Bulletin of the Bingham Oceanographic Collection

BULLETIN

OF

THE BINGHAM OCEANOGRAPHIC COLLECTION

PEABODY MUSEUM OF NATURAL HISTORY

YALE UNIVERSITY

VOLUME XI, ARTICLE 4

A SYMPOSIUM ON FISH POPULATIONS

HELD AT

THE ROYAL ONTARIO MUSEUM OF ZOOLOGY

TORONTO, CANADA

JANUARY 10 AND 11, 1947

Issued May, 1948

New Haven, Conn., U. S. A.

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INTRODUCTORY REMARKS

Dymond: On behalf of the Royal Ontario Museum of Zoology we welcome you all to this Symposium. I shall ask Dr. Huntsman to say something about the background of this meeting.

Huntsman: I would like to say that I have had some interest in this general matter of fish populations for a period going back at least thirty years. Somewhat recently I came most fortunately to be associated with Dr. Van Oosten on the Board of Inquiry for the Great Lakes Fisheries. We were expected to settle all the problems of all the fisheries in all the Great Lakes. We didn't do it, but we did have a good time arguing over what might be done.

As an outcome of our discussions I thought I would get our Canadian Fisheries Research Board interested in the general problem. It forthwith formed a Committee on Depletion, consisting of four persons. The Committee, however, couldn't agree any more than did Dr. Van Oosten and myself, but it reported on the matter and was discharged. It seemed to the members of the Committee that it might be worth-while to get others to help consider this problem of depletion, so we enlarged the group, adding some from the United States.

It was an informal group composed of those who happened to show their interest in arguing over the subject. At first we argued by letter. Then Dr. Merriman, one of the group, proposed that we shouldn't confine ourselves to correspondence but should get together and discuss the problems. To make the results available to others he undertook to have the Bingham Oceanographic Laboratory publish what we produced. Such publication tends to assure more reasoned and guarded statements. I might say that, in addition to having the prepared papers presented, we hope there will be some good discussion, and in order to make the best use of that discussion, a record of it will be made by a stenotypist provided by the University of Toronto for this occasion.

I think it is fitting, because of the history of this affair, that we should have Dr. Van Oosten, who is himself not altogether averse to arguing, preside at our Symposium and guide the discussion.

Van Oosten: For once I am stuck for words—after that introduction! I had wondered why Dr. Huntsman asked me to serve as chairman of this distinguished group. Now that he has given the background I can understand very well why he wants me to sit up here. Apparently my selection is based on the opposition I gave him as a member of the Board of Inquiry. To avoid such opposition at this meeting he thought it best to place me in the chair where I would have to remain neutral!

In one of his letters to me, Dr. Huntsman wrote, "You are not only to preside at the meeting; you are also to be discussion leader for each of the papers." I think he wrote that in a weak moment. At any rate, I threw up my defences, and replied that I did not believe that one man could be an efficient discussion leader for such a variety of papers. So we compromised. We decided that I would serve as chairman but that every man here would be a discussion leader for each paper, except of course the person who was presenting the paper, that is, the victim. The duties, then, are as outlined—I am to sit here on the throne in a neutral capacity and like Nero enjoy the fireworks, and each of you must assume a part in creating the fireworks. In other words, we expect everyone here to participate in the discussions.

Roll Call. The following were present:

Dr. John Van Oosten, U. S. Fish and Wildlife Service, University Museums, Ann Arbor, Michigan.

Dr. F. E. J. Fry, Dept. of Zoology, University of Toronto.

Mr. M. D. Burkenroad, Survey of Marine Fisheries of North Carolina, University of North Carolina, Chapel Hill, North Carolina.

Dr. A. W. H. Needler, Atlantic Biological Station, St. Andrews, New Brunswick.

Mr. W. C. Herrington, U. S. Fish and Wildlife Service, Cambridge, Massachusetts.

Dr. Daniel Merriman, Bingham Oceanographic Laboratory, Yale University, New Haven, Connecticut.

Dr. Thomas H. Langlois, Stone Laboratory, Ohio State University, Put-in-Bay, Ohio.

Dr. W. E. Ricker, Dept. of Zoology, Indiana University, Bloomington, Indiana.
Dr. J. L. Hart, Pacific Biological Station, Nanaimo, British Columbia.
Dr. W. J. K. Harkness, Fish and Wildlife Division, Dept. of Lands and Forests, Toronto.
Prof. H. W. Curran, Dept. of Biology, Queen's University, Kingston, Ontario.
Mr. N. V. Martin, Dept. of Zoology, University of Toronto.
Mr. D. N. Omand, Dept. of Lands and Forests, Toronto.
Mr. N. S. Baldwin, Dept. of Zoology, University of Toronto.
Dr. R. E. Foerster, Pacific Biological Station, Nanaimo, British Columbia.
Mr. L. L. Snyder, Royal Ontario Museum of Zoology, Toronto.
Mr. H. R. McCrimmon, Dept. of Zoology, University of Toronto.
Mr. F. T. Knapp, Dept. of Zoology, University of Toronto.
Dr. A. L. Tester, Pacific Biological Station, Nanaimo, British Columbia.
Mr. Ferris Neave, Pacific Biological Station, Nanaimo, British Columbia.
Mr. W. R. Martin, Atlantic Biological Station, St. Andrews, New Brunswick.
Dr. C. H. D. Clarke, Dept. of Lands and Forests, Toronto.
Prof. C. J. Kerswill, Dept. of Zoology, University of Western Ontario, London, Ontario.
Mr. H. P. Clemens, University of Western Ontario, London, Ontario.
Mr. W. B. Scott, Royal Ontario Museum of Zoology, Toronto.
Mr. Bert Golden, Ontario Federation of Commercial Fishermen, Tobermory, Ontario.
Mr. R. H. Stinson, Dept. of Zoology, University of Toronto.
Mr. J. F. Gage, Dept. of Lands and Forests, Toronto, Ontario.
Mr. C. David Fowle, Dept. of Zoology, University of Toronto.
Dr. J. C. Medcof, Atlantic Biological Station, St. Andrews, New Brunswick.
Mr. C. W. Andrews, Dept. of Zoology, University of Toronto.
Mr. H. H. MacKay, Dept. of Lands and Forests, Toronto.
Mr. E. J. Hamley, Dept. of Zoology, University of Toronto.
Mr. R. N. Johnston, Research Division, Dept. of Lands and Forests, Toronto.
Mr. J. A. Ransbury, Ontario Federation of Commercial Fishermen, Tobermory, Ontario.
Mr. Cecil Martin, Central Lake Erie Fishermen's Association, Port Dover, Ontario.
Mr. Carl F. Kolbe, Ontario Federation of Commercial Fishermen, Port Dover, Ontario.
Mr. W. H. R. Werner, Dept. of Lands and Forests, Toronto.
Mr. D. L. Goodison, Ontario Federation of Commercial Fishermen, Erieau, Ontario.
Dr. W. A. Kennedy, Fisheries Research Board of Canada, Winnipeg, Manitoba.
Prof. D. S. Rawson, Dept. of Biology, University of Saskatchewan, Saskatoon, Saskatchewan.
Mr. Robert Raymond, Dept. of Biology, University of Montreal, Montreal, Quebec.
Prof. Jean Paul Cuerrier, Dept. of Biology, University of Montreal, Montreal, Quebec.
Prof. J. R. Dymond, Royal Ontario Museum of Zoology, Toronto, Ontario.
Dr. A. G. Huntsman, Fisheries Research Board of Canada, Toronto, Ontario.
Mr. F. McCracken, University of Toronto.

Vol. XI, Art. 4.

1. FISHING AND ASSESSING POPULATIONS

BY ARCHIBALD G. HUNTSMAN

Fisheries Research Board of Canada and University of Toronto

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ABSTRACT

Facile apparent solutions of fishery problems, due to their great complexity, have not proved to be effective. The North Sea fishery has been maintained in spite of greatly increased fishing intensity. Its partial stoppage in 1914–1918 resulted in an over-all loss, with doubtful benefit in stock.

Increased fishing intensity will have different effects upon populations of at least one kind of fish (such as *Hippoglossoides*), depending upon whether or not the fish have a short life and rapid growth, growth over many years to a great size, or are stunted from very slow growth. Greatly increased fishing intensity on Passamaquoddy herring, finally involving all ages starting with yearlings, resulted in the take being doubled, with no failure in maintenance but with marked decrease in the large fish.

Regulations to prevent overfishing of salmon in eastern Canada have resulted in some populations being little or not at all used legally. There are very great local differences in the availability of the fish for use. Regulations to permit small fish to become large for a greater take seem to have no basis in fact, to judge from mortality

of salmon freed as grilse. Restriction in fishing to give more spawning seems unwise until there is clear evidence that more spawning is required.

Various fishery conditions have been confused under the terms "overfishing" and "depletion." There is great need for their elucidation, which can come only through knowledge of what is happening to the fish populations, as well as to the fishery. This poses a great need for assessment of the populations. For the most part assessment is possible only through capture of the fish, and can be accurate only by proper interpretation of the given capture. Experiments in capture of known populations seem to be essential for such interpretation. Assumption that a certain method takes practically all the fish is not sufficient.

Interpretation of capture with such great variety in conditions as exists requires very thorough knowledge of fish behavior in regard to capture. This need has revealed that very little is yet known of the response of the individual fish as a whole in movement and survival to what it faces where it lives. There must be knowledge of the principles in this field for assessment of fish populations.

FISHERY PROBLEMS

So many factors affect populations which are fished that any facile apparent solution of a general fishery problem should be suspect. Such a solution swept this continent after the middle of the last century, when a rapidly increasing human population seemed to see its fishery resources dwindling. The amount of fish per person was indeed going down, but the total amount in the water may have been going up for all we know. The solution of the problem was seen to be the newly developed procedure of fish hatching and planting, which was to fill the waters with fish. It has proved to be an *ignis fatuus*. For each case of this nature I ask: Is breeding really at fault?

The Europeans, although first to develop such fish culture, failed to become much enthused over its prospects. Indeed, the British Royal Commission of 1860, headed by Huxley, recommended unrestricted freedom of fishing, at least in the open sea. In its sequel, the British fishing industry, in expanding up to the early part of this century, "enjoyed a period of unexampled prosperity" (Garstang and Mitchell, 1910) and took more fish than all the other European countries put together. Huxley's argument was based largely on herring that were taken mostly in drift nets. The antagonists of unrestricted fishing concentrated on beam and otter trawling for bottom fishes, which method had aroused opposition as new and destructive fishing and began to be officially investigated as early as 1878. Expansion of the fishery was clearly accompanied by such economically adverse factors as decrease in average size of fish and as increase in the effect necessary for a given catch, the latter sending the vessels farther and farther afield. With this background, the present century has been characterized in northern Europe by very thorough fishery investigation, particularly of the centrally important North Sea, under the International Council for the Exploration of the Sea. Thought has become crystallized in a theory of fishing or overfishing (Russell, 1931; Graham, 1935; Thompson, 1937; Russell, 1942; Graham, 1943). This theory has been rather generally accepted on this continent, particularly in the experimental management of the Pacific halibut fishery. Its main argument seems to be that by fishing less you get more through permitting the fish to become larger. For each case of this nature I ask: Does it really pay to let the fish get bigger?

Since this theory has been accepted so generally and is tending to determine international action, it should be considered very critically. In it at least three factors are mixed together, if not confused. In addition to that mentioned (fishing less to get larger fish), there are the profitableness of the fishery and the fishing up of accumulated stock (Thompson, 1937). Since profitableness is largely dependent upon man's wants, which vary greatly in space and time, it may be left out of account for the problem of the fish populations, except as it affects intensity of fishing, although it is of basic importance in the fishery. Attention may be directed to maintenance of the fishery.

WAR CLOSURE OF NORTH SEA

The great war of 1914–1918 reduced fishing in the North Sea very greatly. The countries fishing this Sea had been investigating it cooperatively for some years and had developed the machinery for getting very full records of the fish taken from it. The courses of the takes of the principal kinds of fish and of halibut, from 1910 to 1938 (Fig. 1), as given in the "Bulletin Statistique" of the International Council, reveal some of the apparent effects of the closure on the takes in the following years.

The courses of the annual takes of fish vary greatly from species to species. It has been pointed out in the "Bulletin Statistique" that the courses for haddock, halibut and cod have been more or less similar, as well as those for plaice, sole, whiting and turbot. Of the eight figured, only halibut and haddock show definitely larger takes after the war than before and thus give evidence of a beneficial effect of the closure on the fish population. They also show definite sub-

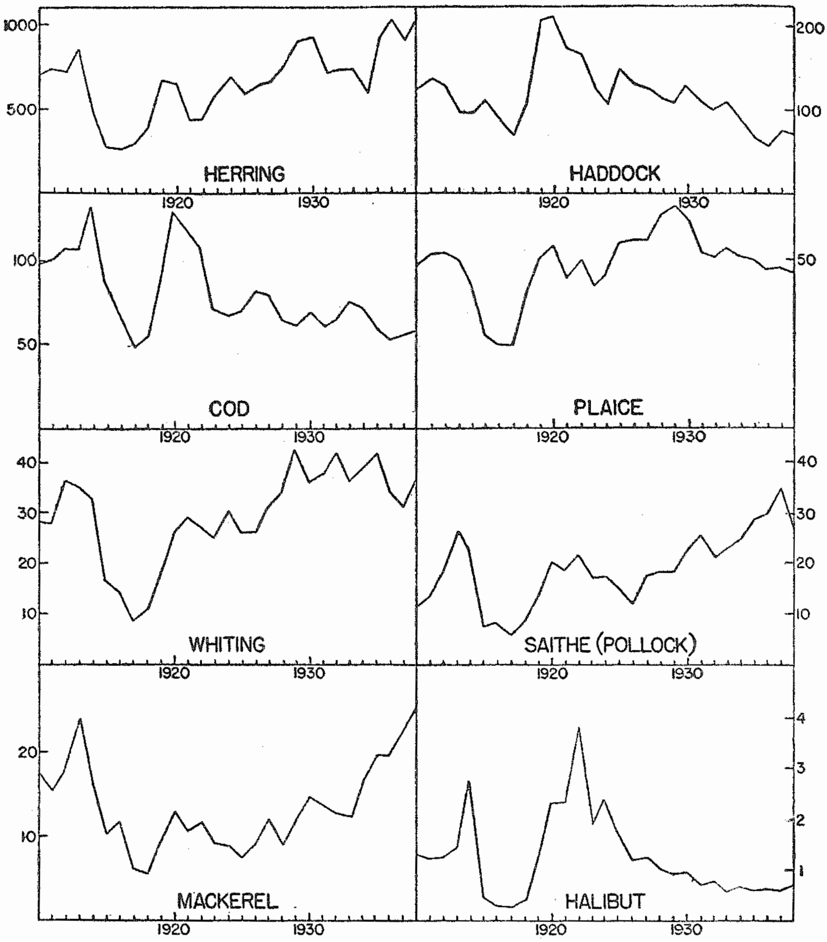

Figure 1. Courses of annual amounts (in thousands of metric tons) of various fishes taken from the North Sea, 1910 to 1938.

sequent declines in take. However, the very large take of halibut in 1914 indicates that other factors may obscure any effect of the closure. Cod, plaice and whiting show about the same take after the war as before, and the two latter show subsequent rises which call for explanation. Herring, mackerel and saithe or pollock, the pelagic rather than demersal species, show lower takes after the war, with a subsequent general rise. The loss through closure in the war years (1914–1918) may be taken as the amount by which the take was less than what would have been expected from the prewar years (1910–1913). This loss is definite in all species (Table I). The six-year postwar period

TABLE I. LOSS OR GAIN IN NORTH SEA FISHERIES FROM CLOSURE DURING THE WAR OF 1914–1918 (EXPRESSED IN METRIC TONS)

Fish	*Prewar annual average (1910–1914)*	*Loss for 1914–1918*	*Loss or gain for 1919–1924*	*A later annual average (1930–1934)*
Total	1,182,779	−2,701,000	−885,219	1,167,709
Herring	744,764	−2,058,317	−1,042,453	737,437
Haddock	120,749	−134,686	+257,472	106,242
Cod	102,565	−122,030	−31,051	68,299
Plaice	50,470	−91,124	−15,283	54,088
Whiting	31,545	−75,681	−36,436	37,985
Mackerel	18,409	−42,921	−48,105	14,071
Saithe (Pollock)	17,322	−33,610	−41,583	23,295
Halibut	1,303	−2,215	+6,104	703

(1919–1924) shows, with similar treatment, gains only for haddock and halibut and a large total loss. A later five-year period (1930–1934), which may be considered as beyond the effects of the war, shows annual takes quite similar to those of the prewar period. How these facts should be interpreted is problematical, but they fail to support the idea that reduced fishing is of any benefit, unless for haddock and halibut. Insofar as the high takes of these two species in the postwar period are the fishing up of stock accumulated during the war years, there can be no hope of maintaining them. They are the inevitable temporary accompaniment of an increase in fishing intensity.

Because of food relationships between the species, the total take (Fig. 2) of fish may be a better index of maintenance of stock than would be the separate takes of the various species. The total take from the North Sea rose to a maximum (1,277,317 metric tons) in 1913, just before the war. It did not again reach such a high level until ten years after the war. In the last three years for which records are available (1936 to 1938), new records were made for sustained as well as high take (1,320,000; 1,354,000; and 1,424,229 tons respectively). So far as maintenance is concerned, there is no evidence of overfishing. It seems indeed doubtful that through "a moderate reduction in fishing power . . . it would be possible to reap a permanent

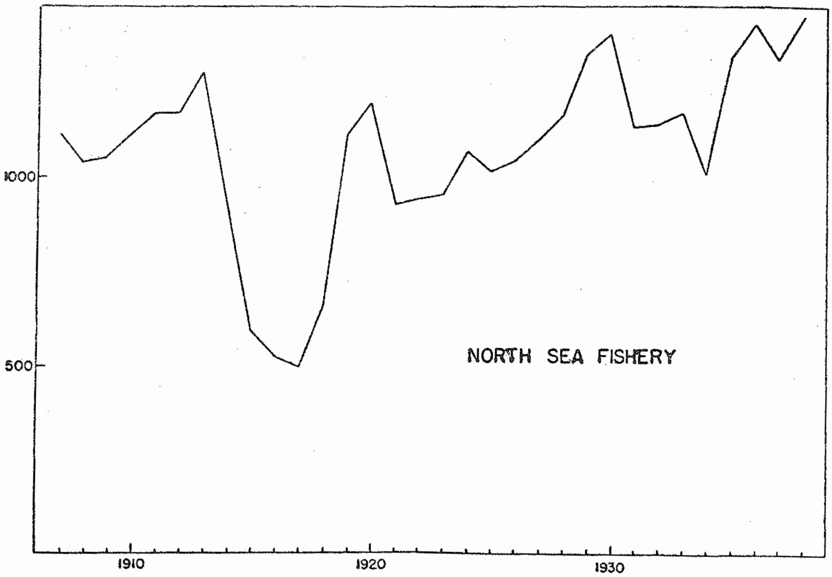

Figure 2. Course of total take of fish (in thousands of metric tons) from the North Sea from 1907 to 1938.

advantage from the increase in fish stocks which is now taking place as a result of the war" (Russell, 1942).

EASTERN CANADIAN CONDITIONS

My investigations have been of waters very different from those of the North Sea. Off Canada's eastern coast are fisheries for which Europeans crossed the Atlantic annually long before they settled this continent. Although these waters formed the avenue by which Europeans first discovered this continent, the neighbouring land has such poor conditions that the local human populations are inadequate to make very full use of the fishery resources, which are in part still exploited by Europeans in annual voyages across about 2,000 miles of ocean. This sparse population is in marked contrast with the heavy human populations around the North Sea. Also there are great local oceanographic and physical contrasts on this side of the Atlantic. Along this side of the continent the Arctic water of the Labrador current gets mixed with the tropical water of the Gulf Stream, and on the multifarious continental shelf the cold water of the north works slowly southward in a series of immense swirls, with fresh water from the continent, sometimes little, sometimes much, exercising its potent effect in vertical differences of strongly stratified water and in differential movements on and off the coast.

Study revealed along the coast strikingly different populations (Huntsman, 1918) of a little used bottom fish, *Hippoglossoides platessoides,* whose scientific name seemed to warrant its being called the Canadian plaice (*platessa* = plaice). At the extremes of their geographical range, the fish were small. At the north in the ice-cold (< 0° C.) bottom water of the Bay of Islands, Newfoundland, they were stunted, showing very slow growth. At the south in Passamaquoddy Bay, with bottom water raised by heavy tidal mixing to 10° C. or more in

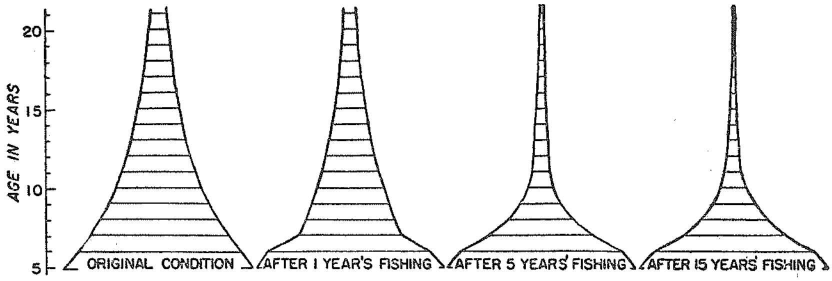

Figure 3. The effect of fishing on the stock (from Huntsman, 1918).

summer, they had grown very rapidly although none were very old. Optimum conditions were clearly in intermediate waters, where large and old fish were found. Fishing a population with such optimum growth would doubtless give the well appreciated decrease in average size as well as in take as the accumulated stock was fished out (Fig. 3). But what would be the effect if there were no particular accumulation of stock as in Passamaquoddy Bay (Fig. 4)? Also, what would be the effect if even the small fish were the result of long accumulation, as in the Bay of Islands? Even for one species on one coast, one theory of fishing or of overfishing may be quite inadequate.

There happen to be fairly good records to show the effects of greatly increased intensity of fishing on a stock of *herring*. About 120 years ago the herring of the Passamaquoddy region of the Bay of Fundy were still being regularly fished by the primitive method of "torching" as used by the aborigines. The fat herring used for smoking were thus dipped when attracted to a boat at night by a light placed in the bow. The large spawning fish, as concentrated outside Grand Manan Island (the outer limit of the region) were taken in gill nets for salting. Reputedly, about 1828 Nova Scotian fishermen introduced to this region the use of large fixed traps or weirs constructed of stakes, brush and netting, which take all sizes of fish. These were particularly useful for taking the three-year-old fat herring in the outer part of the region, these to be hard-smoked as "boneless herring," for which there

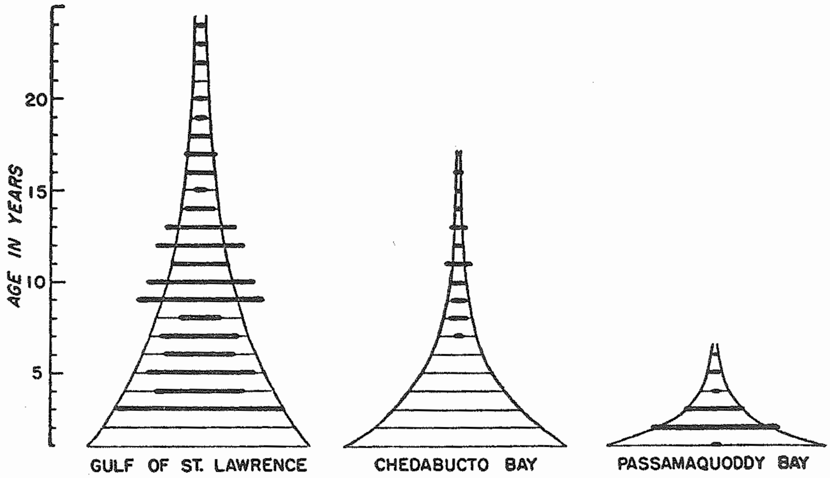

Figure 4. Relative numbers of the various ages in the stock of *Hippoglossoides* in different regions (from Huntsman, 1918).

was a lucrative market. The much smaller yearlings and the two-year-olds had at first only limited use as bait and manure. In 1865 they began to be used as a source of oil and fertilizer, and quite a large industry developed. From 1864 to 1880 further netting of the large fish developed through their capture in increasing quantities in winter for the frozen herring trade. At that time of year they were to be found in deep water in the centre of the region. Finally, the development of canning in the late 1870's provided a very profitable market for the smaller fish as "sardines," which resulted in intense fishing with very many weirs throughout the region, including the innermost parts where the young largely congregate. Even in the early days there was fear of overfishing, which led to restrictions on nets and on fishing season in the spawning area on the outer side of Grand Manan. These restrictions were started in 1834 but stopped in 1837 because of difficulty in enforcement. In 1852 the spawning area was declared closed to fishing from July 15 to October 15 in each year, and in 1868, on Confederation, a special officer was appointed to enforce the law, which law was rescinded only in 1917. With each increase in intensity the ruin of the fishery was foretold, but there has finally been no restriction except to safeguard the licensed weirs from interference by dipping or seining. A limited amount of the latter has been permitted in winter when the fish are too sluggish to enter the weirs.

What has been the outcome? The takes of large, medium and small herring have had very different courses (Fig. 5). These three sizes have been largely separated through different use, the large for "salted herring" and "frozen herring," the medium for smoking, and the small for bait, manure, "guano" or "pomace," and "sardines". The take of the large greatly decreased, the winter fishery passing away with slight, temporary recoveries. The very fat "Quoddy River" herring, the fattest of the fat unspawned herring, which had been taken in moderate quantities in Quoddy River (the main outlet of Passamaquoddy Bay), disappeared. The medium herring or "stringers," used for smoking, increased at first in the 1880's and then decreased to about half. The small "sardine" herring, now fished most intensively, were taken in larger and larger quantities until the total take of herring was more than double what it had ever been prior to this intense fishing for the young. A general level, double the height of the earlier level, has been maintained for about fifty years, with more or less marked fluctuations. In 1911 there was a new high of nearly a hundred million pounds, and in 1941 another of over a hundred million. From 1941 to 1944, war years with strong demand for fish, the take did not fall below 82 million pounds in any year, whereas no previous four-year period held up even to 70 million pounds. Thus there is no evidence that fishing has yet been too intense for maintenance of the stock and the fishery.

Owing to their high value, and to the comparative ease of taking them in the narrow river waters which they enter after feeding in the sea, *salmon* are more apt to be overfished than are strictly marine fishes. Their fishery has long been restricted, whether wisely or not. That the restriction has not been altogether wise is evident from the fact that the stocks of some rivers are taken only illegally, as for

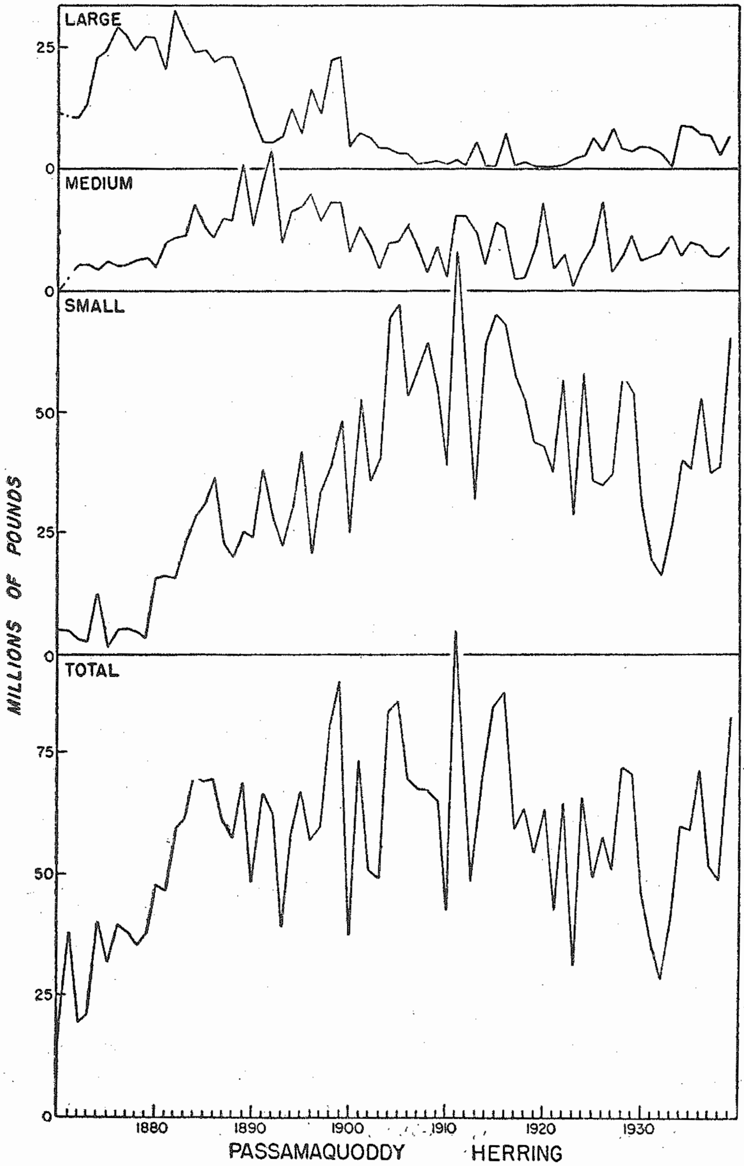

Figure 5. Takes of herring of various sizes from the Canadian part of the Passamaquoddy region of the Bay of Fundy (St. John to Grand Manan) from 1870 to 1939.

example that of the Shinimikas River of northern Nova Scotia. By no legal method have they as yet been taken profitably in the sea there, and they fail to enter the river early enough to give angling. Such zero per cent capture of the Shinimikas salmon is to be contrasted with the capture of 25 per cent of the salmon on the Margaree coast of Cape Breton Island, and of 20 and 70 per cent respectively of the salmon in the outer and inner parts of the outflow of the St. John River into the Bay of Fundy, as shown by tagging experiments. Theories of overfishing should take account of such enormous local variations, even within short distances, in the feasibility of capturing populations that concentrate for river ascent. Doubtless such variations occur for other fishes.

With the idea that it is worthwhile to let them get larger, small salmon are protected by law, which prohibits taking any under a three pound weight. This holds in spite of the fact that in some rivers almost all the salmon are grilse, that is, they weigh from two to six pounds. In the Sackville River, near Halifax, N. S., which is trapped to get salmon for spawning purposes, about half the fish are grilse, and the other half are larger fish and about twice as heavy. Tagging experiments on these fish after spawning have provided data to show whether or not it is worthwhile not to take the grilse in order that they may get larger. From 1932 to 1937, 341 grilse kelts, weighing a total of 1,036 pounds, were tagged and liberated in the Sackville River. Of these, 12 larger salmon weighing a total of about 109 pounds were reported recaptured in later years (Rodd, 1934 to 1940), six being taken in the first and six in the second year after liberation, and six in commercial fishing and six in the river trap. Unless the others went to different rivers, those recaptured represent the survivors. Unless a better outcome from letting salmon grow larger can be demonstrated, it is clearly not worthwhile to stop taking grilse. To drop 1,000 pounds in order to get 100 pounds is not much better than the action of the dog in Aesop's fable that dropped his meat in the brook to snatch at the image.

Should salmon fishing be restricted to provide more spawning fish? This question can be answered only by knowing how few salmon are required for approximately maximal production of smolts in a river. An experiment has been started to determine not only how few spawners, but also how few spawning beds, are required for maximal production of smolts in a stream that has been producing no smolts or only a few. Results from planting experiments indicate that no very large number of underyearling salmon is required for approximately maximal number of smolts.

FISHERY CONDITIONS

"Depletion" and "overfishing" are cries of alarm that cannot properly be restricted by the scientist to precise meanings. By origin, "depletion" means a condition less than full, which, applied to a fishery in ignorance of what fish there are in the water, seemingly signifies a decrease in the fish population that is presumed from a decrease in catch. This has indefinite gradations as well as an indefinitely large number of possible explanations, which make it a comparatively meaningless condition. "Overfishing" clearly means too much fishing for some purpose not defined. If that purpose be to have a big take rather than to reduce a population, this also seemingly signifies a decrease in fish population that is presumed from a decrease in take, but with a difference. While it has infinite gradations, it assumes that fishing is responsible for the decrease, which may not be correct. The scientist may be well advised not to make unwarranted assumptions.

1. The condition, of which complaint is made, may be a decrease in the take-per-unit-of-effort without any decrease in the total take or in the fish population, which may well be termed *overeffort*. This may mean that there has been an increase in fishermen rather than a decrease in fish, as was found in the case of trout (*Salvelinus fontinalis*) angling in the Pomquet River, N. S., in 1938. There was no evidence of any lack of young trout or of any decrease in adult trout at the beginning of the season, but reputedly the number of anglers had become one hundred times as great as it was twenty years earlier. Reduced availability of the fish for any reason other than population size would also give this condition.

2. The condition may be a decrease in total take as well as in take-per-unit-of-effort without decrease in fish population. This will result from prevalent unavailability of fish, as illustrated by the angling take in the Margaree River (Nova Scotia) being down as a result of failure of the salmon to enter the river to any extent during the angling season, and by the angling take in the Moser River (Nova Scotia) being down as a result of high temperature during the season. This may be termed *underavailability*.

3. The condition may be not only a decrease in take but also a decrease in the fish population from a natural cause. The cause may or may not be recognized, and it has proved to be extremely difficult to determine the causes even of marked regular *natural fluctuations* in animal populations. If the cause should be recognized, it may or may not be remediable.

4. The condition may be a decrease in the fish population as a result of human action other than fishing. This is *elimination by man*. Here also, as with the disappearance of salmon from Ontario and New England streams, the cause may be difficult to recognize, with remedial action doubtful.

5. The condition may be a temporary decrease in the fish population as a result of fishing. Fishing clearly decreases the population by the amount removed, and, so long as this is made good by natural increase by the beginning of the next year's fishing, nothing is usually thought of it. This feature of fishing may, however, be overlooked. It means that the more fishing there is in the year, the less is apt to be the take-per-unit-of-effort. Such a condition, when extreme, is properly called *overeffort*.

6. The condition may be a decrease as a result of fishing, in only part of the fish population, that is, a *partial decrease in stock*. This is a usual thing and apt to be recognized, as when the fishing is selective as to size of fish and when the fish are taken at only one stage or in only one part of the area of their distribution. This decrease also may be automatically made good within the year.

7. The condition may be a decrease in the fish population as a result of fishing that is not made good within the year because it represented stock that had taken years to accumulate, that is, old, large fish. This condition is an inevitable aftermath of an increase in fishing intensity for such a stock. There are extreme cases of this for lobsters—local populations made up wholly of old, large individuals resulting from slow immigration. If fishing is profitable only with a large accumulation, the only thing to do when fishing becomes unprofitable is to wait a number of years. This is *exhaustion of accumulated stock*.

8. The condition may be a decrease in old, large fish, but a greater take of all sizes as already described for the Passamaquoddy herring (p. 00). This may be the result of young fish making better use of food in growing than old fish. The *oversenility* has been remedied by fishing.

9. The condition may be a decrease in total take as well as in the take of large fish, to be remedied by restricting the fishing to let the fish get larger, that is, there is *undergrowth* of the fish. It would be expected to result from food for the large fish not being used by the small fish. Haddock in the North Sea and halibut in the Pacific, as well as many other fisheries, have been presumed to show this condition. It is not safe to presume it since death of fish may more than offset any gain in increase in their size. The matter is too complex. To illustrate: Of four hypothetical cases given in Table II, two show

TABLE II. SUM OF TAKES FROM A LOT OF 1,000 FISH IN SEASONS A AND B COMPARED WITH THE TAKE WHEN THE FISH ARE LEFT TO GET LARGER BY FISHING THEM ONLY IN SEASON B.

a. When 30% of the population is taken in a season, the mortality between seasons is 10%, and the increase in weight per fish is from 2 to 4 pounds*

Season	*Population*		*Taken in fishery*	
	Number	*Weight (lb.)*	*Number*	*Weight (lb.)*
A	1,000	2,000	300	600
B	630	2,520	189	756
			489	1,356
A	1,000	2,000	none	
B	900	3,600	270	1,080
			270	1,080

b. When 30% of the population is taken in a season, the mortality between seasons is 10%, and the increase in weight per fish is from 2 to 10 pounds.

Season	*Population*		*Taken in fishery*	
	Number	*Weight (lb.)*	*Number*	*Weight (lb.)*
A	1,000	2,000	300	600
B	630	6,300	189	1,890
			489	2,490
A	1,000	2,000	none	
B	900	9,000	270	2,700
			270	2,700

* If 1,000 fish are subjected to a fishery in season A of 30% intensity, 700 are left. If there is a mortality of 10% from season A to season B, the 700 will be reduced to 630 for capture in season B. Subjected to a fishery then of 30% intensity, the take will be 189 fish.

c. When 30% of the population is taken in a season, the mortality between seasons is 50%, and the increase in weight per fish is from 2 to 10 pounds.

Season	*Population*		*Taken in fishery*	
	Number	*Weight (lb.)*	*Number*	*Weight (lb.)*
A	1,000	2,000	300	600
B	350	3,500	105	1,050
			405	1,650
A	1,000	2,000	none	—
B	500	5,000	150	1,500
			150	1,500

d. When 50% of the population is taken in a season, the mortality between seasons is 50%, and the increase in weight per fish is from 2 to 10 pounds.

Season	*Population*		*Taken in fishery*	
	Number	*Weight (lb.)*	*Number*	*Weight (lb.)*
A	1,000	2,000	500	1,000
B	250	2,500	125	1,250
			625	2,250
A	1,000	2,000	none	—
B	500	5,000	250	2,500
			250	2,500

greater and two less take as a result of letting the fish get larger. The proportion taken in the fishery and the mortality between successive fishing seasons can be determined by tagging. Very great increase in weight (IIa compared with IIb) makes it worthwhile to let the fish get larger. Even very great increase in weight may be more than offset by high mortality (IIc compared with IIb) so that it is not worthwhile to let the fish get larger. But very heavy fishing may reverse this (IId compared with IIc). The proportion taken can be determined by tagging at the beginning of the season and the interim mortality by tagging at the end, as has been done for salmon.

10. The condition may be a decrease in fish population from overfishing that leaves too few spawners, that is, there is a *lack of spawners*. This has frequently been presumed. There is one clear case, namely the River Conon in Scotland, where a trap operated in the river permitted removal of practically every fish that entered. On stoppage of the trapping, the salmon take rose abruptly the correct number of

years afterward as the result of increased spawning. The very high reproductive power of most fishes makes it improbable that many spawners are actually required to produce all the young that will find conditions for survival.

11. The condition may be a decrease in fish population from the operations of other fishermen than those who complain of the condition. The assumption that the fish population is a common one may not be warranted. The extent to which the fish taken in one fishery will affect the take in another (that is, the extent of the fishery interference) can be determined by tagging, as was done for Margaree salmon (Huntsman, 1939).

NEED FOR ASSESSING POPULATIONS

Wise action can be based only upon knowledge of what the fishery condition actually is. It will be evident from the foregoing account that to differentiate the many fishery conditions it is necessary to know not only what fish are caught but also what the fish population is.

Before adopting the rule of restricting fishing to give more spawners, we should know that there is a lack of spawners, which may be indicated by underrecruitment of the fished stock. A correlation must be established between intensity of fishing and both spawning population and recruitment of the population fished. This requires assessment of those populations.

Before adopting the rule of restricting fishing to give a larger take through letting the fish get larger, we should know that it will do so, that is, that there is undergrowth of fish. The proper correlation must be established between intensity of fishing and the proportions of fish of the various ages and sizes fished and between intensity of fishing and the total take in weight. This requires assessment of the population fished. The direct method of finding out whether or not it is worthwhile to let fish become larger is to mark or tag them to see whether they will yield more pounds as recaptured in later years.

If a decrease in the take of fish is attributed to a decrease in the stock either locally or generally, for which a remedy should be sought, we will need to find by assessment that the population has decreased either locally or generally and to correlate such decrease with some factor that may be remedied.

To prevent overeffort—too much fishing effort for the stock of fish in the water—there should be assessment of the population for planning of the fishery.

To have the fish food go into valuable fish, there needs to be assessment of all the populations using the available food in addition to knowledge of the food or predator relationships.

ASSESSMENT

Since a science of fish populations can be based only upon accurate measurements of the populations, we must learn how to measure them.

Capture is necessary to assess fish populations. Marking or tagging a known number of fish is frequently a valuable adjunct. Methods may be divided into those that attempt to take all the fish and those that estimate the total from capture of a part.

Attempts to Take the Whole Population. Methods that have been used are (1) seining, (2) trapping migrants, (3) shocking the fish electrically, and (4) using poison, such as rotenone. It has been generally assumed that these methods take all or nearly all the fish, with reliance perhaps upon repeating the process until no more are taken. The effectiveness of whatever method is used can be determined by ascertaining whether or not, under the conditions in question, all of a known number of marked or tagged fish are taken.

Estimating Total Population from Partial Capture. The take-per-unit-of-effort has been very generally used for comparative estimates of populations. For safe interpretation one needs to know thoroughly how this varies with conditions. As representing the availability of the fish, it is of great economic importance, but it may have little reference to the size of the population if the effort may or may not be put forth when the fish are available. Even with uniform availability, a big effort gives a different result from a little effort for the same population, as Kyle (1928) pointed out. Russell (1931) maintains, however, that, although the take-per-unit-of-effort does not *per se* represent the stock at the beginning of fishing, it can be used as an index of the stock remaining after fishing "if certain conditions be fulfilled." Actually it represents something between the two, and the smaller the proportion of fish removed (not the shorter the time of fishing) the less does it differ from either. How reliable this method is can be determined only by knowing what the populations are, that is, the very thing that we are using it to discover.

To determine what the take-per-unit-of-effort represents and how it varies with conditions we must do something more. We can either (1) put a known number of fish in a discrete body of water that lacks them and try to capture them under different conditions, (2) put a known number of marked fish in a discrete body of water and try to capture them under different conditions, or (3) try to capture the fish in a discrete body of water under different conditions during a short period in which the fish population may be presumed not to change and at the other end of the period attempt to get the whole population by one of the methods mentioned above. We have the greatest need for work of this kind to permit us to interpret properly the data of the fisheries, on which we ordinarily depend for knowledge of fish populations.

FISH BEHAVIOR

Since to measure fish populations we must capture at least some of them, knowledge of the behavior of fish in regard to capture is of basic importance in the study of fish populations. This is what I have called the zoapocrisis of the fish, its response as a whole to what it faces where it lives. The responses involved are those of movement and survival. This is an almost virgin field for study.

As an undergraduate in 1904 I observed at the Georgian Bay Biological Station that young black bass (*Micropterus dolomieu*) in quiet open water formed "solids" of definite size, shape and position, while in the laboratory, under experimental conditions, they behaved as a gas, expanding and contracting within certain limits with the space available. In 1937 I studied similar behavior of young salmon in turbulent current. This can be understood, as in physics, on the basis of forces of both attraction and repulsion between the particles or individuals, although attraction is negligible for the salmon. Repulsion doubtless explains the fact that more fish are taken when nets are lifted frequently (Van Oosten, 1935). In herring, studied from 1911 on, the force of attraction between the individuals is rather great, and the masses flow from place to place (depending upon the forces to which they are exposed) with considerable passive transportation by the water. The masses expand and contract with temperature between 0° and 12° C., at least. Also, in feeding they expand and remain stationary in the water, and, when not feeding, they contract and flow through the water. Like salmon, herring masses in finely turbulent current either remain stationary in relation to the bottom or move up or downstream, depending upon the strength of the current as well as upon other conditions. Herring are taken in weirs, as in the Passamaquoddy region, only when the masses move into them, either by passive transport or by flowing through the water. Temperature and feeding, through affecting the rate of flow, determine how many are captured, as shown by the course of the take of herring through the year (Fig. 6).

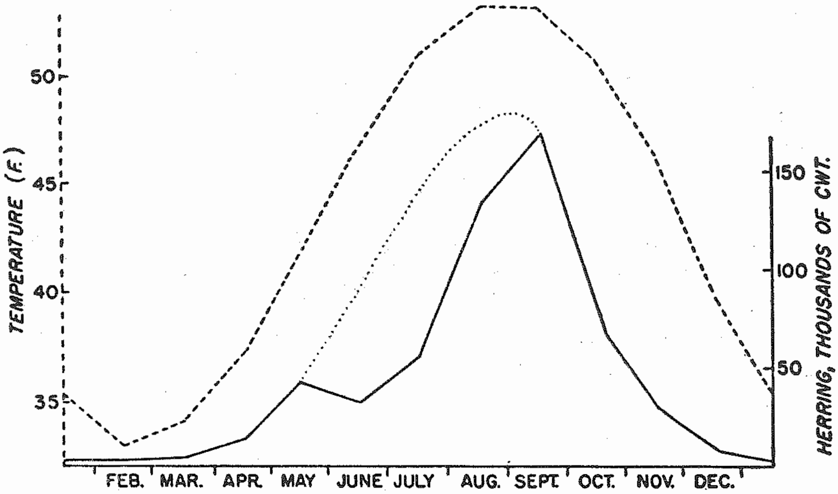

Figure 6. Average course of water temperature (above) and herring fishery (below) in the Passamaquoddy region of the Bay of Fundy throughout the year, from data for the years from 1925 to 1930 (from Huntsman, 1933).

The take is nil in winter (some taken by seining but none in weirs) and highest at the height of summer, with a take lower than would otherwise be expected from June to August, the main feeding season. Bar weirs capture herring on the basis of the movement of the masses in finely turbulent current.

In 1904 I observed that young rock bass were "adsorbed" on the rocky bottom. I refer to the concentration of individuals on the bottom as "adsorption" in order to draw attention to the parallel between this and the behavior of the molecules of physics and chemistry, "adsorption" being used as early as 1882 for the condensation of gases on surfaces of solids. You may prefer to call this behavior of the fish "thigmotaxis." Pots form the best material for "adsorbing" fish with such behavior, perhaps as providing greater contact surface. They are used on our east coast for eels, for hagfish (*Myxine*) taken for scientific purposes only, and for lobsters (cunners [*Ctenolabrus*], rock eels [*Zoarces*] and flounders [*Pseudopleuronectes*] taken incidentally). At Bermuda in 1925 I noticed that most of the fish, as having such "adsorptive" behavior, were taken in pots. Salmon are at times "adsorbed" on the bottom, but this behavior is usually associated with strong light from above, which means that it occurs in daytime only and in comparatively shallow water. The decreasing light of evening brings salmon from the bottom to the surface. Herring are not "adsorbed" on the bottom, but their masses are moved to and from the surface with changing light. Some weirs take the masses of herring as a result of such movement.

Fish that move up and down streams are influenced in movement by the factors mentioned. The movement seems to become nil for our species with the temperature close to 0° C. The movement decreases with the temperature rising above an optimum. At about 21° C. adult salmon do not descend, but move short distances down as well as up, and with warmer water will be carried down stream.

Capture of fish on baited hooks depends upon very many things. If the hooks are stationary, the movement of the fish becomes important. With high temperature, haddock cease to be taken on line trawls, and salmon stop rising to a fly. Results from salmon angling are nil at night and fluctuate during the day, apparently with high temperature rather than light, the picture changing with season as daily range in temperature changes.

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DISCUSSION

Van Oosten: Dr. Huntsman's paper is now open for discussion.

Herrington: Dr. Huntsman, there are two or three points that I would like to bring out at the moment regarding the changes in the North Sea catch which you described. Later on I am going to present some data which may bear upon these changes.

If you accept for the moment the argument that intensive fishing is not causing a decline in over-all productivity in the North Sea, I think you should bear in mind that if you deplete a desirable species and an undesirable species takes its place there still is a loss as far as human needs are concerned. For instance, on Georges Bank if haddock were decreased and a less desirable species took its place, there would be an over-all loss even though the total poundage of all species landed remained the same.

You show growth curves for Canadian plaice where the fish at the southern limit of the range grew much more rapidly than those at the northern limit. I have found several cases of a similar nature, but I also found that while the southern fish start growing more rapidly, the growth drops off and eventually the more northern fish reach a larger size. The older southern fish did not necessarily die off at a younger age than northern fish, but they were smaller because of slower growth. It may be that the considerable reduction in growth rate would lead to erroneous age readings.

In the case of herring your curve showed an increased catch with the shift to small herring. The data I have to show later will offer a possible explanation of these increases.

In considering whether or not heavy fishing can deplete a herring fishery, the experience on the west coast, according to publications I have seen, tends to show that heavy fishing can almost wipe out stocks of herring such as they have out there. The herring population is certainly reduced because of the fishery.

You commented on the possibilities of checking your assessment of population size if you liberate a certain number of tagged fish and then capture them all. Now, there may be a difference in the likelihood of different fish being caught. You could only say with certainty that the ones you caught were "suckers" for the hook or whatever type of gear you used to catch them. If you catch them again, all you prove is that you have assessed the "suckers"; you haven't necessarily assessed the total population. Various census methods have been checked on in New York State. They have used an electrical shocker in a stretch of stream and have repeatedly covered that stretch until they got none back, and then checked by draining the area. They found that by repeated use of the shocker they got all the fish out.

You mention that the trap is the best way to catch "adsorbed" fish. (Incidentally, I question the word "adsorbed." Why not use a simple term like "bottom fish"?) Otter trawls or dredges would appear to be a better gear for bottom forms. Certainly dredges catch a closely "adsorbed" scallop better than would traps.

You are stressing the importance of assessing populations. I agree with you wholeheartedly on the value of accurate assessment.

Huntsman: I entirely agree with you that you have to take account of any peculiarity of the fish which results in the capture of some and not others. When you have marked fish, no matter whether you catch them with the gear you are using or otherwise, they provide a means of determining the effectiveness of your method of capture. Of course, you have to modify your calculations as to what the recapture of a certain number of captured and marked fish means in comparison with the total population of fish. That brings in what I have tried to stress, namely the importance of studying the behavior of the fish. The need to know far more about how the fish react to capture is stressed in my paper.

As to the stock of herring on the Pacific coast going down, that is perhaps comparable with the larger herring going down in the Passamaquoddy region. You see, my point was *not* that the larger herring don't decrease, but that the fishermen could, and apparently did, take a greater total poundage despite the intensity of the fishery.

Herrington: My impression was that they had practically wiped out the population in these areas. Even when they closed the fishery it took a considerable number of years for it to come back.

Tester: I am quite interested in this discussion. I believe that the Alaskan workers have concluded that there has been a decrease in the southeastern Alaskan population as a result of the fishery. It is true that the area was closed for several years and is only now coming back into its own.

I am not in a position to present the reasons that they have advanced for their conclusions, but I can say that, as far as the British Columbia herring fishery is concerned, we still don't know. We have come to the conclusion that the herring fishery should be pursued as intensively as possible consistent with maintaining an adequate supply of young to get maximum sustained yield. We are trying to estimate the minimum number of fish that must spawn to keep the supply of young at an approximately constant level of abundance. We are undertaking an experiment on a large scale to get at that particular point.

At the present time I cannot point to any decrease in the British Columbia herring populations that can be attributed directly to past heavy fishing.

The British Columbia herring is unlike the Passamaquoddy Bay herring in many respects. It is possible for very large catches to be made when the fish gather fairly close to the spawning grounds just before they are ready to spawn. During that period the fish have been protected in British Columbia by a closed season. It is possible—I can't say whether it is probable or not—that if the fishing were thrown open at that time practically the entire stock of mature fish could be wiped out.

There is one more point, Dr. Huntsman, that I would like to mention. It has to do with the figures you showed in connection with the seasonal catch of herring in Passamaquoddy Bay and the relationship between the catch and temperature change. On the west coast of Vancouver Island it would be almost in reverse to the situation you describe. If it can be said that herring "flow," then herring flow into the inshore waters and are vulnerable to the fishery during the winter period rather than during the summer, giving an opposite relationship to that which you describe. That makes me suspicious of assuming that there is a causal relationship between temperature and catch either in your case or in my own.

Huntsman: There is no question that what seems to be a causal relationship may be only an apparent one. There may well be a difference between what you describe and what we have in Passamaquoddy Bay. It is true that our herring are in the region throughout the whole year; they don't come into the region from the outside. Elsewhere on the Atlantic coast this might not be true at all. That they are there the year round makes it possible to recognize the effect of temperature on the catch.

As to your experiments on whether or not intensive fishing of certain grounds will affect the number of offspring, I am inclined to believe that (as has been suggested for the Passamaquoddy region) there will be so many adjacent spawning regions, some of them with relatively unfished stocks, that only the whole picture will tell the story. That is, influx of larvae might offset complete local removal of spawners.

Tester: I would agree, Dr. Huntsman, insofar as one particular area is concerned. However, we are applying this experiment to one major population which occurs along the whole of the west coast of Vancouver Island, and which constitutes a more or less discrete unit.

Huntsman: The potentialities for herring production are apparently much better in British Columbia than anywhere on the Atlantic coast—that is, for producing a large volume of herring.

Herrington: As I understand it, the North Sea herring on the Atlantic coast is known as a high-seas fish. On the west coast I understand that the population enters bays. If you concentrate on a population when it is concentrated, as during the spawning season, it is possible to wipe it out or greatly decimate it. As I understand it, our investigators on the west coast believe that the Alaskan fish have different habits than the Atlantic fish. The question, it seems to me, is whether or not each major bay population is independent.

Huntsman: I wouldn't say it is a high-seas fish.

Needler: I agree with Dr. Huntsman that the herring on the east coast are caught almost entirely close to shore. There are mostly small herring inshore, but the bigger herring also appear to be over the inlying region. The few sonic-sounder records we have had in reporting herring in the Gulf of St. Lawrence indicate schools in close to shore, not out in the middle.

Herrington: What are the depths?

Huntsman: Anywhere from the shore down to thirty fathoms for spawning.

Needler: There are two points I would like to mention. One is that the difference between the expected catch of herring and the actual catch—I say "expected" on the temperature basis—in Passamaquoddy Bay may be the recruitment of a new year-class which bumps the catch up at the end of the year and makes that part higher and the other constantly lower.

The other point is with reference to the use of traps. We showed with smelt experiments that you caught more smelt lifting the trap every second day than you did lifting it every day. These were relatively small catches. It appeared that the small smelts wouldn't go through the trap except when disturbed. If you lifted the trap every day you would disturb them twice as often. You caught the same number of larger smelts whether you lifted it every day, every second day or every third day, but you caught fewer small smelts when you lifted it every day.

I object to the term "adsorbed" because I have an idea of adsorption as not including movement along the surface, while in the case of trapping the very method depends on movement along the surface.

Huntsman: My use of the term "adsorb" does not include movement, but draws attention to a similarity between a certain behavior of fish and an inorganic phenomenon.

Van Oosten: What was that other term you mentioned, Dr. Huntsman?

Huntsman: Thigmotaxis.

Van Oosten: Speaking of results with traps, we have used the records of the commercial fishermen on the Great Lakes. I have not got the exact figures in mind, but when we compared the records of catch for nets which were out one night, two nights, and up to eleven nights—for different types of gear—we found that if you put the catch for one night on the basis of 100, two nights out would produce something like 115 pounds rather than 200, as you might assume theoretically. After two nights there was only a slight increase with each additional night out. It wouldn't pay to keep the nets out much longer than two nights, and in some instances it might not even pay to keep them out two nights. Although we were rather surprised by the results, the trap-net fishermen were not particularly surprised. In fact, after we reported our results many fishermen informed us that they were perfectly aware of this fact, and that they had made visual observations of the fish and could see them swimming back and forth through the tunnel of the trap nets. The fish would move in and go out. Why they moved back and forth I don't know. The strange thing is that the same end results were obtained for gill nets and impounding nets. The fishermen tell us that if any number of dead fish are in a gill net other fish will keep away from that net, but, peculiarly enough, we got the same small increase with traps which take fish alive. We haven't found an explanation.

Huntsman: The fishermen certainly know a lot of such things. I wish they were down on paper.

Van Oosten: We were interested because we were working out some unit of catch-per-fishing-effort. We assumed, as many did, that the best unit would be the catch-per-unit-of-gear per night out, but we found that it was not a satisfactory unit. There wasn't a proportional increase in catch per night, so we discarded the night out and we now use simply the catch-per-unit-of-gear, disregarding entirely the length of time the nets are out. In any specific area the fishermen have about the same general habits year after year with respect to fishing time. So we could very well discard the time element in our unit.

Van Oosten: Is there any more discussion of Dr. Huntsman's paper?

Langlois: From what has been said, there seems to be quite a difference in the habits of the Alaskan herring and those on the east coast. I have a recollection of Rounsefell's remarks concerning Alaskan herring, in which he showed the correlation of year-groups with temperature changes. I am just wondering whether there could be any correlation between your Bay herring (in which the series of dominant year-groups apparently comes through in succession) and discharge of the stream.

Huntsman: The correlations I got with the discharge of the St. John River showed the amount caught in the particular year to agree with the discharge. The peculiar conditions in that region, as far as we can tell, seem to make it practically certain that every year-class will get a good chance. We see no particular evidence of good and poor year-classes, which have been shown so very definitely for other regions of the Atlantic.

Needler: Your point is that the temperature is unusually constant from year to year, is it, Dr. Huntsman?

Huntsman: Yes.

Foerster: I would like to see a little more elaboration as to whether the trap catches of salmon given by Dr. Huntsman can be considered a fair sample of the population, or whether they represent a fringe perhaps of the general population or a unique part of it with particular habits which led to them being caught by traps, and to what extent that might affect the assessment of the whole population. I think that is a very important point in appreciating the importance of assessment of population.

Huntsman: There is no question—you see, we tag at certain traps and then we take all the recaptured . . . .

Foerster: You tag fish caught by traps only?

Huntsman: Some taken by traps and some taken in gill nets. We got the same result for both when in the same general area. For instance, near St. John Harbor the same result was obtained from those tagged from traps or weirs as from those taken in gill nets off Lorneville—70 per cent in each case. The only difference was that those taken in gill nets weren't caught for a little while in any quantity. The biggest returns were about a week afterwards. It seemed to require about a week for them to recover from the struggle in the nets, which they didn't have to undergo in the traps.

Foerster: You think your sample was a true sample of the population?

Huntsman: All I can say is that we had samples from different parts of the St. John River outflow. There was a difference in percentage of recaptures between inner and outer regions, but both lots of fish were parts of the whole population of the river. It is a very complicated thing. I wouldn't maintain that we as yet know how to get a perfect idea of the total population related to any river.

Van Oosten: Any further questions?

Hart: Dr. Huntsman showed some graphs of the production of various European bottom fish and also of herring and mackerel. Have you examined those figures at all, Dr. Huntsman, to detect indications as to the extent to which the fluctuations in yield were influenced by economic conditions? I couldn't read the years very accurately, but it seemed to me there was quite a close relation with the stock market.

Huntsman: I don't know. I haven't tried to correlate them with either sun-spots or the stock market.

Needler: After each war there were differences in the kind of fishing equipment used. I was wondering also what area is included in the North Sea and wondering whether the near and far areas were separated. You won't get the same result in the two, the near area being more intensively fished than the outer. If the two weren't separated I doubt very much whether the total would give the correct picture in view of the economic demand which, for example, now has reached the stage in England where they are only fishing for herring half the time; the boats have agreed to stay in half the time so that their herring catches can be sold. The war not only upsets fishing during the war but after, especially as regards the larger boats that go a distance.

Huntsman: It would be good to have an analysis of all the factors. However, I certainly didn't have time to make such an analysis, so that the only conclusion I have thought proper to draw is that, as it stands, we cannot see any definite evidence that the fisheries as a whole in the North Sea haven't been maintained. Surprise is expressed in the statistical bulletin of the International Council at the way in which the North Sea has stood up under intensive fishing.

Burkenroad: We have been attempting, for the North Carolina region, to get at this economic factor in a very crude way. We are plotting prices in constant dollars parallel to catch. When price and production move in the same direction, change in demand seems indicated. When price goes down and production goes up, and when price goes up and production goes down, change in abundance is indicated. In the case of price down and production up, it seems possible that there might have been an increase in abundance; and in the reverse case you might have a scarcity of fish, since otherwise increased landings ought to lower price. It would be difficult to subject those North Sea figures to such an analysis, because prices or values are not given in the Council statistics.

Huntsman: Even when price goes up and catch goes down you can't necessarily conclude that the population has gone down, because some fishermen stop when they have a certain amount of money. Some of ours behave in that manner.

Herrington: Price ceilings affect that relationship.

Van Oosten: The price of fish certainly has an effect on production, as I have experienced recently with our lake trout. The fishermen were getting 60 to 70 cents per pound, the normal price being around 25 cents. Under these conditions of high price I have seen more than once a crew of three men go out and come back with only 90 or 100 pounds of trout. They kept right on fishing. Normally they would have stopped, but at 60 or 70 cents per pound they kept right on operating.

Huntsman: I once attempted to find the correlation between the take of these Passamaquoddy herring and the days of the week. I found that every alternate day the catch was high. Since they don't run the factories on Sundays, none are reported on that day. The factories can't carry them over the week-end because they go bad, so they take a lot on Monday. They are apt to take too much. They ease off on Tuesday. They come up on Wednesday, and then ease off on Thursday. Monday, Wednesday and Friday were the peaks.

Herrington: The Boston landings of groundfish follow that curve very closely. Friday, however, has lower landings.

Medcof: I was reading an interesting article lately in connection with a clam fishery which is conducted in a very primitive fashion. In the depression time there was a great increase in the number of fishermen. People in poor economic condition were forced into fishing because they couldn't find anything else to do. Naturally enough, inexperienced people make lower catches. And, under the regulations, there was no possibility for improvement in fishing gear. It remained the same. So it is quite different from the condition that Mr. Herrington described, where you have improvement in trawls and what not. You have to deal with each case in itself. When these inexperienced fishermen came into the picture, it is quite certain that the catch-per-man-per-tide would drop because an experienced man could produce two or three times the quantity that an inexperienced man would.

2. NORTH AMERICAN ATTEMPTS AT FISH MANAGEMENT

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ABSTRACT

Following a brief statement of the history and growth of the North American fisheries there is a discussion of the present biological concept of the effects of fishing on fish stocks and the actual inapplicability of this concept to the major fisheries. The new movement, particularly on the part of fishery biologists in the midwestern and eastern states and Canada, exclusive of the U. S. Fish and Wildlife Service, attributes major fluctuations of fish abundance to effects of an environment which fluctuates in its suitability for larval fish rather than to depletion by overfishing. Lake Erie illustrates the necessity for studying entire environments rather than just the fish in a body of water; the relationships of the lake to its bays, tributary streams and headwater areas, as regards fish production in the lake, are presented in some detail. The suggestion is offered that other bodies of water may have "key areas" like that described for Lake Erie, wherein the cycle leading to fish production is either started or kept from starting. Recent efforts of trying to improve fishing in midwestern inland waters are reviewed.

HISTORY AND DISCUSSION

The exploitation of the natural resource of fishes on and adjacent to the continent of North America has a record which extends back to about the year 1500 A. D. It began after Cabot returned to Europe and presented glowing accounts of the fishes he had seen. When Jacques Cartier entered the mouth of the St. Lawrence River in 1534 he found some Norman and Breton fishermen present on the "banks" (Aubert de la Ruë, 1944: 184). The industry expanded southward with local enterprises at each of the colonies from Maine to Florida, and in the Gulf of Mexico. The west coast fisheries expanded with the growth of the settlement after 1849. They were extended northward along the Canadian coast during the early part of the present century, and they became a major Alaskan enterprise during the last three decades. The principal fresh-water fisheries developed rapidly during the period beginning about 1850, when the potentialities of the Great Lakes and Mississippi basin came into use.

Although each region developed its fishery as a local enterprise, the over-all record is in accord with the nation-wide trend of expansion from small to big business. According to a report by Ickes (1945), the magnitude of fish production in the several areas is expressed as follows:

1942.	New England	676,000,000	pounds
1940.	Middle Atlantic and Chesapeake	684,000,000	"
1940.	South Atlantic and Gulf	576,000,000	"
1940.	Puerto Rico and Virgin Islands	3,700,000	"
1942.	Interior of the United States	175,000,000	"
1942.	California	1,173,000,000	"
1941.	North Pacific States	289,000,000	"
1943.	Alaska	577,000,000	"
	Hawaii	14,700,000	"
Total		4,168,400,000	"

The first fish management attempts, consisting of some self-imposed limitations of catch, were made by the men who were operating the early fisheries. Later the fishermen learned the technique of stripping ripe spawn and adding the fertilizing sperm to start egg development, and thus they started an extensive system of salvaging the spawn of the fish in their catch.

Biologists have watched the development of the fisheries from an early date and have helped the fishermen develop methods of taking fish, and of measuring, packaging, transporting and marketing their products. When fish propagation became the vogue, biologists helped develop techniques for increasing the fertilization percentages, for providing proper nourishment for growing young fish, for controlling fish diseases, and for transporting live fish to the areas scientifically selected for liberation.

Biologists also have been attempting to follow the changes that have taken place in the fish populations while this expansion of the rate of exploitation has occurred. Some of them have attempted recently to formulate a generalized history of a fishery in terms of stages of progress, as follows. The start of a fishery is a small scale operation, with fish abundant and prices low. After the field has been opened there is an increase in the number of fishermen, an increase in the total pounds of fish taken and a slight increase in price, but there is a reduction in the average size of the fish. Later there is a great expansion in the number of fishermen and of fishing effort, with violent fluctuations in the abundance of fish. The catch alternates between peaks which glut the market and lows which lose the market, and the price varies quickly from lows which provide little profit when the market is glutted to highs which also provide little profit when there are so few fish to sell.

During some of the least profitable periods, many fishermen discontinue their operations, thus easing the pressure on the fish populations enough to permit some recuperation. The stocks build up again, providing more returns per unit of effort and more profit to the smaller number of fishermen. This leads to another increase in the number of fishermen and to an increase in the amount of fishing effort, thus beginning a second phase of an oscillating rhythm. If allowed to proceed undisturbed, following this law of economics, this type of change occurs over and over again.

In some cases, about the time of the first serious decline, the fishermen have requested help from government, or government has offered help, to stabilize the industry. On the theory that a dependable supply of the marketable product must be the first consideration, biologists have been assigned to the task of finding out what needs to be done to insure more dependable yields, preferably at higher levels, but especially yields which fluctuate less violently. The recommendations of the biologists have tended to follow the procedures which the fishermen think are indicated, *i. e.*, restrictions on the time and length of the fishing season, modifications of the fishing gear so as to permit more small fish to escape, minimum limits on the size of fish which may be taken so that more small fish might attain maturity, and total limits on the catch permitted of particular species in specified areas.

Curiously, however, the above formulation does not seem to fit the record of most of the major fisheries as presented in Ickes' report. For instance, the catch of pilchards on the west coast has shown a consistent increase from about 1914 to its present phenomenal size of about 600,000 tons, without any indications that any restrictions are ever going to become necessary. The Pacific fisheries for shad, anchovies, rockfishes, lingcod, cod, black cod and tunas have been described as not yet developed to their full capacities. The tunas are considered to be a world resource, so little touched by present fishing efforts that no comprehensive studies of their life histories have been started.

Similarly, on the east coast, where the combined catch of the Canadian and American fishermen of codfish totals about one billion pounds, the biology of the species is not known and no regulatory measures are in force or even recommended. The North Atlantic catch of herring ranges from thirty to ninety millions of pounds, with no sign of depletion. The biology of pollock, whiting, cusk, rosefish, lemon sole and menhaden is not known, but the catch of those kinds is less than seems desirable and feasible without harm to the stocks. In Lake Erie, the fishery for blue pike, yellow pike, sauger, sheepshead and carp has reached high levels without apparent detriment to future production (Langlois and associates, 1936–1945).

Some attempts at management have been made for a few of the important oceanic fishes. For instance, hatcheries were operated to supplement natural reproduction of the Alaska salmons until recently when the futility of this procedure was established and the hatcheries were discontinued. Because the salmon migrate out of salt water into streams to spawn they are peculiarly susceptible to another method of management. The crop of salmon can be predicted by counting the number of spawners moving upstream towards the spawning grounds, then by counting or estimating the relative number of newly hatched young as they move downstream towards the ocean, and finally, by checking data on stream and ocean conditions which effect the survival of salmon. This can work only by making these determinations for each stream's population every year, and for Alaska alone this would require twelve field laboratories (Ickes, 1945: 8). Lacking the facilities to handle the task in this desired manner, the U. S. Fish and Wildlife Service has established regulations to define fishing areas, provided weekly closed periods, and prescribed size-limits on fishing gear, opening and closing dates for the fishing season, and maximum catch quotas for certain areas.

In 1936 Pritchard reported finding a significant correlation of the number of pink salmon adults migrating daily from the sea to the spawning areas in a creek with the daily rainfall in the region and the maximum daily water height in the stream. Later, Thompson (1945) reported that an obstruction in the Fraser River could not be passed by ascending salmon and that this barrier was of greater importance than fishing intensity to the salmon of that stream. An expensive fish-ladder has recently been constructed to enable the salmon to bypass this barrier, but Ricker (1947) has expressed doubt as to the value of this procedure on the basis that the barrier kept back only a small percentage of the migrants.

The fisheries for halibut on both coasts have fluctuated greatly, and overfishing has been cited as the cause. The Pacific halibut catch was reported by Thompson (1936) as having dropped from sixty millions of pounds in 1912 to twenty-two millions in 1930, after which it went up to thirty-two millions in 1936. The North Atlantic halibut catch showed a decline from a high of thirteen millions to a low of one million pounds. No major attack has been made on the problems connected with the halibut of the North Atlantic, but the attempts to manage the Pacific halibut have been given wide publicity and acclaim. An International Fisheries Commission was established by presidential proclamation (Hoover, 1931) for this purpose because the same stocks of halibut were supplying the fishermen of Canada and the United States.

After extensive investigations, the conclusion was reached that the abundance of halibut on the fishing banks and the number of spawners could be increased by reducing the amount of fishing, without loss of poundage, until new supplies of young would allow an increase in the catch. The increase in the number of spawners was expected to result in the production of more eggs, this leading to more fish which would grow up to provide more spawners and a surplus to be caught. The Commission was given authority in 1931 to put its recommendations into effect, and it established some new limitations on the catch.

Essentially the same viewpoint was taken by Rounsefell and Dahlgren (1935: 138), as expressed in their statement that the relative abundance of any particular year-class in the catch is influenced by (1) the relative number of larvae of any particular year-class hatching and surviving until of an age or size to enter the catch, (2) the rate of natural mortality, and (3) the increased rate of mortality induced by the fishery. Rounsefell (1930: 262) elsewhere reported finding a correlation between surface water temperatures and the success of spawning. He concluded that this was more likely to be associated with the planktonic food supply than as a result of any direct effect upon the fish eggs.

It is difficult to determine the relative numbers of larvae of any particular year-class, but vast differences are known to occur, and for lack of information about the causes of these differences it is often assumed that the most important factor which determines abundance is the increased mortality induced by the fishery. Tremendous fluctuations of abundance of some kinds of fish, not ascribable to depletion by the fishery, have been noted. Kendall (1908: 292) cited one instance, as follows.

> The effects of the complete extermination of menhaden from the seas may be inferred from the effects of local disappearances for a term of years and where there is no evidence that the fishes that fed upon them there suffered in consequence of their departure. It may with propriety be stated here that such 'unaccountable' disappearances took place long before modern fish traps and purse seines were known. Subsequent like disappearances and reappearances, again disappearances without reappearances, cannot then, logically, be laid to the purse seines and steamers.

In Lake Erie there was a comparable decline of a fresh-water plankton feeder, the cisco (*Leucichthys artedi* LeSueur). Reports by investigators of the U. S. Fish and Wildlife Service have described this as a clear-cut case of decline due to depletion by fishing and have used the case of the missing cisco as the basis for urging the establishment of an International Board of Control to establish limitations on the fishing intensities for all species in the Great Lakes (Van Oosten, 1937, 1939; Gallagher and Van Oosten, 1943). The probability that the principal cause of this relict coregonid's decline was a function of an unfavorable environment for the eggs or larvae has appeared as a result of an independent investigation conducted continuously by the State of Ohio since 1938 in the western part of Lake Erie.

Like the menhaden of salt water, the cisco is a plankton feeder throughout its entire life span, a fact which makes it unique among the commercially important fishes of Lake Erie. This habit establishes the dependence of the cisco upon the primeval lake conditions of clear, cool water. It is one of the two members of the Coregonidae still occurring in Lake Erie, though the upper lakes each contain more of the total of eleven forms described as occurring in the Great Lakes (Koelz, 1929). Lake Erie is the shallowest and warmest of the Great Lakes, presenting conditions which are marginal for this group of fishes and thus taxing their tolerance to exist there at all. The extreme variation found by limnological studies to occur from year to year (Chandler, 1940–1944) well may be interpreted as the cause of the near elimination of this one of the last two survivors of the group in Lake Erie.

The Ohio investigations have been conducted at the Franz Theodore Stone Laboratory on South Bass Island. This island is one of a series which marks the edge of the shallow western part of Lake Erie from the deeper basin to the east. From this island westwards the depth of water grades from a midlake average of thirty-two feet to the shoal areas along the south shore. The island is almost fifty miles distant from Toledo at the mouth of the Maumee River and about the same distance from the mouth of the Detroit River. The drainage from the upper lakes, brought into Lake Erie by the Detroit River, constitutes from 96 to 98 per cent of all inflowing water. This large volume (about 160,000 cubic feet per second) passes as a stream through the west end of Lake Erie, swinging along the north shore, then southward along Point Pelee to enter the middle part of the basin. In contrast, the Rouge, Raisin, Maumee and Portage Rivers discharge into a water mass which acts like a great mixing bowl, stirred up by strong winds, but lacking through-flow current characteristics.

The Ohio limnological studies have reached out from the island to cover nearly the entire western end of the lake, with sampling stations from south to north shores. In general, the water from the upper lakes, coursing along the north shore, remains relatively clear, while there is great variation in the transparency of the water of the stiller mass. A correlation has been demonstrated (Chandler and Weeks, 1945) between these variations of transparency and the variations of discharge of the south shore tributary streams (Figs. 1A, B), while the cause of the reductions in transparency has been shown to be the finely suspended sedimentary clays. In the same paper a correlation was established between the annual cycles of fluctuating abundance of the nitrates and phosphates with the run-off from the lands of the northwestern part of Ohio. The amounts of these inorganic salts increase greatly at times of accelerated stream discharge, and as discharge varies greatly from year to year, so do the amounts of these salts in the lake. Unfortunately, while these plant nutrients are brought into the lake in larger amounts during the seasons and years when the streams are showing maximal discharge, the stream flow is also most violent at those same times, and there is a coincident increase in the amount of silt which is stream-borne into the lake. This silt, fine clays from flat farm lands, makes turbid the west end water mass, curtaining out the sunlight without which the nutrient salts cannot be photosynthesized into plant tissues.

During the last eight years continuous studies of the lake plankton have discovered tremendous variations in the numbers of organisms and in the periods of their abundance (Fig. 1C). Expressed (Langlois, 1946) in terms of fractions of the maximum yet found, that of 1941,

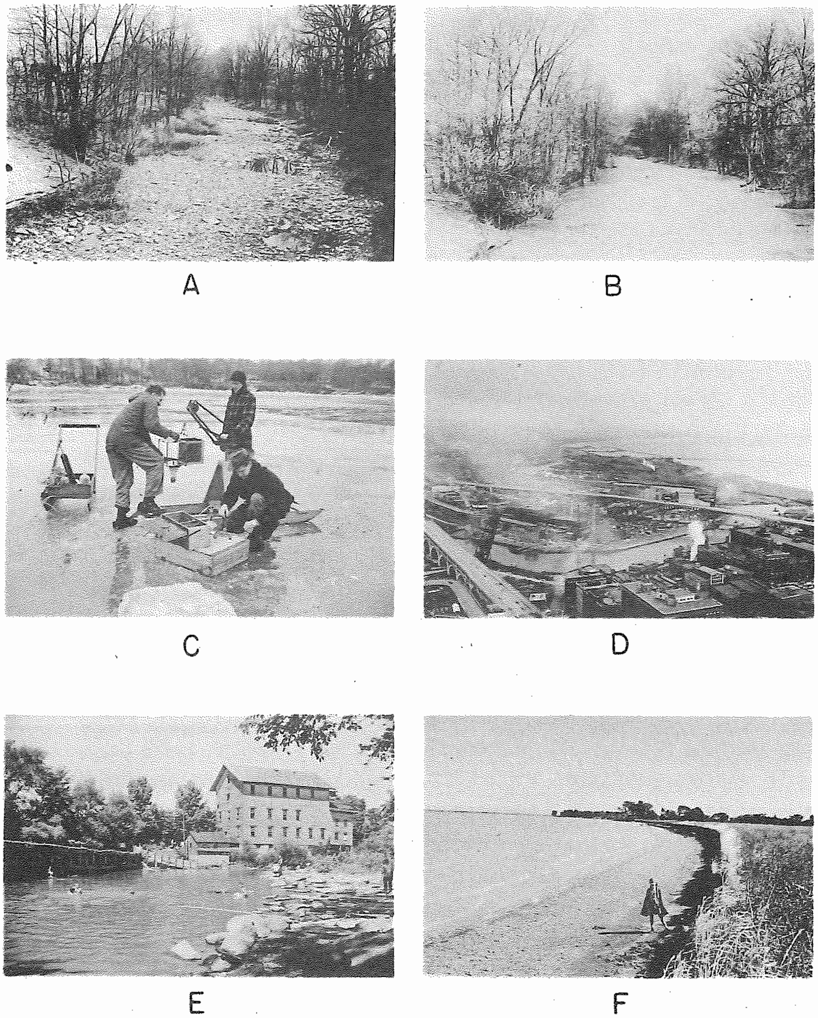

Figure 1. *A,* Honey Creek, a tributary to the Sandusky River, is devoid of flow in November. *B,* The same creek is at flood stage the following March. *C,* Continuous limnological research involves collecting plankton through the ice. *D,* The industrialized mouth of the Cuyahoga River in Cleveland. *E,* The mill dam at Monroeville, Ohio, stops migrations of fish in the Huron River. *F,* The south shore of Sandusky Bay is undercut by waves and is receding, at the cost of good land and to the detriment of the lake.

the yearly maxima were as follows: 1939, 14%; 1940, 23%; 1941, 100%; 1942, 16%; 1943, 8%; and 1944, 78%. The duration of the periods of abundance also varied greatly, being very brief in some years and prolonged in others. These extreme variations of plankton abundance have been found to be correlated with the relative transparency of the water, and they appear to offer an explanation for the variation in survival of larval fish.

The occurrence of dominant year-classes has been shown (Van Oosten, 1938, 1942; Jobes, 1933; Deason, 1936) to characterize the stocks of many kinds of fishes in Lake Erie. Significantly, the dominant year-classes of several kinds of fish were produced the same years. For instance, the hatch of 1926 yielded big year-groups of such diverse forms as yellow pickerel, white bass and sheepshead, and this fact suggests that the critical period for all of these kinds is the period after hatching, when they all depend upon plankton for food. This period occurs in April, May and June in Lake Erie, the identical period of greatest variation in plankton abundance. Of high significance is the fact that the favorable vernal season of 1944 was the one which led to the production of a relatively large number of ciscoes. The ciscoes which hatched that spring yielded a catch by Ohio fishermen of 677,212 pounds in the autumn of 1945. The previous ten-year average was 21,684 pounds per year, and the big hatch of 1944 had been produced by the very small stock present in the lake in 1943. No theory of overfishing can explain this sort of an increase in abundance.

The shallow western part of Lake Erie, into which certain influential streams discharge their waters, and into which most of the shoal-seeking fishes make their spawning migrations, appears to be the "key area" for starting the energy cycle which culminates in crops of fish. Into this water mass the streams pour the principal quantities of plant nutrients, and within this water mass the nutrients are either utilized to start the series of stages of levels of life, or they are not utilized because the silt screens out the sunlight. One of the procedures for permitting dependable annual productions of large numbers of young fish is the establishment of those land-use practices which will hold the top soil on the farm land at the headwaters of the tributary streams.

The tributary streams to a lake have other roles to play in assisting the lake to produce fish. Many kinds of lake fish migrate upstream to spawn on the riffles, and when the young hatch on the riffles they are current-carried down into the vegetated bays where they find some protection during the most helpless stage of their existence. The south shore tributaries to Lake Erie once functioned in this manner. In 1850 Kirtland described the annual spawning migration of muskellunge and sturgeon from Lake Erie up the Cuyahoga River. Pollution from the industries at Cleveland now make an impassable barrier at the mouth of the Cuyahoga (Fig. 1D), and it is possible that the substances carried out into Lake Erie may adversely affect the growth rate of lake fishes. VanOosten (1929: 406) showed that the herring of Saginaw Bay were thus retarded during the first World War by chemical wastes brought in by the Saginaw River. Similar zones of pollution or small dams (Fig. 1E) exist at or near the mouths of *all* of the major streams along the south shore of Lake Erie, so that the streams have discontinued rendering those services which are essential to the fishes of the lake.

While the Ohio fisheries research program has been concerned with this key area of Lake Erie and the tributary streams, it seems probable that the problems of fish production of each of the other Great Lakes may be similarly concentrated on key areas and tributary streams. Saginaw Bay and Potagannissing Bay are known to be two of the key areas for Lake Huron, Green Bay for Lake Michigan, and the Bay of Quinte for Lake Ontario. Significantly, the proposed attempt to reduce the population of marine lampreys has been focussed on these forms while they are in the streams, though the harm they do is done in the lakes.

It may be that the mouths of streams and the oceanic bays are comparable key areas, since most of the principal marine fisheries center in such regions. Bigelow (1926) showed a correlation between stream mouths and plankton distribution, and Huntsman (1934) has indicated that the herring fishery at Passamaquoddy Bay is made possible by the surface and subsurface currents caused by the discharges of freshwater streams. The same approach to problems of such fluctuating marine fisheries as the halibut may show that the mortality of larvae exceeds in importance that of the adults caused by fishing (Eschmeyer, 1944, 1945; Langlois, 1941; Moffett, 1943).

The great reproductive potential of fish, upon which we rely when taking out sizable increments of the stocks, is the compensating factor which permits our use of fish flesh for food. The problem of fish management is one of providing an environment which favors the operation of that factor. The environment must be suitable for the fish to place those eggs, for the eggs to hatch, and for the larvae to grow until they become big fish. This problem is individual for each stream, bay and lake, but it has aspects of stream-bay and bay-lake relationships. It may involve keeping the top soil on the land from which the rainwater drains into the stream, and it may involve checking the bankwash on the bay or lake shores (Fig. 1F). It may or may not include any actions directed towards the fish themselves, but it should involve the elimination of physical or physiological barriers to free movements of the fish. It must be based upon knowledge of the needs of each species of fish, although the scope of information at hand about such needs is truly meager. It is particularly important that we become better informed about the inter-relations of the many species of fish which are present in most bodies of water.

Some of the recent attempts at the management of fresh-water fishes merit attention. Poisons have been used for the collection of whole fish populations for study of the constituent species, and there have been some attempts to do selective poisoning to get only certain kinds out of many present. Some efforts to improve lake fishing have consisted of placing brush shelters on shoals, or of adding fertilizers to increase the plankton. Stream improvement programs have aimed to create better environment by checking eroding banks, shifting currents with deflectors, installing new riffles and small dams, and stabilizing flow with headwater impoundments. The control of such fish predators as turtles, snakes and birds has been tried in some instances. Large scale programs of propagating and distributing game fish species are still in effect, although there is a tendency at present to divert funds from that purpose towards the improvement of habitat. Much hullabaloo has been raised about the evils of pollution, but little real progress has been made towards correcting this misuse of our streams.

The construction of a number of large impoundments during the last few years has created some new problems of fish management. Some of them, like Lake of the Ozarks in Missouri, and Lake Herrington in Kentucky, exhibited early peaks of production which were followed by slumps without noteworthy recovery. Others, such as Lake Mead in Arizona and Nevada, and Lake Texhoma in Texas and Oklahoma, are so new that no appraisal can be made as to their capacities to produce fish. The series of large impoundments on the Tennessee River has been studied by fisheries biologists during its entire history, and the recommendations made by them aim towards a stabilized yield at high levels, without restrictions on cropping methods. In Wisconsin, Schneberger (1945) also advocated cropping as a tool of fish management. Thompson and Bennett (1938) in Illinois have attempted to establish desirable balances between predators and predatees in the fish populations of small lakes as a technique of fish management. In Indiana, Ricker and Gottschalk (1941) reported an instance of improvement of angling in a small lake by the removal of coarse fish. Michigan's program for making better fishing (1945) presents Westerman and Hazzard's brave reversal of previous policies of propagation and commitment to attempts at habitat improvement. The fish program for Ohio (Langlois, 1944, 1945) aims entirely at improving fishing by providing suitable habitat and reducing unnecessary restrictions.

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DISCUSSION

Van Oosten: Dr. Langlois' paper is now open for discussion.

Herrington: You mention that your work has been done in the western end of Lake Erie. Have you any evidence that the turbidity of the water you find there has extended out into the main part of the lake?

Langlois: Not particularly. I should mention that the western end is the shallow end of the lake. I don't think there is any place more than 35 feet deep. That is the edge of a basin, and then it drops off. The deepest part of the lake is the eastern third.

Herrington: Do you believe that when the water level of the streams is high and additional nutrients are brought down to the lake that these nutrients won't work into the eastern end of the lake and thereby cause a heavier production there?

Langlois: We have some evidence of plankton drift. The Cleveland Waterworks maintains some data on plankton. What I am thinking about particularly is that the young of practically all species of fish require plankton as their first food. It has to be present in the area where the young fish are, and in abundance. There has been a westward spawning migration for most of the species in the lake, and the west end is, therefore, the critical area. It probably determines the advent of year-groups into the catch.

Hart: Did you have a big year-group as a result of your comparison with your 100 per cent year?

Langlois: I am not quite sure about that. We had no evidence at that time of a return of herring. I had been rather expecting there might be one following that '41 year. I am not at all sure that this '44 hatch may not have been the result of a slightly increased number in that '41 hatch. That is pure conjecture, however.

Herrington: In other words, until you carry through the chain connecting the low or high production of plankton to production of year-classes, you won't be very sure of the facts?

Langlois: Yes. We are gathering a lot of circumstantial evidence. We piece it together and begin to draw conclusions, and then comes a time to check those conclusions.

Burkenroad: Would it be possible to carry back the river discharge observations by means of rainfall correlations over the eight-year period for which you now have observations? That is, if you could correlate rainfall and discharge, then you could compare weather bureau records running far back with the catch records.

Langlois: We know the effects of exceedingly heavy rainfall and stream flow on leafy aquatic vegetation. Heavy river discharge will eliminate it. We know, for instance, that the mouth of the Maumee River was once exceedingly densely populated with leafy aquatics; they are gone now and Maumee Bay is about as barren as this floor.

Huntsman: It seems that such of our eastern Canadian rivers as we have studied are fairly barren of nutrient salts, perhaps because the salts have been very thoroughly removed by plant growth as the water runs down the rivers. Hence a certain amount of suspended matter may actually be desirable in order to make sure that the nutrient salts are available in the bays or sea. In the sea the comparable case to your situation in western Lake Erie seems to be that of the Gulf of Mexico near the mouth of the Mississippi—certainly that part of the Gulf of Mexico is very highly productive in fish and shrimp. Apparently that is related to a muddy Mississippi where the nutrient salts carried down that river are made available out in the Gulf of Mexico. I was wondering how you would view that point. Presumably there would be no likelihood of reducing the amount of sediment in your streams so that the salts would be used in the streams rather than in the western end of Lake Erie.

Langlois: I don't know what likelihood there might be. The districts of northwestern Ohio are flat, and the farmers have scarcely been conservation-minded. They are hardly aware of the loss of one inch of topsoil, in spite of the fact that one inch from there is worth a great deal more consideration than in southeastern Ohio where the land is relatively unproductive. I think methods are known to control this sheet erosion, such as contouring in certain areas where the land is uneven enough to justify contours.

Ricker: I think all of us on the Great Lakes would be interested in seeing whether some compromise or some point of agreement could be reached between your views and Dr. Van Oosten's. I don't pretend to have found that, and, as you say, it may well be that both fishing and these factors you mention have had some share in the history of the Lake Erie fishery. The thing that strikes me though is the fact that the cisco fishery declined, as I recall it, rather abruptly around 1925, whereas it seems to me this turbidity would have increased gradually over a long period of years. I suppose it would be conceivable that a critical stage would be reached which would be reflected in a rather abrupt turn in the fishery. Have you given that consideration?

Langlois: We have seen several years in a row where turbidity was so excessive as to virtually prohibit the entrance of any successful year-group. It isn't too far-fetched to figure that two or three additional years may have made it worse at the time of that critical decline in production.

Ricker: Can that be shown in the records of turbidity or of stream flow?

Langlois: Dr. Chandler has some data on that. I wish I'd had Dr. Chandler bring his data and his graphs along.

Van Oosten: Have you any records to indicate how the turbidity of Lake Erie has changed during the last 40 or 50 years?

Langlois: We have only this evidence of extreme variations from year to year in the last eight years.

Huntsman: Presumably evidence from the rooted aquatics would be pertinent?

Langlois: I think it is.

Huntsman: What records have you of that?

Langlois: The exact data I am not sure of, Dr. Huntsman, but there are definite records of the upper end of both Maumee Bay and Sandusky Bay having been extensive duck marshes and of there having been dense aquatic leafy vegetation throughout those bays. Turbidity is the probable cause of its elimination.

Herrington: There is a point in your argument I would like to clear up. You just stated that if you had a series of years where you had high turbidity it might reduce the population to a very low level from which it wouldn't recover. If that is the case, suppose a fishery reduced it to a comparable level, what would you have then?

Langlois: The curious thing is that the stock has been at a comparatively low level since 1925, but in spite of that the herring have come back.

Herrington: Thinking in terms of averages, not individual years, on the average have your conditions been very poor during the time the stock did not come back?

Langlois: Yes, they have been poor.

Herrington: It would be desirable to tie together the relationship over a longer period. Without it an hypothesis is about as far as you can go.

Langlois: We think it is a pretty good hypothesis supported by considerable circumstantial evidence; better than the hypothesis of over-fishing for which the evidence also is only circumstantial.

Van Oosten: In the earlier years Lake Erie fishermen were using the so-called bull nets for the cisco primarily. That is a floated gill net some 25 feet deep. After a number of years of use of that net in the eastern end of the lake in New York, it was taken up by the fishermen of Pennsylvania, and finally it was used by the Ohio fishermen in the shallow waters in the western end of the lake. That net, as I said before, is 25 feet deep, and the deepest part in the western end of the Lake referred to by Dr. Langlois is about seven fathoms. If you float that net in that depth you can see that you are practically covering the fishing waters from top to bottom. The custom was, of course, to head off the ciscoes when they were on their spawning run in the fall of the year. The fishermen would follow the schools of ciscoes as they migrated from one end of the lake to the other. Of course, they fished them also during the summertime in deep water. The average annual production had been going down from the earlier years. With the advent of the bull net it almost went back to the normal figures of the early years. That increased yield lasted for a period of about ten or twelve years. Then we had an unusual concentration of the cisco for two successive years in the deep water and the fishermen followed them. It was here that a heavy toll was taken followed by a sudden collapse of the fishery.

It was this sudden collapse that puzzled us when we were first sent down there to investigate. The cisco catches were tremendous right up to the very last day of fishing in 1924. Fifteen or twenty thousand pounds of fish were brought in by a boat in one day out of one lift. Then with the opening of fishing in the spring of 1925 there was a collapse. The annual production of some 26 million pounds dropped to around 5¾ million, and the next year to 3 million, and then for a long series of years it averaged around 250,000 pounds. But in the meantime the bull net had been abolished—that net is no longer in use except on a very small scale in New York waters.

Herrington: It is since then that the recovery has come?

Van Oosten: There has been no recovery.

Herrington: Oh, I understood there had been a recovery.

Van Oosten: No, only a temporary one. There was a temporary recovery in '38 which lasted for two years. The production was around 2,000,000 pounds. The normal annual production was around 26 million pounds in the earlier years. Only one year-class, that of 1937, entered the fishery those two years, just as the 1944 year-class has entered for the last two years.

Herrington: The point I have in mind is this: If Dr. Langlois argues that you can have a series of years where you have poor conditions for survival of young which reduces the total of young to a point where the stock cannot recover easily, he would have to concede that the fishery depleting the stock to the same level would have the same effect. It seems to me that the poor conditions for the survival of young and the intensive fishery would have the same effect.

Langlois: There had been intensive fishing prior to this for a decade. I think the catch before this was 48 million pounds. It stayed high without any such decline of this nature.

Herrington: Is it a combination of poor conditions for survival plus a heavy catch, do you think?

Langlois: Yes, that is possible. But it doesn't seem conceivable to me you can bring it back by limiting the catch.

Huntsman: Do you believe that with the bull nets no longer in operation the recent abundance corrects the condition by providing enough spawners? Will we get back now the abundance there was before?

Van Oosten: It probably would if you'd leave the fish in the lake.

Kolbe: I would like to make the point that commercial fishing will reduce fish only down to a level beyond which it is unprofitable to fish, whereas a change in natural conditions can take the fish down to any level whatsoever. There are three of us here who make our living catching fish. The commercial catch of ciscoes for 1943 may not accurately represent the actual population. In the fall of 1944 when these ciscoes spawned there wasn't a great deal of fishing. There was more money to be made catching something else. There were hundreds of square miles on which there was never a net fished out in the center of the lake where these ciscoes spawned. They are the fish that brought on this big class in the last couple of years. When we fished them heavily last fall the fish weren't fully mature; they went to the bottom. There wasn't a great amount of spawn. In fact we couldn't have begun to take spawn in the boats for hatchery purposes because we wouldn't have found enough. This year, however, the fish spawned heavily. It must have been an eighth of an inch thick because the eel-pouts and perch were just full of it. I venture to say we opened some stomachs that had 80,000 eggs in them. There was one catch in which I think 77 per cent of the eel-pouts and all of the perch were full of it. We can't understand a lot of these things. To us it is largely a matter of egg survival or fry survival. Those are the two things that the fishermen look for and here we can see there is tremendous destruction.

While I am speaking I would like to ask a couple of questions of Dr. Langlois. For instance, do you feel that the turbidity due to storms all over central Lake Erie is vastly detrimental?

Langlois: Well, in general, the fall storms really stir up the bottom. We have records of that, too. However, that is before the spawning season of the herring, so I am inclined to think that it is not highly significant in this case.

Kolbe: We find when the water gets cold it doesn't get in motion as much and we may not have as big a season as we do when the water is warm.

There is another question I would like to ask you also. You said that in one year there was eight times as much plankton as another year. What was the situation relevant to the animal plankton?

Langlois: That pulse falls a little behind, but that was abundant too.

Kolbe: Would it be six to eight times, too?

Langlois: Yes, probably. We have collections and samples and it was abundant.

Kolbe: It is standard knowledge among fishermen in Lake Erie that the green slime, which is the phytoplankton, I'm sure, is very abundant in the spring if it is an open winter, that is, if there is no ice. On the other hand, if it is a winter when the lake has been covered over heavily with ice and perhaps a lot of snow so that the sunlight hasn't penetrated, we go out and the water seems more or less clear of plankton, which then comes on gradually after that. Sometimes our lines are so covered we can't catch a fish, although the fish may be there in abundance.

Van Oosten: I think an important missing link is the fact that there has never been shown any correlation between the abundance of plankton and the abundance of fish. After all, we don't eat plankton; we eat fish. If you can show any correlation between the variations in the plankton crop and the strength of the year-classes of the various fish, then you have got something, but until you can do that you are simply theorizing. It may sound all right to say that young fish have to have plankton, but they may have more than they can eat now in Lake Erie. Also, you must consider the time element. You may have a peak in plankton production which occurs two weeks before or two weeks after the fish have hatched which will do them very little good. As a matter of fact, as far as turbidity is concerned, I have the records of Lake Erie from 1910 on. I have divided the records for two periods. The turbidities of the last 15 years average less than the turbidities of the earlier 15 years. That statement applies to the annual averages as well as to the April–May averages when it has been assumed that the turbidities are critical. That answers Mr. Herrington's question about whether average conditions have changed. According to turbidity records they have not. In fact, they have improved. Certainly, storms are nothing new in Lake Erie. They have always been there. Turbidity has always been there. Certainly turbidity and the storms were present when the fish were plentiful, just as they are present to-day.

Langlois: Dr. Chandler has gone over the turbidity records of the State Department of Health, which I presume are the source of your information, and he has concluded that they are so vague and indefinite that averages of them don't amount to a tinker's damn.

Van Oosten: I wouldn't want to challenge the records of the Ohio State Board of Health, particularly after two of your men including Dr. Chandler used those same records. Your Dr. Doan attempted to show correlation between turbidity and the abundance of fish and failed to do so with respect to three species. He found correlation for one species, but it was a positive correlation—the more turbid the water the more abundant this fish became. If your men can use the State Board of Health records I assumed I would be justified in using the same records. Furthermore, you contend that the sauger is associated with muddy water. The fishermen have contended this a long time. That assertion is not new, but it is another thing to prove it. If the lake has become more turbid in recent years you'd expect the saugers to increase in abundance. As you have stated repeatedly in your papers, the clear-water fish have decreased in abundance because the lake is becoming more turbid. The production records show contrariwise that the saugers are less abundant now than formerly and that the clear-water fish, the walleye pike, are more plentiful than they have ever been. The records don't seem to support your theory at all. In fact, as far as the fish records are concerned, they don't seem to support anything you say with respect to turbidity and abundance of fish. I don't say that the environment is no factor at all, but I do contend that overfishing is a very important factor, and, of course, there is where our so-called feud originated. You say that overfishing has not been a factor in the depletion of the fisheries in the Great Lakes. That is where we disagree.

Herrington: In the North Sea they went into the study of plankton and worked on it intensely for many years. They finally seemed to run into a dead end because, as I recall, they could not obtain a good correlation between the plankton and fish abundance. Until we bridge that gap we can't assume from plankton records very much about what will happen to the fish.

Burkenroad: The most recent Norwegian studies show that survival of herring fry is correlated with occurrence of planktonic food.

Van Oosten: There is one experiment which indicates that a turbidity of less than 100 parts per million has no effect on the abundance of fish. It so happens that the annual averages of turbidity in Lake Erie are all under 40 parts per million. You might have a day where it goes up to 150 or 250 at the highest, but that is not usual.

Langlois: All it takes is one period of turbidity to eliminate the plankton. Averages mean nothing.

Huntsman: In the Passamaquoddy Bay region the facts seem to relate low phytoplankton production to turbidity resulting from very heavy tidal action. High production of fish wasn't correlated with high local production of plankton. My contention was that there really was a correlation between high fish production and high plankton production, which was missed simply because the plankton was brought to that region from where it was produced. It wasn't produced locally because of the turbidity. It was produced farther out in the Gulf of Maine and then was brought to that region and made available locally to the fish, which gave high production. So we had the two things there: The reduced local production of plankton as a result of turbidity and increased fish production as a result of transport and availability of the plankton produced elsewhere. The situation is more complicated than at first appears. The larger picture is needed.

Langlois: The herring in Lake Erie which have showed this decline are, of course, plankton feeders and are therefore most susceptible to that kind of a change. Significantly, of course, the other fishes have not showed a comparable decline. A record of fish production in Lake Erie for the last 30 years will show a succession of peaks but not a sustained yield. Each peak is determined by the abundance in that year-class of fishes—blue pike or yellow pike, yellow perch or what have you—but there is no evidence of any sufficient decline in any of the other fisheries to lead to the concern that might have been expressed. Since we were inclined to think that the decline in the herring was not certainly shown to be associated with the overfishing and might well have been associated with other factors, and since the other fishes were not showing that same decline and consequent cause for concern, we felt that the necessity for an over-all board of control was perhaps untimely.

Herrington: Do I understand you to say that the cisco went down and the others didn't?

Langlois: The others fluctuated greatly.

Herrington: Yet you are arguing that the turbidity caused the cisco to go down but didn't affect the others, is that correct?

Langlois: The cisco is a plankton feeder throughout life and it is therefore particularly susceptible to the changes in plankton abundance caused by turbidity. There is one other kind of forage fish in Lake Erie we are beginning to know something about. That is the all-abundant lake shiner. It is a part of the picture. The problem has to do with the problem of forage fishes as well as plankton.

Herrington: There must be something special happening to cisco that didn't happen to the others.

Kolbe: As a fisherman I would like to add that the herring is a plankton-eating fish. If you are short of plankton the many species of animal-eating fish in Lake Erie would very soon clean up the fry of the herring—especially when the fishermen fished intensively for herring and skipped the blue pike which is a very heavy eater of fish. A scarcity of plankton for one year would have a great effect on the herring, whereas it wouldn't have much effect on the other species of fish.

Herrington: The larger carnivorous fish feed upon young fish. Those young fish must feed upon plankton somewhere in the chain. If you cut off that chain you cause a decrease of the fish farther up the series.

Kolbe: Since the ciscoes disappeared, it has been very easy for all the carnivorous species which are born in the spring of the year and hatch out in a few days time. In fact, since the ciscoes disappeared we have had the biggest perch run and the biggest whitefish run in history. It is the carnivorous fish which seem to survive easily because they spawn in the spring and hatch in a few days.

Herrington: They are feeding on something?

Kolbe: We find that they do feed heavily on the shiner. There are a lot of them in the east end of the lake.

Langlois: It is not a simple problem by a long shot. We recognize it. Let me point this out. I think perhaps some of Walter Koelz' subspecies may not be recognized as valid any longer, but he pointed out that there were 11 species of salmonoids in the Great Lakes and of those only two were in Lake Erie, while there were half a dozen or more in each of the upper lakes. The fact is that Lake Erie is approaching the edge of suitability for that group of fish. What I think we are seeing is the further change in conditions that eliminates one of those remaining forms.

Foerster: In other words, there isn't any hope of restoring them by any fish management policy?

Van Oosten: Of course, the whitefish are in the same boat. They also spawn in the fall and hatch in the spring. However, they have never disappeared like the cisco. They have almost the same habits except they don't feed on plankton throughout life. They have come back in tremendous numbers. In fact, the record production occurred in 1940 if I remember correctly.

Herrington: It seems to me, Dr. Langlois, that there runs through all this argument the fact that you are conceding that if you reduce the spawning population enough the fish doesn't come back. Then you are also arguing that a commercial fishery can't fish down to a point where it makes any difference to the recruitment. But it still isn't proven whether, on the average, a higher spawning stock than the one left by the fishery wouldn't yield a better recruitment.

Langlois: You have shown that there is an optimum spawning stock for the haddock, that you can get too many breeder fish, and this probably is true of other species.

Herrington: There must be an optimum there somewhere. The question is whether it is so low that the stock cannot be pushed below it by the fishery.

Van Oosten: Referring again to plankton, all that is shown is the tremendous variation in the quantity of plankton. You still don't show that even at the minimum the lake isn't rich in plankton. All the investigations made in the past by other people show that Lake Erie is tremendously rich in plankton. I think if you find a year that has eight times more than another year it doesn't necessarily mean that the lowest year was poor at all.

Langlois: The year-round studies have not been made before this series by Dr. Chandler. Other studies, based on a few of the summer months, are wholly inadequate.

ing areas and characterized by average differences in certain morphological characters such as numbers of vertebrae, of scales and of fin-rays.

The discovery that the age of fish and certain characteristics of their life histories could be read from the scales has been basic to many phases of population work. The organization of statistics, especially those on an international scale, has also been an indispensable tool in population studies.

The understanding of populations and of the factors affecting them has reached the stage where in some species fishing probabilities have been attempted with considerable success.

DISCUSSION

Sixty-five years ago Huxley (1881) made some estimates of the population of herrings in the North Atlantic, based on his work as a member of two successive Royal Commissions investigating fisheries. He estimated that there must have been scattered through the North Sea and the Atlantic at one and the same time scores of shoals of herrings, any one of which would go a long way towards supplying the whole of man's consumption of herrings. He did not believe that all of the herring fleets together destroyed five per cent of the total number of herring in the sea in any year. He concluded that:

> the best thing for Governments to do in relation to the herring fisheries, is to let them alone, except in so far as the police of the sea is concerned. With this proviso, let people fish how they like, as they like, and when they like. . . there is not a particle of evidence that anything man does has an appreciable influence on the stock of herrings. It will be time to meddle, when any satisfactory evidence that mischief is being done is produced.

It should be remembered in connection with this conclusion that it was reached in relation to the herring and at a time when trawling by steam-driven vessels had scarcely commenced.

The modern concern of European investigators, such as E. S. Russell (1942) and Graham (1943), with what they call the over-fishing problem is chiefly about demersal species taken by trawling.

Fisheries research in Europe gradually developed during the last half of the nineteenth century, chiefly in the Scandinavian countries, in Great Britain and in Germany. The urge to study the fisheries arose largely from economic necessity. As E. S. Russell (1932) points out, in certain communities, notably in northern Norway where the population is mainly dependent upon fishing for a livelihood, the success or failure of the fishing is almost a matter of life or death.

International Council for the Exploration of the Sea. The Council has played an important part in stimulating and co-ordinating research on population problems in European waters. It was formed in 1902 as a result of preliminary international conferences held in 1899 at Stockholm and in 1901 at Christiana.

The most pressing fishery problem at that time was the supposed depletion of the plaice in the North Sea through excessive fishing, and the chief work of the Council until the outbreak of the first great war was the investigation of the plaice fisheries. However, it had concerned itself also with herring, cod, mackerel, salmon and other food fishes as well as with hydrological and plankton investigations. At its last meeting before the war of 1914–1918 the Council decided on a program for extending its investigations to the North Atlantic generally, because it was recognized that conditions in the Atlantic had an important bearing upon conditions in the North Sea and that the development of steam power in fishing must inevitably extend the horizon of European fishing interests and consequently of fishing investigation.

The Council carries out no investigations of its own, although it has a small staff for recording and co-ordinating data collected by the participating countries. Each of the participating powers undertakes a share in agreed programmes of investigations, to be carried out at its own cost and by the means at its disposal. The co-operative studies undertaken under the auspices of the Council have usually been concerned with such subjects as, factors affecting abundance of fish in different areas, effect of destruction of undersized fish, effect of institution of size-limits of fish that are allowed to be landed, effect of installation of minimum mesh sizes of nets, closed seasons, nursery grounds, and whaling.

The countries supporting the work of the Council have varied from time to time. At present they include Great Britain, France, Spain, Belgium, Denmark, Eire, Holland, Iceland, Norway, Poland, Sweden and Finland.

The publications of the Council include:

Rapports et Procès-Verbaux, Publications de Circonstance, Journal du Conseil, Bulletin Statistique, Bulletin Hydrographique, Bulletin Planctonique, Bulletin Trimestriel, Faune Ichthyologique de l'Atlantique Nord, Annales Biologiques, Current Bibliography, and Special Publications.

Fluctuations in Abundance. Wide fluctuations in abundance are a characteristic feature of animal life in the sea (Kemp, 1938). Because of the effect of such fluctuations on the economic life of Norway, a study of fluctuations was undertaken in that country in 1901 by Dr. Johan Hjort, then Director of Fisheries, aided by Einar Lea and Oscar Sund. A study of the age composition of the herring stocks of successive years soon led to the discovery that different year-classes varied markedly in their contributions to the stock of fish supporting the fishery (Hjort, 1914, 1926) and that wide differences in the success of various year-classes was one of the chief causes of fluctuations in the fishery. This principle was strikingly illustrated by the occurrence of the rich year-class of 1904, which dominated the Norwegian herring fishery for a long period of years. Other good year-classes were those of 1913 and 1918, while those of intervening years were poor.

In the case of the Norwegian cod, specially prolific brood-years were those of 1904 and 1912. Thompson's (1930) work on the haddock showed that in 1920, 1923, 1926 and 1928 the brood was much above the average, while in the intervening years the supply was moderate or poor. A specially good brood-year was found sometimes to contribute to the stock up to 25 times as many young haddock as a poor year. Other workers have found in the case of other species that it is not uncommon to find fish belonging to one year-class fifty or sixty times as numerous as those of another.

The fact that year-classes differ widely in their numerical strength has been demonstrated in the case of most of the important food fishes. This was emphasized in the reports of a meeting of the International Council for the Exploration of the Sea held in London in 1929, at which the problem of fluctuations was given special consideration (Rapp. Cons. Explor. Mer, *65*, *68*). Papers were given (1930) by Hjort, Sund, Thompson, Lea, Hodgson and others on fluctuations in cod, haddock, hake, plaice, herring, pilchard, sprat and lake herring.

The subject of fluctuations was also considered at a special biological meeting of the International Council held in 1936 (*Comparative studies of the fluctuations in the stocks of fish in the seas of North and West Europe*, Rapp. Cons. Explor. Mer, *101* [See, *e. g.*, Sund, 1936]).

In commenting on the problem of fluctuations due to the success or failure of brood-years, Hjort (1930) stated that there was "no agreement between the various species of fish in this respect in the same year. Only in particular cases (herring in the coastal waters of Norway and the sea around Newfoundland, and cod in the coastal waters of Norway and Davis Strait) has it been observed that the same year-classes were unusually abundant, on both occasions in waters situated widely apart."

Years when plentiful year-classes of cod were produced more or less over the whole range of the cod's distribution in the North Atlantic are given as 1924 and possibly 1912, 1917 and 1927. It is also believed that there are probably years of production of poor classes more or less general over wide areas. It is known for certain, however, that there are years in which good year-classes are produced in some regions and moderate or poor year-classes in others. It is assumed, therefore, that the causes of annual fluctuations are usually restricted both in space and time.

Causes of Fluctuations in Abundance. Search for an explanation of the causes of the wide differences in the size of different year-classes has brought out the fact that there is no necessary connection between the number of eggs produced in a particular spawning season and the number of fry which survive. Poor spawning years have often been good brood-years. It is usually assumed that the critical period of great mortality falls in the first few days or weeks after the eggs hatch. Factors suggested as influencing the hatching and survival of young include the following.

1. The origin of a rich year-class would require the contemporary hatching of the eggs and the development of the special sort of plants or nauplii which the newly hatched larva needed for its nourishment (Hjort, 1926).
2. The young larvae might be carried far away out over the great depths of the Norwegian Sea, where they would not be able to return and reach the bottom on the Continental shelf before the plankton in the waters died out during the autumn months of the first year of their life (Hjort, 1926).

Heavy gales may so disturb the sea bottom as to produce conditions unfavorable for the eggs or larvae.

Sund (1924) found a direct correlation between the rich year-classes of Norwegian cod and the years of smallest snowfall.

Long term studies such as those of F. S. Russell (1930–1940) are necessary for the elucidation of factors affecting the success of year-classes. These studies at the Plymouth Station were aimed at determining the extent to which a planktonic population of young fishes, comprising some fifty or more species, ranges in its proportional composition from year to year, and determining also whether or not a good or bad year for one species held good also for certain other species. It was hoped that, if a number of species were affected in the same way in one year, indications of some of the causes of such fluctuations might be obtained.

During the course of Russell's studies it was found that a serious decline in the numbers of young fish was correlated with a marked change in the amount of phosphate in the waters. Renewal of the phosphate in the channel appeared to be largely dependent on the inflow of mixed Atlantic water which is rich in phosphate because it contains water that has upwelled at the edge of the continental shelf. It seemed probable that the normal water movements off the mouth of the channel had undergone changes, and that these changes were indirectly responsible for the decline in the production of young fish. A by-product of the study was the discovery that certain planktonic animals are indicators of water-masses and are thus useful in tracing water movements.

The variation of such important constituents of sea waters as phosphate, silicate, nitrite and nitrate, seasonally and with depth, their replenishment and the part they play as factors of plant growth, have been studied by Atkins (1926) and Harvey (1928). Phosphate appears to be a limiting factor, at least at certain times.

The successful rearing of the fry of marine fish by Rollefsen (1939) is throwing light on the subject of the need of recently hatched fry on food of a certain size and kind. Plaice larvae have been successfully reared by feeding with nauplia of *Artemia*. Cod fry have also been fed on nauplia of *Artemia*, but success is not claimed in rearing this species.

Soleim (1942) has investigated the relation between high mortality of herring fry and poor plankton.

Fluctuations Due to Hydrographic Conditions. In contrast to the fluctuations in the fishery due to differences in the size of year-classes, which tend in most cases to be of short duration, there are fluctuations due to hydrographic conditions, which tend to be of long-term duration. Fluctuations due to differences in the success of brood-years are usually restricted to a certain species in a particular area, while fluctuations due to hydrographic conditions often extend over a period of years and involve much larger areas and large numbers of species.

Fluctuations in migrations of herring to the coast do not necessarily reflect fluctuations in the stock; they produce changes in availability rather than changes in abundance. According to Runnstrøm (1937), in certain years Norwegian herring spawn mainly in deeper water and on more offshore grounds than in other years, and then the fishery bears on only a part of the spawning stock. The most extreme shifting of spawning places seaward seems to have taken place in the 'seventies of the last century when the spring-herring fishery on the southwest coast was a total failure for a series of years. Herring shoals were observed at sea, however, and herring roe was found in deep water. The abundance of herring fry in coastal waters indicated also that there had not been any considerable decrease in the spawning stock.

Through the use of the echo sounder the movements of spawning herring are now followed throughout the season. By this means it has been shown that the fishery has fallen mainly on shoals spawning close to the coast while great herring shoals have remained for weeks unexploited on more offshore grounds.

This type of fluctuation is also illustrated by the Bear Island cod fishery. In 1925, and for several years following, the Norwegians found great numbers of cod on the banks surrounding Bear Island. There had been a former occasion between 1874 and 1882 when cod were plentiful in this area. Between 1883 and 1925 the grounds were examined on a number of occasions but very few cod were found. Another instance is afforded by the cod fishery in West Greenland. At certain times large concentrations of cod appear on this coast and spread as far north as Disko Bay, but after a term of years their numbers suddenly decline and a protracted period of scarcity follows. Both these occurrences apparently were due to the fact that for a period of years in the 1930's the entire area from Greenland to Bear Island had become appreciably warmer. Increased sea temperatures probably of the order of 1.0° to 2.0° C. had allowed various species of fish to extend beyond the usual limits of their distribution. Hydrographic conditions in this case determined the size of that part of the stock that was at the disposal of the fishery in a certain area. The effect of hydrographic conditions may, therefore, mask the effects of fluctuations due to varying year-class sizes and may at times render fishery prediction unreliable.

The study of hydrography, and particularly of the currents, is fundamental for an understanding of the life and movements of the fish. The work of Graham (1924) and Graham and Carruthers (1925) on the relation of currents and other hydrological conditions to the life history and distribution of the cod afford examples of the correlation which can be established between hydrographical and biological conditions. In the study of such relationships the International Council plays a most important role in organizing systematic sampling through such agencies as steamships, lightships and research vessels. The tabulated results, mainly for temperature and salinity, are published annually in the Council's Bulletin Hydrographique.

Fluctuations in the Fauna of the Sea Bottom. Fluctuations also occur in the fauna of the sea bottom. Davis (1923, 1925), in the course of extended investigations on the Dogger Bank, found that certain small bivalves sometimes occurred over enormous areas, thus providing rich feeding for haddock and plaice. Some of these beds covered areas up to six or seven hundred square miles. One bed, whose population was estimated at 4,500,000,000,000 was composed largely of shellfish of a single year-group. These investigations which continued for several years showed that great changes took place from year to year in both extent and location of the beds.

Davis considered that the most probable cause of these fluctuations was changes in the course of the currents by which the larvae are passively transported. Species which are restricted to a particular type of bottom, if they do not happen to be deposited by the currents on suitable ground, produce scant crops. Subsequent investigations have shown that fluctuations in the fauna of the sea bottom, as in the case of the fishes, are the rule rather than the exception and that this holds good also in the littoral region.

Blegvad (1914) has investigated the food-chains of fish and fish larvae down to their ultimate elements.

Petersen and Boysen-Jensen (1911) and Petersen (1914, 1918, 1922, 1924) were the first to apply quantitative methods to the study of bottom fauna of the sea. For use in his studies, Petersen invented a bottom sampler, since known as the Petersen grab, by means of which he was able to bring up the soil and animals contained in it from a definite area of bottom. As a result of his studies of the fauna of sea bottom, Petersen developed the idea of communities, natural groups of species inhabiting more or less well defined areas which could be mapped. He recognized and mapped the location of eight types of communities in Danish waters. These were defined with reference to "characteristic species." One of his communities, for instance, he called the *Macoma* community from the prominence of the small bivalve *Macoma baltica* in it. Each community had fairly definite relations to depth of water, character of bottom, and probably also to such factors as temperature and salinity. Although Petersen recognized the importance of soil texture in determining the distribution and abundance of bottom organisms, this character has been still further emphasized by Davis (1925) who is inclined to substitute for the Petersen community the principle of soil associations.

Fishing Mortality. In regulating fishing in an effort to maintain the maximum continuous yield it is necessary to have information on rates of mortality due to fishing and to natural causes. Attempts to estimate reductions in populations arising from each of these causes have been based on the results of age analysis of fish stocks and of tagging experiments.

At a meeting of the International Council held in Berlin in 1939 the results of such studies were discussed by E. S. Russell, Graham, Thursby-Pelham, Raitt, Jensen and others (Rapp. Cons. Explor. Mer, 1939, *110*). Since the results have also been summarized by E. S. Russell (1942) it is perhaps sufficient for the present purpose to quote one or two examples of the sort of results obtained.

For the haddock of the North Sea, Raitt (1939) concluded:

> Of the second-year frequency of the brood of 1923, for instance, 15% was removed in the third year, a further 50 in the fourth, and 20 in the fifth. Of the second-year frequency of the brood of 1933, 65% was removed in the third, a further 25 in the fourth, and nine in the fifth, leaving only one per cent. as against 15 in the case of the brood of 1923. By the end of its third year the ranks of the 1933 brood were reduced by two-thirds of their second-year strength, which was as much as the 1923 brood suffered in its third and fourth years together. The average age to which the 1923 brood survived was four, and that of the 1933 brood less than three.

These results give a measure of the increase in the rate of mortality between 1923 and 1933.

In extensive plaice-tagging experiments carried out from 1929 to 1932 (Hickling, 1938) on the continental side of the southern North Sea, during which nearly 20,000 fish were marked, it was found that, excluding the smaller fish which are not returned in their true proportions, the percentage recaptured in the first year after tagging varied from 40 to 55 depending on locality. Judging from the numbers recaptured, it was concluded that there was a general rate of decrease in the stock of the order of 70 per cent per annum, a rate which would leave only two fish per thousand marked still surviving at the end of the fifth year of life.

The Overfishing Problem. A great deal of attention has been given in Europe to what is called the Overfishing Problem. Overfishing is defined as that condition in which the more you fish the less you catch. One statement of the situation is as follows:—If we start with an unfished or virgin stock and gradually increase the amount of fishing, we get for some time a continuously increasing yield accompanied shortly by a decreasing catch-per-unit-of-fishing-effort. But the yield does not go up in direct proportion to the amount of fishing; the ascending curve of yield begins to flatten out, and there comes a time when a maximum yield is obtained. Thereafter, if fishing is still further increased, the total yield falls off. That is what is meant by overfishing—the state in which the more you fish the less you catch.

If we wish to obtain the maximum steady yield from a stock, we must fish neither too much nor too little but at an intermediate rate, such that the number caught multiplied by their average weight is, and remains at, a maximum. If we fish too little, we do not catch a sufficient number to give the maximum steady yield in weight. If we fish too much, the average weight of the fish caught is too low to give the maximum yield. There must be, it has been concluded, for every stock of fish an optimum rate of fishing which will give the maximum steady yield (subject, of course, to variations due to natural fluctuations, which, however, cancel out over a period of years, and to variations in growth-rate).

A year-class of fish, after it has survived the heavy mortality incidental to its early life, will, if protected from fishing, increase in total weight for some years, the loss due to natural mortality being well over-compensated by the growth of the survivors. The only comparison I have been able to find between a virgin or unfished stock of fish is that quoted by E. S. Russell (1942). The population of plaice on newly discovered grounds in the Barents Sea was found by Atkinson (1908) to consist almost entirely of large fish, mostly over 40 cm. and mostly mature. In contrast to this the population of plaice in the North Sea, which had been fished commercially, consisted of fish mostly under 40 cm. in length, and the proportion of mature fish was much less than in the Barents Sea. The average size at first maturity is approximately the same in both areas, namely 39–40 cm.

Ever since Petersen's (1894) work on plaice in Danish waters there has been general agreement that it must pay the industry to allow fish to grow to a medium size. His studies emphasized the fundamental importance of rate of growth and of food supply. The limited amount of food restricts the production of fish. "A stock of plaice with a low growth-rate will not yield the same annual production as a stock with rapid growth; a very dense, slowly growing stock will give but a very poor yield, as almost all the food will go simply to the maintenance of life and next to nothing can be used for growing purposes." Rapid production and early cropping were, in Petersen's view, the things to aim at in the regulation of fisheries.

E. S. Russell (1942) points out that in the early days of fishery science most workers thought that the main thing to aim at was to keep up the supply of mature fish so that an abundant supply of eggs and larvae and young fish might be assured. It was thought important, therefore, to prevent the capture or destruction of sexually immature fish, and very high size limits were advocated. Petersen pointed out that such measures might easily defeat their own ends if they resulted in producing overcrowded stocks of young fish, which grew slowly and consumed a great amount of food to little purpose. He advocated size limits of a moderate kind.

Some writers have exaggerated Petersen's view and oppose all measures for the protection of undersized fish. Up to a certain point fishing is good for a stock, since it clears out the accumulated stock of old slow-growing fish. It thus enables the remainder to grow more quickly and makes room for the oncoming brood. The thinning of younger fish should result in increased growth-rate and, therefore, of productiveness. Up to a point, yield can be increased by increasing fishing, but after this maximum is reached, increased fishing produces a less weight of fish (see also Graham, 1943).

There seems to be general agreement on the part of European fishery biologists that there is too much fishing for demersal fish and that the fish are being taken too young. Through the machinery provided by the International Convention on Mesh and Size Limits, undersized fish are protected from capture.

Racial Investigations. One of the aspects of fish populations to which a great deal of research has been devoted in Europe is the existence of so-called local races. Within the total area of distribution of most of the species of fish that have been investigated, local populations have been found which can be distinguished by morphological and other characteristics. Thus the cod of the North Sea, of the Norwegian coast, and of Iceland, are separate stocks, each with its own spawning grounds and areas of distribution, and each distinguished from the others by the possession of morphological characteristics peculiar to it.

One of the first workers who made a careful study of the differences between local populations was Heincke. Matthews (1886), in an account of his studies on differences among Scottish herrings, refers to Heincke's "elaborate investigations into the varieties of the herring of the Baltic, including a few from the North Sea (Peterhead and Norway) and whose results appear in an excellent report published by the German Fishery Commission (Jahrsbericht der Comm. Z. Wissensch. Untersuch der deutschen Meer, 1878. 1882)." Matthews (1886, 1887) used 14 body proportions, as well as counts of fin-rays and keeled scales in his study of differences among the summer and winter herrings of the Scottish coasts. He emphasizes the necessity of examining large numbers of specimens, mentioning the "amount of almost 'drudgery' entailed in an investigation of this nature . . . In my own case, the mechanical work entailed amounted to the taking of about 16,000 measurements on the herrings, with over 20,000 subsequent calculations."

Heincke (1898), who is usually given credit for demonstrating the existence of "races" among herring, showed that fish from different areas have characteristics peculiar to themselves. Local populations, he believed, could be identified by their body proportions and by the number of certain structures. The body proportions he used included length of head and the distance from the head to other parts of the body. Other characters used included number of vertebrae, number of rays in certain fins and number of scales along the underside of the fish.

Williamson (1900) followed with work on the mackerel using 27 characters. Later workers have limited their observations to fewer characters such as vertebral and fin-ray counts, which has enabled them to make their studies on very much larger numbers of individuals.

Thus in Schmidt's (1930) racial investigations on the cod, only two characters were always examined, namely the number of vertebrae and the number of rays in the second dorsal fin. Only occasionally were the number of pectoral and branchiostegal rays examined. His studies involved the examination of about 20,000 specimens from 114 stations distributed over the greater part of the range of the species in the Atlantic.

These investigations showed that the cod of the North Atlantic consist of a number of more or less distinct populations, differing from one another in a number of morphological characters. In vertebrae and fin-rays of the second dorsal it was found that the number increased from south to north in the open waters. Thus, in European waters the lowest values were found west of the British Isles and the highest in northern Norway. Similarly in American waters, the lowest were found off the coast of the United States and the highest off northern Newfoundland and Labrador. There was also a difference in the average values on the two sides of the Atlantic such that the number of vertebrae increased from east to west. From west of Scotland, where the lowest number of vertebrae (51.47) was found, the number progressively increased around the Faroes, Iceland, East Greenland and West Greenland to Labrador and northern Newfoundland, where the highest value (55.46) was found. Paralleling these differences in the number of vertebrae, the average values for the second dorsal fin showed an increase from south to north on both sides of the ocean and an increase from west of the British Isles over the Faroes, Iceland and Greenland to Newfoundland. In European waters, the number of second dorsal fin-rays practically never reached 20, whereas average values above 20 were the rule in American waters.

Typical values were as follows:

Area	*Vertebrae*	*Second dorsal fin-rays*
Nantucket shoals	52.90	19.74
St. John's, Newfoundland.	54.91	20.48
Belle Isle Strait	55.46	20.86
West Greenland	53.60	20.32
East Greenland	53.14	20.04
Iceland	52.29–53.26	19.23–19.94
Northern Norway	53.82	19.84
Southern Norway	52.44	19.55
English Channel	51.75	18.75
Rockall Bank, west of British Isles	51.47	19.46

Marked differences were found between vertebral numbers and number of rays in the second dorsal fin between inshore (or shallower) and offshore (or deeper) water, the former having the lower values. Examples were as follows:

Area	*Vertebrae*	*Second dorsal fin-rays*
Innermost part of Trondhjem Fjord, Norway	52.35	19.24
Outside the fjord	53.76	20.13
In Gulf of St. Lawrence	53.58–53.86	19.96–19.71
Outside the Gulf of St. Lawrence	54.16–54.29	20.00–19.87

Schmidt (1917 to 1930; see also Smith, 1921, 1922), in addition to his racial studies of cod, made a series of very important contributions to the racial investigations of other species. One of the species on which much work was done was *Zoarces viviparus*. This viviparous fish, he pointed out, was exceptionally well suited for such studies. Thus one could compare mother and offspring in respect of a whole series of characters, which were already fully developed in the yet unborn progeny. Moreover, local populations of *Zoarces* differed unusually widely in a number of characters from those of neighbouring populations. Thus populations inside the Danish fjords sometimes had as many as nine fewer vertebrae on the average than those living outside. The middle parts of the fjords occupied an intermediate position in such respects. ". . . no closely investigated fish species," he said, "shows such great differences from population to population."

Analyses of ten successive year-classes from the same locality showed only very small variations, or less than one in the average number of vertebrae. Transplantation of samples of the same population to a new environment produced a significant change in the number of vertebrae, or more than one on the average. He also carried out experiments on hatching three different lots of trout (*Salmo trutta*) eggs from the same parent at different temperatures. A slight variation was observed in the number of vertebrae of fishes from the different lots.

Runnstrøm (1937), in his review of Norwegian herring investigations, points out that there exist different spawning communities in Norwegian waters which do not mix to any great degree. Some of these communities spawn on the coastal grounds while others spawn on more offshore grounds, visiting the coastal waters in the large herring stage only.

The investigation of these localized breeding populations was facilitated by the fact that fish appear on somewhat small sharply defined banks and in shoals consisting only, or for practical purposes only, of one biological group of a species. Therefore, the investigation of local populations was much easier in such waters as those of Norway and Iceland and of the Faroes than in more extended waters like the North Sea where the topographical features of the depths of the bottom are not so distinctly marked.

As to the causes of the morphological differences which characterize races, Hjort (1930), referring to the proceedings of a special meeting of the International Council for the Exploration of the Sea held in 1928 (Rapp. Cons. Explor. Mer, 1929, *54*) reported that there was then a "somewhat sharp division of opinion between those, who regard the formation of races as the result of fortuitous hereditary combinations of characteristics, and those who regard it as due to an interplay of the power of adaptation shown by the animals concerned and the physico-chemical conditions predominating in particular areas of the sea."

One of the reasons for the belief that environmental conditions can and do alter the characters by which races are distinguished is that such characters are not fixed but may vary from year to year in the one localized population. On the basis of such evidence, Jensen (1939b) concluded that "as regards both plaice and the dab the number of anal fin rays seems to be positively correlated with the temperature of the water during the time at which the larvae are quite small. 1 degree C. corresponds to about 0.4 anal fin rays."

Schmidt (1930) gave it as his opinion that "Fishery biologists are evidently unanimous that external factors are capable of altering the average characters by which races in the fishes are determined. This has been proved directly by experiment in the common trout (*Salmo trutta* L.) and in the million fish (*Lebistes reticulatus* [Peters] Regan) by varying the temperature during which the development in the 'critical period' took, place . . .

"It would, however, be quite wrong to ignore the fact that the differences in the average characters by which the races are determined may also be of a hereditary, genotypical nature . . ."

At a meeting of herring experts, held under the auspices of the International Council at the Fisheries Laboratory, Lowestoft, England, in 1935, several papers dealing with the herring stocks of various areas were presented; some of these dealt with "races" in this species (see Andersson, Davis, LeGall, Hodgson, Poulsen, Runnstrøm, Schnakenbeck, Tåning and Wood, 1936).

Statistics. Since many phases of fishery research are based on fishery statistics, systems for the collection of these statistics have been organized in most European countries and the International Council early gave attention to the compiling of international statistics of catch. A summary of the statistics for northwestern Europe is published annually by the International Council as the "Bulletin Statistique."

In Great Britain fishing vessels provide information as to the quantities and kinds of fish landed, classified at least roughly as to size, where they were taken, what gear was used, the length of the voyage, and the number of hours actually spent in fishing. This information is collected daily at all the main fishing ports in Great Britain. An account of the methods used in collecting statistics is given by E. S. Russell and Edser (1925) and Edser (1925).

Supplementing the general information obtained from the commercial statistics, more specialized data as to size-composition of the catches are collected by a special staff working partly on fishing vessels at sea and partly at coastal markets. In 1929, 914,000 fish were measured at sea and 69,500 in the markets. In addition the age-compositiion of the stocks are determined especially for plaice, cod, herring and haddock. 20,000 plaice otoliths were examined by the English staffs in 1929.

Scale Studies. The development of techniques for determining the age and other facts of the life history of fishes from examination of their scales has contributed greatly to the study of fish populations.

Much of the early work on age determination and the correlation between the growth of the body and of the scales was carried out in connection with the Norwegian herring investigations by Dahl, Lea and others. They, of course, based their investigations on earlier work by such men as Hintze (1888) and Hoffbauer (1899), who had interpreted the rings on the scales of carp of known ages. The history of the advancements and refinements in scale-reading techniques have been traced by Lee (1920) and Graham (1929).

The study of scales has been found useful not only in determining the year-class to which fish belong but also in identifying fish of different types of life history. Local populations often differ in spawning times and rates of growth. For instance one type of Norwegian herring was found to have an abnormally small increment of growth in its third year. Such characters as this, which can be read from the scales, have been useful in recognizing populations and in studying the composition and recruitment of fish stocks.

Migrations. One of the first questions investigated under the auspices of the International Council was the extent to which fluctuations in the fisheries might be due to mass movements of fish coming onto grounds where they were taken by fishermen in some years and not in others. As already explained, it has been found that, while some fluctuations in the fishery are caused by variations in the movements of fish, there are enormous actual differences in abundance from time to time. The movements of fish have been traced in part by tagging and in part by the recognition of discrete populations through racial studies.

Several species of fish, including the cod and herring, have been shown during their life-time to carry out a migratory movement between a breeding place and a feeding place often separated by many hundreds of miles. For instance, one large cod population spawns about the latitude of the Lofoten Islands. From here the young are believed to be carried mainly north and east to the Barents Sea by the current which flows up the coast of Norway. On reaching maturity these fish are said to return to the spawning grounds off the west coast of Norway.

E. S. Russell (1932) says that in general "the life-history and migrations of a fish-group . . . take place within a closed circle; as a rule the fish move up-stream to spawn and their eggs and larvae are distributed downstream by the currents; spawning areas and feeding areas are often distinct and may be widely separated, and migrations are mainly for the two purposes of feeding and spawning." Reference in support of this statement is made to the papers of Damas (1909) and Schmidt (1909). Hjort's (1914) paper contains a chapter on the spawning and migrations of the cod.

Hodgson (1934) describes a similar movement for the herring.

. . . we find the spawning migration is against the stream, or contra-natant as it has been called. Thus the herring, in common with many other fish, carries out the obvious movement in going up stream to spawn, so that under normal conditions its young will be brought back to the same area whence the parents came.

Also, in the case of the plaice, Buchanan-Wollaston (1923–1926) found that the great majority of this species in the North Sea collect for spawning in a particular area off the estuary of the Thames in winter, where a tongue of warmish water extends up from the Channel and that their eggs and larvae are carried north and east by the prevailing current to the shallow continental flats, where they find suitable conditions for their further development.

Prediction. Knowledge of the populations of several species and of the factors affecting them has reached the stage where forecasts of probable abundance are possible. This is due in large part to the ability to recognize year-classes and to compare their relative abundance as they first enter the commercial fishery (Hodgson, 1932). Such forecasts have been issued for haddock, cod, herring and mackerel and in the main they have turned out to be remarkably accurate.

It must be remembered that estimates of the relative strength of year-classes based on observations of young fish as they enter the fishery are estimates of abundance and not necessarily of availability. Fish may actually be abundant and not available to the fishermen because they do not appear at times or at places where fisherman have been in the habit of finding them. Runnstrøm (1937), as already mentioned, points out that certain fluctuations in the spring herring fishery are due to variations in the migrations of the herring to the spawning grounds. In certain years the herring spawn mainly in deep water and on more offshore grounds than in other years, and then the fishery bears only on a part of the spawning stock. The use of the echo sounder in recent years has overcome variations to some extent in the fishery due to hydrographical conditions, although this is still one of the least understood factors responsible for fluctuations in the fisheries.

Jensen (1939a) discusses the role of hydrographical factors in determining the yield of mackerel in Danish waters. Their immigration from the North Sea seemed to be determined by the inflow of water. Pelagic fish, having no sense of the direction of water movement, follow the current passively. Predictions based on observations of water movements failed in three years and came true in eleven.

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DISCUSSION

Van Oosten: This paper is now open for discussion.

Huntsman: You apparently consider, Professor Dymond, that the theory of overfishing is based on the conclusion that it pays to let the fish get bigger. Do you think that European investigators have excluded the fishing up of the accumulated stock as well as the purely economic factor to which you have referred, and that they have really shown that it does pay to let these particular fish get bigger?

Dymond: I don't think I can answer the question. The term "overfishing" means exactly what they say: The more you fish the less you catch. That is apparently a fact there.

Burkenroad: The North Sea is supposed to have tremendously more fishing than any of our North American waters. Therefore, we shouldn't necessarily think it is essential to follow European conclusions on this side of the Atlantic. We haven't the same intensity of fishing here.

Herrington: Georges Bank produces much more for its area than the North Sea. The Bank is just a small fraction of the size of the North Sea.

Burkenroad: Is that so? Of all species or just a few?

Herrington: All species.

Needler: I don't think there is much doubt of the greater fishing intensity in the North Sea. The North Sea fishery has succeeded in reducing the size of the commercial species much more than in any of our areas in the west.

Kolbe: Isn't the size of the carnivorous fish important? I like to maintain that the larger a carnivorous fish is, feeding largely on other fish, the less fish flesh it gives rise to in terms of the potentialities of the basic plankton; this is because it is eating a lot of fish that have taken years to grow. Therefore, if your fish become smaller due to fishing in the North Sea, you can maintain a bigger population than you could on your Georges Bank.

Herrington: On Georges Bank the haddock, which is a bottom feeder, doesn't feed on other fishes.

Burkenroad: The productivity relationships are terribly complicated. You have a dynamic situation, not static. When a fish eats food it releases nutrients. A fisherman is interested in standing crops; that is, he cannot fish at a level of population that will not permit him to draw his net through the water and bring in a quantity of material greater than a certain minimum. But you can have a large production of fish with a small standing crop, at a high rate of turnover.

Herrington: Mr. Kolbe, I think your statement is still correct, that the higher you go in the feeding cycle the smaller will be the population. The corn-hog ratio and the corn-beef ratio are examples of that. It takes so many pounds of feed to produce one pound of meat.

Burkenroad: Dr. Taylor has calculated the ratio between phosphate and nitrate in what we take out of the sea in our annual catch in the United States and the amount in the area of the fishery. The fraction we take out is insignificant.

Needler: The overfishing conception in the North Sea is not based on the total production at all. Specific reference is made to certain species of fish. One cannot criticize the conception on the basis of the total productivity and plankton productivity and so on. They still say that, in spite of certain species being overfished, the total production is not yet overfished. There are still very large quantities of herring and other species which are not overfished. Overfishing to the stage that Prof. Dymond says, where the more you fish the less you get, is limited to certain species on certain grounds and not to the entire productivity of any area or to any one species over the entire area. So that it boils down to what I think Mr. Herrington said earlier, that they are concerned not with reducing the total production but with maintaining the proportion of that production which lies in certain species. If certain species are more desirable than others, as they evidently are, it may be an undesirable thing to reduce these species as far as the others. That, I think, is the claim for overfishing.

Huntsman: The herring constitute the great bulk of the catch of the North Sea.

Needler: So that the total take has not been affected—not to the extent of fishing more and getting less. In fact, already, right now with food scarce, the English are using the machinery only to about 50 per cent because they can't get rid of the catch.

Huntsman: The rule that the more you fish the less you catch may be true for the haddock and halibut. However, it isn't a general rule for the bottom fishes.

Dymond: The trouble there is that when you haul your net over a certain bank you get everything there. It is a matter of compromise.

Huntsman: The best case for study seems to be the halibut in the North Sea. I would like to see the results critically studied. I would like to see whether it pays to let them get bigger.

Dymond: The halibut is one of the fish on which they are trying to make a quantitative study. It is a much more difficult situation than off the west coast where there are only two countries to deal with. In the North Sea they have half a dozen countries, and it is very difficult to get them to agree on even a method of research.

Herrington: Why don't we adopt a halibut program on the Atlantic as well as the Pacific? Are we willing to trade 10 for one—that is, 10 pounds of cod or other species for one pound of halibut?

Needler: I think it goes even further than that. You can't build up the production of halibut—at least you can't reduce the catch of small halibut and let them grow bigger—without reducing the catch of other fish that have several times the value.

Burkenroad: I think the point about desirability is a fundamental one. How is one fish determined by long-term policy-makers to be more desirable than another? A fish that is more in demand one year may lose its lead in value the next year because consumers' tastes change. There are no satisfactory studies defining the extent to which the availability of the fish affects the demand for it. Desirability is neither constant nor objectively determinable, and I doubt that we can safely limit our science to attempts to prevent one equally nutritious and harvestable fish from replacing another. Local and temporary changes are important, but they ought not to obscure our thinking about basic principles.

Herrington: Professor Dymond mentioned the belief in a critical point in the survival of the young, which might be one or two days in the early stages of development. With poor conditions during that critical period you'd have a poor year-class. A short time ago Sette published a paper on mackerel which I think for the first time provided some information on the mortality rate of the young from the egg stage to the time they reach several inches. It was based upon a repeated series of hauls taken over the nursery grounds for mackerel, using plankton nets with current meters to measure the volume of water strengths. In that way it was possible to reduce the catch to terms per cubic meter or some such constant. The whole area was covered. As I recall, it was found that there was a relatively constant mortality rate through the egg and larval period with no exceptionally critical point. If you increased the over-all rate only slightly over the entire period of time, that slight increase would cause a big decrease in the number of survivals. The mortality rate over the whole period of the larval life appeared to be the determining factor rather than extremely high mortality at a particular stage.

Dymond: This theory of the Europeans, and your statement about the mackerel, seem to assume that the critical factor is not whether the fish hatch but whether they survive after they are hatched. Do we all assume, and if we do are we correct in assuming it, that the conditions for hatching are not so critical as the conditions for survival after hatching?

Needler: I think there is some evidence that survival is usually more important than the variation in number of eggs and that hatching is less important. It is the conditions in the first year of life or the first few months—not a particular day or week—which, of course, are basic in predictions.

Van Oosten: If there is no further discussion we shall now call for the next paper.

4. FLUCTUATION IN ABUNDANCE OF PACIFIC HALIBUT

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ABSTRACT

Analysis of data published by the International Fisheries Commission indicates that the decline in abundance of halibut on the Pacific coast west of Cape Spencer between 1915 and 1930, and the increase since that date, may both have been much greater than can be accounted for by the changes in amount of fishing. It therefore seems possible that the major fluctuations in abundance of this stock of fish should be attributed to natural causes, perhaps of a regularly cyclical sort. In view of these results, it is suggested that the desirability of applying current theories of biological management to marine fisheries remains to be demonstrated.

ACKNOWLEDGMENTS

The present paper is one of the results of an effort to assess the marine fishery resources of North Carolina. Examination of the biological aspect of this question, not only from an immediate point of view, but in its fundamentals, has been made possible by encouragement and support from Dr. Harden F. Taylor, Executive Director of the Survey of Marine Fisheries of North Carolina, and from Dr. R. E. Coker, Chairman of the Advisory Board.

Criticism, suggestions and information, which have enabled me to correct a variety of blunders and to improve the range of treatment, have been received from numerous colleagues. Of those not mentioned in the text, especial thanks are due to Dr. A. G. Huntsman of the University of Toronto, to Dr. Daniel Merriman and Dr. E. F. Thompson of the Bingham Oceanographic Laboratory, and to Dr. W. E. Ricker of Indiana University. I should like also to offer here, to Professors A. E. Parr and G. E. Hutchinson of Yale University, a grateful appreciation for my introduction to the quantitative theory of fishery and ecosystem dynamics.

On behalf of the Survey of Marine Fisheries, as well as myself, thanks are here expressed to the authorities of the American Museum of Natural History, particularly to the Library and to the Department of Fishes and Aquatic Biology, for their grant of working facilities.

INTRODUCTION

It has been generally considered that the Pacific halibut affords a clear and proven case both of serious reduction of a population of marine fishes by fishing and of the subsequent rehabilitation of the population through restriction of exploitation.[1] This exceptionally

[1] "The Pacific halibut is a classic example of a resource which, after undergoing extreme depletion, has been restored through careful regulation. As a result of the

well documented instance has necessarily exerted a powerful influence upon thought in fishery biology. But there is evidence that the abundance of various marine fishery animals is much more strongly influenced by natural events than by man (*cf.* Huntsman, 1944a). Therefore, too ready a resort to analogy with the case of the Pacific halibut would be undesirable even if this classical example of over-exploitation were unquestionable.

It is the purpose of this paper to demonstrate that, even for a fish so slow growing, late maturing and continuously accessible as the Pacific halibut, the magnificent studies published by Thompson and his collaborators[2] are insufficient to exclude the possibility that natural fluctuation has been the major factor in the long-term decline and recovery in abundance of at least one of the stocks. In consequence of this demonstration, serious question may be raised concerning those frequent imperfectly documented cases which have been attributed by analogy to overfishing, merely upon indication of a decline in production or of yield-per-unit-of-effort.

NATURE OF THE PROBLEM

The question here dealt with is whether or not any important part of the changes in abundance of Pacific halibut were greater than might reasonably be expected to have been caused by the changes in the fishery. The history of the fishery upon the banks west of Cape Spencer provides material especially well adapted for such an analysis.

In the first place, tagging experiments have demonstrated that the stock of mature halibut on the western banks behaves as a discrete unit. Extensive and rapid exchanges of fish occur throughout the range of the western fishery, but there is no significant interchange with the several stocks (long subject to intensive exploitation) which occupy areas south of Cape Spencer (Thompson and Herrington, 1930).

Secondly, the quantitative history of the western fishery is almost complete. The first serious fishing beyond Cape Spencer began around 1910, but there were no extensive operations until 1912, when the total reported catch from the area was still of minor extent (55,000 lb.). A rapid expansion then occurred, to 24 million pounds in 1915.

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rapid development of an intensive fishery between 1910 and 1930 the stocks of halibut in the north Pacific declined alarmingly . . ." (U. S., Senate, 1945: 21).

[2] Int. Fish. Comm., Nos. 1–12, 1928–1937.

Information on the total fishing effort employed in the western fishery is first offered from 1915 (Thompson and Bell, 1934), when the fishery was only three years old.

In the third place, the decline in average catch-per-unit-of-effort upon the western banks was of a highly spectacular sort during the first four years of the fishery, from 266 pounds in 1915 to 125 pounds in 1918. The severity and rapidity of this early decline is made obvious by comparison with over-all accompaniment of the next twelve years of fishing, a fall to 65 pounds by 1930. Since the early decline was accompanied by a fishing effort only about one-quarter as great as the maximum later expended, it is obvious that a particularly critical opportunity is offered for comparing the characteristics of the fishery with its supposed effects upon abundance.

Therefore, it will be attempted in subsequent paragraphs, first, to compare the apparent changes in quantity of halibut living upon the western banks during the early days with the quantities concurrently removed by the fishery, and second, to analyze the less spectacular changes of later years.

ANALYSIS OF THE PHASE OF DECLINE IN ABUNDANCE OF THE WESTERN STOCK OF HALIBUT

Changes in Magnitude of the Stock. A rough measure of the absolute quantity of halibut commercially available within the range of the fishery west of Cape Spencer around 1927 is afforded by tagging experiments initiated at that time. These experiments indicated a rate of capture of about 10 per cent per year of the average stock commercially available (Thompson and Herrington, 1930: 91, 107; Thompson and Bell, 1934: 46).[3] Landings from the western banks at this time were

[3] According to Thompson and Herrington (1930: table 2, figs. 11, 12), average weight of individuals tagged was considerably less than that of fish caught commercially. Therefore, per cent of weight of tagged fish recaptured would not give an accurate picture of fishing intensity in per cent by weight. However, tag returns are given in per cent by number, and it seems legitimate to assume that a commercial catch of 10 per cent by number of tagged fish would be the equivalent of a catch of 10 per cent by weight of the population commercially available.

The commercial catch is obviously not a random sample of the total population of halibut, but is selective for size. The landings thus represent a different per cent of the total population by weight than by number. The phrase "population commercially available" has therefore been used in the present paper to indicate that part of the population within which fishing intensity in per cent by number and by weight would be equal.

around 30 million pounds. The effective western limit of the fishery evidently lay between Kodiak and the Shumagin Islands (according to Bower, 1929: 290). The commercially available stock evidently consisted chiefly of mature fish more than ten years old.[4] Consequently, it would appear that the average stock of halibut more than ten years old between Cape Spencer and the Shumagins in 1927 must have amounted to around 300 million pounds.

An estimate of the magnitude of the commercially available western stock in the early days of the fishery may now be attempted. At that time, the population of the western grounds is indicated to have been much greater than in 1927. Thus, according to Thompson, Dunlop and Bell (1931: table 12), on the easternmost of the western banks (those between Cape Spencer and Cape Cleare) the average catch-per-unit-of-effort in 1915 was 320 pounds, in 1920 it was 143 pounds, and in 1927, 79 pounds. On the middle banks, between Cape Cleare and Trinity Island, the respective values were 237, 152 and 85 pounds. For the far western banks (which were commercially unimportant through 1924 at least) no data are available before 1920, the respective values there for 1920 and 1927 being 156 and 102 pounds. Thus, it may be concluded that, over the range of the western fishery as a whole, the catch-per-unit-of-effort in 1927 was only about one-third of that in 1915. Assuming, for the present purpose, that decline in

[4] Thompson, Dunlop and Bell (1931: 94–95) state that "The halibut fishery on this part of the coast [Cape Spencer to Cape Cleare] was, and still is, directed primarily at fish over 11¾ pounds in weight, cleaned but not headed, this being the lower size limit of first-class fish. This is approximately the average size at which fish on the western grounds mature." Thompson and Bell (1934: 48) give the average weight of 11-year-old Yakutat fish as 11 pounds. Maturity is said to be first attained by western fish between ten and thirteen years.

Thompson and Herrington (1930: 40–41) state that on the western banks "What is brought up on the hooks can as a rule be marketed," extensive culling-out of small fish, as on the southern banks, being unnecessary. Their experimental catches showed average lengths between 77 and 86 cm. (modes between 65 and 75 cm.), which, according to their weight-length curve on p. 75, would correspond to average weights between 10 and 12 pounds.

The proportion of fish weighing less than 12 pounds landed from the banks at Portlock and west rose to 20 per cent by 1927 (Babcock, *et al.*, 1930: 21); but the Yakutat banks, which probably yielded about one-quarter of the total western landings at this time (Thompson and Herrington, 1930: table 5), were the source of fish of larger average size (*ibid.*: 40, 99); and the proportion of fish weighing less than 12 pounds in the total western catch in 1927 may therefore have been as low as 15 per cent.

magnitude of the stock and decline in catch-per-unit-of-effort were commensurate, the commercially available western stock in 1915 would evidently have averaged about three times as great as that in 1927, or 900 million pounds.

Changes in Apparent Magnitude of the Stock Compared to Withdrawals by the Fishery. Between 1912, when the western fishery began, and 1927 the total recorded landings of halibut from this area amounted to about 284 million pounds (according to Thompson and Bell, 1934: 12, table 2). This quantity is less than half of the apparent decline in the western population of halibut from 1915 to 1927, as roughly estimated above on the assumption that decline in population was commensurate with that in catch-per-unit-of-effort, and that average population in 1927 was ten times landings.

It has already been noted that the most spectacular part of the decline in catch-per-unit-of-effort on the western grounds occurred from 1915 to 1918, when the over-all average catch-per-unit fell from 266 to 125 pounds (Thompson and Bell, 1934: 12, table 2). If it be assumed that magnitude of population declined equally with catch-per-unit during this period, then the stock of western halibut commercially available would have fallen from about 900 million pounds to about half that value. Against this apparent decline of some 450 million pounds, landings from the beginning of the western fishing through 1918 totalled only 102 million pounds (or, to make a stricter comparison, landings for 1915–1918 totalled only 71 million pounds, *less than one-sixth* of the apparent concurrent decline in population).

The above indication that withdrawals by the early fishery may have been insufficient to cause the observed rapid decline in abundance (illustrated in Fig. 1 and in Tables III and V, with values obtained by a somewhat more refined method described on p. 93) seem strong enough to warrant a closer examination of this possibility.

Changes in Area of the Fishery Compared to Apparent Changes in Magnitude of the Stock. An objection might be raised to the estimation of western population in 1915 and 1918 by comparison of the catch-per-unit with that in 1927, since the area exploited by the western fishery shifted greatly between these dates. From 1912 through 1915 the catch was evidently drawn almost entirely from the eastern (Yakutat) area (Thompson and Freeman, 1930). From 1916 through 1918 the middle (Portlock) area rose in importance until, according to

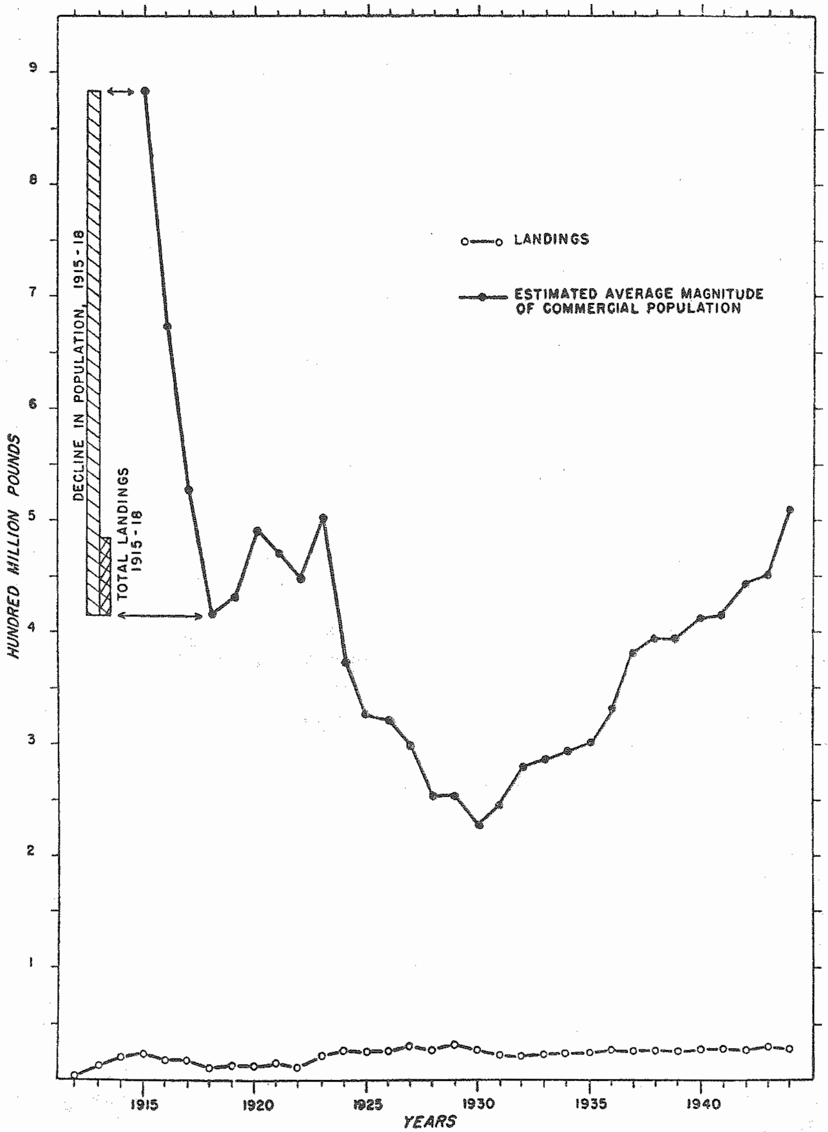

Figure 1. Estimated average commercial population of halibut on grounds west of Cape Spencer, 1915–1944; compared with landings; with histogram contrasting decline of population 1915–1918 with total landings during the same period.

records of vessel landings in Seattle (U. S., Rep. Comm. Fish., 1916–1918), it may perhaps have contributed in the latter years a share of the catch as great as that of Yakutat (Table I). By 1928 the Yakutat

TABLE I. TOTAL NUMBER OF UNITS OF FISHING-EFFORT ON GROUND WEST OF CAPE SPENCER, 1915–1925, COMPARED WITH CATCH-PER-UNIT-OF-EFFORT OVER-ALL AND ON THE DIFFERENT BANKS, AND WITH PROPORTION OF FISH FROM THE DIFFERENT BANKS IN TOTAL WESTERN LANDINGS AT SEATTLE AND PRINCE RUPERT*

Year	*Units of effort (thousands)*	*Catch-per-unit-of-effort (lb.)*				*Yakutat and Portlock-Far Western area fish in total western landings at different ports (%)*			
		Over-all	*Yakutat area*	*Portlock area*	*Far Western area*	*Seattle*		*Prince Rupert*	
						Yakutat	*Portlock and F.W.*	*Yakutat*	*Portlock and F.W.*
1915	89	266	320	237	——	——	——	——	——
1916	92	203	228	143	——	64	36	——	——
1917	108	158	158	157	——	55	45	——	——
1918	85	125	126	125	——	38	62	——	——
1919	98	130	140	116	——	83	17	——	——
1920	91	148	143	152	156	51	49	——	——
1921	104	141	177	115	133	89	11	80	20
1922	80	135	139	132	59	74	26	76	24
1923	143	150	164	138	159	100	0	65	35
1924	233	110	96	115	118	60	40	34	66
1925	273	95	75	103	98	17	83	20	80

* Constructed from U. S., Rep. Comm. Fish., 1916–1926; Babcock, *et al.*, 1931: fig. 9; Thompson, Dunlop and Bell, 1931: table 12; Thompson and Bell, 1934: table 2.

area produced little more than a quarter of the total annual western yield, less than was obtained in the same year from the banks west of Portlock which were practically untouched before 1920 (*cf.* Thompson and Herrington, 1930: 51, table 5).

Consequently, it might be thought that the over-all reductions in catch-per-unit from 1915 to 1918 to 1927 resulted from mere local exhaustion of restricted areas which were originally densely populated, with subsequent expansion of the fishery to less productive but more representative regions. However, the data provided by Thompson, Dunlop and Bell (1913: see particularly their figs. 21, 22, 34, 37, 40; compare also Table I, p. 88, and footnote 12, p. 99) indicate that the changes in catch-per-unit from period to period were parallel on the different banks from Cape Spencer to the Shumagins, regardless of the changes in locality to which the drain by fishing was chiefly applied. Therefore it would seem that, although the Yakutat spawning area may have yielded a higher initial average catch-per-unit than the banks farther west, and although abundance on the banks farther west was somewhat higher than that in the Yakutat area in 1927, the picture of a catch-per-unit reduced to a third of that in 1915 over the entire range is a legitimate one.

The early limitation in range of the fishery might also permit a somewhat different objection to the inference that decline in catch-per-unit from 1915 to 1918 was greater than can be accounted for by the landings during that period. The population of the area that was heavily fished in 1915–1918 would have been only a fraction of the total over the whole range, and in consequence this population might have been reducible to the requisite low degree of abundance by a catch much smaller than would have been required to reduce the total population to this level. However, this objection is met by the same evidence as the preceding one, namely, that abundance fell about as rapidly in areas not heavily fished as in those upon which the fishery of the given period was concentrated.

An explanation of this peculiar parallelism of changes in abundance in different western areas has been supplied by tagging experiments (Thompson and Herrington, 1930). Mature fish (such as were probably almost exclusively taken by the western fishery up to 1918 at least, and which still supplied the bulk of the catch in 1927) were shown to move freely and rapidly over the entire range from Cape Spencer to the Shumagins. The average dispersion of the tagged fish was 250 miles within a year, which is around half the distance from the center of the range to its eastern and western extremes, an amount sufficient to carry a fish from Yakutat to Portlock. Furthermore, the average dispersion in 1927–1928 was least for the smallest fish, which included a proportion of immatures. It is known that the early exploitation yielded fewer small fish than did that in 1927 (Babcock, *et al.*, 1930: 21), and it may be presumed, therefore, that in the early years the commercial population was even more highly migratory than that in 1927. Consequently, the drain of an early fishery, limited to a part of the range, would have been transmitted rapidly to the entire stock (*cf.* Thompson, Dunlop and Bell, 1931: 63).

Drainage even of a highly mobile stock by a fishery situated chiefly in the easternmost quarter of the range (as in the period up to 1918) would obviously result in a gradient of increasing abundance with increasing distance from the fishery. The slope of this gradient would, however, depend upon the rate and extent of movement of the fish; and there is reason to believe that such movement may have been sufficient to prevent any cumulative increase in steepness of the slope from year to year.

The movements of the fish appear to be seasonal migrations from the grounds farther west to more easterly spawning areas, and return. Maximal dispersion of the fish tagged in 1927 was attained in the first year, "indicating but not proving, the migrations to be seasonal" (Thompson and Herrington, 1930). Thompson and Van Cleve (1936: 108) state that "The adaptation of the halibut to the currents in the Gulf of Alaska is therefore sufficiently clear. The mature fish migrate to the eastward within the western areas and spawn . . . for the most part between Yakutat and Kodiak Island . . . [The late post-larvae and metamorphosed young] have been found . . . along the southern coast of the Alaska Peninsula [*i. e.*, from Kodiak westward]." Thompson and Herrington (1930: 102) state that "During this time [summer, 1927–1928] the fishery on Yakutat Spit and the W Ground is practically negligible as very few fish are found on these banks except during or near the spawning season"; Thompson and Freeman (1930: 39) note that "the discovery (in 1913) of this Yakutat Spit, upon which dense schools collected to spawn, gave the fishermen opportunity to make heavy catches late in the fall and early spring . . . [The discoverers of the] W Ground . . . in 1913 . . . had taken from them spawning fish much like those taken from near Yakutat."

A seasonal spawning concentration in the Yakutat area, renewed and dispersed each year by movement of fish to and from banks extending far to the west, would obviously not present the opportunities for cumulative development of a density gradient which would be offered by random diffusion. In fact, the evidence indicates that the Yakutat population must have been renewed annually by contributions from the entire stock. Thus, the population available at Yakutat in a given year would be expected to depend rather upon the magnitude of the total western stock than upon the proportion of the fish at Yakutat which survived the previous season's fishing (especially in the early days of the fishery when the catch was composed to a very large extent of mature fish, and when fishing beyond Yakutat was of minor importance).

This question, of the rate of renewal of the Yakutat concentration, has been discussed by Thompson, Dunlop and Bell (1931) in connection with the surprising temporary rise in catch-per-unit-of-effort on the western grounds from 1919 to 1923. The authors state (*ibid:* 13) that

"Allowing for possible irregularities in the records, it is apparent that the depletion was halted between 1918 and 1921 or 1923, allowing an influx of newly mature fish from the untouched immatures of the western grounds. This halt was probably due to the decline in vessels fishing these banks . . . " Again (*ibid:* 95), "The first intensive exploitation of these banks took place between 1913 and 1918. Evidently mature and immature stocks alike were quickly reduced. But with the slackening of the fishery, particularly in the more distant areas, the migratory mature stock, drawing from distant untouched banks, quickly replaced part of the loss . . . "

The above remarks, which seem to imply that there was a cumulative increase in the slope of the density gradient until a renewal of equilibrium was permitted by slackening of the fishery, do not afford the only possible interpretation of the facts. If the temporary increase in catch-per-unit on the nearer banks after 1918 had been the result merely of a levelling redistribution of the stock, it would not be expected that the farther banks would show an increase in catch-per-unit like that on the nearer banks. Since such a synchronous increase appears to have occurred over the entire range (Thompson, Dunlop and Bell, 1931: fig. 21), its cause may have been other than the levelling out of inequalities in distribution caused by the previously intense fishery.

Furthermore, no clear relationship is evident between the intensity and distribution of fishing in a given year during this period and the catch-per-unit in that or a succeeding year. The modest remission in total fishing effort which occurred in 1918 (followed in 1919 by a halt in the preceding rapid decline in catch-per-unit on Yakutat) in fact appears to have been accompanied by an increase rather than by a slackening of fishing effort on the farther banks (according to the proportion of "Portlock" fish in the western landings at Seattle; see Table I). The amount of fishing on the farther banks evidently fell off greatly in 1919, but the total fishing effort reverted in that year to the second highest level in the history of the fishery. As a matter of fact, there was no average remission of fishing effort in the period preceding the peak of the renewal of abundance in 1923, since the average yearly number of units of effort expended in the four years 1919–1922 was 93,328, as compared with 93,325 in 1915–1919. The data thus do not confirm the conjecture that the rise in catch-per-unit after 1918 was the result of reversal of a cumulative effect of localized fishing on the distribution of the population. Instead, they seem better fitted by the hypothesis that the supply on Yakutat at the beginning of each spawning season was commensurate with the level of the total population, and that the distributive equilibrium was reached anew between one season and the next.

For an explanation of the increase in abundance from 1918 to 1923 other than remission in intensity of the fishery, attention may be directed to Table II. This shows a rapid rise in percentage of halibut

TABLE II. PERCENTAGE OF HALIBUT OF LESS THAN TWELVE POUNDS IN LANDINGS AT ALL PORTS FROM PORTLOCK AND FAR WESTERN BANKS, 1919–1928*

Year	*Per cent*	*Year*	*Per cent*
1919	11	1924	14
1920	11	1925	16
1921	13	1926	19
1922	15	1927	20
1923	16	1928	21

* Derived from Babcock, *et al.*, 1930: 21, fig. 11.

under twelve pounds in landings from Portlock and the far west, from about 11 per cent in 1919 and 1920 to about 16 per cent in 1923 (followed by a drop to about 14% in 1924, and then a renewed rise attaining the 21% level by 1928). Unfortunately, information concerning the percentage of "chickens" in total western landings is not available. However, the combination of a rise in catch-per-unit-of-effort until 1924 with a rise in the proportion of small fish (from some of the banks at least) during the same period is suggestive of the entry of especially numerous year-classes into the fishery. (It should be emphasized, however, that even if fully established, the mentioned combination would not supply entirely conclusive evidence; see p. 107, and note that the drop in over-all abundance from 1923 to 1924 seems much greater than would be expected from the changes in percentage of young fish in combination with those in fishing-mortality.) On the whole, therefore, the rise in catch-per-unit from 1919 to 1923 offers no support for the view that there was a lag in dispersal of the mature population sufficient to permit a density-gradient accentuated from year to year under conditions of severe localized fishing.

In the light of the foregoing considerations, our comparison of the sum of western catches in 1915–1918 with the apparent decline in total western population during that period seems legitimate.

Relationship Between Catch-per-unit-of-effort and Magnitude of Population. In a preceding paragraph an estimate of the western population of halibut in 1915 and 1918 was obtained by comparison of catch-per-unit-of-effort during those years with that in 1927 (when a figure for absolute magnitude is obtainable by use of the results of tagging experiments), on the assumption that a rectilinear relationship existed between catch-per-unit and magnitude of population. Under simple ideal conditions the ratio of catch-per-unit-of-effort to population would indeed remain identical from time to time whatever the changes in fishing-effort and fishing-mortality (*cf.* Ricker, 1940: 69; " . . . catch per unit effort is a valid estimate of the relative size of average populations on hand *during the fishing season* of successive years"); but the conditions with which we have to cope are certainly far from simple and ideal, and the legitimacy of the assumption of rectilinearity requires examination (see also p. 97 ff).

One obvious requirement for qualification results from the circumstance that a given increase in units of effort might be expected to result in a less than proportionate increase in catch. A correction of fishing effort for such effects, by use of the compound interest equation, was therefore introduced by Thompson and Bell (1934: 36–37; see also Ricker, 1940: 63–64). However, the application of such a correction [by means of the equation $w = 100.0 - \text{antilog}_{10}\ (2.0 - 0.00000013225\,x)$, where w = per cent of commercially available population caught during the year, and x = number of units of fishing effort employed on the western banks] does not significantly change the uncorrected estimates given on a preceding page, as is shown by Table III.

TABLE III. ESTIMATED POPULATION OF PACIFIC HALIBUT ON FISHING GROUNDS WEST OF CAPE SPENCER COMPARED WITH CATCH, 1915–1918

Year	*Estimated fishing mortality (in % by wgt. of commercial population)*	*Landings (million lb.)*	*Estimated commercial population (million lb.)*	*Escapement [commercial population minus landings] (million lb.)*	*Loss of population unaccounted for [comm. pop. minus preceding year's escapement] (million lb.)*
1912	——	0.06	——	——	——
1913	——	10.31	——	——	——
1914	——	22.15	——	——	——
1915	2.7	23.66	884	860	——
1916	2.8	18.67	674	655	−186
1917	3.2	17.00	527	510	−128
1918	2.6	10.62	415	404	− 95
1927	10.0	30.03	300	——	——

Justification for the present assumption of a rectilinear relationship between population and catch-per-unit is afforded by the fact that this same assumption is employed by Thompson and his co-workers in reaching the conclusion that the fishery was responsible for the decline in abundance. The proposition is not explicitly stated by the authors cited, but its acceptance by them can readily be demonstrated by analysis, from table 11 of Thompson and Bell (1934: 36), which illustrates their method of calculating changes in the catch-per-unit to be expected from a given change in fishing effort.[5] Accordingly, the remark of Thompson, Dunlop and Bell (1931: 73) that "catch per unit is accepted as a direct measure of abundance" evidently intends "abundance" to mean *poundage per unit of area*, and "direct" to mean *proportional*. Hence, when the same area is in question, "abundance" would evidently refer to magnitude of population, an inference given a degree of confirmation by the remark (*ibid:* 57), regarding the Yakutat grounds, that "The abrupt fall in the catch [per unit] from 1915 to 1918 agrees with what has been found elsewhere on newly and intensively exploited banks, where the accumulated stock is rapidly removed."

Reliability and Comparability of the Data. In the foregoing paragraphs, justification has been presented for the reasoning underlying our suggestion that the reported fall in catch-per-unit-of-effort on the western banks from 1915 to 1918 was nearly *seven* times too great to be accounted for by mortality caused by fishing. This justification consisted in demonstration that the method of reasoning here employed has the same degree of validity as that used by Thompson and his co-

[5] *Catch-per-unit-of-effort* = *Catch/Effort;* and *Population* = *Catch/Fishing-mortality* (in per cent of average population captured). Hence *Population/Catch-per-unit-of-effort* = *Effort/Fishing-mortality.* In table 11 of Thompson and Bell fishing-mortality ("intensity") in years 2–9 is given as a constant, 60 per cent; and fishing-effort (in terms of skates of gear fished) is also given as constant, 179 skates. Consequently, the relation between population and catch-per-unit has evidently been assumed to be rectilinear.

The same fact may be more directly shown by calculation from the values given in the table cited. Taking, for example, years 2 and 9, the respective catches are given as 6,550 and 4,060. Since these catches represent a fishing-mortality or -intensity of 60 per cent, the respective average populations must have been 10,917 and 6,767. The respective catches-per-unit-of-effort are given as 36.6 and 22.7. The ratio of population to catch-per-unit must therefore have been taken to be constant, its value being 298 in both cases.

workers in reaching, from the same data, the conclusion that the decline was caused primarily by the fishery. In the present section, objections will be raised which tell equally against Thompson's interpretation and the one here proposed.

The first point to be considered is the reliability of the data. Our estimate of population in 1927 is based on reports of total fishing-effort and catch, together with a value for per cent of average population caught. The estimate of per cent of average population caught was obtained from the results of limited tagging experiments (Thompson and Herrington, 1930: 89–91) and therefore cannot be regarded as precise. Likewise, the estimates of total catch and fishing-effort (Thompson and Bell, 1934: 12) are presumably not entirely reliable, since there is a discrepancy of more than 20 per cent between the estimates for 1928 given by Thompson and Bell and those for the same year given by Thompson and Herrington (1930: 51).[6]

It will thus be seen that the data basic to our estimate of population in 1927 may be quite imprecise. However, in order to reduce the estimated populations in 1915 and 1918 to a level such that the decline during that time would have amounted to no more than the sum of reported landings (around 70 million lb.), the total western population in 1927 would have to be estimated at no more than 50 million pounds instead of 300 million.[7] This would require that the estimate of per cent of average population caught in 1927 be six times too low, or the estimate of landings in 1927 six times too high. But it seems most probable that the estimate of landings is minimal even if erroneous; and it would be astonishing if an estimate of fishing-mortality which has not been corrected by its authors after ten years of continuing study were even as much as 100 per cent too low.[8] It therefore does

[6] 26,982,962 lb., 370,645 skates, and 72.8 lb. per skate, by Thompson and Bell, as compared with values for areas 19 to 36 totalling 33,822,065 lb., 470,731 skates and 71.9 lb. per skate, by Thompson and Herrington. The account by Thompson and Herrington (*ibid.*: 53) indicates that the estimates of catch and effort were obtained by summation of fishermen's log-records. The discrepancy is therefore a puzzling one, since it cannot (according to the dates of publication) have resulted from additional records collected after completion of the paper by Thompson and Bell.

[7] Let X = population in 1915, Y = 1918, Z = 1927. Assuming, from catch-per-unit-of-effort, that $X/Y/Z$ was about 6/3/2, and if $X - Y = 70$ million lb., then $X = 140$ million lb., and $Z = 47$ million lb.

[8] I am deeply indebted to Mr. H. A. Dunlop, Director of the International Fisheries Commission, for the following information (*in litt.*, January 16, 1947): "I regret that

not appear that imprecision of the data concerning the population in 1927 lies within limits which can seriously affect our results. Estimates of population in 1915 and 1918 are, unlike that for 1927, not subject to invalidation by unreliability of totals for catch and fishing effort, since they may be based upon the ratios of the catch-per-unit-of-effort indicated by the presumably representative samples afforded by available fishing records. A careful examination of the analysis by Thompson, Dunlop and Bell (1931) promotes confidence in the reliability of the 6/3/2 ratio of catch-per-unit-of-effort, at least within limits not seriously affecting our estimates of population.

Finally, it is entirely possible that the reports of total western landings in 1915 and 1918 (Thompson and Bell, 1934: 12) are not precise, but an analysis of other available information makes it seem improbable that actual production in 1921 could have exceeded that reported by Thompson and Bell for that year by more than, say, 50 per cent.[9] If the western landings reported by Thompson and Bell

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I cannot release for outside publication unpublished tagging returns. I can say, however, that in keeping with the increasing intensity of fishing the returns from the 1927 and 1928 experiments in the years immediately following 1928 gave a slightly higher but not significantly different fishing mortality rate than was shown by the first years' returns."

The fact that the rate of return of these tags was maintained in succeeding years seems to ensure that the low initial rate of return did in fact correspond to a low rate of fishing-mortality, rather than a high rate of tag-loss or other artifact (*cf.* Graham, 1938).

[9] Other available information is as follows: Landings from west of Cape Spencer at Seattle in 1921 were about 1.0 million lb., out of total landings there from Alaska of 1.1 million lb., and total landings there of 11.5 million lb. (Radcliffe, 1922: 62). Landings from west of Cape Spencer at Prince Rupert in 1921 are indicated by Babcock, *et al.* (1931: 19) to have been about 5.5 million lb., out of total Alaskan landings there of 11.5 million lb., and total landings there (according to Canada, Fish. Statist., 1922) of 25.3 million lb. Vancouver landings (*ibid.*) were evidently about 7.1 million lb.; their derivation is unknown. Total Alaska landings in 1921 were about 17.2 million lb. (Bower, 1922: 42), of which an unknown proportion came from south of Cape Spencer.

The sum of the official figures for total landings of halibut in Seattle, British Columbia and Alaska in 1921 is thus 61.3 million lb., only 17 per cent higher than the 52.2 million lb. total catch in all areas given by Thompson and Bell (1934: 12).

The sum of reported western landings in Seattle and Prince Rupert in 1921 is 6.5 million lb. Assuming that western landings at Vancouver were in the same proportion to the whole as at Seattle, the landings of halibut at Vancouver from west of Cape Spencer would have amounted to 9 per cent or 0.6 million lb. Assuming that landings in Alaska (probably mostly at Ketchikan) contained fish from west of Cape for 1915 and 1918 are less than the actual ones by no more than seems probable for 1921, the error would be insignificant, since actual landings would have had to be 600 per cent more than those reported, to match the apparent decline in population.

Errors in the various values for catch, effort and fishing-mortality, amounting to less than 100 per cent for each (and therefore within the bounds of reason), could together, if they were all in an appropriate direction, perhaps result in an apparent discrepancy of 600 per cent between decline in population and concurrent landings. However, the likelihood that an entire series of relatively small errors was uniformly in the proper direction, and therefore cumulative, seems no more probable than that a major error exists in any single item.

It is now necessary to give further attention to the problem of the relation between catch-per-unit-of-effort and population. Catch-per-unit-of-effort is a direct measure only of the frequency with which halibut are recovered from the gear. Under simple, ideal circumstances, frequency of capture ought to be proportional to frequency with which the hook is encountered by fish, and this to density of population per unit of area. However, it can be demonstrated that there was a considerable difference in the ratio of catch-per-unit-of-effort to population between the areas south and those west of Cape Spencer in 1926–1927; and in consequence, the possibility of differences in the proportionality of catch-per-unit to density of population at different periods on the western banks must also be entertained.

As has been pointed out in footnote 5, the ratio between population and catch-per-unit is the same as that between fishing-effort and rate of fishing-mortality. Rate of fishing-mortality on the southern grounds was shown by tagging experiments to be about 40 per cent in 1926, as against 10 per cent on the western grounds in 1927. Number of skates of gear set on the southern grounds in 1926 is given as 494,078, as against 345,513 on the western grounds in 1927. The

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Spencer in the same proportion as among fish taken off Alaska and landed at Prince Rupert, then the maximal Alaskan landings of fish from west of Cape Spencer would have been 62 per cent or 10.6 million lb. The sum of known and estimated western landings in 1921 is thus 17.7 million lb., an amount only 20 per cent greater than the western catch of 14.7 million lb. reported by Thompson and Bell (1934). Even if all Alaskan landings were assumed to derive from grounds west of Cape Spencer (which is highly improbable), the total western catch would be only 24.3 million lb., only 65 per cent more than the value given by Thompson and Bell.

ratio of estimated population to catch-per-unit on the southern grounds was therefore 1,235,195/1, while that on the western grounds was 3,455,130/1, nearly three times as great. The higher percentage of the population captured per-unit-of-effort on the southern grounds must correspond to a higher efficiency of the effort, if the lower average catch-per-unit-of-effort (52.2 lb. on the southern banks in 1926, as compared to 86.9 lb. on the western banks in 1927; *vide* Thompson and Bell, 1934: 12, 18) corresponds to a smaller southern population.

This apparent difference in efficiency of the fishing-effort might of course not be real. For example, the percentage of the population caught on the southern grounds might not have been four times as high as on the western grounds, despite the much higher rate of return of southern tags. If real, the difference would presumably refer, for example, to better knowledge of the southern grounds or the habits of the southern fish, less frequent preoccupation of the southern hooks by fish other than halibut, a higher degree of activity among southern halibut, a greater tendency to school, a greater appetite for the bait, etc. The possibility of differences of this nature, not only from area to area, but from period to period in the same area, is obvious. Thus, it is conceivable that a relatively small reduction in the abundance of halibut relative to prey might greatly change the avidity with which the bait was sought; or a small change in mean temperature might have a considerable effect on rate of movement.[10] A further type of possibility (for the suggestion of which I am greatly indebted to Professor A. E. Parr) is, that since a hook-and-line fishery is dependent on the exercise of initiative by the fish, a selective drain of susceptible individuals might in the course of time reduce the catch-per-unit without commensurately reducing the stock.[11] The degree of probability that the ratio of catch-per-unit to population on the western grounds changed from such causes between 1915 and 1927 cannot be assessed.

[10] Thompson, Dunlop and Bell (1931: 82) describe probable effects of seasonal changes in temperature on feeding activity.

[11] Apart from conditioned or genetically inherited differences in normal behavior, such a selective exhaustion of the susceptible individuals might result, for example, from a greater tendency of diseased than sound halibut to take bait, with resultant effects on subsequent rate of spread of infection (*cf.* Thompson and Freeman, 1930: 30, 42, who evidently attribute the drop in frequency of diseased individuals solely to reduction in average age of the population).

With regard to possible change in efficiency of fishing-effort as a result of change in habit of concentration or dispersal, it is conceivable that the same stock, moving about at the same rate within the same area, would yield a higher catch-per-unit if schooled than if scattered, since the fishery may be presumed to operate, not entirely at random, but by sampling until a spot of high yield is found, which is then intensively fished until the yield falls. The possible effects of change in external conditions or in age or magnitude of population of halibut on the formation of schools is unknown. However, it seems possible that, if changes in tendency to concentrate did occur on the western grounds between 1915, 1918 and 1927, these changes might have been such as to cause an under- rather than an over-estimation of the decline in population between 1915 and 1918. Thus, Thompson and Herrington (1930: 52) observe that "It may, of course, be true that where the fish school very densely indeed, as they did in the early days of the industry, the maximum number which can be caught by the unit of gear is the limiting factor, this number forming a variable proportion of the fish on the ground."[12] Also, the fact that efficiency was evidently much higher in 1926–1927 on the sparsely populated southern banks than on the densely populated western ones, suggests as a possibility that reduction in size and abundance of the fish might be correlated

TABLE IV. AVERAGE CATCH-PER-UNIT-OF-EFFORT IN POUNDS, IN THE YAKUTAT AND THE PORTLOCK AREAS IN THE PERIOD MAY–SEPTEMBER, AROUND 1915, 1918 AND 1927*

	1913(14)–1916	1917–1919	1926–1928
Areas 19–23 (Yakutat area)	187	100	62
Areas 24–28 (Portlock area)	198	99	79

* Constructed from data of Thompson, Dunlop and Bell (1931).

[12] It should be noted that the decline in average catch-per-unit on the western banks does not appear to be attributable to a shift in effort from areas or seasons of denser to those of less dense schooling. This point has been discussed in detail by Thompson, Dunlop and Bell (1931: 87–107). Their tables 26 and 31 show that even if comparison is restricted to the months May–September, when catch-per-unit falls to its lowest seasonal level and the fish are not schooled for spawning, the ratio between catches-per-unit in the years around 1915, 1918 and 1927 remains about the same as when all seasons are considered, and is alike on Yakutat and Portlock. Table IV illustrates this point.

with an enhancement rather than with a reduction in efficiency of the fishing-effort.[13]

On the other hand, it is impossible to say whether the corrections applied by Thompson and his co-workers, in their attempt to make the unit-of-effort comparable over long periods of changing fishing-methods, are valid. It cannot be gainsaid that our assumption of a constant ratio between fishing-effort and rate of fishing mortality might conceivably err in amount and direction sufficiently to annul the discrepancy which we have pointed out between estimated decline in population and reported landings (although, on the whole, it seems more probable that this was not the case). But it should be borne in mind that the assumption of an increase in the ratio of effort to mortality with the passage of years, sufficient to bring our estimates of the decline of the early western population into line with the contemporaneous drain by the fishery, would amount to a denial of the validity of evidence of a serious decline in abundance of the western stock of halibut, *and would therefore be as detrimental to Thompson's views as to those here advanced.*

ANALYSIS OF THE PHASE OF INCREASE IN ABUNDANCE OF THE WESTERN STOCK OF HALIBUT

Changes in Apparent Magnitude of the Stock. Since 1931, catch-per-unit-of-effort on the western grounds has been increasing. The changes which have occurred are shown in Fig. 1 and Table V. It will be seen from Fig. 1 that the annual changes in estimated average

[13] If efficiency of effort increased as population declined, the population in 1915 would have been more than three times the one in 1927, and the one in 1918 less than half of the one in 1915. The estimate of magnitude of population in 1927 would not be affected, since it depends on a direct measurement of percentage of population caught.

References to Table V on page 101.

[14] Constructed from data on landings, fishing-effort, and catch-per-unit-of-effort in 1915–1933 as given by Thompson and Bell (1934: 12) and from data on landings and catch-per-unit-of-effort in 1934–1944 prepared by the International Fisheries Commission (British Columbia, Reps. Prov. Fish. Dept., 1935–1945).

[15] *Total increment* equals *landings* plus *change in average population since preceding year.* In Fig. 2, change in population since preceding year has been given as percentage of preceding year's population; whereas in the present Table, change in population since preceding year has been treated as percentage of the current year, resulting in some minor differences.

TABLE V. CIRCUMSTANCES OF THE HALIBUT FISHERY ON BANKS WEST OF CAPE SPENCER, 1915–1944[14]

Year	*Fishing-effort (ten thousand skates)*	*Catch-per-unit-of-effort (lb.)*	*Landings (million lb.)*	*Landings (% of estimated population)*	*Estimated average commercial population (ten million lb.)*	*Total increment (% of estimated population)*[15]
1915	9	266	24	2.7	88	——
1916	9	203	19	2.8	67	−28
1917	11	158	17	3.2	53	−24
1918	8	125	11	2.6	42	−23
1919	10	130	13	3.0	43	+ 6
1920	9	148	13	2.7	49	+15
1921	10	141	15	3.1	47	− 1
1922	8	135	11	2.4	45	− 2
1923	14	150	21	4.3	50	+13
1924	23	110	26	6.8	37	−29
1925	27	95	26	8.0	33	− 6
1926	28	94	26	8.1	32	+ 7
1927	35	87	30	10.0	30	+ 1
1928	37	73	27	10.7	25	+ 1
1929	42	73	30	11.9	25	+11
1930	41	65	27	11.7	23	+ 1
1931	29	72	21	8.5	25	+19
1932	25	82	21	7.4	28	+20
1933	27	84	22	7.8	29	+10
1934	28	86	24	8.0	29	+18
1935	27	88	24	7.9	30	+10
1936	27	97	26	7.8	33	+17
1937	23	112	26	6.7	38	+20
1938	22	116	26	6.5	39	+10
1939	22	115	25	6.5	39	+ 6
1940	22	121	27	6.6	41	+11
1941	23	122	28	6.7	42	+ 7
1942	21	131	27	6.1	44	+13
1943	21	133	28	6.3	45	+ 8
1944	18	151	27	5.3	51	+15

population of halibut during the fourteen years 1917–1930 are approximately balanced by those in a converse direction during the fourteen years 1931–1944. During the former period, the estimated population dropped from 530 to 230 million pounds, averaging 380 million pounds, while during the latter period it rose from 250 million pounds to 510 million pounds, averaging 370 million pounds. The question here to be considered is whether or not the increase ought to be attributed to reduction in amount of fishing.

Changes in Apparent Magnitude of the Stock Compared to Withdrawals by the Fishery. During the period 1917–1930 annual landings averaged 6.3 per cent of the population, while in the period 1931–1944 they averaged 6.4 per cent. Thus, the over-all per cent of the population removed by the fishery, being constant, does not afford any obvious explanation of the reversal of direction of population-change after 1930, from waning to waxing. A more detailed examination of the data likewise fails to show any conspicuous relation between periods of population-increase or -decrease and extent of drain by the fishery. Selecting periods when the population was of comparable magnitude, it is seen in Table VI that the total annual additions to the stock in

TABLE VI. AVERAGE ANNUAL INCREMENT (LANDINGS, PLUS INCREASE OR DECREASE IN THE STOCK AS COMPARED WITH THAT OF THE PRECEDING YEAR) DURING SELECTED PERIODS OF COMPARABLE MAGNITUDE OF ESTIMATED POPULATION

Period	*Range in population (10 million lb.)*	*Average population (10 million lb.)*	*Average annual landings (10 million lb.)*	*Average annual change in population (10 million lb.)*	*Average total annual increment (10 million lb.)*	*Average total annual increment (% of av. population)*
1918–23	42–50	46.0	1.4	−0.4	+1.0	+ 2.2
1924–29	37–25	30.5	2.8	−4.1	−1.3	− 4.3
1931–37	25–38	30.3	2.3	+2.2	+4.5	+14.8
1940–44	41–51	44.6	2.7	+2.4	+5.1	+12.4

the 1930's and 1940's were much greater than can be accounted for by the changes in landings as compared with those of the 1910's and 1920's. Thus, average annual landings were 1.6 per cent of population less in 1931–1937 than in 1924–1929; but the average total annual increment in 1931–1937 was 19.1 per cent of population more than in 1924–1929, leaving a difference in average total annual increment be-

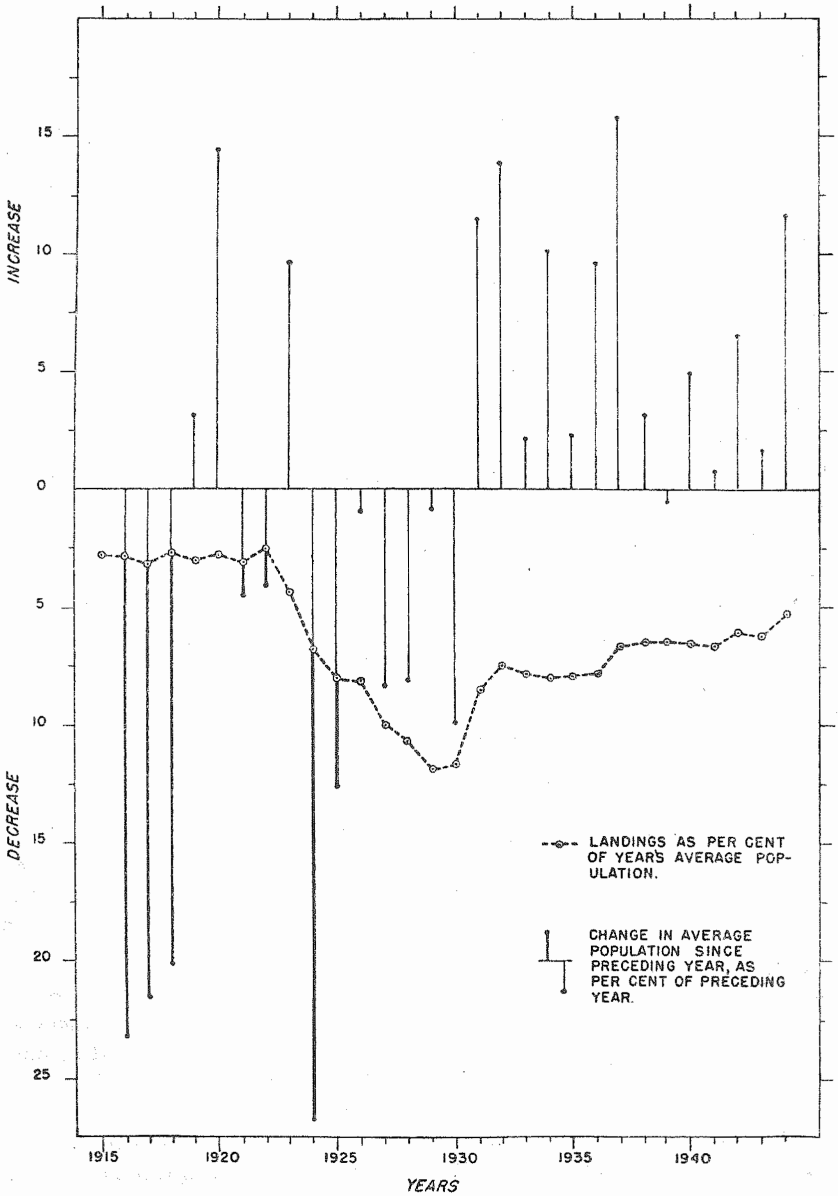

Figure 2. Annual landings relative to year's average population, 1916–1944; compared with change in population since preceding year, relative to population of preceding year.

tween the two periods of 17.5 per cent which is unexplainable by a difference in amount of fishing.

Fig. 2 and Table V, showing the year-to-year percentage changes in population and landings, clearly bring out the fact that total annual increment in population (landings plus increase since preceding year), previously negative in seven out of ten years, became steadily positive after 1925; and that this change began while fishing-effort was still rising both relatively and absolutely. It will further be seen that, although the beginning of the period of maximal increment (in 1931) coincided with a sharp reduction in rate of fishing-mortality and -effort from the high of 1927–1930, the level of exploitation after 1930 remained much higher than that before 1925.

The same lack of relationship between magnitude of catch and changes in population is demonstrated in a different manner in Fig. 3, which deals with absolute quantities. It will be seen that in 1915–1919 and 1920–1924, although the amount of halibut caught was at a low level, the sum of landings was less than shrinkage in population between the first and last years of these periods. In 1925–1929 the catch reached its highest level, but shrinkage in population was more than balanced by landings. In 1930–1934, 1935–1939, and 1940–1944, landings were not so much less than those of 1925–1929 as they were greater than those of 1915–1919 and 1920–1924, yet population increased instead of shrinking.

To describe the same facts in still another way: although the average annual catch since 1932 (26 million lb., or 7% of the estimated average stock) has been lower than that during the five years 1927–1931 (27 million lb., or 9% of the average stock), it has been much greater than the average from 1915 through 1926 (18 million lb., or 4% of average stock). Thus, a stock of estimated average magnitude of only 375 million pounds in 1932–1944, subject to a fishing mortality averaging 7 per cent per year, nearly doubled during the period. In contrast, a stock averaging 488 million pounds in 1915–1926, and then subject to a fishing mortality averaging only 4 per cent per year, declined to one-third during the period.

Changes in Abundance Compared to Changes in Composition of the Stock. Critical evidence concerning the causes of improvement in the western stock of halibut since 1930 would be provided by adequate data on changes in size and age composition of the stock. Unfortu-

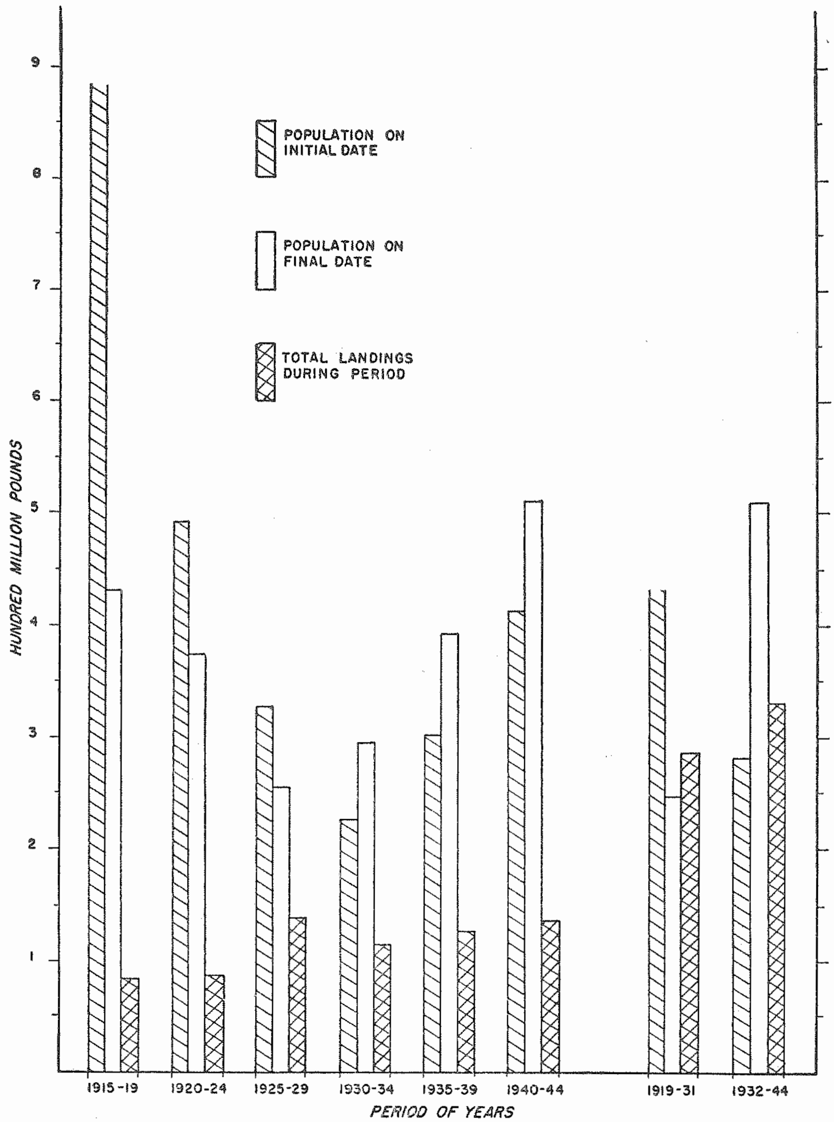

Figure 3. Initial and final population of each four-year period during the interval 1915–1944, and of two thirteen-year periods within the same interval; compared with total landings during each period.

nately, the only information on this subject which has been published (apart from the statement of the International Fisheries Commission [British Columbia, Rep. Prov. Fish. Dept. (1941), 1942: 26] that "The abundance and average size of the fish are both greater . . . ") consists in data on the percentage of under- and over-sized fish in landings from all western banks in 1932–1935 (given by Bell, 1937: 12), and in data on the proportion of "Grade 2" in landings from all western banks at Seattle in 1929–1942 (Fiedler, 1931–1941, 1942–1945, and Anderson and Power, 1946). These numerical data, reproduced in Tables VII and VIII, would be insufficient for our purpose even if

TABLE VII. PERCENTAGE OF SMALL, MEDIUM AND LARGE HALIBUT IN LANDINGS FROM THE WESTERN BANKS, 1932–1935; AND PROPORTION OF SMALL PLUS LARGE HALIBUT IN THE TOTAL

Year	*Small*	*Medium*	*Large*	*Sum, small plus large*
1932	18.0	70.6	11.4	29.4
1933	16.8	69.8	13.4	30.2
1934	17.5	68.3	14.2	31.7
1935	15.5	65.4	19.1	34.6

TABLE VIII. PROPORTION OF "GRADE 2" HALIBUT IN TOTAL LANDINGS AT SEATTLE FROM THE WESTERN BANKS, 1929–1942, AND PRICE OF "GRADE 2" RELATIVE TO "GRADE 1," 1929–1942

Year	*Proportion* (%)	*Relative price* (%)	*Year*	*Proportion* (%)	*Relative price* (%)
1929	26	85	1936	41	93
1930	29	76	1937	36	85
1931	46	85	1938	38	94
1932	44	43	1939	40	95
1933	40	77	1940	43	96
1934	38	86	1941	42	92
1935	40	92	1942	46	90

they were acceptable as indices of the composition of the stock,[16] since

[16] The following obstacles to acceptance of available data as reliable indices of the composition of the stock may be considered:

The proportion of "small" fish in "Grade 2" is unknown and undoubtedly variable.

The proportion of "large" fish in the landings may have been increased by a change in trade classifications which appears to have developed gradually between 1930 and 1935 (for calling the existence of such change to my attention, I am deeply indebted to Mr. H. A. Dunlop of the International Fisheries Commission). Comparing data what we require is knowledge of the changes in relative strength of the different year-classes during their passage through the population for comparison with the changes in fishing mortality (*cf.* Thompson, 1937: 16).

The percentage of under-sized fish in the population commercially available represents a pool, to which incoming year-classes contribute increasingly for a time (from about their seventh through their eleventh years, according to data for the late 1920's given by Thompson and Bell, 1934: 48). At the same time, the pool is being drained not only by fishing and natural mortality but by translation of the small fish to medium size. An increase in the proportion of the total commercial population contained in the pool of small fish during several years, parallel with an increase in the total commercial population (such as is suspected in the period 1919–1923; see p. 92), would suggest an increase in the incoming year-classes, but it does not supply conclusive evidence. This is because such parallel increases might even occur with

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from Thompson and Herrington (1930: 36) with those from Western Fisheries (1933, *7* [1]: 5; 1935, *9* [6]: 8; 1939, *17* [6]: 9; see also Fiedler [1938: 439] and Anderson and Power [1946: 202] for estimates of the shrinkage in weight from round to dressed halibut), it would appear that the change was from an upper limit for "medium" of 80 pounds or more (heads on) to one of 70 pounds. That the change was at first not rigorously applied is suggested by a remark attributed to a fisherman (Western Fisheries, 1934, *7* [4]: 7), "Here they are payin' 8½ for 10-lb. to 80-lb. fish, an' this should be down to 60-lb."

The proportion of under- and over-sized fish landed may, according to the remarks of Thompson and Herrington (1930: 36) have been influenced strongly by changes in price of these grades relative to that of first grade fish and of each other (see Table VII and Fig. 4 for changes in relative over-all price of "Grade 2"; also Bell, 1937: 12; see Western Fisheries, 1934, *7* and *8*, section "Vancouver Halibuteers," for variation in price of "chickens" relative to "large").

The proportion of "Grade 2" fish landed may have been influenced by factors independent of relative price and abundance of under- and over-sized fish, and also of changes in location and season of fishing. "Grade 2" includes not only "large" and "small," but also fish "soft," "gray," "scarred," "torn" or otherwise imperfect (see Thompson and Freeman, 1930: 30, 42; Thompson, Dunlop and Bell, 1931: 21; Western Fisheries, 1935, *9* [6]: 8). The proportion of such fish among those of "medium" size might be affected by changes in average air temperature as related to arrangements for refrigeration, in incidence of sporozoan infection, in crowding or state of nourishment of the stock before capture, etc. That the proportion of imperfect fish among those of "medium" size may be a significant one is suggested by the wide gap between proportion of total under- and over-sized fish landed in 1932–1935 (Table VII) and proportion of "Grade 2" landed at Seattle during these years (Table VIII).

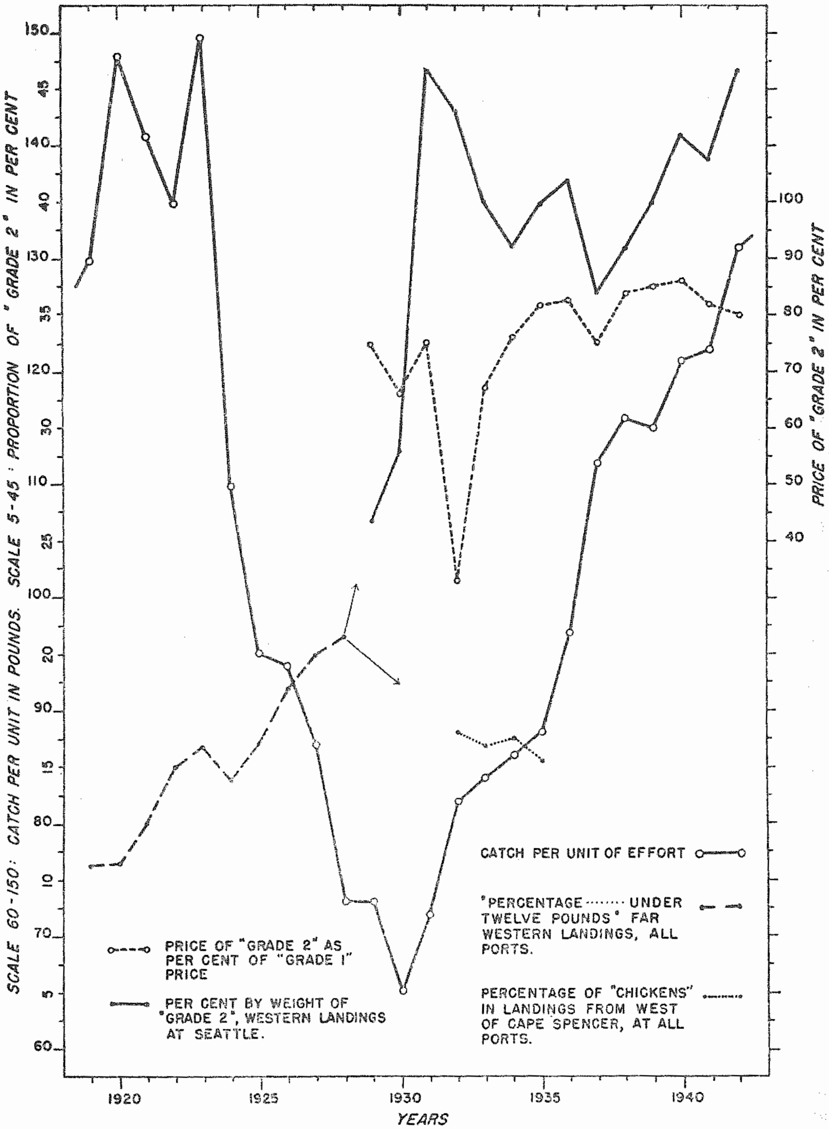

Figure 4. Catch-per-unit-of-effort; compared with proportion of small halibut in landings from far western banks, 1919–1928, and from all western banks, 1932–1935; and with proportion of second-grade halibut and price of second-grade halibut relative to that of first grade, in landings from all western banks at Seattle in 1929–1942.

both a decline in magnitude of incoming year-classes and an increase in fishing mortality, through differential changes in natural mortality and rate of growth. Similarly, a decline in percentage of undersized fish, parallel with an increase in the total commercial stock (such as that from 1932 to 1935, which Bell's [1937] data suggest; see Table VII, Fig. 4), might readily result, for example, from an increase in the pool of small fish during the period before 1932 by accession of unusually large year-classes, followed by translation of this excess to the medium size-class. The tremendous rise from 1930 to 1931 in percentage of "Grade 2" fish landed at Seattle (see Table VIII, Fig. 4) might conceivably in part reflect such an event.

Comparison of Expected with Observed Changes in Abundance. It seems fairly clear from the foregoing various evidences that changes in fishing effort have not been proven sufficient to explain the recent increase in abundance of halibut on the western banks. Therefore, it is possible that the correspondence shown by Thompson and Bell (1934: 46, fig. 17) between the changes in actual catch-per-unit-of-effort and those calculated from changes in fishing-effort (on the basis of an arbitrarily selected constant annual increment of young and assumed constant rates of natural mortality and of growth during the limited period 1920–1929) might represent a special result unobtainable (at the same constants) not only for the period of rapid decline before 1920 but for the period of increase since 1930 as well. That this is in fact the case is demonstrated in Fig. 5, which illustrates the result of calculations of expected catch-per-unit-of-effort for the period 1930–1944, using the same method and the same constants as were employed by Thompson and Bell (1934) for the period 1920–1929.[17]

[17] The calculated catch-per-unit-of-effort has been corrected for competition of gear, but, following the practice of Thompson and Bell, the observed catch-per-unit has not been so adjusted. However, the changes resulting from adjustment of observed catch-per-unit would be insignificant (at a maximum, in the case of 1938, reduction from 178% of 1930 to 170%).

One possible objection to the particular constants employed in this method of calculation lies in the chance that the rate of growth assumed (that of fish from their seventh to their eighteenth year) might not be the same as that at greater ages. The landings from western grounds evidently included a significant proportion of fish older than eighteen years, and a relatively low proportion of those younger than eleven years. Thus, the experimental catches from Yakutat, the W Ground and Portlock in 1926–1927, described by Thompson and Herrington (1930: 39, table 2), included 9 per cent by number of fish more than 115 cm. in length (equivalent to a

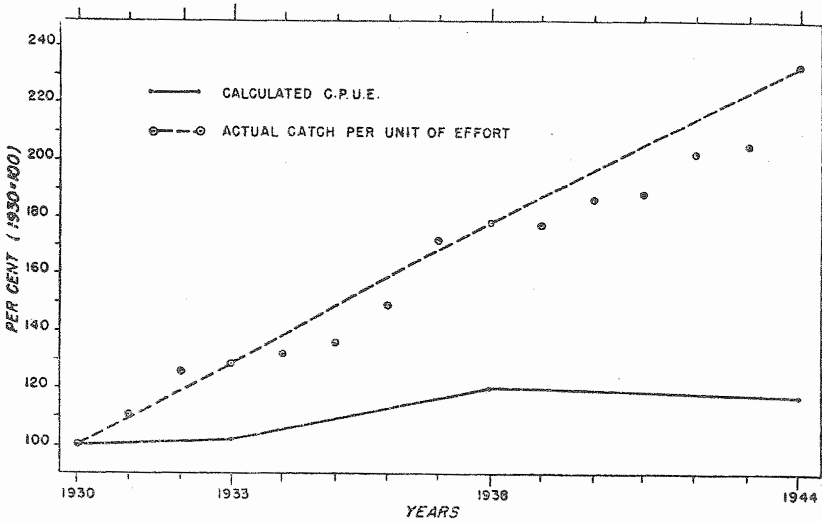

Figure 5. Observed change in catch-per-unit-of-effort, 1930–1944; compared with expected change in 1930–1933–1938–1944 as calculated by the method of Thompson and Bell (1934).

It will be seen that, on the basis of calculated stock in 1929 and observed extent of fishing-effort thereafter, the catch-per-unit-of-effort since 1930 should have risen only slightly from its dead low level in 1930. The actual course of events has been a rapid rise to a level greater than any since 1917.

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weight of 33 lb., according to Thompson and Herrington, 1930: 75, fig. 22; or an age of eighteen years according to Thompson and Bell, 1934: 48, table 15). The same catches, although believed to include a larger proportion of small fish than in the commercial catch (*ibid.:* 36), contained only 44 per cent by number of halibut less than 80 cm. in length (equivalent to a weight of about 11 lb., or an age of about eleven years). In contrast, the proportion of halibut of eleven years or younger in expected landings calculated for the 1920's would be more than 70 per cent.

Further objections to the method of calculation are discussed by Ricker (1944: 39–40); and it is of course the present contention that the rates of increment of young, of growth and of natural mortality have varied significantly from time to time. What has been attempted here is simply an extension of the series constructed by Thompson and Bell, without change in procedure, for the purpose of showing its failure to maintain a correspondence with events.

The laborious calculations involved in obtaining a final term for every year have been omitted, since it has been thought unnecessary to define more points in Fig. 5 than are required to establish the lack of correspondence between the trends of the observed and the calculated values.

POSSIBILITY THAT CHANGES IN ABUNDANCE OF WESTERN HALIBUT HAVE BEEN CHIEFLY DUE TO NATURAL FLUCTUATION

Changes in Rate of Recruitment of the Stock. The rate of natural mortality among the commercially available population on the western grounds in 1927 is suggested by table 18 of Thompson and Herrington (1930: 90) to have been somewhere around 20 per cent. The decline in estimated population between 1915 and 1918 is almost exactly what might be expected from a natural mortality of 20 per cent[18] in addition to the fishing mortality, *if there had been no additions whatsoever either by entrance of succeeding year-classes or by growth of those already commercially available.* The decline, if not caused wholly by a contemporaneous disastrous change in rates of natural mortality and growth, might, therefore, obviously have been in part at least a result of temporary reproductive failure more than ten years before, long antecedent to the commencement of commercial fishing. It has already been pointed out (p. 92) that the simultaneous appearance in 1919–1923 of a rise both in catch-per-unit-of-effort and in percentage of small fish suggests the appearance in the fishery at that time of year-classes considerably larger than those which preceded them.

[18] It is of course possible, and might even be expected on *a priori* grounds, that rate of natural mortality would have been higher than in 1927 at an earlier time when the western population was denser, of greater average age, and not subjected to an appreciable fishing mortality. However, natural mortality among the greatly reduced population on the southern banks around 1926 is estimated at the astonishingly high rate of 36 per cent (Thompson and Herrington, 1930: 106); and it will be seen that if the rate had been much higher there in the 19th century before the population was heavily fished, it would have been at an almost incredible level for adults of a slow-growing predator believed frequently to attain an age as great as fifty years. The extinguishing effects of a combination of rates of natural mortality and growth, such as are indicated by Thompson and his co-workers (21% growth and 36% natural mortality on the southern grounds; about 16% growth and around 20% natural mortality on the western grounds), have already been commented upon by Graham (1935: 210); and it is obvious that such a combination could not be maintained indefinitely by a population, unless its normal condition, even in the absence of fishing, were that of low incidence of old fish.

It should be noted that, although Thompson and Herrington do not attempt to define precisely the rate of natural mortality on the western banks, since the experiments "are as yet too few to justify extensive analysis," they do explicitly state that "The decline [in rate of tag-returns with time since tagging] is not as rapid as in the southern experiments" (Thompson and Herrington, 1930: 107).

As has already been noted, Thompson and Bell (1934: 34–48) have shown that (at a selected constant annual increment of young fish and at rates of natural mortality and growth like those observed) the observed changes in amounts of fishing are such as to cause a decline in calculated catch-per-unit-of-effort somewhat like that actually observed in the western fishery from 1920 to 1929. If the significance of this correspondence is accepted, it follows that, since the brood-stock had begun to decline long before, Thompson and Bell's constant annual increment of young must represent an increasing increment per unit of brood-stock. Such an improvement in rate of replacement per unit of spawning population might be the corollary of a reduction in population (whether fishery-induced or not), as has been discussed by Babcock, *et al.* (1931: 24). However, the indicated improvement might equally well have been the result of changes in natural factors entirely independent of man and halibut, in, for example, temperature, currents, abundance of other organisms, etc.

It is well known that great periodic fluctuations in the abundance of various marine animals do occur, which appear to be entirely independent of human activities (*cf.* Kemp, 1938), and which it may in some cases even be possible to predict empirically, long in advance (see Ottestad, 1942; and the demonstration of a regular 14-year cycle in the starfish by Burkenroad, 1946b). Therefore the possibility ought not to be ignored that the improvement during the 1920's in rate of recruitment of the Pacific halibut, which is suggested by the computations of Thompson and Bell, might have corresponded to a change of phase in a system of periodic natural fluctuations. A phase of rising trend in rate of recruitment of population, of sufficient duration, would ultimately result in an increase in abundance even if fishing were legally unrestricted (unless the demand for halibut is unlimited, which is improbable).

Possible Causes of Change in Rate of Recruitment. In seeking an explanation, other than immediate changes in the extent of fishing, for the early great decline and for the recent much-more-than-expected rise in abundance of halibut, the question of adequacy of the brood-stock comes immediately to mind. However, since halibut of the western stock do not appear to enter the fishery to any great extent before their ninth or tenth year, it will be seen that the brood-stock corresponding to the year-classes entering the fishery in the late 1930's and the 1940's was the greatly reduced one of the late 1920's and early

1930's. Therefore, the potential of egg-production should evidently have been much less favorable to the recruitment of the recent population than it was to the rapidly declining population of the 1920's (assuming a constant relation of gonad to roe-fish; but compare Moore, 1937: 712–714, on variation in development of gonad in sea-urchins).

Explanation might also be sought in a more rapid rate of growth or a lessened rate of natural mortality among fish of commercial size, resulting from a lower level of the contemporary population. However, such an explanation is difficult to invoke in the present case, because the declining and the increasing populations have been of similar magnitudes (see Fig. 3, Table V).

Finally, an explanation of the increase in population during the late 1930's, compatible with the decline in the middle 1920's, might be supplied by the hypothesis that the chief influence upon the magnitude of year-classes entering the halibut fishery is competition offered by the adult population during the time the brood was growing.[19] A broader expression of this sort of density-dependence would be that the relations of the halibut, not only to its own young but to its prey,

[19] Compare Huntsman's remarks (1938) on cyclical fluctuation of sockeye and Atlantic American salmon. Fry (1939) and Herrington (1941, 1944) also regard the interaction of adults with young as a primary influence upon rate of recruitment in the cases dealt with by them (a possibility dealt with for vertebrates in general by Errington, 1946); but both further invoke an inadequacy of brood-stock resultant from over-fishing, a view repudiated by Huntsman (1944b: 535).

Herrington (1941, 1944) interprets the temporary occurrence of reduced crops of New England scrod haddock at intervals during the period 1913–1930 as a result of critical competition between young and adults for food during peaks in adult population. However, he explains the apparently contradictory evidence offered by the uniformly mediocre crops of scrod in 1930–1941 (when the adult population remained steadily at a minimal level) as a result of insufficiency of spawners.

Caution seems to be required in interpreting available data concerning a critical lower level of brood-stock for successful production of American haddock, since the year-classes entering the haddock fishery in the North Sea seem to have fluctuated as greatly after the fishery had reached a very high intensity (Bowman, 1932) as have the year-classes entering the New England fishery at all adult abundances. Indeed, comments in recent Reports of the Director of the U. S. Fish and Wildlife Service suggest that later events in the haddock fishery may not have corresponded to expectation from the hypothesis of inadequate brood-stock (1944: 243: "The haddock population . . . is more abundant [in 1942–1943] than at any time in the past ten years because of the reduction in the number of large trawlers. The larger spawning population which will result should ensure good catches in the next several years." 1946: 194: "Preliminary analysis of abundance indices, size and age data show that the 1941, 1942, 1943 year-classes on Georges Bank were relative failures").

its parasites, its competitors and its predators, might be like those in a Lotka-Volterra periodic cycle or a Gause relaxation-oscillation (*vide* Bodenheimer, 1938: 81–112). Thus, a reduction in the population of halibut, whether caused by fishing or not, might have resulted in a lagging, subsequent increase in the populations of its prey, or a reduction in the populations of its predators, or a diminution in the transmission of its diseases (*cf*. p. 98) such as to have placed the stock of halibut fished in the late 1930's in more favorable circumstances than the one fished in the mid-1920's. If this were the case, it should be noted that the increase in population during the 1930's would be a consequence rather of the preceding decline in population than of the subsequent restrictions upon fishing.

Since the immediate effects of fishing seem not to provide an adequate explanation of the observed occurrences, a description of the early tremendous decline and the recent more-than-expected improvement in the western stock of halibut in simple terms of *change in natural conditions, independent of and overshadowing the immediate effects of fishing,* cannot be avoided. No evidence concerning possible delayed-action effects of change in population upon the halibut and its biotic environment is available. Therefore it is difficult to assess the part which fishing may have played in causing the prescribed changes in natural conditions. However, inasmuch as the early decline seems likely to have been a result of influences exerted before fishing began, we may suspect that the major later role was played by natural biotic adjustments and readjustments, either purely internal to the ecosystem or precipitated by external physico-chemical changes.

The remarks of Atwood (in Baird, 1873: 119, 226) suggest that during the first half of the 19th century haddock may have been much less abundant in New England waters than it had become by 1870. "When I first engaged in the fisheries [1816], haddock was scarce on our coast, and in winter sold much higher than cod. They did not increase for many years after." About 1858, "I proved before the legislature that haddock was much more abundant than it had been at any previous time, . . ." Since then, "this species has been increasing from year to year, until they have increased in vast numbers, so much so that they are too plenty for the fisherman or dealer . . ." If Atwood, an intelligent, experienced and reputable man, is correct, a long-term natural decline in abundance of haddock during the present century ought not to be surprising.

It should be noted that, if the poor crops of scrod in 1930–1943 cannot be unequivocally attributed to reduction of brood-stock below a critical level, the part of Herrington's hypothesis which concerns competition between adults and young is rendered dubious also, however reasonable it seems.

Possible Regularity in Pattern of Fluctuation. Some unsupported speculations concerning the future of the stock of halibut on the western banks may perhaps be tolerated, if their nature is thus plainly labelled. Reference has already been made to the remarkable symmetry of the apparent changes in population of halibut between 1917 and 1944 (p. 102 and Fig. 1). This symmetry suggests the possibility that fluctuations in abundance of halibut might be of a regularly periodic nature.

After 1915, the trend of the population curve is very sharply downward. Before 1915 data are inadequate or lacking, but there is some weak suggestion that the high level in 1915 may possibly have represented the near edge of a peak rather than of a steady plateau. Thus, Thompson, Dunlop and Bell (1931: 57, fig. 17, table 12) summarize extensive records showing a catch-per-unit-of-effort in Areas 19–23 during 1914 only two-thirds of that in 1915 (and they believe the low value for 1914 to be reliable, although they suggest that the subsequent rise is "due to a better knowledge of the grounds," which were not intensively explored until 1913). Reports concerning exploration of the western grounds by the "Albatross" and otherwise, between 1888 and 1900, although difficult to interpret and of very dubious value, may possibly indicate a relatively low level of abundance in these waters during these years (*cf.* Thompson and Freeman, 1930: 20, 28–29).[20]

If abundance in 1915 represented a peak attained only within a few years of that date, and if the changes in the stock are of a regularly cyclical sort, it would be expected that during the next few years after

[20] In view of the difficulty of obtaining evidence concerning abundance of halibut prior to the commencement of intensive fishing, ethnological enquiry for possible traditions of recurrent scarcity of halibut among aborigines of the Northwest, combined with research into the question of whether or not availability of halibut to fisheries of aboriginal type provides a useful index to general abundance, might yield results of some relative worth.

I am deeply indebted to Dr. Clellan S. Ford of the Department of Anthropology, Yale University, for the following comment (1946, *in litt.*):

"From Boas' material on the Kwakiutl of Vancouver Island, it appears that these people surround halibut fishing with a considerable number of taboos and restrictions. This is particularly interesting in view of the relative insignificance of halibut fishing as compared to salmon fishing which is so important as a source of food for the Kwakiutl. Although taboos surround salmon fishing as well, the evidence suggests that past experience has taught the Indians that halibut fishing is less certain than salmon fishing. This uncertainty does not seem to arise from inferior fishing methods

1944 the population of the western grounds might rise rapidly, perhaps even to a level double that of 1943 (when the International Fisheries Commission believed [British Columbia, Rep. Prov. Fish. Dept. for 1943, 1944: 29] that the yield from the western area "is approaching the maximum that the grounds can produce"). At some subsequent time within the next half decade or so, according to conditions assumed at the beginning of this paragraph, abundance might be expected to begin to drop precipitously despite whatever restriction of the fishery.

It would be extremely surprising if the halibut of the western banks were to prove subject to regular cyclical fluctuation of period around thirty-four years, such as has been considered in the preceding paragraph; and it may be emphasized that the indications from which this possibility is suggested are worthless as evidence. However, it seems proper to say that the events of the next half decade deserve close observation and that it would be unfortunate if an increase in fishing, sufficient to obscure the issue, were permitted to occur before the critical period has passed.[21]

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for there is ample evidence to indicate that when halibut are available the Indians catch plenty of them. It seems most likely that their worry . . . stems from a fear that the halibut will disappear. This suggestion is further corroborated by the following quotation: 'The stomach of the first halibut caught in the season is eaten first, next the pectoral fins, then the head. The rest is divided among the people. If this is not done, the halibut would disappear.' (Boas, Franz: *Current Beliefs of the Kwakiutl Indians, Journal of American Folklore,* Vol. XLV, 1932, p. 237.)"

[21] I am greatly obliged to Mr. H. A. Dunlop of the International Fisheries Commission for the following account (*in litt.;* January 16, 1947) of the fishery west of Cape Spencer since 1944:

"Landings from Area 3 in 1945 and 1946 amounted to 28,700,000 and about 30,600,000 pounds respectively. The increase in the latter year resulted from an unexpected increase in the intensity of fishing in the period between announcement of the date of closure and actual closure of the area. It was not intentional.

"The catch per skate in the two areas declined to about 132 pounds in 1945 and to 125 pounds in 1946. Judgment of the significance of this decline must be withheld because of our inability to secure data regarding the changes in the size composition of the Area 3 stock during the war years."

For comparison with Table V, the above values indicate, for 1945 and 1946 respectively, fishing efforts of 217 and 245 thousand skates, landings of 6.4 and 7.2 per cent of estimated population, estimated populations of 449 and 426 million pounds, and total increments of −7 and +2 per cent of estimated population.

The negative value for increment in 1945, the first since 1925, might conceivably be a symptom of the approach of a change in phase of cycle.

NATURAL FLUCTUATIONS IN THE ABUNDANCE OF HALIBUT, IN RELATION TO HUMAN ACTIVITIES

The question proposed in the introduction to the present paper (whether or not any important part of the changes in abundance of Pacific halibut were greater than might reasonably be expected to have been caused by the changes in the fishery) must, according to the foregoing analysis, be answered in the affirmative. It can no longer be assumed, therefore, that the recent annual catch of halibut, as a result of the regulation begun by international agreement in 1932, is "perhaps 20 million pounds greater than the fishery would be taking now had unrestricted fishing continued" (U. S., Senate, 1945: 22). Instead, the evidence suggests that, for the western banks at least, the major portion both of the decline and the increase in abundance may have been independent of the fishery and might have occurred even in its absence or in the absence of other than economic restrictions upon it.

The coincidence in time between regulation of the halibut fishery and the appearance of a rising trend in abundance (which has apparently been taken by some as evidence that the rise was caused by the regulation) is not necessarily a wholly fortuitous one; but the causal sequence might be from change in abundance to regulation instead of the reverse. This results from the fact that the development of a conspicuous scarcity (which is the usual stimulus to measures intended, in the old phrase, "to preserve the stock of fish") is also followed naturally by the development of the next maximum, in periodically varying populations.

The conclusions reached by Thompson and his co-workers with regard to the primary importance of fishing as the cause of changes in abundance of halibut on the western grounds may well be valid for a limited period in the 1920's (a period which begins after two-thirds of the decline in abundance had been accomplished and ends before the renewal of abundance had begun). The societal influences under which fishery biology has been conducted would favor such limited and special conclusions, in that the time of occurrence of that particular phase of a cycle of periodic natural fluctuation, when a fishery of given magnitude would most conspicuously affect the level of abundance, would also be the time most propitious for the inception and support of biological studies of the species. It therefore seems possible that the available data of fishery biology on the whole provide a distorted picture of the relation of fishing to the marine stocks. Correctives might be supplied by the general adoption of adequate programs of continuous collection and publication of data, available like hydrographic data for analysis by workers not involved in maintenance of a particular project; coupled with acceptance and explanation by biologists themselves of the fact that, as yet, fishery regulation is primarily a tool for experimental research rather than a vehicle for expression of proven findings. A means of approach to these correctives might be through professional insistance that biological support for regulation of a marine fishery be dependent, in the state of our knowledge as it is likely to exist in the near future, on provision for adequate and disinterested observation of the results.

Discovery that the major fluctuations of a given stock of fish are not within human control might be thought to indicate that further study of the species would not produce practical benefits. Such is not the case. The ability to predict changes in abundance at sufficiently long range would often be of economic value to the fishing industry almost as great as would be the ability to control the changes; and it may be ventured that the goal most likely to result in enhancement of the practical importance of marine fishery biology is that of development of reliable means of long range forecasting. The scale and complexity of the problems encountered in attempting to control the gigantic self-compensating operations of a marine ecosystem, hinted at by Burkenroad (1946: 55–56), have not perhaps been fully appreciated by those who think in terms of regulation rather than prediction.

The studies of the history of abundance of Atlantic fishery stocks, undertaken by the Survey of Marine Fisheries of North Carolina and the Chesapeake Bay Fisheries Commission, suggest that to achieve reliable forecasting, investigations concerned with individual species may sometimes be insufficient. In certain species, early observation of year-class success may yet prove adequate for short-range forecasting of commercial abundance; in others regularity in pattern of fluctuation may be found, such as to permit long-range empirical prediction; in still others, forecasts of long or short range may be made possible by discovery of correlations between abundance of the given stock and physico-chemical variables (as recently and brilliantly disclosed for the as yet unpredictable hydrographic factors governing the broods of pilchard, by Walford [1946]). But in addition to such cases, it is likely that an important residue of unstable species exists, for which purely biological interactions are so important that successful forecasting will require the integration of knowledge of the state of numerous other stocks. And in all cases, there must be remembered not only the relatively accessible fluctuations but those of longer term which (as perhaps in halibut) spread over human generations and seem sometimes to outweigh the ones of briefer period and immediate concern.

No adequate program for collection of general statistics of current abundance exists, and if one were to be established, a long time must elapse before the clues required for prediction could often be obtained from its results. Our surveys have shown that a wealth of neglected and perishable information can still be unearthed, from which by appropriate unconventional methods the changes in abundance of numerous marine forms during the last century may be approximated. Past neglect to gather, preserve and analyze this material is in part attributable to lack of imagination in those responsible for the formulation of long-range programs; but in part also to the predominance in American fishery biology (ever since the initial unfortunate reference of a scarcity of scup to the increasing use of pound-nets, by the nascent Fish Commission) of the view that a knowledge of fishing pressure is the chief requisite for prediction of changes in abundance. In emphasizing, in the present paper, that the effects of fishing may be more limited than has been generally conceived, it seems proper to urge at the same time that an immediately necessary task of fishery biology is the attempt to reconstruct all possible details of historical change within our marine ecosystems.

An expansion of knowledge of past abundances, such as our surveys during the past two years have shown to be feasible at relatively small cost, would facilitate present search for the simpler predictable changes, and would thereby help to stimulate the required development of an adequate general program for collection of current data. Beyond this accessory function, history supplies at least a guide to long-term possibilities (such as the not improbable future decline or southward shift of the croaker fishery, and expansion of the northern supply of menhaden). Still further, by this means might be confirmed at a relatively early date the existence, if not the nature, of complex internal rearrangements of the marine organism-systems as living wholes; such as are not detectable through investigation directed, in the usual manner, one by one to single forms.

SUMMARY AND CONCLUSIONS

1. The self-contained stock of Pacific halibut on banks west of Cape Spencer appears to have declined in magnitude between 1915 and 1918 by an amount more than six times as great as the quantity removed by the fishery during this period.

2. Analysis of the data bearing on this apparent discrepancy between sum of catches and decline in population tends to confirm its reality, unless the efficiency of a unit of fishing-effort (which may be measured by the ratio of effort to per cent of fishing mortality, and is equal to ratio of average population to catch-per-unit-of-effort) changed greatly between 1915 and 1927. Efficiency on the southern grounds in 1927 appears to have been nearly three times that on the western grounds at about the same time; and possible causes of such a difference, which might operate in time as well as geographically, are pointed out. However, if it were to be assumed that efficiency on the western grounds changed sufficiently from period to period to annul the apparent discrepancy between magnitude of catch and decline in population in 1915–1918, evidence supposedly indicating serious depletion of the stock would likewise be invalidated.

3. The discrepancy between magnitude of catch and decline in population in 1915–1918, if accepted as real, seems to demonstrate that the principal part of the historical reduction in abundance of halibut on the western banks was a result of natural fluctuation, independent of the fishery. Further, the temporary rise in abundance from 1919 to 1923 appears more likely to have resulted from entry into the fishery of year-classes greater in magnitude than those preceding them rather than (as has been believed) from improved utilization through temporary reduction of the fishing effort.

4. The rise in abundance since 1930 appears to be greater than can be accounted for by the diminution in fishing-effort, by an increase in the antecedent brood-stock, or by reference to an improvement in rate of natural mortality or growth proportional to immediate differences in magnitude of population. The likelihood of lagging effects of changes in antecedent population levels resulting from other mechanisms than change in egg-production or in competition between adults and young, is remarked.

5. There exists a bare possibility, concerning which critical evidence should be provided by events of the next half decade, that fluctuation

in the population of halibut on the western banks might be of a regularly cyclical sort with a period of around thirty-four years.

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DISCUSSION

Van Oosten: This paper is now open for discussion.

Herrington: I think you are correct in concluding that the increase in the stock, shown by catch-per-skate, cannot all be accounted for by the regulations. Calculations for the southern area, based on catch, fishing intensity, and catch-per-skate, suggest that there was an increase in recruitment to the stock from younger fish. However, the regulations did contribute a considerable part of the increase, and this should be acknowledged.

Burkenroad: The rise in catch-per-unit-of-effort, which should have been expected by 1944 from the decrease in fishing on the western banks brought about by the regulation, was to 120 per cent of 1930; however, the actual rise was to 230 per cent. The discrepancy is so great that I see no reason to postulate that the regulations had any detectable effect. Furthermore, if the decline in magnitude of the stock before

1930 was far beyond what the fishery could produce, why should regulation of the fishery produce an increase of any significance?

Herrington: In estimating the absolute magnitude of the stock, have you taken natural mortality into consideration?

Burkenroad: If you have 1,000 tagged fish and 10 per cent are caught, and if 10 million pounds are landed that year, then presumably there were 100 million pounds on the grounds. You don't have to deal with natural mortality; it cancels out.

Herrington: If you had 1,000 fish and you got 100 back and 50 tags fell off, then the mortality would be heavier than that, wouldn't it?

Burkenroad: Well, since you reported the tag returns on the western banks for only two years, it is difficult to make sure of the fishing rate, as Dr. Ricker has pointed out to me. But on breaking down your tag-returns into half-years, on the assumption that the fishing was equally distributed during those half-years, I get a logarithmic curve suggesting the 10 per cent rate to have been real, thus confirming your conclusion published in 1930.

Herrington: That would have to be demonstrated.

Burkenroad: You yourself named that 10 per cent fishing rate. If you and Thompson are going to use that in coming to the conclusion that the fishery has been responsible for the decrease in abundance, then it is legitimate for me to use it in an analysis of your conclusions. Look at the curves in Thompson and Bell. You know their correlation between the theoretical effect of fishing and the observed changes. That is based on a 12 per cent rate. The difference would not affect my results concerning discrepancy between shrinkage of population and landings, since I could use 20 per cent and still come to the same conclusions.

Herrington: Whether or not somebody else uses it in making an estimate doesn't justify you in using it if you don't think it is correct.

Burkenroad: You must understand that I do think it is correct. We have stuck our necks out, on the assumption that the data are actually correct, by suggesting that a regular natural cycle may be the explanation of the changes in abundance. The next few years of fishing ought to test that. If there is a regular cycle in halibut such as has been found for the starfish, it is not inconceivable that the abundance of halibut will fall greatly during the next few years. However, the purpose of our North Carolina group is not to settle the Pacific halibut problem. What we are primarily interested in doing is showing that the evidence doesn't have to be interpreted in the fashion in which Thompson has interpreted it. In other words, we want to be in a position to be able to say whether or not the effects of natural fluctuation should be considered more seriously by fishery biologists, and whether or not Thompson's very influential opinions to the contrary are based on conclusive evidence.

Herrington: I think you would get more interesting results in the southern area, south of Cape Spencer.

Burkenroad: I think you showed that there are a number of regions involved in the southern fishery, between which there may be little exchange of stocks. This makes analysis impossible.

Herrington: It would be a better example because the depletion has gone much farther.

Burkenroad: I don't know. I think that the reported western drop in catch-per-unit to one quarter of the early level is quite sufficient. That would be a high degree of depletion, and was so claimed. This chart [indicating] shows here the corrected catch-per-unit at the beginning of the fishery on the western banks and this down here [indicating] is the level in 1930. That is a colossal drop, and I think it provides an ample change to work with. The southern data are much less complete, and we don't know whether the total quantity of fish was ever as great on the southern banks as it is stated to have been on the western banks at the beginning of the western fishery.

Herrington: The principal question is whether fishing caused the decrease. It could be figured just as well for the southern area.

Burkenroad: No, it can't be. Because if there are several southern stocks and they are not migrating over the whole southern area—that is, if you have a number of static stocks on the southern grounds—and if you cannot tell from the available data how landings and population varied from stock to stock, you are in no position to calculate the relation of fishing pressure to abundance.

Herrington: I think you will find that in an area like that, if in any part of that area fish are much more abundant, fishermen soon find it. As a result, on the average an area is fished down pretty much together. You don't find big differences from one spot to another.

Burkenroad: I have indeed suggested to Dr. Ricker that this more difficult southern problem is better adapted to his mathematical capacities which are very much higher than mine. But I still don't see why it is necessary for present purposes to treat both halves of the fishery. Frankly, I feel both that the analysis of the simpler western situation has strained me to my uttermost limit, and that it is sufficient for our North Carolina needs to show that Thompson's conclusions concerning the western fishery are not in accord with the evidence from that area.

Needler: As I understand this, you have two arguments criticizing the soundness of the existing conclusions concerning the fishery west of Cape Spencer by Thompson, *et al.* The first one is that the catch-per-unit-of-effort—if it is an indication of change in amount of fish—changed so much, fell off so much, that it would indicate reduction in the abundance of halibut several times greater than in the actual catch . . . . .

Burkenroad: Seven times greater than the actual catch.

Needler: The other argument is that the restriction saved a certain amount of halibut, but that calculating on the number of halibut which it saved and their growth with an assumed mortality of 10 or 12 or 20 per cent, you still don't produce enough more halibut in the sea to account for the increase.

Burkenroad: That is a very acceptable summary.

Needler: I don't know any of the detailed data, but if those two propositions are sound it would certainly indicate that there are a number of other factors which are just as important as the fisherman.

Kolbe: Are you prepared to suggest what the other factors are?

Burkenroad: I don't think anyone here is yet prepared to offer an explanation of changes in abundance of marine fishes backed by sound evidence.

Needler: I think, Mr. Chairman, we are up against the same thing in assessing the value of lobster rearing in the State of Maine. We are presenting the same kind of argument to show that the lobster rearing is not responsible for the increase. From the records of the number of fourth-stage larvae planted, we find that even if all of them survived to marketable size they would only account for five per cent of the increase. So we concluded that the lobster rearing stations did not produce the increase. This is the same type of argument. It only applies to the validity of the assumption that the lobster rearing stations produced the increase. It doesn't, of course, explain how the increase came about. We can imagine about ten different factors that might have caused it.

Burkenroad: I am prepared to discuss the possibility which has appealed to me most. I am not, however, able to offer any evidence for it. If a 34-year cycle in abundance of halibut, such as I am suggesting to be a possibility, should prove to be the case, it might be argued that the explanation of the cycle toward which I am inclined may have validity. That is not, however, a good argument. It is in fact the sort of argument I deprecate when applied to increases in abundance of fish following regulation. Mere coincidence between a prediction and a result is not necessarily evidence that the prediction was based on sound conceptions.

For example, it appears to me that one should expect to find an increase in fish when regulation has been applied, even though fishing has no effect on the stock. Fish populations, as Professor Dymond pointed out, all appear to fluctuate naturally. When a naturally fluctuating population reaches a dead low, it may be expected to increase in abundance thereafter. When a scarcity occurs, it is a stimulus to study of the fishery, and regulation of it. Consequently, one should expect to find regulations applied at low points in natural periodicities. Therefore, one would as a general rule find increases in abundance following regulation, even if fishing had nothing to do with the scarcity. An increase in abundance is thus not by itself critical evidence for a causal connection between the regulation and the increase.

The view of the causes of fluctuation in abundance of sea animals to which I tend is that we are dealing with extremely complicated interdependences of organisms. Quite apart from precipitating causes of a physicochemical nature, change in any one living part of an ecosystem will, by means which have been mathematically expressed by Volterra and others, result in subsequent changes in other populations of the system, and so on. I believe that in many fisheries it will ultimately be found that fairly regular cycles of abundance are being caused by the pendulum-swing of changes purely internal to the living part of the ecosystem, independent of such external affects as fishing, radiation, precipitation, temperature, and so on.

Huntsman: It seems to me that the importance of this lies in the fact that the halibut is the best case to show the possible value of letting the fish get bigger. I don't know of any better case. I had accepted the experiment on the Pacific coast as proved insofar as it pays to let the fish get bigger, but not as proving that it paid to have larger numbers of spawners. Therefore, I was somewhat surprised to find that this—to me a supposedly proved case—did not stand up. It seems to be similar to the case of the Atlantic salmon with which I am familiar—and here again I had accepted the claims made for beneficial regulation of a fishery, namely, of the Restigouche salmon fishery in northern New Brunswick and southern Quebec. Those responsible for the angling took a variety of measures to increase the stock; over quite a long period of years they seemed to get definite evidence of an increase as shown by an increase in angling catch and also in an increase in net catch; with the latter they were not concerned other than in a negative fashion. After perhaps twenty years the catch went down and they started to blame the net fisheries. They wouldn't give up their original conception. But when you examine the facts, it appears that the rise was coincidental with rises in other rivers that hadn't been subjected to the same management, and that the fall also occurred in other rivers that had not been subjected to the same management. Thus an apparently good correlation of increase in stock with certain management has not been borne out by other facts.

Burkenroad: I am perhaps prejudiced in favor of the view that natural fluctuation may be the cause of most of the changes in our fisheries, because this proved to be the case in my first effort in the field of population study. There appears to be an entirely regular natural cycle in starfish, which are a pest of oysters in Long Island Sound. This cycle cannot be related to any changes in fishing effort. An interesting case of supposed "overfishing" of starfish occurred in the 19th century. In 1884, which was just before a peak in this 14-year cycle, a piece of gear called the mop dredge was invented. It was and still is a very effective method of differentially clearing starfish from the oyster beds, an operation which had previously involved the labor of picking up both starfish and oysters and throwing back only the oysters. The oyster growers mopped assiduously, and the abundance of starfish declined year after year. The official reports during the next seven years, were that the oyster grower, using the means placed at his disposal by modern science, was now able to control this once-feared pest. About this time the low point in the cycle was passed—and no more was heard of scientific management of the abundance of starfish until after this 19th century experience had been forgotten.

Herrington: I wonder if Dr. Huntsman has correctly interpreted your conclusions or what you mean to conclude. Do you think your evidence shows there has been no benefit from the regulations, or merely that they have not accounted for all of the increase?

Burkenroad: Using Thompson's method of calculation, the expected increase as a result of the regulation would have been to 120 per cent of 1930, whereas it was actually to 230 per cent. I think that permits us to say that the regulations were of no demonstrable significance according to Thompson's own method of calculation, since 20 per cent is too small to be regarded as significant.

Huntsman: My point is that it isn't proven. So I have lost faith. I don't say there hasn't been improvement as a result of that control in both cases, but it isn't proven.

Herrington: You are not arguing there was no benefit?

Burkenroad: No proof of biological benefit. The evidence suggests that catch-per-unit-of-effort might have risen to about the same extent in the absence of any legal restrictions. There may have been a benefit to fishermen in that, by agreed limitation of production, prices could be made higher relative to the supply in the water. Such benefit would, however, be counterbalanced by injury to the consumer, and its significance is a matter for economists, sociologists and political philosophers, not biologists.

Herrington: Another question. The length of the fishing season in the area south of Cape Spencer has decreased greatly. In 1930 it was eight months and fifteen days; in 1945, one month and fifteen days. If they simply compare the average for the season, then catching halibut through that short season probably would give a higher catch-per-skate than over a period of eight months. They probably have allowed for that. If not, the increase in catch-per-skate would not indicate a comparable increase in population.

Burkenroad: I think their only correction was for the competition of gear, using the compound interest equation. I don't think that in getting a standard skate they have dealt with possible effects of a shortened season, which are somewhat uncertain.

Ricker: Just so there won't be any misconception, I might say that I became aware of Mr. Burkenroad's interest in the halibut fishery only *after* he had developed the thesis he has presented here. I was asked for comments, and the points I raised were mostly potentially unfavorable to his views, although quantitatively none of them need be of importance, and Mr. Burkenroad evidently believes they are not so. One of these comments concerned the estimated 10 per cent rate of exploitation for the western halibut population in 1927. In the light of some computations I had made on the southern halibut population, I felt that this estimate *might* be considerably too low. However, I believe this would not affect his main argument substantially, one way or the other. Mr. Burkenroad, did you also estimate the effects of possible error in this rate of exploitation, as it affects the later history of the fishery from, let us say, 1930 onward? If the stock in 1927 were really only a half or a third as great as you compute from the published estimate of rate of exploitation, how would that affect your assessment of the recent period of increasing abundance?

Burkenroad: One of my indications of an increase greater than expected is by continuing for later years Thompson and Bell's method of comparing actual with theoretical changes in catch-per-unit. This method of assessment does not depend on the accuracy of the estimate of the 1926–27 rate of exploitation, since my point is that coincidence of actual and calculated abundances cannot be obtained for periods both before and after 1930 at the same constants.

Another method of assessment not dependent on estimates of absolute population, consists in comparing the total landings during paired periods before and after 1930 when catch-per-unit was similar. The only one of my assessments completely dependent on estimates of rate of exploitation is that concerning effects of fishing in early years.

Clarke: In your calculations of total population, did you assume that the catch-per-unit-of-gear was proportional to the size of the population?

Burkenroad: The catch-per-unit-of-effort was used, not per-unit-of-gear. I am not at all sure that the rectilinear relation of catch-per-unit and population is a sound assumption. However, if this assumption is questioned, it bears equally against Thompson's conclusions. In other words, if catch-per-unit is not a rectilinear index of population, then you can't use it as a rectilinear index of depletion.

Clarke: Thompson doesn't find it necessary to make any assumption concerning the actual abundance of fish in order to prove depletion. All he needs to know is that the fisherman can't catch them.

Burkenroad: But if catch-per-unit is not proportionate to population, you have no grounds for talking about depletion until you find out what the relationship is. If the fish were there in much the same quantity, and a decline in catch-per-unit simply meant the fishermen couldn't catch them, then regulations intended to let the little ones grow big and to increase the brood stock would hardly be called for.

5. STUDIES ON THE MARINE RESOURCES OF SOUTHERN NEW ENGLAND

VII. ANALYSIS OF A FISH POPULATION

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ABSTRACT

This study of the species taken in the winter flounder trawl fishery off Rhode Island and Connecticut is based on monthly representative samples of the catch from August 1943 to July 1946. It is an analysis of the population as a whole, with particular reference to its seasonal and annual organization and the relationships of its components. The history of the fishery and its present status are outlined. Of the total catch by weight during the three-year period, it is estimated that 55 per cent was actually marketed and 45 per cent discarded as trash. The adequacy of this method of sampling the population, the relative and seasonal abundance of the different species, and the evidence for interspecific relationships (particularly between the two dominant elements of the catch, winter flounder and skate) are discussed in some detail. The study provides a framework upon which more precise information can be constructed, as well as a basis for future comparison, and so affords an approach to the question of overfishing and related problems.

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INTRODUCTION

The fear of overexploitation of marine resources is as old as the hills. It is the *raison d'être* of the fishery biologist. We talk glibly of the conservation, management and rational utilization of stocks of marine fishes, and those outside the field are often led to hold a somewhat exalted opinion of the state of our knowledge and of our ability to cope with the problems at hand. The truth of the matter is that most of the major issues in fishery biology are still highly controversial. For example, there is no unanimity of opinion as to demonstrable instances of overfishing. We know only a modicum about the causes of fluctuations in abundance. The subject of inter- and intraspecific competition in populations of marine fishes is little understood. And a nice question is posed by the fact that dominant year-classes (the exceptionally high survival of the young born in any one year resulting in ultimate benefit to the fishery) sometimes occur when the adult stock is at a comparatively low level. All this may be taken as a sad commentary on our lack of progress in the half century dating from Hoffbauer's discovery of the possibility of determining ages and growth rates by means of scale analysis. Many reasons can be cited. One is that the field has failed to attract its share of well trained investigators. But more pertinent to the subject of this discussion is the extreme difficulty of procuring catch statistics and ecological data which are capable of yielding the necessary information, the inordinate amount of "patient puttering" which is a part of all fisheries research, and the complex problems involved in sampling, in determining and interpreting the catch-per-unit-of-effort, and in population analysis.

The present paper is the result of a three-year study of the species taken in the winter flounder trawl fishery off Rhode Island and Connecticut (Fig. 1). It is based on monthly samples of the catch from August 1943 to July 1946. The more obvious facts about the seasonal and annual composition of the population and its organization are set forth to form a framework upon which more detailed information can be constructed, and also to provide a basis for future comparison. More specifically, the objectives of this investigation were as follows. 1. To discover the proportions of regularly marketed, occasionally marketed, and discarded or "trash" elements in the catch. 2. To provide information for an understanding of the life histories of the species encountered. 3. To study the population as a whole with

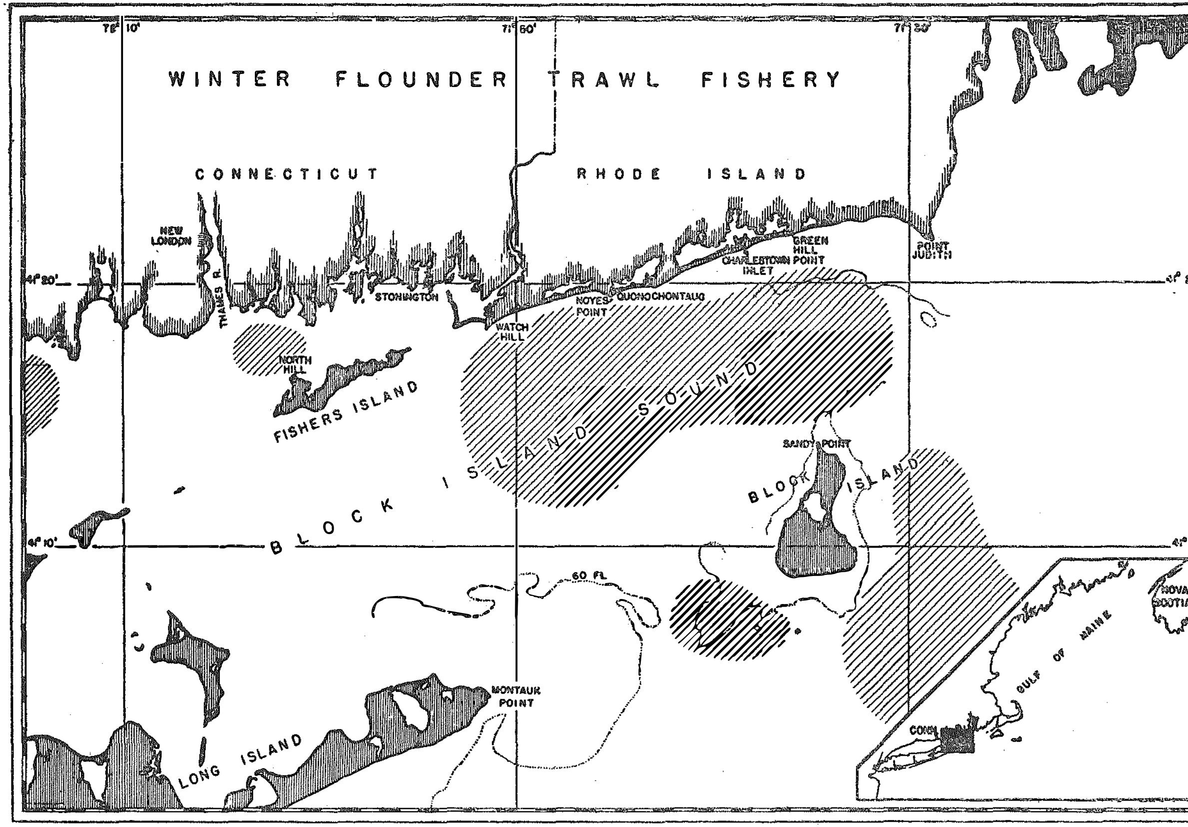

Figure 1. Chart of the southern New England winter flounder trawl fishery. Lined areas are the localities in which most of the effort is concentrated.

particular emphasis on the relationships of its components. The present paper provides information on the first and last of these objectives. With regard to the life-history studies, investigations on the six major species (constituting over 90 per cent of the catch by numbers, p. 157), as well as on three lesser forms, have either been completed for publication or are now in progress.

TABLE I. SCIENTIFIC AND COMMON NAMES OF FISHES TAKEN IN MONTHLY ONE-HOUR HAULS, AND ADDITIONAL SPECIES OBSERVED IN OTHER HAULS ON COLLECTION DATES FROM 1943–1946

From Monthly One-Hour Hauls

1. *Mustelis canis:* smooth dogfish, grayfish.
2. *Squalus acanthias:* spiny dogfish, grayfish, piked dogfish.
3. *Raja erinacea:* little skate, common state, hedgehog skate, summer skate.
4. *Raja diaphanes:* big skate, spotted skate, winter skate.
5. *Raja stabuliforis:* barn-door skate, winter skate.
6. *Clupea harengus:* herring, sardine.
7. *Pomolobus pseudoharengus:* alewife, gaspereau, sawbelly.
8. *Poronotus triacanthus:* butterfish, dollarfish, harvest fish.
9. *Centropristes striatus:* sea bass, black sea bass, blackfish.
10. *Stenotomus chrysops:* scup, porgy.
11. *Menticirrhus saxatilis:* kingfish, king whiting, whiting.
12. *Tautogolabrus adspersus:* cunner, sea perch, bergall, nipper.
13. *Tautoga onitis:* tautog, blackfish.
14. *Stephanolepis hispidus:* common filefish, foolfish, thread filefish.
15. *Spheroides maculatus:* puffer, swellfish, blowfish, globefish.
16. *Myoxocephalus octodecimspinosus:* longhorn sculpin, gray sculpin, hacklehead, toadfish.
17. *Hemitripterus americanus:* sea raven, red sculpin.
18. *Prionotus carolinus:* common sea robin, green-eye.
19. *Prionotus evolans:* red-winged sea robin, striped sea robin.
20. *Macrozoarces americanus:* ocean pout, eelpout, yowler, conger eel, ling.
21. *Merluccius bilinearis:* whiting, silver hake, New England hake.
22. *Gadus morhua:* cod, rock cod.
23. *Melanogrammus aeglifinus:* haddock, white-eye.
24. *Urophycis regius:* spotted hake.
25. *Urophycis tenuis:* white hake, Boston hake, mud hake, ling.
26. *Urophycis chuss:* squirrel hake, snot-head hake.
27. *Paralichthys dentatus:* summer flounder, fluke, plaice, turbot.
28. *Paralichthys oblongus:* four-spotted flounder, Baptist fish.
29. *Limanda ferruginea:* yellowtail, rusty dab, sand dab.
30. *Pseudopleuronectes americanus:* winter flounder, flat, blackback, flounder.
31. *Glyptocephalus cynoglossus:* witch flounder, sole, fluke.
32. *Lophopsetta aquosa:* sand flounder, windowpane, sundial.
33. *Lophius americanus:* goosefish, monkfish, angler, mouth-all-mighty, fishing frog.

From Additional Hauls on Collection Dates

1. *Dasybatus marinus:* sting ray, stingaree, clam cracker. IX-12-'43.
2. *Brevoortia tyrannus:* menhaden, pogy. IX-10-'44.
3. *Scomber scombrus:* common mackerel. VI-23-'44.
4. *Cynoscion regalis:* weakfish, squeteague, sea trout. X-31-'43, XI-19-'44, X-15-'45.
5. *Leiostomus xanthurus:* spot, goody, postcroaker, Lafayette, porgy, yellowtail. XI-19-'44.
6. *Ceratacanthus schoepfii:* orange filefish, foolfish, sunfish. X-26-'44.
7. *Neoliparis atlanticus:* sea snail, lumpsucker, New England sea snail. IV-16-'45.
8. *Liparis liparis:* sea snail, striped sea snail, north Atlantic sea snail. I-14-'46.
9. *Pholis gunnellus:* rock eel, gunnel, butterfish. V-18-'44, III-24-'46.
10. *Pollachius virens:* pollock, Boston bluefish, coalfish, green cod. VI-23-'44.
11. *Microgadus tomcod:* tomcod, frostfish. III-19-'44.

This work represents a co-operative attack on the problem. Tables I, IV, and V[2] show that 44 species, over 37,000 individuals, and 25,000 pounds of fish are involved in the analysis; the magnitude of the undertaking was such that no single investigator could possibly handle all phases of the work. Actually the entire staff of the Bingham Laboratory has had a hand to a lesser or greater extent in the field work, routine laboratory analysis, preparation of the data or other aspects of the investigation. To all of these individuals we express our indebtedness and record our gratitude. It is also a pleasure to make acknowledgement to the Connecticut State Board of Fisheries and Game and to the Woods Hole Oceanographic Institution for financial assistance.

HISTORY OF THE CONNECTICUT TRAWLING INDUSTRY

During the course of this investigation a considerable amount of historical information was gathered from conversations with several of the old-time skippers of eastern Connecticut. Since only part of this material was based on the written record, it was not always possible to obtain absolutely precise data. However, it seems appropriate to record the information here because so little can be found in the general fisheries literature on the subject.

Commercial fishing in Connecticut in the early days of the present century and in preceding decades was carried on by a variety of

[2] The species in Tables I and IV–VI are arranged in order of their appearance in C. M. Breder's "Field Book of Marine Fishes of the Atlantic Coast from Labrador to Texas," G. P. Putnam's Sons, New York, 1929: XXXVII + 332.

methods; among them were the hand line, line trawl, fyke net, pot, purse seine, shore seine and trap net, the last two being relatively more important then than in recent years. As a rule the fishermen of those times did not by any means devote their efforts exclusively to this occupation—they farmed, trapped, ran steamboats, etc., and only fished when circumstances so dictated. But during the first 15 years of the century the demand for fish apparently enjoyed a considerable upswing; individual hand-line fishermen began to make a good living from their efforts, new gear was introduced, and commercial fishing became more and more of a full-time occupation. Proximity to the New York market led some of the larger fishing concerns to establish headquarters in the state, particularly in New London and Noank. Under these circumstances the fishermen of course became alert for any innovation which gave promise of increased productivity. About 1908 Capt. Frank Thompson of New London tried the beam trawl with indifferent success; he was the only fisherman to attempt to handle this rather awkward gear which was apparently not well suited to the small boats then in use. In the same year, however, Capt. Elisha Clark brought the otter trawl from Long Island to Connecticut; he and Capt. Benjamin Chesbro of Stonington appear to have been the first to fish this gear. Its advantages were immediately apparent, and among others who changed to the otter trawl at approximately the same time were the Wilcoxes, Clarks and Capt. Clay of Stonington, Capts. Daboll, Rathbun, Christenson and Fitch of Noank, the MacGregor brothers, and Capts. Clark and Lewis of Mystic, and Capts. Thompson, McLaughlin, Brown and Slade of New London. By 1913 Capt. Thompson was making a full-time business out of otter trawling and several years later a dozen or fifteen other fishermen were similarly engaged. The otter trawls fished by the boats of this time varied considerably; some were as little as 20 feet in width and were lifted by hand. The gear was (and still is for the most part) towed from the mast or boom rather than from gallows frames. The boats in this fishery were not big—often no more than large dories powered with small motors. Some of the boats built in these early days are still in operation and constitute the smaller units of the present fleet. The otter trawl was first used in the winter flounder fishery and the results are said to have been more than gratifying. Old photographs provide some evidence, debatable withal, that the size of the fish averaged considerably larger than those taken today.

About 1916–1917 Capt. Elisha Clark had built the 33-foot "Bessie," Capts. Elmer and George Wilcox the 35-foot "Anna D.," and Capt. Frank Thompson the 36-foot "Eleanor Louise." The latter boat was the largest and most powerful then in operation for the purposes of trawling; she fished a net with a 60-foot mouth and worked out of New London, while the others hailed from Stonington. Other large vessels were Capt. Walter Rathbun's 34-foot "Alden" at Noank and Capt. Asa Clark's "Constance C." from Mystic. The eastern Connecticut catch was probably over a million pounds in 1917; by 1918 another half dozen boats had entered the fishery and the catch was doubled. By 1920 about 35 vessels were engaged in the fishery which yielded several million pounds of winter flounders annually. All of these fish were caught within five miles of shore, and it is of special interest in view of later conclusions in this paper (p. 152) that there were relatively few skates in the catch (an average of not more than a bushel a haul). With reference to changes in relative abundance of different species, Capt. Ellery Thompson has told us that in 1922, after eight years with this fleet, he saw his first haddock; this species provided good inshore fishing for the next ten years, but since the early 1930's the schools have not come onto the grounds to any extent although individual haddock are taken on occasions. In the middle 1920's new boats with added power were built. The engines jumped from a maximum of 40 horsepower to 65 horsepower, with the result that the grounds were fished longer and more intensively, and the competition was such that the boats started moving further afield to grounds off Martha's Vineyard and Nantucket. Sette[3] reports the yield of flounders of Connecticut as nearly six million pounds in 1925 and over seven million in 1926; this increase was due to the expansion of the fishery and the consequent inclusion of the yellow-tail (*Limanda ferruginea*) in the catch. By 1930 Fiedler[4] lists the otter trawl landings of flounders in Connecticut as over 11 million pounds, a further reflection of the trend. These were boom times. For example, in 1929 Capt. Ellery Thompson's two boats took over a million pounds of market fish of all kinds; the "Eleanor," on which the work here reported was done, accounted for 660,000 lbs. alone. There were now some 50

[3] Fishery Industries in the United States, 1926. Appendix V, Rep. U. S. Comm. Fish. (1927), 1928: 337–483, Washington, D. C.

[4] Fishery Industries of the United States, 1931. Appendix II, Rep. U. S. Comm. Fish. (1932), 1932: 97–440, Washington, D. C.

vessels in the fleet. The largest was 80–100 feet. In 1935 the fleet had not increased, and total production apparently fell somewhat, but a half decade later there were approximately 60 vessels, and the total landings rose as butterfish and scup became prominent elements in the marketed catch. By 1943, when this study was begun, still larger and more powerful boats had been built, and their greater cruising radius, speed, and efficiency combined to raise the total landings considerably higher.

We cannot but be reminded by the preceding story of Michael Graham's "The Fish Gate."[5]

> . . . as the fishing power increases the stock falls, but the yield at first rises . . . The inherent weakness of all mechanized fishing is that one day's trawling, or lining, or one setting of one net, continually becomes less profitable. The trouble starts right at the beginning of a fishery: the stock becomes reduced at once by what the fisherman takes; and the catch per net, or the like, starts to fall at once. So the fisherman, if he is to live as he did, must increase his fishing power—buying more nets, installing a motor, building a bigger ship, using a patent trawl, bobbins, bridles, ticklers, and anything else that he can scheme up to increase his power—so that, temporarily at any rate, the reduced catch per unit of fishing power may still provide him with a living. . . . But the increased fishing effort reduces the stock still more . . . the urge to expand still remains, and continues to result in increase of total fishing power. Now comes the snag. Experience has shown that the yield does not continue to rise. After a certain point the total yield of a fishery fails to increase any more, whatever the fishermen do. This is the key to the history of fishing, all over the world.

In the case of the eastern Connecticut fishing industry, it is clear that the trawl fishery for winter flounders began in the second decade of the present century and was sufficiently well developed by 1920 to produce several million pounds annually. For a time the fishery was confined to the general Block Island Sound area, but increasing competition soon forced some of the fleet to shift further afield and to look for new species although the original grounds continued to yield their fair quota of winter flounder. It would appear that the Block Island Sound area has consistently yielded from two to five or more million pounds of winter flounder annually to eastern Connecticut fishermen over the past quarter of a century; in the last decade the Connecticut catch of this fish has ranged from two or three up to five million pounds, with Rhode Island fishermen taking roughly another half to one million pounds of this species from this region each year. This is

[5] Faber and Faber Ltd., London, 1943: 196 pp.

probably not a species which is subject to violent fluctuations in abundance and to the phenomenon of year-class dominance, and since the young fish remain on nursery grounds during the first years of their life and only enter the fishery later, the recruitment to the commercial stock is probably reasonably steady. The Block Island Sound area is fished quite regularly by the smaller and medium-sized vessels of the fleet; these are boats whose day-to-day operation is relatively cheap and which can make a small profit on relatively small catches. If the weather is poor or the fishing slow they can afford to remain idle. When conditions are good they fare well. On occasions when the winter flounders are abundant the larger vessels, which normally go further afield on longer trips for yellowtails and other species, fish the area until it is no longer profitable for them. In short, there is a "limit of unprofitableness" (Graham) which works at different levels on the boats of different size; with the smaller craft the margin between cost and profit is a relatively slim one. And because the grounds are not on a line between major fishing ports (such as Gloucester, Boston and New Bedford) and further offshore banks which are worked intensively by modern trawlers, they are not subjected to the tremendous strain which these vessels could exert at times when it might be profitable for them to work the area. Furthermore, the proximity of New York means a ready market for this high quality fresh fish.

This, then, was the general picture when the present work was begun. The winter flounder fishery is apparently fairly stable as a result of: 1) the life history of the species which affords it good protection in its first years, 2) the various economic factors, and 3) its geographical position. During the period from 1940 to 1945 the average annual catch of winter flounders from this area by Connecticut boats was somewhat higher than in preceding years (roughly an average of four or more million pounds annually)—a fact which is probably explained by the incentive to fish more intensively during a period of high prices.

MATERIALS AND METHODS

The winter flounder trawl fishery off southern New England is conducted mainly by small draggers from 25 to 55 feet in length. Modified otter trawls are used, the width, mesh-size, number of floats on the head rope, dimensions of the doors, etc., varying with the size of the boat, season of the year and individual preference of the skippers. In Rhode Island and Connecticut the industry centers at

Stonington, and the region fished extends from the mouth of the Thames River along the south shore of Rhode Island and through the Block Island Sound area into the open ocean to the east and south (Fig. 1, Table II). Within this whole region the bottoms of the

TABLE II. DATE, LOCALITY, VESSEL AND DEPTH FOR MONTHLY ONE-HOUR HAULS, 1943–1946

Date	*Locality*	*Name of vessel*	*Depth (fathoms)*
VII-16-1943	15 mi. SSE. of Point Judith, R. I.	Eleanor	25
IX-12-1943	14 mi. SSE. of Point Judith, R. I.	Eleanor	22
X-31-1943	3 mi. S. of Green Hill, R. I.	Eleanor	14
XI-21-1943	5 mi. ESE. of Watch Hill, R. I.	Eleanor	12
XII-19-1943	5–8 mi. ESE. of Watch Hill, R. I.	Eleanor	10–14
I-23-1944	1 mi. S. of Noyes Point, R. I.	Eleanor	10–15
II-20-1944	2 mi. S. of Green Hill, R. I.	Eleanor	12
III-19-1944	2 mi. SSE. of Watch Hill, R. I.	Eleanor	15
IV-23-1944	2–3 mi. S. of Green Hill, R. I.	Eleanor	12–15
V-18-1944	Between Fishers I. and mouth of Thames R.	Eleanor	10–12
VI-23-1944	3 mi. N. of Sandy Pt., Block Island, R. I.	Eleanor	20–23
VII-23-1944	3 mi. N. of Sandy Pt., Block Island, R. I.	Eleanor	20
VIII-13-1944	3 mi. N. of Sandy Pt., Block Island, R. I.	Eleanor	20
IX-10-1944	3 mi. N. of Sandy Pt., Block Island, R. I.	Eleanor	20
X-26-1944	Off Noyes Point and Quonochontaug, R. I.	Eleanor	8–12
XI-19-1944	Off Quonochontaug and Noyes Point, R. I.	Eleanor	10–15
XII-18-1944	2 mi. S. of Charleston Inlet, R. I.	Marise	14
I-1945	—	—	—
II-1945	—	—	—
III-5-1945	4 mi. S. of Green Hill, R. I.	Eleanor	20
IV-16-1945	3 mi. NNE. of Block Island, R. I.	Eleanor	20
V-27-1945	Between mouth of Thames R. and Fishers I.	Eleanor	10
VI-18-1945	2 mi. SE. of Watch Hill, R. I.	Eleanor	20
VII-17-1945	1½ mi. SE. of Watch Hill, R. I.	Eleanor	20
VIII-21-1945	5 mi. SSE. of Watch Hill, R. I.	Eleanor	20
IX-23-1945	3½ mi. SE. of Watch Hill, R. I.	Eleanor	20
X-15-1945	1 mi. S. of Quonochontaug, R. I.	Eleanor	10
XI-11-1945	1 mi. N. of North Hill, Fishers I., N. Y.	Eleanor	10
XII-1945	—	—	—
I-14-1946	Off Charleston Inlet, R. I.	Eleanor	10
II-19-1946	2 mi. W. of Noyes Point, R. I.	Eleanor	10–18
III-24-1946	½ mi. W. of Hatchett's Reef, Conn.	Eleanor	15
IV-1946	—	—	—
V-6-1946	3 mi. WSW. of Block Island, R. I.	Eleanor	20
VI-9-1946	4 mi. S. of Quonochontaug, R. I.	Eleanor	20
VII-1946	—	—	—

Figure 2. Typical dragger of the Stonington, Conn., fleet; the "Lt. Thomas Minor" taken from the "Eleanor." Photograph by H. Gordon Sweet.

Figure 3. Part of a typical catch just after it has been dumped on the deck. At least nine species are visible: smooth dogfish, little skate, puffer, longhorn sculpin, sea raven, common sea robin, whiting, winter flounder, and sand flounder. Photograph by H. Gordon Sweet.

specific localities in which the draggers work are similar at least to the extent that the topography must obviously be smooth enough to permit efficient operation of the gear. Off the Thames River the bottom is soft and partly muddy; sea lettuce (*Ulva*) and kelp (*Laminaria*) are abundant. Off the south shore of Rhode Island the bottom is harder, and the sand is overlaid with an accumulation of shells of various mollusks among which grow quantities of sponges (*Haliclona* and *Suberites compacta*). Around Block Island the bottom varies from mud to hard smooth sand with a light admixture of gravel; sponges are present here but never in the quantities that they occur along the south shore of Rhode Island. To the east and south of Block Island the bottoms fished vary from soft to hard and are frequently characterized by scallops (*Pecten grandis*) and mussels (*Modiolus modiolus*). The depths in these different localities range from 10 to 30 fathoms.

The study and ultimate analysis of such a fishery involves many problems and there are various methods of attack. One of the most obvious difficulties is that of gathering data in sufficient quantities to give an adequate picture of the population but at the same time having the numbers of fish in each sample small enough so that it is possible to handle them and accumulate the necessary basic information.

Preliminary survey of the winter flounder trawl fishery on a number of draggers in the spring of 1943 indicated that it might be possible to sample the population by studying single representative hauls at monthly intervals. In order to do this it was first necessary to select a vessel which was as nearly typical of the fleet as possible (Fig. 2). Here we were particularly fortunate, and to Captain Ellery Thompson of the "Eleanor" we owe much. His intelligent co-operation and his interest and understanding were major factors in the success of the undertaking.[6] Although most of the monthly trips were on the "Eleanor," one sample was taken and several other trips were made on Captain Harold McLaughlin's dragger "Marise"; here again we were exceptionally fortunate in the help we received, as well as in the fact that the vessel is also fairly typical of the fleet. The "Eleanor" is 50 feet overall, has a beam of 14.25 feet, and a 65-horsepower gasoline engine. She fished nets with an 80-foot mouth, whose stretched mesh-size in the body and in the cod-end varied from 2½ to 4½ inches. That the variations in gear did not alter the catch significantly for the

[6] For an excellent account of Captain Thompson and fishing activities on the "Eleanor," see *The New Yorker*, Jan. 4 and 11, 1947 ("Profiles").

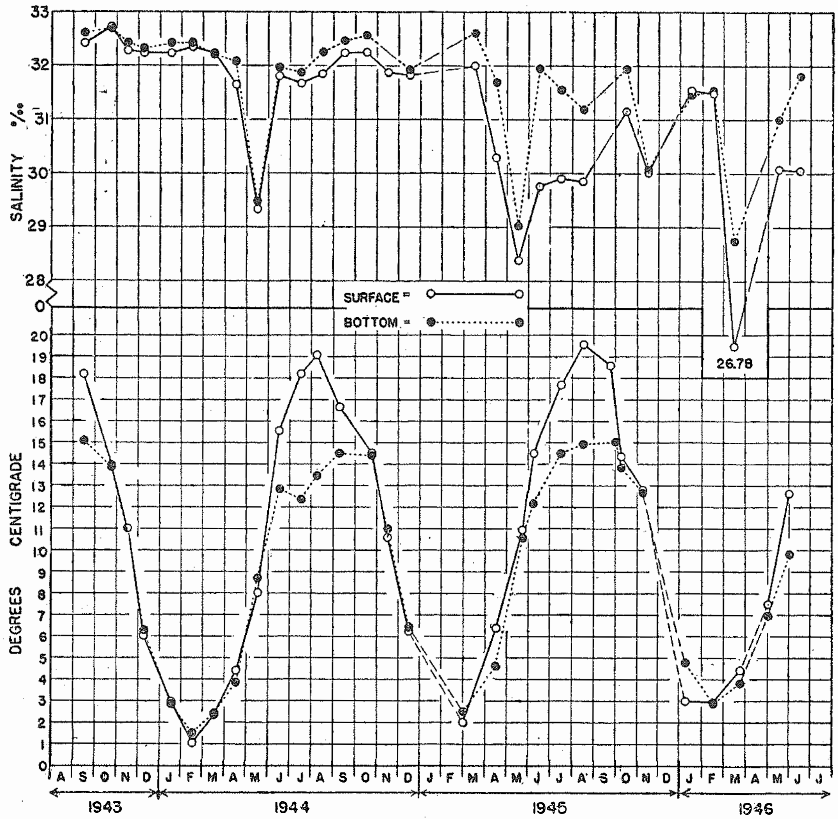

Figure 4. Surface and bottom salinity and temperature records, 1943–1946. Refer to Table II for exact localities. The three low points in the salinity curve are due to the fact that part of the fishing fleet often moves to the west for a brief period in the spring to meet what is apparently an eastward migration of winter flounders, and these samples were taken near the mouths of the Thames and Connecticut Rivers. Since the water samples were collected from different localities within a fairly large area and in no regular annual pattern, it is difficult to be certain whether the general decrease in salinity from 1943 to 1946 shown above is a true reflection of general conditions or the result of variation in the position of the stations. It would appear from Table II that the decrease may be real. The peaks and troughs of the water temperature record show a slight increase over the whole period.

purposes of the work here reported, either in the quantity or in the size-distribution of the various species, was demonstrated by comparisons of different hauls under approximately comparable conditions. Of greatest importance in this study was the knowledge, experience and judgment of the skippers with whom we worked and who did their best to provide us with typical catches and samples which were representative of each month (Fig. 3). Such sample hauls were taken over a 36-month period; during this time at least one haul a month was collected, except on five occasions when the weather, tie-ups or illness caused a break in continuity (Tables II, IV–VI). One or more members of the laboratory were on board for all but three of the collections; full field notes were taken and surface and bottom salinity and temperature records are shown in Fig. 4. It was the usual practice to take the second or third haul of the day after observation of the first or second drag had provided general evidence that the catch was typical of the month. Always the guiding criterion was to obtain a representative haul. By estimating the quantity of fish to be taken after seeing the first or second drag it was possible to judge the length of the succeeding haul necessary to provide a sample for adequate laboratory analysis. As an added means of judging the typicalness of the drag selected for each month, a number of other trips were made for purposes of comparison; these indicated only minor variations insufficient to alter the general conclusions. Each representative haul was barrelled and iced immediately and transported by truck to New Haven; the catches varied from less than a barrel to six barrels (roughly 200 pounds to a barrel). At the laboratory the catches were sorted by species, and each individual fish was weighed, measured and sexed. Additional data was then taken on all species for the life-history studies; where the number of individuals was large, a sample covering the entire size-range was studied, and where it was possible, all the individuals were subjected to detailed analysis. Scales and otoliths were taken, gonads and stomach contents were preserved, vertebral counts were made, etc. Finally, for the purposes of this discussion, all hauls were equalized to one hour's unit-of-effort.[7]

Fig. 5 shows the number of species, individuals and pounds of fish taken on each collection date on an hourly basis over the three-year period. It is immediately apparent that the numbers in all three categories were generally greatest in the summer and fall months and

[7] The sample hauls actually varied from 30 minutes to two hours and 10 minutes in length. It is possible that a small error was introduced by equalizing throughout to one hour's effort, for, assuming an even distribution of fish on the bottom, there is some reason to think that a trawl takes more in the first part of its drag than in any subsequent part. Presumably, as the cod-end fills up with fish the strain increases so that the effective fishing width of the net, as determined by the distance between the otter boards, is decreased.

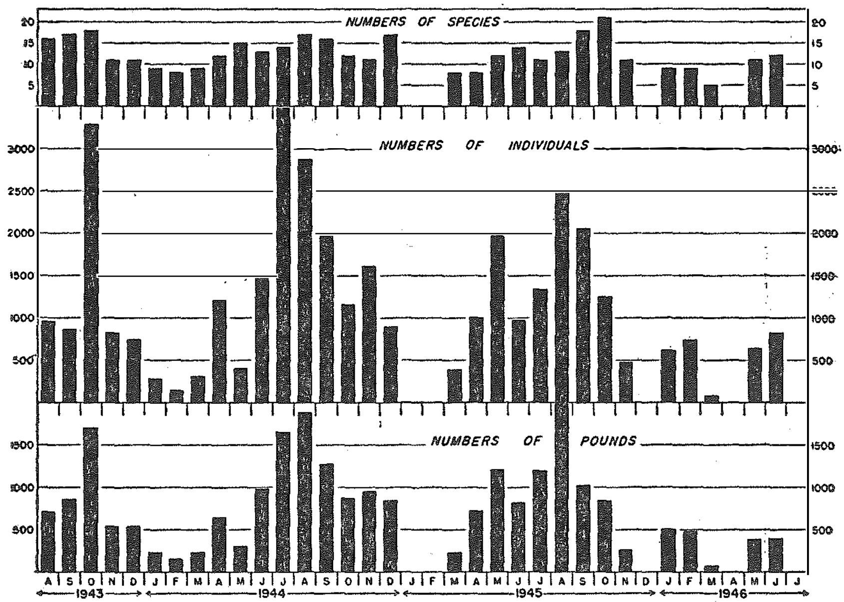

Figure 5. Numbers of species, of individuals, and of pounds for one hour hauls by months from August 1943 to July 1946.

least during the winter and early spring. Also, the peaks in numbers of individuals and pounds did not necessarily coincide with the peaks in numbers of species. Table IV shows that the haul in October 1943 contained an enormous number of sculpins, year-round residents, which were taken in what was apparently a pre-spawning mass movement or congregation. The hauls in July, August and September 1944 were dominated by winter flounders, also year-round residents, as was the catch in May 1945. In the hauls of July, August and September 1945, winter flounders, little skates, sand flounders and whiting—all species which occurred with great regularity in the monthly catches—were the dominant elements; all except the whiting, which probably migrates to the south in the winter, are permanent residents. On the other hand, the peaks in numbers of species in October 1943, August and December 1944, and September and October 1945, were due to immigrants of temporary residence which were not present in great numbers. The maximum number of species was 21 in October 1945, of individuals 3,448 in July 1944, and of pounds 2,008.8 in August 1945.

The smallest catch was made in March 1946—five species and 81 fish weighing 71.3 pounds. The peaks of abundance of demersal fishes by numbers and weight in the summer may be related to an abundance of bottom invertebrates which in turn may be the result of optimal conditions and of the early summer plankton bloom.

TRASH VERSUS MARKETED FISH

At the time this investigation was begun, the war emergency had brought about a demand for increased fisheries production. Since the trawl fisheries take many species which are discarded as "trash" but which could be utilized, and since few figures were available on the proportions of the catch which were marketed, one of the objectives of this study was to provide data on this subject. Leaving aside problems of marketing and other economic considerations which have been discussed elsewhere,[8] analysis is rendered more difficult by the fact that in the period covered by this investigation there was a distinct tendency to market hitherto discarded or partially discarded species. Instead of dividing the catch arbitrarily into marketed and nonmarketed or trash components, therefore, it has been necessary in Fig. 6 and Table III to include an "occasionally marketed" category. The increased tendency to market the forms in this grouping from 1943 to 1946 applies particularly to the whiting, windowpane flounder and two hakes, although all of the species were saved to a greater extent than before. In connection with Fig. 6 and Table III, note that the undersized individuals in the marketed categories which would have been shovelled overboard as trash are included in the figures for each species. This fact renders the numbers, pounds and percentages of the species in each group that were actually marketed slightly too high. In the winter flounder the error from this cause in the period from January to July 1944 is approximately one per cent of the total weight; in the whiting the error in the fall and early winter (*e. g.*, October, November and December 1943), when many individuals too small for market are taken, is as high as 10 per cent of the total weight. However, the over-all alterations in the general results from this factor are small.

[8] See especially pages 11–31 in Olsen and Merriman, "The biology and economic importance of the ocean pout, *Macrozoarces americanus* (Bloch and Schneider)," Bull. Bingham Oceanog. Coll., *9* (4): 1–184, 1946.

TABLE III. NUMBERS, POUNDS AND PERCENTAGES OF THE 20 MOST COMMON FISHES IN THE ONE-HOUR HAULS FROM 1943 TO 1946 BY SPECIES AND BY MARKETED, OCCASIONALLY MARKETED, AND NONMARKETED CATEGORIES. THESE 20 SPECIES REPRESENT 99.8% BY NUMBERS AND 99.5% BY WEIGHT OF THE TOTAL OVER THE THREE-YEAR PERIOD

	1943–1944				*1944–*	
Marketed	*No.*	*% of total no.*	*Lb.*	*% of total lb.*	*No.*	*% of total no.*
Pseudopleuronectes americanus	6,390	45.8	3,603.4	42.3	6,860	48.4
Gadus morhua	65	.5	297.8	3.5	96	.6
Stenotomus chrysops	3	.0	.9	.0	29	.2
Limanda ferruginea	59	.4	43.0	.5	24	.2
Paralichthys dentatus	3	.0	1.7	.0	30	.2
Totals	6,520	46.7	3,946.8	46.3	7,039	49.6
Occasionally Marketed						
Merluccius bilinearis	757	5.4	341.0	4.1	2,199	15.5
Lophopsetta aquosa	464	3.3	259.1	3.0	484	1.3
Urophycis chuss	286	2.1	214.2	2.5	186	1.3
Prionotus carolinus	21	.2	11.8	.1	43	.3
Urophycis tenuis	148	1.1	186.2	2.2	50	.4
Raja stabuliforis	71	.5	220.6	2.6	64	.5
Macrozoarces americanus	34	.2	49.2	.6	44	.3
Spheroides maculatus	—	—	—	—	7	.0
Lophius americanus	36	.3	303.7	3.6	29	.2
Totals	1,817	13.2	1,585.8	18.7	3,106	21.9
Nonmarketed						
Myoxocephalus octodecimspinosus	4,676	33.5	1,864.3	21.9	2,070	14.6
Raja erinacea	618	4.4	771.3	9.1	1,367	9.7
Paralichthys oblongus	180	1.3	91.1	1.1	339	2.4
Raja diaphanes	87	.6	211.8	2.5	179	1.3
Tautogolabrus adspersus	28	.2	21.5	.3	33	.2
Hemitripterus americanus	22	.2	16.9	.2	30	.2
Totals	5,611	40.2	2,976.9	35.1	4,018	28.4
Grand totals	13,948		8,509.5		14,163	

TABLE III. NUMBERS, POUNDS AND PERCENTAGES OF THE 20 MOST COMMON FISHES IN THE ONE-HOUR HAULS FROM 1943 TO 1946 BY SPECIES AND BY MARKETED, OCCASIONALLY MARKETED, AND NONMARKETED CATEGORIES. THESE 20 SPECIES REPRESENT 99.8% BY NUMBERS AND 99.8% BY WEIGHT OF THE TOTAL OVER THE THREE-YEAR PERIOD

1945		*1945–1946*				*Totals 1943–1946*			
Lb.	*% of total lb.*	*No.*	*% of total no.*	*Lb.*	*% of total lb.*	*No.*	*% of total no.*	*Lb.*	*% of total lb.*
4,056.7	40.7	2,327	25.3	1,613.2	23.3	15,577	41.8	9,273.3	36.5
299.1	3.0	9	.1	39.7	.6	170	.5	636.6	2.5
23.8	.2	115	1.3	7.9	.1	147	.4	32.6	.1
18.3	.2	18	.2	19.5	.3	101	.3	80.8	.3
74.4	.7	52	.6	127.2	1.8	85	.2	203.3	.8
—	—	—	—	—	—	—	—	—	—
4,472.3	44.8	2,521	27.5	1,807.5	26.1	16,080	43.2	10,226.6	40.2
902.9	9.1	923	10.1	348.1	5.0	3,879	10.4	1,592.0	6.3
278.0	2.8	1,152	12.5	584.4	8.4	2,100	5.6	1,121.5	4.4
140.1	1.4	164	1.8	122.4	1.8	636	1.7	476.7	1.1
34.5	.3	306	3.3	107.4	1.5	370	1.0	153.7	.6
64.6	.6	105	1.1	47.1	.7	303	.8	297.9	1.1
244.2	2.4	22	.2	174.4	2.5	157	.4	639.2	2.5
127.4	1.3	62	.7	171.7	2.5	140	.4	348.3	1.4
3.0	.0	110	1.2	62.4	.9	117	.3	65.4	.3
404.8	4.1	18	.2	183.4	2.6	83	.2	891.9	3.5
—	—	—	—	—	—	—	—	—	—
2,199.5	22.0	2,862	31.1	1,801.3	25.9	7,785	20.8	5,586.6	21.2
1,016.5	10.1	1,022	11.1	499.1	7.2	7,768	20.8	3,379.9	13.3
1,645.9	16.4	2,197	23.9	2,122.4	30.6	4,182	11.2	4,539.6	17.9
150.6	1.5	376	4.1	179.9	2.6	895	2.4	421.6	1.7
443.6	4.4	177	1.9	483.3	7.0	443	1.2	1,138.7	4.5
15.6	.2	18	.2	24.3	.4	79	.2	61.4	.2
32.4	.3	11	.1	9.5	.1	63	.2	58.8	.2
—	—	—	—	—	—	—	—	—	—
3,304.6	32.9	3,801	41.3	3,318.5	47.9	13,430	36.0	9,600.0	37.8
9,976.4		9,184		6,927.5		37,295		25,413.2	

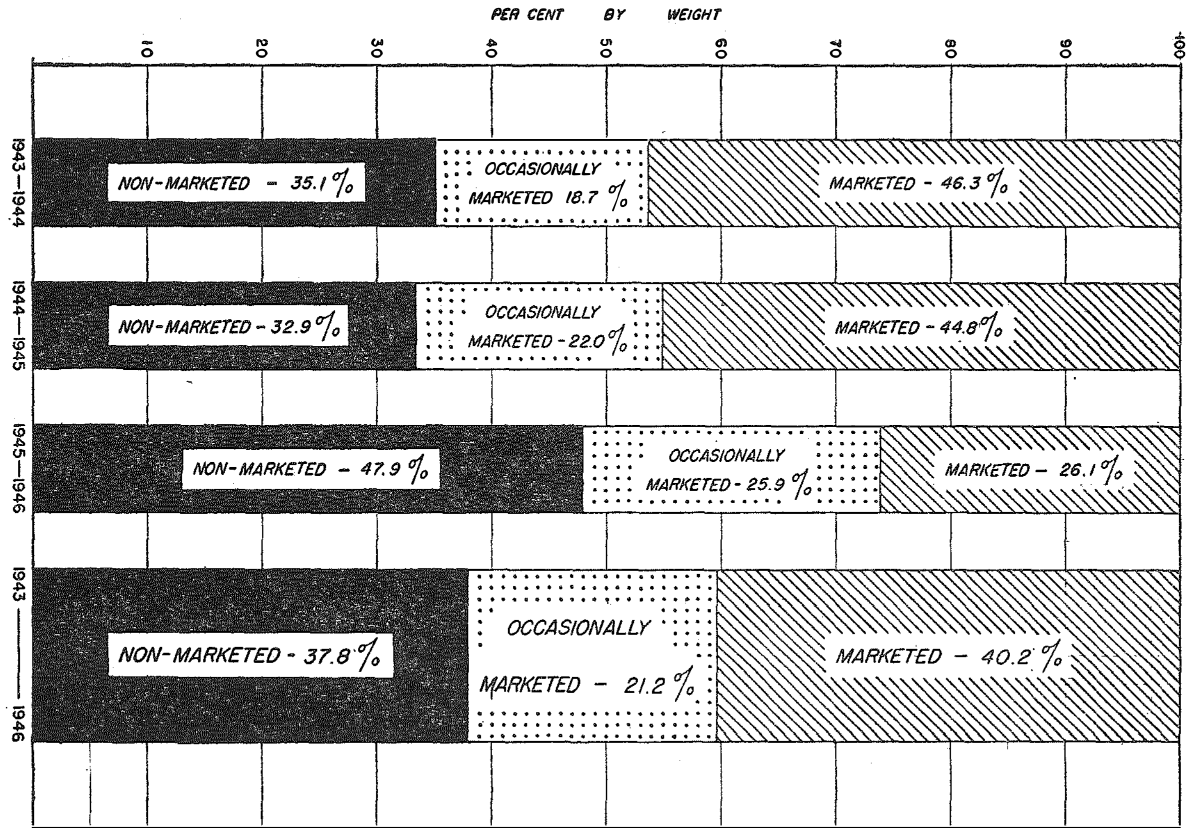

Figure 6. The nonmarketed, occasionally marketed and regularly marketed proportions of the catch as per cent of weight by years and for the three-year total. Data compiled from monthly sample hauls.

In the three-year period from 1943 to 1946, 40.2 per cent of the total catch by weight was marketed, 21.2 per cent occasionally marketed, and 37.8 per cent was discarded as trash. The increased utilization of the occasionally marketed species in the war emergency was encouraging; all of these forms can and should be marketed regularly, especially the whiting and hakes, which suffer heavy mortality even under best conditions when returned to the water after being taken in the trawl. Windowpane flounders (with their exceptionally fine flavor), barndoor skates, and goosefish clearly have a place in the market. Among the nonmarketed fishes the sculpin and little skate are the major elements (Table III). The mechanical difficulties of handling these species and the relatively small edible proportion to be recovered from them has precluded their utilization to date, but similar forms are retained and marketed in fisheries in other parts of the world. Furthermore, as will be shown later (p. 162), the relationship between the winter flounder and small skate may be such that it might be advantageous to fish the skate population down to a lower level. The four-spotted flounder presents difficulties because it spoils so fast, but these could perhaps be overcome, and the big skate could certainly be used, as could both the cunner and sea raven.

Of the 21.2 per cent by weight of the fishes in the occasionally marketed category over the three years of this study, certainly more than half was actually saved. In round numbers we would estimate, therefore, that 55 per cent of the total catch by weight was actually marketed and 45 per cent discarded as trash. Annual variations in the percentages of marketed, occasionally marketed, and nonmarketed categories were not significant except in 1945–1946 when the trash species were relatively more abundant—47.9 per cent by weight; this was due to the much greater proportion of little skates (p. 149).

ANALYSIS OF THE POPULATION

The Adequacy of Sampling

In an analysis of this sort in which conclusions are based on monthly one-hour drags over a three-year period, the adequacy of the sampling is obviously a critical factor. We have already stressed the fact that the knowledge and full co-operation of the captains of the vessels from which the representative hauls were taken were of major importance (pp. 143–145); the judgment of these men as to the typicalness of the drags was invaluable. We have also mentioned the fact that in addition to the days on which the samples were taken we made other trips on the "Eleanor" and other draggers for comparative purposes so that we often had more than one day on which to choose the monthly sample hauls.

Still other means of testing the adequacy of sampling are available from catch statistics. In Fig. 7A we have indicated the shipments of winter flounder (the dominant element of the catch) from Connecticut to the New York market by months in 1945. Since by far the major proportion of the landings of this species from Connecticut is shipped to the New York market, even though the intensity of fishing varies somewhat according to the season of the year, this graph provides considerable evidence as to monthly fluctuations in abundance and availability. In Fig. 7B the catch of winter flounder in the monthly sample hauls over the same period is shown. Note that, except for one month (June), the trends in abundance compare remarkably well with those indicated in Fig. 7A. Furthermore, with respect to June, even in the absence of the New York market statistics, reference to the catch of winter flounder in the sample hauls of that month in 1944 and 1946 (Table V) would have shown that the corresponding sample in 1945 was probably inadequate in its representation of this species. The adequacy of this method of sampling as a means of showing trends and fluctuations in abundance thus receives much support from the comparison of Figs. 7A and B.

As a final check on the sampling method, the captains of the "Eleanor" and the "Marise" were asked to keep specially prepared logs of the catch by species in every haul for over a year. This data, scrupulously taken by both men, provided a basis for comparison of the monthly one-hour samples with the monthly catches. Fig. 7C shows the pounds of winter flounder caught per hour's trawling by months from April 1945 to March 1946 in the sample hauls and in the "Eleanor's" monthly catch. Again the trends in abundance, though by no means perfect, are comparable over the majority of the period covered. However, it is clearly evident from this graph that the captain of the "Eleanor" favored us in the sample hauls. In other words, the sample hauls tend in most months to be much larger than the average haul in the same period—in more than half the months in which comparison is possible the sample drag contained over twice as many winter flounders as the average haul. It is clear, then, that

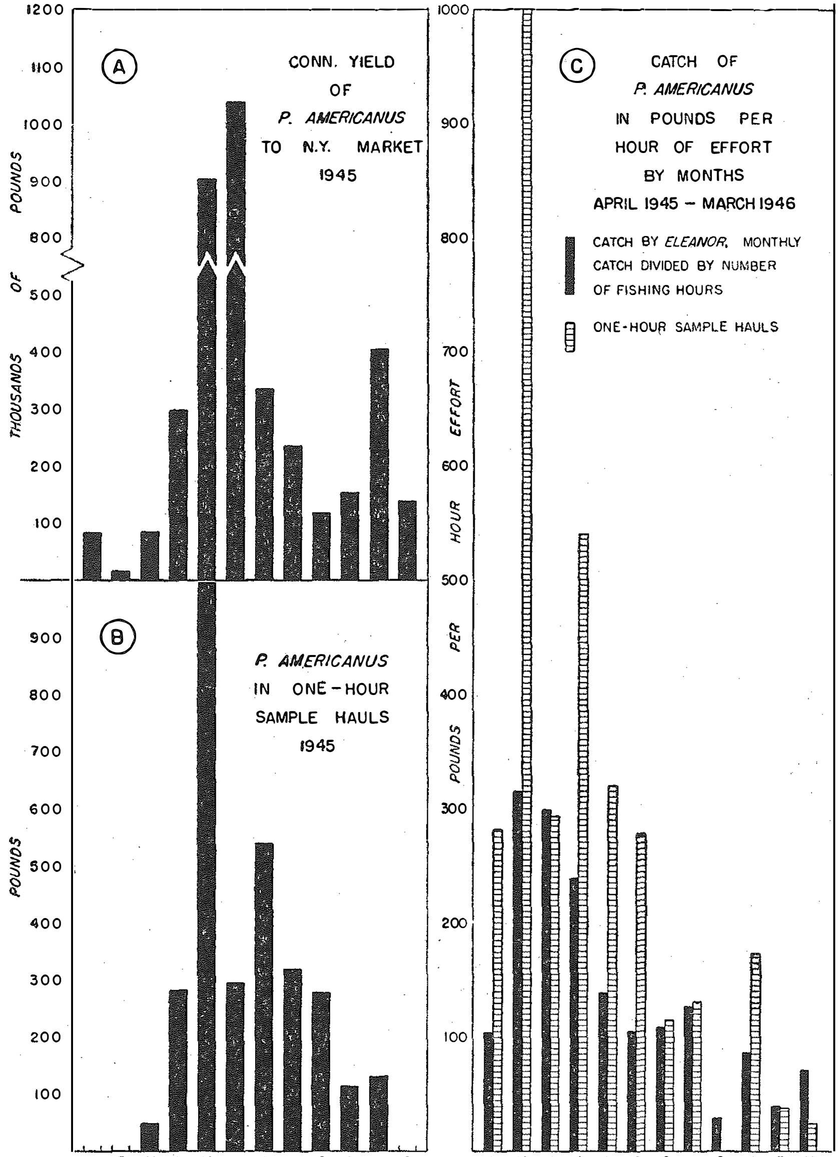

Figure 7. A. Shipments of winter flounder from Connecticut to the New York market by months in 1945. B. Pounds of winter flounder in the one-hour sample hauls from the "Eleanor" by months in 1945. C. Pounds of winter flounder taken by the "Eleanor" per hour's effort by months from April 1945 to March 1946 (lined columns) compared with pounds of winter flounder in the one-hour sample hauls over the same period (black columns). See text for discussion.

while the sample hauls provide evidence of trends in abundance, they are of dubious value in estimating total monthly or annual production; if we attempted to estimate the vessel's monthly or annual catch by multiplying the sample hauls by the number of hours fished, the results would be grossly in excess of the actual take. However, comparison of the composition of the catch in the sample hauls with that of the daily and monthly catches as recorded in the logs indicates, in general, that the proportions of the component species by months is quite accurately represented in samples. Fluctuations in relative abundance of species by months can therefore be demonstrated by this method of sampling.

There are also other limitations to be considered in regard to sampling the population of fishes in an area by taking representative hauls from the commercial vessels. First, the samples are restricted to the localities where the bottom is sufficiently smooth to permit the operation of the trawl; the composition of the population and the relative abundance of the species in those localities within the whole area which cannot be worked are unknown. Second, within the localities which can be trawled, the fishermen of course go to places which they know from experience will give them the best catch at any particular time of year; in short, they try to go where the fishing is best, and under certain circumstances when the boats are crowded into one locality, the drain on the population is such that an early haul may differ considerably from one later in the day. Therefore, the samples are not necessarily typical of even all the smooth bottom within the entire region. Strictly speaking, they are typical only of what are probably the most productive smooth bottom localities each month within the whole area.

Seasonal Organization

Monthly samples in the period from August 1943 to July 1946 were collected in 31 out of the possible 36 months. January, February and December 1945 and April and July 1946 were the periods omitted. Tables IV, V, and VI show respectively the numbers, pounds, and average weights of the individual fish by species per one-hour haul per month during the entire investigation.[9] Where no figure is recorded

[9] The totals for each year (August through July), as well as the grand totals for all three years, are also shown in Tables IV–VI, but no attempt has been made to equalize for the different year's effort, although hauls were made in all 12 months in '43–'44, in only 10 months in '44–'45, and in only nine in '45–'46.

for a species on any particular date it means that none were taken. Examination of this material provides much information on seasonal organization and relative abundance. Block Island Sound is roughly in the middle of the geographical range of the great majority of the more common species encountered, but obviously none of these fish are confined in their distribution to the limited area sampled; some are present on a year-round basis, while others show seasonal trends in their presence or absence, and some are much more highly migratory than others.

The following list considers the different species in the order of number of occurrences out of a possible total of 31:

The *winter flounder* and the *little skate* top the list; they were present in all samples. These two species are permanent residents in the sense that representatives of both were always present, although the actual quantities varied widely. This does not mean that they are non-migratory forms; indeed our tagging experiments show that the winter flounder undertakes considerable migrations in Long Island Sound and southern New England waters.

The *longhorn sculpin* was present in 29 out of the 31 months; it was missing in August and September 1945 and tended to be more abundant in the fall, winter and early spring months. It spawns in the winter and deposits its eggs on the dead-man's finger sponge (*Haliclona*) and other objects in the area directly off the southern coast of Rhode Island which is fished intensively at this time of year. Tagging of this species also shows that it may undertake considerable movements in Block Island and Long Island Sounds, and the enormous catch of sculpins on several occasions indicates mass congregations that must involve migrations.

The *windowpane flounder* was also present on 29 out of the 31 possible occasions. It is by no means as abundant as the preceding forms, and although our tagging again shows that it undertakes considerable movements in southern New England waters, it, like the species mentioned above, is unquestionably present on a year-round basis in this area.

The *big skate,* also apparently in this region in limited numbers at all times of year, was absent from the samples on five occasions. However, this species is more migratory than might be expected, as shown by the fact that one which was tagged by us off Block Island in June 1946 was recaptured six months later off Sandy Hook, New Jersey.

The *whiting* shows a definite seasonal pattern of abundance. It was present in 23 samples, but was absent January–April 1944, March and April 1945, and February and March 1946. It appears in the spring of the year (May)—presumably from the south—and is present in greatest numbers in the fall months.

The *sea raven* was taken in 20 samples out of the possible 31. This species is present in limited numbers only, and the months in which it was absent over the three-year period give no evidence of any seasonal pattern indicative of extensive migration. The fish is apparently a permanent resident of limited abundance.

The *four-spotted flounder*, on the other hand, is clearly a migratory species. It was present in 18 samples and was missing from the catch from November 1943 through April 1944 and over much the same period in 1944–1945 and 1945–1946. The peak of abundance was in August and September in all three years, although the fish is apparently present in the area from May to November.

The *squirrel hake* shows an almost identical pattern of abundance and must similarly be a seasonal migrant. It was taken in 18 samples during the spring, summer, and fall, and obviously tends to be absent in the winter.

The *goosefish* was taken in 17 samples in limited numbers and showed a tendency to be less abundant in the winter and more common in the summer months.

The *cod*, taken 16 times, apparently migrates to this area in the fall and is taken most commonly in the colder months of the year.

The *yellow-tail flounder*, also taken 16 times, was more often present in the winter months.

The *barndoor skate* was caught in 14 hauls and was most abundant in the summer months.

The *white hake* closely parallels the squirrel hake in that it tends to be absent in the winter and is clearly a seasonal migrant.

The *ocean pout*, also taken 13 times, tends to be absent in summer months and is only available to this fishery in any quantity in winter and spring.

The *common sea robin* and the *summer flounder*, present 12 and 11 times respectively, are obviously spring and summer immigrants and do not occur in the winter.

The *cunner* and the spiny *dogfish* are only taken in the trawl in the warmer months and the *scup* shows much the same pattern of occurrence. This is also true of the *butterfish, striped sea robin* and *puffer*.

The *smooth dogfish, herring, alewife, sea bass, kingfish, tautog, filefish, haddock, spotted hake* and *witch flounder* all occurred only once or twice in the 31 hauls. Their numbers in the trawl samples are insufficient to provide much evidence as to migratory patterns or seasonal abundance. Some, like the tautog, alewife, sea bass and kingfish we know from other types of fishing are often present in this region in good numbers. Others, like the filefish, spotted hake and witch flounder are apparently no more than comparatively rare stragglers into the area.

Relative Abundance and Interspecific Relationships

Reference to Tables III and V show that in terms of poundage the six most abundant species over the three-year span were:

	Per cent of total by weight	*Per cent of total by number*
Winter flounder (*Pseudopleuronectes americanus*)	36.5	41.8
Little skate (*Raja erinacea*)	17.9	11.2
Sculpin (*Myoxocephalus octodecimspinosus*)	13.3	20.8
Whiting (*Merluccius bilinearis*)	6.3	10.4
Big Skate (*Raja diaphanes*)	4.5	1.2
Windowpane flounder (*Lophopsetta aquosa*)	4.4	5.6

Together these represent 82.9 per cent of the total catch by weight and 91.0 per cent by number. By weight the next most abundant species is the goosefish (*Lophius americanus*), which accounts for 3.5 per cent of the total, and following it come the barndoor skate (*Raja stabuliforis*) and the cod (*Gadus morhua*), each of which amounts to 2.5 per cent of the total. In terms of numbers, the four-spotted flounder (*Paralichthys oblongus*) ranks sixth with 2.4 per cent of the total, the squirrel hake (*Urophycis chuss*) seventh with 1.7 per cent, and the big skate (*Raja diaphanes*) eighth although it is fifth in per cent by weight. All of these forms are wholly or partially demersal; the only ones which are not strictly bottom-living and bottom-feeding forms are the closely related merlucciid (whiting and hake) and gadid (cod) fishes, although even these commonly feed on or near the ocean floor. Of the six most abundant species in terms of per cent of the total by weight, all except the whiting are resident in the sense that, although they may migrate considerable distances and are by no means confined to the area under consideration, representatives are unquestionably always present; the whiting, as we have seen (p. 156), is highly seasonal in its occurrence and presumably migrates north in the spring and south in the winter.

The catches of the five major resident species in pounds per one-hour haul per month over the three-year span are shown in Fig. 8. Note that the peak catches of winter flounder were made in the spring and early

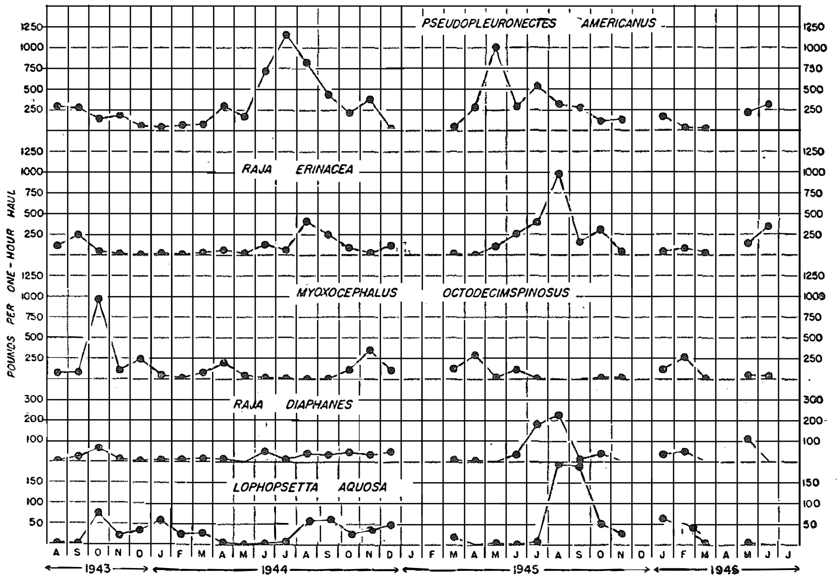

Figure 8. Seasonal fluctuations in abundance of the five major resident species—reading from top to bottom, winter flounder, little skate, longhorn sculpin, big skate, and windowpane flounder. Data given in pounds per one-hour haul by months from August 1943 to July 1946.

summer months, while the peak catches of the little skate follow slightly later in the summer. The big skate and the windowpane flounder show almost identical peaks coincident in point of time, though by no means of equivalent quantity, with those of the small skate. The sculpin peaks of abundance occur in the fall (October–December), except in 1945, and spring (February–April); these peaks may result from pre- and post-spawning migrations, and do not coincide with the times of maximum quantities of the other species. In fact the sculpin population appears to be at its lowest level when first the winter flounder and then the little skate, big skate and windowpane flounder are abundant. There is in these data, then, some indication that either there is competition between species (particularly between winter flounder and little skate), or that the life-history and movement- or migration-patterns of these species fit together in such manner that the peaks of abundance of demersal forms do not coincide. It may be that food conditions on the bottom is the controlling factor. We have seen (Fig. 5 and pp. 145–147) that the peaks in total poundage tend to occur in the midsummer months. The maximum hourly catches are of the order of magnitude of 1500–2000 pounds. Knowing the speed of the boat (1.75–2.00 m. p. h.) and the fishing width of the net (approximately 45 ft.), it is possible to estimate that in an hour's drag on the average the trawl covers roughly 10 (or at a maximum, 12) acres of bottom. This means that under optimal conditions the bottom carries 150–200 pounds of fish per acre at any one time. This figure assumes that the trawl takes all the demersal fish in its path, which is of course not true; however, the small fish and those larger individuals which do escape would probably not raise the poundage figure to any great extent, and we are therefore justified in calling 200 pounds an approximate top figure.[10]

In this connection, there are of course two trophic levels within this community of fishes; one is dependent upon invertebrate food and one depends on fish for food. We estimate that the ratio of invertebrate-eating to piscivorous forms for the three-year span was 5.7 : 1. However, this proportion varied considerably according to the time of year. For January, February and March 1944–1946 it was 7.3 : 1, for the April–June period 13.3 : 1, July–September 11.5 : 1, and October–December 4.9 : 1. This variation is of course due to seasonal changes in the composition of the population. The chief fish-eating forms are the whiting and goosefish, with the cod and hakes being semi-piscivorous, and the sculpin, sea raven and sea robins completely omnivorous but probably depending considerably more on invertebrates than on fish for food in the localities worked by the trawl. The figures given above should not be taken as a strict prey-predator relationship, since a number of the adult invertebrate-feeding forms are too large to serve as prey for predators; especially is this true of the skates, ocean

[10] The amount per acre calculated from the four largest catches in pounds per hour is actually 181.3 lbs. (20.3 g. per sq. m.), and from the six smallest catches 20.2 lbs. (2.3 g. per sq. m.); for the average of the entire three-year span the figure is 82.3 lbs. (9.2 g. per sq. m.).

pout, cod and some flatfish. The matter is further complicated by the fact that some predators (*e. g.*, the whiting) prey on their own species, and that in these estimates all sizes of goosefish, whiting, etc., have been counted as piscivorous. We judge that the ratio between those invertebrate-feeding forms which are small enough to serve as prey and the predators is of the order of 4 : 1 for the three-year period.

Returning to the matter of interspecific competition, Fig. 9 shows the per cent of the total annual catch of the five major resident species for the three years, plotted by three different methods. This approach eliminates seasonal variations and migratory patterns within the annual cycle. Here again the data are somewhat suggestive of an inverse relationship between the winter flounder and the little skate. As the catch of winter flounder goes down from 1943 to 1946, the catch of little skate goes up. The sculpin catch also descends, and the big skate and windowpane flounder catch rises, although to a lesser degree. The inverse correlation between the percentages of winter flounder and little skate is high, but the data are insufficient to have mathematical significance. A fact which partially mitigates the validity of this material is that in the last year (1945–1946) no sample was taken in July. This is a month in which large catches of winter flounder are usually made, and therefore its omission in 1946 might seriously affect the ratio of this species to little skate for the whole year. However, July is also a month in which the little skate is on the ascendancy, and it is significant, too, that the July landings of winter flounder by eastern Connecticut vessels (as judged by shipments to the New York market) was approximately 15 per cent less in 1946 than in either of the preceding years. In connection with the importance of a single month when the data are lumped together in years, note that one month may provide a large percentage of the annual catch. For example, this is particularly true of the October 1943 sample of sculpins as well as of the August 1945 haul of little skates (Table V). Therefore, as we have emphasized before (p. 145), it is essential in such an analysis that each monthly haul be as representative of that period as possible; otherwise an entirely false picture of relative abundance might be obtained.

Further evidence that there may be some sort of competition or reciprocal relationship between the winter flounder and little skate is found in the results of stomach-content analyses, although of course food is by no means the only factor controlling the numbers of indi-

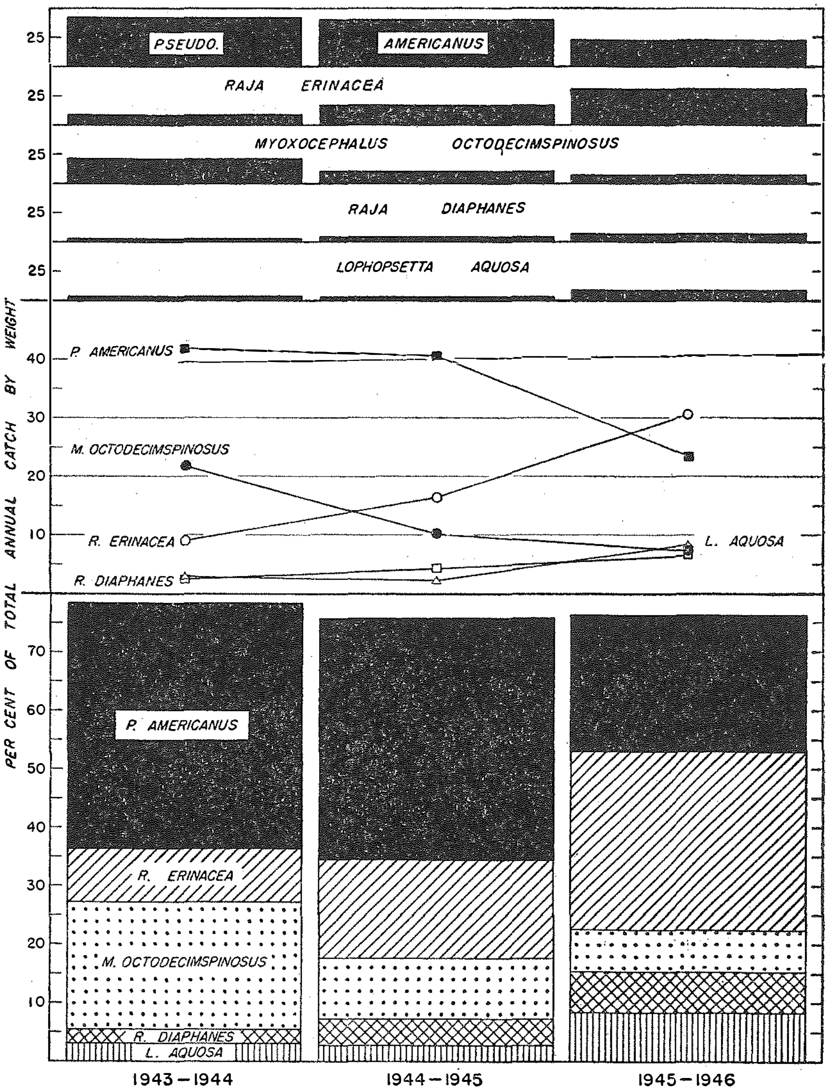

Figure 9. Per cent of the total annual catch occupied by each of the five major resident species in 1943–1944, 1944–1945, and 1945–1946. The same data is plotted by three different methods.

viduals and species in any particular area. Our analyses show that the amphipod, *Leptocheirus pinguis*, is the dominant item of food in both species—approximately one-third by volume. In the winter flounder the two next most important items are *Unciola* and ampeliscids; these forms are also common in the little skate, although *Cancer* and *Crago* follow *Leptocheirus* in per cent by volume. There is, therefore, much in common in the feeding habits of winter flounder and little skate in the area studied. By sharp contrast, we find that in the windowpane flounder by far the dominant item of diet is mysids, which are less than five per cent by volume of the stomach contents of the winter flounder; it is clear that these two flounders do not compete for the same food.

All told, there is a considerable body of evidence that an inverse relationship of sorts exists between the winter flounder and little skate. There are the wholly independent and unsolicited comments of old-time skippers that in the early days of the flounder fishery there were relatively few skates in the catch (p. 137). There is the fact that the seasonal peak catches of these two species, while both occur in the warmer months of the year, do not coincide; the winter flounder is on the decrease as the little skate increases in abundance (Fig. 8). There is also the inverse correlation between the per cent of winter flounder and little skate in the total annual catch in the three-year period covered by this study (Fig. 9). Finally, there is the evidence from stomach content analyses which reveal a high degree of similarity in feeding habits.

CONCLUSIONS

The study of the population of fishes sampled by the winter flounder trawl fishery off the Connecticut and Rhode Island coasts from 1943 to 1946 presents many other possibilities for analysis than those already mentioned. Unlike most marine fisheries investigations which are confined to a single species which is the dominant element of the catch, this is an attempt to make a preliminary analysis of the whole population of demersal and other forms which are taken in the trawl. In general the approach is holological rather than particulate. Quite apart from the data (not included herewith) which the study has yielded on the life-histories of the individual species, the information is essential for a thorough comprehension of all the conditions of the fishery. It also provides a basis for comparison in the future, and so affords a means of approach to the question of overfishing and other problems which should be of utility. The conditions are such that the collection of data can be duplicated at any time, and any changes in the over-all population or in any of its specific parts can therefore be studied.

DISCUSSION

Van Oosten: This paper is now open for discussion.

Burkenroad: I would like to raise one point with regard to the adequacy of your sampling. In our experience a fishery is directed toward the fish which it is most profitable to catch at the moment. There is a considerable amount of difference between the fishes at different spots in a given region, and the fishermen are highly aware of that, so it is entirely possible that your ratios are not representative of anything but the state of the market.

Merriman: That is a fair comment. However, this is predominantly a winter flounder fishery the year round. The samples are obviously taken in those localities within the whole area where the fish are concentrated to best advantage for the commercial fishermen, since we are dependent on the commercial fleet for our analysis. That is the way we sometimes feel about the analysis of tagged fish—the tagging might show where the vessels fish rather than where the fish go.

Burkenroad: Even if the fishery is predominantly for the winter flounder, the other species may represent the margin of profit; and the ratios of species to species in the catch may thus be governed by spot-fishing controlled by changes in price, rather than by ratios of total stocks of each in the area. Therefore, in the same way as Herrington weighted his halibut tag returns according to local fishing intensities, it would seem necessary to compare your ratios with prices before assuming that the changes have any biological significance.

Merriman: I am aware of that possibility. However, from our rather extensive experience in this particular fishery and from simultaneous observation of market prices, we do not feel that this factor affects the results of our analysis materially. In short, we feel that the over-all ratios of species to species in the catch reflect in a general way the actual condition of the population.

Huntsman: The outstanding thing seems to be a difference between winter and summer. Would you say that is due to the fish not remaining in the area in the winter or not being caught?

Merriman: That is due to the fact that they do not remain in the fishable localities. If a man in the wintertime tries one locality and gets very little he tries other localities. I have a table showing the areas fished and you will see that they are distributed pretty evenly.

Huntsman: Would you say there is a movement offshore in winter and onshore in summer? Where are the fish in the winter? Could they be taken somewhere else by some fishermen?

Merriman: Some of the species tend to move to the south. However, in the case of the ocean pout we know that they go into a rocky bottom area where they are not available to the trawl in summer, and some of the flounders move inshore in winter. All these areas are not capable of being dragged.

Huntsman: The tagging done on the cod, which might be considered a representative fish of this sort, seemed to show two different types of movement which you got, more or less, all along the coast—movement offshore in winter and onshore in summer, and then a wandering from the region which involved a relatively small proportion of the population, in some places at least.

Merriman: We would say, judging from our experience, that cod came onshore in the winter. They are present in the winter months.

Herrington: That movement might be affected by temperature changes.

Merriman: Surely.

Herrington: If your fish are not in this area throughout the year, is your figure of production per acre valid?

Merriman: I only quoted that as a maximum that could be expected.

Herrington: What do you mean by that figure? Is that the amount of usable fish that the bottom can feed and maintain and that can be taken off yearly or is it the catch-per-unit-of-effort,—that is, is it the production of the trawl or the production of the bottom?

Merriman: It is actually based on the production of the trawl.

Herrington: I think it is more pertinent to know whether or not your catch per trawling hour is the measure of the productivity of the bottom considered in terms of the area trawlable. What you catch represents the concentration of fish which may have put on their weight and their growth in other places.

NUMBERS OF FISH BY SPECIES PER ONE-HOUR HAUL PER MONTH, 1943 - 1946

TABLE IV.

	SPECIES	1943 AUG. 16	1943 SEPT. 12	1943 OCT. 31	1943 NOV. 21	1943 DEC. 19	1944 JAN. 23	1944 FEB. 20	1944 MAR. 19	1944 APR. 23	1944 MAY 18	1944 JUNE 23	1944 JULY 23	YEARLY TOTAL	1944 AUG. 13	1944 SEPT. 10	1944 OCT. 26	1944 NOV. 19	1944 DEC. 18
1	MUSTELUS CANIS													0					
2	SQUALUS ACANTHIAS		1	2									2	5	14	2			
3	RAJA ERINACEA	89	183	42	17	13	16	6	19	61	21	111	40	618	356	219	65	19	90
4	RAJA DIAPHANES	2	9	16	9	3	6	4	10	7		15	6	87	14	20	17	10	20
5	RAJA STABULIFORIS	6	46	5						1		9	4	71	50	3			2
6	CLUPEA HARENGUS													0					2
7	POMOLOBUS PSEUDOHARENGUS									4				4					2
8	PORONOTUS TRIACANTHUS													0	2	6			2
9	CENTROPRISTES STRIATUS													0					
10	STENOTOMUS CHRYSOPS			1							1	1		3		27			
11	MENTICIRRHUS SAXATILIS													0					
12	TAUTOGOLABRUS ADSPERSUS	1		4						1	11	3	8	28	24	9			
13	TAUTOGA ONITIS										1			1					
14	STEPHANOLEPIS HISPIDUS													0				3	
15	SPHEROIDES MACULATUS													0					
16	MYOXOCEPHALUS OCTODECIMSPINOSUS	170	187	2505	268	530	95	15	159	594	100	39	14	4676	8	9	210	720	116
17	HEMITRIPTERUS AMERICANUS		4	1	1	1	1		1		1	4	8	22	4		7	7	6
18	PRIONOTUS CAROLINUS		7	2							10		2	21		26			
19	PRIONOTUS EVOLANS										1			1					
20	MACROZOARCES AMERICANUS		8			1		1	2	21	1			34					6
21	MERLUCCIUS BILINEARIS	23	10	127	220	22					13	36	306	757	344	464	477	233	438
22	GADUS MORHUA	2	1	6	4	40	2	5	1	4				65			2	7	60
23	MELANOGRAMMUS AEGLIFINUS	1												1					
24	UROPHYCIS REGIUS													0					
25	UROPHYCIS TENUIS	24	1	81									42	148	6	12			10
26	UROPHYCIS CHUSS	42	26	74	2					9	2	1	130	286	32	75	2		6
27	PARALICHTHYS DENTATUS											3		3	8	9	3		
28	PARALICHTHYS OBLONGUS	54	40	7							2	17	60	180	138	134	22		
29	LIMANDA FERRUGINEA	18	2	6	18	5	1	3	1	5				59	2			7	6
30	PSEUDOPLEURONECTES AMERICANUS	510	323	254	242	62	61	69	75	500	235	1245	2814	6390	1762	861	287	537	30
31	GLYPTOCEPHALUS CYNOGLOSSUS	1												1					
32	LOPHOPSETTA AQUOSA	2	1	146	42	64	102	40	42	9	1	3	12	464	102	95	56	68	98
33	LOPHIUS AMERICANUS	10	13	2	5	2	2				2			36	8		9	3	4
	DAILY TOTAL	955	862	3281	828	743	286	143	310	1216	402	1487	3448	13961	2874	1971	1157	1614	898

	SPECIES	1945 JAN.	1945 FEB.	1945 MAR. 5	1945 APR. 16	1945 MAY 27	1945 JUNE 18	1945 JULY 17	YEARLY TOTAL	1945 AUG. 21	1945 SEPT. 23	1945 OCT. 15	1945 NOV. 11	1945 DEC.	1946 JAN. 14	1946 FEB. 19	1946 MAR. 24	1946 APR.	1946 MAY 6	1946 JUNE 9	1946 JULY	YEARLY TOTAL	GRAND TOTAL
1	MUSTELUS CANIS					2			2													0	2
2	SQUALUS ACANTHIAS								16	8	8	8								4		28	49
3	RAJA ERINACEA			15	3	94	205	301	1367	1132	226	250	46		40	60	31		114	298		2197	4182
4	RAJA DIAPHANES			5	27		6	60	179	78	4	16			18	25			36			177	443
5	RAJA STABULIFORIS						6	3	64	4		4								14		22	157
6	CLUPEA HARENGUS								2													0	2
7	POMOLOBUS PSEUDOHARENGUS								2													0	6
8	PORONOTUS TRIACANTHUS								10		2											2	12
9	CENTROPRISTES STRIATUS								0			2	1									3	3
10	STENOTOMUS CHRYSOPS					2			29		12	102	1									115	147
11	MENTICIRRHUS SAXATILIS								0			2										2	2
12	TAUTOGOLABRUS ADSPERSUS								33	10		8										18	79
13	TAUTOGA ONITIS								0													0	1
14	STEPHANOLEPIS HISPIDUS								3		2											2	5
15	SPHEROIDES MACULATUS					7			7		106	4										110	117
16	MYOXOCEPHALUS OCTODECIMSPINOSUS			247	609	31	115	5	2070			32	45		243	519	11		106	66		1022	7768
17	HEMITRIPTERUS AMERICANUS			1		2		3	30			6				2	1			2		11	63
18	PRIONOTUS CAROLINUS					5	11	1	43	26	180	56							44			306	370
19	PRIONOTUS EVOLANS								0		2	2										4	5
20	MACROZOARCES AMERICANUS			6	31		1		44						5	1			56			62	140
21	MERLUCCIUS BILINEARIS					80	88	75	2199	68	448	276	65		10				28	28		923	3879
22	GADUS MORHUA				27				96				1		6	2						9	170
23	MELANOGRAMMUS AEGLIFINUS								0													0	1
24	UROPHYCIS REGIUS								0		2		1									3	3
25	UROPHYCIS TENUIS						22		50	12	52	30	3							8		105	303
26	UROPHYCIS CHUSS						39	32	186	4	70	82								8		164	636
27	PARALICHTHYS DENTATUS					3	7		30	28	10	8							2	4		52	85
28	PARALICHTHYS OBLONGUS					3	18	24	339	220	110	16	2						8	20		376	895
29	LIMANDA FERRUGINEA			4	5				24						13	5						18	101
30	PSEUDOPLEURONECTES AMERICANUS			79	306	1729	446	823	6860	536	432	234	251		177	61	28		234	374		2327	15577
31	GLYPTOCEPHALUS CYNOGLOSSUS								0													0	1
32	LOPHOPSETTA AQUOSA			35		15	2	13	484	382	392	110	72		109	69	10		8			1152	2100
33	LOPHIUS AMERICANUS				1		4		29		4	4							8	2		18	83
	DAILY TOTAL			392	1009	1973	970	1340	14198	2508	2062	1252	488		621	744	81		644	828		9228	37387

NOTE: IV/23/'44, PART OF P. AMERICANUS (30) CATCH ESTIMATED - POSSIBLE ± ERROR OF 15-20 FISH

POUNDS OF FISH BY SPECIES PER ONE-HOUR HAUL PER MONTH, 1943 - 1946

TABLE V.

	SPECIES	1943 AUG. 16	1943 SEPT. 12	1943 OCT. 31	1943 NOV. 21	1943 DEC. 19	1944 JAN. 23	1944 FEB. 20	1944 MAR. 19	1944 APR. 23	1944 MAY 18	1944 JUNE 23	1944 JULY 23	YEARLY TOTAL	AVE. PER DRAG	NO. OF TIMES CAUGHT
1	MUSTELUS CANIS													0	0	0
2	SQUALUS ACANTHIAS		1.8	10.7									9.9	22.4	7.5	3
3	RAJA ERINACEA	112.8	249.7	47.7	19.5	14.6	20.5	8.0	24.3	64.1	22.4	134.9	52.8	771.3	64.3	12
4	RAJA DIAPHANES	2.7	23.1	61.2	11.4	4.4	8.3	10.7	15.1	16.2		49.3	9.4	211.8	19.3	11
5	RAJA STABULIFORIS	3.4	48.5	92.4						1.4		9.7	65.2	220.6	36.8	6
6	CLUPEA HARENGUS													0	0	0
7	POMOLOBUS PSEUDOHARENGUS									1.8				1.8	1.8	1
8	PORONOTUS TRIACANTHUS													0	0	0
9	CENTROPRISTES STRIATUS													0	0	0
10	STENOTOMUS CHRYSOPS			0.2							0.2	0.5		0.9	0.3	3
11	MENTICIRRHUS SAXATILIS													0	0	0
12	TAUTOGOLABRUS ADSPERSUS	0.8		5.9						1.3	5.0	2.1	6.4	21.5	3.6	6
13	TAUTOGA ONITIS										0.6			0.6	0.6	1
14	STEPHANOLEPIS HISPIDUS													0	0	0
15	SPHEROIDES MACULATUS													0	0	0
16	MYOXOCEPHALUS OCTODECIMSPINOSUS	71.9	79.6	961.3	107.4	247.2	45.3	9.3	78.6	196.9	43.4	16.7	6.7	1864.3	155.4	12
17	HEMITRIPTERUS AMERICANUS		2.1	1.5	0.3	0.3	1.7		0.9		0.7	2.7	6.7	16.9	1.9	9
18	PRIONOTUS CAROLINUS		4.9	0.4							5.5		1.0	11.8	3.0	4
19	PRIONOTUS EVOLANS										0.6			0.6	0.6	1
20	MACROZOARCES AMERICANUS		9.5			1.4		3.1	4.0	30.4	0.8			49.2	8.2	6
21	MERLUCCIUS BILINEARIS	16.0	10.2	49.9	74.5	5.7					6.7	26.4	151.6	341.0	42.6	8
22	GADUS MORHUA	3.2	1.2	56.5	12.4	154.3	8.5	35.2	6.5	20.0				297.8	33.1	9
23	MELANOGRAMMUS AEGLIFINUS	1.2												1.2	1.2	1
24	UROPHYCIS REGIUS													0	0	0
25	UROPHYCIS TENUIS	26.1	2.1	100.6									57.4	186.2	46.6	4
26	UROPHYCIS CHUSS	18.7	14.7	74.2	1.4					6.8	1.7	0.9	95.8	214.2	26.8	8
27	PARALICHTHYS DENTATUS											1.7		1.7	1.7	1
28	PARALICHTHYS OBLONGUS	29.2	20.1	3.8							0.9	8.0	29.1	91.1	15.2	6
29	LIMANDA FERRUGINEA	13.2	1.2	4.4	14.4	1.7	0.7	3.1	0.4	3.9				43.0	4.8	9
30	PSEUDOPLEURONECTES AMERICANUS	397.0	280.5	145.5	181.1	60.7	48.4	59.8	78.9	300.0	170.4	728.7	1152.4	3603.4	303.3	12
31	GLYPTOCEPHALUS CYNOGLOSSUS	0.6												0.6	0.6	1
32	LOPHOPSETTA AQUOSA	1.2	0.5	75.9	20.7	34.5	58.4	24.9	27.5	5.3	0.3	2.4	7.5	259.1	21.6	12
33	LOPHIUS AMERICANUS	16.5	68.2	16.9	99.4	19.8	38.8				44.1			303.7	43.4	7
	DAILY TOTAL	714.5	817.9	1709.0	542.5	544.6	230.6	154.1	236.2	648.1	303.3	984.0	1651.9	8536.7		

	SPECIES	1944 AUG. 13	1944 SEPT. 10	1944 OCT. 26	1944 NOV. 19	1944 DEC. 18	1945 JAN.	1945 FEB.	1945 MAR. 5	1945 APR. 16	1945 MAY 27	1945 JUNE 18	1945 JULY 17	YEARLY TOTAL	AVE. PER DRAG	NO. OF TIMES CAUGHT
1	MUSTELUS CANIS										9.4			9.4	9.4	1
2	SQUALUS ACANTHIAS	54.1	1.2											55.3	27.7	2
3	RAJA ERINACEA	407.3	245.8	80.9	21.9	112.2			19.8	4.6	106.9	250.2	396.3	1645.9	164.6	10
4	RAJA DIAPHANES	41.5	36.6	45.0	35.8	50.9			8.5	5.2		37.9	182.2	443.6	49.3	9
5	RAJA STABULIFORIS	125.6	4.7			75.0						36.4	2.5	244.2	48.8	5
6	CLUPEA HARENGUS					0.6								0.6	0.6	1
7	POMOLOBUS PSEUDOHARENGUS					0.3								0.3	0.3	1
8	PORONOTUS TRIACANTHUS	0.6	1.3			0.4								2.3	0.8	3
9	CENTROPRISTES STRIATUS													0	0	0
10	STENOTOMUS CHRYSOPS		21.5								2.3			23.8	11.9	2
11	MENTICIRRHUS SAXATILIS													0	0	0
12	TAUTOGOLABRUS ADSPERSUS	10.0	5.6											15.6	7.8	2
13	TAUTOGA ONITIS													0	0	0
14	STEPHANOLEPIS HISPIDUS				0.4									0.4	0.4	1
15	SPHEROIDES MACULATUS										3.0			3.0	0.3	1
16	MYOXOCEPHALUS OCTODECIMSPINOSUS	2.6	3.5	106.0	348.6	56.6			134.3	287.4	17.3	58.4	1.8	1016.5	101.7	10
17	HEMITRIPTERUS AMERICANUS	2.7		14.1	5.6	4.1			1.5		1.9		2.5	32.4	4.6	7
18	PRIONOTUS CAROLINUS		16.5								2.7	14.1	1.2	34.5	8.6	4
19	PRIONOTUS EVOLANS													0	0	0
20	MACROZOARCES AMERICANUS					9.2			17.3	98.7		2.2		127.4	31.9	4
21	MERLUCCIUS BILINEARIS	181.4	271.4	139.8	79.6	116.6					48.1	32.6	33.4	902.9	112.9	8
22	GADUS MORHUA			5.7	18.5	253.6				21.3				299.1	74.8	4
23	MELANOGRAMMUS AEGLIFINUS													0	0	0
24	UROPHYCIS REGIUS													0	0	0
25	UROPHYCIS TENUIS	9.1	16.4			9.5						29.6		64.6	16.2	4
26	UROPHYCIS CHUSS	28.9	55.1	2.2		3.8						31.1	19.0	140.1	23.4	6
27	PARALICHTHYS DENTATUS	14.1	36.5	7.1							9.1	7.6		74.4	14.9	5
28	PARALICHTHYS OBLONGUS	57.9	57.2	13.0							1.8	9.6	11.1	150.6	25.1	6
29	LIMANDA FERRUGINEA	0.2			6.9	4.4			2.3	4.5				18.3	3.6	5
30	PSEUDOPLEURONECTES AMERICANUS	822.7	441.9	221.8	385.4	20.7			49.6	281.6	1000.3	293.1	539.4	4056.7	405.7	10
31	GLYPTOCEPHALUS CYNOGLOSSUS													0	0	0
32	LOPHOPSETTA AQUOSA	63.1	62.7	27.9	37.0	49.1			20.2		6.9	1.9	9.2	278.0	32.7	9
33	LOPHIUS AMERICANUS	59.2		207.1	17.4	79.4				20.2		21.5		404.8	67.5	6
	DAILY TOTAL	1881.0	1277.9	870.6	957.1	846.4			253.5	723.7	1209.7	826.2	1198.6	10044.7		

	SPECIES	1945 AUG. 21	1945 SEPT. 23	1945 OCT. 15	1945 NOV. 11	1945 DEC.	1946 JAN. 14	1946 FEB. 19	1946 MAR. 24	1946 APR.	1946 MAY 6	1946 JUNE 9	1946 JULY	YEARLY TOTAL	AVE. PER DRAG	NO. OF TIMES CAUGHT	GRAND TOTAL	GRAND AVE. PER DRAG	TOTAL NO. OF TIMES CAUGHT	
1	MUSTELUS CANIS													0	0	0	9.4	9.4	1	1
2	SQUALUS ACANTHIAS	4.8	4.5	5.2								1.3		15.8	4.0	4	93.5	10.4	9	2
3	RAJA ERINACEA	975.1	155.1	299.0	47.1		47.1	78.2	34.7		141.6	344.5		2122.4	235.8	9	4539.6	146.4	31	3
4	RAJA DIAPHANES	229.0	12.5	38.2			39.4	53.7			110.5			483.3	80.6	6	1138.7	43.8	26	4
5	RAJA STABULIFORIS	5.2		9.9								159.3		174.4	58.1	3	639.2	45.7	14	5
6	CLUPEA HARENGUS													0	0	0	0.6	0.6	1	6
7	POMOLOBUS PSEUDOHARENGUS													0	0	0	2.1	1.1	2	7
8	PORONOTUS TRIACANTHUS		0.1											0.1	0.1	1	2.4	0.6	4	8
9	CENTROPRISTES STRIATUS			1.7	0.3									2.0	1.0	2	2.0	1.0	2	9
10	STENOTOMUS CHRYSOPS		4.6	3.2	0.1									7.9	2.6	3	32.6	4.1	8	10
11	MENTICIRRHUS SAXATILIS			0.4										0.4	0.4	1	0.4	0.4	1	11
12	TAUTOGOLABRUS ADSPERSUS	12.2		12.1										24.3	12.2	2	61.4	6.1	10	12
13	TAUTOGA ONITIS													0	0	0	0.6	0.6	1	13
14	STEPHANOLEPIS HISPIDUS		0.2											0.2	0.2	1	0.6	0.3	2	14
15	SPHEROIDES MACULATUS		60.1	2.3										62.4	31.2	2	65.4	21.8	3	15
16	MYOXOCEPHALUS OCTODECIMSPINOSUS			16.3	21.8		118.4	255.1	5.1		46.5	35.9		499.1	71.3	7	3379.9	116.5	29	16
17	HEMITRIPTERUS AMERICANUS			6.1				1.4	1.5			0.5		9.5	2.4	4	58.8	2.9	20	17
18	PRIONOTUS CAROLINUS	20.7	43.9	22.3							20.5			107.4	26.9	4	153.7	12.8	12	18
19	PRIONOTUS EVOLANS		0.3	1.9										2.2	1.1	2	2.8	0.9	3	19
20	MACROZOARCES AMERICANUS						17.4	4.9			149.4			171.7	57.2	3	348.3	26.8	13	20
21	MERLUCCIUS BILINEARIS	44.2	158.9	90.5	29.5		2.7				9.1	13.2		348.1	49.7	7	1592.0	69.2	23	21
22	GADUS MORHUA				4.2		23.3	12.2						39.7	13.2	3	636.6	39.8	16	22
23	MELANOGRAMMUS AEGLIFINUS													0	0	0	1.2	1.2	1	23
24	UROPHYCIS REGIUS		0.4		0.4									0.8	0.4	2	0.8	0.4	2	24
25	UROPHYCIS TENUIS	3.2	20.2	17.4	1.2							5.1		47.1	9.4	5	297.9	22.9	13	25
26	UROPHYCIS CHUSS	2.2	29.4	79.1								8.7		122.4	30.6	4	476.7	26.5	18	26
27	PARALICHTHYS DENTATUS	88.8	15.7	14.5							2.5	5.7		127.2	25.4	5	203.3	18.5	11	27
28	PARALICHTHYS OBLONGUS	105.1	50.5	9.0	0.6						4.6	10.1		179.9	30.0	6	421.6	23.4	18	28
29	LIMANDA FERRUGINEA						17.1	2.4						19.5	9.8	2	80.8	5.1	16	29
30	PSEUDOPLEURONECTES AMERICANUS	319.3	277.7	114.5	130.8		173.5	36.0	24.4		226.9	310.1		1613.2	179.2	9	9273.3	299.1	31	30
31	GLYPTOCEPHALUS CYNOGLOSSUS													0	0	0	0.6	0.6	1	31
32	LOPHOPSETTA AQUOSA	196.0	190.8	51.8	28.1		64.3	42.4	5.6		5.4			584.4	73.1	8	1121.5	38.7	29	32
33	LOPHIUS AMERICANUS		4.1	1.5							174.5	3.3		183.4	45.9	4	891.9	52.5	17	33
	DAILY TOTAL	2008.8	1029.0	796.9	264.1		503.2	486.3	71.3		891.5	897.7		6948.8			25530.2			

NOTE: VIII/21/'45, 2% OF R. ERINACEA (3) SLIGHTLY DEHYDRATED ...... VIII/21/'45, 5% OF R. DIAPHANES (4) SLIGHTLY DEHYDRATED ...... IV/16/'45, PART OF STOMACH CONTENTS OF M. AMERICANUS (20) LOST ...... IV/23/'44, PART OF P. AMERICANUS (30) CATCH ESTIMATED - POSSIBLE ± 10 POUND ERROR

AVERAGE WEIGHTS OF INDIVIDUAL FISH BY SPECIES PER MONTH, 1943 – 1946

TABLE VI.

	SPECIES	1943 AUG. 16	1943 SEPT. 12	1943 OCT. 31	1943 NOV. 21	1943 DEC. 19	1944 JAN. 23	1944 FEB. 20	1944 MAR. 19	1944 APR. 23	1944 MAY 18	1944 JUNE 23	1944 JULY 23	AVERAGE YEARLY TOTAL	1944 AUG. 13	1944 SEPT. 10	1944 OCT. 26	1944 NOV. 19	1944 DEC. 18
1	MUSTELUS CANIS													0					
2	SQUALUS ACANTHIAS		1.8	5.5									5.0	4.5	3.9	0.6			
3	RAJA ERINACEA	1.3	1.4	1.1	1.1	1.1	1.3	1.3	1.3	1.1	1.1	1.2	1.3	1.2	1.1	1.1	1.2	1.2	1.2
4	RAJA DIAPHANES	1.4	2.6	3.8	1.3	1.5	1.4	2.7	1.5	2.3		3.3	1.6	2.4	3.0	1.8	2.6	3.6	2.5
5	RAJA STABULIFORIS	1.6	1.1	18.5						1.4		1.1	16.6	3.1	2.5	1.6			37.5
6	CLUPEA HARENGUS													0					0.3
7	POMOLOBUS PSEUDOHARENGUS											0.5		0.5					0.2
8	PORONOTUS TRIACANTHUS													0	0.3	0.2			0.2
9	CENTROPRISTES STRIATUS													0					
10	STENOTOMUS CHRYSOPS			0.2							0.2	0.5		0.3		0.8			
11	MENTICIRRHUS SAXATILIS													0					
12	TAUTOGOLABRUS ADSPERSUS	0.8		1.5						1.3	0.5	0.7	0.8	0.8	0.4	0.6			
13	TAUTOGA ONITIS										0.6			0.6					
14	STEPHANOLEPIS HISPIDUS													0				0.1	
15	SPHEROIDES MACULATUS													0					
16	MYOXOCEPHALUS OCTODECIMSPINOSUS	0.4	0.4	0.4	0.4	0.5	0.5	0.6	0.5	0.3	0.4	0.4	0.5	0.4	0.3	0.4	0.5	0.5	0.5
17	HEMITRIPTERUS AMERICANUS		0.5	1.5	0.3	0.3	1.7		0.9		0.7	0.7	0.8	0.8	0.7		2.1	0.8	0.7
18	PRIONOTUS CAROLINUS		0.7	0.2							0.6		0.5	0.6		0.6			
19	PRIONOTUS EVOLANS									0.6				0.6					
20	MACROZOARCES AMERICANUS		1.2			1.4		3.1	2.0	1.4	0.8			1.4					1.5
21	MERLUCCIUS BILINEARIS	0.7	1.0	0.4	0.3	0.3					0.5	0.7	0.4	0.5	0.5	0.6	0.3	0.3	0.3
22	GADUS MORHUA	1.6	1.2	9.4	3.1	3.9	4.3	7.1	6.5	5.0				4.6			2.9	2.6	4.2
23	MELANOGRAMMUS AEGLIFINUS	1.2												1.2					
24	UROPHYCIS REGIUS													0					
25	UROPHYCIS TENUIS	1.1	2.1	1.3									1.4	1.3	1.5	1.4			1.0
26	UROPHYCIS CHUSS	0.4	0.6	1.0	0.7					0.8	0.9	0.9	0.7	0.8	0.9	0.7	1.1		0.6
27	PARALICHTHYS DENTATUS											0.6		0.6	1.8	4.1	2.4		
28	PARALICHTHYS OBLONGUS	0.5	0.5	0.5							0.5	0.5	0.5	0.5	0.4	0.4	0.6		
29	LIMANDA FERRUGINEA	0.7	0.6	0.7	0.8	0.3	0.7	1.0	0.4	0.8				0.7	0.1			1.0	0.7
30	PSEUDOPLEURONECTES AMERICANUS	0.7	0.7	0.6	0.7	1.0	0.8	0.9	1.1	0.6	0.7	0.6	0.6	0.6	0.5	0.5	0.7	0.7	0.7
31	GLYPTOCEPHALUS CYNOGLOSSUS	0.6												0.6					
32	LOPHOPSETTA AQUOSA	0.6	0.5	0.5	0.5	0.5	0.6	0.6	0.7	0.6	0.3	0.8	0.6	0.6	0.6	0.7	0.5	0.5	0.5
33	LOPHIUS AMERICANUS	1.7	5.2	8.5	19.9	9.9	19.4				22.1			8.4	7.4		23.0	5.8	19.9

	SPECIES	1945 JAN.	1945 FEB.	1945 MAR. 5	1945 APR. 16	1945 MAY 27	1945 JUNE 18	1945 JULY 17	AVERAGE YEARLY TOTAL	1945 AUG. 21	1945 SEPT. 23	1945 OCT. 15	1945 NOV. 11	1945 DEC.	1946 JAN. 14	1946 FEB. 19	1946 MAR. 24	1946 APR.	1946 MAY 6	1946 JUNE 9	1946 JULY	AVERAGE YEARLY TOTAL	AVERAGE GRAND TOTAL
1	MUSTELUS CANIS					4.7			4.7													0	4.7
2	SQUALUS ACANTHIAS								3.5	0.6	0.6	0.7								0.3		0.6	1.9
3	RAJA ERINACEA			1.3	1.5	1.1	1.2	1.3	1.2	0.9	0.7	1.2	1.0		1.2	1.3	1.1		1.2	1.2		1.0	1.1
4	RAJA DIAPHANES			1.7	0.2		6.3	3.0	2.5	2.9	3.1	2.4			2.2	2.2			3.4			2.7	2.7
5	RAJA STABULIFORIS						6.1	0.8	3.9	1.3		2.5								11.4		7.9	4.1
6	CLUPEA HARENGUS								0.3													0	0.3
7	POMOLOBUS PSEUDOHARENGUS								0.2													0	0.4
8	PORONOTUS TRIACANTHUS								0.2		0.1											0.1	0.2
9	CENTROPRISTES STRIATUS								0			0.9	0.3									0.7	0.7
10	STENOTOMUS CHRYSOPS					1.2			0.8		0.4	0.03	0.1									0.1	0.2
11	MENTICIRRHUS SAXATILIS								0			0.2										0.2	0.2
12	TAUTOGOLABRUS ADSPERSUS								0.5	1.2		1.5										1.4	0.8
13	TAUTOGA ONITIS								0													0	0.6
14	STEPHANOLEPIS HISPIDUS								0.1		0.1											0.1	0.1
15	SPHEROIDES MACULATUS					0.4			0.4		0.6	0.6										0.6	0.6
16	MYOXOCEPHALUS OCTODECIMSPINOSUS			0.5	0.5	0.6	0.5	0.4	0.5		0.5	0.5			0.5	0.5	0.5		0.4	0.5		0.5	0.4
17	HEMITRIPTERUS AMERICANUS			1.5		1.0		0.8	1.1			1.0				0.7	1.5			0.3		0.9	0.9
18	PRIONOTUS CAROLINUS					0.5	1.3	1.2	0.8	0.8	0.2	0.4							0.5			0.4	0.4
19	PRIONOTUS EVOLANS								0		0.2	1.0										0.6	0.6
20	MACROZOARCES AMERICANUS			2.9	3.2		2.2		2.9						3.5	4.9			2.7			2.8	2.5
21	MERLUCCIUS BILINEARIS					0.6	0.4	0.4	0.4	0.7	0.4	0.3	0.5		0.3				0.3	0.5		0.4	0.4
22	GADUS MORHUA				0.8				3.1				4.2		3.9	6.1						4.4	3.7
23	MELANOGRAMMUS AEGLIFINUS								0													0	1.2
24	UROPHYCIS REGIUS								0		0.2		0.4									0.3	0.3
25	UROPHYCIS TENUIS						1.3		1.3	0.3	0.4	0.6	0.4							0.6		0.5	1.0
26	UROPHYCIS CHUSS						0.8	0.6	0.8	1.3	0.4	1.0								1.1		0.7	0.7
27	PARALICHTHYS DENTATUS					3.0	1.1		2.5	3.2	1.6	1.8							1.3	1.4		0.3	2.4
28	PARALICHTHYS OBLONGUS					0.6	0.5	0.5	0.4	0.5	0.5	0.6	0.3						0.6	0.5		0.5	0.5
29	LIMANDA FERRUGINEA			0.6	0.9				0.8						1.3	0.5						1.1	0.8
30	PSEUDOPLEURONECTES AMERICANUS			0.6	0.9	0.6	0.7	0.7	0.6	0.6	0.6	0.5	0.5		1.0	0.6	0.9		1.0	0.8		0.7	0.6
31	GLYPTOCEPHALUS CYNOGLOSSUS								0													0	0.6
32	LOPHOPSETTA AQUOSA			0.6		0.5	1.0	0.7	0.6	0.5	0.5	0.5	0.4		0.6	0.6	0.6		0.7			0.5	0.5
33	LOPHIUS AMERICANUS				20.2		5.4		20.6		1.0	0.4							21.8	1.7		10.2	10.7

SEE NOTES AT BOTTOM OF TABLE V

6. ESTIMATING FISHING INTENSITIES

By Alfred W. H. Needler

Fisheries Research Board of Canada

ABSTRACT

The two principal points in this discussion are: (1) the distinction between availability as indicated by catch-per-unit-of-effort and population as indicated by fishing mortality and catch, and (2) the decline, as fishing intensity increases, in the value of availability as an indication of changes in abundance and the corresponding increase in the importance of knowing fishing mortalities and populations. The latter are essential to any clear understanding of intensive fisheries and whether or how to manage them.

DISCUSSION

Mr. Chairman, I shall try to modify my remarks in the light of preceding presentations and discussions, hoping on the one hand to avoid repetition and on the other to provoke discussion. The title was assigned to me and is perhaps misleading, as I intend to speak of the significance rather than the methods of estimations of fishing intensities and populations.

To offset any apparent over-simplification I would like, first of all, to make a generalization about generalizations. It is quite obvious that no generalizations are valid in these matters unless they are qualified—unless they are what might be called conditioned or dynamic generalizations. We cannot say simply that any one factor is most important in all fisheries, either when assessing the potentialities of all fisheries or attempting to manage them. We cannot even say that any one factor is important or unimportant in all fisheries.

It was interesting, for example, in our discussion on trapping fish to surmise that in time we could probably contrive a sound generalization to the effect that the frequency with which a trap should be hauled to get the largest average catch per day would have a special relationship for each species to the fullness of the trap. On the other hand, we obviously could not generalize more simply and say that the catch either always increases or always decreases with frequency of hauling.

A great many factors affect the estimation of populations, the changes in populations and the devising of management procedures in which, after all, we are all interested in the broad sense of deciding what action may be taken to improve the take of fisheries. There is no fishery in which there are not a great many factors at work, and this brings me to one more generalization; namely, that even though one or more factors may be demonstrated to be particularly important in any one fishery, that does not necessarily mean that others do not have their effects. One might take our discussion of the Pacific halibut fishery as an example. To say that the fluctuations in abundance are principally caused by factors other than the fishery does not mean that the management of the fishery or control of fishing effort might not raise the general levels about which the fluctuations caused by these other factors occur.

Estimating Availabilities and Estimating Populations. There is a great mass of data on the catch-per-unit-of-effort which is practically synonymous with availability or the ease with which fish can be obtained.

Now, this is quite distinct from estimation of the actual population by relating the total catch to the fishing mortality (as measured, for example, by proportion of marked fish recaptured). Although catch-per-unit-of-effort may change in such a way as to indicate changes in the population, there is many a slip 'twixt the cup and the lip, because it has never, I think, been quite demonstrated that the catch-per-unit-of-effort is directly proportionate to the population. A great many other factors may enter in the fishing process.

Importance of Population Estimates Depends on Intensity. Knowledge of availability is always of direct practical importance to the fishery. Its value as an indication of abundance and, consequently, as a basis for management, declines with increasing intensity of fishing, and at the same time the importance of estimating the population increases.

Fisheries with Low Intensities. From the very start of a fishery it is important to know how much effort is necessary to catch fish. That determines the immediate economic prospects.

In a great many new fisheries—for instance, our explorations for herring in the Gulf of St. Lawrence—we are not immediately concerned with the total population. We are most definitely concerned with availability and how it varies with time and place. We are interested in the total population as an indication of the long-term potentialities and of what the expected industry might do to the population, but we are still concerned primarily with availability.

Then there are old fisheries which are still limited by demand as, for example, the herring fishery in the North Sea. I think that there, where the population has supported a very large fishing industry over a very long time and where the fishery is still limited by demand rather than by supply, it is not of much practical importance to know how many herring are in the sea. It is very important to know about availability, how catch-per-unit-of-effort varies from place to place and from time to time; and it is especially important because where there is an economic rather than a biological limitation to the fishery the cost of capture is extremely important. It has an importance which does not enter into such fisheries as those (one might list many: lobsters, whitefish, and so on) in which the demand is very good and in which the industry can afford to use expensive methods of capture.

Fisheries with Moderate Intensities. Now, we might proceed next to what one might call the moderately intensive fisheries, such as the haddock and the halibut. In these fisheries, with fishing mortalities of the general order of 10 to 20 per cent, estimations of fishing mortality and population become more important. Fishing mortality becomes a serious factor in the composition of the population as to size and age. In this connection I would point out that when one speaks of a fishing mortality it is usually in terms of a mortality during a certain period. An annual mortality as low as 10 per cent extended over twenty years of the life of halibut has a tremendous effect on the abundance of the older halibut. A similar fishing mortality applied to a fish like, say, the silverside, which is caught in only one of its years, is much less serious.

Now, in these moderately intensive fisheries we have a great deal of difficulty in making fishing mortality and population estimates, because the fishing mortalities are still so low as to make a high degree of accuracy very difficult, using methods which are effective in really intensive fisheries.

Fisheries with High Intensities. In this arbitrary classification a "really intensive" fishery is one such as the lobster fishery which, in Canadian waters, catches from about 40 to about 80 per cent of the lobsters of marketable size present on the fishing grounds in any one year. A knowledge of the population is important in these very intensive fisheries, and I presume there must be a great many fisheries which are equally intensive. Our knowledge of fishing mortalities is only in its infancy at the present time.

Knowledge of the size of the population and of the fishing mortality is very important in estimating the potentialities of such a fishery. Without such knowledge one might think, "Why, there are plenty of lobsters in the sea. We can greatly enlarge the number of fishermen and they'll all still make about the same kind of living." In an area where 80 per cent of the catchable lobsters are being caught each year, the prospects for a much larger fishing population obtaining almost the same sort of living are very low, and lower than in the places where fishing mortality is very much less.

In these intensive fisheries it is necessary to estimate populations through fishing mortalities in order to understand changes in abundance, because the catch-per-unit-of-effort fails entirely to indicate such changes. In the Canadian lobster fishery the catch-per-unit-of-effort in the first week of the two-months' season, if an adequate sample could be taken, might indicate the abundance of the lobsters at the beginning of the season, but the fishery is so intensive that the abundance is often reduced to a stage where the fishermen stop fishing before the end of the season. Under these circumstances it is very difficult to obtain any estimate of changes in abundance from year to year on the basis of catch-per-unit-of-effort, and the total catch would be a very inaccurate indication unless corrected by some knowledge of the fishing mortality.

Fishing Mortality and Size Limits. There is another value in knowing the fishing mortality which is important in intensive fisheries, and that is in its application to the problem of size limits. Whether or not the capture or retention of fish below a certain minimum size limit should be prohibited depends on whether or not the total take would be increased by catching the fish at a higher average size than would occur without that particular restriction. Knowledge of the fishing mortality is an essential to forming a sound opinion on this question.

For example, if we are catching a known high proportion (such as 80%) of the marketable lobsters in a certain locality, if we know the rate of increase in weight of the individual lobsters near the lower limit of size at which they are caught, and if we can estimate the mortality from other causes than fishing ("natural mortality"), then we can predict whether or not a new or a higher minimum size limit would lead to a greater weight of lobsters being caught. There are obviously many difficulties in the way of making such a calculation. Natural mortality, for example, may be estimated as the difference between total mortality as shown by age frequencies and fishing mortality as shown by the proportion of marked fish returned. Accuracy is obviously difficult and limited but may set reliable limits which permit the sound conclusion that the size at which the lobsters are caught should be increased. There is a further difficulty in that we cannot predict the effects, on the natural mortality and on the growth rate, of increasing the population on the fishing grounds by establishing or raising a size limit. But here, again, we must fall back on population estimates to discover what the effects actually are. We should have them before and after the action is taken.

With these few generalizations about the value of estimating the population through fishing mortalities and of knowing fishing mortalities themselves, I shall close and hope that other points may be brought out in discussion.

DISCUSSION

Van Oosten: Dr. Needler is now open for "needling."

Huntsman: You insist upon the primary importance of availability rather than of the populations. Is that based upon the belief that the problems with which you are particularly concerned will be sufficiently handled without knowledge of populations, or that the whole thing is so vast that you had best take what seems to be the easier way of getting a fair answer?

Needler: The latter. I think the long-term solution of the problem should include an estimate of the population in all cases, but for the immediate practical purpose the availability is most valuable in many instances.

Huntsman: I am entirely in agreement with you. I have been pressing strongly for the assessment of the populations because, to deal effectively with populations, we must measure them. Availability is of first importance economically—the fisherman wants to know whether he is going to get fish or not. Nevertheless, if we are to take account of variability in availability, it is essential to know something about the size of the population, which I think you were trying to indicate.

Needler: I think in those cases where the fishery is not very intensive, availability is a better indication of changes of abundance than it is in the case where the fishery is really intensive and in which the catch-per-unit-of-effort is affected by the fishery as the season progresses as well as by the abundance at the beginning of the fishing season. That, of course, is a lucky thing, because in the less intensive fisheries the catch-per-unit-of-effort is much easier to get than any population estimate, whereas in the more intensive fisheries, such as the one I used for an example, you can get some estimate of population with reasonable accuracy, let us say, within 15 or 20 per cent.

Huntsman: You spoke about the difficulty of determining the natural mortality. Doubtless that would be affected by your so-called fishing mortality. You had 80 per cent fishing mortality and I think you also spoke of 20 per cent natural mortality. That means none were left to grow up.

Needler: I was talking about a two-month season for the fishing mortality, and I mentioned the estimated natural mortality between that season and the next one as in the neighborhood of 10 or 15 per cent of what was left.

Langlois: I don't know a thing about lobsters, being a fresh-water biologist, but I have watched the behavior of crayfish a little bit and maybe there is something comparable. In the case of crayfish there is a definite territorial limitation that is involved. A big crayfish has to have quite a big-sized territory. He is, shall we say, a dominant being. The number of crayfish any pond can support is definitely limited. It can support a great deal more in the way of small ones than large ones. I just wonder if your problem of lobster abundance may not be definitely associated with the territory of the bottom.

Needler: I think it is. The fishermen know that. They keep moving their gear all the time because if they put a trap down in exactly the same place they don't catch their lobsters as quickly as they would if it is moved. Of course, the intensity of the lobster fishery runs into thousands of traps per square mile, and these are constantly being moved about. I think that sampling tends to overcome this very local occurrence of the dominant individual.

Burkenroad: I'd like to applaud Dr. Needler's statement of the importance of regarding regulation as part of the equipment of the fishery biologist; in other words, as an experimental tool. It is customary to apply regulations as though they embodied a complete knowledge of the situation. It is frequently the case that no further adequate observation of a fishery that has shown decline is made, once a set of regulations has been put through on the basis that "We now know enough to regulate." If it could be more widely understood that in the present state of knowledge regulation is only a means of testing various hypotheses—and the only such experimental method available to the fishery biologist—we would rapidly come to command a great deal more information than we do now.

Needler: Mr. Chairman, I wouldn't suggest for a moment a regulation that I didn't think would improve matters. In other words, the range of experimentation that way is certainly limited, but it is true, I think, that the results of a new regulation can give you, as it were, more than one point on your curve. You can regard the thing in a more dynamic fashion—that is, develop a sound generalization over a variation in conditions.

Herrington: I think the reason it hasn't been mentioned before is because fishery biologists take it for granted that every regulation is part of an experiment, to be followed up by observations on the reaction.

Huntsman: The chief need, I think, Mr. Chairman, is that the fishing industry generally should realize that each one of these regulations should be considered as an experiment.

Herrington: Yes, that is right. Frequently the biologist has convinced himself of she validity of his conclusions to such an extent that he attempts to sell the conclusions as established fact. It may be more difficult to get action, saying it is experimental, but I think in most cases it would be more valuable in the long run to sell it on those terms.

In classifying haddock as a fishery of intermediate intensity, you mentioned 20 per cent. We have considerable data which suggest that on Georges Bank the total mortality is nearer 50 per cent.

Needler: In that case it graduates to the intensive category.

Herrington: In regard to it being more difficult to get an abundance measure for the fishery of high intensity, there is the intermediate case of the lobster fishery along the New England coast which is a 12-month affair. By getting the catch-per-unit-of-effort by months or by half-months it is possible to get a relatively good measure of relative changes by comparing the catch-per-trap at the beginning of one lobster year (September or October) with that in another. Comparing month for month you get a good measure of the relative changes in the population or of the availability. If you get an adequate amount of information over your short periods of time you can do this.

Needler: I agree. This lobster fishery of ours is a special case.

Herrington: If you could get the first day or few days of the season, you might be able to use catch-per-trip. It would seem to be just a different type of problem.

Needler: In actual practice it is almost impossible to get a good sample showing the changes in the availability day by day because, unfortunately, at the beginning of the season there are rapid temperature changes which are changing the trapping activity of the lobsters very quickly.

7. COMPUTATION OF FISH PRODUCTION[1]

William E. Ricker
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and

R. E. Foerster
Fisheries Research Board of Canada

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ABSTRACT

The annual production of a fish population is defined as the product of the average population on hand and the instantaneous rate of growth, summed over the whole of the year. A computation of production has been made for the young sockeye salmon of Cultus Lake, British Columbia, where it proved satisfactory to divide the year into

[1] Contribution No. 363 from the Department of Zoology, Indiana University.

half-month periods for this purpose. Published data on seasonal rate of growth and seasonal mortality rate provide the basis of the calculation. Total production varied greatly from year to year and reached a maximum of 41 metric tons, or 6.6 tons per square kilometer.

Production is concentrated in the summer months and falls to zero in winter. The fraction of the total production which appears as "yield" (seaward migrants) has varied. Prior to 1936 the average yearling stock was 28 per cent of the production plus the weight of the fry, but when a program of predator control was inaugurated it increased to about 44 per cent. The increase is about 55 per cent, and the increase in ratio of yield to production-plus-fry is about 65 per cent. This change has been accompanied by a decrease in the weight of fish dying in the lake, which is proportionately somewhat greater because a smaller initial weight of fry now suffices to produce any given yearling stock. Because of the more favorable ratio of yield to production, and probably also because of more efficient utilization of food for growth by the sockeye, no increase in production of the sockeye foods in the lake need be postulated to account for the sharp increases in yields of sockeye obtained while predators were controlled.

The mortality rate is greatest while the sockeye are very small, and the prolongation of this period of small size (hence greater vulnerability) in years when many fry are present appears to be a part of the mechanism whereby the total size of the population is regulated. Seasonal changes in average stomach contents of sockeye, per unit body weight, vary in much the same way as does growth. Little food is eaten by the very small sockeye of May and early June, and the suggestion is made that in years of very large populations some might even succumb to starvation. Approximate estimates of the annual consumption of Entomostraca by the sockeye of the lake can be made both from the production of the latter and from their stomach contents and rate of digestion. The two methods give results of the same order of magnitude. The maximum for a year appears to be about 12×10^{10} gram-calories, or 150 metric tons wet weight, or 24 tons per square kilometer. This is of the order of six times the mean annual standing crop.

Insofar as mortality is the result of predation, the instantaneous mortality rate is a direct measure of the activity of the predators, and rather small changes in amount of predation suffice to produce large changes in the percentage of the fish which survive, when that percentage is not large. At Cultus Lake it is estimated that if no other causes of mortality were present a reduction of the predator population by a little less than a third would have been sufficient to produce the observed increase in survival rate of the sockeye (after predator control was begun) to 2.3 times its former value. No evidence is available that other causes of death are of any great importance to young sockeye, though that possibility cannot be wholly excluded.

Computations of the production of other species of fish in other bodies of water will usually be more difficult than for the Cultus sockeye, but very likely it will often be possible to obtain data from which they can be estimated with sufficient accuracy to be of real usefulness.

INTRODUCTION

Ivlev (1945) and Clarke (1946) define the *production* or *net production* of any organism or class of organisms in a body of water as the total quantity elaborated during a stated period of time, regardless of whether or not all of it survives to the end of that time. Production, in this sense, is not an easy quantity to estimate. Obviously it is the product of the average population on hand and the rate of increase in weight of the fish in that population during the period under consideration. Since both the size of a fish population and its rate of growth can vary with the seasons, this means that each of these must be estimated at rather short intervals, their products computed, and the sum of the products taken, in order to compute the total production for a whole year. At Cultus Lake, British Columbia, information on the seasonal variation in growth and in size of the population of young sockeye salmon has been obtained in the course of investigations conducted from 1925 to 1938. This information can be used to make what is possibly the first factually-based estimate of the net production of a fish population that has ever been attempted.

Production, in this strict sense of the term, is of fundamental importance in respect to all questions concerning the productivity of waters. For example, to estimate the efficiency of conversion of fish food to fish flesh in a body of water it is first necessary to know how much fish flesh has been produced. At Cultus Lake the estimation of production is of particular interest for the following reason. The writers have reported that following a campaign of removal of predacious fishes in the lake there was a threefold increase in survival rate of the young salmon (Foerster and Ricker, 1941). At the same time, in two of the years of control, the weight of salmon leaving the lake greatly exceeded the maximum observed previously. It is of greatest interest, therefore, to determine whether or not this increased *yield* reflects an increased *production* of salmon in the lake.

The sockeye of Cultus Lake spawn from October to December, and the year of spawning is used to designate each *year-class*, that is, the fish from eggs laid, say in 1930, constitute the year-class of 1930. Eggs hatch in the spring and the young begin a free-swimming life during May; for simplicity, all the young are considered to begin their lake life at the middle of May. In most years a large majority of any brood leaves the lake the following spring, during April and early May.

Here we will take April 30 as the mean time of departure, and hence assign 11.5 months of lake life to the young salmon during the time they are in the age-group O, that is, while they are *fingerlings*. Thus the year-class of 1930 lives in the lake from May 16, 1931 to April 30, 1932. In addition to the yearling migrants there are a certain number of young which remain in the lake a second year; in the example of the year-class of 1930, these two-year-old migrants would leave the lake in April 1933, having spent the period May 1, 1932 to April 30, 1933 (approximately) in the lake as age I or *yearling* salmon. The number of these age I sockeye varies greatly; though usually a minority group, occasionally they exceed the number of yearling migrants of the same year-class. There are also a certain number of sockeye which never leave the lake (Ricker, 1938b). The number of these too is very variable, but even at best they appear to be scarce in relation to the number of migrants, and they cannot be included in our computations of production.

The following definitions can therefore be made:

1. The *yield* of sockeye from the lake in the year n consists of the weight of yearling migrants of year-class $(n - 2)$, plus the weight of two-year-old migrants of year-class $(n - 3)$.

2. The *yearling stock* in the lake just prior to migration is equal to the weight of yearling migrants leaving the lake, plus the weight of yearlings which do not leave the lake then, but whose survivors leave a year later.

3. The *production* of sockeye in the lake during a year's time (May 1–April 30) is the sum of (1) the total weight increment within the age O population from the time it hatches (considered as May 15) to the time it appears as age I yearling stock the following April 30; plus (2) the total weight increment within the age I population from May 1 to April 30.

BASIC DATA

Obviously, to compute the production of sockeye for a year we should know, for both age O and age I individuals:

a. the number and weight of the fish present at some time during the year;

b. the rate of growth during successive short periods throughout the year;

c. the rate of mortality during the same periods.

Some information on each of these points is available for the Cultus sockeye, though the data are not always as accurate as would be desirable.

(a) The determination of the number and weight of young sockeye present is easiest at the end of the year, *i.e.*, at time of migration in April. A direct count of the migrants and their average weight is available for all years (Foerster, 1944). The only uncertainty concerns the number and weight of nonmigrants. The majority of the survivors of these nonmigrants will migrate the following year, and their numbers then are available. In a later section (p. 194) evidence is presented that the sockeye suffer about 90 per cent mortality in their second year (as compared with 94 per cent in the first year), and accordingly these numbers are multiplied by 10 to give their initial abundance as yearlings. Following the change in survival rate which accompanied predator control, estimates of the number of nonmigrants are made on a different basis. The number of two-year migrants is multiplied by only 3, instead of 10, to give the number of nonmigrants of the previous year, because the new survival rate is about three times the old.

The average weight of a nonmigrant fish must also be estimated for each year. It is considerably less than that of the migrants of the same year-class, at least in years when nonmigrants are relatively numerous. From computed lengths at the annulus formation (Foerster, 1944: 272) it is possible to estimate that the yearling nonmigrants of the 1927 year-class were 0.55 of the weight of the migrants, on the average, and those of the 1931 class were 0.40. These ratios have been used for the corresponding years in Table I. For other years it is necessary to guess, using the principle that the ratio of average weight of a nonmigrant to a migrant is inversely related to the number of the former (their percentage of the total year-class) and also to the average size of the migrants.

Fortunately nonmigrants usually are few in number compared to the yearling migrants, so any arbitrariness in estimating their numbers and their weight can have little effect on the total result, except in the case of the year-classes of 1928 and 1932. The complete schedule of estimates of numbers and weight of the yearling stock is shown in Table I.

(b) To obtain estimates of the growth of the sockeye throughout the year, samples taken from the stomachs of piscivorous fishes are

TABLE I. NUMBER AND WEIGHT OF YEAR-OLD MIGRANTS, NONMIGRANTS, AND TOTAL YEARLING STOCK

1	2	3	4	5	6	7	8	9	10
Year-class	Migrants			Nonmigrants			Total yearling stock		
	Number (thousands)	Average weight (g.)	Total weight (kg.)	Number (thousands)	Average weight (g.)	Total weight (kg.)	Number (thousands)	Average weight (g.)	Total weight (kg.)
1925	183	8.10	1,480	17	7.0	120	200	8.00	1,600
1926	336	5.04	1,690	83	3.5	290	419	4.73	1,980
1927	2,426	3.06	7,420	666	1.68	1,120	3,092	2.76	8,540
1928	39	6.55	260	52	3.0	160	91	4.62	420
1929	350	7.10	2,490	2	7.0	10	352	7.10	2,500
1930	788	7.32	5,770	0	—	0	788	7.32	5,770
1931	1,571	3.67	5,770	633	1.46	920	2,204	3.04	6,690
1932	121	6.53	790	142	4.0	570	263	5.17	1,360
1933	242	7.55	1,830	4	7.5	30	246	7.55	1,860
1934	502	8.83	4,440	69	8.6	590	571	8.79	5,030
1935	3,101	5.96	18,490	60	5.8	350	3,161	5.96	18,840
1936	1,627	7.2	11,720	10	7.0	70	1,637	7.2	11,790

available. As it is seldom that sockeye from stomachs can be weighed satisfactorily, their lengths form the basis of the calculations. The best data are for the rather large year-classes of 1931 and 1935. The average fork length of the 1931-class sockeye, taken at different times of the year, is shown by Ricker (1937: table 1); similar figures for the 1935 class have been presented graphically (Ricker, 1938c) but are taken here from the original records. For the present purpose it is necessary to convert these lengths to weight. This has been done by using the formula

$$W = 0.0100\ L^3,$$

this being the best cubic equation taken from Foerster's (1944) data on migrants (W, weight in grams; L, fork length in centimeters). Among the very young fish the body is more slender and this relationship does not hold. However, the beginning of the weight curve, each year, can be anchored fairly well by considering 0.15 g. to be the mean weight of the fry at the time they become free-swimming, this time being taken as May 15. (The fact that very young fingerlings do not follow the length-weight equation above is illustrated by the two points for late May and early June in the 1935 growth curve of Fig. 1.) The mean weight of yearlings on April 30 is estimated by the method explained above (Table I, column 9). Complete growth curves are shown, plotted logarithmically, in Fig. 1. It should be observed that in choosing the exact position of these freehand curves we were in-

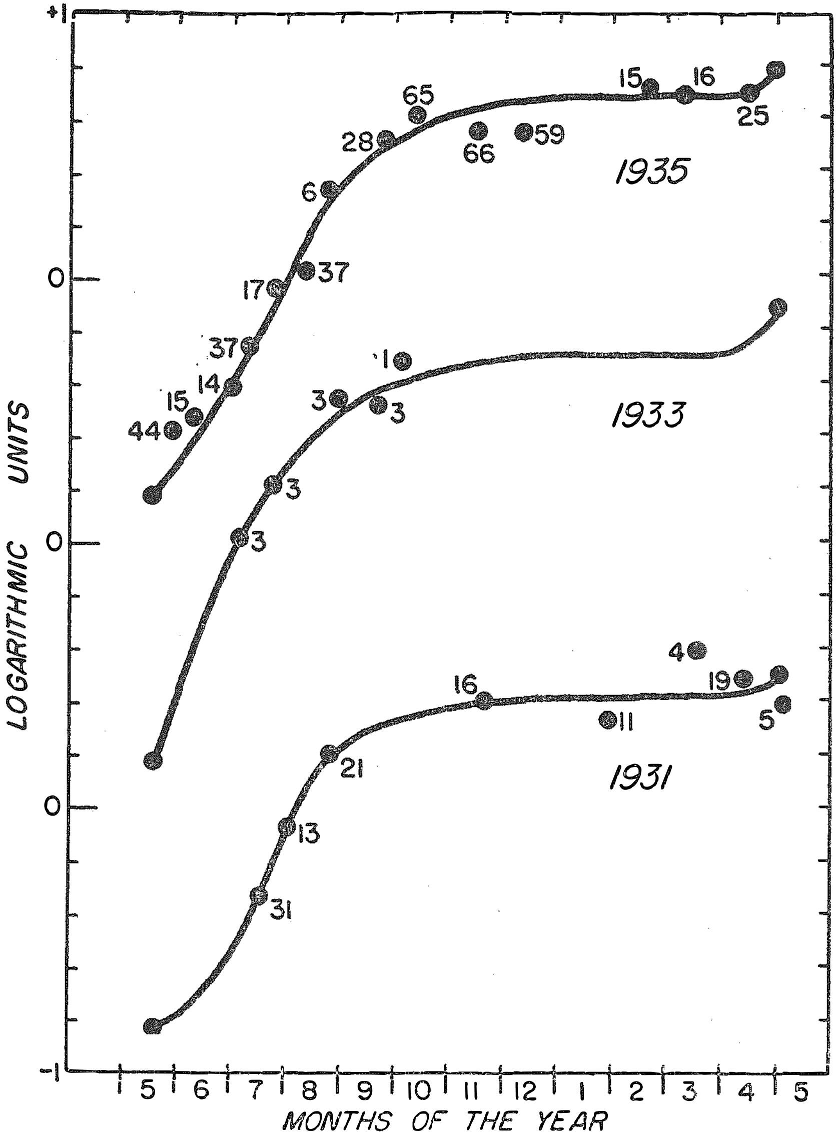

Figure 1. Logarithms of calculated mean weights in grams of young sockeye salmon, taken from stomachs of predators, of the year-classes of 1931, 1933 and 1935. Numbers beside each point indicate the number of fish on which it is based. The first point in each series is the mean weight of free-swimming fry, and the last point is the mean weight of the yearling stock (Table I, column 10). In the ordinate, each zero applies to the curve it stands opposite.

fluenced partly by the apparent amount of feeding done by the fish in each month (cf. Fig. 4).

The similarity of the growth curves among the three year-classes presented in Fig. 1, combined with fragmentary data for other years, justifies the conclusion that seasonal variation in rate of growth is of a rather regular character from year to year. For the purpose of this paper the growth of the 1931 year-class is taken as a model of relative seasonal growth, and seasonal growths in all other years are computed from it, using their observed total annual growths as a basis. In the case of the 1933 year-class of Fig. 1, which pertains to a smaller population than the other two, there is some indication that growth early in life is somewhat greater, relatively. While the data are certainly not sufficient to demonstrate it, this effect is what might be expected of a small population if the early months of life are at a time when food is relatively scarce. The possible influence of this source of error on the calculations is discussed later (p. 193).

The growth data are used in the form of the instantaneous rate of growth for each half-month, found by writing down logarithms from the smoothed curve for 1931 in Fig. 1, taking the differences between successive values, and dividing by 0.4343. The computation is given in Table II, columns 3–5. The sum of the semimonthly instantaneous rates is the instantaneous growth rate for the year, 3.01.

The semimonthly instantaneous growth rates for the 1931 year-class are now applied proportionately to all other years. For example, for the 1934 year-class the mean weight of the yearling stock is estimated as 8.79 g., or $8.79/0.15 = 58.6$ times their weight as fry. From this the instantaneous rate of growth for the year $= k = \log_e 58.6 = 4.07$. Accordingly, each of the semimonthly instantaneous rates for the 1931 class is multiplied by $4.07/3.01$ to obtain the corresponding value appropriate to the 1934 year-class.

(c) Estimates can be made of seasonal changes in mortality from data (Foerster, 1938) which are based primarily on the survival of marked fish of the year-class of 1933, released at various times during the year 1934–1935. The graph of survival is repeated here (Fig. 2, curve A), with the addition of points for time of hatching and time of migration. As regards the last-named, the two-year-old migrants of 1936 numbered 1,400, which means about 4,200 nonmigrants present a year earlier, as compared with 242,000 migrants. Thus the percentage of migration in 1935 can be taken as $242{,}000/246{,}000 = 98.3$ per cent.

TABLE II. COMPUTATION OF SEASONAL GROWTH RATE AND MORTALITY RATE. NOTE THAT INTERVALS LONGER THAN A HALF MONTH ARE USED FROM OCTOBER 31 TO DECEMBER 15, AND FROM DECEMBER 15 TO MARCH 15

1	*2*	*3*	*4*	*5*	*6*	*7*	*8*
		Computation of growth rate			*Computation of mortality rate*		
Date	*Months before migration*	*Logarithm of weight in grams*	*Difference of logarithms*	*Instantaneous growth rate (k.)*	*Percentage survival as migrants*	*Survival rate (s.)*	*Instantaneous mortality rate (i.)*
Apr. 30	0	0.48			0.983		
			0.03	0.07		0.763	0.27
Apr. 15	0.5	0.45			0.750		
			0.02	0.05		0.907	0.10
Mar. 31	1.0	0.43			0.680		
			0.01	0.02		0.961	0.04
Mar. 15	1.5	0.42			0.646		
			0.00	0.00		0.769	0.27
Dec. 15	4.5	0.42			0.497		
			0.03	0.06		0.845	0.17
Oct. 31	6.0	0.39			0.420		
			0.02	0.05		0.938	0.06
Oct. 15	6.5	0.37			0.394		
			0.04	0.09		0.931	0.07
Sep. 30	7.0	0.33			0.367		
			0.04	0.09		0.918	0.09
Sep. 15	7.5	0.29			0.337		
			0.06	0.14		0.911	0.09
Aug. 31	8.0	0.23			0.307		
			0.12	0.28		0.899	0.11
Aug. 15	8.5	0.11			0.276		
			0.18	0.41		0.887	0.12
July 31	9.0	$\bar{1}.93$			0.245		
			0.26	0.60		0.857	0.15
July 15	9.5	$\bar{1}.67$			0.210		
			0.21	0.49		0.824	0.20
June 30	10.0	$\bar{1}.46$			0.173		
			0.15	0.35		0.786	0.24
June 15	10.5	$\bar{1}.31$			0.136		
			0.08	0.19		0.735	0.31
May 31	11.0	$\bar{1}.23$			0.100		
			0.05	0.12		0.600	0.51
May 15	11.5	$\bar{1}.18$			0.060		
Total				3.01		0.0612	2.80

Since there is evidence from the stomachs of predators that mortality from predation increases sharply when the sockeye move inshore prior to migration (Ricker, 1941), the survival curve has been bent sharply upward in April instead of being given a broader slope from the previous observation onward.

It was more difficult to make a decision regarding the first point plotted in Fig. 2A. The ratio of yearling stock to eyed-eggs planted was 5.63 per cent for the 1933 year-class. Since there is evidence for

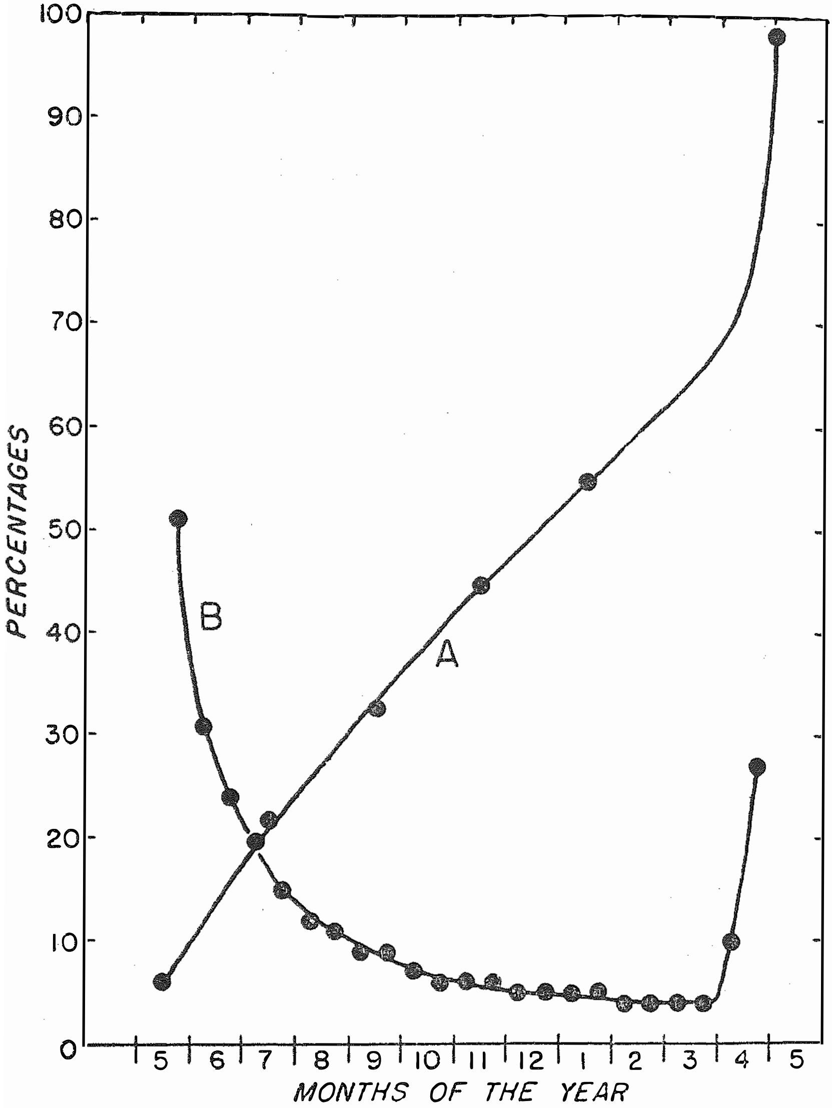

Figure 2. *A* Number of yearling migrants of the 1933 year-class surviving from fingerlings released at dates indicated on the abcissal scale, as a percentage of the number released (for a discussion of the first and last points, see the text). *B* Instantaneous mortality rates, in terms of percentage, computed from curve A for successive half-months.

some loss of eggs before hatching, this figure has been increased, rather arbitrarily, to 6.10 per cent to represent the rate of survival of free-swimming fry. (The representativeness of this figure is discussed below, p. 185.) Multiplying by the 98.3 per cent obtained above, we obtain $0.983 \times 6.1 = 6.0$ per cent for the ratio of fry hatched to yearling migrants. This figure is comparable to those obtained from the marked sockeye, as given in Fig. 2A, and accordingly it is plotted as the first point on that curve.

The computation of semimonthly instantaneous rates of mortality from these data is shown in Table II, columns 6–8. From the smoothed curve A of Fig. 2 percentages were read off at successive fortnights (column 6), and the ratios of their successive values constitute estimates of survival rates, s, during the period in question (column 7). These are converted to instantaneous mortality rates, i, using the relationship $s = e^{-i}$ (column 8). The result is plotted as curve B, Fig. 2. The over-all survival rate of 6.1 per cent corresponds to an annual instantaneous mortality rate of $i = 2.80$. The latter is also, of course, the sum of the semimonthly instantaneous rates.

Unfortunately information on seasonal mortality rates is available for only the one year. It is somewhat risky to assume that a similar seasonal distribution of mortality existed in the other years, yet such an assumption is essential to later computations. Fortunately there is indirect evidence in its favor. It has been demonstrated (Ricker, 1941) that there is a very close and direct relationship between number of yearling migrants and the number of sockeye occurring in stomachs of the lake's important sockeye-eating fishes during the autumn, winter and early spring months. This was true of trout, char, coho salmon and squawfish, and it prevailed over years marked by pronounced differences in both the abundance and the size of the sockeye. It can readily be postulated that at any given season the rate of digestion by the predators was much the same in all these years, because the average weight of the total food in a stomach usually did not vary nearly as much as did the number of sockeye eaten. This was partly because the sockeye were smaller in years of large populations and partly because other foods were substituted when sockeye were scarce, and in any event it appears that moderate variations in amount of food eaten have little effect upon a fish's rate of digestion (Karzinkin, 1935). Since the proportionality was observed over most of the year, for one predator or another, it indicates that the relative seasonal incidence of predation is the same from year to year. Accordingly, insofar as sockeye mortality has been the result of predation, we believe it must have followed much the same seasonal pattern over the period under consideration. An exception is probably to be made for the young sockeye during May and June, as discussed later (p. 192).

There remains the problem of deciding on representative values of the total annual mortality rate, or of its complement, the survival rate, for the young salmon. The yearly seeding of the lake has been carried out by three different methods: natural propagation, planting eyed eggs in tributaries, and release of free-swimming fry. The yearling stocks (*not* yearling migrants) produced in successive years by each of these are shown in Table III. In years of natural propagation

TABLE III. COMPARISON OF THE ESTIMATED YEARLING STOCK WITH THE SEEDING WHICH PRODUCED IT, IN VARIOUS YEARS

Brood year	*Seeding*[a] *(thousands)*	*Yearling stock (thousands)*	*Survival (%)*
A. Fry liberation			
1926	5,916	419	7.07
1929	9,093	352	3.87
1932	4,825	263	5.45
1936[β]	12,468	1,637	13.13
B. Eyed-egg planting			
1928	2,650	91	3.44
1933	4,371	246	5.63
1934[β]	5,590	571	10.22
C. Natural spawning			
1925	17,470	200	2.68
1927	250,000	3,092	1.24
1930	24,900	788	3.17
1935[β]	40,000	2,204	7.90
D. Geometric mean of all methods			
1925–33			3.63
1934–36[β]			10.20

[a] Fry liberated, eyed-eggs planted, or eggs in females spawning naturally.
[β] During these years predator control was in operation.

there is no good way of estimating fry production. Eyed eggs are subject to natural accidents while they lie in the streams, but it has been shown (Foerster, 1934) that under favorable conditions a large fraction of them produce fry—88 per cent was the average obtained in experiments. Hence the *maximum* survival rate of eyed eggs may be close to the usual survival rate of fry. When the fry themselves are planted in the lake it might seem that a direct measure of their survival to the status of yearling stock would be available. However, there is the question of whether planted fry are, initially, as hardy as naturally-produced fry, and whether they may not suffer unrepresentative losses during whatever time it takes them to find their appropriate ecological niche and distribution in the lake.

Considering first the years prior to predator control, there are three figures for fry survival (Table III) which average 5.46 per cent. This is not far from the adjusted value 6.1 per cent estimated earlier for the 1933 year-class on the basis of eyed-egg planting, and accordingly it has been decided to accept the latter figure as representative of all years prior to 1934. Naturally it is subject to considerable limits of error, but any value from 4.0 to 8.0 would necessitate only unimportant changes in the productions which are calculated below.

In the three years of predator control there was a notably greater rate of survival. The average increase in number of migrants produced, considering all methods of propagation used, was from 3.13 to 9.95 per cent, or by 3.18 times (Foerster and Ricker, 1941: 329). This comparison was the suitable one for judging the value of predator control, because it is the number of migrants which determines the number of adult salmon, apparently more or less independently of the age or size of the former. (Or if there is any advantage to larger size, the migrants produced during control possessed it.) For our present purpose it is desirable to compare the total survival of yearling stock, *i.e.*, migrants plus nonmigrants, before and after control. This is done in Table III, using the yearling numbers computed in Table I. The geometric means of the eight survival rates before control, and the three after control, are found to be 3.63 and 10.20 per cent, respectively. These correspond to instantaneous mortality rates of 3.32 and 2.29 respectively, the latter being 0.690 of the former. This then is our best estimate of the fraction by which the semimonthly and the total instantaneous mortality rates for the year-classes of 1933 and earlier years must be multiplied, to correspond to conditions under which the year-classes of 1934–1936 lived. Given the average value $i = 2.80$ for the earlier period, we thus obtain $i = 1.93$ for the later period, corresponding to a survival of 14.5 per cent from the fry stage onward. As with the corresponding figure for the 1925–1933 classes, this percentage is somewhat greater than the fry survival rate actually observed (13.1 %).

COMPUTATION OF PRODUCTION OF SOCKEYE OF AGE O

As defined earlier, the production of a fish population is the sum of the growth made by all its members. Consequently our estimate of production will be the product of the instantaneous rate of growth during a given time interval and the average weight of population present during that same interval. In a simple case where growth and mortality are unchanging through the year, the average population present during the year is

$$\frac{W_0\,(e^{k-i}-1)}{k-i}, \qquad (1)$$

where W_0 is the initial weight of the stock, and k and i are the instantaneous rates of growth and mortality, respectively, for the year (cf. Ricker, 1945; Clarke, Edmondson and Ricker, 1946). The Cultus sockeye differ from the above situation in the fact that the relative magnitudes of k and i change sharply with the seasons, and accordingly it is necessary to carry out separate computations of average population for rather short time intervals. The basic interval used has been half a month, but during the winter when growth was slow or absent, and mortality nearly constant, two longer intervals were used, as noted in Table II. The computation of production for the year-class of 1931 is shown in Table IV. The difference of the instantaneous rates of growth and mortality, shown in column 4, is found by subtraction of column 3 from column 2; it may be either positive or negative. The corresponding change in biomass is found from an exponential table (column 5). In column 6 we start at the top with the arbitrary figure of 100 weight-units of yearling stock at time of migration. During the half-month April 16–30 this stock had decreased, as shown by the negative entry in columns 4 and 5. Its size on April 15 was therefore $100/(1 - 0.18) = 122$ units. Its *average* weight during the half-month can be found from formula (1), an expression for which numerical values have been tabulated for magnitudes of $k - i$ from -2 to $+2$, as an aid in these and similar calculations (Ricker, MS).[2] The average weight, in the case at hand, is 122 times (1), or 110, as shown in column 7. (When $k - i$ lies between the limits $\pm$ 0.10, a simple average is sufficient.) In a similar manner the average stock present during all previous half-months (and other periods) is computed.

[2] Those for positive values of $k - i$ are in column 5 and those for negative values are in column 4 of the appendix of the paper cited, $k - i$ being represented there by i.

TABLE IV. COMPUTATION OF RELATIVE BIOMASS, PRODUCTION AND MORTALITY IN SUCCESSIVE HALF-MONTHS FROM THE DATA OF TABLE II. ALL FIGURES ARE IN TERMS OF A YEARLING STOCK OF 100 WEIGHT-UNITS

TABLE IV. COMPUTATION OF RELATIVE BIOMASS, PRODUCTION AND MORTALITY IN SUCCESSIVE HALF-MONTHS FROM THE DATA OF TABLE II. ALL FIGURES ARE IN TERMS OF A YEARLING STOCK OF 100 WEIGHT-UNITS

Column	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*9*	*10*	*11*	*12*
Date	*Computation of biomass, production and mortality for the year-class of 1931*								*Biomass, production and mortality for the year-class of 1935*		
	k	*i*	*k–i*	*Change in biomass*	*Biomass*	*Average biomass*	*Production*	*Mortality*	*Biomass*	*Production*	*Mortality*
May 1					100				100		
	0.07	0.27	−.20	−.18		110	8	30		10	20
Apr. 16					122				111		
	0.05	0.10	−.05	−.05		125	6	12		7	8
Apr. 1					128				112		
	0.02	0.04	−.02	−.02		130	3	5		2	3
Mar. 16					131				113		
	0.00	0.27	−.27	−.24		151	0	41		0	24
Dec. 16					172				137		
	0.06	0.17	−.11	−.10		181	11	31		10	17
Nov. 1					192				144		
	0.05	0.06	−.01	−.01		192	10	12		9	6
Oct. 16					193				141		
	0.09	0.07	+.02	+.02		191	17	14		15	7
Oct. 1					190				133		
	0.09	0.09	.00	.00		190	17	17		14	8
Sep. 16					190				127		
	0.14	0.09	+.05	+.05		185	26	17		21	7
Sep. 1					181				112		
	0.28	0.11	+.17	+.19		165	47	18		33	8
Aug. 16					152				86		
	0.41	0.12	+.29	+.34		131	54	16		35	6
Aug. 1					113				57		
	0.60	0.15	+.45	+.57		91	55	14		31	4
Jul. 16					72				30		
	0.49	0.20	+.29	+.34		62	31	13		15	3
July 1					54				19		
	0.35	0.24	+.11	+.12		51	18	12		7	3
June 16					48				15		
	0.19	0.31	−.12	−.11		51	10	16		3	3
June 1					54				14		
	0.12	0.51	−.39	−.32		66	8	34		2	6
May 16					80				17		
Totals	3.01	2.80	+.21	+.23	81		322	302	17	216	133

It was noted earlier that the production during a half-month is equal to k times the average population, and this product is shown in column 8. Similarly the weight of fish dying is i times the average population (cf. Ricker, 1944: 29), as shown in column 9. Finally, it is necessary to change from terms of the arbitrary 100 weight-units of yearling stock to terms of the actual stock shown in column 10 of Table I. In the present instance the production is $322 \times 6690/100 = 21500$ kg., and the mortality is $302 \times 6690/100 = 20200$ kg.

The above calculations offer numerous opportunities for accidental errors, but fortunately they can be checked very conveniently at two points. The initial stock of 80 weight-units, found by the successive divisions down column 6, can be checked by a direct computation from the total of the $k - i$ column. This equals $+ 0.21$, corresponding to a change of $+ 0.23$, and hence the initial stock $= 100/1.23 = 81$ units —the same as 80, closely enough. The second check is a balance of gains and losses for the year. The initial weight of the fry, plus the production, should equal the weight of the yearling stock, plus the deaths, *i.e.*, $80 + 322 = 100 + 302 = 402$. When these two agree satisfactorily the only possibility of error lies in the estimation of average population in each half-month.

The computation of growth rates and mortality rates for year-classes other than that of 1931 was explained earlier, and the computation of production and mortality for them presents no new features. The detailed seasonal calculation cannot be presented for every year, but one for the year-class 1935, during predator control, is included (Table IV, columns 10–12). The total productions and mortalities for all the years are given in Table V. It should be observed that during the years in which the year-classes of 1925, 1928, 1932 and 1933 inhabited the lake as age O fish, the figures given in Table V are considerably less than the total sockeye production of the lake, because in those years important bodies of age I sockeye were present too. For the remaining years, however, the figures tabulated represent the great bulk of the sockeye production of the lake.

As mentioned earlier, there are two different sets of mortality rates used in Table V: those for the 1925–1933 and those for the 1934–1936 year-classes. For each of the two mortality rates, considered separately, it is evident that the slower the rate of growth the greater is the total mortality in comparison with the production or with the size of yearling stock (Table V, column 7). In the case of the year-

TABLE V. PRODUCTION OF, AND MORTALITY AMONG, AGE 0 SOCKEYE DURING THEIR YEAR OF LAKE LIFE (IN KILOGRAMS)

1 Year-class	*2* Weight of yearling stock	*3* Initial weight of fry	*4* Mortality	*5* Production	*6* Ratio of production to yearling stock	*7* Ratio of production to mortality	*8* Summer production
1925	1,600	500	3,750	4,850	3.03	1.29	2,960
1926	1,980	1,030	5,280	6,230	3.15	1.18	4,140
1927	8,540	7,500	26,500	27,500	3.22	1.04	19,300
1928	420	220	1,130	1,320	3.15	1.17	880
1929	2,500	870	7,620	5,020	3.05	1.29	4,720
1930	5,770	1,900	13,700	17,600	3.06	1.29	11,000
1931	6,690	5,300	20,200	21,500	3.22	1.06	14,900
1932	1,360	650	3,520	4,270	3.14	1.21	2,760
1933	1,860	610	4,390	5,700	3.05	1.30	3,300
1934	5,030	590	6,140	10,700	2.13	1.74	6,000
1935	18,840	3,300	25,100	40,700	2.16	1.62	23,700
1936	11,790	1,700	15,100	25,200	2.14	1.67	14,500

class of 1927 there was scarcely any difference in weight between fry and yearlings. On the other hand, for any given mortality rate the ratio of production to yearling stock is almost constant, in spite of rather large changes in rate of growth (Table V, column 6). This fact at first appeared rather remarkable to the writers, but trial computations showed that the observation is in accord with expectation, at least over the range of growth rates encountered here. The reason can be expressed briefly as follows. Going backward from any fixed yearling stock at migration time, a small growth rate during the year just completed means that, on the one hand, the stock "produced" only a small fraction of its weight during any given time interval, but on the other hand the stock itself was larger. These two opposed effects compensate each other fairly well, though not exactly, and produce the rather stable ratios observed.

Some of the interesting features of the calculated productions and mortalities may now be discussed.

Seasonal Change in Bulk of the Stock. Considering the detailed seasonal account of the 1933 year-class, shown in Fig. 3, it appears that the biomass (standing crop) of the fry suffered a sharp decrease during late May and early June, reaching a low point about mid-June. Thereafter it began to gain; it rapidly increased throughout the summer, and had practically achieved its maximum size by the middle of September, this being about 1.8 times the migration size. Through late autumn and winter, growth slowed down and finally ceased, while mortality remained appreciable, so that the stock was reduced to 118 per cent of migration size by April 1. During April both growth and mortality increased sharply, but the latter apparently had the edge, resulting in a final decrease of the stock to its size at migration. The net result is that during their year in the lake the young salmon of the 1933 year-class increased to three times their initial bulk.

In the years, prior to predator control, when the growth rate was less than for the 1933 year-class, the above picture was considerably modified, though its general features remained the same. An example is the 1931 year-class shown in Table IV. The initial decrease in bulk was relatively greater than in 1933, so that the stock soon decreased to less than half its weight at hatching. The rapid summer growth did not achieve so high a level as in 1933, and mortality during winter continued to be relatively higher. As a result the final stock at migration time weighed only about a quarter more than it did at hatching.

In the years of predator control, beginning in May of 1935, the 1933 picture was considerably modified in the other direction, as shown by the example of the year-class of 1935 in Table IV. In the three years of observations the weight of the yearling stock was 5.7 to 8.5 times as great as that of the fry (Table V), since growth had a much greater edge over mortality.

Seasonal Changes in Production. In all years production was concentrated during the summer, from June 15 to September 15, to the extent of ⅔ to ¾ of the year's total (Fig. 3). There was a rapid rise in production during the following April, but the fish left the lake soon after it started. During winter, growth apparently ceased and production dropped to zero.

Seasonal Changes in Mortality. The weight of fish dying was more evenly distributed through the year than was production, but it too had a low point in winter, and a high in April. Prior to predator control its most conspicuous level was reached just after the fry appeared in May and early June, but since 1935 this has been less important because of the *relatively* smaller number of fry present (Table III).

Mortality Among Very Young Fish. The question of the mortality of the very young fish deserves special mention. The estimates of seasonal instantaneous mortality rates (Table IV) show that mortality during May was very high (0.51 for the half-month), then dropped to 0.31 in early June and to 0.24 in late June, levelling off rapidly. Now these estimates pertain to the year-class spawned in 1933, which consisted of the fish which made the most rapid growth of any year-class prior to predator control. There seems little doubt that the large mortality rate of May was directly related to the small size of the sockeye then or to behavior associated with small size, rather than to peculiarities of the predators or of their environment at that time of year. Consequently these 1933-spawned fish, which grew most rapidly and hence would pass through the vulnerable stage most rapidly, probably suffered less "infant" mortality than did any other year-class prior to that of 1934. Earlier we pointed out that predation on sockeye appeared to be in proportion to abundance, as estimated from a comparison of stomach contents of predators with the size of the yearling stock. However, the data on which this relationship was founded did not include stomach contents in May and June, so that the observation is not in conflict with the possible existence of a relatively greater early mortality rate in years of slow growth. Direct evidence *for* the latter cannot be obtained from the stomachs, however, because years of really slow growth were all years of natural propagation, when no good estimate of fry present is available.

We should expect, therefore, that the years of large initial sockeye populations, and hence of slow growth, should be years of poor survival rate, because of the prolongation of the period of unusual vulnerability which followed the emergence of the fry from the redds. It is even likely that the difference is greater than our method of computation suggests (Table IV), for in Fig. 1 there was an indication that the year-class of 1933, which was numerically small, exhibited even a *relative* rate of growth in May and early June greater than that observed in years of large populations.

The likelihood that the mortality rate of the very young sockeye varies a great deal with the size of the population is of great theoretical and practical importance. On the one hand, it has long been supposed on theoretical grounds that the efficiency of reproduction of a fish population must decrease as the population approaches its upper limit of size, but there have been relatively few indications of exactly how and when the extra mortality takes place. The picture presented here suggests a very nice regulatory mechanism: the more fry present, the less each eats, hence the slower it grows, and hence the longer it remains at a size especially vulnerable to predator attack.

From the point of view of the computations in this paper, it can be concluded that the procedure of estimating all seasonal mortality rates from that of the year-class of 1933 may considerably underestimate the mortality rate in May and June during years in which growth was slow. In its effect on total mortality or total production, however, error of this sort is not important, because production especially is rather small in May and June, and even doubling it would make little difference in the final result for the whole year. If, however, we had started each year with an estimate of the fry present as a constant fraction of the number of eggs in spawning females, then for such a year-class as that of 1927 both production and mortality would have been greatly overestimated.

PRODUCTION OF SOCKEYE OF AGE GROUP I

In the majority of the years of our study the production of age I sockeye in the lake was so small in comparison with that of age O fish that it is not of any great importance. The exceptions consist, in part, of the largest year-classes, which produced more two-year-old migrants, even relative to their total abundance, than did most of the smaller ones (in years prior to the increase in survival rate associated with predator control). Thus important bodies of age I sockeye lived in the lake as a result of the large spawnings of 1927 and 1931. Also, the years following these two, 1928 and 1932, produced the largest observed *proportion* of two-year-old migrants. With them the estimated number (though not the weight) of the yearling nonmigrants somewhat exceeded that of the migrants of the same year-class (Table I). In the case of the 1927 and 1931 year-classes the two-year-old migrants exceeded in bulk the yearling migrants of the following spawning which had lived in the lake with them. Thus the production of age I fish cannot always be disregarded.

The data available for estimating the production of age I sockeye are not as good as those used for the age O fish. As far as growth is concerned, an estimate of the average size of the nonmigrant yearlings has been presented (Table I), which is good for the 1927 and 1931 year-classes but much less reliable elsewhere. Also, there are good estimates of the size of the same fish a year later, for five year-classes (Foerster, 1944: table I). To estimate the seasonal distribution of growth, we have used the relative seasonal rates for the age O fish for successive half-months from July 16 to April 30. It is felt that the growth rates prior to July 16 for age O fish would be too small relatively, because their small food consumption at that time contrasts sharply with fragmentary indications of a rather large rate of food consumption by the age I fish (see specimens taken May 20, 1933, in Table VIII). As an estimate, therefore, the relative rate of growth for July 16–31 has been applied to the period June 1–July 16, while slightly smaller values are used for the two halves of May (Table VI, column 2). The semimonthly instantaneous rates established in this way are used to define the *relative* seasonal growth rates for all the age I populations. From these the *absolute* seasonal growth rates can be computed. As an example, for the year-class of 1927 the average weight of two-year-old migrants was 16.44 g., and that of the yearling nonmigrants was 1.68 g. The instantaneous rate of growth for the year, therefore, was $\log_e (16.44/1.68) = 2.28$. This is divided among the successive half-months in proportion to the successive entries of column 2, Table VI, the result being in column 3.

In estimating the mortality rate of age I sockeye we are somewhat worse off than we are in respect to their growth, for there is no direct estimate of total mortality for any year. We can only cite the observation mentioned earlier, that rate of predation seems to be more or less independent of size after the first few months of life. On this basis the mortality rates estimated for age O sockeye in successive half-months from July 16 to April 30 are applied directly to the older ones. For the period May 1–July 15 the same mortality rate is used as for July 16–31, namely 0.15 (Table VI, column 4), except that during one fortnight 0.16 is used in order to bring the total for the year to 2.30, corresponding to the even 10 per cent survival rate used in calculating Table I. As further justification for this procedure it may be observed that the size discrepancy between age O and age I is not necessarily very great. The July 16–31 rate of mortality was originally established for the fish of the 1933 year-class, which at that time averaged about 1.7 g. in weight. The nonmigratory yearlings of the 1927 class weighed 1.7 g. and those of 1931 only 1.4 g. Hence in these two years the July 16–31 rate of the 1933 class is being carried over to fish of quite comparable size, initially at least.

Given these data, the computation of age I production is done in the same manner as for the younger fish. Five examples are shown in Table VII. In general the ratio of production to migrant stock is

TABLE VI. COMPUTATION OF PRODUCTION AND MORTALITY OF AGE I SOCKEYE OF THE 1927 YEAR-CLASS. ALL WEIGHT FIGURES ARE RELATIVE TO 100 WEIGHT-UNITS OF TWO-YEAR-OLD MIGRANTS

1	2	3	4	5	6	7	8	9	10
Date	*Relative growth*	*Estimated growth rate*	*Estimated mortality rate*	*Instantaneous rate of change*	*Fractional change in weight*	*Estimated biomass*	*Average biomass*	*Production*	*Mortality*
April 30						100			
	.07	.04	.27	−.23	−.21		113	5	31
April 16						127			
	.05	.03	.10	−.07	−.07		132	4	13
April 1						136			
	.02	.01	.04	−.03	−.03		138	1	6
Mar. 16						140			
	.00	.00	.27	−.27	−.24		162	0	43
Dec. 16						185			
	.06	.03	.17	−.14	−.13		199	6	34
Nov. 1						212			
	.05	.03	.06	−.03	−.03		215	6	13
Oct. 16						219			
	.09	.05	.07	−.02	−.02		221	11	15
Oct. 1						223			
	.09	.05	.09	−.04	−.04		228	11	21
Sep. 16						233			
	.14	.07	.09	−.02	−.02		235	16	21
Sep. 1						237			
	.28	.14	.11	+.03	+.03		234	33	26
Aug. 16						230			
	.41	.21	.12	+.09	+.09		221	46	27
Aug. 1						211			
	.60	.30	.15	+.15	+.16		197	59	30
July 16						182			
	.60	.31	.15	+.16	+.17		169	52	25
July 1						156			
	.60	.31	.16	+.15	+.16		145	45	23
June 16						134			
	.60	.30	.15	+.15	+.16		125	38	19
June 1						116			
	.50	.25	.15	+.10	+.11		110	28	16
May 16						104			
	.30	.15	.15	.00	.00		104	16	16
May 1						104			
Totals	4.46	2.28	2.30	−.02	−.02	102		377	379

TABLE VII. ESTIMATED PRODUCTION AND MORTALITY OF AGE I SOCKEYE (IN KILOGRAMS)

1	2	3	4	5	6	7
Year-class	*Weight of nonmigrant yearlings*	*Weight of two-year-old migrants*	*Mortality*	*Production*	*Ratio of production to two-year-olds*	*Lake's total production for year indicated*
1926	290	105	540	350	3.36	27,800 (1928–29)
1927	1,120	1,095	4,150	4,130	3.77	5,450 (1929–30)
1928	160	118	470	430	3.66	6,350 (1930–31)
1931	920	763	3,030	2,860	3.75	7,130 (1933–34)
1932	570	288	1,320	1,040	3.63	6,740 (1934–35)

greater for age I than for age O sockeye; its value lies between 3.4 and 3.8, as compared with about 3.1 for the younger fish during the same period. What is more interesting is the fact that the mortality of age I sockeye, in terms of weight, tends to be high, and there is no suggestion that any of these age I stocks increased in weight during their second year in the lake. At best they approximately held their own (1927 year-class), while most of them seem to have decreased considerably in bulk, sometimes by half or more.

The age I productions are added to the age O productions of the same year (*not* the same year-class) in column 7 of Table VII to give the total production for that year. While some of the age I productions constitute a large part of the total production for their year, none of them are very large in absolute terms. In years like 1928–1929 which had really large age O productions, the age I production was insignificant because age I fish were not very numerous, and what there were grew slowly. Thus, in considering the question of a possible maximum level of productivity for the lake, it is scarcely necessary to know anything about age I production.

PRODUCTION AND FOOD CONSUMED

Further light is shed on the course of sockeye production in the lake by a computation of the amount of food in the stomachs of the specimens of the year-class of 1931, taken in 1932–33. These have been computed in terms of body weight (Table VIII) and are presented graphically in Fig. 4. In general, the ratio of food to body weight varies with water temperature and with food supply, reaching a maximum in August–September. The sharp decline in late September and October is associated with the near-disappearance at that time of the sockeye's favored food (*Daphnia*) rather than with temperature.

TABLE VIII. MEAN LENGTH AND WEIGHT, AND QUANTITY OF FOOD CONSUMED BY SOCKEYE TAKEN 1932–1934, OF THE YEAR CLASSES OF 1931 AND 1933

Date	*Number of stomachs*[a]	*Size of Sockeye*		*Stomach contents*	
		Mean length (mm.)	*Calculated weight (g.)*	*Mean weight (mg.)*	*Per cent of body weight*
1932					
May 10	15	—	0.15	0.15	0.10
May 18	50	23	0.15	0.3	0.20
June 3	9	—	0.21[γ]	0.7	0.33
July 14	58	36	0.47	4.5	1.25
July 31	52	44	0.85	14.3	1.68
Aug. 25	40	54	1.58	31.1	1.97
Oct. 10	14	—	2.24[γ]	10.7	0.48
Nov. 18	56	63	2.50	21.6	0.86
1933					
Jan. 13	9	—	2.64[γ]	6.1	0.23
Jan. 28	28	60	2.16	9.6	0.44
Mar. 17	10	73	3.89	13.0	0.33
Apr. 12	26	67	3.01	36	1.20
Apr. 30[β]	—	—	3.54	—	—
May 2	9	62	2.38	22	0.92
May 20[δ]	4	—	2.00[γ]	45	2.25
1934					
July 4	3	47	1.04	8	0.77
July 23	4	55	1.66	(32)	(1.9)
Aug. 29	2	70	3.43		
Sept. 19	5	69	3.29	38	1.15
Oct. 2	1	78	4.75	(25)	(0.5)
1935					
Apr. 30[β]	—	—	7.55	—	—

[a] The average lengths and weights are based on smaller numbers of fish than these, as shown in Fig. 1.
[β] These samples are the yearling migrants plus nonmigrants.
[γ] These weights are estimated by interpolation.
[δ] These are in all likelihood nonmigratory yearlings.

Temperature and food both may combine to keep consumption at a low level in winter and to permit a sudden rise in April (Ricker, 1937). An interesting anomaly, however, is presented by the feeding of fingerlings from May to early July. Their food is much less than what might be expected on the basis of temperature or food available, as is shown by the fact that the nonmigratory yearling sockeye feed very actively in May (Table VIII). Of course it may be that stomach contents are not proportional to the daily ration throughout the whole size range represented here: *i.e.*, the young ones may digest their stomachful more rapidly, and so their rations may be larger than they

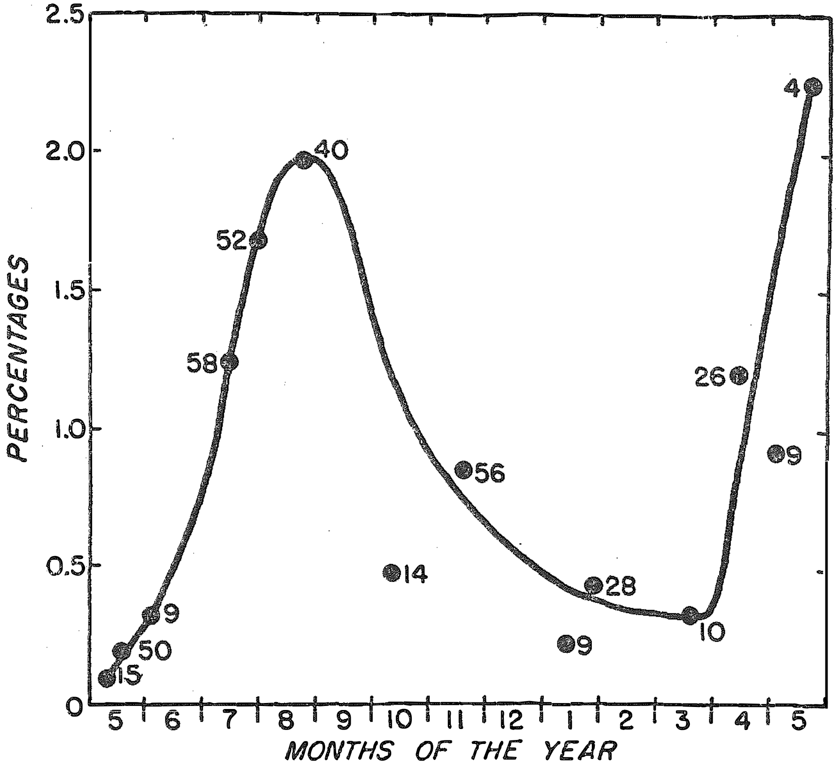

Figure 4. Mean weight of food in stomachs of young sockeye taken from predacious fishes, as a percentage of their body weight, throughout the year 1932–1933 (year-class of 1931). The number beside each observation indicates the number of stomachs examined.

seem. Still, the discrepancy is so great (0.1% as compared with 2%) that only a small part of it could be explained in that way. One suggestion would be that, while plankton crustaceans in general are abundant in May and June, there might be a scarcity of foods suitable for fry, at least in the parts of the lake they inhabit (wherever that may be). A comparison of the qualitative composition of the food in the sockeye stomachs with the entomostracans present in the pelagic region of the lake (Ricker, 1937) showed that the fingerling sockeye ate relatively few *Cyclops*, which was the abundant species in May and June, "preferring" the much scarcer *Bosmina* when very small, and later *Daphnia*. Remembering that the calculated original weight of the fry of the 1931 year-class was quite large (four-fifths of the final weight of the yearlings), it is evident that there may well be a period of serious scarcity, in the early part of the season, of the types of food suitable for the very young fish.

The above situation may suggest another possible cause of mortality among very young sockeye. If the observed short rations of May and June, 1932, were even less for the much larger population present during the same season of 1928, might not a point be reached where some fry would actually die from loss of weight? We offer this suggestion with considerable reserve and would probably not have mentioned it except that exactly the same idea has been put forward by Einsele (1941) to explain the poor survival of the fry of *Coregonus* in southern German lakes. He found that these fry, when first hatched, died in large numbers when fed plankton at the density of its occurrence in the lake, but that this mortality could be almost wholly eliminated by increasing the concentration of food in the medium. The same effect has been postulated by some marine biologists to account for the tremendous mortalities of pelagic fish fry that occur in certain years.

We do not suggest, of course, that the above hypothesis and the one proposed earlier—greater predation on fry of large populations because of their slow growth—exhaust the possible causes of poor survival from naturally-spawned eggs, or even from eggs or fry that have been planted. Thus, the survival of the year-class of 1925 to the yearling stage was as small as that of 1927, though it consisted of rapidly growing fish.

In order to estimate approximately the actual quantity of Entomostraca consumed by the sockeye of the lake in the course of a year, two approaches are possible. On the one hand, Ivlev (1945) shows that the efficiency of conversion of food to body substance achieves a maximum of about 35 per cent in well fed young animals, comparing calorific equivalents of predator and prey. To convert wet weight of young sockeye to calorific value, we use the factor 1000 gram-calories per gram, in default of exact analyses; it is true that adult sockeye *flesh* yields much higher factors (1500–2000 calories), but their rich fat content is largely responsible for this, and also the fact that no bone is included. At this rate the 1931 year-class's production of 21.6 metric tons in 1932–33 corresponds to 2.2×10^{10} gram-calories, and if it had been converted from Entomostraca under the most favorable conditions it would have required $2.2 \times 10^{10}/0.35 =$

6.2×10^{10} calories of the latter. This figure, however, must be considered minimal, because the slow growth rate of the 1931 year-class suggests that conversion efficiency was probably considerably less than 0.35—possibly only half or a third as great. The largest estimate of food consumed, obtainable by use of this factor, is for the year-class of 1935 in 1936–37: 11.6×10^{10} calories.

Another way to reach an approximate estimate of consumption is from the observed stomach contents. In Table IX is given a computation of the daily ration and total consumption of the sockeye of 1932–1933. Its weakest point is, of course, the estimate of "turnover," *i.e.*, the ratio of the observed stomach contents to the daily ration. Ricker (1937: 458) experimented briefly on the rate of digestion among sockeye and found that when held at 12° C. without food, half of a group of 10 had emptied their stomachs in four hours and considerable progress had been made by the others. He concluded that a *conservative* estimate of sockeye feeding in summer would be that they consume their average observed stomach contents every day. For our present purpose a *most probable* estimate will be better than a conservative one, and this we consider to be four times the observed contents, in summer. (The earlier estimate was unduly influenced by the fact that the experimental animals contained much less food than do wild ones.) For other seasons reductions to three and two times are made (Table IX). On this basis, admittedly very poor, the estimate of the total consumption of plankton by this brood of sockeye comes to 103 metric tons wet weight. This can be converted to calorific content using Iablonskaia's (1935) figure of 3,770 calories per gram dry weight, and a moisture content of 80 per cent,[3] making 7.8×10^{10} calories. The latter figure agrees well enough with the minimum of 6.2×10^{10} calories found by the other method, but this does not mean that each could not be 100 per cent or so in error. In fact we are inclined to regard them both as low, because an efficiency of conversion as high as 35 per cent for such slow-growing fish seems improbable, and because a minimum food consumption of 11.6×10^{10} calories was achieved in a later year with a much smaller initial population.

Taking 11.6×10^{10} calories, or 154 metric tons wet, as the best available estimate of the possible consumption of plankton food by

[3] Moisture contents of *Daphnia* are quoted as in excess of 90 per cent (Iablonskaia, 1935; Geng, 1925); but the stomach contents considered here appeared to be partially dehydrated by the animals before their death.

TABLE IX. COMPUTATION OF TOTAL FOOD CONSUMED BY SOCKEYE OF THE 1931 YEAR-CLASS, IN 1932–1933

		Mean weight (g.)	*Stomach contents (% of body weight)*	*Estimated "turnover"*	*Daily ration (% of body weight)*	*Semi-monthly ration (% of body weight)*	*Population weight (metric tons)*	*Food consumed (tons per half-month)*
1933	May II	—	2.32	4	9.3	—	—	—
	I	—	1.80	4	7.2	—	—	—
	Apr. II	2.90	1.24	4	5.0	75	7.4	5.5
	I	2.74	0.66	3	2.0	30	8.4	2.5
	Mar. II	2.66	0.33	2	0.7	11	8.7	1.0
	I	2.64	0.33	2	0.7	10	9.0	0.9
	Feb. II	2.64	0.34	2	0.7	10	9.3	0.9
	I	2.64	0.36	2	0.7	10	9.7	1.0
1933	Jan. II	2.64	0.40	2	0.8	13	10.2	1.3
	I	2.63	0.45	2	0.9	13	10.7	1.4
1932	Dec. II	2.61	0.53	2	1.1	18	11.2	2.0
	I	2.57	0.61	2	1.2	18	11.7	2.1
	Nov. II	2.51	0.71	3	2.1	32	12.2	3.9
	I	2.44	0.83	3	2.5	38	12.6	4.8
	Oct. II	2.34	1.02	3	3.1	50	13.0	6.5
	I	2.22	1.27	3	3.8	57	12.9	7.4
	Sep. II	2.06	1.59	4	6.4	96	12.8	12.3
	I	1.84	1.91	4	7.6	114	12.5	14.2
	Aug. II	1.50	1.97	4	7.9	127	11.2	14.2
	I	1.08	1.87	4	7.5	112	8.9	10.0
	July II	0.64	1.49	4	6.0	96	6.2	6.0
	I	0.40	0.99	4	4.0	60	4.2	2.5
	June II	0.29	0.61	4	2.4	36	3.4	1.2
	I	0.22	0.39	4	1.6	24	3.4	0.8
1932	May II	0.17	0.23	4	0.9	14	4.4	0.6
Total								103.0

sockeye in a year, it is of interest to compare it with estimates of the standing crop of the plankters concerned (Ricker, 1937, 1938a). Practically all sockeye food consists of the four entomostracans—*Daphnia, Cyclops, Bosmina* and *Epischura.* Their abundance in the lake was estimated and converted approximately to a wet weight basis in terms of "Units" of 0.005 mg. size (Ricker, 1937: table 4). The average abundance of entomostracans over 1932–1935 is about 20 units or 0.1 milligram per liter throughout the year, equivalent to 4 grams per square meter of lake surface, or 4 metric tons per square kilometer. The area of the pelagic region of the lake is 5.9 square kilometers, so the 154 tons consumed by sockeye represents 26 tons per square kilometer. Thus the ratio of yearly consumption to mean stock is 6.5 to 1. This would constitute a minimal estimate of the "turnover" of the entomostracan population—6.5 times a year, but naturally a poor one. A similar computation for the summer months only indicates that the *Daphnia* consumed each month is equal to 1.5 times its average population at that time. This suggestion of rather heavy consumption is interesting in the light of an observation made earlier, that the *Daphnia* stock declined more rapidly during two summers of large sockeye populations than during two summers having small populations (Ricker, 1937), suggesting that the *Daphnia* population was actually depleted by the feeding of the salmon.

SOCKEYE AND PREDATORS

Effect of Predator Control Upon Production. One of the most interesting features of Table V is a comparison of the productions before and during the predator control campaign. For example, comparing the two largest populations in each category, the yearling stock produced by the year-class of 1935 was 2.21 times that produced by the 1927 class, but the production for the 1935 class was only 1.48 times that for the 1927 class. Considering production during the important May–August period of rapid growth, the figure for the 1935 class was only 1.23 times that for 1927 (Table V, column 8). While we should not attach too much significance to the exact size of these ratios, it is clear that the production of sockeye during the years of predator control can almost always be matched by comparable years during the earlier period, and accordingly there is no reason to suppose that the capacity of the lake to *produce* sockeye had been appreciably increased during predator control, either by way of an increased food supply or in any other manner.

There is also another factor which undoubtedly has a bearing on production and food supply, though unfortunately there are no data from which to estimate its effect quantitatively. A number of authors have shown that the efficiency of conversion of food to flesh by fish increases with increase in food consumed, up to rather large daily rations. That is, relatively more food is used for growth and less for maintenance, other factors being constant. To cite data for another salmonid, Pentelow (1939) found that at 5°–10° C. brown trout used a rapidly increasing proportion of their food for growth as their daily ration increased, up to the maximum amount they would eat—six per cent of their weight per day. It seems very likely, therefore, that the sockeye of the smaller (initial) populations, which presumably eat more food per fish, as shown by their more rapid growth, are also using a larger fraction of their food for growth. If this is so, we should expect any given amount of sockeye food in the lake to produce more sockeye flesh if invested in a smaller number of normally-growing fish than if invested in a larger number of slow growing fish. Thus the larger total production of sockeye by the 1935 year-class may well be based on an actual food consumption no greater than, or not as great as, that eaten by the 1927 year-class, because the latter population consisted of less well fed fish.

Even without the benefit of the above analysis, the opinion has already been expressed (Foerster and Ricker, 1941) that the favorable effect of removing predacious fishes from the lake has been a result of improved survival rather than of improved food supplies. Some of our colleagues, in oral or written comment, have proposed the opposite view, which evidently appears more reasonable to them in the light of their experience on other bodies of water. For example, Rounsefell (1946), after examining these data in some detail, concludes that "clearly the removal of competing species greatly raised the level of maximum productivity over that prevailing under natural conditions." Presumably, Rounsefell's use of "productivity" here means the quantity of sockeye food produced by the lake; if so, we submit the analysis above as additional evidence that such an increase need not be postulated. In fact the data suggest that no important increase in food supply could have occurred, otherwise the production of the 1934 and 1936 year-classes would surely have been greater. And as was shown earlier (Ricker, 1941), there is little food competition between the sockeye and the species which have been removed from the lake, so it is difficult to see how the suggested increase in food production could have come about.

Since the 1935 year-class of sockeye grew considerably less rapidly than those of 1934 and 1936, it may well be that any further increase in number of fry would result in a decrease instead of a further increase in production. If so, 41 metric tons, or 6.6 tons per square kilometer, may represent almost the lake's maximum capacity to produce sockeye, this figure being achieved only if the sockeye are sufficiently numerous, but not so numerous that they fail to make reasonably rapid growth.

Predator Control and Yield. The ratios of production to yearling stock tabulated in Table V, column 6, have characteristic values before and after the reduction of the lake's predators. For the 1933 and earlier year-classes the yearling stock represents about 30 per cent of the production; later it is 47 per cent of the production. This comparison is not the best one, however, for it takes no account of the original contribution of the fry to the weight of the stock. Expressing the weight of yearling stock as a percentage of production-plus-weight-of-fry, the following series of figures is obtained:

Year-class	*Percentage*	*Year-class*	*Percentage*
1925	30	1931	25
1926	27	1932	28
1927	24	1933	30
1928	27	1934	44
1929	29	1935	43
1930	29	1936	44

The yearling stock is thus 28 per cent of the lake's total gain of sockeye biomass in years before control, and 44 per cent of it after control, on the average. The apparent improvement in utilization of production is therefore about 55 per cent. However, yearling stock is not exactly the same thing as yield, and in some of the years before control a large part of it did not migrate. Thus the mean improvement in the ratio of *yield* to production-plus-fry-weight is somewhat greater than 55 per cent; approximately 65 per cent. Even this does not take into consideration the migrant-production relationship for the age I stock, a consideration of which would make the situation after control seem still more favorable.

Efficiency of Predator Removal. In assessing the change in survival rate which occurred after predator control was begun, reliance has been placed upon the laws of chance to exclude the possibility that a *natural* change could have accomplished the same result (Foerster and Ricker, 1941: 329). While this procedure showed that the "accidental" explanation was very improbable, it could not make it appear impossible, and hence it is desirable to explore also the question of whether or not the average improvement in survival is consistent with the observed change in predator populations. In an earlier section (p. 185) we calculated the average age O survival rates to be in the ratio of 6.1 per cent before control to 14.5 per cent after, corresponding to instantaneous mortality rates of 2.80 and 1.93 respectively. It is these instantaneous mortality rates which should be proportional to the predator populations. This fact may be made clear by means of the following illustration, which also illustrates the general nature of instantaneous rates. Suppose that the mortality had occurred evenly throughout the year—that is, at every moment a constant fraction of the sockeye present was eaten. Then, dividing the year into a large number of equal time intervals—1,000 will be sufficient—there will be 2.80/1000 = 0.280 per cent of the available sockeye eaten during each such interval. If the initial stock is 1,000,000, then 2,800 are eaten during the first interval with 997,200 remaining; next time 0.28 per cent of 997,200 = 2,793 are eaten, with 994,407 remaining. Repeated 1000 times, this predator activity leaves $1{,}000{,}000\ (1 - 0.0028)^{1000} = 61{,}000$ survivors. Now, on the assumption that predation is proportional to the abundance of both predators and prey, a reduction of the predator population by 31 per cent means that during each of these thousandths of the year the fraction of sockeye killed will be reduced from 0.280 per cent to 0.193 per cent. The action of this mortality rate throughout a year leaves $1{,}000{,}000\ (1 - 0.00193)^{1000} = 145{,}000$ survivors. Thus a 31 per cent reduction in predators results in an increase in survival from 61,000 to 145,000, or to 2.4 times the original value. The fact that predation actually varies in its seasonal incidence does not affect the applicability of the above illustration to the observed data, as trial calculations can easily show. (This represents the increase in survival rate from fry to yearling stock; the average increase in migrants was considerably greater because a larger fraction of the yearling stock went to sea during the years of predator control.)

It appears, therefore, that if all sockeye mortality in the lake is the result of predation, then to produce the observed change in survival the predator population of the lake must have been reduced to 0.69 of its original size, or by about a third. Estimates of the decreases in fish predator populations have already been made (Foerster and Ricker, 1941). They indicate a serious reduction of squawfish and char of sizes above 200 mm., amounting to ¾ or more of the original population. For trout, however, no complete demonstration of any change was obtained, though there was some evidence of a decrease considerably less than the above. In assessing these results it should be remembered that (1) char, though heavy consumers of sockeye, have apparently never been very common; (2) squawfish, though numerous, eat sockeye only during cool weather and in small quantities individually (except during April); (3) trout, which eat many sockeye at all times of year, are at least fairly numerous, but they are the fish least affected by the control program. Another thing to bear in mind is that the fish less than 200 mm. long, of all these species, were practically untouched by the gill-netting program. Though these smaller fish ate relatively more of other foods than did those larger than 200 mm., they did contain some sockeye, and it is well known that smaller fish tend to eat more per unit body weight than do larger ones. For example, in the food tables given for these predators (Ricker, 1941), the fish are divided into length classes 100 mm. wide, and there is a tendency for the average stomach content to remain about the same in spite of increase in fish size, from the 100–200 to the 200–300 mm. range, or even beyond. Finally, there is a certain amount of predation by fish-eating birds on the lake, which may not be wholly negligible; no attempt was made to interfere with these. In view of all this, it is entirely possible that the control program reduced the effective number of predators by only about a third, in spite of the much more serious losses suffered by the medium-to-large individuals of two of the piscivorous fishes. On the other hand, it seems clear that the reduction could scarcely have been much *less* than a third.

Another point must be considered in this connection. It is perhaps conceivable that the predacious fishes have never accounted for the whole, or for even the greater part, of the mortality among the sockeye, even after discounting the mortality among the very young fry, as discussed earlier (p. 199). If this were so it would, of course, require a reduction of predators by more than a third to have achieved the observed increase in survival. Among the sockeye, mortality not due to predation would be difficult to detect, considering their pelagic habitat. It appears very improbable that death from senility would occur in such young fish, which would leave disease, parasites or congenital weakness as possibilities. The only observation having a direct bearing on this subject was made in March of 1937, when the lake was completely ice-covered for two weeks or so; which, incidentally, is an almost unheard of event. On one occasion a trip was made across the central part of the lake. A previous thaw had produced holes in the ice up to a foot or so in diameter, which holes later filled in with clear ice. It was noticed that some of these clear lenses had fish enclosed in them, and chopping several out revealed them to be fingerling sockeye. They were found over most of the area traversed, and if the whole lake were similar, then there were at least several hundred in all, and possibly several thousand. No cause of death was ascertained; of course there was no depletion of oxygen which might make an air hole attractive. The number of sockeye in the lake at this time can be computed as about 2,900,000 from data given earlier; hence, if 1000 fish were dead, and if they represented one day's loss, that would correspond to an instantaneous mortality rate of 0.005 per half-month. This can be compared with the 0.03 per half-month earlier estimated for this time of year, to give an idea of the possible order of magnitude of the mortality. However, there is no way of knowing if these fish were killed by conditions peculiar to a period of ice-cover, or if the ice merely served to entrap what normally die anyway. The net result of this observation is to make it appear perhaps a little more likely that an appreciable amount of nonpredatory mortality occurs, without giving any clue as to its cause or its quantitative importance.

If there were good estimates of the predator populations in the lake, together with their daily sockeye ration in successive months of the year, it might be possible to compute their total sockeye consumption and compare it with the estimate of sockeye mortality, to see if any considerable residuum remained to be accounted for. What is actually fairly well known, however, is only the average number and volume of sockeye present in stomachs of the important predators, in several years. Under such circumstances it is impossible to compute their total consumption of sockeye with enough accuracy for this purpose. It can only be said that it seems entirely *possible* that the fish predators may have been abundant enough to account for the entire number of sockeye which die. The question of whether or not there were additional important causes of mortality must await further study.

DISCUSSION

The Cultus Lake data have been used to illustrate a method of computing fish production and to demonstrate some of the uses to which such a computation may be put. It is evident, however, that the kinds of data used here to calculate seasonal mortality and seasonal growth rate are by no means universally available. Possibly the only other kind of population for which production could be computed quite easily from data now available are the pelagic young of marine fishes, which have been sampled, using tow nets in a quantitative and systematic manner, over their whole range. Among larger fishes, while seasonal changes in growth rate have been determined for a number of populations, information on the seasonal distribution of mortality is for the most part nonexistent. Possible exceptions may be found among heavily-exploited populations in which fishing is known to be the principal cause of mortality.

However, in spite of these difficulties we believe that computations of production could be made for a considerable number of fish populations with sufficient accuracy to have real usefulness. The seasonal growth patterns already determined for a number of species could be carried over to other similar species living in similar environments. Since we should expect much less seasonal variation in mortality among older fish than has been found for the age O salmon considered here, the total instantaneous mortality rate, determined from a "catch curve" (Ricker, MS) or from a marking experiment, could even be divided up equally throughout the year, as an approximation. If fishing mortality can be separated from natural mortality, and if the seasonal distribution of the former is known, then only the natural deaths need be arbitrarily distributed throughout the year. Pond experiments have already been started, from which it is hoped to obtain information on the seasonal distribution of natural mortality among some warm-water fishes of Indiana.

As information of this type accumulates, it is not too much to hope that computations of fish production will be made as a matter of course on any body of water being intensively studied. They need not be especially accurate in order to be far superior to the estimates of *yield* which have usually been used in the past as a measure of fish production in a body of water. With the young sockeye we have found values between 2.1 and 3.6 for the ratio of production to yield, but there are good reasons to expect that much larger or much smaller ratios may prevail among other species, or at other ages, or in other habitats. Thus, if a computation of production differs from the true value even by 50 per cent, it is still a much better piece of information than is the yield for the purpose of estimating the utilization of fish food resources, or in connection with most other questions involving the "trophic-dynamic "aspect of aquatic ecology.

As far as Cultus Lake is concerned, the picture of production and food relationships obtained is incomplete from the standpoint of the lake's economy as a whole. Even the information on the sockeye is quite imperfect in places and some of the data used in the computation of production should be checked as soon as possible. If a similar study is attempted elsewhere, nothing would be more valuable than the discovery of a practical method for obtaining good-sized samples of the young sockeye when they are in the lake. Possibly a trawl could be developed for this purpose that would not require too large a boat to haul it, or experiments with a "trawl" hauled vertically might be made. In our work it was always tantalizing to realize that while millions of young salmon were present in the lake, it was necessary to depend on partly digested stomach samples for information on growth and feeding, and to rear in artificial ponds the specimens needed for experimentation. If this hurdle can be passed, a small sockeye lake similar to Cultus presents an unusually favorable opportunity for the quantitative study of the process of production as a whole, including the sockeye, their enemies and their food organisms. As Ivlev has suggested, it is entirely possible that such a study might reveal important principles which would be of general applicability to aquatic productivity everywhere.

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DISCUSSION

Van Oosten: Is there any discussion on Dr. Ricker's paper?

Huntsman: How important would you consider it to be to carry out experiments dealing with these points in an area or pond where you had a much better chance of measuring your primary factors? In dealing with the whole problem of computation of production, is it important to get actual facts from a body of water where you can obtain what might be called the necessary data?

Ricker: I think experiments of that sort on small bodies of water would certainly be valuable. It might be, as has been suggested, that some general principles might emerge of which we are ignorant now but which might be applicable to larger bodies as well. However, even if you wanted to apply them to larger bodies of water it would have to be under experimental conditions.

8. PROSPECTS FOR MANAGING OUR FISHERIES

By R. E. Foerster

Fisheries Research Board of Canada

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ABSTRACT

Fisheries management is practicable only where adequate information is available. This exists at the present time in few instances. Prediction of sizes of populations, based on knowledge of existing stocks and effect of new-age classes, is suggested as a valuable feature of management. Many basic factors still have to be studied, *e. g.*, relationship of spawning to recruitment, factors limiting early survival, mortality rates in the ocean, adequate statistics, inter-specific relationships, variation in oceanographic conditions. Setting up of quotas may be a useful means of regulation provided that these are allowed flexibility to be altered as new data indicate. Limitation of fishermen may be required. Fisheries management policies to provide maximum sustained yield are the objective of all fisheries. Progress is being made but the rate is dependent on the extent to which pertinent data can be accumulated.

DISCUSSION

It is very apparent at the present time that a very significant evolution is taking place in fisheries biology. This has developed partly from the natural extension of our interest from the individual to the group or population as a whole, but especially from the wide demand on the part of government and industry for definite practical recommendations by which the commercial stocks of fish may be protected from over-zealous exploitation and consequent economic depletion in order to obtain maintenance at a high level of production. This newer approach has been termed "fisheries management" and suggests a definite effort to regulate commercial exploitation of a stock of fish in such a manner that a maximum quantity may be removed from year to year without endangering the production of new supplies. In other words, a maximum sustained yield is the objective.

It is now generally accepted that the resources of the sea are not unlimited and inexhaustible, and that the ocean does *not* represent a magic basin from which can be withdrawn at any time or in any place an endless quantity of fish or other forms. On the contrary, it is now commonly conceded that the sea has a definitely limited productive capacity, like that of land, and that therefore there is a limit to what can be harvested from it.

This relatively new conception, when coupled with the increased demand for fish products and for the desire to capitalize as much as possible on available marine resources (especially those of coastal waters), has led to an appreciation of the need for a proper policy of balancing exploitation or harvesting against the amount of fish available and also of attempting to regulate the catch against the renewing recruitment of the stocks of fish present. In other words, it is desired to remove from the sea only those quantities of fish that constitute what might be considered *the surplus* and to leave, for spawning purposes, a sufficient supply to maintain the stocks at a high level of production.

Every country with a fishery that is either presently-existent or potential is exhibiting keen interest in fisheries management, and many of them are actively studying ways and means of initiating proper regulation procedures. It is not a simple problem, however, and the further fisheries biologists delve into the problems of fish populations and their maintenance the more complex and complicated become the mechanics for suitable manipulation of catch versus natural production of the stocks being exploited. The literature is replete with reports of studies being conducted in many countries and on many species of fish. These may eventually bear fruit.

Is Fisheries Management Practicable?

At the outset it may be profitable to enquire as to whether or not a scheme of fisheries management for any species of fish is wholly practicable. Can we evaluate the productiveness of certain bodies of water and assess the yields of fish which may safely be removed, as agriculturalists do for land and crops and as ranchers do for pasturage and stock? An agriculturalist, knowing the type of soil, the length of the growing season, the conditions for average growth, and the average yield of grains, can estimate fairly accurately what a given tract of land should produce. His estimates will be affected only by unusual environmental circumstances, such as excessive rain, drought, early frost, disease, etc. Can the fishery biologist do equally well?

If by "maximum sustained yield" it is inferred that it will be practicable to define, in course of time, how many millions of pounds of a species of fish can be removed from a certain area year after year or how many millions of cases it will be possible to pack annually, I would hazard the opinion that such an objective will be achieved in few instances. It is not in the nature of things for animals to act in such a convenient manner. A cyclic rhythm seems to be a natural phenomenon, and superimposed on this there are all the natural variations produced by a host of varying environmental factors which have an intimate effect on production. Of most of these we know very little, actually, and it will be a long time before they are adequately delineated.

Value of Prediction

It seems reasonable to anticipate, however, that in course of time it may be possible to predict in advance the size of populations of fish and to indicate what amount of fish may be made available to the fishery and what should be reserved as a spawning escapement. Whenever fisheries research has advanced (with respect to any species of fish) to the point where reasonably accurate estimates of existing populations can be made and the relation to them of incoming age or year-classes determined, it may be feasible to set up some form of tentative management policy.

Among those species of fish which have a long life and in which the same population is fished over a number of years, such as the halibut, a relatively good picture of the trends in the stocks can be obtained. Variations both in the extent of recruitment of young fish to the population and in natural mortality rates are not likely to be so severe, and the effects can be foreseen well in advance. With fish having a shorter life and fewer age-classes represented in the fishery, such as the herring and pilchard, the trends in the sizes of the stocks can still be reasonably well traced, but action to counteract any sudden decline in one age group must be more quickly taken to restore the population to a maximum level. For anadromous species, such as the Pacific salmon, which die after the first spawning and where only one or two age groups are involved, an estimation of populations is definitely more difficult and regulatory measures have to be essentially more drastic.

The likelihood of success of any managment policy for any species of fish will depend on the possibility of reasonable prediction estimates being obtained. Where such prediction estimates indicate fairly clearly the effect on the accumulating stock of cyclic changes in survival and of reduction in recruitment due to unfavorable climatic or environmental conditions, a flexible system of regulation seems feasible and should tend to establish the fishery on a sound basis fairly quickly. Fishery biologists are bending every effort to advance their research along those lines that will reveal to them (1) the status of existing populations of fish, (2) the trends occurring, (3) the factors causing or influencing such trends, and (4) the feasibility of controlling, in whatsoever way possible, the factors limiting survival or production of fish. It is definitely a long-term problem requiring at the outset the accumulation and analysis of many years' data before even a preliminary conception of the status and trend of a population can be had, but once commenced the addition of each season's records denotes progress toward an eventual solution.

Basic Factors Still to Be Revealed

Before much progress can be made in practical fisheries management there are a number of fundamental relationships that still must be determined.

Relationship of Spawning to Recruitment. E. S. Russell (1942: 83) has stated that "so far as we know at present, there is no obvious correlation between the number of eggs spawned and the number surviving to reach the catchable stock, in any of the important species." He has also pointed out with much truth (*ibid.*: 71) that "in the early days of fishery science most workers thought that the main thing to aim at was to keep up the supply of mature fish so that an abundant supply of eggs and larvae and young fish might be assured." This is still an axiom in many quarters, that there must always be a large spawning escapement of mature fish in order to guarantee an abundant supply of eggs and, *ipso facto*, of young fish.

That this may not be the correct approach for Pacific herring has recently been advanced by Dr. A. L. Tester of the Fisheries Research Board of Canada, who has been conducting an investigation of the British Columbia herring fishery. Some ten years ago concern was felt about the maintenance of the herring fishery of the east and west coasts of Vancouver Island. It was decided to test out the quota system of regulation whereby the commercial fishery would be limited to an arbitrarily set quota and a suitable supply of fish for spawning would be assured. The results to 1943–44 are reported by Tester (1945). The investigation has now reached a point where the relationship of extent of spawning to extent of actual recruitment of new fish to the stock constitutes a basic consideration of regulation. If there is a direct relationship between spawning and recruitment, then provision for large spawning must be made, but if there is no significant correlation, or in other words, if the recruitment is of equivalent extent whether the spawning within limits be large or small, then attempts to ensure a large spawning or seeding are unnecessary and may even produce an unnecessary waste of food fish. An experiment on the west coast of Vancouver Island has recently been commenced to determine, by appreciably increasing the fishing intensity and thereby cutting down the spawning escapements, the relationship between spawning and recruitment by speedier methods than is possible under the quota system.

Nowhere is the need for definite knowledge of the value of spawning in relation to recruitment more pressing than in the salmon fisheries, where the importance of large spawning escapements and heavy seedings has been stressed for many years. All that is known at present is that mortality during spawning, incubation, and early fresh water residence is high. For Alaska red salmon which migrate to sea as two- and three-year-old smolts the mortality has been reported

(Barnaby, 1944: 292) at 99.55 per cent of the presumed egg deposition; for Cultus Lake sockeye, migrating principally at the end of the first year, the loss is 98.2 per cent (Foerster, 1938: 154); for fry-migrating pink salmon, the mortality varied at McClinton Creek, Queen Charlotte Islands, from 93.1 to 76 per cent (Pritchard, 1939), and for chum salmon in a small stream (Nile Creek) on the east coast of Vancouver Island, 97 per cent (Neave, unpublished data). Except for the McClinton Creek pink salmon experiments (Pritchard, 1939), where an inverse relationship was demonstrated between spawning escapement and percentage fry production, there are insufficient data available to define the relationship of varying amounts of spawning to resulting production of young fish. The salient information is badly needed.

Factors Limiting Early Survival. To what extent losses occurring during spawning and early life can be controlled or reduced depends largely on the responsible factors and on the feasibility of control or reduction. Obviously the greater the survival of eggs and young the greater the recruitment and the more rapid the increase in the stock to its upper limit; greater also, the catch which can be allowed to fishermen.

For marine species the factors involved in limiting survival of eggs and young, if known, are probably largely beyond control. For shore or reef spawning species there may be some means of improving spawning and survival conditions, but the most promising possibilities appear to exist in the case of the salmon, where, by stream improvement, water-flow control, elimination of predators, etc., or perhaps by some effective measures of artificial propagation, production of young may be appreciably increased.

Irrespective of the present likelihood of practical control, the limiting factors in all cases should be investigated and revealed. Until they are known our knowledge is incomplete and the practicability of dealing with them effectively remains undetermined.

Mortality Rates in the Ocean. For many of the commercial fishes the mortality rates during ocean residence can be determined. By comparison of survival of year groups and by tagging it has been possible in many cases to compute reasonably accurately the mortality, both natural and fishing; such information is essential to a full understanding of the fishery and the development of a management policy.

For salmon, however, such data are conspicuously lacking. Only for sockeye salmon are there any pertinent data. These were obtained (1) in connection with propagation experiments, conducted by the Fisheries Research Board of Canada at Cultus Lake, British Columbia (Foerster, 1936), which revealed a survival to the adult stages of approximately 10 per cent of the seaward migrants leaving the lake, and (2) by the United States Fish and Wildlife Service for Karluk Lake, Alaska (Barnaby, 1944), which showed a return of 21.0 per cent. The Cultus Lake results were obtained from marked yearling migrants, while those for Karluk were derived from marked two-year-old smolts. These findings require confirmation.

Obviously in developing any management policy, even in attempting any prediction procedure, it is essential that some approximate estimate of the return from the sea, whether computed from spawning adults or seaward migrating young, must be established. For salmon this remains one of the important unknowns in our knowledge and constitutes a challenge for workers in this field.

Adequate Statistics. In all population studies it is imperative that there be available as complete statistics as possible of the catches of fish, particularly in relation to place of capture. On the British Columbia coast this phase of the work has been progressing very slowly and cannot be considered adequate in any of the fisheries.

Migration studies by means of tagging have shown that certain species of commercial fish are caught in several fishing areas along the coast, each of the same general population. In developing a management policy it is necessary to know where the species are being exploited and to what extent. Otherwise the measures of abundance or the indices of trends are not accurate. In other species there are discrete populations in various parts of the coastal area. It is necessary to know the limits of these populations and to obtain the specific data pertaining to them. This can be achieved only by collecting proper catch statistics and by adequate sampling of the catches.

Slow progress is being made in the development of a satisfactory system of statistics. In many respects the sincere and honest cooperation of individual fishermen has to be relied upon to obtain the data as to place of capture, and where such assistance is lacking the results obtainable are of limited value. In a ling cod study attempted in the Strait of Georgia a few years ago the whole investigation broke down because the fishermen (at that time many were Japanese) refused to reveal where their catches were being made. Without this information neither proper catch records nor suitable sampling procedures could be completed. There are indications that the attitude of the fisherman is changing. This should facilitate future efforts to acquire the essential basic data.

Inter-specific Relationships. It is reasonable to assume that in the water, even as on land, there is a constant conflict for existence, for food and for space, between populations of species. When one population declines or increases, whether predator, prey or competitor, it has an effect on the others. In some instances heavy fishing of a predator of other fishes, whether it be a food fish or a fish valuable for liver or body oils or for other products, relieves the pressure on the preyed-upon group and permits the latter to increase. This may be advantageous or otherwise. When steps are taken by regulation to curtail fishing on certain species there is an effect on others, perhaps beneficial, perhaps the contrary.

How significant such relationships between species are in the development of management policies depends largely upon the species being managed. In certain cases the reactions may be highly significant and important; in others they may be only of minor concern. Nevertheless they should be included in any investigation and the part they play clearly determined, even though only as factors causing variation in the populations being managed.

For salmon, as an example, there is available certain evidence (Foerster and Ricker, 1941) that control of predator fish can result in appreciable increase in survival of young sockeye. This suggests one means of management. Young sockeye during their year in the lake have also certain competitors for plankton food. Reduction in numbers of these fish should result in greater growth and survival of the more desirable sockeye. Where the latter have been severely reduced in abundance through various causes, the competitors may now be well established, and sufficiently so to make it impossible to restore the former sockeye populations. Only by clearing out these competitors can restoration of the sockeye, then, perhaps be accomplished. This would also be a phase of fisheries management.

Other examples of important relationships could be cited, such as the probable effect on some of our coastal fisheries of the protection of the fur seal and its notable increase in abundance, the heavy war-time exploitation of our grayfish (dogfish) populations, the alleged increase in sea lions and hair seals, the establishment of halibut nursery areas in certain coastal regions and the effect on crab populations. All such population changes undoubtedly have a bearing on the conditions prevailing in other fisheries.

Variations in Oceanographic Conditions. Conditions prevailing in the inshore and offshore ocean waters have a direct bearing not only upon availability of fish to the fishermen but also upon survival. To cite but one example, the recent near-failure of the pilchard fishery on the west coast of Vancouver Island in 1946 is attributed partly to decreased population, to the failure of new age-classes to enter the fishery, and partly to changed oceanographic conditions which cut short the normal northward annual migration.

Little is known of the real relationship of oceanographic conditions to the well-being of our Pacific coast fishes, but since spawning of the marine species is intimately associated with environmental conditions, it is evident that a study is essential before a proper understanding can be reached. Although it is unlikely that any measure of control can be instituted, a knowledge of the conditions, and particularly of existing trends, if any, can be of great significance in prediction and may play a major part in this important feature of fisheries management. The initiation of an oceanographic investigation is urgently needed. Its results will have wide application to fisheries.

Establishment of Quotas

In view of our existing limited knowledge of the exact status of many of our fisheries, and in view of the demand for management of some kind to build the stocks up to a reasonable maximum level and maintain them at that level with a maximum sustained yield, it may yet be considered feasible in many cases to adopt a quota system of regulation or management, thus limiting the extent of commercial exploitation and thereby ascertaining how the populations of fish react. Undoubtedly there will be variations in abundance from year to year as well as variations in availability of fish to the fishermen due to weather, late running, etc., but if the quota be allowed a moderate flexibility dependent upon information and data made available to the biologists, such a system would seem to have genuine merit. It would at least provide a control on one phase of the fishery, especially if it be a highly-exploited fishery, and it would achieve a quicker understanding of the maximum desirable level of exploitation to be reasonably allowed. It would not be expected at any time to provide a uniform level of exploitation or a uniform sustained yield or catch, for cyclic variations in abundance are likely to occur, perhaps of some magnitude over a period of years, but it would tend to cut the extremes of these cyclic variations and would at least lead to an earlier understanding of their existence and probable extent. Quotas may therefore prove effective as the first step in fisheries management, and a very useful one. They might even lead to the conclusion that in certain fisheries no management is required. Even this would be a progressive step, but the writer is dubious of the likelihood of its occurring.

One argument against limitation of catch by quotas or by any other means is that under such a system no attention is given to economic demand, price levels, etc. In those years, for example, when there exists a keen demand for certain fish products due to failures in the supply of other food products or because of the failure of fisheries in other areas, there is no opportunity of appreciably increasing the catch and relieving the critical situation. If prices happen to be high, there is no means of capitalizing on them. It is argued that, since there is little danger of depleting a stock of fish beyond recovery, it may be found advisable to exploit it heavily at opportune times, even though it lead to temporary economic depletion subsequently. Such a practice, though meeting immediate expediencies in unusual instances, inevitably results in highly fluctuating fisheries with no assurance that the low levels of abundance may not occur at times when abundant supplies are sorely needed. It would not appear to be a wise system of management.

Limitation of Fishermen

Quotas are suggested as a means of definitely limiting the total extent of exploitation. They limit the amount of the catch of fish, irrespective of the number of fishermen. A further means of management might be the limitation of licenses, thus stabilizing the number of fishermen involved and assuring to each a reasonable catch. This has already been suggested for the salmon fisheries of British Columbia by the Assistant Commissioner of Fisheries (Alexander, 1939: 18) and has been discussed in general terms as a method of fisheries management by Herrington and Nesbit (1943).

There is much merit in the contention that such limitation would benefit the fishermen as well as the supply of fish, for the licensed fishermen would then be more definitely interested in the conservation of the fish and the maintenance of his means of livelihood at a high level. It might lead to the development of a more stable group of experienced, highly-efficient operators. On the other hand, it might be difficult to bring such a system into being, and for some of our fisheries it might lead to wastage of fish.

The subject is included only as a reference to a further method of fisheries management.

CONCLUSION

That some measure of fisheries management should be developed to maintain a high sustained yield for our commercially-important fisheries seems highly desirable. While for some species a reasonable management policy may now be possible, for others more pertinent information is required. Quota systems of regulations leading eventually to final management policies are suggested, but the quotas should retain sufficient flexibility to be altered as conditions warrant. Quotas may quite quickly reveal the effect of fishing-effort on the stocks of fish and indicate the general reaction to varying degrees of exploitation.

Prediction is considered a valuable phase of management. It can indicate for certain species the trends in the populations, even if it does not reveal the total abundances, and can be used as a guide to effective regulation of fishing-effort in order to guarantee an adequate spawning population.

The fishing industry and government departments charged with the administration of fisheries resources are vitally interested in the establishment of suitable management policies that will result in maximum sustained exploitation consistent with perpetuation of the resource. Restriction of fishing-effort is in some instances the only means of rebuilding the stocks to high levels of abundance, but wherever possible these restrictions should be supplemented by other means of increasing production of fish to the end that the restrictions can be reduced and maintenance of stocks of fish at high levels of abundance assured by other phases of management. Definite progress is being made as pertinent facts accumulate. Methods used and results obtained in all parts of the world are critically examined to determine their usefulness in other situations, and gradually the value and practicability of useful management policies are becoming clarified.

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DISCUSSION

Van Oosten: Dr. Foerster's paper is now open for discussion.

Huntsman: I wonder about the economic side which you almost seemed to exclude from your plans for future management. I understood from Dr. Needler's remarks that he would put that in the forefront. Could it be considered as proper procedure to place the most importance upon the purely economic factor of catch-per-unit-of-effort, and attempt primarily to manage on that basis, bringing in the matter of determining availability in due course?

Foerster: I think you have to have a scientific basis on which to operate—in other words, some principles for your fisheries management.

Huntsman: This would be a principle. You would base your fishery upon catch-per-unit-of-effort as the fishermen, I think, really have to do, but you help them to do it well.

Herrington: Isn't it preferable to take a medium course? If you decide to do something from the biological angle, then you must consider how those measures would bear on the fishermen.

Let's assume that it has been determined that a certain fish would benefit by raising the size limit from 20 to 30 inches. A large part of the fish population lies between 20 to 30 inches. If you raised the size limit in one jump you would wipe out the fisherman's livelihood for a period of perhaps three years. That would obviously be economically and sociologically undesirable. So you compromise and raise the limit slowly so that each step will have very little effect each year. Isn't that the way it is done?

Huntsman: Yes, but suppose we take the Pacific halibut experiment which has been under criticism. Hasn't it been worth-while from the aspect of catch-per-unit-of-effort? Looking at that part of the experiment, or the management, surely it has been worth-while, irrespective of the part that has been criticized.

Burkenroad: You evidently mean that the price to the fisherman has been raised by management, because there is no evidence that it is the regulation which has improved the catch-per-unit-of-effort. The fisherman is getting a better price, relative to catch-per-unit-of-effort. The public is paying a higher price, relative to the availability of the fish.

Huntsman: I am under a misconception. I thought there was a decided improvement in the catch-per-unit-of-effort.

Burkenroad: Yes, but there is no evidence that it was due to the regulations.

Huntsman: I thought that was an actual result.

Burkenroad: I don't think the evidence requires that it be considered as anything but an unforeseen natural change.

Herrington: Wouldn't the evidence plus experience show that the size of the fleet was a factor. If the fleet grows and if they are fishing the full season, rather than just two or three months, what usually happens is that the total catch, not the catch-per-unit-of-effort, goes up. In the halibut case the catch was held down so that the returns-per-skate went up.

Burkenroad: As landings go up the price goes down, other things being equal, and effort would then be expected to decline. This is a complicated relationship which we are trying without much success to analyze for the North Carolina Survey. But to assume, in the lack of satisfactory analysis, that the fisheries would not regulate themselves at the level socially optimal is equally without foundation.

Huntsman: I thought if anything was clearly established it was that the restriction of effort would increase the catch-per-unit-of-effort, both in the European and the Pacific halibut.

Burkenroad: The only thing that is established is the theoretical possibility. I would like to raise the point that, even if we grant that management based on sound biological principles should have a beneficial effect on a given species of fish, and even if we disregard the probability that benefit to one species will have detrimental repercussions on other members of the ecosystem, the question remains whether the magnitude of the changes caused by the fishery is really at all comparable with the magnitude of the uncontrollable natural changes. For example, if you are aiming to create, by restrictions of fishing, a small improvement over what you could get without restriction, but if natural fluctuations are causing very large changes, then the effort required for a management program may not be worth the cost. It all depends on the ratio in magnitude of effect between the natural causes and the human causes. It seems to me that, for most if not all fisheries, it has not yet been demonstrated that the natural or the indirectly human effects do not far overshadow the effects of fishing.

Foerster: That is perfectly true. Sometimes, though, I wonder whether we are not exaggerating the possibilities of natural variations.

Huntsman: What is the position now as to fishery management for the future? The fisheries are bound to be managed by the fishermen themselves, but can the fisheries investigators see, more or less clearly, certain parts of the picture which enable them to help the fishermen manage the fisheries more effectively? What can we see most clearly? We should take full account, it seems to me, of this very important matter of the catch-per-unit-of-effort, as Dr. Needler has pointed out, so as to know whether or not the fisherman is going to make a living, and advise him accordingly. How much farther we can see is the question. We may be in doubt about these natural fluctuations. We should try to separate them out if we can.

Needler: Certainly I didn't intend to suggest that management should be based only on a knowledge of the catch-per-unit-of-effort. Management, as most highly developed, should be based on a knowledge of the population as well. It depends on the definition of management. The knowledge of the catch-per-unit-of-effort and prediction of the catch-per-unit-of-effort could contribute, of course, to management which attempts to even up production; and it could contribute to the economic use of next year's crop of fish.

Burkenroad: One question is, does the particular fishery considered have an effect on the next year's crop? For example, in peneid shrimp a high proportion seems to be removed, but there does not seem to be any evidence that that removal has any effect on the next year's crop; thus the field for rational legal restriction there is probably limited to the question of how rapidly each crop of shrimp should be harvested, and by whom. The biological question of whether delayed harvesting would really increase the crop is subsidiary to unsolved socioeconomic questions. If the next year's stock is going to reach the level that natural conditions permit, without reference to the preceding year's fishery, what does the biologist manage?

Needler: That's the whole point. You have to know what your mortality is going to be and, of course, you have to bring in the length of life of the animal concerned. With the halibut it would be a reasonable assumption that a large proportion of the larger halibut would be there next year. Now, with silverside, it is a reasonable assumption that any you left wouldn't be there at all.

Fry: It's a little hard for a mere neutral person to get a word in edgewise. It would seem to me, listening to the managers and nonmanagers in the course of the last day and a half, the one thing you have not gotten down to is the actual application of the principal of limiting factors, which is really the thing you are both invoking. That is, a factor that is potentially limiting does not operate until you get down to a certain point. I don't quite see why you don't get together and say, "There is a possibility of one fishery reducing the stock below the minimum and thus getting it into this limiting range where it is going to affect the next year's crop. However, in this other fishery that is not so."

Needler: I think you have stated what I was trying to say, that is, that the applicability of these methods depends on the intensity of the fishery.

9. LIMITING FACTORS FOR FISH POPULATIONS[1]

SOME THEORIES AND AN EXAMPLE

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[1] This paper draws extensively upon results of the work carried on by the "Haddock Investigations" of the Fish and Wildlife Service of the United States Department of the Interior, under the direction of the writer. A number of other investigators have assisted in this work from time to time, notably John R. Webster, Mildred S. Moses and Howard A. Schuck. The population index for haddock and for other groundfish has been handled since 1937 as a separate project, "Groundfish Abundance Analysis," started in 1938 under George A. Rounsefell. Field work at sea was done on commercial trawlers and on the "Atlantis," through co-operation of the Woods Hole Oceanographic Institution. Data on the commercial catch were obtained by various interviewers stationed on the Boston Fish Pier. Dorothy B. Monahan and Edward S. Phillips provided assistance in preparation of charts and analysis of data for the present manuscript. Correction of script and proofreading was handled by Erna L. Milch.

[1a] Proofs not seen by author.

ABSTRACT

The purpose of this paper is to determine the factors having most influence on the *average* productivity of certain fish populations; to develop the theoretical relationships expressing the effect of these factors on fish stocks; to test the validity of the theoretical relationships by using actual data for certain fisheries; and to apply the conclusions to the problem of explaining the present poor condition of the haddock population and how it can be improved.

The theoretical relationships developed indicate, under the conditions considered, that average relative recruitment to the usable stock of fish is dependent chiefly upon the size of the spawning stock and of the competitive stock. The correlation between adult stock and recruitment for actual haddock data is very similar to the theoretical correlation curve. By varying the supply of food, changes in the theoretical curve are obtained which are similar to recent changes in the actual haddock correlation curve.

The conclusion that recent supplies of food available to haddock have been reduced materially is supported by independent evidence from studies of adult stock distribution on the fishing grounds and from growth rates. Increases in the population of other species have not been sufficient to explain the decrease in haddock food.

This study shows that the recent scarcity of haddock resulted from reduced food supplies for haddock and from underfishing during the war. It also indicates that recruitment should increase during 1947–48, and that, to maintain a high yield in the future, the adult population must be held within the limits required for good spawning and minimum intraspecific competition.

The basic objective of the major proportion of the work in fishery biology, at least of that part financed by Government, is to determine how man can obtain the maximum continued yield from our fishery resources. The maximum objective of the work is the accumulation of such knowledge that the controllable elements of the environment can be managed so that productivity can be held at the maximum; the minimum objective is to discover causes of variability in productivity, whether controllable or not, so that useless expenditure of effort and funds on ineffective management measures can be avoided. There are many intermediate objectives which may be of value in situations where the maximum cannot be achieved.

THE PROBLEM

The wide variety of procedures and programs adopted by fishery biologists suggests that the field is broad and the approach to the problem not well defined. Perhaps it will help if some of the essential parameters can be determined; that is, what parameters must be known if we are to determine the optimum yield and its concomitant conditions.

On the average, the number of fish of usable size which man can remove annually from an independent population of fish is equal to the annual recruitment to this population from the upgrowth of young, minus the natural mortality of the usable stock. Thus:

$$P_1 + R - M_n - M_f = P_2,$$

in which P_1 equals the population of usable size at the beginning of the year, R equals the annual recruitment, M_n equals natural mortality through the year, M_f equals the mortality from fishing (the catch), and P_2 equals the population at the beginning of the next year, with all of the values given in numbers of fish.

When the fishery is stabilized $P_1 = P_2$ and $M_f = R - M_n$.

In the interest of simplicity, let us temporarily forget natural mortality of fish of usable size. Then, since $M_f = R$, we can define the conditions of maximum sustained yield as those which result in the maximum sustained recruitment. Consequently, our problem is to determine the quantitative relationships or correlations between recruitment and the various environmental factors, in order that the conditions of maximum recruitment can be defined.

This statement is an oversimplification, of course. The commercial fisherman at least is more interested in the weight of fish caught than in the number. Therefore, recruitment in weight through growth to a larger size must be considered in addition to recruitment in numbers.

In the following sections of this paper it will be shown that increase in weight or mass of the usable and adult stock will have effects on recruitment which may outweigh the direct effect of increased size of the individual fish. The complete interrelationships have not yet been worked out, but in the case of Georges Bank haddock it appears that the size at which the fish are taken for market is much less important in determining the maximum yield than is the mass of the adult stock maintained in the area. This may be equally true for many other species.

THEORETICAL CONSIDERATIONS

It will be of help in examining this problem to set up hypotheses covering some of these relationships, which then can be tested by application to actual data. The hypotheses have been derived to apply particularly to populations such as Georges Bank haddock, which are predominant among the larger fish in that area and which are noncannibalistic. However, it is probable that with certain modifications the hypotheses may be more generally applicable. The basis for the hypotheses will include factual information, reasoning and speculation.

Recruitment equals reproduction (numbers of fertilized eggs or young) minus the mortality they experience before reaching usable size. Since reproduction generally is roughly proportional to the mass of the spawning stock (number and size of spawners), relative reproduction can be represented by a straight line starting at zero when the spawning stock is zero, increasing with the mass of the spawning stock, and reaching a maximum of 100 per cent when the spawning stock reaches a maximum (Fig. 1., Table I).

The mortality experienced between the egg or newly-spawned young stage and the time the fish reach usable size is caused by numerous factors including predators, food limitations, and unfavorable conditions in respect to temperature, salinity and currents.

Temperature and salinity are of primary importance in delineating the area outside of which M_n is so high that survival is poor or impossible. Within this area, year-to-year variations in temperature and salinity may cause annual variations in natural mortality, and therefore, in annual recruitment. However, in such cases it is not likely that either is the limiting factor in determining the *average* recruitment *over a period of years.* Therefore, in general, within the favorable

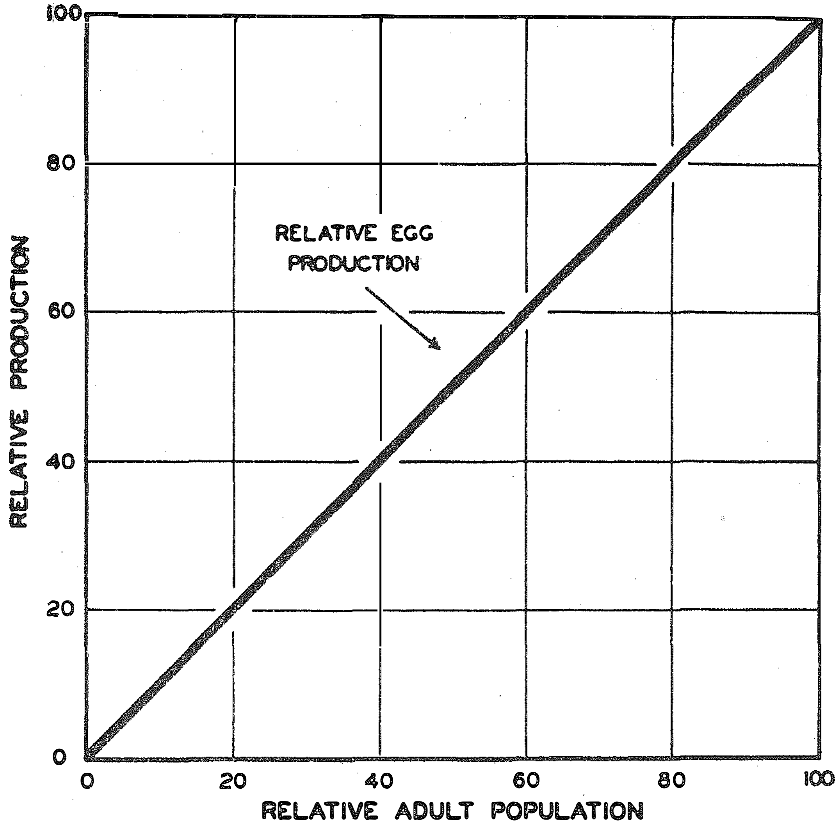

FIGURE 1. Relationship of the adult stock to production of eggs. Correlation between the relative adult population size (mass), plotted as a percentage of the maximum, and the relative number of eggs or larvae produced, plotted as a percentage of the maximum.

temperature and salinity ranges of a species, food and predators are likely to be much more important in determining *average* survival than are temperature and salinity. Food is directly related, for in the final analysis it is the amount of food available which provides the over-all limitation on the amount of life which can be supported in a given area. Thus, at high population levels intraspecific competition for food should be dominant. However, when the population is considerably below the maximum which the food will support, interspecific predation probably becomes more important in determining the average survival or recruitment.

TABLE I. CHANGES IN EGG PRODUCTION AND THEORETICAL MORTALITY OF YOUNG FOR VARIOUS ADULT STOCK MAGNITUDES

Category	*Unit*	*Relative values*											*Figures in which used*
Adult Stock	% of maximum	0	10	20	30	40	50	60	70	80	90	100	—
Eggs	% of maximum	0	10	20	30	40	50	60	70	80	90	100	1, 2
Interspecific Predation	% of eggs	—	90	78	67	58	50	42	36	31	28	25	2
Interspecific Predation (I. P.)	Relative number	0	9	16	20	23	25	25	25	25	25	25	2
Survivors	Relative number	0	1	4	10	17	25	35	45	55	65	75	2, 3
Intra-Year-Class Mortality (I_a-Y. C.)	% of I. P. survivors	—	4	8	12	16	20	43	56	64	69	73	3
Survivors	% of I. P. survivors	—	96	92	88	84	80	57	44	36	31	27	—
Survivors	Relative number	0	1	4	9	14	20	20	20	20	20	20	3, 4
Inter-Year-Class Mortality	% of I. P. and I_a-Y. C.	—	2	4	6	8	10	80	90	92	94	95	4
Survivors	% of I. P. and I_a-Y. C.	—	98	96	94	92	90	20	10	8	6	5	—
Survivors	Relative number	0	1	4	8	13	18	4	2	2	1	1	4, 7

In this and in the following sections "available food" is used in the sense of food available to the species being considered. Interspecific competition for food will reduce the amount available to this species, and therefore it has the same effect as a reduction in the supply from some other cause. The effect of such changes in the supply of food will be considered in a later section (p. 241).

Interspecific predation and intraspecific competition and the mortalities arising therefrom operate concurrently, but, as just pointed out, it is probable that the first reaches a maximum rate at low population levels and the latter at high levels. It is also probable that the two types of mortality attain their maximum influence at different times in the life cycle of the fish. In the case of haddock, mortality from interspecific competition probably is greatest during the first year or two of life on the bottom. For the sake of simplicity in argument these two types of mortality will be considered as if they occurred successively rather than concurrently. This will yield somewhat different values for mortality rates than if concurrent rates were used, but it should not change the general shape of the adult stock-recruitment correlation curve.

Mortality from Interspecific Predation

When the number of eggs and early-stage larvae is small, mortality from interspecific predation probably reaches a very high percentage for the egg, larval and young fish stages. However, the number of potential enemies in a given season must have some practical limit, so that as the quantities of eggs and young increase a saturation point will be reached beyond which the actual numbers of young taken will not increase greatly. In this event the rate of mortality will decrease as the population of young approaches the saturation level. The relationship of mortality rate to the adult population size will be similar to that between mortality rate and the number of eggs and early larvae, for the magnitudes of population size and eggs and early larvae are at least roughly proportional (Fig. 1).

If the mortality of the eggs and young from interspecific predation is of the type discussed above, it will be related to population size more or less as shown in Fig. 2 and Table I. The values shown do not pretend to represent the actual mortality rates and percentage of survivors, but rather only the type of change in rate which exists. The mortality rate could be greatly increased above that shown with-

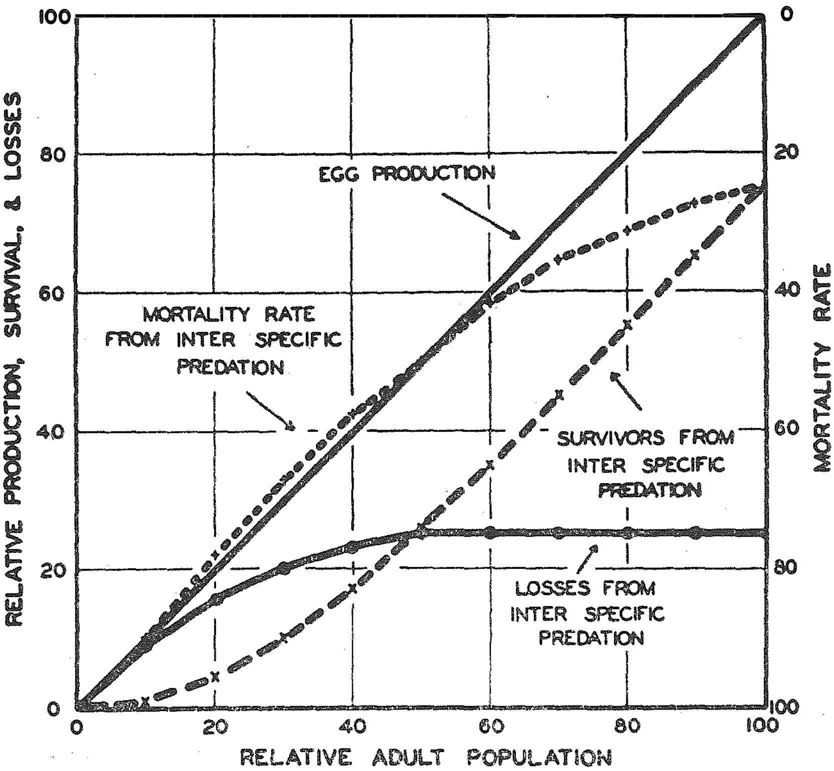

FIGURE 2. Effect of interspecific predation on survival of young. Theoretical correlation between the relative adult population size and the losses, mortality rate and survivors from interspecific predation. The egg production curve is from Fig. 1; the relative losses are assumed (see text); the mortality curve and survival curve are derived from the first two curves. These curves do not represent actual numbers and rates but only the type of change in number or rate which accompanies changes in the adult population size.

out changing the shape of the survival curve. The only assumptions involved are that predators take a high proportion of the eggs and early larvae when the latter are relatively scarce (*i. e.*, at low population levels) and that a decreasing proportion is taken as the numbers increase. The actual numbers destroyed, therefore, approach an asymptotic limit determined by the number of predators (Fig. 2). Probably the fixed limit to the number destroyed, indicated in Fig. 2, does not exist in nature, although it should be approximated. With increasing population size and number of eggs, the young probably would be dispersed over a somewhat greater area, even for increases at high population levels. This greater distribution would subject them to more predators, so that the asymptotic limit at high population levels would not be fixed but would increase slightly with an increase in population.

Mortality from Intraspecific Competition

The mortality arising from intraspecific competition for food should be closely related to population size. The rate would be related to the average amount of food per fish, and with a given supply of food the average food per fish would be determined by the size of the population. In the following line of reasoning we will assume a constant supply of food available to haddock. The effect of changing interspecific competition for food will be referred to later (p. 241).

At population levels well below the maximum that can be supported in an area the competition would be low, and with increasing population size this competition would increase at a low rate until the most accessible kinds of food and most suitable grounds had been utilized. Thereafter the rate would increase more rapidly with further increases in population level and egg production, in order to hold the numbers of young to the level which the food supply would support.

If the competition were principally within year-classes, this increase in mortality rate at higher population levels should be about proportional to the increase in number of eggs and, therefore, of the adult stock. This relationship would be necessary to hold the survivors to the number which the supply of food could support. Under actual conditions it is probable that the number of survivors would not level off at an absolute ceiling, for with a continued increase in the adult population the young would be spread over a somewhat greater area. This would make available at least some additional supplies of food.

This type of mortality (competition within year-classes) is shown in Fig. 3. Mortality at low population levels is light but increases as the population increases, until the most accessible supplies of food are utilized. From there on the mortality increases to keep the surviving population in balance with food supplies.

In the case of haddock at least, the principal competition at higher population levels is between year-classes instead of within classes. The principal nursery grounds are outside of the areas apparently preferred by the adult fish (Figs. 18, 19). Consequently, the competi-

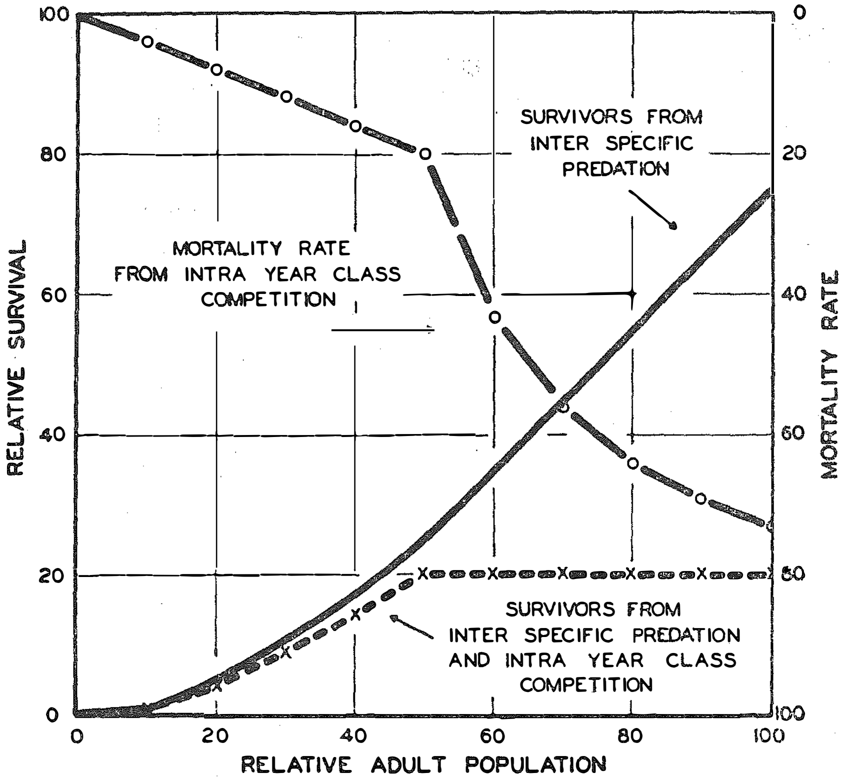

FIGURE 3. Effect of intra-year-class competition for food. Theoretical correlation between the relative adult population size, the mortality rate from intra-year-class competition for food, and the survivors from interspecific predation and intra-year-class competition. The interspecific survival curve is from Fig. 2; the mortality rate curve is assumed (see text); the curve representing interspecific and intra-year-class survivors is derived from the preceding curves. The mortality curve represents only the relative change in rate which accompanies changes in the adult population size.

tion between the old and young is limited, except when the population of adults increases until growing population pressure forces them to spread out in search for food to areas not covered at lower population levels. Competition with the young then increases rapidly. If the adults are migratory and the young are not (as with haddock), it is probable that the nursery grounds are stripped of food, the adults then moving on, leaving little food for the young. Under these conditions the mortality rate of the young would increase slowly with increasing population size until the adult population reached the level where it

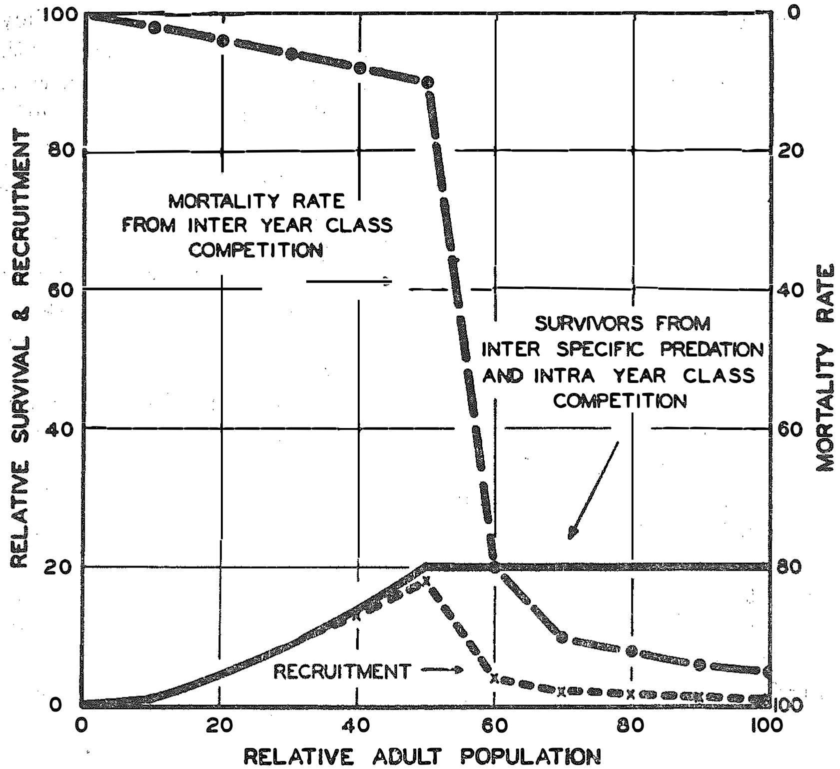

FIGURE 4. Effect of inter-year-class competition for food. Theoretical correlation between the relative adult population size, the mortality rate from inter-year-class competition for food, and recruitment. The survival curve from interspecific predation and intra-year-class competition is from Fig. 3; the mortality rate curve is assumed (see text); the recruitment curve is derived from the preceding curves. Recruitment to the adult population or usable stock consists of the young fish which survived interspecific predation and intra-year-class and inter-year-class competition for food. The mortality curve represents only the relative change which accompanies changes in population size.

began to overrun the principal nursery grounds. Further increases in the adult population would cause a rapid rise in the mortality rate until it approached 100 per cent. From there on further increase in rate would be slow, for it is probable that a few young could continue to find food in out-of-the-way localities and in particularly favorable areas. The mortality curve of this type should approximate some such shape as shown in Fig. 4.

If both intra- and inter-year-class competition are present, their effects would be combined at the lower population levels, since they both serve to reduce the amount of food available per fish. Both would increase as the adult population increased, for competition with the adults would become greater as the adults increased, and the within-year-class competition would rise as the eggs and larvae increased in numbers. These increases would be proportional to the spawning stock. At higher population levels the relationship may be more complicated, depending on whether or not the competition between adults and young is present throughout the years before the young reach usable size or is concentrated in a particular year or season. In the case of Georges Bank haddock there is considerable evidence which indicates that at high population levels this type of competition is concentrated mainly in the first winter of the young haddock's life. At that time the young are 8–12 months old, the adults are most dispersed, and production of food probably is at its minimum. If such is the case, then at high population levels the mortality caused by competition within the year-class before the first winter would not be important. The bottleneck on survival would be determined by the competition furnished by the adult population during the first winter.

Inter-year-class competition after the first winter probably is not critical, for haddock in their second and third years become more migratory, and thus they are able to seek new grounds for food if one area is stripped. During the years covered by our data there is no evidence to indicate that there has been abnormally high mortality of older fish at times of maximum population level.

It does not appear essential at this point to determine the relative importance of mortality caused by intra- and inter-year-class competition, or to determine whether or not the acceleration in mortality from the two types of competition occurs at the same population level. If inter-year-class competition is most important, as in the case of haddock, the survival curve will be of the type shown in Fig. 4, while if intra-year-class competition is the most important, the survival curve will be of the type in Fig. 3.

In the foregoing discussions adult stock is used to represent spawning stock as well as competitive stock. This condition is approximated for species such as haddock, where the fish mature at about the time they reach usable size. For other species such as the New England lobster and rosefish, the fishery begins taking the young several years before they reach spawning size. In such cases the adult stock and the competitive stock (as represented by the catch) will have different values and must be plotted on different scales to obtain the recruitment-stock correlation.

Effects of Decrease in Food

This problem can be subdivided into two parts, (1) decrease in food for the larval and early bottom stages (first summer) and (2) for the older stages.

Decreases in food for the larvae and juveniles only would cause the point of inflection in the intra-year-class mortality curve (Fig. 3) to move to the left to whatever extent was required to keep the surviving

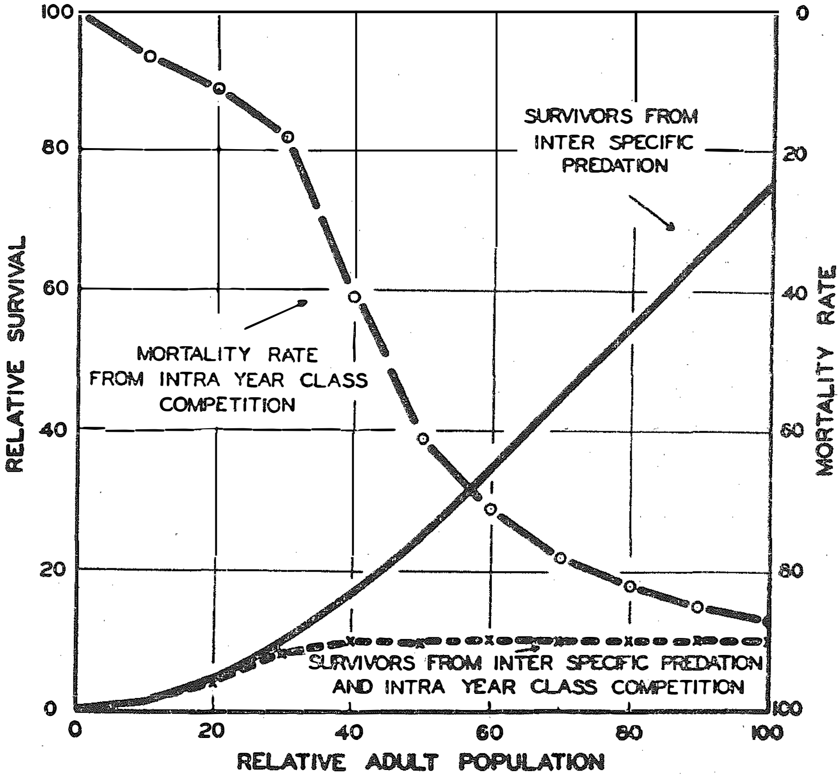

Figure 5. Effect of 50 per cent reduction in food supply on intra-year-class competition. These theoretical correlation curves are similar to those in Fig. 3, except for changes caused by reducing the food supply for the juveniles by 50 per cent.

TABLE II. EFFECT OF REDUCED FOOD SUPPLIES ON THEORETICAL MORTALITY AND SURVIVAL OF YOUNG

Category	*Unit*	*Relative values*											
Adult Stock	% of maximum	0	10	20	25	30	40	50	60	70	80	90	100
Survivors from Interspecific Predation (Table I)	Relative number	0	1	4	7	10	17	25	35	45	55	65	75
Intra-Year-Class Mortality[a] (I_a-Y. C.)	% of I. P. survivors	—	7	12	15	18	41	60	71	78	82	85	87
Survivors	% of I. P. survivors	—	93	88	85	82	59	40	29	22	18	15	13
Survivors	Relative number	0	1	4	6	8	10	10	10	10	10	10	10
Inter-Year-Class Mortality[a]	% of I. P. and I_a-Y. C. survivors	—	4	8	10	80	92	95	—	—	—	—	—
Survivors	% of I. P. and I_a-Y. C. survivors	—	96	92	90	20	8	5	—	—	—	—	—
Survivors	Relative number	0	1	4	5	2	1	½	—	—	—	—	—

[a] Food reduced to 50 per cent of original amount assumed in Table I.

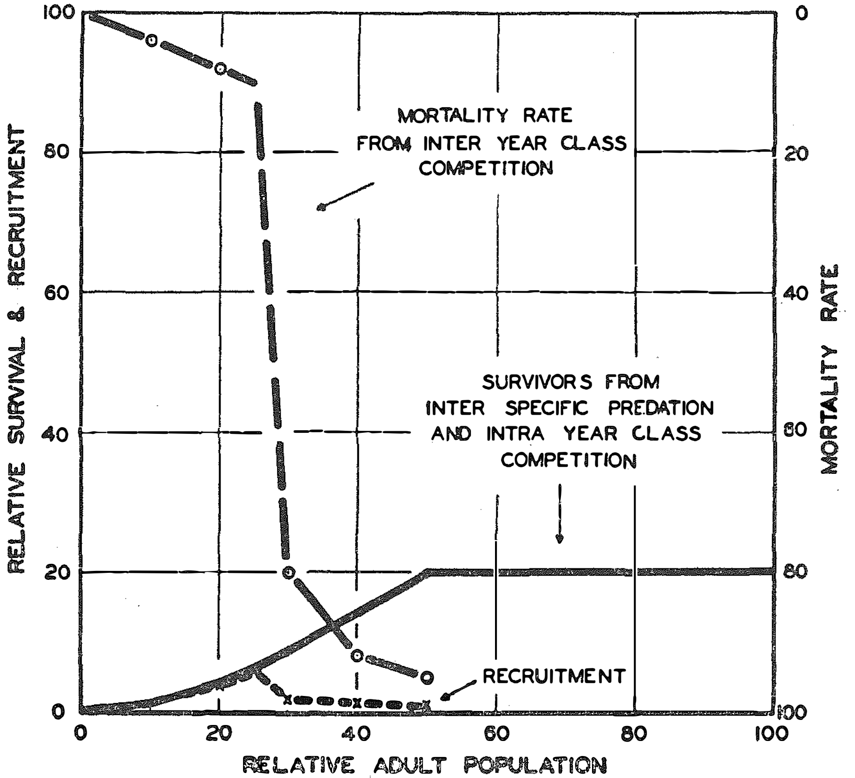

FIGURE 6. Effect of 50 per cent reduction in food supply on inter-year-class competition. These theoretical correlation curves are similar to those in Fig. 4, except for changes caused by reducing the food supply for the older year classes by 50 per cent.

population within the limits of the reduced supply of food. This would lower the maximum level for the numbers surviving; it would round off the peak but would not otherwise greatly change the shape of the recruitment-adult population correlation curve; and it would depress the location of the modal recruitment value in relation to adult population size to only a minor extent. These effects are shown in Fig. 5 and Table II, and in the Fig. 7 curve, for 50 per cent reduced food for juveniles.

A reduction in the supply of food for the older fish would have a more noticeable effect on the recruitment-population correlation curve. The decreased amount of food would cause the adults to spread out in the search for food at a lower population level than before. This

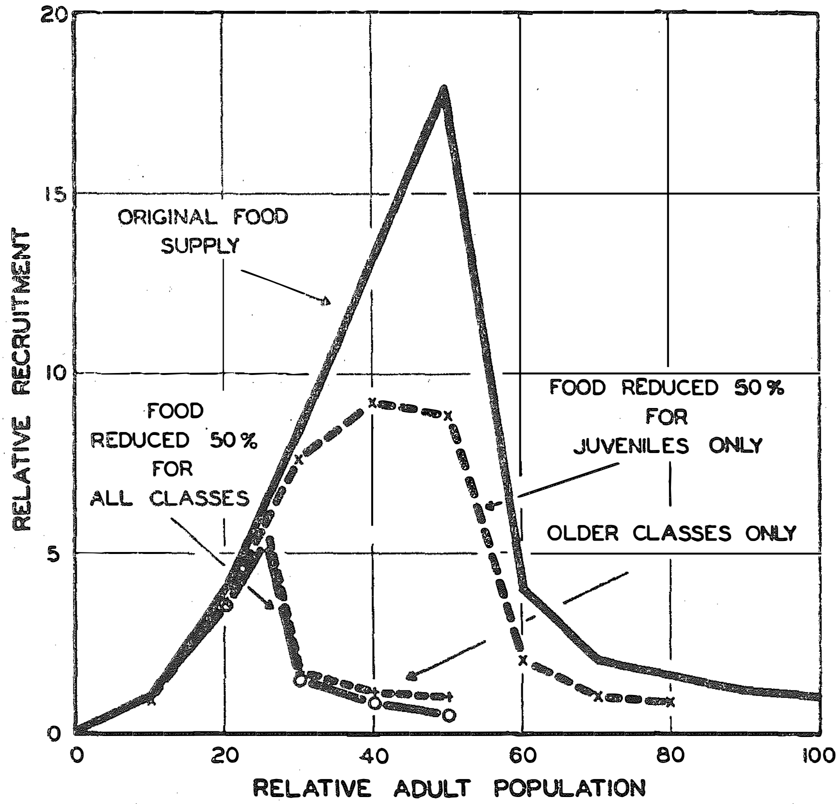

FIGURE 7. Adult population-recruitment correlation curves for various conditions of food supply. Theoretical curves showing effects of 50 per cent reduction in the food supply for juveniles only, for older classes only, and for both juvenile and older classes.

would shift the first inflection point in the mortality curve (Fig. 4) in the direction of a smaller adult population, more or less in proportion to the reduction in food supplies. As a result, the modal recruitment value in the recruitment-population correlation curve would be shifted in the same direction. Fig. 6 and Table II show the effect of a 50 per cent reduction in food for the older year-classes.

The effects of reduction in food supply for juveniles only, adults only, and for both juveniles and adults, are shown by the recruitment-adult population correlation curves in Fig. 7. Reduction in juvenile food reduces the maximum recruitment but does not materially shift the mode in relation to adult population size. The effects are much greater when food supplies are reduced for older year-classes and for all year-classes. The modal value is reduced and shifted in the direction of lower population level.

SECURING THE ESSENTIAL PARAMETERS

It seems probable that *average* reproduction and survival to usable size (recruitment) is determined primarily by mortality correlations of the types represented by the curves developed in the course of the preceding reasoning and speculation. In these relationships the quantity and type of food available to a given population is the factor which is most important in setting the over-all limit on recruitment. Furthermore, within the limits set by food supplies, it appears that population size is most important in determining the success of average recruitment.

Population size is subject to control by man. It follows then that if we hope to manage our fisheries so that the maximum sustained yield can be obtained it is essential that these relationships be understood and evaluated. Until this is accomplished it will be impossible to state what conditions relating to spawning stock and population size will produce the maximum sustained recruitment. Increasing the size of the spawning stock or total usable stock by minimum size limits, catch limits, of by other controls on fishing, may be harmful if it results in greatly increased intraspecific competition. Decrease in recruitment from this cause may more than compensate for gains achieved by larger size of individual fish and more spawners. In some cases perhaps the soundest conservation measure would be to stimulate the decrease of the stocks by decreasing protection.

This line of argument leads to the conclusion that the first problem of the fishery biologist usually should be to determine the above relationships. The problem can be attacked through study of the present and past fishery. If suitable data are available covering years during which the population has varied through a wide range of productivity, it is likely that it will be possible to determine the recruitment-population correlation curve over a considerable proportion of the total population range. In such a case the optimal condition of spawning stock and population size can be estimated. When data are available covering only a limited part of the recruitment-population correlation curve, and not including the modal recruitment section, then conclusions concerning optimal conditions will not be possible, but the biologist may be able to point out the direction in which spawning stock and population should be changed to produce a greater yield. By the collection of suitable data it will be possible to determine when the optimum population size has been deviated from, and management efforts then can be concentrated on returning the population to and maintaining it at the optimum level.

To solve the problem it is necessary that the several basic factors be evaluated quantitatively so that their relationships can be determined. These basic factors are recruitment, spawning stock and usable population size. Total catch (M_f) also is an essential element, for it is the final measure of productivity, and usually management of the catch is the most effective method for control of population and of spawning stock size.

Evaluation of annual recruitment, spawning stock and population size in general requires an accurate abundance index for the usable population. From such an index it is possible by means of size or age analysis, age at maturity and other data to determine the relative or actual numbers of fish reaching usable size each year (recruitment), the relative or actual numbers of spawners during any year (spawning stock) and the relative or actual numbers of fish of any size or year-class.

Measurement of abundance can be approached in several ways. The simplest (but not simple) case is that of anadromous fish such as salmon, where the spawning run makes up practically the entire usable population. Accurate records of the catch, plus a count of the upriver migrants made at a dam or weir, provide a complete record of the adult stock. This can be broken down into the respective age groups by means of suitable scale samples. The total number of fish of each year-class, on their first return to the river, is the recruitment from that class. The total number of fish escaping upriver to spawn is the spawning stock. The number of fish of any particular size or age-class can be obtained by sampling procedures. Compared to this, the accurate evaluation of abundance for a fish population in a large river, lake, bay, or ocean, when the usable and mature fish do not pass in review, is progressively, and in some cases almost immeasurably, more difficult.

In small streams and lakes an absolute measure of the total population can be obtained by poisoning, drainage, shocking, etc. However, with the exception of shocking, there may be some question concerning the use of these methods in a continued study of productivity, for they are likely to considerably alter natural conditions in the water body being studied.

All other approaches to this problem, using present methods and equipment, are indirect. Since it is impossible to obtain direct counts of the population, it is necessary to make use of sampling methods utilizing the commercial or sport fisheries, tagging procedures, or special gear operated from research vessels. Such methods can provide the needed data, but the errors in the values obtained are unfortunately large. Probably the greatest challenge to the fishery biologist today is improvement in his methods of measuring fish populations. Possibilities for improvement include technological developments such as subsurface photography, sampling mechanisms, etc.

Recruitment

Evaluation of recruitment can be based upon an idex showing the relative abundance of the fish population from year to year, the total annual catch, and the age composition of the population and catch. From these data the relative numbers of fish reaching usable size from each year-class can be derived. The accuracy of the evaluation will be limited by the accuracy with which abundance and age composition can be measured.

Absolute recruitment also can be evaluated but requires somewhat more data. Rough values for recruitment can be obtained from the following simplified formula given earlier in this paper:

$$P_1 + R_1 - M_{f_1} = P_2$$

$$R_1 = P_2 - P_1 + M_{f_1},$$

in which P_1 equals the relative population in numbers of fish of usable size at the beginning of the year, R equals the recruitment during the year, M_f equals the catch during the year and P_2 equals the relative population size at the beginning of the second year. The values are in numbers of fish, and natural mortality has not been considered.

In a stabilized fishery (in which the population is neither increasing nor decreasing from year to year) $P_2 = P_1$. Then $R_1 = M_f$.

These conditions rarely exist, for usually P, M_f and R vary from year to year. However, if recruitment can be stated as a proportion of the population at the beginning of the year, the values for P and R still can be obtained from the data for a single year. This is shown in the following example:

Yr.	*P*	*R*	*C*
1	1.00	.50P	70
2	.80	1.00P	60
3	1.20	—	—

$$1.00P + .50P - 70 = .80P \qquad .70P = 70 \qquad P = 100\ R = 50$$
$$.80P + 1.00P - 60 = 1.20P \qquad .60P = 60 \qquad P = 100\ R = 100$$

If data are available for two or more years, actual values also can be obtained for P and R by means of simultaneous equations, even though the R values are relative rather than in terms of P.

The data needed for these solutions are:

1. An accurate index of the population size (usable fish).
2. An accurate index of the annual recruitment (requiring age composition in addition to the population index).
3. An accurate record of the total catch in number of fish.

If the relative R and P values could be obtained with a high degree of accuracy, then the calculated values of R and P would be very close to the real values. However, I know of no case where the real accuracy of R and P indices has been determined. (In fact there have been few attempts to measure R or P.) It is possible to obtain the standard errors of the R and P indices, but these simply represent the consistency with which the gear samples the fish population or with which we sample the gear, but they do not indicate the accuracy with which the indices represent the population.

Because of the large errors in the calculated values for P and R caused by relatively small errors in relative P and R, the value of this method for obtaining real values may be limited. More exploratory work needs to be done on this subject to determine what degree of accuracy can be obtained by different methods of computation.

Even though it is not possible to obtain accurate real values for P and R, the relative values secured from population indices and age analysis can be used in analyzing the relationship between population size and recruitment.

TOTAL STOCK AND SPAWNING STOCK

The relative and actual spawning stocks and immature stocks of usable size fish can be estimated from the population index using information on age or size at maturity. The relative value will serve if actual values cannot be obtained.

DISCUSSION

The preceding argument covers only a few of the factors affecting recruitment. Usually, numerous subsidiary problems not covered here also will be involved. For some populations, particularly in the case of pelagic species, other elements of the environment may be so influential from year to year as to obscure the over-all influence of spawning stock, predation, and intraspecific competition. This also may be true for species which make up a minor part of the fish population of an area, for the food supply available to such a species will be heavily influenced by the abundance of competing species. Then interspecific competition for food may have a paramount influence. In the calculations described in computations of P and R, natural mortality also has been ignored, but it will be considered in the examples to be discussed later (p. 250). The foregoing argument also assumes that the fish population being studied is completely independent of other populations of the same species. If this is not true, then the differential migration between this and other populations must be taken into account.

The various causes of variability in survival may, in particular cases or years, cause wide deviations from the theoretical relationships discussed in the preceding argument and in some cases may make special problems of dominant importance. However, it is doubtful whether or not one is justified in assuming this to be so until the population relationships have been worked out at least approximately. In any event, the management of a fishery usually is possible only through control of mortality caused by human activities in order to bring spawning stock and competitive stock into the most productive relationship. Unless these relationships are understood, management is blind. Furthermore, the effect of other factors on recruitment cannot be determined unless recruitment itself has been evaluated and the effect of population relationships removed. Thus it appears essential, in any study designed to obtain an understanding of the factors controlling productivity of a stock of fish, that the elements we have discussed should be included among the primary objectives of the investigation.

In the following section of this paper the correlation curve showing the relationship between adult population size and recruitment will be derived for an actual fish population and compared to the theoretical curves developed above.

NEW ENGLAND HADDOCK (AREA XXII SOUTH)

Index of Population Size

Special data concerning fishing effort, locality, etc. have been collected from the haddock fishery since 1931, and from these catch-per-unit-of-effort has been derived. In addition, extensive collections and analyses of older records obtained from boat owners, old government reports and from fishery publications have made it possible to obtain a comparable, but not an equally reliable, measure of abundance back to 1914. Less dependable estimates also have been obtained for 1913 and 1912. The effects of major changes in fishing methods, gear and boats have been evaluated and brought into proper relation, but it is impossible to determine exactly the comparability of the unit of effort used over wide intervals of time. Furthermore, as with any abundance measure of this kind, it must be remembered that the catch-per-unit-of-effort may not represent the entire population, but rather only a part, particularly in the early years when the fishery was not intensive. However, the haddock population index for Area XXII South (Georges Bank, South Channel, Nantucket Shoals, etc.) constitutes one of the longest existing series of reasonably reliable measurements of the variations in magnitude or availability of a fish population (Fig. 8, Table III).

Up to the present, the best check on the accuracy with which the index shows changes in the population is the intrinsic consistency of the seasonal and annual values obtained. One method for testing this is available from the calculations used to estimate the total population of fish of marketable size. The formula used for this purpose is similar to the one referred to in the first part of this paper (p. 231). Using pounds instead of numbers of fish, and allowing for natural mortality:

$$P_1 + R_1 + G_1 - M_n - M_{f_1} = P_2 ,$$

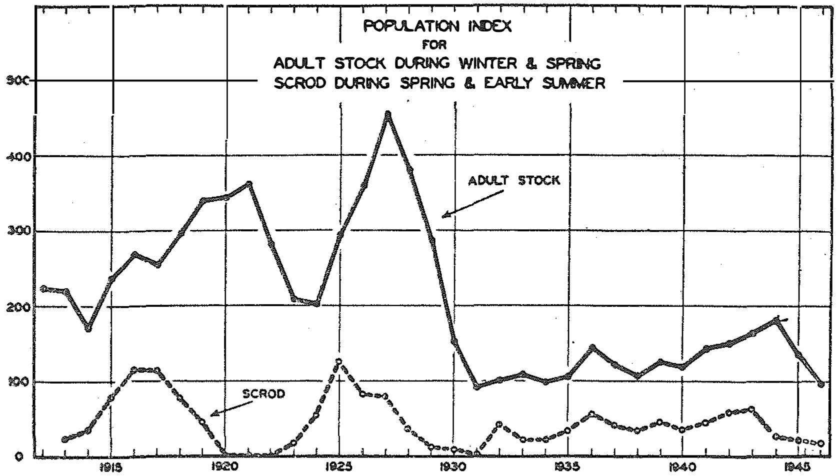

FIGURE 8. Changes in the size (mass) of the population of adult haddock and of scrod haddock (1½ to 2½-lb. fish) in Area XXII South (Georges Bank, South Channel, Nantucket Shoals). The winter and spring population of adults represents spawning fish, the spring and early summer population of scrod represents recruitment of 3-year-old fish. The vertical scale is in terms of hundred-weights of haddock caught per day by a standard group of large otter trawlers. The 1946 indices are estimated from incomplete data.

where P_1 equals the population index at the beginning of the year, P_2 the index at the beginning of the next year, R_1 the recruitment through upgrowth of young fish, G_1 the increase in weight through growth of fish present at the year's beginning, M_n the reduction in the population by natural mortality, and M_{f_1} the reduction in population through fishing operations.

From our population index, P_2 can be stated as a percentage of P_1, or both can be stated as percentages of the index for some other year. M_{f_1} is equal to the total catch during the year. R_1 can be calculated in terms of P_1 from an age analysis of the catch, and G_1 can be determined from growth studies and expressed as a percentage of P_1 and P_2. From various kinds of indirect evidence M_n has been estimated to lie between 5 per cent and 20 per cent. For the purpose of obtaining an inclusive estimate of population size, values of 0, 10 and 20 per cent have been used.

Estimates of the population at the beginning of 1927 (P_1) were obtained, using data for 1927–1931, years during which recruitment (R_1) was negligible or could be calculated from the scrod catch. It

TABLE III. ADULT STOCK AND SCROD INDICES FROM CATCH-PER-UNIT-OF-EFFORT ANALYSIS, AREA XXII SOUTH

Year	*Season[a] indices[β] of adult stock*			*Season indices of scrod*			
	D *Preceding year*	*A*	*Average*	*A*	*B*	*Average*	
	(lb.)	(lb.)	(lb.)	(lb.)	(lb.)	(lb.)	(No.[γ])
1912	22,300	22,600	22,450	—	—	—	—
1913	22,800	21,300	22,050	3,100	1,600	2,400	1,200
1914	16,700	17,500	17,100	3,300	3,700	3,500	1,750
1915	22,900	24,500	23,700	8,600	6,900	7,800	3,900
1916	26,900	26,900	26,900	9,900	13,100	11,500	5,750
1917	26,000	25,000	25,500	13,700	9,200	11,400	5,700
1918	28,900	30,200	29,550	11,200	4,100	7,600	3,800
1919	33,000	35,100	34,050	5,600	3,400	4,500	2,250
1920	34,000	34,600	34,300	0	0	0	0
1921	36,600	35,900	36,250	0	0	0	0
1922	29,600	26,800	28,200	0	0	0	0
1923	22,000	19,500	20,750	3,150	180	1,660	830
1924	19,200	21,200	20,200	5,550	5,290	5,420	2,710
1925	28,500	30,400	29,450	13,940	11,210	12,580	6,290
1926	34,100	37,700	35,900	6,660	9,710	8,180	4,100
1927	45,400	45,500	45,450	7,930	7,890	7,910	3,960
1928	39,200	36,900	38,050	4,520	2,580	3,550	1,780
1929	30,400	27,000	28,700	1,570	870	1,220	610
1930	16,700	13,800	15,250	940	870	900	450
1931	9,700	8,800	9,250	470	1,140	800	400
1932	9,400	10,700	10,050	3,970	4,300	4,140	2,070
1933	11,200	10,400	10,800	2,250	2,200	2,220	1,110
1934	9,800	9,800	9,800	2,200	2,170	2,180	1,090
1935	10,300	10,800	10,550	3,160	3,470	3,310	1,650
1936	14,300	14,600	14,450	4,630	6,490	5,560	2,780
1937	12,600	11,900	12,250	3,490	4,830	4,160	2,080
1938	10,600	10,800	10,700	2,490	4,250	3,370	1,680
1939	12,500	12,700	12,600	3,820	5,370	4,600	2,300
1940	11,800	12,000	11,900	1,830	5,470	3,650	1,820
1941	14,000	14,600	14,300	3,520	5,480	4,500	2,250
1942	15,000	15,100	15,050	4,020	7,840	5,930	2,960
1943	16,600	16,200	16,400	5,410	7,240	6,320	3,160
1944	18,100	17,900	18,000	3,480	2,120	2,800	1,400
1945	13,600	13,400	13,500	1,140	1,290	1,220	610
1946	—	—	[δ]9,600	—	—	—	[δ]860

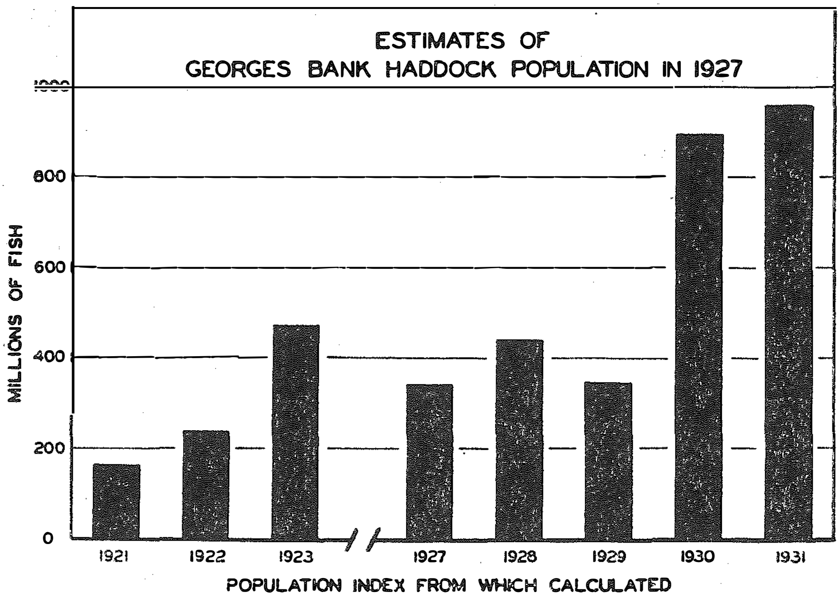

FIGURE 9. Estimates of the number of haddock in Area XXII South at the beginning of 1927. The estimates were obtained from the relationship between changes in the population index, the commercial catch and other data for the years shown along the horizontal axis. An annual natural mortality of 15 per cent was assumed.

will be possible to extend the calculations to other years when age analysis of the catch has been completed. Fig. 9 shows the values obtained, using a natural mortality of 15 per cent.

If the population index accurately represented the year-to-year changes in the total haddock population of commercial size fish in the area, then the calculated values of P_1 would be much the same or would

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References to Table III on page 252

[α] The year was divided into four seasons: A, Feb.–Apr.; B, May–July; C, Aug.–Oct.; and D, Nov.–Jan.

[β] The indices for the four seasons, A, B, C, D, were smoothed by a moving average of 4, then of 2, to reduce amount of variability caused by seasonal short-term factors. The Season D and A indices for adult stock used in this table are from smoothed figures. Scrod indices are unsmoothed.

[γ] Weight divided by 2, since scrod average about 2 pounds each.

[δ] Preliminary estimate based on decline in Season C. The boats used in this study were tied up during all of Season A and most of Season B.

fluctuate around an average value, regardless of the years from which they were calculated. Actually, the values obtained differ considerably, particularly those calculated from 1930 and 1931 data. The explanation lies in the fact that the fishery was not sampling the entire population in 1921–1929; furthermore, the expansion of operations in 1930 and 1931, stimulated by declines in prices and decrease in the daily catches of haddock, resulted in improvement of fishing methods greater than we were able to measure and bring into adjustment and in the inclusion of sections of rough bottom and new elements of the population not previously fished. Therefore, the index values in 1930 and 1931 did not decline as much as did the population itself, and this resulted in abnormally high calculated values for the population size in the base year (1927) when obtained from these data. Analysis of other data relating to the distribution of fishing operations, changes in gear, etc., support this explanation.

These abnormally high calculated values for population size were based upon data for years during which extreme scarcity of haddock exerted the maximum stimulus for improvements in gear and expansion of the area fished. Much more stable values can be expected from data for years when this stimulus was lacking.

The relatively consistent values obtained from the 1923, 1927, 1928 and 1929 data, using natural mortality rates of 10 and 15 per cent, suggest that these figures may provide the best estimate of the actual population size. The average of the calculated population values, using 10 per cent mortality, was about 325 million fish, and the average of the values, using 15 per cent mortality, was about 400 million fish.

Some further information on the reasonableness of these estimates can be obtained by other calculations.

From data on population size, mortality and catch, it is possible to calculate the decrease in the 1927 stock of fish during 1927–1931. Recruitment in 1928 and 1929 was very small and that in 1930 and 1931 can be evaluated from the scrod index. The average annual weight of haddock surviving from the 1927 stock can be estimated as increasing from 2.2 pounds at the beginning of 1927 to 4.9 pounds at the beginning of 1931. This is based upon the fact that there was a heavy recruitment of scrod in 1925–1927, so that the stock at the beginning of 1927 must have averaged about four years old. The age of this stock would have increased to eight years at the beginning of 1931. Age-weight data for Georges Bank haddock collected in 1936 give the weight of haddock for these ages (Table IV). The average ages and weights for the haddock taken during these years would be intermediate between the weight given. The 3.3-pound average for 1928 checks very well with the 3.4-pound average obtained from length-frequency samples taken in 1928.

TABLE IV. DATA ON AGE, WEIGHT, AND COMMERCIAL CATCH FOR THE 1927 STOCK OF HADDOCK IN AREA XXII SOUTH (GEORGES BANK)

Year	*Age 1927 stock*[a]		*Average weight*[β]		*Commercial catch*[γ]	
	Beginning year (yr.)	*Mid-year* (yr.)	*Beginning year* (lb.)	*Mid-year* (lb.)	(lb. in millions)	(No. in millions)
1927	4.0	4.5	2.2	2.6	143	55
1928	5.0	5.5	2.9	3.3	191	58
1929	6.0	6.5	3.6	4.0	223	56
1930	7.0	7.5	4.3	4.6	175	38
1931	8.0	8.5	4.9	5.2	94	18
1932	9.0	9.5	5.5	5.8	—	—

[a] Estimated from consideration of recruitment magnitude in 1925–1931.

[β] From age-weight curve for haddock sampled in 1936. Midyear average for 1928 checks against size samples for that year.

[γ] Scrod landings in 1930 and 1931 not included; considered new recruitment.

By using the above figures for average weight the commercial catches in 1927–1931 can be converted from pounds to numbers of fish (Table IV).

Now, if it is assumed that the total population of haddock of commercial size was 400 million at the beginning of 1927, and we subtract from this the natural mortality (15%) plus the commercial catch, an estimate of the population at the beginning of 1928 will be obtained. This can be done successively for the remaining years and gives a series of population figures which can be converted to an index with 1927 as the base (Table V).

TABLE V. DECREASE IN THE 1927 HADDOCK STOCK, ASSUMING (1) AN ORIGINAL STOCK OF 325 MILLION FISH WITH 10 PER CENT NATURAL MORTALITY ANNUALLY AND (2) 400 MILLION FISH WITH 15 PER CENT NATURAL MORTALITY

Year	*Total stock*	*Natural mortality*	*Fishing mortality*	*Total mortality*	*Ratio to 1927*
	(millions)	(millions)	(millions)	(millions)	(%)
1927	325	32	55	87	100
1928	238	24	58	82	73
1929	156	16	56	72	48
1930	84	8	38	44	26
1931	40	4	18	22	12
1932	18	—	—	—	6

Year	*Total stock*	*Natural mortality*	*Fishing mortality*	*Total mortality*	*Ratio to 1927*
	(millions)	(millions)	(millions)	(millions)	(%)
1927	400	60	55	115	100
1928	285	43	58	101	71
1929	184	28	56	84	46
1930	100	15	38	53	25
1931	47	7	18	25	12
1932	22	—	—	—	6

Calculations similar to the above can be carried out using an original stock of 325 million haddock and a natural mortality of 10 per cent. The index curve obtained is practically the same as that derived from the use of a 400-million original stock and a 15 per cent mortality rate.

The population indices calculated from the 400- and 325-million bases are compared (Fig. 10) to the indices obtained from the catch-per-unit-of-effort analysis. The latter have been converted to numbers of fish (Table VI).

The two series of indices show a similar trend, but the catch analysis series appears to be considerably too low, particularly in 1930. The two series again approach each other in 1931 and 1932. This relationship of the calculated and catch analysis index curves agrees with observed conditions. From 1927 to the beginning of 1930 the fishing fleet was not exploiting the entire population. Therefore, the heavily-fished portion was reduced to a greater extent than the population as a whole. In 1930 and 1931 fishing operations were expanded to include most of the additional area of the bank. Thus, during these years the catch analysis index did not drop as much as did the population itself.

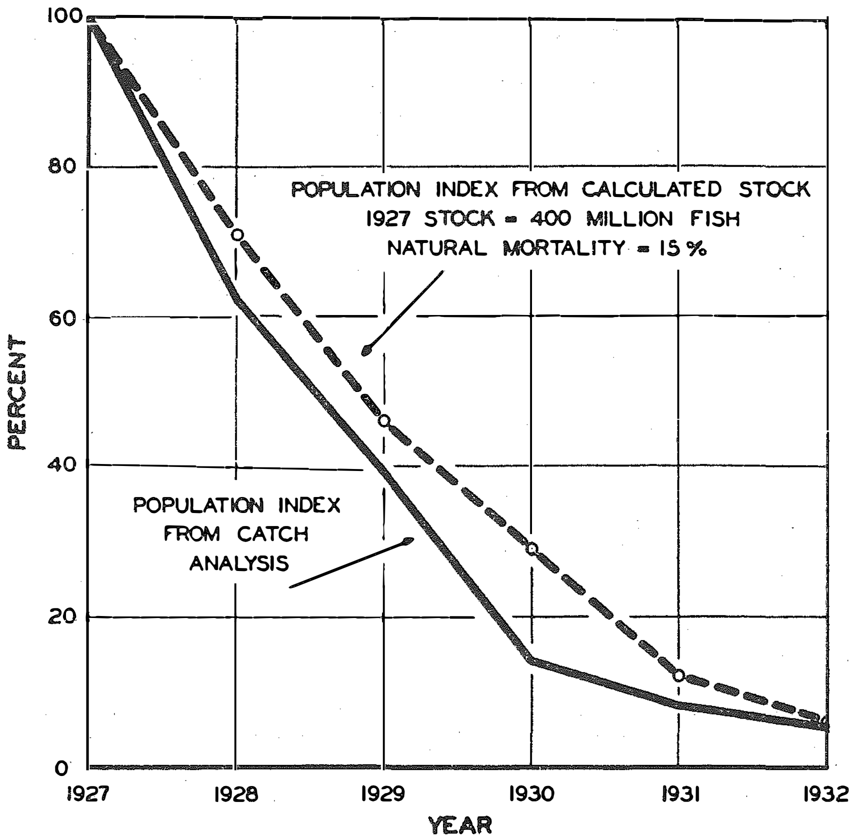

FIGURE 10. Decline in the 1927 haddock stock shown by two methods. (1) Using a calculated initial stock of 400 million fish, annual catch and natural mortality were subtracted to obtain the surviving stock in successive years. (2) The population index obtained from catch-per-unit-of-effort analysis was converted to numbers and adjusted to 1927 as a base. See Tables V and VI.

If values below 325 million are used for the original stock, a natural mortality of less than 10 per cent must be assumed to avoid negative values for the stock at the beginning of 1932. On the other hand, if values above 400 million are used, a natural mortality of more than 15 per cent must be assumed to avoid values for the 1932 stock which are much in excess of that indicated by the catch analysis data. Therefore, it seems very probable that the actual population of marketable fish at the beginning of 1927 was between 325 and 400 million fish, and

TABLE VI. DECREASE IN THE 1927 HADDOCK STOCK, AS SHOWN BY THE CATCH-PER-UNIT-OF-EFFORT ANALYSIS FOR SEASON D (NOV., DEC., JAN.) 1926–1931 AND SEASON A (FEB., MAR., APR.) 1927–1932

Season D					
Year	*Total haddock*	*Scrod haddock*	*Total haddock adjusted for recruitment*[a]		*Ratio to 1926*
	(lb.)	(lb.)	(lb.)	(No.)	(%)
1926	29,400	5,200	29,400	13,400	100.0
1927	24,600	2,600	24,600	8,500	63.4
1928	18,300	1,100	18,300	5,100	38.1
1929	8,700	500	8,200	1,910	14.3
1930	4,900	200	4,700	960	7.2
1931	6,500	3,200	3,300	600	4.5

Season A						*Average*
Year	*Total haddock*	*Scrod haddock*	*Total haddock adjusted for recruitment*[β]		*Ratio to 1927*	
	(lb.)	(lb.)	(lb.)	(No.)	(%)	(%)
1927	57,000	7,900	57,000	25,900	100.0	100.0
1928	45,300	4,500	45,300	15,600	60.2	61.8
1929	33,400	1,600	33,400	9,300	35.9	37.0
1930	16,600	900	15,700	3,650	14.1	14.2
1931	11,500	500	11,000	2,250	8.7	8.0
1932	11,900	4,000	7,900	1,440	5.6	5.0

[a] The 2,600 pounds of scrod in 1927 and 1,100 pounds in 1928 were considered to be fish from the 1926 recruitment which had not yet grown beyond scrod size. The scrod in the following years must have come from new recruitment, since the time interval was too great for carry-over from the 1926 scrod.

[β] The 4,500 pounds of scrod in 1927 and 1,600 pounds in 1928 were considered to be fish from the 1926 recruitment which had not yet grown beyond scrod size. The scrod in the following years must have come from new recruitments, since the time interval was too great for carry-over from the 1926 scrod.

that the average mortality during the following years averaged between 10 and 15 per cent.

These calculations must be considered only as preliminary explorations of the possibilities of estimating the representativeness of population indices. If the sensitivity of the methods is sufficient, they may provide a means, under some conditions at least, for measuring the bias in the index arising from such factors as changes in the efficiency of fishing methods, crews' skill, shortcomings in methods of sampling the entire population, and the effect of schooling habits of the fish.

This examination of some of the characteristics of the haddock population index indicates that the annual indices probably are relatively accurate indicators of population changes. However, when the fishery is drawing upon only part of the population, the indices will be somewhat too low.

Recruitment and Spawning Stock

Studies of age, growth and maturity have shown that the scrod catch for the haddock population found on Georges Bank and South Channel (Area XXII So.) during the spring and early summer (Feb. to April and May to July) is made up mostly of three-year-old fish, with most three-year-old fish mature. Some four-year-olds are included, particularly when the four-year-old year-class is very large, and some two-year-olds are occasionally included, notably in 1941. However, in general the spring and early summer population index for scrod represents the abundance or availabliity of three-year-old haddock.

The data on relative abundance and size give relative estimates of (1) the annual recruitment (scrod index during the spring and early summer), (2) the spawning stock (index for large plus scrod during the winter and spring), and (3) the total usable stock (index for large and scrod during any season of the year).

By plotting the recruitment index for each year against the index for the spawning stock which produced the year-class of which it was composed, the relationship between spawning stock and recruitment is obtained (Fig. 11). Data for 1912 and 1913 were not used because of their lesser reliability.

By plotting the recruitment index against the index for the population on the grounds, when that recruitment year-class was one year old, two years old, or some other age, the relationship is obtained between the number surviving to usable size and the number of adults competing with them when they were yearlings or of some other given age (Fig. 12). Analysis by this method showed that recruitment at the higher competitive stock levels was inversely related to the competitive stock size when that recruitment year-class was about one year old. The negative correlations with the stocks at other ages of the recruitment year-class were lower. This relationship, and the distri-

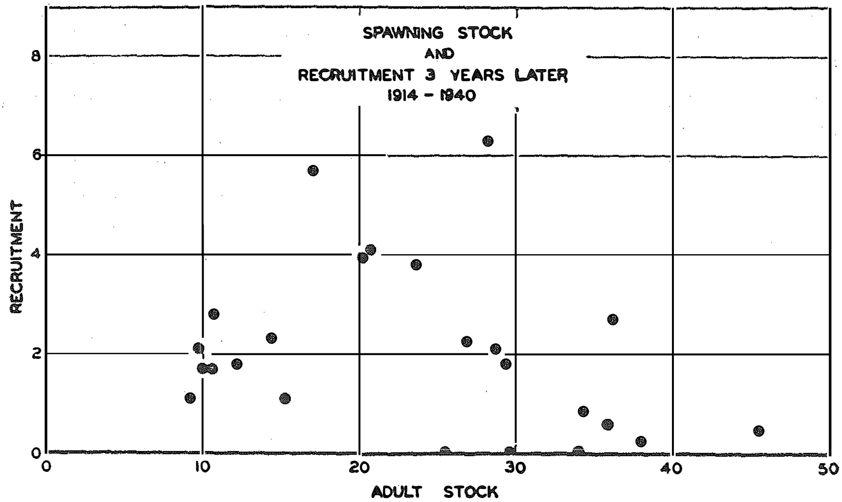

FIGURE 11. Correlation between the adult stock (spawning stock) and recruitment of young to the commercial stock three years later. Spawning stock is represented by adult population indices during the winter and following spring in terms of thousands of pounds per day's fishing. Recruitment is represented by scrod indices during spring and early summer in terms of thousands of fish-per-day.

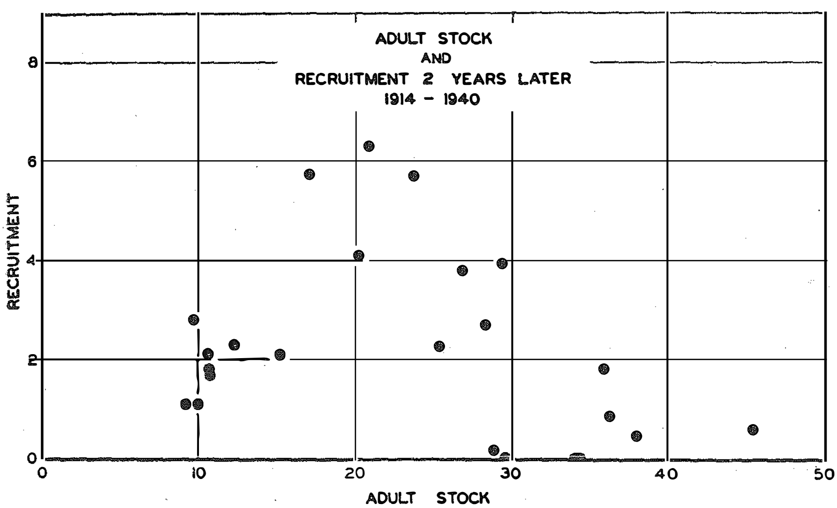

FIGURE 12. Correlation between the winter adult stock (competitive stock) and recruitment of young two years later. Winter competitive stock is represented by adult stock indices during winter and spring. Recruitment is represented by scrod indices during spring and early summer. Units are the same as in Fig. 11.

bution of the adults in relation to the nursery grounds, indicate that the most critical competition comes during the winter when the young are 8–10 months old. Probably this is the season when the production of bottom food is at a minimum.

If our preceding argument is sound, then we are justified in concluding that in the left-hand part of the correlation chart, where the average recruitment trend is rising, the effect of increasing spawning

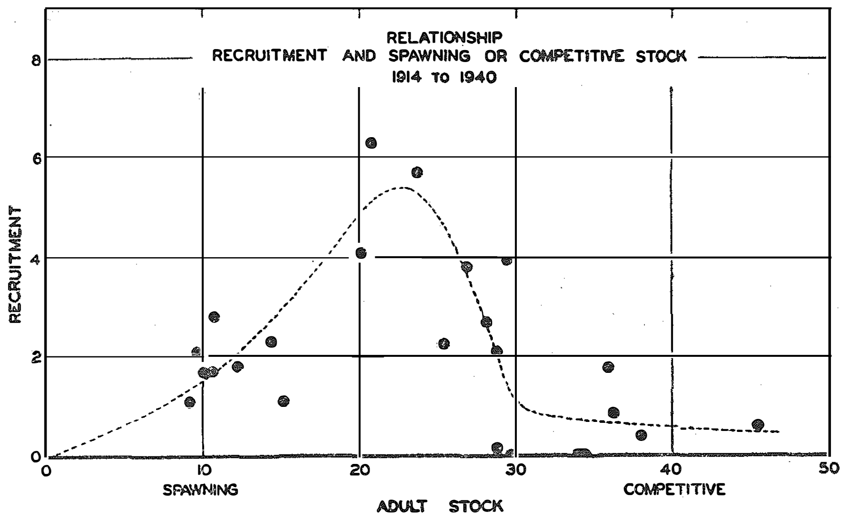

FIGURE 13. Correlation between adult stock and recruitment during 1914–1940. Recruitment was plotted against the spawning (3-year lag) when the adult stock index was less than 20 thousand pounds per day and against competitive stock (2-year lag) when the adult stock index was more than 20 thousand pounds per day. The units used are the same as in Figs. 11 and 12. The curve was fitted by eye.

stock is dominant; while in the right-hand part of the chart, where the recruitment trend is declining, the competition with the adult stock is dominant. As a first approximation we can therefore combine the left-hand section of Fig. 11 and the right-hand section of Fig. 12, and obtain Fig. 13, which expresses the correlation between recruitment magnitude and spawning stock or competitive adult stock.

Deviations from the average correlation line shown in Fig. 13 can arise from a multiplicity of causes, including errors in our data and the effect of various environmental factors, such as temperature, currents, etc., which vary from year to year.

It will be noted that the shape of the curve fitting these data (Fig. 13) closely approximates the theoretical curve shown in Fig. 4. This suggests, for species having characteristics similar to haddock, that the theoretical interpretations of mortality relationships in the first section of this paper are reasonably correct.

Correlation in Recent Years Between Recruitment and Adult Stock

The wide variations in recruitment in the early years of the fishery (1914–1930), and the consistently fair-to-good recruitment during the 1930's, are explained by the correlation with the adult stock shown in Fig. 13. This correlation led us to expect improved recruitments from the increasing adult stock in 1941, 1942, 1943 and 1944. Instead, recent work has shown that the 1941–1943, and possibly the 1944, year-classes were very poor. For a number of reasons discussed in a recent paper (Herrington, 1946), it seems possible that the amount of haddock food in the Georges Bank area might have been affected by intensive otter trawling with the heavy gear which came into use in 1929–1931. In order to examine this possibility, the adult stock and recruitment data for the years since 1931 have been plotted (Fig. 14). It will be noted that data for 1931–1940 were used in the correlation charts for both the early and more recent years (Figs. 13, 14). This will be discussed later.

The rough curve fitted by eye for the Fig. 14 data has about the same shape as the one shown in Fig. 13. The left-hand section, showing the relationship at the lower adult stock levels, is similar to the left-hand section of the Fig. 13 curve, but the mode comes at about the adult stock 13 index, instead of at 23. By referring back to Figs. 6 and 7, it will be seen that this shift in the position of the mode toward a smaller adult population is similar to that which was caused by decreased supplies of food in the theoretical case considered on page 241. Decrease in food supply, therefore, is the most probable explanation for the shift in the mode of the recruitment curve for recent years.

The use of 1931–1940 data in both correlation charts does not measurably bias the comparisons, for the adult populations in these years were below the level at which the intraspecific mortality rates were greatly increased, even under recent conditions. The calculations illustrated in Fig. 7 indicate that changes in food supply do not

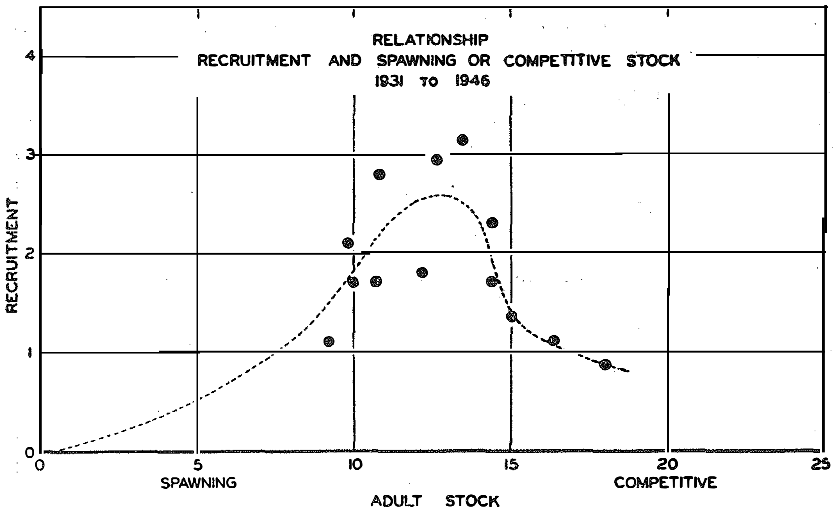

FIGURE 14. Correlation between adult stock and recruitment during 1931–1946. Recruitment was plotted against the spawning (3-year lag) when the adult stock index was less than 13 thousand pounds per day and against the competitive stock (2-year lag) when the adult stock index was more than 13 thousand pounds per day. The open circles represent adjusted values for 1941 when abnormal quantities of baby haddock (2-year fish) were marketed. These amounted to 10 per cent of total haddock in 1940D, 10.5 per cent in 1941A, and 5 per cent in 1941B. The curve was fitted by eye.

affect recruitment materially until the stock approaches the level at which most of the food supply is utilized.

On the basis of the relationships discussed on page 241 and illustrated in Fig. 7, it is also possible to draw tentative conclusions about the types of food which had declined in abundance. In the discussion it was shown that in order to considerably shift the mode of the recruitment curve toward a lower adult population level the supply of food for the older fish must decrease. Thus, the shift shown from the conditions illustrated in Fig. 13 to recent conditions illustrated in Fig. 14 indicates that food for the older haddock (probably 1 + year-classes) had decreased by perhaps 40 to 50 per cent. However, this shift provides no information concerning changes in food for the juveniles.

OTHER EVIDENCE BEARING UPON THESE INTERPRETATIONS

Several projects are under way to check the validity of the foregoing interpretation of the haddock data. These include work on distribution of adults and juveniles on the fishing grounds, growth, and studies of the total production of all species by years and subareas.

Geographical Distribution of Adults and Young. The low recruitment at high adult population levels has been interpreted as resulting from high mortality of the young when the adults overrun the nursery grounds and compete with them for food. This is based on the tentative conclusion that the adults prefer areas separate from the nursery grounds, but that at high population levels they are forced to spread

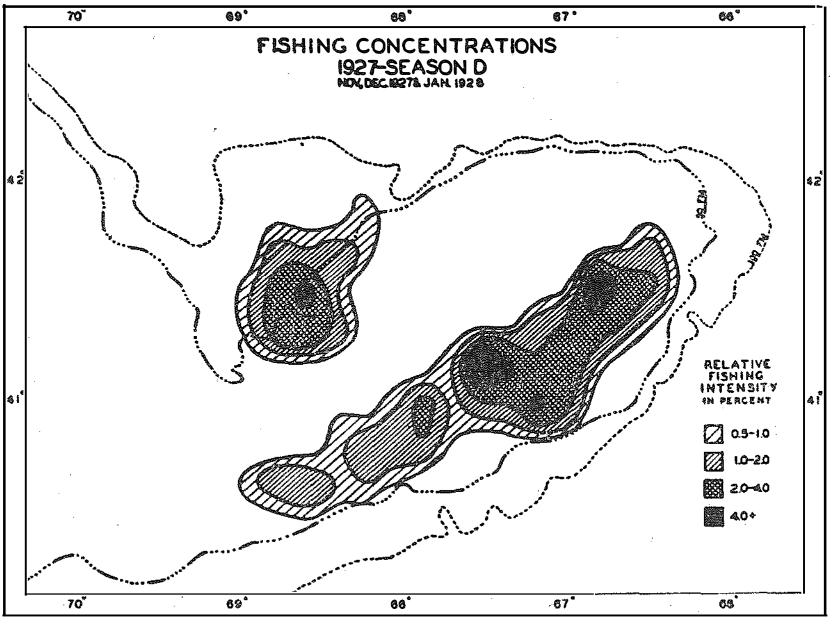

Figure 15. Fishing concentrations on Georges Bank and South Channel in the winter of 1927–1928 (Nov.–Jan.). Obtained from fishing locations of the Portland Trawling Company fleet.

out in the search for food. Such spreading is greatest during the winter months.

Failure of recruitment from the 1941–1943 year-classes has been interpreted to be the result of competition with the adults. If this is true, then the distribution of adults in the winters of 1942–1944 should be comparable to the distributions in 1926–1928 and should be more extended toward the nursery grounds than distributions during 1931–1940.

The actual distribution of adult haddock in the three periods indi-

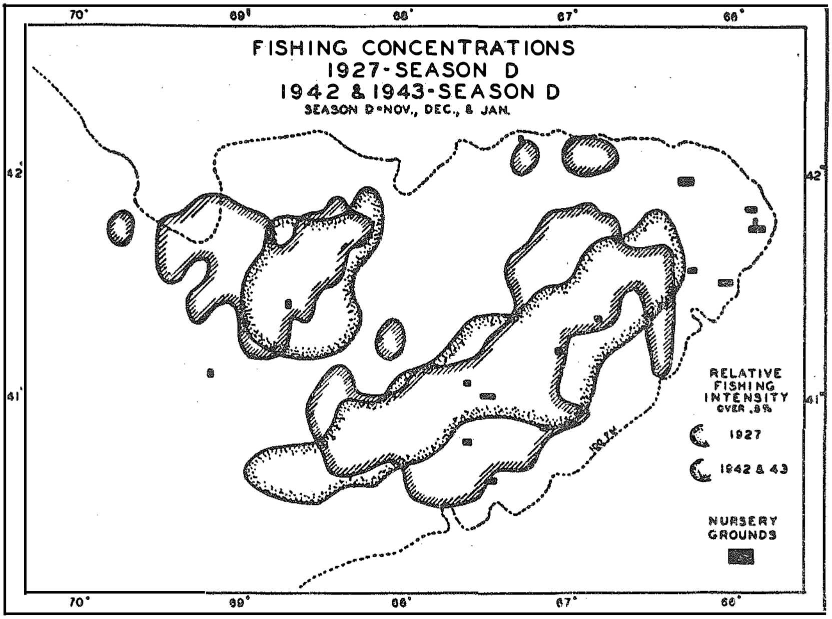

FIGURE 16. Fishing concentrations on Georges Bank and South Channel in the winters of 1927–1928 and 1942–1944, in relation to the nursery grounds. Concentrations include all areas in which fishing intensity was 0.5 per cent per-unit-area or over. Black rectangles show locations where one-year-old haddock were taken during young-fish surveys, using special small-meshed trawls. Length of rectangles represents relative number of young haddock taken per hour's trawling.

cated has been examined through an analysis of the distribution of the fishing fleet during those years. It has been demonstrated time and again that in an intensively fished area no large concentration of a sought-after species long escapes the attention of the fishermen. Consequently, the distribution of the fishing fleet is a reasonably good indicator of the distribution of the principal bodies of fish, insofar as fishable bottom is concerned.

Records of the Portland Trawling Company, covering daily radio reports from their large fleet of trawlers which operated in 1927–1931, provide data for the early period. These reports included the daily positions of the trawlers and the amounts of fish caught. The number of days the fleet fished in each unit area (10-minute rectangles) was plotted, and the numbers were converted to percentages of the total amount of fishing during that month or season. Contour lines then

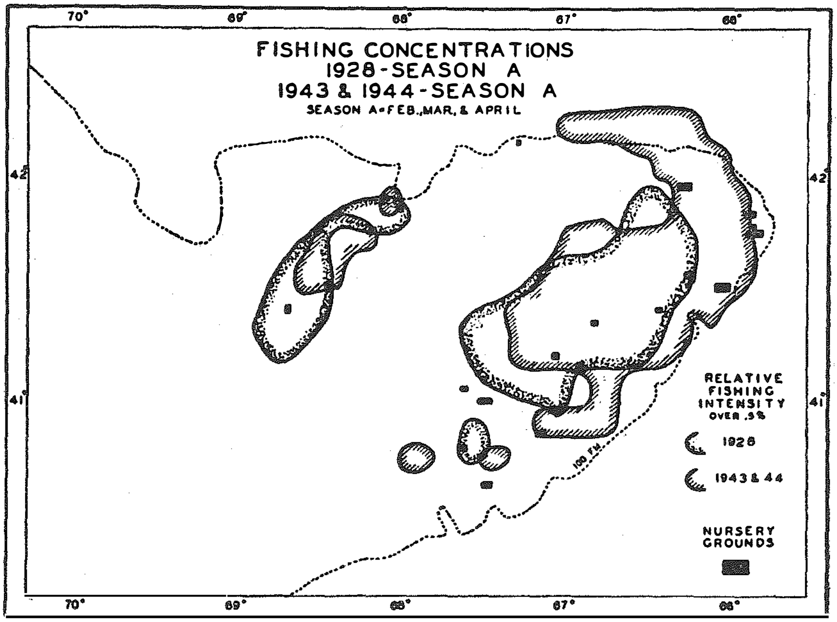

FIGURE 17. Fishing concentrations on Georges Bank and South Channel in the springs of 1928 and 1943–1944, in relation to the nursery grounds. The northeastern edge of the bank was not fished in 1928 because of the rough bottom. In 1930 and 1931 gear was developed which could fish such areas.

were drawn through points of equal fishing intensity. These contours are shown in Fig. 15 for Season D (Nov.–Jan.) 1927–1928.

In 1931–1946 similar information on fishing concentrations is available from data on fishing locations and time fished, these data being obtained from interviews of captains or mates of all boats fishing out of Boston. These have been analyzed in a similar manner for November, December and January, 1936–1937, 1939–1940 and 1942–1944, and for February, March and April, 1937, 1940 and 1943–1944.

The distribution of fishing, as indicated by the area within the 0.5 per cent fishing intensity contour, is shown in Figs. 16 and 17 for the winter and spring seasons (Nov.–Jan. and Feb.–March) of 1927–1928 and for the average of the winter and spring seasons of 1942–1943 and 1943–1944. The average distributions for the winter and spring seasons of 1935–1936 and 1939–1940 are shown in Figs. 17 and 18. It will be seen that the distributions in 1927–1928 and 1942–1944 are

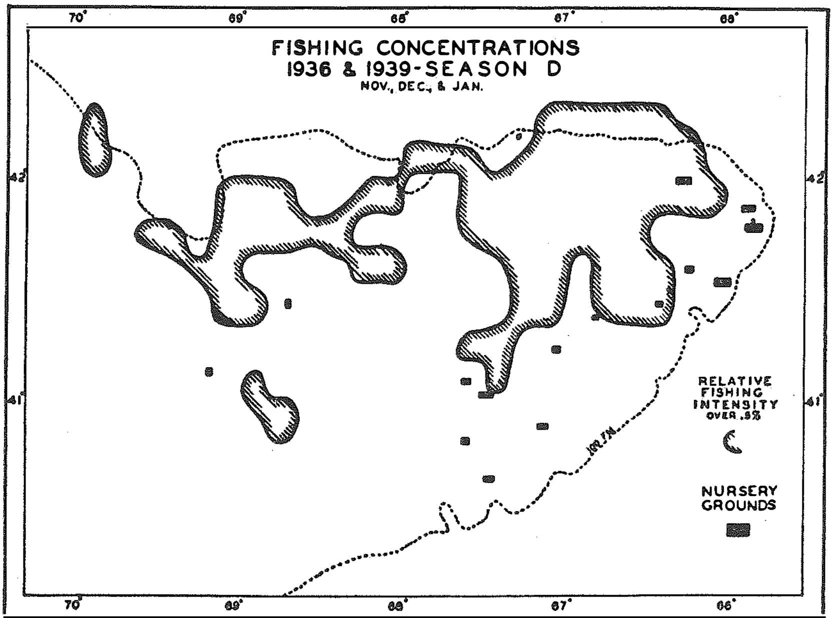

FIGURE 18. Fishing concentrations on Georges Bank and South Channel in the winters of 1936–1937 and 1939–1940, in relation to the nursery grounds.

similar, except that the 1927–1928 distributions do not cover as much of the northeastern section of the bank. In those years the northeastern section could not be fished with the kind of gear then in use because of the roughness of the bottom. Judging from the quantities of haddock found in this area in later years when more rugged gear was used, it is reasonable to assume that haddock were concentrated in this area during 1927–1928, as well as in the area fished by the fleet. Thus, the distributions of adult haddock during the winters and springs of recent years (1942–1944), which produced poor recruitments, was very similar to the distributions in 1927–1928, which also produced poor recruitments. In contrast to this, the distributions of haddock in the winters of 1935–1936 and 1939–1940 were more northerly and did not extend as far toward the eastern edge of the bank.

The locations and relative quantities of one-year-old haddock taken in the course of survey trips on the "Atlantis" in the springs of 1935 and 1936 also are shown in Figs. 16 to 19. Special small-meshed

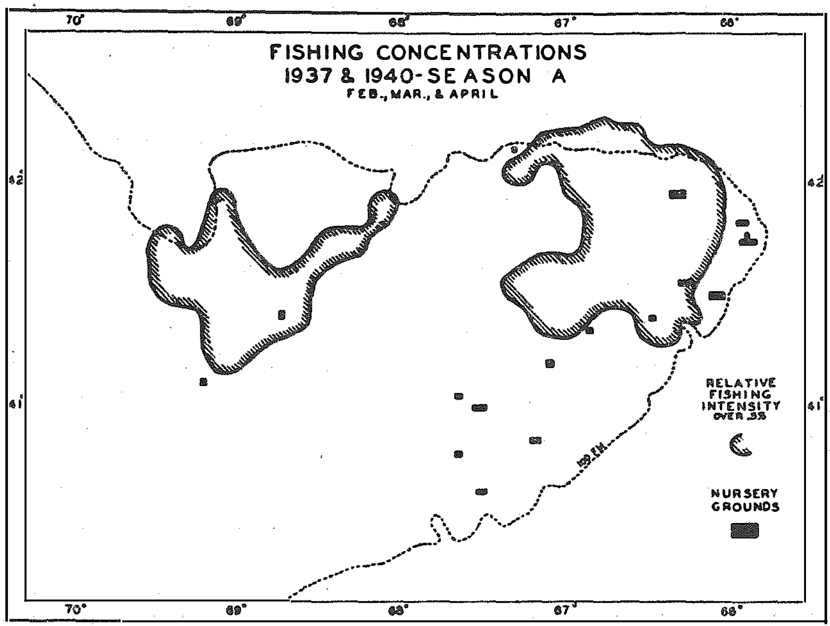

FIGURE 19. Fishing concentration on Georges Bank and South Channel in the springs of 1937 and 1940, in relation to the nursery grounds.

trawls were used, and tows were made at a grid work of stations covering Georges Bank, South Channel and Nantucket Shoals. Incidental sampling at other seasons and records from the fishing fleet indicate that small haddock are concentrated principally in these general areas until their second and third years, when they move farther in on the bank and probably increase the range of their movements.

Figs. 16 to 19 show that a much larger proportion of the nursery grounds was overrun by the adults in years which produced low recruitments (1927–1928 and 1942–1944) than in years which produced fair to good recruitments (1935–1936 and 1939–1940). This is in agreement with the predicted distributions, and helps to confirm the conclusion that reduced recruitments from 1941–1943 year-classes were caused by intraspecific competition for food.

Growth. The spreading of the adult haddock over the nursery grounds in years when the population level was high has been explained on the basis of population pressure resulting from intraspecific competition for food. If this is so, then the competition for food in 1942–1944 must have been comparable to that in 1926–1928 and much more intense than in 1931–1940.

The intensity of intraspecific competition for food should be more or less inversely proportional to the amount of food per fish. Therefore, the amount of food per fish should be relatively less during years when the adults spread over the nursery grounds (1926–1928 and 1942–1944) than during years when they do not spread so extensively (1931–1940). Growth studies of haddock collected in 1930–1935 have shown that, following the drastic reduction in the population level from 1927–1931, the growth rate increased considerably. Presumably this was caused by a greater amount of food per fish when the population was reduced. Therefore, it seems safe to assume that changes in the amount of growth reflect to some extent the relative amount of food per fish.

From these relationships it can be reasoned that the growth of haddock during 1931–1940 should have been considerably greater than growth during 1926–1928 and 1942–1944.

Work on the age composition and growth of the haddock stocks, being carried on by Howard Schuck of the North Atlantic staff, has been extended to include the study of growth during the several years mentioned above. A complete discussion of the work will be covered in a later report, but preliminary results now are available. These show that growth of group I haddock (second season's growth) in 1942, 1943 and 1944 (years when recruitment was very poor) averaged 13.3 cm. Average growth of group I haddock in the years 1931–1940 (years when recruitment averaged "good") was 14.5 cm. Average growth of group I haddock in 1926–1928 (years when recruitment was very poor) was 11.6 cm. The last average may be somewhat too low, for it was based upon two-year-old fish collected by the radio operator of a commercial trawler. The samples were obtained from culled haddock and there may have been some bias toward small fish.

Differences similar to those for group I fish were found in the growth of group II fish, while the differences for group 0 fish were not significant.

These results are in line with our previous reasoning. Decreased growth of group I and group II haddock, indicating a shortage of food for these sizes, was found for those years when our interpretation indicated that recruitment was reduced by food competition between adults and juveniles. The lack of considerable differences in the growth of group 0 haddock may indicate that food for the juveniles was not a limiting factor in any of these years. This is in line with the theoretical conclusion that shift in the recruitment mode toward a lower population level results from reduction in food for the older fish rather than in food for the juveniles.

Shortage of Haddock Food in Recent Years

Considerable evidence has been presented in the preceding sections of this report which strongly indicates that the poor recruitment from the 1941–1943 year-classes resulted from a reduction in the supply of food available to adult haddock. The cause of this shortage has not been discussed.

Possibly the first explanation which will occur to the student of animal populations, to account for the indicated decrease in haddock food, is interspecific competition for food. It will be recalled that mortality from this cause was not considered in the theoretical discussion in the first section of this paper (p. 232). Competition of this type causes a reduction in the food supply, and therefore it will affect the haddock population in the same way as would a reduction in food from any other cause.

Following this line of reasoning, the indicated decrease in the haddock food supply might be explained as follows. The decrease in the haddock stocks from 1927–1931 released large quantities of food. The numbers of other species which could use this food would therefore increase. The amount of food available to haddock in later years would be decreased by the competition from these expanded populations, which in turn would prevent rapid recovery of the haddock population to its previous level. If this explanation is valid, then competing species must have increased more or less in proportion to the decrease in haddock.

Nearly all of the bottom fish taken on Georges Bank are captured by otter trawls. This type of gear is nonselective in regard to most species and sizes of fish, for it sweeps over the bottom taking all objects in its path which are not too small to sift through the mesh, not too active to be caught, or not too solidly secured to the bottom to be torn loose. Therefore, the otter-trawl catch provides a reasonably good index of the kinds and relative quantities of fish on the bottom. The catches of commercial species other than haddock have been analyzed to obtain the catch-per-unit-of-effort, using the same methods applied to haddock data. These records show that the landings of these species averaged about 5,000 pounds per day for 1926–1928, compared to about 7,900 pounds per day for 1941–1943 (Table VII). This increase is not great and may reflect the increased marketability of these species more than an increase in their populations.

TABLE VII. CATCH PER DAY OF HADDOCK AND OF ALL OTHER MARKETED SPECIES FOR CERTAIN YEARS, AREA XXII SOUTH

Year	*Total haddock*[a]	*Miscellaneous fish*	*Total fish*[β]	*Ratio: total haddock to total fish*[γ]
	(lb.)	(lb.)	(lb.)	(%)
1926	41,290	4,400	45,690	——
1927	43,780	5,140	48,920	——
1928	34,460	5,620	40,080	——
Total	119,530	15,160	134,690	——
Average	39,843	5,053	44,897	——
1929	22,370	6,170	28,540	——
1930	11,520	6,340	17,860	——
1931	9,120	4,540	13,660	——
Total	43,010	17,050	60,060	——
Average	14,340	5,680	20,020	——
1941	15,460	8,100	23,600	65.6
1942	16,500	7,700	24,200	68.3
1943	16,250	7,800	24,000	67.6
Total	48,210	23,600	71,800	——
Average	16,070	7,900	23,970	——
Change 1926–28 to 1941–43	−23,773	+2,847	−20,927	——

[a] From haddock population index.

[β] Data for 1926–1931 from population index calculated for haddock and other species. Data for 1941–1942 calculated from haddock index and ratio of haddock to total marketed fish.

[γ] Percentages obtained from landings by all large otter trawlers.

In addition to the fish caught and marketed, the otter trawls catch many species and sizes which are not saved for market. These are termed "trash." No continuous records of the quantities of trash fish caught are available, but in the course of numerous field trips on otter trawlers in 1931 and 1932 members of the North Atlantic research staff obtained records of the quantities of trash fish caught on many trips to Georges Bank. More recent data on trash fish (Herrington, Rounsefell and Perlmutter, 1942) are available from records made by members of the crew of a large trawler for six months of 1940 and 1941 (Table VIII). The differences between the quantities reported in

TABLE VIII. CHANGES IN THE RELATIVE ABUNDANCE OF "TRASH FISH" FOR CERTAIN YEARS[a]

Year	*Total haddock* (lb.)	*Ratio trash to haddock* (%)	*Trash fish* (lb.)
1931	9,120	35	3,200
1932	11,570	35	4,000
Average	——	——	3,600
1940	12,590	58	7,300
1941	15,460	58	9,000
Average	——	——	8,150
Change 1931–32 to 1940–41	——	——	+4,550

[a] Data from Herrington, Rounsefell and Perlmutter (1942).

1931–1932 and 1940–1941 correspond to an increase in the average catch-per-day of about 4,500 pounds.

These two sets of records provide a poor basis for estimating the changes in abundance of "trash" species during the years when food for adult haddock became less available. However, if we accept them as the most probable figures and add to them the increases indicated for miscellaneous market fish, an increase of 7,400 pounds per day is obtained. Since the decrease in the average haddock catch-per-day between 1926–1928 and 1941–1943 was 23,770 pounds, the increase in miscellaneous market species and trash would compensate for only about one-third of it, even though we assumed that all of these species were direct competitors for food with haddock. It does not appear, therefore, that interspecific competition for food can account for the indicated reduction in the amount of food available for adult haddock.

Total Catch of All Groundfish

The final measure of the productivity of an area is the total amount of fish which can be removed annually over a long period of years. Data of this kind are not available from the published records except for recent years. Data for earlier years are being assembled from Fish and Wildlife Service records and from records of trawler operators. These compilations have been completed for the years of greatest landings, 1928–1930, and compared to the three recent years with the highest production, 1940–1942.

During the last ten years fisheries have developed for two important species which are caught in the Georges Bank area. Rosefish have been taken in large quantities in South Channel. Yellowtail flounders are taken chiefly in the area around Nantucket Lightship and south of Massachusetts. Both species are found mostly in areas (or on bottom) not much frequented by haddock. Production from these areas has been included in the Georges Bank production figures.

The average production of haddock in 1928–1930 was almost 100 per cent greater than the 1940–1942 average. The production of all groundfish in 1928–1930 was about 30 per cent greater than in 1940–1942, in spite of the addition of rosefish and yellowtail flounders to the catch in recent years.

Pelagic fish such as mackerel and swordfish have not been included in these figures, for they are present in the area for only brief periods and most of their growth must be acquired elsewhere. Therefore, they should not be an important factor in the Georges Bank balance of fish and fish food.

These data indicate that the total productivity of the Georges Bank area has been considerably less in recent years than in the past. The decline in production of haddock has not been compensated for by increased production of other species.

POPULATION CYCLES

The information now available on growth, mortality rates, distribution and fishing intensity largely accounts for the cyclic or semicyclic changes in the Georges Bank haddock population during the years covered by the population index (Fig. 8). As indicated by this analysis, the population changes and their causes were as follows. The cyclic changes between 1912 and 1931 resulted from the varying competition, related to population size, between adult and juvenile haddock, and from the two- and three-year lag between changes in competition and recruitment to the adult stock. The accelerated and extreme decline from 1927–1931 was caused by coincidence of depressed recruitment and greatly-increased fishing intensity. The protracted partial depression in recruitment from 1930–1940 resulted chiefly from a suboptimal spawning stock which gradually recovered from the extreme low point reached in 1931. Severe depression of recruitment in 1944–1946 resulted from increased competition between the adults and juveniles similar to that in 1918–1922 and in 1926–1928, but at a lower population level, probably because of decreased food supplies.

Under virgin conditions with no fishery, it is probable that the population changes would be similar to those in 1912–1927, but with the cycle stretched out another year or two. During these years the mortality from fishing was relatively minor, for the catch and fishing intensity were much less than in recent years (Herrington, 1944). The greatly increased fishing intensity since 1927 reduced the competitive stock and eliminated the downward phase of the cycle until 1942. Then a moderate increase in the adult population resulting from decreased wartime fishing, and a presumable decrease in haddock food, again set in operation biological interactions of the type which caused the declines in 1921–1924 and 1927–1931.

If cyclical forces outside of the haddock population itself have been factors in the situation, it appears that they have not had a major influence in determining the range of variation in the population or its average level in recent years. Characteristics of the haddock's life history and of the commercial fishery have been the controlling factors in determining changes in population level, with the supply of food available to haddock setting the over-all ceiling.

It is possible that there may be some basic cycle which affects the supply of haddock food. The negligible recruitment of young haddock to the adult stock in certain years, as shown by the scrod index in Fig. 8, has been explained as resulting from unusually intense competition for food two years earlier. This indicates that such competition occurred in 1910–1912, 1918–1921, 1926–1928, and 1942–1945. There also is the suggestion of a slight depression in the rising recruitment trend in 1937–1940, which might be the result of increased competition in 1935–1938.

Let us assume a seven- to nine-year cycle in the food supply for haddock above juvenile sizes. Then the low years in the food cycle would about coincide with the peak years for usable population because of the lag between spawning and recruitment and that between intra-year-class competition and recruitment. Thus, the minima in the food cycle would have occurred around 1910–1912, 1918–1921, 1926–1929, 1935–1938, and 1942–1945. The approximate coincidence of peak periods of adult haddock abundance with food supply minima would cause an even more intense competition for food during these years than would occur with a more uniform food supply. Under this interpretation, the decrease in food during 1935–1938 did not cause intensive competition and a resulting high mortality of young, since the population had not recovered to the level at which food supply was the limiting factor. The decrease in recruitment in 1944–1946, indicating intense competition for food in 1942–1944, would require a decline in food during those years, whether cyclic or not, to a level considerably below the 1910–1912, 1918–1921 and 1926–1929 minima.

The principal effect of a food cycle would be to determine the length of the haddock population cycle during years when the adult stock increased beyond the optimum level in relation to food supply. The changes in the adult population level still would be caused by intraspecific competition of the types discussed, and the lowered level for optimum adult stock in 1942–1945 would require a much lower food level than that prevailing in 1918–1921 and 1926–1929. Thus, it does not appear that the conclusions concerning the factors affecting recruitment would be changed materially by the presence of food cycles. However, the latter would provide a possible explanation for the reported scarcity of haddock on the Nova Scotian banks in 1930–1932 and in 1945–1946 and for the regular spacing of haddock recruitment minima.

RECRUITMENT-USABLE STOCK CORRELATIONS FOR OTHER SPECIES

In an early section of this paper (p. 232) it was mentioned that the theories developed in respect to the factors determining recruitment magnitude applied particularly for species with life histories similar to Georges Bank haddock. Some data are available which suggest that these theories may be more generally applicable.

Production figures for North Sea haddock before, during and after World War I suggest a relationship between the magnitude of the usable stock and recruitment which is similar to that found for Georges Bank.

The interpretation of the North Sea data would be as follows. The accumulation of older fish during the war caused increased intraspecific competition which reduced the survival of young. Consequently, the postwar catches, after a temporary increase, dropped below the prewar level as soon as the accumulated stock had been caught up and the reduced survival of young had caused a decline in recruitment. The succeeding increases and decreases in the annual landings might also have some relationship to spawning stock and competitive stock.

Indices for catch-per-boat-week for California sardines covering 1932–1942 (Silliman and Clark, 1945) (Table VII) show some interesting relationships not dissimilar in some respects to those obtained for the population index for haddock. For a fish population as intensively exploited as the California sardine, it seems reasonable to assume that the annual average catch-per-boat-week is influenced considerably by recruitment. A relatively low catch indicates that recruitment was poor, while a relatively high catch indicates that recruitment was good. Since the sardine reaches commercial size in about three years, it is possible, by plotting the catch-per-boat-week for one year against the catch three years following, to obtain an approximate correlation between the relative stock and recruitment. When this is done with the sardine data for 1932–1942 a correlation curve is obtained with a shape somewhat similar to that for haddock.

Recruitment during these years should show a considerably greater variation than catch-per-boat-week, which is influenced by the survivors from the previous year. In the years with the lowest catch-per-boat-week, recruitment probably would be very small. If this is the case, use of relative recruitment instead of catch-per-boat-week would yield a correlation curve even more closely resembling that obtained for haddock.

It may be that the similarity between the correlation curves for the two species is purely coincidental or the catch-per-boat-week indices may not provide even approximate measures of the relative stock and recruitment. However, the results suggest that a more detailed analysis of this kind might be fruitful.

Data for a number of other species and fisheries have been noted which appear to have a somewhat similar relationship between usable stock and recruitment. The great increase in the Maine lobster catch between 1939 and 1945 so far has been explainable only on the basis of changes in the spawning stock and competitive stock during previous years. The results of this study of the lobster fishery will be reported in the near future.

In the above discussion, similarities have been indicated in the relationship between usable stock and recruitment for a number of species of fish. If further work shows that these similarities are real, it may indicate that the types of inter- and intraspecific mortalities discussed in the first part of this paper are rather generally applicable. If this proves to be the case, then the type of analysis discussed in this paper will provide a useful method for exploring some of the population conditions required for maximum recruitment.

APPLICATION OF THE CONCLUSIONS TO THE HADDOCK FISHERY

The results of this study of the Georges Bank haddock population make it possible to formulate limited predictions for the future and to suggest what action should be taken to obtain maximum production. These predictions are based on data up to October 1946.

Because of favorable spawning stock and competitive stock conditions in 1945 and 1946, the 1945 year-class should be considerably more numerous than those of 1941–1944. As a result, there should be a material increase in the abundance of baby haddock (1–1½-lb. fish) during the summer of 1947. The trawling fleet, stimulated by the scarcity of large haddock, probably will concentrate on these small haddock unless protective measures are adopted. If such a concentration occurs, the 1945 class will be decimated greatly before the members reach spawning size, and there will be no chance for the spawning stock to recover from the low point reached in 1946 and 1947. If this is continued during the following years it can be expected that the catches on Georges Bank will continue at a low level.

These conclusions indicate the great desirability of adopting minimum mesh and market sizes, so that the young haddock will be protected until they reach about two pounds in weight. This will allow them to spawn at least once and will provide a greater poundage because of their larger size. It will increase the spawning stock considerably and result in improved recruitment in later years.

The results of the work further indicate that, if the above measures are adopted, care should be exercised to prevent the adult stock from increasing to the level where competition with the young becomes an important cause of mortality. By increasing the accuracy of the abundance index from a more extensive study of growth rates from scales and collections of small haddock, and by improved knowledge of population size and distribution from "Albatross III" surveys, it should become possible to determine when the adult stock approaches the level at which intensified competition with the young begins. At that point restrictions on mesh size and fish size should be relaxed and the taking of scrod haddock encouraged to prevent the accumulation of an excessive competitive stock and the consequent heavy mortality of the juveniles.

If there is a cycle in the supply of haddock food, which present data do not confirm or deny, the benefits to be gained by varying protection of the young to suit conditions are even greater. By encouraging the building up of the spawning stock when food is increasing, and by reducing the competitive stock when food supplies are decreasing, it should be possible to obtain much fuller use of the supply of haddock food and thereby arrive at a greater and more regular production of fish than otherwise would be possible.

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DISCUSSION

Van Oosten: Mr. Herrington's paper is now open for discussion.

Fry: I should like to ask Mr. Herrington if he is familiar with the population figures for the lake trout in Algonquin Park.

Herrington: I am not.

Fry: They show the same characteristic quite markedly.

Herrington: A number of population curves seem to show it.

Fry: We actually use a master curve as an index to compare our fisheries at the present time.

Herrington: Does it work?

Fry: Yes, it seems to fit at the moment.

Burkenroad: I should like to say that Mr. Herrington's suggestion of change in relationship between spawning stock and recruitment at different levels of spawning stock seems theoretically a reasonable one. However, Mr. Herrington hasn't included in his previous papers on this relationship a consideration of the effect on the haddock stock of changes in the crops of its predators and its prey. It appears to me that what he has done today is to assume his original hypothesis as if it had been proven, and then to reconcile it with the more recent contradictory evidence by assuming changes in the food crops. In other words, he didn't get the expected increase in young when his spawning stock went up to what was thought to be the optimum level, and his explanation is that the amount of food produced by the ground has fallen off. But if there has been a great change in the crop of food, one would tend to attribute that to a natural change, and one might suspect that such changes may have had more effect than the changes in the amount of fishing, during the whole course of the fishery as well as during the last few years.

Herrington: Again, I am trying to provide what is the most reasonable interpretation of the data. The evidence indicates that the food was the limiting factor in

1942 to 1945, but not in the previous years since 1926–1929. The apparent reduction in the food ceiling between 1926–1929 and 1942–1945, as you say, indicates a change in food. But that change in food, judging by the data I have presented, did not limit recruitment between 1929 and 1942. At least it was not the dominant factor. Another problem is: "What caused the change in food?" I didn't touch on that. I don't think your comments bear on my argument.

Burkenroad: But the assumed change in food is obviously the important one here and not the change in fishing. Could it not be change in basic production of food which is controlling the changes in abundance of haddock at any time rather than change in stock of haddock caused by fishing?

Herrington: From the relationship obtained it appeared that, during these periods (1926–1929 and 1942–1945), food was the limiting factor. It seemed valid to me also to conclude from this relationship that during the years at this level [indicating on chart] the stock was below the optimum and recruitment was limited by spawning stock. Therefore, you might say that during these years there was underfishing and during these [indicating] overfishing.

Burkenroad: That is a perfectly reasonable explanation but there is no evidence to support it. There is nothing to exclude the hypothesis that some other factor than overfishing was limiting during 1929–1942 also; for example, size of the crop of food, such as is invoked for other years. Your evidence for a causal relationship between brood-stock and brood is therefore no longer conclusive, because the correlation has failed to hold up, and there is no independent evidence concerning change in crop of food.

Herrington: Can you provide evidence? If I provide evidence for my theory and you provide none for yours, mine seems more reasonable.

Burkenroad: I don't see that you have provided evidence for yours. If you had gotten an increase in the brood when your spawning population recently went up toward the presumed optimum, then you would have taken it as evidence for your hypothesis. But when the population doesn't rise as expected and you explain that by assuming that the food-crop is no longer as large as it used to be, the justification for your hypothesis of the relation of brood-stock to brood becomes circular. You now have only one reasonable explanation out of numerous other equally reasonable ones.

Herrington: You are unwilling to concede anything, as far as I can see. I say I presented evidence that food during these years was limited and during the other years was not. From that I reasoned that the growth rate should be affected in a certain way. We went out and studied growth rate and found that growth rate was affected in the manner we predicted from our interpretation of these relationships. We also have gone further into trying to figure out what happened to the food supply. However, that really isn't part of the argument to this point. We have three lines of evidence. We have this interpretation; we have the evidence from growth; and, we have the evidence from fish distribution. They are independent lines of evidence, and they all fit into this particular theory. Until you can provide more lines of evidence for another interpretation, it seems my interpretation must stand.

Burkenroad: It seems to me all I have to do is refer to your '44 paper for comparison with this. You were satisfied in '44 with your interpretation on the basis of a constant food-production level. Now you are not.

Herrington: I think this fits in directly with the interpretation of '44. At the high population levels food was the limiting factor. I provided additional evidence that the food for haddock has changed. Therefore, it seems to me I am justified in saying this is the most probable interpretation.

Burkenroad: Isn't the change in food the important thing here (indicating on chart)?

Herrington: The change in food is the important thing at the population levels in 1942–1945, but not in 1930–1941. It seems to me that, in the last two days, there has been a consistent refusal on the part of some participants to admit that spawning stock has any bearing on the recruitment of fish. It doesn't seem to me that such a position will stand up. We know that at some levels it must be a limiting factor. The question is where that level is.

Huntsman: There doesn't seem to have been brought into the discussion a condition which is sometimes referred to as "overpopulation." Dr. Miller of Alberta told me of an instance in which increase in the intensity of a fishery for whitefish in a lake gave larger fish.

Needler: I think that is true in McFadden Lake, N. B., too. As the number of fish went up the size went down. There was an indication that the larger fish got thinner. They couldn't feed in competition with the smaller fish.

Fry: You have that in lake trout populations too, though it is greatly complicated by the fact that you don't get the growth rate in proportion to the density in all cases. There are many other complications. As far as we can see in regard to these lake trout, the two major food fishes are whitefish and perch. In small lakes there aren't the whitefish although there are the perch, but the trout can't seem to get them for various reasons. You don't necessarily have any improvement in the growth rate by pulling the population down.

Martin: I might say that in Nova Scotia, where there is not much otter-trawling, the catch of haddock has gone down in a comparable fashion to that on Georges Bank. Perhaps an alternative explanation is that dragging the bottom is not as important as interspecific competition. The catch of cod has doubled from 1943 to 1946.

Herrington: I am quite ready to concede that there are a lot of other possible explanations. However, on Georges Bank we have eliminated cod, since we have available index records of that species. Perhaps there has been a cycle in the productivity of the bottom food. There may be a lot of other explanations. But, so far this is the only thing which seems to tie in with the available data.

Tester: Mr. Chairman, I don't think I completely follow the presentation in several places. In this very first graph, Mr. Herrington, you show that under certain conditions doubling the number of spawners will double the number of recruits.

Herrington: No. Doubling the number of spawners, roughly speaking, will double the number of *eggs*. I think there is general agreement on that.

Tester: In your subsequent considerations you have dealt with mortality as extending over a considerable period of time and being influenced by two things: interspecific competition and intraspecific competition. I can't see how intraspecific competition would actually enter into a consideration of mortality. By that, you mean actual competition for food?

Herrington: Right.

Tester: Do you believe then that competition for food will cause mortality as well as reduce the growth rate?

Herrington: The first effect is on growth rate, but if you keep on expanding the population you reach a point where apparently the population must be limited, perhaps by starvation, perhaps by other factors to which semistarvation makes them susceptible.

Tester: I am thinking of exceptions to this type of mortality. In the case of some of the marine species there has been some evidence that when the eggs are deposited on the bottom in layers, only the top eggs will survive—that would be one of the exceptions.

Herrington: That would follow this type of curve at the lower levels. That would be intraspecific competition, but not for food. As you increase the quantity, the mortality increases because you are limited by space.

Tester: It is a different type of mortality in that it occurs at one particular time.

Herrington: That is right, and it would be one of the other factors that would affect a particular species.

Tester: In a case like that you wouldn't necessarily expect your theoretical survival curve, as derived, to apply.

Herrington: If that type of mortality fits this form of curve, then it would. If you have a saturation level from the point of view of space, then you get a curve of this type. Therefore, it wouldn't alter the shape of the survival curve I have derived.

Tester: I don't know. I probably haven't followed you very closely, but it seems to me from what evidence I have come across that it doesn't conform to this type of curve and that you can have cases similar to those which Dr. Fry mentioned. He referred to fluctuations due to meteorological causes. Perhaps . . .

Herrington: Wait a minute. If you recall the correlation curve I showed you, you will remember that there were fluctuations from the average curve, major fluctuations, doubling and tripling of values, causing variations of hundreds of per cent. What I have said is that the average of these values over a period of time will be determined by the level of the spawning and competitive stocks. There is room within this theory for almost unlimited fluctuations from year to year. I am only saying the average is governed by spawning and competitive stock. As I said before, I am leaving plenty of latitude for other factors.

Hart: I don't know how seriously Mr. Herrington is presenting his information on pilchards. I don't feel satisfied that the relationship between availability and abundance of spawners is close enough to warrant the assumption which I think he made.

Herrington: I made no assumptions. I said, when you treat the data like this, this is what you get. Therefore, it might indicate that the treatment I have described would be applicable.

Hart: I have no objection to that.

* * * *

Van Oosten: I see here under "Discussion" the two subjects "Nomenclature" and "Assessment." Do we want to continue the discussion on these?

Herrington: Since this group started off with a discussion of terms, that would seem to be a proper subject.

Dymond: That will take another Symposium, won't it?

Merriman: Probably two.

Van Oosten: Do we want a discussion on the subjects mentioned here—on one or both?

Dymond: I doubt if we could get any satisfaction out of it in the time at our disposal.

Ricker: I am in favor of postponing it until later.

Van Oosten: Before we adjourn, Dr. Huntsman, I would thank you very much for calling this Symposium. I think it is one of the finest I have ever attended on fishery subjects. I am sure that everyone of us now knows a lot more than we did two days ago. This conference probably changed some of our views on various aspects of the fishery problems. We certainly have acquired more knowledge. I would also like to thank Professor Dymond for the accommodation he has given us. He made some comment that the room was not suitable for our meeting, at least not as suitable as he would like to have it, but I think it has been an ideal spot. I also want to thank those who participated, and I am particularly happy to see some of our commercial fishing friends here sitting in on this meeting. I wish we could get them to attend all of the scientific meetings.

If there is no further business, I shall call this meeting adjourned and hope that we may all meet again in the not too distant future.