Stock Discrimination in Marine Fishes*

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Abstract

Various methods of stock discrimination in marine fishes are reviewed, especially tagging and migration studies, meristics, parasites, serology, and biochemical-genetic differences from electrophoresis, with particular attention to Atlantic cod, *Gadus morhua*, of the Northwest Atlantic. The advantages and disadvantages of these methods for stock discrimination are noted, together with principles regarding the use of these and other methods for delineating natural fish populations. The conditions leading to stock formation, especially of large stocks, are discussed and an illustration given of the uses of stock concepts for management and their inherent dangers.

Introduction

When I was invited to participate in the Special Session on Stock Discrimination in Marine Fishes, I rashly accepted, although, apart from a contribution in 1975 (Templeman, 1976) on consideration of Flemish Cap as a region for research on year-class recruitment of cod and redfish, I have not attended a meeting of ICNAF or NAFO since 1971. However, my involvement with ICNAF goes back to its beginning in February 1949 when I signed, on behalf of Newfoundland, the original ICNAF Convention in Washington, D. C. I was a member of the Standing Committee on Research and Statistics that established the statistical divisions of the ICNAF Convention Area, I took part in the gradual unfolding of research knowledge on fish biology and stock discrimination in the area, and I collaborated with John Gulland in 1965 (Templeman and Gulland, 1965) in recommending conservation actions which formed the basis for control of catches by ICNAF during 1972-79 and subsequently by NAFO.

It is inevitable that I shall lean heavily on personal knowledge of the cod stocks of the Northwest Atlantic and, since this is an overview paper, I shall introduce some of the subjects and ideas to be presented in more detail by others. Only a small part of the great volume of literature on stocks of marine fishes can be mentioned, with emphasis on cod of the Northwest Atlantic as examples to illustrate and provide commentary on the major methods used to discriminate between fish stocks.

Stock Definition

There have been many definitions of a stock (variously called population unit, management unit, or unit stock), most of them not differing greatly. Templeman (1979) gave the following definitions: a population is a group of fish occupying an area at a particular time; a stock is a recognizable unit which has certain areaoccupying and migratory patterns but whose spawning area (or spawning season in that area) is separate from those of other stocks; a stock complex is a recognizable group of adjacent stocks which at periods other than spawning intermingle or overlap greatly and are different in migratory behavior from adjacent stocks or stock complexes. The primary location base of a stock is its spawning area, where mature spawning individuals are separated from other stocks of mature fish of the same species spawning at the same time.

Marr (1957) defined a population unit as a fraction of a population that is itself self-sustaining. A unit stock was defined by Parrish (1964) as a relatively homogeneous and self-contained population, whose losses by emigration and accessions by immigration, if any, are negligible in relation to the rates of growth and mortality. Ideally, according to Cushing (1973), the stock should be isolated, it should suffer neither loss by emigration or gain by immigration (the loss to emigration can be disregarded if it is not too large), and mating within the stock should be randomly distributed.

Cross and Payne (1978), from a biochemicalgenetic viewpoint, defined a fish stock as a panmictic group of individuals that share a common gene pool and are more or less isolated during the reproductive period from all other conspecific populations. Such stocks may be distinguished by investigating the geographic distributions of allelomorphic genes over the species ranges. However, according to Parrish (1964), the characters used for differentiation between management units need not necessarily be genetypic and

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unaffected by environmental influences, and some of the management units may not even have diverged sufficiently to produce differences in the genotype.

Principal Methods of Stock Discrimination

Tagging and migration

The method most generally used for stock discrimination has been tagging and migration studies, as illustrated for the Arcto-Norwegian cod stock by Trout (1957), for the Icelandic cod by Tåning (1937), for cod stocks of Newfoundland and adjacent areas by Thompson (1943), Templeman and Fleming (1962), Postolaky (1966) and Templeman (1974, 1979), for cod off the Canadian Maritimes by McKenzie (1956), for the Gulf of St. Lawrence cod stocks by Martin and Jean (1964), and for the cod stocks off northeastern United States by Wise (1958, 1963).

Meristic characters

After Heincke's (1898) attempt to use meristic characters to distinguish between various races of herring in the Northeast Atlantic, vertebral and fin-ray counts, but also gillraker and scale counts, have been used as aids in distinguishing fish stocks. Schmidt (1930) used vertebral and dorsal fin-ray averages to distinguish cod from various parts of the North Atlantic. Since that time, vertebral counts were found useful in distinguishing cod stocks at West Greenland (Hansen, 1949; Templeman, 1962). For the Newfoundland area, Templeman (1981) found sufficient differences in vertebral averages and in high and low vertebral numbers to distinguish cod of West Greenland from those of Labrador, and cod of the Labrador-East Newfoundland stock from the northern Gulf of St. Lawrence and southern Grand Bank stocks and from the Avalon stock complex. McKenzie and Smith (1955) found differences in vertebral averages of cod off the Canadian Maritimes, and McKenzie (1940) reported lower vertebral numbers in autumn-spring cod off Halifax and vicinity than in spring spawners.

Parasites as indicators of fish stocks

Parasites may be useful as biological tags when the source and site of the infection are known and the parasite has a sufficiently long life, and especially when infection by the parasite occurs on a spawning ground in the sea or in freshwater. The latter was illustrated by Margolis (1963) for young sockeye salmon. Of more than 50 species of mainly metazoan parasites found to occur in sockeye salmon, only two, the cestode *Triaenophorus crassus* whose infection of young sockeye occurred in western Alaskan rivers and a nematode, *Dacnitus truttae*, whose infection of young sockeye occurred in some Asian rivers, proved to be subsequently useful for separating these stocks of sockeye salmon in the sea.

In the Newfoundland area, from studies on the infection of cod by the nematode Phocanema (Porrocaecum) decipiens (Templeman et al., 1957) and by the copepod Lernaeocera branchialis (Templeman et al., 1976), parasite incidence was found to be indicative of the extent and the degree of inshore-offshore migration of cod and to be useful in delineating cod on Flemish Cap as a separate offshore stock. Khan et al. (1980) reported that the infection of eastern Newfoundland cod by the protozoan Trypanosoma murmanensis, which is transmitted by the cold-water leech Johanssonia arctica, was of considerable use in discriminating broadly between cold-water and warmerwater cod stocks. However, because the areas of infection were not precisely known, there were difficulties in interpreting the data for areas where intermingling occurs such as off southeastern Newfoundland.

Serological and biochemical methods

It can often be demonstrated from serological data and biochemical-genetic studies of various proteins that allele patterns are consistent with simple Mendelian ratios (e.g. two alleles A and B should be present in the ratios AA:2AB:BB), as postulated by the Hardy-Weinberg law (sometimes called the Castle-Hardy-Weinberg law) (Castle, 1903; Hardy, 1908; Weinberg, 1908). Agreement with the Hardy-Weinberg law indicates a separate stock, whereas significant disagreement (i.e. an excess of homozygotes) indicates a mixture of stocks. The regions of relative stock purity and of intermingling can be located if there is enough difference in the proportions of the two or more alleles in the adjacent stocks. Differences between populations or stocks can be tested for significance by comparing the postulated gene frequencies with those observed in samples of the population.

Among many studies of blood groups in fishes, those of Møller (1966a, 1967, 1968) on cod in the Northeast Atlantic may be considered typical of work in this field. He found that data for Arcto-Norwegian and coastal cod stocks off Norway, distinguished by otolith type, showed differences in two blood groups, the ranges being well separated for one of the groups.

The most useful and most extensively used protein systems examined by electrophoresis for separating cod populations have been haemoglobin polymorphism and blood serum transferrins. There are three main genotypic patterns of haemoglobin polymorphism from a pair of different allelic genes. These patterns have been very useful in showing differences in cod populations and stocks of the northeastern and north-central Atlantic (Frydenberg *et al.*, 1965; Sick, 1965a, 1965b; Jamieson, 1968) but not so useful in the North American area where the differences were much smaller (Jamieson, 1975; Sick, 1965b; Odense *et al.*, MS 1966). Blood serum transferrins have been found useful for separating cod populations in the major regions of the North Atlantic (Møller, 1966a, 1966b, 1968; Jamieson, 1968, 1975; Cross and Payne, 1978; Jamieson and Turner, 1979). Transferrins offer much genetic polymorphism from a series of nine codominant alleles at the genetic locus (Jamieson and Jónsson, 1971), some of these being rare mutations. In Jamieson's (1975) study of 11 populations of North American cod, there were six transferrin (T_f) alleles, giving the possibility of 21 genotypes (6 homozygotes and 15 heterozygotes) of which 20 were noted. Cross and Payne (1978) also interpreted their transferrin polymorphism studies on Northwest Atlantic cod in terms of six alleles segregating at a single locus.

Among other proteins investigated for polymorphism in the North Atlantic cod were: general serum proteins (Ullrich, 1967, 1968), enzymes such as esterase (Nyman, 1965; Jamieson, 1975), lactate dehydrogenase (Odense *et al.*, MS 1966, 1969; Jamieson, 1975), and phosphoglucose isomerase (Dando, 1974; Cross and Payne, 1978). These studies provided useful results for separating some cod populations. Serological and biochemical studies of fish populations were reviewed by DeLigny (1969).

Additional methods of stock discrimination

Among other methods that have been used in attempts to discriminate between fish populations and stocks and a few examples of their use are: differences in growth and sexual maturity of cod (Fleming, 1960); differences in spawning period, especially useful for herring (Johansen, 1924; Cushing, 1967; Hodder and Parsons, 1971; Parsons, 1972) but also to some degree for cod (McKenzie, 1940; Templeman, 1979); differences in color of cod (Dannevig, 1953; Love, 1970, 1974); evidence from otolith structure, used for differentiating Arcto-Norwegian and coastal cod off Norway (Rollefsen, 1933; Trout, 1958); differences in weight and size of otoliths for haddock (Templeman and Squires, 1956) and for cod (Rojo, 1977); differences in scale circuli for cod (Thompson, 1943) and for salmon (Lear and Sandeman, 1979); discriminant function analysis of meristic or morphometric characters or both for pink salmon (Amos et al., 1963), for Atlantic herring (Parsons, 1972) and for capelin (Sharp et al., 1978); and correlation or lack of correlation among recruiting year-classes of different stocks (Cushing, 1973). There are numerous references to the above methods, only a few of which are noted for illustration.

Discussion and Conclusions

A marine fish stock is a recognizable population unit for management purposes, with its own spawning area or spawning time or segregation for spawning and with patterns of egg and larval drift and migration made possible by a water current system. It may be genetically different from an adjacent stock if the barriers to migration of adults and drift of larvae and the lack of intermingling at spawning time are great enough. The degree of genetic difference is an indication of the length of the period of stock separation. The following discussion refers specifically to cod stocks of the Northwest Atlantic.

Comparative results from different techniques

Tagging and migration studies form the primary attack on stock discrimination. Their success depends on an adequate level of fishing effort throughout the area being investigated to provide the opportunities for recapture and on an adequate level of tag returns and recapture information. Tagging should be carried out during the spawning season on different parts of the spawning grounds of adjacent stocks and during the feeding season in their nursery and feeding areas. Also, tagging should be undertaken in overwintering areas when these are different from the spawning areas.

Meristic differences may be present and useful when spawning times and temperatures differ sufficiently to produce them. In such cases, also, the extreme numbers in a frequency can be used as tags, being absent or very scarce in one stock and the reverse in an adjacent stock. Furthermore, in an area such as Flemish Cap where there is little variation in temperature during egg development, the variances associated with cod meristic frequencies are usually smaller than those for adjacent stocks where spawning occurs and eggs develop under more variable temperature conditions. Genetic factors may also influence the production of meristic differences (Hempel and Blaxter, 1961).

Parasites are useful as indicators of fish movements when the parasite lives long enough and the source of infection is known. Their importance for stock discrimination occurs in the rare cases in the sea where the main source of infection is on the spawning ground of one stock but not, or in much lesser degree, on the spawning grounds of adjacent stocks.

The biochemical-genetic studies of cod populations in the western Atlantic thus far have shown great genetic distinctions between major areas, such as between West Greenland and Labrador, the areas north and south of the Laurentian Channel, and especially between Flemish Cap and the adjacent Grand Bank. In each case, the bank areas are separated by deepwater channels and current patterns restrict the movement of eggs and larvae from one to the other. In the case of the West Greenland and Labrador areas, distance is an important restriction. That the cod populations of these areas were essentially separate was already known from migration and meristic and sometimes parasite studies before biochemical-genetic studies were undertaken, but the latter are useful to indicate how long the populations have been essentially separate. Apart from the above, although differences between samples may be readily found, the biochemical-genetic studies have not been extensive enough and have depended too much on chance sampling to offer much assistance in separating cod stocks of the western North Atlantic. As for meristic and parasite studies, there can be difficulties in interpreting data from nursery and feeding areas, and biochemicalgenetic studies may indicate significant differences between samples of cod from the spawning area and from the feeding or overwintering area of the same stock. The primary reason for such differences is that the feeding and overwintering areas contain a mixture of stocks.

General principles in using stock discrimination methods

Stock discrimination studies should be aimed at mature fish on the spawning ground at spawning time. For large stocks of pelagic spawners such as cod, this is often a difficult task. The spawning grounds of the Labrador-East Newfoundland cod stock (or stock complex) extend about 800 nautical miles from north to south (Templeman, 1981). Although it has been convenient to consider this complex as one stock, one would expect to find some differences between the groups of cod which spawn in various parts of this vast spawning area. The more northern coastal populations of this stock are more related to more northern spawning grounds than are the southern coastal populations of the stock (Templeman, 1979). In cod tagging and other stock discrimination studies, it must be remembered that not all mature cod spawn in the area of the spawning grounds where they were caught and tagged or sampled. The spawning of cod of the Labrador-East Newfoundland stock proceeds for several months, and cod which spawn early in the northern part of the area may rapidly move as spent fish to more southerly spawning areas of the stock (Postolaky, 1966). When sampling this stock for discrimination studies, it is essential, therefore, to note the condition of the gonad with regard to sex and maturity stage. This is not readily done in tagging except for fish with running eggs and milt, but it is essential for other studies. Immature cod whose nursery ground is the spawning ground of the stock under consideration may not belong to the same stock as the spawning fish. Furthermore, immatures of a stock whose nursery area is remote from the spawning ground usually do not migrate to the spawning ground with the mature fish except possibly for some large immature individuals. Trout (1957) found that a "dummy" run of large immature cod migrated with matures of the Arcto-Norwegian stock toward the spawning ground but to a lesser distance.

After spawning, the cod proceed to feeding grounds which are usually close to the areas where they existed as immatures (Templeman, 1979). Again, the sampling for biochemical or other methods of stock discrimination should include the recording of size, sex and gonad condition, and the age is useful, especially in parasite studies. The usual weakness of tagging in the feeding and nursery areas is the lack of information on maturity stage of individual fish in the overlapping length ranges of immatures and matures. Also, one must be cautious in using differences in parasite infestation of immature fish and in such environmentally-affected parameters as growth or size at sexual maturity from samples obtained in feeding and nursery areas as evidence of differences between stocks, because these areas may contain a mixture of several stocks.

Apart from the possibility of changes in biochemical indicators with size and age, the small and large fish in a feeding area may be from different stocks. For example, in the studies of Odense *et al.* (MS 1966, 1969), the cod samples taken near St. John's, Newfoundland, showed marked deviation from the Hardy-Weinberg law, indicating the presence of more than one stock. Templeman (1979) reported that the smaller cod from the St. John's area were predominantly highvertebral-count fish from the northern (Labrador-East Newfoundland) stock, whereas the large cod were mostly low-vertebral-count fish of more southerly stocks.

Studies on growth and size at sexual maturity, year-class differences, otolith, scale, morphometric and similar characteristics are most useful for stock discrimination purposes when the data pertain to spawning cod on the spawning grounds. In a stock, such as the Labrador-East Newfoundland cod stock, with apparent egg and larval drifts of 600 nautical miles or more, fish on the nursery grounds may exhibit different growth, age and length at maturity, and parasite infestation patterns, even though they belong to the same stock (Fleming, 1960; Templeman, 1962, 1979, 1981).

Determination of stocks

Stocks of cod and other marine fishes are made possible by appropriate current, temperature and salinity conditions, and suitable spawning times and areas, accompanied by suitable nursery areas for the young and adequate quantities and varieties of food for larvae, juveniles and adults. The maturing fish in the nursery areas must have the stimulation and energy and the swimming ability to return against the current to the spawning grounds from which they originated as eggs and larvae. Iles and Sinclair (1982) related the existence and size of herring stocks of the North Atlantic to oceanographic conditions, resulting in larval retention areas of various sizes. For the Arcto-Norwegian cod stock, which spawns at Lofoten and vicinity, the long drift northward to the Barents Sea under cool temperature conditions and relatively deep water for the settling of the young allow a very large nursery area for the stock. Similarly, for the Labrador-East Newfoundland cod stock, the large spawning area and the low temperature of the upper water layers at spawning time in March-May (mainly March-April), with consequent long period to hatching of the eggs and the slow growth of larvae during their drift southward in the Labrador Current, enable the young to settle over a very large area (Templeman, 1979, 1981). For the three Northeast Atlantic cod stocks, which spawn in March, the North Sea cod settle to the bottom in early July at about 3.5 cm in length, Icelandic cod settle in early August at about 4.5 cm, and Arcto-Norwegian cod settle in the Barents Sea in late August and September at about 7.5 cm. Thus, the larvae drifting in the coldest water and the fry settling in the deepest areas have the longest pelagic life and consequently are more widely dispersed (Corlett, 1958). For smaller cod stocks, the oceanographic conditions create smaller retention areas, such as that produced by the eddy system around Flemish Cap (Templeman, 1976; Kudlo and Boytsov, 1978; Borovkov and Kudlo, 1980).

Use of stock concepts for management and an example of inherent difficulties

The application of assessments to stocks of cod and other species in the Northwest Atlantic is very much limited by the established statistical divisions for which the basic data are provided, and hence the projected total allowable catches (TACs) are not finely tuned, even in relation to the available information on stocks. To take the Labrador-East Newfoundland cod stock as an example, the TACs for the northern part of the stock in Div. 2GH and for the major part of the stock in Div. 2J+3KL are established separately. In such a stock, it might be expected that cod in the northern extremity of the area could, on the average, have less larval survival than stock units farther south and thus be quickly damaged by overfishing. This apparently occurred in 1965-69 (May et al., MS 1981, table 3). Hence, it is wise to have a separate TAC for the northern part of this stock which should be watched closely. In fact, this part of the stock should probably not be fished at all except for the small traditional coastal fishery. The southern part of the stock in Div. 3L intermingles greatly with several other cod stocks (Templeman, 1979, 1981). In years when ice conditions are severe, the TAC for Div. 2J+3KL may be taken mainly in the southern divisions with consequent excessive reduction in that part of the stock. In years when fishing is possible in the northern divisions in winter and spring and cod are abundant there, the fish are so concentrated by water temperature that excessive exploitation by trawlers may occur on the offshore grounds. This apparently happened in the late 1960's following which the stock size declined rapidly, with consequent greater detrimental effects on the coastal fisheries of Labrador and northeastern Newfoundland than in Div. 3L. Consideration should be given to imposing TAC's for cod in individual divisions of 2J, 3K and 3L.

References

- AMOS, M. H., R. E. ANAS, and R. E. PEARSON. 1963. Use of a discriminant function in the morphological separation of Asian and North American races of pink salmon, *Oncorhynchus gorbuscha* (Walbaum). *Bull. INPFC*, **11**: 73-100.
- BOROVKOV, V. A., and B. P. KUDLO. 1980. Results of USSR oceanographic observations on Flemish Cap, 1977–78. ICNAF Sel. Papers, 6: 47-52.
- CASTLE, W. E. 1903. The laws of heredity of Galton and Mendel and some laws governing race improvement by selection. *Proc. Amer. Acad. Sci.*, **34**(8): 223–242.
- CORLETT, J. 1958. Distribution of larval cod in the western Barents Sea. *ICNAF Spec. Publ.*, 1: 281-288.
- CROSS, T: F., and R. H. PAYNE. 1978. Geographic variation in Atlantic cod, Gadus morhua, off eastern North America: a biochemical systematics approach. J. Fish. Res. Bd. Canada, 35: 117–123.
- CUSHING, D. H. 1967. The grouping of herring populations. *J. Mar. Biol. Assoc. U.K.*, **47**: 193–208.
 - 1973. Recruitment and parent stock in fishes. Div. Mar. Resour., Univ. Washington, Seattle, Sea Grant, 73-1, 197 p.
- DANDO, P. R. 1974. Distribution of multiple glucosephosphate isomerases in teleostean fishes. Comp. Biochem. Physiol., 47B: 663–679.
- DANNEVIG, A. 1953. The littoral cod of the Norwegian Skagerak coast. ICES Rapp. Proc.-Verb., **136**: 7–14.
- DeLIGNY, W. 1969. Serological and biochemical studies on fish populations. Annu. Rev. Oceanogr. Mar. Biol., 7: 411-513.
- FLEMING, A. M. 1960. Age growth, and sexual maturity of cod (Gadus morhua L.) in the Newfoundland area, 1947–50. J. Fish. Res. Bd. Canada, 17: 775–809.
- FRYDENBERG, O., D. MØLLER, G. NAEVDAL, and K. SICK. 1965. Haemoglobin polymorphism in Norwegian cod populations. *Her-editas*, 53: 257–271.
- HANSEN, P. M. 1949. Studies on the biology of the cod in Greenland waters. *ICES Rapp. Proc.-Verb.*, **123**: 1-77.
- HARDY, G. H. 1908. Mendelian proportions in a mixed population. *Science*, **28**: 49-50.
- HEINCKE, H. 1898. Naturgeschichte des Herings. Teil 1. Arb. Dtsch. fisch.-verb., 2: 1-223.
- HEMPEL, G., and J. H. S. BLAXTER. 1961. The experimental modification of meristic characters in herring (*Clupea harengus* L.). *ICES J. Cons.*, 26: 336–346.
- HODDER, V. M., and L. S. PARSONS. 1971. Comparison of certain biological characteristics of herring from Magdalen Islands and southwestern Newfoundland. *ICNAF Res. Bull.*, 8: 59–73.
- ILES, T. D., and M. SINCLAIR. 1982. Atlantic herring: stock discreteness and abundance. *Science*, **215**: 627–633.
- JAMIESON, A. 1968. Cod transferrins and genetic isolates. *In* Eleventh Env. Conf. Anim. Blood Groups and Biochem. Polymorph., Warsaw, 2-6 July 1968 (p. 533-538). Dr W. Junk, The Hague, 607 p. 1975. Enzyme types of Atlantic cod stocks on the North American banks. *In* Isozymes, III, Genetics and Evolution, Acad. Press, N. Y., p. 491-515.
- JAMIESON, A. and J. JONSSON. 1971. The Greenland component of spawning cod at Iceland. ICES Rapp. Proc.-Verb., 161: 65-72.
- JAMIESON, A., and R. J. TURNER. 1979. The extended series of T_f alleles in Atlantic cod (*Gadus morhua* L.). *In* Marine organisms: genetics, ecology and evolution, B. Battaglia and J. Beardmore (ed.), Plenum Press, N. Y., p. 699-729.
- JOHANSEN, A. C. 1924. On the summer and autumn spawning herrings of the North Sea. Medd. Komm. Dan. Fisk. Havunders.,

Ser. Fisk. 7(5), 119 p.

- KHAN, R. A., J. MURPHY, and D. TAYLOR. 1980. Prevalence of a trypanosome in Atlantic cod (*Gadus morhua*), especially in relation to stocks in the Newfoundland area. *Can. J. Fish. Aquat. Sci.*, **37**: 1467–1475.
- KUDLO, B. P., and V. D. BOYTSOV. 1978. The effect of water dynamics on year-class strength of cod on Flemish Cap. ICNAF Sel. Papers, 5: 7-9.
- LEAR, W H., and E. J. SANDEMAN. 1979. Use of scale characters and discriminant functions for identifying continental origin of Atlantic salmon. *ICES Rapp. Proc.-Verb.*, **176**: 68–75.
- LOVE, R. M. 1970. The chemical biology of fishes. Acad. Press, London and New York, 547 p.

1974. Colour stability in cod (*Gadus morhua* L.) from different grounds. *ICES J. Cons.*, **35**: 207–209.

- MARGOLIS, L. 1963. Parasites as indicators of the geographical origin of sockeye salmon, Oncorhynchus nerka (Walbaum), occurring in the North Pacific Ocean and adjacent areas. Bull. Int. N. Pacif. Fish. Comm., 11: 101–156.
- MARR, J. C. 1957. The problem of defining and recognizing subpopulations of fishes. Spec. Sci. Rep., U.S. Fish. Wildl. Serv., 208: 1-6.
- MARTIN, W. R., and Y. JEAN. 1964. Winter cod taggings off Cape Breton and on offshore Nova Scotia banks, 1959–62. *J. Fish. Res. Bd. Canada*, **21**: 215–238.
- MAY, A. W., R. G. HALLIDAY, R. WELLS, and E. DUNNE. MS 1981. Management of Canadian cod stocks. *NAFO SCR Doc.*, No. 141, Serial No. N449, 18 p.
- McKENZIE, R. A. 1940. Nova Scotian autumn cod spawning. J. Fish. Res. Bd. Canada, 5: 105–120.

1956. Atlantic cod tagging off the southern Canadian mainland. Bull. Fish. Res. Bd. Canada, **105**: 93 p.

- McKENZIE, R. A., and G. F. M. SMITH. 1955. Atlantic cod populations along the southern Canadian mainland as shown by vertebral count studies. J. Fish. Res. Bd. Canada, **12**: 698–705.
- MØLLER, D. 1966a. Genetic differences of cod in the Lofoten area. Nature, 212: 824.
 - 1966b. Polymorphism of serum transferrin in cod. *Fiskeridir*. *Skr. (Fisk.)*, **14**: 51-60.
 - 1967. Red blood cell antigens in cod. Sarsia, 29: 413-430.

1968. Genetic diversity in spawning cod along the Norwegian coast. *Hereditas*, **60**: 1-32.

- NYMAN, O. L. 1965. Inter- and intraspecific variations of protein in fishes. *Ann. Acad. Regia Sci. Ups.*, **9**: 1–18.
- ODENSE, P. H., T. C. LEUNG, and T. M. ALLEN. MS 1966. An electrophoretic study of tissue proteins and enzymes of four Canadian cod populations. *ICES C.M.*, Doc. No. G:14.
- ODENSE, P. H., T. C. LEUNG, T. M. ALLEN, and E. PARKER. 1969. Multiple forms of lactate dehydrogenase in the cod, *Gadus morhua* L. *Biochem. Genet.*, **3**: 317–334.
- PARRISH, B. B. 1964. Notes on the identification of subpopulations of fish by serological and biochemical methods, the status of techniques and problems of their future application. *FAO Fish. Tech. Pap.*, **30**: 1-9.

PARSONS, L. S. 1972. Use of meristic characters and a discriminant function for classifying spring- and autumn-spawning Atlantic herring. *ICNAF Res. Bul.*, **9**: 5-9.

- POSTOLAKY, A. I. 1966. Results of cod tagging in the Labrador and North Newfoundland Bank regions, 1960–64. *In* Results of investigations in the Barents, Norwegian, White seas and the Northwest Atlantic in 1964, PINRO, Murmansk, No. 6, p. 89–90. (Fish. Res. Bd. Canada Transl. Ser., No. 859, 1967.)
- ROJO, A. L. 1977. The otolith, discriminating factor of codfish (*Gadus morhua* L.) stocks in the Northwest Atlantic. *Invest. Pesq.*, 41: 239–261. (Fish. Aquat. Sci. Transl., No. 4690, 19 p.)

ROLLEFSEN, G. 1933. The otoliths of the cod. Fiskeridir. Skr. (Fisk.),

4(3): 1-14.

- SCHMIDT, J. 1930. The Atlantic cod (Gadus callarias L.) and local races of the same. In Racial investigations, X, C. R. Lab., Carlsberg, 18(6): 1-71.
- SHARP, J. C., K. W. ABLE, W. C. LEGGETT, and J. E. CARSCADDEN. 1978. Utility of meristic and morphometric characters for identification of capelin (*Mallotus villosus*) stocks in Canadian Atlantic waters. J. Fish. Res. Bd. Canada, 35: 124–130.
- SICK, K. 1965a. Haemoglobin polymorphism of cod in the Baltic and the Danish Belt Sea. *Hereditas*, **54**: 19–48.

1965b. Haemoglobin polymorphism of cod in the North Sea and the North Atlantic Ocean. *Hereditas*, **54**: 49-69.

- TÅNING, Å. V. 1937. Some features in the migration of cod. *ICES J. Cons.*, **12**: 3-25.
- TEMPLEMAN, W. 1962. Divisions of cod stocks in the Northwest Atlantic. *ICNAF Redbook*, 1962 Part III: 79–129.

1974. Migrations and intermingling of Atlantic cod, *Gadus* morhua, stocks of the Newfoundland area. J. Fish. Res. Bd. Canada, **31**: 1073-1092.

1976. Biological and oceanographic background of Flemish Cap as an area for research on the reasons for year-class success and failure in cod and redfish. *ICNAF Res. Bull.*, **12**: 91-117.

1979. Migration and intermingling of stocks of Atlantic cod, Gadus morhua, of the Newfoundland and adjacent areas from tagging in 1962–66. *ICNAF Res. Bull.*, **14**: 5–50.

1981. Vertebral numbers in Atlantic cod, *Gadus morhua*, of the Newfoundland and adjacent areas, 1947–71, and their use for delineating cod stocks. *J. Northw. Atl. Fish. Sci.*, **2**: 21–45.

- TEMPLEMAN, W., and A. M. FLEMING. 1962. Cod tagging in the Newfoundland area during 1947 and 1948. J. Fish. Res. Bd. Canada, 19: 445–487.
- TEMPLEMAN, W., and J. A. GULLAND. 1965. Review of possible conservation actions for the ICNAF area. ICNAF Ann. Proc., 15: 47-56.
- TEMPLEMAN, W., and H. J. SQUIRES. 1956. Relationships of otolith lengths and weights in the haddock, *Melanogrammus aeglefinus* (L.), to the rate of growth of the fish. J. Fish. Res. Bd. Canada, 13: 467–487.
- TEMPLEMAN, W., V. M. HODDER, and A. M. FLEMING. 1976. Infection of lumpfish (*Cyclopterus lumpus*) with larvae and of Atlantic cod (*Gadus morhua*) with adults of the copepod. *Lernaeocera branchialis*, in and adjacent to the Newfoundland area, and inferences therefrom on inshore-offshore migrations of cod. J. Fish. Res. Bd. Canada, 33: 711–731.
- TEMPLEMAN, W., H. J. SQUIRES, and A. M. FLEMING. 1957. Nematodes in the fillets of cod and other fishes in Newfoundland and neighbouring areas. J. Fish. Res. Bd. Canada, 14: 831–897.
- THOMPSON, H. 1943. A biological and economic study of cod (*Gadus callarias* L.) in the Newfoundland area. *Nfld. Dep. Natur. Resour. Fish. Bull.*, **14**: 160 p.
- TROUT, G. C. 1957. The Bear Island cod: migrations and movements. *Fish. Invest. Lond.*, Ser. 2, **21**(6): 1–51.

1958. Otoliths in age determination. *ICNAF Spec. Publ.*, 1: 207-214.

ULLRICH, H. 1967. Erste Mitteilung zur Serumelektrophorese. Fischerei-Forschung., 5(2): 57-59.

1968. Zweite Mitteilung zur Blutserumelectrophorese von Kabeljau des Nordwestatlantiks. *Fischerei-Forschung.*, **6**(1): 37-39.

- WEINBERG, W. 1908. Uber den Nachweis der Vererbung beim Menchen. Jahresh. Ver. Vaterl. Naturkd. Wuerttemb., 64: 368-382.
- WISE, J. P. 1958. The world's southermost indigenous cod. *ICES J. Cons.*, **23**: 208–212.
 - 1963. Cod groups in the New England area. *Fish. Bull. U. S.*, **63**: 189-203.