Seasonal movements of shorebirds in relation to spacing behaviour and prey availability

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Dugan, Patrick Joseph (1981) Seasonal movements of shorebirds in relation to spacing behaviour and prey availability. Doctoral thesis, Durham University.

Seasonal Movements of Shorebirds
in relation to Spacing Behaviour
and Prey Availability.

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being a thesis presented in candidature for the degree
of Doctor of Philosophy in the University of Durham,
February, 1981.

To my parents

SEASONAL MOVEMENTS OF SHOREBIRDS IN RELATION TO SPACING BEHAVIOUR AND PREY AVAILABILITY

Abstract

Data on counts of shorebirds and information from ringing and colour-marking studies are examined and integrated to provide detailed information on seasonal changes in distribution, and movements of Knot, Bar-tailed Godwit and Grey Plover in North- West Europe, particularly Britain.

Several factors which may lead to the movements observed, particularly those factors affecting energy balance, are considered. Published information on seasonal changes in weather conditions in Britain and Europe, and on prey abundance in different estuaries, is reviewed and supplemented by studies from Morecambe Bay and the Tees and Humber estuaries. It is suggested that late autumn movements of Knot and Bar-tailed Godwit from the eastern North Sea to Britain permit birds to avoid severe winter weather conditions. Movements of many Knot northward from the Wash along the east coast of Britain also occur in November, perhaps to reach estuaries less influenced by cold air masses from Europe. The reasons for most other movements are unclear. No evidence was found of major differences between estuaries in the timing of breeding or growth rates of invertebrate prey, which might have led to the differences in timing of peak prey biomass for shorebirds to exploit.

Differences/

Differences have been found in the seasonal patterns of depth distribution of Macoma balthica between Morecambe Bay, the Wash and Humber. However, the timing of movements of Knot between these estuaries could not be related to these differences in availability of prey. Availability of Macoma on Morecambe Bay in spring is high and may partly explain why high numbers of Knot collect there to put on pre-migratory fat reserves.

Movements of Knot through the Tees estuary appear to be unrelated to changes in prey abundance or availability. Two alternative survival strategies are suggested for this species: (1) itineracy, visiting two or more British estuaries after moult, and (2) sedentary behaviour, visiting only one estuary after moult, or staying on the moulting area.

Seasonal use of the Tees estuary by, and movements to and from there of, Grey Plover were studied in relation to spacing behaviour and prey availability. Two strategies of use of space by Grey Plover were found. Territoriality was shown to be particularly advantageous during periods of severe, particularly windy, weather. Flock feeding was adopted by some birds which could not, and by some individuals which chose not to, obtain a territory. Some movements of Grey Plover from the estuary were probably determined by social status. A few of those which were unable to obtain a territory in autumn left the estuary. No evidence of movement in relation to prey availability was obtained.

Findings/

Findings of the study are discussed in terms of proximate and ultimate factors determining the timing and survival value of shorebird movements.

Contents

Acknowledgements

This research was performed while at the University of Durham, and I thank Professor D. Barker for the facilities provided in the Department of Zoology.

The study was financed by a postgraduate research studentship from the Natural Environment Research Council, for which I am very grateful.

I am pleased to have this opportunity to thank the many people who assisted at various times with fieldwork at Teesmouth, particularly C. McCarthy, N.C. Davidson, F. Symonds and D.J. Townshend. Special thanks are due to L.R. Goodyer for catching the Grey Plovers and Knot marked during the study and to the many people who assisted in cannon-netting. Throughout the study at Teesmouth, Tees and Hartlepool Port Authority gave permission for access to their land. In the Zoology Department J. Richardson gave much assistance in the use of constant temperature facilities for processing mud samples.

During my survey of information on intertidal invertebrates of other estuaries many people provided help and the benefit of personal knowledge of their research areas. To all these workers I am very grateful but thank particularly Drs. R. Key, N.V. Jones and P. Ratcliffe of Hull University for information on the invertebrate populations of the Humber estuary and

M. Tasker/

M. Tasker who gave much information on shorebirds of that estuary.

The British Trust for Ornithology, kindly allowed me to examine ringing recoveries of Knot, Bar-tailed Godwit and Grey Plover and counts of these species from the Birds of Estuaries Enquiry. This task was made much easier through the readily given assistance of A.J. Prater.

The study of colour-marked Knot would not have been possible without the generous cooperation of Ciba-Geigy in supplying dyes. In 1979-80 the Wash Wader Ringing Group marked birds on the Wash. For their help in organising this I am especially grateful to N. Branson, W.J.A. Dick, P. Ireland and M. W. Pienkowski. Studies of shorebird movement using colour-dyed birds depend very heavily for their success on the observations of bird watchers. To all those who sent records of, and to those who looked without success for, marked birds I am very grateful.

Throughout this study I have benefitted greatly from discussion with, and information readily supplied by, many colleagues at the Zoology Department, University of Durham, particularly, D.M. Brearey, N.C. Davidson, M.W. Pienkowski and D.J. Townshend.

In the production of this thesis I am particularly grateful to D. Hutchinson for producing the photographic plate/

plate and to Mrs. Anne Peddie for her cooperation and speed in typing the manuscript.

Finally, to my supervisor Dr. P.R. Evans, I owe a great debt not only for his advice, encouragement and criticism during this study but also for his help and enthusiasm throughout my stay in Durham and for his interest in encouraging my study of migratory habits.

General Introduction

At the end of the breeding season in June and July each year many hundreds of thousands of shorebirds migrate from their arctic, and north temperate breeding grounds to moult on the coasts of North West Europe (e.g. see Rooth, 1966; Evans, 1981). Others stop here only briefly to renew their fat reserves before moving further south to moult and winter in southern Europe and South and West Africa (Minton, 1975). At the end of autumn, on completion of moult, many birds also move further south (Boere, 1976). However, many remain to pass the winter on the coasts of the North and Irish Seas. In spring, birds which have wintered further south return north, often stopping in North West Europe to rest and renew energy reserves before moving on to the breeding grounds (Minton, 1975; Smith and Greenhalgh, 1977). At this time birds which have wintered in North West Europe also move northwards.

This description of migration from and to the breeding areas is similar to that of many other groups of palaearctic migratory birds, e.g. passerines (Moreau, 1972); many seabirds and wildfowl (Cramp and Simmons, 1977). However, within the past twenty years it has become evident that even within North West Europe, particular areas are used at particular stages of the seasonal migration cycle of shorebirds. In autumn, not only do birds/

birds move south after moult, but within North West Europe they may move from one coastal area where they have moulted to others where they winter. Similarly, in spring some birds leave areas where they have wintered and move to other areas where they moult into breeding plumage and lay down fat before migration.

Even more recently, as studies at Durham University have examined shorebird movements, it has become evident that the movements which occur are considerably more complex than previously thought. Even in mid-winter, outwith the conventional peak migration times, shorebirds have been shown to move between estuaries. Thus published information and more recent observations suggest that many shorebirds use (and may possibly require) not just one, but a network of estuaries each winter. Why these movements occur and what mechanisms control them are not understood at present. This thesis forms a preliminary investigation of these two questions.

My investigation has taken the form of three related studies.

(1) Analysis of available information on seasonal changes in shorebird use of, and movement between, estuaries in North West Europe, and particularly in the British Isles.

(2) Examination of regional variation especially within Britain, and seasonal changes, in those factors of importance/

importance in the energy balance of shorebirds which may be potentially correlated with shorebird movements. These include climatic features, such as temperature and wind speed, and prey abundance.

(3) Detailed investigation of one shorebird species, the Grey Plover *Pluvialis squatarola* on the Tees estuary in North East England, in order to examine at first hand seasonal movements and the factors to which these may be related.

In studies (1) and (2) attention has been confined to three shorebird species: Knot *Calidris canutus*, Bar-tailed Godwit *Limosa lapponica* and Grey Plover. Of these shorebirds which regularly use British and European estuaries in large numbers each year, these three species, together with Dunlin *Calidris alpina*, obtain almost all their food intake from intertidal estuarine mudflats. Among other wader species, Curlew *Numenius arquata* and Golden Plover *Pluvialis apricaria* many use neighbouring pastures in large numbers (McLennon 1979; Townshend 1981a). Redshank *Tringa totanus* also use areas of pasture and many subsidiary freshwater feeding areas (Tubbs and Tubbs 1980). Oystercatchers *Haematopus ostralegus* and Turnstone *Arenaria interpres* also use fields occasionally but obtain most of their daily food intake in many estuaries from mussel beds and rocky shores. Sanderling *Calidris alba* obtain most of their intake from sandy marine beaches. Thus, the use by these other shorebird species, of areas other/

other than intertidal mud makes considerably more complex and tenuous any analysis of movement which could be performed. For example, reduction in number of Curlew using certain estuaries may not indicate movement to another estuary but simply movement to adjacent pasture. Also, although any proven movements of Curlew between estuaries could be due to depletion of intertidal food resources, they may also be due to depletion of prey stocks in the pastureland, or on nearby rocky shores. Investigation of these problems is clearly possible but in the present study it was decided to concentrate on species for which information on both movement of individuals and prey abundance was available. Dunlin were excluded from consideration in this study because very little information is available from any estuary on seasonal variation in abundance of the wide range of small invertebrate prey species of major importance in their diet (Evans et.al., 1979).

Further justification for the intensive investigation of Grey Plover on the Tees estuary is given in Chapter 3.

Chapter 1. Distribution and movement of shorebirds within the British Isles in the non-breeding season.

INTRODUCTION

In the past ten years several authors have reviewed seasonal use of British estuaries by shorebirds, described monthly change in numbers and suggested origins and destinations of birds arriving and departing. Wilson (1973) examined ringing and count data relevant to Morecambe Bay and concluded that Knot which moult on the Wash and Dee move to Morecambe Bay in mid-winter, as do Bar-tailed Godwit from the Ribble. Smith and Greenhalgh (1977) concurred with these views but added that Knot which moult on the Ribble also may winter on Morecambe Bay. Minton (1975) reviewed the results of shorebird ringing on the Wash and supported the idea that many Knot which moult on the Wash winter on the west coast of Britain, especially on Morecambe Bay, the Dee and the Ribble, but he also concluded that others moved south to France. He suggested that Knot which moulted in the Waddenzee arrived on the Wash in November to winter. Prior to these studies, Evans (1968) made radar observations of inter-estuarine movements of shorebirds. He described south-easterly movements from the Forth estuary in August, but southerly and southwesterly movement in September. From Teesmouth, southwesterly movements to the Ribble were recorded.

As a result of these analyses of counts, ringing data, and/

and radar observations the direction and time of movements between a few of the major estuaries are known. However, to date, no attempt has been made to amalgamate the information presented in these studies with counts and ringing data from other estuaries. Yet, such a synthesis of available information forms an essential framework from which to consider the reasons for inter-estuarine movement of shorebirds and the factors which may control their timing. In this Chapter I present such a synthesis.

METHODS

Counts

To determine major seasonal change in the distribution of shorebirds within Britain, count data from the Birds of Estuaries Enquiry of 1970-75 have been examined. This enquiry organised jointly by the British Trust for Ornithology, the Royal Society for the Protection of Birds, and the Wildfowl Trust is the only attempt so far to document comprehensively the use of British estuaries by shorebirds. During the Enquiry counts were made each month from August to April and supplemented, when possible, with counts in July and May. Whenever possible counts took place at highwater on spring tides when the birds were assembled on roosts or flew to these sites. On all major estuaries, counts involved a team of observers, each counting one particular section at the same time on each day, in the hope that this would prevent the omission or duplication of birds (Prater, 1971). However, the counts from the Birds of Estuaries Enquiry, although of great value, are subject to/

to many sources of error, and little information is available for periods between monthly counts. Thus, a low count made on a day of poor visibility may be a true indication of low numbers of birds but may also be entirely a consequence of poor visibility and consequent observer error. In more intensive studies although similar poor observing conditions are encountered the count can be checked within a few days when visibility improves. Similarly on at least some estuaries, such as the Tees and Humber, birds may change roost site from one side of the estuary to the other, from day to day. Frequent visits to the estuary increase observer awareness of these changes and early detection of any new roost sites used. In contrast, the one-monthly Birds of Estuaries Enquiry counts do not allow such observer awareness to develop and the possibility of oversight, during a count, of an inaccessible or previously unused roost site arises. Consequently, in some areas at some times of year, fluctuations in total numbers of birds counted may reflect, not change in population size, but change in visibility or roosting habit. Thus although in most years of the Enquiry most of the major estuaries were censussed the accuracy of the counts must be treated with caution. It is not possible to claim that small changes in observed population size on an estuary reflect true changes in numbers of birds present on that estuary. Consequently in my analysis of these count data I have considered only major seasonal changes/

changes in shorebird distribution on British estuaries. The data do not permit definite conclusions as to which movements occur between which estuaries. To investigate this recoveries of ringed birds were analysed.

Ringing Recoveries.

Where possible I have considered only recoveries on one estuary of birds ringed on another during the same non-breeding season, as only these provide definite proof of change of area within a winter. Other recoveries concern birds recaptured some years later than that of first capture. In these cases the presence of the same individual on another estuary after the year of first capture does not allow definite conclusions to be made. While it is possible that the individual in question has followed the same route as in the year of first capture, this need not necessarily be so, as will be shown for some Grey Plover (Chapter 3). In view of the ambiguity of these data they have been excluded from the analysis (with the exception of those for Bar-tailed Godwit where this ambiguity does not influence the conclusion from the data).

Not only is the proportion of ringed birds which have been recovered on another estuary within the same non-breeding season very small, but also on only a few occasions can the time of movement be determined to within one or two months. Yet, the timing of each is crucial/

crucial to an understanding of the advantage accruing from movements.

Colour-marking.

In order to identify more precisely both the times and routes of some movements a programme of colour-dyeing of Knot was started on the Tees estuary in 1978-79 and expanded to include the Wash in 1979-80. The most important advantage of dyeing over conventional ringing as a method of studying inter-estuarine movement of shorebirds is that identification of the origin of an individual does not require recapture, but can be determined by colour and/or position of the dyemarks. Birds caught on the Tees in 1978-79 were marked on the underparts with a green, resin-based dye which persisted on the plumage for about eight weeks. In addition some birds in December 1978 were marked with temporary coloured P.V.C. leg flags (Goodyer et.al. 1979) which also allowed identification of origin of an individual without requiring recapture. In 1979-80 birds on the Tees were marked with a yellow dye (Picric Acid). To distinguish between catches those birds caught in November were marked on the breast and those caught in January on the rump. Birds caught on the Wash were marked with the green dye, on the rump before 1st January and on the breast after this date. Sightings of marked birds were obtained from research workers and bird watchers who had been notified of the dyeing programme by letter and/or through ornithological societies and bulletins. Because of the limited time available/

available for the dyeing study no attempt was made to achieve regular coverage of all major sites. Consequently absence of records from an estuary does not necessarily indicate absence of movements to that site. Similarly, it is likely that the absence of regular coverage, particularly on larger estuaries may result in oversight of marked individuals for several weeks. Consequently the accuracy of estimates of arrival dates is unknown and may be low. However despite this some sightings in other estuaries were recorded within a few weeks of marking. Consequently the accuracy of estimates of time of movement of these birds is high.

Thus, the following accounts of seasonal movements of Knot, Bar-tailed Godwit and Grey Plover are syntheses of data available from counts, conventional ringing and colour-marking schemes.

KNOT

Introduction

Almost all Knot which occur in Britain in the non-breeding season breed in Greenland and north east Canada (Minton, 1975). Adult birds reach Britain in July and August and concentrate on the Wash, Ribble, Dee and Morecambe Bay (Prater, 1974). Other adults arrive at this time in the Danish, German and Dutch Waddenzee where birds which breed in the western Palearctic and Holarctic mix with birds from the Siberian breeding population (Dick et. al. 1976). Juveniles are first seen/

seen in Britain in mid August and early September (Minton, 1975; Smith and Greenhalgh, 1977).

Movements from and into the Wash.

Most ringing of Knot has been done on the Wash (ca. 30,000 between 1959-1978), Dee (ca. 3,000) and Morecambe Bay (ca. 7,000 until 1973). Recoveries within the same winter of adults ringed during moult, ie. from July until the end of October (Minton, 1975), are shown in Fig. 1. Recoveries within the same winter of adults ringed after October are shown in Fig. 2. These data indicate that most movements of adults from the Wash occur at the end of moult and few later. Although ringing data are subject to many biases it is likely that the predominance of post-moult movement is a genuine result. Although most Knot have been caught on the Wash during autumn many thousands have been caught there at other times of year. Clearly the likelihood of detection of movement depends upon the length of winter left in which both to move and to be caught at the destination. It also depends on the activities of ringers and ease of capture in different months at these sites. Thus it is not surprising that most movements recorded are of autumn caught birds. However, despite the considerable length of time that a bird may remain on an estuary before being captured, many of the movements have been detected within two months of capture on the Wash. Thus if movements occurred throughout the winter, birds caught on the Wash in November, December/

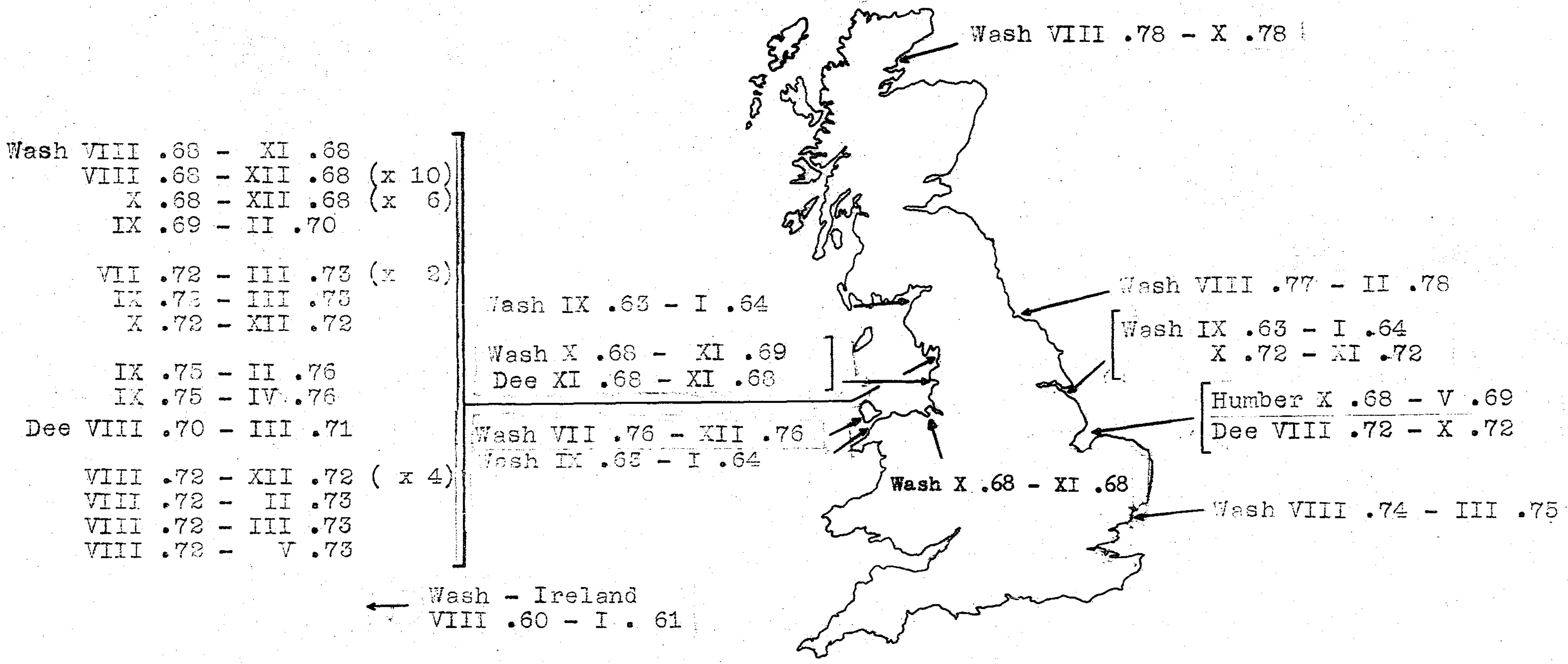


Fig. 1. Recoveries in Britain within the same non-breeding season as that of ringing, of adult Knot ringed in Britain during the moult period i.e. August until the end of October. For each bird, estuary, month and year of ringing and month and year of recovery are indicated at the estuary of recovery.

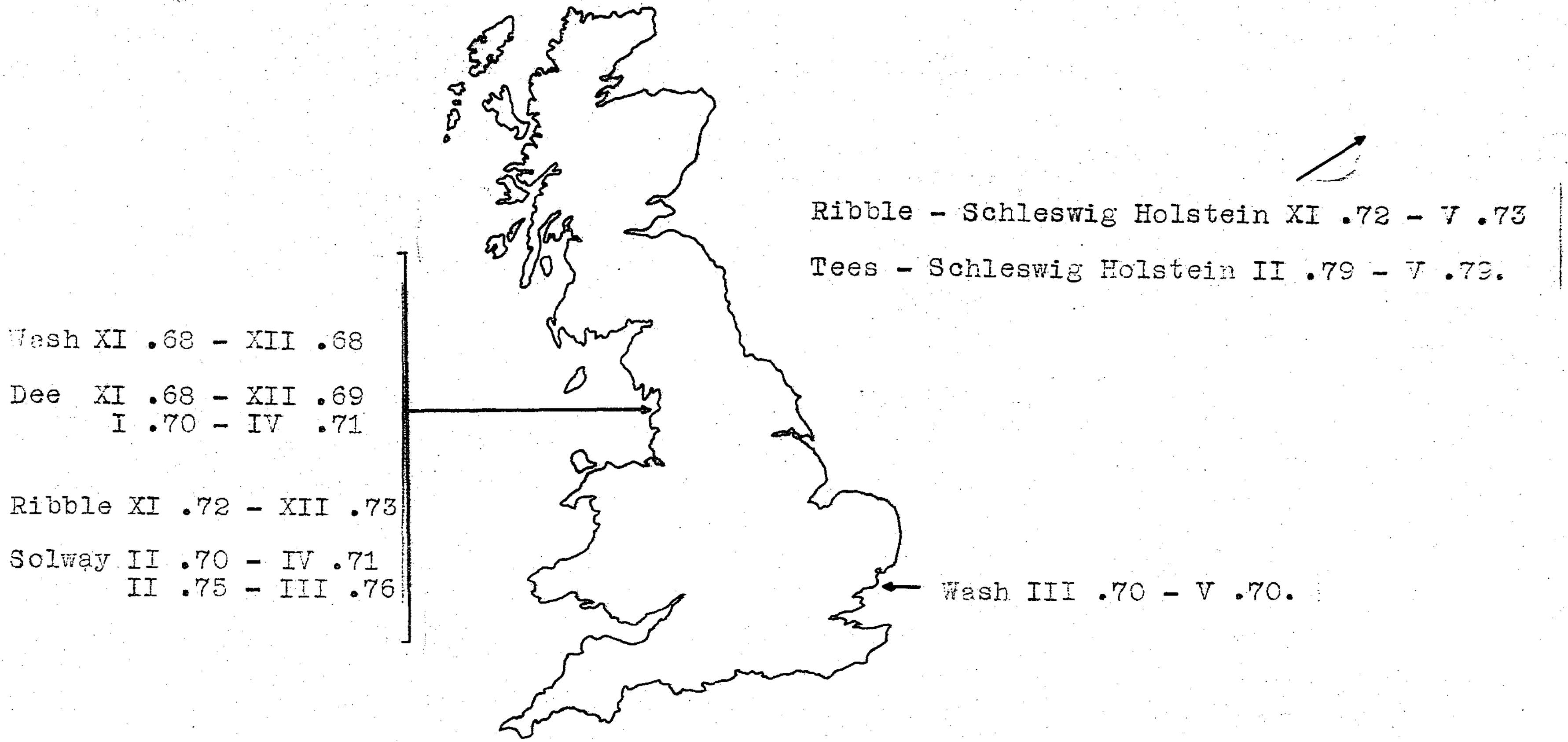


Fig. 2. Recoveries in Britain and Schleswig-Holstein within the same non-breeding season as that of ringing, of adult Knot ringed in Britain after moult i.e. after 31st. October. Explanation as for Fig. 1.

December, and January should have been represented in catches in the spring. This has occurred very rarely and indicates that, most movements do occur in the autumn and early winter.

Movements of juveniles follow a similar pattern to that observed in adults (Fig. 3) but data are too few to permit a detailed comparison between adults and juveniles. However Minton (1975) concluded that most juveniles pass through the Wash by mid-October and winter in France, Iberia and possibly West Africa.

In autumn juveniles form only a small proportion of the total population and by winter usually less than 5% of the Knot on the Wash. Consequently the overall picture given by counts is likely to reflect adult movements, irrespective of the juvenile pattern.

Counts on the Wash reinforce the conclusion from the ringing data that an exodus occurs in late October, at least in some years. In three of the five years for which data are available the number of Knot present on the Wash rose steeply in July and August to a peak in September and October but dropped again before numbers rose for a second time in November and December to a winter maximum (Fig. 4). In the other two years no peak was evident in September. In 1971-72 numbers in September were as high as in those years in which a September peak was/

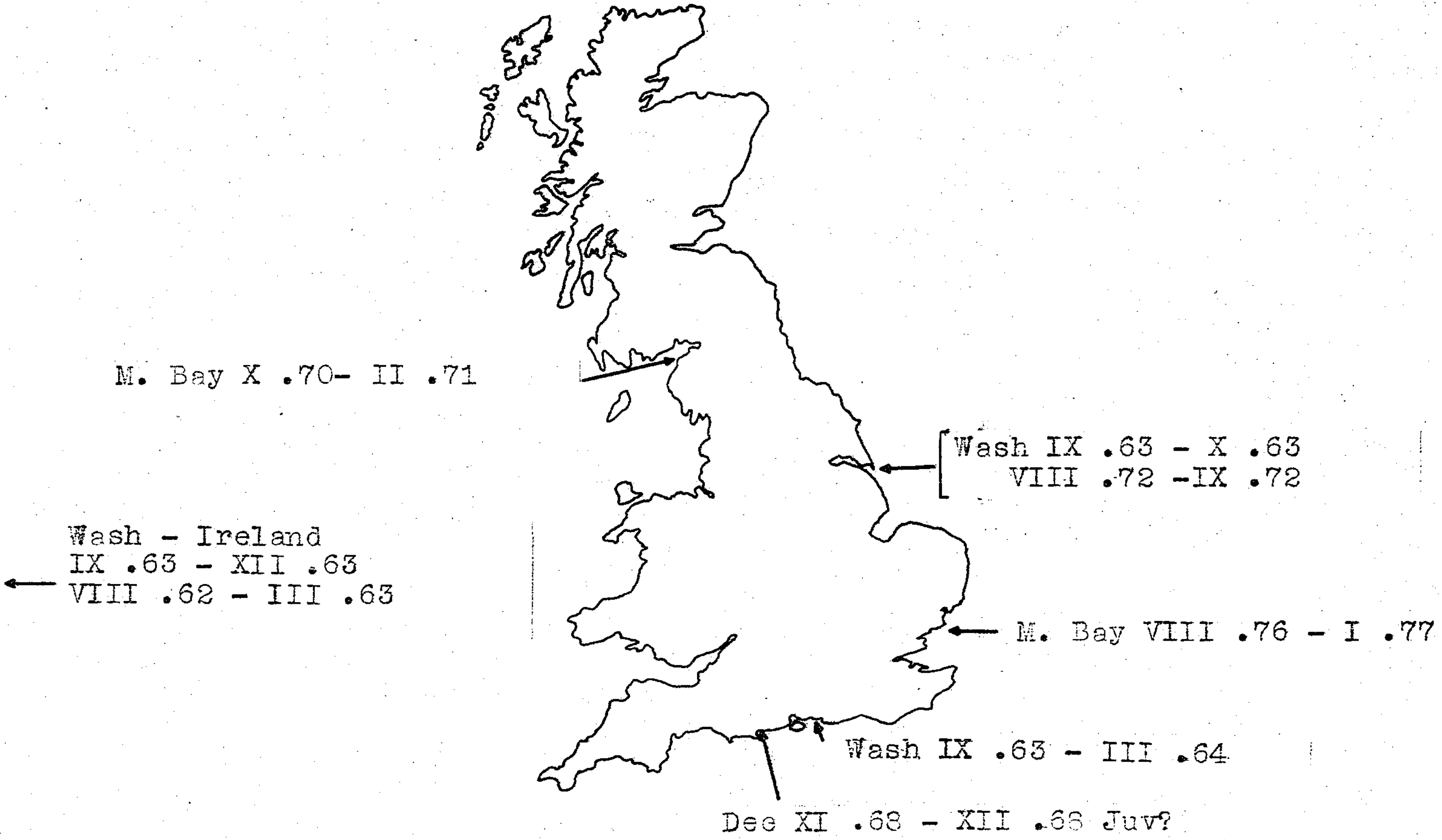


Fig..3. Recoveries in Britain within the same non-breeding season as that of ringing, of juvenile Knot ringed in Britain. Explanation as for Fig. 1.

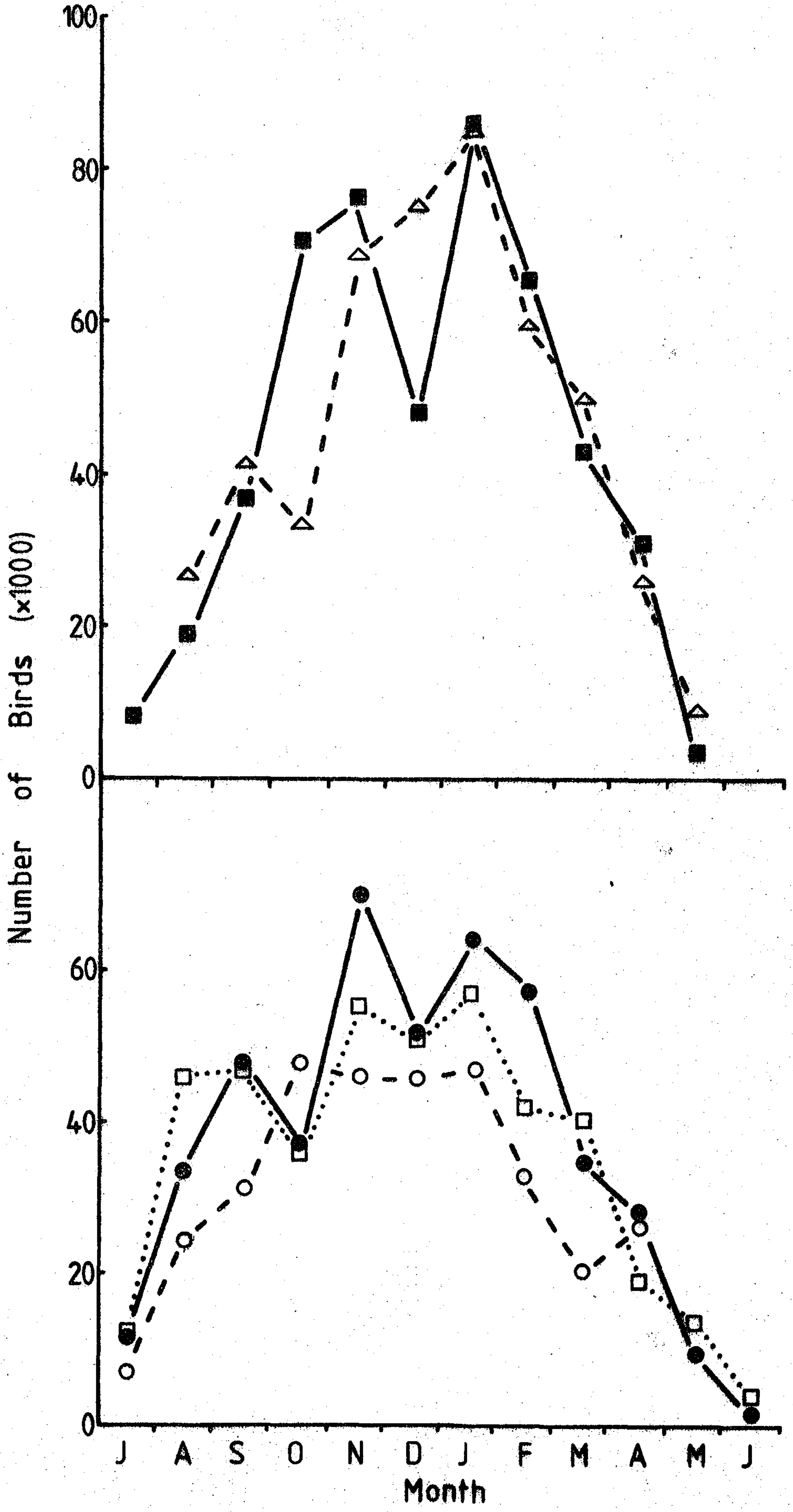


Fig. 4. Monthly counts of Knot present on the Wash.
(○ 74/75); (● 73/74); (□ 72/73); (■ 71/72);
(△ 70/71).

was recorded, but they continued to rise to November. A drop in numbers was apparent in December but an increase again in January (Fig. 4). These data suggest that in 1971 the same number of birds arrived but that no departure occurred until December. However, the count data do not allow examination of any turnover of individuals on an estuary. It is possible that, although numbers appeared to rise continuously from September to November in 1971, many of the individuals present in September may have departed before November. Indeed the monthly intervals between counts mean that rapid fluctuations in numbers could be missed. Unfortunately, no large captures of Knot were made on the Wash in October or November of 1971 and consequently the extent of any turnover cannot be investigated.

Movements along the east coast.

At the same time as numbers of Knot on the Wash rise in November and December, following the October decrease, numbers using the estuaries on the east coast of Britain, north of the Wash, increase greatly (Fig. 5), often continuing to do so when the numbers on the Wash (Fig. 4) level off e.g. in 1972-73; 1974-75. It is likely that birds which arrive in Britain at this time have moulted on the eastern North Sea coast. Numbers of Knot on both the German and Dutch Waddenzee fall at this time (Prater, 1974). However, six of the within-year recoveries indicate that some of the birds which use/

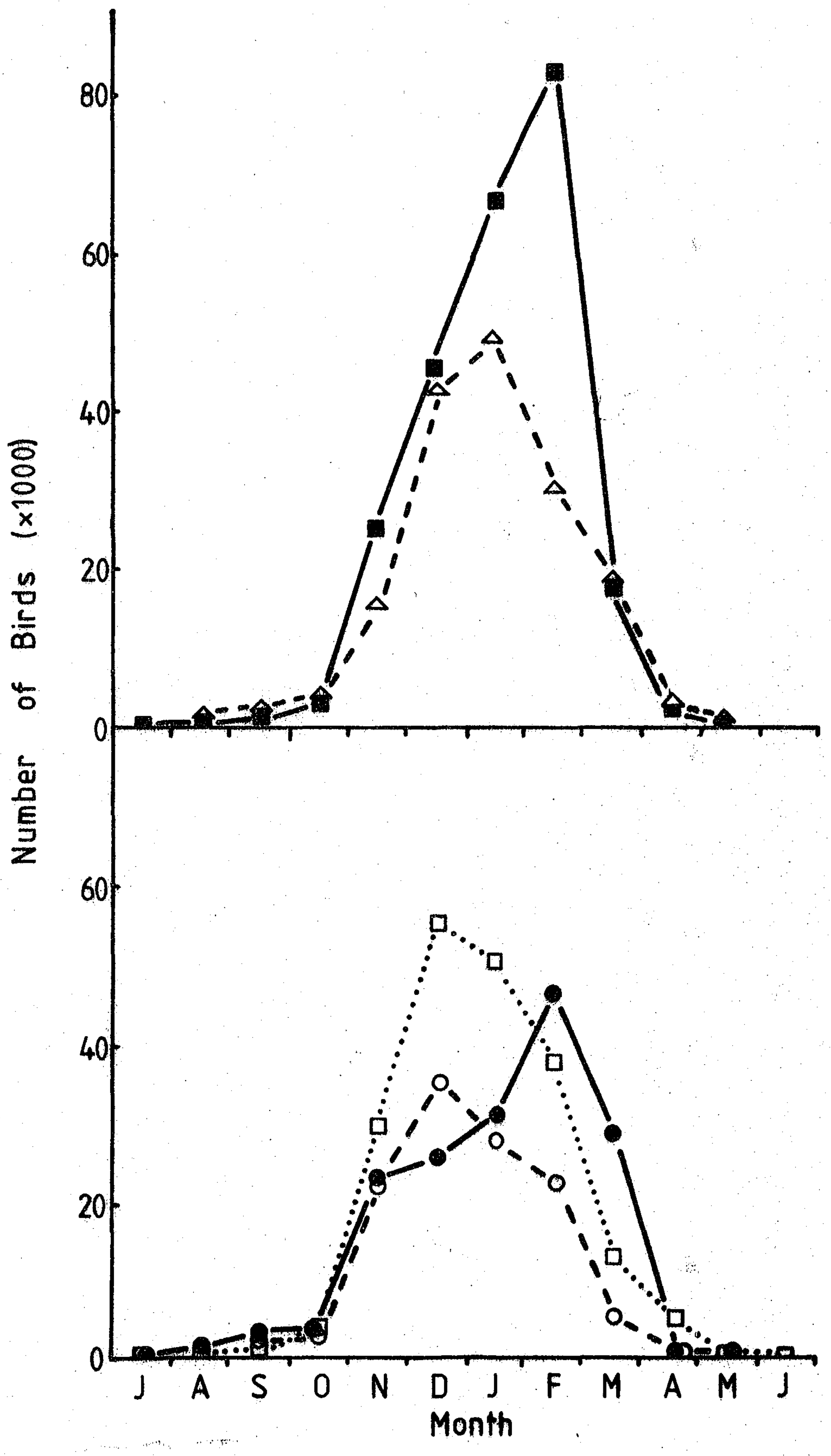


Fig. 5. Monthly counts of Knot on the estuaries on the east coast of Britain, north of the Wash i.e. Humber Tees, Lindisfarne and Forth. (Symbols as in Fig. 4.)

use the north-east coast estuaries during, or after, October have spent the earlier part of the autumn moulting on the Wash. Of these movements two to the Humber and one to North-East Scotland occurred before the time of the major influx on the east coast. The other three were also ringed before this period of influx but recovered after. Thus is it not possible to conclude precisely when, in relation to the time of the large influxes on the east coast, the movements occurred. Only for one dye-marked bird can the time of movement, in relation to the time of the influx on the Tees estuary be determined. This individual, dyed on the Wash in October, was seen on the Tees in November, a few days after the first influx of Knot on the Tees occurred. (Fig. 6). On the Tees estuary the small area and regular observer coverage at this site mean that it is very unlikely that a marked bird would have been missed for more than a few days. Furthermore, in October and November each year there are only very small numbers of adult Knot (less than fifty individuals) on the estuary (Fig. 6). Consequently it is very unlikely that the dyed bird was present, but was missed, before the first influx at the beginning of November. The very low number of Knot present on the estuary prior to November each year (see Fig. 7) also suggests that the ringed bird caught on the Wash in August 1977 and retrapped on the Tees in February 1978 also arrived on the estuary after the beginning of November.

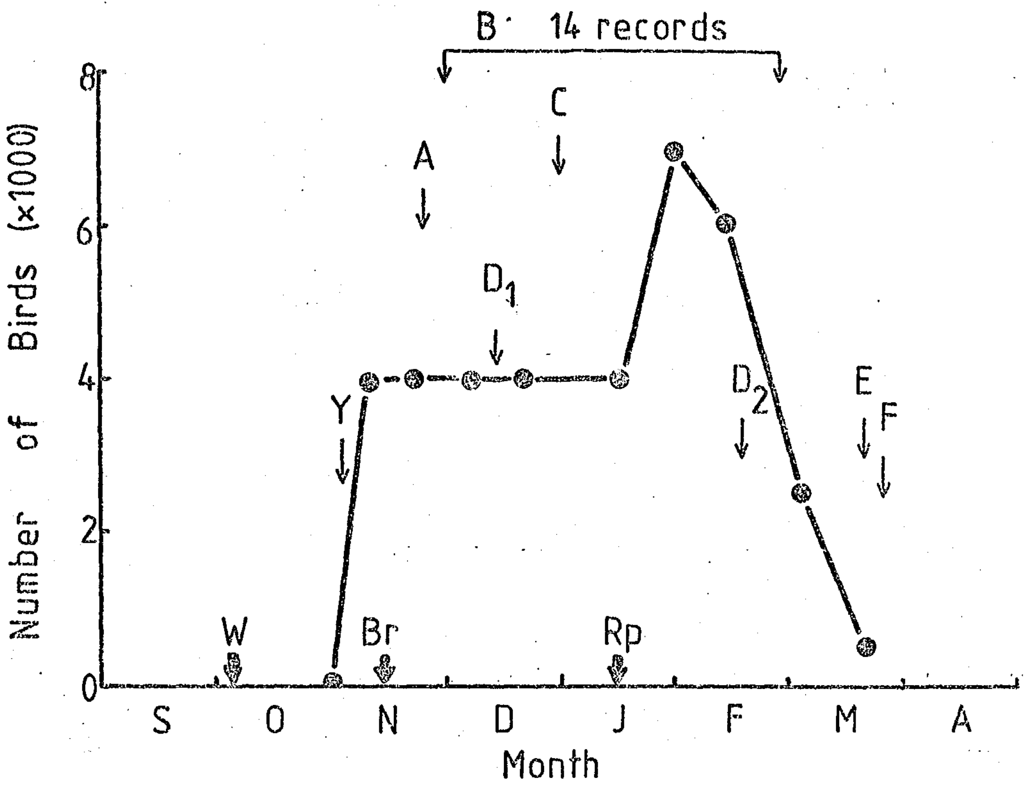


Fig. 6. Movements of colour-dyed Knot from and change in numbers of Knot present on the Tees estuary in 1979-80.

Sightings of birds:-

(i) Dyed 14-11-79 = Br

A - Humber 1 bird

B - St. Mary's Island/Seaton Sluice, Northumberland
14 records, 1-6 birds.

C - Bamburgh, Northumberland 1 bird

D_1D_2 - Forth 1 bird on each occasion

(ii) Dyed 17-1-80 = Rp

E - Wash 1 bird

F - Forth 1 bird

(iii) Dyed 6/7-10-79 on Wash = W

Y - Tees 1 bird

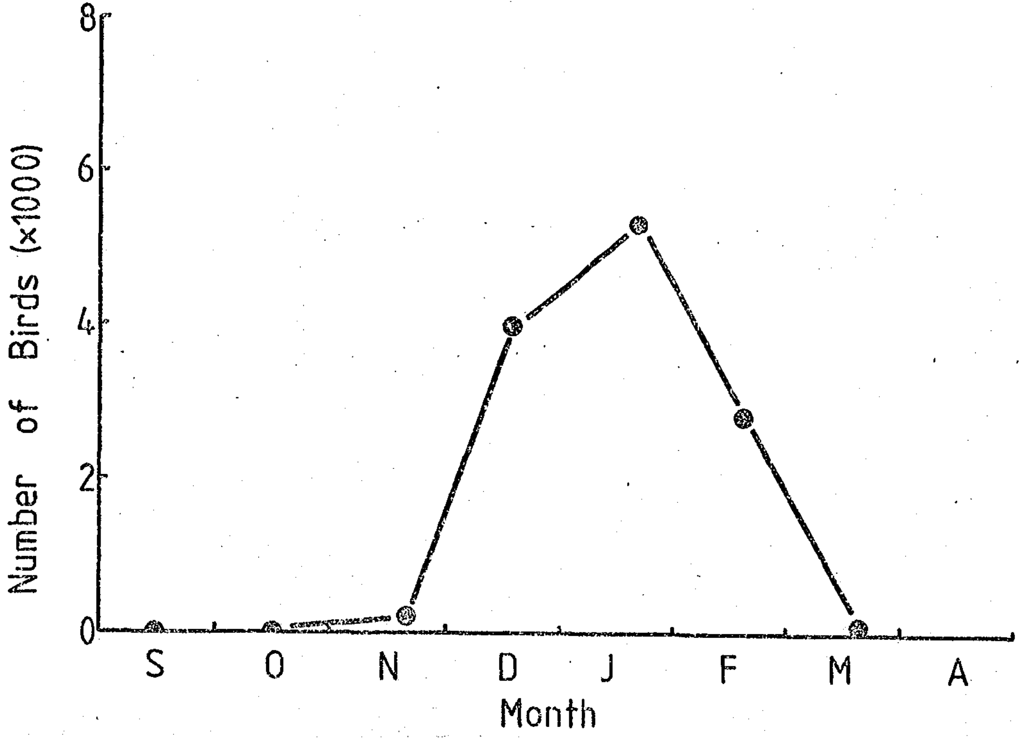


Fig. 7. Monthly counts of Knot on the Tees estuary 1977-78.

Thus it is likely that at least some of the birds arriving on the Tees estuary in November originate from the Wash. This may be true of those arriving in November on other east coast estuaries. It should be noted that the two marked birds which moved from the Wash to the Tees had been present on the Wash since August and October, and had not arrived there with the November influx. Thus at the time of the November influx on the Wash, there was considerable turnover of birds there. Whether the northward movements of birds which have moulted on the Wash is voluntary or through displacement is not known.

It is possible that some birds go directly from the Waddenzee to the estuaries of the north-east coast of Britain in November. Certainly, if all birds move through the Wash turnover must be very rapid. For example, if turnover had occurred in 1972-73 the 25,000 birds which arrived on the north-east estuaries between October and November must have left the Wash within a maximum of one month of the arrival of 20,000 birds (by which amount total numbers on the Wash increased in this month) on the Wash during this period. Similarly, the 25,000 arriving on the north-east coast between November and December must have left the Wash within one month of the arrival of another 20,000 (i.e. assuming 25,000 birds did move from the Wash to the north-east coast between November and December 20,000 birds is the size of the influx which must have occured on the Wash to/

to account for a decrease of only 5,000 birds there between November and December) on the Wash between November and December. However, such rapid onward movement, although involving much smaller numbers of birds, occurred at this time on the Tees, as documented below. Thus similar rapid onward movement might possibly accompany the turnover which occurs on the Wash. Consequently at the present time it is not known how much, if any, movement to the north-east estuaries is direct from the Waddenzee. This may be solved by dye-marking on the Waddenzee.

In 1979-80 dye-marking of Knot in November provided evidence of turnover and rapid onward movement from the Tees. Of 270 birds colour-dyed on the Tees on 14-11-79 three were seen along the Northumberland coast fifteen days later and one seen on the Forth estuary after one month. Over this period numbers of Knot on the Tees remained approximately constant (Fig. 6). However, the percentage of colour-marked birds in the population decreased, which indicates that a small exodus of Knot, replaced by a small influx, had occurred (Table 1). If all 270 birds dyed on 14-11-79 had remained on the estuary during November and December when the total number of birds on the estuary was approximately 4,000, the actual proportion of birds dyed would have been 6.8%. However, over this period the mean percentage of birds observed which were colour-marked was 5.4%. Thus assuming random mixing/

Table 1. Proportion of Knot on the Tees observed to be colour-dyed in November and December, 1979. Figures given are the mean number of colour-marked birds seen in flocks checked on each date.

Date	No. of flocks checked	Mean flock size	% of birds colour-marked	
			$\bar{x}$	S.E.
18.11.79	2	63	4.1	0.2
23.11.79	6	156	5.0	1.1
26.11.79	1	110	9.1	0.0
6.12.79	7	83	5.8	0.7
10.12.79	1	162	4.3	0.9
Nov. & Dec.	17	112	5.4	0.6

using the Waddenzee decline. It is not known how many, if any, of the birds arriving on each of the north-east estuaries arrives directly from the eastern North Sea. This would require north-west movements which have not been seen by radar in autumn (P.R. Evans, Pers. Comm.). Certainly some of the birds arriving on the Tees and Humber at this time spent part of the early autumn on the Wash. It is possible that rapid turnover and northward movement from the Wash occur. There is considerable evidence of much onward movement out of the Tees estuary chiefly to the north, but also south and even east across the North Sea. These exoduses were accompanied by balancing influxes of Knot on the Tees. It is not clear whether birds were forced out or left voluntarily.

Movements to the west coast.

In the five winters for which data are available, at the time of the autumn decrease in numbers of Knot on the Wash, numbers increased on Morecambe Bay (Fig. 9) where most of the ringing recoveries within the same non-breeding season have been obtained. However, much of this increase in numbers on Morecambe Bay might be explained by movements from other west coast estuaries alone. At the same time as birds leave the Wash, the distribution of Knot changes markedly on the west coast. Numbers on the Ribble drop sharply (Fig. 10) as those on Morecambe Bay and the Solway (Fig. 11) gradually increase. On the Dee, a similar early autumn peak occurs but in most years it is much smaller than

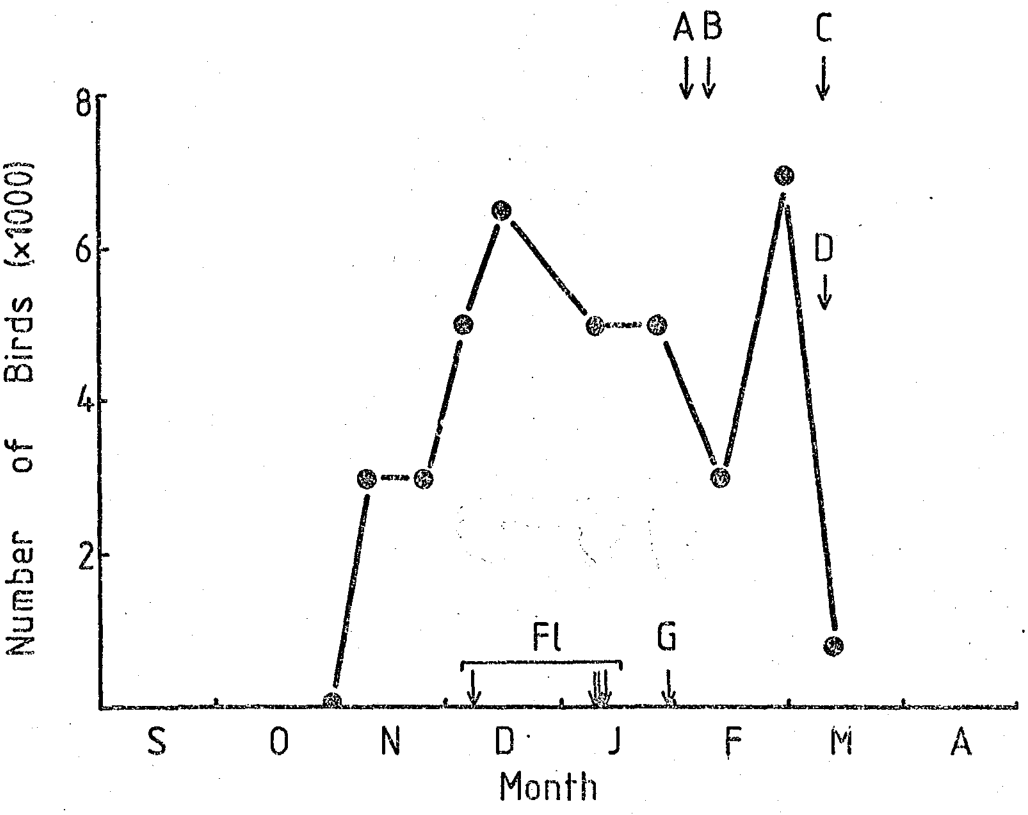


Fig. 8. Movements of colour-marked Knot from and change in numbers of Knot present on, the Tees estuary in 1978-79.

Sightings of birds:-

(i) P.V.C. Flags put on : 11.12; 9.1; 10.1; 12.1 = F1.

A - Forth 1 bird

B - Loch Ryan 1 bird

(ii) Dyed 28-1-79 = G

C - Forth 1 bird

D - Humber 2 birds

to that on the Ribble (Fig. 12). Furthermore, there are recoveries on Morecambe Bay in winter of birds ringed both on the Dee and the Ribble a few months earlier. During this period when numbers on individual west coast estuaries are changing, the total population on the west coast remains fairly constant, rising gradually in some years but decreasing slightly in others (Fig. 13). Thus any post-moult movement from the Wash to the west coast would need to be approximately balanced by emigration from the west coast at this time. Consequently it is not possible, from count data alone, to obtain even a minimum estimate of the numbers of birds moving onto the west coast at this time. It is therefore not possible at present to say with confidence how great or regular is the movement from the east to west coasts in November. Similarly it is not possible to calculate precisely the relative size of the southward movements from the west coast and the Wash at these times. However, whereas there are many records in southern Europe in winter of birds ringed in autumn on the Wash, only two are known from the west coast estuaries. But fewer Knot have been ringed on the west coast in autumn.

Thus some birds which spend the early autumn moulting on the Wash, move in some years to the west coast by mid-winter. Other individuals move in some years to southern Europe after moulting on the Wash. It is not clear whether a constant proportion of birds moulting on the/

the Wash use the two destinations in all years. However, the predominance of recoveries from southern Europe in years when none were obtained from the west coast (Table 2) suggests that they may be alternative destinations for many individuals.

Movements in spring (March to May).

There is little detailed information on movements of birds in spring. In some years. e.g. 1970-71; 1973-74 and 1974-75, numbers on Morecambe Bay rose steeply (Fig. 9) when numbers on the east coast declined (Figs. 4,5). This decrease in numbers on the east coast as numbers rose on Morecambe Bay may reflect movement from the east to west coast at this time of year. However, there are no recoveries, of ringed birds within the same non-breeding season, to confirm this. In contrast, there are two recoveries (one of a bird ringed on the Tees in January, and one ringed on the Ribble in November) in Schleswig-Holstein in May, within the same non-breeding season. Indeed between February and April numbers on the east coast have always declined (Fig. 14), while those on the whole of the west coast have also declined or remained constant (Fig. 13), and total numbers in the whole of Britain have declined sharply (Fig. 15). Numbers of Knot increase on the Waddenzee in spring (Prater 1974). Thus, although many birds, most probably those wintering on the west coast, go to Morecambe Bay for pre-migratory fattening (Prater and Wilson, 1972), many others, mostly from the Wash and estuaries/

Table 2. Recoveries on Morecambe Bay and in southern Europe within the same non-breeding season of Knot ringed on the Wash.

Adults

	Wash to Morecambe Bay			Wash to southern Europe		
Year	Month of capture	Month of recovery	No. of birds	Month of capture	Month of recovery	No. of birds
1964-65				Sept.	Nov.	1
				Nov.	Dec.	1
1968-69	Aug.	Nov.	1			
	Aug.	Dec.	10			
	Oct.	Dec.	6			
	Nov.	Dec.	1			
1969-70	Sept.	Feb.	1			
1970-71				Nov.	Dec.	1
1972-73	July	Mar.	2			
	Sept.	Mar.	1			
	Oct.	Dec.	1			
1973-74				Aug.	Oct.	1
1974-75				July	Feb.	1
1975-76	Sept.	Feb.	1			
	Sept.	April	1			
1976-77				Aug.	Jan.	1
Juveniles						
1969-70				Aug.	Sept.	1
1973-74				Sept.	Oct.	1

Figs. 9-15. Monthly counts of Knot. Symbols as in Fig. 4 plus ▲ 69/70.

Fig. 9. Morecambe Bay.

Fig. 10. Ribble.

Fig. 11. Solway.

Fig. 12. Dee.

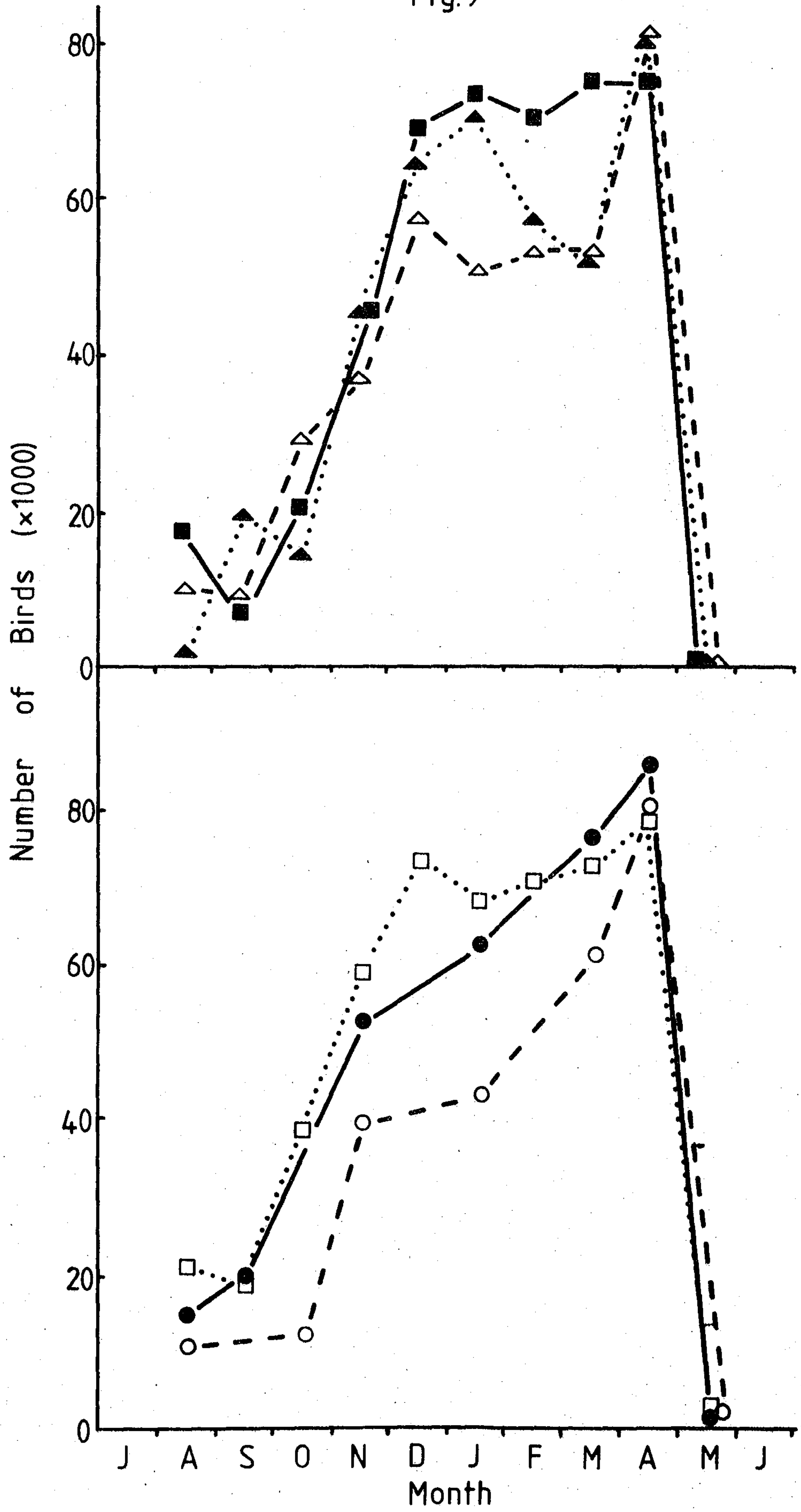
Fig. 13. All major estuaries on the West Coast, combined.

Fig. 14. All major estuaries on the East Coast, combined.

Fig. 15. All major British estuaries, combined.

Note: For the Solway, counts for 1969-70; 1970-71; 1971-72 and 1973-74 are for the south side of the estuary only. For 1972-73 and 1974-75 counts are of the whole estuary.

Fig. 9



80
60
40
20
0
Number of Birds (×1000)
80
60
40
20
0
J
A
S
O
N
D
J
F
M
A
M
J
Month

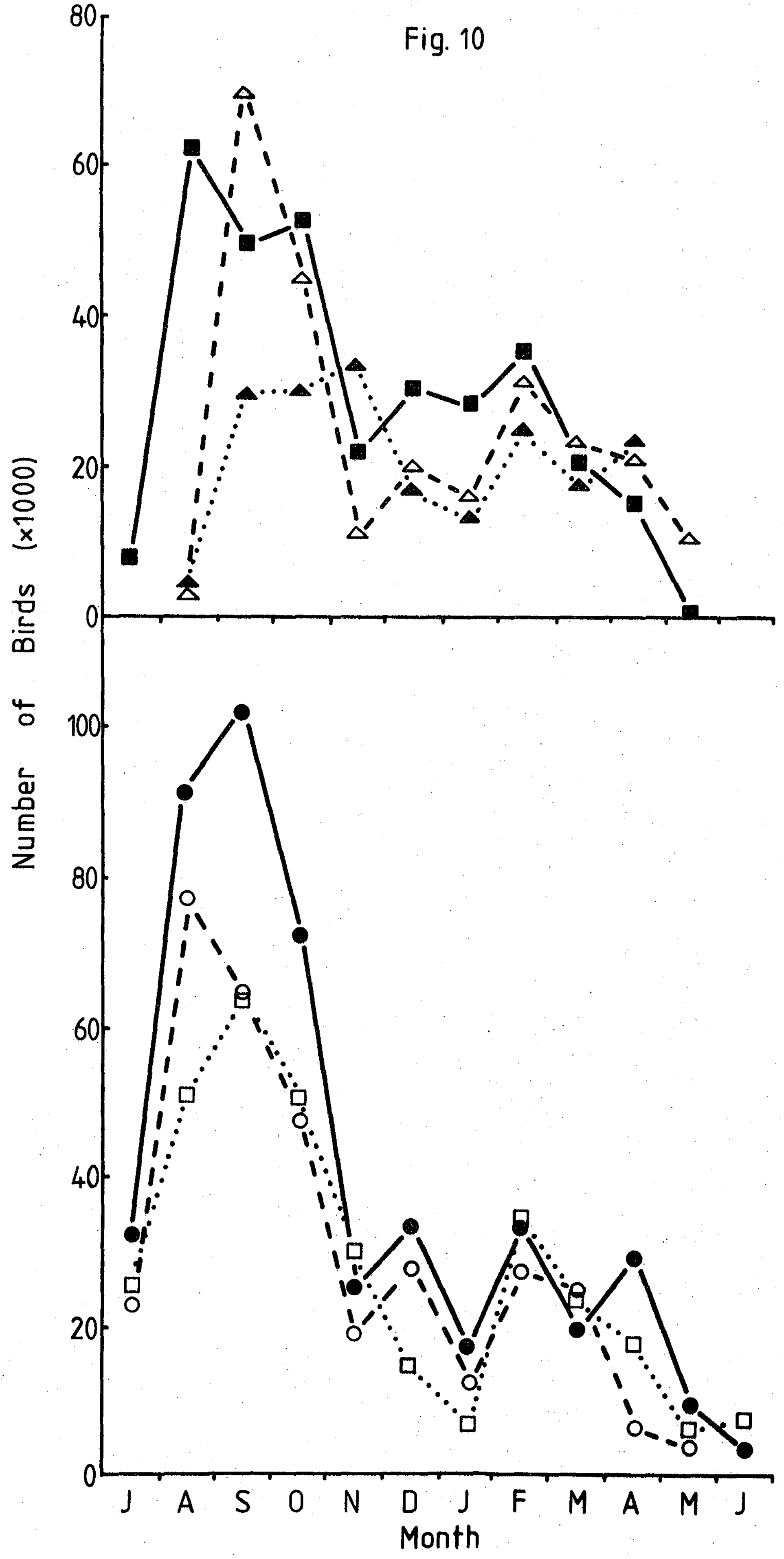


Fig. 10
Number of Birds (×1000)
80
60
40
20
0
100
80
60
40
20
0
J
A
S
O
N
D
J
F
M
A
M
J
Month

Fig. 11

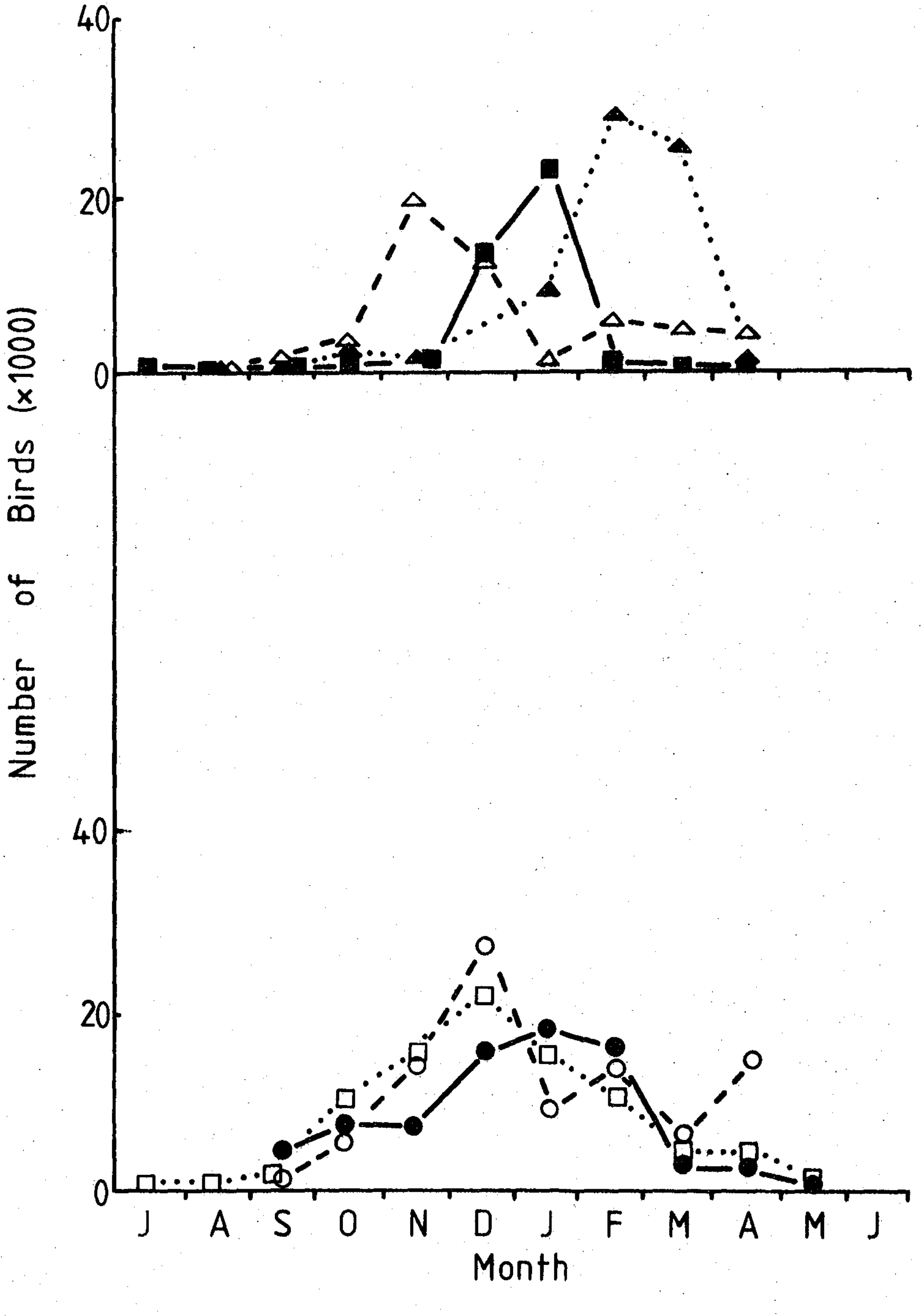
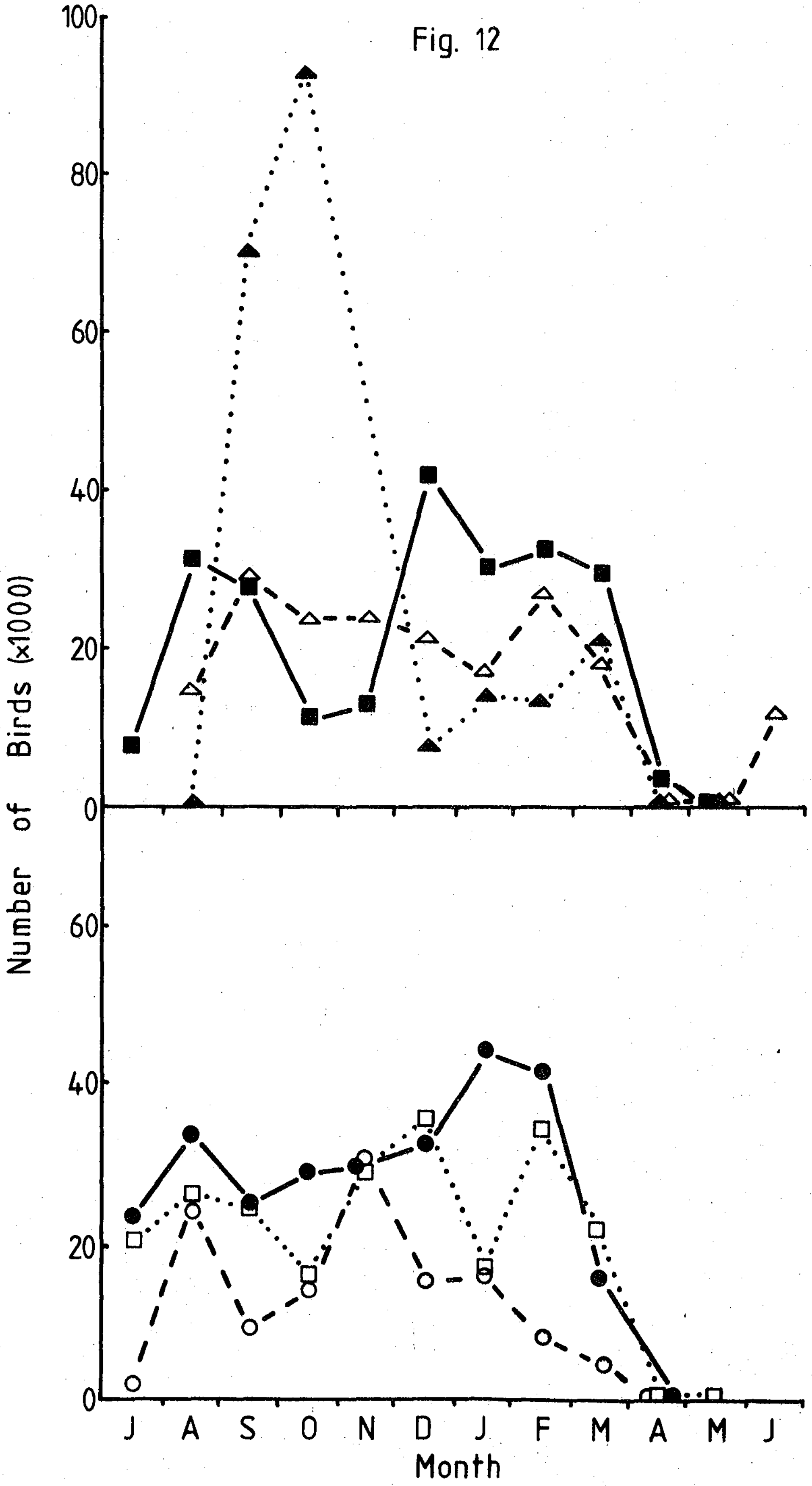


Fig. 12



100
80
60
40
20
0
60
40
20
0
Number of Birds (×1000)
J
A
S
O
N
D
J
F
M
A
M
J
Month

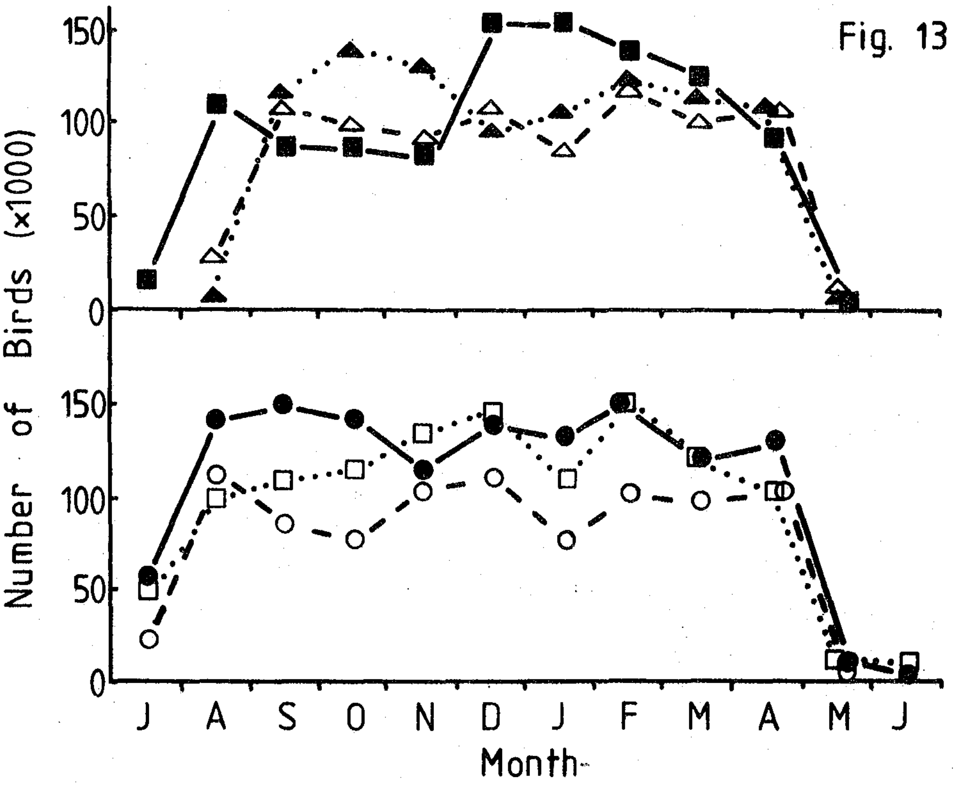


Fig. 13
Number of Birds (×1000)
150
100
50
0
150
100
50
0
J
A
S
O
N
D
J
F
M
A
M
J
Month

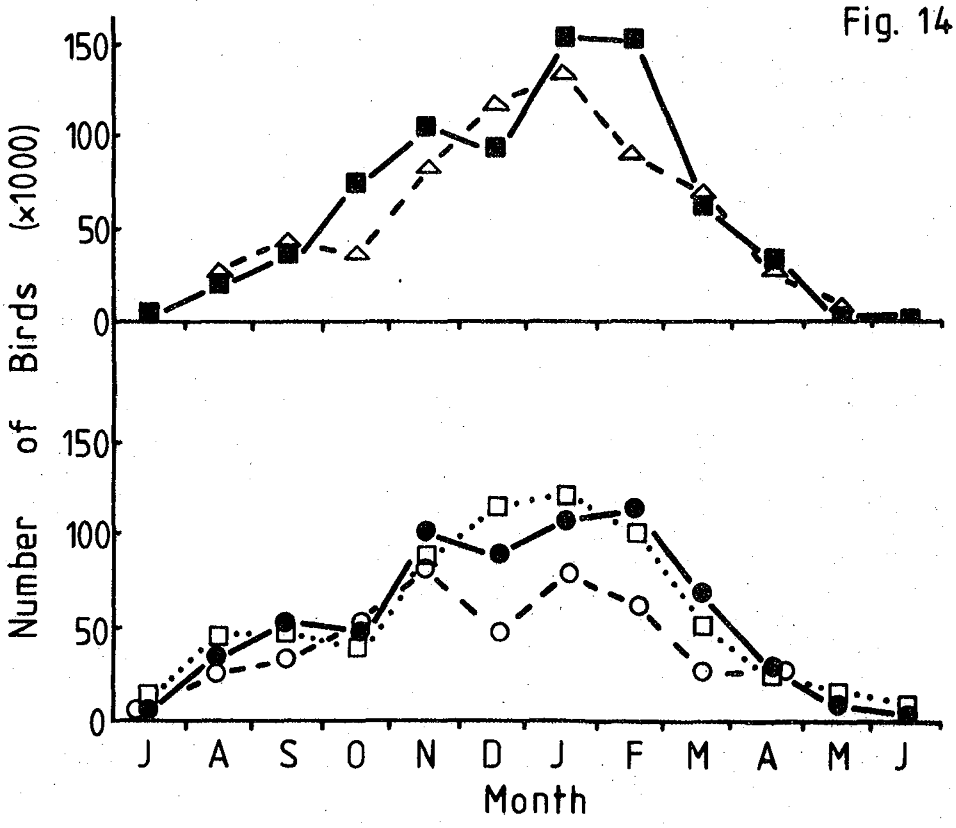
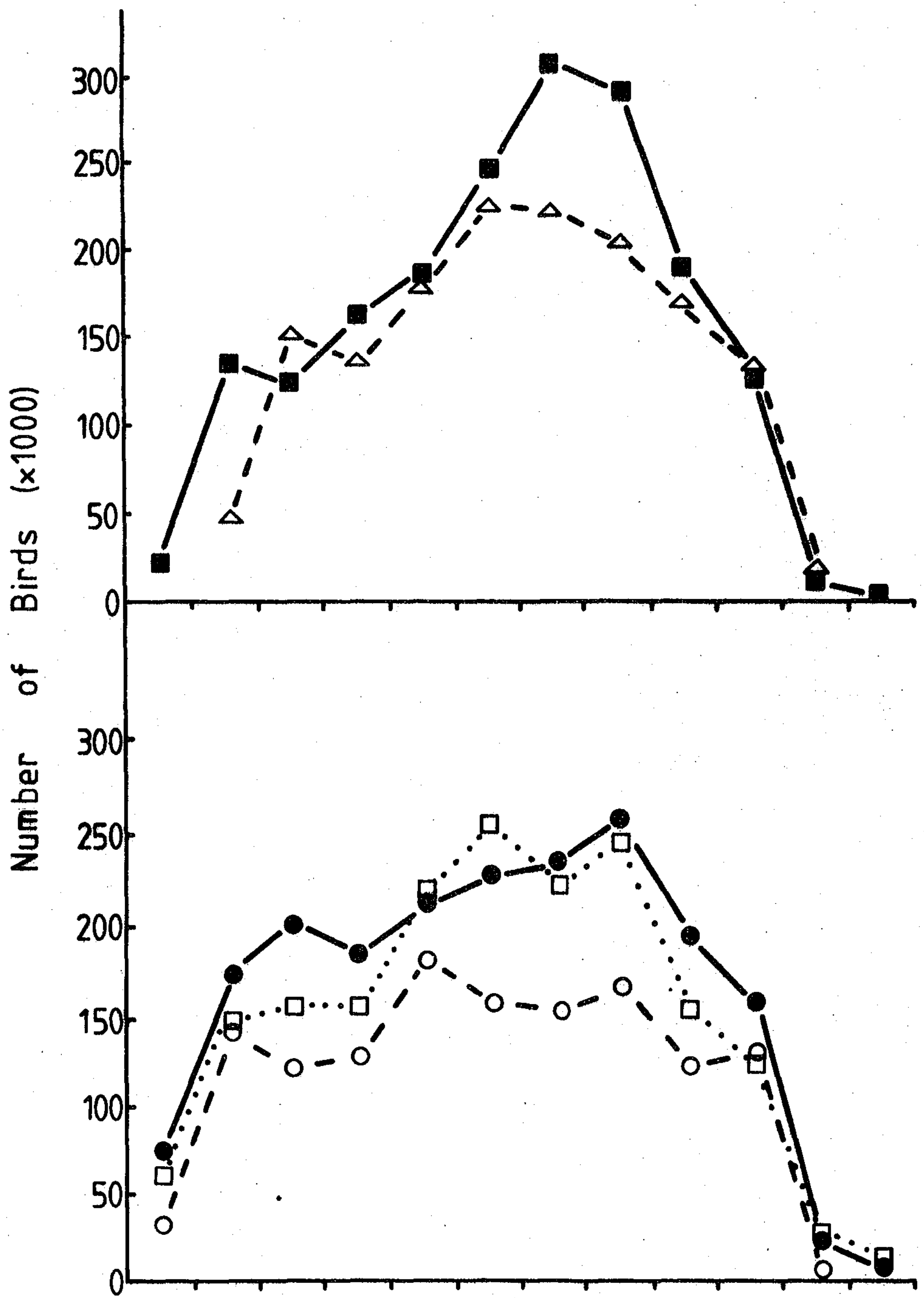


Fig. 14
Number of Birds (×1000)
150
100
50
0
150
100
50
0
J
A
S
O
N
D
J
F
M
A
M
J
Month

Fig. 15



Number of Birds (×1000)
300
250
200
150
100
50
0
300
250
200
150
100
50
0
J
A
S
O
N
D
J
F
M
A
M
J
Month

estuaries on the north-east coast, return to the Waddenzee between February and April. There is some evidence from the dye-marking study on the Tees that this movement to the eastern North Sea coast may not be direct. In 1979 two birds marked on the Tees in January were seen on the Humber in early March, after numbers had decreased on the Tees (Fig. 8). Again in 1980, one bird marked on the Tees in January was seen on the Wash in March, and another, marked at the same time was seen on the Forth, also in March, after the majority of the birds which used the Tees in mid-winter had departed (Fig. 6). Thus it is possible that some birds may move to another east-coast estuary prior to movement across the North Sea. Similar observations have been made of Dunlin from the Forth and Tees (Pienkowski and Clark, 1979 ; L.R. Goodyer, Pers. Comm.).

BAR-TAILED GODWIT

Unlike Knot, Bar-tailed Godwit breed only in northern Russia, (e.g. see Evans, 1981). After breeding, adults move west, the first arriving in Britain in July where they settle on their moulting areas. Although some birds are present, and presumably moult, on most major estuaries at this time e.g. Lindisfarne and the Forth (Figs. 16,17) the main moulting areas are the Wash and Ribble (Figs. 18,19) (see also Minton, 1975; Smith and Greenhalgh, 1977). Juveniles begin to arrive in late August, but most reach Britain in September (Minton 1975; Evans and Smith, 1975). However, very little is known/

known of the extent to which the movements of juveniles differ from those of adults. Consequently most of the following discussion refers to adults.

Following the completion of moult in late October and early November (Evans and Smith, 1975), counts indicate departures from the Wash and Ribble and arrival on other estuaries (Figs. 20-23). However, only on the east coast is there confirmation of direct movement between estuaries used for moulting and those used later. One ringing recovery and one sighting of a colour-marked bird indicate movement from the Wash to the Humber and from the Tees to Lindisfarne (Fig. 24). Thus it appears that on the east coast there is some movement along the coast similar to that documented for Knot. However, the extent to which the increase in numbers on the estuaries of the north-east coast is due to movement from the Wash is not known. Indeed, since numbers on other moulting areas, particularly the Waddenzee, decline at this time of year (Boere, 1976), many of the birds arriving on the estuaries of the north-east coast of Britain might come from there.

On the west coast of Britain the increases on the Dee, Morecambe Bay and Solway in October and November (Figs. 21-23) are only rarely matched by a decrease of similar magnitude on the Ribble (Fig. 19). Consequently, it seems unlikely that many of the birds move after moulting on the Ribble to winter on the west coast estuaries. More probably these wintering birds come from other moulting areas/

Figs. 16-23. Monthly counts of Bar-tailed Godwit.

Fig. 16. Lindisfarne.

Fig. 17. Forth.

Fig. 18. Wash.

Fig. 19. Ribble.

Fig. 20. North-East Coast.

Fig. 21. Morecambe Bay.

Fig. 22. Dee.

Fig. 23. Solway.

Note: For the Solway, counts for 1969-70; 1970-71; 1971-72 and 1973-74 are for the south side of the estuary only. For 1972-73 and 1974-75 counts are of the whole estuary.

Fig. 16

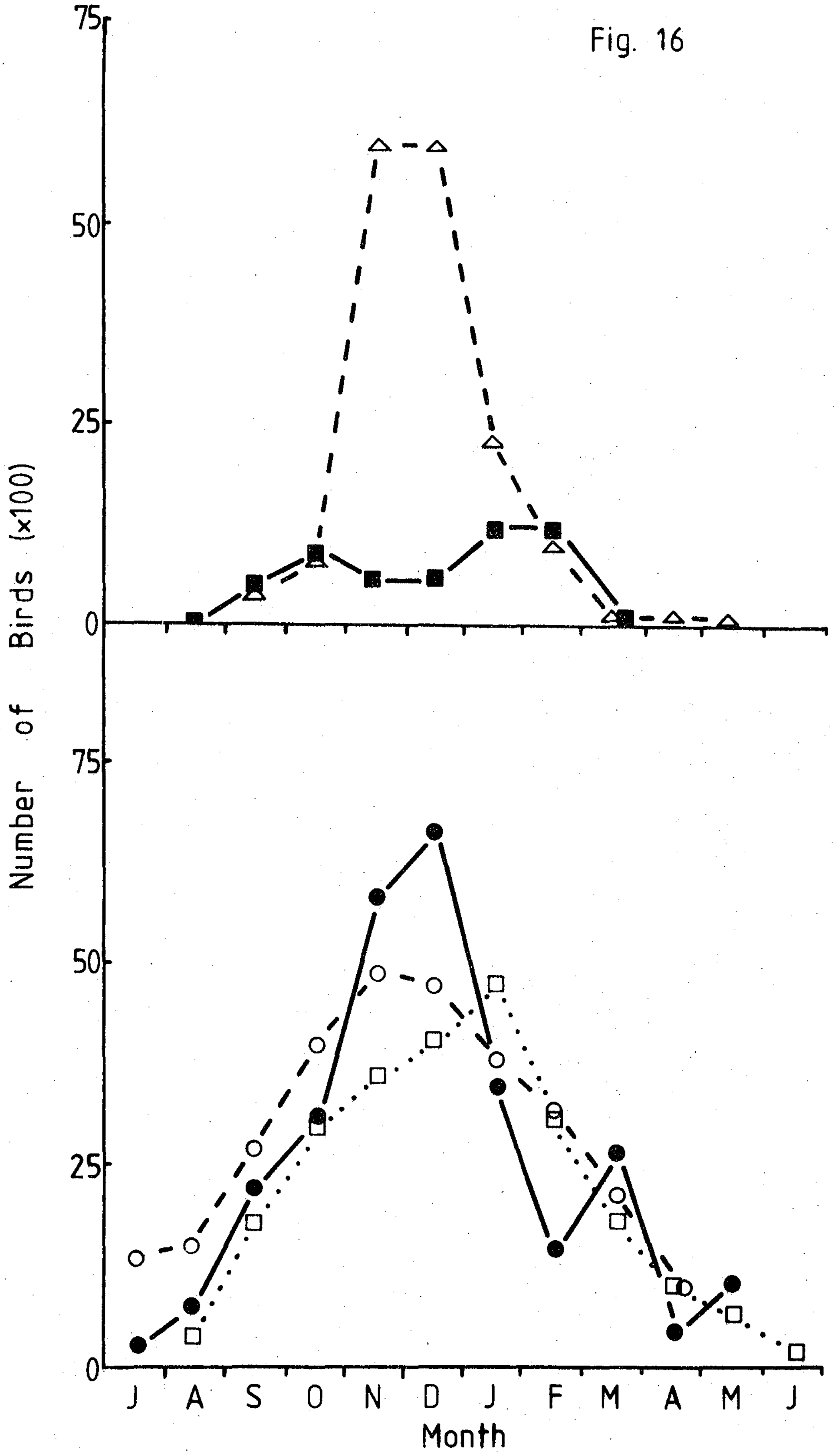


Fig. 17

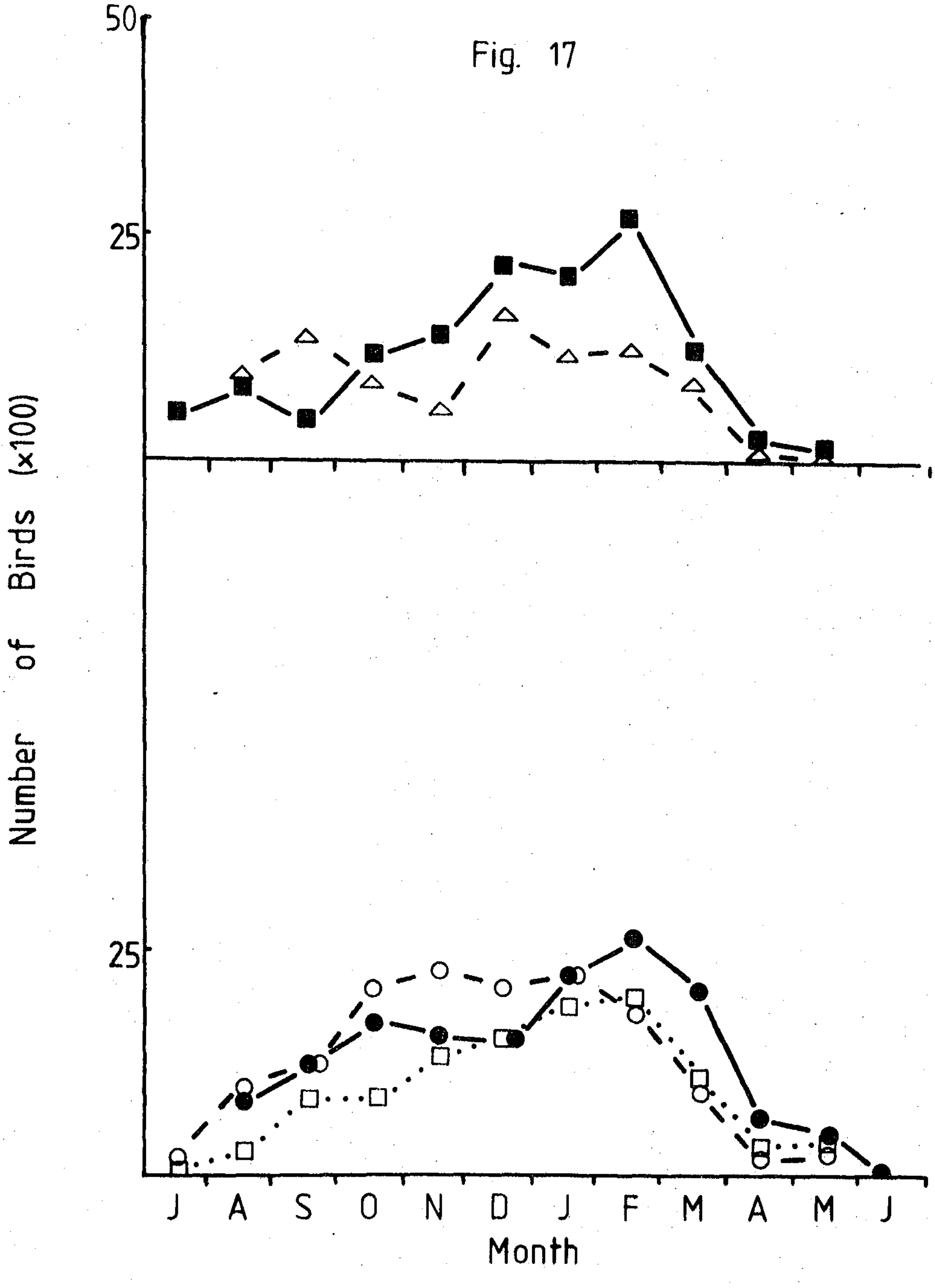
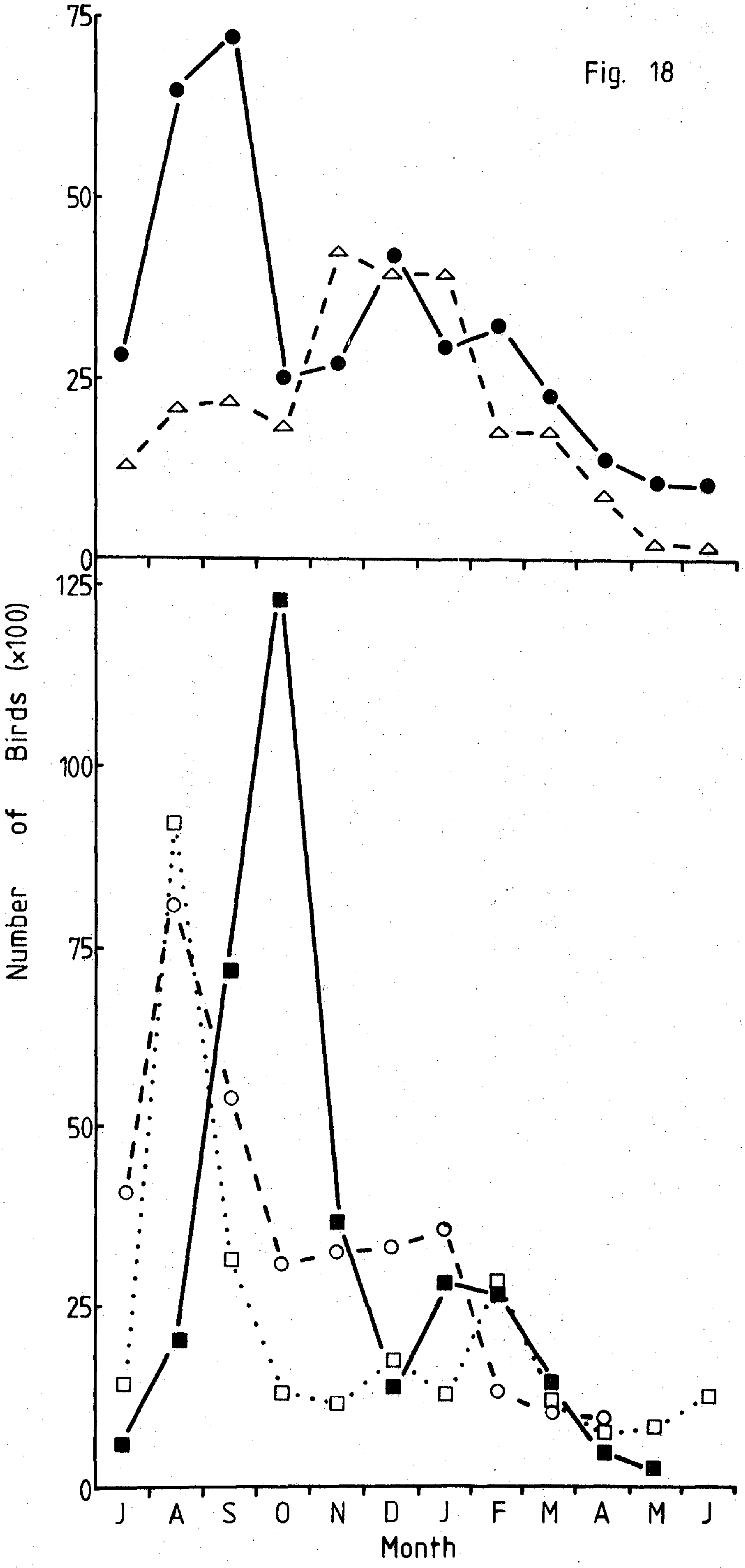


Fig. 18



75
50
25
0
125
100
75
50
25
0
Number of Birds (x100)
J
A
S
O
N
D
J
F
M
A
M
J
Month

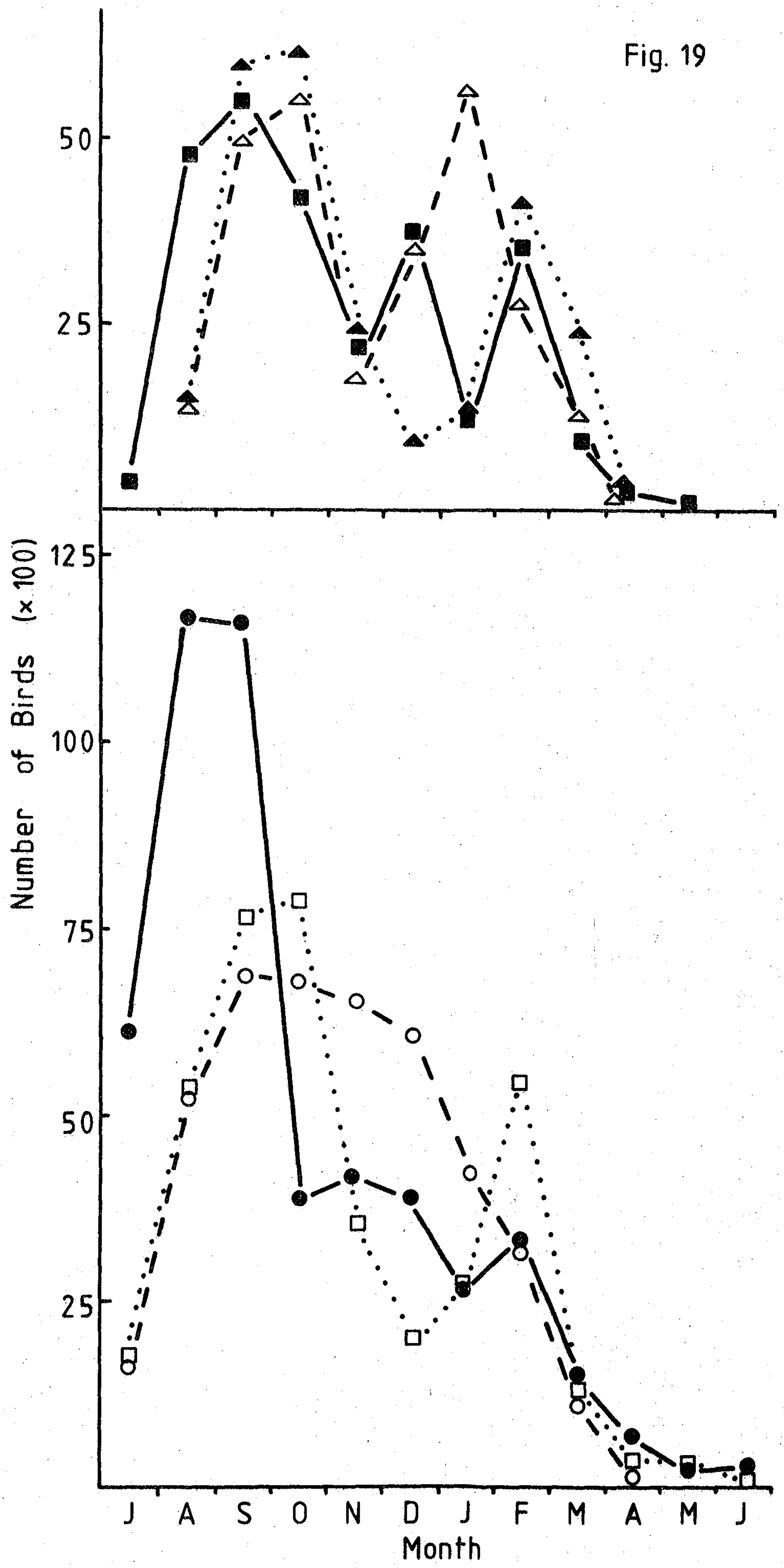


Fig. 19
50
25
125
100
75
50
25
Number of Birds (×100)
J
A
S
O
N
D
J
F
M
A
M
J
Month

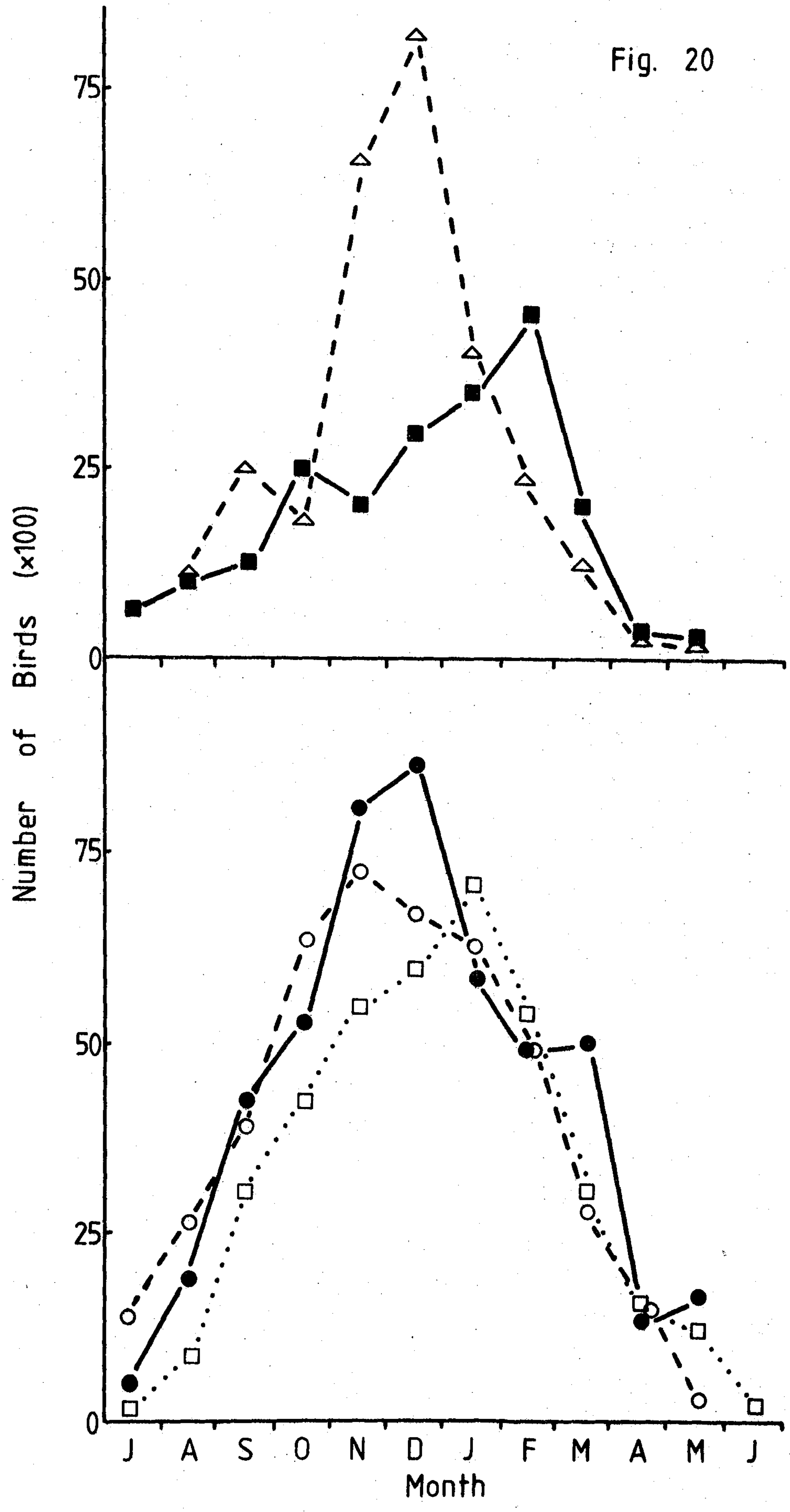


Fig. 20
Number of Birds (×100)
75
50
25
0
75
50
25
0
J
A
S
O
N
D
J
F
M
A
M
J
Month

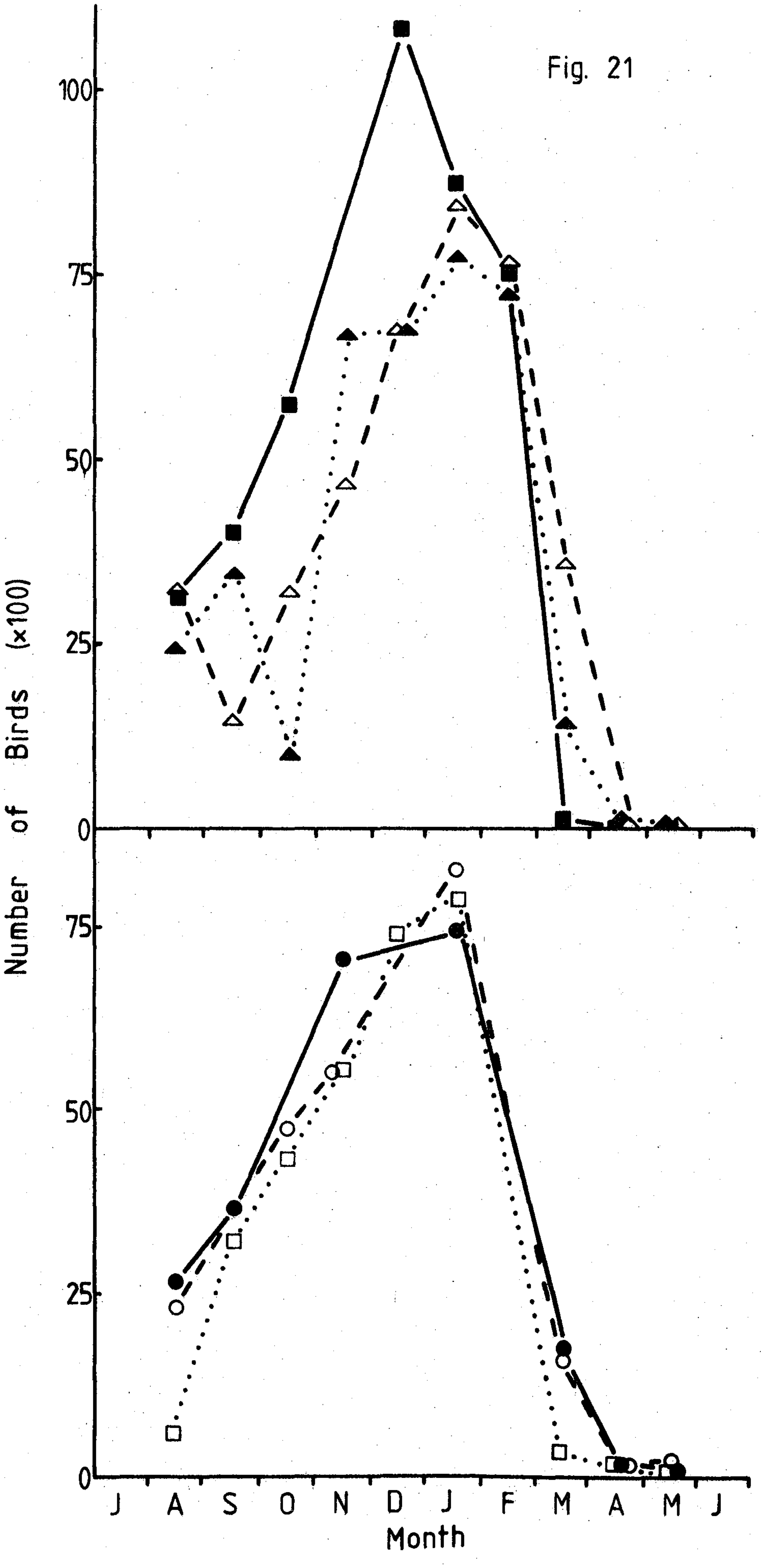


Fig. 21
Number of Birds (×100)
100
75
50
25
0
75
50
25
0
J
A
S
O
N
D
J
F
M
A
M
J
Month

Fig. 22

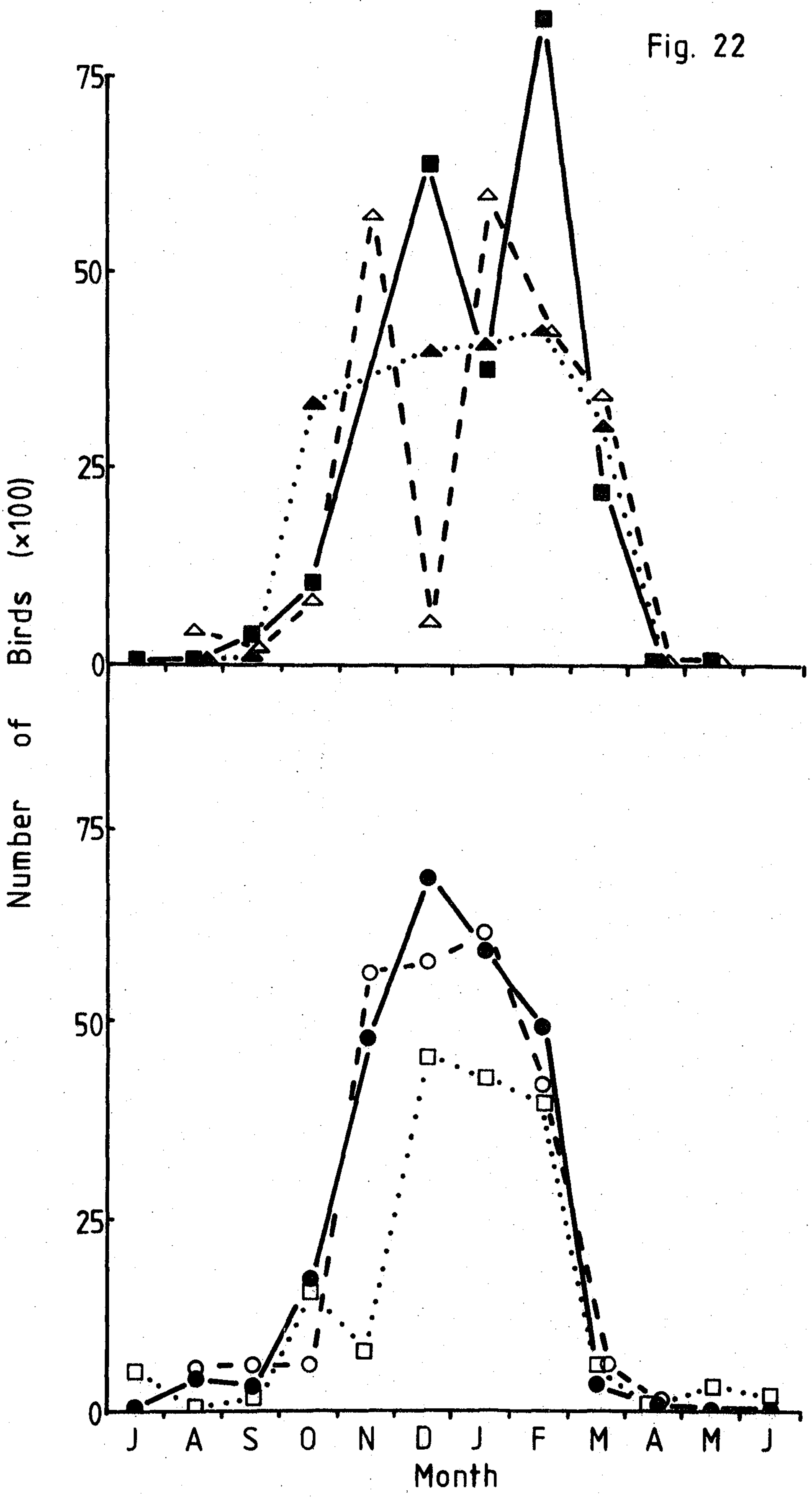
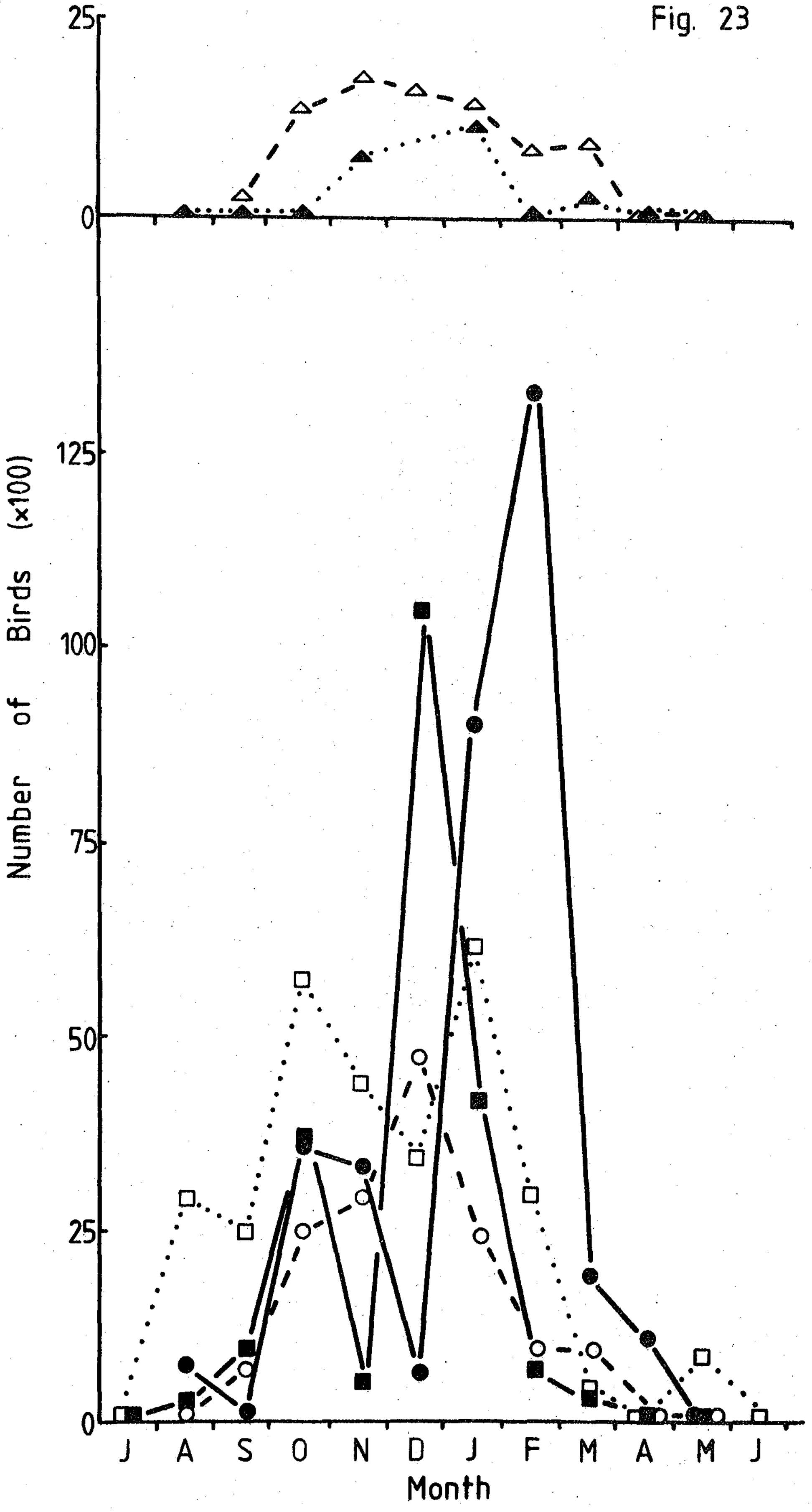
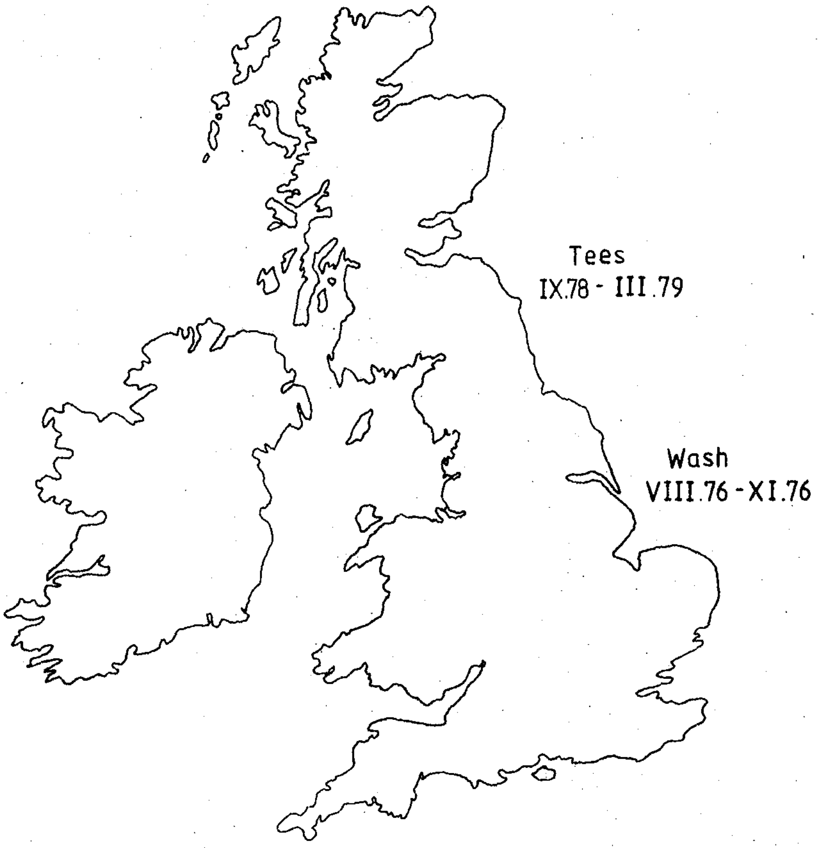


Fig. 23





Juvenile VIII.77 Cornwall ⟶ I.78 France (Brittany)

2nd. year bird VIII.72 Wash ⟶ X.72 Spain (Santander)

Fig. 24. Recoveries, within the same non-breeding season as that of ringing, of Bar-tailed Godwit ringed in Britain. Explanation as for Fig. 1.

areas, particularly the Waddenzee. However, it is not known where birds, which do move after moulting on the Ribble, winter. Some of the birds present in other areas of the British Isles in autumn have been found to the south a few months later (Fig. 24), so birds from the Ribble may also move south. However, ringing data concern only one first year and one second year bird and it is possible that only the younger birds move south for winter.

There is no evidence of movement, within the winter of ringing, of Godwit after moult from the east to west coast, or vice versa, as observed in Knot. Indeed, there is not even a single record of a bird ringed on one coast and recorded on the other coast in subsequent years (Table 3). One bird ringed in Ireland in August was caught on the Wash in October the following year. This may suggest that some birds which are present on the Wash in October spend part of early autumn in Ireland. However, it is possible that this ringed individual may have followed a different route each year. The absence of recoveries on the opposite coast from that of ringing may be partly a consequence of the small number of Godwit that have been ringed in Britain.

In the spring of most years numbers of Godwit on most estuaries (and consequently in Britain) drop sharply between February and March (Figs. 16-23). Very few birds remain in April or May to undergo pre-breeding moult or pre-migratory fattening in Britain. Most of the Godwit which/

Table 3. Between winter recoveries of Bar-tailed Godwit within Britain away from the estuary of first capture.

Date and place of ringing		Date and place of recovery	
13.3.71	Dee	24.1.73	Solway[1]
30.11.70	Dee	3.9.75	Morecambe[2] Bay
14.8.69	Morecambe Bay	13.6.76	Ribble[3]
26.10.73	Roe estuary, N. Ireland	18.8.74	Wash[2]

1. Remains found
2. Controlled
3. Found shot

which leave British estuaries in February and March probably go to the Waddenzee, where large numbers arrive at this time (Boere, 1976). However, there is no direct proof from ringing recoveries of this.

Immediately prior to the spring decline in numbers, count data suggest that an influx of birds occurs in most years, at least on some estuaries, particularly on the west coast e.g. Ribble (Fig. 19) (see also Smith and Greenhalgh, 1977). As discussed for Grey Plover in Chapter 3 these birds may come from wintering grounds further south in southern Europe or West Africa. However, once again, there is no ringing data to support this.

GREY PLOVER

All Grey Plover which spend the non-breeding season in western Europe and Africa breed in Siberia (Branson and Minton, 1976). Adults first arrive in Britain in late July and early August when numbers increase on most estuaries but particularly on the Wash (Fig. 25-27). Most birds which arrive at this time stay to moult. However, some move rapidly on (Minton, 1975; see also Chapter 3). On the Wash numbers of birds decrease rapidly by October (Fig. 25). At this time many birds which have completed moult move south to wintering grounds in France, Iberia and West Africa (Minton, 1975; Branson and Minton, 1976). However, some of these departing/

departing birds may not have completed, but instead arrest, moult (Branson and Minton, 1976). Numbers also drop on other estuaries after moult e.g. Essex (Fig. 26) and on the Tees (see Chapter 3). However, birds continue to depart in late October and November from the Tees (Chapter 3) and Ribble (Smith and Greenhalgh, 1977).

Juveniles begin to arrive in Britain in September (Minton, 1975; see also Chapter 3) at which time many are found on isolated open coastal sites e.g. on the Northumberland coast (P.R. Evans Pers. Comm; Pers. Obs.). From the Wash, southward passage of juveniles continues into November (Minton, 1975). Several weeks after the departure of moulting adults from the Wash, count data indicate an increase in numbers in the period from December to January in three of the four years for which data are available (Fig. 25). Similar peaks in numbers in mid-winter occur on other estuaries e.g. the Essex estuaries, the South Coast Harbours, the Ribble (Figs. 26-28) and the Tees (see Chapter 3). However, the timing of the increases on different estuaries do not always coincide, either with one another or with the timing of general increases in total numbers in the British Isles. For example, although numbers on the Essex estuaries (Fig. 26) peaked in January and February, at the same time as total numbers present in Britain also peaked (Fig. 29), only in one winter (1974-75) did this coincide with the timing of the mid-winter peak on the Wash (Fig. 25). Thus the time of highest numbers in mid-winter/

Figs. 25-29. Monthly counts of Grey Plover.

Fig. 25. Wash.

Fig. 26. Essex.

Fig. 27. South-Coast Harbours.

Fig. 28. Ribble.

Fig. 29. All major British estuaries, combined.

Fig. 25

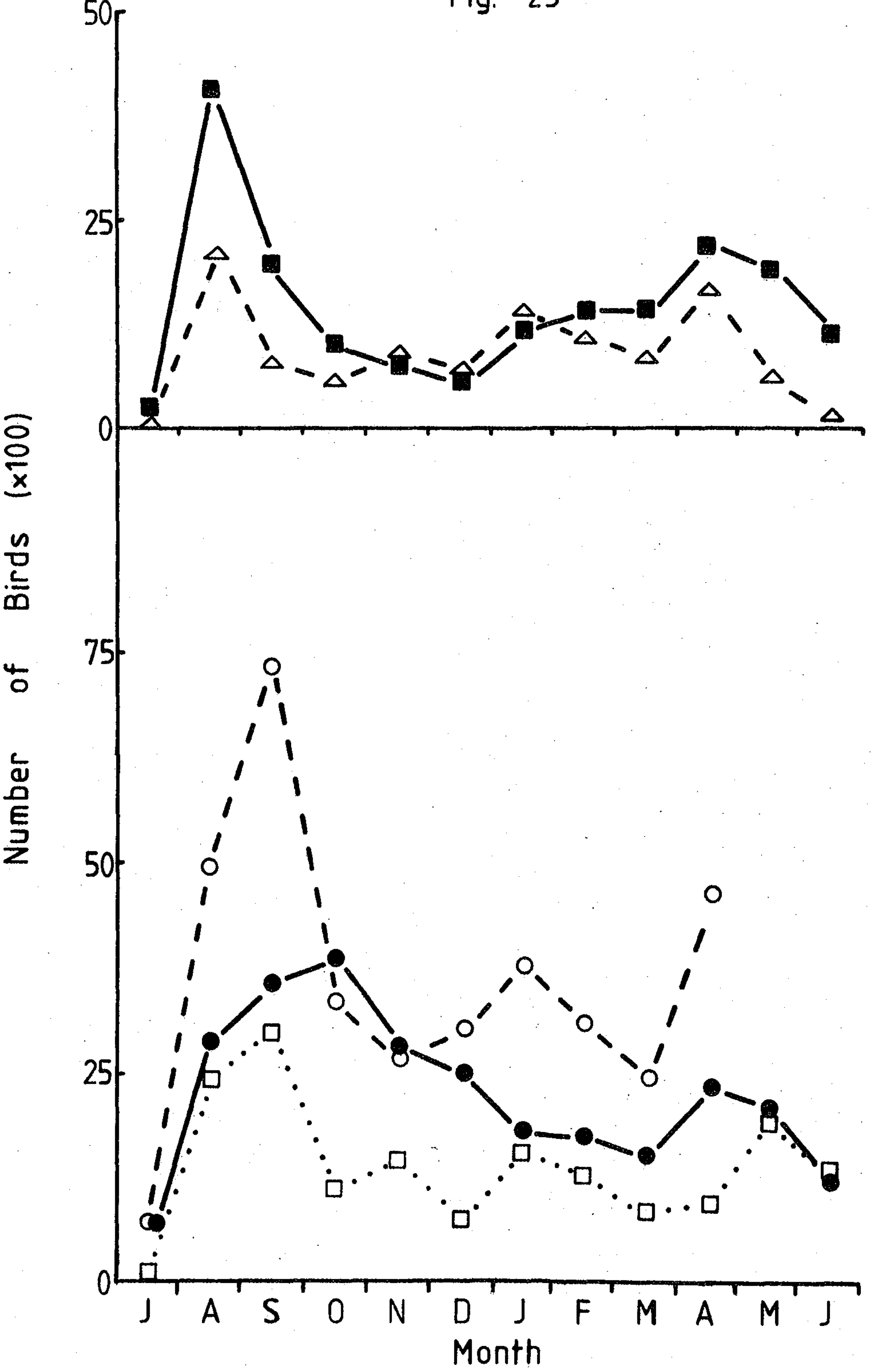


Fig. 26

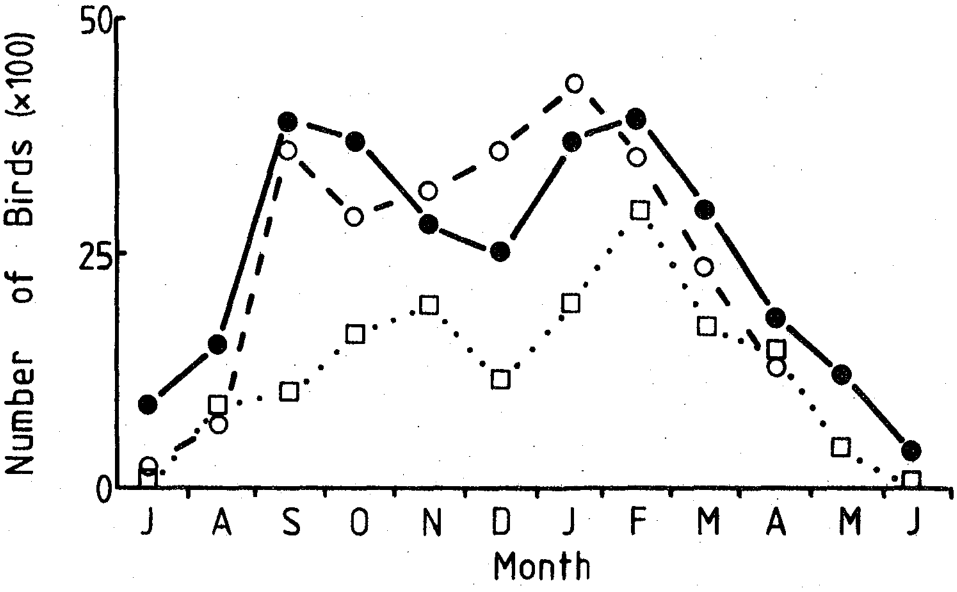

Number of Birds (×100)
50
25
0
J
A
S
O
N
D
J
F
M
A
M
J
Month

Fig. 27

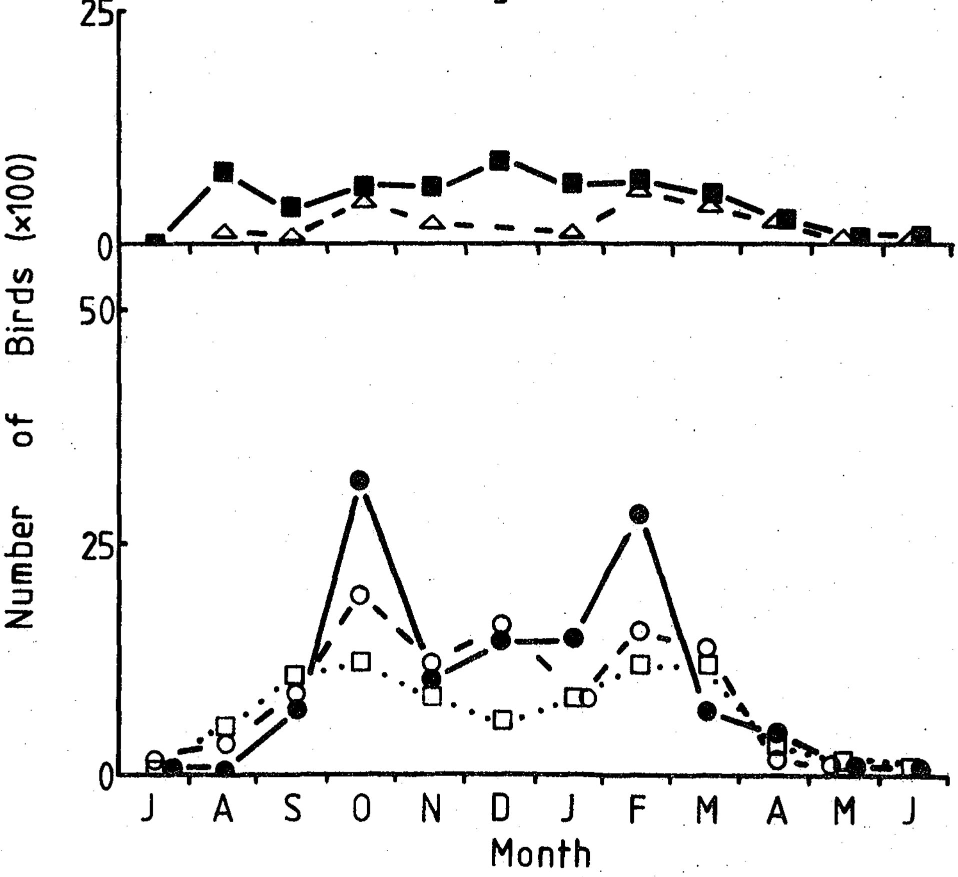
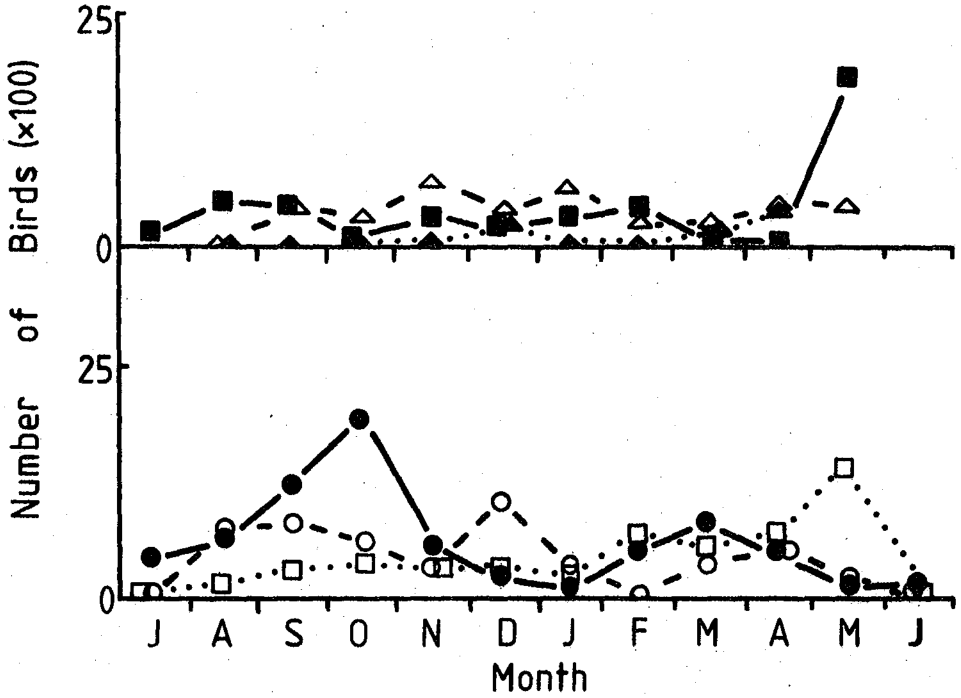
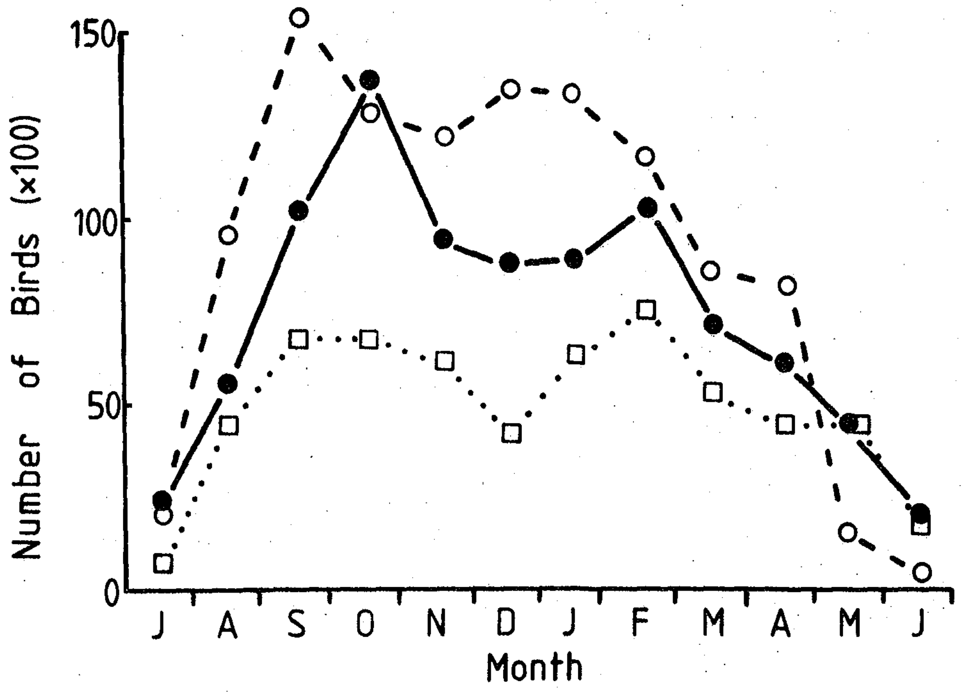

Number of Birds (×100)
25
0
50
25
0
J
A
S
O
N
D
J
F
M
A
M
J
Month

Fig. 28



25
0
25
0
Number of Birds (×100)
J
A
S
O
N
D
J
F
M
A
M
J
Month

Fig. 29



150
100
50
0
Number of Birds (×100)
J
A
S
O
N
D
J
F
M
A
M
J
Month

mid-winter varies between estuaries. Prater (1971), has argued that the peaks in January and February on the Essex estuaries represent spring passage of birds which have wintered further south. Ferns (1977) and Smith and Greenhalgh (1977) have suggested the same explanation for similar rises in numbers on the Severn and Ribble. As described in detail in Chapter 3, on the Tees estuary, two distinct peaks in numbers occur during some winters, the second of which may contain passage birds. However, the first peak, which I argue in Chapter 3 is probably the result of movement from the Waddenzee where numbers fall at this time (Fig. 30), has occurred at somewhat different times in successive years, varying between November and February. Consequently it is not possible to conclude that the peaks in Essex and the South Coast Harbours, or on the Ribble, are definitely, or even solely, of passage birds. Indeed it seems likely that because the Birds of Estuaries counts are made only at monthly intervals these peaks may be the result of several influxes within a few weeks of birds from different origins. Indeed the data from 1972-73 indicate that numbers in Essex and the South Coast Harbours increased in both January and February. These increases may have been the result of two influxes of differing origin. Similarly, although the peak in numbers of Grey Plover on the Wash in November probably represents an influx from the Waddenzee, the influxes in January or February could indicate either immigration from the eastern North Sea, or passage from wintering areas further south.

On/

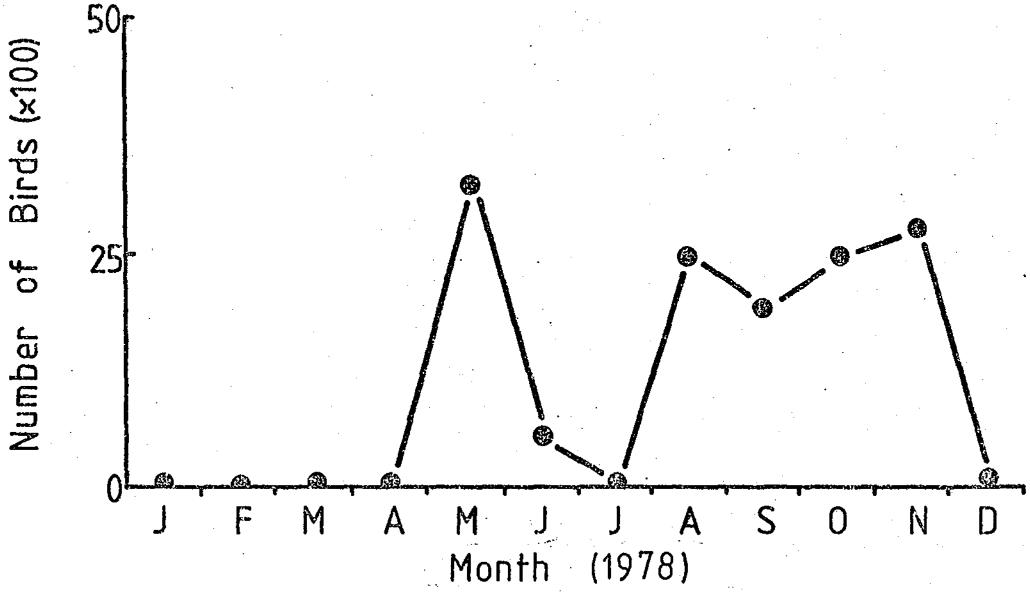


Fig. 30. Monthly counts of Grey Plover in Denmark 1978. Data from Meltofte, 1979.

On both the Wash and Ribble, numbers of Grey Plover rise in late April or May. The use of the Ribble by Grey Plover has been reviewed by Smith and Greenhalgh (1977) who report that this second spring peak consists almost entirely of adults in summer plumage and suggest that these are birds from African winter quarters making a brief refuelling stop en route to the high arctic breeding grounds. Minton (1975) has suggested a similar explanation for the peak at this time on the Wash. Neither the Birds of Estuaries counts nor other published information provide evidence of late spring passage on other estuaries. However, the observation of Buxton (reported by Smith and Greenhalgh, 1977) of a flock of 500 Grey Plover on the Dee in May 1975 suggests that this may occasionally occur on other estuaries.

Thus, to summarise, numbers of Grey Plover in Britain are highest in autumn when large numbers moult on the Wash, after which, many birds move further south. However, autumn peaks in numbers are also evident on many other estuaries, including the Tees, even though total numbers are relatively low at this time. Also in August, on both the Wash and the Tees, there is rapid through passage of birds which may move further south before moulting. In winter, a number of influxes of Grey Plover occur on both the east and west coasts. Some are thought to be from the Waddenzee but those in February probably represent northward migration. However, the variable timing of the former and the low frequency of counts does not/

not allow discrimination between these influxes to be made. There is no definite evidence for within-winter movement between British estuaries and data from the Tees suggest that, outwith the periods of major influx and departure, little movement of Plovers occurs (see Chapter 3). However, more detailed study is required to quantify the extent of those movements which do occur. In late spring influxes occur regularly on the Wash and Ribble, but irregularly and for only short periods on other estuaries. It is thought that these consist of birds which have wintered further south and which stop briefly to replace fat reserves before moving to their high arctic breeding grounds.

Chapter 2. Factors affecting energy balance in shorebirds: regional and seasonal variation.

INTRODUCTION

In order to survive from one breeding season to the next every individual shorebird must achieve sufficient food intake to meet its energy demands and to obtain essential nutrients over this period, while at the same time avoiding predation. Shorebirds may occur at higher densities (during breeding) in the Arctic than further south because predation in the Arctic is less (Pienkowski, 1980); Evans, 1981). However, although there is very little information on the risk of predation to shorebirds in North-West Europe it is difficult to conceive that, within the non-breeding season, shorebird populations move to avoid predation as predators will presumably follow their food supply. In view of this and the more obvious importance of energetic and nutrient demands as factors leading to changes in shorebird distribution, the role of predation, except where this influences energy expenditure, is not discussed further.

Little is known of any changes in specific nutrient demands of shorebirds through the non-breeding season, although in both sexes during moult and in females prior to departure to the breeding grounds, protein demands must be especially high. The shortage of information concerning/

concerning nutrient demands of the birds and seasonal change in body composition of their prey does not permit detailed consideration of the potential role of these factors in determining shorebird movements. However, where relevant they are discussed.

Evans (1976) has reviewed the main purposes for which shorebirds require energy in the non-breeding season. These are:- (1) to maintain body temperature and normal metabolic processes including digestion, (2) to fly, to and from its feeding grounds, and possibly to escape predators, and (3) to cover the costs of food gathering.

(1) The amount of energy required to maintain body temperature rises as ambient temperature decreases. Within the thermoneutral zone no additional energy is required as body temperature is maintained through changes in the insulative capacity of the plumage, accomplished by small muscular adjustments of feather posture. However, once ambient temperature falls below the lower critical temperature chemical thermogenesis is required to maintain body temperature. Several attempts are in progress to measure the rate of increase of metabolic rate with falling temperature and its effects on the energy budgets of wintering shorebirds, but at present data for only two species, the Little Ringed Plover Charadrius dubius and Woodcock Scolopax rusticola have been examined (Gavrilov and Dol'nik cited in Kendeigh et. al., 1977). In the Little/

Little Ringed Plover metabolic rate increases by about 56% of Basal Metabolic Rate (B.M.R.) and in Woodcock by 46% of B.M.R. for every 10°C drop in temperature below the lower critical temperature of the respective species. Lower critical temperatures of few shorebird species are known. Gavrilov and Dol'nik obtained values of 22°C for Little Ringed Plover and 18°C for Woodcock. It seems likely that these values of both lower critical temperature and rate of increase in metabolic rate with falling temperature below this point are good approximations to these values in other species of shorebirds. As suggested by Evans (1976) it is likely that most shorebirds wintering north of the Mediterranean will experience temperatures below this. Indeed it is probable that in most parts of Britain temperatures experienced will be consistently ten or more degrees below the lower critical temperature.

The increase in heat loss and consequently in metabolic rate with decreasing temperature under calm conditions is accentuated in conditions of forced convection resulting from an increase in wind speed. Again little information is available on the magnitude of this increase at different wind speeds. However Gessaman (1973) reports that metabolic rates of Snowy Owls *Nyctea scandia* almost doubled when wind speed rose from calm to 9 metres/sec at temperatures of -20°C and -30°C.

(2) Although large day to day changes in energy needed/

needed for flight seem unlikely it is possible that during the course of a winter shorebirds may require to fly further from the roost to feed as a result of prey depletion nearby. Hamilton, et.al. (1967) suggest that the energy expended in flying to those feeding grounds may be offset by reduced intraspecific competition and/or higher prey availability encountered there. However, in only one study (Zwarts, 1974) has evidence been produced to show that shorebirds did indeed fly further from the roost later in the winter. Consequently it is not possible in the present study to consider in any detail the importance of seasonal increase in distance of feeding grounds from a safe roost site as a factor leading to movements of shorebirds between estuaries in winter. Similarly predation pressure and energy expended in anti-predator behaviour in different areas is not known. However as discussed previously it is very unlikely that predators influence the distribution of shorebirds in winter, but rather that the converse is true.

(3) Energy costs of food gathering, i.e. those incurred in locating, catching and handling the prey, can vary greatly throughout the non-breeding season. As the density of available prey decreases (either because of reduction in its accessibility or detectability) the time and therefore the energy, required to detect and capture individual prey items increases.

Reduction in absolute density may occur through predation or other forms of mortality or because of migration/

migration of at least part of the prey population out of the intertidal zone. Similarly, in a number of prey species, including Macoma balthica (L.) and Nereis diversicolor O.F. Muller, seasonal reduction in the percentage available, occurs as a result of vertical migration within the substrate (Reading and McGrorty, 1978; Muus, 1967). Further to these changes in density of accessible prey, day to day changes in environmental conditions can greatly influence the available density by affecting the detectability of the prey (Smith, 1975; Goss-Custard et. al. 1977a; Pienkowski, 1980).

In this chapter I review data relating to seasonal changes within Britain and other coastal regions of North-West Europe, in the distribution and severity of factors affecting energy balance in shorebirds. I discuss first climatic factors affecting body temperature. I then consider, for each estuary for which information is available, prey density and prey quality. Finally I examine both short and long term changes in availability.

FACTORS AFFECTING BODY TEMPERATURE AND METABOLIC RATE

Temperature

In North-West Europe the seasonal temperature regime of low lying areas is the product of both latitude/

latitude and distance from the Atlantic Ocean. In winter the ocean is considerably warmer than the land and isotherms lie in a north-westerly direction (Fig. 1). Conditions become progressively colder along a line from the west of Britain across the North Sea to Denmark and the Baltic where the proximity to the continental airstream has a marked cooling effect on the climate. In spring and autumn when the continental land mass is warming and cooling respectively the temperature of land and sea at the same latitude is about equal. Although the 5°C isotherms do not permit precise comparison of Britain and the eastern North Sea coast at this time it is apparent that temperatures are very similar. In March and October when the winter temperature pattern is respectively receding and developing, the pattern of isotherms lies mid way between that in summer and winter. In summer the land is warmer than the sea. Consequently at this time coastal regions in the eastern North Sea experience higher temperatures than similar areas at the same latitude in Britain (which experience the cooling influence of the Atlantic).

Within the British Isles lowest air temperatures are experienced in January and February and highest in July and August. However, as discussed above, the precise pattern and scale of seasonal temperature changes experienced in each area depend greatly upon the longitude of that area and the relative strengths of/

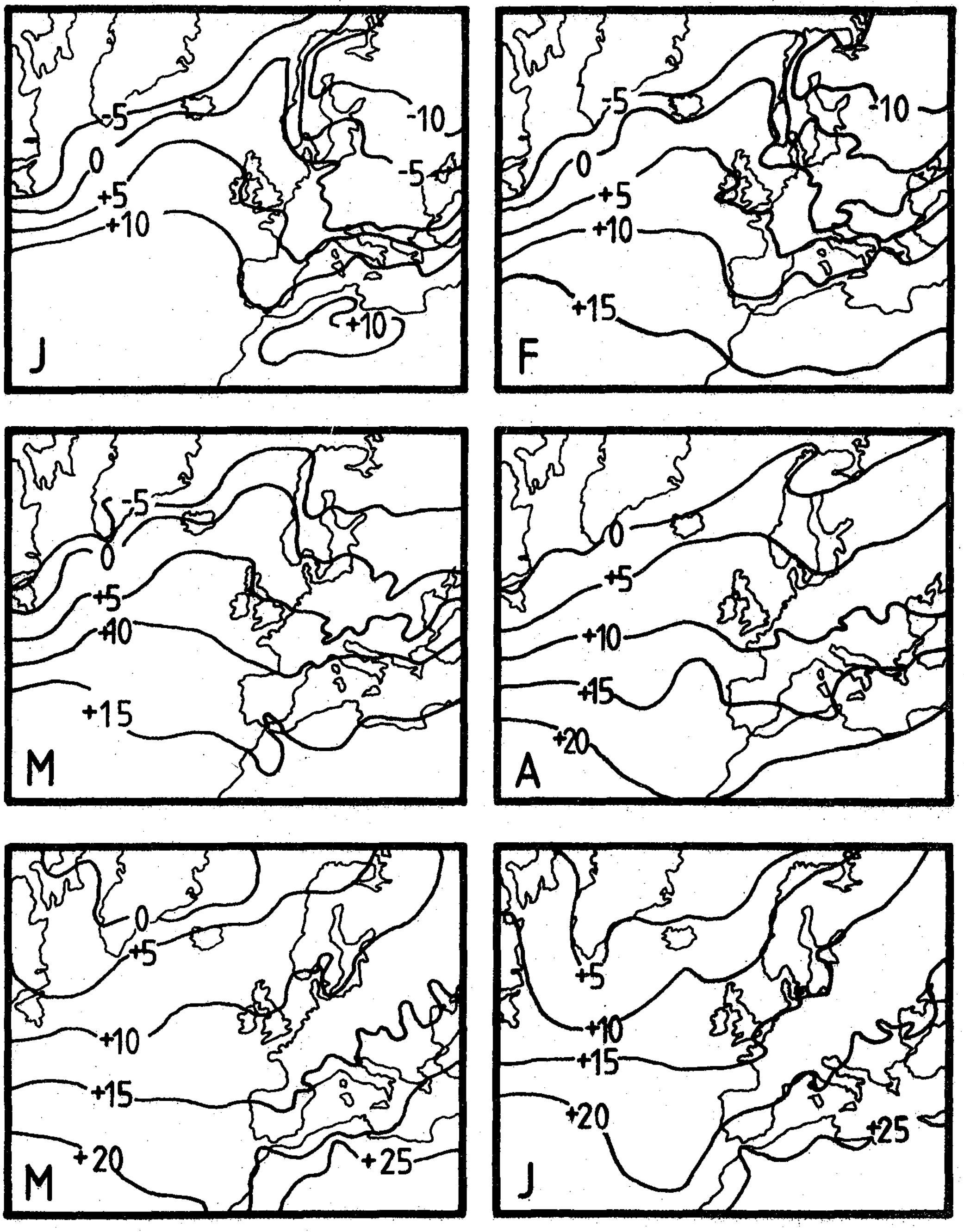


Fig. 1a. Monthly mean surface air temperatures (°C) January to June (1931-60). Figures from Met. Office 1975.

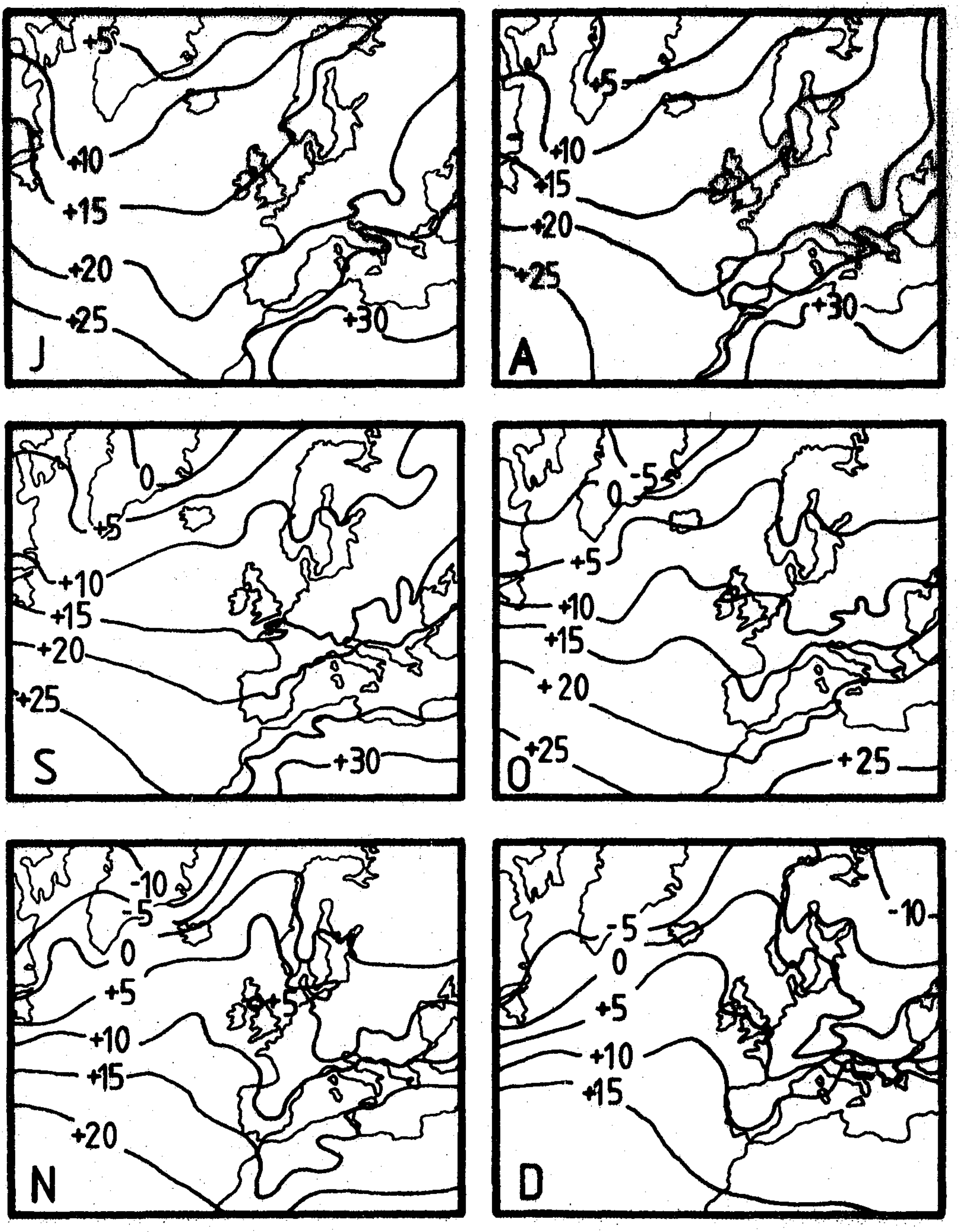
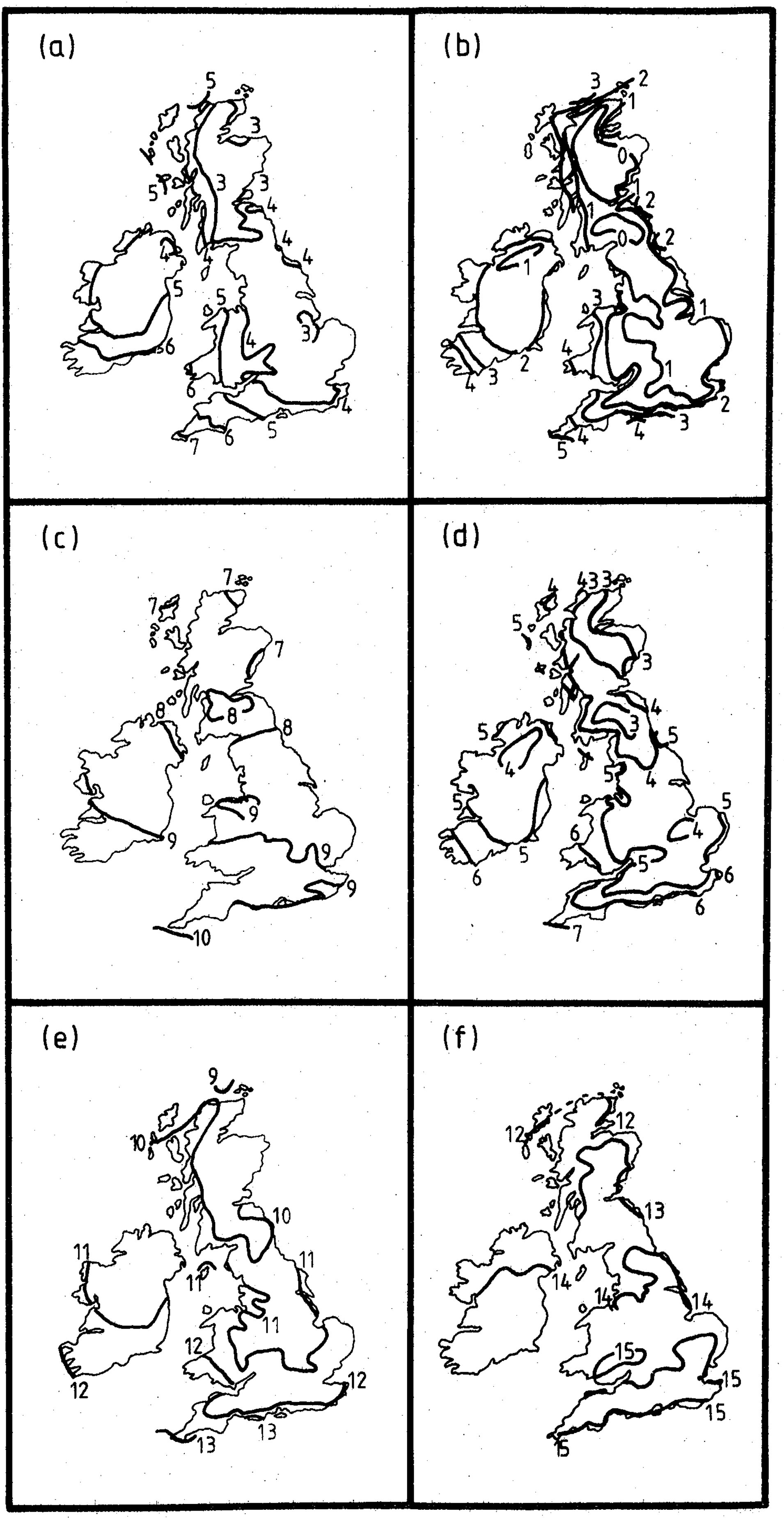


Fig. 1b. Monthly mean surface air temperatures (°C), July to December (1931-60). Figures from Met. Office 1975.

of maritime and continental climatic influences. Of the coastal areas under consideration in the present study, those in the south-east, particularly the Essex estuaries and the Wash, are most subject to the influence of continental airstreams (Tout, 1976) and those in southern Ireland and South-West England least subject. This is reflected in the January mean temperatures and more particularly in the mean daily minima, experienced by these areas. In this month, the Wash and the Essex estuaries are on average subject to lower temperatures than all other estuaries on the east coast south of the Forth. On the west coast, only the Solway is colder (Fig. 2). It is perhaps surprising that temperatures at more northerly latitudes are higher. However, a cold easterly airstream falling on the north-east coast of England will have crossed a considerably longer stretch of relatively warm sea than the same airstream falling on the coast of Essex, which is much closer to the continental land mass.

However, it may not be the average pattern (over 20 to 30 years) of winter temperature distribution within Britain that is likely to be most important in affecting the evolution of shorebird movements. Rather it may be the pattern of temperature distribution in those few winters when conditions are most severe that is the most important selective factor. If we consider two estuaries (A) and (B), if (A) experiences low/

Fig. 2. January, April and October air temperatures 1941-70 in °C, reduced to sea lvel.
(a) mean January; (b) mean daily minimum January;
(c) mean April; (d) mean daily minimum April;
(e) mean October; (f) mean daily maximum October.
Figures from Tout, 1976.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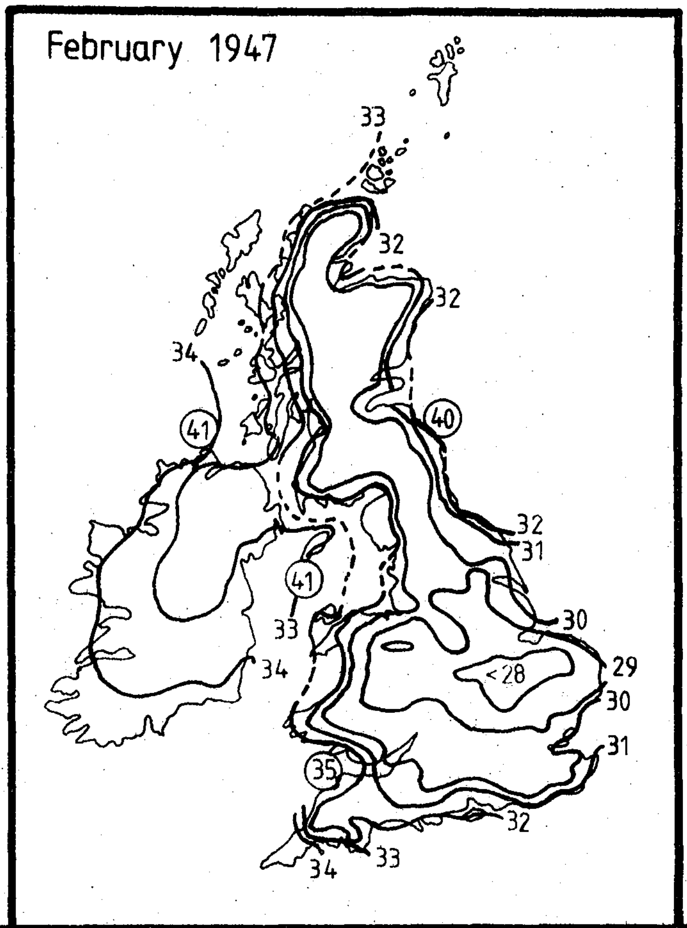
low January temperatures e.g. a monthly mean ca. 2.0°C every year it will have a lower average January temperature than (B) experiencing mean January temperature in most years of ca. 4.0°C. However, if in severe winters (B) experiences colder conditions e.g. -3.0°C instead of 0.0°C at (A) it is likely that greater mortality will occur at (B). Consequently I would expect selection for a pattern of movement away from area (B) to area (A) before the coldest months. This would not be predicted from average temperature values alone. In the most recent severe winters, 1978-79, 1962-63 and 1946-47, the pattern of distribution of mid-winter temperatures (Fig. 3) was very similar to the average pattern for 1941-70 (Fig. 2). More importantly in all three years the areas of the Wash, East Anglia and Essex were the coldest of the major shorebird wintering areas in Britain. One difference, however is apparent between these cold winters and the average for 1941-70. The east coast of Scotland, where the mean temperature for 1941-70 was as cold as the Wash, was warmer than the Wash in all three severe winters. The relatively mild conditions in these areas in severe winters might have been an important factor in the evolution of the northward movement of birds from the Wash to these areas, if temperature is the most important selective agent.

In spring, latitude is of more importance in determining average temperatures than longitude (Fig. 2) and/

Fig. 3. Mean air temperature, February, 1947 (°F); January, 1963 and January 1979 (°C) reduced to sea level. Sea temperatures are shown in circles. Figures from Met. Office, 1947, 1963, 1979.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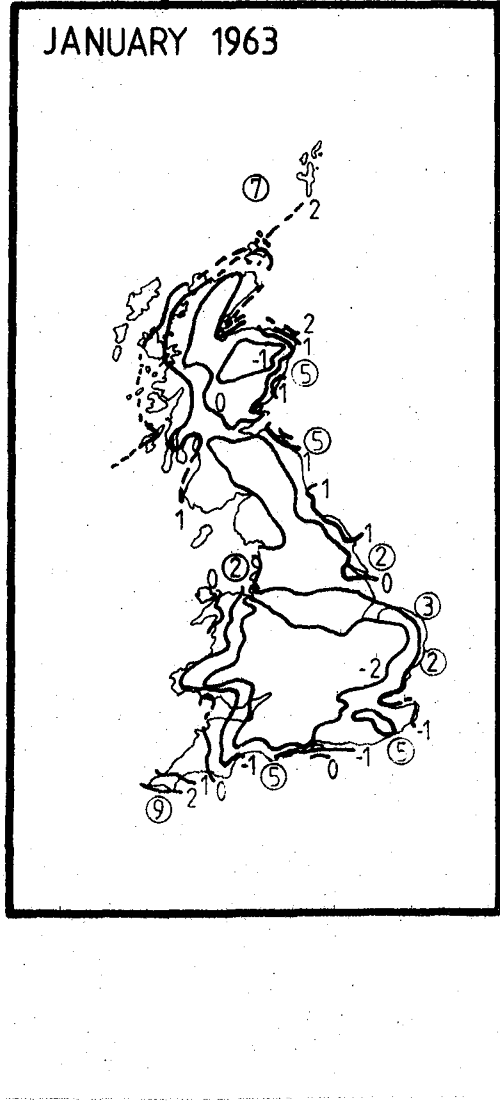
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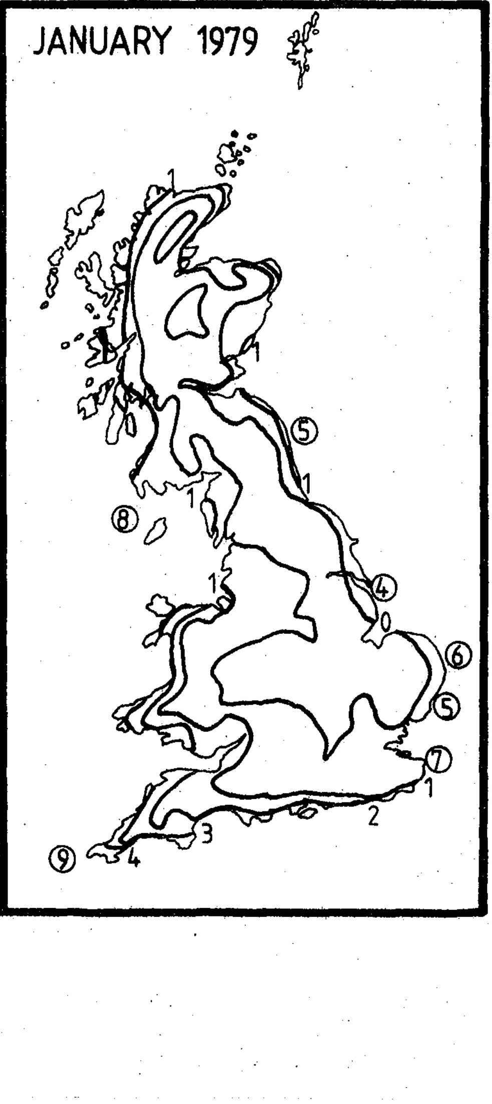
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and highest mean daily minima occur mainly on the south and west coasts. In addition, if persistent onshore winds occur at this time of year the North Sea can have a marked cooling effect upon temperatures on the east coast. For example, Tout (1976) cites the example of 4th April, 1974 when there was a temperature gradient of 16°C from a maximum of 5°C at Tynemouth (where the cooling effect of the North Sea was evident) to one of 21°C at Blackpool.

In October also, the sea has a great influence on the temperatures encountered in different areas. On the east coast the cooling influence of the North Sea is particularly marked and the isotherms of mean daily maximum temperature dip steeply southwards (Fig. 2).

Wind speed

Wind speed, much more than temperature, is affected by local topography. Most coastal weather stations are on promontories and measure wind speed at a height of 30 feet above ground level. Consequently the figures available from these stations do not usually refer to the wind speed that shorebirds experience while foraging and roosting. In view of this limitation in the data, it is possible to make only very broad comparisons of wind speed on British coasts. However the west coast is much windier than the east coast. Throughout the year, winds of force

5+, and gales (force 8+) are both much more frequent in the West (and North) than in the East (and South) of Britain, (Shellard, 1976 ; H.M.S.O., 1975; Fig. 4). **However** in the severe winters of 1962-63 and 1978-79 (Fig.5) no such clear pattern is apparent. On both east and west coasts highest average wind speed usually occurs in one of the months November to March, most commonly in March. However gales are much more frequent in January (Shellard, 1976).

Wind chill

Moving north from the Wash along the east coast of England and west to Morecambe Bay, mean and average daily minimum temperatures in mid-winter, increase. However wind speeds also increase. Thus from these figures alone it is not possible to determine precisely the relative energy requirements for maintenance of body temperatures of shorebirds in each area. To determine this, comparison of the degrees of wind chill is required. However, calculation of this parameter suffers from the same limitation as do the wind speed data i.e. they refer to wind chill at 30 feet above ground level at the site of the weather station. Consequently care is needed in interpretation of published wind chill data.

Howe (1962) computed mean wind chill using the formula developed by Siple and Passel (1945), namely $H = (\sqrt{100\,V} + 10.45 - V)(33 - t)$

where/

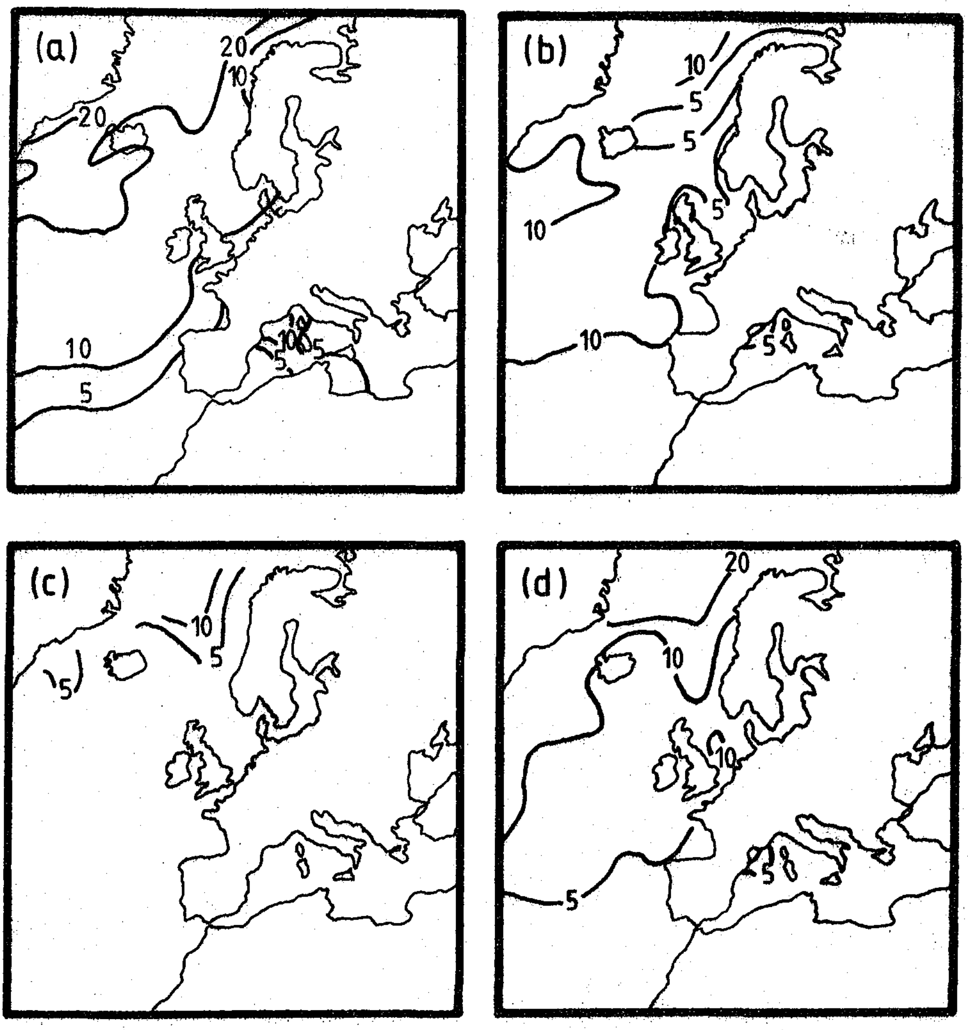


Fig. 4. Percentage frequency of wind speed of Beaufort force 8 or more (> 34 kt) in (a) January, (b) April, (c) July, (d) October. Figures from Met. Office 1975.

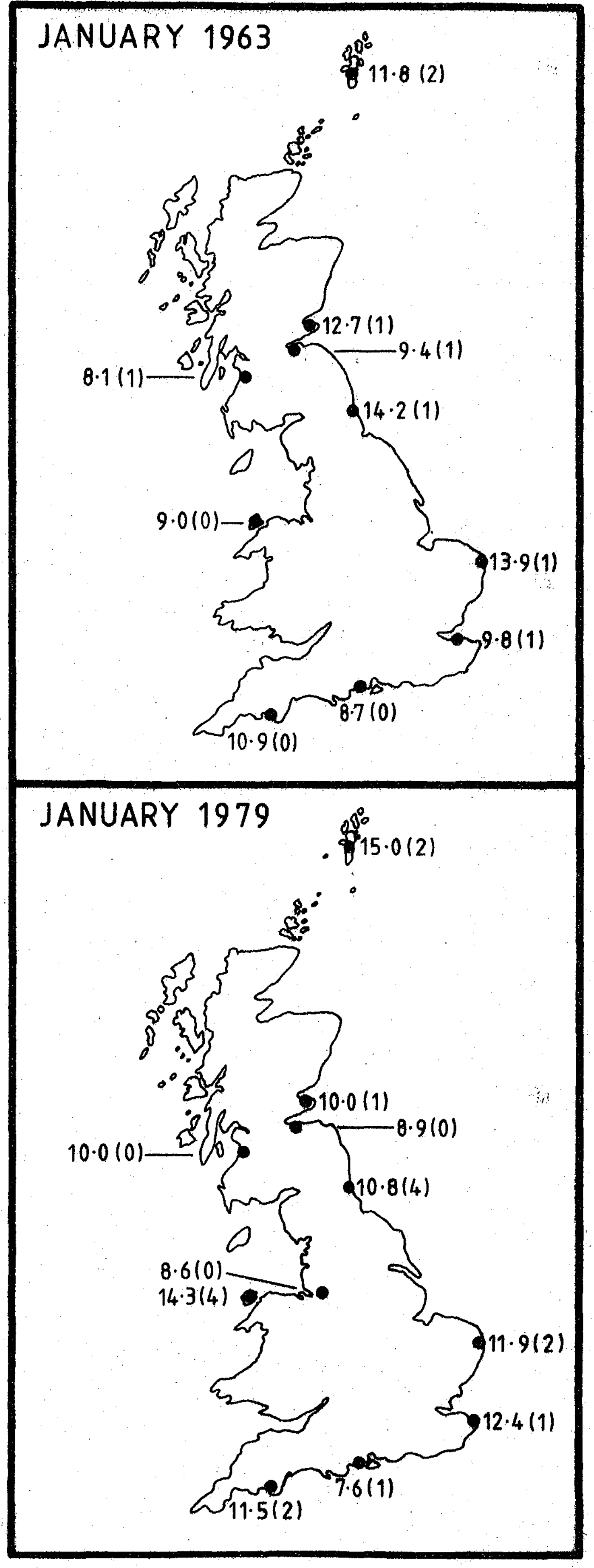


Fig. 5. Mean hourly wind speed and number of days with gales (figures in parentheses) in January 1963 and 1979. Data from Met. Office, 1963, 1979.

where H represents heat loss (wind chill) in kilogram calories per square metre of exposed surface per hour, V the wind speed in metres per second and t the air temperature in degrees Centigrade. This formula was derived from observations of the freezing rate of water, sealed in a small plastic cylinder, at various temperatures and wind speeds. Consequently the values given are of limited relevance to birds which possess insulation in the form of a layer of feathers (although these may be flattened by strong winds). However, the formula derived by Siple and Passel is very similar to that used by Dugan et. al. (In press),

namely $W = TV^{\frac{1}{2}}$

where T is the temperature deficit (of the mean daily temperature below 10°C) and V is the mean daily windspeed (Knots). This formula isbased on the finding of Gessaman (1973) that oxygen consumption of a Snowy Owl Nyctea scandia increased with the square root of wind speed at constant temperature. Thus the findings of Siple and Passel for water in plastic cylinders are not greatly dissimilar from those for living birds. Furthermore, it is the relative severity of wind chill in different areas, rather than the absolute values, which is of most importance to the present study. The data given by Howe (1962) allow such comparisons of wind chill in different estuaries to be made.

The iso-cooling lines drawn by Howe (Fig. 6) indicate that among the areas under consideration that where/

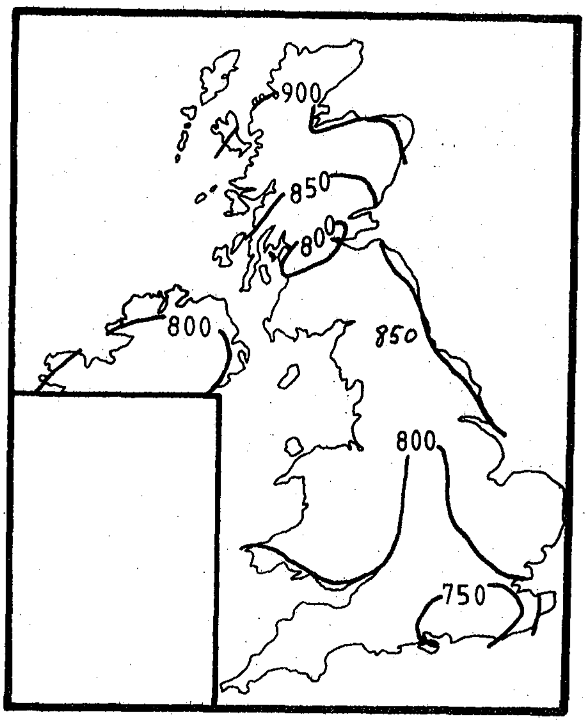


Fig. 6. Mean windchill, January 1956-61. Iso-cooling lines in Kg cals/M^2 Hr. (From Howe, 1962).

where average rates of heat loss in mid-winter are greatest is the north-east of England. Cooling rates for the Humber, Wash, Essex and the west coast of England all fall within 800-850 KG cals/M^2Hr. Thus although on average it is warmer on the Tees and Lindisfarne in mid-winter than on the Wash, wind chill is usually greater. Consequently, even when the errors involved in deducing wind speeds relevant to shorebirds are considered, the possibility exists that northward movements from the Wash in November do not take birds to areas where energy requirements are less in mid-winter. However, the data for 1962-63 suggest that in at least one severe winter the average pattern may not be observed. In January 1963 wind chill was less on the north-east coast of England than in East Anglia and Essex (Fig. 7a). This however was a consequence of the very low temperatures in the south of England in this month (Fig. 3) rather than because of higher wind speeds there (Fig. 5). In January 1979 the distribution of wind chill within Britain (Fig. 7b) was more similar to the average calculated by Howe (1962) than it was in 1963, However, wind chill experienced in the area around the Wash was slightly higher than in areas further north on the east coast. Thus, these data suggest that wind chill experienced by shorebirds in severe winters may be more intense in the area surrounding the Wash than further north on the east coast. However, much more precise data on wind speed from/

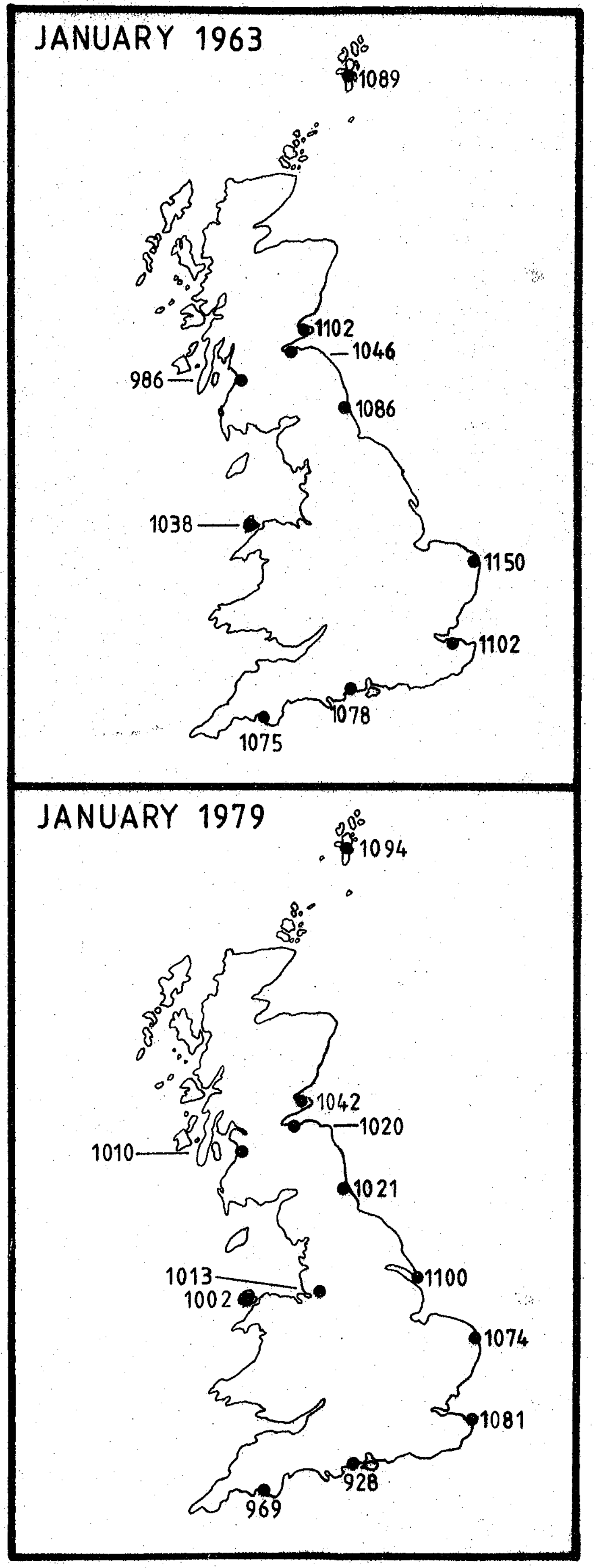


Fig. 7. Wind chill (in KG cals/M^2Hr) for January (a) 1963 (b) 1979. Values were calculated using the formula of Siple and Passel (1945). Data from Met. Office 1963, 1979.

from the feeding areas used by the birds, rather than from weather stations, are required to confirm the relative severity of wind chill experienced by shorebirds in different estuaries.

PREY ABUNDANCE

Introduction

In order to examine profitably the data available on invertebrate prey species as part of the present investigation of factors affecting shorebird movements, it is necessary to recognise two distinct groups of questions:-

(1) What determines the number of shorebirds using different estuaries? e.g. Why do more birds use the Wash than the Severn each year?

(2) Why is there a seasonal pattern in use of particular estuaries by shorebirds? Why does the pattern differ between estuaries? Why do birds move from one estuary to another?

Prater (In press) has used data from the Birds of Estuaries Enquiry to show a positive correlation between numbers of birds and estuary size, among estuaries on the east coast of England. Perhaps this is not surprising. However, this finding does not hold for the large estuaries of the west coast of England, where peak numbers of Knot, Grey Plover and Bar-tailed Godwit are not related to estuary size (Table 1). Goss-Custard/

Table 1. Estuary size and numbers of shorebirds on the west coast of England.

Estuary	Total area[1] (hectares)	Average annual peak count		
		Knot	B-t Godwit	Grey Plover
Morecambe Bay	28,967	80292 ±1485	8432 ±463	230 ±48
Ribble	7,358	75279 ±6439	7271 ±858	1369 ±262
Dee	9,555	36416 ±2669	5972 ±542	571 ±103
Severn	19,700	6668 ±2025	194 ±31	520 ±135

Note: 1 Area on spring tides.

Custard et. al. (1977**b**) have used data from the Essex estuaries to show that densities of Curlew, Redshank, Oystercatcher and Dunlin are positively correlated with prey density in these sites. However, they were unable to correlate densities of Knot with that of any of its main prey species in these estuaries. Also they did not attempt to investigate the relationship between Grey Plover and Bar-tailed Godwit and their prey because of the range of prey species taken by both birds. Thus, although some relationships are suggested by these analyses, they hold true only for some areas and for some species. Much further study is required of the mechanisms underlying the correlations obtained and the reasons for the absence of any clear relationship for some species and some areas. However, at present, sufficiently detailed invertebrate information does not exist for most British estuaries for such analysis to be carried out. Furthermore, detailed understanding of the relationships between numbers of each shorebird species and density and availability of different prey species is required before a clear understanding of the behavioural mechanisms underlying the correlations observed can be achieved. Detailed discussion of factors determining peak numbers of shorebirds on estuaries must await such information.

In the present study I have been concerned primarily with the second set of questions i.e. why do movements occur/

occur at the times and in the directions they do? The seasonal pattern of use of estuaries and movements between these by the shorebirds described in Chapter 1 could result from seasonal changes in prey abundance and differences between estuaries in the timing of these. If invertebrate prey species differ between estuaries in the timing of their reproduction, settlement and/or growth, differences in time of peak prey abundance between these estuaries could be produced. Since it appears possible that the most abundant estuarine invertebrates may be reproductively isolated from one estuary to another (Evans, 1979), differences in life cycles might be expected.

Timing of settlement - peak density

In any analysis of seasonal variation in prey abundance it is not the abundance of all size classes i.e. total abundance, but that of the size classes composing the preferred prey of each shorebird species that must be considered. Furthermore, each shorebird species does not take the same invertebrate prey species on every estuary. On many estuaries e.g. the Wash, Ribble and Humber, Knot feed mainly on *Macoma balthica* but in others, large quantities of *Mytilus edulis* L. are taken in addition to *Macoma* e.g. Morecambe Bay (Prater, 1972), or instead of *Macoma* e.g. Tees (Pers. Obs.). However because *Mytilus* is generally found only on the rocky periphery of estuaries it is not normally included in most estuarine sampling programmes. Consequently/

Consequently it is rarely possible, from the results of estuarine surveys, to establish accurately the prey resources of Knot on each estuary.

The main prey of Bar-tailed Godwit also varies between estuaries. On the Ribble it is *Macoma* (Greenhalgh, 1975), on the Tees *Nereis diversicolor* (Evans et. al. 1979), and on Lindisfarne *Arenicola marina* (L.) (Smith, 1975). For Grey Plover the main prey species on the Tees is *Nereis* (see Chapter 3) but on Lindisfarne *Arenicola* and *Scoloplos armiger* and and *Notomastus latericeus* are taken (Pienkowski, 1980). Different prey species differ in their profitability i.e. the net amount of energy obtained per item as a proportion of the total amount of energy obtained. This varies not only between prey species but also between size classes. Some species of prey may be numerous and easily found but be of low energy content e.g. *Scoloplos*. Other may occur at lower densities but provide a larger energy intake per item e.g. *Arenicola* and *Nereis*. However, if the appropriate density data for the size classes taken by each shorebird were available it would be possible to equate the profitability of different densities of different prey species.

Thus to compare seasonal change in the value to shorebirds of the prey populations of different estuaries/

estuaries, data on seasonal change in abundance of different size classes of each prey species taken by the shorebirds are required. (In addition, data on prey availability are required. These are considered in a later section.) However, few data of this type are available. One of the original aims of the present study was to examine the results of recent extensive and intensive surveys of the intertidal invertebrate macrofauna in many British estuaries. By analysing material from these it was hoped to be able to investigate the role of prey abundance and the timing of growth and reproduction as factors determining the timing and direction of shorebird movements. However, during the course of this review, it became apparent that, because of the varied aims and methods of each survey, the form of the data obtained varied considerably. Because of a lack of detail or standardisation in the data, very little meaningful analysis was possible, and consequently the following review is of a very superficial nature.

Several of the studies, those of Morecambe Bay, (Anderson, 1972); the Essex estuaries (Kay and Knights, 1975); the Dee (Gillham, 1978); Medway (Wharfe, 1977) and Severn (Boyden and Little, 1973 and Little and Boyden, 1976) have been concerned primarily with distribution of the macroinvertebrates in relation to biological, chemical and physical parameters of the sediments. These surveys have involved extensive sampling/

sampling to allow the production of faunal distribution maps for each area. However, in all these studies, not only was each area sampled on only a few occasions (and the sampling of different sites often carried out in different months), but in the analyses of the material, little or no attention was paid to the density of different size classes. Thus few data on seasonal change in density are available from any large estuaries and in most cases these data refer to density of all size classes combined.

Many more intensive studies have been carried out, in which density of a number of invertebrate species has been monitored regularly in a very few specific sites on an estuary for twelve months or more. However, in some of these studies, as in the extensive surveys little attention has been paid by workers to the different size classes of prey e.g. Martin (1972) in Langstone Harbour. Consequently any changes in density of the larger size classes of the macrofauna - those of most importance to the shorebird species under consideration in this thesis - are obscured by annual spatfall and mortality. In others, the subdivisions of size and age classes that have been effected are not sufficiently detailed for the purposes of the present study e.g. Chambers and Milne (1975b); Elliott (1979); Evans et. al. (1979). In only a few studies are detailed size data presented e.g. those of Chambers and Milne (1975a); Ratcliffe (1979). Using these, and the data from material on *Macoma* and *Nereis* I collected/

collected during the present study, it has been possible to obtain an indication of the extent of year-to-year, and inter-estuarine variation in the date of peak densities of prey, both of total numbers and of large size classes only. Methods of sampling and detailed invertebrate data from the Tees are given in Chapter 3 and Appendix 8.

Within each species, although there are marked differences in maximum total densities of Nereis, Macoma and Hydrobia ulvae (Pennant) between estuaries, seasonal changes in density follow a very similar pattern in different areas. Peak densities of all three species occur in late summer or autumn, normally July or August for Nereis and Macoma, and August or September for Hydrobia (Figs. 8-10). Following the peak, numbers decrease steeply through winter until spring when lowest densities occur. Inspection of data for Nereis from the Severn (Mettam, 1979) and Tees (present study) (Fig. 11) and for Macoma from the Humber (Ratcliffe, 1979 and present study) and Morecambe Bay (present study) (Fig. 12) indicates that the major fluctuations in density are due to spatfall and subsequent mortality. Percentage changes in density of large Nereis are as great as among small animals, but absolute densities are consistently lower. On the Tees, numbers declined from June to March, the greater part of this decline occurring after November (Fig. 8). On the Severn numbers of large Nereis also decreased after July, but after fluctuating in mid-winter (possibly/

Fig. 8. Seasonal change in density of Nereis diversicolor on selected British estuaries. Density is expressed as percentage of maximum recorded during the year for which data are given. Where two values of 100% are given the larger, depicted by closed symbols joined by solid lines, refers to total density and the smaller, depicted by open symbols joined by dotted lines, refers to density of animals 4 cm body length.

Ythan; Chambers and Milne, 1975a.		100%=950/m^2 100%=216/m^2
Tees; Herdson Pers. Comm.		100%=924/m^2
Tees (sub-areas 22 & 23); Present study.		100%=1460/m^2 100%= 556/m^2
Humber (Skeffling); Ratcliffe, 1979.		100%=2890/m^2
Chalkwell, Essex; Dales, 1951.		100%=280/m^2
Medway (Colemouth creek); Wharfe, 1977.		100%=10,000/m^2
Langstone Harbour (Portsea A); Martin, 1972.		100%=200/m^2
Severn (Caldicot); Mettam, 1979.		100%=2090/m^2 100%=505/m^2
Dee (Gayton 29); Gillham, 1978.	1973	100%=340/m^2
	1975-76	100%=880/m^2
	1976-77	100%=520/m^2

Fig. 8 a

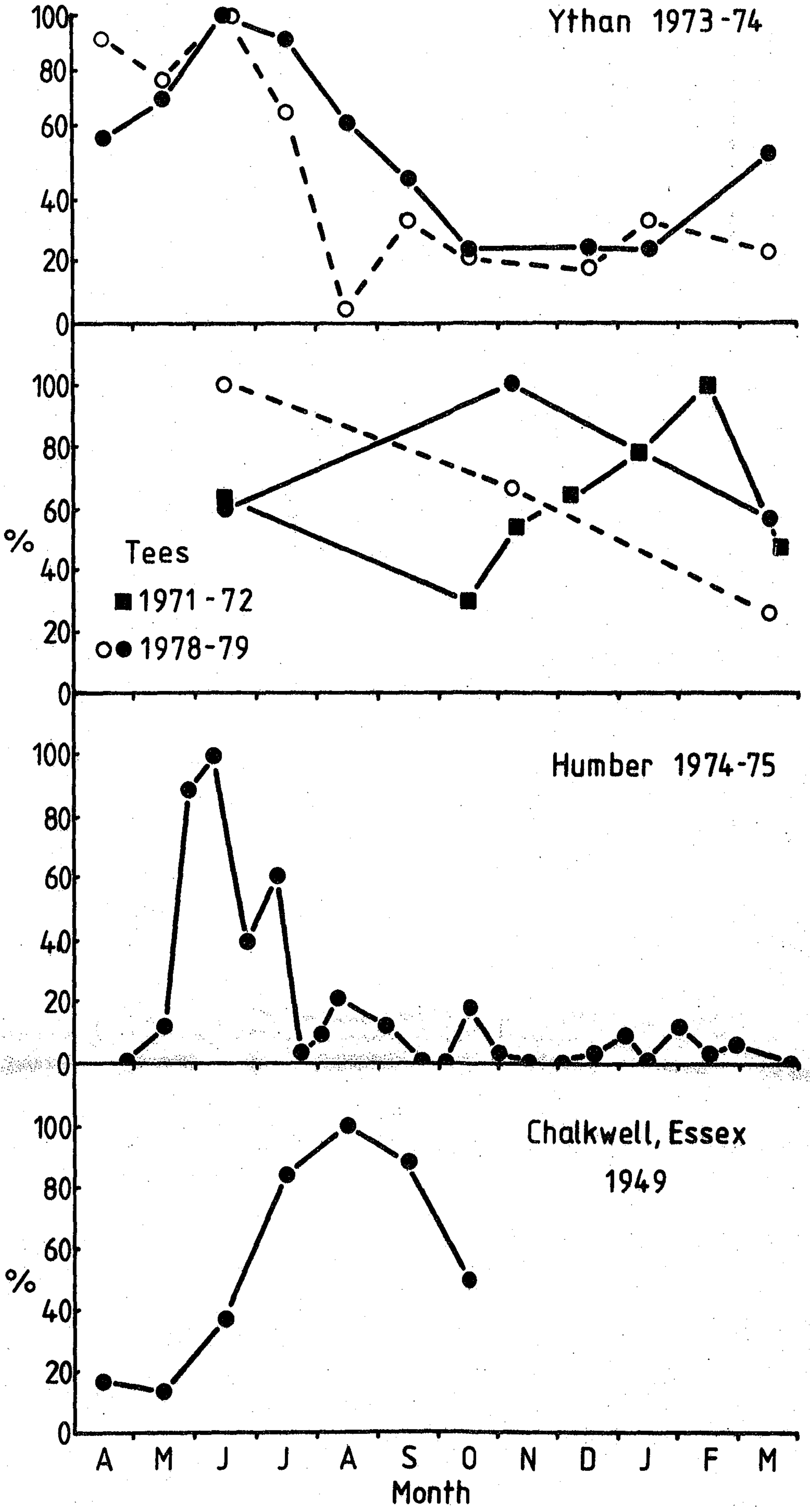

Ythan 1973-74
100
80
60
40
20
0
%
Tees
■ 1971-72
○● 1978-79
Humber 1974-75
Chalkwell, Essex
1949
A
M
J
J
A
S
O
N
D
J
F
M
Month

Fig. 8b

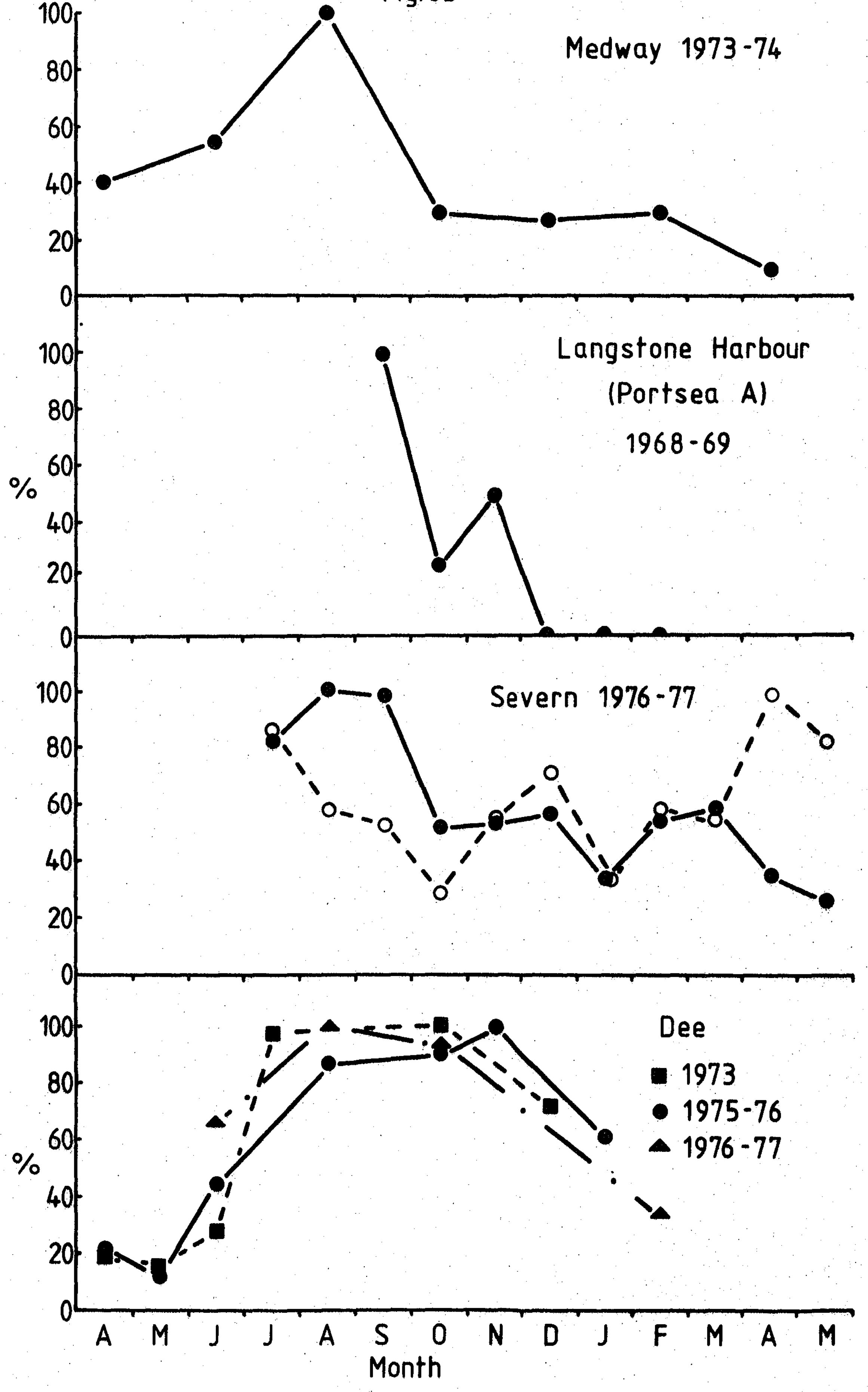

Medway 1973-74
Langstone Harbour
(Portsea A)
1968-69
Severn 1976-77
Dee
■ 1973
● 1975-76
▲ 1976-77
%
100
80
60
40
20
0
A
M
J
J
A
S
O
N
D
J
F
M
A
M
Month

Fig. 9. Seasonal change in density of *Macoma balthica* on selected British estuaries. Density is expressed as percentage of maximum recorded during the year for which data are given. Where two values of 100% are given the larger, depicted by closed symbols joined by solid lines, refers to total density and the smaller, depicted by open symbols joined by dotted lines, refers to density of animals in the 9-13 mm shell length size class.

Ythan; Chambers and Milne, 1975b. 100%=6028/m^2

Forth (site B.3); Elliott, 1979. 100%=4100/m^2

Humber (Skeffling); Ratcliffe, 1979.

1974-75 100%=23679/m^2
100%=1403/m^2

1975-76 100%=15786/m^2
100%=1491/m^2

Present study 1978-79 100%=3990/m^2
100%=650/m^2

Dee (Gayton, 22); Gillham, 1978.

1973 100%=8700/m^2

1975-76 100%=9200/m^2

1976-77 100%=12600/m^3

Morecambe Bay (Hest Bank);
Present study 100%=5300/m^2
100%=271/m^2

Fig. 9a

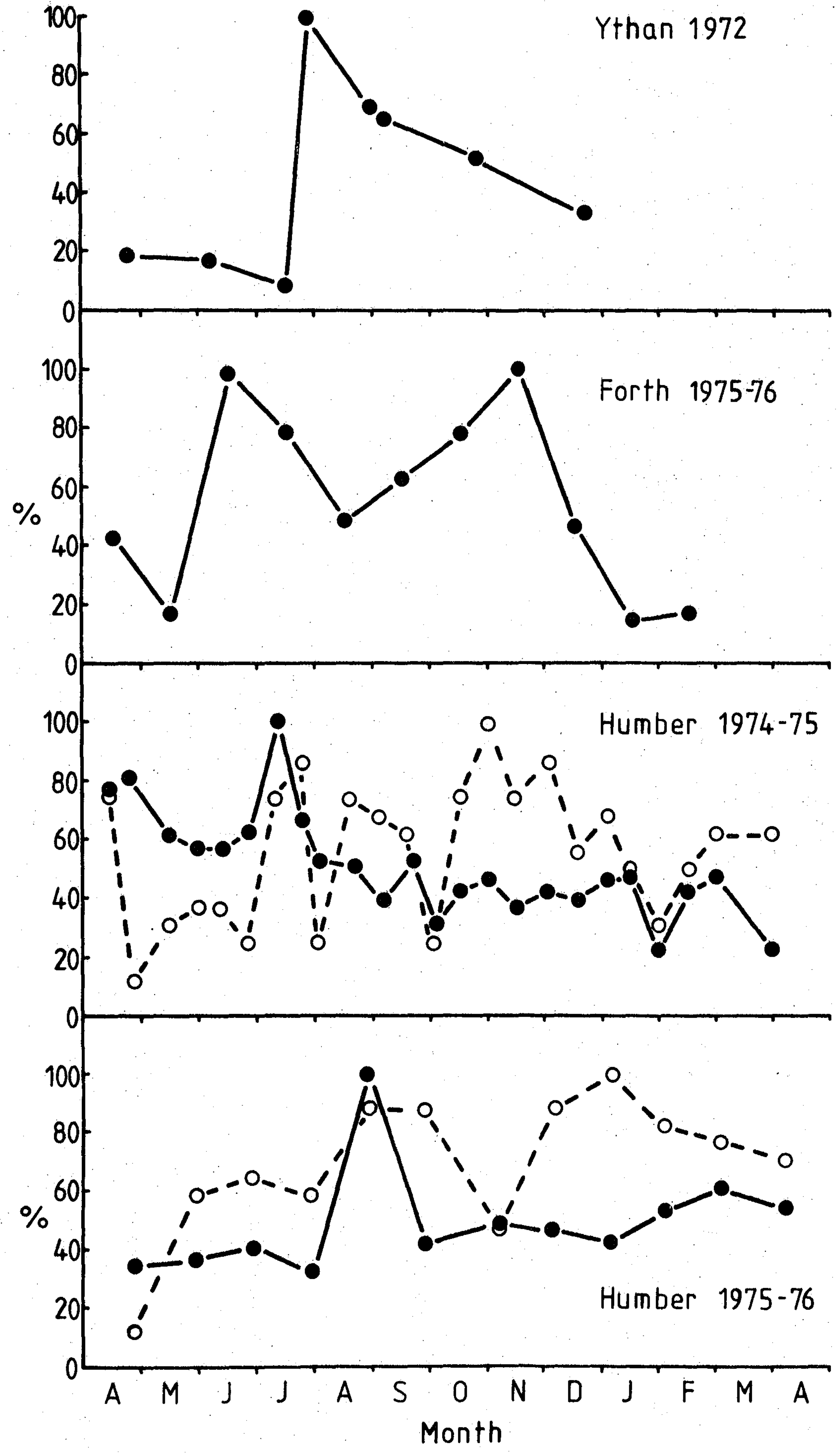

Ythan 1972
Forth 1975-76
Humber 1974-75
Humber 1975-76
%
%
0
20
40
60
80
100
A
M
J
J
A
S
O
N
D
J
F
M
A
Month

Fig. 9b

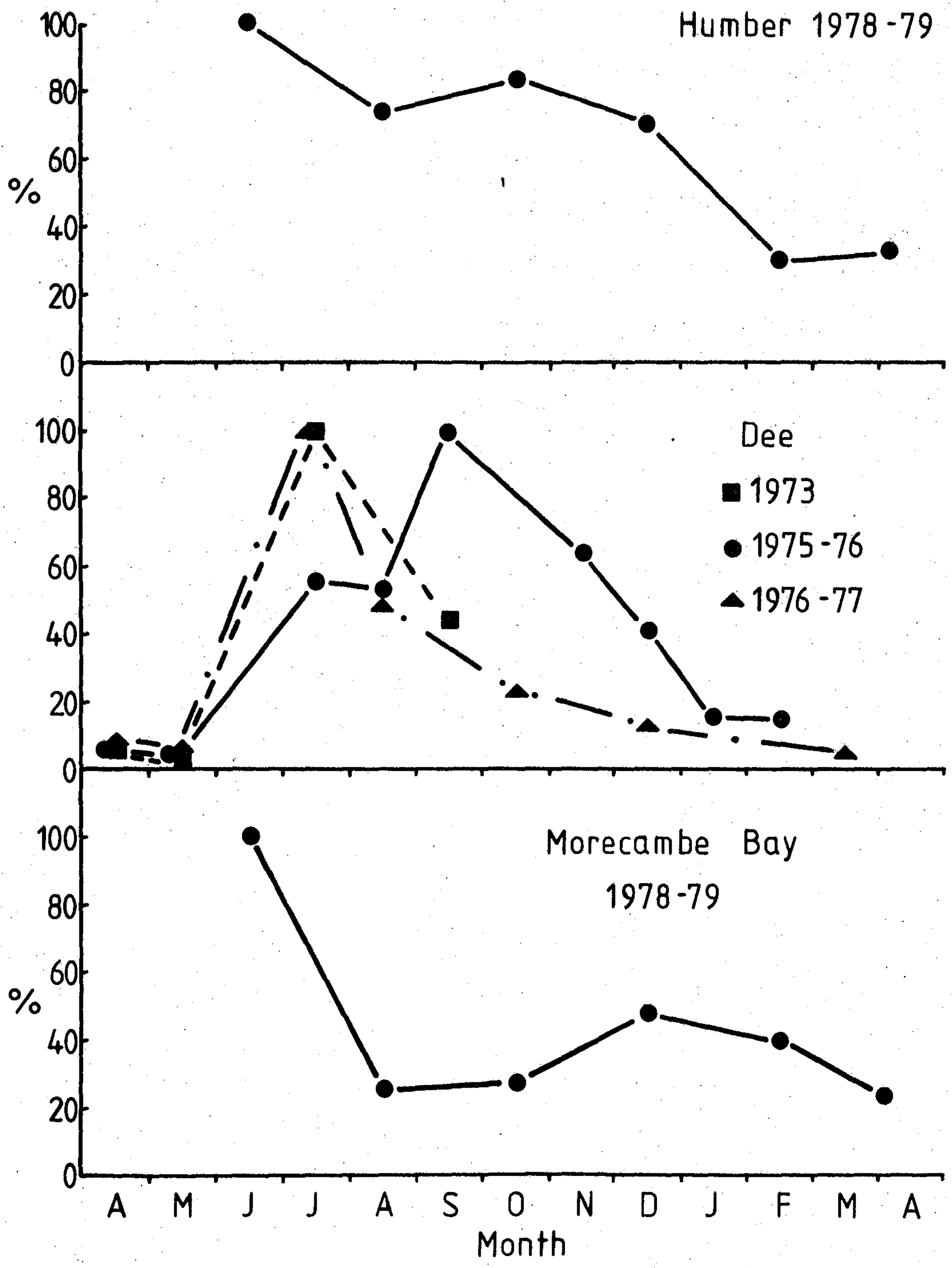

Humber 1978-79
%
100
80
60
40
20
0
Dee
■ 1973
● 1975-76
▲ 1976-77
100
80
60
40
20
0
Morecambe Bay
1978-79
%
100
80
60
40
20
0
A
M
J
J
A
S
O
N
D
J
F
M
A
Month

Fig. 10. Seasonal change in density of Hydrobia ulvae on selected British estuaries. Density is expressed as percentage of maximum recorded during the year for which data are given.

Forth (mean of all sites); Elliott, 1979.		$100\% = 37,300/m^2$
Tees; Herdson Pers. Comm.		$100\% = 33450/m^2$
Tees (sub-area 8); Present study.		$100\% = 9745/m^2$
Medway (Hoo); Wharfe, 1977.		$100\% = 92166/m^2$
Langstone Harbour (Portsea A); Martin, 1972.		$100\% = 3700/m^2$
Dee (Gayton 22); Gillham, 1978.	1973	$100\% = 1505/m^2$
	1975-76	$100\% = 3956/m^2$
	1976-77	$100\% = 5590/m^2$

Fig. 10a

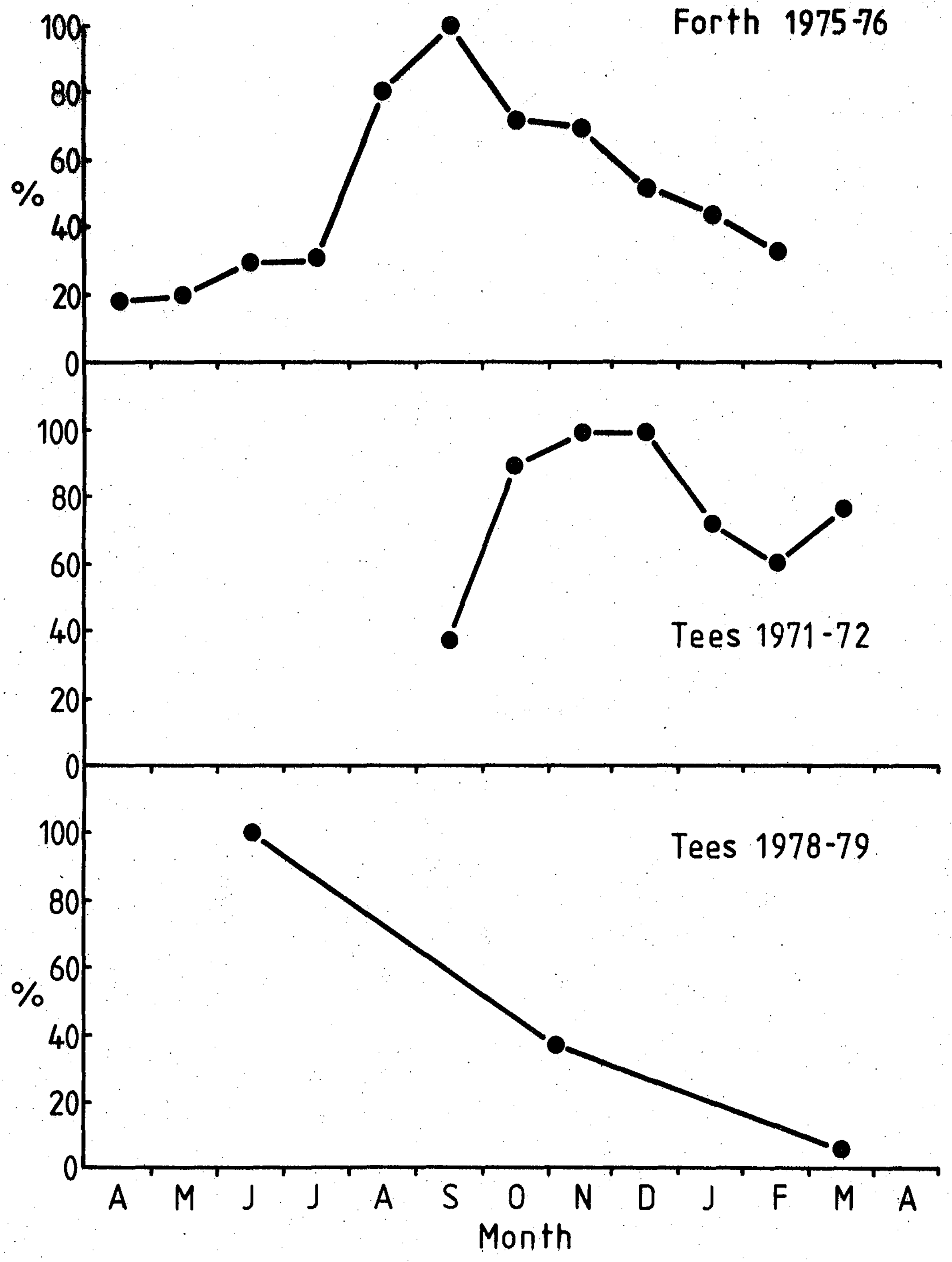
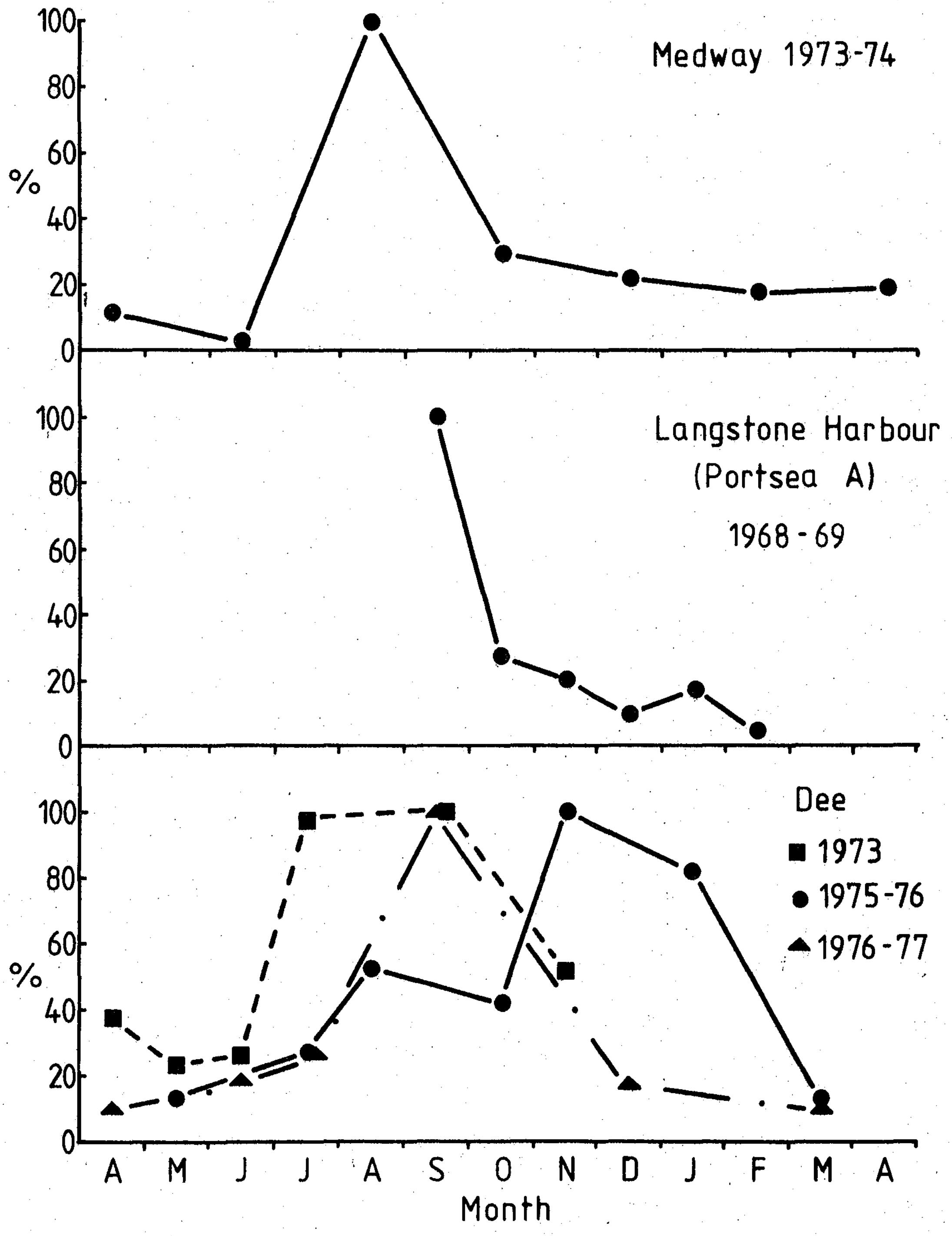

Forth 1975-76
Tees 1971-72
Tees 1978-79
%
100
80
60
40
20
0
A
M
J
J
A
S
O
N
D
J
F
M
A
Month

Fig. 10b


Medway 1973-74
Langstone Harbour
(Portsea A)
1968 - 69
Dee
■ 1973
● 1975-76
▲ 1976-77
%
100
80
60
40
20
0
A
M
J
J
A
S
O
N
D
J
F
M
A
Month

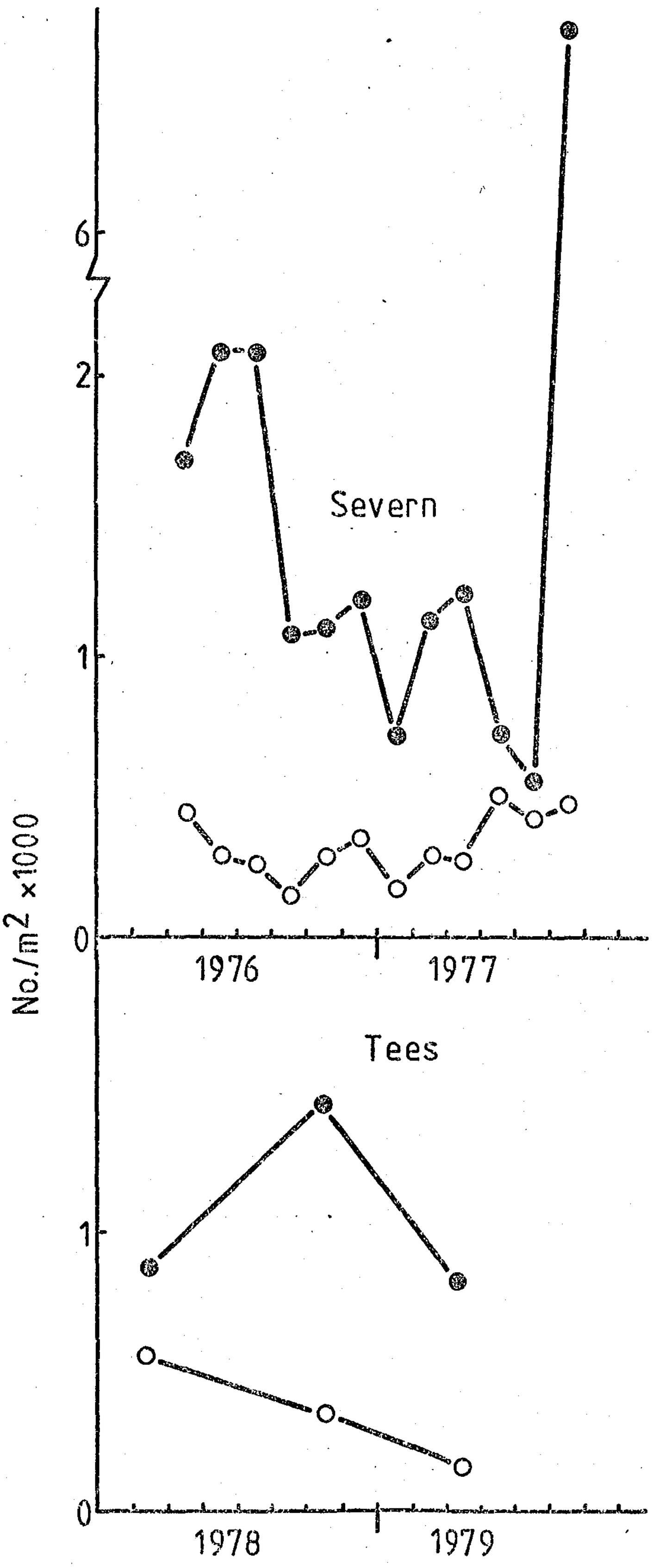


Fig. 11. Seasonal change in density of Nereis diversicolor on the Tees (present study) and Severn, Caldicot (Mettam, 1979). ● Total density; ○ density of Nereis of body length > 4 cm.

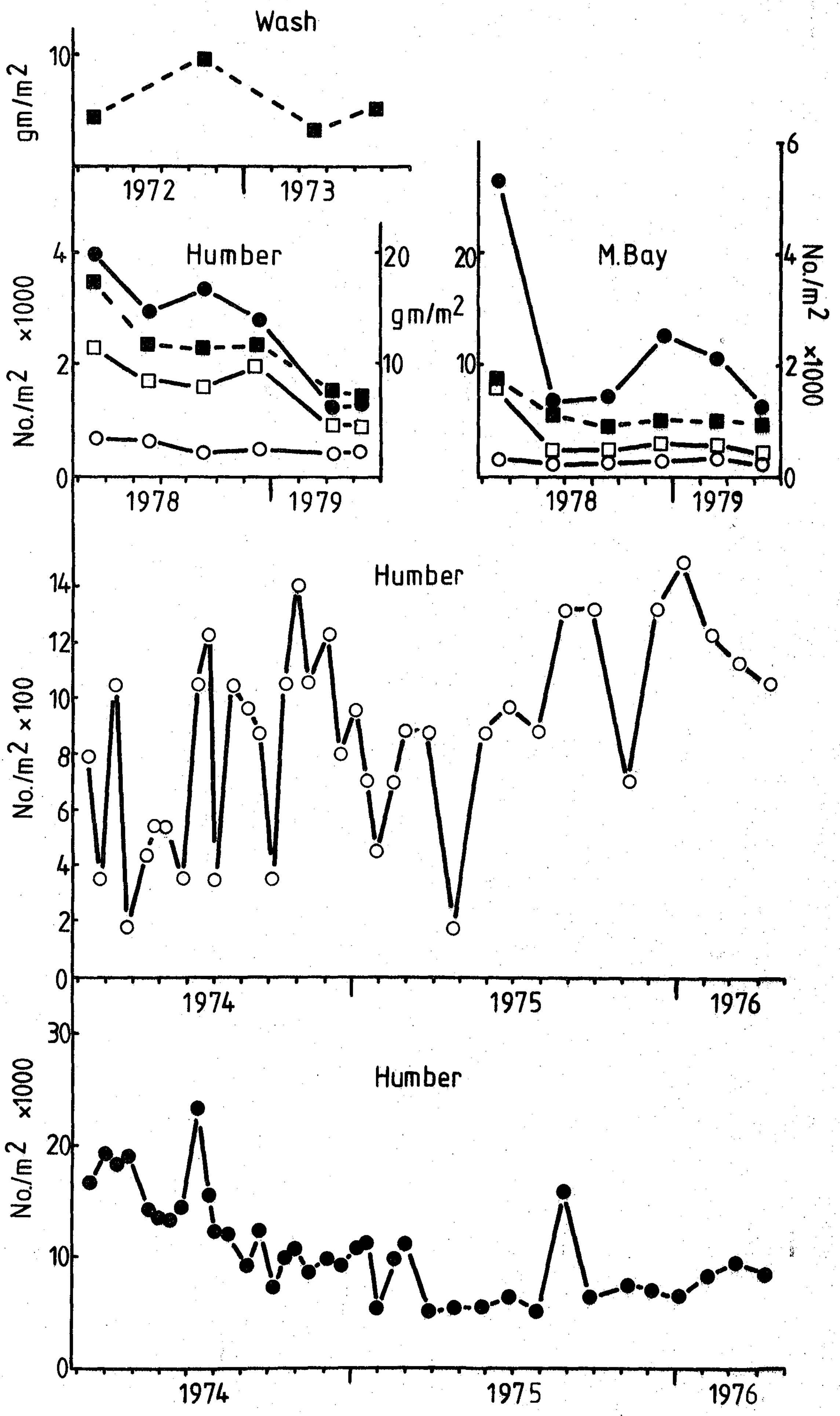
Fig. 12. Seasonal change in density of *Macoma balthica* on the Humber estuary, Skeffling (Ratcliffe, 1979 and present study), Morecambe Bay, Hest Bank (present study) and the Wash (Goss-Custard et. al., 1977a).

● Total density (No./m^2).

○ Density of 9-13 mm shell length size class (No./m^2).

□ Density of 6-15 mm shell length size class (No./m^2).

■ Density of 6-15 mm shell length size class (biomass (g)/m^2).


Wash
gm/m2
10
1972
1973
Humber
No./m2 ×1000
4
2
0
20
10
gm/m2
1978
1979
M.Bay
20
10
6
4
2
0
No./m2 ×1000
1978
1979
Humber
No./m2 × 100
14
12
10
8
6
4
2
0
1974
1975
1976
Humber
No./m2 ×1000
30
20
10
0
1974
1975
1976

(possibly through immigration and emigration) rose again after March as a result of growth of smaller animals (Mettam, 1979).

Percentage changes in density of large *Macoma* (Fig. 9) are much less marked than in *Nereis*. This is a consequence of the long (6-7 year) life cycle of *Macoma* compared to the short (2-3 year) life cycle of *Nereis*. The short term fluctuations observed by Ratcliffe (1979) of animals in the 9-13 mm shell length category are almost certainly due to sampling error.

Where data are available for one estuary in more than one year these indicate little variation between years in timing of settlement of first year animals e.g. *Nereis* (Dee) (Fig. 8); *Macoma* (Humber and Dee) (Fig. 9). However in 1975-76 on the Dee the time of peak density was noticeably later in all three species, *Nereis*, *Macoma* and *Hydrobia* (Figs. 8-10). This suggests that spawning was delayed in all three species in this year as a result of unfavourable conditions, perhaps low temperature early in the season. On the Tees estuary, the time of peak density recorded during the present study was much earlier than that recorded by Herdson (Pers. Comm.). However Herdson determined density by sieving substrate cores (see Evans et. al. 1979) and it is likely that many of the smaller size classes ca 2 cm were broken up, forced through/

through the sieve and lost. It seems possible that the later peak in density observed by Herdson is a consequence of some overwinter growth of these smaller individuals, resulting in their retention in the sieve several months after settlement.

Thus the data available do not suggest major variation between years in the timings of settlement and peak density. Rather, the time of peak density is reasonably predictable from year to year. In contrast however, the size of peak density is not predictable in the same way. In some years spatfall can be very poor, e.g. in 1972 settlement of both *Nereis* and *Macoma* on the Dee was very low (Figs. 13,14). However, the effect of this poor settlement on the size of the population of size classes taken by shorebirds is likely to be complex. For the shorebird species under consideration in the present study the small first year animals which settle are unimportant in the diet. Only after growth has occurred do they enter the size classes preferred by the shorebirds. Consequently only when growth to the size taken by shorebirds has occurred will a bad settlement be reflected in the density of size classes taken by Knot, Bar-tailed Godwit and Grey Plover. Thus the effect of poor settlement will become apparent in the population of large *Nereis* only in the second winter after settlement. In *Macoma* the same effect will not be apparent until the third or fourth winter after settlement.

Unfortunately/

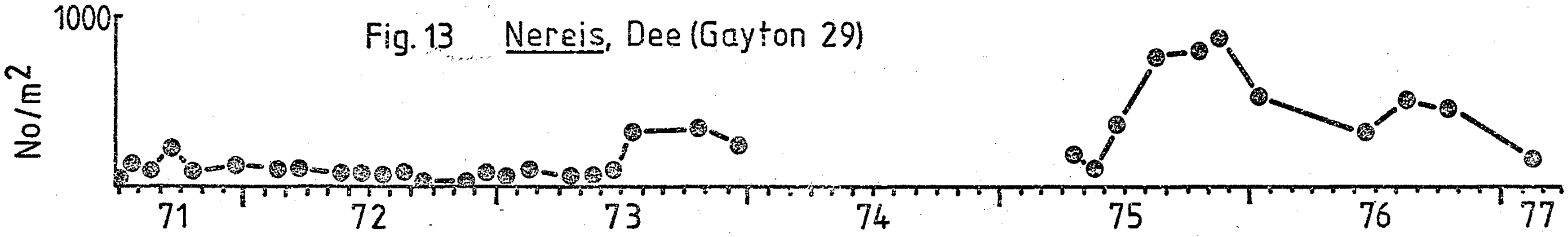


Fig. 13. Seasonal change in density of Nereis on the Dee estuary 1971-77. (From Gillham, 1978).

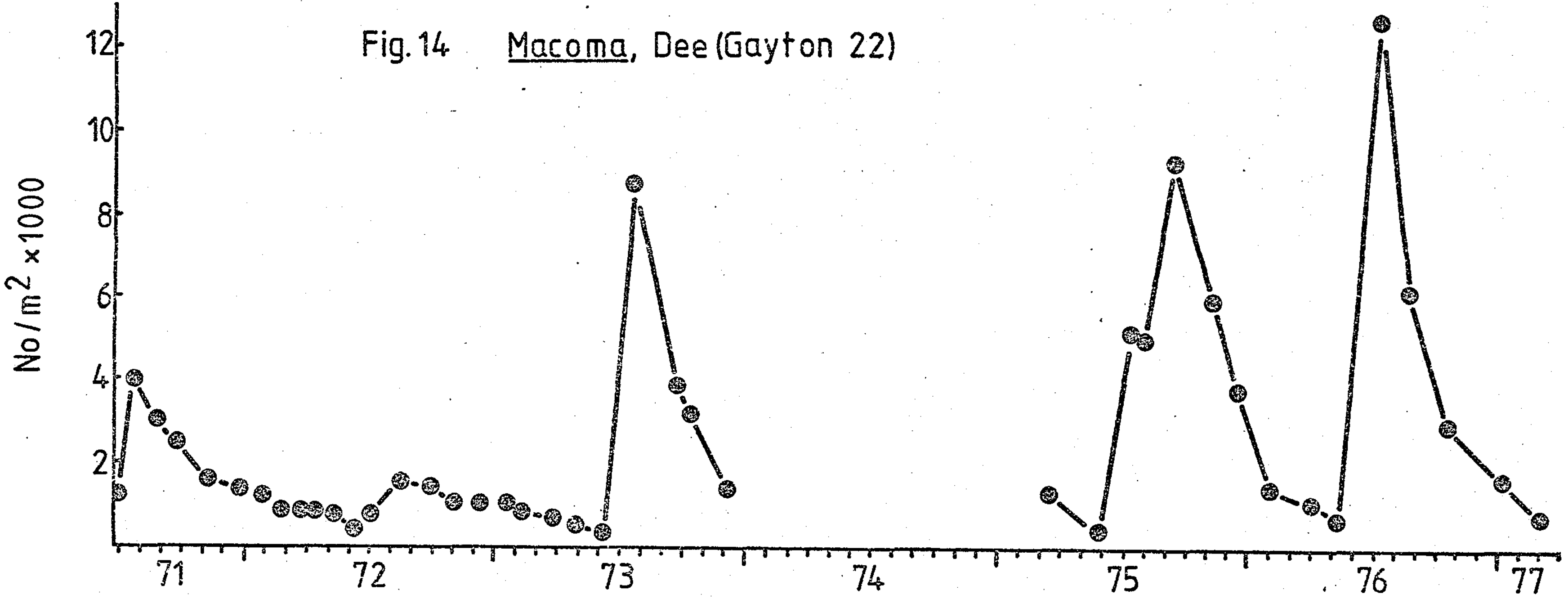


Fig. 14. Seasonal change in density of Macoma on the Dee estuary 1971-77. (From Gillham, 1978).

Unfortunately Gillham, on the Dee estuary, did not sample the macrofauna in 1974 and it is therefore not possible to compare densities of Nereis in that year with those in 1972, before the poor settlement. However, assuming that the lowest densities immediately prior to spatfall are the best indication of the size of the population of large Macoma (i.e. because the proportion of spat in the population is least at this time) the data for Macoma for 1975-76 do not indicate any marked change in the density of large animals. Although no count data are available for 1975-76, the data for autumn 1974 indicate that the average number of Knot present on the Dee in August and September was the lowest recorded there in these months during the Birds of Estuaries Enquiry. This may possibly be a consequence of the poor spatfall of Macoma in 1972. In 1969-70 the number of Knot moulting on the Ribble was lower (Chapter 1, Fig.10), and the number on the Dee higher (Chapter 1, Fig.12), than in other years. These data suggest a switch of moulting area of many individuals in one year from the Ribble to the Dee. This change of moulting area may be a response to lower prey density, possibly a consequence of poor settlement two or three years previously.

Growth rate

Nereis

Density data suggest that most invertebrate species settle at approximately the same time of year in different/

different estuaries. Thus, if differences exist in timing of peak abundance of the size classes taken by shorebirds, these must be as a result of differences in growth rate. Mettam (1979) has reviewed available information on growth rate of Nereis in different estuaries, concluding that the rates on the Ythan and Severn are very similar but much lower than that observed by Dales (1951) on the Thames. Ratcliffe (1979) reports the growth rate of Nereis on the Humber to be very similar to that observed on the Ythan, and in Denmark by Muus (1967). It is not possible at present to explain the exceptionally fast growth rate reported by Dales. However the very large size (20 cm) attained by Dales' animals at Chalkwell, compared to those reported on the Humber (6 cm), Ythan and Severn (7 cm) and Tees (12 cm), and the one-year life cycle reported by Dales, rather than a 2-3 year life cycle as reported by Mettam (1979), Evans et. al. (1979), Chambers and Milne (1975) and Ratcliffe (1979), suggest that the Thames population was exceptional in a number of ways. The data concerning seasonal changes in density of large animals on the Tees, Severn and Ythan also indicate that no major differences in growth rate exist between these areas. The times of peak and lowest abundance are very similar, i.e. early summer and winter respectively, in all three areas. Thus, at present it is possible to conclude that in most areas studied, growth rates of Nereis are very similar.

Macoma

Macoma is much longer lived than Nereis. Individuals of six years of age are common in most areas in North-West Europe (Lammens, 1967; Chambers and Milne, 1975b; Warwick and Price, 1975; Wolff and de Wolf, 1977 and Ratcliffe, 1979). Consequently the size range of Macoma taken by shorebirds spans several year classes. As a result, the density of Macoma of the size taken by the larger shorebirds is likely to fluctuate much less than the density of Nereis taken by these shorebirds which come mainly from a single year class (2+). (Many smaller Nereis are taken by Dunlin and Redshank. However these shorebirds are not considered here.) Similarly differences in growth rate between estuaries will be of less importance in determining the density of the size class preferred by shorebirds in these areas.

Growth rates of Macoma have been reviewed by a number of authors, e.g. Gilbert (1973), Ratcliffe (1979) and Elliott (1979). Data from these authors relevant to North-West Europe, and from the published work of Lammens (1967), Boyden and Little (1973), Chambers and Milne (1975b) and Warwick and Price (1975) are presented in Fig. 15. Ratcliffe (1979) considers it likely that Lammens, Boyden and Little, and Warwick and Price failed to collect animals during their first winter of life, or to recognise first winter rings and consequently that/

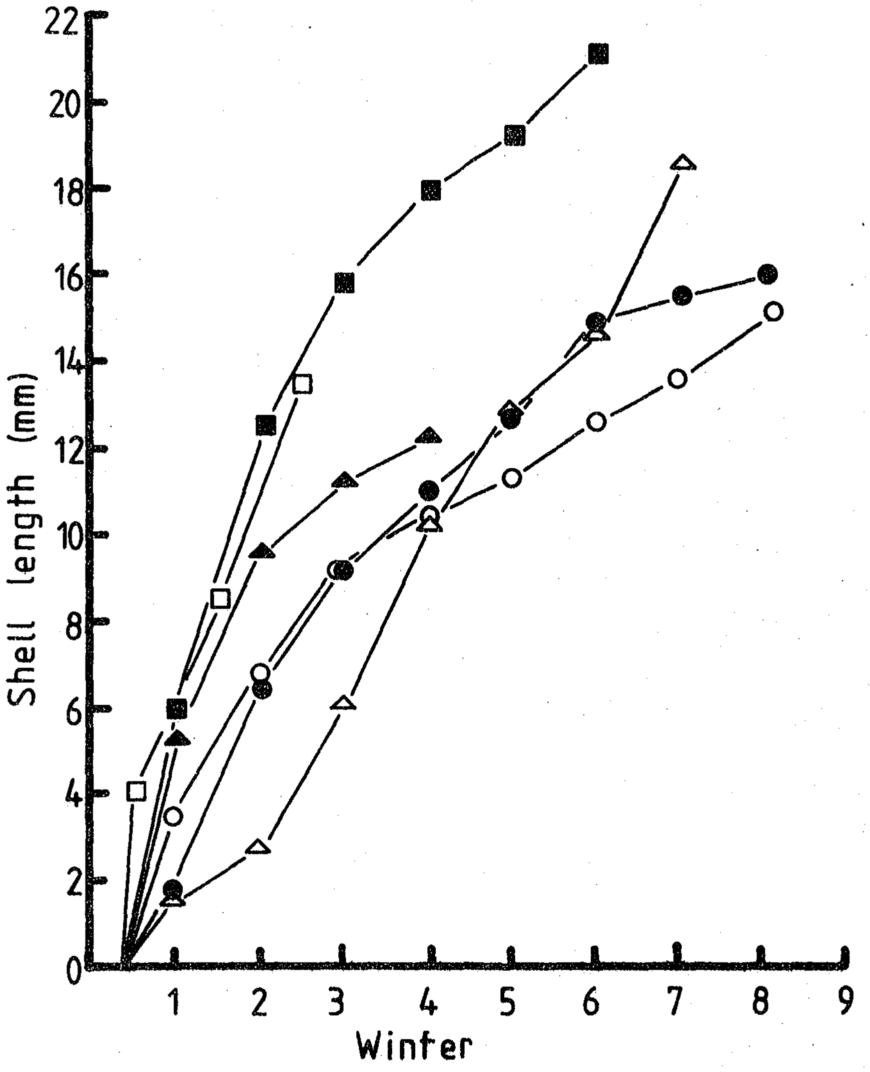


Fig. 15. A comparison of growth curves of *Macoma balthica* recorded by different authors.

■	Lammens, 1967
□	Boyden and Little, 1973
▲	Warwick and Price, 1975
△	Chambers and Milne, 1975b.
●	Ratcliffe, 1979
○	Elliott, 1979

that their growth curves appear shifted one year to the left. Even if this is true, it is clear that within Britain growth curves are very similar. What differences are apparent seem to be related to the temperatures experienced in the areas studied. The growth rates recorded by Warwick and Price, and by Boyden and Little, who worked in South-West England, were the highest. Those observed by Chambers and Milne, and Elliott who worked on the east coast of Scotland, were the lowest. The growth rate recorded by Lammens for the Waddenzee is clearly higher than that observed in Britain. Thus differences in growth rate are very similar within Britain but lower than in the Netherlands. However care must be exercised in interpreting these data, as both Green (1973) and Elliott (1979) have described differences in growth rate between different areas of the intertidal zone within one estuary. Unequivocal interpretation of growth data from different estuaries requires very precise standardisation of the environmental conditions e.g. the substrate type and tidal height of the study site.

Although differences in growth rate between estuaries are apparent, Macoma has, in most areas studied, a very short growing season (Table 2). By August growth in most areas has stopped. This suggests that, irrespective of differences in growth rates in different areas, the time of maximum weight of individual animals of a given/

Table 2. Growing season of <u>Macoma</u> <u>balthica</u> in different geographical areas.

Estuary	Authority	Growing season
Ythan	Chambers and Milne, 1975b	0+ until October 1+ March-late October 2+ March-August.
Forth	Elliott, 1979	1+ April-June or August
Humber	Ratcliffe, 1979	1+ March/April - August/September 2+ March/April - July/ August
Waddenzee	Lammens, 1967	mainly spring - slows in summer - stops in winter
	de Wilde, 1975	February/March-June/July
	Beukema, 1974	mid March-June/July
Grevelingen	Wolff and de Wolf, 1977	0+ little growth from settlement until March/April of following year 1+ max. weight in autumn > 1+ max. weight June/July

given size will be the same in each area. Available data tend to support this. For example, peak weight of animals of 15.5 mm shell length occurred on the Forth in May to July, on the Ythan in June, the Wash in August and the Humber in October (Fig. 20). The one major exception is Morecambe Bay where peak weight was recorded in December (Fig. 20). (This may be due to warmer sea temperatures on the west coast allowing a longer growing season.)

Thus, slight differences in growth rate are apparent between estuaries. Furthermore, although the data suggest that the growing season may extend to December on Morecambe Bay, in other estuaries the length of the season appears to be very similar, ending in late summer. The absence of marked variation between areas in these features of growth and the similarity in timing of settlement of first year animals in different areas, suggest that data for peak density of the size classes taken by shorebirds give a true indication of the food resources and that this relationship is not likely to vary markedly between estuaries. Indeed the data for Morecambe Bay indicate that the time of peak density is much more important than time of maximum body weight of *Macoma* in governing the period of peak biomass. Thus, the peak biomass per square metre occurred in June at the time of peak density, rather than in December when maximum weight per/

per individual was recorded (Fig. 12). In contrast, on the Wash, highest weights of individual animals were observed in June, yet peak biomass did not occur until November (Goss-Custard et. al., 1977a). This suggests that between June and November movement of <u>Macoma</u> into the study site may have occurred, to produce the increase in biomass observed over that period. (Fig. 12.)

SEASONAL CHANGE IN NUMBERS OF KNOT AND ABUNDANCE OF ITS MAIN PREY <u>Mytilus edulis</u> ON THE TEES ESTUARY

<u>Introduction</u>.

In few of the invertebrate studies reviewed in the preceding section were the populations of shorebirds feeding on a particular prey species monitored. Consequently it has not been possible to relate directly the changes in numbers of birds to changes in invertebrate abundance. However, on the Tees estuary, the main prey of Knot is <u>Mytilus edulis</u> which occurs on rocky outcrops at the mouth of the estuary. On spring tides almost all birds present on the estuary feed there. In 1978-79 I monitored seasonal changes in abundance of <u>Mytilus</u> to discover whether fluctuations in numbers of Knot on the estuary were related to these.

<u>Methods</u>

<u>Mytilus</u> were sampled on Coatham rocks, the main mussel/

mussel scar in September and December 1978 and in February 1979. On each occasion the area covered by Mytilus, density within this area and size-frequency distribution was determined. Using a 1x1 m wire quadrat, sub-divided into 100 units of 100 cm^2, the percentage coverage of the rocks by Mytilus was estimated at 20 metre intervals along three transects (Fig. 16). This was done by recording the number of 10 cm squares which were covered by Mytilus. At each 20 m interval four estimates of percentage coverage were obtained by randomly throwing the quadrat on the rock surface. Areas where the Mytilus were spread evenly and those where animals occurred in heaps, as a consequence of wave action were recorded separately. At sites on transects 1 and 2 (Fig. 16) sample cores were taken to measure density (core area = 11.00 cm^2.). At each site, two cores were taken for clumped and two for evenly distributed Mytilus. In the laboratory, the Mytilus from each sample were counted and measured to the nearest mm.

Results and discussion

Although the area covered by Mytilus decreased from September to December on two transects it increased on the other (Fig. 17). Between December and February there was no significant decrease in coverage on any of the transects (Fig. 17). Similarly although the density of 1-5 mm and of 5-10 mm shell length Mytilus increased through the year on both transects/

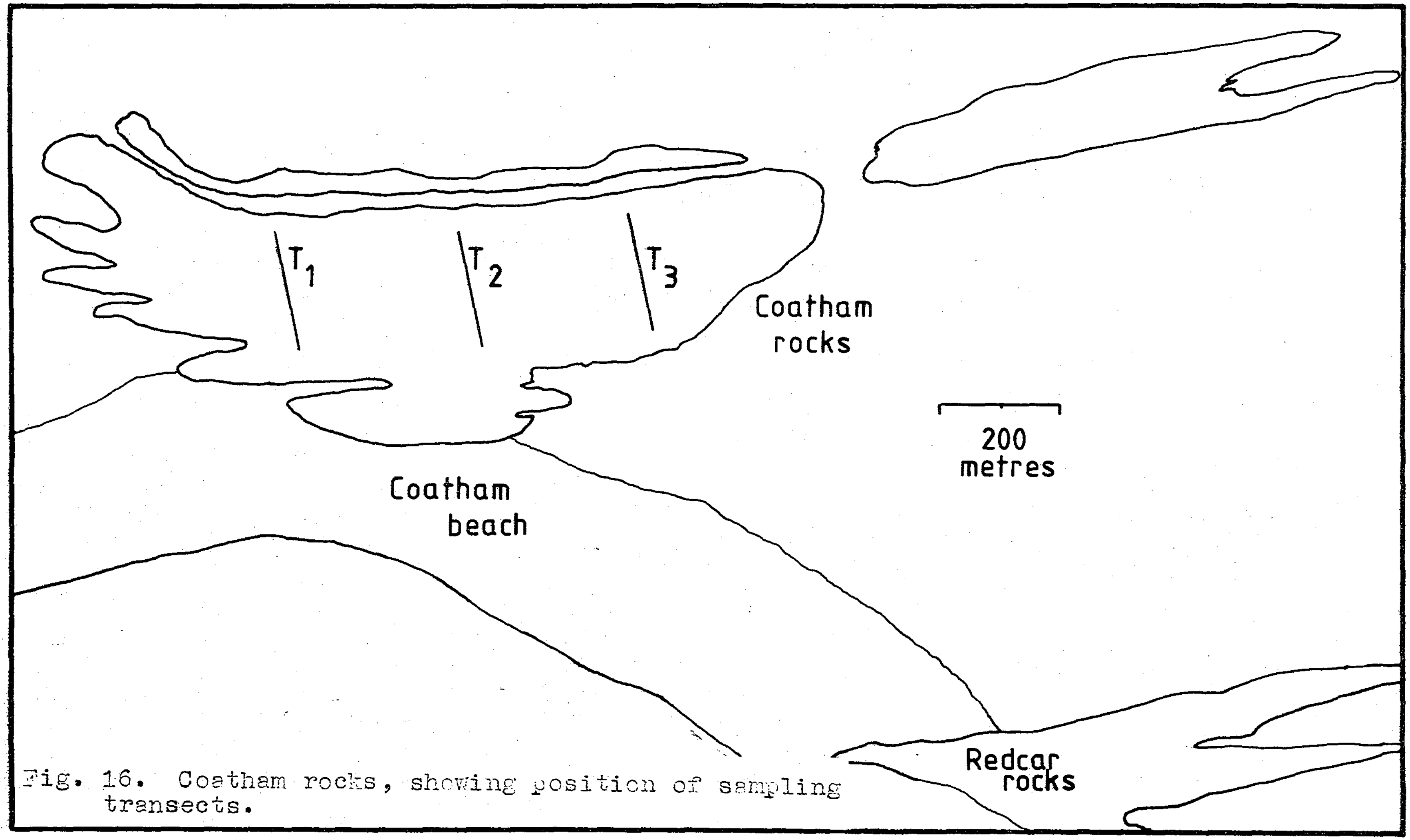


Fig. 16. Coatham rocks, showing position of sampling transects.

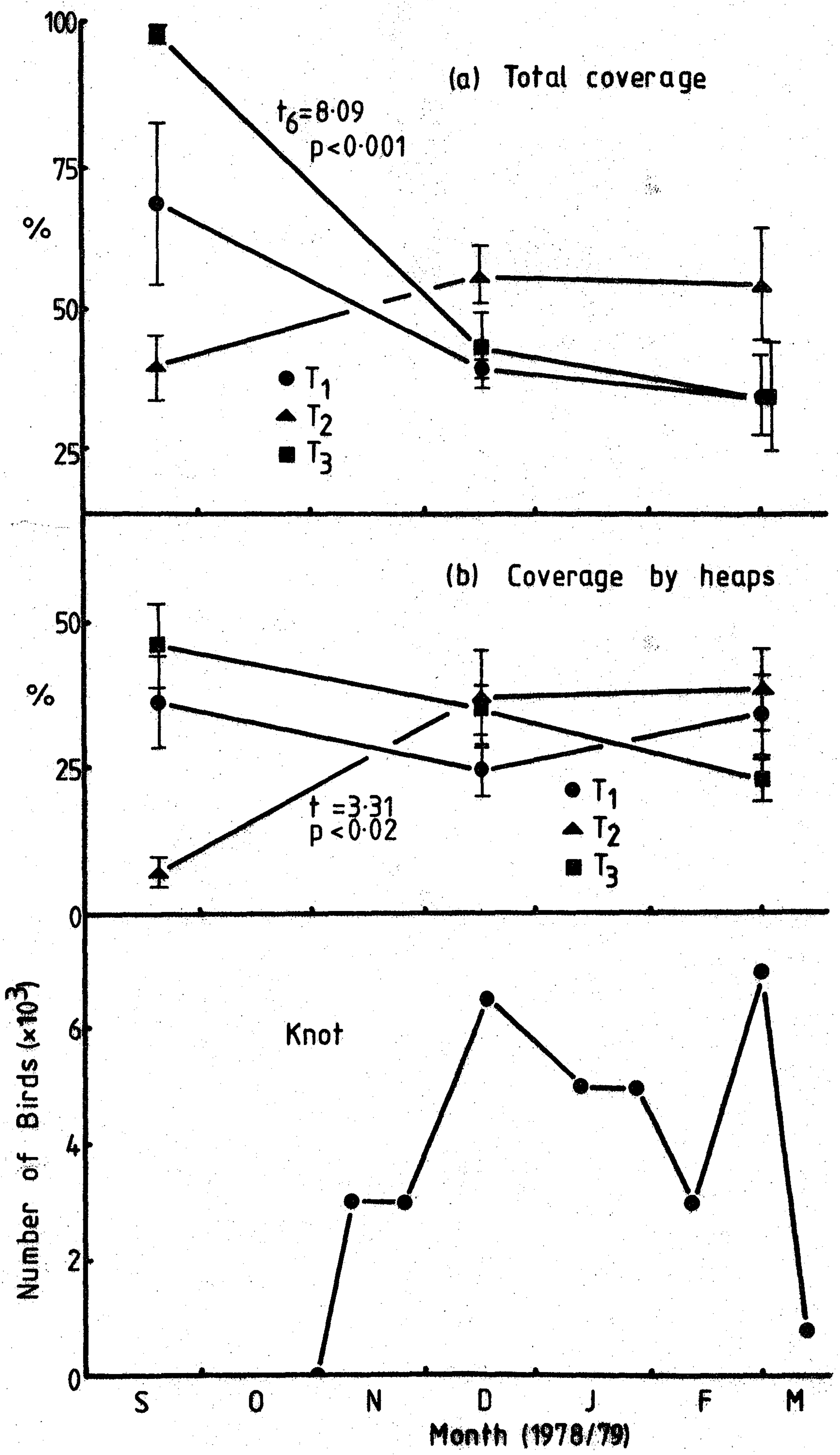


Fig. 17. Seasonal change in coverage of Coatham rocks by Mytilus edulis (a) Total coverage (b) coverage by heaps of Mytilus. Figures given are mean and one standard error of estimates of percentage coverage within eight sample quadrats (see text). Counts of Knot for 1978-79 from Chapter 1, Fig. 8 are given for comparison.

transects 1 and 2, particularly between December and February, density of 10-15 mm and 15-20 mm Mytilus remained relatively constant (Fig. 18 a,b). Prater (1972) concluded that Knot took mainly small Mytilus ($\leqslant$ 5 mm) and casual observations made of birds feeding on Coatham rocks agree with this. However I have also seen larger size classes (5-15 mm) being taken. Clearly a few items of this size can contribute the equivalent biomass of many smaller individuals. Consequently the precise importance of large and small Mytilus to the energy intake of Knot is not clear. However the data do not indicate rapid changes in density of either large or small Mytilus on Coatham Rocks of the magnitude necessary to correlate with the fluctuation in numbers of Knot observed in 1978-79. Clearly sampling was infrequent and some changes in the prey population may have occurred without being recorded. However the major changes in abundance and availability are likely to be due to dislodging of Mytilus by wave action during storms. The absence of any change in coverage between December and February suggest that this did not occur to any great extent on Coatham Rocks in 1978-79.

PREY QUALITY/

Fig.18a

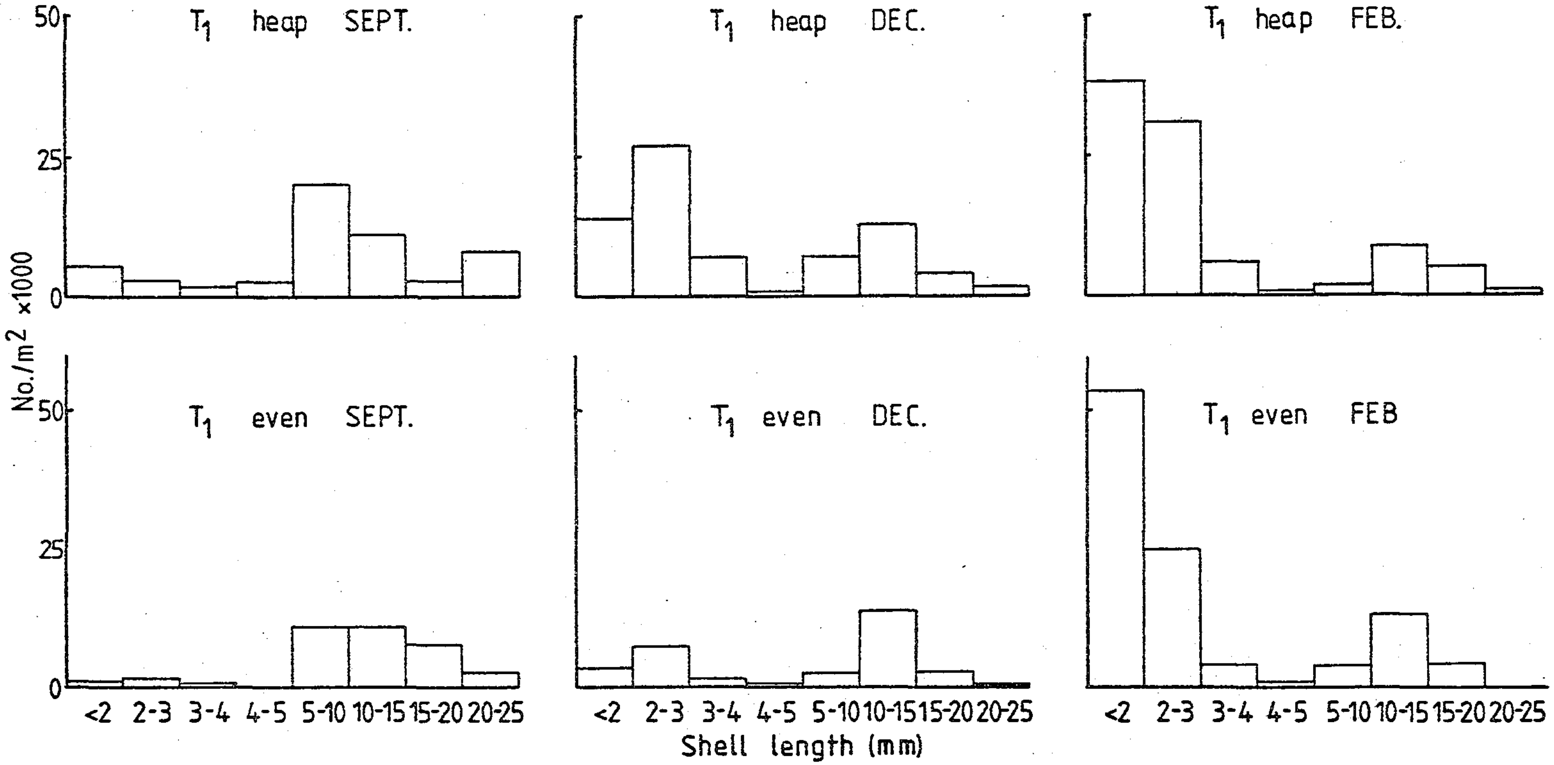
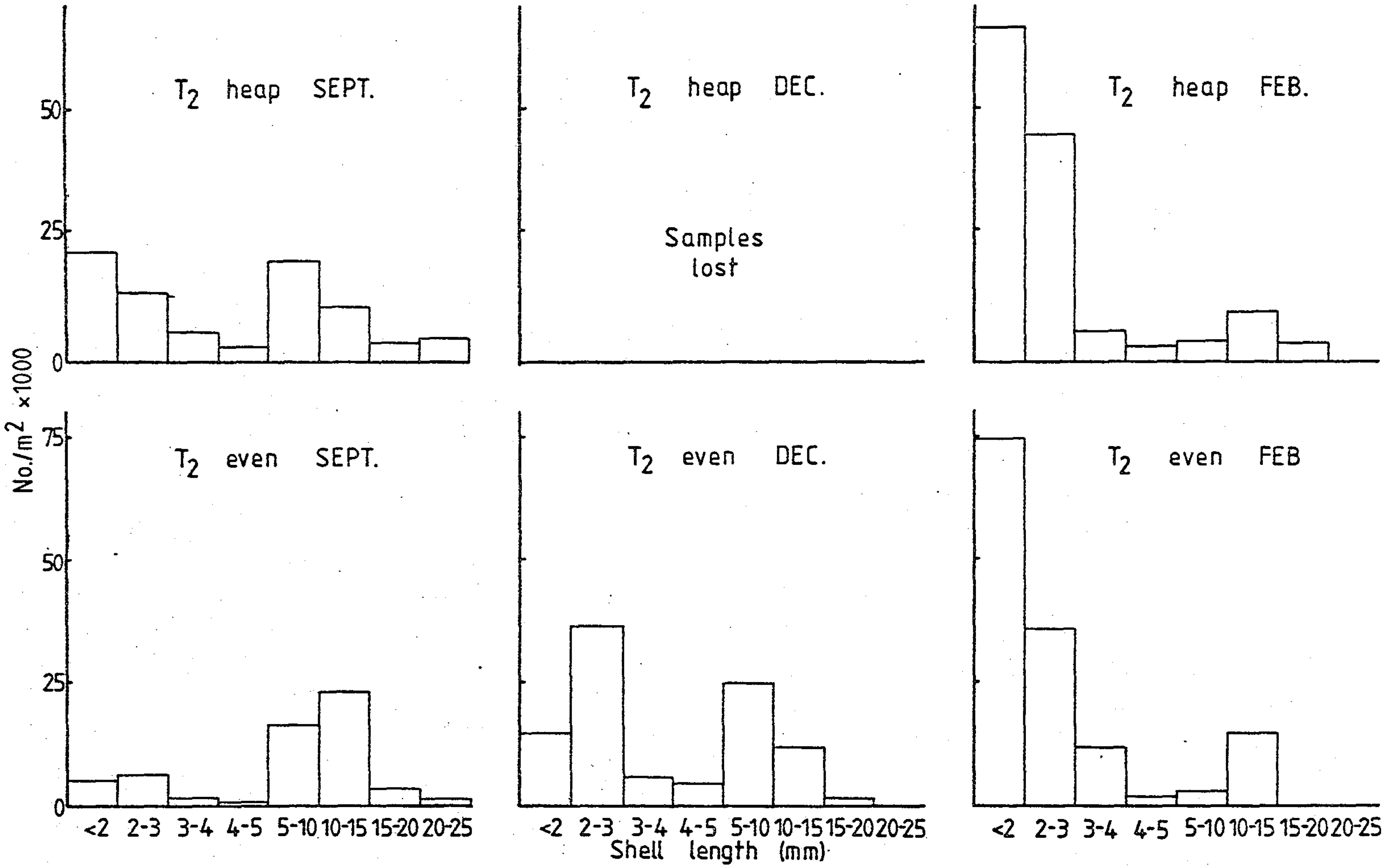


Fig. 18. Size frequency distribution of Mytilus edulis from Coatham rocks in September and December 1978, and February 1979. (a) Transect 1 (b) Transect 2.

Fig. 18b


T$_2$ heap SEPT.
T$_2$ heap DEC.
Samples lost
T$_2$ heap FEB.
T$_2$ even SEPT.
T$_2$ even DEC.
T$_2$ even FEB
No./m^2 ×1000
0
25
50
75
<2
2-3
3-4
4-5
5-10
10-15
15-20
20-25
Shell length (mm)

PREY QUALITY

Introduction

The data presented so far suggest that neither major differences in timing of peak density or biomass, nor in growth rate, exist between the estuaries under consideration in this study. However, it is possible that shorebirds might gain an advantage in moving if the relative quality of the prey changes in different estuaries at different times. During the course of a year the body weights of most individual prey items are known to change as development of reproductive tissue and body reserves, followed by their emaciation, takes place. Differences between estuaries in the precise timing and extent of these changes might thus explain the movements of shorebirds feeding upon these species. Ansell and Trevallion (1967) have outlined a seasonal cycle of body condition for boreal bivalves.

(1) A winter period of inactivity during which gametogenesis proceeds slowly and body reserves are used to supply reduced metabolic needs.

(2) A short period following the renewal of feeding activity in spring when the body reserves are renewed, growth recommences and rapid gonad proliferation and gametogenesis occurs.

(3) A reproductive period during the summer when the temperature rises above a certain threshold level and body growth, gonad growth and spawning proceed together.

To these should be added a fourth period during which growth may stop if temperatures rise too high in summer.

There is now considerable evidence confirming the reality of this cycle in a number of bivalve species (Carduim edule L., Hancock and Franklin, 1972; Donax vittatus (da Costa), Ansell, 1972; Macoma balthica, Chambers and Milne, 1975b; Scrobicularia plana (Da Costa), Hughes 1970), and in polychaetes (Chambers and Milne, 1975a).

It is with parts (1) and (2) of this cycle in which no increase in body size (e.g. shell length in Macoma) occurs, that I am concerned here. (Part (3) and the later stages of (2) are accompanied by growth in shell size. It is this growth period which leads to the annual peak in density of the size classes preferred by shorebirds. Thus the relevant data has already been discussed in the preceding section.)

Macoma

Data on seasonal change in body condition of Macoma are available for a number of estuaries. However, as with data on density, not all the data on body condition are comparable. I collected data from the Humber estuary and Morecambe Bay from animals left in clear sea water for 24 hours, to permit them to empty/

empty their gut contents, and then dried under vacuum at $60^{\circ}C$. Values given are ash-included dry weights. Of the other studies for which data have been obtained, only that of Goss-Custard et. al. (1977a) followed the same procedure. Elliott (1979) left the animals in sea water for only six hours. Consequently not all guts may have been empty. Animals were dried at $60^{\circ}C$, but not under vacuum, and so some water may have been retained. Chambers and Milne (1975b) kept animals in sea water for 24 hours but obtained dry flesh weights after freeze drying. It has been shown that this method is only 95% as efficient as vacuum drying (Giese, 1967). Consequently figures from the Ythan and Forth are not directly comparable with those from other estuaries, although they indicate timings of change in body condition of Macoma within each estuary.

The data available indicate little seasonal change in body weight of smaller animals (those of importance to Knot); see for example the 10.5 mm size class (Fig. 19). Seasonal changes in larger size classes (of importance to Bar-tailed Godwit) are more marked. Among these, peak weight for a given size e.g. 15.5 mm (Fig. 19) was recorded in May on the Forth, in June on the Ythan, in August on the Wash, in October on the Humber and in December on Morecambe Bay. Minimum values were recorded in February on Morecambe Bay, April on the Humber and Ythan but in May on the Wash. In/

Fig. 19. Seasonal variation in dry flesh weight of *Macoma balthica*. Upper symbols refer to animals of 15.5 mm shell length and lower symbols to those of 10.5 mm shell length.

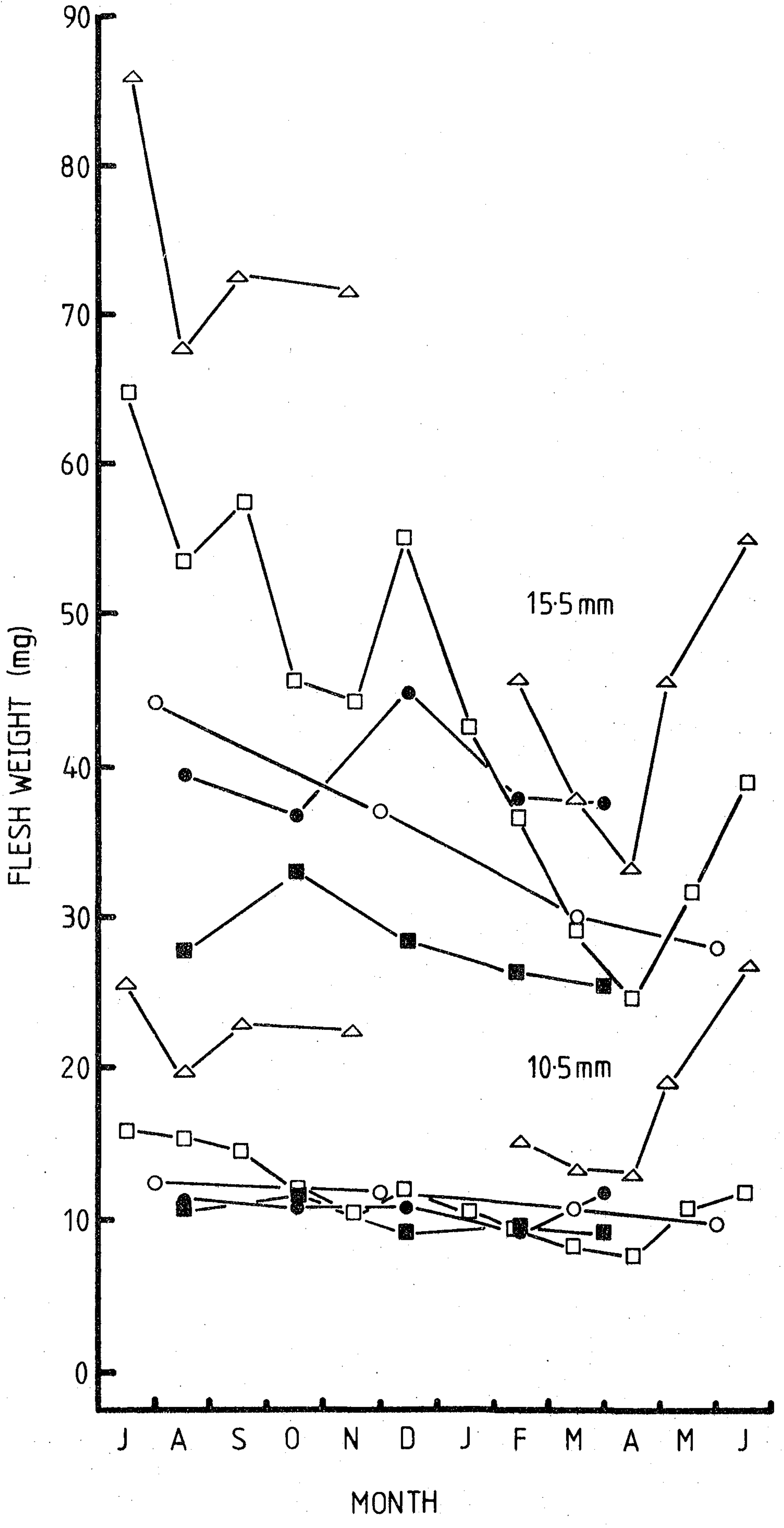
△ Ythan, Chambers and Milne 1975b.

□ Forth, Elliott, 1979.

○ Wash, Goss-Custard et. al. 1977a.

● Morecambe Bay, Present study.

■ Humber, Present study.


FLESH WEIGHT (mg)
90
80
70
60
50
40
30
20
10
0
15·5 mm
10·5 mm
J
A
S
O
N
D
J
F
M
A
M
J
MONTH

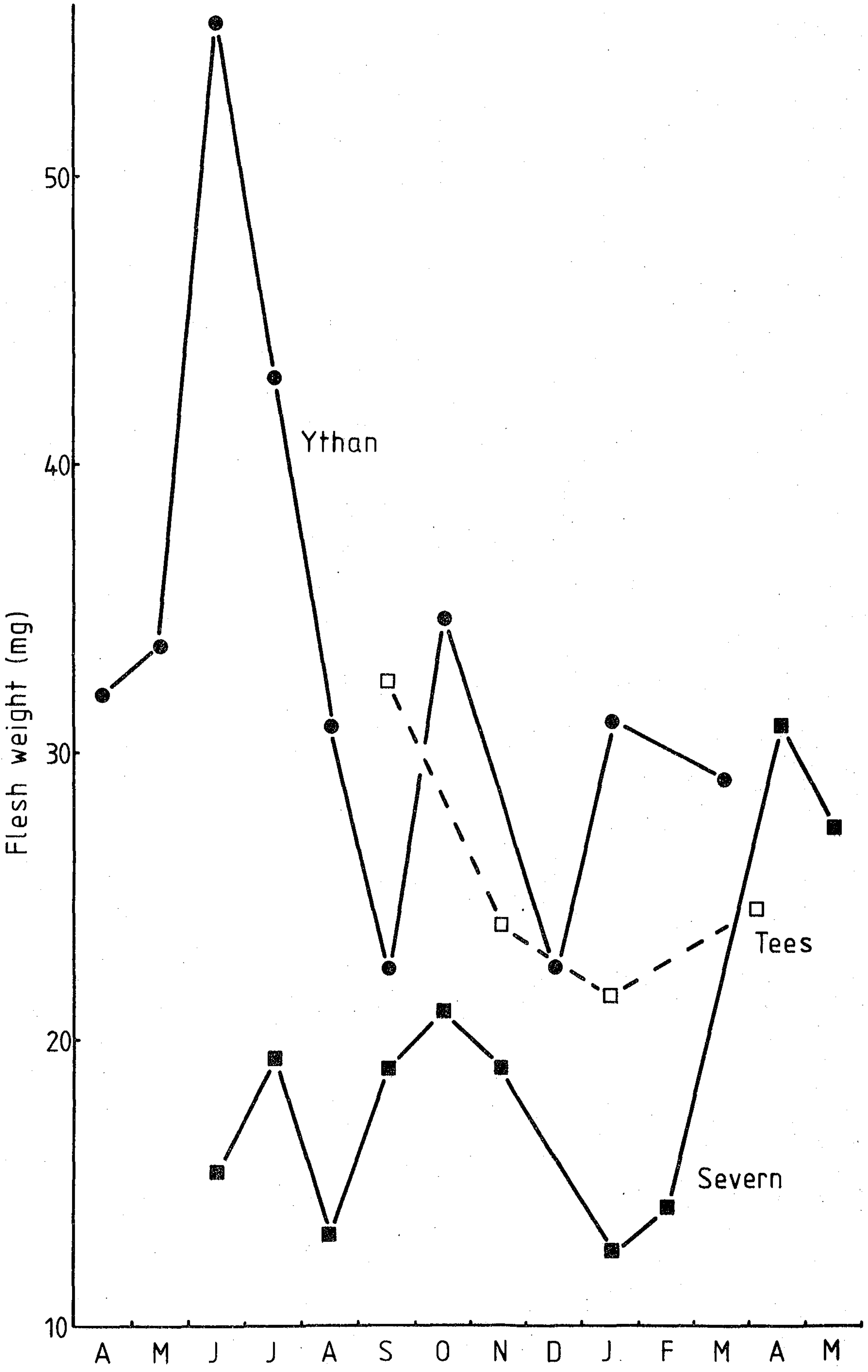
In the Waddenzee, Beukema and de Bruin (1977) reported maximum weights in June/July and minima in March. These data suggest that the growing season begins earlier and lasts longer on Morecambe Bay, and begins earlier on the Forth, than in the Waddenzee, Ythan, Humber, or Wash. Despite this, inter-estuarine variation in dry weight is not great, although more evident in the larger size classes. Highest values in summer for a given size class are recorded on the Wash and thereafter on Morecambe Bay. However, as data from the Wash are expressed as ash-free dry weights, it is clear that differences in body condition between these two areas are not great. Lowest values were always found on the Humber.

Nereis

Data on body condition of Nereis are available from the Tees, Severn and Ythan. However, these data are, as for Macoma, not directly comparable because animals from the Severn and Ythan were freeze dried (Mettam, 1979; Chambers and Milne, 1975a). However, the pattern of seasonal change in weight is similar in all three areas, with minimum weight in December or January (Fig. 20). On the Ythan and Severn low weights were recorded also in autumn. The differences in timing of peak weights are probably due to regional differences in timing of gonad development /

Fig. 20. Seasonal change in dry flesh weight of *Nereis diversicolor*.

●	Ythan, Chambers and Milne, 1975a.
□	Tees, Present Study.
■	Severn (Caldicot), Mettam, 1979.



Flesh weight (mg)
50
40
30
20
10
Ythan
Tees
Severn
A
M
J
J
A
S
O
N
D
J
F
M
A
M
Month

development, to which the rapid rise in weight, seen on the Severn between February and April and on the Ythan between May and June, is attributed (Mettam, 1977; Chambers and Milne, 1975a).

Although animals from the Severn were freeze dried and so retained some water they are consistently lower weight than those from the Tees and Ythan. The reasons for this are unclear. The rich nutrient source on the Tees estuary (Gray 1976) may contribute to high weight there. However, the studies in the three estuaries occurred in different years. Hence the possibility of annual, as well as regional, differences in body condition cannot be discounted. Thus although for Nereis the available data suggest that differences in body condition occur between areas the same pattern of seasonal change in body condition is apparent in each estuary.

PREY AVAILABILITY

Tidal exposure

The environmental factor which has the greatest influence on the daily pattern of activity of estuarine feeding shorebirds is the ebb and flood of the tide. In most species feeding takes place only when the mudflats are exposed. At high water most of the birds' time is spent roosting, and preening. However the times of exposure of the feeding grounds do not remain constant from/

from day to day. Over a period of a week the times of high and low water become progressively later, changing by a total of ca. 6 hours. Furthermore, the amplitude of the tides and consequently the area of shore exposed in gently shelving estuaries also varies on a fortnightly semi-lunar rhythm. On some days low water occurs in the middle of the day, which allows maximum feeding time during daylight hours, while a week later high water occurs at this time of day, which allows little time for diurnal foraging, especially in mid-winter.

In some estuaries, e.g. the Tees low water in the middle of the day occurs during spring tides. Such conditions provide the longest feeding periods during daylight on the largest feeding areas. The lowest tidal levels may contain high densities of unexploited prey because they are exposed infrequently. Although it has been suggested that for many Grey Plovers on the Tees estuary food intake during darkness is greater than during daylight (Dugan, 1981) it remains a basic assumption that for most species in most areas the main feeding period is during daylight low water (Goss-Custard, 1969; Pienkowski, 1980; Smith, 1975). Thus, on estuaries such as the Tees where low water on spring tides occurs in the middle of the day these tides provide very good feeding conditions. However, because of the weekly cycle of neap and spring tides, in these same areas, a week later the period/

period of neap tides coincides with high water in the middle of the day. In these conditions very little feeding time will be available during daylight in mid-winter and on a much more restricted area. Thus on the Tees estuary tidal conditions very cyclically from providing very good daytime feeding conditions on spring tides to very poor feeding conditions on neap tides. In other estuaries e.g. those in Essex and Morecambe Bay, low water on spring tides occurs in the early morning and late evening. Conversely low water on neap tides occurs in the middle of the day. Thus in these areas, it is on spring tides that little time is available for daylight feeding, but the area exposed is still large. On neap tides a longer period is available for foraging during daylight, but the area exposed is smaller. Thus on the Essex estuaries and Morecambe Bay, although feeding conditions vary with the spring-neap cycle, the variation is not as marked as on the Tees and Forth. In these latter areas, unless birds operated a spring-neap cycle of deposition and utilisation of fat reserves, the favourable feeding conditions during spring tides would be of little value to them during neap tides. Consequently if severe weather on the Tees coincided with periods of neap tides, it is likely that severe feeding stresses would occur.

Assuming that all other factors are equal, birds should winter in areas where the risk of feeding stress is/

is as low as possible. It is likely therefore that estuaries where feeding conditions vary least during the spring-neap tidal cycle would be favoured over those e.g. the Tees estuary, where feeding conditions vary greatly during such a cycle. On this basis, I would predict that birds should favour areas in mid-winter where the time of low water on spring tides is at dawn and dusk i.e. where the variation in feeding conditions between spring and neap tides is least. In Britain these conditions occur on the Wash, in Essex, on the south and north-west coasts of England and on the north and west coasts of Scotland (Fig. 21). Conversely, variations in feeding conditions between spring and neap tides are greatest on the estuaries of the east and north-east coasts i.e. the Humber, Tees, Lindisfarne and the Forth.

These arguments indicate that the northward movements observed along the east coast of Britain in autumn and winter are not a response to more favourable tidal conditions on the estuaries of the North-East. Furthermore, on the west coast of England tidal conditions are very similar on all the major estuaries, yet movements occur between them. Therefore it seems unlikely that tidal conditions are of major importance in controlling the timing and direction of movements on this coast also.

Thus, although there is much variation in tidal regime between estuaries, and this is potentially of great/

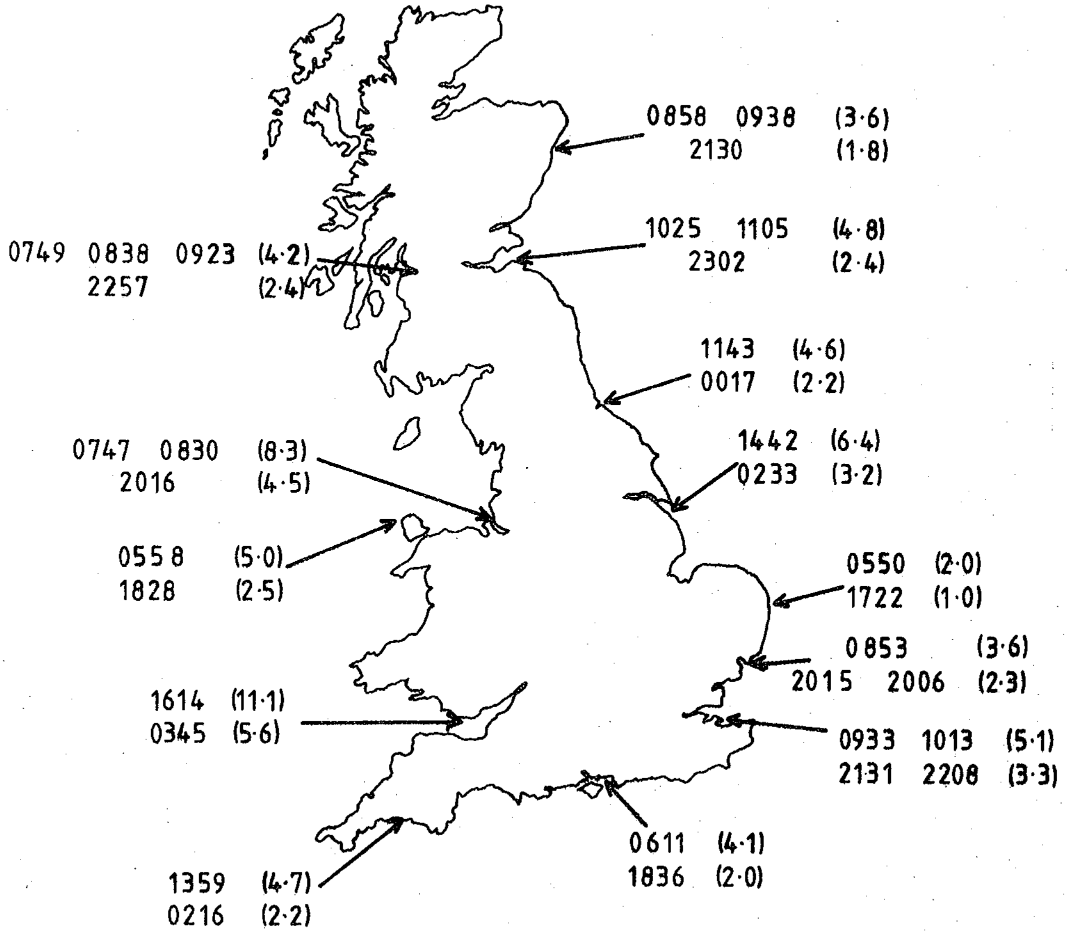


Fig. 21. Time of lowest low water during daylight (upper) and darkness (lower) in January 1973 at selected sites around the British coast. Mean tidal range (in metres) for each site is given in parentheses, spring (upper), neap (lower).

great importance for maintenance of energy intake by shorebirds, there is no evidence that these factors do in fact lead to shorebird movements.

Prey behaviour

Seasonal patterns of behaviour which can result in seasonal changes in availability of intertidal invertebrates are of three main types, (1) migration between different tidal levels, (2) vertical migration within the substrate and (3) activity.

(1) Naylor (1962) reported downshore migration of *Carcinus maenas* in autumn and the reverse in spring. Also evidence of this temperature related movement has been observed in other areas. On the Tees estuary Curlew and Whimbrel *Numenius phaeopus* feed in autumn on *Carcinus* along rocky parts of the intertidal area where many small individuals stranded at low water hide under stones and algae. In winter very few *Carcinus* are present in these areas and few birds feed there. Similarly Goss-Custard and Jones (1976) reported *Carcinus* in pellets of Curlew collected from the Wash in summer and autumn but not from those collected in winter.

In the Dutch Waddenzee the chief food in summer of the Greenshank *Tringa nebularia* is *Crangon vulgaris* which moves offshore in winter (Swennen, 1971). By this time most of the Greenshank present in summer and autumn have migrated further south although it is not known/

known whether the decrease in availability of Crangon is an important causal factor in this.

Smaller downshore movements in winter have been reported in Nerine cirratulus Della Chiaje the most important prey of Sanderling Calidris alba in North-East England (Brearey, 1981). However as Evans (1979) has discussed this does not lead to absence of Nerine from the diet but may merely aggravate foraging difficulties in winter by restricting, on neap tides the amount of time that it is possible to feed on Nerine. Similar difficulties may also be encountered in some areas by species feeding on Arenicola which has been shown on the Forth to migrate downshore on neap tides and upshore on spring tides (Darby, 1975) and generally downshore in winter.

(2) Many intertidal invertebrates are known to occur deeper in the substrate in winter than in summer. Smith (1975) demonstrated that at a substrate temperature of -1°C the proportion of Scoloplos armiger in the top 5 cm. fell from about 50 to 30% and that this reduction in accessibility led to a reduction in their capture rate by Bar-tailed Godwit feeding upon them. Several authors report that Nereis diversicolor is found at greater depths in winter than in summer. In Denmark Muus (1967) found worms at 55 cm depth in February but in June the maximum burrowing depth for all size classes was/

was 25 cm. These observations agree well with that of Linke (1939) who found individuals at 40 cm. depth during periods of frost. They have also been cited by Townshend (1981a) to explain the movement in December of Curlew, which capture Nereis by probing into the burrow, from the mudflats of the Tees estuary to feed on earthworms in nearby pastures. Birds which behave in this fashion are short-billed individuals (chiefly males) which, Townshend argues, in December cannot meet their requirements because of the downward migration and consequent reduced accessibility of Nereis. Although little information is available for Godwit feeding on Nereis it is likely that as they effect capture by the same method they experience a similar reduction in prey availability. In contrast, the rate of prey capture by short-billed Plovers is not affected by this change in depth distribution. They rely on capture of Nereis while at the surface either defaecating, or irrigating their burrows, activity which does not appear to be affected by winter increase in burrow depth (see Chapter 3).

Seasonal changes in depth distribution of Macoma balthica have been described by a number of authors. On the Ribble Greenhalgh (1975) reported 14% of the total population below 3 cm in June/July but 20% in September/October and 40% in January/February. This pattern of change was also found on the Wash where monthly/

monthly sampling was carried out. Maximum depth was observed in December when, of the size classes preferred by Knot (9-13 mm length), only 4% of the biomass lay within probing range of a Knots bill (33 mm)(Reading and McGrorty, 1978). However, on the Ythan estuary in North-East Scotland, Chambers and Milne (1975b) observed little variation in depth distribution between December and May, but in June a greater proportion of large animals were found at deeper levels.

Thus although in each area studied the depth of the population varied seasonally the precise pattern observed, although similar on the Wash and Ribble differed on the Ythan. In order to investigate more fully such inter-estuarine variation in pattern of depth distribution I monitored the depth of <u>Macoma</u> on Morecambe Bay and the Humber estuary, once every two months between June 1978 and April 1979. A stainless steel corer 10 cm square and 10 cm deep with a slit at 33 cm (the length of a Knots bill) in two opposing walls was used. To reduce the possibility of movement of animals within the sample during removal from the mud isolation of the two parts of the sample was effected by inserting a stainless steel plate in the slit at 33 cm while the corer was still in situ. After removal, upper and lower sections were sieved and preserved separately. Samples from the Humber were collected at Skeffling, the main study site of Ratcliffe (1979). Those/

Those from Morecambe Bay were collected from Hest Bank.
Both sites are major feeding areas of Knot on these estuaries. Ten samples were collected on each occasion.

The results of this study of Macoma indicate that the pattern of seasonal change in depth distribution of both population density and biomass on Morecambe Bay and the Humber is very similar to that on the Wash (Figs. 22-25). In all three areas the population is nearest the surface in summer and deepest in mid-winter. However, differences in timing of increase in depth are apparent between estuaries. On the Wash and Morecambe Bay the proportion of the biomass of animals in the size range 9-13 mm available to Knot, falls between August and October from ca 60% to 10%. In contrast, on the Humber the decrease at this time is only from 94% to 82%. Here the corresponding increase in depth does not occur until between October and December after which there is a rapid rise from December to February. On Morecambe Bay no, and on the Wash little, upward movement is apparent until after February after which this is rapid.

Reading and McGrorty (1978) considered the environmental factors to which seasonal change in depth of Macoma might be related. Of these factors, that to which the pattern of depth distribution was most closely related was daylength although they were unable to suggest a reason for this relationship.
Evans/

Fig. 22. Density of Macoma balthica in the size range 9-13 mm accessible to Knot Calidris canutus with a mean bill length of 33 cm.
(○) Morecambe Bay, (●) Humber.

Fig. 23. Percentage of the population of Macoma balthica in the size range 9-13 mm accessible to Knot with a mean bill length of 33 mm. Symbols as in Fig. 22.

Fig. 24. Biomass of Macoma balthica in the size range 9-13 mm accessible to Knot with a mean bill length of 33 mm. Symbols as in Fig. 22.

Fig. 25. Percentage of the biomass of Macoma balthica in the size range 9-13 mm accessible to Knot with a mean bill length of 33 mm.
(○) Morecambe Bay, (●) Humber, (■) Wash, from Reading and McGrorty (1978).

Fig. 22

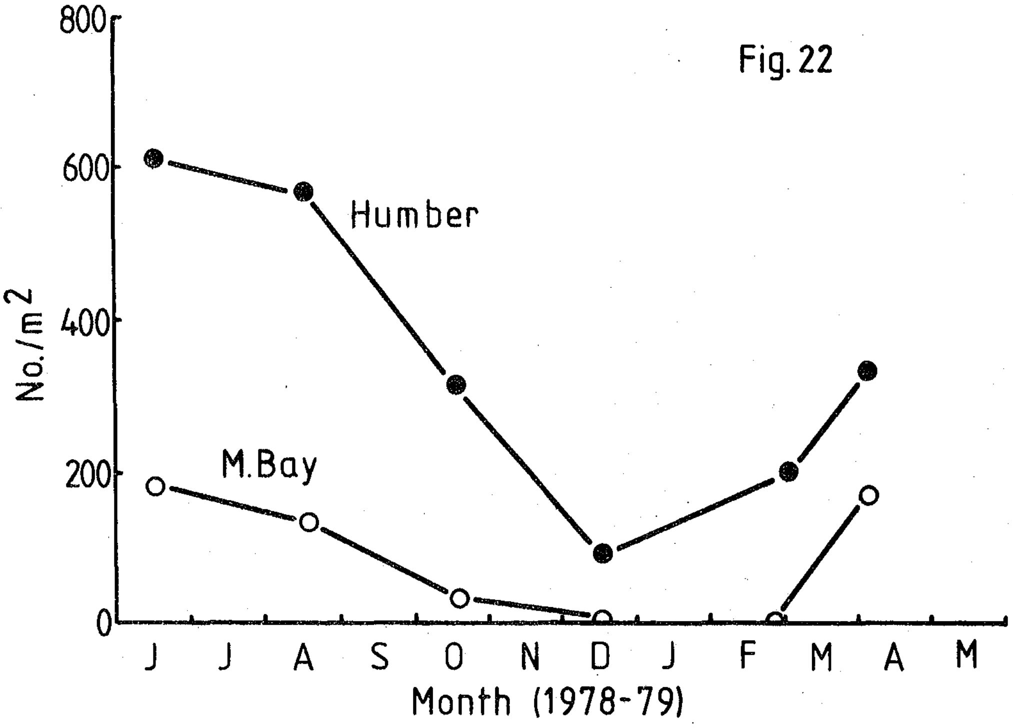
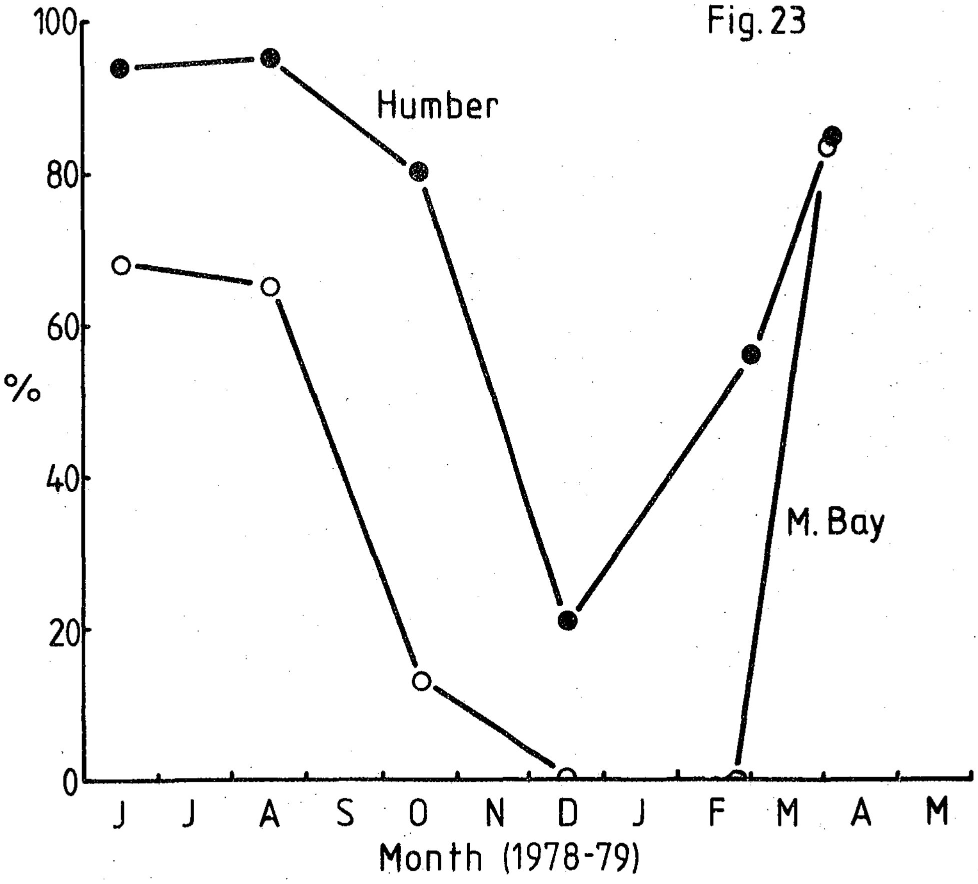

800
600
400
200
0
No./m2
Humber
M.Bay
J
J
A
S
O
N
D
J
F
M
A
M
Month (1978-79)

Fig. 23


100
80
60
40
20
0
%
Humber
M. Bay
J
J
A
S
O
N
D
J
F
M
A
M
Month (1978-79)

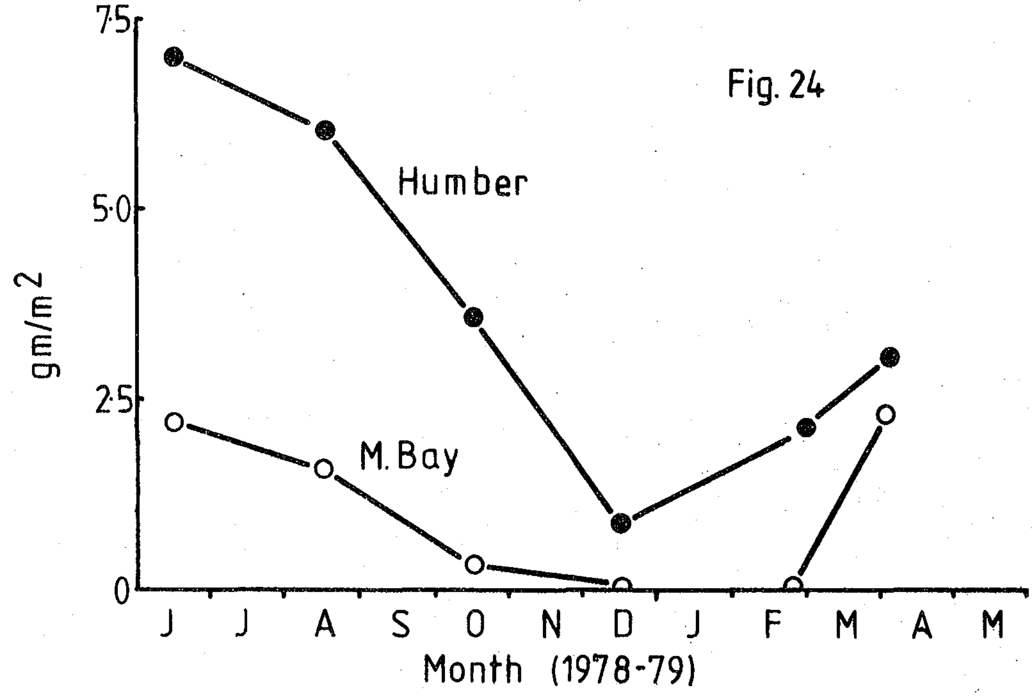


Fig. 24
7·5
5·0
2·5
0
gm/m²
Humber
M. Bay
J
J
A
S
O
N
D
J
F
M
A
M
Month (1978-79)

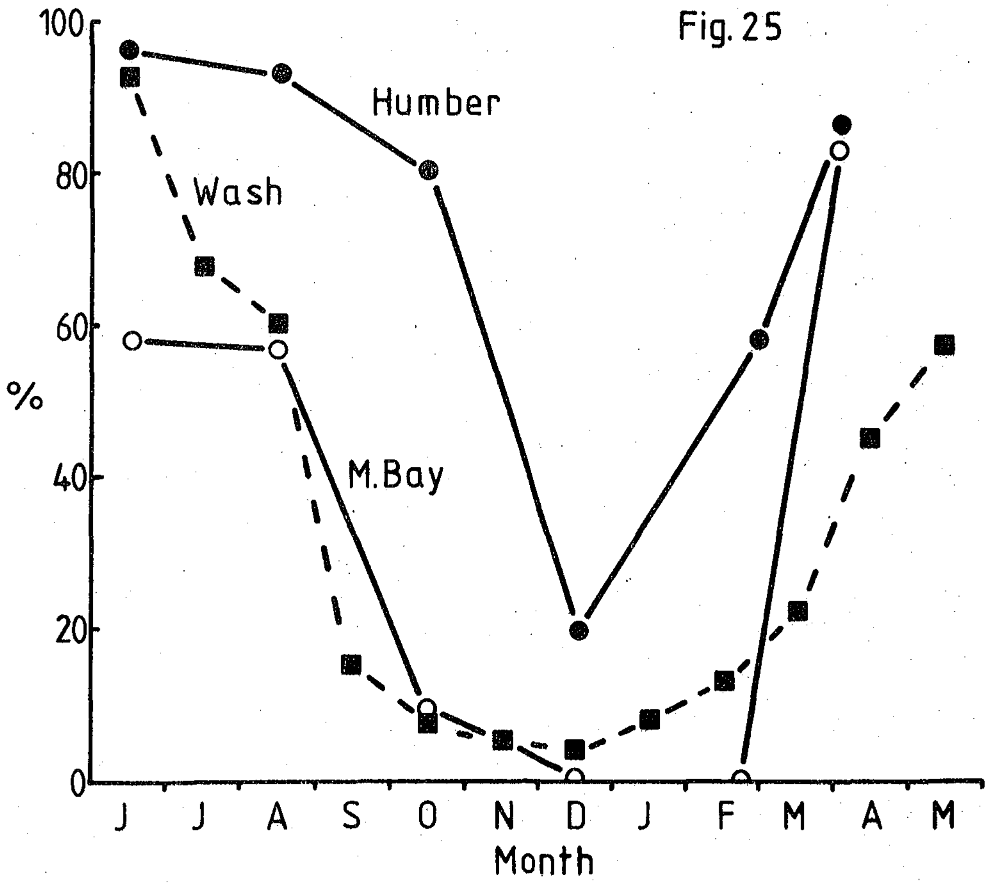


Fig. 25
100
80
60
40
20
0
%
Humber
Wash
M. Bay
J
J
A
S
O
N
D
J
F
M
A
M
Month

Evans (1979a) has suggested that deeper burrowing of Macoma is an anti-predator response, the bivalves occurring close to the surface when the Knot are absent in summer. However this is clearly not true for Morecambe Bay from February to April, where availability of Macoma increases at the same time as do numbers of Knot.

Series of mean monthly temperatures are not available for Morecambe Bay and the Humber for 1978-79. However, mud temperatures on my sampling dates indicate that, at both sites, maximum depth was recorded on days when temperature was lowest and minimum depth when temperature was highest. However these data are too few to speculate as to whether this is a causal relationship. Indeed if this were the case the higher biomass available in December on the Humber than on Morecambe Bay (where the temperature was 6°C higher) is difficult to explain. Perhaps the precise extent of the burrowing response is limited by the higher density of Macoma on the Humber.

One environmental factor which Reading and McGrorty did not consider specifically is the depth of the deoxygenated layer in the substrate. It is possible that Macoma might move upward in summer to avoid more de-oxygenated conditions in the substrate. The difference in depth distributions between the Humber and/

and Morecambe Bay is consistent with this hypothesis. The substrate on Hest Bank is clean sand whereas at Skeffling on the Humber is silty mud with a clear de-oxygenated layer near the surface. Perhaps Macoma on the Humber burrow both deeper and later and to a lesser depth than on Morecambe Bay because of the de-oxygenated conditions in the deeper mud, only doing so as the de-oxygenated layer becomes deeper as conditions become colder. However this suggestion does not explain the observation of Chambers and Milne (1975b) that on the Ythan Macoma burrow deeper in summer. Clearly the factors controlling the burrowing behaviour of Macoma merit further study.

Thus, at present it is not known whether the seasonal changes in depth of Macoma are controlled directly by environmental changes or are under internal control, and, if the latter, to what the behaviour is adapted. Clearly this distinction is of major importance in any consideration of the year-to-year consistency of the pattern of availability I have described. However, of the factors to which the movements may be related i.e. temperature, daylength and depth of the de-oxygenated layer (which will be greatly affected by both temperature and sunlight), all three vary in a predictable seasonal manner. Consequently it is likely that the availability of Macoma/

Macoma will itself be predictable and therefore a factor to which the regular seasonal pattern of shorebird movements may be related.

The seasonal changes in depth distributions may indeed be a factor determining the timing and direction of the movements of Knot described in Chapter 1. Throughout the winter the availability of Macoma to Knot is higher on the Humber than on the Wash. Thus any birds which leave the Wash in November and move to the Humber will encounter not only a higher biomass/m^2 there (Fig. 24) but also higher availability. Why then do not more Knot move to the Humber earlier in the autumn when availability of Macoma is much higher than in mid-winter? Perhaps adult Knot do not move at this time because they are still in moult. Indeed, of the proven movements of Knot from the Wash to the Humber, the two earliest recoveries, one in September and the other in October were of Juveniles (Chapter 1, Fig. 3) which would not have been moulting flight feathers in those months (Minton, 1975). However, as discussed in Chapter 1, the influxes on the estuaries of the north-east coast occur at a time when numbers on the Wash also increase. Thus, prey abundance and availability is sufficiently high to support increased numbers on the Wash. This indicates that if timed by external factors movement from the Wash to the Humber at this time is more likely to be a consequence of competition on the Wash rather than directly/

directly related to the low prey availability there. Thus, although the higher availability of *Macoma* on the Humber in November and December may be an important factor in determining the direction of movement of birds from the Wash it seems unlikely that it is important in determining the timing of movement. Rather the factors which cause birds to leave the Waddenzee and arrive on the Wash at this time of year may be indirectly the cause of the timing of this exodus. Similarly, it is unlikely that changes in availability of *Macoma* on Morecambe Bay are an important element in determining the timing and direction of movements on the west coast. For example, numbers of Knot using Morecambe Bay increased greatly from July to December yet availability of *Macoma* declined. Indeed on Hest Bank in December and February no *Macoma* in the 9-13 mm shell length size range were found within reach of a Knots bill (Fig. 22). In these months Knot feeding on Hest Bank must have taken predominantly smaller-sized *Macoma*. It is possible that the high availability of *Macoma* on Morecambe Bay in spring is one reason for this area's importance as a pre-migratory fattening ground. However while an increase in availability will increase the number of birds the area can support at this time it is likely that the observed difference in size of the Knot population of Morecambe Bay and the Wash in April (Chapter 1, Figs. 9,4) is a consequence primarily of/

of the higher temperature regime on the west coast at this time of year (Fig. 3).

Throughout this discussion I have had to rely upon one winters data on depth distribution of Macoma in each area, but counts of birds from several winters. However as argued previously, of the factors to which the seasonal change in depth distribution of Macoma may be related i.e. temperature, daylength and depth of the de-oxygenated layer, all three vary in a predictable seasonal manner each year. Therefore it seems likely that the patterns of change in depth distribution described will remain constant from year to year. Similarly, count data from the Humber (Tasker and Milsom, 1979) and Tees (Chapter 1, Figs. 6,8) estuaries in recent years (1978-80) suggest that the timing of movements of Knot in these years is not markedly different from that of movements revealed by the Birds of Estuaries Enquiry counts from 1969-75 (Chapter 1). Thus although the data on depth distribution of Macoma and numbers of Knot were collected in different years the consistency between years in pattern of both seasonal change in depth distribution of Macoma and seasonal change in numbers of Knot on each estuary suggests that the comparisons I have made are valid.

(3) Changes in availability of prey, through changes in their accessibility, are probably gradual. However/

However there is also much weather-dependent variation in the activity of prey, and hence their availability. Although activity can vary greatly and vary rapidly, for example as air temperature fluctuates during the day, the seasonal pattern of temperature and wind conditions can also induce seasonal patterns in activity. Smith (1975) and Pienknowski (1980) have shown that capture rate of Arenicola by Bar-tailed Godwit and Grey Plover decreases as temperature decreases and attribute this to a reduction in defaecatory activity of Arenicola with a fall in temperature. Similarly Goss-Custard et. al. (1977a) have shown that capture rate of Macoma by Knot decreases as temperature declines. This may indicate variation in burying depth with temperature. However low capture rates at low temperatures and high capture rates at higher temperatures have been observed in one day (J.D. Goss-Custard, Pers. Comm.). This suggests that the variation in capture rate is due largely to variation in activity, and hence detectability, of prey with temperature. Strong winds can also affect the detectability of prey. For Plovers, which rely almost entirely on visual detection of prey at the surface of the mud, it is likely that buffetting by strong wind can severely reduce their ability to detect movement of prey. Indeed evidence is presented in Chapter 3 to show that on the Tees estuary Grey Plovers feeding in exposed areas on Nereis diversicolor stop feeding and roost at wind speeds in excess of 25-30 Knots. Pienkowski (1980) has also shown a decrease/

decrease in capture rate of Arenicola by Grey Plover with increasing wind speed. However in this situation the effect is not as marked as when feeding on Nereis on the Tees because of the larger cues used in detecting the presence of Arenicola. Thus during the winter as conditions become colder and more windy, not only does the energy expended in maintaining body temperature increase but the detectability of most invertebrate prey decreases at the same time.

Evans (1976) has also considered the effect of wave action on birds foraging at the tide edge. Bar-tailed Godwit which often feed in water up to 15 cm deep will be affected by this. However although there are little data available on the magnitude of these effects it is likely that they are less important than those of wind and temperature on both prey availability and metabolic rate. Similarly it is likely that the effects of different substrate type upon the energy demands of food gathering discussed by Evans (1976) are of relatively little importance in causing movements between estuaries.

DISCUSSION

Movements of shorebirds in relation to factors affecting energy balance.

Of the factors affecting energy balance in shorebirds, that to which most movements can be related is temperature. The movement of Knot, which have moulted in/

in the Waddenzee, to the Wash and other east coast estuaries occurs at a time (early November) when the increasing cooling influence of the continental land mass on temperatures experienced on the eastern North Sea coast is clearly apparent. Grey Plover also leave the Danish Waddenzee at this time. Thus birds which make this westward movement encounter at their destination temperatures less severe than those they would have encountered in mid-winter at their point of departure.

Knot and Bar-tailed Godwit which move northwards from the Wash in November encounter, on average, higher mid-winter temperatureson the Tees but wind chill may, on average, also be higher here. However birds which move from the Tees to the Forth in most years encounter both lower temperatures and possibly higher wind chill at their destination. Thus whereas movement westwards across the North Sea in early winter can be described as movement to a region where winter weather is less severe, the movement northwards from the Wash cannot be described in these terms. However it may be the most severe rather than the average conditions experienced by shorebirds in winter which are most likely to be the major selective factor determining the pattern of movement observed. Consequently it is the geographical distribution of low temperature and high wind speeds during severe winters, rather than the average pattern of distribution over thirty or forty years/

years of mostly mild winters which will govern the pattern of movement. Thus it is possible that the northward movement from the Wash to the east coast of Scotland, where average January temperatures are about the same as those recorded on the Wash, has arisen because temperature and wind chill in Scotland are less severe and shorebird survival here greater than on the Wash during severe winters. Thus individuals which move away from the moulting areas (the Wash) before winter will have a selective advantage during severe winters. However this does not explain the northward movement from the Tees to the Forth as even in the severe winters temperatures were the same, or higher on the Tees than on the Forth.

Although the timing of low water on spring tides differs between estuaries along the east coast of Britain , the variation in feeding conditions over a series of spring and neap tides (and consequently of food intake and probably of mortality during severe weather) is greater on the Tees, Lindisfarne and the Forth than on the Wash. Yet birds move from the Wash to the north-east coast at the end of autumn. The available invertebrate data do not indicate major differences between estuaries in seasonal timing of peak biomass densities of prey. Nor are differences in timing of changes in prey body weight indicated. It is possible that birds move to particular estuaries in/

in response to specific nutrient requirements e.g. protein. However the cycle of biochemical composition of invertebrate prey species follows that of body weight (Ansell and Trevallion, 1967; Beukema and de Bruin, 1977). Thus not only is it unlikely that major differences in nutrient content of particular prey will vary between estuaries in the non-breeding season sufficiently to cause the scale of movements observed, but that any such changes would be reflected in changes in body weight, whose timing does not vary markedly between estuaries. Through the winter, considerable differences exist in availability to Knot of Macoma on the Wash and Humber, at least in one year. However as I have argued above, although the higher availability on the Humber in winter may be an important factor in allowing large numbers of Knot to use the estuary at this time, the lower availability on the Wash is not the factor which causes the movement to occur, as higher numbers of birds are present there in mid-winter than in autumn. However, why some birds leave the Wash and some stay at this time is not known. Similarly, on the Tees the data do not indicate any clear relationship between abundance of Mytilus and numbers of Knot using and moving through the estuary.

On the west coast of Britain there are no seasonal differences/

differences in temperature between the Dee and the Ribble estuaries and Morecambe Bay. However marked seasonal differences in usage of each area do occur. I have interpreted these as suggesting that most Knot on the west coast in autumn moult on the Ribble, and afterwards move to the other estuaries, particularly to Morecambe Bay. Bar-tailed Godwit may also move after the moult to other west coast estuaries, but may also move to southern Europe and West Africa. The reasons for this pattern of usage of areas on the west coast is unclear. The invertebrate data reviewed in this chapter suggest that it is very unlikely that marked seasonal differences in timing of peak density, body weight or biochemical composition of one or more prey species occur between these estuaries on the scale required to explain the usage by Knot or Bar-tailed Godwit. Consideration of other factors also do not reveal major differences which can explain the pattern of usage observed. The decrease in availability of <u>Macoma</u> in winter, reported by Greenhalgh, (1975) may reduce the potential rate of food intake by Knot on the Ribble below that on Morecambe Bay, as, although a similar decrease in availability of <u>Macoma</u> occurs on Morecambe Bay, large mussel beds are also available there and are used extensively by Knot (Prater, 1972; Dare, 1969). This suggestion is supported by the increase in numbers of Knot on the Ribble after mid-winter at a time when availability of <u>Macoma</u> is probably increasing. However the/

the importance of the role of prey abundance or its availability in controlling movement is questioned by the minimal use made of Morecambe Bay by Knot in autumn, when the total abundance of available Macoma is almost certainly always very much greater than on the Ribble.

In this review of factors affecting the energy balance of shorebirds and the seasonal change in the severity of these in different estuaries I have considered each factor in isolation. Clearly all factors affect shorebirds at the same time in what may conceivably be a very complex way. Thus the step by step approach adopted here may fail to investigate these relationships in sufficient depth. To investigate this problem more fully a multivariate approach could be considered. However before such an analysis could be undertaken much fuller and more precise data on prey density, quality and availability from most major estuaries are required. However, even with such information a multivariate approach would tell little of the mechanisms which lead to the movements observed. To elucidate these, detailed study of the interelationships between shorebirds, their prey and different substrates within each estuary is required. It is my opinion that a series of such studies, although labour intensive, on a range of estuaries, are likely to lead to a more sound basis of/

of information from which predictions on numbers of birds and factors affecting movements can be made for other estuaries.

History of movements.

Up to this point I have concentrated discussion on the distribution at the present time of factors which may lead to shorebird movements. However to attain full understanding of the reasons for the presence of inter-estuarine movements, the extent to which movements observed at the present time have been pre-programmed through selective mortality in past years, rather than occurring in direct response to conditions encountered by birds on an estuary in the year of movement, must be considered. Clearly if selective mortality in past years has been of major importance in the origin of movements seen at present it may not be possible to relate the movements observed at present to the present-day distribution of factors affecting energy balance. This might provide an explanation for the moulting areas used in North-West Europe. In this region, the Waddenzee, Wash and the Ribble are the three most important post-breeding moulting areas. The first two are the largest estuarine areas in North-West Europe, but the Ribble is relatively small. Movement from the Waddenzee after moult can be related to temperature and wind chill. However on the Ribble there is no conclusive evidence of/

of any factors which explain the great use of this area in autumn, but a reduction in its use in winter, nor of the lack of use of Morecambe Bay, a much larger area in autumn. Although data on the seasonal abundance of the food supply are lacking it is unlikely that this changes in such a marked way to result in the marked change in usage observed. Furthermore, even if the food supply on the Ribble is particularly good in autumn it seems unlikely that it will be that much better than on Morecambe Bay (where high densities of *Macoma* are present throughout the autumn) to explain the restricted use of Morecambe Bay in autumn. Unfortunately, few data are available on numbers of shorebirds using the Ribble and Morecambe Bay before the start of the Birds of Estuaries Enquiry counts. Thus it is possible to examine only superficially whether the use of Morecambe Bay and Ribble has changed greatly during the past 100 years. Counts given for the Lancashire coast for 1967-68 and 1968-69 by Greenhalgh (1969) cannot be used to investigate this. Only parts of the coast were counted e.g. only the north shore of the Ribble, not the whole estuary. Thus in view of the local movements of birds between roosts that have been reported it seems likely that the low numbers of Knot and Bar-tailed Godwit reported by Greenhalgh (1969) for the Ribble may be a result of incomplete coverage rather than to small numbers of birds actually present. Indeed large numbers of Knot have been reported/

reported to use the Ribble, especially in autumn, since the early 20th century (Oakes, 1953; Wagstaffe, 1926). In contrast however Holder and Wagstaffe (1930) reported that in autumn 1921-29 only about 200 Bar-tailed Godwit used the Ribble. However it is not possible to conclude, without data from other estuaries for this period, whether the low numbers using the Ribble indicate that fewer birds moulted in Britain at this time or whether other British estuaries were used instead in autumn. Thus it seems that the Ribble has been used as a moulting area by Knot for at least the past 60-70 years but that this may not be true of Bar-tailed Godwit.

Consideration of the evolution of use of the Ribble as a moulting area rather than the larger area of Morecambe Bay requires knowledge of the history of the topography and prey populations in each area. The Quaternary history of both areas is well known (Huddart et. al., 1977). Over this period the size of each area has increased and contracted as the sea level rose and fell. However the most recent incursion by the sea occurred ca. 800 years ago and affected only the Ribble (Huddart et. al., 1977). Thus it seems likely that since this last incursion the Ribble has been or has become a more favourable moulting area than Morecambe Bay. However how this may have come about is unclear. Although no information on the topography or invertebrate populations of the two areas is available it is possible that sediments on Morecambe Bay/

Bay may have been more mobile more recently and, because of this, unable to support large prey populations. Thus at some time within the past 800 years birds may have used the Ribble as a moulting area and in winter moved further south to southern Europe or Africa. More recently, as sediments stabilised and prey populations became established these birds may have begun to move from the Ribble to Morecambe Bay to winter rather than moving further south. However this scenario does not explain why birds leave the Ribble at the end of moult. This may be because of the downward migration and decrease in availability of Macoma in winter. Also the suggestion that at the present time birds moult on the Ribble, even although prey are available on Morecambe Bay, because they have not adjusted to the recent development of prey stocks on the Bay, suggests that shorebirds are very slow in adapting to changing food distribution. Yet the mobility of Knot described in this thesis and by other workers e.g. Greenhalgh (1969) suggests that this is unlikely. Perhaps the possibility that birds during moult require specific types of roost site which are not available on Morecambe Bay but do occur on the Ribble requires more consideration.

Further speculation on the evolution of these shorebird movements is not worthwhile as data are so limited. However future consideration of the persistence from year to year of the movement patterns described will/

will allow more sound hypotheses to be advanced as to the evolution of these movements. In this respect I suggest that long term monitoring of shorebird numbers and their invertebrate food supply in selected estuaries, wherever possible combined with long-term marking of individual birds, to identify changes in seasonal use of estuaries, will provide much insight into the problems I have discussed.

Individual differences in movement pattern.

The seasonal pattern of use of the Wash by Knot cannot be explained by changes in the food supply. After birds have moulted on the Wash, some leave, but more birds arrive in November and December; yet no similar fluctuations in the food supply are evident. Thus the data suggest that some individuals are pre-programmed to move south after moult on the Wash, whereas others from the same area move north, along the east coast and at least in some years west to the Irish Sea coast. Following this departure other individuals which have moulted elsewhere arrive and replace them on the Wash.

The advantages of moving from the Waddenzee to the Wash and from the Wash further south are clear. As discussed above, average temperatures and the risk of severe weather are lower on the Wash than the Waddenzee. However even on the Wash the risk of severe weather is considerably/

considerably greater than further south, for example on the west coast of France. Thus both movements take birds to areas where the risk of cold-induced energy stress is less than at their origin. However it is not clear in what way birds arriving on the Wash from Holland differ from those leaving the Wash, nor from those which remain in Holland in mid-winter. Possibly those birds remaining in colder areas are more efficient foragers i.e. expend less energy in gathering a given biomass of food. Also it is likely that the effects of such differences will be accentuated where dominance hierarchies form. Aggression does occur in flocks of Knot (Goss-Custard 1970; Pers. Obs.) although it is not known if a constant hierarchy exists. Further it is possible that metabolic rates of birds which remain in colder areas may be slightly lower than of those which move further south. However, there are ringing records of birds present on the Wash in one winter and in France in another at the same time as, or earlier than, caught on the Wash (Table 3). Thus the individual variation I have suggested may not result in movement to the same place every year. However how birds choose where to go (or are forced to go) each year is not known.

Similar individual variation in movement pattern occurs among Grey Plover. In the study on the Tees estuary (Chapter 3) great variation in timing of movement was apparent. The data suggest that in autumn/

Table 3. Recoveries in France in subsequent years of Knot ringed on the Wash.

Date of capture on the Wash	Age at 1st capture	Date of capture/ recovery in France	Area of France
27-8-68	Adult	14-8-70	Charente-Maritime
26-10-68 13-9-69	"	6-9-70	Gironde
10-1-70 27-2-71	Juvenile	29-10-71	Calvados
7-3-70	Adult	20-8-72	Gironde
7-3-70	"	19-9-70	Gironde
19-2-72	"	27-7-72	Gironde
22-8-78	"	27-7-79	Gironde

Note: Only records of recoveries which occurred earlier in the year than the date of first ringing are included as these provide the best indication that birds have changed their movement pattern between years.

autumn many birds leave the estuary voluntarily, some after a very short stay, but others after several months. However others leave in autumn after being unsuccessful in establishing a territory. These enforced emigrations can be attributed to differences in dominance status. However no information is available on why individual variation occurs in the timing of apparently voluntary movements.

Thus among shorebirds using each estuary there is great intraspecific variation in timing and direction of movement. Some of this variation can be attributed to differences in dominance status of individuals. However the reasons for most of the variation are unclear. It seems possible that different individuals may be physiologically better adapted to wintering in colder conditions, and that these stay in North-West Europe, while those less well adapted to survival during cold weather move south. However no information is available to test this. Hence detailed study of individual variation in metabolic physiology of shorebirds could prove to be of great value in understanding the intraspecific variation in movement patterns described.

Movement strategy of Knot using the Tees estuary.

Movements of birds through the Tees estuary in 1978-79 and 1979-80 cannot be related to the food supply. In/

In 1978-79 the marked fluctuations in numbers of birds present were not accompanied by similar fluctuations in availability or abundance of *Mytilus edulis* the main prey species. Similarly, although in 1979-80 the prey population was not monitored, movements of birds both north and south from the Tees in November (within a few weeks of arrival of birds on the estuary) did not coincide with the occurrence of storms and associated wave action, the factors most likely to cause changes in abundance of *Mytilus*. These fluctuations in numbers and movement of Knot, which are apparently unrelated to changes in prey abundance, are similar to those described for Sanderling which feed on the exposed marine beaches at the mouth of the Tees estuary (Brearey, 1981; Evans, 1981) and also reported from California by Myers (1980). Evans (1981) has discussed such movements in terms of the predictability and constancy of the food resources utilised in these areas. The marine beaches are exposed to considerable wave action which, when especially severe, can remove large areas of substrate and the prey populations these contained. Thus it is to a bird's advantage to be aware of alternative food resources on neighbouring areas of coast which may be used in the event of such removal of prey occurring. This concept can be extended to Knot, although on a larger scale. Birds which arrive on the Tees in November and then move to another area, after a few days or weeks at Teesmouth, will obtain knowledge of the status of the prey population/

population in several areas. Thus if, for example, severe wave action removed all Mytilus from the rocks on the Northumberland coast individuals which have visited the Tees will have experience of whether prey stocks were large there and likely to provide a sufficient food supply if they return there. Thus the risk to one of these transient (itinerant) birds of moving to an area with insufficient resources is less than the risk to a bird which did not possess knowledge of other areas. It is likely that further long-term study of individually colour-marked individuals on the Tees would allow investigation of year to year variation in time of arrival, length of stay on the estuary and location of mobile individuals along the Northumberland coast. It is hoped this will lead to more detailed understanding of the extent of movement through the Tees estuary each year, the year to year survival of transient and sedentary individuals, and allow more confident speculation as to the reasons for the behaviours observed.

Chapter 3. Seasonal change in numbers of Grey Plover using the Tees estuary, in relation to spacing behaviour and prey availability

INTRODUCTION

Few intensive studies of the dynamics of wintering populations of shorebirds have been made. Attention has normally been directed towards ringing and biometric studies e.g. Minton (1975) or feeding ecology and behaviour (Goss-Custard, 1969; Prater, 1972; Smith, 1975; Pienkowski, 1980; Townshend, 1981). Rarely has a synthesis been attempted of these subjects with population parameters such as survival and emigration. However, it is readily apparent from Chapters 1 and 2 that full understanding of the interrelationships between shorebird movements and the population parameters of their invertebrate prey, environmental conditions and the social organisation of shorebird populations during winter requires such a synthesis.

Most previous discussions of population processes in wintering shorebirds have been restricted to consideration of factors affecting flock density. Goss-Custard (1970) reviewed these, concluding that compact foraging flocks were formed primarily as an antipredator response, wherever this was compatible with the foraging behaviour of the birds. Thus birds feeding by touch can afford to feed in compact flocks as the cues used to detect prey are not suppressed by activity of birds on the mud surface whereas the levels of invertebrate activity needed by visual/

visual predators are depressed and therefore these birds are more dispersed over the feeding grounds. However, while such mechanisms are certainly of major importance in regulating flock density in a particular prey patch, little information is available to indicate how such studies can be extrapolated to regulation of estuarine population size. That behavioural control of flock density may lead to regulation of population size during times of food stress has been shown in Woodpigeons Columba palumbus (Murton, 1968) and suggested in Rooks Corvus frugilegus (Patterson, 1975). However, although there is some evidence of mortality among Grey Plovers at Teesmouth, and of other species in other areas (see Evans, 1976), during severe weather, there is little convincing evidence of shorebird movements in direct response to either reduced rates of energy intake or increased energy demands during such severe conditions (Evans, 1976). Further, the social organisation of many shorebirds has been shown to be considerably more complex than that described in the Woodpigeon and Rook. For example some individuals of many shorebird species have been found to exhibit territoriality on some of the wintering grounds, but not on others (Myers et.al. 1979a). While many of these territories are short term, lasting only a few hours, some have been shown, in a number of species, to last for several months e.g. Sanderling (Myers et.al. 1979b); Grey Plover (Knights, 1979); Curlew and Grey Plover (Townshend, 1981) and Curlew (Zwartz Pers. Comm.). Although many individuals/

individuals of the same species may be present in flocks on the same wintering site the potential importance of territoriality in affecting numbers on a wintering area is clear. However, to date, no studies of this have been attempted in any shorebird species. Consequently the role of territoriality in regulating numbers of shorebirds present on an estuary in winter remains open to speculation.

On the Tees estuary in North East England the number of Grey Plovers present in winter varies between 100 and 300 yet both long term territoriality and flock feeding are found. Since 1976 a sizeable proportion of the birds have been marked with unique combinations of colour rings allowing individual identification. Taking advantage of this situation, a study of seasonal change in numbers and movements of Grey Plovers using the Tees estuary was undertaken with the aim of furthering understanding of the relationship between these phenomena and potential controlling factors particularly shorebird social behaviour and prey availability.

STUDY AREA

Since the beginning of the nineteenth century much of the original intertidal sand and mudflats (2,400 ha) of the Tees estuary (54° 37'N 1° 12'W) has been reclaimed (Evans et.al. 1979). Today only two major areas, Seal Sands (140 ha) and Bran Sands (60 ha) (Fig. 1) remain, of which the former is much the more important feeding area for shorebirds. To the north and south, the mouth of the estuary is bounded by sandy marine beaches and rock outcrops. During daylight hours the majority of Grey Plovers on the estuary feed on Seal Sands, although when numbers are high some feed at low water on parts of Bran Sands and the rocks at the mouth of the estuary. However at night more birds feed at the lower tidal levels on Bran Sands and North Gare Sands, a marine beach on the north side of the estuary (Dugan, 1981). The study of Grey Plover reported in this chapter was carried out entirely on Seal Sands.

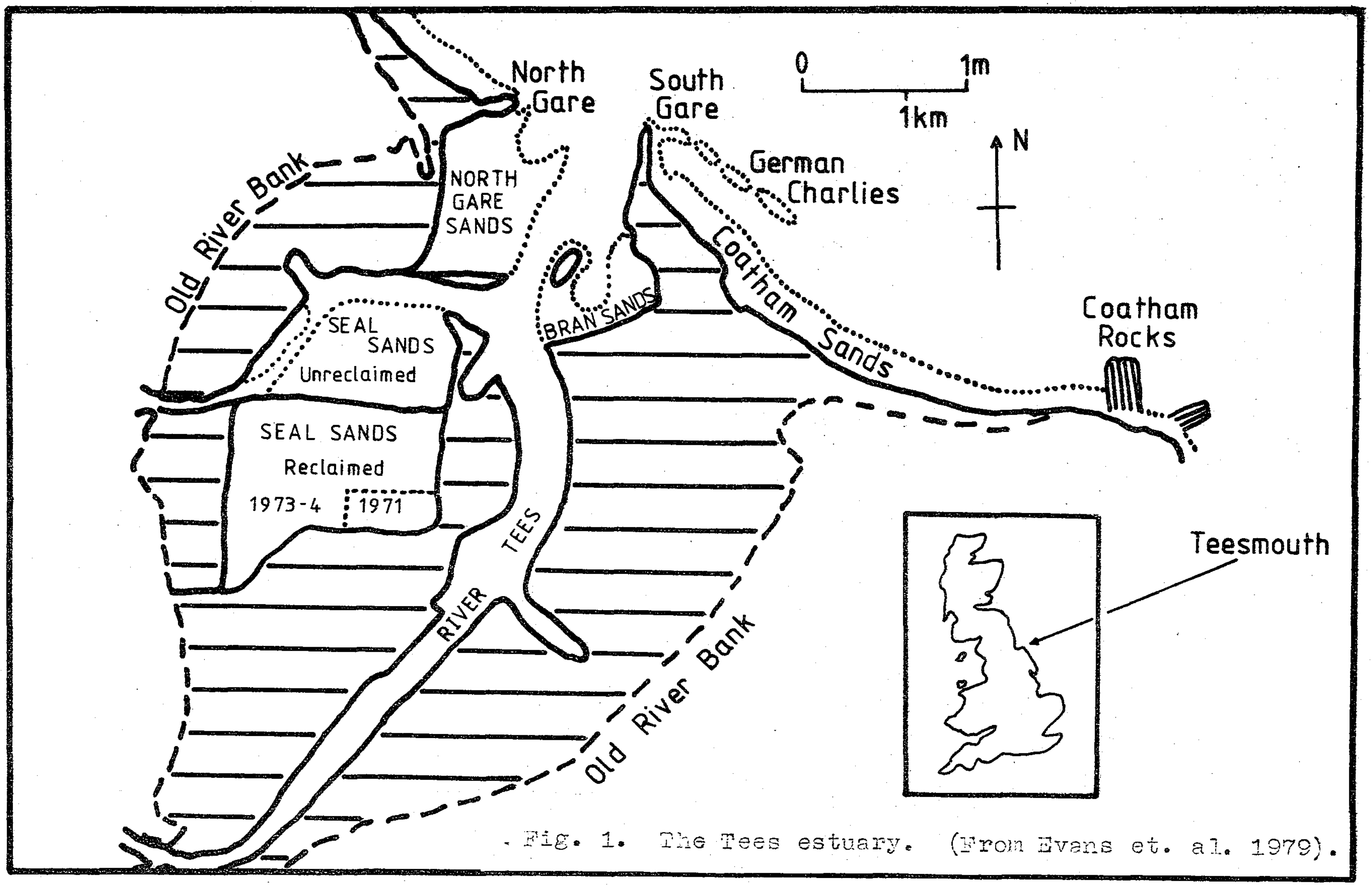


Fig. 1. The Tees estuary. (From Evans et. al. 1979).

METHODS

A. Invertebrates

1. Distribution

On Seal Sands four species of macroinvertebrate are common. These are Nereis diversicolor; Hydrobia ulvae; Macoma balthica and Corophium volutator (Evans et.al. 1979). However of these species only Nereis and Hydrobia are abundant. The macrofauna was surveyed extensively in June and November 1978 and March 1979, following a preliminary sampling in February 1978. An aluminium corer, diameter 11.0 cm and surface area 133 cm^2 was used. Samples were taken to a depth of 30 cm to ensure that Nereis which were observed to burrow to this depth in mid-winter were not missed. Access to firmer areas of the mudflats was achieved by walking, but areas of softer substrate were reached by wading behind a rubber dinghy, using this as a support. Because of the viscous nature of the mud over much of the study area, sieving of samples could be accomplished only by use of a high pressure water jet which resulted in most Nereis being broken up, or forced through the sieve. As it was important to know the length of all the animals sampled, an alternative method of invertebrate extraction was developed. Samples were placed in 5 - litre plastic containers and clean sea-water poured on top to a depth of about 3 cms. They were then left for three days. During this period Hydrobia coming to the surface were picked off. After this, numbers of Hydrobia coming to the surface diminished almost to zero. The sea water was then replaced by salt water twice the concentration of sea water (75 ml. salt/litre). The samples/

samples were left for a further three days during which all Nereis and Corophium coming to the surface, to escape the adverse environment, were collected. Almost all Nereis were extracted from the mud in this way. During the preliminary sampling the efficiency of this method of extraction was determined as ca. 95% by sieving all the samples at the completion of the procedure (Appendix 1.).

2. Quality

In addition to the extensive sampling programme, other Nereis were collected, by digging, from several areas for determination of dry weights and calorific values. Worms were left in clear estuarine water for 24 hours, killed by immersion in alcohol for approximately 60 seconds, measured to the nearest millimetre and dried at 60°C in a vacuum oven. Animals were subsequently weighed to 0.1 mg. using a Mettler balance. For each sampling date and for each area from which animals were collected regression equations relating dry flesh weight to body length were calculated. These are given in Appendix 2.

Hydrobia collected during the extensive sampling programme were prepared in a similar way to Nereis, i.e. kept in clear sea water for 24 hours, before drying in a vacuum oven. The shells were then removed with dilute hydrochloric acid, and flesh dried again before weighing.

Calorific determinations were made using a Phillipson Microbomb Calorimeter (Phillipson,1964).

B. Grey Plovers.

1. Numbers.

a. Individually marked birds

Forty five birds were colour marked during the previous study (Townshend 1981). This total was increased to 200 during the present study. 128 were caught in 1978-79 and 27 in 1979-80. Of these, 153 were caught with cannon nets at daytime roost sites and two mist-netted at night. Each bird was weighed, measured, ringed with a numbered metal (B.T.O.) ring and given an individual combination of coloured darvic rings, before release. Initially, combinations of three coloured rings were used but this was increased to four at the end of January 1979 when all unambiguous three-ring combinations had been used. Loss of rings, from four-ring combinations, which might have led to confusion with three-ring combinations, has not been known to occur.

b. Counts

Only counts of birds (i) at all known high water roost sites, (ii) flying to these roost sites, or (iii) at pre-roost gathering sites have been used to measure total numbers of birds present on the estuary (See Appendix 3). The usefulness of low water counts for this purpose is limited since it is possible consistently to miss large numbers of birds because of the topography of the habitat, the creek feeding habit of many individuals, the distance over which these counts of some areas have to be made and the often restricted visibility during the counts. Furthermore, because of day to day changes in the/

the location of flock-feeding birds, it was not possible to use low water counts to detect and measure accurately trends in population size, as birds could not be counted with equal accuracy in all feeding sites used by the flock.

Particularly in winter, it was possible to attempt accurate counts of the total population on only a few days of each tidal series. Furthermore on some of these same days, it was necessary to search for colour ringed birds. Hence confident accurate counts were made on relatively few occasions each winter, and the timings of population changes thus cannot be determined very precisely from them. To identify the periods of influx and departure it was necessary to supplement the counts with data on arrival and departure of individually marked birds (see Appendix .4.). Furthermore, these data from marked birds were used to determine whether birds moved into and out of the estuary at times which were not detectable from count data alone (since if immigration equalled emigration no change in numbers of birds present would occur). Only in autumn was evidence of this obtained. All influxes of colour marked individuals in winter occurred during periods of population increase.

During both years of the study six main periods when numbers of birds changed, or remained approximately constant, were recognised. Autumn when numbers fluctuated as birds arrived and departed; Post-Autumn - when the population remained constant in size; 1st Influx - the time of the first large increase in numbers; Post-Influx - when following/

following the 1st Influx numbers remained constant or decreased; 2nd Influx - the time of the second large increase in numbers; and Spring - the time of pre-breeding departure. The precise dates of these periods varied somewhat between years, as will be shown later. However as descriptions of time periods they are of much more relevance than calendar months, to the population of Grey Plovers at Teesmouth. Consequently, throughout the text, these terms are used to describe the occurrence of events within the population.

C. Distribution.

All counts of birds feeding on Seal Sands were made, by X 15 - X 60 telescope, from a Land Rover, functioning as a mobile hide, driven along the reclamation walls along two sides of the mudflats. The route and locations of census points are shown in Fig. 2. An 8 x 8 grid of colour-coded stakes at 100 metre intervals had been erected, during a previous study (Townshend,1981), on Central Bank, the largest expanse of mudflat. Using this and the natural heterogeneity of substrate type in other parts of Seal Sands the feeding area was divided into sub-areas and the birds in each counted separately. However, after study of the numbers and behaviour of birds using each sub-area, these have been reduced to nine by grouping (Table 1). Areas were measured from aerial photographs taken in 1976.

2. Behaviour./

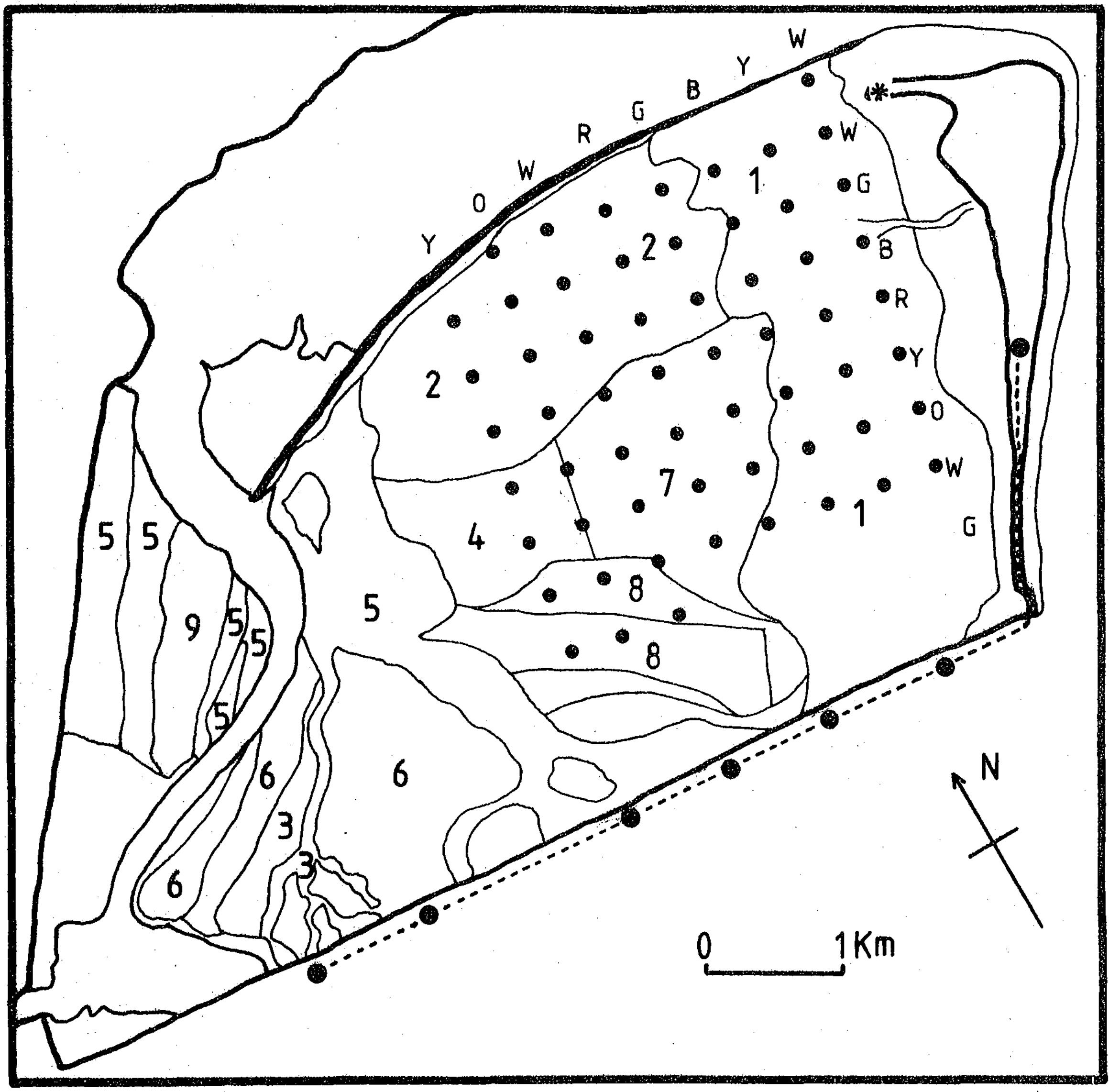


Fig. 2. Seal Sands. Grey Plover feeding areas are numbered 1-9, see Table 1 for descriptions. Letters refer to rows of coloured posts in 100 x 100 metre grid on Central Bank and Eastern Channel. -----●---- Route taken during low water counts and points from which counts and other observations were made. ✱ Site from which detailed observations of territories in Eastern Channel were made.

Table 1. Description of principal Grey Plover feeding areas on Seal Sands.

Area[1]	Size (ha.)	Description
1. Eastern Channel (E.Ch.)	40	Mainly sandy substrate but finer at north and south ends. One deep creek (Plate 1) runs the length of the area but ramifies at the northern end.
2. Central Bank. Far *Enteromorpha*	22	Firm sand underlying a shallow covering (ca. 2 cm) of mud on which grows a thick sward of *Enteromorpha*. Greatly dissected by wide, deep creeks (Plate 1).
3. Scalloped Mud East Ridge and Creek	4	A ridge of firm mud bordering a deep creek[2].
4. Central Bank (mud). Orange post to Central Channel (O-C.Ch.).	5	Firm viscous mud ca. 30-40 cm. deep, overlying sand and criss-crossed by small, narrow creeks (Plate 1).
5. Greenabella Bank + Central Channel, lower tidal levels.	27	Low lying areas of the mudflats. Soft mud with a high water content.
6. Scalloped Mud Main + Side	18	Predominantly firm viscous mud.
7. Central Bank (Mud) Orange to green posts (O-G).	15	The area adjacent to O-C.Ch. and of similar substrate type and topography.
8. Central Bank Sand + *Enteromorpha*	11	Sand, the southern part of which is overlain by firm mud varying in depth from ca. 2-15 cm. on top of which grows a thick sward of *Enteromorpha*.
9. Greenabella Bank. High tidal levels.	4	Firm viscous mud, the surface of which is criss-crossed by narrow creeks and dotted with shallow pools which retain water for several hours after the tide has receded.

Notes. 1. These subdivisions of Seal Sands differ from those described by Evans et.al. (1979).

2. Area 3 divides area 6 but counts were separated because of the territorial behaviour of birds in 3.

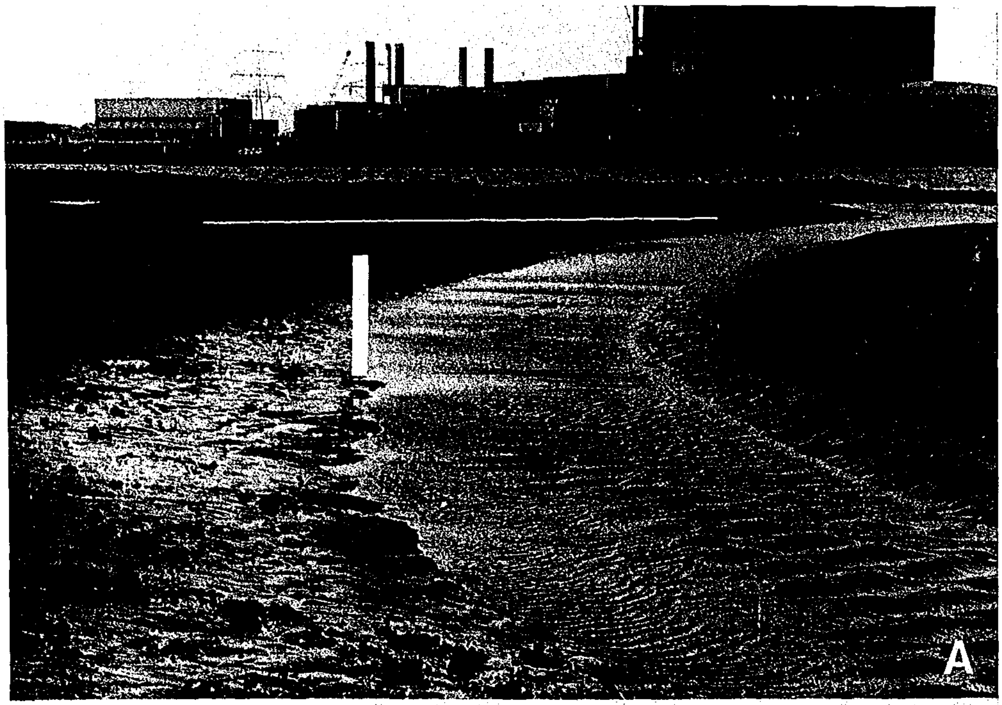
Plate 1. Grey Plover feeding areas 1,2 and 4.

(a) 1. Eastern Channel - showing creek in territory of Y Y/O.

(b) 2. Central Bank, Far Enteromorpha - showing one of the deep creeks which dissect the area.

(c) 4. Central Bank, O-C.Ch. - showing one of the small drainage creeks.

In each area thick vertical white bars represent one metre height. Thin horizontal white lines drawn across the top of each creek allow comparison of the depth of the creeks in each area.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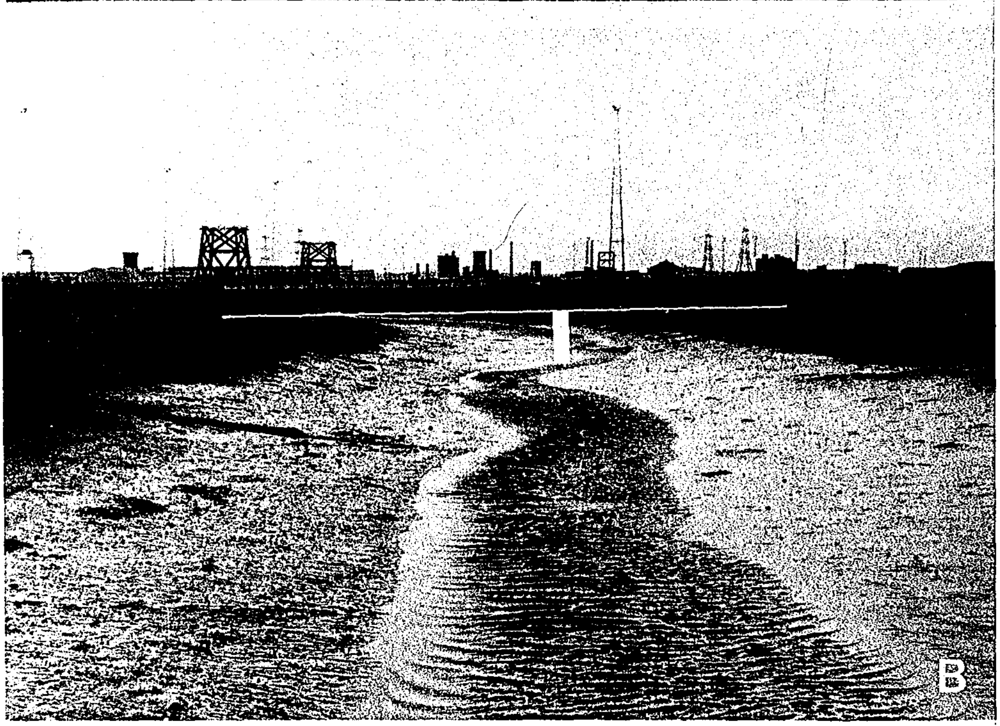
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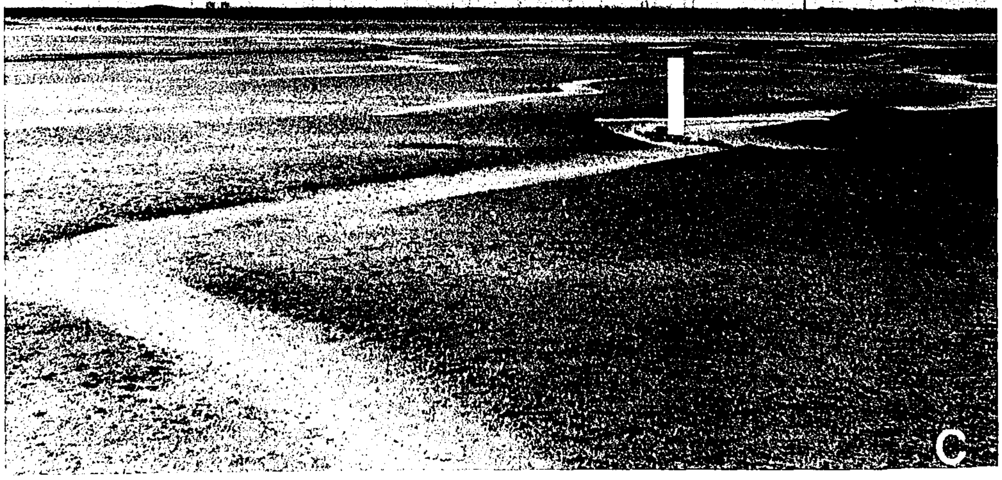
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2. Behaviour

a. Flocking birds

Observations of flock birds were made from a hide mounted on a rubber dinghy and beached on the mud on the ebbing tide, on different sites on different days. Birds showed no adverse reaction to the hide and regularly approached to within ten metres. Rates of food intake were measured by direct observation (by telescope) and recorded on a portable cassette taperecorder. In view of the limited variety of macrofauna each prey taken was normally identified with confidence. The sizes of Nereis taken were estimated by comparison with the bill-lenghts of the birds. Unlike the situation in most waders the variation in bill lengths of individual adult Grey Plovers is fairly small ($\bar{x}$ = 30.1 mm ± 0.1, n=852; Branson and Minton, 1976). The estimates of worm length made by comparison with bill length are clearly open to some error. However, a check on their accuracy revealed the error to be small and enabled correction for this (Appendix 5.).

For analysis of food intake rates only birds watched for three or more consecutive minutes were used. After this point variation in mean intake rate per minute for each individual remains relatively constant with increasing observation time. (Appendix 6.).

During all feeding observations the durations of all other activities i.e. preening, roosting, aggression and anti-predator behaviour were measured and used in constructing time budgets.

b./

b. Territorial birds

The dissected topography of Grey Plover territories made the use of a dinghy-mounted hide impractical for good observations of feeding birds, since these were frequently out of sight in creeks for long periods, or if feeding on the high-level mud continually disappeared behind small bumps. For this reason, detailed observations of territorial birds were confined largely to those feeding within observation distance of the reclamation wall, which provided raised vantage points. However, even from these positions, many birds in Eastern Channel were frequently hidden from view. Observations, like counts were made from a Land Rover.

Both the rates of food intake, and the time budgets of birds whose intake was studied, were measured in the same way as for flock birds. Territory distribution within Eastern Channel and activity of these territory holders was determined by systematically scanning each territory in turn, as frequently as possible, (ca. every 10 minutes), during one or more 45 minute periods, and recording the position and activity of each bird on a cassette recorder. Positions of birds were subsequently plotted on large scale maps of the area (drawn from aerial photographs) and the frequency of each activity calculated. During each circuit of territories some birds were not visible and it is likely that, as a result, observations will be biased in favour of the activities, particularly aggression, which increase conspicuousness. However, as discussed in the appropriate section, the effect of this bias on the conclusions from these data is small. Also attention was sometimes directed towards particular/

particular individuals involved in long periods of one activity e.g. long territorial encounters. This may also have led to bias in the activity analysis. However, the systematic nature of the observations i.e. through a series of visual circuits of the territories, scanning each equally frequently within an observation period, were designed to avoid such bias.

C. Territorial bird R W/G.

Intake and time budget data were recorded in the same way as for flock birds, but observations were made from a Land Rover positioned at the tip of Eastern Channel. The position of the territory boundary was recorded both while recording those of the other territorial birds in the area and during feeding observations. While recording feeding data the position of the bird was noted as frequently as possible using physical features of the territory as reference points.

3. Quantification of energy intake.

a. Intake of worms.

Using the regression equations for body weight of *Nereis* against body length, given in Appendix 2., mean body weights of *Nereis* ranging (in $\frac{1}{4}$ bill length divisions) from $\frac{1}{4}$ bill length (0.75 cm) to 4 bill lengths (12.0 cm) were calculated. Using the calorific values for *Nereis* appropriate to each sub-area, weights were then converted to energy contents of animals, of each body length class for each date on which *Nereis* was sampled. Energy contents of/

of Nereis , corresponding to each date of observation of feeding Grey Plovers, were then obtained by extrapolating from a plot of seasonal change in calorific content of Nereis in each body length category. In 1979-80 this procedure was repeated to obtain data for Eastern Channel and Central Bank O-C.Ch. Values used in calculating energy intake in other areas were estimated from the previous year's data.

b. Intake of Hydrobia.

Using values for the average dry weight of each of the larger size classes (i.e. 2.5 - 3.4 mm and 3.5 - 4.4 mm shell height), given in Appendix .7., the biomass of these size classes per core for Scalloped Mud, Central Bank O-C.Ch ., and the higher tidal levels of Greenabella Bank, was obtained by multiplying the mean number of each size class per core in these areas by average body weight and summing the values obtained. This was then converted to calories using the calorific values given in Appendix 8. The calorific value of an average Hydrobia taken by Grey Plovers (assuming that only animals of sizes between 2.5 mm and 4.4 mm are taken) in each feeding area was then calculated by dividing total calories per core i.e. 133 cm^2 by the mean number of 2.5 mm - 4.4 mm animals per core.

c. Intake of Macoma

Two sizes of Macoma were taken by Grey Plover (1) slightly greater than 1/3 bill length and (2) ca. 1/5 bill length/

length. Using my data from the Humber, the dry weight of a *Macoma* of 11.0 mm shell length was estimated as 10.5 mg. For small *Macoma* (1/5 bill length) dry weight was estimated as 2.0 mg. Calorific value was taken as 5.1 cals/mg as given by Evans et.al. (1979). Using these figures values for calorific content of 54 cals and 10 cals were obtained for *Macoma* ca. 1/3 bill length and 1/5 bill length respectively.

d. *Intake of Corophium*

Millard (1976) gives a value for mean dry weight of 4-7 mm body length *Corophium* as 0.428 mg. Goss-Custard (1977) assumed a calorific value of 4.35 cals/mg. Using these figures a value of 1.9 cals/item was obtained. Thus all *Corophium* recorded were given a value of 2 cals.

NUMBERS OF BIRDS

My data for 1978-80 reveal marked seasonal changes in the number of Grey Plovers using the Tees estuary. In autumn numbers fluctuated but gradually rose to a peak in October, decreased in November and rose again in winter when two major influxes occurred (Fig. 3). The autumn peak was composed of passage and potential wintering birds, both adult and juvenile. Most of the adults moulted on the estuary (Table 2). Numbers fell as passage birds left (Table 3). However, not all adult birds arriving on the estuary in autumn stayed to moult. Many arriving in August and September spent only a few days on the estuary and much turnover occurred at this time (Fig. 4). It is possible that many of the birds which passed rapidly through the Tees in early autumn were in suspended moult. Of the birds caught on 18-9-78 five were in suspended moult. Of these, four were not seen again after capture, which suggests rapid departure. (The fifth was found dead.) None of these birds was seen in the following autumn and consequently the possibility that they died, rather than migrated, after capture cannot be excluded. Some evidence suggests that other birds arriving in August and September, although staying longer also do not moult. Four individuals caught in September 1978 were of very high weight and non-moulting (Table 2). Of these two were not seen after 9-10-78 and one after 3-11-78. The other bird remained until late in November. However, during/

Table 2. State of moult and body weight of Grey Plover caught on the Tees estuary on 18-9-78.

Age and stage of moult	No. of birds	Body Weight (grams).			
		Max	Min	$\bar{x}$	S.E.
Adult. Moulting	27	270	207	231	3
Adult. Arrested moult	5	256	216	229	6
Adult. Non-moulting	4	362	273	325	16
Juvenile	1	-	-	193	-

Table 3. Estimated dates of departure of individually colour-marked birds present on the Tees estuary in autumn only. Dates given are those on which the individual was last sighted. The periods given are those of calculated departure time (see Appendix 4.).

A = Autumn 1st W = 1st Winter Influx P.I. = Post Influx.

Individual	Time of Departure			
	1978-79		1979-80	
	Date	Period	Date	Period
L W/R	22-9-78	A	15-9-79	A
R L/G	31-10-78	A	30-9-79	A
L G/O	9-10-78	A	22-10-79	A
R O/L	8-11-78	A	25-10-79	A
R R/L	18-11-78	A	11-10-79	A
L G/W	9-10-78	A	11-10-79	A
R R/W	9-10-78	A	11-10-79	A
R W/O	30-11-78	A/1stW/P.I.	22-10-79	A
R G/L	3-11-78	A/1stW/P.I.	15-8-79	A

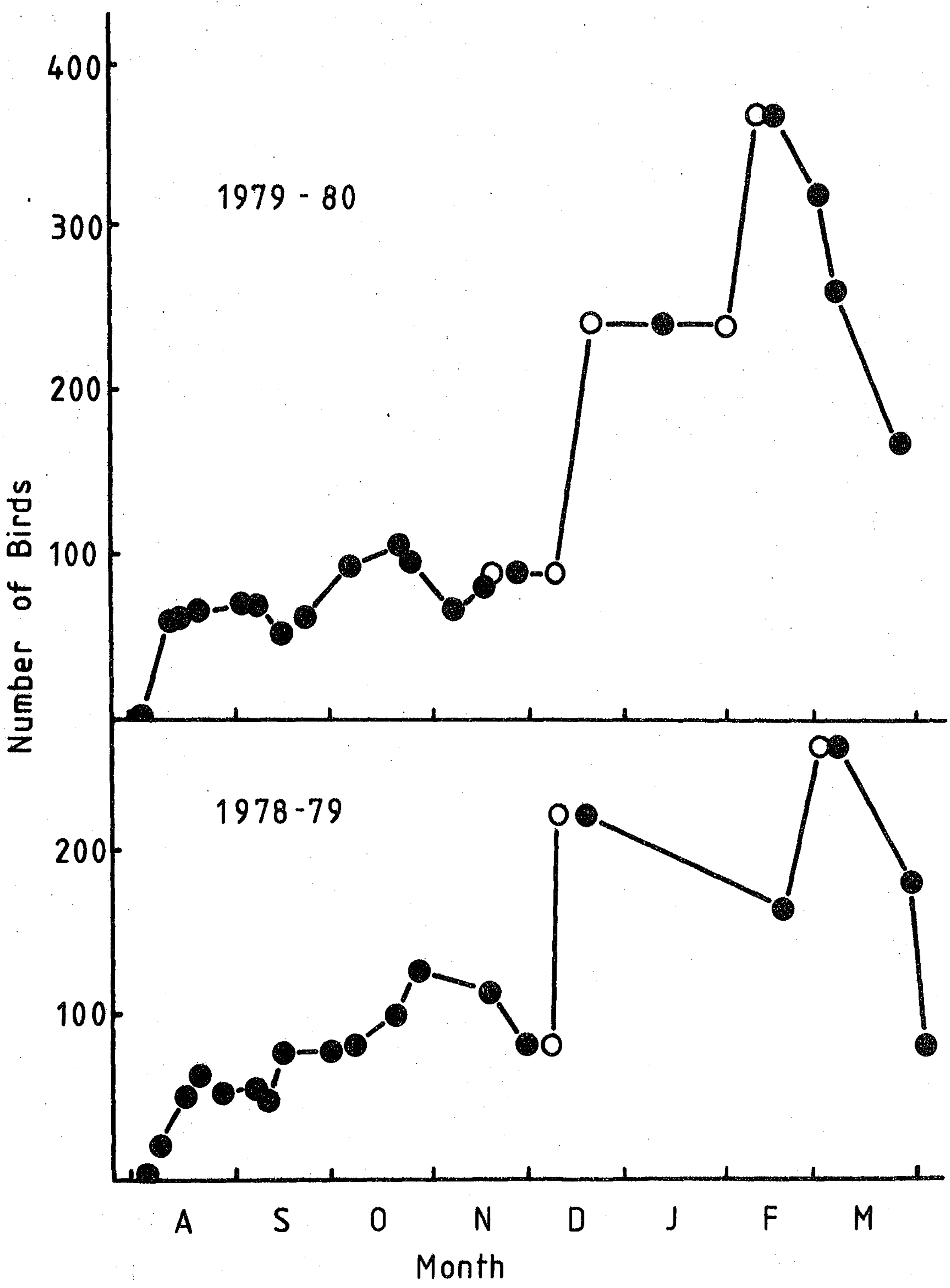


Fig. 3. Seasonal changes in numbers of Grey Plover using the Tees estuary. ● = count ○ = estimated value using sightings of colour-marked birds to indicate time of influx and departure (see Appendix 4).

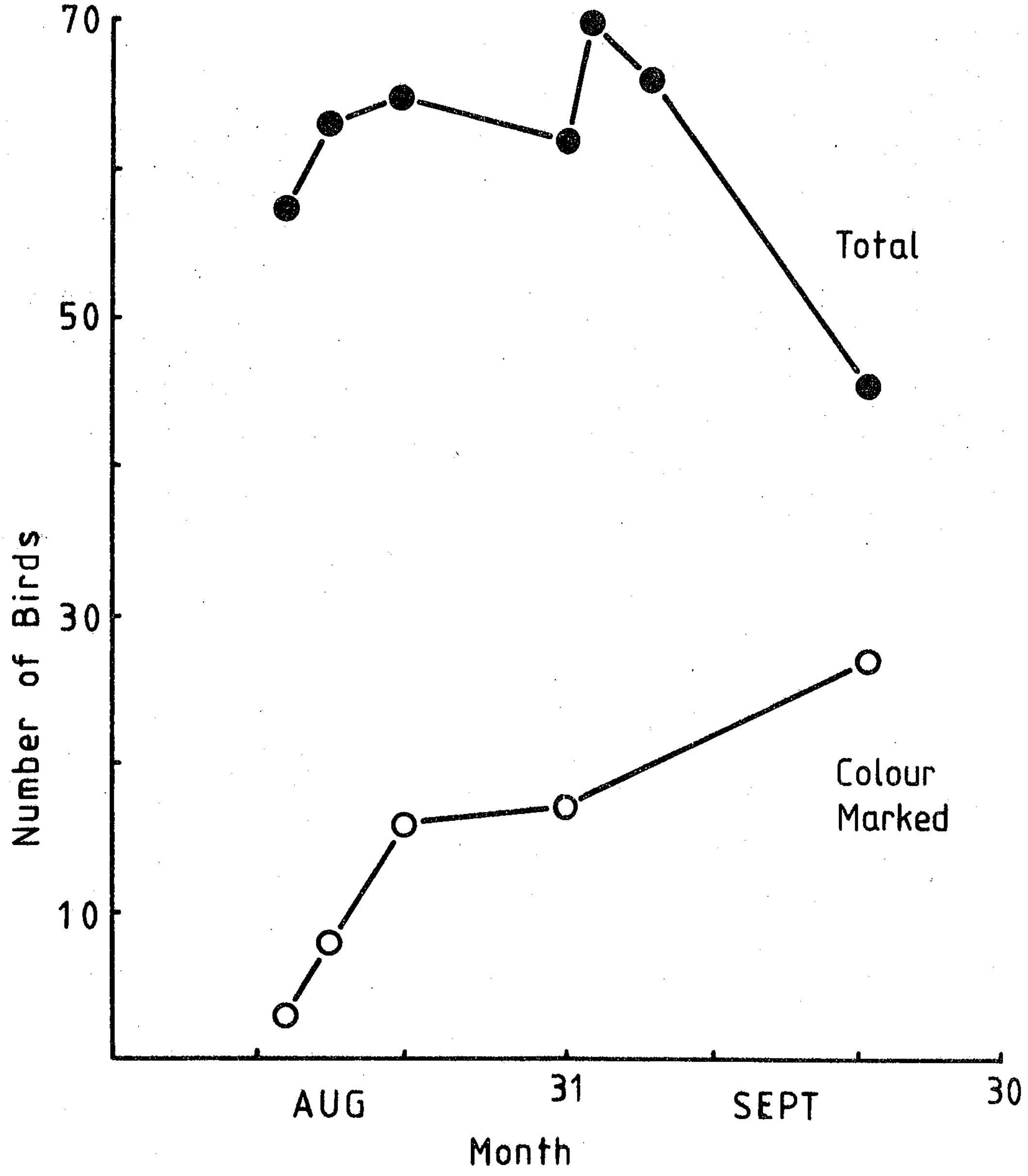


Fig. 4. Total numbers and numbers of colour-ringed Grey Plovers present on the Tees estuary in early autumn 1979.

during this time it retained the same extent (about one third) of black, summer breast plumage as when caught, indicating that body moult was suspended. Why birds of such high weight and presumed high fat and protein reserves did not fully moult their body plumage is unclear.

The seasonal pattern of change in numbers was very similar in both years of the study. Furthermore the composition of each influx and decrease was very similar in each year. Only two changes in time of arrival and seven in time of departure of colour marked individuals were recorded (Table 4). No clear differences between adults and juveniles in regularity of time of arrival and departure were revealed but data are few. The proportion of adults and juveniles among birds present on the estuary followed a similar pattern in the two years. Initially, no, or very few, juveniles were present, the first arriving in September each year. The proportion of juveniles present at Teesmouth, as measured by the percentage in cannon-net catches, then increased through the winter with the early and late winter influxes (Table 5). A similar increase through the winter in the proportion of juveniles present was observed by Townshend (1981).

Return rates of adult birds were high (Table 6). A large proportion of both overwintering and autumn passage individuals present in one year were seen again on the Tees estuary in the following year. (These figures are equal to minimum survival rate.) In contrast birds which departed/

Table 4. Fidelity in time of arrival and departure of individual Grey Plover.

a. Arrival	Time of Arrival 1978-79	No. of Birds Ad.	Juv.	Time of Arrival 1979-80	No. of Birds Ad.	Juv.
	Autumn	29	1	Autumn	29	0
				1st Winter influx	0	1
				Autumn	1	0
	1st Winter influx	9	0	1st Winter influx	8	0
	[1]1st Winter influx or before	31	4	1st Winter influx or before	31	4
	[2]2nd Winter influx or before	19	5	2nd Winter influx or before	19	5

b. Departure	Time of Departure 1978-79	No. of birds Ad.	Juv.	Time of Departure 1979-80	No. of Birds Ad.	Juv.
	Autumn	6	0	Autumn	6	0
	Post influx	5	0	Post influx	3	0
				Spring	2	0
	Spring	55	10	Post influx	4	1
				Spring	51	9

Notes. 1. Birds caught in early and mid-winter and which may have arrived in the 1st winter influx or before.

2. Birds caught after the 2nd winter influx had occured.

The times of arrival and departure of all **individuals** included in the analysis could be identified with sufficient precision to be unambiguously assigned to one of the periods in the population cycle. For simplification and because of the short duration of the post autumn period in the two years of the study, this interval has, for this analysis been lumped with autumn.

Table 5. Seasonal change in proportion of juvenile Grey Plover caught 1978-79.

	1 Autumn		2 Early and Mid-winter		3 Late winter	
	No	%	No	%	No	%
Adult	38	92.7	47	85.5	41	82.0
Juvenile	3	7.3	8	14.6	9	18.0
Total	41		55		50	

1 vs 2 $\chi^2_1 = 4.3137$ $p < 0.05$

1 vs 3 $\chi^2_1 = 8.4200$ $p < 0.01$

2 vs 3 $\chi^2_1 = 0.4636$ $p < 0.01$

Table 6. Rates of return of Grey Plover in 1979-80 in relation to time of arrival/ capture and length of stay in 1978-79.

Only colour-marked individuals whose time of arrival could be identified with sufficient precision to be unambiguously assigned to one of the periods in the population cycle are included in the Table. For simplification and because of the short duration of the post autumn period in 1978-79 this interval has for this analysis been lumped with autumn.

	Adults			Juveniles		
Time of Arrival (or Capture) and Departure	No. present 78-79	No. returned 79-80	% returned	No. present 78-79	No. returned 79-80	% returned
[1]Autumn-Autumn	7	7	100.0	2	0	0.0
[1]Autumn-Spring	25	20	80.0	1	1	100.0
[2]1st Winter-Post influx influx	12	4	33.3	1	0	0.0
[2]1st Winter-Spring influx	44	34	77.3	2	1	50.0
[2] 2nd Winter-Spring influx	26	18	69.2	11	7	63.6

Notes. 1 = Time of arrival 2 = Time of capture.

departed in January or February 1979 (mid-winter) irrespective of their time of arrival had a very low return rate. However, of the eight birds which did not return in 1979-80 three were seen after the severe weather in January 1979 had ended. Thus although the data suggest that the low return rates of birds which departed in mid-winter were at least partially a result of mortality of these birds during the cold weather in January, it is not possible to conclude that this was definitely so. The data for return rates of juveniles are more limited, since only a small number of birds were marked. However, a similar pattern of high return rates of overwintering birds and low rates for birds departing in mid-winter, is shown in Table 6.

The pattern of seasonal change in numbers observed in 1978-80 was similar to that observed in earlier studies of Knights (1979) and Townshend (1981) (Fig. 5). However the precise magnitude and timing of these changes differed between years. Most noticeable among these year-to-year differences are (1) the very high numbers in October 1973 and 1976, (2) the occurrence of two major winter influxes in 1978-79 and 1979-80 but only one, which occurred at different times each year, in 1976-77 and 1977-78 and none in 1973-74 (although counts were made only monthly in this year so that a peak could have been missed) and (3) the variation in size of the winter peaks.

(1) the large autumn peaks in 1973 and 1976 may have been due to large numbers of birds moulting on the estuary in/

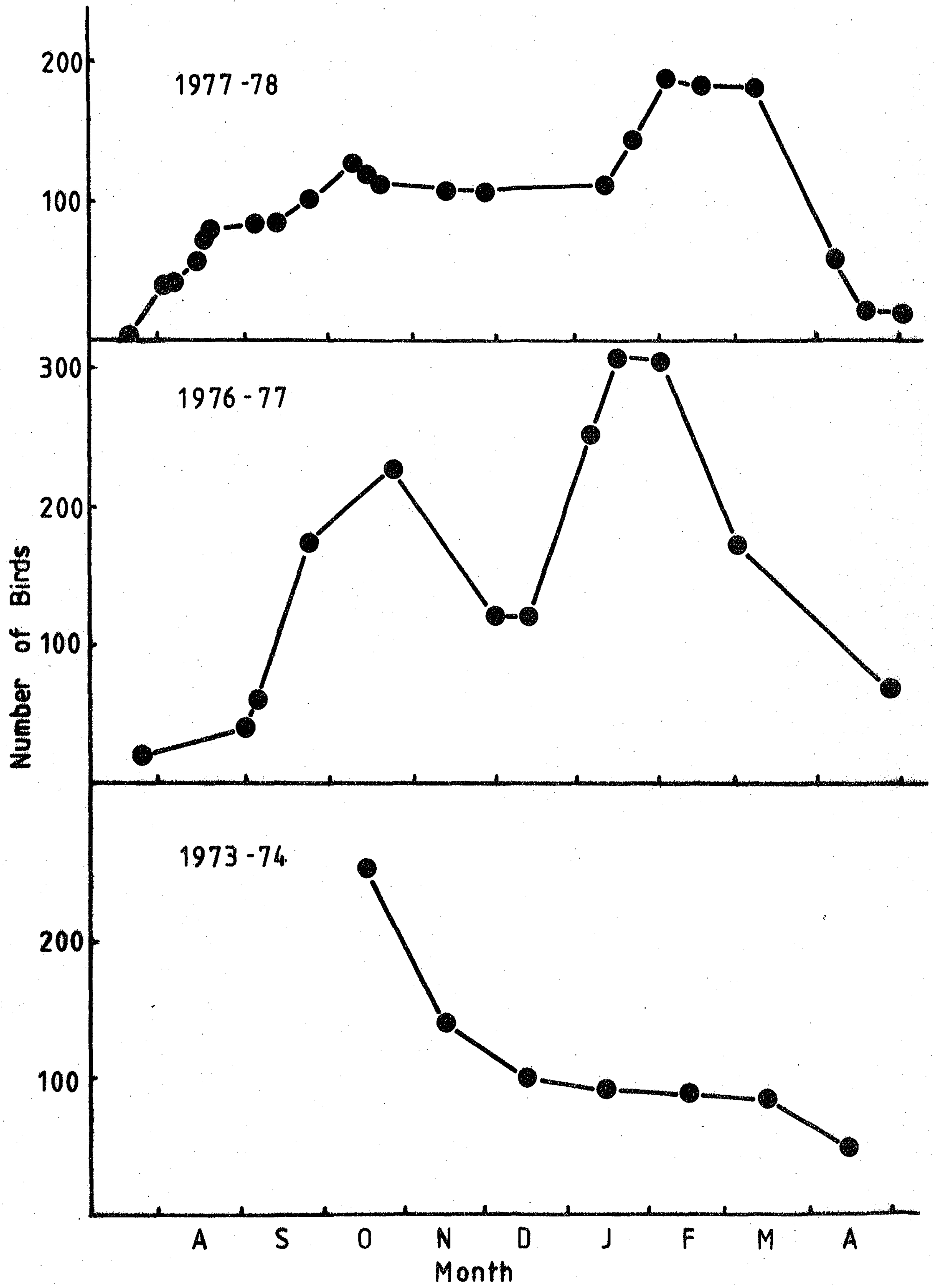


Fig. 5. Seasonal change in numbers of Grey Plover using the Tees estuary. Data from 1973-74 are low water counts from Knights (1979). Those from 1976-78 are high water counts from Townshend (1981).

in these years. However, why the number of birds moulting at Teesmouth might vary from year to year is not known.

(2) From count data alone it is not possible to establish in what way, if any, the winter peaks recorded in 1976-77 and 1977-78 by Townshend (1981) correspond to the two distinct peaks observed in both 1978-79 and 1979-80. However, of a group of birds caught on 12-2-77 i.e. after the peak had occurred in that winter, six were first seen after the peak in the following winter of 1977-78 (Townshend, 1981). Of these individuals five were still alive during my study and all of these returned in the first winter influxes in both 1978-79 and 1979-80 (Table 7). These data indicate that the influxes observed by Townshend correspond to the first winter influxes reported in the present study.

(3) In 1977-78 the winter influx was smaller than in either 1976-77 or the two later years. Seventeen of the birds caught in the 1976-77 winter (on 12-2-77) were not seen, and probably did not return, in 1977-78. However, of these, seven returned at the time of the early winter influx in 1978-79 and three returned a second time in 1979-80, again all in the early winter influx. These data and those for individuals which did return in the first influx in 1977-78 (Table 7) suggest that more birds leave from the source of the early winter influx in some years than others and that when many birds leave it is

the/

Table 7. Dates of first sighting and periods of return to the Tees estuary of colour-ringed Grey Plover first caught on 12-2-77.

Individual combination	Age at capture	Year 1977-78		1978-79		1979-80	
		Date	Period	Date	Period	Date	Period
Y O/R	A	31.10	Autumn	31.10	Autumn	4.11	Autumn
Y R/L	A	10.11	Autumn	24.11	Autumn	31.12	Autumn/ 1st winter influx
L W/L	J	29.8	Autumn	16.8	Autumn	3.9	Autumn
L W/R	J	N.Ob.	-	20.9	Autumn	13.9	Autumn
O W/O	A	12.1	1st winter influx	13.12	1st winter influx	19.11	1st winter influx
Y L/O	A	17.1	1st winter influx	3.1	1st winter influx	N.ob.	-
L O/W	A	13.1	1st winter influx	8.1.	1st winter influx	14.1	1st winter influx
O R/W	A	9.2	1st winter influx	8.1	1st winter influx	14.1	1st winter influx
O L/O	A	16.2	1st winter influx	11.1	1st winter influx	23.1	1st winter influx
Y L/R	J	30.12	1st winter influx	8.1	1st winter influx	4.1	1st winter influx
Y O/L	A	N.Ob.	-	8.12	1st winter influx	N.Ob.	-
Y R/W/							

Individual combination	Age at capture	1977-78 Date	1977-78 Period	Year 1978-79 Date	Year 1978-79 Period	1979-80 Date	1979-80 Period
Y R/W	A	N.Ob.	–	21.12	1st winter influx	N.Ob.	–
Y G/O	A	N.Ob.	–	8.1	1st winter influx	N.Ob.	–
Y Y/Y	J	N.Ob.	–	10.12	1st winter influx	1.2.	1st winter influx
L L/W	J	N.Ob.	–	13.12	1st winter influx	20.1	1st winter influx
L O/G	J	N.Ob.	–	4.1	1st winter influx	N.Ob.	–
O O/O	J	N.Ob.	–	8.1	1st winter influx	9.1	1st winter influx

A = Adult
J = Juvenile
N.Ob. = Not Observed

the same individuals each year which do so. In 1973-74 the absence of a winter influx suggests that no birds left. However the counts in this year were made only monthly and it is possible that a rapid influx and departure of birds may not have been observed. This seems unlikely however as in no other year did the numbers return to the level observed in autumn within a month of influx.

The origin of birds in the early winter influx is not known. Weather conditions on the eastern North Sea coast become very cold in December and movements might occur to avoid these. However, numbers of Knot using the Tees in 1978-79 and 1979-80 increased markedly at approximately the same time as the first winter influxes of Grey Plovers. Some, and possibly all, of these Knot come from the Wash (Chapter 1), Such movements might occur as the result of intra-flock competition for feeding space. For example, a flock of subordinate birds displaced to an inferior feeding area on an estuary might leave when conditions begin to deteriorate in November or December. However, there is no evidence that this occurs in Grey Plover. Indeed if such a mechanism were operating the constancy of composition observed in the first winter influx requires that the composition of the subordinate flock, i.e. that the social status of individuals remains constant from year to year. It is difficult to see how this will occur. Rather the data suggest movement of a discrete population of varying social status from another small estuary or part of a large one.

The two documented changes in time of arrival of individuals between years involved the autumn and the first winter influx, and might thus suggest a common origin for some of the birds arriving in autumn and those arriving in the first winter influx. For example it is possible that some individuals spending early autumn in one particular part of the eastern North Sea coast move to the Tees in autumn while others remain until later and then form the first winter influx. The likelihood that this does occur is supported by the nature of the autumn influxes. In contrast to the sudden winter influxes which probably result from arrival of single large flocks, those in autumn result from a seriesof small flocks (Fig. 3). Furthermore, the individual (W Y/Y) which in 1979-80 returned in the first winter influx (rather than in autumn as it had done in 1978-79 (Table 4) returned again in autumn 1980-81 (Townshend, Pers. Comm.). This individual was observed in Denmark in August 1980 (Pienkowski, Pers. Comm.). Thus some birds arriving on the Tees in late autumn probably spend early autumn in Denmark. Assuming that birds which arrive in the first winter influx occur in autumn in the same area as some of the birds which arrive at Teesmouth in autumn, this observaion of movement of W Y/Y suggests that at least some of the birds arriving at Teesmouth in the first winter influx also originate in Denmark. This suggestion is supported by count data. Numbers of Grey Plover in Denmark in 1978 decreased markedly between November and December (Meltofte, 1979; see Chapter 1).

The/

The absence of evidence of birds changing time of return from late to early winter or vice versa suggests that the origin of birds arriving in early and late winter may be different. Indeed Prater (1971) has argued that a February influx of Grey Plovers on the Essex estuaries is due to birds, having wintered in southern Europe or West Africa, moving north at this time. The occurrence of influxes of birds on estuaries in some years but not in others is a noted feature of passage movements (Smith and Greenhalgh, 1977; Wilson, 1973). It seems likely that the late winter influxes which occurred in 1978-79 and 1979-80 but not in the two previous years represent such passage movements. However if birds do migrate northwards at this time, when severe conditions may still occur on the estuaries around the North Sea, the advantage in doing so is not clear. At this time the Arctic coast of Russia remains inaccessible. Thus later departure from southern wintering grounds could result in birds arriving on the Siberian breeding areas (as snow melt occurs) at the same time as birds which had left in February or March. Siberian breeding Knot do not migrate through the North Sea until May (Dick et. al. 1976 ; Dick, 1979). However it is possible that migration in two or three movements, well spaced in time and allowing a long rest in between each, places a bird at an advantage when it finally arrives on the breeding grounds. The precise nature of any such advantage is unknown. Clearly birds which/

which migrate north earlier have longer to lay down body reserves before departure to the breeding grounds. Evans (1979b) suggested that by moving early to fattening grounds there was greater time available both to moult into breeding plumage and to lay down body reserves and less chance that departure to the breeding grounds would be delayed. However laying down of fat and protein reserves normally occurs rapidly immediately before migration (Davidson, In prep.). Thus it is difficult to see how return to northern Europe in February and/or March two months before movement to the breeding areas is of major advantage to the birds in acquiring these pre-breeding reserves. Rather, the advantage of early movement north may instead lie in avoiding competition at the origins of the movement. Piersma et. al. (1980; Pers. Comm.) have suggested that shorebirds wintering in Mauritania may have difficulty in meeting energy requirements. Measurements in January 1980 indicated that the invertebrate prey biomass density was low and time spent feeding by all species of shorebirds high. If all birds wintering in this area were to wait until April and/or May, before moving north the increased daily food requirements related to preparation for migration by all individuals would coincide. By departing early from this wintering area the pre-migration demands of some individuals would occur before those of birds departing later. It is possible that two conditions prevail in Mauritania (1) that absolute prey density is normally low in April, as suggested/

suggested by Piersma et. al. (Pers. Comm.), and (2) that prey availability does not increase at this time, which seems likely as temperatures are high in winter and therefore unlikely to limit availability at this time as reported from North-West Europe (Smith, 1975; Goss-Custard, et. al. 1977a; Pienkowski, 1980). If these conditions do exist in the wintering areas in West Africa then early departure by some individuals in February/March may enable these birds to avoid or encounter less competition before migration than would be likely if all birds departed at the same time in April. It is likely that subordinate birds which encountered such competition would be unable to achieve sufficient intake to attain pre-migration weight. Consequently it may be to the advantage of subordinate individuals to depart early despite the risk of severe weather upon arrival in North-West Europe.

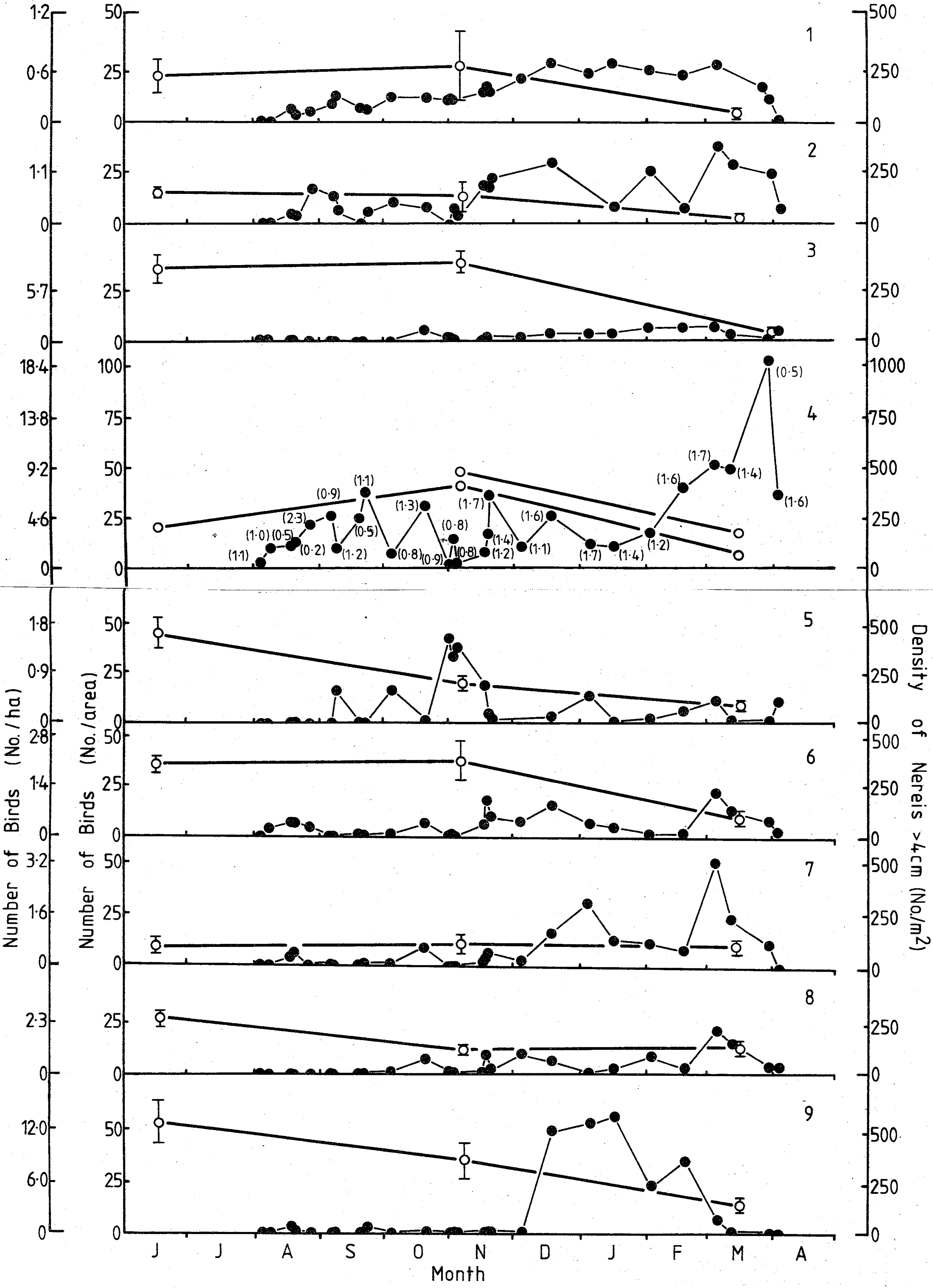
FEEDING DISTRIBUTION OF GREY PLOVER ON SEAL SANDS

In relation to prey distribution.

Seasonal use of each feeding area on Seal Sands varied in a complex way (Figs. 6,7). In some areas, e.g. Eastern Channel, birds were territorial and numbers here remained almost constant throughout the winter. In others, e.g. Central Bank, O-C.Ch., birds fed in a flock and numbers fluctuated, but to varying degrees and at different times of year. To examine the reasons for this pattern of distribution, three parameters/

Fig. 6. Seasonal changes in numbers of feeding Grey Plovers and in density of large *Nereis* on the 9 main feeding areas of Seal Sands in 1978-79. All counts were made between low water - 1 hr and low water + 1 hr. Figures in parentheses refer to tide height at low water. When sampling *Nereis* 2 or 4 samples were taken from a total of 23 sub-areas (see text and Appendix 8). Where more than one sub-area was sampled within a Plover feeding area, density is expressed as the mean, and the standard error given of the average densities within the sub-areas. When only one sub-area was sampled the mean sample density is given. n = number of sub-areas.

Fig. 6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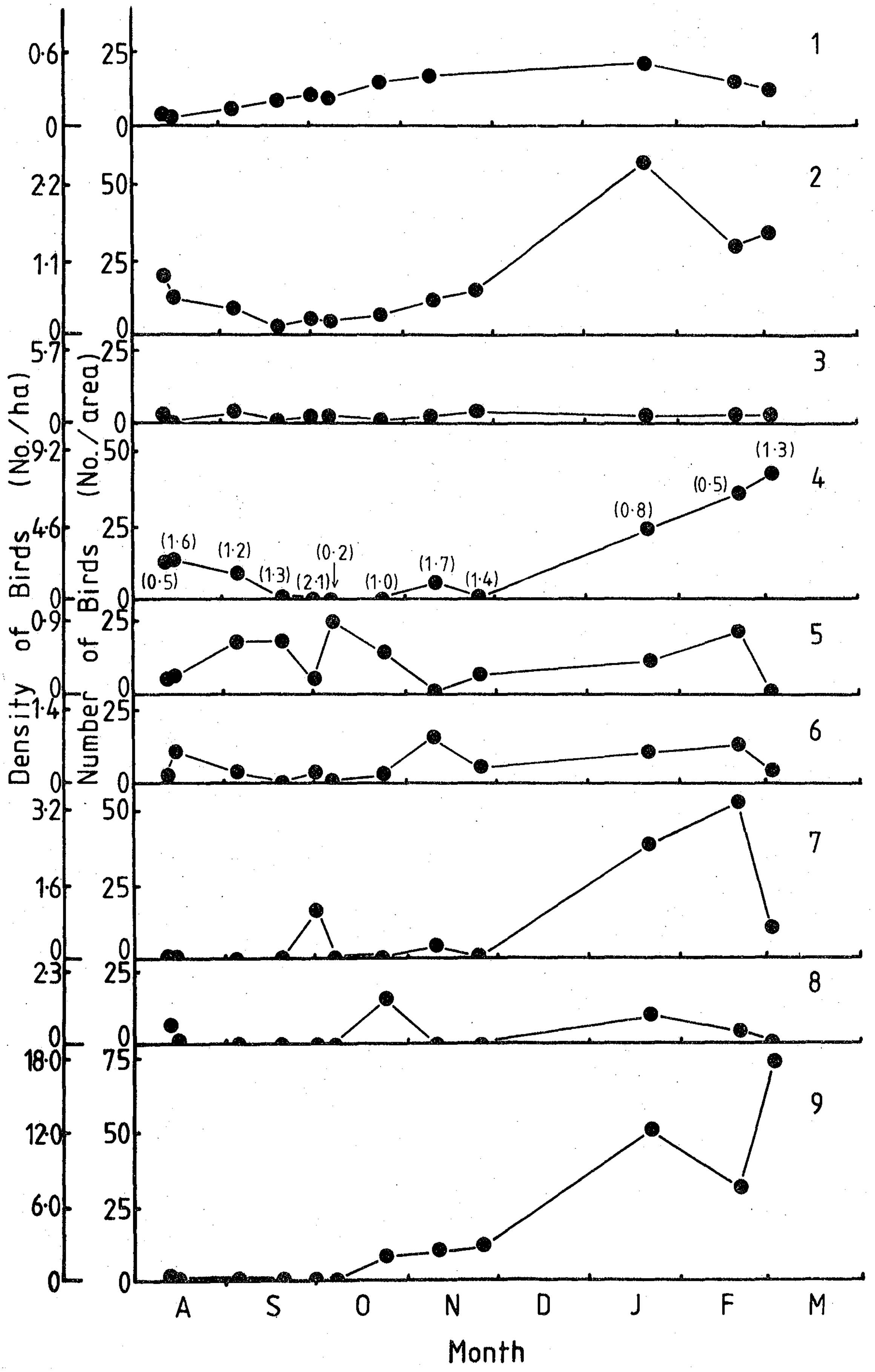


Fig. 7. Seasonal changes in numbers of feeding Grey Plovers on the main feeding areas of Seal Sands in 1979-80. All counts were made between low water -1hr. and low water +1hr. Figures in parentheses refer to tide height (in metres) at low water.

parameters of the prey population have been investigated (i) absolute density,,(ii) prey quality, (iii) availability.

(i) Consideration of prey density in different feeding areas (Figs. 6,8,9) does not explain the pattern of use observed. On most days and in most areas of Seal Sands *Nereis* of body length > 4 cm contributed at least 60% of the energy intake of Grey Plover during my study period (Table 8). Yet although considerable differences existed in absolute density of this size class of *Nereis* between the major feeding areas, the pattern of seasonal change in *Nereis* density was similar in different areas (Fig. 6). Furthermore, although on all days for which data are presented a positive correlation between bird density and prey density is revealed these relationships are not significant. Although thesepositive correlations suggest that some relationship between bird density and prey density exists several anomalies in pattern of seasonal use of the nine feeding areas are evident. For example during much of early autumn when birds first arrived on the estuary, the high levels of Greenabella bank held among the highest densities of large *Nereis*, yet this area was not occupied by plovers until Decembe In contrast, the lower tidal levels of Greenabella Bank held consistently lower densities of large *Nereis*, yet they were used as feeding areas several months earlier. Similarly, no clear correlation exists between the densities of small *Nereis* or *Hydrobia* and bird density (Table 9).

Among the three areas on which territories were established in November, Eastern Channel held the highest density of large *Nereis*. However the densities both there and on Scalloped Mud (E. Ridge) were very similar to/

Table 8. Diet of Grey Plover on the Tees estuary.

Date	No. of observation periods	Occurrence in diet (% calorific intake)									
		Nereis >4 cm		*Nereis* ≤4 cm		*Hydrobia*		*Corophium*		*Macoma*	
		$\bar{x}$	S.E.	$\bar{x}$	S.E.	$\bar{x}$	S.E.	$\bar{x}$	S.E.	$\bar{x}$	S.E.
Central Bank											
9.10.78	15	77.8	5.1	5.2	2.1	8.3	1.4	0.3	0.2	8.4	4.9
21.10.78	11	69.6	7.7	17.6	5.1	10.9	2.5	1.9	0.9	0.0	0.0
4.1.79	15	64.0	7.8	9.1	2.8	26.9	7.8	0.0	0.0	0.0	0.0
Greenabella Bank											
3.1.79	14	67.5	8.8	5.2	3.7	24.5	8.7	0.0	0.0	3.0	2.2
Eastern Channel	Observation time (Mins.)										
6.10.79	9	98.4	-	1.6	-	0.1	-	0.0	-	0.0	-
24.11.79	37	29.6	-	35.6	-	21.5	-	0.0	-	13.3	-
7.1.80	75	92.6	-	6.7	-	0.7	-	0.0	-	0.0	-
9.1.80	24	64.6	-	25.8	-	9.6	-	0.0	-	0.0	-
16.2.80	61	91.1	-	8.1	-	0.9	-	0.0	-	0.0	-

Figures for central Bank and Greenabella Bank are the mean of the means of all observation periods of 3 or more minutes on each date. Figures for Eastern Channel are the proportions of the intake on each date of bird R W/G only. All values are given as per cent of calorific intake. Discrimination of *Corophium* was possible only on occasions when birds were foraging very close to the observation position. Misidentification is most likely to have led to inclusion of *Corophium* as small *Nereis*. However in view of the limited distribution of *Corophium* on Seal Sands it is likely that such errors were infrequent.

Table 9. The relationships between the density of Grey Plover and density of its main prey in each of nine major feeding areas on Seal Sands.

Date	*Nereis*		*Hydrobia*
	>4 cm.	$\leqslant 4$ cm	
	r_7	r_7	r_7
22-9-78	0.3246 0.2872[1]	-0.0444	-0.0043
4-10-78	0.0220 0.1623[1]	-0.2446	-0.4045
19-11-78	0.5022 0.5003[1]	-0.2533	0.1765
5-1-79[2]	0.4694 0.4313[1]	0.7328 (p 0.05)	-0.4962
5-3-79	0.4834 0.3328[1]	-0.2333	0.4083

Notes:

1 Correlation coefficients calculated for only 6 of the 9 areas. Eastern Channel, Far *Enteromorpha* and the lower tidal levels of Greenabella Bank and Central Channel, areas where the topography restricts visibility and results in counting error, were excluded from the analysis.

2 Values on this day are based on 8 areas since poor visibility prevented counting of Far *Enteromorpha*.

Count data used in the analysis are given in Fig. 4. Invertebrate densities were estimated for each date using Figs. 6,8,9.

Fig. 8a

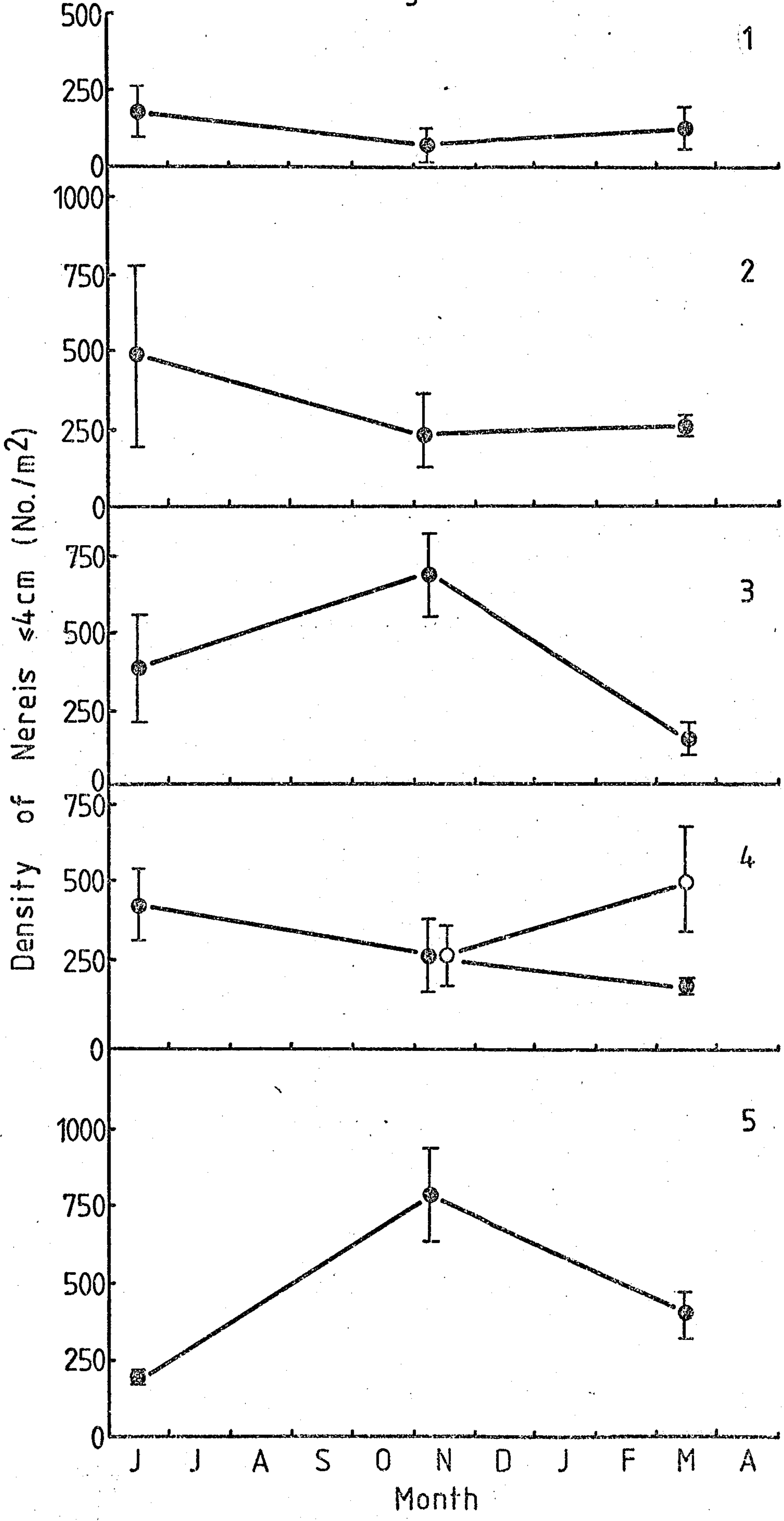
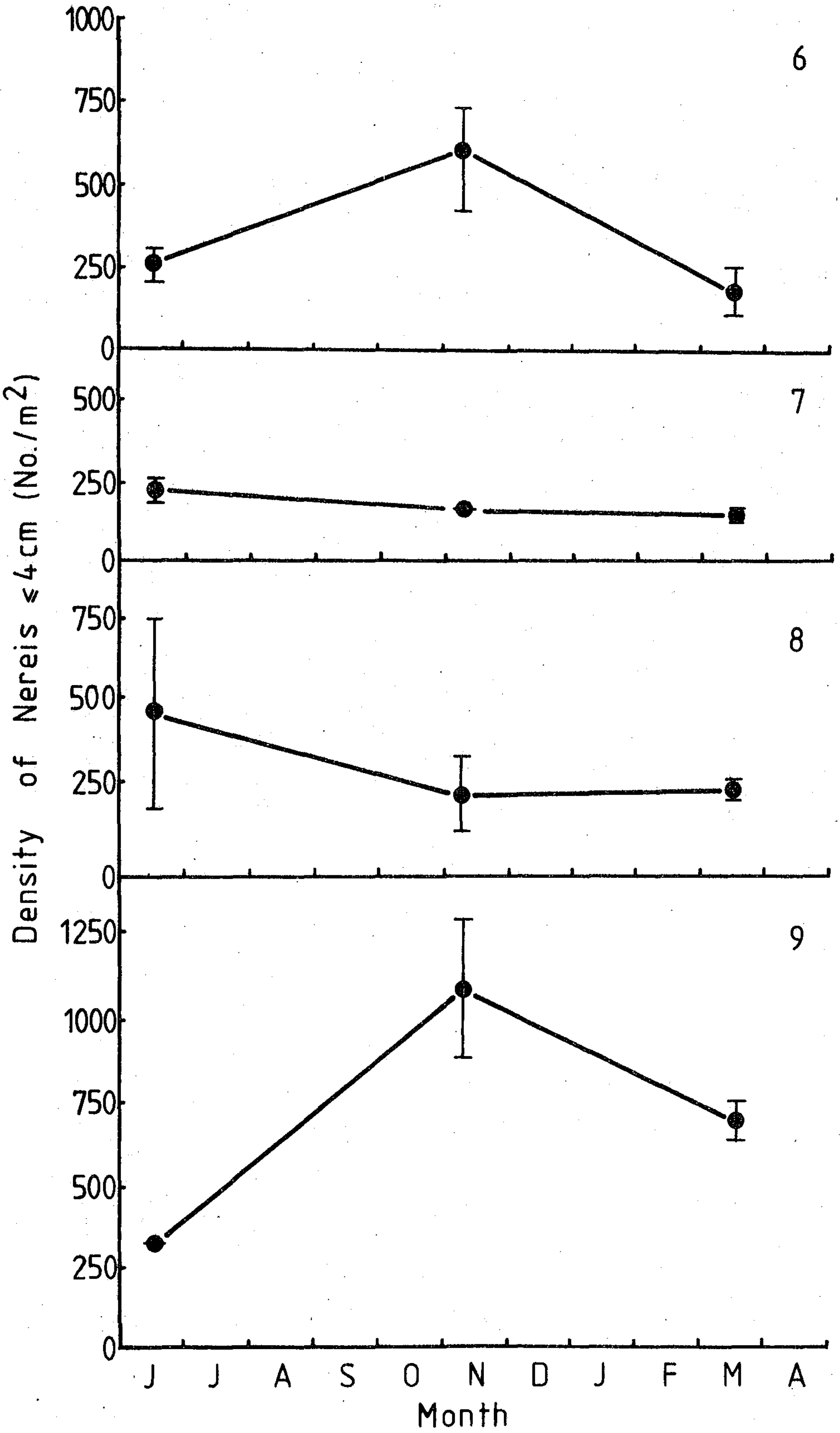


Fig. 8. Seasonal changes in density of small (≤ 4cm) Nereis diversicolor in Grey Plover feeding areas 1978-79. (Data presented as for large Nereis in Fig. 6.)

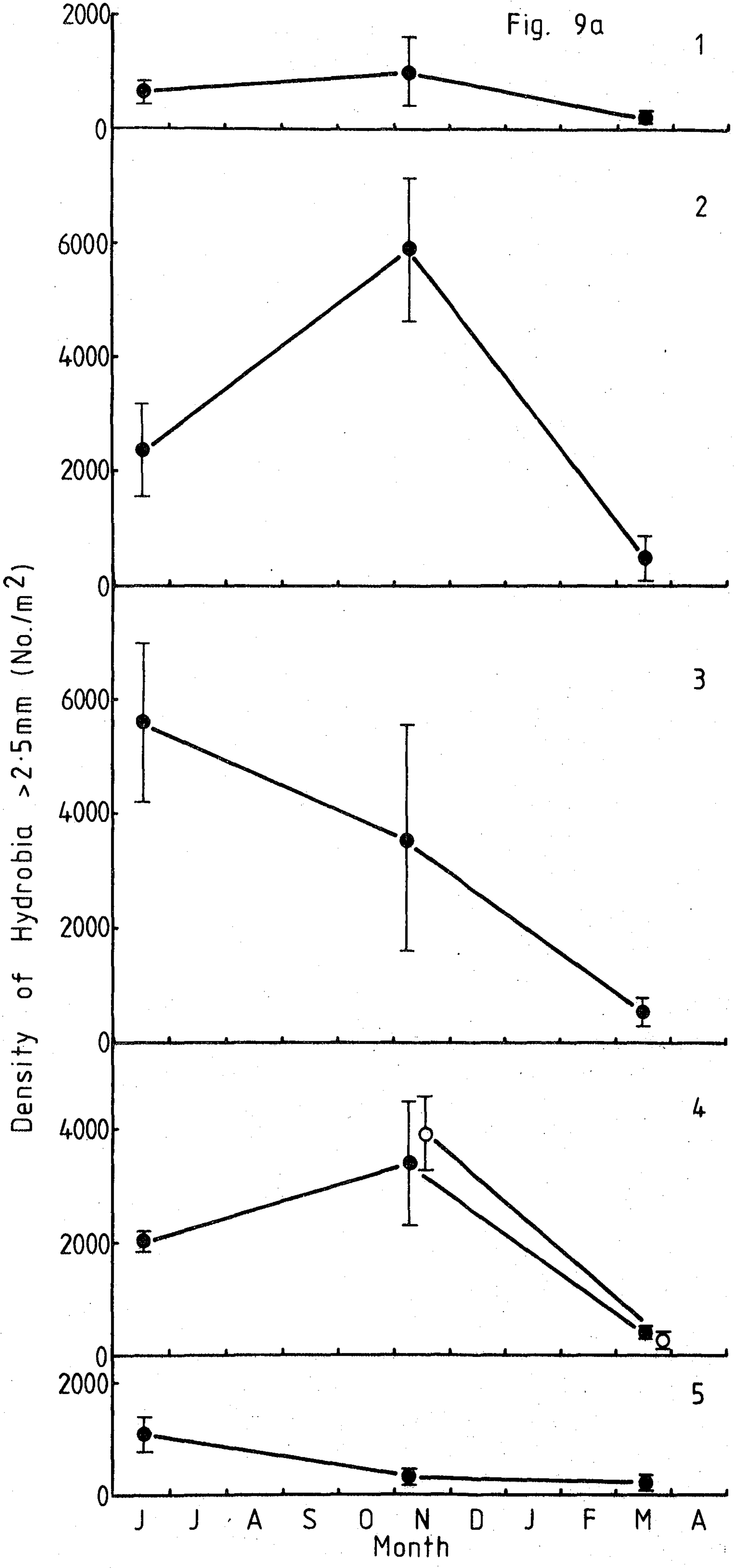
Fig. 8b



6
7
8
9
1000
750
500
250
0
1250
Density of Nereis ≤4cm (No./m^2)
J
J
A
S
O
N
D
J
F
M
A
Month

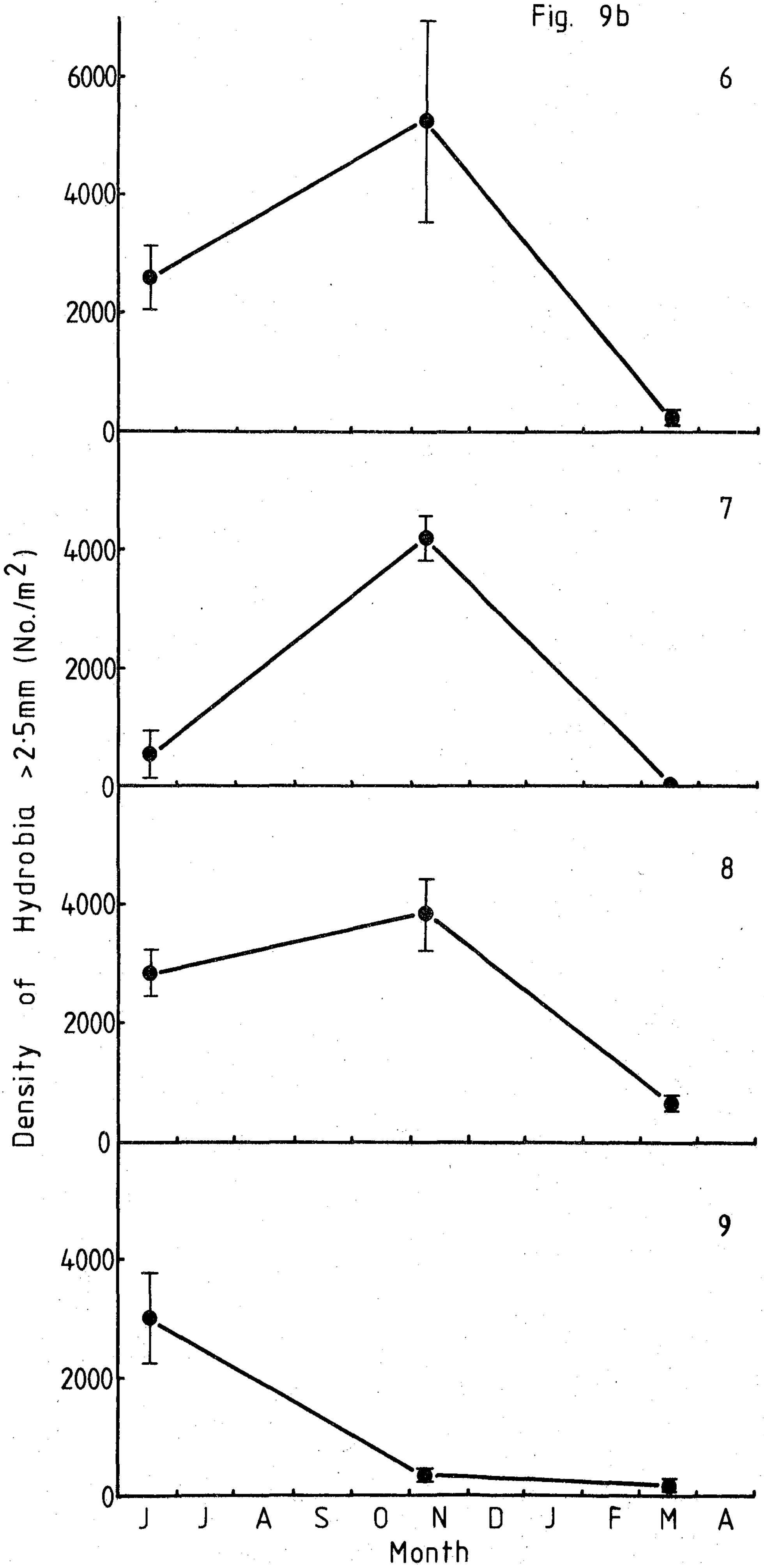
Fig. 9. Seasonal changes in density of *Hydrobia ulvae* ≥ 2.5 mm shell height in Grey Plover feeding areas 1978-79 (Data presented as for large *Nereis* in Fig. 6).

Fig. 9a



1
2
3
4
5
2000
0
6000
4000
2000
0
6000
4000
2000
0
4000
2000
0
2000
0
Density of Hydrobia >2·5mm (No./m2)
J
J
A
S
O
N
D
J
F
M
A
Month

Fig. 9b


6
7
8
9
6000
4000
2000
0
Density of Hydrobia >2·5mm (No./m^2)
J
J
A
S
O
N
D
J
F
M
A
Month

to those on the areas used by the flocking birds. The Far Enteromorpha area of Central Bank, where territories were also established, consistently held the lowest prey density throughout the winter. Clearly the holding of territories was not limited to areas of high prey density.

(ii) Various measures of prey quality e.g. body length, body weight, and calorific value also did not vary either seasonally or between areas in a manner which could explain the observed pattern of use of areas by the plovers. For example, although the mean body length of large Nereis present in each area did vary through the year, the lengths recorded in November and March on Central Bank (O-Y) were among the lowest in all areas at this time (Table 10). Yet in these months, this part of Central Bank was one of the most important feeding areas. Also, whereas the numbers of birds using territorial areas remained almost constant from autumn to spring, the relative quality of these areas, in terms of mean body length of large Nereis in the samples, varied markedly. Sample sizes were, however, small.

Within each size class of Nereis, body weight was consistently higher in Eastern Channel, but very similar in all other areas (Fig. 10). The data for calorific values are more limited, but indicate few significant differences between habitats (Fig. 11).

(iii) Clearly prey availability, rather than absolute prey density, is more likely to be a factor to which use/

Table 10. Mean body length (cm) of large Nereis (>4 cm) in each of the main Grey Plover feeding areas on each of the sampling dates. Figures are calculated only for large Nereis obtained in the 133 cm^2 cones. (n = number of worms measured).

Feeding area		June				November				March			
		n	$\bar{x}$	S.E.	Rank	n	$\bar{x}$	S.E.	Rank	n	$\bar{x}$	S.E.	Rank
1		2	4.8	0.2	7	2	7.5	0.7	1	1	4.8	0.0	7
2		3	5.1	0.4	6	2	6.4	1.0	3	1	7.0	0.0	1
3		2	5.2	0.5	5	2	6.4	0.2	3	1	4.5	0.0	9
4	Y-C.Ch.	11	5.3	0.2	3	21	5.9	0.3	7	8	5.4	0.4	8
	O-Y					17	5.6	0.3		3	4.6	0.1	
5		8	5.6	0.1	2	8	5.5	0.1	8	7	6.1	0.6	2
6		5	5.3	0.2	3	5	6.2	0.3	5	4	5.0	0.1	5
7		1	4.6	0.0	8	2	7.1	0.0	2	2	5.7	0.1	3
8		2	4.6	0.0	8	2	5.5	0.5	8	2	4.9	0.3	6
9		2	5.7	0.1	1	2	5.8	0.1	6	2	5.7	0.3	3

Note: Feeding areas are numbered as in Fig. 2.

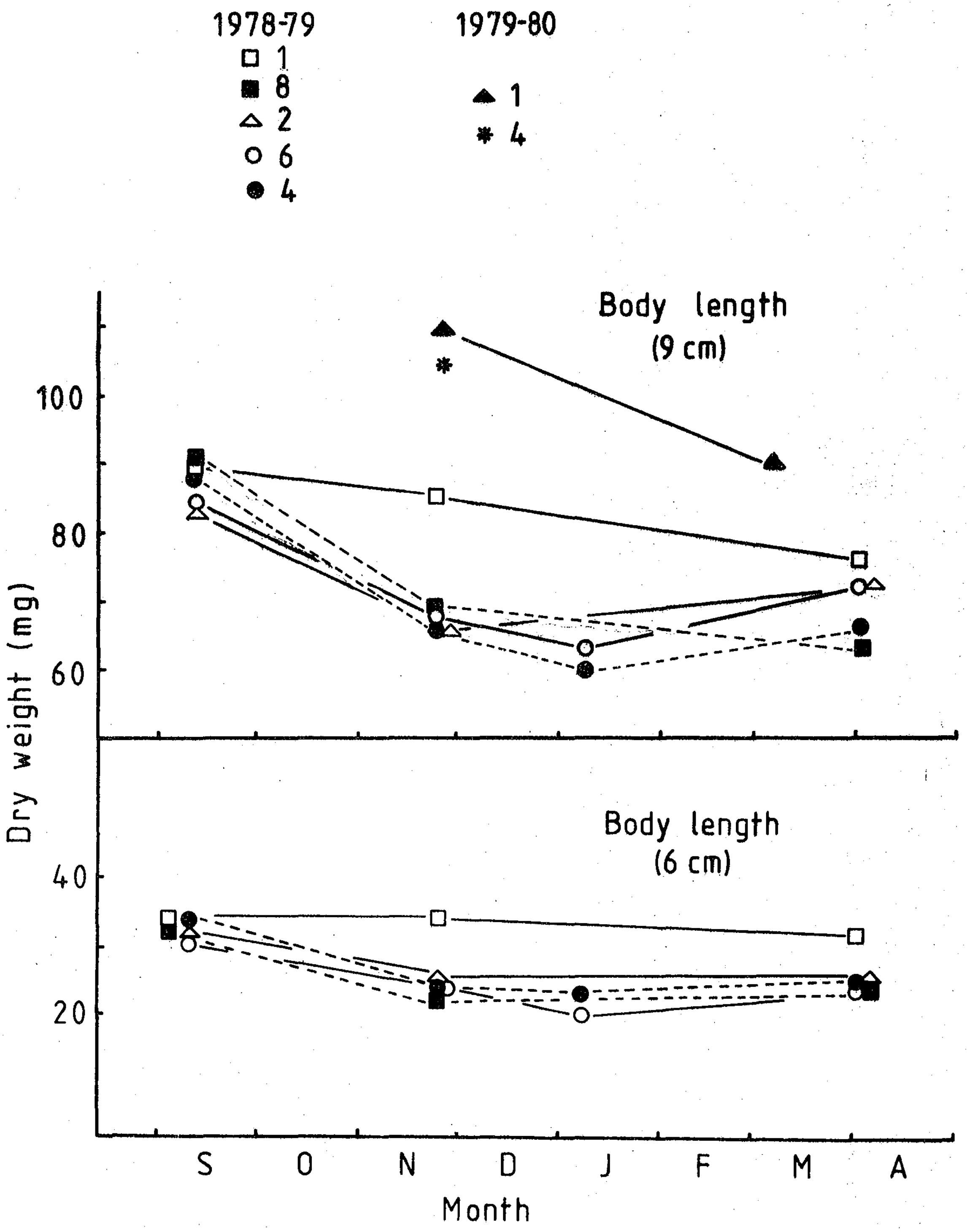


Fig. 10. Seasonal changes in dry weight of <u>Nereis diversicolor</u> in Grey Plover feeding areas 1978-79 and 1979-80. Values given were calculated from the regression formulae given in Appendix 2. Feeding areas are numbered as in Fig.2.

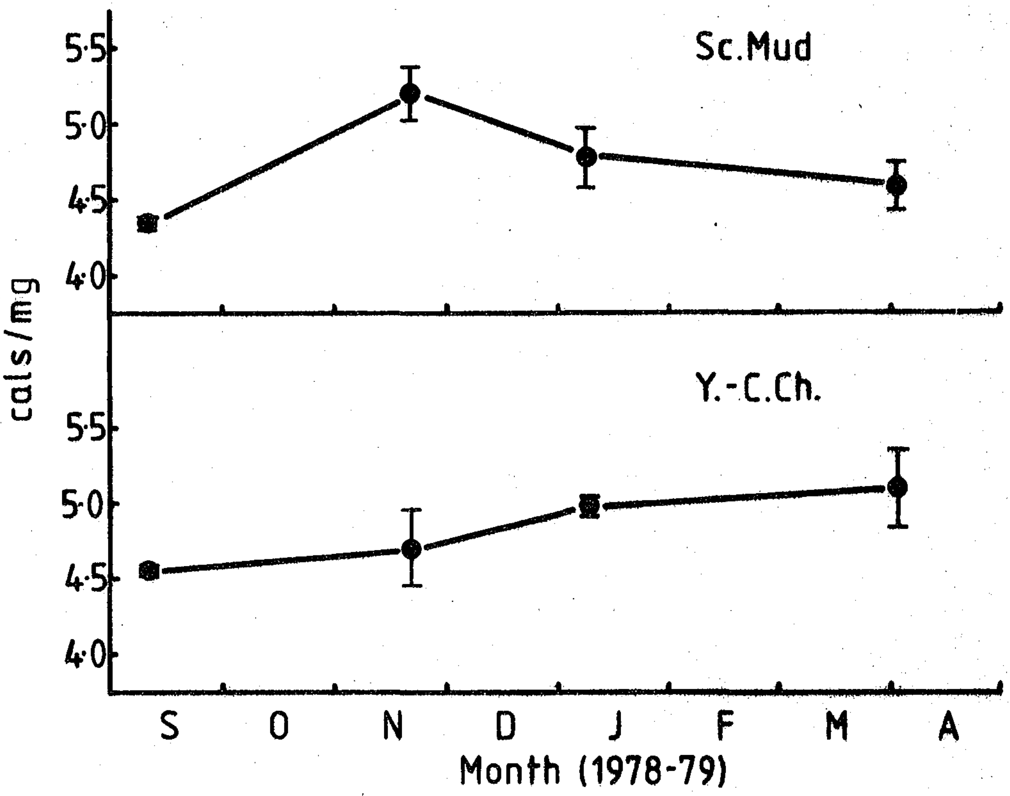


Fig. 11. Seasonal changes in calorific value of *Nereis diversicolor* from Seal Sands. For both Scalloped Mud and Central Bank Y-C.Ch. the significance of differences between values from adjacent sampling dates was determined using students t-test. Only for Scalloped Mud between September and November was this significant $t_{10} = 4.48$ $p < 0.002$. The values for Y-C.Ch. in September and November are significantly different from those for Scalloped Mud $t_{10} = 2.99$ $p < 0.02$ and $t_{12} = 2.26$ $p < 0.05$ respectively. No other significant differences between calorific values of *Nereis* from Scalloped Mud and Central Bank Y-C.Ch. and other areas of Seal Sands were recorded.

use of feeding areas is related. Several authors have been able to measure directly the availability of a number of prey species. Smith (1975) showed that availability of Arenicola marina to shorebirds foraging visually, declined with time after exposure of a site by the ebbing tide. Feeding success of Bar-tailed Godwit (Smith 1975) and Grey Plover (Pienkowski, 1980) taking lugworms, declined in parallel. Pienkowski (1980) also demonstrated a decline in availability and rate of capture by Grey Plover of Notomastus latericeus. However no-one has yet obtained direct measures of the diurnal activity of Nereis diversicolor. Townshend (1981b) has shown, by measuring the search areas of territorial Grey Plovers that, at least on some occasions, prey availability decreases towards and after low water. I have collected similar data for Grey Plovers feeding in flocks, but although similar trends are apparent, none are statistically significant (Fig. 12).

The capture rate of Nereis varied greatly between obsërvation days in a manner unrelated to changes in prey density over these periods. For example, the capture rate of large Nereis on the area of Central Bank referred to as O-C.Ch., was very low on 21-12-78 but higher on 4-1-79 and 4-2-79 (Fig. 13), even though, during the period from November to March, density of large Nereis in this area declined (Fig. 6). These data suggest that availability of Nereis on 4-1-79 and/

Fig. 12. Area searched by flock feeding Grey Plovers in relation to time of low water while foraging in area O-C.Ch. Area searched is expressed as number of paces moved between pauses. Each value refers to one individual. Calculated regression lines are drawn.

Fig. 12a

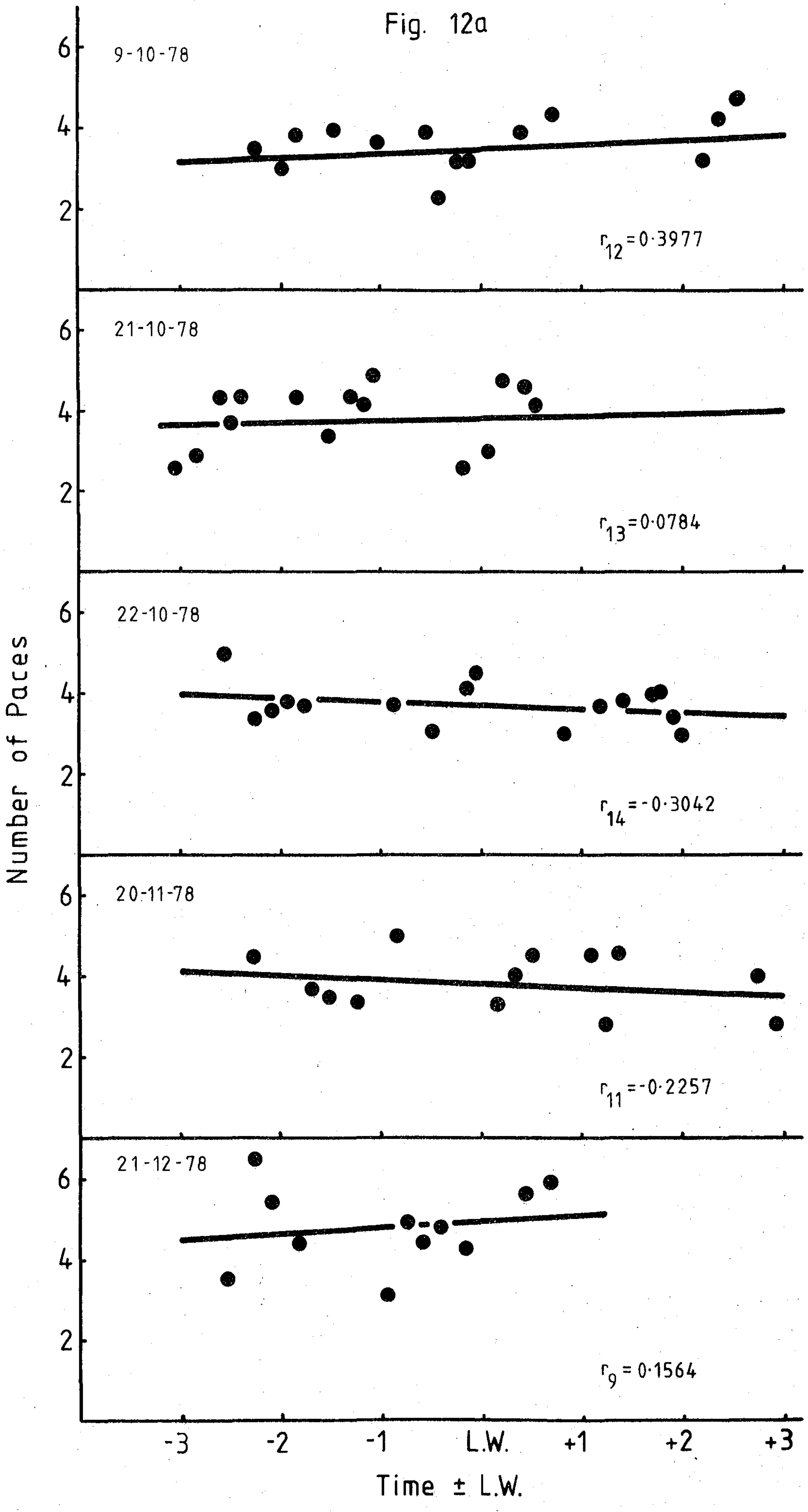
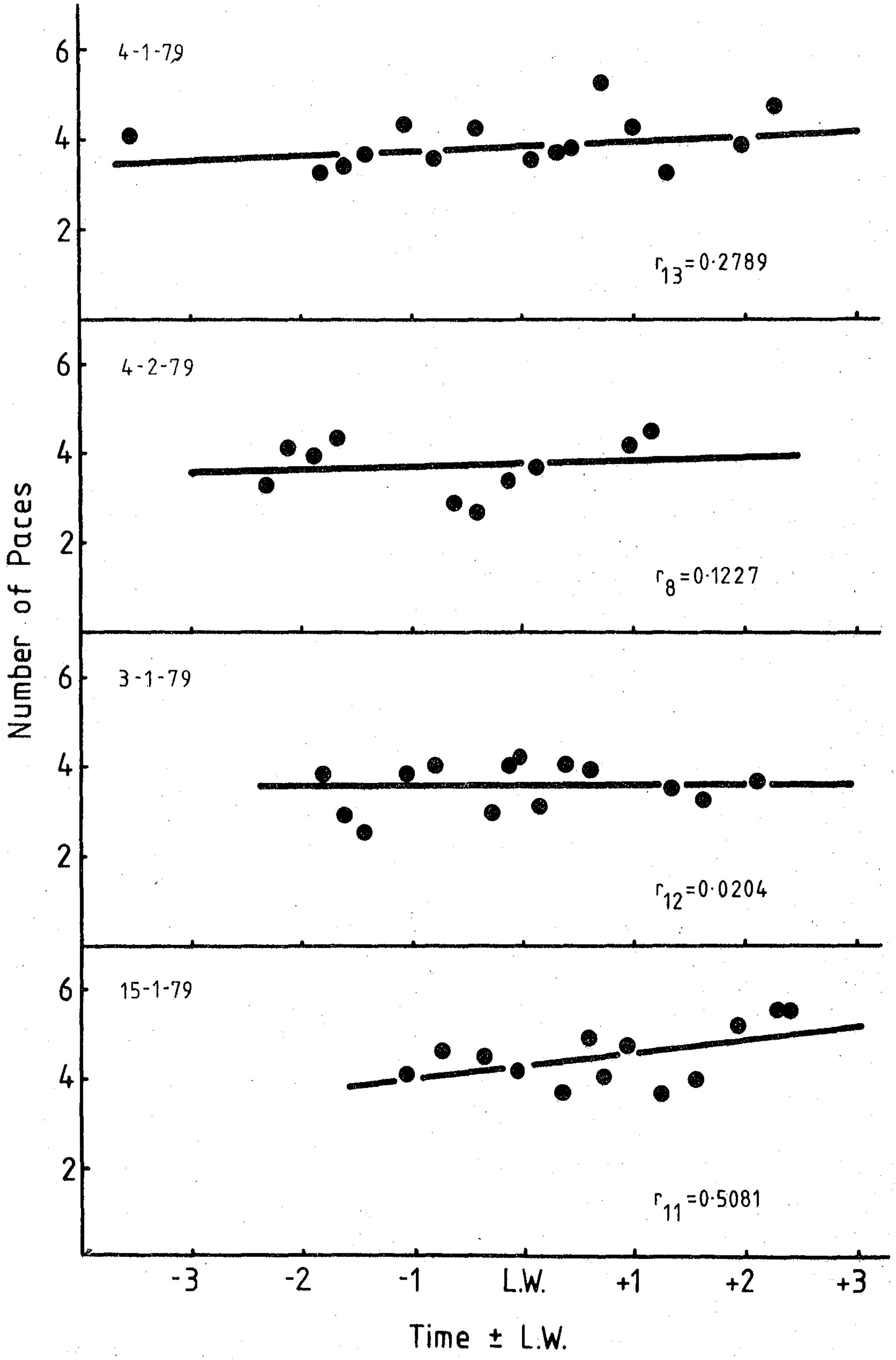

9-10-78
$r_{12} = 0{\cdot}3977$
21-10-78
$r_{13} = 0{\cdot}0784$
22-10-78
$r_{14} = -0{\cdot}3042$
20-11-78
$r_{11} = -0{\cdot}2257$
21-12-78
$r_9 = 0{\cdot}1564$
Number of Paces
6
4
2
-3
-2
-1
L.W.
+1
+2
+3
Time ± L.W.

Fig. 12b


4-1-79
r13=0·2789
4-2-79
r8=0·1227
3-1-79
r12=0·0204
15-1-79
r11=0·5081
6
4
2
Number of Paces
-3
-2
-1
L.W.
+1
+2
+3
Time ± L.W.

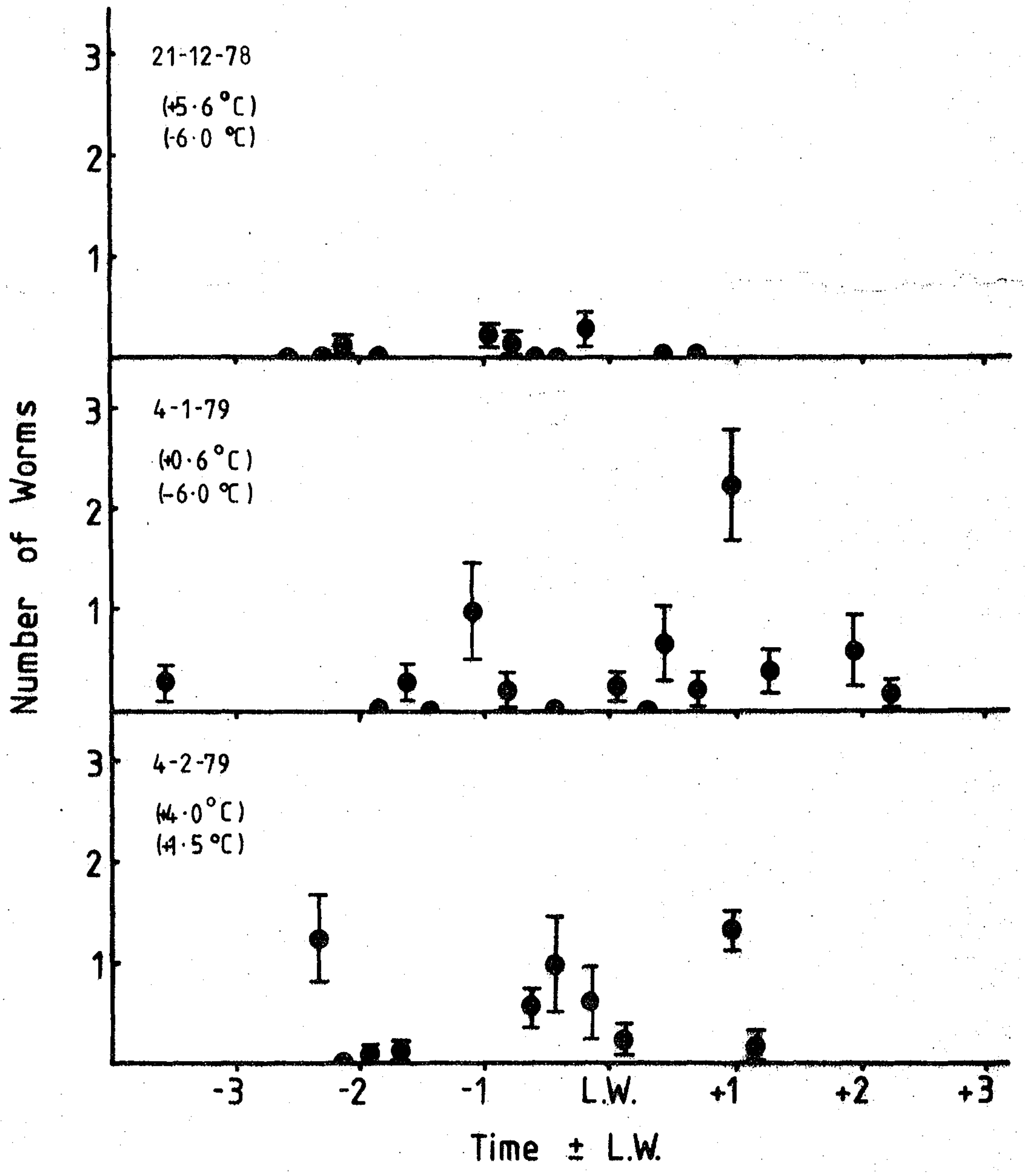


Fig. 13. Day to day variation in capture rate of large (> 4 cm) Nereis diversicolor by flock feeding Grey Plovers in area O-C.Ch. Rates are expressed per minute of feeding time observed. The mean and one standard error are given for each individual. Minute intervals during which non-feeding activity e.g. preening, aggression, occurred were excluded from the analysis as were birds watched for less than 3 feeding minutes. Temperatures given are maxima and minima recorded on each date at Hartlepool.

and 4-2-79 was higher than on 21-12-78 although 4-1-79 was one of the coldest days of the winter (Fig. 13). Thus availability within flock feeding areas appeared to vary from day to day, although it is not possible at present to measure this accurately and independently of capture rate. Combining this knowledge with the detailed counts presented here it is possible to relate the distribution of the flock birds to availability of their prey.

In 1978-79, when birds first returned to the estuary and until the first winter influx occurred in December, most flock feeding birds fed on Central Bank, O-C.Ch. However on days of spring tides many moved to lower tidal levels at low water when prey availability in O-C.Ch. presumably declined (Fig. 6, Table 11). These movements were almost certainly governed by prey availability on Central Bank rather than by tidal height alone, since plover numbers in O-C.Ch. were also low on a neap tide on 8-9-78. When total numbers on the estuary rose in December, birds began to use areas which had previously been mostly ignored. These were particularly the higher tidal levels of Greenabella Bank and Central Bank O-G, where numbers increased markedly.

The numbers of birds using Scalloped Mud (Main) and Central Bank Sand also increased at this time. These areas were previously used mainly on neap tides, when/

Table 11. Changes in the feeding distribution of Grey Plover in relation to the time and heights (in m. above Chart Datum) of low water.

Date	Time	Tide height at low water (metres)	No. of birds in each feeding area			
			O-C.Ch. (4)	G-O (7)	Sand/Ent (8)	Low tidal levels (5)
27.8.78	L.W.	2.3	21	0	0	0
	L.W. + 1 hr.		23	0	0	0
6.9.78	L.W. - 1 hr.		26	7	0	0
	L.W.	0.9	25	1	0	0
	L.W. + 1 hr.		28	3	0	0
22.9.78	L.W. - 1 hr.		21	5	0	0
	L.W.	1.1	37	1	0	0
3.11.78	L.W. - 1 hr.		20	4	5	1
	L.W.	0.8	2	0	0	37

Note. Figures in parentheses refer to the number given to each feeding area in Table 1.

when numbers of birds using Central Bank O-C.Ch. were usually high but when lower tidal levels of Greenabella Bank and Central Channel were covered by the tide and so unavailable.

By January, numbers on Central Bank O-C.Ch., and on the lower tidal levels of Greenabella Bank and Central Channel, had decreased to approximately half the autumn levels, although the reasons for this are unknown. However at this time numbers of Bar-tailed Godwits in both these areas increased dramatically (Fig. 14). Smith (1975) reported that, in interspecific encounters, Plovers were normally displaced by Godwits. Consequently, the reduction in numbers of Plovers on Central Bank O-C.Ch. and at the lower tidal levels of Greenabella Bank and Central Channel may have been as a result of interspecific competition. Indeed, over the period when numbers of Godwits were high, numbers of each species in both areas were negatively correlated. However the numbers of days on which counts were made at that time are very small and correlations not significant at 95% level (O-C.Ch. $r_3 = 0.8515$, $0.05 < p > 0.10$; Greenabella Bank and Central Channel lower tidal levels $r_2 = -0.2854$, $p > 0.1$). Zwarts (1974) has observed similar slight negative correlations between numbers of Avocets Recurvirostra avosetta and Black-headed Gulls Larus ridibundus. Numbers using the areas first occupied in numbers at the time of the first winter influx remained high through December, January and February, but started to decline, particularly on the higher/

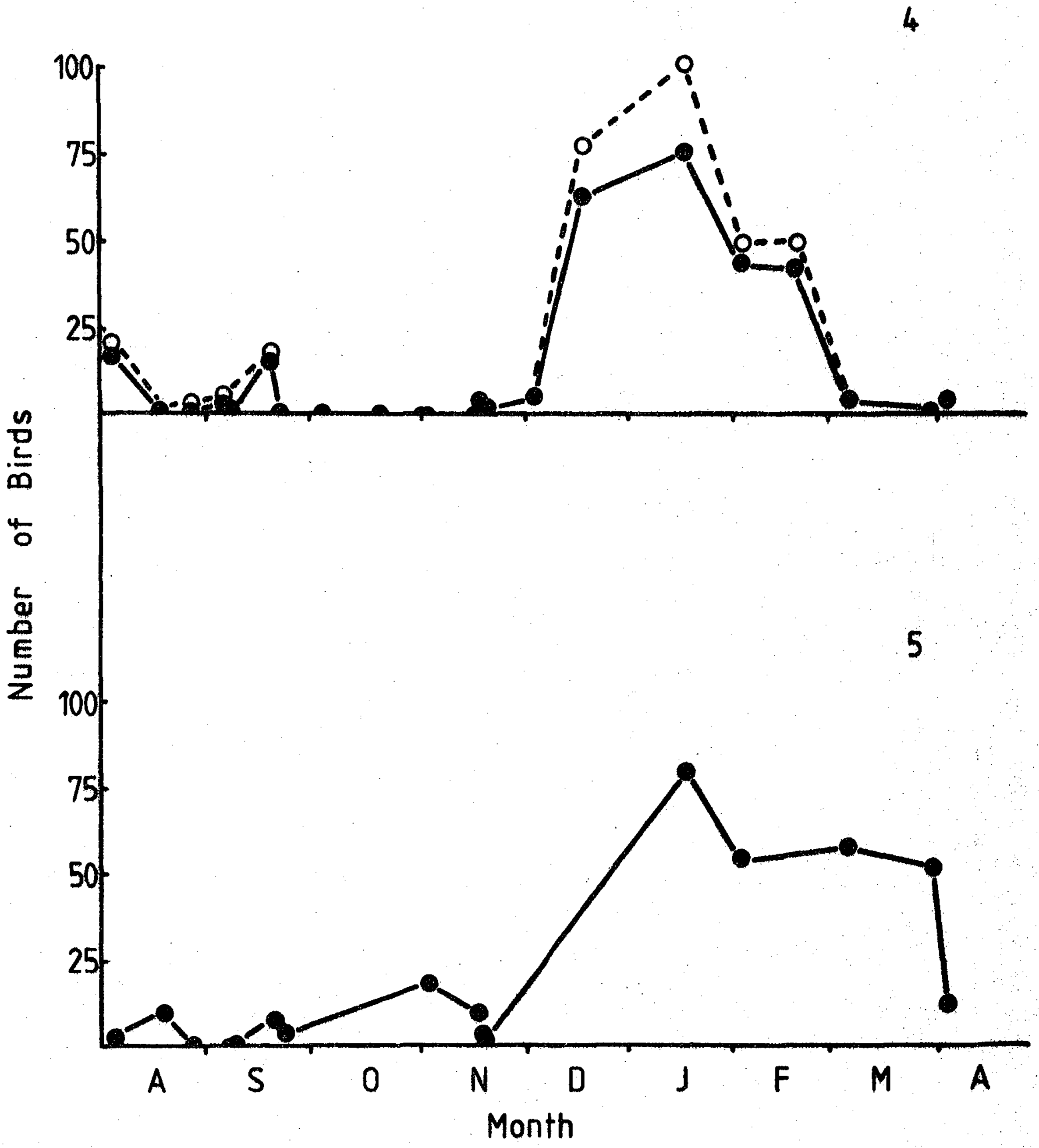


Fig. 14. Seasonal changes in numbers of Bar-tailed Godwit feeding on Central Bank O-C.Ch. and on the lower tidal levels of Greenabella Bank and Central Channel. Solid symbols joined by solid lines refer to feeding birds, open symbols joined by dotted lines to the total number present i.e. including roosting individuals. See Appendix 9 for low water counts of Bar-tailed Godwit and Curlew in other areas.

levels of Greenabella Bank, in March. In this month, however, larger numbers, occasionally even higher than in autumn, again used Central Bank O-C.Ch.

In 1979-80 the basic pattern observed in 1978-79 was repeated. However, particularly in the autumn of 1979, the lower levels of Greenabella Bank and Central Channel were used in preference to Central Bank O-C.Ch. on more neap tides than in the previous year (Fig. 7). This difference in use of these areas between years may reflect lower absolute prey density and consequently lower densities of available prey on Central Bank O-C.Ch. or higher densities in the other areas in 1979-80. However no data are available with which to test this hypothesis.

Territory establishment.

Although consideration of prey availability helps to explain some features of the complex pattern of changes in distribution of the flock, neither this nor prey quality suggest reasons for the area specific differences in social behaviour, or for the constancy of the number of birds in the territorial areas. To understand this more detailed analysis is needed of the pattern of territory establishment.

During autumn while the total number of birds present on the estuary fluctuated, the number of territorial birds gradually rose and that of flock birds/

birds decreased (Fig. 15). By November, a few weeks before the early winter influx, the number of territorial birds, in both years, exceeded that of flock birds. This gradual increase in the number of territorial birds did not result solely from new arrivals immediately occupying new territories. Although some birds took up territories immediately upon their arrival (e.g. W R/O (Fig. 16) which was first seen on the estuary and in its territory on 3-11-79) many spent several months in the flock before doing so (Table 12). Of twelve colour marked birds, present in the flock at the beginning of October 1978 and which stayed to winter at Teesmouth, most had left the flock by mid November and only three remained in the flock throughout the winter months. Thus, at least during daylight, most individuals initially fed in a flock, and established territories only late in autumn or in early winter. Of these individuals which arrived in autumn only a few continued to feed in the flock throughout the winter. In contrast, most of those which arrived in the first winter influx fed in a flock. At first sight, the simplest explanation of these observations would appear to be that those individuals remaining in the flock are subordinate and are not allowed to take up territories. Unfortunately, none of the birds which remained in the flock after December was observed in aggressive encounters in autumn and consequently there is no direct evidence of their social status. However, of the birds which did leave the/

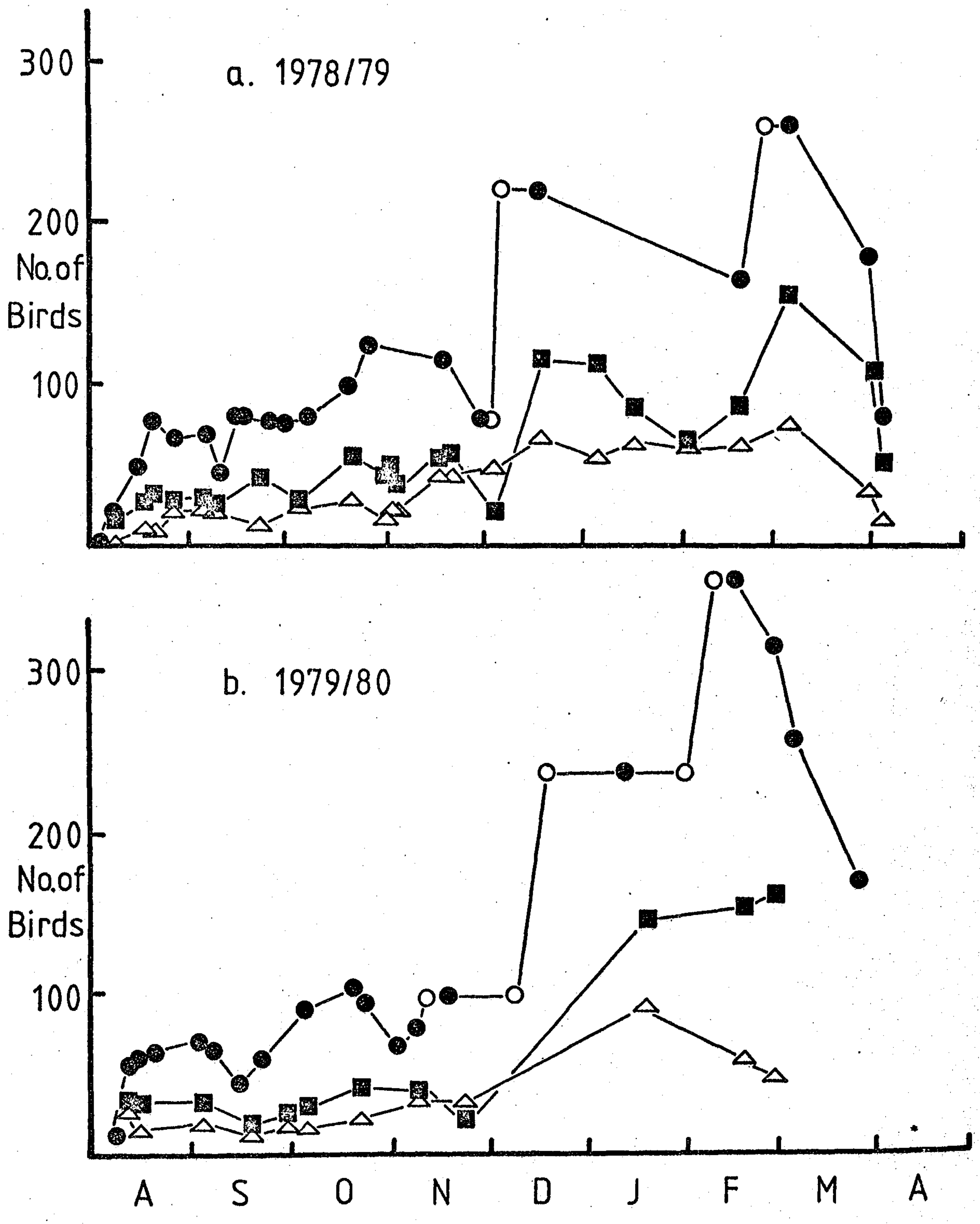
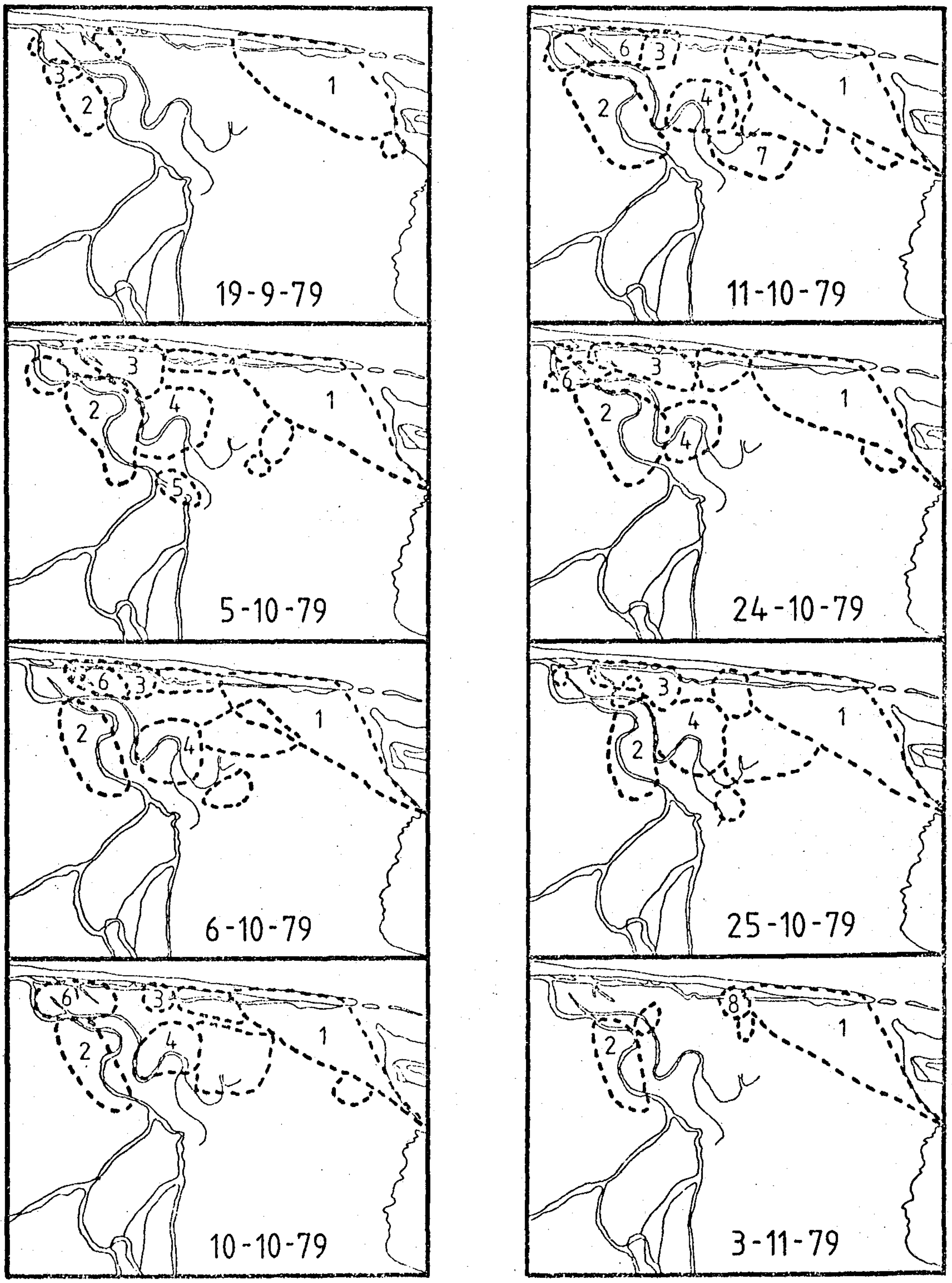


Fig. 15. Seasonal changes in total population of Grey Plover and number of flock feeding and territorial birds ●○ Total, ■ Flock, △ Territorial.

Fig. 16. Seasonal change in territory distribution in Eastern Channel.

Territory boundaries (----) have been drawn for each observation day by surrounding (1) positions of birds on each date plotted on large scale maps (see text) and (2) areas not used by an individual on that day but used previously and subsequently by it and which on the day in question was not used by another Grey Plover. Days marked with an asterisk are those on which the area was scanned only once. Territories occupied by unmarked individuals have been left blank and those defended by colour-marked birds numbered:-

1 (R W/G); 2 (W R/W); 3 (R O/L); 4 (G Y/R);
5 (R/G R/G): 6 (Y Y/O); 7 (G/Y W/O); 8 (W R/O);
9 (L G/L); 10 (G/Y O/W); 11 (L W/G); 12 (R/W R/Y);
13 (R O/Y); 14 (O/W G/Y).


1
2
3
19-9-79
1
2
3
4
5
5-10-79
1
2
3
4
6
6-10-79
1
2
3
4
6
10-10-79
1
2
3
4
6
7
11-10-79
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4
6
24-10-79
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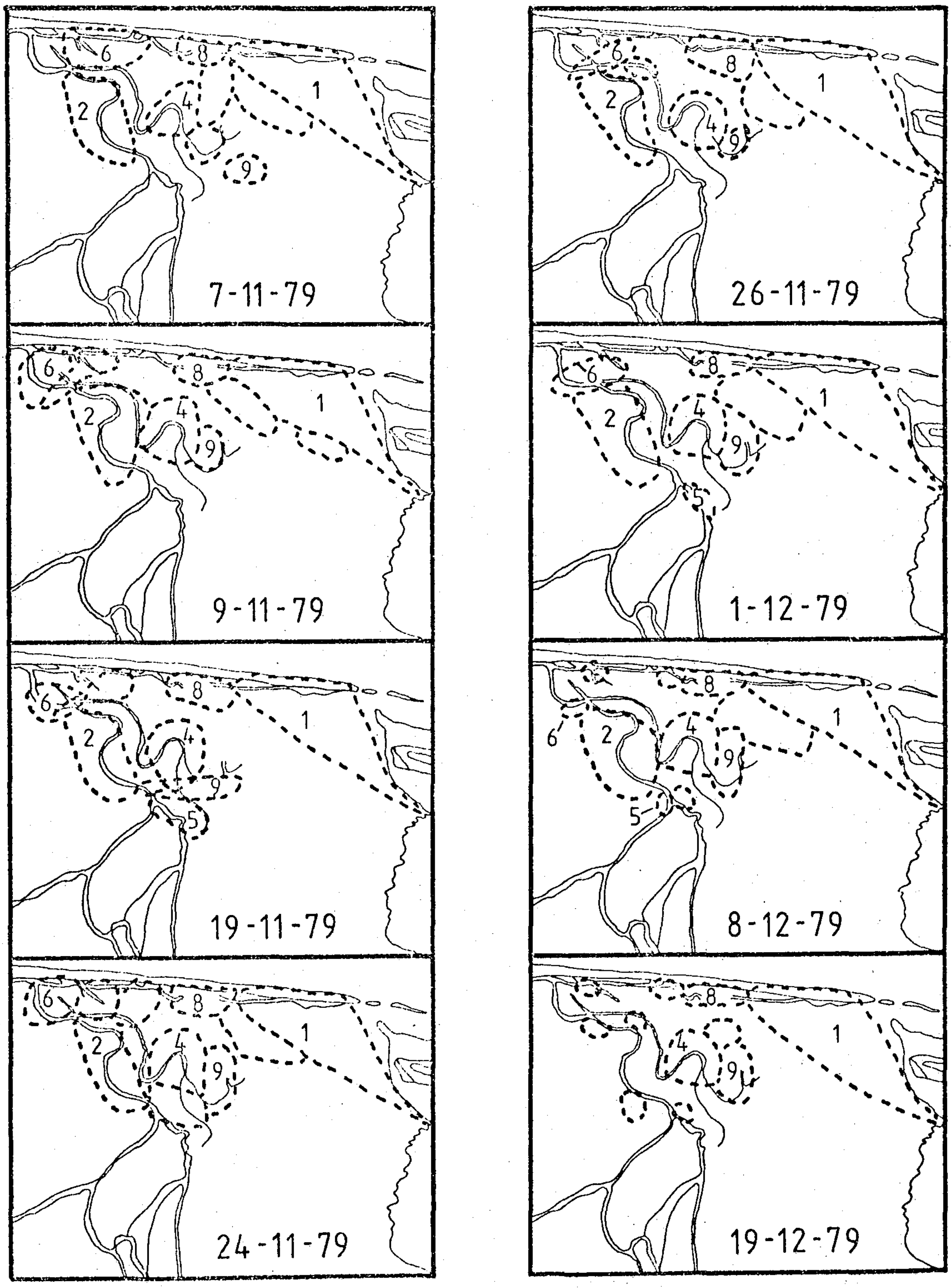
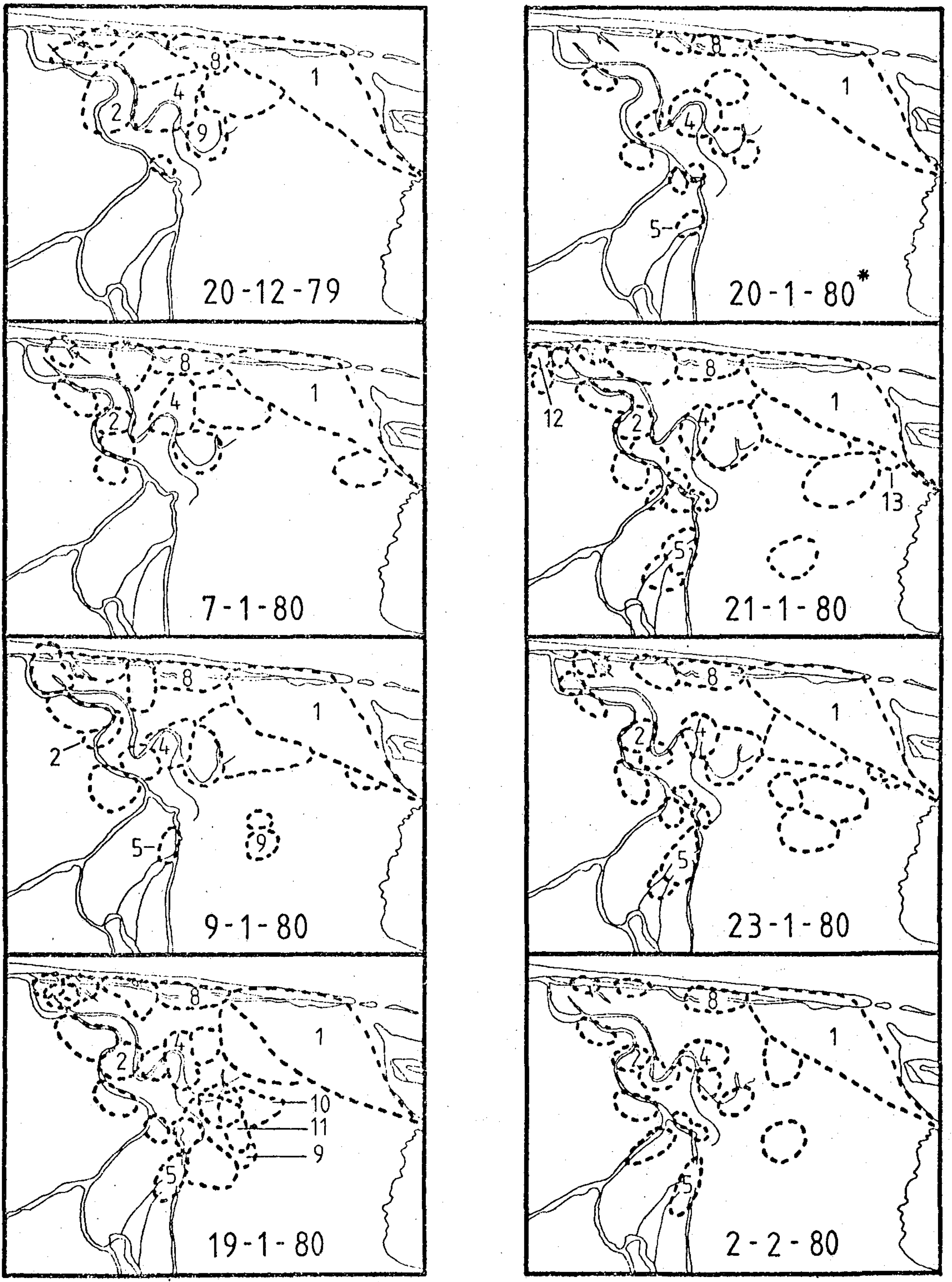
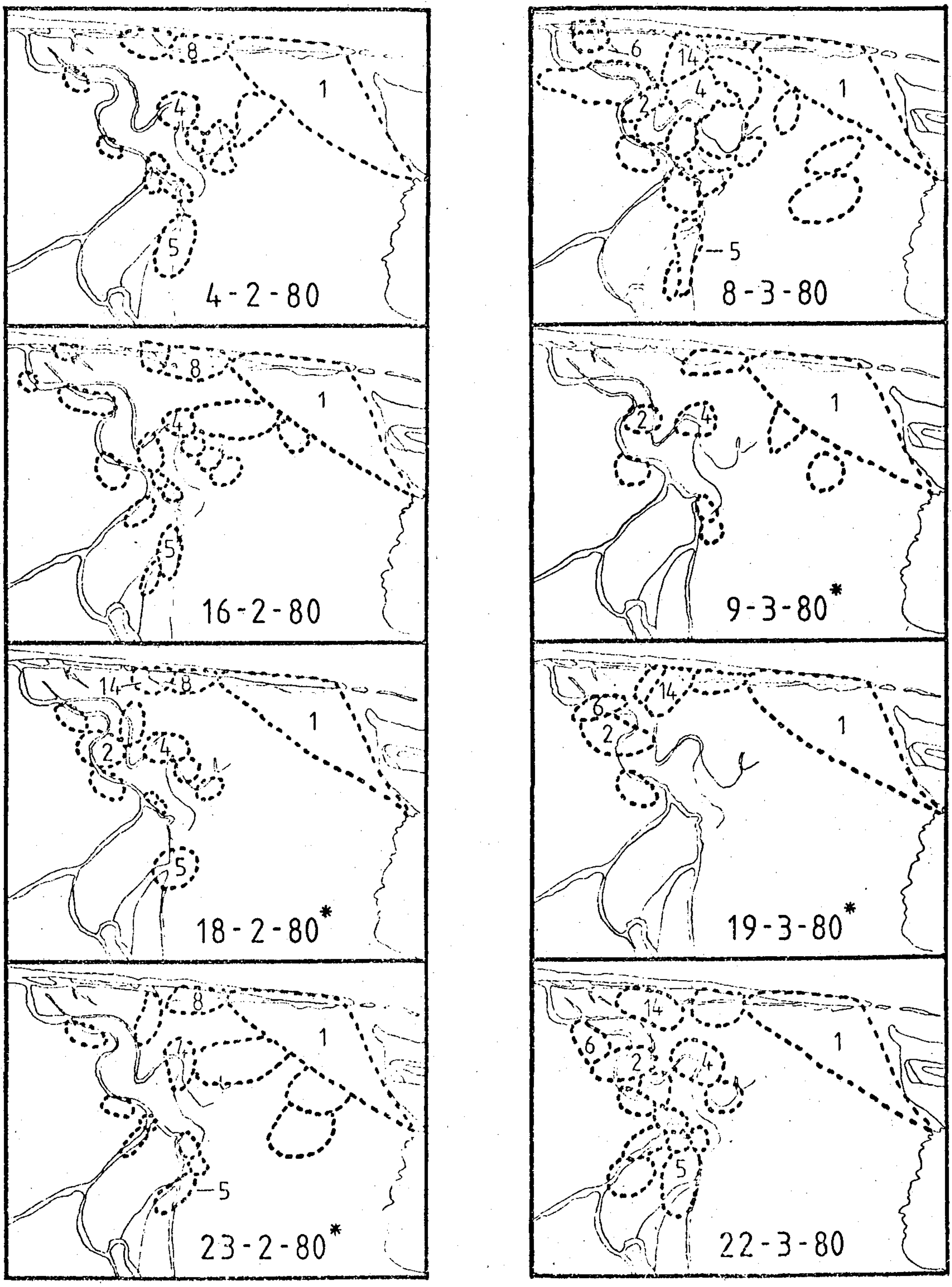
4
25-10-79
1
2
8
3-11-79


6
8
1
2
4
9
7-11-79
6
8
1
2
4
9
26-11-79
6
8
1
2
4
9
9-11-79
6
8
1
2
4
9
5
1-12-79
6
8
1
2
4
9
5
19-11-79
8
1
6
2
4
9
5
8-12-79
6
8
1
2
4
9
24-11-79
8
1
4
9
19-12-79


1
2
4
8
9
20-12-79
1
2
4
8
7-1-80
1
2
4
5
8
9
9-1-80
1
2
4
5
8
9
10
11
19-1-80
1
4
5
8
20-1-80*
1
2
4
5
8
12
13
21-1-80
1
2
4
5
8
23-1-80
1
4
5
8
2-2-80


8
1
4
5
4-2-80
8
1
4
5
16-2-80
14
8
1
2
4
5
18-2-80*
8
1
4
5
23-2-80*
6
14
1
2
4
5
8-3-80
1
2
4
9-3-80*
14
1
6
2
19-3-80*
14
1
6
2
4
5
22-3-80

the flock to become territorial, the dominant bird was last to do so (Table 13). This suggests that the remaining birds may also have been dominants. Furthermore, those birds that arrived in the first winter influx and established territories, did so not only by squeezing between, or displacing birds from already occupied territories, but also by occupying previously unoccupied areas. Thus birds remaining in the flock in November did not do so because of an absolute shortage of potential territories i.e. flock feeding was not forced on these individuals. Therefore, irrespective of the relative social status of the territorial and flock birds, the disappearance of birds from the flock and their occupation of territories indicates that, at least for some individuals the benefits of territoriality relative to flock feeding increased as the autumn progressed. This led to territoriality in some birds, but others remained as flock feeders, which presumably for them, was the more profitable behaviour.

To understand in more detail the reasons for territoriality in Grey Plover wintering at Teesmouth an investigation of measureable costs and benefits of territoriality and flock feeding was undertaken.

COSTS AND BENEFITS OF FLOCK-FEEDING AND TERRITORIALITY

Introduction./

Table 12. Disappearance of colour-marked birds from the flock.

Date	Birds remaining in Flock (%)
9.10.78	100
21.10.78	92
22.10.78	92
20.11.78	58
22.11.78	42
21.12.78	33
3.1.79	25
4.1.79	25
15.1.79	25
4.2.79	25

Values refer to individually colour-marked birds originally seen in the flock in October which were known to still feed in the flock on, or after, each date. Birds which left the estuary have been excluded from the analysis.

Table 13. Departure of colour-marked birds from the flock in relation to dominance status. All aggressive encounters involving the individuals listed are included in the Table.

Individual	Aggressive encounters		Date last seen in flock
	No.	% won	
Y W/O	10	90	22.11.78
L L/R	3	33	22.10.78
W O/G	3	0	"
L W/L	1	0	"
Y W/W	1	0	"

COSTS AND BENEFITS OF FLOCK-FEEDING AND TERRITORIALITY

Introduction.

In recent years the value of flocking in birds has been the subject of much discussion. The benefits gained from enhancement of food intake e.g. Murton (1971) and increased protection against predators e.g. Pulliam (1973), Vine (1971), have received particular attention.

An individual bird may enhance its food intake by copying other birds in either of two ways: (1) by following more successful birds from a communal roost site to feeding grounds - the information centre hypothesis of Ward and Zahavi (1973); and (2) by learning of the location of patches of high prey density on the feeding grounds by watching more successful individuals in the flock (Krebs et. al., 1972). Of these two mechanisms however, the former is an advantage of communal roosting rather than of feeding in flocks.

As both flock and territorial Grey Plovers on the Tees estuary roost together, it is unlikely that this behaviour is of major importance in determining which feeding stragegy is adopted by individuals. However if high densities of available *Nereis* occur in patches it is possible that flock-feeding birds may learn the location/

location of such patches by watching other individuals c.f. Krebs et. al. (1972). However I have not collected data to test this.

Flocking by shorebirds might give greater protection against birds of prey, which in some areas are important predators (Page and Whitacre, 1975; Smith, 1975). The risk of predation may be reduced within a flock in several ways: (1) earlier detection of predators e.g. Barnard (1980); Pulliam (1973) (2) confusion of predators e.g. Owens and Goss-Custard (1975); Neill and Cullen (1974) or (3) by reduction in the probability that any one individual will be caught e.g. Hamilton (1971); Pulliam (1973).

The response to avian predators of Grey Plovers, whether territorial or flock-feeding, is normally to crouch in a gully or small depression, rather than to fly and form a compact flock. Allied to the scattered feeding distribution and consequent difficulty in rapidly forming a tight flock, these behaviours suggest that avian predation is a relatively unimportant factor in determining spacing behaviour in Grey Plovers. However, a few individuals do take flight in response to alarm calls and mingle with flying flocks of smaller waders, particularly Dunlin and Knot. These smaller species feed in the greatest numbers where the flocking Grey Plovers feed. Hence, although potential avian predators of Grey Plover seldom occur on the estuary, it/

it is possible that in the past such predation has been an important factor in the evolution of interspecific flocking in the species.

Mammalian predation may be of much greater importance on the Tees estuary and possibly on many other, particularly small, estuaries with relatively long shorelines. Foxes *Vulpes vulpes* are known to frequent Seal Sands regularly at night, and the relatively isolated territorial birds, many of which feed in creeks, must be particularly at risk to predation. However, there is no firm evidence that such predation on Grey Plovers has occurred and this suggestion must, at present remain speculative.

Even if a reduction in the chances of predation is a major advantage of flock-feeding, it is unlikely that predation pressure on the Tees estuary varies seasonally in a manner which alone will explain the seasonal change in social behaviour, observed there. Other costs and benefits of flocking and territoriality must also be considered. These are, where possible, most easily considered in energetic terms.

Energy expenditure.

Evans (1976) listed three main purposes for which a shorebird needs energy in the non-breeding season: (1) to maintain its body temperature and normal metabolic processes (2) to fly, to and from its feeding grounds, and/

and possibly to escape predators and (3) to cover the costs of food gathering. To these I would add a fourth: to defend a territory (or an individual distance within a flock).

(1) In each species of bird there is a range of ambient temperatures within which, at rest, the metabolic rate is minimal. As temperature falls below this a steadily increasing expenditure of energy is required to maintain body temperature. In addition, with increasing wind speed the rate of heat loss due to forced convection (and, therefore the metabolic rate required to compensate for this) increases further. Although the magnitude of these wind induced losses is not known, they could, as argued by Evans (1976), be considerable. The metabolic rate of Snowy Owls *Nyctea scandia* almost doubled, as wind speeds increased from calm to 9m/sec at temperatures of -20^{o} and $-30^{o}C$ (Gessaman, 1973).

On Seal Sands, as wind speeds rise above about 25 knots, Grey Plovers feeding in flocks on exposed mudflats cease feeding and start to roost (Table 14). It is possible that birds do so because at these wind speeds the rate of energy production needed to balance heat losses through forced convection is too great to be met by the rate at which prey biomass can be obtained. However many individuals of other shorebird species - those/

Table 14 Effects of wind speed on feeding by Grey Plover on open mudflats.

Date	Wind Speed (kts)	% birds feeding	Sample Size
18-2-79	8	100	31 birds
4-12-78	9	100	6
18-12-78	10	100	18
22-10-78	15	100	19
2-2-79	18	100	15
3-11-78	21	100	14
20-11-78	21	100	7
17-1-79	25	7+	15
22-11-78	31	6++	17
14-2-79	36	0	15

\+ Refers to a single individual which fed in the lee of an embankment, but with low success in spite of the shelter. (Mean intake rate 15 cals minute compared with 60 cals/min on 4th December 1978, 39 cals/min on 18th February 1979 and 73 cals/min on 5th January 1979).

++ Refers to a single individual which tried to feed for 10 minutes and then gave up because of lack of success.

those which feed by tactile means, such as Knot and Dunlin - continue to feed in these conditions. Furthermore, the response of the Plovers to high wind speeds is sudden, rather than gradual as would be expected if wind chill were the main causal factor. Thus it is likely that Grey Plovers cease feeding because buffetting by the wind interferes with their run-stop-peck feeding method, as suggested by Evans (1976). Davidson (in press) has shown that Redshank respond to gales by moving to sheltered feeding sites. This also is a sudden response as winds exceed 25 knots.

The response of Grey Plover to strong winds is a result of their dependence on specific visual cues for detection of <u>Nereis</u>. These are different in other invertebrate species; consequently the influence of wind on foraging behaviour of Plovers in other estuaries may be different from that on the Tees. At Lindisfarne, Grey Plover feed on <u>Arenicola</u> and Pienkowski (1980) has shown that, although their prey capture rate was reduced at wind speeds over 25 knots, birds continued to feed successfully. The implications of this variation between estuaries in the effect of wind on feeding success is discussed in detail later.

Territorial areas used by Grey Plover at Teesmouth differ in topography from those used by the flock. They are of firmer substrata and dissected by creeks (Table 1). These creeks vary in size from 2 m deep and/

and 4 m across to 0.5 m deep and 0.7 m wide (see Plate 1 a,b). During gales, when it is not possible for flock birds to feed, territorial birds frequently can do so in the creeks (Table 15), where wind speed is much reduced (Table 16). Thus it is possible for most territorial birds to maintain a sufficient rate of intake to achieve a net gain of energy during windy conditions, whereas most flock birds cannot and lose weight (Dugan et. al. In Press).

(2) The magnitude of daily energy expenditure incurred in flying to and from the roost sites and escaping predation cannot be quantified accurately. However both territorial and flocking Grey Plovers use the same roost sites, usually between 2 and 4 Km from the feeding grounds. Furthermore, while feeding most birds of both behavioural types respond to predation in the same manner, viz. by crouching, as mentioned earlier. Thus these activities are unimportant to the explanation of seasonal changes in behaviour of foraging Grey Plovers and need not be examined further.

(3) As argued by Evans (1976), if prey become less available, a bird will take longer to find a given quantity of food and will therefore expend more energy in finding it. However, as discussed previously, availability of Nereis to Grey Plover appears to vary independently/

Table 15. Calorific intake and rate of capture of <u>Nereis</u> by territorial Grey Plovers feeding in creeks during gale conditions.

Individual Date Area	Wind Speed (Knots)	Cal. Intake Cals/min.			*Nereis* capture Total			Large	
		No. Mins.	$\bar{x}$	S.E.	No. Mins.	$\bar{x}$	S.E.	$\bar{x}$	S.E.
L W/L 14-2-79 Sc. Mud	36	20	11.0	7.7	11	0.64	0.19	0.09	0.9
R W/G 18-3-80 E.Ch.	36	14	313.2	81.7	8	2.50	0.47	1.63	0.35

Note: Calorific intake was calculated for total observation time. Rate of *Nereis* capture was calculated only for periods of continuous feeding.

Table 16. Wind speed in creeks within territories and on the nearby open mudflat.

Creek	Wind speed Above creek m.p.h.	 Knots	 In creek m.p.h.	 Knots	Significance of Difference	
R W/G Territory	11.0± 0.4	9.5± 0.3	7.8± 0.3	6.7± 0.3	$t_{10}=6.4$	p 0.001
"	10.0± 0.5	8.6± 0.4	4.4± 0.8	3.8± 0.7	$t_{10}=6.0$	p 0.001
Y Y/O Territory	10.1± 0.5	8.7± 0.4	3.8± 0.2	3.3±0.2	$t_{10}=11.7$	p 0.001
W R/W Territory	7.6± 0.5	6.5± 0.4	7.0± 0.2	6.0±0.2	$t_{14}=1.11$	N.S.
Far *Enteromorpha* Central Bank	9.2± 0.1	7.9± 0.1	5.6± 0.3	4.8±0.3	$t_{6}=11.3$	p 0.001

Note: All measurements were made with a Casella anemometer.

independently of temperature. Thus it seems unlikely that, in the situation investigated in this study, major seasonal changes in prey availability exist.

(4) Intra specific aggression occurred throughout the study period from August to April. Within the flock the highest levels were recorded in autumn. However data are too few to conclude that a seasonal pattern in intensity exists. However the time spent in aggression was higher on Central Bank than on Greenabella Bank on most days (Fig. 17). In the territorial area in Eastern Channel, aggression declined from autumn onwards (Fig. 18), though with much day to day variation in levels. After December the level stabilised somewhat, at about that observed in the flock. Although different methods were used to measure the average rates of aggression among flock and territorial birds, it is unlikely that the differences observed are a result of this. The data for the territorial bird R W/G (Fig. 19) were obtained in the same way as for the flock birds, yet the seasonal change in aggression wasvery similar in this and other territorial birds, except in mid-winter, when the level displayed by R W/G was much lower than the mean for all territorial birds in this area. However, although the method used to measure the activity of all territorial birds (recording the activitiy of visible birds at regular intervals) is biased towards recording aggression, the main cause of the difference between R W/G and other territorial/

Fig. 17. Seasonal variation in level of aggression among flock birds 1978-79. The time spent in aggression is expressed as a % of total observation time. The figures are mean values and one standard error for all birds watched for 5 or more minutes on each date.

● Birds feeding on Central Bank.

○ Birds feeding on Greenabella Bank.

Fig. 18. Seasonal variation in level of aggression among territorial birds in Eastern Channel 1979-80. The number of aggressive encounters involving each colour-marked individual recorded on each day during scans of all territorial birds (see text for details) is expressed as a percentage of all sightings on that day of that colour-marked individual. The figures presented are the mean and one standard error of these values for colour-marked individuals seen 3 or more times during scans on each day. Only days when values were obtained for 3 or more birds are included in the figure.

Fig. 19. Seasonal variation in time spent in aggression by R W/G, 1979-80. The values are expressed as a percentage of total observation time.

Note.
As Figs. 17 and 18 are derived by two different methods of estimating time-budgets it is not possible to perform rigorous statistical analysis with the small sample size available. Further, as in Fig. 18 each point is not derived from the same individuals on each day it is not possible to analyse statistically the data presented.

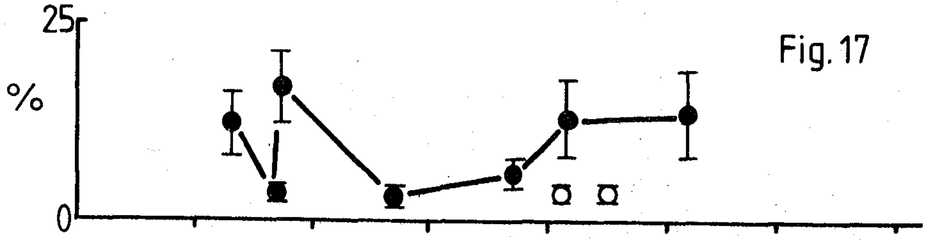


Fig. 17

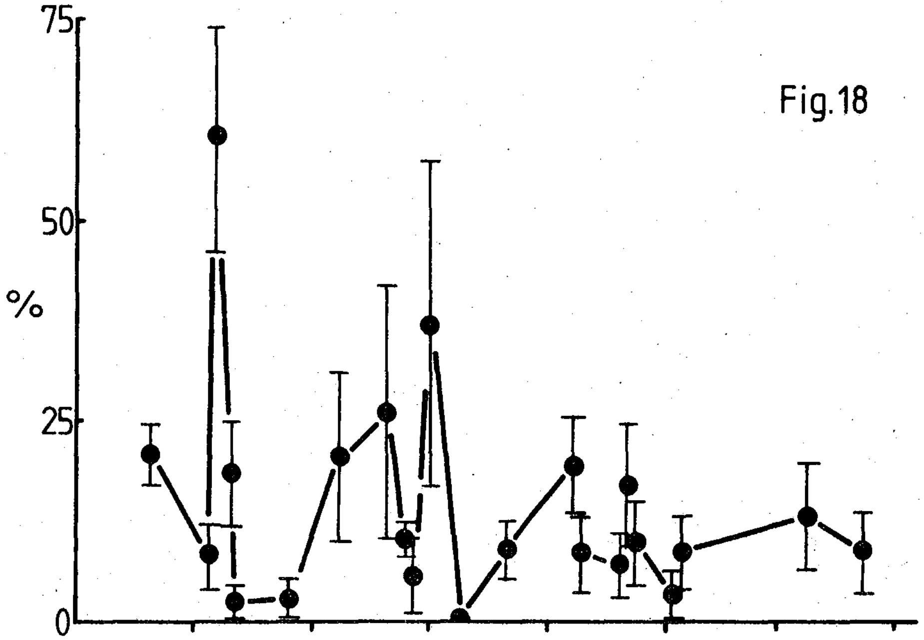


Fig. 18

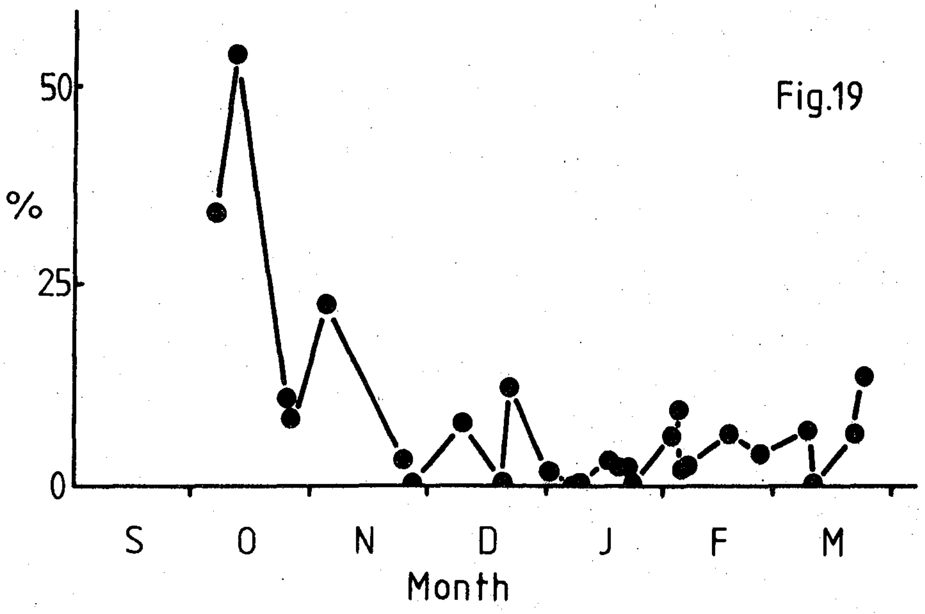


Fig. 19

territorial birds was the position of R W/G's territory. This was bounded along most of its perimeter by either sand dunes or Seaton Channel i.e. unsuitable feeding habitat. Thus R W/G had only 2 or 3 immediate neighbours against which to defend its boundary, compared with 6 or 7 of some of the other birds (Fig. 16).

It seems likely that seasonal variation in levels of territorial aggression suggested in Figs. 18 and 19 was due to seasonal variation in rate of boundary and ownership change. During autumn the distribution of territories in Eastern Channel was continually being modified, the rate of change slowing in early winter (Fig. 16). However when numbers of birds on the estuary increased again in December, many changes in territory distribution occurred (Table 17; Fig. 16). Some birds established territories by squeezing into and reducing the size of existing territorial areas in Eastern Channel (compare e.g. the territory of W R/W on 8-12-79 and 7-1-80 (Fig. 16). Indeed one colour-marked bird left Eastern Channel at this time i.e. L G/L (Table 17; Fig. 16). This territorial activity resulted in increased complexity of territory distribution and maintained aggression at a high level.

At the time of the first winter influx of Grey Plovers a few instances of swamping of territorial areas by flock birds also occurred e.g. G/Y O/W and L W/G fed in Eastern Channel once, on 19-1-80, but these /

Table 17. Changes in size and location of Grey Plover territories in Eastern Channel in the month following the first winter influx.

Birds which maintained territory size	Birds whose territory was reduced in size	Birds which left their territories	Other birds which were recorded in E. Ch. but did not establish territories
R W/G	W R/W	L G/L	L W/G
W R/O	R/G R/G	(Y Y/O)	R O/Y
G Y/R	(Y Y/O)		G/Y O/W
			R/W R/Y

Note: It is not known whether Y Y/O left its territory or whether this was reduced to an area in which the individual was not visible from the observation position.

these incidents were too infrequent to have any significant effect on aggression within the area. Similarly, on one occasion (4-2-79) one individual was observed to defend a territory within the flock for only one low water period. This behaviour is similar to the short-term territoriality observed by Myers et. al. (1979b), in Sanderling and may have been the result of a patch of high density of available prey. However, such territorial defence is too infrequent to greatly influence the level of aggression within the flock.

In summary, energy spent in aggression by territory holders was greatest in autumn. At this time, such birds spent more time than flocking birds engaged in this behaviour. However, by winter, aggression amongst territory holders had declined. At this season territorial and flock feeding birds spent approximately equal amounts of time in aggression.

Energy intake.

No consistent difference in mean rate of prey capture or energy intake is apparent between territorial and flock birds (Figs. 20, 21, 23, 24.) although because of the small sample sizes and heterogeneity of the data it is not possible to examine this rigorously statistically.

However, in Eastern Channel for most of the winter R W/G maitained a very high energy intake rate, normally higher than that recorded in either flock or for other territorial birds (Figs. 22,25). The extensive data for intake rates of R W/G reveal two peaks of intake, the

first/

Fig. 20. Seasonal variation in rate of energy intake of flock feeding birds. Intake values refer to the mean rate, among all individually recognisable birds observed during the low water period on each date. Rates were calculated for total observation time i.e. feeding time plus time engaged in other activities such as preening, aggression. Only data from birds watched for 3, or more minutes, were used. Figures given refer to number of birds. Thick and thin vertical lines represent one standard error and the total range of values, respectively. Symbols indicate values from feeding areas:

●	4 (1978-79)
■	4 (1979-80)
○	9 (1978-79)
□	9 (1979-80)
△	5 (1979-80)

Fig. 21. Seasonal variation in rate of energy intake of territorial birds on Scalloped Mud. Explanation as for Fig. 20. Symbols indicate birds observed:

×	Y W/W 1979-80
○	mean of Y W/W & L W/L 1979-80.
●	mean when 2 or more birds observed, 1978-79
✱	Y W/W 1978-79
△	W Y/Y 1978-79
□	L W/L 1978-79

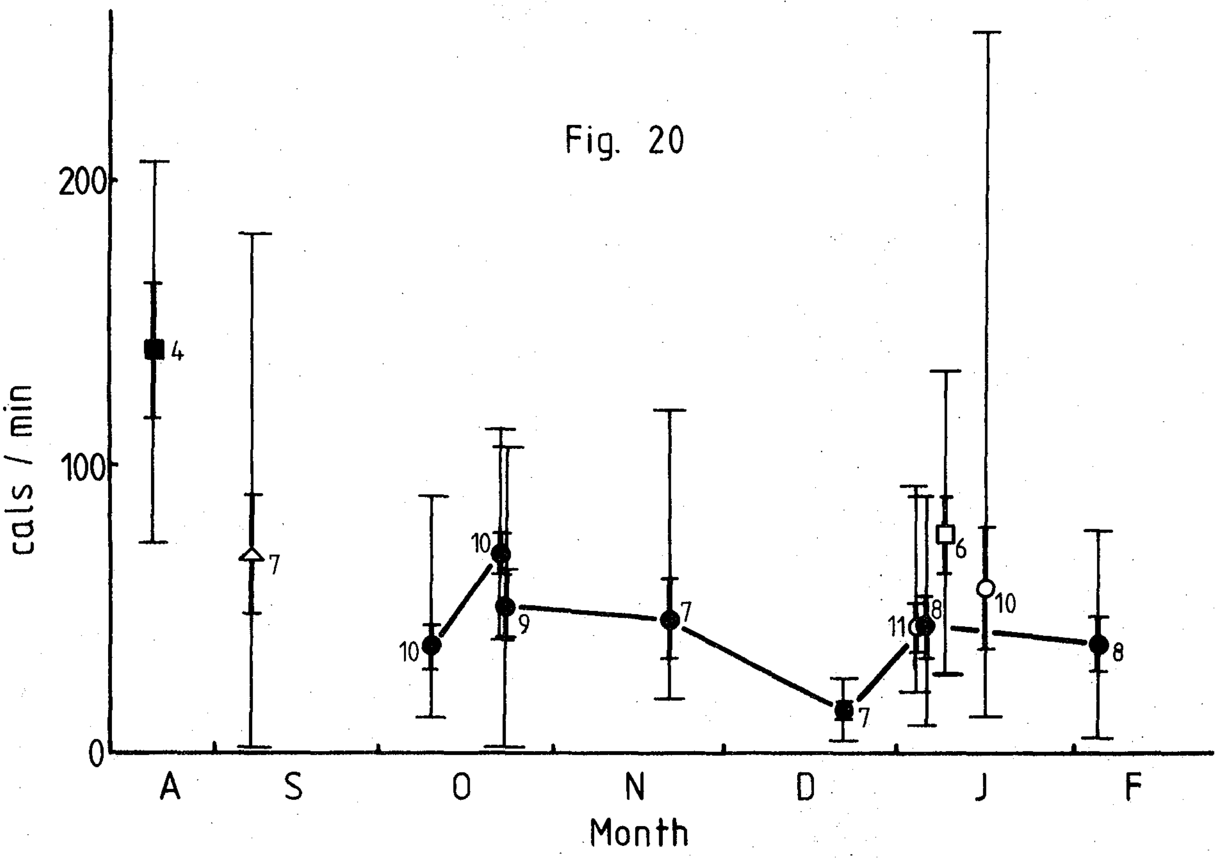

cals / min
0
100
200
4
7
10
10
9
7
7
11
8
6
10
8
A
S
O
N
D
J
F
Month

Fig. 20

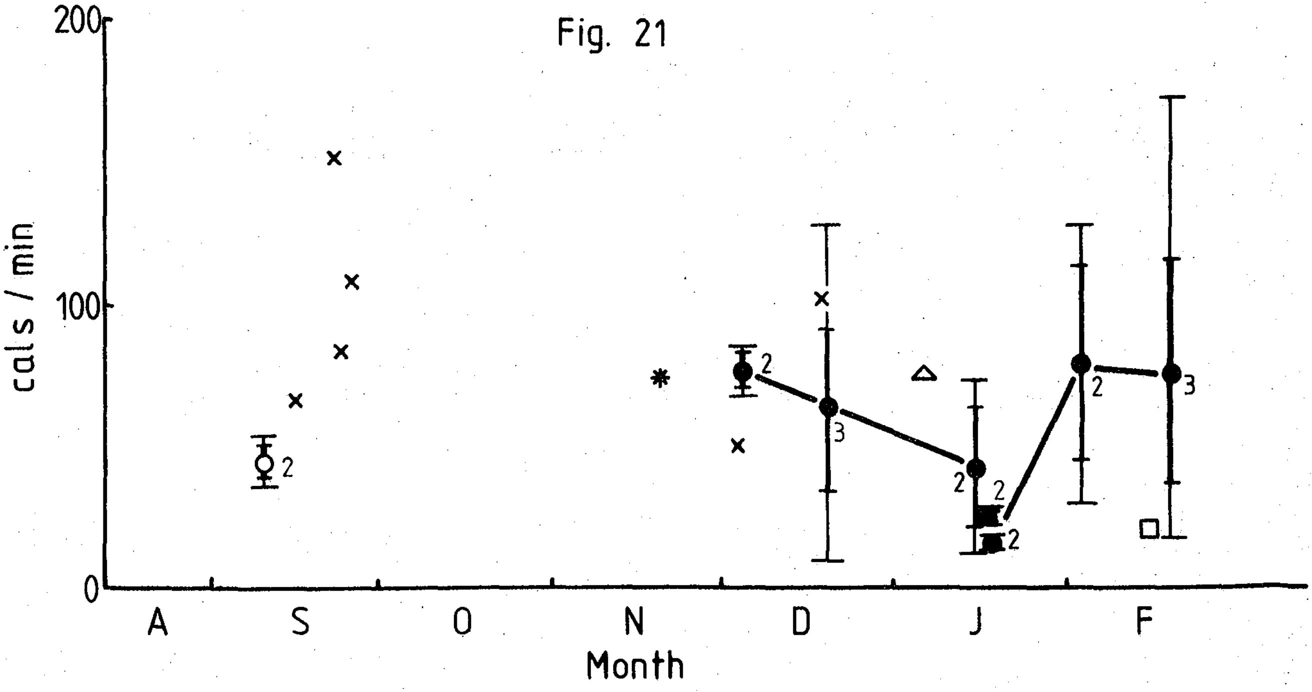

cals / min
0
100
200
2
2
3
2
2
2
2
3
A
S
O
N
D
J
F
Month

Fig. 21

Fig. 22. Seasonal variation in rate of energy intake of R W/G, a territorial Grey Plover in Eastern Channel, in 1979-80. Intake values refer to the mean rate during the total period of observation on each date. Figures given refer to the number of minutes for which the bird was watched on each date. Only data for days when this was equal to or exceeded, 15 minutes are presented. Thin vertical lines represent one standard error.

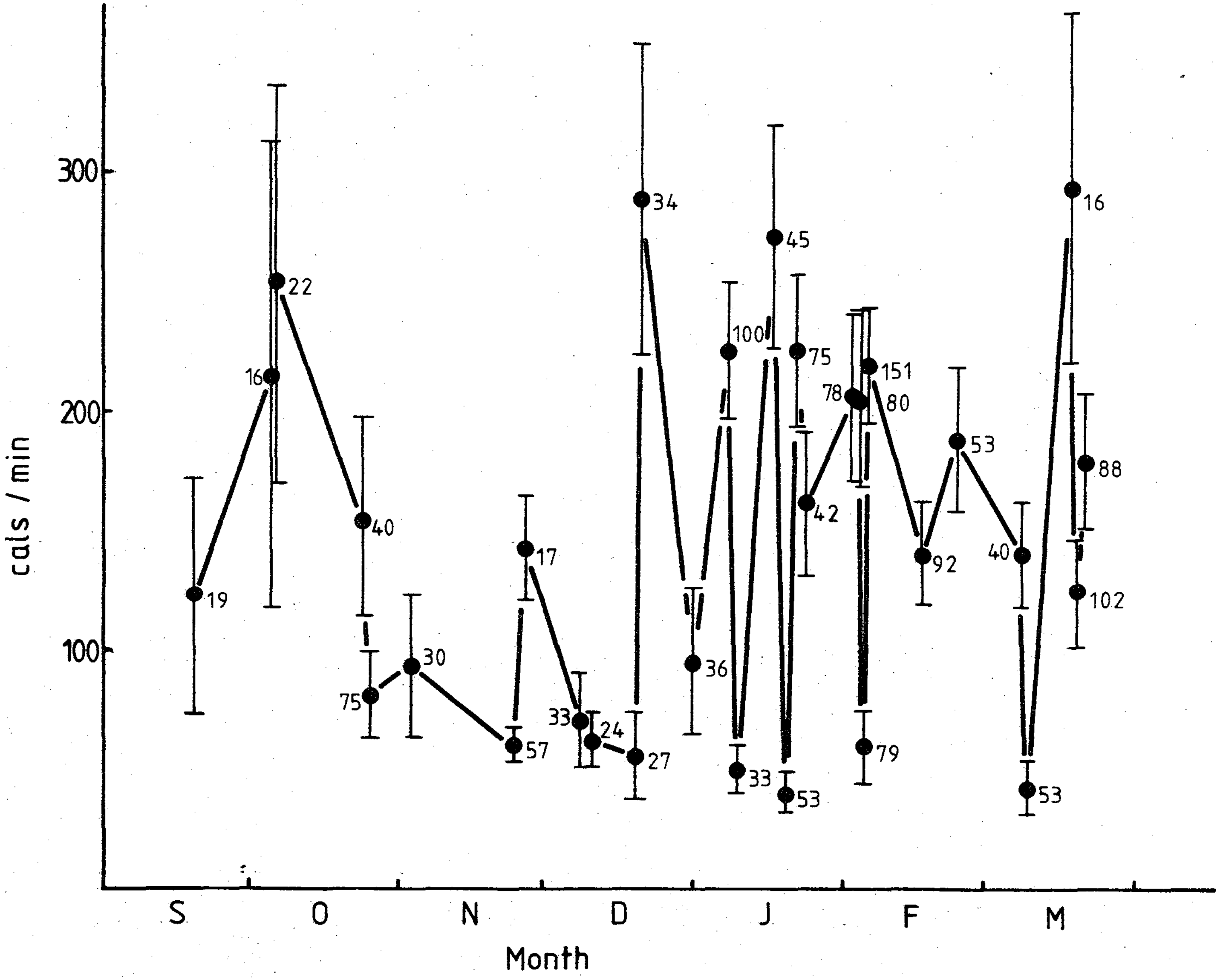

cals / min
300
200
100
S
O
N
D
J
F
M
Month
19
16
22
40
75
30
57
17
33
24
27
34
36
100
33
45
53
75
42
78
151
80
79
53
92
40
53
16
88
102

Fig. 23 Seasonal variation in rate of capture of large (> 4 cm. in length) _Nereis_ by flock feeding birds. Explanation and symbols as for Fig. 20.

Fig. 24. Seasonal variation in rate of capture of large _Nereis_ by territorial birds on Scalloped Mud. Explanation and symbols as for Fig. 21.

Fig. 25. Seasonal variation in rate of capture of large _Nereis_ by R W/G. Explanation and symbols as for Fig. 22.

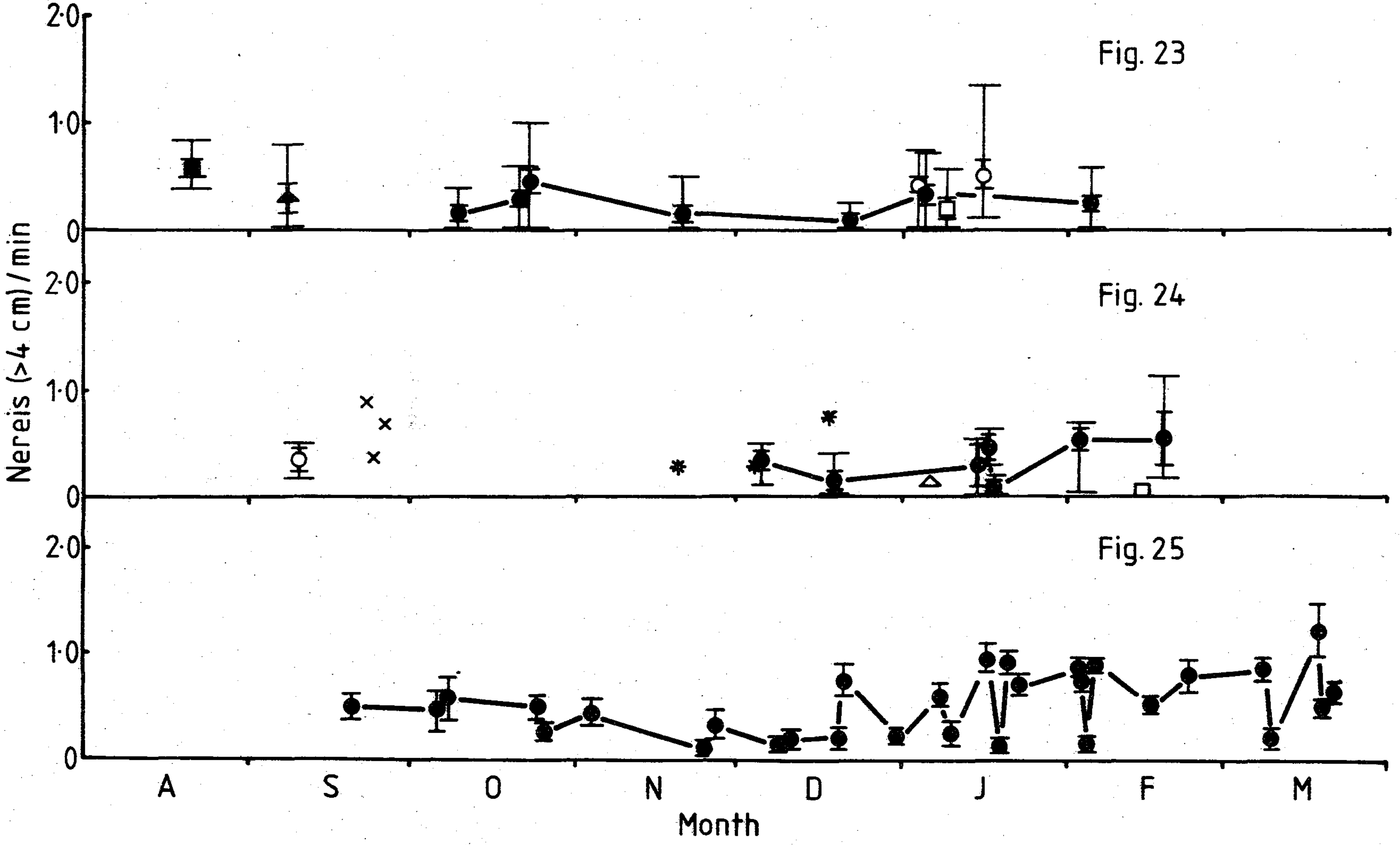


Fig. 23
Fig. 24
Fig. 25
2·0
1·0
0
Nereis (>4 cm) / min
A
S
O
N
D
J
F
M
Month

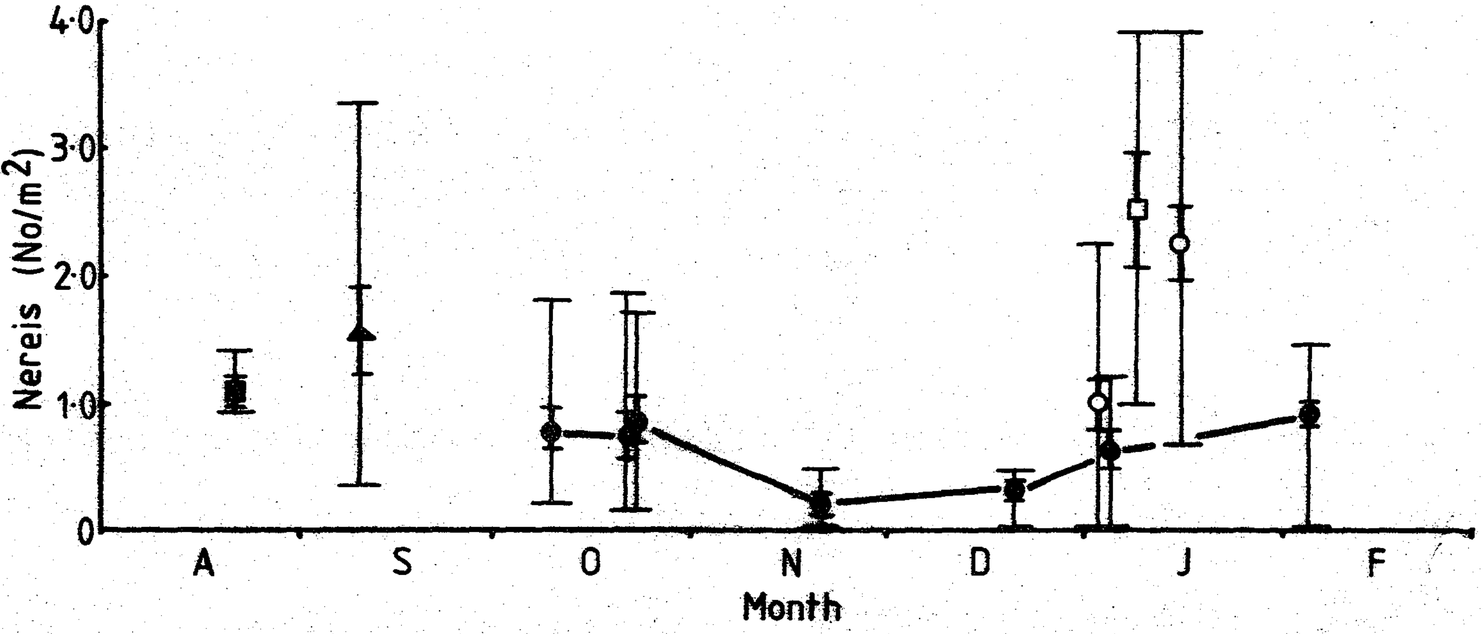


Fig. 26. Seasonal variation in rate of capture of Nereis of all sizes by flock feeding birds. Explanation and symbols as for Fig. 20.

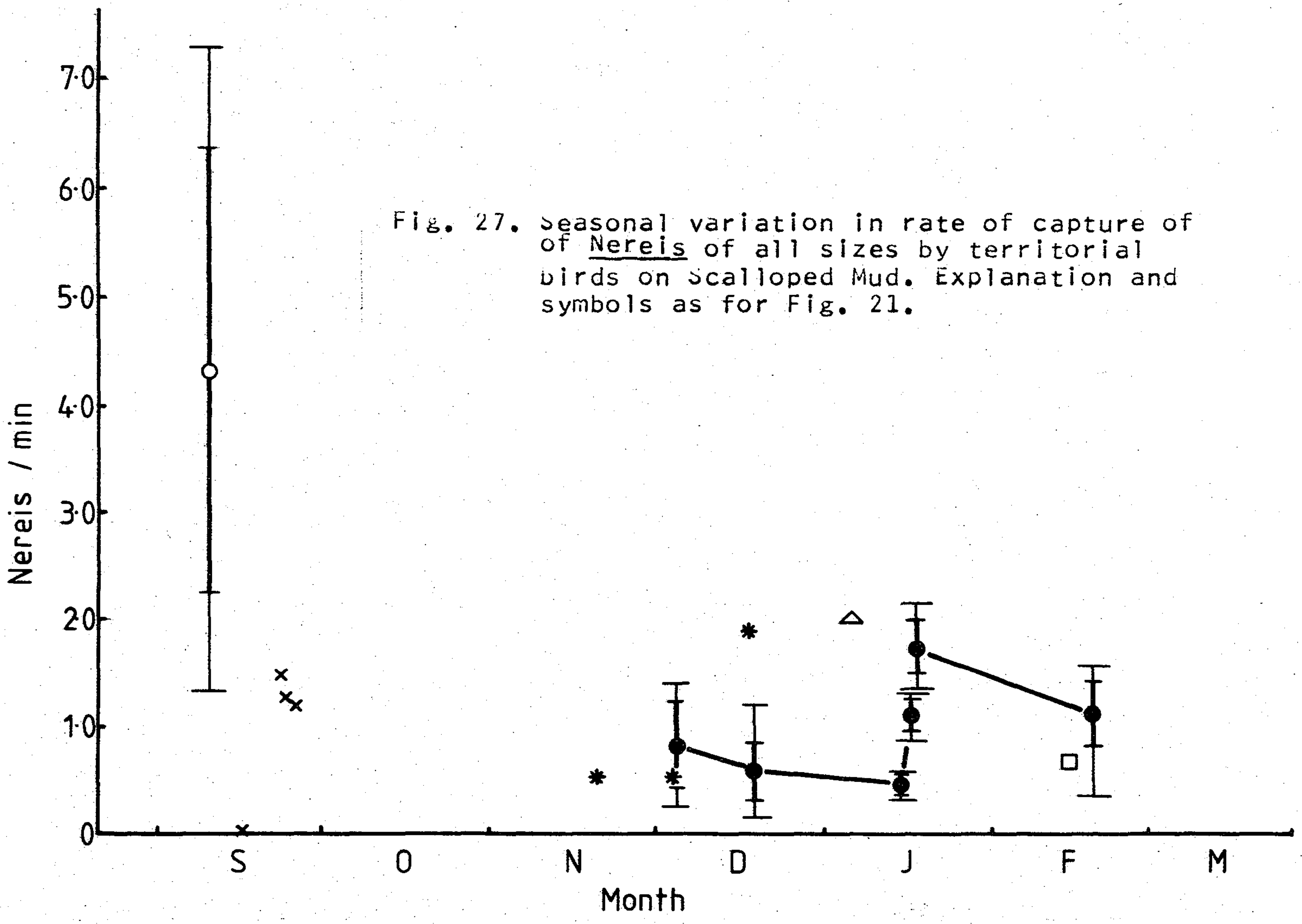


Fig. 27. Seasonal variation in rate of capture of of *Nereis* of all sizes by territorial birds on Scalloped Mud. Explanation and symbols as for Fig. 21.

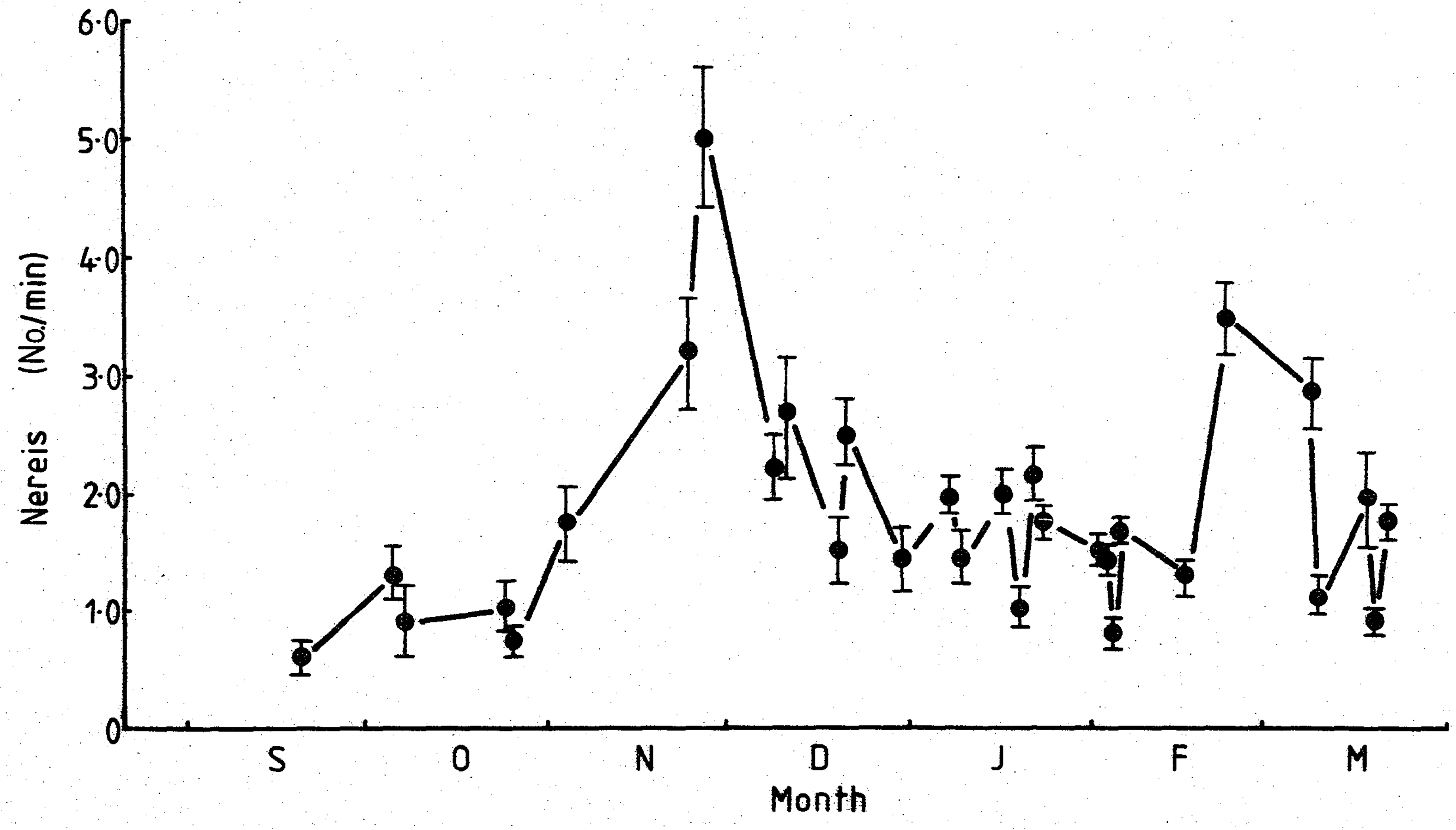


Fig. 28. Seasonal variation in rate of capture of Nereis of all sizes by R W/G in winter 1979-80. Explanation and symbols as for Fig. 22.

first in autumn and the second from late December until the end of the winter (Figs. 22, 25, 28). It is most unlikely that the pattern of seasonal variation in intake observed in this individual is an artefact of inadequate data. Furthermore, although dry weights of *Nereis* in Eastern Channel in autumn 1979 were high the two peaks described are apparent, not only in calorie intake rate, but also in capture rate of large *Nereis*. When R W/G was caught on 18-9-78 it was in moult and the autumn peak in intake in 1979 must also have coincided with the moult. However, aggression was also highest at this time (Fig. 19) and therefore it is not possible to distinguish unequivocally between the energy demands of territorial defence and moult. Nevertheless in early November, when aggression was still high but moult would have finished, the energy intake had already decreased suggesting that the higher energy intake may have been principally due to moult.

The low intake by R W/G observed during November and early December was not a result of less time spent foraging for that remained high (Fig. 29), but to a decrease in intake of large *Nereis* (Fig. 25). In contrast, the intake of all *Nereis* (and therefore, by subtraction, also of small individuals) was highest at that time (Fig. 28). The increase in energy intake, following the November and December low, was due to an increase/

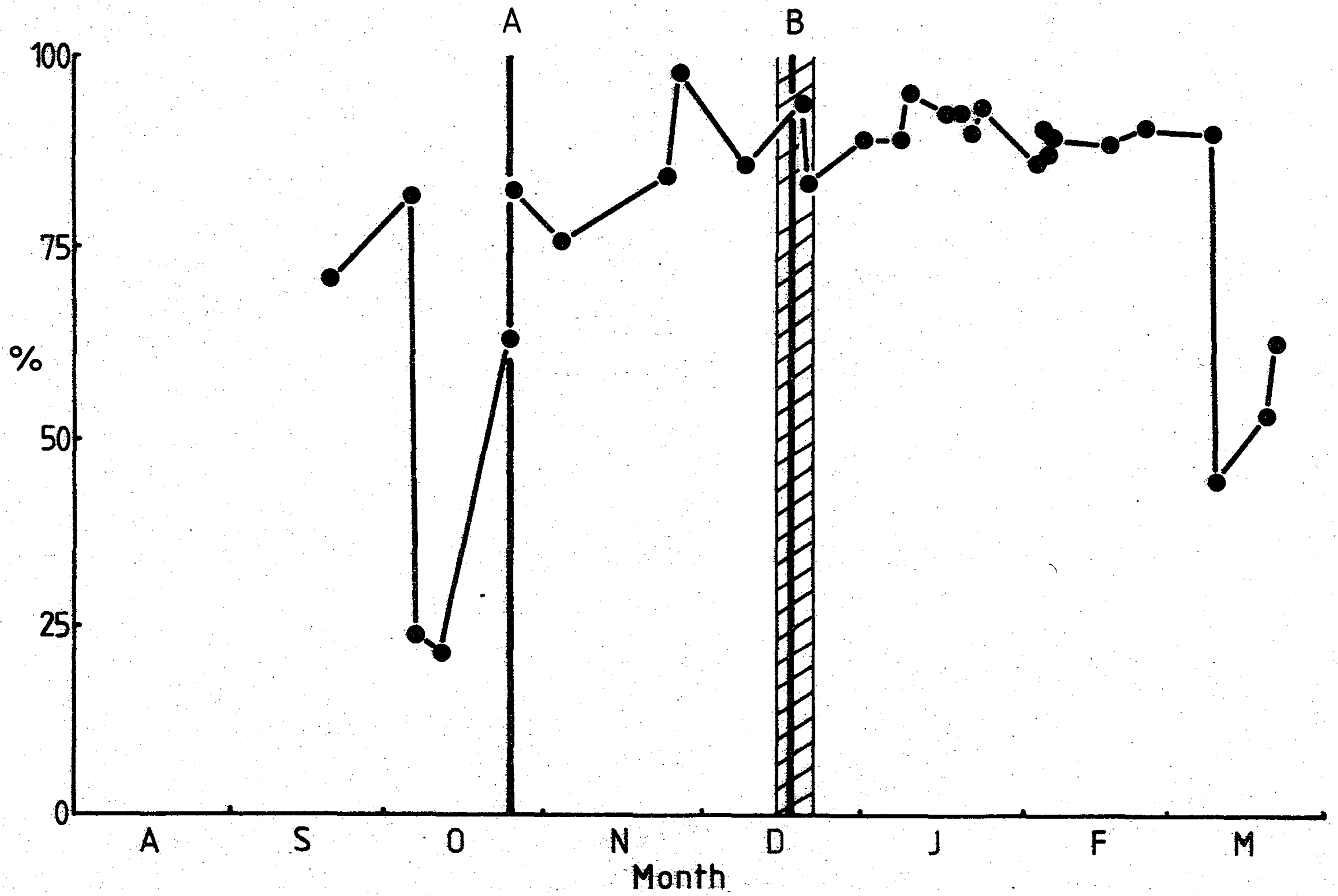


Fig. 29. Seasonal change in percentage of time spent feeding by R W/G in winter 1979-80. Values present the amount of time spent feeding expressed as a percentage of total observation time. Single vertical line A indicates the time of the drop in intake rate of R W/G. Single vertical line B indicates the time of the December increase in intake rate of R W/G. Hatched bar indicates the start of the period of prolonged cold weather.

increase in capture rate of large, and a decrease in that of small, Nereis.

Discussion.

a. Energy intake and expenditure of flock-feeding and territorial individuals.

Because of the high incidence of aggression among territorial birds, it seems possible that, in autumn, daily energy expenditure under calm conditions may be higher among these than among flock birds. However, offsetting this greater rate of energy expenditure among territorial birds, evidence suggests that high rates of energy intake are achievable in some territories. In the absence of more daylight and detailed nocturnal observations, the overall advantage and frequency of such high intake rates is not known. The low total calorie intake during daylight hours of most flock and territorial birds indicates that they must obtain a large proportion of their total intake at n night. Observations of radio-tagged birds at night are consistent with this hypothesis since they may feed in different areas and on larger prey than by day (Dugan, 1981).

Thus assuming that both flock and territorial birds are capable of feeding at night, a high diurnal intake must be a true advantage, however slight.

Under/

Under very windy conditions the value of territorial possession increases markedly. Shelter is essential for efficient foraging and is available within a territory in creeks. Absence of such features in flock foraging areas can lead to starvation during prolonged gales and periods of low temperatures (Dugan et. al. In Press). Indeed, in the winter of 1978-79, of 5 birds which disappeared from the estuary in mid-winter, and whose social behaviour prior to departure was known, all were flock feeders. Of these, only one (20%) was seen in the following winter of 1979-80, whereas 13 out of 15 (87%) of the flock feeding birds which left in spring returned. However at present with only a few years data it is not possible to be absolutely certain that all birds which disappeared in mid-winter in 1978-79 and did not return in 1979-80 died. Thus, although there is evidence that flock birds, but not territorial birds, disappeared from the estuary during severe weather it is not possible to conclude that this was definitely due to mortality. More data from future years are required to clarify whether mortality during severe conditions is greater among flock than territorial birds.

b. Optimal use of territories.

At times of greatest energy demands, high energy intake by R W/G was achieved by increased intake of large *Nereis*. In contrast, Pienkowski (1980) has shown that among Grey Plover feeding in flocks on *Arenicola* at Lindisfarne smaller proportions of large worms were taken/

taken under cold conditions. However, the birds studied by Pienkowski foraged in the same site in both mild and cold conditions, whereas in my study, the increase in capture rate of large Nereis by R W/G in severe weather was associated with change in use of parts of its territory. During the period of low intake from 25-10-79 to 19-12-79 use by R W/G of areas where low calorie intake was achieved averaged 37% of total feeding time. In the period of high intake preceding this, the corresponding figure was only 18% (Fig. 30). After 19-12-79, use of areas where low intake was achieved decreased to 13% with the onset of severe conditions (Fig. 31). Furthermore, from 25-10-79 to 10-12-79 there is a negative correlation between area quality and use (Fig. 32). This becomes positive after mid-December (Fig. 33). These relationships are due in part to the large size of the poor quality areas and the negative correlation in Fig. 32 is reduced when expressed as % per area ($r = -0.3095$ $p > 0.1$). However, the size and direction of change in the use of the sub-areas between the two time periods is significantly positively correlated with the quality of the area (Fig. 34) i.e. use of good areas increases from 25-10-79 - 10-12-79 to 19-12-79 - 8-3-80 while that of poor areas decreases. A similar correlation is obtained when area quality is expressed in terms of capture rate of large Nereis achieved there (Fig. 35). This pattern of territory use is not consistent with short term optimisation of enrgy intake. This hypothesis/

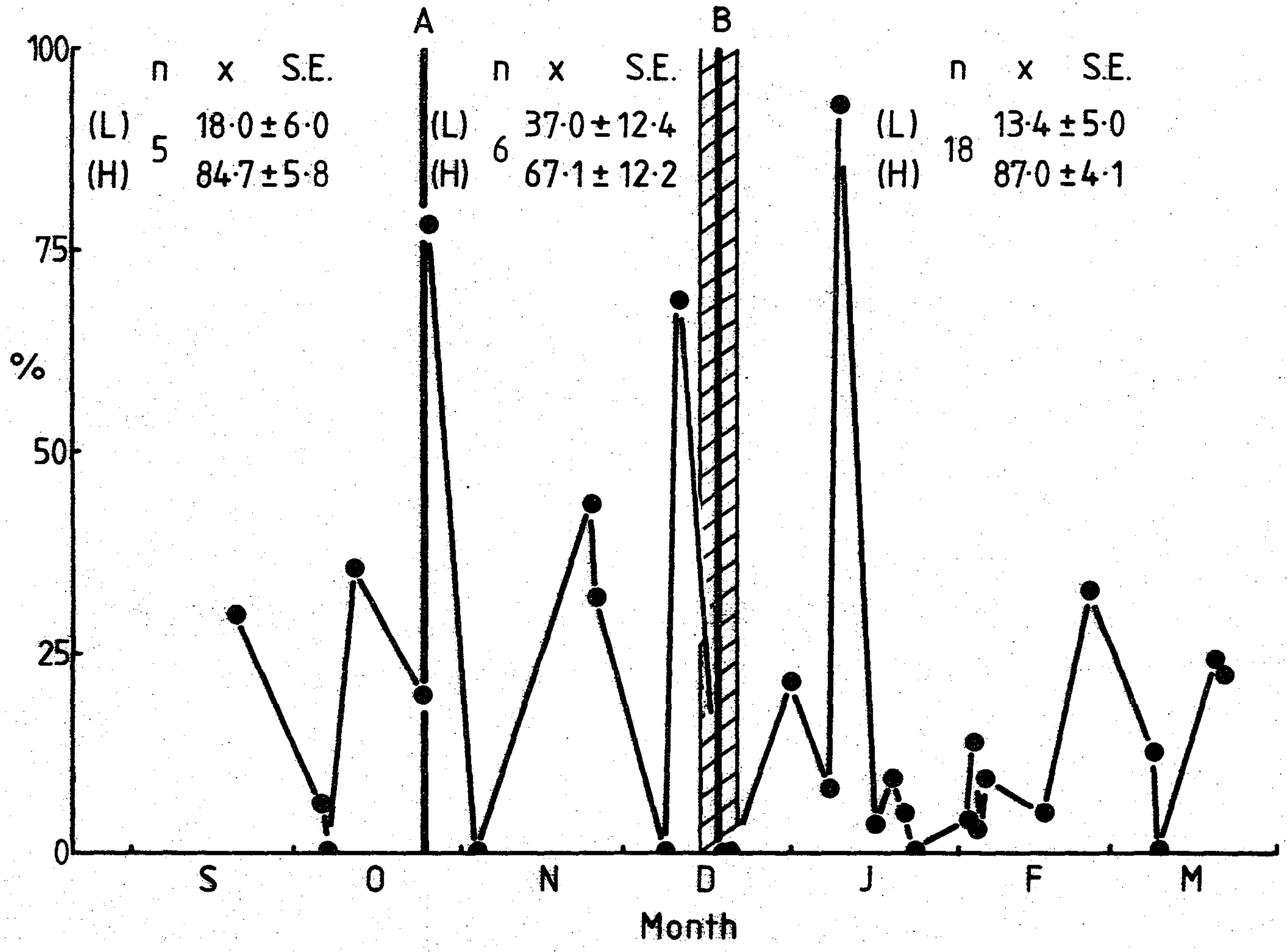


Fig. 30. Seasonal variation in use of low and high intake areas by R W/G in winter 1979-80. For each observation day is shown the percentage of total feeding time i.e. excluding time engaged in other activities, spent in areas of low calorific intake (< 125.0 cals/min). Vertical lines and bar are as in Fig. 29. Mean daily percentage of time spent in low (L) and high (H) intake areas are given for three periods: two of high intake 19-9-79 to 24-10-79 and 20-12-79 to 21-3-80, and one of low intake 25-10-79 to 19-12-79. n = number of days.

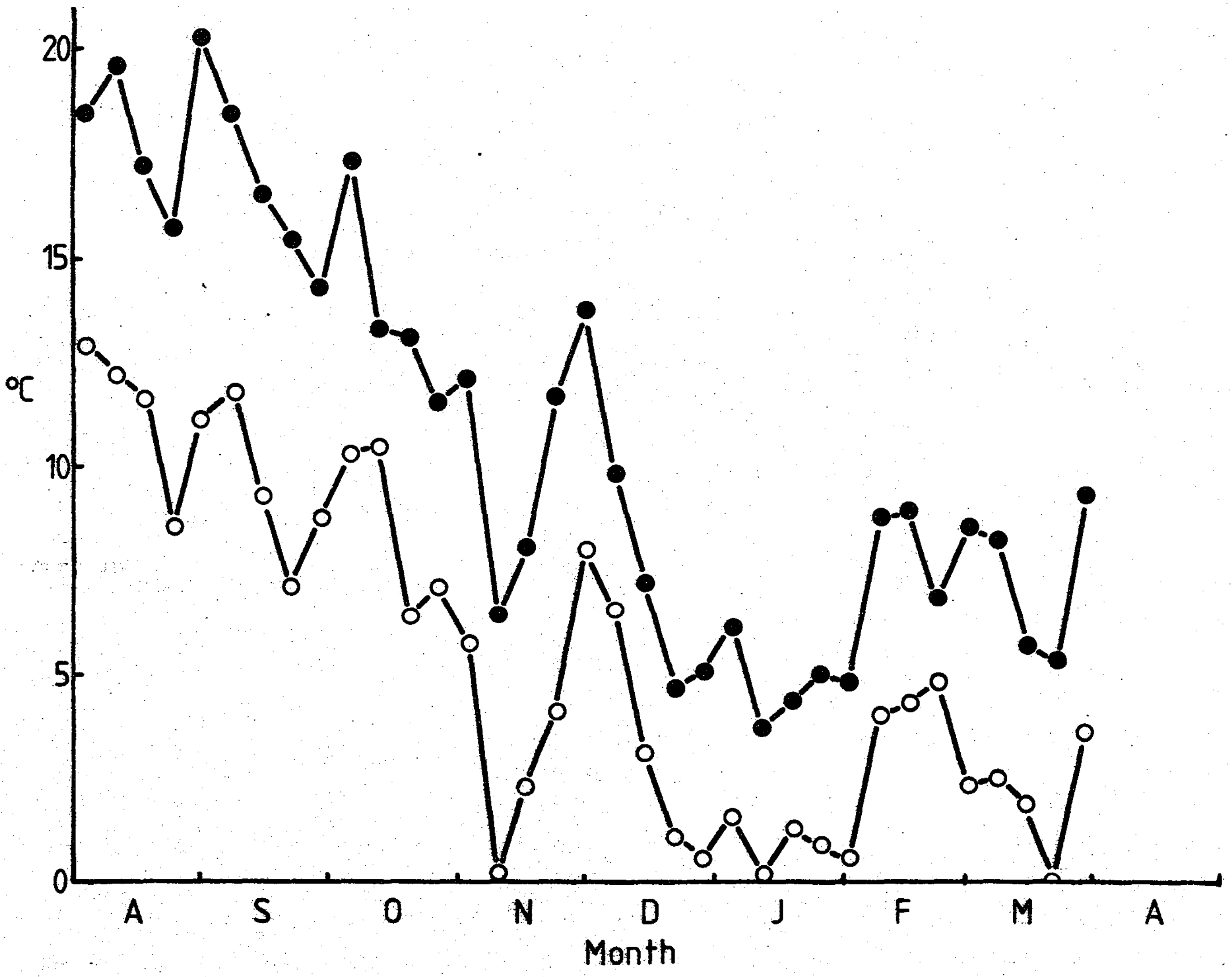


Fig. 31. Seasonal temperature variation 1979-80. Values given are mean daily maximum (●) and minimum (○) temperatures (°C) recorded in each week at Hartlepool.

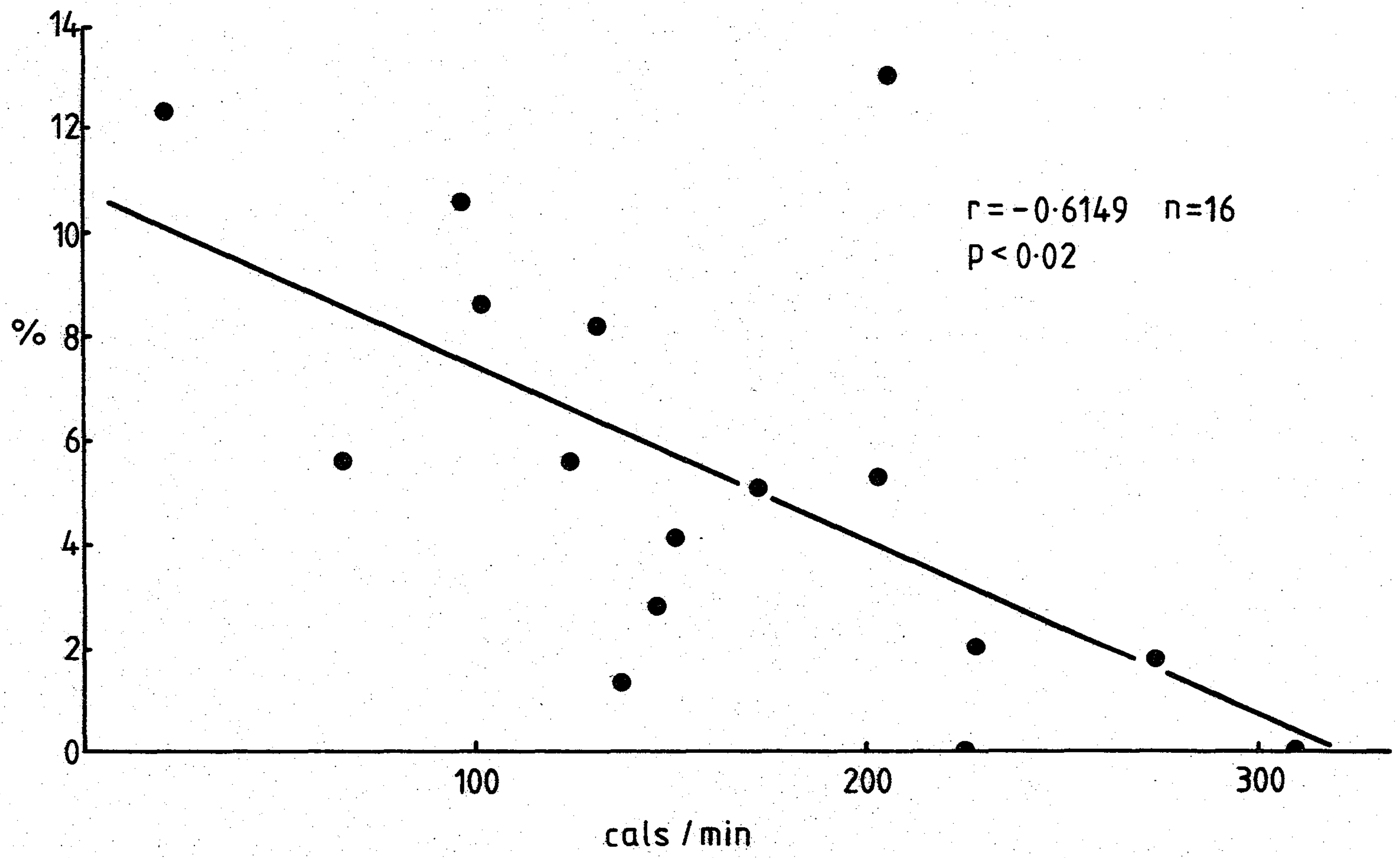


Fig. 32. Relationship between the percentage of total feeding time spent by R W/G in each part of its territory between 25-10-79 and 10-12-79 and the quality of those parts of the territory. Area quality is expressed as mean intake (cals) achieved there per minute of feeding time i.e. excluding activities such as aggression, preening.

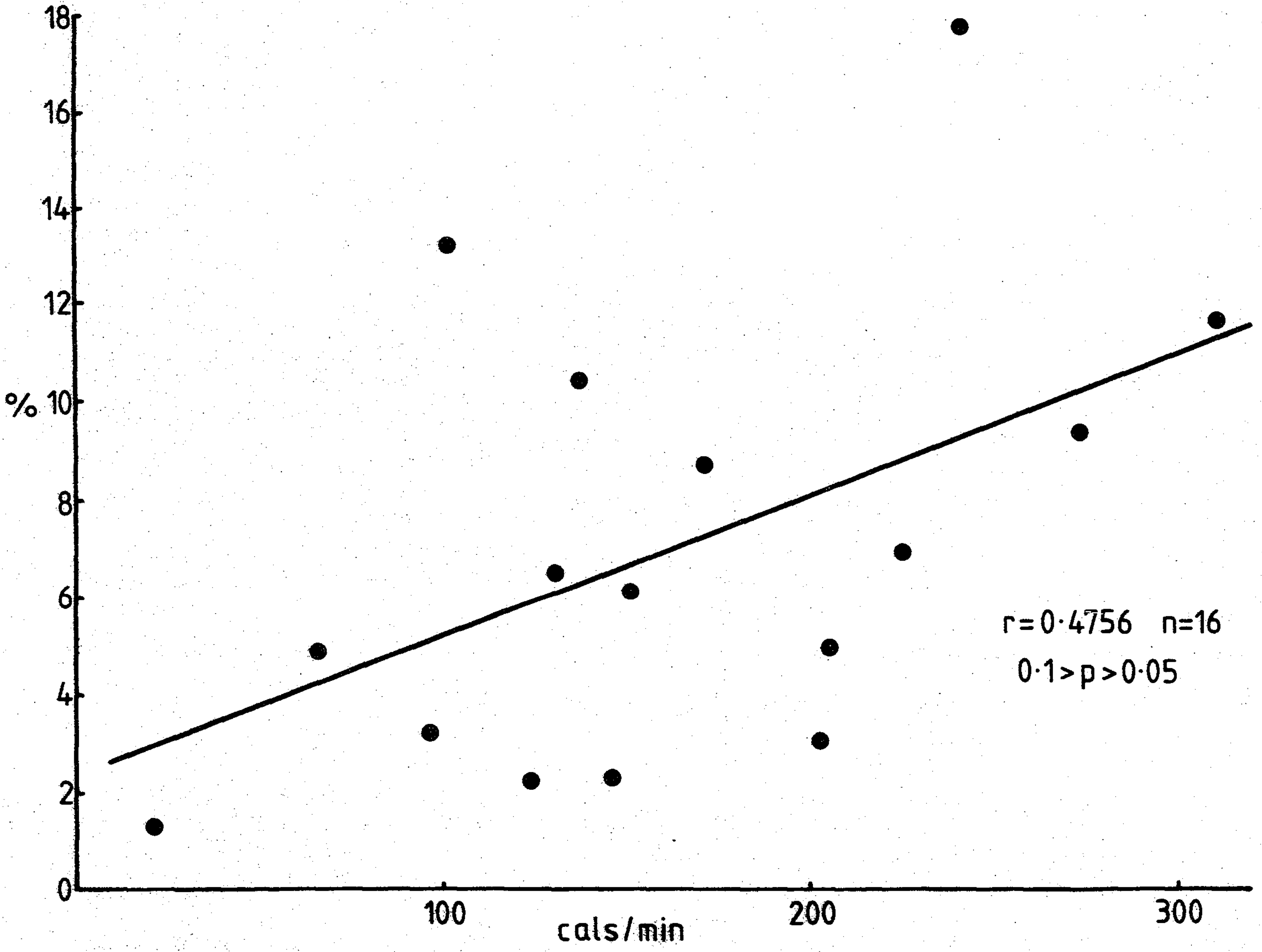


Fig. 33. Relationship between the percentage of total feeding time spent by R W/G in each part of its territory between 19-12-79 and 8-3-80 and the quality of those parts of the territory. Explanation as in Fig. 32.

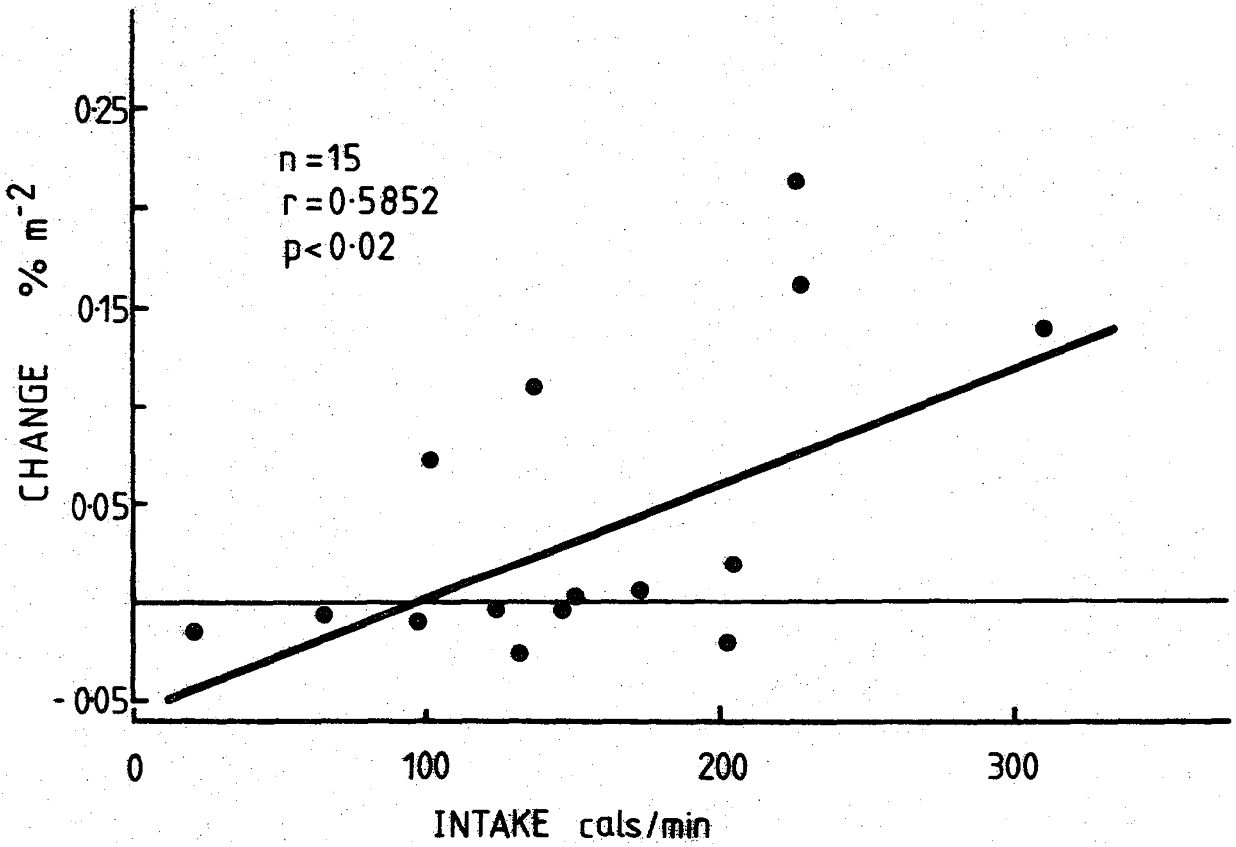


Fig. 34. Change in use by R W/G of parts of its territory from 25-10-79 - 10-12-79 to 19-12-79 - 8-3-80 in relation to rate of energy intake in each area. Use of each sub-area of the territory expressed as a percentage of total feeding time spent in the territory was converted to a measure per unit area by dividing each percentage by the size of the sub-area. Change in use of each sub-area is expressed as the change (+ or -) in this figure (%/area) between the two time periods for which figures were determined.

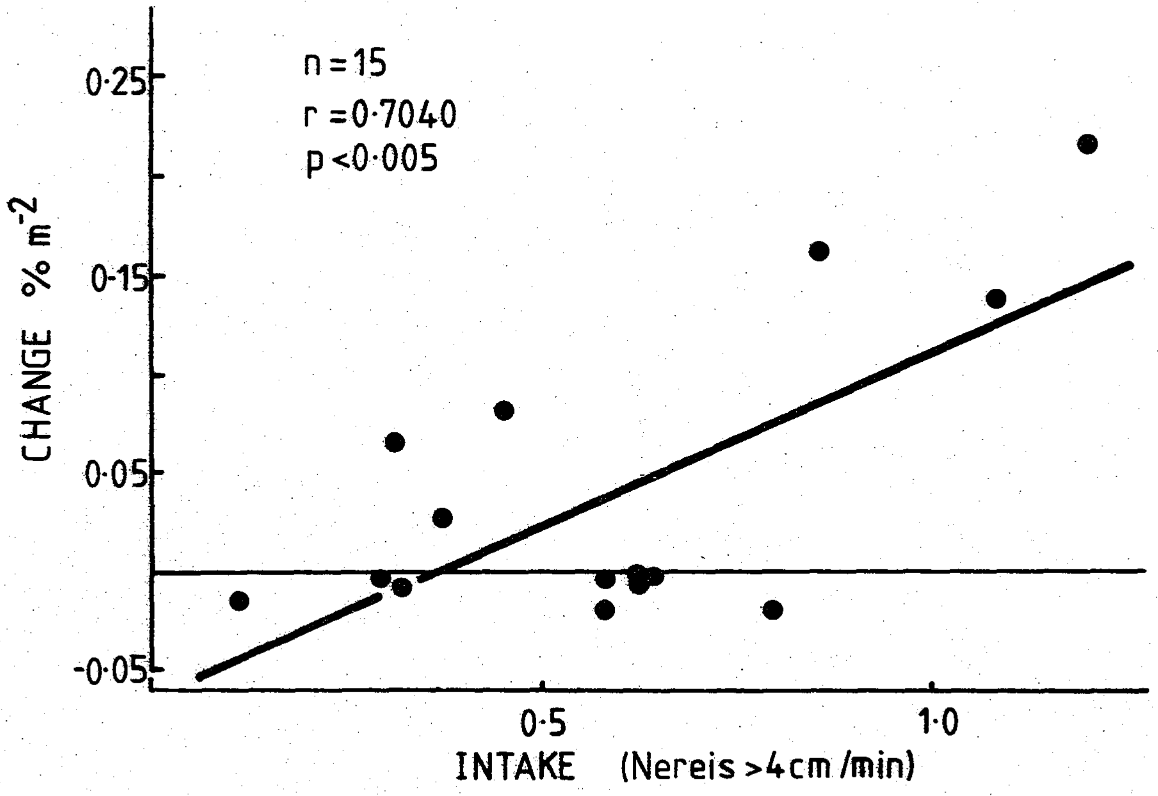


Fig. 35. Change in use by R W/G of parts of itsterritory from 25-10-79 - 10-12-79 to 19-12-79 - 8-3-80 in relation to rate of capture of large Nereis in each area. Explanation as for Fig. 34.

hypothesis predicts that an individual should forage in areas of highest potential prey intake irrespective of season and so minimise the amount of time spent foraging (see for example Schoener, 1971). Clearly this does not occur. Rather, although after 24-10-79 time spent feeding was consistently high, the data indicate that over this period during mild conditions the bird used less areas where high intake was possible using these only when weather conditions became severe. One interpretation of this reduced use of high intake areas during mild conditions is that the birds avoided them. For wintering adult shorebirds the aim is not just to survive from day to day, but to survive the whole winter and to breed successfully in the following spring. Consequently, while wintering, an individual should not behave so as simply to maximise rate of net energy gain each day, but to minimise its risk of winter mortality and of being in poor condition at the beginning of the breeding season. Thus a bird which utilises and depletes the most profitable prey patches within its territory i.e. those yielding highest energy intake per calorie expended, during autumn, when the daily energy demands are not high, will not be able to use these later in the winter when conditions are more severe and the need for a high rate of energy intake correspondingly greater. Consequently, such a bird will be at a disadvantage relative to one which reduced its use of the best areas in autumn and therefore to which these will be available later in the winter. This conservation of resources in analagous to hoarding exhibited by many Corvids/

Corvids (see e.g. Bossema, 1970) and Tits (J.R. Krebs,Pers.Comm) and its occurrence has been suggested in breeding Sparrowhawks <u>Accipiter nisus</u> (I. Newton Pers. Comm.). However its existence has not previously been demonstrated.

Although territorial Grey Plovers have occasionally been observed to displace Redshank and Turnstone from specific feeding sites within their territories I have no evidence that the Plovers attempt to maintain inter-specific territories. Among other shorebirds which winter at Teesmouth, both Curlew and Bar-tailed Godwit take <u>Nereis</u> as their main prey (Evans et. al. 1979). Why, therefore, should Grey Plovers attempt to conserve the food supply of their territories if they do not exclude other species of shorebirds as well as conspecifics? However, most of these other species do not attempt to defend their territories within the Plover territories, and the numbers which feed in the areas where Grey Plovers maintain territories are fairly small (see Appendix 9). Consequently it is possible that even if individuals of another species feed within the Plover territories it is not energetically worthwhile for Plovers to chase these off as they will eventually leave of their own accord. In contrast most Grey Plover would attempt to occupy a territory permanently and therefore need to be excluded. Nevertheless if individuals of other species which move through Grey Plover territories/

territories feed in those parts within a territory where each Plover achieves the highest prey intake rate, these resources will gradually be depleted and not be available to the Plover at times of severe weather. However, the best feeding areas for Plovers need not be the best for other shorebirds. For example the cues used by Plovers and those used by Curlew and Bar-tailed Godwit to find and capture *Nereis* are probably different. The long-billed species do not need to wait for the ascent of *Nereis* to the surface, and can use the entrances of burrows as indicators of the likely presence of *Nereis*, which they can then attempt to capture by probing into the mud. Plovers cannot do this and require cues which indicate the presence of *Nereis* at the surface of the mud. Consequently the location of patches of *Nereis* of highest availability for Curlew and Godwit may be different from those for Plovers. Indeed, during over forty hours of observations of Grey Plover territories in mid-winter I have no records of Curlew or Godwit feeding in the areas preferred by the Plovers. In view of this, the absence of interspecific territoriality, and indeed the possibility of overlapping territories of Grey Plover and Curlew, is compatible with the conservation of resources described for R W/G.

Thus, in summary, possession of a territory allows conservation of the most profitable prey resources. These/

These may then be used during times of high rates of biomass intake. Such an increase in intake rate under severe conditions is not possible in the flock and the advantage of territoriality is accentuated at this time.

c. <u>Sequence of territory occupation</u>.

The incidence of days of high wind speeds, particularly of gales (i.e. > 34 Knots), and of low temperatures, when the two principal advantages of territoriality described above (namely high rates of prey intake and availability of shelter) are greatest, increases markedly between October and November (Fig. 36). By November in each year, most occupation of territories has occurred by those birds which have arrived in autumn. These data suggest that territoriality is a strategy which enhances survival during periods of severe weather, especially gales. However this does not explain the sequence of territory occupation. Why do many birds spend the early autumn in a flock and wait until October and November before establishing territories?

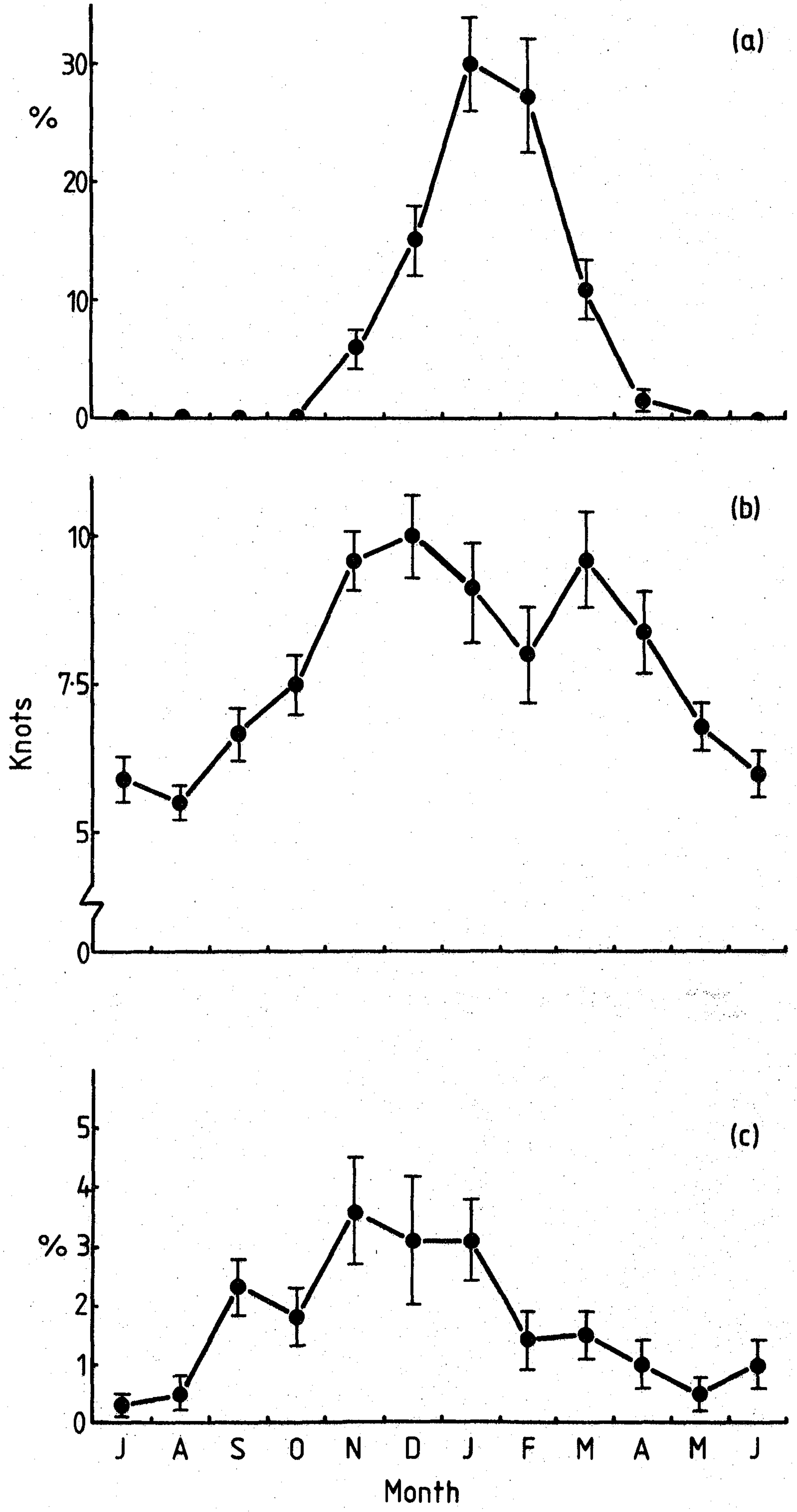
Some Grey Plovers establish territories soon after they arrive in early autumn. As described earlier, those that do, encounter a high incidence of aggression. However, this intense aggression does not appear to reduce the rate of calorific intake at this time (see the data for early October for R W/G in Fig. 22). By November, most territorial boundaries have stabilised. Thus/

Fig. 36. Seasonal change in severity of weather conditions in North-East England.

a. Percentage of days when maximum temperature $< 40^{o}F = 4.6^{o}C$. Values given are mean and one standard error for Hartlepool 1951-75.

b. Mean wind speed Durham 1967-78.

c. Percentage of days with gales. Hartlepool 1952-80. A day with gales is defined as one on which mean wind speed ≥ 34 Knots and/or gusts ≥ 43 Knots were recorded.



(a)
%
30
20
10
0
(b)
Knots
10
7·5
5
0
(c)
%
5
4
3
2
1
0
J
A
S
O
N
D
J
F
M
A
M
J
Month

Thus a bird waiting until to November to occupy a territory will encounter a lower incidence of intrusion within its territory by other individuals. Reduced aggression in late autumn may, in some way, be advantageous e.g. it may reduce "stress" which might otherwise reduce an individuals capacity to defend a territory later in the winter. However, there is no documentary evidence that such stress occurs. Delaying the time of territory occupation until late autumn involves the risk that birds waiting until this time to occupy a territory will find most good territories already occupied. However if, as suggested earlier, it is the dominant birds which are last to leave the flock, these will be able, if necessary, to displace either birds which have left the flock earlier to take up territories or some of the birds which occupied territories immediately on return to the estuary. Such displacement does occur e.g. R O/L (Fig. 16, 25-10-79 to 3-11-79). However, none of the individuals which displaced birds in Eastern Channel at any time of year had previously been seen in the flock. Consequently their dominance status is unknown.

Delayed occupation of a territory may also reduce the risk of predation. If, as suggested, territorial birds are more at risk to predation the risk of mortality will be reduced by delaying occupation of a territory until the risk of starvation due to severe weather outweighs that of predation. Thus I suggest that the pattern/

pattern observed on the Tees estuary of territory occupation by Grey Plovers during the autumn and winter is the consequence, for each individual, of a balance between minimising the risk of predation and possibly the degree of stress whilst seeking to maximise the chance of survival during severe conditions. Information given by Krebs (1974) suggests that parallel strategies may exist in the Great Blue Heron _Ardea herodias_. In this species the mean intake rate of flock birds was three times that of territorial birds, which had to forage for three times as long. However flock birds fed on an ephemeral food resource, fish stranded in tidal pools by the receding tide, whereas territorial birds fed in permanent freshwater creeks and ditches. Thus although when food abundance was high the flock birds had a higher rate of intake the risk of failure of the food resource and starvation was also higher than for territorial birds.

The preceding discussion does not explain why, in November, some territories taken up later in the winter remained vacant, yet some birds present during the autumn remained to feed in the flock throughout the winter. These observations suggest that in mid-winter two different strategies exist. In contrast to the risks of predation and stress which are present each year, severe weather conditions of the type encountered in 1978-79, which may lead to mortality, are rare. Indeed/

Indeed the winter of 1978-79 was one of the worst this century in Britain. Considering the frequencies of occurrence of high risks of mortality from predation and starvation, dynamic balance between territorial and flock-feeding birds within a population (assumed to be faithful to a given estuary) can be conceived (Fig. 37). Among flock-feeding birds predation risk is low. However, occasionally, about every 10 - 20 years, a high percentage suffer mortality as a result of severe winter weather. Thus numbers of flock feeding birds will remain high while winter conditions are mild, and possibly increase gradually from year to year if recruitment has been good, but fall sharply as a result of a severe winter.

Among territorial birds predation risk is higher but survival during severe weather is very good. Thus it is likely that these birds will suffer approximately constant mortality, probably higher than among flock birds, from year to year but be little affected by severe winters. At present these suggestions must remain speculative. To advance the study further, more information on feeding success of both flock-feeding and territorial birds throughout the autumn and winter and of relative survival rates from year to year is required. Further for a comprehensive approach to this problem the effects on breeding success, other than through survival of adults, of winter territoriality and flock-feeding, need to be measured.

d./

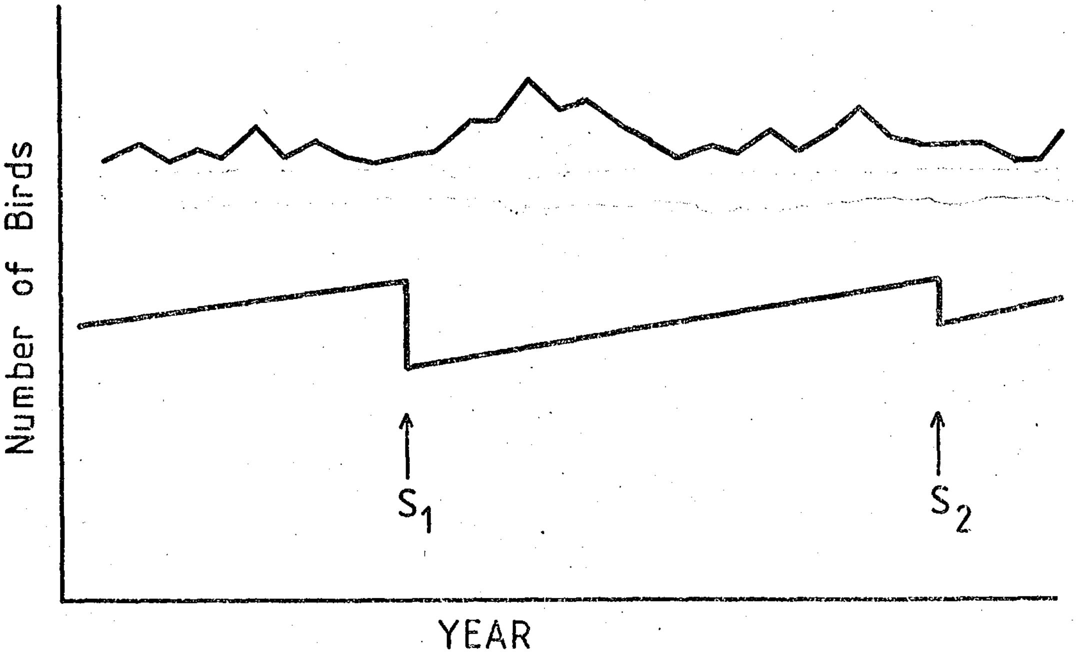


Fig. 37. Model of the effect of severe winter weather conditions on year to year changes in numbers of territorial and flock feeding Grey Plover which arrive on the Tees estuary in autumn and remain through the winter. S_1 and S_2 indicate severe winters. It is assumed that the number of territories established will vary from year to year independently of weather conditions as the distribution of competitive abilities among the birds arriving in autumn varies (see text).

d. Strategy choice of birds arriving in the first winter influx.

This discussion has been concerned primarily with strategy choice when made prior to the onset of winter conditions. However, birds arriving in the winter influxes must make the same choice. For these individuals, however, the need for the correct decision is much more immediate than for those which arrive in autumn. In autumn, if an individual tries to establish a territory and in so doing utilises stored energy reserves by spending most of the day involved in aggressive encounters, it will take only a few days to replace these. However, from November onwards, the risk of a period of gales is high. In these conditions the risk is high that a bird, particularly if unsuccessful in competition for a territory, may not restore body condition as rapidly as in autumn and may die. Furthermore, birds which are unsuccessful in obtaining a territory in autumn may move to another estuary in Britain, or move further south to southern Europe or West Africa. In winter the risks encountered in moving to these areas are greater. On other British estuaries competition for space may be as great as on the Tees. Furthermore, some fat and protein reserves will be used in moving, and upon arrival at another estuary, an individual may not be any more successful in foraging. Hence in moving it may have decreased its chances of survival during severe weather. Migration further south may also be hazardous, even in autumn. Dick/

Dick and Pienkowski (1979) reported many birds arriving in North Africa in an emaciated condition in the autumn of 1973. In winter, any southward movements would normally have to be made during more severe conditions than in autumn. Winter temperatures, and particularly wind chill, can at times be severe on the Atlantic seaboard of southern Europe and North Africa. Thus the energy demands of migration are greater and consequently the risk of starvation are greater at this time of year. However, some birds do disappear from the Tees in mid-winter (see earlier section) suggesting that the options of movement within Britain, or further south, has been taken. Nevertheless, most remain. Consequently it is likely that in November the flock is composed primarily of birds which choose not to establish a territory. However after the first winter influx the flock then contains in addition, individuals which were unable to establish territories upon arrival in the first winter influx. If indeed, as suggested earlier, individuals which choose not to establish territories in autumn are dominant, the birds which arrive in the first winter influx which are unable to occupy territories will be more likely to suffer mortality during severe conditions. Of the four flock birds which are thought to have died during the cold weather in January and February 1979 two, for which definite arrival periods are known, arrived in the first winter influx.

Thus/

Thus to birds arriving in winter, the advantage of a territory remains as high as in autumn, but the risk in trying to obtain one is much higher. For those birds unsuccessful in establishing a territory, the advantage of the flock remains as high as in autumn but the risks are greater. For birds which choose the flock in preference to territoriality the risks and advantages are the same as for birds arriving in autumn.

DISCUSSION

As a result of the processes described, some regulation of the numbers of Grey Plover on Seal Sands occurs. In autumn the number of territories established is limited by a combination of the size of the area available and the distribution of competitive ability within the group of birds present on the estuary. Although the area remains constant from year to year I assume that the distribution of competitive abilities among the individuals present will vary between years. Thus in years when there is a large number of individuals among the birds which arrive in autumn whose ability to obtain and maintain a territory is high, a large proportion of the territories established during autumn will survive until the time of the first winter influx. Therefore numbers present on the estuary before the first winter influx will also be high. In other years more subordinate birds may arrive in autumn. In such years/

years, even if the total number of birds arriving is the same as in other years many of these subordinate birds may not take up, or lose their territories at the expense of larger territories for the more dominant individuals. Thus in these years the number of territorial birds and therefore total population will be lower. Dhondt and Hublé (1968) have shown that similar variation in population size occurs with variation in age structure of territorial birds in a study of the population dynamics of breeding Great Tits Parus major. This argument does not necessarily invoke the concept of a superterritory suggested by Verner (1977). Although the initial size of some territories is large and these are subsequently subdivided as a result of competition e.g. W R/W (Fig. 16) the large initial size of the territory may be interpreted as the individual maintaining as large an unexploited food resource as possible for use during severe winter conditions.

Thus on the Tees estuary much movement out of the estuary in early autumn is voluntary. Some birds do so in October after moult but others move through rapidly in, August and September, presumably to moult elsewhere. In contrast, other birds which leave the estuary later in autumn are displaced territorial birds. Why some individuals are "preprogrammed" to move out of the estuary while many stay, and others attempt to do so, is not known.

In/

In mid-winter the population size is determined primarily by the size of the first winter influx and the size attained in autumn. When the influx occurs, the size of the increase in the number of territorial birds may be limited by the competitive ability of the individuals. Birds of similar, or greater, ability than birds which established territories in autumn can displace or squeeze in between these earlier established individuals (see Table 17; Fig. 16). Those individuals which cannot obtain a territory or are displaced will join the flock as will those birds which flock feed by choice. In 1979-80 after the first winter influx the population remained approximately constant, and only a little emigration occurred. In 1978-79 the population decreased at this time. Some emigration did occur. However it is thought likely that some of the decrease was due to mortality.

Thus after the first winter influx some birds leave the estuary in both mild and severe winters. However it is not known whether birds which leave at this time do so as a result of competition either within the flock or from territorial birds, or if these movements are also preprogrammed. Perhaps Grey Plover are similar to Knot but with only a small proportion of the birds arriving on an estuary voluntarily moving to other estuaries soon after arrival. In the absence of information on the destinations of Grey Plover which leave the Tees in mid-winter, it is not possible to speculate further.

As/

As discussed in Chapter 1 the pattern of change in numbers seen at Teesmouth is similar to that observed on a number of British estuaries. However, the extent to which the population processes observed in this study operate in these other areas, is not known. No similarly comprehensive study of Grey Plovers has been attempted elsewhere although Pienkowski (1980) studied the feeding ecology of this species on Lindisfarne, N.E. England, and did not find territoriality. However, the hypothesis put forward here is that territoriality reduces the risk of mortality at times of greatest energy demands. On the Tees estuary these occur when prolonged periods of high wind speed prevent feeding. However this need not be so in every estuary. As discussed previously the important influence of wind on foraging capabilities of birds on the Tees is a consequence of the dependence of Plovers on detecting Nereis at the surface of the mud. Despite several attempts to identify and quantify the cues used, it has not been possible to do so and I conclude that these are subtle and probably difficult to detect for Grey Plover, as well as for a human observer. Hence their detection by Plovers is likely to be greatly impaired by buffetting from high winds. In contrast, the cues used by Plovers in detecting some other prey species are more obvious. Birds feeding on Arenicola use production of defaecatory casts to indicate the presence of the prey at the surface (Pienkowski, 1980),

a/

a cue which is easily detected by a human observer. In view of this it is not surprising that high wind speed does not have the same marked effect on Grey Plover feeding on Arenicola as on those feeding on Nereis. Although intake rate decreases with increasing wind speed this remains high at wind speeds of 33 knots (Pienkowski, 1980). However as shown by Smith (1975) and Pienkowski (1980) the availability of Arenicola is very dependent upon temperature. In contrast, as reported earlier it was not possible to relate availability of Nereis, as measured by capture rate by Grey Plovers, on Seal Sands to this variable. Clearly the influence of temperature and wind speed varies from area to area depending upon the prey species present and the nature of the cues used in their detection. At Lindisfarne it is likely that among birds feeding on Arenicola territoriality is more likely to be exhibited where the effects of low temperature are reduced. However, not only are the effects of low temperature on feeding success more difficult to avoid (being independent of topography) than those of high wind speed, the areas where mud temperatures are likely to be highest i.e. at low tidal levels, are not in winter used by Grey Plovers probably because of interspecific competition with Bar-tailed Godwit (Pienkowski, 1980). However, a further feature of Arenicola availability, its dependence on the stage of the tidal cycle suggests that among birds feeding on this prey, territoriality is unlikely. Cast production by Arenicola is greatest immediately after the substrate surface is exposed by the/

the ebbing tide and thereafter declines. The resultant mobility of the zone of peak prey availability makes territorial defence unlikely.

However, while it is not surprising that Pienkowski (1980) did not report territoriality among Grey Plovers feeding on Arenicola he did not study in detail birds feeding in other areas at Lindisfarne. Indeed some of these are similar in substrate, topography and invertebrate fauna to Seal Sands and it is possible that a similar system to that described for Seal Sands may exist. This is also true of other areas in Britain, particularly the small Essex estuaries. Here, not only are there many suitable creeks of the type described on Seal Sands which can provide shelter for foraging Plovers, but overall wind speed is almost certainly reduced over large areas by the proximity of the shoreline. In the British Isles the highest winter concentrations of Grey Plover occur in Essex and on the Wash. It would be premature to suggest that the high numbers on the Essex estuaries are a definite consequence of the features described here. However, these areas and the Grey Plover wintering there are undoubtedly worthy of detailed study. The Wash, the only large British estuary with a high mid-winter population of Grey Plover is also the most dissected of the large estuaries. A study of the social behaviour of Grey Plover here in relation to topography and prey distribution would be of great value.

Final Discussion

The ecological factors which lead to most long distance migrations are fairly obvious. For example, the severity of Arctic winters make the breeding grounds of many shorebird species uninhabitable in winter. The absence of an abundant insect fauna in Northern Temperate areas in winter makes southward migrations of hirundines and many insect-feeding passerines essential for their survival. However the ecological and behavioural factors which may control the distribution, movements and destinations of these groups of birds within their wintering ranges are not clear and have received little detailed consideration. My study has examined some factors which may lead to movements of shorebirds in North-West Europe within the non-breeding season. I now discuss the extent to which this study has added to understanding of the ecological factors leading to the evolution of the movements observed and of the proximate environmental cues which may serve as stimuli for movement. Also I discuss differences between adults and juveniles in pattern of movement and reasons for these. Finally, I consider fidelity and lack of fidelity to the wintering sites. Although much has been written about recurrence of individuals in certain sites little attention has been paid to those individuals which change wintering or moulting area from year to year and the possible advantage of this.

Ultimate factors governing migration depend on the aim of the migration. Most movements I have discussed concern survival through the winter. The ultimate factor in response to which Knot, Bar-tailed Godwit and Grey Plover move from the eastern North Sea coast to the British Isles is most probably the severity of mid-winter conditions at the origin. Such weather conditions can affect the energy balance of shorebirds in a number of ways, most directly by increasing heat loss, and by preventing birds from foraging because of high wind speed, or a covering of the mudflats with ice. Also, prey availability and hence the density of available prey may be reduced to levels which prevent birds feeding fast enough. The precise importance of each of these pathways is not known in most species. However it seems most likely that the direct effects are of great importance to all species while the indirect effects will have a greater effect upon visual foragers, particularly plovers.

It might be supposed that the movements of Knot from the Waddenzee could be related to a decrease in the availability of <u>Macoma</u> in November and that because of this birds move then rather than later in the severe weather conditions of December, January and February. However for none of the other movements of Knot, between British estuaries, is there evidence that changes in availability/

availability of prey are of major importance in determining their timing. Consequently it cannot be concluded that the movement from the Waddenzee is related to changes in density of available prey.

The regularity of timing of the influx to Britain in November of Knot and Bar-tailed Godwit suggest that these birds use a constant proximate cue, which anticipates the arrival of cold weather, to time movements. If an external cue is used it seems most likely that this is decreasing daylength. However the importance of completion of moult in 'releasing' birds to be able to move is not known.

In contrast to the influxes of Knot and Bar-tailed Godwit, the first winter influx of Grey Plover on the Tees estuary is not constant in its timing from year to year. This suggests that this movement of Grey Plover is not initiated by a seasonally regular proximate cue such as daylength. Rather it seems that these movements of Grey Plovers may be initiated by a stimulus which is variable in timing and strength between years. This suggests that the proximate factor stimulating the movement of Plovers might be the actual arrival of severe weather (which is also the ultimate reasons for the movements). Why Grey Plovers alone should wait for the arrival of severe conditions before moving rather than anticipating these conditions is/

is not clear. Other plover species, Lapwing Vanellus vanellus and Golden Plover Pluvialis apricaria seem to behave in a similar fashion. Among many African passerines the environmental change which provides the proximate stimulus for movement is also the ultimate cause for migration e.g. the beginning and end of the rainy season (Elgood et. al. 1973; see also Ward, 1971).

The factors which control movement between British estuaries are not clear. Movement of Knot north along the east coast may reduce the risk of mortality during cold weather which is more severe on the Wash. The regularity of timing of this movement from year to year suggests that, if there is external control, the proximate cue which initiates movement may be change in daylength. However as it is thought that much of this movement comes after turnover on the Wash in November, it is not possible to distinguish the extent to which the northward movement is initiated by competition on the Wash which results from arrival of birds from the eastern North Sea coast.

Thus there is at present, no evidence that movements of shorebirds within the non-breeding season are controlled by seasonal changes in density of available food. In contrast in Africa there are several examples of movements which it is thought are a response to depletion/

depletion of food stocks in the source area e.g. juvenile Great Spotted Cuckoos *Clamator glandarius* arrive from October onwards in Senegal, where they stay only until food abundance decreases sharply from December onwards (Moreau, 1972). However present evidence suggests that the ultimate factor controlling the movements of shorebirds within the area surrounding the North Sea is the severity of winter weather conditions. However precisely how different weather conditions affect energy balance are not known for every species.

Some movements, particularly those northwards and eastwards in the late winter and early spring have normally been interpreted as preparation for breeding (Prater, 1971; Evans, 1979b). The movements of Knot, Bar-tailed Godwit and Grey Plover eastwards across the North Sea in March and April may allow birds to exploit a food resource that was unexploited during the winter, either because it was unavailable due to low temperatures or because prey capture rates would not have been sufficiently high to meet the high energy intake required by the birds at this time. However, reasons for other northward migrations such as those of Grey Plovers and Bar-tailed Godwit which reach Britain in February and March are unclear. The advantage may lie in avoiding competition in the wintering areas, as suggested earlier in relation to birds wintering in Mauritania, or may allow early moult into breeding plumage/

plumage to occur before the requirements of pre-migratory fattening.

Among birds using each estuary or group of estuaries, not all individuals respond in the same way to changing conditions. Many Knot and Grey Plover which have moulted on the Wash move south, while more Knot arrive from the eastern North Sea coast and replace those which have left. Similarly, on the Tees estuary differences in migration pattern of individual Grey Plovers have been shown to exist. The reasons for these intraspecific differences in movement pattern are at present little known. However the study of spacing behaviour of Plovers on the Tees estuary has suggested that some of the Grey Plovers which move do so because they are unsuccessful in establishing or maintaining a territory. I have suggested that the advantage of territory possession is that these enable the owners to achieve a greater energy intake during cold and windy conditions than would be possible by flock feeding. Thus again the ultimate reason for the movement is the severity of weather conditions in winter. However, the proximate cue which affects whether or not a bird moves is its success in obtaining a territory. Similar behaviour is displayed by Chaffinches Fringilla coelebs which remain to winter in Scandinavia. Some males establish winter territories. Those which cannot do so migrate. Similar behaviour was observed in Kestrels Falco tinunculus in Dumfriesshire by Village (1980).

The/

The two groups of Knot described i.e. those which are (1) itinerant and (2) sedentary, represent a further incidence of individual variation in movement pattern. Studies of other shorebirds suggest that these two types of individual are found in other species. However at present the relative selective advantage of each behaviour under different weather and feeding conditions is not clear. Neither is it known whether the strategy employed by an individual varies from year to year, either with or independently, of age.

Most of this study has been concerned with adults, as counts of total numbers consist predominantly of these. Little is known of the way in which the patterns of movements of juveniles differ from those of adults. Data indicate that juvenile Knot tend to winter further south than adults (Minton, 1975). This may also be true of Bar-tailed Godwit. The reasons for this are unclear. Perhaps they move to areas where winter conditions are least severe, as survival for juveniles is relatively more important than for adults, since juveniles have yet to attempt to breed. However this does not take account of any cost in migrating. It has been argued earlier that the risk of mortality during migration may be high, perhaps higher than the risk of mortality during severe winter weather. Perhaps juveniles are less efficient foragers. They may be unable/

unable to achieve sufficient intake in North Temperate areas in winter during cold weather and therefore may have to migrate south even though the risks of mortality during migration may be high. However juveniles may move because they are forced to do so through competition. On the Tees estuary observations of Grey Plovers suggest that although some juvenile birds are of high competitive ability and can chase off other Grey Plovers encroaching on their territories more quickly, than can many adults, the majority of juveniles were of poorer competitive ability.

In some species of shorebirds e.g. Bar-tailed Godwit and Knot, immature (1st and 2nd year) birds move north in summer, but do not go as far as the breeding areas (Minton, 1975). Why these birds do so is unclear. However it seems possible that in Mediterranean and equatorial regions, where these birds have wintered, high summer temperatures may depress prey availability (see Evans, 1976). Thus it may not be possible to feed there at a sufficient rate in summer. These birds may then stop northward movement as soon as feeding conditions are suitable. Movement further north towards the breeding grounds would take them to areas where prey density is low (Evans, 1979).

Little is known of changes in movement patterns within the life of an individual. Many juvenile Grey Plover return to the Tees each year, but others do not. Absence of some individuals in subsequent years is probably/

probably due to mortality but may be due partly to change in movement pattern. The high return rates of Plovers suggest that such changes are few. However the amount of change in movement pattern between years may be much greater among birds which have wintered further south in their first year.

Data has been presented to show that some adult Knot occur in different wintering and moulting areas in different years. Such lack of fidelity may provide the same advantage as suggested for itinerancy within a non-breeding season, i.e. that an individual may, by visiting different sites in different years obtain knowledge of areas which may be used if the food supply is poor, or weather conditions severe in one area in a future year. However lack of fidelity may also be a disadvantage. Birds may be forced to move to different areas in different years as a result of competition. As stated above, some Grey Plover did not recur on the Tees estuary every year. However most of these cases are of individuals which did not return in the first winter influx. The absence of these birds from the Tees in one year was probably a consequence of favourable conditions in the moulting area (from which it is thought they come to form the first winter influx on the Tees) as a result of reduced competition, high prey density, or mild weather conditions. There is also some variation between years in time of arrival of/

of a few Grey Plovers on the Tees estuary. Some Grey Plovers have been observed to spend early autumn on the Tees in some years but have not returned to the estuary until later in others, and vice versa. However there is no evidence that early movement by these individuals from the area occupied first in autumn is voluntary and it may be induced either through competition or deteriorating weather or feeding conditions. Similarly it is not known whether the change of moulting area observed for some Knot is voluntary or enforced. Thus at present, although possible advantages of lack of fidelity are apparent, there is no evidence to confirm that these advantages are real, nor even to suggest that lack of fidelity is adaptive.

The presence of itinerancy during the non-breeding season in some shorebird species suggests that the effects of reclamation of some of the estuarine areas used in mid-winter, on total numbers of these species, may not be great. Some mortality may occur but the itinerant behaviour observed indicates that these species may be pre-adapted to encountering difficult feeding conditions in some areas and be able to move to alternative feeding areas (Evans, 1981). In contrast for species such as Grey Plover, which the evidence suggests are more sedentary in mid-winter, it is likely that reclamation of sites used in mid-winter will have a more serious effect upon total numbers. However most of both 'itinerant' and 'sedentary' species use predictably specific moulting sites. It seems likely that reclamation/

reclamation of these areas may lead to a serious decrease in total numbers of these species. The precise effects of such reclamation are difficult to predict as at present the precise reasons for the use of specific estuaries as moulting areas are not known. However if the changes in moulting site reported here are, as suggested, enforced in some way, this suggests that, at least in some years these preferred moulting sites are full. Thus reduction in the size of these areas will result in redistribution of birds to less preferred moulting areas, and possibly in mortality.

Summary

This study reviews published information on inter-estuarine movements of Knot, Bar-tailed Godwit and Grey Plover in North-West Europe, especially Britain. An attempt is made to relate these movements to seasonal changes in factors, particularly weather conditions and prey abundance, of importance to the energy balance of shorebirds. Seasonal changes in numbers and movements of Grey Plover using the Tees estuary, in relation to spacing behaviour and prey availability, are considered in detail.

In early autumn Knot moult mainly on the Waddenzee, the Wash and the Ribble estuaries. After moult many birds from the Waddenzee move to the Wash. It is thought that others go via the Wash to estuaries on the north-east coast of England. (Some also move to the west coast of England, particularly Morecambe Bay.) Prior to the arrival of birds from the Waddenzee many birds from the Wash move to southern Europe. However, the proportions of birds present in early autumn which move to these areas and the proportion which stay on the Wash are not known. It is suggested that a smaller proportion of birds move to the west coast from the Wash than has previously been suggested, and that this movement may not occur every year. Few precise data on movements between west coast estuaries are available. It is suggested that most birds which moult on the Ribble probably winter on the west coast estuaries, particularly Morecambe Bay.

Colour/

Colour-marking of Knot on the Tees estuary indicated rapid onward movements, to coastal areas further north, of a small proportion of the birds which arrived in November.

Bar-tailed Godwit also moult chiefly on the Waddenzee, Wash and Ribble, but others moult on the Forth and at Lindisfarne. Subsequent movements are not well documented. Counts suggest that many birds from the Waddenzee move to Britain, particularly to the estuaries of the West Coast. Some birds from the Wash move to the north-east coast of England, but it is likely that at least part of the wintering population in these areas moults on the eastern North Sea coast.

Grey Plover are more widely distributed during autumn than either Knot or Bar-tailed Godwit. However large concentrations occur on the Waddenzee, Wash, Ribble and Essex estuaries. After moult, many birds move to southern Europe. Others, probably from the Danish Waddenzee, move to British estuaries in mid-winter. Numbers in Britain increase in February - March, probably as a result of birds which have wintered further south returning north.

In winter, conditions on the eastern North Sea coast are more severe than in Britain. Movements of all three species after moult, westwards across the North Sea, reduces their risk of encountering severe weather in mid-winter. Reasons for the other movements described are/

are unclear. Average winter temperatures, and temperatures during the last three very severe winters, are higher on the east coast, north of the Wash, than on the Wash itself. Northward movement of many Knot in November may be to avoid the colder conditions on the Wash. None of the invertebrate data examined suggest that movements are related to inter-estuarine differences in timing of peak prey biomass or abundance. Timing of larval settlement and growth rates of prey are similar in most estuaries for which data are available. No major differences between estuaries in the timing of peak quality of prey are apparent.

In November more Macoma are within reach of a Knot's bill on the Humber than on the Wash or Morecambe Bay. However, the absence of Knot from the Humber in autumn, when availability of Macoma is even higher, suggests that the timing of movement to the Humber in November and December is probably not related to availability. High availability of Macoma on Morecambe Bay in spring may however be an important factor allowing large numbers of Knot to use this area for laying down fat reserves before departure to the breeding grounds.

Birds which move south from the Wash after moult probably do so voluntarily, not as a result of competition. These are then replaced by birds moving from the Waddenzee. The reasons for such intraspecific variation in movement strategy are unknown.

It/

It was not possible to relate movements of Knot from the Tees to changes in abundance of Mytilus edulis, its main prey. Information from dye-marked birds suggest that, after arrival on the Tees from the Wash, some Knot stay only a few weeks before moving north to the Northumberland coast and the Forth estuary. However, others are sedentary. It is suggested that the itinerant behaviour is an adaptation to an unpredictable food supply. However the reasons for lack of movement by some individuals, and the survival rates of each group, are not known.

Detailed study of Grey Plovers on the Tees estuary indicated that in autumn some adults move through the estuary rapidly, but others stay to moult before moving on. These movements are "voluntary". In autumn many individuals attempt to obtain territories. Some of those which cannot, or are displaced from territories, then leave the estuary. Others stay in a flock while feeding. It is suggested that territoriality is a strategy permitting maintenance of food intake during severe, particularly windy, weather conditions in winter. The creeks contained in territories provide shelter for feeding birds and permit intake to be achieved during gales. Birds which cannot obtain territories are more likely to suffer mortality. For these individuals it is advantageous to move further south. It is suggested that the number of territories established in autumn is limited by the distribution of competitive ability within the population of Grey Plovers attempting to establish territories. The data has also suggested that some birds/

birds which remain in winter do not attempt to obtain territories, but choose to flock feed. A simple graphical model is presented to indicate how the proportion of flocking and territorial birds in the population will change, following severe and mild winters.

The reasons for movements of shorebirds and their timings during the non-breeding season are discussed in the light of the findings of the study.

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Appendix 1. Table A1. Success of salt extraction as a technique for removing *Nereis diversicolor* from mud samples.

Details of the procedure are given in the text.

Description of substrate	No. of Nereis picked from surface	No. retained in 40 sieve	% success of salt extraction
Sand	13	0	100
"	6	0	100
"	15	0	100
Sand/Mud	5	0	100
"	3	1	75
Firm mud	6	1	86
"	9	0	100
Viscous mud	6	0	100
"	7	0	100
"	7	0	100
"	11	0	100
"	1	0	100
Soft mud	4	0	100
"	8	0	100
"	1	0	100

$\bar{x} \pm$ S.E. = 97.6 ± 1.7

Appendix 2. Table A2. The values of terms from the relationship log (dry flesh wt. in mg.) = a + b $\log_{10}$ (relaxed body length in cm) for Nereis diversicolor from Seal Sands.

Area	Date	No. animals measured	a intercept	b regression coefficient	r correlation coefficient
Sc. Mud	11.9.78	16	-0.422	2.459	0.94
C.Bank (Y-C.Ch)	"	10	-0.281	2.333	0.98
C.Bank (Sand)	"	12	-0.520	2.600	0.99
C.Bank (Ent)	"	11	-0.340	2.365	1.00
E.Ch.	"	11	-0.353	2.420	0.96
G. Bank	5.11.78	12	-0.646	2.737	1.00
Sc. Mud	23.11.78	13	-0.607	2.560	0.99
C. Bank (Y-C.Ch.)	"	14	-0.528	2.460	0.99
C. Bank (Sand)	"	11	-0.823	2.787	1.00
C. Bank (Ent)	"	13	-0.336	2.255	0.98
E. Ch.	"	10	-0.266	2.305	0.92
Sc. Mud	7.1.79	12	-0.907	2.840	0.98
C.Bank (Y-C.Ch)	"	13	-0.442	2.330	1.00
Sc. Mud	1.4.79	11	-0.676	2.652	1.00
C.Bank (Y-C.Ch.)	"	13	-0.455	2.388	0.99
C.Bank (Sand)	"	4	-0.453	2.359	1.00
C.Bank (Ent.)	"	12	-0.575	2.558	0.99
E.Ch.	"	9	-0.177	2.153	0.96

C. Bank/

Appendix 2./

Area	Date	No. animals measured	a intercept	b regression coefficient	r correlation coefficient
C.Bank (Y-C.Ch)	12.12.79	10	-0.310	2.461	1.00
E.Ch.	"	9	-0.274	2.458	1.00
G. Bank	8.1.80	13	-0.381	2.475	1.00
E.Ch.	22.3.80	10	-0.382	2.393	0.99

Appendix 3. Determination of population size.

Early in autumn when the number of birds on the estuary is small it is normally possible to check all roost sites at high water. Because of this, the small number of birds present and the open topography of the roost sites used at this time, accurate counts of total numbers present can be made. However, as the number of birds increases in October individuals begin to use the main winter roost site where, because of the rocky substrate, large numbers are hidden from view. Consequently accurate high water counts are no longer possible.

As high water roost counts become inaccurate, but while the numbers on the estuary remained small, counts of birds flying from the feeding grounds to the main high water roost site were used in measuring the total number of birds present. In these months, the number of birds in each flock is sufficiently small to permit accurate counts. After the feeding grounds were completely submersed, all other birds which had gone to subsidiary roost sites, and had therefore been missed, were counted by visiting each subsidiary roost.

When numbers increased in winter the flocks flying to roost were too large to permit accurate counts. At this time counts were made at pre-roost gathering sites. As the main intertidal area nears complete submersion, birds gather on one or both of two small areas of high level/

level mud, close to the reclamation wall, where they can be counted quickly and accurately. Small numbers of birds leaving before completion of the counts were, if not already included, counted as they flew off, or when they landed. On occasions when large numbers of Plovers flew before being counted the count was abandoned because of difficulty in making accurate counts of large flying flocks of Plovers, since these normally occur in association with Dunlin, Knot and Bar-tailed Godwit.

Appendix 4. Determination of times of influx and departure.

(1) Influx

In both 1978-79 and 1979-80, but particularly in the later year, large numbers of colour-marked Grey Plovers, which had been caught in previous years, returned to the estuary. Using sightings of these birds only, an 'Index of Influx' was calculated (Figs. A1,A2) for each date on which 25% or more of the colour-marked birds known to be present on the estuary at that time, were seen on one of the high water or pre-roost sites. The percentage of colour-marked individuals seen on a particular day that were seen then for the first time in that non-breeding season was calculated.

(2) Departure

In 1978-79 the number of colour-marked birds, known to have visited the estuary in that winter, that were not seen (1) on and after the date of each high water count and (2) after a period of influx were determined as a measure of the size of a departure from the total population on the estuary.

Clearly not all birds were seen on the day before departure. Indeed a few may have remained on the estuary without being identified for several weeks before departure. To take account of this source of inaccuracy two error levels were determined on each count date (Figs. A3,A4).

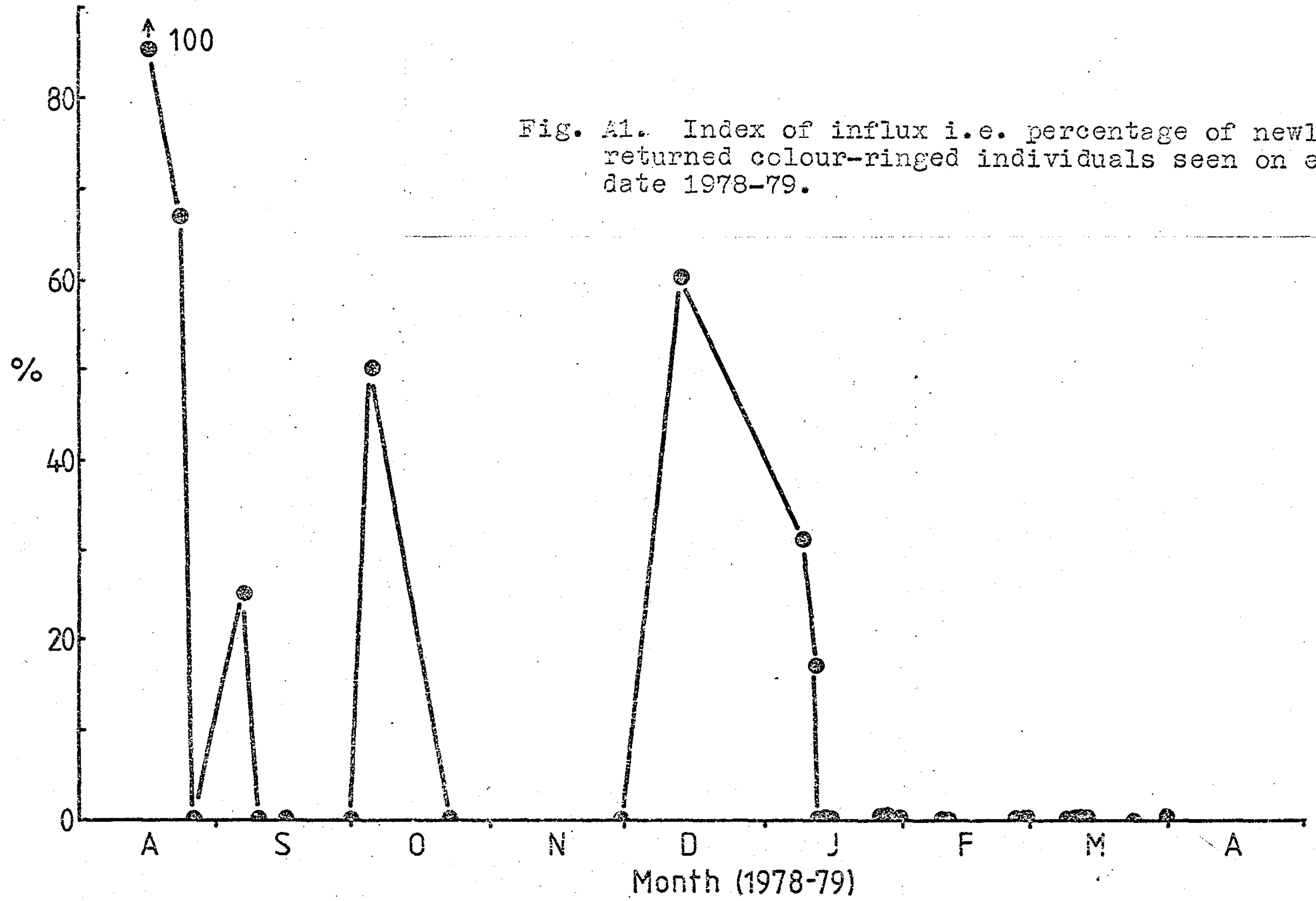


Fig. A1. Index of influx i.e. percentage of newly returned colour-ringed individuals seen on each date 1978-79.

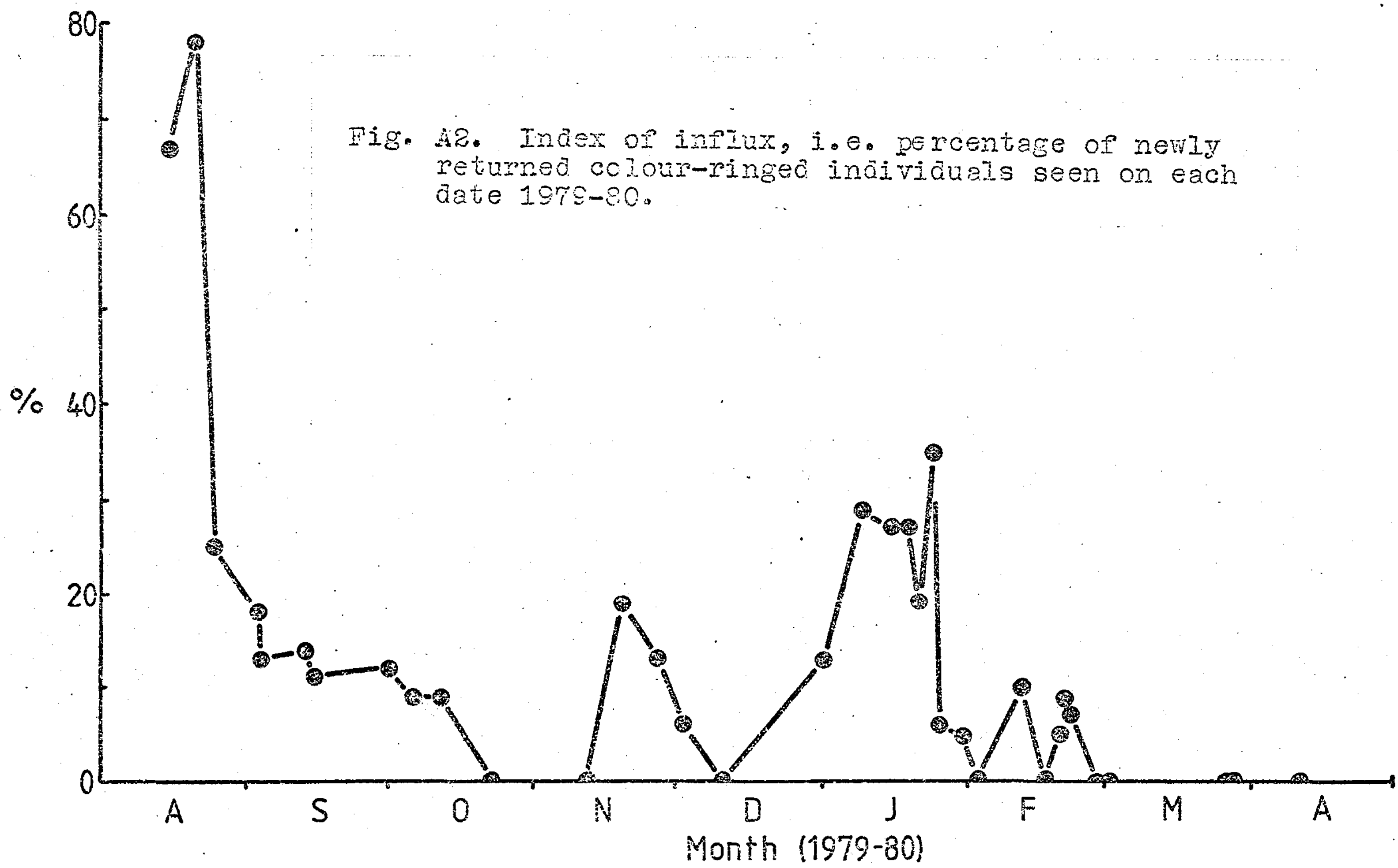


Fig. A2. Index of influx, i.e. percentage of newly returned colour-ringed individuals seen on each date 1979-80.

(a) The number of birds last seen 10 days prior to that date.

(b) For each individual the maximum interval between sightings was determined. The number of days in this interval was then added to the date of last sighting of the individual. If on doing this the date reached was on or after the date for which the error level was being calculated, then it was assumed that the bird may have been missed and been present on this date.

The procedure was repeated in 1979-80, but in this year only the birds marked before 1979-80 were used.

Using these estimates of "error" the number of colour-marked individuals lost from the population was compared with the total population figures and used to identify and/or confirm periods of population decrease. This was particularly needed in the January, February, March period of 1979 when no reliable high water counts could be made because of severe weather conditions and unusual pre-roost behaviour of the birds.

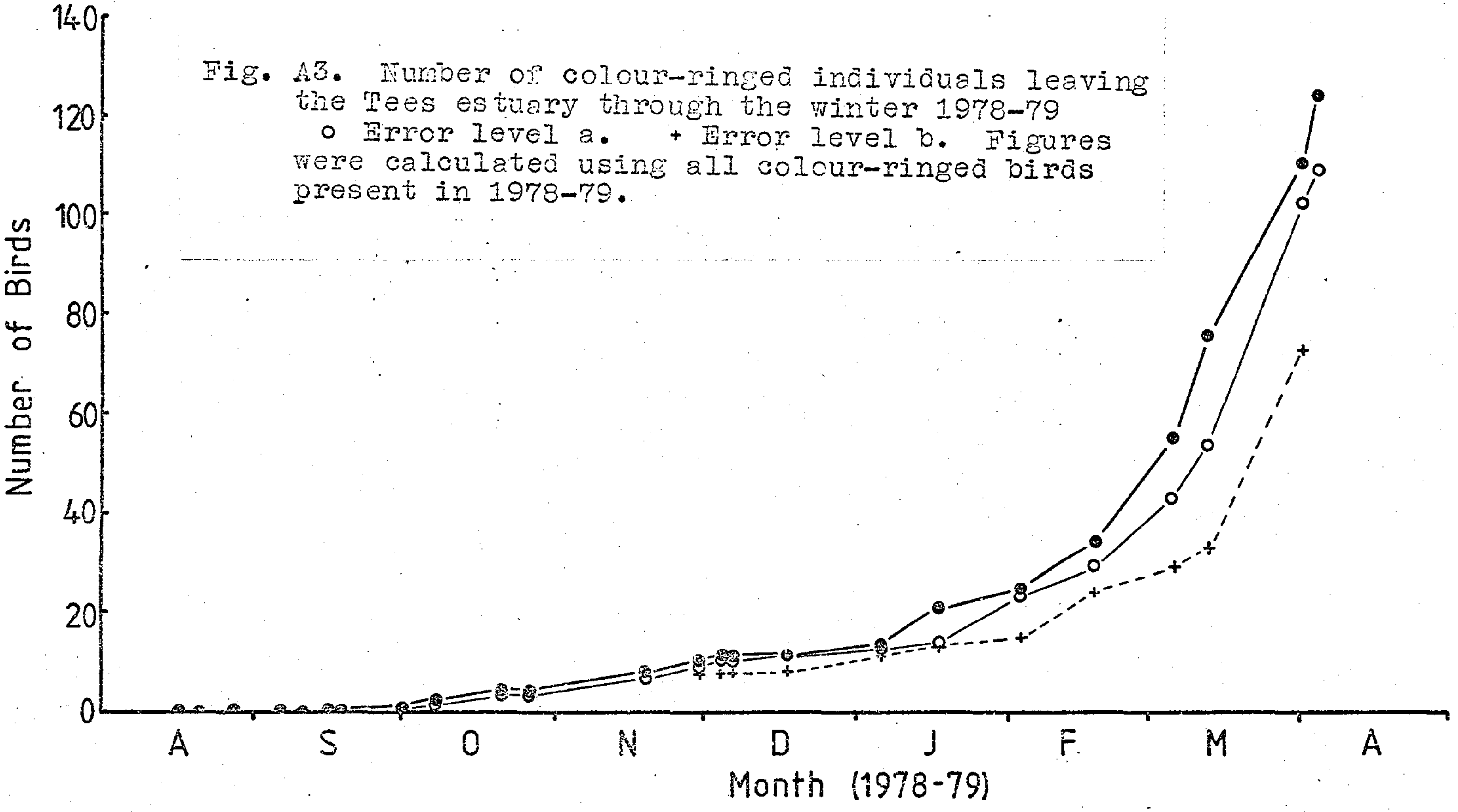


Fig. A3. Number of colour-ringed individuals leaving the Tees estuary through the winter 1978-79 ○ Error level a. + Error level b. Figures were calculated using all colour-ringed birds present in 1978-79.

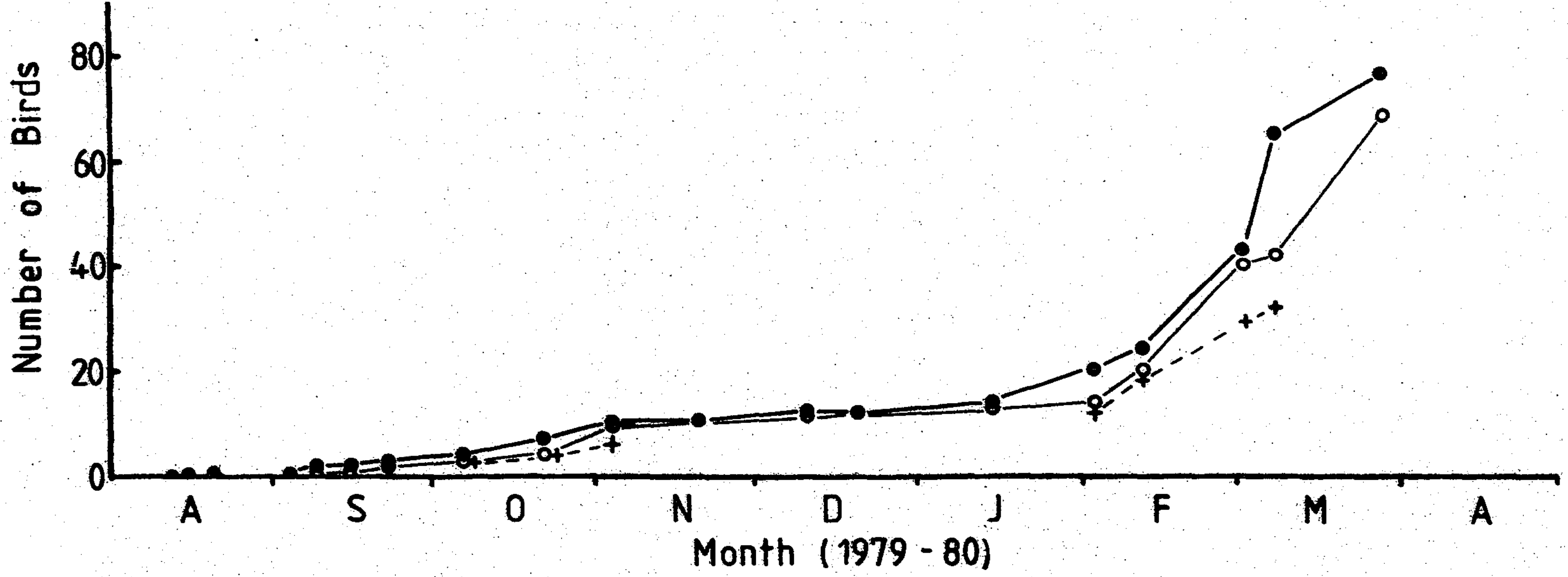


Fig. A4. Number of colour-ringed individuals leaving the Tees estuary through the winter 1979-80 ( ). o Error level a. + Error level b. Figures were calculated using birds ringed before 1979-80 only.

Appendix 5. Correction of estimated *Nereis* body length

Twenty-five *Nereis* of a range of body lengths were collected. Using forceps held so that only 3 cm (ca one Grey Plover bill length) protruded from the hand, an assistant picked up and stretched each live animal in turn, in order to simulate the observed stretching of *Nereis* when pulled from the mud by Grey Plovers. I watched this procedure by telescope at 30 metres distance, and estimated the lengths. Each animal was individually bottled and, on return to the laboratory, killed in alcohol, and measured. The relationship between estimated (stretched) and measured body length was then determined (Fig. A5). Estimated values were then corrected to true length (Table A3) before inclusion in intake and capture rate calculations.

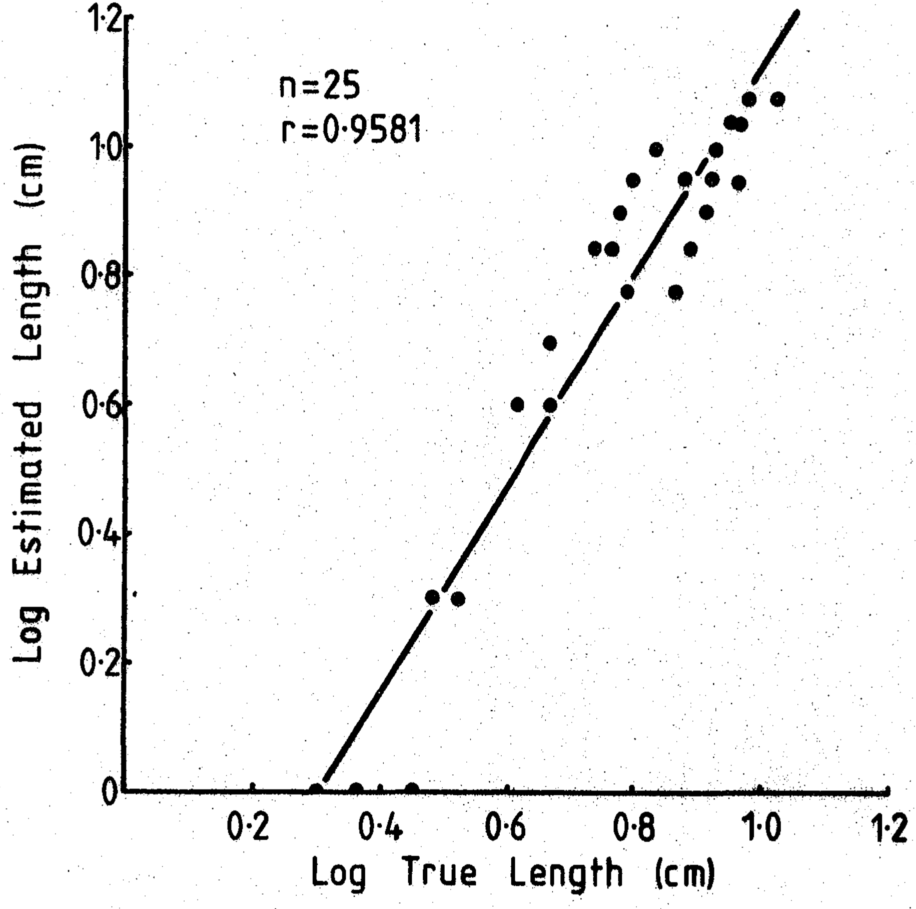


Fig. A5. Relationship between true body length of <u>Nereis diversicolor</u> and estimated length (log/log).

Appendix 6. Length of observation period - its effect on variation in observed intake rate.

In order to determine the smallest time period for which a bird should be observed to reduce observed variation for each individual to an acceptable level, the standard deviation of mean intake rate per minute was plotted against increasing number of minutes of observation for seven periods of observations (Fig. A6). Variation around the mean, although great both between individuals and in the same individual in different observation periods remained relatively constant with a sample size of three or more minutes.

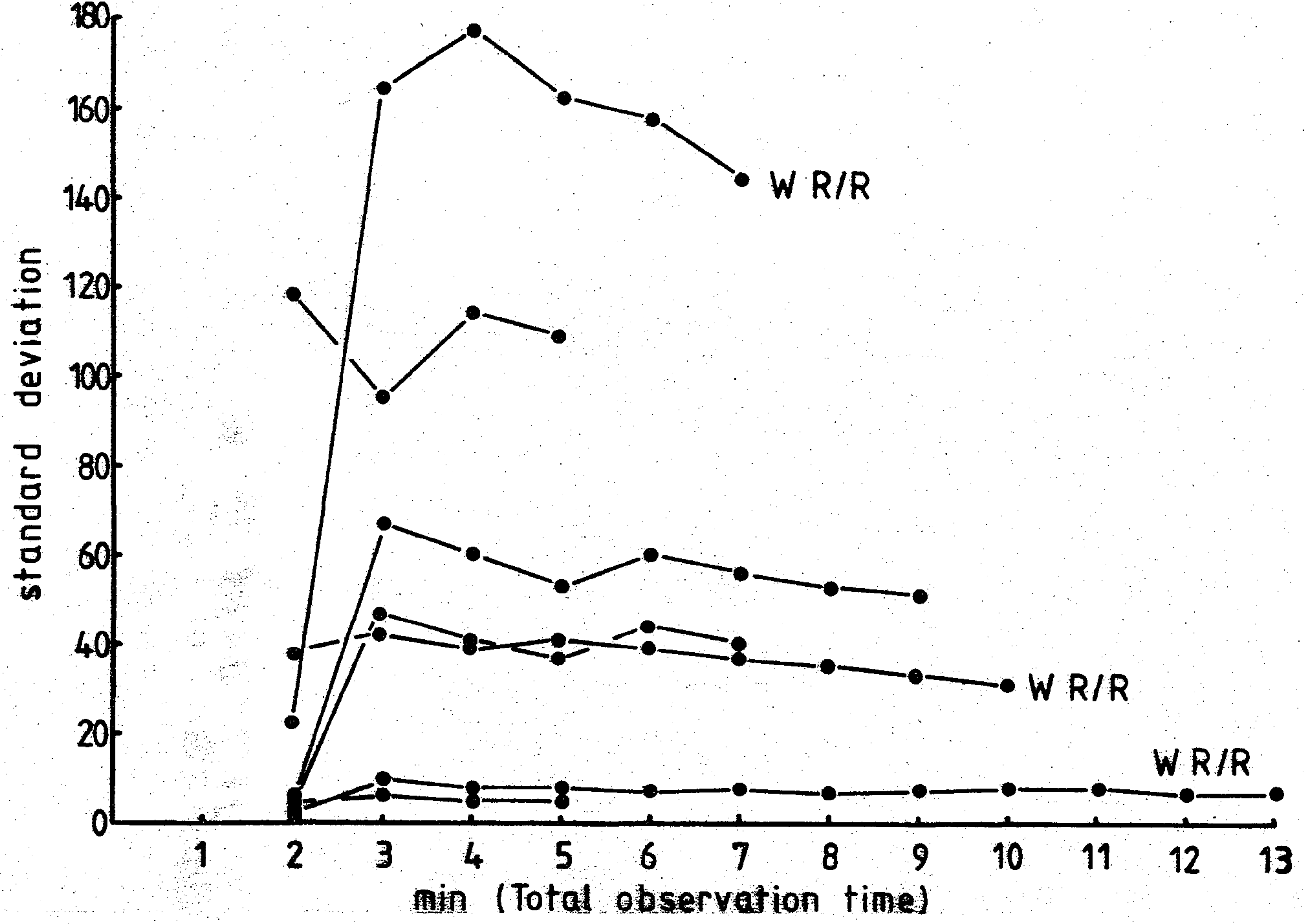


Fig. A6. Relationship between legth of observation period and standard deviation of calculated mean intake rate.

Appendix 7. Table A4. Dry weight and calorific values of Hydrobia ulvae used in calculation of energy intake of Grey Plovers.

Month + Area		Mean dry wt/individual shell height (mm)		shell height (mm)	Mean calorific value (cals/mg) shell height (mm)	Average calories/individual (cals) shell height (mm)
	n	2.5 - 3.4	n	3.5 - 4.4	2.5 - 4.4	2.5 - 4.4
June	12	0.562	28	1.085	5.62	4.9
	12	0.562	28	1.085	5.62	3.9
	27	0.342	13	0.715	4.90	2.2
	14	0.295	10	0.590	5.09	1.6
November						
	29	0.509	22	0.832	5.07	3.3
	29	0.509	22	0.832	5.07	3.3
	10	0.391	18	0.601	5.30	2.4
March						
	15	0.560	20	0.850	5.00	3.6
	15	0.560	20	0.850	5.00	3.6
	28	0.461	16	0.699	5.07	2.7
		-	5	0.604	5.88	3.5

Calorific values given are based on single determinations

Appendix 8. Tables A5a,b. Densities of *Nereis diversicolor* on Seal Sands.

Values given in Figs. 6 and 8, Chapter 3, were obtained from data presented here by calculating the mean density of *Nereis* in the sub-areas within each feeding area. Sub-areas from which *Nereis* were collected are shown in Fig. A7.

* Values given for these areas are those used in Figs. 6 and 8.

n = number of samples taken in each sub-area.

Table A5a. *Nereis* > 4 cm.

Feeding area	Sub-area	June			November			March		
		n	$\bar{x}$	SE	n	$\bar{x}$	SE	n	$\bar{x}$	SE
1	1	1	301	0	2	527	107	2	76	53
	2	2	151	53	2	38	27	1	0	0
2	3	4	151	46	2	339	240	2	0	0
	4	3	201	89	2	0	0	2	0	0
	5	2	113	27	4	94	62	2	38	27
3	6*	4	358	67	4	395	56	2	38	27
4	7*	-	-	-	4	477	74	4	151	0
	8*	4	207	56	3	427	109	3	75	0
5	9	4	264	94	4	339	86	4	38	19
	10	2	301	0	2	113	80	2	38	27
	11	2	528	53	2	0	0	2	151	0
	12	2	490	80	2	301	160	2	0	0
	13	2	603	53	2	264	80	2	113	80
	14	2	113	27	4	113	42	4	132	31
	15	2	339	133	2	189	27	2	75	0
	16	2	942	80	2	226	53	2	151	53
6	17*	5	361	45	5	377	95	5	105	34
7	18	3	25	20	4	188	62	4	56	16
	19	2	151	0	2	75	0	2	151	53
8	20	2	226	0	2	151	0	2	113	27
	21	2	339	80	2	76	53	2	151	106
9	22	4	565	57	4	545	126	4	151	46
	23	4	546	173	4	188	42	4	132	56

Table A5b. Nereis $\leq$ 4 cm.

Feeding area	Sub-area	June			November			March		
		n	$\bar{x}$	SE	n	$\bar{x}$	SE	n	$\bar{x}$	SE
1	1	1	301	0	2	0	0	2	58	27
	2	2	75	0	2	151	53	1	226	0
2	3	4	509	163	2	76	53	2	226	0
	4	3	377	163	2	25	0	2	0	0
	5	2	716	133	4	19	16	2	0	0
3	6*	4	377	173	4	678	141	2	151	53
4	7*	-	-	-	4	301	96	4	546	165
	8*	4	471	108	3	301	123	3	201	20
5	9	4	188	68	4	1695	381	4	207	137
	10	2	189	27	2	678	267	2	377	53
	11	2	264	80	2	603	0	2	226	0
	12	2	264	133	2	716	27	2	754	106
	13	2	226	53	2	980	373	2	678	53
	14	2	75	0	4	188	62	4	132	41
	15	2	189	27	2	791	133	2	452	0
	16	2	151	53	2	565	80	2	339	133
6	17*	5	256	50	5	588	157	5	181	69
7	18	3	150	62	4	151	38	4	113	62
	19	2	264	27	2	151	53	2	151	53
8	20	2	76	53	2	415	186	2	226	0
	21	2	904	267	2	75	0	2	301	0
9	22	4	320	101	4	1394	371	4	772	200
	23	4	320	86	4	791	221	4	603	208

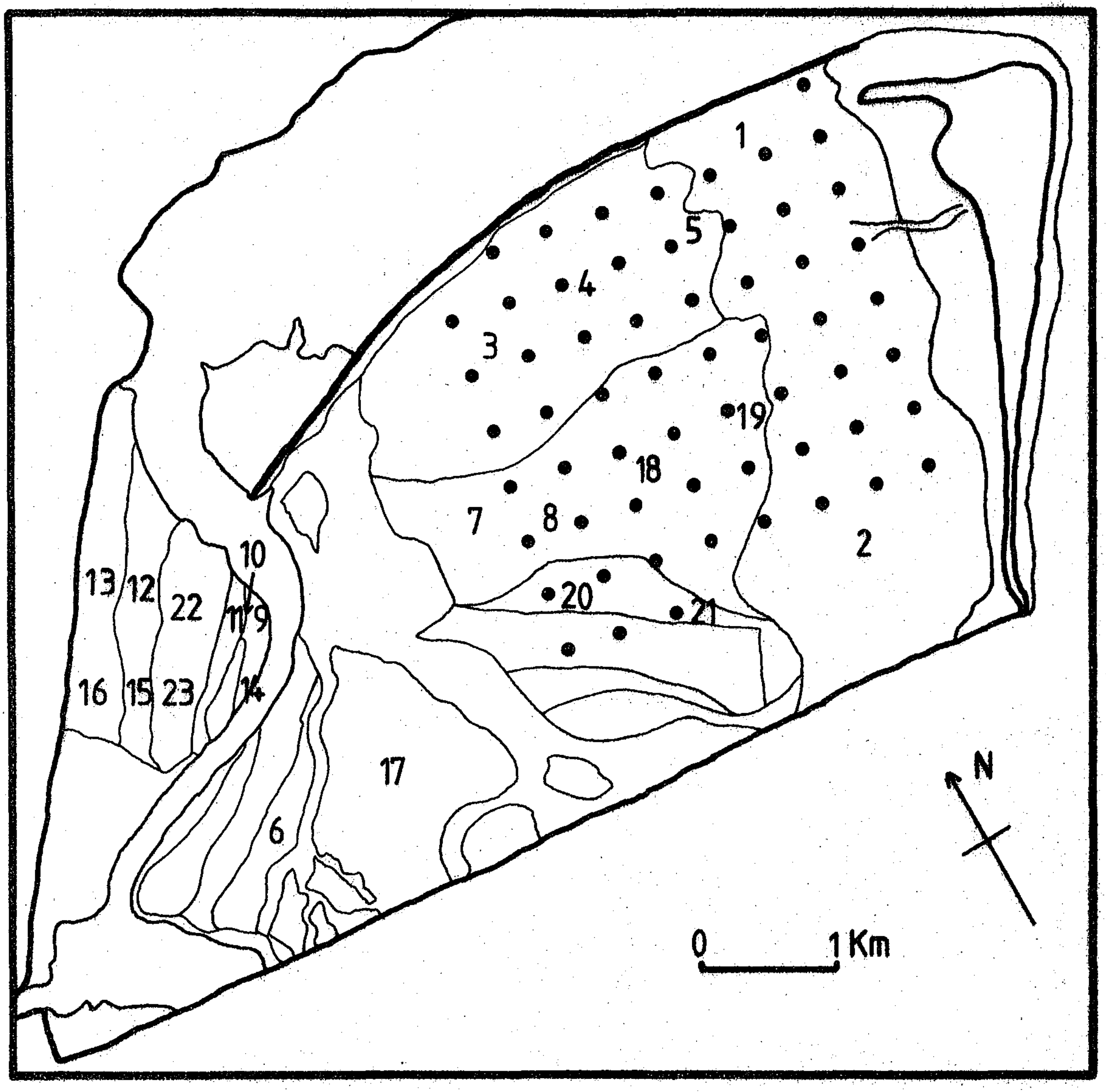
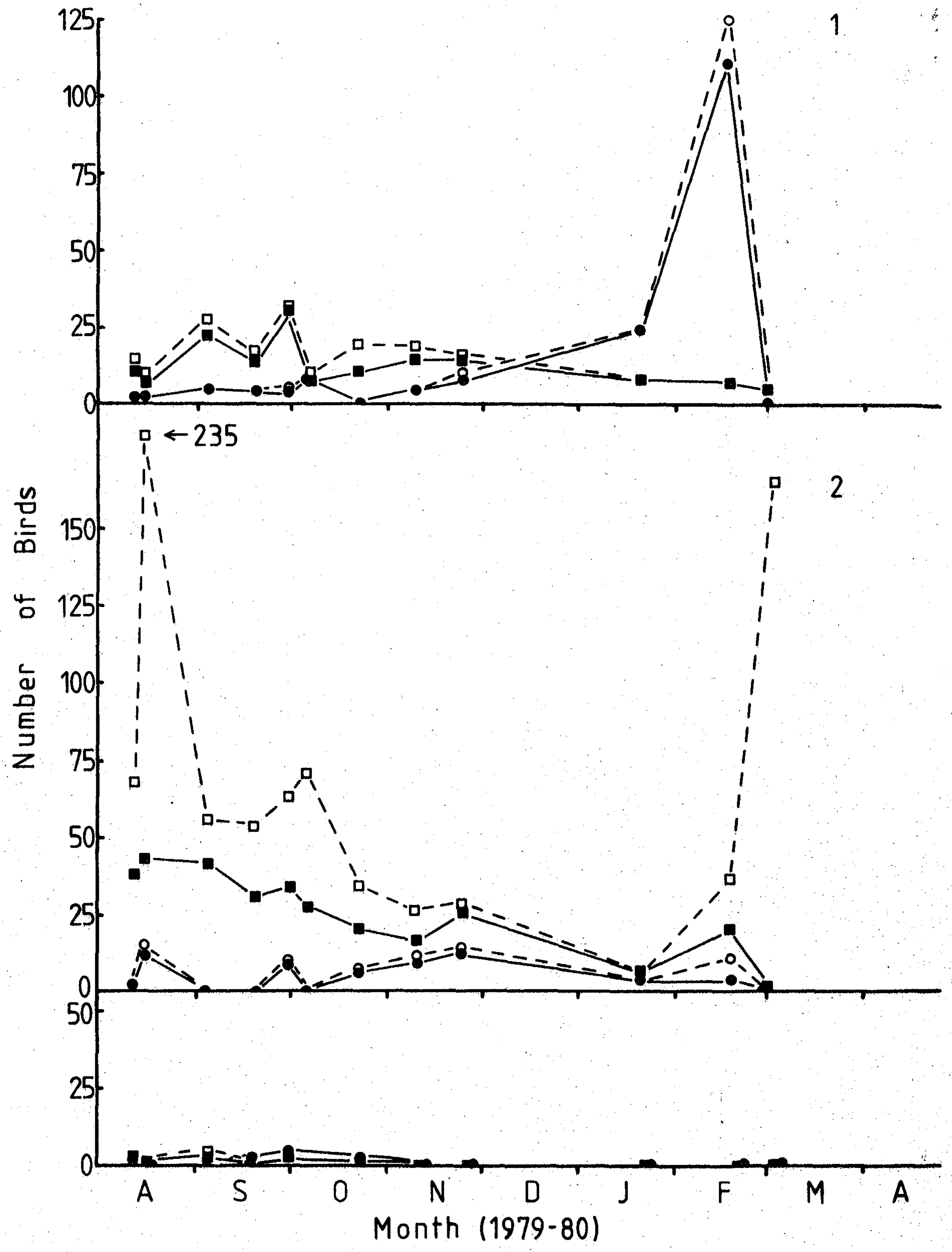
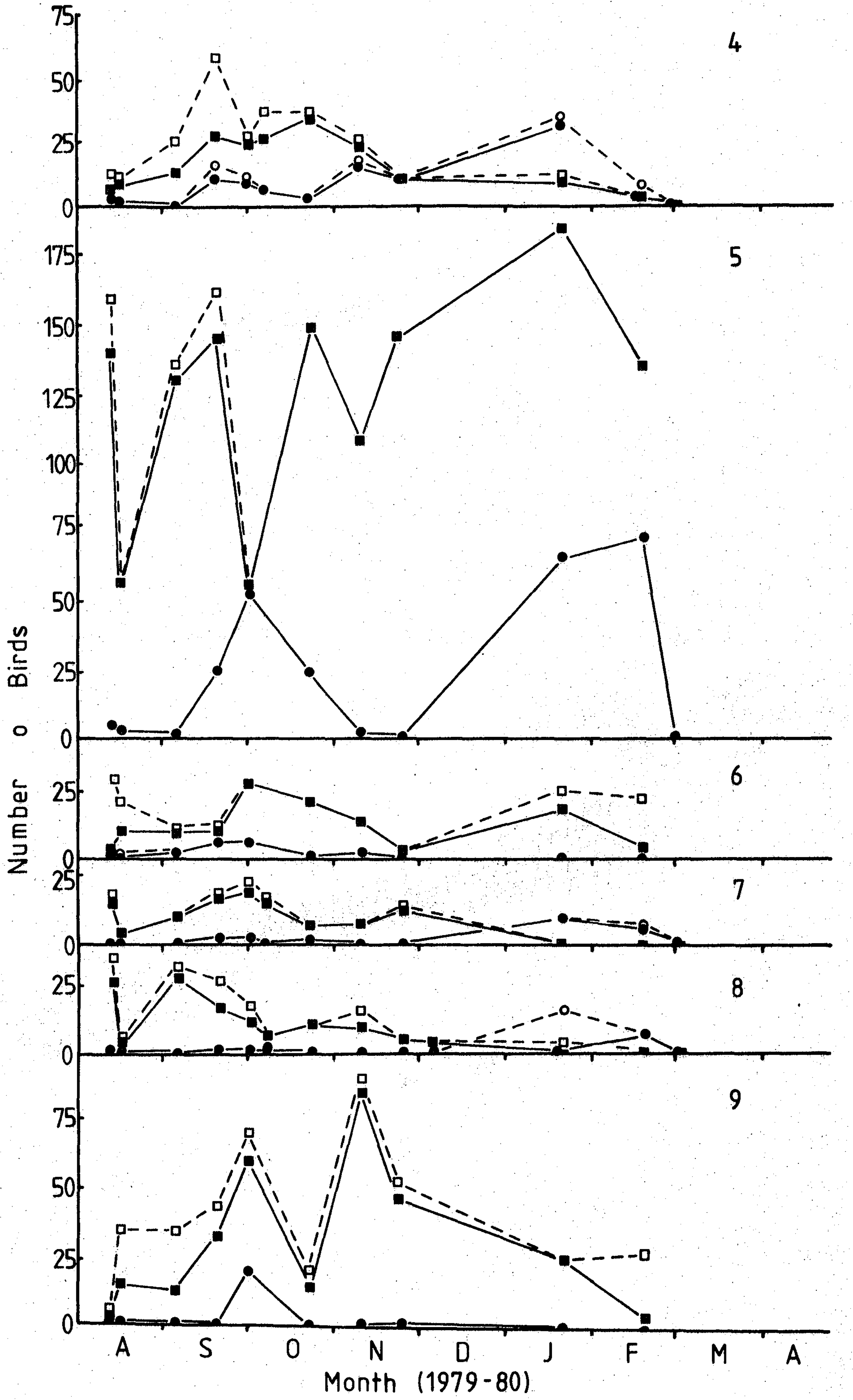


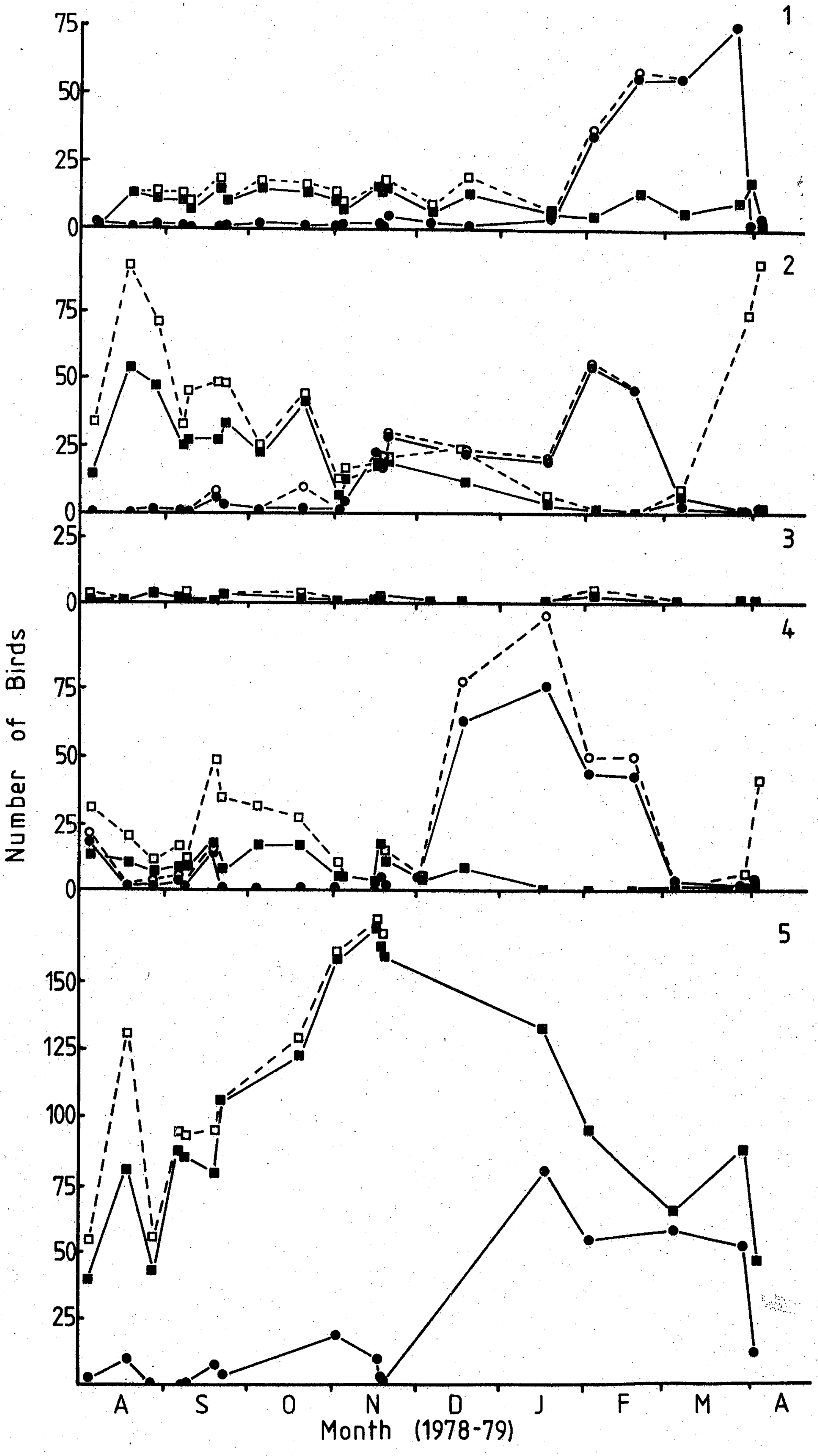
Fig. A7. Seal Sands, showing sub-areas referred to in Table A5.

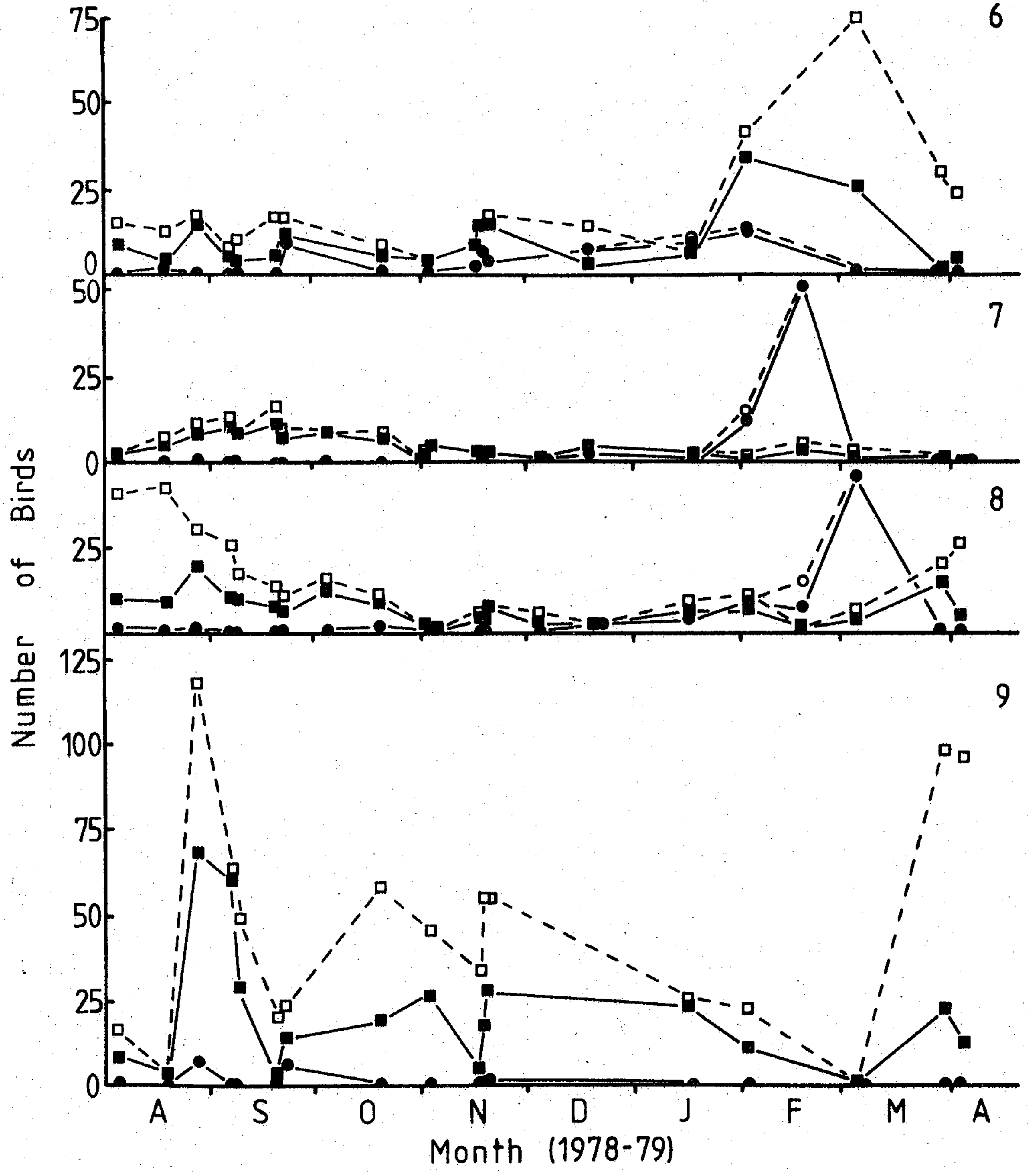
Appendix 9. Seasonal changes in low water distribution of Curlew and Bar-tailed Godwit. (Fig. A8).

Counts were made at the same time (between low water - 1 hr and low water + 1 hr) as those of Grey Plover to allow investigation of the possibility that the distribution of Plovers was affected by that of Curlew (■□) and Bar-tailed Godwit (●○). Solid symbols joined by solid lines refer to feeding birds, open symbols joined by dotted lines to the total number present i.e. including roosting individuals.


1
2
← 235
Number of Birds
125
100
75
50
25
0
150
125
100
75
50
25
0
50
25
0
A S O N D J F M A
Month (1979-80)


4
5
6
7
8
9
Number o Birds
75
50
25
0
175
150
125
100
75
50
25
0
25
0
25
0
25
0
75
50
25
0
A S O N D J F M A
Month (1979-80)


1
2
3
4
5
75
50
25
0
150
125
100
Number of Birds
A S O N D J F M A
Month (1978-79)


6
7
8
9
75
50
25
0
125
100
Number of Birds
A S O N D J F M A
Month (1978-79)