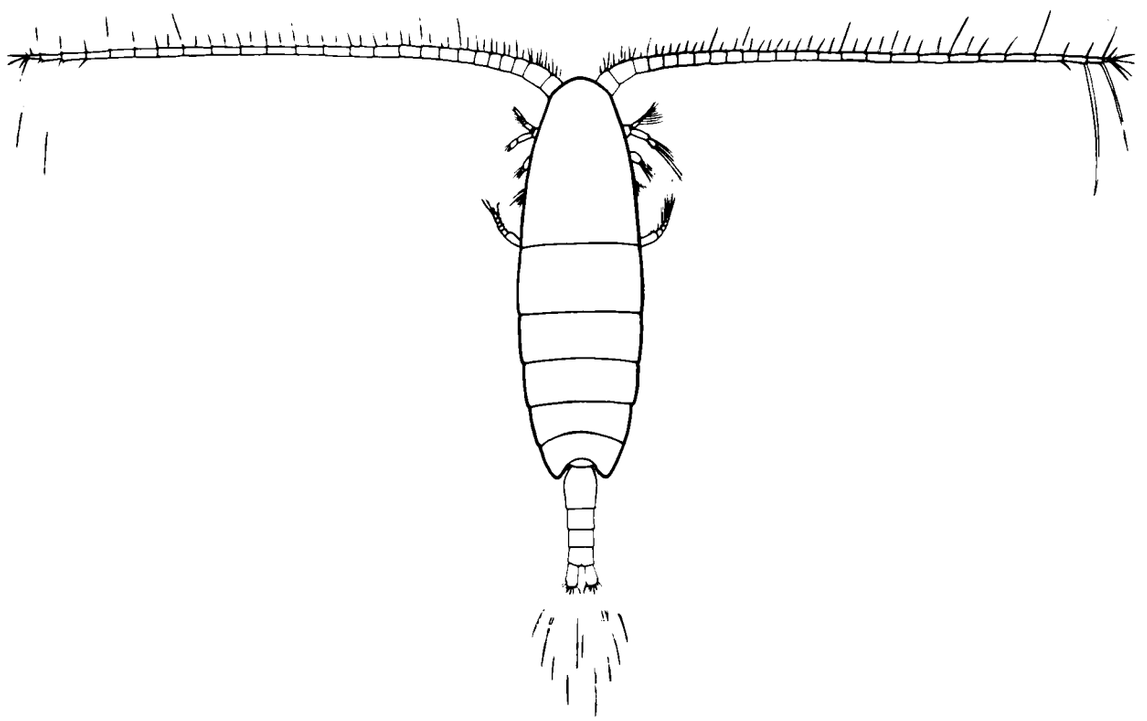


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INVESTIGATIONS ON THE SYSTEMATICS AND ECOLOGY OF *CALANUS FINMARCHICUS* S.L. (CRUSTACEA, COPEPODA)

By

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CONTENTS

Abstract i

Acknowledgements viii

General Introduction 1

Historical 1

Taxonomy and general morphology 3

The Continuous Plankton Recorder 6

The NORWESTLANT Surveys 12

The present investigations 13

PART I. ON THE SYSTEMATICS OF CALANUS FINMARCHICUS S.L.

Biometric investigations on Calanus finmarchicus s.l. 15

Introduction 15

Methods 17

Comparison of Calanus finmarchicus s.str. and C. glacialis . 18

Comparison of Calanus finmarchicus s.str. and C. helgolandicus 22

Mixed sample 22

Geographical variation 24

Conclusions 27

Experimental investigations on Calanus finmarchicus s.str. . . 29

Introduction 29

Material and methods 29

Results 32

Size variations 32

Morphological variations 36

Conclusions 38

General discussion 42

PART II. ON THE ECOLOGY OF CALANUS FINMARCHICUS S.L.

Some comparisons between Calanus f. finmarchicus and other copepods in the Atlantic Ocean south-east of Greenland 50

Introduction 50

Material and methods 51

Results 53

Systematic account 53

Temperature and depth groupings 59

Discussion 61

The distribution of Calanus finmarchicus s.l. in the North Atlantic and North Sea 65

Introduction 65

Material 66

Results 66

Total distribution 66

Seasonal distribution 68

Timing of seasonal fluctuations in abundance . . . 75

Conclusions 79

Calanus finmarchicus on the continental shelf between Newfoundland and the Gulf of Maine 83

Introduction 83

Material and methods 84

Results 85

Seasonal changes in population composition 85

Seasonal variations in size 86

Calanus biomass and the phytoplankton 88

Occurrence of *Calanus f. glacialis* 89

Conclusions 89

The spring generation of *Calanus f. finmarchicus* in the waters around Greenland 93

Introduction 93

Material and methods 95

Results 96

Geographical pattern 96

Association with temperature 98

Discussion 100

Concluding discussion 106

Bibliography 111

ABSTRACT

Calanus finmarchicus sensu lato belongs in the order Copepoda of the class Crustacea. It is probably the most widespread marine copepod, being found throughout the world in all but the tropical seas. Over much of its distribution it is the dominant member of the zooplankton and is an essential part of the food web on which many economically important fish depend. An understanding of its ecology will play a fundamental part in the scientific management of fisheries. The aim of the thesis is to attempt an understanding of certain aspects of this vast subject. The scope of the thesis has been broadened, paradoxically perhaps, by previous work which has produced various opinions on the systematic status of populations in different water masses. It has been necessary, therefore, to define the main populations in systematic terms and then to use these definitions in a number of ecological studies.

The scientific history of Calanus finmarchicus s.l. began two hundred years ago with its discovery and description, as Monoculus finmarchicus, by Gunnerus. Today it has been suggested that it should be regarded as a complex of seven species, each characteristic of different water masses. Three of these, C. finmarchicus, sensu stricto, C. glacialis and C. helgolandicus are known from the North Atlantic and they form the subject of the present investigations. Morphological separation of these species is based mainly on the structure of the fifth (last) pair of limbs; in adult females and stage V copepodids the shape of the inner border of the coxopodite and the size of the teeth on this border

are the main characters. In C. finmarchicus the teeth are small and the border approximately straight; C. glacialis, which is larger than the other two, also has small teeth on a concave border; and C. helgolandicus has larger teeth on a strongly concave border. Adult males are distinguished mainly by different proportional lengths of the rami of this pair of limbs.

The material for the investigations has come for the most part from samples obtained by the Continuous Plankton Recorder in the course of the Survey of the North Atlantic and North Sea conducted from the Oceanographic Laboratory, Edinburgh; these samples have all been taken at a depth of 10 m. Some experimental work was carried out at the Marine Station, Millport, in the Firth of Clyde, and net samples obtained during the International NORWESTLANT Surveys of 1963 have formed the basis for two ecological studies.

Mixed samples formed the basis for the comparisons of C. finmarchicus with C. glacialis and C. helgolandicus. The routine analysis conducted by the staff of the Oceanographic Laboratory provided the information on occurrence necessary for the selection of samples. Measurements were taken of metasome length and of all features of the fifth limbs mentioned in previous descriptions; the most important of these was the curvature of the toothed border, but the number and size of teeth and the presence or absence of an extra seta on the endopodite were included as well. These characters were all considered in relation to metasome length and, in the case of curvature of the toothed border, an angular measure was

devised which also took account of size. The results showed that there was little difference in length between C. finmarchicus and C. helgolandicus, the mean for the latter being slightly greater; values for tooth size also overlapped but there was complete separation between the two on the basis of curvature. This separation held good when measurements were made of over a thousand specimens from a wide range of different positions in the North Atlantic and North Sea. The mixed sample of C. finmarchicus and C. glacialis showed a bimodal length frequency but continuity of all morphological characters, including curvature, in relation to length. The experimental investigations demonstrated inverse relationships between length and temperature and between concavity and temperature. The individuals in the experiment thus tended at low temperatures towards features characteristic of C. glacialis. These results are considered, on the one hand, to support the specific separation of C. finmarchicus from C. helgolandicus, as is now widely accepted, but, on the other, to indicate that the apparent differences between C. finmarchicus and C. glacialis are the result of scarcity of specimens of intermediate size and that the characters are affected by temperature. The scarcity of individuals of intermediate size is considered to be explicable in terms of the comparatively small quantities of stable sub-Arctic water compared with the North Atlantic and the Arctic. Since recent authors have shown C. glacialis to be zoogeographically distinct from C. finmarchicus, it is proposed to

retain the former as a subspecies of C. finmarchicus.

In introducing the ecological studies, results are presented which were obtained from a series of plankton samples taken during the NORWEST-LANT Surveys. These demonstrate above all the dominance of Calanus f. finmarchicus among the herbivorous copepods in the region south-west of Greenland. In addition to C. f. finmarchicus and C. f. glacialis, ten species of larger copepods (greater than 3 mm in body length) were obtained and the distribution and abundance of each is recorded. The occurrence of each species is analysed further in relation to sea temperature and depth in a way which enabled them to be classified as warm, intermediate or cold water and as slope, intermediate or oceanic species. It is suggested that the temperature characteristics of C. f. finmarchicus indicate that the sampled population is relatively stenothermic.

The primary aim of the Continuous Plankton Recorder Survey is zoogeographical and the abundance of Calanus finmarchicus s.l. makes it an ideal subject for distributional studies even in the areas to have come most recently within the Survey. Charts of distribution show that C. f. glacialis occurs only in those areas influenced by an outflow from the Arctic, i.e. the Labrador and Greenland coastal currents; that C. f. finmarchicus is found throughout the Survey area except for the extreme south-east and is most abundant in the colder oceanic regions of the North Atlantic; and that C. helgolandicus is a more southerly form which is most common in the south-east of the Survey area and in the

waters of the Gulf Stream System. Low numbers of each form are generally found during the winter months. In spring, C. f. glacialis is the first to increase in numbers near the surface, starting in the regions most strongly affected by the Labrador Current and later in the more mixed waters south of the Newfoundland Grand Banks. C. f. finmarchicus is next to increase, first in the southern coastal areas and later further north and out into the open ocean. C. helgolandicus is last to increase in numbers, starting in the south and becoming progressively later towards the north. Where they overlap, C. f. finmarchicus is the spring-summer form, C. helgolandicus the summer-autumn one. Seasonal fluctuations in numbers are, with a few exceptions, closely similar throughout the Survey area. The most notable exception concerns C. f. finmarchicus on the Grand Banks where the cycle is a complete inversion of the typical pattern.

The Continuous Plankton Recorder provides samples which can also be used in a detailed investigation of the ecology of abundant epiplanktonic species in a part of the Survey area. In the present study the annual cycle of C. f. finmarchicus on the continental shelf between Newfoundland and the Gulf of Maine has been investigated, as well as some aspects of the relationships with temperature and phytoplankton. There are two main generations in the year, in spring and summer, and a suggestion of a third one in the autumn. Timing was a little earlier in the vicinity of the Gulf of Maine than further to the north-east.

Copepodids showed clearer relationships with environmental conditions than did adults, presumably because they had had less time to encounter and be affected by different conditions. An inverse relationship was apparent between metasome length of stage V and sea surface temperature two months previously. Fluctuations in the estimated biomass of younger copepodids (stages I - IV) closely followed those of estimates of the total phytoplankton at all times of year except the spring; in the four months from March to June the increase in phytoplankton was at first greatly in excess of that of young Calanus, to be followed two months later by signs of overgrazing before the balance was achieved again in July. It is suggested that the total biomass of Calanus did not fluctuate greatly through the year; stocks increased steadily during spring and summer and became depleted just as steadily during late autumn and winter.

Hensen net samples taken in April, June and July, 1963, during the NORWESTLANT Surveys, formed the basis for an investigation of the speed and geographical pattern of development of C. f. finmarchicus in the waters around Greenland. The spring generation, the only important one in the year, began almost simultaneously throughout the area. It is suggested that light, rather than temperature, was associated with maturation of the population. Thereafter the speed of development varied from region to region, so that in July the generation was most advanced in the open Atlantic and southern Labrador Sea, less advanced further north and in shallower water. A temperature effect was apparent in this

pattern. It was possible to define three regions within the Survey area, namely the Labrador Sea and Baffin Bay, the Irminger Sea south to the Reykjanes Ridge, and the open Atlantic south-east of the Ridge. The relationships between sea temperature and the speed of development of Calanus in each region differed in such a way that, for a given temperature, development was fastest in the Labrador Sea and slowest in the open Atlantic. This is taken to indicate acclimatisation of the populations in each of the three regions. It is suggested that in this way populations of Calanus f. finmarchicus can complete a generation during the summer months, both in the cold water of the Labrador Sea and in water, some 8 - 11^{o}C warmer, in the open Atlantic.

In conclusion, the importance of the population as the basic unit in ecological investigations is emphasised. A high degree of ecotypic adaptation of populations is suggested as the means whereby Calanus finmarchicus s.l. has become widely distributed and reached high levels of abundance. Prominence must be given, therefore, to the identification of such populations in future studies. The vitality and adaptability of this copepod remain to be explained in terms of a wide range of biological disciplines.

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My thanks are due to Mr R.S. Glover, Director of the Oceanographic Laboratory, for suggesting that I work on *Calanus*, an important animal of the plankton, for supervising the investigations and for offering critical and helpful advice. I have discussed the problem with many members of the staff at the laboratory, in particular with Dr L.T. Jones, Dr J.M. Colebrook, who introduced me to many statistical techniques and helped me to apply them, Mr G.A. Robinson and Dr G.A. Yarranton. Mr J. Roskell and Mr D.H. Jones have given valuable help in the reproduction of the figures. The Survey conducted with the Continuous Plankton Recorder, on which so much of this study depends, requires much team-work for effective operation; I am indebted to those who prepare the Recorders, to those who tow them at sea and to all members of staff at the laboratory for their part in the routine analysis which provides the essential data. The experimental work was carried out at the Marine Station, Millport, by kind permission of the former Director, Dr C.H. Mortimer, F.R.S. Then and later I have benefitted greatly from the advice of Dr S.M. Marshall, O.B.E., F.R.S. Mr V. Bainbridge kindly made available to me the data from the NORWESTLANT Surveys.

The extension of the Recorder survey into the north-west Atlantic, which has proved so important an area in the present investigations, has been aided by Contracts N62558-2834 and N62558-3612 between the Office of Naval Research, Department of the United States Navy and the Scottish Marine Biological Association.

The work was carried out whilst I was a member of the staff of the Oceanographic Laboratory, Edinburgh, and was supported by grants from H.M. Treasury through the Development Commission, succeeded in 1965 by the Natural Environment Research Council.

I wish to record my sincere thanks to Sir Alister Hardy, F.R.S., for his active interest in this work and his encouragement, which have played a large part in bringing about the presentation of this thesis.

GENERAL INTRODUCTION

HISTORICAL

Calanus finmarchicus (Gunnerus) was the first free-living copepod to be described and the two hundredth anniversary of its discovery in Hammerfest, Norway, occurs this year. In 1770 the Bishop of Trondheim described it as Monoculus finmarchicus, sufficiently accurately for there to be no doubt of the identity of the species he had in front of him. For the next century there was considerable difficulty with its name until Giesbrecht (1892) reviewed the nomenclature carefully. Since then the nomenclatural problem has given way to the systematic problem of just what Calanus finmarchicus comprises. In 1863 Claus described, as Cetochilus helgolandicus, a copepod which occurred commonly in the North Sea and Mediterranean. This was included by Giesbrecht as a synonym of C. finmarchicus. Then Sars, in 1903, revived the name, Calanus helgolandicus, for the more southerly populations found by him in his studies of Norwegian copepods. This was accepted by some, rejected by others and left as a probable example of geographical races by many, until in 1949 Rees made the structure of the fifth limb the basis of a new definition and used samples taken with the Continuous Plankton Recorder to chart their distributions in the North Sea. Although this paper and Brodsky's description (1948) of C. pacificus were not universally accepted (e.g. Vervoort, 1957), they started the fragmentation of C. finmarchicus sensu lato and this may be said to have prepared the ground for the descriptions of C. glacialis Jaschnov,

1955, C. australis Brodsky, 1959, C. chilensis Brodsky, 1959 and C. sinicus Brodsky, 1965, from populations previously referred to C. finmarchicus. By this time C. helgolandicus was widely considered a distinct species, a step further than Rees' reference to it as a form of C. finmarchicus. As their names suggest, they are in general characteristic of various geographical regions.

The problem of C. glacialis dates back to 1902, when Mràzek published an account of the Copepoda collected by the German Expedition to the Arctic in 1898. He noted the great size range of C. finmarchicus and investigated its morphology in an attempt to discover characters which might divide his specimens into two or more groups. He was unable to come to a firm conclusion but thought it likely that there were more than one species (Formenkreisen); a definite answer would need to await the results of statistical analysis. Since that time numerous investigations into Arctic copepods have demonstrated a bimodal size frequency for Calanus finmarchicus and several explanations have been forthcoming. Stǿrmer (1929) examined material from the west coast of Greenland and suggested the large specimens underwent a two-year life cycle while the small specimens had an annual reproductive cycle. Bogorov (1934) demonstrated an inverse relationship between temperature and body weight and concluded that temperature was the most important factor controlling weight. Jespersen (1934) and Ussing (1938) also found bimodality in sampled populations from West Greenland. Jespersen was unable to confirm

or deny Størmer's suggestion though there was little difference in the stage of development of the generations to suggest that the speed of one cycle was twice that of the other. In the absence of distinguishing characters he suggested that different temperatures at development were responsible for the bimodality. Ussing also decided in favour of conspecificity but thought that food supply was the deciding factor in the production of large or small individuals. Following so much speculation, the next reports (Wiborg, 1954; Digby, 1954) were more strictly factual. A new complexion was put on the subject in 1955 when Jaschnov raised the large specimens to the rank of species, proposing the name C. glacialis. A series of papers by the same author (1957a, b, 1958, 1961, 1962, 1963) gave further details of ecological and morphological differences. The name C. glacialis has become widely used, e.g. by Brodsky (1959), Grainger (1961, 1962, 1963), Grice (1962), Heinrich (1962b), and Johnson (1963a, b), and the ecological relationship between it and C. finmarchicus has become much better understood. Their distributions have been well summarized by Grainger (1963): "Arctic water is indicated by the presence of C. glacialis without C. finmarchicus, boreal water by C. finmarchicus without C. glacialis, and subarctic (mixed arctic and Atlantic) water by the presence of both species".

TAXONOMY AND GENERAL MORPHOLOGY

Calanus finmarchicus s.l. belongs in the order Copepoda within the Crustacea. It has been made the typical representative of its

sub-order, the Calanoida, by Sars (1903). These copepods are all free-living, almost always planktonic and generally marine. They are characterised by a body which is clearly divided in two parts, an oval cephalothorax or metasome and a narrow, cylindrical abdomen or urosome; in the other free-living copepods the division occurs one segment forward, so that the last thoracic segment is incorporated in the urosome. The anterior part of the body of calanoids consists of the cephalosome, made up of the head and first thoracic segment, and the mesosome, made up of the second to sixth thoracic segments. The urosome consists of the five abdominal segments and a pair of post-anal rami known collectively as the caudal furca. Some fusion of segments is general within the sub-order but in Calanus this is confined to the first two segments of the urosome in adult females. There are five pairs of appendages on the head, namely the first and second antennae, the mandibles and the first and second maxillae. The last pair of mouthparts, the maxillipeds, are found on the first thoracic segment (i.e. the last segment of the cephalosome) and a pair of swimming limbs on each of the other five thoracic segments. The last of these is often highly modified in the male and reduced or even absent in the female. The structure of these limbs plays a prominent part in the taxonomy of the calanoids and Calanus is no exception in this, though the fifth limbs are comparatively little modified. There are no appendages on the urosome.

The other species in the genus and in the closely related Neocalanus are separated from the complex, C. finmarchicus s.l. (i.e. those species listed on pagesl and 2), on such clear characters as the shape of the head and the last metasome segment and the absence of teeth on the coxopodite of the fifth pair of limbs. Within the complex some slight differences in head shape may sometimes be useful but clear morphological characters are only to be found in the structure of the fifth limbs. In the male this involves different proportions in the lengths of the rami of both limbs; in the females it involves the curvature of the toothed border and the size of the teeth themselves on the inner margin of the coxopodite. Jaschnov (1958) has suggested a further division of the species within the complex: those with small teeth in the female and the least asymmetry in the limbs of the male belong to one group and those with large teeth on a strongly concave border in the female and more asymmetrical limbs in the male belong to the other. The first group consists of C. finmarchicus sensu stricto and C. glacialis, both of which occur in the North Atlantic. The second group contains C. helgolandicus, C. pacificus, C. sinicus, C. chilensis, and C. australis; only the first of these has been reported in the North Atlantic.

Calanus finmarchicus s.l. has been recorded in all the major water masses of the world, from polar to sub-tropical regions. It is usually a prominent member of the planktonic community and plays a vital role, as a herbivore, in the food chain. Thus it is not surprising that it

was the first free-living copepod to be described and probably no accident that its systematics are among the most controversial in the Copepoda; many less well-known copepods give promise of systematic difficulties, but so far Calanus affords the best example of the problem. It can reasonably be hoped that the solution of problems concerning Calanus will help when other species are tackled, for what is true for one may well be true for another.

Systematic studies perhaps have their chief justification in the foundation they lay for further studies. Such is certainly the intention in this case. The aim has been, first, to define the populations present by means of systematics and, secondly, to study relationships within and between them in a series of ecological investigations.

THE CONTINUOUS PLANKTON RECORDER

The basis of these investigations has been the Continuous Plankton Recorder and the Survey of the North Atlantic and North Sea in which it is used. The Recorder was devised originally by Dr A.C. (now Sir Alister) Hardy for use with R.R.S. Discovery in the South Atlantic. He had noted in earlier investigations that the shoaling of planktonic organisms could cause adjacent plankton samples taken with a conventional net to yield widely different results. The present instrument was designed to smooth out such patchiness and also to take advantage of the periods at sea when the ship was under way between stations and normally

unable to collect biological information. For these purposes it had to be robust, reliable, easy to operate and able to provide plankton samples whose position of capture could be determined.

Results with the early models encouraged Dr Hardy, by this time Professor of Zoology and Oceanography at the University College of Hull, to develop the Recorder as the instrument for a synoptic survey, which started in 1931, in the southern North Sea. Since then the structure of the instrument has remained virtually unchanged. One of those currently in use is shown in Fig. 1 and a diagram showing its mode of operation in Fig. 2 (see Hardy, 1936, 1939, for complete descriptions of the instrument and the original survey). Externally the Recorder is equipped with a diving plane near the front and beneath the point of attachment of the towing wire. The downward component of the water thrust on the diving plane counteracts the upward component on the towing wire and the body of the instrument at all speeds between 8 and 16 knots, so that the Recorder samples at a constant depth according to the length of wire. The depth chosen for the Survey is 10m. The body of the Recorder tapers towards the rear and is equipped with tail-planes and a fin incorporating a rudder which can be pre-set. A propeller mounted at the rear is turned by water passing over the blades during towing. A small aperture, $\frac{1}{2}$ inch square, at the front opens into a tunnel 2 x 4 ins. in cross-sectional area and this in turn opens to the outside towards the rear of the body. The middle section of this tunnel and the associated mechanism can be removed for ease of maintenance and

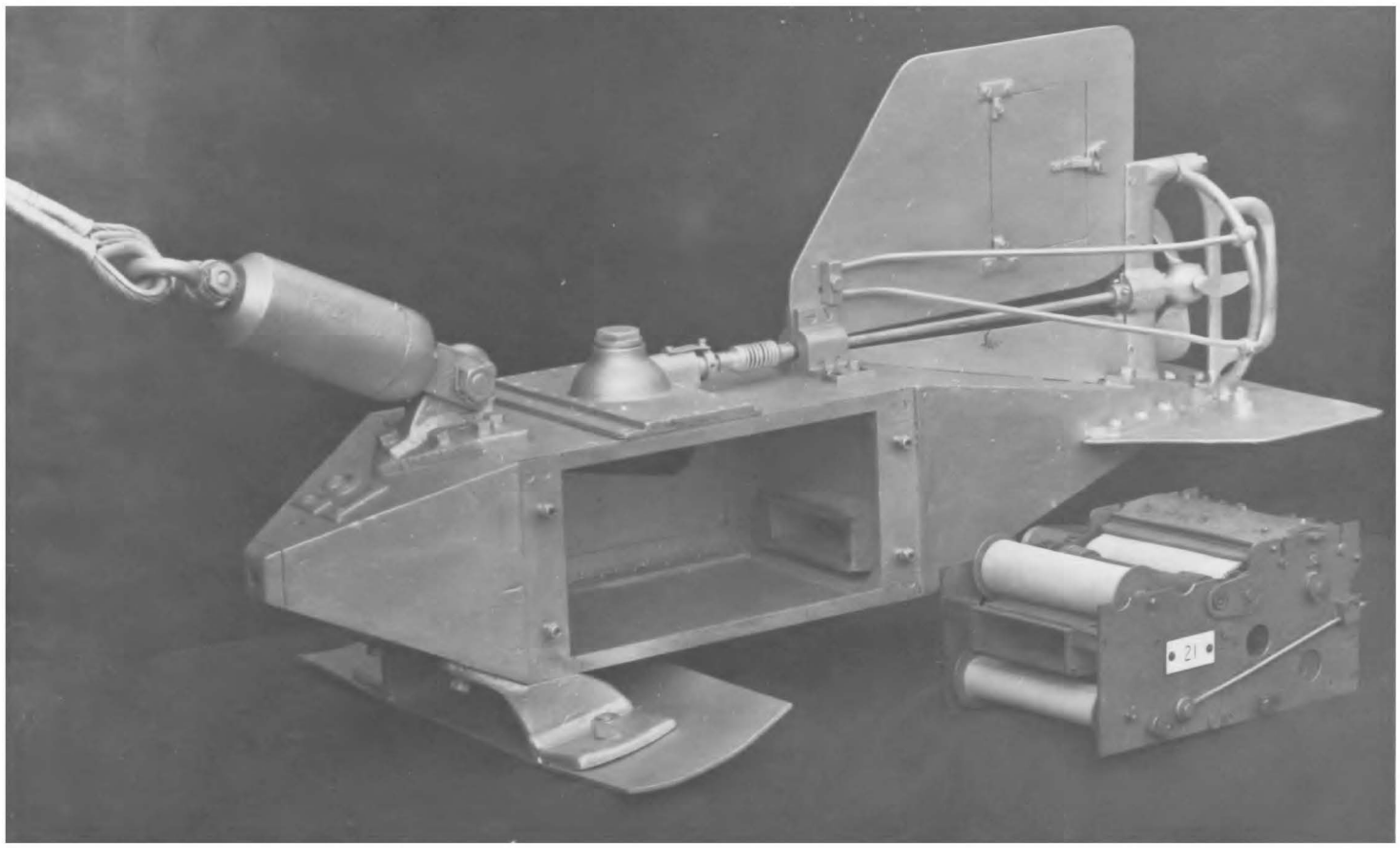


Fig. 1. The Continuous Plankton Recorder: photograph showing the body and the inner mechanism.

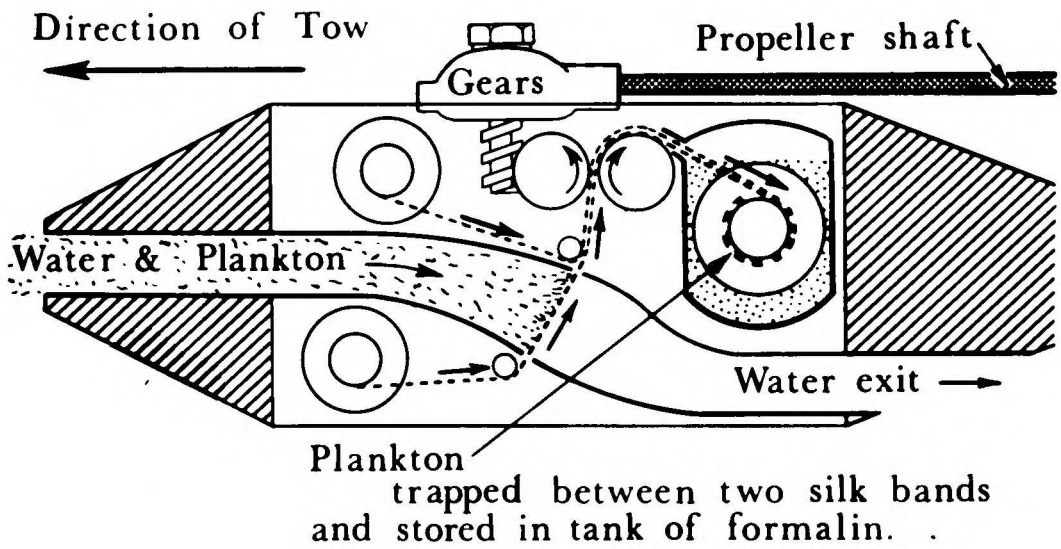


Fig. 2. The Continuous Plankton Recorder: diagram showing the working of the instrument. The arrows show the direction of water flow through the Recorder.

preparation for sampling. This section comprises two spools mounted at the front, one above and one below the water tunnel and a third spool at the rear in a tank with a close-fitting lid. Two long strips of fine meshed silk (0.3mm aperture size) are rolled on the forward spools, the leading end of each strip being attached to the third spool in the storage tank. In so doing the strip from the lower spool, the filtering silk, passes over a roller and across the water tunnel. Immediately above the water tunnel it is covered by the second strip of silk, passes over a second roller and between two driving rollers which grip the silk tightly at the edges and thence into the storage tank. Formalin seeps into the tank slowly from a reservoir underneath. The driving rollers and the spool in the storage tank are themselves driven by the propeller through a gear on the top of the casing. The gearing is adjusted so that the strips of silk are advanced as nearly as possible four inches during every ten miles of tow. The spools take up to 17 feet of silk and one tow can continue for 500 miles; on the longer routes this means replacing the inner mechanism two or three times on a voyage.

The plankton which is required to be sampled occupies a considerable size range, from Nitzschia delicatissima, a diatom 55-90μ long and 2μ wide, up to Meganyctiphanes norvegica, a euphausiid crustacean which may be 3.5 cm long. No one mesh could filter this size range with equal efficiency but, for any given size, it can be assumed that samples

are comparable and may be considered quantitatively. In comparing species of different sizes or shapes this cannot be assumed. There are two main aspects to this problem; first, avoidance, chiefly by the larger and more powerful animals, and, secondly, escape through or round the filtering silk. The extent to which avoidance reduces the size of the samples has not yet been fully investigated, though the high speed (usually 9-15 knots) at which the Recorder is towed and the absence of a bridle at the front may well make this less of a problem than in other plankton samplers. Colton and Marak (1962) say, "the Recorder appears to catch more of the larger, active, [cod and haddock] larvae than are taken by conventional nets". Escape from within the Recorder has been studied by Robertson (1964. A method for studying herbivore standing crop with the Continuous Plankton Recorder. Ph.D. Thesis, University of Michigan) who related the proportion of certain species of small copepods retained on the silk to the length of the metasome. For Calanus the data only concern stage I and II copepodids and are, therefore, scarcely applicable to the present work. It may be mentioned that the amount of plankton which does escape through the mesh is certainly less than it might be, since the widening of the water tunnel behind the aperture reduces the overall filtering rate to 1/29 of the towing speed; this value allows for obstruction from supporting bars behind the filtering silk.

The plankton sample reaching the laboratory consists of a spool

onto which is wound the double layer of silk with the plankton in between. The route the ship has followed while towing the Recorder is known and, by relating this to the length of silk used, the position in the sea at which any given part of the silk was filtering can be calculated. The silk is cut into sections approximately four inches wide and corresponding to ten miles of sampling. While being towed, the strips of silk are, of course, moving continuously, approximately at the rate of two inches (the width of the filtering area) every five nautical miles. The sampling of each section thus overlaps the preceding and succeeding ones but in quantity provides a measure of the plankton in ten miles of sampling; in that distance approximately $3m^3$ of water are filtered. Alternate sections of the silk are distributed among the scientific staff of the laboratory in Edinburgh, the remainder being stored and kept available for specialist study. Analysis of the plankton is conducted in three stages. First, twenty microscope fields, 0.3mm in diameter, are examined on the filtering silk under high power magnification for phytoplankton; presence, but not number, of the various species is recorded for each field, the maximum value thus being 20. Secondly, a traverse of the sections of both the filtering and covering silks, covering 1/40 of the total area, is made using low-power magnification and the numbers of each species of small zooplankton (under 2mm in length) are estimated by means of a series of categories based approximately on a logarithmic scale (Table I). Finally, the larger species of zooplankton from the whole area are identified and

Table I. The categories and their accepted values used during routine analysis of samples from the Continuous Plankton Recorder.

Estimated no. present	Category	Accepted value
1	1	1
2	2	2
3	3	3
4-11	4	6
12-25	5	17
26-50	6	35
51-125	7	75
126-250	8	160
251-500	9	310
501-1000	10	640
1001-2000	11	1,300
>2000	12	2,690

estimated, again using categories. Care is taken during analysis to ensure that the sample is disturbed as little as possible so that its use for further study is not impaired. It is mainly the results from the last stage of the analysis which have been used in those sections of this work which deal with the distribution and abundance of Calanus. These results are further processed in order to produce a chart of distribution and abundance for the common species and groups in the plankton for each month of each year. "Accepted values" (Table I) have been established on the basis of extensive tests of the actual numbers occurring most frequently within each category and these are used to calculate mean monthly values for each species or group occurring in each rectangle, 2° long., 1° lat., covered by the Survey. The methods of analysis can be found in greater detail in Colebrook (1960).

Since the Survey started in 1931 it has expanded enormously. Before being interrupted by the Second World War it had extended into the northern North Sea. Soon after the Survey was resumed further areas in the north-east Atlantic were included and in 1959 a route was added across the Atlantic between Iceland and Newfoundland. Since then gaps have been filled and extensions made so that now the area covered stretches from the Gulf of Main to the Norwegian Sea and from Greenland to north-west Spain (Fig. 3). This work is conducted entirely from merchant ships and weather ships of various nations. The aim is to sample along each route once a month throughout the year. Since 1962

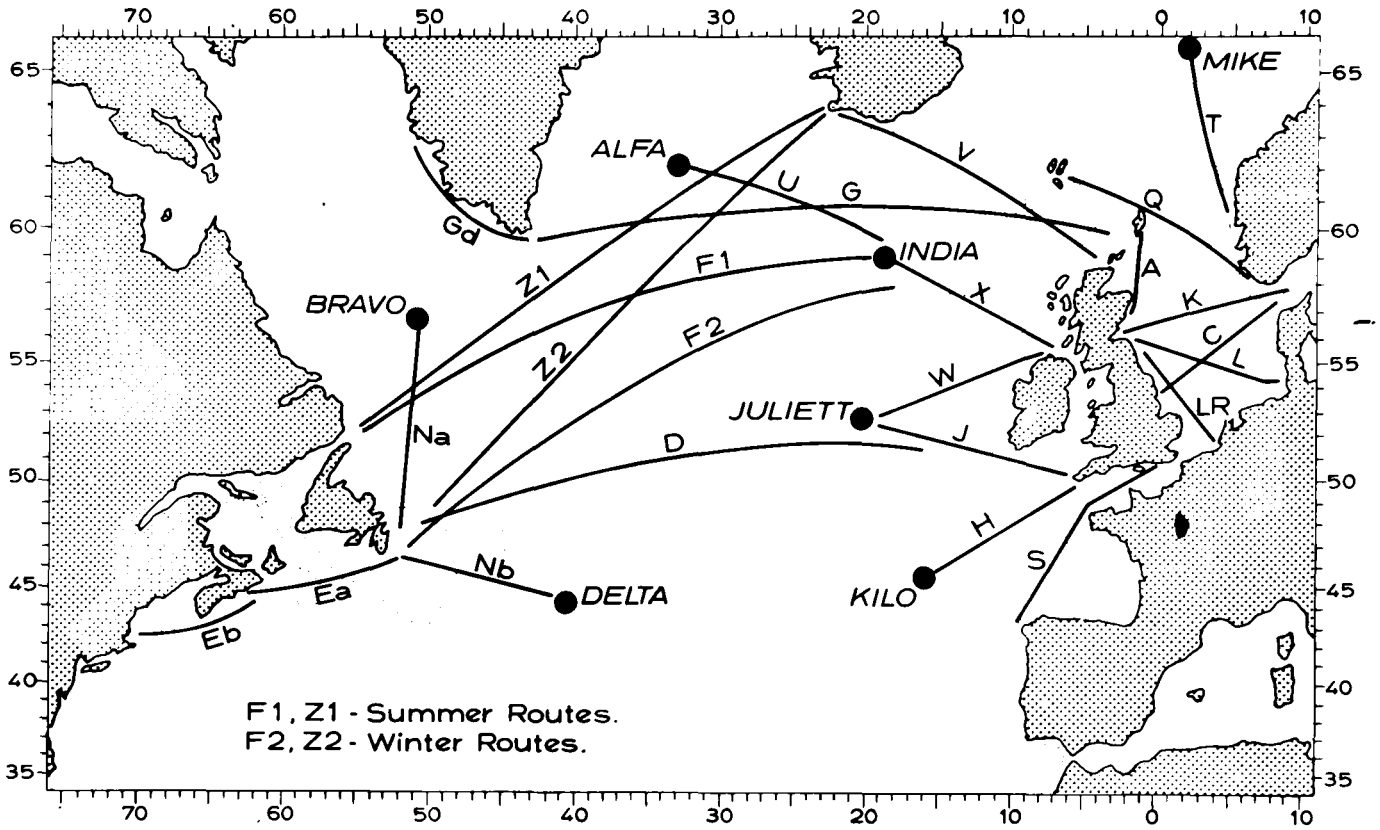


Fig. 3. The Continuous Plankton Recorder Survey: chart of the North Atlantic showing the routes regularly sampled by the Recorder. The ocean weather stations are named.

over 100,000 miles of sampling have been obtained each year. For further details of the Survey, see Glover 1962.

THE NORWESTLANT SURVEYS

Colton and Marak (1962) comment that the Continuous Plankton Recorder and other instruments may be used to supplement each other in a research vessel programme. The present study is in no way such a programme but it has nevertheless proved possible to introduce investigations on samples taken with conventional nets to bring in other ecological aspects. The opportunity to do this work arose when the Oceanographic Laboratory was invited to help in the analysis of samples taken during the NORWESTLANT Surveys of 1963. These Surveys were conceived and planned by the International Commission for the Northwest Atlantic Fisheries and carried out by eight member countries, Canada, Denmark, the Federal Republic of Germany, France, Iceland, Norway, the United Kingdom and the Soviet Union. The first survey was conducted in April, the second in late May and early June and the third mostly in early July. The main concern of the surveys was with the drift of cod eggs and larvae and redfish larvae in relation to environmental conditions. Food being an important part of the environment, high priority was given to the analysis of those species in the plankton which are considered important to the fish larvae. Adult Calanus were included in this. Analysis of the samples was in fact carried further at the Oceanographic Laboratory and by most other participants, so that the available data

include the numbers of each post-naupliar stage (copepodids I-V and adults) in many of the samples taken with Hensen nets. These nets had a mouth diameter of 72 cm, were made of No. 3 silk and were hauled vertically from 100 m or, where the depth of the sea was less than this, from a few metres above the bottom to the surface. Some stramin net samples were also received at the Oceanographic Laboratory and the results from these have been used, briefly, in presenting a picture of the associations of Calanus finmarchicus, in terms of occurrence and abundance, with other copepods. The stramin net, as used in the Surveys, has a mouth diameter of 2m and netting composed of 500 threads per metre.

THE PRESENT INVESTIGATIONS

In conclusion to this introductory section, the main aims of the present investigations are set out below:

a) to determine the systematic status of the three forms of C. finmarchicus in the North Atlantic.

b) to define specific differences where these are considered to exist.

c) to determine whether there is evidence of further division and to assess the population units which may be of ecological significance.

d) to survey the distribution of each such unit in the North Atlantic and North Sea.

e) to study seasonal changes in distribution and abundance throughout the Survey area.

f) to use the Continuous Plankton Recorder in a study of the annual cycle of Calanus in a restricted geographical area, namely the continental shelf between Newfoundland and the Gulf of Maine.

g) to use samples obtained by conventional nets to supplement these results by providing information on the breeding and development of Calanus.

PART I

ON THE SYSTEMATICS OF *CALANUS FINMARCHICUS* S.L.

BIOMETRIC INVESTIGATIONS ON *CALANUS FINMARCHICUS* S.L.

INTRODUCTION

The questions posed at the end of the general introduction are of two types, the systematic and the ecological. It has seemed better to consider the systematic questions first for two main reasons. First, since populations are the basic units of ecology, an evaluation of their systematic status forms an essential part of any ecological investigation and it is desirable to define them at an early stage. Secondly, the systematics of *Calanus* have been studied far longer than its ecology and, perhaps for this reason, more controversy surrounds the problem than has yet been engendered around ecological studies. An attempt has been made, therefore, to resolve the conflicting opinions on the systematics of *Calanus finmarchicus* s.l. as far as the area of the North Atlantic covered by the Continuous Plankton Recorder Survey is concerned, before going on to investigate less studied aspects of its ecology.

Rees (1949) demonstrated that the Continuous Plankton Recorder was sampling two forms, "*finmarchicus*" and "*helgolandicus*" in the eastern North Atlantic and the North Sea. Since 1958 they have been separated in the routine analysis of Recorder samples at the Oceanographic Laboratory and no undue difficulty has been encountered in their identification. Soon after the extension of the Survey into the western North Atlantic in 1959 large *C. finmarchicus* s.l. were recorded in some samples from the Labrador Current. Specimens were sent to

Professor Jaschnov in Moscow who confirmed their identification as C. glacialis. Separation of C. glacialis from C. finmarchicus in routine analysis, however, did not prove to be so straightforward and a number of specimens could not definitely be assigned to one or the other on the basis of published descriptions. The nature of Recorder sampling is such that numerous samples, which individually may be small, combine to produce extensive data on distribution, abundance and fluctuations near the sea surface. It is thus essential for correct identification and estimation of the numbers of the species in each sample to be made. The present investigation, therefore, had as its immediate objective the laying down of fixed criteria to be used in the separation of C. finmarchicus from C. glacialis in Recorder samples.

Jaschnov (1955, 1957a) used body length and the structure of the fifth limb to distinguish C. glacialis from C. finmarchicus s.str. and it was clear at the outset that the best chance of making a morphological definition lay in the structure of that limb. The possibility of other differences, never recorded by previous workers but yet clear enough for use in routine analysis, seemed remote but could not be overlooked. A few specimens of typical C. finmarchicus and C. glacialis were obtained from Recorder samples and a check on their gross morphology was carried out, with particular attention being paid to the setation of all appendages. No structural differences which had not been reported previously were observed between the two and it was clear that any definition would need to be based on the structure of the fifth limb or,

less desirably, on body length. The structural details of the fifth limbs which could be expected from Jaschnov's description to yield a definition were the curvature of the toothed border on the coxopodite, the number and size of the teeth and the number of setae on the outer border of the last segment of the endopodite (see Fig. 4). Since these characters are all amenable to biometric analysis, large numbers of individuals have been measured in the hope that differences might be found which showed no overlap between species and which thus would prove valid definitions for the identification of all individuals. For the comparative studies samples were chosen where the routine analysis had shown two species to be present; for the geographical studies the samples were chosen from those where routine analysis had shown C. finmarchicus s.l. to be present.

METHODS

All specimens were measured from the tip of the head to a line joining the postero-lateral corners of the last thoracic segment; this is termed the metasome length. The fifth swimming limbs, which provide the chief taxonomic characters within Calanus finmarchicus s.l., were mounted in polyvinyl lactophenol stained with ink (Carrie, 1959). The external setae on the endopodite (Fig. 4, S) were counted and the limb measured for length (Fig. 4, L) and for curvature of the toothed border on the coxopodite (Fig. 4, X). For measurements of a concave border a movable eyepiece hair-line was adjusted to lie across the

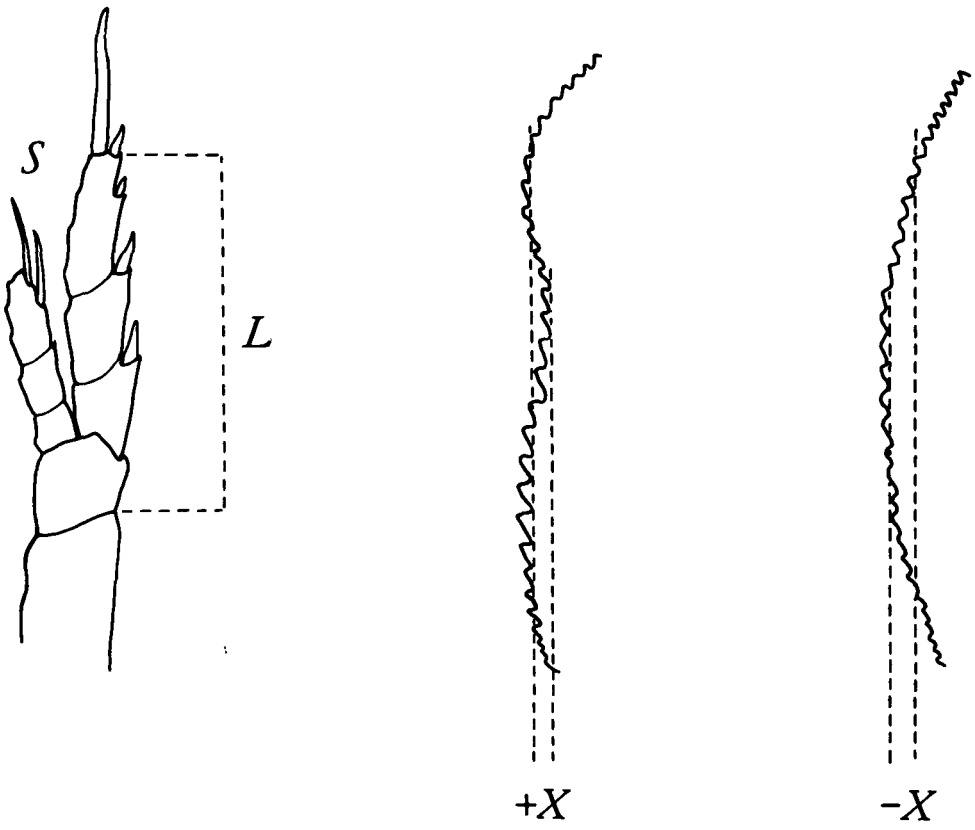


Fig. 4. Measurements of the fifth limb: L, length excluding coxopodite; S, setae on the outer margin of the endopodite; + X, concavity of the inner border of the coxopodite; - X, convexity of the same.

shoulders of the border; the distance the line travelled to reach the bottom of the concavity was then recorded. It was found that the shoulders on concave borders coincided with the position of the seventh tooth from the proximal end and the ninth from the distal end of the toothed border. The positions of these teeth, therefore, have been taken as the base line for measurements of convex borders.

COMPARISON OF CALANUS FINMARCHICUS AND C. GLACIALIS

This comparison is based on a detailed analysis of Plankton Recorder samples taken along a stretch of 180 miles east of the Newfoundland Grand Banks, between 48°N, 45°W and 45°40'N, 46°30'W, on 10th - 12th March 1961. The routine analysis had shown high numbers of Calanus, mostly C. finmarchicus but with some C. glacialis. Nearly 700 adult females were obtained and they were all measured. The results, converted to running averages and on a logarthmic scale, are shown in Fig. 5. The sample divides into two at around 3.6 mm metasome length. In accordance with recent practice (see Grainger, 1961) the smaller specimens will be referred to as C. finmarchicus, the larger ones as C. glacialis. The data on length, expressed as cumulative percentages, have been plotted on probability paper in Fig. 6. This technique enables mixed samples to be separated and mean values and standard deviations to be obtained (Harding, 1949). A point of inflection at 97.5% separates the two groups. Superimposed on the figure are the lines AB and CD, derived from the cumulative percentages

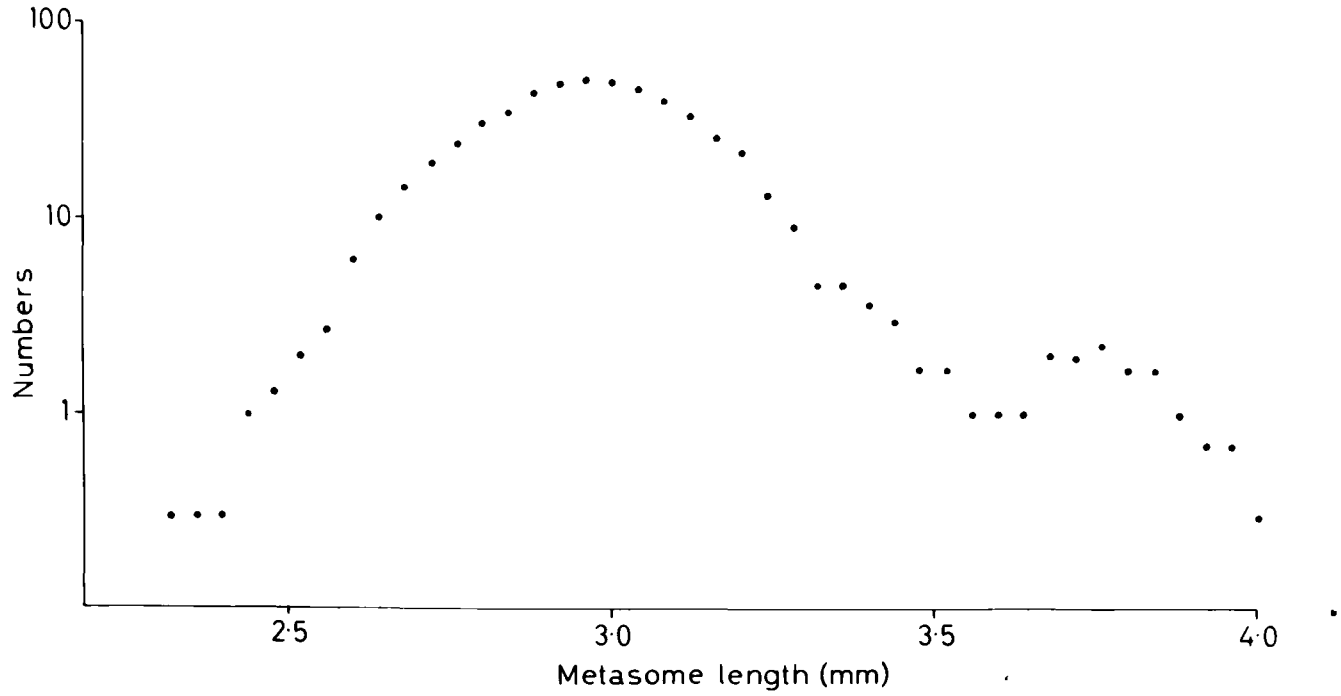


Fig. 5. Adult female Calanus from east of Newfoundland, showing the length frequency, using running averages.

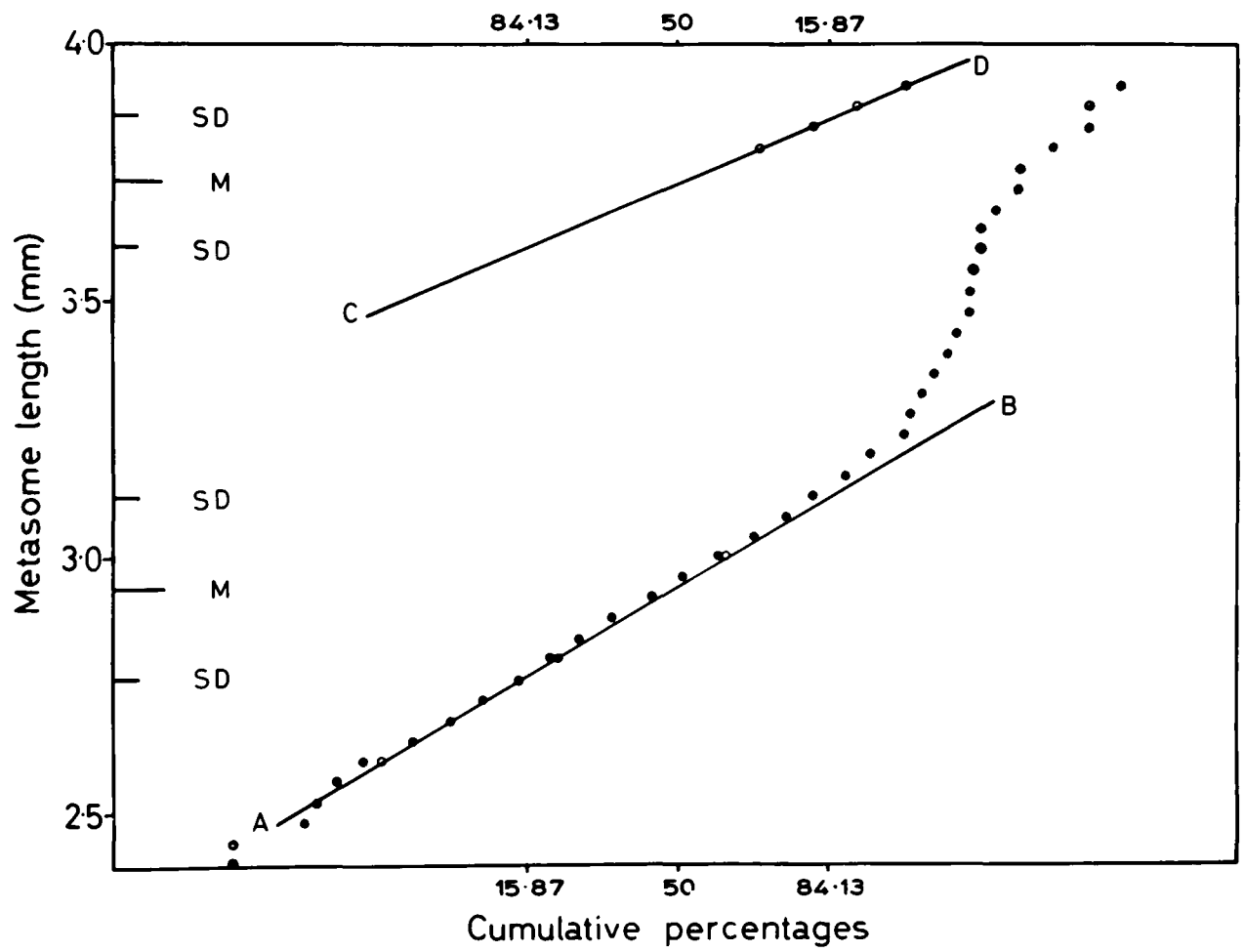


Fig. 6. Adult female Calanus from east of Newfoundland, showing the length frequency plotted on probability paper. Lines AB and CD represent the separate length frequencies of Calanus finmarchicus and C. glacialis respectively. M, mean metasome length; SD, standard deviation.

for each group treated separately. The mean metasome length of C. finmarchicus was 2.94 mm (standard deviation 0.18) and of C. glacialis 3.73 mm (standard deviation 0.13).

In previous descriptions of the species within Calanus finmarchicus s.l., the toothed border of the fifth limb has been described as convex, straight or concave. This takes account of the deviation of the border from a straight line in the way that the value X in Fig. 4 attempts to measure. The results of these measurements are shown in Fig. 7. The full size range was sampled, wherever possible eight specimens from each size category (0.04 mm) being measured. The arrow in this and subsequent figures indicates the separation between C. finmarchicus and C. glacialis on the basis of size frequency. A single value has been calculated for each specimen by averaging the measurements for the two limbs in order to reduce the variability and bring out more clearly any separation which might be inherent in the sample. No separation between the finmarchicus and glacialis sections of the sample is apparent. There is instead a continuous trend from a border which is slightly convex in the smallest specimens to a markedly concave border in the largest.

It is important to take the size of the specimens into account before studying this apparent trend further. Fig. 8 shows the relationship between the lengths of the metasome and the 5th limb, using scales adjusted to produce a line at 45^{o} for an isometric relationship. The fitted line has a gradient of 44^{o} - 45^{o}, indicating a constant ratio between metasome and fifth limb length throughout the size range.

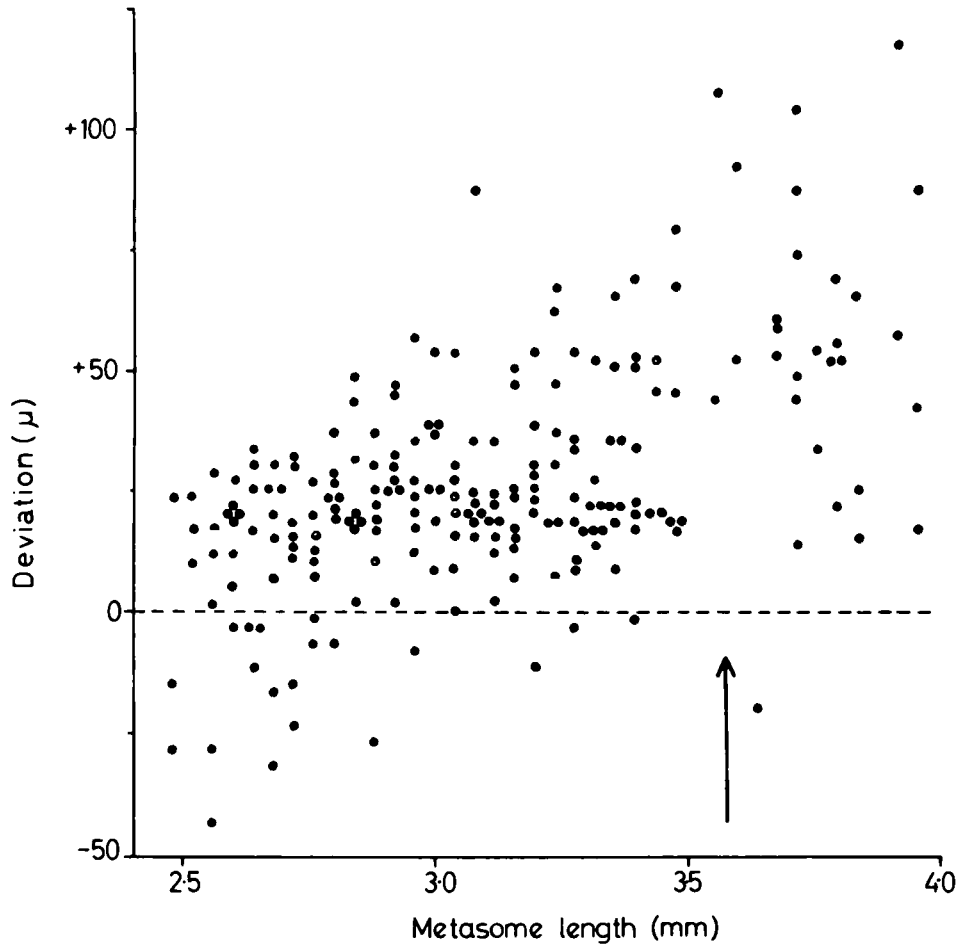


Fig. 7. Adult female Calanus from east of Newfoundland, showing the curvature of the toothed borders of the fifth limbs, expressed as the deviation from a straight line. Positive values represent concave and negative values convex borders. The arrow indicates the separation between small and large Calanus.

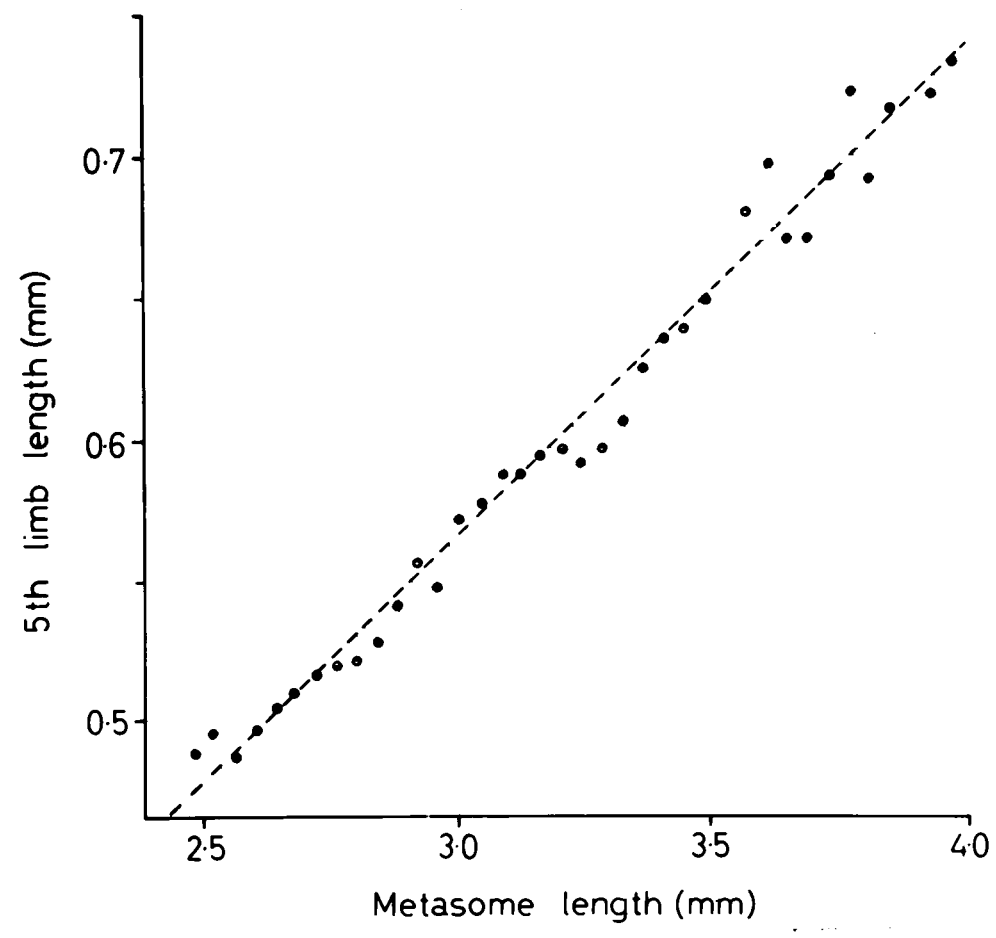


Fig. 8. Adult female Calanus from east of Newfoundland, showing the relationship between the lengths of the metasome and of the fifth limb.

The length of the toothed border was found to be approximately a fifth of the limb length, L. An angular measure of curvature, $\underline{\theta}$ (Fig. 9) derived from X and L/10, thus relates curvature to metasome length. This has been expressed as $(100-200/\pi)$ radians in order more easily to contrast concave and convex borders; positive values are concave, negative ones convex.

The mean values of $\underline{\theta}$ for each size group have been plotted against metasome length in Fig. 10. Some scatter occurs towards the upper end of the size range where numbers were low. Despite this there is a clear trend from slight concavity in the smallest specimens to distinct concavity in the largest, equivalent to an angle, $\underline{\theta}$, of approximately 84^{o}. Since a similar trend to that shown in Fig. 7 is apparent in Fig. 10, it is clear that concave curvature does increase with metasome length and is not simply an increase of the value, X, commensurate with an increase of L/10.

The number of setae present on the outer border of the endopodite of the fifth limb (Fig. 4, S) was counted on 97 specimens. Of these at least six had dissimilar counts on the two limbs but, as there were a further 28 which had only one intact endopodite, it has been decided to treat the limbs separately.

There was an extra seta on the endopodite of 33% of the 5th limbs. Taking the finmarchicus and glacialis groups separately, the percentage occurrence was 26 and 52 respectively. This agrees closely with

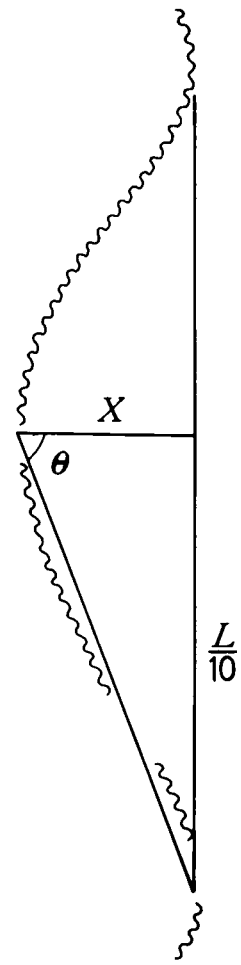


Fig. 9. The method for determining the angular measure of curvature. L and X have been obtained as shown in Fig. 4.

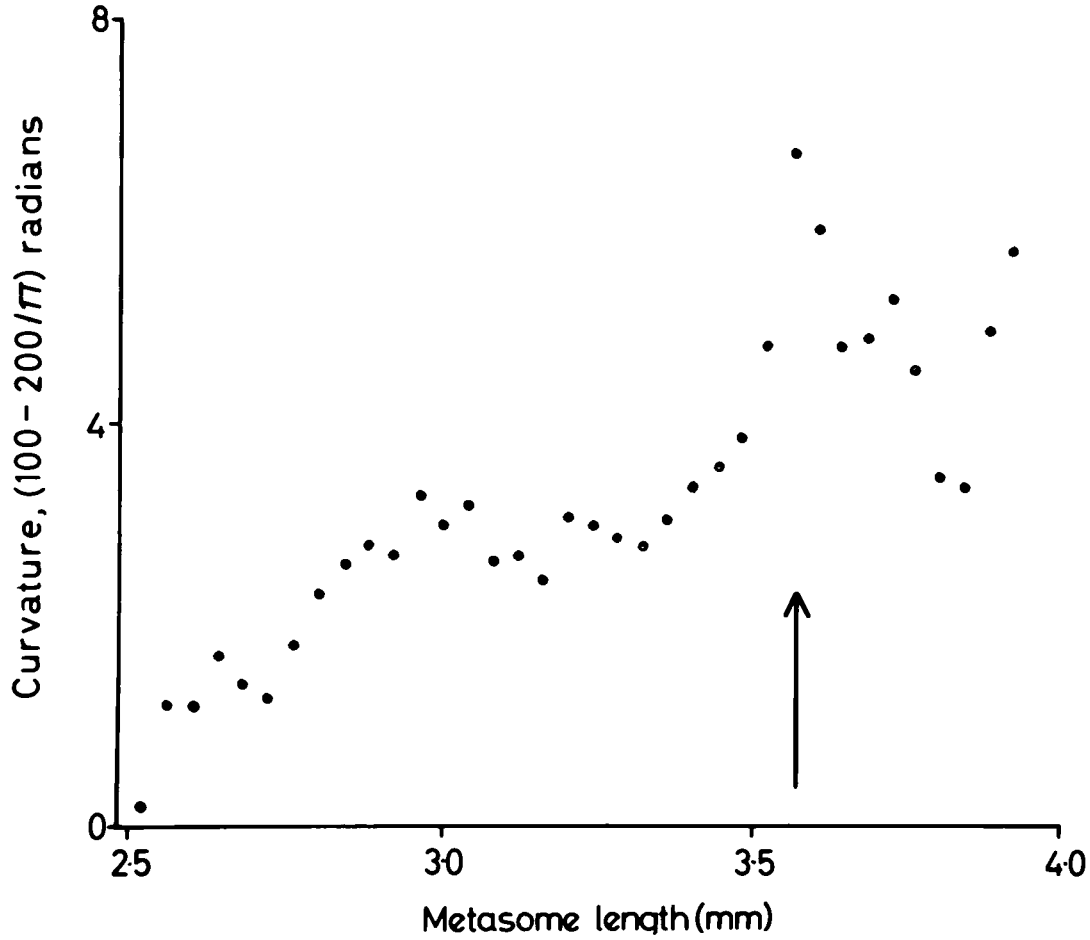


Fig. 10. Adult female Calanus from east of Newfoundland, giving the mean values for curvature of the toothed borders of the fifth limbs. The arrow indicates the separation between small and large Calanus.

Jaschnov's (1957a)figures of 27% for C. finmarchicus from the Norwegian Sea and 49% for C. glacialis from the Kara Sea. In Table II the whole size range has been subdivided to investigate possible trends in relation to size. The extra seta occurred in 6 - 13% of the small C. finmarchicus and in 50 - 53% of C. glacialis. The largest C. finmarchicus, however, occupied an intermediate position with 38% of the specimens having double setation.

TABLE II - The percentage occurrence of an extra seta on the endopodite of the fifth limb in each of six size groups. Groups 1 - 4 contain C. finmarchicus alone, group 6 contains C. glacialis alone and group 5 contains both.

Group	Metasome length range (mm)	Percentage occurrence of extra seta
1	2.50-2.74	13
2	2.74-2.98	8
3	2.98-3.22	6
4	3.22-3.48	38
5	3.48-3.70	50
6	3.70-3.94	53

Counts of the teeth on the border of the coxopodite and measurements of the maximum tooth length have been made over the full size range (Fig. 11a). The mean number of teeth throughout the size range of C. finmarchicus is slightly higher than the mean number for C. glacialis, due to a marked lowering of the upper limit in the latter. The break

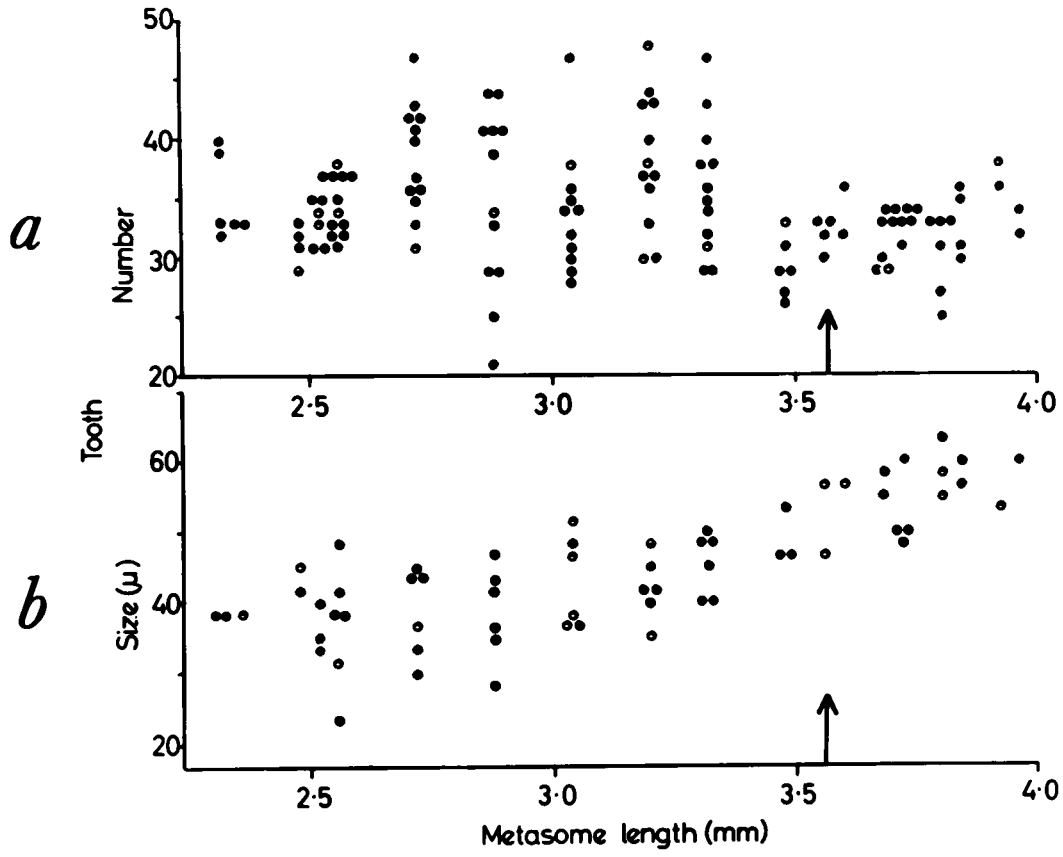


Fig. 11. Adult female Calanus from east of Newfoundland, showing, a, the number of teeth on the toothed borders of the fifth limbs and b, the maximum tooth size on these borders. The arrows indicate the separation between small and large Calanus.

in continuity between the two groups is thus due to an apparent decrease in variability in C. glacialis. This also agrees with Jaschnov's (1957a) findings. Maximum tooth length (Fig. 11b), on the other hand, shows no discontinuity. The data indicate either a steady increase in tooth size directly proportional to metasome length or a tooth size constant in the lower part of the size range, gradually becoming larger in the upper part.

COMPARISON OF CALANUS FINMARCHICUS AND C. HELGOLANDICUS

Mixed sample.

Results of routine analysis of Recorder material were again used to select a suitable sample for the comparison. The sample chosen, in which both Calanus finmarchicus and C. helgolandicus had been recorded, was taken on a 10 mile stretch of the northern North Sea, approximately $57^{\circ}50'N$, $1^{\circ}40'W$, on the night of 11th-12th September, 1961. A total of 96 specimens was obtained, 64 adult females and 32 stage V copepodids.

Examination of the size frequencies of both adult females and copepodids revealed no sign of a separation into two groups. When the curvature of the toothed border of the fifth limbs was studied, separation was immediately apparent (Fig. 12). In one group the border rarely diverged from a straight line by more than 25μ; in the other group there was a minimum concave deviation of over 50μ. This separation agrees with the descriptions of Calanus finmarchicus and C. helgolandicus respectively (see Rees, 1949).

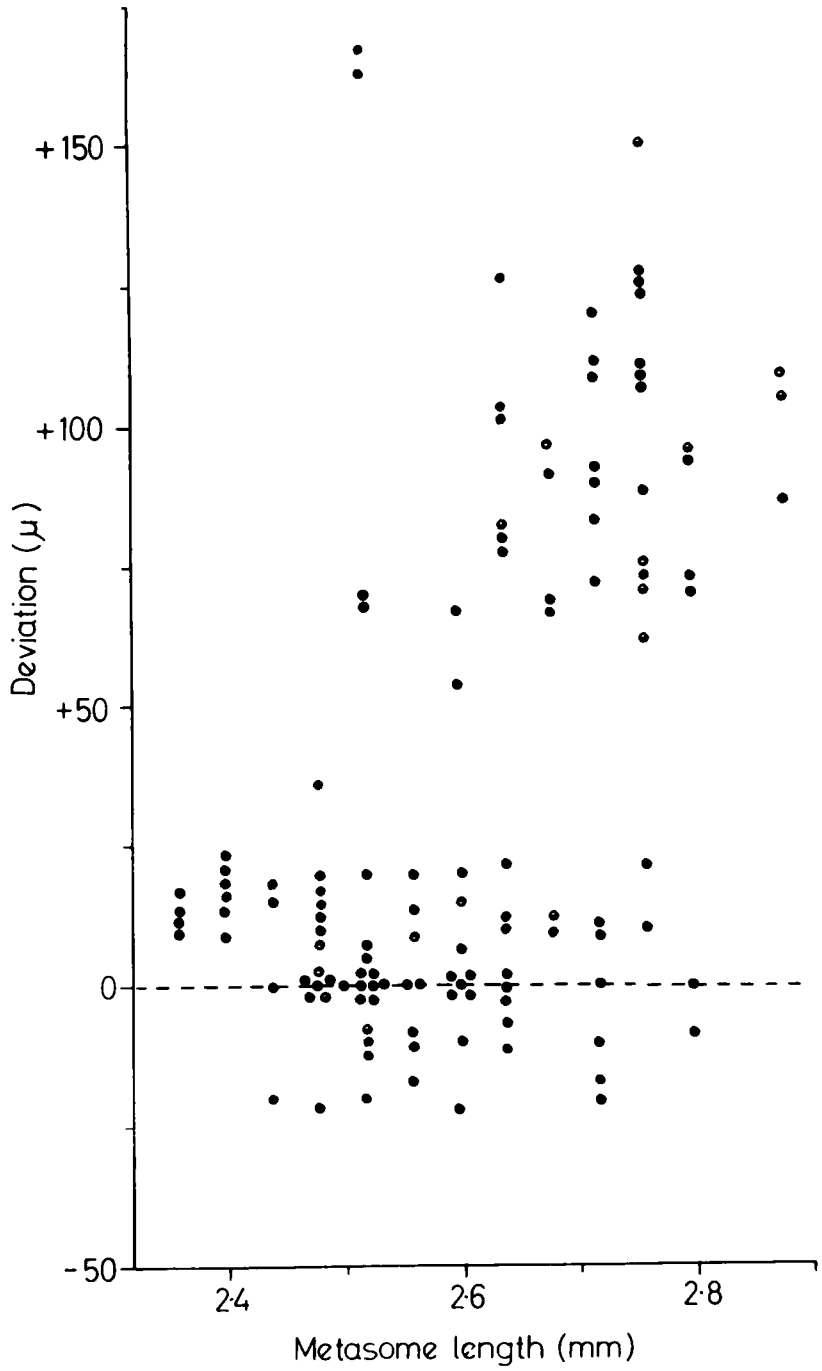


Fig. 12. Adult female Calanus from the North Sea, showing the curvature of the toothed borders of the fifth limbs, expressed as the deviation from a straight border. Positive values represent concave and negative values convex borders.

Using the curvature of the coxopodite to separate C. finmarchicus and C. helgolandicus, size frequencies were re-examined. The adult length range of each was a little less than the total, C. helgolandicus having the slightly greater mean size (Fig. 13); the few stage V C. helgolandicus were scattered throughout the range.

The fifth limbs were further examined to determine the relative frequency of one and two setae on the outer margin of the last endopodite segment. In adult females of both species single setae predominated; in C. finmarchicus 10.2% of the total had two setae and in C. helgolandicus 8.4%. This is too small a difference for any conclusion to be drawn, though it is a difference in the same direction as that discovered by Jaschnov (1957a) who gave percentages of 27 and 4 respectively. There were only four whole limbs of C. helgolandicus at Stage V, two with one seta, two with two. For C. finmarchicus at this stage, where figures are available for 41 limbs, double setation occurred on 80.5%. This fits in with Jaschnov's figures (1957a) of 91-95% double setation in more northerly samples. Double setation in the adults was more common among the larger specimens and at stage V this was even more marked.

The maximum size of the teeth on the coxopodite border of the adult females was also measured (Fig. 14). There was incomplete separation on the basis of this character, though the average maximum size of the teeth of C. helgolandicus (62μ) was 1.75 times that of C. finmarchicus (35μ).

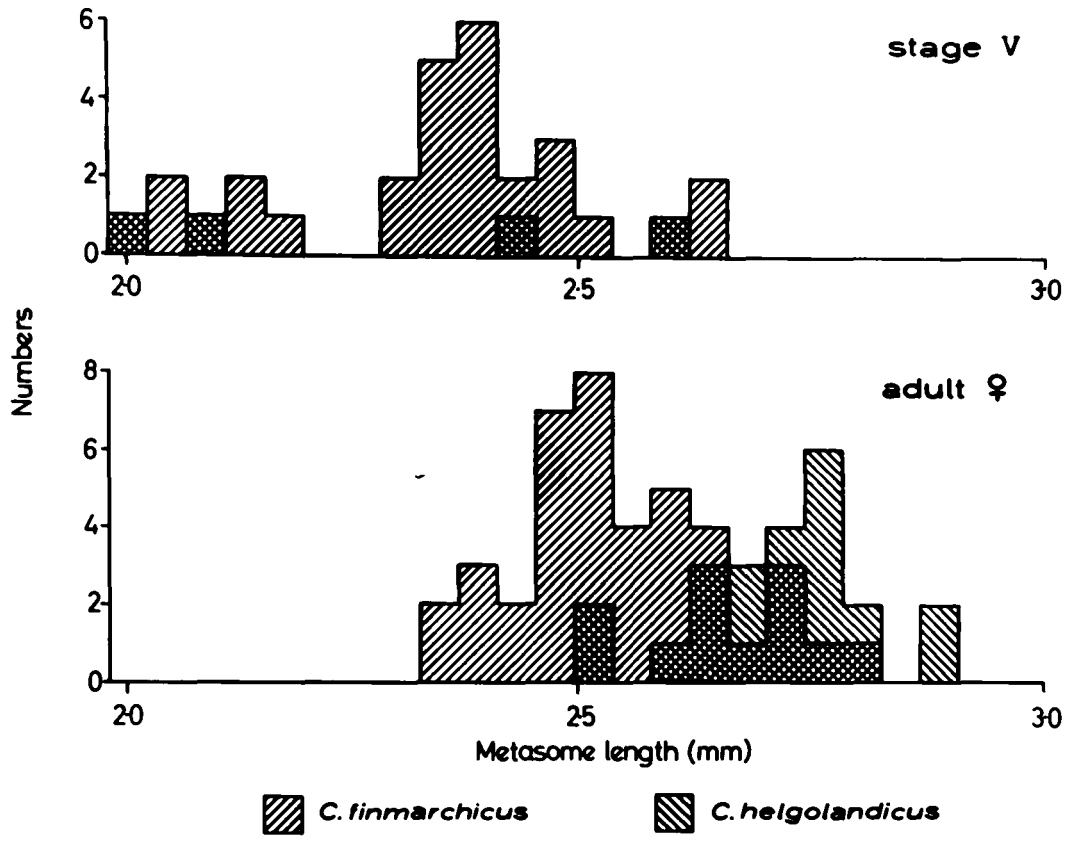


Fig. 13. Stage V and adult female Calanus from the North Sea, showing the length frequencies of C. finmarchicus and C. helgolandicus.

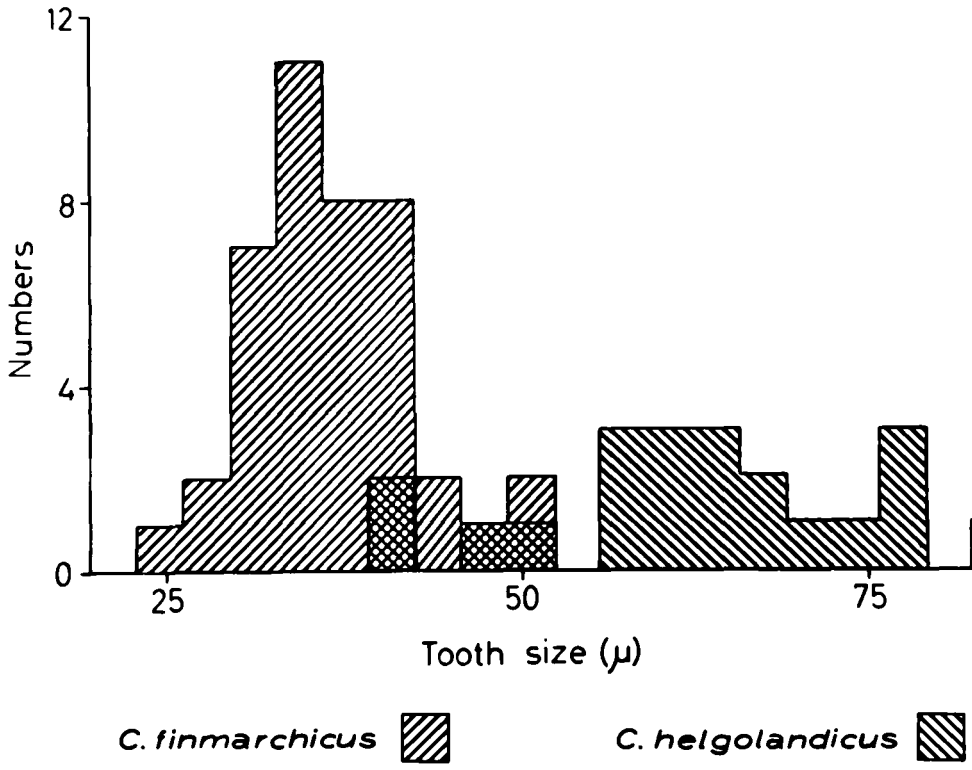


Fig. 14. Adult female Calanus finmarchicus and C. helgolandicus from the North Sea, showing the maximum tooth size on the toothed border of the fifth limbs.

Geographical variation.

The second part of the investigation was concerned with geographical variation within the area of the Recorder Survey. The standard areas into which the survey is divided have been used. Samples were chosen from each area in which Calanus had been recorded. As far as possible, 20 stage V copepodids and 20 adult females of both C. finmarchicus and C. helgolandicus were obtained from each area, all sampled in July 1963. The sample of C. finmarchicus from area D8 contained a few specimens of C. glacialis. Fig. 15 shows the standard areas and the position of samples chosen. Just over a thousand specimens were examined and every one was assigned either to C. finmarchicus or to C. helgolandicus on the basis of curvature of the toothed border of the fifth limb. C. helgolandicus occurred only sparingly at this time off the European continental shelf and the areas B5, C5 and D5 have been combined for the adult females.

The data on curvature obtained from all the samples were first combined to see whether the separation apparent in the sample from the northern North Sea held good for the whole of the area. All the C. helgolandicus examined had a toothed border deviating by more than 50μ from a straight line and all but two C. finmarchicus gave values less than this figure; the two exceptions were large specimens from the Labrador Sea. There was complete separation, however, in both stage V copepodids and adult females when curvature was expressed as an angular measure (Fig. 16). The morphological difference between C. finmarchicus and C. helgolandicus may thus be defined as:

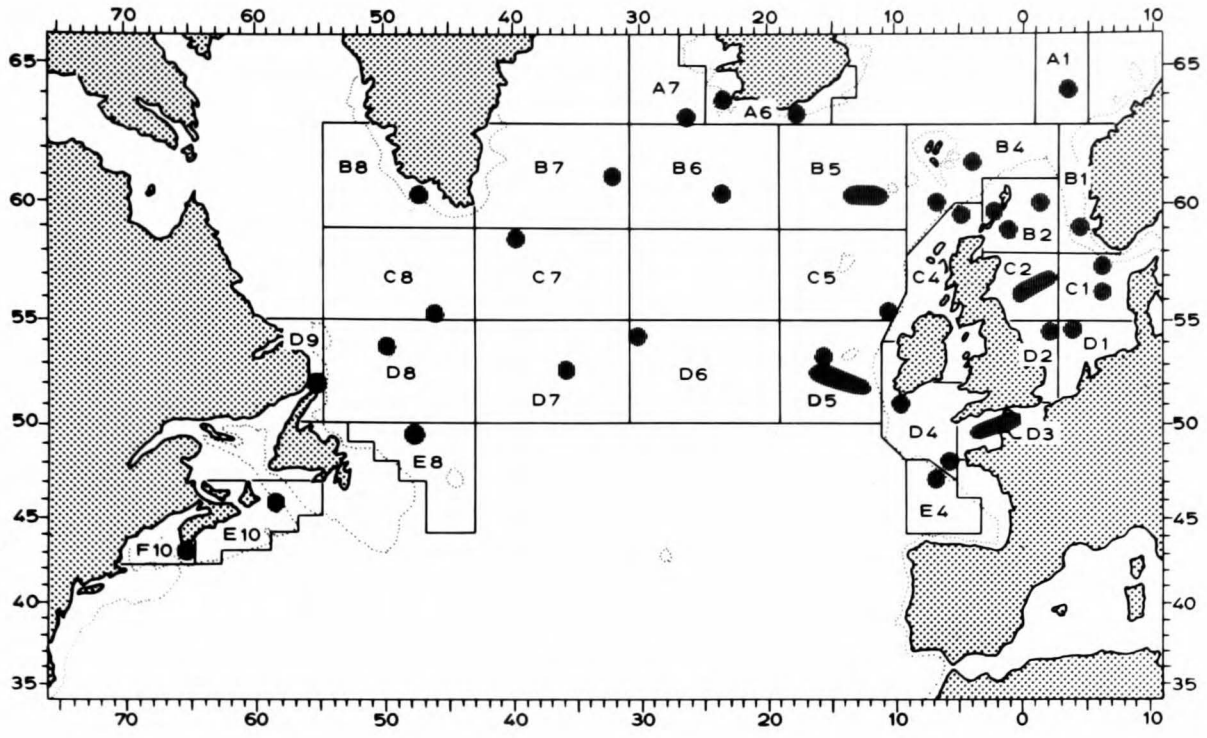


Fig. 15. The area of the Recorder Survey with the standard areas and the position of the selected samples of Calanus taken in July 1963.

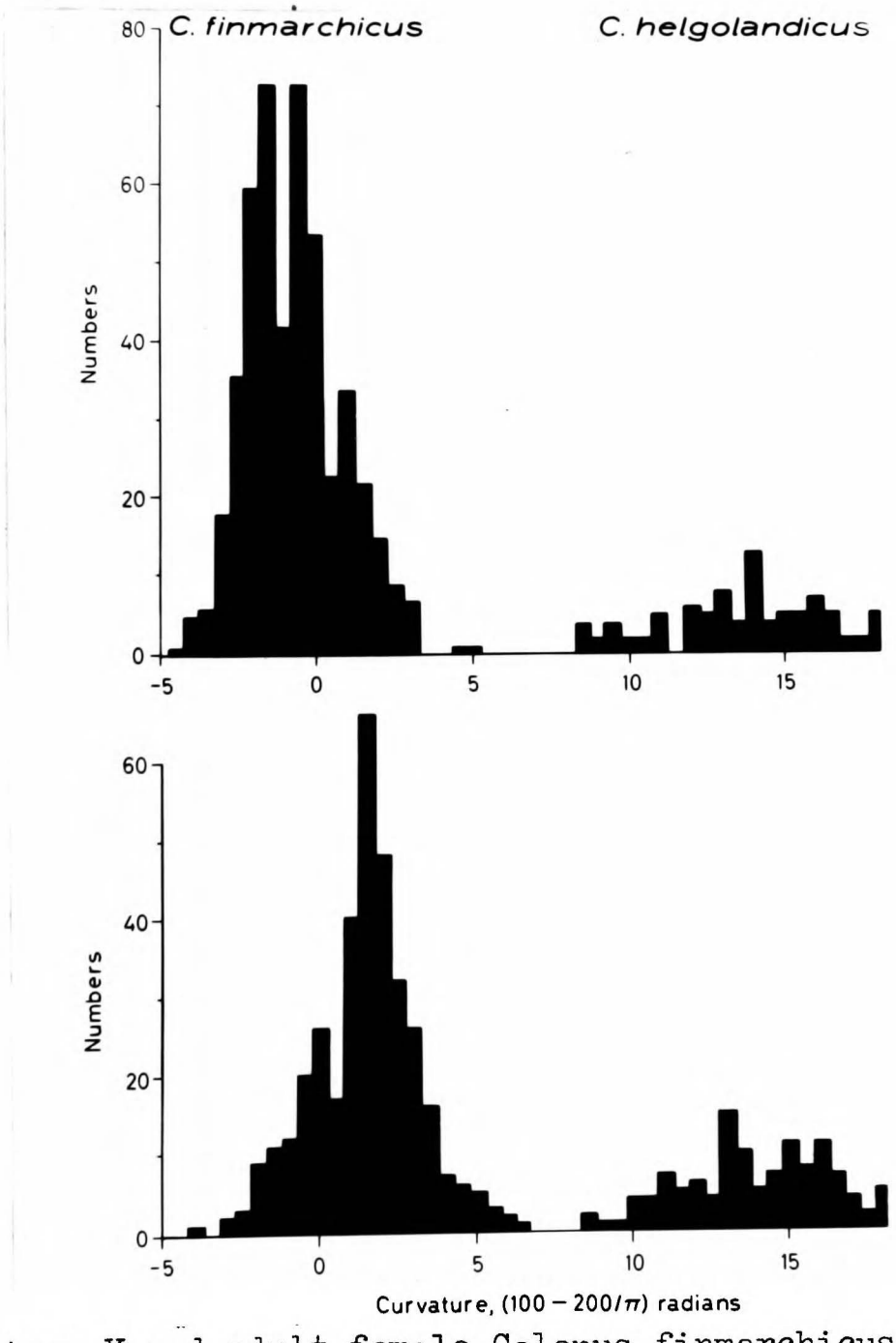


Fig. 16. Stage V and adult female Calanus finmarchicus and C. helgolandicus from the North Atlantic and North Sea, showing the curvature frequency of the toothed borders of the fifth limbs.

C. finmarchicus: Curvature = $100 - \frac{200}{\pi} (\arctan L/10X) < 7$

C. helgolandicus: Curvature = $100 - \frac{200}{\pi} (\arctan L/10X) > 8$

Where L = length of the outer margin of the fifth limb (basipodite and exopodite), in mm.

X = deviation of toothed border of fifth limb from a straight line, in mm.

The mean metasome lengths of Calanus finmarchicus and C. helgolandicus, stage V and adult female, are shown in Fig. 17. There was quite a wide range of size in C. finmarchicus within the area. C. helgolandicus, on the other hand, varied much less in size. In C. finmarchicus there was an increase in size towards the north-western Atlantic while in C. helgolandicus, which was never recorded far from the European continential shelf, the smallest adult females were found in the English Channel, the Bay of Biscay and west of the British Isles. In that part of the area in which both species occurred, adult female C. helgolandicus were found to be slightly the larger, the ratio being 1 : 1.05. The overall difference between the stage V copepodids was negligible. In both adults and stage V copepodids, a geographical pattern in the size ratios emerged: adult females of both species east of the Faeroes, off western Norway and in the mouth of the Skagerrak were nearly identical in size, while everywhere to the south and west, C. finmarchicus were the smaller; at stage V, C. finmarchicus were larger than C. helgolandicus in the mouth of the Skagerrak and to the north of Scotland but were the smaller to the south and west of the British Isles. In other words, over

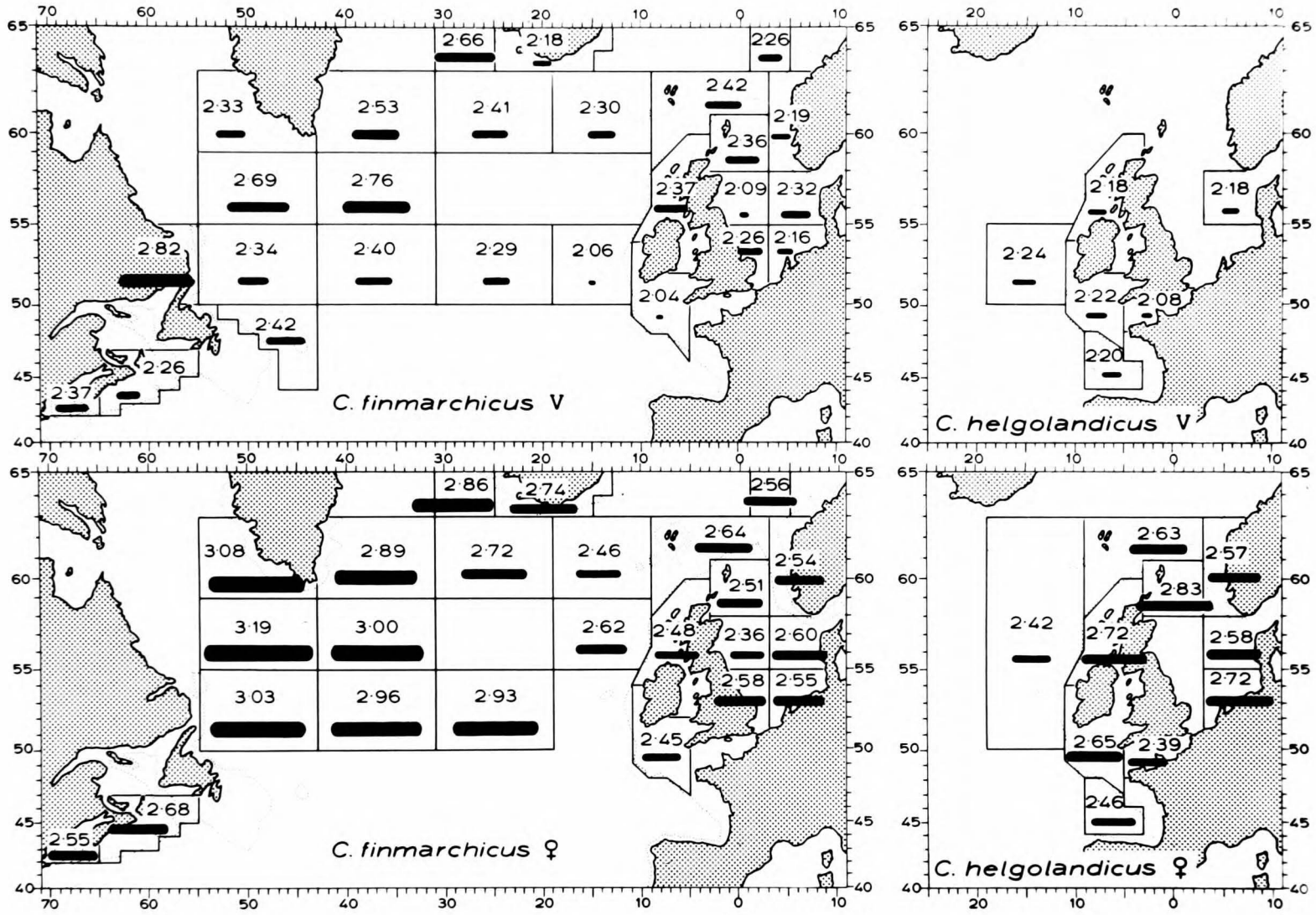


Fig. 17. Stage V and adult female Calanus finmarchicus and C. helgolandicus from the North Atlantic and North Sea, showing the mean lengths of the metasome in July 1963.

the same area, C. finmarchicus varied in size more than C. helgolandicus. It may be that in this area environmental factors have a more marked effect on C. finmarchicus than on C. helgolandicus, which is near the northern limit of its distribution.

Investigation of the curvature of the toothed border on the fifth limb (Fig. 18) revealed a geographical pattern only in the case of adult female C. finmarchicus, the limb borders being more concave in three neighbouring standard areas (shown hatched) in the western Atlantic than elsewhere. Otherwise there was an apparently random variation within fairly narrow limits for each stage and species. There was little difference in curvature between stage V and adult female C. helgolandicus. In C. finmarchicus, on the other hand, adult females invariably had more concave borders than the corresponding stage V copepodids.

Setation of the fifth limb varied widely between stages and species and also throughout the area (Fig. 19) but no geographical pattern could be discerned. In both species, the extra seta was more frequent in stage V than in the adult females; this is to be expected since stage V includes males which always possess the additional seta in the adult stage.

Surface temperatures for the survey area were obtained for the months of May, June and July 1963 from charts compiled by the Marine Division of the British Meteorological Office and by the U.S. Navy Hydrographic Office. In C. finmarchicus an inverse relationship between metasome length and temperature was apparent. The closest relationship existed

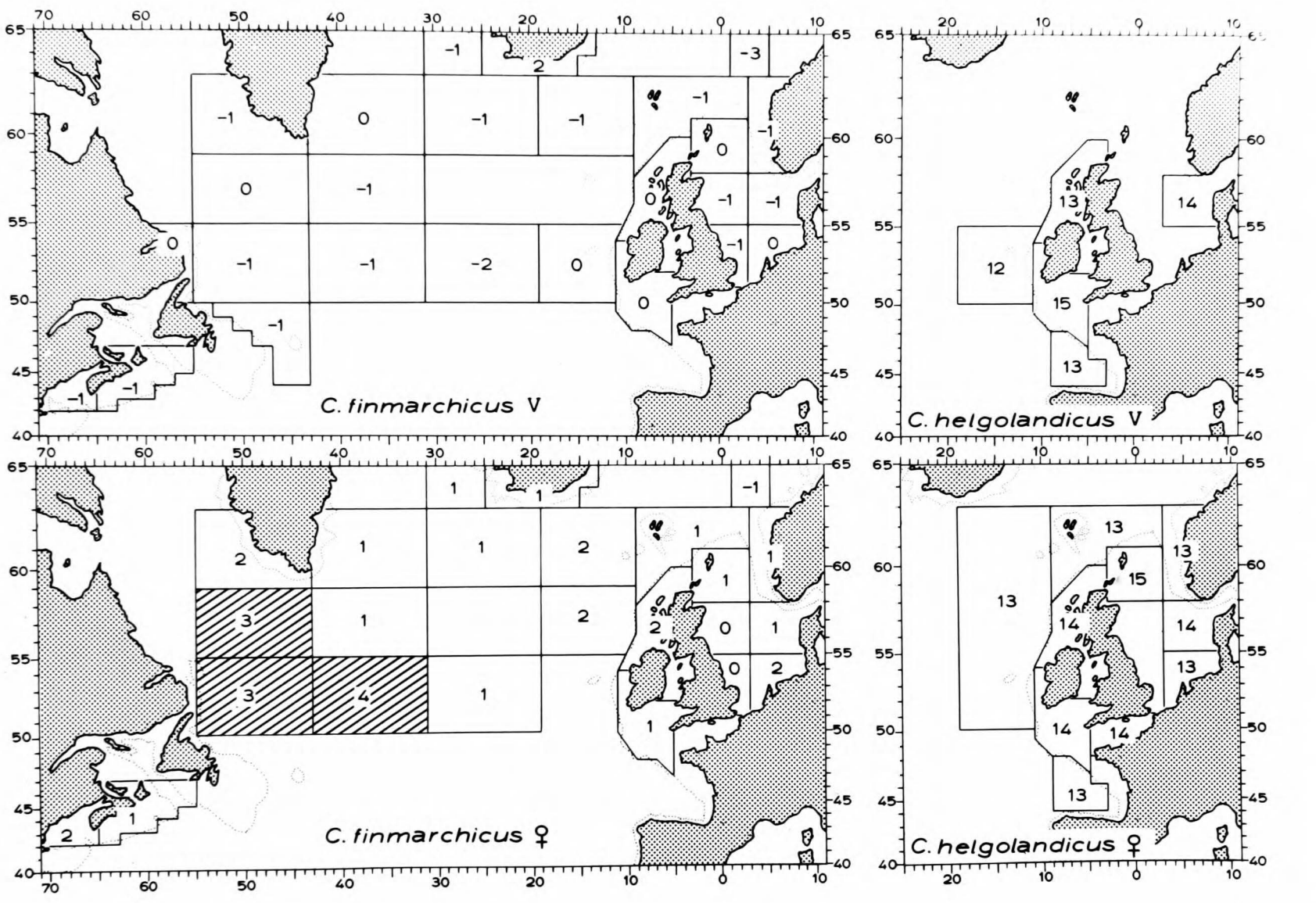


Fig. 18. Stage V and adult female Calanus finmarchicus and C. helgolandicus from the North Atlantic and North Sea, showing the mean values for curvature (100-200 π radian units) of the toothed border of the fifth limbs in July 1963.

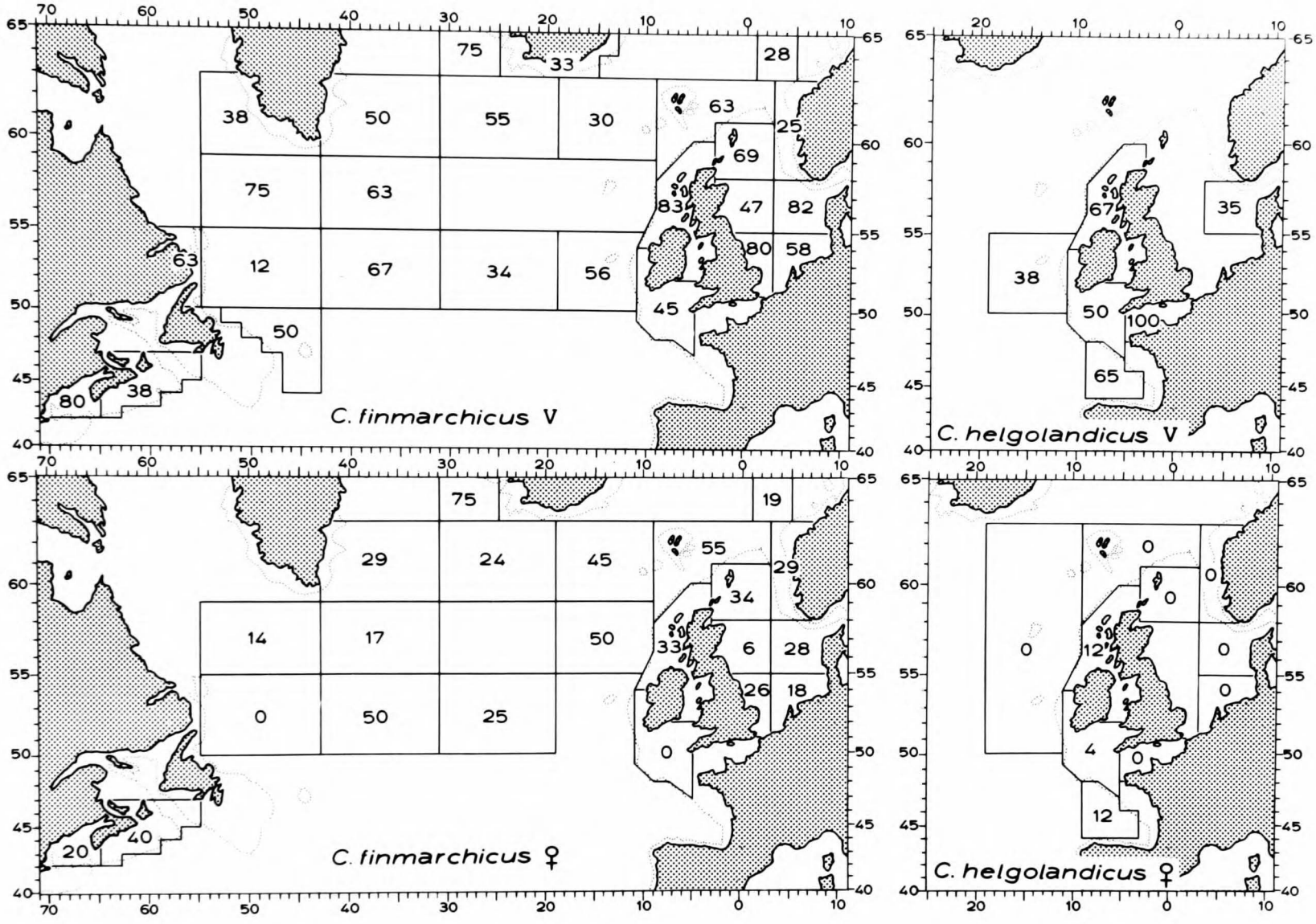


Fig. 19. Stage V and adult female Calanus finmarchicus and C. helgolandicus from the North Atlantic and North Sea, showing the percentage occurrence of an extra seta on the endopodite of the fifth limbs in July 1963.

between length and the temperature in June, approximately one month before the sampling described here (Fig. 20). The correlation coefficients between size and temperature in the samples of Calanus finmarchicus from the North Atlantic and North Sea were - 0.636 for stage V and - 0.844 for adult females, both coefficients being significant at the 0.1% level.

When C. helgolandicus was considered, a much weaker relationship with temperature emerged; the best was obtained with adult females and the temperatures in July (Fig. 21). The correlation coefficient was - 0.551, which is just significant at the 5% level. No significant relationship with temperature was observed in stage V C. helgolandicus, but there were only a few standard areas with samples of this stage as well as available temperature values.

CONCLUSIONS

These results confirm that the samples considered here contained three recognisable forms of Calanus finmarchicus s.l., identifiable as C. finmarchicus s. str., C. glacialis and C. helgolandicus. C. helgolandicus could be identified on morphological grounds alone and showed complete separation from the other two. C. glacialis, on the other hand, showed morphological continuity with C. finmarchicus and was best separated on the basis of the length of the metasome. These findings require further discussion but, first of all, they call into question the grounds for making a specific distinction between C. finmarchicus and C. glacialis.

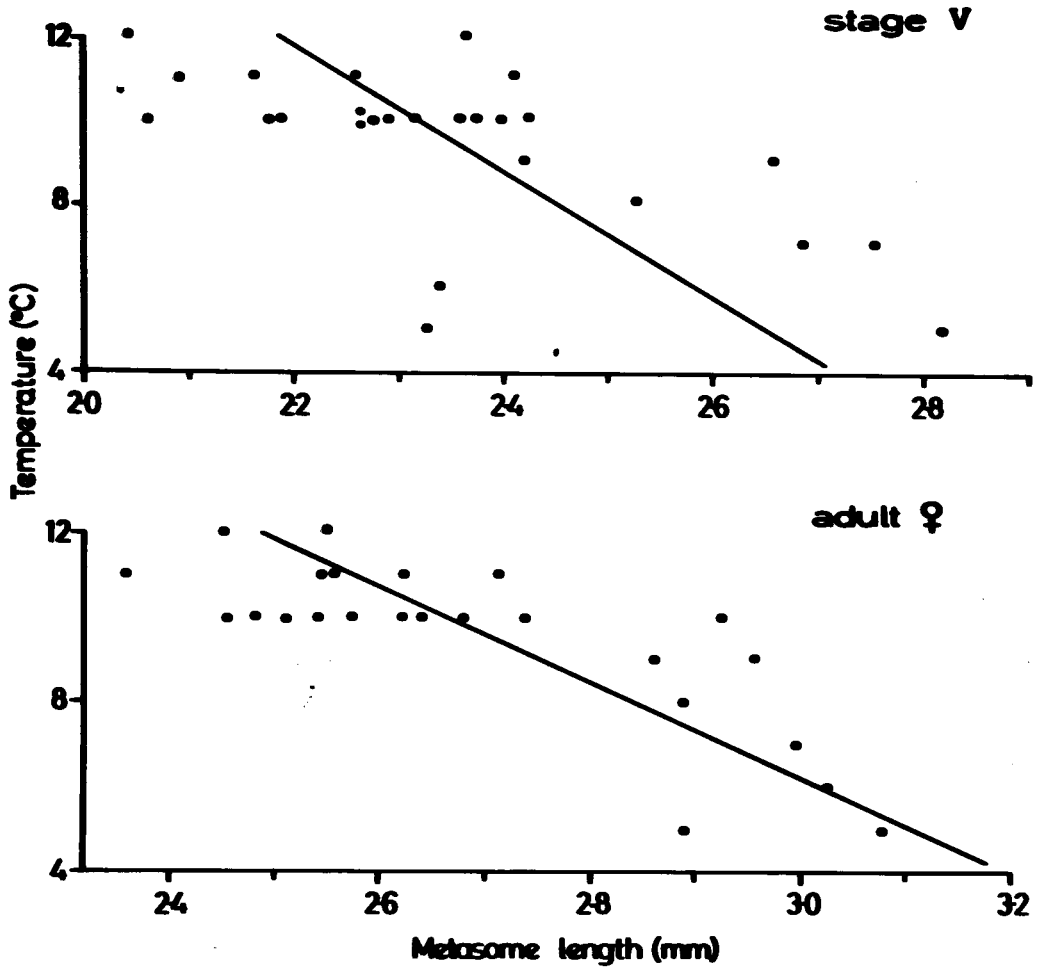


Fig. 20. Stage V and adult female Calanus finmarchicus from the North Atlantic and North Sea, showing the mean lengths of the metasome in July 1963 plotted against the estimated mean temperatures in the same large areas during June 1963. The regression of length on temperature has been projected.

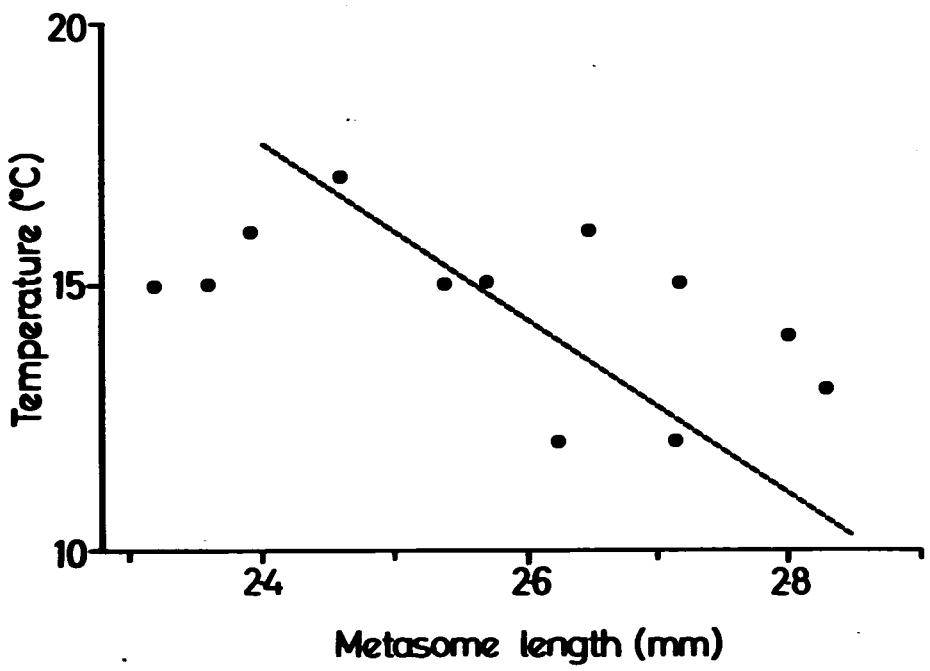


Fig. 21. Adult female Calanus helgolandicus from the North Atlantic and North Sea, showing the mean lengths of the metasome in July 1963 plotted against the estimated mean temperatures in the same large areas during the same month. The regression of length on temperature has been projected.

Morphological continuity between populations may be due either to genetic variation in a cline, resulting in subspecific differences or even the formation of a ring-species, or to allometry associated with changing environmental conditions; a combination of these alternatives is also possible.

The study of geographical variation showed significant relationships between sea surface temperature and the length of the metasome in C. finmarchicus. The morphological characteristics of C. glacialis were shown also to be related to the length of the metasome. It seems, therefore, a logical step at this stage to investigate the effect of temperature on the morphological characters investigated here and in this way to assess whether the basis for the observed allometry is phenotypic or genotypic.

EXPERIMENTAL INVESTIGATIONS ON *CALANUS FINMARCHICUS* S.STR.

INTRODUCTION

An inverse relationship between environmental temperature and body size is well known in many groups of poikilothermal animals. Relevant data on marine planktonic Copepoda have been collated by Deevey (1960, 1964, 1966). Huxley (1932) gives many instances of allometric relationships between size and various morphological characters. So far a direct relationship between temperature, or any other environmental factor, and a variable morphological character has not been demonstrated in any marine planktonic copepod. Yet information of this sort is essential if the basis of differences between populations is to be properly understood.

The following experiment was carried out with this aim in view, i.e. to assess the extent to which observed allometry was genetically controlled or environmentally induced. The allometric relationship with size particularly considered here was the curvature of the toothed border on the coxopodite of the fifth limbs. Other aspects of the effect of temperature on *Calanus finmarchicus* s.str., such as body length, development and growth rate, became apparent in the results of the experiment and are included here to indicate the range of effects controlled, at least partly, by temperature.

MATERIAL AND METHODS

The experiment was started on 16 April 1964 and concluded on 13 May.

Plankton samples were obtained from a single locality (off Garroch Head, Bute, in the Firth of Clyde) using plankton nets with 60 and 180 meshes per inch. Individuals required for the experiment were sorted as soon as possible after capture. Four individuals of stage I or II copepodids or two individuals of stage III or IV were placed in 100 ml beakers which were distributed between four constant temperature tanks. Each tank contained at least ten gallons of water in which the beakers were immersed almost to the brim. The warmest tank was supplied with a thermostatically controlled heater with a stirring propeller while the others each had a refrigerating coil, thermostatic control and aeration to ensure mixing. Glycol was added as an antifreeze to the water in the two coldest tanks. The degree of temperature control is shown in Table III.

TABLE III. Temperature control in the experimental tanks.

Tank	Temperature (^{o}C)
1	16 ± 1.2
2	10 ± 1.5
3	5 ± 1.3
4	0.5 ± 1.0

The tanks were checked on alternate days. The water in each beaker was replaced with recently collected water which had stood for some hours immersed in the same tank. At first the sea water was rich in phytoplankton, particularly Skeletonema, but as this later became scarcer, it was decided on the 13th day of the experiment to augment the food with

Syracosphaera. Standard quantities of concentrated culture were added to each beaker: for the first four days three drops per beaker on the days between checks, thereafter increased by the addition of one drop per beaker on check days.

Note was taken of any changes in condition of the copepods at each check and moulted cuticles were preserved in labelled tubes; adults and any dead specimens that had moulted at least once in the experiments were similarly preserved. Each specimen was stored with its own exuviae so that the development of each individual could be followed. Specimens were preserved in 5% formaldehyde solution. It was unfortunately necessary to end the experiment before all the specimens had completed development. This was more serious in the colder tanks where development was slow.

Investigation of the results was begun some three weeks after the end of the experiment, when all specimens were considered to have reached settled dimensions after possible distortion at preservation. The number of specimens obtained from each tank is given in Table IV. As the emergence of the copepod caused distortion of the moulted carapace, it was not possible to obtain total body or metasome lengths from the exuviae. In practice it was found convenient to measure exuviae and whole animals from the anterior border of the 1st antennal insertion to the postero-lateral tips of the metasome. A 4% addition converts this value approximately to the total metasome length.

TABLE IV. The number of moults into each copepodid stage.

Temperature (nominal)	Stage				
	II	III	IV	V	VI
15°C	4	10	29	49	11
10°C	1	9	24	46	21
5°C	5	9	29	33	2
0°C	1	6	15	10	0

Four specimens developed into Calanus helgolandicus. They have not been included in any of the calculations.

RESULTS

Size Variations

The speed of development was usually proportional to temperature, though in two cases development was as fast at 10°C as at 15°C. The former temperature was nearer that of the sea; the individuals kept at that temperature were therefore subjected to less environmental change on introduction into the experiment than the rest and might thus be expected to develop more satisfactorily. Table V shows the mean length of time spent at each stage using all specimens which passed through at least one complete stage in the experiment; only two specimens passed through two moults in the 0°C tank.

TABLE V. Mean length of time (in days) at each copepodid stage.

Temperature (nominal)	Stage			
	II	III	IV	V
15°C	4.0	8.2	8.9	9.3
10°C	4.0	8.5	8.0	10.0
5°C	8.4	10.5	11.8	16.7
0°C	16.0	18.0	-	-

The percentage increase in body length at moulting has been calculated in order to eliminate the effect of initial size differences between the groups. Table VI gives the mean increase in size and the level of significance for the trend at each moult, using the t-test. At each moult there was a discernible trend towards larger increases at lower temperatures. This was most marked in the case of the second and third moults where there was a high level of significance. The values obtained from the colder tanks do not always continue the trend. They are based on the few individuals which moulted quickly and may be lower than would have been obtained from the whole sample.

No attempt has been made on the basis of the present results to calculate the expected mean size of natural populations occurring in water masses of known temperature. Apart from the fact that such populations invariably develop in an environment with constantly changing hydrographic conditions and apart from the likelihood that they have been

subjected to such conditions over many generations, the specimens in the experiment showed a marked 'experimental effect' tending to reduce growth. Fig. 22 shows that individuals started in the experiment at Stage III were smaller on average at stage V than those started at stage IV. Despite this effect the temperature-dependent trends in each were closely similar.

TABLE VI. Mean percentage increase in metasome length.

Temperature (nominal)	Moult				
	I-II	II-III	III-IV	IV-V	V-VI
15°C	12.2	31.9	19.2	15.6	11.8
10°C	31.3	32.7	24.9	17.6	12.8
5°C	29.2	42.5	26.3	17.7	12.4
0°C	-	40.2	24.8	22.2	-
Significance *t*-test	10% (15-5°)	1% (15-0°)	1% (15-0°)	5% (15-0°)	- -

The percentage size increase of the fifth limb at the moult from stage IV to V has been chosen for investigation of the relative effects of temperature and time. This limb, which is first functional at stage IV, grows proportionately more than the body at the moult to stage V. The relationship between the two size increases, based on the present material, is:

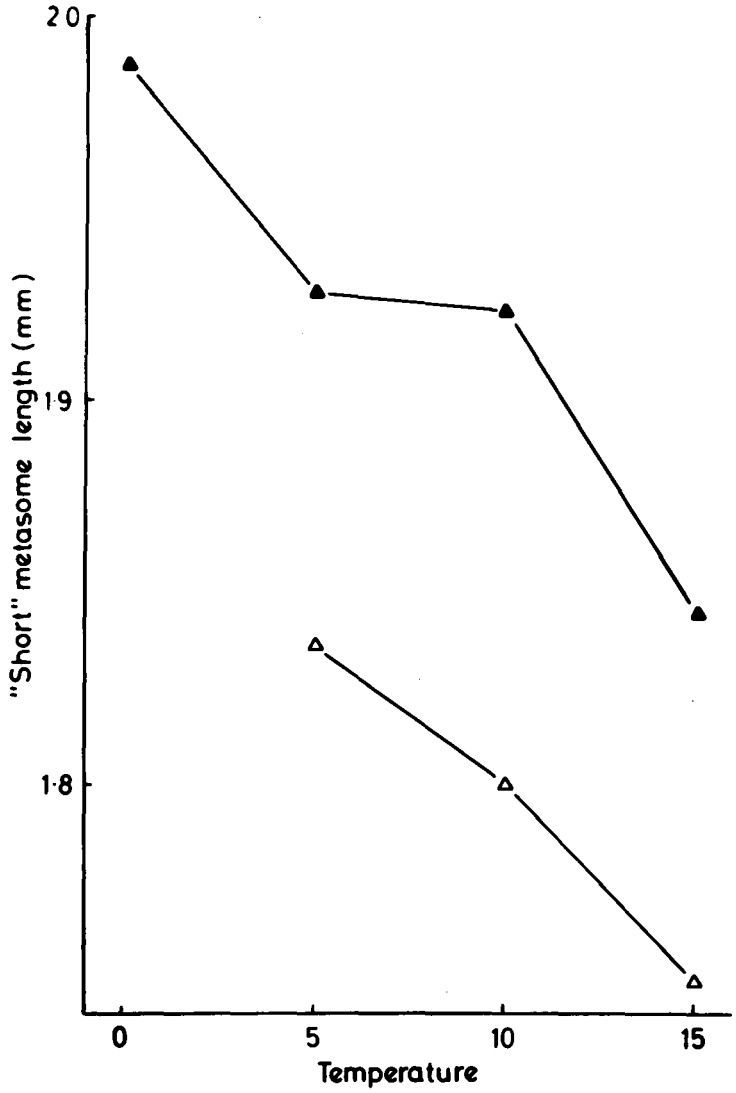


Fig. 22. Calanus finmarchicus, stage V, from the Clyde Sea Area. Mean length from the anterior insertion of the first antenna to the end of the metasome for specimens developing at four temperatures; open triangles - specimens introduced to the experiment at stage III; solid triangles - specimens introduced at stage IV.

$$G_1 = 1.4G_m + 15$$

where G_1 = % size increase of 5th limb,

G_m = % size increase of metasome.

It appears, therefore, that a lowering of temperature reduces the rate of development of Calanus copepodids while at the same time it increases their eventual size. It remains to be seen whether the temperature effect on growth is simply the result of the temperature effect on the rate of development or whether there is an additional direct effect. Fig. 23 shows the same set of data treated in two ways. The solid dots represent the mean percentage increase in size attained after a given number of days at the previous stage, regardless of temperature. Individuals from the 15°C tank tend to dominate at the left hand end, ones from the 0°C tank at the right. To eliminate this, the data have been weighted according to the mean temperature, the results being plotted as open dots. Scatter is greatly increased, showing that temperature exerts strong control over growth. The weighted data indicate a clearer relationship between growth and time; percentage size increases are greater after long periods, smaller after short periods. The scatter of temperature-weighted results may well be due to the emergence of a combination of factors not all of which act in the same direction; thus damage to an individual may delay development without encouraging growth, as will food shortage, while an abnormal hormone balance may delay moulting without affecting growth. The indication that temperature has a direct limiting

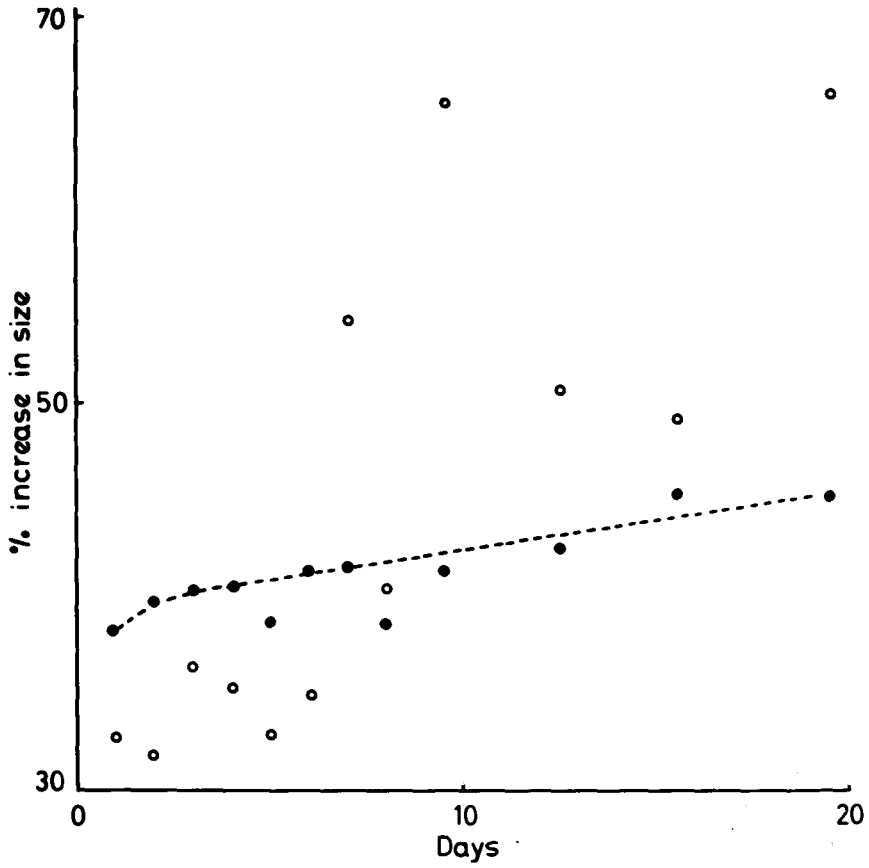


Fig. 23. C. finmarchicus, stage V, from the Clyde Sea Area. Mean percentage increase in length at moult from stage IV; solid dots, broken line - unweighted values; open dots, - values weighted for temperature.

effect on growth is best demonstrated by a study of the growth rate at each temperature expressed as the percentage increase per day, i.e. percentage increase at moulting divided by the time in days spent at the previous stage (Fig. 24). The regression equation for the growth rate of Calanus finmarchicus under the present experimental conditions is:

$$G^2 = 6.88\sqrt{t} + 9.0$$

where, t = temperature in degrees Centigrade at which development takes place,

G = growth rate, expressed as % increase per day.

Morphological Variations

The concavity or convexity of the inner coxopodite border of the fifth limbs has been measured and the mean results are presented in Fig. 25; all stage IV and V specimens started in the experiment at stage III or IV have been included (no stage III copepodids reached stage V in the 0°C tank). The figure demonstrates a positive relationship between temperature and the convexity of the border, a trend which culminates at 0°C in stage V copepodids showing a mean concave value, after one moult at this temperature. There is statistical significance, using the t-test at the 1% level, between 15° and 5°C and between 10° and 0°C.

Although the mean convexity of the border was closely similar among all stage IV copepodids put into each tank, there was a significant (0.1% level) trend towards greater convexity at lower temperatures among the stage IV copepodids produced during the experiment (Fig. 25). Despite this, the trend in curvature at stage V was the same whether the specimens

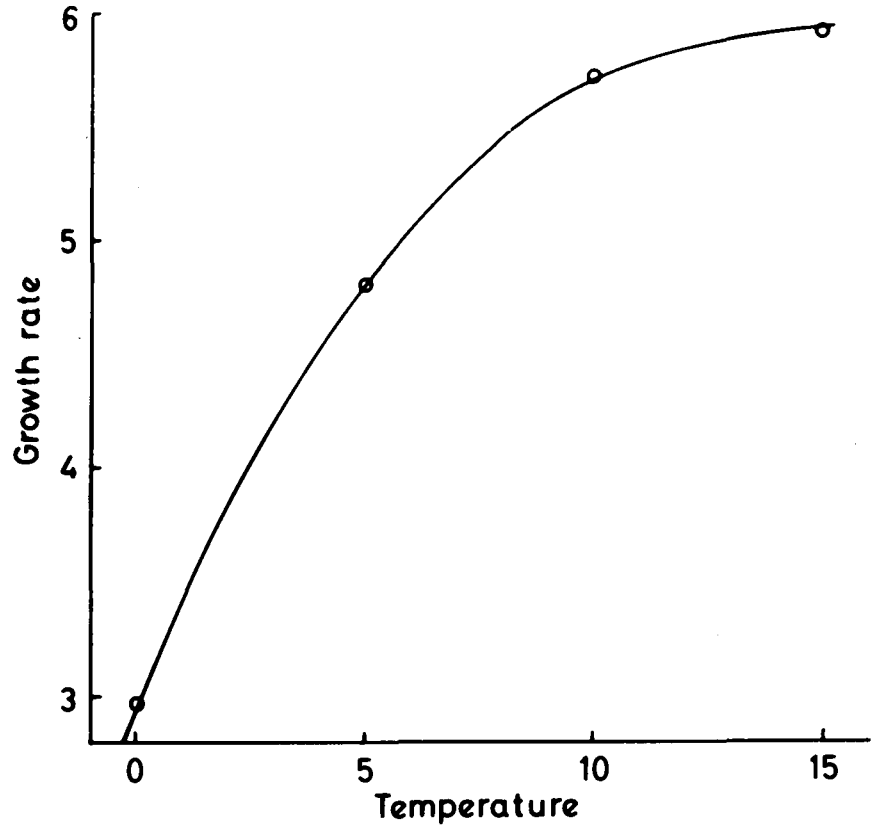


Fig. 24. C. finmarchicus, from the Clyde Sea Area. Mean growth rates of stage IV copepodids, calculated from the growth at the moult to stage V and the length of time spent at stage IV.

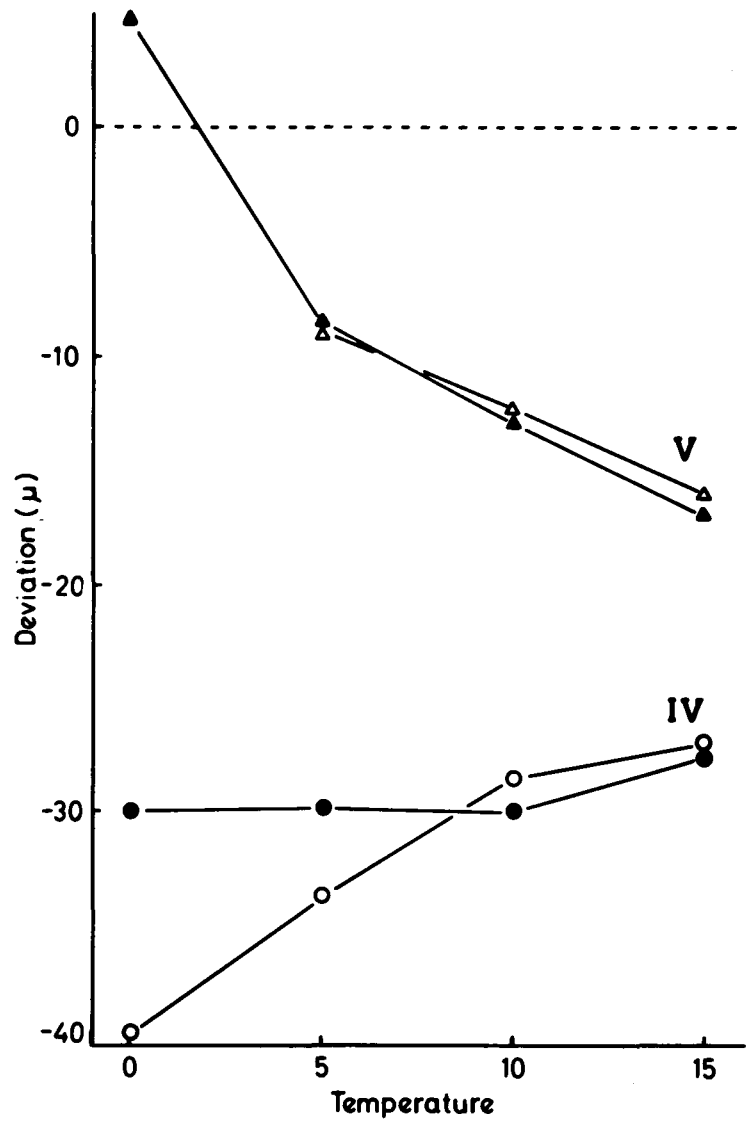


Fig. 25. C. finmarchicus, from the Clyde Sea Area. Mean deviations from a straight line of the fifth limb toothed border. Broken line represents a straight border; negative values represent convexity; open symbols - specimens introduced to the experiment at stage III; solid symbols - specimens introduced at stage IV.

had been introduced into the experiment at stage IV or at an earlier stage. It seems, therefore, that the curvature of the border was determined by conditions at the time of moulting rather than by the history of conditions during development.

In order to assess correctly any allometry shown by Calanus, angular measures of curvature have been calculated (see Fig. 9) which incorporate the size of the specimens. Fig. 26 shows the results of these calculations; all specimens which moulted at least once in the experiment have been included. There was a clear progression from strongly convex borders in stage IV towards straighter or even concave borders in stages V and VI. Whereas the stage IV borders were more convex at low temperatures, the trend was reversed at stage V and there was an indication that this was asmarked or more so at stage VI.

The frequency with which a second seta occurred on the outer margin of the last endopodite segment (see Fig. 4, S) was next investigated. The percentage occurrence of double setation is given in Table VII. Very few specimens (6 out of 159) had one seta on one limb and two on the other, so these have been ignored and the percentage calculated from single limbs. One specimen which had single setation in stage V developed double setation in the adult, the second setae developing at the positions of small notches discernible in stage V; otherwise all adults had the same setation as the stage V. No specimens at stage IV were found with double setation. There was a marked increase in the occurrence of double setation at lower temperatures, a trend which occurred in both the larger groups (starting stages III and IV) separately as well as combined.

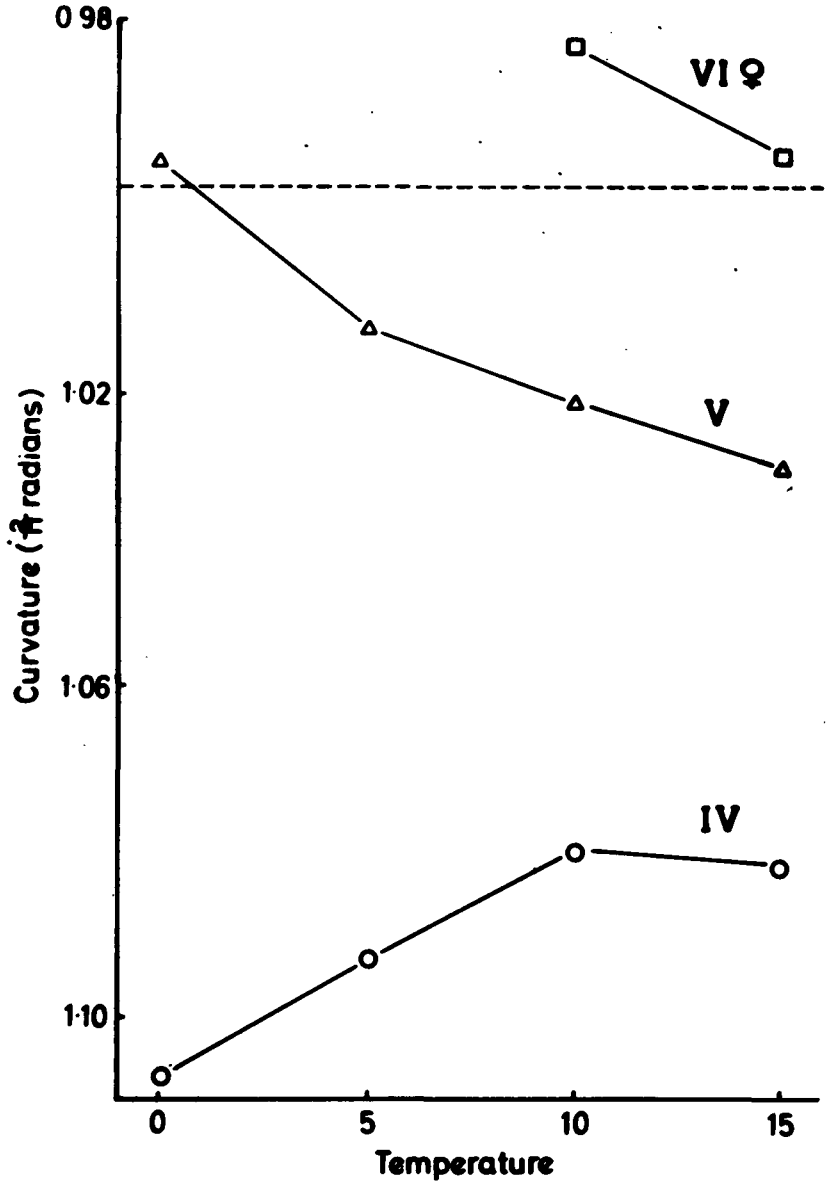


Fig. 26. C. finmarchicus, from the Clyde Sea Area. Mean curvature of all specimens after at least one moult under experimental conditions. Values above the broken line represent concavity, those below convexity.

TABLE VII. Percentage occurrence of double setation on 5th limb endopodite.

Temperature (nominal)	Stage V
15°C	37.3
10°C	37.0
5°C	52.4
0°C	66.7

The number and size of the teeth on the coxopodite of the fifth limb were also investigated. These teeth first appeared at stage IV, grouped towards the inner margin of the coxopodite about half-way along its length; there might be up to ten or eleven but the average was about three. At stage V, the teeth were much more numerous and were arranged in a single marginal row, sometimes with some doubling near the base. In the present material the mean value dropped steadily with temperature from 27.2 teeth at 15°C to 25.4 at 0°C; this is not, however, statistically significant. At the final moult the number again increased, to mean values around 31. At stage IV, when the teeth were dispersed and their bases distinct, values for tooth size tended to be greater than at stages V and VI where the bases of the teeth had coalesced. It is doubtful, however, if there was any real difference in tooth size during development. No trend was discernible with temperature.

CONCLUSIONS

Numerous investigations (e.g. Gurney, 1929; Ruud, 1929; Bogorov,

1934; Clarke and Bonnet, 1939; Deevey, 1960, 1964, 1966; McLaren, 1963; Kovalev, 1964; ElMaghraby, 1965; Nesmelova, 1966) have shown an inverse relationship between size and temperature in marine copepods and the same is well known in other groups. Coker (1933) demonstrated this temperature effect on size in experiments with Cyclops. The present results confirm this effect on Calanus and show that it is due to the retardation of the growth rate at low temperatures being correspondingly less than the retardation of the rate of development.

Foremost among the morphological characters used in the identification of C. glacialis (Jaschnov, 1955, 1957a) is the shape of the toothed coxopodite border of the fifth limbs. The results from the experiment show that a trend towards greater convexity at lower temperatures in stage IV copepodids is reversed in stage V and adult females; there is an association in these stages between cold water and concave borders. The other characters used were only applicable to whole samples. For the first of these, the number of teeth on the coxopodite border, Jaschnov found that the range of variability was greater in C. finmarchicus than in C. glacialis. The size range of specimens in the experiment was not wide enough for a change of this nature to be detected. The second character, endopodite setation, is applicable to the experimental results. The experiment showed there to be an inverse relationship with temperature consistent with Jaschnov's findings (1957a) that double setation was more common in C. glacialis than in C. finmarchicus.

There is, however, one point of difference between the experimental results and those of Jaschnov (1957a) in the setation of stage V copepodids and adult females of Calanus finmarchicus s. str. Jaschnov found 93% double setation in his samples of stage V, compared with 27% in adult females. Even allowing for 50% of males, this still suggests that many individuals lost a seta in the final moult. No specimens in the experiment lost a seta and one gained a second on each fifth limb at this moult. Jaschnov's widely different counts may be due to a seasonal effect resulting in a difference between generations. Seasonal variation in size associated with different generations has been demonstrated in many areas (e.g. Adler and Jespersen, 1920; Marshall, 1933). Since larger specimens have a higher percentage of double setation, it is conceivable that, when large copepodids appear together with small adult females from the previous generation, setal counts of copepodids and adults will be very different. This argument can only be applied to populations with more than one generation in the year, as is the case with Calanus in the Norwegian Sea (Wiborg, 1954) where the adults investigated by Jaschnov were obtained. Conversely, a population with only one generation in the year should show similar counts in stage V and adults. This is borne out by Jaschnov's figures for C. glacialis. Adult females had a percentage occurrence of double setation of 49%. Allowing for a maximum ratio of one male to one female (this cannot be calculated from the proportion in the plankton since males are short-lived) this percentage is equivalent to a maximum

of 75% for all adults. The value given of 65% for stage V copepodids is thus consistent with the experimental finding that setae are not lost in the final moult.

GENERAL DISCUSSION

The biometric investigations into C. finmarchicus and C. helgolandicus support the conclusions of most authors in recent years that they are distinct species. Morphological discontinuity between the two, despite breeding distributions that are at least partly sympatric, is a firm indication of specific difference. Other points in favour of this view are the ecological differences in seasonal fluctuations and annual cycles (Rees, 1949; Russell, 1951; Jaschnov, 1958), a different pattern of egg-laying behaviour (Marshall and Orr, 1955), indications of chromosome differences (Harding, 1963), independent variations in body length (cf. Sars, 1903; Rose, 1933; Mauchline, 1956; Brodsky, 1959) and differences in enzyme composition (Manwell, Baker, Ashton and Corner, 1967). The experiment on C. finmarchicus, moreover, showed no sign of a temperature-dependent trend towards features characteristic of C. helgolandicus. Concavity of the toothed border was greater at lower, not higher, temperatures, so that the trend was in the opposite direction from that expected from the field data if there had been a morphological link between the two species.

The relationship between C. finmarchicus and C. glacialis, on the other hand, appears to be much closer. Bimodality in length frequency is certainly a regular feature in samples from mixed Atlantic and Arctic water. The connection between Arctic water and the large specimens and between Atlantic water and the small specimens has been well established

(e.g. Jaschnov, 1961, Grainger, 1963). This is not, however, sufficient evidence for sustaining the specific identities of the groups; size is too variable a character to be useful taxonomically and its dependence on temperature has been established experimentally in copepods (e.g. Coker, 1933) and, in Calanus, in particular, in the previous section. Numerous investigations on various copepods (e.g. Gurney, 1929, Ruud, 1929, Clarke and Bonnet, 1939, Deevey, 1960, McLaren, 1963, Kovalev, 1964, El-Maghraby, 1965) have shown this inverse relationship between size and temperature in the sea. A wide range of size may, therefore, be expected in a species with a wide range of temperature tolerance.

Morphological characters may be expected to be a more reliable systematic guide but care is needed to ensure that such characters are not the result of allometric growth and are not affected by environmental conditions. Foremost among these characters is the form of the toothed border of the fifth limb in the female and stage V copepodids. The results described here show a trend associated with size and give no indication of separation into two groups; the apparent rarity of specimens with borders of intermediate concavity is due to the rarity of specimens of intermediate size. The relationship between this character and temperature during development has been confirmed in the experiment on Calanus described above. The remaining characters that Jaschnov (1957a) used could be applied only to the identification of populations (as "finmarchicus" or "glacialis") and not to individuals. Neither tooth

size nor endopodite setation showed any discontinuity when considered in relation to the length of the metasome; and the only suggestion of separation came from the restriction in the range of tooth number but this occurred at a point which did not exactly correspond with the separation based on size. Setation, moreover, showed an inverse relationship with temperature in the experiment, consistent with Jaschnov's findings (1957a) that double setation was more common in C. glacialis than in C. finmarchicus. Jaschnov added that two external setae were more common in northern than in southern species. It may be that this is related to the need to maintain functional efficiency with increase in size; the number of setae sufficient to provide an efficient swimming web around a small limb will be inadequate when spaced out around a larger limb. It is worth noting that in males of Calanus finmarchicus s.l. and C. hyperboreus where the fifth limb exopodites are devoid of setae, the endopodite invariably has two external setae.

Grainger (1961) has said that specimens of a size intermediate between C. finmarchicus and C. glacialis could usually be identified on the basis of the curvature of the toothed border. It can be misleading, however, to use two alternative characters in identification. The mean relationship established between size and curvature has been obtained from a large number of individuals, most of which possessed a border either more or less concave than normal for their size. Thus of the few specimens of intermediate size whose identities were in doubt, still fewer

possessed a border of intermediate curvature (see Huxley, 1932, pp. 210-212, for a discussion of transgressive characters).

Grainger (1963) also noted that samples obtained from Nova Scotia northward to Baffin Bay appeared to indicate that C. finmarchicus s. str. was largest in the centre of the region, decreasing in size towards both south and north. He attributed this decrease to increased mixing of Arctic with Atlantic water. As far as the decrease in the south is concerned it seems difficult to assess the relative effects of mixed water and of increase in temperature at lower latitudes. In the north, ice prevents surface sampling in the winter and such sampling in the spring starts later the further north one penetrates. Thus the samples which Grainger considered from the North Labrador Sea and east Hudson Strait were obtained in June and early July, the samples from east and north-east Davis Strait and from Baffin Bay not until late July and September. Experience in other areas (e.g. Adler and Jespersen, 1920, Marshall, 1933, Clarke and Zinn, 1937, Ussing, 1938) suggests that the observed differences may be explained by a seasonal change in size.

There has been a suggestion that the eggs of C. glacialis may be different from those of C. finmarchicus. The former apparently lay eggs with a distinct space between the outermost membrane and the egg itself, while the eggs of the latter typically show no such space. Eggs of the "glacialis" type have been obtained in the laboratory from C. glacialis caught in the Gulf of Maine (Conover, personal communication) and from

individuals, which may have been C. glacialis, caught near Tromsø in northern Norway (Marshall and Orr, 1955, p.7). No eggs intermediate between these two types have been recorded. Having noticed the existence of different types of eggs, the late Dr A.P. Orr made some further observations during a cruise of F.R.S. Scotia north of Scotland in 1953 (Marshall, personal communication). Ripe female Calanus were collected daily and the eggs they laid were examined one day later. Females laying "glacialis" eggs increased from 0% at 60°10'N to 17% at 63°45'N, although C. glacialis itself (or "large C. finmarchicus" before 1955) has not been recorded from the area. This suggests that there is variation in the proportion of females of C. finmarchicus laying eggs of the "glacialis" type and that this proportion increases from south to north, within the area where C. finmarchicus occurs without C. glacialis. The laying of such eggs by C. glacialis might thus represent the end of the trend.

It seems, therefore, that the only indication of separation into C. finmarchicus, s. str. and C. glacialis is the difference in size between Arctic and Atlantic specimens and the bimodality of the size frequency of samples from mixed water. There is no difficulty in accounting for the size difference on the basis of varying environmental factors, chiefly temperature, but it still remains to elucidate why so few specimens occur in the intermediate size range.

The sub-Arctic region of the Atlantic sector of the world's ocean system is small and indistinct in comparison with the great volumes of water in both the Arctic and the temperate North Atlantic. Sub-Arctic

conditions are restricted to the currents, chiefly the East Greenland Current, flowing out of the Arctic basin by way of the Irminger and Norwegian Seas, to the variable but narrow boundary between Arctic and Atlantic water in the Barents Sea area and to Baffin Bay and part of the Labrador Sea. The Labrador Sea and Baffin Bay form the only part of the sub-Arctic which might be stable enough for the establishment of indigenous populations. The capacity of Baffin Bay has been estimated as 536,000 km^3 (Kossinna, 1921) and of the Labrador Sea, very approximately, as 1,000,000 km^3. Hachey (1961) estimated the annual inflow into the area at 157,000 km^3 from the West Greenland Current and 45,000 km^3 from the Canadian Archipelago. Excluding any backwaters in the system, there is thus a complete change of water in approximately eight years.

This estimated rate of changeover allows little opportunity for an indigenous population to become established under sub-Arctic conditions; the fauna instead will be characteristic of the mixed waters of origin. A planktonic species occurring in both the North Atlantic and the Arctic and showing evidence of clinal variation may, therefore, be expected to show bimodality of the variable characters in any sample from sub-Arctic regions. Such bimodality in the length of Calanus finmarchicus/glacialis cannot, therefore, be taken as evidence of specific differences between the populations.

The morphological, experimental and ecological evidence thus indicates no specific difference between Calanus finmarchicus and C. glacialis. It

is suggested, accordingly, that C. glacialis should be relegated to the rank of sub-species, C. finmarchicus glacialis, Jaschnov 1955, whose distinguishing characters are associated with an Arctic distribution. This conclusion is based entirely on material from the Atlantic sector of the world's ocean system and can be expected to have most relevance in that sector. Elsewhere rather different situations may occur as either subspecies meets other populations within C. finmarchicus s.l.

It must be emphasized that this conclusion in no way invalidates the ecological and zoogeographical work that has been carried out in the western North Atlantic on the assumption of specific differences. In fact, since the emphasis has now moved from genetic to environmentally induced differences between the populations, the value of C. f. finmarchicus and C. f. glacialis as indicators of water masses is enhanced. Metridia longa, Calanus hyperboreus and Acartia longiremis are all found far north in the Arctic but their distribution is not restricted entirely to such waters. The occurrence of these species outside the Arctic does not, therefore, imply the presence of Arctic water. Since C. f. glacialis is a product of Arctic conditions its occurrence in the North Atlantic does imply the presence of Arctic water.

Some remarks by Sewell (1948, p. 386) form an apt conclusion to this discussion: "It seems to me that the evidence that we have been studying indicates that the copepods are extremely plastic, and that as we trace the distribution of any given species along the current system in which it

is living, the parent form, when it reaches an area of different physical and chemical composition, may give rise to offspring that differ from the parent in size and even in structure, so that, perhaps not infrequently, the two forms have been described as different species. The presence of two such forms in different oceans must not therefore be taken to be evidence in favour of the specificity of the fauna of the two regions but rather as evidence of continuity, either at the present time or in the past, of distribution".

PART II

ON THE ECOLOGY OF *CALANUS FINMARCHICUS* S.L.

SOME COMPARISONS BETWEEN *CALANUS F. FINMARCHICUS* AND OTHER COPEPODS IN THE ATLANTIC OCEAN SOUTH-EAST OF GREENLAND.

INTRODUCTION

Ecological investigations may be divided conveniently into those which concern the actions of single populations and those which concern the interactions between the populations within a community. The investigations which comprise the second part of this thesis are chiefly of the first type and concern the geographical and seasonal distributions of *Calanus f. finmarchicus*, *C. f. glacialis* and *C. helgolandicus*, the annual cycle of *C. f. finmarchicus* on the Scotian Shelf and the timing of its spring generation in the waters around Greenland. In concentrating on *Calanus* in isolation from the rest of the planktonic community in which it lives, however, it is easy to lose sight of one of the most striking characteristics of its ecology. Sars (1903) states, "Of all the marine calanoids of Norway, this form /*C. f. finmarchicus*/ is by far the most common, occurring often in enormous shoals", and Grainger (1961) comments, "The copepod *Calanus finmarchicus* has long been considered as one of the most abundant and most important planktonic species in all northern seas".

In introducing these investigations on the ecology of *Calanus finmarchicus* s.l., this section is intended to take note of its extraordinary abundance. For this purpose, results from a series of plankton samples taken during the second NORWESTLANT Survey are used to study associations between *C. f. finmarchicus* and a number of other large

calanoids, greater than 3mm in body length. Since no account has been taken of the representatives of the other groups present in the zooplankton at the same time, this investigation is necessarily limited in scope; but, nevertheless, as the copepods form one of the most abundant groups of animals in the plankton, a general impression of the importance of Calanus may be gained.

MATERIAL AND METHODS

During the second NORWESTLANT Survey, R.V. Anton Dohrn sampled a series of about 150 stations extending over an area south-east of Greenland, between 24th May and 24th June, 1963 (Fig. 27). 73 stramin net samples containing copepods were sent to the Oceanographic Laboratory, Edinburgh, for analysis.

Additional information given for each station included the time and duration of hauling, the sea depth and surface temperature.

Preliminary sorting of the material had been carried out before dispatch from Germany. As copepods usually formed the bulk of the samples they had been left as the main constituent of the residue after the other main groups had been removed. In the larger samples, of known total volume, a suitable sub-sample was removed, its volume determined and the copepods analysed. In the smaller samples a Hopkins tray (Hopkins, 1962) was used and 1/25th removed for analysis; occasionally the whole sample was examined. All these samples had been taken from approximately 50 m. to the surface but, as the length of haul varied

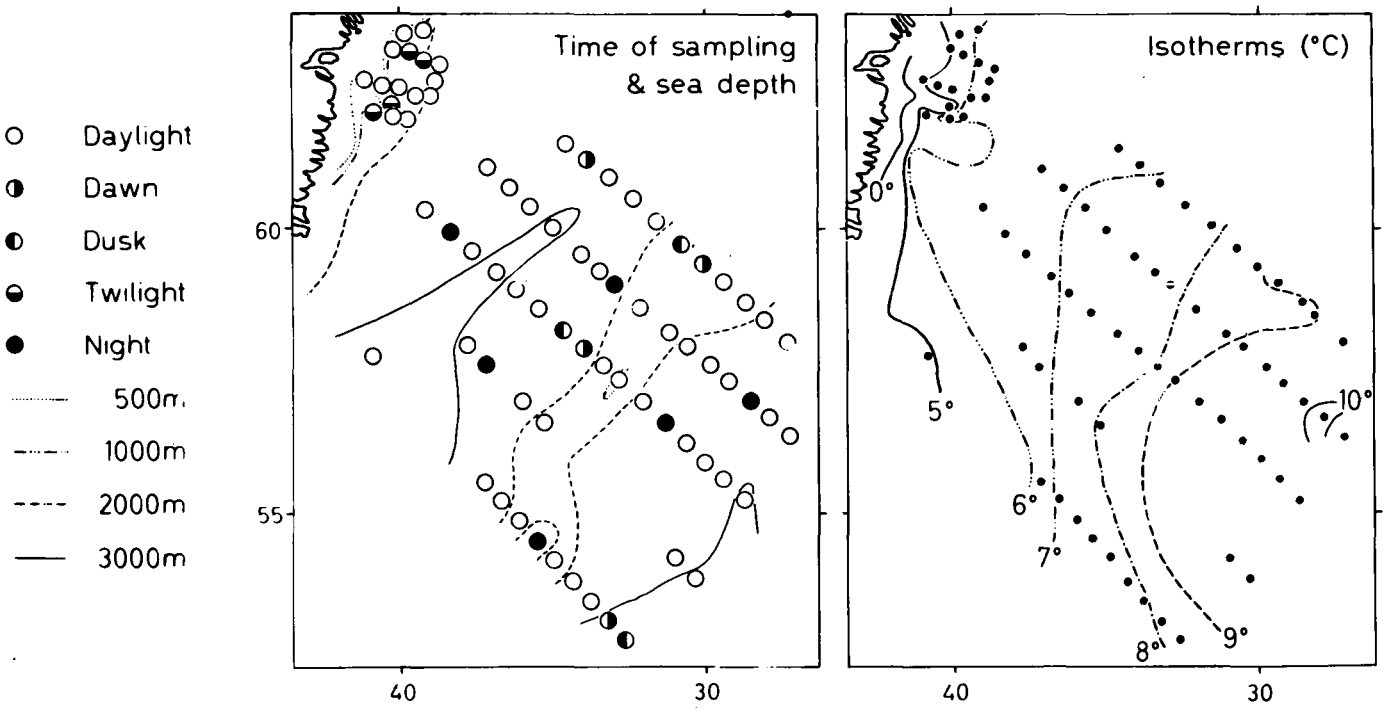


Fig. 27. The stramin net samples taken by R.V. Anton Dohrn during NORWESTLANT II, showing the time of sampling, depth contours and surface isotherms.

from 20 to 40 minutes, the results were converted to a standard half-hour haul.

The lower size limit for satisfactory retention by the stramin net appeared to be about 3 mm in body length. Smaller specimens were occasionally found but it is considered that these cannot be investigated further. 12 species or subspecies of larger calanoids were recorded in the samples. Calanus f. finmarchicus or Euchaeta norvegica dominated in all samples; occasionally Calanus hyperboreus was present in comparable numbers and in these samples its biomass exceeded that of the other species. The other widespread species were Heterorhabdus norvegicus, Euchirella rostrata and Rhincalanus nasutus, the last two being rather patchy.

In some species the size of the sample was evidently affected by the time of day when the haul had been taken. In these cases the number of individuals in each sample was plotted against the time of day (defined as the nearest quarter-hour to mid-haul) and the mean for each four-hour period calculated; these means were all based on 11 to 13 samples. Where these values showed a clear pattern of diurnal rhythm, a conversion factor was calculated for each quarter hour, in order to standardise all values to the highest point on the curve. The converted values have been termed night standard values (n.s.v.).

Temperature and depth characteristics have been calculated for each species and are presented as the mean temperature or depth for the occurrence of the species. Attempts have been made to classify the

copepod species in relation to these parameters, using the difference between the species and Survey means. Over most of the Survey area there was little relationship between temperature and sea depth. The three shallowest samples were, however, the coldest, due to the East Greenland Current flowing close to the coast. Since these three stations showed such a strong bias, they have been excluded from all studies of depth characteristics.

RESULTS

Systematic Account.

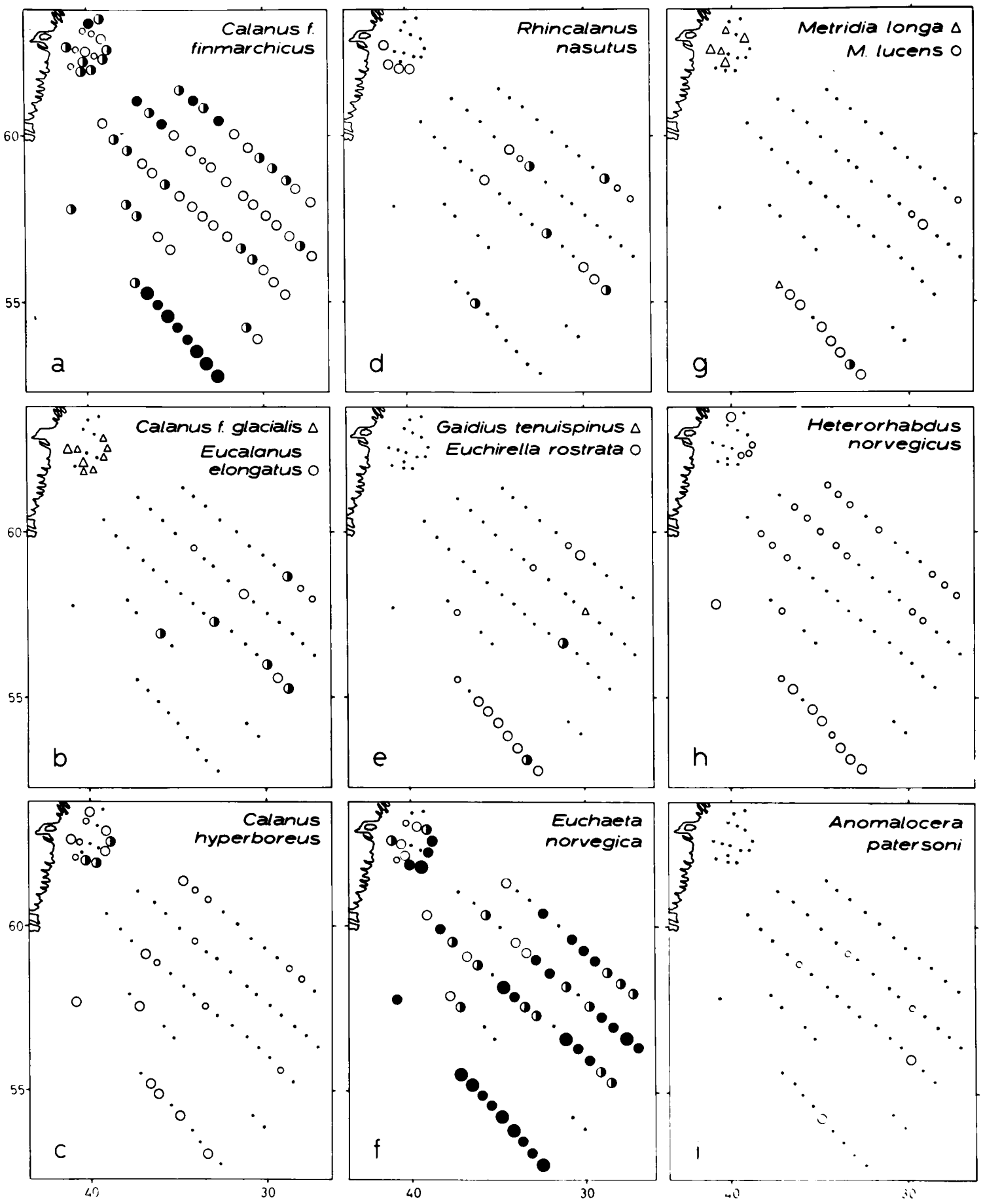
Calanus f. finmarchicus (Fig. 28a)

Adults and stage V copepodids were satisfactorily retained by the net. It was the most widespread copepod species and occurred at every station for which there was a copepod sample. Adult females were most abundant in the southern part of the Survey area. Adult males were similarly distributed, though they occurred in much smaller numbers. Stage V copepodids were also most abundant in the south but were quite common, too, in the more northerly parts of the Survey area where they sometimes predominated over the adults.

C. f. finmarchicus occurred throughout the full range of temperature in the Survey. Its mean temperature of occurrence was close to the mean for the Survey, suggesting that its centre of distribution approximates to the centre of the Survey. The mean depth over which C.f.finmarchicus was caught was considerably greater than the mean for the Survey

	a	b	c	d	e	f	g	h	i
·	0	0	0	0	0	0	0	0	0
o	<100	<10	<100	<10	<100	<100	<100	<100	1
O	<1000	<50	<1000	<100	<1000	<1000	<1000	>100	>1
◑	<10,000	>50	>1000	>100	>1000	<10,000	>1000		
●	<100,000					<100,000			
●	>100,000					>100,000			
△		<100			1		<100		
△		>100					>100		

Fig. 28. Charts of distribution of calanoid copepods. The key indicates the levels of abundance represented by the symbols in each of the charts, a - i.


Calanus f. finmarchicus
a
Rhincalanus nasutus
d
Metridia longa △
M. lucens ○
g
Calanus f. glacialis △
Eucalanus elongatus ○
b
Gaidius tenuispinus △
Euchirella rostrata ○
e
Heterorhabdus norvegicus
h
Calanus hyperboreus
c
Euchaeta norvegica
f
Anomalocera patersoni
i
60
55
40
30

although again it occurred throughout the available range of sea depths. This suggests that the main distribution of this species is in oceanic areas.

Little can be deduced about a possible diurnal rhythm. Adult males, females and stage V copepodids all followed closely similar patterns of sample size in relation to time of sampling (Fig. 29). There was a progressive rise in the average size of sample from midnight until a peak was reached between 8 a.m. and 12 noon after which there was a decrease until about 6 p.m. A second, smaller, peak, represented by the mean values for the period 8 p.m. to midnight, then occurred. There was, therefore, no tendency for catches to be highest in the dark and conversion factors seem not to be justified.

Calanus f. glacialis (Fig. 28b)

This species was restricted entirely to the coldest water in the Survey, close to the east coast of Greenland. It was the most strongly Arctic of all the copepod species with mean temperatures of occurrence of 1.7 (adult females) and 2.2°C (Stage V) and a maximum of 6.1°C. No deduction as to its distribution in relation to sea depth can be made, since such cold water was restricted to the Greenland continental shelf.

So far north there was little darkness at night and no diurnal rhythm was apparent.

Calanus hyperboreus Krøyer (Fig. 28c)

Adult females and stage IV and V copepodids were present in the samples. The species was widely distributed throughout the Survey area

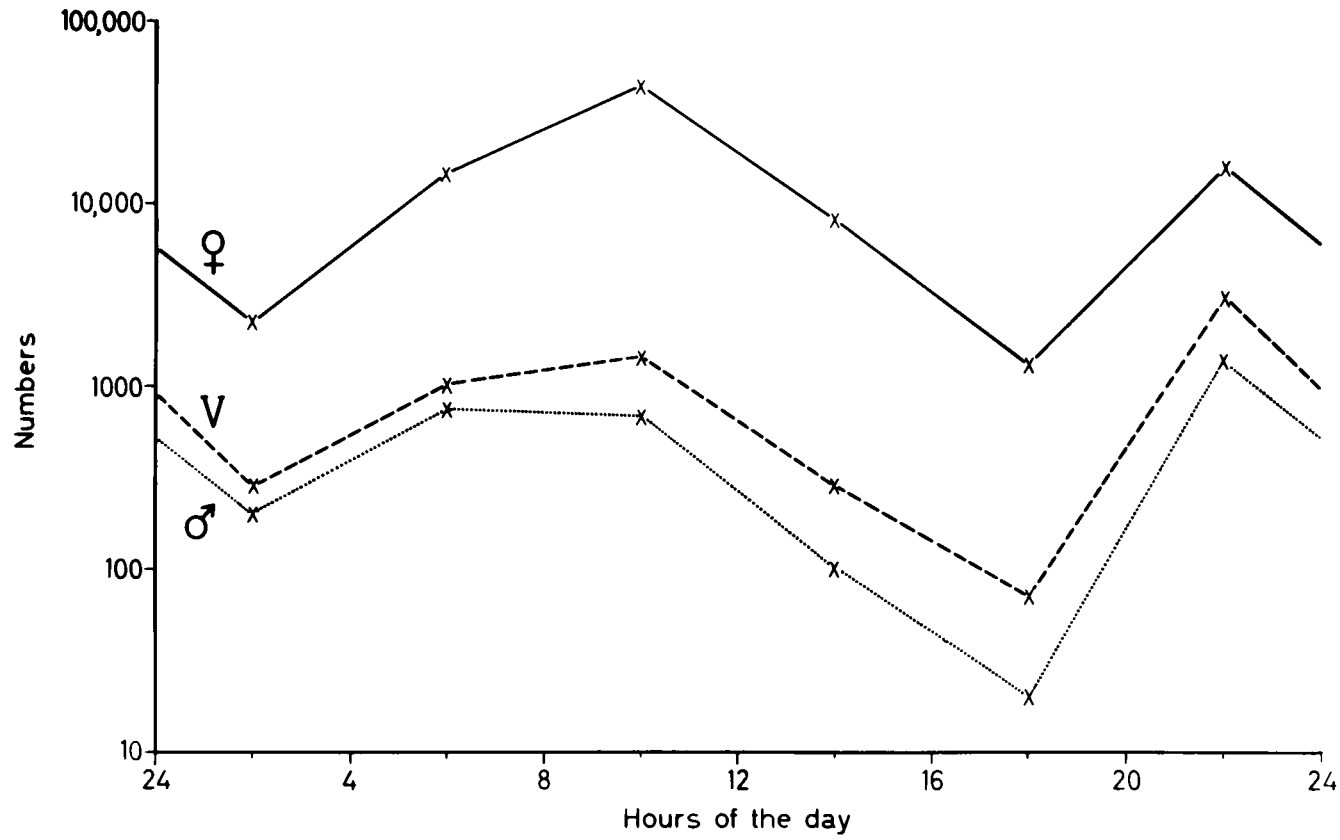


Fig. 29. The mean size of sample of Calanus f. finmarchicus obtained during each four-hour period of the day.

though it showed a tendency towards greater concentrations in the coastal and off-shore region near Greenland; only here did samples exceed 1,000 individuals.

The mean temperatures of occurrence were between 6.0 and 6.3°C, with adult females having the highest average. This is 1 - 1½°C lower than the Survey mean and seems to indicate that the centre of distribution of this species lies to the north of the centre of the Survey.

Despite the exclusion of the cold shallow water samples, Calanus hyperboreus still occurred mainly in the samples taken over shallower depths; the mean depth of sea for the occurrence of this species was 280 to 500 m less than the mean for the Survey. No diurnal rhythm was apparent.

Eucalanus elongatus (Dana) (Fig. 28b)

Adult females predominated with a few stage V copepodids present. Numbers were small, reaching 100 in one sample, and the distribution was restricted to the south-eastern part of the area.

No specimens were taken where the surface temperature was less than 7.3°, and the average was 9.0°C, 1½° above the mean for the Survey. This was the highest mean value obtained and it seems certain that the centre of distribution of the species lies in warmer water than that of the Survey.

The mean depth of sea for the occurrence of this species was a little less than the mean for the Survey, suggesting that it is not wholly

oceanic in its distribution. The low numbers obtained showed no diurnal rhythm.

Rhincalanus nasutus Giesbrecht (Fig. 28d)

The records of this species come from two distinct areas. The first, in the south-east, is similar to that of Eucalanus elongatus; the other, separated from the nearest record in the south-east by 200 miles, is a patch of four samples on the southern edge of the area sampled near the coast of Greenland. The presence of this patch exclusively in the south of the coastal area suggests that it had not been carried south by the East Greenland Current.

The mean temperature for the records of Rhincalanus was only slightly (0.7°C) higher than that for the Survey as a whole. Its centre of distribution, therefore, may not be far removed from the centre of the Survey.

The mean depth of sea for the occurrence of this species was close to the mean for the Survey. No diurnal rhythm was apparent.

Gaidius tenuispinus (Sars) (Fig. 28e)

Only one specimen, an adult female, was obtained. It occurred in a haul taken at 19.00 hrs. in a depth of 2410 m and at a temperature of 9.0°C.

Euchirella rostrata (Claus) (Fig. 28e)

This species only occurred on or to the south-east of the Reykjanes Ridge, most commonly on its south-eastern slope. Though it never occurred at a temperature below 6°C, its mean temperature of occurrence

was a little less than 1° above the Survey mean. The mean depth of sea for the occurrence of this species was almost 200 m greater than the Survey mean. These facts suggest that this species is distributed mainly in the deeper parts of the North Atlantic with a centre of distribution displaced only slightly south of the centre of the Survey. Only five out of the 13 records of the species were from daytime hauls but the data were insufficient for the calculation of night standard values.

Euchaeta norvegica Boeck (Fig. 28f)

This abundant and widespread species occurred in all but 17 of the samples and on several occasions was the dominant species of copepod. Adult females and stage IV and V copepodids were present.

The relationship between size of sample and the time of day when it was taken revealed a diurnal pattern (Fig. 30). Conversions to night standard values were made accordingly and further study has been based on these values.

The species was consistently abundant in the south-western part of the Survey area and extended in two bands of abundance along the south-eastern and north-western slopes of the Reykjanes Ridge and again over the lower part of the continental slope off Greenland.

The mean temperature of occurrence was very close to that of the Survey, suggesting that the centre of distribution of this species is near the centre of the Survey, although it is known to range widely to the north and south. The mean depth of sea for the occurrence of E. norvegica was also near that of the Survey as a whole. Though

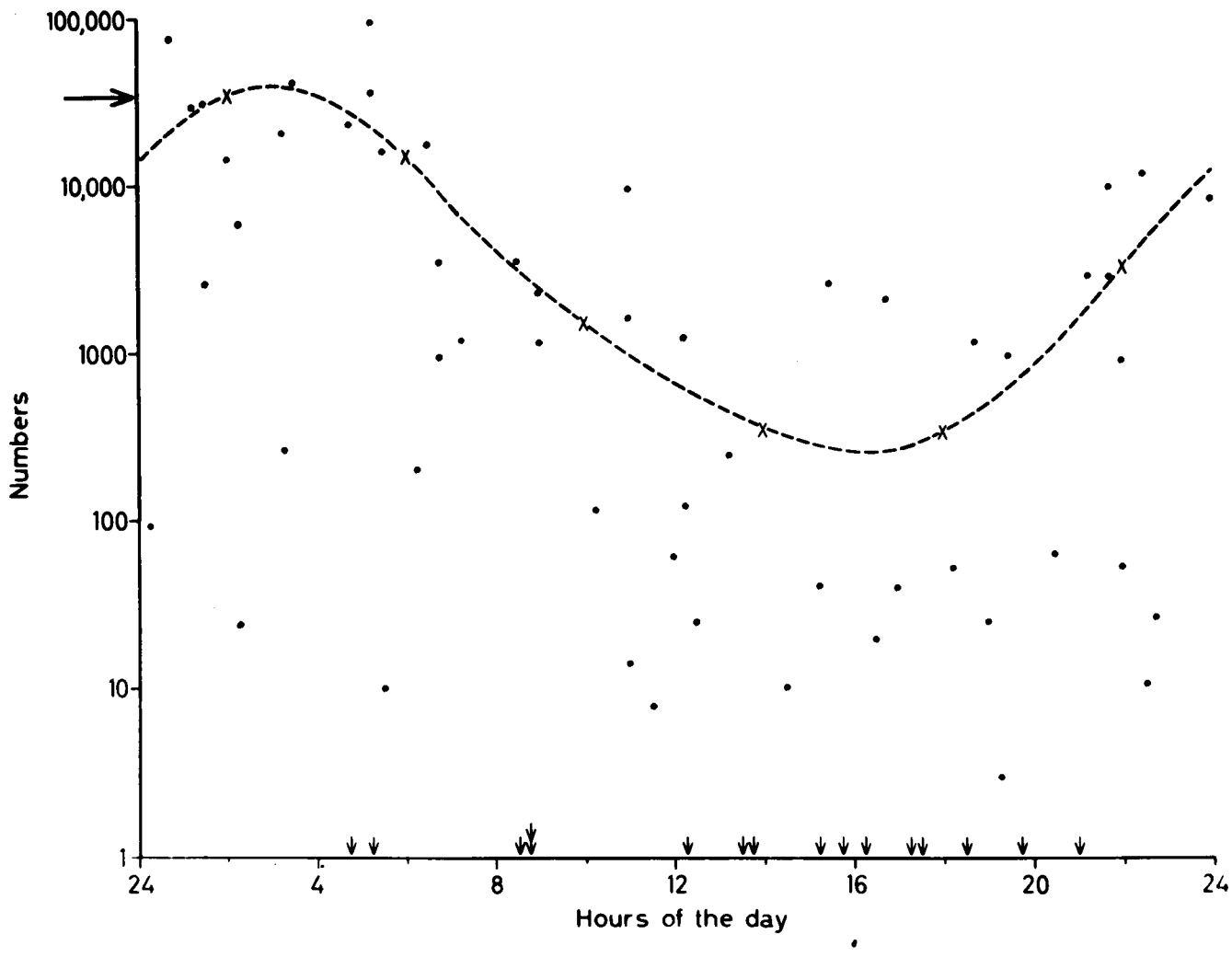


Fig. 30. The numbers of Euchaeta norvegica obtained in relation to the time of sampling; the small arrows indicate samples from which E. norvegica was absent. The mean values (X) for each four-hour period are shown joined by the broken line. The position of the highest point on the curve (equivalent to a mean of 40,000 specimens per sample) to which the four-hour means were converted is indicated by the large arrow.

present over the whole range of depth there were signs of decreasing abundance towards the extremes.

Metridia lucens Boeck (Fig. 28g)

Two restricted patches occurred; the one in the south was the larger with seven samples containing between 150 and 2,200 specimens; the one in the east consisted of three samples with from one to 150 specimens.

Although showing a much more restricted distribution than Calanus f. finmarchicus the temperature and depth characteristics of Metridia lucens were closely similar. On the evidence of temperature the centre of distribution is probably a little to the south of the centre of the Survey and it appears to occur more in oceanic water than over the continental slope. The ten records all came from daytime hauls.

Metridia longa (Lubbock) (Fig. 28g)

Four records, including two of numbers in the hundreds, came from the coastal part of the Survey. The fifth, 250 miles away, was in the south-west, close to but not overlapping the patch of M. lucens.

M. longa showed itself to be a cold-water species, second only to Calanus f. glacialis. Most of the records can be taken, therefore, to indicate a species whose southern limit, as far as regular occurrence near the surface is concerned, only just reaches the north of the present area. The solitary record in the south-west indicates that it does occur further south but probably only rarely near the surface. No diurnal pattern was discernible from the limited data available.

Heterorhabdus norvegicus (Boeck) (Fig. 28h)

This species was quite common in the south-west and extended in smaller numbers north-eastwards between the coast of Greenland and the Reykjanes Ridge. A smaller patch occurred on the eastern edge of the area but no records were obtained from the higher slopes of the Reykjanes Ridge

This distribution over deeper water is reflected in the study of the depth characteristics of the species. These show H. norvegicus to occur over a mean depth of 2575 m, 250 m greater than the Survey mean. It seems reasonable to conclude that this is an oceanic species.

The mean temperature of occurrence for H. norvegicus is very close to the mean for the Survey. It seems likely, therefore, that this is a species whose centre of distribution is similar to that of the Survey. There did not appear to be a diurnal pattern in the size of samples.

Anomalocera patersoni Templeton (Fig. 28i)

Only five records were obtained for this species and numbers were always low. All the records were in the neighbourhood of the Reykjanes Ridge.

The temperature and depth characteristics suggest that this is a species found mainly over the continental shelf or slope and centred only a little south of the centre of the Survey. All records were from day time hauls.

Temperature and depth groupings

In order to compare the characteristics of each species or subspecies

in relation to sea temperature and depth, the two sets of values have been tabulated. In both cases the species divide into three main groups. In the species-groupings according to the mean temperature of occurrence (Table VIII) the separations occur at around 1.0°C above and below the mean for the Survey; the range of temperature is greatest in the cold-water group and sub-divisions can be made at 4° and 2°C below the Survey mean. Calanus f. glacialis is distinctly the most Arctic in its temperature preference. Metridia longa is somewhat less extreme and Calanus hyperboreus, the last of the cold-water group, still less so. The intermediate group is compact in its mean temperature of occurrence, the range being less than 1°C. It is also the largest group,with seven species; this is perhaps not unexpected since these species must be the true natives of the region. The warm-water group comprises two species only and of these there is only a single record of Gaidius tenuispinus. Larger numbers obtained of Eucalanus elongatus enable a firmer deduction as to its preference for higher temperatures to be made. Included in Table VIII are the standard deviations from the mean temperatures of occurrence for the eight species which occurred in at least ten samples. Metridia lucens deviated least from the mean; of the two most widely distributed species, Calanus f. finmarchicus showed much less deviation than did Euchaeta norvegica.

Calanus f. glacialis and Metridia longa have had to be excluded from any consideration of depth preferences because of the bias introduced by the shallow cold water of the East Greenland Current (see p. 53).

TABLE VIII. Species groupings according to temperature; the mean temperature for the Survey was 7.4°C.

Species	Difference from Survey mean	Standard deviation
Calanus f. glacialis ♀	- 5.7°C	
" " V	- 5.2	
Metridia longa Adults	- 2.8	
Calanus hyperboreus V	- 1.4	0.64
" " IV	- 1.2	
" " ♀	- 1.0	
Heterorhabdus norvegicus Adults	- 0.1	0.78
Calanus f. finmarchicus ♀	0.0	0.69 (♀,♂,V)
Euchaeta norvegica IV, V, ♀ (n.s.v.)	+ 0.3	1.26
C. f. finmarchicus V	+ 0.4	
Metridia lucens Adults	+ 0.4	0.48
Calanus f. finmarchicus ♂	+ 0.5	
Rhincalanus nasutus ♀	+ 0.7	1.27
Anomalocera patersoni ♀	+ 0.8	
Euchirella rostrata V, ♀, ♂	+ 0.8	0.66
Eucalanus elongatus V, ♀	+ 1.6	0.81
Gaidius tenuispinus ♀	+ 1.6	

Divisions separating the remaining species into three groups may be made at values 100 m above and below the mean depth of the stations in the Survey (Table IX). Since the Survey mean was over 2000 m, even those species, Calanus hyperboreus and Anomalocera patersoni, in the "shallow-water" group can hardly be classed as neritic, but rather as "slope" species. The remaining eight species are divided equally between the intermediate and oceanic groups; the relative size of the latter group is not surprising since the Survey was conducted to a large extent over oceanic depths.

DISCUSSION.

Sewell (1948) has given the most comprehensive review of the distribution of the marine free-living copepods. Of the species recorded here, Calanus finmarchicus, Rhincalanus nasutus (there is some confusion with R. cornutus in Sewell's work) and Anomalocera patersoni are classed as epiplanktonic species, the rest as meso- and bathy-planktonic, and all are listed as occurring in the North Atlantic. Calanus hyperboreus, Gaidius tenuispinus, Euchaeta norvegica, Metridia longa and Heterorhabdus norvegicus are also included in the Arctic fauna and the remaining five species are mentioned as occurring in boreal regions (the north-west coast of Norway or the north coast of Iceland). Vervoort (1963, 1965) has recorded Eucalanus elongatus, Rhincalanus nasutus, Euchirella rostrata and Heterorhabdus norvegicus from the Gulf of Guinea; Sars (1925) recorded Euchaeta norvegica as far south as

TABLE IX. Species groupings according to sea depth; the mean depth of sea for the Survey was 2,327 m.

Species		Difference from Survey mean
Calanus hyperboreus	V	- 482 m
" "	♀	- 365
" "	IV	- 284
Anomalocera patersoni	Adults	- 259
Eucalanus elongatus	V, ♀	- 68
Rhincalanus nasutus	♀	+ 27
Euchaeta norvegica	IV, V, ♀ (n.s.v.)	+ 38
Gaidius tenuispinus	♀	+ 83
Euchirella rostrata	V, ♀, ♂	+ 197
Heterorhabdus norvegicus	Adults	+ 248
Calanus f. finmarchicus	♀	+ 253
Metridia lucens	Adults	+ 388
C. f. finmarchicus	V	+ 635
" "	♂	+ 802

the Azores; and Metridia lucens is known to occur in the Mediterranean (Giesbrecht, 1892, as M. hibernica) and again in the southern hemisphere (Farran, 1929; Vervoort, 1957) but has not so far been recorded from tropical or subtropical regions. The Arctic distribution of C.f. glacialis and the restriction of C. f. finmarchicus to cold temperate regions have been indicated by Jaschnov (1961) and Grainger (1963).

The classification of these species according to their temperature preferences, as given here, is in general agreement with their previously known distributions. Thus the most Arctic of them all, C.f. glacialis, is found to have preference for the coldest water while the other two members of the cold-water group are the only species recorded here which occur regularly in the Arctic and the North Atlantic but not in lower latitudes. The intermediate group consists of those, like C.f. finmarchicus and M. lucens, whose distribution is largely confined to cold temperate regions and those, like Euchaeta norvegica and Heterorhabdus norvegicus, which range north towards the Arctic and south towards the tropics. The only warm-water species, Eucalanus elongatus, for which there are adequate data in the present study, is known from equatorial regions but has not been recorded further north than the north coast of Iceland. Since the Survey was conducted almost entirely over depths greater than 1500 m, these species are all essentially oceanic. The groupings of species noted here really represent, therefore, sub-divisions of this one type of distribution. The preferences of the species with regard to sea temperature and depth are summarised in Table X.

TABLE X. Temperature and depth preferences.

	Slope	Intermediate	Oceanic
Cold	Calanus hyperboreus	———	———
Intermediate	Anomalocera patersoni	Rhincalanus nasutus Euchaeta norvegica	Calanus f. finmarchicus Euchirella rostrata Metridia lucens Heterorhabdus norvegicus
Warm	———	Eucalanus elongatus Gaidius tenuispinus	———

If the mean temperature of occurrence of a particular species within an area, such as that of the present Survey, can be taken to indicate its temperature preference, the argument can be extended to suggest that the standard deviation from the mean for a species provides a measure of its tolerance to different temperatures; those species with a narrow range of temperature tolerance would deviate little from the mean and vice versa. On this basis, Metridia lucens would appear to be the most stenothermic species, followed in order by Calanus hyperboreus, Euchirella rostrata and Calanus f. finmarchicus; Heterorhabdus norvegicus and Eucalanus elongatus are rather more eurythermic while Euchaeta norvegica and Rhincalanus nasutus are markedly so. In some respects this suggestion seems to fit in with known

distributions, for example the "stenothermic" M. lucens ranges through some 30° latitude in the North Atlantic while Eucalanus elongatus is more "eurythermic" and ranges through some 65°. Euchirella rostrata, however, has a recorded range of 60° and yet is relatively "stenothermic". This is, however, probably not a valid test to make, as the total range of a species is often, if not usually, constituted by a number of different populations, each of which may be adapted to different environmental conditions.

Fager and McGowan (1963) have described species associations in the zooplankton of the North Pacific and Colebrook and Robinson (1964) have related some of the commoner species in the eastern North Atlantic and North Sea to each other. The importance of such integrated ecological studies as these cannot be doubted, but at the same time the need to recognise and understand the ecological units, i.e. the populations rather than the species, must not be overlooked. The subsequent sections are intended as contributions towards such an understanding.

In conclusion, one feature of the biology of C. f. finmarchicus makes it stand out from all other species in the present area. It is estimated that the 73 samples examined contained a total of 1,260,000 adults and stage V copepodids of this species, almost twice as many as the specimens of Euchaeta norvegica and a hundred times more abundant than C. hyperboreus, which were respectively the second and third most common species in the samples. E. norvegica is a carnivore, so the dominance of C. f. finmarchicus among the herbivores was unrivalled.

THE DISTRIBUTION OF CALANUS FINMARCHICUS S.L. IN THE NORTH ATLANTIC AND NORTH SEA.

INTRODUCTION

The dominance of Calanus f. finmarchicus among the herbivores of the zooplankton is so striking in the area to the south-east of Greenland that its importance in the economy of that part of the North Atlantic cannot be doubted. It is logical to consider next how extensive is the range over which Calanus finmarchicus s.l. occurs and exerts its influence, and to study the geographical relationships between the three forms as they have been defined in Part I.

The main outline of the distribution of Calanus has been known for a long time. This information has been gathered from investigations, too numerous to list completely, based on material collected at different times by a variety of methods and often from quite limited geographical regions, thus making quantitative comparisons difficult. Earlier investigations of Calanus within the area now covered by the Continuous Plankton Recorder Survey (see Fig. 3) include those of Fish (1936), who described its biology in the Gulf of Maine, and Grainger (1963), who summarised its distribution from Newfoundland to Baffin Bay; With (1915) reported on Calanus from the Danish Ingolf Expedition to the Irminger Sea and neighbouring waters and Wiborg (1954) studied Calanus in the Norwegian Sea; further south, Rose (1929) reported on the epiplanktonic copepods, including Calanus, taken during the cruises of Prince Albert 1er of

Monaco and Grice (1963) found it off the eastern American seaboard in part of the Gulf Stream System. Now, with the results from the Continuous Plankton Recorder, it is possible for the first time to chart the patterns of distribution and abundance of Calanus near the sea surface over the whole of this area.

MATERIAL

Results from the analysis of Recorder samples form the basis for this study. These results are processed as a matter of routine by members of staff at the Oceanographic Laboratory to provide monthly mean values for all "statistical rectangles" (1^{o} lat. x 2^{o} long.) sampled in the month. All available results are included from 1958 to 1965 inclusive. Since the westernmost part of the Survey was not effectively under way until 1962, results from that area, i.e. that in which C. f. glacialis occurs (see Fig. 31), cover the period 1962-65 inclusive. Stage V copepodids and adults are combined during routine analysis and estimates of abundance of these stages are made for each of the three forms of C. finmarchicus s.l. separately. The data used here only concern these stages and do not include the younger copepodids.

RESULTS

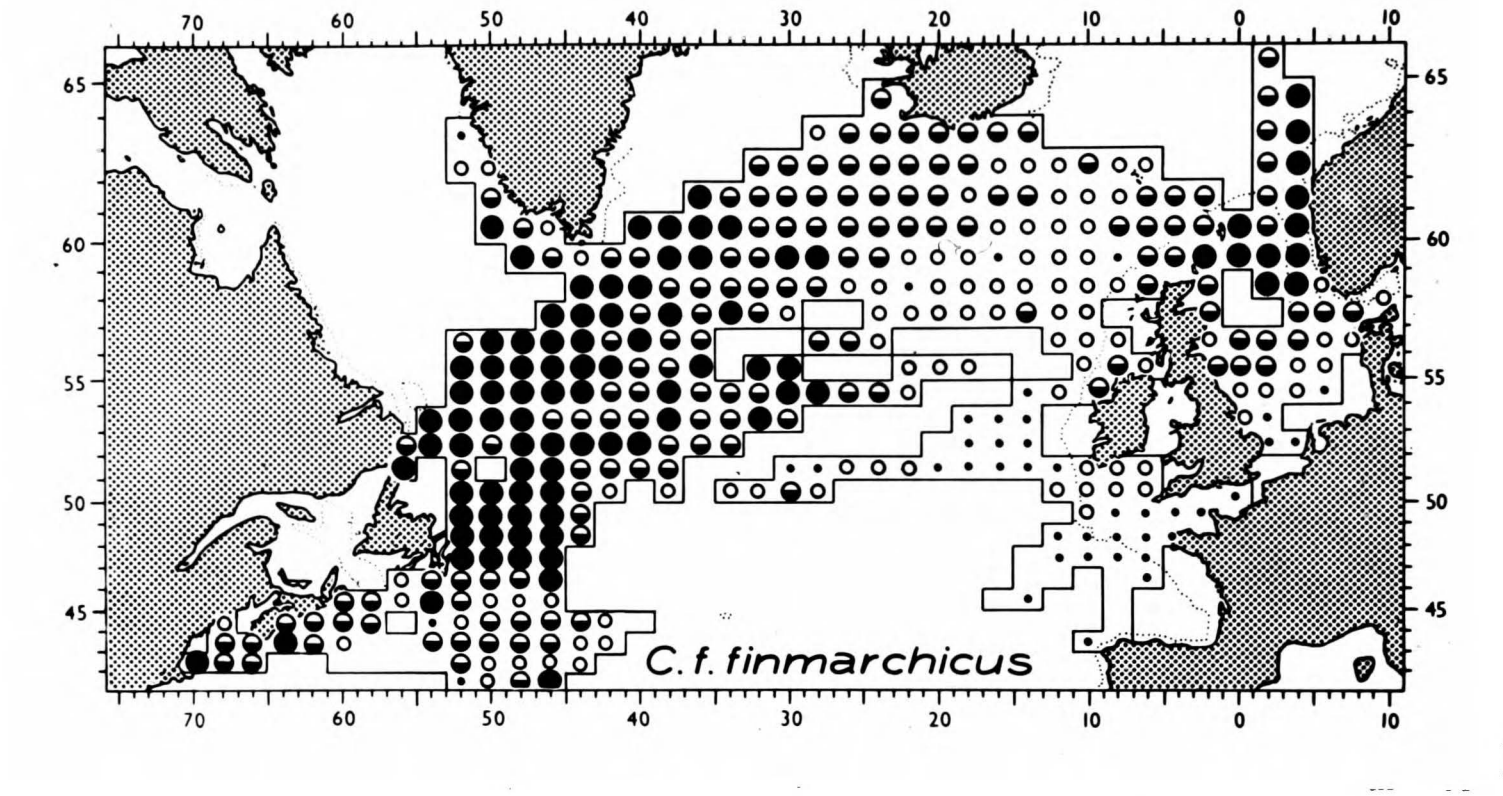
Total distribution

A single, long-term, mean has been calculated for each statistical rectangle from all available monthly means. The results for

C. f. finmarchicus, C. f. glacialis and C. helgolandicus are presented in Fig. 31. It must be noted that the levels of abundance indicated by the symbols are different in the three charts; higher numbers of C. f. finmarchicus than of C. helgolandicus are usually obtained and the numbers of C. f. glacialis are always low. Only those rectangles which have been sampled at least five times are included, except for a few to the south and east of the Newfoundland Grand Banks which have been retained because of their apparent zoogeographical significance, especially in the case of C. helgolandicus.

C. f. finmarchicus occurs throughout almost the whole of the Survey area. It is remarkably cosmopolitan and occurs quite commonly in shallow coastal seas and in the open ocean. Its main centre of abundance, however, is quite clearly the oceanic area south of Greenland and east of Labrador and Newfoundland; long term means of 15 individuals per sample (approximately $3m^3$) are common. Part, at least, of what appears to be a second centre of abundance can be seen in the Norwegian Sea and the northern part of the North Sea. Few specimens have been recorded in the south-eastern part of the Survey area.

C. f. glacialis occurs only in the western part of the Survey area. It is most frequent off south-east Labrador and along the north slope of the Newfoundland Grand Banks, where the Labrador Current flows into the Survey area. It also occurs quite regularly to the south of the Grand Banks where the influence of the Labrador Current is known to extend. It has been recorded on a few occasions in the open ocean,

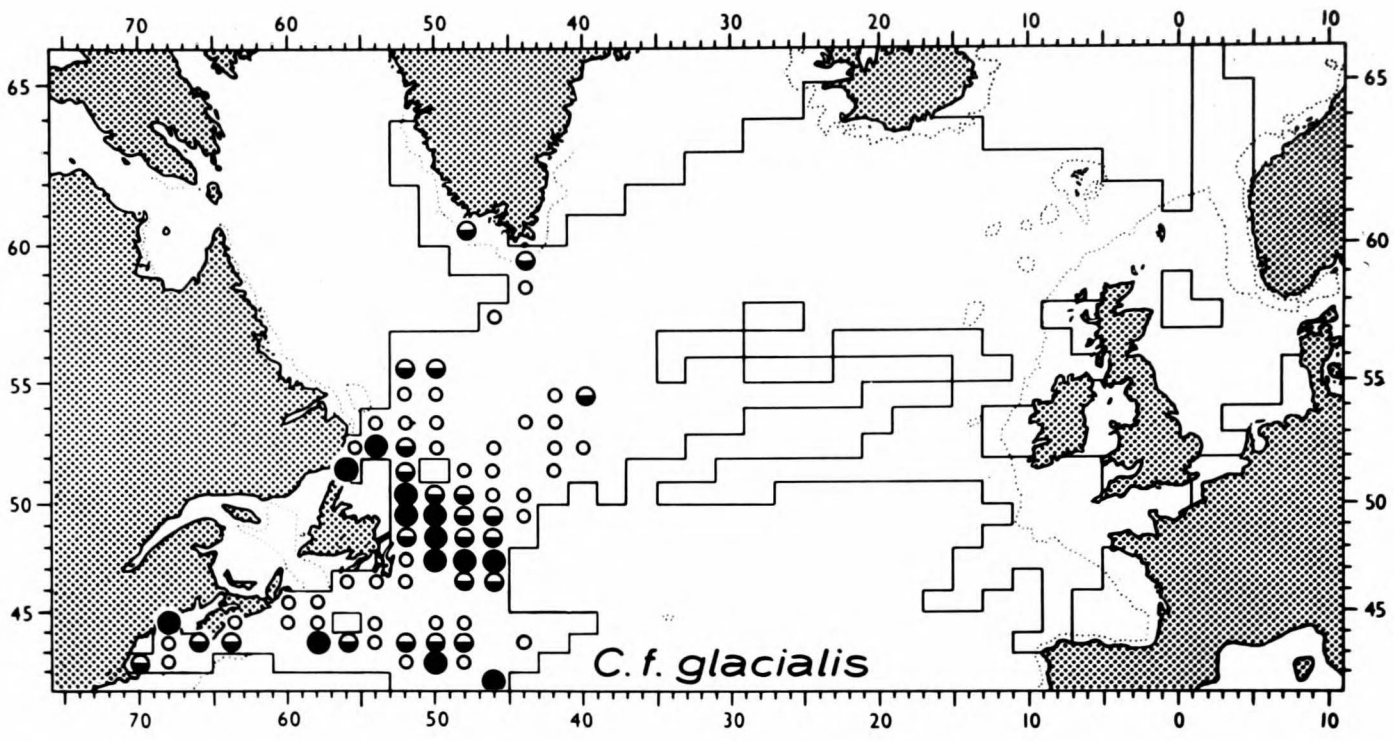


A. C. f. finmarchicus, using all data from 1958 to 1965 inclusive.

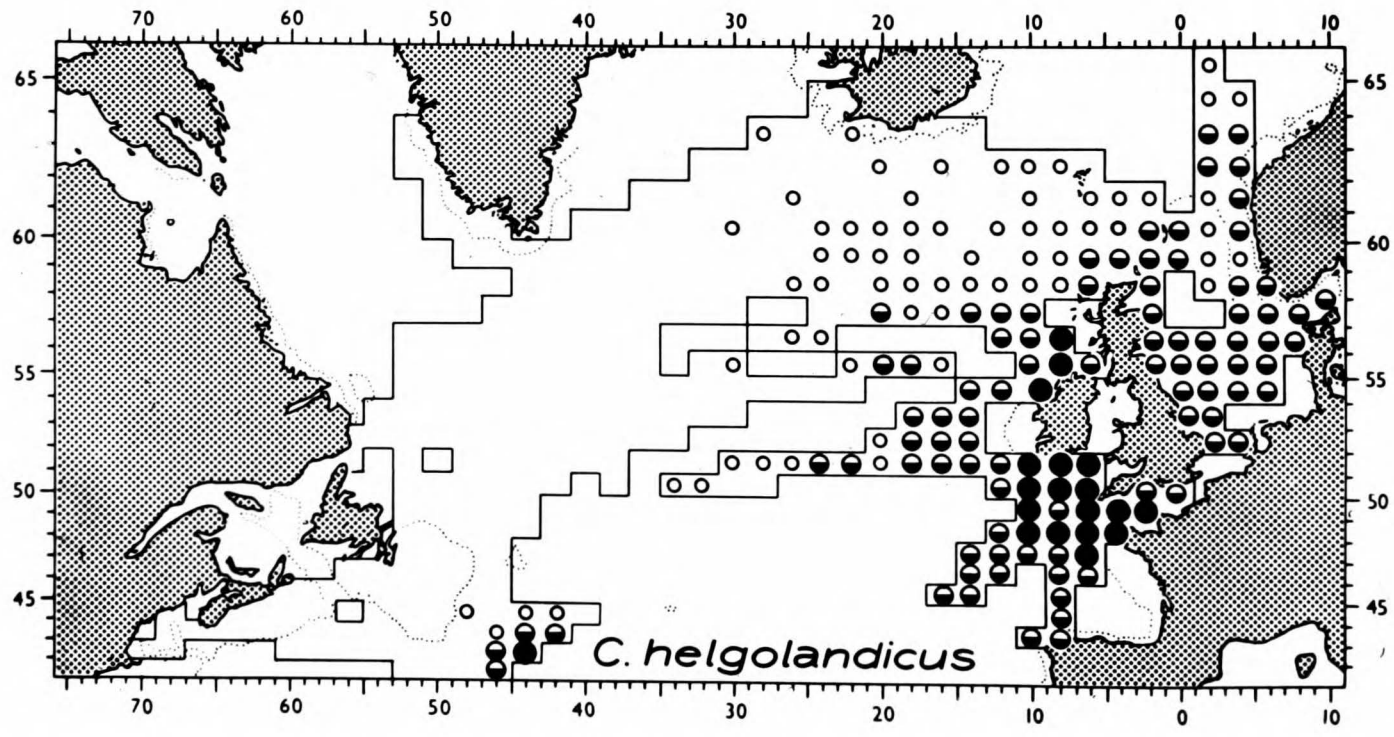
	·	○	◒	●
C. f. finmarchicus	<0·40	0·40–2·20	2·20–9·00	>9·00
C. f. glacialis	—	<0·10	0·10–0·25	>0·25
C. helgolandicus	—	<0·25	0·25–2·20	>2·20

Fig. 31. Distribution charts of Calanus finmarchicus s.l.

The values in the key represent mean numbers per sample (approximately $3m^3$).



B. C. f. glacialis, using all data from 1962 to 1965 inclusive.



C. C. helgolandicus, using all data from 1958 to 1965 inclusive.

Fig. 31. (Continued)

where eddies of the same current mix with Atlantic water, and in the East Greenland Current as it flows round the south of Greenland to form part of the West Greenland Current. Elsewhere, C. f. glacialis appears to be entirely absent.

The main centre of abundance of C. helgolandicus within the Survey area, to the east and south-east of the British Isles, occurs very near the apparent south-eastern limit of C. f. finmarchicus. Further north, both to the west of Ireland and Scotland and in the North Sea, C. helgolandicus becomes rarer as C. f. finmarchicus becomes more abundant; further west the isolated records of C. helgolandicus in the open Atlantic do not reach the main centre of abundance of C. f. finmarchicus. In the south-west, as in the south-east, there are signs that C. helgolandicus may be the commoner species where the warm influence of the Gulf Stream System becomes stronger. These records show that C. helgolandicus is not just a coastal species from the eastern North Atlantic but occurs in oceanic regions as well.

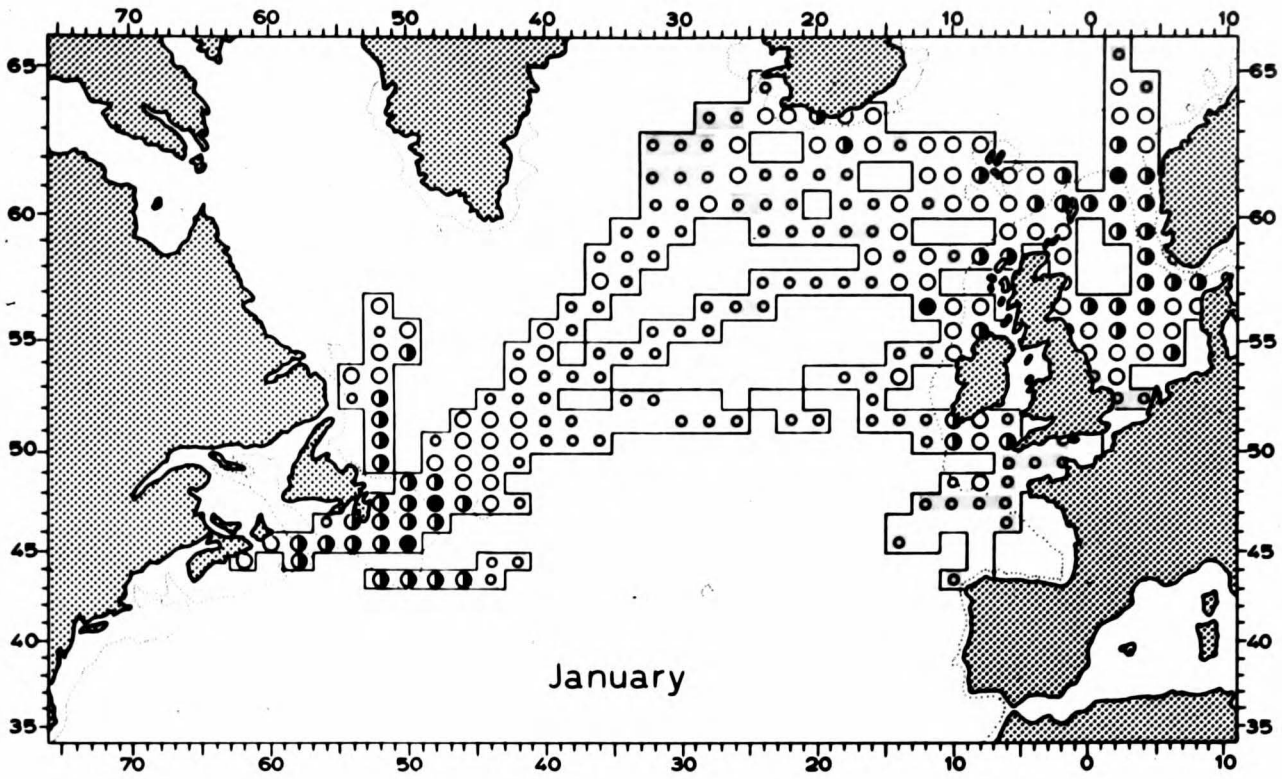
Seasonal distribution

Over the period of sampling considered here there is still some patchiness of sampling; coverage is more extensive in some months than in others and sampling in the western oceanic regions tends to be more northerly in summer than in winter, as the ships head for Belle Isle Strait rather than sail round Cape Race, Newfoundland. Nevertheless, over the main part of the Survey area it is now possible to use the accumulated data for each month separately in order to trace the seasonal changes in abundance.

It is necessary at this point to anticipate some of the findings given later under this heading and state that the seasonal changes in abundance of Calanus f. finmarchicus are, with few exceptions, closely similar in all parts of the Survey area. Such differences in the timing of increase and decrease as do occur between regions are on a much smaller scale than the differences in abundance; monthly charts of abundance thus do little more than repeat the pattern shown in Fig. 31. If the pattern of seasonal fluctuations is to become apparent, it will thus be essential to eliminate local differences in overall abundance. At the same time, for a description of the main pattern of fluctuations and of any variations, a geographical presentation is desirable. C. f. glacialis and C. helgolandicus show greater differences in seasonal fluctuations between regions but it is considered that the treatment of results should be the same for all three forms. A set of charts for each form of Calanus finmarchicus s.l. has been prepared accordingly in which the levels of abundance shown are relative to the overall mean for the respective rectangles. To do this, monthly mean values for all years combined were obtained first and then the ratio, expressed as a percentage, of these values to the overall means for all months and years combined was calculated. Each chart shows the area sampled in the respective month. Within the sampled area blank rectangles indicate total absence and the symbol for 0% indicates absence in the month concerned; the other symbols indicate low (1 - 50% of the overall mean), intermediate (51 - 200%) and

high (> 200%) relative abundance. Changes in mean abundance of C. f. finmarchicus and C. helgolandicus from month to month are, on the whole, fairly gradual and continue throughout the year so alternate months only are presented here. In the case of C. f. glacialis, on the other hand, most of the changes occur in the early months of the year, so all months have been included.

The charts for C. f. finmarchicus (Fig. 32) show that, near the surface, this form increases generally in numbers from January to May, the peak month of the year. Thereafter there is a period of four to five months during which numbers remain near the overall means for the respective rectangles. After September numbers start to decrease and continue to do so until January. Within this very general pattern, however, it can be seen that there are some marked local differences. The most pronounced of these is found on the Newfoundland Grand Banks where numbers are high in January and low in May and July; this is in fact a complete inversion of the pattern found in most other parts of the Survey area. Other variations involve differences of a month or two in the timing of the fluctuations and different lengths of the season during which these late stage C. f. finmarchicus are present in the surface waters sampled by the Recorder. Thus the few numbers well above average in March occur mostly in the areas associated with the Gulf Stream System in the western Atlantic, to the west of the British Isles, in the southern North Sea and, perhaps surprisingly, off the south-west



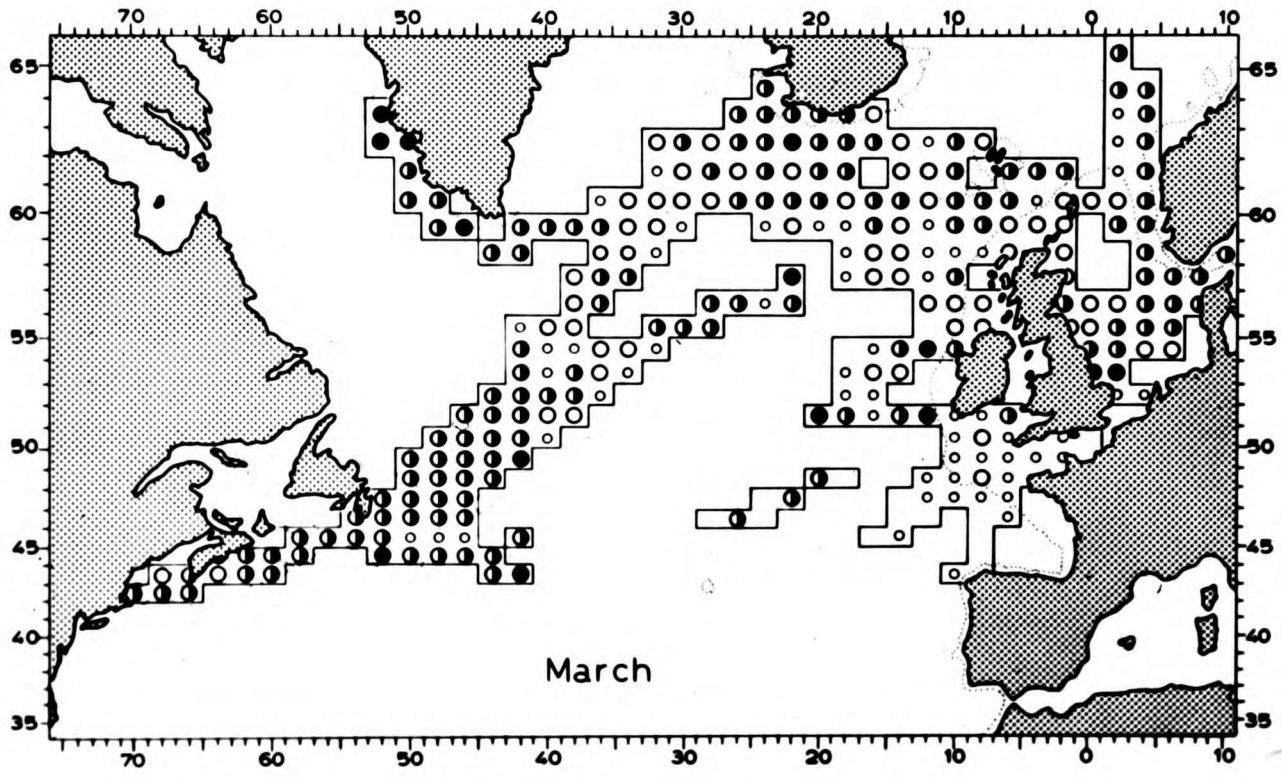
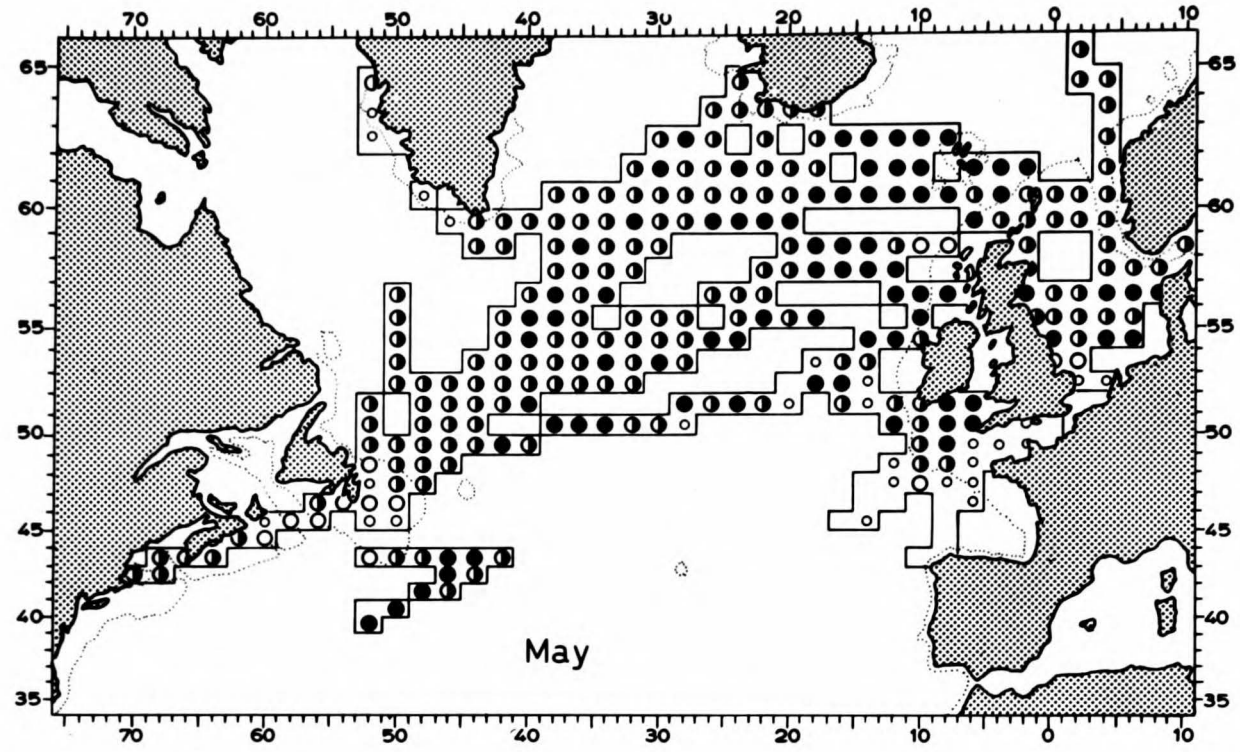


Fig. 32. The mean levels of abundance of C. f. finmarchicus in alternate months. The monthly means for each rectangle have been expressed as percentages of the overall mean for the respective rectangle. The results have been assigned symbols (see key) which indicate absence and low, average and high values for each month in each rectangle.

∘	0 %
o	1-50 %
◑	51-200 %
●	> 200 %



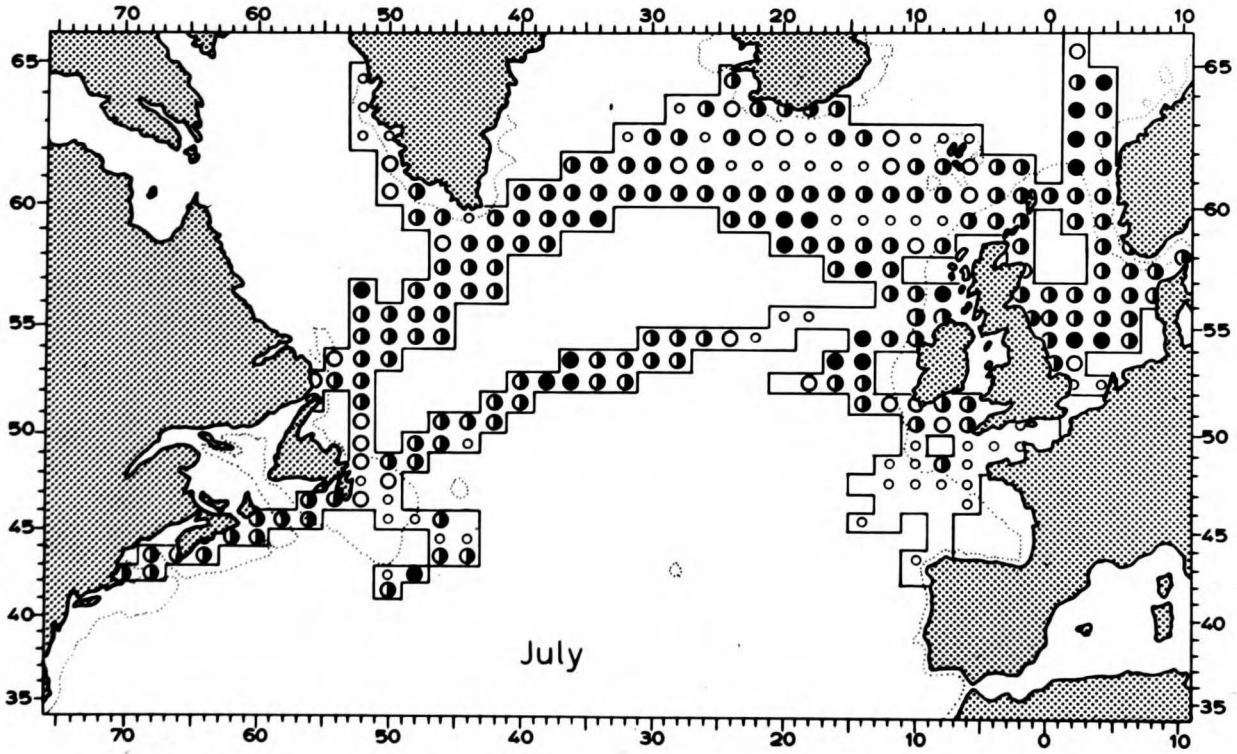


Fig. 32. (Continued).

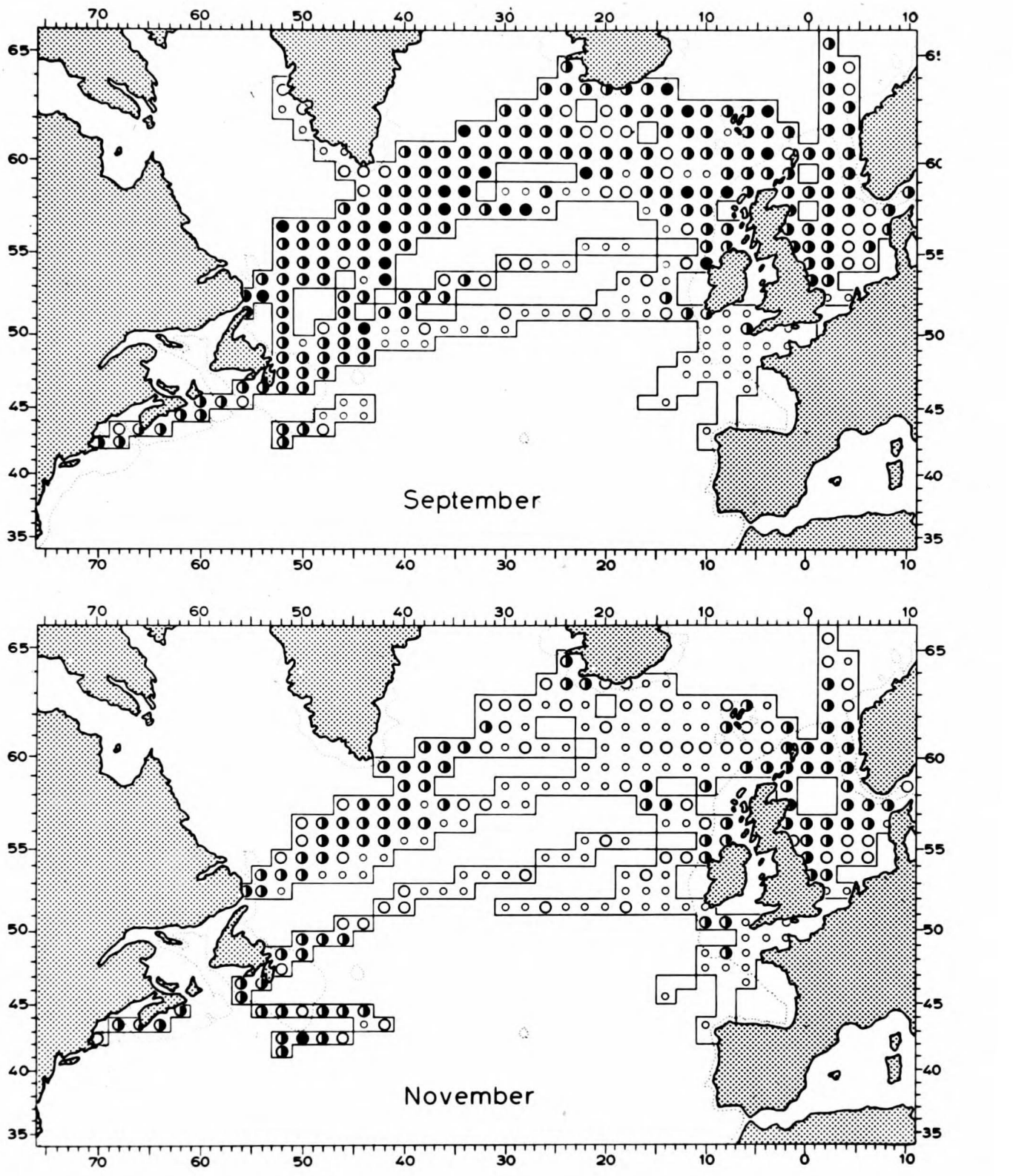


Fig. 32. (Continued).

coast of Greenland; in May such high percentage values are found more in the region south-west of the Faeroe-Iceland ridge and in the open Atlantic north of the main influence of the North Atlantic Drift; and in July high values occur in the Norwegian Sea. Records of populations maintaining themselves at or near the mean level in January are almost entirely confined to the continental shelves or neighbouring regions while the numbers of C. f. finmarchicus are well below the average in all parts of the open ocean at this time of year.

This presentation depicts the patterns of seasonal fluctuations and indicates in what way they differ between regions but it is also desirable to know to what extent the patterns differ; for this, statistical techniques of correlation are appropriate. Even if it were practical to apply such techniques to the 400 or so rectangles which have been sampled at one time or another and present the results in an intelligible fashion, the smallness of the samples, with proportionally wide margins of error in consequence, would render such results of little value. The rectangles have been combined, therefore, into 34 large areas (Fig. 33) most of which have been well sampled at all times of year. Monthly means of abundance have been calculated for each of the three forms of Calanus finmarchicus s.l. in each area where they were recorded. For purposes of comparison the monthly values for the areas needed to be standardised in such a way that they had a mean of zero and a variance of one. Correlation coefficients were then calculated for each pair of large

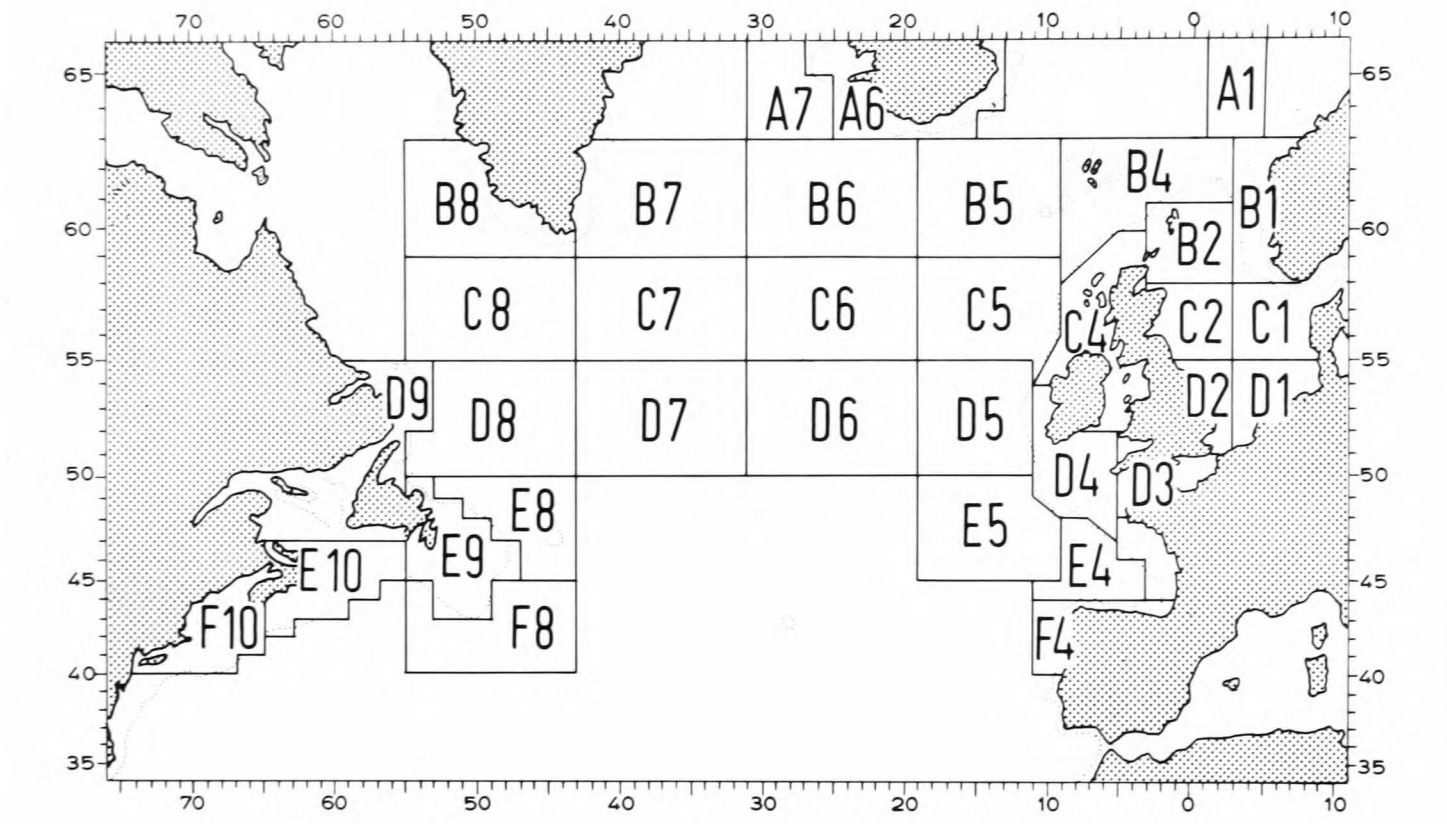


Fig. 33. Map of the North Atlantic giving the large areas into which the area of the Recorder Survey is divided.

areas and the results presented in the form of matrices.

There was adequate data for this purpose in 33 large areas in the case of C. f. finmarchicus; the area F4 has had to be excluded as there was only a single record. After standardisation of the monthly values, correlation coefficients were calculated between all the areas and the results, multiplied by ten, are presented in Fig. 34; the ranking of areas in the matrix has been done by trial and error. Nine of the areas showed consistently low correlations and have been placed separately, on the right of the main body of the matrix. All but two of the remainder were highly correlated throughout, indicating a similar cycle of seasonal fluctuations over the whole of the North Atlantic in the Survey area north of 50°N, the North Sea and Norwegian Sea and coastal areas off Ireland, Scotland, Iceland and Labrador. The two-dimensional scope of a matrix is inadequate for the satisfactory representation of all the relationships but the suggested ranking does indicate a general progression from a cold region (D9) associated with the Labrador Current to more southerly and warmer regions (F10 and D1) in the Gulf of Maine and southern North Sea respectively. Eight areas (C1 to D2 in the matrix) are particularly highly correlated to each other and to others higher up the matrix. These areas, showing what may be called the typical cycle of seasonal fluctuations, occur in the central North Sea, off Western Norway and in the eastern and central oceanic regions; other areas, e.g. C8 and D8, with which the typical group also show high correlations,



Fig. 34. Correlation matrix of seasonal fluctuations in number of C. f. finmarchicus. The correlation coefficients have been multiplied by ten.

occur in the western oceanic regions. Altogether, therefore, the "typical" areas cover the main range of C. f. finmarchicus. In four of the areas, D3, E8, E9 and E10, which have been excluded from the main body of the matrix, sampling has been good and the low correlation coefficients reflect a real difference in the seasonal fluctuations in numbers. In other cases, B8, D4, E4, E5 and F8, the anomalous pattern may well be due to irregular sampling (B8, to the west of Greenland, has been sampled best in summer and is, in fact, a coastal area of a type not found elsewhere in the Survey area) or to irregular occurrence of C. f. finmarchicus near the edge of its range; the consequent low numbers in such areas would result in large proportional fluctuations from month to month and high correlations are therefore unlikely.

Although the records of C. f. glacialis are based only on four years of sampling and are consequently rather scattered, the charts of seasonal distribution (Fig. 35) show quite clearly that the occurrence of this form in the Survey area is concentrated early in the year. In the first three months of the year records come mainly from the coastal or near-coastal regions strongly affected by the Labrador Current. The greatest numbers have been recorded in April and May and at this time of year there are records from as far east of Newfoundland as 40°W and south to 41°N. There are very few records from the succeeding months until a slight increase in December.

The matrix (Fig. 36) brings out clearly the distinction between the areas strongly affected by the Labrador Current (C8, D8, E8, E9 and, to

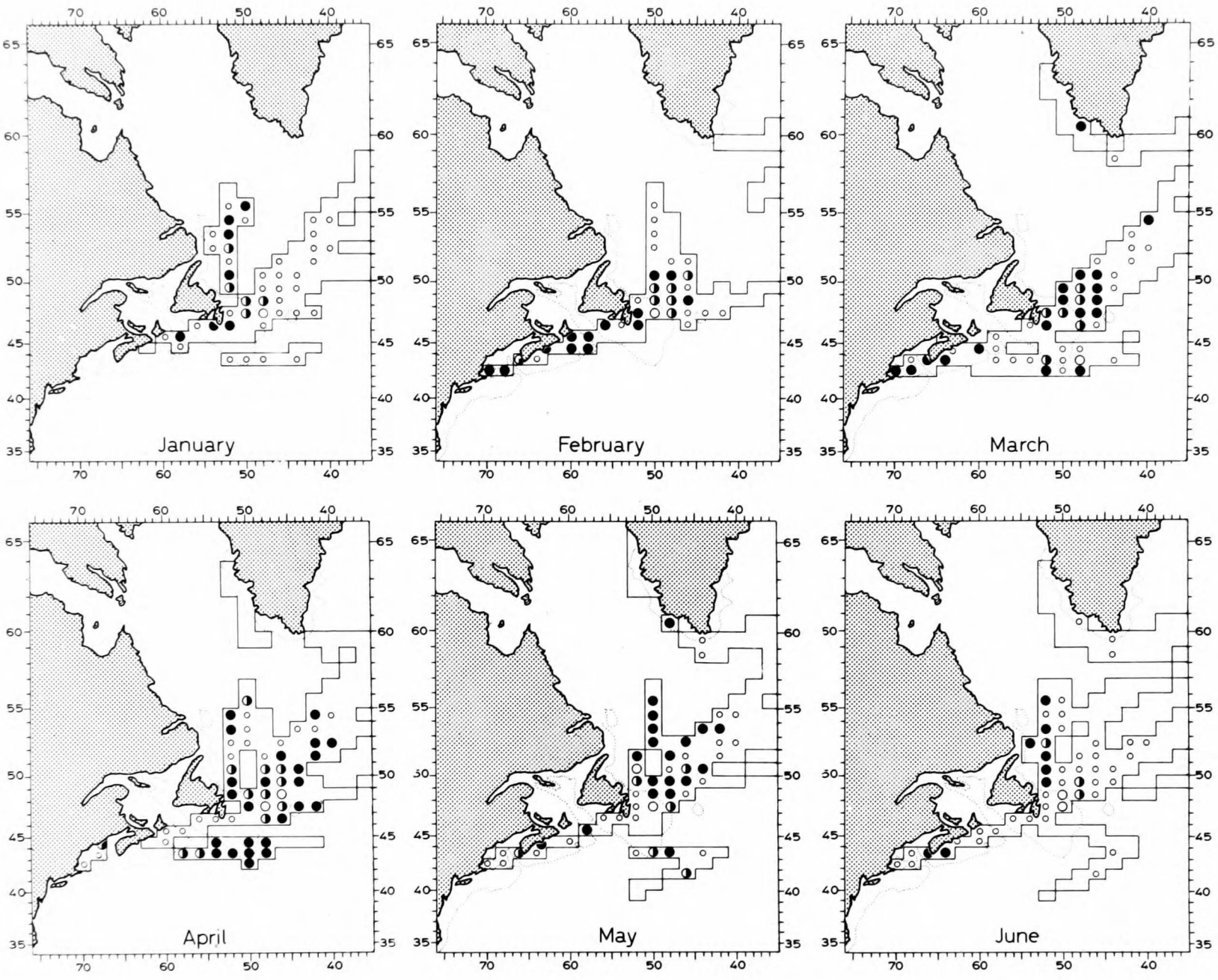


Fig. 35. The mean levels of abundance of C. f. glacialis in all months. The monthly means for each rectangle have been expressed as percentages of the overall mean for the respective rectangle. The results have been assigned symbols (see key to Fig. 32) which indicate absence and low, average and high values for each month in each rectangle.

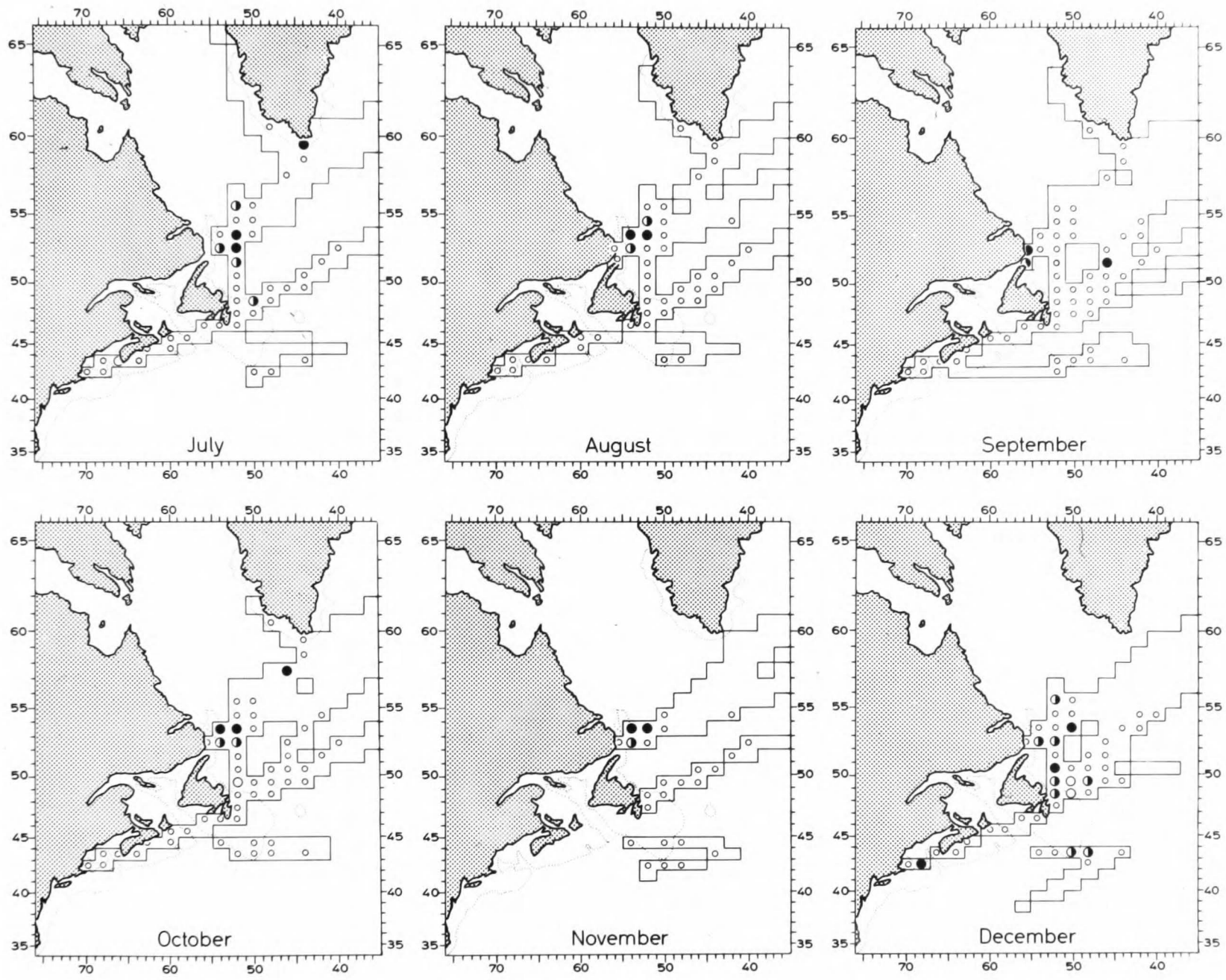


Fig. 35. (Continued).

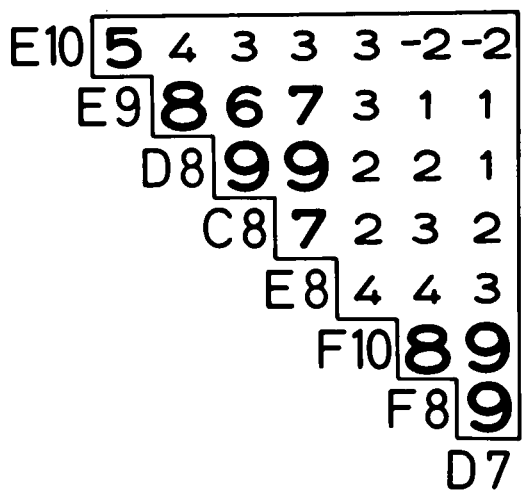
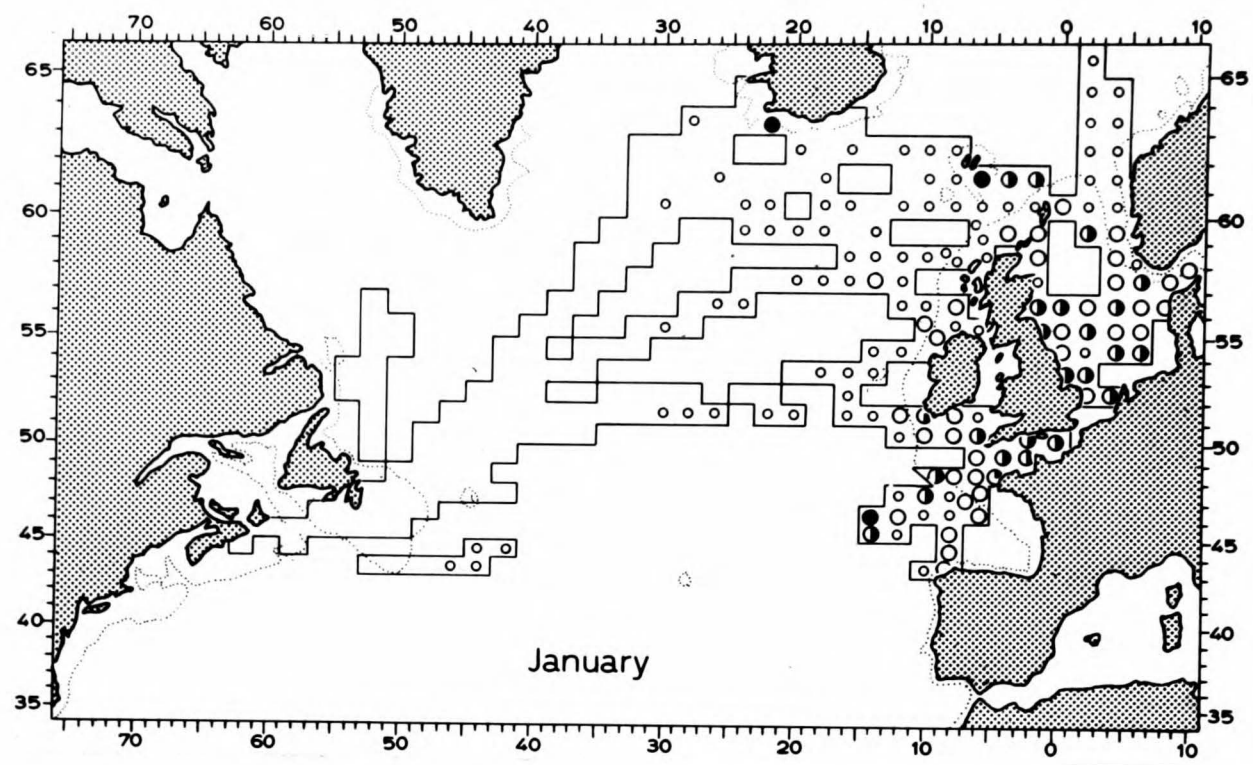


Fig. 36. Correlation matrix of seasonal fluctuations in number of C. f. glacialis. The correlation coefficients have been multiplied by ten.

a lesser extent, E10) and those of a more temperate nature (D7, F8 and F10).

The winter populations of C. helgolandicus (Fig. 37) in the surface waters sampled by the Continuous Plankton Recorder do not appear to be as consistently low in numbers as was seen in the case of C. f. finmarchicus. This may be due to the fact that, within the area of the Survey, C. helgolandicus is found relatively less frequently in the oceanic regions; certainly it has never been found far from the continental shelf between November and March. The spring increase starts in March, particularly in the south-east North Atlantic. In May values well above the local averages are found in the Gulf Stream System south of Newfoundland, off the west coast of the British Isles and to the south of Iceland. Populations are maintained to the east, south and west of the British Isles in July but the oceanic range appears to contract; there is some increase in the northern North Sea at the same time. The highest values of the year around the Faeroes and in the Norwegian Sea occur between September and November, by which time some decrease in the more southerly populations is apparent.

C. helgolandicus occurred in sufficient numbers in 20 large areas for purposes of correlation analysis and the results are shown in Fig. 38. The correlation coefficients are generally considerably lower than those of C. f. finmarchicus, making ranking of the areas rather easier. Two large areas, one a cold-water area and the other in the southern North Sea, could not be included satisfactorily and two others, B4 and C5, are



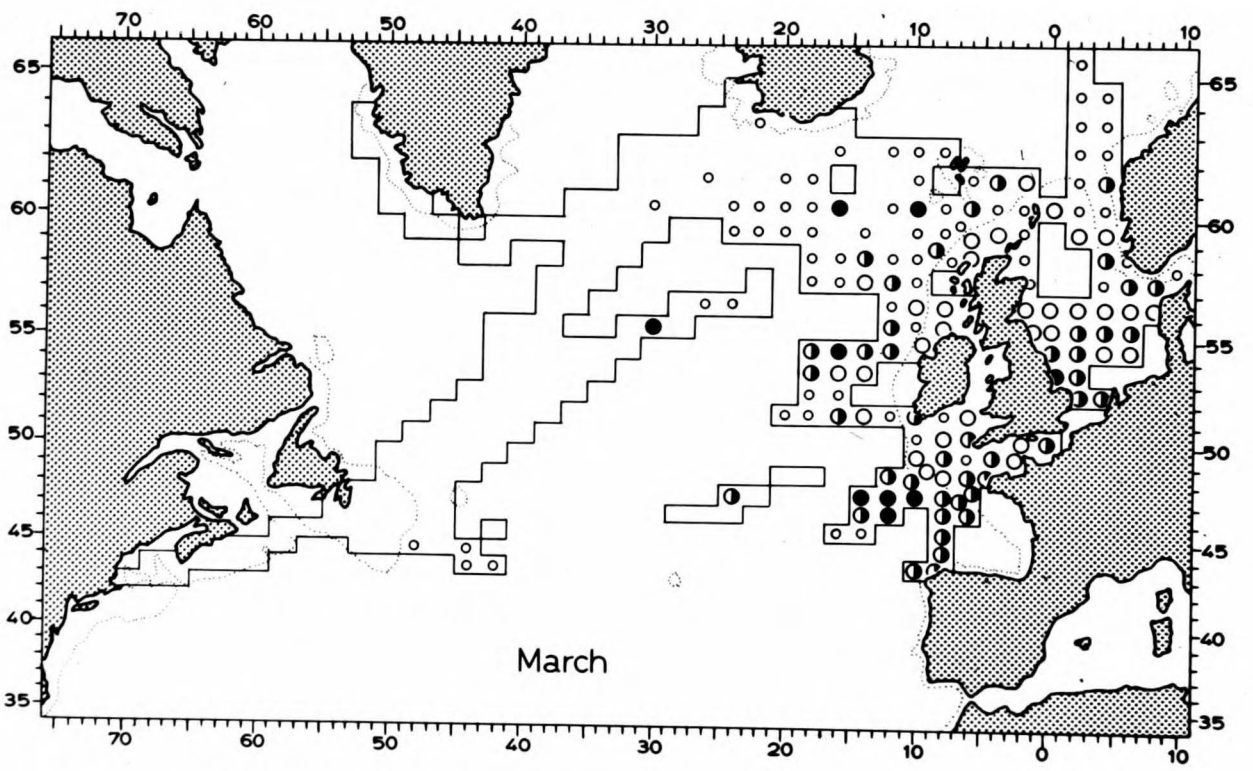


Fig. 37. The mean levels of abundance of C. helgolandicus in alternate months. The monthly means for each rectangle have been expressed as percentages of the overall mean for the respective rectangle. The results have been assigned symbols (see key to Fig. 32) which indicate absence and low, average and high values for each month in each rectangle.

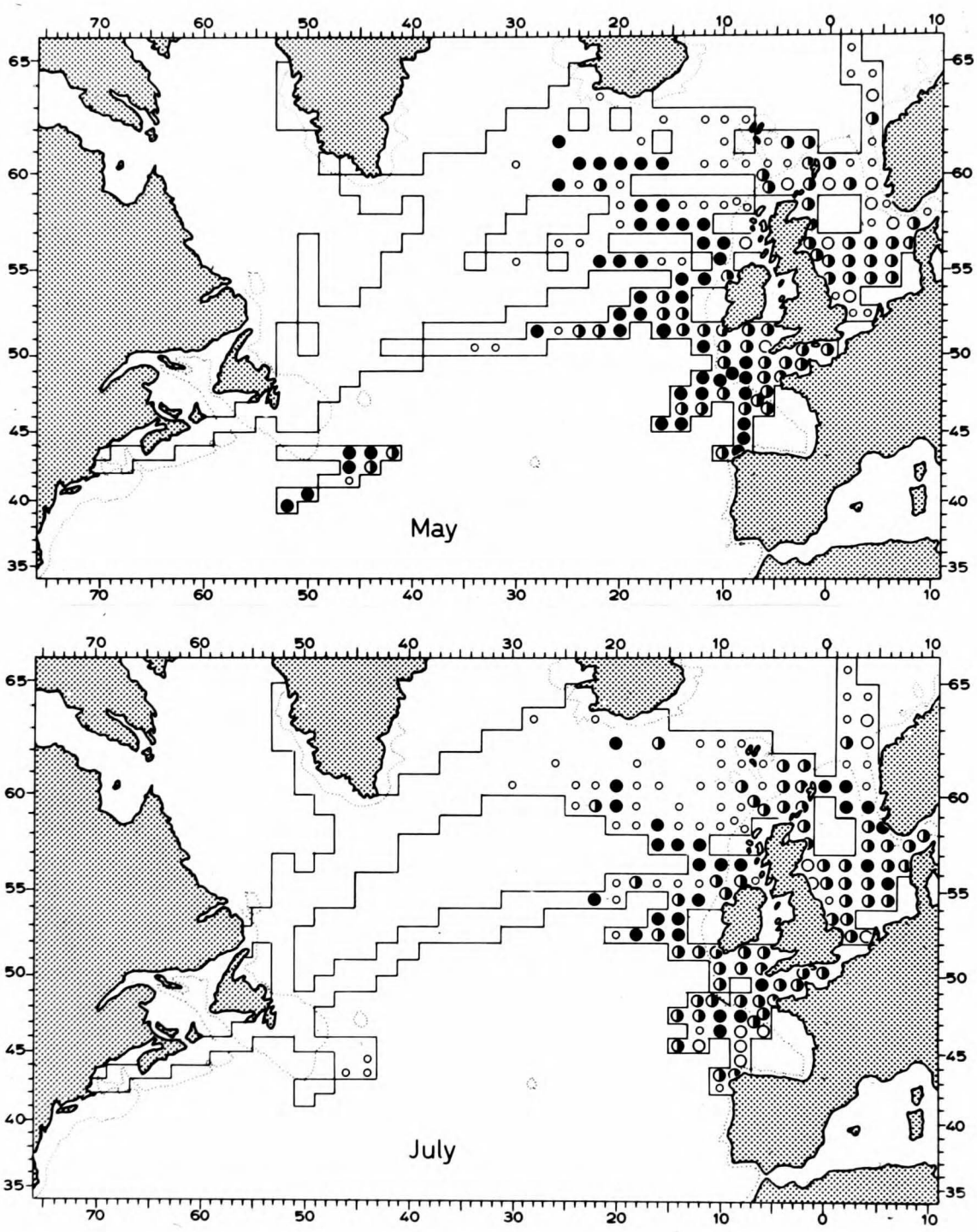


Fig. 37. (Continued).

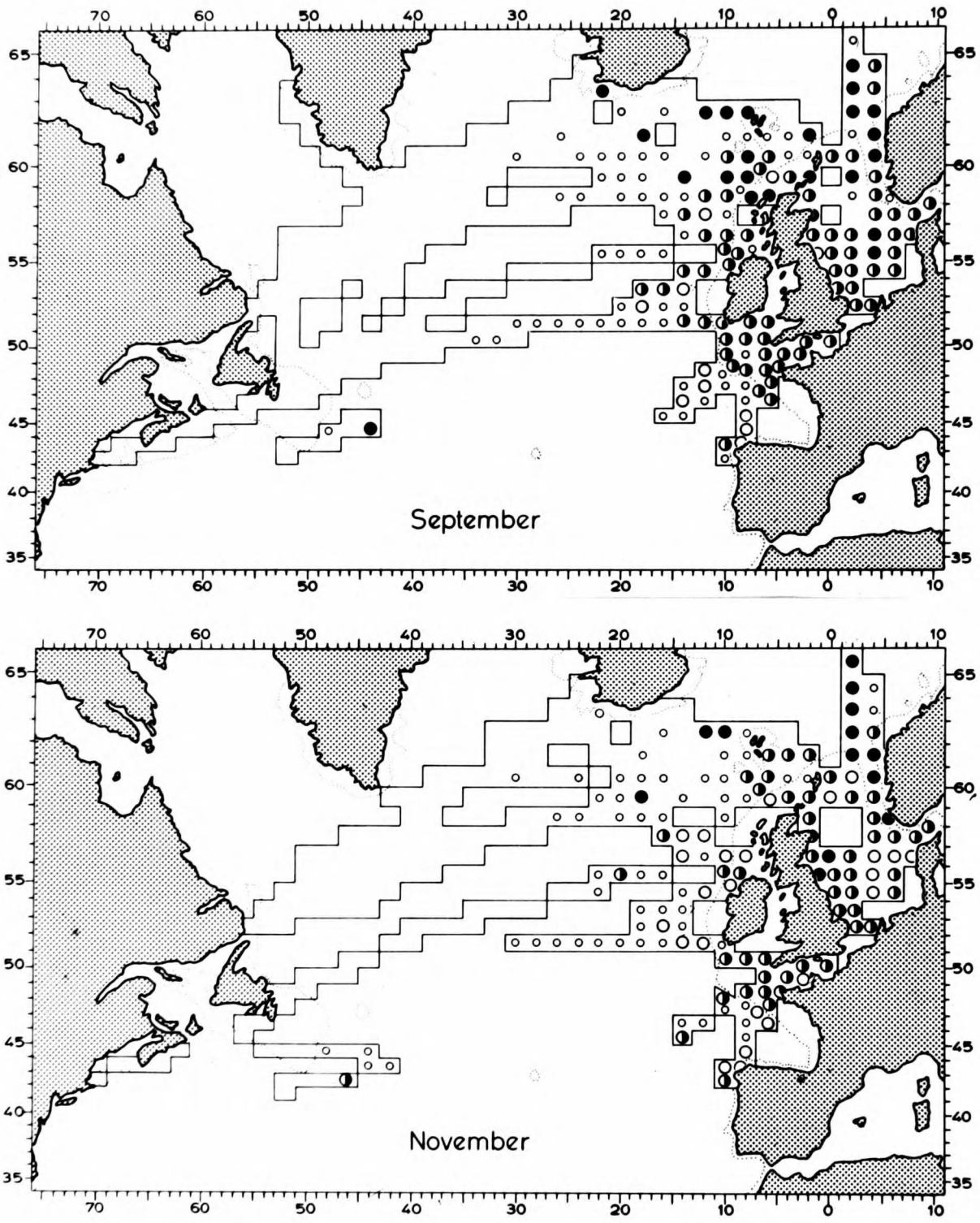


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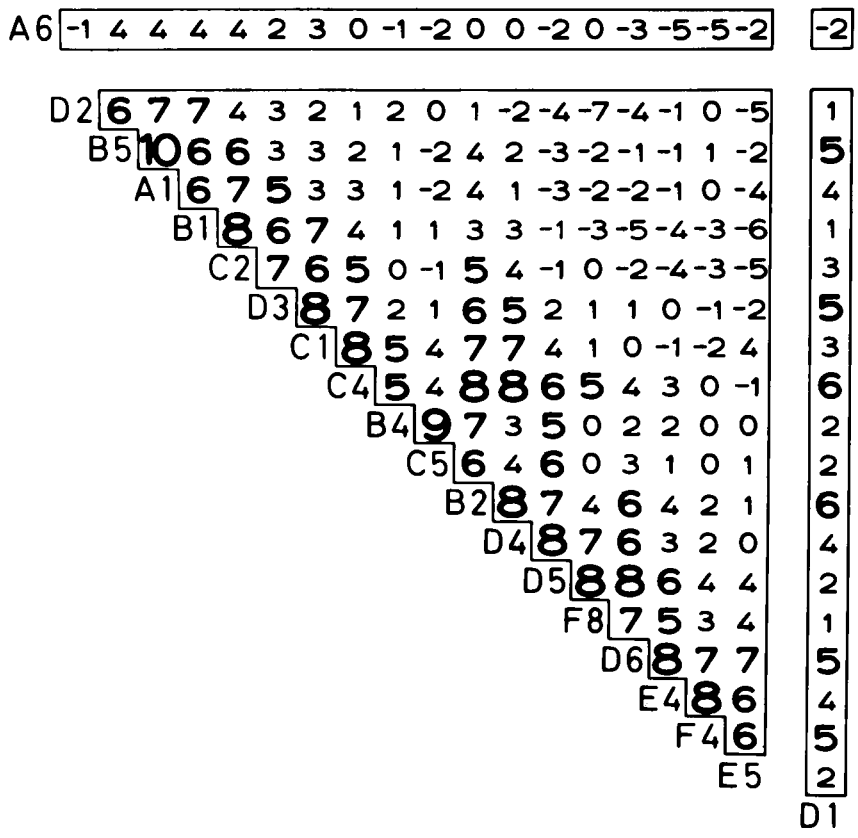


Fig. 38. Correlation matrix of seasonal fluctuations in number of C. helgolandicus. The correlation coefficients have been multiplied by ten.

a poor fit in the main body of the matrix; the last two have been included, however, because reasonably high correlations with other areas occurred at one position only in the main order of ranking. In general the cold areas are found high in the matrix, with a progression to the warmer areas towards the bottom. There is little sign of grouping of similar areas.

Timing of seasonal fluctuations in abundance.

Under the previous heading the patterns of seasonal fluctuations in numbers of Calanus finmarchicus s.l. have been examined and the extent to which they differed between large areas evaluated. In all three matrices the ranking seems to be related primarily to differences in timing of the fluctuations while differences in their nature seem only to be of secondary importance. For the purposes of a general comparison between the timings of the three forms, the following calculation of "mean time of occurrence" (M) has been made:

$$M = \frac{\Sigma mn}{\Sigma n}$$

where, m = the month, assigned a value in sequence from 1 to 12

n = the large-area mean for the month.

Fractions of a month are expressed in terms of days and weeks, for example a mean of 4.33 would be expressed as the 10th day of April.

This "mean time of occurrence" has been calculated for each of the three forms in each large area in which it occurred together with at least one of the other two forms. The results show that

C. f. glacialis is the earliest of the three forms to increase in numbers at a depth of 10 m in the spring. The cycle is from one and a half to just over three months in advance of that of C. f. finmarchicus in all large areas where they both occur, except to the south of the Grand Banks where there is a difference of little over a month. C. f. finmarchicus is next to develop. Only in area D6 is C. helgolandicus earlier than C. f. finmarchicus; elsewhere, C. f. finmarchicus is the earlier by between ten days and two and a half months. Those areas where there is the least difference in timing occur to the south-west and west of the British Isles, in the Gulf Stream System and in the north-western North Sea. In the central and southern North Sea and in the vicinity of the Faeroes, the difference is approximately one month, while on the northern fringe of C. helgolandicus' range there is a difference of more than two months.

The ecological effect of either C. helgolandicus or C.f. finmarchicus is probably very small at the extremes of their distribution. Where they co-exist in high numbers, however, their inter-relationships may be an important aspect of their ecology; the North Sea is a good example of such a region. Fig. 39 shows their relative frequency in the south-western North Sea through the year. C. f. finmarchicus forms the greater part of the Calanus population from March to August, while C. helgolandicus is the more common from September to February. There is similar succession in all those areas where the calculations of timing show C. f. finmarchicus to be earlier than C. helgolandicus.

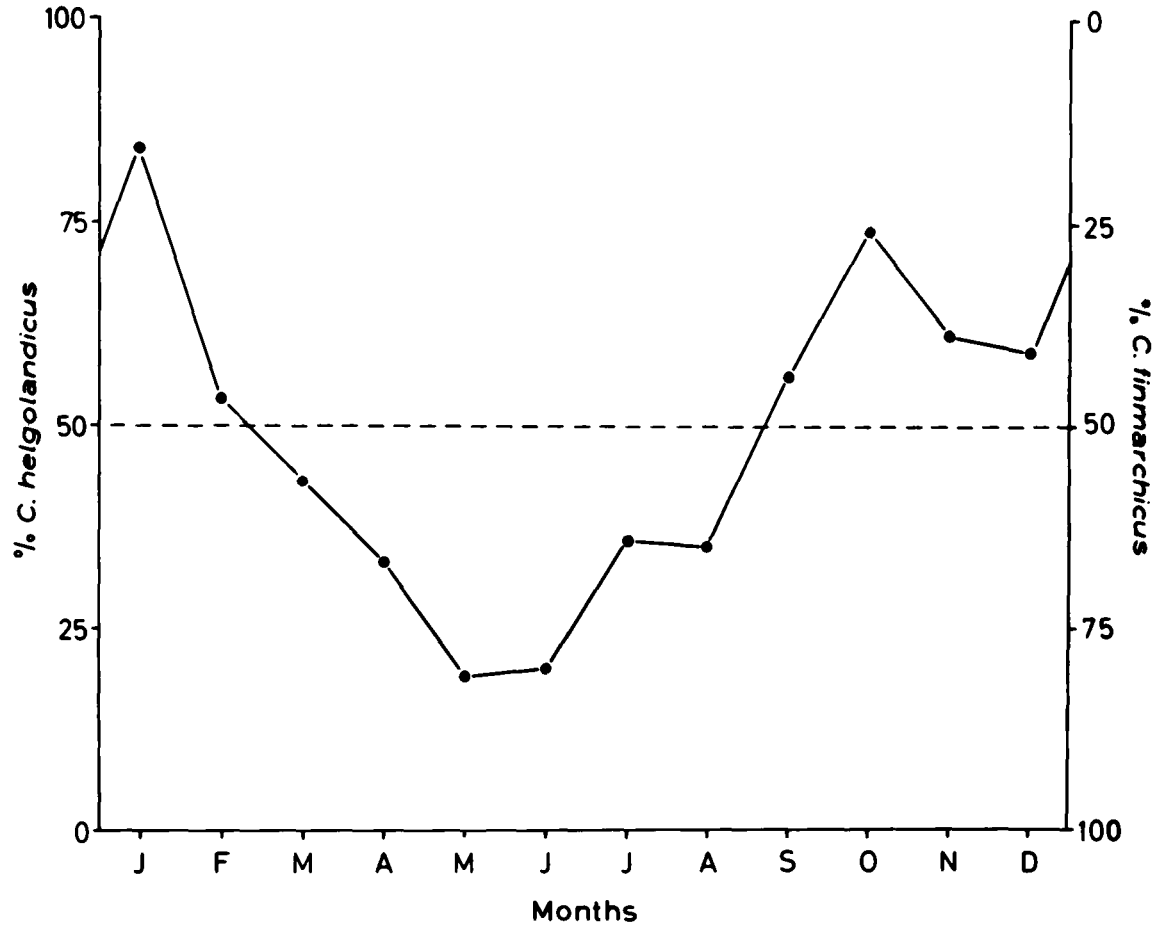
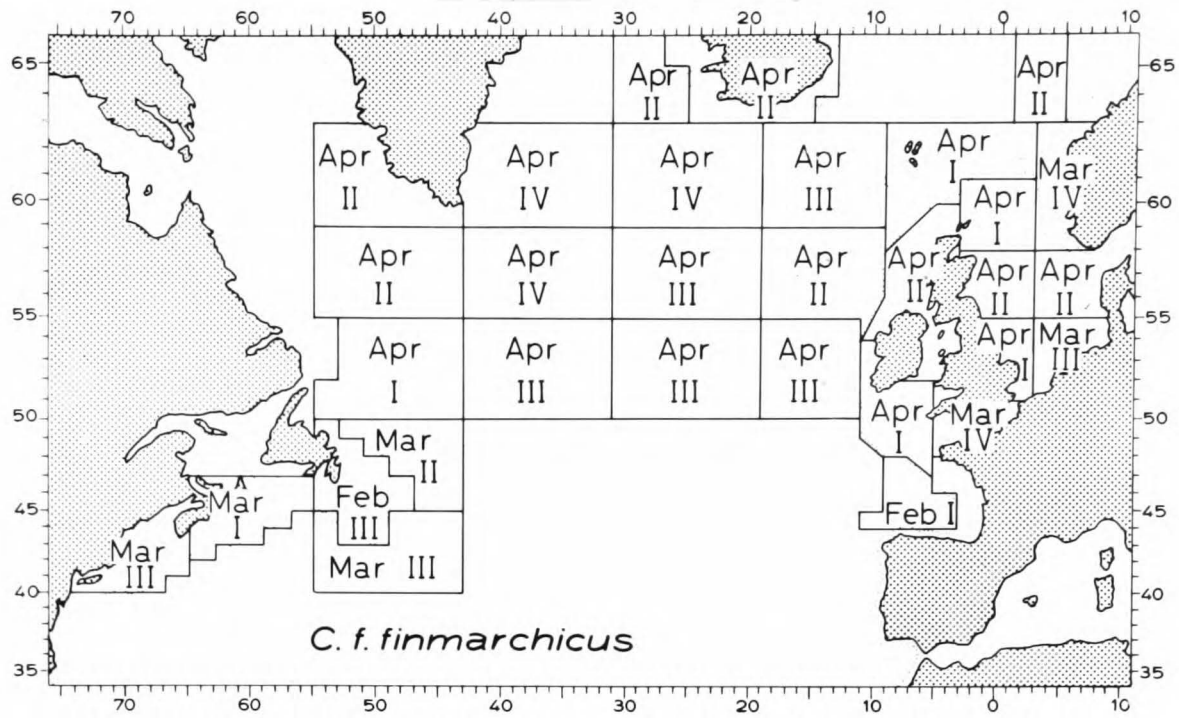


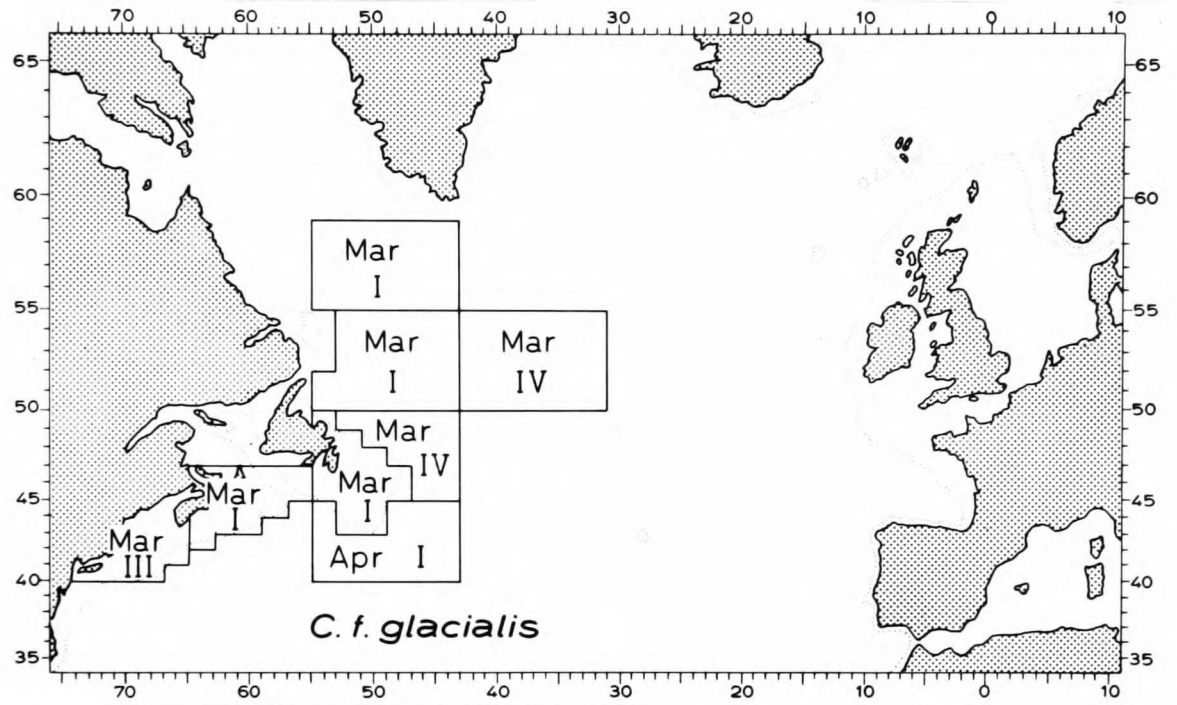
Fig. 39. Calanus finmarchicus s.l. in the south-western North Sea (large area D2), showing the changes in proportional composition between C. f. finmarchicus and C. helgolandicus through the year.

As indicated above, differences in the seasonal fluctuations of each form of Calanus between different large areas seem to be mainly in the timing of increase and decrease. The calculations of mean time of occurrence, as already made, incorporate a number of these aspects of timing, not all of which may be inter-related; for example, the length of the active season, during which high numbers are recorded near the surface, may vary geographically independently of the timing of the spring increase. By superimposing two or more such variables, the geographical pattern of each may well be obscured. An attempt has been made, therefore, to compare the timings of the spring increase independently of the other variables by recalculating the mean time of occurrence, using data from the first six months of the year only. The results are shown in Fig. 40 a - c. In C. f. finmarchicus the increase only occurs before the beginning of April in the extreme south-west of the survey area, the Bay of Biscay, the English Channel and the south-east corner of the North Sea. It occurs right at the beginning of April in the areas between Norway and the Faeroes. During April it gradually spreads through the North Sea and into the Norwegian Sea, northwards along the west coast of the British Isles, northwards from the Grand Banks towards Greenland and in a north-westerly direction across the Atlantic to reach the last area, off the south-east of Greenland, by the end of the month. The two areas in the north where coastal sampling predominates, off the south of Iceland and the south-west of Greenland, indicate that the timing of the increase is more

a



b



c

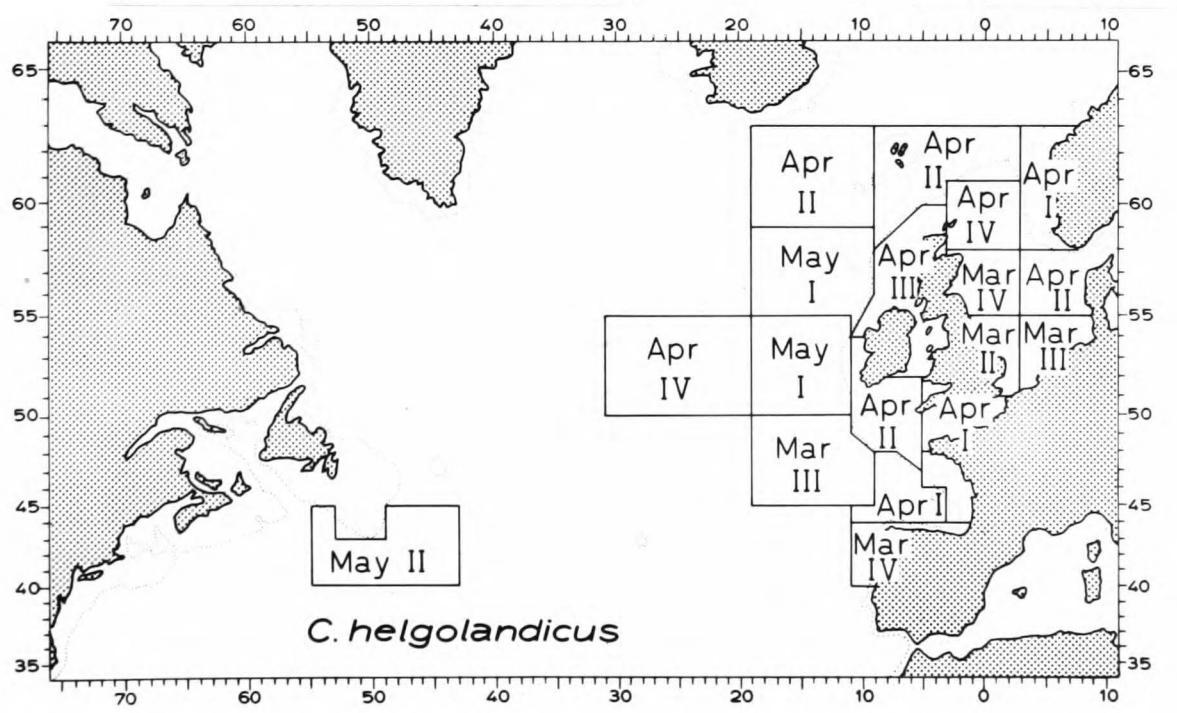


Fig. 40. The timing of the spring increase in numbers of late stage Calanus finmarchicus s.l. at the sea surface. Roman numerals indicate the quarters of each month.

advanced close to land than in the open ocean. In C. f. glacialis the main period of increase occurs in March or at the very beginning of April. It takes place in the first week of March off Labrador, Newfoundland and Nova Scotia and in the last ten days of March and the first week of April in the Gulf of Maine and in the open Atlantic to the north-east and to the south of the Grand Banks. This is the same distinction as the one noted earlier in the consideration of statistical correlations between large areas; since this form occurs only rarely in the latter half of the year, the calculations of spring timing and of correlation coefficients are based on almost the same data. The pattern of spring timing of C. helgolandicus is in general similar to that of C. f. finmarchicus as far as they overlap, though there are differences in detail. Although the maintenance of a relatively high winter population near the surface has exaggerated the indication of early development in the southern North Sea, this region and that in the Atlantic off north-west Spain appear to be the first to show signs of development in the Survey area. By the beginning of April such activity has spread more widely through the North Sea, into the English Channel and onto the Spanish continental shelf. In a fortnight, from the 7th to the 22nd of April, the increase has spread northwards from the Bay of Biscay to the north-west of Scotland, by which time the remaining areas in the northern North Sea and to the east of the Faeroes have also recorded their spring increase. C. helgolandicus in the open ocean seems to develop a week or two later, by early May in the

east but not until near the middle of the month in the area south of the Grand Banks.

CONCLUSIONS

The results show that Calanus f. finmarchicus is widespread throughout that part of the North Atlantic sampled by the Continuous Plankton Recorder; it is, in fact, the most widespread of all the zooplankton species of the region. Only in the extreme south-east, in the region of the Bay of Biscay, is there an indication that its normal limit of distribution has been reached. Low numbers near the southern edge of the oceanic part of the Survey suggest that this limit extends in an arc not far to the south of the Survey area; this is in agreement with its distribution as determined in previous studies, e.g. by Jaschnov (1961). Although recorded quite commonly in neritic areas, its main centres of abundance mark this form as primarily an oceanic species of cold temperate (boreal) regions.

The restricted distribution of C. f. glacialis in the North Atlantic may be defined as those regions in which there is an Arctic influence. It appears to be confined entirely to areas reached by an outflow from the Arctic, through the Labrador or East Greenland Currents.

C. helgolandicus is associated equally clearly with the warmer water within the Survey area. It is limited to those regions where there is a warm Atlantic influence or, nearer the coast, where temperatures are relatively high in the summer. While its northern

limit is reached within the Survey area, C. helgolandicus clearly extends well to the south of present sampling with the Recorder. Jaschnov (1961) indicated its presence in the eastern Atlantic as far south as 20°N. It seems reasonable, therefore, to classify this as a species of the warm temperate regions of the Atlantic. The sampling of warmer regions of the open ocean, though limited, is sufficient to suggest that this species, like C. f. finmarchicus, is widespread in oceanic as well as neritic regions.

The close juxtaposition of C. helgolandicus and C. f. glacialis south-east of the Newfoundland Grand Banks indicates how waters of entirely different origins come together in this area. C. f. finmarchicus, the intermediate form, occurs with C. f. glacialis where Atlantic water has mixed with Arctic; it overlaps to the greatest extent with C. helgolandicus in those areas where seasonal changes in hydrographic conditions provide a suitable environment for one and then the other.

The seasonal fluctuations in numbers of Calanus show that the summer values may be comparable in neritic and oceanic areas, while in winter numbers at 10 m are maintained at a proportionally higher level over the continental shelf than over deep water. It is known that Calanus overwinters in deeper layers of water than it occupies during the summer (e.g. Marshall and Orr, 1957; Kashkin, 1962). It seems likely that the greater depths to which Calanus can penetrate in the open ocean allow it to disappear more completely from the surface than

is possible in shallow water. The almost complete absence of Calanus from the surface of the ocean in winter contributes to a more regular cycle of seasonal fluctuations than is usually found near the coast. Another important factor in this is probably the more even seasonal change in hydrographic conditions where the mass of water is greater and the disrupting influence of land is less. As a result geographical patterns in the timing of the spring increase are regular over great distances of open ocean and correlation coefficients between oceanic areas tend to be high. Contrasts between the areas of the North Sea, on the other hand, can be sharp. It is possible at the moment to do little more than describe these patterns and contrasts, and relate them to gross geographical and environmental factors. Synoptic hydrographic observations will be invaluable in analysing further the dependence of these copepods on their environment. In all this the anomalous cycle of C. f. finmarchicus on the Newfoundland Grand Banks stands out, a problem which again needs such data for its solution.

The available data are, however, well suited to the study of relationships between different members of the plankton. In the present investigation, the seasonal succession of the forms of Calanus is an example of such a study. It is likely that every planktonic species inhabiting a current system will have a total distribution greater than the area in which it can reproduce and maintain itself satisfactorily; the species will be an expatriate in those regions outside its normal limits of environmental tolerance to which current

systems can transport it. Such regions are probably unimportant to the species as a whole and expatriate species similarly unimportant to the endemic community.

For these reasons only those regions where breeding populations of two forms of Calanus occur together satisfy the initial conditions for biological succession. It is not yet clear whether the samples of C. f. glacialis are derived from a population which breeds and maintains itself somewhere in the region of Arctic outflow along the east coast of North America, but the complete absence of records for a part of the year from all sampled areas, except the northernmost part of the Labrador Current, does suggest that it is an expatriate form within the Survey area. Similarly, C. helgolandicus is an expatriate species in the more northern and western parts of its range. The most suitable overlap between forms for the study of succession is thus that between C. f. finmarchicus and C. helgolandicus in the North Sea and off the west coast of the British Isles. Since both these forms are known to be primarily herbivores (Marshall 1924, Petipa, 1965) and the morphology of their mouthparts is almost identical, the relationship between them appears to be a good example of biological succession: as environmental conditions change from favouring one species to favouring another, the second replaces the first in fulfilling essentially the same ecological role in the community.

CALANUS FINMARCHICUS ON THE CONTINENTAL SHELF BETWEEN NEWFOUNDLAND AND THE GULF OF MAINE

INTRODUCTION

Recent investigations have emphasised the importance in the ecology of marine copepods of such factors as temperature and phytoplankton in the environment (e.g. Deevey, 1960) and the timing of generations within the population (Beklemishev, 1954; Heinrich, 1962a). Deevey has demonstrated an inverse relationship between ambient temperature during development and body length in natural populations and in some cases a positive relationship between food supply and body length. Beklemishev grouped copepods according to the relative timing of breeding cycles and phytoplankton blooms. He pointed out that, for maximum use to be made of an increasing stock of phytoplankton, the herbivore biomass needs to be increasing concurrently at its maximum rate. This maximum rate of growth occurs fairly late in the development of a new generation, in the older copepodid stages. Breeding in such cases must, therefore, start before the phytoplankton bloom. There are, however, other ecological situations where breeding cannot start before the phytoplankton blooms, cases where, for example, a population over-winters as juveniles and requires the spring outburst of phytoplankton before it can mature. The timing of the bloom of phytoplankton and the breeding behaviour of copepods are an important aspect of studies of annual cycles in the plankton, studies which can be undertaken on material collected by the Continuous Plankton

Recorder. It was noted in the previous section that there were differences in seasonal fluctuations within the area of the Recorder Survey so only one part of it, the continental shelf from Cape Race, Newfoundland, to Boston, Massachusetts, is considered here.

MATERIAL AND METHODS

Sampling of the chosen area is in two parts, the first from St. John's, Newfoundland, to Halifax, Nova Scotia, the second from Halifax to Boston. Fig. 41 shows the approximate route taken by the ships towing Plankton Recorders (there is some variation from month to month), bottom topography and the basic current system (after Hachey, Hermann and Bailey, 1954). A period of fourteen months of sampling, from July, 1961, to September, 1962, was covered in the course of the investigation. During this period twelve sets of samples were obtained, with a break in September, 1961, and incomplete sampling in November, 1961, and January, 1962, on the eastern part of the route. About 45 samples, each equivalent to approximately $3m^3$ and representing 10 miles of sampling, were taken between Cape Race and Halifax and 35 samples between Halifax and Boston. Alternate samples have been studied and the results combined into three sections, the first from Cape Race over St Pierre Bank and the Laurentian Channel as far as the north-eastern end of the Scotian Shelf, the second over the north-eastern part of the shelf as far as Halifax and the third from Halifax to Boston, again passing over some deeper water in the Fundian Channel.

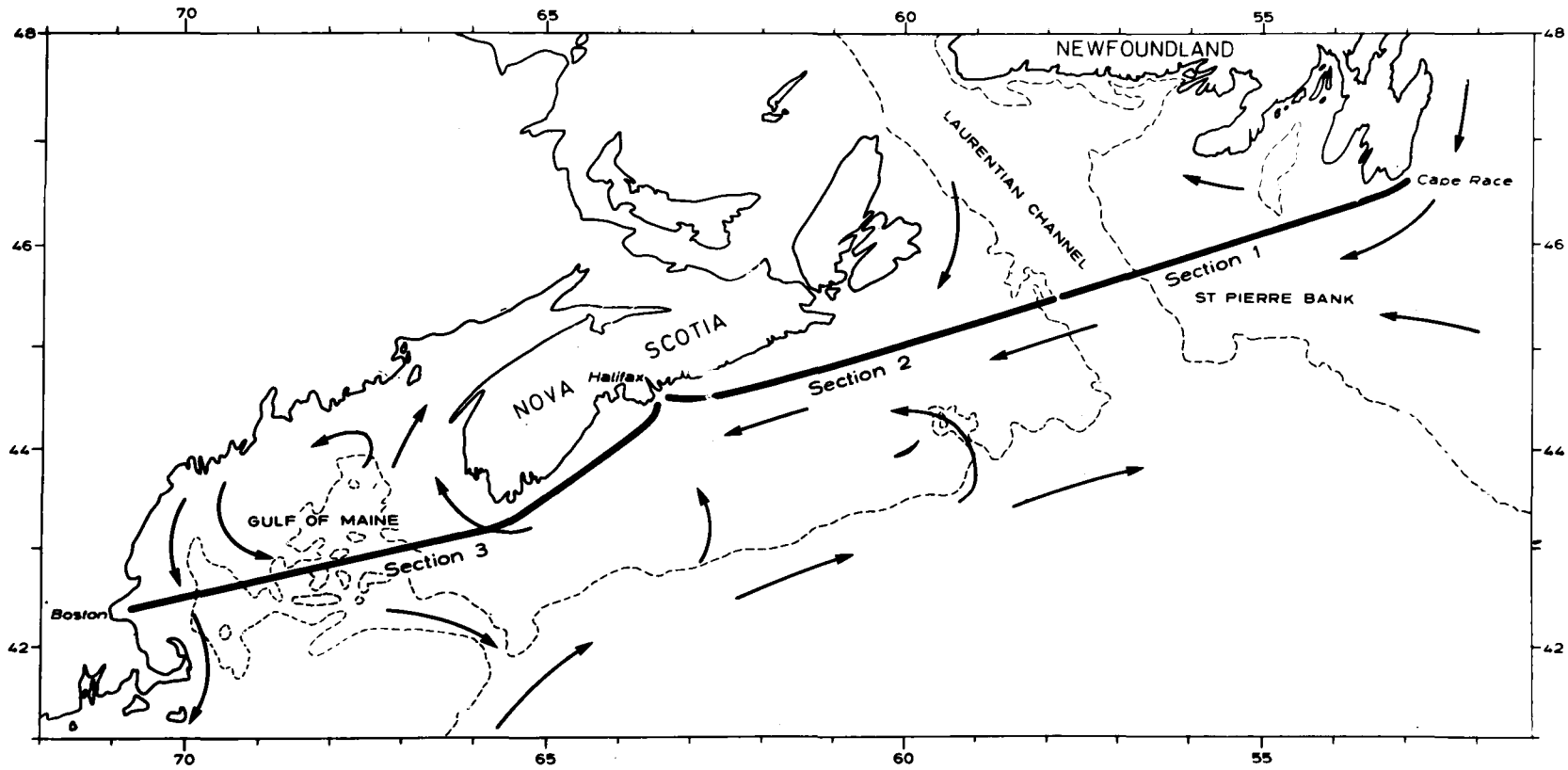


Fig. 41. The investigated area, from Cape Race, Newfoundland, to Boston, Massachusetts, with the approximate sampling route and its three sections. The 100 fm contour is marked and the main current patterns indicated.

Adults and stage V copepodids were counted in each of the samples examined. "Accepted values" for the categories recorded during routine analysis (see p. 11) have been used to estimate the numbers of young copepodids (stages I - IV combined).

RESULTS

Seasonal changes in population composition.

The composition of the populations, expressed as percentages of adults, stage V and younger copepodids, is shown in Fig. 42 a - c. The patterns in the three sections are similar; young copepodids predominated for three to four months in spring and early summer, and again in the autumn. Older stages were proportionally more common in early spring and mid-summer. Since the proportion of younger stages retained by the filtering silk is less than that of older stages (see p. 9), a developing generation tends to become more apparent as the copepodids become older and larger. Thus, as shown in Fig. 42b, the numbers of stages I - IV retained by the silk increased steadily from February to July after which there was a sudden drop in their percentage occurrence as moulting to stage V took place. Nevertheless recruitment to the stocks appears to have occurred over two quite short periods, as indicated by the rapid fall in proportion of adult females. In all three sections the first generation started to appear in the samples in February and March. In sections 1 and 2 the second started in August while in section 3 it occurred rather earlier, in July or even late June.

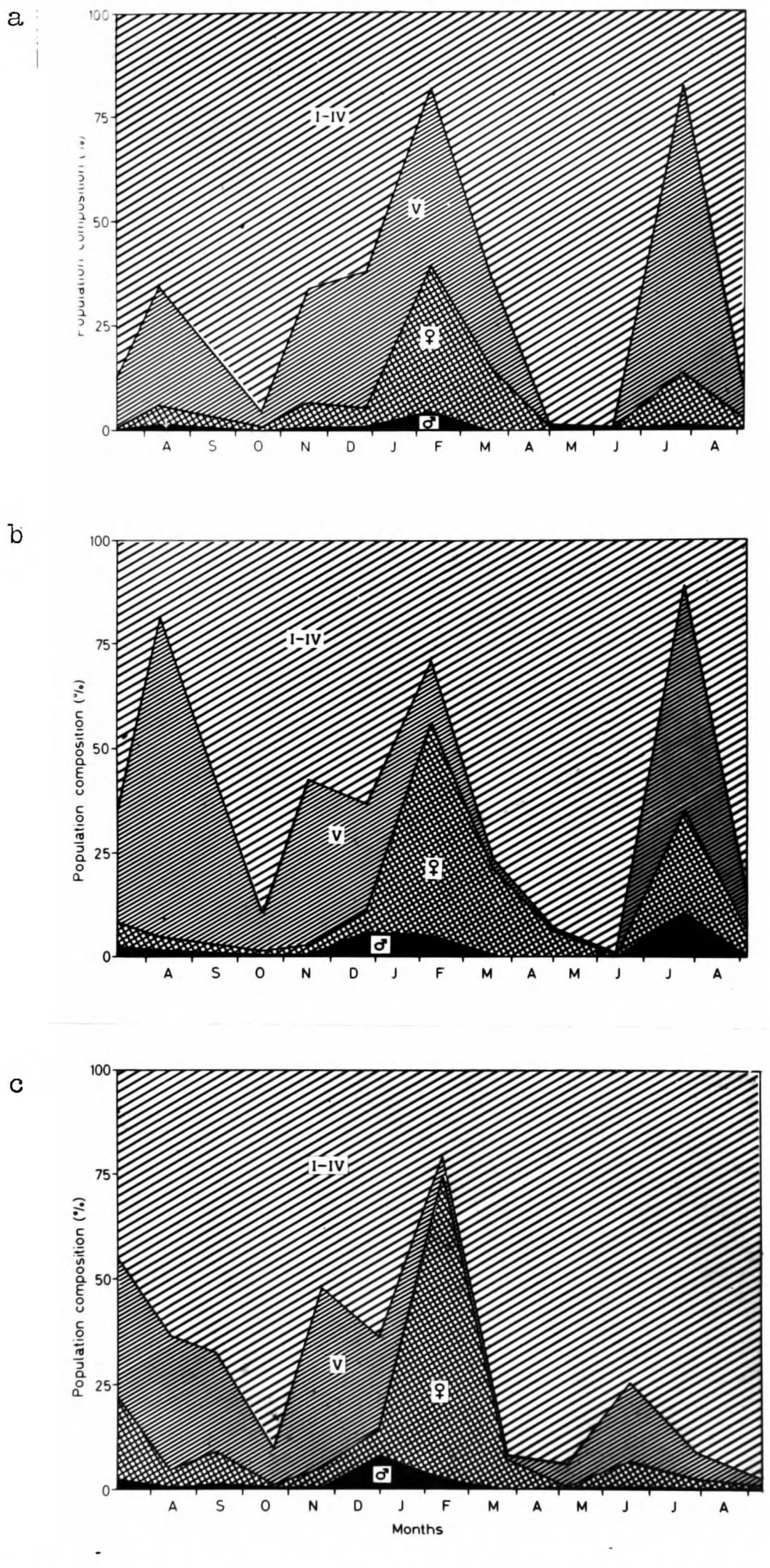


Fig. 42. Calanus f. finmarchicus; population compositions in the samples taken from July 1961 to September 1962.
a. Section 1. b. Section 2. c. Section 3. (For the position of the sections see Fig. 41).

There is a suggestion, too, of a third generation in the late autumn and early winter at least in section 3; in all sections the reduction in young copepodids from October to January was interrupted in December. In section 1 this was merely a slight check in the decline in numbers of stage I - IV but in the other two sections, particularly the third, the proportion of these copepodids increased again in December.

The fluctuations of stage V copepodids and adult females generally coincided with each other. It seems likely that the females did not usually remain long at stage V; the overwintering generation, for example, seemed to be maturing steadily from October to January. The appearance of males sometimes preceded the main abundance of females; in sections 2 and 3 they reached their winter peak of proportional frequency a month before the females and two months before the apparent start of the generation.

Seasonal Variations in Size.

The length of the metasome in adults and stage V copepodids was measured from the tip of the head to a line joining the postero-lateral margins of the metasome. Mean values for this measurement in stage V copepodids and adults are given in Fig. 43. Separate values for stage V are given for the three sections; this stage was absent from the samples from section 1 taken in September 1962. Combined results are given for adult females and males since there were apparently no local patterns in size variations.

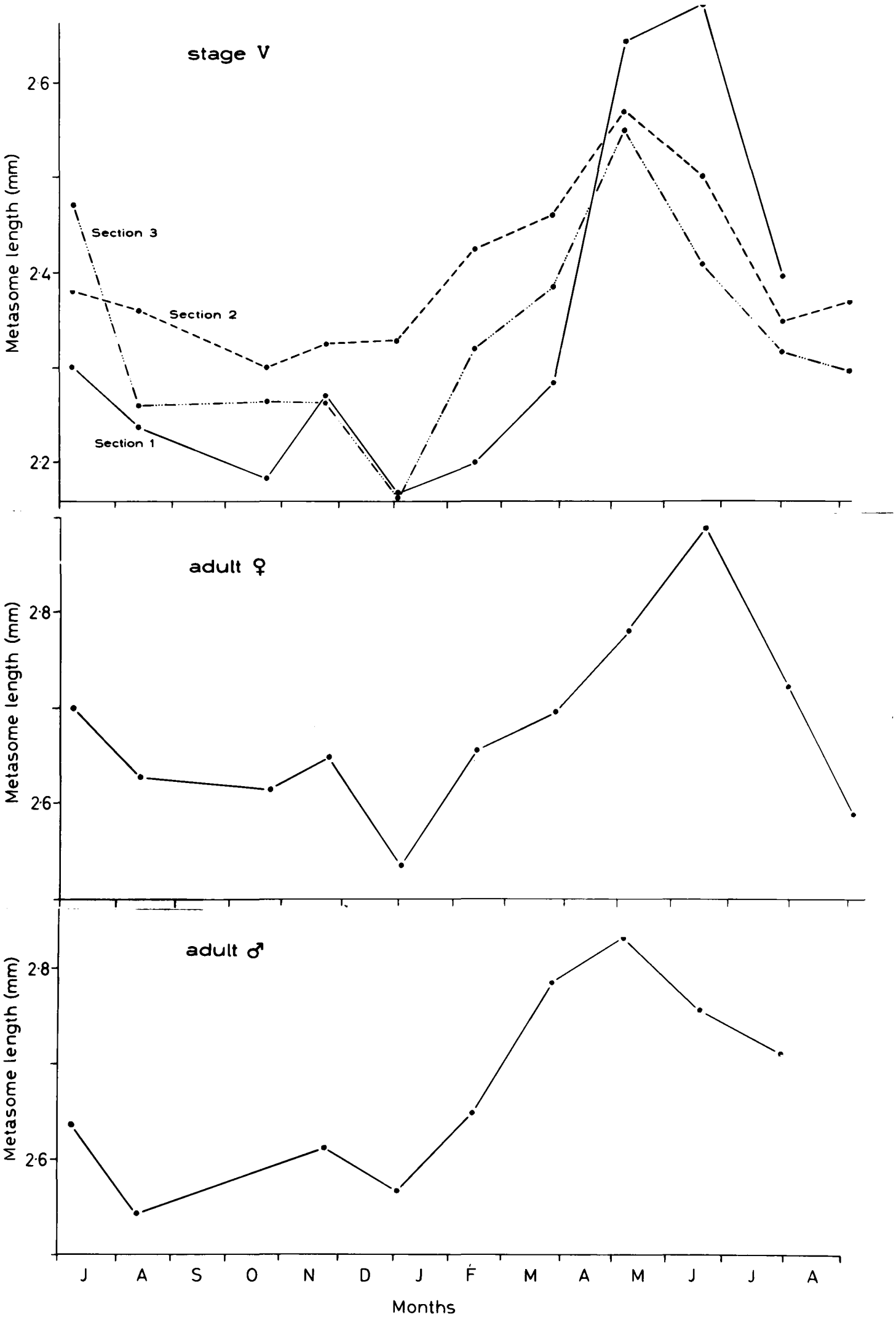


Fig. 43. Calanus f. finmarchicus: mean metasome lengths throughout the investigated period. Values for the three sections of the route are shown separately for stage V copepodids but have been combined for the adults.

Each set of values shows a distinct pattern of seasonal variation in length, the maxima occurring in May or June, the minima most commonly at the beginning of January. The largest stage V copepodids were found in May in sections 2 and 3, in June in section 1. The annual cycles of size variations of adult females and males do not exactly coincide, the former being a month later in achieving their greatest length. There appeared to be some local differences in length of stage V between sections, the range of variation being greatest in section 1 and values for section 3 being rather smaller than those for section 2.

Sea surface temperatures for the area have been obtained from the monthly charts issued by the U.S. Navy Hydrographic Office. Seasonal changes in temperature and mean lengths of Calanus were compared. An inverse relationship was apparent which was strongest in adult females when metasome length was compared with sea temperature three months previously and in stage V when a two month delay was used (Fig. 44).

There was no sign of a relationship between the metasome length of adult Calanus and the quantity of phytoplankton at the same time or at any time previously. There was a suggestion of a positive relationship in the case of stage V copepodids when considered in relation to the phytoplankton one month previously; in particular the two samples of Calanus stage V with the greatest mean length of metasome occurred one month after the highest concentrations of phytoplankton in their respective areas. It may be that fluctuations in abundance of phytoplankton during the development of a generation of Calanus gradually obscure any

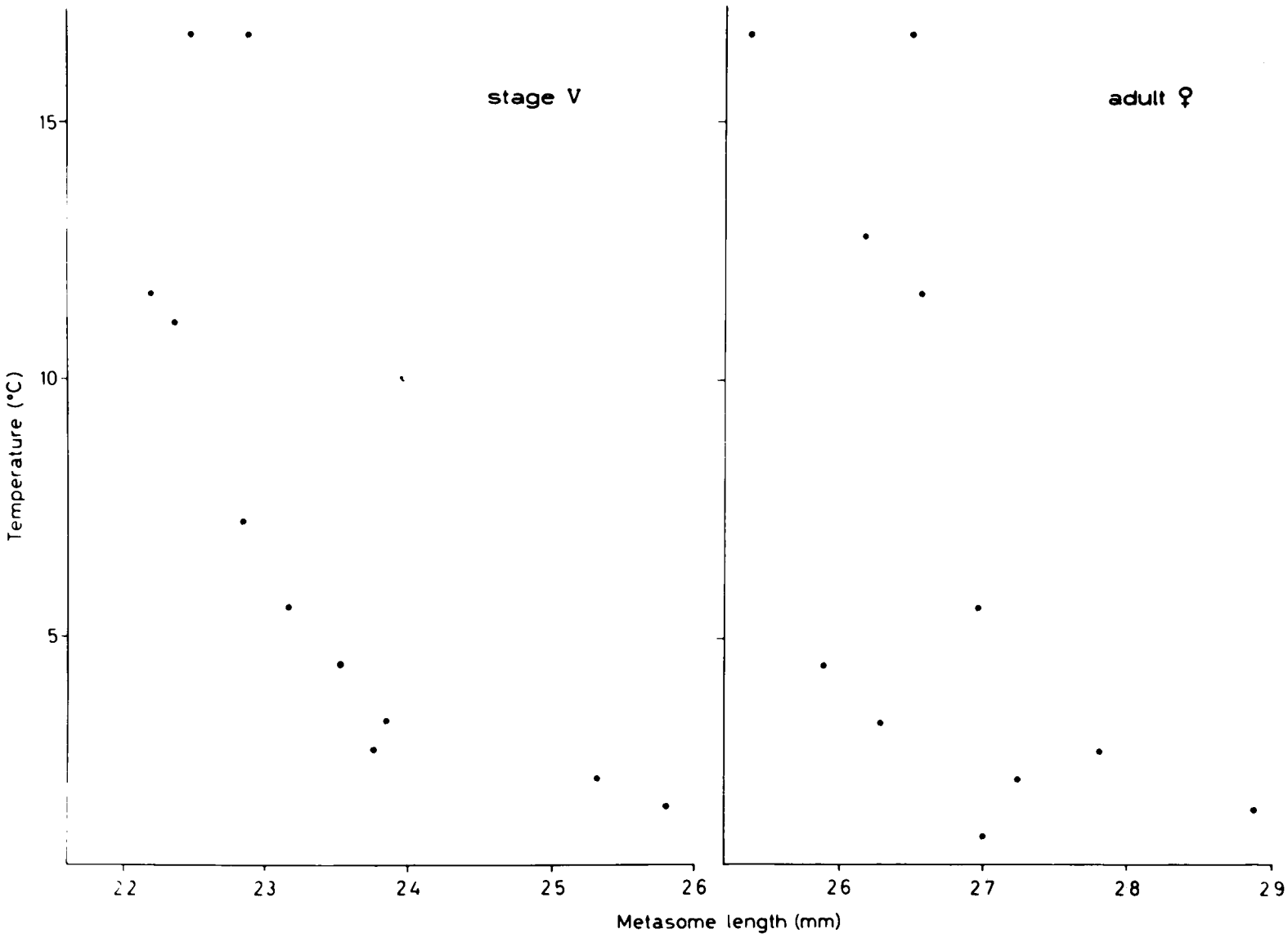


Fig. 44. Calanus f. finmarchicus: the relationship between metasome length of stage V copepodids and adult females and surface temperature two and three months before sampling respectively.

relationship which may exist. The phytoplankton, therefore, has been considered further only in relation to the younger copepodids, stages I - IV.

Calanus Biomass and the Phytoplankton.

Copepodids I - IV have been grouped together in the present investigation. A standard value of 1.2 mm metasome length, based on published values for these stages (Marshall and Orr, 1955), has been taken in order to derive values for biomass using the formula calculated by Kamshilov (1951). Since various approximations are involved in the conversion and only one part of the water column is represented in the samples, the units of biomass are not considered to be absolute values and therefore have not been expressed in terms of milligrams per unit volume of water. The estimates of the total phytoplankton are based on a visual assessment of "greenness" of the filtering silks. In the absence, at present, of any more precise method the results obtained in this way seem to justify the method (see Colebrook and Robinson, 1965).

The fluctuations in abundance of phytoplankton and the biomass of Calanus stages I - IV are shown in Fig. 45. The curves follow each other quite closely except that the increase of phytoplankton occurred rather earlier and was greater than the increase in young Calanus. This may be partly accounted for by the omission of nauplii from the estimates of young Calanus and by the loss of more of the smaller than the larger copepodids through the Recorder. The similarity between the fluctuations of phytoplankton and young Calanus other than during the spring may

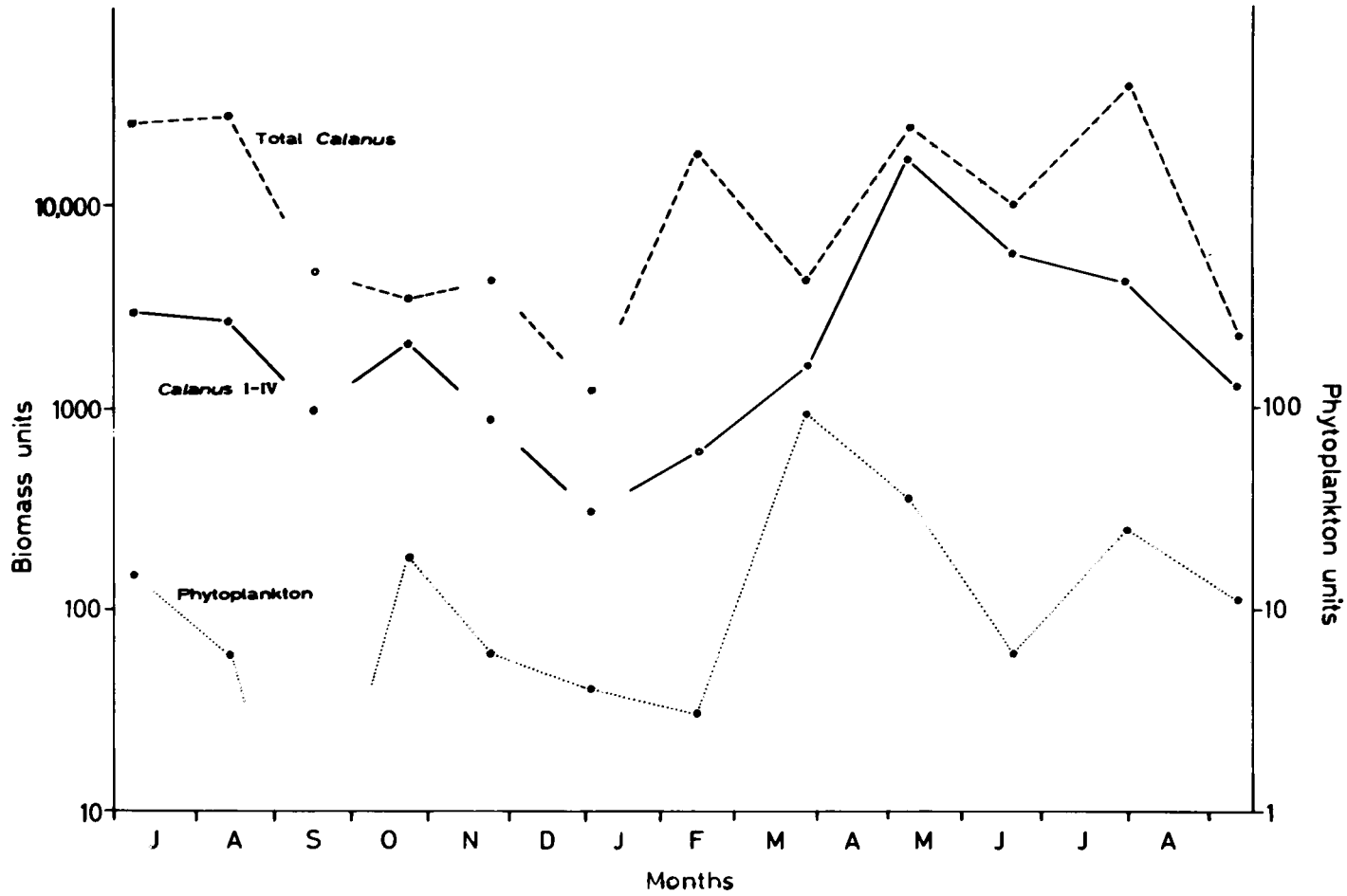


Fig. 45. Fluctuations in abundance of phytoplankton, young copepodids of Calanus and all stages of Calanus. The phytoplankton units have been obtained from colour analysis of the samples (see. p. 88), and the biomass units by application of Kamshilov's formula (1951) to the numbers of Calanus recorded in the samples. The open circles indicate samples which were not fully quantitative.

suggest that food was an important limiting factor on the stocks of Calanus in the area.

Estimates of the total biomass of Calanus are also given in Fig. 45. Seasonal fluctuations were fairly small, consisting of an apparent drop during the autumn and rise in early spring, followed by a small but steady increase during the summer months. There was little sign of breeding by the time of the apparent increase of biomass in February, so this increase must have been due to the return of the over-wintering population to a level at which they could be sampled by the Recorder.

Occurrence of Calanus f. glacialis.

The size frequency of C. finmarchicus in the area (Fig. 46) shows that there was a number of specimens over 3.5 mm in metasome length which could be referred to C. f. glacialis. The geographical and seasonal occurrence of these specimens is shown in Fig. 47. C. f. glacialis was most common over the shallow parts of the Scotian Shelf and at times when the sea temperature was low but formed too small a part of the Calanus populations to indicate reliably the nature of the ecological relationship between it and C. f. finmarchicus.

CONCLUSIONS

The biology of Calanus finmarchicus in the Gulf of Maine and Bay of Fundy has been investigated by Fish (1936). The western end of the area covered in the present investigation also covers a part of the Gulf of Maine and there is thus an overlap to provide a check on results.

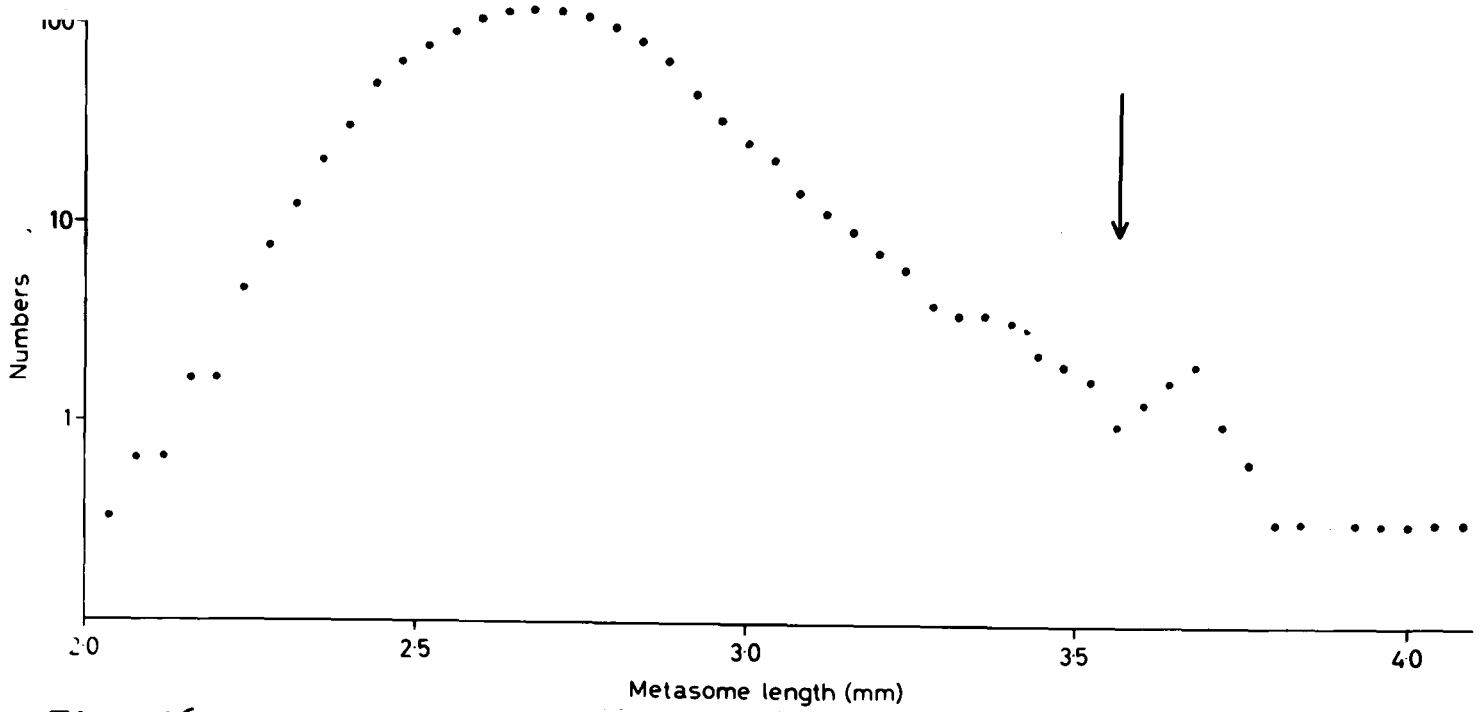


Fig. 46. Calanus finmarchicus, adult ♀, from all samples; the metasome length frequency, plotted on a logarithmic scale and using running averages. The arrow indicates the apparent separation between C. f. finmarchicus and C. f. glacialis.

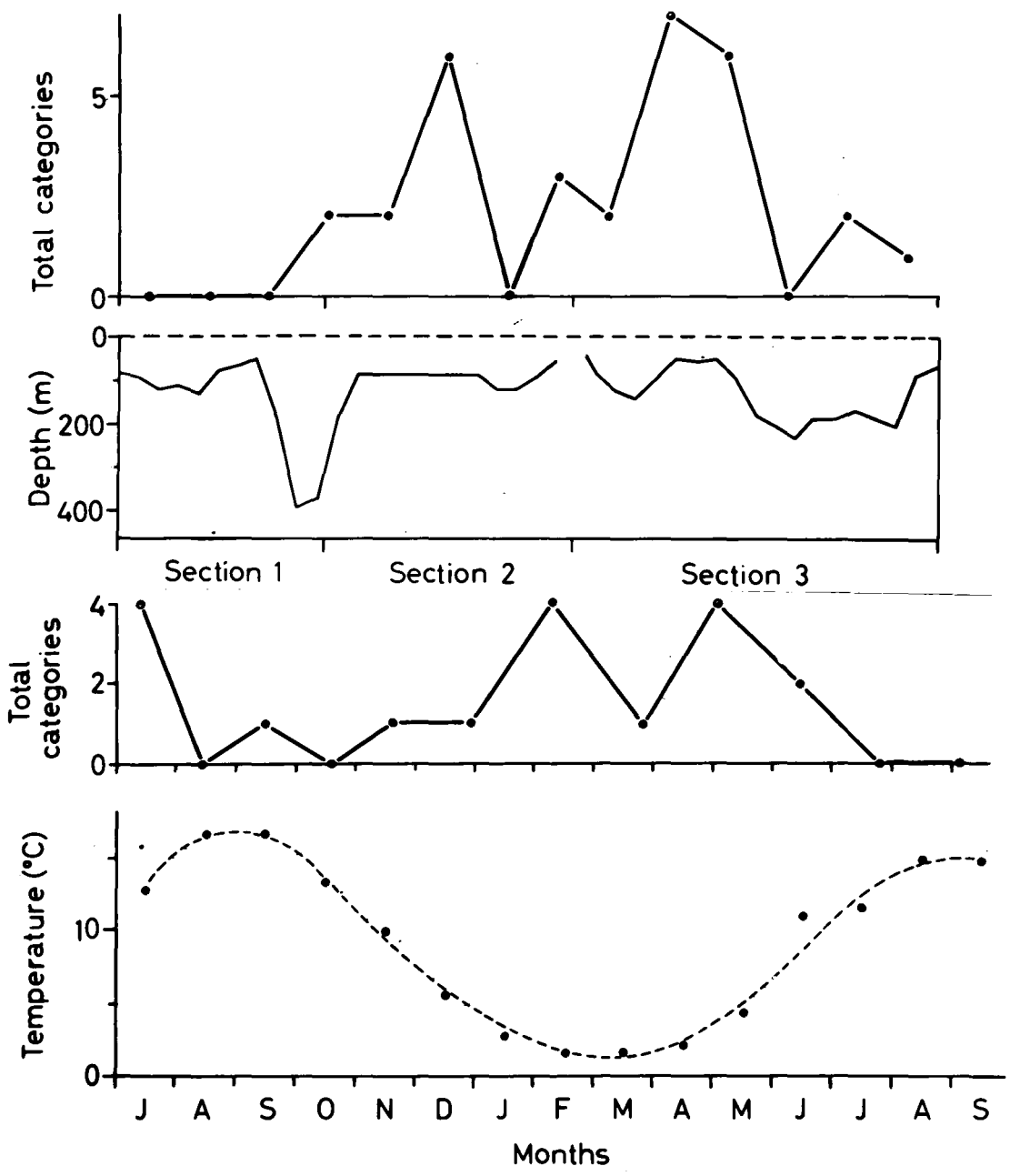


Fig. 47. The occurrence of C. f. glacialis along the three sections from Cape Race, Newfoundland, to Boston, Massachusetts, and throughout the investigated period. The corresponding sea depths and surface temperatures are shown.

Fish found that the largest stocks of Calanus in the area were to be found in this western part of the Gulf of Maine and that there were two main generations in the year, starting in March and June respectively, and a small one in September. Similar results for this area have been obtained in the present study, although the generations seem to have been rather more widely spread, the first starting in February, the second in July and the third in October or November. Some of this apparent difference may be due to different methods of recognising the beginning of a generation but it is likely that there are also variations in timing from year to year; in particular, the length of the breeding season in 1961 (from February to November) seems to have been longer than in 1931-2. Stocks further to the north-east, both in the Bay of Fundy and along the continental shelf off Nova Scotia and southern Newfoundland, show little or no sign of a third generation but, whereas Fish concluded that populations of Calanus in the Bay of Fundy were regularly augmented from richer areas to the south-west, the populations along the shelf outside seem to be indigenous.

It has been established in many areas that males of Calanus finmarchicus mature earlier than the females (see Woodhead and Riley, 1959, p. 467) and that one copulation is usually enough to fertilise the whole egg production of a female (Marshall and Orr, 1955). The fact that adult males appeared rather earlier than the females supports these observations.

The temperature of the sea surface in the area ranged between 2°

and 17°C. Deevey (1960) found that there was an inverse relationship between length and temperature with such a range, while an additional direct relationship between the body length of copepods and the phytoplankton was only apparent within ranges of less than 14°C. Not unexpectedly, stage V copepodids showed a closer relationship with environmental temperature than did adult females and the interval in time between observations of sea temperature and metasome length was shorter in the case of the former. The environmental factors of temperature, light and quantity of phytoplankton are closely inter-related (e.g., Braarud, 1945; Nielsen and Hansen, 1959) and it seems difficult, therefore, to try to assess the effects on copepods of two of these, temperature and phytoplankton, independently. A wide range of temperature through the year implies a rapid change in temperature between the maximum and minimum and phytoplankton would thus be expected to change rapidly too. In Calanus, on the other hand, changing conditions over several months affect the ultimate mean length of the copepods so that any relationship between phytoplankton and copepod size may be effectively obscured. Under less variable conditions, temperature, phytoplankton and copepod size may all be seen to be related.

Estimates of the biomass of young stages of Calanus finmarchicus indicate a relationship to estimates of contemporary phytoplankton from July to February (Fig. 48). In the remaining months, on the other hand, there was a swing from abundant phytoplankton and low values for young Calanus in March to relatively scarce phytoplankton and high values for

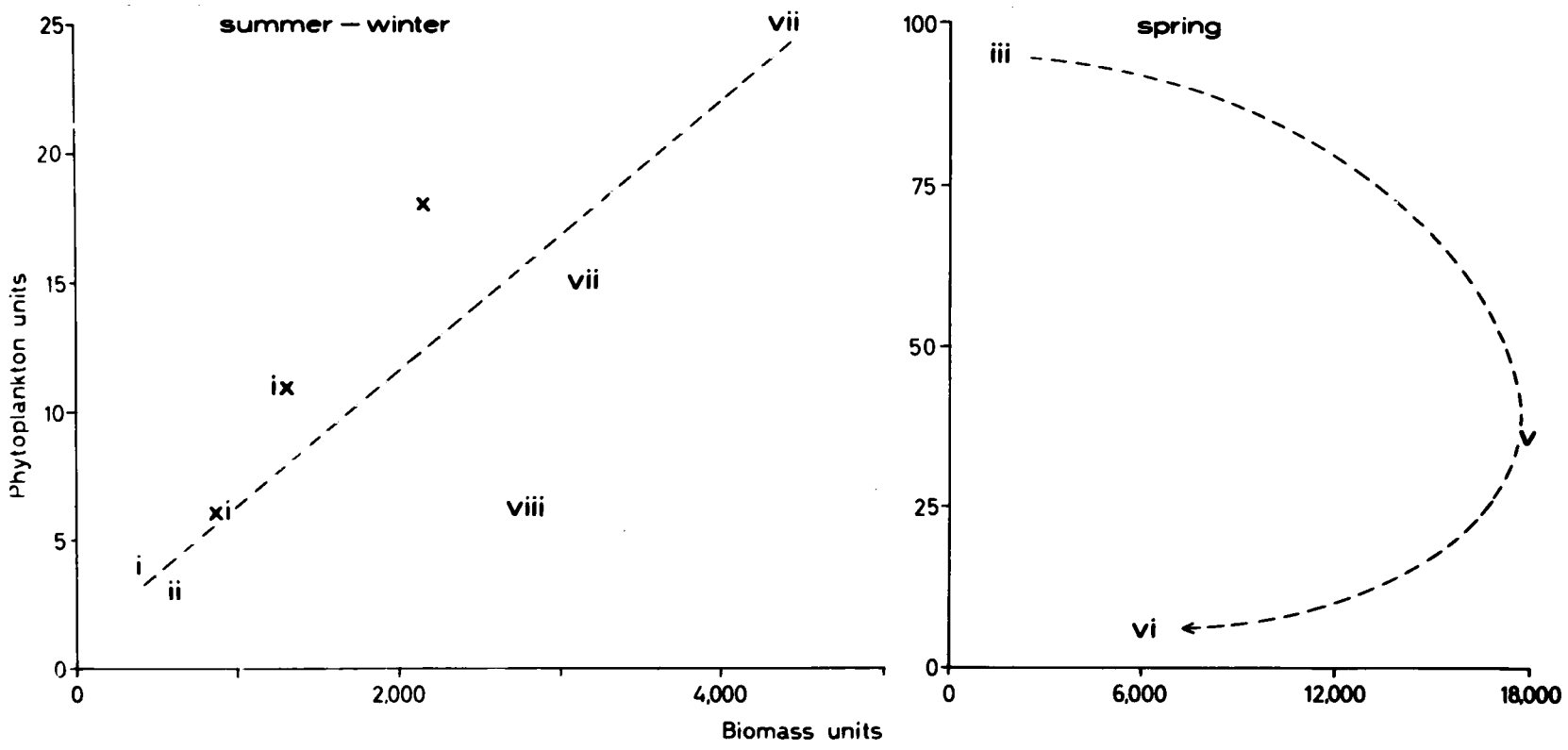


Fig. 48. Phytoplankton and Calanus; left, their relative abundances from July to February; right, the same from March to June. The broken lines indicate a suggested linear relationship from summer to winter and a succession of phytoplankton by Calanus in spring.

young Calanus in May and towards a return to the usual relationship in June. There was thus a balance between phytoplankton and Calanus which only broke down during the rapid spring outburst of phytoplankton and the ensuing increase in young Calanus during the first generation of the year. This supports the suggestion made by Baklemishev (1954) and Heinrich (1962a) that Calanus finmarchicus breeds soon after the spring development of phytoplankton.

THE SPRING GENERATION OF *CALANUS F. FINMARCHICUS* IN THE WATERS AROUND GREENLAND

INTRODUCTION

The changes in population composition from month to month south of Newfoundland and along the Scotian Shelf were shown in the previous section of the thesis to indicate an annual cycle of two main and one subsidiary generations. The most clearly defined of these was the first, but before this had been completed the second was already under way. This overlapping of generations makes it difficult to examine more closely any relationships which may exist between reproductive activity and environmental conditions. The period of abundance of phytoplankton, some five or six months in this coastal area off North America, is approximately twice as long as in the oceanic regions around the south of Greenland (Robinson, personal communication). The shorter period of abundant food in the north can be presumed to constrict the season of zooplankton production and, with lower sea temperatures, reduce the number of generations per year; it is under such conditions that any relationships between the breeding of *Calanus* and the environmental conditions will be most apparent. The importance of a few months of early summer in the replenishment of stocks has been emphasised, in fact, in previous work on the annual cycle of *Calanus f. finmarchicus* in the northernmost parts of its range (e.g. Jespersen, 1934; Ussing, 1938). It has been suggested that in these areas there is a single generation in the year and that this starts in April

or a little later. The information collated by Marshall and Orr (1955) shows that C. finmarchicus usually overwinters in deep water as stage IV or V and that the copepods rise towards the surface about the time that they mature in the early spring. Grainger (1959) has shown that in the extreme north of its range C. f. finmarchicus sometimes overwinters as stage III or even II, but this does not seem to apply in any region of the Atlantic. It should be, therefore, easy to distinguish the overwintering population from the spring generation in areas where development is relatively slow.

Since the present intention is to study further the timing of breeding activity and the speed of development of Calanus f. finmarchicus, in particular to examine the suggestions of environmental effects made in the previous section, a northern region of the North Atlantic has been chosen in order to achieve the conditions of simplicity which are desirable. Under such conditions it should be possible to provide an exception to the statement by McLaren (1965, p. 533) that, "Development rate is generally obscure in field collections". The area chosen, to the east, south and west of Greenland, was sampled during the NORWESTLANT Surveys in 1963 (see p. 12). As the period covered by the Surveys, from April to July, coincides with the time of greatest breeding activity in the area (see Jespersen, 1934) the results obtained should yield information on an important part of the annual cycle and how this varies geographically and with changes in the environment.

MATERIAL AND METHODS

The data used here are the results for Calanus f. finmarchicus from all the Hensen net samples, where developmental stages were analysed, in the Surveys NORWESTLANT I - III. These results have been presented by Corlett and Bainbridge (In press) as a series of 18 charts which show the abundance of each developmental stage of C. f. finmarchicus in each rectangle, 2^{o} long. x 1^{o} lat., sampled during each of the three Surveys. A single value representing the degree of development of the generation has been obtained for each rectangle by calculating the mean developmental stage; for this purpose each copepodid stage was assigned a numerical value, from 1 to 9, starting with the overwintering stage IV and ending with the adults of the spring generation. As suggested in the introduction to this section, it was clear from the composition of the population in each plankton sample whether the older copepodids (stage IV and V) and the adults belonged to the overwintering or to the spring generation.

It should be noted that the nature of the sampling introduces a bias towards the larger stages. Cushing and Tungate (1963) state that Calanus stage I is not sampled adequately by the Hensen net using 60-mesh silk. The efficiency of catching increases with the size of Calanus so that the proportion of young stages in the population will always be underestimated. The efficiency of capture of each stage, however, can be presumed to be more or less constant, so that comparisons between samples are valid.

RESULTS

Geographical pattern

Samples obtained from NORWESTLANT I (Fig. 49) were considerably more limited in area than from either of the subsequent Surveys. This was due in part to the ice in the extreme north-west still being impenetrable and in part to analysis of the greater part of the samples from the Irminger Sea being confined to adults and stage V copepodids. The samples nevertheless covered quite an extensive area, from 52° to 67°N and from 34° to 60°W, and included ranges at 50 m of temperature from -1.5° to 6°C and salinity from 33.6°/oo to 34.9°/oo. Despite such differences in the environment, however, the development of the Calanus generation was fairly uniform over the whole area and showed no obvious pattern associated with geographical location or environmental conditions. In a few samples the Calanus were on average still at stage V; in most, however, adults dominated and there were early signs of the spring generation; in three areas the generation was a little further advanced with copepodid I the mean developmental stage. The total range of development was equivalent to only 1.8 stages.

Sampling was good during NORWESTLANT II (Fig. 50) and extended northwards well into Baffin Bay and westwards across much of the Labrador Sea, as well as covering the Irminger Sea and reaching south-eastwards beyond the Reykjanes Ridge. By this time, June 1963, a geographical pattern had begun to emerge. The most advanced development was found on the south-eastern margin of the Survey and on the

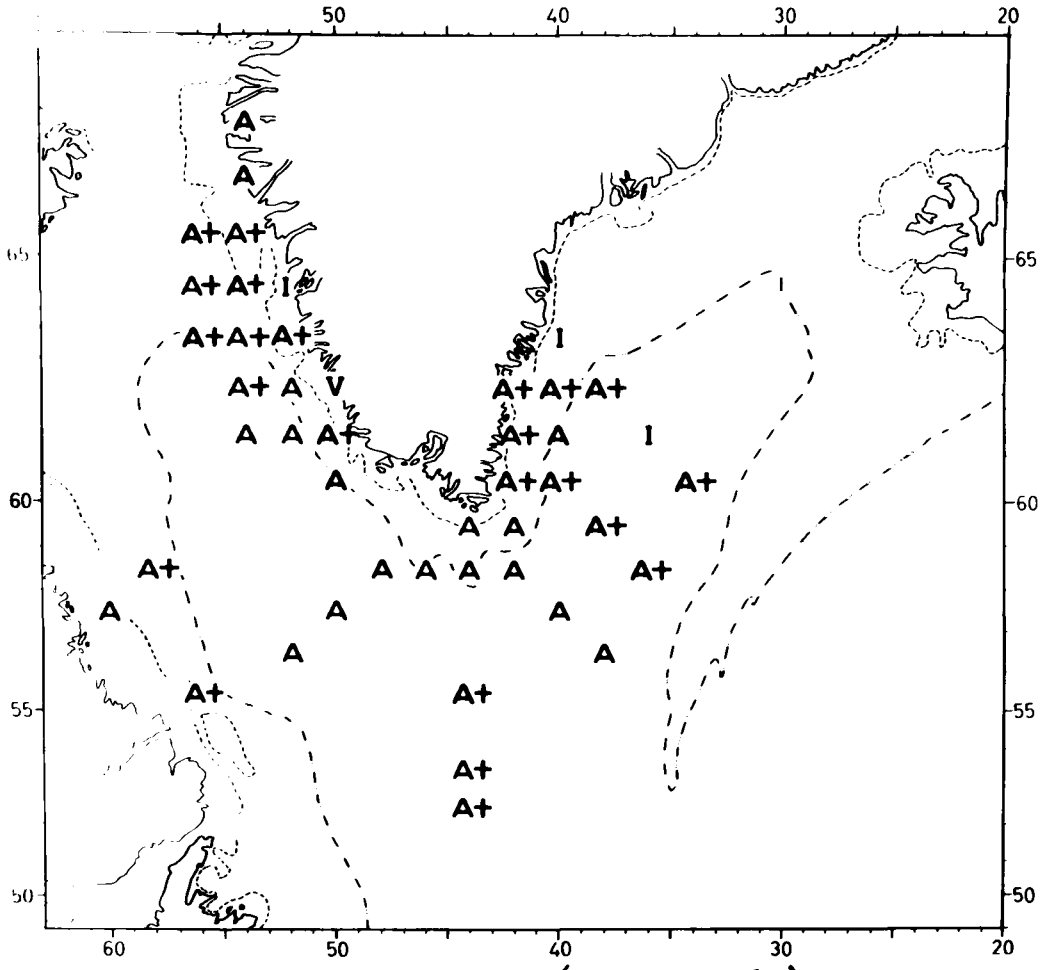


Fig. 49. The area of NORWESTLANT I (April 1963) showing the mean stage reached by the spring generation of Calanus f. finmarchicus in each sampled rectangle, 2° long. x 1° lat. Depth contours at 200 and 2000 m. V - overwintering copepodid V; A - adults (+ - copepodids I - III present) I - copepodid I.

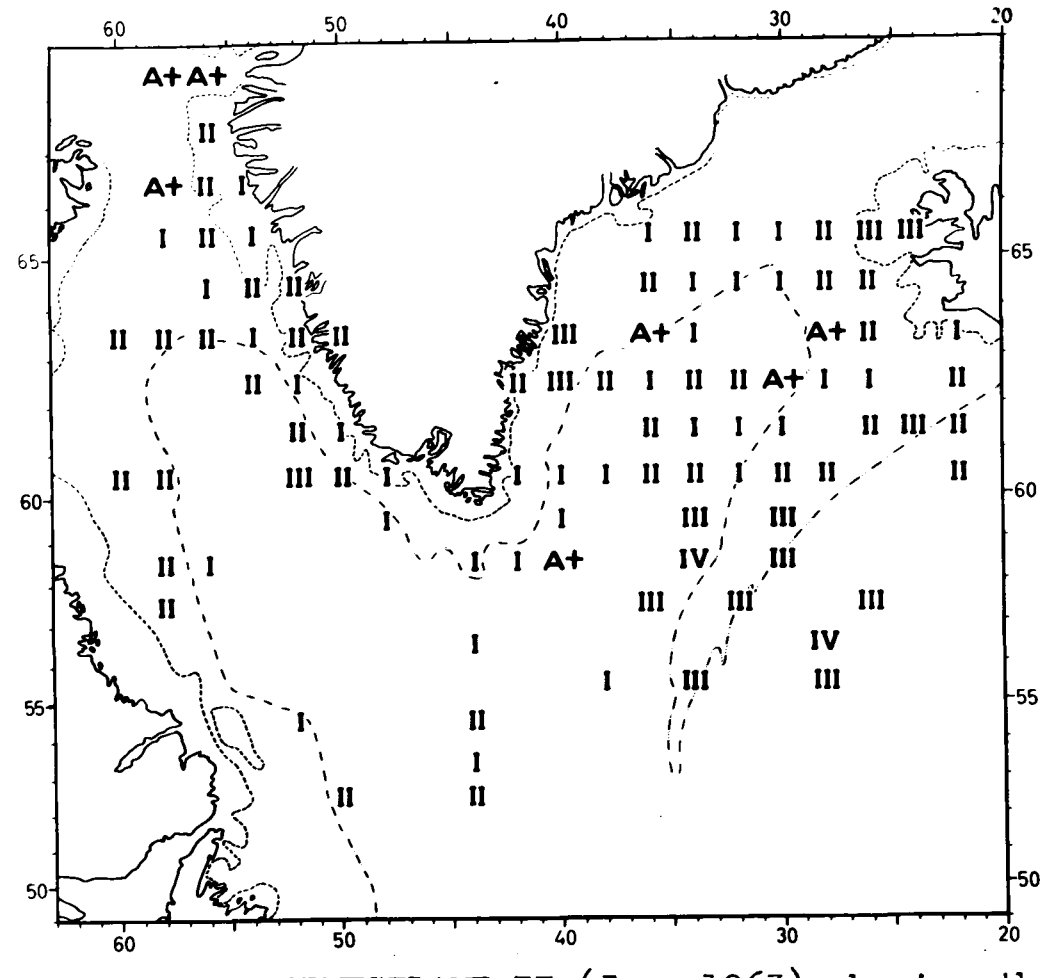


Fig. 50. The area of NORWESTLANT II (June 1963) showing the mean stage reached by the spring generation of C. f. finmarchicus. Symbols are as in fig. 49; additional Roman numerals refer to appropriate copepodid stages.

Icelandic Shelf while least advance had been made in Baffin Bay and the western Labrador Sea, the coastal regions around Greenland and, rather surprisingly, in some rectangles to the south of Greenland. By this time the total range of development of the generation within the area had increased to the equivalent of 4.2 stages.

The area covered during NORWESTLANT III (Fig. 51) was similar to that of the previous Survey though rather less complete. The gaps, however, do not obscure the fact that the geographical pattern had emerged still more clearly. Advanced development was apparent towards the southern end of the Reykjanes Ridge, in the Irminger Sea, excepting the north-western part, and in the central Labrador Sea. Conversely, samples from Baffin Bay and near the Labrador and Greenland coasts showed the least advanced development.

A precise calculation of the speed of development during the period of the Surveys is only possible for the 37 rectangles which were sampled during both NORWESTLANT I and III; the difference between these values (Fig. 52) indicates the number of developmental stages through which the generation passed in three months, April to July. Development in the open Atlantic, in the central part of the southern Labrador Sea and in the off-shore regions of the Irminger Sea was about twice as fast as in Baffin Bay and the coastal regions around Greenland. Intermediate speeds occurred in the vicinity of the edge of the Greenland shelf, off-shore in the northern Labrador Sea and in the Labrador Current.

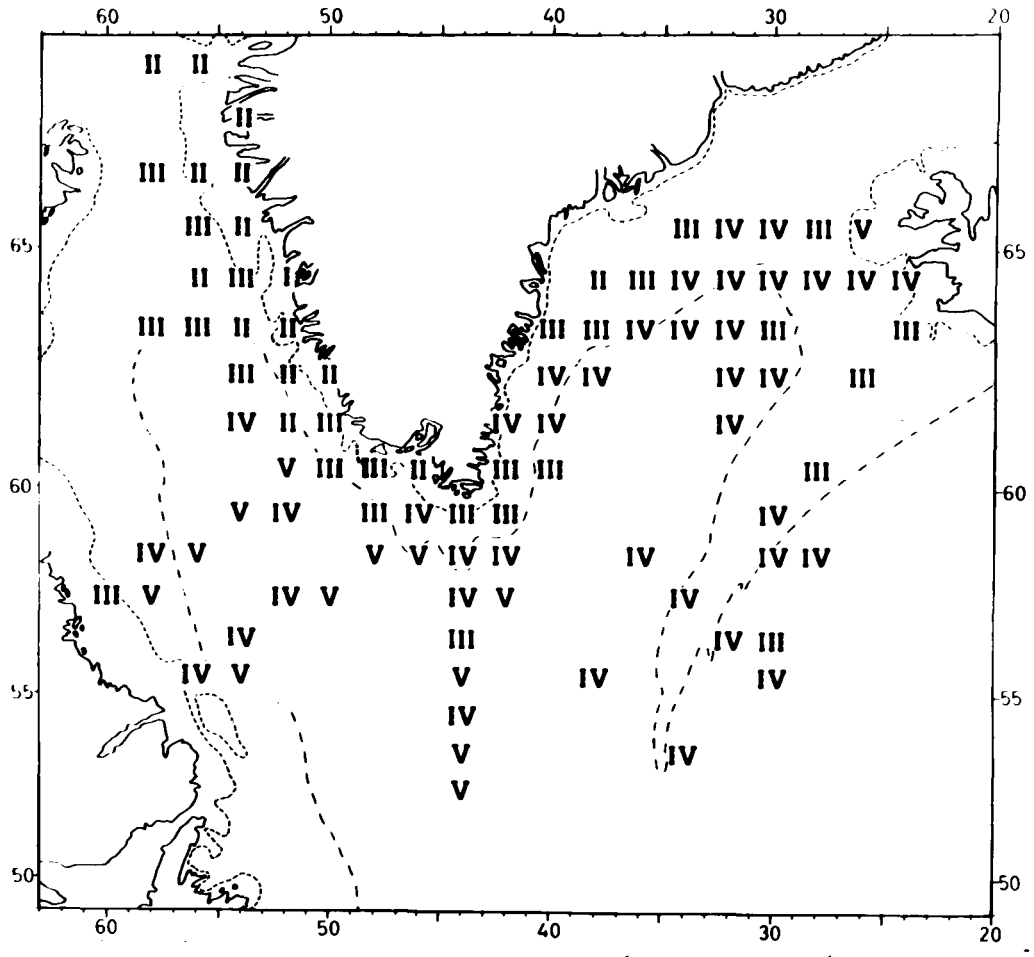


Fig. 51. The area of NORWESTLANT III (July 1963) showing the mean stage reached by the spring generation of C. f. finmarchicus. Symbols are as in figs. 49 and 50.

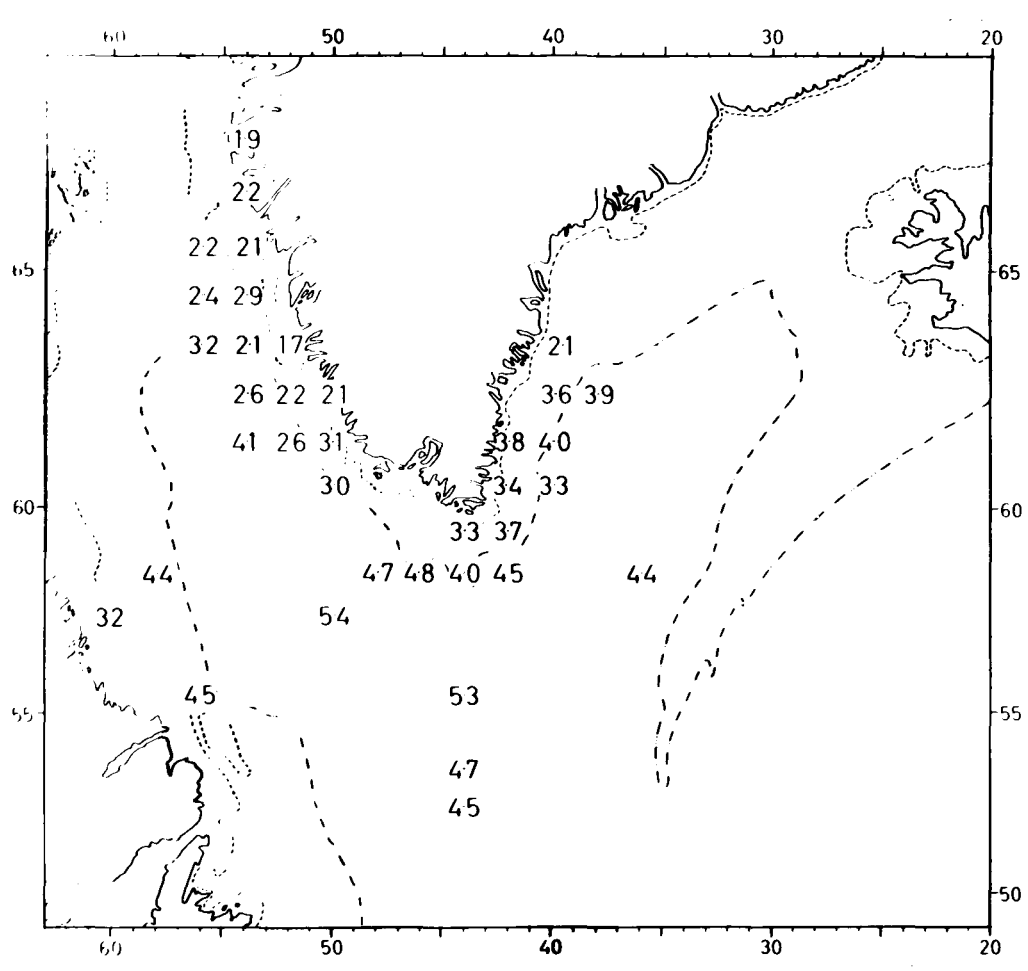


Fig. 52. The mean number of developmental stages passed through by C. f. finmarchicus between April and July, being the difference between the values obtained from NORWESTLANT I and III in all rectangles sampled on both occasions.

Since the values obtained from NORWESTLANT I showed a general uniformity throughout the area, it is possible to use the values obtained from NORWESTLANT III alone as an alternative estimate of speed of development. Development was progressively more advanced towards the south and over deep water (Fig. 53). Where great depths occurred at low latitudes development tended to be fastest, with a trend culminating in the slowest development in shallow water at high latitudes. The results from the Icelandic shelf were exceptional in showing rapid development at a high latitude and shallow depth and have been omitted from the figure. The need to make this omission indicates that the relationship is more accidental than real. The Arctic inflows into the area of the Surveys are known to be the East Greenland Current, which, diluted to some extent by Atlantic water, continues round Cape Farewell to become the West Greenland Current, and the Labrador Current. All these currents flow close to the coasts so that sub-Arctic conditions prevail in the shallow waters of the area with the exception of those round Iceland. It is reasonable, therefore, to study the speed of development in relation to temperature, probably the most obvious physical difference between the Atlantic and the Arctic.

Association with temperature.

A positive relationship is apparent between sea temperature at 50 m during NORWESTLANT II and the stage of development reached by Calanus during NORWESTLANT III (Fig. 54). When all points are

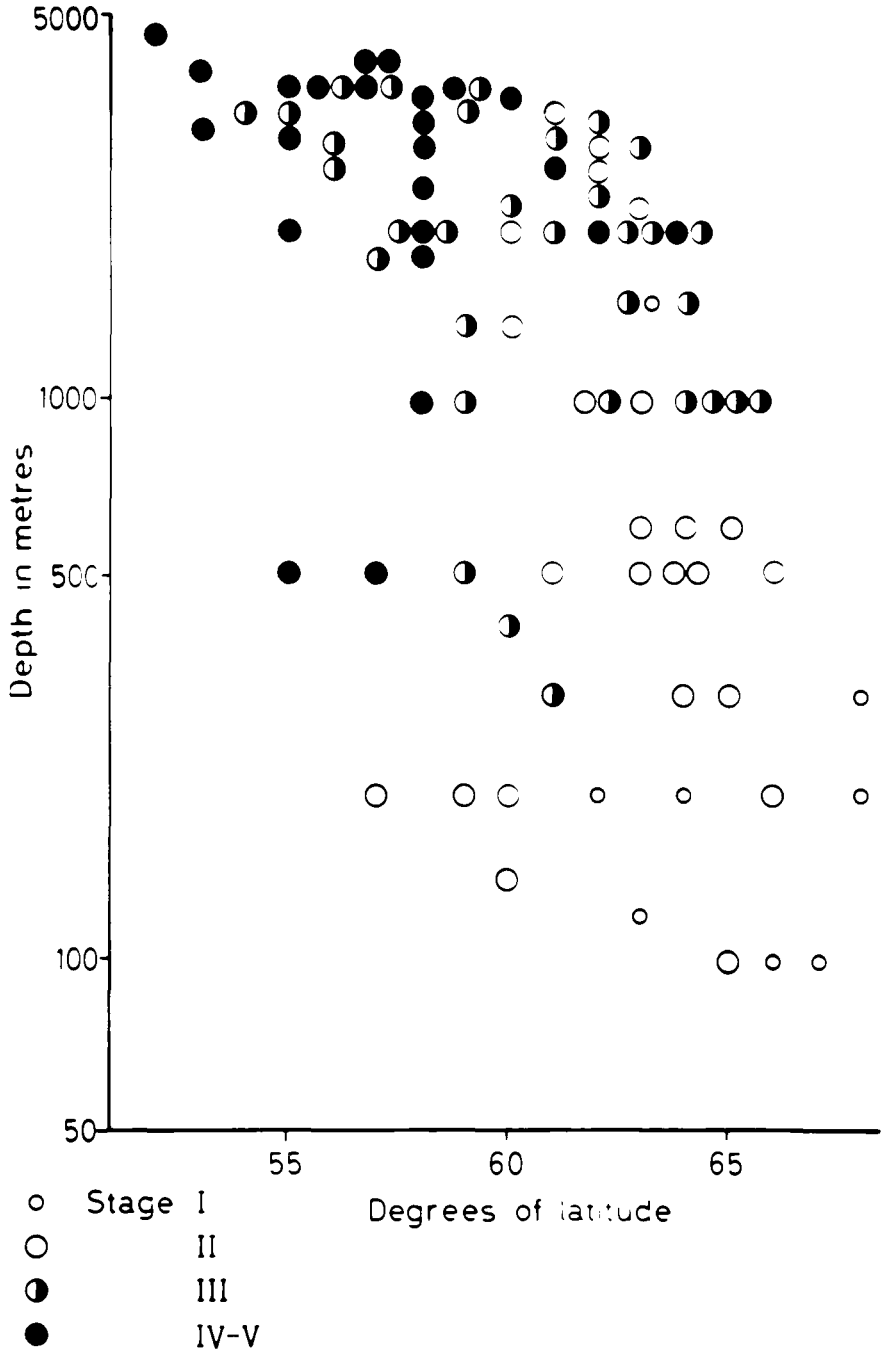


Fig. 53. The mean stage of development reached by C. f. finmarchicus in NORWESTLANT III related to geographical features of latitude and sea depth.

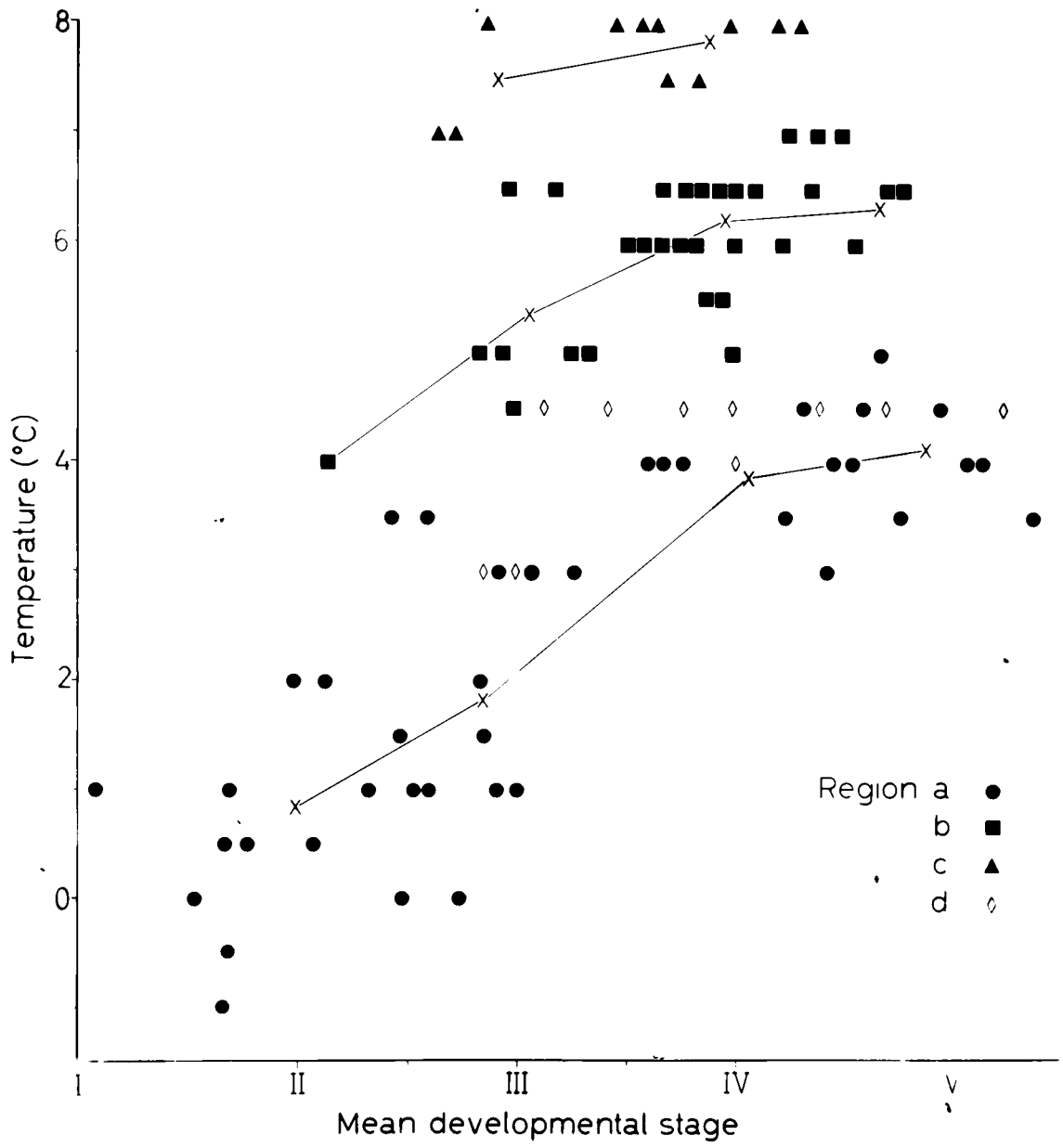


Fig. 54. The relationship between temperature at NORWESTLANT II and the mean stage of development reached by C. f. finmarchicus in NORWESTLANT III in the three defined regions (a - Labrador Sea; b - Irminger Sea; c - Open Atlantic) and the intermediate region (d).

considered there is a fairly wide scatter. During plotting of the results, however, it was noticed that values for rectangles in the Labrador Sea were situated low in the figure and values for the Reykjanes Ridge and the rectangles to the south-east occurred at the top. Geographical boundaries were therefore drawn up within the Survey area and different symbols assigned to the values from each of these regions. These regions are (a) the Labrador Sea and Baffin Bay, bounded by a line from Cape Farewell to Belle Isle, (b) the Irminger Sea and north-west Atlantic, from Iceland to the edge of the Greenland shelf, extending south to the northern slopes of the Reykjanes Ridge and to a line parallel to and 250 miles south-east of the boundary of the Labrador Sea, (c) the open Atlantic over and to the south-east of the Reykjanes Ridge, (d) the remaining samples, from a composite and poorly definable area comprising the coastal shelf of East Greenland and the rectangles to the south of Greenland between the first two regions.

When each of the three main regions are considered separately, there is a significant relationship between temperature during NORWESTLANT II and the development of the generation of Calanus during NORWESTLANT III. While the apparent relationship is similar in all three regions, there is no overlap between them. For given temperatures development appears to have been fastest in the Labrador Sea and slowest over and to the south-east of the Reykjanes Ridge. Over the range of development present, displacement between adjacent regions is some

2 to 3°C. Regression equations have been calculated for the three defined regions, for purposes of discussion only, and are given below:

$$(a)\quad D = 0.57t + 1.82$$

$$(b)\quad D = 0.48t + 1.01$$

$$(c)\quad D = 0.88t - 3.26$$

where D = mean stage of development reached during NORWESTLANT III,

t = temperature (°C) at 50 m during NORWESTLANT II.

Over the whole area of the Surveys, except in the Labrador Current, there was found to be a relationship between salinity and temperature at 50 m. The water of the Labrador Current differed in having a proportionally lower salinity than the rest. A relationship, therefore, between salinity at 50 m during NORWESTLANT II and the stage of development of Calanus reached by the time of NORWESTLANT III was to be expected. It was found, however, that it was a looser relationship than that obtained with temperature and has not been pursued further.

DISCUSSION

Russell (1926) and Bogorov (1946) have emphasised the apparent importance of light in the control of the vertical distribution of Calanus. It appears that seasonal and diurnal changes in illumination can affect the behaviour of Calanus in two distinct ways: where there is alternation between light and dark through the day, as in temperate latitudes and during the polar spring and autumn, the copepods are

distributed near the surface at night and in rather deeper layers during the day; where there is permanent daylight during summer and permanent darkness during winter, however, the effect is reversed and Calanus is to be found nearer the surface in summer than in winter. In the former situation Russell and Bogorov have adduced evidence to suggest that Calanus keeps as far as possible within an optimum light intensity. Experiments carried out by Hardy and Bainbridge (1954) showed that Calanus exhibited a negative reaction towards strong light and a positive reaction towards weak light, thus reinforcing the suggestion of an optimum light intensity. Absence of light, however, did not invoke a reaction. Somewhere between darkness and low light intensities it may be presumed, therefore, that there is a threshold value for response to light.

The present results show that within the area of the NORWESTLANT Surveys Calanus was widely distributed by April in the uppermost 100 m and that the sampled populations consisted mainly of mature individuals which already showed signs of starting to breed. At first there was no geographical pattern in the timing of the generation but one gradually emerged over the next few months, despite the fact that the temperature range in the area during NORWESTLANT III was only slightly greater (1/6) than during NORWESTLANT I. The range of salinity, and probably of other chemical conditions of the water as well, was also similar in the two Surveys. These facts suggest that such local conditions of

the environment as these could not be responsible for inducing maturation and spawning. It seems likely, instead, that the stimuli which cause Calanus to rise to the surface layers and to start reproduction operate on a much wider scale and may be associated with the threshold value of light mentioned above. Riley (1942) demonstrated the effects of light and turbulence in promoting the onset of phytoplankton production and Sverdrup (1953) devised an equation emphasising the importance of light in this respect. As discussed previously (p. 92) Calanus finmarchicus on the Scotian Shelf is ready to breed when the phytoplankton bloom starts in the spring, so it is reasonable to suggest that conditions of light similar to those which induce the onset of phytoplankton production also induce the overwintering population of Calanus to rise to the surface layers and to mature.

Investigations on the annual cycle of Calanus finmarchicus by With (1915), Ussing (1938), Kielhorn (1952) and Digby (1954) indicate that reproduction is concentrated largely in a single generation over the most part of the area considered here. Grainger (1959) has shown C. f. glacialis to be biennial in the Canadian Arctic. If the onset of breeding is controlled by environmental conditions, as suggested above, there can clearly be no intermediate length of reproductive cycle, since this would involve the cycle getting out of phase with seasonal changes in the environment. Yet it is clear from the results given here that, once reproduction had started, the speed of development was related to the ambient temperature. Temperature conditions, however,

differ quite considerably within the NORWESTLANT area; charts of sea surface temperature prepared by the Meteorological Office show that throughout the year the surface water south-east of the Reykjanes Ridge is some 8 - 11°C warmer than the surface water in the Davis Strait. If the relationship between temperature and speed of development were the same in the three well-defined regions the values from region (c) would lie about an extension of the mean line for region (b) and this in turn would be in line with that for region (a) (see Fig. 54). They are, instead, displaced until they come to lie one above the other; in other words the regression coefficient has remained approximately the same, but the intercept constant is lower the warmer the region. As a result the speed of development of Calanus is sufficient for at least one generation in the year, whether it be in the open Atlantic in a region affected by the North Atlantic Drift or under sub-Arctic conditions in Baffin Bay.

In 1936, Fox produced the first of a series of papers by him and by Wingfield on the activity and metabolism of poikilothermal animals in different latitudes. Starting with the observation that species in cold climates are about as active as the same or related species in hot climates and the fact that oxygen consumption of individual animals is directly related to temperature, the investigations were designed to elucidate the relative oxygen requirements of related populations. Representatives of the Annelida, Crustacea (Tanaidacea, Amphipoda, Decapoda Natantia) and Echinodermata were studied. It was

found that in general the relationship, a direct one, between oxygen consumption and temperature was similar in the cold and warm water populations, so that oxygen consumption was greater in the latter. Pandalus montagui was found to be an exception, in that the two populations showed different relationships which resulted in the consumption of oxygen remaining similar; these populations thus showed evidence of acclimatisation. When the activity of warm and cold water populations, in the form of respiratory movements or heart beats, was compared, similar levels, indicating acclimatisation, were found to be more common. Thus Perinereis cultrifera, Pandalus montagui and Caprella acanthifera, as well as some pairs of closely related species, showed similar rates of heart beat or respiratory movement in the cold and warm water populations, despite the fact that in each case activity was related to temperature. Athanas nitescens and Spirontocaris cranchi showed a somewhat higher level of activity in the population from the warm environment but even in these cases the relationship with temperature was not the same between populations. Fox (1939) discussed these various types of physiological adaptation, comparing the results with work on other aquatic poikilothermal animals, and considered the question of a phenotypic or genotypic basis for such differences between populations. The evidence is still inconclusive but suggests that examples of both individual and genetic adaptation occur.

So far there has been little indication of physiological adaptation in marine planktonic animals in general, copepods in particular. Results given by Marshall, Nicholls and Orr (1935) and by Clarke and Bonnet (1939) do indicate regional differences in respiration rates. In this case, however, the relationship with temperature is obscure since the areas concerned, the Clyde sea area and off Wood's Hole respectively, have similar mean values for temperature, the main difference being the much greater annual range off Wood's Hole. Halcrow (1963) studied the changes in oxygen consumption of Calanus finmarchicus following exposure to changes in temperature. He demonstrated acclimatisation within the temperature range normally found in the area where the copepods had been collected. Despite the fact that the temperature range within which C. finmarchicus has been reported (the range given by Halcrow is further enlarged by the inclusion of C. helgolandicus) is considerably greater than that for C. hyperboreus, he found that the capacity for thermal acclimatisation of the former was little greater than that of the latter, using values given by Conover (1961). He suggested the presence of "temperature races" of C. finmarchicus to account for its wide distribution. The different positive relationships between temperature and the speed of development of the population in the three regions considered here support such a suggestion. The displacement of each relationship relative to the others indicates that Calanus finmarchicus exhibits physiological adaptation to the environment similar to that of Perinereis cultrifera, Caprella acanthifera and Pandalus montagui (Fox, 1939, pp. 150-151).

CONCLUDING DISCUSSION

"Successful species are usually widespread and rich in genetic variability, but they tend to be rather conservative from the evolutionary point of view. Populations within such species display much ecotypic adaptation and clinal variation" (Mayr, 1954, p. 178). This statement contains several far-reaching propositions which may be applied to Calanus finmarchicus s.l., apparently a good example of a successful species. It is not the intention here to test the validity of the propositions but rather to use the quotation as the connecting theme in concluding this study. In doing this the scope of the statement has been extended to cover, not a single species, but a species-complex or superspecies, Calanus finmarchicus s.l.

Calanus finmarchicus s.l. is undoubtedly one of the most "successful" creatures in the plankton. Its dominance within the community and its widespread distribution, as considered in the introduction to, and the subsequent section of, Part II of the thesis, demonstrate this success forcibly. The richness of its genetic variability is, in effect, the basis for the whole of Part I; even here only a part of its variability, that represented in the North Atlantic, is considered.

Mayr's use of the word 'conservative' to describe a successful species is perhaps a less objective concept than his other propositions; but in the implication of resistance to change the use of this term is readily appreciable in the context of the traditional view of the taxonomic position of Calanus as a primitive genus of the calanoid copepods.

This view, however, is now giving way to the idea that the absence of certain morphological features, such as a geniculate first antenna in the adult male, may be the result of loss rather than a primitive condition. Perhaps, then, a conservative species is one in whose evolutionary history there is more morphological simplification than elaboration.

The traditional view of Calanus as a primitive genus has also been justified in the past by its occurrence throughout the oceans of the world, the corollary being that it was the more advanced forms which had become specialised to one particular environment or another. But it is hard to reconcile this view of Calanus, particularly C. f. finmarchicus, with its extraordinary abundance over such a wide area and always in company with a number of other herbivores potentially capable of competing with it. This success alone must indicate, as Mayr has propounded, a degree of adaptation to the environment which is unlikely to be primitive.

Aspects of the way in which Calanus finmarchicus s.l. does fulfil these propositions of ecotypic adaptation and clinal variation have occurred in the present study. The relationship between phytoplankton and the biomass of young C. f. finmarchicus on the Scotian Shelf and the different relationships between speed of development and sea temperature in different parts of the North Atlantic indicate a high degree of adaptation to the environment. Clinal variation in morphology exists between C. f. finmarchicus and C. f. glacialis and a "physiological cline" can be postulated in the rates of development of the spring generation in the waters around Greenland; the warmest and the coldest

regions show the greatest difference between their relationships of speed of development to sea temperature, while the regions of intermediate temperature also show intermediate relationships.

All Mayr's propositions are thus readily applicable to Calanus finmarchicus. They also serve two additional purposes: first, they suggest a possible key to the success of Calanus and, secondly, they emphasise the need to apply other well-known branches of biology to the study of plankton. The emphasis that Mayr places on populations may well prove significant in the search for the cause of the success or otherwise of a particular species. The evidence of acclimatisation and the suggestion of stenothermy indicate that populations of Calanus are highly adapted to their immediate surroundings. It is, therefore, the populations which emerge as the important objects for study and prominence must be given to their identification in future investigations.

At the beginning of this discussion it was pointed out that Mayr's statement was to be applied to a species-complex rather than a single species. It is arguable that this extension of a quotation from an infraspecific context through the "species-barrier" to a superspecific use is unjustified. But to argue this is, I think, to lose sight of the ecological understanding that is being sought. Except insofar as C. f. finmarchicus and C. helgolandicus are able to occur sympatrically to a greater extent than C. f. finmarchicus and C. f. glacialis, specific or subspecific status matters little from an ecological point of view.

That the difference in status is merely relative is illustrated by an analogy drawn by Dillon (1966) between the evolutionary history of a species and the life cycle of an organism. He has recognised four phases, summarised in Table XI, in the evolutionary cycle of a species. He has also pointed out that all phases need not be passed through by all species, in particular that many populations within the "mesospecies" undergo speciation and return thereby to the "neospecies" phase.

TABLE XI. Biogeographic patterns and species types (after Dillon, 1966).

Distributional patterns		Species		
Range	Subspeciation	Stage	Type	Relative abundance
Expanding	Absent	New or young	Neospecies	Very high
Stable	Extensive	Young adult	Mesospecies	High
Stable	Low or absent	Mature	Euspecies	High to moderately high
Contracting	Absent	Senescent	Telospecies	Low, diminishing

With its extensive subspeciation and speciation, a wide and apparently stable distribution and high numbers, Calanus finmarchicus s.l. is a good example of a "mesospecies". This phase is characterised by marked morphological variation and by an extremely vital and highly plastic condition (Dillon, loc.cit. pp. 121, 125). As is perhaps usual with concepts developed from analogies, the idea of a "mesospecies" is useful in description but not in explanation. It is helpful here in pointing out some of the major problems which still remain to be solved

before we can understand the success of Calanus finmarchicus s.l.: what are the features of the complex which produce the vitality and plasticity which enable it to dominate the marine zooplankton throughout vast areas of the world's oceans? The answers to this question will require a synthesis of existing and new knowledge from many fields, including physiology, genetics, biochemistry, ecology and animal behaviour. These branches of biology have still, as emphasised by Mayr's proposition, much to contribute to our understanding of Calanus, in particular, and plankton, in general.

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