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RECRUITMENT AND PARENT STOCK
IN FISHES

By David H. Cushing

WSG 73-1

July 1973

DIVISION OF MARINE RESOURCES
UNIVERSITY OF WASHINGTON 98195

Prepared under the
National Sea Grant Program

A WASHINGTON SEA GRANT PUBLICATION

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ACKNOWLEDGMENT

This publication was supported by the Washington Sea Grant Program, a part of the National Sea Grant Program. The National Sea Grant Program is supported by the National Oceanic and Atmospheric Administration, U. S. Department of Commerce.

Printed in the United States of America

Price \$7.50

Distributed by University of Washington Press, Seattle 98195

(Washington residents please add sales tax)

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FOREWORD

In 1971, the University of Washington was designated as a Sea Grant College by the U.S. Department of Commerce with grants administered by the Division of Marine Resources at the University. One of these grants, "Aquatic Stock Management," under No. 1-35320, was established to promote innovative teaching related to management of renewable resources, and to supplement and broaden instruction being given at the College of Fisheries and in the Center for Quantitative Science. To help satisfy these objectives a series of guest lectureships was established. In the fall of 1972 Dr. David H. Cushing, Senior Principal Scientific Officer, Ministry of Agriculture, Fisheries and Food, Fisheries Laboratory, Lowestoft, Suffolk, England, presented the second series entitled "Recruitment and Parent Stock in Fishes." His lectures are presented here in published form in order to serve a broader audience--students, researchers, and resource managers engaged in studies of quantitative fishery biology.

Editing and production by Ms. Carol Ovens and Ms. Patricia Peyton of the Division of Marine Resources and Ms. Dorothy Beall of the College of Fisheries and typing of the manuscript by Ms. Muriel Mobley of the College of Fisheries are gratefully acknowledged.

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Chapter 1

THE NATURE OF A FISH STOCK

Introduction

Because nearly all the herring fisheries in the Northeast Atlantic have failed (Burd, in press) and there is a very strong threat to the recruitment of the Arcto-Norwegian cod stock under the pressure of heavy fishing (Garrod, 1967), the study of stock and recruitment in European waters has evolved in recent years. The problem of growth overfishing, in short, has been replaced by that of recruitment overfishing--that is, the stock has been reduced by fishing so far that the recruitments, or incoming year-classes, have been reduced also.

One of the lesser consequences of the study of growth overfishing has been that questions of stock unity have become somewhat less interesting. Not only has it been possible to consider male and female plaice as separate populations because of their differences in growth rate, but mixed fisheries might have been treated in the same way, so long as the vital parameters were properly averaged in a proportionate way. Indeed, one might envisage grouping animals by the values of their vital parameters only. Further, there are problems in exploitation in which the stocks are necessarily ill defined, for example, Antarctic krill and some coastal shellfish.

The study of recruitment overfishing requires that the high variance within the stock and recruitment relationship be generated neither by the mixture of stocks nor by an invasion of recruits. The survival of recruit from egg is the most important information in the study, and the variance about the stock and recruitment curve must express differences in it. Hence the stock must be considered as a pure stock. If the vital parameters of such a population are to be determined, the geneticist's assumptions should be recalled: (1) that the stock be isolated; (2) that it suffer neither loss by emigration nor gain by immigration; and (3) that mating within it be randomly distributed.

Large populations of fishes are nearly always migratory, and for their sizes the animals travel very great distances and depend upon the current system to do so. The migration circuit (Harden Jones, 1968) provides the seasonal and geographical regularity of certain fisheries, spawning fisheries like that for cod in the Vestfjord in northern Norway and feeding fisheries like those for herring that used to occur on the polar front between Iceland and Jan Mayen. But more important for our present purpose is the mechanism by which the stock retains its isolated character.

Early History of Racial Studies

In describing and defining animal species, we may say that each is a group of animals, every individual of which can be distinguished from those of closely related species. A stock of fish is a group of lower taxonomic status; across the North Atlantic, there are many isolated stocks of cod (*Gadus morhua* Linnaeus), but the individuals of one cannot be reliably distinguished from those of another with the external characteristics usually employed by taxonomists.

The early fisheries biologists referred to such groups as races and distinguished them with meristic characters. With distributions of fin rays and of vertebrae, Schmidt (1930) showed small differences in the means between the Arcto-Norwegian cod stock and its close neighbors. The differences are minimal, a small fraction of a vertebra, and as will be shown below, they may indicate much more important differences, which have a genetic basis. The most important work on races from a historical point of view was that by Heincke (1898) on the herring. With four morphometric measurements made on samples taken from a large number of fisheries in European waters, he distinguished between spring- and autumn-spawning races. They were, however, scattered in local groups and such local races were said to frequent a particular spawning ground, because they returned each year to spawn there. Not all Heincke's results can be repeated today because many stocks have disappeared, either from natural causes or from heavy fishing. He thought that the racial characters reflected average physical conditions in the environment and because the environment differs so much from place to place, the local races are distinct merely because such characters are environmentally determined.

It should be recalled that Heincke's papers were published two years before the "rediscovery" of Mendel's findings. Like Schmidt's conclusion on the Arcto-Norwegian cod, Heincke's on the nature of herring races have a modern ring in that there are many small local groups, even though the methods are long ago out-of-date. The work of Le Gall (1935) on the herring was based on an analogous approach and it forms the basis of much of the present separation of stocks in European waters. In the Pacific halibut, two stocks, or races, were distinguished partly on morphometric differences and partly on the distribution of tags (Thompson and Van Cleve, 1936; Thompson and Herrington, 1930). Various combinations of morphometric measurements still play a part today in the statistical separation of stocks of fish.

Although Heincke's conclusions are pleasing to a modern ear, his statistical treatment did not really convince his contemporaries or their successors. Some groups designated by him as spring or autumn ones did not survive later examination (Jenkins, 1920). Morphometric studies were not

continued much in herring work, but the collection of samples of meristic characters proliferated. During the high days of the development of genetics, racial studies in fisheries biology were restricted to the study of characters believed to be environmentally determined.

Meristic Characters

A meristic character is one that is measured in a sample of perhaps a hundred fish caught at a particular locality and it is the mean of a distribution (continuous in morphometric measurements and discontinuous in counts of vertebrae, etc.). Average numbers of vertebrae, keeled scales, or fin rays are typical meristic characters that have been used in the study of herring populations. The locality at which such samples are taken plays an important part in the procedure because the distribution of localities reflects the unspoken views of the investigators and it is here that Heincke's influence has really been exerted: his successors have tended to place their samples as closely in space as he did and to some extent they eventually confirmed his conclusions.

Figure 1 shows the cline in vertebral counts in herring off the coast of British Columbia (Tester, 1935). The difference between the smallest interval of latitude is very small, but it persists in time. Downs herring spawning near the Sandettié Bank in the Straits of Dover have vertebral counts of about 56.56 and those from the same stock spawning in the eastern English Channel have counts of about 56.66. There are differences in magnitude from year to year, but each year there is a persistent difference between the two groups of about one tenth of a vertebra (Zijlstra, 1958). In contrast, the difference between the European and American eels, which spawn relatively close to each other in the Sargasso Sea, is of the order of seven vertebrae. The question then arises whether the number of vertebrae is genetically or environmentally determined.

Tester's results imply that the number of vertebrae changes with water temperature: in cooler water the number is a little higher. Such a relationship was first noticed by David Starr Jordan (1891). Tåning (1952) showed that the number of vertebrae in sea trout was determined during the period of gastrulation and that the number of fin rays was determined just before hatching (Figure 2). The lowest vertebral count was found at 6° C and at both higher and lower temperatures, higher counts were observed. Hence the ecological hypothesis was confirmed experimentally. Much earlier, Schmidt (1917, 1920) had established a similar relationship in the viviparous blenny (*Zoarces viviparus* L), but he also showed that the numbers of vertebrae in these fishes were genetically determined to some degree and that the very local populations of blennies along the Norwegian coast were genetically isolated. More recently, Purdom and Wyatt (1969) crossed North Sea and Irish

Sea plaice and incubated the eggs under the same temperature conditions. The results suggested that the differences in vertebral count between two groups of animals had a genetic basis.

Large numbers of observations on meristic characters have been tabulated by fisheries biologists on the assumption that the differences are real enough, in a genetic or an environmental sense, to distinguish races. But the genetic and environmental factors have only rarely been distinguished. The differences observed are often so small as to make the statistical treatment unmanageable. The real trouble is that to make sense of the differences in vertebral counts, larger samples are needed in smaller areas and such a laborious procedure has never been justifiable, particularly if the genetic basis has been by and large obscure.

The Stocks as Defined by Fisheries Biologists

Stocks were first recognized as fisheries that recurred at the same place each year. Because fisheries exploit spawning, feeding, or migrating animals, they are found in regular positions on the migratory circuit of the stock at the same season each year (Harden Jones, 1968). If such a circuit is considered as characteristic of a particular stock, then the classification of stocks by fisheries is a reasonable first approximation. A later development was to group fisheries by the degree of isolation as determined by tagging experiments. For example, large numbers of cod have been tagged throughout the North Atlantic and only a very small proportion have shifted from their original areas where each area is rather large, as the Grand Banks, Barents Sea, Iceland. An exception is the extensive movement of cod from a spawning ground in Iceland to southern Greenland. However, a cod has been recorded as crossing the Atlantic from the North Sea to the Grand Banks off Newfoundland (Gulland and Williamson, 1962). Fisheries biologists used to say that the cod at the Faroe Islands are retained on the shelf around the islands and that they do not cross the deep water to Iceland, the Norway coast, or to the North Sea. The single traveller has thus been regarded as an exception to the more general rule that the cod are retained in particular localities in the shelf seas.

An extension of this approach is to regard stocks as originating from statistical areas. If the latter are large, like those into which the two groups of Pacific halibut were classified, the areas include the stocks. The smaller the statistical area, the more detailed the information, provided there is enough of it; in the North Sea, squares of one degree of longitude by half a degree of latitude are used. The statistical areas for the British Columbian herring are about the same size, there being one group in the Straits of Georgia and another seaward of Vancouver Island. In this fishery a considerable tagging program has been executed; up to 100,000 tagged fish were released. The results by statistical squares

are given in Harden Jones (1968) and they show that up to 20% stray from one square to another in the first year after tagging, but that this proportion decreases with age. Indeed there is no stray between squares among the oldest animals. The fish tend to return to the ground of first spawning and there is no exchange between squares remote from each other. The division between the remote squares represents a true separation of stocks, but that between adjacent squares may represent a difference between stocklets, between which interchange is expected (*see below*). The fact that such interchange decreases with age implies that the statistical square was large enough to detect the presence of the stocklet. (A stock may be defined as a large isolated population and a stocklet is one of a small part that exchanges individuals with other stocklets.)

Recently, catch quotas have been introduced for haddock and for yellow-tailed flounder in the International Commission for Northwest Atlantic Fisheries (ICNAF) area. Because variations in catch are mainly variations in recruitment, the quotas must be related to stocks. It is convenient to group catches by statistical areas and in the case of the Georges Bank haddock, the statistical area may correspond with that occupied by the stock. However, some of the areas are extensive and evidence of stock unity by statistical area need not exist. As such evidence becomes available in the future, it is likely that smaller areas will be needed to manage the catch quota system effectively.

The vital parameters of a fish population are recruitment, growth, and mortality. To a limited degree they can be used to distinguish stocks. For example, there were three stocks of autumn-spawning herring in the North Sea and they differed in their growth rates, among other things, the bigger fish living in the north; for example, at four and five years of age, there was a difference of 1.5-2.0 cm in length between the three groups and considerable differences in weight. But a much more valuable index is the correlation or lack of it between recruiting year-classes. Between the three stocks the year-classes were not correlated, but within one of them, between three separate fisheries exploiting the same stock they were highly correlated (Cushing and Bridger, 1966). If recruitment is highly correlated in such a way, it is in itself good evidence of stock identity, if only because the variability of year-classes is so very high.

Many of the cod stocks in the North Atlantic were erected (in a quasi-taxonomic sense) by the fisheries biologists. The evidence they used was suggestive but never decisive. However, the combination of biological evidence on the nature of the migration circuit, on which the separate stocks are fished, with the genetic evidence of difference between them, is quite decisive as will be shown in subsequent sections.

The Hydrographic Containment of a Stock--Arctic Cod

The Arctic cod, or Arcto-Norwegian cod, spawn in the Vestfjord inside the Lofoten Islands in northern Norway and are caught there and in the Barents Sea, where they feed. It is a large stock of fish capable of supporting high catches (of hundreds of thousands of tons), although at the present time it suffers from a recruitment failure due to heavy fishing (Garrod, 1967). Figures 3-a, 3-b, and 3-c show: the catches of eggs made on the major spawning ground (Hjort, 1914) (Figure 3-a), the distribution of echo traces during March 1955 at the height of the spawning season (Boström, 1955) (Figure 3-b); and the local recaptures from Hjort's (1914) (Figure 3-c) tagging experiment. The spawning occurs on the edge of the deep water in the fjord below a layer of freshish water, and the shoals persist in the same position for a considerable time. The spent fish drift away down the fjord or between the Lofoten Islands and eventually move away north in the Atlantic current. The eggs, and subsequently the larvae, drift down the fjord into the same current that carries them north to the nursery grounds on the Svalbard Shelf or in the eastern Barents Sea. From taggings in the summer feeding fishery on the Bear Island Shelf, Trout (1957) has shown that although the great majority of tagged fish were recaptured in the Vestfjord, a small proportion were recovered further south. Records of the fishery in the Vestfjord go back to the twelfth century and show that it had occurred at the same place at the same time of year for a very long time.

The outward migration is shown in the pattern of recaptures in the Barents Sea from taggings in the Vestfjord (Figure 4-a). They are spread all over the Barents Sea, on the Svalbard Shelf, and on the shallow banks in the eastern Barents Sea (Figure 4-b). The boundary of their migration on the Svalbard Shelf is the boundary on the seabed of the 2° C isotherm [as shown by Richardson *et al.*, 1959; Beverton and Lee, 1965; and Hylan *et al.*, 1961 (Figure 4-c)] at the edge of the Arctic water mass. Figure 4-c also shows echo surveys for large midwater fish, that is cod, in the Barents Sea in spring and autumn (Hylan *et al.*, 1961); effectively, the cod enter the eastern Barents Sea through a gate formed by the North Cape current as it passes between the Arctic water and the coast and they return in autumn by the same route. The outward migration is probably a drift along the North Cape current to the eastern Barents Sea and along the West Spitsbergen current to the Svalbard Shelf and Spitsbergen. The adult fish move from deep water on to the shelf during a short period of about 10 days in early June (Richardson *et al.*, 1959) and spread across it during the summer to feed (Beverton and Lee, 1965).

The inward migration is shown in Figures 5-a, 5-b, and 5-c; fish were tagged in the eastern Barents Sea during the summer and the pattern of recaptures shows the westerly movement of the fish toward the Vestfjord apparently against the North Cape current (Mastov, 1944, Figure 5-a; Idelson, 1931, Figure 5-b). An interesting point is that of the inward migration toward the

spawning ground, the fish travel at 5.67 miles/day, but on the outward one with the current, they move only 1.64 miles/day. Harden Jones (1968) suggested that there might be a south-bound countercurrent. The final section of the inward migration is shown by a series of echo surveys (Saetersdal and Hysten, 1959) (Figure 5-c), in which the fish move down the Norway coast in the gullies on the shelf edge to the Vestfjord. They move around the island of Røst, the outermost Lofoten island, and into the fjord.

The migration circuit of the Arctic cod depends on the fixed spawning ground in the Vestfjord and on the larval drift in the Atlantic current to the nursery grounds on the Svalbard Shelf and in the eastern Barents Sea. Their range across the shelves in summer is limited by the position of the mass of Arctic cold water at a temperature of less than 2° C on the bottom and the fish return to the Vestfjord in the Atlantic current system, perhaps in a countercurrent. Figure 6 shows Mastov's (1944) diagram of the migration of the immature fish from the shelves in the Barents Sea into deeper water during the winter. The nursery ground lies at the end of the larval drift and the adolescent fish join the adult stock by migrating from the nursery into deeper water off the shelf edge in the autumn. The fish leave the Atlantic current in June by migrating up the Svalbard Shelf into shallower water and they return to it by moving back into deeper water. Thus the migration circuit is completed within the current system, although the water moves perpetually in one direction. Figure 7 shows an idealized migration circuit.

A stock is contained within a current system in which the migration circuit is maintained. From the nature of the system there must be small gains and losses, which account for the very long distances sometimes recorded by marked cod. Because they are of small magnitude, the stock retains its identity despite the gains, the losses being of no account in the question of identity. The stock may comprise a group of stocklets, between which there is mixture, but it is itself isolated. Since the spawning season lasts for nearly four months, peaking in March, larvae are being produced for a long period. In terms of metamorphosed fish, the spread in time will be increased by diffusing processes during the larval drift, which, in time, must occupy a major part of the production cycle. Hence there is no room for a competitive cod in the Barents Sea that spawns at the same season; there is, however, a fjord cod that spawns in the Vestfjord and elsewhere during spring, but that presumably does not migrate into the Barents Sea. The length of the spawning season, combined with the area of nursery grounds fed by the spreading larval drift, ensures that only cod of the Arcto-Norwegian stock reach the Svalbard Shelf and the eastern Barents Sea. In this way the structure of the migration circuit ensures the isolation needed to maintain the identity of the stock for long periods. One would expect then to find a number of species in roughly the same migratory circuit, but only one stock of each species.

Results of considerable interest from tagging experiments confirm the isolation of fish stocks. Figure 8 shows the spread of tagged halibut from the point of liberation; numbers recaptured are plotted on distance. Numbers decay with distance, irrespective of direction, in a way that suggests a form of diffusion from a point source. An interesting point is that the degree of spread is markedly different between the two stocks, the southern group in tens of miles and the western in hundreds of miles. But the spread is slow and the chance of mixture with the other stock about a thousand miles away is very low. In complete contrast, Figure 9 shows the transpacific migration of albacore, in which the fish travel across the ocean in the comparatively short time of about a year or so. It would be reasonable to suppose that the North Pacific subtropical anticyclone is the current system within which the stock is contained and the speed of the crossing suggests that the fish take a course in the faster current around its edge where the fisheries lie. If this suggestion is true, the stock is contained in the world's largest oceanic structure. Figure 10 shows on a very much smaller scale in the southern North Sea the recaptures of plaice that were tagged on their spawning grounds and recovered there one year later. None strayed from the Flamborough spawning ground and four out of 56 strayed from the German Bight spawning ground to a very small one near Botney Gut. None of the Southern Bight spawners were recaptured on either of the other spawning grounds. Fish that were presumably mixed on their feeding grounds segregated to their spawning grounds. The three examples show the greatly different scales of spread from which maturing fish rejoin each other on their spawning grounds.

Terrestrial populations have the appearance of very great complexity, from the beetles in the meadow to the elephants that range the African plains. In the sea, however, much of the complexity of life is not visible and we are surprised when complicated mechanisms start to emerge. In evolutionary terms, the migration circuit has fitted itself into the current structure in a way that ensures reproductive isolation. Indeed the passive larval drift may be considered as the immutable section of the circuit about which the rest of it has to be fitted in order to secure this isolation. It will be suggested below that essential parts of the population control take place predominantly during the larval drift and on the nursery ground.

Genetics in Stock Studies

In the southern North Sea and the eastern English Channel, the Downs herring spawns on five or six small but well-established spawning grounds. Each is about 2 km across and they are about 30 km distant from each other. Recruitments in three different fisheries on this stock are highly correlated, but there are no differences in morphometric or meristic characters (Le Gall, 1935) except the small and persistent one in vertebral count, referred to above; however, there is a difference in blood proteins between the Sandettié and eastern Channel stock (de Ligny, 1969). The stock appears

to be composed of a number of stocklets and such a structure may be a general rule. There appears to be an analogous structure in the British Columbian herring; and in his description of the Norwegian herring stock, Runnström (1941) referred to herring spawners as February (early or late) or early March fish that came repeatedly to the same patches of gravel year after year at the same season. It is possible that the North Sea cod can be separated into stocklets, as shown by the results of tagging experiments, which is not yet confirmed by any blood protein. There are three groups of plaice in the southern North Sea (Harden Jones, 1968) and three groups of Californian sardine (Sprague and Vrooman, 1962; Vrooman, 1964). The prime example of a large stock comprised of an array of stocklets is that of the Fraser River salmon; the fish return to the parent stream and the chance of straying is very low (Foerster, 1936; Pritchard, 1938). Li (1955), a population geneticist, has pointed out that to obtain maximum variation, a large population having no exchange with its neighbors should comprise a number of stocklets that mix with their neighboring stocklets.

In animals other than fish (and indeed in one or two fishes), the genetic basis of blood group differences has been established in breeding experiments. In a sample of fish taken on a particular ground, two alleles should segregate by the Hardy-Weinberg law (i.e., the distribution of the alleles A and B is $AA + 2AB + BB$). This law assumes that mating has taken place randomly and that there has been neither immigration to or emigration from the stock, nor mutation in the two alleles or selection upon them. Because the blood proteins are common to vertebrates and fish, it is reasonable that the blood proteins of fish segregate themselves by the Hardy-Weinberg law. A fit to the law is then considered to justify the assumptions. Further, a deviation from the law, for example a preponderance of homozygotes, is taken to indicate a mixture of populations.

Since the middle fifties a large amount of work has been done on the blood groups of fishes, together with some work on other proteins. One of the best examples is the study of the North Atlantic cod. Figure 11 shows distributions of two proteins (de Ligny, 1969). In Figure 11-a is shown a cline in the hemoglobin HbI' along the coast of Norway, with high values in the north and low values in the south. There are two samples, which deviate from the Hardy-Weinberg law (just south of the Lofoten Island) and have an excess of homozygotes, and they may indicate mixture perhaps with coastal cod. In the Lofoten fishery itself, a distinction has been drawn for a long time between Arctic and coastal cod in the nature of their otoliths. The two forms were shown to differ in the blood groups A and E and in the hemoglobin HbI', but not in transferrins. So within the Lofoten spawning fishery, there must be a mechanism that allows the Arctic and coastal cod to segregate to breed separately.

The distribution of the hemoglobin HbI' across the North Atlantic is shown in Figure 11-b (de Ligny, 1969). The most remarkable point is the sharp distinction between the North Sea (and the adjacent areas) and the

rest of the North Atlantic. The cod in the northern Baltic, however, are closer to those in the open Atlantic than they are to those in the North Sea. But in the western Baltic the fish resemble the North Sea animals. The distribution in the transferrin TFC across the North Atlantic is given in Figure 11-c. There are distinctions between each group shown and across the whole ocean there is a cline, which suggests that the cod on the North American coast have been separated from those on the European coast for a very long period of time. If we combine two distributions, we will see that there is a complex network of many stocks throughout the North Atlantic.

A difference between stocks can be established by comparing gene frequencies in a (2×2) table. For a single allele, differences in proportion of about 20% are significant. Some of the differences between adjacent groups shown in Figure 11 are not very great under this criterion, but others are certainly quite different. However, seven transferrins and three hemoglobins have been identified in the North Atlantic cod populations. With such an array of characters, difference is estimated with a $(2 \times n)$ table and then each group shown in Figure 11 is a distinct one. In other words, the chance of mixture between such populations is very low indeed, perhaps 1 in 10^6 .

The Unit Stock and Recruitment

In the Introduction it was suggested that problems of growth overfishing could find solutions that were to some extent independent of stock unity; it would not necessarily be desirable, but one might imagine stock unity is being defined only by the homogeneity of its vital parameters. A solution to the problem of recruitment overfishing, however, does require the establishment of a proper degree of stock unity, because the variance of recruitment must not include any component from another stock. Conversely, if the unity of the stock has been established in a satisfactory manner, the variance about the stock and recruitment curve must be restricted to recruitment only.

For the present study, however, a much more important point is the dependence of stock unity upon the current structure, which I have called the hydrographic containment of the stock. One part of the structure, the larval drift from the spawning ground to the nursery ground is immutable because the larvae are drifted passively in the regular current from the spawning ground, which is fixed in position (at least in temperate waters). They are spawned into it and they sink out of it, at least in the case of the Arctic cod. In an evolutionary sense, the larval drift forms a geographical base to the stock, for the rest of the migration circuit has to be established to secure its continued existence. It was suggested earlier that the combination

of a longish spawning season and the diffusive processes during the larval drift secure the isolation of the stock on the nursery ground. Later, it will be suggested that the control of numbers occurs mainly during the larval drift and that the control of weight occurs on the nursery ground. Of course the two are not separated processes, but the distinction can be loosely made, as will be shown later.

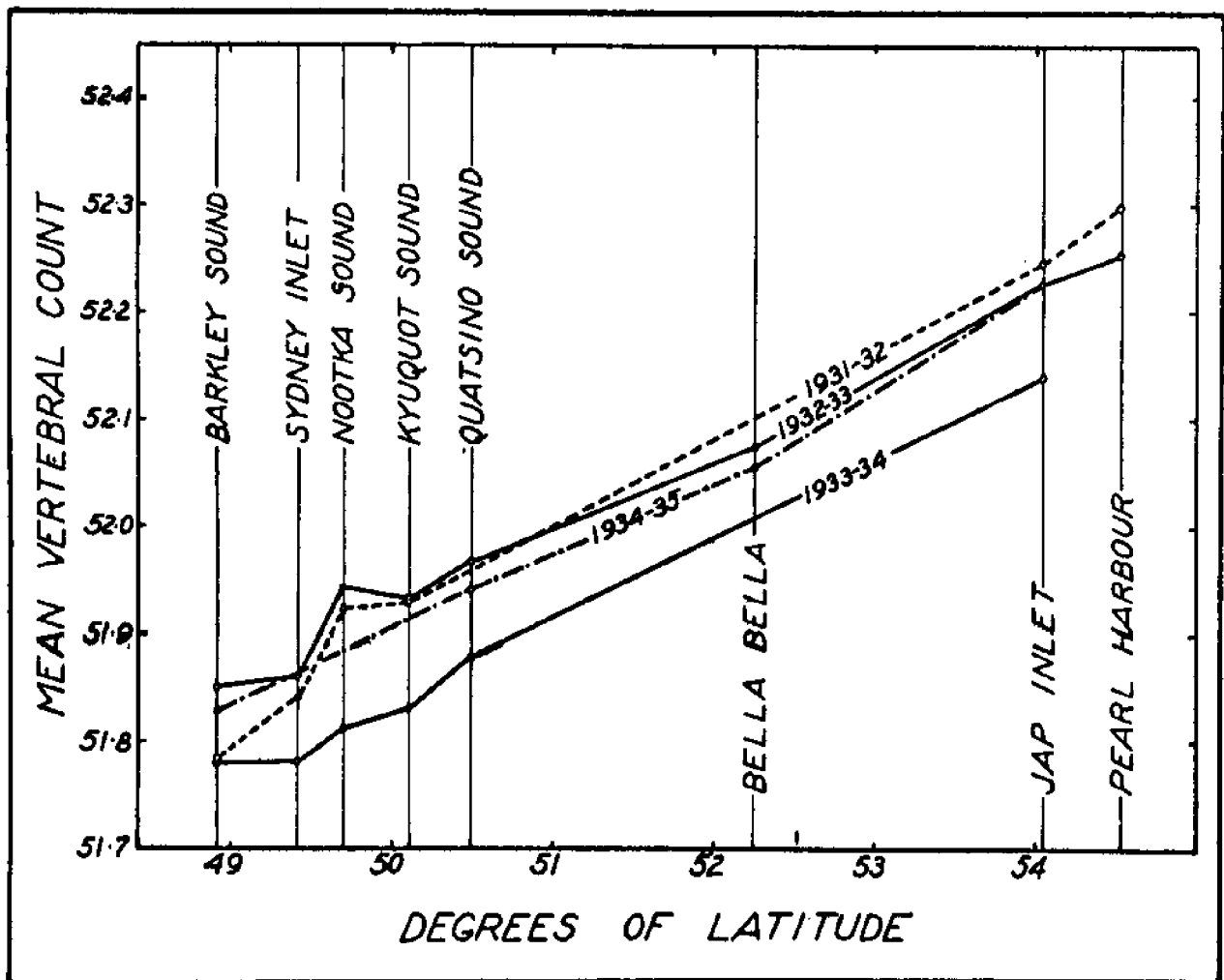


Figure 1. The trend in the number of vertebrae with latitude in British Columbian herring off Vancouver Island (Tester, 1935).

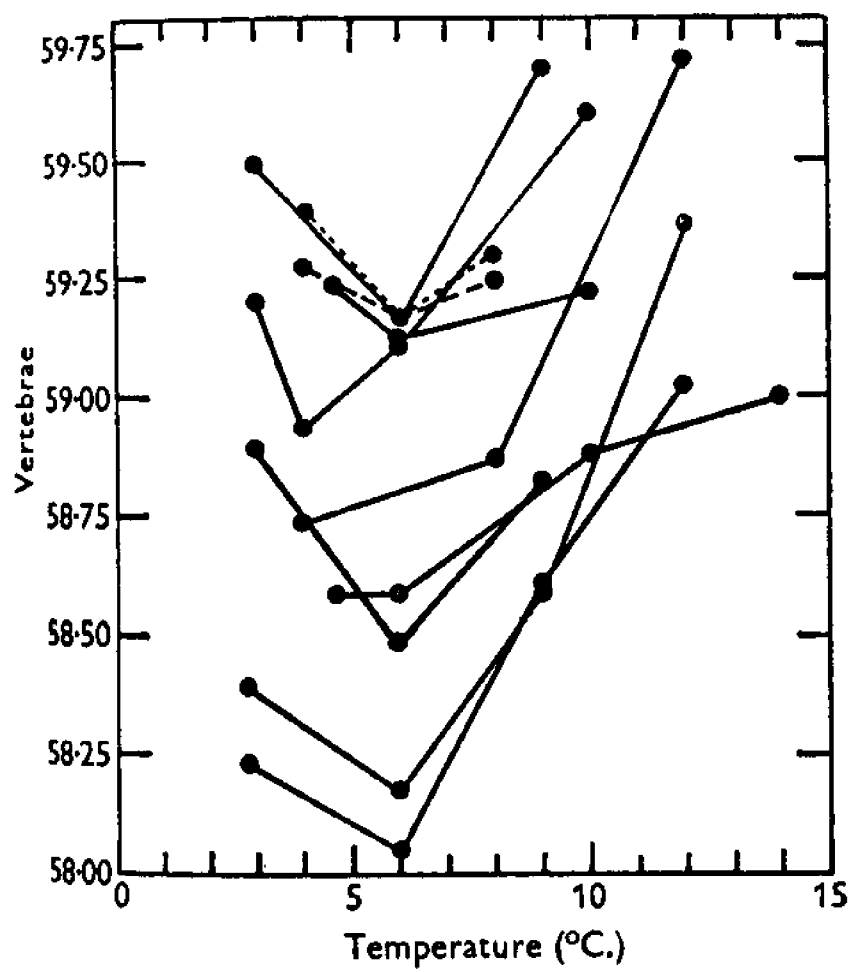


Figure 2. The effect of temperature upon the vertebral counts of trout (Taning, 1952).

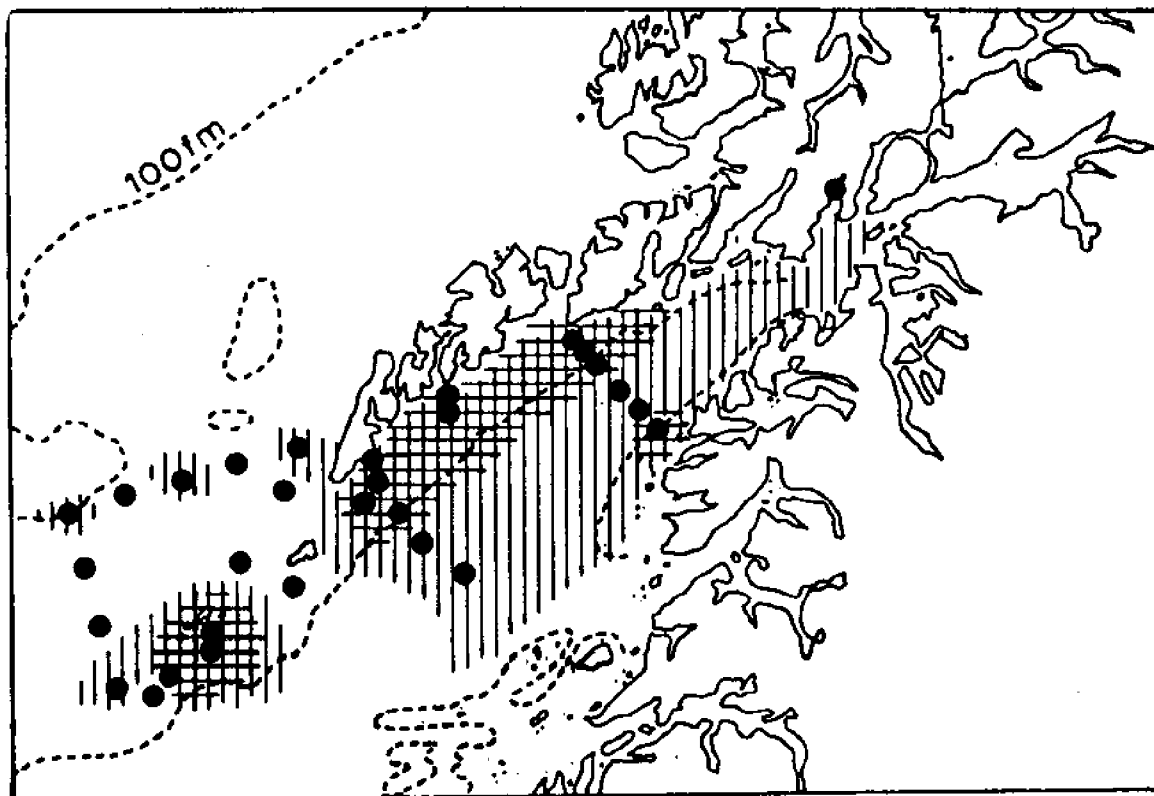


Figure 3-a. The spawning ground of the Arctic cod: distribution of cod eggs (Hjort, 1914).

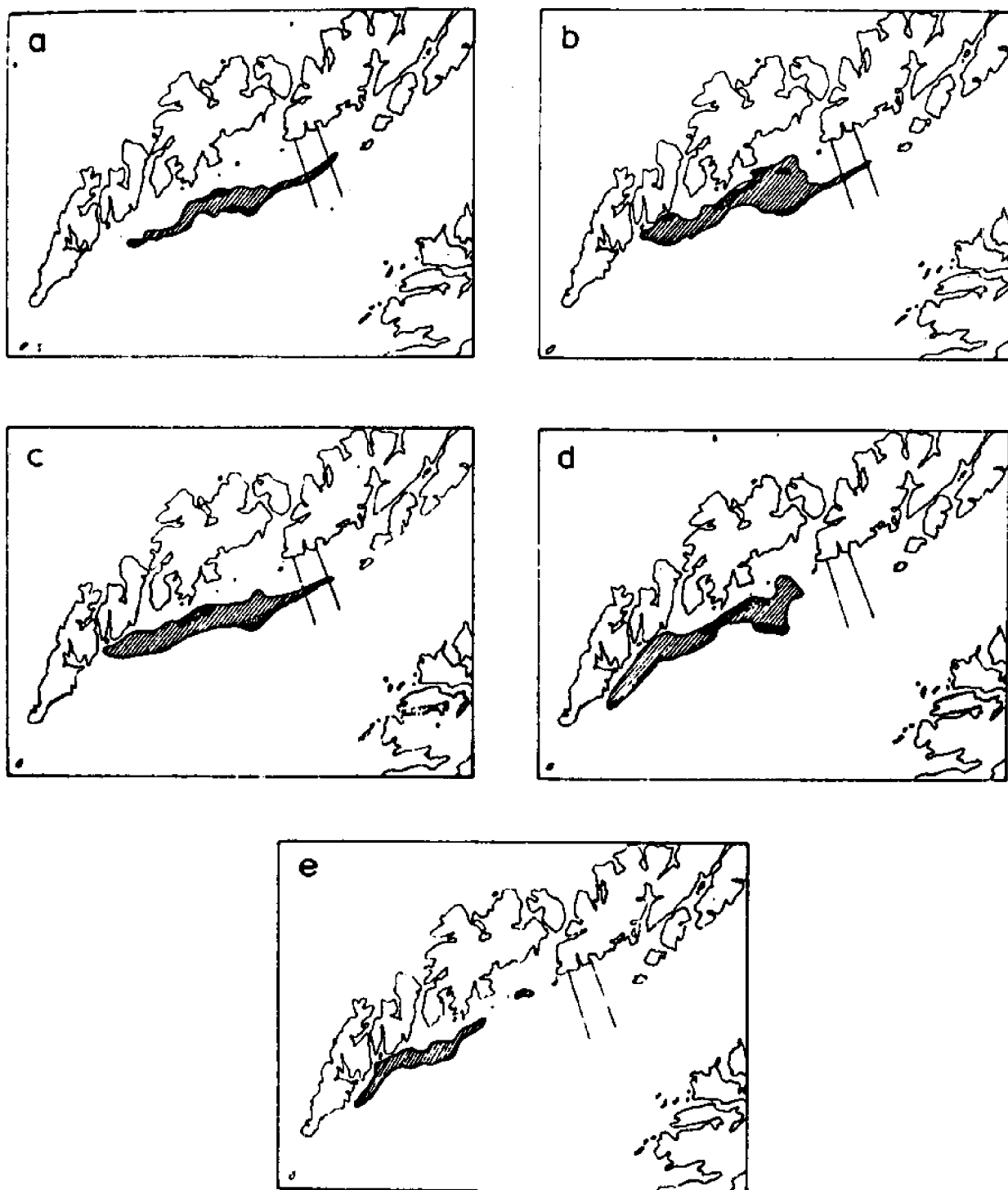


Figure 3-b. The spawning ground of the Arctic cod: distribution of echo traces in March 1955 (Bostrøm, 1955), in successive weeks, a-e.

- a. 1-5 March 1955
- b. 7-12 March 1955
- c. 14-19 March 1955
- d. 21-26 March 1955
- e. 28 March to 2 April 1955

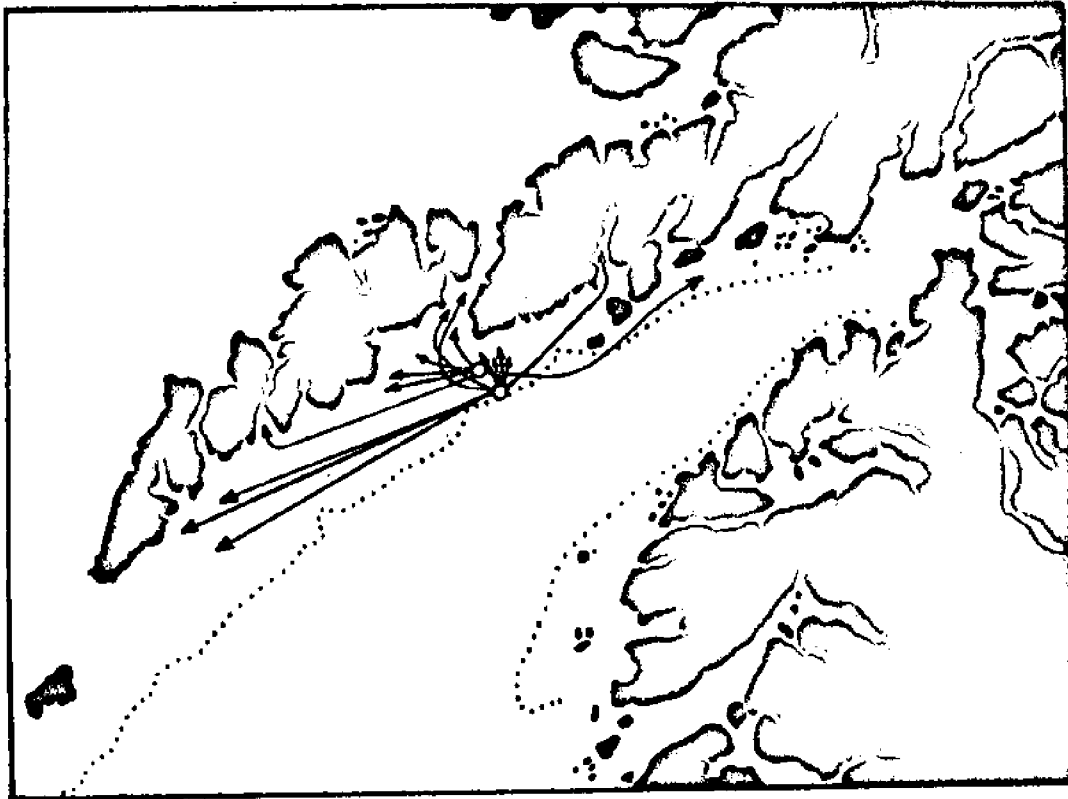


Figure 3-c. The spawning ground of the Arctic cod: local recaptures from tagging on the spawning ground (Hjort, 1914).

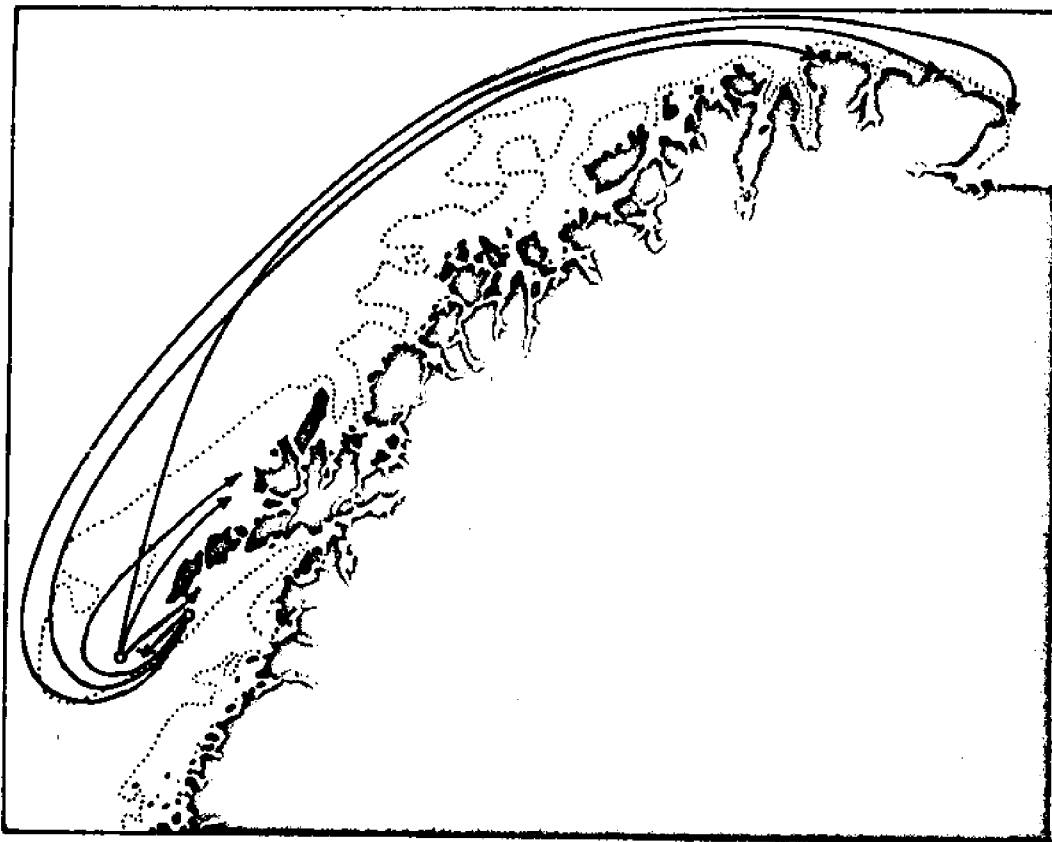


Figure 4-a. The outward migration of the Arctic cod: recaptures in the North Norwegian coast (Hjort, 1914).

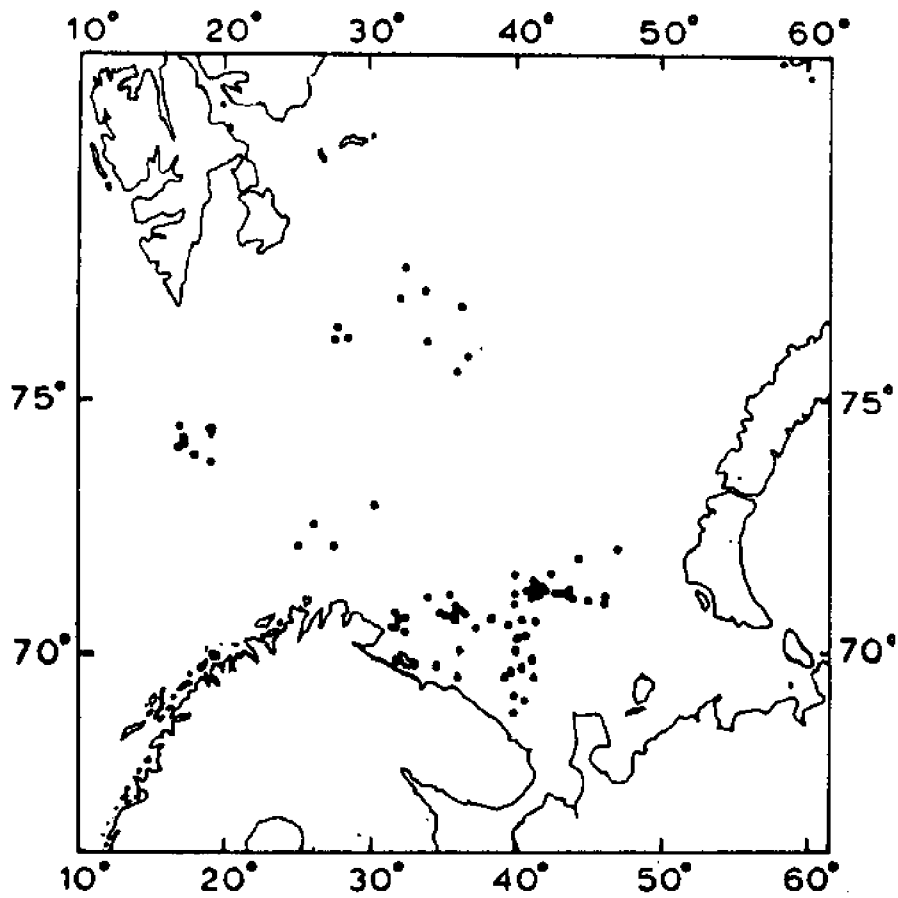


Figure 4-b. The outward migration of the Arctic cod: recaptures in the Barents Sea (Dannevig, 1953).

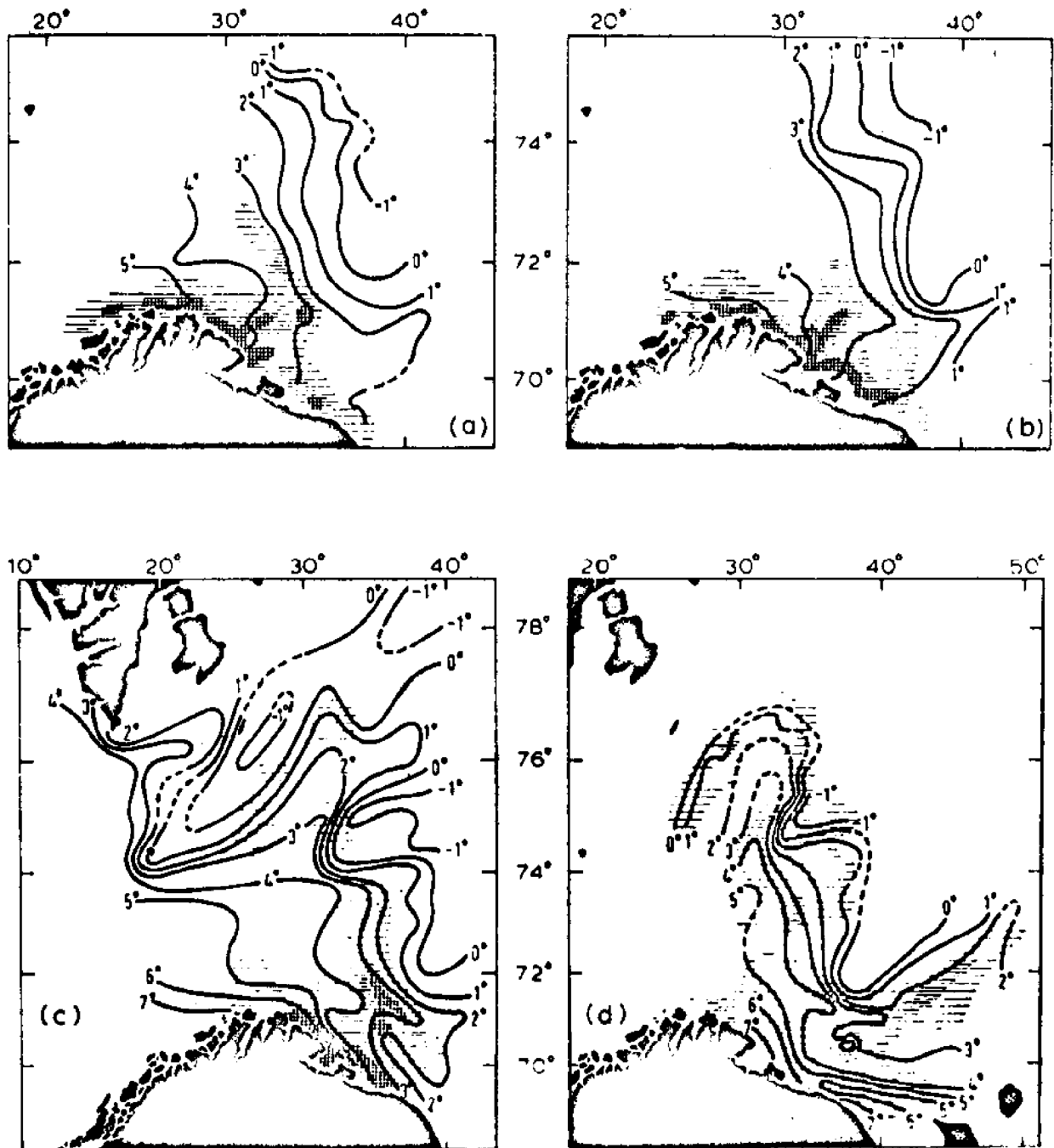


Figure 4-c. The outward migration of the Arctic cod: distribution of echo traces off the North Cape in spring and autumn 1959 (Hysten et al., 1961).

- a. 23 March to 20 April 1959
- b. 22 April to 12 May 1960
- c. 20 September to 24 October 1958
- d. 23 September to 20 October 1959

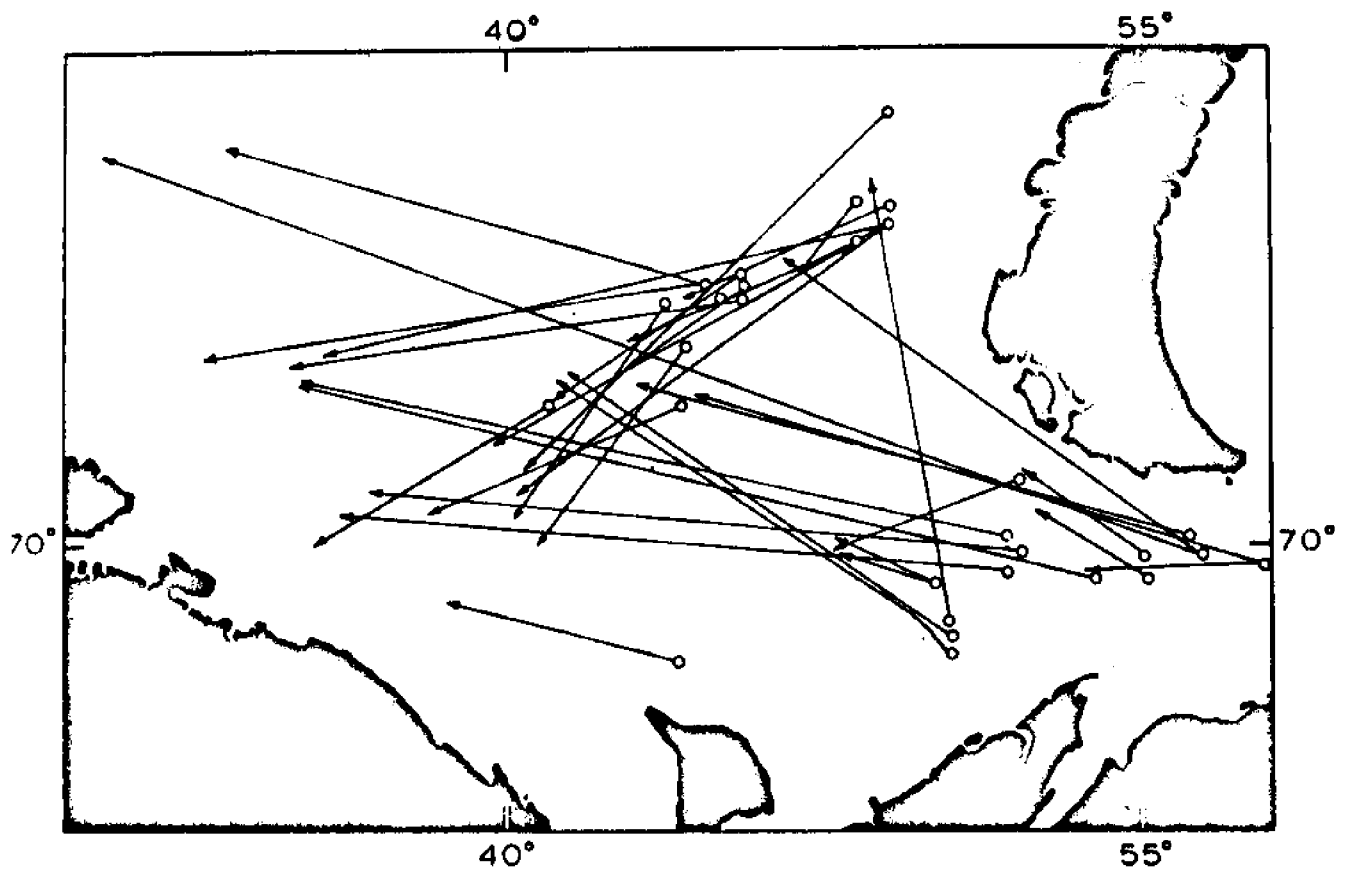


Figure 5-a. The return migration: recapture from the eastern Barents Sea (Mastov, 1944).

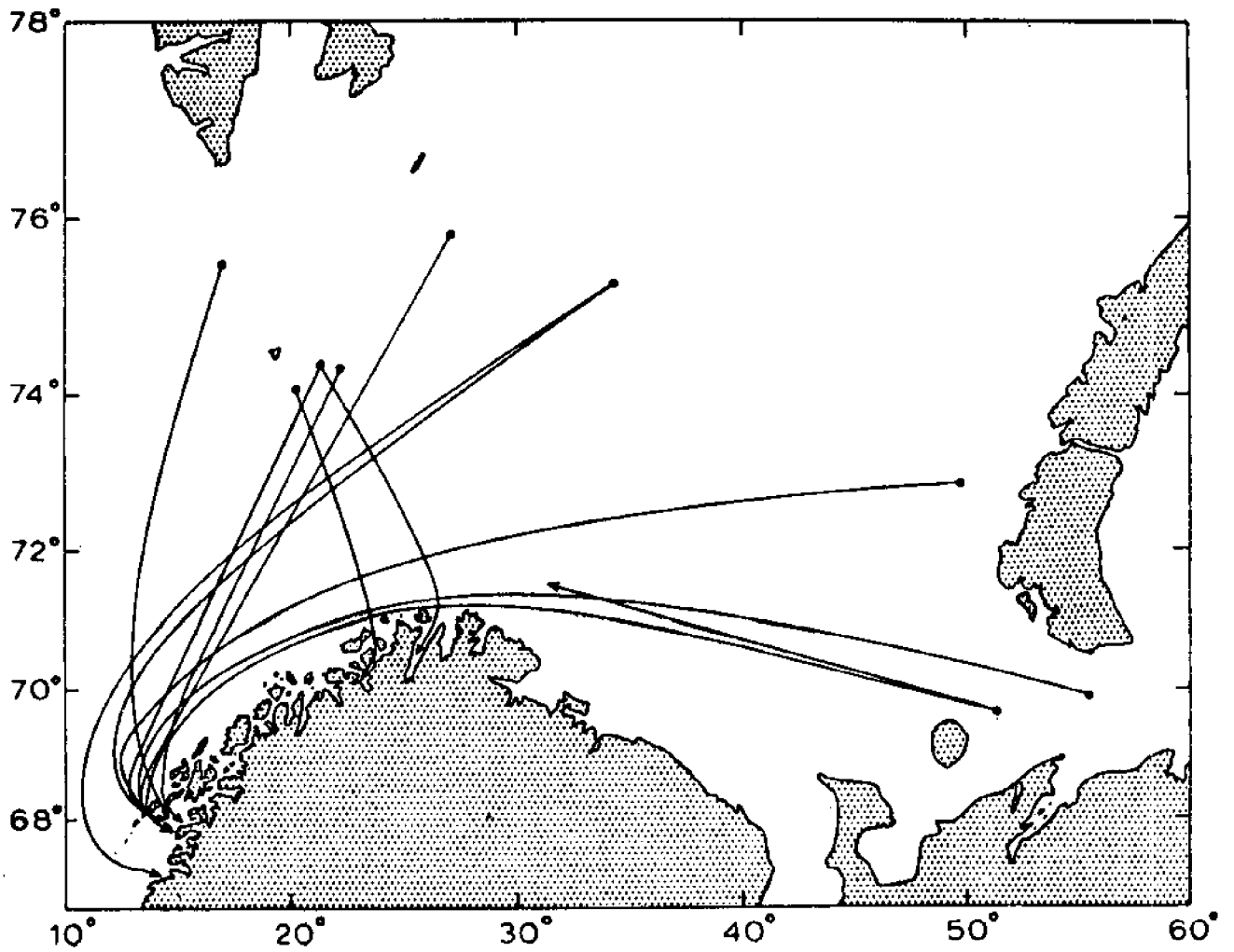


Figure 5-b. The return migration: recapture from the eastern Barents Sea (Idelson, 1931).

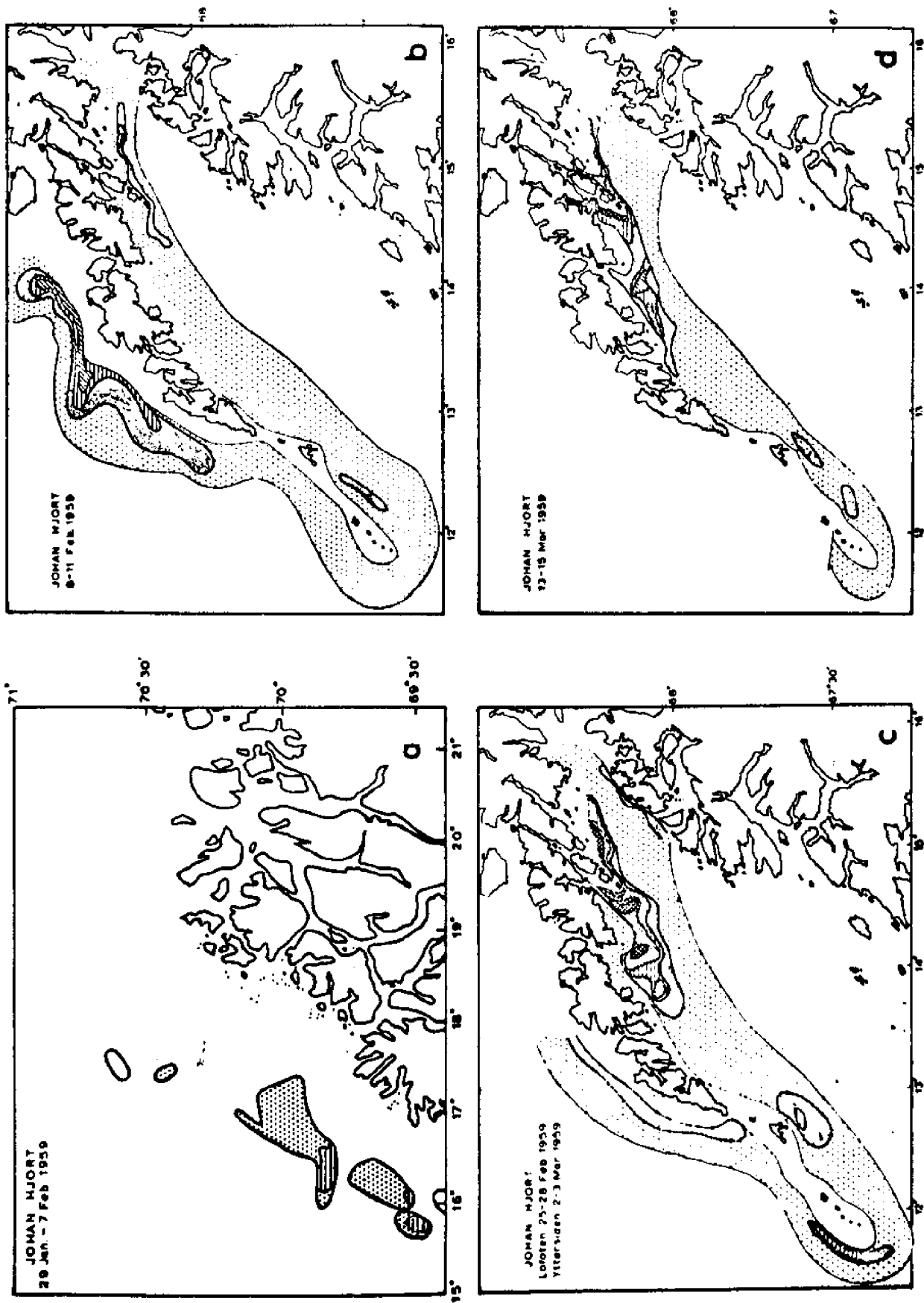


Figure 5-c. The return migration: an echo survey showing the approach of the cod to Vestfjord (Saetersdal et al., 1959).

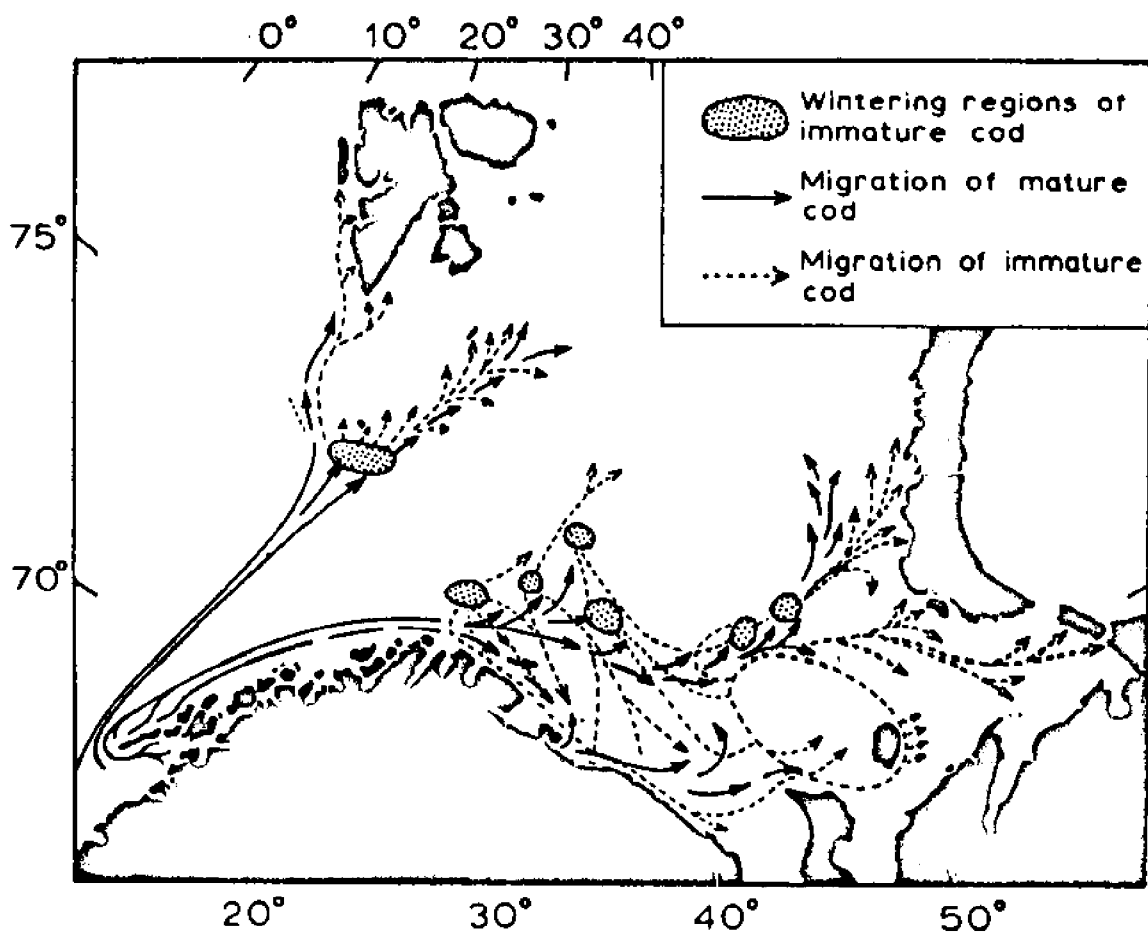


Figure 6. Migration of immature cod in the Barents Sea (Mastov, 1944).

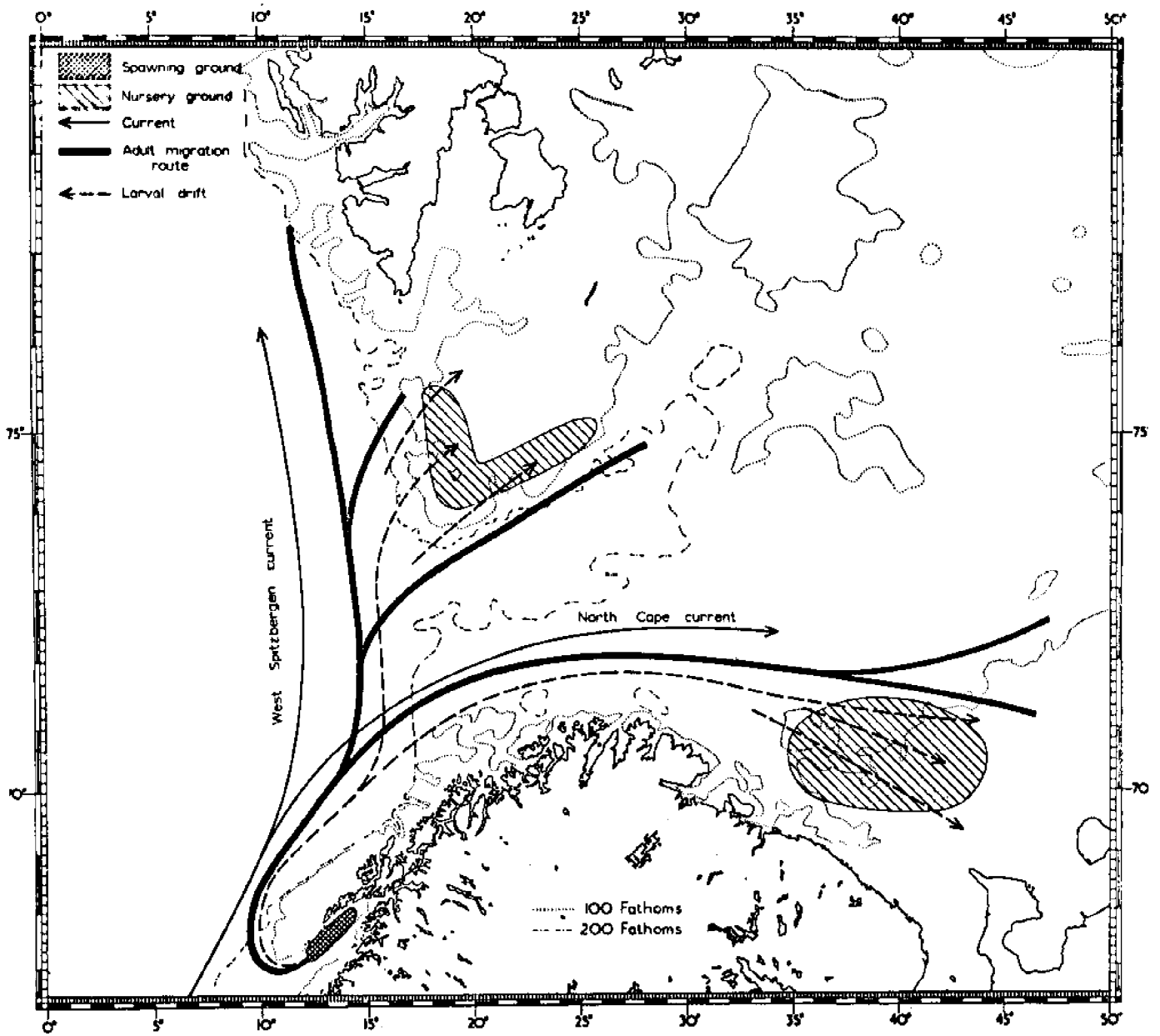


Figure 7. An ideal picture of the migration circuit of Arctic cod.

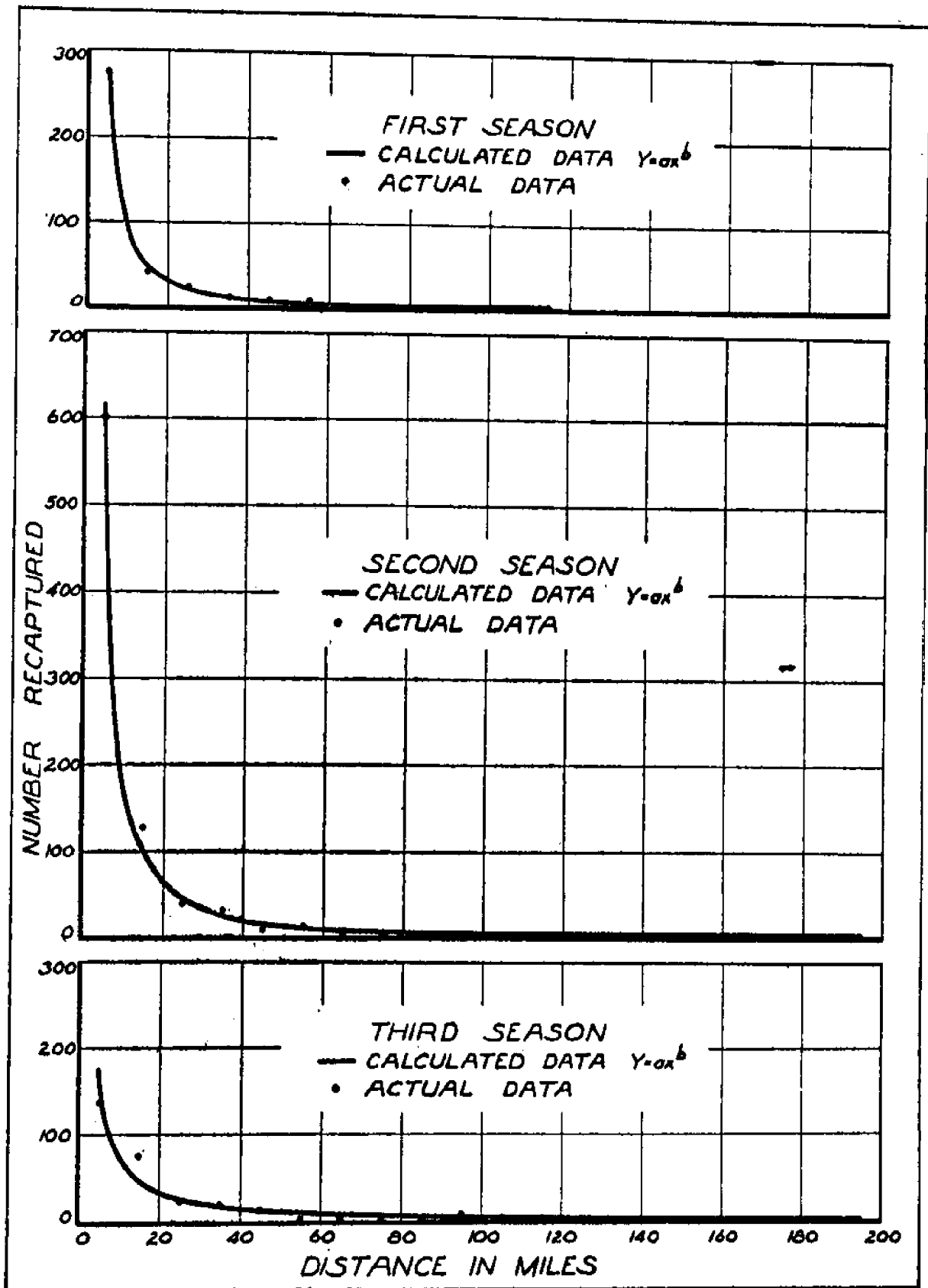


Figure 8. The spread of tagged halibut from the point of liberation (Thompson and Herrington, 1934).

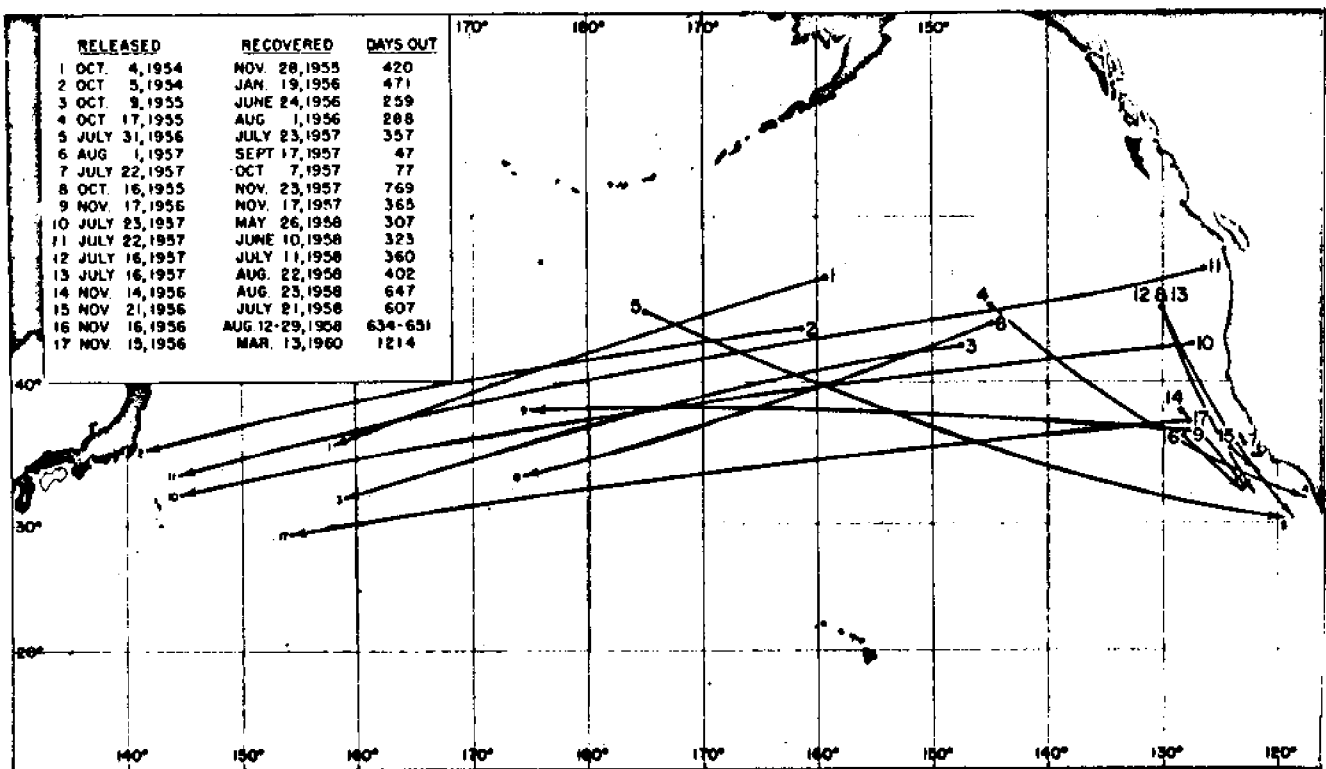


Figure 9. The transpacific migrations of the albacore (Otsu, 1960).

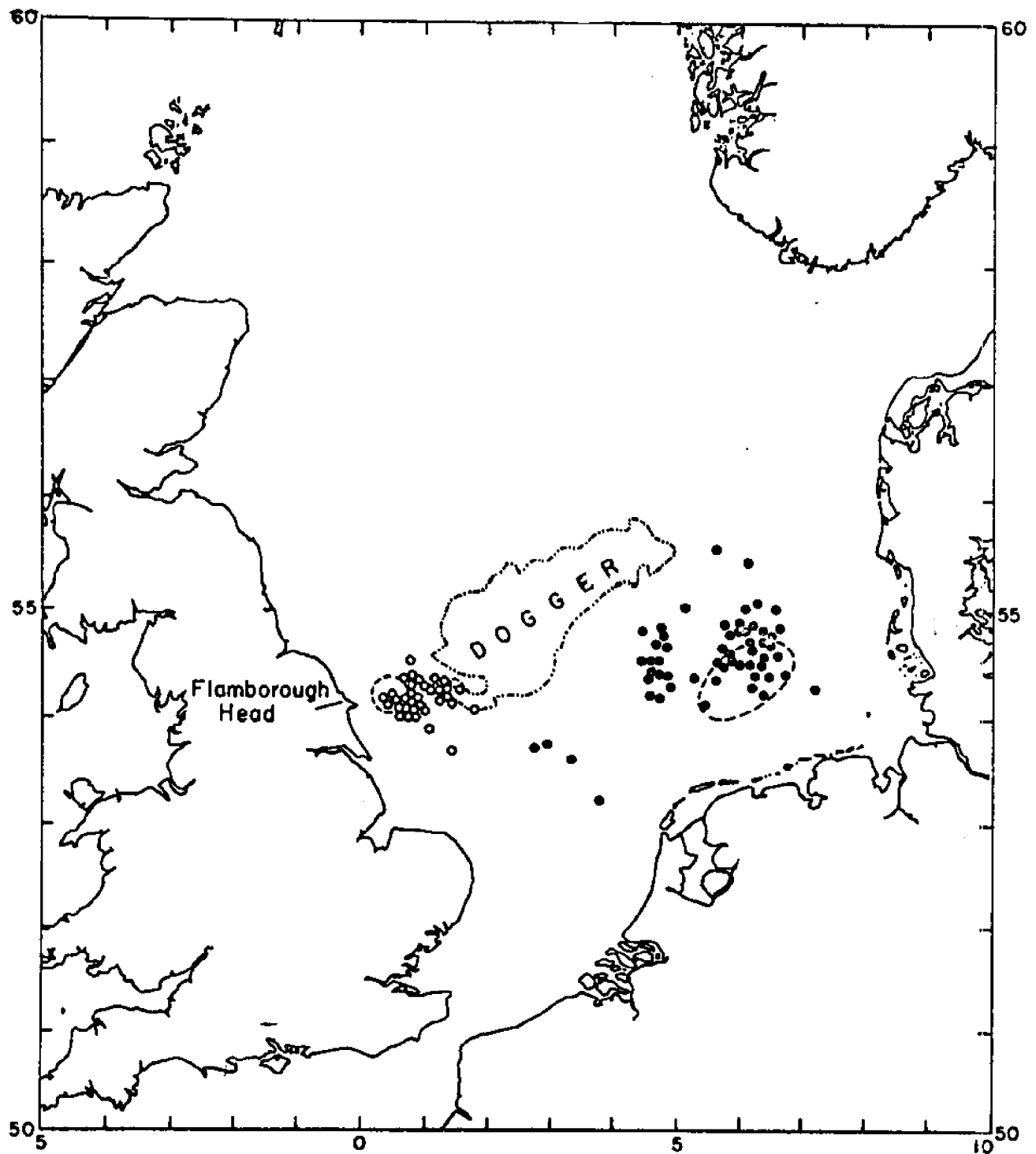


Figure 10. The recovery of plaice tagged on their spawning grounds one year later (de Veen, 1961).

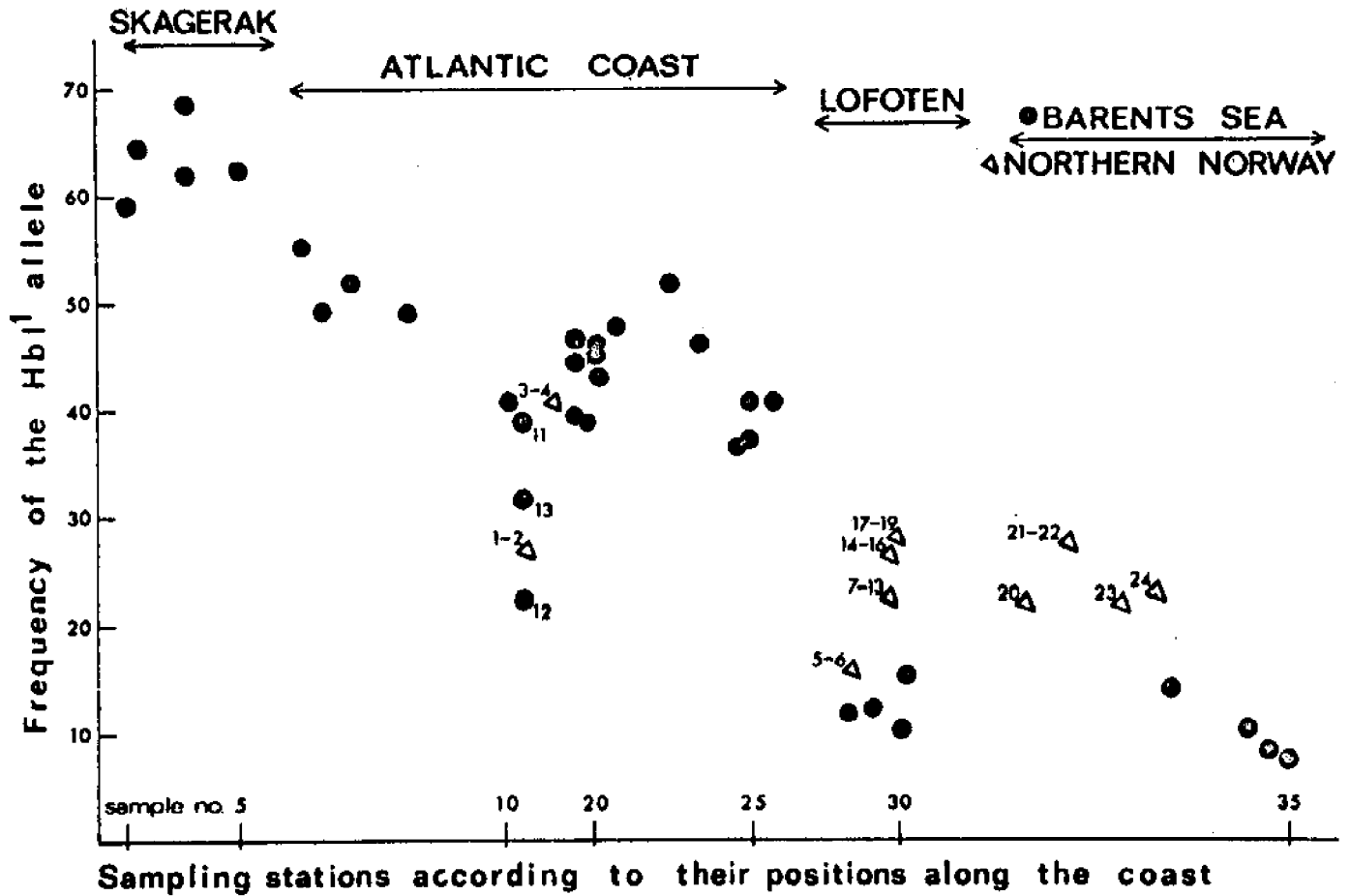


Figure 11-a. The distribution of isozymes in the North Atlantic cod: a cline in hemoglobin in cod along the coast of Norway (de Ligny, 1969).

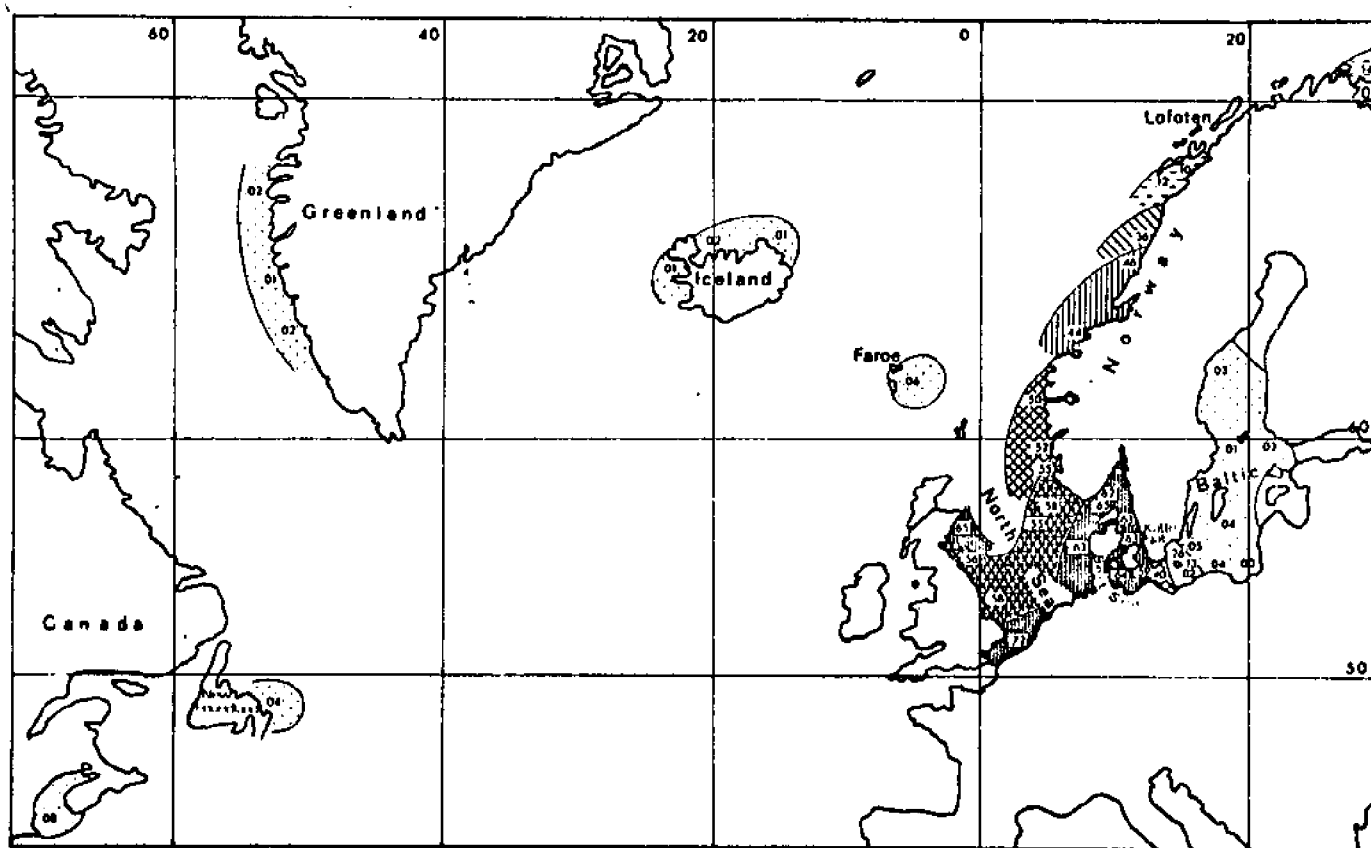


Figure 11-b. The distribution of isozymes in the North Atlantic cod: distribution of the hemoglobin HbI' in the North Atlantic (de Ligny, 1969).

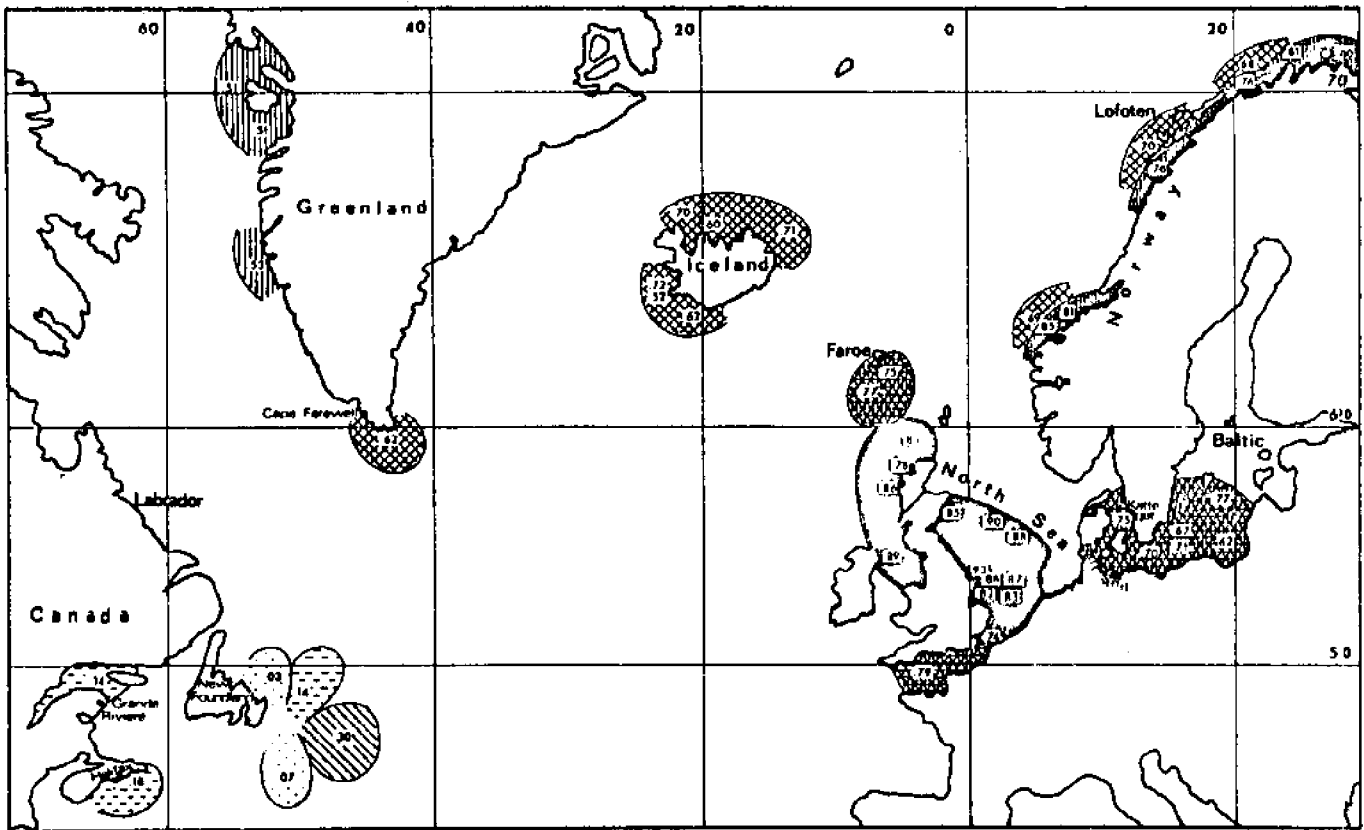


Figure 11-c. The distribution of isozymes in the North Atlantic cod: distribution of the transferrin, Tf^C in the North Atlantic (de Ligny, 1969).

Chapter 2

THE MECHANISMS OF RECRUITMENT

Introduction

Like other vertebrates, fish live for a considerable number of years. In tropical waters a life span of up to 10 years is common and in high latitudes some fishes may live for 20 years or more. A sturgeon 157 years of age has been recorded, but at the other end of the life span scale, *Labidesthes* lives for less than a year (Beverton and Holt, 1959). Because fish live for a long time, a stock has many age groups and recruitment is the annual increment to a stock. The youngest year-class of recruits is the most abundant; it may, however, recruit in parts over a number of years and then the youngest age-group may be less abundant than one perhaps a year or so older. The Pacific salmon lives for about four years, recruits, spawns, and dies in the last year of its life. The exploited stock is effectively a single-aged one, although there is a little spread in other age-groups.

The variability of recruitment is high, both independently and as a proportion of the stock. That of the Downs herring in the southern North Sea varied by a factor of three, whereas that of the Norwegian herring may have changed by two orders of magnitude during periods of 30 to 50 years (Cushing and Bridger, 1966; Marty and Fedorov, 1963). The year-classes of both the North Sea and Georges Bank haddock stocks have also varied by about two orders of magnitude for periods of about 40 years (Jones, in press; Grosslein and Hennemuth, in press). During the sixties the recruitments to the cod, haddock, and whiting stocks in the North Sea increased dramatically and the 1962 haddock brood was 25 times greater than any of its predecessors (Cole and Holden, in press). The high variability and the large number of age-groups may explain why the Leslie matrix has never been used much in the dynamics of fish populations.

Very roughly, the number of age-groups in a stock is a function of the variability of recruitment: the Norwegian herring with 20 age-groups is much more variable in recruitment than the Downs herring with only seven or eight. The variation in recruitment is damped by the number of age-groups in the stock. Under conditions of constant adult mortality, the numbers of eggs generated each year in a multi-age stock must be about the same, so the variability in recruitment is environmentally generated. The Pacific salmon is a single-age stock and the variability of recruitment is not too high. The benign environment of lakes and streams is one in which the stock can survive without damping the variability of recruitment with contributions from many age-groups. The study of the Pacific salmon is very rewarding because the system of stabilization must be the least perturbed by environmental variation.

Conversely, the many age-groups in most fish populations provide the capacity to resist environmental variation. If a stock is to survive, it must retain stable numbers and hence a stabilization mechanism. The study of recruitment and its dependence on parent stock is really the study of such a mechanism. If the mechanism provides stabilization, the stock is insulated to some degree from environmental change in terms of numbers. Hence severe environments would be colonized by populations with effective mechanisms of stabilization.

Fish lay very large numbers of eggs, whether they be Pacific salmon (a few thousand eggs) or old cod (tens of millions of eggs). Elasmobranchs lay eggs in ones or tens and some fish are viviparous, but most are very fecund. A multi-age stock is replaced by the sum of recruitments generated by a year-class; n age-groups in the stock generate n recruitments, the sum of which replaces two parents, or n gonads generate $2/n$ adults in a single recruitment. The mortality between hatching and recruitment is thus very high. The variance of recruitment, however, is very low indeed as compared with the loss in numbers before recruitment (0.3-2.0 orders of magnitude as compared with 5 to 7) and so there must be a very fine control mechanism. Variance is lowest among those stocks that do not experience the worst of environmental change, so their control should be the most precise. If we suppose that mortality is a density-dependent function of age, that is from n gonads to two replacing adults, the problem has been placed in another compartment. The mystery of the fine control has disappeared and the Malthusian sting is blunted, but the new problem is to imagine a chain of predators, each of which appears on stage at the right moment. The growth and death of the little fishes must be matched to the predator system to achieve the control.

Larval Drift

An essential component of the migration circuit is the larval drift from spawning ground to nursery ground, and in temperate waters the larvae move passively with the current from a fixed spawning ground to a fixed nursery. Although the sites of some spawning fisheries, such as that for cod in the Vestfjord, have been known for centuries, the evidence that fish in temperate and high latitudes spawn in fixed positions has been obtained only slowly. The spawning grounds of the Pacific salmon are known in very great detail (Anon, 1950-1966). Those of the Atlantic herring in the North Sea, however, were discovered in two stages: first, by plotting the positions of "spawny" haddocks, which gathered on patches of herring spawn (Hodgson, 1928) and second, by herring trawlers equipped with echo sounders that located the spawning shoals. The latter were particularly successful in the southern North Sea after the Second World War. The herring spawning grounds are of limited extent, for example, 2 km x 500 m at the Sandettié Lightvessel (Bolster and Bridger, 1957) in the southern North Sea; there are five others of the

same limited extent, between the Thames and the Seine, to which the fish returned exclusively each year for a decade at least. Beverton (1962) examined all the plaice egg surveys that had been executed in the Southern Bight of the North Sea since the first decade of the century and showed that the distribution of plaice eggs was a remarkably constant one, between the Thames and the Rhine (Figure 12). Similarly the Norwegian herring spawned on narrow grounds described in some detail by Runnström (1936), although none of them now support a fishery. The evidence that temperate fishes spawn on specific and restricted grounds is not very extensive, but the cod, herring, and plaice are among the commonest in northern waters.

Spawning grounds of such a precisely fixed nature are probably found only in waters poleward of the subtropical anticyclones. In tropical and subtropical waters, the positions of spawning grounds are perhaps less well determined. Ahlstrom's (1966) distributions of sardine eggs off California during a period of nine years show no regularity in spawning position. Tuna larvae are distributed all over the North Pacific anticyclone (Matsumoto, 1966; Ueyenagi, 1969) and maturing yellowfin tend to be found in the eastern North Equatorial Current and off the Philippines (Nakamura, 1969). The diffuse spawning grounds of the open ocean in low latitudes may be associated with the continuous production cycles characteristic of them. Those in upwelling areas also in low latitudes are perhaps variable in position because of differences in the points of upwelling from year to year. In high latitude waters, the production cycle is discontinuous and a fixed position of spawning, together with a fixed spawning season, probably gives the best chance of making the best of a variable production cycle.

The larval drift is well described for the plaice spawning in the Southern Bight of the North Sea. As noted above, the spawning ground lies between the Thames and the Rhine and the eggs hatch after about three weeks, on the average. The spawning ground lies in the center of the main Channel stream. It is water of relatively high salinity and relatively low turbidity and the plaice larvae live in it as they are drifted northeastward. Before the larvae metamorphose and sink to the seabed, the larval drift has carried them to a point off Texel Island in northern Holland (Figure 12).

Production in the Southern Bight is governed by the turbidity. It is a region of swift tidal streams, and Joseph's (1957) figure, which shows the distribution of particles in depth for a number of tidal cycles, provides the evidence that the depth of mixing was just the depth of water. The compensation depth is shallow enough not to be affected much by the tidal variations in turbidity. Lee and Folkard (1969) showed that turbidity increased with rising wind strength and so the compensation depth decreased. Figure 13 shows how critical depth and production ratio change with season and different turbidities. If the depth of mixing is the depth of water, and if turbidity increases in the rising wind, the critical depth is affected by the wind and so is the compensation depth. The course of production is governed by the production ratio D_c/D_m (where D_c

is the compensation depth and D_m the depth of mixing). The production cycle is thus restrained by the wind. An interesting point is that along the course of the larval drift, the water is deeper to the west and to the north. Consequently, production begins off the southern Dutch coast and proceeds along the coast in a northerly direction and then westerly to the open sea. As the larvae drift northeasterly, they move into regions of later production, delayed by as much as a month on average (Cushing, 1967). Thus, the larvae are provided with food all along the course described as the larval drift.

The larval drift ends off Texel Island and the metamorphosed fish are found in the Waddensee, the flats inside the Friesian Islands (Figure 14; Zijlstra, 1972). They are found there almost exclusively. A most interesting point is the mechanism by which the little fish migrate inshore. Dietrich (1954) has shown that near the boundary of Channel water and Dutch coastal water, the bottom water moves shoreward during part of the tidal cycle and the surface water moves seaward in the opposite direction. It is convenient that the larval drift ends at a point at which there is such a mechanism to carry the little fish inshore to the Waddensee. Dietrich also showed that the conditions for this "mill" are uncommon, and that they depend upon the tidal streams flowing parallel to the coast. Such a hydrographic gate occurs in only one other position on the continental coast--north of Esbjerg--and it presumably marks the end of the larval drift of the German Bight plaice stocklet.

The mortality rates of the plaice larvae during the larval drift in the Southern Bight have been estimated by Harding and Talbot (in press). The baby fish were caught with a development of a Gulf III sampler towed at 5 knots; it was fished from surface to bottom and back to the surface again (Beverton and Tungate, 1967). The larvae are retained by the meshes and do not dodge the net to any appreciable degree (D. W. Harding, personal communication). The area of spawning and larval drift is sampled very fully (Harding and Talbot, in press). Because the sea is rough and well mixed during the period of sampling, the patchiness is slight and indeed the coefficient of variation of a single haul can be as low as 10%. The mortality rate is 80%/month and there is every reason to suppose that this estimate is a firm one. Figure 22 shows the trend in numbers with time for four periods.

During the period of larval drift, the density of the animals is maximal and so the density-dependent processes must be at their most intense. In that of the plaice in the Southern Bight there are other fish larvae present, for example cod, whiting, dab, sand eel, and herring. Plaice and sand eel feed mainly on *Oikopleura* and the others feed on copepod nauplii. There is thus the simplest form of food chain, with two groups of larvae competing for two groups of food. Not only is the density at its highest point, but also the opportunity for competition is greatest.

The Nursery Ground

The nursery grounds of fishes have not been well studied until quite recently, but in the last decade some flatfish nurseries have been examined in considerable detail. The first was Percy's (1962) work on the winter flounder in the Mystic River in Connecticut (Figure 15); Riley and Corlett (1965) examined plaice in Port Erin Bay on the Isle of Man. Macer (1967) studied a similar plaice population in Red Wharf Bay on Anglesey off the north-west coast of Wales. Steele and his coworkers have analyzed the population processes in Firemore Bay in Loch Ewe (Northwest Scotland) in a number of publications, some of which will be referred to below. Figure 16 shows the decline in numbers of 0-group and I-group winter flounders on the nursery ground with a similar fall in the mortality rate with age. The initial mortality was 29%/month and during the second year it declined to about 5%/month. Riley and Corlett (1965) examined the decline in density of plaice larvae in Port Erin Bay (Isle of Man) and found that the average mortality rate from July to December was 30-50%/month. The postage-stamp plaice were eaten by I- and II-group plaice, I- and II-group dabs, I-group turbot, and other fishes.

Macer (1967) showed that a new brood of plaice appears in Red Wharf Bay in April or May and at this time some of the little fish have not metamorphosed. The recruitment to the bay is complete by July, but during their first weeks or months on the beach the animals die at the rate of 40%/month. Figure 17 shows the decline in stock density right through the winter; like that in the Mystic River, it rises in January, February, and March presumably after some availability change; perhaps the little fish bury themselves in the sand in midwinter. Consequently, the mortality rate may be said to decrease from 40%/month in the first summer to about 10%/month in the following spring. In Port Erin Bay, however, no such availability change was noticed in midwinter, but no reason for this can yet be adduced. Edwards and Steele (1968) reported a mortality rate for plaice between June and December of about 50%/month; that of dabs declined from 92%/month in the first month to 34%/month subsequently.

The 0-group plaice feed on worms and molluscs. Bregnballe (1961) working in the Limfjord in northern Denmark showed that they fed predominantly on the oligochaete *Paranais literalis*, but also on *Macoma* siphons and *Pygospio* tentacles. In the first days on the Danish beach, the fish put on up to 11% body weight/day. In Red Wharf Bay, plaice, dabs, and gobies feed on *Pectinaria* (up to 7800/m²), *Nephtys*, *Phyllodoce*, and *Ampelisca*. Figure 18 shows the growth of plaice in Firemore Bay, which fed on *Tellina* siphons and polychaete tentacles. But the most remarkable point is the increase in spread of length during the season on the beach, which indicates a sharp competition in growth. Relatively to the mean the increase in spread is not very great, but absolutely it is considerable, particularly if translated into cruising speed or escape speed.

In a study of the exploitation of *Tellina* siphons by 0-group plaice, Trevallion *et al.*, (1970) showed that the initial growth rate on the beach was governed by the numbers of *Tellina* siphons eaten. The growth rate was proportional to the quantity of food available following the traditional form of Ivlev curve, so the increment of weight depends on the quantity of food. Steele and Edwards (1969) showed that the energy intake of the population remains uniform throughout the season for four years, so the growth of individuals depends upon the mortality rate. Figure 19 shows the dependence of weight increment (per unit of energy metabolized) on mortality, with the apparently surprising result that the greatest energy transfer occurs when the death rate is greatest. The figure represents a time series, with high mortality and high growth during the first days on the beach and the low values in the winter. If the curve is really convex as suggested in the figure, the proportion of growth to mortality increases with time on the nursery ground.

In each of the bays examined, there are I-group and II-group fish, survivors of earlier year-classes. In Red Wharf Bay, 70% of the fish are 0-group plaice and 5-7% are I-group plaice and dabs, both of which live in rather deeper water. In Port Erin Bay, the 0-group plaice are eaten by I- and II-group plaice, I- and II-group dab, I-group turbot, and other fish. It is possible that codling play the same part in Firemore Bay (Edwards and Steele, 1968). The fish may represent only a part of the predatory system, but the important question is whether there are enough I-group plaice to generate a critical mortality; in other words, is cannibalism an essential part of the regulatory system?--or is mortality merely part of a predatory net?

The earliest statement on the generation of recruitment was that of Hjort (1914), who suggested that there was a critical phase in the life history when the failure to feed after the absorption of the yolk sac was responsible for fluctuations in recruitment. In detail, Hjort's thesis is no longer maintained, but the idea of a critical phase has survived, for example, the period of larval drift or the period on the nursery ground. However, if density-dependent mortality were considered to continue throughout the life cycle, there should be no critical phase. If density-dependent mortality continues, density-dependent growth might do so also, but both processes would be expected to decay with age. Then the important factor is the difference between growth and mortality, which declines in the life cycle.

The Variation in the Production Cycle

The production cycle continues throughout the year in subtropical and tropical waters and stops in winter as in higher latitudes. Colebrook (1965) has pointed out that the discontinuous cycle of temperate and high

latitudes (a roughly bell-shaped curve) can vary in amplitude, timing, and spread. The variability of the cycle depends upon the critical depth and the development of the production ratio, as described above.

Figure 20 shows differences in the production cycle in British waters; the curves are of "greenness" sampled with the plankton recorder (which collects plankton at 10 m along standard routes once a month) and are averaged for a period of 14 years (Colebrook and Robinson, 1965). There are three groups of production cycle: (a) those in the central North Sea with spring and autumn peaks of equal magnitude, (b) those elsewhere on the shelf with a dominant spring peak, (c) those in the Ocean beyond the continental shelf with a single summer peak. Associated with these groups of production cycle are three groups of herring--autumn, winter, and spring spawners. The autumn group spawns in the northern and central North Sea and their larvae grow up during the period of the autumn production cycle. Blaxter and Hempel (1963) have shown that there is a point of no return for yolk-sac herring larvae, after which they die even if food becomes available. Cushing (1967) estimated the point of no return after the midpoint of the spawning period and showed that it occurred in the middle of the production cycle, so the larvae had the best chance of survival. The winter-spawned herring were linked to production cycles in late winter or very early spring. The spring spawners depended on a later cycle in early summer: an exception was the Norwegian spring spawners in the Baltic outflow, linked to the spring production cycle, which occurs in March. The Baltic outflow is a shallow layer of freshish water over saltier water in the Norwegian deep waters. Thus the three spawning groups of herring are linked to three forms of production cycle.

Between the three groups of herring, there are considerable differences in growth and reproduction (Cushing, 1967). From winter and autumn to spring spawners, W_{∞} increases and K decreases--that is, the spring spawners are the biggest and the winter spawners the smallest. In the winter and spring spawners, the maturation stage V lasts for many months, whereas in the summer spawners it endures for only three or four weeks. The eggs of the winter and spring spawners are twice as big as those of the autumn spawners. Such differences are profound ones and imply that the spawning groups have perhaps the status of races. If during a long period of time, in an evolutionary sense, the three groups have segregated into three races, then the links with the production cycles are of considerable importance. Differences are established through the isolating mechanisms, but the fact that the differences are associated with the three forms of production cycle implies that they originate in the early stages of life.

There are two sorts of variability of importance in a study of year-classes. The first is manifested in the random variation in the timing of the production cycle, which may be expressed in the variability

of recruitment to some fish stocks. The second is the response in brood strength to the long-term climatic trends. In European waters, there are continuous trends between periods of westerlies and southerlies, between climatic deterioration (nasty), and climatic amelioration (nice). The Norwegian and Swedish herring periods occur alternately within the framework of this climatic periodicity. Within any one period, the year-classes of the Norwegian herring vary about a mean, but at particular points in the climatic periodicities they decrease or increase sharply, extinguishing or reincarnating the fishery. The fish stock has effectively rectified the climatic variation by living at two successive levels of abundance and within each of these levels, and to a certain variability, the stock in numbers is insulated from the climatic variation.

The Times of Spawning

If the production cycle, the source of food for the larvae, varies randomly in timing, the fish should spawn at some point in time to take the best advantage of it. If spawning time were correlated with the timing of the production cycle, the fishes would have to mature and spawn in some way dependent upon the weather. A more conservative procedure would allow the fish stock to spawn at a fixed season.

Figure 21-a shows how the date of peak spawning has remained steady (with one or two exceptions) for a number of streams in the Fraser River system; there is no upward or downward trend in the time series except in two or three instances out of the fifty-one stocklets. Figure 21-b gives the dates of spawning from grab samples for the Norwegian herring for a short period of years. In Figure 21-c, the dates of peak catches of the Arcto-Norwegian cod in the Vestfjord are given for a long period of years; in each year, catches are recorded by weeks and the peak catch is taken as indicating the peak spawning. There is a trend in the data which resembles that of recent climatic changes in the Northeast Atlantic, but the range of the trend is only seven days. An examination of all the plaice egg surveys that have been carried out in the Southern Bight of the North Sea revealed that the average date of peak spawning occurred on 19 January, each year with no trend in time. Different methods were used for each of the four species and between them the four comprise a large proportion of the fish catches in the northern hemisphere. The standard errors of the mean peak spawning date ranged from three to six days. This account is taken from Cushing (1971).

The spawning season in each species lasts for quite a long time, perhaps three months, yet the standard error of the peak date may be less than a week. I have already noted that the long spawning season secures the reproductive isolation of the stock, but the wide spread of spawning ensures that late spawners at least would profit from a late production cycle. An interesting point from Figure 21-c is that there is a slight

trend towards later spawning, of about seven days, in a 70-year time series for the Arcto-Norwegian cod. It is possible that this small trend is associated with the climatic change in the twenties and thirties of the present century; if so, there is some evidence of adaptation to climatic change, even if it is rather slight.

Seasonal timing is often achieved in animals by photoperiod. There is no evidence yet that the spawning time of any of the four species is governed by photoperiod. However, the trend in the catches of Arcto-Norwegian cod could be related to an increase in cloud cover in the later winter during the climatic trend, and then the spawning date might be delayed with none in the photoperiod itself, in terms of the daily period of sunlight at 70 m, (the depth at which the Arcto-Norwegian cod spawn).

When the spawning times of the Californian sardine were examined for a period of about a decade, no regularity at all was detected; indeed the error in any date of peak spawning would be estimated in months rather than in days or weeks (Cushing, 1971). The summer spawners in the English Channel, from Russell's evidence (1934), also spawn irregularly. In British waters, the summer spawners, southern animals, tend to be serial spawners, whereas the northern fish, the spring spawners, spawn as quickly as water can be taken up by the ripening eggs. The division between northern and southern animals in British waters may represent a boundary that corresponds to the subtropical convergence in the open ocean. Poleward of this boundary, the production cycle is discontinuous and towards the Equator it is continuous; perhaps the serial spawners were originally associated with the continuous production cycles of tropical and subtropical waters.

There appear to be two generalizations. First, poleward of the subtropical convergences, spring (and perhaps some autumn) spawners have a fixed season, extending for about three months. The larvae are hatched in an average season in the midst of the spring production cycle; but in an aberrant season, the same larvae may be hatched into empty water. Second, in low latitudes, serial spawners may spawn at any time, like the tuna, in nine months of the year. Whenever the larvae are hatched, food is available. In the upwelling areas, where the production cycles are possibly homologous with those of higher latitudes, spawning times are variable, perhaps because after upwelling has started, food is generally available.

The Match of Spawning to the Production Cycle

The fixed time of spawning is associated with the variable timing of the production cycle in temperate waters. In any one year, however, the temporal distribution of the production of fish larvae in time should match that of their food in order to obtain the maximum survival. Under conditions of constant stock quantity, differences in survival from egg to recruit are responsible for differences in the magnitudes of recruitment. The highest recruitment may be generated by the best match of the two distributions in time, that

of fish larvae and that of their food. Conversely, a mismatch between the two distributions will generate the least recruitment. Such a thesis requires that recruitment be determined predominantly during the larval drift. A number of predictions have been made of recruitments from the numbers of 0-group fish just after metamorphosis (for example Wimpenny, 1960; Nizovtsev, 1968). Such predictions presume that density-dependent processes are in the main complete and that recruitment has been more or less determined by the time of metamorphosis. However, density-dependent processes may continue throughout the life history and recruitment may not be finally determined until the young fish actually join the adults in the open sea.

In broad terms, the variance of recruitment about the stock/recruitment curve is a function of the match or mismatch of larval production to that of the larval food. The timing of larval production is a function of the time of spawning and the variation of development rate with temperature. Figure 22 shows the observed loss rates of plaice larvae in the Southern Bight of the North Sea for a few year-classes (Harding and Talbot, in press); this diagram provides the evidence for the mortality rate in larvae of 80%/month. But the important point here is that for the 1963 year-class, hatched during the cold winter of 1962-1963, the rate of development was very much slower and the egg mortality was much less. Figure 23 shows the development of the 1963 year-class in subsequent years (Harding and Bannister, unpublished MS). In 1963 the production cycle itself was probably not delayed very much because the cold winters in European waters occur during anticyclonic conditions and therefore fairly calm seas, and the rate of photosynthesis is not affected very much by temperature. The match of larval production to that of their food in 1963 might well have been optimal because the larval production was delayed by the cool water and the production of their food might have been advanced by the calm weather.

Recruitment and Stabilization

In broad terms, the variance of recruitment about the stock/recruitment curve is a function of the match or mismatch of larval production to that of the larval food. The stabilization mechanism works in the match/mismatch process by altering the number of eggs produced; with a larger number of eggs, the food/larva is reduced and so the chance of survival is reduced. In such a way is a density-dependent mortality introduced into the system. If recruitment is always greater than stock at low levels of stock and less at high levels, the form of density-dependent mortality creates a stabilization mechanism by which recruitment always returns the stock to a middle level. The magnitude of recruitment is generated in an evolutionary time period by competition. My present thesis is that the three processes--the determination of recruitment, the stabilization of numbers by density dependence, and the establishment of the magnitude of the stock by competition--all achieve their greatest effects during the larval drift. Another way of putting it is to say that all three are components of the single process, the way in which fish larvae grow and survive upon the available food.

Numbers are stabilized in the face of high environmental variability, which is reflected in the variation of recruitment. Indeed the latter may be a direct reflection of the changes in the weather. Recruitment variation is, however, damped by the number of year-classes in adverse environments and by the stabilization mechanism in all environments. The population is thus insulated from the variation in the environment as expressed in stock numbers. However, it was pointed out above that climatic change is a continuous process, and the period in the Northwest European waters is of 70-100 years. So far as we can see, some stocks like the Arcto-Norwegian cod stock vary only moderately in the face of climatic change, whereas others, like the Norwegian herring, vary drastically. Such capacities must be accounted for in the mechanism of recruitment.

Figure 24 shows a diagram of the dependence of recruitment upon parent stock and the stock stabilizes itself about the point where the curve cuts the bisector. The variability of recruitment is indicated by the two ordinates, a and b, and the arrows show the direction of stabilization: for example, a high recruitment to a low stock (a) returns the stock towards the point of stabilization. But another condition is shown when recruitment is below the bisector at low stock or above it at high stock. Then the addition of recruitment is in the direction of instability. If in response to climatic change, a number of such low or high recruitments occur in sequence, the magnitude of the stock must change considerably. Such a mechanism suffices to describe the disappearance and resurgence of the Norwegian herring fishery in its periodic fluctuations and to account for the enormous increases in numbers on colonization of new areas.

The recruitment mechanisms, as envisaged here, are subtle and complex. There is a simplicity in design, however, in the part played by the larval drift. It is fixed in time by the fixed spawning season and in space by the fixed spawning ground and the inability of the larvae to do anything but drift with the current. In this sense it forms the geographical base of the migratory circuit, from which the animals spread and to which they return. In addition, because of the high densities in the planktonic environment and because of the relatively simple food web there (for the fish larvae), density-dependent processes are at their most active and competition is most effective. At the same time, the magnitude of recruitment is probably determined during this period and so the three most important components of numerical stabilization are in fact parts of a single and essential process, the conversion of food into growth by the larvae in the face of mortality. It is unlikely that the density-dependent processes stop there, but may continue in decaying fashion throughout life. Lastly, if the stock and recruitment curve describes the stabilization mechanism properly, means are also provided by which the stock can increase or decrease in numbers enormously in the face of climatic advantage or disadvantage. Thus, the larval drift provides not only the geographical base for the stock's existence but also the conditions for the natural regulation of numbers that provides the temporal base for its evolutionary existence.

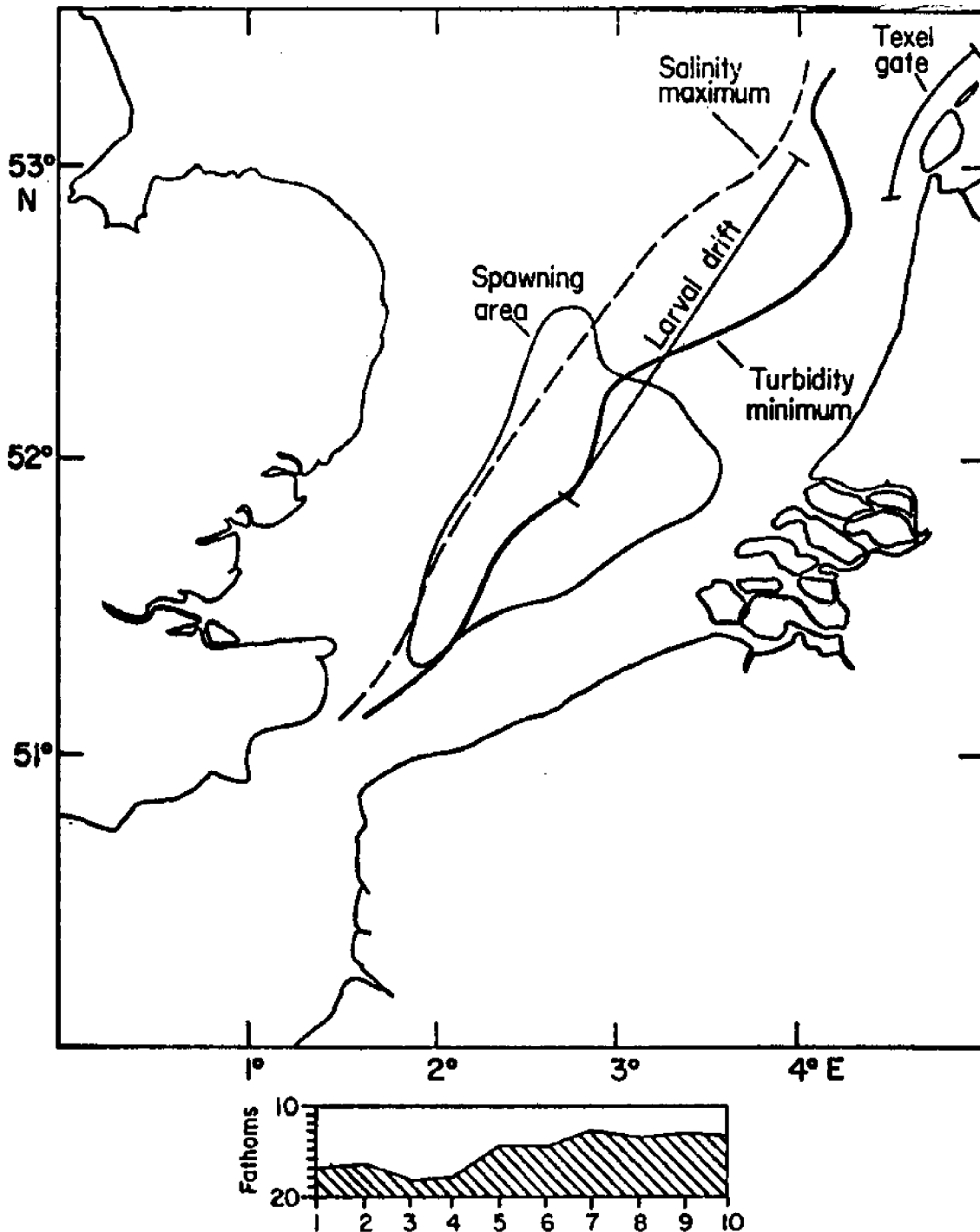


Figure 12. The center of the spawning ground of plaice in the Southern Bight (after Simpson, 1959), the larval drift in the water of maximum salinity and minimum turbidity and the Texel gate to the inshore region (Dietrich, 1954). Inset below shows the average depth along the larval drift, with fifteen miles on either side.

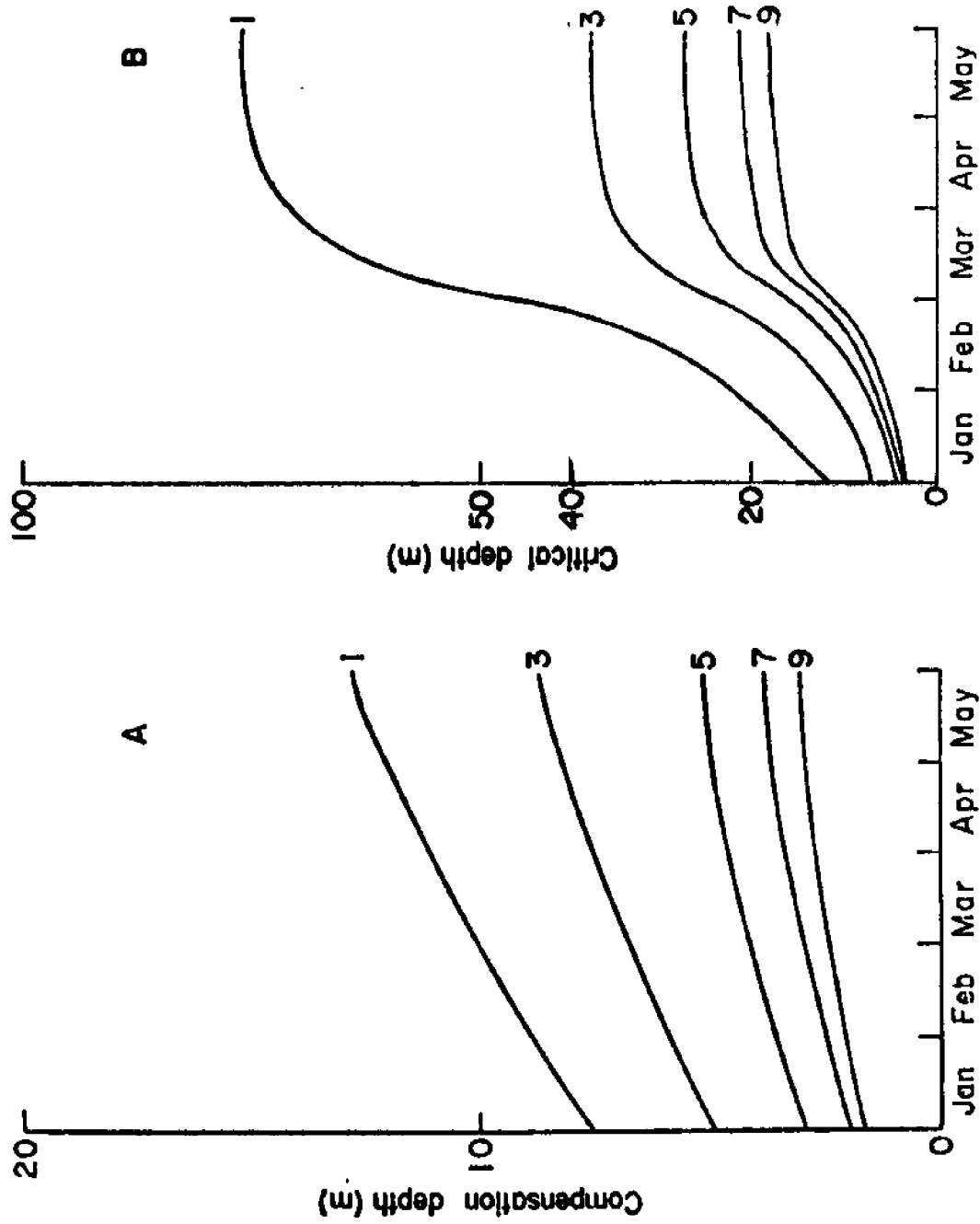


Figure 13. (a) Compensation depths in the Southern Bight of the North Sea from January to May in coastal water types 1, 3, 5, 7, and 9. (b) Critical depths in the Southern Bight of the North Sea from January to May in coastal water types 1, 3, 5, 7, and 9.

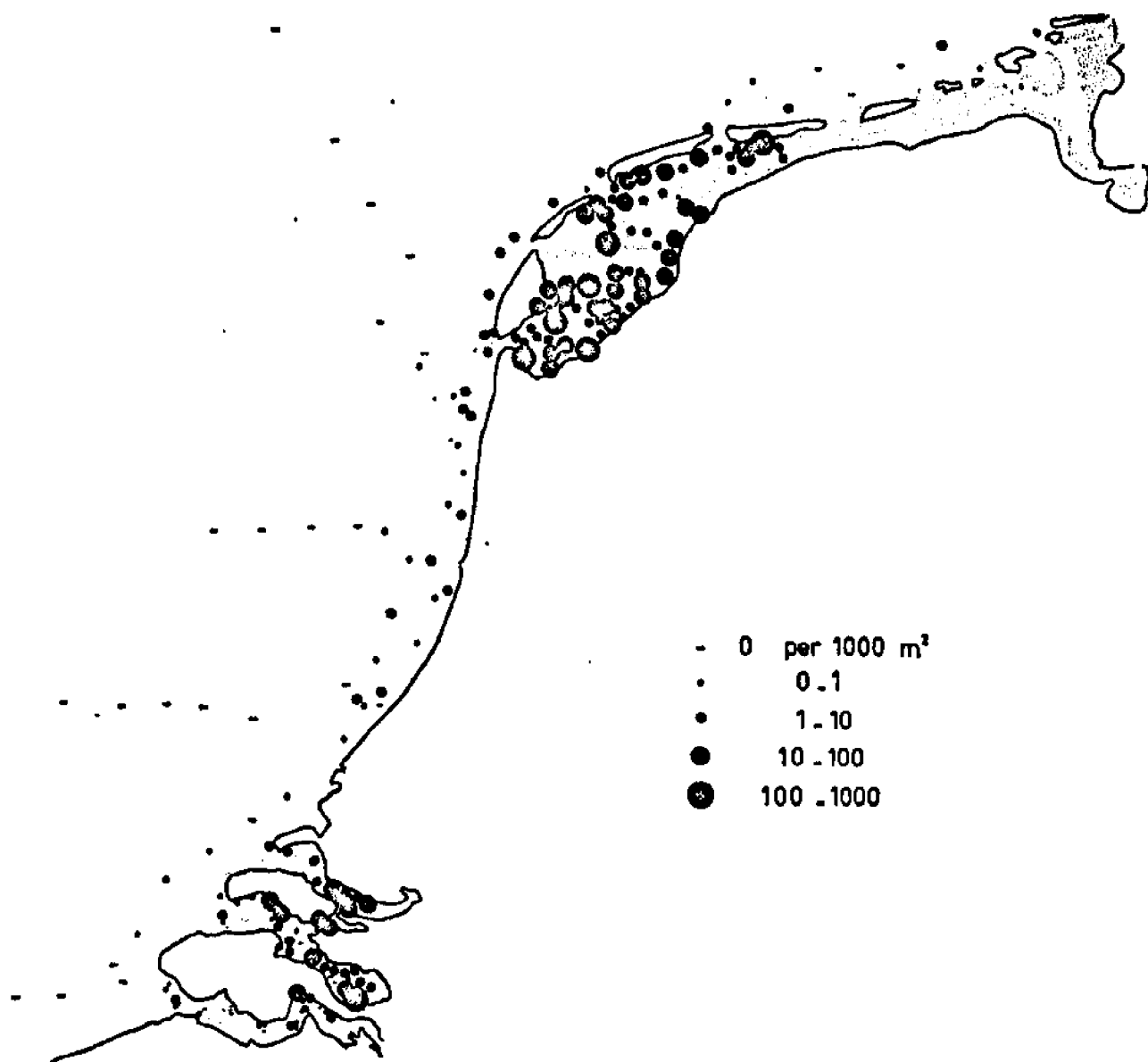


Figure 14. The distribution of 0-group plaice on the Dutch coast particularly in the Waddensee (Zijlstra, 1972).

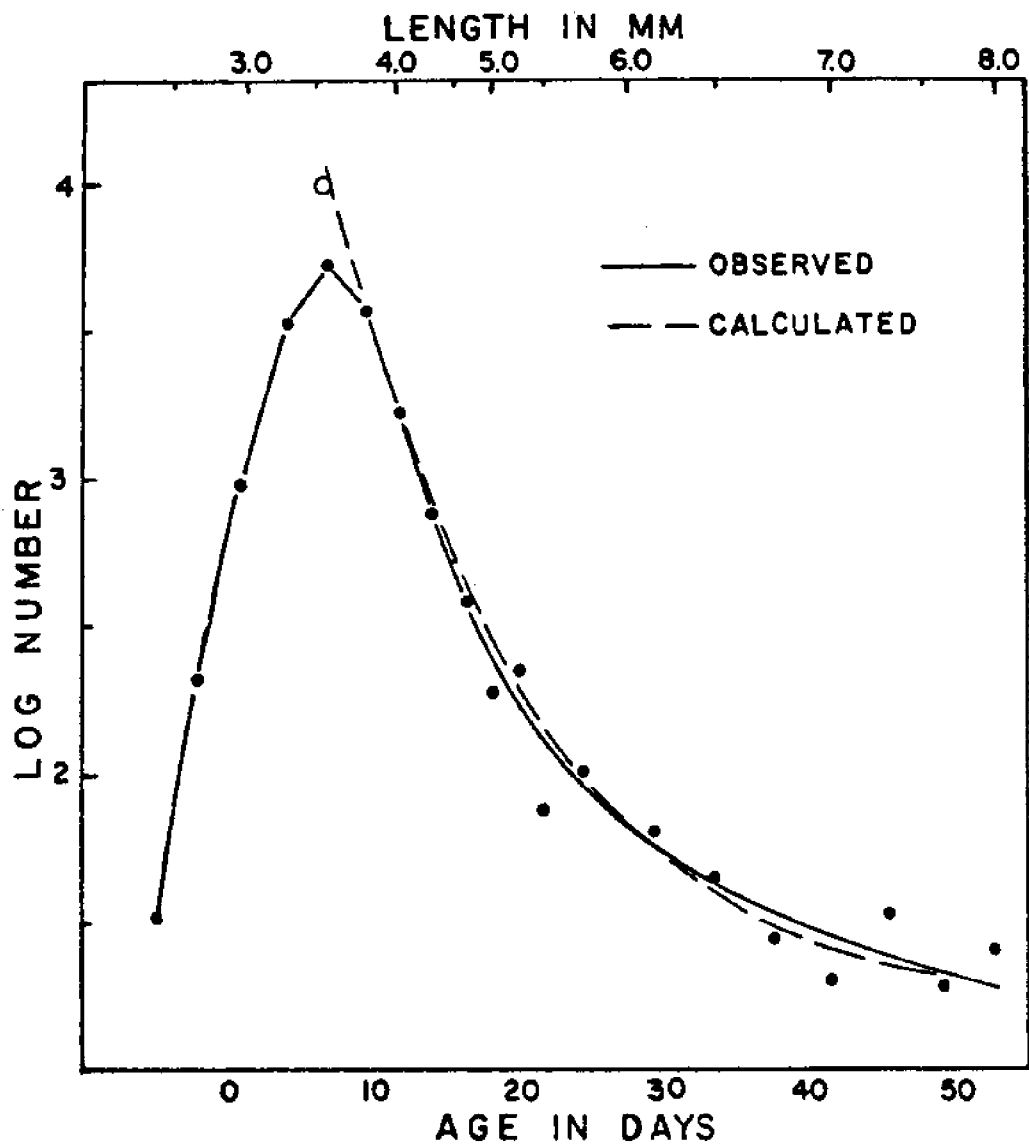


Figure 15. Catch curve for larval winter flounder. The calculated curve computed is based on an independently estimated translocation rate from the estuary of the Mystic River and upon two estimates of mortality.

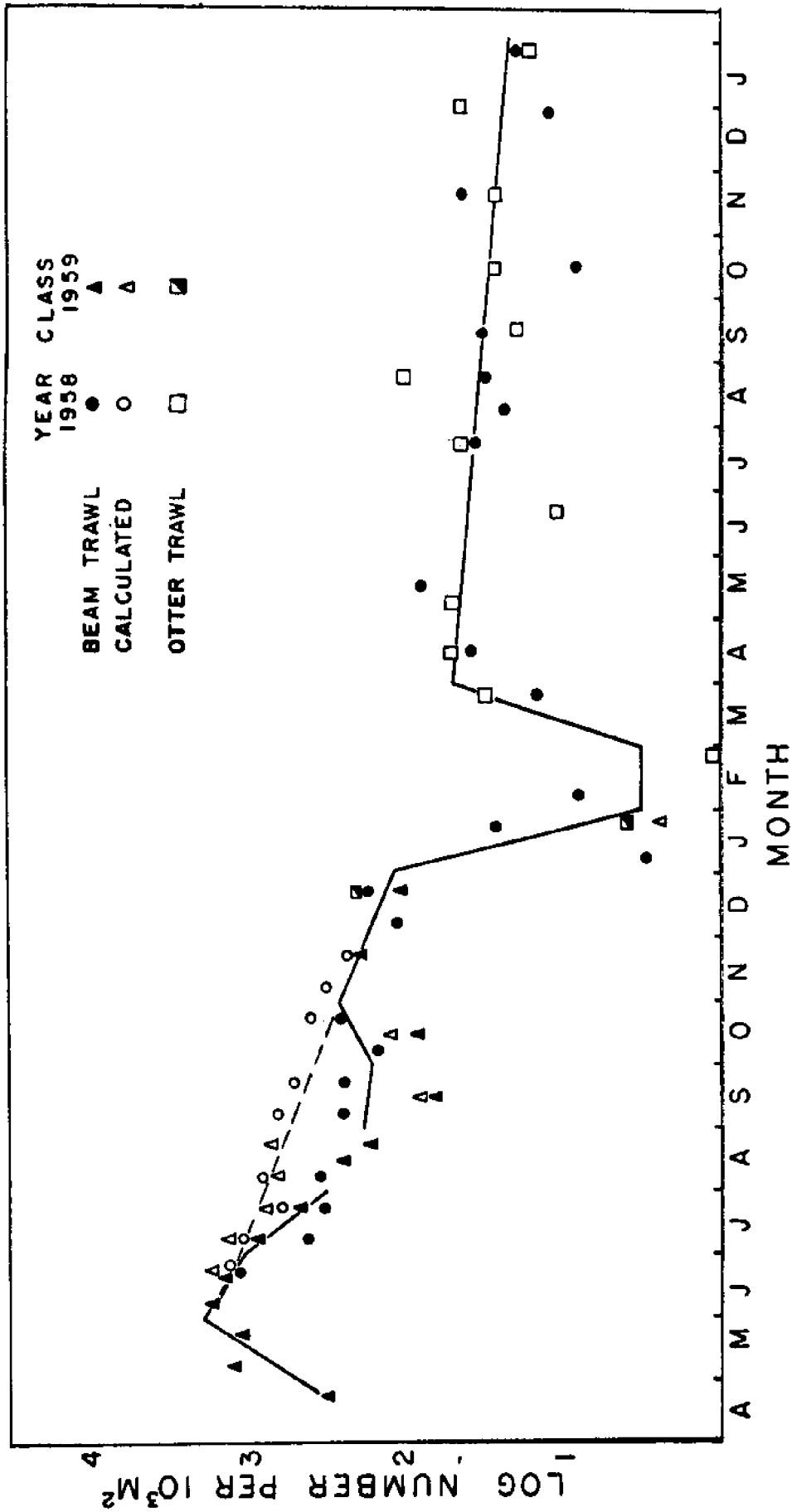


Figure 16. Catch curve for juvenile flounder of age-groups 0 and I of the 1958 and 1959 year-classes in the Mystic River Estuary.

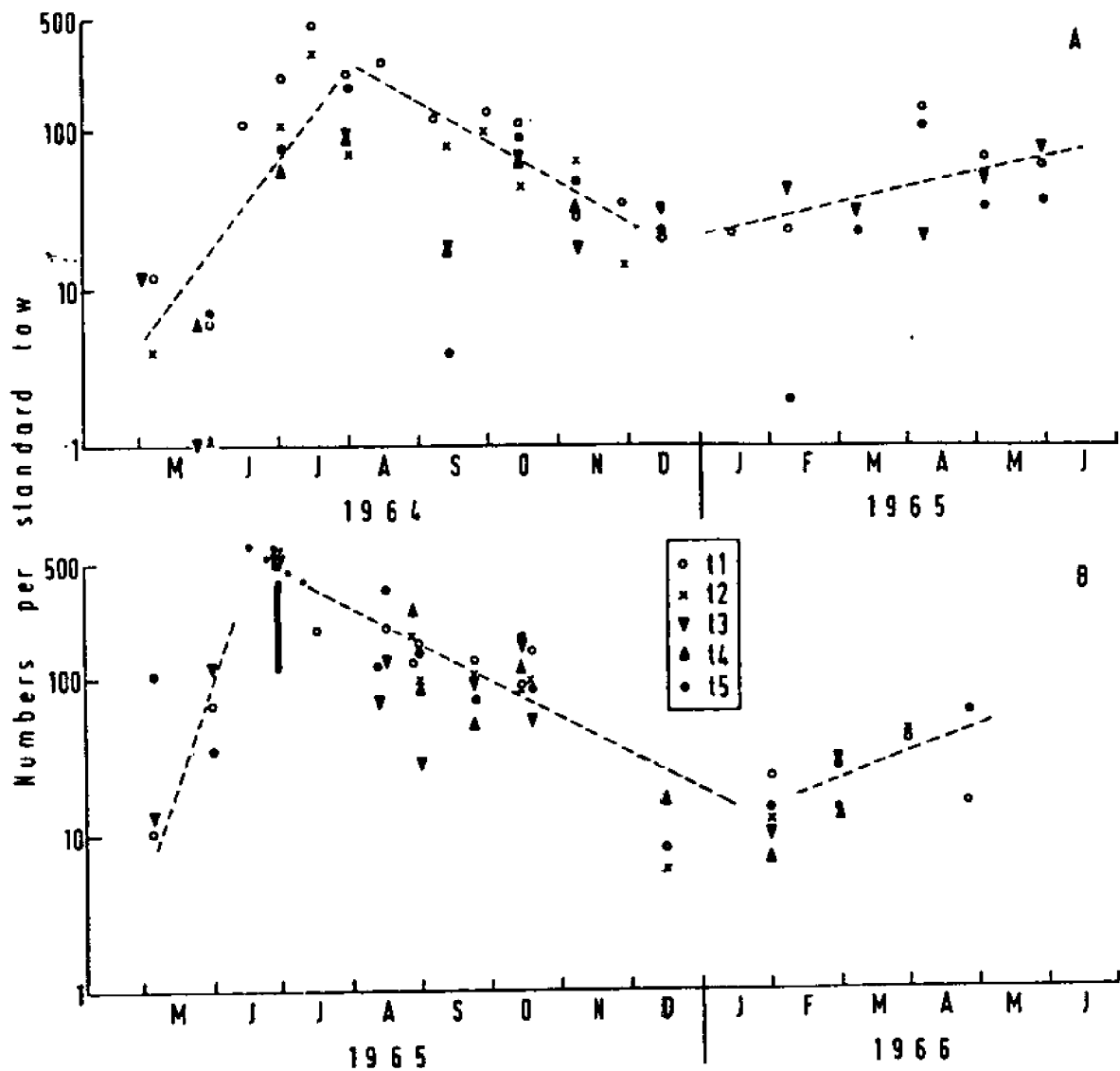


Figure 17. Numbers of 0-group plaice of the 1964 and 1965 year-classes caught per standard tow at five positions in Red Wharf Bay, Anglesey, U.K.

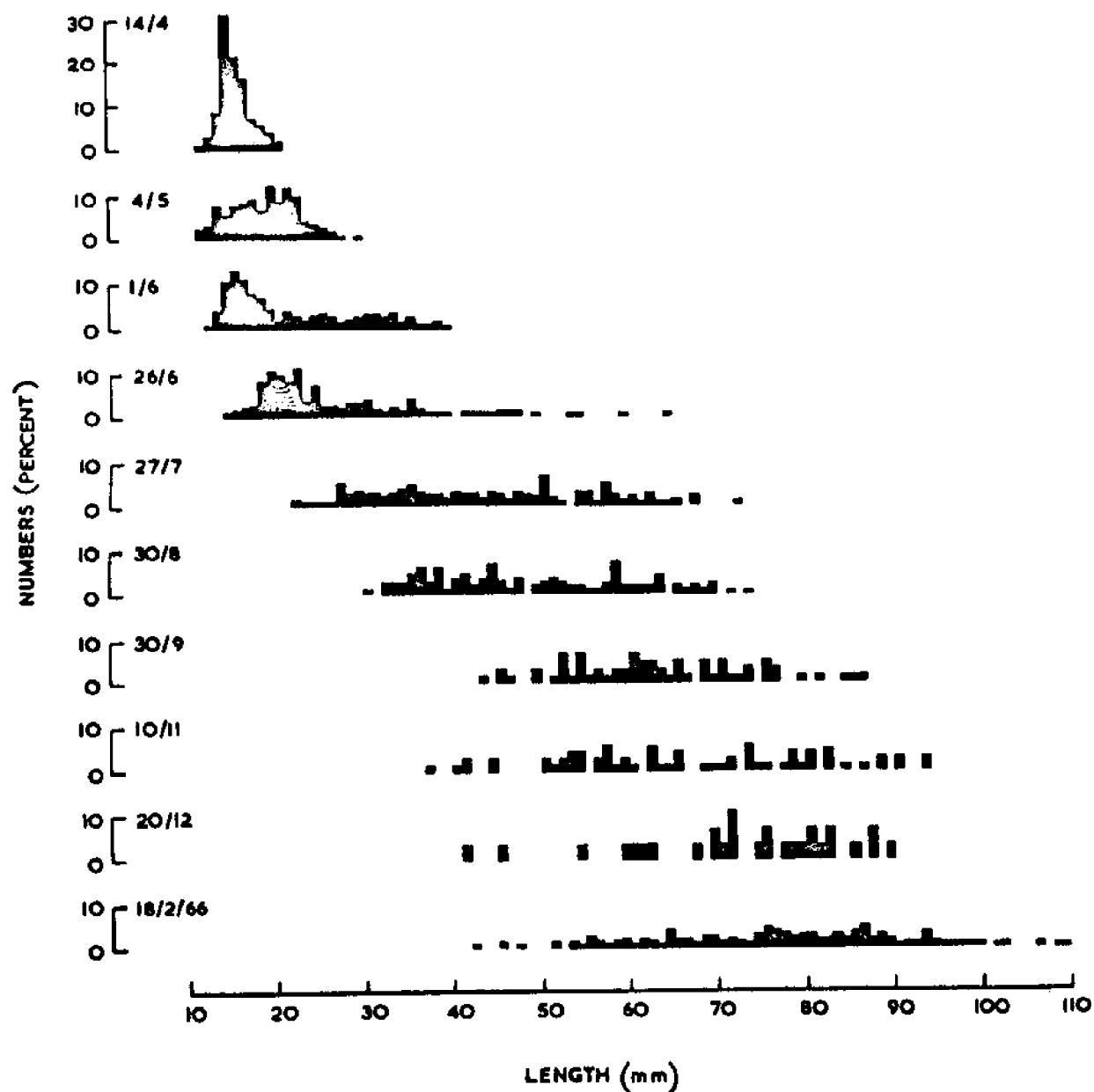


Figure 18. Size distribution of 1965 year-class of plaice, by months in Firemore Bay, Loch Ewe, Scotland.

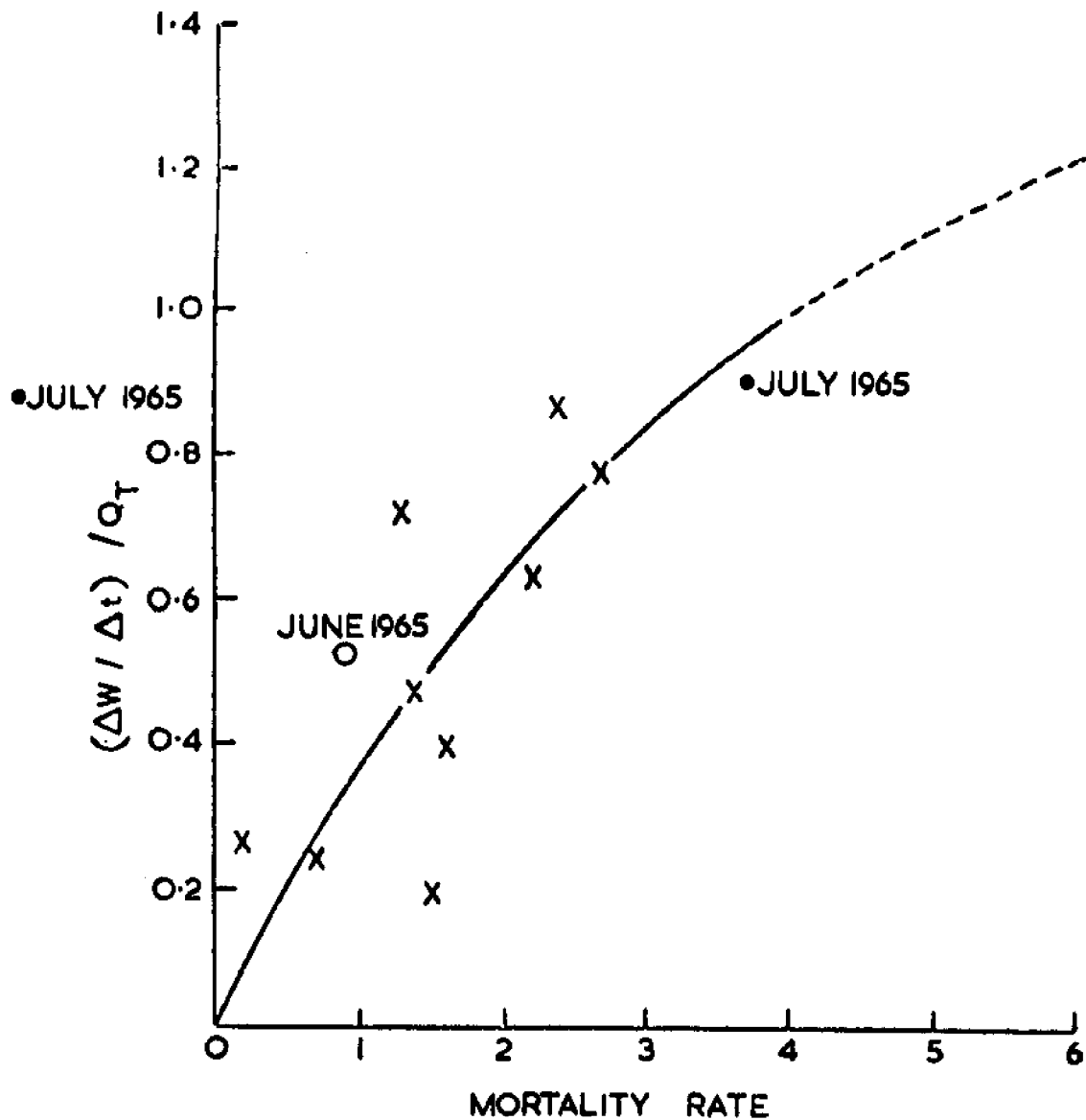


Figure 19. The dependence of growth rate of 0-group plaice upon their mortality rate in Firemore Bay, Loch Ewe, Scotland. The growth increment is corrected for differences in temperature.

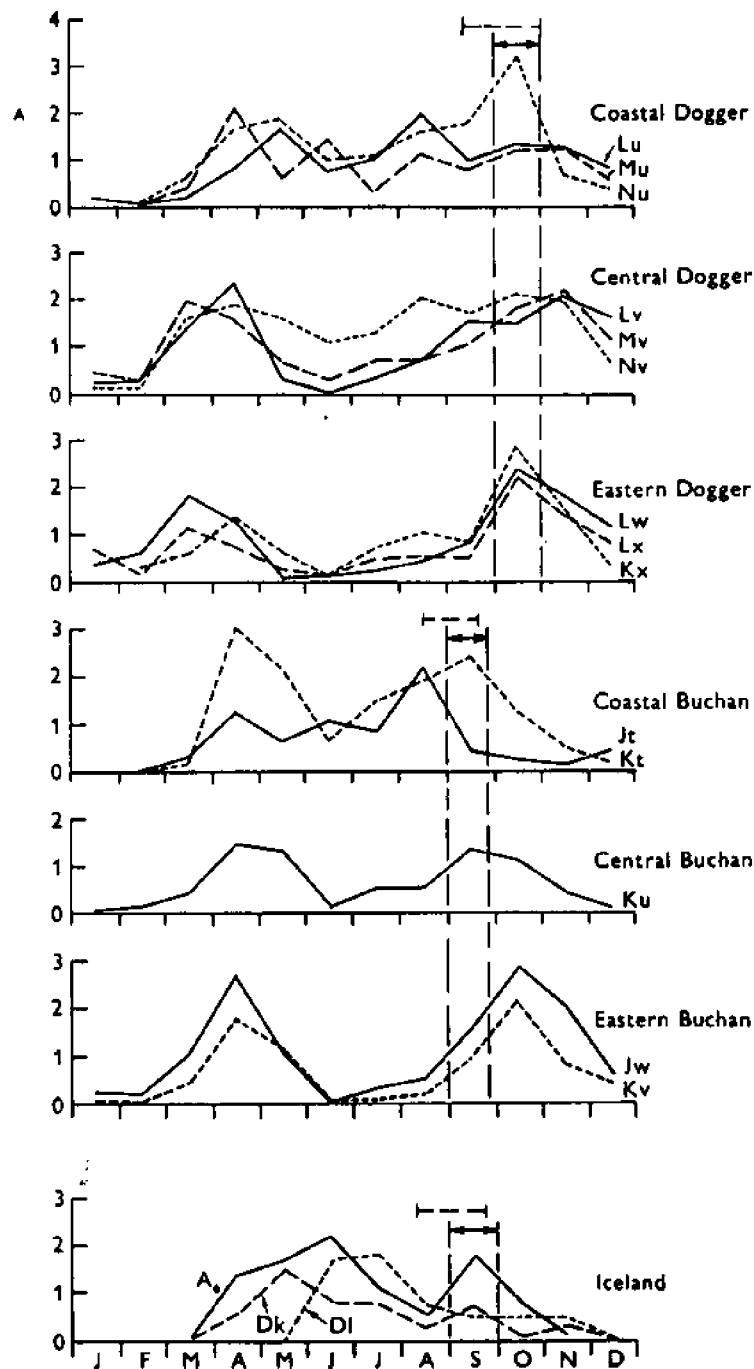


Figure 20. The three types of production cycle in phytoplankton color: (A) central North Sea (and Iceland), (B) coastal Atlantic, and (C) oceanic Atlantic. For each herring stock the period of larval survival, from fertilization to 50% survival under starvation (Blaxter & Hempel, 1963), is indicated by arrows, from the middle of the spawning period in time. The statistical squares used are indicated as Mu, Lu, etc. (See Cushing, 1967, for a more detailed explanation).

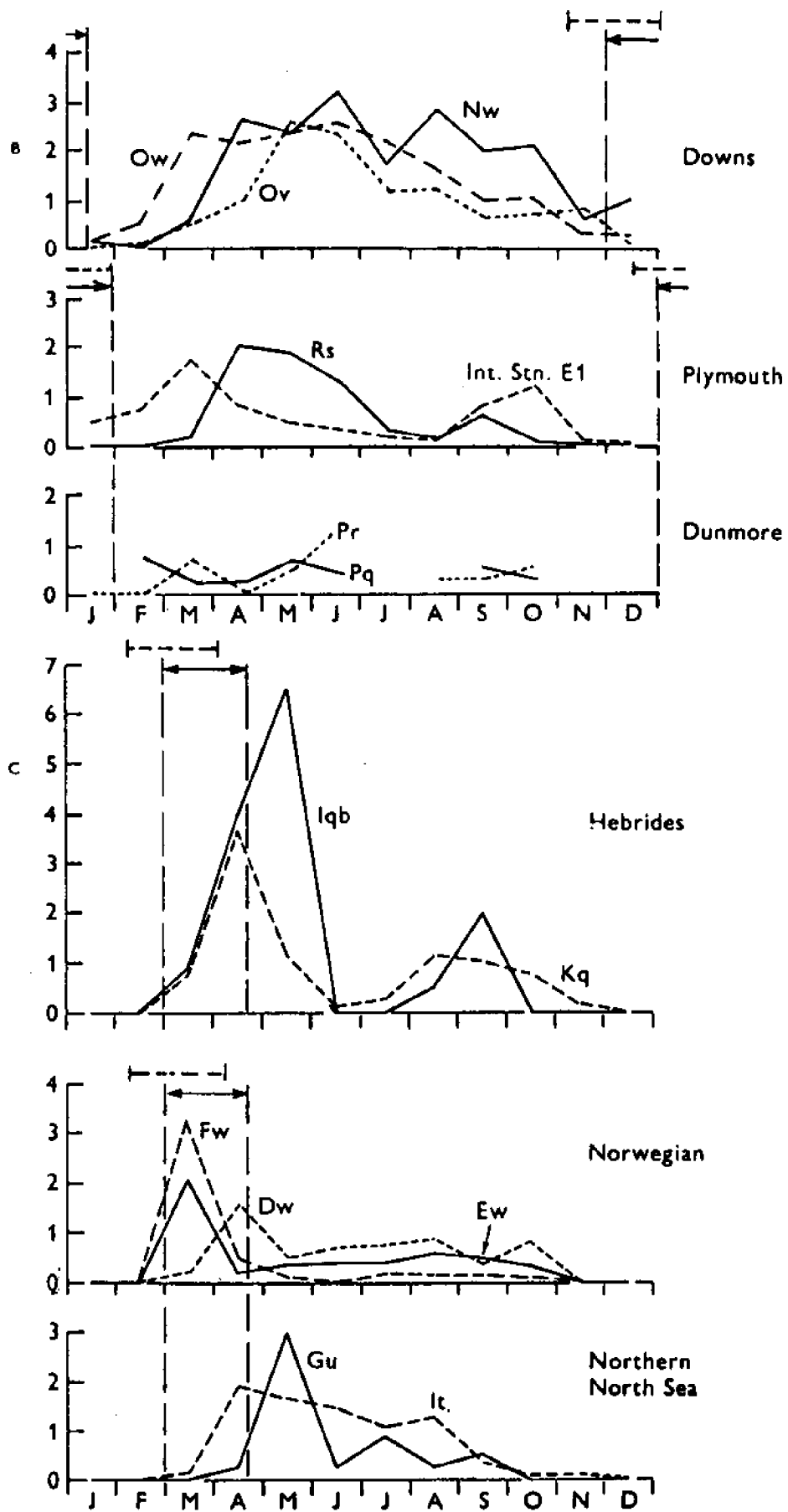


Fig. 20. (Continued).

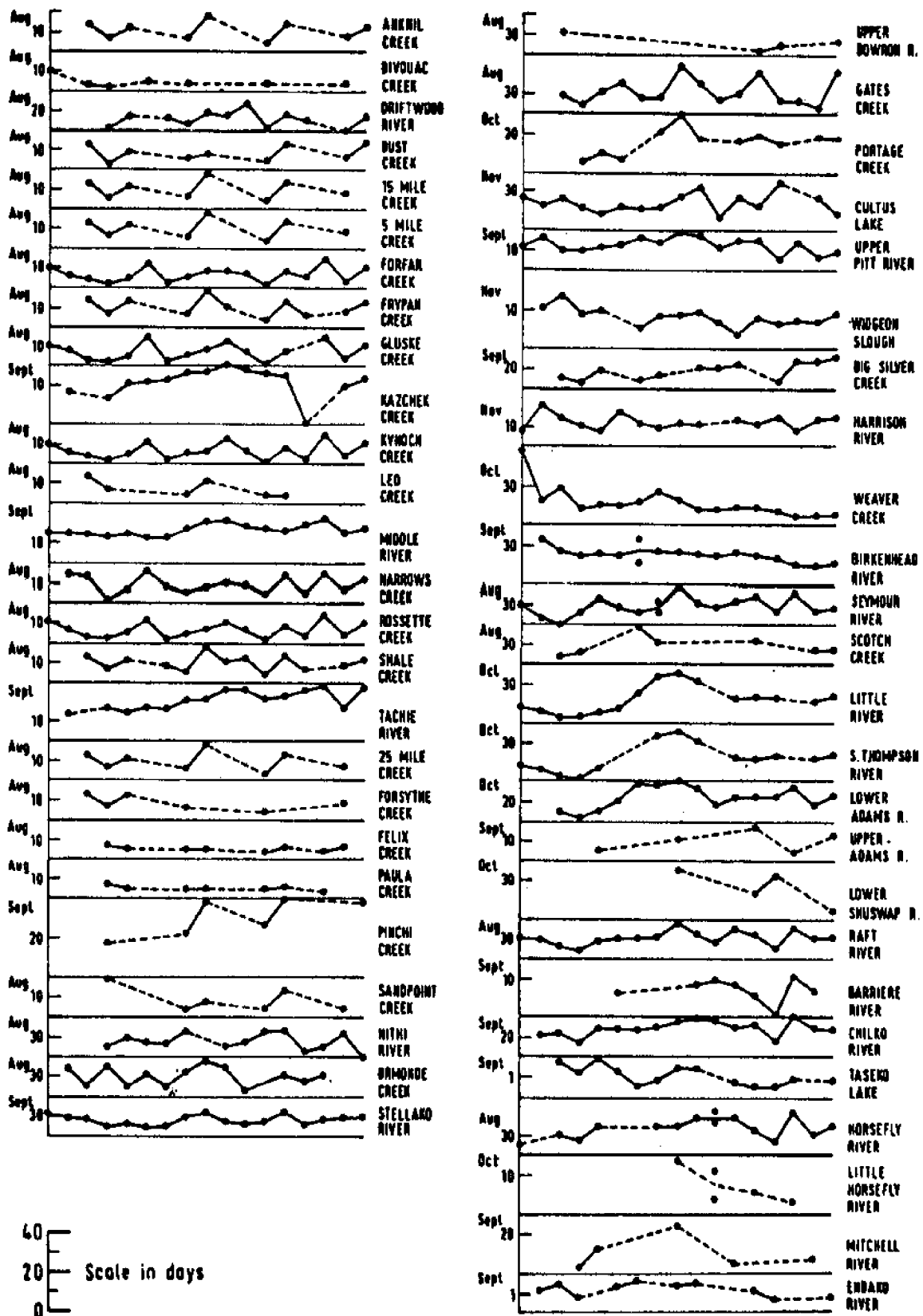


Figure 21-a. Time series of peak spawning dates for sockeye stocklets in the Fraser River system (Anonymous, 1950-1966; Cushing, 1970).

Spawning ground	Days from first positive sample																																			
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	
I.....	1	1	1	1	1	1	2	1	1	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
II.....	1	1	-	-	-	1	1	2	1	1	2	1	1	1	1	1	1	-	-	-	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-	
III.....	1	1	-	1	1	-	1	2	1	1	-	1	2	2	1	1	1	1	-	1	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-	
IV.....	1	1	-	1	-	2	3	3	2	1	1	-	2	3	2	-	-	-	-	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-	
V.....	1	1	1	-	-	-	-	-	-	2	2	4	2	2	1	3	4	2	1	1	1	2	2	2	2	2	2	1	1	-	-	-	-	-	-	
VI.....	1	1	1	1	1	1	1	1	1	1	1	1	3	3	3	3	2	2	3	5	3	1	1	1	1	1	2	2	1	-	-	-	-	-	-	
VII.....	1	1	-	-	1	-	-	-	1	1	1	2	2	2	3	4	4	3	3	3	3	3	1	2	1	1	-	1	1	-	-	-	-	-	-	
VIII.....	1	1	1	-	-	-	-	3	3	1	1	1	2	1	3	4	5	5	5	2	-	-	1	1	1	1	1	1	-	-	-	1	2	-	2	
IX.....	1	3	2	2	3	3	2	3	3	4	3	2	3	2	3	2	3	3	2	2	1	1	1	2	1	1	1	1	1	1	-	-	-	-	-	
X.....	1	2	1	-	-	-	-	-	-	-	-	1	1	-	1	1	3	4	4	5	5	-	2	1	1	1	1	1	-	-	-	-	-	-	-	
XIII.....	1	1	1	2	3	4	4	4	3	3	3	3	3	2	2	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
XIV.....	1	-	1	1	1	-	-	-	-	-	3	4	3	2	2	1	-	-	-	1	-	-	1	1	-	-	-	-	-	-	-	-	-	-	-	

	Mean date of first spawning	Mean day of spawning	S.D. of the mean date of spawning	S.E. of the mean date of spawning
I.....	2. Mar	6.45	2.90	0.92
II.....	23. Feb	11.94	5.19	1.26
III.....	23. Feb	12.38	6.90	1.54
IV.....	21. Feb	10.50	5.94	1.24
V.....	10. Feb	16.80	6.64	1.06
VI.....	7. Feb	17.06	7.44	1.04
VII.....	4. Feb	17.50	6.31	0.94
VIII.....	27. Jan	17.53	7.86	1.14
IX.....	3. Feb	13.00	7.42	0.98
X.....	5. Feb	18.00	6.74	1.14
XIII.....	10. Feb	8.98	5.43	0.61
XIV.....	10. Feb	12.17	7.72	1.20

Figure 21-b. Distribution of days of spawning after the date of first spawning of the Norwegian herring, estimated from the age of spawn in a grab sample (Runnström, 1941); the numbers in the upper table give the number of positive samples on a given day.

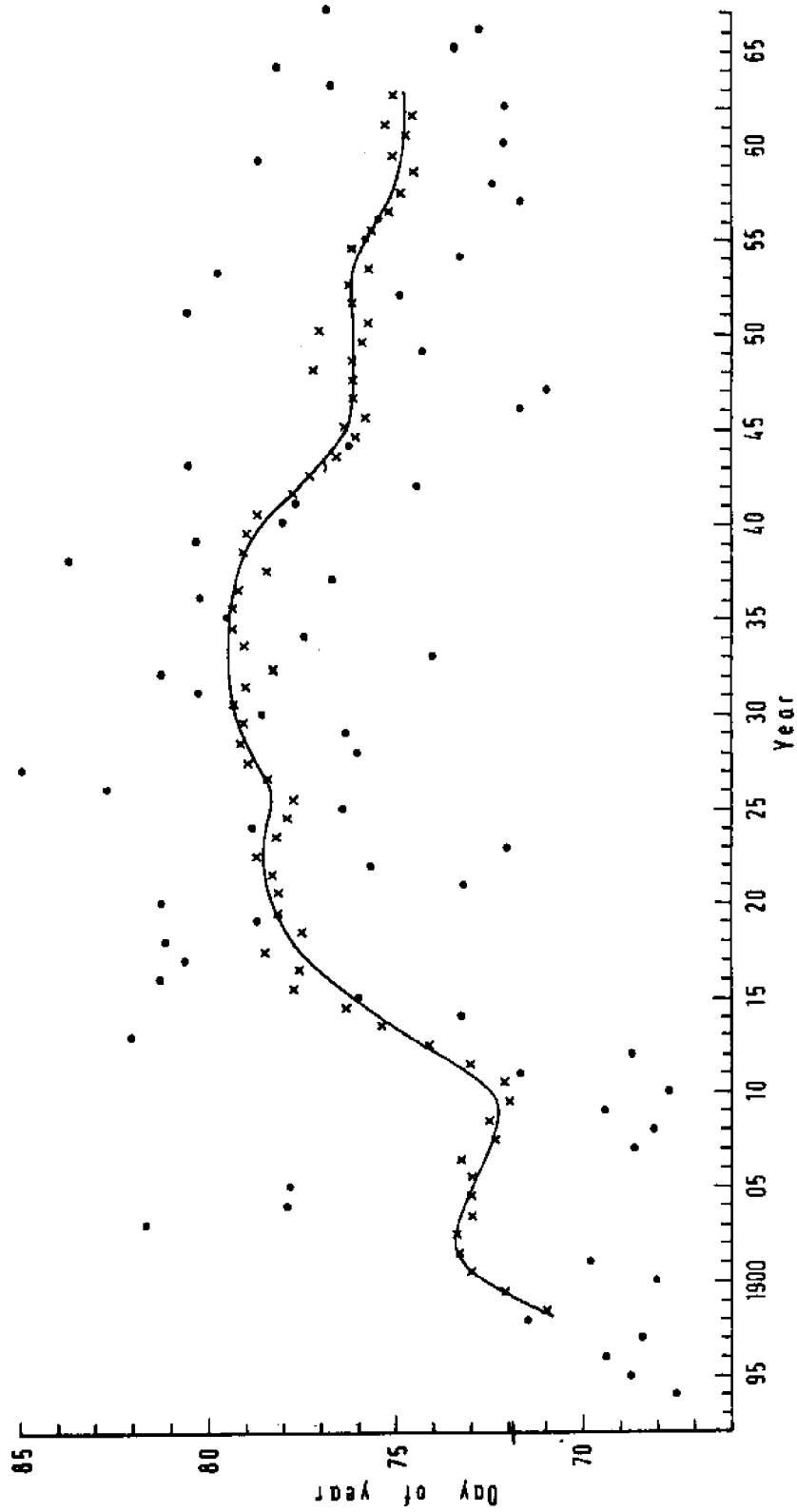


Figure 21-c. Mean dates of peak catches of cod in the Lofoten fishery, 1894-1967 (Anonymous, 1894-1968); the trend line (x---x) is fitted by moving means.

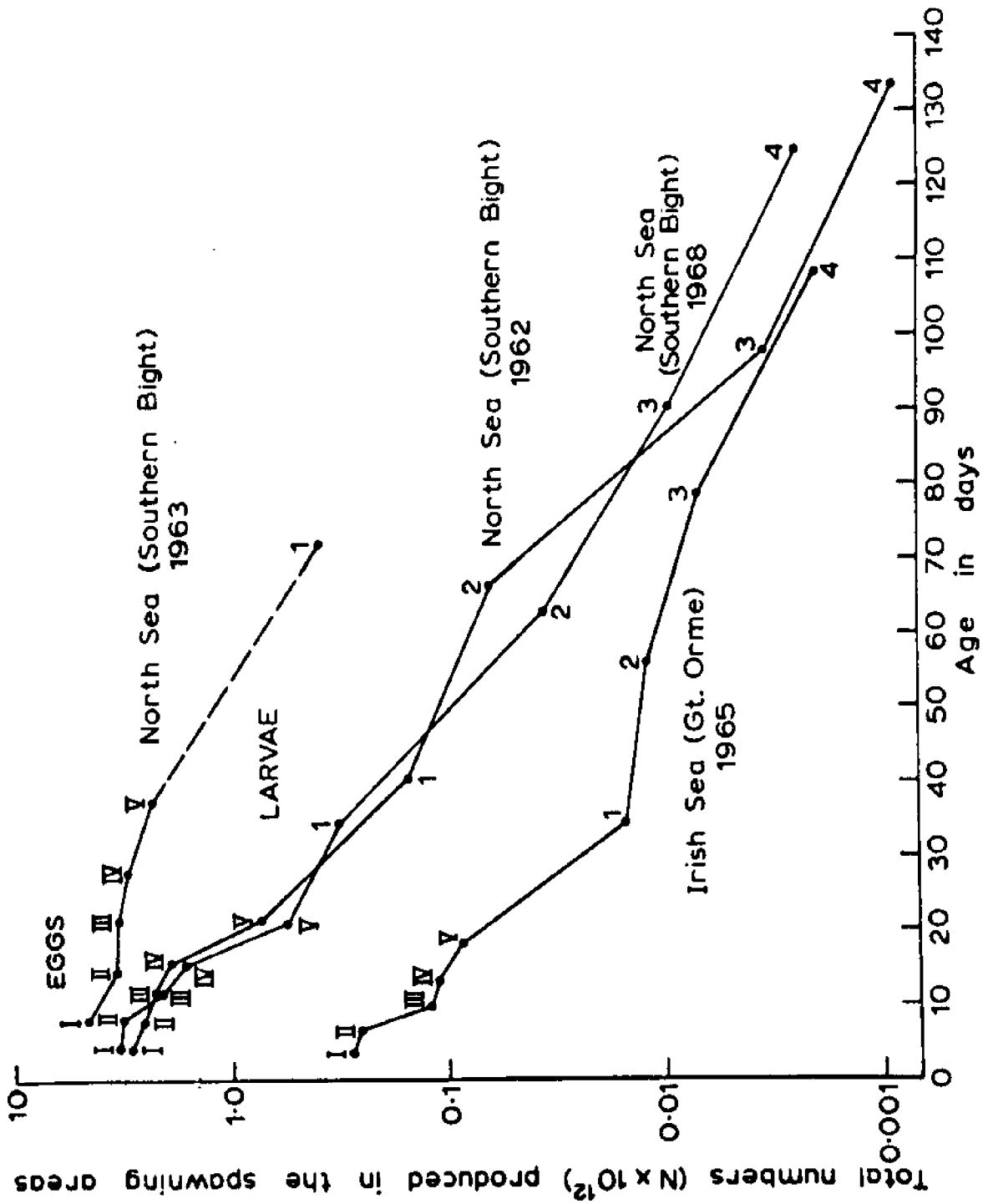


Figure 22. Survival curves for plaice eggs and larvae in the Great Orme spawning area of the Irish Sea in 1965 and the Southern Right of the North Sea in 1962, 1963, and 1968 (Harding and Talbot, in press).

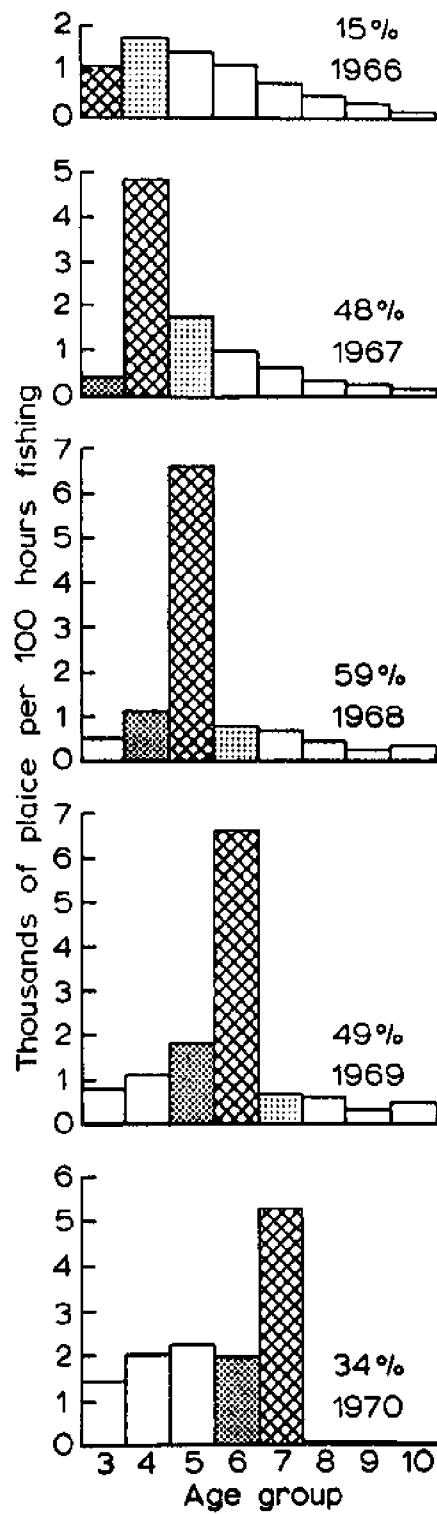


Figure 23. The importance of the 1963 year-class of plaice in the Southern North Sea (D. W. Harding and R. C. A. Bannister, unpublished manuscript).

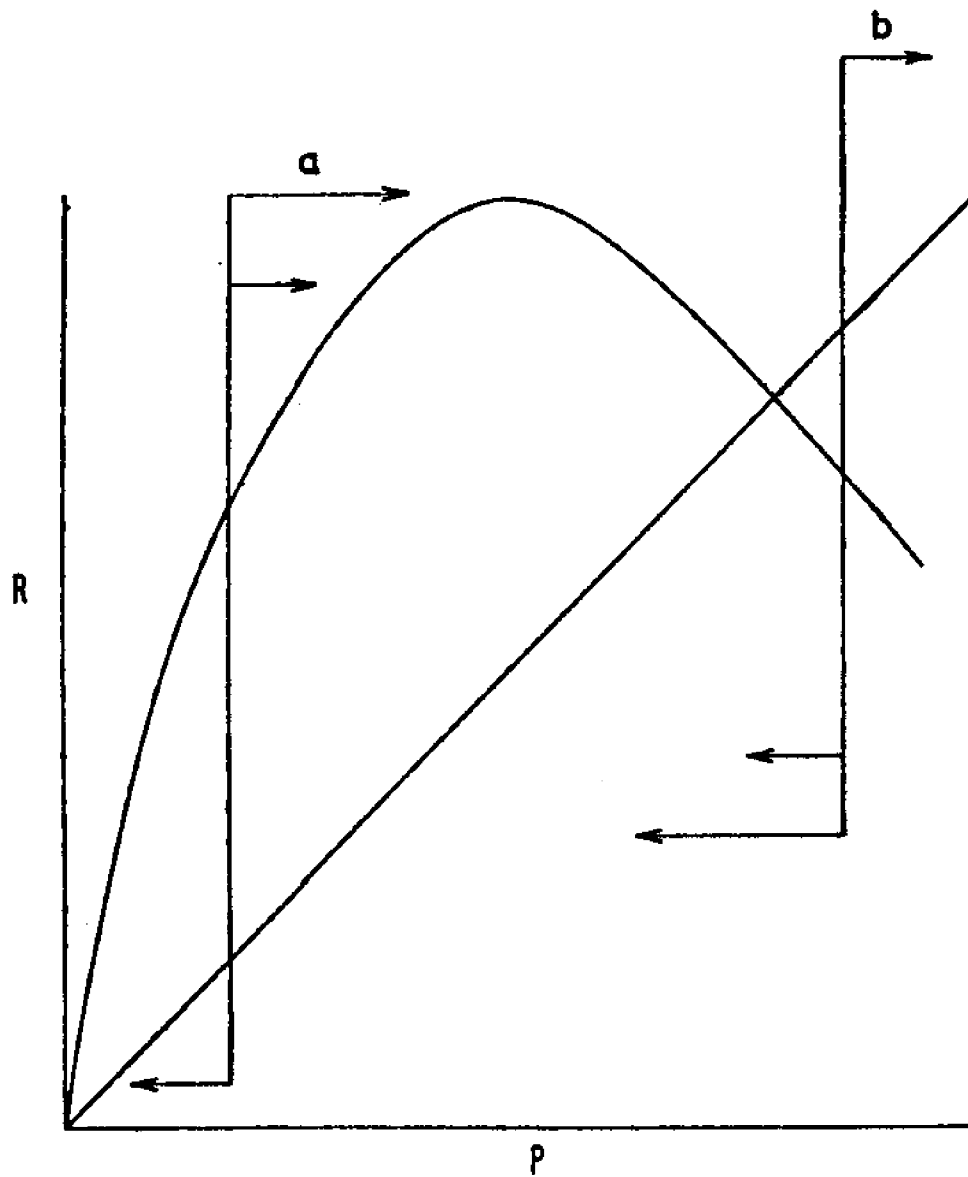


Figure 24. The three sources of variance in recruitment shown on a stock and recruitment curve (Cushing, 1968).

Chapter 3

THE STABILITY OF NUMBERS

Introduction

The Malthusian principle states that whereas the food intake of a population is additive, its potential in reproduction is geometric. Then by the deaths of their siblings, the survivors flourish and it is this mortality, or the struggle for existence, that results in stable numbers. In general numerical stability is attained by density-dependent processes. Howard and Fiske (1911) suggested that such a density-dependent control is mediated either through fecundity or through mortality. The most important step was made by Lack (1954), who wrote that the reproductive rate is determined by natural selection and not by the magnitude of mortality. In fishes, eggs are about the same size and weight, a fact which determines fecundity, as given in evolution and the growth of the adults is not density-dependent. Their stability from generation to generation must be generated by mortality.

The Stability Observed

After the International Council for the Exploration of the Sea was established, trawling surveys were conducted by a number of research vessels. When the results appeared, the three experts on overfishing (Garstang, Petersen, and Heincke, in Cushing, 1972a) were so dismayed by the variance between trawl hauls that they could see no solution to the problem of overfishing based on them. The name of the "Overfishing" Committee was changed to "the problem of small plaice," because the little fish were discarded in large numbers by the British trawlers working on the coasts of Holland and Germany. Garstang and Petersen turned their attention to the transplantation of small plaice from the overcrowded continental coast to the more spacious and richer grounds on the Dogger Bank, which eventually was shown to be unprofitable. The overfishing problem did not return to the Council until the late thirties. However high was the variability of the trawl hauls, from year to year they expressed considerable stability as can now be seen by hindsight.

To Hjort (1914), the fluctuations due to recruitment were probably more important than the effect of fishing because until 1930 or later the Norwegian herring and the Arctic cod were lightly fished. He would have liked to forecast the fluctuations because they generated so much variability in the catches; the Norwegian herring at least provided a fishery that was highly variable from year to year. The stock had between ten and twenty age-groups of mature fish and it tended to be dominated by single, sporadic, and outstanding year-classes, as, for example, that of 1904 and

that of 1950. Today, when fishing pressures are much greater, the need for managing the fluctuations has become imperative. For example, the present recruitments to the Arcto-Norwegian cod stock are very low indeed because of recruitment overfishing, and they have fortunately been more or less correctly forecast. In contrast there have been sharp increases in the recruitments of haddock, whiting, and cod in the North Sea of nearly an order of magnitude, which were quite unforeseen (Cole and Holden, in press). But despite these manifest needs of the industry, my point is now that the variability of recruitment expresses considerable stability in numbers.

Figures 25, 26, and 27 show some long-term series of recruitments to fish stocks. Figure 25(d) shows the total run of the Karluk River sockeye salmon in Alaska from 1887-1953 (Anonymous, 1962); the total run is the sum of catch and escapement and the latter is the remainder of the stock that escapes to spawn and die. The Pacific salmon recruits, spawns, and dies at four years of age, although there are a few spawners of other ages, particularly in Alaska. However, it is reasonable to represent the total run as recruitment. In Figures 25(a), 25(b), and 25(c) are given the recruitments to three herring stocks. From 1904-1953, the recruitment to the Norwegian herring is represented by Derzhavin's original form of virtual population analysis, Figure 25(c) (Marty and Fedorov, 1963). Hanamura (1961) has estimated the accumulated catches by year-classes for the British Columbian herring from 1915-1952, Figure 1(b). The recruitment to the Downs herring from 1925-1962 in numbers/drifter shot (corrected for an efficiency change) was estimated by Cushing and Bridger (1966) (Figure 25(a)). The recruitments to three Atlantic cod stocks from 1924 to about 1960 as estimated by the modern form of virtual population analysis are shown in Figure 26 (Garrod, 1967); the three stocks are those at West Greenland, Iceland, and the Barents Sea. The material for the Georges Bank haddock stock from 1929-1967 is taken from Grosslein and Hennemuth [in press]. Recruitments to the North Sea sole population estimated by virtual population analysis (Anonymous, 1970) from 1930-1966 are shown in Figure 27. The three figures summarize information from cod, herring, haddock, salmon, and sole stocks, which represent a fair proportion of commercial fish catches; the most important point is that recruitment in each stock is properly estimated. The recruitments are calculated in different ways, but the variability is fully comparable between stocks. The periods of time are long, about 30 to 90 years, and upward or downward trends in time can be clearly established.

There is a slow downward trend in the recruitment to the Karluk River sockeye salmon by a factor of two to three and the variability about this trend reaches a factor of about six. In the Norwegian herring there is a rising trend up to the 1950 year-class by a factor of about five, but the subsequent year-classes declined by two to three orders of magnitude: the range about the rising trend varies between 10 and 40 times. In the British Columbian herring, there is also a rising trend of about a factor

of three and the range varies between three and 12 times. There was no trend in the recruitment of the Downs herring before the Second World War, but it declined after it by between three and 10 times; about both pre- and postwar sets of data, the range of recruitment varied between three and five times. In the cod stocks, there is neither upward nor downward trend at West Greenland, but a slightly rising trend at Iceland of about a factor of two. The range of recruitments is less than an order of magnitude except in the pre-Second World War series at Iceland; indeed the variance of recruitment (by inspection only) to the cod stocks is surprisingly low. In contrast, that of the North Sea sole, with no upward or downward trend, extends over a factor of 60.

An interesting generalization emerges from these data. The range of recruitment to the Norwegian herring is much higher than that to the Downs herring: indeed if other North Sea stocks (the Dogger and Buchan stocks) are drawn into the comparison, it can be shown that the variance of recruitment increases with depth of water. If it is related to the variance of the production cycle, which increases with depth of water, the result is not unexpected. In contrast, the variability of recruitment to the cod stocks, two of which live in the Arctic Circle, is low, much less than that to the Norwegian herring, which live in the Norwegian Sea a little to the southward of the area of the cod stocks. The highest variation of recruitment was found in the North Sea sole stock, an animal at the northern edge of its range. Perhaps the lowest variability of recruitment is found in the center of the geographical range of a given species.

The most important point, however, is that the variance of recruitment is less than an order of magnitude, except at the edges of the geographical range. The variance of stock in any multi-age stock will be less by two factors, (a) the number of age-groups in the stock, (b) the number of years during which a given recruitment joins the adult stock. The stocks represented in Figures 25, 26, and 27 are all exploited and so there are fewer age-groups than in the natural state. Consequently the variance of recruitment as observed may be rather greater than that of the virgin stock. The variance about a stock and recruitment curve increases with exploitation because the number of age-groups becomes reduced. The salmon stocks are not as variable as those of the herring or of the sole, but the recruitment is not damped by a number of age-groups or the spread of recruits in age. Of the cod stocks shown in Figure 26, when unexploited, most would have been between nine and 16 abundant age-groups and, in most, recruitment would be spread over two to five years. Thus, if the variance of recruitment as presented is on average about an order of magnitude, that stock is reduced to a factor of three, or somewhat less. Hence, fish stocks have a considerable capacity for stabilization.

In the larger stocks of commercial fishes, such as we have examined, the numbers are about 10^{10} or somewhat less and they might range from, for example, $0.67-2.0 \cdot 10^{10}$. Each of the species examined is very fecund, 5,000 for a female sockeye salmon and 10,000,000 for a female cod. The

numbers of eggs laid range from 10^{13} to 10^{17} . The spawning season is long, two to five months, and the spawning area may be extensive or restricted. Then the density of eggs of different species in the sea may be a function of the population fecundity.

It has already been suggested that the variability of recruitment is linked to the match or mismatch of larval production to that of their food. Figure 28 shows the variation in numbers and in timing of the stock of *Asterionella formosa* in Windermere (Lund, 1964). Compared with the open sea, a lake like Windermere is a very special case. Production starts in spring when the lake overturns and so the start of production is related primarily to temperature rather than to wind and sunlight, although of course they must play some part in the subsequent development of the cycle. The series of production cycles for 16 years shows the variability in quantity produced during the cycle and variation from year to year amounts to about a factor of three. The range in timing is about two months with a standard deviation of about one month. The variability of the production cycle in the open sea is probably greater, particularly in the open ocean in high latitudes. For example, Corlett (1953) showed that the peak of algal stock at Ocean Weather Ships "I" and "J" differed by six weeks in three observations. The quantities of primary production may not differ too much from year to year, but the variability of recruitment is probably rooted in the differences in timing of the cycle that are observed from year to year. As they grow through the life cycle, fish eat a few algae, then become carnivores of the first or second orders. The critical phase in this development is when the little fish start eating herbivores, for example copepod nauplii and their analogues. In temperate waters, the overwintering generation of copepods spawns during the early stages of the production cycle. Hence the timing that is of interest is probably closely related to the timing of the critical depth. The variability in the amplitude of the production cycle is of the same order as the variability in year-class strength.

The Stabilization Mechanism

The stabilization mechanism is well described in Figure 29, from Ricker (1958). Recruitment is expressed as a function of stock in numbers of eggs, that is, numbers of recruits or numbers of spawning adults, both multiplied by fecundity, in appropriate ways. The curve cuts the bisector at the average value of stock in its unexploited state, the stabilization point. Below it, at low stock, recruitment is greater than stock and so it will tend to return the stock to the point of stabilization; at high stock, the reverse process must take place. If the curve is slightly convex with respect to the bisector, the stabilization mechanism is weak, but if it is sharply convex, drawn like a dome, the capacity for stabilization is strong and the stock returns quickly to the stabilization point. The variance in stock, due to variable recruitment in the unexploited state, reflects its capacity to tolerate environmental changes. In the exploited stock, the

point of stabilization is found at lower levels of stock, according to the degree of exploitation. Ricker (1954, 1958) calls the stabilization point in the virgin stock the replacement stock, which it must be in a single age spawning stock like that of the Pacific salmon. In a multi-age spawning stock, however, the point of replacement cannot be defined unless the trend of natural mortality with age is known and even then it may not be desirable to do so: I will return to this point in a later chapter.

Without describing Ricker's curve at the moment, it is now well enough known that recruitment/unit stock declines with increasing stock. Figure 30 shows the decline in survival as recruitment per unit stock with increasing stock for the southern North Sea plaice (Beverton, 1962). In other words, the curve as shown (without yet specifying its nature) describes the recruitment mechanism in fishes in the barest terms. The question arises whether the essential mechanisms are those of density-dependent mortality (and growth) or whether they are mediated through fecundity as a consequence of density-dependent growth in the adult parents. First, the generations should be independent. Second, the control of the magnitude of recruitment occurs between hatching and recruitment; in the Downs herring, the number of larvae hatched is a linear function of stock, but is a curvilinear function of subsequent recruitment (Cushing and Bridger, 1966). In the Pacific salmon, however, some density-dependent control may occur in the redds (Hunter, 1959; McNeil, 1963). In any case density-dependent growth in adult fishes is difficult to detect (except in the Pacific halibut, Southward, 1967), although, of course, size for age might be determined by density-dependent growth at an earlier age. If that were the case, recruitment might be determined by juvenile density-dependent processes in the previous generation; it is simpler to say that it is determined by the same processes in the one generation, between hatching and recruitment. Then fecundity is a design feature, evolutionarily determined, as Lack suggested.

Ricker's initial equation represents the dependence of recruitment on parent stock in a convenient way: $R = APe^{-BP}$, where R is recruitment, P is stock, A is the coefficient of density-independent mortality, and B that of density-dependent mortality. There are three processes summarized in the equation. The first, the magnitude of the stock, is the most important and it is the result of competition that has continued for long periods of time. Because food is shared between fish larvae of about the same size during the larval drift, competition must occur there and perhaps exclusively. In later life, adult fishes may lead somewhat isolated lives in which competition can be only thinly expressed; indeed if recruitment is determined in early life, the competition in later life can find expression only in fecundity changes. The second component is the density-dependent mortality ($-BP$), which must occur during the period of larval drift if recruitment is forecast successfully from the numbers of 0-group fishes. The third component in stabilization is the part played by density-independent mortality in the generation of recruitment. In Figure 27 it is expressed as variance about the curve or as the capacity of the stock to stabilize itself, in the face of environmental variability.

The most important contribution in imagining the mechanism of stabilization is that of Ricker and Foerster, (1948). They suggest that the larvae grow at different rates through a critical size range within which they are vulnerable to predation. Growth depends upon food and if the quantity of food is initially constant, then the conversion of food to growth depends upon the number of larvae between which the food is shared. If the number is small, growth is rapid and the critical period of predation is short; if large, growth is slow and the period of predation is long. Beverton and Holt, (1957) expressed the idea formally in an equation, which I have described as the initial Ricker equation. The development of these equations is somewhat different and I will return to them later.

Models of the Density-dependent Mechanism

Jones (in press) and Jones and Hall (in press) have developed a model of the dependence of fish larvae upon their food. They assume that larvae die if they fail to capture a specified number of food organisms, and that searching capacity increases exponentially with age. The initial numbers of haddock eggs were taken to be $0.8-4.0 \cdot 10^8/\text{km}^2$ and the initial numbers of food organisms were taken to be $0.4-1.2 \cdot 10^{11}/\text{km}^2$. Rosenthal and Hempel (1970) have shown that the Downs herring larva searches 15-20 liters/day at the end of the yolk sac stage and 30-40 liters/day at a length of 12-14 mm. A larval haddock increases its weight at 12%/day and feeds on the nauplii and copepodites of *Calanus*.

The probability of encounter of food organisms depends upon the rate of encounter of the mean number. The least number of food organisms for survival is given as function of that mean number, the search volume, and the mortality rate. Then the dependence of survival on food can be elaborated. Haddock larvae grow at 12%/day and die at 10%/day and a minimum food requirement of 0.2-0.7 *Calanus*/day (for larvae of t days of age) was established, below which the larvae died. The numbers of larvae alive after 45 days were calculated for different numbers of food organisms and fish larvae and different minimal food requirements. The model showed that a density-dependent mortality was generated, that the number of food organisms was not really affected, but that variation in the initial numbers of food organisms ($\times 4$) led to differences in survival of three orders of magnitude. The order of variation in year-class strength is very much less and Jones suggested that shoaling played a part in damping this variation. During the first year of life, the increment of weight is 10^5 , but the decrement in numbers is 10^4 , so the gain in biomass is one order of magnitude. Hence the difference between growth and mortality must be maintained. Jones writes that there would be: "considerable biological advantage in the existence of a single mechanism able to influence both growth and mortality simultaneously and hence control this balance in the long term."

An analogous model has been developed by Cushing and Harris (in press). Larval plaice grow and as they do so they swim more quickly and evade capture by a particular predator. They feed and reduce the density of food and so the increase in length and increase in speed during a time interval are reduced; the period under predation becomes extended. If the numbers of fish larvae are increased, the density of food becomes reduced more quickly and the period under predation becomes extended still further. Hence, a density-dependent mortality is generated by the availability of food, as suggested by Ricker and Foerster (1948) and Jones (in press).

It is at first sight unrealistic to limit the model to the pressure exerted by a single predator. However, one might imagine that the fish grow through the search fields of a succession of predators, each larger, and less numerous than its predecessors. Such a structure might generate density-dependent mortality in age throughout the life cycle, as will be suggested below. Then, although only one artificial predator exists in the model, it represents similar processes supposed to occur later in the life cycle.

Because food intake depends on weight and because speed is a function of length, a length/weight relationship is needed. Ryland (1963) gives data for plaice larvae from which the following equation was derived:

$$W = (L^3 - 0.35)/0.115,$$

where W is wet weight in mg and L is length in cm.

Ryland (1963) estimated the cruising speed of plaice larvae:

$$C = 1.7 + 2.83 L^{1.192},$$

where C is the cruising speed in cm/sec.

The escape velocity was set at $6C$ from some preliminary observations made by my colleague, Dr. G. P. Arnold.

Ryland (1964) made observations on the diurnal variation in the fullness of the guts of plaice larvae and showed that they were full for 14 hours in each day. Harris (1968) developed an expression to describe the volume searched by a plaice larvae, G :

$$G = 3\pi R^2 C t / (3 + \pi k R^3),$$

where R is the attack range of the larvae in cm ($0.7L$);

where t is the time spend feeding each in sec i.e., $14 \times 3,600$;

where k is the density of food organisms, in n/ml .

It was assumed that the plaice larvae ate *Artemia* nauplii, each of which weighed 0.057 mg wet weight (they range in radius from 0.18 to 0.28 mm, or 0.022-0.095 mg, the mean of which is 0.057 mg). The quantity eaten is the product of the density of the nauplii, the weight of each nauplius and the daily volume searched.

Riley's (1966) experiment gives the daily ration for a plaice larvae in numbers of *Artemia* nauplii. Then, $I = 0.08W$, where I is the daily ration in mg. It is an average ration, not a maintenance ration; a maximum ration was set at 1.4 body weights/day to prevent the larvae from becoming overfed in the model.

The effect of starvation was adapted from Blaxter's (1965) work on herring larvae:

$$W' = W [1 - (0.072 - 0.032L)(1 - F/I)],$$

where W' is the weight of a fish larva after a period of time of food lack

where F is the food intake/day, i.e., kg.

The effect of food on growth is given by $W' = W + H(F - I)$, where H is a food conversion coefficient ($= 0.05$; from Figure 4 in Riley, 1966). Because of lack of evidence, food intake cannot be specified as a proportion of a maintenance ration. However, at the expense of the larvae being overfed, the differences in food availability can be shown upon the growth rates and death rates of the fish larvae.

As the model progresses in time, new estimates of length and cruising speed are derived from the changed values of weight:

$$L' = (0.35 + 0.115W')^{0.383} \text{ and } C' = 1.72 + 2.83L'^{1.192},$$

where L' and C' are estimates of L and C after a time interval.

The predator's cruising speed was assumed to be 3L/sec and the attack range, 6L. From Bainbridge's (1960) data on grown fish, a curve of acceleration with time reveals a point at which speed reaches a maximum, 12L/sec after 0.5 sec. The distance reached in the short burst of half a second is 6L, which may be considered both as the escape distance or attack range. The generalization applies to finned and grown fish and it is an extension to apply it to planktonic predators (including fish) more generally.

Harris (1968) developed an equation that expressed the volume searched by a predator, with an attack speed, $R_p = 6C$ cm/sec. Predation, P , in liters/day is given by:

$$P = 3\pi R_p^2 C_p T_1 t / (3 + T_1 R_p^3) ([3C_p / A_p] - 2),$$

where R_p is the attack range or escape range of the predator;

where C_p is the cruising speed of the predator;

where $A_p = R_p - C_p$;

where T_1 is the density of larvae.

Predation reduces the number of larvae: $T_1 = T_1(1 - UP)$, where U is the density of predators, T_1 is the density of fish larvae after a time period.

As originally published in Cushing and Harris (in press), the model did not describe density-dependent growth at all because I was uncertain whether the food of plaice larvae declined during the season or not. Wyatt (in press) has shown that the populations of *Oikopleura* do decline under predatory pressure by the larvae of plaice and sand eels. In its present form, the density of food organisms is reduced by larval feeding. The original model represented an underestimate of density-dependent mortality, because the constant quantity of food available was shared among increasing densities of larvae and if that had been reduced then the density-dependent mortality would have been greater.

From Beverton (1962), figures are available on the density of larvae produced by an average stock size, and an extension both to low and high stock is possible. From the fitted curve (using the equation $R = APe^{-BP}$), the observed density-dependent mortalities can be estimated (i.e., e^{-BP}). In the following they are compared with those under estimated in the model because Wyatt's findings were not then known:

n larvae/m ³	-BP	e ^{-BP}	Model mortality rate
0.5	0.134	0.875	0.533
2.8	0.751	0.472	0.159
10.0	2.680	0.0686	0.046

The trend of density-dependent mortality is correctly estimated; it is an increase of 12 times (e^{-BP}) or 11 times in the model, for an increase in larval density of 20 times. But the magnitude of larval mortality at the average density of larvae is underestimated by three times and at the extremes by about one and one-half times, perhaps because the effect of density-dependent growth was not included.

Figures 31-a, 31-b, and 31-c show the results of model investigations made with both growth and mortality density-dependent; Figure 31-a shows how larval mortality during a 30-day period increases with numbers of larvae; Figure 31-b shows that the weight of a larva varies with food after 30 days and Figure 31-c illustrates the dependence of mortality (as percentage per month) on food. Thus mortality (and growth) are density-dependent and both are functions of the available food. The range of growth and mortality in the model match the observations in the sea and the densities of larvae are those found in the sea. The model is, however, unfinished because each component has not been tested as well as it might have been and the links between the components have not been fully investigated.

However a model has been developed in which mortality is density-dependent through the availability of food and because of this link growth is density-dependent also. The relevance of these facets of construction will become clear later.

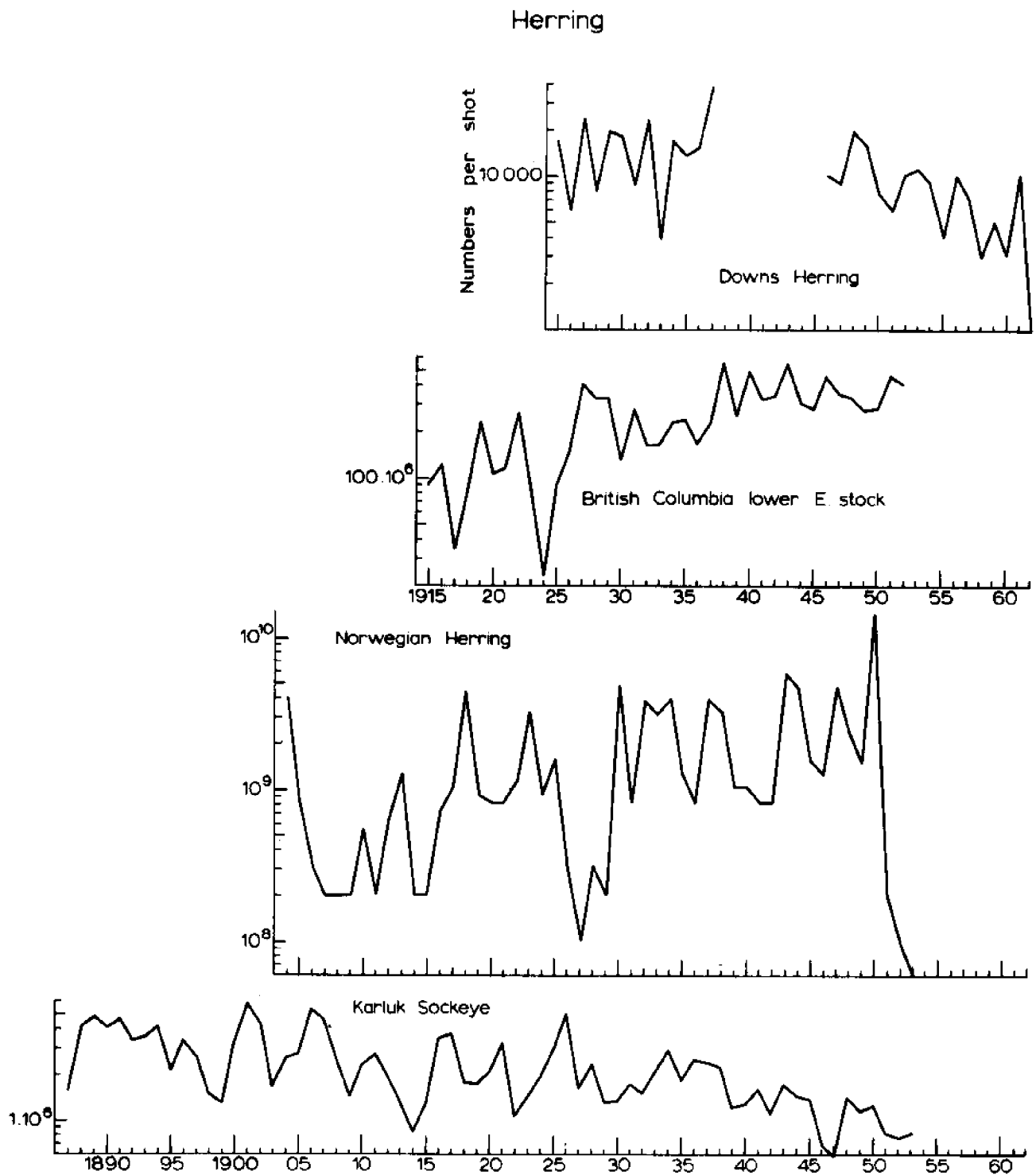


Figure 25. Herring and salmon recruitments
 (a) Downs herring, 1925-1962 (Cushing and Bridger, 1966)
 (b) British Columbian herring, Lower East stock, 1915-1952
 (c) Norwegian herring, 1904-1953 (Marty and Fedorov, 1963)
 (d) Karluk River salmon, 1886-1953 (Anonymous, 1962).

Cod

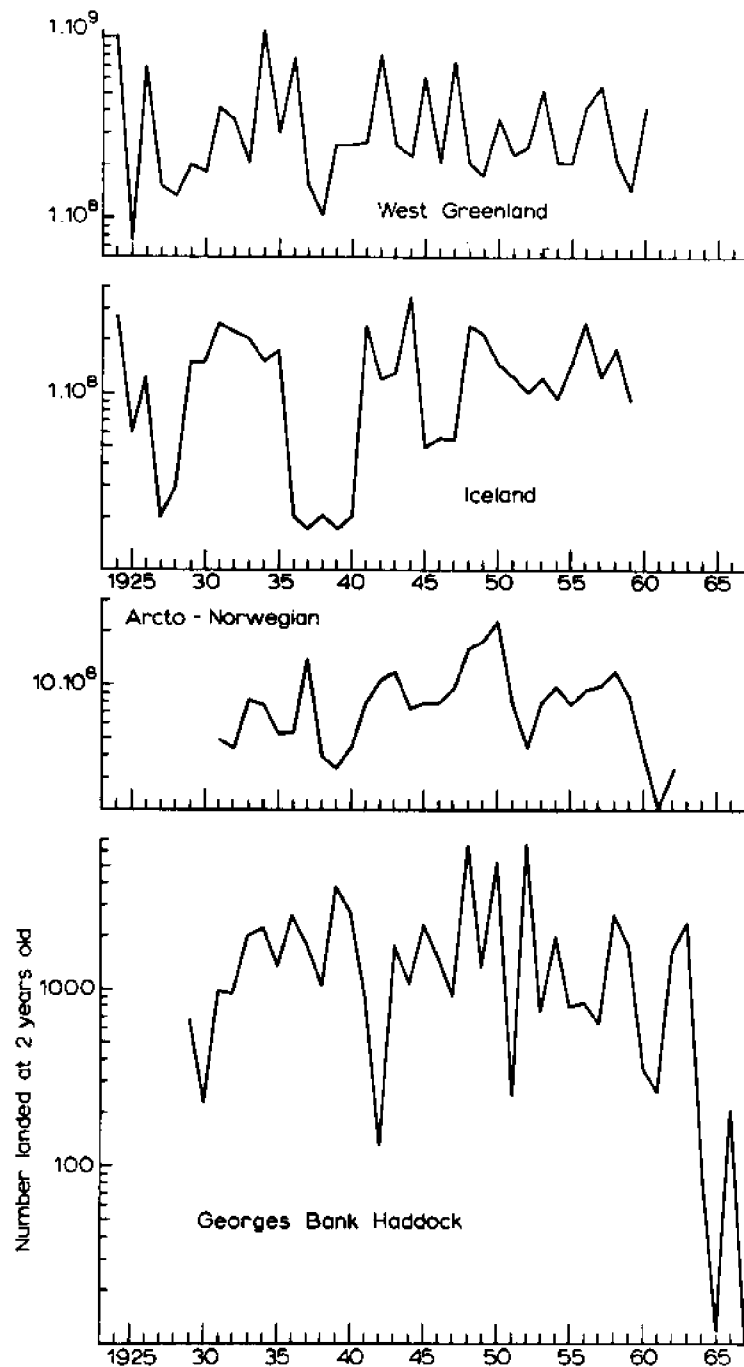


Figure 26. Gadoid recruitments
 (a) West Greenland cod, 1924-1960 (Garrod, 1968)
 (b) Iceland cod, 1924-1959 (Garrod, 1968)
 (c) Arcto-Norwegian cod, 1931-1962 (Garrod, 1967)
 (d) Georges Bank haddock, 1929-1967 (Grosslein and Hennemuth, in press).

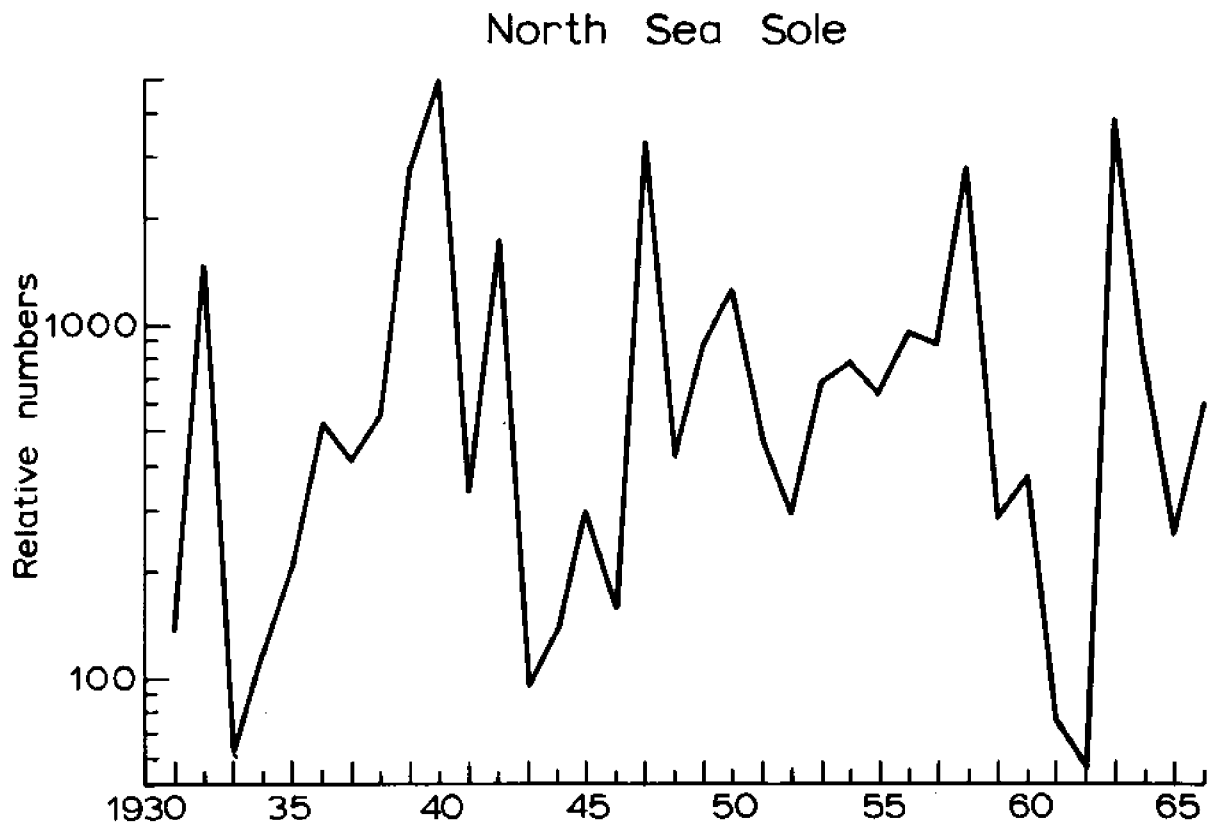


Figure 27. Flatfish recruitments, North Sea sole (Anonymous, 1970).

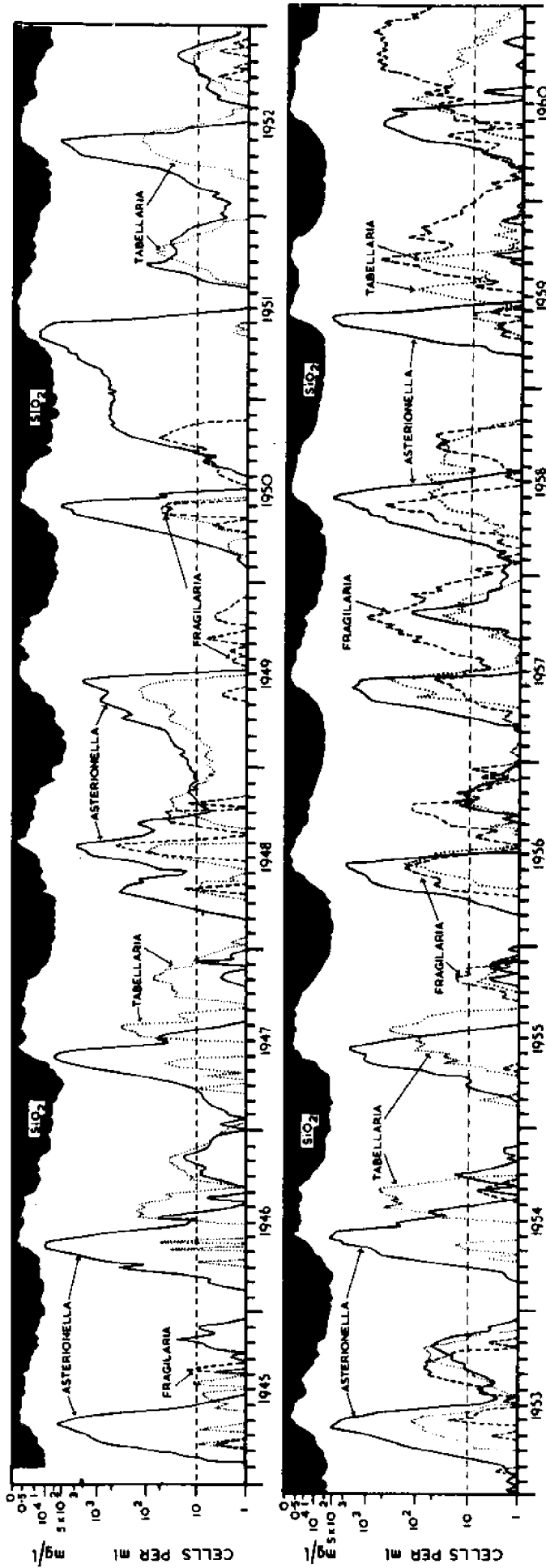


Figure 28. Variation in numbers and in timing of the outburst of *Asterionella formosa* in Windermere (Lund, 1964).

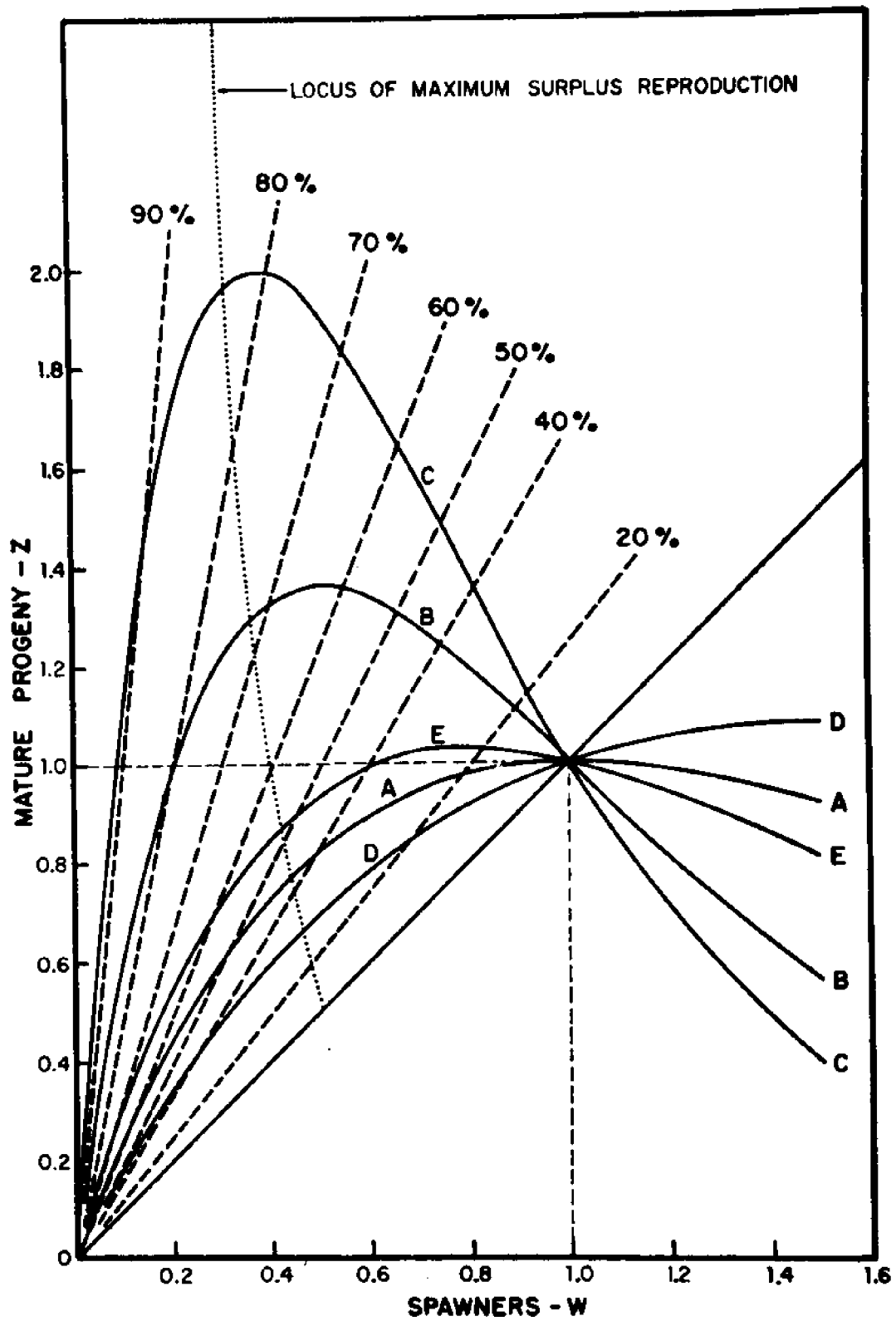


Figure 29. Ricker's stock and recruitment curve (Ricker, 1958).

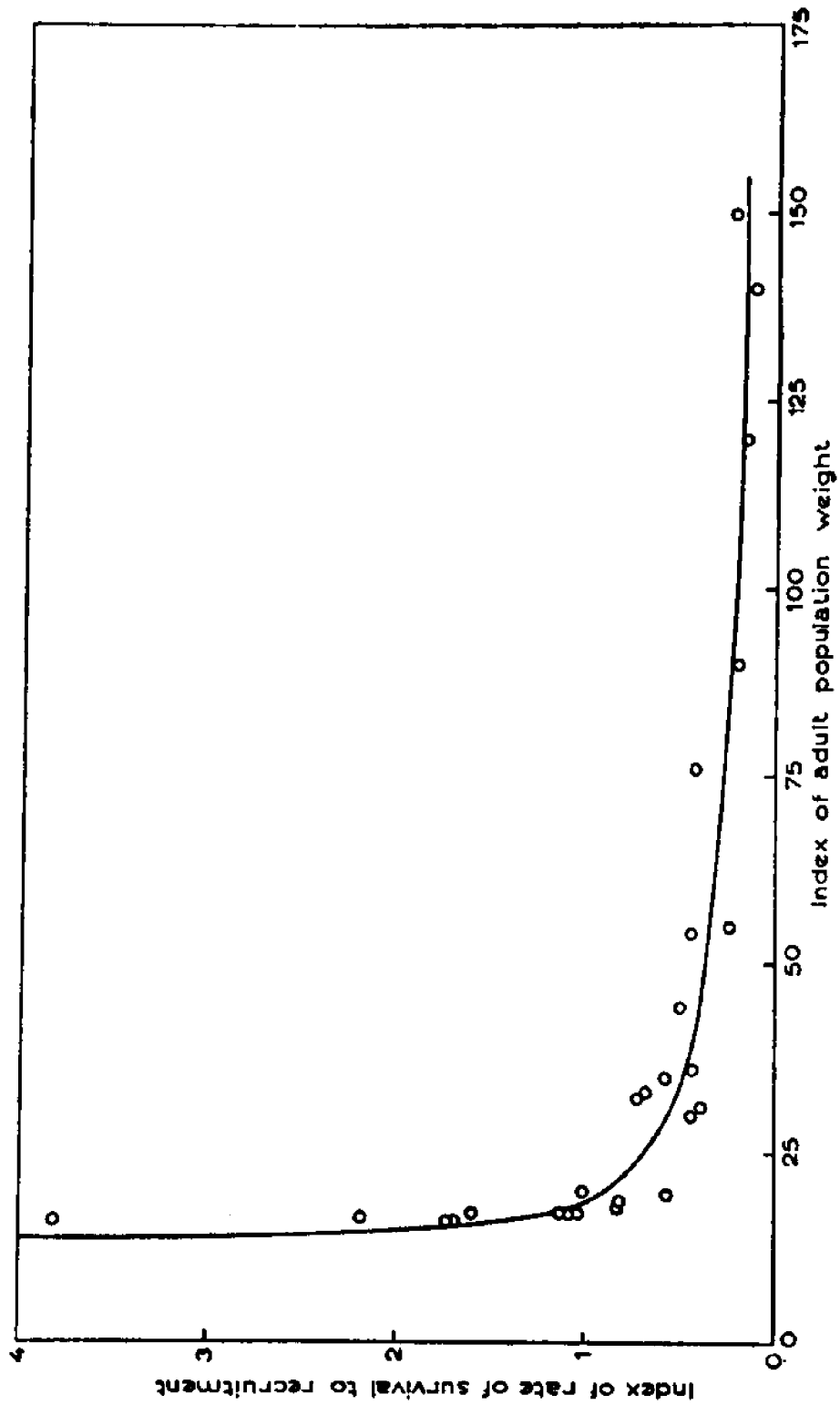


Figure 30. The decline in survival (as recruits/stock) with increasing stock in the southern North Sea plaice (Beverton, 1962).

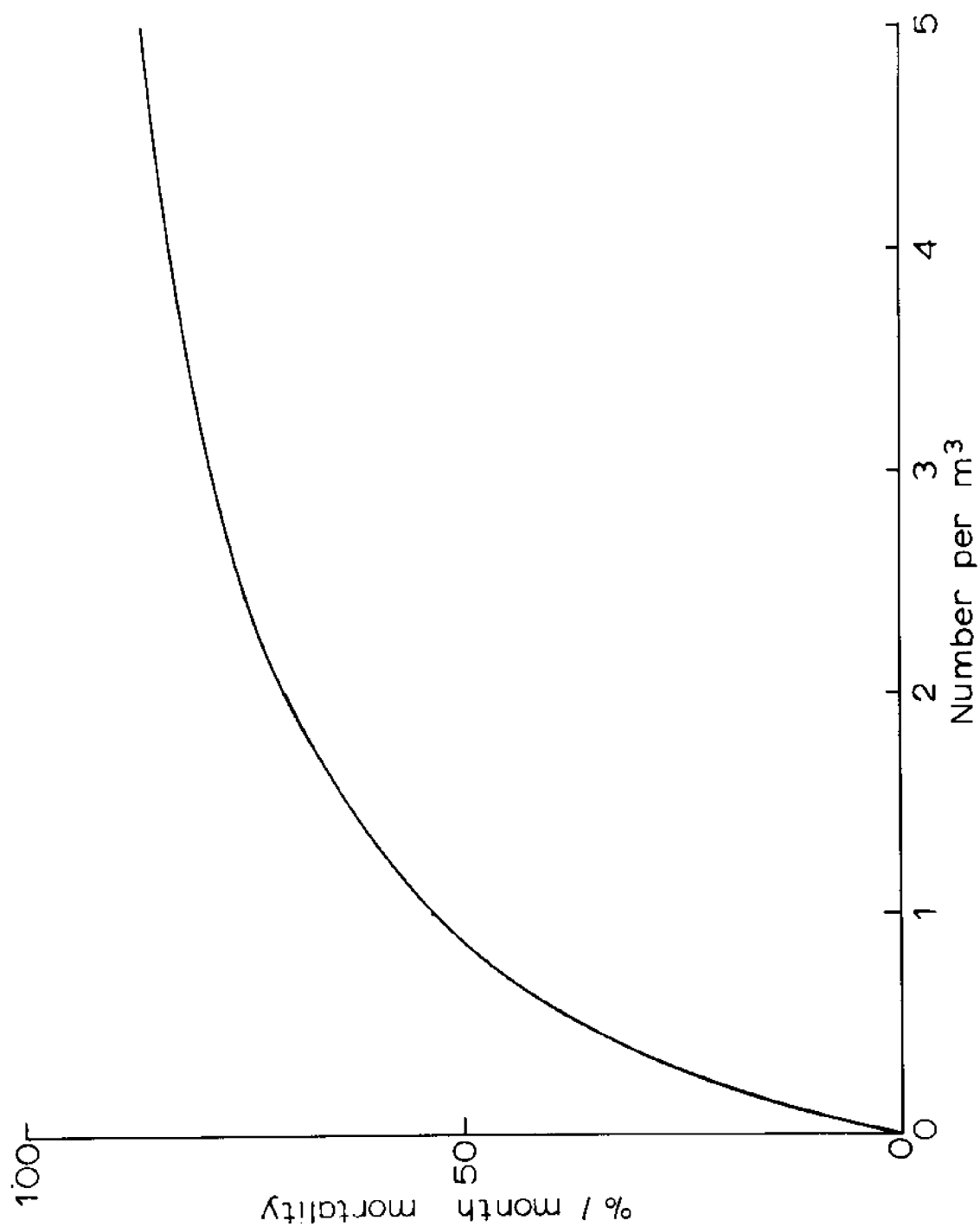


Figure 31-a. Results of model investigations: dependence of mortality on density.

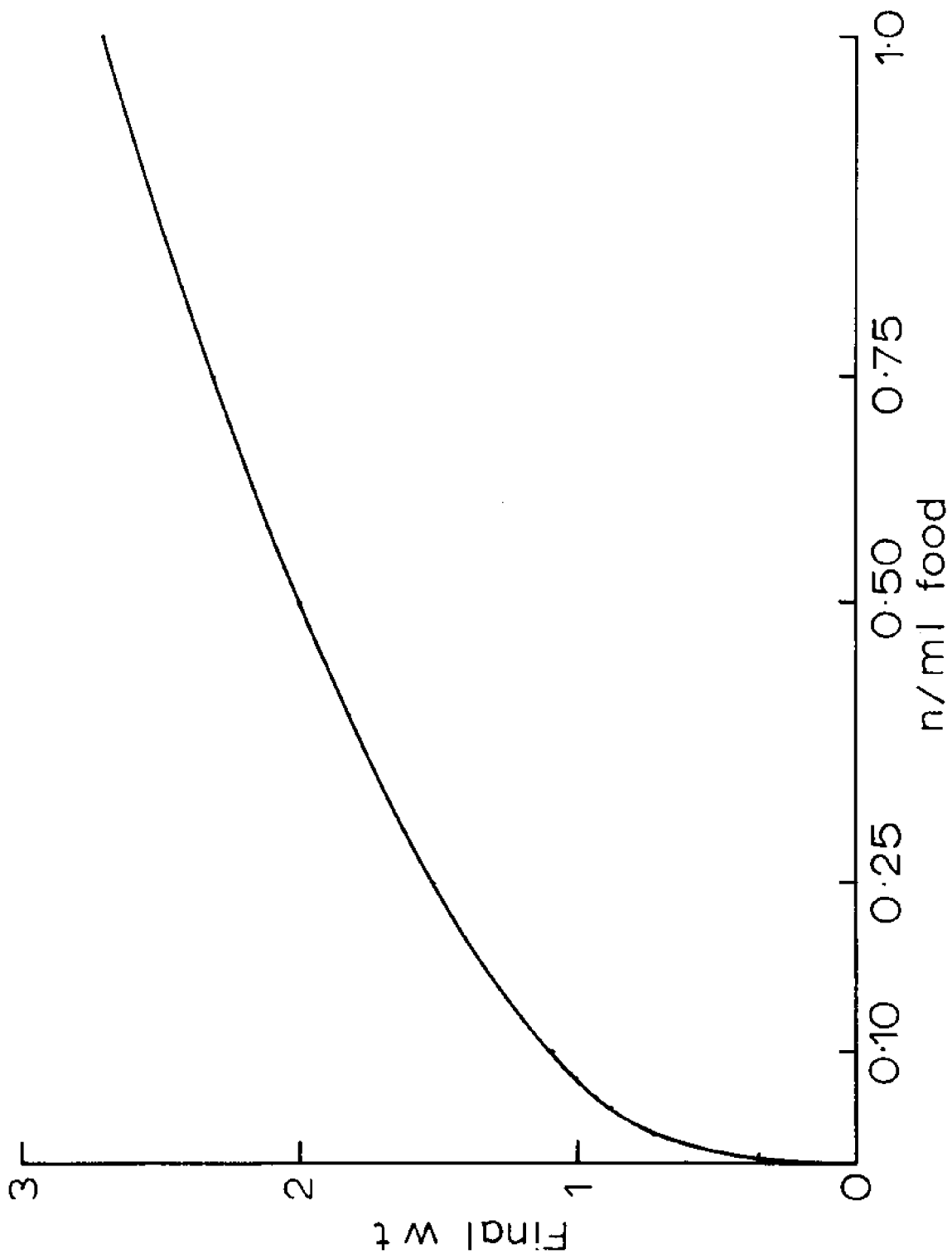


Figure 31-b. Results of model investigations: dependence of final weight on food.

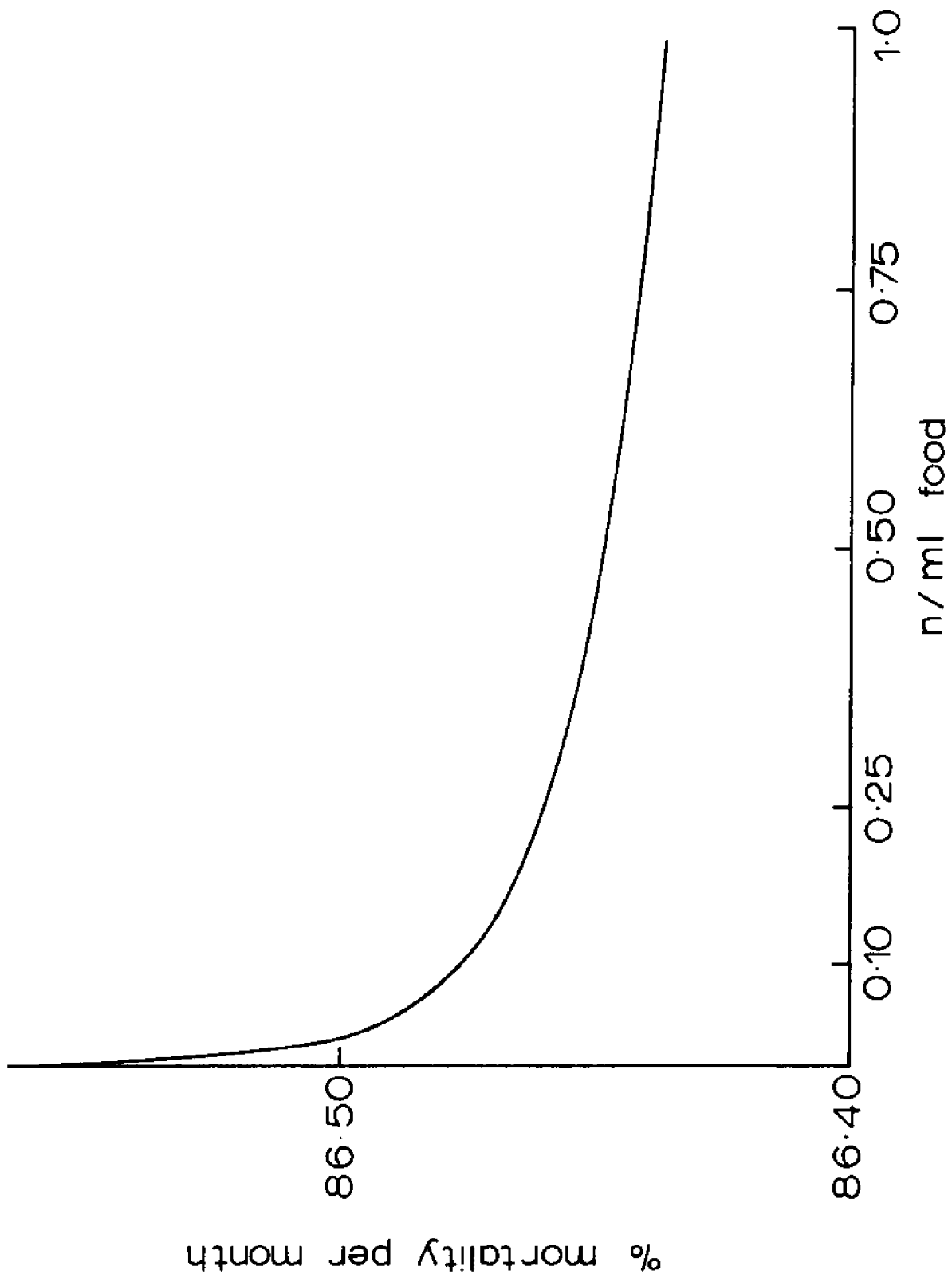


Figure 31-c. Results of model investigations: dependence of mortality on food.

Chapter 4

THE STOCK AND RECRUITMENT CURVES

Introduction

In the population dynamics of fishes, descriptive models are usually based on the logistic curve, and the effects of growth and recruitment are included in the differences in stock, or stock density, which they describe. Such models have now passed into history except in those stocks for which age estimates are lacking. Because it was assumed that growth and reproduction were balanced by mortality (as they must be to obtain stability in numbers), it was thought unnecessary to measure such parameters independently. The earlier descriptive models have been replaced by analytic ones in which the population is synthesized from measurable parameters.

There are two forms of stock/recruitment curve, that of Ricker and that of Beverton and Holt. The first cannot be applied easily to multi-age stocks and the second perhaps should not be applied to gadoid stocks.

The Biology of the Pacific Salmon in the Development of the Ricker Curve

Ricker (1954) distinguished three forms of predation: first, where the predator takes a fixed number of prey; second, where the predator takes a fixed proportion of prey numbers; and third, where the predator takes all in excess of a given number of prey. When a fixed number is taken, mortality declines with increased density; when a fixed proportion is eaten, mortality remains constant; if all are taken in excess of a given number, mortality increases with density, but as shown above it need not be the only way of generating density-dependent mortality. Density-dependent mortality in this sense is generated by an increase in predation. If a fixed number is taken, at low levels of numbers, mortality must increase in an inversely density-dependent manner. Neave (1953) named such a death rate depensatory, as opposed to a compensatory one, which increases with density.

Neave, and others, suggested that the mortality of salmon eggs in the redds is compensatory, because too many eggs/unit area might exhaust the limited oxygen supply. Hunter (1959) showed that the percentage survival from egg to emergent fry decreased with increased numbers of pink and chum salmon, when he expressed spawning success as an asymptotic function of numbers/unit area. Depensatory mortality was first demonstrated by Neave (1953) by marking chum salmon fry in groups of one hundred (out of thousands) about 300 yards upstream from a counting weir; the percentage survival to the weir increased with increased numbers in Hooknose Creek and in Nile Creek. Hunter (1959) showed that the percentage of pink and chum fry eaten by coho and sculpin decreased with increasing quantity of emergent fry. He also established that the number eaten was virtually constant.

The possibility of compensatory mortality was first raised by Ricker (1950), when discussing the dominance of cycles of Fraser River sockeye. Because the fish of a year-class spawn and die together at the age of four, a spawning group in one year is distinct in time from that in any other in the four-yearly cycle except its parents. There is exchange at a low level in time because a small proportion spawn at ages other than four; it is analogous to the low degree of stray from one parent stream to another. Having noticed that one cycle in the Fraser River was dominant to the other three (after the Hell's Gate landslide), Ricker suggested that the dominance was maintained by the mortality of the fry of the weaker cycle, caused by predation from fish of the dominant cycle one year older. Hence, cannibalism might explain the observed phenomenon of dominance.

The common curve that Ricker developed is:

$$R/R_r = (P/P_r) e^{(P_r/P_m)(1 - P/P_r)}, \quad (1)$$

where R is recruitment;

where R_r is recruitment at the replacement point of stock, P_r , so

$$\text{that } R_r = P_r;$$

where P is stock;

where P_m is the stock at which maximum recruitment is found.

In Ricker's terminology, $(R/R_r) = Z$, $(P/P_r) = W$, $(P_r/P_m) = a$, so $Z = We^{a(1-W)}$. Because in the accepted terminology today, Z is the coefficient of instantaneous total mortality, I write: $(R/R_r) = We^{a(1-W)}$. The replacement level of a single-age stock, P_r , where the curve cuts the bisector, is the point at which the unexploited stock replaces itself and about which it stabilizes; as noted earlier an exploited single-age stock replaces itself and stabilizes at lower levels. The constant $a (= P_r/P_m)$ (Figure 29) describes the shape of the curve; if low, the curve is slightly convex, and if high, it is a sharp dome. In general, the curve takes a dome-shaped form with respect to the bisector because $R > P$, when $P < P_r$. The development of this curve will be discussed below. Chapman (1972) has described the right-hand limb of such a dome-shaped curve as overcompensation because, mathematically, recruitment is reduced to very low levels indeed if density-dependent mortality is very high.

Larkin and Hourston (1964), starting with Ricker's three types of predation, discussed various forms of depensation. They separated the life cycle in various stanzas, in which different mortality structures might be expected. The Pacific salmon grows through a number of well-defined stages: eggs in

the redds, fry in the lakes, smolts in the rivers, adolescents in the open ocean, and spawning adults back in the river again. Larkin and Hourston (1964) described the development of a model with different mortality structures; Ward and Larkin (1964) describe its application to the Adams River stocks, and Larkin and MacDonald (1968) its application to the Skeena River stocks. The form of depensatory mortality was expressed.

$(R/R_r) = We^{a(W-1)}$, which generates a concave curve with respect to the bisector rather than a convex one, as in the usual Ricker curve.

The first stage of mortality in the life cycle is the compensatory one in the redds. It is modified at stock values beyond the point of stabilization ($=P_r$), by writing:

$$(R/R_r) = (1 - D)e^{a_3(W-1)} + D.$$

where a_3 is a coefficient of depensation.

At such high levels of stock, the density-dependent mortality in the usual Ricker curve is so high (in the particular stocks considered) that recruitment is reduced to very low levels indeed (as noted above), and this equation modifies the curve by bringing it to an artificial asymptote, D. In the Pacific salmon stocks, the variance in stock is the same as that in recruitment and so the nature of the curve beyond the point of stabilization has some practical importance; in a multi-age stock such importance would be less, because the variance in stock is less than that of recruitment (by the square root of the number of age groups). During the first part of the life of the fry in the streams, they are exposed to random chances of death (or extrapensatory mortality in Neave's terminology) as opposed to a positive aggregation by predators. Then as they come within range of larger predators, this mortality is considered to be depensatory. A fourth component is called buffered depensation, when the one-year-old smolts eat the fry as they emerge. The fifth and last form of mortality is an extrapensatory one in the open ocean.

For the Adams River stock, the model was run for many simulated years, and in the course of time the subdominant cycle gradually develops just after the dominant one. An interesting point is that at low stock level, the recruitments are grouped rather close to the bisector (Shepard and Withler, 1958) as if depensatory mortality were indeed an important factor. Recently, Larkin (1971) examined the sensitivity of the model by varying the parameters, and showed how dominance can be reduced. Although the evidence presented by Neave and Hunter showed that depensatory mortality could be generated in an experimental sense, Larkin's models establish

that it can occur as an important part of the stock/recruitment relationship itself, as Ricker originally suggested. Compensatory mortality alone does not explain the dominance of one cycle over its successor in the Pacific salmon stocks.

Densatory mortality probably occurs in the lacustrine phase of the life history of the sockeye salmon. The question is: What part does it play in the life history of marine fishes more generally? It is generated when a fixed number is taken from a small stock by predation, and it decreases with increasing stock. For each equal increment of stock, mortality decreases until their decrements become very small indeed. Then the proportion taken by predation is effectively constant, if not precisely so. Densatory mortality is related inversely to stock, but at higher stock levels it becomes effectively density-independent. It is apparent in the Pacific salmon because the exclusive nature of the cycles amplifies the initial effects into the phenomenon of dominance. On the other hand, the same form of mortality may very well occur and not be noticed; indeed on a flatfish nursery ground, metamorphosing animals migrate inshore through a barrier of I group fishes, which are predatory. If no aggregation takes place, such mortality is density-independent except at low stock levels, unless of course such predators generate density-dependent mortality in the manner outlined in the previous chapter. As stock is reduced, densatory mortality may play a part in multi-age stocks, particularly when reduced to single-age stocks by the effect of fishing. Indeed, predators on a herring spawning ground like "spawny haddocks" may have densatory effects. Burd and Parnell (in press) have shown that the dependence of larval numbers on stock in the Downs herring takes a concave form at very low stock values, which indicates such a possibility.

There is a question of terminology. Neave (1953) introduced the terms compensatory and densatory mortality as synonyms for direct density-dependent and inverse density-dependent mortality, as being less cumbersome. In fields of ecology other than fisheries, the distinction between the two forms of density-dependence has been drawn and because the densatory form is uncommon, the direct form of density-dependence (the compensatory one) has been called density-dependent. Densatory mortality plays an important part in the dynamics of the Pacific salmon population, but in the general field of fisheries biology in the sea, mortality has been classified as density-dependent and density-independent.

It was suggested above that during the larval drift, three population processes are mediated in a single process, that is, those of competition, density-dependent mortality, and year-class determination. It is possible that the last, which involves a mortality that Larkin has called extrapensatory, might be eventually predicted from climatic information. Further, as more is known of the development of growth and mortality during the larval stages, the term density-dependent mortality itself may disappear except as a Malthusian reminder. The essential mechanism must maintain the ratio of growth to mortality at given ages, and we will remind ourselves from time to time that it is density-dependent.

The Ricker Curve

Ricker's (1954) first study of the dependence of recruitment upon parent stock assumed that the density-dependent or compensatory control was generated by cannibalism. In lakes and rivers Pacific salmon of one year-class feed on the class a year younger, as suggested above, and analogous processes could be found in the sea. The question really is whether such animals are more than accidental cannibals, that is whether their absence would make any difference to the general network of predators. Poor year-classes are often succeeded by good ones, in multi-age stocks, but a good one does not need a poor precedent.

Ricker (1954) postulated two stock sizes: P_1 and P_2 ; $P_2 = WP_1$.

Then recruitment $R_1 = KS_1 P_1$,

where density-independent factors reduce survival S_1 , to the fraction K ;

$R_2 = KS_2 P_2 = KS_2 WP_1$, where cannibalism or predatory abundance occurs for a brief period; that is S_2 represents density-dependent survival.

$$R_2/R_1 = \frac{KS_2 WP_1}{KS_1 P_1} = W \frac{S_2}{S_1}$$

$$W = \log S_2 / \log S_1 \quad \therefore S_2 = S_1^W$$

$$\therefore R_2/R_1 = WS_1^{W-1} \quad (2)$$

To locate the maximum,

$$WS_1^{W-1} \ln S_1 + S_1^{W-1} = 0$$

$$\therefore -\ln S_1 = 1/W \text{ or } S_1 = e^{-1/W}$$

Let $W = 1$ and substituting $1/e$ for S_1 in equation (2)

$$\therefore R_2/R_1 = We^{1-W}$$

The two processes of density-dependent and density-independent mortality have been considered separately in distinct stocks. If they work together,

because $W = P_2/P_1$, it is an easy step to write $W = P/P_m$, where P_m is the stock at which maximum recruitment is found, or

$$\text{or } R/R_m = (P/P_m) e^{1 - P/P_m}. \quad (3)$$

The next stage in the development is to extend the argument from cannibals to predators that aggregate on to their prey or increase in numbers in proportion to the prey (Ricker, 1958).

$$N = N_o + K_1 P,$$

where N_o is the initial abundance and N the abundance of predators;
where P is the prey, K_1 is a coefficient of aggregation.

The mortality generated by the predators is given by

$$Z_o + K_2 (N_o + K_1 P) = Z_o + K_2 N_o + K_1 K_2 P,$$

where Z_o is the initial mortality rate of the prey.

The survival of the prey, that is, of the little fish, is attributed to density-independent causes, S_n , and to density-dependent causes, S_c . The density-dependent mortality is a function of the initial numbers of fish.

$$S_n = e^{-(Z_o + K_2 N_o)}$$

$$S_c = e^{-K_1 K_2 P} = e^{-KP}, \text{ where } K_1 K_2 = K = B.$$

$$\text{Then } R = S_n P S_c = A P e^{-BP}, \text{ where } A = S_n. \quad (4)$$

By maximization we obtain equation (3). Then the concept of replacement stock, P_r , was introduced, which is the point in stock at which the curve cuts the bisector. In a single-age stock, recruitment is then equal to stock, and in a multi-age stock, I have called it the point of stabilization. The final form of Ricker's equation is

$$R/R_r = W e^{a(1-W)}, \quad (5)$$

$$\text{where } a = P_r/P_m.$$

I have called equation (4) Ricker's initial equation, not because it was the first, but because it stated his essential formulation in the simplest possible way.

There are two points of criticism of Ricker's development. The first is that cannibalism or an aggregation of predators is perhaps not needed to control numbers from generation to generation. Ricker (1958) wrote that predators "must be so numerous as to decrease the number of prey survivors."

In the formulation as applied to fitted data, a mean abundance is assumed because the rates of increase of predation cannot be specified. But if density-dependence is generated, as suggested earlier, as an effect of food availability, then the prey survivors are decreased and predatory mortality varies inversely with the availability of food: so if food has to be shared among more larvae, mortality increases and so is density-dependent. With increased numbers of larvae, predatory mortality increases as if the predator was aggregating, as in the development of equation (4). This process can start on the initial numbers, as in the Ricker equation. This is the position of Beverton and Holt's second equation (see below), in which numbers are also controlled from generation to generation.

The second point of criticism concerns the maximization step that ends in equation (5). In a multi-age stock, the replacement point is inaccessible because the trend of natural mortality with age is unknown; any constant mortality with age is inconceivable because then the population cannot be terminated in age. In a single-age stock like that of the Pacific salmon, fish that die after spawning, the replacement point remains valid. At a later stage it will be suggested that the trend of natural mortality with age can be approximately specified in a multi-age stock. Hence recruitment might be considered as the sum of repeated spawnings for a number of years, and the problem really becomes the same as that for the single-age stock as Ricker (1958) suggested. The difficulty about this approach is that recruitment and stock are distinguishable only in a transitory sense. In the Pacific salmon recruitment is stock that spawns four years after its parents. In the multi-age stock, the annual recruitment replaces the annual deaths. Although stocks must replace themselves, the point of replacement is not made use of here although some didactic use is made of an analogous point of stabilization.

The Beverton and Holt Curve

Ricker's most important point was that a constant fraction of the population of little fishes is taken by predators, and when there is a larger population, the fraction increases because the predators aggregate. Beverton and Holt (1957) attacked the problem from a different point:

$$\frac{dN}{dt} = (\mu_1 + \mu_2 N) N, \quad (6)$$

where N is the number of larval fish;

where μ_1 is the instantaneous coefficient of density-independent mortality;

where μ_2 is the instantaneous coefficient of density-dependent mortality.

For a short time period,

$$N_t = \frac{1}{\frac{\mu_2}{\mu_1} (e^{\mu_1 t} - 1) + \frac{e^{\mu_1 t}}{N_t}}$$

$$\text{If } \alpha = \frac{\mu_2}{\mu_1} (e^{\mu_1} - 1) \text{ and } \beta = \frac{e^{\mu_1 t}}{N_t}$$

$$R = \frac{1}{\alpha + \beta/P} \quad (7)$$

so long as the short time period is extended to the total time period from hatching to recruitment. The density-dependent mortality is proportional to N_t and not N_0 although if the period is short $N_t \approx N_0$; the conditions of population stability were fulfilled. This equation is asymptotic in recruitment.

Although equation (7) represents the curve that they fitted to some limited data, Beverton and Holt examined another possibility. They followed Ricker and Foerster (1948) and defined t_c as the time to reach a critical size at which mortality is changed and it is proportional to stock; in other words, if t_c is short, food availability is high and if long, food availability is low.

$$N_c = P e^{-\mu'_1 t_c}$$

where μ' is a constant mortality coefficient

$$\text{Then, } R = P e^{-[(\mu'_1 - \mu'_2) t_c + \mu'_2 t_r]}$$

where μ'_2 is a density-independent mortality coefficient between t_c and t_t , the age of recruitment.

$$\text{Let } e^{-\mu'_2 t_r} = A'$$

$$\text{Let } t_c \text{ vary with } P; \text{ then } (\mu'_1 - \mu'_2) t_c = B'P$$

$$R = A'P e^{-B'P} \quad (8)$$

Strictly, A^1 and B^1 operate in successive periods. Superficially, equations (8) and (4) are identical. However, the density-dependent mortality is generated in different ways in the two equations. In equation (4) it is due to the aggregation of predators or cannibals, whereas in equation (8) it depends on food availability such as indicated in the last chapter. However, the curves can be fitted to data in a provisional way because the separate formulations of the density-dependent mortality cannot yet be independently derived. As will be shown later, the data for the gadoid stocks tend to group themselves into dome-shaped curves, one or two markedly so. Hence the asymptotic curve of Beverton and Holt is not generally applicable. They faced this problem in the data for the Georges Bank haddock stock, which Herrington (1948) had grouped into a very marked dome. The curve fitted to these data was of the form:

$$R = A' P e^{-(B'_0 P + B'_1 P^2)}, \quad (9)$$

where the increment of density-dependent mortality with stock was attributed to cannibalism. There appears to be a relationship between density-dependence and fecundity, (as will be shown below); the dome-shaped curve characteristic of gadoids need not be a special case.

Present Developments

The main present developments by Larkin are in simulation models based on the curves given above. Larkin has used the Ricker curve to express both compensatory and depensatory effects as noted above. Paulik, Hourston, and Larkin (1967) have pointed out that the Beverton and Holt rectangular hyperbola can be readily used in the development of multiple strategies, because in exploited populations, the important part of a stock/recruitment curve is the left-hand limb, which describes the reduction of recruitment with fishing. However, if we seek understanding, the distinction between the two curves is of some importance.

Recently, Harris (in press) has reviewed the present equations relating recruitment to parent stock. He distinguishes between density-dependent mortality (as at any time t between hatching and recruitment) and stock-dependent mortality, which depends on the initial number of larvae. Beverton and Holt's first equation expresses the effect of density-dependent mortality and Ricker's initial equation and Beverton and Holt's second equation expresses the effect of stock-dependent mortality. They express the effects from generation to generation, whereas Beverton and Holt's first equation need not do so (in practice it does so).

If mortality varies with the K^{th} power of density, the stock/recruitment curve is an asymptotic one in recruitment like the first one of Beverton and Holt. Generalizing,

$$M = f(N)$$

$$\therefore \frac{dN}{dt} = -f(N)N$$

$$\int_{N_0}^R \frac{dN}{Nf(N)} = - \int_{t_0}^{t_r} dt = -(t_r - t_0),$$

where t_0 is the time at hatching when N_0 is the initial number and t_r is the time of recruitment, R . As this cannot be integrated, let us assume that

$$\int \frac{dN}{Nf(N)} = \phi(N) + C \therefore \frac{d\phi}{dN} = \frac{1}{Nf(N)} \quad (10)$$

$$\therefore \int_{N_0}^R \frac{dN}{Nf(N)} = [\phi(N) + C]_{N_0}^R = \phi(R) - \phi(N_0)$$

$$\therefore \phi(R) - \phi(N_0) = -(t_t - t_0)$$

Differentiating,

$$\frac{d\phi(R)}{dN_0} \cdot \frac{d\phi(N_0)}{dN_0} = 0$$

$$\text{or } \frac{d\phi(R)}{dR} \cdot \frac{dR}{dN_0} - \frac{d\phi(N_0)}{dN_0} = 0$$

Substituting from equation (10)

$$\frac{1}{Rf(R)} \cdot \frac{dR}{dN_0} - \frac{1}{N_0 f(N_0)} = 0 \quad (11)$$

$$\text{or } \frac{dR}{dN_0} = \frac{Rf(R)}{N_0 f(N_0)} \quad \text{or } \frac{RM_r}{N_0 M_0}$$

where M_r and M_0 are the instantaneous mortality coefficients at recruitment, t_r , and time of hatching, t_0 .

This expression can only be zero at $N = \infty$, so the dome-shaped curve cannot be generated by density-dependent mortality alone.

In Beverton and Holt's second equation, which is identical in form to Ricker's initial equation, two levels of larval mortality are assumed and the transition from one to the other occurs at the time t_c . Now $t_c \propto 1/W_\infty \propto \text{food eaten} \propto \text{density} \propto N_0$. This is a stock-dependent mortality, in which growth varies inversely as stock. Harris then investigated the relationship between t_c and N_0 . In the von Bertalanffy equation,

$$L_t = L_\infty(1 - e^{-Kt}).$$

$$\text{Differentiating, } L_\infty K e^{-Kt} \frac{dt}{dL_\infty} + (1 - e^{-Kt}) = 0,$$

$$\text{or } \frac{dt}{dL_\infty} = - \frac{(1 - e^{-Kt})}{L_\infty K e^{-Kt}} = - \frac{L_t}{KL_\infty(L_\infty - L_t)}$$

For small values of L compared with L_∞ , this approximates to

$$\frac{dt}{dL_\infty} \approx - \frac{L}{KL_\infty^2}$$

Integrating, $t = L/KL_{\infty}$

Then the relation between t_c and N_0 might be more accurately expressed as $t_c \propto (N_0)^{1/3}$

$$\text{Then } R = APe^{-BP^{1/3}} \quad (12)$$

. This equation is of the same form as the earlier one, but perhaps it is the distance between the larvae that is important in generating the density-dependent processes.

Harris then asks whether mortality can be a function of both stock (N_0) and density (N_t), i.e., $M = f(N)$ and $f(N_0)$. He finds that

$$\frac{dR}{dN_0} = \frac{R \cdot Mr}{N_0 M_0} + R \cdot Mr(t_r - t_0) \cdot f(N_0) \frac{d}{dN_0} \cdot \left(\frac{1}{f(N_0)} \right)$$

The first term is identical with that of equation (2). Differentiating part of the second term:

$$\begin{aligned} f(N_0) \cdot \frac{d}{dN_0} \cdot \frac{1}{f(N_0)} &= - \frac{(N_0)}{(f[N_0])^2} \cdot \frac{d(f[N_0])}{dN_0} \\ &= - \frac{1}{f(N_0)} \cdot \frac{d(f[N_0])}{dN_0} \end{aligned} \quad (13)$$

This term is negative if $f(N_0)$ increases with N_0 and vice versa. If mortality were a product of N_t and an increasing function of N_0 , dR/dN_0 might reach zero at $N_0 < \infty$. Summarizing, if mortality is a function of density alone, the stock/recruitment curve increases to an asymptote only; if it is a function of N_0 and N_t , a dome is possible. The important point is that this development is possible in Beverton and Holt's second curve, whereas Ricker's initial equation depends only on stock-dependent mortality (in cannibalism or the aggregation of predators). Similarly, Beverton and Holt's first curve relies on density-dependent mortality only. The most interesting point is the part played by density-dependent growth in the relationship between N_0 and N_t . Whether it occurs in the form postulated by Jones (in press) or Cushing and Harris (in press) is so far unknown.

Chapter 5

THE ROLE OF FECUNDITY

Introduction

In the large populations that support commercial fisheries, fish spawn eggs of about the same size, that is, about 1 mm across; exceptions are salmon and halibut, the eggs of which are 4 to 5 mm in diameter, which are, of course, up to two orders of magnitude larger by volume. Differences in size are to some extent differences in quantity of yolk, which are adaptations of the match of larval production to the variability in timing of the production cycle; a notable exception is the pilchard egg, which has a large perivitelline space. Most eggs in the sea hatch in a fairly short time, from two days to three weeks, but those of the salmon have to live in the redds for five months or more. Fecundity is a function of weight, so if eggs are more or less of the same size, bigger fish are more fecund than smaller ones.

When the eggs are laid in the sea, they take up water and increase their volume considerably (up to five times in the plaice, Fulton, 1897). The gonad volume is roughly one-fifth or one-sixth of the total volume of the fish, so the volume of eggs in the sea is approximately equal to that of the parent. Obviously, the eggs cannot be laid all at once. The density of eggs in the sea cannot be expressed as fecundity/m², but is some small fraction of that quantity. It is possible that the fraction of the gonad used in each spawning is approximately the same in all fishes. On the other hand, the number laid is the product of fecundity and the number of females. The density of eggs in the sea is an index of the stock of eggs and hence the stock of females. If density-dependent mortality takes place predominantly during the larval drift, it should be some function of fecundity. Preliminary attempts to establish a relationship between estimates of density-dependent mortality in different groups of fishes with either Ricker's final equation or the Beverton and Holt first equation failed because the material was highly variable.

The First Method (Cushing, 1970)

Figure 32 shows Ricker's family of stock and recruitment curves. If recruitment is variable and the numbers of observations are low, the estimates of the constants must also be variable. However, in exploited stocks, the data must be grouped to the left of the point of stabilization (= P_r in Ricker's terms). By inspection, it appears that some herring and some salmon stocks can be described as low domes (curves a, b, and c) and that two cod stocks (Arcto-Norwegian and St. Lawrence) can be described as high domes (curves d and e). In an attempt to express such differences, the

following equation was used as an approximation: $R = kP^b$, where k is a constant and b an index of density-dependence (Cushing, 1970). If data are distributed about the curves in Figure 32, between P_r and the locus of maximum surplus reproduction, then $b < 1$. Now R/P is an index of survival, so

$$R/P = kP^{(b-1)},$$

$$\text{or } \log (R/P) = \log k + (b-1) \log P.$$

Hence $(b-1)$ is the decrease in survival generated by a proportional increase in stock; as stock increases, b decreases from (< 1) to 0 and to negative values.

Figure 32 shows, as a dotted line, the locus of maximum surplus reproduction for the family of curves. For lightly exploited stocks, that is, up to the point of maximum surplus reproduction, the index may be fairly reliable. For stocks with slight domes (i.e., a, b, and c), it may be reliable however heavily they are exploited. For stocks with marked domes (i.e., d and e), the index is underestimated when the exploitation is heavy. The main point, however, is that the index cannot be overestimated in exploited stocks.

Thirty-one stocks were examined, for which data on stock and recruitment were available; the groups of fish were pink salmon, chum salmon, red (or sockeye) salmon, Atlantic herring, Pacific herring, California sardine, flatfish, tuna, and gadoids. Because some series of recruitments were distributed about an obvious dome, the slopes were recalculated for all observations greater than the mean in stock. This exercise was restricted to those stocks for which there were more than 20 observations. Of 20 such stocks, in six no change in the index was found, i.e., less than the standard error of the slope in the original analysis. In 12 stocks, differences greater than the standard error of the original analysis were found, but they were less than that of the second treatment, which included fewer observations. Only in two stocks (Skeena sockeye and Arcto-Norwegian cod) was a marked difference found in the second treatment. In the Skeena sockeye, the slope was reduced from 0.679 to 0.315, a difference which, however, was not significant; but the direction of change suggests the presence of a dome in a well-exploited stock as is shown in the treatment by Shepard and Withler (1958) and by Larkin and MacDonald (1968). In the Arcto-Norwegian cod, the index of density-dependence was increased from -0.067 to -1.989 (SE 0.449), a significant difference, as might be expected in a heavily exploited stock if there is a dome in the stock recruitment relationship; this modified value was subsequently used. Another conclusion is that the indices of density-dependence are probably fairly well estimated.

The relationships between recruitment and parent stock are shown in Figures 33-39. Each figure includes a number of plots of log recruitment on log stock; the dotted lines indicate the 95% confidence limits to the

slope drawn through the mean and the slope rotates between the confidence limits. Figure 33 shows the relationship for four pink salmon stocks. Figure 34 shows the slopes for eight red salmon stocks and one of chum salmon. They include well-known stocks like those of the Fraser, Karluk, and Skeena to which dome-shaped curves were originally fitted. By inspection, a fair fit to the data has been obtained, particularly when it is recalled that the point of interest is the slope at the mean value of stock. Figure 35 gives the data for the Northeast Atlantic herring, the stocks of which are the Downs and Norwegian herring, Buchan and Dogger herring; the slopes for the winter/spring spawners (Downs and Norwegian) are obviously greater than those for the autumn spawners (Buchan and Dogger). In Figure 36 are shown the relationships for the Pacific herring, the stocks of which are the British Columbia, both Lower East and North, Southeast Alaska, and Sakhalin. In general, in the herring stocks, the slopes appear to be less than those of the salmon and, in the Pacific herring, they approach zero; the data are more variable, as in the chum salmon and the autumn-spawning Atlantic herring. The data for the California sardine are shown in Figure 37, together with some for the yellowfin tuna. The data for flatfish are given in Figure 38--Pacific halibut, Petrale sole, and southern North Sea plaice. The index of density-dependence for the halibut tends to be negative and that for the plaice is zero, with not too much latitude from the confidence limits. Figure 39 shows the data for the gadoids, two of which are sharply negative and one of which is positive; that for the Arcto-Norwegian cod stock has a negative slope in the adjusted data as noted above.

By inspection there is a trend from positive to zero, from zero to negative slope as one passes from salmon to herring, flatfish, and gadoids, which is a trend in increasing fecundity. Figure 40 gives the slope and their errors as twice the standard error in an order of groups, pink salmon at the top and gadoids at the bottom, which is also an order in fecundity. There is a trend in the index of density-dependence with increasing fecundity. Within the red salmon group, the southern group (Columbia, Fraser, and Skeena) differs a little from the Bristol Bay group, with the Karluk River perhaps intermediate. Within the Atlantic herring, there is a distinct difference between the winter and spring spawners, Downs and Norwegian, and the autumn spawners, Buchan and Dogger, and this difference is associated with a difference in fecundity; the winter/spring herring fecundity is about 45,000 and that of the autumn fish is about 75,000. The figure shows significant differences between the St. Lawrence cod and the Arcto-Norwegian cod and all other stocks examined. The indices for the Egegik red, Skeena red, and Puget Sound pink salmon differ from the index of Georges Bank haddock. Further, the indices for plaice and halibut differ from those of some salmon stocks and Atlantic herring. Estimates of the indices for Karluk pink salmon, North Sea haddock, Southeast Alaska, and Sakhalin herring are poor ones because the data are highly variable.

Estimates of fecundity are given in Cushing (1971) and in general they are not of high quality because the samples have usually been taken casually and have not always been distributed in weight. However, the differences between groups of fish in fecundity are so considerable that the poor sampling may not matter too much. Figure 41 shows the relation between the index of density-dependence and the cube root of the fecundity; density-dependence is thus a function of the distance apart of the eggs, or larvae, in the sea, a point that was made in the previous chapter.

There are two important points about the regression shown in Figure 40. The first is that density-dependence is linked directly to the density of eggs or larvae in the sea and that the importance of the larval drift is emphasized as the period at which control processes dominate. Second, the regression does not depend on the gadoids like the St. Lawrence and Arcto-Norwegian cod, but is a continuous trend in fecundity from salmon to flat-fish. Therefore the gadoid dome-shaped curve is not a special case as Beverton and Holt (1957) implied in their treatment of Herrington's data on the Georges Bank haddock (1948). If it is not a special case, then the use of their asymptotic relationship should be rejected.

The Second Method (Cushing and Harris, in press)

Because the first method was no more than a piece of statistical brutality, there was a need to repeat it with a more recognizable form of stock and recruitment curve. For this purpose, Ricker's initial curve was used, i.e., $R = APe^{-BP}$. This form was used because the replacement stock, P_r , is inaccessible with our present knowledge of the trend of natural mortality with age and because in a multi-age stock replacement is achieved over a period of years. Another point is that an annual recruitment is only a small proportion of the stock and the stock is in a steady state with its annual increment of recruits, equivalent to the annual loss by death. Then the stock is at its replacement point at any stable population level.

The curve of the equation was fitted by the least squares technique, i.e., so as to minimize $\Sigma(R - APe^{-BP})^2$. The technique consists of estimating minimal values A_K and B_K for the parameters and setting up the normal equations:

$$\delta A \cdot \Sigma \left(\frac{\partial F}{\partial A} \right)^2 + \delta B \cdot \Sigma \left(\frac{\partial F}{\partial A} \cdot \frac{\partial F}{\partial B} \right) = -\Sigma \left(F \cdot \frac{\partial F}{\partial A} \right)$$

$$\delta A \cdot \Sigma \left(\frac{\partial F}{\partial A} \cdot \frac{\partial F}{\partial B} \right) + \delta B \cdot \Sigma \left(\frac{\partial F}{\partial B} \right)^2 = -\Sigma \left(F \cdot \frac{\partial F}{\partial B} \right),$$

where F represents the function $R - A_K P e^{-B_K P}$.

$$\frac{\partial F}{\partial A} = -P e^{-B_K P} = -R/A_K \text{ (when } F = 0)$$

and
$$\frac{\partial F}{\partial B} = A_K P^2 e^{-B_K P} = R P \text{ (when } F = 0).$$

These equations are then solved for δA and δB , which are then added to A_K and B_K to give new estimates A_{K+1} ($= A_K + \delta A$) and B_{K+1} ($= B_K + \delta B$), and the process is repeated, using new values, until a satisfactory accuracy is attained.

The accuracy of the results was investigated as follows:

Let σ = standard deviation of residuals; therefore

$$\sigma^2 = \frac{\sum (R - A P e^{-B P})^2}{(N - 2)}$$

Having calculated σ^2 , it is possible to calculate standard errors of the parameters A and B and of the calculated value of R at any given value of P . The latter item enables us to draw a confidence band on either side of the calculated curve (a 95% confidence band lies between +2 standard errors of the curve).

Let σ_A = standard error of A, σ_B = standard error of B, and σ_R = standard error of R; σ_A , σ_B , and σ_R are obtained by inverting the matrix

$$M = \begin{vmatrix} \Sigma\left(\frac{\partial F}{\partial A}\right)^2 & \Sigma\left(\frac{\partial F}{\partial A} \cdot \frac{\partial F}{\partial B}\right) \\ \Sigma\left(\frac{\partial F}{\partial A} \cdot \frac{\partial F}{\partial B}\right) & \Sigma\left(\frac{\partial F}{\partial B}\right)^2 \end{vmatrix} \quad \begin{array}{l} \text{used in setting} \\ \text{up the normal} \\ \text{equations} \end{array}$$

If we write

$$M^{-1} = \begin{vmatrix} c_{11} & c_{12} \\ c_{21} & c_{22} \end{vmatrix},$$

then

$$c_{11} = \Sigma\left(\frac{\partial F}{\partial A}\right)^2 / \psi$$

$$c_{12} = -\Sigma\left(\frac{\partial F}{\partial A} \cdot \frac{\partial F}{\partial B}\right) / \psi$$

and

$$c_{22} = \Sigma\left(\frac{\partial F}{\partial B}\right)^2 / \psi,$$

$$\text{where } \psi = \Sigma\left(\frac{\partial F}{\partial A}\right)^2 \cdot \Sigma\left(\frac{\partial F}{\partial B}\right)^2 - \left[\Sigma\left(\frac{\partial F}{\partial A} \cdot \frac{\partial F}{\partial B}\right)\right]^2$$

$$\text{and } \sigma_A^2 = c_{11} \sigma^2, \quad \sigma_B^2 = c_{22} \sigma^2$$

$$\text{and } \sigma_R^2 = \sigma^2 \left[c_{11} \left(\frac{\partial F}{\partial A}\right)_P^2 + 2c_{12} \left(\frac{\partial F}{\partial A} \cdot \frac{\partial F}{\partial B}\right)_P + c_{22} \left(\frac{\partial F}{\partial B}\right)_P^2 \right],$$

where the suffix P indicates values at P.

Figure 42 shows the fit of the equation to three stocks of red salmon; the same information is used as in the first method. The full line gives the best fit to the curve and the dotted line, the 95% confidence limit to that line. For each curve, the constants A and B were calculated, with their standard deviations. The standard deviation of B was expressed as a percentage of B, at the mean of P, in order to assess the quality of the material. The Atlantic herring, Buchan and Dogger stocks, are shown in Figure 43 and the Pacific herring in Figure 44. Flatfish are shown in Figure 45 and the gadoids in Figure 46.

This method does not add anything to the detailed analysis by groups given above. The average indices of density-dependence (as b) by groups are compared with averaged values of $-B\bar{P}$ for the same groups.

Group	Group	$-B\bar{P}$	b
	Pink salmon	0.61	0.48
	Red salmon	0.77	0.53
	Chum salmon	1.13	0.77
	Atlantic herring	0.45	0.56
	Pacific herring	1.06	0.84
	California sardine	1.14	0.55
	Flatfish	1.02	1.18
	Gadoids	1.75	2.17
	Yellowfin tuna	1.41	1.34

The correlation between the two estimates is 0.85 ($p < 0.01/DF 7$). However, between stocks exploitation must vary considerably. In general terms, fecund fishes are fished harder than the less fecund ones, so the trend of density-dependence with fecundity is, if anything, underestimated. The conclusion that density-dependent mortality is a function of the distance apart of the larvae in the sea is reinforced. Further, the gadoid dome-shaped curve is probably not a special case, but is merely a consequence of high fecundity. The value of $(-B\bar{P})$, from a mean stock value, assumes that the degree of exploitation was common to all stocks.

It is reasonable to suppose that the stock and recruitment curve characteristic of Atlantic herring is nearly a linear one with a slight dome with respect to the bisector, whereas that characteristic of the Arcto-Norwegian cod stock has a pronounced dome. If a herring stock and a cod stock with the same number of age groups are compared, that of cod

would be expected to have a much greater capacity for stabilization merely as a consequence of the more pronounced dome. The gadoid stocks thus should be able to withstand more fishing than the herring and should also be able to survive in harsher environments. It is no accident that the Norwegian and Swedish herring stocks have alternated in abundance in the face of climatic variation since the early Middle Ages, whereas during the same period the Arcto-Norwegian cod stock provided a fishery in the Vestfjord in Northern Norway since the twelfth century. During the late fifties and sixties, the fishery for the Norwegian herring collapsed through recruitment overfishing (*see* Chapter 6). The capacity for stabilization is a biological property revealed as a function of fecundity, which provides the developed gadoids with an insulation from environmental change. The more primitive herring lack this capacity and are more vulnerable to climatic change.

An unexpected consequence of the second method is that the maximum to the stock and recruitment curve can be estimated from the confidence limits to the curve. Figure 47 shows the stock and recruitment curves of four well-known stocks. The confidence limits to the curve have been used to establish confidence limits to the maxima. The position in stock of the maximum recruitment to the Arcto-Norwegian cod stock is defined within fairly narrow limits.

Conclusion

Fecundity is a function of weight, and in the long term of evolution, fishes have grown to large sizes and considerable ages perhaps to generate effective mechanisms of stabilization. The model of density-dependent processes described above suggests that the larval fish grow to avoid death; that is, if they succeed in feeding well, growing well, and swimming well, a larger proportion evade predation. In the longer term, fish grow large perhaps in order to stabilize their numbers in the face of environmental variability. To avoid death by growing quickly is in effect the process within one generation that leads to the population stability between generations.

In the sea, fish are large animals, high in the pyramid of numbers. However, fish are rarely the top predators. At the top of the food chain structure in the ocean are sharks, porpoises, and toothed whales. None of the top predators are as fecund as fish like cod and tuna. As fish grow from larva to adult, they move up the food chain to end just below the top predators. The whole structure of high fecundity, pelagic eggs, larvae of a standard size, metamorphosis, and intense growth on the nursery ground exploits the whole food chain structure in an evolutionary sense. The enormous loss in numbers to the fish is gain to other parts of the food chain and thus fish populations sustain the food chain they exploit.

Holden (in press) has summarized the information on the forms of reproduction in elasmobranchs in saying that the teleost larval stage has been eliminated. He distinguished two groups, of relatively high and low fecundity (but much lower than in other fishes), in which natural mortality appears to be about equal. It is possible that fecundity increases under exploitation, which would provide a neat density-dependent recruitment mechanism. It is suggested that the curve of recruitment on parent stock is a lightly convex one, which can be varied slightly by changes in natural mortality rate and fecundity. The real point is that unless some such mechanism is available, yields from elasmobranch stocks could not be sustained.

There are four conclusions in management:

- a. The stock and recruitment curve for the Atlantic herring is lightly convex. Herring fisheries have probably been exploited to extinction and many small stocks have in fact disappeared in the past perhaps because of natural causes. Such stocks should be exploited at the point of maximum surplus recruitment (not the maximum recruitment, which may sometimes be near the virgin stock value).
- b. For flatfish, recruitment may possibly be considered as independent of stock over the exploited range (Thompson and Bell, 1934, for the Pacific halibut, and Graham, 1935, for the Southern North Sea plaice assumed that the rate of natural increase or reproduction was proportional to fishing mortality).
- c. The curves for the cod suggest that there is a marked absolute maximum in recruitment. Cod stocks are less vulnerable than the herring to overexploitation because of their greater capacity for self-regulation, but they should also be exploited at the point of maximum surplus recruitment (which may be quite close to that of the maximum recruitment).
- d. Elasmobranchs can be exploited, but the limits to fishing are unknown.

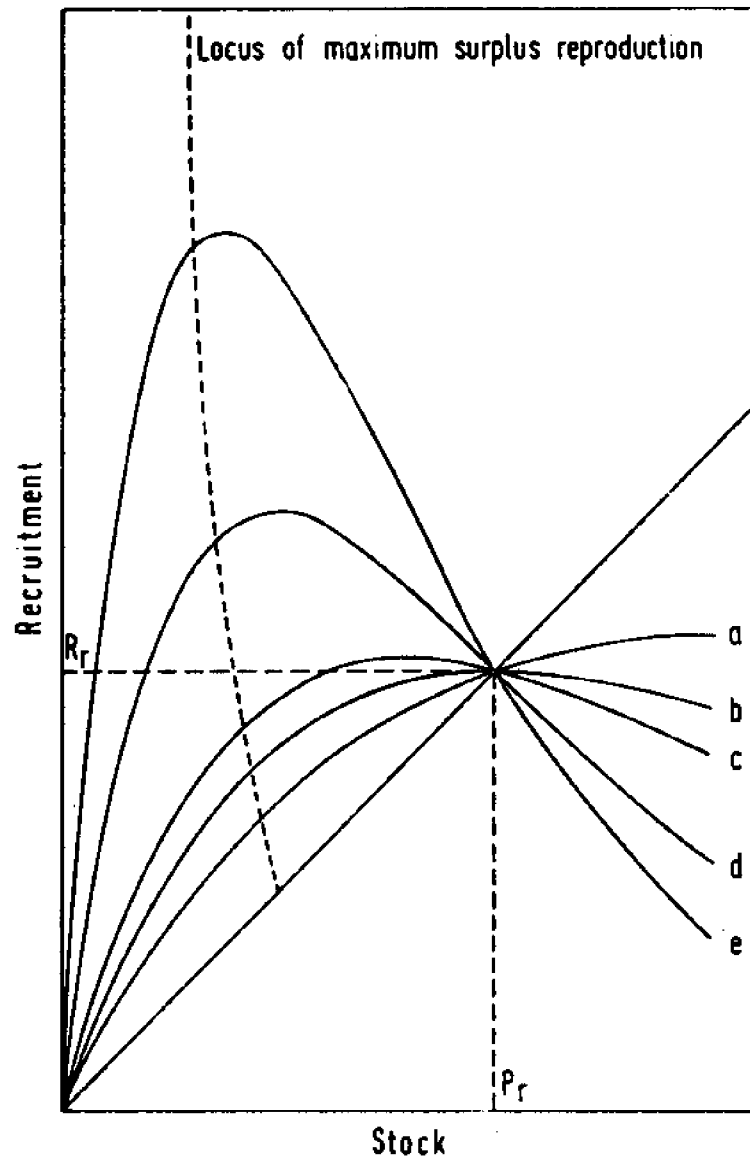


Figure 32. Ricker's (1958) family of stock/recruitment curves.

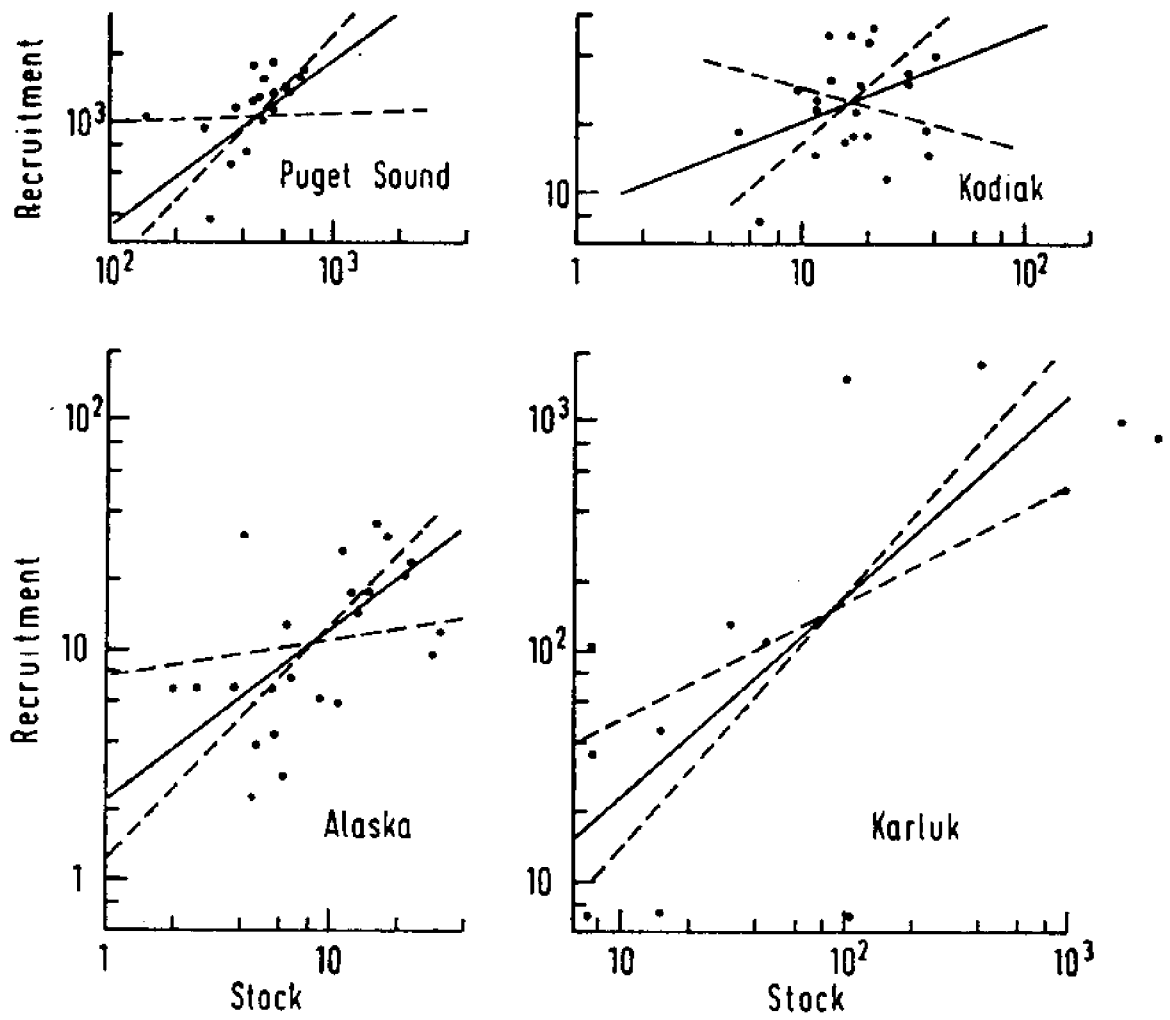


Figure 33. The index of density-dependence for four stocks of pink salmon.

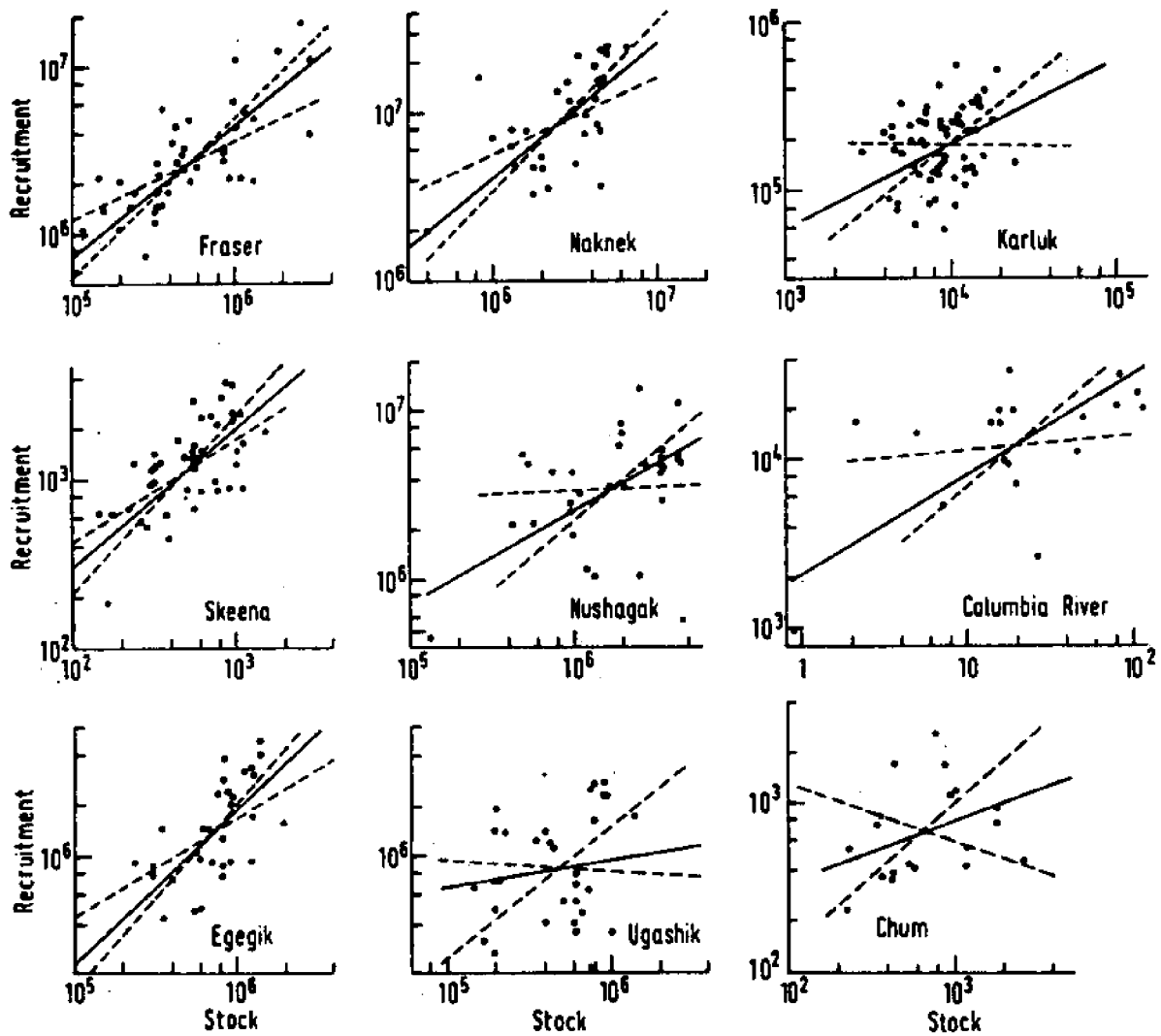


Figure 34. The index of density-dependence in eight red salmon stocks and one chum salmon stock.

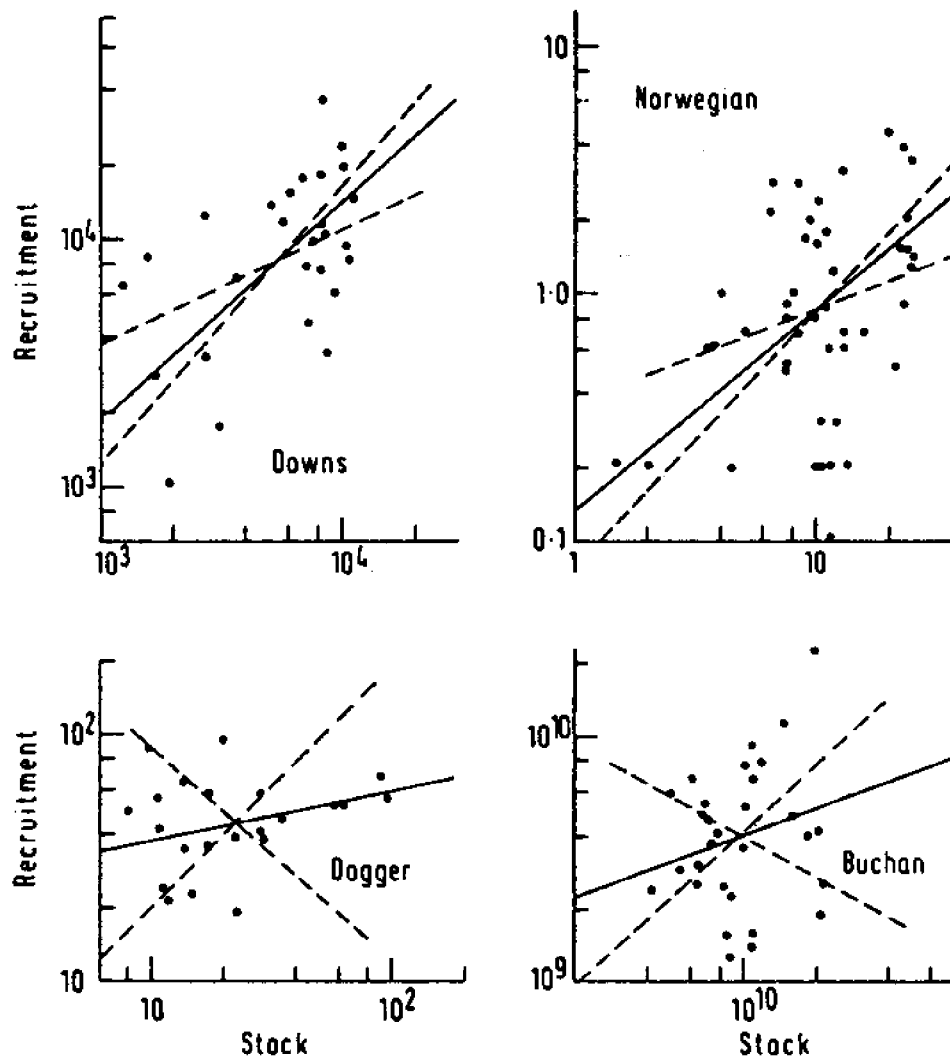


Figure 35. The index of density-dependence in four Atlantic herring stocks.

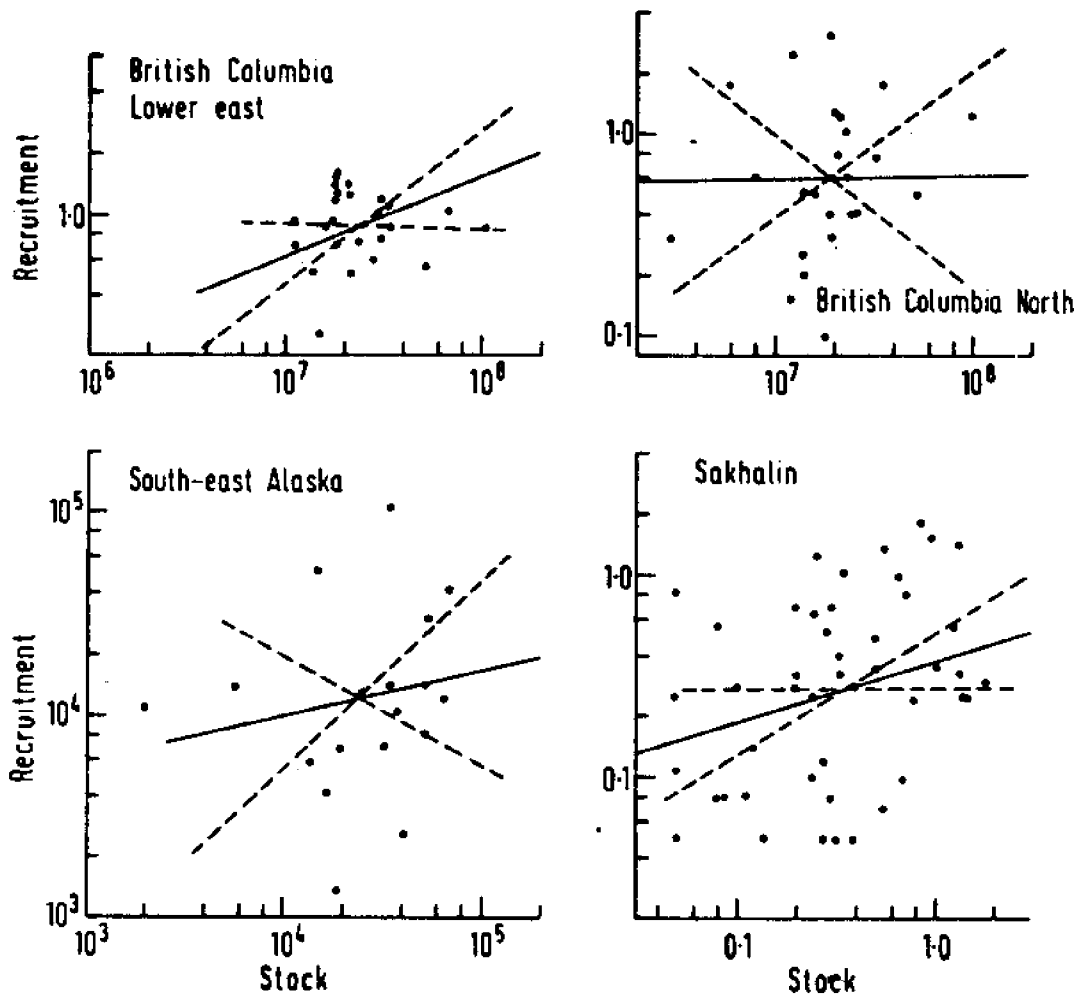


Figure 36. The index of density-dependence in four Pacific herring stocks.

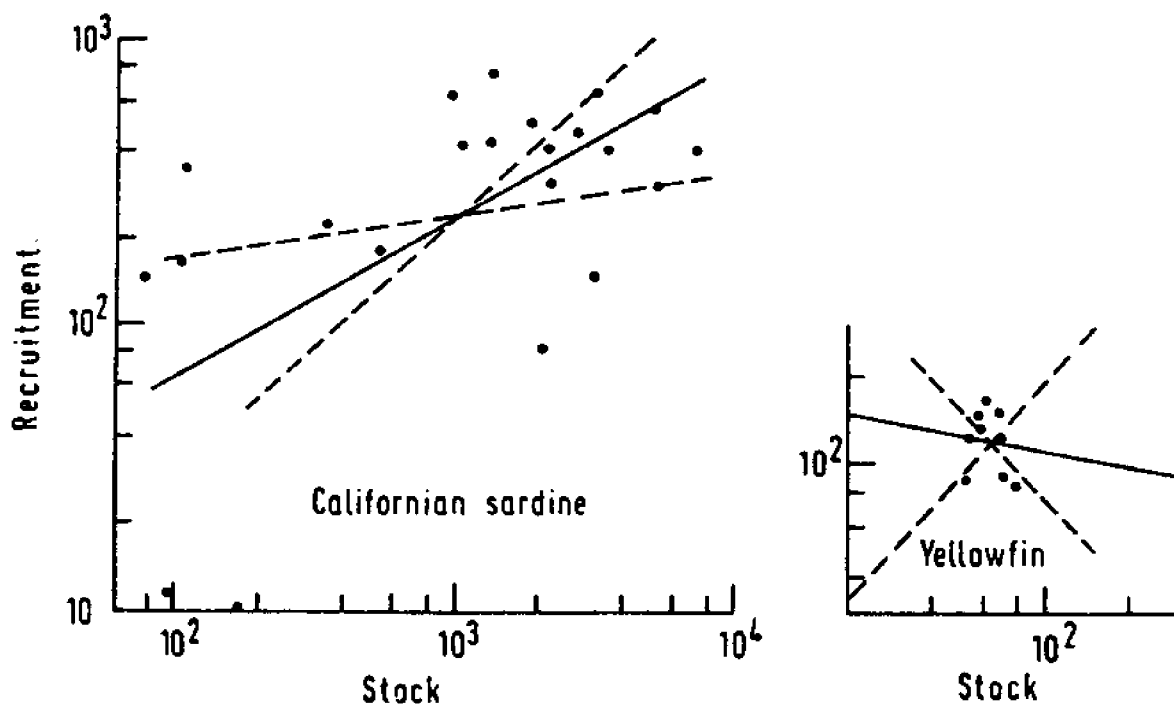


Figure 37. The index of density-dependence for the Californian sardine and the yellowfin tuna.

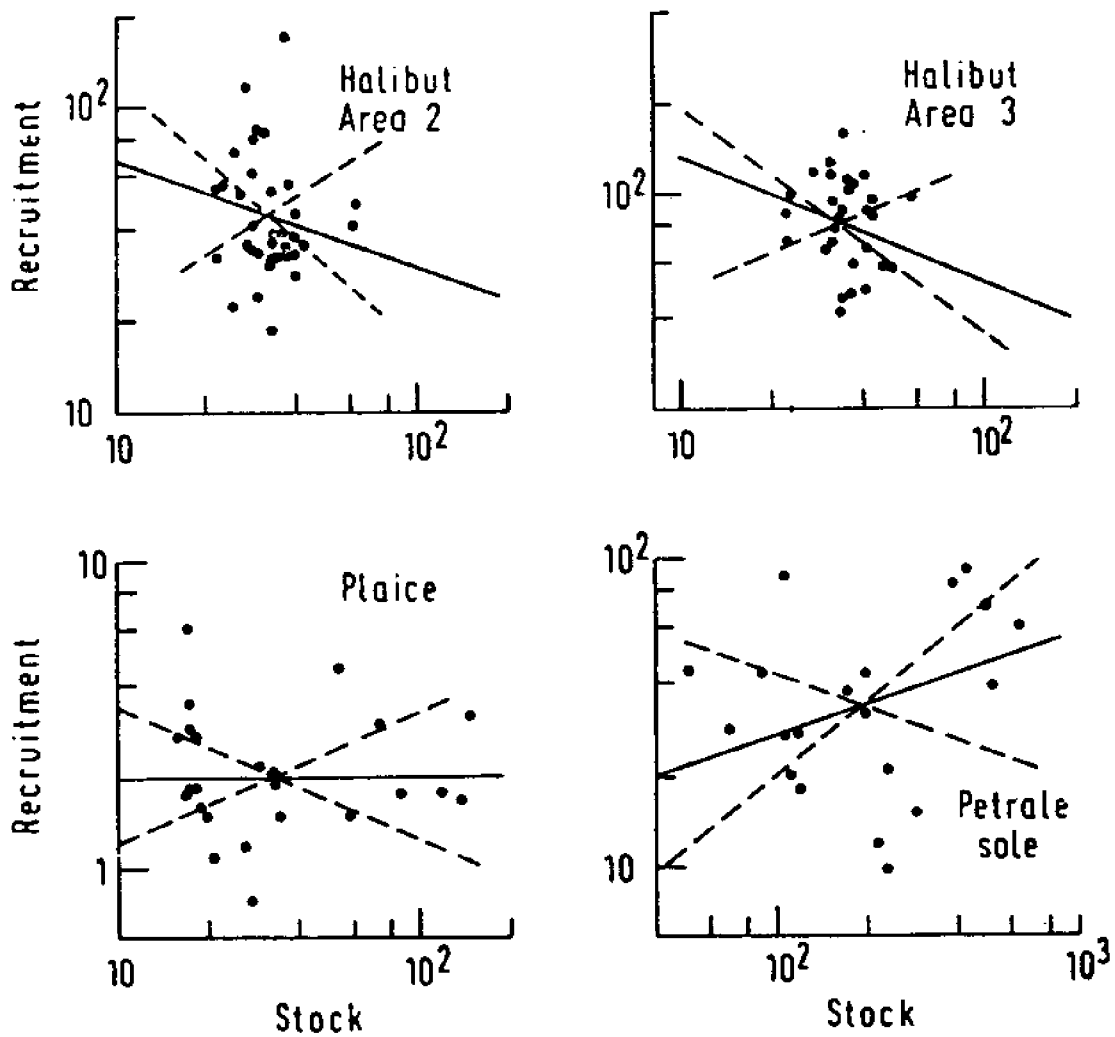


Figure 38. The index of density-dependence in four stocks of Flatfish.

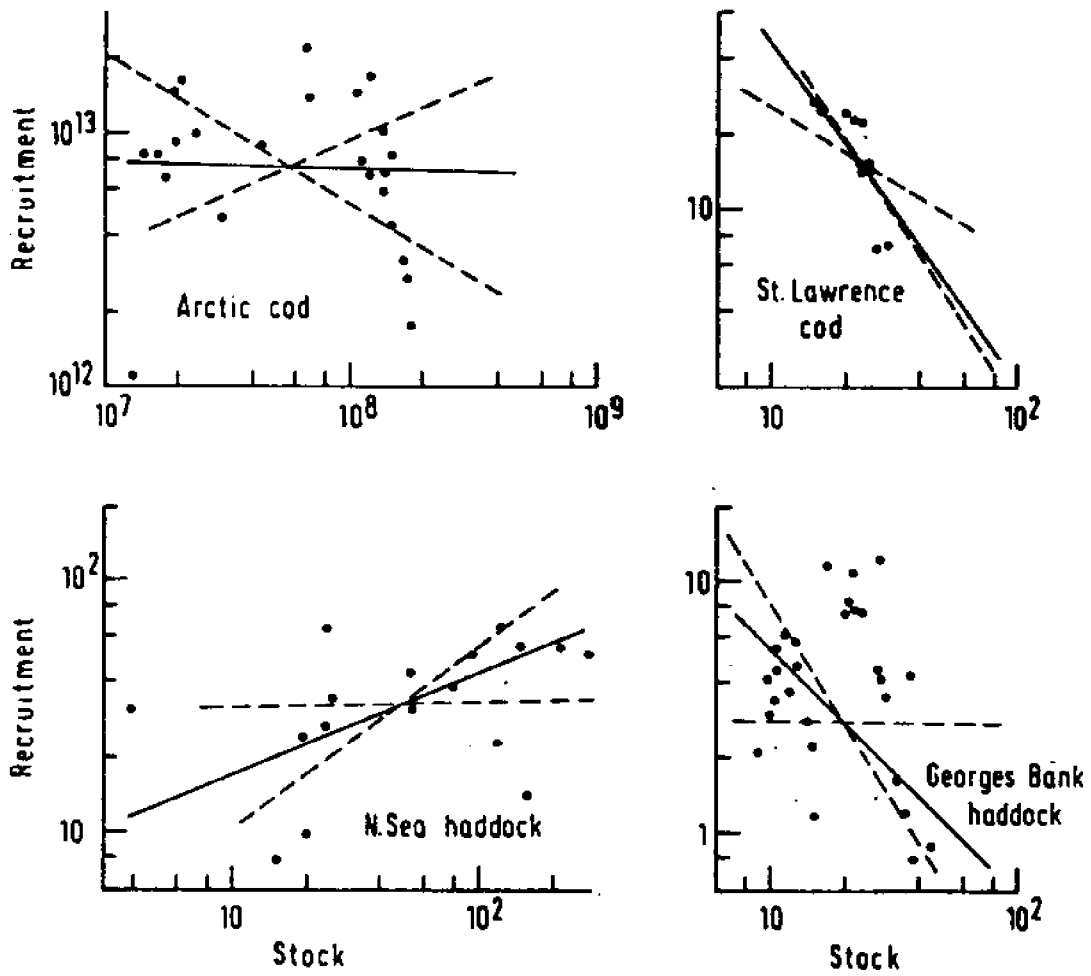


Figure 39. The index of density-dependence in four stocks of gadoids.

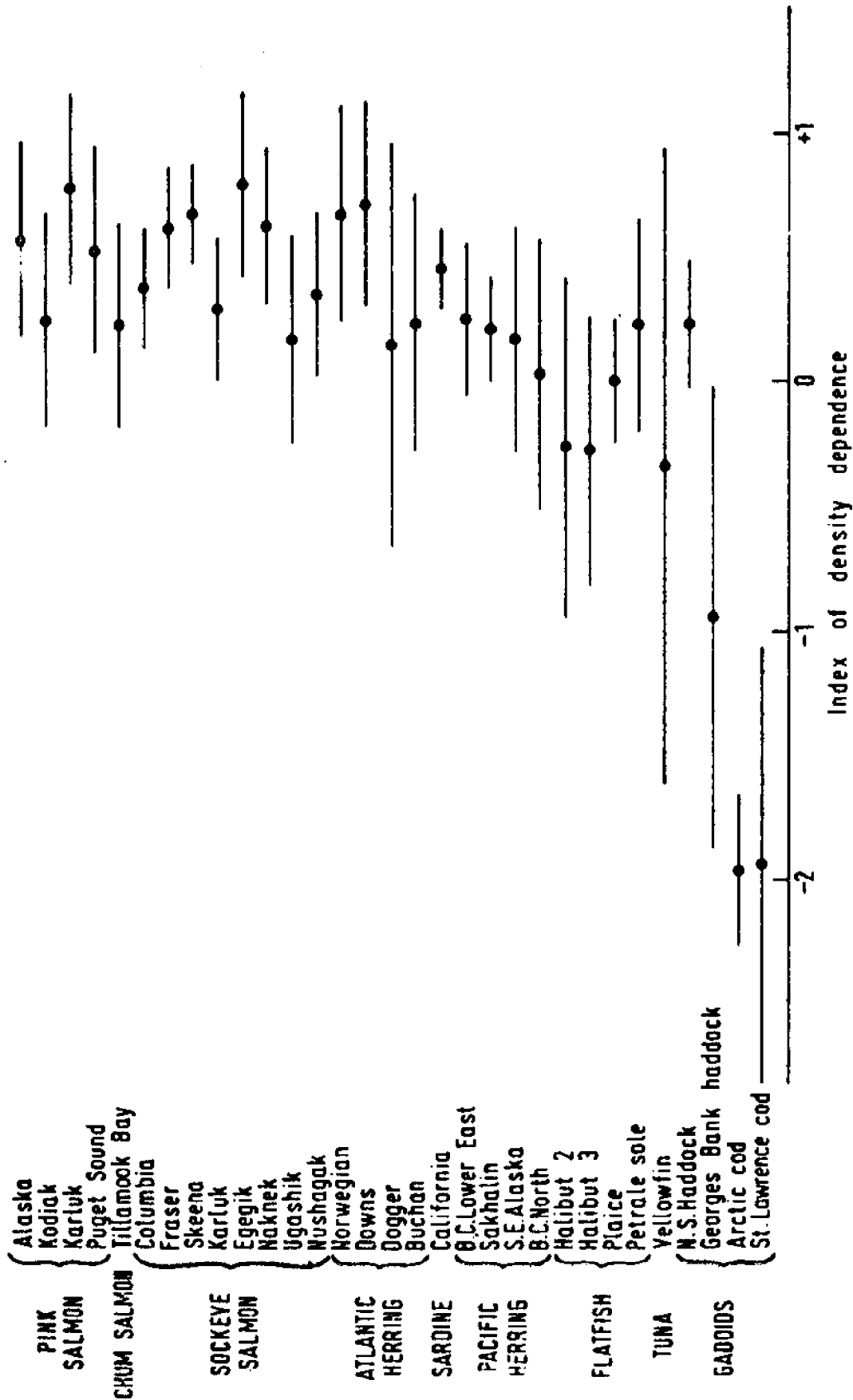
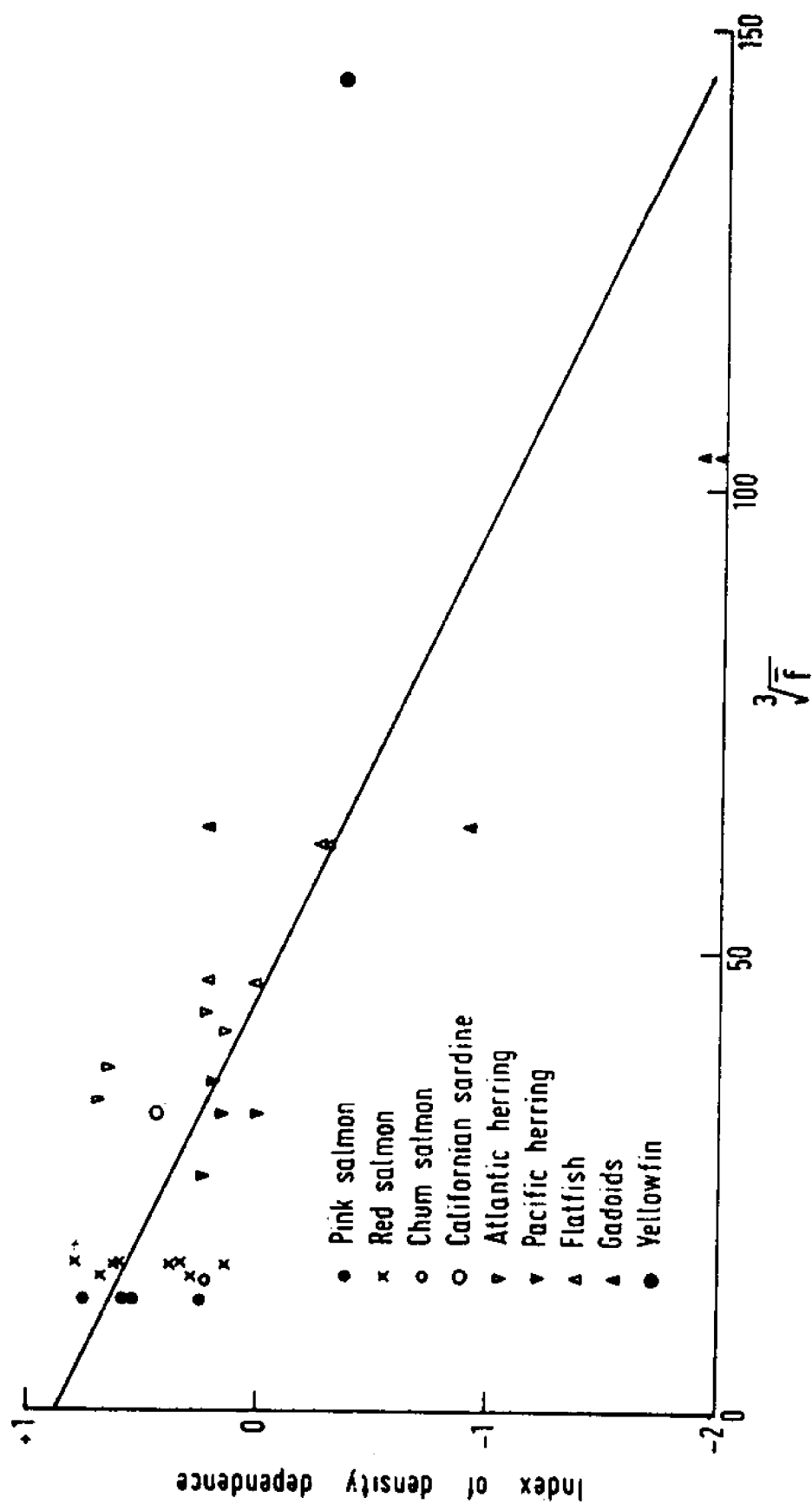


Figure 40. The indices of density-dependence and their errors (at twice the standard error) arranged in order of fecundity, lowest at the top.



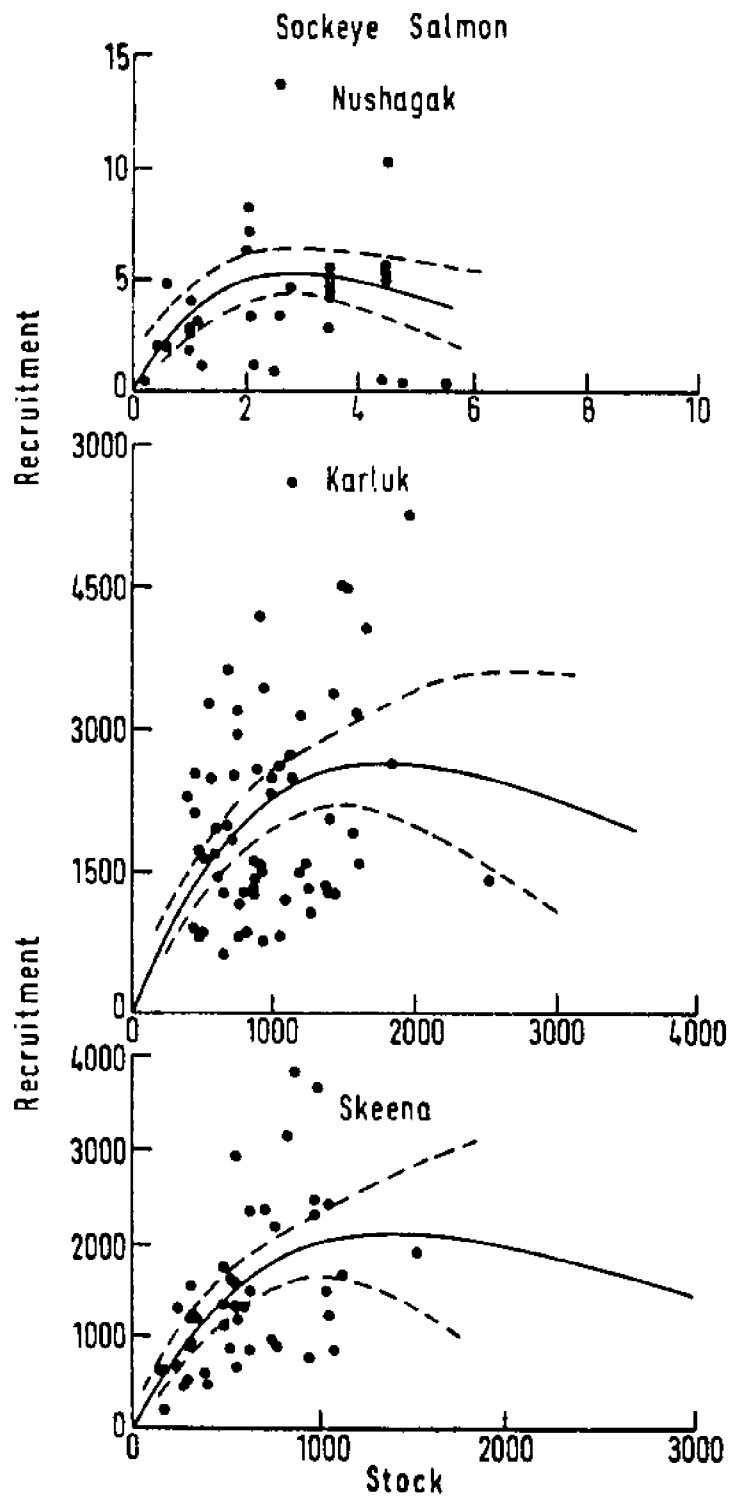


Figure 42. Stock/recruitment curves for three stocks of red salmon.

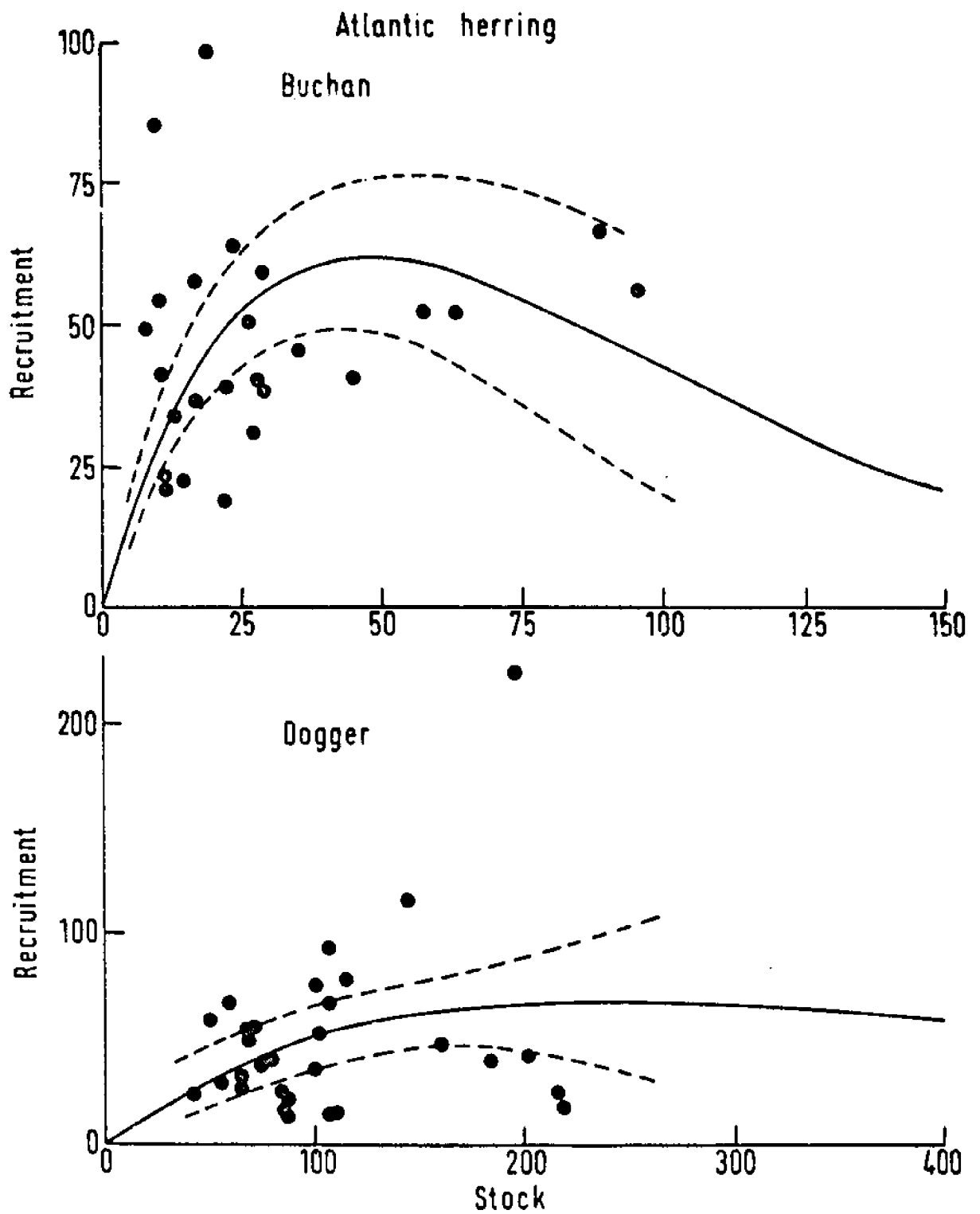


Figure 43. Stock/recruitment curves for two Atlantic herring stocks.

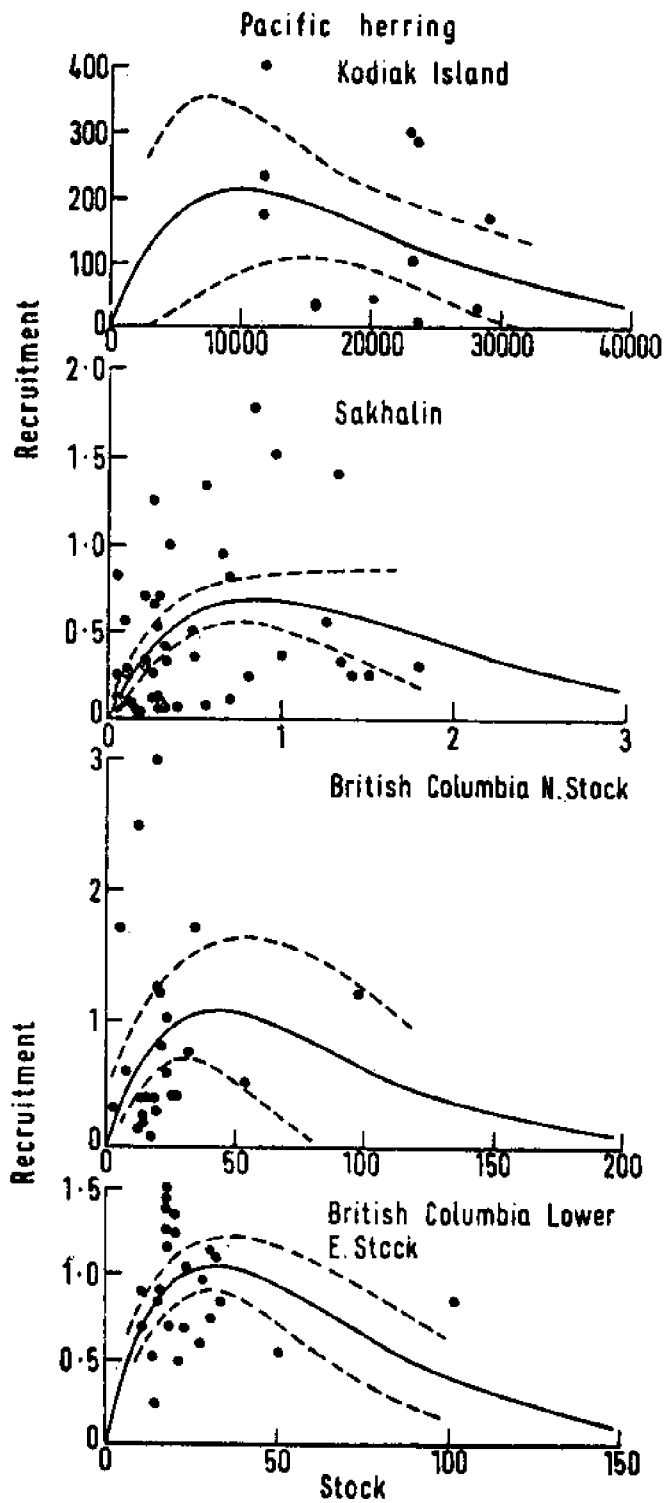


Figure 44. Stock/recruitment curves for four Pacific herring stocks.

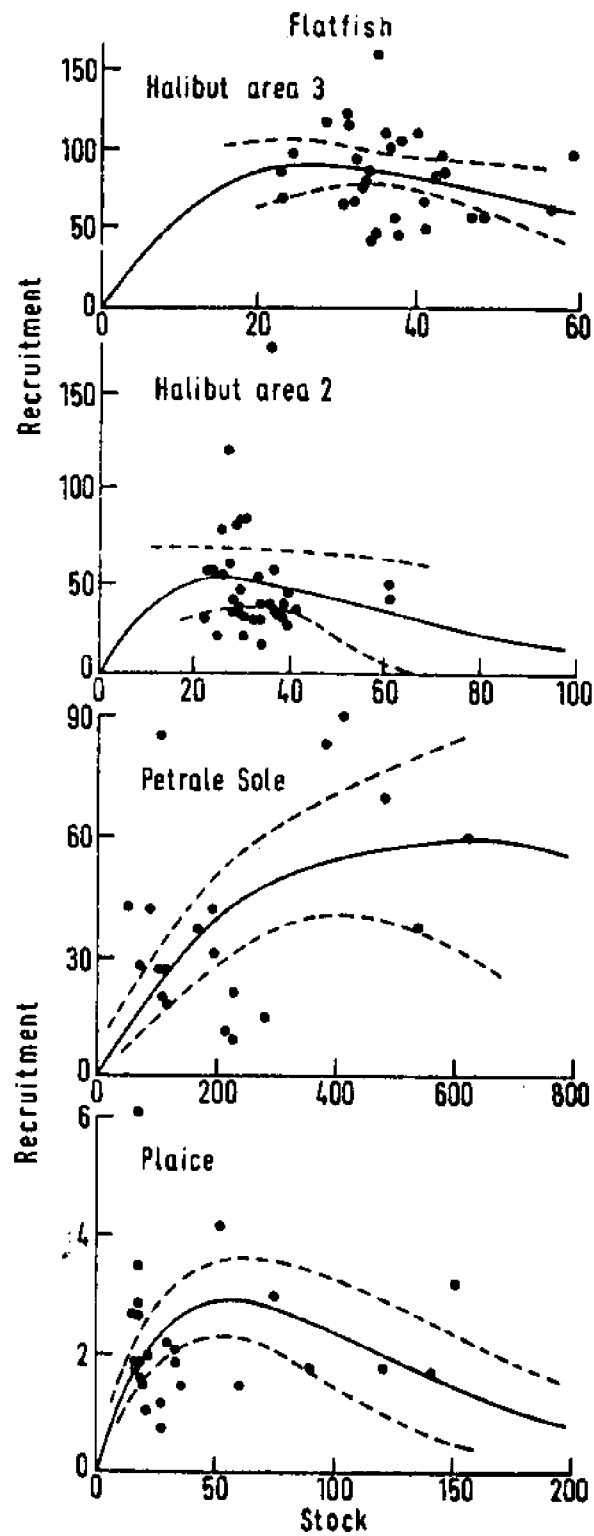


Figure 45. Stock/recruitment curves for four flatfish stocks.

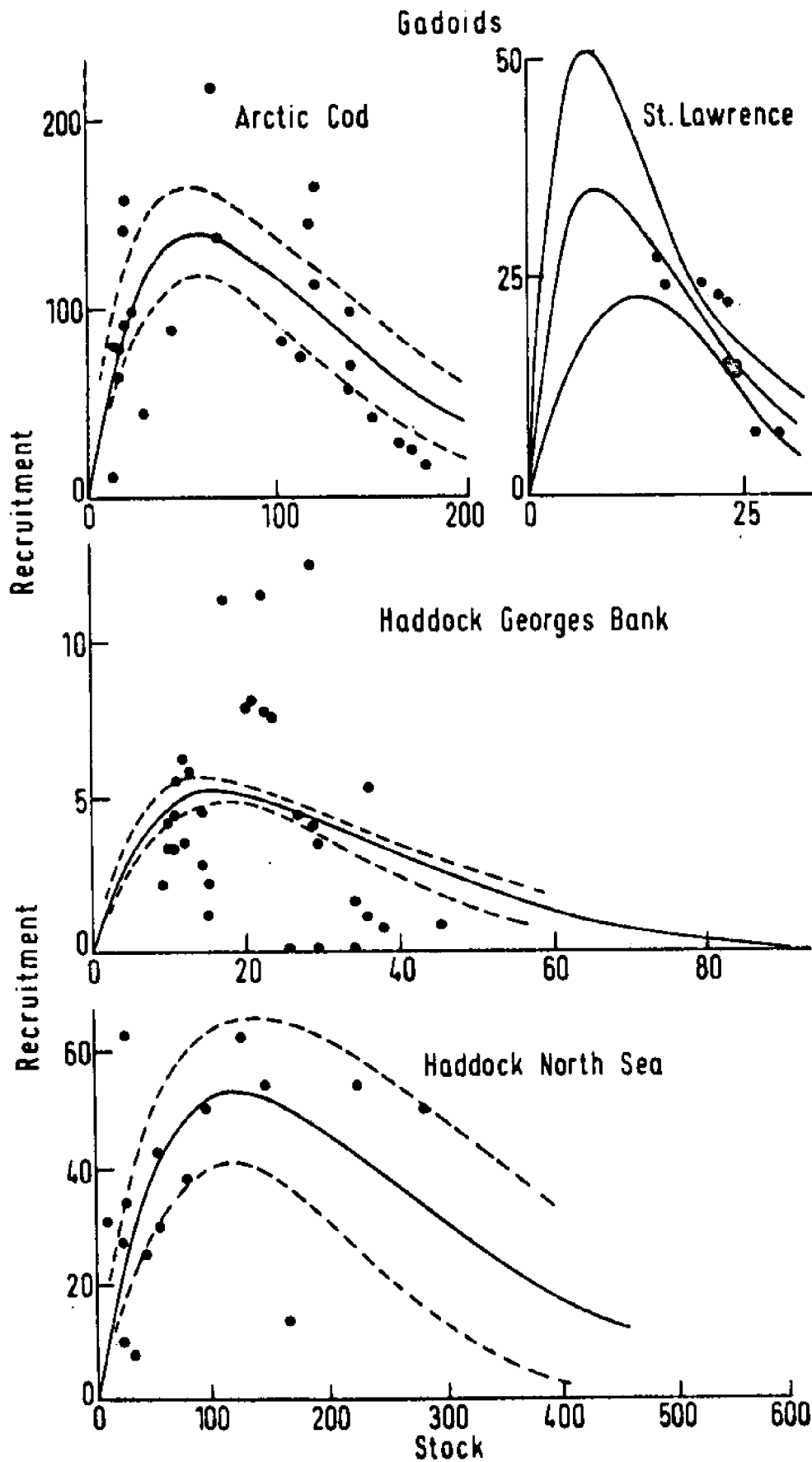


Figure 46. Stock/recruitment curves for four gadoid stocks.

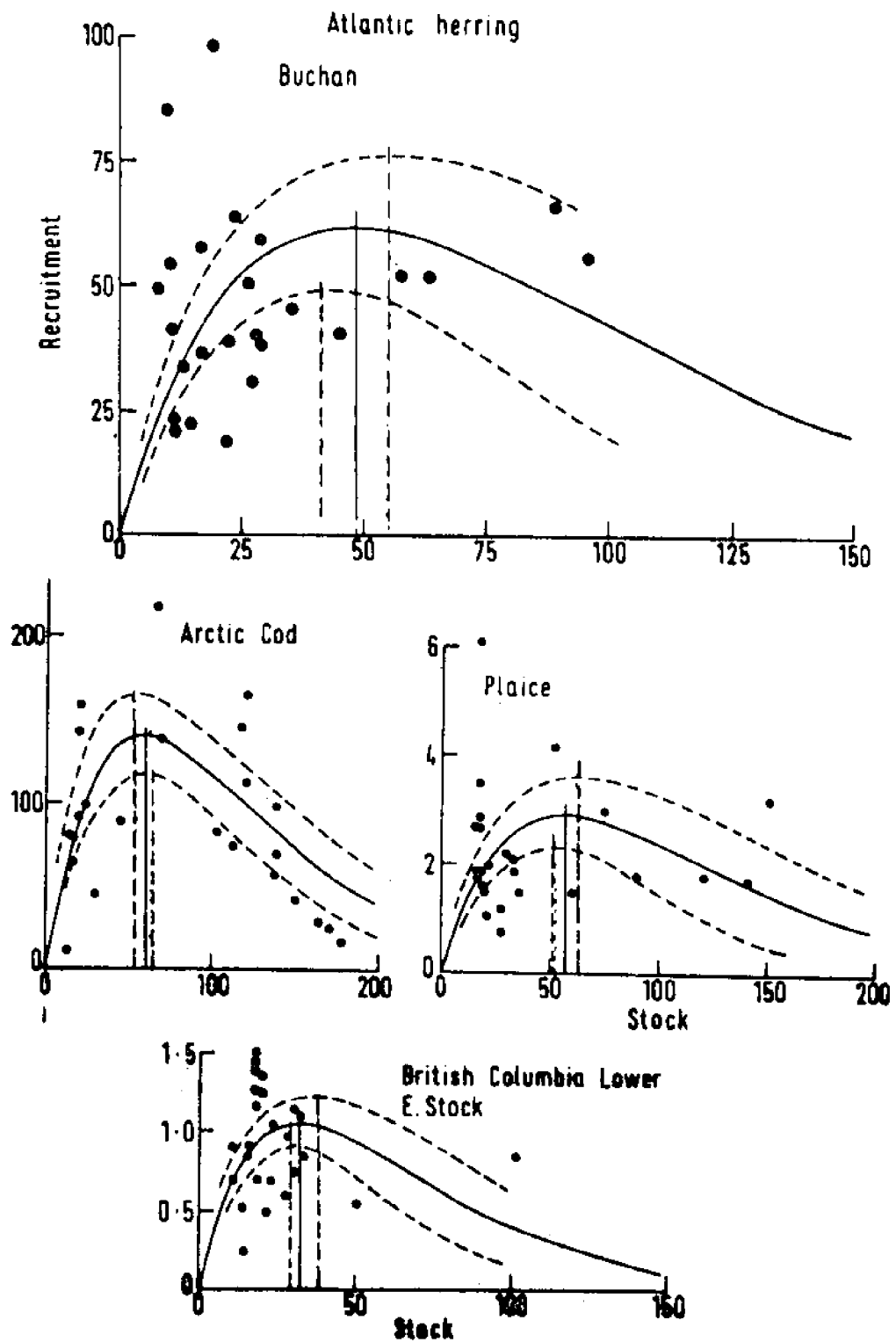


Figure 47. The maxima of four stock/recruitment curves with errors.

Chapter 6

RECRUITMENT OVERFISHING

Introduction

The term "overfishing" is an old-fashioned one. Fishermen used it when stock densities had declined to less profitable levels. Fisheries biologists used it to describe a stock exploited too heavily to obtain the maximum sustainable yield in either the sense of Schaefer (1954) or in that of the yield per recruit (Beverton and Holt, 1957). Today, restrictions on fishing are enforced in the international commissions, which may take a number of factors into account, and the word "overfishing" has tended to disappear.

In the early stages, fisheries biologists considered that fishing destroyed small fish before they had a chance to put on much weight by growth. Thompson and Bell (1934) and Graham (1935) faced this problem of growth overfishing in the Pacific halibut and the southern North Sea plaice, respectively, and both stated that fishing effort would not reach such levels as to reduce recruitment to the stocks. It was believed that with increased mortality, there should be compensating increases in growth and in recruitment. However, all three were aware of the possible dangers of reducing recruitment. The problem of growth overfishing was solved scientifically by Beverton and Holt (1957), and in the North Atlantic commissions, it has been mitigated by agreed measures of minimum landed sizes and minimum mesh sizes in the trawls. In the yield/recruit solution to growth overfishing, the possible effects on recruitment were both implicitly and explicitly dismissed. The Schaefer model does not distinguish the effects of growth and recruitment, but the maximum sustainable yield determined from it must take into account the trend of recruitment with stock.

The phrase "recruitment overfishing" has some value for two reasons: (a) it states the implicit failure of the yield/recruit solution; (b) there is often real danger of the complete collapse of a fishery (particularly of herringlike fishes), even if the extinction of the stock by fishing must be very unlikely. The term is used here only to indicate that recruitment has declined under the pressure of fishing. There is no implication that a maximum sustainable yield can yet be estimated reliably from any form of stock/recruitment relationship, although a provisional method is described in the last chapter.

This chapter describes the collapses or near collapses that have occurred because of the failure of fisheries scientists to understand the nature of the stock/recruitment relationship.

The East Anglian Herring

The East Anglian herring fishery was practiced by drift netters in October and November each year off the east coast of England. It was a very old fishery, records of which extend back into the early Middle Ages, but it is not known whether the record is continuous. Cushing (1968b) gives an account of stock densities between 1750 and 1789. The first decade of the present century was the heyday of the steam drifter, and in 1913 more than 300,000 tons of herring were handed in the ports of Lowestoft and Yarmouth.

The fishing effort exerted on the Downs stock was estimated in drifter shots, each one of which comprises a night's fishing by a curtain of net two miles long and two fathoms deep that drives in the tide. The stock was exploited by pair trawlers and bottom trawlers in the southern North Sea and by drifters and bottom trawlers in the central and northern North Sea. Between 1946 and 1956, catches and fishing effort on the stock increased sharply, (Cushing and Bridger, 1966). During the period 1955-1966, catch declined sharply, total mortality remained steady at about 1.20, and the abundance of larvae fell by a factor of 2.5; indeed, between 1946 and 1966, stock density declined by a factor of 9. If larval abundance is an index of stock, then stock declined. Crude fishing effort (as the number of drifters' shots) declined between 1955 and 1966, but mortality remained steady, which suggested that the catchability had changed. It had been observed that the driftermen's pattern of search had changed from within-square searching to between-square searching. A change in catchability was detected in the ratio of stock density to stock:

$$\frac{C}{f} \cdot \frac{qf}{C} \frac{(1 - e^{-Z})}{Z} = q \frac{(1 - e^{-Z})}{Z}$$

where C is catch;
 f is fishing effort;
 q is the catchability; and
 Z is the instantaneous total mortality coefficient.

Then it was shown that the decline in corrected stock density was matched by the fall in larval abundance. Hence the increase in catchability was confirmed.

The lack of upward or downward trend in mortality was associated with constant fishing effort when corrected for the change in catchability. As stock density declined, so did stock and with it recruitment; hence the decline in catch was explained; recruitment fell during the period 1946-1966 by a factor of 9 times. Figure 48 shows the dependence of recruitment on parent

stock, both in stock density. The estimates of stock were based on the mixing rates of the Downs stock in the northern and central North Sea, which although reasonable were unsupported by independent evidence. Whatever their magnitude, however, there was no upward or downward trend during the period 1955-1966. The question of the mixing rate does not therefore enter the argument and the estimate of the change in catchability was secured by the estimates of change in larval abundance. Consequently, the simplest explanation of the decline in catch is recruitment failure as stock diminished under the pressure of fishing.

The stock recruitment curve itself, Figure 48, is peculiar in that it is a nearly linear one with neither dome nor asymptote, but the first exploitation of the Downs stock must have started many centuries ago and the first records must have been of a well-exploited stock. Recruitment declined slowly and the fishery took nearly fifteen years to die; such a slow decline might be expected from the shape of the stock/recruitment curve. During the middle sixties, the total true effort exerted on the stock declined and with the shrinking stock, mortality rates remained high until the fishery was extinguished. In 1969 and 1970 the larval abundance in the Eastern Channel recovered sharply to the levels of the early fifties, so within the stock there is the capacity for recovery. There were two groups of herring in the Downs stock, those spawning in the Eastern Channel and those spawning in the southern North Sea. So far, the latter group has not recovered. But the fishing here must have been one of the most intense recorded. For ten days or so each year for ten years (1950-1960), up to 150 large distant-water trawlers worked in ranks of seven to ten ships each about 20 yards apart in an area of about one by three miles. On the eastern Dogger Bank a fishery for immature herring from most of the North Sea stocks has been practiced since about 1950. A tagging experiment then showed that the fishing rate was about 15-20%/per year, i.e., recruitment to all North Sea stocks was reduced by that fraction. Recently, this experiment was repeated and it was shown that the fishing rate was much higher, as might be expected from shrinking stocks subjected to the same effort. Much more important, however, it is likely that the fishing effort exerted in this immature fishery is now high enough probably to prevent recovery when it is trying to take place.

When the East Anglian fishery collapsed in 1955, the herring was considered to be only lightly fished, the stock was ill-defined, and most were supposed to be eaten by gannets or whales. The yield/recruit solution to growth overfishing, although by then well known, had not been published and the climate for any stock/recruitment solution in Europe, at least, was chilly.

The Arcto-Norwegian Cod

The Arcto-Norwegian stock of cod has been fished in the Vestfjord and on the coastal banks of northern Norway for a very long time. The feeding grounds and nursery grounds in the Barents Sea were exploited by British and

German trawlers from 1928 onwards and the same boats worked the Norway coast for the large cod on their way to spawn. Russian trawlers had worked on the stock in the White Sea from Murmansk from an earlier period, but in the late fifties the Russian fleets increased considerably.

Garrod (1967), in a study of the stock, showed that fishing effort increased in 1956, that it remained high until 1963, and that during these years the stock density dropped by nearly half. Garrod applied a form of virtual population analysis to estimate the recruitment to the stock. Let $E_t = C_t/V_t$, where E_t is the exploitation rate, C_t is the catch, and V_t is the virtual population, all in the year t . Catches are summed from the last age-group, λ , of a cohort, or year-class, back in time to the age of recruitment. The natural mortality, M , is estimated independently and so $N_\lambda = C_\lambda/E_\lambda$ where N_λ is the stock in numbers at age λ ; $V_\lambda = (C_\lambda/E_\lambda) F_\lambda/Z_\lambda = C_\lambda/(1 - e^{-Z_\lambda})$. There is an important separation in time between $C_{\lambda-1}$ and N_λ . the catch $C_{\lambda-1}$ is caught until the end of the year $t_{\lambda-1}$, whereas the stock N_λ is exploited from the beginning of the year t_λ . So the ratio $N_\lambda/(C_{\lambda-1})$ is expressed in quantities at the same point of time. Then,

$$\frac{N_\lambda}{C_{\lambda-1}} = \frac{N_{\lambda-1} e^{-Z_{\lambda-1}} Z_{\lambda-1}}{N_{\lambda-1} F_{\lambda-1} (1 - e^{-Z_{\lambda-1}})} = \frac{e^{-Z_{\lambda-1}} Z_{\lambda-1}}{F_{\lambda-1} (1 - e^{-Z_{\lambda-1}})}.$$

From tables of $(e^{-Z}/F(1 - e^{-Z}))$, $F_{\lambda-1}$ is determined

$$\text{Then } E_{\lambda-1} = (F_{\lambda-1}/Z_{\lambda-1}) (1 - e^{-Z_{\lambda-1}}) + (e^{-Z_{\lambda-1}} E_\lambda)$$

and $N_{\lambda-1} = V_{\lambda-1}/E_{\lambda-1}$ so estimates of N , E , and F are obtained by ages within the year-class.

As calculation proceeds from the last age-group to the first in the year-class, the estimate of F tends towards a true value, within the limits imposed by the independent estimate of M . Therefore, the more age-groups in the year-class, the better. The method gives useful estimates of recruitment in numbers in fisheries where estimates of stock density are poor. Further, the catch at each age produces an estimate of fishing mortality for that age.

Figure 32 shows Garrod's data of recruitment and stock fitted by the initial Ricker curve by the method described in an earlier lecture. At the present time, recruitment is very low indeed; in fact four year-classes are effectively absent. As a consequence of the excessive fishing effort in the early sixties, the stock was reduced so much that the chance of good recruitment is considerably reduced. Garrod and Dickson in Cushing (1971) have

correlated recruitment to the stock of cod with components of climatic change. The variation of recruitment as deviation from the stock/recruitment curve must be environmentally generated. However, the reduction in recruitment at low stock as compared with the maximum possible is quite considerable, as shown in Figure 32.

Four Pelagic Stocks

In discussing the effect of fishing in a stock/recruitment context, Ricker (1958) expressed the exploitation as $(R - P)/R = (Pe^{a(1-W)} - P)/(Pe^{a(1-W)})$ or $E = 1 - e^{-a(1-W)}$. There is a limiting rate of exploitation, E_∞ , at which any increase in effort will reduce the stock to zero. Then if $P = 0$, $P/Pr (=W) = 0$, and the limiting rate of exploitation, $E_\infty = 1 - e^{-a}$, where $a = Pr/Pm$ in Ricker's terminology. In his initial curve, $E_\infty = 1 - 1/A$. From our study so far, clupeid stocks are possibly vulnerable to recruitment overfishing. From Figure 32, for the clupeid stocks, $a (= Pr/Pm)$ ranges from 0.50-0.75 and to 2.0+ for the gadoid stocks. From the study on fecundity, it can be shown that for maximum catch for clupeid, $E_s \approx 0.30-0.40$. Such an estimate can be compared with independent estimates of $E (= [F/Z][1 - e^{-Z}])$. If $a = 0.50$, $E_\infty (= 1 - e^{-a}) = 0.40$ and if $a = 0.75$, $E_\infty (= 1 - e^{-a}) = 0.52$. Hence the limiting level of exploitation is not very far beyond that for maximum recruitment. In applying such levels to any particular stock, it must be recalled that only a general value of a has been used and the true value might be different. I have not estimated a directly for any of the four pelagic stocks, but have used values of $E_\infty = 0.35-0.50$, directly. The description of stocks and the estimation of exploitation rates are taken from Cushing (1971).

Figure 49 shows the catches in hundreds of thousands of tons of the Hokkaido herring and the fishing effort in hundreds of nets from 1870 to 1960. Catches peaked in 1897, oscillated till 1931, after which they declined. The survival rates from 1910 to 1950 were 0.46-0.53. In 1944-1948, the survival rate was 0.79; if the natural mortality was well estimated during the latter period, then the exploitation rate was probably high during the earlier period of peak effort. Perhaps catches declined after 1931 because stock had been pressed low enough to reduce recruitment, that is, less than the stock at which Ricker's maximum surplus recruitment occurs (Figure 51). The point of evidence is that catch declined under high effort, when the exploitation rate was probably high.

Trends of catch and fishing effort in the Norwegian herring fishery from 1946 to 1963 are shown in Figure 50. Catches had increased since the early decades of the present century and further catches were made during the sixties. Since the early Middle Ages, the Norwegian and Swedish herring fisheries have alternated in a periodicity of 70-100 years and any decline of either fishery

might be interpreted as the end of a natural period. However, the decline during the late fifties shown in Figure 50 was not accompanied by any indications of climatic change; for example, during a Swedish period that follows a Norwegian one, the Baltic freezes in winter--and it did not do so.

The figures of fishing effort include indices of purse seine and drifter effort in the international fleet. Dragesund and Jakobsson (1963) analyzed tagging results for the Atlanto-Scandian stock exploited in the Norwegian fishery for the period 1952-1959. Their maximum estimate of natural mortality was 0.23; because this estimate must include a proportion of tagging mortality, it is an overestimate. The inset figure in Figure 50 shows the exploitation rate between 1952 and 1959, together with the value of E_1 supposedly characteristic of clupeids. Catches declined from the peak in 1956 after the exploitation rate approached 0.35. This value is close enough to E_1 (even if $a = 0.75$) to make it likely that recruitment was reduced, not only absolutely but also relatively to the maximum surplus recruitment, particularly if the clupeid stock/recruitment curve was nearly linear. Fishing effort increased sharply after the year of peak catch with no increase in exploitation rate, but it remains possible that the limiting rate was in fact exceeded in subsequent years. In 1955 and 1956, the 1950 year-class reached its peak; their successors may not have reached their full potential.

Figure 50 represents catches and exploitation on spawning grounds, partly south of Bergen and partly off Stadt, to the north of Bergen. Runnström (1933, 1934) showed that there were three spawning groups of Norwegian herring, off Utsira, Stadt, and Lofoten. During the sixties fishing moved north of Lofoten and by the end of the decade, the Norwegian herring fishery no longer existed.

Figure 51 shows the trends in catch and effort for the Japanese sardine between 1925 and 1957; the peak was reached in 1935 and 1936. Yamanaka (1960) suggested that $M = 0.37$ and that $F = 0.50-0.70$, so $E_{0.38}$. The failure of the year-classes in the late thirties was recognized at the time and was attributed to climatic events. It is, however, simpler to suggest that recruitment was reduced as stock was reduced by fishing. The dramatic reduction in catch suggests recruitment failure even if the exploitation rate did not reach the limiting level.

In Figure 52 are shown the trends of catch and effort in the California sardine fishery from 1920 to 1957. The insets show the exploitation rates calculated in two ways, together with the limiting levels of exploitation considered appropriate for clupeids. Clark and Marr (1955), from tagging experiments, suggested that the natural mortality rate was 33-39% [$M = 0.40-0.50$]. The top inset shows the exploitation rate estimated from figures of natural and fishing mortalities; it also shows the exploitation rate estimated from the ratio of total population to available population. The lower inset shows exploitation rates calculated from the ratios of catch to stock during the crucial period.

The fishery collapsed in three stages, after 1936, after 1944, and finally in 1950. The rate of exploitation reached high levels in 1936; indeed in that year it reached the limiting level--but the subsequent year-classes were not in fact reduced. During the years 1943-1945, exploitation approached E_1 in all three estimates shown in the insets; and the year-classes 1943, 1944, and 1945 were low in consequence. The year-classes 1947 and 1948 recovered to some degree, but those of 1949 and 1950 collapsed completely. The inset figures show that with two methods the exploitation rate exceeded the limiting level. One of the methods does not show it and that is Widrig's (1954), in the ratio for the total population to available populations. But Widrig's method requires constant recruitment and his method failed with the three failing year-classes--1943, 1944, and 1945. It is concluded that the fishery collapsed because the exploitation rates were too high and probably reached the limiting level at the end. On completely different grounds, Murphy (1966) has suggested that the collapse of the Californian sardine fishery was due to recruitment failure under the pressure of fishing. Marr (1962) published a correlation between recruitment to the Californian sardine and the temperatures off Scripps' pier. It represents another correlation between deviations from a stock/recruitment curve and temperature. Hence the correlation and the reduction of recruitment by fishing do not exclude each other. Conversely, the reduction of recruitment through natural causes would be credible if the exploitation rate were that expected at the maximum surplus recruitment.

The four clupeid fisheries at their peak yielded in sum more than five million tons of sardines and herring and now very few fish are caught from any of them. At the time of collapse, each failure was attributed to environmental conditions. It was thought above that clupeids were more sensitive to environmental change than gadoids and fishermen had recognized it for a very long time, and we have substantiated this belief; in the past, many herring fisheries appeared and disappeared. However, just as clupeids are vulnerable to climatic variability, they are also vulnerable to the pressure of fishing. However, the Hokkaido herring fisheries had persisted for centuries (Motoda and Hirano, 1963). The stocks of the Japanese sardine and the Californian sardine have been replaced by anchovies; it is possible that pilchards off South Africa are being replaced by anchovies at the present time. Such competitive effects could occur naturally, but they would be accelerated by recruitment failure due to fishing. This and the fact that the clupeid stocks did collapse at about the limiting rate of exploitation suggest that recruitment can be finally reduced by fishing.

Conclusion

The distinction drawn between growth overfishing and recruitment overfishing is perhaps not as superficial as first appeared. Most fisheries biologists have been concerned with establishing the maximum sustainable yield or some analogue. The problem of growth overfishing was really one

of the conservation of profit. In the Pacific salmon, the problem of recruitment has been resolved in considerable detail, but the character of the salmon's peculiar life history cannot be easily extended to other fishes in the sea. The reasons are twofold: (a) in the fishery, they do not grow; (b) the fishery is so brief that natural mortality does not matter. Any extension to the multi-age stocks at sea requires two forms of information: (a) the trend of natural mortality with age, if there is any general rule; (b) the generation of stock in weight, not numbers, with density-dependent recruitment and age-dependent natural mortality. Beverton and Holt (1957) devised a self-generating yield curve by replacing recruitment in the yield/recruit formulation with their stock recruitment curve, the rectangular hyperbola. Neither is satisfactory today because (a) the rectangular hyperbola does not describe the dome that the data appear to require for the gadoid stocks at least; (b) the replacement stock in the Ricker curve is inaccessible and probably inappropriate; (c) the trend of natural mortality with age is not yet described.

Until the stock/recruitment problem is solved, fisheries will fail, particularly the clupeid ones and perhaps from time to time a gadoid one. The early problems of fisheries biology were concerned with the profitability of the fishing industry rather than its very existence, although everybody--scientists and fishermen--knew the danger of recruitment failure existed. As science and the industry developed, the fishermen became more efficient and the scientists were perhaps misled by the high variance of recruitment.

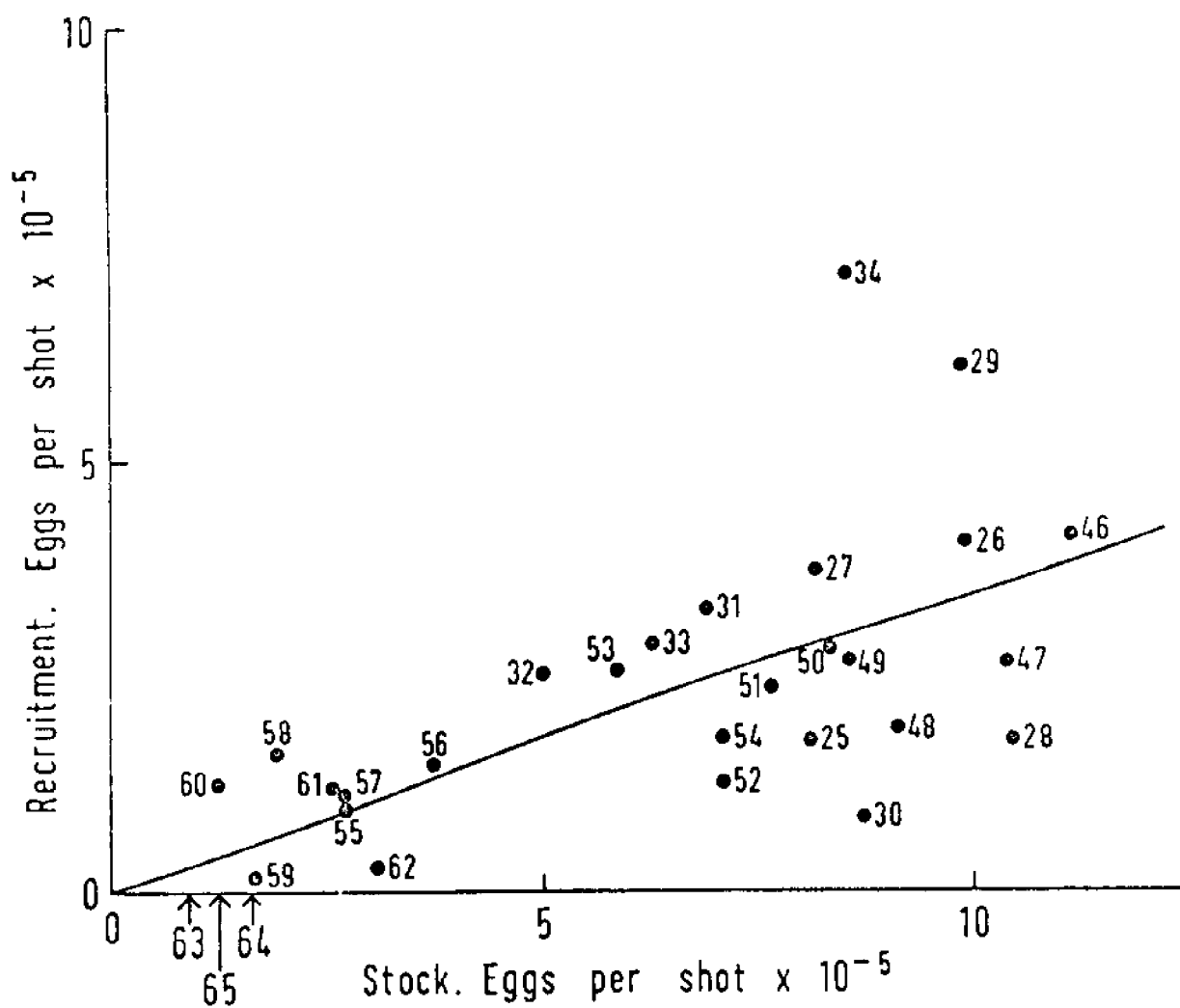


Figure 48. The dependence of recruitment upon parent stock for the Downs herring (Cushing, 1968a).

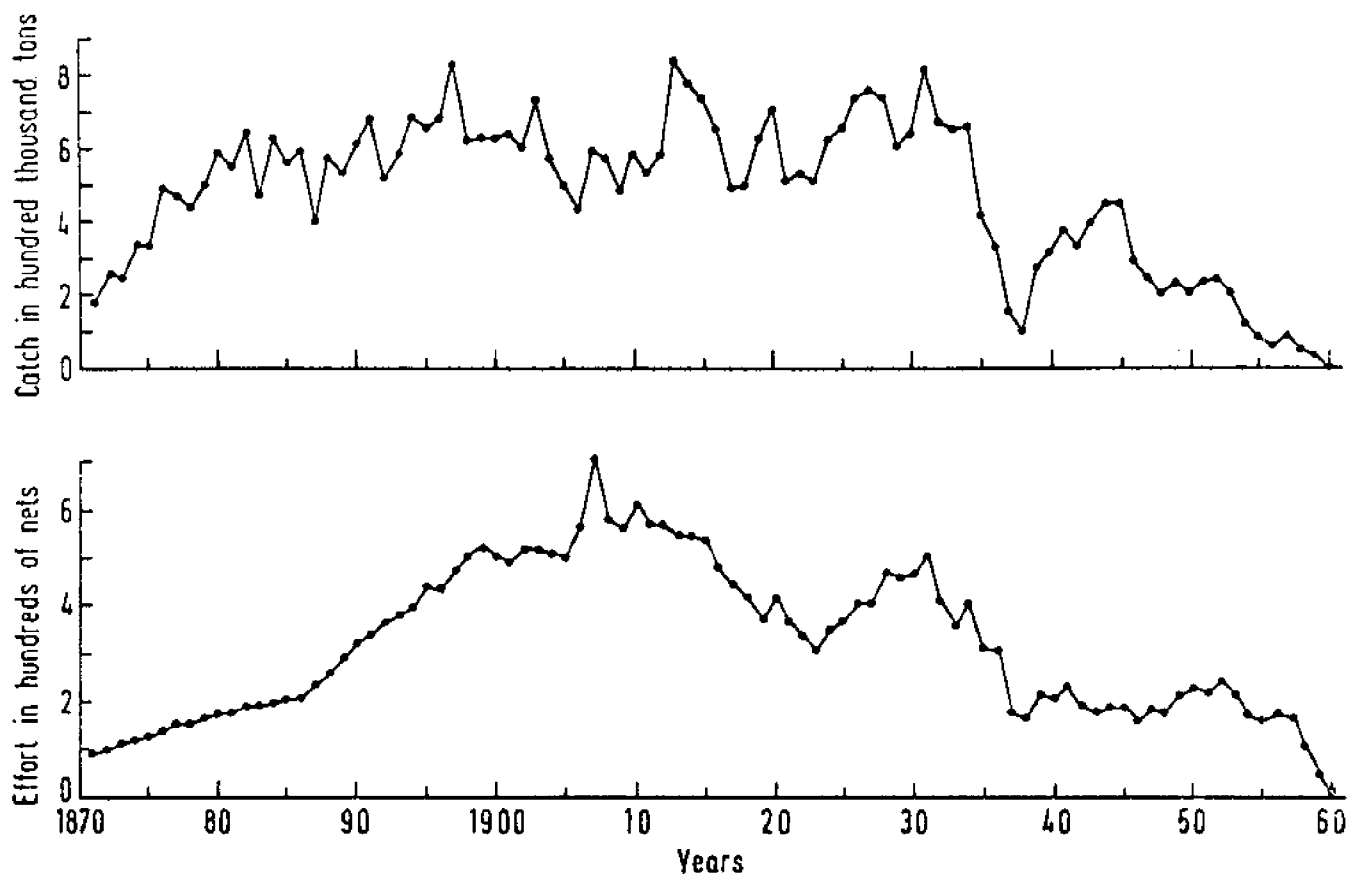


Figure 49. Catches of the Hokkaido herring and the fishing effort exerted on the stock (Cushing, 1971).

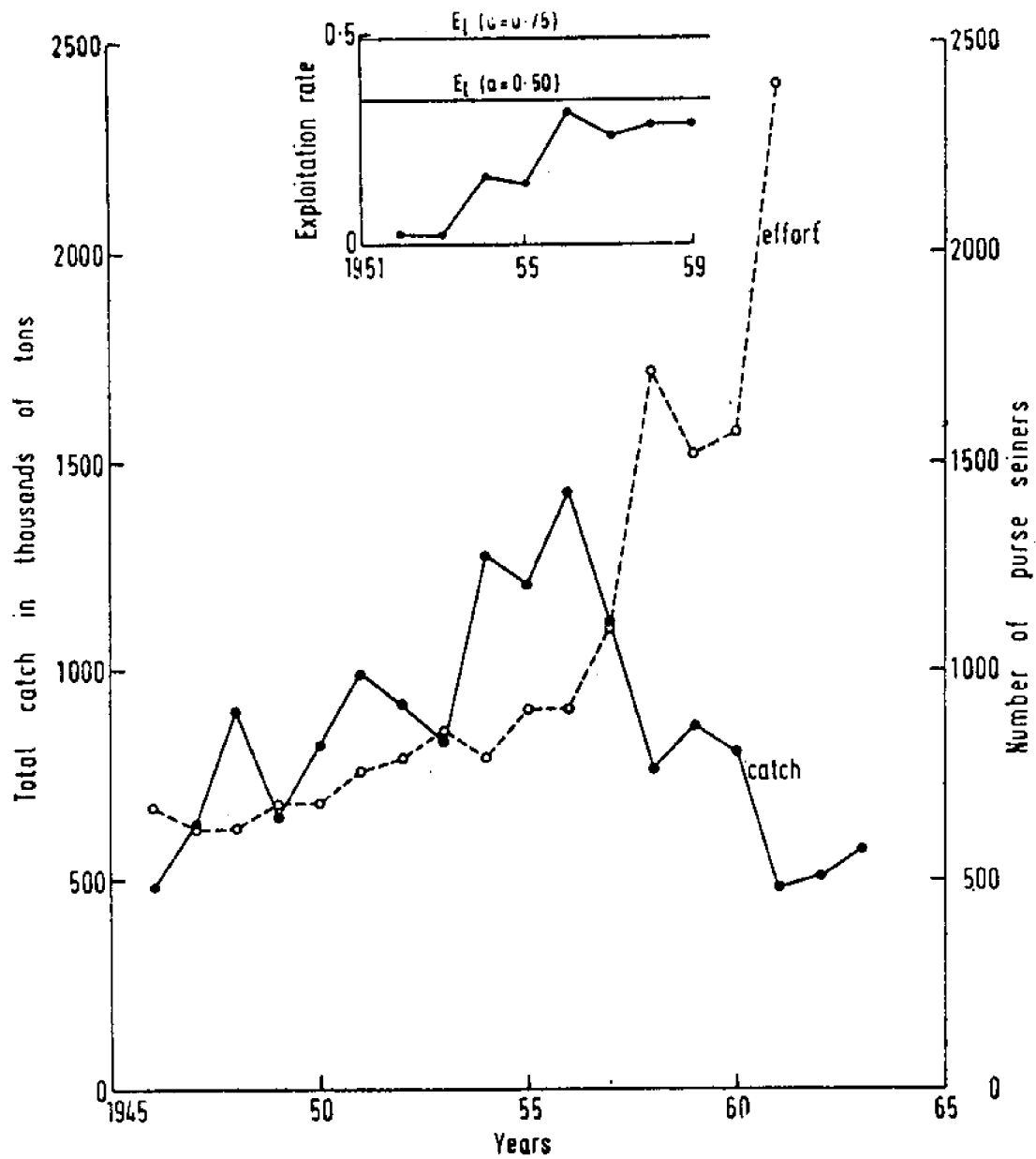


Figure 50. Catches of the Norwegian herring and the fishing effort exerted on the stock (Cushing, 1971); the inset figures show the limiting exploitation rates.

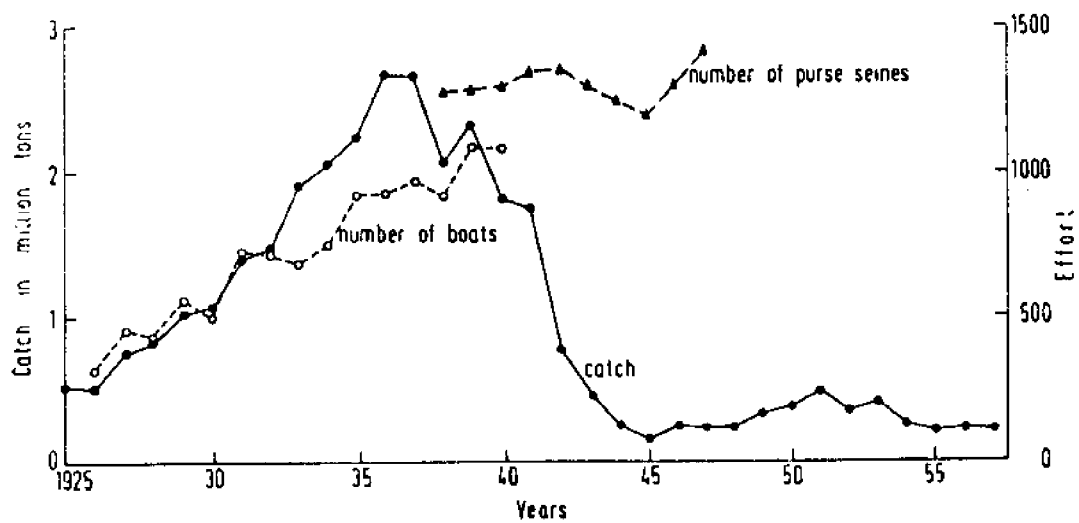


Figure 51. Catches of the Japanese sardine and the fishing effort exerted upon the stock (Cushing, 1971).

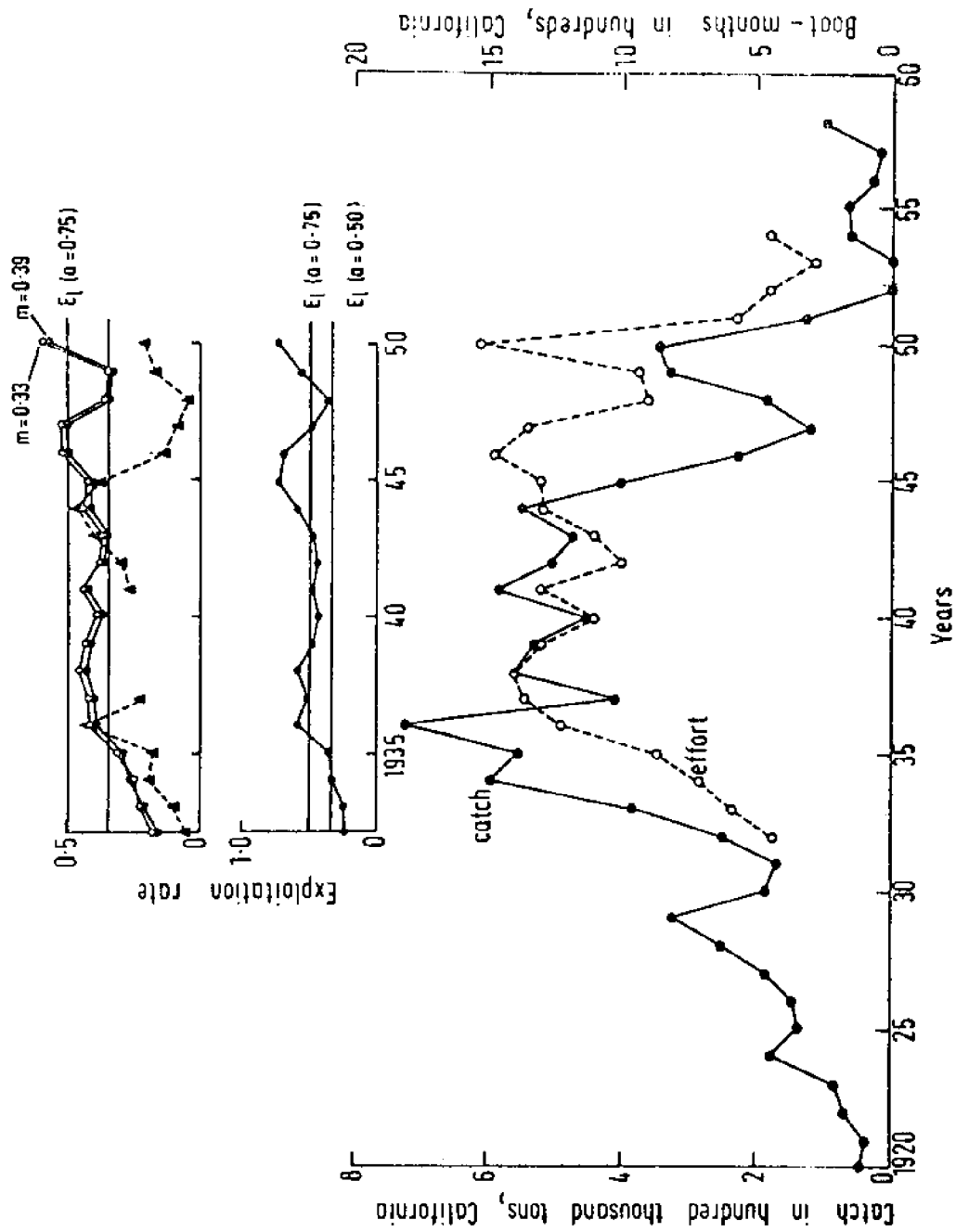


Figure 52. Catches of the California sardine and the fishing effort exerted upon the stock (Cushing, 1971); the inset figures show the limiting exploitation rates.

Chapter 7

THE AGE STRUCTURE OF A POPULATION

Introduction

The age structure of a marine fish population has rarely been described in full. Ricker and Foerster (1948) made a detailed study in age of the sockeye salmon population in Cultus Lake, British Columbia. Gulland (1970) showed a rough trend in age from larval mortality to adult mortality in the southern North Sea plaice. Beverton and Holt (1957) proposed that the natural mortality of such a population was perhaps density-dependent up to and throughout adult life, but that for practical purposes it could be taken as constant with age in a yield per recruit model. However, in order to formulate a stock and recruitment relationship in a multi-age stock, the trend of natural mortality in age should be known. A death rate that is constant in age is unlikely because the population cannot be terminated in age. The virgin stock would then be improperly estimated. There must be a senility function of some sort, like the Gompertz Law, as Beverton (1963) noticed. Deevey (1947) summarized much information on mortality in the form of life tables for a number of animal groups and showed that in adult age-groups it increased in old age.

If the gadoids are not considered a special case, there are two forms of stock/recruitment curve--Ricker's initial one and the second one of Beverton and Holt, which are identical in final form, but which differ in derivation as indicated in an earlier chapter. Harris distinguishes between stock-dependent and density-dependent mortality; the first is a function of the initial numbers of eggs, for which Ricker's equation is appropriate, and the second is a function of density at some later date, for which the first equation of Beverton and Holt may be used. In the latter, the density-dependent processes are assumed to occur during a period of time, the larval drift or the 0-group stage on the nursery ground; in the earliest part of the life cycle, they could equally be regarded as stock dependent. It is proposed to extend this period into adult life until the onset of senescence, whenever that may be. If the density-dependent processes are adequately described in the model linking growth and mortality presented above, a generalized form of such predation could apply to all stages in the life fishes, indeed to any animal in the sea that lives by attack and escape. Models of predation (for example, Holling, 1965) are based on the proportion of time to capture and eat to time to search. As the latter is inversely related to density, predatory mortality must also be density-dependent. The extension of density-dependent natural mortality to the adult age-groups may not be unreasonable.

Density-dependent Natural Mortality

A female fish may spawn for n years, and to replace itself, it must generate two spawning adults by the end of its life or $2/n$ per year. Ricker (1945) has defined a critical length in a population as that at which the growth rates and mortality rates are equal. There should equally be a critical age at which the specific annual growth rate, G (in weight or fecundity), equals the specific annual mortality rate, M^* .

$$G = (1/t) \ln W_2/W_1$$

where W_1 is weight in a given year and W_2 that one year later;

$$M^* = (1/t) \ln N_2/N_1$$

where N_1 is the number in a cohort in a given year and N_2 , that in the same cohort one year later.

The age distribution of biomass (or fecundity) reaches a maximum at this critical age in the unexploited stock. No increment in the biomass (or fecundity) can be expected at a greater age, and if senescence is to start at any age, it should start then. Older fish will of course contribute to the fecundity of the population; but under average conditions in the virgin stock, the population should replace itself by the critical age. The virgin stock is variable: if it has more than replaced itself, the density-dependent processes in the subsequent generation will reduce the excess, and if it has failed to replace itself by the critical age, then the fecundity of the older fish should make up the deficit. Hence the senility function should reduce the biomass of older fish in such a way that the ratio of older stock to total stock corresponds to the coefficient of variation of the virgin stock.

Let us suppose that natural mortality is a density-dependent function of age between hatching and the critical age.

$$N_t = N_{(t - \delta t)} e^{-kN_t \cdot \delta t}$$

$$\dot{N} = N_{(t - \delta t)} [1 - kN_t \delta t + \dots]$$

$$N_t - N_{(t - \delta t)} = \delta N_t = kN_t^2 \delta t$$

$$\int \frac{\delta N_t}{N_t^2} = \int k \delta t$$

$$\left[-\frac{1}{N}\right]_{N_0}^{N_t} = [-kt]_0^t$$

$$-\frac{1}{N_t} + \frac{1}{N_0} = -kt$$

$$N_t = \frac{N_0}{1 + N_0 kt},$$

the initial approximation is valid so long as $M < 0.5$.

Let $kN = M$

$$N_t = N_0 / (1 + M_0 t);$$

$$M_0 = (N_0 - N_t) / N_t \cdot t,$$

where N_t is the number at time t ;

where N_0 is the initial number i.e., at hatching;

where M_0 is the initial mortality, i.e., during the larval stages.

The development of these equations was carried out by my colleague, J. G. K. Harris.

Let N_0 , the initial number, be that at hatching or at first feeding and let T be the critical age. Then $M_0 = (N_0 - N_T) N_T^{-1} \cdot T$. In the virgin stock of plaice $N_T = 2$ and $T = 16$ (see below). M_0 can be estimated if the ratio (N_t/N_0) is known, for example, the initial mortality of plaice larvae; then N_0 can be estimated. Trial calculations have shown that if N_0 is large, M^* is the same at any age greater than three.

Cod, herring, and sprat may have the same specific mortality rates at a given age, but their average natural mortalities throughout adult life differ considerably because they mature at different ages and survive to different ages. So long as there is no density-dependent growth in adult life, the critical age can be determined directly from $(G - M^*) = 0$. In the Pacific halibut, density-dependent growth persists into the early adult age group, but this is probably an exception to the general rule (Southward, 1967).

The Natural Mortality of the Plaice of the Southern North Sea

It has already been noticed that M^* is the same at any given age, provided that N_0 is large and $t > 3$ years. The critical age then depends upon the growth rate. Hempel (1955) showed that density-dependent growth could not be detected in the adult age groups of plaice in the southern North Sea. I have examined the data from 1929-1970 and could also find no density-dependence by plotting $\Delta W/W$ on stock density at the age of five. However, the mean length of five-year-old fish increased by about 5 cm during the fifties, and Gulland (1968) has suggested that there was a shift in the major effort expended from the Southern Bight to the German Bight, that is, on to the larger fish in an age group. The year-classes 1942-1944 were chosen because the increase in length was least in these year-classes. For females only, the parameters were:

Year class	K	L_{∞}	t_0
1942	0.1140	61.0	
1943	0.0748	71.67	
1944	0.1054	61.76	
Mean	0.0981	64.81	-1.935

The parameters were established for females only because the initial number N_0 is considered to be a function of one or n ovaries. From the parameters averaged for three-year-classes, the growth rate was calculated. Figure 53 shows the trend in $(G - M^*)$ with age and at the age of 16, $(G - M^*) = 0$ i.e., $T = 16$.

During the sixties, an average value of fishing mortality in the adult age-groups of females is $F = 0.215$. Hence $N_t \neq 2$ at the critical age of 16 but $2 \cdot e^{-F} = 1.613$; or the value of 2 is reached at 13. This does not mean that the critical age shifts from 16 to 13, because neither G nor M^* has changed; it does mean that under exploitation, the stock can replace itself at a lower level, which is a familiar concept in the Ricker family of curves.

The trend in N_t from hatching to the critical age can be established if the initial mortality is known. The loss rates of the plaice larvae are known: 80%/month or 99.20%/three months (the estimate of 80%/month is based on the observations for three months; Harding and Talbot, in press).

$$\text{In days, } N_{30}/N_0 = 0.2 = N_0/1+30M_0 \therefore M_0 = 0.133.$$

$$\text{Then } M_0 = N_0 - 2e^{-F}/2e^{-F} \cdot 13 \therefore N_0 = 1026.5.$$

N_t can be calculated for any number of ages. Figure 54 shows the trend in numbers with age, exploited at $F = 0.215$, assuming that $M_0 = 0.0522/d$. The mortality during the first quarter of life is 80%/month as given above. The mortality rates of 0-group fish of 40%/month at recruitment (in June) or 10-20%/month during the following winter are marked on the figure; these estimates of 0-group mortality are summarized from recent work by Lockwood [in preparation]. The adult natural mortality is taken from the loss rates of the transwarthime year-classes (Beverton and Holt, 1957): between the

ages of 5, 6, or 7 before the Second World War to 13, 14, or 15 after it. The mortality rate estimated in this way was 0.1, although Beverton (1964) in a later analysis of the data suggested that $M_0 = 0.08$ and $M_{\sigma} = 0.12$. For the ages 5 to 15, it can be shown that the average mortality rate calculated to N_t is 9.7%/yr. From hatching to the critical age, the trend of mortality with age can be fairly well simulated. This calculation depends entirely upon the estimate of larval mortality.

Senescent Mortality in the Plaice

Beverton (1963) put the Gompertz Law in the following form:

$$N_t = N_1 e^{-e^{(m_0 + m_1 t)}}$$

Where m_0 is the initial natural mortality rate at age N_1 ;

where m_1 is the rate at which senescent mortality increases with age;

where t is the age at which senescent mortality starts.

Since 1963, otoliths of the plaice population in the southern North Sea sampled at Lowestoft have been burned (Christensen, 1964) with the result that ages are determined routinely to the 21st year. From the otolith samples, my colleague, Mr. T. Williams, made age determinations up to the age of 35. The samples were taken from the year-classes 1933-1950.

The numbers of female plaice per 100 ton-hrs fishing at each age between 1964 and 1969 were averaged by years. Then total mortality was estimated from the ratio of the numbers per 100 ton-hrs fishing averaged for the six years at successive ages. The same data were averaged in age by moving means of threes to obtain a second estimate of total mortality. For the ages 5-16, the density-dependent mortality, was subtracted. By this means it was estimated that $F = 0.215$ for the ages 5 to 16 and that $m_0 (= M^*)$ at age 16 = 0.078. My colleague, Dr. R. C. A. Bannister, has found that the mortality of females during the same period estimated by virtual population analysis was also low.

A "catch curve" does not provide good estimates of total mortality because it can conceal a trend in time. Indeed, Gulland (1968) has suggested that there have been changes in the distribution of effort exerted on the plaice population during the late fifties. The estimate of fishing mortality on the younger age groups is not very different from that obtained by virtual population analysis in which trends in time are not concealed. The "catch curve" was used because to apply other methods completely would not be possible until 1992. Any estimate of the trends of mortality in the older

age groups would be biased by their mortality history in earlier years. In general the trend in mortality on the plaice population has been declining. The oldest year-classes sampled entered the fishery in 1938 when F (on both sexes) was 0.73. Then followed a period of no fishing during the war. Subsequently the value of $F = 0.5$ (Gulland, 1963) declined during the fifties and perhaps it fell further during the sixties. The mortality of females might have always been lower than that on both sexes. The natural mortality of the plaice was well estimated from the transwar-time year-classes (Beverton and Holt, 1957; Beverton, 1964) : $M = 0.1$. The trend of mortality might have been as follows:

1938-39	F 0.7	Z 0.8
1940-45	0.0	0.1
1946-54	0.5	0.6
1955-63	0.3	0.4
1964-70	0.2	0.3

It is assumed that the difference between the sexes in mortality tends to decrease with increasing fishing; however, it is possible that the downward trend in mortality on the females is a little overestimated. For a constant number of recruits, stock densities were calculated with this set of mortality for the year classes 1943-54, summed as a catch curve in the years 1964-70. The average mortality was 0.42, whereas the "catch curve" mortality was 0.58, so mortality was overestimated by the catch curve. Earlier year-classes back to that of 1934 were subject to no mortality during the war and then the "catch curve" mortality would underestimate the true mortality. In fact the "catch curve" mortality for all age groups was 0.26, and the average mortality was 0.38, so the catch curve underestimates mortality in the age group 16 to 31 in the period under investigation. Figures 55a and b show the observed catch curve and the one calculated by the method given above. The calculated one tends to overestimate mortality between the ages 16 to 21, but to underestimate it overall, with the effect that the shape of the curve is concave (Figure 55c); the concavity is a combined result of declining mortality in the postwar years and of no fishing mortality during the war itself. If the decline in mortality is a little overestimated, the initial slope is a little too high, but the effect would be to reduce the concavity to some extent - the overall underestimate of mortality from 16 to 31 would remain, if reduced a little. The observed catch curve is convex (Figure 55d), as if a senescent mortality did occur. The contrast between the two is enough to justify fitting Beverton's (1963) equation; the study of the possible nature of the catch curve shows that any estimate of fishing mortality used between the ages of 16 and 31 is an underestimate by as much as 50%. Further, it is assumed that fishing mortality is constant in the catch curve and so the changes in time have to be incorporated in an average figure.

Beverton's equation was used as follows:

$$N_t/N_1 = e^{-[Ft + e^{(m_0 + M_1 t)} - e^{m_0}]}$$

$N_1 = 34.3$; $N_t = 0.5$; $t = 15$; $m_0 = 0.078$; m_1 was calculated for a range of values of F ($= 0.0, 0.10, 0.15, 0.20$). Then the curve was fitted to the observed data between the ages of 16 and 31. The calculation was made

in this form because at the lower limit, when $t = 0$, $N_0 = N_0 e^{-(e^{m_0})}$. The observations are not independent of each other so a statistical comparison between the calculated curves and the observations cannot be made. An attempt was made using differences from the observations, but the variance was too high and statistical tests had to be abandoned.

Figure 56 shows the observations between the ages of 16 and 31 and curves of senescent mortality calculated at different levels of fishing mortality. The curves with $F = 0.0$ and $F = 0.2$ do not fit the data at all. The observations appear to be grouped in two parts, in ages 16-24 and in ages 25-31; the first period would be fitted by $F < 0.10$ and the second day by $F = 0.10-0.15$. Hence it is likely that there was a change in mortality in the catch curve. It will be recalled that the catch curve probably underestimates the fishing mortality by about 50%. Hence a true average value might be between 0.15 and 0.21. The point of evidence is that the observations in the form of a catch curve cannot be described by the trends in mortality in the cohorts that contribute to them and that they can be described by a form of senescent mortality. At $F = 0.1$, $m_1 = 0.0855$ and at $F = 0.15$, $m_1 = 0.0728$ and it would appear that either value would be applicable; the values of fishing mortality are underestimated, and perhaps in better data in future years, better estimates of m_1 might emerge.

The Age Structure in a Fish Population

There are four stages in the life history: (a) the larval drift before metamorphosis; (b) life on the nursery ground just after metamorphosis; (c) adult life, the period of fecundity; and (d) senescence. Figure 57 shows the trends in specific mortality rate and specific growth rates (by quarter years) for the first four or five years of life. The mortality rates follow the type of trend shown in Figure 54, but the growth rates increase sharply on the nursery ground, presumably because food is plentiful and predators are relatively few. During the larval drift, the specific mortality rates are very much greater than the growth rates. During life on the nursery ground, the specific growth rate becomes greater and remains

so until the critical age, after which senescence may supervene with a mortality rate greater than growth rate. The period of excess growth is that in which fecundity is built up and in an average condition, fecundity and egg production in the virgin stock are determined by the growth rate. Variability in stock produces variability in egg production and hence the subsequent density-dependent processes.

In this chapter it is proposed that the natural mortality of fishes is predominantly density-dependent. Knowing the larval mortality of plaice, it is possible to predict the subsequent death rate as far as it is at present known. The model of density-dependence in the larval life cycle described above is based on the success of an animal in exploiting food as it passes through a predatory field. It could be generalized to other marine life cycles so long as growth continues. In a sense this is sufficient justification for senescence, because in old age the specific growth rate is very low indeed.

However, fisheries biologists are accustomed to separating density-dependent from density-independent mortality because any stock recruitment curve appears to comprise large variability in recruitment for small differences in stock. Hence density-dependent mortality should perhaps be a small proportion of total mortality. Consider a trend in N_t with time and let a proportion be killed in an adventitious manner. In mathematical terms, it is as if N_0 and M_0 were reduced [in $N_t = N_0 / (1 + M_0 t)$]. Then let the density-dependent mortality continue in time and a correction has been made for the adventitious deaths. Perhaps the variability of recruitment is the result of what is effectively a density-dependent control over other forms of mortality.

Harris distinguished stock-dependent and density-dependent mortality. In the formulation used here N_t , the numbers at time t , depends upon N_0 , the initial numbers of eggs and upon M_0 , the initial mortality. However, Harris also suggested that the two forms of mortality were interdependent or if N_0 is high, M_0 is high and N_t is low. Just as density-independent processes modify the course of numbers in time, one might imagine that a difference in N_t might modify M_0 as if N_0 had changed, resulting in a later difference in N_t . Such variance about the design form of the curve of N_t in time would be generated by differences in food availability and in predator abundance.

The other question raised at this point concerns the nature of senescence. Because fish continue to increment growth at all ages, Bidder (1925) suggested that they were immortal, or that senescence started at an age well beyond the life span commonly experienced in an exploited stock. Graham (1957) has referred to very old fish in the Kavirondo Gulf of Victoria Nyanza. Recently, Greer-Walker (1970) has examined the muscle fibers of the cod and has shown that the cross-sectional area of white

muscle fibers reaches a maximum at a length of about 100 cm and that at 120 cm, there is a reduction in area of 20%. The white muscle generates the escape and attack speed, so between 100 and 120 cm, the capacity of the fish to feed and escape attack must decrease. Trout (1957) has shown that cod in the Barents Sea of 100-120 cm are 12-16 years of age and perhaps a little more. Later it will be shown that the critical age for cod is 16. Dr. Green-Walker has examined some female plaice in the last year or so; he shows that there is a peak in white fibers diameter at 600 g in plaice and that it declines to about 50% at 1400 g, that is not far from an age of 16. However, the calculation of $(G - M^*)$ was made on fish of the 1943-1946 year-classes before the apparent increase in length for age occurred. All we can conclude is that there is a little independent evidence that senescence is a possible cause of mortality.

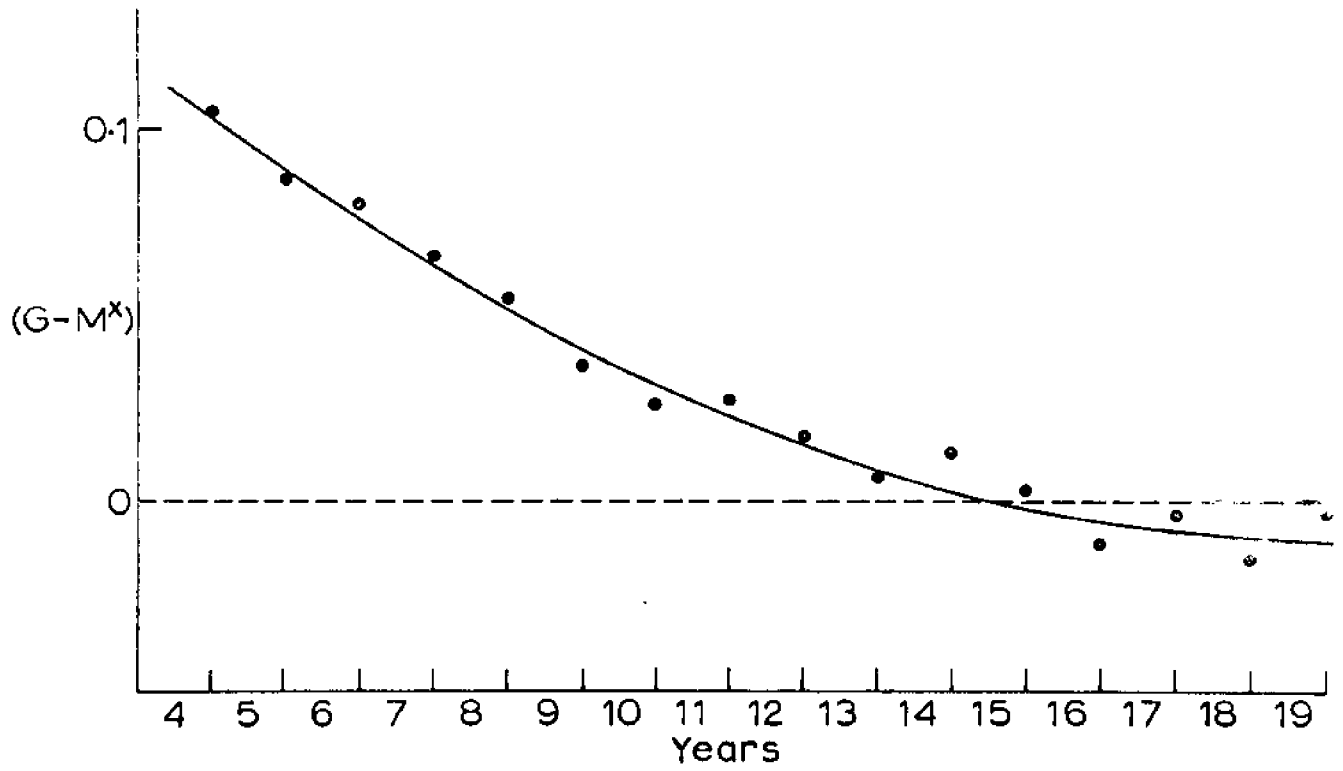


Figure 53. The trend in $(G - M^*)$ with age for female plaice of the year-classes 1942-1944.

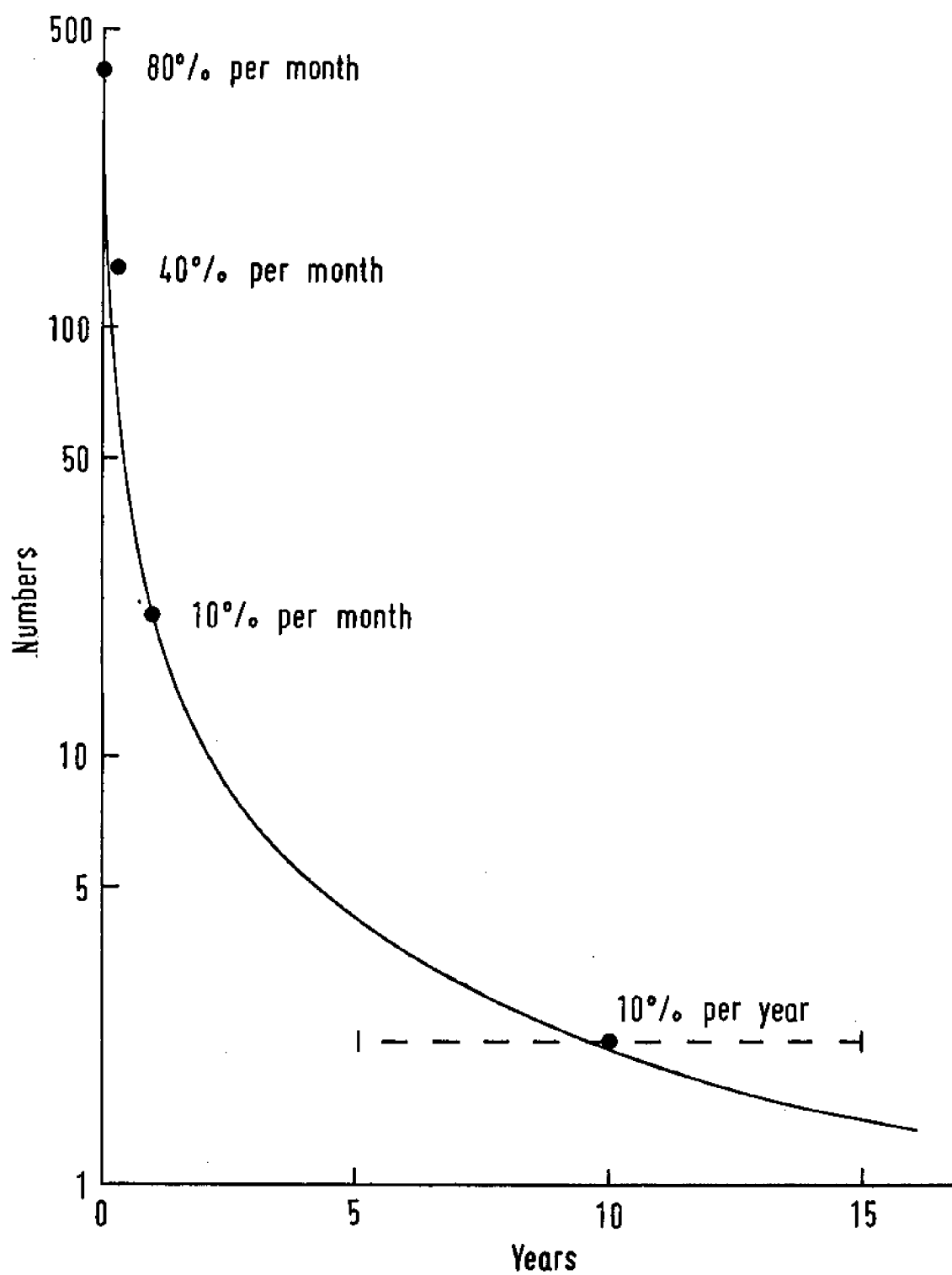


Figure 54. The trend in N_t with age for plaice from hatching to the age of 16.

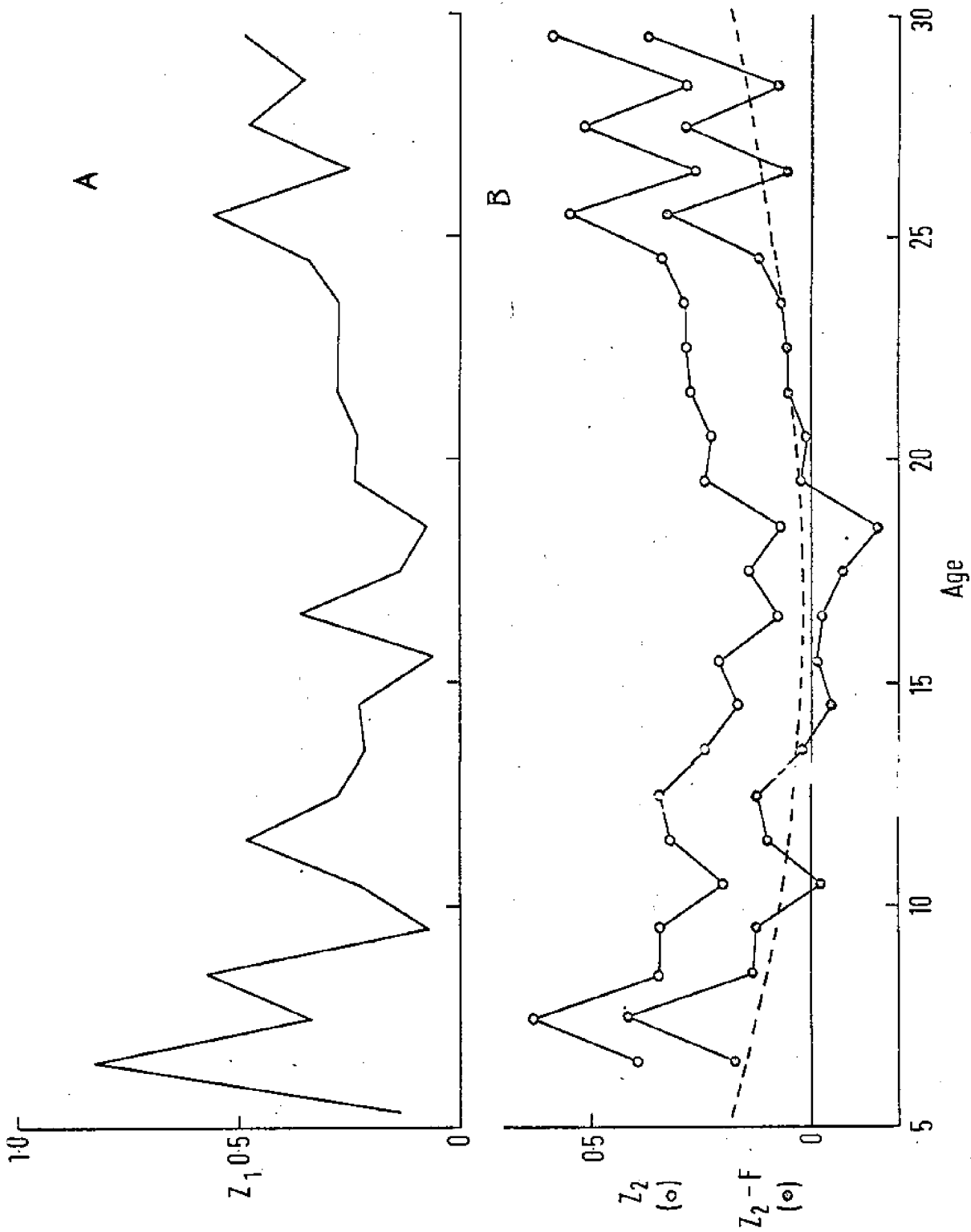


Figure 55. Trends in total mortality with age:

- (a) trend in total mortality (Z_1) estimated from the ratio of numbers per 100 ton-hr fishing (averaged for six years) at successive age groups.
- (b) trend in total mortality (Z_2) from the same data averaged in age by moving means of three.

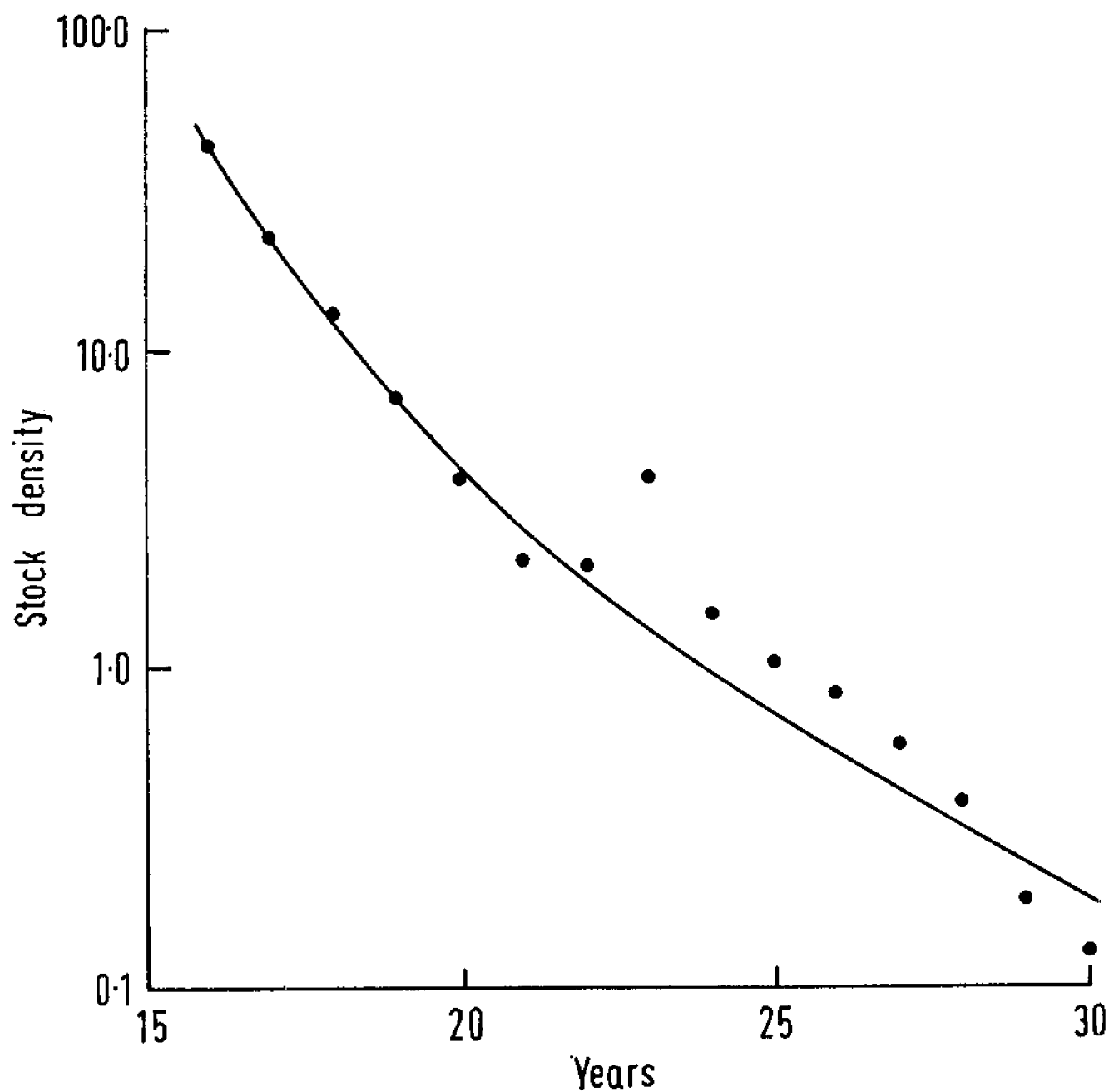


Figure 55-c. The modeled trend in stock density in a catch curve between 1964 and 1969 assuming no fishing during the war and the decline in mortality subsequently.

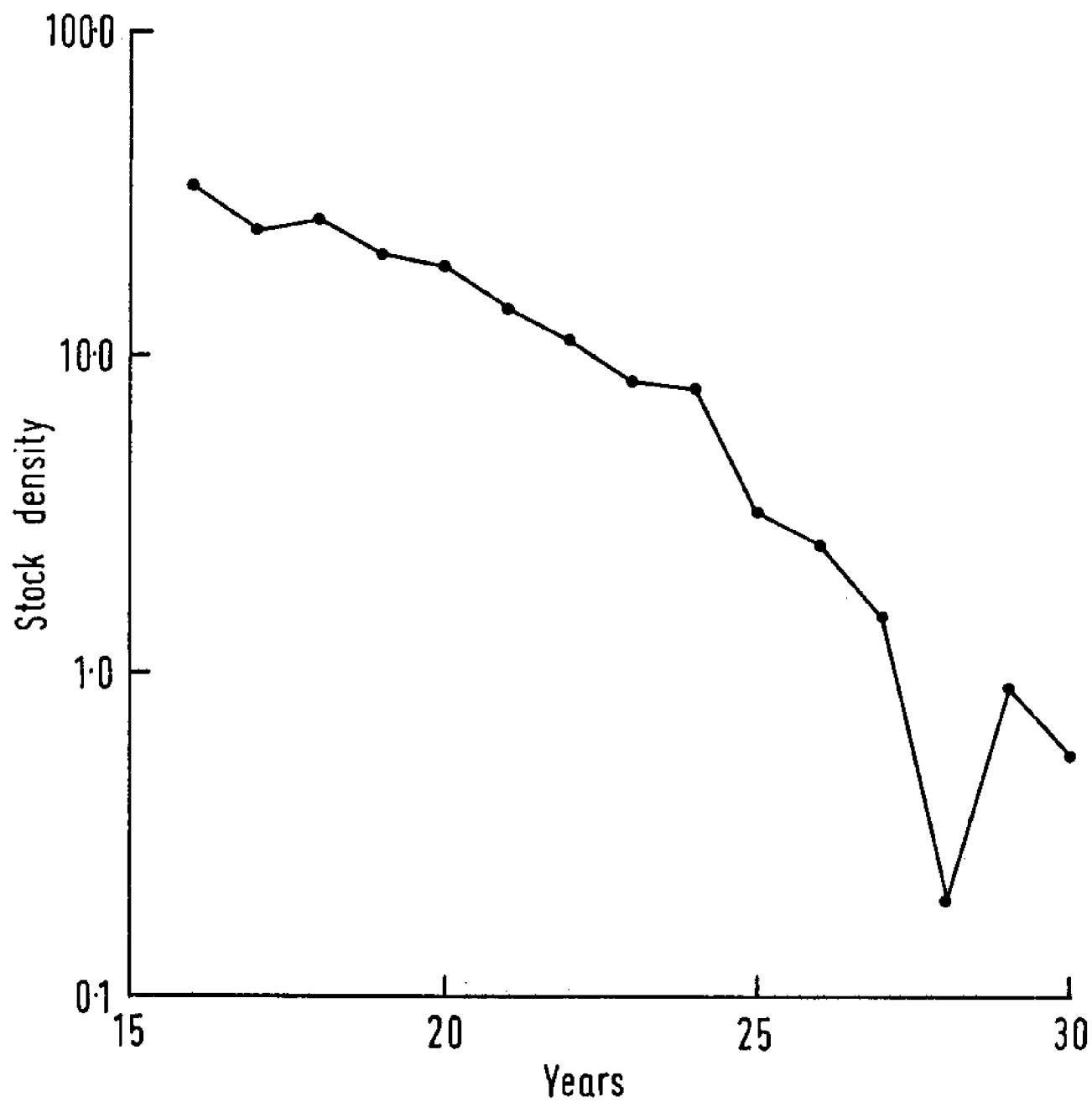


Figure 55-d. The observed trend in stock density as a catch curve between 1964 and 1969.

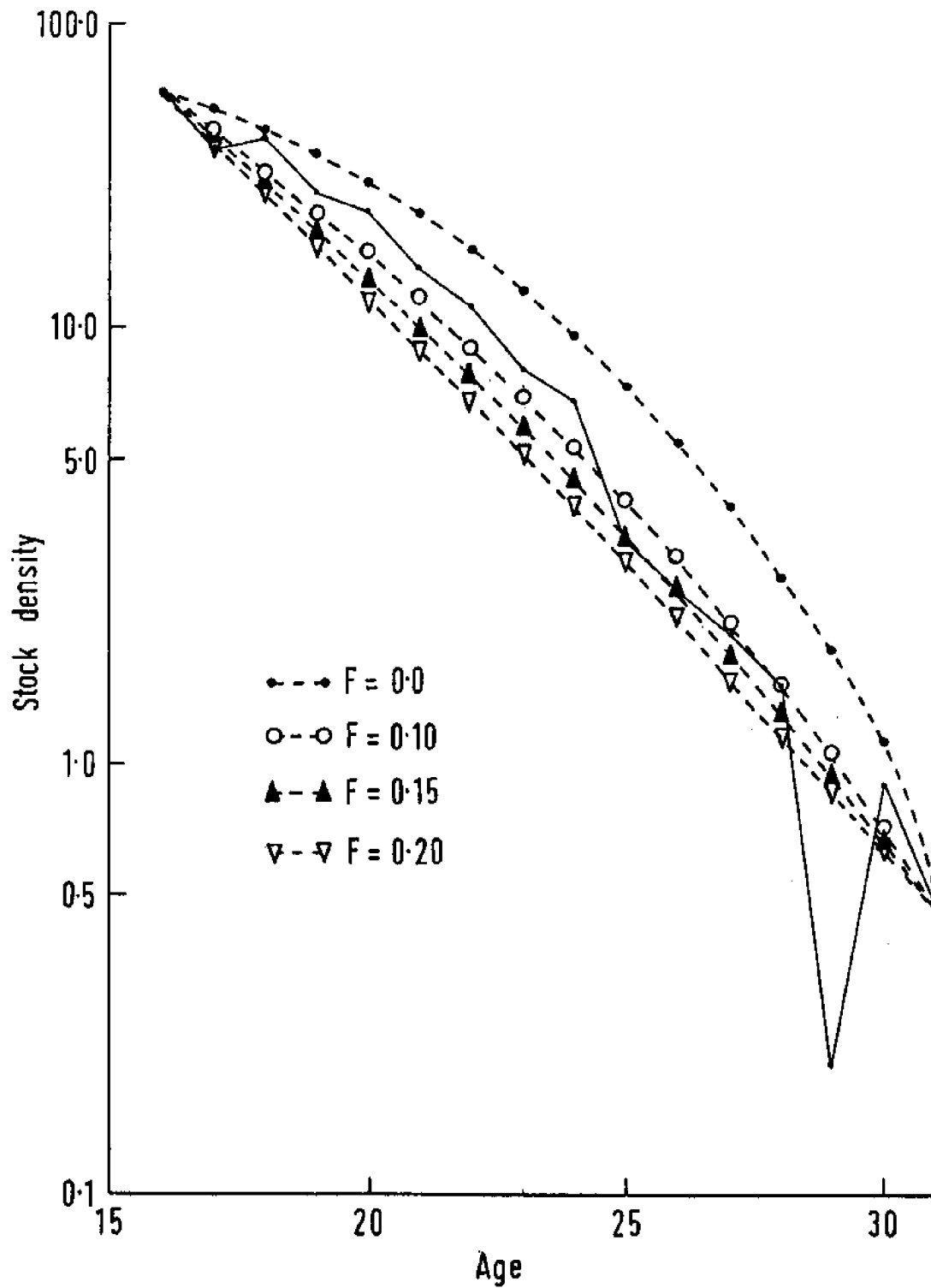


Figure 56. The observations of stock density in a catch curve between 1964 and 1969 fitted with Beverton's equation using different values of fishing mortality.

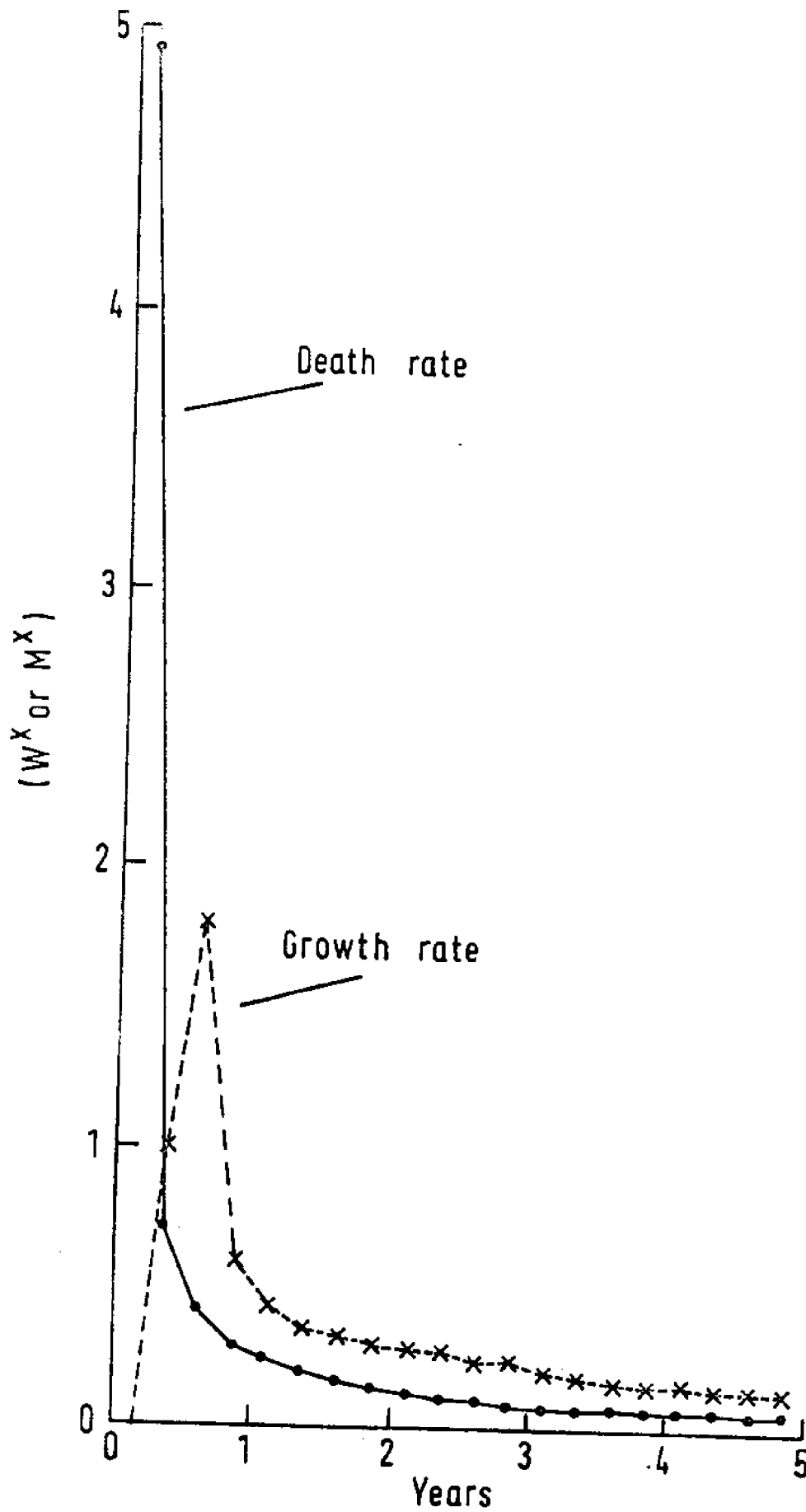


Figure 57. Trends in specific mortality rate (M^*) and specific growth rate (G) by quarter years for the first four years of life.

Chapter 8

CLIMATE AND RECRUITMENT

Introduction

In the models of the mortality of the Pacific salmon between birth and recruitment, Larkin (1964) has described extrapensatory effects that are given random values in the calculation. In any time series of recruitments with no upward or downward trend, the observations are often randomly distributed. However, variation in recruitment is often correlated with differences of a climatic character. Although weather forecasting is a short-term art, the ocean itself (and at a further remove the recruitment mechanism of fishes) damps the variability in climatic trends. In the future recruitment may be predicted to some extent from observations on solar radiation and on wind strength and direction.

The Correlation Between Year-class Strength and Climatic Change

In the history of fisheries biology, a number of correlations have been found between recruitment and particular components of climatic change, but most have failed with increasing number of observations. Carruthers (1938) correlated the year-class strength of the Downs herring with the strength of southerly winds in the area of spawning. Recruitment to the North Sea haddock stock was also related to southerly winds (Carruthers et al., 1957), to westerly winds (Rae, 1957), and to the quantity of *Calanus finmarchicus* (Cushing, 1966). Each of these correlations failed in subsequent years. Hermann et al. (1965) showed a positive correlation between the year-class strength of west Greenland cod and sea temperatures (between 0°C and 4°C), and Martin and Kohler (1965) have demonstrated a negative correlation between annual cod catches and temperatures (between 5°C and 9°C) off St. Andrews, N.B. Between them these two correlations represent conditions at the northern and southern edges of the geographical range of the North Atlantic cod. Neither of the latter correlations has yet failed with additional observations. Many such correlations have lived and died in the history of fisheries biology, and the attitude they indicate implies that recruitment is modulated by climatic factors.

Another form of evidence emerges from the examination of individual year-classes. For example in the southern North Sea, very strong year-classes of cod, sole, and plaice originated in the very cold winter of 1962-1963; a general explanation may be that the development of eggs and larvae was delayed by the colder water till food for the larvae was fully available. Templeman (1965) has studied the outstanding year-classes of cod, haddock, and herring stocks throughout the North Atlantic between 1902 and 1962; the year-classes

were not expressed in numbers or in stock density but were classed qualitatively--"abundant," "very abundant," etc. In ten stocks, nine were "abundant" in 1950: the famous 1904 year-class was not only "abundant" in the Norwegian herring, but also in the Arcto-Norwegian cod and Icelandic haddock. In 1922, there were "abundant" year-classes of cod off West Greenland and Lofoten in northern Norway and of haddock off Iceland; the same groups were "abundant" in 1934 with the addition of the Icelandic cod. All cod year-classes and that of Grand Bank haddock were "abundant" in 1942. In 1955, Icelandic cod and the Grand Bank haddock were "abundant" and in 1956, nine of the ten stocks listed were "abundant" or "very abundant." It will be shown below that all these dates are significant in a climatic context. But the most remarkable point is the contemporaneous appearance of good (or bad) year-classes in different parts of the North Atlantic, which can only indicate a phenomenon that is fairly pervasive in nature.

A third point of evidence is the correlation between the catches of the Arcto-Norwegian cod stock and the widths of annual rings on pine trees in the area of the Lofoten Islands in northern Norway where the cod spawn (Ottestad, 1942). For a term of fifty-five years, periodicities in the pine tree data were detected with a form of harmonic analysis in order to establish temporal changes in climate. The periodicities were correlated (Figure 58) with the catches ($r=0.84$; $n=55$); the differences were correlated with events themselves mediated by climatic changes. A similar analysis of Yugoslav fisheries in the Adriatic has been made by Zupanovic (1968) from a long series of data on catches for a number of species; an important point is that he was able to forecast a general increase in sardine catches in Yugoslavia. Some of the correlations of recruitment with particular factors have had a transient life, but these two correlations survive probably because the independent variable is the general result of climatic change and not a particular factor, like the wind strength from a particular direction.

The fourth point of evidence is derived from the same Arcto-Norwegian stock of cod in the years since the Second World War. Garrod (1967) has estimated the recruitment to this stock by virtual population analysis as described in an earlier chapter. Dickson and Garrod (1972) have correlated the survival indices (i.e., R/P) with differences in surface salinity in the German Bight and with temperature differences on the Kola meridian (Figure 59). It might seem perverse to correlate recruitment to an Arctic stock of cod with events more than a thousand miles away in the North Sea. However, as will be described in the next section, climatic change is widespread and differences in quantities in the North Sea are closely correlated in time with those in the Barents Sea, presumably because the waters of both seas are replenished by the common North Atlantic drift. Both areas are also affected by a common wind system.

The four points of evidence are, first, the failing correlations with particular factors, second, the widespread appearance of contemporaneous year-classes of different species across the North Atlantic, third, correlations with indices that reflect general climatic change and, fourth, correlations with detailed indices of climatic change. Some of the early correlations

were based on a false premise, that larval fish were blown by the wind in the surface waters into areas in which survival was good or into others where it was bad. For example, Carruthers et al. (1957) believed that the correlation of haddock year-classes with wind strength was generated by larvae being lost, or not, over the Norwegian deep water in the North Sea. However, Saville (1959) showed that the larvae never reached the deep water, so this form of physical explanation must be rejected. Fish in temperate waters spawn at fixed seasons and the production cycles vary in amplitude, timing, and spread. The match or mismatch of larval production and the production of larval food are probably sufficient causes of the variability of year-classes. The variations in the production cycle are generated by differences in wind strength or radiation, and this is the basis of the correlations with indices of climatic change.

The Nature of Climatic Change

The sun's energy is nearly constant, although small trends are perhaps noticeable. At the earth's surface, however, it varies with the sun's altitude, which itself varies daily and seasonally, and with differences in dust and moisture in the air. Hence, the input of heat to the earth's atmosphere and oceans varies seasonally and latitudinally; it is modified by mountain ranges and continents and markedly by snow and ice, which reflect it. Thermal gradients tend to increase over middle latitudes as an effect of the main icefields towards and at the poles. The inequalities in heating generate density differences in the atmosphere and hence winds. Warm air rises in low latitudes and cold air sinks nearer the poles; and in the middle latitudes, the air streams westerly at the center of the heat engine at a height of several km. Variations in the trends of these winds or the upper westerlies (partly as Rossby waves or partly in detailed response to geographical features) generate the differences in the distribution of cyclones and anticyclones, which cause the variations in wind strength and direction right across the globe.

Such variations in climate at one position are apparent in cycles of different periods. The longest periodicity of interest to fisheries biologists is about 50-60 years, which is, for example, the approximate half wavelength of the Norwegian and Swedish herring periods. Figure 60 shows the number of days classed as "Westerly" over the British Isles between 1873 and 1963 (Lamb, 1966). The alternation of Norwegian and Swedish periods may be associated with a shift from westerly to southerly winds and back again, as will be described below. The main wind systems flow between the centers of low and high pressure, the cyclones and anticyclones. If the prevailing winds shift in season or as the years pass, it is because the average tracks of depressions change with the varying distribution of the heat budget across the earth.

Figure 61 shows the trend in surface temperature between 1880 and 1960 for sea areas in the Northeast Atlantic (Smed, 1947-1969). The chart shows the annual anomalies from a mean; the latter was calculated for only an initial

part of the periods; consequently the absolute values are biased, but the trend in time is not. In each area, the sea was coolest during the first two decades of the 20th century; but subsequently in the thirties, forties, and fifties, the sea became warmer by about one degree centigrade or so. Bjerknes (1963, 1964) has explained the warming of the Northeast Atlantic by the decrease in westerly winds, which resulted from the dwindling pressure difference between the Iceland low and the Azores high. With the failing winds the quantity of heat remaining in the sea increased and so the sea temperature rose. In the mid-19th century, the Iceland low was weak, but in the eighties it intensified, giving low pressures, and high differences in pressure between it and the Azores high to the south and hence strong westerly winds. Subsequently, by the thirties and forties of the present century, the pressure difference between the two systems had diminished and the westerlies slackened. Thus, Figures 60 and 61 show different expressions of the same phenomenon.

The analysis of climatic change has been carried a stage further by Dickson (1971). He examined the anomalies of surface salinity in months from a grand monthly mean, for each year in the waters around the British Isles. They were averaged by moving means for different areas, for example, Western Approaches, German Bight, etc. Figures 62a-d show a summary of the whole time series: 1905-1925 in the Western Channel; 1920-1940 in the central North Sea and German Bight; 1934-1955 in the Irish Sea; and 1940-1970 in the German Bight. The different areas used are those in which the data were available. The continuous time series show peaks in the high salinity anomaly:

1904-1906, 1920-1921, 1925-1926, 1930-1931, 1934-1935, 1939, 1950,
1954-1955, 1959-1960, 1964-1965.

The series of years is an important one and recurs in the biological history of the British waters and the North Atlantic--for example, the famous 1904 year-class of the Norwegian herring and the prominent 1950 year-classes of both the Arcto-Norwegian cod and the Norwegian herring. The changeover from herring to pilchards in the Western English Channel may have taken place in three stages, 1925-1926, 1930-1931 and 1934-1935 (Cushing, 1961, 1966). There are many other examples. Many of these series of years can be picked out in detail from the long period of westerlies shown in Figure 60.

Dickson's explanation is as follows. Namias (1964) had examined the climatic events in 1959, which was a long hot summer in the British Isles. The anomalously warm sea temperatures in the waters around the British Isles were generated by a protracted northerly advection of warm and saline water throughout the eastern Atlantic. A west Atlantic low and an anticyclone over Europe led not only to the northerly advection of warm water in the eastern Atlantic, but in the same season there is a southwesterly advection of cold water along the coast of Labrador. The basis for the pervasive correlation of year-classes across the whole North Atlantic begins to emerge. There are certain factors that tend to enforce persistence in such climatic events. By

examining the pressure distributions in the North Atlantic for 21 years, Dickson showed that southerly winds occurred during those years of high salinity inflow. Indices of meridionality (or southerliness) and cyclonicity in Europe were developed and were correlated with the salinity anomalies. Hence Namias' hypothesis was extended from the single year 1959, by Dickson, to the long time series from 1905-1970.

Figures 60 and 62 show different aspects of the same phenomenon. In the eastern Atlantic, the prevailing winds shift from south to west and back again in the long-term and this shift is linked to the variability in the high salinity anomalies. The wind system contains within itself the capacity to vary in the short-term (as shown in the salinity anomalies) and in the long-term (as shown in the shift from southerly to westerly). On an oceanic scale, fish tend to spawn close to the coast, so differences in wind strength and/or direction can become amplified by the shape of the coastline, merely by modifying the degree of fetch in the ocean wave system. The climatic structure has the capacity to vary both in the short-term and the long-term at one position in the sort of way that the recruiting year-classes to the fish stocks vary. One of the most interesting points about Dickson's account is that the same pressure system generates warm water in the eastern Atlantic and cold water in the western Atlantic. Outstanding year-classes of cod common to both sides of the Atlantic are then perhaps associated with decrement of temperature in the eastern Atlantic and with an increment in the west; those in the east would be at the southern edge of their range and those in the west at the northern edge. The converse condition is also possible.

Johansen (1924) listed the Swedish herring periods: 1307-1362, 1419-1474, 1531-1586, 1643-1698, 1784-1808, 1878-1918 and each lasted about 53 years and the alternate Norwegian periods each lasted about 56 years. The Swedish herring are probably North Sea fish (Höglund, 1972) that penetrate the Skagerrak at certain times, which may be periods of abundance or periods at which the salinity inflow is above average. Considerable variations in the inflow of Atlantic water into the Baltic have been recorded for a long time; small populations of cod are sustained by such sporadic invasions. The North Sea herring spawn close to the British Isles and so a westerly wind with a short fetch might generate a closer match of spawning to a production cycle than a southerly wind with a long fetch. Runnström (1933) found three main spawning areas off the coast of Norway, off Utsira near Haugesund, off Stadt (north of Bergen), and north of the Lofoten Islands. Devold (1963) has recounted how these stocklets died out from south to north and so the fishery ended in the far north at the end of the Norwegian herring period in the sixties and seventies of the last century. The decline of the stock occurred as the wind shifted from southerly to westerly in spring (Figure 60). The shape of the Norwegian coastline with respect to the prevailing winds plays a part here as it runs northeasterly from Bergen to the Lofoten Islands. Provided that the Swedish and Norwegian stocks are distinct as described, the alternation may occur as the wind system shifts back and forth in a periodic manner.

Ishevskii (1964) divided the northern hemisphere into five subregions--Greenland and North America, Atlantic, Europe/Asia, E. Siberia, and Pacific. Changes in one are out of phase with those in an adjacent area and the whole system is that of planetary or Rossby waves. Ishevskii believed that temporal differences in properties were generated by the effects of tidal periods of up to 18 or 20 years on seasonal heat budgets. Catches of cod and herring set back in years by the modal age of the stock were correlated with temperatures or with events during the first year of life. Figure 63 shows a correlation between catches of Caspian Sea pike perch and the temperature on the Kola meridian. An inverse correlation between temperature in the Labrador Sea and that in the Barents Sea was shown. Correlations between Black Sea systems and Barents Sea systems were established on the assumption that they were out of phase with each other. Hence the association between the long-term herring periods in the northeast Atlantic and similar periods in the catches of tuna in the Pacific established by Uda (1960) is perhaps a reasonable one.

There is some evidence of a regular and long-term periodicity of about 110 years, which may be a dominant feature of the climatic regimes of temperate seas. Over a long period of time, fish stocks have probably adapted themselves to it in modifying their recruitments, slightly in the gadoids and violently in the clupeids. Climatic change can be expressed by changes in temperature, radiation, and wind strength or direction. It can be shown that such factors modify the timing and amplitude of the production cycle; it is difficult to imagine how recruitment is modified by climatic factors if it is not through the medium of the production cycle.

The Biological Response to Climatic Change

In temperate waters production stops in winter. Production cannot start until the depth of mixing is exceeded by the critical depth. The critical depth is that at which photosynthesis equals respiration when both are integrated in depth. Subsequently, the rate of production depends on the rate of development of the production ratio ($=D_c/D_m$, where D_c is the compensation depth and D_m the depth of mixing). The compensation depth, D_c , is that at which the rate of photosynthesis equals the rate of respiration. As the sun's angle rises in the spring, the compensation depth increases. Just as the sunlight increases in spring, so the wind strength falls and the countervailing factors ensure that the production ratio increases sharply.

In a small and arbitrary model, Figure 64 shows how the amplitude, spread, and timing of the production cycle depend upon the variations in the rate of change of the production ratio. Let $dP/dt = P(R - G)$, where P is the algal population, R is the algal reproductive rate, G is the algal mortality due to grazing, and t is time. The algal reproductive rate was arbitrarily increased from 0.1 to 1.0 in steps of a variable number of days (2.0, 2.5, 3.0, 3.5, and 4.0). At $R = 0.35$, grazing mortality was started and it was increased to equal R at $R = 1.0$ and to exceed R by 25%. Thus in an arbitrary model, a delay period was introduced and the cycle was controlled

when $R < G$. A bell-shaped curve like the real production cycle is the result. The figure shows how the timing of the production is delayed as the production ratio develops more slowly (as indicated by the slower rate of development of the algal reproductive rate) and how the amplitude varies also with the rate of change of the production rate. The model was not intended to predict the magnitude of the changes in the production cycle, but only to show that amplitude and timing were modifiable in the way suggested.

In Figure 65 is given a pictorial representation of the match of larval production to that of their food. Three conditions of timing are shown: early, middle, and late production relative to the fixed spawning time of the fish. The nauplii are the main food of fish larvae and the number of nauplii per larva is an index of the availability of food to them. In the early production cycle, food availability is positive from an early date and it increases to a low level. In the late production cycle, food availability becomes positive much later and it increases very rapidly to a high level. In the early cycle, survival may be always low because the larvae feed poorly, grow slowly, and suffer heavy predation. In the late cycle, survival is very low until the food becomes superabundant, after which survival is high. However, the late cycle is potentially dangerous because if there is no food when the yolk has been exhausted, the larvae will starve. The middle production cycle may be the effective one representing the average condition. This account is taken from Cushing (1972b).

There is, however, another form of modification. Figure 22 shows the mortality rates of plaice in the Southern Bight of the North Sea for three years (Harding and Talbot, in press). In the cold winter of 1962-1963, the mortality rate of larvae was less than that in the other years, but the development rate was very slow indeed. Figure 23 shows the strength of the 1963 year-class in 1971 at the age of eight. It is the strongest year-class that has appeared since 1945 and it was generated in the cold winter, with low larval mortality and a slow rate of development, and the production may have been advanced in the calm weather of anticyclonic conditions. The cold winter is characterized by an anticyclone over the North Sea. There are thus two components to the match or mismatch of larval production to that of their food--the variability of the production cycle and the rate of development of the larvae.

Conclusion

For a long time, biologists have been aware of an association between the highly variable recruitment of fishes and the manifestation of climatic change. Recruitment and wind strength or direction appeared to be correlated for limited periods of time. Across the North Atlantic, abundant year-classes of disparate stocks appeared in particular years. One important correlation was related by differences in catches to the effects of climatic change, the

width of rings on local pine trees. Finally, correlations of year-class strength on indices of climatic change have been developed on the basis of a wider understanding of its nature.

The description of climatic change in the Northeast Atlantic is based on the switch from westerly to southerly winds and back again during periods of about 110 years. Within the long-term variation, there are years of high salinity inflow that appear to be correlated with the emergence of good year-classes in the same year in different parts of the Northeast Atlantic. Perhaps in the future, recruitment will be forecast from meteorological studies.

The mechanism at the root of the successful correlations between year-class strength and climatic factors is probably the match or mismatch of larval production to that of larval food, because it is the only means by which recruitment can be modulated by the weather.

In general biological terms, one would expect a population in evolutionary terms to reduce environmental variability to a minimum. If recruitment is environmentally modulated, then the stabilization mechanism ensures least variation in the stock. On the other hand, it is possible that the control of stability is in fact linked to the determination of recruitment.

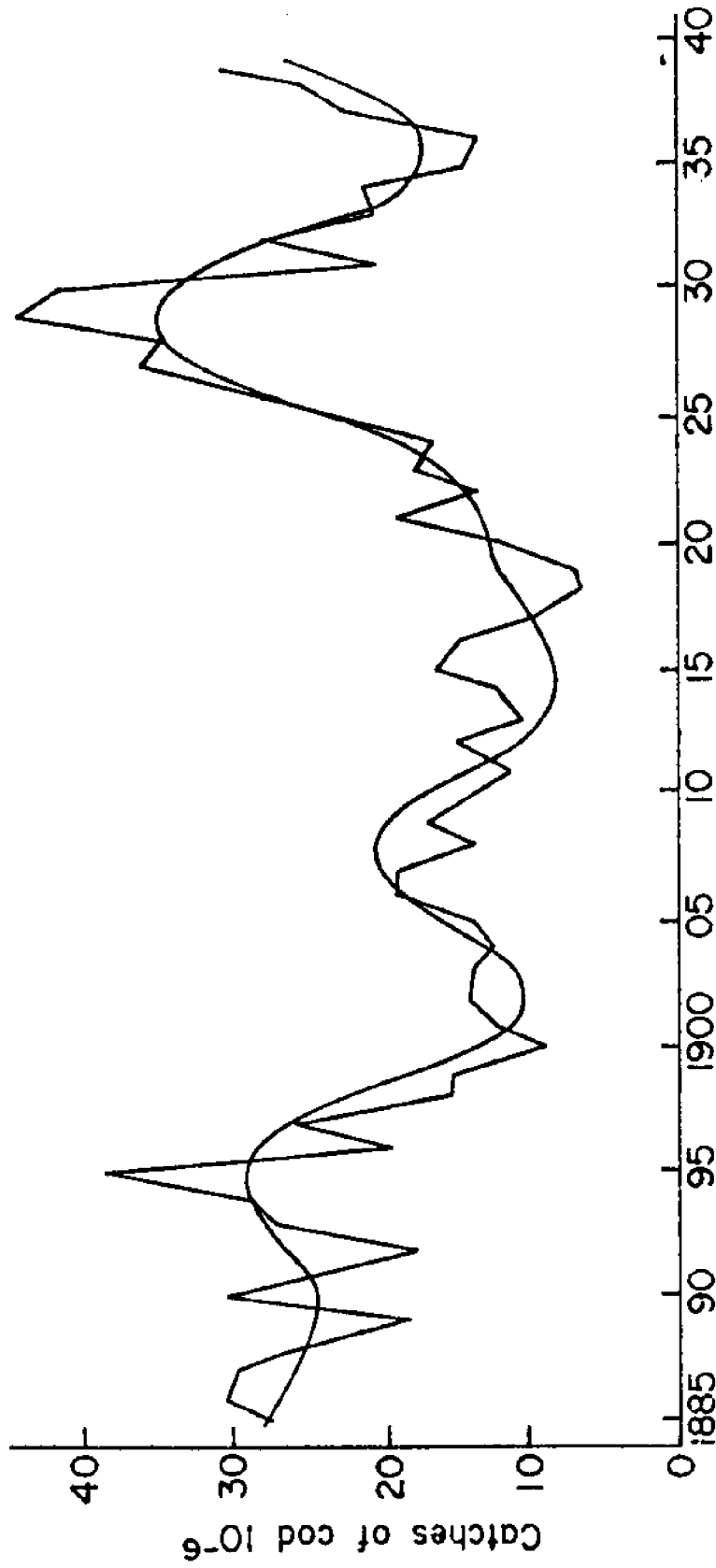


Figure 58. Correlation between cod catches in the Vestfjord and the periodicities in pine tree rings in the same region (Ottestad, 1942).

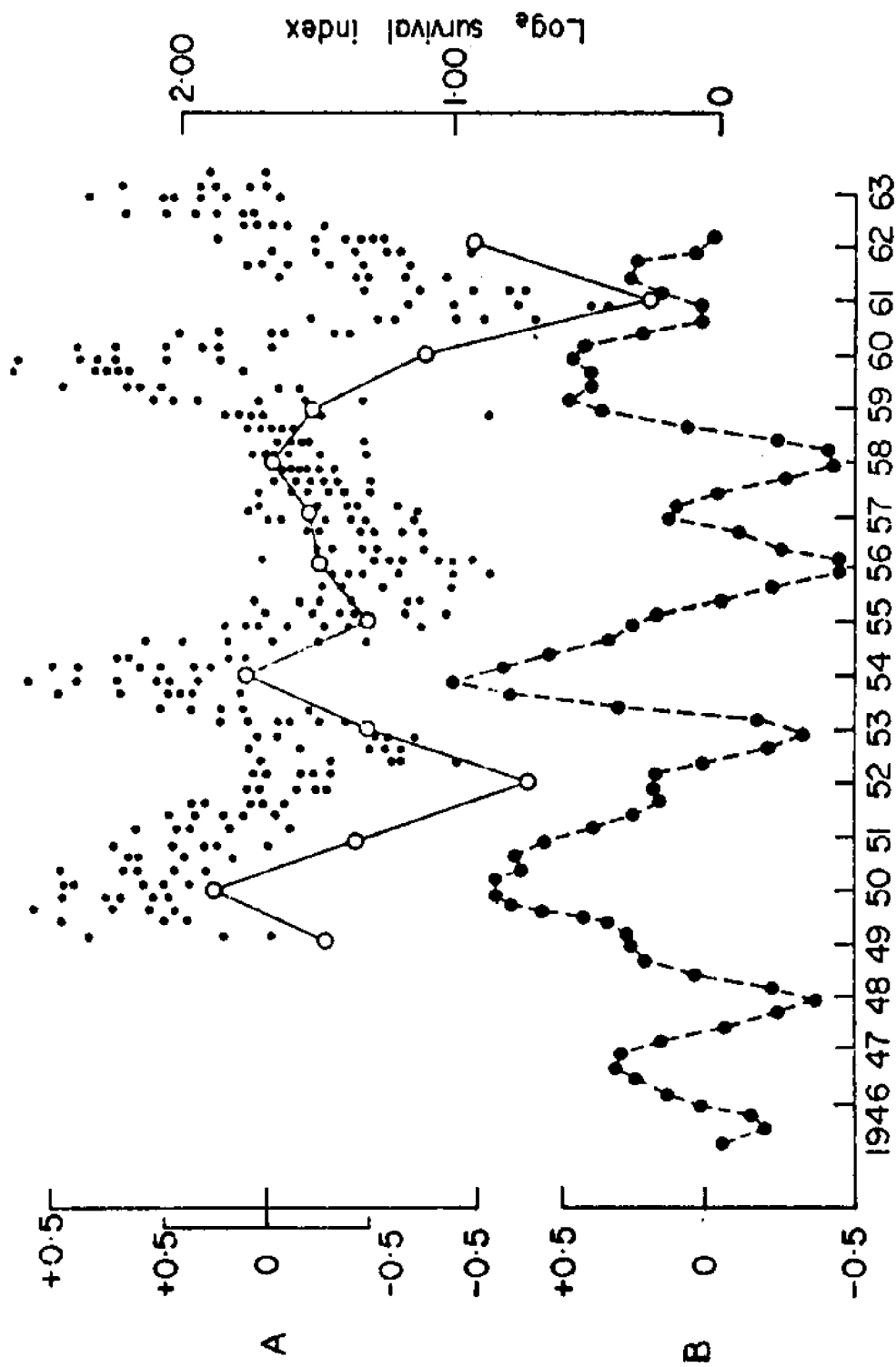


Figure 59. Correlation between the year-classes of Arcto-Norwegian cod and (a) salinity anomalies in the German Bight; (b) temperature anomalies on the Koia meridian (Dickson and Garrod, 1972).

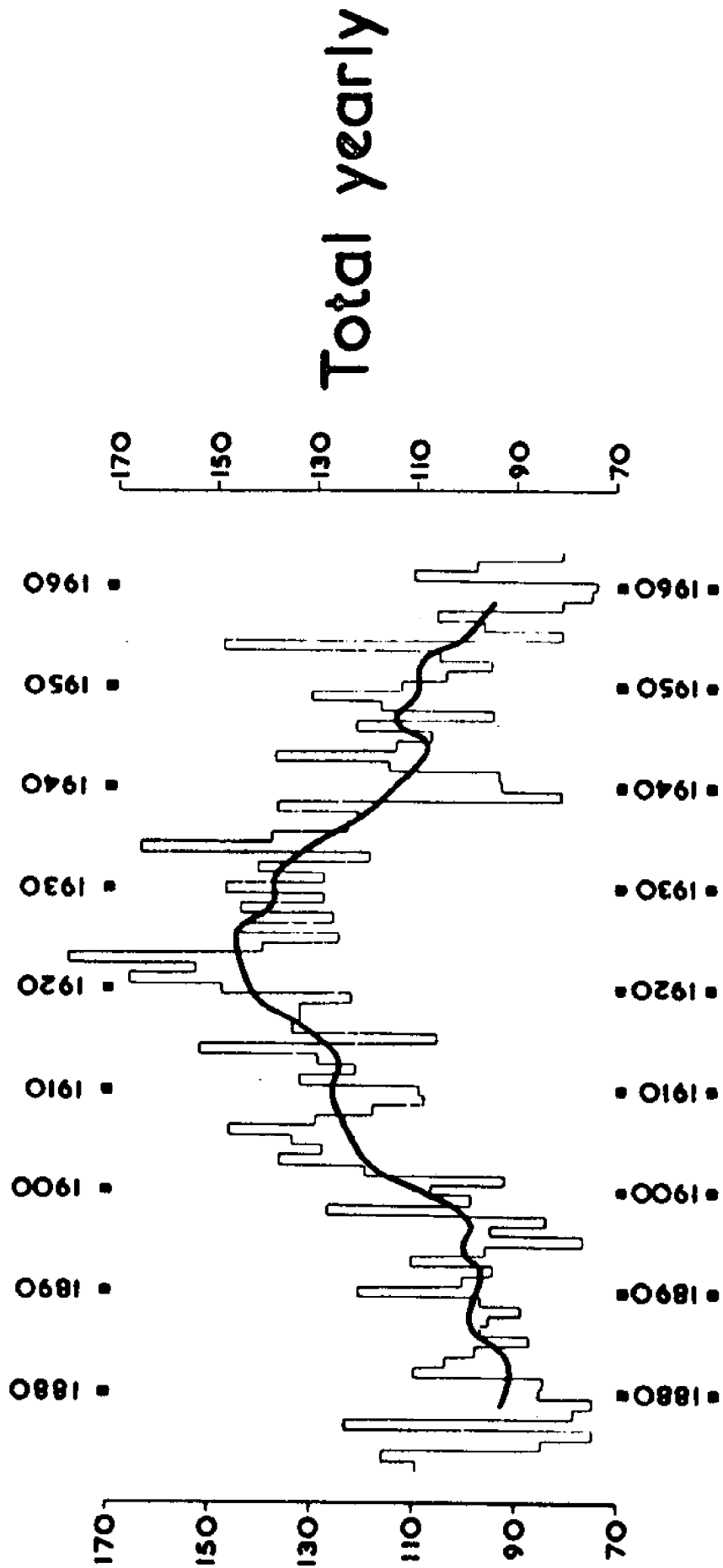


Figure 60. The number of days classified as "westerly" over the British Isles 1875 and 1963 (Lamb, 1966).

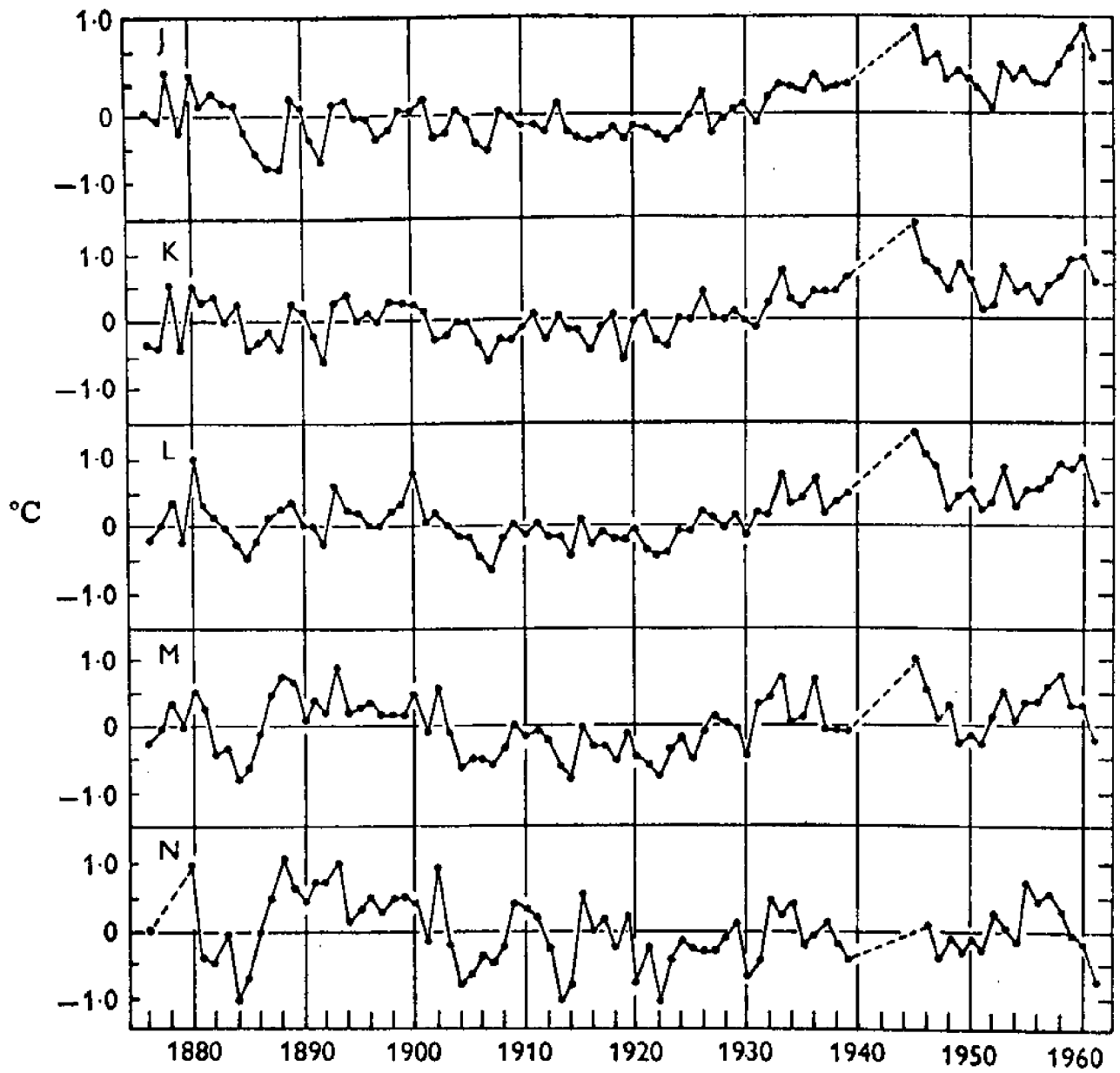


Figure 61. The trend in surface temperature in northeast Atlantic waters between 1880 and 1960 (Smed, 1947-1969).

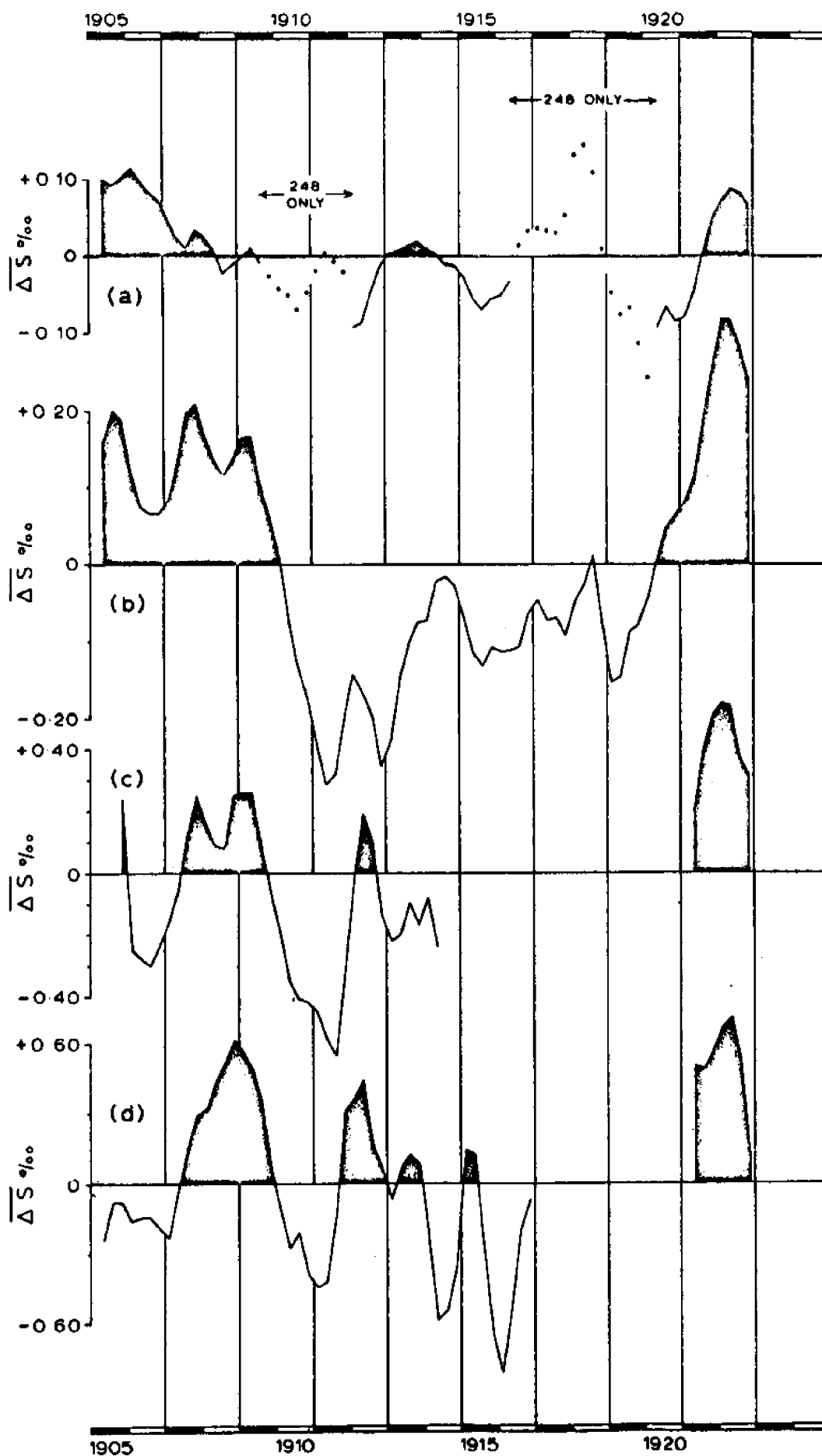


Figure 62-a. Anomalies of surface salinity between 1905 and 1925 in the western English Channel (Dickson, 1971).

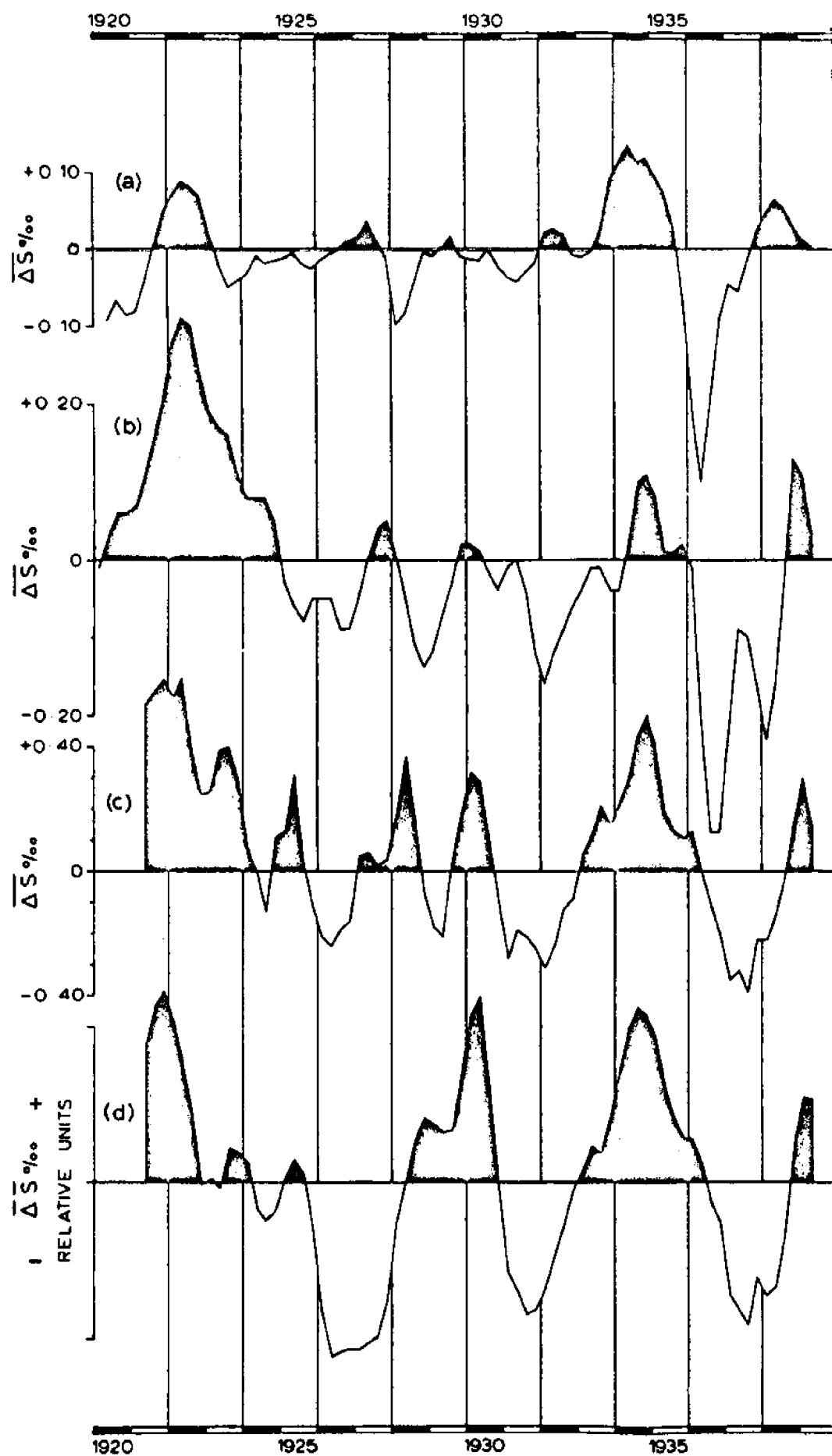


Figure 62-b. Anomalies of surface salinity between 1920 and 1940 in the central North Sea (Dickson, 1971).

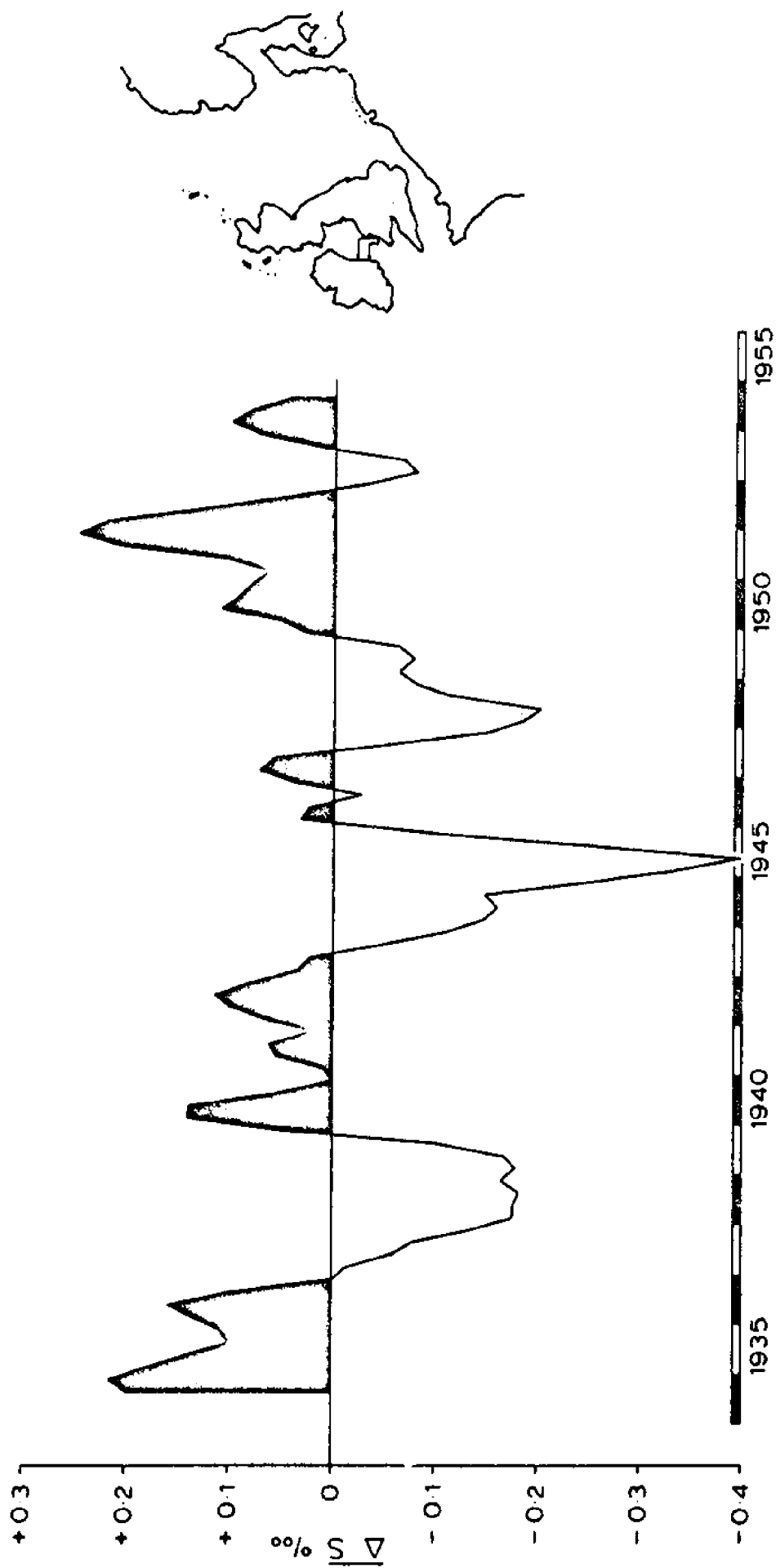


Figure 62-c. Anomalies of surface salinity between 1934 and 1955 in the Irish Sea (Dickson, 1971).

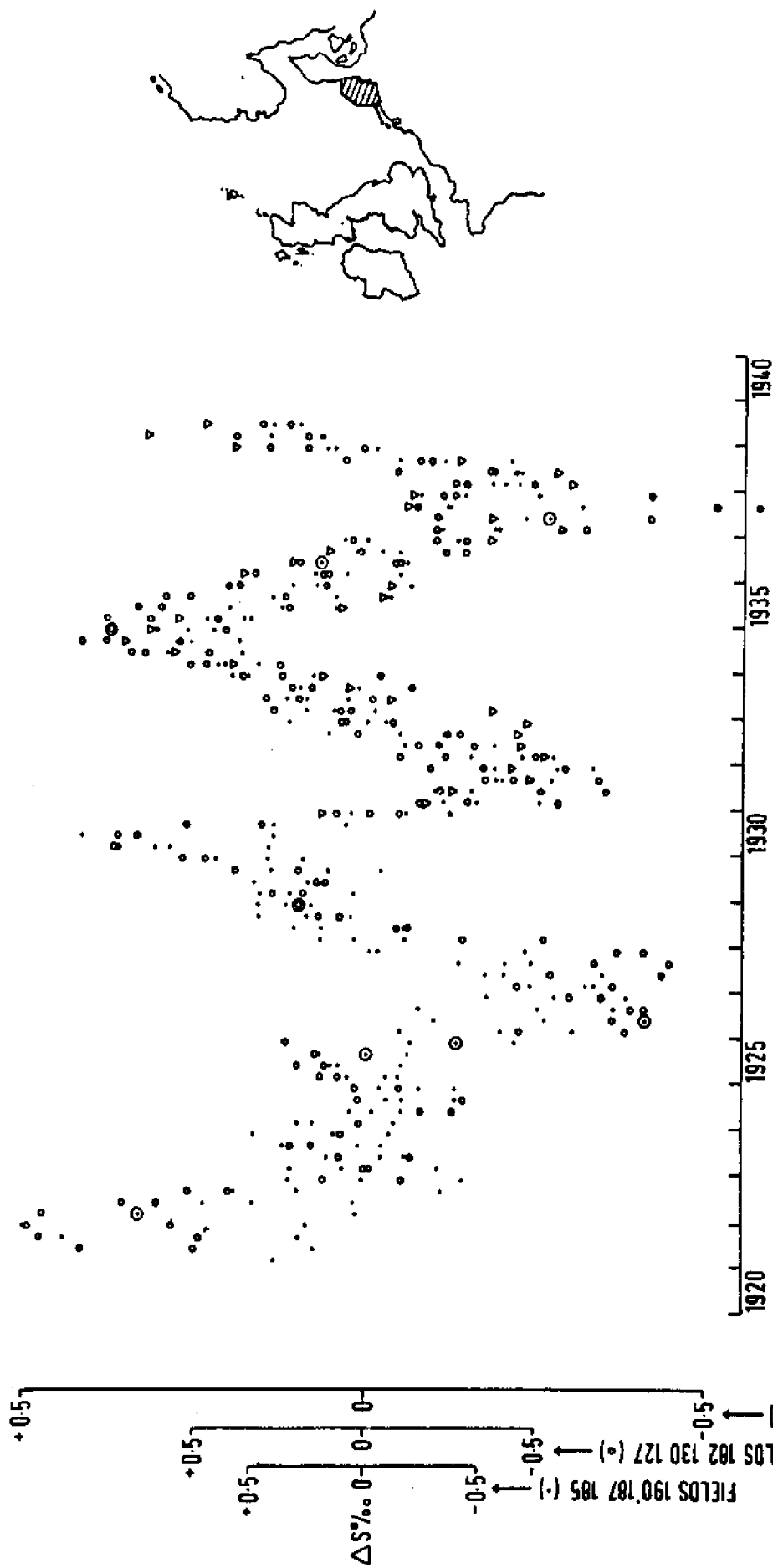


Figure 62-d. Anomalies of surface salinity between 1920 and 1940 in the German Bight of the North Sea (Dickson, 1971).

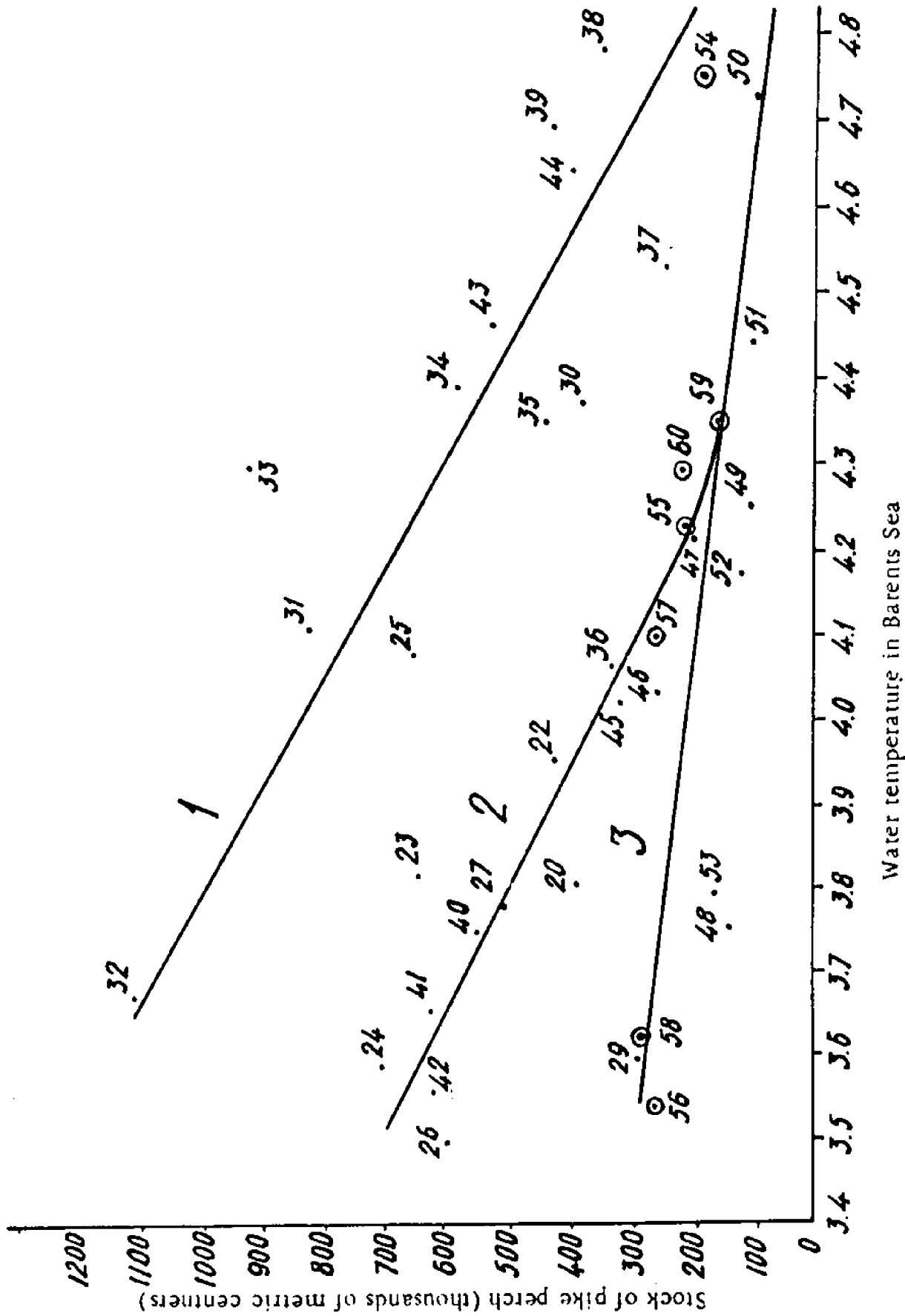


Figure 63. Correlation between catches of the Caspian Sea pike perch and the temperature anomalies on the Kola meridian (Ishevskii, 1964).

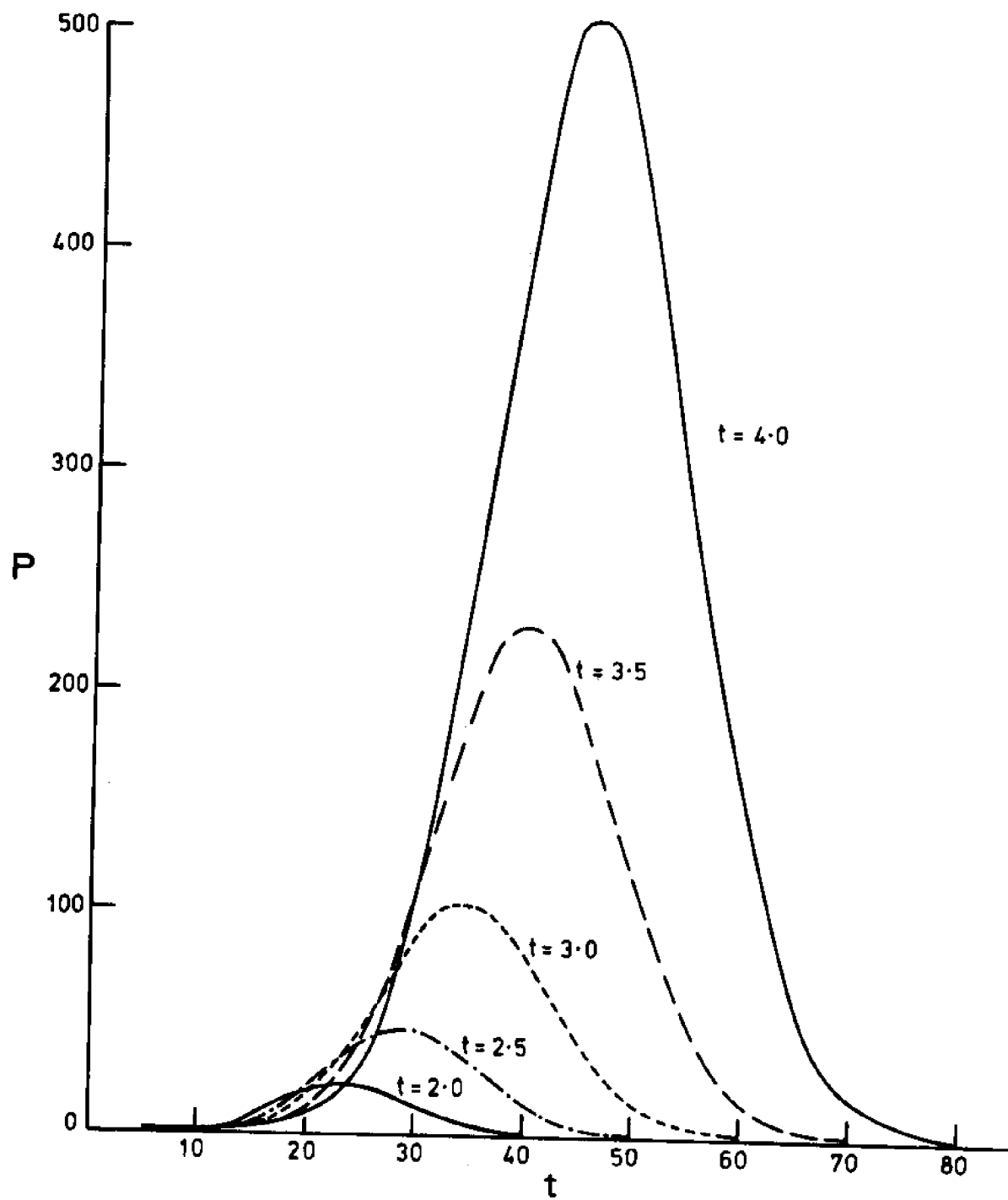


Figure 64. The variation in timing of the production cycle generated by different rates of development of the production ratio.

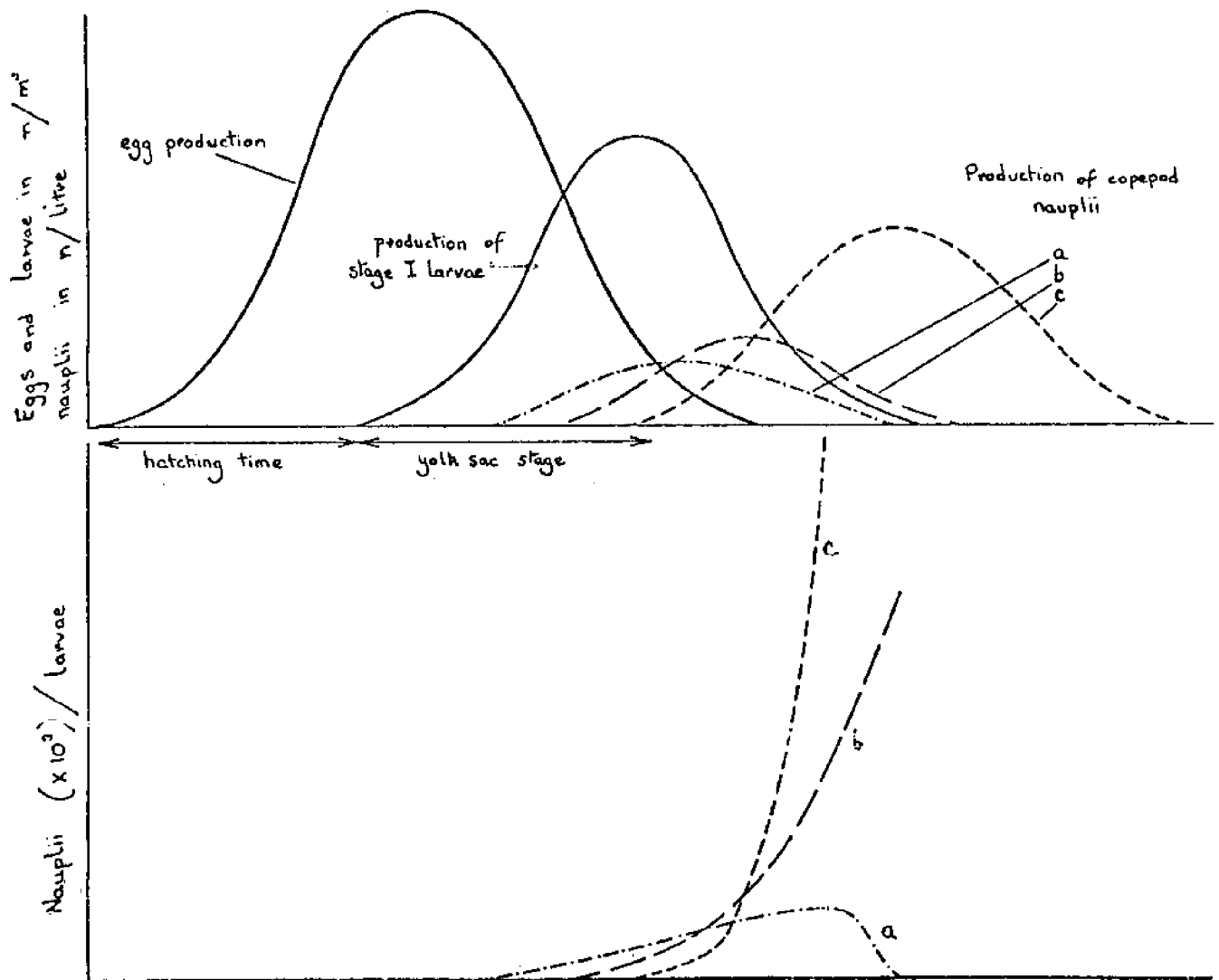


Figure 65. The match or mismatch of the production of fish larvae to that of their food.

Chapter 9

THE SINGLE PROCESS

Introduction

There are three components in the natural regulation of fish populations--the generation of recruitment, the stabilization of numbers, and the competition with other fish species. The stability of a population in numbers represents its capacity to take energy from the environment and insulate itself from physical variability in the world in which it lives. It seems unlikely that any one process could be responsible for such a pervasive phenomenon. It is more probable that stability is the result of a network of processes that operate throughout the life cycle. In this chapter, the whole life cycle will be examined in some detail in order to understand how such processes are interrelated.

Fecundity, Spawning, and the Density of Eggs in the Sea

The number of eggs laid is proportional to the weight of stock, and differences in stock from generation to generation are responsible for the stock-dependent processes, including mortality. With a fixed value of stock, variation in year-class strength is generated by density-dependent processes between hatching and the time of recruitment. Lack's (1954) dictum that the reproductive rate of an animal population was determined by the force of natural selection might suggest that fecundity played no part in stabilization apart from variation in stock. However, if growth were density-dependent throughout adult life, high stock in numbers would produce a reduced number of eggs and vice versa. Such a mechanism might be sufficient to achieve stabilization if density-dependent growth were effective in the older age-groups. But, in general, it is absent in adult animals or at most limited to the younger age-groups. Southward (1967) has described density-dependent growth in the Pacific halibut and found that it was pronounced in the younger age-groups, decreasing with age. Because density-dependent growth seems, at most, to be limited to the immature fish, which are not fecund, its effect can only be to trim major events achieved in other ways. If, however, it is recalled that stock is biomass, it must be generated by both growth and mortality, and density-dependence need not be confined to one of them.

Ricker's formulation of the stock and recruitment relationship requires that the mechanism is only stock-dependent, either by cannibalism or by the aggregation of predators. Such a mechanism accounts for events in the life of the Pacific salmon because cannibal smolts can and do aggregate, but it need not be the essential explanation. In the more general case of marine fishes, it is difficult to see why cannibalism or the aggregation of predators should be restricted to larger fishes, if the index of

density-dependence is really a function of weight or fecundity. The opportunities for cannibalism or the aggregation of predators are equally present in herring and flatfish, but the dome-shaped curve (which would be characteristic of extreme cannibalism) is found only among gadoids. Let us suppose that the gadoid dome is generated by cannibals; then as stock is doubled, recruitment can be halved. If stock is five times the recruitment, one tenth of the stock diet is composed of recruits whatever their age; as codling, the numbers need not be very great, <100/yr per adult, but at lesser ages, the numbers could be enormous. The point whether stock-dependent mortality is alone enough to generate the gadoid dome cannot be decided on these arguments. Harris pointed out that so long as stock- and density-dependent processes can interact between hatching and the age of recruitment, stock-dependence as the aggregation of cannibals or other predators is not needed.

The density of eggs in the sea is a function of stock, if only fractionally. The spawning season of most fish, in temperate waters, lasts for a long time, up to three months. The eggs are laid in sequence during a period of about three weeks or so, because of the need to take up water. For both reasons, the density of eggs in the water must tend to be a fraction of one gonad beneath a square meter. Further, Beverton (1962) published the average egg distributions for the plaice in the southern North Sea from survey cruises from a number of years and it can be shown from his results that the average distance apart of female plaice is 80 m. Hence, in unit volume, there is one contribution from part of one gonad and another from other gonads in the stock, although the relative proportions are probably inaccessible at the present time. The question is raised whether there is a limiting density above which the stock, in all its millions, becomes effective. Or to put the problem another way, the spawning season is so long that it is difficult to imagine how stock-dependent differences are generated.

In the stock recruitment formulation $R = APe^{-BP}$, the constant A is taken to represent density-independent mortality, being the tangent to the curve at zero stock. An alternative explanation is that it represents the density-dependent mortality generated by one fish, as each spawns large numbers of eggs and larvae. In the equation, density is the number in the stock, but in the sea there can be no distinction between the number of larvae produced by one fish and the number produced by more than one. Further, if mortality were in the main density-dependent, as suggested earlier, then density-independent mortality is not needed except as variance to recruitment. Despite the caveats expressed above, stock-dependent effects will be expressed in the initial density of larvae. Then density-dependent ones are expressed in the density of little fish in the sea at any time in the subsequent life history.

Egg and Larval Development

It has already been pointed out that in temperate waters, the production of larvae may be matched or mismatched to that of their food. If fish spawn at fixed seasons, the availability of food is governed by the variability of the production cycle in timing and in amplitude. Because photosynthesis is highly dependent upon light intensity and not very dependent on temperature, the variability of production depends upon that of the production ratio, D_c/D_m . But the development of eggs and larvae is highly dependent on temperature. Since development is an inverse power function of temperature, cold water delays it to a much greater extent than warm water accelerates it. To put it another way, variability in temperature is much more important at the colder end of an animal's range than at the warmer.

Dickson, et al. (in press) has correlated the year-class strength of North Sea cod along two "bateaux routiers" lines in the North Sea for a number of years in each month at a number of positions. The "bateaux routiers" lines are lines of stations at which observations of surface temperature and salinity are taken each month by merchant ships. A spatial correlation for a number of years was obtained for each month of the year. Good year-classes were inversely correlated with temperature in March and April (which is the spawning season) on grounds west and east of the Dogger Bank, where the fish spawn. The correlation coefficients showed trends in time at any one position, indicating that egg and larval development starts before March and continues after April (Figure 66). The spatial and temporal correlations showed the position and timing of the spawning group, which is not well known in any other way. With the use of Apstein's (1909) observations of the rate of development of cod eggs at different temperatures, Dickson was able to estimate the standard deviations of the developmental rate from the variability of temperatures in the North Sea by months for a considerable period of years. In egg development, the variability due to temperature is relatively low, but the effect of cold winters is considerable--as was described earlier for plaice.

The power function of egg development with temperature is probably not very different from that of larvae. It is possible that the extreme variation in egg and larval development is something less than a month. But because the delay to development in cold water is much greater than the acceleration in warm water, the curve of larval production in time can become skewed, being drawn out in time in cold water. The main effect of the slower development is to improve the match of larval production to that of food (Figure 67). Warmer water would accelerate development and reduce the delay, but the range of this effect is small. Further, small differences in temperature must have considerable effects at the cold edge of an animal's range, but at the warm edge the same effects can be achieved only by large differences in temperature. In tropical and subtropical waters, there may be no real differences because development is rapid. In any case in a system of continuous production, there is no need for the larval production to be matched in time to that of their food.

It is known that the production cycle is variable in timing, as described earlier. However, it is rather difficult to establish the degree of variability. At International Station E1 off Plymouth in southwest England, the peak of the production cycle differed by about a month in two successive years (Harvey, 1934; Harvey et al., 1935). Corlett (1953) showed that in three years the timing of the production cycle at *Weather Ships I* and *J* differed by six weeks. Davidson (1934) examined the production cycle for a number of years off Passamaquoddy Bay, New Brunswick, Canada, and found that their timing varied by about two months in five years. From the plankton recorder results, the standard deviation of timing appears to be as low as 10 days, but this may be an artefact--because it differs so much from the few direct observations that exist. It seems possible that the variation in timing may be as much as two months, depending upon the position. The variability, however, is not biased in one direction, but is equally spread. Consequently, the effect of cold winters or indeed of cooler years must be to improve the match of larval production to that of their food.

There may be a general trend in wind direction from westerly to southerly and back again every 110 years in the Northeast Atlantic. Associated with it may be a trend in timing of the production cycle. At the same time the sea temperatures vary, and it is possible that a delay in the production cycle may be accompanied by delayed larval production in cooler water.

The main source of variability in the whole system of recruitment must lie in the availability of food during the larval stages. The physical mechanisms that determine the variability are known and the biological responses can be indicated. However, the variation in timing of the production cycle remains unknown and with it the degree of variability of food.

Feeding and Density-dependent Processes

The interrelation between growth and mortality in larval life was described earlier. An animal that feeds well and swims quickly avoids predation and vice versa. If the number of animals is increased, food has to be shared among the increment in number and so mortality increases. This is true in the comparison between generations in which stock-dependence is predominant, but also in time during the life cycle, in which density predominates. Just as mortality is density-dependent, so must growth be if food is to be shared among varying numbers of fish larvae. In general, mortality rate may decrease with increasing food and growth rate may increase. But at two levels of numbers, $n_2 > n_1$, mortality is higher and growth rate lower in the greater numbers. The relationship is illustrated in Figure 68. The specific mortality rates and growth rates are thus linked directly to the availability of food. Neess and Dugdale (1959) analyzed the Allen curve, in which the numbers of a cohort are plotted on weight in such a way that

age moves to the right from birth on the ordinate to death on the abscissa. The slope of the curve for a particular insect population was shown to be M/K . In ecological terms a fish puts on weight to avoid the chance of death, or the population extracts energy from the trophic level below at the least chance of being transferred itself to one above.

In a food chain, fish grow through the trophic levels and as an individual grows out of one predatory field into another, mortality decreases. Figure 69 shows how growth and mortality might change with time for two populations, $n_2 > n_1$. G and M^* are linked in the same way as in their dependence upon food. Ivlev (1961) has shown that there is a distribution in size of the food that a predator takes. If the prey grows and survives through such a size distribution, its standard deviation can represent in the time scale of the growth of prey, the period of predatory activity. It is short when growth is quick in plenty of food and long under conditions of starvation.

The size distributions of the food of predators must overlap, if the ratio of predator weight to prey weight is constant. The fish grows out of one predatory field into another. As growth decelerates in the life cycle, the period of passage through each succeeding field becomes progressively longer. In this way the average mortality for a fish stock may take the density-dependent function with age that was suggested earlier. In adult life, the degree of density-dependence declines as the specific rates tend towards zero, but the special effect of senescence may also be density-dependent; very old fish may become vulnerable to smaller predators.

Figure 69 shows the trend of growth and mortality with time under conditions of constant food. If the initial numbers are changed in a stock-dependent manner, both growth and mortality are changed. But with constant numbers, the same result can be obtained by changing the food density. If food density supplied to a population n_2 is increased, mortality for a short time period decreases and growth increases as if the trend of mortality had shifted from n_2 to n_1 .

Let us suppose that the augmentation of food persists for a period of time. Then during this period the rates of changes of mortality, in the trends yielding the numbers n_1 and n_2 , are different. At the end of the time period, the food density returns to its original level and then the trend in mortality is a new one, yielding new numbers, n_3 . The effects of this temporary change in food density are: (a) the population responds by increasing growth rate and decreasing mortality and it exploits the food patch in increasing its biomass; and (b) when the food density has been restored to its original value, the relatively higher mortality rate and relatively lower growth rate compensate for the temporary change. Hence, as food is patchy in time and space, there is a continuous oscillation in the density-dependent processes, resulting in high exploitation of food and a continuous fine control of the ultimate recruitment (Figure 70). This is the real distinction between stock-dependent and density-dependent mortality. The first is an initial density that is a function

of the stock achieved by the parent generation. The second is a response to a present density following a period of time: after the increase in food, mortality and numbers reach new values after a period of stabilization.

Environmental Modulation

Fisheries biologists have tended to ascribe much greater importance to density-independent mortality than to density-dependent mortality, because the variance of recruitment is much higher than its component of variance due to stock. If density-dependent mortality were to be considered a general rule, the question arises: How does the environment modify recruitment directly?

Fish may die from a variety of causes--disease, oxygen lack, red tides, the confluence of warm and cold currents, to mention only those which have produced spectacular death rates. Let us suppose that a proportion die from some unnamed effect. Because numbers have been sharply decreased, mortality rate declines and growth rate increases since more food is available to the survivors. Then the density-dependent mortality continues as if at a lower level of numbers. But because death is permanent, there is no feedback in mortality, as there might be with a temporary (as opposed to a permanent) augmentation of food. The effect of such adventitious death is to reduce the numbers transiently, after which density-dependent mortality continues towards a lower level of numbers but with more food to share.

There are two sorts of environmental modulation of importance to developing fishes, adventitious death and variations in the quantity of food. As shown above, N_t is continuously modified by variations in food density contemporaneously with concomitant modifications to growth. The detailed analysis of immature growth in the Downs herring by Iles (1967, 1968) shows how closely the variations in food quantity must be modulated in differences in growth, some of which are density-dependent. It is possible that variations in food density can switch successive values of N_t from low to high and back again. The losses due to adventitious environmental death, however, are not reversible. If it is true that in the life of fishes, density-dependent mortality predominates, it is possible that the range of variation of recruitment in numbers as a proportion of the total loss in numbers from hatching to recruitment estimates the proportion of density-independent mortality.

Stabilization

As Harris has distinguished between stock-dependent and density-dependent processes, we may also distinguish stabilization from generation to generation from stabilization within a year-class. In the virgin stock, the stabilizing mechanism provides relatively more recruits at low stock and relatively fewer at high stock with the result that the stock always returns

to the point of stabilization. The process of stabilization takes place through a number of generations. In view of the continuous response of recruitment to climatic change, a slow upward or downward trend is always possible. Then stabilization is accelerated or decelerated in time. A rapid upward or downward trend is unstable because the mechanism of stabilization does not succeed.

Within a year-class, there is a continuous process based on the availability of food by which N_t is adjusted successively in time. It is the fine control by which recruitment is in the end determined. The variability of recruitment is determined first by the initial stock number, N_0 , and second by the density N_t , continuously adjusted to the availability of food. It recalls Gulland's (1965) coarse and fine control of year-class strength. As cohort succeeds cohort from year to year, each recruitment is stabilized as far as possible in the face of food availability and the stock is stabilized with a number of recruitments. Thus the distinction between the terms "stock-dependent" and "density-dependent" introduced by Harris has acquired biological meaning.

If the fine control depends upon the availability of food, the density-dependent processes cannot start until the larvae start to feed. The level of food must be set by the match or mismatch of larval production to that of their food. Because the densities are highest during the larval drift, the processes are then sharpest and perhaps most critical. Hence, the initial stock-density which is relevant is that of the first feeding larvae. Subsequently, density-dependent processes continue and decrease as a function of age.

There are three processes that are important in the regulation of animal population--the stabilization of stock, the generation of recruitment, and the maintenance of competition. The first two have been discussed in some detail, but the third has been established in evolutionary history. However, competition has been maintained in each generation. Fish larvae are all about the same size and compete for the same foods in rather simple food chains. Highly evolved fishes are often large and fecund with efficient mechanisms of stabilization, which they achieve by gaining weight in the face of death. In the studies of larval fish populations, the maintenance of competition might be expressed as the gain in biomass per death by given size or age groups.

Adult Life

From egg to recruit, the magnitude of year-class strength is determined. During adult life, a population of eggs is spawned each year. The first is concerned with density-dependent processes and the second with starting the stock-dependent ones. It is true that density-dependent processes might be considered as continuing throughout adult life, but they are low. The contrast between juvenile and adult life may be theoretically artificial. However, consider the lonely lives of adult fishes; stabilization has been

achieved, density-dependent processes are low, and competition is least. Food rarely limits the growth of adult fishes and all they have to do is to feed and spawn even if they have to travel hundreds or thousands of miles a year to collect their food. On the other hand, the juveniles grow in the face of death to extract the largest biomass that the food chain will allow.

The Single Process

In the introduction, it was considered unlikely that any single process could be responsible for extracting energy from the food chain and at the same time insulate the population from the physical variability of the sea. However, the distinction made somewhat artificially between juvenile and adult lives corresponds to density- and stock-dependent processes. In an evolutionary sense fish grow big, to spawn and to achieve stability in numbers. Then the stabilization mechanism within a year-class from hatching to recruitment is perhaps the single most important process in the lives of fishes.

The density-dependent processes in the juvenile stage may depend upon the variability in food supply to maintain the continuous adjustment of density-dependence in time. It is the environmental variability that stimulates the single process by which the maximum biomass is extracted from the food chain. Paradoxically, the long-term purpose of this mechanism is to achieve the stability in numbers by which the population insulates itself from the same environmental variability. It is a perpetual mechanism for assessing the variability of food (in the main) and extracting the most energy from it.

Because fisheries biologists have believed that the regulation of numbers occurred during larval life, they have expressed both recruitment and parent stock as numbers of eggs, which is a function of biomass. The essential mechanism, which may be the continuous adjustment of density-dependent processes during larval life, acquires biomass by the detailed interlocking of growth and mortality. Although stability in numbers is obtained in this way, there is a sense in which the mechanism achieves stability in biomass or numbers of eggs.

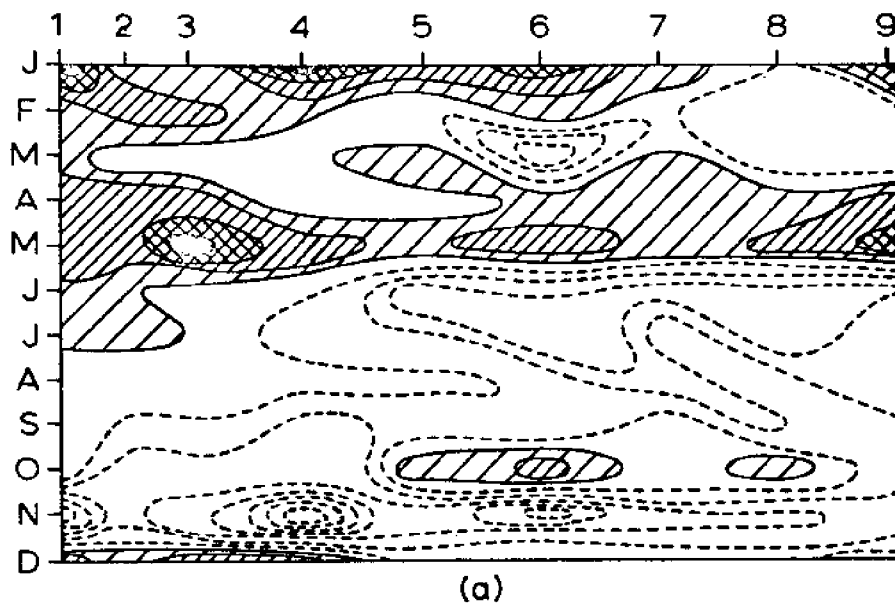


Figure 66. Correlation between temperature and year-classes by stations and months in the North Sea.

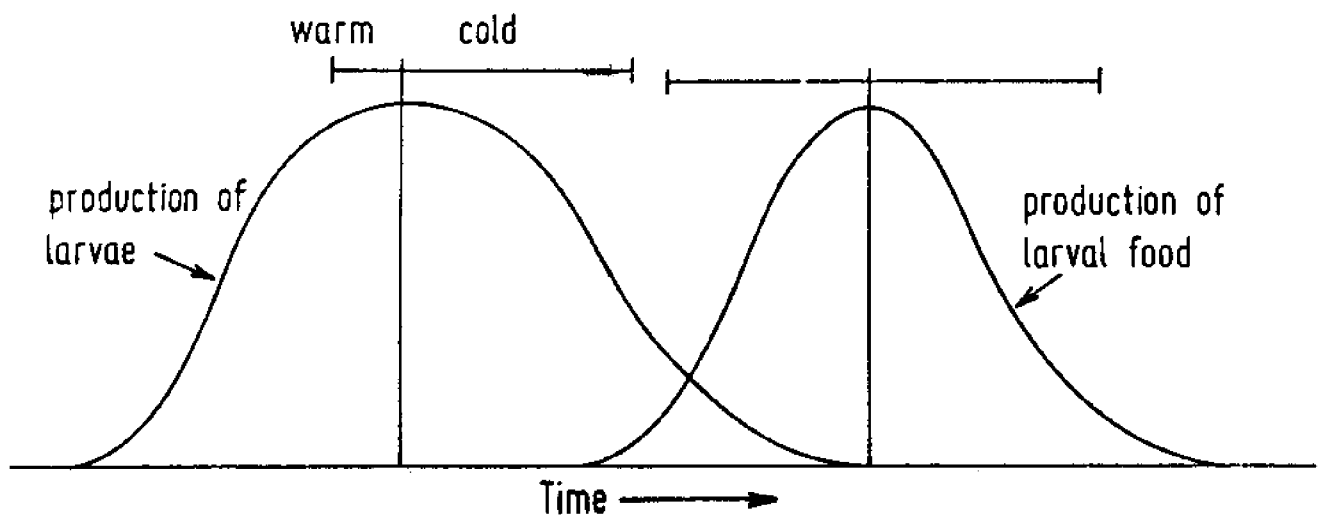


Figure 67. Effects of temperature on the match/mismatch of larval production to that of their food.

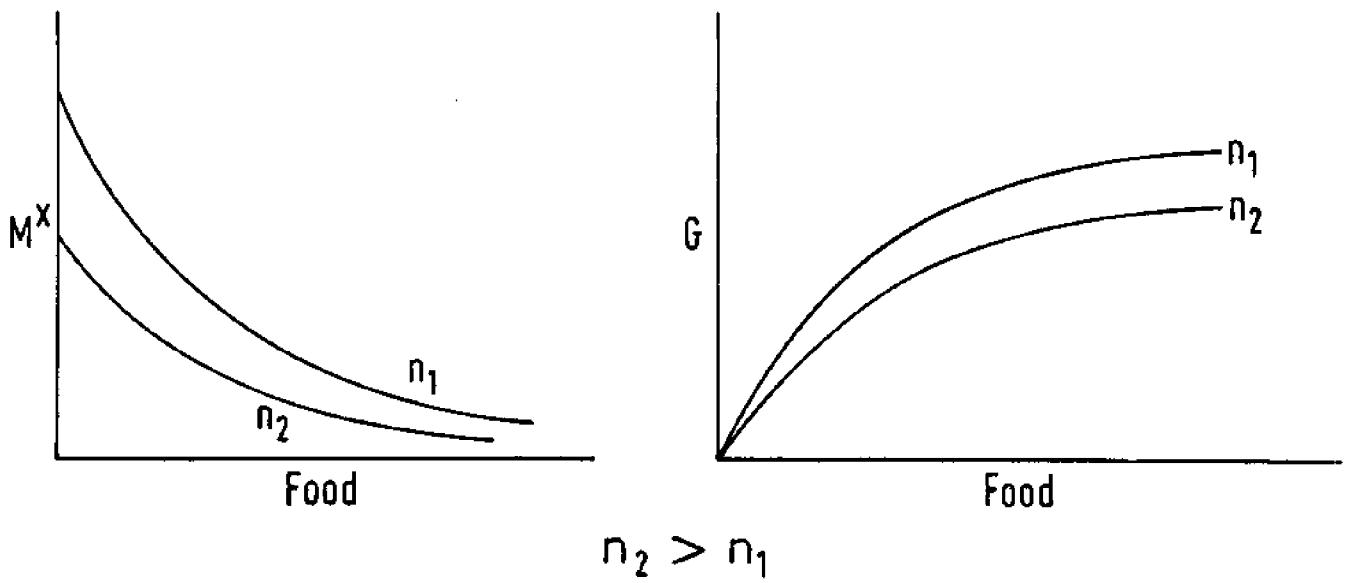


Figure 68. Trend of G and M^* on time for two levels of food.

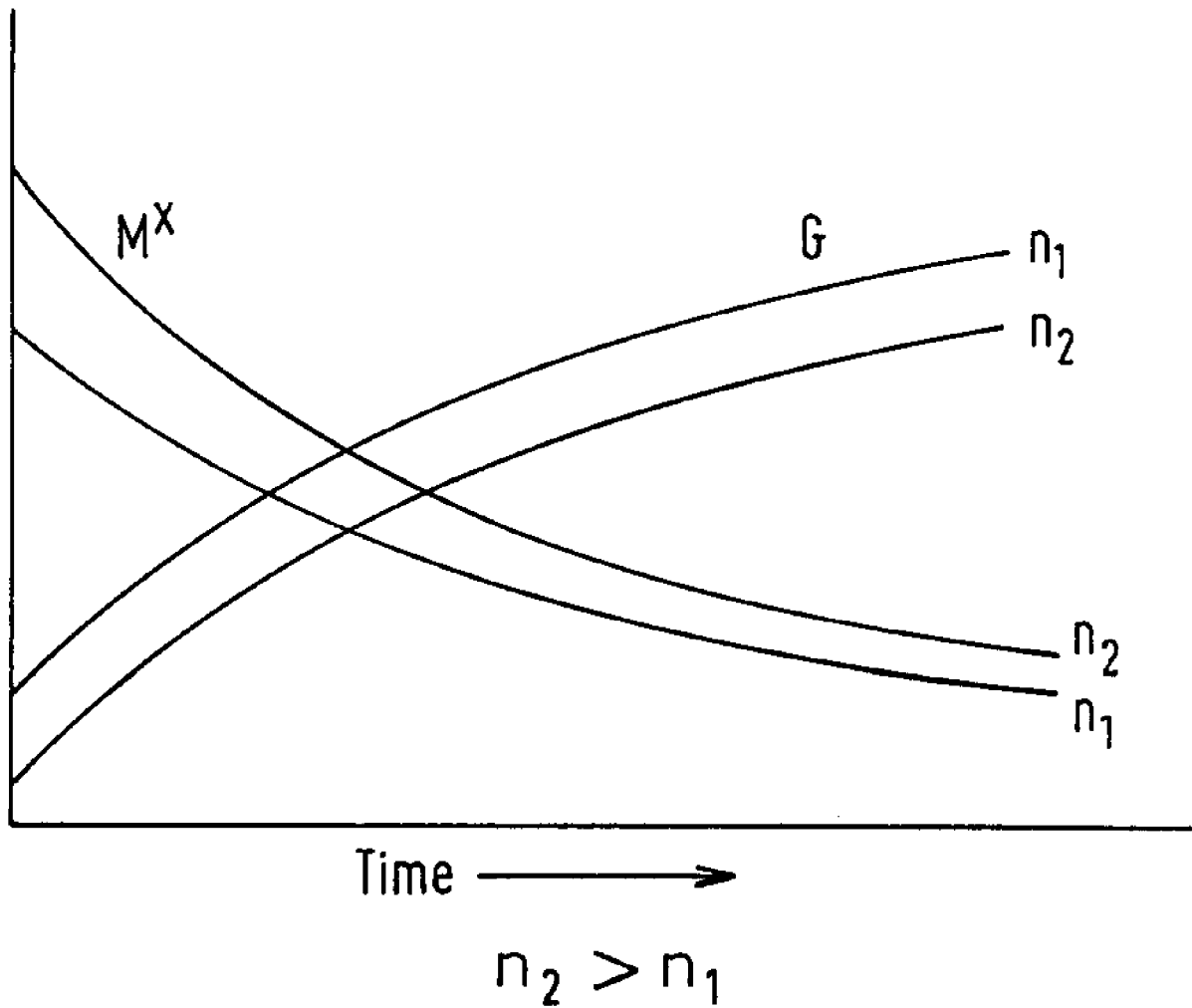


Figure 69. Trend of G and M^* on food for two levels of numbers.

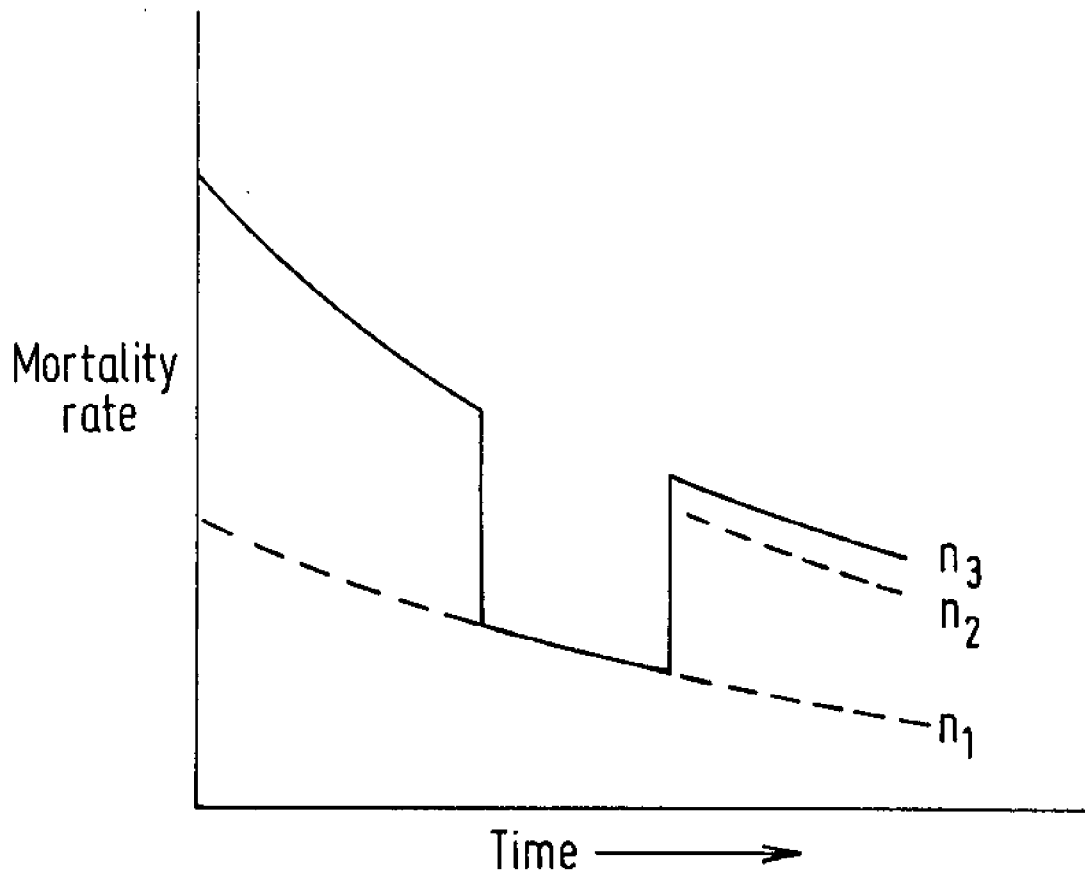


Figure 70. The effect of a change in food availability on mortality rate in time (*See text for explanation*).

Chapter 10

THE PRESENT STATE OF THE STOCK AND RECRUITMENT PROBLEM

Introduction

The purpose of any study in fisheries biology is to improve the quality of management. For some fish stocks, perhaps the minority, management has failed and this failure is a scientific one. This is perhaps because the recruitment mechanisms have not only been poorly understood, but have possibly been oversimplified. As shown earlier, a population of fishes, both within a single cohort and on an evolutionary time scale, exploits a large part of the food web. To simulate the generation of recruitment in a detailed way would require the collection of data on scales of time and space that would be prohibitive. In any case, the problems of management will not wait. Then the complex biological problems must be approximated. This chapter is in two parts--first a summary of the biology of recruitment that represents the overwhelming complexity of the processes, and second an approximate yield curve for multi-age stocks, with recruitment varying with stock.

The Biology of Recruitment

The enormous fecundity of fishes has always impressed students of the struggle for existence that such a wastage of potential life be supported to obtain the survival of the population. If the possible mechanisms described in the previous chapter are true, then the apparent profligacy is not wasted at all, but is part of a very complex mechanisms indeed. If eggs are wasted, they must die by density-independent causes--generated by an array of environmental factors. Hence the direct effects of wind, temperature, and so on upon larval survival have been examined in some detail by fisheries biologists. However, as suggested above, density-dependent mortality may express the real form of environmental modulation.

Fecundity is a function of weight, and the index of density-dependence increases with it. Fish that grow a great deal live long enough to have many age-groups in the stock and so the population fecundity of such fishes is high. Differences in weight for age from generation to generation appear to be small, and so fecundity is nearly always about the same. The population fecundity differs from generation to generation mainly by the strengths of the component year-classes. There are three arguments suggesting that stock expresses itself in the early life of the larvae. First, the initial larval mortality is a function of the population fecundity, that is, it is stock-dependent. In the comparison between groups of fishes, the indices of density-dependence were correlated with the cube root of the fecundity, or the distance between eggs or larvae in the sea. Second, Harris developed the stock/recruitment equation to the form $R = APe^{-BP^{0.33}}$, which again implies that the

density-dependent processes are linked to the distance between larvae. Third, when the larval mortality rate of plaice was used to calculate the trend in mortality, the estimated initial number was low. On the scale that nine gonads should generate two adults, by the age of sixteen, such a value of N_0 corresponds to the age at which the larvae start feeding, which is when the density-dependent processes might be expected to begin. If true, there is then a density-independent loss of numbers during the egg and yolk sac stages. If the density-dependent processes derive from the availability of food, the initial number could not be expected to be effective at a greater age. The initial number is still stock-dependent at that age and, perhaps subsequently, numbers are continuously modified until the age of recruitment.

The mechanism by which mortality becomes a density-dependent function of age should be considered as an average condition. The initial number is the stock-dependent component and the trend of numbers with age is a function only of the initial number and the critical age. The real point here is what assumptions are implicit in the function in age of stock-dependent mortality. Stock-dependent mortality is described in such a way that under average conditions (design conditions, so to speak), the population replaces itself by the critical age in the virgin stock. Despite the fact that the trend of natural mortality with age is successfully described with this formulation, there is a sense in which it is little more than a useful trick; that is, it does not appear to describe that mortality which depends on density as opposed to that which depends on stock save under an average condition. Earlier I referred to the work of Neess and Dugdale (1959), who analyzed the nature of an Allen curve when applied to a single cohort of an insect population: from a plot of $\ln n$ on $\ln wt$, the slope is (M/K) . Weight increases as a function of time, and the life history of the cohort in the Allen curve is represented along the abscissa. Using G and M^* in the plaice, the same linear trend of (M^*/G) can be established on a similar Allen curve. In other words, the trend of growth with age is linked to that of mortality. Here we return to Harris' suggestion that density-dependent growth plays an important part in the determination of recruitment. The initial mortality of larvae can only be stock-dependent, but later the linked processes of growth and mortality may very well be density-dependent in age. Then the expression that has been used as on the average condition may also express in any one cohort the mortality that depends on density.

In the previous chapter on the single process, a density-dependent mechanism was described. Differences in numbers are generated during short time periods, possibly in response to variance in food availability. The model of the dependence of growth and mortality on food was described and it is relevant in that the density-dependence was generated over a time period; in the formulation, it is initially stock-generated, but it is modified during 30 days by the availability of food. In general terms, one might well expect the natural regulation of an animal population to be rooted in the amount of food available. Perhaps the most interesting point to be raised was that the density-dependence might be generated by the variability of food. Ivlev's (1961) well-known experiment on feeding showed that fish obtained more nourishment from patchy food than from evenly distributed food.

If natural mortality were density-dependent throughout life, then regulation is a continuous process. The variability of the food may be said to modulate it in time. Further, the postulated process allows the greatest quantity of energy to be extracted from the food chain at each level as the fishes grow. It has always been recognized that the regulatory function of a population should be intimately dependent upon the carrying capacity of the environment. The continuity of the process means that every variation in food in time and space is exploited. Perhaps the most important point is that the spawning stock each year represents the averaged modulation of the regulatory process by the environment on each cohort. Consequently, the initial numbers in the next generation that contribute the stock-dependent mortality summarize the environmental modulation of all the cohorts in the stock for a long period before the density-dependent processes continue into the next generation.

Hence, the functions of stock-dependent and density-dependent mortality may be distinguished. The density-dependent processes express the detailed and continuous adaptation of numbers to the availability of food, which is the fine control of recruitment. The stock-dependent process damps the variance due to recruitment. The two functions are distinct and in a sense are opposed, the one responsive and the other, conservative.

It was suggested earlier that differences in food availability are in their turn modulated by climatic changes in detail. The process by which the population is regulated is also that which determines the magnitude of recruitment. It is closely dependent upon the climatic factors from which the population becomes insulated from them. An old physiological maxim states that the constancy of internal environment of an animal renders it independent of the external one. Similarly, the stabilization mechanism secures the population from the variability of the external environment. The continuous exploitation of the food chain in time not only ensures the extraction of the maximum energy but also ensures the most efficient exploitation.

In the last decade or so, ecologists have discussed problems of stability and diversity. Each population in any web or chain of food must have some form of stabilization mechanism, perhaps of analogous form to that described here for some fishes. If there are few predators succeeding each other in the life cycle of a cohort, the variance in recruitment to any population must be much greater than if there are many. Or there is less chance to extract energy from the food chain and the populations are less abundant.

If this mechanism is at the root of the fine control of the generation of recruitment, it is in detail a very complicated one. In principle, however, it may be less complex. Obviously a detailed model of the whole process would need very large quantities of information on a routine basis and this would cost too much. To manage a stock taking into account the dependence of recruitment upon it, a provisional model is needed. However incomplete, it may suffice for our present purpose, because some form of solution is urgently needed.

A Provisional Yield Curve Incorporating the Dependence of
Recruitment on Parent Stock

When Ricker faced the problem of a multi-age stock, he wrote (1958) that if recruitment should be expressed as the sum of numbers throughout the cohort less the total natural mortality, then the problem is reduced to that of the single-aged stock. But it requires that natural mortality be estimated independently; any mortality approximation leads to a wrong estimate of the virgin stock and hence a bias on the yield curve, at low values of fishing mortality (where indeed it might not matter much). It is possible that replacement in a multi-age stock should be regarded a little differently. Any one recruitment is usually a rather small fraction of the unexploited stock. In the year of recruitment, the gain in numbers by recruitment is balanced by the loss in deaths. The gains and losses are averaged throughout the life span, which represents replacement but is being modified in time continuously. Although stock must be replaced by recruitment, the concept of a replacement stock, in Ricker's sense, is perhaps not needed in a multi-age stock.

It would be idle to suppose that the values of specific annual mortality (M^*) at successive ages represent more than average values for any stock and that there may be variations between species due to a variety of conditions. However, in the plaice, at least, there is some evidence that the natural mortality across a number of age-groups is well represented. Given P , R , F , and the trend of natural mortality with age, the stock in age can be reconstituted and compared with the initial value from the stock/recruitment curve itself, appropriate to the value of recruitment used. The number of fish at four years of age is given by $R/(W_t \cdot \phi)$, where R is in eggs/100 hours fishing, W_t is the mean weight at age of four-year-old female plaice, and ϕ is the fecundity constant (143.92 eggs/g in the plaice; Simpson, 1951). N_t is then calculated for each age from $N_{t+1} = N_t e^{-(F+M^*)}$ etc. The stock densities in numbers at each age are raised by the weight at age to give biomass as kg/100 hours fishing at each age. They are summed from ages 4 to 21 to give P for that value of F . The reconstituted value of stock only corresponds with the initial value (from the stock/recruitment curve corresponding to R) if F is correctly estimated. At the present time, most values of F are obtained from $Z-M$, with M constant with age; the reconstituted value of stock can only rarely equal the initial one.

$$\text{Let } N_1 = N_0 e^{-(F + M_1)}$$

$$\therefore \quad dN_1/dF = -N_1 e^{-(F + M_1)} = -N_1$$

$$N_2 = N_1 e^{-(F + M_2)}$$

$$\therefore \frac{dN_2}{dF} = N_1 \frac{d(e^{-(F + M_2)})}{dF} + \frac{dN_1}{dF} e^{-(F + M_2)}$$

$$\therefore = -N_1 e^{-(F + M_2)} - N_1 e^{-(F + M_1)} = -2N_2$$

$$N_3 = N_2 e^{-(F + M_3)}$$

$$\therefore \frac{dN_3}{dF} = -N_2 e^{-(F + M_2)} - 2N_2 e^{-(F + M_3)}$$

$$- 3N_2 e^{-(F + M_3)} = -3N_3$$

The biomasses at age were multiplied by 0, 1, 2 ... 18 from ages 4 to 21, summed and raised by the fecundity coefficient to give dP/dF .

$$\text{Then } F_1 = F_0 - \frac{(P_0 - P_1)}{dP/dF}$$

(This use of Newton's method was carried out for me by my colleague J. G. K. Harris.) By iteration, a true value of F for each stock value was obtained. The catch in numbers from one age to the next was taken from $F/Z (N_0 - N_1)$ [or $qf/Z (N_0 - N_1)$] and Y_n was raised by the average weight during the year to give catch in weight. In this way, a yield curve in numbers or in weight was constructed from the stock recruitment curve.

Figure 71-a shows the stock and recruitment curve for the southern North Sea plaice based on catches/100 hours fishing in kg by age-groups between 1929 and 1970. The value of the virgin stock is shown and it was calculated using the above method, when $F = 0$. Figure 71-b shows the yield curve in weight calculated in this way, with a maximum at $F = 0.2$. Figure 71-c shows the same curve and the yield per recruit curve, in values relative to the maximum. The yield per recruit curve was calculated first with $M = 0.1$ and second with the density-dependent values calculated from equation 8. Thus for the plaice, the maximum of the yield curve differs little from the yield per recruit curve; however the reduction in yield beyond the maximum is sharper, which indicates that it should not be exceeded. If this model is compared with one using a constant mortality in age, two general biases should be considered. First,

from the age of maturation to the critical age, the mean age in M^* is less than the median, so $F^* < F$ by a constant but small quantity. Second, because M^* decreases with age, the exploitation ratio (F^*/Z) increases with age and catches from older age-groups form a relatively greater part of the total than if M were considered constant. This bias is low, but F^* generates about 5% more catch than F . The yield curve for plaice (Figure 71-b) suffers from a particular form of bias because length for age has increased during the period of examination. A constant weight for age has in fact been used, so the reconstituted biomass is less than it should be and F is underestimated. When such a growth change takes place, each point should be calculated with the appropriate weight for age if F is to be correctly estimated. Unfortunately this cannot be attempted until the nature of the change in length for age is understood.

Figure 72-a shows the stock/recruitment curve for Arcto-Norwegian cod and Figure 72-b shows yield curves calculated in the same way for the Arcto-Norwegian cod. Because the variance of recruitment in this stock is not very different from that of the plaice, the same senescence function has been used; as noted above, if these values are incorrect the yield curve becomes slightly biased at very low values of fishing mortality, but the position of the maximum is not displaced. Both curves differ considerably from the corresponding yield per recruit curves.

There are three important characteristics of the yield curve calculated in this way: (a) at rates of exploitation less than Ricker's limiting value, the condition of population stability is fulfilled; (b) the curve could be fitted to total catch data in much the same way as is the Schaefer curve; (c) estimates of fishing mortality are free from bias within the limits imposed by the estimate of natural mortality and the stock/recruitment curve. The main disadvantage to the method is that it includes the variability inherent in the stock and recruitment curve; although the variability of recruitment can be very high, the variability of the curve itself is often not too great as noted in an earlier chapter.

Conclusion

An indication of the essential processes in the natural regulation of a fish stock has been given. A provisional yield curve has been developed. It must be obvious that much depends on the interpretation of the course of natural mortality with age. There are many general reasons that have been cited for supporting the interpretation, but only for the southern North Sea plaice is there any concrete evidence.

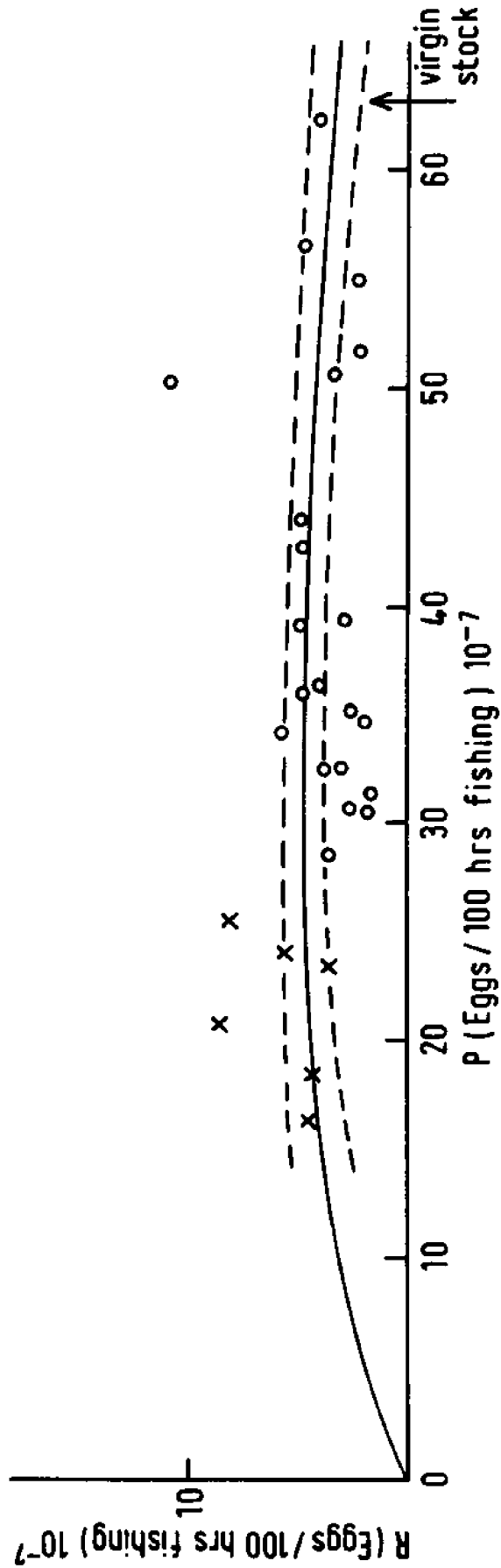


Figure 71-a. The stock recruitment curve for the southern North Sea plaice. The dotted lines indicate the 95% confidence limit to the curve. Crosses show prewar observations and the circles postwar ones.

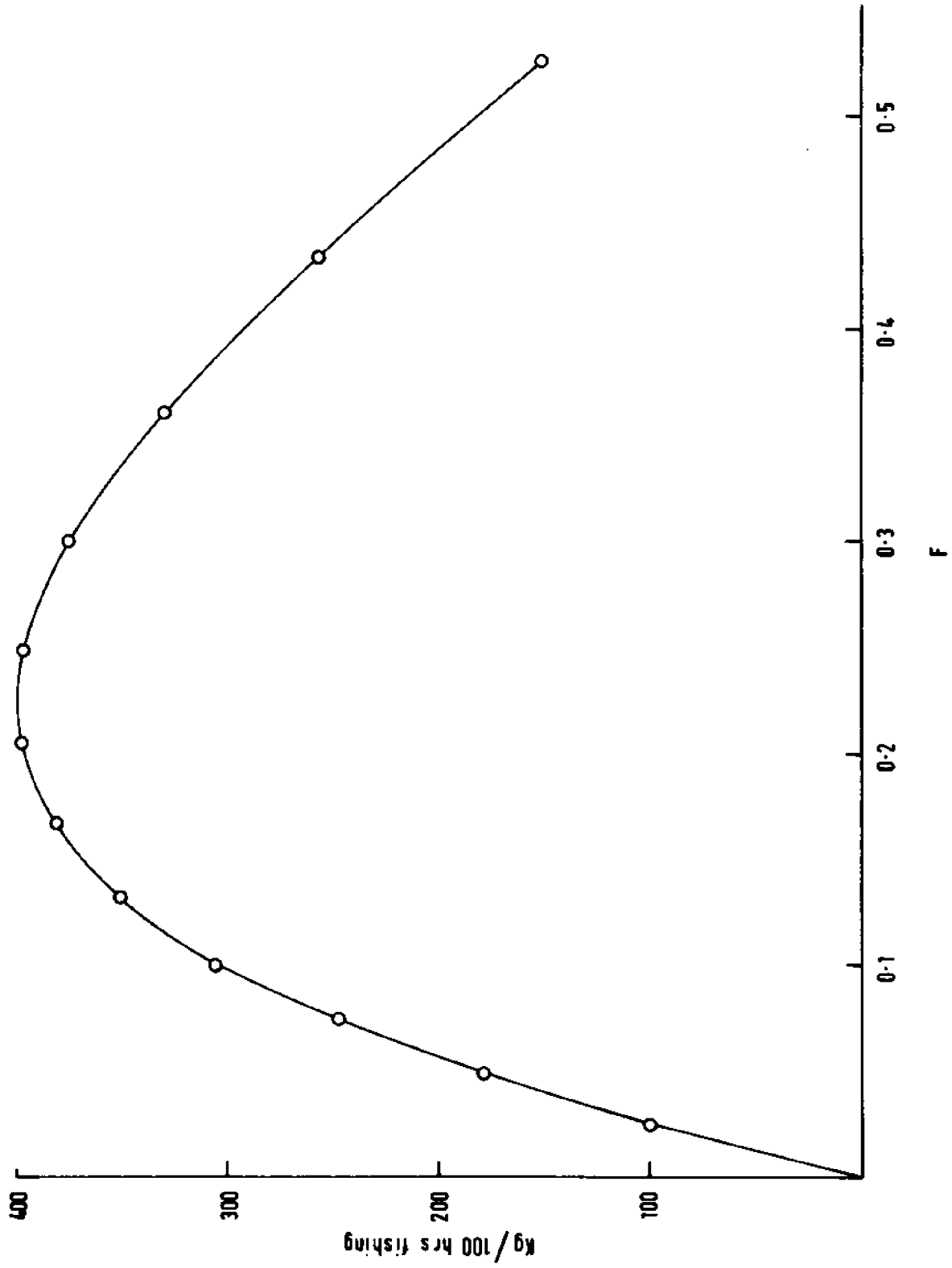


Figure 71-b. Yield curve for plaice.

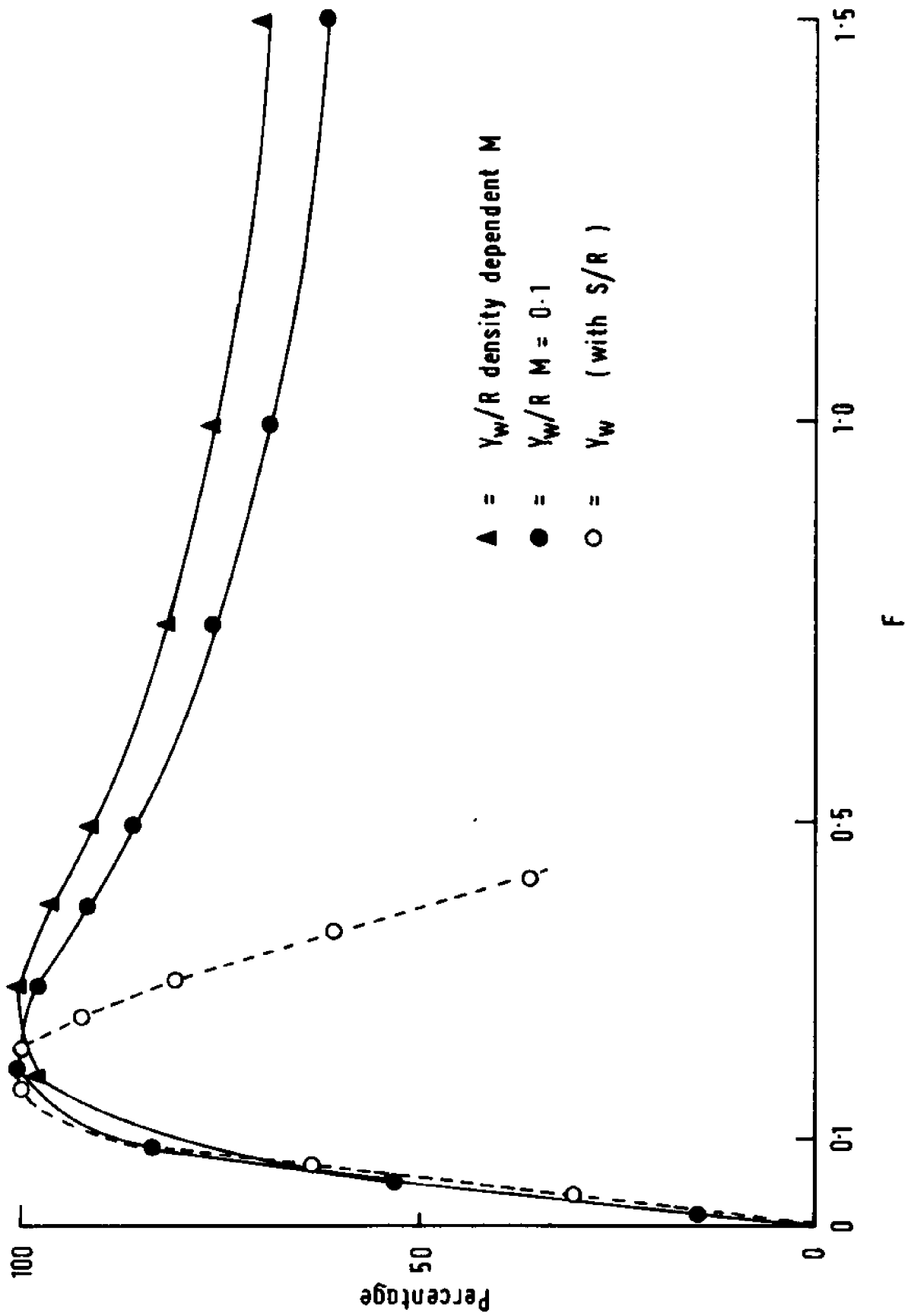


Figure 71-c. Yield curve for plaice compared with the yield per recruit curve (which is also calculated for density-dependent natural mortality).

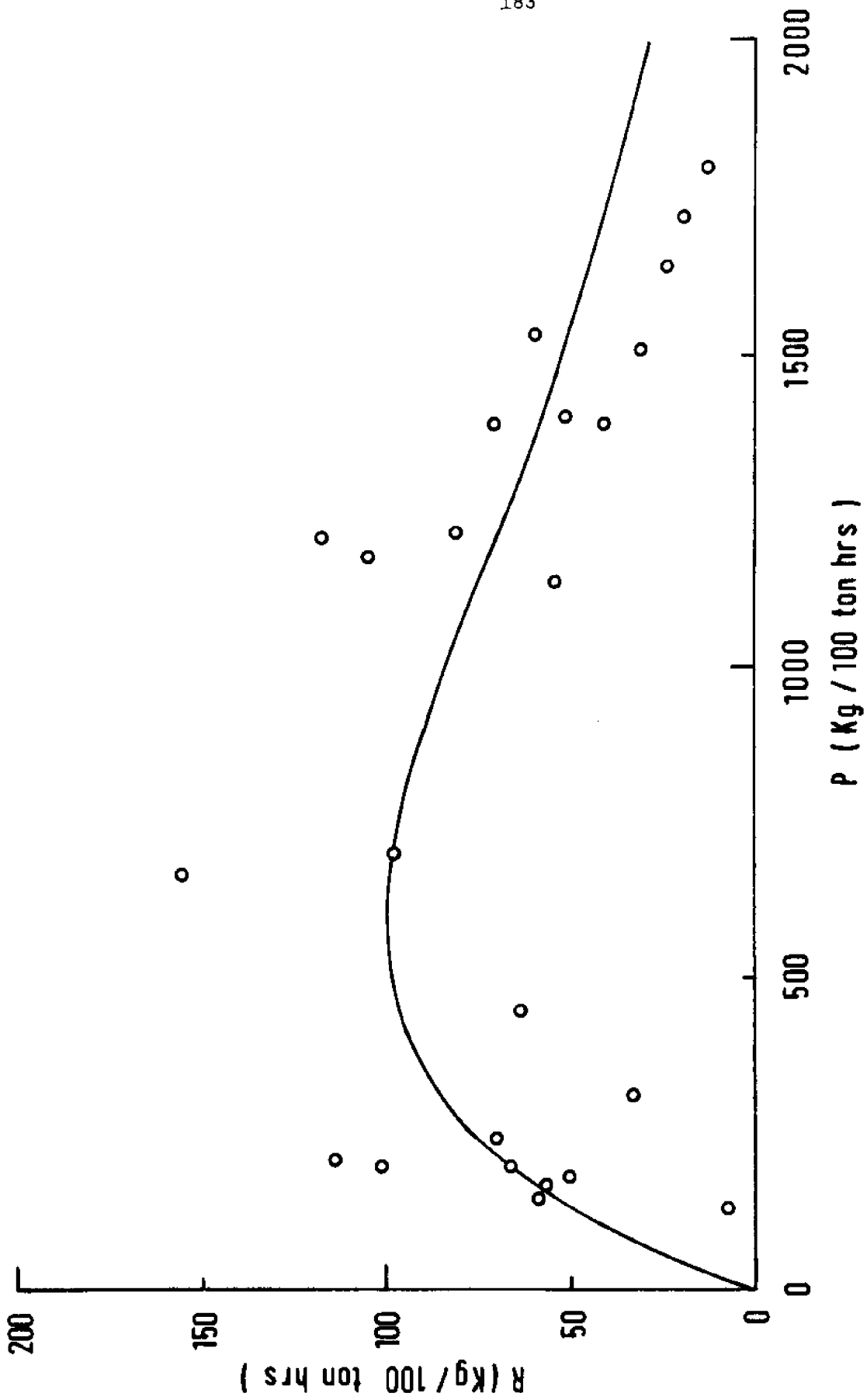


Figure 72-a. Stock recruitment curve for the Arctic cod.

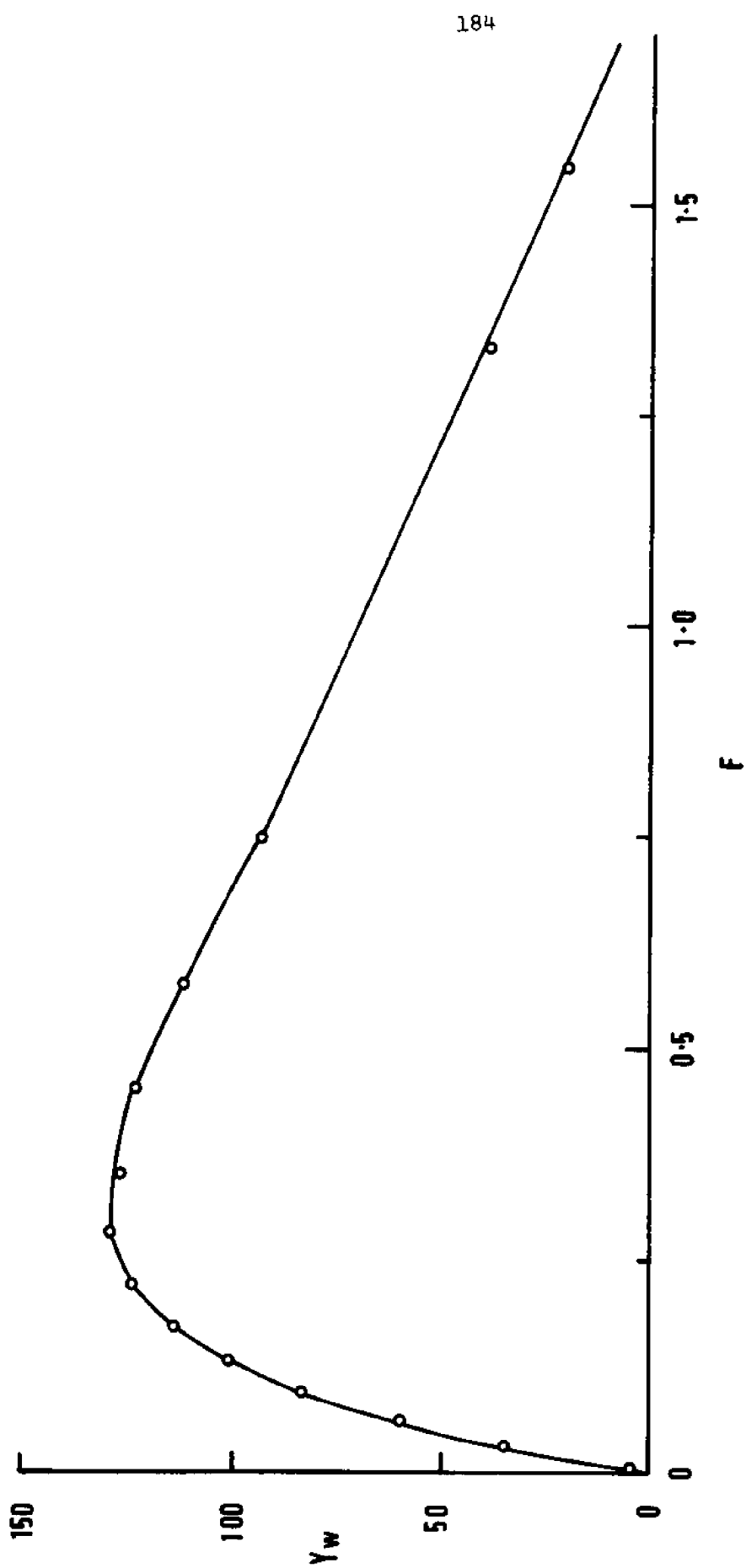


Figure 72-b. Yield curve for the Arctic cod.

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