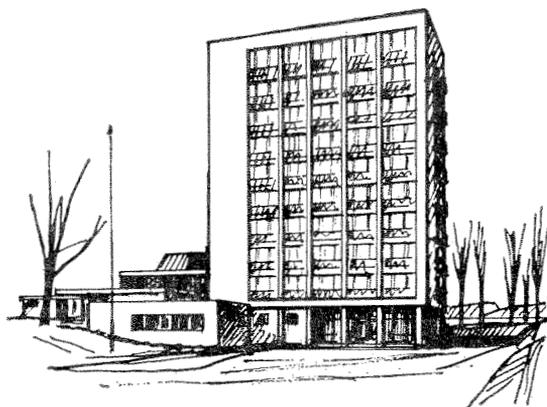


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FISKERIDIREKTORATETS SKRIFTER

SERIE HAVUNDERSØKELSER

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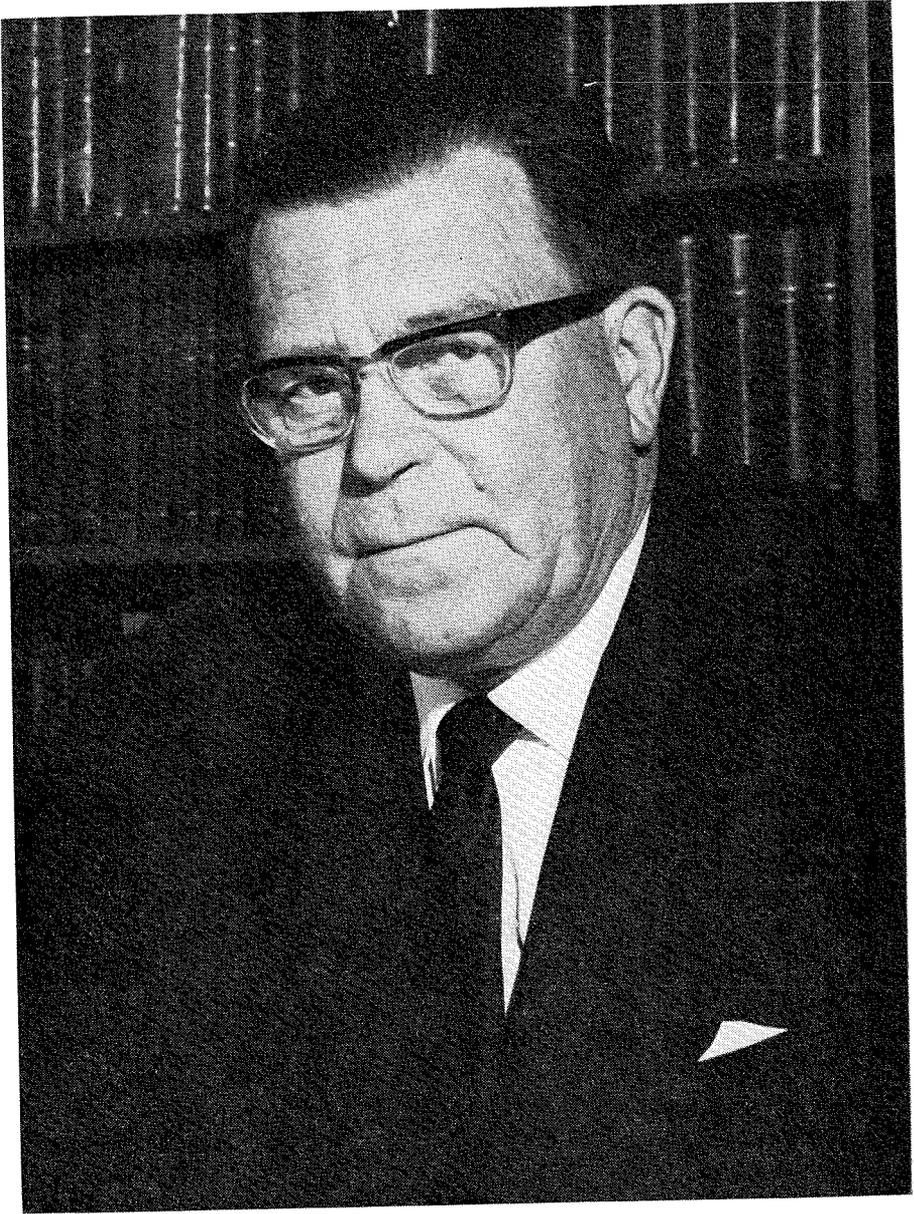
DIRECTORATE OF FISHERIES

BERGEN · NORWAY

1969

CONTRIBUTIONS
GIVEN IN HONOUR OF
GUNNAR ROLLEFSEN
AT HIS 70TH BIRTHDAY

EDITORS:
ERLING BRATBERG ERLING BAKKEN
ODD NAKKEN



Gündas Kalliper

FOREWORD

Gunnar Rollefsen was born November 20, 1899. His parents were factory owner, later bank manager, Hans Georg Rollefsen and Anna Marie, n. Christensen. The family lived in Larvik, a town by the Oslofjord, and here Gunnar Rollefsen finished his pre-university education in 1920. His boyhood interest in living organisms of all kinds led him on to a study of zoology at the University of Oslo.

In 1927, before Rollefsen had completed his university studies, he was offered a fellowship to take up research at the scientific department of the Directorate of Fisheries in Bergen. At that time he was working on his thesis on freshwater fish. In Bergen, however, Rollefsen started investigations on marine plankton, and soon concentrated on fish eggs, especially eggs of cod. From simple, discarded parts of mechanical equipment he succeeded in making an apparatus that automatically at short intervals photographed the development of cod and flounder eggs. This made it possible to describe in detail the hatching process under various conditions. During this period he also studied the effect of mechanical influences on the cod egg, and demonstrated that the action of waves and breakers are responsible for a heavy mortality among the eggs.

During his first years in Bergen Rollefsen took part in many cruises, and enjoyed the work aboard the first ship named "Johan Hjort". This was a small cutter able to operate in inshore or nearshore waters only.

The scientific staff was small and Rollefsen undertook investigations in biology as well as physical oceanography. Rollefsen's principal interest, however, was in studies of the cod in Lofoten. He worked on the age determination of this fish and found that the otoliths gave a more reliable indication of age than the scales. In addition he discovered that the two subpopulations, the coastal cod and the "skrei", could be separated by their otolith patterns, and he was furthermore able to distinguish the zones in the otoliths representing the years of spawning. The details in the life history of each cod, as revealed from the otoliths, formed the basis for a series of prognoses on the strength of the year-classes and the prospects for the cod fishery.

Supported by grants from research funds established by the fishing industry, Rollefsen initiated a new approach to a major problem in fisheries: what causes the great fluctuations in year class strength in fish stocks? And further: is it possible to diminish these fluctuations by artificial hatching and rearing? In 1934 experiments were started in Trondheim to rear a hybrid between two species of flounders. The hybrid is very rare in nature, but ecologically fully competitive and easy to recognize. Millions of these "marked" fry were released in an enclosed fjord and their further destiny closely watched. The hybrid turned out to be superior compared to the natural flounders. However, some estimates of mortality could be made, and a lot of practical experience on artificial propagation on fish was collected. In particular, the problem of finding suitable food for the larvae was solved. Unfortunately, the experiments had to be discontinued when World War II broke out.

During the war it was impossible to carry out usual field work, and investigations had to be concentrated on providing samples from the greater seasonal fisheries, mainly cod and herring. An unbroken series of observations on the age composition in these stocks was therefore maintained.

A great interest in applied research had developed when war ended in 1945. Rollefsen realized this, and he started to work hard on obtaining what he regarded as a major requirement for further studies: an ocean-going research vessel. Despite the fact that a shortage of steel, engines and equipment existed, his persistent argumentation resulted in the go-ahead from the Government. The ship was built from a hull intended for a whaler and completed as "G. O. Sars" in 1950.

The design of the 170-foot ship proved very successful for all the varied purposes for which she was needed. Her general layout was copied when the new "Johan Hjort" was built 8 years later. But this time the need for a new research vessel was advocated strongly by the fishermen's organizations as well.

Rollefsen was appointed director of the Institute of Marine Research in 1947 after acting as head for some years. As director he had to devote an increasing part of his work to planning and administration. The staff increased from 25 persons to more than 100 under Rollefsen's leadership, and many new research projects were taken up. Not only was the biology of commercially important marine species studied, but investigations of the physical and chemical environment, the biochemistry and physiology of fishes, applications of hydroacoustics, and studies of invertebrates became increasingly important.

Besides his work at the Institute Rollefsen played a prominent part in international organizations. He attended the meetings of the International Commission for the Exploration of the Sea (ICES) for the first

time in 1934. Later he met regularly in several of the ICES' committees and became chairman of the Northeastern Area Committee in 1945 and of the Gadoid Fish Committee in 1954, an office he filled until 1958. He was elected Vice President in 1957 and First Vice President a year later. Rollefsen took an active part in the meetings, and as chairman he arranged several group meetings of expert biologists on specially important topics. He realized that ICES would benefit greatly if organized as a completely independent international body. In cooperation with other members of the Bureau he contributed to an agreement with the Danish Government and a Convention for ICES in order to clarify the status of the body.

Rollefsen's contribution to international cooperation among scientists and fisheries administrators was not limited to ICES, but included international fisheries commissions as well. He took part when the International Commission for the Northwest Atlantic Fisheries (ICNAF) was established in Washington D. C. in 1949, and attended all annual meetings of that commission as a delegate until 1961. Within ICNAF he always emphasized the importance of a rational management of the resources, but at the same time put the case for the Norwegian fisheries when needed.

On the east side of the Atlantic, especially the North Sea, management of the marine fisheries was organized internationally under the Permanent Commission of the International Fisheries Convention of 1946. On the Commission Rollefsen met as a delegate from the time the organization was established until it was reorganized as the North East Atlantic Fisheries Commission in 1958, and he was the Vice President between 1953 and 1956. His work here was mainly related to studies of the effect of mesh sizes and of size limits of fish, and he was the chairman of a committee established to report on these problems.

The trawler fleets of all nations increased greatly after World War II. It was felt by many that their exploitation of the fish stocks on the banks along the Norwegian coast was a threat to the livelihood of the Norwegian fishermen who traditionally depended on these resources and mainly used gillnets and longlines.

Rollefsen's view was that the Norwegians ought to develop a trawler fleet of their own, but apart from this, needed protection of the near-shore waters. He therefore gave very valuable assistance at the International Court of Justice in the Fisheries Case between United Kingdom and Norway in 1951 where the Norwegian base lines determining the fishery limit fixed by the Royal Norwegian Decree of July 12th 1935, in order to protect the coastal fisheries, were declared not to be contrary to international law.

Besides the demanding work on the international arena, Rollefsen had projects in Norway that required his participation. One important task was to provide new facilities for the Institute. In 1960, after many years of planning and negotiations the Institute moved into a new building near the waterfront in Bergen harbour. This greatly improved the working conditions. Earlier the staff of about 70 were scattered in several houses, most of them in converted flats.

In 1950, following a lecture by Rollefsen, a committee established by Bergen Commercial Association promoted a collection of funds from private contributors and the planning of a public aquarium began. The aquarium was to be constructed in connection with the new building for the Institute of Marine Research. Rollefsen had in this way initiated a project he later followed up in every detail. The planning challenged both his artistic mind and biological knowledge. Right from the outset, he emphasized the importance of making the aquarium attractive to the general public, but at the same time making it suited for experimental purposes so that it thereby could serve science and the fisheries.

When Rollefsen in 1947 became the director of the Institute of Marine Research he needed in a great measure all the varied abilities he possessed. He had to lay aside his own research projects and devote himself to leading the Institute with all the administrative tasks this involved. Norwegian marine research was faced with extensive work after the war. Research on a wider range of fish species was required, and a closer contact between the scientists and industry as well as the general public had to be established. Moreover it was necessary to bring new methods and technical equipment into use in marine research. With the ideas Rollefsen has always had about fisheries investigations and their relation to the fisheries, he had the best qualifications to achieve valuable results within his field.

Rollefsen is a scientist and administrator with considerable scientific imagination. He also has a strongly developed sense of scientific accuracy and always stresses the integrity of research. At the same time, however, he is a true artist and combines an eye for artisticly and esthetical values with a creative imagination more forceful than usually found among scientists. These qualities of Rollefsen's character are not only noticeable in company with friends and colleagues, but are perhaps most clearly manifested by the creation of the Aquarium in Bergen. The Aquarium bears evidence of a successful combination of extensive knowledge about life in the sea, a thorough understanding of the technical problems involved and an ability to give the plans an artistic implementation. Through the Aquarium Rollefsen has brought the life in the oceans as close to man as technically possible, and at the same time given the

visitors an illusion of descending into the sea to there discover a completely new world.

Gunnar Rollefsen, an artist within his field, is gifted with personal talents which have influenced his work as a fishery biologist. His scientific papers, therefore, bear a very personal stamp and this holds for his work as administrator and head of the Institute as well. His manner of proceeding at conferences and meetings has always reflected his rich personality, and one has the impression that Rollefsen during all his work has managed to transform his own high hopes and plans into realities. Other scientists may point to greater practical implementations of their work, but few have like him been able to illuminate important aspects of life in the oceans.

Also as a writer and a lecturer he has shared his knowledge with many interested people, and his readers and listeners are not only found among persons associated with the fisheries, but include the general public as well. This part of his work reflects still other aspects of his distinctive personality.

For his important and varied work Rollefsen has been honoured in various ways. Thus in 1960 the University of Bergen conferred on him an honorary Doctor's degree for his contribution to scientific research. He has received the Knight's Cross, First class, of the Order of St. Olav of Norway, the Commander's Cross of the Swedish North Star Order, and the Knight's Cross, First Class, of the Royal Danish Order of Dannebrog. Of his honorary scientific distinctions may be mentioned the Hans Strøm Medal of the Academy of Ålesund Museum, the Gold medal of the Association for the Development of the Norwegian Fisheries and the Oscar Sund Price medal. Rollefsen is a member of the Norwegian Academy of Science and corresponding member of the Zoological Society, London.

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AN APPRECIATION

It gives me great pleasure as President of the International Council for the Exploration of the Sea, to express, on behalf of the Council, our deep appreciation of the life and work of our old friend Gunnar Rollefsen. Gunnar Rollefsen first attended the annual conferences of ICES in 1934 as an expert for Norway. He was a delegate in 1945 and, with the exception of 1951, from 1948 to 1961 also. He was elected a Vice-President in 1957 and First Vice-President in 1958. We all very much regretted when he had to retire from the Council in 1962 owing to ill health. Had he been able to continue I have no doubt he would have eventually been elected President. He was Chairman of the North-Eastern Area Subcommittee from 1945 to 1954 and of the Gadoid Fish Committee from 1954 to 1959. Gunnar Rollefsen was, therefore, very much a "man of the Council".

At the annual meeting in Bergen in 1957 Rollefsen suggested that an approach should be made to the Danish Government with a view to having the Council accorded proper international status in Denmark. With George Lienesch of the Netherlands he and I interviewed the then Danish Prime Minister, who received us sympathetically, as well as a number of high ranking officials of the Danish Government. Eventually, as is common knowledge now, the Danish Government called a meeting to discuss a Convention which was ultimately signed and ratified by all member nations. In the 1964 Convention there was provision for a host agreement with Denmark and when I came to sign this on behalf of the Council I felt that I was usurping the place of Rollefsen, who had done so much to bring this matter to fruition.

Rollefsen's advice was frequently sought in the Council and he always made valuable contributions to the discussions of the many problems which confronted us. As Chairman of the Consultative Committee I valued his help in the work we had to perform, especially as the Council's

Contribution given in honour of Gunnar Rollefsen at his 70th birthday.

new relationship with the former Permanent Commission, established under the International Fisheries Convention of London of 1946 necessitated new thinking on many problems.

Shortly after the War when Rollefsen was seeking funds for his new institution and the aquarium in Bergen we were all enthralled by his vivid accounts of his search for new materials and for new ideas, of which he himself was never short.

He never hesitated to assist the young fishery scientist. I well remember visiting Bergen as a young student in 1936 when Rollefsen, a busy man preparing to go off on a cruise, devoted almost a full day demonstrating to me his interpretation of the reading of otoliths of cod.

His obvious enthusiasm for the job, whatever it might be, was infectious. Kindly, generous, hospitable in the extreme, a good companion Gunnar Rollefsen made many friends at our Council meetings.

The International Council for the Exploration of the Sea takes just pride in having had as one of its foremost members Gunnar Rollefsen who will be long remembered by all those who regard him as a friend. On behalf of the Council I wish to offer Gunnar Rollefsen our congratulations on his seventieth birthday and to express our best wishes to him for his future health and happiness.

ARTHUR E. J. WENT

President of the International Council
for the Exploration of the Sea.

TRIUMPHS AND FRUSTRATIONS OF THE FISHERY BIOLOGIST

It is the fishery biologist's main duty to acquire knowledge on the causes of the fluctuations observed in the catches of fish and shellfish. Both in space and in time the catches may vary widely. Scientific analysis has revealed that both natural factors, as a rule beyond control by man, and the fishing industry, acting as extra predator, can be held responsible. A good quantitative insight in this complex matter requires knowledge on reproduction, growth, migrations, natural mortality, and fishery mortality in the species concerned. To achieve this, the fishery biologist should have the disposal of laboratory and research-vessel facilities, equipped with sufficient staff and apparatus, operating on the basis of an adequate budget, all this adapted to the character and extent of the natural range of the fish populations under consideration. There is something else required, not to be bought for money: a good dosis of enthusiasm to tackle the intricate problems both in the field and in the laboratory.

The results obtained step by step are not intended for the protection of nature or to prevent rare and interesting species to become extinct, but rather to lead the way towards a rational exploitation of the fish stocks. The scientist produces the material for a sound governmental management programme.

One should realize that the exploitation of the aquatic resources is of quite an exceptional nature: here one harvests jointly what nature produces voluntarily. For the terrestrial resources, both animal and vegetable, this system has been abandoned long ago, leaving out of consideration some forgotten corners of the world where human society still works on a truly prehistoric level. Agriculture and animal husbandry replaced the free exploitation of the terrestrial natural resources since time immemorial. All the major products of nature are nowadays grown

on privately owned plots in which one counts on due repression of poaching and other infringements. Tillage and manuring, control of predators, parasites, and diseases requires investment of money and labour, but the net results of all this fall in the hands of the farmer, gardener, cattle breeder, poulter or apiarist who works his own plot of land. Scientific advice helps him to increase the yield both quantitatively and qualitatively as well as to mechanize and industrialize his working.

How far the fishery lags behind in this respect! Fishing usually means little more than jointly harvesting what nature yields, and this not only in the open sea but also in territorial waters, and in most of the fresh water. For a very limited number of species, predominantly of a non-mobile nature, the big jump forward to real farming has been made. This involves abolishment of the former free fishery, putting the suitable areas into the hands of fish and shellfish farmers, and adequate policing; further, adopting appropriate cultivation techniques as well as control of predators, parasites, and diseases based on scientific information. In several cases striking results have been obtained, demonstrating that nature, left to itself, does not necessarily lead to the maximum production. The biological potentialities are often remarkably greater than fully natural conditions suggest.

Terrestrial experience indicates that adequate reglementation of a joint exploitation of resources of mobile species can lead to better annual yields and can prevent eradication of more vulnerable species. This experience has been applied in the field of fisheries, which gradually led to the following development:

I

Checking evident cases of wasteful exploitation such as use of destructive fishing methods leading to the untimely death of great numbers of immature fishes. Examples are the prohibition of the use of explosives and poison, and the abolishment of fishing for young specimens of commercial species for the purpose of manuring the land. Though introduction of such measures seems a rather obvious matter, hardly requiring scientific advice, we have to admit that it was not so very long ago that one ruthlessly and purposely fished for immature fish in the nursery areas in inshore waters of the North Sea. The Government concerned (Netherlands) found it a difficult decision to put those trash fishers out of business even though it was clear that the benefits for the offshore fishery for consumption fish, in which more than one nation participates, would largely surpass the immediate losses.

II

A further step towards a more rational exploitation of the aquatic resources was the introduction of minimum legal sizes for species of commercial importance. Everywhere one noticed that large, presumably older, specimens invariably became scarcer according as one fished more intensely. Fishery biologists pointed out that in many a case fishes were harvested before they could participate in reproduction. Would this be done on too large a scale, there would be reason to fear that the level of reproduction could be drastically reduced, especially in fish populations with a limited range. It was not difficult to determine at which length the species under consideration becomes sexually mature, and hence to establish a minimum legal size permitting a fish to reproduce at least once before being caught.

Since taking such measures requires only a limited amount of scientific information, and since a minimum legal size is rather easy to control, one would expect that all modern countries had adopted this system long ago, in an effort to safeguard their aquatic resources both in fresh water and in the sea. Unfortunately this is not the case:

A) One can point out many a case in which governments are reluctant to adopt such a minimum legal size because the species under consideration are of considerable commercial interest before they attain sexual maturity. In such cases fishermen strongly oppose introduction of a minimum legal size based on this principle, and will abuse such a measure whenever possible if their government imposes it on them.

B) In case feeding habits are such that one strongly prefers the very young stages above exploitation of the larger fishes, few countries are willing to introduce a minimum legal size for such a species. Therefore one still fishes on a large scale for eelers in countries where the larger eels are less appreciated.

C) The same happens when the species under consideration is only within reach of the national fleet when immature, to migrate to other areas at a more advanced age.

D) Fish is often used as raw material for the production of fish meal, a crude product which finds its way predominantly to poultry farming and pig breeding. This is a sound principle when species are used which are in no developmental stage interesting as human food. Still, one can adduce quite a few examples in which the contrary is the case. When one started the production of fish meal from immature specimens of commercially important species, one often assumed that the stocks were so great that some thinning out of the schools of juveniles would not noticeably affect the catches of mature specimens (e.g. North Sea herring).

Another case is that of the brown shrimp for which one assumed that the small specimens were all males and would never grow up to commercial size, hence could safely be used as raw material for fish meal. We now know that this is not true, and that protection of small shrimps will lead to a noteworthy increase in the catches of larger shrimps. Still, it seems difficult to suppress the established shrimp meal plants, even when this would be financially very interesting for the shrimp industry as a whole.

III

Fishery biologists continued their scientific work and gradually managed to get a grip on the dynamics of aquatic resources, considering man as an extra predator. Quantitative information on reproduction, growth and mortality formed the basis of this better knowledge and mathematics helped to build up the fishery theory. It appeared to be necessary to collect information on reproduction, growth, and mortality for every species separately and often within one species for every separate population. It then became clear that a minimum legal size based on attainment of sexual maturity was a rather primitive tool in fisheries management. If sufficient knowledge was acquired for a given species and population, one could calculate how the fishing industry could make the highest catches in such a manner that it would not adversely affect the catches to be made in future years. This is the "optimum sustainable yield". It appeared to be possible to indicate rather precisely at which size the fish could best be harvested if one is really after the highest catch, expressed in tons of fish. For both social and commercial reasons it is as a rule wise not to catch the whole year-class in too short a span of time, therefore to start fishing some time before the calculated size has been reached, and to continue fishing for some time after that supreme moment. The biologist is further acquainted with the often considerable fluctuations in the strength of the consecutive year-classes, and can give advice how to avoid too strong a reflexion of these fluctuations on the market through harvesting of several year-classes simultaneously.

It was the fishery biologist's pride and joy to be able to provide the material for a sound fishery management leading to a high and sustainable level of production. His advice could be translated to minimum legal sizes (often considerably higher than those formerly based on attainment of sexual maturity) and hence on the type of gear (e.g. mesh size of nets) to be used at a given level of fishing intensity. The biologist demonstrated how one can catch more fish by adoption of larger mesh

sizes, and when the fishery intensity is already too high, how one can catch more fish by reducing the fishery intensity, which means increase of the catch per "unit of effort". The best results will be obtained if the fishermen concentrate their efforts on one single species and avoid mixed catches as far as possible. To attain this, the biologist tries to gain more information on the behaviour of the fish to enable the technical experts to develop specialized apparatus and gear to find and to catch the species under consideration. Meanwhile he goes on collecting information on year-class strength, growth, and mortality in species of commercial importance, for these are data influenced by a variety of factors, man's activities included.

It must be possible to build up a sound fishing industry on the scientific basis produced by the fishery biologist. For obvious reasons, this goal will be reached easier in waters over which the government has complete jurisdiction, and somewhat more difficult in international waters. But there too it is in principle possible to come nearer to the optimum sustainable yield provided one manages to develop a good system of international control on the measures jointly taken. In Europe it was the setting up in the year 1946 of the Permanent Commission for the Overfishing of the North Sea, which promised international agreement on the measures to be taken for a sound management of the marine resources in the North Sea and adjacent waters. Later, its range was considerably broadened by the rebaptism into the North East Atlantic Fisheries Commission, on which occasion the measures to be discussed went far beyond establishment of minimum legal sizes for fish and for the mesh size of nets.

Were the high hopes nourished by the fishery biologists of many a nation justifiable? Three examples, one from outside, two from inside the NEAFC area, will elucidate this question:

A) The post-war revival of the Antarctic whaling industry was spectacular. An international commission had to watch against possible overfishing of the whales. Whales reproduce but slowly and the scientists had to admit that a fool-proof system of age determination in whales had still to be developed. Hence data on growth and on reproduction rate should be handled with caution. One could agree on a minimum legal size and on a system of annual quota, expressed in "blue-whale units". When the catch per unit of effort began to decrease, the countries interested in whaling refused to believe in overfishing.

The scientists, realizing that the data on which they had to base their conclusions were not so dependable and complete as they would have wished, worded their reports with the under such conditions customary caution, which led the representatives of the industry to wave all their

apprehension aside. In a later phase all one was willing to agree on was a very slight reduction in the annual quota, so slight that it would have been virtually impossible to determine whether this reduction would have any effects at all. The reducing stock made remunerative exploitation soon impossible for the western countries. Perusal of the scientific information available leads to prediction of the number of decades required for the rehabilitation of the stocks if one stopped whaling completely and immediately. This forecast shows whaling cannot be a profitable industry for a long time to come. One also concluded from the available data that one had trusted in the overall observation of the minimum legal size one had agreed upon, but that evidently a great number of whales must have been stretched administratively.

This is a sad and disheartening story, especially for those who believe in a rational exploitation of marine resources based on scientific evidence.

B) Cod and haddock once abounded in the Barents Sea and adjacent waters. In the old days it were especially the Norwegian fishermen who caught the adults during their spawning migration to the Lofoten area. Later, a trawl-fishery evolved in the Barents Sea itself. The mesh size of the nets in use was rather small, and the fish got less chance to reach an appreciable size according as the fishery intensity increased. The fishes caught showed a gradual decline in average size and the catch per unit of effort decreased alarmingly. Scientific evidence collected by fishery biologists clearly showed what happened, and one finally agreed to use larger mesh sizes to protect the younger fishes. As usual, the industry tried to compensate for the declining catches by increasing the fishing effort. Thus the positive effect of the increase in mesh size is easily obscured. Another adverse effect of an increased fishing intensity is a reduction in the number of year-classes caught simultaneously. The fluctuations in the strength of the consecutive year-classes are as a rule considerable in gadoid fishes. Therefore, some degree of stabilization in the annual catches can only be achieved when a greater number of year-classes is found in the cod ends of the trawl nets. One strong year-class may predominate in the catches for several years in succession. The smaller the number of year-classes caught simultaneously the greater the chance that there is sooner or later no rich year-class available at all, which makes the annual catches drop alarmingly. It is often assumed that the number of eggs produced in the spawning season is never a limiting factor in reproduction in fishes such as gadoids, which produce a great number of small-sized eggs. Still, unless the amount of food for the larval stages is the limiting factor in reproduction, it is hard to see how a considerably reduced number of eggs spawned (e.g. because only

a small number of adults participates in reproduction) will on an average lead to the same year-class strength as in periods with a more ample egg production. Fishery biologists from several countries have now stated that the stocks of cod and haddock in the North East Atlantic's Arctic section have come down to an alarmingly low level. The year-classes which will enter the fishery in the years to come are so poor that the annual catches in this area will drop to an unprecedented level. One hopes that a rich year-class will be produced in 1969 or 1970 so that the catch will improve in due course, but the small number of adults which will participate in reproduction in those years make many a biologist wonder whether the chance for a really good year-class to spring up is not very small, indeed.

Trawl-fishery will not be remunerative in this area for at least several years to come, and the number of fish migrating to inshore waters will no doubt be small for a longer period. What will the industry do? The fertility of the sea is not adversely affected by the fishery, and even very seriously reduced fish stocks will get a chance to recover when left in peace for several years. There is little hope that the countries concerned will agree to stop the fishery in this area to give the stocks a chance to recover, or even to reduce the fishing intensity drastically, to achieve the same goal somewhat slower. At most one is willing to restrain from a further increase in fishing intensity. The disappointing catches will sooner or later force the larger units to try their luck elsewhere (increasing the fishery intensity there), whereas the smaller vessels, operating inshore, will not be in a position to escape, and have to face disaster.

This, too, is a sad and disheartening story, especially for those who produced the scientific material on which a sound management could have been based timely, and who welcomed the international agreement to increase the mesh size as a first step in the right direction, only to see later that one is unwilling to control the fishing intensity.

C) Herring has for ages been the most important fish in the North Sea, and for some countries the herring fishery was traditionally the most important section of the sea fishery. Herring used to be superabundant in the North Sea, and the total annual catches fluctuated but slightly. Fishery investigators used more of their time for the study of other species of fish, since the herring fishery gave no reason for concern. When the Permanent Commission for the Overfishing of the North Sea started its work, the herring was not listed among the protected species, and neither did one consider a minimum legal size for the herring or a minimum mesh size for the herring nets. Scientific evidence demonstrated that the catches were usually composed of a great number of year-classes, among which

one or more strong year-classes dominating in the catch pattern for years in succession.

In the post-war period the fishing effort gradually increased in the North Sea. More and/or greater ships and stronger engines came into use, electronic apparatus to find the fish schools were introduced, active fishing (trawl nets) replaced the passive gear (drift nets). The total herring catches from the North Sea remained after an initial increase at about the same level, despite the strong increment in fishing intensity. Analysis of the catches revealed that they were no longer composed of 10 to 12 year-classes, as in the past, but of fewer and fewer year-classes. In recent years it is virtually the year-class entering the fishery for the first time (the recruits, 3 years old) which dominates in the catches. Hence greater fluctuations in the annual catches in our time and the risk that some poor year-classes in succession bring down the total landings from the North Sea to an unprecedented level. The Downs stock, the herring population which always gave rise to an important fishery in the southern North Sea in autumn, and which spawns in the Channel towards the end of the year, suffered so much from the high fishing intensity that the fleets found it in recent years hardly worth while to continue fishing on it.

The growing concern in the herring sector led to international efforts to elucidate the causes of the decline of the herring stocks. One was in the beginning very reluctant to admit that the increased fishing intensity had anything to do with it. One rather blamed adverse weather conditions and unusual hydrographical patterns for the poor recruitment. An international tagging scheme should throw more light on the effect of fishery for young herring carried out in the German Bight (the Bløden fishery) has on recruitment of adult herring, and hence on the catches of herring for human consumption. The Bløden fishery produces raw material for fish meal plants in Denmark and Germany. Though herring has many natural enemies it cannot be denied that fishing away of great numbers of young immature herring must have some adverse effect on the stocks of adult herring. The tagging results seemed to warrant the conclusion (1957) that only some 15% of the immature North Sea herring fell victim to the Bløden fishery. Hence, the Bløden fishery can only be held responsible for a reduction in the catch of adult herring up to 15%. Just now, tagging of immature herring is undertaken on a larger scale, to find out whether the 1957 conclusions can be corroborated. However this may turn out, it seems always an unwise management to use young individuals of a fish species which is in adult stage fit for human consumption as raw material for the production of fish meal or other low-level products.

The situation aggravated when an improved fishing technique (the purse seine) made it possible to catch entire schools located with the aid of electronic equipment. Though a better fishing technique is in principle always welcome if it means less labour and lower expenses to catch a given quantity of fish, there was reason for serious concern in this case. The fish caught in large quantities could not get appropriate treatment on board of the ships and was, when landed, only fit as raw material for fish meal plants. Thus only a small percentage of the fish protein will indirectly—through mediation of chickens and pigs—come as human food on the market, though there would have been an excellent direct market for the herring itself. This sharp increase in the herring fishing soon led to a noteworthy reduction of the stocks and now the purse-seiners are in search of juvenile herring, which means destruction of still greater numbers of herring than at the time one found adult herring in sufficient quantities.

The situation is alarming for the strength of the year-classes which will recruit now and next year is very disappointing, indeed. The large-scale destruction of young herring continues. So much money has been invested in this industry that one is not inclined to consider to stop using herrings as raw material for the production of fish meal. On the contrary, one will fish with increased effort when the catch per day fishing is insufficient.

When the herring is left in peace, it can be expected that new stocks build up again, provided another species—like for instance the sprat—has not taken its place and its food, which phenomenon has been observed after heavy fishing on sardine stocks off the coasts of California and South Africa. In such cases the old situation may never return.

This again is a sad and disheartening story. Fishery biologists of all countries concerned agree now that herring can suffer from overfishing, and that it is unwise to reduce the stocks so much that the annual catches virtually depend on the strength of one or at most two year-classes. Use of food fishes as raw material for a fish meal industry seems very unwise, indeed. Everybody waits for a miracle and points out that dramatic changes in the herring population have been recorded from past ages. Nobody is really inclined to reduce the level of this herring fishery drastically to give the herring a chance to recover. Whenever there are signs of recovery, like was the case in the southern North Sea in 1968, one jumps immediately on it with a great number of ships, instead of exerting one's efforts to assist the stocks to come back to the old level.

No small wonder that the fishery biologist suffers from frustration. Did not he produce the scientific basis for a wise fisheries management,

and did not he put down in exact figures how one could reach the optimum sustainable yield for a given body of water or, if one preferred, the optimum sustainable profit? This optimum sustainable yield appeared to be a *fata morgana*. Many efforts were made to come closer and closer to this ideal situation. International agreement has been reached on the use of larger mesh sizes, and a system of international control was worked out step by step. But one did not reduce the number of fishery units according as the efficiency of these units went up.

One did not even seriously consider to prevent a further increase in the fishing intensity. The effect of mesh size increase is nullified by increment in fishing intensity and the desired stabilisation of the annual catches can only be reached when the fishing intensity is brought down to such a level that more year-classes are caught simultaneously.

Did the biologist fail to explain in clear terms what would happen if no concerted action was taken? Did he word his conclusions too cautiously so that all one wanted to do was asking for more detailed studies to clear up the points on which he expressed some doubt? The biologist certainly underestimated the resistance of economical and political nature. Reducing the fishing intensity means that capital already invested in ships and plants will be annihilated. One will prefer to continue working with a smaller profit or to ask for governmental subvention in some form or another. Politically it is difficult to prevent noteworthy numbers of employers and employed to continue their activities in such a specialized industry as the fishery is. Here, too, governments prefer to subvent the fishing industry and to cherish the hope that things will take a favourable turn.

What will happen now that the *fata morgana* called "optimum sustainable yield" seems more unattainable than ever? The sea fishery will in all probability split up in four directions:

A) The *tramp fishery*, a form of free enterprise not hampered by restrictions, which hunts for fish wherever fish can be found and wants to use all conceivable technical means to catch that fish. This form of fishery does not worry about the future. If a fish population shows signs of serious overfishing, one goes elsewhere. Distance should not hamper, therefore larger units equipped with facilities for deep-freezing, which can stay away from their home ports for weeks and months, are required. Whenever a stock of predatory fish is depleted, and nature, abhorring a vacuum, puts large schools of cephalopods in their place, one will fish for those squids and cuttlefishes instead.

Such a tramp fishery is already in existence and countries where wages are relatively low and/or where the sources of food rich in animal protein are scarce, will be in the best position to continue the tramp

fishery on a remunerative basis. The countries of western Europe will certainly not be among those who can easily compete in this field. The assistance of fishery biologists will only be invoked for this type of fishery to scout for fish schools, to follow their migrations and to develop efficient methods to catch the fish, based on detailed knowledge of their behaviour.

B) A type of fishery which could be described as *managed fishery*. The highest yields over a longer period of time can no doubt be expected from a given fish population if it receives proper management from the larval phase of the fish till the day of capture. This includes safeguarding spawning grounds and nursery areas from the adverse effects of pollution; keeping losses by predation within bounds as far as possible; protecting the young fishes against the danger of being caught in small meshed nets such as used by shrimpers; avoiding of wasteful fishing methods; catching the adult fish with nets of which the mesh sizes are scientifically prescribed so that one approaches the optimum sustainable yield as close as possible; and above all avoidance of a fishery intensity greater than strictly necessary. Proper management of a fish population is theoretically so attractive, since it promises the optimal use of the fertility of the sea and a minimum of fluctuations in the annual landings, that many a country will continue its efforts in that direction, despite the many disappointing experiences encountered thus far. The more countries participate in the fishing on a given population, the more difficult it is to agree on the necessary management measures. Palliatives will never lead to proper management. Since control of the fishing intensity on an international basis is not only the most important measure to be taken, but also the most unpopular and legally the most difficult, it is to be expected that countries, which want to make a serious effort in the direction of a managed fishery, will sooner or later follow other paths. Most probably the only way out to higher yields and more stabilized landings at a moderate fishing intensity will be proclamation of territorial rights so far offshore that the fish populations under consideration do not surpass those boundaries during their migrations. This may in due course lead to a sharing out of fishing grounds, as has already been done for the mineral resources on the continental shelf. Such a system requires the same rigid control as now applied in the present narrow strips of territorial waters. Species such as sole, plaice, and shrimp are among the first to benefit from such a managed fishing pattern. Still, experience gained within national waters demonstrates that the control of fishing intensity based on the number of units, the size or horse-power of the boats, or the size of the nets to be used, is a very difficult and intricate matter and that there are many ways to get around

such regulations, sometimes even leading to loss of seaworthiness of the ships used. Concerted action of experts or various description will be required to develop a workable formula to control the fishing intensity.

The alternative is to work out a basis of quota. This is only feasible where the landings are to a high degree centralized and conscientiously recorded. A quota system has moreover the economic disadvantage that there will always be a rush to get within the shortest time possible the quantity of fish allowed, which leads to inefficient use of fleet and personal and to an irregular supply of the market, hence to lower prices.

For the fishery biologist such a trend towards a truly managed fishery is certainly most interesting. This will give him a fair chance to demonstrate that he is worth his money, for he knows that the yield will increase substantially if his proposals for regulation of the fishery are put in practice. Now his own government is free to impose the measures he deems necessary for a rational exploitation of the fish stock under consideration. He feels no longer frustrated because his scientific proposals are amended to such an extent in efforts to reach unanimous international agreement that the net results will hardly be measurable. He knows now, that the results of his painstaking efforts to evaluate the strength of the year-classes, to measure the growth of the fishes, to follow their migrations, to study their hazards, will be used efficiently and that the measures he proposes to increase the yield quantitatively and qualitatively, measures such as prescribing the number of fishing units required, defining the characteristics of the gear to be used, and protecting the young fishes on the nursery grounds, will no longer be nullified by an uninhibited increase in fishing intensity, and by destruction of countless immature specimens by an industrial fishery.

C) A third line, already in operation on some scale is *fish cultivation*. Instead of harvesting the mature fish as nature produces it, one keeps it for a longer or shorter period in confinement as private property. This can only be done in well-protected waters where only the proprietor has the right to fish and from which the fish cannot escape. Usually this means keeping the fish in denser concentrations than occur in nature, which involves a careful control of the oxygen level, of the food supply, and of predators, parasites, and diseases. In fresh water, fishes like carp and trout are produced on commercial scale this way, in sea water it is in the first place immobile species such as oysters and mussels which are cultivated. In this latter case one should rather speak of a semi-culture. One offers the shellfish a suitable substratum, protects them against predators, parasites, competitors, and diseases as far as feasible, but one does not control their food supply. Dense concentrations of molluscan shellfish can only be grown successfully where tidal currents see to a steady

supply of the natural plankton. As a rule a semi-culture yields a far greater crop than nature would ever have produced without man's intervention, but one cannot step up the production beyond the ceiling set by the natural food supply.

A true cultivation of fishes in the marine environment, in which extra supplies of food have to be offered, has just been started. In the second half of the 19th century hatcheries have been set up in many a country in an effort to check the decline of the fish stocks by producing small fry of fish and lobsters, which was then brought back to the natural environment. This because one assumed that the earliest developmental phases might be the bottleneck determining eventually the strength of the fish stocks. That one hardly ever picked the fruits of these efforts should in the first place be ascribed to a lack of quantitative insight. We appreciate that one persevered until well in the 20th century, for psychologically spoken it must have given a great feeling of satisfaction to put out into the sea great numbers of young fishes in return for all the fish harvested commercially.

In recent years cultivation of marine fish has been resumed, first on experimental scale, later in pilot plants. One had in mind to rear young flatfish from the egg till "postage stamp" size, and then to transfer those young fishes to areas where flatfish food abounds, but where stocks of flatfish are virtually absent. Should the flatfish grow up successfully in these areas, then it had to be expected that fishermen from more than one country would try to harvest this bounty. In a later phase one diverted to rearing valuable flatfish species to consumption size. Warm water discharged by electric plants could be used to speed up the growth of the fishes. It remains to be demonstrated whether production of valuable species of consumption fish can be remunerative in such plants. If so, application can be expected in several countries possessing well-sheltered sites with unpolluted and undiluted sea water.

The fishery biologist interested in cultivation projects will find a rich field for his activities here. He should evaluate all environmental factors involved in cultivating dense stocks of fish in captivity, should work out a suitable diet which promotes growth of the fish, which food should be relatively cheap and to be kept in stock, and should study parasites and diseases which could cause harm, and develop methods to control those.

D) The fourth line in the sea fishery could be described as the *sport-fishery*. Already now sportfishermen turn more and more to the sea, not only because many fresh waters become so badly polluted that sport-fishing is hardly longer possible there, but also because boats and equipment required for sport-fishing in sea gradually come within reach of a

greater number of people. Sport-fishing can be of considerable recreational and economical value for a country, but that not in the first place because of the consumption fish caught. The fish often comes in the last place and is not seldom left behind or displayed on the ship in such a way that it spoils. It is not important either what it costs to catch one fish. Especially in tropical and subtropical countries sport-fishing in sea will show a rapid increase and exert a greater economical impact than the commercial fishery ever did there.

The fishery biologist can assist the development of the sport-fishery by providing information on the migration of the species concerned and by disseminating knowledge on the habits and whereabouts of the species the sportfisherman is interested in. Sport-fishing contributes to the fisherman's happiness and well-being, partly because of the nostalgia a man in a modern civilization feels when he thinks of his ancestors in ages long gone by, trying to squeeze a living out of the hostile waters by outwitting the denizens of the sea. And thus prehistoric times merge into our modern world.

Will all this really happen, which means radical changes in the present fishery pattern, and disaster in many of its sectors? In principle a joint fishery on a truly rational basis does still belong to the possibilities, but if one seriously wants to reach that goal a rapid and drastic change of gear is a prerequisite. The fishery biologists are certainly ready to take up the challenge.

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STUDIES ON BLOOD PROTEINS IN HERRING

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INTRODUCTION

An investigation on blood proteins of herring, *Clupea harengus* L., was started in 1965 in order to find characteristics to be applied on the problem of identification of stock units. As part of this programme a report on serum esterase polymorphism has been published (NÆVDAL 1969). The present report deals with the electrophoretic analyses of hemoglobins and serum proteins. A complete description of ontogenetic variations in herring hemoglobin has been published (WILKINS and ILES 1966), and in the present report most attention has therefore been paid to the serum proteins.

MATERIAL AND METHODS

Blood sampling, treatment of blood and sera, analyses by electrophoresis, staining of proteins, autoradiography etc. were carried out in the same way as described for investigation on sprat (NÆVDAL 1968). PARKER and BEARN (1963) and CANN (1966) found multiple electrophoretic zones rising from protein-buffer interaction in the presence of boric ions. The buffer used in the present routine analyses contained boric acid, and to find out whether boric ions had any influence upon the protein zones, part of the material was analyzed by a buffer without boric acid but otherwise under identical conditions.

The type of herring investigated, date and locality of sampling and numbers in the samples are listed in Table 1. Age, sex, vertebrae numbers and otolith and scale type have been determined for part of the material. The specimens of samples 9 and 10 were caught as 0-group in August 1965 and separated into two batches which were kept isolated in tanks under simulated North Sea and Barents Sea temperature conditions (HARALDSVIK, personal communication).

Contribution given in honour of Gunnar Rollefsen at his 70th birthday.

RESULTS AND DISCUSSION

BIOLOGICAL VARIATION

Hemoglobin

The results of the hemoglobin analyses were, except for insignificant differences, in accordance with the ontogenetic variations described by WILKINS and ILES (1966). The relationship between hemoglobin types and growth may be different in the various populations, but as long as this is not completely understood, hemoglobin types cannot be used for identification of stock units. Therefore a further discussion of the hemoglobin types have been omitted.

Serum proteins

All serum proteins moved towards the anode at pH 9.0. Considerable variations were noted in several groups of proteins. A representative selection of protein patterns (electrophoretograms) are shown in Fig. 1.

The serum transferrins, identified by autoradiography, had less anodic mobility than any other serum proteins. Two transferrin bands were common. They were named Tf A and Tf B, the first had the greatest anodic mobility. Each specimen might possess one or two of the transferrin bands, and the phenotypes were named Tf AA, Tf AB and Tf BB according to the components they possessed.

Specimens which contained a single strong transferrin band only, often showed a faint band at the position of the lacking transferrin band

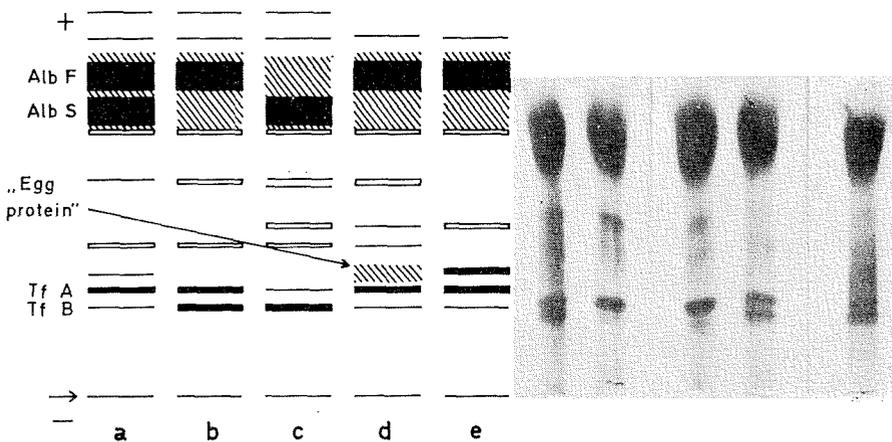


Fig. 1. Outline of serum protein patterns in herring obtained by combined starch and agar gel electrophoresis at pH 9.0, and photograph of electrophoretograms obtained by routine analyses. Filled in bars: Strong bands. Hatched bars: Moderately strong bands. Single lines: Faint bands. The point of application is indicated by the smaller arrow. From left to right the photographed types are: Tf AB, Tf AA, Tf AA, Tf AB, and Tf BB.

(Fig. 1). These specimens were classified as if the weak band was absent (Tf AA or Tf BB phenotype). The faint bands varied in strength among specimens and sometimes even between repeated analyses of the same specimen. The determination of the transferrin phenotypes were consequently to some degree unreliable.

A few specimens had one band close to Tf A at the cathodic side. A fourth band, seen on the anodic side of Tf A in a few specimens, probably represented a second rare transferrin component (Fig. 1e). The two rare bands were not tested autoradiographically since sera were not available when the tracing experiments were made, and they were both classified together with Tf A when calculating frequency distributions.

Presence of great amounts of hemoglobins in the serum slowed down the mobility of the transferrin molecules, especially Tf A, and consequently several specimens might be incorrectly determined as Tf BB. The relation between hemoglobins and transferrins was not clear, but the transferrins did not stain with *o*-dianisidine and consequently had no hemoglobin-binding capacity. Evidently sera containing considerable amounts of hemoglobins could not be used for determination of transferrin types.

Freezing and thawing of sera had no influence on the mobility of the transferrins or other serum proteins. However, a prolonged storage of sera in deep freezer had a similar effect on the transferrins as the presence of hemoglobins, namely reduced anodic mobility, making the type determination unreliable.

A broad and diffuse band was found on the anodic side of Tf A in females near spawning. Position and strength differed, but it was always located near Tf A, and therefore the classification of transferrin types in these cases was difficult. This band probably represented the "ripe female protein" observed in species of the genus *Oncorhynchus* (TSUYUKI and ROBERTS 1966) and the rainbow trout, *Salmo gairdneri*, (THURSTONE 1967).

Several protein bands were seen between the transferrins and the albumins. Although great variations were observed, these bands were too weak or too diffuse to form the basis of classifying the specimens into well-defined groups. Some of these patterns are outlined in Fig. 1. Since one of the mentioned bands stained with *o*-dianisidine, it probably represented haptoglobin/hemoglobin complexes.

Two main albumin components could be distinguished. One or both were present in each specimen (Fig. 1). The faster moving component was named Alb F and the slower Alb S. The three phenotypes were named Alb FF, Alb FS and Alb SS. The differences between the albumin types were often insignificant, and accordingly the albumin type determinations could only be accomplished in a few samples. In front of the albumins one or two faint pre-albumin bands were observed.

Table 1. Observed distributions (obs) of transferrin types in herring compared to expected Hardy-Weinberg distributions (exp).

Sample no.	Locality and date of sampling		Indications of sample		Transferrin groups			No.	q_A
					Tf AA	Tf AB	Tf BB		
1	Håvik i Fusa, Hordaland	5 Oct. 65	O-group	obs	60	17	1	78	0.88
				exp	60.4	16.5	1.1		
2	Fensfjorden, Hordaland	15 Oct. 65	O-group	obs	57	24	17	98	0.70
				exp	48	41.2	8.8		
3	Fensfjorden, Hordaland	23 Oct. 65	O-group	obs	86	20	4	110	0.87
				exp	83.3	24.9	1.9		
4	Buagrunden, off Møre	10-11 Febr. 66	Adult Norwegian spring spawners	obs	196	124	17	337	0.77
				exp	199.8	119.4	17.8		
5	Røstbanken, Lofoten	10 March 66	Norwegian spring spawners	obs	68	33	8	109	0.78
				exp	66.3	37.4	5.3		
6	Fana fjorden, Hordaland	14 April 68	Adult spring spawners	obs	43	50	20	113	0.60
				exp	40.7	54.2	18.1		
7	57° 40' N, 04° 30' E North Sea	24-25 May 66	Autumn spawners	obs	14	55	83	152	0.27
				exp	11.1	59.9	81.0		
8	58° 00' N, 05° 00' E North Sea	27 June 66	Autumn spawners	obs	17	38	23	78	0.46
				exp	16.5	38.8	22.7		
9	Lysefjorden, Hordaland	18 Aug. 66	See text	obs	12	51	35	98	0.38
				exp	14.2	46.2	37.7		
10	Lysefjorden Hordaland	23 Aug. 66	See text	obs	12	46	38	96	0.36
				exp	12.4	44.2	39.3		
11	Myking, Hordaland	April 67	Adult spring spawners	obs	37	33	13	83	0.64
				exp	34	38.3	10.8		
12	Duesund, Mastj. Hordaland	12 June 67	1-group	obs	69	25	2	96	0.85
				exp	69.4	24.5	2.2		
13	Halifax, N.S. Canada	June 68	Adult	obs	74	20	4	98	0.86
				exp	72.5	23.6	1.9		

None of the observed variations could be correlated with age or sex, except for the "ripe female protein".

The variations also occurred when boric acid was omitted in the buffer. Therefore the observed variations cannot be due to a protein-buffer interaction caused by boric ions. However, it is possible that other substances in the buffer or medium may interact with the proteins and thus cause artificial multiple zones.

Two allelomorphic genes (named Tf^A and Tf^B), each controlling one transferrin component, would explain the intraspecific variation in the herring serum transferrins. This corresponds to the transferrin variation in cod (MØLLER 1966) and in some other gadoid fishes (MØLLER and NÆVDAL 1966). The observed distributions of transferrin types in herring are shown in Table 1, and assuming the above gene combinations, gene frequencies were calculated from the observed distribution in each sample. Good agreements between observed and expected distributions were found in most cases. The deviations were not statistically significant, except for sample 2. This sample, which showed an excess of hypothetical homozygotes compared to expected numbers, might represent a mixture of two or more populations. Consequently, control by two allelomorphic genes may be accepted as an explanation of the herring transferrin variations.

The rare transferrin components are believed to be controlled by other alleles belonging to the same genetic system. However, because these components occurred only in a few specimens, this hypothesis could not be tested statistically. The presence of weak components in addition to the stronger transferrin components do not necessarily cause any difficulties in explaining the transferrin variations in herring. Simultaneous variation of a major and a minor component has been reported for the serum transferrins in mouse (SCHREFFLER 1960), and the herring transferrins may be controlled in a similar way. However, the minor components of the mouse transferrins were invariably present, whereas in herring they might differ in strength and even be lacking. This indicates a more complicated genetic control by modifying genes or dependence upon non-inherited factors.

The albumin variations may also be controlled by two alleles, each controlling one main albumin component. In the few samples where the albumin types could be determined with a reasonable degree of reliability, fairly good agreement was found between observed and expected distributions. Consequently, the albumin variation in herring and its control may be similar to the albumin variation in man (KNEDEL 1958, EFREMOW and BRÆND 1964), chicken (McINDOE 1962), and horse (BRÆND 1964).

No hypothesis of genetic control of the other serum protein variations can be put forth due to the protein bands in all cases being too weak for proper classification.

GEOGRAPHICAL VARIATION

Assuming that the hypothesis of genetic control of the transferrin types in herring is correct, their frequency distributions may be used for identification of population units. The variations in the other blood proteins are at present not revealed clearly enough to be of any value for this purpose. Table 1 gives observed distributions of transferrin types and the frequencies (q_A) of the hypothetical gene Tf^A , taken as a characteristic sample parameter. All these samples have been analyzed fresh or fresh frozen, and sera with considerable amounts of hemoglobins have been omitted. Due to difficulties caused by the weak transferrin zones, statistical methods for comparing samples have not been applied. However, the considerable variations of q_A among samples may allow some tentative conclusions.

The highest value of q_A was found in some samples of young herring from inshore waters of western Norway (samples 1, 3 and 12). Sample 2 collected in the same area and approximately at the same time as sample 3, showed somewhat lower q_A -value, and the distribution of phenotypes in this sample was not in accordance with expected Hardy-Weinberg distribution, indicating a mixture of populations differing in q_A . The q_A -values of the samples 9 and 10 also indicate that herring of different origin is populating the inshore waters of western Norway. The herring in these samples had been caught in inshore waters south of Bergen and kept for one year at the Institute of Marine Research. These two samples of herring, exposed to different temperature conditions, showed nearly the same q_A -values. The values were much below the values of samples 1, 3 and 12, but similar to those observed in samples of North Sea autumn spawners (samples 7 and 8). The mean vertebrae number and otolith characters indicated that these young herring originated from North Sea autumn spawners (HARALDSVIK, personal communication).

No significant differences were observed between the samples from the southern (off Møre) and northern (off Lofoten) spawning grounds of the Norwegian spring spawning herring, but differences should not be expected since the northern group was recruited from the southern area in 1959-61 (DEVOLD 1968). The q_A -values of these samples were higher than for samples of mature spring spawning herring from inshore waters of western Norway south of Møre (samples 6 and 11). Differences have been found in age composition, scale pattern and growth rate between Norwegian spring spawning herring and spring spawners from inshore

waters of western Norway (HARALDSVIK 1968). Samples 6 and 11 also differed from samples of young herring in the same fjords indicating that the adult and young herring in the same area may originate from different populations (local populations, spawning migrations of other populations and eggs and larvae from offshore waters).

In the two samples (7 and 8) of autumn spawners from the North Sea the q_A -values were significantly lower than for the other samples, but the q_A -values in these two samples did not agree. It is suggested that the samples consisted of a mixture of different groups of autumn spawners and this may explain the observed differences.

The sample from Canadian waters showed that variations in serum transferrins are present also in herring in the west Atlantic. The same phenotypes occurred as far as could be stated by the present electrophoretic methods, indicating control by homologous genes. The sample showed a gene frequency near the highest observed in samples from Norwegian waters.

SUMMARY

1. Hemoglobins and serum proteins of herring have been analyzed by agar gel electrophoresis (hemoglobins) and combined starch and agar gel electrophoresis (serum proteins). The material comprises twelve samples from the Norwegian coast and the North Sea and one sample from the east coast of Canada, a total of 1,546 specimens.
2. The results of the hemoglobin analyses were in general agreement with the ontogenetic variation described by WILKINS and ILES (1966).
3. Intraspecific variation was noted in the transferrin components. Three common transferrin types were found and assumed to be controlled by two allelomorphous genes. No relation to age or length was found. Presence of additional weak components complicated the type determination. Hemoglobins in the sera as well as prolonged storage made the type determination unreliable.
4. Observed albumin variations could be explained assuming control by two alleles, while observed variations in other serum protein groups were too weak or too diffuse for classification. A broad and diffuse band was found on the electrophoretograms from ripe females.
5. Considerable variations in the frequencies of the genes supposed to control the transferrin types were observed among samples. The type determinations were in some specimens complicated, but the observed variation were greater than what could be explained by incorrect type determination or sampling error. The variation therefore probably represent real differences among population units.

ACKNOWLEDGEMENT

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BALANUS BALANOIDES (L.) ON THE ATLANTIC COAST
OF FRANCE: FURTHER OBSERVATIONS ON THE
SMALL ISOLATED POPULATION AT THE SOUTHERN
LIMIT OF ITS DISTRIBUTION AT ARCACHON

By

HAROLD BARNES and MARGARET BARNES

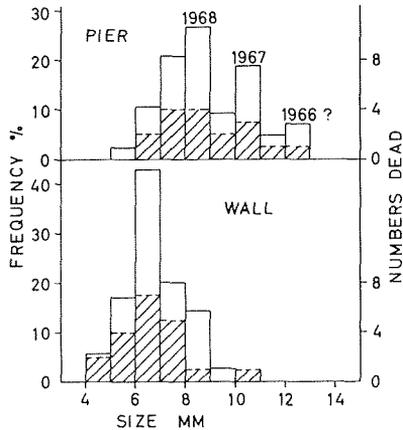
The Dunstaffnage Marine Research Laboratory, Oban, Scotland and
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The behaviour of an animal near the limits of its distribution is always of considerable ecological interest. On western European coasts *Balanus balanoides* (L.) is one of the most common components of the littoral fauna of rocky and relatively open coasts (for a summary of the literature see BARNES 1957a, 1958, BARNES and BARNES 1962). In its distribution and behaviour it may be regarded as a typical boreo-arctic species, characteristics typical of a northern species accompanying it to the southern limits of its distribution (BARNES 1957b). It is present in quantity on the eastern Channel coast of France although much less abundant in the western channel; there seems, however, to have been an increase in population density in the western region during the past ten years (BARNES and BARNES 1966). On the French Atlantic coast it is fairly common, although somewhat unevenly distributed, with the southern limit in quantity at La Rochelle. There is then a complete break in the distribution with a reappearance in moderate quantity in north-western Spain, in the Asturias and Galicia. Some details of competition at Pornic, near to the southern limit, with the warm-temperate littoral *Chthamalus stellatus* have recently been given and an account of the effect of abnormal temperatures (BARNES and BARNES 1968).

BARNES and POWELL (1966, *q.v.* for a discussion of the validity of some older records) have drawn attention to a small "isolated" population south of La Rochelle at Arcachon. Very small numbers were originally (in 1963) recorded on a concrete wall—one of the very few suitable areas

Contribution given in honour of Gunnar Rollefsen at his 70th birthday.

Fig. 1. *Balanus balanoides* at Arcachon; size (basal diameter)- frequency (%) distribution of animals in two localities, with estimated year classes on the pier; hatched area, size frequency (actual numbers) of empty shells.



in this locality—between the Jetée Anglais and the Jetée de la Chapelle; subsequently (in 1964) a few individuals were found on stakes from the Bassin itself. The animals on the wall were recorded as too far apart to breed and were estimated to be one year old; all were present under well-developed *Fucus vesiculosus* at about M.T.L.; by 1967 this population had markedly increased (BARNES and BARNES 1968). Those on the stakes appeared to represent two year classes and consisted of a small group of animals, all of which had well-developed egg masses.

Further observations on the “wall” population—the total lateral extent of which is about 1.0 km—are now recorded. The basal diameters of all the animals, living and dead (empty shells), found during a thirty-minute survey of both the wall and the piles of the Jetée Legallais were recorded. On the wall 35% of the population was dead, on the piles only 17%. The size distribution of each population is shown in Fig. 1. The wall population has a well-marked peak at a diameter of 6.0–7.0 mm which may be confidently assigned to the settlement of the spring of 1968; no further year classes can be recognized but a skewness to the right suggests the admixture of small numbers of an older year class; individuals larger than 10.0 mm were not found and all the evidence suggests that on the wall animals do not live beyond two years. On the piles the first year class is represented by the 8.0–9.0 mm size group; a peak at 10.0–11.0 (1967 spat) and possibly an earlier settlement can be recognized. Almost 30% of the pile population had a size greater than 10.0 mm and empty shells up to 14.0 mm were found. It seems clear that both survival and growth are better on the piles; this may be due to greater protection from high summer temperatures which would be inimical to an essentially boreo-arctic species.

The original records were for the wall; on that occasion the piles were

not examined carefully since at that time Mr. H. T. POWELL's interest centred largely on the occurrence of *Fucus serratus* which is restricted to the wall. It seems possible that the piles were first colonized. The density is now sufficient to give an expanding but still very local population some of which settles on the nearby wall annually, and there lives only for about one year. In view of the distance from La Rochelle it is very unlikely that planktonic larvae are brought into the Bassin each year—even though this (or a vector from the same place) was responsible for the original colonization.

SUMMARY

Balanus balanoides is present as a small, isolated and even locally restricted population on the west coast of France at Arcachon. Observations of the past few years indicate an increase in numbers. Growth and survival are best in shaded places—possibly due to these affording some protection from high summer temperatures.

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NOTES ON GREENLAND HALIBUT, *REINHARDTIUS HIPPOGLOSSOIDES* (WALBAUM), IN THE EASTERN NORWEGIAN SEA

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DISTRIBUTION

Very little is known about the distribution and development of Greenland halibut, *Reinhardtius hippoglossoides* Walbaum 1792, in the Norwegian Sea and the Barents Sea. In the eastern Norwegian Sea the mature stock is distributed from the Norwegian coast along the slope of the continental shelf northwards W of Bear Island to Spitsbergen. Lower abundance is found off the coast of South Norway, and in the southern part of the Barents Sea eastwards to the Kanin Peninsula and the SW coast of Novaya Zemlya and at the coasts of Spitsbergen (Fig. 1). The species is rarely found in the Norwegian fjords. Greenland halibut is also distributed in the southern part of the Norwegian Sea between the Faroes past E and N of Iceland and the SE coast of Greenland.

In the fjords and along the coast of West Spitsbergen Greenland halibut was not very common in the first half of this century (HOGNESTAD

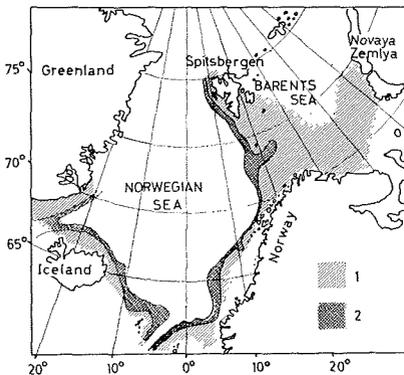


Fig. 1. 1 and 2. The distribution of Greenland halibut in the Norwegian Sea and the Barents Sea. 2. The area between 400 and 1000 m depth along the slope of the continental shelf.

1961), but later the abundance of young age groups seems to have increased considerably. The species was found in this area in 1946 and 1947 (DEVOLD pers. comm.), and in 1958 young age groups seemed to be quite common in the fjords (HOGNESTAD 1961). In recent years it has been frequently found in Spitsbergen waters. Young age groups (0-4) have not been found in other parts of the Barents Sea (ANDRIYASHEV 1954) nor along the Norwegian coast. Very little is known about spawning and development in this area, but some observations were made in 1964 and 1965 (SOROKIN 1967).

An increasing Norwegian fishery is taking place in the eastern part of the Norwegian Sea from February to September at depths between 400 and 800 m. The fishing grounds are located along the slope of the continental shelf from off the coast of North Norway to off the coast of Spitsbergen. In the W-E direction they are located in a relatively narrow band due to the depth conditions along the slope (Fig. 1). Similar conditions are found along the slope of the continental shelf N of Iceland (KONSTANTINOV 1968). Judging from the locations of the fishery from time to time, it seems that mature Greenland halibut migrate slowly from the area outside North Norway to the waters W of Bear Island and Spitsbergen from February to July. From the same area some migration takes place eastwards to the southern Barents Sea in the same period (SOROKIN 1967) but this is probably mainly the immature part of the stock.

OBSERVATIONS ON O- AND I-GROUP GREENLAND HALIBUT

Bottom-trawling was carried out with R/V *Asterias* during the summers of 1958 and 1960 on the banks and in the fjords of West Spitsbergen both along the W and N coasts. Juvenile Greenland halibut were found in the fjords at depths varying from 190-300 m, and in temperatures between

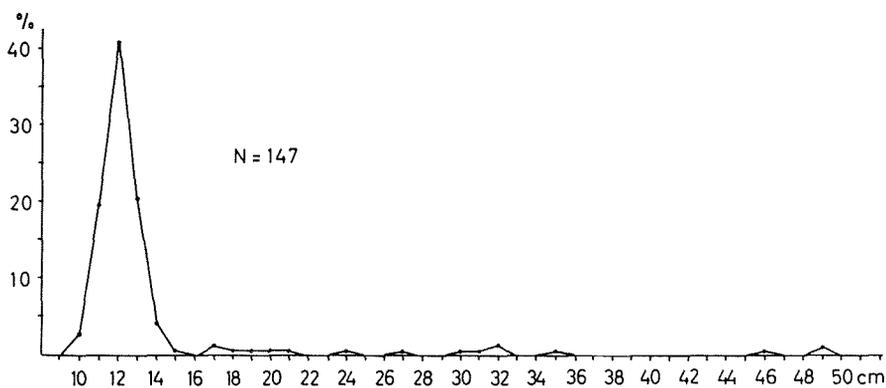


Fig. 2. The length distribution of Greenland halibut from the fjords of West Spitsbergen 1958.

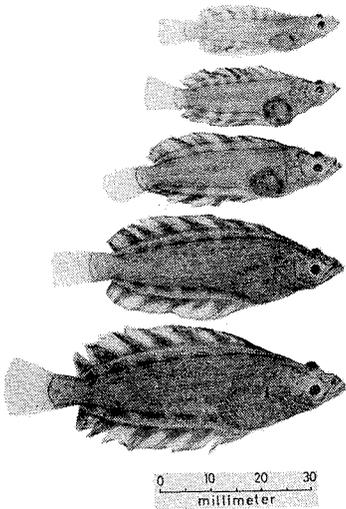


Fig. 3. O-group Greenland halibut of 36, 40, 47, 58 and 67 mm length from the Woodfjord, Spitsbergen, 10 August 1960.

1–2°C. Weak echo-recordings were made of a layer which consisted of planktonic organisms together with larvae of Greenland halibut, Long Rough Dab and Cottidae.

In 1966 a few O-group Greenland halibut were caught in early September with pelagic trawl at 25–35 m depth at almost 79°N, off the coast of West Spitsbergen (Fig. 4). In August–September 1968 some O-group Greenland halibut were taken with pelagic trawl both along the W coast of Spitsbergen and between Bear Island and Spitsbergen (Fig. 4). The catches were made at 10–50 m depth in temperatures from 0°–2°C. The highest abundance was recorded at approx. 78°N (Sentinellaflaket). The length distribution (Fig. 5) varied from 33–69 mm (mean 45.7 mm). The recordings in 1966 and 1968 were made during the combined

–0.7° and 1.3°C, mainly around 0°C. The size distribution varied between 10 and 50 cm, but generally more than 90% of the catches consisted of fish of 10–15 cm length (HOGNESTAD 1961, Fig. 2).

In August 1960 some O-group Greenland halibut of 36–67 mm length (mean 49.6 mm) (Fig. 3) were caught with mid-water trawl in Woodfjord on the N coast of Spitsbergen at 60–80 m depth (Fig. 4). Larvae of 36–40 mm length had not completed their metamorphosis, but showed signs of the imminent turning of the head. The larvae were half transparent, and their intestines were filled with red-coloured food, mainly small unidentified crustaceans. The temperature of the water layer where the larvae occurred varied from

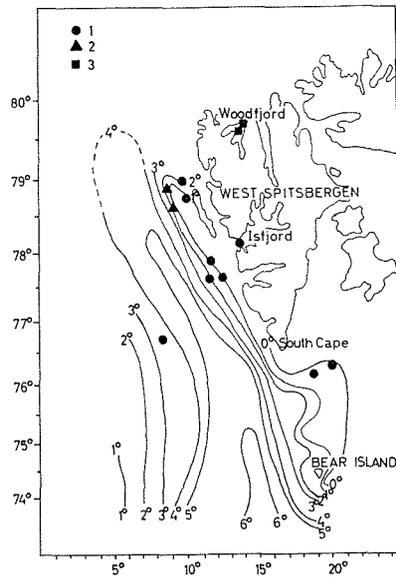
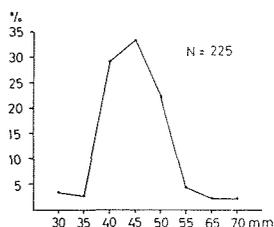


Fig. 4. Catch localities of O-group Greenland halibut in (1) 1968, (2) 1966 and (3) 1960. Isotherms at 50 m depth in early September 1968.

Fig. 5. The length distribution of O-group Greenland halibut from the Spitsbergen area August–September 1968.

English–Russian–Norwegian O-group fish survey in the Barents Sea. The above-mentioned observations of O-group Greenland halibut are the only ones known so far in the Barents Sea area.



DISCUSSION

The spawning and development of the Greenland halibut are described from West Greenland (JENSEN 1935). In these waters spawning takes place at 600–1000 m depth in temperatures between 3.5° and 4°C and a salinity of 34.5‰. Assuming that the Greenland halibut require the same hydrographical conditions for spawning in the Barents Sea area, which means temperatures between 2° and 4°C, one can to some extent locate the spawning grounds in this area.

According to ANDRIYASHEV (1954) Greenland halibut migrate to 800–1200 m depth for spawning. At the eastern parts of the Norwegian Sea these depths are only found along the slope of the continental shelf from the Norwegian coast northwards to W of Spitsbergen. Along this slope the temperature as a rule decreases to 0°C at 800–1000 m depth (HELLAND-HANSEN and NANSEN 1909). This has also been shown by several observations during recent years. In the same area the 2°C isotherm is located at 600–800 m, but W of Bear Island it can be found at 300–400 m (MORK 1968). The temperature range 2°–4°C is thus generally found at 300–800 m depth along the slope from the coast of Norway to West Spitsbergen.

The finds of O-group Greenland halibut indicate that spawning must take place along the slope of the continental shelf between North Norway and Spitsbergen, and recent Russian investigations also seem to confirm this (SOROKIN 1967). Judging from the locations of the temperature range 2°–4°C in this area, it is most likely that spawning takes place no deeper than 800 m.

The time of spawning in West Greenland waters is from April to June (JENSEN 1935). In the eastern Norwegian Sea area it is supposed to take place from March or April to July (MILINSKY 1944, ANDRIYASHEV 1954). The size of the O-group fish observed in August–September indicate that the main spawning takes place in April–June, but Soviet scientists have observed considerable spawning in November–December in the same area (NIZOVTSSEV pers. comm.).

Off West Greenland larvae with yolk sac of 10–18 mm length are found at 600–1000 m depth. Larvae longer than 16 mm are found near

the surface and near land. The larvae are still bilateral symmetrical at a size of 54–57 mm. In August–September the larvae reach the length of 60–70 mm at which size the pelagical period ends and the larvae seek bottom life. At the same time pigmentation on the blind side disappears, and does not appear again until the fish reaches about 15 cm (JENSEN 1935).

In the Barents Sea area young Greenland halibut (age groups 0 and 1) have been found in Spitsbergen waters only (HOGNESTAD 1961, Fig. 4), and the development seems to be similar to that in Greenland waters. In Spitsbergen waters, however, the movement of the left eye probably starts before the larvae reach a length of 35 mm and is found to be completed on larvae of 60 mm length compared with 85 mm in Greenland waters. In both areas the larvae seem to reach the maximum pelagical size in August–September, but the metamorphosis is completed before the larvae seek bottom. The observations of the pigmentation are the same in Spitsbergen and West Greenland waters.

The smallest larvae hitherto found in the investigated area is 33 mm, and the reason for the lack of smaller sizes is certainly that investigations have not been carried out in the deep layers where Greenland halibut are supposed to spawn. The only area where I-group fish have been found is in inshore Spitsbergen waters. This indicates that the nursery grounds are located here, and a southwards migration takes place later on.

The main spawning grounds must be located along the slope of the continental shelf between 70°N and 75°N at 400–800 m depth, judging both from the distribution of the O-group fish and the hydrographical conditions. If spawning took place further to the S, O-group fish should have been observed in the Barents Sea as well according to the prevailing currents.

SUMMARY

The distribution of *Reinhardtius hippoglossoides* (Walbaum), Greenland halibut, in the Norwegian Sea is described with special reference to the distribution in the eastern part of the area.

The only records of O- and I-group Greenland halibut in this area are made in Spitsbergen waters.

The distribution of O- and I-group fish together with the hydrographical conditions along the slope of the continental shelf between Norway and Spitsbergen lead to the conclusion that the main spawning area of Greenland halibut must be along the slope between 70°N and 75°N in April–June at depths between 400 and 800 m.

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THE SCIENTIFIC NAME, DISTRIBUTION AND
CHARACTERISTICS OF THE BLUE LING,
MOLVA DYPTELYGIA (PENNANT), FROM
WEST GREENLAND AND NEWFOUNDLAND AREAS

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INTRODUCTION

Morphometric characteristics have been described previously for only one blue ling from the western Atlantic (TEMPLEMAN and SQUIRES 1962) and meristic characteristics for only four, and two of these were described as *Molva molva* (L.) by JENSEN (1948). Hence more morphological and meristic data are needed for comparison with specimens from the Northeast Atlantic. Data for three new specimens are presented (Tables 1, 2). Unless otherwise noted, morphometric and meristic data were obtained by the methods of HUBBS and LAGLER (1958).

There is, moreover, considerable confusion regarding the scientific name of the blue ling and this subject is discussed and conclusions drawn.

Additional scientific records help to outline the present distribution of the blue ling in the western Atlantic (Figs. 1, 2, Table 3) and an attempt is made to bring order to the statistics of blue ling and ling as reported to ICNAF and to correct some of the major errors in these reports.

SCIENTIFIC NAME OF THE BLUE LING

Neglecting the previous period when even more variations of scientific names were used (see SVETOVIDOV 1948 and FRASER-BRUNNER and PALMER 1951 for lists of these), in recent years two main scientific names, with some variations of spelling, have been used for the blue ling. Some of the references to these names are: *Molva byrkelange* (Walbaum, 1792)

Contribution given in honour of Gunnar Rollefson at his 70th birthday.

by FRASER-BRUNNER and PALMER (1951), KOTTHAUS and KREFFT (1957), RAHARDJO (1961), TEMPLEMAN and SQUIRES (1962), NIELSEN (1963) and NETZEL and STANEK (1966). On the other hand, SVETOVIDOV (1948) and TÅNING (1958) have used *Molva dipterygia* (Pennant, 1784) and KOTTHAUS and KREFFT (1967) *Molva dipterygia* (PENNANT, 1784).

STRØM (1765) in Danish and (1767) for the same paper in German introduced a recognizable description and figure for the blue ling referring to the common name "Byrkelange". The paragraph from STRØM (1767) containing this description is quoted below:

"Dem Lysing (*Gadus Merluccius*) ist er in gewissen Stücken, nämlich in Ansehung des Unterkinnnes, und der Beschaffenheit des Fadens unter der Kehle, zwar am ähnlichsten; hingegen aber ist er von demselben, in Betrachtung der Anzahl der Strahlen in den Finnen oder Flossfedern, und anderer Eigenschaften, so in der Beschreibung von Sundmöer bereits angeführt worden, und daher nicht nöthig hier zu wiederholen, doch zu unterscheiden. Da aber Linnaeus in Syst. Nat. Edit. 10 p. 254, den Lysing *Gadus dipterygius, cirratus, maxilla inferiore longiore* nennt, und diese Beschreibung sich eben sowohl vor den Byrkelange schickt, so kann ich nicht besser unterscheiden, als wenn ich den letztern so nenne: *Gadus dipterygius, cirratus, maxilla inferiore longiore, pinna ani ossiculorum 70.*"

MÜLLER (1776) refers to the blue ling and I quote below three of his entries of which no. 346 refers to the blue ling:

- "345. *G. Mustela dipterygius cirratus cirris quinque, pinna dorsali priore exoleta*. D. *Kroll-Qyabbe, Moer-Qyabbe, N. Rødbrunne Tang-Brosme*.
 346. *G. dipterygius, cirratus, maxilla inferiore longiore, pinnis analibus LXX*. N. *Byrke-Lange* Str. S. 275. Act. nidr. 3, 446 t. 8. Aph. 1, 494.
 347. *G. Aeglefinus tripterygius cirratus albicans, cauda biloba, maxilla superiore longiore*. D. *Kuller N. Kollie, Hyse*. I. *Ise*. Isl. R. 528 t. 26. Aph. 4, 537."

The use of "Byrke-Lange" by MÜLLER is quite definitely as a common name. He lists it in his index of Danish and Norwegian vernacular names.

PENNANT (1784) says: "Among the fishes which have hitherto shunned our shores are the *Raia Clavata*, Müller no. 309; ... *Squalus Spinax*, 312; ... *Chimera Monstrosa*, 320, a most singular fish; ... *Gadus Brosme*, 341; *G. Dypterygius*, or *Byrke-lange*, 346; ...

Thus STRØM (1765, 1767) produced a description, figure, genus, common name and location that are sufficient to recognize the species in comparison with other lings, MÜLLER (1776) quoted STRØM, and PENNANT (1784) gave MÜLLER as his reference.

MÜLLER italicizes his specific but not his generic names and begins his specific names with a capital letter, but his "dipterygius" of *G. dipterygius* is not italicized and does not begin with a capital. It is

evident that the "dipterygius" of STRØM as used in referring to "Byrkelange", the blue ling, is the same word he has used immediately above in his description of the hake (Lysing) and consequently is descriptive, meaning two-finned (dorsal) in the same way that the next word "cirratus" and the phrases following are descriptive.

Similarly in MÜLLER's account "G. *Mustela* dipterygius, G. *Aeglefinus* tripterygius, G. dipterygius", it is evident that the dipterygius (two-finned) and tripterygius (three-finned) are descriptive and that because also it is not italicized nor does the dipterygius begin with a capital, dipterygius is not presented as a species name.

Apart from his slip in naming the blue ling, MÜLLER (1776) is consistently binominal and his names are recognized. PENNANT's (1784, p. 76) fish names are quoted from MÜLLER's binominal list, and in addition the blue ling scientific name is made binominal. It is my conclusion that PENNANT's name can be accepted both on the basis of the rules set down by INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE (1964), Article 11C, and on the basis also that PENNANT's reference to MÜLLER fulfils the requirements of Article 16(a) as a valid indication.

Since the word dipterygius as used by STRØM (1765, 1767) and MÜLLER (1776) is descriptive and not specific, PENNANT (1884), who first set up the name as a scientific name *Gadus Dypterygius*, was perfectly at liberty to use the species term *Dypterygius* instead of the descriptive word dipterygius. FLEMING (1828, p. 192) introduced the genus *Molva* (type *Gadus molva* L.) for the ling group. I conclude, therefore, that the scientific name of the blue ling is *Molva dypterygia* (Pennant, 1784).

MORPHOMETRIC AND MERISTIC CHARACTERS

The morphometric and meristic characters of the north-west Atlantic specimens (Tables 1, 2) are usually within or occasionally overlapping the range of *Molva dypterygia* from the north-east Atlantic. (Compare SVETOVIDOV 1948, FRASER-BRUNNER and PALMER 1951, TEMPLEMAN and SQUIRES 1962, RAHARDJO 1961, NIELSEN 1963, allowing for the fact that SVETOVIDOV's and NIELSEN's body proportions of this species are based on the total length. See later.) The pelvic fin ending anterior to the posterior end of the pectoral separates them from *M. macrophthalmia* (Rafinesque). The ratios of the length of the 1st dorsal base in 2nd dorsal base (6.5-7.4) are intermediate between and separate from those of *M. molva* (3.5-4.5) and *M. macrophthalmia* (9.2-11.0) but are included in the range of this ratio for *M. dypterygia* of the north-east Atlantic (5.3-7.5).

The least height of the caudal peduncle is similar to that of *M. dypterygia* of the north-east Atlantic and lower than that of *M. molva*.

Table 1. Morphometric characteristics of the blue ling, *Molva dypterygia*, from the north-west Atlantic. (S.L. = standard length, H.L. = head length. Otherwise all percentages are of standard length. Apart from the total length occasionally measured fresh at sea, all other measurements were taken in the condition on examination, item No. 43.)

Item	Body character	No. 1 Dana Bank, W Greenland, 17 Aug. 1965	No. 2 Fylla Bank, W Greenland, 14 Aug. 1965	No. 3 Hermitage Bay, Nfld., 17 Sept. 1959. TEMPLEMAN and SQUIRES (1962)	No. 4 SE slope Grand Bank, 24 Nov. 1964
1	Total length: sea, fresh, mm ¹	777.0	858.0	1150.0	—
2	Total length: shore, mm ¹	—	847.0	1121.0	1241.0
3	Standard length: snout—end hypural, mm	723.0	783.0	1047.0	1152.0
4	Head length: snout—end bony operculum, mm	147.2	160.0	235.0	250.8
5	Head length: snout—end bony operculum, %	20.4	20.4	22.4	21.8
6	Snout length, % S.L.	6.4	6.6	6.9	7.1
7	Snout length, % H.L.	30.9	32.2	32.1	33.3
8	Orbit: horizontal diameter, % S.L.	5.3	4.5	4.9	4.9
9	Orbit: horizontal diameter, % H.L.	25.8	22.1	21.7	22.4
10	Orbit: vertical diameter, % S.L.	4.1	3.5	4.3	4.1
11	Orbit: vertical diameter, % H.L.	20.4	17.0	19.1	19.0
12	Cornea: horizontal diameter, % S.L.	3.7	3.6	ca. 3.4	4.2
13	Cornea: horizontal diameter, % H.L.	18.3	17.5	ca. 15.3	19.3
14	Interorbital: width, least fleshy, % S.L.	2.8	2.6	2.8	—
15	Interorbital: width, least fleshy, % H.L.	13.8	12.5	12.3	—
16	Interorbital: width, least bony, % S.L.	1.7	1.6	2.0	1.9
17	Interorbital: width, least bony, % H.L.	8.2	7.9	8.9	8.6
18	Post-orbital length: to end bony operculum, % S.L.	9.2	9.3	9.2	9.2

¹ Anterior tip lower jaw, with mouth closed, to post. end of caudal fin.

Table 1 (continued).

Item	Body character	No. 1 Dana Bank, W Greenland, 17 Aug. 1965	No. 2 Fylla Bank, W Greenland, 14 Aug. 1965	No. 3 Hermitage Bay, Nfld., 17 Sept. 1959. TEMPLEMAN and SQUIRES (1962)	No. 4 SE slope Grand Bank, 24 Nov. 1964
19	Post-orbital length: to end bony operculum, % H.L.	44.7	45.4	42.6	43.1
20	Lower jaw: protrusion beyond upper, % S.L.	0.7	0.6	0.5	0.9
21	Lower jaw: protrusion beyond upper, % H.L.	3.4	2.8	2.1	4.0
22	Barbel: length, % S.L.	1.9	2.2	0 ²	3
23	Barbel: length, % H.L.	9.5	10.8	0 ²	3
24	Body: greatest height, %	12.1	12.3	ca. 10.9	18.7
25	Caudal peduncle: least height, %	2.6	3.0	—	2.6
26	Snout—ant. base 1st dorsal, %	27.7	28.8	28.7	29.4
27	Snout—ant. base anal, %	45.2	46.0	47.5	48.8
28	1st dorsal base: length, %	7.5	7.9	7.8	8.2
29	2nd dorsal base: length, %	55.5	55.4	51.7	52.8
30	1st dorsal: greatest height, % ⁴	7.9	8.4	8.4	7.6
31	2nd dorsal: greatest height, % ⁴	5.7	6.1	6.1	5.7
32	Tip pelvic anterior to vertical from posterior end pectoral, %	3.7	4.1	5.6	6.5
33	Interorbital width, least fleshy, in length of head	7.3	8.0	8.1	—
34	First dorsal base in 2nd dorsal	7.4	7.1	6.6	6.5

² Absent, only a stub present.

³ Unsuitable for measurement.

⁴ Longest fin ray.

Table 1 (continued).

Item	Body character	No. 1 Dana Bank, W Greenland, 17 Aug. 1965	No. 2 Fylla Bank, W Greenland, 14 Aug. 1965	No. 3 Hermitage Bay, Nfld., 17 Sept. 1959. TEMPLEMAN and SQUIRES (1962)	No. 4 SE slope Grand Bank, 24 Nov. 1964
35	Height 2nd dorsal in height 1st dorsal	1.4	1.4	1.4	1.3
36	Sex	♀	♀	♀	♀
37	Sexual maturity	Imm.	Imm.	Mat. (spent)	Mat.
38	Ovary weight, kg	—	—	—	0.94
39	Egg diameter, mm	5	5	—	0.5
40	Round weight, sea, kg	1.41	2.36	—	—
41	Round weight on examination, kg	1.36 ⁶	2.18	3.8	9.9
42	Gutted and gilled weight, after examination, kg	—	1.96	—	7.1
43	Condition on examination	Excellent, measured fresh 1-1½ hr after capture	Good, fresh after freezing on ship and thawing in ice	Good, ex 10% formalin	Good, fresh after freezing on ship and thawing in ice

⁵ Eggs not visible to naked eye.

⁶ Weight on shore after freezing on ship, and thawing in ice on shore.

Table 2. Meristic characters of the blue ling, *Molva dypterygia*, from the north-west Atlantic.

Body character	1	2	3	4	5 ¹	6 ²	7 ³
1st dorsal rays, No.	12	13	12	13	13	14	12
2nd dorsal rays, No. ⁴	76	77	73	78	76	78	72
Anal rays, No. ⁴	74	76	68	74	73	74	69
Pectoral rays, No.	19	20	20	21	19	20	18, 20
Pelvic rays, No.	6	6	6	6	6	7	7, 6
Vertebrae, No.	79 ⁵	78 ⁵	77 ⁵	79 ⁵	—	77	75

1-4, author, from St. John's Station specimens. Numbers from Table 1.

¹ Off S Labrador, February 1965 (NETZEL and STANEK 1966).

² Off outermost islands near Narssalik, Frederikshaab District, SW Greenland, September 1928 (JENSEN 1948).

³ Near Narssak, Julianchaab District, SW Greenland, 1939 (JENSEN 1948).

⁴ In my counts all rays counted, i.e. last two rays counted as two.

⁵ Including urostylar half-vertebra as one vertebra.

The relative head length (20.4-22.4 S.L.), the predorsal length (27.7-29.4 S.L.), and the preanal length (45.2-48.8 S.L.) of the four western Atlantic blue ling are considerably greater than those of blue ling from the eastern Atlantic in NIELSEN (1963). These measurements of NIELSEN attributed to standard length, are, however, taken from SVETOVIDOV (1948) and are based on total length. When SVETOVIDOV's measurements are adjusted upward for a standard length of 92.9% of total length (average of the four western Atlantic specimens in Table 1) the relative length ranges for the eastern Atlantic specimens become: for the head length (18.5-19.0 S.L.), for the predorsal length (25.5-27.2 S.L.), and for the preanal (40.8-47.6 S.L.). These eastern Atlantic ranges are close to or overlapping with those of the western Atlantic but the head and the predorsal (a large part of which is the head) measurements are still somewhat greater for the western Atlantic. SVETOVIDOV's ranges are presumably for blue ling from the north-eastern Atlantic and the western Atlantic blue ling are presumably related to those of Iceland. Icelandic blue ling have higher meristic counts than those of northern Norway (RAHARDJO 1961) suggesting lower temperatures and the possibility of slower growth rate and consequently a larger head at Iceland than in northern Norway.

In meristic characters, the number of 1st dorsal rays (12-14) is within the range of *M. dypterygia* of the eastern Atlantic (11-15), higher than that of *M. macrophthalmalma* (10-11, rarely 12) and lower than that of *M. molva* (13-16). The number of 2nd dorsal rays (72-78) is within the range of the eastern Atlantic *M. dypterygia* (69-83) and of *M. macrophthalmalma*

(74–82) but higher than that of *M. molva* (57–70). Anal ray count (68–76) is within the range of eastern Atlantic *M. dypterygia* (62–81) and that of *M. macrophthalma* (70–79) and higher than that of *M. molva* (55–67).

Vertebral number (75–79) is within the range of eastern Atlantic *M. dypterygia* (72–79), but higher than that of *M. molva* (62–67) and below that of *M. macrophthalma* (80–84). The number of pectoral rays (18–21) overlaps with that of *M. dypterygia* from the eastern Atlantic (18–20), is the same as that of *M. molva* and is higher than that of *M. macrophthalma* (15–18).

The meristic counts of the western Atlantic blue ling are high on the average and, apart from those of the 1st dorsal, are higher than the Icelandic averages which in turn are higher than those for the north-east Atlantic (RAHARDJO 1961).

DISTRIBUTION

Records from scientists, and research and exploratory vessels

These records (Fig. 1, 2, Table 3) show a distribution of the blue ling from 66° 32' N, ICNAF (International Commission for the Northwest Atlantic Fisheries) Division 1B, southward along the west coast of Greenland to ca. 60° 56' N, Division 1F (see Fig. 2 for ICNAF area, Subareas 1–5 and divisions). There are no records for the Labrador subarea, ICNAF Subarea 2, three records from Subarea 3 and none south of this point, the most southerly record being at 43° 35' N, Division 3N.

These records represent all the published and unpublished records of blue ling from the Canadian and West German research vessels.

A few of these are documented for meristic and morphometric characteristics (Table 1). Also, the blue ling is so different in appearance from the common ling that no errors in separation should be made by scientists and the European scientists are familiar with both species. Only one specimen of the common ling, *Molva molva*, has been reported in published records from the western Atlantic (from Subarea 3, TEMPLEMAN and FLEMING 1954). Also, Mr. ERLING BRATBERG (letter, 13 March 1969) says that he observed one common ling caught by a Norwegian research vessel on bottom longline in West Greenland waters several years ago, but that no other data are available regarding this capture. He also says that blue ling have not been observed on Norwegian research vessel cruises to the ICNAF area.

The two ling from West Greenland, reported by JENSEN (1948) as the common ling, *Molva molva*, were actually blue ling, *Molva dypterygia* (TÅNING 1958; Table 2). Canadian fisheries research vessels which have fished in all ICNAF subareas and for twenty years in Subareas 2–4 and

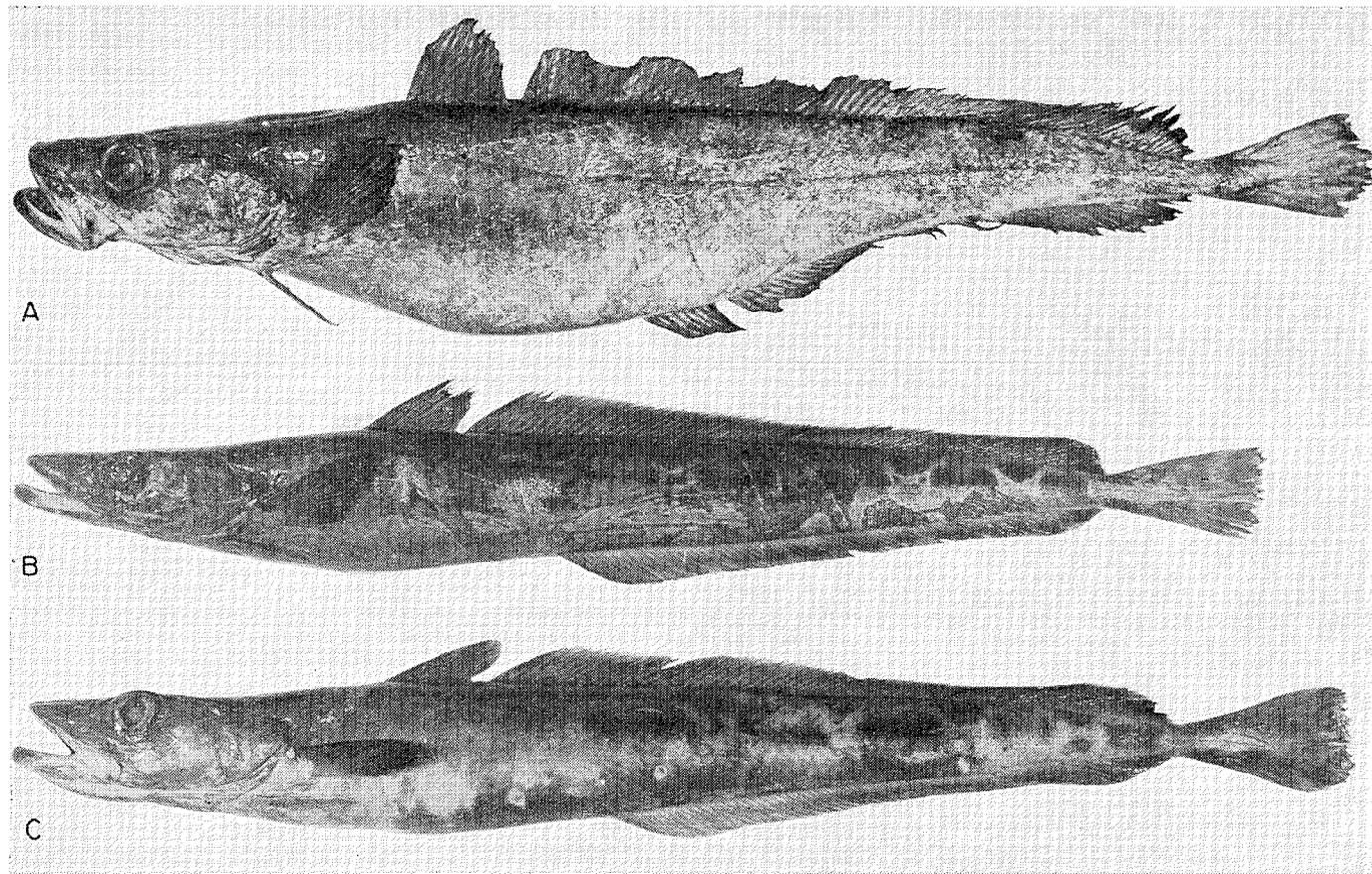


Fig. 1. Blue ling, *Molva dypterygia*: A, 1241 mm in total length, from the SE slope of the Grand Bank, November 1964, Table 1, No. 4, B, 858 mm in total length, from Fylla Bank, W Greenland, August 1965, Table 1, No. 2; C, 777 mm in total length, from Dana Bank; W Greenland, August 1965, Table 1, No. 1.

Table 3. Records of the blue ling, *Molva dypterygia*, from scientists and research vessels in the ICNAF area.

ICNAF div.	Year	Month	Position		Depth (m)	Bottom temp. (C)	No. fish	Length (cm)	Observer or reporter, ship, etc.
			N lat.	W long.					
1B	1967	27 Oct.	66° 32'	56° 25'	285-300	3.8	2	79, 86	Walther Herwig, J. MESS-TORFF.
1C	1955	28 Sept.	65° 05'	54° 45'	250-300	—	1	77 ♂	KOTTHAUS and KREFFT (1957). Anton Dohrn, A. MEYER.
1C	1965	25 July	64° 42'	54° 33'	260	4.6	1	1	Anton Dohrn, H. H. REINSCH.
1C	1965	25 July	64° 37'	54° 28'	260	4.6	6	—	Anton Dohrn, H. H. REINSCH.
1C	1965	25 July	64° 30'	54° 25'	260	—	1	—	Anton Dohrn, H. H. REINSCH.
1C	1965	24 July	64° 18'	54° 08'	220	4.6	1	—	Anton Dohrn, H. H. REINSCH.
1D	1959	3 Jan.	64° 10'	53° 33'	270	—	1	—	Trawler <i>Island</i> , explor. cruise, H. KOOPS.
1D	1965	14 Aug.	63° 34'	53° 00'	455-485	5.61	2	86, ca. 115 ¹	A. T. Cameron, longline, author.
1D	1965	17 Aug.	62° 45'	51° 50'	385-395	5.3	1	78	A. T. Cameron, longline, author.
1D	1967	2 Nov.	62° 58'	52° 14'	300-315	5.1	6	70-90	Walther Herwig, J. MESS-TORFF.
1D, 1E	1959	30 Apr.- 15 May	ca. 62°	ca. 51°	—	—	ca. 50	—	JOENSEN (1960). Faroese otter trawler <i>Skalaberg</i> with research personnel on board.
1E	1928	Sept.	ca. 61° 38'	ca. 49° 25'	0	—	1	108	JENSEN (1948). Reported as <i>Molva molva</i> .

¹ Floated away from close to ship. Observed by author.

Table 3 (continued).

ICNAF div.	Year	Month	Position		Depth (m)	Bottom temp. (C)	No. fish	Length (cm)	Observer or reporter, ship, etc.
			N lat.	W long.					
1F	1939		ca. 60° 56'	ca. 46° 04'	—	—	1	133	JENSEN (1948). Reported as <i>Molva molva</i> .
3K	1965	5 Feb.	52° 10'	55° 00'	236-260	—	1	99	NETZEL and STANEK (1966). <i>Feniks</i> (Polish factory trawler).
3N	1964	24 Nov.	43° 35'	48° 50'	510-550	3.84	1	124	A. T. Cameron, E. J. SANDEMAN.
3Ps	1959	17 Sept.	47° 33'	56° 06'	240	—	1	115	Nfld. otter trawler <i>Pennyworth</i> .

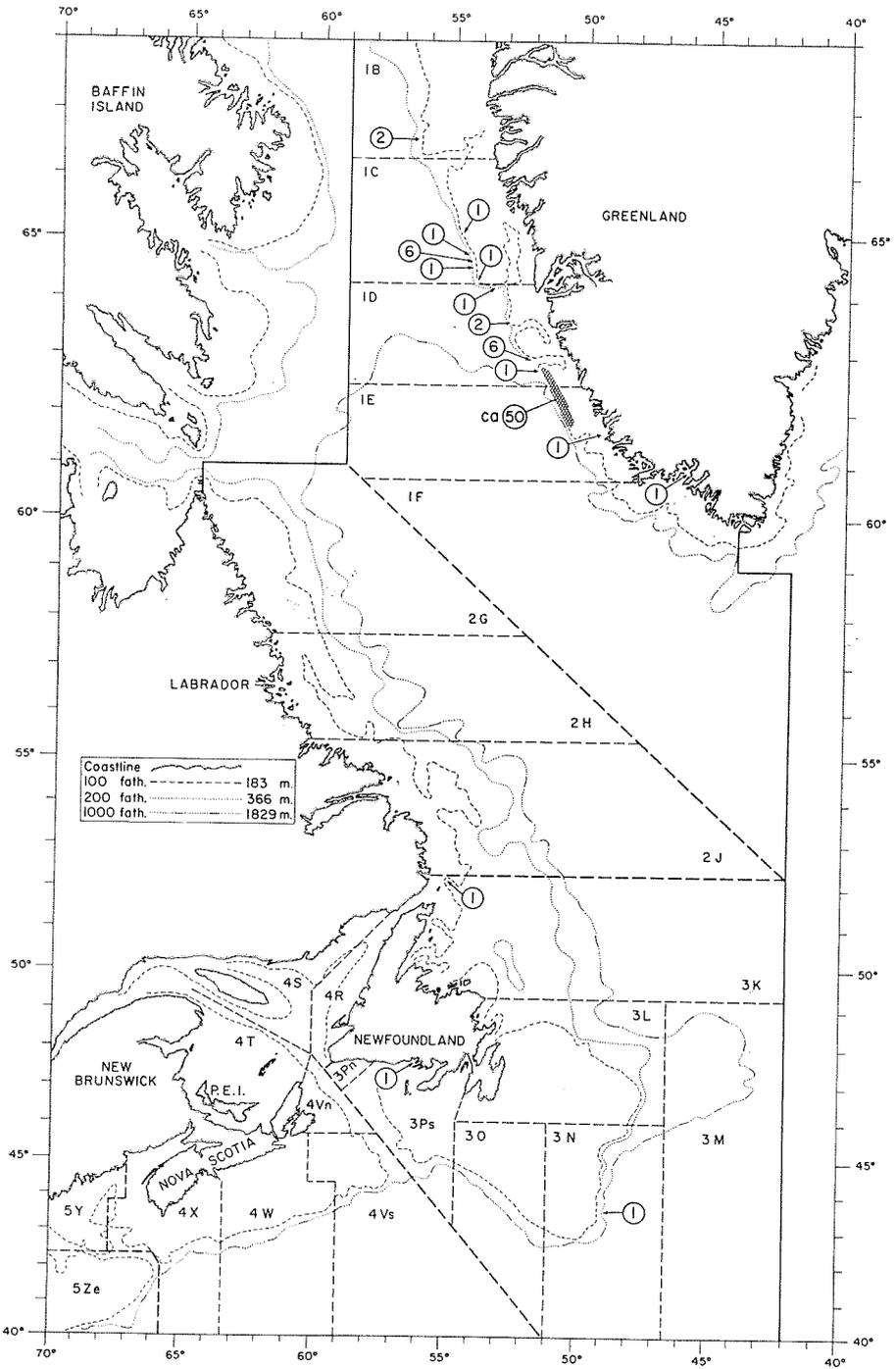


Fig. 2. Distribution of the blue ling, *Molva dypterygia*, as recorded from the ICNAF area by scientists.

for over half this period down to 730 m have never caught a common ling. Dr. J. MESSTORFF has informed me (June 1968) that research vessels of the Federal Republic of Germany have never caught a common ling in the ICNAF area although a number of blue ling were captured (Table 3).

SEREBRYAKOV (1965) reported four eggs of *Molva molva* from the Scotian Shelf portion of Subarea 4 from Soviet ichthyoplankton collections in 1959–1962. I am not certain whether or not eggs of blue ling can be distinguished from eggs of common ling and if so at what stages.

The blue ling are usually reported from deep water, 220–485 m, in West Greenland and 236–550 m in the Newfoundland area but one of the West Greenland fish reported by JENSEN (1948) was harpooned at the surface near shore. Temperatures for the deep water catches were between 3.8 and 5.6 C (Table 3).

Although only the blue ling in Table 3 have been reported by scientists, and only the smaller number of Tables 1 and 2 further authenticated by morphometric and meristic characters, much larger quantities of ling and blue ling have been reported in commercial statistics from the ICNAF area.

The ICNAF Statistical Bulletins, 1955–1967, indicate (Table 4) small commercial landings of ling, *M. molva*, usually from Subarea 1 (West Greenland) but also from Subarea 2 (Labrador) and Subarea 3 (the Newfoundland area).

At my request, Dr. B. J. KOWALEWSKI of ICNAF has supplied the ling catch records in all the national submissions of fisheries statistics to ICNAF

Table 4. Landings of ling (metric tons) from ICNAF subareas (as published in ICNAF Statistical Bulletins after screening out probable errors.

Ling always defined in ICNAF list of species as *Molva molva* (L.)).

Year	ICNAF Subareas					Total 1-5
	1	2	3	4	5	
1954	2	0	0	0	0	2
1955	18	0	0	0	0	18
1956	2	0	0	0	0	2
1957	6	0	0	0	0	6
1958	0	22	0	0	0	22
1959	0	0	0	0	0	0
1960	5	0	4	0	0	9
1961	3	0	1	0	0	4
1962	1	0	0	0	0	1
1963	4	1	0	0	0	5
1964	0	0	0	0	0	0
1965	0	0	10	0	0	10

since 1952. The result is Table 5 which is not very much different from the published records (Table 4) except for the considerably larger landings in 1964. All the ling except the small amount caught by the Faroese fishermen (which was caught by longline) were taken by otter trawl in redfish, cod or mixed cod and redfish fishing.

There are seventy-four records of ling, *M. dypterygia*, from West Greenland by scientists, and apart from BRATBERG's sight observation of a single specimen, *M. molva* has not been recorded from this area. Although in my cruise in West Greenland in July–August 1965 on the *A. T. Cameron*, three blue ling were taken among the small number of fish caught by longline, in about twenty years of groundfish dragging by the *Investigator II* since 1946 and by the *A. T. Cameron* since 1958, in Subareas 2, 3 and 4 at depths in many cruises to 730 m, no ling have been caught by the *Investigator II* and only one by the *A. T. Cameron*. Ling are thus apparently very rare in Subareas 2 and 3, no records of *M. dypterygia* having been reported by scientists from Subarea 2 and only three specimens from Subarea 3.

The larger landings of 1964 (Table 5) from Subareas 1 to 3 and the small landings from Subarea 4 were all reported by Germany except for three tons by the United Kingdom in Subarea 1. Moreover Germany reported 259 tons as blue ling and the remaining 26 tons as ling. Also the one ton of ling caught by Germany (the remaining five tons were landed by Iceland) in Subarea 1 in 1957 and the two tons caught by Germany in Subarea 1 in 1959 were reported as blue ling. All the remaining catches were reported as ling with no indication of separation into common ling or blue ling except that ling was designated in the ICNAF list of species as *Molva molva* and ling is the European name (in English) for *Molva molva*. Dr. ARNO MEYER, in his letter of 26 February 1968, says that *Molva molva* is always reported in German statistics as ling and *Molva dypterygia* as blue ling.

The 601 tons of ling from Subarea 5 (Gulf of Maine-Georges Bank) in 1964 (Table 5) were reported by Poland and must refer to one or both of the hakes, *Urophycis chuss* or *Urophycis tenuis*. Ling is one of the common names for these hakes in eastern Canada and eastern United States.

After the ICNAF Statistical Bulletin for 1963 (1965) the ling, *Molva molva* (L.), was deleted from the list of common and scientific names used in the Statistical Bulletin.

Although the relatively large quantities of ling caught by Poland in Subarea 5 in 1964 (Table 5) were presumably hake, it is not possible to explain the reported landings of ling from Subareas 2 and 3 in this way. The total landings from Subareas 2 and 3 between 1958 and 1966 are in metric tons from ICNAF Divisions 2G(1), 2H(12), 2J(47), 3K(33),

Table 5. Landings of ling from the ICNAF area (metric tons round fresh. Original data as reported to ICNAF).

Year	ICNAF subareas					Total
	1	2	3	4	5	
1953	Ø (Iceland)	—	—	—	—	Ø
1954	—	—	—	—	—	—
1955	14 (Iceland 14, Germany Ø)	—	—	—	—	14
1956	1 (Germany)	—	—	—	—	1
1957	6 (Iceland 5, Germany 1 ¹)	—	—	—	—	6
1958	—	22 (Germany)	Ø (Germany)	—	—	22
1959	2 (Germany) ²	—	—	—	—	2
1960	5 (UK 1, Germany 1, Iceland 3)	—	4 (Iceland)	—	—	9
1961	3 (Germany)	—	1 (Germany)	—	—	4
1962	1 (UK 1, Germany Ø)	—	—	—	—	1
1963	4 (Germany 3, UK 1)	1 (UK)	—	—	—	5
1964	220 (Germany 217 ³ , UK 3)	37 (Germany) ⁴	28 (Germany) ⁵	Ø (Germany Division 4W) ⁶	601 (Poland)	886
1965	1 (Denmark (Faroes))	—	12 (Iceland 9, Denmark (Faroes) 2, UK 1)	—	—	13
1966	4 (Denmark (Faroes) 2, UK 2)	—	—	—	—	4

¹ Blue ling.

² Blue ling only.

³ Blue ling plus ling—197 tons of blue ling included.

⁴ 35 tons of blue ling included.

⁵ 27 tons of blue ling included.

⁶ Ling plus blue ling.

Ø Magnitude more than zero but less than $\frac{1}{2}$ ton.

3L(1), 3M(5), 3P (less than 0.5) and Subarea 3, Division unknown (6). Thus the reported landings are from Subarea 2 and mainly the northern sections of Subarea 3. Of these ICNAF divisions, only 3P possesses any but rare specimens of hake. The only fish in Subarea 2 at all hake-like and which occurs in modest numbers in the deep water is the small blue hake, *Antimora rostrata*, which is presumably unlikely to be called ling. In any case 52 tons of these ling from Subareas 2 and 3 are reported by Germany in 1964 as blue ling which shows that it is not hake that is being reported.

Dr. ARNO MEYER has written me (26 February 1968) that the German blue ling statistics reported to ICNAF for 1964 are incorrect. These blue ling reported by West-German vessels were caught off East Greenland and were referred to the ICNAF area by wrong assignments of areas when splitting mixed trips, mainly of cod and redfish, which were caught in the different areas on the same trip.

For Subarea 1 (West Greenland), neglecting the incorrect West-German records for 1964, in the years from 1955 to 1966 where records are available for the divisions of Subarea 1, the following total landings of ling (occasionally reported as blue ling) are reported (in metric tons): 1A(0), 1B($<\frac{1}{2}$ ton), 1C(2), 1D(3), 1E(2), 1F(11). If the monthly records of $<\frac{1}{2}$ ton are equated as $\frac{1}{4}$ ton each the landings from these divisions become: 1A(0), 1B($\frac{1}{4}$), 1C($2\frac{1}{4}$), 1D($5\frac{3}{4}$), 1E($3\frac{3}{4}$), 1F(12). It is apparent that most landings come from the southern divisions of Subarea 1 where deep-water fishing is carried out for cod and redfish. Although some of the ling statistics from Subarea 1 may still be incorrect assignments from mixed landings from East and West Greenland, the quantities and locations appear to be reasonable and possible.

It is presumed that all ICNAF landings of blue or common ling reported from Subareas 2 and 3 are falsely assigned in the same way from the landings of vessels which had fished East and West Greenland waters. Some of the very small catches of one to several tons of blue ling in West Greenland are presumably local catches in this area, but there is no certainty that they are always correctly allotted between the divisions of Subarea 1, as assignment of ling, pro rata with landed catches of cod and redfish, may spread the blue ling into more divisions and may also divide some East Greenland blue ling among the West Greenland divisions.

CONCLUSION

From the data presented, it is concluded that, apart from rare specimens, the common ling, *Molva molva*, is not present in the ICNAF area.

The blue ling is scarce but not rare in West Greenland but is rare in areas south of West Greenland, the most southern records being from ICNAF Subarea 3.



SUMMARY

1. A discussion of the various scientific names used for the blue ling leads to the conclusion that the correct name is *Molva dypterygia* (Pennant, 1784).
2. Meristic and morphometric characteristics are provided for two blue ling from West Greenland and one from the Newfoundland area.
3. The morphometric and meristic characters of blue ling from the north-west Atlantic specimens are usually within, overlapping or close to the ranges of these characters for *Molva dypterygia* from the north-east Atlantic.
4. The commercial statistics for ling in the ICNAF area are discussed and attention called to some of the errors.
5. It is concluded that blue ling are present in small numbers in the West Greenland area and rare in the remaining areas, the most southern definite records being from ICNAF Subarea 3.

ACKNOWLEDGEMENTS

I am very grateful to Dr. ARNO MEYER, Dr. J. MESSTORFF and Dr. H. H. REINSCH of the Institut für Seefischerei, Hamburg for providing information on the distribution of the blue ling, to Mr. ERLING BRATBERG of the Fiskeridirektoratets Havforskningsinstitut, Bergen for information on ling catches in the ICNAF area by Norwegian research vessels, and to Mr. E. J. SANDEMAN, scientist-in-charge of the *A. T. Cameron* when the second St. John's Station specimen of the blue ling from Subarea 3 was obtained. I am also grateful to Mr. L. R. DAY and Dr. B. J. KOWALEWSKI of the ICNAF staff at Dartmouth, Nova Scotia, who provided unpublished information on reported catches of ling in the ICNAF area.

I have consulted Mr. G. PALMER of the British Museum, Natural History on the correct scientific name for the blue ling and have benefited much from my correspondence with him on this subject.

Photographs are by Mr. E. L. ROWE.

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THE PLASTIC SEABED “OYSTER” FOR MEASURING BOTTOM CURRENTS

By

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Many of his friends will recall that Gunnar Rollefsen had a genius with simple materials—as witness his achievement in taking a cine-film of cod spawning with simple gear at a time when others possessing expensive apparatus had had but scant success.

The recollection has emboldened the present writer to submit for publication in the volume now honouring Rollefsen’s seventieth birthday, a small paper which deals with the first employment of a device for measuring bottom currents whose very keynote is simplicity. It is not unreasonable to maintain that there are various problems in oceanographical research where a simple and cheap apparatus can have real merit on grounds other than those of economy and simplicity. Sometimes the use of such a device may be the only way of tackling a problem hopefully, and although that to be described does not produce a continuous record but makes only easily-repeatable single observations, these latter can be just what is wanted for certain purposes.

In what follows we shall give an account of a modest tool for investigating seabed currents, without depth limitation. The broad nature of the device can be conveyed at the outset by merely quoting the legend carried on a large diagram from which our present figures have been cut out. The legend in question reads:

“This device is meant to be thrown out anywhere from any kind of ship over any ocean depths. It is designed to sink to bottom to make a single record of bed current speed and direction. Some time later it will rise to surface to travel as does a drift bottle until cast ashore. It carries a multi-language questionnaire paper, the perusal of which should result in the investigator receiving back by post the directional pendulum bearing permanent interpretable grooves.”

Contribution given in honour of Gunnar Rollefsen at his 70th birthday.

Any serious paper dealing with current measuring would of course be expected to make many citations from the nigh-staggering literature which now exists, and any writer on bottom currents would equally be expected to quote from the many papers which give the results of effort spent to measure them. Because there is (not surprisingly!) a real paucity of data on currents right down on the deep ocean bed, and because much of what is known about them has come from photographic studies of their effects of various kinds, we can here justifiably abstain from citations on the grounds that we have attempted a novel approach. We were concerned to produce a device which would not require the possession and operation of deep sea cameras, would involve only very modest expenditure of money, would not call for the availability of a specialist ship, could be used more or less anywhere without any concern at all for weather, and would require no line attachments at all to an attendant ship or to a mooring. Because our aim was to measure actual bed currents there would be no similarity with the well-known seabed drifter.

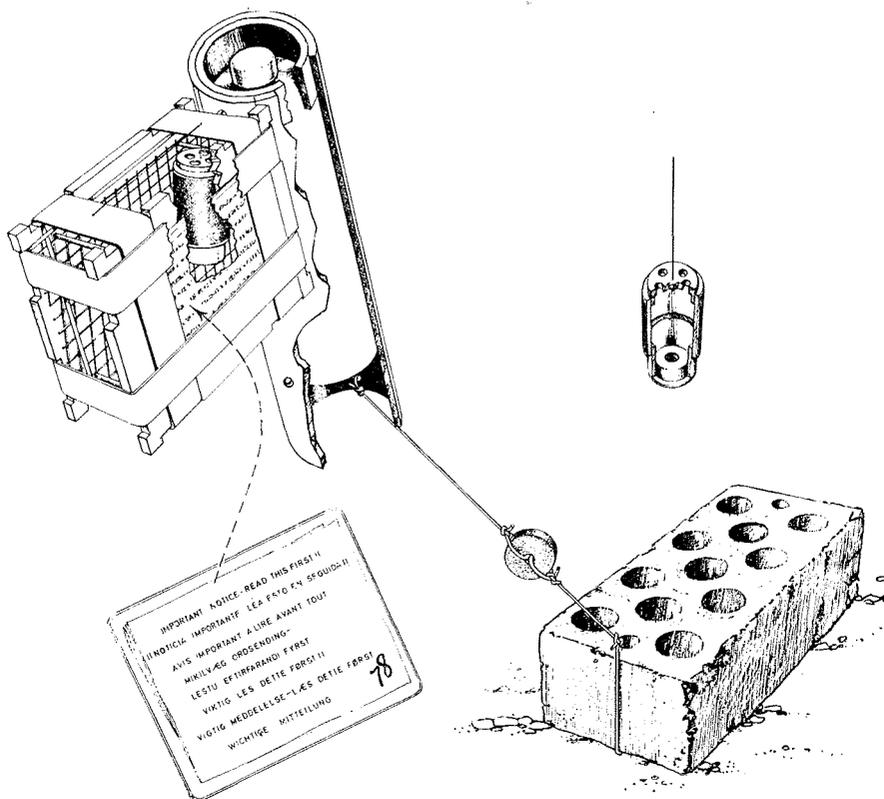


Fig. 1. The construction of the device as described in the text. The suspended directional pendulum is shown (in section) — as also is the come-loose tether to the brick.

Fig. 2. The device in operating situation on the seabed (below), and the way in which the grooves-slope is easily determined (above).

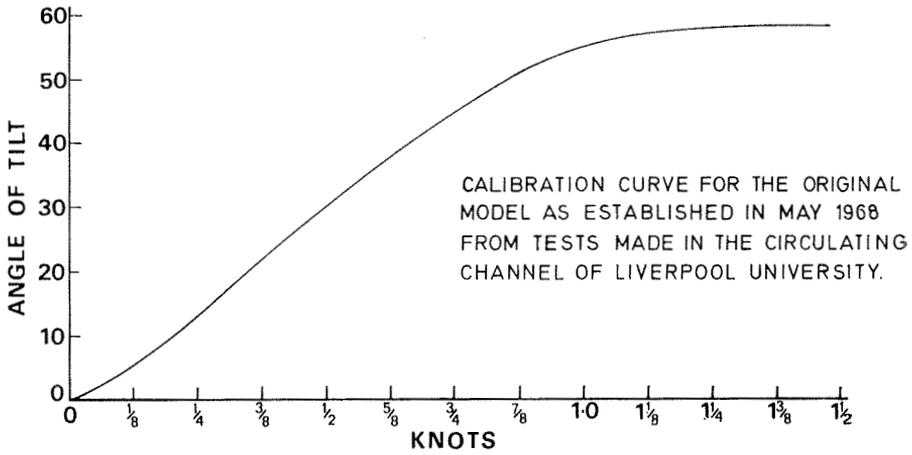
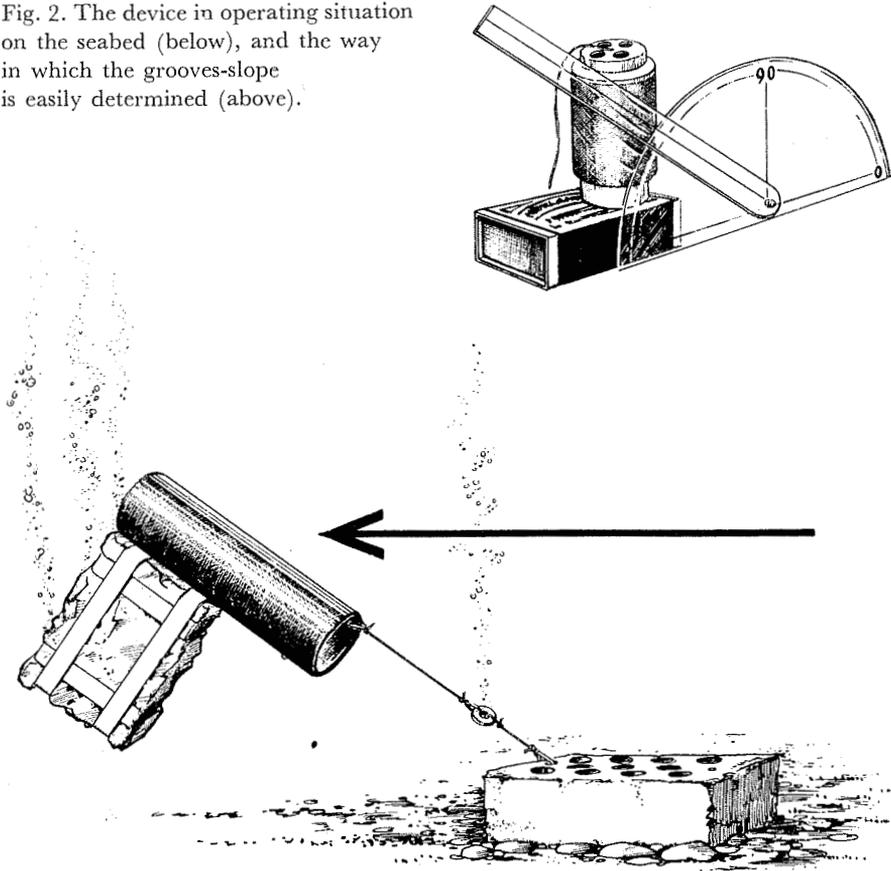


Fig. 3. Tilt/speed curve.

This paper can be kept brief and realistic if we do little more than reproduce (1) the memorandum which we sent to finders of the stranded "oysters" and (2) the diagram which we also posted to them. For publication purposes however, we have cut the large diagram into three illustrations, Figs. 1, 2, and 3.

We particularly wished to avoid the trouble of paying rewards, and we therefore relied upon the desire of finders to receive promised information about their finds proving sufficient to bring in returns. In the event it certainly did so, and some finders even asked that we should not bother to refund their postage costs.

A sufficient description of the "oysters" is afforded by reproducing the memorandum sent to finders—and we here give it as posted to the latest of these:

*MEMORANDUM FOR THE INFORMATION OF PERSONS WHO
HAVE FOUND ONE OF OUR "STRANGE OBJECTS" STRANDED
AND HAVE KINDLY SENT BACK TO US THE PART ASKED FOR
BY THE MULTI-LANGUAGE YELLOW PAPER WHICH THEY
FOUND BOUND INTO IT.*

At the outset it is to be said that the object which you found relates to a new method of sea research which could be called: "Seabed Currents by Post" to use rather picturesque language. You will be best able to appreciate what is involved if you read what follows whilst looking at the artist's diagram now sent to you. It is convenient for workshop and stock purposes to have a nickname for various sorts of device when many exist—and the thing you found goes conveniently under the name: "Plastic Seabed Oyster". The use of the word "Oyster" will become obvious we think. The object which you found and which we shall call a "P.S.B.O." from now on, was originally tossed overboard from the survey launch *Waterwitch* (Lieut.-Cdr. J. Paisley, R.N. (retd.)) at a spot near Alderney in the Channel Islands on 23rd September, 1968. It was sent to the bottom in the depth of about 172 metres in a long deep trough in the sea-floor called the Hurd Deep. This deep is of interest for a number of reasons, and in the old days masters of home-bound sailing ships liked to find it with their leadlines to assist their positioning. A number of the devices were thrown out each hour round the clock so that we could hope to learn what changes in speed and direction the bottom tidal streams might display in this area where they are strong (and known) on the surface. There would have been real difficulty in measuring the bottom currents in the wild weather which prevailed at the time, and the occasion was therefore very suitable for trying a new way of working which does not require a ship to keep an instrument captive on a suspension line. The following is a description of the P.S.B.O. as it was when

thrown out to sink to bottom. Two small rectangles of buoyant stiff polythene held about two inches apart by four strong perishable stiff rods (3.9 mm in diameter) set into little pits drilled in their corners on their inwards sides, were bound round with powerful stretched "garters" made of non-perishable butyl rubber. Extra strong bands of ordinary rubber were added to increase the squeeze force. These bands were disposed both across the length (14.5 cm) and the width (11.0 cm) of the polythene rectangles. The hold-apart rods were made of a corrodible alloy which fizzes away in sea water. On the inwards face of one of the polythene plates was fixed an equal-sized rectangle of green square-meshed plastic material such as is used for making meat safes etc. This material has stiff and pronounced raised ribs and the sheet of it used in the P.S.B.O. has these prominent hard ribs running parallel to the 14.5 cm edges of the plastic rectangle.

Hung midway between the polythene rectangles (at one end) is a cylindrical pendulum suspended on a terylene thread set into the centre of its top. This pendulum is about the size of a wine bottle cork. It is made from a polythene tube such as pharmacists use for keeping capsules in. The tube has holes in it to allow it to fill with water. Over the tube is a sleeve of soft rubber tubing and, over this latter, a strip of thin pure copper foil (0.7 mm thick) is wound to encompass the whole circumference of the tube. The copper foil is held secure from twisting movements by means of a thread tied suitably through it and the cylinder. The circular base of the pendulum contains a tight-fitting disc compass made from ceramic steel. This compass is very powerfully magnetized across its diameter which means that one point on the circumference seeks north, and the opposite one south. As so far described, if you held the cylindrical pendulum by the suspension thread, it would always rotate to come to rest in the same position. The suspension of the pendulum between the polythene rectangles is so arranged that it stays always midway between them so long as the hold-apart rods are intact. As so far described, if you tilted the plates the pendulum would remain vertical, but, if whilst you held them tilted the rods could suddenly crumble, the "oyster" would close with a powerful grip. The result would be that the plastic mesh would press its ribs into the copper and would make deep grooves in that soft covering of the directional pendulum. If you now forced the plates apart again and removed the pendulum, you would of course find that the grooves were on the slope—that is, not parallel to the top and bottom of the pendulum. These remarks explain how the grooves which you may have noticed on the pendulum which you returned to us were made.

Let us return to the device as so far described. The next step in its manufacture was to fasten the box affair comprising the two plates, the

hold-apart rods, the rubber binders and the pendulum—at right angles to the top of a short length of plastic tubing (6 cm wide and 26 cm long) containing a thin-skinned plastic detergent bottle filled with junk oil. This addition is made to give the gadget more buoyancy—more flotation power. From a point on the circumference of this tube (at its bottom) a string leads away which has to act as a limp tether. We next tie the free end of this string to a brick—using for convenience one of the holed kind of brick known to builders as “airbricks”. We allow about 20 cm for the length of the limp tether. We next sink the whole affair in a glass tank of sea water. It “floats” of course but at first the box part rides up somewhat above the horizontal. We then wind some thick solder wire round the box at the end away from the tube until it (the box) is horizontal. If we could now set the sea water in motion (thereby imitating a current), the tube would incline from the vertical and the box would dip below the horizontal—but the directional pendulum would always hang vertical. Clearly, the faster the current the greater would be the angle of tilt. Thanks to suitable laboratory tests made in water moving at various known speeds, we know the connection between angle of tilt and speed of current. Obviously we want the current to tilt the whole device without “blowing” directly on the pendulum. We therefore enclose the box part within a close-fitting cellophane bag such as is used for packing sandwiches—but we put some holes in the top of the bag to allow the escape of air and of the gas which will be produced when the rods fizz away.

The way of using the devices is as follows: we take them in our ship to a place where the bottom currents are of interest to us. Then we toss them overboard separately with the tether of each tied to a brick—but, in the tether, we incorporate a washer of the same corrodible alloy as the rods are made of. This washer takes much longer to fizz away and crumble than the rods do. When the P.S.B.O. reaches the bottom, if there is a current it tilts of course. When the hold-apart rods crumble the oyster snaps to and squeezes the pendulum very tightly to produce grooves whose slope is in proportion with current speed, and whose position on the pendulum (when referred to the known north-seeking vertical of the latter) reveals the direction of the current. Some time after the answer has become securely squeezed within the P.S.B.O., the tether washer crumbles and lets the device rise to the sea surface. Thereafter it floats on and on much under wind influence until such time as it fetches up on a beach. This makes one think of drift bottles and of the thousands of records of their travels which we hold—but, with the P.S.B.O., we want the winds to blow them along so that we shall not have to wait so long for returns as we might in the case of drift bottles carefully ballasted to escape wind influence.

We do not of course care where the P.S.B.O.'s go ashore; it is all the same to us so long as we get returns from them—their message having been securely locked within them ever since they closed on the seabed.

One thing remains to be explained. Clearly we had to have a way of hearing from persons who might find P.S.B.O.'s stranded on beaches. Obviously we could not accept the expense of much printing on plastic even if space sufficed. We therefore had recourse to multi-language questionnaire sheets enclosed in heat-sealed wallets of clear thin polythene. We tested these latter in water pressurized to more than 1,400 kilograms per square metre which is a much greater pressure than exists anywhere in the deepest parts of the oceans.

After the P.S.B.O. which you found stranded had risen to the surface, it travelled up the whole length of the English Channel under the influence of currents and winds. It rounded Kent and travelled on along the coasts of Essex and Suffolk to reach Norfolk after accomplishing a journey of about 280 miles. At the time of writing this twenty-one of the forty P.S.B.O.s put out near Alderney have been found stranded on the Norfolk coast. It may well be that some not urged ashore there by the north-easterly winds then prevailing, may travel on to go ashore very much further afield.

The recipient of this memorandum is warmly thanked for his help, and is informed that he is completely free to make any use of the story he may wish.

Your number was:—

Your finding date was:—

Your bottom current was:—

Addendum.

Since the above was written, two further P.S.B.O.s have been returned—of which yours is one. That returned from near Saltburn on the northernmost part of the Yorkshire coast and also that from Whitley Bay in Northumberland have travelled on about 130 miles further than those returned from the Norfolk coast. In other words they have covered a track of about 410 miles from the place where they were put on the sea bed.

[Memorandum ends here]

The multi-language yellow questionnaire paper referred to in the foregoing memorandum brought very pleasing success indeed, and we became accustomed to the postman bringing neat little parcels with the two supplied adhesive labels affixed to them.

The wording of the questionnaire paper (folded to the size 11.5 cm by 9.0 cm) was as follows:

- (a) The portion visible through the polythene envelope on recovery read thus:

IMPORTANT NOTICE – READ THIS FIRST !!

!!NOTICIA IMPORTANTE—LEA ESTO EN SEGUIDA!!

AVIS IMPORTANT – A LIRE AVANT TOUT

**MIKILVÆG ORDSENDING –
LESTU EFTIRFARANDI FYRST**

VIKTIG – LES DETTE FØRST !!

VIGTIG MEDDELELSE – LÆS DETTE FØRST

WICHTIGE MITTEILUNG !

- (b) the subsequent wording was the following printed successively in English, Spanish, French, Icelandic, Norwegian, Danish, and German:

The strange object which you have found stranded, should contain within itself information relating to the speed and direction of the water movements on the deep ocean bed at a spot very far away and on an occasion perhaps very many months ago.

If you will very kindly help us by acting as requested in what follows, the whole story will be told to you by letter as soon as we hear from you.

We particularly need to receive from you the little polythene tube coated with thin copper foil which you should have found squeezed within the object which you discovered stranded. This should have marks upon it which we can interpret for our purposes, and we accordingly beg you to send it back to us wrapped in a way which will preserve those marks. You will find enclosed with this two small printed labels which become strongly adhesive when their brown paper covers have been removed. Please affix them both to the little parcel which we strongly hope you will send to us. One of them will save you the trouble of writing our address, and the other will let the British Customs know what is contained. Please tear out from this sheet this portion which is in your own language, and please post it back to us with the undisturbed tube after having filled in the little questionnaire beneath. If you have difficulties, please solicit the help of a local official—and please tell us whether you require the postage expenses to be refunded.

As time goes on we shall hope to give finders more information than that obtained from the single object found by them. Please tell us very clearly your own name and address, and please state where and when you found the stranded object.

Our address is:

The National Institute of Oceanography,
WORMLEY, GODALMING, SURREY, ENGLAND.

Your name:

Your address:

.....

Date of finding:

Place of finding:

Our identity number marked on the paper:

It is pleasing to be able to state that all the directional pendulums returned to us were in excellent condition and had been carefully packed. The "grooves in copper" method of recording had been chosen after much pondering how best to achieve a record which would be virtually indestructible by the handling the pendulum would get from finders, and which would stand up to much rough usage due to wave motions on beaches. The reader might wonder how the method would work miles deep when the rubber sleeve under the copper would be "bone hard" before the oyster closed. This was checked by tests in a pressure tank. It was expected and proved that once the oyster had closed tight upon hard rubber whilst down below, it would maintain its powerful grip and make the grooves as the rubber softened again on ascent to surface. When the oysters were put out in the Hurd Deep a violent storm was raging and the tides were top equinoctial springs. As already remarked, all the returned pendulums were easily interpretable and there is no reason at all to doubt any of the speed values which, "round the clock", ranged from slack to one-knot on bottom below the 172 metres of water. It is however unfortunate that the directions are not so credible from this first experiment. It is clear that the hung pendulums must have spun somewhat from touching the side plates during surgings of the oysters. This is a fault which has now been rectified in preparation for another experiment. The pendulums are now pivotted on a swinging bracket in such a way that they cannot touch the sides of the oysters before closure.

Oysters furnished with the new pivotted pendulum have had their behaviour effectively checked in the following way. Some of them adapted to close in ten minutes were put on bottom from a lightship moored in the estuary at Harwich. They were used both on the seagoing and land-going stream along with infallible current-measuring jelly bottles of the same timing. In all cases a complete direction check was obtained. It is now intended to use the oysters in the greatest depths of the Bay of Biscay. When this is done they will probably have been modified a little to increase their sensitivity still further at lowest speeds. It is easy enough to cater for very slow speeds and equally easy to cater for speeds up to and beyond three knots—but there are of course real problems in making an oyster which will be satisfactory for both. Ideas are not lacking but they are a matter for the future. We may conclude by expressing the hope that publicity given by the B.B.C. might help towards future success.

ACKNOWLEDGEMENTS

I am indebted to my colleague Mr. D. BOOKHAM for all the constructional work involved, and to our artists Mr. N. R. SACHEL and Miss P. E. WILLIAMSON for all the drawings.

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GROWTH OF SOCKEYE SALMON IN RELATION TO ABUNDANCE IN THE KVICHAK DISTRICT, BRISTOL BAY, ALASKA¹

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INTRODUCTION

Intensive exploitation of Bristol Bay sockeye salmon (*Oncorhynchus nerka*) by both domestic and high-seas fishing has spurred the effort to formulate rational management procedures. Regardless of approaches to the formulation, two elements are indispensable: an accurate forecast of the run of adult salmon and a reliable estimate of the escapement that will produce the largest return.

Sockeye salmon leave the Kvichak River for the sea either in the second year of life (age I smolts) or in the third year (age II smolts). Nearly all survivors from both groups return after two or three years in the sea; thus practically all of the total production from an escapement is realized in instalments of 4, 5, or 6 years after the year of spawning. (Other age groups are generally negligible in number.)

RICKER (1962) compiled the available data on ocean survival of smolts and average length at the time of seaward migration for both North American and Asian sockeye salmon stocks. Survival generally was highest for the stocks that produced the largest smolts; but within one river system survival was generally not related to size. Where there is cyclic variability in run magnitude, as in the Kvichak River stock, a new dimension is added. Since the progeny from a given year of spawning return 4, 5, and 6 years later, the cyclic pattern of salmon abundance would not persist if the survival rate of the progeny were not higher in the peak cycle year than in off cycle years. For the Kvichak stock, there is a return of more than three mature fish per spawner of the peak year class, but of only

¹ Contribution No. 292, College of Fisheries, University of Washington.

one or two mature fish per spawner of the off year classes or even less. On the other hand, smolts during the peak cycle year may be 10–20 per cent smaller in length on the average than smolts during the off cycle years.

The interactions between the strength of year classes of salmon, primary and secondary production in the nursery area, and abundance of predators and food competitors, which result in a cyclic run abundance in the Kvichak River, can best be studied by a simulation model. But if such a model shall be useful for predictive purposes it must be a realistic one and not only one of verisimilitude. In order to achieve this a number of functional relationships must be determined. The present paper represents an effort to this end by discussing some functional relationships between growth of salmon and population density in the Kvichak River system.

SMOLT SIZE IN RELATION TO MAGNITUDE OF PARENT ESCAPEMENT

It has been observed in many river systems in North America and in Kamchatka that an inverse relationship exists between the average size of smolts and population size (KROGIUS 1961, JOHNSON 1965, BURGNER *et al.* 1969).

During the period 1953–1968, for which data are available on escapement and corresponding smolt abundance for the Kvichak stock, there were seven years in which less than one million fish escaped to the spawning grounds, three years in which escapements ranged from 2.5 to 3.7 million spawners, and three years in which escapements were exceptionally large. In 1956 the escapement numbered 9.4 million fish; in 1960, it was 14.6 million fish; and in 1965, it was 24.3 million spawners (Table 1). The total number of smolts produced increased over these last three cycle years, but the number of smolts produced per spawner declined. Nevertheless, it is informative to determine whether the average length of smolts has been a function of escapement size over the years.

The average lengths of age I smolts and age II smolts are plotted against the magnitudes of parent escapements in Fig. 1. In both cases, average length decreased as parent escapement increased until parent escapement reached a certain level, after which average length stabilized. For age I smolts this level was about four million spawners. Despite exceptionally large escapements in 1956, 1960, and 1965, the average length of age I smolts produced varied only from 82 to 86 mm. For age II smolts, the level at which the smolt length stabilized itself was about nine million fish. For the two largest escapements during the period under consideration, the average length of age II smolts was about 100 mm.

Table 1. Sockeye salmon escapements and average lengths of smolts produced, Kvichak River, 1952-1965.¹

Year	Escapement, thousands	Average length of smolts, mm		Index catch of age I and II smolts, thousands
		Age I	Age II	
1952	5,970	—	109	—
1953	321	89	116	66
1954	241	92	120	39
1955	250	96	114	89
1956	9,443	84	99	6,045
1957	2,964	80	108	639
1958	535	91	117	72
1959	680	92	110	98
1960	14,630	82	98	5,247
1961	3,706	83	108	1,717
1962	2,581	87	109	2,206
1963	339	90	114	89
1964	957	94	118	475
1965	24,326	86	105	8,341

¹ Data for 1952-1964 are from PENNOYER and STEWART (1967) and from ALASKA DEPARTMENT OF FISH AND GAME (1968); remaining values are preliminary estimates furnished by the Alaska Department of Fish and Game.

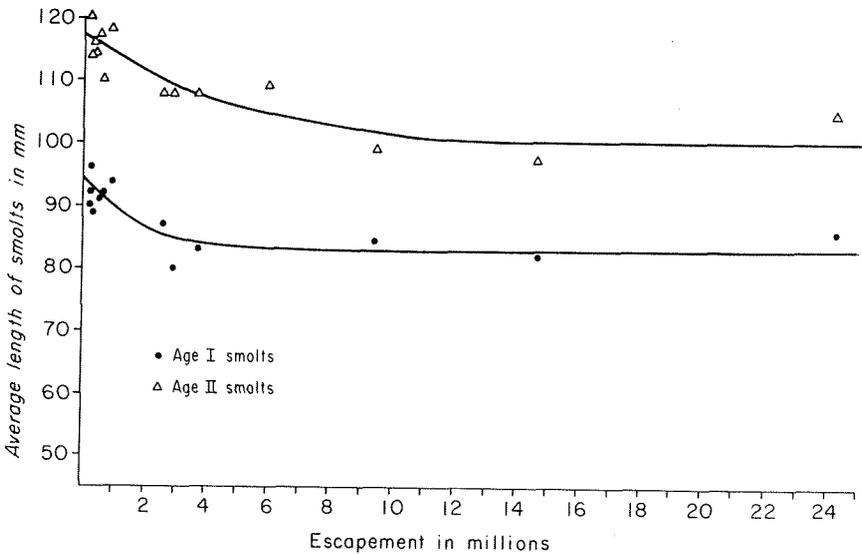


Fig. 1. Average lengths of age I and age II smolts as a function of parent escapement size in the Kvichak River, 1955-1968. Equation for the curve fitted to the age I smolt data is $y = 83.22 + 11.26 \cdot e^{-.63x}$, and that for the age II smolt data is $y = 101.02 + 16.22 \cdot e^{-.24x}$.

The observed relationships are expressed by negative exponential curves of the form $y = a + be^{-cx}$, fitted to the data by a non-linear regression technique (GALES 1964).

It may be assumed that the escapement of close to 25 million spawners in 1965 is perhaps the largest escapement to the Kvichak River since the inception of the commercial fishery. The data suggest that, for the observed escapement range, the young fish will not migrate to sea as age I smolts unless they have reached an average length of about 80–85 mm, and smolts of age II have reached an average length of about 100 mm or more. Since kokanee salmon have never been observed in Iliamna Lake and age III smolts constitute a negligible group, either the food supply is sufficient for all fish which do not migrate at age I to reach an average size of about 100 mm or the slower growing fish are more easily captured by predators.

The statement on average minimum size at time of migration as age I smolts can be verified by observations on the juvenile salmon in Iliamna Lake. Personnel of the Fisheries Research Institute have sampled the juvenile salmon in Iliamna Lake every year in August and September since 1962 (KERNs 1965, 1966, 1968). The maximum and average sample mean lengths of fingerlings calculated as of September 1 are given in Table 2. Also given is the computed daily increase in length, based on repeated sampling each year at the same locality from the latter half of the summer season; this growth rate is assumed to have been maintained from June to September. Such data may yield a higher growth rate during the first part of the summer than actually took place. In some years the maximum sample mean length of fingerlings, computed as of June 1, approached the length at which smolts migrate to sea as age I, but the computed average lengths were substantially smaller with one exception. In Iliamna Lake, the smolt out-migration is brief and essenti-

Table 2. Growth in length of yearling sockeye salmon in Iliamna Lake from June to September, 1962–1967.

Year	Sample mean length on Sept. 1, mm		Estimated average daily increase in length, mm	Calculated length on June 1, mm	
	Maximum	Average		Maximum	Average
1962	102.1	90.8	.18	85.9	74.6
1963	104.1	100.0	.20	86.1	82.0
1964	108.8	96.2	.37	75.5	62.9
1965	117.3	110.3	.58	65.1	58.1
1966	114.8	110.7	.56	64.4	60.3
1967	104.0	90.4	.27	79.7	66.1

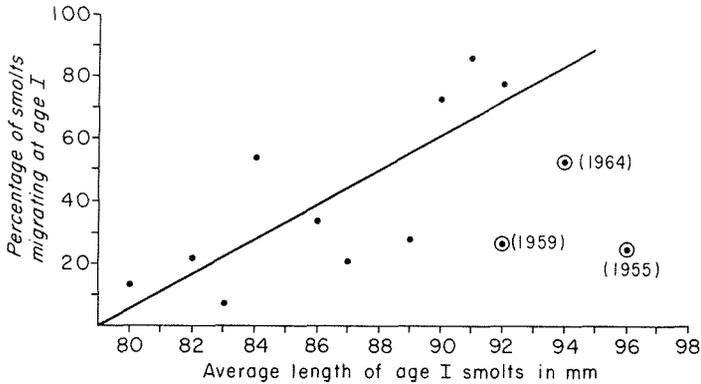


Fig. 2. Regression line of percentage of smolts migrating at age I on the average size of age I smolts, 1953–1965. Data for the years 1955, 1959, and 1964 are not included in the calculation of the regression line $y = -437.3 + 5.54x$.

ally over by the first week of June, unlike in some other lakes of Bristol Bay, where migration may extend through the month of June and part of July. In the Kvichak River system, therefore, it is possible to specify the time at which smolts must average a minimum size to migrate.

Finally, one could expect the proportion of age I smolts produced from an escapement to increase with an increase in average length of age I smolts. Data published by PENNOYER and STEWART (1967) on average smolt length and proportions of smolts of age I and age II produced from an escapement have been plotted in Fig. 2. At first glance a linear relationship seems to be nonexistent. However, when the three aberrant points representing the proportions of smolts from the spawnings in 1955, 1959, and 1964 migrating at age I are excluded, a reasonably well-defined relationship emerges. The larger the average length of age I smolts, the larger the proportion of the year class that migrated at this age.

An explanation for the three aberrant points must be sought elsewhere. All three represent production from a pre-peak year class of the Kvichak River sockeye salmon cycle. The low percentages of age I smolts produced from the spawning in 1955, 1959, and 1964 should be viewed perhaps as a result of the cyclic variability in run magnitude. The age II smolts spent their last year of freshwater residence together with the fry of the subsequent peak year, and they may have survived better than smolts in the other years of the cycle since the rate of primary production shows a tendency to increase in the year following a peak cycle year (BAXTER 1968).

Furthermore, the proportion of fish migrating to sea as age I smolts may only increase linearly with length of the juvenile salmon over a

certain size range. In years with a low biomass of juvenile salmon and a high growth rate and average length, the proportion of age I smolts produced from an escapement may decrease in a parabolic manner. This presumably was the case for the three aberrant years prior to the peak cycle year. KROGIUS (1961) has presented similar data from Lake Kuril pointing to a prolonged freshwater residence in years with low biomass of juvenile salmon relative to the food supply and hence increased growth rate. The secondary production in Iliamna Lake has remained fairly stable since observation started in 1962. Such suggestions can only be verified by further studies, but the substantially identical relationship for the three pre-peak years for which data exist strongly suggests that such a mechanism must be operating.

LENGTH AT MATURITY OF THE KVICHAK SOCKEYE SALMON

Since 1957 the mean length of the returning mature sockeye salmon to the Kvichak River has varied from about 540 to 580 mm for three-ocean females and from about 480 to 520 mm for the two-ocean females. Although the males are larger, a similar range of size variation has been observed for the males (Table 3). Length is defined as the distance from the middle of the eye to the fork of the tail.

Population density has been expressed as the total size of the run in any one year by combining the catch and escapement of all age groups which returned to the Kvichak River in a year. A negative exponential

Table 3. Average lengths of Kvichak sockeye salmon in the escapements, 1957-1968 (mm).

Year	Total Kvichak/Naknek run in millions	Male		Female	
		2-ocean	3-ocean	2-ocean	3-ocean
1957	8.183	518.6	571.6	503.2	552.0
1958	1.830	537.2	591.1	516.8	567.7
1959	5.427	521.4	582.4	510.5	558.9
1960	26.547	488.1	567.5	471.4	535.0
1961	12.314	515.1	574.1	503.6	563.2
1962	5.676	524.0	578.3	511.3	562.3
1963	2.405	529.3	599.1	513.7	571.7
1964	4.799	501.7	577.4	487.1	567.2
1965	44.358	493.9	560.8	477.2	540.4
1966	10.364	521.8	577.4	503.8	556.0
1967	6.512	537.6	597.1	518.6	578.1
1968	4.963	510.9	591.1	493.3	574.8

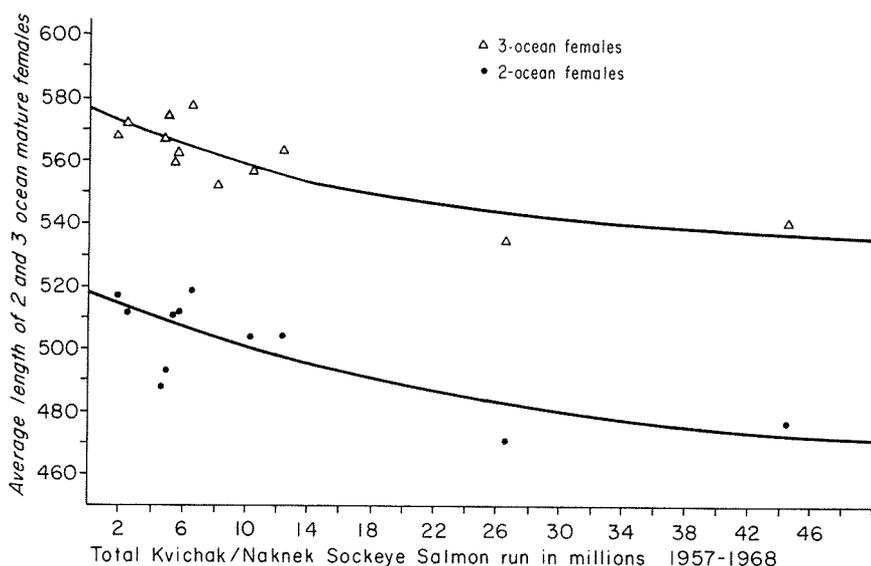


Fig. 3. Average length of returning female sockeye salmon as a function of total return, 1957-1967. Equation for two-ocean females is $y = 462.64 + 53.64 \cdot e^{-.037x}$ and that for three-ocean females is $y = 532.23 + 44.61 \cdot e^{-.53x}$.

relationship was found between the two variables for runs up to 26 million fish; but no further reduction in average length was observed, for example, in 1965 when 44 million fish returned (Fig. 3).

Changes in average length of a given age group of mature salmon have been described for other populations. KROGIUS (1960) describes regular periodic fluctuations in length of sockeye salmon from Lake Dalnee. BIRMAN (1964) brings out the interesting fact that not only is length of the salmon feeding in the sea inversely related to population density, but the total quantity of feeding salmon of all species affect the final size of a species, even in a year where this species may not be particularly abundant. He demonstrated that the size of the mature Bolsheret chum salmon was inversely related to the magnitude of the pink salmon runs in the same year. EGOROVA (1964) relates age at maturity of the Ozernaya sockeye inversely to the magnitude of the runs.

The authors cited above relate these manifestations to competition for food. However, it does not seem reasonable to postulate a general shortage of food in the ocean since the two ocean age groups of Kvichak sockeye salmon together number in any year at most between one and two hundred million individuals which migrate widely. Even if all species of salmon were considered together the magnitude is small compared with the abundance of other marine species. Still this does not preclude the existence of local shortage of food.

Table 4. Average index catches and weights of pelagic fish in Iliamna Lake, 1962-1967.

Year	Fry		Yearlings		Threespine sticklebacks		Relative total biomass
	Average catch per set	Average weight, in g	Average catch per set	Average weight, in g	Average catch per set	Average weight, in g	
1962	21.8	1.3	93.3	9.4	141.3	.8	1018
1963	27.8	2.1	12.0	9.0	24.3	.8	186
1964	.9	1.5	20.6	8.0	96.3	.9	253
1965	4.4	2.2	3.6	11.2	86.7	.9	128
1966	151.7	1.5	.9	13.1	40.4	.7	268
1967	67.6	2.1	80.9	6.6	38.3	.7	703
Average for all years		1.78		9.55		.8	

In the sea it is a difficult task to ascertain the abundance of food at one specific place and at a specified time. But, since growth of juvenile salmon in the Iliamna Lake nursery area and length at seaward migration seemingly follow the same pattern as growth of maturing salmon and their length at maturity in the sea, these problems can better be studied in a restricted freshwater ecosystem such as that of Iliamna Lake.

GROWTH OF JUVENILE SOCKEYE SALMON IN RELATION TO FOOD SUPPLY

Threespine sticklebacks, sockeye salmon fry and yearlings inhabit the limnetic zone of Iliamna Lake. Ninespine sticklebacks, smelts, and a few fish of other species are found also; but they make up a negligible part of the biomass of pelagic fish and can be ignored. The average weights of age I threespine sticklebacks and sockeye fry and yearlings in index catches in the years 1962–1967 are given in Table 4, based on data published by KERNs (1965, 1966, 1968). Whereas the average weight of age I sticklebacks has remained almost the same in the last 6 years, the weights of fry and yearlings have varied and have reflected changes in total biomass of limnetic fish. For all years, the average weight of fry was 1.78 and that of yearlings 9.55, or a ratio of 5 : 4. But within the lake

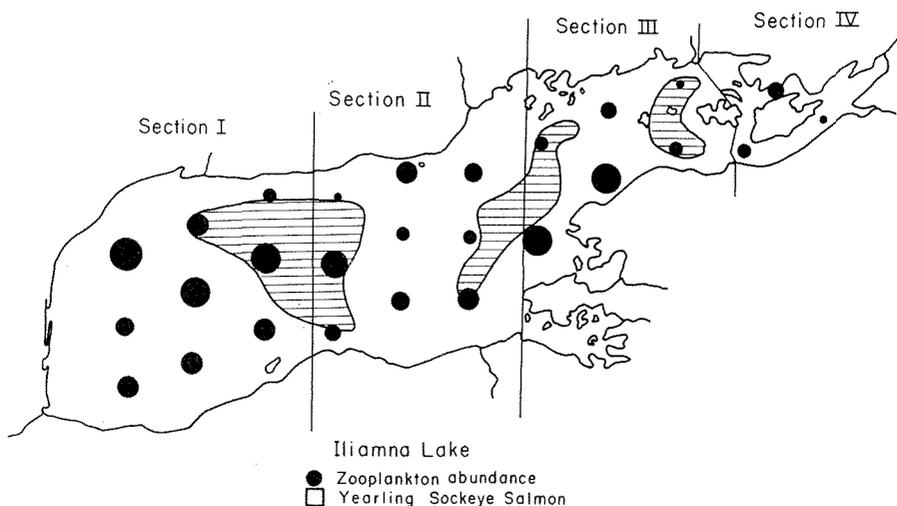


Fig. 4. Standing crop of zooplankters and maximum density of sockeye salmon yearlings in Iliamna Lake, August, 1967. Cross-hatched areas correspond to average catches of 300 yearlings or more per tow. Smallest circle indicates 3–4,000 and largest circle, 12–14,000 zooplankters per cubic meter. (Data on fish abundance given by KERNs (1968) and plankton abundance from unpublished data provided by Mr. T. GUNNERØD.)

there are great differences in length. For the sake of convenience the lake is divided into four main sections, numbered I to IV, from west to east (Fig. 4). It has been known for some time that the average length of yearlings in any one year in the western part of the lake (section I) is greater by about 20 per cent than that of fingerlings in the eastern part (section IV) (KERNs *et al.* 1963). These differences can be related to the standing crop of zooplankton which has been estimated from samples taken with a No. 6 mesh, $\frac{1}{2}$ -m open net from bottom or 100 m to surface. Although such a sampling does not yield any absolute estimate of the rate of production, the standing crop of zooplankters toward the end of August, when sampling of juvenile sockeye salmon normally takes place, serves as a relative measure of the food potential at this time of the year.

The average number of zooplankters per cubic metre in sections I to IV for the years 1963–1968 were 10,050, 8,938, 7,196, and 6,201 respectively. This seemingly direct relationship to average length of yearling sockeye salmon which decreased from section I to section IV for the same years disappears when the average length of yearlings within a section is plotted against the standing crop of zooplankters there in any one year (Fig. 5). If a regression line is fitted between observed average length and corresponding zooplankton abundance, the hypothesis that the slope

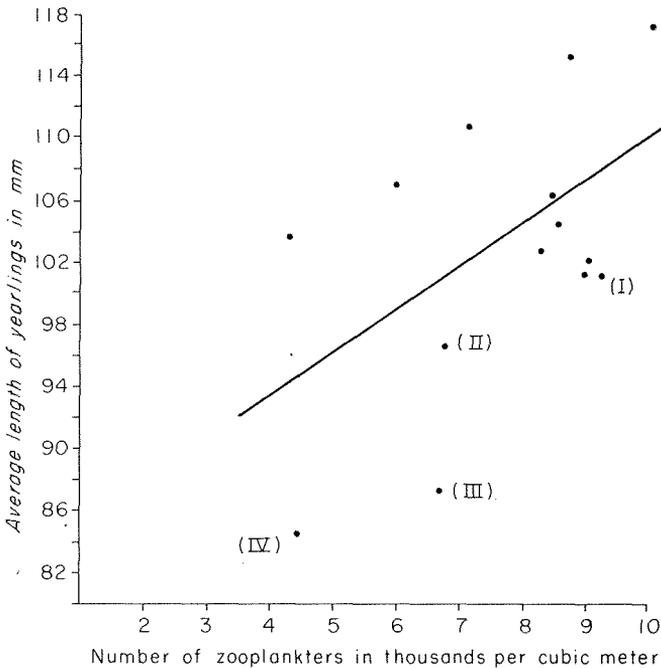


Fig. 5. Regression line of average lengths of yearling sockeye salmon and standing crop of zooplankters by lake sections (sections indicated in parentheses for 1967).

of this line is zero is barely rejected at the 95 per cent confidence level. ($t = 2.33$, 15 d.f.) and the hypothesis is accepted at the 99 per cent level.

Two factors add to this variability. First, the larger average lengths of yearlings in the two lower sections I and II may be due to an immigration of the fastest growing fish from the two upper sections III and IV and length may not be directly related to observed plankton abundance. A majority of fish spawn in sections III and IV and the resulting progeny move down Iliamna Lake to the outlet in the western end of section I during their freshwater residence.

Secondly, the distribution of yearlings in 1967 (Fig. 4) in relation to observed plankton abundance registered at the different stations in that year include heavy abundance of yearlings at places both with high and low abundance of zooplankton. This raises doubt as to the suitability of an average zooplankton abundance for a section as an index of food potential unless the juvenile salmon constantly and rapidly move around feeding. It is difficult to pass judgment on this question from the existing tow net data which give fish abundance only once during each season. A rapid dispersal of the juvenile salmon is not apparent. Since 1962 a centre of heavy yearling concentration in the lower part of Iliamna Lake has been associated with a large biomass of juvenile salmon and ensuing population pressure which forces a more widespread dispersal.

Too many factors are therefore confounded at the present time to state clearly the dependence of growth of juvenile salmon upon the availability of food except in a rather approximate manner.

There are indications that other growth inhibiting factors related to population density are operating. Two points deserve mention. In 1967, a year with the largest biomass of juvenile salmon present for those years where corresponding plankton data are available, the average length of the yearlings in all sections were substantially lower (sections I, II, and III) or equal (section IV) to the smallest average length observed in other years at a corresponding plankton density. Secondly, there is an asymptotic lower limit for average length of migrating smolts, both of age I and age II smolts. Both facts lead one to hypothesize that the depression of growth rate in years with a high biomass of juvenile salmon is due to space factors. The same may be true for the immature fish feeding in the sea. These results are in accord with those presented by JOHNSON (1965) from Babine Lake. As to the nature of such growth inhibiting factors related to population density JOHNSON summarized pertinent studies. But to date the proposed factors are merely indicative of those operating in sockeye populations and worthy of further investigations. It should be illustrative to study not only the total number of zooplankters but also their availability to sockeye salmon under different fish densities.

As a consequence, the capacity of the nursery area in Iliamna Lake can be measured adequately by the number of smolts produced from an escapement, especially since the survival rate of smolts to mature salmon is not closely tied to average length of the smolts.

SMOLT PRODUCTION IN THE KVICHAK SYSTEM IN RELATION TO MAGNITUDE OF PARENT ESCAPEMENT

Basically, two groups of points are available for placing an upper limit on the nursery capacity. One group includes the numbers of smolts produced from a series of small escapements, and another group the numbers of smolts produced from three peak years. In Fig. 6 are plotted the numbers of smolts produced and the magnitudes of the corresponding parent escapements for all years. The smolt production from the 1960 escapement may have been underestimated because heavy iceflow prevented sampling for extended periods when age II smolts migrated to sea in spring of 1963. Another estimate can be made by assuming that the ratio between index catches of smolts by fyke net in 1963 and 1968 should approximate the ratio of the average number of fingerlings caught by tow net in Iliamna Lake in the previous fall. In 1962, an average of 93.3 fingerlings was caught per haul, whereas an average of 80.9 yearlings was taken per haul in 1967. Thus, the expected index catch for age II smolts in 1963 would have been 7.7 million instead of the observed index catch of 5.2 million; the true value may lie somewhere between.

Two logistic curves of the form $y = a/(1 + e^{-(b + cx)})$ were fitted to the data, and the two values for the smolt index for 1963 were used. Smolt production increased as magnitude of parent escapement increased until an asymptotic limit was reached. In both cases it appears that the asymptotic limit for the number of smolts that can be produced from one

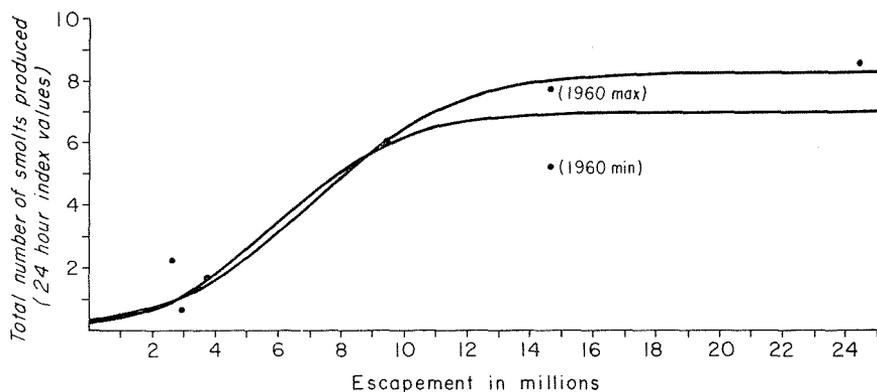


Fig. 6. Total numbers of smolts produced from escapements in the Kvichak system, 1953-1965. Equations for the two logistic curves are $y = 8.14/(1 + e^{3.20-.46x})$ and $y = 6.83/(1 + e^{3.19-.55x})$.

escapement in Iliamna Lake is close to the 1965 production value, although substantially smaller escapements will yield about the same number of smolts. Some confirmation may be derived from historical data for the Kvichak stock. In order to arrive at an escapement of 25 million spawners, it is necessary to postulate unrealistic low fishing mortalities except for the period 1936–1938. In 1936 the Kvichak catch numbered 16.8 million fish, in the following year 14.0 million, and in 1938 21.0 million; and the escapements must have been at least the same size (MATHISEN 1965). In other years the commercial catches never reached such magnitudes and it is not reasonable to suspect the escapement to have reached the 1965 value.

It is an important fact that during the period 1936–1938 the pattern of the Kvichak cycle changed from a peak run and one or two very strong subdominant runs to one exceedingly strong peak run and small runs. The latter pattern has persisted to the present. Were several strong year classes to be produced again in succession, there would be a sustained cropping rate of zooplankters and the total standing crop may decline drastically relative to the present-day situation. Zooplankton production may then exert a more direct effect on growth and survival of the juvenile sockeye salmon than observed today.

SUMMARY

1. Catch and escapement of Kvichak River sockeye salmon (*Oncorhynchus nerka*) and smolt production from Iliamna Lake, the nursery area, have been determined annually since 1955. Since 1962, information has been collected on growth and abundance of fry and yearlings and zooplankton production in Iliamna Lake.
2. Growth in length of smolts can be expressed as a negative exponential function of population density. A similar relationship exists for maturing salmon on their return from the ocean to the Kvichak River.
3. There is no strong correlation between the growth of juvenile salmon in Iliamna Lake nursery area and the standing crop of zooplankters. Other effects of crowding on growth need to be investigated.
4. An asymptotic limit for the number of smolts produced in the nursery area has been computed, but it may be valid only for a single-peak cycle, the current pattern of run variability in the Kvichak River.

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THE HALIBUT GILLNET FISHERY IN WEST FINNMARK

Analysis of Landings Data from Øksfjord 1955–65

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INTRODUCTION

In 1936 gillnet fishing for halibut was started in Norway (DEVOLD 1938). One of the main localities for this autumn–early winter fishery is the deep parts of Altafjord in West Finnmark with its tributaries and entrances.

Detailed studies of the fishery and the stock of halibut in this area were carried out during the years 1956 to 1960 (OLSEN 1956, TJEMSLAND 1960, OLSEN and TJEMSLAND 1963, MATHISEN and OLSEN 1968). The findings of these investigations provided the main basis for revisions of existing regulations being in force for this fishery since 1937. The first revision was introduced in 1956 when the fishing time was increased to the end of December from, previously, December 15; and the second one in 1962, from which year the closed season started on January 21.

Estimates of mortality and the likely effects of the fishery on the stock were reported by MATHISEN and OLSEN (1968). The present data throws some further light on the dynamics of this stock of large mature halibut, which for most practical purposes can be considered as exploited by the gillnet fishery only during the short period of the year when these large fish penetrate into the deep fjords of Northern Norway to spawn.

MATERIAL AND METHODS

The Official Statistics of Norway give catch of halibut by months, but no published commercial statistics exist for the gillnet fishery alone or for the effort extended in this fishery.

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Table 1. Records of gillnet caught halibut landed in Øksfjord during the seasons 1955 to 1964-65.

Year	Month	Landings in kg	No. of men per vessel	No. of landings	No. of men times no. of landings	CPUE
1955	Oct.	1.580	3.5 ¹	90 ¹	315	5.0
	Nov.	5.782	3.8 ¹	100 ¹	380	15.2
	Dec. ²	7.768	4.1 ¹	60 ¹	410	18.8
	Nov.-Dec.	13.550	—	160 ¹	790	17.2
1956	Nov.	8.232	3.8 ¹	140 ¹	532	15.5
	Dec.	20.286	4.1 ¹	143	586	34.6
	Nov.-Dec.	28.518	—	283 ¹	1118	25.5
1957	Oct.	2.146	3.5 ¹	47	165	13.0
	Nov.	5.100	3.8 ¹	54	205	24.9
	Dec.	19.489	4.1 ¹	96	394	47.9
	Nov.-Dec.	24.589	—	150	599	41.1
1958	Oct.	2.369	3.5 ¹	35	123	19.3
	Nov.	3.039	3.8 ¹	38	144	21.1
	Dec.	13.523	4.1 ¹	53	217	62.3
	Nov.-Dec.	16.562	—	91	361	45.9
1959	Oct.	2.270	3.5 ¹	27	95	23.9
	Nov.	2.817	3.8 ¹	32	122	23.1
	Dec.	8.443	4.1 ¹	44	180	46.9
	Nov.-Dec.	11.260	—	76	302	37.3
1960	Oct.	1.576	3.5 ¹	37	130	12.1
	Nov.	4.172	3.8 ¹	35	133	31.4
	Dec.	5.691	4.1 ¹	42	172	33.1
	Nov.-Dec.	9.863	—	77	305	32.3
1961	Oct.	1.946	3.5 ¹	40	140	13.9
	Nov.	5.256	3.8 ¹	44	167	31.8
	Dec.	9.842	4.1 ¹	47	193	51.0
	Nov.-Dec.	15.098	—	91	360	41.9
1962	Nov.	3.128	3.8	18	68	46.0
	Dec.	12.969	4.1	46	187	69.3
1963	Jan.	9.310	4.6	31	143	65.1
1962	Nov.-Dec.	16.097	—	64	255	63.1
1963	Oct.	1.162	2.3	9	21	55.3
	Nov.	2.535	3.1	12	37	68.5
	Dec.	14.745	3.8	43	163	90.4
1964	Jan.	3.170	4.4	8	35	90.6
1963	Nov.-Dec.	17.280	—	65	200	86.4
1964	Oct.	2.064	2.9	13	37	55.7
	Nov.	5.039	3.0	20	59	85.4
	Dec.	7.748	3.5	36	126	61.5
1965	Jan.	489	2.8	5	14	34.9
1964	Nov.-Dec.	12.787	—	57	185	68.0

¹ Estimated figures. ² Closed season starting 15 December.

Table 2. Monthly weight distributions for gillnet caught halibut landed at Øksfjord.

W kg	1961-62					1962-63					1963-64					1964-65				
	O	N	D	J	Σ	O	N	D	J	Σ	O	N	D	J	Σ	O	N	D	J	Σ
5-9	2	4	2	35	43	—	1	14	16	31	35	64	34	10	143	—	2	29	44	75
10-14	3	11	13	72	99	4	3	28	49	84	30	37	61	26	154	2	7	42	72	123
15-19	9	8	14	90	121	2	6	20	36	64	20	17	59	17	113	2	8	31	62	103
20-24	5	13	11	54	83	2	7	33	17	59	19	10	61	21	111	5	14	28	46	93
25-29	11	23	28	44	106	3	11	60	29	103	12	20	70	20	122	11	43	67	43	164
30-34	11	23	28	29	91	1	19	59	22	108	18	22	97	16	153	17	56	83	22	178
35-39	10	22	27	23	82	5	26	56	13	100	7	20	54	13	94	10	25	43	21	99
40-44	2	19	16	13	50	4	11	19	11	45	4	10	29	8	51	10	18	32	20	80
45-49	5	5	10	18	38	—	1	11	6	18	1	1	14	5	21	6	8	13	8	35
50-54	—	2	5	15	22	2	—	11	3	16	3	1	14	3	21	1	1	8	7	17
55-59	—	4	1	10	15	—	3	2	3	8	—	—	5	5	10	1	2	5	2	10
60-64	1	—	2	8	11	1	—	—	3	4	1	—	6	—	7	—	1	5	7	13
65-69		3	—	10	13	—	—	—	4	4	—	—	2	1	3	—	—	2	5	7
70-74		1	1	8	10	—	—	—	1	1	—	—	6	1	7	—	—	2	2	4
75-79		1	—	6	7	—	1	3	2	6	1	—	2	—	3	—	—	—	3	3
80-84		—	1	5	6	1	—	2	3	6	—	—	1	1	2	—	—	2	3	5
85-89		1	—	7	8		1	1	2	4		2	—	2	4		—	2	3	5
90-94		1	1	2	4		—	1	—	1		—	2	1	3		—	2	4	6
95-99							1	1	2	4		—	2	3	5	2		1	3	6
100-104								1		1		—	—	3	3			3	1	4
105-109												—	3	2	5			3	4	7
110-114												—	1	2	3			1	3	4
≥115												1	1	5	7			7	4	11
Total	59	141	160	448	808	25	90	322	222	659	151	205	524	165	1045	67	185	411	389	1059
\bar{W}	29.5	33.5	32.6	29.3	30.7	33.5	34.1	29.4	27.6	30.5	21.0	20.7	29.8	35.9	27.7	36.1	31.5	33.3	29.5	31.2

Through the courtesy of Njord Handels og Industri A/S, the only fish packing and processing company in Øksfjord, where a fair proportion of all gillnet caught halibut in West Finnmark is landed, a series of detailed landing statistics for this fishery was compiled for the period 1955–1965 (Table 1). Some data on relative effort were also collected and the material thus comprises monthly (since 1961 also weekly) records of all landings of gillnet caught halibut; the number of landings made, and since 1962 also the number of men, and some information on the amount of gear in relation to vessel size and number of men. For the four last seasons data are available on the size distribution of the landings in terms of weight (Table 2).

Records are available of the number of landings from 1957 onwards and for the last three seasons also of the number of men for each vessel and landing. These data show quite clearly that the average number of men per vessel increases from October to December–January, probably because the larger vessels do not start halibut fishing until the latter part of the season when catches are best.

For the season of 1962–63 there are also data on the amount of gear used, and these reveal a nearly linear relationship (Table 3) between number of nets and number of men per vessel. Thus the effective effort is directly proportional to the number of men per vessel, and the landing data have to be corrected for the seasonal change in vessel size, or average number of men per vessel, to facilitate unbiased estimates of catch per unit of effort (CPUE). In recent years there has been a continuous trend of reducing the number of men required to operate these fishing vessels, and the monthly estimates of average number of men per vessel for 1962 were therefore used as weighting factors for all previous years.

Table 3. No. of men and average no. of nets used for 11 vessels in the 1962–63 season.

No. of men	Average no. of nets
2	23.3
3	24.5
3	26.4
4	31.5
4	31.8
4	38.6
4	45.0
5	36.0
6	72.0
6	77.0
7	88.3

The estimates for November and December of CPUE were applied to the official statistics of total catch of halibut in Finnmark during the last quarter of each year to calculate the total effort required to catch an equivalent quantity of halibut if fishing with gillnets only (Table 4). Since halibut landings in October are always relatively small the bias introduced by using the combined CPUE estimates for November–December only is probably not very significant.

SIZE DISTRIBUTION

Table 2 gives the monthly weight distribution in 5 kg groups of all gillnet caught halibut landed in Øksfjord during the fishing seasons 1961–62 through 1964–65. Frequency distributions for the total material, October–November–December combined and for January respectively are plotted for each year on Fig. 1. The bimodal type of distribution is probably caused by the great sex difference in growth rate.

In all seasons except 1963–64 the halibut caught during October–December were generally larger than those taken in January. This is in keeping with previous findings from the detailed investigations of 1956 to 1960 (OLSEN 1956, TJEMSLAND 1960) that the older fish which have spawned earlier generally arrive on the spawning grounds before the first time spawners; which for halibut in the Altafjord area usually do not appear before some time in January.

However, in the 1963–64 season the spawning run apparently occurred earlier than normal and many relatively small-sized halibut were caught before Christmas. When January came catches were declining and most of the season was presumably over by then.

The figure shows no general trend of decreasing fish size over the years. If anything, there was a slight increase in the relative numbers of medium sized fish and the proportion of large halibut, over 50 kg say, remained fairly constant. This size distribution is very similar to that established for the period 1956 to 1960, and although it is known that a gradual increase from 16" to 18" mesh size of the halibut nets did take place in recent years, it is nevertheless safely concluded that no dramatic change in size composition has occurred from the first to the second five-year period.

CATCH AND EFFORT

On the top of Fig. 2 are plotted the landings in Øksfjord during October–November–December, of all gillnet caught halibut and the corresponding total landings of halibut in the county of Finnmark. These also include a quantity taken with longlines and trawl (mainly immature fish).

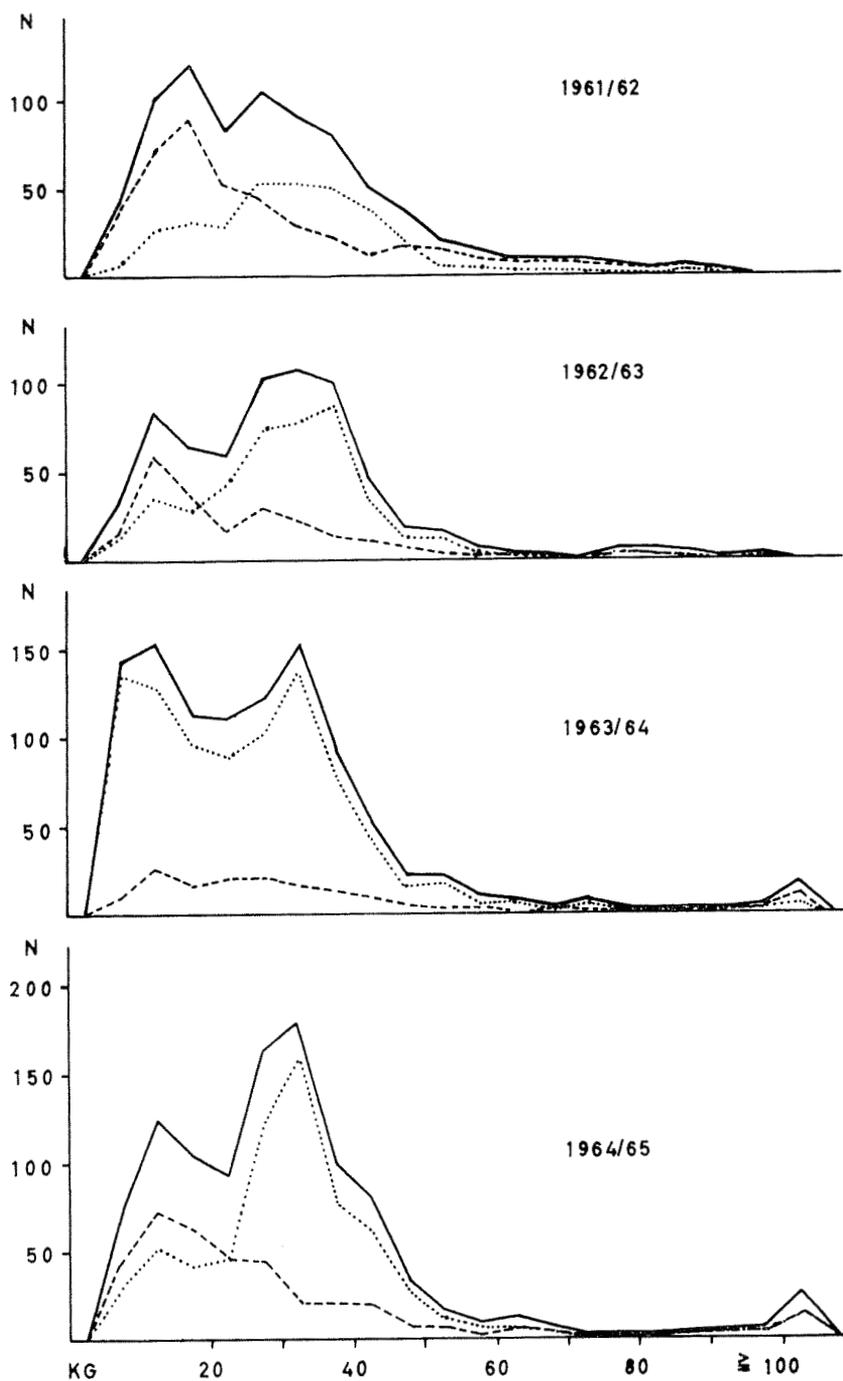


Fig. 1. Size distributions of gillnet caught halibut landed at Øksfjord. Solid line: total. Dotted line: October/November/December. Broken line: January.

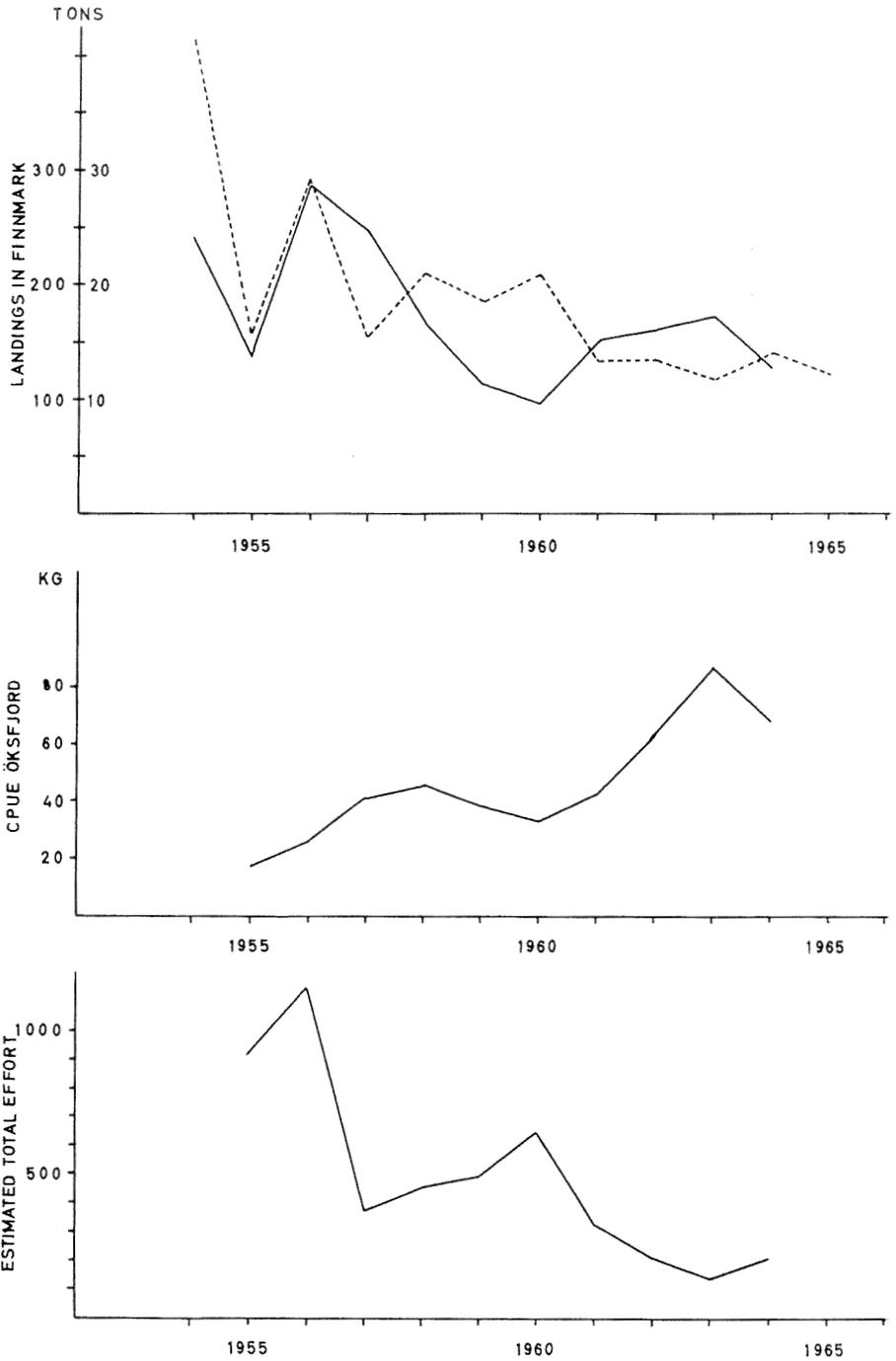


Fig. 2. Top, solid line: gill net caught halibut landed at Øksfjord in November/December. Broken line: total halibut landings in Finnmark during October/November/December. Middle: catch per unit of effort (CPUE) estimated from statistics of landings at Øksfjord in November/December. Bottom: estimated total effort of the halibut fishery in Finnmark during last quarter of the year.

The figure confirms that Øksfjord is a main landing place for the halibut gillnet fishery in the area and accounts for about 10 per cent of all halibut landed in Finnmark. Thus, there is good reason to assume that any trend in the halibut stock of the area would be manifest in the fishery out of this port.

The landing statistics for 1955 to 1965 shows a general trend of decreasing halibut landings in the last quarter of the year both for the whole county and for the gillnet fishery out of Øksfjord.

This decrease has taken place at the same time as a marked increase in CPUE has been experienced (Fig. 2, middle) and, consequently, the estimated total effort of the fishery has decreased to about one-fifth of the level in the mid-1950's (Fig. 2, bottom, Table 4).

The rise in CPUE has been most spectacular and continuous for the month of November, but also for December and October a great increase was apparent (Table 1), and on an average for November and December combined, CPUE more than tripled during the ten-year period studied.

DISCUSSION

There may be several reasons for the spectacular rise in CPUE during the period covered by this study. For December there was at first a great increase in the years 1956, 1957 and 1958. This was most probably a direct result of the new regulations extending the season to the end of December and the changeover from hemp to nylon nets, which took place gradually during these years. This gear innovation was followed by a gradual increase in mesh size from the usual 16" nets to 18", and even

Table 4. Total catch of halibut landed in Finnmark during October/November/December and estimated total effort for the same period.

Year	CPUE Nov./Dec.	Catch in Finnmark Oct./Nov./Dec.	Estimated total effort
1955	17.2	157	913
1956	25.5	292	1145
1957	41.1	153	372
1958	45.9	210	457
1959	37.3	184	493
1960	32.3	209	647
1961	41.9	136	324
1962	63.1	134	211
1963	86.4	119	137
1964	68.0	142	209

Table 5. Records of catch and effort in 1962/63 for 12 vessels using nets of different mesh sizes.

Week No.	16" and 18" mesh			18" and 20" mesh			All nets		
	Catch kg	No. of nets	kg/net	Catch kg	No. of nets	kg/net	Catch kg	No. of nets	kg/net
46	320	186	1.7	644	215	3.0	964	401	2.4
47	469	204	2.3	31	30	1.0	500	234	2.1
48	421	165	2.6	409	220	1.9	830	385	2.2
49	1719	556	3.1	1944	400	4.9	3663	956	3.8
50	1264	392	3.2	549	205	2.7	1813	597	3.1
51	1714	485	3.5	1595	320	5.0	3309	805	4.1
52	169	70	2.4	—	—	—	169	70	2.4
1	199	60	3.3	179	30	6.0	378	90	4.2
2	1761	248	7.1	2887	355	8.1	4648	603	7.7
3	2451	332	7.4	1118	105	10.6	3569	437	8.2
4	337	55	6.1	3101	270	11.5	3438	325	10.6
45-48 (Nov.)	1469	627	2.3	1084	465	2.3	2549	1092	2.3
49-52 (Dec.)	4866	1503	3.2	4088	925	4.4	8954	2428	3.7
1-4 (Jan.)	4748	695	7.0	7285	750	9.7	12033	1445	8.3
Total	11183	2825	4.0	12457	2130	5.8	23540	4955	4.8

20" used by some vessels, while the dimensions of the nets themselves remained unchanged. It is interesting to note that the shift to larger mesh sizes was already started voluntarily before the 18" mesh was prescribed by the new regulation in 1961 as a direct result of the successful experiments with large meshed nets carried out by the Institute of Marine Research from 1957 to 1960.

This mesh increase was probably partly responsible for the more than doubling of CPUE which occurred after 1961 and which was apparent throughout the season. Some data from 1962-63 (Table 5) of catch rates for 16" and 18" nets compared with 18" and 20" nets suggest that the immediate effect of the mesh size increase would be of the order of 40% to 50%. Any long term effects of increasing the exploitation age, as discussed by MATHISEN and OLSEN (1968) would not take effect immediately, and hence, the rising CPUE must also have been caused by other factors than the use of larger meshed nets.

There is no evidence suggesting that the rise in CPUE estimates could be related to increased effective fishing time of the nets in recent years; in fact, any trend here would be towards decreasing fishing time when nylon nets were introduced because the fish die quickly in such nets and the quality then deteriorates.

One possible cause is the increase in the minimum landing size of halibut from 50 cm to 65 cm introduced in 1956. This regulation certainly reduced the fishery for small, immature halibut at the Finnmark coast, and any effects of the reduced fishing mortality of these age groups (3-5 years) would not be felt in the gillnet fishery for mature halibut until at least 6-7 years later.

Finally, one should consider the apparent fall in total effort of the Finnmark halibut fishery, which in itself is probably related to a gradual change during the same period in the structure of the fishing fleet and the overall reduction in the number of fishermen. In Fig. 3 CPUE is plotted against the two years sum of estimated total effort. This indicates a direct relationship between CPUE and effort which for the range in total effort experienced during the 1955-65 period could well account for the observed increase in CPUE.

This relationship might be composed of two components. Firstly, it could reflect a true density change resulting from variations in fishing mortality. However, it is also likely that the reduced and low participation in this fishery in recent years, which is conducted in fairly restricted localities, has had a direct and immediate effect on the efficiency of the operations for the individual vessels, allowing more careful selection of the fishing places for the nets and practically eliminating any chance of entangling or conflict between different vessels.

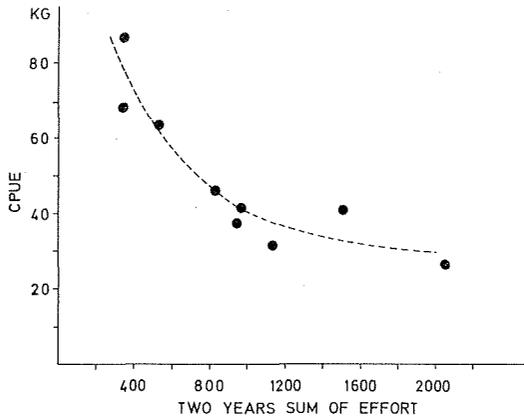


Fig. 3. Estimates of catch per unit effort (CPUE) at Øksfjord for November/December plotted against two year sums of estimated total effort for the county of Finnmark during October/November/December.

The present data have thus demonstrated that the trend of decrease in the halibut landings in Finnmark from 1955 onwards was most likely caused by reduced fishing effort, while in the gillnet fishery for mature halibut the CPUE increased greatly. This increase was partly caused by more efficient nets and less competition on the fishing grounds, but it also reflects a real increase in fish density resulting from the lower fishing mortality in the mature stock, the increased exploitation age, and possibly improved recruitment to the mature stock resulting from the raising of the minimum landing size introduced in 1956.

SUMMARY

1. This study was based on statistics of gill net caught halibut landed at Øksfjord, West Finnmark from 1955 to 1965. For the most recent years some data on relative effort and weight distribution of the catches were also available.
2. Small annual fluctuations in size distribution of the catches occurred, but no consistent trend over the years were apparent.
3. During the 10 year period studied, halibut landings in the last quarter of the year decreased markedly both in the county of Finnmark as a whole and at Øksfjord. However, during the same period catch per unit of effort in the gill net fishery increased greatly, and consequently, the estimated total effort was very much reduced.

4. It is concluded that the reduced landings resulted mainly from reduced fishing effort while the increase in catch per unit of effort was partly caused by improved fishing nets and less competition on the fishing grounds, but was also reflecting a real increase in fish density.

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ON THE PROBLEM OF THE EFFECT OF FISHERIES ON FISH STOCKS

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When we consider the problem how the fisheries affect the fish stocks and their reproduction the most important and principal question arises whether the fish have ever encountered the influence of any factor similar to that of the fisheries. In other words, we ask if the fish have been able to adapt themselves to some influence which can help them to stand the fishing effect, or whether the fisheries are quite a new factor to them, and they are not prepared at all.

In ichthyological literature the effect of fisheries is, to some extent, considered similar to that of predators on the fish stock. The suggestion seems to be true for small sized abundant species which are, in fact, subject to such an influence under natural conditions. However, the fishing and predatory effects differ substantially. The fishery is usually based on the adult portion of the population, and due to longer contacts between the fishery and older age groups the numerical strength of the latter is drastically reduced. The “rejuvenation” process is always a consequence of the fishery. Predators, on the contrary, take younger age groups. The predatory effect never leads to rejuvenation of the population. Thus, the fishing effect is of specific character, and the majority of fish in their development and during the adaptation process to the environment have never encountered influences resembling the fishing effect under natural conditions. Furthermore, many biologically adapted features which are acquired due to evolution and advantageous to the fish under natural conditions are turning into disadvantageous habits, thus increasing the effect of fisheries on the stocks and the reproduction.

This can be illustrated by a number of examples (Table 1). In many fish species the bodies are covered with bone knobs, hooks and thorns,

Contribution given in honour of Gunnar Rollefsen at his 70th birthday.

Table 1. Adapted features in fish, their biological significance and negative role under condition of intensive fishing

Adapted features	Biological significance	Negative role under fishing conditions
1. Knobs, hooks and thorns on fish bodies, thorny rays in fins	Protection of fish, especially young from predators	Tangling in nets and difficulty in escaping through meshes
2. Height and width of fish bodies	Lower predatory effect on young fishes	Enmeshing in nets with relatively large meshes
3. Shoaling	Lower predatory effect	Efficient detection of shoals by echosounders and asdics
4. Multiage composition of a population	Increase in the reproductive ability of the population	Decline in the reproductive ability as a result of rejuvenation of the stock caused by intensive fishing
5. Gradually maturation of eggs and spawning in batches	Increase in the reproductive ability of a species	Due to longer stay spawners are more easily caught on spawning grounds
6. Low metabolism in winter during the period of maturation	Savings in energy	Higher accessibility to the fisheries
7. Ability of burying themselves in the ground	Protection from predators	Failure in escaping fish nets
8. Well developed receptive system in tuna	Detection of prey	Increase in the space between hooks and extension of longlines
9. High speed of movement in tuna	Chasing for prey, escape from predators	Spread of the area fished by a longline
10. Habit of avoiding zones with high velocities of water in the river in many anadromous fishes	Savings in energy during anadromous migrations	Better access to the fisheries in shallow localities in the river

and the fins have thorny bone rays. These peculiarities can be looked upon as an adapted protection of the species, especially the young, against predators. Due to these features the bycatch of young increases under intensive fishing since it is difficult for them to escape through the meshes of nets and trawls and easy to get tangled in the meshes of the different gears. The best evidence of the negative role of the morphological peculiarities is tangling of the young of sturgeon in fixed and drift nets. This greatly affects the fish stock.

Great width and height of a fish body protect the fish from predators.

In the fishery, due to the height of the body, young specimens are entangled in nets with rather big meshes. Flounder, bream and some other species may exemplify this fact. The peculiarities of their body form impede selective fishing.

Shoaling can, to a certain extent, be considered a means to protect the fish from predators. However, the fishery with modern scouting techniques is facilitated by the shoaling and yields good catches.

A multiage composition of a spawning population leads to some increase in the reproductive ability of a species. Intensive fishing may result in a rejuvenation of the stock by reduction in the older age groups in the spawning population and finally, lowering of the reproductive ability of the species.

The fecundity of fish increases when the eggs mature gradually and is spawned in batches. This enables the fish to use much more of the energetic resources of the body as compared to the case where all the eggs ripen at the same time. Under fishing conditions a gradual maturation makes females stay on the spawning grounds much longer, chances for catch, thus, increases.

A lower rate of metabolism in winter, in the period of gonad maturation is observed in many species of fish. The phenomenon enables a species to save some energy for spawning. Low mobility of fish in this period makes them more vulnerable to fishing gear. The winter fishery for carp is based on this peculiarity as the fish are taken in deeper hollows.

Many species of flat fishes bury themselves in the ground to escape predators. The same reaction in fish to a coming trawl is observed, but all their efforts are in vain when the trawl is too near.

Tuna possess a well developed receptive system which enables them to locate prey over a radius of several dozen meters. Owing to this peculiarity hooks can be arranged with wider spaces, say 70–100 m apart, and the longline stretched to over 100 km.

The great swimming speed of the tuna causes an expansion of the efficient area of a longline, and the efficiency increases in proportion to the speed of the tuna moving over the area. As a result, a harmless gear, as it may seem at first sight, turns into one of the efficient means in the marine fisheries. Let us assume that the average speed of tuna is as low as 5 km per day when the longline is arranged in the water; a longliner then can cover the area of 500 square km. Even if not more than 20% of the fish inhabiting the area are caught, the catch per day per longliner will correspond to a yield from an area of 100 square km. Actually, the tuna is moving much faster.

The sturgeons moving upstream to their spawning areas, avoid zones with high velocities of water. To save their energy they migrate over

shallow places where they are more easily caught by seines than in deeper places of the river.

It is very likely that far more examples can be given as evidence for how adapted features, biologically advantageous, may turn into disadvantageous habits under the condition of intensive fishing.

All these facts reveal that the effect of fisheries on fish stocks is related not only to the technical progress and its excessive scale, but also with the aspect that some adapted features in fish is counteractive under conditions of intensive fishing, thus making the effect of fisheries more pronounced.

Programmes of further investigations should include examination of adapted features in fish which tend to have counteractive effect under fishing conditions, as well as comparative studies of these features under natural and fishing conditions.

SUMMARY

It is demonstrated by examples that morphological, physiological and behavioural features of fish developed evolutionary and normally of protective value are directly disadvantageous to the fish when subjected to intensive fishing.

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EFFECTS OF OCEAN THERMAL STRUCTURE ON FISH FINDING WITH SONAR

By

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THE ACTIVE SONAR FORMULA

The sonar equipment has become in common use in most modern offshore fisheries in the North Atlantic. The performance of the sonar in fish finding depends on a multitude of factors, such as the technical properties of the sonar itself (e.g. the frequency used), the self noise of the vessel, the skill of the operator and, not least, the environment in which the sound propagates. This paper deals with the effects of the ocean thermal structure on the sound propagation.

The noise limited active sonar equation can be presented in a general form:

$$M_n = (S_o + T - 2H) - (N + \Delta R)$$

where M_n is the signal to noise ratio (or the recognition differential), S_o is the original signal strength, T is the target strength (or its scattering cross section) and $2H$ is the two-way propagation loss in the water. N and ΔR present the self noise and the directivity index (i.e. the gain of the signal due to receiving directivity) respectively. In reverberation limited condition, the last term ($N + \Delta R$) represents the reverberation level.

The noise level N depends on environmental noises, such as those caused by breaking waves, by noise making marine animals, rain, traffic, and first of all, by the ships' own noises carrying the sonar.

EFFECTS OF OCEAN ENVIRONMENT ON THE PROPAGATION OF SOUND

The sound impulse emitted by a sonar or an echo sounder is subject to a number of losses during its travel through the water: the absorption

Contribution given in honour of Gunnar Rollesfsen at his 70th birthday.

loss in water, the geometrical spreading loss, surface scattering (reverberation), volume scattering and bottom reflection or scattering loss.

The absorption loss in water is greatly dependent on the frequency used by the sonar, and also depends on the temperature of the water:

$$a = \frac{0.17}{T + 18} f^2$$

where a is absorption loss, T is temperature of the water and f is the frequency. The surface scattering depends on the roughness of the surface (e.g. the wave height) and sonar frequency. The bottom scattering is a relatively complex function of the type of sediment, bottom roughness and frequency. The volume scattering depends on frequency and on the amount of scatterers (such as air bubbles, plankton and fish).

The geometrical spreading loss depends on the vertical distribution of the sound speed in the water. This aspect of the sound propagation is described in this paper in relatively easily measured and/or predicted ocean thermal structure parameters—sea surface temperature (SST), mixed layer depth (MLD) (the depth of the top of the thermocline), and the gradient of temperature between the surface and the MLD (“in layer gradient”, INGRAD).

EFFECTS OF OCEAN THERMAL STRUCTURE ON THE PROPAGATION OF SOUND

GENERAL SOUND PROPAGATION MODEL IN RELATION TO THERMAL STRUCTURE

The sound waves, as most true wave motions, follow the SNELLIUS law, i.e. they refract towards the lower velocity of propagation. It is most appropriate to present the propagation paths in the form of sound rays which are perpendicular to the wave front.

A typical sound speed structure and a few significant sound rays are given in Fig. 1. The following features of interest are depicted in this figure: (a) the sound propagation in the surface duct, (b) the distance of the “partial shadow zone”, and (c) the width and distance of the bottom bounce beam. The dependence of these features on the thermal structure were investigated, using a precision ray tracing technique (AYRES, WOLFF, CARSTENSEN and AYRES 1966) on the CDC 1604 computer. This ray tracing technique uses a time step of 1/124 second and a space step of 10 metres and includes the effects of the curvature of the earth. A ray bundle of 16° ($+8^\circ$ to -8°) was used corresponding roughly to the average beam width of sonars in use.

The ray traces of various thermal structure profiles (33 in number) with varying SST, MLD and INGRAD were computed. A few examples

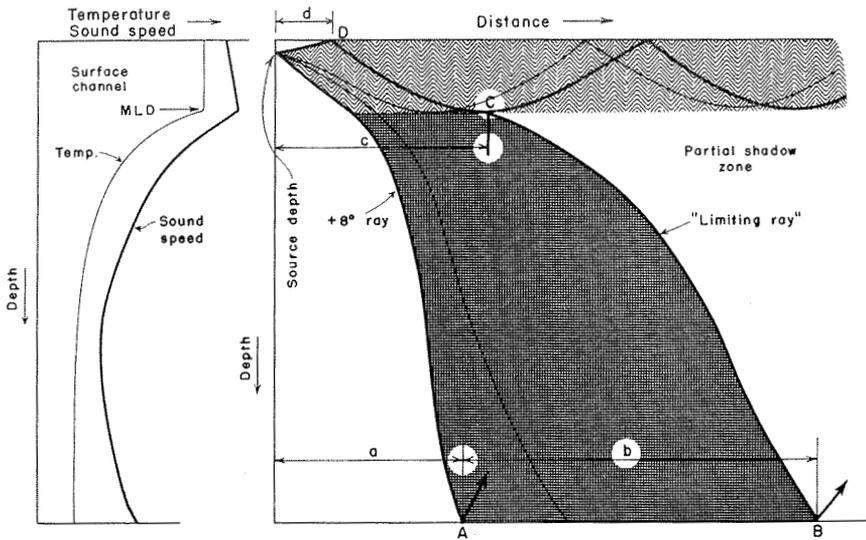


Fig. 1. A typical temperature and sound speed profile and significant sound rays.

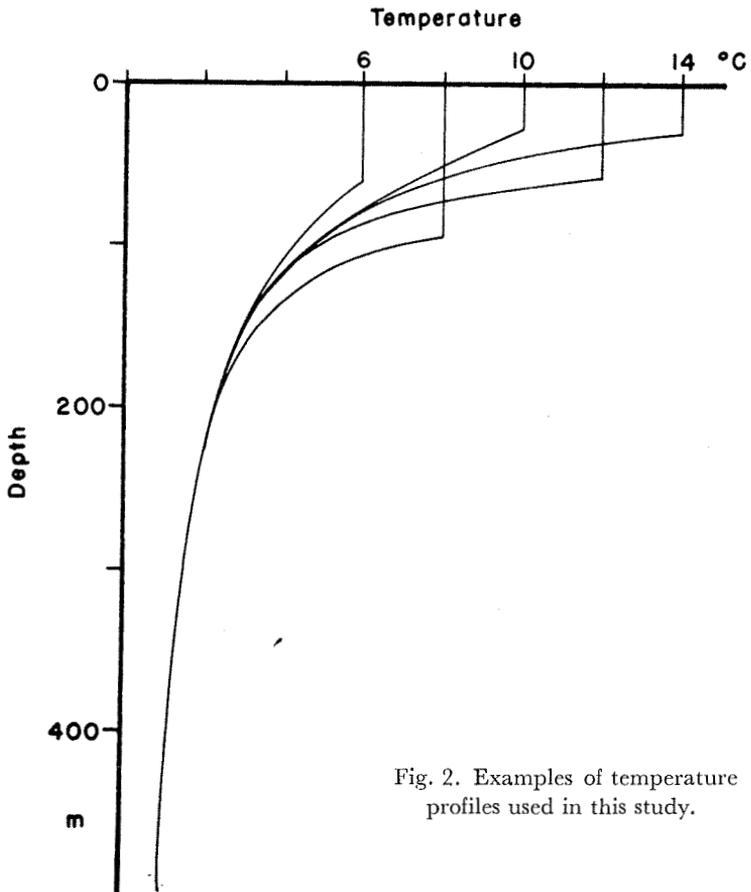


Fig. 2. Examples of temperature profiles used in this study.

of the selected profiles are shown in Fig. 2. The study of the influence of SST and MLD on the sound propagation parameters of interest was made with an isothermal layer from surface to MLD. Thus, the sound speed increases from the surface to the MLD where it reaches a maximum due to pressure effects on sound speed. Some of the nearly horizontal sound rays will become trapped in the surface mixed layer as the sound rays bend slightly towards the surface above the MLD. A separate study was made of the effects of negative temperature gradients between the surface and the MLD.

The ray tracing was computed to a maximum depth of 500 metres and to a maximum distance of 10 kilometres. The salinity was taken constant from the surface to 500 metres. The effect of salinity on sound speed is considerably smaller than that of temperature. Furthermore, it is relatively easy to ascertain the synoptic thermal structure (e.g. with bathythermograph cast) from a fishing vessel, whereas the determination of synoptic salinity structure from fishing vessels is, at present, not possible.

SEA SURFACE TEMPERATURE, MIXED LAYER DEPTH AND "IN LAYER GRADIENT" AS BASIC PARAMETERS FOR ESTIMATION OF SOUND PROPAGATION PATH IN NEAR-SURFACE LAYERS

The portion of sound energy, trapped in the surface layer and measured here in terms of the width of the trapped beam, depends greatly on the MLD (Fig. 4) and partly on source depth. However, Fig. 4 indicates that this beam width is also slightly dependent on SST. This latter dependence is mainly caused by the non-linearity of the sound speed dependence on temperature and depth (see Fig. 3).

The relation of the width of the bottom bounce beam to the SST and MLD is shown on Fig. 5. The "inner limit" (distance a on Fig. 1) is independent of MLD but dependent on SST. The relation to SST, although statistically a very good and reliable one, is, however, an indirect relation, the direct cause being the thermocline gradient and magnitude. It can be noted that if the transducer/receiver beam width is 16° and if it is horizontal, the area with a radius of a (see Fig. 1) is not sonified by such a sonar beam. This area, however, is sonified by vertical beams (such as an echo sounder beam).

The width of the bottom bounce beam (distance b) depends on depth (taken constant, 500 m in Fig. 5), SST and MLD. Again, the relation to SST is an indirect one via thermocline gradient and magnitude.

Fig. 6 presents the relations between SST, MLD and the closest point immediately below the top of the thermocline where the "partial shadow zone" starts (distance c in Fig. 1). The term "partial shadow zone" is



Fig. 3. Sound speed at different temperatures (0 and 500 m depth, salinity = 35‰).

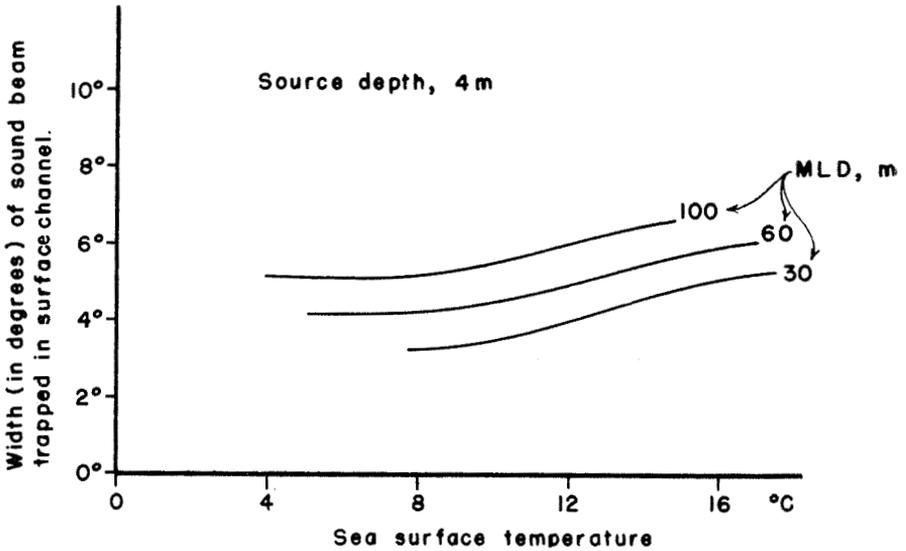


Fig. 4. Beam width of sound trapped in surface channel at different SST and MLD (source depth 4 m).

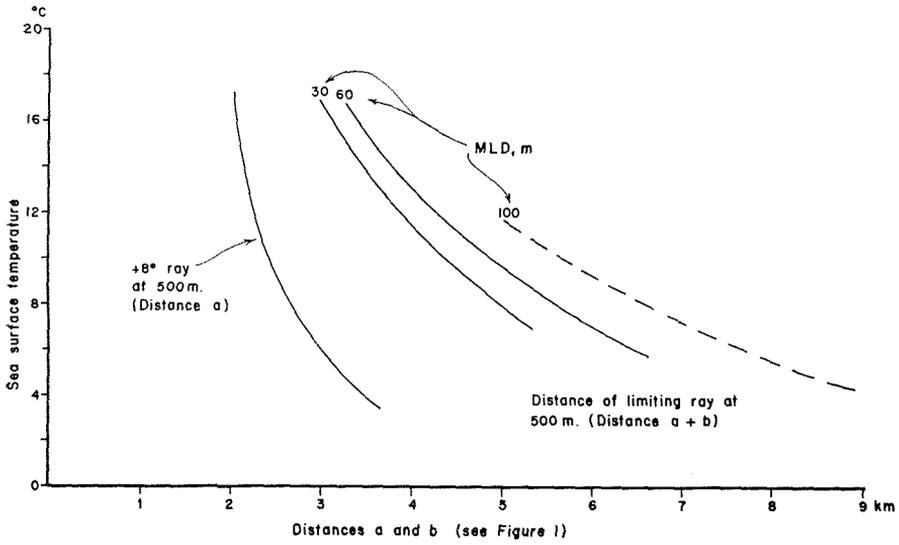


Fig. 5. Horizontal distance and width of the bottom-bounce beam in 500 m depth in relation to different SST and MLD.

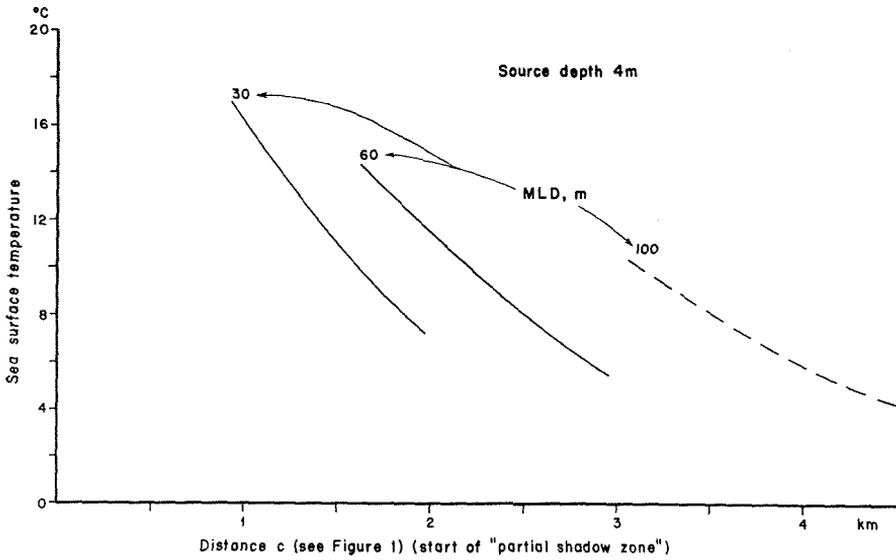


Fig. 6. Closest distance to "partial shadow zone" immediately below MLD in relation to different SST and MLD.

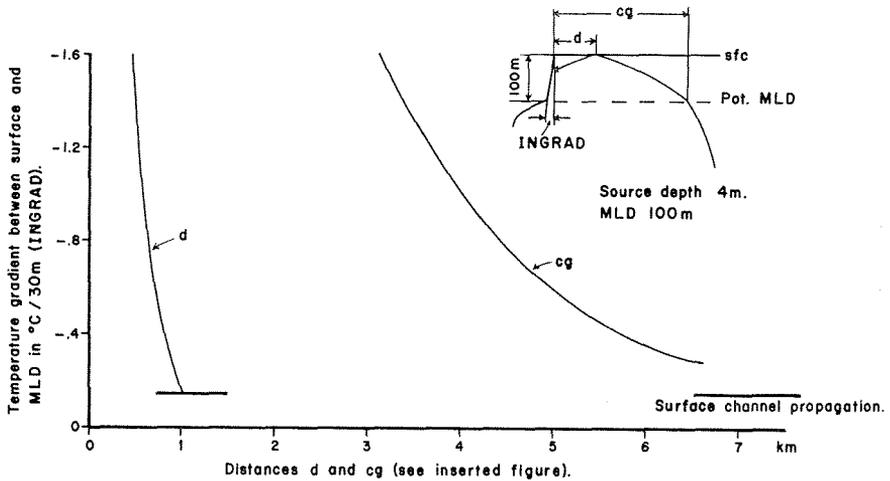


Fig. 7. Maximum grazing distance at the surface and distance at which last surface grazing ray leaves surface channel at different "in layer gradient" (INGRAD) (source depth 4 m, MLD 100 m).

used because this zone is not entirely void of sound (derived from bottom bounce and from bounce on irregular surface and irregularities in the interface (MLD)). The "distance c " is obviously greatly dependent on MLD and source depth, but also depends on SST, as Fig. 6 indicates. This latter dependence is directly caused by the sound speed change with temperature and by the non-linearities in this change (Fig. 3).

The above described relations referred to the isothermal surface mixed layer. However, this layer is not always isothermal and contains small transient thermoclines, especially during the heating season in spring and early summer. Computations with different negative temperature gradient above the top of the thermocline were made, and the results are presented in Fig. 7.

When the temperature gradient (INGRAD) in the surface layer is more negative than -0.15°C per 30 m, there is no surface channel propagation. The distance at which the last ray leaves the surface layer depends on the MLD and the INGRAD (see Fig. 7).

Finally, it is emphasized that the relations described above referred to the delineation of the sonified field. The computation of fishing sonar ranges must include propagation loss computations and other parameters, as briefly outlined in the first two chapters.

SUMMARY

1. The width of the sound beam trapped in the surface channel depends, besides on MLD and INGRAD, also on SST. The latter relation is brought about by nonlinearity in the sound speed dependence on temperature and depth (Fig. 4).
2. The bottom bounce beam width depends primarily on the temperature gradient and magnitude of change in the thermocline. With limited sonar beam width, the area near the ship below the thermocline is not accessible to horizontal beams (Fig. 5).
3. The distance to the "partial shadow zone" depends primarily on MLD, but is also affected by SST (Fig. 6).
4. If the INGRAD is more negative than -0.15°C per 30 m, there is no surface channel propagation. The distance at which the sonified field in the surface channel ends, depends on INGRAD and MLD (Fig. 7).

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DESIGN OF A SONAR FOR FISH COUNTING

By

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INTRODUCTION

Some three years ago the Marine Laboratory commenced a study of the feasibility of making population assessments by echosounder. The species of prime interest was the herring of the northern North Sea.

The study involved a review of work in progress elsewhere, a decision about the most suitable kind of equipment to use, and consideration of the statistical mathematics required for the interpretation of results. The choice of equipment, and of the resolution required, was of course influenced by the known facts about the distribution of herring.

It was felt that the counting and sizing of individual echoes would provide more information than an integration method, as it offered the prospect of classifying fish in accordance with their target strength (T decibels). To make this a practical method for routine surveys a degree of automation was required, so that the observational task aboard ship could be kept to reasonable proportions.

Since the population density of herring can be at times very high (as much as 10 or 20 per cubic metre in daylight schools) it was decided to aim for the highest degree of resolution attainable within the available funds. Our previous experience suggested that an acoustic frequency of 400 kHz was about the optimum, offering a practical range of about 150 m, and a total beamwidth of about $1\frac{1}{2}^\circ$, using a transducer small enough to mount in a towed body of reasonable weight, around 80 kg (Fig. 1).

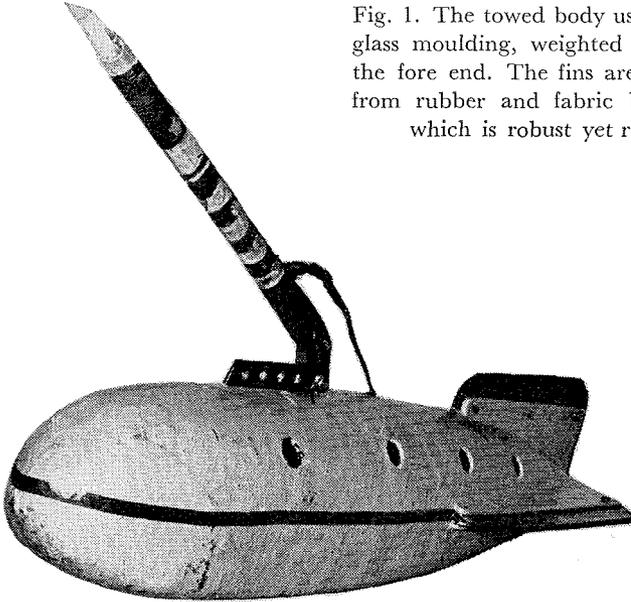
EQUIPMENT

ECHOSOUNDER

A trial equipment incorporating a commercial pulse height analyser was manufactured and used from "Explorer" in July 1967 and 1968. This proved reasonably successful, and a more compact equipment is now

Contribution given in honour of Gunnar Rollefsen at his 70th birthday.

Fig. 1. The towed body used is a fibre-glass moulding, weighted with lead at the fore end. The fins are constructed from rubber and fabric belt material which is robust yet resilient.



under construction, incorporating improved techniques. The principal characteristics of the new echosounder are as follows:

Frequency 400 kHz.

Transducers—circular PZT of 18 cm or 48λ diameter.

Nominal beamwidth 0.011 radians or 0.75° half angle to 3 db point.

Range resolution—better than 15 centimetres, nominal pulse length 100μ sec.

T.V.G. as $40 \log R \times 0.18 R$ (R = range in metres).

Acoustic transmit power about 400 watts. Source level about 138 db ref. 1μ bar at 1 metre.

Transducers in a towed body which also houses a preamplifier of 40 db gain.

Very low noise levels; the RMS noise referred to the transducer is about 0.1μ V.

Effective range for fish counting about 160 metres; for sea-bed echoes about 400 metres.

All timing functions are now controlled by a 100 kHz crystal oscillator. The output of this is divided by a series of 9 decades in integrated circuit form. By conventional use of inverters and gates, output pulses are derived to control transmissions, T.V.G. start and stop, and analyser functions, which will be described later. The 1 kHz decade output is used also to control the motor speed of a precision paper recorder, which acts

as a monitor on the correct working of the whole system, and also provides short-term information about targets. The transmission is derived by gating a crystal oscillator to a conventional transistor push-pull output stage.

The receive system consists at present of a preamplifier with a gain of around 40 db feeding an Eddystone radio receiver to which the time-varied gain (T.V.G.) is applied. The intermediate frequency (I.F.) output of the Eddystone receiver at 720 kHz is tailored to suit the pulse analyser, and the audio circuits left feeding a speaker which is quite distinctive in alerting the operator to fish echoes.

The T.V.G. voltage is derived as the sum of two exponential sweeps, the start and rate of both being accurately controllable.

PULSE HEIGHT ANALYZER

The analyser used is a Laben 400 channel machine, slightly modified to suit the particular application. Such analysers are adaptable to many modes of use, but we confine ourselves here to a standard procedure. Analysis begins 10 milliseconds after transmission, and sorts echoes into 20 time intervals each of 10 milliseconds duration. In other words echoes are classified into twenty depth intervals, the first being from 7.5 m to 15 m, and the last being 150 m to 157.5 m.

Echoes falling into each of these time intervals are classified into twenty amplitude channels, each of 80 millivolts amplitude, and a back-bias of 80 millivolts is applied. Thus the first amplitude channel is 80–160 millivolts, and the last amplitude channel is 1.60 to 1.68 volts. By using a logarithmic amplifier these channels can be converted to decibel levels.

At the end of a predetermined period, the analyser feeds the stored data to a teletype machine to provide both a printed record and a punched tape for subsequent computer processing. At the same time, the stored information is erased, so that after print out the sequence can be repeated.

Thus we have the potential, using a standard instrument, to make a detailed analysis of echo information.

In water less than 157 m depth, the sea-bed echo would give rise to spurious counts. Hence it is necessary to eliminate it. This general problem of sea-bed elimination (S.B.E.) was originally dealt with by stopping the analyser 3 milliseconds before the appearance of the sea-bed echo. The timing for this function was derived from the previous sea-bed echo. This is not precise enough to allow demersal fish to be counted, hence an alternative is being adopted. This is the provision of a transmitted pre-pulse at 300 kHz, which can be used in two ways.

- (a) The pre-pulse is transmitted 200μ seconds in advance of the main transmission. Receipt of the 300 kHz sea-bed echo shuts down the analyser. Thus we have an S.B.E. system allowing fish to be counted to a distance of 20 or 30 cm above the sea-bed.
- (b) Where detailed analysis of the depth distribution of demersal fish is required, the pre-pulse can be made to occur 20.2 milliseconds before the main transmission. The 300 kHz sea-bed echo is now used to start the analyser, which then is swept through its time channels in 20 milliseconds instead of its standard 200 milliseconds, thus sampling a 15-metre layer above the sea-bed.

GENERATION OF SAMPLING PULSES

The pulse analyser is designed to deal with pulses of rise times less than 1 microsecond, whereas rise times of fish echoes in this case are of the order of 80 microseconds. The envelope of the echo signal thus has the characteristic of a slowly varying signal so far as the machine is concerned, and in such a case sampling pulses are required to select the instants for amplitude measurement. The principle used for this is illustrated in Fig. 2. If the incoming pulse is differentiated, a zero-crossing

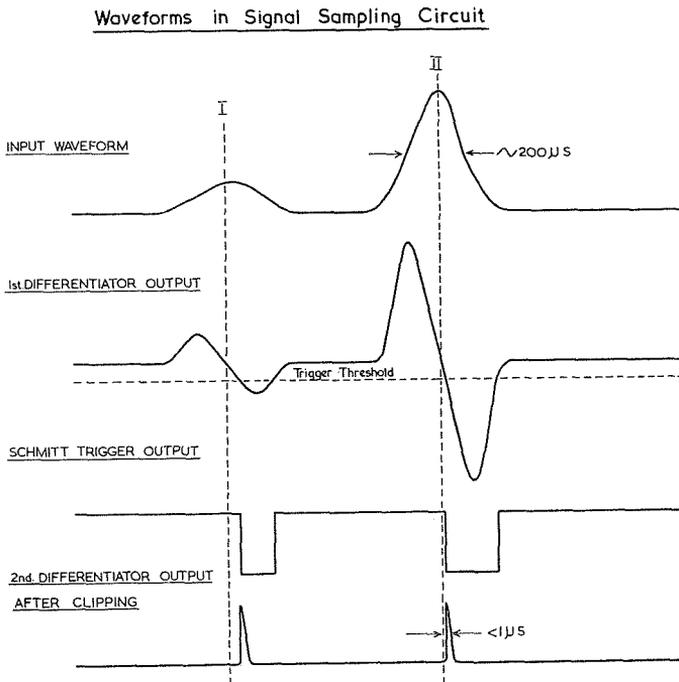


Fig. 2. Waveforms in the signal sampling circuit.

occurs very close in time to the pulse peak. If this differentiated signal is over-amplified to square it, and differentiated again, we can by selecting the appropriate polarity obtain a sampling pulse suitable to trigger the analyser, and occurring at the appropriate instant. The squaring amplifier is in fact a Schmitt trigger, whose threshold is set at a low level to avoid timing errors, as shown in I and II. It is important that this "signal selector" system should be of adequate sensitivity so that it is not itself the limiting factor in echo detection. It is desirable rather that calibrated back-bias control on the analyser should determine the minimum echo height for a count.

RECORDING MONITOR

The working of the analyser produces information pulses when an echo goes into the magnetic core store, and for instance when an echo overflows the top channel. Bearing in mind the original concept, it was desired to ensure that the working of the system could be made obvious and the information displayed immediately in a conventional form. To do this a Mufax paper recorder was employed, the speed being controlled by the same crystal clock as programmed the transmit and analysis cycles. Thus the recorder runs in synchronism with the transmissions in the usual way. It was arranged that storage of an echo by the analyser would generate a 1 millisecond marker pulse, and overflow of the top channel would produce a 7 millisecond marker pulse. Thus fish echoes counted produce small ticks, and the sea-bed echo produces a long mark. If the system is working as intended, a normal-looking recording results which is closely analogous to that of a conventional echo-sounder. It should be noted, however, that the recorder cannot be made to carry as much information as the analyser, as the range resolution on paper cannot be pushed to much less than 1 m. The analyser by contrast gives the full resolution of the acoustic system, its own internal limits in this respect corresponding to a range resolution of about one cm or less.

ANALYSIS

It is easy to predict the distribution of echo amplitudes from a known distribution of targets, but the inverse process is a little more difficult. In the treatment that follows no attempt is made to sort out all the statistical implications, a task we feel to be more appropriate to a professional mathematician. Thus we attempt here to lay down the problem, and an outline solution in such a way as to stimulate more sophisticated mathematical analysis. It will however be evident that the nature of the

directivity function is the determinant of the statistical accuracy attainable. If it were practical to produce a beam of definite angular width, at the edge of which the acoustic energy dropped from a standard value to zero sharply, then very significant results could be obtained even from small numbers of targets. However it will be well enough understood that such a situation can only be approached by the adoption of parameters much more extreme than have been contemplated here, though if a much smaller maximum range were acceptable, as it might be in a plankton counter, one could greatly improve matters in this respect.

The prime assumption made in the present treatment is that the T.V.G. has been so arranged that the echo from a small target is independent of range, i.e. allowance has been made for spreading loss and for attenuation in the medium.

Information is obtained in the form of signal levels. It is based on 20 or 50 minutes' survey, and is printed out and punched on paper tape by the teletype machine.

However the information is wanted in another form, as a distribution of target strengths.

Since the T.V.G. is a full correction, the echo of any target is independent of range. The amplitude depends only on the angular coordinates of the targets.

The essential part of the treatment is to assume some density of fish, and deduce the echo distribution that would result. We then use this to deduce density from echo distribution.

Consider any range slice lying between R_1 and R_2 in the beam, and let the solid angle be k . The volume in the range slice is

$$\int_{R_1}^{R_2} kR^2 dR = 1/3 k (R_2^3 - R_1^3)$$

Thus if there be N_1 targets per cubic metre in this range slice, of target level -40 db, the number contained in the solid angle k is $1/3 N_1 k (R_2^3 - R_1^3)$.

We now have to consider the directivity pattern of the equipment. This can be obtained theoretically by combining the transmit and receive directivities. Better, it can be obtained by direct field trial at some suitable range, e.g. 100 m. The complete way to show the results is to plot a cross-section of the beam and we may suppose this to have been done. (Fig. 3.) The levels chosen are arbitrary and have been chosen so as to include a suitable gain for our purpose. Since the beam angle is small, the area within a contour measured in (radian)² corresponds to the solid angle in steradians.

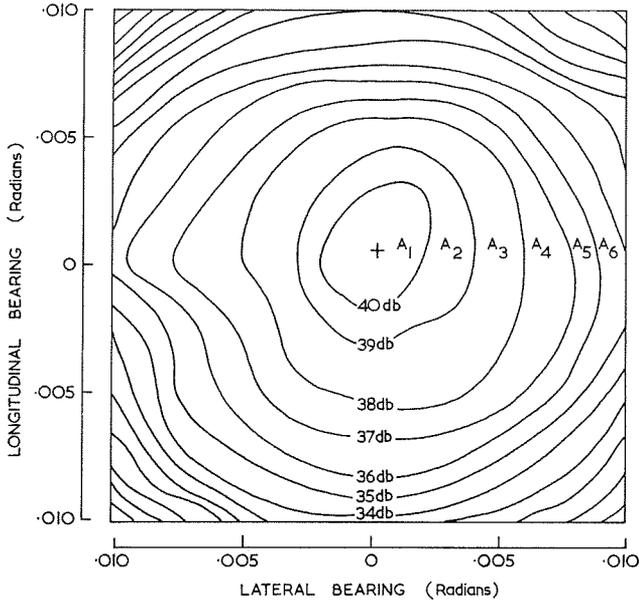


Fig. 3. Cross-section of acoustic beam pattern.

The -40 db targets will be detected only in the centre area A_1 , and the echoes will be between 0 and 1 db. We call this channel 1. The number of echoes in this class is $N_1 \cdot 1/3 k(R_2^3 - R_1^3)$ where we now know $k = A_1$.

Now consider there to be N_2 targets present of target level -39 db. These will give $N_2 \cdot 1/3 A_2(R_2^3 - R_1^3)$ echoes in channel 1 plus

$$N_2 \cdot 1/3 A_1(R_2^3 - R_1^3) \text{ echoes in channel 2}$$

— and so on.

Suppose an eventual count in this depth slice was n_1 echoes in channel 1, n_2 in 2, n_3 in 3 and so on. Then we see that

$$\left(\frac{3}{(R_2^3 - R_1^3)} \right) \cdot n_1 = A_1 N_1 + A_2 N_2 + A_3 N_3 \dots + A_{20} N_{20}$$

$$\left(\frac{3}{(R_2^3 - R_1^3)} \right) \cdot n_2 = A_1 N_2 + A_2 N_3 \dots + A_{19} N_{20}$$

$$\left(\frac{3}{(R_2^3 - R_1^3)} \right) \cdot n_3 = A_1 N_3 \dots + A_{18} N_{20} \text{ etc.}$$

giving 20 sets of equations.

A general solution can be found in the form

$$\begin{aligned} \left(\frac{R_2^3 - R_1^3}{3}\right) N_1 &= B_1 n_1 + B_2 n_2 + B_3 n_3 \dots + B_{20} n_{20} \\ \left(\frac{R_2^3 - R_1^3}{3}\right) N_2 &= B_1 n_2 + B_2 n_3 \dots + B_{19} n_{20} \\ \left(\frac{R_2^3 - R_1^3}{3}\right) N_3 &= B_1 n_3 \dots + B_{18} n_{20} \text{ etc.} \end{aligned}$$

where the coefficients $B_1, B_2 \dots B_{20}$ are dependent only on the acoustic beam shape. A computer can put in the range corrections and print out the desired data in the form of target density as a function of target strength.

The estimate of mean density has finally to be divided by the number of transmissions.

ACCURACY

In order of importance, the accuracy of the system is dependent on (a) knowledge of the attenuation of sound in sea water, which determines the constants of the time-varied gain; (b) accuracy of determination of the beam pattern. When these are sufficiently known to give confidence, it may be worth introducing a correction for ship speed, which causes the transmit and receive beam patterns to be displaced relatively by a small angle. It must also be accepted that roll or pitching of the towed body, if accurately known, would give rise to calculable corrections.

PRELIMINARY SURVEY

A preliminary survey was carried out east of the Shetlands during August 1968. As, at this stage, the analyser output was being printed, not punched, a full analysis cannot be presented. However, some indication of the nature of the observations will be helpful. Transmissions were made every two seconds, data were recorded for twenty minutes in every half hour and printed out during the remaining ten minutes. The total number of counts in any half hour period varied enormously, from zero to over one thousand. During preliminary trials the gain was set at a level where very few counts were recorded in the highest amplitude channel, and during the survey only a very few echoes overspilled this level, indicating that the gain setting was about right for the population being sampled. Two samples of Mufax record are shown in Figs. 4 and 5, Fig. 4 showing a large mid-water school with some fish traces near the bottom in 110 m, while Fig. 5 shows a more scattered population.



Fig. 4. Sample record from the Mufax precision recorder, used to monitor the system. The record shows a large shoal and demersal fish and covers 2 miles in 110 m depth.

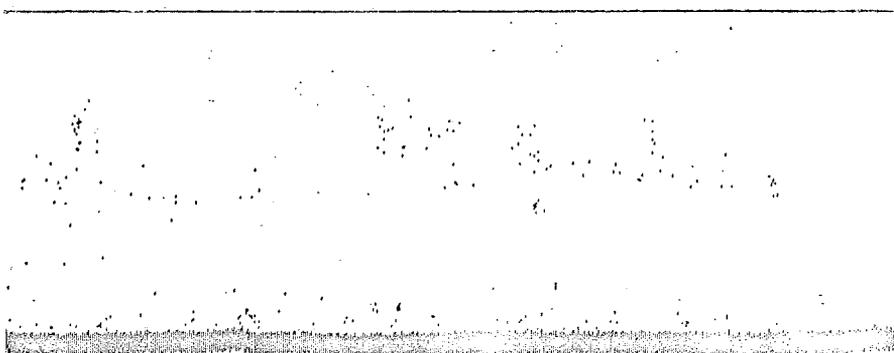


Fig. 5. Sample record from the Mufax precision recorder, used to monitor the system. The record shows scattered fish and covers 2 miles in 130 m depth.

Total counts recorded during a selected 24-hour period amounted to 845 for the region of depth of less than 52.5 m, and 6,561 for the region below 52.5 m. After applying corrections for range, this gave a pelagic fish estimate of 845 per million cubic metres for the upper zone, and 322 per million cubic metres for the deeper region. The selected period involved a north-south steam about fifty miles east of the Shetland Islands. Since paper tape was not in use at that stage, a full analysis cannot be given, nor were the various calibrations sufficiently advanced for this to be offered as a serious fish assessment.

It will be clear that a great deal of work remains to be done, in particular on transducer measurements, and in general on acoustical target strengths of fish. It appears, that the technique can give a great deal more information about pelagic fish populations and distribution than has been hitherto available.

SUMMARY

The paper described (a) A very high resolution echo-sounder, (b) A method of sorting echoes by amplitude and range, (c) A study of the analysis required to transform from distribution of echoes to distribution of targets.

Under (a) the main parameters were—frequency 400 kHz—range resolution 15 centimetres—beam angle to half-power point 0.011 radians.

The equipment for recording echoes (b) is a pulse height analyser. Echo information is stored in twenty range intervals, each subdivided into 20 categories of amplitude.

It was shown (c) that the process of determining target distribution from echo distribution can be dealt with by computer, and resolves itself into a correction for angular spread of the beam, followed by a transformation to allow for the directivity pattern. This latter transformation is equivalent to solving twenty simultaneous linear equations for each range element. The coefficients of the equations are constants for the equipment, thus the set can be solved once, and the result applied to each successive range element by a simple programme.

ACKNOWLEDGMENTS

The authors wish to express their thanks to Messrs. R. G. LAWRIE, I. B. PETRIE and R. L. CRAIG for aid in design and construction of the equipment, and to Mr. R. BROOMFIELD of Nuclear Enterprises Ltd., Edinburgh, for his work in modifying the pulse analyser.

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THE RELATIONSHIP BETWEEN ARCTIC AND
COASTAL COD IN THEIR IMMATURE STAGES
ILLUSTRATED BY FREQUENCIES OF
GENETIC CHARACTERS

By

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INTRODUCTION

The cod, *Gadus morhua* L., which inhabit the Norwegian coast and the Barents Sea, form two genetically separate populations (MØLLER 1968a). In spite of the simultaneous spawning in the same areas the two groups of cod have significant differences in frequency of the haemoglobin *HbI*¹ allele (SICK 1965) and of the blood types A and E (MØLLER 1967). The investigations did not record possible gene flow from one gene pool to another, implying that the Arctic and the coastal cod should be regarded as two sibling species (MØLLER 1968b).

The present paper describes the variation of the *HbI*¹ allele and the blood type E frequencies of samples of immature cod, which have been collected inshore and offshore at the bottom along the Norwegian coast and in the Barents Sea. Since Arctic and coastal cod are characterized by certain frequencies of these characters (MØLLER 1968a), this variation also gives expression for the relationship between immature Arctic and coastal cod.

Portions of this material have been published previously either as a part of other investigations (FRYDENBERG, MØLLER, NÆVDAL, and SICK 1965; MØLLER 1967) or as a preliminary report (MØLLER, NÆVDAL and VALEN 1967).

MATERIAL AND METHODS

The material consists of two main parts: fourteen samples of cod fry, totalling 914 specimens, from the Vestfjord, Troms, and Finnmark area (Table 1, Fig. 1); and forty-eight samples of young cod, of which the

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Table 1. Date, locality and number of specimens of, and gear used for collected cod fry samples.

Sample No.	Date	Locality	Number of specimens	Gear
1	4 Oct. 63	Øksfjorden	60	Shore seine
2	4 Oct. 63	Øksfjorden	65	Shrimp-trawl
3	27 Oct. 64	Øksfjorden	60	Shrimp-trawl
4	3 Oct. 63	Gausvik, Vågsfjorden	81	Shore seine
5	28 Oct. 64	Gausvik, Vågsfjorden	73	Shore seine
6	3 Oct. 63	Rolla, Vågsfjorden	77	Shrimp-trawl
7	28 Oct. 64	Rolla, Vågsfjorden	80	Shrimp-trawl
8	5 Oct. 63	Eidsfjorden	22	Shore seine
9	5 Oct. 63	Eidsfjorden	84	Shrimp-trawl
10	9 Oct. 63	Ulsfjorden	85	Shore seine
11	9 Oct. 63	Ulsfjorden	67	Shrimp-trawl
12	8 Oct. 63	Altafjorden	68	Shore seine
13	8 Oct. 63	Altafjorden	15	Shrimp-trawl
14	1 Nov. 64	Varangerfjorden	77	Shrimp-trawl

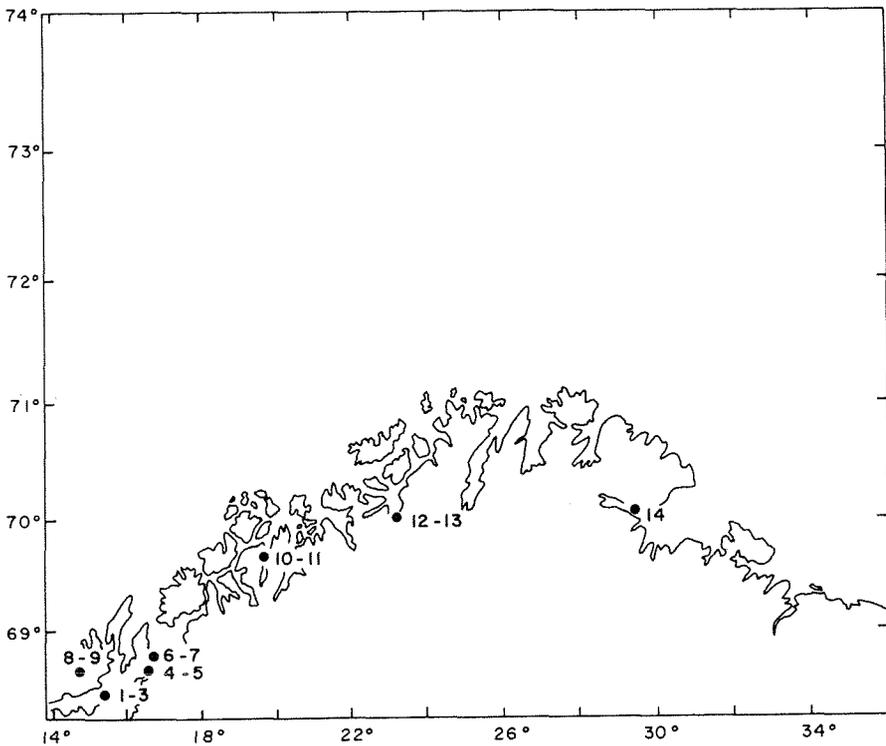


Fig. 1. The location of capture of fourteen cod fry samples.

Table 2. Date, locality and number of specimens of, and gear used for collected samples of young cod.

Sample No.	Date	Locality	Number of specimens	Gear
1	4 Oct. 63	Øksfjorden	57	Shrimp-trawl
2	27 Oct. 64	Øksfjorden	80	Shrimp-trawl
3	25 Oct. 65	Øksfjorden	109	Shrimp-trawl
4	3 Oct. 66	Øksfjorden	115	Shrimp-trawl
5	3 Oct. 63	Gausvik, Vågsfjorden	28	Shore seine
6	26 Oct. 65	Rolla, Vågsfjorden	26	Shrimp-trawl
7	28 Oct. 65	Målsnes, Malangen	85	Shrimp-trawl
8	30 Sept. 66	Målsnes, Malangen	97	Shrimp-trawl
9	10 Oct. 63	Tromsø	191	Trap-net
10	9 Oct. 63	Breivik, Ulsfjorden	20	Shore seine
11	7 Oct. 63	Breivik, Ulsfjorden	156	Shrimp-trawl
12	11 Nov. 64	Breivik, Ulsfjorden	115	Shrimp-trawl
13	16 Sept. 66	Breivik, Ulsfjorden	120	Shrimp-trawl
14	29 Oct. 65	Grøtnes, Ulsfjorden	59	Shrimp-trawl
15	28 Sept. 66	Årøy, Kvenangen	120	Shrimp-trawl
16	29 Sept. 66	Rødøy, Kvenangen	114	Shrimp-trawl
17	8 Oct. 63	Bosekop, Altafjord	156	Shrimp-trawl
18	30 Oct. 64	Bosekop, Altafjord	95	Shrimp-trawl
19	30 Oct. 65	Bosekop, Altafjord	39	Shrimp-trawl
20	19 Sept. 66	Bosekop, Altafjord	120	Shrimp-trawl
21	28 Feb. 66	Sørøya N 71° 03', E 23° 31'	98	Trawl
22	2 Nov. 65	St. Tamsøy, Porsangerfjorden	173	Shrimp-trawl
23	16 Mar. 66	St. Tamsøy, Porsangerfjorden	119	Shrimp-trawl
24	20 Sept. 66	St. Tamsøy, Porsangerfjorden	120	Shrimp-trawl
25	27 Sept. 66	Svaerholt, Porsangerfjorden	118	Shrimp-trawl
26	6 Nov. 64	Mårøy, Laksefjord	96	Shrimp-trawl
27	5 Nov. 64	Kjeldneset, Tanafjord	120	Shrimp-trawl
28	21 Sept. 66	Kjeldneset, Tanafjord	119	Shrimp-trawl
29	26 Sept. 66	Losvik, Tanafjord	120	Shrimp-trawl
30	14 Mar. 63	Tanasnaget N 71° 06', E 29° 00'	115	Trawl
31	20 Apr. 64	Tanasnaget N 71° 00', E 29° 04'	40	Trawl
32	2 Mar. 66	Tanasnaget N 71° 01', E 29° 06'	118	Trawl
33	15 Jan. 67	Tanasnaget N 70° 58', E 28° 59'	120	Trawl
34	12 Nov. 65	Makkaur	119	Long line
35	2 Nov. 64	V. Jacobselv, Varangerfjorden	93	Shrimp-trawl
36	23 Sept. 66	Vadsø, Varangerfjorden	118	Shrimp-trawl
37	16 Jan. 67	Kiberg, Varangerfjorden	120	Trawl
38	4 Mar. 66	Malangsgrunnen N 69° 51', E 16° 42'	97	Trawl
39	21 Nov. 64	Malangsgrunnen N 70° 00', E 17° 10'	79	Trawl
40	19 Nov. 64	Bear Island N 73° 55', E 18° 15'	133	Trawl
41	28 Feb. 64	Nordkapp Bank N 72° 12', E 24° 25'	123	Trawl
42	1 Mar. 66	Nordkapp Bank N 71° 55', E 25° 10'	120	Trawl
43	20 Apr. 64	Nordkyn N 71° 14', E 27° 55'	90	Trawl
44	18 Jan. 67	East Bank N 70° 16', E 32° 25'	117	Trawl
45	12 Mar. 63	East Bank N 70° 06', E 33° 45'	138	Trawl
46	13 Mar. 63	Skolpen Bank N 70° 54', E 34° 00'	80	Trawl
47	10 Mar. 63	Skolpen Bank N 70° 10', E 34° 50'	150	Trawl
48	26 Jan. 67	Skolpen Bank N 71° 21', E 35° 31'	120	Trawl

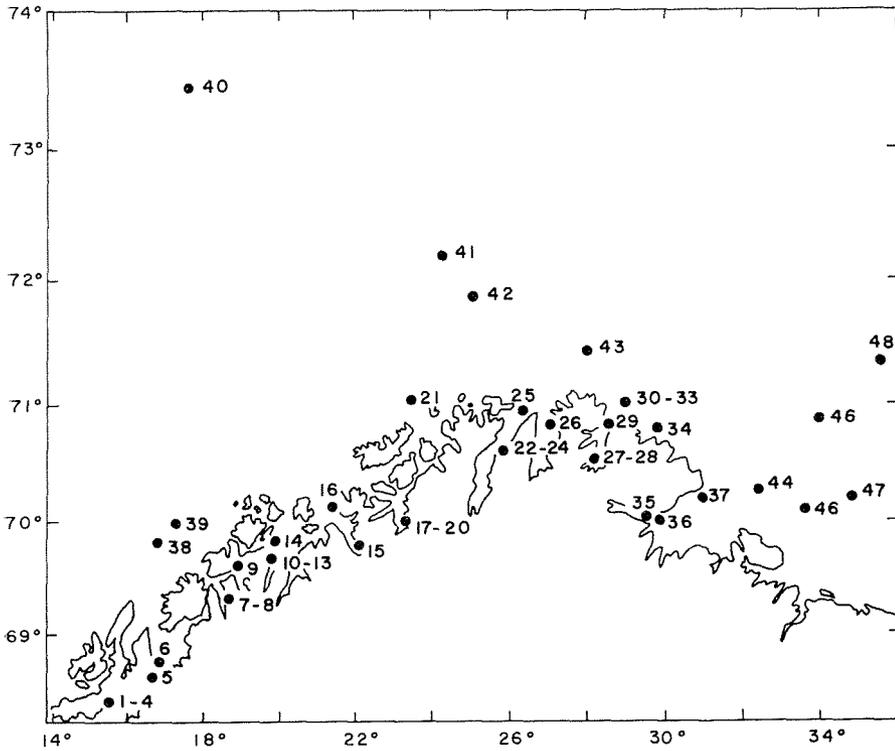


Fig. 2. The location of the forty-eight sampling stations of immature cod.

majority were from three to six years old, totalling about 5,000 specimens, from different localities in northern Norway and in the Barents Sea (Table 2, Fig. 2).

Both in Table 1 and 2 the samples are listed in geographical order from south to north and east. In Table 2 the samples from the coast are presented first and then the samples from the coastal banks and the sea. Samples taken from the same fjord are listed after locality in order from the bottom to the mouth of the fjord.

In addition to date, locality, and the total numbers of specimens in each of the samples, the tables also give information about the fishing gear used. Most of the fish were caught with the help of fishery research vessels, except for the fish caught by trap-nets and the fish in sample 34 (Table 2), which were caught by professional fishermen.

During trawling and long line fishing the depths were recorded by an echo sounder, and the approximate mean depth of the different sampling localities are given in Table 3 and 4. In the same tables the depths for the shore seine and the trap-net fishing are estimated as 2 and 15 m, respectively.

The fry blood specimens were acquired from live fish by cutting the tail, while the other blood specimens were obtained by heart puncture of live cod. The handling of the specimens, the method used in haemoglobin determinations, the blood grouping technique, and the explanation of the nomenclature used in this paper, have been described elsewhere (SICK 1965; MØLLER 1967). However, the blood type E frequency of nine samples, collected in 1963, was not determined due to lack of antisera at that time.

All specimens were analysed at the Institute of Marine Research, Bergen, except for the samples 32 to 35 which were sent to the Institute of Genetics, Copenhagen, where the electrophoresis was carried out (FRYDENBERG *et al.* 1965).

RESULTS

THE VARIATION OF THE FREQUENCY OF THE HbI^1 ALLELE IN SAMPLES OF COD FRY

Table 3 gives the distribution of the haemoglobin patterns, the frequency of the HbI^1 allele (q^1), and the depth of the cod fry samples. The frequencies of the samples vary between .088 (sample 7) and .432 (sample 8), and the frequencies differ significantly among samples taken in the same fjord (samples 1-3, 4-7, and 8-9) and in the same year (samples 4

Table 3. The distribution of the haemoglobin patterns, the frequency of the HbI^1 allele (q^1), and the depth of the cod fry samples.

Sample	HbI^1/HbI^1 homozygotes	HbI^1/HbI^2 heterozygotes	HbI^2/HbI^2 homozygotes	Total of rare types	q^1	Depth of sample in meter
1	4	19	37	0	.225	2
2	4	22	39	0	.231	200
3	3	14	43	0	.167	200
4	8	19	54	0	.216	2
5	7	32	34	0	.315	2
6	0	15	62	0	.097	300
7	2	10	68	0	.088	240
8	4	11	7	0	.432	2
9	4	36	44	0	.262	250
10	6	29	50	0	.241	2
11	7	28	32	0	.313	125
12	9	25	34	0	.316	2
13	2	6	7	0	.333	70
14	3	21	52	1	.175	200

and 6, 5 and 7, and 8 and 9). The differences between these pair of samples from the same fjord are similar with high values of q^1 in shallow water and with low values in deep water.

However, the frequencies have about the same value in the samples 1 and 2, or the difference is contrary with slightly higher values in deep water in the samples 10 and 11, and 12 and 13. Regarding the difference in depth between the samples 11 and 13, and the samples 2, 3, 6, 7, and 9, the main impression is that the frequency of the HbI^1 allele varies to a certain degree with the depth; the lowest values being in deeper water.

This relationship is supported further by treating the samples as grouped data. The depth versus the mean frequency of the samples belonging to the same 50 m class is plotted in Fig. 3. Only the frequencies between 51 and 150 m do not appear to fit in the diagram of correlation between depth and frequency of the HbI^1 allele.

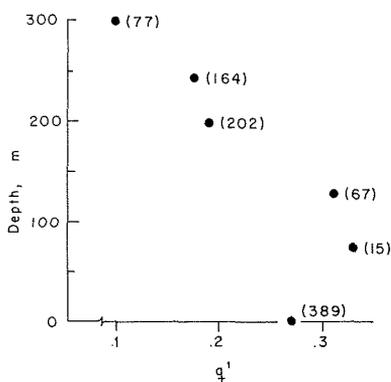


Fig. 3. Relationship between frequencies of the HbI^1 allele (q^1) in samples of cod fry and sampling depths. Figures in brackets represent the number of specimens.

THE VARIATION OF THE FREQUENCIES OF THE HbI^1 ALLELE AND THE BLOOD TYPE E IN SAMPLES OF YOUNG COD

The distribution of the haemoglobin patterns, the values of q^1 , and of the frequency of the blood type E (p^E), together with the depth of the collected samples of young cod are listed in Table 4.

In Figs. 4 and 5 the values in samples from different localities of q^1 and p^E , respectively, are represented on a map of northern Norway and the Barents Sea. In localities which in Table 4 are shown with two or more samples, the values on the maps represent the means.

The highest values both of q^1 and p^E are found inshore (Figs. 4 and 5), whereas mostly all of the values in samples from the banks appear to be comparatively low. In most of the fjords with more than one sample the

Table 4. The distribution of the haemoglobin patterns, the frequencies of the HbI^1 allele (q^1) and the blood type E (p^E), and the depth of the samples of young cod.

Sample	HbI^1/HbI^1 homo- zygotes	HbI^1/HbI^2 hetero- zygotes	HbI^2/HbI^2 homo- zygotes	Total of rare types	q^1	p^E	Depth of sample in meter
1	4	19	34	0	.237	—	200
2	7	20	48	5	.216	.385	200
3	5	31	72	1	.188	.426	200
4	6	33	70	6	.196	.487	200
5	2	13	13	0	.304	—	2
6	1	6	18	1	.154	.269	240
7	3	20	62	0	.153	.476	200
8	5	40	52	1	.255	.674	110
9	19	83	88	1	.317	.917	15
10	2	7	11	0	.275	—	2
11	9	42	105	0	.192	—	115
12	4	38	70	3	.200	.708	110
13	1	23	96	0	.104	.458	120
14	4	17	38	0	.212	.568	175
15	6	37	76	1	.204	.508	110
16	1	18	89	6	.088	.343	295
17	9	61	86	0	.253	—	70
18	3	35	57	0	.216	.637	70
19	1	10	27	1	.154	.645	70
20	3	45	70	2	.213	.825	70
21	6	23	69	0	.179	.155	220
22	6	44	122	1	.162	.606	210
23	1	32	86	0	.143	.419	230
24	5	34	79	2	.183	.592	230
25	1	25	86	6	.114	.283	230
26	5	10	80	1	.104	.152	220
27	3	23	92	2	.121	.432	175
28	4	30	82	3	.160	.310	180
29	1	22	96	1	.100	.263	310
30	3	26	86	5	.133	—	290
31	0	9	31	0	.113	.233	220
32	3	22	89	4	.119	.164	220
33	5	28	85	2	.158	.383	100
34	2	29	87	1	.139	.187	215
35	2	31	56	4	.188	.641	200
36	1	26	91	0	.119	.244	230
37	7	39	72	2	.221	.368	110
38	1	16	80	0	.093	.208	260
39	5	19	55	0	.184	.575	220
40	3	31	90	9	.139	.101	250
41	2	23	98	0	.110	.048	265
42	1	23	96	0	.104	.112	255

Table 4 (continued).

Sample	HbI^1/HbI^1 homo- zygotes	HbI^1/HbI^2 hetero- zygotes	HbI^2/HbI^2 homo- zygotes	Total of rare types	q^1	p^E	Depth of sample in meter
43	3	14	73	0	.111	.097	250
44	5	21	90	1	.132	.068	180
45	1	21	136	2	.072	—	220
46	1	14	63	2	.100	—	180
47	0	25	124	1	.083	—	230
48	1	17	102	0	.079	.100	190

sample with the lowest value of q^1 and p^E is found near the mouth of the fjord:

Vågsfjorden	q^1 : .304 and .154	p^E : —
Ulsfjorden	.173 and .212	.360 and .343
Kvenangen	.204 and .088	.299 and .189
Porsangerfjorden	.163 and .114	.330 and .154
Tanafjorden	.140 and .100	.215 and .141
Varangerfjorden	.188 and .119	.401 and .130

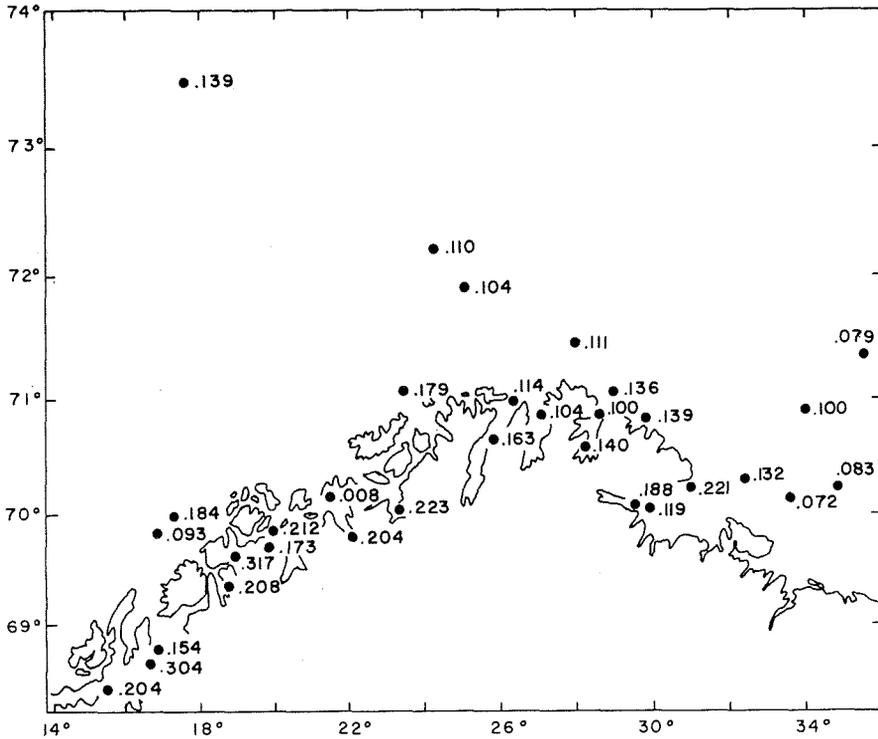


Fig. 4. The frequencies of the HbI^1 allele in the different sampling localities.

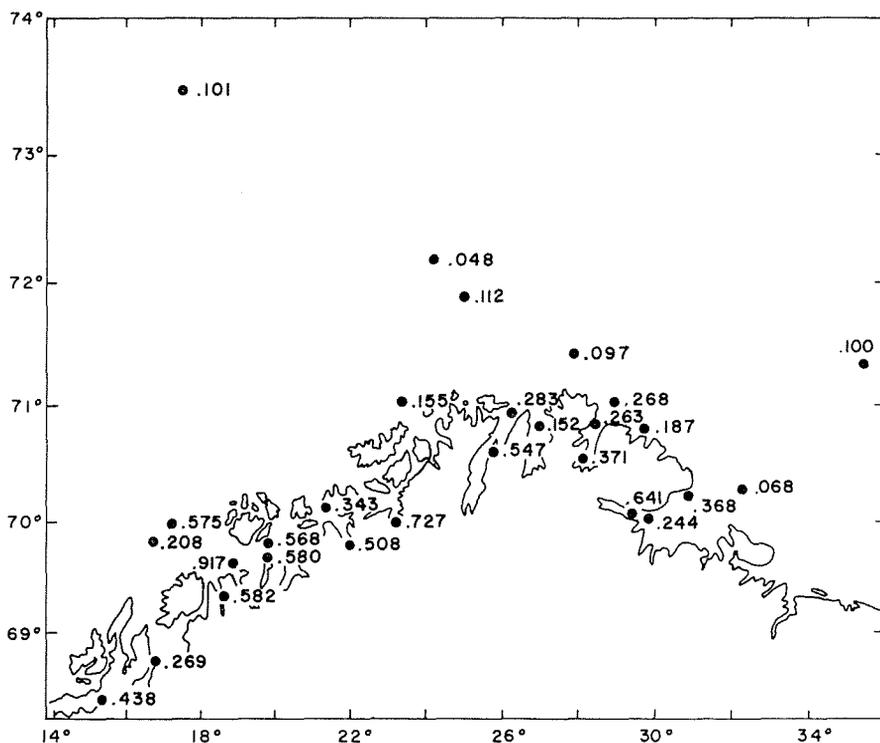


Fig. 5. The frequencies of the blood type E in the different sampling localities.

However, the figures contain more frequencies which do not fit in this general pattern, in Fig. 4 for instance, the values .212, .179, .141, and .225; and in Fig. 5 the values .917, .268, and .368. Therefore, the values of q^1 and p^E according to the depth of the sample are plotted in Figs. 6 and 7, respectively. Incidentally, the samples collected inshore and the samples within the coastal locality form four different groups as indicated on the figures.

Both in Figs. 6 and 7 the frequencies are decreasing with increasing depth. Although there are large variations from one sample to another, the values of the estimated means in each of the groups both for q^1 and p^E are decreasing continually with the values .312 and .920, respectively, near the surface to .109 and .300 at 300 m. The decline in the values of the frequencies appears greatest in the first 100 m.

The values of q^1 and p^E in samples from the sea are low (Figs. 6 and 7). Only one sample (sample 39) has intermediate values of q^1 and p^E , while the others have as low or lower values than the samples collected inshore on corresponding depth.

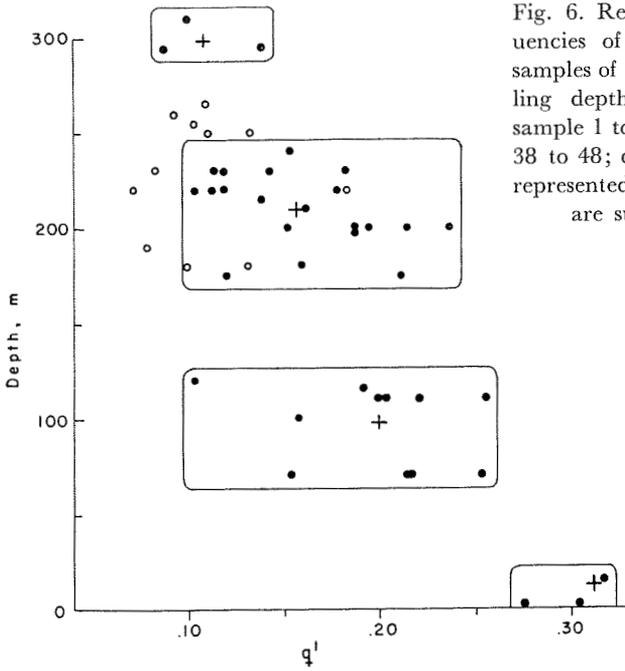


Fig. 6. Relationship between frequencies of the HbI^1 allele (q^1) in samples of immature cod and sampling depths. Legend: Black dots, sample 1 to 37; open circles, samples 38 to 48; crosses, means of samples represented by black dots and which are surrounded by a line.

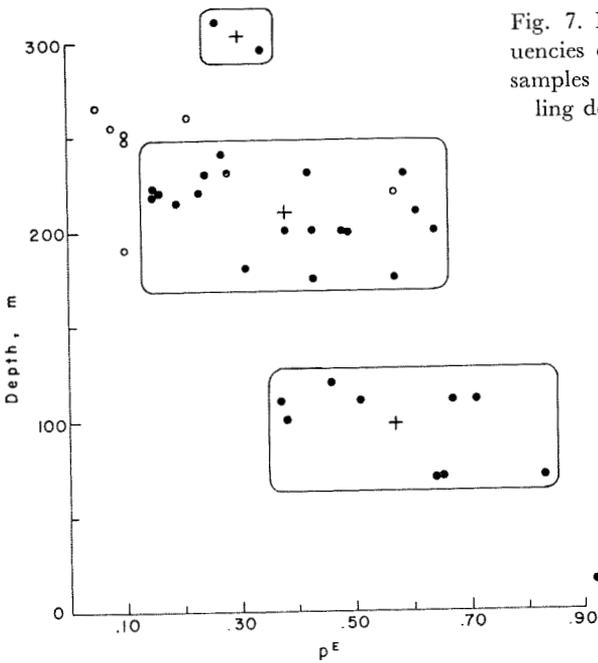


Fig. 7. Relationship between frequencies of the blood type E (p^E) in samples of immature cod and sampling depths. Legend: See Fig. 6.

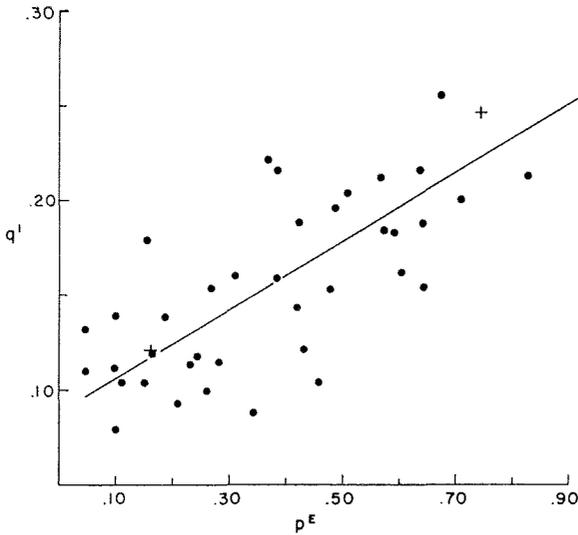


Fig. 8. Relationship between frequencies of HbI^1 allele (q^1) and frequencies of the blood type E (p^E) in the samples. Legend: Black dots, values of the samples; regression line, $y = .089 + .179x$; crosses, mean values of the spawning groups of Arctic and coastal cod.

The value of q^1 according to the value of p^E in the same sample are plotted in Fig. 8, together with values representing spawning groups of Arctic and coastal cod in the Vestfjord and north to the Laksefjord (MØLLER 1968 a).

Here too there are large variations from one sample to another. However, the values correlate (correlation coefficient .77), and the data fits a straight regression line ($y = .089 + .179x$; linear regression coefficient = .179, highly significant $P > .01$). The mean values of the Arctic cod spawning groups fit this line, while the values of the coastal spawning groups are slightly different.

THE DISTRIBUTION OF THE HAEMOGLOBIN PATTERNS

Tables 2 and 4 list the haemoglobin patterns, the homozygotes HbI^1/HbI^1 and HbI^2/HbI^2 ; and the heterozygote HbI^1/HbI^2 , in the cod fry and young cod samples, respectively. The total numbers of individuals in several of the samples are low, and the observed numbers of the different patterns of the individual samples in the tables deviate slightly from the expected numbers calculated from the Hardy-Weinberg law of genotype distributions in large random mating populations. However, by treating the samples in larger units it is possible to detect unconformity. The observed and expected distributions of the haemoglobins in cod fry is not in accordance:

	<i>HbI¹/HbI¹</i>	<i>HbI¹/HbI²</i>	<i>HbI²/HbI²</i>
obs.	63	287	564
exp.	46.6	319.7	547.7
	$\chi^2 = 9.561$; d.f. = 1; $P < .005$		

Similarly, the samples collected inshore or on localities near the coast (samples 1 to 37) of young cod do not fit the Hardy-Weinberg law:

	<i>HbI¹/HbI¹</i>	<i>HbI¹/HbI²</i>	<i>HbI²/HbI²</i>
obs.	150	1051	2633
exp.	118.8	1112.0	2603.2
	$\chi^2 = 11.881$; d.f. = 1; $P < .005$		

DISCUSSION

The main purpose of the present study is to investigate the relationship between Arctic and coastal cod in their immature stages by the variation of the frequencies of the *HbI¹* allele and of the blood type E.

Due to the sampling gear the report is restricted to cod staying near or at the bottom of the sea.

The significant differences found between the observed and the expected numbers both of samples of cod fry and of young cod, demonstrate that the samples were collected from two or more genetically separated populations.

The values of q^1 and p^E correlate (Fig. 8, page 230). The estimated values appear to represent different mixtures of individuals from two distinct populations. The mean values for Arctic cod spawning groups fit in this correlation, while the values of coastal cod spawning groups have slightly higher values of q^1 for corresponding values of p^E . Rather than sampling error the reason for this is that the two groups of samples represent genetic diversity in the coastal cod in that area. While the values of the spawning groups mostly represent samples from the Vestfjord area, the values of young cod represent samples caught in different localities all over northern Norway.

In spawning groups of Arctic and coastal cod in the Vestfjord and north to the Laksefjord the mean frequencies of the *HbI¹* allele were .121 and .247, respectively; and of the blood type E .162 and .722 (MØLLER 1968a). The specimens in these spawning groups were classified as Arctic and coastal cod according to the otolith type (ROLLEFSEN 1933), however, otolith types are not a well-defined character. Therefore, the actual values of the Arctic cod groups are somewhat lower than these estimated values, while those values for the coastal cod groups are higher.

The low values of q^1 and p^E in a sample signify a high percentage of Arctic cod, while relatively high values of q^1 and p^E represent a high percentage of coastal cod.

Both the values of q^1 in cod fry samples and the values of q^1 and p^E in samples of young cod were decreasing with increasing depth (Figs. 3, 6 and 7). Although there are large variations from one sample to another, these variations are probably caused by the large geographical differences in sampling localities, both in latitude and in distance from the shore. All localities in the sampling area are not given equal representation. Shallow water east of the Altafjord is poorly represented. The reason for the large drop in frequencies both of q^1 and p^E in the first hundred meters is probably due to inadequate sampling. However, the coastal cod appear to prefer the shallow waters at the coast, while the deep water are preferred by the Arctic cod; an apparent feature which is also characteristic of first year cod in late autumn.

Only one of eleven samples collected from the sea appears to contain a high percentage of coastal cod (sample 39) (Figs. 4 and 5), although the depths of these samples were not deeper than the sampling depths inshore or near the coast (Figs. 6 and 7). The frequencies of the samples show that the samples primarily consist of Arctic cod. Thus, the Arctic cod is found in the open sea, while the coastal cod strain is restricted to the coastal waters.

Despite the restricted area of sampling and the limited number of samples it is convincingly demonstrated that the relative strength of Arctic and coastal cod in northern Norway and the Barents Sea appear to depend on depth and distance from the shore.

The result confirms the results of previous studies concerning the distribution of Arctic and coastal cod, such as tagging experiments and determination of the otolith types (HYLEN 1964 and 1967; SÆTERS DAL 1956).

Differences found previously between the adult stages (MØLLER 1968a) are supported by the different environmental preferences demonstrated here in the immature stages. There is every reason now to regard the two cod forms as two sibling species.

SUMMARY

The frequencies of the *HbI¹* allele and of the blood type E are recorded for samples of cod fry and of young cod at different localities in northern Norway and the Barents Sea.

Using the frequencies as an expression for the relationship between Arctic and coastal cod it is demonstrated that the relative strength of the

two cod forms appear to depend on depth and distance from the shore. The coastal cod prefer the shallow waters at the coast, while the open sea and deeper waters both offshore and inshore are preferred by the Arctic cod; thus, the two cod forms are regarded as sibling species.

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THE LOGARITHMIC SERIES AND THE LOGNORMAL DISTRIBUTION APPLIED TO BENTHIC INFAUNA FROM PUGET SOUND, WASHINGTON, U S A ¹

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INTRODUCTION

Collections from natural communities of organisms are characterized by unequal abundances of the various species, and several mathematical models have been proposed to represent the distribution of specimens among the species (TAYLOR 1953, WILLIAMS 1964). Two of the most frequently used models are the logarithmic series (FISHER, CORBETT and WILLIAMS 1943) and the lognormal distribution (PRESTON 1948). The present paper is an attempt to test the validity of these models for communities of benthic organisms.

R. A. FISHER demonstrated that the negative binomial distribution could be applied to the frequency distribution of species abundances in samples from natural communities where the species were distributed randomly and the abundances of the various species were distributed in accordance with a Gamma-function. The proportion of species with abundance n in a sample is then expressed by:

$$P_{(n)} = \frac{(k + n - 1)! p^n}{(k - 1)! n! (1 + p)^{k+n}}$$

where p is a parameter related to the sample size and k is an inverse measure of the variability in the abundances of the species. When applied to a collection the zero term may be omitted, since no information is available about the number of species present in the community but not included in the sample. Furthermore, the range of species abundances is

¹ Contribution No. 505, Department of Oceanography, University of Washington.

normally so large that k becomes nearly zero. Thus, by omitting the zero term and setting $k = 0$, and by substituting α for $1/(k - 1)!$ and x for $p/(1 + p)$ in the formula for the negative binomial distribution, FISHER arrived at the logarithmic series:

$$P_{(n)} = \alpha x^n/n$$

where $P_{(n)}$ is the proportion of species in the sample with n specimens. The relationship between number of species (S) and number of specimens (N) in the logarithmic series is:

$$S = \alpha \ln \left(1 + \frac{N}{\alpha} \right)$$

Total number of specimens in replicate samples from a community satisfying the logarithmic series will be distributed according to the negative binomial distribution and total number of species according to a POISSON-series (QUENOUILLE 1949). KENDALL (1948) showed that the logarithmic series could originate from various types of population growth, and a comprehensive account of the application of the logarithmic series to various aspects of quantitative biology is given by WILLIAMS (1964).

PRESTON (1948) questioned two consequences of the logarithmic series model, namely, that species with few specimens in a community are more numerous than species with intermediate abundances, and that no upper limit to the number of species is defined. He stated that the number of species is limited, and that it is not reasonable to expect that a major part of the species are of very low abundance; in reality the majority of the species are of intermediate abundance. PRESTON showed that the distribution is normal when the abundances are grouped in geometric classes differing by a factor of two, i.e., the distribution is lognormal. However, if a collection is small compared to the total number of species present in the community the distribution is a truncated lognormal; in such situations many of the species appear to be rare and the data fit a logarithmic series. By doubling the sample size the mode of the lognormal distribution shifts to one higher class and the distribution thus becomes less and less truncated with increasing sample size.

WILLIAMS (1953) agreed that the lognormal distribution often is preferable to the logarithmic series; however, he found that classes differing by a factor of three are better, because by PRESTON's method half of the number of species with two specimens are included in the first class and the other half in the second class. By WILLIAMS' $\times 3$ classes the species in the first class have one specimen, in the second class two to four, in the

third class five to thirteen, and in the fourth class fourteen to forty specimens, such that the midpoints of the classes are one, three, nine and twenty-seven specimens.

MATERIALS AND METHODS

The present material was collected quarterly (seven cruises) during 1963–64 at eight stations in Puget Sound in from five to ten replicate samples with a 0.1 m² van Veen grab (LIE 1968). All the polychaetes, crustaceans, lamellibranchs and echinoderms from the first two cruises (January–February and April–May 1963) were identified and counted; in the samples from August and November the polychaetes were identified only from stations 2 and 7; in the samples from 1964 (three cruises) polychaetes were not identified. Therefore, the logarithmic series has been applied only to the data from the two first cruises when the number of species was sufficiently high for meaningful plotting of the first ten classes of the series (species with from one to ten specimens).

The logarithmic series was fitted by finding x from table 146, page 308, in WILLIAMS (1964), and α was calculated from the formula:

$$\alpha = N(1 - x)/x$$

The logarithmic series can be fitted when x and α are known (page 235). The deviation of the logarithmic series from observed frequencies was estimated by the formula:

$$D = \left[\sum_{i=1}^n (\log A_i - \log B_i)^2 / n \right]^{1/2}$$

where A_i is the observed frequency, B_i the frequency expected from the logarithmic series, and n the number of classes.

The lognormal distribution was tested by plotting the cumulative percentage of the $\times 3$ classes on logarithmic probability paper; a lognormal distribution is represented by a straight line on such paper (AITCHISON and BROWN 1957).

The SHANNON–WIENER function of information theory (SHANNON and WEAVER 1963):

$$H = - \sum_{i=1}^s p_i \log_2 p_i$$

is a measure of the complexity of an animal community; the more similar the abundances of the various species and the higher the number of species, the higher the diversity of the community as measured by the

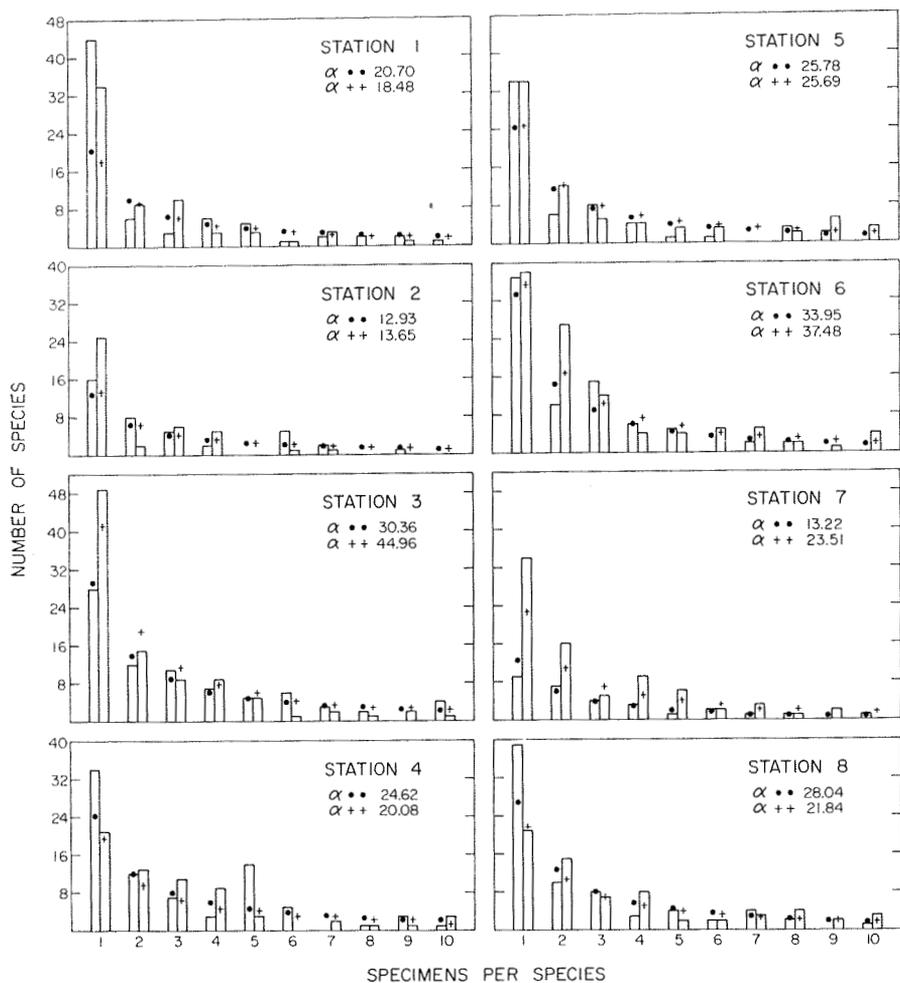


Fig. 1. Observed frequencies of specimens per species (bars) and frequencies expected from the logarithmic series in January-February (dots) and April-May (crosses) 1963 of benthic infauna from eight permanent stations in Puget Sound.

formula. The relative diversity (H_r) or "evenness" (PIELOU 1966) is the ratio between the observed diversity and the maximum diversity the community could contain, i.e., if all the species were equally abundant:

$$H_r = H/H_{\max} \quad (H_{\max} = \log_2 S)$$

Thus the relative diversity represents only the distribution of specimens among the species and is unaffected by variation in the total number of species in a sample. SHANNON and WEAVER (1963) defined redundancy as one minus the relative information, and the redundancy for a com-

munity of organisms is therefore a measure of the level of dominance in the community. Redundancy expressed in percent by the formula:

$$R = 100(1 - H_r)$$

has therefore been used in the present paper as a measure of the dominance of the faunal assemblages in Puget Sound.

RESULTS AND DISCUSSION

THE LOGARITHMIC SERIES

Fig. 1 shows the observed frequencies and the frequencies expected from the logarithmic series of species with from one to ten specimens in the samples from the eight stations in Puget Sound during January–February and April–May 1963. There is generally a reasonably good fit, but in seven of the sixteen cases the discrepancy between observed and expected frequencies was larger than could be expected when tested by a Chi^2 test (Table 1). Since the logarithmic series were fitted by determining two parameters, x and α , the degrees of freedom in the Chi^2 tests equal the number of classes minus two.

Table 1. Chi^2 test of goodness of fit of observed frequencies to frequencies expected from the logarithmic series for benthic infauna from eight stations in Puget Sound.

Station	Date	Chi^2	Degrees of Freedom	p(0.05)
1	February 1963	37.8	5	11.07
1	April 1963	25.2	5	11.07
2	February 1963	2.8	3	7.81
2	May 1963	21.0	3	7.81
3	February 1963	3.7	6	12.59
3	April 1963	8.6	6	12.59
4	January 1963	25.7	5	11.07
4	April 1963	10.6	5	11.07
5	February 1963	11.5	5	11.07
5	April 1963	8.2	5	11.07
6	February 1963	8.6	5	11.07
6	April 1963	12.9	6	12.59
7	February 1963	2.2	3	7.81
7	April 1963	21.8	5	11.07
8	February 1963	9.8	5	11.07
8	April 1963	6.4	5	11.07

The discrepancy between the observed and the expected frequencies was particularly high at stations with a high degree of numerical dominance, and the deviation from the logarithmic series (D) for the first five classes (species with from one to five specimens) appeared to be positively correlated to the redundancy (R) (Fig. 2). The correlation is weak, probably largely because of sampling variability for the rare species, but KENDALL's rank correlation coefficient was 0.61 ($p < 0.01$). A test of the relationship between goodness of fit to the logarithmic series and redundancy could be performed if the redundancy could be manipulated and the subsequent change in the goodness of fit studied. Stations 1 and 3 were quite similar in species composition and about the same species were numerically dominant at the two stations (LIE 1968); however, station 1 had a very high and station 3 a very low redundancy. When the data from these two stations from February 1963 were pooled, the combined redundancy as expected became lower than at station 1 but higher than

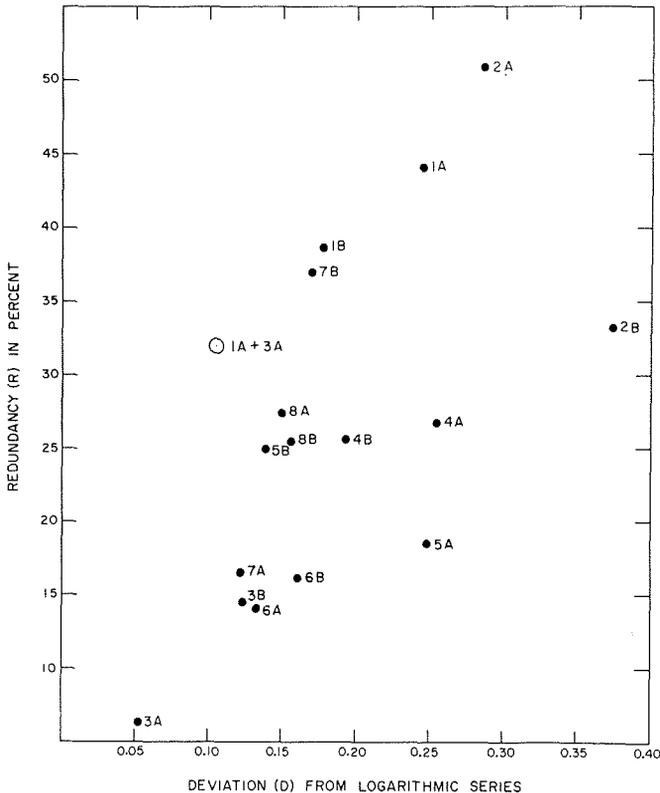


Fig. 2. The relationship between redundancy and the deviation of observed frequencies from frequencies expected from the logarithmic series at eight stations in January-February (A) and April-May (B) 1963.

at station 3. Consequently the deviation from the logarithmic series (Fig. 2) became lower than for station 1 but higher than for station 3.

Several examples of poor fit to the logarithmic series in collections of insects with strong numerical dominance by one or a few species are discussed by WILLIAMS (1964). A characteristic feature of these situations, as for the benthic infauna, was a too high number of species with only one specimen. In communities with strong dominance the basic assumption of a Gamma-distribution of the species abundances may not be satisfied.

One of the underlying assumptions for the logarithmic series is that the species are randomly and independently distributed. However, non-randomness of spatial distribution occurs frequently in nature (HAIRSTON 1959) and LIE (1968) showed that most of the numerically dominant species at the stations in Puget Sound had varying degrees of patchiness. The measured patchiness is in part a function of sampling design and sampling techniques. Certain sampling techniques, such as using light traps to attract and capture insects (WILLIAMS 1964) and trawling for bottom fish (TAYLOR 1953), have provided data with particularly good fit to the logarithmic series. However, these sampling techniques tend to obscure real patchiness of the fauna and thus they induce randomness. In the benthic communities in Puget Sound a considerable portion of species are commensal (viz. members of the polychaete family Polynoidae and the crustacean family Pinnotheridae), and consequently the requirement of independence is often not satisfied.

Benthic communities, particularly in the arctic and boreal regions, are characterized by dominance in abundance or biomass by a small number of species (THORSON 1957) and normally there is patchiness and a considerable degree of interdependence among the species. As the basic assumptions for the logarithmic series are randomness of spatial distribution and independence among the species, and as the series appears to be adversely affected by numerical dominance, it is doubtful if the series generally is a representative model for the relationship among species and specimens in a benthic infaunal community.

THE LOGNORMAL DISTRIBUTION

The data from January–February and April–May 1963 were grouped in $\times 3$ classes (WILLIAMS 1953) and the cumulative percentages were plotted on logarithmic probability paper (Fig. 3). The curves are reasonably straight, which indicates that the distributions are close to the lognormal. However, all the curves are characterized by having the median (50% probability) in the first or second class, indicating that half or more of the species had not been sampled. By increasing the sample

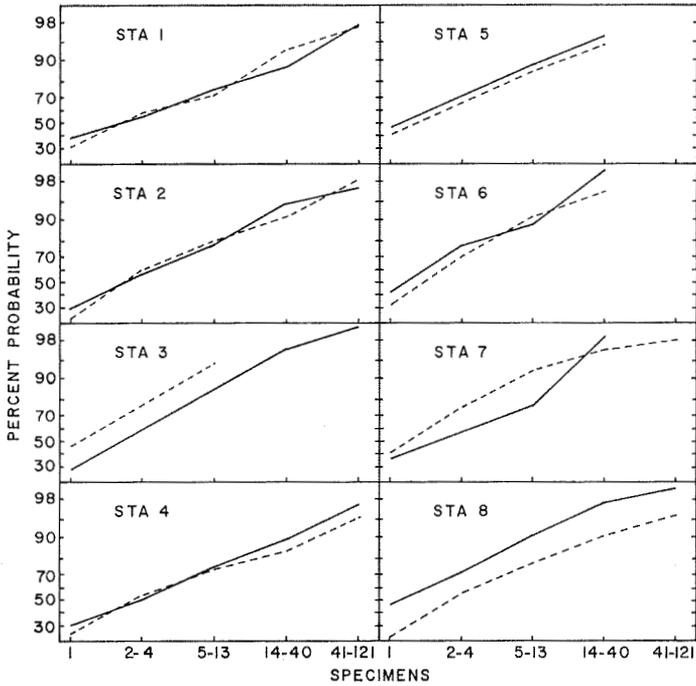


Fig. 3. Cumulative percentage distribution of species in $\times 3$ classes of abundance. Solid line; January—February 1963; broken line: April—May 1963.

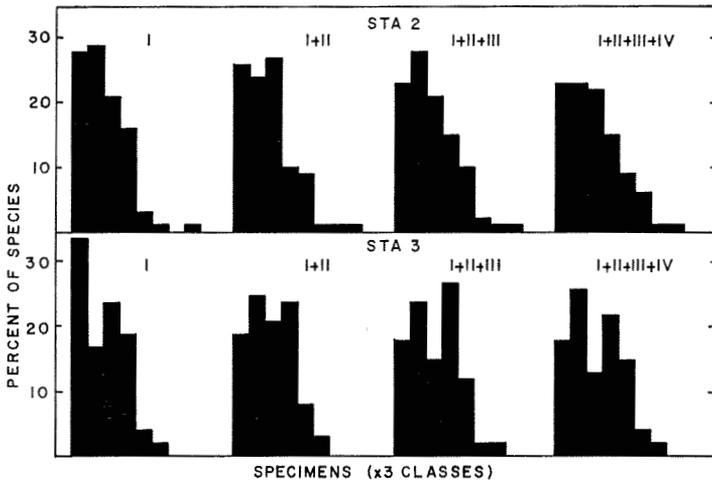


Fig. 4. Percentage frequency distribution of species in $\times 3$ classes of abundance at stations 2 and 3. Combined data from January—February (I), April—May (II), August (III), and November (IV) 1963.

size the median should shift to the right on the abscissa (PRESTON 1948), i.e., the first class should contain a progressively lower percentage of the total number of species. WILLIAMS (1953) showed that the mode of the lognormal distribution of insects caught in light traps shifted to the right when the sampling time was increased from an eighth of a year to eight years. The faunal assemblages in Puget Sound exhibited small variations in number of species and the numerically dominant species remained largely the same throughout the investigated period (LIE 1968). Combining the data from different cruises for a station would then, as for WILLIAMS' insect data, in effect be increasing the sample size. Fig. 4 shows the percentage frequencies of the total fauna at station 2 and the non-polychaetes at station 3 when data were combined for the four cruises in 1963. A significant shift of the mode can hardly be ascertained; even after combining all four cruises the curves are strongly truncated, although a reduction in the percentages of the first class did take place.

The constancy of total number of species during the investigated period does not necessarily imply that the same species always were present. Fifteen of the species (23%) found at station 2 in May were not found in February, eleven species (17%) found in August were not found during the two preceding cruises, and nine species (12%) found in November were not found during the three preceding cruises. Similarly, twenty-five of the species (45%) found at station 3 in April were not found in February, eleven species (19%) found in August were not found during the two preceding cruises, and seven species (12%) were not found during the three preceding cruises. Therefore, by increasing the sample size it appears that the chance of encountering new species was nearly as high as the chance of adding new specimens to earlier recorded rare species. HAIRSTON and BYERS (1954) did not find a significant shift of the mode of the lognormal distribution with increasing sample size, and they argued that the reason for this was the extreme patchiness of the rare species.

When communities are considered more or less well defined stages in a "continuum" (WHITTAKER 1967), a certain number of the rare species will be representatives of neighbouring communities. Increasing the sample size will lead to discovery of more of these rare, transient species, and the lognormal distribution will always be strongly truncated. An upper limit of the number of species in a community cannot be defined (BRIAN 1953), except the limit set by the respective zoogeographical regime. LIE (1968) found a gradual transition in faunal composition among the eight Puget Sound stations. The benthic communities appear to be arrayed in a continuum that is directly related to physical properties of the substrate. When the data from all seven seasons were

combined for each station and for all the stations, thus effectively increasing sample size, the lognormal distributions were still strongly truncated for the individual stations (Fig. 5). In contrast, the distribution for the combined data was considerably less truncated. Therefore, it appears that the sampling at the eight stations in Puget Sound during 1963-64 was sufficient to encompass the majority of the species in this relatively well defined geographical area.

Complete or nearly complete lognormal distributions have been demonstrated in large samples from well defined geographical areas such as islands (PRESTON 1962) and in samples covering a very large area or collected over a very long time (WILLIAMS 1964). Such samples will contain species from more than one community, and the lognormal distribution is therefore a model for the "between habitat" species diversity (MACARTHUR 1965).

Benthic communities may be identified as "statistical units" based on the presence of characteristic species (THORSON 1957) or ordinated in multi-dimensional space by multivariate analysis (CASSIE and MICHAEL 1968), but regardless of technique of analysis the communities must be considered "open" in the sense that there are no distinct borders between them. The lognormal distribution in such communities will be strongly truncated and therefore not be a better model for the distribution of specimens among the species than the logarithmic series.

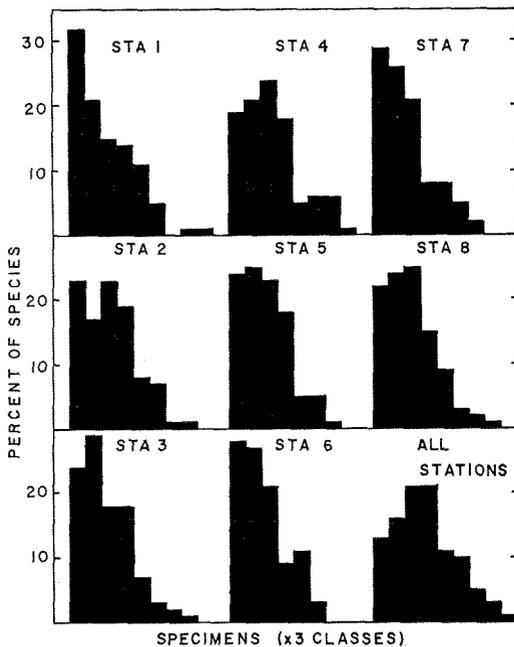


Fig. 5. Percentage frequency distribution of species in $\times 3$ classes of abundance. Combined data from 1963-1964 for single stations and for all stations.

SUMMARY

1. Benthic infauna collected at eight stations in Puget Sound during 1963-1964 was tested for agreement with the logarithmic series and the lognormal distribution.
2. The data agreed only moderately well with the logarithmic series; seven of sixteen cases showed statistically significant differences between observed frequencies and frequencies expected from the logarithmic series. Furthermore, there was an inverse relationship between goodness of fit to the logarithmic series and the level of numerical dominance of the faunal assemblages. This relationship, and the fact that the underlying assumptions for the logarithmic series are not applicable in benthic communities, makes the series a doubtful model for the relationship between species and specimens in a benthic community.
3. The lognormal distribution fitted the data reasonably well, but the curves were always strongly truncated. Increasing the sample size reduced the percentage of species in the first class somewhat, but only when the data from all the seasons and all the stations were combined was a significant part of the distribution "unveiled". The lognormal distribution therefore represents the geographical region reasonably well, but for each station the curves are too truncated to represent better models than the logarithmic series.

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FEEDING RATES OF CETACEA

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INTRODUCTION

A variety of porpoises and dolphins of the superfamily Delphinoidea, ranging through three magnitudes of weight from the harbour porpoise *Phocoena* to the killer whale *Orcinus*, have now been kept in captivity. From aquarium records of body weights and weights of food ingested, daily food consumption can be determined. Following IVLEV (1961) I shall call this index the daily ration. There is no suitable term in the literature for the index daily ration expressed as percent of body weight which I shall therefore call the feeding rate. The purpose of this paper is to attempt to discover the feeding rates of whales which are too large to have yet been kept in oceanaria.

MATERIAL AND METHODS

Table 1 summarises the results of a literature search on feeding rates, supplemented by unpublished information obtained by correspondence with curators of various oceanaria. Least information was obtained for body weight, since curators are loath to weigh living animals, especially those of large size, and estimates of weight are usually too inaccurate to be useful. An independent search of literature and unpublished records on length and weights of whales, however, allowed construction of curves from which weight could be determined knowing body length; this information was useful for the killer whale *Orcinus*, for example. Data on body weight and daily ration, from which feeding rate could be calculated, were found for 8 genera of Delphinoidea maintained in captivity, ranging through 2 orders of magnitude of body size. Details are as follows:

Contribution given in honour of Gunnar Rollesen at his 70th birthday.

Table 1. Summarised data on feeding rates of Delphinoidea in captivity.

Species	Number of animals	Location	Mean body length	Mean body weight	Mean food weight per diem	Food as per cent body weight	Number of daily feeds
			m	kg	kg		
<i>Phocoena phocoena</i>	8	Strib, Denmark	1	40	4.3	10.8	3-4
<i>Lagenorhynchus obliquidens</i>	2	Vancouver, British Columbia	2	87	6.8	7.9	?
<i>Phocoenoides dalli</i>	1	Pt. Mugu, California	2	120	15	11.3	5
<i>Tursiops truncatus</i>	2	Pt. Mugu, California; Montreal, Quebec	2	168	7.0	4.2	2
<i>Globicephala macrorhyncha</i> juv.	1	Marineland, Florida	1	ca 190	24.1	12.7	?
<i>Delphinapterus leucas</i>	2	Vancouver	2.8	238	23	5.5	2
<i>Delphinapterus leucas</i>	4	New York City	3.4	468	23	5.1	?
<i>Pseudorca crassidens</i>	1	Marineland of the Pacific, California	3.6	437	20.9	4.7	?
<i>Globicephala scammoni</i>	3	Marineland	5	842	33.2	4.0	?
<i>Orcinus orca</i>	4	Vancouver, Sea World, Calif.	4.75	1258	51	4.05	?

(Data on animals or groups of animals used in calculating feeding rates in Table 1 are shown by an asterisk in the text.)

Phocoena phocoena.

Harbour porpoise. ANDERSEN (1965, Tables 1 and 2) gave weights and daily rations of 7 porpoises held in captivity at Strib, Denmark. All but two of the animals were weighed at death, the other two at a point midway through experiments. Most of the animals presumably increased in weight during this period. The food was fish: herring, *Clupea harengus* and whiting, *Gadus merlangus*. From ANDERSEN's data I calculate that the mean weight at death was 51 kg, and the mean ration was 4.3 kg per diem. Hence the minimum estimate of feeding rate is 8.26%. ANDERSEN gives the mean body weight during captivity as

40 kg and the mean feeding rate about 10% (accurately 10.8%).* I have used this figure in calculating the feeding rate in Table 1, but necessarily weight at death in calculating its variability between animals in Table 2.

Table 2. Feeding rates of individual *Phocoena* (data from ANDERSEN 1965; Tables 1 and 2).

Animal number	Season (summer, winter)	Duration (months)	Food per diem (kg)	Animal weight (kg)	Feeding rate (Weight of food × 100
					Weight of animal)
1	W	5	3.0	—	—
2	S	1	2.0	38	5.26
3	S	2	4.1	32	12.81
4	W	3	5.4	63	8.57
5	W	3	4.8	55	8.73
6	S	2	4.1	30	13.67
7	W	5	4.1	68	{6.03
7	S	5	4.8		
8	S	5	4.2	71	{5.92
8	W	5	5.1		
Mean of animals 2 to 8			4.2	51	8.26
Range			2.0–5.4	32–71	5.26–13.67

Lagenorhynchus obliquidens.

Pacific white-sided porpoise. ANON (1968 a) gave the length of a male as 6 ft (183 cm) and weight 198 lb (90 kg); the weight of a companion female 185 lb (84 kg). Their food consumption was 15 lb (7 kg) of herring, *Clupea pallasii* and mackerel, *Pneumatophorus diego*, per diem (ANON. 1967 a).*

Phocoenoides dalli.

Dall porpoise. RIDGWAY (1966) gave the daily feeding rate of a specimen of weight 120 kg as 15 kg of mackerel, *Pneumatophorus diego*, in 4 feeds per diem.*

Tursiops truncatus.

Bottlenose porpoise. RIDGWAY (personal communication), gave the feeding rate of a female *T. truncatus* of weight 390 lb (177 kg) as 16 lb (7.3 kg) per diem of mixed fresh mackerel, *Pneumatophorus* and smelt, *Osmerus mordax*. Mr. BRIAN BECK (personal communication) from experience at the Montreal Aquarium gave the feeding rate of a female *T. truncatus* of weight 350 lb (159 kg), fed on herring and smelt, as 30 lb

(13.6 kg). However at this rate of feeding, the animal soon reached satiety and ceased to feed. With a free choice, the average daily intake levelled off to 15 lb (6.8 kg) per diem after 11 days. Feeding rate for both experiments agrees at 4.2% (Table 1).*

Delphinapterus leucas.

White whale. ANON. (1968 a) gave the current lengths of two white whales as 10.5 and 8 ft (320 cm, 244 cm) and the lengths at capture, on September 16 1967, as 10 ft 4 in and 7 ft 5 in (315 cm, 226 cm). ANON. (1967 b) gave the weight of the calf as 490 lb (223 kg) having increased from 238 lb (108 kg) at capture. ANON. (1967 a) gave the feeding rates as 50 lb (23 kg) of herring and salmon (*Onchorhynchus* sp.) for the adult and 25 lb (11.5 kg) for the young animal, but the calf was reported to be taking some food from the adult. I calculate the adult's weight to have been 300 kg, the weight of the young animal in November–December 165 kg, giving estimated feeding rates of 4.1 and 6.9%.*

Mr. R. MORRIS (personal communication) gave me details of two male and two female white whales held at the New York Aquarium. Lengths ranged from 10 to 13 ft with a mean of 11 ft 3 in (3.43 m). Weights were estimated at from 700 to 2000 lb with an average of 1250 lb (567 kg), and feeding rates from 40 to 60 lb per animal per diem with an average of 50 lb (23 kg) in two daily feeds, giving an estimate of feeding rate of 4.1%. These weights however, were estimates and may have been high. Known weights of the four animals were given to me by MORRIS and Mr. P. MONTREUIL as: two females at capture in August 1967—625 lb (284 kg) each; the larger male, on May 17, 1965—1181 lb (538 kg). Dr. J. R. GERACI (personal communication) estimated the weight of the two males in 1967 at 900 and 1100 lb. All these weights had presumably increased by February 1968 when the feeding rate was given by MORRIS. Using the known weights one obtains a mean weight of 369 kg and a mean feeding rate of 6.2%. The mean of the two estimates of feeding rate for the New York animals is 5.1%.*

Pseudorca crassidens.

False killer whale. BROWN, CALDWELL and CALDWELL (1966) gave the cumulative food consumption of a captive female false killer whale between November 4, 1963 and August 31, 1965 as 30,650 lb (13,903 kg) of fish and squid. I calculate a mean daily ration of 45.95 lb (20.84 kg). The animal weighed 825 lb at capture and 1100 lb at writing. Taking the mean weight at 962.5 lb (456.6 kg) I find a mean daily feeding rate of 4.7% of body weight.*

Globicephala macrorhyncha.

Southern Atlantic pilot whale. KRITZLER (1952) gave a total food consumption of a young captive pilot whale at Marineland, Florida, between October 6, 1948 and July 5, 1949 as about 7 tons of squid, plus small, unmeasured quantities of fish. Weight at capture was estimated at 300 lb and at death 505 lb. Daily food consumption was at least 53.03 lb (squid only) and mean weight during this period at least 400 lb, giving a daily feeding rate of 4.7% of body weight.*

Globicephala scammoni.

Pacific pilot whale. BROWN (1960, 1962) and GILMORE (1962) gave the weights and daily feeding rates of three Pacific pilot whales held at Marineland of the Pacific, California, in about September, 1959: the smallest weighed an estimated 1100 lb and ate 40–45 lb of food daily; the median animal weighed 1360 lb and ate 80 lb daily; the largest weighed an estimated 3000 lb and ate 100 lb of food daily. For the median animal, of known weight, the feeding rate was 5.9% of body weight per day. Taking the mean of the three weights, known and estimated, as 1850 lb, and the mean daily ration as 74 lb, the mean feeding rate is calculated at close to 4.0% of body weight per diem.*

Orcinus orca.

Killer whale. A female at the Vancouver Aquarium on January 16, 1968 measured 16 ft 2 in (4.9 m) along the curve of the back, or 15 ft 6 in (4.7 m) in a straight line (ANON. 1968 a). In November, 1967 this animal ate 110 lb (50 kg) of herring and ling cod, *Ophiodon elongatus*, daily (ANON. 1967 a). The weight of this animal was estimated at 2500 lb (1136 kg), giving an estimated feeding rate of 4.4% per diem.* A previously-captured male, length 15 ft 4 in (4.67 m), weighed 2300 lb (1040 kg) and ate a steady diet of 100 lb (45 kg) daily (NEWMAN and MCGEER 1966), giving a feeding rate of 4.3% of body weight per day.* A male killer whale of length 16 ft (49 m) held at Pender Harbour, British Columbia, ate 130 lb (59 kg) of herring daily before its escape (ANON. 1968 b). From a weight/length curve I calculate its weight to have been about 1500 kg, giving a feeding rate of 3.9%.* [Data for construction of the weight/length curve for *Orcinus orca* were obtained from the compendium of SCHEFFER (MS 1967), from SLEPTSOV (1961) and BURGESS (1968)]. BURGESS (1968) gave the daily food intake of a killer whale at Sea World, San Diego California, as between 36 and 63 kg, or a mean of 49.5 kg. The length at capture in October, 1965 was 4.1 m and the

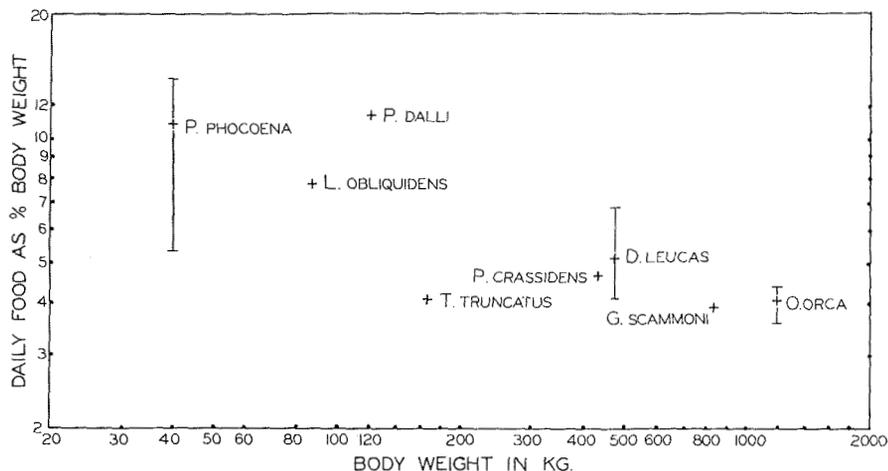


Fig. 1. Feeding rates of Delphinoidea.

weight 1088 kg. The length after 17 months was 4.5 m and the weight had increased about 270 kg, implying a weight at writing of about 138 kg. I calculate a daily feeding rate of 3.6% of body weight daily.*

RESULTS

Fig. 1 shows that the feeding rate decreases from the smaller genera of Delphinoidea to the larger, but levels off at about 4 to 5% of body weight for genera of length 2 m (weight 650 kg—adult *Tursiops*) or greater.

This pattern is complicated by several factors:

(a) Differences occur in feeding rates between young and adult animals.

Best data are those of ANDERSEN (1965) for *Phocoena* which show a variation in feeding rate of from 5.26 to 13.67% for 7 animals (Table 2). With the exception of one short-lived and probably sick animal (No. 2), which was small yet fed at a low level, feeding rate was inversely proportional to body weight. Only two animals, having weights of less than 30 kg, showed feeding rates in excess of 10% of body weight. MØHL-HANSEN (1954) gave birth weight of Danish porpoises as 6–8 kg, weight at full weaning as 25 kg, so that the animals below 30 kg in weight were young.

A young pilot whale, *Globicephala macrorhyncha*, showed a feeding rate of 13% (KRITZLER 1952). This is twice as high as the feeding rate of an adult *G. scammoni*, which was 6% of body weight (Table 1).

The young *Delphinapterus leucas* held in captivity consumed about 6.9% of body weight per diem compared to its mother's consumption of about 4.1%. However the account makes clear that the young animal

stole food given to the mother, which would increase further the disparity between the feeding rates.

(b) Species differences occur between genera of the same weight.

Phocoenoides dalli has a higher feeding rate than the slightly smaller *Lagenorhynchus obliquidens*, as well as the larger *Tursiops truncatus*. *Phocoenoides dalli* is exceptional also in having a high metabolic rate, large heart, thin fat layer and ability to dive very deep (RIDGWAY 1966). RIDGWAY and JOHNSTON (1966) gave the heart weights of these three species, which I have included in Table 3. Heart weights are exactly proportional to daily feeding rates, being close to $0.11 \times$ feeding rate, as follows:

Species	Body weight kg	Feeding rate %	Heart weight	$\frac{\text{Heart weight}}{\text{Feeding rate}}$
<i>L. obliquidens</i>	87	7.8	8.5	0.109
<i>P. dalli</i>	120	11.3	13.1	0.116
<i>T. truncatus</i>	168	4.2	5.0	0.119

This result is not unexpected since both heart weight and feeding rate are expressions of metabolic rate. *P. dalli* appears to be exceptional also in the number of daily feeds necessary in captivity to maintain its high metabolism; 5 compared with 2 for *Tursiops truncatus* and *Delphinapterus leucas*; 3 or 4 for *Phocoena phocoena*. While the metabolic rate of many genera is not known, we now have three measures of it: proportional heart weight, feeding rate, and number of daily feeds.

DISCUSSION

The measures of the metabolic rate give us a key to discovering the feeding rate of large whales which cannot yet be kept in captivity. The assumption involved is that heart weight retains the same proportionality to feeding rate in large whales as in the Delphinoidea. I made a literature search on total weights and heart weights of whales starting from the paper of SLIJPER (1958). The main references were: BJARNASON and LINGAAS (1954); FUJINO (1955); KLEINENBERG (1956); KLEINENBERG *et al.* (1964); LAURIE (1933); NISHIWAKI (1950); OHNO and FUJINO (1952); OMURA (1950, 1957); QUIRING (1943); RIDGWAY and JOHNSTON (1966); SLEPTSOV (1961); SLIJPER (1958); and TOMILIN (1967), the last quoting several Soviet authors. Results are summarised in Table 3 and Fig. 2.

Adults of the large whalebone whales (Mysticeti) are seen to have heart weights of 3.5 to 6% of body weight. For good numbers of 4 species

Table 3. Body and heart weights of Cetacea.

Species in order of increasing size	No. of specimens	Body length cm	Mean body weight kg	Heart weight \times 1000 Body weight	
				Range	Mean
<i>Phocoena phocoena</i>	27	67-171	35.9	6.5-12.2	8.4
<i>Delphinus delphis</i>	50	—	54.2	—	4.84
<i>Phocoenoides dalli</i>	3	—	97	12.5-13.4	13.1
<i>Lagenorhynchus obliquidens</i>	5	—	110	7.0- 9.2	8.5
<i>Tursiops truncatus</i>	50	—	133	—	5.00
<i>Kogia breviceps</i>	1	298	417	—	3.26
<i>Delphinapterus leucas</i>	20	327-425	821	3.7- 6.9	5.7
<i>Globicephala melaena</i>	1	—	1,230	—	4.4
<i>Orcinus orca</i>	3	495-650	2,288	5.0- 7.3	6.41
<i>Balaenoptera acutorostrata</i>	1	790	4,846	—	4.75
<i>Berardius bairdi</i>	1	—	8,560	—	6.30
<i>Balaenoptera borealis</i>	17	1160-1460	12,551	3.4- 4.9	4.04
<i>B. brydei</i>	20	1220-1380	13,077	2.3- 6.8	4.6
<i>Eubalaena glacialis</i>	2	1160-1250	22,556	6.9- 7.9	7.4
<i>Eschrichtius glaucus</i>	1	1335	31,466	—	5.47
<i>Megaptera novaeangliae</i>	4	1250-1390	31,913	3.6- 5.8	5.31
<i>Physeter macrocephalus</i>	30	1110-1800	31,525	2.4- 6.1	3.32
<i>Balaenoptera physalus</i>	29	1860-2320	51,632	2.3-11.0	3.96
<i>B. musculus</i>	32	2130-2710	85,520	3.7- 6.7	3.99

of rorqual (*Balaenoptera borealis*, *brydei*, *musculus* and *physalus*) the mean figure was close to 4‰; for smaller numbers of humpback, *Megaptera novaeangliae* and right whales, *Eubalaena glacialis*, the figure was about 5 to 6‰. It was significantly lower at 3.4‰ in a good series of sperm whales, *Physeter catodon* and, perhaps also significantly, in one specimen of the related pigmy sperm whale, *Kogia breviceps*. Data were scarce for medium-sized whales: a single specimen of lesser rorqual, *Balaenoptera acutorostrata*, gave 4.8‰ and SLIJPER without stating details of size gave a figure of 5.1‰ for a second specimen of this species. A heart weight/body weight ratio of 6.3‰ for one specimen of *Berardius bairdii* is too little to provide a reliable figure for the Ziphiidae. I have been able to find less data for the Delphinoidea than for large whales. Three adult specimens of adult killer whales, *Orcinus orca*, gave a proportional heart weight of 6.35‰; 20 white whales, *Delphinapterus leucas*, 5.7‰; 50 *Tursiops truncatus* 5.1‰; 50 *Delphinus delphis* 4.8‰; and 27 *Phocoena phocoena* 8.4‰. The data do not disagree with the previous conclusion that the heart weight/body weight ratio is equal to about one tenth of the feeding rate.

Heart weight is higher for young than for adult Cetacea of the same species. For *Delphinus delphis*, KLEINENBERG (1956) gave heart/body weight

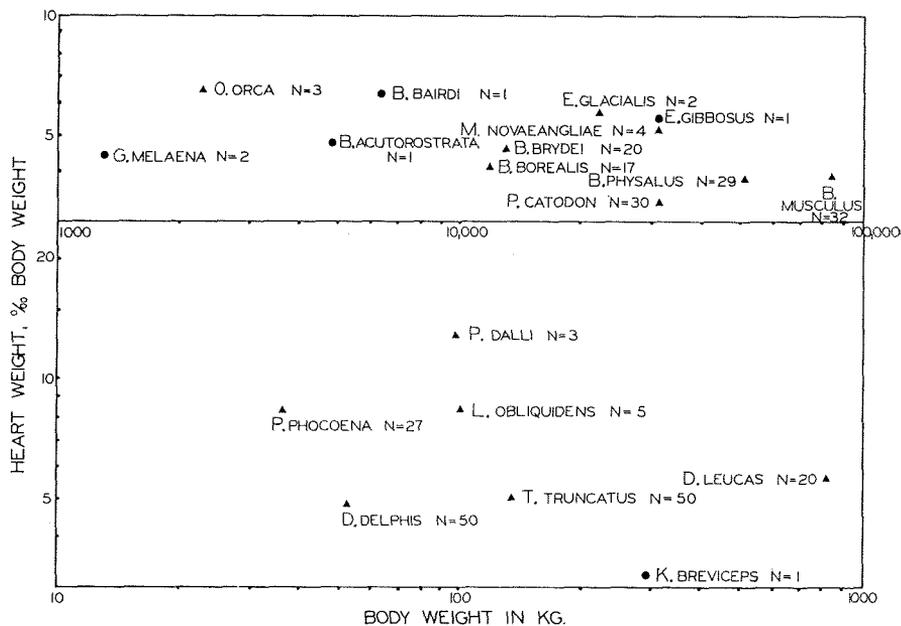


Fig. 2. Heart weight/body weight ratios of Cetacea. Solid circle—single animal; triangle—mean of more than one animal. N = number of animals from which data obtained.

ratios of 7.59‰ for late embryos, 6.93‰ for underyearlings and 4.84‰ for older animals. The data of SLIJPER (1958) suggest the same for *Tursiops truncatus*: 9.4‰ for a juvenile compared with 5.0‰ for KLEINENBERG's adult sample; and also for *Lagenorhynchus acutus*: 17.7‰ for a newborn animal compared with 8.5‰ for RIDGWAY and JOHNSTON's (1966) adult sample of the related *L. obliquidens*. However SLIJPER's (1958) data for 27 *Phocoena phocoena* show no decline in heart weight/body weight ratio with increase in body weight (age). This exception suggests that *Phocoena* (like *Phocoenoides dalli*) may retain a high metabolic rate throughout life. However, KLEINENBERG's data for Black Sea *Phocoena phocoena* gave a mean heart weight/body weight ratio of only 4.5‰ for 50 Black Sea *Phocoena*, indicating that the question must be re-examined.

Assuming that the ratio of heart weight to body weight equals approximately one tenth of the feeding rate in large whales, I conclude that the large rorquals eat some 4% of their body weight daily. A lower figure for *Physeter* seems quite reasonable since *Physeter* feeds through the ear, but the large rorquals feed during the summer months only.

KLUMOV (1963) has deduced from data on maximal stomach con-

Table 4. Weights of full stomachs of some Mysticete whales.

Species	Region	Length (m)	Body weight (metric tons)	Weight of stomach contents (metric tons)	Ratio
Blue	Antarctic	24	65	1.10 <i>a</i>)	1.7
Fin	N. Pacific	22	57 <i>f</i>	0.85 <i>b</i>)	1.5
Fin	N. Pacific	18.5	35	0.75 <i>c</i>)	2.0
Fin	N. Pacific	18.5	35	0.76 <i>d</i>)	2.2
Sci	N. Pacific	12	10 <i>e</i>	0.60 <i>d</i>)	2.0

a) KLUMOV 1963 p. 141, *b*) KLUMOV 1963 p. 149, *c*) KLUMOV 1963 p. 154, *d*) NEMOTE 1959 pp. 218-220, *e*) OMURA 1950, *f*) NISHIWAKI 1950.

tents of Mysticeti and the biomass of planktonic food that "the whale-bone whales require about 30-40 g per kg of live weight daily." This conclusion agrees well with my own. "Proceeding from the above indices" says KLUMOV "the 24-hour long requirement of food for the blue whale of average size and weight (23.5-24.5 m, 60-70 tons) is 2-2.5 tons." KLUMOV makes clear that this level of feeding is optimal, depending on an adequate biomass of plankton or pelagic fish. Table 4 shows data on maximum stomach volumes of large rorquals. With KLUMOV's suggested feeding rate, the ratio of stomach volume to body weight suggests a twice-daily feeding rate for blue, fin and sei whales. By contrast IVASHIN (1961) suggests that the daily food consumption of a humpback whale, *Megaptera novaeangliae*, in Antarctic seas in February is about 4 metric tons, with feeds every 3-4 hours. Assuming a body weight of about 25 tons the feeding rate would be 16%, which would demand a much higher metabolism of *Megaptera* than of the genus *Balaenoptera*. Such a feeding rate would be comparable with that of *Phocoenoides dalli* among the Delphinoidea and would necessitate a large heart. The average heart weight for 4 large specimens of *Megaptera* is 5.3‰, which is higher than for the species of *Balaenoptera*, but not as high as IVASHIN's suggestion would require. I conclude that KLUMOV's assumptions on feeding rates are probably closer to reality than IVASHIN's.

The data of KLUMOV (1963) and NEMOTO (1959) on stomach contents suggest that baleen whales rarely find optimal quantities of food, at least in the North Atlantic and Pacific Oceans; this would imply that they must actively search out feeding concentrations. The sensory and navigational basis of this search has yet to be discovered.

SUMMARY

1. The feeding rate of a whale is defined as the weight of daily food ingested expressed as percentage of body weight. Records of daily rations of Delphinoidea (porpoises and dolphins) in captivity allow calculation of feeding rates for eight genera having adult body weights of 10^1 to 10^3 kg.

2. There is an inverse relation between feeding rate and body weight, both between species and between young and adult Delphinoidea. The range of feeding rates is from 12–13% to 4–6%. Above a body weight of 6×10^2 kg, represented by adult *Tursiops truncatus*, feeding rate remains constant at 4–6% up to the largest species in which it has been measured, the killer whale, *Orcinus*, of body weight 2×10^3 kg.

3. Heart weight expressed as proportion of body weight varies directly with feeding rate and is equal to about one tenth of it. Young animals of all species, as well as adults of *Phocoenoides dalli* and possibly *Phocoena phocoena* have high feeding rates and heart weights, showing that both indices measure metabolic rate. From their heart weight/body weight ratio an attempt has been made to calculate feeding rates of whales too large to be kept in aquaria.

4. Heart weight/body weight ratios of adults rorquals of the genus *Balaenoptera* are about 4‰; of sperm whales, *Physeter* and one example of the small, related *Kogia*, lowest of all at 3.5‰. These data suggest a feeding rate of 4% for adult rorquals, so that from curves relating body length and body weight, their daily food consumption may be calculated.

ACKNOWLEDGMENTS

My debt to a number of skilled curators of aquaria is, I hope, adequately expressed by mention of their names in the text. Dr. E. D. MITCHELL gave valuable stimulus and criticism in the development of the paper.

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INTRASPECIFIC STRUCTURE AND VARIABILITY IN RELATION TO FISHERIES MANAGEMENT

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INTRODUCTION

Cod is nothing but cod, a fish species, *Gadus morhua* L. This species is caught nowadays with trawls in the north Atlantic and on the Newfoundland banks, in the Barents Sea as well as in the northern Pacific, near the coasts of northern Asia and northern America. This fish is also caught with long lines and hooks in the Norwegian fjords and the White Sea and is known to have been fished by pomors in the last century and by middle age vikings. Cod was fished by the stone age man who populated the Norwegian coast, the Russian Murman and the Pacific coastal areas thousands of years ago.

It is yet uncertain when cod originated as a species, but as far as a number of other species of the same boreal faunistic complex, mostly fresh water fishes, are concerned, they are known to have originated in the mid tertiary period. Most zoologists nowadays regard species as an objective reality, as a form of existence of the living matter. Animal species is not a conventional concept, it is not “what a taxonomist considers a species”, but an actually existing multitude of specimens which possess some specific-qualitative properties characteristic for the given species and relatively stable in time and space. It means that a species which once originated exists a more or less long period of time (so far as the specific environment exists) retaining its specific properties.

As regards freshwater fishes, perch, pike, pike-perch, catfish and some others, they are known to have undoubtedly existed since pliocene time and possibly earlier. At approximately the same time most species representative of the boreal sea fauna complex, cod, oceanic herring, plaice and flounders, etc. were formed (NIKOLSKY 1968). However, the

Contribution given in honour of Gunnar Rollefson at his 70th birthday.

stability of the species over thousands, and possibly, millions of years is ensured by the intraspecific variability, by its elasticity, so to say.

Stenobiotic species adapted to live under relatively stable, abiotic and biotic life conditions reveal a lower variability, lower elasticity. Usually, their intraspecific structure is simpler. An example of this type of stenobiotic fishes with a very low variability could be supplied by most of the species populating coral reefs, e.g. Pomacentridae. These species are extremely low-variable, occupying as a rule, a very limited distribution area and being adapted to very stable life conditions. They perish when these conditions change beyond the limit of this fish's very low specific adaptability.

Eurybiotic species, such as Arctic charrs and cod, possess a much wider range of adaptability, a considerable intraspecific variability and a more complex intraspecific structure. Thus, every species represents an open self-regulating system in a permanent interaction with the environment which incessantly keeps adapting to the changing conditions. This system possesses at the same time certain morphological, physiological and ecological characters distinctive for the species as a system.

INTRASPECIFIC VARIABILITY

For fishery biologists, endeavouring to develop a scientific basis for fish resource exploitation, the knowledge of the elasticity and the structure of the given species-system of economic importance is quite essential. Principal mechanisms operating in the populations provide changes in number and biomass due to respective environmental changes, first and foremost in the food supply rate which is manifested in growth changes. As is known, the increase in growth rate is related to a faster achievement of maturation age and an increase in fecundity. A faster growth is related to reduction of mortality rate, for, as a rule, bigger fish fall prey to predators on a larger scale than the smaller ones. Principle mechanisms of population self-regulation in connection with food supply changes have been rather well studied (NIKOLSKY 1950, 1962 and 1969, ROLLEFSEN 1954, SCHAEFER 1956 and others) and a detailed account is uncalled for here.

However, the process in question is often found not to be as direct as in the above scheme, being considerably affected by a number of factors, and, in particular, by mutual interactions of fish in different number of year-classes. A numerous year-class may handicap the growth rate of both preceding and following generations. The problem calls for further investigation for it is of a great theoretical and practical interest, first and foremost, in forecasting of the mature stock recruitment. A review of the data on the problem was reported by POLYAKOV (1962).

Changes in spawning periodicity appear to be an essential form of self-regulation. In fact, in years when the stock of White Sea herring is numerous a part of the females may leave out a spawning period. Due to food supply insufficiency they fail to fatten during a single feeding period (CHEPRAKOVA 1966). This phenomenon is also observed in some freshwater species, e.g. in whitefish (RESHETNIKOV 1967). It should be noted that many species inhabiting the northern part of the distribution area reproduce every other year, southern populations reproducing annually. Besides whitefish, this has been found in bream and some other species (KOSHELEV 1966). It is interesting that in some species in the southern part of the distribution area, e.g. in bream, portioning in spawning is observed, i.e. the reproduction rate speeds up.

An essential, though yet poorly investigated, mechanism of self-regulation is change in the variability of specimens in the population. Food supply increase is, as a rule, related to a reduction in the year-class size variability. This has been most clearly demonstrated in Baltic herring larvae (ANOKHINA 1969). Strong year-classes are distinguished by a wider variability range that weaken year-classes. The food supply is determined not only by the numbers of fish in an age group, but by the development of its food resources, and equally important, the coincidence of the food plankton period with fry development. This regularity, though manifested in a more complicated way, is noted for cod fry (NIKOLSKY, BELYANINA, PONOMARENKO and SYSOEVA 1968). In the case of cod fry, the variability of characters is largely dependent on the size of the concentrations formed due to the dispersal over one or the other branch of the Atlantic current. Besides, in recent years, due to a low level of reproduction no feedback between the total number of cod fry and the food supply has been observed. This relationship was, however, revealed in specifically rich generation years, e.g. 1963.

The relationship between character variability and the quantity of cod fry is better demonstrated in coastal forms. In such stocks, as a rule, numerous populations prove to be most variable. An increase in variability makes it possible for the population to cope with more diversified environmental conditions. It has been most explicitly demonstrated for characters related to feeding and diet diversity. It is noteworthy, as was revealed in Murman coastal cod, that the diversity of characters in it slightly reduces with age in connection with a higher food supply level in fish at the age 1+ and 2+ as compared with specimens at the age of 0+.

One of the most essential specific characters which secure the existence of a species as a relatively stable unit, is the intraspecific structure. To a certain extent, all the intraspecific forms can be subdivided into four groups.

1. Geographical forms or subspecies, e.g. Atlantic cod and Pacific cod. The formation of subspecies enables the species to fill in a greater distribution area.

2. Ecological forms or infraspecies, e.g. fjord and migratory cod forms. The existence of various ecological forms enables filling in diversified habitats within the distribution area.

3. Seasonal forms, e.g. spring and autumn forms in salmon, autumn and spring spawning herring forms. This means of variability ensures filling in the same biotope to a greater extent in different seasons of the year.

4. Temporary forms, the forms which originate in the same biotope under changed life conditions in a population of any species. Such temporary forms are most markedly observed in numerous freshwater species, e.g. roach in the course of transition to the life in a reservoir newly formed at the river. In mammals such temporary subspecies are found in some fossil forms from the quarternary period, e.g. in Baltic region elk. The adaptive value of temporary subspecies lies in the capability of filling in the same biotope under changed conditions.

The diversity of the four intraspecific forms may be quite different ranging from a clear cut distinguishability to a gradual transition of one form to the other, clinal variability being in evidence. It should be mentioned in this connection that I do not find justifiable the fact that in the latest edition of the zoological nomenclature code taxonomic values are solely attributed to geographical categories, subspecies, the remaining intraspecific forms, being left out. Ecological and seasonal forms, however, often prove to be distinguishable to a greater extent than subspecies.

In many cases the appearance of ecological and seasonal forms is of a parallel character. The phenomenon faced is reminiscent of Vavilov's law of homologous rows (NIKOLSKY 1969). Possibly, as was suggested by BERG (1948) it is expedient to attribute the same specimens to such similar forms in different species, e.g. deep-water forms, infraspecies profundicola, lacustrine forms, infraspecies lacustris, etc. I believe that this scheme should be employed in zoological nomenclature code, subspecific individual names being retained.

IMPORTANCE FOR FISHERIES MANAGEMENT

For fishery biologists, the existence of intraspecific group forms within a species is extremely essential. When exploiting a certain population, dynamics of its number and distribution area should be taken into consideration. For example, the Arcto-Norwegian cod stock, being a unified self-recruiting form distributed over a great area, calls for a definite

exploitation scheme. If, as in the case of the northwestern Atlantic cod, some local forms are found, rational fishery should be arranged on a different basis than in the case of the Arcto-Norwegian stock. It is interesting to note that morphological indices in different age groups of the same form do not differ greatly in local forms of western Atlantic cod. In the Arctic cod, however, the distinctions in the morphology of different age groups within a form may be quite pronounced. This appears to be accounted for by highly variable life conditions in different age groups (ПОРОВА 1968). In numerous species there occur both large migratory forms and small coastal ones distinguished by a slower growth as well as an earlier maturation onset. The degree of isolation in these forms may range widely in some cases as in north Caspian roach. A coastal, smaller form may result from reproduction by a semi-migratory fast-growing one, and, evidently, vice versa. In other cases these forms may be isolated, one not reproducing the other.

In red salmon, *Oncorhynchus nerka* (Walb.), the migratory form reproduces in lakes a land-locked form, the so-called residual. In turn from this land-locked form a migratory form can be reproduced under certain conditions (КРОКХИН 1967).

It should be noted that in the course of the dwarf red salmon development some caryotypic changes occur, a great number of polyploid specimens appearing. This is of particular interest if polyploidy is related to an increased morphological variability. It is noteworthy that in migratory red salmon the caryotype is peculiarly stable (CHERNENKO 1968). The relationships between seasonal forms prove to be likewise diversified. If, e.g. in autumn- and spring spawning Baltic herring, a partial transition of one form to the other is evidently possible, in chum salmon this appears to be out of the question. It is natural that a fishery biologist aims at elucidating the relationships between the intraspecific forms, in particular, the possibility and conditions under which specimens of one form appear from the specimens of another form, i.e. whether one form can be reproduced by another and to what extent.

Thus, investigation of the theoretical aspects of the problem of species, further elucidation of the concept of species as a self-regulating system appears to be extremely essential for the solution of a number of fishery problems, and, first and foremost, for developing the basis of a rational exploitation of commercial species.*

* Dr. Rollefson's paper on cod and cod fishery which he kindly sent me bears the following dedication: "To Dr. Nikolsky who also struggles with these mysteries". I believe that joint efforts of scientists the world over will eventually do away with numerous mysteries that still have currency in fishery biology and help to organize rational fishery in international waters, a work which Dr. Rollefson has been contributing greatly to.

CONCLUSIONS

Every animal species is relatively stable in time and space. This relative stability is provided by adaptive intraspecific variability which makes it possible for the species to exist under certain changes of its biotic and abiotic environment. Species is an open self-regulating system. Eurybiont species usually possess a more complex intraspecific structure and a wider range of self-regulation mechanisms than stenobiont species adapted to more stable conditions.

The knowledge of specific structure as well as its regulatory parameters is essential for rational exploitation of commercial species populations and the ensurance of their reproduction. The most essential system of regulatory mechanisms manifests itself in food supply and reproduction rate variability. Disturbances in this regulatory system affect recruitment and bring about a lack in resources of the given commercial species, i.e. overfishing in the biological sense.

An essential regulatory mechanism which secures the existence of the species is an adaptive morphological variability of its specimens. Every year-class is somewhat distinguishable from adjacent year-classes due to the specificity of its living conditions. At the same time adjacent year-classes specifically in the species with a long life cycle mutually interact, affecting the growth rate, fecundity and other year-class characters.

In specific structure the relationships between intraspecific forms is its essential property. To meet the requirements of fisheries, not only the information of the size and properties of the different species forms are essential, but also the possibilities of reproduction of one of the forms by another, i.e. the character of their relationships.

The knowledge of the peculiarities of commercial species regulatory mechanisms and their structure are prerequisite for developing productive fishery.

SUMMARY

The paper presented deals with the problem of intraspecific structure and variability in fishes. Four forms of intraspecific groups are noted. The necessity to study the intraspecific structure and variability for fishery management is emphasized.

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PHYSICAL VARIABILITY IN THE SEA AND THE CONSEQUENCES FOR FISHERIES HYDROGRAPHY

By

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INTRODUCTION

Fisheries hydrography relies on physical, chemical and biological oceanography and as a marine science tries to solve practical problems in fisheries by understanding the behaviour of various organisms in connection with the natural environment. A broader basis of studies was given by the foundation of the International Council for the Exploration of the Sea (ICES) in 1902. General and detailed facts could be established: the stocks of commercial fish are integrants of ecological systems in which interrelated physical and chemical conditions of great complexity operate and fluctuate from year to year. These systems exercise decisive influence on reproduction, growth and mortality of the organisms, and no rational study of fish can be undertaken without exhaustive inquiry on the physical-chemical conditions. Among the factors of the ecological systems are water temperature, salinity, depth, pressure, currents, content of different nutrients, oxygen, light, osmotic pressure, hydrogen-ion concentration, food (DIETRICH, SAHRHAGE and SCHUBERT 1959). Measuring and understanding of the physical and chemical factors have developed enormously during the last ten years. This is not without influence on fisheries hydrography as such factors have to be taken into account in biological oceanography. New important environmental factors could still be discovered.

The great development in physical and chemical oceanography in the last decade became possible by the introduction of modern electronics to measurements and data processing. Stratification and motions were revealed and showed surprising variations, periodic and non-periodic. Physical oceanography was challenged to measure and to ex-

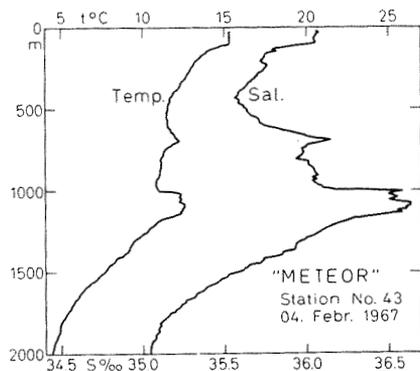


Fig. 1. Vertical profile of temperature and salinity based on a bathysonde record 40 n.m. west of Cap São Vicente ($\varphi = 36^{\circ}53'N$, $\lambda = 9^{\circ}50'W$). (After SIEDLER 1968).

plain these phenomena and to give the biological oceanography a base to study the consequences on the behaviour of the species. Under the topic "variability" these processes and their interrelation in space and time became one of the central tasks of present oceanography.

PHYSICAL VARIABILITY IN TIME AND SPACE

What is the meaning of the general term "variability" in the sea? The answer is demonstrated in five examples using the recordings of modern instruments. The first one (Fig. 1) shows the vertical distribution of temperature and salinity with the fine structure of layering. The continuous records were taken during an anchor station of R/V Meteor during the Atlantic seamounts cruises 1967 near Cap São Vicente in the mixing area of Atlantic and Mediterranean water masses. The second example (Fig. 2) shows the variations in time of temperature and current

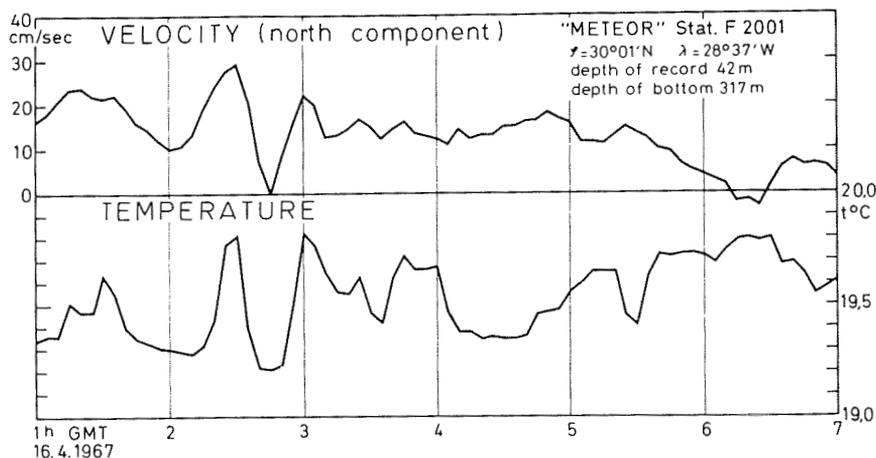


Fig. 2. Time variations in current velocity and temperature on the Great Meteor Seamount over a period of 6 hours. (After MEINCKE 1969).

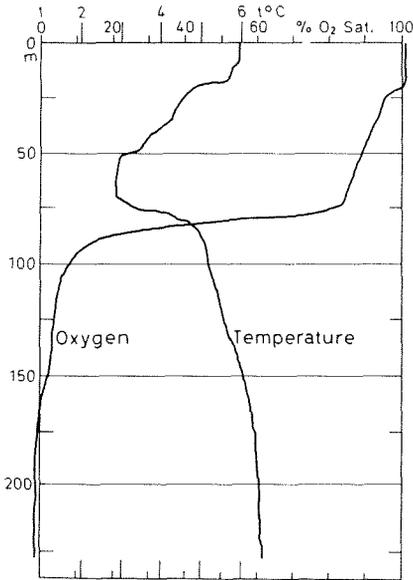


Fig. 3. Vertical profile of temperature and oxygen in % of saturation based on an oxygen-sonde record in the central Baltic 8 May 1968 ($\varphi = 57^{\circ}03'N$, $\lambda = 19^{\circ}50'E$). (After GRASSHOFF 1969).

velocity (north component) recorded from a moored instrument system. This example covers six hours and is a small part of a series of long records in the area of the Great Meteor Seamount, showing that even in the open ocean short term changes govern the current and temperature recordings. In a third example (Fig. 3) the vertical distribution of oxygen and temperature in the central Baltic is presented, showing the fine structure of layering. The oxygen changes from 90% to 10% saturation in a thin discontinuity layer at about 80 m depth. In depths more than 150 m the curve is below the zero line, i.e. hydrogen-sulphide appears in the water. In the fourth example (Fig. 4) is demonstrated that a recording

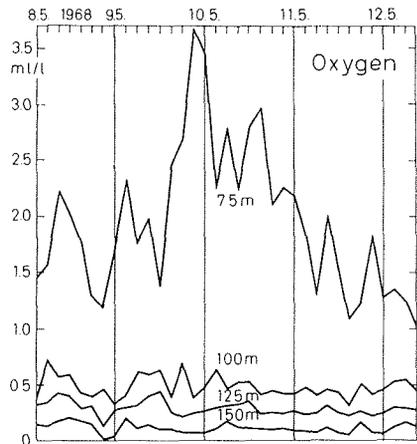


Fig. 4. Time variations of oxygen at different depths during 8-12 May 1968 in the central Baltic ($\varphi = 57^{\circ}03'N$, $\lambda = 19^{\circ}50'E$). (After GIESKES and GRASSHOFF 1969).

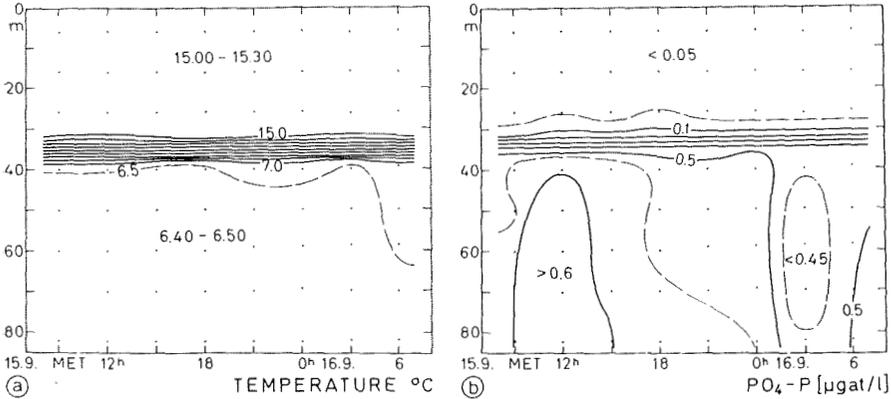


Fig. 5. Time variations during 24 hours, 15-16 Sept. 1968 in the central North Sea represented as isopleths ($\varphi = 56^{\circ}21'N$, $\lambda = 1^{\circ}3'E$). (After EHRHARD and SCHOTT 1969).

as in Fig. 3 is not representative, even for some hours. There are time variations in the oxygen content at the same point in the central Baltic. The reasons are vertical movements in internal waves as well as horizontal movements transporting different horizontal water masses which, in the Baltic, are of relatively small dimensions. Such a local inhomogeneity of the water can exist in a sea like the Baltic with extremely small tidal currents. But even in the North Sea with strong tidal currents and great mixing short term changes of chemical parameters are pointed out (Fig. 5b) as opposed to the temperature (Fig. 5a). Both figures are based on repeated observations during an anchor station of R/V Alkor. The changes of phosphate content in the deeper layers are about 50% of the absolute value, although the temperature is constant. This means that short term chemical-biological processes exist, which qualify to differentiate between water masses where temperature and also salinity show homogeneous water. Results like these reveal that the sea is much more complicated in stratification, motion and variations with time than physical and chemical oceanographers had imagined only ten years ago. This, of course, is not without consequences for the fisheries hydrography.

The following facts of common validity may be summarized:

1. The stratification has a rather fine structure, i.e. temperature and salinity may vary strongly in only a few meters of vertical distance. These abrupt changes influence the vertical distribution of currents and chemical parameters and therefore, the environment of the organisms.
2. The fine structure of the stratification changes in time and space.
3. The changes in time consist partly of periodically vertical move-

ments. They are partly unperiodic, and partly they belong to local inhomogeneities in the water.

A single hydrographic station is only representative within a wide range when measuring the fine structure of the vertical distribution of the main physical and chemical components (temperature, salinity, sound velocity, current-shear, oxygen). These measurements must be taken by research ships, since new principles in instrumentation have been developed in the last ten years (bathysonde, sound-velocity meters, current-shear meters, oxygen sonde, etc.).

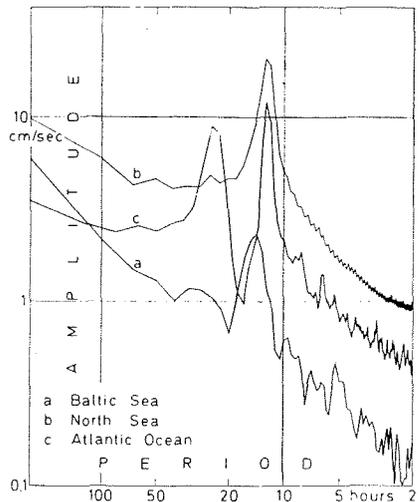
The observed facts require further special instrumentation to obtain continuous records from moored measuring systems of at least temperature, salinity and current speed and direction. As carriers of instruments different systems are used:

1. Surface buoys damped against surface wave oscillations.
2. Submerged buoys, released from the mooring by an acoustic signal.
3. Masts or posts at the bottom.
4. Underwater winches moving sensors up and down regularly.

The two last systems are usable only in the shelf regions as it was done in the Baltic (KRAUSS 1960, SIEDLER and KRAUSE 1967).

By the period analysis of longterm registrations general conclusions can be drawn in spite of the special local characteristics in different areas. Examples from the central Baltic, the central North Sea and the subtropical Atlantic Ocean may illustrate this fact. Figs. 6 and 7 show the amplitude spectra of current velocity components from these records. In Fig. 6 curve a) from the Baltic Sea indicates a significant peak at the

Fig. 6. Amplitude spectra of current velocity, north component, from a) Baltic Sea ($\varphi = 55^{\circ}3'N$, $\lambda = 13^{\circ}51'E$), depth of record 39 m, depth of bottom 45 m, 4-25 Aug. 1965. (After KRAUSS, unpubl. results). b) North Sea ($\varphi = 56^{\circ}20'N$, $\lambda = 1^{\circ}0'E$), depth of record 10 m, depth of bottom 85 m, 14-27 Sept. 1968. (After SCHOTT 1969). c) Atlantic Ocean ($\varphi = 29^{\circ}60'N$, $\lambda = 28^{\circ}37'W$) depth of record 50 m, depth of bottom 322 m, 30 April-30 May 1967. (After MEINCKE 1969).



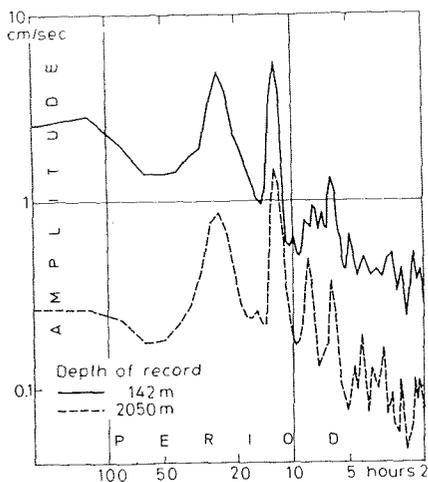


Fig. 7. Amplitude spectra of velocity, north component, from current meters moored by R/V Meteor ($\varphi = 29^{\circ}05'N$, $\lambda = 29^{\circ}02'W$, depth of bottom 4630 m, 13–28 April 1967. (After MEINCKE 1969).

inertial period. Curve b) gives the spectrum from a 14 days-record of the homogeneous upper layer in the central North Sea and shows that the half day-tidal component is the only motion of importance. In curve c) the spectrum from a 30 days-record in the Atlantic measured on top of the Great Meteor Seamount, the tidal periods of 12.4 and 24 hours and the inertial period predominate. Two spectra from different depths of a deep sea mooring with water depth 4630 m (Fig. 7) demonstrate that the spectra may differ on different levels even at the same location.

The general features revealed by spectral analysis are:

1. The amplitudes of motion decline towards shorter periods.
2. Records in close vicinity—vertical as well as horizontal—may show low coherence.
3. Only three main types of motion exist in almost all areas of the sea: the tidal currents of half and one-day periods, inertial oscillation with its latitude-dependent period, and the stability oscillation with a period determined by the density stratification.
4. In addition to these narrow bounded sectors of the period spectrum a multitude of periodic and non-periodic motions of almost unknown origin complicates the picture.

Measurement and interpretation of these processes and of the fine structure of stratification are among the main tasks of modern physical oceanography, and this requires further use of moored systems of instruments.

INSTRUMENTS REQUIRED FOR STUDIES OF THE VARIABILITY

The instruments available for mooring are prepared to record up to two months. A longer time interval is not realistic unless sufficient fouling protections for the sensors are developed. The time interval between two single measurements can be between quasi-continuity and one hour, but further changes are not difficult. The measuring depths desired are mainly down to 500 m, in some cases to the bottom in 5000 m.

The accuracy requirements of the measurements depend on the variability in the ocean areas and may, therefore, only be stated for certain ranges. The necessary high accuracies are not fulfilled in all cases as they can be made available only with great technical efforts, e.g. $\pm 0.01\%$ in salinity or ± 0.01 dbar in pressure:

The standard lower limits of accuracy are:

Temperature	± 0.01 to $\pm 0.1^\circ\text{C}$
Salinity	± 0.01 to $\pm 0.1\%$
Current direction	± 1 to $\pm 5^\circ$
Current speed	± 1 to ± 10 cm/sec
Pressure (gauge)	± 0.01 to ± 0.1 dbar
Pressure (depth)	± 1 to ± 10 dbar.

The attention is focussed on better reliability of the measuring systems under the hard conditions at sea and also on better mooring systems. The methods must be improved, the losses of instruments must be diminished thus increasing the efficiency of the measurements.

CONSEQUENCES FOR FISHERIES HYDROGRAPHY

As demonstrated new sophisticated methods have been developed in physical and chemical oceanography. The progress in fisheries hydrography, however, seems to be inadequate because the correlations between nonbiological and biological factors are not fully understood. Two steps should be made:

1. To study the processes causing the physical and chemical variability.
2. To investigate the biological variability and its relationship to the physical and the chemical variability.

Both can be done in form of experiments in selected areas of the ocean. One of such tests is prepared in the Norwegian Current on the continental slope in autumn 1969 with scandinavian, icelandic and german scientists and with a concentrated effort of research ships and moored re-

ording systems. The results may among other things give criteria, e.g. sampling positions, for moored buoys with data-telemetering systems. Even if no other relationship is known but that between the temperature and the fish distribution such buoys may prove to be as useful as a multinational project of synoptic surveys with research ships as discussed in the ICES and demonstrated by the usefulness of the pilot project in 1966 (EGGVIN 1966).

SUMMARY

Progress in fisheries hydrography depends on progress in the knowledge of physical and chemical variability in the sea. This variability is caused by short term changes in the fine structure of layering in temperature, salinity, current and chemical parameters and revealed by the new ways developed in instrumentation. Some examples of the results, achieved in the North Atlantic, the North Sea and the Baltic, are represented.

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THE GAS CONTENT IN THE COREGONID SWIMBLADDER

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INTRODUCTION

The gas content in the swimbladder of coregonid fishes has been described from different species and localities by several authors (HÜFNER 1892, SAUNDERS 1953, SCHOLANDER, VAN DAM and ENNS 1956, SUNDNES, ENNS and SCHOLANDER 1958, SUNDNES 1959 and SUNDNES 1963). The swimbladder gas in the investigated species is found to contain 99 vol% N₂. The classical example is HÜFNER's paper on *Coregonus acronius* Rapp. In *Coregonus lavaretus* (L.), however, the gas composition was different to other investigated coregonids (SUNDNES, ENNS and SCHOLANDER 1958). In this species the O₂ percentage increased with depth as for physoclist fish (SCHOLANDER, CLAFF, TENG and WALTERS 1951).

Rete structures are found both in the vascularisation of the swimbladder wall of *C. lavaretus* (FAHLÉN 1959) and *C. acronius* (FAHLÉN 1967), and there are seemingly no anatomical background for expecting a different gas mixture to be deposited in the two species.

The findings of 15.2—18.2 vol. % O₂ in the swimbladder of *C. acronius* in the autumn (SUNDNES 1959) and the different distribution of *C. acronius* and *C. lavaretus* with respect to depth (SUNDNES 1963) lend support to the theory that the higher nitrogen content in the coregonid swimbladder is a secondary result of the swimbladder physiology. In the present paper a comparative investigation of the swimbladder gas in two coregonid species is presented.

MATERIAL AND METHODS

The species investigated in the present paper are *Coregonus acronius* from Bodensee (Lake Constanze), Germany and *Coregonus lavaretus* from the lake Randsfjord, Norway.

Contribution given in honour of Gunnar Rollesfsen at his 70th birthday.

The fish were caught by gillnets at depths varying from 15–35 m in Bodensee, and at 70 m in Randsfjord in October and November respectively. The gas samples were drawn from live fish immediately after reaching the surface. The gas analyses were performed in the 0.5 cc gas analyzer (SCHOLANDER 1947). The O₂ content of the fish blood was analysed in a syringe analyzer (SCHOLANDER and VAN DAM 1956). A few specimen of *C. lavaretus* were transported live to the Institute of Marine Research, Bergen for shallow water experiments.

RESULTS

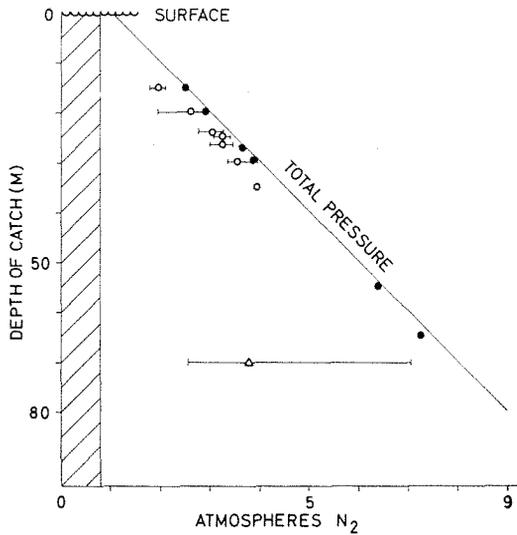
C. acronius was only found in depths down to 35 m probably due to the increasing pollution of the deeper fishing grounds. A single specimen caught at 25 m had a N₂ content in the swimbladder of 98 vol.%. The highest O₂ content measured in *C. acronius* was 33.9 vol.% in a specimen caught at 20 m. Among *C. lavaretus* from 70 m depth in Randsfjord the highest N₂ content was 88.6 vol. %.

The variation in the swimbladder gas content of *C. acronius* and *C. lavaretus* at different depths are shown in Table 1.

Table 1.

Number of fish	Depth in meters	Total range in gas content			
		<i>C. acronius</i>		<i>C. lavaretus</i>	
		vol.% N ₂	vol.% N ₂	vol.% O ₂	vol.% N ₂
5	15	11.5–28.8	70.8–87.4	—	—
48	20	2.0–33.9	63.4–97.5	—	—
15	24	1.8–17.0	82.3–97.5	—	—
3	25	1.2–12.1	87.5–98.3	—	—
2	27	5.1–17.7	82.8–94.2	—	—
6	30	4.2–14.9	84.4–94.9	—	—
1	35	12.0	87.7	—	—
42	70	—	—	10.6–68.8	30.7–88.6
3	Shallow water aquarium	—	—	9.3–25.6	70.4–90.1

The mean values and the range of pN₂ for the two species at different depths are plotted against the total hydrostatic pressure in Fig. 1. The pN₂ in the swimbladder of *C. acronius* caught at different depths in May are also plotted against total hydrostatic pressure. Using average values is not quite correct since the spread of data really reflects different biological situations of the fish.



Figur 1. Mean pN_2 in the swimbladder of coregonids in relation to depth. ● *C. acronius*, May. ○ *C. acronius*, October. △ *C. lavaretus*, November. — indicate total range. ▨ partial pressure of dissolved N_2 in the lakes.

DISCUSSION

The primary gas deposited into the swimbladder has an O_2 content higher than that of the air. This is definite in *C. lavaretus* which inhabits relative shallow water. During the spawning period it migrates to deeper areas and has a much higher O_2 content than that of air. (SUNDNES, ENNS and SHOLANDER 1958). A prolonged stay in the deep areas without even small vertical migrations would result in an absorption of the oxygen. It is very unlikely that the oxygen exposed to living tissue in the swimbladder behave like inert gases. The gas will immediately enter the energy metabolism. During a prolonged stay at a certain depth, the O_2 in the swimbladder lost by metabolism will be replaced by a mixture of O_2 and N_2 to keep the fish buoyant at that depth. By a continuous replacement of the O_2 partly by N_2 , the N_2 content of the swimbladder gas will increase asymptotically. This is seemingly the process in *C. acronius* which is abundant in deeper areas. A similar process is also possible in *C. lavaretus*, as shown by the high N_2 values in Table 1. Also in shallow water the same situation occur when vertical migrations are possible. *C. lavaretus* kept for 2 months in a 40 cm deep tank had a swimbladder gas consisting of 90.1 vol. % N_2 and 9.3 vol. % O_2 .

Like *C. lavaretus* also *C. acronius* is able to deposit a gas mixture into the swimbladder having an O_2 higher than that of air. (Table 1). Due

to the different vertical distribution of the two species (SUNDNES 1963), a high O₂ content as found in *C. lavaretus* should not be expected in *C. acronius*.

As an example, a stationary, buoyant *C. acronius* at a depth of 30 m will have a swimbladder gas consisting of about 99 vol. % N₂. By migration to a depth of 10 m, the volume of the swimbladder is kept constant by releasing gas. The gas left in the swimbladder has the same high N₂ content. When migrating back to 30 m, the swimbladder will be compressed to half the volume. To be neutrally buoyant a gas deposition corresponding to half the volume of the swimbladder in that depth is necessary. E.g. a maximum mixture of O₂ like those found in *C. lavaretus* consisting of nearly 70% O₂, will give a maximum O₂ content of 35 vol. % O₂ in the swimbladder of a buoyant *C. acronius*. In the present investigation a O₂ content of 33.9 vol% is found in the swimbladder of *C. acronius*.

CONCLUSION

The present findings support the theory that the high N₂ content found in the coregonid swimbladder is a compensation of the loss of O₂ to the surrounding tissue and not due to a primary deposition of a gas mixture containing a high percentage of N₂.

The replacement of the gas volume is made by a mixture of O₂ and N₂, and the continuous loss and replacement function gives an increase in the N₂ content.

The high O₂ content in both species support the theory that the gas is deposited into the coregonid swimbladder from the vascular system of the fish.

The underlying mechanism of the deposition of gases into the coregonid swimbladder, however, is still an open question.

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SUMMARY

The present investigation support the theory that there are no differences in the swimbladder physiology of *Coregonus acronius* in Bodensee and *Coregonus lavaretus* in Randsfjord. The high N₂ content found in *C. acronius* is due to absorption of the O₂ content of the swimbladder.

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NOTES ON THE DISTRIBUTION AND ECOLOGY OF *MYXINE GLUTINOSA* L.

By

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The hagfish (*Myxine glutinosa* L.) is very common on muddy bottoms along the west coast of Norway, and has for at least 80 years been a favourite subject for anatomical and histological research. Its life history is not, however, correspondingly well known, and although it may live for a long time (several months) in aquaria, it does not breed there. The embryology is practically unknown.

In recent years Foss (1962) has made important contributions to the knowledge of the ecology of the species by discovering its burrows (in Ulvikpollen in Hardanger, West Norway) and by tagging experiments.

The present notes are concerned with the distribution and ecology of the species, based on observations made by the author during 11 years of field work in the Bergen area and the Hardanger Fjord, and also on an analysis of the available literature.

The hagfish has figured in Norwegian scientific literature since the time of LINNÉ, and several authors have taken part in the discussion of its relation to the major systematical groups. (For instance GUNNERUS 1763, and KALM 1753). KRØYER (1852–53) stated that the species is found all along the Norwegian coast, and NILSSON (1855) mentioned its abundance on some parts of the Scandinavian coasts. COLLETT (1875) said that it is found in all suitable localities along the Norwegian west coast, and NANSEN (1886 and 1888) mentioned that several hundred specimens could be collected at Alverstrømmen (north of Bergen) (cf. BRINKMANN 1961), and that it is “more common than any other fish” in the fjords around Bergen.

Contribution given in honour of Gunnar Rollefson at his 70th birthday.

According to GRIEG (1914 p. 52), it is found down to a depth of 500 metres around Bergen, is abundant in the Hardangerfjord, and "occurs quite commonly up to about a depth of 10 metres in the innermost part of Jondalsbugten on muddy bottoms". TAMBS-LYCHE (1954) found that the species occurred almost everywhere in Sørffjorden and Osterfjorden in North Hordaland, on muddy bottoms up to a depth of about 100 metres.

Throughout its area of distribution, the hagfish is a characteristic animal on the muddy bottoms which cover most of the fjord deeps.

As mentioned above, GRIEG (1914) found that the hagfish occurred down to 500 metres around Bergen. In later years, however, it has repeatedly been caught, sometimes in large numbers, at a depth of 690 metres in Korsfjorden near the Biological Station Espegrend; and LYNNGES (1930) mentions catches taken at a depth of 1100 metres in the Sognefjord. At one station (ZF 176) in the Hardangerfjord (Samlafjord near Ålvik), 473 specimens were caught in baited eel-traps at a depth of 864 metres. The greatest depth mentioned by BIGELOW and SCHROEDER (1948) is 524 fathoms (985 metres). One may therefore conclude that there is, at present, no real indication of the maximum depth at which it may be found.

It is also of greater interest to find the upper limit of its occurrence.

As mentioned above, GRIEG (1914) found the species "quite commonly" at a depth of 10 metres in Jondalsbukten in Hardanger. In July 1959, the present author thoroughly investigated the locality but was unable to find the species between 8 and 24 metres, from which depth the bottom of the bay descends steeply. In any case the bottom of the bay is not suitable for the hagfish as the mud is mixed with coarse sand and gravel. It is therefore probable that GRIEG's statement is erroneous, or perhaps more likely, the figure 10 may be a misprint for 100 metres. The species, in any case, does not occur at the depth stated.

All available information shows, however, that *M. glutinosa* ascends to lesser depths as one passes from the open coast towards the inner fjords. In the relatively open waters of the outer areas, for instance, near the Biological Station Espegrend, it has so far not been caught above 95 to 102 metres (near Ospøya in Raunefjorden), although several attempts have been made to find it in shallower localities where it might be studied. Near Herdla (the site of the Biological Station before 1940), it was known to occur regularly in Ypsøy sound, where the depth varies between 30 and 70 metres (Herdla collecting station No. 12). It is probable that the species was caught at the greater of these depths rather than at the lower. Ypsøy sound is near the "bottom" of the Herdla fjord, and forms a small, rather closed basin with sills at both ends. There is a considerable amount

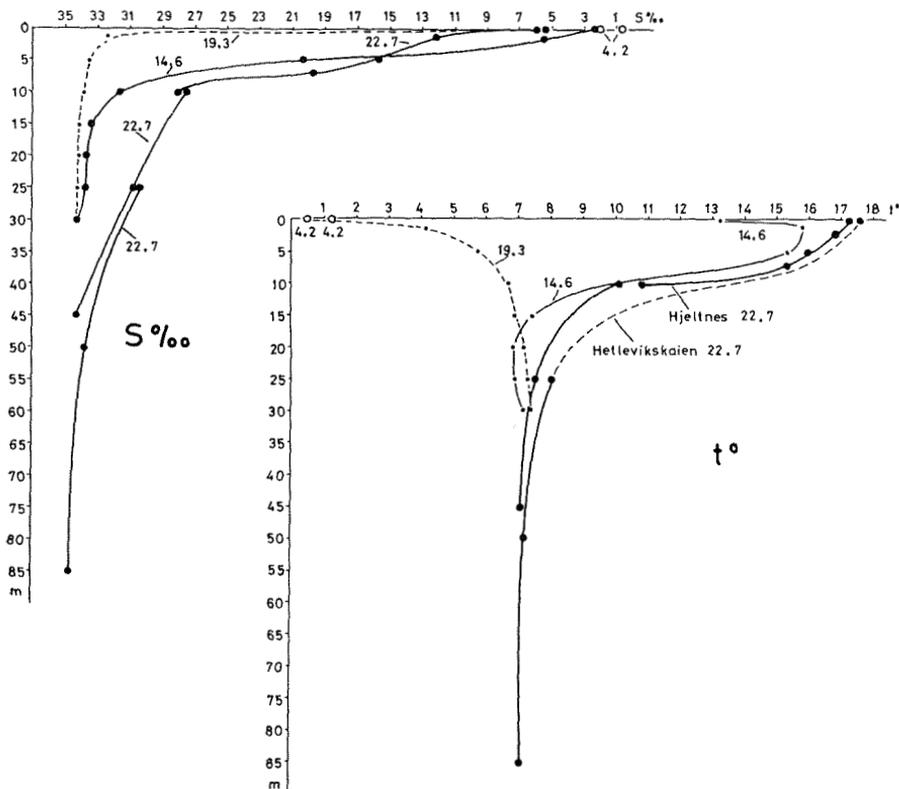


Fig. 1. Hydrographic observations in Ulvikpollen, Hardanger 1959 (July) and 1960 (winter and June). Open rings: winter observations. Filled dots: summer observations. Observations on 22 July were made at three different localities; in the bay proper (bottom at about 15 metres), at the opening of the bay (bottom at about 50 metres), and near Hetlevikskaien (bottom about 90 metres).

of fresh water run off from the nearby Rosselandspollen and from lakes on Holsenøy.

In Ulvikpollen, in the innermost part of the Hardangerfjord, *M. glutinosa* has been caught regularly between 24 and 48 metres in relatively large numbers during the Hardanger fjord investigations (see also Foss 1962). Trials at depths of 9 to 10 metres were always negative.

The available information on the hydrography of Ulvikpollen has been plotted in Fig. 1. It shows that there are large annual variations in temperature and salinity in the layers above 30 metres, but from that depth to the bottom, the temperature and salinity conditions are remarkably constant throughout the year. This figure should be compared with a corresponding one from a locality very similar to the one at Raunefjorden by BURDON-JONES and TAMBS-LYCHE (1960 p. 19). It shows that

a corresponding stability throughout the year in the outer fjord districts, is found only at a depth of 90 to 100 metres, the minimum depth where *M. glutinosa* occurs in that area.

It may be that a high and constant salinity (32 to 35‰), and also a constant and not particularly high temperature (<about 8°C) are the limiting factors for the distribution of the species. But the physical features of the bottom are evidently also of importance.

Observations of the minimum depth of the species' occurrence in other parts of its area of distribution correspond well with what is known from the Bergen coast.

KRØYER (1852-53) mentions 12 to 20 fathoms as the common depth at which it is found in the Kattegat, and says that it has been found repeatedly at 7 to 8 fathoms. However, PETERSEN and LEVINSEN (1900) found it only in trawlings between 300 and 40 fathoms, the only exception being a single specimen caught north of Læsø at a depth of 20 fathoms. KRØYER received his information from fishermen, and their depth figures may not have been so accurate as PETERSEN and LEVINSEN's records.

BRATTSTRÖM (1948) found one specimen near Kullen at the northern entrance to Øresund, at a depth of 20-23 metres (length 380 mm.)

LYNGNES (1930) found the species up to 20 fathoms on the Møre coast, and COLLETT (1875) also mentions 20 fathoms as the minimum depth, while in 1905 he said that it "may be found in shallow bays of only 20 metres depth".

LILLJEBORG (1891) mentions 15 fathoms as the upper limit on the Swedish west coast, and RETZIUS (in SMITT 1875) gives 16 to 17 fathoms as the minimum depth in Gullmarfjorden. GUSTAFSON (1934) mentions 30 metres as the upper limit in the same fjord.

The North Atlantic distribution of *M. glutinosa* extends from Murmansk to Gibraltar. It has been found a short distance east of the Straits of Gibraltar, but does not occur elsewhere in the Mediterranean. It has been found in the Sound (see above), but not in the Baltic. Possibly the salinity is too low. It seems to be more common in the northern part of the area of distribution than in the southern. It has been recorded near the east coast of Iceland at a depth of 940 metres by KONSTANTINOV and SCHEGOLEV (1958). IVERSEN (1936) found two specimens at East Greenland (63°40'N 39°6'W). FABRICIUS (1780), KRØYER (1852-53) and JENSEN (1926) record it in West Greenland waters. The species is also distributed from the Gulf of St. Lawrence (VLADYKOV 1951) to Delaware Bay and Cape Fear in North Carolina.

BIGELOW and SCHROEDER (1948) compared North American specimens with Norwegian ones, but did not find sufficient difference to consider them as separate, either at the species or subspecies level. They

therefore considered *Myxine limosa* GIRARD 1859, described from North America, as a synonym for *M. glutinosa*.

There is, however, one difficulty not mentioned by BIGELOW and SCHROEDER. The largest European hagfish recorded were 470 mm (COLLETT 1875) (from Øksfjord in Finnmarken) and 455 mm long (NILSSON 1955) (from West Norway). The present author, in the course of his stay at Espegrend, measured a total of 1682 specimens from the vicinity of Bergen and the Hardanger fjord, and found the largest animal to be 382 mm long. The average length in most catches was not above 260 to 280 mm. However, a maximum size of 790 mm has been reported from U.S.A., and CONEL (1917) mentions a series with an average length of 620 mm.

The size of the animals caught depends to some degree upon the size of the gear used to catch them. At Espegrend, common eel-traps were mostly, but not exclusively used. It may be that some other gear might have caught individuals larger than 382 mm. There is no indication as to the gear used by CONEL, but it seems very unlikely that this should be the reason for the great difference in size recorded. It seems therefore worthwhile to make a closer investigation as to the size-distribution of the species on both sides of the Atlantic. If a difference in the maximum size, such as the one mentioned above, is confirmed, that would indicate that at least different subspecies occur in the eastern and western Atlantic.

SUMMARY

The distribution and ecology of the hagfish, *Myxine glutinosa*, in the Bergen area is discussed, especially its depth occurrence. The ascent of the species to lesser depths in the inner fjords is seen in relation to the stability of the water masses. The total distribution of the species is reviewed, and it is suggested that a pronounced difference in size of the animals on both sides of the Atlantic may, if confirmed, indicate that there are different subspecies.

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ON THE HYDROGRAPHY OF THE SHELF WATERS OFF MØRE AND HELGELAND

By

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INTRODUCTION

The coastal banks between Stad and Lofoten (Fig. 1) are an important spawning and hatching area for several fish species. The hydrography in this area is, however, insufficiently described, especially the conditions in winter and spring when the spawning and hatching of some of the most important commercial fish species take place.

The topography of the area is presented in Fig. 1. The extension of the shelf in this area is greater than off other parts of the Norwegian coast. In average the width is more than 100 nautical miles, except off Møre where the shelf is narrow.

Basic studies of the hydrography of the coastal banks were carried out by HELLAND-HANSEN and NANSEN (1909). Sea surface temperatures in the area were presented by EGGVIN (1966), and LJØEN (1962) discussed the hydrography in summer.

The present work presents a description of the general hydrography on the coastal banks in winter. The upper layers are dealt with in detail since their relationship with biological phenomena are of particular interest.

MATERIAL AND METHODS

The analysis is based on hydrographic observations made during two cruises. The first, in February 1956, covered the entire shelf and the adjacent deep sea between Grip and Lofoten (Fig. 5). The second, in early March 1968, covered the shelf between Stad and Frøyabanken (Fig. 7). At all stations observations were taken in standard depths to the bottom, and the temperature at 4 m depth was recorded continuously with thermograph.

Contribution given in honour of Gunnar Rollefson at his 70th birthday.

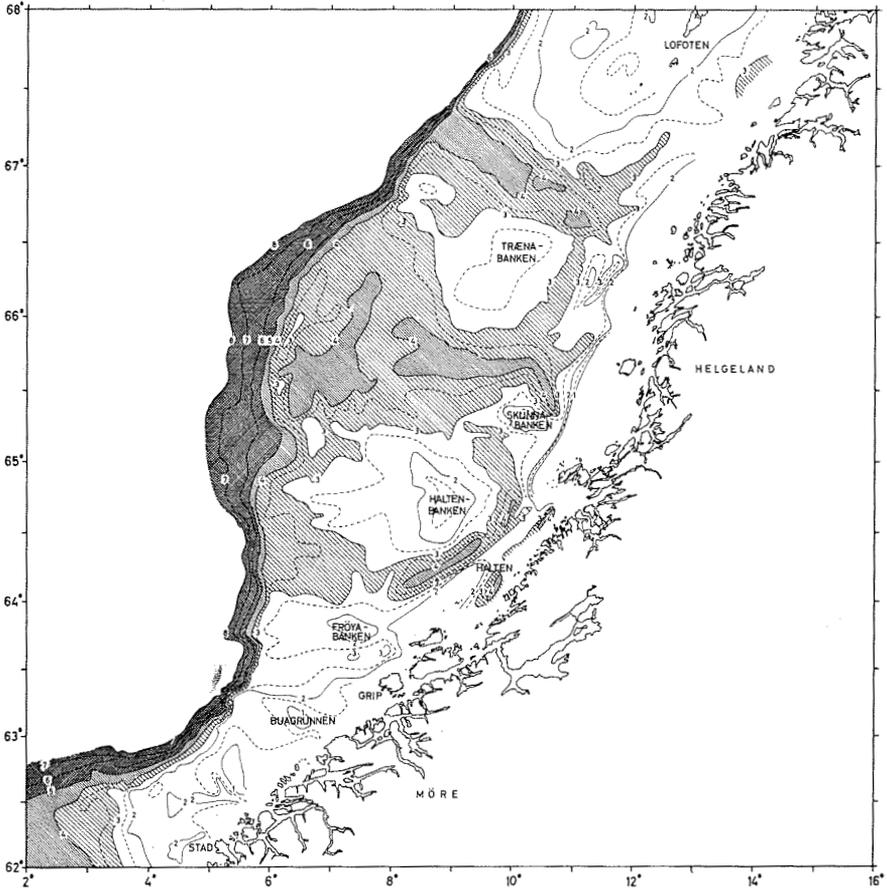


Fig. 1. Bathymetric map of the investigated area. Depths in hectometers.

THE WATER MASSES

Plots of temperature versus salinity from all points of observation are presented in Fig. 2, which gives a view of the different water masses in the investigated area. Three main water masses may be defined: Coast water, Atlantic water and Slope water. The latter is mainly a mixture of Atlantic water and the upper part of the deep water in the Norwegian Sea. The other two, Coast water and Atlantic water, are brought by the currents into the area where their characteristic parameters are altered due to mixing and heat exchange with the air.

Extreme Coast water is characterized by salinities and temperatures lower than 34.5‰ and 5.5°C. A_1 on Fig. 2 represents the core of Atlantic water of the Norwegian Atlantic Current in the southern part of the area. This water is partly protected from direct heat loss to the air by overlying

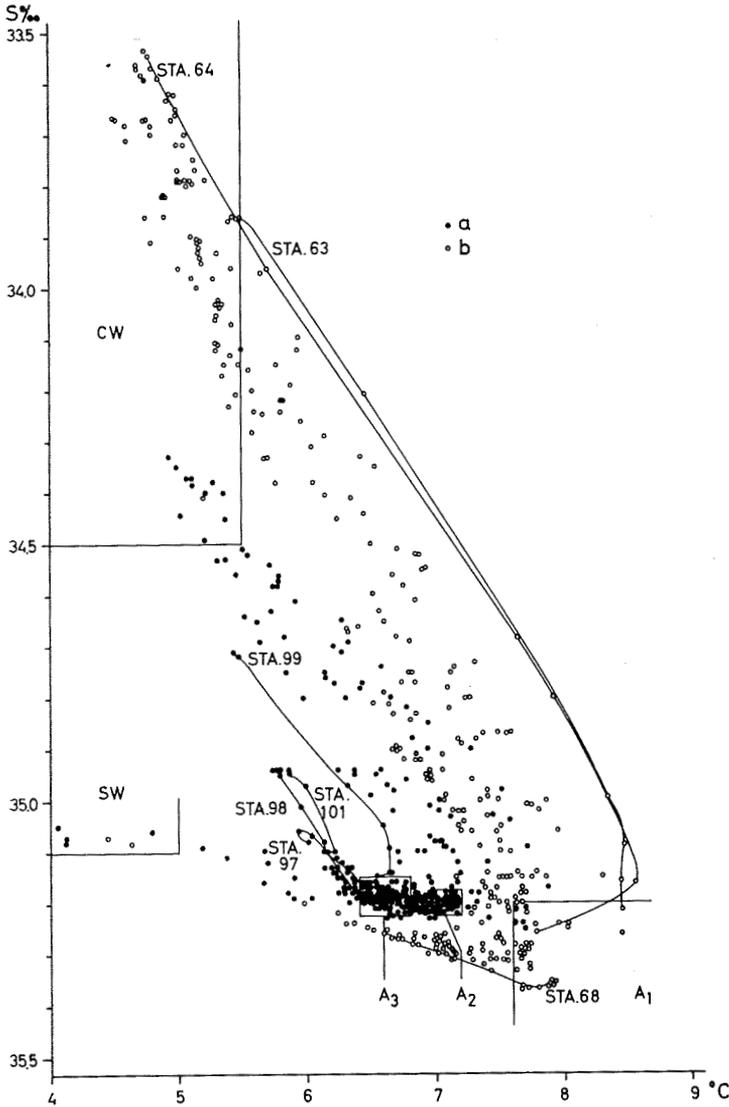


Fig. 2. Temperature-salinity diagram. (a) Observations in 1956. (b) Observations in 1968. CW: Coast water. SW: Slope water. A₁, A₂ and A₃: Phases of Atlantic water.

Coast water. A concentration of temperature-salinity points around 35.20‰ and 7.0–7.2°C indicates a larger bulk of nearly homogeneous water, A₂, a phase of Atlantic water. This water also gives the main contribution to a water mass, A₃, with salinities 35.15–35.22‰ and temperatures 6.4–6.8°C which have been formed mainly by cooling and a slight mixing with less saline water.

Slope water has salinities and temperatures below 35.10‰ and 5.0°C, and is located at the upper edge of the continental slope. There is no direct connection between Coast water and Slope water.

The temperature–salinity curves in Fig. 2 illustrate clearly that the extreme values of Coast water and Atlantic water are found in the southernmost part of the area. Corresponding to earlier findings (HELLAND-HANSEN and NANSEN 1909), both salinity and temperature of Coast water increase further north while the values in Atlantic water decrease. These changes are due to mixing between the water masses and the fact that both masses mainly move to the north.

THE DISTRIBUTION OF TEMPERATURE AND SALINITY

THE 1956 SURVEY

The section

The water mass A_2 is present in a width of 60 nautical miles (between Station No. 70 and 74) and has a thickness of about 250 m (Fig. 3). The water mass is brought into the area by the Norwegian Atlantic Current and makes a trough in the water mass A_3 . On the coastal side A_3 is formed as a result of mixing between A_2 and Coast water, and on the offshore side by mixing between A_2 and water from the central part of the Norwegian Sea where the salinity is slightly less than in A_2 . The main process, however, underlying the formation of the mass A_3 in the bankarea, is the exchange of heat with the air. This results in a vertical mixing from the surface to the bottom and a decrease in temperature.

Coast water appears in a narrow zone near the shore. The isohalines slope steeply, indicating a strong northward current relative to the bordering mass.

At Station No. 77 an intermediate maximum in temperature appears with extreme values at 50 and 75 m depths. Originally, this water was of the type A_2 , but receives admixture of Coast water in the upper part without significant heat loss to the air.

A ribbon of relatively cold water occurs in the Atlantic phase A_3 in the intermediate and deep layers at Station No. 78. This water has a slightly higher density than the surroundings and is probably formed on Haltenbanken, which partly is shallower than 150 m. Here, the vertical convection from surface to bottom occurs earlier in winter than in the deep waters surrounding the bank.

Another ribbon of relatively cold and less saline water in the Atlantic phase A_2 occurs outside the edge of the shelf. This minimum in the values of the parameters is partly due to an ascent of deep water and not caused by admixture of Coast water.

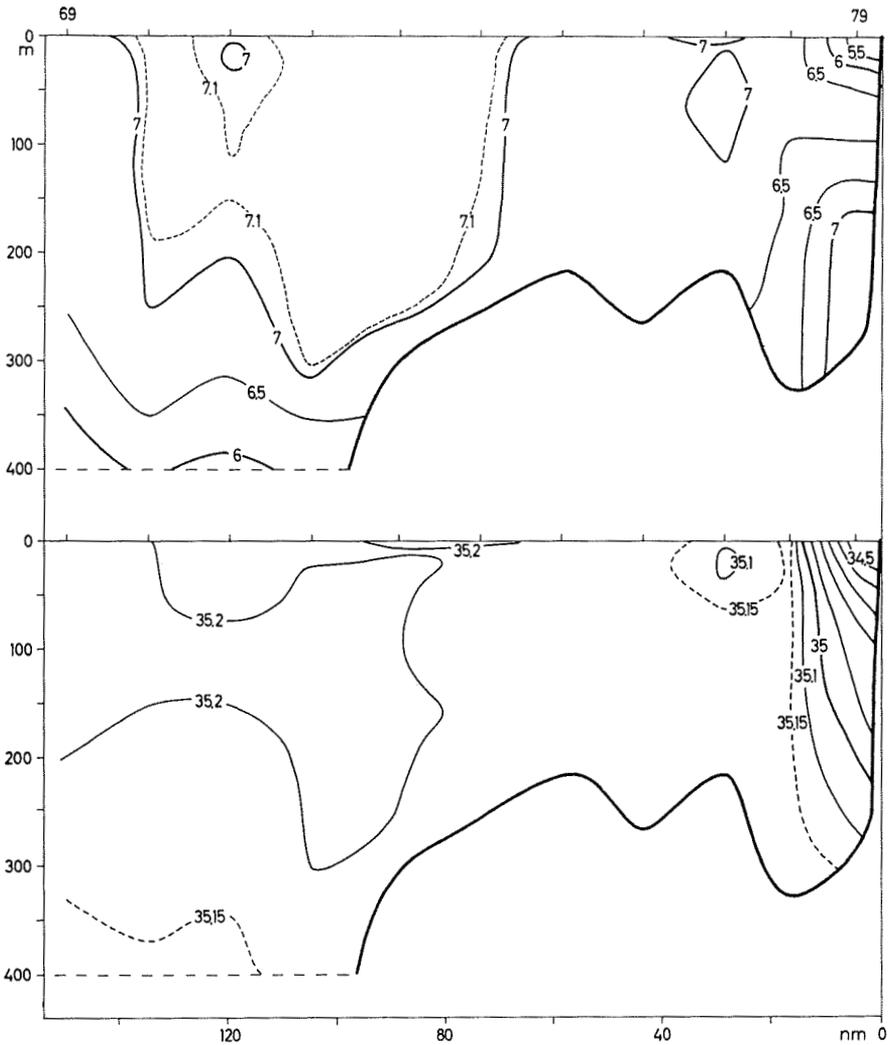


Fig. 3. Temperatures ($^{\circ}\text{C}$) and salinities (‰) off Halten 20–21 February 1956.

The upper layer

The distribution of temperature at 4 m depth (Fig. 4), recorded continuously, permits more explicit studies than is possible by using the stations only. A change in the temperature in the upper layer is caused by mixing between Coast water and Atlantic water and by heat loss to the air only. The temperature, therefore, is a useful parameter for examination of the distribution of the main masses of the top layer, assuming that the heat exchange with the air is similar throughout the area investigated.

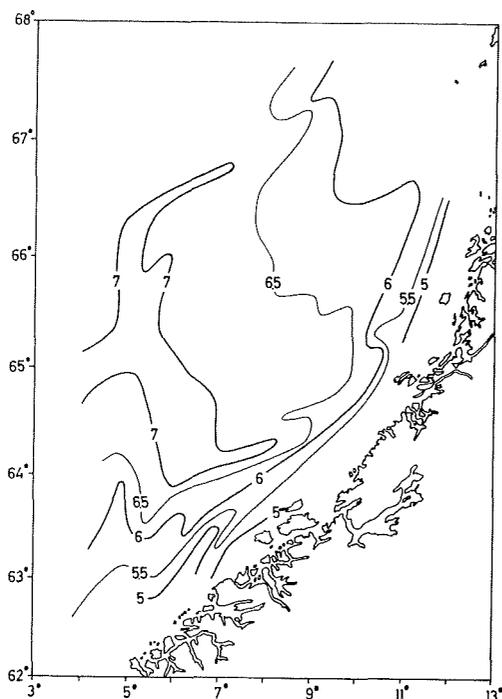


Fig. 4. Temperatures ($^{\circ}\text{C}$) in the surface layer 18–24 February 1956.

It is evident that the Coast water splits into two branches outside Møre. The main branch runs parallel and close to the coast, whereas the other follows the edge of the continental shelf on top of the Atlantic water. The thickness of this branch was about 50 m in the southern part of the area, but was hardly traceable farther north in the section (Fig. 3).

The Atlantic water seems to move northward along the edge of the shelf, and one branch pushes towards the shore along the channel between Frøyabanken and Haltenbanken.

The intermediate layer

A general characteristic of the Atlantic waters A_1 and A_2 is that high temperature is associated with high salinity (Fig. 5). The distribution of these parameters show that the bulk of these masses moves northwards along the slope, and that two branches are pushed towards the coast in channels between the banks.

The minimum in salinity at Station No. 67 is due to admixture of waters from the outer branch of the coastal water.

The ribbon of ascended water in the phase A_2 , mentioned before, gives rise to a minor minimum of temperature above and along the outer part of the slope.

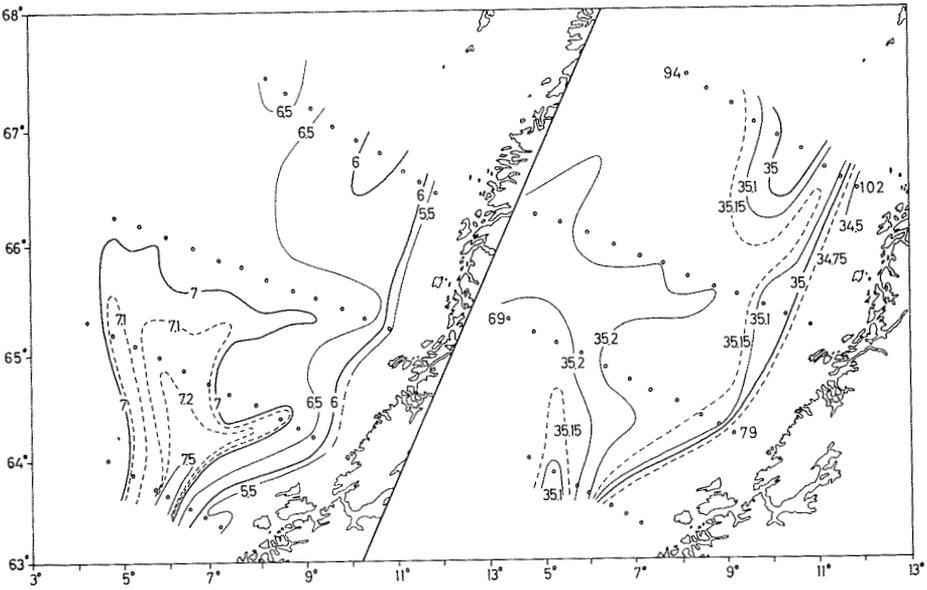


Fig. 5. Temperatures ($^{\circ}\text{C}$) and salinities (‰) at 50 m 18–24 February 1956. Station grid is indicated.

THE 1968 SURVEY

Observations from 1968 give a more detailed account of the hydrographic conditions in the southernmost part of the investigated area. Fig. 6 shows that Coast water is found across the whole continental shelf as a wedge above the Atlantic water. The extreme values of the parameters in the Atlantic water occur at the inner end of the slope just below the Coast water. The transition layer between the two masses is thin, and

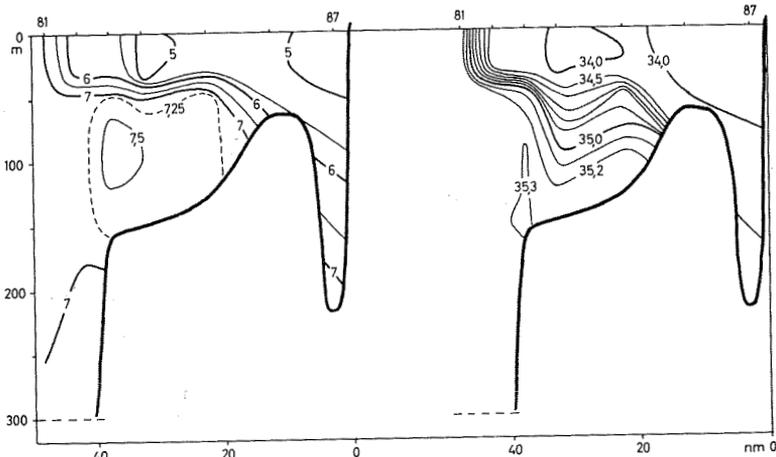


Fig. 6. Temperatures ($^{\circ}\text{C}$) and salinities (‰) across Buagrunden 10 March 1968.

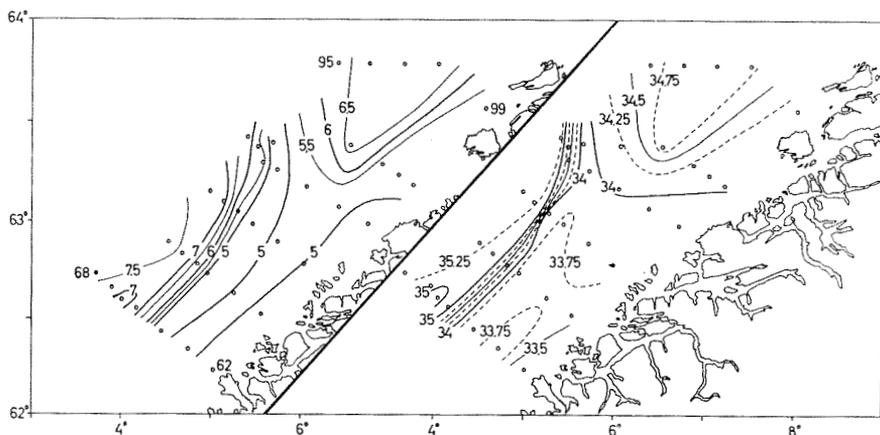


Fig. 7. Temperatures ($^{\circ}\text{C}$) and salinities (‰) at the sea surface 7–12 March 1968. Station grid is indicated.

relatively large vertical and horizontal gradients occur both in temperature and salinity.

In the upper layer (Fig. 7), above the outer part of the shelf, there is a ribbon of water with low temperatures and salinities which seems to continue northwards along the slope. To the north of Buagrunnen temperature and salinity increase in northward direction.

The distribution of temperature and salinity at 50 m depth is illustrated in Fig. 8. There is a narrow zone of water with temperature maximum following the continental slope. This zone divides into two branches west of Grip. One part follows the continental slope northwards, the other bends to the east and follows the northern slope of Buagrunnen towards Grip.

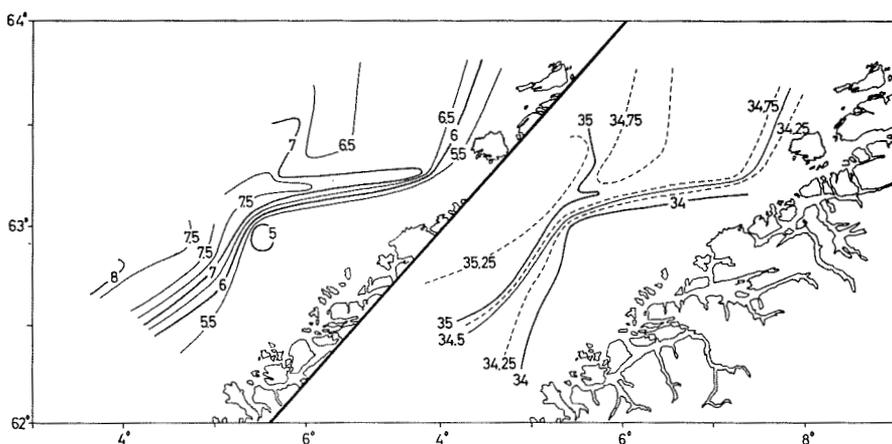


Fig. 8. Temperatures ($^{\circ}\text{C}$) and salinities (‰) at 50 m 7–12 March 1968.

DISCUSSION AND CONCLUSIONS

From Fig. 2 it may appear as if the temperature and salinity of the Atlantic water were higher in 1968 than in 1956, and that the values of the corresponding parameters of the Coast water were lowest in 1968. This is mainly a geographical variation. The 1968 cruise covered the area where the two water masses recently had come into contact. Therefore, the largest vertical and horizontal gradients were found here. As reported earlier by HELLAND-HANSEN and NANSEN (1909), the gradients were smaller farther north due to mixing between these two water masses.

The seaward extension of the Coast water is as a rule larger in summer than in winter (HJORT and GRAN 1899). In the summer 1957 (LJØEN 1962), the 35.0‰ isohaline at the surface had an average distance of about 150 nautical miles from the shore. The corresponding distance in the winter 1956 was 10–40 nautical miles, except for an area just south of Lofoten. Besides the variation in time also large geographical variations appeared in the extension of Coast water. Off Møre the 35.0‰ isohaline intersected the surface at a distance of 40–50 nautical miles from the shore, while farther north, at Helgeland, this distance was only 5–10 nautical miles.

Off Møre the temperature and salinity of the Coast water were lowest at the outer part of the shelf (Fig. 7). This situation supports the suggestion of HELLAND-HANSEN and NANSEN (1909) that the northward velocity of the Coast water in this area is greatest at the edge of the shelf. On the main part of the banks the velocities are lower and may have various directions (DRAGESUND and NAKKEN 1968). The branch of Coast water which followed the slope northwards from the area west of Buagrunden also seems to be present in summer (LJØEN 1962, Fig. 4B). The water of this branch mixed in all directions with water masses of higher temperature and salinity and therefore soon lost its original characteristics.

North of Buagrunden the main bulk of Coast water probably flowed to the east and followed the coast northwards from Grip on. The strongest northward movement of the Atlantic water occurred outside the upper edge of the continental slope. However, there is evidence of a splitting of this current by longitudinal zones with discontinuity in the transversal distribution of the parameters. As in summer (LJØEN 1962), branches of Atlantic water pushed towards the coast in the channels between the banks. This pattern is obviously an effect of the bottom topography.

SUMMARY

1. The distribution of temperatures and salinities off the west coast of Norway have been studied, based on observations from cruises in February 1956 and March 1968.
2. The main flow of Coast water follows the edge of the shelf between Stad and Grip. West of Grip it divides into two branches. One follows the slope northwards, the other flows to the east and follows the coast northwards.
3. The Atlantic water follows mainly the slope, but branches of Atlantic water move to the east in the troughs between the banks.

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THE EFFECT OF FISHING ON SIZE COMPOSITION AND SEX RATIO OF OFFSHORE LOBSTER STOCKS

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INTRODUCTION

The initial effects of exploitation on marine stocks seldom have been thoroughly documented, because the stocks usually are not studied until a species has experienced a history of exploitation. The fishery for lobsters, *Homarus americanus*, in offshore waters of southern New England offers an opportunity to record the chronological changes due to exploitation. The fishery is in the early stages of development and fishing effort is expended disproportionately on relatively discrete grounds.

In this preliminary account of the data collected from the offshore fishery, I compare the size distribution and sex ratio of lobsters from several fishing grounds, and hypothesize that the differences are due mainly to fishing. The hypothesis was developed on the basis of work on sex ratio of lobsters by THOMAS (1955) and from data on size distribution collected from research cruises. Data are not yet available, however, on such aspects as seasonal migrations and total catch and effort by area, which must be considered if the effects of fishing are to be fully assessed.

THE OFFSHORE LOBSTER FISHERY

The history of the fishery for offshore lobsters has been reconstructed by SCHROEDER (1959). Lobsters were taken incidentally in the bottom trawl fishery for various species of groundfish in the early 1900's. In ensuing years, effort was expended specifically for lobsters, but catches through 1946 were less than 50 metric tons. SKUD (in press) described the recent increase in landings, which surpassed 500 metric tons in 1955

Contribution given in honour of Gunnar Rollesfsen at his 70th birthday.

and 2500 metric tons in 1965. Fishing is conducted with a standard bottom trawl to the edge of the continental shelf, 100 to 400 km offshore, and is concentrated at depths between 100 and 500 meters. The use of the bottom trawl and the depth of fishing are in sharp contrast to coastal fisheries where lobsters are captured in pots, usually at depths less than 50 meters.

The offshore fishery is concentrated near submarine canyons at the edge of the continental shelf (Fig. 1). Five of these canyons have been sampled more intensively than others and can be grouped into three categories by distance from major ports of landing. Hudson and Veatch Canyons are 200 to 250 km offshore, Oceanographer and Lydonia between 250 and 300 km, and Corsair Canyon is about 400 km from the nearest port. Though historical catch records were not tallied by canyon, the canyons closest to shore generally have been fished more heavily than more distant canyons during the development of the fishery. In my analysis, I occasionally combined data from canyons that were equidistant from shore and that had lobsters of similar size.

Samples were drawn from commercial landings; interviews with vessel captains provided information on the vessel, gear, area and depth of fishing, days fished, and total catch in pounds. At least 100 lobsters were measured and sexed in each sample. (Unless otherwise noted, all measurements refer to carapace length.) Data from research cruises included hydrographic data, time, distance, and the range in depth of each trawl tow. Sampling was concentrated in areas regularly fished by the commercial fleet. Each lobster was sexed, measured, and weighed, and the number of berried (egg-bearing) females was recorded. Research cruises provided information on prerecruits which was not available from commercial landings. Though the fishery operates in international waters, state laws apply to the landings; offshore catches are therefore subject to minimum size (approximately 8 cm) regulations that control the inshore lobster fishery.

CATCH PER UNIT OF EFFORT

To test the generalization that more distant canyons were less intensively fished, catch and effort of commercial vessels were compared by canyon. Effort was measured in days fished—length of the total trip, less fishing days lost. A vessel may fish at several canyons during a single trip but only those trips during which effort was concentrated in the vicinity of one canyon were compared. Further, the comparison was limited to vessels which had fished on at least two occasions in both areas being compared.

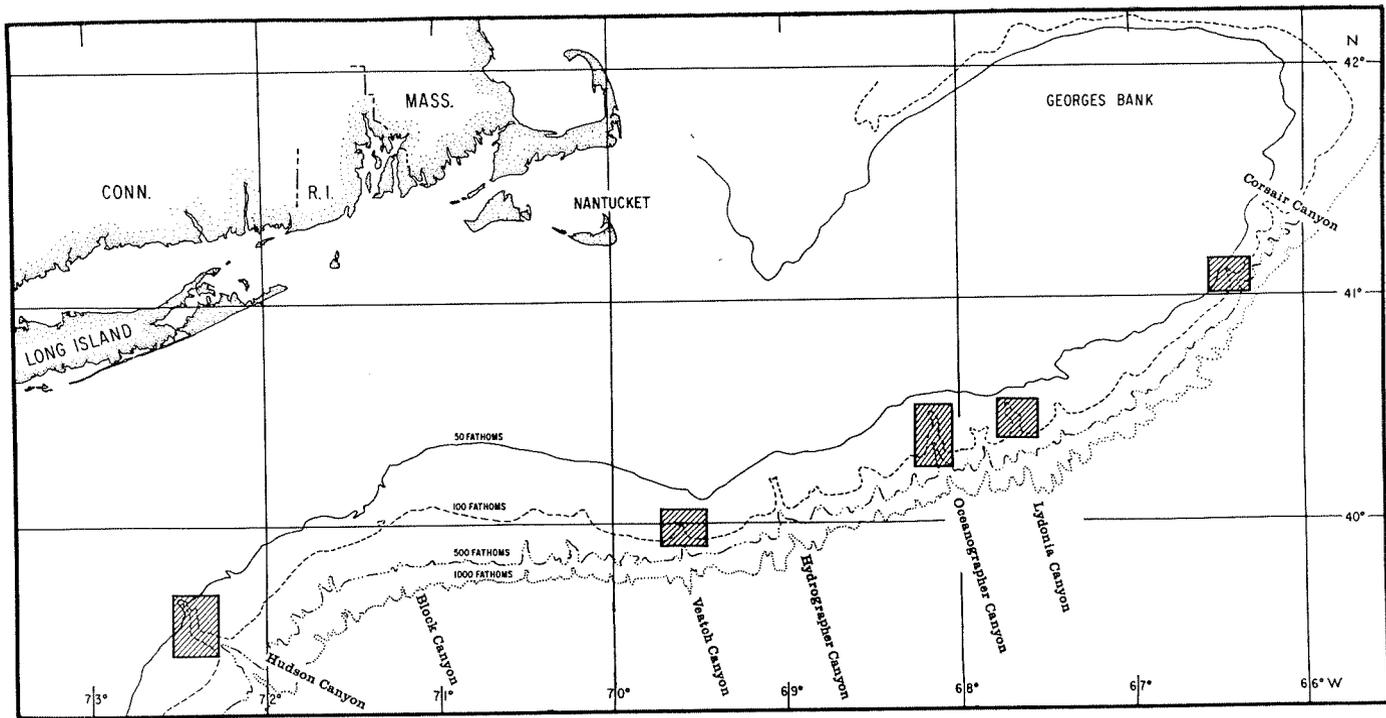


Fig. 1. Sampling locations for lobsters on the continental shelf off New England.

These criteria restricted the selection to six vessels, but included 63 interviews or trips. The average catch per day or catch per unit of effort (CPE) for each trip was determined for each vessel (Table 1). The mean CPE for the vessels ranged from 451 to 621 kg (average, 552) in the Hudson-Veatch area, from 539 to 706 kg (average, 670) in the Oceanographer-Lydonia area, and from 680 to 801 kg (average, 741) in Corsair

Table 1. Average daily catch (kilograms) of lobsters by six vessels in the offshore canyons, 1965-1967. [Entries in the table are the averages for each fishing trip.]

Canyon area	Vessel						A-F
	A	B	C	D	E	F	
Hudson-Veatch	363	665	389	794	486	499	
	605	806	455	303	616	403	
	377	340	713	907	489	—	
	455	340	766	831	756	—	
	562	737	—	495	583	—	
	357	455	—	395	455	—	
	499	377	—	—	455	—	
	801	—	—	—	368	—	
	1264	—	—	—	544	—	
	314	—	—	—	523	—	
	—	—	—	—	455	—	
	—	—	—	—	455	—	
—	—	—	—	756	—		
Mean CPE	560	531	581	621	534	451	552
Number of trips	(10)	(7)	(4)	(6)	(13)	(2)	(42)
Number of days fished	(77)	(30)	(17)	(19)	(85)	(9)	(237)
Oceanographer-Lydonia	—	826	495	—	529	777	
	—	624	583	—	480	1021	
	—	484	—	—	907	777	
	—	—	—	—	624	907	
	—	—	—	—	990	428	
	—	—	—	—	—	837	
	—	—	—	—	—	408	
	—	—	—	—	—	324	
	—	—	—	—	—	706	
	—	—	—	—	—	—	
Mean CPE		645	539		706	687	670
Number of trips		(3)	(2)		(5)	(9)	(19)
Number of days fished		(17)	(18)		(36)	(62)	(133)
Corsair	—	—	—	—	—	680	
	—	—	—	—	—	801	
Mean CPE						741	741
Number of trips						(2)	(2)
Number of days fished						(16)	(16)

Canyon (only two trips, 16 fishing days, available for comparison). CPE at Hudson–Veatch, the area closest to the coast, was lower than at more distant canyons.

Assuming that the population densities at the canyons were comparable prior to exploitation, this trend in CPE indicates a more intensive exploitation at the canyons closest to shore. Though early records of total catch and effort are not available to establish this premise, the statistics now being collected and subsequent changes in CPE may help determine the distribution of past fishing effort. The size composition data in the following section do lend support to this thesis.

SIZE COMPOSITION

The mean size of lobsters was related to the distance from shore. Length-frequencies of lobsters were smallest at Hudson and Veatch Canyons, intermediate at Oceanographer and Lydonia Canyons, and largest at Corsair Canyon (Fig. 2). This trend in size follows the expected diminution from fishing, i.e., Hudson and Veatch Canyons lie closest to the coast and presumably have been more intensively fished. CPE was lowest at the Hudson–Veatch area, higher in Oceanographer–Lydonia, and highest at Corsair Canyon.

The data from Veatch Canyon are more extensive than those from the other canyons, and show marked changes in size composition during the three years of sampling. The cumulative percentage of catch of

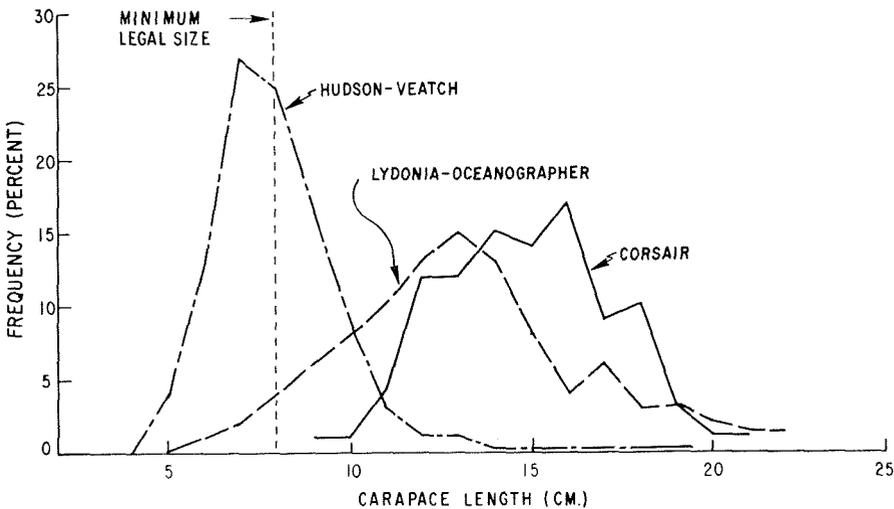


Fig. 2. Length-frequencies of lobsters in catches by research vessels at offshore canyons, 1965–67.

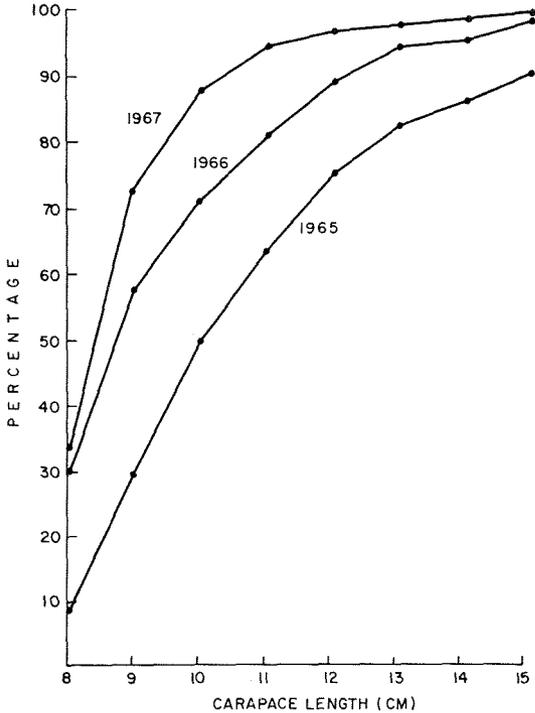


Fig. 3. Cumulative percentage of the catch of legal-sized lobsters at Veatch Canyon, 1965-67.

lobsters 8 cm and larger showed that smaller lobsters accounted for progressively more of the catch (Fig. 3). For example, the percentage of lobsters in the 8 to 10 cm size group was 50 in 1965, 70 in 1966, and nearly 90 per cent in 1967. This progressive change is assumed to be caused by fishing.

Additional evidence that differences in size distribution are related to fishing was obtained by comparing the present data with that reported by McRAE (1960) from exploratory cruises made 10 years ago. The modal size of lobsters from Veatch and Lydonia Canyons was smaller in 1965-67 than in 1956 and the decrease in size was greatest in Veatch Canyon which is closest to shore (Fig. 4). The depth of water in which samples were taken ranged from 200 to 500 meters in 1956, however, and from 100 to 300 meters in 1965-67. Since the size of lobsters generally increases with depth, the differences in depth fished in the two periods have contributed to the apparent change in size distribution (SKUD and PERKINS, in press). To examine this relationship of size with depth, data from recent research cruises have been grouped by depth for comparison (Table 2).

The maximum increase in size with depth was 1.1 cm, whereas the difference in size between canyons was as much as 6.7 cm. Thus a

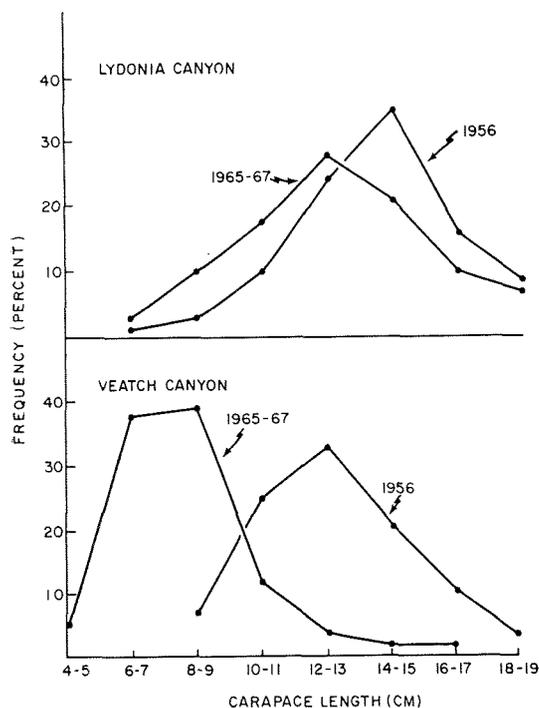


Fig. 4. Comparison of length-frequencies of lobsters collected in 1956 and in 1965-67 at Veatch and Lydonia Canyons.

Table 2. Average carapace length of lobsters by depth of capture.

Canyon	100-200 meters Mean size (cm)	200-300 meters Mean size (cm)
Hudson-Veatch	8.0	8.7
Oceanographer-Lydonia	11.9	13.0
Corsair	14.7	15.4

factor other than depth accounted for most of the difference between the size distribution of the lobsters in 1956 and 1965-67.

TEMPLEMAN (1936) and others have correlated size of lobsters with temperature and undoubtedly the growth in offshore stocks can be similarly affected. However, it seems unlikely that temperature differences could account for the magnitude and the progressive nature of the changes in size recorded at the canyons.

SEX RATIO

THOMAS (1955) constructed a model of a lobster population with a uniform mortality rate, and showed the expected change in sex ratio with size (Fig. 5). The model assumed that mature females molted

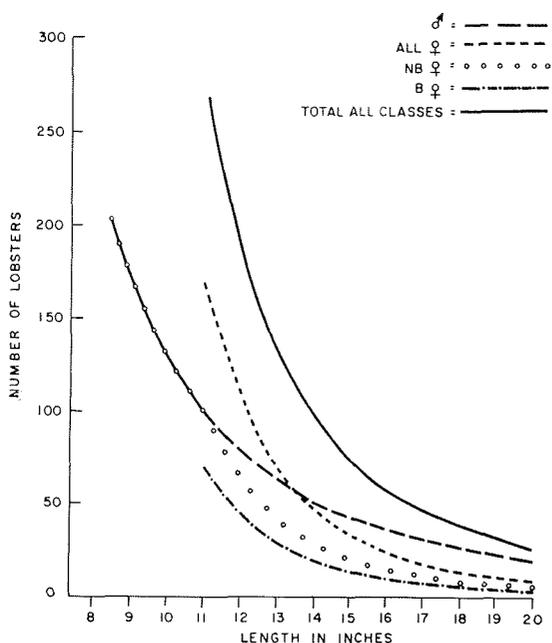


Fig. 5. Size comparison in a model stock, based on a uniform recruitment of 100 males and 100 females at a maturity size of 11 inches (total length) and a 30% total mortality rate. B = berried; NB = Non-berried. (After THOMAS 1955).

only once in 2 years, whereas males molted every year. Biennial molting by females was reported by GARMAN (1892) and later supported by HERRICK (1896) and others. Exceptions do occur but WILDER's (1953) data showed clearly that the proportion of non-molting females increases with size at or near maturity. He also showed that males do not always molt annually. Nor is the molting cycle consistent in the offshore populations, particularly in the largest individuals (15 cm or more) that may molt but once in 3 years. However, I do not consider these exceptions as a serious defect of the model, for regardless of the source, the data indicate that, collectively, males molt more frequently than females.

In the model, the sex ratio of immature lobsters is assumed to be 1 : 1. After maturity, the less frequent molting of females causes them to outnumber males at any given size. For example, mature females at 8 cm would remain in this size category and be joined by previously immature females that had molted, whereas males at 8 cm would have molted and progressed to the next size group. If no mortality occurred for either sex, and if all females matured at precisely 8 cm, the ratio of females to males would double at that size. In actuality, all females do not mature at the same size and, as natural and fishing mortality reduce the numbers, the proportion of females increases gradually and the sex ratio can never be expected to reach 2 : 1 (Fig. 6).

Growth rate also influences the observed changes in sex ratio. In

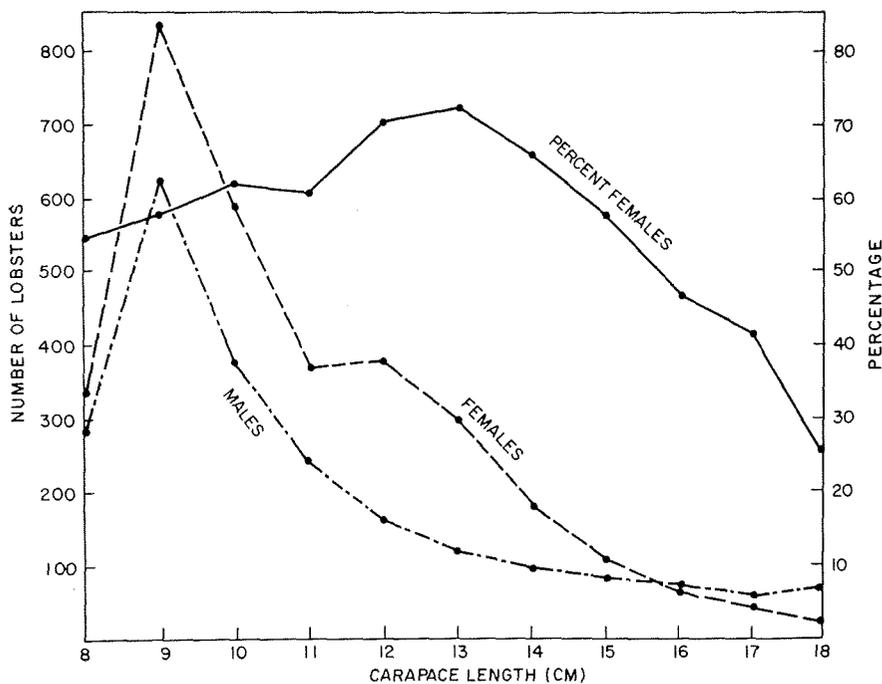


Fig. 6. Numbers of males and females and percentage of females in commercial samples from Veatch Canyon, 1965-67.

the model, the growth increment per molt was considered to be 14 percent. For the offshore lobsters, preliminary estimates showed that growth between molts was 15 percent for mature females, whereas, the increment for mature males was 18 percent. TEMPLEMAN (1936) also observed differences in growth between the sexes after maturity. This difference concentrates the number of females in smaller length classes and the slower growth, coupled with the less frequent molting, results in an increase in the proportion of females at given sizes.

The increased number of females over males with size is apparent in offshore lobster stocks and can be followed over a greater size range than in coastal stocks (Fig. 6). The increase in the proportion of females with increasing size does not continue indefinitely, but the decline in the rate of increase depends on the rate of mortality. THOMAS (1955) concluded that the change in sex ratio could be used to estimate mortality and showed the expected differences in sex ratio in two models, one with a total annual mortality of 70 percent and another with a 30 percent mortality. When annual intermolt mortality of males is 70 percent, mortality between biannual molts of mature females is 91 percent. Or,

if mortality is 30 percent for males, the intermolt mortality of females is 51 percent.

In offshore lobster stocks the proportion of females continues to increase until 12 or 13 cm. In the model the proportion of females was highest at a size class 2 or 3 cm smaller than in the offshore stocks; the difference suggests that offshore lobsters mature at larger sizes than that assumed in the model. However, it is possible to compare the decline in the percentage of females (larger than 13 cm) in the offshore stocks with the changes of sex ratio in the model. The rate of decline at Veatch Canyon most closely approximates that of a 50-percent annual mortality, whereas that from Oceanographer and Lydonia conforms most closely to a 30-percent mortality; these rates suggest a 20-percent greater fishing mortality at Veatch Canyon, if the natural mortality in the two areas is equal (Figs. 6 and 7).

RECRUITMENT

COLE (1954) provided an excellent summary of "population consequences" expected from changes in birth rates and death rates. Under exploitation, he listed three expected changes: (1) a decrease in longevity; (2) an increase in the population's birth rate; and (3) the obvious in-

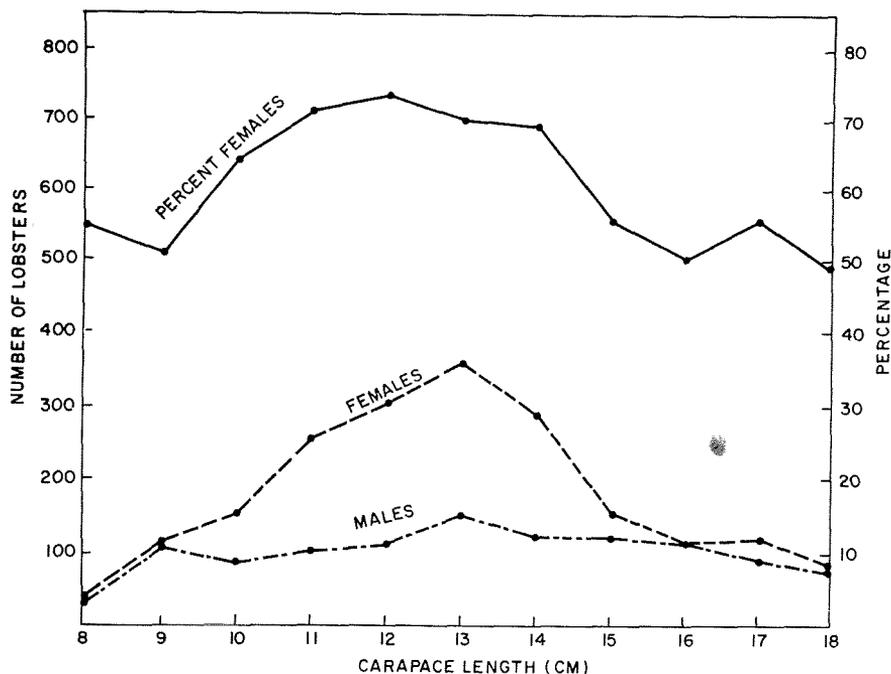


Fig. 7. Numbers of males and females and percentage of females in commercial samples from Oceanographer and Lydonia Canyons, 1965-67.

crease in the proportion of young. Items 1 and 3 are demonstrated clearly in the length-frequencies of lobsters presented earlier, and also from the data on catch per unit of effort (CPE). The average weight of legal-sized lobsters from Hudson and Veatch Canyons approached 1 kg; conversion of the mean CPE (552 kg) from weight to numbers indicated a catch of over 500 lobsters per day. At Oceanographer and Lydonia Canyons, where the average weight was about 2 kg, the converted CPE (670 kg) was 335 lobsters per day. Lobsters at Corsair Canyon averaged 2.7 kg and the converted CPE (741 kg) was 257 lobsters per day.

Item 2, an increase in the birth rate, is difficult to measure in the offshore fishery. Increased birth rate in a population may be reflected in changes of the age or size at first maturity. For lobsters, such a change can be measured by comparing the number of egg-bearing (berried) females to the total number of females at a given size. I have tallied the percentage of berried females taken during the research cruises in 1956 (from McRAE 1960) and 1965-67 (Table 3). In 1956, no females were berried at 8 or 9 cm and less than 20 percent were berried at 10 and 11 cm. In 1965-67, a few females were berried at 8 cm, over 20 percent at 9 cm, and more than 30 percent at 10 and 11 cm. This change, which could be due to an increased growth rate, may indicate an increased birth

Table 3. Percentage of berried lobsters among females of different size groups collected in canyons off New England during exploratory cruises in 1956 and research cruises in 1965-67.

Length (cm)	1956		1965-67	
	All females (Number)	Berried females (Percent)	All females (Number)	Berried females (Percent)
6	0	0.0	363	0.0
7	2	0.0	464	0.0
8	12	0.0	441	1.6
9	31	0.0	343	22.7
10	45	11.1	232	33.2
11	122	18.9	133	30.8
12	98	25.5	168	25.6
13	191	35.1	163	27.0
14	131	35.1	121	30.6
15	225	31.1	94	29.8
16	134	26.9	64	37.5
17	52	32.7	46	19.6
18	36	38.9	40	40.0
19	11	45.5	16	18.8
20	3	33.3	3	66.7

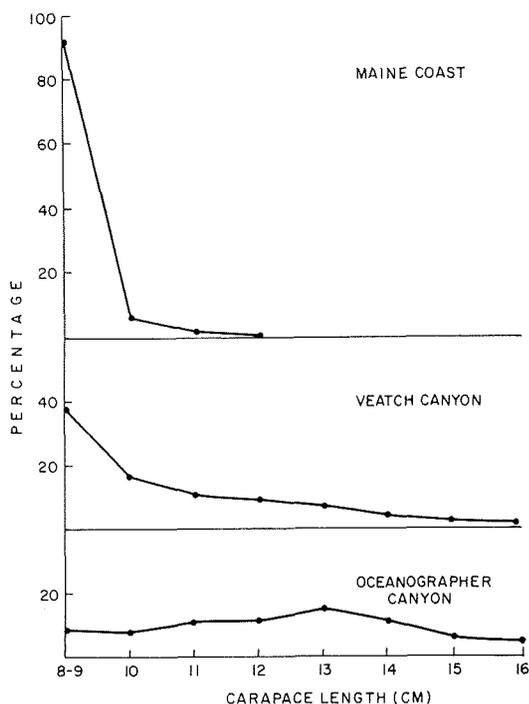


Fig. 8. Size composition of lobsters from inshore and offshore areas (both sexes).

rate and suggests that the increasing proportion of small lobsters in the offshore catches is not only the result of cropping the larger individuals. However, additional information is necessary to determine whether total egg production has increased or whether the improved recruitment of immatures and young adults has been influenced by other factors such as emigration.

COMPARISON WITH THE COASTAL POT-FISHERY

The inshore lobster fishery in Maine is very intense; at the peak of the fishing season more than 4,000 fishermen (including 2,000 part-time) fish more than 750,000 lobster pots. Dow (1964) estimated that recruit lobsters (8 to 9 cm) accounted for 80 to 90 percent of the Maine landings (Fig. 8). The size distribution in the coastal waters is in sharp contrast to that of lobsters offshore, even in the most intensively fished areas. In canyon areas that are fished less intensively, recruits account for only 5 percent of the catch and the dominant size group at some canyons is 13 cm or more.

The proportion of females in the inshore fishery is seldom more than 51 or 52 percent. I examined the sex and size data from 2,500 lobsters

collected along the Maine coast.¹ In the size class from 8 to 10 cm, the proportion of females was 49.8 percent, whereas in the 11 to 12-cm size group only 45.1 percent were females. Male and female lobsters of over 11 cm accounted for only 4 percent of the sample.

The relatively low proportion of females at sizes from 8 to 12 cm and the small contribution of lobsters over 11 cm in the inshore sample are consistent with a total mortality of 90 percent in THOMAS' (1955) model and confirms Dow's (1964) estimate. The model shows an expected 52 percent females in the 10-cm size class, and shows that only 5 percent of the population remains at the next molt (approximately the 11-cm size class). The proportion of females at 11 cm is higher in the Maine sample than the model predicts, but this proportion may be influenced by the release of berried females that are protected by law.

Exploitation of the Maine fishery is apparently so high that there is little or no increase in the proportion of females. TEMPLEMAN's (1936) data from the coastal fishery at Seal Island, Nova Scotia does show a moderate increase in the proportion of female lobsters between the 7 to 10 cm length classes. The proportion of females increased to 58 percent at 10 cm and then declined. The sample excluded berried lobsters, which suggests that the increase was greater than indicated; and this exclusion precludes any detailed comparison with the model. However, the changing sex ratio with size does conform and the proportion of females at 10 cm would indicate a fishing intensity less than that in Maine but greater than that offshore.

SUMMARY

The lobster fishery in the offshore waters of southern New England is in the early stages of development. The assumption that canyon fishing grounds closest to shore are the most heavily fished was supported by a lower catch per day (CPE), a smaller mean size, and a higher total mortality than exists in more distant canyons.

At Hudson and Veatch Canyons, less than 250 km offshore, the average CPE was 552 kg; Oceanographer and Lydonia Canyons extend 300 km offshore and had a CPE of 670 kg; and at Corsair Canyon, which is 400 km from shore, CPE was 741 kg. Lobsters were smallest at the canyons which were closest to shore and had the lowest CPE. The size frequency was higher at the canyons of intermediate distance and the CPE was higher. The largest lobsters were from Corsair Canyon, which is the furthest from shore, and had the highest CPE.

The modal carapace length of lobsters at Veatch Canyon was over 12 cm in 1956 and is now less than 9 cm. In three successive years of

¹ Data provided by JAMES THOMAS, Maine Department of Sea and Shore Fisheries.

sampling (1965-67), the contribution of small lobsters has increased and in 1967 more than 90 percent of the legal-sized lobsters were from the 8 to 10 cm length class. The progressive change at Veatch Canyon and magnitude of size differences among canyons are greater than expected from the influence of temperature or depth of fishing.

Observed changes in sex ratio support the basic assumptions made in THOMAS' (1955) model and follow the expected changes at different levels of mortality. The proportion of females to males increases gradually from 8 cm to 13 cm and then declines. Because females molt less frequently than males, their numbers at a given size decline more rapidly. The model assumes that females molt only every two years; whereas, males molt annually and have a lower intermolt mortality. The change in sex ratio was used to estimate mortality in the offshore fishing grounds. The more distant canyons had a lower mortality, higher catch per unit of effort, and larger size composition. The size composition and sex ratio of coastal lobster fisheries indicated that exploitation was more intense than in offshore fisheries.

The increased proportion of young lobsters in the offshore catches followed expected changes from exploitation, but also suggested an increase in the population birth rate. This possibility was supported by the observation that in ten years the percentage of berried females at smaller sizes of maturity had increased substantially. However, additional data are needed to determine whether the improved recruitment has resulted from other factors.

Additional data and analyses are needed to test the hypothesis that fishing has caused the changes in size composition, sex ratio, and catch rates. If the assumptions hold and the level of fishing continues or increases, the more distant canyons are expected to experience changes in lobster size, sex ratio, and catch rates—comparable to those at the canyons closest to shore.

The size at maturity, frequency of molting, and rate of growth used in the model are not entirely consistent with observations in the offshore fishery. However, the basic concepts seem applicable and the necessary adjustments and corrections can be incorporated into the model when sufficient data are available.

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DATA ON LIFE HISTORY AND CHARACTERS OF
GALEUS PIPERATUS, A DWARF SHARK OF
GOLFO DE CALIFORNIA¹

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INTRODUCTION

The purpose of this paper is to amplify information on the life history and characters of *Galeus piperatus* SPRINGER and WAGNER, a dwarf cat shark that has just recently been described from an oceanographically distinctive area in the northern part of Golfo de California, on the Pacific side of northern Mexico. In a way, this contribution supplements the recent account (HUBBS, IWAI and MATSUBARA 1967) of an even smaller, pelagic, squaloid shark, *Euprotomicrus bispinatus* (QUOY and GAIMARD).

Galeus piperatus was described by SPRINGER and WAGNER (1966) from two adult females only 296 and 302 mm in total length and one immature female 256 mm long, all from a series of five specimens trawled in Golfo de California. The capture of the type specimens had been discussed by LAVENBERG and FITCH (1966) under the name of *Galeus* sp., and the species has been briefly diagnosed with a copy of the original figure by KATO, SPRINGER and WAGNER (1967, p. 23, fig. 4), who have assigned it the vernacular name, "peppered shark". For this supplementary account of the species we have had available, in addition to the two mature female types and one additional adult female, three adult and two early juvenile males, and one egg case that, we believe, pertains to this species (Table 1). The types were taken in 1964 by the R/V Alaska of the California Department of Fish and Game; all other specimens, in 1967–1969, by the R/V Velero IV of the University of Southern California, and the research vessels Thomas Washington and Ellen B. Scripps of the Scripps Institution of Oceanography.

¹ Contribution from the Scripps Institution of Oceanography, University of California, San Diego (La Jolla, California 92037).

HABITAT

All known specimens of *Galeus piperatus* have been taken in the northern part of Golfo de California, in the Salsipuedes basin—in a region that is well known for a rather high incidence of endemism and for extreme fluctuations in physical parameters: the annual temperature range of surface waters is extreme (warm like tropical waters in summer, as cool as southern California waters in winter); tidal currents are strong; and vertical and horizontal turbulence are exceptional (RODEN 1958 and 1964, RODEN and GROVES 1959, HUBBS and RODEN 1964). The species has not been taken by recent trawling in other parts of the Gulf, nor along the open coast of the Baja California peninsula, nor along the coast south of the Gulf. However, it should be looked for in those areas.

The region where this shark occurs is not only one of considerable endemism, but is also one where a number of northern (warm-temperate) fishes and other organisms occur, apparently as Pleistocene relicts, sympatrically with a reduced assemblage of tropical forms (WALKER 1960). Thus, although the fauna of the whole Gulf is largely to be characterized as depleted-tropical, the occurrence of this scyliorhinid in the upper part of the Gulf is not wholly inconsistent with SPRINGER's indication (1966, pp. 583–584) that the “cat sharks appear very rarely in warm waters and inhabit shore waters only in the higher latitudes or in comparatively cool-water areas”. The group appears to be mildly anti-tropical, using this term, as originally proposed (HUBBS 1952), to include subtropical and warm-temperate species.

The specimens have been taken through a wide range of bottom depths, from barely over 400 m to hauls at 732–1215 m and 1097–1326 m (Table 1). Similarly, a new hagfish (*Eptatretus* sp.) has been trawled in the same area repeatedly, but nowhere else, at depths from 198 to 1180 m, over a far greater bathymetric range than that inhabited by any of the six other myxinooids we have been collecting in large quantity in Baja California and the Gulf.

Some of the ship records have indicated that this shark at times may enter the midwater zone, in this area of great vertical turbulence. The three type specimens and two others that were misplaced were taken in a large midwater trawl that reportedly was fishing at a depth of approximately 275 m (SPRINGER and WAGNER 1966), but LAVENBERG and FITCH (1966, pp. 92–95) have stated that the trawling depth for the station was determined as 275 m by measuring the cable angle and ship speed [a dubious determination, especially in an area of notoriously fast currents]. They added that the Precision Depth Recorder during the trawling “showed a constant bottom depth of 220 fathoms (400 m)” — close to the

Table 1. Collection data on known specimens of *Galeus piperatus*.

Specimen no. ¹	Ship	Station	Method of capture	Depth of water (m)	Lat. (N)	Long. (W)	Date
SIO 68-89	<i>Thomas Washington</i>	MV68-I-59	40' balloon otter trawl	556-635	29°40.2'– 29°43.9'	113°55.4'– 113°58.0'	1968-I:18
SIO 68-90	<i>Thomas Washington</i>	MV68-I-60	40' balloon otter trawl	545-630	29°39.5'– 29°43.5'	113°55.5'– 113°59.0'	1968-I:18
SIO 69-203	<i>Ellen B. Scripps</i>	MV69-II-6	Free-vehicle trap	746	28°40'	113°53'	1969-III:2
LACM 30063-1	<i>Velero IV</i>	11821	Beam trawl	731-1215 ⁴	28°33.0'– 28°46.75'	112°49.5'– 113°06.0'	1967-XI:30
LACM 30303-1 ²	<i>Velero IV</i>	11837	Beam trawl	1097-1326	28°37.0'– 28°40.5'	112°56.0'– 113°01.5'	1967-XII:2
LACM 7552 Holotype	<i>Alaska</i>	64A2-16	Large mid-water trawl	402-412	28°55'	112°50.5'	1964-IV:6
LACM 8818-9 (Paratype)							
USNM 200413 ³ (Paratype)							

¹ LACM = Los Angeles County Museum; SIO = Scripps Institution of Oceanography; USNM = United States National Museum.

² The egg case was taken at this station.

³ This paratype is the only specimen that was not examined or measured by us.

⁴ According to the collection records, the beam trawl was calculated from wire angle and ship speed to have fished at the midwater depth of 530-630 fathoms, at least about 100 m off the bottom (see text).

depth of 402–412 m furnished us—and they further stated: “During retrieval, the net actually travelled to the bottom where it rode for sufficient time to pick up several thousand heart urchins . . . mollusks . . . and several kinds of bottom living fishes” (including, in addition to *Galeus*: *Hydrolagus colliei* (LAY and BENNETT), *Coelorhynchus scaphopsis* GILBERT, *Sebastes* spp., *Xeneretmus ritteri* GILBERT, *Symphurus* sp., and others that probably came from the bottom). It therefore seems certain that the trawl did fish on the bottom. Consequently, there is no reason to think that the cat sharks must have been taken above the bottom. One of several large hake, *Merluccius angustimanus* GARMAN, taken at this station spewed up a partly digested *Galeus*.

The collection records for Velero IV Station 11821, where specimen LACM 30063-1 was taken, indicate, again through measurements of cable angle and ship speed, that the beam trawl was fishing at 530–630 m, or about 100 m or more above the minimum water depth of 731 m. The chief technician therefore thought that there is no reason to believe that the trawl ever hit the bottom. However, such calculation of trawl depth proved erroneous in the station just discussed and we regard it as unreliable, especially where currents and turbulence are so strong. A macrourid recorded as having been caught in the trawl further suggests the probability that the trawl reached the bottom.

We think it highly probable that all the specimens of *Galeus piperatus* have been taken on or very near the bottom.

DESCRIPTION OF EGG-CASE

It has generally been assumed that all scyliorhinid sharks are egg layers, but the discovery that one species, *Galeus polli* CADENAT, gives birth to free-living young (CADENAT 1959) calls for an examination of the mode of reproduction in all the species. (We avoid the terms oviparous, ovoviparous, and viviparous, since among fishes there is a complete spectrum from the fertilization of eggs some time after deposition to the bearing of virtually mature offspring).

Fortunately we have an egg-case (Fig. 1) that we think almost certainly is that of *G. piperatus*, for the following reasons:

(1) The egg-case was trawled along with an adult of *G. piperatus* in the limited area where this species has been taken.

(2) The minute size of the elongate egg-case is consistent with the dwarf size of the species. Young only 71 and 80 mm long (in preservation) are well formed, and the 80-mm juvenile on being trawled uninjured swam long and very vigorously in a tray of water. The egg-case seems to be of a size adequate to hold a coiled embryo about as long as the smaller free-living juvenile. The three adult males although only 280 to 293 mm in total length have fully elaborated claspers and, therefore, had attained their final size.

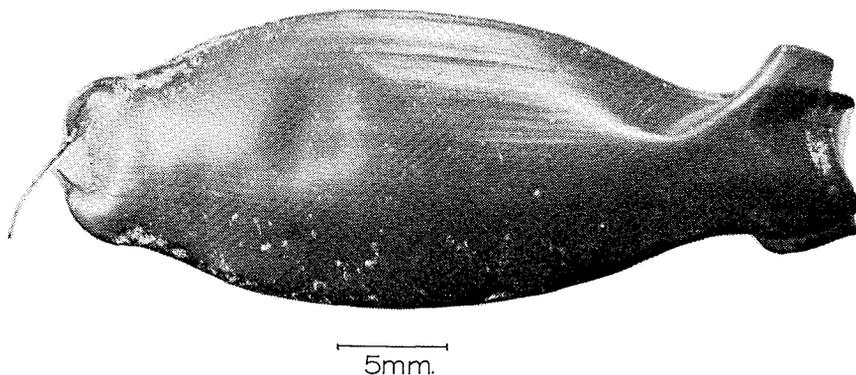


Fig. 1. Scyliorhinid egg-case 35 mm long, thought to represent *Galeus piperatus*, taken in trawl with adult male at R/V Velero IV Sta. 11837.

The two largest known females, only 296 and 302 mm in total length, each has "a few large eggs about 7 mm in diameter in the functional right ovary, and are considered sexually mature" (SPRINGER and WAGNER, 1966, p. 8). The proportion of the size of the egg-case (35 mm long) to the estimated total length of the mature female is about the same as in other scyliorhinids. The ratio in this species is 118; in *Cephaloscyllium uter* JORDAN and EVERMANN, regarded by KATO, SPRINGER and WAGNER (1967) as synonymous with *C. ventriosum* (GARMAN), 124, on basis of averaging measurements of nine eggs; in *Apristurus brunneus*, 100 (five measurements); in *Schroederichthys maculatus* SPRINGER (data from SPRINGER 1966), 129; in *Galeus melastomus* (data from TORTONESE 1956), 112.

(3) The egg-case closely resembles that of *Galeus melastomus* (RAFINESQUE) as figured by TORTONESE (1956) and shows points of resemblance as well as difference when compared with figures of egg-cases referred by SPRINGER (1966) provisionally to *Scyliorhinus meadi* SPRINGER, *S. retifer* (GARMAN), and *Schroederichthys maculatus* SPRINGER.

(4) The egg-case is surely that of a scyliorhinid and it seems improbable that it pertains to any of the three other species of the family that occur in Golfo de California. Of these, the *Cephaloscyllium* reaches the length of about 1 m and is known to have much larger egg-cases (nine in the Scripps collection average 100 mm in midline length). *Parmaturus xaniurus* attains a length of about 0.5 m, and almost surely has larger egg-cases. *Cephalurus cephalus* (GILBERT) is incompletely known from a few immature specimens (BIGELOW and SCHROEDER 1941) and its egg-case has not been identified.

The tiny, empty egg-case is translucent-brown. It is rather evenly elliptical, and moderately expanded at the truncate anterior end (now slit open), without evident tendrils. The posterior end becomes somewhat thickened as the two closely approximated sides, each ending in the base of a tendril, are arched very closely together. Very fine longitudinal striations parallel the margin.

DESCRIPTION OF JUVENILE

Two juveniles of *Galeus piperatus*, both males, have been collected. The larger (Fig. 2), SIO 68-89, 85 mm in total length in life, 80 mm on preservation, is the one that was noted to swim long and vigorously. The smaller one, SIO 68-90, measures only 71 mm in alcohol, though the yolk-sac is completely absorbed. The larger one was taken with an adult male (SIO 68-89), and both came within the limited area from which adults and the egg-case have been collected.

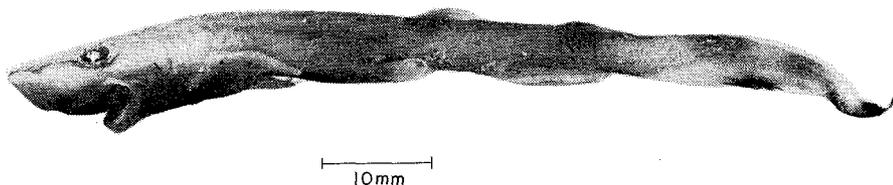


Fig. 2. Juvenile male of *Galeus piperatus*, 80 mm in total length (SIO 68-89).

In coloration the juveniles differ strikingly from the adults. In addition to the large melanophores—the “fine pepper-like spots” (Fig. 3, upper, and Fig. 7) that prompted SPRINGER and WAGNER to name the species *piperatus*—the juveniles bear a series of blackish areas (Fig. 2) formed by the concentration of melanophores. A dark area extends from midsides well onto each dorsal fin. Five distinct dark areas mark the caudal fin. Three are on the upper lobe: one at and below the upper caudal origin, another midway along the dorsal lobe, and an intense black area on the upper part of the caudal tip, leaving the extreme end of the caudal axis unpigmented. The ventral lobe bears two dark blotches, one at the extreme end and one below the pale area between the first two upper spots. This color pattern is similar to that figured for juveniles of *Galeus polli* CADENAT (1959, Fig. 17), and seems to homologize with the dark saddles and caudal blotches described and figured by SPRINGER (1966) for the adults of several species referred to *Scyliorhinus*, *Galeus* and *Halaaelurus*.

In life, the larger juvenile was pale purplish-brown on the upper and posterior parts and silvery on the belly. The dusky to black markings were very conspicuous, and the extreme tip of the caudal lobe was milky white.

The inside of the mouth is not as intensely dark as in adults. The melanophores are limited to the posterior half of the roof of the buccal cavity and the anterior half is quite pale. No denticles are borne in this region in juveniles, but the anterior section bears numerous fleshy tubercles about as large as the teeth. These appear to be sensory papillae, which in the adult are retained, though obscured by the denticles that largely cover this region (as noted below).

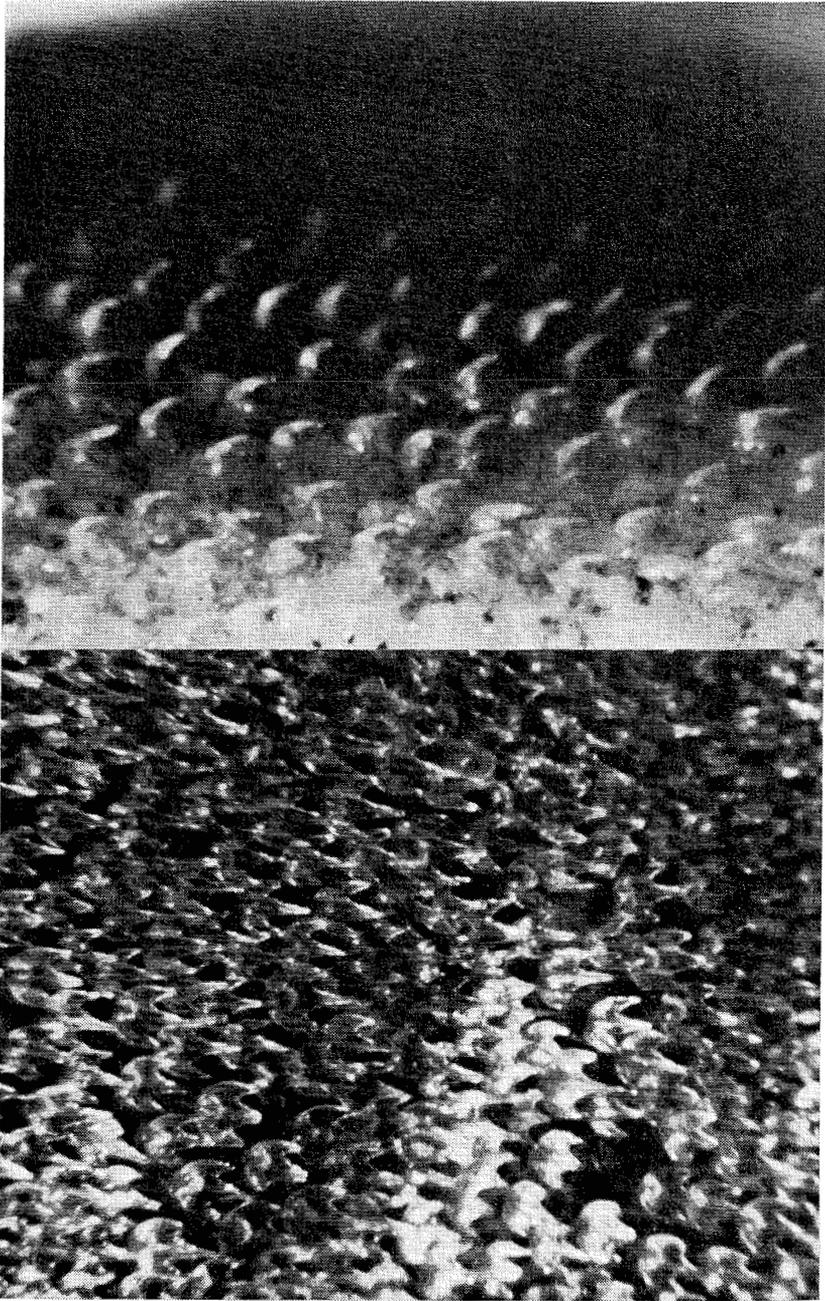


Fig. 3. Denticles of *Galeus piperatus*. Above: denticles of SIO 68-89, an 80-mm juvenile male. Below: denticles of SIO 68-89, a 284-mm adult male. Both views are of areas below the first dorsal fin and are magnified about $70\times$ (anterior to the left).

The denticles on the body (Fig. 3) of the juveniles differ notably from those of the adult. Instead of being trident-shaped and bearing a high central ridge and a less elevated marginal ridge above and below, the denticles on the juveniles are long, hooked spines with only the median element apparent. Instead of being borne on a pedicel, they are sessile. The specialized denticles that form the crest on the caudal fin—a feature of the genus *Galeus*—resemble those of the adult.

The teeth of the juveniles, both males, resemble those of the adult males (as described below). The lower jaw bears a total of only ten to thirty irregularly arranged teeth. At the lip line there is a definite transition between the teeth and the denticles.

The vertebrae are apparently completely formed in this species by the time a length of 70–80 mm has been attained, for the numbers in young and adult are approximately equal (Table 3), even in the caudal region, with the possible exception of one or a very few terminal rudiments, because they are not all completely calcified. Thus, the early development of adult characters in this dwarf species is highlighted. The contrast in relative lengths of monospondylous and diplospondylous vertebrae seems greater in the juveniles than the adults, but the penultimate monospondylous vertebra is much less elongate in form in the juvenile than in the adult, yielding a lower “B” ratio (Table 3). However, as noted below, this ratio is of somewhat dubious significance.

Although essentially adult form is attained at an exceptionally small size, the juveniles differ from adults in various morphometric features (Table 2). As is usual in elasmobranch development the urosome is markedly elongated in juveniles, as is shown by measurements 5, 6, 10, and 56, most notably for the caudal-fin dimensions (44, 45). In compensation, the predorsal lengths (1, 2) are shorter. The relative shortening of the anterior regions involves primarily the anterior trunk (the measurement from insertion of pectoral fin to origin of first dorsal, 7, constitutes 16 or 17 instead of 19 to 25 per cent of the total length). Measurements involving the head do not change markedly. Oddly, the orbit-length proportion (30) remains essentially constant. The caudal peduncle (14, 16) is proportionately deeper and wider in the juveniles. The vertical fins have longer bases (39, 42, 45, 55), and, correlatively, interdorsal space (4) is shorter. The paired fins (46–52) are much smaller. The gill-slits (18) are more closely approximated ventrally, but the interorbital width and interspiracular distance (31, 32) seem to be somewhat greater. In certain changes with age, especially the elongation in the dimensions of the snout (19–22, 34), the shortening of the mouth-projection measurement (28), and the broadening of the mouth (29), the abrupt transformation apparently occurs over the size range of our two young specimens (71 to 80 mm in total length).

MORPHOMETRY

All known specimens of the species, with the exception of the two mislaid individuals that were trawled with the types and of one paratype (USNM 200413), have been measured for fifty-seven dimensions (Table 3). This has been done to illustrate morphometric differences between juveniles and adults, as just indicated and to determine what differences, if any, distinguish the sexes. These measurements, furthermore, provide data for future comparisons of *G. piperatus* with other species, particularly with the western North Atlantic cognates, *G. arae* (NICHOLS) and *G. cadenati* SPRINGER (1966), and with the three species described from eastern Asia: *G. eastmani* (JORDAN and SNYDER) from Japan, *G. sauteri* (JORDAN and RICHARDSON) from Taiwan, and *G. hertwigi* (ENGELHARDT) from Japan (references in SPRINGER and WAGNER 1966).

For greater accuracy measurements were taken from point to point. The only projection measurement was "mouth length" (Number 28 in Table 2). Precision dial calipers were used on the larger specimens, under magnification as needed. The two juveniles were measured with an optical micrometer. Origins of vertical fins and insertions of paired fins were located by gently pushing one point of the calipers against the anterior base of the fin until slight resistance was felt. Depending on obvious context, either the minimal or the maximal measurement was employed. In general, the methods follow the recommendations of HUBBS and LAGLER (1964), and, with some exceptions and additions, are those used in HUBBS, IWAI and MATSUBARA (1967) in describing another dwarf shark. The method of measurement was somewhat modified for several parts, numbered as in Table 2:

- 2, "Length to D2", and all other dimensions, were measured linearly and none were computed by addition.
- 10, "D2 origin to upper C origin", and all other measurements involving the upper lobe of the caudal fin, were made considering the upper caudal origin to occur at the extreme front of the row of modified denticles cresting the caudal fin (Fig. 5).
- 13, "Body depth (greatest)" and 15, "Body width (greatest)", and other dimensions were measured as the specimen, if distorted by preservation, was manipulated to approximate its normal form in life.
- 20, "Snout length (preoral)", was taken by us from tip of snout to the margin of the lip on the midline.
- 21, "Prenarial length, outer" represents distance from tip of snout to nearest point of margin of outer opening of nostril.
- 22, "Prenarial length, inner" represents distance from tip of snout to extreme inner-posterior angle of nostril.
- 28, "Mouth length (projection)" was measured from margin of upper lip along a mid-sagittal line to a straightedge laid between extreme ends of gape.

29, "Mouth width" is the distance between extreme corners of the gape.

44, "Upper lobe C (extreme)" and 45, "Lower lobe C (extreme)" are measured between the appropriate origin and the extreme tip of the caudal fin.

All measurements are expressed as thousandths of the standard length. The abbreviations used for fins are: P1 = pectoral, P2 = pelvic, D1 = first dorsal, D2 = second dorsal, and C = caudal.

Comparison of the measurements of three adults of each sex (Table 2) disclosed hardly a trace of sexual dimorphism. The length of the abdomen, as measured between the insertions of the paired fins (dimension No. 12) averages slightly higher in females (189) than in males (178), but the difference is much less notable than was indicated for the pelagic dwarf shark *Euprotomicrus bispinatus* by HUBBS, IWAI and MATSUBARA (1967, pp. 13-14, Fig. 1). In that form the greater length of the abdomen in females was suggested "as an adaptation to fecundity in a dwarfed shark". The difference may be related to the simultaneous development of the whole brood by *Euprotomicrus bispinatus* and the presumable development of mature eggs one by one in *Galeus piperatus*.

COLOR

In the original description of *Galeus piperatus* stress was placed on the uniformity of the coloration, with the exception of the sprinkling of large melanophores (such as shown in Figs. 3, upper, and 7) in the largest known specimen, the holotype (LACM 7552, 302 mm in total length). The somewhat smaller paratypes were described as having "irregular and indistinct blotches that contrast little with the background color". Our subsequently collected specimens show moderately conspicuous dark markings set off by a narrow, light, subhexagonal reticulum, approaching that figured by SPRINGER (1966, Fig. 20) for a specimen of *G. arae* (NICHOLS) of comparable size. The figure of the holotype and the specimen itself show almost no trace of a blackish margin along the anal and caudal fins and little blackening on the dorsal fins, but our specimens show these markings strongly. We suspect that the lack of contrast in the types is attributable at least in part to the method of preservation.

Life colors were recorded on a 280-mm fully adult male (SIO 68-89-5A1). Dorsally the color is rather rich brown. The ventral region of the trunk is gray, with bright-blue reflections. A wide dorsolateral stripe, extending to between the dorsal fins, is marked by a pale subhexagonal network colored like the belly. In contradistinction to the original description, there is a sharp contrast between the dorsal and ventral color. A mid-dorsal stripe is slightly lighter and yellower than the reticulum. There is an irregular trace of the reticulations on the tail.

Table 2. Measurements of *Galeus piperatus* in thousandths of total length.

Specimen no.	Male					Female		
	SIO 68-90	SIO 68-89	SIO 69-203	SIO 68-89	LACM 30303-1	LACM 8818-9 ²	LACM 30063-1	LACM 7552 ¹
Total length (mm)	71	80	280	284	293	256	295	302
1. Length to D1	427	417	464	451	451	430	468	440
2. Length to D2	592	569	621	623	608	598	624	613
3. Between dorsal origins	159	152	161	165	163	157	158	171
4. Interdorsal space	75	62	88	89	87	81	85	88
5. D2 origin to end C	408	435	379	380	403	406	369	383
6. Tip D2 to end C	335	352	305	301	318	329	302	308
7. P1 insertion to D1 origin	170	160	208	194	226	209	251	200
8. Prepectoral length	211	227	238	224	223	219	234	195
9. Prepelvic length	390	373	386	391	375	363	393	358
10. D2 origin to upper C origin	111	130	98	89	92	107	96	99
11. P2 insertion to lower C origin	255	227	225	244	232	238	214	262
12. Between P1 and P2 insertions	182	176	186	177	171	200	192	176
13. Body depth (greatest)	82	77	99	103	100	73	94	115
14. C peduncle depth (least)	44	40	39	39	38	36	38	36
15. Body width (greatest)	89	95	93	89	89	100	87	86
16. C peduncle width at front C	23	22	20	18	19	16	21	16
17. Length to first gill-slit	177	181	188	175	183	174	201	163
18. Width between first gill-slits (ventrally)	80	97	111	97	110	101	104	108
19. Snout length (preocular)	82	91	85	83	83	88	86	77
20. Snout length (preoral)	58	79	80	72	76	80	86	70
21. Prenarial length, outer	49	53	55	55	52	55	57	51
22. Prenarial length, inner	51	68	64	61	61	59	63	56
23. Nostril width (maximum)	26	30	25	25	26	25	29	26

Specimen no.	Male					Female		
	SIO 68-90	SIO 68-89	SIO 69-203	SIO 68-89	LACM 30303-1	LACM 8818-9 ²	LACM 30063-1	LACM 7552 ¹
24. Internarial width (least)	29	31	27	28	27	27	28	27
25. Between tips of narial flaps	57	55	56	54	62	62	58	61
26. Nostril to orbit (least)	29	34	34	29	30	24	35	27
27. Nostril to mouth (least)	16	17	18	19	18	21	25	20
28. Mouth length (projection)	64	58	49	43	43	36	41	37
29. Mouth width	85	90	108	100	103	132	104	95
30. Orbit length	41	42	39	43	41	41	42	40
31. Interorbital width (fleshy)	89	110	86	85	84	82	87	86
32. Interspiracular distance (dorsally)	107	109	105	95	100	101	106	96
33. Spiracle length (maximum)	9	10	6	5	9	10	4	7
34. Spiracle to snout tip	134	148	137	132	131	128	138	127
35. Spiracle to P1 insertion	138	146	159	150	151	153	159	141
36. Between fronts of gill-slits 1 and 5	60	70	49	55	60	67	49	61
37. Height, first gill-slit	28	21	21	26	26	19	20	20
38. Height, fifth gill-slit	19	13	13	19	17	11	13	15
39. D1 base	54	57	45	45	43	50	50	49
40. D1, origin to extreme tip	89	97	75	76	76	88	84	78
41. D1 height (insertion to extreme tip)	36	39	38	39	45	49	42	32
42. D2 base	58	57	49	43	47	48	47	49
43. D2, origin to extreme tip	87	95	74	68	74	75	72	71
44. Upper lobe C (extreme)	314	322	281	286	307	292	278	284
45. Lower lobe C (extreme)	325	362	289	290	319	311	287	303
46. P1 base (fin appressed)	41	49	70	69	67	67	77	67
47. P1, lower-anterior edge	85	110	121	128	120	127	119	117
48. P1, lower-distal edge	44	47	103	86	90	95	91	101

Specimen no.	Male					Female		
	SIO 68-90	SIO 68-89	SIO 69-203	SIO 68-89	LACM 30303-1	LACM 8818-9 ²	LACM 30063-1	LACM 7552 ¹
49. P2 base	60	70	84	77	74	76	100	79
50. P2 origin to tip of rays	74	99	118	101	99	116	116	113
51. P2 origin to tip clasper	64	78	162	159	157	—	—	—
52. Cloaca to tip clasper	31	35	107	105	102	—	—	—
53. Cloaca to tip P2 rays	42	69	70	52	52	74	71	65
54. Snout to anal-fin origin	514	492	561	553	533	504	536	540
55. Length anal base	132	125	112	108	122	128	134	123
56. End of anal fin to lower C origin	35	16	14	20	9	14	11	12
57. Length anal fin	141	151	127	129	140	146	146	146

¹ Holotype.

² Paratype.

DENTICLES

To supplement the original account of denticles on the body of adults we include (Fig. 3, lower) the reproduction of a photomicrograph of the pedunculated tridents, which contrast boldly with the simple, hooked, sessile spinelets of the juveniles (Fig. 3, upper), as already noted. The denticles on the body also contrast sharply with the minute lanceolate oral denticles noted and figured by SPRINGER and WAGNER (1966, pp. 3-4, Fig. 2) for *G. piperatus* and found by them in all species of *Galeus* that they examined. The occurrence, distribution, and form of denticles on the surfaces of the buccal cavity provide diagnostic characters in sharks, as the late Swiss paleontologist BERNHARD PEYER found during unpublished research at Scripps Institution several years ago.

The specialized form and pattern of the denticles on the clasper are mentioned below.

TEETH

The collection of males makes it possible to point out sexual dimorphism in the tooth structure of adults, somewhat in the direction of, but far less extreme than, the sexual dimorphism of the teeth in *Apristurus riveri* BIGELOW and SCHROEDER, as described and figured by SPRINGER (1966, pp. 591-593, Fig. 10). The females exhibit a greater degree of heterodonty than the males. The teeth of females vary from tricuspid anteriorly, with a long central cusp near the symphysis, to posterior teeth with cusps, of more uniform length, numbering four or five in the upper jaw and five to seven in the lower jaw (Fig. 4). In males, tricuspid teeth continue to the end of the jaw, with some reduction in relative length of the central cusp. One male (SIO 69-203) bore a few pentacuspoid teeth near the end in each jaw. Generally, all teeth of the adult males are similar to the anterior tricuspid teeth of the females. As already noted, small juvenile males have teeth similar to those of adult males.

In adults of each sex the tooth rows range from twenty-nine to thirty-two on each side of the jaw.

VERTEBRAE

As determined by radiography, the vertebrae in eight specimens vary in number as follows (Table 3): monospondylous vertebrae 30 to 33 (mean 32.7), precaudal diplospondylous vertebrae 36 to 39 (37.4), total precaudals 66 to 72 (69.1), caudals 41 to 49 (45.6), total count 112 to 118 (114.7). In all the radiographs the monospondylous vertebrae give way to the diplospondylous condition clearly and abruptly over the insertion

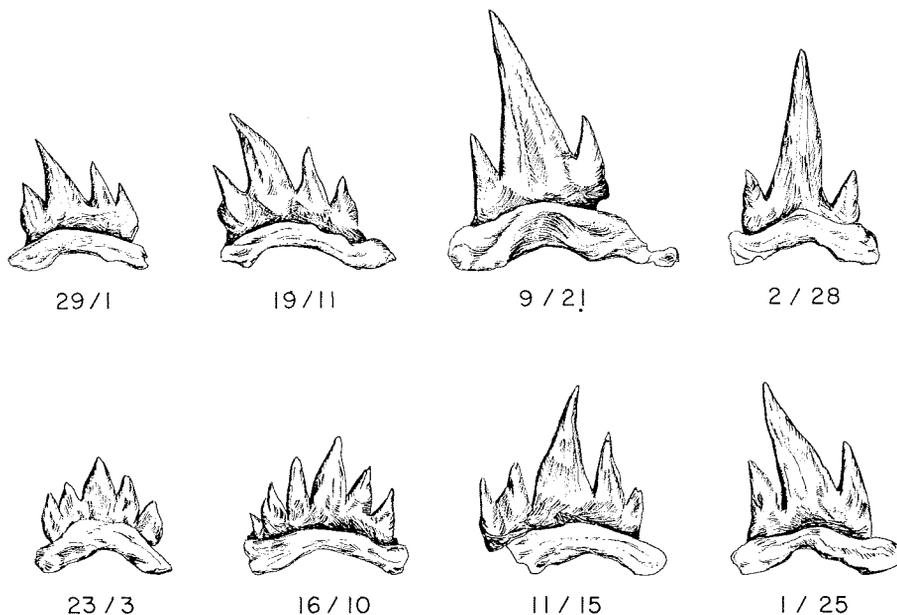


Fig. 4. Teeth from the left jaw of an adult female of *Galeus piperatus* (LACM 8818-9, a paratype, 256 mm long). Upper jaw, above; lower jaw, below. The first figure represents the number of teeth between that tooth and the symphysis; the second figure, the number of teeth between that tooth and the end of the jaw.

of the pelvic fins (Fig. 5), thus rendering precise the counting of monospondylous centra. The diplospondylous vertebrae are designated as pre-caudal and caudal, by the definition of the first caudal (Fig. 6) as the first vertebra lying wholly or by any part below the beginning of the double row of tubercles that dorsally crest the caudal fin (the same point that is regarded by us, for measurements, as the origin of the caudal fin).

The very early virtual completion of vertebral formation reflects the dwarfed nature of the species, as already noted in discussing the juveniles.

Our counts of the holotype and one paratype show some divergence from those by SPRINGER and WAGNER (1966). The counts of monospondylous vertebrae agree, but the diplospondylous pre-caudal counts (obtained by subtraction from their Table 3) differ by as much as three and the caudal counts by as much as five. Perhaps those workers chose a different point for the caudal origin, or counted caudal rudiments differently. In his review of western Atlantic scyliorhinids SPRINGER (1966) presented counts of monospondylous vertebrae only, stating that "diplospondylous vertebrae near the tail tips were difficult to count". Whereas monospondylous and pre-caudal diplospondylous counts are quite precise, the number of caudal vertebrae is subject to some counting error due to

Table 3. Vertebral characters in eight specimens of *Galeus piperatus*, from radiographs.

Specimen no.	Sex	T. L. (mm)	Precaudal vertebrae		Total precaudal vertebrae	Caudal vert.	Total vert.	A ¹	B ²
			Mono-spondylous	Diplo-spondylous					
SIO 68-89	♂	284	31	39	70	46	116	146	130
SIO 68-89	♂	80	31	38	69	45	114	188	93
SIO 68-90	♂	71	33	39	72	41	113	186	85
SIO 69-203	♂	280	33	36	69	47	116	143	142
LACM 30303-1	♂	293	30	36	66	47	113	149	142
LACM 7552 (Holotype)	♀	302	33	36	69	49	118	136	127
LACM 8818-9 (Paratype)	♀	256	31	39	70	46	116	178	124
LACM 30063-1	♀	295	32	36	68	44	112	156	140
Averages			32.7	37.4	69.1	45.6	114.7	160.3	122.9

$$^1 A = \frac{\text{length of penultimate monospondylous centrum}}{\text{length of first diplospondylous centrum}} \times 100.$$

$$^2 B = \frac{\text{length of penultimate monospondylous centrum}}{\text{diameter of penultimate monospondylous centrum}} \times 100.$$

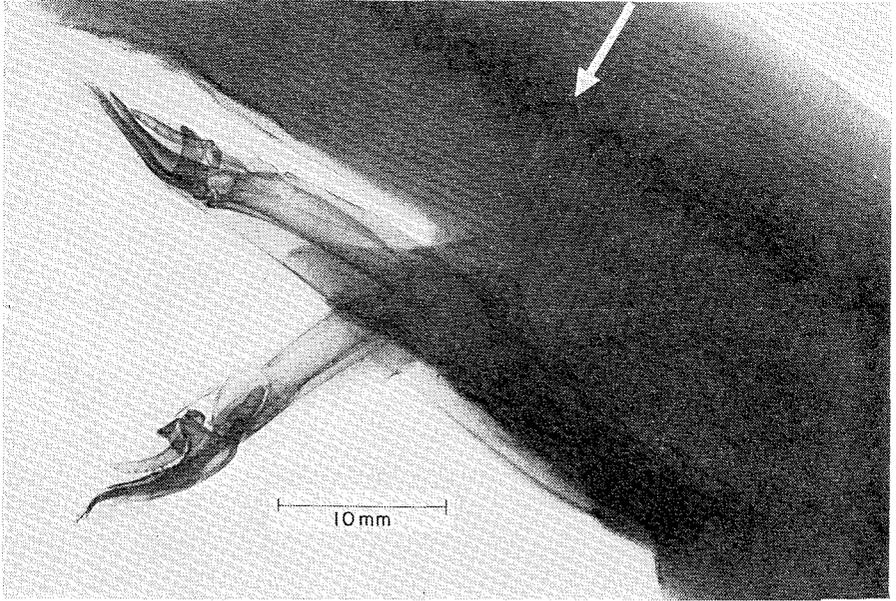


Fig. 5. Radiograph of pelvic claspers and median vertebrae of adult male *Galeus piperatus* in right lateral view (SIO 68-89). Arrow indicates point of change from monospondyly to diplospondyly.

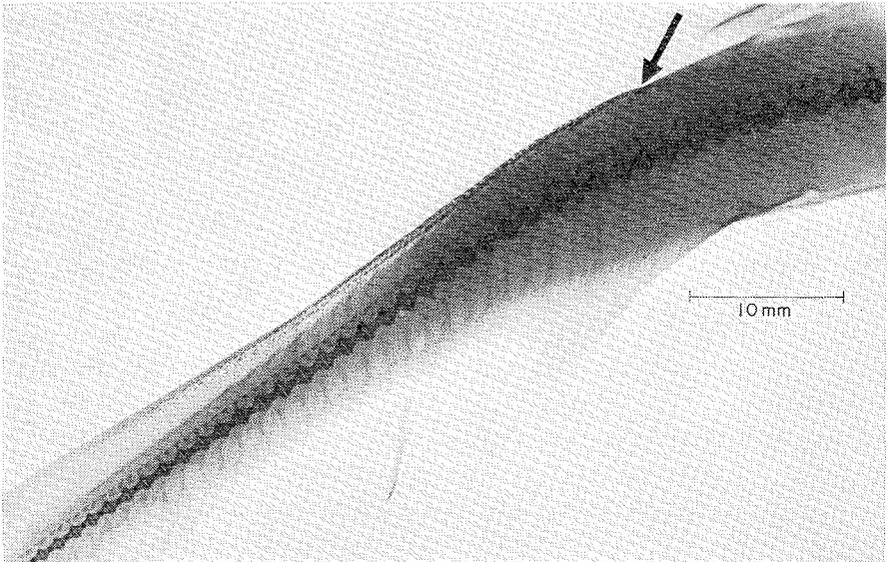


Fig. 6. Radiograph of caudal fin of holotype of *Galeus piperatus*. Arrow indicates beginning of double row of enlarged denticles used as a marker for origin of caudal fin and caudal vertebrae.

the minute and irregular size of the centra and the distorted shape of the last few elements. Nevertheless, we feel that with good X-ray equipment, and with due care in exposures and in counting, that reasonably reliable counts can be obtained for the diplospondylous vertebrae—certainly for the precaudal ones, if a precise point for the start of the precaudal count is established.

Other striking differences occur between our values and those of SPRINGER and WAGNER (1966) for the "A" and "B" ratios (defined in Table 3), which were originally proposed and utilized by SPRINGER and GARRICK (1964). Furthermore, the range of variation for each ratio is very large. In small sharks, such as *Galeus piperatus*, a typical vertebra is about 2–3 mm long. Measurement under magnification is essential, but is complicated by the large grain size that appears under such enlargement. The limits of the centra are difficult to ascertain with certainty. In addition, different exposure times can cause measurements for the same specimen to diverge. This results from the circumstance that inadequate X-ray exposures fail to represent the full length of the centra, because the thin fore and aft ends of the amphicoelous vertebrae fail to register, whereas the width of the centrum remains scarcely altered. Until exposure times and methods of measuring can be standardized, we feel that the "A" and "B" ratios will be of little value, especially for small sharks.

CLASPERS

The claspers of *Galeus piperatus* (Fig. 7) are large, robust, and highly complex, particularly as shown by radiography (Fig. 5). They are very mobile and are jointed about midway of their length. The siphons open laterally at about 0.9 of the distance out from the cloaca. The pattern of grooves and of hard and soft flaps, folds, and prominences is complicated but consistent. The detailed structures and homologies are yet to be worked out, and we are pleased to learn that STEWART SPRINGER has undertaken a study of the claspers of the Scyliorhinidae. In gross features, the clasper of *G. piperatus* conforms with SPRINGER's (1966, Fig. 4B) sketch of the claspers and general pelvic region in a western North Atlantic species, *G. arae* (NICHOLS), and definitely contrasts with LEIGH-SHARPE's (1920) non-detailed brief account and figures for the European species *Scyllium catulus* = *Scyliorhinus catulus* (L.) and *Scyllium canicula* = *Scyliorhinus canicula* (L.). We feel that in all probability the finer structure of the diverse elements of the clasper will provide key value in the recognition of genera and species of Scyliorhinidae and in the interpretation of their relationships.

The denticles on the clasper are distinctively modified in pattern and

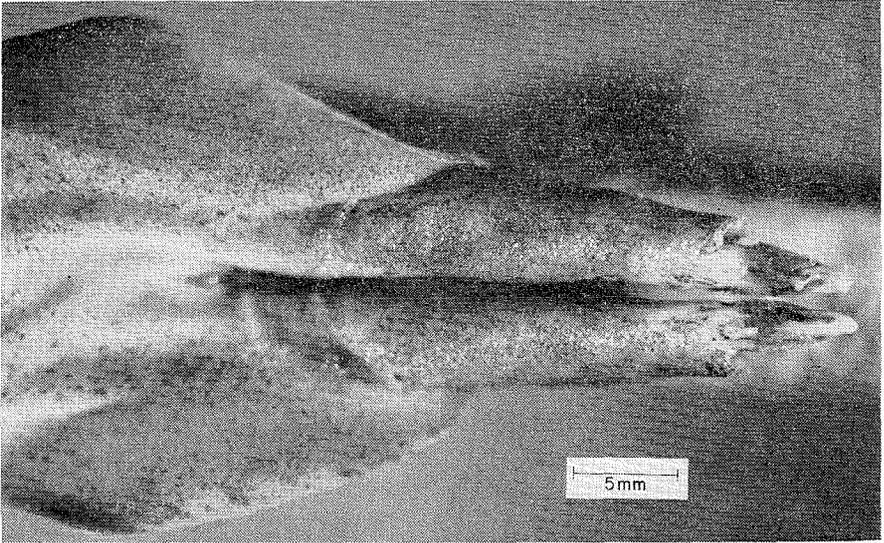


Fig. 7. Pelvic claspers of adult male of *Galeus piperatus* (SIO 68-89).

form. They completely cover a large area over the ventral surface basally. Distally, this area spirals laterally and dorsally. This major patch is continuous with the squamation of the flat lower surface of the pelvic fins, though the intervening denticles are weak. The patch ends abruptly against the smooth denticle-free skin, which is irregularly marked with black (Fig. 7). Beyond the subterminal notch in the clasper as seen in ventral view (Fig. 7), and just proximal to the whitish flesh-covered tip of the clasper, there is a discrete patch of denticles, which are mostly loose and lanceolate, but outward and upward, where concealed by a prepuce-like hood, they become strong and fixed. On the opposite side, opposite the basal part of the terminal patch and extending farther proximally, is a second discrete patch of denticles, which are moderately flattened, slender and sharply pointed.

Most notable among the diverse denticles on the clasper are the very slender, mostly loosely attached hooks that biserially line the edge of the spiralling sperm duct on the outer and upper sides of the organ. A few occur at the outer tip of the subterminal notch as seen in ventral view (Fig. 7), but the main part of the double file is along the firm edge that angles proximad and entad. The hooks arise from a dorsal terminal cartilage (Fig. 6). These hooks closely approach the denticles on the body of the juveniles (Fig. 3, upper).

An example of the finding of profound differences in clasper characters between two species of squaloid sharks that were long thought, probably

erroneously, to be very closely related, has recently been presented (HUBBS, IWAI and MATSUBARA, 1967, pp. 33-36, Fig. 7, pls. 2, 6, 7). Thorough critical, detailed, and comparative studies of myxopterygial structures in all sharks are, indeed, long overdue.

SUMMARY

Information is presented on a recently described dwarf shark, *Galeus piperatus*, which occurs through a wide range of depth in turbulent waters of highly varying physical parameters in Golfo de California, Mexico. It barely exceeds 300 mm in total length and an egg-case presumed to be of this species is only 35 mm long. Young about 80 mm long are well formed and very active. The sexes are remarkably alike in most respects but differ in tooth structure. The denticles of the young bear a single hooked spine, but are pedunculated tridents in the adult. The claspers are large, robust, and of highly complex external and internal structure.

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ON THE MIGRATIONS OF THE COD IN THE SKAGERAK SHOWN BY TAGGING EXPERIMENTS IN THE PERIOD 1954—1965

By

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INTRODUCTION

Tagging experiments on cod carried out in the skerries and fjords on the Norwegian Skagerak coast have shown that the cod population or populations in the area undertake only short migrations and are more or less isolated from the cod in other areas of the Skagerak (DAHL 1906, RUUD 1939, LØVERSEN 1946). Two tagging experiments conducted from the Biological Station in Flødevigen in 1953 and 1954 showed, however, that cod from the Skagerak coast could undertake longer migrations along the Norwegian coast as well as into the Skagerak (unpublished data). These contradictory results, as compared with previous years tagging experiments, inspired the former director, Dr. A. DANNEVIG, to initiate tagging experiments also from the Danish side of the Skagerak. This paper describes the results of eleven tagging experiments carried out in the years 1954 to 1965.

MATERIAL AND METHODS

The tagging experiments were carried out in the years 1954, 1955, 1956, 1958, 1960, 1961 and 1965 during cruises with R/V G. M. Dannevig. The cod used for tagging were caught with hand line, and only fish in good condition were tagged. In all the years the fish were released at Robben (N 57°42', E 09°12') about 25 n.m. from the Danish Jylland coast. In 1954 and 1958 tagged fish were also released at Rubjerg (N 57°30', E 09°35'), and in 1956 near Hanstholm (N 57°15', E 08°00').

The Lea hydrostatic tag was used in all the experiments except in one experiment in 1954 when a tag consisting of impregnated paper printed

with necessary text, and rolled together to about the same size as the Lea tag was used.

All the tags were fixed in front of the first dorsal fin with a nylon thread.

The total length of the tagged fish ranged from 22 to 110 cm with a mean length of 56 cm, and the greatest frequencies were in the size groups 41 to 70 cm.

The number of tagged fish each year varied from 87 in 1956 to 309 in 1960, totalling 1,244 fish. The number of tagged fish and recaptures are given in Table 1.

RESULTS AND DISCUSSION

Of the 1,244 tagged fish a total of 367 or 29.5% had been recaptured within the end of May 1969. Tags (14) which have been reported found on the shore along the Danish, Norwegian and Swedish coast are not included in this figure. Of 44 fish tagged in 1954 with the impregnated paper tag, 11 fish have been recaptured compared to 12 recaptures of 45 fish tagged at the same locality and the same year with the Lea tag. The two tags are therefore treated in the present report as having the same tagging efficiency.

The recapture percentage from the different tagging years shows a variation from 24.9 to 35.6. The number of recaptures decreased rapidly after the first year in liberty (Table 1). The two experiments in 1954 gave no recaptures in the third year, and in general the number of recaptures in the third year was very small. The longest time in liberty was 83 months. In the total material the mean number of months before recapture is about the same in the different length groups.

The total material shows that the recapture percentage was higher in the larger length groups than in the smaller ones. Of 110 tagged fish in the group 41–45 cm 14.6% were recaptured compared to 43.2% recaptured from the group 66–70 cm with 111 fish (Fig. 1). This could either be due to availability, mortality, a higher shedding percentage among the smaller fish, or a combination of these factors. LEFRANC (1967) also got fewer recaptures from the smaller cod and assumes that the mortality could be higher among the smaller ones. The same decreasing recapture tendency with decreasing size at tagging was also shown on whiting by KNUDSEN (1964).

All the recaptures in the Skagerak have been taken on the Danish side of the Norwegian Channel. No fish from any of the three tagging localities was recaptured on the Norwegian Skagerak coast though the nearest tagging position, Robben, is only about 40 n.m. from the coast. Tagging experiments in the skerries on the Norwegian Skagerak coast in the years

Table 1. Number of cod tagged and recaptured in the years after tagging, and the percent returns from the different tagging years.

Date	Locality	Number of cod tagged	Years at sea							Sum recaptured	Total % returns tagged in the different years	
			1	2	3	4	5	6	7			
1954 Aug.	Robben	64	8	4							23	25.8
1954 Aug.	Rubjerg	25	10	1								
1955 April	Robben	129	22	7	6	5	2	1	1		44	34.1
1956 April	Robben	49	11	2	1				1			
1956 April	Hanstholm	38	7	6	2		1				31	35.6
1958 Aug. Sept.	Robben	110	20	2	2							
1958 Aug. Sept.	Rubjerg	104	26	10	2	2	2				101	34.1
1958 Nov.	Robben	82	22	10	3							
1960 May	Robben	188	33	16	9		2				83	26.9
1960 Aug.	Robben	121	16	4	1	1	1					
1961 Aug.	Robben	195	31	13	1	1		1			57	24.9
1961 Nov.	Robben	34	6	3	1	1						
1965 March	Robben	105	17	9	1		1				28	26.7
Total		1244	229	87	28	10	9	2	2		367	29.5

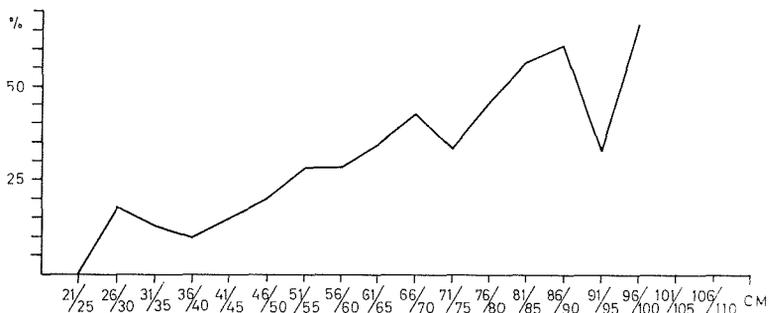


Fig. 1. Percent recaptured cod according to length when tagged. (Number of tagged fish in each of the 5-cm groups: 33, 47, 42, 110, 148, 140, 211, 225, 111, 62, 52, 30, 18, 3, 3.)

1953 and 1954 gave some returns from the Danish side of Skagerak (unpublished data). As the fish in these experiments had been kept in a spawning basin at Flødevigen for some weeks before tagging, the long migration may, however, have been an effect of the captivity. It seems reasonable to conclude therefore, that there usually is no connection between the cod populations on the Danish and the Norwegian Skagerak coast.

Most of the recaptures are taken near the tagging localities. From the Robben experiments 25.6% have been caught within 10 n.m. of the Danish coast, mostly from October to December (Fig. 2). No one was taken near the coast in July, only one in August and one in September. Farther off the coast most of the fish were taken from July to September. DANNEVIG (1966) mentions that the cod on the Norwegian Skagerak coast migrate to deeper water in the summer due to the warm surface water and return to shallow water in the autumn. A similar seasonal variation in recaptures is also shown in this material and could possibly be due to migration to deeper water in the last part of the summer and early autumn, and to shallow water in the late autumn.

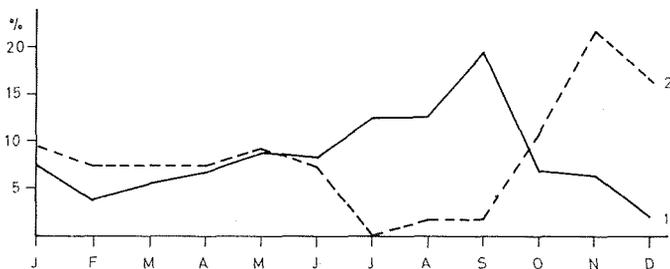


Fig. 2. Monthly variations in the recaptures in the Skagerak. 1) outside and 2) inside a limit of 10 n.m. off the Danish coast.

From the Hanstholm experiments one cod has been recaptured near Robben and four near Hanstholm on the Danish coast. Five have been caught in the eastern part of the North Sea and four near the tagging position.

Table 2. Total number of recaptures in Skagerak, the North Sea and Kattegat from each tagging year (Hanstholm experiment excluded).

Year	Skagerak	North Sea	Kattegat	Total
1954	18	2	2	22
1955	34	7	1	42
1956	10	5	0	15
1958	83	5	6	94
1960	58	10	3	71
1961	37	9	3	49
1965	19	5	0	24
Total	259 (81.4%)	43 (13.6%)	15 (4.7%)	317

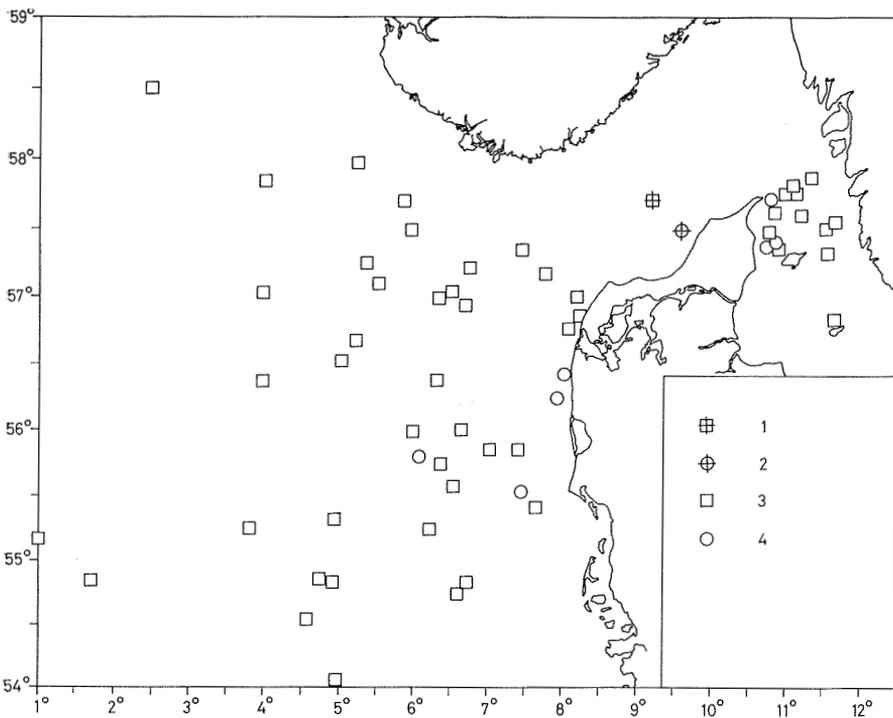


Fig. 3. Recaptures from the North Sea and Kattegat. Tagging positions. 1) Robben and 2) Rubjerg. Recaptures from 3) Robben and 4) Rubjerg.

As shown in Table 2 only 4.7% of the recaptures are from Kattegat (the border between Skagerak and Kattegat defined by a straight line from Skagen to Paternoster Lighthouse), and they have all, except one recaptured near Anholt, been taken in the area between Læsø and the border to Skagerak (Fig. 3). With two exceptions they have all been caught in the period from November to February.

From the Robben and Rubjerg experiments 13.6% of the recaptures have been caught in the North Sea, which should indicate a connection between the cod in the Skagerak and the eastern part of the North Sea. As Fig. 3 shows, all the cod except three are taken east of E 03°50' and between N 54°00' and N 58°00' with a random distribution in the area. Most of them have been taken in the first months of the year. In the southern and middle part of the area, south of N 57°00', most of the cod were caught during the first six months of the year, mainly from February to April (Table 3). Only three individuals have been taken from July to December. According to BEDFORD (1966) the central North Sea cod have in the summer (May to September) a northerly movement. Although the number of recaptures from the North Sea in the present material are few, the numbers are higher from the northern part (north of N 57°00') than from the southern part in this period.

Two fish from these tagging experiments made very long migrations. One cod, 72 cm long, was tagged on Robben in March 1965 and recaptured 49 months later on the Norwegian Helgeland coast. It is interesting to note that HYLEN (1964) reported a similar migration, but in opposite direction of a cod tagged on the Trøndelag coast and recaptured west of Skagen. The longest migration was made by a fish tagged on Robben in May 1960 and recaptured 34 months later on the Fyllas Bank on West Greenland. The shortest possible distance between the two places is 2,300 nautical miles. The total length of the fish was 65 cm at tagging and 93 cm when recaptured. A similar long journey, from the North Sea to the Grand Banks, has earlier been reported by GULLAND and WILLIAMSON (1962). Long migrations of cod have also been observed in other areas, as for example between Iceland and Greenland, from Iceland to the Faeroes and from the Faeroes to the North Sea (TÅNING 1934).

Table 3. Number of cod recaptured in the North Sea in the different months.

	Jan.	Feb.	Mar.	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
North of 57°N	1	1		1	1		1	5	1	2		
South of 57°N	3	7	7	5	3	2	2					1

SUMMARY

1. A total of 1,244 cod was tagged from 1954 to 1965. The recapture percentage from the different tagging years varied between 24.9 and 35.6 with a mean of 29.5 for the whole period.
2. No cod has been recaptured on the Norwegian Skagerak coast, indicating that there is no connection between the cod populations on the Danish and Norwegian side of the Skagerak.
3. The recaptures in the Kattegat have been very small (15 individuals). The migration into the eastern part of the North Sea somewhat greater (43 individuals), and they were mainly caught in the first part of the year.
4. One cod has been recaptured on the Fyllas Bank on the West Greenland 34 months after the tagging, and one on the Norwegian Helgeland coast after 49 months at sea.

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PREDICTED EFFECTS OF FERTILIZERS UPON THE ALGAE PRODUCTION IN FERN LAKE¹

By

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INTRODUCTION

Fern Lake is situated about 60 km south-west of Seattle in Kitsap County, Washington, U.S.A. (Fig. 1). The lake was, in 1958, made the object of a 10-year research project by the Laboratory of Radiation Biology, University of Washington, with the Washington State Department of Game and the U.S. Atomic Energy Commission as sponsors. The objective was to study the mineral metabolism in the entire watershed in an attempt to accumulate knowledge for the improvement of natural resources (DONALDSON, OLSON and DONALDSON 1959).

Limnological descriptions of the lake are given by GELDIAY, DONALDSON and OLSON (1959) and by OLSEN and OLSON (1966). Details of the metabolism of certain elements have been gathered through tracing radioactive isotopes such as P-32, Ca-45, I-131 and Mo-99, using the whole lake as experimental field (DONALDSON 1962), (DONALDSON 1964), (PALUMBO *et al.* 1963).

The lake has been extensively studied both with respect to the rate of gross production by phytoplankton, composition and quantities of zooplankton and insects, as well as the growth of the fish. Originally the fish population consisted of eight species. To simplify the whole ecosystem to better control the fish production, the lake was depopulated in 1957 and again in 1960. Restocking has annually been made with 7,000–20,000 steelhead broods (*Salmo gairdneri*). The production of the lake is low, for fish in the order of 1/10 of the nearby Bay Lake, which has been used for comparison. OLSEN, CHAKRAVARTI and OLSON

¹ Contribution No. 314, College of Fisheries, University of Washington. Atomic Energy Commission Contract No. AT(45-1) 1385. Principal investigator Dr. LAUREN R. DONALDSON.

Contribution given in honour of Gunnar Rollefson at his 70th birthday.

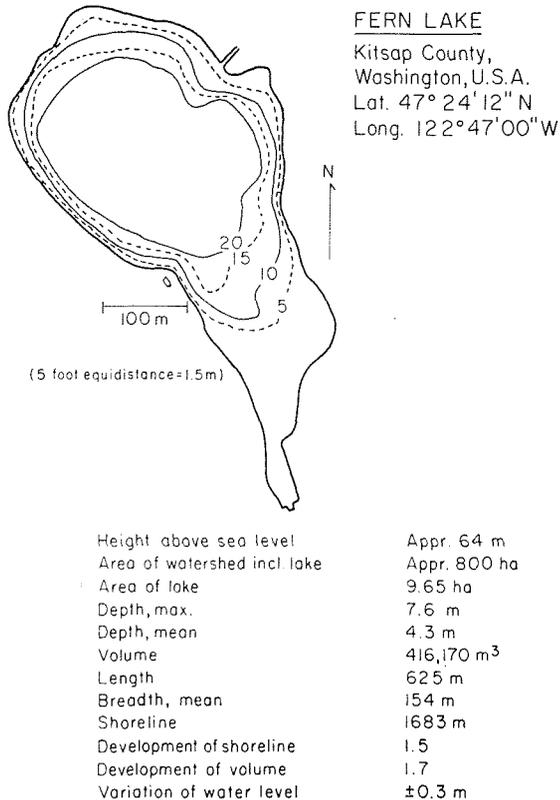


Fig. 1. Fern Lake. Morphometric data (OLSEN and OLSON 1966).

(1967) analyzed the spectrum of macro- and micro-element composition of the water, and demonstrated extremely low levels for most of the plant nutrients. They concluded that a nutrient deficiency was seriously limiting the production of the lake. By comparing the mineral composition of Fern Lake with that of the productive Bay Lake it seemed reasonable that the productivity of Fern Lake could be improved by fertilizing the water with the whole spectrum of elements, bringing them to the levels of Bay Lake. On the basis of such evaluations, OLSEN (1965) suggested the composition and amounts of fertilizers to be used (Table I).

Before the fertilization of the lake was initiated, pilot experiments were carried out in two of four plastic silos anchored in the lake. The silos each enclosed a water column of 154 m³ lake water with a surface area of 30 m². They were both treated with fertilizers, one with the proposed concentration exclusive of iron and the other with iron included. The experiments revealed slowly increasing chemical reactions in the iron-treated silo, forming colloids resulting in a 75% decrease in transparency

after a week (OLSON, personal communication). In the other silo no such effects were observed within the first week. A strong growth increase in the phytoplankton was recorded in both silos, after a short period of inhibition. About nine weeks after application the maximum rate of gross production was recorded in the iron-treated silo with a value in surface waters of 180 times the original gross production (OLSON, personal communication). Some doubt existed as to what degree the responses in the silos could be indicative of the lake itself due to the prehistory of the silo waters since the implantation of the silo in 1964 (OLSEN 1965). Also, since no information concerning optimum fertilizer concentrations could be obtained from the pilot experiment, a bioassay analyzing effects of different quantities of fertilizers and specifying the importance of iron upon the rate of gross production in lake water was scheduled.

Different approaches have been used in measuring limiting nutrient factors in natural phytoplankton populations since RHYTER and GUILLARD (1959) and GOLDMAN (1960) applied the C-14 technique on similar problems for seawater and lakes, respectively. A review of this literature is given by WETZEL (1965) and GOLDMAN (1965). The present investigation is in principle similar to the bioassays of limiting factors made by RYTER and GUILLARD (1959), since the analyzes are made on water enriched with different degrees of the whole spectrum of fertilizers and deals with the effect of removing one of the trace elements. It deviates, however, in that respect that a large volume of water was applied and that the analyzes of effects were carried out until a maximum level in the rate of primary production seemed to be reached.

MATERIALS AND METHODS

The bioassay was carried out in Fern Lake during the period 9 August–1 September 1966 in a series of fourteen 5-gallon glass bottles. Previous to the experiment the bottles were washed and rinsed in hot 2% Na_2CO_3 solution followed by hot 1% HCl solution and finally rinsed several times in lake water. Fifteen litres of lake water, collected 10 cm below surface from a raft anchored in the lake was filled into the bottles, and fertilizers added as follows:

Container No.	1 and 5	No	fertilizers added
	2 and 9	$\frac{1}{4}$ (c-Fe)	» »
	3 and 10	$\frac{1}{2}$ (c-Fe)	» »
	4 and 11	1 (c-Fe)	» »
	6 and 12	$\frac{1}{4}$ c	» »
	7 and 13	$\frac{1}{2}$ c	» »
	8 and 14	1 c	» »

where c refers to the composition and concentrations given in Table I, c-Fe to the same concentrations omitting iron.

The fertilizers were made from p.a. grade chemicals in five separate solutions in order to avoid precipitations:

Sol. 1	Sol. 2	Sol. 3	Sol. 4	Sol. 5
MgSO ₄	Ca(NO ₃) ₂	H ₃ BO ₃	NH ₄ H ₂ PO ₄	FeSO ₄
K ₂ SO ₄	CaCl ₂	MnCl ₂	NaHCO ₃	
ZnSO ₄		CoCl ₂		
		H ₃ MoO ₄		
		KI		

The containers were plugged with rubber stoppers perforated with 1 cm glass tubing (30 cm long) with a bent plastic tube at the upper end. This system allowed free gas exchange and acted, at the same time, to guard the cultures from accidental contamination. Arranged in numbered sequence, the containers were left floating in the lake attached to a line anchored between the raft and the western shore (Fig. 2).

At intervals as given in Table II, parallel samples were collected from the containers into 125 ml Pyrex glass bottles for productivity measurements. Sampling was made with a squeeze-ball pump, after a thorough mixing of the content was secured by squeezing air into the bottom of the containers. The samples were placed in an incubator, injected with 2,5 microcuries C-14 as NaHCO₃, and incubated under artificial light for four hours (STEEMANN-NILSEN 1952). Similarly, bottles wrapped in aluminium foil were used to evaluate C-14 dark fixation during the same time. The temperature in the incubator was controlled to that of the lake. After four hours, the samples were filtered on Millipore filters (HA), preserved and removed of inorganic ¹⁴CO₃²⁻ by afterfiltering of 10 ml 10% formalin. Following drying in a desiccator, β counting

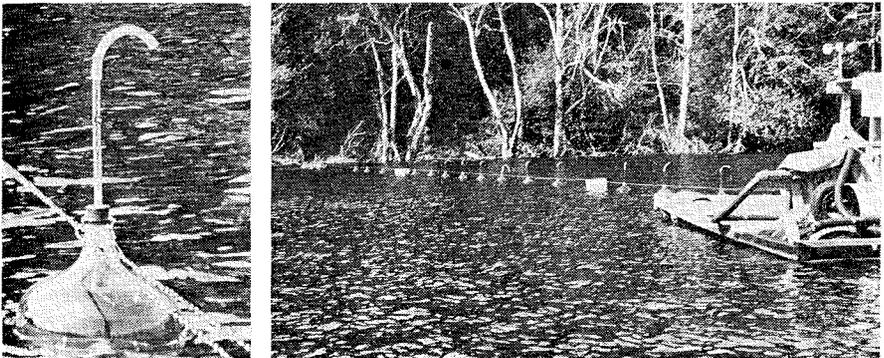


Fig. 2. Fern Lake bioassay. Experimental set-up.

of the MP filters was made on a Nuclear Chicago low-level β counter. The efficiency of the system was 6%.

Total alkalinity was determined from titrations with 0.02 N HCl in 200 ml samples, and the total available CO_2 was calculated as mgC/l using the conversion tables given by SAUNDERS, TRAMA and BACHMANN (1962). The rate of gross production under the standardized condition was calculated from the net count of the light and dark bottles as follows:

$$P = \frac{(\text{cpm}_L - \text{cpm}_D) \cdot 1.1 \cdot \text{total CO}_2}{R}$$

where cpm_L and cpm_D = counts per min. net from light- and dark-exposed samples,

R = dpm C-14 added times counter efficiency times correction for MP filter absorption (SAUNDERS *et al.*, 1962),

1.1 = correction for isotope discrimination and respiration.

Estimates of *in situ* rates of gross production were made according to BERGE (1958).

RESULTS AND DISCUSSION

The net cpm from the duplicate C-14 light incubator measurements are listed in Table II. Dark bottles were run only for one of the controls and for containers 13 and 14 (half- and full-fertilized lake water). These results are listed in Table III as net count per minute.

The data demonstrate generally good agreement between the duplicate C-14 measurements. On the 96% confidence level the average of the C-14 measurements are accurate to 14.8% on the whole, and for the first four days better than 7.7%. Within these errors of measurement, the results from the parallel series of experiments mostly agree very well. An exception demonstrate the duplicates with $\frac{1}{2}$ (c-Fe) fertilizer by the end of the experiment where the deviation from their mean is greater than 60%. The container with the higher of the values had, by the tenth day of observation, lost the stopper and glass tube protection. During the application of fertilizers to the lake initiated that day, contamination of this container likely has happened. In the following evaluations, this value has therefore been omitted.

No serious bacterial activity occurred in the samples, the dark fixation of C-14 being rather constant throughout the experiment (Table II), and constituting a decreasing significance in the C-14 measurements. It appears that day to day variations in the rate of photosynthesis occurred and had the same trend in the controls and in the other containers. Such variations were expected as effects of day to day changes in environmental

conditions. Since the effects presumably act proportionally on the activities in the cultures, they are eliminated in analyzing changes in the rate of gross production for each of the containers relative to those of the controls at the same time. Such data have been calculated as percentages of the average from the two controls and are listed in Table 1.

Table 1. C-14 fixation in the fertilized containers as percentages of that in non-fertilized lake water. Values are averages of duplicate measurements in four-hour light box incubations.

c = full proposed concentration of fertilizer in lake water.

c-Fe = full proposed concentration of fertilizer less iron in lake water.

	Time after fertilization						
	4 hrs	24 hrs	2 days	4 days	7 days	11 days	17 days
$\frac{1}{4}$. (c-Fe)	80	98	123	236	673	1223	1533
$\frac{1}{4}$. (c-Fe)	85	111	147	200	455	1400	1356
$\frac{1}{4}$. c	84	119	164	242	392	1688	2101
$\frac{1}{4}$. c	79	109	152	226	748	1647	2072
$\frac{1}{2}$. (c-Fe)	75	87	99	188	607	1804	10019
$\frac{1}{2}$. (c-Fe)	75	86	117	187	413	3231	2484
$\frac{1}{2}$. c	76	103	143	268	617	4131	5841
$\frac{1}{2}$. c	65	81	105	244	397	3038	3335
1. (c-Fe)	56	63	83	208	490	2817	7445
1. (c-Fe)	56	61	73	205	493	2505	8061
1. c	61	84	112	211	414	1227	20732
1. c	57	70	87	291	423	2583	15317

It is evident that no increase in the C-14 fixations was obtained in the fertilized containers before closely one day after application and in some instances, not before the second and third day after application (Fig. 3). On the contrary, inhibitions in the rate of C-14 fixations after four hours were evident in all the fertilized containers. The inhibitions, demonstrated by the maximum depressions in the curves are highly significant as confirmed by a t-test, and are increasing with increasing amounts of fertilizer applied. However, they are not significantly different for the series with and without iron as demonstrated by Table 2 and the diagram in Fig. 4 (left).

The intervals before the cultures have recovered increased with the amount of fertilizers used, but they were also significantly different for the series with and without iron: consistently, the iron-treated containers showed more rapid recovery (Fig. 4, right).

The inhibition was probably due both to sudden changes in the osmotic pressure of the water and to toxic effects from one or more of the elements introduced (GOLDMAN 1965) and (WETZEL 1965). The difference

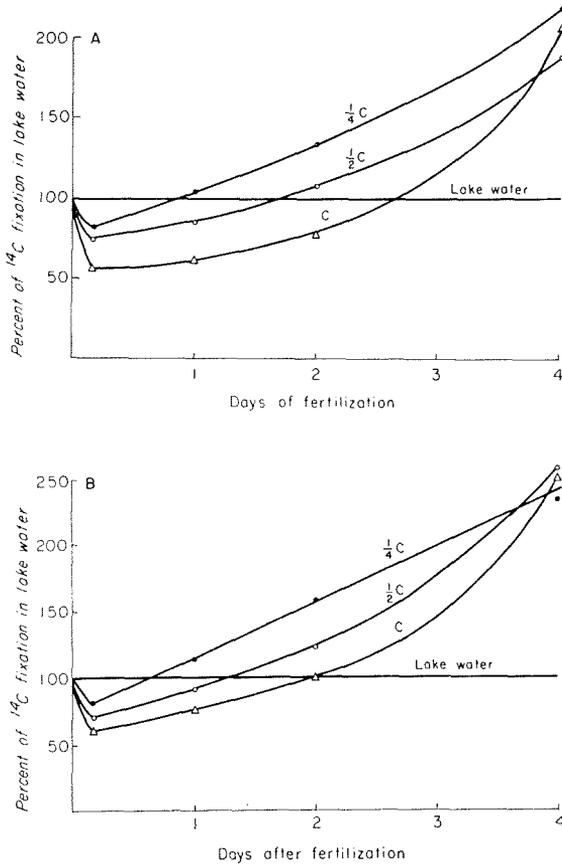


Fig. 3. Effects of fertilizers upon the rate of gross production during the first four days of the experiment. (A) without iron, (B) with iron, c = proposed concentration of fertilizers.

Table 2. Inhibition in C-14 fixation four hours after fertilization (%) and the time until recovery (hrs).

Concentration of fertilizer	Fertilizer inclusive of iron		Fertilizer exclusive of iron	
	% inhibition at 4 hrs.	Duration in hrs.	% inhibition at 4 hrs.	Duration in hrs.
$\frac{1}{4}$ c	17.6	20	18.5	16
$\frac{1}{2}$ c	25.1	40	29.4	31
c	43.9	64	41.0	46

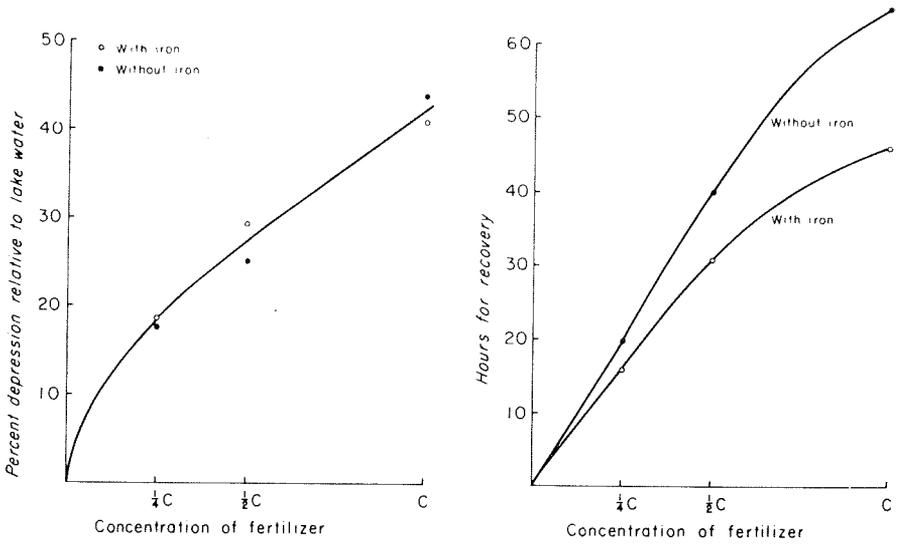


Fig. 4. Maximum inhibition of ¹⁴C assimilation (left) and time before recovery (right) for different degrees of fertilization. c = proposed concentration of fertilizers.

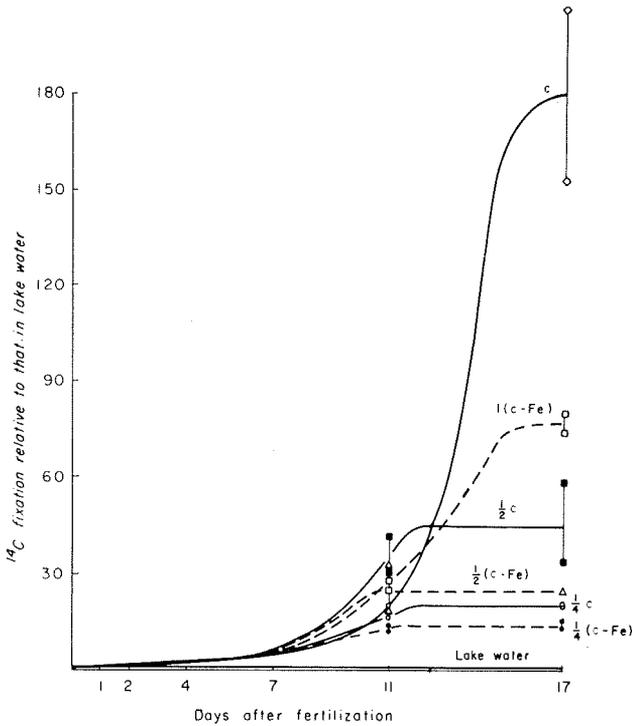


Fig. 5. Effects of fertilizers upon the rate of gross production. c = proposed concentration of fertilizers, c-Fe = proposed concentration of fertilizers less iron.

in times when the inhibitions were effective in containers with and without iron, can be explained by the chemical reactions iron created in lake water, slowly forming colloidal materials less available to the plankton and with reduced effect on the osmotic pressure.

The data from Table 1 have been plotted in the diagram of Fig. 5 and growth curves are matched to the average of each of the duplicate series. It is evident that very high increases occurred in the rate of production in all the fertilized containers following a rather long lag phase. The final effects increased with increasing amounts and were higher in the series with iron than without. By the end of the experiment the production in the containers had apparently reached a steady state. For $\frac{1}{4}$ (c-Fe), $\frac{1}{2}$ (c-Fe) and c-Fe these levels seem to be limited by iron deficiency, since the corresponding series with iron all reached considerably higher values (Fig. 6). The highest effect was demonstrated in the container with full proposed fertilizers, where the rate of gross production had reached levels 180 times higher than in the non-treated lake water. Similarly, the rate of production in the fully fertilized containers without iron was 75 times that of lake water. The trend in the curves (Fig. 6) further indicates that stronger fertilizations than made both with and without iron would still increase the rate of production. The necessary quantities to reach maximum effects are not predictable from this experiment.

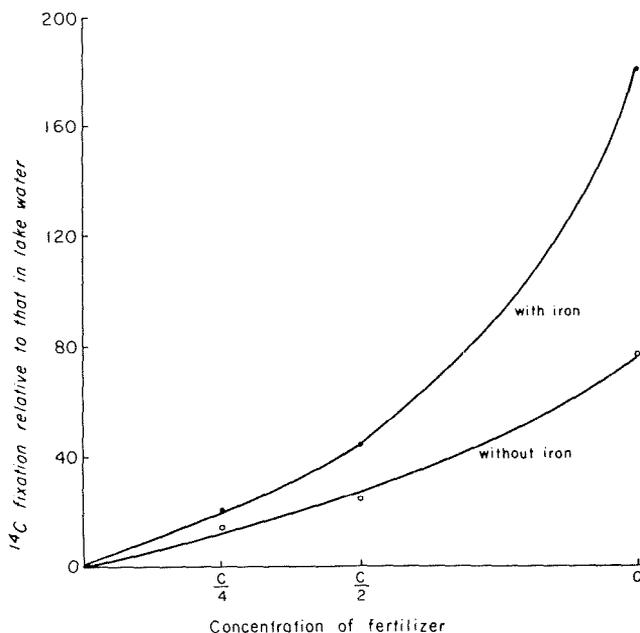


Fig. 6. Relations between rates of gross production in fertilized lake water with and without iron, seventeen days after treatment.

Using the average cpm for the duplicate experiments and 2.3 mg C/l as a representative average value for the total available CO₂ (Table IV), the ultimate rates of production reached in the differently treated containers have been calculated and are shown in Table 3.

Table 3. Rates of gross production in the fertilized and non-fertilized containers at the end of experiment. Values are average of the series.

	Av. cpm at 17 days	P mg C/m ³ day	Rel. to lake water
Lake water	689	24.8	1.0
Lake water $\frac{1}{4}$ (c-Fe)	9,952	358	14
Lake water $\frac{1}{2}$ (c-Fe)	17,113	924	25
Lake water 1 (c-Fe)	53,419	1923	78
Lake water $\frac{1}{4}$ c	14,376	518	21
Lake water $\frac{1}{2}$ c	31,608	974	40
Lake water 1 c	124,190	4470	180

Although iron, where not applied, evidently became the limiting factor at the increased rates of productivity, it is interesting to note that increased applications of fertilizers without iron still caused increased growth. These findings seem to indicate that the iron possibly was available as contaminant in the other fertilizers. The present materials do not allow analyzes in this regard, and several possibilities for its explanation exist. It might be suggested that some other element partly can replace iron in metabolic processes or that the increased fertilizer concentration changes the redox potential enough to alter the availability of naturally existing iron. Also, selection of different communities of organisms having different iron response rates might likely have occurred.

Care should be used in interpreting results from the experiments to the situation in the lake. The enclosure of small volumes of lake water in containers creates a serious change in the plankton ecology. Significant is the increased ratio of surface to volume of water; also the effects from changes in light intensity, wind mixing, and air temperature are seriously altered, and together these factors could influence both the composition and the activities of the primary producers. It is also obvious that the 15 litre samples do not represent a complete miniature of the ecosystem of the lake, and the intereffect by organisms in the containers is more or less artificial. However, using the results obtained relative to those from non-treated containers, the mentioned effects are minimized or, in some cases, even eliminated. It is thus felt that the general conclusions drawn

should be valid also to the lake itself under steady state conditions. It is interesting to note that the effect of full proposed fertilization with iron included was identical to the maximum effects recorded in the pilot experiment with the plastic silo. However, with respect to maximum effects, these should be considerably lower in the lake under natural conditions where dispersion and dilution would reduce the amount of fertilizers available to the primary producers.

The total rate of gross production of the lake is the sum of all the rates per unit volume at any place and depth, $P_{a,z}$. The latter is again related to the rate of gross production measured under standardized conditions (P_i) in the incubator the following way

$$P_{a,z} = P_i \cdot \frac{I_{a,z}}{I_i}$$

where $I_{a,z}$ = effective light at a,z and I_i = effective light in the incubator. The relation is valid as long as light intensities are below saturation for the producing population. For the major part of the lake's annual gross production, the relation is assumed to be valid. Forming the relation between the rates of production in fertilized water ($P'_{z,a}$) and in non-fertilized water ($P_{a,z}$), we have

$$\frac{P'_{a,z}}{P_{a,z}} = \frac{P'_i}{P_i} \cdot \frac{I'_{a,z}}{I_{a,z}} = \frac{P'_i}{P_i} \cdot \frac{T'}{T}$$

where T and T' are the light transmissions of the water before and after fertilization. The total effect of the fertilization on the *in situ* rates of production at any place and depth of the lake is thus equal to the relative change in the rate of production at standardized conditions of the same sample times the relative change in light transmission of the water.

CONCLUSION

From the results presented, the following conclusions can be drawn.

Application to Fern Lake water of the proposed concentration of fertilizers, with and without iron, acts as a preliminary inhibitor upon the photosynthetic activity of the phytoplankton. For each of the two compositions of fertilizers used, the extent and duration of the inhibitions are nearly proportional to the amount of fertilizers introduced; addition of iron sulfate reduced the duration of the inhibition.

Following preliminary inhibition, a strong increase in the rate of production per unit volume and light occurs, increasing with increasing amounts of fertilizers. The trend of the results points out that the optimum effects will be reached with higher applications than proposed.

At the raised levels of photosynthetic activity, iron became a limiting factor if not applied. Application of iron raised the effect of fertilizers on the ultimate rate of gross production in the containers with an average factor of about 2. However, chemical reactions occurred in the water, forming colloidal materials which decreased the light transmission. The pilot experiments with Fern Lake water showed a 75% reduction in light transmission, a situation that seemed to persist over several months. Even with a twofold gain in the rate of gross production under standardized conditions relative to that of the iron-free parallels, the counteracting effect of the reduced transparency of the lake would cause a probable loss in the total gross production of the lake, as long as the colloidal materials persisted.

Since technical grade chemicals were planned to be used in the fertilization of the lake, it was anticipated that iron might be present as a contaminant, sufficiently not to become limiting.

The following advices for a successful improvement of the primary productivity can be given:

1. Fertilizers should be added to the lake in the full proposed concentration, exclusive of iron. By extrapolating the results, it seems evident that higher effects can be reached with higher applications.

2. Application of 100 ppb of iron (Fe^{2+}) increases the effect of fertilizers upon the rates of gross production under standardized light conditions. However, due to the effect of this amount upon transparency, it will reduce the integrated rate of gross production of the lake, and should, therefore, not be included.

3. After completed fertilization as above, bioassays with lake water should be repeated to investigate whether iron had become the limiting factor on the rate of production, and from similar experiments, possibly indicate quantities of eventual later additions.

4. The applications of fertilizers should be made sequentially, using one quart or less at a time, in order to minimize inhibition of the primary producers. For the same reason, rapid and thorough mixing with the whole water column seems important. The time intervals between applications should be three days or more to ensure rehabilitation in the plankton productivity between applications.

SUMMARY

1. With the object of predicting effects of different amounts of fertilizers, upon the rate of primary production in Fern Lake, a bioassay was carried out in a series of 14 twenty liters glass carboys.
2. The experiment revealed that the rate of gross production increased nearly proportionally with the amounts of fertilizers added and a maximum increase of 180 times the original rate of gross production was obtained.
3. When iron was included with the fertilizers colloidal substances were formed acting upon the transparency of the water. When it was excluded it became limiting on the rates of primary production.
4. It is demonstrated that due to reduced transparency the inclusion of 100 ppm iron would not increase the total primary rate of production of the lake any further.
5. Suggestions for the fertilization of Fern Lake are given.

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APPENDIX

Table I. Fern Lake water analysis together with the proposed addition of fertilizers.
(Data from Olsen *et al.* (1967) and Olsen (1965).

Macro-elements mg/l	Lake Surface	Water Bottom	Proposed added (c)	Fertilizers Sources and Amounts
Ca	1.4	1.6	2.5	Ca(NO ₃) ₂ 5.12 mg/l
NO ₃			3.8	
NH ₄			0.1	CaCl ₂ 3.46 »
Cl	2.8	3.1	2.2	
Mg	0.3	0.2	0.5	MgSO ₄ ·7H ₂ O 05.0 »
SO ₄			2.6	
K	0.2	0.1	0.5	K ₂ SO ₄ 1.42 »
Na	1.5	0.5	1.0	NaHCO ₃ 3.66 »
HCO ₃			2.7	
PO ₄ -P	0.004	0.009	0.2	NH ₄ H ₂ PO ₄ 0.74 »
Micro-elements µg/l				
B			10	H ₃ BO ₃ 57.1 µg/l
Co	6.4	11	10	CoCl ₂ 22.0 »
I			50	KICl 65.4 »
Mn		24	50	MnCl ₂ 179.8 »
Mo	0.2	0.2	10	H ₂ MoO ₄ ·H ₂ O 18.8 »
Zn	18.6	30.5	15	ZnSO ₄ ·7H ₂ O 65.9 »
Cu	7.0	15	0	
Ni	5.4	2.5	0	
Fe	110	134	100	FeSO ₄ ·7H ₂ O 500 »

Table II. C-14 fixation in plankton from containers with untreated and with fertilized Fern Lake water. Values in net CPM of C-14 assimilated from $2\frac{1}{2} \mu\text{Ci } ^{14}\text{CO}_2$ per 125 ml of sample. Parallel runs in four hours light-box incubations. c = full proposed concentration of fertilizer in lake water. c-Fe = full proposed concentration of fertilizer less iron in lake water.

Container # and contents	Time after fertilization						
	9/VIII-4 hrs. CPM	10/VIII-1 day CPM	11/VIII-2 days CPM	13/VIII-4 days CPM	16/VIII-7 days CPM	20/VIII-11 days CPM	26/VIII-17 days CPM
No. 1: Lake Water	968	1379	1119	760	987	992	683
		1275		761	1077	937	664
5: Lake Water	1079	1143	1140	529	807	2062 (b)	714
	1151	1312	1304	542	906		694
2: $\frac{1}{4}$ (c-Fe)	858	1273	1491	1528	6927	12804	12031
	806	1223	1397		6007	11611	8992
9: $\frac{1}{4}$ (c-Fe)	853	1423	1716	1297	4678	14269	8992
	927	1419	1725	1297	4064	13682	9692
3: $\frac{1}{2}$ (c-Fe)	798	1124	1109		5831	17840	66650
	760	1094	1205	1221	5831	18165	71411
10: $\frac{1}{2}$ (c-Fe)	784	1106	1426	1276	4256	32241	18851
	688	1090	1323	1142	3673	32241	16376
4: 1 (c-Fe)	603	807	988	1580	4933	31233	52615
	588	808	941	1115	4487	24983	49963
11: 1 (c-Fe)	574	761	808	1352	4791	24376	55539
	591	798	888	1287	4678	25624	55539
6: $\frac{1}{4}$ · c	897	1500	1943	1432	3593	15778	14476
	856	1545	1895	1704	3935	15856	14476
12: $\frac{1}{4}$ · c	840	1349	1772	1424	9157	37020 (a)	13872
	813	1423	1788	1510	5218	31233 (a)	14689
7: $\frac{1}{2}$ · c	762	1270	1646	1655	5033	45437	37020
	832	1351	1692	1818	6832	37020	43461
13: $\frac{1}{2}$ · c	669	1016	1216	1588	3361	29395	23239
	687	1039	1241	1570	4312	31233	22710
8: 1 · c	570	1091	1381	1397	4202	13141	142840
	698	1064	1342	1331	3756	11347	142840
14: 1 · c	573	1349	1024	4098 (a)	4064	27761	111094
	624	1423	1008	1678	1503	23793	99983

(a) $5 \mu\text{Ci}$ added (b) Two samples on one filter

Table III. ^{14}C fixation in dark bottles during four hours incubator experiments. Values are net cpm of ^{14}C fixed from $2\frac{1}{2} \mu\text{Ci } ^{14}\text{CO}_2$ per 125 ml sample.
 c = full proposed concentration of fertilizers.

	Time after start of experiment			
	2 days	4 days	11 days	17 days
Lake Water	94	90	110	103
$\frac{1}{2} \cdot c +$ Lake Water	104	107	200	300
$1 \cdot c +$ Lake Water	113	93	219	269

Table IV. Physical-chemical properties in the experimental containers.

	Total Alk.	t°C	pH	CO_2 mg C/l
Lake water, before exp.	8.20	22.5	7.2	2.26
Lake water, at end of exp.	7.92	23	6.65	2.87
Lake water with $\frac{1}{4} c$ fert. at end of exp.	9.08	23	9.30	2.00
Lake water with $\frac{1}{2} c$ fert. at end of exp.	9.60	23	9.80	2.11
Lake water with $1 c$ fert. at end of exp.	10.20	23	9.70	2.24
Average total CO_2 as mg C/l =				2.30

COMPARISON OF PACIFIC SARDINE AND ATLANTIC MENHADEN FISHERIES

By

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INTRODUCTION

The rise and fall of the North American Pacific coast sardine fishery is well known. Once the most important fishery in the western hemisphere in weight of fish landed, it now produces virtually nothing. The meal and oil industry based on the Pacific sardine (*Sardinops caerulea*) resource no longer exists. The sardine fishery (Fig. 1A) began in 1915, rose fairly steadily to its peak in 1936 (with a dip during the depression), maintained an average annual catch of more than 500 000 tons until 1944, then fell off sharply. Annual production has not exceeded 100 000 tons since 1951, and commercial sardine fishing now is prohibited in California waters. A much smaller fishery for the southern sub-population developed off Baja California in 1951.

The decline of the west coast sardine fishery gave impetus to the much older menhaden (*Brevoortia tyrannus*) fishery (Fig. 1B) along the Atlantic coast of the United States. Fishing for Atlantic menhaden began early in the nineteenth century. From the 1880's until the middle 1930's the annual catch varied around about 200 000 tons. In the late 1930's annual landings began to increase and from 1953 to 1962 inclusive remained above 500 000 tons. The peak year was 1956, with a catch of nearly 800 000 tons. After 1962 the catch began to fall off sharply, reaching a low of less than 250 000 tons in 1967.

The remarkable similarity in history of landings of the two species is illustrated in Fig. 1. If the sardine curve is shifted in time about twenty years the coincidence is startling (Fig. 1C). The following questions arise:

1. Is the Atlantic menhaden fishery doomed to extinction?

Contribution given in honour of Gunnar Rollefson at his 70th birthday.

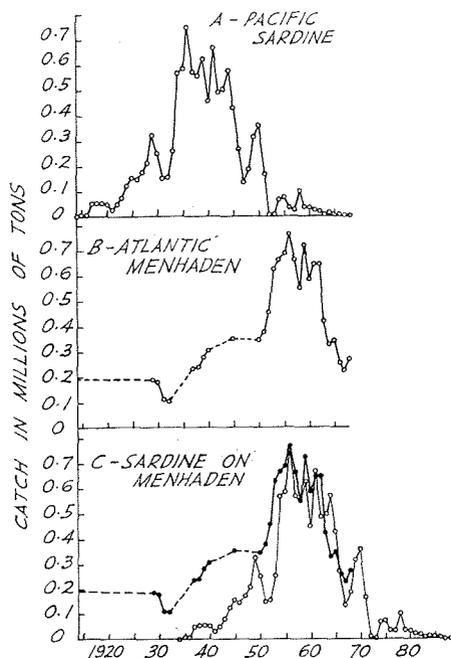


Fig. 1. Historical record of Pacific sardine landings (A), Atlantic menhaden landings (B), and sardine landings shifted twenty years and superimposed on menhaden landings (C). Data from AHLSTROM (1960), HENRY (1968), and Statistical Digests of the Bureau of Commercial Fisheries.

2. Is there anything in the history of the Pacific sardine fishery or in knowledge of the biology of the species that would lead to inferences about the future of the menhaden resource and its fishery?

3. Does the history of the sardine fishery offer any lessons that might help the menhaden industry or other fishing industries anywhere in the world to avoid the fate of the sardine industry?

In this paper these questions are examined only briefly.

COMPARISON OF LIFE HISTORIES

Both species have relatively wide ranges of distribution along coasts that trend generally north and south (Fig. 2). The Pacific sardine once ranged from south-eastern Alaska to the Gulf of California (55° to 23° N. Lat.). The Atlantic menhaden has been taken from Nova Scotia to southern Florida (46° to 23° N. Lat.). It does not pass around the southern tip of Florida into the Gulf of Mexico, but another species, *Brevoortia patronus*, supports the important menhaden fishery in the Gulf.

Within these geographic ranges, samples of the commercial catch of Pacific sardine and Atlantic menhaden usually contain larger and older fish with increasing latitude. Not only do the older fish go farther north, but also apparently the larger fish of each age, for the apparent growth

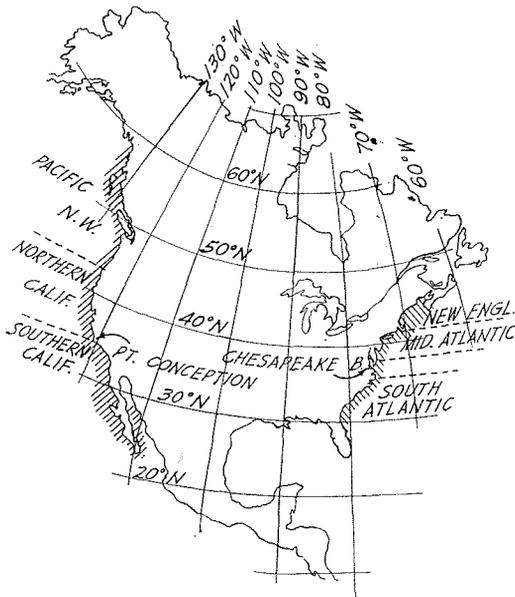


Fig. 2. Geographic distributions of Pacific sardine and Atlantic menhaden along North American coasts.

rate increases from south to north (Fig. 3). Both species are found in northern oceanic waters usually only in summer. Usually, adults are found farther north than young, and young farther north than the pelagic eggs. Adult Pacific sardines and juvenile Atlantic menhaden sometimes spend the winter in northern inlets or tributaries. From these observations it has been inferred that most spawning occurs towards the southern part of the range of each species and that most of the mature fish make an annual northward migration in spring and summer, returning south in late fall and winter, and moving farther northward with increasing size and age. These inferences have been confirmed by tagging. In

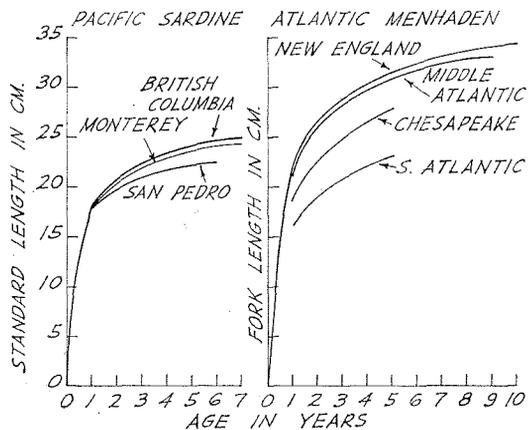


Fig. 3. Apparent growth rates of Pacific sardines and Atlantic menhaden from commercial catches at different latitudes.

common with many clupeoid fishes there is also a tendency for older and larger fish to be farther offshore. Both species are divided into sub-populations, which do not intermingle completely, although their geographic ranges overlap considerably.

Plankton studies have confirmed the inferences about major spawning areas, but Pacific sardine spawning progresses in a wave from south to north, winter to summer, whereas Atlantic menhaden spawning apparently progresses from north to south, summer to winter. The location and intensity of spawning of both species may vary widely from year to year, and survival to the stage of recruitment into the commercial fishery varies widely.

Scientific studies of the Pacific sardine and its fishery have been under way since the early days of the fishery, and the biology and ecology of the species and the response of the stocks to fishing are reasonably well understood. Substantial continuing studies of the Atlantic menhaden and its fishery began little more than a decade ago, and scientific investigations are still not adequate to obtain all the information necessary to understand the population dynamics and ecology of the species and to stabilize the economics of the fishery. For both species funding of scientific investigations was difficult to obtain until substantial declines in the resource and the catch created responsive political climates.

COMPARISON OF THE FISHERIES

Although the Pacific sardine fishery began off California, toward the southern part of the geographic range, and the Atlantic menhaden fishery began to the northward, off New England, the reaction of the two resources to fishing has been similar. As could have been predicted from knowledge of the biology of the species and of the known effects of a developing fishery on fish stocks, fishing reduced the life expectancy. Thus the northern fisheries were affected first (Fig. 4). The peak of the sardine fishery in the Pacific North-west covered the period from 1929 to 1943, and the fishery collapsed before 1950. In northern California the peak was from 1934 to 1944 and the collapse in the early 1950's. In southern California landings were substantial from 1934 to 1950, with a peak in 1950, and fishing continued at a lower level of catch into the early 1960's, after the industry in the north had suspended operations.

The history of menhaden landings has been similar (Fig. 4). In New England the catch reached a peak in 1899, then fell off virtually to nothing in the 1930's and 1940's. There was a resurgence in the 1950's, which lasted until about 1960. The peak of the fishery in the middle Atlantic region covered the period 1953 to 1963, and by 1965 that segment

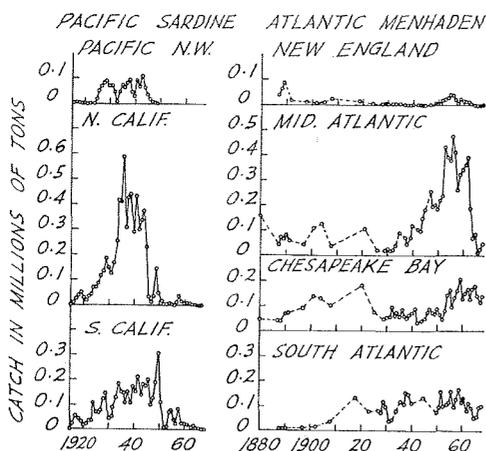
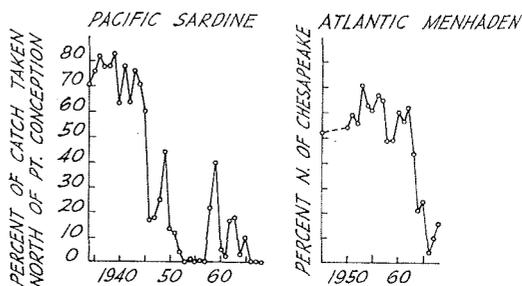


Fig. 4. Historical catch records of Pacific sardine and Atlantic menhaden at different latitudes.

of the industry was virtually dormant. In Chesapeake Bay a high level of catch has been maintained since 1954, with some decline in the last two years. The catch in the Chesapeake has been maintained only at the expense of a substantial increase in fishing effort. In the area south of Chesapeake Bay the catch has fluctuated about the same level since 1936.

The decline and collapse of both fisheries from north to south is demonstrated better by considering the trends in percentage of the total catches taken in the northern parts of the species range. For the Pacific sardine the northern area includes waters north of Point Conception, for the Atlantic menhaden it is the area north of Chesapeake Bay. From the peak of the fishery in the decade beginning about 1934 the percentage of the sardine catch taken to the north fell from about 80 per cent in the late 1930's to zero in the late 1960's (Fig. 5). From the peak of the Atlantic menhaden fishery in the middle 1950's the percentage of the total catch taken north of the Chesapeake fell from over 70 per cent in 1953 to less than 20 per cent after 1965 (Fig. 5). For both fisheries, once the peak was reached the percentage of the catch taken in northern waters was a direct

Fig. 5. Trends in percentage of the total catches of Pacific sardine and Atlantic menhaden taken in northern waters as each fishery declined from its peak.



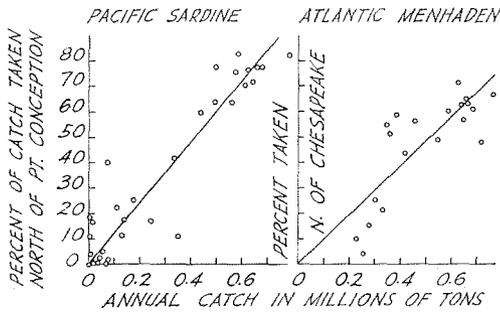


Fig. 6. Relation between total annual catches of Pacific sardine and Atlantic menhaden and percentage of the catch taken in northern waters.

function of abundance as reflected in the total catch (Fig. 6). Such declines do not necessarily connote overfishing, but they do throw the bulk of fishing effort on the younger fish to the south, and increase the risk of overfishing.

ROLES OF OTHER FACTORS DETERMINING ABUNDANCE

The evidence is strong that there has been no reduction in total biomass of pelagic fishes in the California Current System. The drop in sardine abundance has been offset by increases in other species, especially anchovy. McHUGH and AHLSTROM (1951) suggested that fuller utilization of species such as anchovy, saury (*Cololabis saira*), and jack mackerel (*Trachurus symmetricus*) should be encouraged. The possibility exists that similar compensatory changes may be taking place in the environment of the Atlantic menhaden but the research program has not been broad enough to determine if this is so. Several species could be involved in such ecological adjustments, including sea herring (*Clupea harengus*), thread herring (*Opisthonema oglinum*), and jacks (*Caranx crysos*, *Trachurops crumenophthalma*), to name just a few. The catch of sea herring has increased steadily in the last few years, and the fishery (mostly by nations other than the United States) now extends south to Cape Hatteras (about 35° N. Lat.). Whether this southern herring fishery has been made possible by an increase in abundance favored by the menhaden decline is not known. The relationship between menhaden abundance and biomass of other species such as thread herring also is not known. It is important that such ecological interactions be understood.

LESSONS TO BE LEARNED FROM THE SARDINE FISHERY

Many people have contributed to scientific knowledge of the Pacific sardine resource and the effect of fishing on it. Particularly useful references are the work of AHLSTROM (1960, 1966), CLARK and MARR (1955),

MARR (1960, 1963), MURPHY (1966) and RADOVICH (1962). Scientific studies have shown beyond reasonable doubt that the sardine stocks were reduced by a combination of intense fishing and poor spawning success, and that the Pacific northern anchovy (*Engraulis mordax*) invaded the environmental niche vacated by the sardine. It has been estimated that the sardine resource has dropped to 5 per cent or less of its former biomass, and that the standing crop of anchovy has increased at least twenty-fold over the same period.

A fishery based on a single species, highly variable in abundance, is not likely to be a stable fishery. If there is a profitable market for the product, capital investment in boats, fishing gear, and processing plants will grow. The exigencies of natural fluctuations in abundance, and the stimulating effect on survival to recruitment caused by reduction of the total stock, make it highly probable that as the fishery develops towards maturity, two or more strong year classes will follow each other in a relatively short span of time. Encouraged by this unusually high productivity the industry will continue to enlarge its capacity to catch and process the fish. Inevitably the time will come when biological productivity of the species drops from environmental causes. Since in a fully developed fishery the standing stock usually is about half the size of the unexploited population, other species may be given a competitive advantage which may inhibit production of strong year classes in the species being fished. Moreover, the time lag of a year or two in building vessels and plants usually may provide maximum catching and processing capability when the resource is already declining. In the absence of effective fishery regulation disaster is probably almost inevitable. Even with an effective regulatory mechanism, backed by adequate scientific knowledge, management is far from easy. There is no single optimum sustainable yield in a widely fluctuating resource. Only in certain salmon fisheries has a widely flexible scale of annual catch quotas been applied successfully.

When the sardine fishery was at its peak, there was no interest in alternative resources. Each species has different habits and reactions to fishing gear, and the industry had no time to waste in learning how to catch other species when sardines were present. As the resource declined many units in the fleet were preoccupied with searching for the absent schools of sardines, buoyed by the persistent optimism of fishermen that next year would be better. This optimism was strengthened by a brief resurgence of the resource in 1949 and 1950, and by a lesser increase in the middle and late 1950's. The concern of industry is illustrated by its action in imposing a voluntary tax on landings, the funds to be used in support of research. The industry was aware of the existence of a substantial anchovy resource, and in 1953 landed more than 40 000 tons.

But they were unable to develop a viable market for canned anchovies, and opposition to use of anchovies for oil and meal was already strong.

As the sardine stocks declined, the political climate for developing alternate resources for the fish meal and oil industry on the Pacific coast was becoming more difficult. The powerful sportfishermen's organizations in the State of California, convinced that disappearance of the sardine was reducing the availability of forage fishes, successfully sponsored restrictive legislation and regulations. This placed increasing restrictions on the commercial sardine fishery and also made it difficult to develop an anchovy fishery. Commercial fishing for sardines in California waters is now prohibited entirely. Attempts to develop a viable commercial anchovy fishery in the last few years led to a proposal by the scientists for an annual quota of 200 000 tons, with provision for carefully controlled scientific monitoring. This quota was selected because it was about the smallest catch that could be expected to produce a measurable effect on the resource, yet offer no threat of overfishing. A much lower quota of 75 000 tons finally was adopted, but this small quota has never been reached, partly because it has been divided into sub-quotas by areas, partly because the uncertainty of being permitted to continue a commercial anchovy fishery may have discouraged commercial fishermen from acquiring modern, efficient catching equipment, but probably mainly because such a small quota offers little promise of developing a profitable industry. If a fishery for anchovy and other suitable pelagic species had been allowed to develop while the sardine resource was still in good condition there might still be a prosperous fish meal and oil industry on the Pacific coast. It would be unfortunate for American fishermen if fishermen of other nations were to demonstrate successfully that these unutilized resources are abundant and can be taken economically in international waters.

As often happens in fishery investigations, scientific studies were not adequately supported until the sardine resource was already well on its way to obscurity. When the expanded investigations of the California Cooperative Oceanic Fisheries Investigations (CalCOFI) began in 1948 the catch was down to about 25 per cent of its former levels. CalCOFI has sponsored an impressive series of scientific studies, which have advanced fishery science considerably, but this knowledge came too late to be of much value to the sardine industry. The ecological implications of this valuable work should not be ignored in funding, investigating, and managing other fisheries.

PRESENT CONDITION AND FUTURE PROSPECTS FOR
ATLANTIC MENHADEN

The literature on the menhaden fishery is by no means as extensive as that for the sardine. The principal references used were HENRY (1968) and REINTJES (1969).

Although it has not been demonstrated conclusively that the menhaden resource has been overfished, the striking similarity in trend of landings should give cause for concern (Fig. 1). It should be noted especially that the sardine catch improved substantially for a period of two or three years following the poor catch of 1947. This caused most people in industry, and some scientists, to say that the sardine decline was temporary. Actually, no one knew at that time exactly what was happening. The catch fell almost to nothing in 1952 and 1953, and following two brief and much smaller upsurges in 1955 and 1958, the fishery soon collapsed. If the Atlantic menhaden fishery were to follow the same trend, the point of collapse could come as early as 1972, and certainly no later than the early 1980's (Fig. 1C). This cannot be regarded as a valid prediction, but the possibility should not be dismissed lightly.

The menhaden industry was encouraged in 1968 by an increase in the catch in the middle Atlantic and Chesapeake areas. The middle Atlantic catch was almost double the catch in 1967 and the Chesapeake catch increased by more than 20 per cent. There is some evidence that the 1966 year class was larger than any year class since 1963, and this could account for improved catches in 1968, but the 1966 and the 1963 year classes were much smaller than the dominant year class of 1958 and the other large year classes that supported the peak years of the fishery.

The Atlantic menhaden fishery has not declined to quite the low level that finally led to increased scientific attention to the sardine resource some twenty years ago. Indeed, it cannot be predicted with assurance that the Atlantic menhaden fishery will take the same course as the sardine fishery, although there is no scientific basis for optimism. To some it may appear that neither the industry nor fishery managers have drawn any lessons from the history of the sardine fishery. The industry remains optimistic that the situation will improve, and has hailed the improved catches of 1968 as evidence that the decline may have been temporary, especially in the area north of Chesapeake Bay. The three peaks in sardine catches after 1947 were also accompanied by increased catches north of Point Conception (Fig. 4) as would be expected from the migratory habits of the resource. Meanwhile, sport fishermen on the Atlantic coast are becoming increasingly concerned about the menhaden fishery, and pressures for restrictive legislation are increasing in each session of several State legislatures.

MURPHY (1966) estimated that the maximum sustainable yield of Pacific sardines for the period ending in 1946 was about 470 000 tons a year. From 1937 to 1945 the sardine fishery took an average annual harvest of about 570 000 tons, or about 100 000 tons per year over the estimated surplus production. This intense fishery was removing about 79 per cent of the stock of sardines of commercial size each year. Considering the geographic range of the Atlantic menhaden resource as compared with the Pacific sardine, the similarity in life histories, and the remarkably similar patterns of landings during the peak years of the two fisheries, it would have been prudent to assume that the maximum sustainable yield of Atlantic menhaden would not exceed 470 000 tons annually. The average catch of menhaden from 1953 to 1962 inclusive was about 658 000 tons. Thus, if the assumption about maximum sustainable yield of menhaden is tenable, the stock was being overfished by about 40 per cent.

Concentration of the fishery for menhaden or sardine in the southern part of the species range has other disturbing biological and economic implications. This forces the fishery to take increasing proportions of younger fish, many of which have never spawned. A menhaden fishery conducted exclusively north of Chesapeake Bay would take larger and older fish, increasing the odds that substantial numbers would be able to spawn at least once before capture. Moreover, if menhaden are like other clupeid fishes, the average oil yield should be considerably greater in northern waters, but the yield of meal should not be substantially less. Thus, the economic return per unit weight of fish could be greater. It is unlikely that the industry in the south would be willing to restrict its operations in favor of operators in more northern waters, although this might prove to be the simplest way to manage the fishery. The question has not been examined carefully, but it would merit study.

The menhaden industry, with government assistance, has been giving attention to the need for alternate resources, not only along the Atlantic coast, but also in the Gulf of Mexico, where menhaden catches have been dropping since the early 1960's. Thus, some of the lessons have been heeded, but they may have been heeded too late and with too little sense of urgency by industry and scientists alike. For example, no scientific evidence is available to show whether other species in the same geographic areas are reacting in any way to the changed abundance of menhaden. Essentially, history may show that the menhaden industry today is at the critical stage reached by the sardine industry two decades ago. Here is an opportunity for government and industry to build on the experience of the sardine industry, before it is too late, in a joint effort to broaden the resource base of the Atlantic fish meal and oil industry and to take

advantage of the considerable advances in fishery science that have been made since the end of World War II.

It is not necessary to wait until indisputable scientific evidence is available before taking action to manage a fishery. History has shown that such caution usually leads to disaster. The history of the Pacific sardine fishery, and present knowledge of the ecology of the resource, suggest that the industry might have been prospering today if the knowledge necessary for appropriate action had been available, and such action had been taken. The menhaden industry has taken some tentative voluntary steps in this direction. It is to be hoped that industry will recognize the need to continue seeking a rational fishing policy.

SUMMARY

The Pacific sardine resource, which once supported an important American fishery, declined abruptly in the late 1940's and early 1950's, and the fishery is now defunct. Scientific research during the peak of the sardine fishery and subsequent to the decline has demonstrated fairly clearly that the cause was overfishing, fluctuations in abundance from natural causes, and invasion of the vacated niche by the Pacific northern anchovy. It has been concluded that it may not be possible to harvest a sustainable yield from a highly fluctuating resource like the Pacific sardine, for the reduced population will yield available energy to other ecologically similar species. Thus, the concept of a broad resource base made up of several species may be essential to the economic viability of most fishing industries. Perhaps the best documented example of the effect of selective fishing on the ecology of a large body of water is the history of the fishery resources of Lake Michigan (SMITH 1968).

About twenty years later the Atlantic menhaden fishery went through a remarkably similar cycle. The northern fishery is virtually defunct, but the southern fishery is still in operation. The total annual catch now is a little more than one-third as large as the average catch from 1953 to 1962. Although it has not been demonstrated that the Atlantic menhaden resource is overfished, it might be prudent to borrow from the experience of the sardine industry and develop management plans accordingly. An important consideration would be to determine as soon as possible which species in the environment of the menhaden are utilizing the energy released by the decline of the resource. It is unlikely that fishery management in the ocean will ever be generally successful if action is postponed until absolute proof of overfishing is available.

ACKNOWLEDGMENTS

My interest in herring-like fishes and their variations in abundance was stimulated very early in my professional life by the work of Dr. GUNNAR ROLLEFSEN. I am honored to dedicate this paper to him.

It was not possible to make a thorough literature review in preparing this article. I believe I have consulted most of the major recent comprehensive papers on pertinent aspects of the two fisheries. If I have missed important papers or have not given appropriate emphasis to the recent literature it was not intentional. I apologize to authors whom I may unwittingly have slighted.

I am indebted to JOHN C. MARR, KENNETH A. HENRY, and MILNER B. SCHAEFER for reviewing the manuscript.

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THE FLUCTUATION OF YEAR-CLASSES AND THE REGULATION OF FISHERIES

By

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INTRODUCTION

Fishermen contrast the considerable regularity in the positions of capture of fish with the variation in quantities caught at those positions from year to year. The regularity is that of the migratory circuit from spawning ground to feeding ground and back again (HARDEN JONES 1968); for example, spawning cod have been caught in the Vestfjord for centuries (ROLLEFSEN 1956) and, since the thirties, fish of the same stock have been caught on the Svalbard Shelf west of Bear Island in early June. Similarly, the East Anglian herring have been caught in October and November off Lowestoft and Yarmouth for centuries as they migrated southward to spawn. But both stocks, cod and herring, vary from year to year due to differences in the recruiting year-classes. These differences can be grouped in three categories:

1. Annual changes due to density independent effects.
2. Density dependent changes following changes in stock.
3. Long term changes associated with changes in climate.

THE THREE CATEGORIES OF VARIANCE IN RECRUITMENT

Fig. 1 shows how the three categories of variation may be represented on a stock and recruitment curve. The curve of recruitment cuts the bisector at the point at which stock replaces itself in recruitment; in effect, it is the level of stock about which it stabilizes itself under natural conditions without fishing. Variance in recruitment about the stock and recruitment curve is represented on the ordinate (a) below the replace-

Contribution given in honour of Gunnar Rollefsen at his 70th birthday.

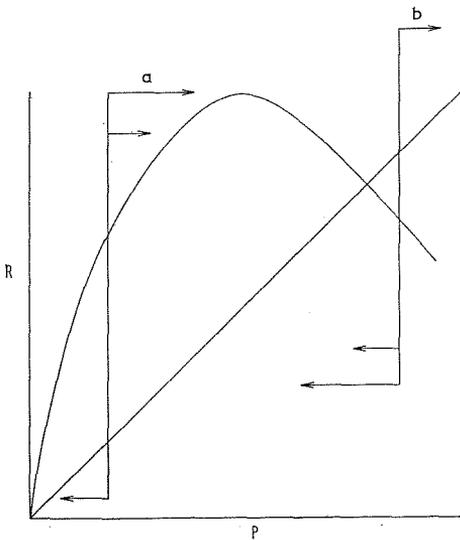


Fig. 1. The three sources of variance in recruitment shown on a stock and recruitment curve; see text for discussion.

ment point in stock and on the ordinate (b) above it in stock. Both represent the first category of fluctuation, variance in recruitment from year to year due to density independent causes. The second category is represented by the stock and recruitment curve itself; as stock increases, the recruitment per unit stock decreases and this is the effect of density dependence. The third category of variation occurs if recruitment falls below stock when stock is very low and then downward instability in stock is generated, which is represented in Fig. 1 by the variance of recruitment on the ordinate (a) falling below the bisector; an upward instability—at high stock—can be generated in an analogous way by the variance of recruitment on the ordinate (b) appearing above the bisector. If such instabilities occur randomly, subsequent recruitments must return the stock in the direction of stability. If, however, they occur in sequence, the stock collapses or expands, which are the conditions under which climatic change can affect the fluctuations.

PROCESSES DURING THE PERIOD OF LARVAL DRIFT

To survive, the larvae need food, not only when the yolk-sac is exhausted, but all through their lives during the period of larval drift. Although algae are often found in the guts of larvae at the first stages of active feeding, the baby fish subsist in the main on copepod nauplii (LEBOUR 1918a, b and 1919) and their analogues. In temperate seas, the production of nauplii is linked to the feeding of adult copepods in the early stages of the production cycle (MARSHALL and ORR 1952). So food

is available to fish larvae at a fairly early stage in the cycle and this accounts for the link shown below between the herring populations and the form of production cycle.

However, the production cycle is variable in timing, in amplitude and in spread (COLEBROOK 1965) and if fish in temperate seas spawn at relatively fixed seasons (CUSHING 1969a) then the food available to the larvae must vary as the cycle varies. The variability of the production cycle tends to increase with depth of water as it depends much upon the vagaries of the depth of mixing, largely governed by wind strength and direction. This accounts for the greater variability in recruitment observed in stocks living over deep water in temperate seas. In the relation of spawning and the production cycle, time is critical to the survival of the larval fish, and the observed variance implies that the major processes determining recruitment may lie between spawning and nursery ground.

The separation of the three categories of variance in recruitment is perhaps a little artificial as all three may be but facets of a single set of processes. In temperate seas, the variance of recruitment to herring stocks tends to increase with depth (CUSHING 1967) and it has been shown that the three groups of autumn-, winter- and spring spawning herring stocks are associated with three forms of production cycle in the north-east Atlantic (CUSHING 1967). The increased variance in recruitment with depth can be associated with increased instability in the timing of the production cycle providing food for the larval fish. The two results lead to the conclusion that the processes determining the major proportion of larval mortality must lie between spawning ground and nursery ground because the production cycles on the nursery ground must differ from those in the open sea, if only because of differences in depth. The argument depends on the biology of the herring; it can be extended to other species when it is recalled that fish of many species spawn at about the same time. For example, in the Southern Bight of the North Sea, when herring spawn there so do cod, whiting, dabs, sandeels and plaice.

Of the three sources of loss to which the larvae are subject, predation, diffusion and advection, it is likely that predation is by far the most important. The loss rate of plaice larvae in the Southern Bight of the North Sea is 80 per cent per month as an apparent mortality (HARDING, in preparation), which is considerably more than might be expected from the physical causes. It is assumed that a larva, which has moved out of the larval drift and fails to reach the usual nursery ground, is lost to the stock, i.e. it fails to return to the native spawning ground as an adult. The real question is how can predation in the larval drift effect the three categories of fluctuations which are illustrated in Fig. 1.

The fish larvae feed and as they feed they grow. As they grow they

swim more quickly and reduce the chance of predation. If they fail to feed adequately they swim more slowly and the chance of predation is increased. So with constant predation, variations in mortality rate can be generated merely by differences in the availability of food. Then, variations in stock change the food availability and so the mortality rate generated by the predators is also density dependent. The assumption of constant predation may appear to be unreal, especially if a particular predator is in view. The fish moves through three trophic levels as it grows and within any one level it is likely to be subject to a succession of predators, each larger than the last, but each less numerous. The differences between densities of each predator may tend to average out and then the low variability of recruitment as proportion of total mortality between egg and adult is not surprising. It is possible, in an evolutionary sense, that the fecundity of a fish stock is a function of the mortality generated by the network of predators along the larval drift and on the nursery ground.

VARIANCE OF RECRUITMENT ABOUT THE STOCK AND RECRUITMENT CURVE

Although it is unlikely that year-classes are completely determined during the period of larval drift, because by then only a small fraction of life to recruitment has elapsed, much of the variance of recruitment might be attributed to variance in food availability, itself due to variation in the timing of the production cycle. Many attempts have been made to correlate recruitment with environmental factors, but usually they have failed. An important exception is the correlation of catches of cod at Lofoten with the number of rings on pine trees in northern Norway for a long time period (ORTTESTAD 1942). The reason for success is that a well-known result of climatic change was correlated with the catches. A particular cause was not specified, like the strength of a wind from a given direction over a very broad area, but a general result was indicated. The variation in the production cycle is governed by the rate of change of the algal reproductive rate, which in its turn is controlled by the rate of change of the ratio D_c/D_m , where D_c is the compensation depth and D_m is the depth of mixing (CUSHING 1962). Very roughly, this ratio is affected by changes in sunlight and by changes in wind strength and direction. It follows that these climatic parameters need be sampled only on the track of the larval drift from spawning ground to nursery ground.

Correlations between recruitment and winds were often successful for a period of years, after which they failed catastrophically. Any examination of trends in wind strength and direction, at one position at the same

season for a long time period, shows that there are shifts in strength and direction of wind all the time (DIETRICH 1954). Hence to take wind strength variations from a single direction is to ignore perhaps the most important source of variation. In temperate seas, the track of larval drift is usually not far from a coastline, where a small shift in direction can have considerable effects.

A considerable source of variation can lie in the stock and recruitment curve itself. That for the Arctic cod is dome-shaped as has been shown by GARROD (1966). At middle levels of stock, average recruitment is considerably higher than at low levels and at high levels. In contrast, the curve for the East Anglian herring is not far from a linear one, with only a slight dome before it passes through the replacement point. Differences in recruitment at different levels of stock are considerable. So if we need to know the true relationship between recruitment and environmental factors, recruitment should be measured as deviation from the stock and recruitment curve. If it is believed that such a curve should be fitted from the data on recruitment and data on stock only, then the argument is circular. The circle can be broken if it is assumed that there is a curve characteristic of any fish species and that differences, for example between that for the Arctic cod and that for the East Anglian herring, are real and not merely statistical fantasies.

AN INDEX OF DENSITY DEPENDENCE AND ITS CONSEQUENCES

CUSHING (1969b) has examined the possible stock and recruitment curves for thirty-one stocks. No differences between constants were found using the RICKER equation (1954, 1958) or the BEVERTON and HOLT (1957) equation. An index of density dependence, b , was calculated from the equation $R = KP^b$ (where R is recruitment, P is stock, and K is a constant), used at mid to high stock levels. It was found that $b = a \bar{f}^{1/3}$, where \bar{f} is the average fecundity of the stock, over a range in b from $b = 0.8$ to $b = -1.95$. In effect, this means that there is a series of curves ranging from the near linear curve of the East Anglian herring to the pronounced dome of the Arctic cod, each of which is specified by the fecundity of the fish. Fecundity is a function of weight, and density dependent growth decreases with size in fish (RAITT 1939, ILES 1967, SOUTHWARD 1967) and so it is effectively independent of the index, i.e. density dependence must be achieved in density dependent mortality. Thus, we return to the point that in an evolutionary sense, fecundity is a function of the network of predators along the track of the larval drift. Because there is a fixed

quantity of eggs available, fecundity may be regarded as a homeostatic mechanism which creates stability in a variable environment.

Larval density is a function of the density of spawning females and of fecundity. With fish like the herring which do not grow much during their mature lives, fecundity must play less part in determining larval density than the density of spawning females. With fish like the cod which grow a great deal as mature animals, fecundity may not stabilize the population: a stock at the replacement point which suffers a recruitment failure must suffer an increase in average weight and fecundity, which by itself must generate instability. At the same time, after a recruitment failure, the density of spawning females must decline which will generate greater recruitment per unit stock which is a stabilizing change. So it is likely that stock differences affect larval density merely through differences in the densities of spawning females. Then fecundity controls differences in the degree of density dependence between stocks as might be expected from its supposed homeostatic character of evolutionary origin.

A DIFFERENCE BETWEEN HERRING-LIKE FISHES AND COD-LIKE FISHES

On Fig. 1 variance in recruitment due to differences in stock density is expressed in the stock and recruitment curve itself. In larval density, differences in stock affect the availability of food, more being available to the larvae at low stock and less at high; and from the preceding argument such differences within a stock are generated by differences in the densities of the spawning females rather than fecundity. The question of how much of the variance of recruitment is due to density dependent causes and how much to density independent causes cannot readily be answered in general terms. However, D. J. GARROD has analysed the variances in the recruitment of spawners to the Arctic cod stock and has separated those due to environmental changes and those due to stock changes. Because the stock and recruitment curve for the Arctic cod is markedly dome-shaped, it is likely that for other fish stocks the ratio of density independent variance to density dependent variance may be greater. Indeed, it is possible that the ratio is correlated with the index of density dependence, or with fecundity. As further consequence, it might be concluded that the herring-like and salmon-like fishes were more vulnerable to environmental change than the cod-like fishes. Another way of saying the same thing is that the cod-like fishes have a greater capacity for stabilizing their populations than have the herring-like fishes. The stock of the Arctic cod has varied in quantity to some extent during the long centuries of its recorded existence (ROLLEFSEN 1956). In contrast, the Norwegian herring

fishery, which is worked in a somewhat less adverse environment than the Arctic cod, has suffered a series of temporary extinctions over about the same historical period (DEVOLD 1963).

The dramatic changes in pelagic fish stocks are exemplified well by the Norwegian herring periods which have been correlated with ice cover periods north of Iceland by BEVERTON and LEE (1965). There are periods in climatic change lasting about fifty to a hundred years of somewhat irregular occurrence. A recent change in climate has been expressed as a warming of the north-east Atlantic since the late twenties which may have ended in the early sixties of the present century (BJERKNES 1964). A decline in the average strength of the westerlies in the North Atlantic left more residual heat in the water. Towards the European coasts the decline of the westerlies allowed southerly winds to predominate (DICKSON, in preparation). Over a long time period the wind direction slowly shifts and the long-term consequence may be that the production cycle shifts away in season from the time of spawning of a fish stock. Equally, a production cycle may shift towards the time of spawning of a fish stock. Fig. 1 shows how a marginal instability in sequence (shown where the variance of recruitment falls below stock at low stock and where it rises above stock at high stock) can lead to the marked reduction or the full expansion of a stock. Such a capacity to respond to environmental change by changes in numbers is the means by which the herring-like fishes survive under adverse conditions. The lack of homeostasis is a primitive character and perhaps the evolutionary step from the primitive herring to the developed cod was the use of growth and hence fecundity to achieve a more powerful mechanism by which the population could be stabilized.

In Fig. 1 are shown the three sources of variation which might affect recruitment, the year to year environmental changes, the larger scale climatic changes and the differences due to stock density. It is possible that all three are mediated by the same processes in food availability during the period of larval drift. A perennial problem facing fisheries biologists is how to distinguish the effects of environmental change on recruitment from those induced by the fishery. The first distinction to be made is between the year to year density independent effects and those associated with large-scale climatic change. The year to year effects, although contributing perhaps a high variance, are considered to be randomly distributed about the stock and recruitment curve and therefore are of no further interest. If the stock and recruitment curve for a given fish species is established independently of the values of recruitment and parent stock then we may consider the curve as given and recruitment as distributed about that curve.

An assumption here is that within an environmental period, recruitment fluctuates randomly and that when the environment changes, recruitment changes markedly and sharply. This concept follows from the supposed homeostatic nature of fecundity, i.e. that the fixed fecundity insulates the stock from minor environmental changes, but allows it to adapt in a favourable or unfavourable manner to major changes.

CONSEQUENCES IN THE REGULATION OF FISHERIES

The more important problem is whether a large scale climatic change has effects on recruitment which can be distinguished from those following a reduction of stock due to fishing. Consider a virgin stock oscillating in time about its replacement point. A failure of recruitment, complete as that in the Plymouth herring (CUSHING 1961), would yield a series of points along the abscissa, decreasing in stock as stock fell in consequence. In general, the recruitment/unit stock should decline more quickly with stock than that expected from the stock and recruitment curve. In a stock with a dome-shaped stock and recruitment curve the distinction could perhaps still be made as long as the stock were not too heavily exploited. For herring-like fishes, in which the curve of stock and recruitment is only lightly convex, there would be a real problem of distinction. One would depend upon the difference between the average falling recruitment and that expected about the stock and recruitment curve. If it becomes possible to specify the variance to a stock and recruitment curve, a failing recruitment due to abnormal environmental causes might be distinguishable by ordinary statistical procedures. There is, however, a strong possibility that failure would take place quickly and so there would not be enough information on which to base a judgement. There is, however, a more practical way of achieving the same end. On any stock and recruitment curve there is a point in stock at which recruitment is maximal—RICKER's (1958) point of maximum surplus reproduction at stock P_s with a corresponding exploitation rate E_s . At stock levels below this point, if fishing effort is constant, yield will be reduced and if fishing effort increases at such levels, there is considerable danger that the fishery will be extinguished, if not the stock. There is a limiting exploitation rate, E_1 ($= 1 - e^{-a}$ where $a = P_r/P_m$, P_r is the replacement level of stock and P_m is the level of stock at which maximum recruitment occurs) beyond which the stock is extinguished. If the stock in numbers collapses when the exploitation rate is set at E_s , it must do so through a failure of recruitment due to environmental change. So any stock can be exploited down to the stock level, P_s , at which maximum recruitment is obtainable. Then,

if environmental collapse occurs, the maximum yield has been obtained until the point of collapse.

From a regulatory point of view this means that environmental changes in recruitment can be to some extent ignored. The value P_s can be established from the character of the stock and recruitment curve, i.e. to some extent from the fecundity of the fish. The effect of growth can be taken up in a self-regulatory yield curve of the form proposed but not fully developed by BEVERTON and HOLT (1957). The maximum of such yield curves may tend to lie at stock levels of $P < P_s$, because the exploitation rate E_s may tend to be too high to exploit the benefits of growth to the full. The effect of variance in recruitment about the curve is an important one. In the extreme case of a one-year-class stock under heavy fishing pressure, the variance of stock is essentially the variance of recruitment and so collapse of the fishery could occur near the level of P_s ; obviously the variance of the stock is that of the recruitment divided by the number of year-classes.

It might be suggested that if the stock were fished to the maximum sustainable yield on a yield-per-recruit basis, the stock is not vulnerable to recruitment failure through heavy fishing. Fig. 2 (after GULLAND 1967) shows a yield per recruit curve and a yield curve calculated in terms of a stock and recruitment curve. The obvious point is made that the new maximum is at a lower level of stock than that on the yield per recruit curve. But, where yield decreases from the maximum at increasing levels of fishing mortality, and $P < P_s$, the variance of recruitment might generate sufficient variability in stock to endanger it. The danger is greater for the herring-like fishes with a slightly convex stock and recruitment curve than for the cod-like fishes with a curve which is markedly dome-shaped. Indeed the limiting rate of exploitation for herring may

occur at levels of fishing mortality hitherto considered as comparatively low.

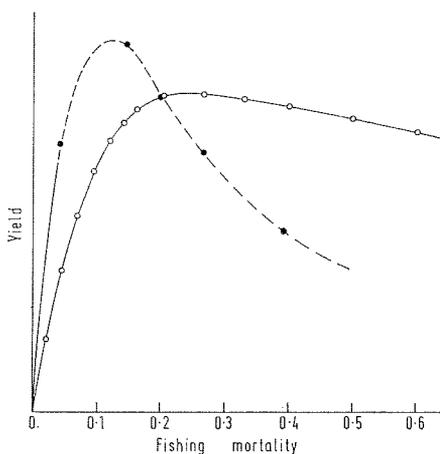


Fig. 2. A yield-per-recruit curve for plaice (full line) and with a stock and recruitment curve (broken line) incorporated (After GULLAND 1967).

The failure of the East Anglian herring stock was one in which $E < E_s$ for a long period during the fifties (CUSHING and BRIDGER 1966) and so the ascription of failure is to fishing. An interesting point is that the fishery took a long time, about a decade, to finally vanish. This was because the variance in recruitment (and hence stock, because during its last decade, it was a one-year-class fishery) was rather low, and because the stock and recruitment curve is only slightly convex. The Arctic cod stock is in danger at the present time, because recruitment has been reduced under pressure of fishing. If we were given the chance to solve the problems of these ancient fisheries again, we should recommend that the stocks be exploited at the best rate of exploitation for the recruitment (either at E_s in numbers, or at the maximum of a self-regulatory yield curve). Then if collapse occurred subsequently through an environmental effect on recruitment, the best yield to that point had been taken. Thus, from the point of view of regulation the environmental factors need not concern us unduly, which is not to say that they should not be predicted.

SUMMARY

There are three sources of variation of recruitment; first that due to random fluctuations alone, secondly that, due to variations in stock and thirdly variations which are extreme at low and high levels of stock and if these occur sequentially can cause catastrophic declines or sharp increases in stock density. From a study of stock/recruitment curves of a number of fish species, it appears that the curve for herring-like fishes differs markedly from those, for example, of cod-like fishes or in more general terms that the shape of the stock/recruitment curve is really a function of its fecundity. That for the herring-like fishes is a near linear curve whereas that for the cod-like fishes is markedly dome-shaped. It follows that the herring-like fishes are very vulnerable to long-term climatic changes and that the cod-like fishes are able to stabilize their populations through long-term climatic changes merely because the increased recruitment when stock is slightly reduced is very much greater than that for the herring-like fishes. If stocks of fish are to be managed then the stock/recruitment relationship has to be taken into account; a form of self regenerating yield curve combining stock/recruitment and yield-per-recruit was in fact put forward by BEVERTON and HOLT. A development of such a curve is needed and one of the uses of such a curve would be that management need not take too much notice of environmental change, because if it occurred the stock would have been exploited at its best rate before any environmental collapse took place.

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