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Emigration of fish: a change in opinion*

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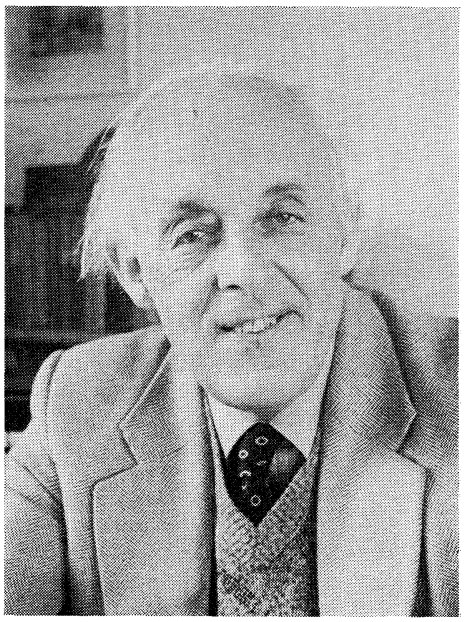
1. Introduction

Today the International Council for the Exploration of the Sea collects information on the gut contents of many fishes in order to make estimates of natural mortality by age and to improve estimates of recruitment. In other words predation is considered the main agent of natural mortality. Many years ago such a project might not have been undertaken because it was thought that fish emigrated from their native stocks to perhaps a significant extent.



2. The distant recoveries from tagging experiments

TANING (1934, 1935) reported the results of tagging experiments on adult cod at Iceland and West Greenland and discussed the distant recoveries from these sites and also from earlier work on Faroe Bank and from the shelf around the Faroe Islands. His results are summarized in Table 1. From the four tagging sites fish were recaptured from Newfoundland, East Green-

Table 1. Distant recoveries of cod from tagging experiments in Iceland, West Greenland, Faroe and Faroe Bank (from TANING, 1934, 1937) (% recovered shown in brackets)

Position of tagging	Number tagged	Numbers recovered from:— Newfoundland	W Greenland	E Greenland (Denmark St)	Iceland	Faroe	Faroe Bank	Norway	Orkney	Northern North Sea
Iceland (1925-35)	4939	1 (0.02%)	17 (0.34%)	1 (0.02%)	—	2 (0.04%)	—	2 (0.04%)	—	—
West Greenland (1924-32)	8500	—	—	—	256 (3.0%)	—	—	—	—	—
Faroe (1909-32)	6183	—	—	—	—	—	2 (0.03%)	—	1 (0.016%)	1 (0.016%)
Faroe Bank (1910)	585	—	—	—	—	2 (0.3%)	—	—	—	—

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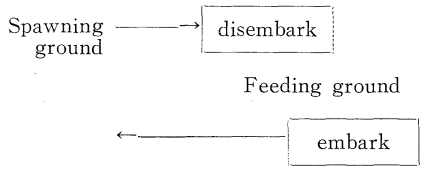
land, Faroe Islands, Faroe Bank, Norway, the Orkney Island and the Northern North Sea. There are two classes of recovery, those at a low level 0.02–0.04% and those at a high level between Iceland and West Greenland (and vice versa), 0.34%–3.0%. The exchange between the Faroe Islands and Faroe Bank is perhaps intermediate, 0.03%–0.3%. SIGURDSSON (1982) reported 4 tags recovered off Norway and 2 off Shetland from taggings off Iceland; the percentage recovered were 0.01% (for two tags off Norway) and 0.03% (for one tag off Shetland). LEBED *et al.* (1983) reported thirteen recoveries at Iceland and Faroe from tagging in the Barents Sea (62,286 cod were tagged, a return of 0.02%).

In general genetic studies have shown that the chance of exchange between major cod stocks is low (excluding that between Iceland and West Greenland); with two haemoglobins and seventeen transferrins. JAMIESON and TURNER (1979) have shown that the chance of mixture between such stocks is as low as 0.01%. The low level recoveries quoted above (0.01% to 0.04%) are of the same order, if a little higher, but the numbers recovered are very low. The exchange between West Greenland and Iceland is very much greater; as yet the genetic evidence of distinctness of these stocks is indecisive (JAMIESON and JONSSON, 1971). JAMIESON and JONES (1967) have found a difference of one transferrin locus between the stocks of cod on Faroe Bank and those on the Faroe Island shelf. Hence there is some agreement between the evidence from genetic studies and that from tagging.

3. The hydrographic containment of a stock

The simple model of how a stock is contained within a current or tidal system is expressed as part of JONES (1968) triangle of migration:—

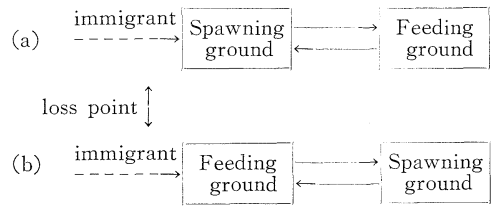


The arrows indicate the denatant and contranatant migrations in a current or tidal system. The point of disembarkation might be relatively close to the spawning ground whereas that of embarkation might be relatively far; however distance between the two is not a necessary part of subsequent argument.

Each migration may be relatively quick. From the Vestfjord in northern Norway to the Svalbard Shelf in the Barents Sea is about 800 km; at 24 km d^{-1} (JONES, 1968), the distance might be covered in 29 d. JONES *et al.* (1979) have shown that plaice in the Southern Bight of the North Sea migrate to the spawning ground on the south bound tide and sit on the sea bed on the north bound, selective tidal transport; after spawning they change the procedure, migrate north on the north bound tide and sit on the bottom on the south bound. If the average tidal fetch is 14 km, the migration to and from the Central North Sea takes about 22 d.

If the migrations are quick, the points of embarkation and disembarkation become important. One might imagine that cod disembark from the West Spitsbergen current near Bear Island and spread north towards Spitsbergen and east across the Svalbard Shelf. Then they feed all summer and later embark on the currents and return to the Vestfjord. An analogous argument could be made on the migration structure of the Southern North Sea plaice.

The embarkation point may well be downstream of the point of disembarkation. Further downstream there may be a loss point beyond which the fish must look elsewhere for its migration circuit. There are two ways in which new circuits might arise.



If the animal were a plaice it switches behaviour on the spawning ground. The second alternative (b) is to be preferred because in (a) it would have to return across the loss point to the old feeding grounds. The West Greenland cod established its migration circuit (JONES, 1968) in the second form, (b). Hence the im-

migrant found a new point of embarkation and after spawning in the north of West Greenland, a new point of disembarkation on the new feeding ground. I assume that the West Greenland spawning arose on the offshore banks from Iceland immigrants and not from the fjord stocks.

4. The West Greenland cod stock

The West Greenland cod stock built up from 1912 with good year classes, 1917, 1922, 1924, 1926, 1934 and 1936 and high catches were made in the fifties and sixties (CUSHING, 1982). Between 1917 and 1936 the fishery progressed northwards on the coast of West Greenland. It is likely that larvae and immature cod drift in the Irminger current to the East Greenland current round Cape Farewell to West Greenland (JONES, 1968).

The West Greenland tagging experiment (1924-36) showed that recaptures at Iceland started in 1930:-

	Recaptures	
	Greenland	**Iceland**
1924	1	0
1925	15	0
1926	16	0
1927	16	1
1928	6	0
1929	9	0
1930	16	7
1931	32	47
1932	44	35
1933	22	57
1934	48	53
1935	58	44
1936	31	12
	314	256

During the thirties there were many changes in distribution particularly between 1930 and 1935, as a consequence of climatic change (see CUSHING, 1982). The percentages recovered at Iceland from West Greenland on a longer time scale were:-

1924—8	1.8%
1929—33	54.5%
1934—9	42.1%
1944—4	38.7%
1945—9	3.2%
1950—2	5.7%
1968—9	5.8%

Thus the period 1930-44 was one of high recapture rate at Iceland. The fishery declined in the late sixties.

The West Greenland stock lies downstream of the Icelandic in the Irminger and the East and West Greenland currents. The high rate of return between 1930 and 1944 suggests perhaps a strong Irminger and a strong countercurrent. The period of the fishery lasted from 1912 to 1970 (however it still persists at a low level). Before that period cod did not reach West Greenland and did not survive on the offshore banks. Then the loss point may have been in the Denmark Strait, but in the thirties it must have shifted westward. As the climate ameliorated, cod (perhaps as larvae and immature fish as well as adults) colonized West Greenland and a spawning ground was established there, downstream from Iceland; in other words the immigrants survived on the new feeding ground for a significant period — and they returned to Iceland at a high rate. The migration and the establishment of a new stock may have been an abnormal event.

5. Natural mortality

Taning's figure (Fig. 1) shows the spread of distant recoveries from Newfoundland to Norway, tagged on the Icelandic spawning grounds; it was reproduced in Russell's (1937) paper on fish migration. The extensive migration to West Geenland was also shown. The proportions recovered were not shown and one might have believed that the emigration was significant. Any student of populations hopes that loss by emigration is balanced by a gain in immigration, but in fishes such a balance depends on the distribution and strength of the currents. But if either immigration or emigration were high, the stocks would not necessarily be genetically distinct.

However, an opinion emerged — that any estimate of natural mortality may include a component of emigration. BEVERTON and HOLT's (1957) estimate of natural mortality from the transwartime year classes of Southern North Sea plaice (0.1) was and remains the only well established measure, but such animals were not visualized as particularly vigorous migrants.

The genetic studies on North Atlantic cod

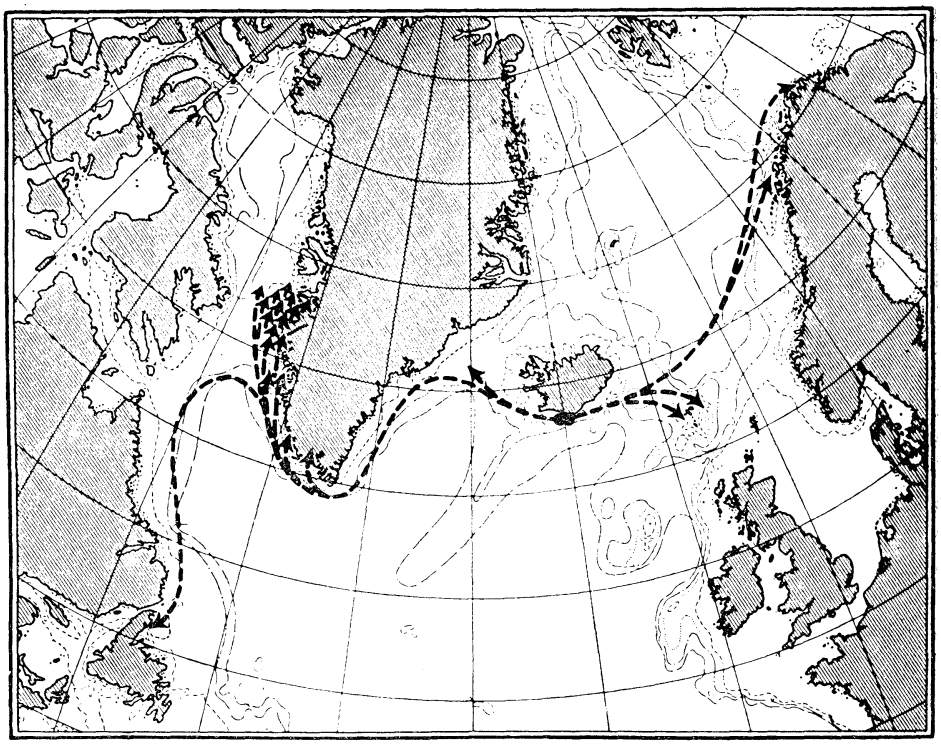


Fig. 1. The distant recoveries of cod from liberations on the Iceland spawning ground (TANING, 1937).

stocks (summarized in JAMIESON and TURNER, 1979) showed that the chance of mixture was low. There is no conflict between this result and that of the low recovery rates (In Table 1) — even if the number of tags returned is very low. The high recoveries between Iceland and Greenland and vice versa are probably the result of a temporary colonization; because of such an exchange, a genetic distinction would not be expected until many generations had elapsed i. e. towards the end of the period of the fishery.

The results of the genetic studies was a change in opinion, that emigration need not be considered a necessary component of natural mortality. Then such death is due to disease or predation. If we except the recorded disasters due to disease (see SINDERMANN, 1971). the predators take amongst their prey, the normally sick, and the problem of natural mortality becomes a study of predation. Even senescent fish may be killed by predators and need not die of old age.

6. The unit stock

In any population study the stock under examination must be defined. In the early days of fisheries research a common sense approach sufficed. For example, the cod stocks in the North Atlantic were separated from each other by deep water, which a demersal fish would not cross. But cod crossed the Denmark Strait in numbers and TANING (1937) quoted examples of the pelagic capture of cod. SIGURDSSON (1982) makes the same point for the plaice.

However, the need for stock definition differs with circumstance. BEVERTON and HOLT (1957) devized a model for the mesh regulation of cod, haddock and plaice in the North Sea. In other words, the stock with respect to a given mesh size comprised a number of species. In the Gulf of Thailand the "stock" comprises a much larger number of species. But the more usual problem is to define stocks at a subspecific level, such as the cod stocks in the North Atlantic. To understand the dependence of recruitment on parent stock, the stock must be properly

defined or the estimates of recruiment will be biased. So long as recruitment is estimated quantitatively by cohort analysis, the stock must be properly defined — for the same reason.

There is a difference between evidence from the distribution of fish tagged on the spawning ground and that from genetic evidence. The spread of tags describes the stock area on the feeding ground (provided that fishermen are there) and the genetic evidence provides evidence of the discrete nature of distinct stocks, that is, a low rate of mixture. The evidence of the low rate of mixture from tagging is of the same order (always excepting the West Greenland colonization) but that from tagging is more expensive: ten tags recovered from distant grounds require 100,000 released on the spawning ground. From the nature of the hydrographic containment of the stock, it is possible that the distant recoveries are distributed by the differences in current and counter-current.

7. Discussion

The purpose of this paper is to portray a change in opinion. Taning's chart of distant recoveries from Iceland (with no indication of the proportion recovered) appeared to be a picture of emigration. Despite BEVERTON and HOLT's (1956) estimate of the natural mortality of plaice, gossip on the natural mortality of other species always included the possibility of emigration.

The genetic estimate of mixture in the North Atlantic cod stocks showed that emigration and immigration need not be considered under normal circumstances: the colonization of West Greenland is seen as an anomalous event. Then the central problem in the estimation of natural mortality becomes the measure of predation. The genetic study of stocks has not developed as might have been expected, perhaps because the dramatic results for the North Atlantic cod stocks have not been repeated in other species, possibly for technical reasons. It is possible, of course, that such differences do not exist in other species. It is however, my view that population studies will remain for ever suspect unless supported by studies on genetics and migration.

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