STUDIES OF THE FOODS AND FEEDING ECOLOGY OF WADING BIRDS

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by

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ABSTRACT

In this thesis are described the populations of waders (Aves: Charadrii) occurring on the Ribble Estuary, Lancashire, special reference being made to the eleven species comprising the bulk of the shore wader population. The daily routine of these birds is described including the time spent in feeding.

The feeding areas are described together with the foods taken from gut and pellet analysis and direct observation.

The distributions of invertebrates, and especially those of major importance as wader food, are described as well as the factors affecting these distributions. Variations in density of prey in relation to O.D., general geography of the estuary, and time of year are included. Depth distribution and variations in prey size are outlined for the main species.

Food intake was studied in the eight main waders. Daily intake through the year is described.in relation to energy requirements. Variations of feeding rates with several factors are included.

All data are combined to enable calculation of the total biomasses of the main prey taken by waders in the course of a year. These are compared with total minimum annual production of the prey. Future work, including a computer study based on these and extra data, is outlined.

Frontispiece

a. The author counting a flock of 45,000 Knot
25 August, 1972

b. Crossens roost from the air
12 October, 1973

Bar-tailed Godwit - top left

Knot - left middle

Oystercatcher - centre to right middle

Dunlin - centre to bottom right

ACKNOWLEDGEMENTS

Firstly, I must thank Dr. W. G. Hale who has supervised this work and given me, not only the use of the facilities in his Department, but also much encouragement and advice. Dr. P. H. Smith also gave much encouragement and also provided many data on wader numbers; for these I am grateful.

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Finally, this study would not have been possible without the encouragement of my family and especially my wife. She has tolerated my absence from home for days on end and, over the past ten months, has put up with the bulk of books and papers necessary to the writing of this thesis.

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VIII THE FOOD INTAKE OF WADERS

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INTRODUCTION

During the past decade several plans have been published or discussed which would result in the development of several major British estuaries. Some of these will possibly have been completed during the 1980's if government and industry ignore the arguments put forward by conservationists and, as natural estuaries, these areas will be no more. There is a real possibility that many British estuaries, now in more or less a natural state, will be developed into major industrial complexes similar to the Rhine area of the Netherlands.

Foremost amongst these, at present (May 1974) are the Maplin Sands, off Foulness Island (North Thames) where it is proposed to build London's third airport, a seaport, several road and rail links with existing transport systems and a city in South East Essex to house the half million people who would be employed by the two Maplin projects and also the industries which Maplin would attract.

Elsewhere on the coasts of England and Wales the following projects have been proposed which would have similar effects on estuarine environments:

1. The Wash - some form of barrage to form a reservoir for water storeage,
2. Medway and Swale - a large industrial complex,
3. Humber - a terminal for receiving North Sea gas and oil, and possibly an oil refinery,
4. Dee (Cheshire - Flintshire) - a barrage for a reservoir including an extensive water-sports area,
5. Morecambe Bay - plans, now suspended, for a reservoir with possibly a motorway across the barrage to improve communication between Furness and the main motorway network and hence attract industries to settle on the Furness coast (including N.W. Morecambe Bay),
6. Duddon - a reservoir,
7. Solway Firth - a reservoir, with separate schemes for a marina-water sports area.

Besides these the following estuaries are to a great extent affected by industry and are likely to be affected in a greater way in the future: Tees, Tyne, Wear, the estuaries entering Southampton Water, the estuaries of South Wales and the Mersey. In Scotland there is not the pressure that exists in England though many of the Firths, especially those on the east coast (e.g. Moray and Dornock) are likely to become increasingly affected as a result of the exploitation of offshore fuel deposits.

Thus, few large estuaries are not scheduled for development, and one such is the Ribble Estuary, Lancashire.

Estuaries have long been known as important areas for birds, especially non-breeding flocks of wildfowl (Anseriformes) and waders (Charadriiformes). The former order has been well studied in view of its interest to wildfowlers - in Britain there is the review of Atkinson-Willes (1963) and a series of booklets dealing with individual estuaries is being prepared by the Wildfowlers' Association of Great Britain and Ireland dealing with populations, whilst teams at the Wildfowl Trust and Royal Society for the Protection of Birds have been investigating wildfowl feeding ecology. Until recently however, the wader situation was poorly known. Rooth (1967) for instance stated that "in *Britain* it is particularly the Wash .... and surrounding area with 150,000 waders that is important; also such areas as the Norfolk Broads .... and the North Norfolk Marshes......." (!) The chief exception to this was the Fishery Section of the M.A.F.F. studies of the Oystercatcher *Haematopus ostralegus* dealing with population (Dare 1966), and feeding ecology (e.g. Drinnan 1957, Davidson 1967).

It was because of this dearth of information and the increasing pressures on estuaries that it was felt that regular censuses ought to be carried out of waders over the major estuaries and these started in the mid-1960's with the Ribble and Morecambe Bay whilst in 1969 other estuaries were incorporated under the banner of the *Birds of Estuaries Enquiry* of the British Trust for Ornithology.

At the same time studies were begun on the factors which attract waders to estuaries. Out of the breeding season the main factor is food.

It has been attempted, therefore, in this study to examine potential wader-food, species, populations, wader populations and the amount of food that these wader populations consume. From these it was hoped to gain an insight into whether the Ribble could hold more waders than it already does, and possibly whether it could absorb waders displaced from elsewhere. Furthermore, although no two estuaries are completely alike and thus wader feeding ecology is likely to vary to some extent from area to area, it is also hoped that the data presented here may supplement similar studies now in progress in the Tees Estuary and Lindisfarne areas (Durham University), Ythan Estuary (Aberdeen University), Wash and Foulness (N.E.R.C.) and other projects. From such projects a clearer understanding is being obtained of the predator-prey interactions in the wader-invertebrate food chains in the estuary ecosystem.

The statistical tests of Bailey (1959) were mostly used in this study though reference was also made to Elliott (1971). Throughout the text means are given followed by standard error wherever possible. Graphs involving the plotting means also include one standard error either side of the mean by a vertical bar corresponding to the standard error.

THE STUDY AREA

The tidal area of the Ribble Estuary (figure 1) is funnel-shaped, extending 24 Km. westwards from Preston to the Irish Sea where it reaches its maximum width of 18 Km. The total area is about 84 Km^2. At low tide the majority of this is exposed, when just two narrow channels contain water. The largest of these is the Ribble Channel which has been canalised by the Preston Port Authority and is a shipping lane: this includes about 5 Km^2. of the estuary. To the south is the Pinfold Channel, draining the mud and sandbanks as well as the large area of mossland (low-lying peaty farmland) to the south of the estuary: this takes up to about 3 Km^2 of the estuary. The remainder consists of mud and sand, separated by the two main channels into three areas, the major wader feeding areas.

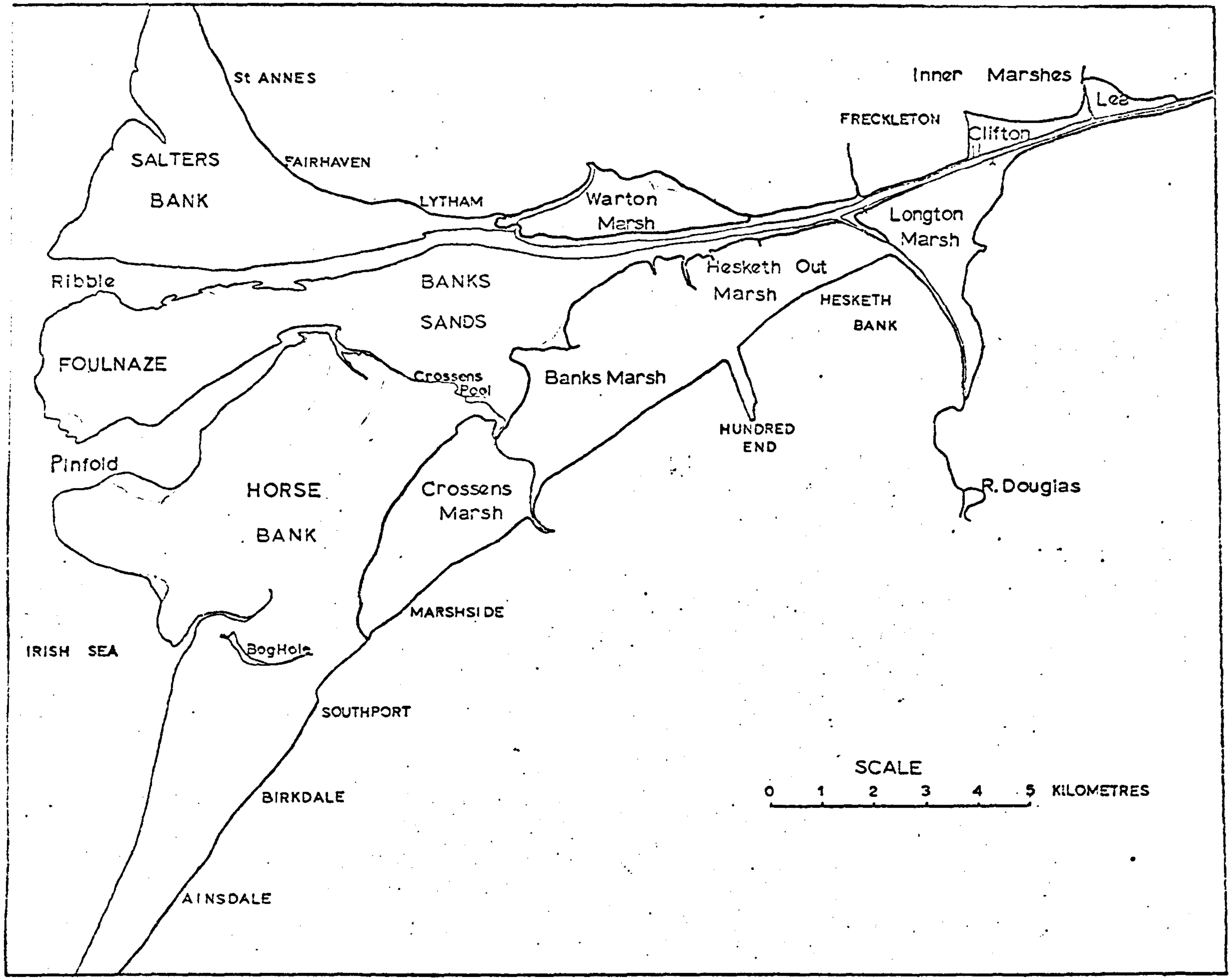
North of the Ribble Channel is Salter's Bank (about 16 Km^2), between the Ribble and Pinfold is Foulnaze (7 Km^2) and Banks Sands (12 Km^2), and to the south of the Pinfold is the vast Horse Bank which stretches down to Formby Point as Birkdale and Ainsdale Sands (38 Km^2). From Lytham and Hundred End eastwards narrow strips of mudflat border the Ribble Channel and also the River Douglas (which opens into the Ribble at Hesketh Bank) to the points at which these cease to be tidal. The physical characteristics of these areas are dealt with in Chapter VI.

Backing the mud and sand banks along most of the south and part of the north side is a large expanse of saltmarsh, totalling (in 1973) about 13.35 Km^2. This is mainly the typical "west coast" Festuca rubra and Puccinellia maritima saltmarsh with varying amounts of Cochlearia anglica, Armeria maritima, Glaux maritima, Halimione portulacoides, Suaeda maritima, Aster tripolium and Plantago maritima. Over large areas this floral variation is reduced due to heavy grazing by sheep and cattle whilst on some of the higher inner marshes (e.g. Clifton) turf is removed for gardens.

Since the early 1950's large areas of mudflat have become fixed as saltmarsh due to the increased rate of accretion caused by the appearance and spread of Spartina: since 1954 about 2.7 Km^2 have been

Figure 1

Map of the Ribble Estuary


St ANNES
SALTERS
BANK
FAIRHAVEN
LYTHAM
Warton
Marsh
FRECKLETON
Inner Marshes
Lea
Clifton
Longton
Marsh
Ribble
BANKS
SANDS
Hesketh Out
Marsh
HESKETH
BANK
FOULNAZE
Crossens
Pool
Banks Marsh
HUNDRED
END
Pinfold
HORSE
BANK
Crossens
Marsh
R. Douglas
MARSHSIDE
IRISH SEA
BogHole
SOUTHPORT
SCALE
0 1 2 3 4 5 KILOMETRES
BIRKDALE
AINSDALE

formed. Before the arrival of *Spartina* colonisation of the higher exposed mud/sand was performed by the slower spreading *Salicornia herbacea* and *Puccinellia* but it is probable that the increased colonisation of sand by halophytes has been encouraged somewhat by the completion of the Ribble Channel "training walls" and the construction at Southport of a large marine lake and coastal road which extended into the tidal zone. These have produced a longer period of slack water at high tide and therefore increased sedimentation. Indirectly, this increase of sedimentation rate and saltmarsh spread affects feeding wader populations in that few waders feed on the highest areas of intertidal zone due probably to a poorer prey fauna (see later) and thus at present the real feeding area is decreasing. This loss of intertidal feeding area is however compensated for an increase of saltmarsh breeding habitat.

This study deals only with waders which feed on the saltmarshes and mudflats. However, some of these (e.g. Oystercatcher, Curlew, *Numenius arquata* and Redshank *Tringa totanus*) also spend some time feeding on fields around the estuary and thus these areas had to be considered. Observations were made, therefore, on the peaty mossland fields around the south side of the estuary and behind the towns of Lytham and Blackpool, and on reclaimed saltmarshes immediately adjacent to the unreclaimed marshes. These have been described by Greenhalgh (1971 and in press).

CHAPTER II WADER POPULATIONS OF THE RIBBLE ESTUARY

Introduction

For many years the Ribble Estuary has been known as a major haunt of waders; T. A. Coward (1920) mentioning the large numbers of Knot, and J. Charnley and W. Heathcote (1933), R. Wagstaffe (1929), E. Hardy (1941) and C. Oakes (1953) recording some data on the Ribble's waders. With F. W. Holder, R. Wagstaffe also published several papers dealing with waders on the south Ribble during the 1920's - 1940's (e.g. 1930 on Bar-tailed Godwits). Only since the last war, however, has a great deal of systematic censusing been carried out. N. Harwood (1955) published many counts from the north Ribble and, with H. Shorrock, A. Harrison and others maintained regular coverage also of wader migration through Freckleton sewage farm and its associated Inner Ribble Marshes. On the south side of the estuary less was done in this period though F. W. Holder and R. Wagstaffe carried out observations into the 1950's and visitors to the area made less regular counts (e.g. W. G. Hale, C. Oakes and K. G. Spencer).

In 1960 the present writer began a programme of wader counts on the north side of the estuary and, from 1967 extended them to the south side. From 1968 - 9 also, the B.T.O.'s Estuaries Enquiry was commenced. To carry out as full a census as possible for this Dr. P. H. Smith organised a team which has, since 1970, made complete counts of all the waders on the shore. From 1972 these have been supplemented by aerial surveys by Dr. W. G. Hale.

Methods

Only in species which feed on fields (e.g. Golden Plover, Snipe and Ruff), the tops of saltmarshes (e.g. Whimbrel, Green Sandpiper and Green Shank) and Freckleton sewage farm can counts be made which give accurate results irrespective of either time of day or state of tide. For the vast majority of birds on the estuary the only time at which accurate counts can be made is when all the birds gather into a few high tide roosts for a few daylight hours each day. A further

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In all species except Oystercatcher, Curlew and Redshank it was certain that, during the main years of this study (1971-74) all waders feeding on the Ribble Estuary were counted at the high water roosts. All areas were thoroughly checked, including fields inland, and no roosts were found there. Further checking was carried out by Dr. W. G. Hale from a light aircraft on several occasions. Thus it can be taken that the wader censuses gave valid estimates of the Ribble populations.

constraint is provided by the effects of the various tide heights, for on neap tides (less than 24 feet (7.8 metres)) not all birds use these roosts, many remaining on exposed feeding areas out in the estuary, and those that do go to roost usually scatter themselves along the edge of the tideway in such a fashion that counting is almost impossible. It is normally the case, therefore, that counts are made only on the higher (27 feet (9 metres) or more) tides and these occur in two short periods each of up to five days per month. It is thus impossible to locate subtle variations in wader numbers on the shore as might be observed from more frequent censuses on sewage farms etc. However, general trends can be seen clearly and good estimates of the numbers of most species obtained.

Counts are made by estimation in the case of large flocks, and most observers who have contributed data (though most presented here are by P.H.S. and the author) have had their ability to deal with such estimates checked several times. In no case have independent estimates of the same roost by experienced observers varied by more than about 5%.

The method of estimating involves initially the counting or careful estimating of a manageable proportion of the flock (e.g. 100 in a species occurring in numbers up to about 5,000, 1,000 in species numbering 20 - 30,000 and 5,000 in species in excess of 30,000). The whole flock is carefully checked against this proportion and the number of these in the flock estimated. This gives the estimate: usually it is checked several times, especially in the case of larger flocks, whilst when two or more observers are involved in the census they can carry out independent counts and, where these differ, argue and re-check until they reach agreement. Different roosts are counted by different variations of the above method, for no two roosts on the Ribble are * identical and each requires certain modifications of the usual method.

In this analysis personal data are included from the following areas in the years given below:

1. Inner Ribble Marshes : mainly January 1963 to the present but including some data from 1960,
2. Lytham to Squires Gate (including the three roosts of Warton Marsh, Fairhaven and Squires Gate) : 1960 - 70 with some data since,

3. Southport - Crossens area : 1967 onwards,
4. Banks - Hundred End : some counts 1966 - 7 but regular counts from 1968.

Many of these counts have been included in the B.T.O. Estuaries Enquiry and through the offices of Dr. P. H. Smith, the regional organiser, all data collected under that scheme have been included in the analysis. Other observers have given extra information. A full list of observers who have contributed to this study is included in the acknowledgements.

In the text, data from the Estuaries Enquiry are given in graph form whilst counts from other sources are given in the tables. Also given for all species in Table 1 is an estimate of the number of bird-days per annum for the years 1971-2 and 1972-3. These have been calculated from the Estuaries Enquiry data by weighing the graphs (it was intended to use a computer for this analysis, but the inaccuracy due to the time between censuses and the errors in estimation made such precise "bird-day per annum" calculations untenable: the method used gives a figure which is as reliable a guide as is required). This figures gives a good impression of total pressure of waders on the estuary better than simple numbers can, and can be more easily incorporated into estimates dealing with the overall impact of such waders on invertebrate populations.

In Table 2 are given the average peak (calculated by taking the average of the maximum counts for the years 1970-1 to 1973-4) and the maximum peak (the highest number recorded during the same years) for each species. These are compared with the most recently published data on the British totals (anon. 1973) and the estimated European (including Britain and North Africa) populations from Spitz (1969) as amended for Great Britain by Prater (1972).

Nine species of wader have bred around the Ribble Estuary during the period of this study and estimates of their populations are given in Table 3, taken from Greenhalgh (1969 a and b, 1971, 1972 and unpublished M.S.) supplemented from further unpublished data.

List of waders (Charadruforms : Charadru) recorded on the Ribble Estuary

Altogether 48 species of wader have been recorded on the Ribbel Estuary and these are shown in the list below.

Oystercatcher	*Haematopus ostralegus* (Linn.)
Lapwing	*Vanellus vanellus* (Linn.)
Grey Plover	*Pluvialis squatarola* (Linn.)
Golden Plover	*Pluvialis apricaria* (Linn.)
Ringed Plover	*Charadrius hiaticula* (Linn.)
Little Ringed Plover	*Charadrius dubius* (Scolopi)
Kentish Plover	*Charadrius alexandrinus* (Linn.)
Dotterel	*Eudromias morinellus* (Linn.)
Black-winged Stilt	*Himantopus himantopus* (Linn.)
Avocet	*Recurvirostra avosetta* (Linn.)
Whimbrel	*Numenius phaeopus* (Linn.)
Curlew	*Numenius arquata* (Linn.)
Black-tailed Godwit	*Limosa limosa* (Linn.)
Bar-tailed Godwit	*Limosa lapponica* (Linn.)
Spotted Redshank	*Tringa erythropus* (Pallas)
Redshank	*Tringa totanus* (Linn.)
Lesser Yellowlegs	*Tringa flavipes* (Gonelin)
Greenshank	*Tringa nebularia* (Gunnerus)
Green Sandpiper	*Tringa ochropus* (Linn.)
Wood Sandpiper	*Tringa glareola* (Linn.)
Common Sandpiper	*Actitis hypoleucos* (Linn.)
Turnstone	*Arenaria interpres* (Linn.)
Short-billed Dowitcher	*Limnodromus griseus* (Gmelin)
Great Snipe	*Capella media* (Latham)
Snipe	*Capella gallinago* (Linn.)
Woodcock	*Scolopax rusticola* (Linn.)
Jack Snipe	*Lymnocryptes minimus* (Brunnick)
Knot	*Calidris canutus* (Linn.)
Sanderling	*Calidris alba* (Pallas)
Semi-palmated Sandpiper	*Calidris pusillus* (Linn.)
Little Stint	*Calidris minuta* (Leisler)
Temminck's Stint	*Calidris temminckii* (Leisler)

Least Sandpiper	*Calidris minutilla* (Vieillot)
White-rumped Sandpiper	*Calidris fuscicollis* (Vieillot)
Baird's Sandpiper	*Calidris bairdii* (Coues)
Pectoral Sandpiper	*Calidris melanotos* (Vieillot)
Purple Sandpiper	*Calidris maritima* (Brunnich)
Dunlin	*Calidris alpina* (Linn.)
Curlew Sandpiper	*Calidris ferruginea* (Pontoppidan)
Stilt Sandpiper	*Micropalama himantopus* (Bonaparte)
Broad-billed Sandpiper	*Limicola falcinellus* (Pontoppidan)
Buff-breasted Sandpiper	*Tryngites subruficollis* (Vieillot)
Ruff	*Philomachus pugnax* (Linn.)
Grey Phalarope	*Phalaropus fulicarius* (Linn.)
Red-necked Phalarope	*Phalaropus lobatus* (Linn.)
Wilson's Phalarope	*Phalaropus tricolor* (Vieillot)
Stone Curlew	*Burhinus oedicnemus* (Linn.)
Collared Pratincole	*Glareola pratincola* (Linn.)

Nine of these have been recorded only once in the area, nine others have been recorded on five or less occasions and fifteen, though occurring every year, never occur in flocks exceeding one hundred. Of the fifteen common species which remain, four feed primarily on farmland or saltmarshes (Lapwing, Golden Plover, Snipe and Ruff). This leaves eleven species of common waders which are primarily feeders on the intertidal zone, and it is with these that this account mainly deals: Oystercatcher, Grey Plover, Ringed Plover, Curlew, Black-tailed Godwit, Bar-tailed Godwit, Redshank, Turnstone, Knot, Sanderling and Dunlin.

Three of these have, therefore, been exluded from a detailed investigation of feeding ecology: Grey Plover and Ringed Plover because a high proportion of their numbers feed predominately outside of the Ribble boundaries, and Turnstone which feeds in most cases almost entirely on the *Mytilus* Church Scar area.

Table 1 Number of bird-days for eleven common waders on the Ribble Estuary

	1971 - 2	1972 - 3
Oystercatcher	574,000	637,000
Grey Plover	142,000	161,000
Ringed Plover	34,500	5,600
Curlew	92,000	132,000
Black-tailed Godwit	-	58,000
Bar-tailed Godwit	876,000	1,186,000
Redshank *	485,000	785,000
Turnstone	-	30,400
Knot	9,733,000	9,885,000
Sanderling	739,000	955,000
Dunlin	5,231,000	9,429,000

* data from 1 July to 31 March

Note: 1971-2 data for Black-tailed Godwit and Turnstone inadequate.

Table 2 Comparison between Ribble population of eleven wader species and populations of British Isles and Europe

	Ribble Estuary		European Peak	British Peak	Ribble average peak as % of	
	Average Peak (1970–73)	Maximum Peak (1970–73)			European Peak	British Peak
Oystercatcher	3,043	4,066	470,000	193,614	0.6	1.6
Grey Plover	1,312	1,800	-	7,350	-	17.8
Ringed Plover	1,110	1,210	-	18,392	-	6.2
Curlew	918	1,383	110,000	61,405	0.8	1.5
Black-tailed Godwit	978	1,330	-	4,043	-	24.2
Bar-tailed Godwit	7,667	11,635	70,000	41,512	11.0	18.4
Redshank	3,682	5,891	84,000	69,365	4.4	5.3
Turnstone *	397	450	11,500	12,891	2.0	3.1
Knot	72,038	91,205	435,000	387,345	16.6	18.7
Sanderling	7,526	9,450	-	23,794	-	31.6
Dunlin	32,774	44,790	830,000	464,214	3.9	7.6

* Turnstone data from 1967–1970 data of Table 13.

Notes: The maximum European populations are from Spitz (1969) amended for British numbers by Prater (1972).
The maximum British populations are from anon. (1973).
Both sets of data give estimates of peak population for each species irrespective of the month in which the peak occurred.

Table 3 **Maximum breeding populations (in pairs) of waders around the Ribble Estuary : area shown in Figure 1**

	Unreclaimed Saltmarsh	Reclaimed Saltmarsh	Sandy Beach	Mossland	TOTAL
Oystercatcher	16	4	1	8	29
Lapwing	56	1,012	0	640	2,208
Ringed Plover	3	2	4	0	9
Little Ringed Plover	0	0	0	1	1
Curlew	0	1	0	2	3
Black-tailed Godwit	?	1	0	?	1+
Redshank	231	32	0	7	270
Snipe	0	9	0	(30)	(39)
Woodcock	0	0	0	(1)	(1)
Dunlin	6	0	0	0	6
Ruff	1	1(?)	0	?	2+

Results

The results presented here deal with the eleven commonest species which feed on the intertidal zone of the Ribble Estuary. Some data on these, together with the other species, have been published (Greenhalgh 1967, 1968a and b, 1971, M.S. 1973 and in press).

OYSTERCATCHER

The density of Oystercatchers breeding on the Ribble marshes and surrounding farmland (Table 3) is much lower than the density around nearby areas such as Morecambe Bay and the Cumberland coast though there are signs from recent years of a slow increase (Greenhalgh 1969a, 1971, 1973).

Small numbers of Oystercatchers (up to 350) remain through the summer and the majority of these (75% in 1971, 87% in 1972 and 80% in 1973) show at least a trace of immature plumage. First immigration occurs in late June and early July of birds which, from their plumage and behaviour, appear to be to some extent family parties, presumably of birds originating from northern England and Scotland (see Dare 1970). A significant proportion (30% in 1973) appear to be adults independent of young (possibly failed or non-breeders) which moult on the estuary. In July 1973 a party of 51 adult Oystercatchers spent three weeks on Longton Marsh during which time they moulted some primaries and body plumage.

There is a suggestion of an autumn peak in August and September recalling the pattern in Morecambe Bay (Wilson 1973) though in some years no such pattern occurs. Instead counts vary from fortnight to fortnight, possibly as waves of migrants pass through the area. During the winter months numbers appear to fluctuate on the estuary much more than they in fact do. This is due to a variable proportion spending the daylight hours or just the high tide period feeding or roosting on fields: these are usually missed during roost-censuses though some counts are available. In the years 1967 - 70 P. A. Greenhalgh and the present writer made nineteen thorough counts of the numbers of Oystercatchers roosting at high tide on the shore and fields of the north Ribble. Out of a grand total of 17,900 counted, 7,454 roosted inland (41.6%), the range of inland roosting birds being from less than 1% to 88% of the north Ribble birds. Of these at least 60% returned to the shore to feed at low tide whilst observations showed that the other birds left the fields at dusk and returned at dawn.

On the south Ribble similar counts were made in the period November - February 1970 - 74 and these have shown that between 80 and 330 feed during the day on fields (up to 30% of the total population). At high tide these may be joined by up to 450 roosting birds. All these inland birds are excluded from the censuses given in Figure 2 and Table 4 (which gives the numbers feeding on the Mytilus scar off Fairhaven), except those made in severe weather when inland feeding areas are frozen and all Oystercatchers must resort to the intertidal feeding areas. During recent winters the weather has been generally extremely mild, with just a few frosty days. However, in 1967 and 1969 the effects of hard weather on the inland feeders can clearly be seen : in Table 4 counts made in such conditions are shown underlined.

Inland feeding is a recent phenomenon, having been first noticed on a large scale from Morecambe Bay following the exceedingly hard 1962 -3 winter, which decimated the Cardium stock, the main food of Oystercatchers in Morecambe Bay. These stocks never recovered and some of the Oystercatchers which remained turned to lumbricids and insect larvae from fields in the following winters (Dane 1966). There are not the records for the early 1960's to show whether any food stocks on the Ribble have decreased, except that fishermen from Marshside and Crossens used to collect cockles from the Horse Bank and now the species is very sparce. It was after the 1962 - 3 winter that Oystercatchers began to feed regularly on fields around the Ribble.

Oystercatchers begin to leave from mid-February and by mid-April only the summering birds remain: this decrease parallels the arrival of Oystercatchers back on their breeding grounds (Greenhalgh 1969a).

GREY PLOVER

This holarctic wader breeds in the tundras of northern America and Eurasia and winters south to Australia, Cape Province and Brazil (Vavrie 1965). To the Ribble it is chiefly a bird of passage with a variable number wintering.

Figure 2

Oystercatcher numbers on the Ribble Estuary
1971 - 2 to 1973 - 4 winters

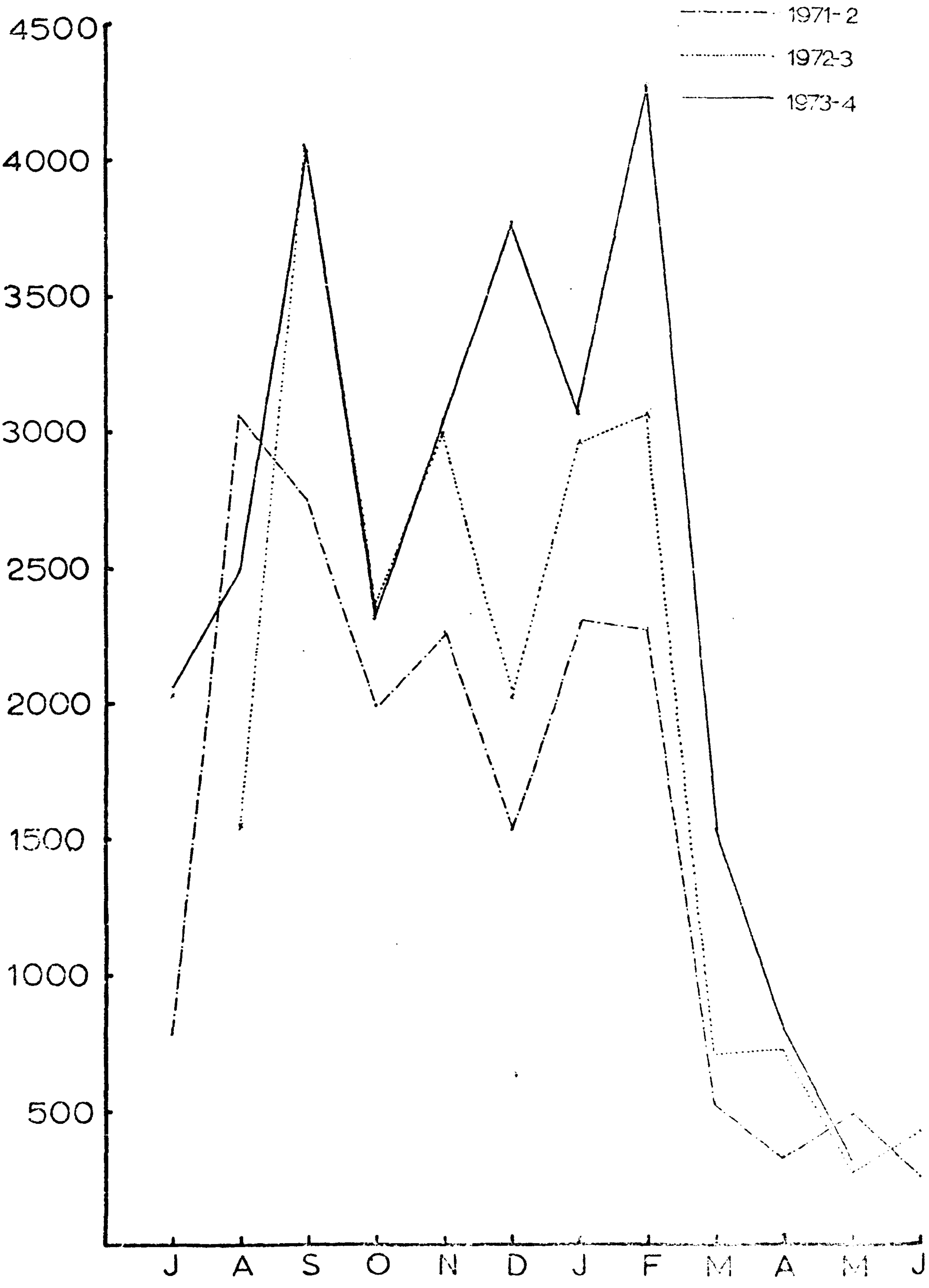
1971-2
1972-3
1973-4
4500
4000
3500
3000
2500
2000
1500
1000
500
J
A
S
O
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Table 4 Maximum monthly counts of Oystercatchers feeding on *Mytilus edulis* on Church Scar, 1966 - 69

	1966-7	1967-8	1968-9
July	61	36	52
August	446	317	500
September	397	355	480
October	482	529	433
November	131	210	366
December	180	126	207
January	340	290	145
February	270	175	305
March	65	38	118

Note: Counts underlined are those monthly maxima made during hard weather (snow, frost).

Small numbers summer (less than 50) and these usually retain a non-breeding plumage whereas arrivals from the beginning of July and early August are adult birds which presumably have come straight from the breeding grounds (in summer plumage). Further influxes, which include juveniles, occur through to November, often resulting in a small autumn peak (e.g. 400 at Lytham, 2 September, 1964; 300 at Formby Point, 15 October, 1966; 1,150 at Crossens, 24 November 1968). In other years no distinct autumn peak can be discerned, or the peak may be very slight (figure 3 for 1971 - 2 to 1973 - 4).

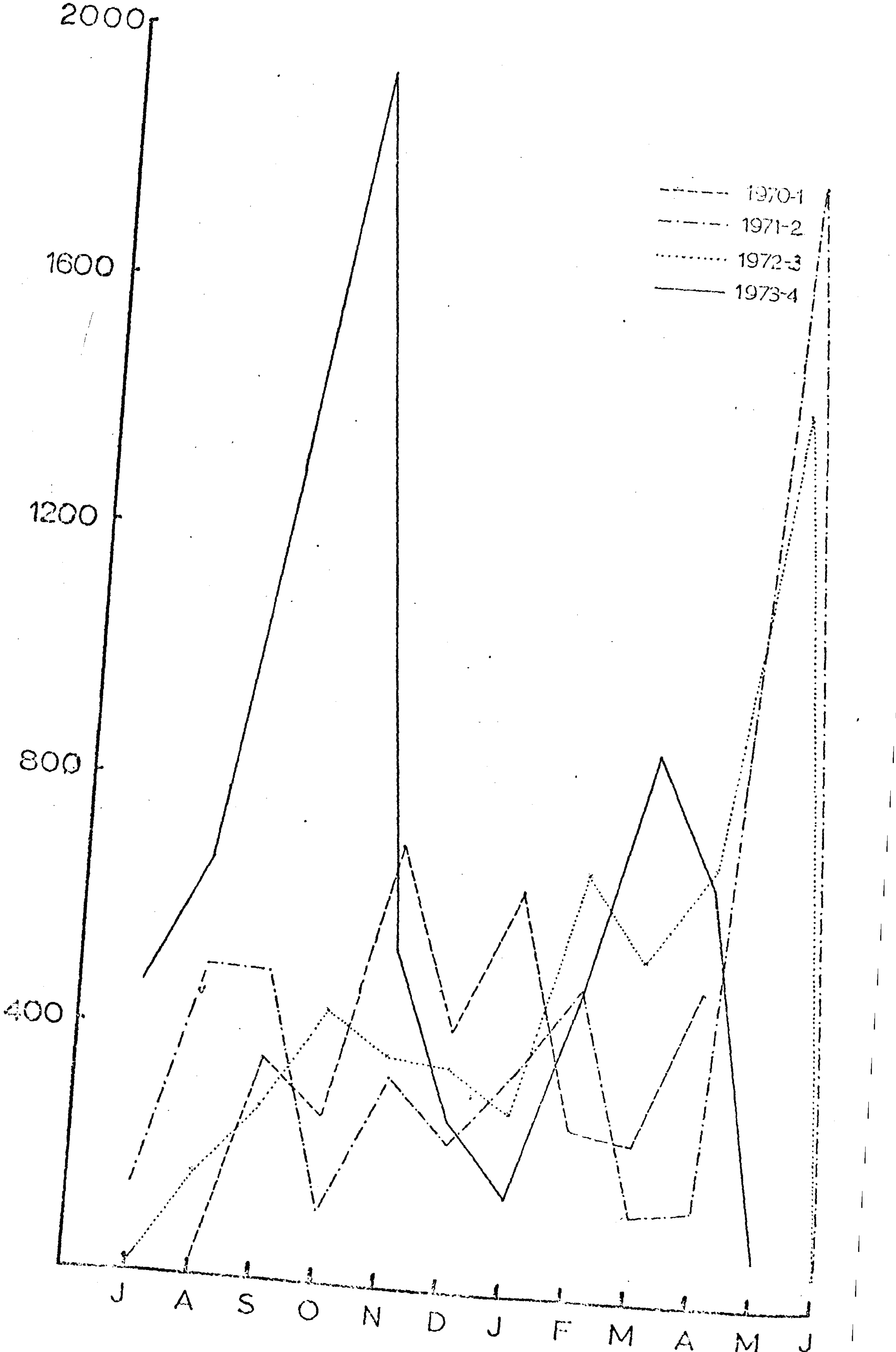
Numbers are relatively small through the winter (the maximum roost count being in the order of 350) and numbers fluctuate widely, possibly as birds move from one estuary to another. Indeed, thorough searches of the Ribble feeding areas seldom yield 100 individuals suggesting that many which roost on the Ribble feed outside the area, along the Fylde coast and south to the Mersey and Dee. Furthermore, observations off Formby Point and Squires Gate and the Fylde coast show some movement into the estuary at high tide and departure on the ebb.

By February spring passage commences, data from recent censuses showing tow peaks (figure 3): a smaller one in February - early March and a second larger one in late April - mid May. The first spring peak appears to consist of a high proportion of first-year birds: the second of adult birds in breeding plumage.

Wilson (1973) reported that the Morecambe Bay population departed from late February whilst the overall British Grey Plover population, as shown by recent Estuaries Enquiry censuses, also gives a peak in February (anon. 1973). It may be that the North European winter population moves in February - early March resulting in decreases on some estuaries with influxes to others. The second peak, consisting almost entirely of adults, was first demonstrated by N. Harwood working on the north Ribble (e.g. 320, 8 May 1953; 270, 17 May 1955; 300, 15 May 1956) but its full extent was not appreciated until May 1972 when the first complete May census was carried out (figure 3).

Figure 3

Grey Plover numbers on the Ribble Estuary 1971 - 2 to 1973 - 4 winters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The size of the May peak in 1972 (1,800) was 24.5% of the peak British number in that year (anon. 1973), though the number of Grey Plover-days on the Ribble is not large (table 1) due to the rapid build-up and departure of such peaks.

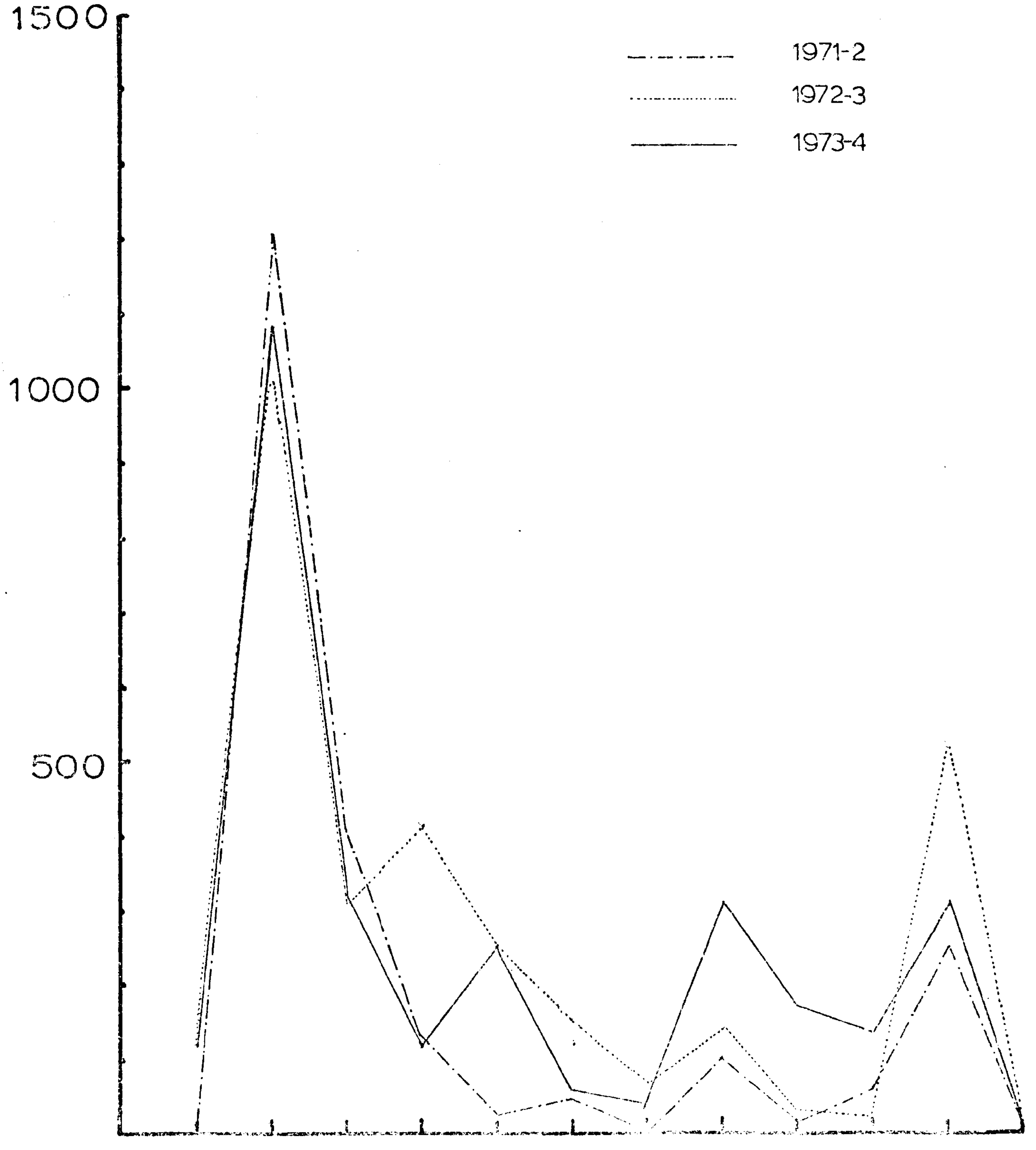
RINGED PLOVER

The small and decreasing population of Ringed Plovers which breed aroung the Ribble Estuary remains on the breeding areas into late July. It is then lost amidst the first returning migrants which appear in early July and increase through the month. From data from the Inner Marshes (Greenhalgh 1968) and from the Lytham - Squires Gate area (Greenhalgh 1969 unpublished M.S.) two peaks of passage can be discerned from more frequent counts (Table 5): the first in late July to early August and a second from late August to September. From monthly counts, whether from the roosts over separate years (Figure 4) or from pooled data over several years from the Inner Marshes (Table 6) such close but separate peaks are not discernable, a general autumn peak of migration occurring in August - September.

Accounts of Ringed Plover autumn passage from other British areas show a range of times of peaks, none completely agreeing with the Ribble late July - early August and late August - early September. Mason (1969) reported late August and late September peaks from Leicestershire (his first probably being equivalent to the second Ribble peak), Brady (1949) found peaks from Fenham Flats (Northumberland) in late August and early September as did Nisbet (1957) from Cambridge sewage farm (their two peaks being included in the duration of the second Ribble peak). The present writer believes that the first peak, not discerned at these other areas, is that of the British and nearer European breeders whereas the second consists of Ringed Plovers from northern areas (including the arctic race *tundrae*) (Greenhalgh 1968). Observations of Ringed Plovers on the various breeding grounds, some ringing data and measurements of Ringed Plovers taken in these two peaks on the Inner Marshes also suggest that this is the case (Greenhalgh 1968 and unpublished). Furthermore, both peaks contain juvenile birds, indicating that the separation of peaks is certainly not from an age basis.

Figure 4

Ringed Plover numbers on the Ribble Estuary
1971 - 2 to 1973 - 4 winters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Through the winter months Ringed Plovers are scarce, though numbers begin to rise in early February to a peak in late February to March as the nominate hiaticula pass through. This is followed by a separate peak in mid-April to early May as, possibly, northern birds including tundrae pass. The latter peak has long been recognised (e.g. Nisbet 1957, Evans 1966, Mason 1969) though the earlier one has been recorded nowhere else though the overall Estuaries Enquiry monthly British totals indicate a small but clear peak in January (anon. 1973), which may be associated with the Ribble February peak. Certainly February and early March is the time that the British and nearer European populations would be expected to return from more southerly wintering grounds, for they have territories by mid-March.

Ringed Plovers are essentially passage migrants during very brief periods on the Ribble Estuary, and thus their importance on the estuary expressed in terms of bird-days per annum is very low (Table 1).

CURLEW

One or two pairs of Curlew breed on farmland or saltmarshes around the Ribble Estuary though in nearby Pennine areas very large numbers breed. These begin to leave the breeding grounds as their young fledge from late June, resulting in a peak of passage on the estuary in late June to July. A similar peak also occurs in Morecambe Bay (Wilson 1973) and N. E. England (Evans 1966). There is a second peak during September - early October probably of Fenno-Scandinavean Curlews which arrive in Britain from September (Norrevang 1959), some of which winter here.

Numbers decrease steadily through the autumn to a "low" in December. Certainly, however, this decrease can partly be explained by a variable proportion of Curlews feeding and also roosting inland. This is dealt with in Chapter III, though estimates made of the total numbers feeding inland are included below:

a) years 1967 - 70 on the north mosslands average count 71 (range 0 - 181),
b) years 1970 -74 on the south mosslands average count 135

Table 5 Totals of weekly peaks of Ringed Plovers at the Inner Ribble Marshes, 1967 - 69

1 Jul	2 Jul	3 Jul	4 Jul	1 Aug	2 Aug	3 Aug	4 Aug	1 Sep	2 Sep	3 Sep	4 Sep
3	15	28	44	196	61	86	168	105	47	12	9

Table 6 Totals of monthly peaks of Ringed Plovers at the Inner Ribble Marshes, 1963 - 69

Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
32	9	7	131	182	18	72	465	281	26	4	0

(range 0 - 273),

c) years 1971 - 74 on farmland behind the south Inner Marshes average count 38 (range 17 - 110).

The counts made at the roosts (Figure 5) exclude such inland feeders.

The lowest numbers feeding inland were recorded during frosts whilst the maxima were recorded during wet periods when many fields were flooded: such fields generally held the largest Curlew numbers.

Through the early spring (February - March) numbers reach a peak due to the passage of Curlews back to the breeding grounds, territories being taken-up from February onwards. This passage ends during early April, leaving very few summering birds.

BLACK-TAILED GODWIT

Though the Black-tailed Godwit has bred on the Ribble Marshes in recent years, it is mainly known as an autumn passage migrant in relatively large numbers mostly to the Salter's Bank - Warton Marsh area. Smaller though variable numbers occur through the winter and there is a small spring passage.

Autumn migration has been described by Greenhalgh (1973). First immigrants arrive in late June to early July, numbers increasing rapidly during late July and early August to a peak occurring from late August to early October (Table 7). From this peak numbers decrease rapidly to the small winter population. From plumage the first arrivals appear to be adults in breeding plumage, the first juveniles being recorded from late July or early August.

Autumn peak counts are now available for 22 out of the past 25 years and these are given in table 8. From these it will be seen that numbers have increased to a regular autumn peak of 1,000- 1,500. In 1970, and for many Estuaries Enquiry censuses, the Black-tailed Godwit roost was poorly covered: what counts are available under that scheme being unreliable or gross underestimates.

Winter numbers have decreased since 1960, for whereas up to 360

Figure 5

Curlew numbers on the Ribble Estuary
1971 - 2 to 1973 - 4 winters

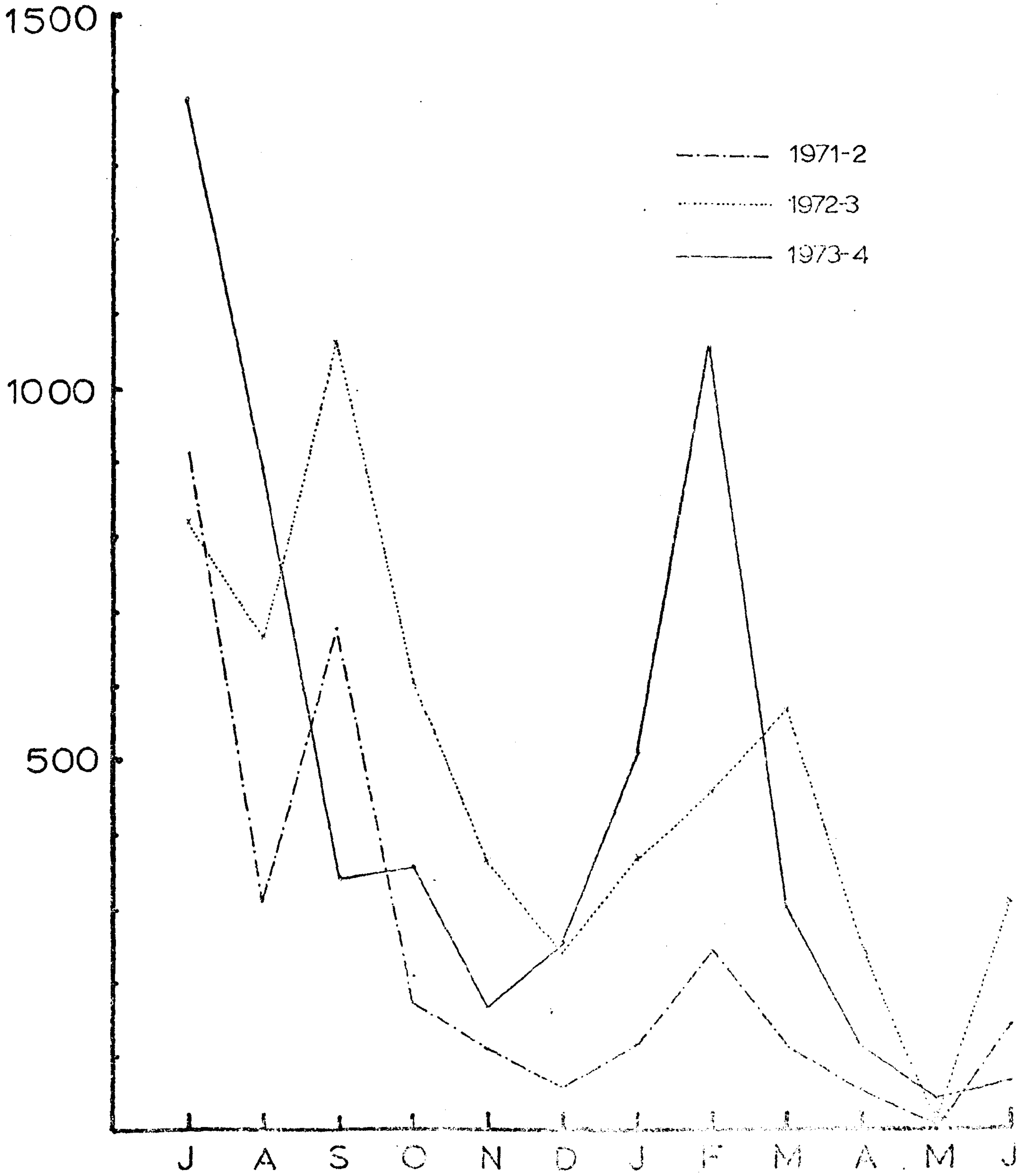
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Table 7 **Fortnightly counts of Black-tailed Godwits on the Ribble Estuary, 1967 - 69 and 1972 - 73**

	-2 Jun	-1 Jul	-2 Jul	-1 Aug	-2 Aug	-1 Sep	-2 Sep	-1 Oct	-2 Oct
1967	19	47	520	620	1,100	890	240	89	15
1968	1	2	40	200	430	1,500	320	150	5
1969	11	141	430	903	-	400	1,500	-	-
1972	2	85	180	890	910	1,240	500	-	85
1973	44	120	443	710	900	977	380	-	-

Note: data for 1967 - 8 are from Greenhalgh (1973), for the other years collected by the author, for the B.T.O. survey or P. Carah (pers. comm.).

Table 8 Peak counts of Black-tailed Godwits in autumn on the Ribble Estuary

1948	145	1963	640
1952	240	1964	570
1953	180	1965	1,050
1954	290	1966	1,150
1955	193	1967	1,100
1956	330	1968	1,500
1957	260	1969	1,500
1958	400	1970	362
1959	415	1971	703
1960	500	1972	1,240
1961	350	1973	977

were recorded in the late 1950's and early 1960's, in the past ten years (1964 onwards) only up to 20 have been recorded in winter. The data from the Estuaries Enquiry for the Dee Estuary, to the south, suggests that those which formerly wintered on the Ribble now winter on the Dee.

Both from observations of plumage and measurements of dead birds, the Ribble Black-tailed Godwits appear to be entirely of the Icelandic race _islandica_. The adults show a deep chestnut-red neck and breast coloration quite unlike the paler drabber salmon-pink and dull orange breeding plumage of the nominate race _limosa_ of continental Europe. They also attain a high degree of breeding plumage which _limosa_ never does, always retaining a proportion of grey winter feathers. These characters typical of _islandica_ can be discerned in the field with no difficulty. Measurements are likewise characteristic of _islandica_ being outside of the size range of their respective sexes of the continental European populations (Greenhalgh unpublished). It is this form which in recent years has been recorded summering around the estuary and which now breeds on the saltmarshes of the Solway Firth to the north (personal observation).

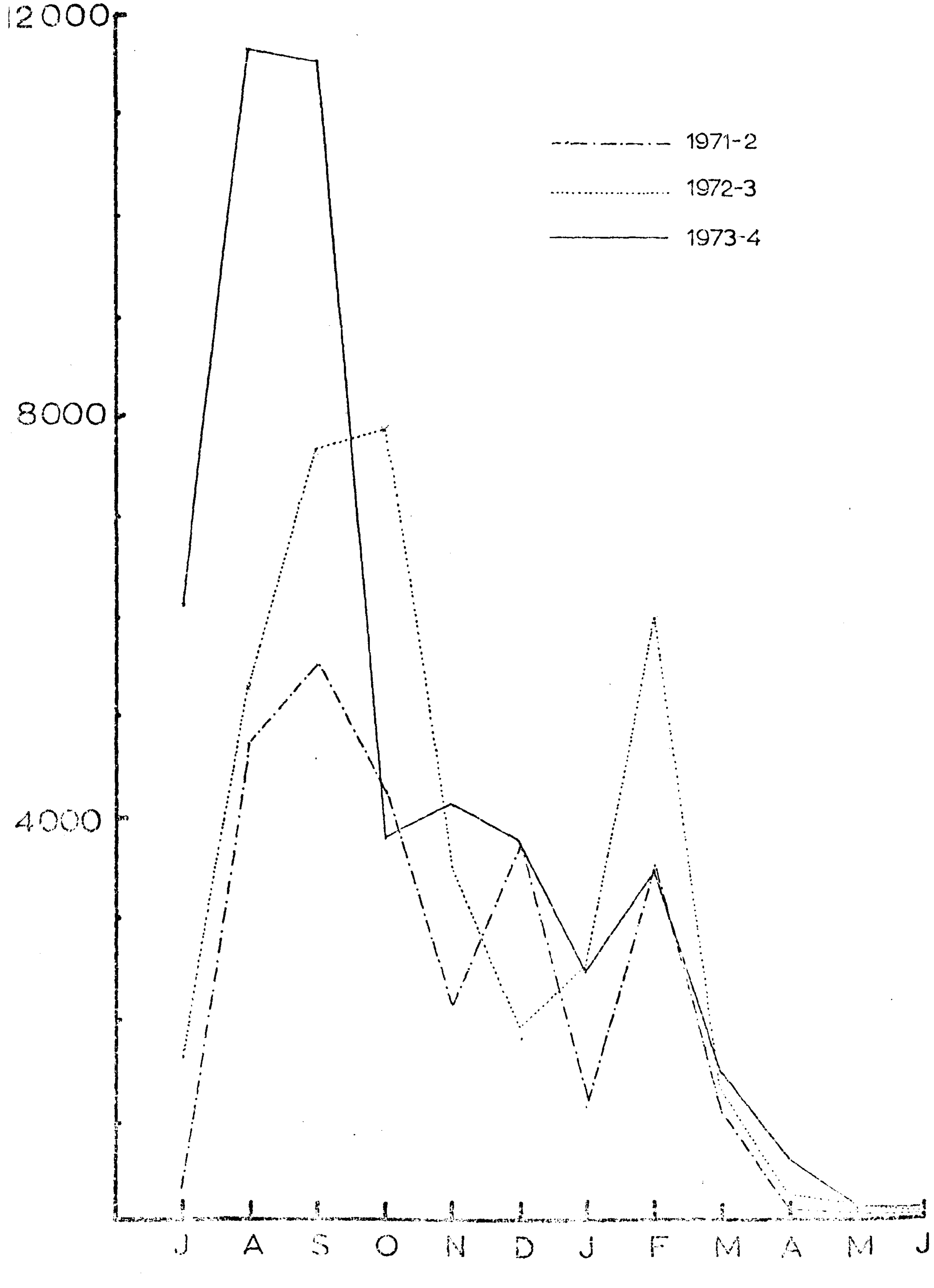
BAR-TAILED GODWIT

The Bar-tailed Godwit, an arctic and subarctic breeding species, is a very numerous passage migrant and winter visitor to the Ribble Estuary (Figure 6). The first autumn immigrants which arrive from late July are usually adults in breeding plumage, remaining on the Ribble until early September during which time they moult body plumage and flight feathers (some already arrive in primary moult). Many (an indeterminate proportion) of these move on and are replaced by influxes of juveniles and possibly also winter-plumaged adults during September and October. At this time the peak occurs, estimated in 1972 at about 12,000 on 16 September (49% of the September British total given by anon. (1973)). Numbers then decrease during November to a winter population which is swollen by an early passage in late January to early March after which there is a rapid departure with only the small number of summering birds remaining after April.

The autumn passage is similar in Morecambe Bay, whilst in some years there are suggestions that the birds which leave the Ribble in

Figure 6

Bar-tailed Godwit numbers on the Ribble Estuary 1970 - 1 to 1973 - 4 winters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1972-3
1973-4
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November may winter in Morecambe Bay (Wilson 1973). However, in N. E. England Evans (1966) traced a small adult passage in July - early August, the first main peak there consisting of the late August juvenile passage whilst adults in winter plumage pass through that area in late September - October. Spring migrations are similar except that in N.E. England Evans (1966) indicated the occurrence of a rapid passage of adults in May, about the same time that Morecambe Bay receives a small influx which summers (Wilson 1973). Holder and Wagstaffe (1930) also noted a spring passage on the Ribble during the 1920's (numbers of Bar-tailed Godwits on the south Ribble however were much smaller than present numbers "from 200 to 300 birds"). It would seem, therefore, that the strength and timing of movements may change to a large degree over the years.

REDSHANK

This species breeds commonly around the estuary on saltmarshes and wet farmlands (Greenhalgh 1969b, 1971, in press and Table 3) whilst small numbers (less than 100) of non-breeders summer along the shore. By mid-July nearly all the breeding population has left the marshes and joined with the first autumn migrants which arrive from early July, numbers building up to a peak in mid-August to September (Figure 7 and, data from Warton Marsh roost, Table 9). A rapid decline occurs from the peak through October and early November to a low population which remains through the winter into early March. During this period a variable proportion either roost or spend the whole day feeding inland (c.f. Oystercatcher and Curlew) and these are missed in censuses from the shore roosts. Unlike the Oystercatcher but as in the Curlew, some Redshanks remain inland in nocturnal roosts during mild full-moon periods (see Chapter III) though in frost and periods with less than about half-moon most Redshanks go to the shore at night. P. A. Greenhalgh and the present writer made estimates of these (1967 - 70) on the north Ribble whilst the present writer made similar observations on the south Ribble (1970 - 74): these are presented in Table 10.

In some years there are suggestions of a spring passage in February - March (Table 9) from the north Ribble though the Estuaries Enquiry has not found this (Figure 7). Generally, however, numbers decrease through March and early April leaving the few summering birds.

This decrease parallels the main return of breeding Redshanks to the saltmarshes and inland breeding areas.

The autumn Redshank passage on the Ribble is identical to that observed in Morecambe Bay (Wilson 1973) and N. E. England (Evans 1966), but spring passage is different in both areas for distinct peaks of passage have been noted in late April - early May in N. E. England (Evans 1966) and late March - early April (Wilson 1973) in Morecambe Bay. Both supposed that this movement was the return passage of the Icelandic Redshanks *robusta* which, from evidence of ringing and measurements, passes through and winters in Britain (Ogilvie 1963, Hale 1974).

TURNSTONE

This holarctic coast and tundra breeder, wintering south to Australia, New Zealand, South Africa and South America (Vaurie 1965), occurs in relatively small numbers on the Ribble compared with Morecambe Bay (Wilson 1973) and other similar areas. There can be no doubt that this is due mainly to the sparsity of suitable feeding habitat on the Ribble compared with these areas, the only *Mytilus* scar of any significance being the poor one at Fairhaven (Church Scar) and there is no stony habitat save relatively small sterile man-made ones (training walls by the river channel and sewage outfalls).

The monthly Estuaries Enquiry censuses (Figure 8) however, probably overlook many Turnstones for only the main wader roosts are counted and most Church Scar Turnstones roost on the beach close to the feeding area when this beach is not badly disturbed. For instance, in the years 1971 - 2 to 1973 - 4 there was no Estuaries Enquiry count of over 200 Turnstones (Figure 8) yet during visits to Church Scar up to 370 were recorded feeding. Data for 1967 - 70 are thus included to show more accurately the numbers feeding on the main area (Table 11).

Only very small numbers summer, the first migrants appearing from late June to July, adults up to 40% of which are in full summer plumage. Numbers build up through August and September to a peak in late September - October though in 1968, when very frequent counts

Figure 7

Redshank numbers on the Ribble Estuary
1971 - 2 to 1973 - 4 winters

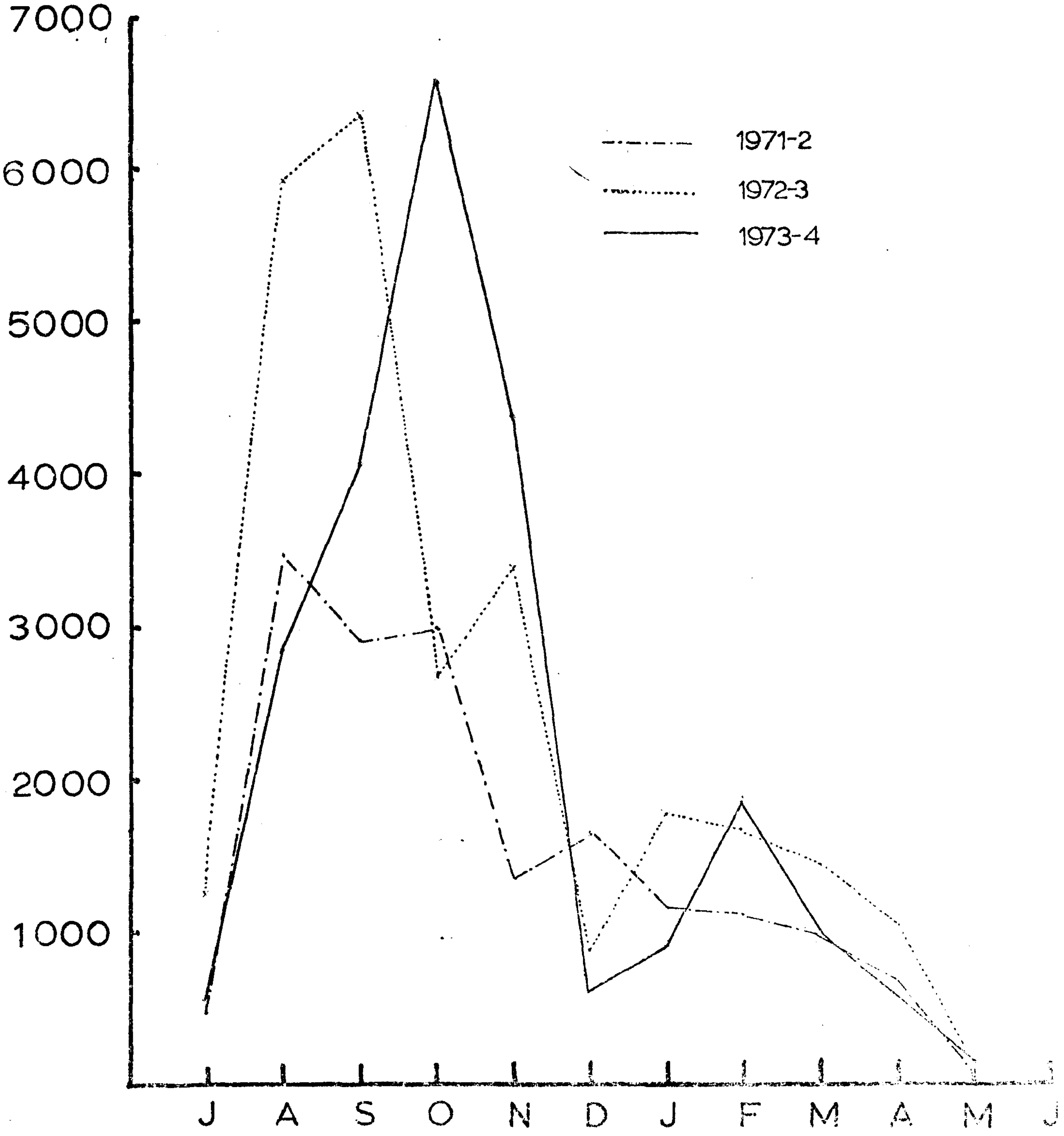
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Table 9 Redshank numbers on Warton Marsh roost, 1967 - 73

	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar
1967–8	6	500	1000	900	1300	900	–	–	570	–
1968–9	31	284	973	1108	740	209	218	193	406	69
1969–70	–	–	1185	620	54	50	38	91	387	480
1970–1	–	–	–	–	–	85	308	367	–	121
1971–2	26	–	2300	785	320	77	171	380	129	52
1972–3	–	–	2300	3450	–	–	80	–	–	260
1973–4	–	48	700	1847	388	–	65	100	350	200

Table 10 **Numbers of Redshanks feeding and roosting inland around the Ribble Estuary**

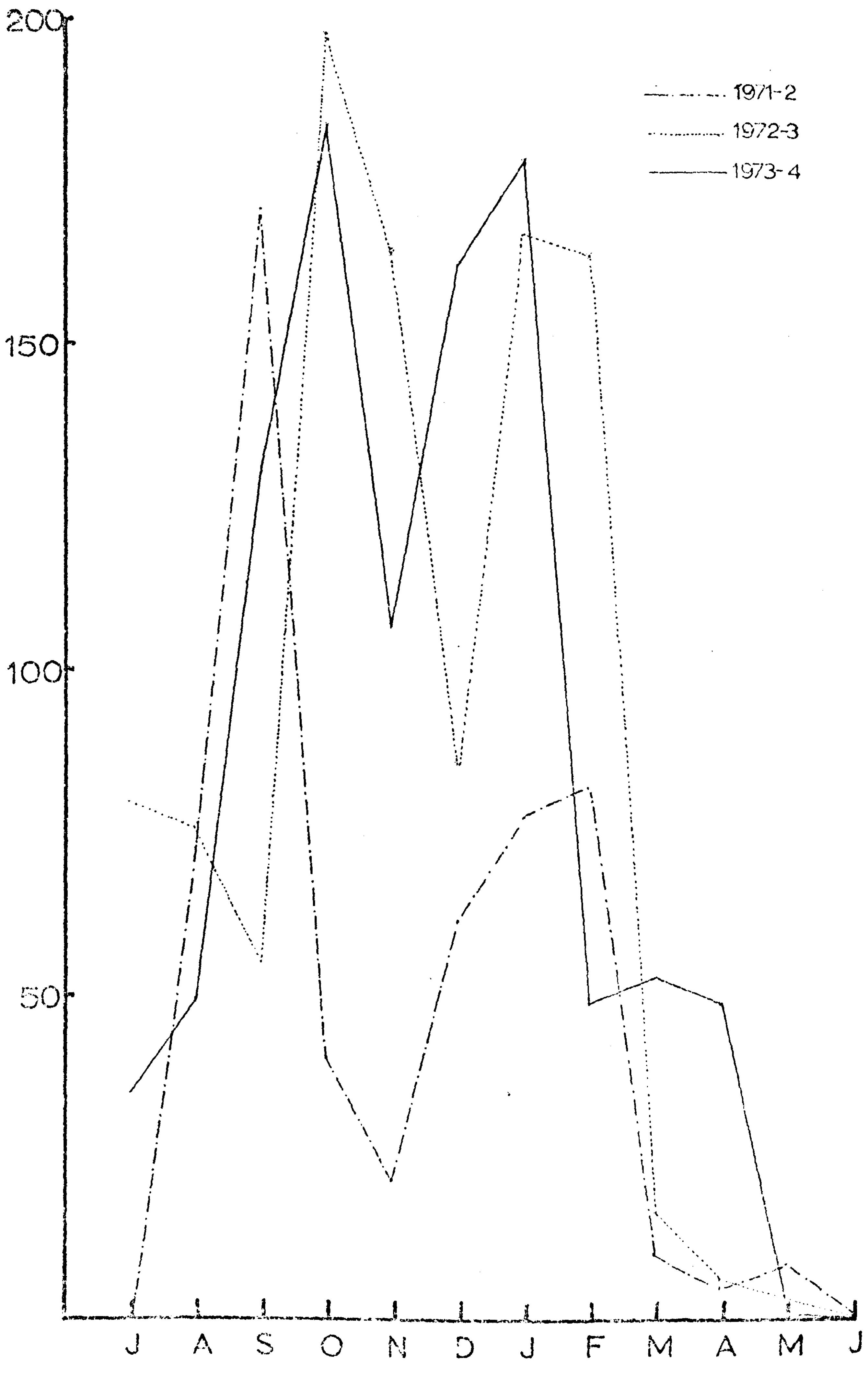
	Numbers feeding inland through day			Numbers feeding inland only at high tide			Numbers roosting at night inland		
	Mean	Range	N	Mean	Range	N	Mean	Range	N
North Ribble (1967 - 70)	127	5–540	68	62	29–260	68	82	19–394	11
South Ribble mosses (1970 - 74)	69	11–615	41	185	49–490	41	44	0–90	38
South Inner Marshes (1970 - 74)	32	20–155	53	-	3	18	-	-	-

Note: N = the number of counts made

Figure 8

Turnstone numbers on the Ribble Estuary 1971 - 2 to 1973 - 4 winters

(N.B. see text for validity)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1971-2
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Table 11 Monthly peak counts of Turnstones on the North Ribble, 1967 - 8 to 1969 - 70

	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May
1967 - 8	9	27	129	170	240	230	180	450	310	180	330	68
1968 - 9	4	39	258	260	270	210	130	260	311	137	321	95
1969 - 70	3	51	195	325	235	288	195	390	420	270	190	60

Note: these were counted on the feeding areas

Table 12 Weekly counts of Turnstones on the North Ribble, 1968

Weeks in

Jan				Feb				Mar				Apr			
1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4
260	-	210	220	153	246	311	106	-	137	128	-	321	-	-	-

Weeks in

May				Jun				Jul				Aug			
1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4
95	7	-	-	-	3	-	5	-	11	-	31	56	-	158	260

Weeks in

Sep				Oct				Nov				Dec			
1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4
191	104	113	-	-	260	270	-	205	-	210	-	-	160	-	130

were made (Table 12) peaks occurred in August and late September - early October, the first passage being the adults in full plumage or moult and the second being juveniles and winter-plumaged adults. Numbers decrease slightly through December with numbers again building up in January and February (possibly these are birds driven from northerly feeding areas by hard weather). A decrease during March is followed in some years (e.g. 1968 and 1969) by a short passage of adults in April, the last birds departing during early May.

KNOT

This species which breeds in Greenland, arctic Canada and arctic Russia (Vaurie 1965) is the most numerous (Table 2) and commonest in sheer weight of numbers throughout the year (Table 1 and Figure 9) of all the Ribble waders.

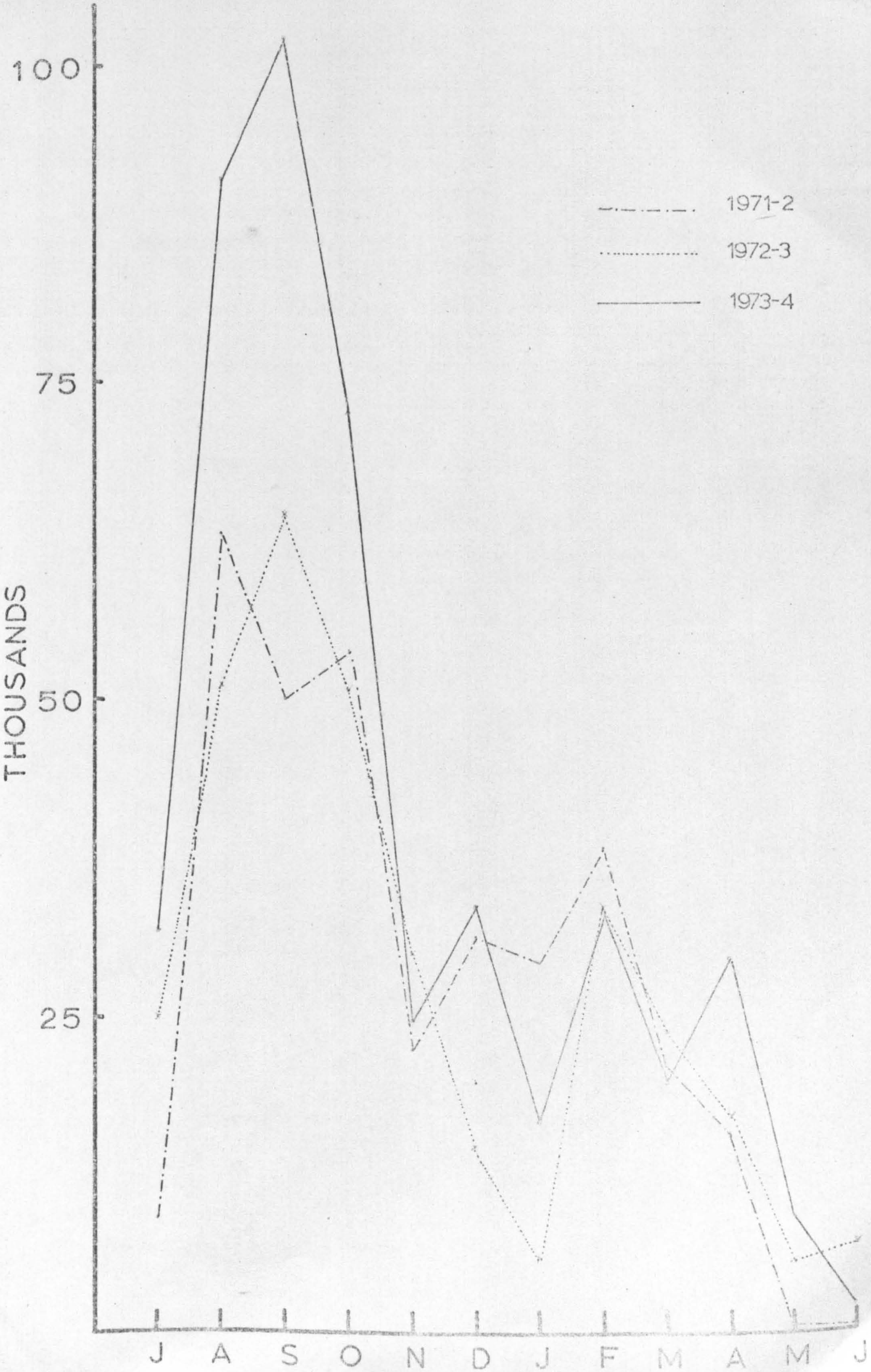
The 5,000 - 10,000 which summer is well over half the British summer population (anon. 1973). Some of these attain a trace of breeding plumage though most retain winter plumage. Then, from mid-July flocks of migrants, adults in summer plumage and mostly in body and flight-feather moult, arrive resulting in a large August - September peak. Many adults appear to move on after their moult but as they do so they are replaced by the juveniles and other adults already moulted into winter plumage from early September. Following this peak numbers rapidly decrease leaving the winter (November - January) population.

Similar passage has been recorded at several localities (e.g. Cambridge sewage farm (Nisbet 1957), N.E. England (Evans 1966)) though in Morecambe Bay the population increases as the Ribble Knot population decreases (Wilson 1973) recalling to some extent the situation in the Bar-tailed Godwit. Ringing has shown that at least some of the birds which have moulted on the Wash and Dee in early autumn winter in Morecambe Bay (Wilson 1973) as possibly do also some of the Ribble moulting population.

Spring passage begins from late January with a relatively small February - March peak and the last passage in April leaving the summering birds from May. In Morecambe Bay peak spring passage is later than on

Figure 9

Knot numbers on the Ribble Estuary
1970 - 1 to 1973 - 4 winters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1971-2
1972-3
1973-4

the Ribble, and is much larger (up to 95,000), falling in April - May.

SANDERLING

This arctic breeding species is one of the latest migrants passing through the Ribble in spring, there being a very strong late April - May peak, and one of the first to return with an autumn peak in July - early August (Figure 10). At these times Sanderlings occur all around the estuary, though from late September to late March most are concentrated on the outermost estuary in the Formby - Birkdale and St. Annes - Squires Gate areas. Fluctuations through this winter period are possibly due to birds from adjacent areas (Alt-Dee and Fylde coast) moving into or out of the Ribble to roost.

Though numbers are not as large as in the other two common calidrines, Knot and Dunlin, the number of Sanderling-days per year being about 10% of the Knot and Dunlin-days per year (Table 1) the 6,500 spring peak is 1972 was over 27% of the British 1972 spring peak (given as 23,794 by anon. (1973)) whilst the 1972 autumn peak of 9,450 on the Ribble was larger than the peak 1971 Sanderling count for the whole of Britain (anon. 1973)! Furthermore, if Spitz (1969) estimate of the European (including Britain and N. Africa) wintering population of 7,400 is correct then the Ribble area holds up to 37% of this, for a winter maximum of 2,750 was counted in January, 1972.

DUNLIN

In terms of bird-days per annum the Dunlin rivals the Knot as being the most abundant wader on the Ribble (Table 1) though the Dunlin peak is never as high as that of the Knot (Table 2).

Dunlin numbers on the Ribble show an almost identical pattern to that recorded by Wilson (1973) from Morecambe Bay. Autumn passage begins in July resulting in a peak in early August - early September. These, shown by Wilson to be either *schinzii* or *arctica* are mostly in full summer plumage when they arrive and during their stay on the Ribble they moult some body plumage and flight feathers. During September and early October these depart and are replaced from mid-October

Figure 10

Sanderling numbers on the Ribble Estuary 1971 - 2 to 1973 - 4 winters

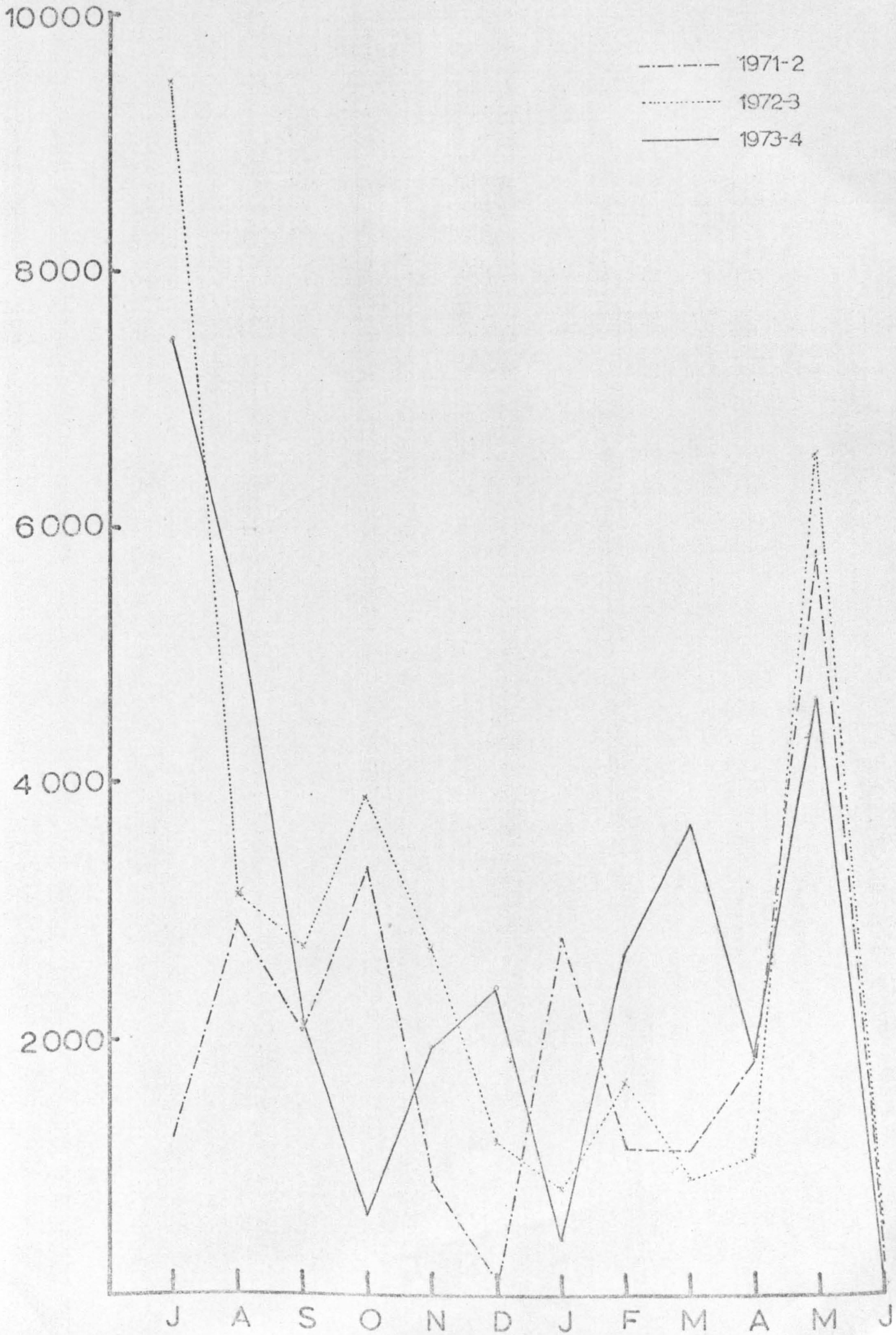
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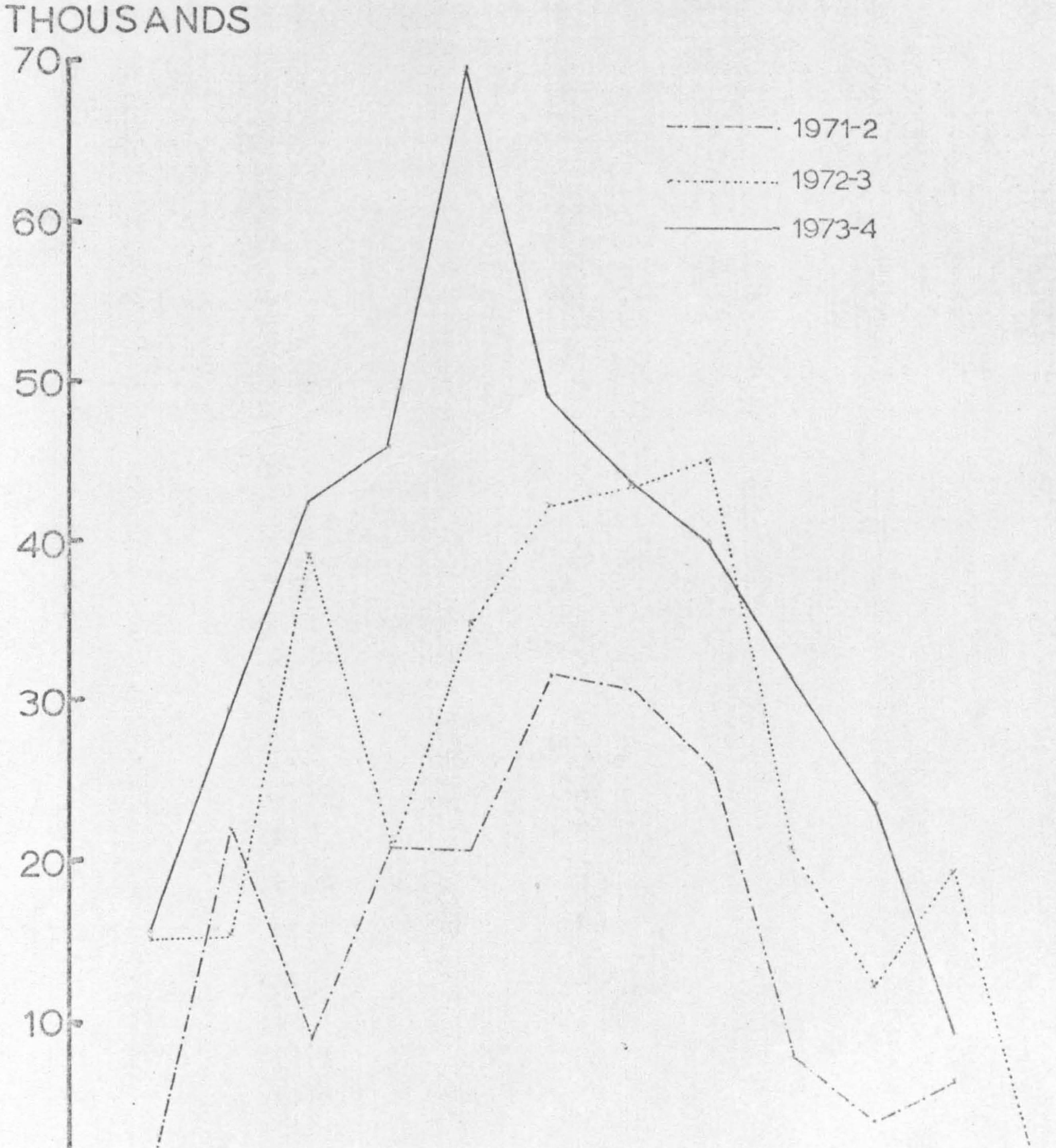
Figure 11

Dunlin numbers on the Ribble Estuary
1971 - 2 to 1973 - 4 winters


THOUSANDS
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1971-2
1972-3
1973-4

by winter-plumaged adult and juvenile Dunlins, ascribed to _alpina_ by Wilson (1973). These form the large winter population, peaking in December - February. Numbers then decrease during March and early April whilst in late April - early May a short but clear passage occurs of summer-plumaged birds (according to Wilson (1973) the returning _arctica/schinzii_ which have wintered from Iberia southwards).

Figure 11 shows this pattern from the roost counts, whilst from the Inner Marshes the August - September and April - May peaks can be discerned but not the winter peak (Table 13).

One or two pairs of Dunlin breed in most years on the saltmarshes of the Ribble Estuary (Greenhalgh 1969b).

Discussion

The importance of the Ribble Estuary to waders falls into three main categories:

1. _Moulting Ground_ - it provides feeding for large numbers of adult waders on their post-nuptial moult in July - September, the following species being involved at the Internationally important * level: Black-tailed Godwit _islandica_, Bar-tailed Godwit, Knot and Sanderling, and at the Nationally important * level: Redshank and Dunlin. Many of these depart after the moult though in some cases the birds which have moulted here and departed are replaced by birds which have already moulted elsewhere.

2. _Wintering Ground_ - internationally important populations of Sanderling and Dunlin winter in the area whilst the populations of Grey Plover, Bar-tailed Godwit and Knot are of national importance.

3. _Passage area_ - in autumn, internationally important numbers of Black-tailed Godwits _islandica_ and Bar-tailed Godwits, Knot and Sanderling occur whilst the peaks of Grey Plover and Dunlin are nation-

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* Importance is classified as 'International' if the Ribble population reaches 5% of the European, and 'National' if the Ribble population reaches 10% of the British total, after Spitz (1969) and anon. (1973).

Table 13 **Totals of monthly peaks of Dunlins on the Inner Ribble Marshes, 1963 - 69**

Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
180	210	470	2,370	1,360	31	920	2,060	210	425	290	120

ally important.

In spring the peaks of Grey Plover and Sanderlings are internationally important whilst the Dunlin peak is of national importance.

The Ribble Estuary is also of national importance for three saltmarsh-farmland waders not considered here: Lapwing, with a mid-winter peak of up to 14,000 (Greenhalgh 1973 unpublished M.S.), Golden Plover, with a spring altifrons peak of over 3,000 (Greenhalgh in press) and Ruff, with an autumn and winter regular population of over 100 and peak of 176 (Greenhalgh 1967, 1971).

There is no doubt, therefore, that for waders the Ribble overall is of great International importance. However, as has been indicated in the previous section, the Ribble should not be considered in isolation. Other British estuaries are used to a large degree by the main British waders: the Ribble autumn Black-tailed Godwits probably winter on the Dee, many autumn Bar-tailed Godwits probably move to winter in Morecambe Bay as do probably many of the adult Knot which moult in August and September on the Ribble. Data available from ringing returns show connections between the major British wader estuaries: Wash, Dee, Morecambe Bay and the Ribble for most species which have been ringed in any numbers. It may well be that all these areas must remain intact if present wader stocks are to be maintained. The same applies to wintering areas for Sanderlings and some Dunlins, etc. further south in Iberia and Africa and to the stopping-off and moulting grounds used by many species in Fenno-Scandinavea, for the pressure put on these areas by Man is sure to increase.

Most waders, it appears, require a series of stopping-off areas including moulting and wintering areas on their migrations between breeding seasons. The Ribble is just one of the links in this chain of important areas.

CHAPTER III THE DIURNAL CYCLE OF WADERS ON THE RIBBLE ESTUARY

There are two main external factors which might affect the amount of time that is available to waders for feeding which may interact and upon which other factors might apply:

1. Solar Cycle: in mid-summer (21 June) at this latitude the hours of darkness (sunset to sunrise) last for 6 hours 59 minutes whilst in mid-winter (21 December) darkness last for 16 hours 31 minutes. One might expect waders to be able to spend less time feeding as daylength shortens in winter. However, many (if not all) species make use of moonlight when the moon is greater than half-phase and feed to some extent at night.

2. Tide Cycle: at approximately every 12 hours 20 minutes is a period of high water alternating with a period of low water. The height which the tide reaches up and ebbs down the shore varies daily depending upon the position of moon and sun. On neap tides large areas of sand and mud are exposed at high water, whilst at high water spring tides little if any substrate is exposed and, with a westerly wind, even the salt-marshes may be flooded, though at neap low water less substrate is exposed than at low water spring.

At high water waders are generally excluded from the intertidal feeding grounds though on neap tides some may remain.

During the winter months when daylight is short, effects of tide cycle may cause a great deal of variance in the light hours available for feeding. At one extreme, with high water at about 0600 and 1820 hours G.M.T. when it may still be dark, the whole of the daylight period will be available for feeding whilst when high water occurs between 1100 and 1300 hours the light hours available for feeding will be reduced by up to 60% depending upon the species of wader and height of tide.

By feeding inland either during the hours of high water or throughout the day some members of some species (mainly Oystercatchers, Curlews and Redshanks) avoid losing feeding time. Otherwise lost feeding time must be made up by feeding at night.

This chapter presents the results of investigations into the amount of time spent in feeding and in other activities by the major wader species on the Ribble Estuary.

Methods

Observations were made of the length of time the birds spent at the roost by recording the numbers present in the roosts at half-hourly intervals from the time of the first arrivals at roost to the last departures. At roosts not easily counted at such intervals (e.g. Warton and Banks Marsh roosts) the numbers passing in and out of the roost every half-hour interval were counted. The extent of feeding, preening and other activities at the roost was noted as was also the tide height on that particular day. This information was obtained from the whole range of tide heights, though with more counts being made on spring tides rather more data were obtained on such tides. From these it was possible to calculate the amount of time per tide cycle (taken in calculations as 12 hours) spent roosting by all the wader species for each category of tide heights.

It was clear that provided they were not prevented by tide conditions, waders generally spent daylight hours feeding or at least on the feeding grounds. However, it was important to obtain some idea of the extent of feeding during periods of darkness and this was done in three ways:

1. Direct observation: provided that cloud was not covering the moon, during full moon periods it was possible to walk across the mudflats and watch waders directly, using binoculars (8.5 x 44) from up to about 30 metres (depending upon species). Approach to this distance usually resulted in some disturbance and so results comparable with daylight observations at 50 - 100 metres using a telescope could not be obtained. However, it was clear that many birds were feeding and attempts were made to estimate the feeding rates.

2. Collected birds: under conditions that it was possible to make direct observations (above), confirmation of these observations was obtained by shooting samples of as many species as possible and examining gut contents. This was a somewhat difficult task and few birds were obtained.

3. During the periods when the lunar phase was less than half, or during periods of heavy cloud which obscured the moon, it was impossible to see the birds at night. The birds were clearly not on the high tide roosts, save at high water and they rapidly left them as the tide ebbed presumably either to feed or avoid mammalian predators which frequented most roosting areas (foxes _Vulpes vulpes_ at Crossens, domestic cats at Squires Gate and Fairhaven, and possibly occasional otters _Lutra lutra_ and feral mink _Mustella vison_ which occurred from time to time around the estuary). Walks across the feeding areas showed the birds to be there.

In an attempt to gauge the extent of feeding under such conditions, mist-nets were errected across the main feeding areas of the south Ribble (mainly Crossens Pool and Banks Sands) to collect birds moving across the feeding areas. Many birds were caught and some killed (under N.E.R.C. Licence) and the gut contents analysed.

Results

1. High Water Roosts

Table 14 gives the mean number of minutes spent by each major species in high water roosts on the Ribble at the whole range of tide heights experienced on the Ribble. Some data are lacking on the lower tide ranges, for it is very difficult to obtain realistic measurements of roosting time with the birds spread along the tide edge.

In most cases the variance in roosting time was great, though impossible to state in statistical terms because a) the roosting times of individual birds was not known, b) estimates of flocks, often very large, were involved and c) timings were made at only every half hour and thus exact roosting times were not known. The situation is complicated further by the fact that different methods of data collection had to be employed at different roosts (see above), birds at some roosts were affected by disturbance (horses, dogs, wildfowlers) and that the tide did not always (or often) make exactly the predicted height due to weather factors.

Figures 12 a, b and c give the general locations of the main wader species on the sand roost at Squires Gate, the sand-mud roost at Crossens and the saltmarsh roost at Banks. These show well the characteristic separation between the species in the roosts.

OYSTERCATCHER

This species spends more time at roost than any other though a high proportion may feed inland (chapter II) either through the day or just at high water. On the Ribble, however, the time spent in roost is much less than that by Oystercatchers in Morecambe Bay which roost for at least 120 minutes at every high tide besides spending up to 60% of the low tide period at 'intermediate sand roosts' (Drinnan 1958, personal observations). This is probably due to the greater abundance of Oystercatcher foods in Morecambe Bay, noteably *Macoma balthica*, *Cardium edule* and *Mytilus edulis* (Dare 1966, Anderson 1972) and the Oystercatchers can generally obtain the daily food requirements in less time than they need on the Ribble (Dare *in litt.*, personal observations).

Even so, most Oystercatchers roost on the Ribble to almost half-ebb (on higher tides) before moving across the higher exposed sandflats to the main feeding areas on the lower shore. The tendancy which this species has of lingering at the roost suggests that the energy it would expend in attempting to find food whilst following the ebbing tide (as do Dunlins for example) would not be adequately repaid by the prey obtained, and thus the birds wait until the richer lower feeding areas are exposed by the tide.

The Oystercatchers which feed on *Mytilus* in Morecambe Bay roost for less time on neap tides than spring tides, as do the Ribble birds (on a 7-metre tide 149 ± 21.2 minutes and on an 8.8 - metre tide

Table 14 Mean time (in minutes) spent in roosting by waders at various tide heights (actual) on the Ribble Estuary

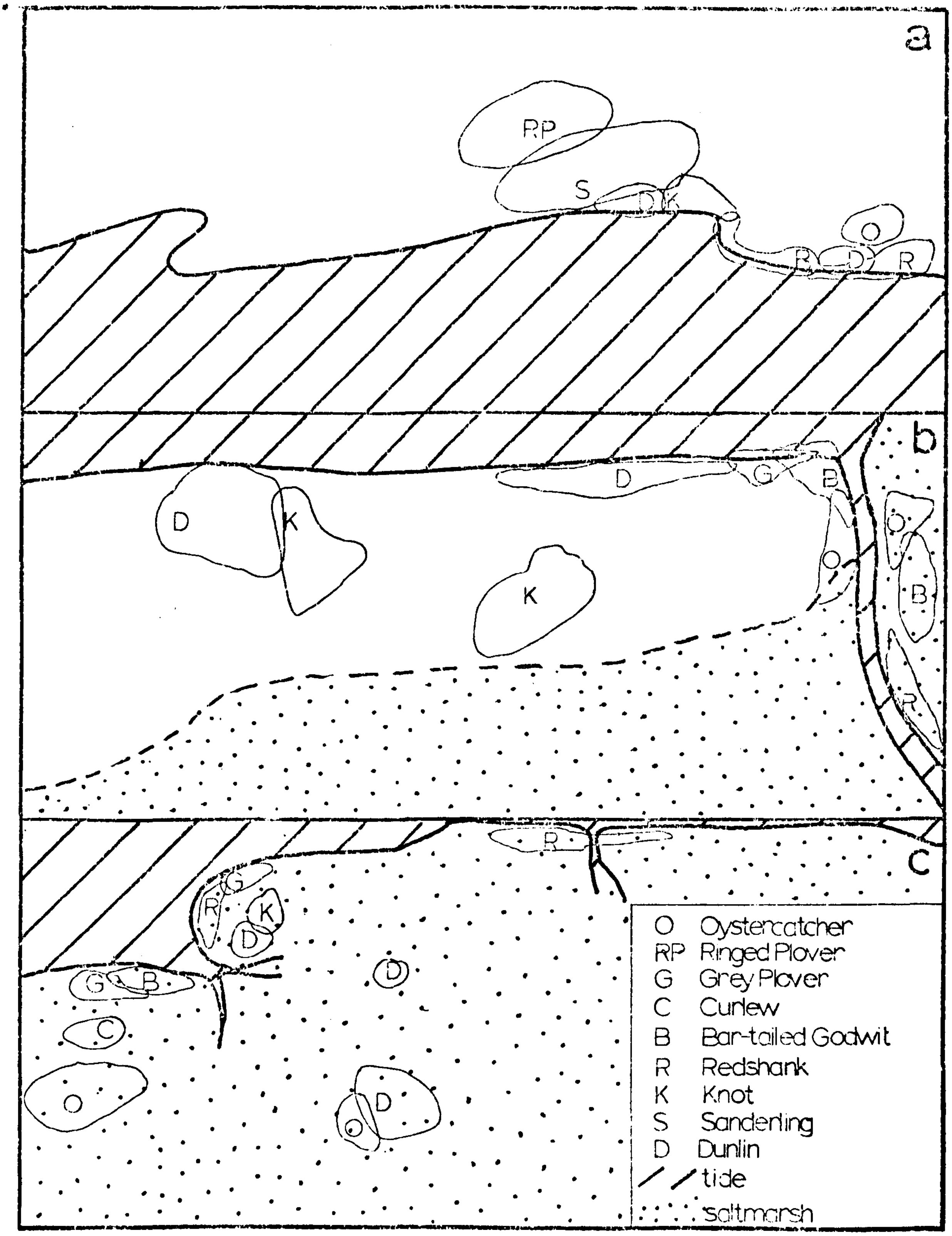
	Height of tide (in metres)										
	7.3	7.6	7.9	8.2	8.5	8.8	9.1	9.4	9.7	10.0	MEAN
Oystercatcher	102	83	115	166	197	184	248	244	316	318	184
Turnstone	–	–	27	91	73	101	195	182	176	209	136
Curlew	–	–	–	–	143	176	234	221	236	270	178
Black-tailed Godwit	–	109	–	148	–	188	261	276	288	307	191
Bar-tailed Godwit	–	89	–	92	–	156	167	178	226	251	162
Redshank	0	0	*	67	100	145	139	200	191	214	141
Knot	!	!	43	69	148	167	180	185	230	245	155
Dunlin	!	!	!	61	119	118	114	130	188	220	112
Sanderling	!	!	!	12	35	52	88	121	157	142	87

* less than 15% roosted for between 18 and 28 minutes

! no real roosting, just loose associations at the tide edge

Figure 12

Locations of the main species in the wader roosts at a) Squires Gate, b) Crossens and c) Banks Marsh


a
RP
S
D
K
O
R
D
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b
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G
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O
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B
R
c
R
G
R
K
D
G
B
D
C
O
D
O
O Oystercatcher
RP Ringed Plover
G Grey Plover
C Curlew
B Bar-tailed Godwit
R Redshank
K Knot
S Sanderling
D Dunlin
tide
saltmarsh

271 ± 29.8 minutes). On spring tides the Mytilus beds are exposed for less time than on neaps, but the tide ebbs further exposing high densities of younger mussels which remain covered on neap tides. By waiting for these rich young mussels to be exposed the Oystercatchers can quickly obtain their daily requirement whilst on neap tides they take more time to obtain the same amount of food on the higher poorest mussel areas (see chapter VIII).

Oystercatchers generally occupy a position high on the roost either in ranks at the rear of the smaller waders or as a separate roost on the saltmarsh. It is rare for this species to feed at a shore roost.

As shown in chapter II, a proportion of shore-feeding Oystercatchers roost inland and the data in Table 16 have included these. A certain amount of feeding occurs on such roosts, particularly if the roost is also used by Oystercatchers feeding thoughout the daytime.

TURNSTONE

This is a species which generally roosts as close to its feeding site as possible and moving off these only when forced to do so by the tide. Thus, on a 6.5 - 7.0 metre tide when Church Scar is not completely submerged, the birds roost there at the water's edge where they may continue feeding.

On the highest tides, when all feeding areas are covered, Turnstones roost for longer periods, often on roosts well away from feeding areas (e.g. St. Annes and Blackpool piers, on saltmarshes). They may remain there to late ebb and then leave for the lowest feeding areas, ignoring the higher feeding areas used on neap tides (c.f. Oystercatchers).

CURLEW

Most Ribble Curlews roost with the Bar-tailed Godwits on Banks Marsh, moving into and out of the roost with the godwits. On the lower tides, however, a distinct Curlew roost is only occasionally formed and it is possible that on such tides more Curlews tend to remain inland rather than feed on the shore. However, the situation on all tides is confused by a movement of Curlews from inland feeding areas onto Banks Marsh around mid-day (thus coinciding with the higher tidal range) and some birds remaining on the marsh throughout the day, roosting.

The inland origin of many Curlews roosting on Banks Marsh has been confirmed from pellet analysis and gut contents (chapter V).

BLACK-TAILED GODWIT

In a previous paper (Greenhalgh 1973) the roosting of Black-tailed Godwits on higher tides was described. As the main feeding areas occur very close to the low tide mark this species tends to roost for much longer than Bar-tailed Godwits, which feed on higher sandbanks. Thus, Black-tailed Godwits leave the main feeding areas about three hours after low tide, as they are flooded by the tide, and form 'intermediate sand roosts' in a similar manner to Oystercatchers in Morecambe Bay. Like this latter species, on the highest spring tides (8.5 metres or more) Black-tailed Godwits remain in roost late into the ebb.

On lower tides this species still roosts for much longer than most other waders, though for much less than they do on spring tides.

BAR-TAILED GODWIT

This species is fairly consistent in roosting pattern, usually most birds arriving at and departing from the roost on the higher tides (8.5 metres or more) within a very short space of time (± 5 - 8% of the mean time of arrival) whereas in most other species arrival and departure are more staggered.

On lower tides roosting times are more variable though on even the lowest tides all Bar-tailed Godwits roost over the high water period.

REDSHANK

Generally, the feeding areas for this species (chapter IV) are fairly high on the shore and consequently only higher tides (8 metres or more) affect all Redshanks to any great extent. On the lowest tides virtually all Redshanks continue feeding, following the tide up the shore, whilst on tides between about 7.5 metres and 8 metres only the Redshanks which feed on the lowest feeding areas roost, the others continuing to feed. There are some indications on these medium-low tides that more roosting occurs on rising tides, (i.e. those building up to the spring peak) compared with falling tides. Possibly this is due to a higher proportion of the food in the mudflat being available on falling tides, when the mud remains wet, whereas on rising tides the mudflats are often hard and dry.

On higher tides the Redshanks form loose packs in Spartina on Warton Marsh and around Crossens Pool - Banks Marsh whilst a variable proportion also roost on the fields behind the shore (see chapter II). These latter may continue feeding.

KNOT

On the lowest neap tides (up to 7.6 metres) no real roosts are formed, many birds (estimates varying between 20% and 45%) continuing to feed. Tides above about 8 metres exclude Knot from their main feeding areas and then definite roosts are formed, the higher the tide the higher the roost until, on tides exceeding 9 metres the roosts may extend onto the saltmarshes. Generally, when roosting on saltmarshes Knot (as well as the other calidrines Dunlin and Sanderling) prefer the lower grazed grass to the Spartina - Aster zones used by godwits and Redshank.

Whereas Knot arrival at roost is staggered over an hour or more, departure is very rapid, the birds leaving in two to five large flocks. This pattern is closely related to feeding pattern (chapters IV, V and VIII).

DUNLIN

Though most Dunlin enter a 'roost' (in the case of this species, a congregation of birds above the high water mark) on tides of 8 metres or more, even on the highest tides a proportion continues to feed, though at a reduced rate (chapter VIII). On tides above 9 metres in which the birds still remained on the mudflats and were not forced onto the marsh top, sample flocks were scrutinised and the number feeding estimated (Table 17). Overall 21.7% of Dunlins were seen to be feeding at any one time though it was observed that some birds would stop feeding for several minutes, suggesting that a higher percentage fed to some extent at high water.

It is clear from Table 15 that the proportion feeding at high water in winter (32.1% in November - February) was higher than that in autumn (11.1% in August - October) and spring (3.1%). This may possibly be a reaction to the reduced daylength in winter, the birds attempting to compensate by feeding over the tide. However, from November - February data (Figure 13) the amount of feeding at the roost appears to be related with mud temperature, especially at mud temperatures below 3°C.* This reduction of feeding at low temperatures may be a result of less food being available in the surface of the mud at low temperatures.

Dunlins also continue feeding up the shore with the tide, unlike most other species which head to the roost as soon as the major feeding grounds are covered by the tide whilst usually they immediately begin to follow the tide down as it ebbs. The only exception to this is when the tide forces the roost onto saltmarsh, the birds feeding less and often remaining until a large area of mud is exposed. The roost breaks up gradually in such circumstances. Thus, the Dunlin roosts for less time than most waders besides being conspicuous in continuing to feed over most high tide periods.

SANDERLING

As with the Dunlin, on tides of less than about 8 metres Sanderling fail to form proper roosts, continuing to feed along the tide's edge or forming loose congregations which may include sleeping birds. On tides between approximately 8 and 8.5 metres a small proportion of birds roosts, the rest continuing to feed by the tide: this is illustrated by the small mean roosting times on such tides. With tides over 8.5 metres however, most birds form roosts where up to 85% of the Sanderlings sleep over the high water period.

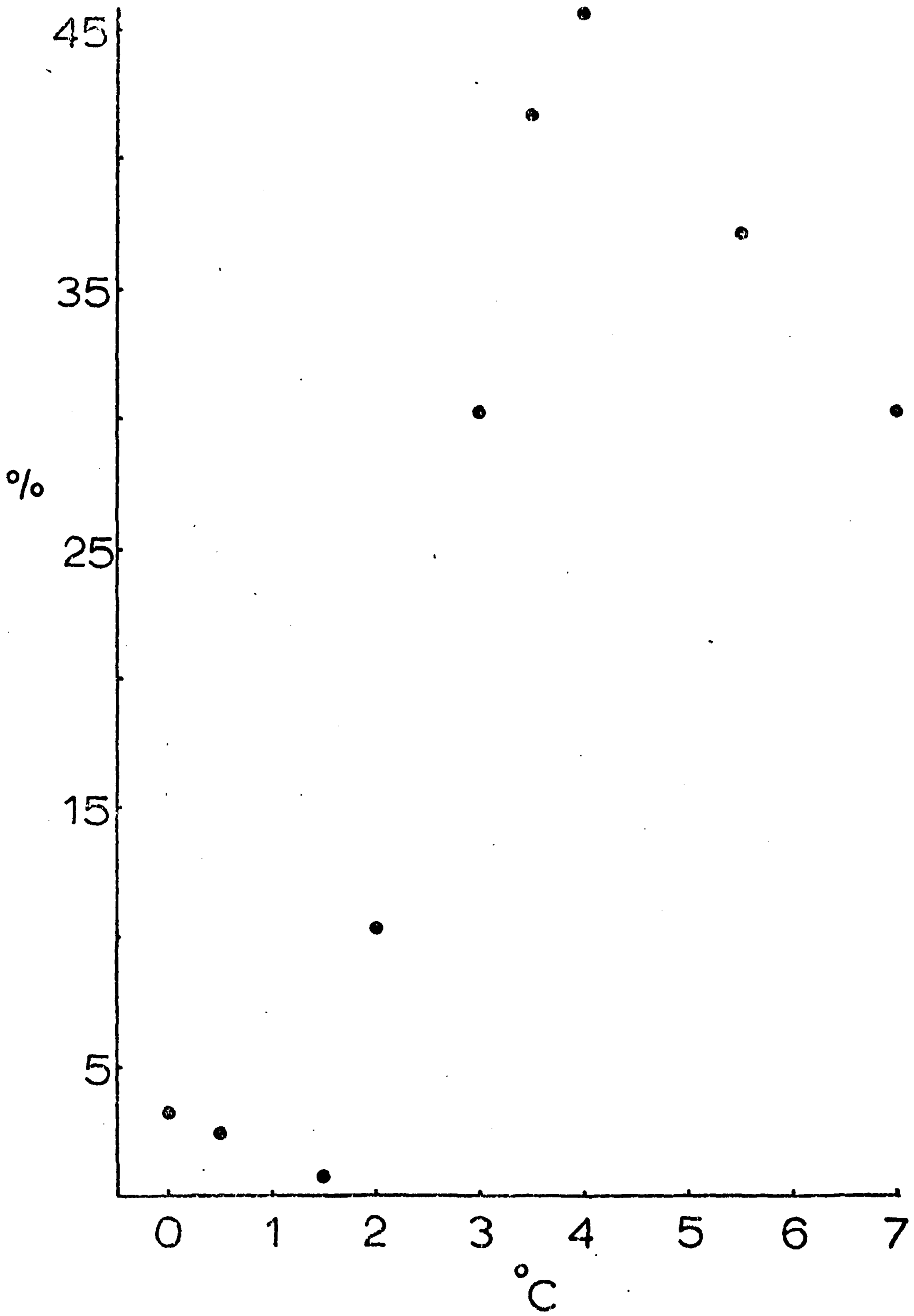
*The regression coefficient is 0.71098, the slope 5.38571 and the intercept 5.66507 for 7 degrees of freedom. The relationship between temperature and feeding is significant (P = 0.05).

Table 15 Numbers and percentages of Dunlins feeding at high water roosts (Crossens - Squires Gate)

	Number Observed	Number Feeding	% Feeding
August	14,350	1,145	8.5
September	11,400	920	8.1
October	9,200	1,800	19.6
November	13,950	5,150	36.9
December	17,000	4,860	28.6
January	21,500	7,420	34.5
February	8,400	2,040	24.3
March	2,600	35	1.4
April	3,250	120	3.7
May	2,180	94	4.4
Overall	103,730	22,584	21.7

Figure 13

The percentage of Dunlins feeding during the high water period at Crossens roost, in November - February, in relation to mud temperature (°c)


45
35
25
15
5
%
0
1
2
3
4
5
6
7
°C

The main Sanderling roost at Squires Gate is badly disturbed by humans and consequently the birds rarely spend the high water period on one site. They tend, therefore, on the highest tides to form a compact roost only when forced to do so by the tide, and the roost breaks down quickly with the ebb. It may be that, given a relatively undisturbed roost site the Sanderlings would spend more time in roost. As it is, they spend on average less time roosting than any other species.

2. Activities on the inter-tidal zone

There were five main categories of activity carried out by waders on the intertidal zone and an attempt was made to estimate the amount of time spent on the intertidal zone in each of these by all species. This was done in a very crude way in January - February and August - September 1971 by observing selected groups of the major species for long periods and noting the time spent by individuals within these groups in the various activities. The data obtained are presented in Table 16: whilst they are not as comprehensive as could be hoped for, probably they give a good indication of the actual state of affairs.

a) Sleeping: some species slept frequently at certain stages of the tide cycle, noteably Oystercatchers and Godwits, and it is possible that such behaviour was in some way connected with 'intermediate sand roosts' and thus part of the roosting cycle.

Curlews slept for the longest periods and it seems likely that these were inland feeders which has spent the previous night feeding and were sleeping on the shore prior to returning to the fields (see section on roosting in Curlew (above) and chapters IV and V).

b) Preening: an occupation usually carried out in the roost but also indulged in on the feeding areas, mostly as the tide was flowing and feeding intensity decreasing (chapter VIII).

c) Movement: this category excludes walking whilst feeding, including flights across the feeding areas, besides walking when the bird was not searching for food. Knot and Dunlin spent the most time in such movements, probably because of the complex routes they take around the feeding grounds (chapter IV). By contrast, Turnstones and Black-tailed Godwits, having the most confined feeding areas had least movement.

Table 16 The percentage of time spent in five main categories of activity by waders on the intertidal zone of the Ribble Estuary

	Sleeping	Preening	Movement	Display	Feeding	No. birds
Oystercatcher	14	2	3	1	80	79
Turnstone	6	3	1	1	89	51
Curlew	31	5	2	0	62	27
Black-tailed Godwit	12	3	2	0	83	114
Bar-tailed Godwit	9	2	4	1	84	302
Redshank	2	1	2	2	93	48
Knot	5	2	8	1	84	2,156
Dunlin	3	1	6	1	89	1,980
Sanderling	4	1	3	1	91	377

d) Display: this included time spent in communication (aggressive or sexual) with others of the same species. In general this was extremely small, with the exception of the Redshank some individuals of which spent up to 9% of the low tide period in late February in display. Recher and Recher (1969) described this aspect of wader ecology out of the breeding season in North America, similarly finding that very little time was taken up in inter- and intra- specific displays.

3. Night-feeding

Observations on night feeding are best considered under two headings, those made on nights when the moon was full and sky clear and those made when the moon-phase was around 'new' or when the lunar-phase was less than half and sky heavily overcast.

a) Moonlit nights.

Six species were observed from close range through binoculars at full moon on clear nights and all were seen to be feeding on the main feeding areas. Gut contents were examined from specimens of three species,

OYSTERCATCHER

Feeding rate on *Mytilus* on Church Scar was estimated at 49% of the daylight rate, mean ingestion rate 22.2 ± 7.1 per hour (n = 41) compared with a mean of 45.04 ± 6.9 (n = 580) in daylight.

The night feeding rate on *Macoma* was lower, 19% of the day rate, with a mean ingestion rate of 27.3 ± 8.2 per hour (n = 56) compared with 144.4 ± 16.7 per hour (n = 1,692) in daylight. Both differences are significant ($p < 0.001$).

BAR-TAILED GODWIT

Full-moon night feeding rate was observed in the Fairhaven Bay area of Salter's Bank where, in daylight, the mean peck rate is 13.1 ± 2.4 pecks per minute and the number of probes 2.96 ± 0.21 per minute. Both these were estimated for night feeding, the mean peck rate being 12.6 ± 1.8 (n = 110) and the probe rate 1.83 ± 0.31 (n = 142). Whereas the difference between peck rates is not significant, the difference between probe rates is significant ($p < 0.001$). However, as ingestion rate (ie swallowing rate) appears to be correlated with probe rate rather than peck rate (chapter VIII) in this species, these data do suggest that the feeding rate of Bar-tailed Godwits on moonlit nights is about 62% that of the daylight rate.

Though no gut contents were obtained, knowledge of the site and prey seen suggested that most food taken was Nereis diversicolor.

REDSHANK

This species was too easily disturbed to yield any satisfactory data by direct observation. However, three guts were obtained from the upper feeding zones of Horse Bank which contained a mean of 52.3 Hydrobia ulvae (47, 51 and 67) and 2.7 Corophium (4, 2 and 2). In this area, guts collected in daylight (chapter V) contained a mean of 18.1 Hydrobia and 53.8 Corophium.

These data, though very small, suggest that even under the most favourable nocturnal conditions food intake is approximately 75% that of daytime and that diet changes from the more active burrowing Corophium to the surface dwelling Hydrobia. Goss - Custard (1969) similarly noted that Redshanks on the Ythan Estuary fed mostly on Hydrobia(and other surface-dwelling gastropods) at night.

KNOT

Estimates of feeding rate on moonlit nights were obtained at two sites on Horse Bank. At the first Knot feed in daylight mostly on Hydrobia and, to a very small degree, Corophium with a peck rate of 80.4 ± 7.9 per minute (chapter VIII). At night the mean peck rate was estimated as 42.7 ± 11.8 (n = 30), though pecks were not as clear as in daytime, the bill being scooped through the substrate surface rather than stabbed with clear pecks. The one bird collected at this site held 17 Hydrobia and three Macoma in the gizzard.

Similar measurements were made on a lower Macoma - rich area, peck rate averaging 3.9 ± 1.2 (n = 27) compared with 28.5 ± 6.3 in daylight. One bird collected here had a gizzard content of nine Macoma.

These suggest that on moonlit nights the feeding rate of Knot is reduced, roughly 55% of the daytime rate when feeding on Hydrobia and 15% of the daytime rate when feeding on Macoma. Prater (1972) found a similar reduction in food intake in Knot feeding at night on Macoma in Morecambe Bay.

DUNLIN

Observation was possible from close range only on Lytham shore, elsewhere disturbance being too great. The mean peck rate at night was estimated at 51.0 ± 14.0 (n = 32), about 70% of the daytime rate of 71.3 ± 9.1 for the same area.

Three birds were collected, their guts containing a mean of 36.9 food items (total of three Corophium and 108 Hydrobia). This is 68% of the mean content of 54.0 items from birds collected at the same site during daylight, but as with Redshank the Corophium, Nereis and Macoma fractions were greatly reduced and the Hydrobia fraction increased.

SANDERLING

Estimates of peck rate were made at night at Squires Gate, the mean of 38.5 ± 5.2 (n = 60) being significantly lower than the daylight rate of 59.4 ± 9.4 ($p < 0.001$), suggesting a moonlit night feeding rate of about 65% of the daylight rate.

b) Moonless nights.

Gut contents were analysed from four species collected in mist-nets on moonless nights: in all cases these were at new moon, for with any significant moonlight waders can see mist-nets and avoid them. Only birds taken from the nets immediately after capture were killed, for birds left for any great length of time rapidly digest the food in the gizzard (see chapter V).

OYSTERCATCHER

Two birds were obtained on Horse Bank, their gizzards containing two Macoma and four Macoma respectively, a reduction of about 90% of the daylight Macoma fraction of the gizzard content from Horse Bank

Oystercatchers.

REDSHANK

Four birds from Horse Bank had a mean gizzard content of 4.25 Hydrobia, a figure of about 6% of the daytime content of 67.6 (chapter V) from this area.

KNOT

Excluding two birds with empty gizzards, four birds from Horse Bank contained 95 Hydrobia and two Macoma. The mean Hydrobia content (23.8) is approximately 24% of the daytime mean (98.9 per gizzard) from this site.

DUNLIN

Seven Dunlins were collected from Horse Bank, two having empty guts, the other five containing a mean of 18.8 Hydrobia. This was approximately 26% of the daytime content of 71.3 .

Conclusions on night feeding rates

It must firstly be stressed that the data presented above are extremely sparse and thus any conclusions drawn from them must necessarily be treated with great caution. However, until more gut analyses are available, or better still an optical aid such as a light-intensifying telescope used then the above estimates will have to be used. More data are required for the whole range of lunar conditions for observation could be made only on the clearest full-moon nights at certain sites whilst mist-nets were only efficient on the darkest new-moon nights (the author spent many nights, with the moon at or about half, patrolling mist-nets with absolutely no success). Thus no data are available for the majority of the lunar cycle: and to obtain such data a light intensifier must be used.

However, the data obtained thus far do suggest that there is some overall reduction in feeding rate at night and it seems that the extent depends upon the food species and state of the moon. In some instances there also appears to be a change of diet at night in some species.

Discussion

From the data presented in this chapter have been calculated (Table 17) the mean number of minutes per tide cycle spent by each wader species in actually obtaining food.

Of course, the actual number of minutes on any one day will depend upon tide height (Table 16) and will be doubled to allow for the two low tide periods per day.

Also, in future analysis it will be taken that one low tide period (i.e. feeding period) per day is at night and that feeding rates are reduced at night to the levels suggested from the very sparse data outlined earlier.

In a short-term analysis (week or month) these figures may give an erroneous picture though when examining the balance over a whole year the figures are probably as precise as need be for the present purpose and until a more accurate picture can be obtained.

Table 17 Mean number of minutes spent in feeding per tide cycle

Oystercatcher	426
Turnstone	527
Curlew	337
Black-tailed Godwit	439
Bar-tailed Godwit	470
Redshank	486
Knot	475
Dunlin	541
Sanderling	578

Note: the estimation of standard errors for the above figures is not practical for the reasons given earlier.

CHAPTER IV THE FEEDING AREAS

Introduction

Though there appears to be vast areas of inter-tidal zone suitable for waders, it is clear from cursory examination that much is not used. A short visit at low tide to Crossens or Banks where the two largest roosts are situated would leave the casual observer with the impression that few, if any, waders occurred in the area and only droppings and foot-prints at the roost-sites would provide a clue to the true picture.

To some extent this is due to the unsuitability of the substrate on the upper shore around the more accessible parts of the Ribble. It has been well established (e.g. Recher 1966) that most waders generally feed in areas where the substrate is covered by a film of water or close to or by the water's edge. Much of the sandier (see chapter VI) south Ribble lacks this water film (especially during neap tide periods) and so waders appear few at low tide. On the north, off Lytham and Fairhaven, the shore beneath the promenade is generally wet and consequently very large numbers of waders can be watched within a few metres of the seawall.

The distribution of the food species is also bound to have some influence on the distribution of feeding waders, though some studies (e.g. Prater 1972) have yielded unexpected and slightly confusing results. This aspect is dealt with in Chapter VII.

This chapter does not deal with why or how the waders select their feeding areas: it is hoped however, that some light may be shed on these problems later. Rather, in attempting to assess the effects of waders on prey densities, and the numbers of waders that an estuary can hold, it is important to include an assessment of the areas from which the present wader populations obtain their food. This chapter attempts such an assessment.

Methods

Throughout the study the location of the main feeding areas for the major Ribble Estuary waders were plotted on sketch maps and the states of the tide when these were used. Observations were carried out also on the movements made by the waders from roost to feeding areas and across the feeding areas. From the mappings the sizes of the feeding areas used by the majority (at least 95% as censused at the roosts) of each wader species have been calculated. In most cases there is a variation in size throughout the year and so calculations of area were made on a monthly basis.

Results

Table 18 presents calculations of size of the feeding areas of nine wader species whilst a series of maps given in the text shows the main feeding ranges of these species throughout the year.

OYSTERCATCHER (Figure 14)

Only the Mytilus bed of Church Scar (0.3 km^2) and the rich Macoma sandflats of Horse and Salter's Bank provide regular feeding sites for large numbers of Oystercatchers, other than these being of a temporary nature. In most years small beds of Cardium edule may develop as a consequence of a local spot fall and occasionally beds of Mactra corallina may be washed out and rapidly exploited by Oystercatchers.

Once Oystercatchers have arrived on the feeding grounds movements to other feeding areas are rare, unless the birds are disturbed.

GREY PLOVER

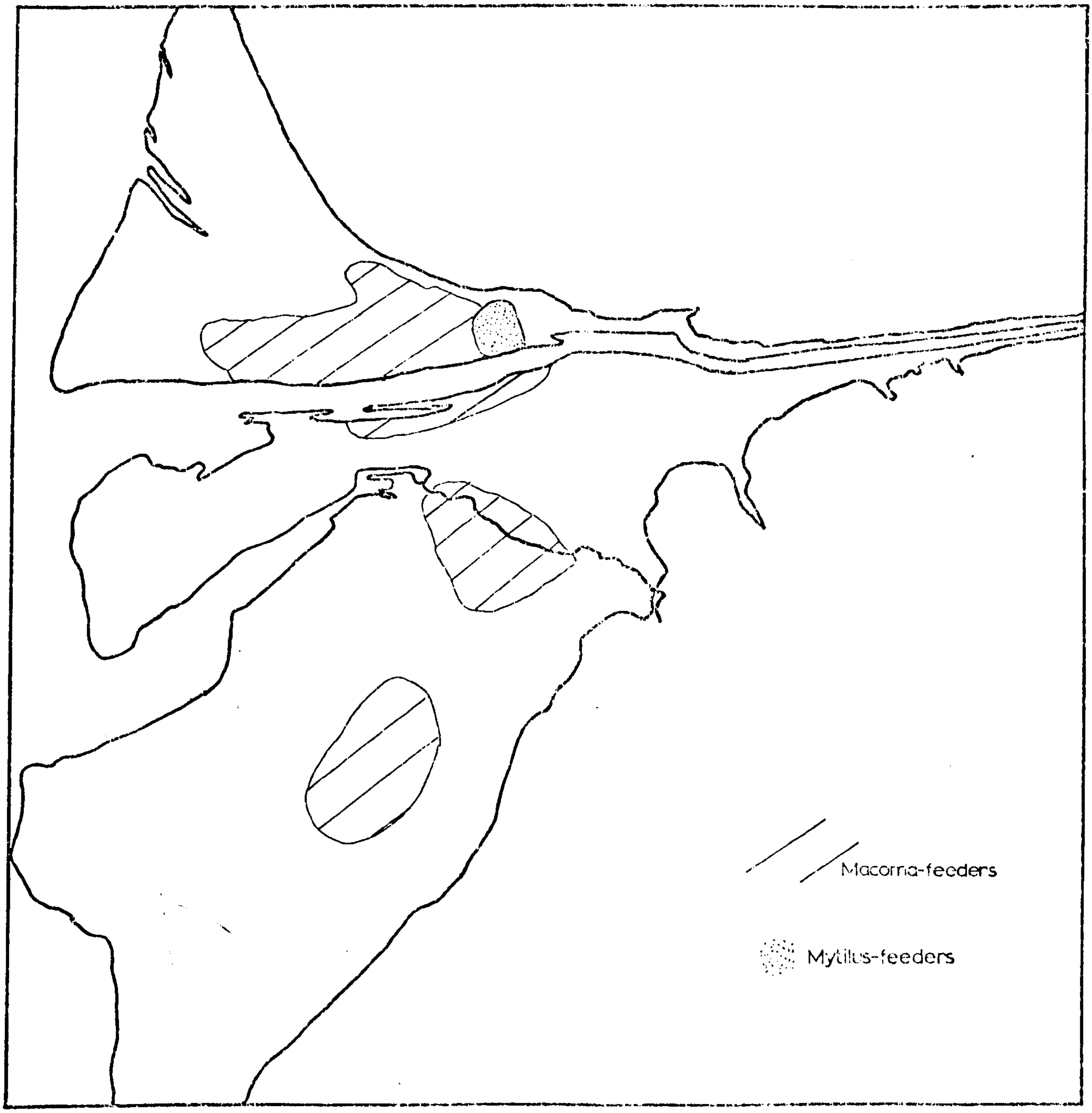
Though relatively large and nationally important numbers of Grey Plovers occur at the Ribble roosts, the majority appears to feed outside of the Estuary, judging from counts and other observations made on the feeding grounds.

Table 18 Sizes (in km^2) of the main inter-tidal zone feeding areas of waders on the Ribble Estuary

	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr/May
Oystercatcher	6.7	6.3	9.8	10.9	7.6	10.2	11.1	5.9	3.1	1.6
Curlew	2.0	2.9	2.6	1.8	1.4	2.1	1.7	1.9	0.3	0.1
Black-tailed Godwit	0.8	1.0	1.2	0.8	-	-	-	-	-	-
Bar-tailed Godwit	2.1	6.6	13.7	10.4	10.1	8.4	7.2	3.5	4.1	3.6
Redshank	3.9	8.6	8.2	6.5	4.0	4.0	4.1	4.0	4.4	-
Turnstone	-	0.6	0.6	0.6	0.6	0.6	0.6	0.6	0.6	-
Knot	12.2	16.4	17.8	18.0	16.1	13.0	12.5	13.0	12.9	9.6
Sanderling	22.4	20.0	11.7	12.9	10.4	10.4	9.6	8.8	7.6	19.8
Dunlin	8.3	9.4	12.2	11.6	15.2	16.0	14.8	16.3	15.5	9.9

Figure 14

Feeding areas of the Oystercatcher on the Ribble Estuary


Macoma-feeders
Mytilus-feeders

CURLEW (Figure 15)

The majority of Curlews which feed on the inter-tidal zone do so north of the Ribble Channel on Salter's Bank though up to 38% feed around Crossens Pool and on Horse Bank, especially in early autumn and late winter. Movements between roosts and feeding areas is usually in association with Bar-tailed Godwits (see below).

BLACK-TAILED GODWIT (Figure 16)

This species is faithful to the 0.8 - 1.2 km^2 of feeding area on the north Ribble, only very small numbers occasionally occurring in autumn in Crossens Pool. Movement to and from these feeding areas is direct, occurring after these have been exposed by the receeding tide and as the tide flows (chapter III).

BAR-TAILED GODWIT (Figure 17)

Like the Black-tailed Godwit, this species also has fairly fixed feeding areas covering about 14 km^2 and in autumn when peak numbers are on the estuary, these are more or less completely used. When lesser numbers occur (through winter and spring) less of this same feeding area is used. The majority of Bar-tailed Godwits feed on Salter's Bank (up to 78%) with up to 34% feeding around the edges of Foulnage and on the north and west of Horse Bank.

These feeding areas reach much higher up the shore than do those of the Black-tailed Godwit (Figure 18) and consequently this species roosts for less time than the Black-tailed Godwit. After leaving the roost most birds fly directly to the upper feeding areas, moving down with the tide to the lowest feeding areas and then returning in front of the advancing tide.

REDSHANK (Figure 19)

During the autumn peak passage period this species extends its

Figure 15

Feeding areas of the Curlew on the Ribble Estuary

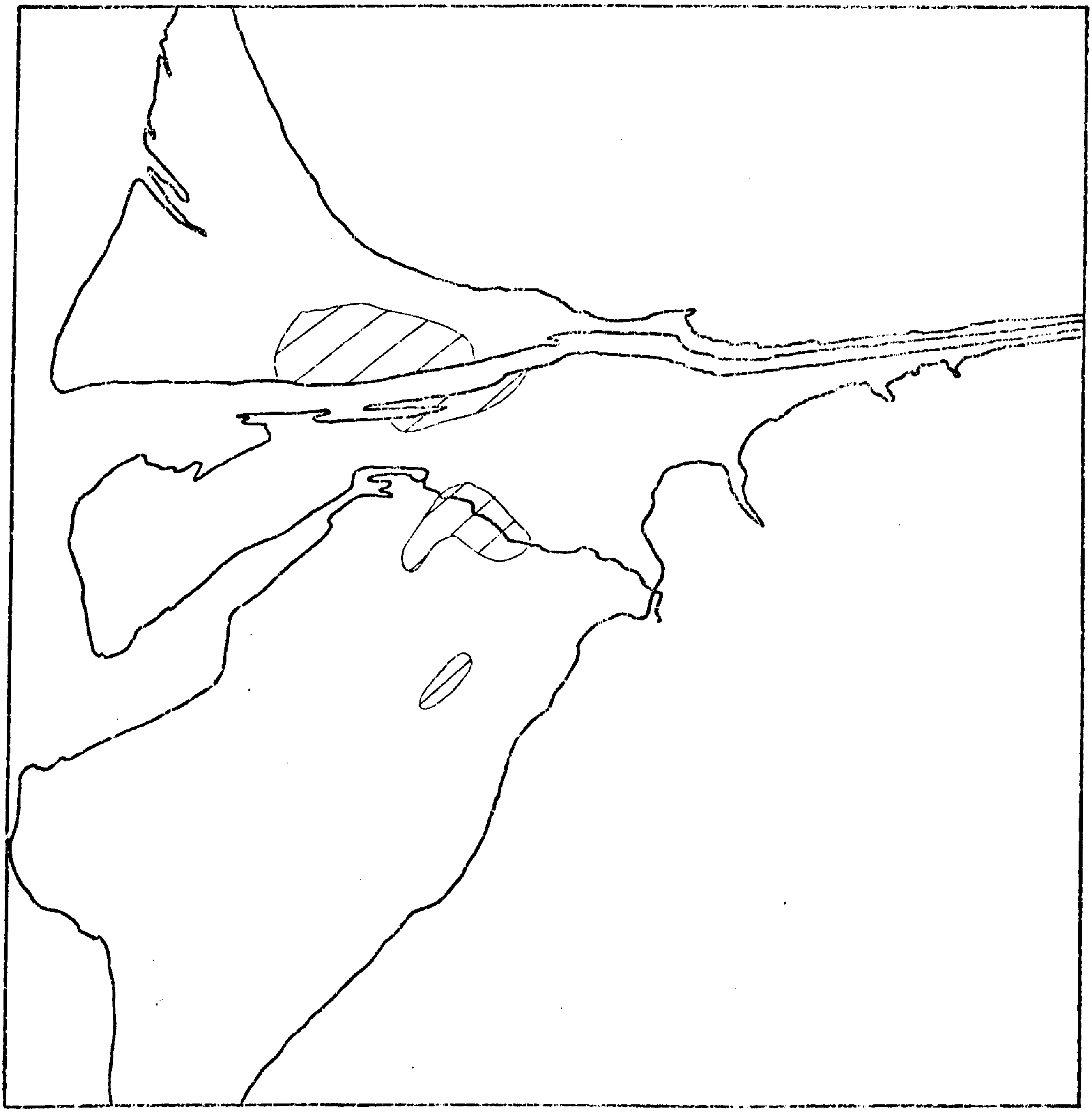
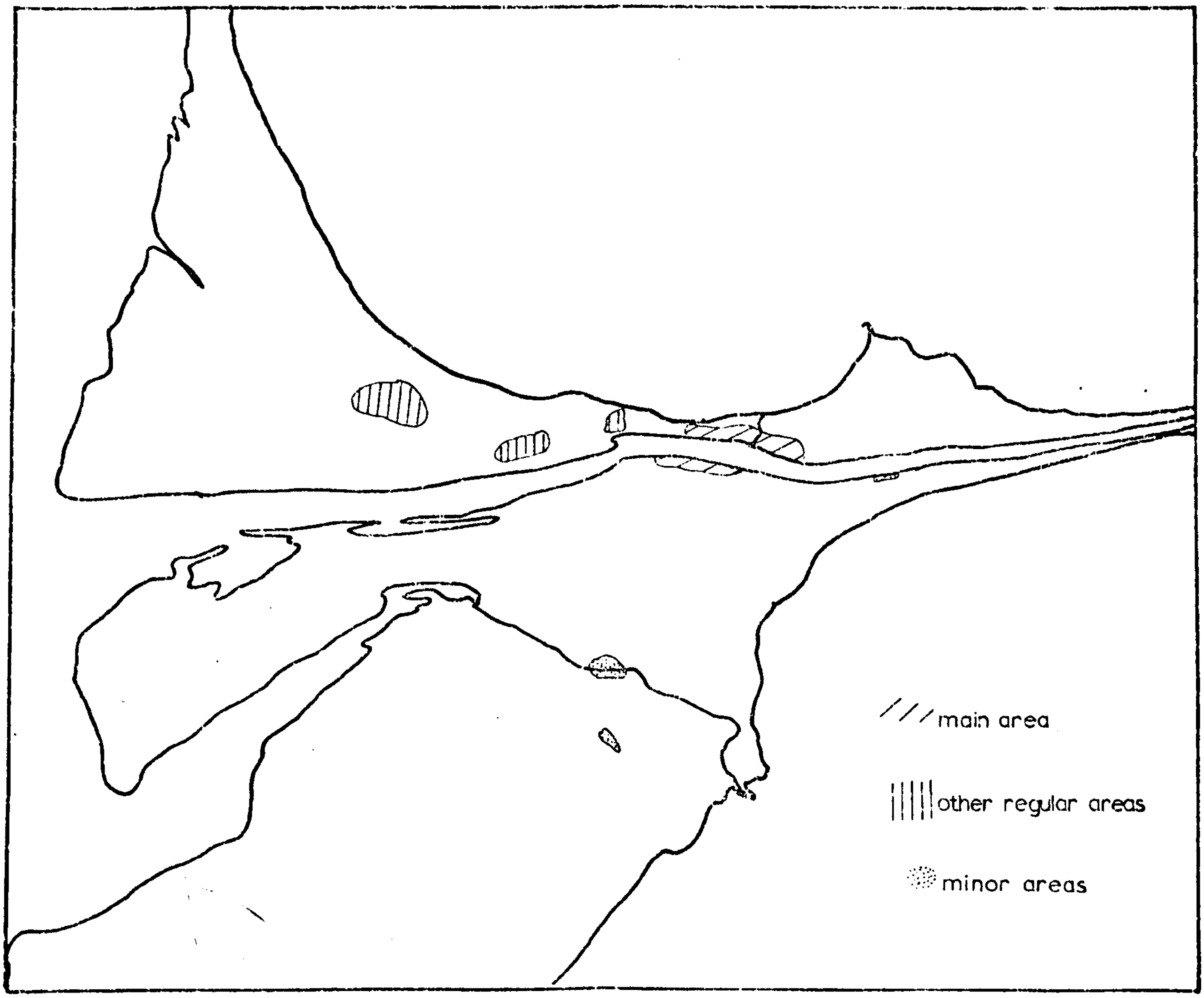


Figure 16

Feeding areas of the Black-tailed Godwit on the Ribble Estuary


main area
other regular areas
minor areas

feeding range over a considerable area of mud and sand which it retreats from during the remainder of the year. This pattern appears to be related especially on the north Ribble with the large Redshank population roosting at Warton Marsh and which feeds on Banks Sands and Foulnage close to the Ribble channel and the eastern half of Salter's Bank. A similar, but less conspicuous autumn increase in roost size on the Banks and Crossens roosts is marked by a more extensive feeding area compared with the winter roosts and related feeding areas (c.f. Figures 19a and b).

The Redshank is primarily an inner estuary and upper shore feeder (Figure 20), relatively few feeding at levels below +1 metre O.D. On the south Ribble where feeding areas are more adjacent to the roosts many Redshanks therefore follow the tide down the shore feeding and similarly feed up in front of the advancing tide to roost, flying just the occasional few metres across channels or the final metres into the roost, (this applies especially to those roosting at Warton and feeding on Salter's Bank) fly directly to the highest and nearest feeding areas as soon as these have been exposed.

TURNSTONE (Figure 21)

This species is mainly restricted to Church Scar and the training walls of the Ribble channel, only very small numbers occurring elsewhere. Movements, other than between roosts and feeding areas, are thus extremely few.

KNOT (Figure 22)

The majority of Knot follows a regular sequence of movements from the roosts (mainly on the south Ribble) across the upper sand and mud banks to the main low tide feeding areas of Salter's Bank.

The Knot roosts split up as they leave the roost into feeding flocks of up to about 15,000 which subsequently break down into flocks of up to

Figure 17

Feeding areas of the Bar-tailed Godwit on the Ribble Estuary

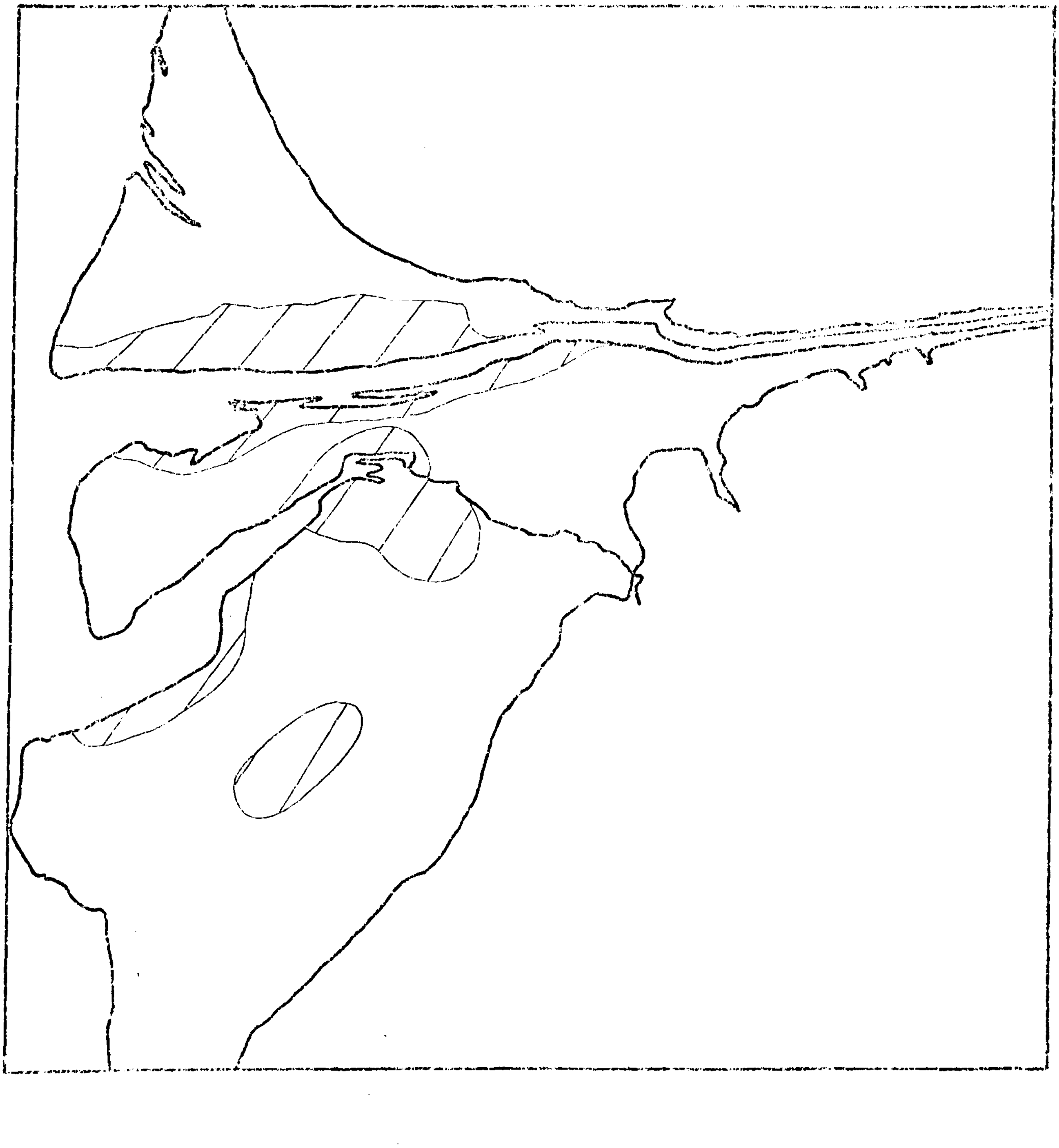


Figure 18

The percentage of the Black-tailed Godwit and Bar-tailed Godwit populations feeding at different shore levels at low water.

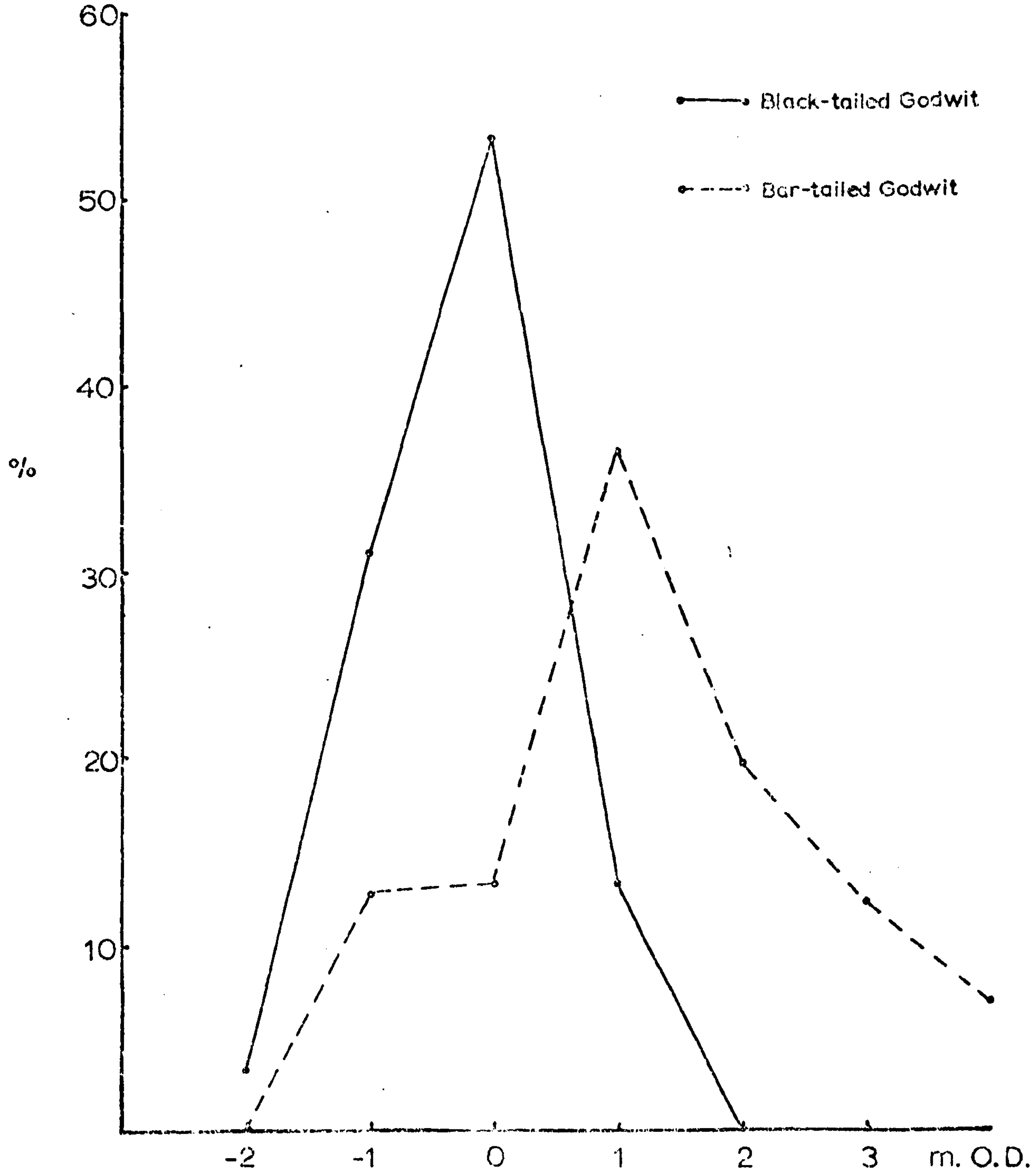

Black-tailed Godwit
Bar-tailed Godwit
%
60
50
40
30
20
10
-2
-1
0
1
2
3
m. O.D.

Figure 19

Feeding areas of the Redshank on the Ribble Estuary a) in autumn and b) in mid-winter

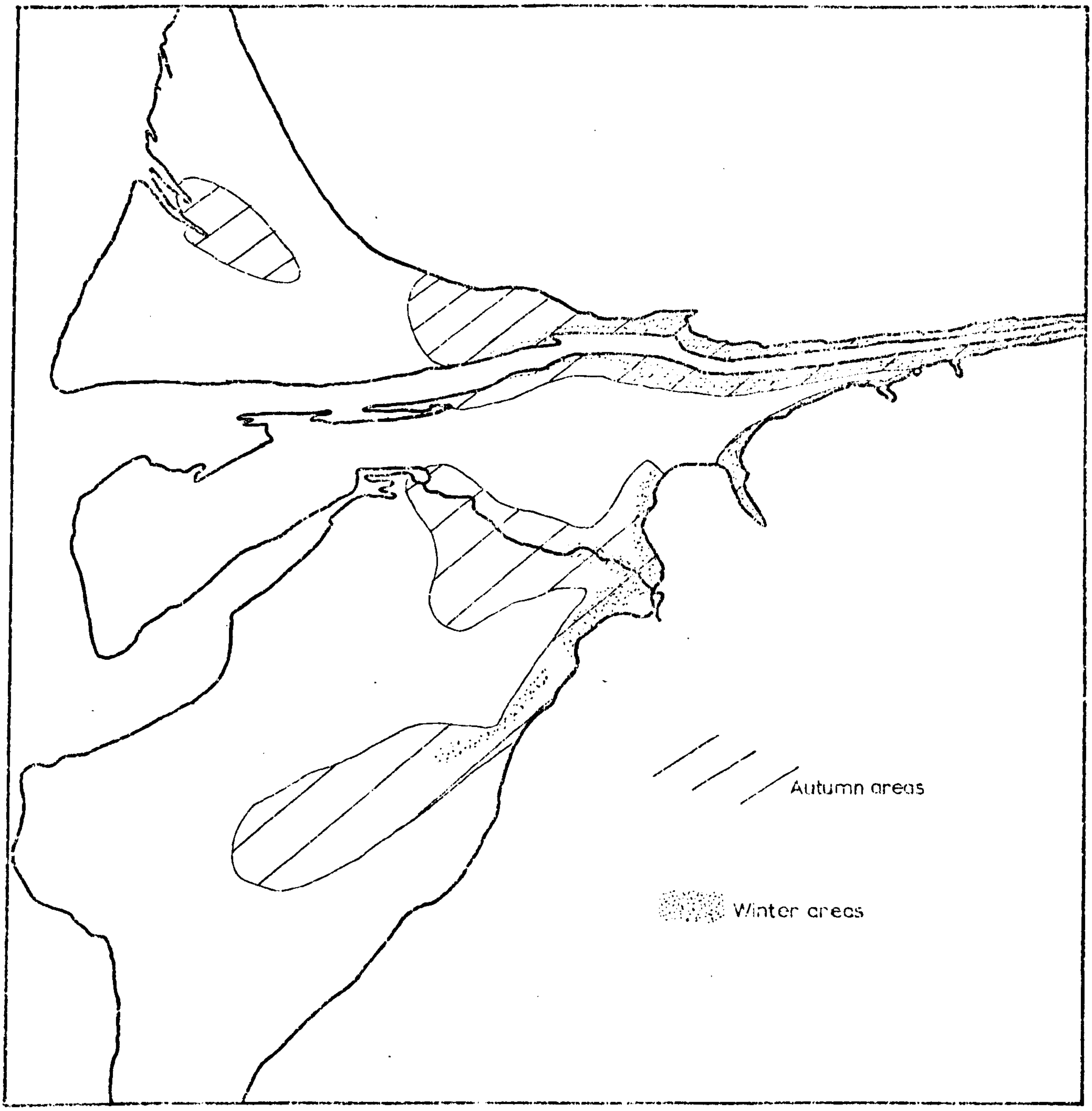

Autumn areas
Winter areas

Figure 20

The percentage of the Redshank population feeding at different shore levels at low water (autumn data, N. Ribble)

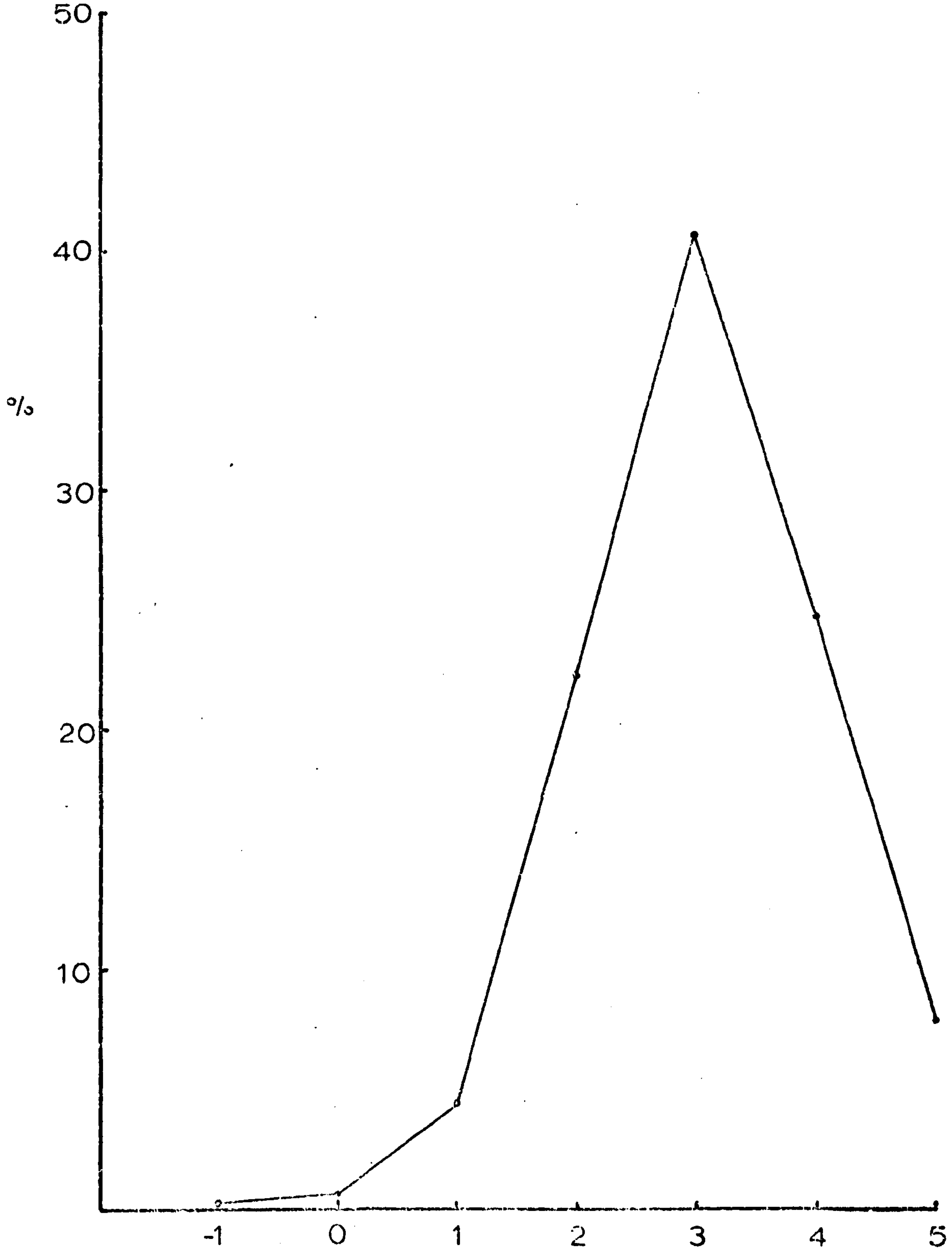

50
40
30
20
10
%
-1
0
1
2
3
4
5
metres O.D.

Figure 21

Feeding areas of the Turnstone on the Ribble Estuary

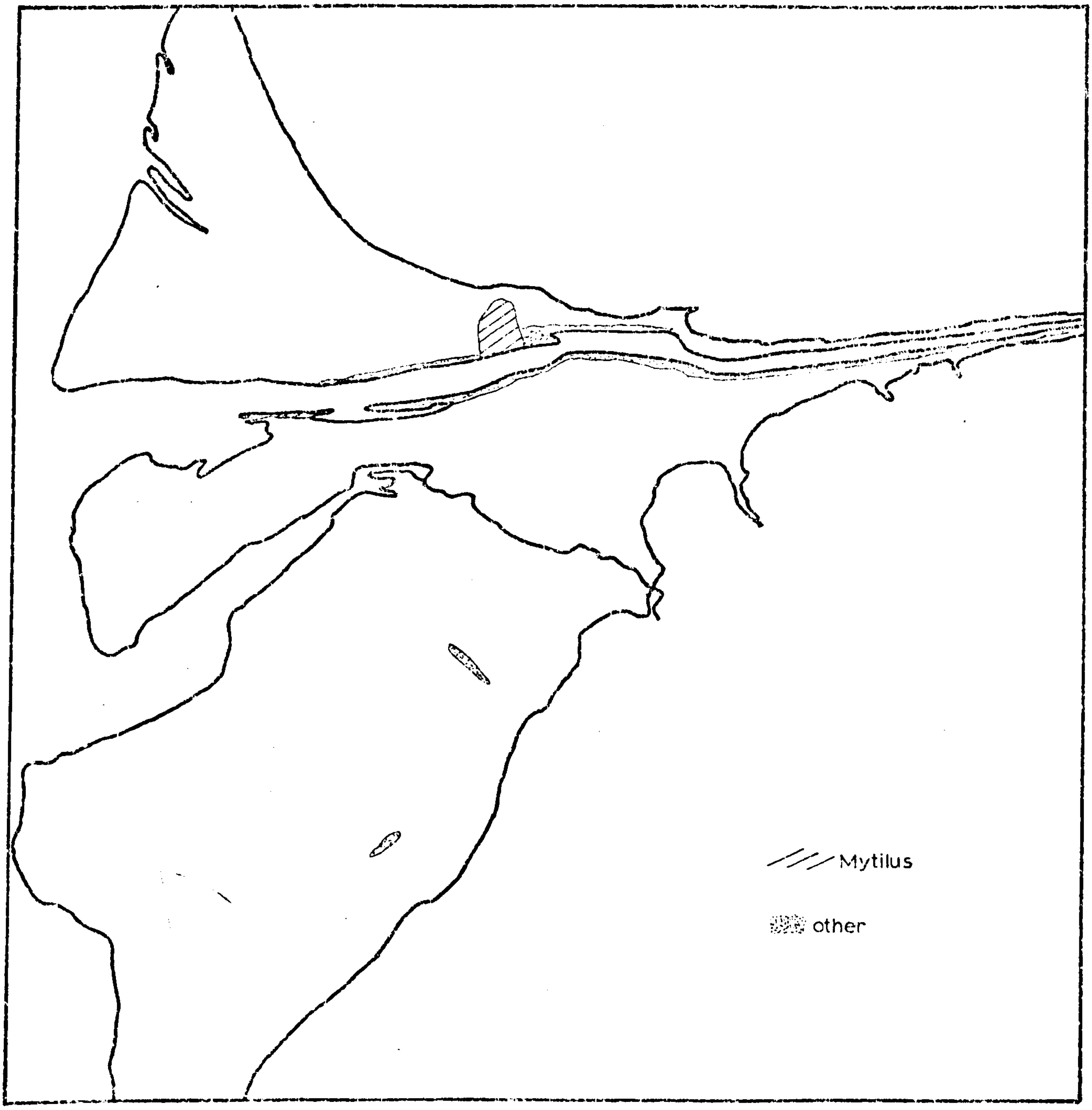

Mytilus
other

Figure 22

Feeding areas of Knot on the Ribble Estuary

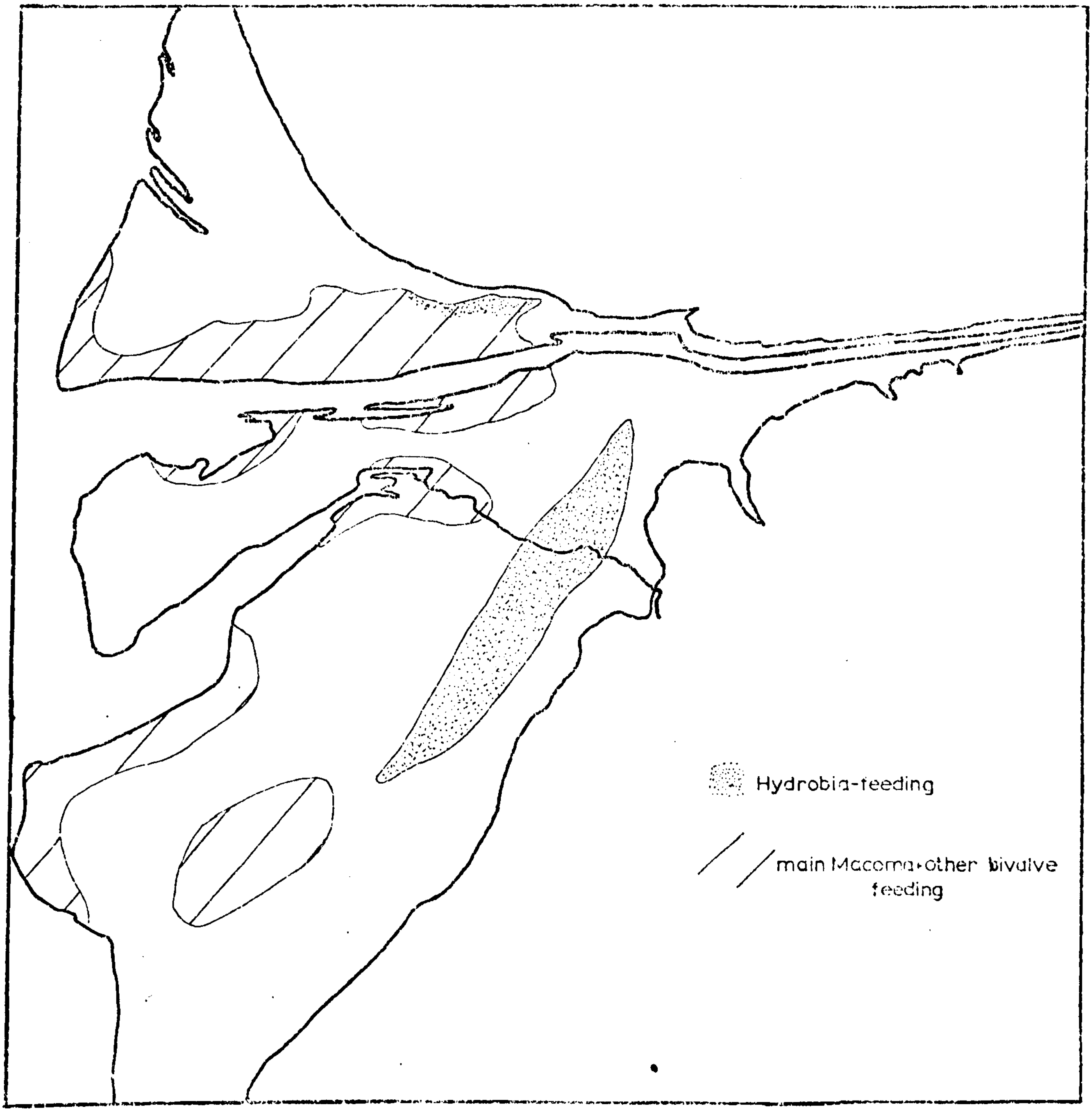
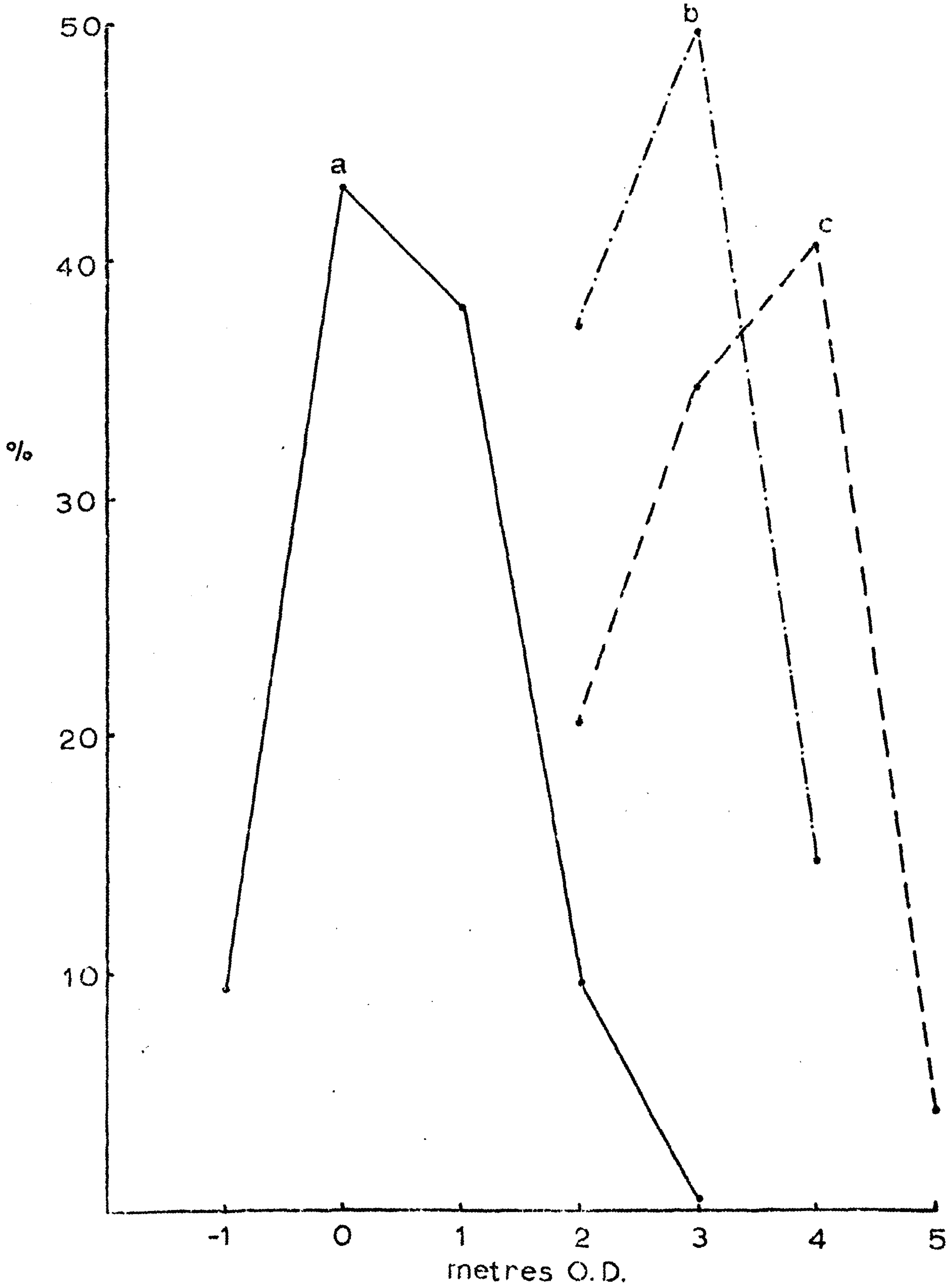

Hydrobia-feeding
main Macoma+other bivalve feeding

Figure 23

The percentage of the Knot population feeding at different shore levels at a) mid-ebb, b) low-tide andc) mid-flow tide.



50
40
30
20
10
%
a
b
c
-1
0
1
2
3
4
5
metres O.D.

about 8000 on the feeding areas. These flocks leave the roosts, flying to the tide's edge when it has reached +4.5 metres O.D. and they then feed down on the shore with the tide, occasionally flying distances of up to 3 Km. to other banks as they become exposed. As they approach the +2.0 - 2.5 metre O.D. shore-level longer movements occur to Salter's Bank where most of the Ribble's Knot spend the low tide period at shore levels between low-water and about +2.0 metres O.D. (Figure 23). Apart from these, up to 28% of the Knot population may move westwards to the area on Horse Bank around and to the north of the Bog Hole where they feed over low-water whilst up to 20% may remain around Crossens Pool and its associated channels where they continue to feed at the slightly higher level of +1.5 - 3.5 metres O.D.

The return movement is similar with birds moving up the shore in front of the flowing tide until they reach about +3.0 metres O.D. when many head directly to roost, others continuing to feed in advance of the tide until they also are forced to roost.

SANDERLINGS (Figure 24)

Like the Redshank this species has much more extensive feeding areas during periods of peak passage than when a stable winter population is present (c.f. Figures 24a and b). In winter only the Squires Gate roost holds significant numbers of Sanderlings and these feed entirely along the sandy shores of the outer estuary and also spread along the Fylde and S.W. Lancashire beaches out of the Ribble Estuary area.

However, during spring and autumn passage the Crossens roost also holds large numbers of Sanderling whilst smaller roosts occur elsewhere. There is then a tendency for the species to occur more widely across the Estuary, though it still avoids the muddy inner estuary.

On the Ribble, Sanderlings are primarily a tide-edge feeder, following the tide in and out. Thus at low-tide most Sanderlings occur on the lowest tide levels (Figure 25).

Figure 24

Feeding areas of the Sanderling on the Ribble Estuary in a) winter and b) Spring and autumn

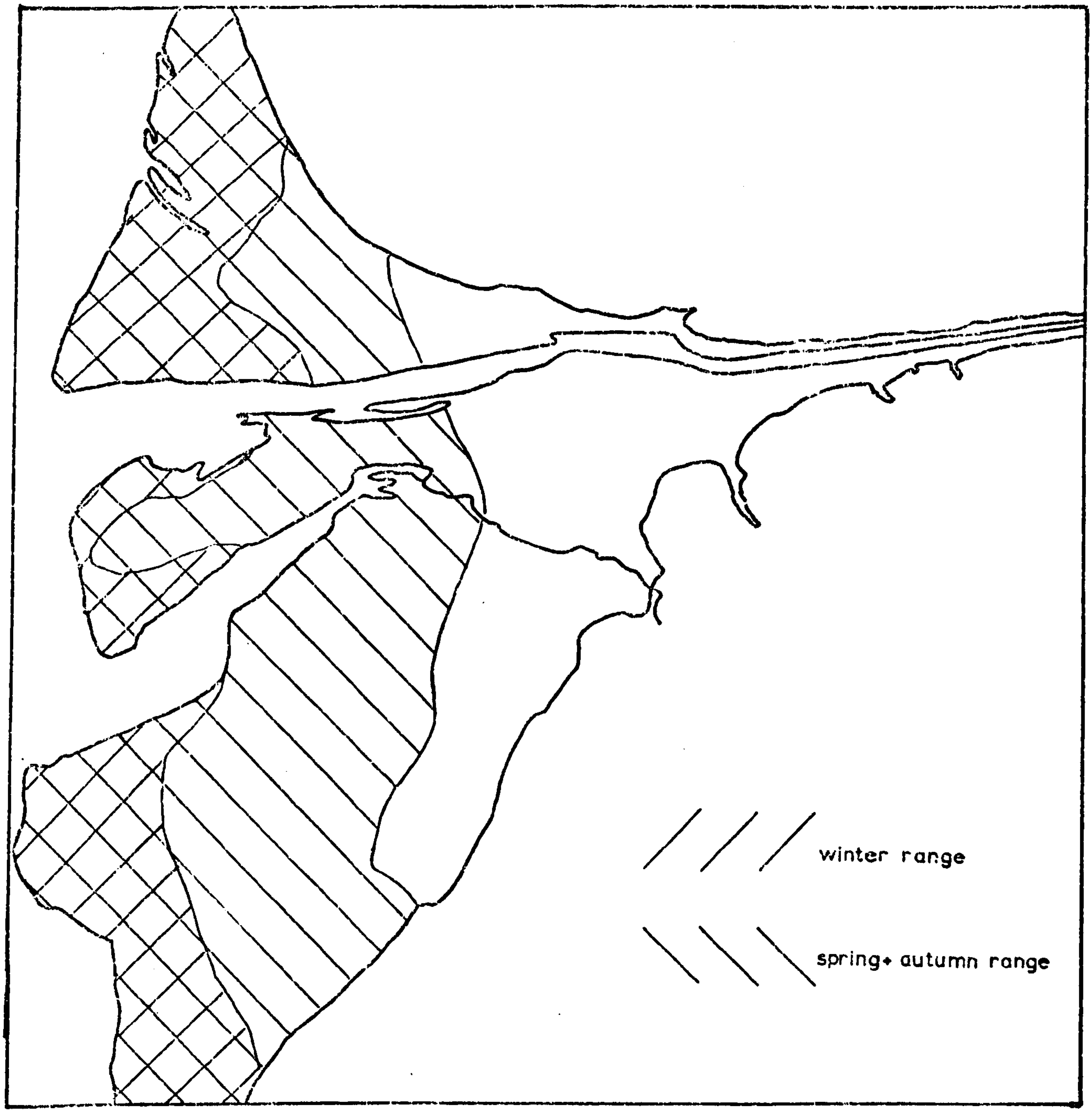
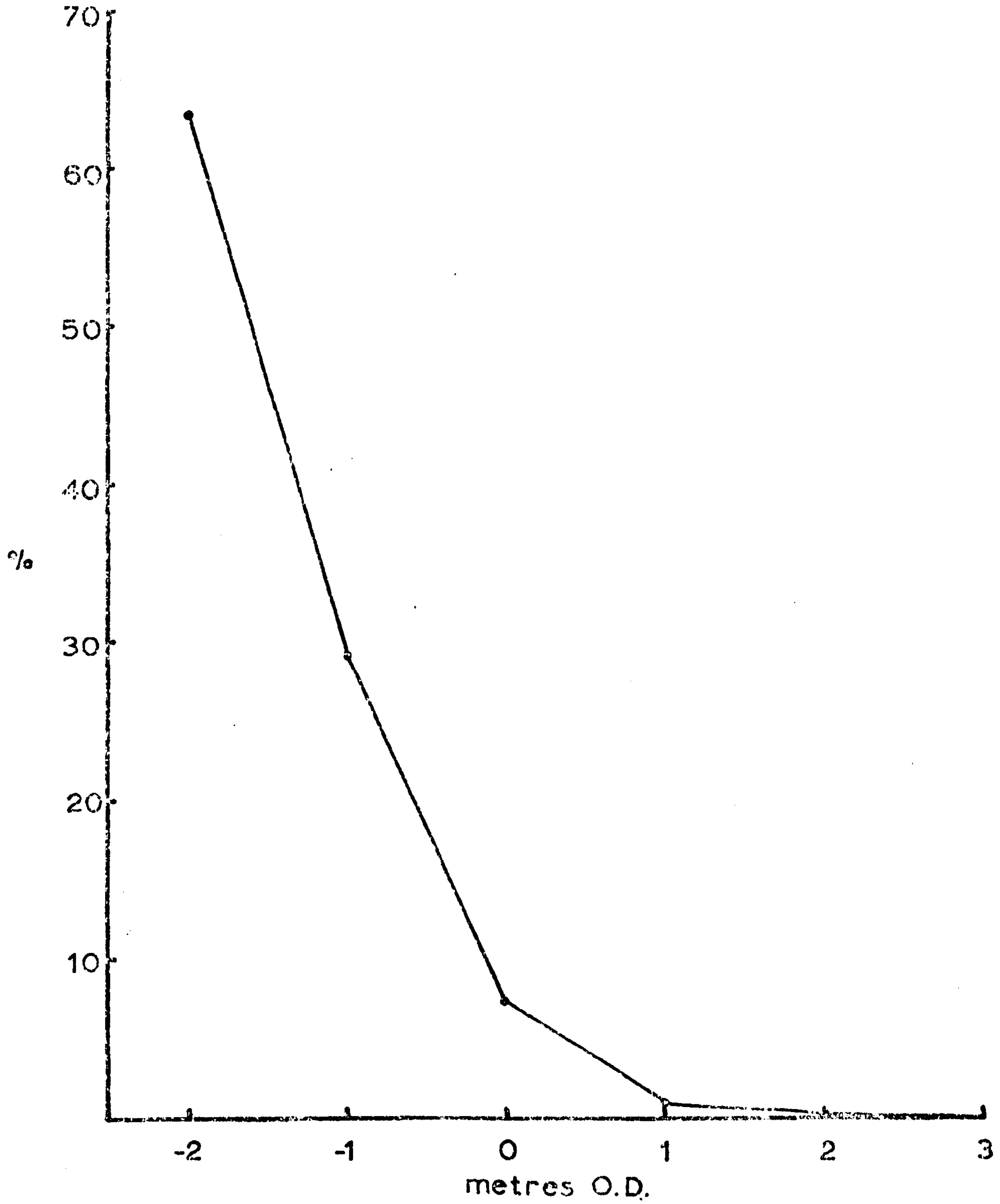

winter range
spring+ autumn range

Figure 25

The percentage of the Sanderling population feeding at different shore-Levels at low water


70
60
50
40
30
20
10
%
-2
-1
0
1
2
3
metres O.D.

DUNLIN (Figure 26)

The majority of Dunlin feeds on the upper shores of the inner estuary and, when the saltmarshes are wet, a high proportion (up to 8,000) may also feed on the saltmarshes. Within the large area of inter-tidal zone used by this species however, there is a great deal used only at certain stages of the lunar cycle. The highest shores, for instance, which dry out during periods of neap tide, are used only on and immediately following periods of spring tides.

Like the Sanderling, the Dunlin tends to feed down the shore with the tide, or where the feeding areas not adjacent to roosts, move out from the roosts as soon as the highest feeding areas are exposed by the tide. Most Dunlin feed above the -0.5 - O.D. shore-level (Figure 27).

Discussion

Most Ribble waders appear to have restricted feeding areas out of which they rarely occur. Most obviously this applies to the Oystercatchers and Turnstones feeding on Church Scar though not in the case of Oyster-catchers feeding on the mud and sand banks where temporary irregular food sources are of some importance.

In some cases, these specifically restricted feeding areas result in very clear separation between congeneric species.

Of the Godwits, Black-tailed Godwits are inner estuary feeders on finer mud substrates close to the low-tide mark whereas Bar-tailed Godwits occur over a larger feeding area of sandy-mud and sand in the outer estuary. Incidentally, it may well be that the Ribble Black-tailed Godwits annual maximum of 1,000 - 1,500, which has developed over the past twenty years, is the maximum that the restricted 1.2 Km^2 feeding area is able to support. Indeed, the maximum average density of Black-tailed Godwits over this area of approximately 0.1 godwit per hectare of substrate is close to the maximum density of Bar-tailed Godwits recorded (about 12,000 over 1,370 hectanes of feeding area). P. J. Dare (pers. com.) has found a similar difference in feeding dispersion of godwits in the Exe Estuary (Devon).

The three common species in the genus Calidris on the Ribble show a similar separation of feeding areas to the godwits though there is a great deal of overlap. Sanderlings are the most isolated, being restricted to the sandy shores, save on passage when they occur on the mid-estuary (but only for short periods). The Knot and Dunlin, occurring on the middle and (Dunlin) inner estuary, are separated mostly by shore-level of the feeding areas (c.f. Figures 23 and 27). However, as Chapter V shows, these calidrines are also separated by diet.

There must be a basic positive advantage to the waders in having restricted feeding areas other than the negative one of reduction of competition in congeners: for restricted feeding areas occur even in single representatives of genera (e.g. Curlew, Redshank). In any case, most species are separated from others by diet (Chapter V).

It is more likely that the feeding areas are selected by the birds. They may learn in some way that a particular area holds large and available food stocks which they return to at every low tide period. There is thus no need for them to search the whole estuary for food at each low tide period. Then when immigrants arrive they may learn of the major food stocks by following others of the same species which already know where to find food.

Two series of observations illustrate how rapidly new food stocks may be discovered. In October 1973, the author discovered a small (300 x 110 metres) Cardium bed on Horse Bank containing high density of cockles of 10 - 20 mm diameter. On 5 November three Oystercatchers were watched feeding on the cockles and by 19 November, 87 Oystercatchers were present. By 6 January 1974, the cockle stocks had been depleted to the extent that no Oystercatchers were present.

Figure 26

Feeding areas of the Dunlin on the Ribble Estuary

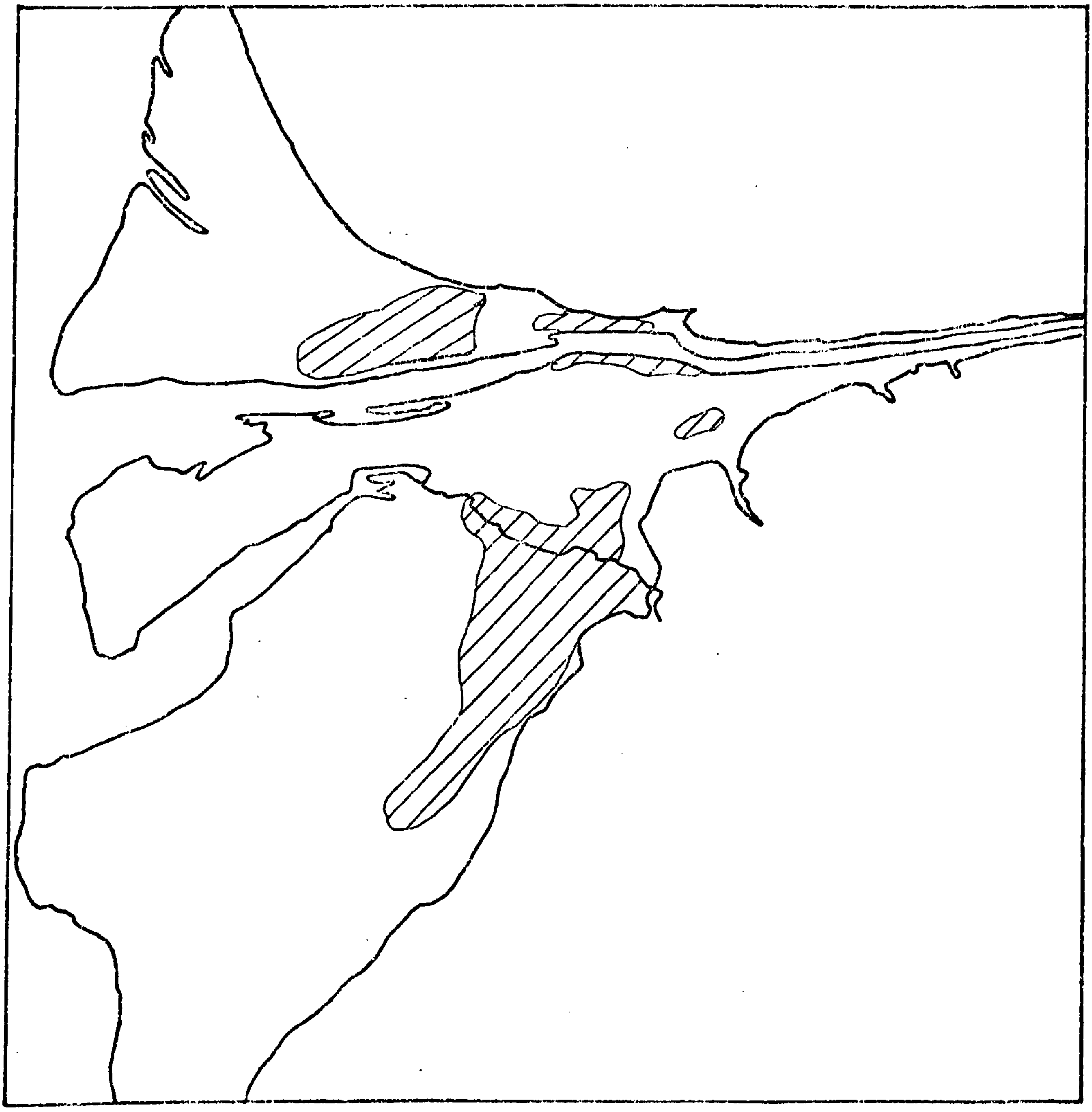
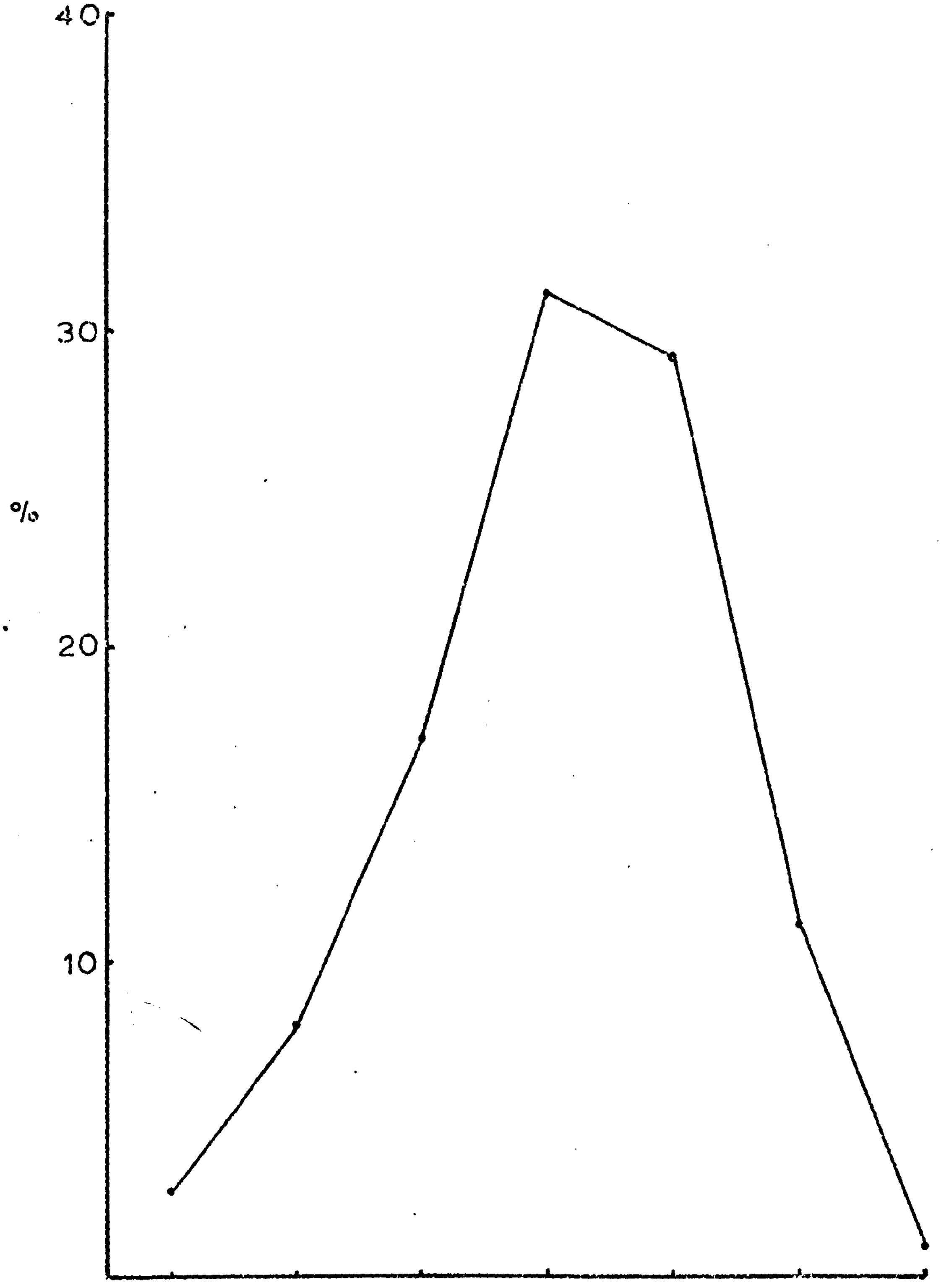


Figure 27

The percentage of the Dunlin population feeding at different shore-levels at low water


40
30
%
20
10
-1
0
1
2
3
4
5
metres O.D.

Likewise, a gale and tidal surge washed-out large numbers of Mactra corallina onto Salter's Bank in February 1972 and within two tide cycles 380 Oystercatchers had discovered and were exploiting the food source.

Waders rapidly learn of food supplies provided by man. There have been many published instances of waders feeding on bread whilst the author used to bait a clap-net in Morecambe Bay with the remains of domestic rabbits to catch Turnstones. Similarly, Redshanks in Morecambe Bay and the Ribble and Alt Estuary learn where the shrimpers discard the shrimp husks and even stand about waiting for the daily provision (personal observations).

It would seem, therefore, that if a food source is located outside of the main feeding area of a species but is discovered by stray individuals then that area and food source can be incorporated into the feeding area of that species either permanently or until the food source is depleted. Far more observations are needed, however, over the following years in order to discover whether the main feeding areas (and prey distribution) vary as have these atypical cases mentioned above.

CHAPTER V THE FOOD OF WADERS

Introduction

Almost as many methods have been used in studying foods of birds as there have been studies. Traditionally have been used gut content analyses, usually taking the crop (in species which have a crop) or oesophagus and gizzard in those species which lack a crop. There are several methods of analysis and presentation of results of such studies (reviewed by Hartley 1948 and Goss-Custard 1973), each of which is open to bias in favour of some prey species against others. Goss-Custard (1973) has discussed such biases and other problems in describing diets by gut analysis.

Less use has been made in wader studies of the pellets ejected from the gizzard, which contain the undigestible remains of the food. This is surprising, for the majority of studies of owls Strigidae and diurnal raptors have centred upon pellet analysis whilst one of the earliest accounts of wader food, that by Hibbert-Ware and Ruttledge (1945) on Curlew dealt with pellet analysis. The only recent study relying heavily on this source of data is that of Swennen (1971) on Greenshank food in the Dutch Waddenzee though Spitz (1971) and others have used pellets in their studies of gull Laridae feeding.

Obtaining qualitative data by direct observation on wader diets is generally impossible with very small prey (e.g. Corophium, Hydrobia) but for the larger invertebrates is, as Goss-Custard (1971) pointed out an excellent method of collecting a large amount of data. In such cases data of feeding rates can be collected (chapter VIII) knowing exactly the foods being taken.

Faecal analysis has not been used in this study, the identifiable remains in the faeces being less easy to identify and quantitatively record than either pellet or gut analysis.

Methods

a) Gut analysis

Birds were shot with 12-bore or .410-bore shotgun (shot size 5 or 6) under licence from N.F.R.C. Immediately 20% formalin was injected into the gut via the buccal cavity until the gizzard and oesophagus could hold no more so as to arrest digestion. In most cases the guts were removed immediately after death and placed in bottles of formalin, this being a more sure way of preventing further digestion of food (P. Morgan pers. com.). Besides these birds collected by the author, many local wildfowlers also gave the guts of the specimens of unprotected species which they had shot. Again, the guts were removed and placed in formalin though it was usually 2 - 6 hours after shooting before this was done and so some digestion had occurred after death.

The contents of the oesophagus and gizzard were examined separately in the laboratory using a X15 Baker stereomicroscope. The presence of each food species was ascertained and the number of whole animals and items counted (Table 19 gives the items counted in this study in gizzard analyses). Then the percentage contribution by volume of the total gut content of each identifiable species was estimated to the nearest 5 or 10%, depending upon the amount and variety of food in the gut.

In the cases of Dunlin and Redshank feeding on Hydrobia, Macoma and Corophium, Bar-tailed Godwit feeding on Macoma and Nereis and Sanderling feeding on Bathyporeia and polychaetes the gizzard contents were multiplied by various correction factors which allowed for certain softer preys being digested more rapidly than harder prey and thus being unrecorded (see Goss-Custard 1969). These correction factors, used in later analyses, and the method of calculating them are given in Appendix I.

b) Pellet analysis

An attempt was made to collect pellets on a monthly basis in the period December 1972 to March 1974. This was not always possible,

Table 19 Items counted in gizzard analysis

Polychaeta:	whole animals, fragments with heads, mandibles/2.
Gastropoda:	whole animals, shells in which height could be measured.
Lamellibranchiata:	whole animals, complete shells/2, hinges/2, fibrous tip of foot in *Cardium*, *Macoma* and possibly *Scrobicularia*.
Crustacea:	whole animals, fragments with heads, complete carapaces, chelae/2, second antennae in *Corophium*.
Insecta:	whole animals, fragments with heads, elytra of Coleoptera, wings of diptera.
Other groups:	whole animals, fragments with heads. Where any fragment existed in a gizzard which indicated a prey species, then this was noted.

however, as periods of heavy rain or the fortnightly spring tides destroyed them. A satisfactory number of pellets was obtained for the five species Curlew, Redshank, Knot, Sanderling and Dunlin though totals of less than ten pellets were obtained for Grey Plover, Turnstone, Snipe, Black-tailed Godwit, Bar-tailed Godwit and Ruff. Oystercatchers also produce pellets though these were not included in the study as observation supported by gut analysis provided ample data of Oystercatcher diet.*

In the laboratory the pellets were dried to constant weight and stored in a dessicator. After weighing they were then broken down in 50% ethanol and the species-remains occurring in each pellet noted. Results were then calculated as the percentage occurrence of each species in the diet. It was considered that counting individual items in the pellets would have been pointless, as those in greatest abundance would generally be from those animals with a greater amount of indigestible structure (*Hydrobia* shells, nereid jaws etc.). In any case, it is probable that by even using percent occurrence, such prey would be over-estimated.

c) Direct observation

Throughout the study any foods ingested and which could be identified were noted. Much of this was observed in making measurements of feeding rates and hence it was possible, knowing the total number of swallows per unit time (chapter VIII) together with the swallows involving identifiable prey, to obtain an estimate of the proportion of these larger prey in the whole diet and, by subtraction, the proportion of the smaller prey (*Hydrobia*, *Corophium* etc.). In most cases it was possible to deduce the species of the smaller prey from the knowledge of invertebrates in that area of substrate or from gut contents.

Observations were made with X15 - 60 Nickel Supra telescope, X30 ex-army telescope and 8.5 x 44 and 8 x 30 binoculars. A "tally-counter" was used in counting.

Throughout this part of the survey data were collected on the major feeding areas unless stated otherwise. Thus it was considered reasonable to summarise the data in the form of composite tables which provide indications of the proportions of foods taken by each wader species population.

*

Only when it was certain that a pellet had been produced by a certain species (usually because only that specied fed or roosted at the site or the bird was seen to regurgitate that pellet) was it included in the analysis.

Results

OYSTERCATCHER

Table 20 presents the data from gut analyses of Oystercatchers on various habitats around the Ribble Estuary.

1. Mussel - scar.

Mytilus is the chief prey, occurring in all guts and forming almost 100% of the gut content by volume. From Morecambe Bay, Dare and Mercer (1973) found that the vast majority of mussel-scar feeders (1186 out of 1222 guts) contained only mussels whereas four of the eleven from the Ribble (admittedly a small sample) contained other prey beside mussels. This greater variability of the Ribble data may be due in some part to the Fairhaven mussel scar being relatively small and the mussels of poor quality and density (chapter VII).

2. Mud- and sand-flat.

The three main prey are the lamellibranchs Cardium edule, Macoma balthica and Scrobicularia plana. In Oystercatchers collected from the Fairhaven area of Salter's Bank Macoma and Scrobicularia occur in approximately equal proportions though on Horse Bank Macoma is the main prey and, on Banks Sands, where relatively few Oystercatchers feed and only four guts were examined, Scrobicularia seems to be most important.

Compared with nearby Morecambe Bay (Dare and Mercer 1973) there is a great diversity of Oystercatcher gut contents on the Ribble, possibly as a consequence of the more varied invertebrate fauna on the Ribble and the lack of an overall major Oystercatcher invertebrate prey. In Morecambe Bay Cardium occurred in vast numbers and was taken to the exclusion of most other prey by Oystercatchers up to the hard winter of 1963, since when the similarly superabundant Macoma has been the major prey.

Plate 1

A Loose pellet of an Oystercatcher containing *Macoma balthica*

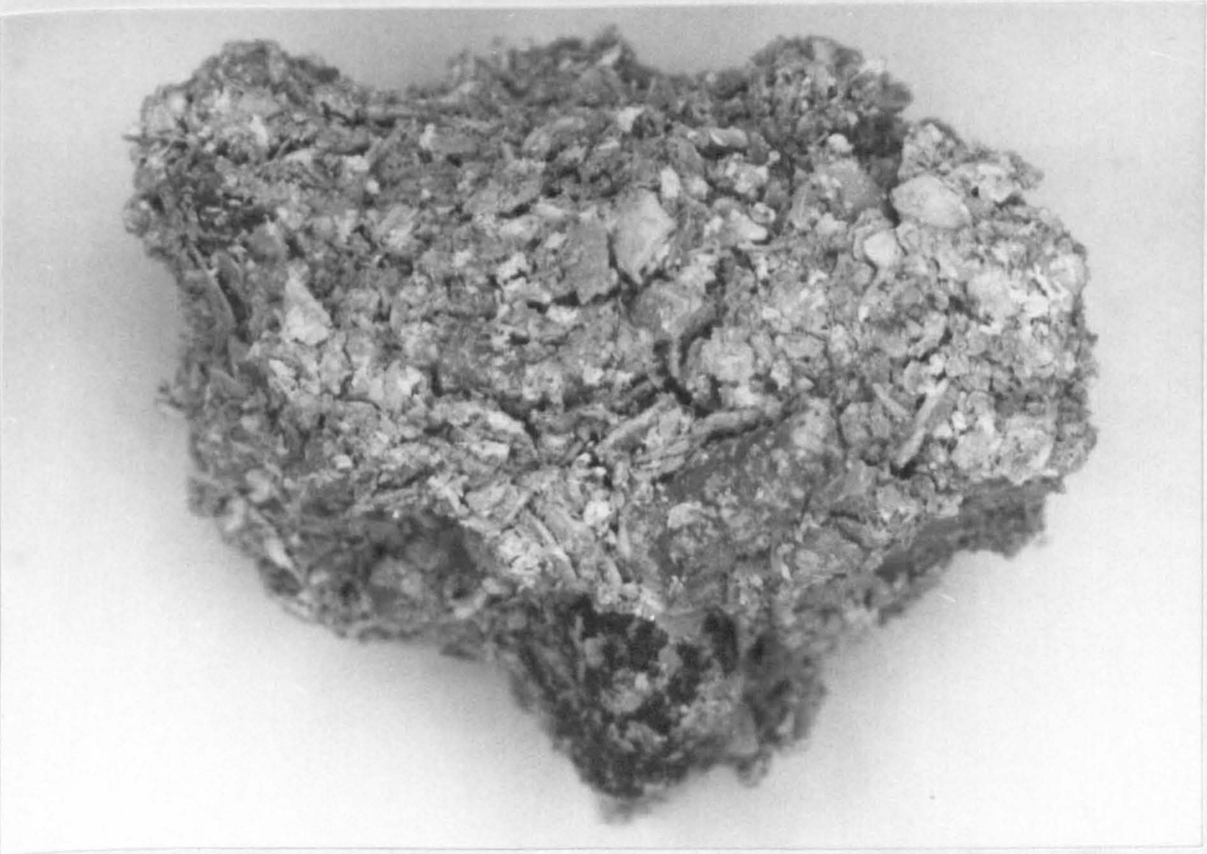


Table 20

Gut contents of Oystercatchers from the Ribble Estuary (1967 - 1973)

a) from the *Mytilus* scar of Church Scar (n = 11)
b) from Fairhaven Bay mudflats (n = 19)
c) from Banks Bay mudflats (n = 4)
d) from Horse Bank mudflats (n = 9)
e) from grasslands (see text) (n = 8)

	No. guts	% guts	Total no. items	items per gut	% by volume of gut content
a)					
Carcinus	1	9	2	0.2	0.1
Littorina	2	18	6	0.6	1.1
Mytilus	11	100	98	8.9	98.8
Macoma	1	9	1	0.1	+
Vegetable matter	9	82	-	-	-
b)					
Nereis	3	16	4	0.2	0.1
Arenicola	1	6	1	0.1	+
Carcinus	1	6	1	0.1	+
Littorina	1	6	2	0.1	0.1
Mytilus	2	10	3	0.2	1.1
Cardium	2	10	5	0.3	1.0
Macoma	16	84	109	5.8	51.6
Scrobicularia	18	95	62	3.3	46.8
Vegetable matter	4	21	-	-	-
c)					
Nereis	1	25	1	0.3	0.1
Macoma	1	25	3	0.8	5.8
Scrobicularia	4	100	29	7.3	94.1
Vegetable matter					
d)					
Nereis	1	11	1	0.1	+
Cardium	3	33	21	2.4	4.7
Tellina	1	11	1	0.1	+
Macoma	9	100	90	10.0	92.2
Scrobicularia	3	33	6	0.7	3.1
Vegetable matter	2	22	-	-	-
e)					
Earthworms	8	100	64	8.0	82.2
Tipulid larvae	4	50	43	5.4	17.8
Coleoptera imago	1	16	1	0.2	+
Gastropoda (Limax?)	1	16	1	0.2	+
Vegetable matter	6	75	-	-	-

+ = present

Table 21

Foods of Oystercatchers on the Ribble Estuary as assessed by direct observation:

a) from the *Mytilus* scar of Church Scar
b) from Fairhaven Bay mudflats
c) from Banks Bay mudflats
d) from Horse Bank mudflats

		Number observed	% observations
a)	*Littorina*	17	3.3
	Mytilus	461	89.4
	unidentified	38	7.3
	N	516	
b)	*Nereis*	2	0.5
	Cardium	45	10.0
	Macoma	327	72.5
	Scrobicularia	51	11.4
	unidentified	25	5.6
	N	450	
c)	*Macoma*	72	41.1
	Scrobicularia	96	54.9
	unidentified	7	4.0
	N	175	
d)	*Cardium*	294	17.2
	Macoma	1181	69.0
	Scrobicularia	163	9.4
	unidentified	76	4.4
	N	1714	

3. Inland grassland.

The six birds were collected from pasture near Scarisbrick and playing fields at Southport. Earthworms (mostly of the genera Lumbricus and Allolobophora) were the major prey found in all guts, with tipulid larvae occurring in three guts.

Data from direct observation are presented in Table 21. These in general confirm the data from gut analyses except that observation revealed less variation in diet than did gut analyses. For instance, 5.9% of food items observed taken by Oystercatchers on the mussel scar were not mussels whereas 8.4% of the items in the guts were not mussels. Similarly direct observation revealed only four regular prey on the inter-tidal zone whereas nine species were recorded from gut analyses. These differences were probably due to birds being collected after they have fed at several sites, different prey possibly being obtained at each.

CURLEW

The Curlew, more than any other wader considered here, is an inland-feeder as well as shore-feeder. Though Oystercatchers and Redshanks do feed inland to varying extents this is largely a secondary food source as far as the whole Ribble populations of those waders is considered. For the Curlew, however, it is the main food source and only relatively small numbers feed on the shore (chapters II , III, and IV). During the years of thisstudy guts have been examined from both areas whilst pellets have been collected from winter roosts (November - February on the south Ribble mosslands. In 1973 pellets were also obtained from birds feeding on the shore. These data are summarized in Tables 22 - 24.

Shore-feeders.

Like the godwits, Curlews are primarily polychaete/bivalve mollusc feeders on the shore, taking mainly the two commonest species Nereis

Table 22

Gut contents of Curlews from the Ribble Estuary:

a) from the shore (n = 12)

b) from inland (n = 11)

		No. guts	% guts	Total no. items	items per gut	% by volume of gut content
a)	*Nereis*	10	83	89	8.9	62.9
	Arenicola	3	25	6	0.5	8.8
	Cardium	1	8	1	0.1	0.4
	Macoma	5	42	57	4.7	26.7
	Scrobicularia	1	8	2	0.2	1.3
b)	Earthworms	9	82	127	10.6	39.5
	Tipulid larvae	5	46	129	10.7	16.3
	Coleoptera imago	1	9	3	0.3	0.5
	Spider	1	9	1	0.1	0.5
	Gastropoda (*Limax* sp.)	1	9	1	0.1	0.5
	seeds	9	82	394	35.8	40.4

Table 23

Analysis of Curlew pellets from the Ribble Estuary:

a) from the inter-tidal zone

b) from inland

		No. pellets	% pellets
a)	Nereis	9	53
	Cardium	1	6
	Macoma	16	94
	Scrobicularia	2	12
	Vegetable matter	4	24
	N	17	
b)	Tipulid larvae	6	9
	Tipulid pupae	1	1
	Diptera imago	2	3
	Coleoptera imago	2	3
	Seeds	51	75
	Other vegetable matter	68	100
	N	68	

Plate 2

Pellet of Curlew consisting of fragments of *Macoma balthica* and *Carcinus maenas*

Table 24

Foods observed taken by Curlews on the Ribble Estuary inter-tidal zone

	No. observed	%
Nereis	187	55.3
Arenicola	21	6.2
Macoma	56	16.6
unidentified	74	21.9
N	338	100.0

diversicolor and Macoma balthica. From the gut contents Nereis appears to dominate the diet whereas Macoma was commonest in pellets (though the number of pellets was small). Such differences were possibly due to the Macoma shell fragments being more likely to be produced in pellets whereas most Nereis jaws may pass out with the faeces. Thus pellets probably underestimated such soft prey fragments in some cases, even when analysis is based on the simple presence or absence criteria. This is further borne out by the absence of Arenicola marina in pellets whereas it forms an important minor food in the gut. Direct observation (Table 24) confirmed the predominance of Nereis and the importance of Arenicola as a minor prey species.

Diet on the shore did not appear to vary through the year, though as shown earlier, the proportion and numbers of Curlews feeding on the shore varies through the year.

Inland-feeders

Analysis of pellets collected from winter roosts are shown in Table 23, where a high proportion of plant material is seen to figure in the diet. However, from gut analysis earthworms and tipulid larvae appear to be more frequent than pellet data suggest. It is clear, therefore, that such soft-bodied prey are grossly underestimated in pellet analysis.

Most of the south Ribble mosslands comprise arable farmland and this probably accounts for the high frequency of plant material in the Curlew guts and pellets. The guts of two December birds taken on pasture held almost entirely earthworms: all other guts contained some cereal seeds.

Hibbert-Ware and Ruttledge (1945) reported from their analysis of Curlew pellets that the early autumn diet from pasture was predominantly insect and seed, earthworms and other soft prey comprising the bulk from November. They found also that Curlews feeding on soft prey produced very much fewer pellets which were smaller in size than the autumn insect/seed pellets ("size of a small pea"). It is possible that some such pellets were overlooked in this survey.

BLACK-TAILED GODWIT

Only four Black-tailed Godwit guts were examined, partly due to the difficulties of approaching the birds feeding on the oozy feeding areas and partly because of the national rarity of the species and the feelings of local conservationists (including the author). These four birds were necessarily collected as they flew onto the marsh immediately after feeding. They held a total of: Nereis 5 whole, 50 in various late stages of digestion but with heads at least still retaining the mandibles and 89 jaws; Scrobicularia one with valves broken and body partly digested but hinges still attached.

This preponderance of Nereis in the diet is borne out by direct observation off Lytham and Fairhaven in autumn (Table 25), where Nereis comprised 82.4% of the food identified with certainty. This is to be expected from the potential prey in the restricted Black-tailed Godwit feeding areas, which is dominated by Nereis.

BAR-TAILED GODWIT

It was possible to collect only 22 Bar-tailed Godwits during the study due mainly to the difficulties of approach within range on the main feeding grounds. Table 26 presents the analysis of the gut contents of these birds.

Two species predominate in the Bar-tailed Godwit diet on the Ribble, Nereis and Macoma. However, only three guts contained both species, the rest having either one or the other almost exclusively except for four birds collected on an Arenicola - rich area of Horse Bank and which held that species. Two guts from birds collected in the sandy-shore area of Ainsdale and Birkdale contained the remaining species given in Table 26.

Table 25

Foods of Black-tailed Godwits from direct observation on the Ribble Estuary in autumn

	No. observed	%
Nereis	686	68.0
Arenicola	29	2.9
Macoma	47	4.6
Scrobicularia	70	6.9
unidentified	177	17.6
N	1009	100.0

More extensive data were obtained by direct observation (Table 27) and these indicated a change-over in main prey on the middle estuary from Nereis in autumn and early winter to Macoma in late winter-spring. From the combined August-January data, Nereis formed 59% (332 out of 560) of the Nereis - Macoma fraction of the diet whilst in February-April Nereis formed only 27% (75 out of 282). This difference is significant ($x^2 = 51.6$; $p < 0.001$). Arenicola was confirmed by these observations to be an important minor prey of Bar-tailed Godwits on the middle estuary.

On the outer estuary, observations showed the Bar-tailed Godwits diet to be composed again mostly of polychaetes including the very low-shore tubicolous Lanice conchilega and Pectinaria koreni.

REDSHANK

Table 28 gives the analysis of gut contents of Redshanks collected during the period 1967 - 73 on the Ribble Estuary outside of the breeding season (April-July).

Saltmarsh.

Those Redshanks feeding on saltmarshes take a large variety of prey, which fall generally into four groups corresponding to the four invertebrate habitat groups on the saltmarshes. (Greenhalgh unpublished):

1. The outer marsh-edge, with Corophium and Hydrobia predominating. Macoma was found in three guts in this zone and these had presumably been collected by the Redshanks on the mudflats before the tide had forced them to the marsh edge.
2. The higher marsh pools where Sphaeroma rugicauda and Gammarus duebeni predominate. The beetle Ochtebius impressicollis was taken in one Redshank gut from a saltmarsh pool.
3. The vegetation-soil of the saltmarsh where arachnids, the beetle Phaedon acmoraciae, diptera and lumbricids occur.
4. The saltmarsh creeks in which, besides Corophium, tubificids occur

Table 26

Gut contents of Bar-tailed Godwits from the Ribble Estuary (N = 22)

	No. guts	% guts	Total no. items	items per gut	% by volume of gut content
Nereis	12	54.5	87	4.0	49.4
Phyllodoce	2	9.1	5	0.2	0.5
Glycera	1	4.5	3	0.1	0.3
Arenicola	4	18.2	6	0.3	1.1
Bathyporeia	1	4.5	8	0.4	0.3
Macoma	12	54.5	140	6.4	47.9
Tellina	2	4.5	3	0.4	0.5

Table 27 Foods observed taken by Bar-tailed Godwits on the Ribble Estuary intertidal zone

	Aug-Oct	%	Nov-Jan	%	Feb-Apr	%	Total	%
Nereis	161	63.5	271	60.6	75	25.2	507	50.7
Phylladoce/Glycera	0	0.0	14	3.1	0	0.0	14	1.4
Nepthys	6	2.4	22	4.9	0	0.0	28	2.8
Lanice	28	11.0	0	0.0	0	0.0	28	2.8
Arenicola	11	4.3	38	8.6	12	3.8	61	6.2
Pectinaria	1	0.0	4	0.9	0	0.0	4	0.4
Corophium	1	0.3	0	0.0	0	0.0	1	0.1
Cardium	0	0.0	7	1.6	0	0.0	7	0.7
Tellina	0	0.0	3	0.7	3	1.0	6	0.6
Macoma	47	18.5	82	18.5	207	70.0	336	33.8
Scrobicularia	0	0.0	5	1.1	0	0.0	5	0.5
Totals	254	100.0	446	100.0	297	100.0	997	100.0

in numbers of up to 4 million per m^2 in anaerobic mud. The one bird collected whilst feeding in a gutter on Banks Marsh had 12.3 g fresh weight of Tubifex sp. in its oesophagus and gizzard.

Spartina edge.

A high proportion of Redshank on the Ribble feed at or within about 100m of the edge of the main Spartina zone (chapter IV). As would be expected from the invertebrate fauna of these areas (chapter VII) Corophium forms the bulk of the diet. Some birds collected in these areas and which had a high proportion of Hydrobia in the gizzard had probably been pushed into the Spartina zone by the flowing tide just before they were collected.

Data from pellet analysis in this zone (Table 29) contained a high proportion of the remains of Hydrobia and other species which occur only occasionally in this zone. This again was possibly due to birds feeding over the low tide period further down the shore depositing pellets containing such remains at roosts in the Spartina. Bias is also caused, however, by the fact that Hydrobia has more undigestible material than Corophium and is thus more apparent in pellets, causing over-estimation of Hydrobia. Furthermore, pellets composed mostly or wholly of Corophium remains seem to disintegrate more readily than those containing a high Hydrobia content. It may also be that Redshanks feeding on Hydrobia produce more pellets than those feeding on Corophium, owing to the larger bulk of undigestible material in Hydrobia.

These factors have been taken into account in the final analysis (chapter X).

Mud and sand-flats.

From both pellet and gut analysis, Hydrobia appears to form the bulk of Redshank diet on Horse Bank whereas on Salter's Bank Corophium

Table 28 Gut contents of Redshanks from the Ribble Estuary (1967-74)

a) from *Festuca*-*Puccinellia* saltmarshes of the south Ribble (n = 38),
b) from inner Horse Bank and Banks Sands (within 100m of edge of *Spartina* marsh) (n=22),
c) from Horse Bank beyond the edge of the *Spartina* zone (n=9),
d) from the inter-tidal zone of the north Ribble (n=15)
e) from grassland (see text) (n=11).

		No. guts	% guts	Total no. items	items per gut	% by volume of gut content
a)	Lumbricids	1	3	2	0.05	-
	Tubificid	1	3	see text		-
	Sphaeroma	15	39	42	1.1	-
	Gammarus	14	37	51	1.3	-
	Corophium	23	61	259	6.8	-
	Tipulid larva	6	16	31	0.8	-
	Diptera imago	9	23	23	0.6	-
	Coleoptera imago	2	5	2	0.05	-
	Araneida	2	5	4	0.1	-
	Hydrobia	2	5	57	1.5	-
	Macoma	3	8	13	0.3	-
	Enteromorpha) *Chaetomorpha*)	13	34	-	-	-
b)	*Nereis*	3	14	3	0.2	+
	Corophium	20	91	1182	53.8	76.8
	Hydrobia	9	41	397	18.1	17.4
	Diptera imago	1	5	2	0.1	+
	Enteromorpha) *Chaetomorpha*)	22	100	-	-	-
c)	*Nereis*	1	11	1	0.1	+
	Corophium	2	22	117	13.0	17.2
	Hydrobia	7	78	609	67.6	55.4
	Macoma	6	67	15	1.7	5.2
	Enteromorpha) *Chaetomorpha*)	9	100	-	-	-
d)	*Nereis*	7	44	32	2.1	13.3
	Corophium	10	67	392	25.9	38.7
	Littorina	2	13	3	0.2	1.0
	Hydrobia	4	27	298	19.7	21.3
	Macoma	6	40	59	4.0	22.3
	Enteromorpha) *Chaetomorpha*)	1	7	-	-	-
e)	Lumbricids	6	54	22	2.0	-
	Tipulid larvae	9	82	96	8.7	-
	Diptera imago	3	27	29	2.6	-
	Lepidoptera imago	1	9	1	0.1	-
	Coleoptera imago	1	9	1	0.1	-
	Araneida	4	36	11	1.0	-
	Myriapoda	1	9	1	0.1	-
	Gastropoda	3	27	6	0.5	-
	Barley-Oat seeds	4	36	28	2.5	-

Table 29

Analysis of Redshank pellets from the inter-tidal zone of the Ribble Estuary (August-March)

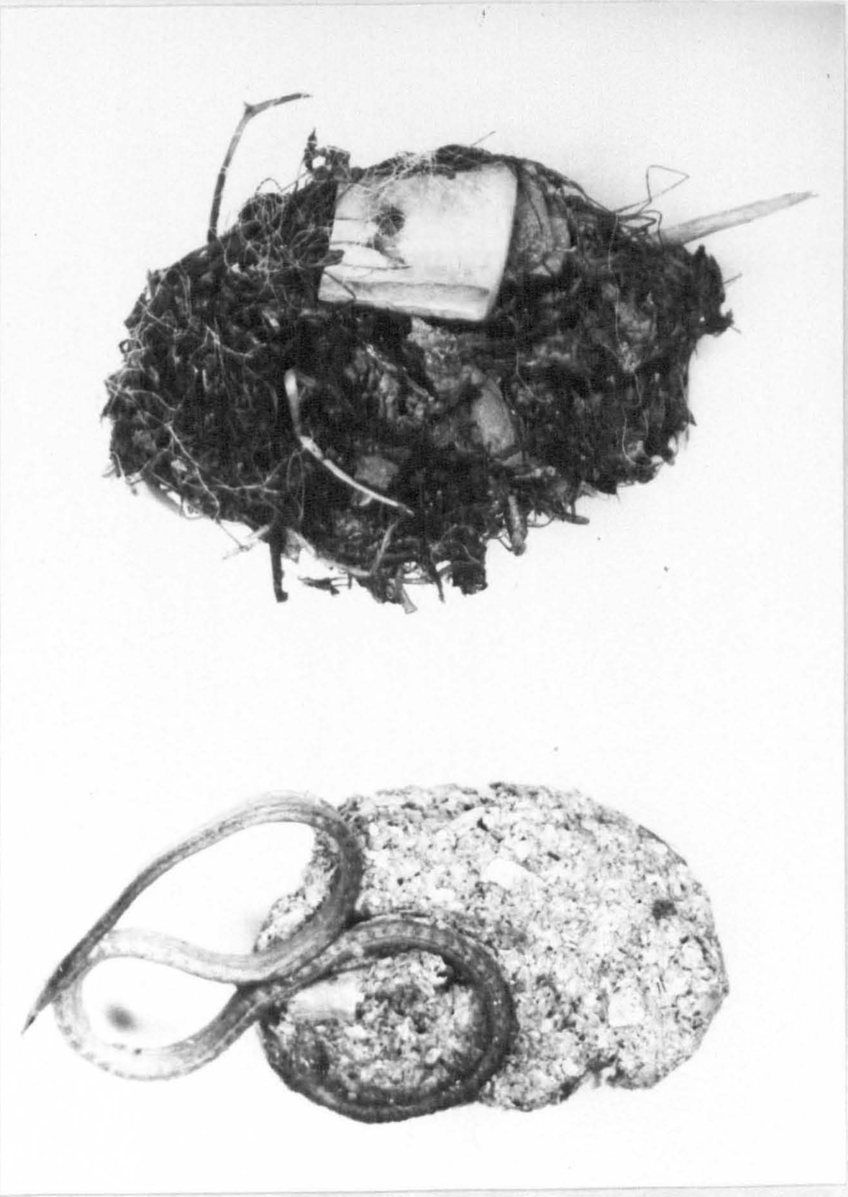
	Within 100m of Spartina marsh		Horse Bank beyond 100m of marsh edge	
	No. pellets	% pellets	No. pellets	% pellets
Nereis	135	32.8	124	38.7
Pygospio (?)	15	3.7	2	0.6
Oligochaeta	3	0.7	0	0.0
Nematoda	31	7.5	23	6.9
Carcinus	29	7.0	57	17.8
Sphaeroma	2	0.4	0	0.0
Gammarus	4	1.0	0	0.0
Corophium	320	77.9	96	30.0
Diptera larva	12	2.9	0	0.0
Diptera pupa	7	1.7	0	0.0
Diptera imago	37	9.0	14	4.4
Hydrobia	299	72.7	257	80.2
Mytilus spat	10	2.4	16	5.0
Macoma	34	8.3	153	47.8
Seeds	21	5.1	0	0.0
Other vegetable matter	350	85.2	298	93.4
N	411		320	

Plate 3

Pellets of Redshank

Top - Pellet consists of Macoma balthica and one Nereis diversicolor

Bottom - Pellet consists of Mytilus edulis



forms an equal or slightly larger proportion of the diet than the Hydrobia fraction. Corophium would appear to be underestimated in such crude data (see Appendix I and above) and in the analysis of chapter X correction factors (Appendix I) have been applied following Goss-Custard (1969) and Greenwood and Goss-Custard (1970).

On both Horse and Salters' Bank Macoma forms an important fraction of the diet, especially in autumn, whilst Nereis reaches its peak contribution in the diet during the winter (Tables 28 - 29).

Grassland.

Redshanks collected from grassland from playing fields at Southport reclaimed saltmarshes at Hundred End and on the Inner Ribble Marshes. On such areas diets were very varied, three birds collected from the latter site in autumn containing each having five different foods in the gut.

KNOT

As can be seen from Table 30, giving the analysis of pellet contents of Knot from the Crossens - Banks area, the food of Knot does not appear to vary through the year to any great extent, the diet being possibly just a little more varied in winter and early spring than in autumn. This is suggested by the fact that only 41 out of 175 autumn pellets (23.4%) contained more than a single prey species compared with 48 out of 91 winter and spring pellets (52.8%). ($x^2 = 16.1$, $p < 0.001$). All these pellets were collected over the same area of the upper-middle shore.

Knot diet does vary however according to the period in the tide cycle, as also Prater (1972) found in Morecambe Bay (Table 31). On the upper shore (above about 3m O.D.) the food consists primarily of Hydrobia collected immediately after the birds have left the roosts and possibly, but not certainly, before the birds enter the roosts. On this latter point, it should be recalled that a high proportion of Knot do not feed on the upper zone as they enter the roosts (chapter IV), flying directly into roost from the middle shore.

Table 30 Analysis of Knot pellets from the Crossens and Banks areas of the Ribble Estuary

	August - November		December-April		TOTAL	
	No. pellets	% pellets	No. pellets	% pellets	No. pellets	% pellets
Nereis	15	9	14	15	29	10.9
Carcinus	2	1	3	3	5	1.9
Corophium	10	6	11	12	21	7.9
Littorina	3	2	1	1	4	1.5
Hydrobia	80	46	49	54	129	48.4
Tellina	0	0	1	1	1	0.4
Macoma	123	70	71	78	194	72.8
N	175	-	91	-	266	-

Table 31 Gut contents of Knot from three tidal levels on the Ribble Estuary

a. ± 1 hour of roost : "upper zone" (n = 11)

	No. guts	% guts	Total no. items	items per gut	% volume
Nereis	1	9	1	0.1	-
Corophium	5	45	65	5.9	7.3
Hydrobia	10	91	563	51.1	87.2
Macoma	2	18	40	3.6	5.3

b. 2 - 3 hours before and after low water : "mid zone" (n = 12)

Nereis	6	50	18	1.4	1.0
Carcinus	1	8	1	0.1	-
Corophium	5	41.5	47	3.9	8.9
Hydrobia	10	83.5	1187	98.9	38.6
Cardium	1	8	1	0.1	-
Macoma	6	50	68	5.7	34.1

c. ± 1 hour of low water : "lower zone" (n = 20)

Nereis	3	15	7	0.4	0.1
Cardium	4	20	18	0.9	2.4
Tellina	2	10	5	0.3	0.3
Macoma	20	100	554	27.7	92.6

On the mid-shore level (approximately 1 - 3 m O.D.) Hydrobia still comprises the bulk of the food in some Knot gizzards, though in others Macoma appears to be the major prey. Probably the birds containing Hydrobia had obtained that species from the higher feeding areas, for the majority of food observed to be taken by Knot at these shore-levels was definitely or probably mostly Macoma. Furthermore, only seven Hydrobia were found in the oesophagus at this level whereas on the upper shore a mean of 51 per gut occurred there. This again suggested that the birds were feeding less on Hydrobia on the middle shore.

Finally, over the lower shore below 1m O.D. Macoma forms the bulk of the diet. Also, except for Nereis (which was identified at this level only from the jaws in the gizzard and thus had possibly been collected higher up the shore), the remainder of the lower zone diet consisted of other bivalves, though these contribute a relatively tiny fraction to the Knot's diet.

SANDERLING

Sanderlings principally are sandy-shore feeders and Table 34 presents an analysis of Sanderling guts from such areas in the Formby-Birkdale and St. Annes-Blackpool areas. A comparison between the data of Table 32 and that presented in chapter VII on invertebrate distribution shows that Sanderlings take the whole range of species occurring in these shores, but mainly the most abundant sandy-shore amphipod Bathyporeia pelagica and its associates. These are mostly collected, as explained in chapter IV, at the tide's edge.

Birds feeding on the lower shore took some Nephthys caeca, whilst others which remained around pools, channel edge or wet rippled sand were found to contain the polychaete Pygospio elegans and, in one case, a small specimen of Carcinus maenas in the gut. Pygospio is probably a major food on parts of the middle shore, but is almost certainly underestimated in the gut analysis owing to very rapid digestion and lack of hard parts.

Table 32 Gut contents of Sanderling from the Ribble Estuary (n = 38)

	No. guts	% guts	Total no. items	items per gut
Glycera	1	2.6	1	-
Nephthys	7	18.4	34	0.9
Scoloplos	1	2.6	2	-
Pygospio	4	10.5	23	0.6
Carcinus	1	2.6	1	-
Eurydice	10	26.3	27	0.7
Bathypoeia	28	73.9	537	14.1
Haustorius	5	13.2	9	0.2
Corophium	5	13.2	13	0.3
Hydrobia	1	2.6	1	-

That some Sanderlings feed in the middle estuary during periods of heavy passage is borne out by the gut analysis of one taken in a flock feeding on Horse Bank: its gizzard contained Corophium volutator and a single Hydrobia ulvae.

DUNLIN

As described in chapter III, a variable proportion of Dunlin feeds throughout the low tide period on the upper shore zone with the remainder having a cycle similar to, although less extensive than, that of the Knot: they move down the shore to the middle zone on the ebb where they feed over low water, advancing before the tide to the roost. A small proportion of Dunlin also feed at high tide in the roost and a similarly small proportion at low tide on the lowest shore zone.

On the upper zone (including roost) the diet consists mainly of Corophium (Table 33) for on this zone Hydrobia is very sparse (chapter VII). The remains of Hydrobia in the gizzards from this level had probably been obtained on the lower shore.

On the mid-shore level Corophium and Hydrobia are co-dominant components of the diet, except for the period around low water when Hydrobia is the main prey and the Corophium fraction of the diet greatly diminished. This may be due to the very low proportion of Corophium in the upper 1cm of substrate at low tide (chapter VII) and this species being to some degree temporarily inaccessible. Relatively few Dunlins appear to feed on the lower middle-shore (up to about 2m O.D.) where Corophium are very sparse.

The small numbers of Dunlins feeding on the lowest shores feed almost exclusively on Macoma, the bird collected and shown in Table 33C having 38 remains of Hydrobia in its gizzard probably having moved down from the upper and middle shores just prior to collection, for Hydrobia are very sparse on the lower shore (chapter VII).

Table 33 Gut contents of Dunlin at three tidal levels on the Ribble Estuary

a. Upper shore (above 3m O.D.) (n = 11)

	No. guts	% guts	Total no. items	no. items per gut	% volume
Nereis	1	9	3	0.3	-
Corophium	11	100	173	15.7	82
Hydrobia	3	27	42	3.8	18

b. Middle shore (0.5 - 3m O.D.) (n = 29)

	No. guts	% guts	Total no. items	no. items per gut	% volume
Nereis	10	34	20	0.7	0.2
Corophium	17	59	289	10.0	33.5
Hydrobia	19	66	825	28.4	64.1
Macoma	6	27	46	1.6	2.2

c. Lower shore (bleow 0.5 m O.D) (n = 5)

	No. guts	% guts	Total no. items	no. items per gut	% volume
Nereis	2	40	14	5.4	9.2
Hydrobia	1	10	38	7.6	2.4
Macoma	4	80	96	19.2	88.4

SIZES OF MAJOR PREY

Measurements were taken from specimens of prey, mostly from gut and pellet analyses, which showed the sizes of the ingested prey. In some cases the intact animals could be measured (height of Hydrobia shell, diameter of Macoma valve, etc.). Most prey items recovered had, however, been digested to some extent and full measurements could not be made. In these cases measurements were taken of characters which bore a relationship to body size.

The following measurements were taken from whole or fragments of prey: in Nereis jaw size measured with a microscope fitted with an eye-piece micrometer; in Hydrobia maximum height of shell; in bivalve molluscs maximum shell width; in crustaceans body length. Dry weight of the ingested prey could be ascertained from the curves and other data showing the relationship between these characters and dry weight, presented in chapter VII.

Sufficient data have been obtained for only the main prey and these are presented here (Table 34). Further analyses for other prey may be possible in the future when more data are available.

It is clear from these data, that although the bulk of waders are feeding on a small number of prey species, there is relatively little overlap in sizes of prey taken, differences in the mean size of any one prey taken by two or more wader species being significant ($p < 0.05$). An exception is in the sizes of Macoma taken by Bar-tailed Godwits and Redshanks (p 0.10).

In the cases where data are sufficient to allow seasonal comparisons of the sizes of prey taken by single wader species, the sizes taken reflect to some extent the variations in prey size through the year in the substrate. This is dealt with in Chapters VII and IX.

Table 34 Sizes of the major invertebrate prey species taken by waders on the Ribble Estuary

Prey	Predator	N	Measurement	x	S.E.	Season
Nereis	Bar-tailed Godwit	98	Jaw-size	0.34	0.012	Aut-winter
	Redshank	116		0.32	0.031	Aut-winter
	Knot	46		0.28	0.022	Aut-winter
	Dunlin	37		0.27	0.018	Aut-winter
Hydrobia	Redshank	490	Shell height	3.81	0.22	Aut-winter
	Knot	1180		3.79	0.21	Aut-winter
	Dunlin	615		2.04	0.11	Aut-winter
Mytilus	Oyster-catcher	680	Valve length	24.7	3.94	Jul-Sep
		910		33.8	3.17	Oct-Dec
		455		31.2	2.88	Jan-Mar
Cardium	Oyster-catcher	416		23.5	2.1	Winter 1968-9
		670		21.6	1.8	Winter 1973-4
Scrobicularia	Oyster-catcher	43		17.6	3.2	Aut-winter
Macoma	Oyster-catcher	68		12.7	0.47	Aug-Oct
		95		11.4	0.62	Nov-Feb
	Bar-tailed Godwit	79		8.41	0.78	Aut-winter
	Redshank	74		8.27	0.91	Aut-winter
	Knot	168		6.29	0.63	Jul-Sep
		92		7.03	0.58	Oct-Nov
		80		6.41	0.71	Dec-Jan
		117		5.96	0.39	Feb-Mar
	Dunlin	63		4.70	0.31	Aut-winter
Corophium	Redshank	289	Length	5.41	0.41	Jul-Sep
		310		6.37	0.48	Oct-Dec
		388		6.21	0.39	Jan-Mar
	Dunlin	166		3.82	0.29	Jul-Nov
		71		5.19	0.46	Dec-Feb
		49		4.86	0.53	Mar-Apr
Bathyporeia	Sandlering	210		3.36	0.19	Jul-Aug
		61		4.58	0.24	Dec-Jan
		90		4.11	0.36	May

CHAPTER VI FACTORS AFFECTING THE DISTRIBUTION OF PREY SPECIES

Previous workers have investigated many environmental factors which might influence invertebrate distribution in estuaries. Some have restricted their analyses to salinity measurements and crude descriptions of substrate (sand, sandy-mud, etc.) . At the other extreme are those who have sought correlations between not only particle size, salinity and organic component of the substrate and invertebrate populations but also chemical characteristics such as phosphate and carbonate content. The analysis of physical characters is extremely time consuming and, as only a small proportion of time could be spent on these, it was decided to examine the following:

1. Sediment size distribution.
2. Water content of surface at low tide.
3. Loss on ignition: a crude estimation of organic content of the substrate.
4. Salinity of water in and over the substrate.
5. Tide coverage of substrate.
6. Temperature of substrate.

1. Sediment Size Distribution

Method: Samples were collected during the regular invertebrate sampling from May to September 1973 throughout the estuary and were oven-dried at 105°C. Each sample was then divided through the standard Wentworth Scale Seives into the four fractions: silt (< 0.0625 mm.), very fine sand (0.125 - 0.0625 mm.), fine sand (0.25 - 0.125 mm.) and medium-coarse sand (1 - 0.25 mm.). Larger granules, small stones and organic debris (i.e. pieces of Spartina, Salicornia, small twigs, etc.) were removed. Each of the four samples was then weighed to the nearest one milligram and each expressed as a percentage of the total dry weight of the sample. These data were then expressed cumulatively and a hyperbolic tangent curve ($y = \tan h\ x$) fitted. From this the 50% point was found and thence the abscission value, which gave the seive-size which would allow 50% of the sample through the seive. This value is known as the 'median particle diameter size' (Morgans 1956). Essentially the same method was employed by McLusky (1971).

Results: In general median particle size varied between 30 and 245 microns though samples from saltmarsh creeks on Longton and Clifton marshes had a median particle size of approximately 15 - 20 microns and the mud trapped by the stone training walls off Warton Marsh approximately 20 - 25 microns.

Taken as a whole, the distribution of sediment particle size follows the pattern observed elsewhere e.g. Morecambe Bay (Anderson 1972) in which median particle size is smallest highest up the shore and is coarsest lower on the shore. Also, particle size is lowest towards the head of the estuary (around the Inner Marshes) and decreases towards the open sea (Formby - Squires Gate). This can be seen from Figure 28 showing the median particle diameter size along five transects across the estuary.

2. Water content of surface substrate at low tide

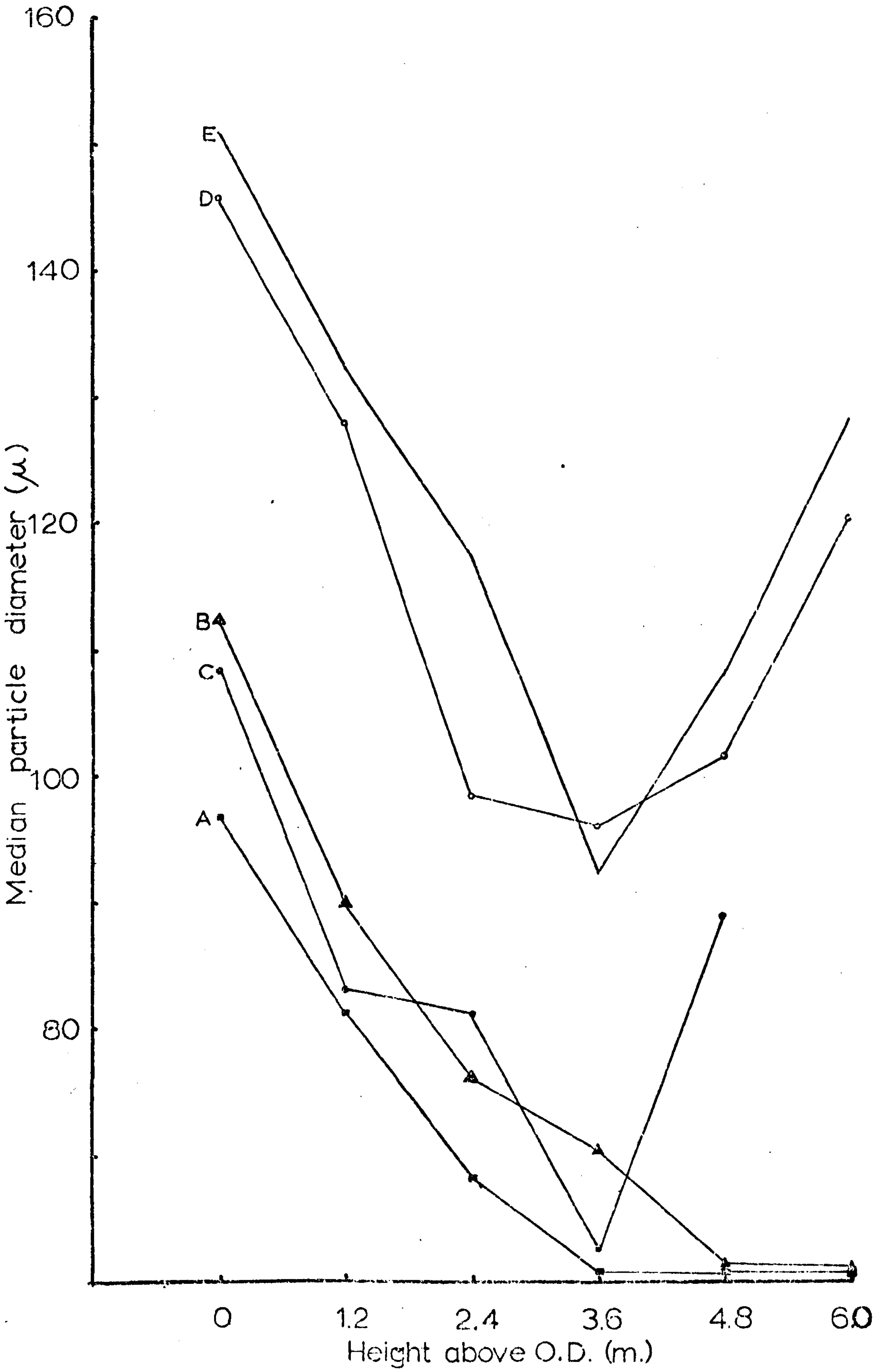
Method: Samples of approximately 150g of the upper 1 cm. of the substrate were collected and immediately placed in small, dry polythene bags which were securely fastened. The samples were weighed to the nearest milligram and the bags then removed and weighed, this weight being subtracted from the total weight of the sample. The sample was then dried in an oven at 105°C to constant weight. The percentage loss of weight due to water evaporation was calculated.

Results: The results from five transects at various points across the intertidal zone are given in Figure 29.

On the inner and central estuary there is a general tendency for water content to decrease down the shore. This is to be expected somewhat from particle size analysis, for substrates with smaller particle sizes will generally hold more water by capillarity. Also in these areas the highest

Figure 28

Median particle diameter size at six shore levels along five transect lines at A. Banks Sands, B. Horse Bank, C. Salter's Bank (east of 33 longtit. O.S. line on map SD32), D. Salter's Bank (west of 33 longtit. O.S. line on map SD32), E. Birkdale Sands.


160
140
120
100
80
Median particle diameter (μ)
0
1.2
2.4
3.6
4.8
6.0
Height above O.D. (m.)
E
D
B
C
A

banks have least gradient and frequently up to 15 mm. of standing water covers the substrate. On the outermost estuary, consisting of very coarse sand, this did not apply: steeper gradients and less capillary attraction results in a low water content at most levels, the lower shore having slightly more water possibly as a consequence of it having been wetted by the sea more recently than the upper shore.

3. Loss on ignition

Method: Weighed samples of oven-dried substrate were burnt in a muffle-furnace at about 500°C for three hours. Losses in weight were mostly accountable to the combustion of organic material, though as Morgans (1956) and McLusky (1971) have pointed out, a small proportion of this loss will be due to evaporation of water held in soil colloids and CO_2 evolved from carbonates. Results were expressed as percentage loss, and a measure of organic carbon in the samples.

Results: The smallest losses on ignition were recorded at Birkdale and Squires Gate (0.42% and 0.53% respectively) and increased up the river reaching maxima at Freckleton Naze (4.98%), on the River Douglas at Tarleton (5.09%) and Longton Marsh (4.17%). A gradient also exists on transects running across the shore, the highest loss on ignition being closer to the high tide levels and the lowest at the low tide marks (Figure 30).

4. Salinity of water in and over the substrate

Method: Samples of water from the Irish Sea were collected, and at hourly intervals from six sample points on the Ribble Estuary: the Pinfold (SD32 314232), Horse Bank (SD32 331208), the Ribble Channel at two sites (SD32 315258 and 352264), Frekleton Naye and off Lea Marsh. All samples were collected and analysed in June 1973. For the Irish Sea the mean concentration of chloride was estimated by titrating 100 cc. samples with sodium nitrate using potassium dichromate as indicator. This gave a mean salinity of 34.2‰. The remaining samples from the Ribble Estuary were analysed

Figure 29

Water content of the upper 1 cm. of substrate along the five transect lines given in Figure 28

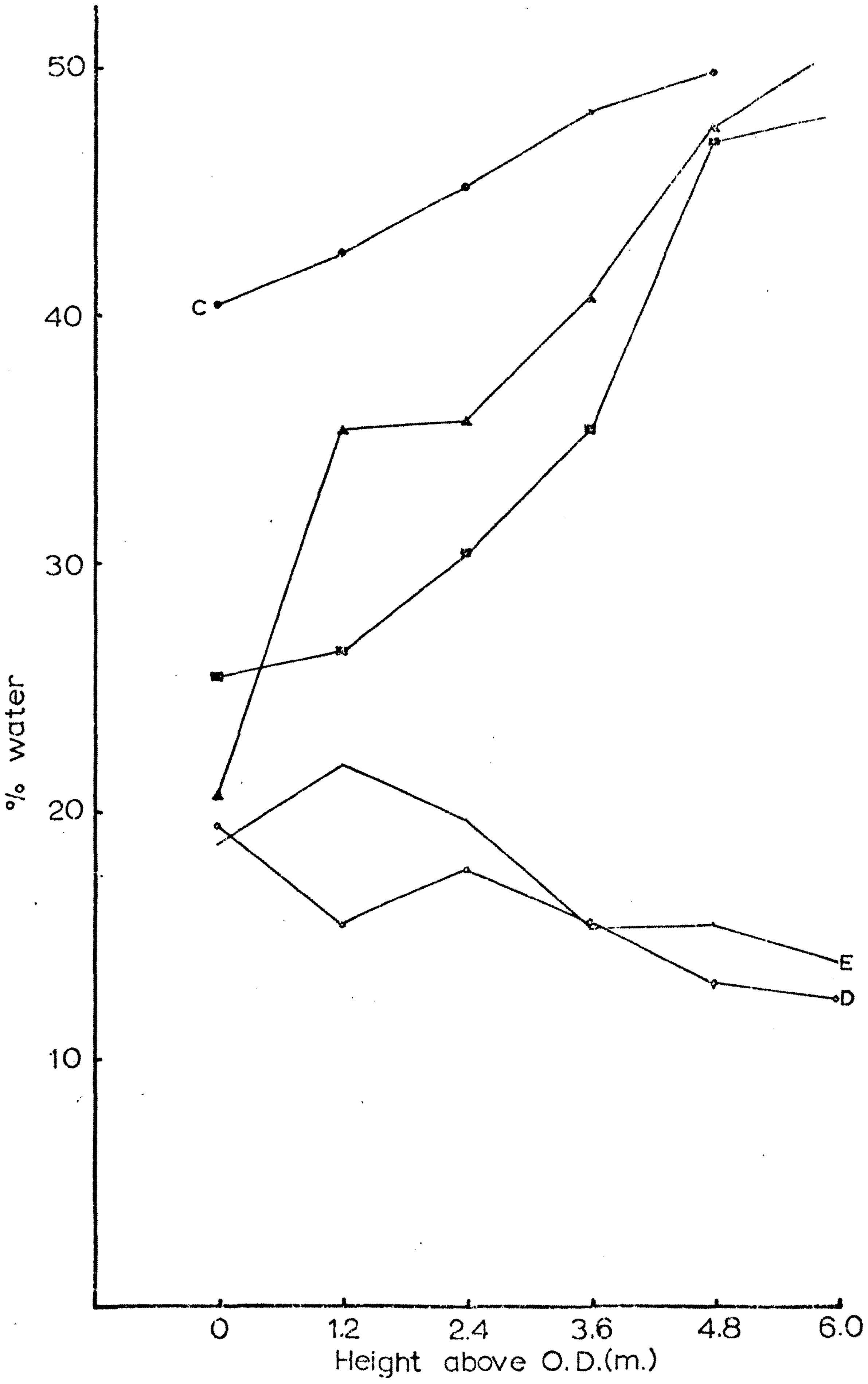
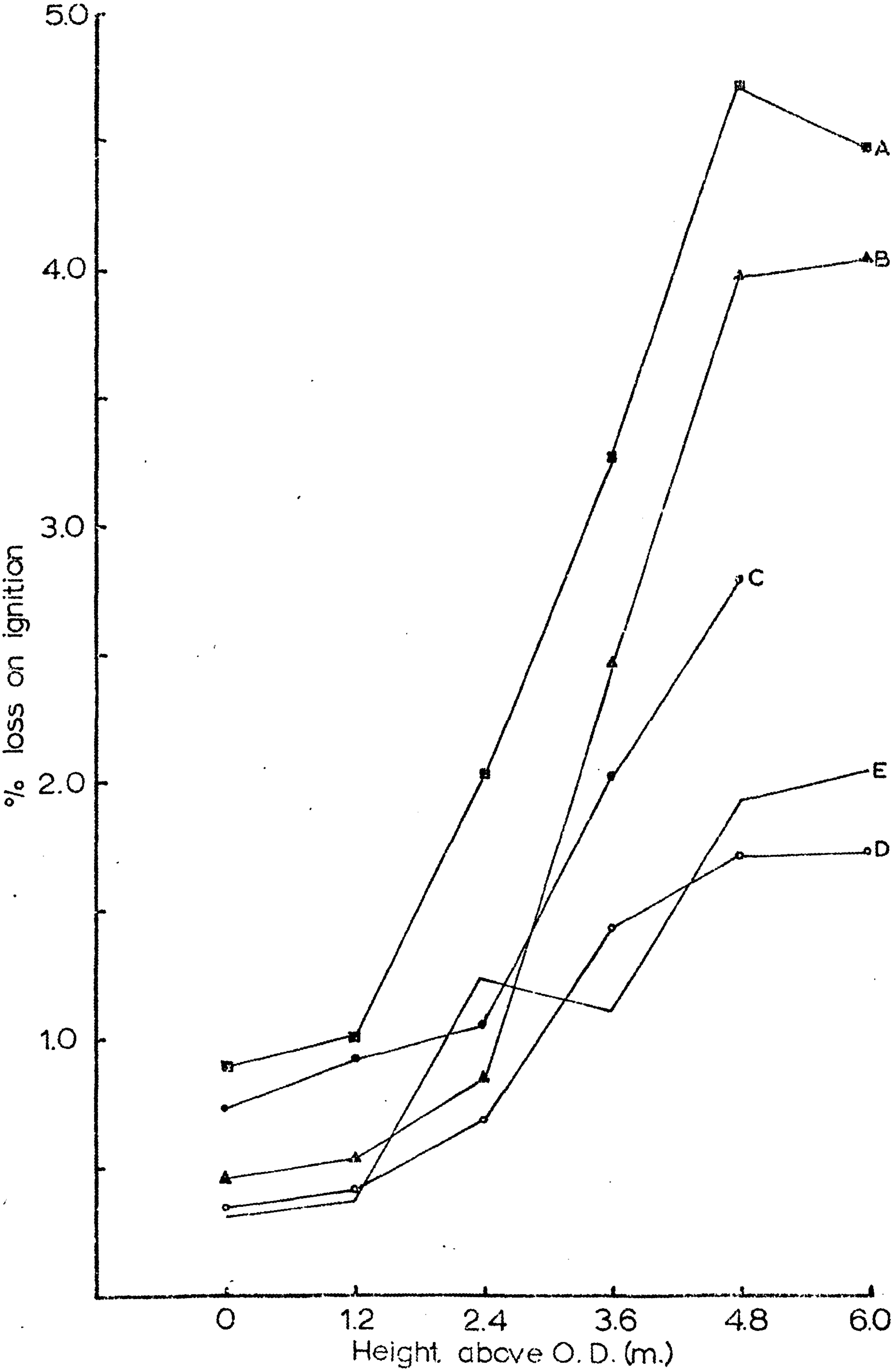

50
40
30
20
10
% water
0
1.2
2.4
3.6
4.8
6.0
Height above O.D.(m.)
C
E
D

Figure 30

Percentage loss on ignition on the five transect lines given in Figure 28


5.0
4.0
3.0
2.0
1.0
% loss on ignition
0
1.2
2.4
3.6
4.8
6.0
Height above O.D. (m.)
A
B
C
D
E

in the same way, though results have been converted to 'percentage seawater' a method adopted by several workers (e.g. Popham 1966 a and b) and one which makes comparison between samples easier.

Results: At low tide the dilution due to fresh water being carried down the river resulted in almost fresh water in the two channels, the Pinfold having the highest low tide salinity possibly as a result of very little freshwater passing down it (there is relatively little overflow from Crossens Sluice in summer, when these samples were taken) and the Pinfold being probably the major channel for drainage of the intertidal zone.

Increase of tide resulted at all sample points in an increase of salinity, though as expected points nearer the sea always had a higher salinity (Figures 31 - 32). Popham (1966 a) correlated this pattern of salinities with the distribution and abundance of invertebrate species in the Ribble Estuary, finding a progressive decrease of marine estuarine species in a series of samples up the estuary.

It has generally been considered that water in estuaries in temperate regions at high tide is stratified; due to its higher specific gravity, seawater tends to lie below the freshwater flowing down-river. Such a situation is known as a 'positive estuary' (Eltringham 1971, McLusky 1971). The Ribble, however, like the Mersey (D.S.I.R. 1938), and Dee (Stopford 1951) shows no clear stratification, at least in the main part of the estuary west of the Naze and Longton Marsh due to the relatively small amount of freshwater being carried down the channels rapidly being mixed with the huge amount of saltwater being carried into the estuary. Samples taken from various depths in July 1973 through the tide cycle from a pylon on Salter's Bank showed an identical salinity at the surface with the deepest water. It is quite likely, however, though this was not investigated, that at certain times (e.g. when the freshwater passing down the main channel is large due to heavy rain inland) that stratification occurs on the inner estuary.

Figure 31

Tidal changes in salinity expressed as % seawater through the neap tide cycle at six sites on the Ribble Estuary.

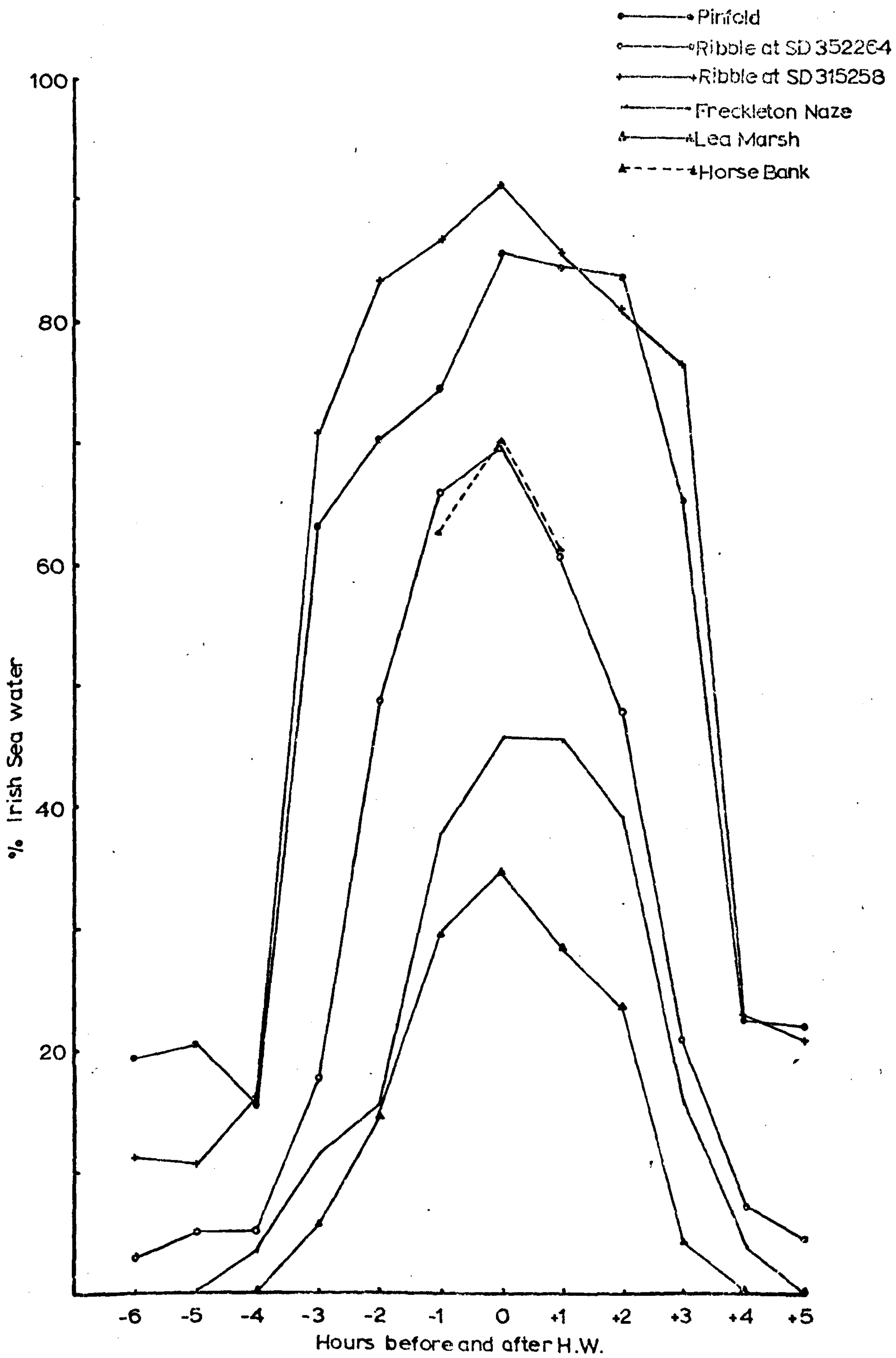
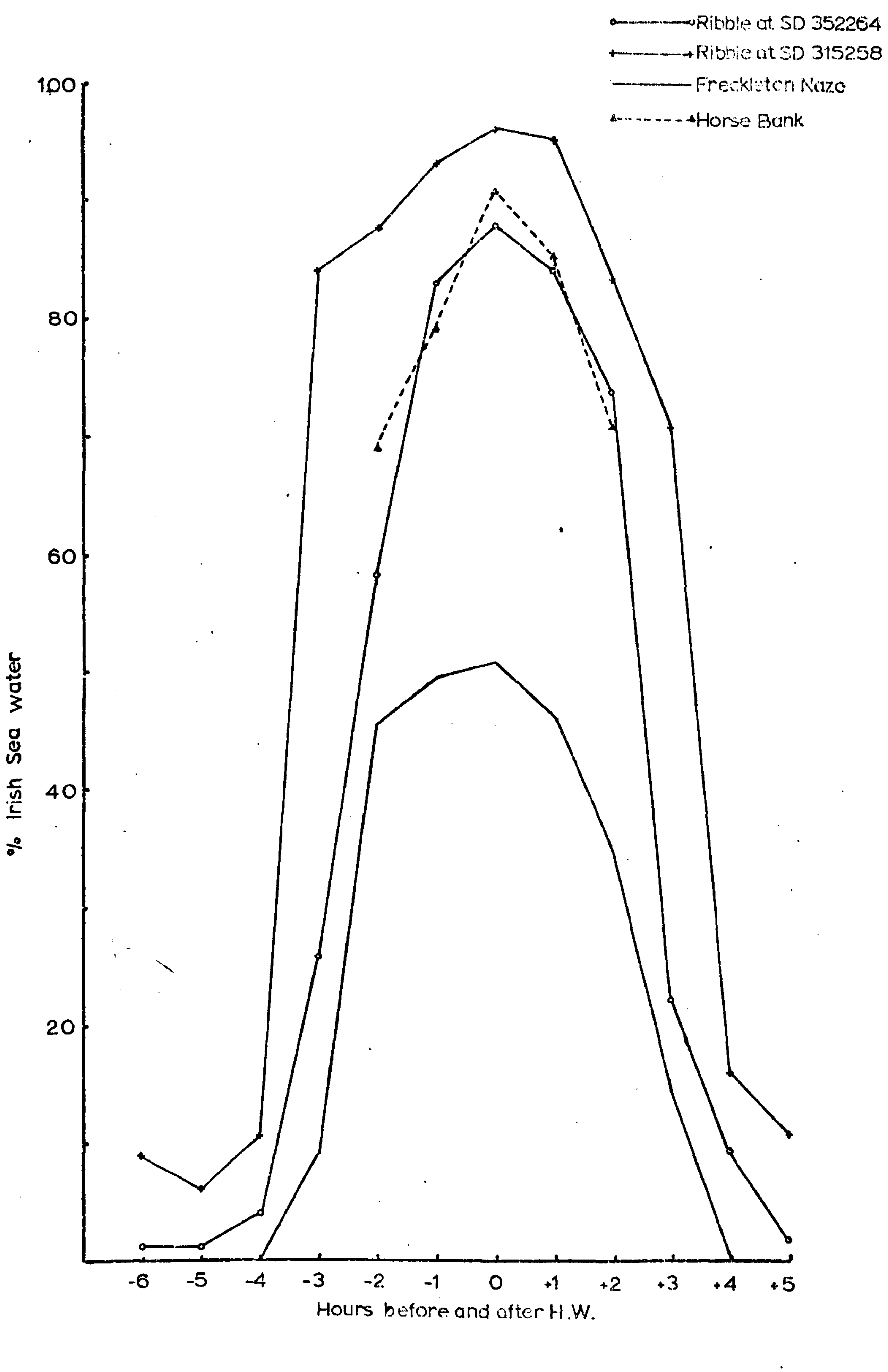

Pinfold
Ribble at SD 352264
Ribble at SD 315258
Freckleton Naze
Lea Marsh
Horse Bank
% Irish Sea water
100
80
60
40
20
-6
-5
-4
-3
-2
-1
0
+1
+2
+3
+4
+5
Hours before and after H.W.

Figure 32

Tidal changes in salinity expressed as % sea water through the spring tide cycle at four sites on the Ribble Estuary.



Ribble at SD 352264
Ribble at SD 315258
Freckleton Naze
Horse Bank
100
80
60
40
20
% Irish Sea water
-6
-5
-4
-3
-2
-1
0
+1
+2
+3
+4
+5
Hours before and after H.W.

The effects of neap and spring tides on coverage of the estuary at high tide has been considered, and salinity differences on two such contrasting tidal regimes was also examined. Figure 31 shows the salinities at six points in the estuary on neap tides whilst Figure 32 shows salinities at four points on spring tides. At low tide concentrations are lower on spring tides than neap tides whilst salinity is greater at all points on a high spring tide compared with a high neap tide. These effects are presumably due to the greater bulk of seawater entering the estuary on the spring tide producing the higher salinity at high tide, with the greater fall in tide and consequently faster ebb producing a lower salinity on spring tide ebbs.

Salinity of interstitial water

Samples were collected by digging a hole in the substrate and collecting the water which percolated into the hole. Altogether seven samples were collected: these are shown in Table 35. As with water in the channels and over the substrate at or around high water, salinity of interstitial water tends to decrease up-river, being highest in the sandy shores of the outer estuary and being almost freshwater at points east of Freckleton Naze. Thus, whilst euryhaline species of invertebrate such as Nereis diversicolor and Corophium volutator might be able to regulate their body fluid concentration to the extent that they might be able to adapt to the whole range of salinities along the estuary, polystenohaline species such as Bathypoeia pelagica and Tellina tenuis on the outer estuary would be more restricted in range and consequently waders preying on such polystenohaline species would be similarly restricted.

5. Tide coverage of substrate

The difference between the highest spring tides (about 9.5 metres) and the lowest neap tide (6.0 metres) is about 3.5 metres. Also, the spring tide ebbs much lower than the neap tides (by up to 3.2 metres). Thus, with the slight gradients of the Ribble Estuary intertidal zone, the amount of shore covered by the tide varies considerably. For instance, on a nine

Table 35 Interstitial water salinities at seven points on the Ribble Estuary

Sample Point	Grid Ref.	Salinity (%)	% Sea water
Formby Point	SD 264067	30.5	88
Birkdale	302166	27	77
Horse Bank	320226	16	46
Foulnaze	302235	25	72
Salter's Bank	324262	14	40
Salter's Bank	300261	18	51
East of the Naze	437272	3	9

metre tide all 84 km^2 of intertidal zone are covered by the tide whilst on an eight metre tide 71 km^2 are covered and on a six metre tide 65 km^2 are covered. This means that invertebrates on the upper shore are not emersed by the tide often for many days on end, whereas during neap tides the lowest shores, exposed during spring tide ebbs, are covered by water throughout the low tide period.

Not only might this affect invertebrate distribution and densities, but also it means that on spring tides the waders have less time on the feeding areas, being excluded from them for up to three hours at each tide cycle, though a greater area of feeding area is exposed whereas on neap tides the waders need not leave the feeding areas, though less is exposed.

6. Temperature of the substrate

Temperature of the substrate was recorded on most visits in order to examine the effects of temperature on variation in depth distribution of invertebrates and on feeding rates and patterns of the waders. Goss-Custard (1969) found that in the Redshank feeding rate, success and ingestion rate fell-off when substrate temperature fell below 5°C: this was investigated.

Conclusion

The distribution of varying physical characteristics on the Ribble Estuary is related with position in the estuary. By influencing the distribution of the major estuarine invertebrates, these physical characteristics will have an indirect influence on the distribution and feeding of the wader species which prey on those invertebrates.

CHAPTER VII THE DISTRIBUTION OF PREY SPECIES IN THE INTERTIDAL ZONE

Introduction

The invertebrate epifauna and infauna of many British estuaries have been studied to varying degrees, though in most cases the amount of quantitative work has been small. Popham (1966 a and b) carried out a small study of the Ribble Estuary, publishing a list of the species he encountered but giving no quantitative data. Other studies have been more thorough: Fraser (1932) and Bassindale (1938) from the Mersey Estuary set a pattern continued by Beanland (1940) from the Dovey Estuary, Spooner and Moore (1940) from the Tamar Estuary, Holme (1949) from the Exe, Brady (1943) from Northumberland, Stopford (1951) and Perkins (1952) from the Dee, Howells (1964) from the Towey and Anderson (1972) from Morecambe Bay. All these gave some idea of numbers, at least of the more abundant members of the macrofauna and attempted correlations between densities and physical characteristics.

Other studies have concentrated on single species or groups which form an important proportion of the macrofauna, the following being relevant to this study in that they deal with species which are important wader foods on the Ribble: Watkins (1941), Meadows (1964), McLusky (1967, 1968, 1970) on Corophium volutator, R. C. Newell (1962, 1964, 1965) on Hydrobia ulvae, Brafield and G. E. Newell (1961), R.C. Newell (1965) and Lamens (1967) on Macoma balthica, Wells (1945), G.E. Newell (1948) and Longbottom (1970) on Arenicola marina and Hughes (1970 a and b) on Scrobicularia plana.

In the present study emphasis was put upon those species important as wader foods. Not only were distribution and density studied but also fluctuations of the populations.

Distribution of sampling sites In July 1971 when the sampling was planned, a preliminary series of samples was taken to locate the major invertebrate populations of the estuary. The following sampling surveys were then undertaken:

1. Extensive surveys

These involved five ~~grid~~ area surveys in which the sampling points were chosen randomly:

a) Salter's Bank grid in November-December 1972: 100 samples
b) Church Scar grid in November 1972: 53 samples
c) Fairhaven Bay grid in November 1972: 8 samples
d) Horse Bank grid in January-February 1973: 150 samples
e) Bog Hole grid in June-July 1972: 40 samples
f) Training walls by Ribble Channel in November 1973: 20 samples

Eight transects were also carried out between M.H.W. and M.L.W. across the intertidal zone as follows:

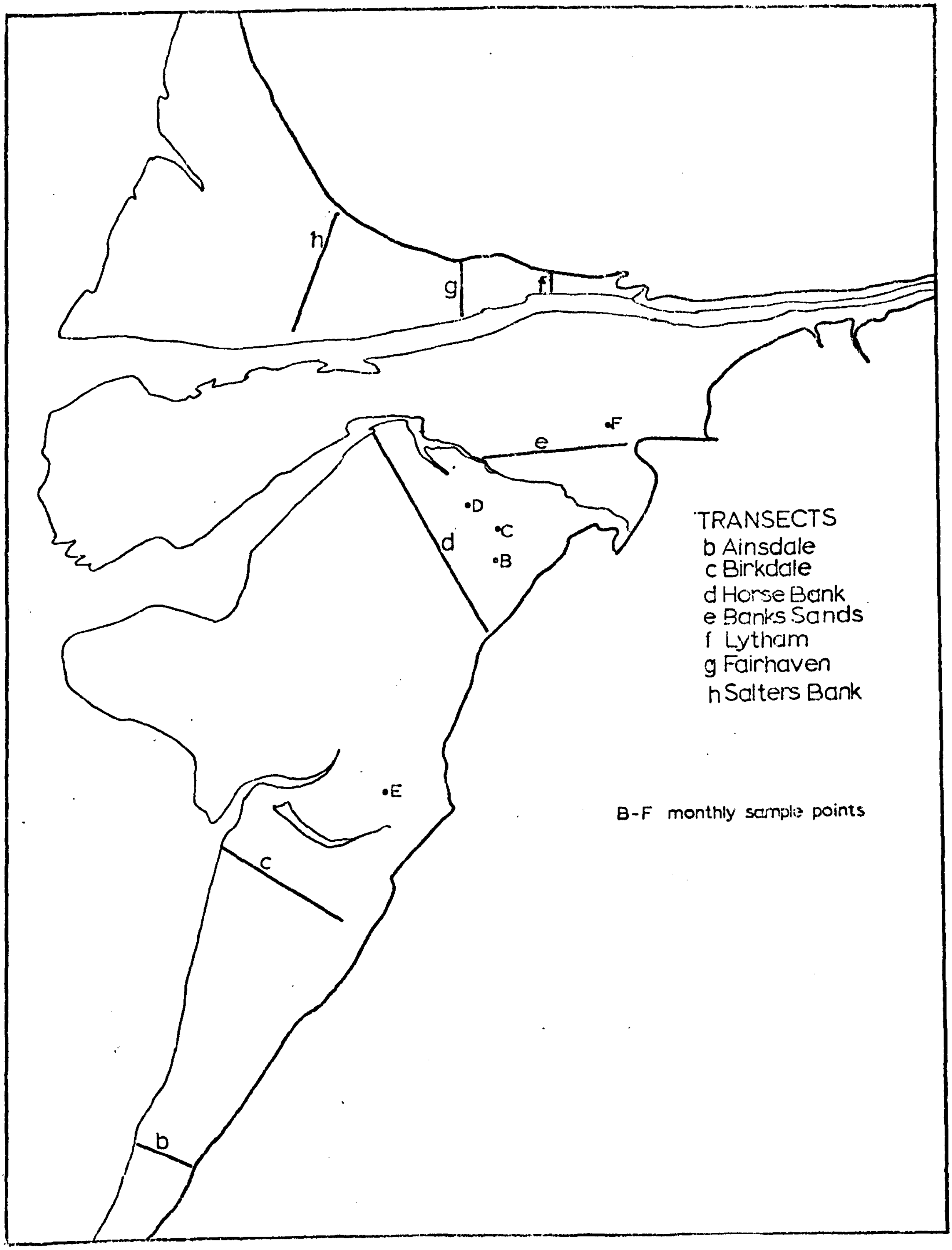
a) Formby Point in February 1972: 60 samples
b) Ainsdale Sands in July 1972: 56 samples
c) Birkdale Sands in July-August 1972: 60 samples
d) Horse Bank in July-August 1972: 64 samples
e) Banks Sands in August 1972: 52 samples
f) Lytham shore in July 1972: 28 samples
g) Fairhaven Bay in August 1973: 84 samples
h) Salter's Bank in September 1973: 108 samples

2. Monthly samples

These were carried out for two of the most abundant members of the macrofauna *Corophium volutator* and *Hydrobia ulvae* at five sample points on Horse Bank and Banks Sands:

Figure 33

Positions of transect lines and selected sampling points



h
g
f
e
•F
•D
•C
•B
d
TRANSECTS
b Ainsdale
c Birkdale
d Horse Bank
e Banks Sands
f Lytham
g Fairhaven
h Salters Bank
•E
B-F monthly sample points
c
b

Point B	SD 32	347214
Point C		348225
Point D		341236
Point E		328188
Point F		371243

and sizes and biomass of the wader food species throughout the year.

METHODS

Sampling Unit Initially a sampler of size $0.25m^2$ was considered suitable but the transport and seiving of such large samples proved to require excessive time. A much smaller unit was, therefore, chosen which would give a reasonable number of organisms in each sample (usually between 30 and 100 of the most abundant species such as Hydrobia, Corophium and Bathyporeia): a cylinder with a diameter of 10cm and a depth of 10cm. Such samples were quickly obtained with little disturbance to the surrounding substrate, and easily carried in polythene bags. By using this sampler, many small samples could be taken at one sampling point rather than just one or two larger ones. Within 24 hours in the laboratory the samples were placed into a seive of mesh diameter 0.5 mm and the sand/mud was hed out. The seive retained the macrofauna which was kept for counting.

Such a sampler was not satisfactory for larger, less numerous and deeper - dwelling invertebrates such as Arenicola, Macoma and Scrobicularia and for these a quadrat was used of $0.25m^2$ and the sample dug out onto a polythene sheet, worked through by hand and counted in the field. The animals obtained were then taken back to the laboratory.

For both types of sample the numbers recorded were expressed as number per m^2, a procedure carried out by most previous workers who have used similar small samples (e.g. Anderson 1972) and one which makes results between studies more comparative. At each point on every visit ten samples were taken at random on a grid 20 metres square based on a fixed point which marked the sample point. Visits were made as near to the end of the month as possible from July 1971 to June 1973 with samples also in October and December 1973. Occasionally sampling was not possible in a particular month.

Investigation of invertebrate size and biomass

From some samples numbers of each species were retained and measurements made, which could generally be taken as a gauge of body size (these are given later in the account) taken. The animals were then separated into size categories and dried to constant weight in a silica gel desiccator. Thence, the mean dry weight of each size class was calculated.

Dried animals from each major prey were 'pelleted' and combusted in a Phillipson microbomb calorimeter and the calorific value per mg. dry weight (ash free and ash included) was calculated.

RESULTS

The locations of the eight main transect lines are given in Figure 33, and the results (expressed as mean number of organisms per m^2, following the method of presentation of previous workers) as well as details of sampling points are given in Tables 36 - 43.

Samples were also analysed from other selected sites: the man-made stony substrate around Southport Sewage outfall and adjacent areas (Table 44), the shingle Fairhaven Bay (Table 45), Church Scar (Table 46) and the stone training-walls by the Ribble shipping channel off Salter's Bank and Foulnaze (Table 47). Data from other surveys will be incorporated in the text.

Table 36 Results of Formby Transect (numbers per m^2)

Transect Point	VI	VII	VIII	IX	X	XI	XII	XIII	XIV	XV
Approx. height (O.D.) in m.	6.8	6.1	5.4	4.0	3.2	2.2	1.0	O.D.	-1.0	-2.0
Nereis diversicolor	0	6	5	3	0	0	0	0	0	0
Phyllodoce maculata	0	0	0	0	2	17	22	9	2	0
Glycera convoluta	0	0	0	0	1	14	8	39	21	0
Nephthys caeca	3	11	19	14	26	87	41	18	2	3
Scoloplos armiger	0	0	0	0	1	0	14	93	42	76
Lanice conchilega	0	0	0	0	0	0	0	0	0	2
Corophium arenarium	0	0	0	28	620	1600	3220	860	203	14
Bathyporeia pelagica	18	109	916	284	2108	3429	3714	4927	1018	5214
Haustorius arenarius	0	0	0	0	11	40	76	32	14	12
Eurydice pulchra	0	0	208	184	381	457	100	180	260	400
Tellina tenuis	0	0	0	0	0	1	3	0	2	16

N.B. No animals were obtained from higher sampling points (I - V)

Table 37 **Results of Ainsdale Transect (numbers per m^2)**

Transect Point	IV	V	VI	VII	VIII	IX	X	XI	XII	XIII	XIV	XV
Approx. height (O.D.) in m.	4.0	3.0	2.5	2.0	1.5	1.0	0.5	O.D.	-0.5	-1.0	-1.5	-2.0
Nereis diversicolor	0	0	0	254	4	0	0	0	0	0	0	-
Phyllodoce maculata	28	0	0	382	0	0	0	0	0	0	0	-
Nephthys caeca	0	0	0	0	0	0	3	46	32	20	28	-
Scoloplos armiger	0	0	0	0	0	2	8	14	108	42	24	-
Arenicola marina	0	0	3	2	0	0	0	0	0	0	0	-
Pygospio elegans	0	0	0	0	0	0	0	0	1000	80	190	-
Spiophanes bombyx	0	0	508	1085	760	0	0	0	0	0	0	-
Lanice conchilega	0	0	0	0	0	0	0	0	0	0	20	98
Pectinaria koreni	0	0	0	0	0	0	0	0	0	0	1	2
Corophium arenarium	0	0	30	60	40	0	0	0	0	0	0	0
Bathyporeia pelagica	890	1018	1230	510	910	328	196	256	1164	840	636	1780
Haustorius arenarius	0	0	0	0	0	0	0	0	0	279	123	146
Eurydice pulchra	0	0	0	0	0	0	0	82	208	132	381	426
Carcinus maenas	0	0	2	0	0	0	0	0	0	0	0	0
Macoma balthica	0	0	1	0	0	0	0	0	0	0	0	0
Tellina tenuis	0	0	0	0	0	0	0	0	8	31	28	14

N.B. No animals were obtained at low water from higher sampling points.
Where no sample taken, shown in table by '-'

Table 38 Results of Birkdale Transect (numbers per m^2)

Transect Point	VII	VIII	IX	X	XI	XII	XIII	XIV	XV
Approx. height (O.D.) in m.	3.0	2.5	2.0	1.2	1.0	O.D.	-0.4	-0.9	-1.7
Nereis diversicolor	0	3	0	0	9	0	0	0	0
Nereis pelagica	0	0	0	0	0	3	0	16	4
Phylladoce maculata	0	18	96	87	164	271	216	22	8
Glycera convoluta	0	0	5	16	120	92	178	397	202
Nephthys caeca	9	34	94	8	7	12	0	0	0
Scoloplos armiger	0	0	0	0	0	1	4	9	3
Pygospio elegans	20	0	0	0	0	0	0	0	0
Lanice conchilega	0	0	0	0	0	0	0	0	3
Pectinaria koreni	0	0	0	0	0	0	14	0	0
Corophium sp. *	21	9	6	0	0	0	0	0	3
Bathyporeia pelagica	95	418	2290	5960	5320	3760	4100	2055	1840
Haustorius arenarius	0	0	23	465	198	226	315	26	34
Eurydice pulchra	0	87	429	1420	1395	1120	685	186	221
Macoma balthica	0	14	3	27	19	1	0	0	0
Tellina tenuis	0	0	0	0	0	0	2	14	6
Donax vittatus	0	0	0	0	0	0	0	0	1
Mactra corallina	0	0	0	0	0	0	1	0	0

* see text

N.B. No animals were obtained at low water from higher sampling points.

CONTAINS

PULLOUTS

Table 40 Results of Banks Bay transect (numbers per m^2)

Transect Point	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	XIII
Nereis diversicolor	0	0	190	136	98	276	392	589	139	186	202	181	116
Arenicola marina	0	0	0	39	0	21	96	42	117	26	0	3	0
Pygospio elegans	0	0	0	0	0	174	0	1120	640	86	57	30	3620
Corophium volutator	254	5207	7210	6477	4064	2413	2159	3810	3556	1200	4699	2413	28
Hydrobia ulvae	3302	1121	90	28760	127	254	508	286	0	0	220	0	0
Macoma balthica	0	0	0	80	122	142	253	514	111	261	69	183	161
Scrobicularia plana	0	0	110	132	104	97	41	9	4	0	3	6	0
Mya arenaria	0	0	0	0	0	0	0	0	0	0	0	0	2
Cardium edule	0	0	0	0	0	0	0	0	0	0	7	19	0

Sample point I in edge of Spartina ,
rest on wet mud and sandy mud.

Table 41 Results of Lytham shore transect (numbers per m^2)

Transect Point	I	II	III	IV	V	VI	VII
Nereis diversicolor	180	273	420	325	596	284	473
Arenicola marina	0	0	94	16	0	21	13
Pygospio elegans	0	1142	920	0	57	230	0
Corophium volutator	1480	6250	3710	2920	1140	320	195
Jaera marina	5	0	0	0	0	0	1
Carcinus maenas	0	0	3	0	2	0	0
Hydrobia ulvae	640	320	11400	280	935	450	75
Macoma balthica	36	71	118	1421	410	186	321
Scrobicularia plana	4	27	31	9	8	14	5
Mya arenaria	0	0	0	0	0	0	2
Cardium edule	0	0	0	0	0	1	0

CONTAINS

PULLOUTS

Table 44 Macrofauna of a) Stone substrate and b) mud substrate around Southport sewage outfall at the Bog Hole

a.	Mean per m^2	S.E.	n
Nereis diversicolor	286.0	47.9	40
Cirratulus cirratus	27400	384.6	40
Corophium volutator	660.8	76.8	40
Gammarus zaddachi	132.4	29.6	40
Carcinus maenas			
large (25 mm <)	9.5	1.3	20
small (25 mm >)			
(i) Enteromorpha	8940	103.6	20
(ii) Stones	3230	41.7	20

Also Palaemonetes varians 5 specimens, Hippolyte varians 1 specimen, Littorina littorea 2 specimens, Hydrobia ulvae 3 specimens.

b.	Mean per m^2	S.E.	n
Nereis diversicolor	1140	94.4	10
Arenicola marina	7.8	2.1	10
Corophium volutator	4820	78.9	20
Hydrobia ulvae	455	34.6	20
Macoma balthica	915	41.0	10
Scrobicularia plana	30.8	6.3	10

Also Carcinus maenas 9 small specimens

TABLE 45

Fauna of muddy shingle shore of Fairhaven Bay

	Mean no. per m^2	S.E.
Corophium volutator	117.8	15.3
Jaera marina	78.4	9.0
Ligia oceanica	336.6	19.4
Carcinus maenas	9.3	1.7
Littorina littoralis	3.2	0.8

Also *Marinogammarus marinus* 7 specimens, Hydrobia ulvae 16 specimens.

TABLE 46 Fauna of Church Scar, North Ribble

	Mean no. per m^2	S.E.
Nereis diversicolor *	470	-
Corophium volutator *	1200	-
Gammarus zaddachi	7.6	2.14
Jaera marina	320.5	21.79
Ligia oceanica	92.6	11.21
Carcinus maenas:		
2.5 cm <	11.4	0.93
2.5 cm >	21.6	5.88
Hydrobia ulvae	13.9	4.16
Littorina littorea	4.9	0.82
Mytilus edulis	323.0	14.69

* open to great error due to sampling difficulties.

Also recorded at edge of Scar: *Macoma balthica* and *Scrobicularia plana*.

TABLE 47

Fauna of training walls of Ribble Channel off Foulnaze, November 1973

	Mean no. per m^2	S.E.
Nereis diversicolor	abundant *	
Corophium volutator	present *	
Gammarus zaddachi	0.9	1.21
Jaera marina	4.1	1.90
Ligia oceanica	3.6	2.11
Carcinus maenas:		
2.5 cm<	4.6	0.22
2.5 cm>	8.1	5.36
Littorina littorea	6.5	2.30
Mytilus edulis	17.4	4.12

Only those species taken by waders are considered here. Nomenclature follows Barrett and Yonge (1958) and Eales (1967).

POLYCHAETES

Nereis diversicolor

This is by far the most abundant species taken over the estuary as a whole, showing typical euryhaline distribution extending from coarse sand at Formby and, to a lesser extent, Squires Gate in which salinity reaches sea water concentration (Figures 31, 32), to the upper estuary reaches around Freckleton Naze, the Douglas Estuary and the Inner Marshes where water concentration is almost fresh (Figures 31, 32). It also occurs on the lowest shore levels down to - 2m O.D. in the middle estuary reaches of Horse Bank, Banks Sands and the eastern part of Salter's Bank off Fairhaven and Lytham up to beyond M.H.W.N. Occasionally *Nereis* has been obtained from samples taken in saltpans high on *Festuca* saltmarshes at between 6 and 7 m O.D.

Highest densities tend to occur in the middle estuary at about mid-shore level (-1m to 1.5m O.D.), being especially abundant in areas of smaller particle size close to channels. Highest densities were recorded from such sites on Banks Bay (up to 589 per m^2), Lytham shore (596 per m^2), Salter's Bank off Fairhaven close to channels associated with the water pipe of Fairhaven Lake (up to 865 per m^2), a system of freshwater channels from Crossens Marsh crossing Horse Bank (932 per m^2) and around the Bog Hole off Southport sewage outfall (986 per m^2).

Previous authors (e.g. Anderson 1972 and Spooner and Moore 1940) attributed high density to either mud or the effects of freshwater, both factors with which *Nereis* density seems to be correlated ($r = 0.912$, p 0.001) on the Ribble. However, it may well be that the higher densities are a result of the higher organic content of such muddy areas (Figure 30). This is further suggested by two sets of samples collected in December 1973 in two muddy creeks at Conder Green on the Lune Estuary, Lancashire. In one the *Nereis* density was 483 per m^2 ± 19.8

(n = 15) and in the other, into which a pipe opened carrying waste milk and raw cattle sewage from a dairy farm, density was 2,847 per m^2 ± 246.7 (n = 10).

Ribble Estuary densities of Nereis are slightly higher than those reported from Morecambe Bay by Anderson (1972), but much lower than those reported by Spooner and Moore (1940) from the Tamar (3,000 per m^2) and Howells (1964) from the Towy (1,212 per m^2).

Nephthys caeca

This errant polychaete showed less euryhaline distribution than Nereis, occurring at most shore levels below M.H.W.N. in the areas west of Southport pier (Birkdale to Formby) and St. Annes to Squires Gate whilst on the middle estuary on eastern Horse Bank and Salter's Bank it occurred only on the lower levels (usually below O.D.) in the more sandy areas. East of Fairhaven Bay and Horse Bank Nephthys was not recorded. Such a distribution suggests that Nephthys is a species requiring substrata with larger particle size (median particle diameter of at least 90μ) and this occurs only in the outer estuary at most shore levels and on the lower shore of the middle estuary (Figure 28). The species may, however, be reacting more especially to the higher salinities of the outer estuary areas, a conclusion Bassendale (1938) and Spooner and Moore (1940) came to. Certainly, at Ainsdale and between St. Annes and Squires Gate Nephthys density is maintained in the occasional muddy pools which occur on these sandy areas.

Nephthys density is much lower than Nereis, the maximum recorded being 294 per m^2. Spooner and Moore (1940) regarded 100 - 300 as "normal" in the Tamar whilst Holme (1949) recorded a maximum of 104 per m^2 from the Exe and Anderson (1972) gave a range of 25 - 100 per m^2 in Morecambe Bay.

Scoloplos armiger

Scoloplos armiger shows a pattern of distribution similar to Nephthys caeca though in general it occurs slightly lower on the shore (usually below about 1m O.D.) in the outer Formby - Birkdale and Squires Gate areas, though in the middle estuary it can be found on western Horse Bank almost up to M.H.W.N. Density is generally lower than that of Nephthys, with a maximum of 190 per m^2 on Foulnaze.

On the Tamar Estuary, Spooner and Moore (1940) found Scoloplos density highest in areas with Zostera sp. (up to 152 per m^2), Brady (1943) found densities of up to 618 per m^2 in Northumberland shores and Holme (1949) recorded a maximum of 108 per m^2 in the Exe Estuary. At Skalling in Denmark, Thramdrup (1935) reported up to 460 per m^2. It seems remarkable, considering the apparent suitability of substrate, that Anderson (1972) did not record the species in Morecambe Bay.

Pygospio elegans

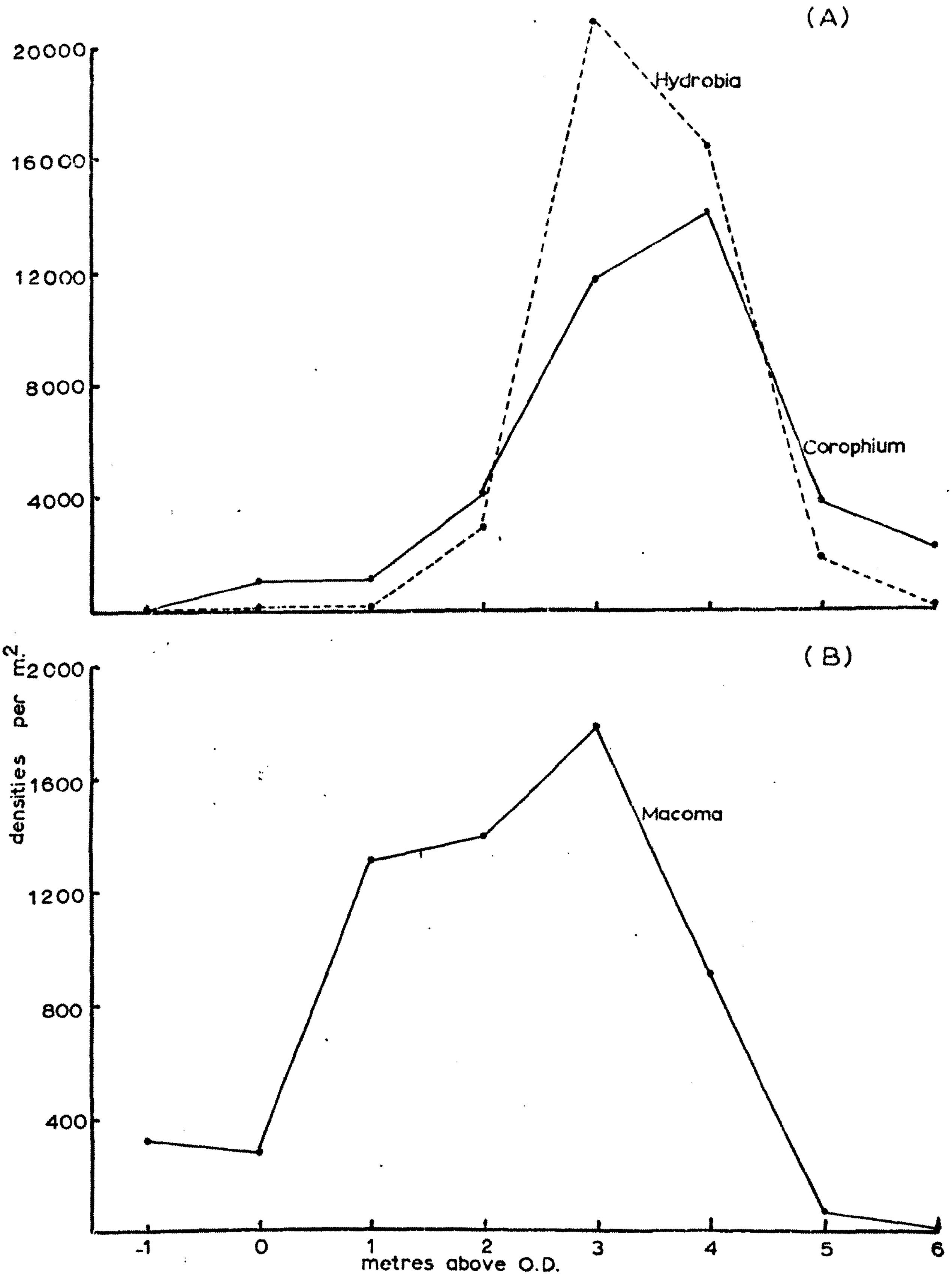
This tubiculous polychaete showed an extremely patchy distribution though it occurred in substrates from mud to silty sand (as in pools at St. Annes and Ainsdale). It was not recorded in the wettest mud east of Lytham and Banks Sands, nor in the coarse sand of Formby, Ainsdale and Squires Gate. Highest densities (maximum 3,620 per m^2) were recorded on the mid-estuary, especially Banks Sands and Salter's Bank.

Arenicola marina

If Popham (1966 a, b) was correct in describing Arenicola as being "exceptionally abundant in the sandy mud between H.W.N. and M.L.T. from Fairhaven to St. Annes" then there has been a drastic decline in stocks. On the south Ribble only three areas hold significant populations of Arenicola, two near the Bog Hole, and one around a small complex of channels draining into Crossens Pool: the maximum densities here were 128 per m^2 whilst on Salter's Bank 123 per m^2 was maximum. Anderson (1972) commented on the relationship in Morecambe Bay and also appertaining to the Ribble between Arenicola occurrence and damp sand, with absence of Arenicola on the higher dry banks. The feeding and

Figure 34

Distribution of a) *Corophium volutator* and *Hydrobia ulvae*, and b) *Macoma balthica* in relation to shore level on the Ribble Estuary (June - August 1972 data)


(A)
20000
16000
12000
8000
4000
Hydrobia
Corophium
(B)
2000
1600
1200
800
400
Macoma
densities per m.^{2}
-1
0
1
2
3
4
5
6
metres above O.D.

method of irrigation in Arenicola described by Wells (1949) require the animal to live in such wet areas.

Lanice conchilega

Together with Pectinaria koreni, Lanice conchilega occurs in large numbers at very low tide levels (close to L. W. S.) on the outer estuary. At low water neap tide these species usually remain covered by the tide, thus being available as food for waders on only about half of the days in each lunar cycle.

CRUSTACEA

Corophium volutator

This is one of the most abundant members of the macro fauna, occuring from Birkdale - St. Annes (where it possibly overlaps with Corophium arenarium) eastwards to the Inner Ribble. Density is highest in the middle estuary, on eastern Horse Bank, eastern Salter's Bank and Banks Sands, with peaks of 22,000 per m^2 from Horse Bank, 22,000 per m^2 from Banks Sands and 8,000 per m^2 from Fairhaven Bay.

The species is found on all shore levels in the main zone though on its western limits it tends to occur higher on the shore than C. arenarium which tends to occur well below O.D. on its eastern limit (see Tables 36 and 37). At its easternmost limits on the Ribble, around the Freckleton Naze area, C. volutator occurs mainly on saltmarshes, reaching densities of up to 4,000 per m^2 in saltpans. Over its main range, however, peak densities are found from about 2m to 5.8m O.D. (Figure 34). These are areas with fairly low median particle diameter (Figure 28), generally a fine sandy mud, though in the finest muds Corophium tends to be sparse, possibly as a result of anaerobic conditions in such mud. These areas also have high organic content (Figure 30) and thus high food content, the factor which Meadows (1964) thought to be of greatest importance in holding high densities of C. volutator. On the Ythan Estuary, Aberdeenshire McLusky (1967, 1968, 1970) has shown that C. volutator reacts, not so much to substrate and organic content than to salinity, being abundant wherever salinity exceeded 5% , reproducing wherever salinity was greater than 7% and exhibiting maximum growth over the range 5% - 20% . From a comparison between *Corophium* distribution and Table 35 it will be seen that the areas with salinity within this range have the highest *Corophium* densities.

In general, peak densities of *Corophium* on other British Estuaries are similar to those from the Ribble. Spooner and Moore (1940) recorded up to 11,000 per m^2 on the Tamar, Stopford (1951) 24,000 per m^2 from the Cheshire Dee, Howells (1964) 17,136 per m^2 from the Towy whilst from Morecambe Bay Anderson (1972) reported a maximum density of 8,700 per m^2.

Corophium arenarium

A species encountered in samples taken in wetter areas, usually on the lower shore (below about 1m O.D.) on the sandy shores of the outer estuary, also being found in the sandier areas of Foulnaze and the outer Horse Bank and Salter's Bank. Though the two species of *Corophium* have never been identified in the same sample, they have been recorded at the same sample point on three occasions: off Birkdale, Horse Bank by the Pinfold and on Foulnaze. They may well overlap therefore to some extent.

C. arenarium tends to select areas with coarser clean sand whilst *C. volutator* is a species of sandy-mud shores (Crawford 1937). It is also possible that *G. arenarium* is selecting for higher salinity than *C. volutator*, areas with high salinity being also areas with larger substrate particle size (see Figures 28, 31, 32 and Table 35).

Density of *C. arenarium* is lower than *C. volutator* , the peak being 3,220 per m^2. Other studies show similar lower density (Holme (1949) for example giving a maximum density of 360 per m^2 in the Exe Estuary).

Bathyporeia pelagica

Bathyporeia pelagica occurs in all sandy substrates west of Southport and St. Annes, as well as the sandier areas of outer Horse Bank and Foulnaze, wherever the substrate holds water. It does not occur on the higher dry beaches. Highest densities occur, therefore, close to low tide marks (up to about 1m O.D.) though in areas of wet rippled sand or shallow pools concentrations may occur up to M.H.W.N. (e.g. sample sites 11 - 14 on Western Salter's Bank, Table 43). Densities in the substrate vary, therefore, probably due to water content, reaching peaks of 4,200 per m^2 off Horse Bank, 3,000 per m^2 off western Salter's Bank, 6,800 per m^2 off Birkdale and 4,200 per m^2 off Formby. Such figures are similar to Holmes' (1949) maximum of 2,180 per m^2 on the Exe Estuary, though Watkin (1942) recorded densities of up to 17,000 per m^2.

There appears to be a movement of *B. pelagica* over the whole inter-tidal zone with the tide. As the tide flows, so *Bathyporeia*, together with *C. arenarium*, *Haustorius arenarius* and *Eurydice pulchra* moves up at the tide edge and retreats as the tide ebbs. Those recorded in pools or wet rippled areas have possibly been stranded by such movements. Thus, over areas lacking these crustaceans at low tide, many hundreds can be taken in hand-nets at the edge of the tide in water up to 20cm deep.

Haustorius arenarius

With *B. pelagica* and *E. pulchra* this species occurs in low density on the outermost sandy shores. Density is low, the maximum recorded being 480 per m^2 at Ainsdale. Pelagic movements with the tide are referred to above (under *B. pelagica*).

Eurydice pulchra

Generally, this occurs with *B. pelagica* on the lower sandy shores with maximum densities of 960 per m^2 on western Horse Bank and 1,420 per m^2 at Birkdale. As with *B. pelagica* during high water the inter-tidal zone is invaded with *E. pulchra*, it occurring in very large numbers (up to 200 in one sweep of a hand-net) at the tide's edge.

Carcinus maenas

This shore-crab occurs wherever adequate stone substrate provided shelter, though highest densities occurred at Southport sewage pipe and on Church Scar. This was especially noticeable in summer samples when numbers were swollen by the large numbers of small (carapace diameter up to 10 mm) young. At this time (June - August) small numbers of young occurred on all shores.

Whereas crab numbers on the open shore are generally very small, the saltmarsh creeks and permanent saltpans hold large numbers, suggesting that density is related to the availability of cover on the estuary.

Other crustaceans

Jaera marina and Ligia oceanica occur wherever there is stone or shingle as in Fairhaven Bay, the training walls of the Ribble channel, Church Scar and Southport sewage pipe. Occasional ones were recorded elsewhere in similar situations.

Sphaeroma rugicauda is a common species in the saltpans and amongst vegetation at the edges of creeks on the highest saltmarshes. Details of its density will be published elsewhere.

Three species of Gammarus have been recorded: G. locusta was taken from a wrecked wooden ship close to L.W.S. off Birkdale, and G. zaddachi from amongst thick Enteromorpha sp. at Southport sewage pipe, Church Scar and the Ribble Channel training walls off St. Annes. G. duebeni occurs in large numbers in saltpans on the highest Festuca saltmarshes. The closely related Marinogammarus marinus was found in very low density in muddy shingle at Fairhaven.

The two species Crangon vulgaris and Palaemonetes varians occurred throughout the estuary either in pools or the tidal waters. C. vulgaris was especially abundant off the sandy/muddy sand areas of Salter's Bank, and Horse Bank south to Formby Point, being the centre of the local shrimping industry. Occasionally it occurred also in shore pools and saltpans on the outer saltmarshes. *P. varians* occurred in the more brackish saltpans and pools on inner Horse Bank, Banks Sands and Lytham shore. *Hippolyte varians* was taken only once at Southport sewage pipe.

MOLLUSCA

Hydrobia ulvae

Though *H. ulvae* has the highest density of any member of the intertidal macrofauna, it has a much narrower range over the shore (mainly 3 - 5.9 m O.D.) than other high density species such as *N. diversicolor*, *C. volutator* and *Macoma balthica*. As in these species, *Hydrobia* occurs mainly on the sandy - mud banks of the mid-estuary: eastern Horse Bank, western Banks Sands and eastern Salter's Bank. Smaller numbers extend up the shore and onto the outer lower saltmarshes (Figure 34), *H. ulvae* being replaced to some extent by *Potamopyrgus jenkinsii* on the highest *Festuca* marshes.

At maximum density numbers generally range from 15,000 - 38,000 per m^2, though one sample from Banks Bay gave a density of 47,000 per m^2. Lower maximum densities have been reported from most other estuaries: 8,000 per m^2 from Aberlady Bay (Forth) (Nichol 1935), 2,840 from the Tamar (Spooner and Moore 1940), 4,000 per m^2 from the Tamar (Holme 1949), 12,500 per m^2 from the Cheshire Dee (Stopford 1951) and 8,525 per m^2 from Morecambe Bay (Anderson 1972). Certainly, maximum numbers on the Ribble are far in excess of the 5,000 - 9,000 range considered by Green (1968) to be 'normal', being in the range of 30,000 - 60,000 per m^2 recorded by Thamdrup (1935) from Denmark.

In studies on the Thames and Essex estuaries Newell (1962, 1964) found a distribution similar to the Ribble with a peak aggregation of up to 10,000 per m^2 on the upper 'muddy - sand' zone. His investigations showed a cycle of pelagic feeding, in that the animals floated and fed on the water surface film at high tide, and then attached onto any solid substrate as the tide receded. Most then burrowed into the substrate as they were exposed to the air, re-emerging as the flowing tide covered them. Following Bascom (1958), Newell suggested that *Hydrobia* would tend to settle on the parts of the shore with least gradient and this is the upper limit of 'muddy sand', below the 'mud' zone of the higher shore. This also would account for the pockets of high *Hydrobia* density in areas of shallow rippled substrate and pools, these being areas where large *Hydrobia* numbers would be expected to be stranded. Newell also showed that *Hydrobia* generally avoided salinities outside the range 2 - 20 % and this factor resulted in an inability to colonise the most inner estuary mudflats as well as limit their extension seawards. On the Ribble such salinities occur on the areas in which highest *Hydrobia* densities were recorded. There appears, however, to be some variation in salinity preferences of *H. ulvae* from estuary to estuary and McMillan (1948) has suggested that there are different biologically races of *H. ulvae*, each being adapted to the main conditions prevailing in a particular area.

Certainly, *Hydrobia* appears to have far narrower requirements in its choice of habitat than the other three dominant members of the mid-estuary fauna : *Nereis*, *Corophium*, *Macoma*.

Macoma balthica

Except for the outermost sandy shores, *Macoma* is the major lamellibranch of the intertidal zone, showing tolerance to a variety of substrate particle size, salinity and organic content in its distribution from Ainsdale to the mudflats east of Lytham and Hundred End.

Maximum densities were 500 per m^2 in Banks Sands, 1,490 per m^2 from Salter's Bank, 2,150 per m^2 from Fairhaven and 2,440 per m^2 from E. Horse Bank. These last two figures, which included about 70% spat, were just within the range of 2,000 - 4,000 per m^2 which Anderson (1972) recorded from Morecambe Bay and well below her maximum of 56,000 (mainly spat). From the Cheshire Dee, Stopford (1951) regarded *Macoma* as the dominant invertebrate though the densities she recorded were generally smaller than both Morecambe Bay and Ribble densities. From the Mersey, Fraser (1932) recorded a range of densities 2,000 - 5,900 per m^2

generally higher than the Ribble and similar to the Morecambe Bay range.

Within the middle estuary where highest Macoma densities were recorded, the species occurred mainly from 4 - 5 m O.D. down to just below O.D. (approximately - 0.5 m O.D.), with only occasional ones above and below this range. It generally is distributed lower on the shore than the high densities of Corophium and Hydrobia (Figure 34).

Tellina tenuis

This bivalve replaces Macoma on the sandy beaches of the outer estuary. Its main distribution is below O.D., possibly in response to wetter substrate at low tide and longer periods of tide cover than the higher shore which, especially on the sandy shores, rapidly dry out. The maximum density of T. tenuis recorded was from Birkdale sands (365 per m^2), though most areas had less (under 100 per m^2).

Other authors (e.g. Holme 1949, Perkins 1956, Anderson 1972) recorded similar distributions and low densities.

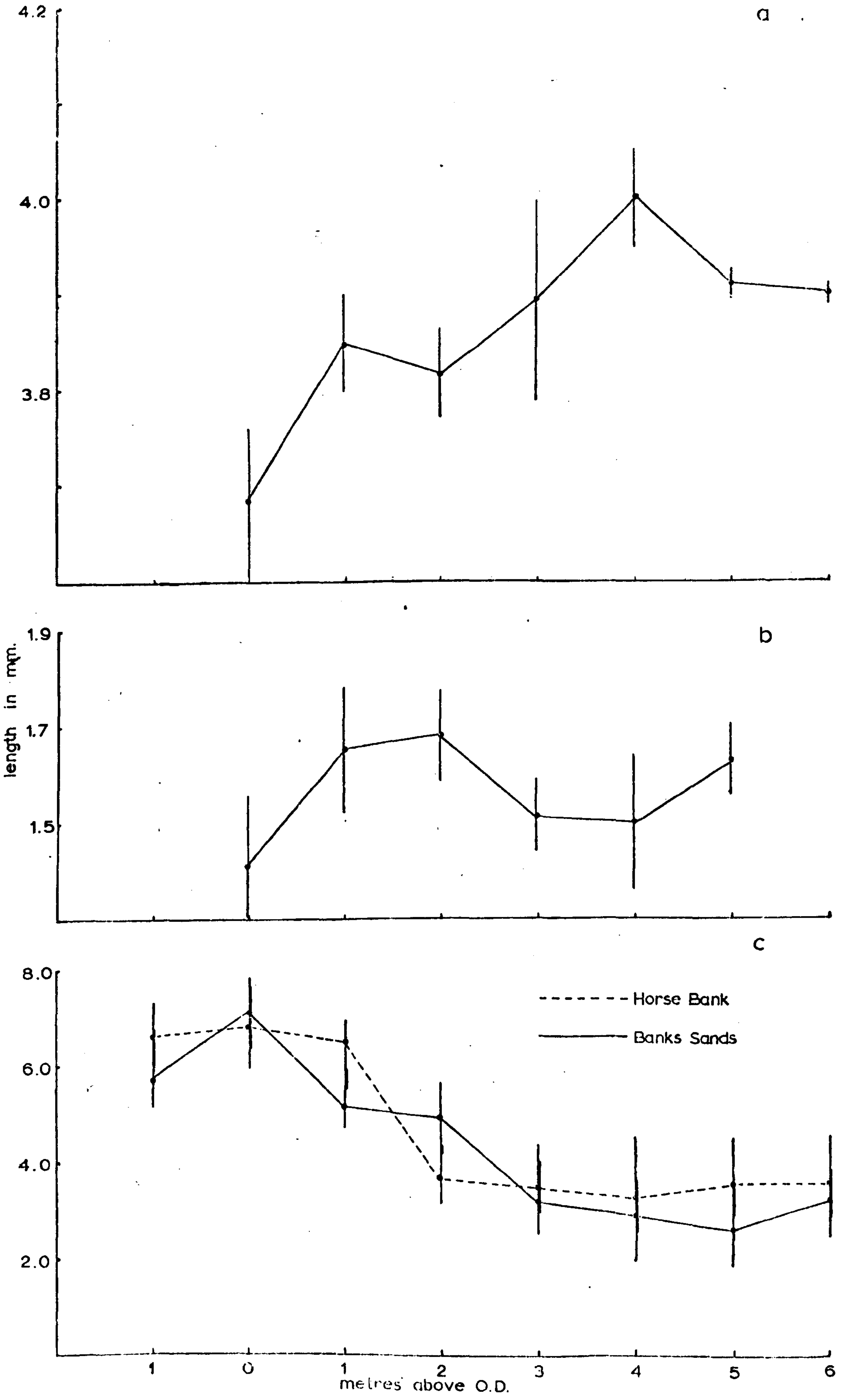
Scrobicularia plana

A widespread species of the muddy middle and inner estuary, occurring from around the Bog Hole east to Hundred End on the south of the estuary and from the muddy creeks in the middle of Salter's Bank east to Warton Marsh. In the west of its range S. plana occurs mainly on the upper part of the tidal range (3m O.D. to M.H.W.S.), though in the eastern area around Banks Sands - Warton Marsh it mainly occurs from -1m O.D. to 2m O.D. with a few up to 4m O.D.

Densities are generally low, reaching over 100 per m^2 at four sites with a peak of 132 per m^2 on Banks Sands. This is close to the maximum recorded by Hughes (1970) of 140 per m^2 from the Lavan Sands, Caernarvonshire and 104 per m^2 from Northumberland (Brady 1942).

Figure 35

Sizes of a) Corophium volutator, b) Hydrobia ulvae and c) Macoma balthica in relation to shore level


a
4.2
4.0
3.8
b
1.9
1.7
1.5
length in mm.
c
8.0
6.0
4.0
2.0
Horse Bank
Banks Sands
1
0
1
2
3
4
5
6
metres above O.D.

Mytilus edulis

Table 46 gives details of density of this species on its major site on the Ribble Estuary. Very small numbers also occur on training walls of the Ribble Channel and pylons by that channel.

Cardium edule

This species was abundant in the estuary in the 1950s, possibly having been hit by the hard winter of 1962 - 3 which decimated the cockle stocks of Morecambe Bay (Anderson 1972). Now it is very sparse, generally occurring in densities of up to 40 per m^2 in the zone between O.D. and 2.7 m O.D. in the middle estuary. Pockets of higher density have occasionally been found (attention being drawn to them by feeding Oystercatchers) but these are rapidly exploited by the Oystercatcher population.

Other molluscs

Littorina littorea and L. littoralis are very sparse, occurring on rocky substrates.

Donax vittatus was found in one sample. Mactra corallina was occasionally taken in samples collected on the lower shores of the outer estuary. It obviously is far more abundant below L.W.S. for many have been washed onto the intertidal zone following gales and heavy seas. In February 1972, for instance, hundreds of intact animals were washed-up onto Salter's Bank at St. Annes.

Mya arenaria occurs in small numbers close to low tide on the middle estuary.

Variation in size of invertebrates in relation to shore level

Variation in size at various shore levels was investigated in three major food species in July - September 1972 on Horse Bank and Banks Sands. Samples were collected at each shore level and all animals of each species measured as follows:

1. Corophium volutator - length from tip of cephalothorax to tip of abdomen
2. Hydrobia ulva - maximum height of shell
3. Macoma balthica - maximum diameter of valves

The data are presented in Figure 35.

Corophium size is larger on the higher shore (over its main range), the smaller mean body size on the lower shore possibly being a consequence of that zone being colonised by young Corophium and few reaching maturity than on the main zone. When these samples were collected, large numbers of small young were present.

Macoma shows a similar pattern, with the mean diameter on the mid-shore, again the main range, and extending down to low tide level, being larger than on the upper shore which presumably is colonised by spat from the lower shore but, due to exposure, cannot hold a large mature population.

Hydrobia however, show no trend in size on the shore in relation to level, probably due to the pelagic feeding habits of the species resulting in a mixing of all Hydrobia sizes. Also, Hydrobia tends to be less static than Macoma and Corophium, which keep to set burrow areas, moving up and down the shore as tide height changes through the lunar cycle.

Unfortunately, there was not opportunity during the study to obtain comparative data for mid-winter.

Vertical distribution of invertebrates in the substrate

Just because organisms occur in an area and are thus potential prey does not mean that they are readily, if ever, available to the predator.

They may be hidden or camouflaged or protected in some way so that the predator is unable to capture them. This seems likely to apply to invertebrates dwelling in or on the intertidal zone, for the deeper they burrow the less likely is it that they will be captured. Once they have burrowed further under the substrate surface than the feeding apparatus of the predator can reach, then they cannot be caught. Only if they venture within reach can they be taken.

An attempt was made, therefore, to calculate the proportion of the major prey species which were within reach by the various wader species through the tide cycle. This, of course, would be dependant upon the length of the particular wader species' bill as well as the sex of the individual wader as in most waders females tend to have longer bills than males.

This part of the study concentrated on the four main prey of the middle estuary, Nereis diversicolor, Corophium volutator, Macoma balthica and Hydrobia ulvae.

Two variants of the normal sampling method were used. Firstly a cover with slits at intervals which enabled thin metal plates to be inserted and thus split the sample into sub-samples from different depths was used. The sampler was pushed into the substrate and then left for 10 - 15 minutes, thus allowing prey which had moved to return to their original position. Rapidly the sampler was then removed and the metal plates rammed in to break up the sample into depth categories. Seiving was then carried out. Many animals were broken during the sampling and the depth at which the part carrying the head occurred was counted.

As a rough check to this a second method was used. A sample was rapidly taken from the upper 3 cm and analysed. A second adjacent sample was then taken down to 10 cm and again analysed. Then, by subtracting the first sample data from the second, the number of animals occurring deeper than 3 cm was estimated. The proportions in the upper

Table 48 Comparison of two methods of analysis of depth distribution at two sites on Horse Bank

	% in upper 3 cm	
	First method (Sampler)	Second method (Subtraction)
SITE 1		
Nereis	8.5	3.0
Corophium	74.8	62.4
Hydrobia	98.3	99.4
Macoma	62.5	65.1
SITE 2		
Nereis	11.2	4.3
Corophium	86.9	65.7
Hydrobia	99.2	99.8
Macoma	69.0	66.4

3 cm and the lower 3 - 10 cm were compared at two Horse Bank sites using the two methods and the results given in Table 48.

The data for Macoma and Hydrobia in both sample types are similar whilst at both sites the proportion of Corophium and Nereis were higher in the sampler (first) method. It would appear that the rapid collection of a sample of 3 cm depth caused sufficient disturbance so as to cause some Corophium and Nereis to move rapidly downwards and escape from the sample. Of course, it is possible that some Corophium and Nereis escaped from the sampler (first) method. However, as this seemed to be less affected than the second, its results were accepted for analysis in this section.

Results

Corophium volutator

Figure 36 shows the percentage of Corophium at three levels in the substrate through the tide cycle. At high water up to 76% of Corophium occur within 3 cm of the substrate surface. As the tide recedes the Corophium move deeper into burrows so that over the low tide period about 90% of Corophium are at least 1 cm below the surface, and up to 55% below 3 cm.

As the tide covers the area, so Corophium move up their burrows and there is some evidence that this movement begins before the tide reaches the animals (see Figure 36).

Animals from the three levels were measured (length) and the means from each were not significantly different (4.01, 4.12 and 3.96 mm at three levels).

Nereis diversicolor

N. diversicolor moves deeper than most members of the macrofauna, for though most occur in the upper 10 - 12 cm, a minority occur to 30 cm

Figure 36

Percentages of Corophium volutator in a) upper 1cm, b) between 1 - 3 cm and c) below 3cm of substrate on Horse Bank and Banks Sands through the tide cycle.

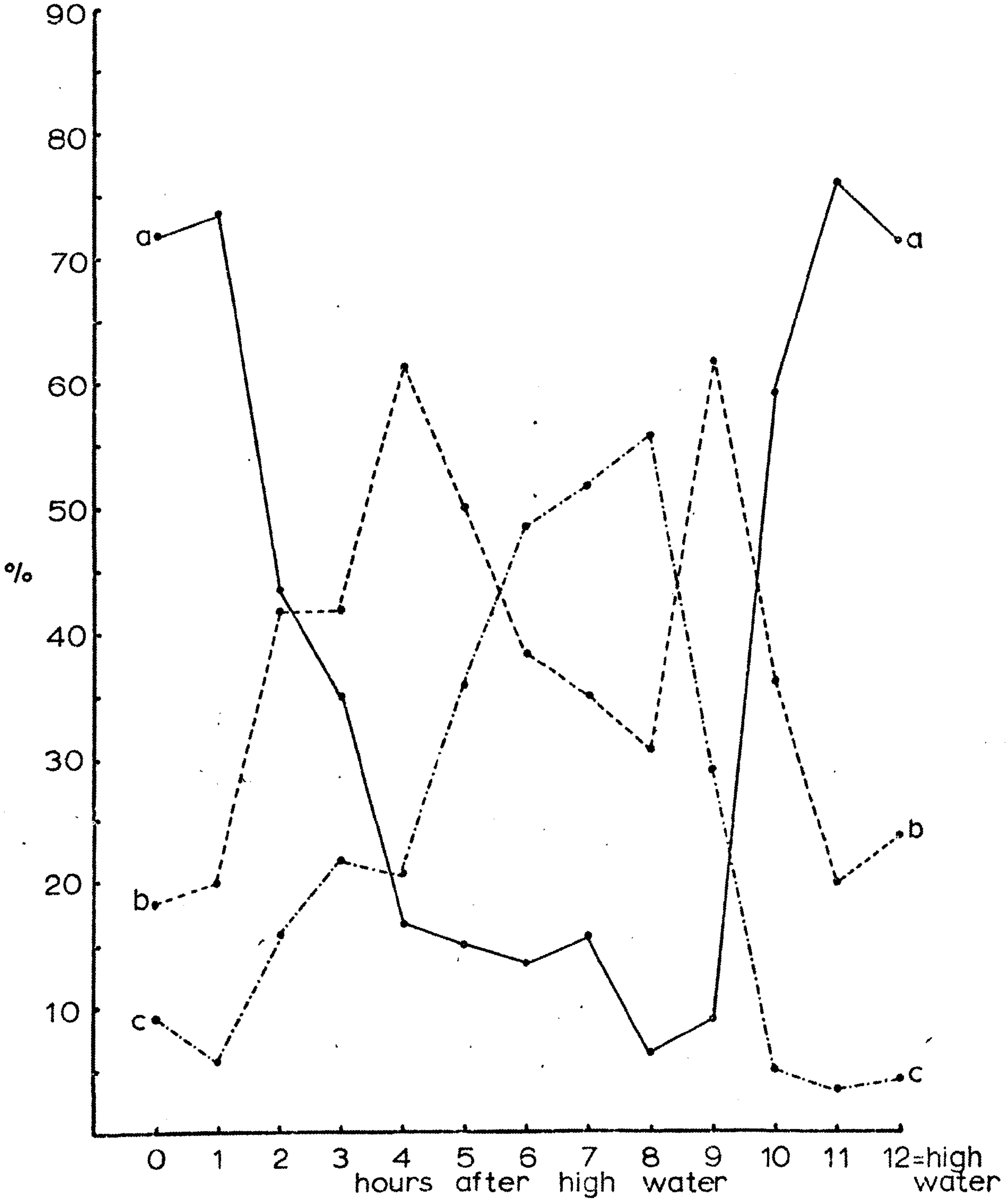

90
80
70
60
50
40
30
20
10
%
a
a
b
b
c
c
0
1
2
3
4
5
6
7
8
9
10
11
12=high water
hours after high water

Figure 37

Depth distribution of *Nereis diversicolor* on a) Salter's Bank and b) Horse Bank, June- August, 1972.

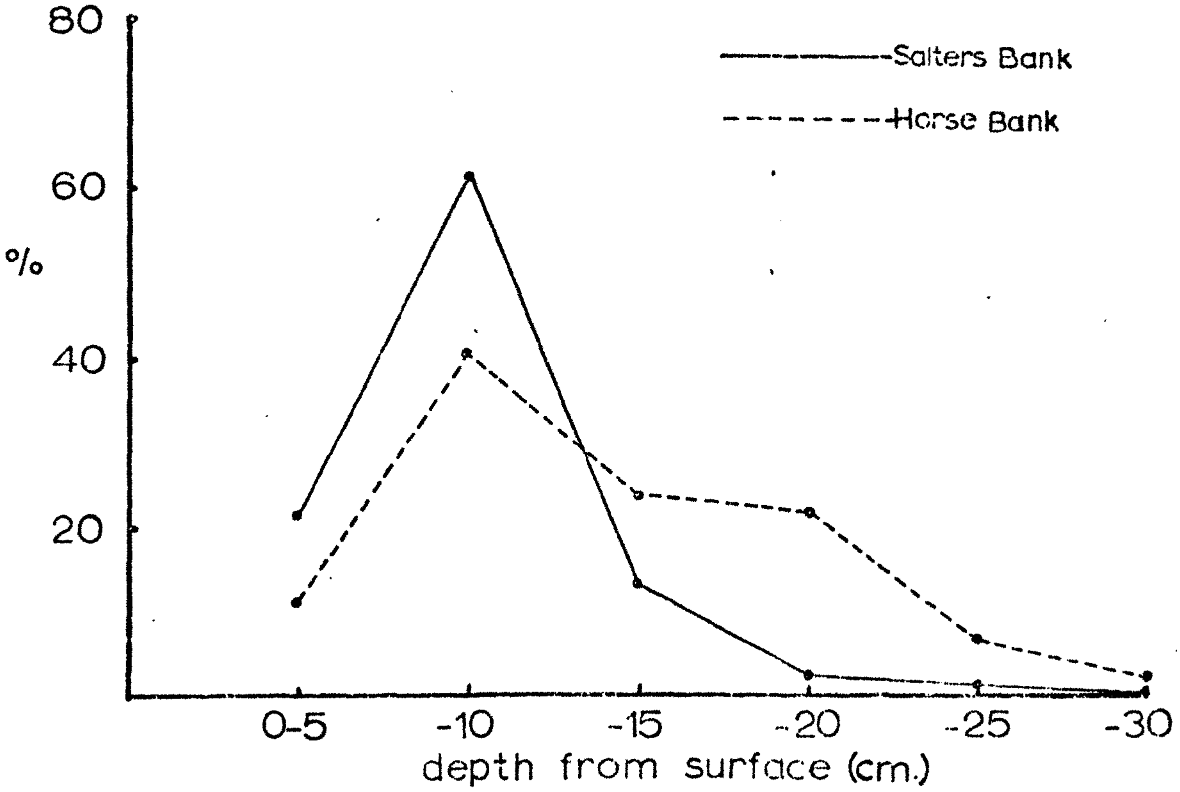
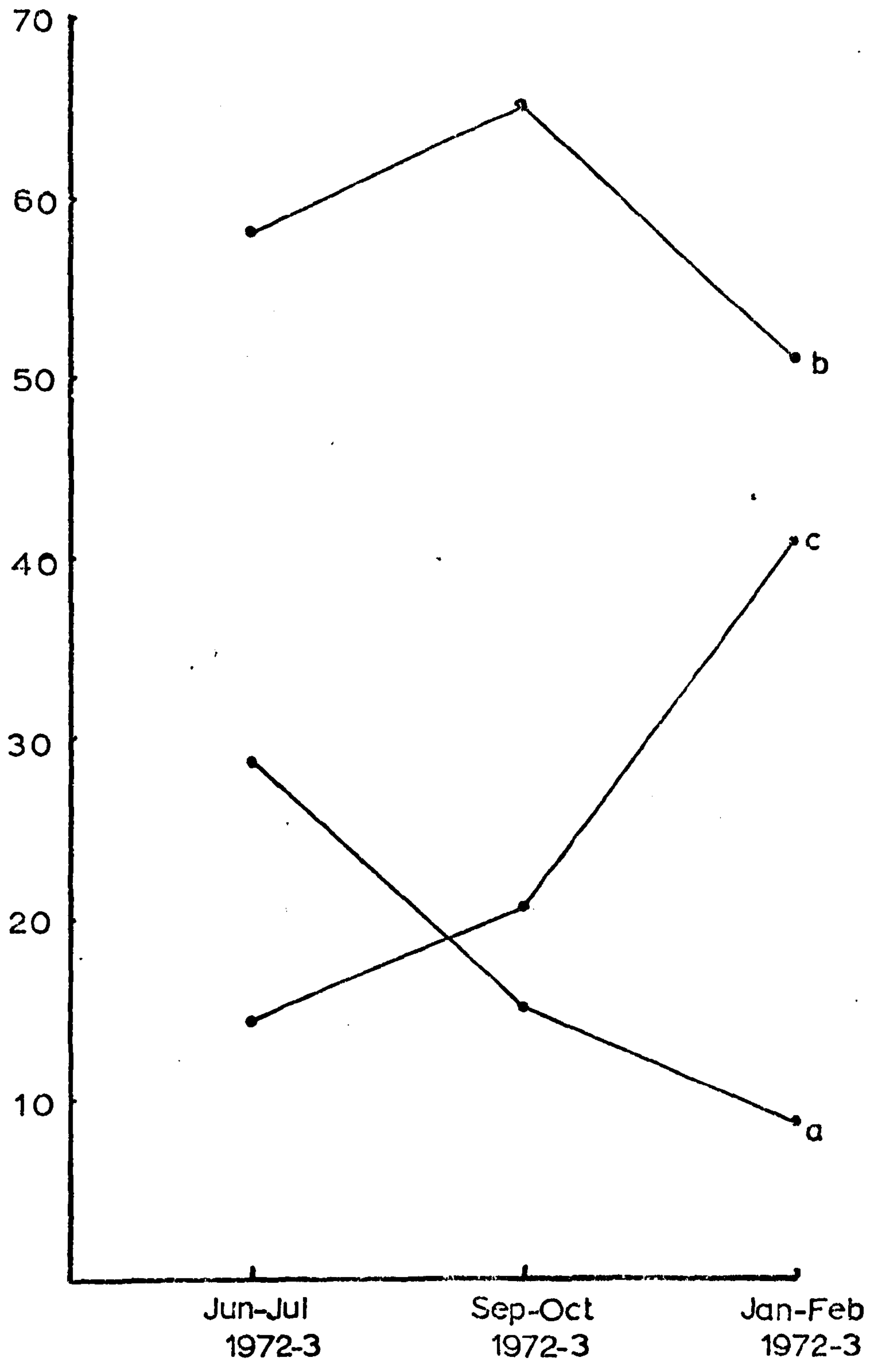

80
60
40
20
%
Salters Bank
Horse Bank
0-5
-10
-15
-20
-25
-30
depth from surface (cm.)

Figure 38

Percentages of Macoma balthica in a) upper 1cm, b) between 1 - 3 cm and c) below 3cm of substrate in Horse Bank and Banks Sands.


70
60
50
40
30
20
10
b
c
a
Jun-Jul 1972-3
Sep-Oct 1972-3
Jan-Feb 1972-3

or deeper (Figure 37). Checks made at various stages through the tide cycle indicated little variance over the low tide period of this pattern. In all cases at least 50% of the Nereis occurred within the upper 10 cm of substrate, and 60% in the upper 15 cm.

Macoma balthica

From Figure 38 and Table 49 it will be seen that throughout the year most Macoma occur between 1 - 3 cm deep under the substrate surface. However, after spat fall which begins in May a large proportion occurs in the top 1 cm and, from their sizes they are mostly young (very small) individuals. This proportion decreases, probably due in large part to predation but possibly due to a general movement down through the substrate. Accordingly, the September-October data in the 1-3 cm and below 3 cm levels increase as the upper 1 cm decrease.

By late winter the proportion of Macoma in the upper 1 cm is very small, whilst that in the 1-3 cm level also has decreased, thus resulting in a correspondingly large rise in the proportion of depths of greater than 3 cm. Again, this may indicate a movement downwards through the substrate or, more likely, to a proportionally higher mortality in the upper substrate levels, these higher Macoma being within the range of more potential predators.

There appeared to be no significant variance in depth distribution through the tide cycle though it is well known (e.g. Brafield and Newell 1961) that bivalves such as Macoma do make horizontal movements under some circumstances through the low tide period. To some extent it is also possible that vertical movements also occur.

Hydrobia ulvae

Depth distribution of H. ulvae varies through the tide cycle (Figure 39) as one would expect, following Newell (1962, 1964). As the tide exposes the mudflat a high proportion of Hydrobia , many or most of which have been

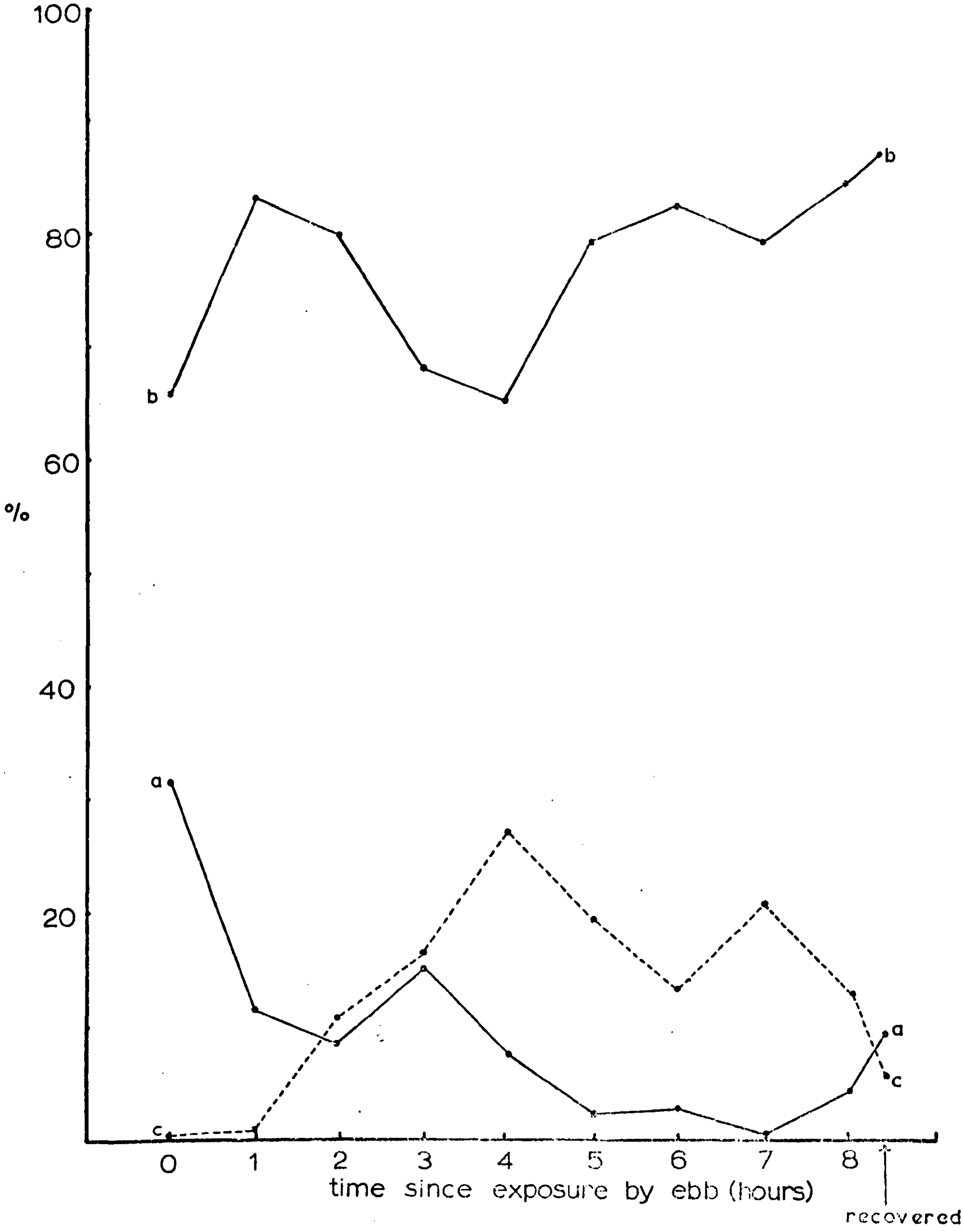
Table 49

The distribution of Macoma balthica in its main range on Horse Bank, Banks Sands and Salter's Bank in relation to size

	Category of shell Length	% of whole population	% of population of upper 3cm
a.	3.0 mm	19.3	29.4
Sept - Oct	3.1 - 5.0	47.1	55.5
1972, 1973	5.1 - 7.0	13.8	6.3
	7.1 - 9.0	8.4	4.2
	9.1 - 11.0	4.8	2.7
	11.1 - 13.0	3.9	1.8
	13.1 - 15.0	1.8	0.2
	15.0	0.9	0.0
b.	3.0	1.9	5.7
Jan - Feb	3.1 - 5.0	8.3	16.7
1972, 1973	5.1 - 7.0	29.8	48.2
	7.1 - 9.0	36.2	22.0
	9.1 - 11.0	19.5	4.5
	11.1 - 13.0	0.8	1.2
	13.1 - 15.0	4.1	1.6
	15.0	2.4	0.1
c.	3.0	51.7	74.4
Jun - Jul	3.1 - 5.0	29.5	14.2
1972, 1973	5.1 - 7.0	3.9	5.1
	7.1 - 9.0	2.7	1.2
	9.1 - 11.0	6.5	2.8
	11.1 - 13.0	8.0	1.9
	13.1 - 15.0	5.9	0.3
	15.0	1.6	0.1

Figure 39

Percentages of *Hydrobia ulvae* a) on surface, b) in upper 1cm of substrate and c) below upper 1cm of substrate, from time of being exposed by the tide to being covered by the tide.


100
80
60
40
20
%
b
b
a
a
c
c
0
1
2
3
4
5
6
7
8
time since exposure by ebb (hours)
recovered

feeding pelagically, are still on the surface of the substrate. Many of these crawl over the mud, possibly continuing to feed, and then burrow into the mud. After about 2 hours of being exposed, the only Hydrobia still remaining on the surface are either in shallow pools or in wet ripples. Thus a movement occurs down through the substrate, over 20% continuing to penetrate beyond the top 1cm by low tide, this resulting, not only in very few occurring on the surface, but also just under (within 1cm) the surface.

There appears to be a return towards the surface layer of substrate before the tide reaches the Hydrobia zone, beginning (judging from the figures for upper 1cm and below 1cm data given in Figure 39) shortly after low water. Such a movement could not be directly triggered off by the tide, but is one which results in the Hydrobia in the upper 1cm of substrate reaching a peak just as the tide returns to cover the area.

General observations on other species

On the outer estuary Corophium arenarium, Bathyporeia pelagica and other crustaceans in this area, which tend to occur close to low tide or in wetter areas, either occur very close to the substrate surface or lead a somewhat pelagic existence at the tide's edge. Certainly, all are easily within the range of even the most short-billed wader such as the Sanderling. Presumably the coarser looser particles making up the shore in these areas make it impossible for these animals to construct burrows as do similar organisms on the sandy-mud and mud shores.

In February 1974 one set of data was collected from creeks draining into Crossens Pool of the depth distribution of Cardium edule and Scrobicularia plana. The results are given in Table 50.

Though C. edule size did not appear to vary significantly with depth (mean valve diameter 18.6 ± 0.24 mm down to 6.0 cm in substrate and 19.2 ± 0.17mm deeper than 6.0 cm), S. plana were significantly larger

Table 50 Depth distribution of Cardium edule and Scrobicularia plana on Horse Bank, February, 1974.

Depth under substrate (cm)	% of population of C. edule	S. plana
0 - 3.0	9.50	3.60
3.1 - 6.0	38.25	21.40
6.1 - 9.0	49.50	32.10
9.1 - 12.0	2.75	31.00
12.1 - 15.0	0.00	7.85
15.0	0.00	4.50
n	240	180

Figure 40

Densities of a) *Corophium volutator* and b) *Hydrobia ulvae* on Horse Bank and Banks Sands, 1971 - 1974

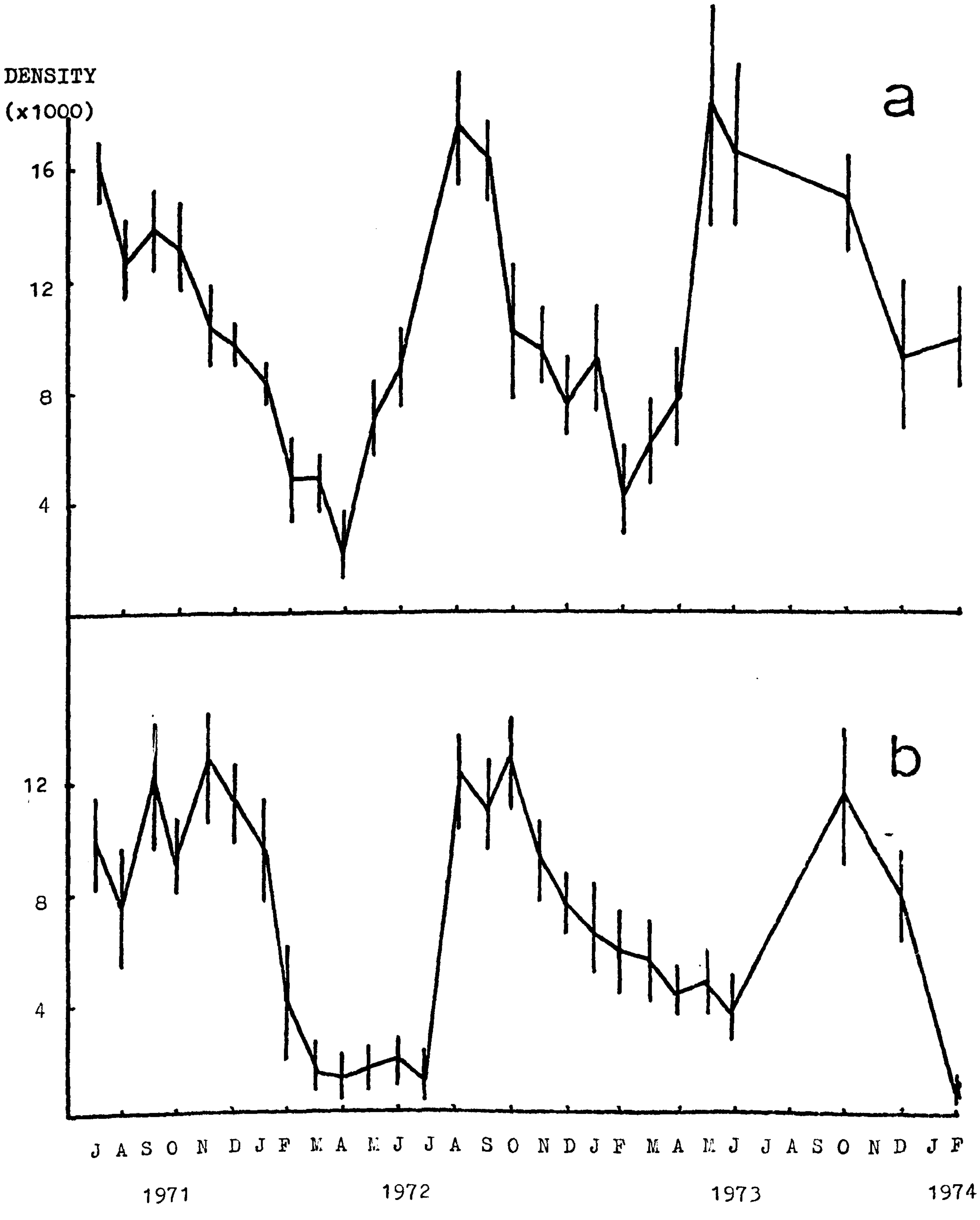
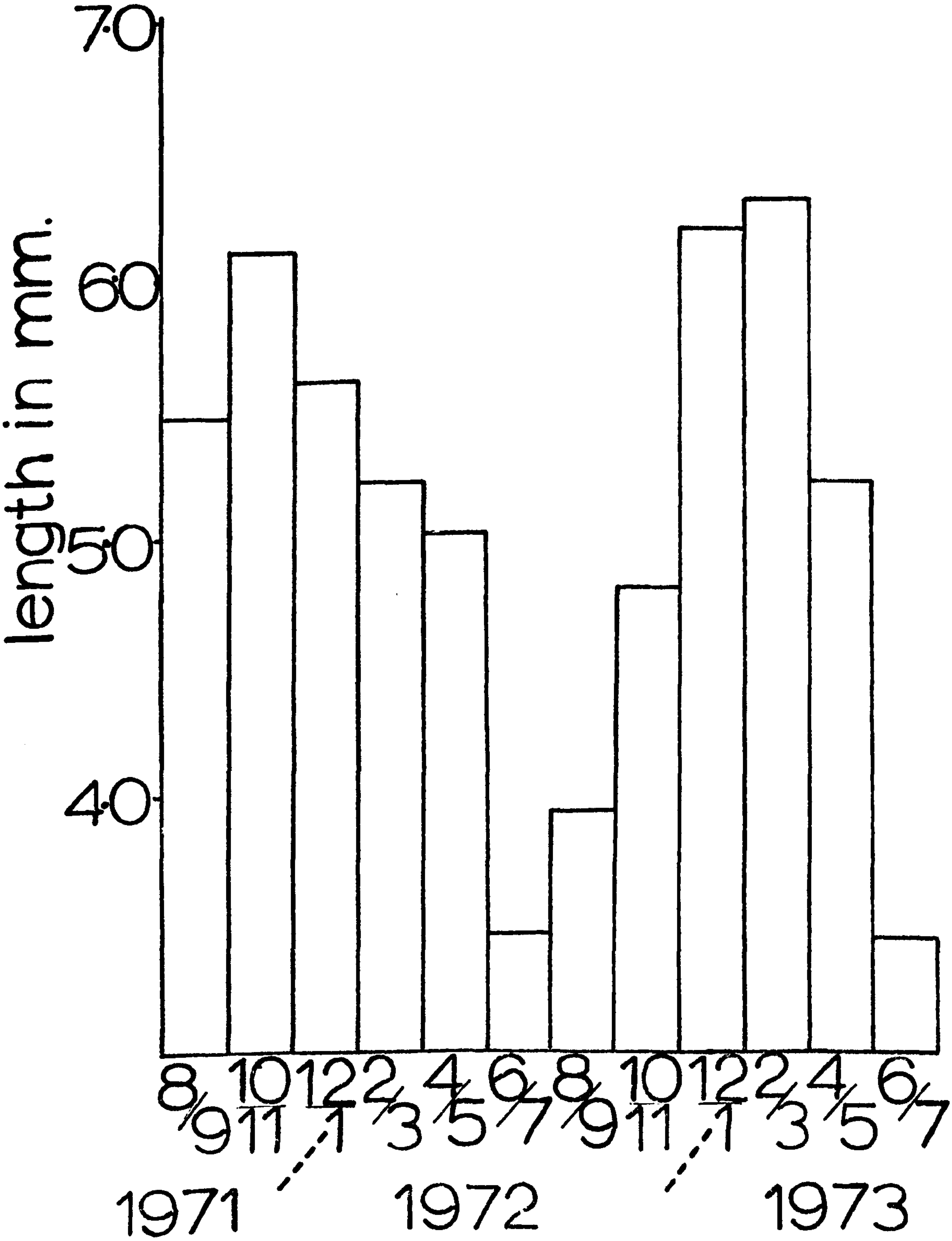

DENSITY
(x1000)
16
12
8
4
a
12
8
4
b
J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D J F
1971
1972
1973
1974

Figure 41

Mean lengths of Corophium volutator on Horse Bank and Banks Sands, 1971 - 1973.


length in mm.
70
60
50
40
8/9
10/11
12/1
2/3
4/5
6/7
8/9
10/11
12/1
2/3
4/5
6/7
1971
1972
1973

at below 6.0 cm than above 6.0 cm (mean diameters 13.2 ± 0.74 and 25.1 ± 0.45 mm respectively, $p < 0.001$). This is probably because the area holds a regular S. plana population, thus animals of different ages will be present whereas the C. edule population largely results from a single spat settlement, probably in autumn 1972.

Seasonal variation in density

Figure 40 gives the results of monthly samples over five sample sites on Horse Bank and Banks Sands for Corophium volutator and Hydrobia ulva. At each sample site ten samples were normally taken, though in some months time and assistance in carrying the samples meant that a reduction had to occur and on these occasions eight samples were taken.

Corophium volutator

In each year the minimum population density occurred in late winter - early spring, though the minimum density recorded in 1972 was only 55% of the 1973 mean minimum whilst in February 1974 mean density was over twice as high as the 1973 minimum. These suggested that mortality of Corophium has been lower in these more recent years, possibly as a consequence of the series of extremely mild winters experienced in N. W. England.

In all years the first young were recorded in late February though these did not produce an increase in the population density until late May and June when these young Corophium comprised the bulk of the population. This can be seen from Figure 41 which gives mean body lengths of Corophium from these monthly samples. During the winter there is a slight reduction in mean length, possibly due to the older and larger animals dying or being selectively predated, there being a sudden decrease in mean length in the June samples due to the large numbers of minute Corophium.

The population peak is reached in the period June- August, thereafter the population rapidly decreases in number. As this density decrease occurs however, so the size of animals remaining in that population rapidly increases to a maximum means size in mid - winter (December - February). This may be due to a disproportionally higher mortality of the smaller individuals through the autumn, but this seems to be unlikely as the waders at least tend to select the larger Corophium (Chapter IX). Far more likely is this due to a rapid growth of the young Corophium.

Watkin (1941) noted in his study on the Dovey Estuary of C. volutator that the death rate of Corophium of length greather than 7mm was very high. He showed that in February-March the bulk of the population was large, in June-October the bulk consisted of smaller individuals whilst the main growth of the young occurred between October and January. On the Ribble the cycle is extremely similar, but the peak size is reached earlier, usually by December.

Hydrobia ulvae

The minimum population density has been recorded in each year between February and June and, in 1973, to July. As with Corophium , this annual minimum has varied, being larger in 1973 than 1972, but much smaller in 1974 when, in February, the lowest density was recorded. In this period the animals have overall a fairly similar shell height: in February 2.68 ± 0.13mm (n = 450).

From late July density increases rapidly due to the settlement of spat approximately 0.6mm long. These grow quickly from August to October, during which time further settlement occurs. In this period the population consists of two groups: adults with a mean shell height of 3.16 ± 0.26mm (n = 78) and young with shell height varying from 0.6 to 1.75mm (see Table 51).

Density decreases from this autumn peak to the low late winter population, the mean size of the Hydrobia increasing (Table 51). This increase of mean size may be due to a higher mortality of the smaller Hydrobia as well as growth.

Biomass of four major prey and calorific values

At present (September 1974) sufficient data of biomass in terms of dry weight and calorific value have been obtained for only the four main prey of the middle and inner estuary, though tentative results are available for Bathyporeia pelagica. It is also possible to make some estimates of the biomass of Mytilus edulis, Scrobicularia plana and Cardium edule by incorporating the findings of Dane (1973), Hughes (1970) and Hancock and Franklin (1972) respectively for those species.

In Nereis, Corophium and Macoma there was a correlation between size and dry weight (Figure 42), at least over the main size range. The regressions of figure 42 could thus be used to estimate the mean dry weight of these species within any particular sample, provided that the mean size of the sample was known. No such correlation was obtained for Hydrobia, mean dry weight through the winter being fairly constant at 0.28 ± 0.002 mg.

Table 52 presents estimates of calorific values of these four prey, using ash - included data. Variance of these estimates is possibly high as a consequence of variable amounts of inorganic detritus within the animals. It is reasonable to use such ash - included values, rather than ash free values, for waders will take such variable amounts of detritus into the gut and this will provide a contribution to the weight of food. For example, an Oystercatcher taking 1g of Mytilus meat into the gut will be obtaining more food value than one taking in 1g of Lumbricus, which may contain a high proportion of soil. Similarly, a Bar-tailed Godwit taking 1g of Macoma will take more indigestible material in the form of shell than one taking 1g of Arenicola which may contain a variable weight of sand and mud. For this reason ash-included estimates are given.

Table 51

Shell heights of young Hydrobia ulvæ through autumn and early winter (1972 - 3 data)

	Height (mm)	S.E.	n
August	1.09	0.20	65
September	1.18	0.27	58
October	1.62	0.15	94
November	2.20	0.29	60
December	2.46	0.31	75

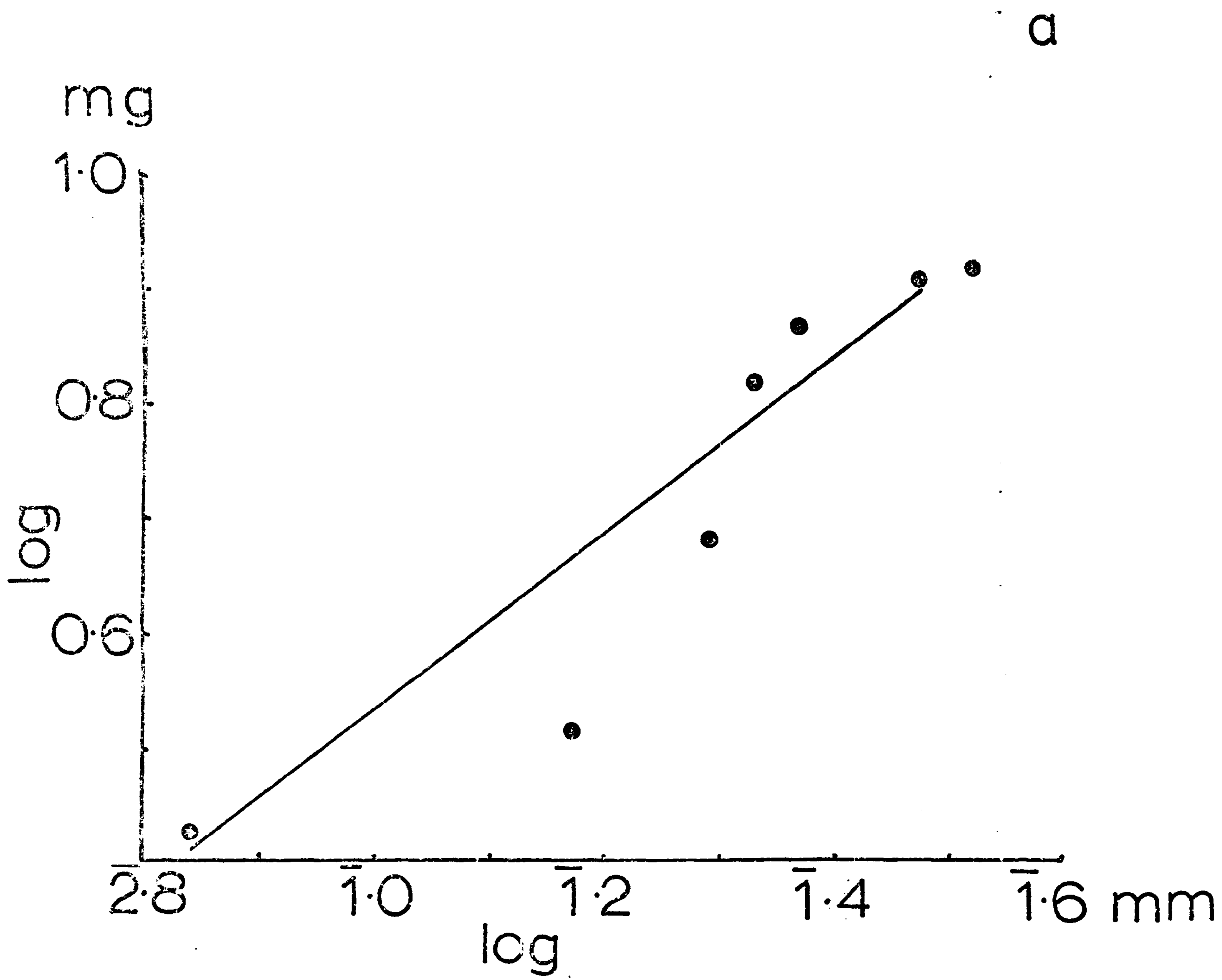
Table 52 Energy values of four major invertebrate prey species on the Ribble Estuary

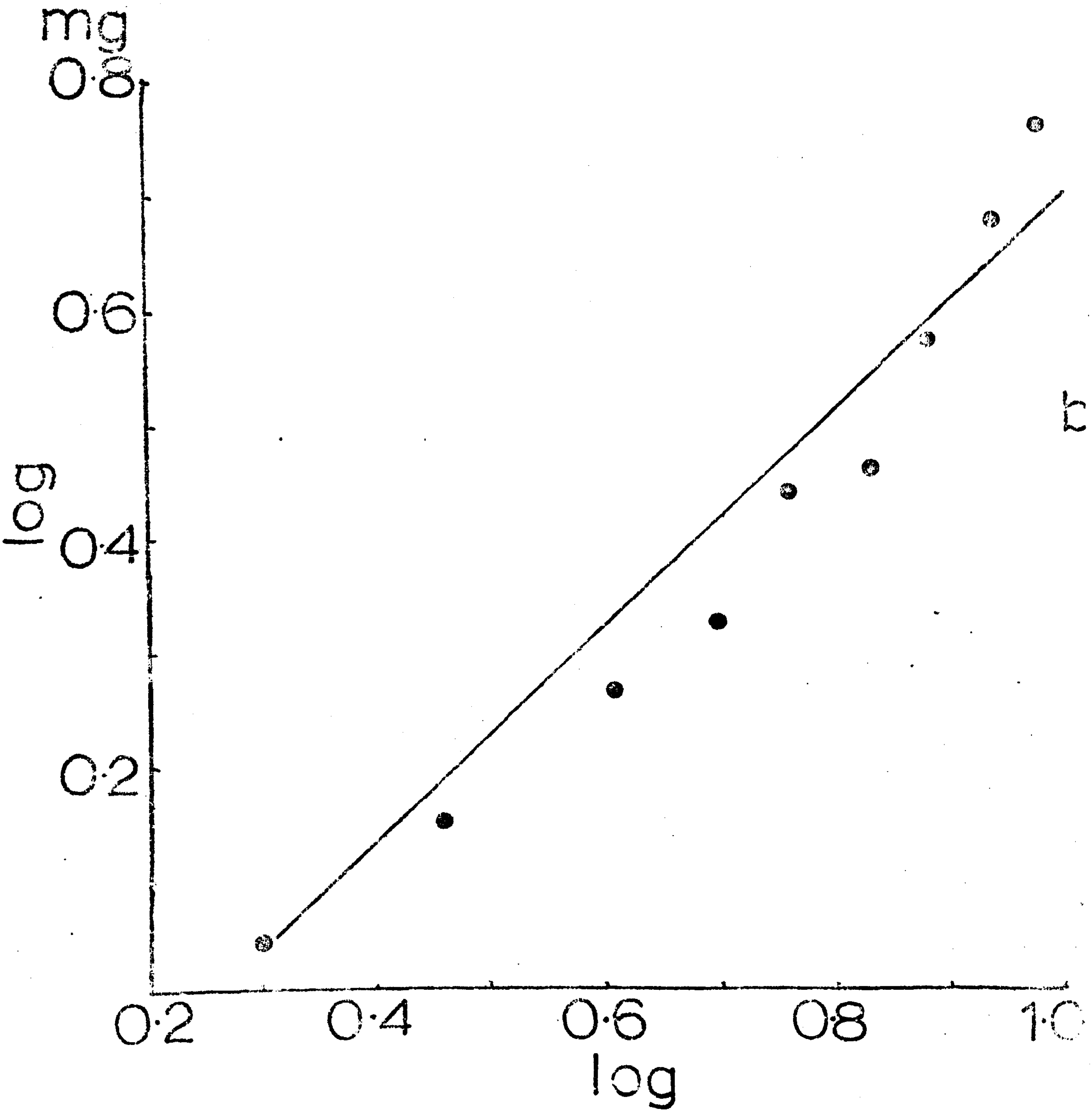
	N	K Cal/g	KJ/g	% ash
Nereis	6	4.91 ± 0.62	20.6 ± 2.61	16.6
Corophium	6	5.54 ± 0.47	23.3 ± 1.98	10.2
Hydrobia	4	1.86 ± 0.29	7.8 ± 1.22	19.6
Macoma	5	4.03 ± 0.24	16.9 ± 1.01	13.8

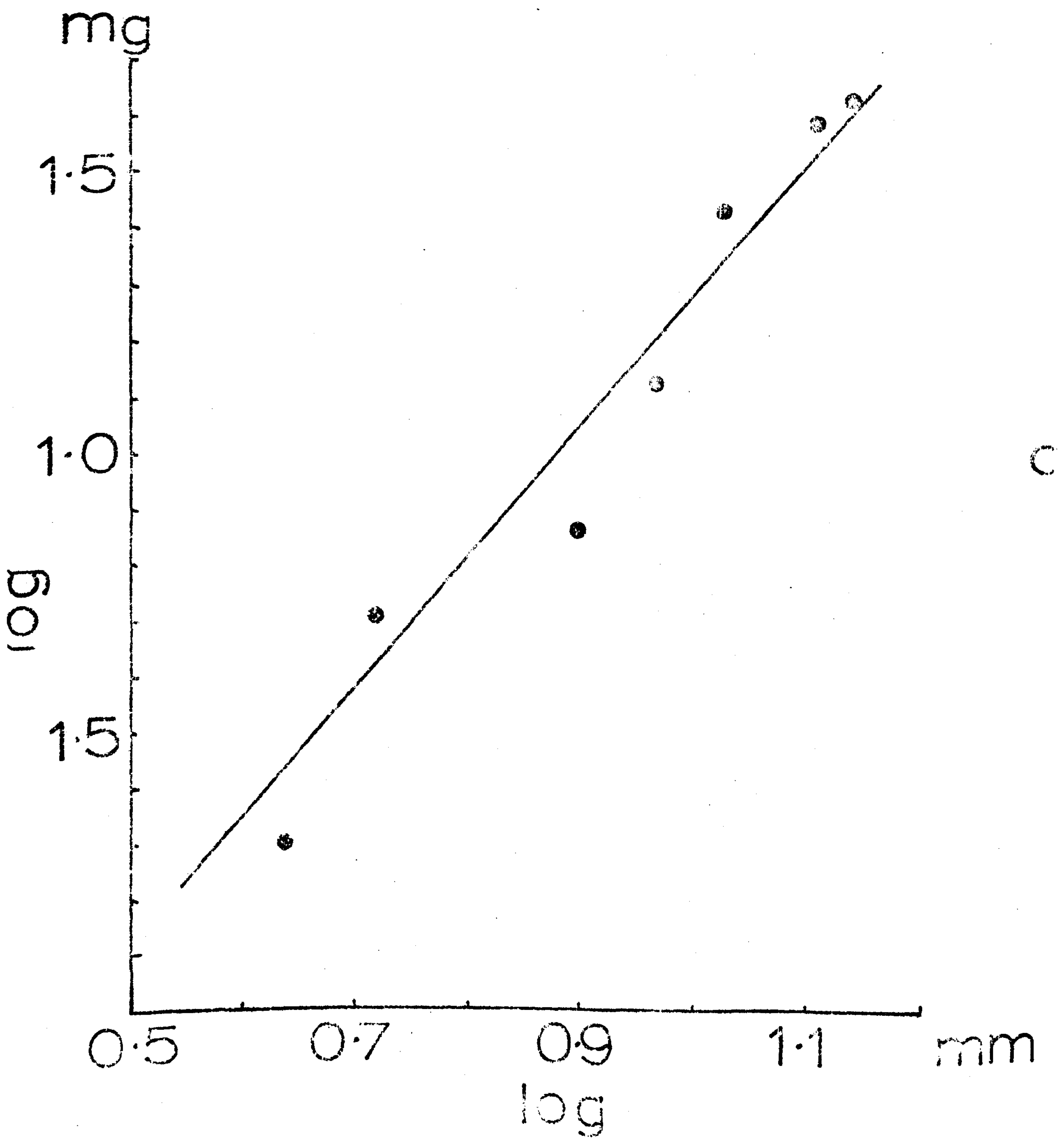
Note: values are given ash-included.
figures after means are 95% confidence limits

Figure 42

Dry weight plotted against a) jaw-length in Nereis, b) body-length in Corophium and c) valve-diameter in Macoma. Correlation coefficients are given next to the regression lines.


a
mg
1·0
0·8
0·6
log
$\bar{2}$·8
$\bar{1}$·0
$\bar{1}$·2
$\bar{1}$·4
$\bar{1}$·6 mm
log


mg
0·8
0·6
0·4
0·2
log
0·2
0·4
0·6
0·8
1·0
log


mg
1·5
1·0
log
1·5
0·5
0·7
0·9
1·1
mm
log
C

Calorific value varies seasonally in many species such as *Mercenaria mercenaria* (Ansell *et al*. 1964), *Tellina tenuis* (Ansell and Trevallion 1967), *Cardium edule* (Hancock and Franklin 1972), *Donax vittatus* (Ansell 1972) and *Mytilus edulis* (Dare 1973). Seasonal variance in energy value may well occur in the species considered here though it was not possible to investigate this aspect during the study. It must be borne in mind, however, that a wader may obtain significantly less food value from a given weight prey in winter than it would have obtained from the same weight in spring and summer.

CHAPTER VIII

THE FOOD INTAKE OF WADERS

Introduction

It is only in very recent years that attempts have been made to estimate the amount of food waders consume in a given time, most earlier authors being content to describe the composition of the diet. Economic problems associated with Oystercatchers feeding on *Mytilus* and *Cardium* fishery stocks prompted MAFF workers to put emphasis on this aspect (Drinnan 1957, 1958 and Davidson 1967), others also having carried out similar food intake measurements in Oystercatchers (e.g. Hepplestone 1971).

Food intake in Oystercatchers is easy to measure due to the sizes of prey and the intricate methods employed in capturing the prey (Drinnan 1957, Davidson 1967, Tinbergen and Norton-Griffiths 1964). Goss-Custard (1969, 1970 a and b) was the first to examine food intake seriously in another species, the Redshank, in which food intake was more difficult to measure. Such studies have paved the way for others: for examples Prater 1972, Smith and Evans 1973 and the present one.

Basically, what is required is a measure of the amount of food taken per unit time the birds are actually feeding. This may vary due to a variety of reasons depending upon the species of wader (for examples, whether tide is neap or spring, whether substrate is wet or dry, time since high water, number of birds in the feeding flock, sex of birds, age of birds, density of prey and mud temperature). Each of these factors should ideally be examined for each major prey of each predator. This study, with a somewhat broader base than the others referred to above, examines food intake for the eight main Ribble waders but as yet not all facets of feeding rate have been examined for all species. Emphasis has been put on their feeding on the major prey over the main feeding range. Further work will be required to fill gaps for these species besides incorporating data on other less important shore waders (e.g. Ringed Plover, Turnstone) on the Ribble.

Methods

The methods of obtaining measurements of feeding rate are well established (e.g. Drinnan 1957, 1958, Feare 1966, Davidson 1967, Goss-Custard 1969, 1970a, Hepplestone 1971, Prater 1972), though different authors have used slightly different modifications to get the same results. The method used here varied slightly from species to species depending on prey and wader, in order that the required data could be ascertained.

Peck rate

This can be taken as a measure of feeding rate (i.e. the rate at which a bird attempts to take food).

Birds were chosen as randomly as possible and the time for the birds to make 30 (or in some cases, 10) pecks at the substrate recorded using a X15 - 60 x 60 telescope, stopwatch and tally-counter. These timings were then converted into pecks made per minute.

In the larger waders (Oystercatchers, Curlew and godwits) however, the calculation of feeding rate seemed a little superfluous in that the actual number of prey ingested could easily be seen and the rate calculated directly. Peck rate was of greatest use in species which peck rapidly but extra counts are required in order to calculate the proportion of pecks which are followed by the swallowing of a prey item.

Feeding Success

The proportion of pecks followed by swallowing was calculated, the main difficulty being that in some cases one could not be certain that a food item had been swallowed.

There was little difficulty in the larger wader species feeding on large prey. In Redshank, Knot, Dunlin and Sanderling the problem was more difficult in that most prey were very small so that swallowing movements were generally difficult to observe.

Goss-Custard (1973) showed by reliability tests that the swallowing movement was a good guide that a food item had been swallowed in Redshank and similar tests were carried out on Redshank and the three calidrines. These tended to confirm faith in the method for Redshank feeding on *Corophium*, though for *Hydrobia* variation in the estimates made by three observers was about 10% suggesting that occasionally prey may be swallowed which one observer may overlook, or a movement may be made which one observer may record as a swallowing. Similar discrepancies occurred in success estimates of Knot feeding on *Hydrobia*, though the author has known times when in wet or cold weather, when the birds have kept hunched-up with feathers fluffed out, it has been impossible to discern swallowing movements. No such problem exists where Knot are eating *Macoma*.

For both Sanderling and Dunlin which, for the most part, are feeding on very small prey, it is virtually impossible to estimate feeding success. This is due, in part, to the rapid peck-rate, for where peck-rate was low on some occasions, (less than about 50 per minute) swallowing movements could often be discerned.

Much more work is required therefore in calculating feeding success of these four wader species, and much of this must involve experimental work with captive birds. Goss-Custard (1970 b) and J. B. Hulscher (pers. com.) have made initial experimental investigations in Redshank and Oystercatcher respectively. Though time and facilities were not available for such work in this study, it is hoped to carry out the necessary experiments and observations at the Wildfoul Trust reserve at Martin Mere once the necessary cages have been constructed.

Ingestion Rate

The number of prey taken per unit time could be ascertained directly with a high level of accuracy in Oystercatcher, Curlew, Black-tailed Godwit and Bar-tailed Godwit for most prey, though smaller ones may have occasionally been overlooked.

For Redshank and Knot ingestion rate had to be computed from peck rate and success data and for Dunlin and Sanderling ingestion rate was estimated from peck-rate, the few records of feeding success and the data for Redshank and Knot feeding on the same or similar prey.

Once the number of prey taken per unit time is known, then the number of prey taken per tide cycle or day can be calculated employing the data on roosting time and time on the shore spent in feeding (chapter III). Where one wader species takes more than a single main prey (e.g. Oystercatcher and Mytilus, Macoma and earthworms , Knot and Hydrobia and Macoma) then using the previous data on foods and feeding areas (chapters IV and V) this can be allowed for in calculating total daily food intake. By knowing mean sizes of prey taken (chapter V), the mean dry weight can be ascertained and thus the total biomass of each prey in terms of grammes dry weight and calorific value taken by a wader per day or tide cycle.

Other factors were often involved in the final analysis; these are given where necessary.

Results

OYSTERCATCHER

The ingestion rate during daylight hours of Oystercatchers on Mytilus edulis are given in Table 53, on Macoma balthica in Table 54, on Scrobicularia plana in Table 55 and on earthworms in Table 56. In Tables 53, 54 and 56 the ingestion rates are given and then, having taken into account the variable amount of time available for feeding (chapter III) the average total daily intakes of the three species are given by mouth. Using data on size of prey taken by Oystercatchers (chapter V) the dry weights of the prey have been calculated and then, using values obtained in this study, from publications or from P. J. Dare (in litt. 11-1-1974), the energy value in terms of KCalories or KJoules. For earthworms (Table 56) have been calculated the intake by birds which spend the whole daylight period feeding and also the intake by those which feed on fields solely at highwater. As only a small proportion of Oystercatchers feed on Scrobicularia, and then probably for only a small part of the low tide period the food intake has been calculated on an hourly basis.

Peck-rate on the Mytilus scar increases through the winter from a mean of 31.41 ± 4.2 per minute (n = 115) in August to 45.04 ± 6.9 (n = 580) in December - January ($p < 0.001$). This is manifested by a significant overall increase in the number of Mytilus consumed per hour (Table 53) through autumn and early winter ($p < 0.001$). In late winter the intake decreases possibly as a consequence of the massive decrease in young mussel-stocks in the area at this time (see Dare 1973). Hepplestone (1971) found a similar increase of feeding rate from October to December and generally a rate of similar order (31.4 to 45.6 Mytilus per hour) of ingestion by Oystercatchers in Aberdeenshire whilst in Morecambe Bay in 1965 - 66 the author found that Oystercatchers there took 35.6 to 47.5 Mytilus per hour. This latter site is a much richer mussel-scar than Church Scar and this presumably accounted to some extent on the higher ingestion rate in Morecambe Bay. At the Morecambe Bay site Oystercatchers roosted longer and spent much more time in activities other than feeding than those on the Ribble (about 270 minutes on a 9m tide at roost compared with about 248 minutes on the Ribble, and between 55% and 75% of the time on the feeding area was spent in obtaining food compared with about 80% on the Ribble). With prey easier to obtain generally on the Morecambe site then less time had to be spent in feeding.

Hepplestone (1971) found that rates of food intake for spring and neap tides were similar in Aberdeenshire though this was not the case on the Ribble (1967-69 data), nor for Morecambe Bay (1965-66). As shown in chapter III, Oystercatchers roost for different amounts of time on the Ribble and Morecambe Bay depending upon tide height. Less time is thus available for feeding on spring tides. Even so, a large proportion of the low water period of spring tides is spent at 'intermediate sand roosts' (Drinnan 1957) so that only 55-60% in Morecambe Bay and 65% on the Ribble of time is spent

Table 53. Ingestion rate of Oystercatchers feeding on *Mytilus edulis* on Church Scar during daylight hours.

Month	No. observations	Mean no. mussels per hour	No. mussels per day	g dry wt	Daily intake expressed as KCal	KJ
Aug	71	35.8 ± 4.3	342	50.1	248	1044
Sep	186	35.4 ± 6.2	355	52.3	259	1087
Oct	362	38.8 ± 4.5	363	58.4	290	1218
Nov	291	48.1 ± 3.9	378	61.0	302	1266
Dec	643	45.0 ± 4.1	364	58.4	290	1218
Jan	322	37.3 ± 3.7	358	56.7	281	1180
Feb	408	34.9 ± 3.9	343	51.2	254	1067
Mar	216	35.8 ± 4.2	316	50.0	248	1044
Apr	103	36.5 ± 4.0	324	51.3	255	1072

Calorific value of *Mytilus* 4.95 KCal/g with ash, taken from Dare (1973)

Table 54. Ingestion rate of Oystercatchers feeding on *Macoma balthica* during daylight hours.

				Daily intake expressed as		
Month	No. observations	Mean no. *Macoma* per minute	No. *Macoma* per day	g dry wt	KCal	KJ
Aug	90	3.24 ± 0.38	1690	37.4	151	646
Sep	251	3.52 ± 0.41	1720	37.9	153	653
Oct	170	3.47 ± 0.36	1420	31.2	126	530
Nov	60	3.12 ± 0.34	1130	19.3	78	328
Dec	105	3.46 ± 0.37	830	14.2	58	244
Jan	84	3.71 ± 0.40	870	14.8	59	248
Feb	152	3.60 ± 0.39	1210	20.6	83	349
Mar	46	3.55 ± 0.37	1740	29.6	109	459

Calorific value of *Macoma* taken as 4.03 KCal/g ash-included.

Table 55. Ingestion rate of Oystercatchers feeding on *Scrobicularia plana* on Banks Sands during daylight hours.

Period	No. observations	Mean no. Scrobicularia per hour	Hourly intake expressed as g.dry wt	KCal	KJ
Jul-Sep	196	13.6 ± 1.9	10.1	45.4	190
Oct-Nov	347	14.4 ± 2.1	10.7	48.0	202
Dec-Jan	563	16.4 ± 1.8	12.4	55.6	234
Feb-Mar	248	8.9 ± 1.1	8.9	40.0	168

Calorific value of *Scrobicularia* taken as 4.4 KCal/g ash-included. Hughes (1970) published a figure of 4.475 KCal/g ash-included.

Table 56. Ingestion rate of Oystercatchers feeding on earthworms *Lumbricidae* on fields.

	No. observations	Peck-rate per min.	Ingestion rate per minute	Daylight period intake expressed as				Highwater period intake expressed as			
				No.	g.dry wt	KCal	KJ	No.	g.dry wt	KCal	KJ
Oct-Nov	372	27.1±1.28	1.07±0.02	640	76.9	291	1212	192	23.1	87	367
Dec-Jan	624	33.4±1.22	1.14±0.03	545	65.4	248	1024	205	24.6	93	392
Feb-Mar	480	34.7±1.09	1.11±0.025	680	81.7	308	1299	200	24.0	91	384

Note: High water period taken as the mean time spent by Oystercatchers, feeding inland, which feed on the shore over the low water period.

feeding on spring tides compared with at least 80% in Morecambe Bay and 85% on the Ribble on neap tides. These different feeding regimes are further marked by different feeding rates and sizes of mussels taken. On neap tides mean feeding rates of 36.8 ± 2.9 mussels per hour on the Ribble and 37.4 ± 1.2 on Morecambe Bay (from data collected in 1965-68) were significantly less than the spring tide feeding rate of 50.4 ± 3.4 and 57.1 ± 4.1 ($p < 0.001$) and the mean mussel sizes 32.4 ± 0.7mm and 32.7± 0.5mm respectively on neap tides and 20.4 ± 1.1 and 17.9 ± 1.4 mm on spring tides ($p < 0.001$). This is equivalent to a daily intake (in September - October) of 57.0 g dry weight on the Ribble and 55.0 g on Morecambe Bay on neap tides and 35.3 g on the Ribble and 37.0 g on Morecambe Bay on spring tides.

It would seem that Oystercatchers take between 30% and 40% less food on spring than neap tides, though this is not necessarily so for there are indications from Morecambe Bay and the north Ribble that more birds feed on the fields at high water on spring tides than on neap tides. It should also be pointed out that on spring tides Oystercatchers spend less time in obtaining food than on neap tides, and can thus conserve more energy in roosting. On spring tides the Oystercatchers feeding on Mytilus can apparently be satisfied by feeding for a minimum amount of time on the very small mussels exposed at lowest tide which can be obtained very quickly whereas on neap tides, when these small mussels are not exposed by the tide the birds must feed actively for longer periods on less rich higher feeding areas of larger mussels.

Feeding behaviour parallels the different feeding patterns. On the higher mussel scar on neap tides most are taken by stabbing the adductor muscles of those individuals in shallow pools or at the tide edge, the valves generally being undamaged. On the lower mussels on spring tides the valves are smashed open on the smaller mussels. This latter technique is a much more rapid procedure than the stabbing procedure, which requires careful selection of suitable mussels with valves open. Tinbergen and Norton-Griffiths (1964) described these two main methods of feeding whilst Norton-Griffiths (1967) showed that at Ravenglass most small mussels were opened by smashing and larger ones by stabbing, the larger ones requiring considerably more blows by the bill (and hence, more time) to open by smashing than smaller ones. It is thus more economical in time when feeding on large mussels to employ the stabbing method, even though searching for suitable open mussels is required.

Macoma balthica provides the main intertidal food source for the Oystercatchers which feed on mud and sand flats though it is quite probable that up to the hard 1962-3 winter when, like Morecambe Bay, the Ribble mudflats held large cockle *Cardium edule* stocks (see later) that this was the preferred prey. In Morecambe Bay Oystercatchers fed almost exclusively on *Cardium* (other than the mussel-feeders) until the *Cardium* stocks were depleted in 1963 since when the remaining Oystercatchers have turned mainly to *Macoma*.

The mean ingestion rate on *Macoma* increases through the winter and decreases in early spring (Table 54), though this is offset by the reduced day length of mid-winter. Hence in mid-winter Oystercatchers take much less *Macoma* than in autumn and spring. Hepplestone (1971) observed overall a lower ingestion rate (3.3 *Macoma* per minute), an average consumption of 25.42 g dry weight per low tide cycle. In mid-winter it is possible for one low tide cycle to take-up the daylight period, though with a tide at about midday possibly only two or three daylight hours may be available for feeding. In autumn or spring, on the other hand, with dawn at 0600 hours and dusk at 0900 hours and a midday tide at least ten daylight hours will be available for feeding. This is of some significance when some observations (chapter III and Hepplestone 1971) indicate a significant reduction in feeding rate during the hours of darkness. This point will be taken up again later.

Feeding success of Oystercatchers on *Macoma* appears to be related to:

1. Wetness of substrate. On mud and sand with a very shallow covering of water peck rate was significantly higher than on dry substrates (23.16 ± 1.58 per minute compared with 16.82 ± 3.44, $p < 0.001$), whilst ingestion rate on wet substrates was considerably higher (3.49 ± 0.27 compared with 0.40 ± 0.17). It may be that activity, either movements of the whole animal

(Brafield and Newell 1961) or of the syphon (Vader 1964), is greater in the wet areas so that the prey are most easily located by the Oystercatchers. Certainly, the location and extraction of Macoma does not seem to be a random hit-and-miss affair. The birds walk slowly in a zig-zag track over the substrate pecking the substrate as they go. When a peck is followed by ingestion, the bird rapidly digs the bill into the substrate and pivots round thereby twisting the Macoma out of the substrate. Similar extraction methods are used for Cardium and Scrobicularia. It is likely that the initial peck causes the Macoma to make some response: cessation of movement, closure of valves or retraction of syphons. This requires further study.

2. Flock Size. Timings were made on Horse Bank in January 1971 of the ingestion rate of Oystercatchers feeding on Macoma in loose flocks and singly. Such timings had to be made under as similar conditions as possible though this could not always be ensured. However, the data suggested that those birds feeding in flocks do have a higher ingestion rate than those feeding singly (3.61 ± 0.31 Macoma per minute in a flock compared with 3.48 ± 0.26 with single birds, $p < 0.05$). This difference is probably related to the time each individual in a flock spends on alert, looking for predators compared with the time spent by a solitary bird (see Lack 1968).

Relationships between ingestion rate and prey density and mud temperature were not investigated. In the former case it has been mentioned that Oystercatchers regularly feed only in areas of higher Macoma density (chapter IV). In the latter case, as will be explained later, on very few days since this study commenced has the temperature of the mud fallen to near freezing point, especially on areas covered by every tide. Thus any relationship between ingestion rate and lower mud temperatures would be of very minor overall importance during the course of this study.

Scrobicularia plana forms a relatively minor part of the overall food intake of Oystercatchers on the Ribble (Table 55) and it seems likely that no birds rely heavily on this for their daily intake. Certainly an Oystercatcher could not survive very long on the amount of food it would obtain from Scrobicularia without using other additional resources.

Though Cardium edule is now a minor Oystercatcher prey on the Ribble it is worthwhile including some details of intake obtained by the author in Morecambe Bay in 1965-68 for comparison with other prey. The average intake was 278 cockles per day on the main cockle bank (Cartmel Wharfe) remaining after the heavy loss of stocks in 1962-3. This compared with intakes of up to 315 cockles per day in the pre-1962 period (Drinnan 1957). The mean length of cockles taken in 1965-68 on this area was 24.61 ± 0.9 mm, equivalent to a dry weight of 0.29 g. The total intake would thus be approximately 81 g dry weight per day. On richer cockle banks such as the Burry Inlet (Davidson 1967) and Morecambe Bay in the pre-1962 years (Drinnan 1957) intakes could well exceed 90 g per day. Taking the energy value of the food as 4.59 KCal per g. ash-included. (P. J. Dare in litt.) then the intake will be 384 KCal per day (1630 KJ) on the 1965-68 data and over 400 KCal per day (1680 KJ) on richer cockle beds.

By feeding on fields at high water the daily food intake can be greatly increased (Table 56). For example, an Oystercatcher in October and November feeding on Mytilus will take an equivalent of about 295 KCals (123 KJ) on the shore and can obtain a further 87 KCals (367 KJ) from fields. The benefit to be had by a Macoma -feeding Oystercatcher of turning to earthworms at high water is even greater, for their winter-day food intake can be approximately doubled by earthworms. Even so, the intake of Macoma -feeding Oystercatchers (about 200 KCals, 840 KJ) is much less than the intake of Mytilus feeders, especially when these are taking earthworms at high water (total day intake in winter approximately 380 KCal, 1350 KJ). This adds to the impression stated earlier that Macoma is a secondary prey of Oystercatchers, utilized only because the primary prey Cardium is almost absent. Further, support for this is given by the analysis of cockle-intake given earlier.

Allowing for the fact that some food intake occurs at night (chapter III) (though there is some controversy as to the extent, Drinnan (1958) and Davidson (1968) assuming night and day rates equal whilst Hepplestone (1971) concurs with the present study) then the total daily intake of food by

*

More recently it has been demonstrated that a factor of three is far too low and the implications of this has been considered in the Discussion (Chapter X).

Oystercatchers feeding on any one of the following groups of items would be as follows:

Cardium alone	380-400 KCal (1600-1680 KJ)
Mytilus alone	260-330 KCal (1090-1390 KJ)
Mytilus with earthworms at low tide	350-420 KCal (1470-1770 KJ)
Macoma alone	80-190 KCal (340-800 KJ)
Macoma with earthworms at low tide	170-260 KCal (730-1090 KJ)

These will be the maxima, for a proportion will be lost in pellets, faeces and meat not actually ingested.

The average weight of an Oystercatcher in north west England in autumn and winter is about 500 g (Dare and Mercer 1973, personal data). From the equation of Lasiewski and Dawson (1967):

$$\log M = \log 78.3 + 0.723 \log W \pm 0.068,$$

the standard metabolic rate for such a bird would be 47.6 KCal per day (200 KJ).

Previous workers have considered the energy requirements in the wild to be at least twice the standard rate (e.g. Hepplestone 1971) though Hulscher (pers. com.) has found the requirements to be about three times the standard value. Thus, on this basis Oystercatchers in the wild will require approximately 143 KCal per day (603 KJ) whilst in hard weather it is likely that the birds will require more, up to 200 KCal (840 KJ) per day.*

It is quite clear that, for shore-feeding Oystercatchers, only those taking *Mytilus* or *Cardium* have an intake covering the requirement. These are the traditional prey of the area (Dare 1966). It is also likely from these data that *Macoma* could not sustain for long periods a large resident Oystercatcher population.

Indeed, the behaviour of feeding on fields through the daylight period, which is presumed to be an extension of the high water feeding (Dare 1966), yields a higher energy intake than if the birds moved back to the shore at at low water to feed on Macoma (Table 56). Fields are however far more vulnerable to frost and snow temporarily making the prey unavailable. Even so, such field-feeders, which probably take some food at night on the shore, may well obtain over 320 KCal (1320 KJ) per day in autumn and spring and 280 KCal (1170 KJ) per day in mid-winter.

Most Oystercatchers would seem, therefore, to have an abundance of food on the Ribble, being able to obtain with relatively little difficulty the daily requirements. The only problem may be for those birds which depend on inland foods to supplement their shore-feeds: in very hard weather they are excluded from fields.

CURLEW

As was shown earlier, it would seem from observations on the estuary that only a small proportion of Curlews feed to any great extent on the shore, probably all feeding for part of the day on fields. When these are frozen in hard weather most birds emigrate to Ireland or West Europe. Furthermore, a high proportion of Curlews feed inland at night, especially around the full moon period. For this reason data on feeding rates of Curlew on the shore are presented simply as peck and ingestion rates, any attempt at making concrete estimates of daily food intake from the shore being inaccurate due to the inland feeding. This latter aspect of Curlew ecology requires more study, especially the time spent in obtaining food in relation to different prey through the year.

The two main prey of Curlew on the shore are Nereis and Macoma (chapter V), most taking Nereis with just occasional Macoma, though a minority (probably about 30%) appear to take a preponderance of Macoma. Measurements of feeding rate have been thus divided into those taking Nereis and those taking Macoma (Tables 57 and 58). No significant variations were observed in feeding rates through the year so data have been pooled.

Feeding and ingestion rates were in all cases significantly different in the three classes of niche on the shore. Feeding activity was lowest on dry substrates, with no standing water or water film, and highest in areas of shallow water ($p < 0.001$ in all cases). Macoma was not observed to be taken regularly in deeper water, though Nereis was taken in deep water at a slower rate than in shallow areas ($p < 0.01$) but a faster rate than in dry areas ($p < 0.001$).

The vast majority of feeding Curlews occurred in the tide-edge, shallow runnels crossing the sand banks or in shallow pools. For instance, in November-December 1972, 487 out of 520 (93.7%) of observed feeding Curlews were in these zones and it is in these that peck and ingestion rates are highest. It is likely that the Curlews here were reacting to visual stimuli in obtaining prey, such as defaecation of polychates or syphon movements in bivalves, for these movements are more frequent in wet areas than dry areas (see earlier, P. Smith pers. com.). Prey density was often not significantly lower on the dry areas of the sand banks frequented by Curlews.

Those Curlews which feed throughout the daylight tide cycle on the shore do so for some 337 minutes (chapter III). From the gut contents available Curlews seem to take similar sized prey to Bar-tailed Godwits (see later) and, knowing the ingestion rates and these two pieces of information it is possible to make a crude estimate of the total daily intake by Curlews on the two main prey.

When feeding in optimal conditions (shallow water) a Curlew taking Nereis ingests about 5.7 g dry weight per tide cycle (equivalent to 21.2 KCal, 89.0 KJ) and one taking Macoma ingests 11.0 g dry weight (44 KCal, 185KJ).

From Lasiewski and Dawson (1967) a Curlew weighing about 450 g would have a standard metabolic rate of 44 KCal (185 KJ) per day.

A wild Curlew would thus require at least 132 KCal (554 KJ) per day assuming that wild birds in winter require three times the basal metabolic rate per day. The food ingested in a single tide cycle could, therefore, amount to 16 - 33% of this requirement.

It seems clear, therefore, as was suggested earlier (chapters II - V),

Table 57. Peck and ingestion rates of Curlew feeding on *Nereis diversicolor*

	n	Peck rate (per min)	Ingestion rate (per min)
Dry sand	34	16.4 ± 3.8	0.6 ± 0.24
Shallow water	148	22.9 ± 1.3	2.1 ± 0.19
Deep water	55	21.5 ± 4.1	1.8 ± 0.21

Table 58. Peck and ingestion rates of Curlew feeding on *Macoma balthica*

	n	Peck rate (per min)	Ingestion rate (per min)
Dry sand	40	27.6 ± 5.2	0.9 ± 0.44
Shallow water	70	35.7 ± 4.9	5.1 ± 0.37

Note: Shallow water is that which is not as deep as the tarsus length, water deeper than this (often up to the bird's belly) being classified as deep.

Table 59. Feeding and ingestion rates of Black-tailed Godwits feeding in flocks on four areas of the Ribble Estuary in autumn (July-September).

	No. observations	Feeding rate	Ingestion rate
Lytham	367	30.9 ± 2.1	3.47 ± 0.38
Fairhaven Bay	104	28.8 ± 2.4	2.71 ± 0.29
near Church Scar	42	26.0 ± 3.2	2.59 ± 0.38
Crossens Pool	19	23.5 ± 3.6	1.64 ± 0.33

that the intertidal zone provides little for the Curlew population on the Ribble, the bulk of the food coming from inland sources.

Because of the sparse distribution of Curlews on the intertidal zone and the above data, no investigations were made of the effects of other factors on Curlew ingestion rates.

BLACK-TAILED GODWIT

Table 59 presents the basic data on feeding and ingestion rates of Black-tailed Godwits from four different areas of the Ribble Estuary. Data are pooled for the late June to early October period out of which the population is very small (chapter II).

On the main area, at Lytham, both feeding and ingestion rates were significantly higher than on the less important Fairhaven and Church Scar ($p < 0.001$). At these latter two sites feeding statistics were fairly similar. Feeding and ingestion rates at the fourth site examined, Crossens Pool, were much lower that at the regular feeding areas. These data were from autumn observations of single birds and one party of four (September 1973). The vast majority of food taken at all sites was Nereis (see chapter V).

Smith and Evans (1973) showed that in Bar-tailed Godwits the larger females had a significantly higher ingestion rate, especially in deeper water, than males. A similar size dimorphism also occurs in the Black-tailed Godwit, the mean bill length of the Icelandic race which predominates on the Ribble in autumn males being 83.2 mm and females 100.3 mm ($p < 0.001$). In autumn 1973-4 the feeding of Black-tailed Godwits at Lytham was re-examined to see whether different feeding ecologies occurred in the two sexes. Only individuals which were readily identified to sex were included. These results are given in Figure 60.

Parties or small flocks of Black-tailed Godwits composed of a single sex do not have significantly different feeding or ingestion rates than mixed-sex flock though it is possible that with more data statistical significance may be found.

Table 60. Feeding and ingestion rates of Black-tailed Godwits in single-sex and mixed-sex flocks in three types of feeding situation.

		Single-sex Flock			Mixed-sex Flock		
		Wet Mud	Shallow	Deep	Wet mud	Shallow	Deep
MALES	Feeding Rate	33.4±1.8	25.6±1.9	19.2±2.1	31.6±2.0	25.9±1.7	20.1±1.9
	Ingestion Rate	3.49±0.38	3.10±0.35	1.8±0.42	3.23±0.36	3.18±0.29	2.02±0.21
FEMALES	Feeding Rate	34.3±2.1	29.4±2.2	26.5±1.7	34.0±2.7	31.0±2.3	29.1±1.7
	Ingestion Rate	3.46±0.31	3.21±0.34	2.9±0.40	3.41±0.34	3.35±0.26	2.36±0.42

Note: 'shallow' refers to water not as deep as the tarsus length, 'deep' to water deeper than the tarsus length.

Table 61. Feeding situations of Black-tailed Godwits at Lytham.

	Wet Mud	Shallow	Deep	n
Male	78%	18.5%	3.5%	250
Female	72%	22%	6%	327
n	430	118	29	577

The main differences are between feeding rates of male and female Black-tailed Godwits. Whether feeding in single-sex or mixed-sex parties, females generally have significantly higher feeding rates than males ($p < 0.01$) the one exception, on wet mud, being possibly due to small sample size. Females also tend to have higher ingestion rates though in only those feeding in deep water are rates significantly higher than in the male ($p < 0.01$ in single-sex flocks and $p < 0.02$ in mixed-sex flocks).

Table 61 shows the main feeding stations of the two sexes at Lytham on the days the data of Table 60 were obtained. Overall, significantly more females were counted on the feeding areas than males ($x^2 = 10.4$, $p < 0.01$). This is unlikely to be due to confusion of the sexes: indeed, it is more likely that some females were recorded as males for the bill length (used in the separation) is not fully grown until late autumn in juvenile godwits and thus very short-billed female godwits could be counted as males.

Males tend to feed higher up the shore than females, a higher proportion of which feed in water at the tide edge. Such differences are not, however, significant ($x_2^2 = 2.961$, $p \quad 0.2$).

The weight of male Black-tailed Godwits in autumn is about 360 g and of females 400 g. Thus a male Black-tailed Godwit will have a standard metabolic rate of 37.4 KCal (157 KJ) and a female 40.2 KCal (169 KJ) using data from Lasiewski and Dawson (1967). Allowing a factor of three in estimating the food-energy requirement per day of wild Black-tailed Godwits (probably a realistic factor in autumn when temperatures are never very low) these will be 112 KCal (470 KJ) for a male and 121 KCal (510 KJ) for a female.

In autumn a Black-tailed Godwit spends approximately 439 minutes per tide cycle in obtaining food whilst during the night it could be expected that feeding might occur on moonlit nights though at a reduced rate. By combining these points with the data presented above it would appear that a male Black-tailed Godwit takes about 20.0 g dry weight of *Nereis* and a female about 20.7 g in autumn over the 24 hour day. These are equivalent to intakes of 84.5 KCal (356 KJ) in males and 87.4 KCal (367 KJ) in females.

The discrepancy between expected requirements and intake could be due to the birds not needing three times the standard metabolic rate (as pointed out earlier, there is some argument as to whether wild birds need intakes of food two or three times the standard requirements). In autumn weather is generally mild and Black-tailed Godwits spend more time roosting than most other waders. It may be also that the godwits obtain far more food at night than has been suggested by this Study.

One point of interest here is that Black-tailed Godwits do not over-winter here: possibly they can manage well on the resources in autumn, but not winter (see chapter IX). They used to winter in the 1950s and early 1960s but have not done so in any number since 1962. The odd ones encountered in winter usually occur on stubble where they appear to glean for seeds and probe for invertebrates. There is evidence (see chapter II) that the autumn Ribble godwits winter on the Dee and it would be interesting to examine the ecology of this winter flock.

BAR-TAILED GODWIT

Table 62 presents basic data on feeding and ingestion rates of Bar-tailed Godwits on polychaetes on Salter's Bank and Foulnaze. Peak ingestion rate occurs in autumn during the period of peak passage and it may be that this high rate of feeding and ingestion is a response to the loss of fat on the migration to the Ribble, to provide energy and protein for the replacement of feathers during the moult which occurs on the Ribble (C.F. Knot) and for the build-up of fat reserves for migration in these godwits which leave the Ribble in late autumn.

Most godwits feed in fairly loose flocks, scattered either along the tide-edge or over areas of wet substrate. A very small proportion of Bar-tailed Godwits (certainly less than 5%) feed solitarily and, on the same area, such 'non-flock' birds have significantly lower feeding and ingestion rates: 22.6 ± 2.8 and 1.17 ± 0.41 per minute respectively C.F. Table 62 ($p < 0.001$).

Smith and Evans (1973) recorded similar differences in feeding and ingestion rates from Lindisfarne.

The ingestion rate of Bar-tailed Godwits on polychaetes on the Ribble was probably significantly faster over the main feeding zone than that measured by Smith and Evans (1973) from Lindisfarne (Table 62 C.F. 1.02 ± 0.2 given by Smith and Evans).

At Lindisfarne, however, <u>Arenicola marina</u> was the main prey whereas on the Ribble just over 10% of polychaete prey consisted of <u>Arenicola</u>, the remainder being <u>Nereis</u>.

Not all of the prey was ingested at every successful capture. On 26 February 1972 a spot-check revealed that in 9 out of 26 (35%) <u>Arenicola</u> and 7 out of 161 (4%) of <u>Nereis</u> captured only fragments were taken and the remainder, broken off, escaped. When such fragments were taken the godwit, instead of taking the food to a pool for washing before swallowing, immediately swallowed the fragment and the bill inserted in an attempt to catch the remainder. In calculating overall food intake such losses have to be taken into account.

For <u>Nereis</u> they are probably slight, though in <u>Arenicola</u> where most of the heavier anterior portion may escape, the losses may be great (at least two-thirds if only the tail region is ingested).

The main Bar-tailed Godwit feeding zones, shown in Chapter IV were either covered by a thin film of water at low tide or were used as the tide was covering or exposing them. A few birds were observed feeding in dry areas, their ingestion rate of 0.8 ± 0.15 per minute being significantly lower than birds feeding in typical wet habitat : Table 62 ($p < 0.001$).

Godwits feeding predominantly on <u>Macoma</u> had faster feeding and ingestion rates than those feeding on polychaetes. The feeding rate, which consisted of a forward sweeping or shovelling movement with the bill inserted up to approximately 3 cm deep into the substrate rather than deep probes, was 39.2 ± 2.6 per minute and the ingestion rate was 6.1 ± 0.08

Table 62. The feeding and ingestion rates of Bar-tailed Godwits feeding on polychaetes on the Ribble Estuary.

	n	Feeding rate (per minute)	Ingestion rate (per minute)
Jul-Aug	42	31.2 ± 2.1	2.86 ± 0.27
Sep-Oct	94	30.4 ± 1.7	2.91 ± 0.34
Nov-Dec	66	29.7 ± 1.8	2.64 ± 0.21
Jan-Mar	78	28.2 ± 2.5	2.68 ± 0.38

per minute. On some occasions, Macoma-feeding godwits would use a rapid pecking movement of the surface few millimetres of substrate followed by bill insertion which usually resulted in some food being obtained. Both feeding movements suggested strongly that the godwits were testing or raking through the substrate for prey rather than following clear visual clues which they were probably using when feeding on polychaetes.

Most Bar-tailed Godwits feeding on Macoma did so in loose flocks and no measurements were taken of the rates of ingestion on the few (certainly less than 2%) which fed solitarily.

Smith and Evans (1973) have recently shown that the feeding ecology of male and female Bar-tailed Godwits differs significantly. This was not investigated here. Such differences which probably exist will probably not affect the overall estimates of food intake, the sex-ratio of Bar-tailed Godwits on the Ribble appearing to be 1:1 (of dissected birds 21 male and 26 female ($x^2 = 0.53$, p 0.7)), and the birds from which feeding data were obtained were chosen as randomly as possible.

On only two days when mud temperature was below 5°C was ingestion rate of Bar-tailed Godwit calculated. The mean of birds feeding on polychaete at Fairhaven was 2.51 ± 0.35, a figure which did not differ significantly from the data obtained for godwit flocks on days with mud temperatures greater than 5°C (p = approximately 0.2).

From Lasiewski and Dawson (1967) the standard metabolic rate of a Bar-tailed Godwit of mean winter weight of 320 g is 34.3 KCal (144KJ) and, assuming an energy requirement of three times this figure in winter, the daily requirement would be about 103 KCal per day (435 KJ).

A Bar-tailed Godwit feeding entirely on polychaetes over the 470 minutes of the tide cycle used in feeding will take about 23 g dry weight of food equivalent to about 97 KCal (408 KJ). One feeding on Macoma will take 36.6 g dry weight through the tide cycle, equivalent to about 148 KCal (620 KJ).

For those feeding on polychaetes there is reasonable agreement between the figures though the godwits feeding on Macoma seem to be taking more than the basic requirements: certainly more than the polychaete feeders. However, a higher proportion of the food value of Macoma will be lost in pellets than of Nereis or Arenicola.

It should be recalled that there appears to be a seasonal swing from polychaetes to Macoma in the diet of Bar-tailed Godwits from February (chapter V) when, in any case, there are very small numbers of godwits remaining on the estuary (chapter II). An increase of food intake caused by a change in main prey would be of some value in early spring, leading to fat deposition prior to migration and breeding.

Those godwits which included Macoma in their diet in autumn and winter obtained most on the lowest feeding areas at low water though none of the data in this study suggested tidal variation in the diet. It is suggested, however, that some Bar-tailed Godwits take Macoma at low water, feeding mainly on polychaetes during tidal movements (C.F. Knot and Hydrobia and Macoma).

REDSHANK

A great deal of background data on food intake in Redshanks during winter was available around the time that the present study was commenced from the work of Goss-Custard (1969, 1970a and b) on the Ythan Estuary, Aberdeenshire. On this relatively small estuary Corophium was the main prey, feeding and ingestion rates on this species being dependent upon mud temperatures below 6°C whilst above that temperature rates were independant of mud temperature. At one site fewer Corophium were taken at lower temperature but more Macoma, whilst at a second site Nereis replaced Corophium as the major prey. Such variation Goss-Custard (1969) attributed to differences in prey behaviour at lower temperatures.

It was also clear that, whilst the sizes of Nereis and Macoma taken on the Ythan remained constant through the year, the sizes of Corophium taken by Redshanks decreased through the winter as size in the substrate decreased. Goss-Custard did not record an increase of peck and ingestion rates parallel to the decline in Corophium prey size through the winter. Consequently, with the size of prey decreasing through the winter and with the reduction of day-length, it was calculated that the Ythan Redshanks obtained less than 50% of their daily food requirements from the estuary in daylight. Goss-Custard thus presumed that the deficit had to be collected either at night or during high water from fields.

Goss-Custard (1970a) also showed that Redshank densities were correlated with prey densities though there was conflicting evidence as to whether feeding rate increased with prey density. In some areas there were slight increases in feeding rate with increasing prey density, in others such a relationship did not occur.

In planning the part of this study dealing with feeding rate of Redshank the points brought out by Goss-Custard's study were considered. Feeding rates were measured at regular intervals through the non-breeding season at Crossens (Horse Bank) in a section of 'Spartina-edge' on which prey was almost exclusively Corophium (Table 63).

Lower down the shore Hydrobia is taken as well as Corophium and during the winter months (November-February) measurements were made of ingestion rate in this zone at seven sites where densities of both prey and also proportions of each in the diet were known. In each case data were collected at low water. At sites B and C Nereis was also taken and at sites B and F Macoma. In all cases these two species contributed a very minor part of the diet so they are excluded from Table 64.

To test whether Redshanks on the Ribble follow a similar pattern of feeding with low mud temperature as Goss-Custard (1969, 1970 a) found on the Ythan, data on the feeding rates from Horse Bank were pooled with similar data from Banks Sands and Warton Marsh from days where mud temperature was known. These data are presented in Figure 43.

In two sites at Lytham and Fairhaven where the prey is mainly Nereis no significant differences were found in either peck or ingestion rates so data were pooled (Table 65). These are areas used in autumn by Black-tailed Godwits. Measurements of feeding rate were also made on a lower shore level on Horse Bank adjacent to Crossens Pool where Redshank feed mostly on Macoma. These are summarised in Table 66. Other data are included in the text.

The mean peck rate of Redshank feeding on Corophium on Horse Bank (Table 63) peaks in autumn (August - September) and early spring (February - March), being fairly constant through the remaining months. Success likewise peaks during September then decreases through the winter with a slight recovery during March. A combination of these statistics together with details of size of prey (chapter VIII) shows that intake, in terms of biomass ingested per hour of daylight, decreases only slightly from a September peak until January when lowest ingestion rate is reached. By March, however, ingestion rate recovers to the autumn level.

This pattern has a profound effect on the daily intake of Redshank through the non-breeding season. In autumn when the birds may be on the feeding areas for over ten light hours, over 90% of the time being spent in feeding (chapter III), a bird could take in at least 10.8 g (46 KCal; 192 KJ) of food. In mid-winter, however, with only eight hours of daylight, probably about two of which would be lost due to high water, the intake would be about 6g (25 KCal; 105KJ).

From the equation of Lasiewski and Dawson (1967) the standard metabolic rate of a Redshank weighing 180g would be 22.6 KCal (95.9KJ). As explained earlier, in the wild the daily intake would be at least twice and possibly three times this rate. The requirements would be greater in winter with lower temperatures, there being an increase in metabolic rate of about 1.5% for each °C temperature decreases (Wallgren 1954). In any case, accepting the factor of three in calculating the energy requirements of waders, the daily requirement would be 68 KCal (286 KJ). Redshank feeding in autumn on Corophium would take about 67% on the shore in daylight whilst in winter about 37% would be obtained in this way.

That Redshank are generally selecting Corophium as food is suggested by Table 64. Data are from the zone where both Corophium and Hydrobia occur in high density and are from days when mud temperature was at least 7°C. Ingestion rate was not correlated with either Corophium or Hydrobia densities and, with the exception of site A where Hydrobia was in very high density and Corophium at the edge of its main range, Corophium was heavily selected compared with Hydrobia (overall $p < 0.001$).

Ingestion rates at the sites given in Table 64 were generally similar to those given in Table 63 with the exception of site D where intake was significantly higher than other sites for the mid-winter period ($p < 0.001$). This site was covered by a deeper film of water than other sites, so it may be that the prey, by responding to the greater water cover, were more readily available.

It was from this zone where both Corophium and Hydrobia occur in high density, also with Nereis and Macoma, that the data in Figure 43 were obtained. Unfortunately, relatively few days with mud temperatures below 6°C were experienced during the study. It was clear, however, that as Goss-Custard (1969) found, Corophium intake decreases with temperatures below 6°C. Hydrobia occupied a larger part of the diet at such temperatures, something which Goss-Custard (1969) did not observe on the Ythan. The proportion and rate of intake of Macoma in the diet did not vary with temperature whilst the only suggestion of an increase of Nereis intake was from two days with mud temperature of 4°C when at sites B and C of Table 64 intake of Nereis was high.

Generally, mud temperature only occasionally falls to below 6 °C on the Ribble, the most vulnerable area being that area covered for only an hour or so during high water. It is this zone which provides Redshank on the Ribble with most winter-feeding (chapter IV). On several of the days on which data in Figure 43 were obtained, mud temperature on the upper shore was between 2 - 6°C (all temperatures at which Redshank suffer from a reduced ingestion rate) whilst on the lower zones where other waders were feeding (Oystercatcher, Bar-tailed Godwit and Knot) mud temperature was at least 2°C higher.

In very prolonged hard weather, last experienced in this region during the 1962-3 winter, Redshank are the worst affected of all the inter-tidal-feeding waders. Not only are they excluded from fields where their food intake is supplemented at high water, but their food intake on the shore is greatly reduced for days on end. In the 1962-3 winter Redshanks had the highest mortality of the shore birds, the British breeding population being reduced by up to 95% (Dobinson and Richards 1964).

Some Redshanks on the Ribble appear to feed exclusively on Hydrobia, especially on Horse Bank. In the period July-October the mean peck rate was 64.7 ± 6.15 per minute and success estimated at 88% whilst in the period November - February mean peck rate was 67.1 ± 7.2 per minute and success 89%. Over an hours continuous feeding such a Redshank would ingest about 1.1 g dry weight equivalent to only 2.5 KCal (8.6 KJ) or about half the ingestion rate when feeding on Corophium.

Hydrobia is an easily obtainable prey, lying exposed at certain states of the tide or just below the mud surface in vast numbers (chapter VII). However, it would be hardly possible in the available time for Redshanks to feed exclusively on this species and obtain sufficient energy-value. Those Redshanks which do take Hydrobia to any extent probably do so for only short periods. However, Hydrobia provides a useful food at night (chapter III) in that the birds have simply to collect the prey from the mud surface and in so doing often employ more of a sweeping, random seiving movement rather than the discrete selective peck.

The two other prey are taken by only a minor fraction of the winter Redshank population. Those feeding on Nereis have a feeding rate higher than that of Black-tailed Godwit in the same area whilst the biomass ingested by such Redshank amounts to double that of those feeding on Corophium. Redshanks feeding on Nereis at Conder Green (S. Morecambe Bay) in December 1973 had lower ingestion rates, equivalent to 7.8 KCal (32.9 KJ) whilst in September 1973 rate was 6.6 KCal (27.9 KJ). Both rates are still higher than those of the majority of Redshanks which feed on Corophium. It must be pointed out that the Morecambe Bay and both Ribble sites where Redshanks regularly feed on Nereis are small, and of a very small substrate

Table 63. Peck rate per minute (P.R.) and percentage of successful pecks (P.S.) of Redshanks feeding on Corophium volutator on Horse Bank study area

				Intake per hour expressed as			
	No. observations	P.R.	P.S.	No.	g dry weight	KCal	KJ
August	186	64.7±7.6	87.5	3400	1.20	5.1	21.4
September	114	66.3±90.6	90.6	3620	1.27	5.4	22.7
October	68	59.8±84.2	84.2	3030	1.24	5.3	22.3
November	49	61.3±9.8	81.3	3000	1.23	5.3	22.3
December	135	62.1±9.0	79.2	2920	1.19	5.1	21.4
January	102	62.3±11.1	65.7	2420	0.92	3.9	16.4
February	50	65.5±10.5	69.3	2730	1.04	4.4	18.5
March	91	71.5±8.3	74.0	3180	1.21	5.2	21.8

Note: calorific value of Corophium measured in this study 4.26 KCal per g dry weight ash-included (17.9 KJ)

Table 64. Estimates of ingestion rate and proportion of Hydrobia in the diet in relation to Corophium and Hydrobia density on Horse Bank (winter 1970-1).

Site ref.	Ingestion rate	Densities of Corophium	 Hydrobia	% of Hydrobia in the diet
A	58.7	7800	16500	24.0±16.8
B	61.3	8450	11400	6.5±7.1
C	55.4	8100	6000	7.4±5.7
D	67.6	12200	7150	0.5±0.8
E	62.8	15700	8000	3.7±2.1
F	59.3	13000	9500	5.0±3.6
G	61.7	10800	8600	0.9±1.1

The sites are seven where details of food intake as well as prey density were known.

particle size. Only Dunlin and, on the Ribble, Black-tailed Godwit occupy the same niche regularly. No Redshank feed on Nereis on areas of sandy mud or sand (areas used by Bar-tailed Godwits).

Macoma is an important food of the autumn passage flocks of Redshank, being taken by probably 20% of the July-September population. Later, when the Redshank population is smaller very few feed to a large extent on Macoma . As can be seen from Table 66 ingestion rate tends to decrease through the year being highest in August-September (the time when most Redshank are feeding on Macoma) and is lowest in spring. These data are, however, combined from many sites and the significance of such trends is questionable. It is of note, however, that the intake in terms of calorific value is fairly similar to those from birds feeding on Corophium , though possibly the August-September intake of Macoma is higher than the Corophium intake in this period.

General observations would suggest that no Redshanks feed through the tide cycle exclusively on either of these last two prey. They all probably take Corophium around high water when the Nereis and Macoma beds are covered by the tide. Some certainly move inland at high water and roost and possibly feed on fields. Also, at night they probably turn to Hydrobia to some extent as do the Corophium-feeders.

No data are available on the amounts of food consumed on inland habitats by Redshank. This may be a considerable amount, especially in terms of total biomass taken by all the Redshanks feeding inland. Such observations that have been made suggest that a cross-section of the available soil or grassland invertebrates are taken (Goss-Custard 1969, chapter V). It is from these sources that the deficit between requirement and intake incurred on the shore, must be taken.

KNOT

From observations on the roosts and feeding areas it is clear that the Ribble Knot population comprise one homogenous population feeding for the most part on a fairly constant diet consisting of Hydrobia on the upper shore

Table 65. Peck rate per minute (P.R.) and percentage of successful pecks (P.S.) of Redshanks feeding on <u>Nereis diversicolor</u> at Lytham and Fairhaven.

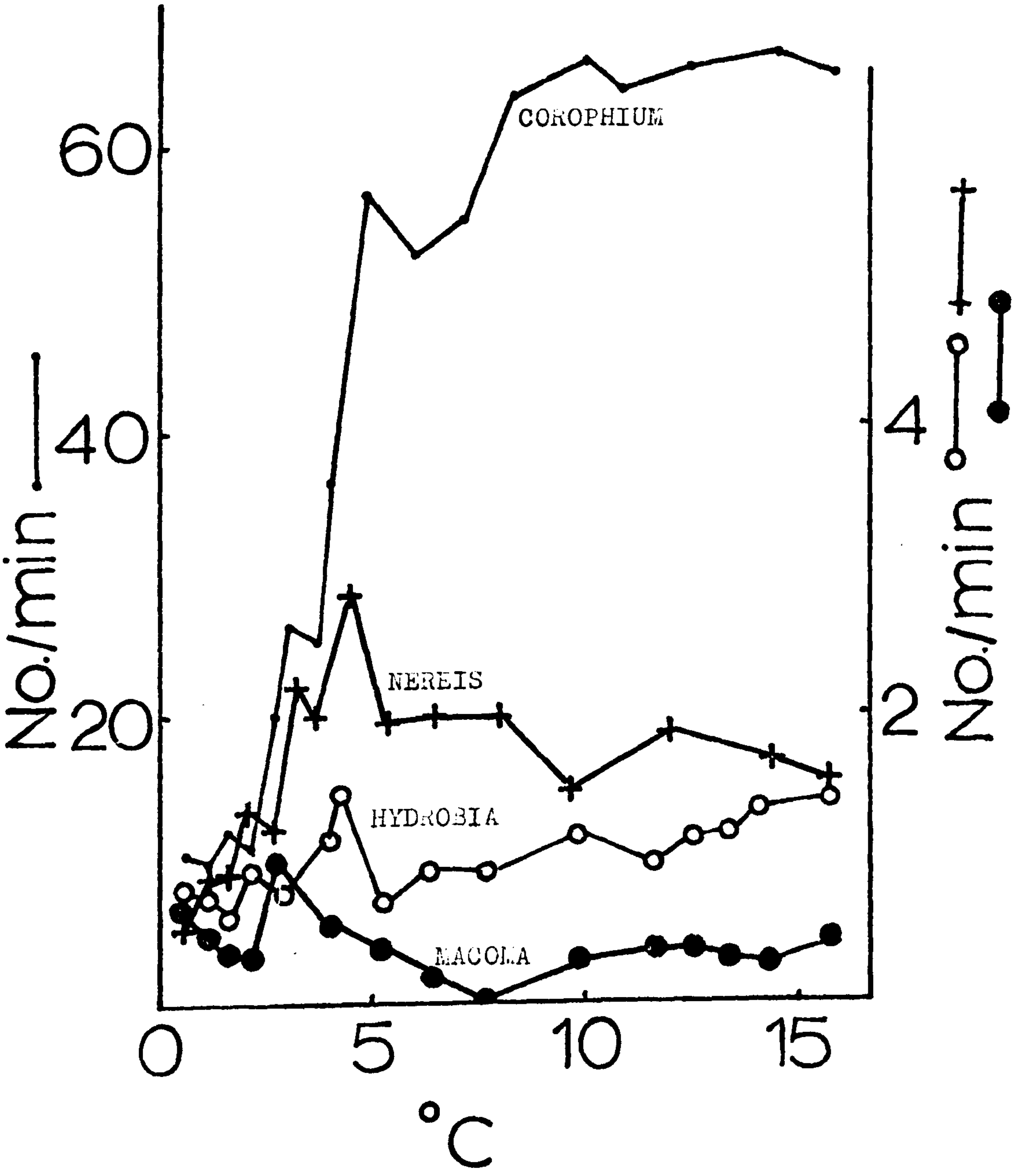
				Intake per hour expressed as			
	No. observations	P.R.	P.S.	No.	g dry wt	KCal	KJ
Aug-Sep	21	32.8±5.8	19.0	376	2.78	10.2	42.6
Oct-Nov	22	35.9±4.8	14.2	306	2.34	9.9	41.6
Dec-Jan	20	37.6±4.1	11.6	262	1.93	8.3	34.8
Feb-Mar	20	36.9±4.0	9.5	350	2.59	10.9	46.0

Table 66. Peck rate per minute (P.R.) and percentage of successful pecks (P.S.) of Redshanks feeding on *Macoma balthica* on Horse Bank.

				Intake per hour expressed as			
	No. observations	P.R.	P.S.	No.	g dry wt	KCal	KJ
Aug-Sep	27	23.4±6.2	11.9	168	1.52	6.1	25.6
Oct-Nov	41	22.1±3.9	9.7	129	1.16	4.7	19.8
Dec-Jan	34	27.6±4.1	10.2	163	1.47	5.9	24.8
Feb-Mar	19	25.7±4.7	7.1	109	0.99	4.0	16.8

Figure 43.

Ingestion rates of Redshank feeding on *Nereis diversicolor*, *Corophium volutator*, *Hydrobia ulvae* and *Macoma balthica* on the Ribble Estuary (mostly Horse Bank and Banks Sands) at different mud temperatures.


COROPHIUM
NEREIS
HYDROBIA
MACOMA
No./min
60
40
20
No./min
4
2
0
5
10
15
°C

around high water and Macoma on the middle and lower shores. Some Knot do not feed on the upper Hydrobia zone and this is especially the case during movements into the roosts (chapter V). Investigations of food intake was therefore centred on these two prey species.

Basic data on feeding on Hydrobia on Horse Bank are given in Table 67. Whilst estimates of feeding rate wére easily ascertainable, calculations of feeding success on Hydrobia were difficult to obtain. However, as the prey was readily available to the birds there seems no reason why feeding success should not be high. Attempts at very close range from a hide gave readings of 85%, 91% and 94% success, estimates fairly close to the success of Redshanks feeding on Hydrobia (see earlier). Experiments on captive birds, however, seem necessary before firm conclusions are drawn and thus the statistics calculated in this section should be treated with some caution.

Peck rate on Hydrobia does not vary to any great extent until February-March when it is significantly lower ($p < 0.001$) possibly due to the lower Hydrobia population at this time. Peck rate on the Ribble is higher than that of Knot feeding on the upper shore, presumed to be on Hydrobia, in Morecambe Bay: 71.6 ± 5.8 per minute (Prater 1972). This may be related to the much greater Hydrobia density on the Ribble (chapter VII).

Prater (1972) did not estimate the intake of Hydrobia. However, for the purposes of this study a success rate of 80% has been used to calculate the biomass of Hydrobia taken per day by Knot (Table 67), allowing for the fact that Knot feed on Hydrobia for only part of the tide cycle.

Basic data on feeding on Macoma are given in Table 68. Though peck rate does not vary very much through the autumn and winter (with the exception of the December figure) to February, there is a suggestion of a consistently slightly lower rate late in the spring. This, together with the fact that feeding success is certainly lower from February onwards than in autumn and winter ($p < 0.05$) results in a significantly lower overall ingestion rate in spring ($p < 0.001$ for August-January and February-May data pooled). This may be a consequence of the lower population of the size of Macoma taken by Knot in spring.

It is interesting that Prater (1972) found a lower peck rate of Knot in Morecambe Bay when feeding on Macoma (23.9 per minute). Further his estimates of feeding success were lower than those from the Ribble ("it was observed that on average, Knot take 1.78 bivalves ..... of 6+ mm in length per minute during the low water period"). The density and size of Macoma in the substrate and the size of Macoma selected by Knot were greater in Morecambe Bay than on the Ribble (chapters V and VII). From his data (Prater 1972, Table 7) the average of 751 bivalves (mostly Macoma) taken by Knot in one tide cycle would have a dry weight of about 11.64 g. In comparison the 775-800 Macoma taken in autumn and early winter on the Ribble have a dry weight of between 9 - 11 g (Table 68).

Feeding rate on Macoma varies with both wetness of habitat and whether the birds are feeding in a flock and probably also the size of that flock.

Both peck rate and ingestion rate are significantly lower on areas of substrate which are not covered in a film of water compared with areas which are, even when the two occur together in a mosaic over the sandflat. On Salter's Bank in January 1974 peck rate was 11.2 ± 4.9 per minute on dry areas and 30.1 ± 5.6 on wet areas ($p < 0.001$) whilst the birds on dry areas took a mean of 0.31 Macoma per minute and on wet areas 3.04 per minute ($p < 0.001$). However, generally only very small proportions of Knot feed on dry areas and then only as they move across from one patch of wet mud to the next. In this context it is of interest to compare pacing-rates of Knot on the two types of substrate. On wet substrate when actively feeding on Macoma pacing-rate was 44.9 ± 38.6 per minute whilst on dry mud the pacing-rate was much higher at 79.1 ± 42.0 per minute. These data again suggested that the Knot were moving across the dry areas quickly but continuing to feed and, upon reaching a suitable area (wet) they reduced pacing-rate (i.e. speed) and peck and ingestion rates increased.

As explained earlier (chapter IV) most Knot feed in fairly large flocks of up to 8,000 few feeding in parties of less than 100. Feeding rates were examined on Salter's Bank in December 1973 and February 1974 in flocks of various sizes. Peck rates in very small flocks (less than 100) averaged

26.8 ± 8.9 and in flocks over this size 28.1 ± 9.3 . These were not significantly different. Success did vary significantly however being 6.5% ± 2.1 in flocks of less than 100 and 9.3% ± 3.0 in larger flocks ($p < 0.001$). In the same period birds feeding in very large flocks of between 7900 and 11600 had success rates of 8.4 ± 1.9% which though not significantly differing from other flocks ($p > 0.2$) is suggestive of a lower rate amongst these very large flocks.

This aspect requires further investigation. It is likely that small parties are not feeding in as profitable areas as larger ones, though sampling over such areas did not reveal such contrasting differences. Smaller flocks possibly do not provide the security of larger ones and hence the birds comprising them cannot concentrate fully on the acquisition of food. Possibly the birds in the larger flocks feed in areas which, either for distributional or behavioural activities of the prey, make the prey more easily available. Had the smaller flocks discovered such a site, and thus increased their feeding success, it can only be conjectured whether birds would join them from other flocks.

One point of note is that after late January the numbers of Knot on the Ribble decrease rapidly (chapter II). This is also manifested in smaller feeding flocks. Feeding success on Macoma decreases markedly from February (Table 68) and it seems possible that the lower spring success is related in some way to these smaller flocks. It may be, of course, that Knot numbers decrease because the food is less available.

No significant differences were found between feeding rates when substrate temperature was above 5°C and than when the temperature was below 5°C. Mean peck rates on Horse Bank were 28.6 ± 6.9 at temperatures above 5°C and 27.1 ± 7.1 below 5°C and ingestion rates 2.93 ± 0.32 at above 5°C and 2.86 ± 0.40 at below 5°C. Low temperatures of substrate did not appear to have an effect on the intake of Macoma by Redshanks, (see earlier).

The mean weight of Knot in winter is 162 g n = 683 (pers. obs.) and from Lasiewski and Dawson (1967) such a bird would have a standard metabolic rate of 21.0 KCal (88.0 KJ). The factor of three would yield a metabolic rate for wild Knot in winter of 63 KCal (264 KJ) per day.

Knot spend about 475 minutes per tide cycle on the feeding area and about 84% of this time in actually obtaining food (chapter III). Estimates of total intake can be made from these data and the above presented in this chapter. In August, with up to 15 light hours a bird taking Hydrobia on the upper shore around high water and Macoma for the remainder of the low water period will take about 67 KCal (282 KJ) of Macoma and 7 KCal (29 KJ) of Hydrobia. The total of 74 KCal (311 KJ) is in excess of the requirements. However, at this time of the year Knot will probably need extra to the basic requirements for moult and for replacing fat lost in the migration from the breeding grounds.

Later, however, in mid-winter, the total intake will be less. This is partly the result of the slightly smaller size of Macoma taken at this time (chapter V), but mainly to the reduction of light hours available for feeding: only eight hours in mid-winter and a high proportion of this may be lost due to the tide. In December-January the intake could be as low as 37 KCal (152 KJ).

It is of interest that coincidental with the reduction in light hours and size of Macoma in late October - early November the population of Knot on the Ribble rapidly decreases. It may well be that these move to areas where Macoma size is generally larger (e.g. Morecambe Bay) or emigrate to regions where day length is longer (e.g. W. Africa).

It is also of interest to note that no strong return migration of Knot occurs on the Ribble in spring. Possibly the resources available at this time are not sufficient to maintain a large transit flock and provide the fat reserves necessary for the return movement to the breeding grounds.

SANDERLING

As explained earlier, Sanderlings are chiefly birds of the outer estuary sandy shores where they feed on Bathyporeia pelagica and associated crustacea, and polychaetes. The data presented here are from the main

Table 67. Peck rate per minute (P.R.) and intake over the tide cycle of Knot feeding on *Hydrobia ulvae* on Horse Bank.

			Intake per tide cycle expressed as		
	No. observations	P.R.	g dry weight	KCal	KJ
Aug-Sep	91	76.3 ± 4.6	2.29	4.12	17.3
Oct-Nov	37	78.7 ± 5.7	2.36	4.38	18.4
Dec-Jan	55	78.8 ± 5.2	2.41	4.48	18.8
Feb-Mar	33	73.5 ± 4.1	2.21	4.11	17.3

Note: see text for data on success rate

Table 68. Peck rate per minute (P.R.) and percentage of successful pecks (P.S.) of Knot feeding on *Macoma balthica*

	No. observations	P.R.	P.S.	Intake per tide cycle expressed as			
				No.	g dry weight	KCal	KJ
August	35	28.1±4.9	11.0	775	9.99	41.4	174
September	71	28.5±7.7	11.1	800	10.30	42.6	179
October	53	29.4±9.6	10.6	775	9.92	27.9	113
November	32	31.2±8.7	9.9	775	9.92	27.9	113
December	34	27.6±7.2	11.6	800	8.91	23.8	100
January	47	29.1±7.8	10.0	725	8.38	21.6	91
February	28	28.9±9.2	6.2	450	7.13	12.6	53
March	42	27.0±6.1	5.9	400	6.78	11.2	47
April	29	27.2±7.3	6.2	425	6.94	11.8	50
May	16	27.0±5.4	5.2	350	6.41	9.7	41

feeding areas on the north side of the estuary where, through most of the year, most Sanderlings occur.

Table 69 presents data on peck rate on three different feeding areas. Birds feeding on crustaceans (judging from gut contents and examination of feeding area) around high water at the tide edge feed at a much higher rate than those feeding on similar prey at low water (p 0.001). In both cases peck rate differs through the year, being slightly higher in spring than autumn.

Unfortunately, feeding success on such small prey is almost impossible to ascertain in the field and as yet it has not been possible to make such calculations on captive birds. Such measurements will have to be made before the real intake of Sanderlings can be calculated.

Feeding success has been calculated however for the birds feeding on areas of mid-shore in the St. Annes - Fairhaven area of western Salter's Bank where prey are mostly the polychaetes Nephthys caeca and Pygospio elegans. In these cases peck rate is lower than when feeding primarily on crustaceans (Table 69).

Success when feeding on these polychaetes does not significantly differ through the year, overall there being a mean success of 14.3 ± 4.8%. Thus, the mean intake is 8.2 per minute in autumn and 7.8 per minute in the remainder of the year. Relatively few Sanderling, however, feed on these prey.

Although it is not possible to present details of total intake from data on feeding success, some indications of the numbers of Bathyporeia and other crustaceans taken by Sanderlings can be obtained by a rather indirect method. From Lasiewski and Dawson (1967) a Sanderling of weight 80 g would have a standard metabolic rate of 12.6 KCal per day (52.9 KJ) and for a wild Sanderling the daily energy requirements would be 37.8 KCal (158.0 KJ). In the period July-August Sanderlings take Bathyporeia of mean length 3.36 mm (equivalent to 0.13 mg dry weight), in December-January 4.58 mm (0.22 mg) and May 4.11 mm (0.20 mg) (Chapter V). The calorific value of Bathyporeia is 4.41 ± 0.71 KCal per g dry weight ash included

Table 69. Peck rate of Sanderlings at three feeding situations on the north side of the Ribble Estuary.

a) At the tide edge within two hours of high water.

	N	Peck rate
July-August	204	71.2 ± 6.7
September-October	76	72.8 ± 8.2
November-March	42	74.7 ± 9.1
April-May	93	73.6 ± 7.3

b) At the tide edge within three hours of low water.

	N	Peck rate
July-August	51	61.8 ± 4.9
September-October	47	62.7 ± 6.3
November-March	32	59.9 ± 7.1
April-May	40	64.8 ± 6.8

c) On silty-sand where prey mostly polychaetes.

	N	Peck rate
July-August	48	57.9 ± 6.2
September-October	34	54.7 ± 7.0
November-March	37	53.9 ± 6.8
April-May	51	54.2 ± 7.3

Table 70. Peck rate and ingestion rate of Dunlins feeding on _Nereis_ at Lytham.

	n	Peck rate	Ingestion rate
July-September	109	59.1 ± 4.8	4.2 ± 0.47
October-December	81	61.7 ± 7.2	4.6 ± 0.39
January-March	46	62.0 ± 5.5	4.8 ± 0.50

Table 71. Peck rate of Dunlins feeding mainly on _Corophium_ and _Hydrobia_ on Horse Bank and Banks Sands, in the period two hours either side of low water.

	n	Peck rate
July	46	72.3 ± 6.9
August	82	74.7 ± 4.2
September	104	73.7 ± 3.8
October	65	76.5 ± 4.1
November	116	74.1 ± 2.8
December	56	74.2 ± 4.0
January	40	75.8 ± 4.8
February	61	76.4 ± 5.6
March	39	75.9 ± 7.9
April	47	78.3 ± 6.9
May	76	79.4 ± 5.0

(18.6 KJ).

Thus, to obtain 37.8 KCal of food per day a Sanderling would have to ingest about 8.5 g dry weight of Bathyporeia, equivalent to approximately 65,000 in July-August, 38,000 in December-January and 42,000 in May.

Sanderlings feed for 578 minutes per tide cycle and, if the daylight period includes approximately $1\frac{1}{2}$ low tide periods in autumn and spring and one low tide period in mid-winter, the birds would have to average an intake of 75 per minute in July-August, 65 per minute in December-January and 48 per minute in May. There is very probably a certain amount of feeding during dark hours, so these estimated rates of ingestion could be reduced accordingly.

Except for the May estimate, the figures arrived at for ingestion rate are higher than the observed measures of peck rate. It is possible, however, that the factor of three by which standard metabolic rate has been multiplied to give daily requirement is too high (possibly it should be nearer two). It is also likely that some of the excess is accounted for by ingestion of larger prey such as Haustorius or polychaetes. Nevertheless, it remains clear that success rate must be fairly high in order for ingestion rate to meet metabolic requirements.

DUNLIN

As described earlier, Dunlins generally feed on the inner-mid estuary zones, mainly on Nereis, Corophium and Hydrobia with some Macoma and feeding rates have been calculated for these. On most main foods, however, it has been impossible to obtain satisfactory data in the field on ingestion rates as it is difficult in most cases to see whether a peck has resulted in the swallowing of a food item. It is hoped to carry out the necessary experiments to provide these data once adequate facilities have been constructed at the Martin Mere reserve.

Table 70 presents basic data of Dunlins feeding in flocks on Nereis in the Lytham area. Both peck rate and ingestion rate tend to increase through the year, though this is significant only in the case of peck rate ($p < 0.001$), not in the case of ingestion rate ($p > 0.1$).

Birds feeding isolated from flocks have the significantly lower peck rate in July-September of 51.1 ± 7.0 pecks per minute (n = 40) and ingestion rate of 2.2 ± 0.34 per minute ($p < 0.001$). Solitary feeding is the exception in this species, as in most other shore waders and it is likely that the low feeding rate of solitary feeders is due to them feeding in poorer (in terms of availability of prey) feeding areas than the flocks, or to them having to spend far more time on the alert for potential predators than flock feeders (see earlier). It is also likely that a high proportion of solitary waders of species which normally feed in tight packs are, in fact, sick.

No relationship was found between substrate temperature and ingestion rate, though data were collected on only four days with the substrate temperature below 4°C. There was also no relationship observed between peck or ingestion rates and tide cycle, though this may have been a result of inadequate data.

Table 71 presents data on peck rate of Dunlin on the two main intertidal prey Corophium and Hydrobia over the low water period on Horse Bank and Banks Sands. In terms of biomass taken, these are the main prey for the whole Dunlin population on the Ribble.

Peck rate at low water varies little through the year except that in April-May it is significantly higher than in the remainder of the year ($p < 0.001$). This may be in response to the need to lay down fat for the return to the breeding grounds and also the extra requirements of breeding (C.F. for example, Redshank).

Peck rate does however vary considerably through the tide cycle being highest in the period immediately after high water (November-January mean peck rate 94.3 ± 11.7, n = 49) and lowest just before and on high water (mean peck rate 47.9 ± 8.6, n = 33). There is, therefore, a rapid switch to high feeding rate as the tide begins to ebb. This may be a response to prey behaviour in that on the ebb prey are at or close to the substrate surface and thus readily available to the Dunlins as they feed down the shore with the ebb. The prey then burrow deeper into the substrate after exposure

Table 72. Estimates of peck rate and proportion of Hydrobia in the diet of Dunlin in relation to Corophium and Hydrobia density on Horse Bank (winters 1970-1 and 1971-2).

Site Ref.	Peck Rate	Density of Corophium	Density of Hydrobia	% Hydrobia in diet	
A	87.4	7800	16500	100	(2)
B	74.6	8450	11400	92	(1)
G	61.3	10800	8600	76	(3)
H	81.0	2900	12000	80	(1)
I	76.3	5600	6400	85	(4)
J	72.1	3000	8000	43	(2)

Notes: The figures in parentheses are the numbers of guts examined from each site.

The sites are those where details of food intake from gut analyses as well as prey density were known.

Sites A, B and G were also investigated for Redshank food intake (Table 64).

and peck rate decreases to 77.8 ± 3.8 (n = 147) in the period between one and four hours after high water and is slightly lower still over the low water period (table 71).

Estimates of peck rate were made at six sites on Horse Bank where density of both Corophium and Hydrobia and the diet from gut analyses were known. This zone on the middle and upper zone of eastern Horse Bank is that from which similar data for Redshanks were collected (see earlier) and in which these two waders are the main predators. The data are presented in Table 72.

It is clear that Dunlin were selecting Hydrobia, as distinct from the Redshanks which selected Corophium. Also, although the data are small, peck rate was higher at higher Hydrobia densities whilst it was independent of Corophium densities. The Dunlins were thus apparently reacting to the Hydrobia density rather than Corophium.

There is no reason to doubt that birds feeding on Hydrobia have a high success rate in that their food is lying almost motionless on or close to the substrate surface. In the Knot a suggested rate of 80% was used in calculating total intake and this will be used here though it may err on the low side. It is hoped, however, to have more accurate estimates available in the future.

The sites recorded above were typical wet habitat and Dunlin feeding on such wet habitat had significantly higher peck rates than those feeding in dry substrate areas ($p < 0.001$) where peck rate was 41.7 ± 8.6 . Few Dunlins feed on dry areas, and then only for short periods. The effects of temperature of the substrate on peck rate was not investigated.

On the south Ribble sites where Corophium and Hydrobia were the main prey Nereis and Macoma were taken but in very small proportions, judging from observation. Overall, means of 2.1% of the pecks resulted in Nereis and 0.6% in Macoma being ingested. Some of the latter may have been overlooked however due to their small size. Lower down the shore on Horse Bank where Macoma comprises more of the diet (Chapter V) a mean ingestion rate of 2.7 ± 0.42 Macoma per minute (n = 57) was observed in the November-February period.

For the purposes of calculating food intake over a whole tide cycle it must be stressed that probably all of the Ribble Dunlin feed at and after high water on Hydrobia and Corophium, the majority continuing to do so through the whole tide cycle except that a small proportion of Nereis and Macoma may be included (see above). At only Lytham and an area of mud-flat at Fairhaven do large numbers of Dunlin (up to about 3000 in mid-winter) feed over the low tide period to an almost exclusive degree on Nereis whilst an almost insignificant proportion do likewise on Macoma on Horse Bank. Estimates of intake take these points into account.

From Lasiewski and Dawson (1967) the standard metabolic rate of a Dunlin weighing 60 g is 10.2 KCal (42.8 KJ) and thus on the basis of earlier points the daily energy intake would have to be about 30 KCal per day (126 KJ) for a wild bird.

Dunlins spend a mean of 541 minutes per tide cycle in feeding (Chapter III). If 80% of pecks are successful (see earlier) then a bird feeding for this time on Hydrobia and Corophium, taking an average of 70% of the diet as Hydrobia, will ingest 19.3 KCal (81.2 KJ) in the tide cycle. As the proportion of Corophium was increased then intake would be greater as a consequence of the higher biomass of Corophium, though success may be lower in the mobile Corophium compared with the relatively stationary Hydrobia. The intake would probably be higher than this however, due to the Nereis and Macoma fraction.

Birds feeding for about 300 minutes at low water on Nereis or Macoma would have a much higher intake. They would obtain about 8.5 KCal (35.7 KJ) from Corophium and Hydrobia on the upper shore either side of high water and about 30 KCal (126 KJ) from Nereis lower on the shore or about 21 KCal (88 KJ) from Macoma. These birds would easily obtain their daily energy requirements in the one tide cycle.

In autumn and spring when the daylight period may include 1½ low tide periods the birds will have little difficulty in obtaining food requirements whilst even in mid-winter the intake at night (chapter III) would probably make up any deficit.

The Dunlin is one of the few wader species on the Ribble which occurs in maximum numbers through the mid-winter and it is also one of the few which would appear to have little difficulty in obtaining maximum food requirements in mid-winter. Some Oystercatchers would seem to have great difficulty in scraping together the daily requirement as would Curlews if they had to survive soley on shore foods. Both of these have lower winter populations than autumn ones (chapter II). Black-tailed Godwits certainly would be hard pressed in obtaining their daily requirements in mid-winter on the Ribble, assuming that their feeding rate was similar to the autumn mean rate. They do not winter on the Ribble (chapter II0, but do so on the Dee: it would be interesting to calculate their energy intake there in mid-winter. Similarly, the Redshank population in winter is very low on the Ribble whilst the Knot population declines rapidly in early winter and in both cases daily food intake would seem to be lower than the expected requirement.

These conclusions are heavily dependant upon Lasiewski and Dawson (1967) and the factors by which the standard metabolic rate has to be multiplied to obtain requirements in the wild. Nevertheless, the overall pattern appears to hold, that the Dunlin with its largest numbers in mid-winter has a relatively higher (based on standard metabolic rate) food intake than those species which have a low winter population. Thus, although there may be abundant food in the substrate, the waders might not be able to get enough of it in the short winter days and thus be forced to move on either to areas where their intake (ingestion rate) is higher (some go to the Dee and Morecambe Bay) or where they can feed for much longer in daylight (e.g. West Africa and Southern Europe). This is one important factor to take into account when predicting the wader populations an area might be able to support.

CHAPTER IX

IMPACT OF WADERS ON THE FOOD RESOURCES OF THE RIBBLE ESTUARY

The amount of food available for waders and the proportion of this actually consumed are difficult parameters to assess over a large estuary such as the Ribble. Inevitably, some variables will not adequately be appreciated until late in the study whilst the size of the area over which data have to be acquired is huge. Therefore, main lines are concentrated on : for examples Knot feeding on Macoma, Redshank feeding on Corophium and Oystercatchers feeding on Mytilus. Less important waders and prey are excluded. However, even at this relatively early stage, it is of value to make an initial estimate of the overall picture and this is done in two ways: firstly, in a preliminary way, manually, and secondly by computer analysis.

Preliminary estimate

1. Food availability.

In order to make an estimate of the total amounts of food available to waders a minimum number of parameters have to be considered. In this preliminary estimate monthly mean densities of the main mudflat invertebrates Nereis diversicolor, Corophium volutator, Hydrobia ulvae and Macoma balthica and the mussel Mytilus edulis were taken and, from estimates made from these monthly samples, the mean monthly biomass, in terms of grammes dry weight and kilo-calories per m^2, was calculated.

Such figures of monthly standing crop fail to account for the quantities of foods taken by the waders in each month. Thus, to each month's standing crop measurement an estimate of the amount taken in that month was added. This monthly intake was estimated by combining the following : daily food intake, biomass of that intake (involving size of prey and energy content) and monthly wader populations. The intake for the whole estuary was then converted into the intake per m^2 of substrate and added onto the monthly standing crop.

Table 73. Monthly mean biomass per m^2 and productivity of prey species (1971-74 data pooled by month) over the whole feeding area of waders (6800 hectares)

	Nereis		Corophium		Hydrobia		Macoma		Mytilus	
	g	KCal	g	KCal	g	KCal	g	KCal	g	KCal
Jan	5.7	20.7	5.8	24.7	7.2	13.4	10.9	54.0	94.0	466
Feb	4.5	16.2	4.8	20.4	6.4	11.9	8.3	41.2	95.6	474
Mar	2.9	10.5	5.1	21.7	5.1	9.5	6.4	31.7	86.4	429
Apr	2.5	9.1	5.9	25.2	4.6	8.6	7.3	36.1	98.1	496
May	3.0	10.9	5.3	22.6	4.3	8.0	7.8	38.4	146.3	726
Jun	3.4	12.6	5.9	25.2	3.5	6.5	9.3	46.3	159.9	791
Jul	4.9	17.6	6.7	28.5	5.1	9.5	12.1	59.8	170.6	847
Aug	5.7	20.7	9.4	40.1	8.6	16.0	15.6	78.0	194.4	963
Sep	8.0	29.0	8.3	35.4	12.9	24.1	14.4	71.4	208.1	1030
Oct	7.7	28.1	8.4	35.8	12.0	22.4	15.6	77.4	213.1	1060
Nov	8.1	29.4	7.2	30.7	12.4	23.1	14.1	70.0	169.1	839
Dec	7.1	25.6	8.2	35.0	13.4	24.9	11.9	59.0	102.3	501
Positive biomass increase (P)	5.9	21.2	6.3	27.0	10.8	20.1	10.4	52.3	131.3	641
Mean standing crop (B)	5.2	18.6	6.5	27.8	7.9	14.7	11.1	55.0	142.3	702
P/B	1.14		0.97		1.37		0.94		0.91	

Table 73 gives the results of this analysis together with positive biomass increase (P), mean standing crop (B) and the ratio between positive biomass increase and mean standing crop (P/B). In this case positive biomass increase is taken as a measure of the minimum production of the invertebrate prey populations. However, although it takes into account the amount of food taken by waders, it excludes the amounts taken by other predators. Fish (especially the flounder Pleuronectes flesus and goby Gobius minutus), birds of the duck family(especially Shelduck Tadorna tadorna, Wigeon Anas penelope and Pintail Anas acuta) and gull family (especially Black-headed Gull Larus ridibundus, Herring Gull L. argentatus and Lesser Black-backed Gull L. fuscus) and other shore invertebrates such as the crab Carcinus maenas take vast quantites of which no measurements are yet available. These will cream off some of the production during the months when biomass is being produced which will not be registered during sampling at the month-end. Thus, positive biomass increase gives but a minimum value (and certainly an underestimate) of production.

Other authors working solely with intertidal invertebrates under both field and laboratory conditions have found higher measurements of P/B, due to their value of productivity (P) being closer to the real value and not simply an estimate of minimum biomass increase. For example, Kay and Brafield (1973) gave a value of P as 45.2, B was 27.68 (from their figures) and hence P/B was 1.63 for a population of Neanthes virens. The P/B ratio, using minimum positive biomass increase (calculated by W.G.Hale from their data), was much lower at 1.34. Similarly, Hughes (1970) gave values of "net increase in energy content on standing crop" as 23.4 KCal/m^2 per year, a figure similar to the positive biomass increase used in the present study, whilst from all sources he calculated productivity as 70.8 KCal/m^2 per year for a mudflat Scrobicularia plana population. Though he gave no estimate of mean standing crop, it is clear that a P/B ratio using the former figure would be much lower than if the latter estimate of P was used.

Other estimates of production (P) have been generally higher than the minimum positive biomass increase used in the present study. Odum and Smalley (1959) gave a value of 40.6 KCal/m^2 /year for a Littorina irrorata population, and Milne and Dunnett (1972) 1300 KCal/m^2/year for a *Mytilus edulis* population. This latter species varies enormously in its productivity however, due to a variety of environmental and management reasons (see Dare 1973).

The P/B ratios in this study are especially low for *Corophium*, *Macoma* and *Mytilus*. In the latter two this is probably due not only to the monthly mortalities due to other organisms (see above) but also to the high mortality of spat which is washed-out from more exposed banks by spring tides and gales. In *Corophium* deaths during the growth and reproductive months due to desiccation of the exposed mudflats reduces the value of P. Such a reduction does not occur in *Hydrobia* probably because it moves down the shore with the falling tides (see chapter VII).

From the P/B figures have been obtained the following estimates of overall production in the five prey species:

Nereis	7.8 g/m^2/year	27.9 KCal/m^2/year
Corophium	9.8	41.7
Hydrobia	11.9	22.1
Macoma	16.7	82.5
Mytilus	213.5	1053.0

2. Food taken.

The total amounts of foods taken by each species of wader in each year were calculated by taking the mean tidal cycle or day intake per bird (chapter VII) and mutiplying this by the monthly population of that species on the Ribble. In this consideration had to be made for the cases (most) when two or more prey were taken by different birds, for instance Dunlins feeding on *Corophium* and *Hydrobia* or *Macoma* or *Nereis*, or where the diet of individual birds changed through the tide cycle (for example Knot taking *Hydrobia* and *Macoma*) or through the diurnal cycle (for example Redshank taking *Corophium* and *Hydrobia*). All the data and factors involved are summarised in Chapters II, III, IV, V and VIII.

Table 74 presents the analysis of the total intake of the four main prey

Table 74. Total intake (expressed in g. dry weight and KCals) of the four major prey of the intertidal mudflats by the main waders on the whole of the feeding area of the Ribble Estuary (taken as 6800 h) in the years 1971-2 and 1972-3.

A. Nereis	1971-2		1972-3	
	g	KCal	g	KCal
Curlew	540,000	1,932,000	762,000	2,772,000
Black-tailed Godwit	-	-	1,495,000	4,988,000
Bar-tailed Godwit	23,400,000	83,972,000	31,800,000	115,042,000
Redshank	553,000	1,940,000	869,000	3,140,000
TOTAL	24,493,000	87,844,000	34,946,000	125,942,000

B. Corophium	1971-2		1972-3	
	g	KCal	g	KCal
Redshank	4,560,000	19,400,000	6,110,000	26,155,000
Dunlin	7,380,000	31,400,000	11,100,000	47,145,000
TOTAL	11,948,000	50,800,000	17,210,000	73,300,000

C. Hydrobia	1971-2		1972-3	
	g	KCal	g	KCal
Redshank	651,000	1,213,000	1,050,000	1,963,000
Knot	36,700,000	68,131,000	37,300,000	69,195,000
Dunlin	70,000,000	130,700,000	126,000,000	235,700,000
TOTAL	107,351,000	200,044,000	164,350,000	306,858,000

D. Macoma	1971-2		1972-3	
	g	KCal	g	KCal
Oystercatcher	17,400,000	86,100,000	19,300,000	95,550,000
Curlew	818,000	4,048,000	1,180,000	5,808,000
Bar-tailed Godwit	26,200,000	129,648,000	35,500,000	175,528,000
Knot	132,000,000	652,110,000	134,000,000	663,345,000
Dunlin	8,980,000	44,464,000	16,300,000	80,097,000
TOTAL	185,398,000	916,371,000	206,280,000	1,020,328,000
GRAND TOTALS	329,190,000	1,299,523,000	422,786,000	1,606,957,000

of the mudflats by the main waders in terms of g. dry weight and KCalories. From this table the mean annual intake of each prey by waders per m^2, for comparison with the data summarised in Table 73, are as follows:

Nereis	0.44 g. per m^2	1.57 KCals per m^2
Corophium	0.21	0.91
Hydrobia	2.00	3.74
Macoma	2.88	14.26

A similar estimate of *Mytilus* intake by Oystercatchers on the Church Scar area gave a mean intake per m^2 of 5.31 KCals in 1966-7, 4.93 KCals in 1967-8 and 4.42 KCals in 1968-9; a mean annual intake of 4.89 KCals per m^2.

Effect of predation on invertebrate populations.

From the simple analyses carried out above it is clear that only a small fraction of the overall productivity of the five invertebrate prey species dealt with here is taken by the wader populations. In terms of mean biomass taken per m^2 per year the following are estimates of the percentage of overall production of each prey species taken by all the studied waders:

Nereis	5.6%	of	productivity	taken	by	waders
Corophium	2.1%	"	"	"	"	"
Hydrobia	16.8%	"	"	"	"	"
Macoma	17.3%	"	"	"	"	"
Mytilus	0.5%	"	"	"	"	"

This, however, is a percentage of the whole 6800 hectares of feeding area, except in the case of *Mytilus* where the data refers solely to Church Scar. Most species are taken by waders over a small part of their total ranges (Chapters IV and VII) and thus a higher proportion of the prey production in these areas will be taken whereas pressure in non-predated parts of the range will be little affected by the wader populations. It is quite likely in the more mobile species, especially *Hydrobia*, that mixing will occur from such less-predated to more predated areas.

Tidal variations also affect feeding range and on neap tides pressure will be put on smaller areas of the invertebrate prey zones. On such tides

Table 75. Mean standing crop and an estimate of productivity (see text) of the four main invertebrate prey over that part of their main range in which predation by waders is highest (1971-3 data).

	Mean standing crop (m^2)		Productivity (m^2/year)	
	g dry weight	KCals	g dry weight	KCals
Nereis	9.2	32.8	12.9	46.1
Corophium	14.3	61.3	13.9	59.6
Hydrobia	24.8	46.2	34.1	63.3
Macoma	14.7	79.2	13.4	74.7

NOTE: P/B data given in Table 73.

Table 76. Total intake (expressed as g. dry weight and KCals per m^2) of the four major prey of the intertidal mud-flats by the main waders (see Table 74) on the main feeding ranges of the Ribble Estuary in the years 1971-2 and 1972-3.

	Area in hectares	1971-2 g	1971-2 KCal	1972-3 g	1972-3 KCal	% Productivity taken by waders
Nereis	3900	0.45	1.59	0.63	2.26	3.5 - 4.9
Corophium	600	1.39	5.92	2.01	8.55	10.0 - 14.4
Hydrobia	500	15.0	28.0	23.1	42.8	38.0 - 46.0
Macoma	4000	3.25	16.2	3.61	17.9	24.2 - 25.3

the drying of the upper shore will virtually remove half of the Corophium zones whilst the failure of the tide-ebb to expose the lowest shore will exclude many waders from their lower Macoma and polychaete food zones. This again will result in a greater pressure on part of the invertebrate population zones though migration into these from areas of lesser pressure may relieve this to some extent.

For the four main species have been calculated the mean standing crop and, on the basis of productivity estimates the standing crop per year and the annual productivity in terms of g. dry weight and KCals per m^2. over their main ranges and where they are most predated by waders. These are presented in Table 75. Such figures are relevant for areas used by waders on tide heights of less than about 8.0 m above O.D. and exclude that part of the ranges little used by waders (Chapter IV). At least 70% of feeding occurs in these areas overall, though this is to some extent an arbitary figure as many other factors are involved, affecting this on a day-to-day basis. A computer analysis will, it is hoped, be fluid enough to allow for all these variables (see later). However, on the basis of this one figure total intake over these main feeding areas is given in Table 76.

Intake is still only a relatively small proportion of both standing crop and productivity except in the case of Hydrobia, the waders being responsible for creaming off between three and five percent of the Nereis, 10-15% of the Corophium production, and about 25% of the Macoma production. Such an analysis for Hydrobia is misleading in that, as explained earlier, the population of this species is somewhat pelagic during the highwater period and thus there is likely to be a mixing of the population over the whole of a mudflat area in such a way that heavy predation over one area will be negated to an unknown extent by immigration from adjacent, less-predated areas.

Effects of season on the wader predation of invertebrates on the Ribble Estuary.

Invertebrate production both in terms of recruitment of new individuals by reproduction and growth of the individuals generally occurs in the period April to November. During the months November to March little biomass is added to the standing crop by either method. So far, these two periods have been kept together and in this section an attempt is made to compare intake during the growth period with that in the months with no real growth.

To do this a reanalysis has been carried out as follows. The total number of bird-days for each major wader species was calculated for the two periods July-October and October-May. From data on foods and feeding rates the daily intake by waders of the four main mudflat prey was then assessed (Chapter VIII) and then the total amounts of these prey in the two periods. Again it must be stressed that the errors in such an analysis are large. However, it is instructive to consider these figures which are given in Table 77 in the form of g. dry weight and KCals per m^2 of substrate (6800 hectares).

During the autumn period the amount taken by waders is compensated for by the production of new individuals and the growth of animals already in the population. Even with this cropping during the growth period, mean standing crop increases. Thus, during the autumn there would appear to be an abundance of food which continues to be produced as the wader flocks remove it.

However, in the winter months little, if any, production takes place and the waders must take their food supplies from an ever decreasing standing crop. This decrease and the mean standing crops in the months of November and May are given in Table 78. It seems likely that, as the winter progresses and standing crop decreases, the waders will have to search more diligently to obtain the same amount of food per unit time though the data in Chapter VIII lend evidence both for and against such an hypothesis. Thus, whereas the feeding rates of some waders on some prey appear to decrease in mid-winter, in others the rates stay at approximately the autumn rate or even higher. Certainly, however, over the main feeding ranges prey densities are still high in late winter and the birds that remain can still generally take food at roughly the same rate as in autumn.

It would appear therefore, as was suggested in Chapter VIII, that food is superabundant and the limiting factor in winter is availability: the reduced daylength is not sufficient for the birds to take the required amounts of food even though they are there. This will be considered further in the final chapter.

The development of a computer programme

There are so many variables contributing to the one link ('prey : wader') in the estuarine food web that a manual analysis cannot properly account for all of them. The estimate presented above has been made to give an approximate series of estimates for the purposes of this discussion. Other variables must be considered before a more accurate assessment is possible.

Eventaully it is hoped to feed all these variables for which data are available concerning the amount of food taken by all the waders on the Ribble Estuary per year into a single computer programme. The following are the variables for which data are available, either in the present thesis or elsewhere:

1. Wader population fluctuations throughout the year.
2. Area of substrate exposed in terms of hectares/hours of known feeding areas: some of this has been included (feeding areas), but other data from tide tables, topography of the estuary, the effects of winds (especially onshore) and the effects of juxtaposition of sun and moon in different terms must be eventually included.
3. Daylength : such data are available from the Meteorological Office.
4. Proportions of feeding areas which are wet (i.e. covered at least by a film of water). This data has not yet been obtained.
5. Numbers of days when substrate temperature falls to below 5°C. There have been few such days during this study : since 1965, only in 1967 and 1969 was the substrate normally used by Redshanks on the upper shore frozen, and then only for very few days.
6. Effect of reduced success rate by low substrate temperature: some data are enclosed (but see 5. above for frequency of such low temperature conditions.)
7. Effects of vertical movements of prey.
8. Effects of different sizes of prey (biomass) throughout the year.

Table 77. Total intake (expressed as g dry weight and KCals per m^2) of the four major prey of the intertidal mudflats by the main waders (see Table 74) on the overall feeding area of the Ribble Estuary, data pooled for the periods July-October and November-March.

	July-October		November-March	
	g	KCals	g	KCals
Nereis	0.31	1.11	0.13	0.46
Corophium	0.09	0.39	0.12	0.52
Hydrobia	0.71	1.31	1.29	2.43
Macoma	1.92	9.50	0.96	4.66

Table 78. Mean standing crop (expressed as g. dry weight and KCals per m^2) of the four major prey of the intertidal mudflats on the Ribble Estuary in the months of November and May (pooled data 1971-74) with the decrease over this period.

	November		May		Decrease	
	g	KCals	g	KCals	g	KCals
Nereis	7.94	28.2	2.95	10.5	4.99	17.7
Corophium	6.98	30.3	5.26	22.8	1.72	8.5
Hydrobia	12.23	22.6	4.29	7.9	7.94	14.7
Macoma	13.88	68.7	7.95	38.4	6.13	30.3

9. Effects of varying prey density.
10. Effects of breeding cycle of prey : recruitment to the food-pool. For this aspect published data are still sparse. Some measurements have been made, however, for some species (e.g. Corophium) on breeding season, and number of young or spat produced.
11. Effects of variable proportion of some waders feeding inland either for high water or whole daylight period.
12. Effects of dark-hour feeding : some information is included but it would be desirable to obtain more extensive data.
13. Effect of diet change
    a) through the year (e.g. some Bar-tailed Godwits tend to change from Nereis to Macoma through the winter).
    b) through the tide cycle (many species appear to switch from one prey to another on the ebb and possibly switch back on the flow, e.g. Knot on Hydrobia and Macoma).
14. The proportions of each species of wader feeding on all the main prey and any variation of this through the year.
15. Variation of time spent feeding with different tide heights.
16. Variation of ingestion rate through the tide cycle.
17. Variation of ingestion rate through the year.

It will be apparent from the above that further data are required for many aspects of the work, and the collection of these is in progress.

From this computer programme it is hoped that it will be possible to give an estimate of the total biomass taken by all the waders in one year, the annual production of prey species and thus, the proportion of this potential food which the waders are taking. If data can be included on productivity of the prey species (as opposed to mean monthly biomass i.e. standing crop) then the amount of prey available for food over and above that needed to replace the total standing crop can be ascertained. Not all of this will be available to waders, of course, for fish, birds other than waders as well as carnivorous invertebrates within the substrate will remove a proportion. It may be possible however, to obtain some insight into whether the Ribble can hold more waders and alleviate the problems caused by a loss of habitat elsewhere.

It may well be possible to expand the computer assessments to include the whole of the north-west England complex of estuaries, by utilizing readily-available data on physiographical features and wader populations of these estuaries. As was suggested in Chapter II, the series Solway, Morecambe Bay, Ribble, Mersey and Dee provide a series of major wader estuaries between which some interchange occurs. Ideally, therefore, they ought to be considered under one 'umberella' study to assess their overall capacity for waders.

CHAPTER X

Discussion

Original aims

The initial aims of this study were to census the wader populations of the Ribble Estuary and to try to assess, from data on potential food distribution and density and food intake, whether the food supplies are limiting the size of these populations. Hence, it was hoped to predict whether the Ribble could support waders displaced from other estuaries affected by development.

These aims required a broad spectrum study rather than a narrow predator-prey survey. Thus, many aspects of the ecology of the prey and certain aspects of wader feeding had to be neglected.

Estimates of the numbers of waders present were made at monthly intervals, though counts of some species or areas were made more frequently. The number of wader-days per year was then calculated for the main species.

From regular samples at certain points over the main feeding areas the pattern of food densities through the year was assessed and this was supplemented by broader sampling programmes, either by transect or area samples, for the remainder of the estuary.

Food intake was estimated from mean peck rate and success rate for some species in which it was difficult or impossible to count accurately every food item taken. In those species, e.g. Oystercatchers and Godwits, where large foods are taken, the number actually obtained per unit time was estimated. These observations were supplemented by food analysis from gut contents and pellets. These data also provided information on size of prey taken.

To work out the total amount of food taken per day by each wader species, it was necessary to calculate the proportion of the day the birds spent feeding. Some allowance had also to be made, however, of the amount of food which was taken during the hours of darkness. Obtaining this parameter proved time-consuming and difficult though some estimates were obtained. Food intake at night appeared to be critical since during the winter months (November - February) well over half the possible feeding time, i.e. the time when the feeding areas were exposed by the tide, was within the hours of darkness.

It was decided from the onset that the energy value of the food would be the unit of biomass thus avoiding the errors in using dry weights which could include much indigestible material. To allow for the fact that the birds take into the gut all of the food including ash, ash-included energy values were used. However, in those cases in which the shell of a bivalve was not investigated (e.g. Oystercatcher feeding on Mytilus), the shell was excluded from the energy value.

The factors which were investigated to achieve the proposed aims are listed on pages 241 and 243 (Chapter IX).

Errors

Quantification of error terms has proved difficult during this study and the problems are discussed below.

a) Wader numbers

The important figures used for analysis are those for the whole estuary, mainly collected by the author and Dr. P. H. Smith but also including others made by helpers of the B. T. O. Estuaries Enquiry. As was explained in Chapter II counts of individual roosts or wader flocks are considered accurate in that independent counts by several observers of the same roost were closely similar. Furthermore, aerial photography carried out by Dr. W. G. Hale confirmed the accuracy of the normal ground counts.

On the Wash and Tees Estuary, however, it appears that high water roost counts miss a significant proportion of the birds which feed at low water on the intertidal zone. Thus, using roost counts at these sites to produce a figure of bird-days per month or yearly grossly underestimates the wader impact on the intertidal zone (J. Goss-Custard pers. com.). It is thus important to know whether the Ribble wader roost counts give a reliable estimate of the numbers actually feeding in the estuary.

During the first three years of the Estuaries Enquiry censuses, efforts were concentrated on the known roosts: Crossens, the Inner Ribble Marshes, Warton, Fairhaven and St. Annes. In 1971 the large Banks Marsh roost complex was discovered and from then all Ribble saltmarshes have been counted on a monthly basis, including those on which few waders roost. P. H. Smith also examined the shore at high water between Ainsdale and Southport, discovering other roosts which have been included in the censuses since 1972. Thus it can be assumed that in recent years no wader roosts have been missed on the shore or marshes.

It is unlikely that any large roosts have been missed on fields inland during the survey, for these have been generally well covered several times each year. Except for Oystercatcher, Curlews and Redshanks (see Chapter II) few waders go inland. On very high spring tides some roost on the reclaimed saltmarshes at Crossens and Hundred End and Martin and Lytham mosses. That all roosts of any significance have been located and included in the censuses has been confirmed by the aerial surveys which failed to locate any other previously unknown roosts.

Furthermore, with few exceptions, counts of birds on the feeding areas approximated to numbers roosting. Turnstones may roost near to the feeding areas and may not join traditional roosts. Most Grey Plovers and Sanderlings appear only to roost in the estuary rather than feed there; these probably move into the estuary from the Fylde and south west Lancashire beaches. These species are not included in the final analysis.

b) Time spent feeding

As indicated in Chapter III, the data obtained on the time spent feeding are such that it is impossible to calculate standard errors. Few individuals can be watched throughout a tide cycle and tide height varies from day to day depending not only on lunar and solar cycles but also on meteorological conditions. Thus combining data obtained by watching one or two birds through the tide cycle for several days would be pointless. In some species it is also likely that seasonal variation occurs (e.g. Oystercatcher), when more time is spent feeding in winter than autumn and spring. However, even at the most favourable time of the year a high percentage of time on the feeding grounds was spent feeding so seasonal variations could not have been large. This factor requires further examination in other species. Owen (1972) and Martin (1965) found similar seasonal variations in feeding time in the White-fronted Goose Anser albifrons and Woodpigeon Columba palumbus respectively.

More recent observations of individual birds throughout a tide cycle (in autumn 1975) suggested that the errors in the Tables 16 and 17 are generally small; in August and September three Mytilus-feeding Oystercatchers spent 71%, 78% and 74% of the tide cycle in feeding. Similar figures for a Macoma-feeding Oystercatcher, a Black-tailed Godwit and two polychaete-feeding Bar-tailed Godwits were 84%, 77%, 89% and 87% respectively. This suggests that the error in the estimate of time spent in feeding is probably overall less than 10%.

c) Night feeding rate

The amount of food taken at night is critical in the analysis of daily food intake especially in winter when up to 1.5 low-tide feeding periods fall with the hours of darkness. Estimates of intake made on moonlit nights are subject to large errors (Table 79) of between 17% and 34% of the means. These error terms are 1.4 - 2.8 times the standard errors of daylight mean feeding rates. Unfortunately the data for moonless nights are too sparse to allow the estimation of errors, though the reduction of feeding rate compared with light hours appears to be large. However, it is unlikely that the error on the estimated level of feeding in full darkness would be of a similar magnitude.

d) Day feeding rate

The standard errors expressed as a percentage of the mean feeding rate lies between 7% and 22% (Table 79), depending on the prey species. These data exclude means of feeding rates away from the main feeding zones.

e) Prey sizes

In the calculation of biomass intake then two statistics - mean dry weight of food items and mean calorific values - were used. Each of these has a standard error affecting the analysis.

The standard errors in the sizes of prey taken by waders (Table 34) varies, the minima (expressing standard errors in terms of percentage of the mean) being:

Nereis	3.5
Hydrobia	5.4
Mytilus	9.3
Cardium	8.3
Macoma	3.7
Corophium	6.3
Bathyporeia	5.2

Thus for the six major prey used in later calculations a standard error on the size taken by waders is less than 10% of the means.

Using these means, in conjunction with the regression lines (Figure 42) and other data of size and dry weight, the biomass of prey was estimated. On the means of dry weight for any size class standard errors lie between 3% in Nereis and 7% in Mytilus. Similarly, the standard errors of the mean calorific value of the various prey lie between about 2% in Cardium and 6% in Hydrobia.

Table 79. Errors of mean feeding rates of certain waders in winter on the Ribble Estuary.

Standard errors expressed as a % of mean

	Food	Day	Night
Oystercatcher	*Mytilus*	15.3	32.0
	Macoma	15.6	33.3
Bar-tailed Godwit	*Macoma* and *Nereis*	7.1	16.9
Knot	*Hydrobia*	9.8	27.6
	Macoma	22.1	30.7
Dunlin	*Hydrobia* and *Corophium*	12.7	27.4

One possibly important source of error in estimating prey sizes lies in the assumption that the waders are taking 'average' food items. It is possible that they select in some way the prey which, size for size, would yield more energy. From size measurements and the appropriate standard errors the energy value for a mean size of prey might vary by ± 10%. It is possible that waders are selecting those higher in the range and ignoring the others. There is, as yet, no evidence for this and it is difficult to see how they might be able to discern between the quality of different prey items when these are buried. Experiments might resolve this point.

It has also been shown that the calorific values of prey meat in some species (notably bivalves) vary significantly on a seasonal basis (Ansell _et al._ 1964, Hancock and Franklin 1972). In autumn meat calorific value is highest and decreases through the winter. Thus, in late summer and autumn waders will get more energy from a unit weight of food than they will in winter. This may be small in some species but on the Wash the decline in biomass of animals of given size during the winter is large, being up to 50% in several species (J. Goss-Custard _in litt._). In this study maximum (autumn) calorific values are used and it is possible therefore that the estimates of winter intake are on the high side.

f) Prey distribution

The major prey species included in the analysis show a contagious distribution with a variance greater than the mean. _Corophium_ and _Macoma_ on Satter's Bank and Horse Bank show no significant departure from a negative binominal distribution ($p > 0.05$) (using Elliot 1971 p. 53) though in _Hydrobia_ and _Nereis_ neither Poisson nor negative binominal distribution fit the data, the contagion being less extreme. The standard errors are:

Corophium	18% of mean
Hydrobia	16% of mean
Nereis	11% of mean
Macoma	14% of mean
Mytilus	9% of mean

The combined effect of these errors

(a) The calculation of daily food intake

The erros involved in these calculations are those relating to prey size, day and night feeding rates and time spent in feeding.

As has been pointed out above, the latter error is impossible to estimate, for example: in mid-winter, high water at 0800 hours means that about one full low water period will be available for feeding in daylight after the ebb; the other feeding period will be at night. With high water at 1200 hours (mid-day tides are usually highest) the birds may roost from about 1000 hours, giving them about two hours feeding prior to this in the light, and after the ebb they may have about two hours feeding before dusk. Up to 1.5 low water periods will be available for feeding in the dark. It is hoped that by assessing intake on a monthly basis these seasonal variations in day-length will have been taken into account.

The remaining erros can be considered as follows:

i prey size up to 10% of the means
ii night feeding rate 20-30% of the means
iii day feeding rate 10-20% of the means
iv time spent feeding estimated as up to 10% of the means.

Summation of error terms gives a total error of approximately 40-60% of the mean daily food intake. Furthermore, it seems likely that in factors i - iii that the true means are larger, rather than smaller than, the observed means. Thus the errors should be added to the observed means to yield the possible mean maximum of daily food intake.

Oystercatcher

Allowing for the standard errors, daily intake could be as high as:

Cardium	660 Kcal	
Mytilus	550 Kcal	
Mytilus	with earthworms at high water	690 Kcal
Macoma	300 Kcal	
Macoma	with earthworms at high water	420 Kcal

However, recent observations of intake suggest that these maxima are far too high and that the earlier estimates are closer. Single Oystercatchers were watched through single low water periods feeding on Mytilus and Macoma in August and September, 1975. All food taken was noted and the energy value calculated, using sizes of the prey taken and converting to dry weight and hence calorific value. The following intakes were noted:

Mytilus - feeding	248 Kcal
	271 Kcal
	206 Kcal
Macoma - feeding	110 Kcal
	122 Kcal

These figures are still open to the errors involved in converting the number of prey items ingested to biomass, but would lead to a daily intake of 315 - 380 Kcals for *Mytilus* and 155 and 190 Kcals for *Macoma* (with possibly another 60 Kcals from earthworms at high water giving a total daily intake of 215 and 250 Kcals).

Black-tailed Godwit

Earlier estimates (p. 200) suggested a daily intake of 84. 5 Kcals by male and 87. 4 Kcals by female Black-tailed Godwits in autumn. From the accumulation of standard error these could be as large as 140 Kcals for male and 144 Kcals for female Black-tailed Godwits, though observations in autumn 1975 suggest that the original calculations were sound. Intake was recalculated from single birds on the main Lytham feeding area which were watched through whole low tide periods. Foods taken were counted and size estimated from the comparison with the Godwit's bill length. Five birds, on five days, took an estimated 58. 5, 64. 1, 71. 5, 52. 4 and 57. 4 Kcals.

Bar-tailed Godwit

The daily intake, estimated as approximately 97 Kcals, could be as large as 152 Kcals based on the accumulated standard errors. Observations of four birds feeding off Fairhaven through single low water periods suggested that the earlier estimate was too low (132, 108, 123 and 145 Kcals with a mean of 127. 0 Kcals).

Redshank

The mid-winter intake was estimated at about 25 Kcals, whilst allowing the maximum error this might be up to 40 Kcals per day. Similarly, in autumn the estimated intake of 46 Kcals might actually be as high as 75 Kcals per day.

Knot

Initial calculations of food intake varied from about 74 Kcals per day in autumn to 40 Kcals per day in mid-winter. Allowing for the possible accumulation of errors these intakes could be as large as 110 Kcals in autumn and 67 Kcals in winter.

Dunlin

The mid-winter intake, calculated as 38.5 Kcals per day may be up to 64 Kcals on the basis of the accumulated errors.

(b) The problem of using standard metabolic rates

Standard metabolic rates are the energy required by an organism to maintain its basic resting metabolism at a constant temperature (20°C). In the wild state the requirements will be much greater. Temperature fluctuations and at certain seasons, notably times of moult and fat deposition, all combine to increase energy requirements far above standard metabolic rate.

Initially in this study a factor of three was used by which the standard metabolic rate was multiplied to give requirements in the field. This factor was chosen after much discussion, and it was stressed earlier that it might have to be modified later. Recently, Hulscher (1974) has shown that Oystercatchers feeding in captivity on Cardium took the equivalent of 4.3 times the standard metabolic rate in summer. In the wild in autumn and winter it is likely that this factor might be increased to give six times or more. Similarly, P. Smith (pers. com.) has found that Bar-tailed Godwits at Lindisfarne take in an equivalent of five times the standard metabolic rate in winter. This does not necessarily mean that the birds require such a high intake (5-plus time standard metabolic rate) even if body weight remains constant. It does seem likely however, that the factor of three, used so far, is too low and that a factor of at least four or five is more realistic.

For the purpose of this section, therefore, the factor by which standard metabolic rate must be multiplied in order to estimate requirements has been calculated from known energy increase. The best data for this are those for Oystercatchers feeding on Mytilus and Macoma/earthworms and Bar-tailed Godwits feeding on polychaetes presented earlier in this chapter. These are from autumn data, so the errors inherant in assessing night intake are very small. Also the data are from observations of single birds throughout single tide cycles. The modified factors are as follows:

Oystercatcher S.M.R. 47.6 Kcals Observed Intake:
Mytilus 380 Kcals
Macoma and earthworms 250 Kcals

Factor: 8 for Mytilus and 5.2 for Macoma and earthworms

Bar-tailed Godwit S.M.R. 34 Kcals Observed Intake: 137 Kcals

Factor: 4

These provide further evidence to the suggestion that the factor should be greater than three, possibly about five times the standard metaboliv rate.

By multiplying standard metabolic rates by five an estimated of daily requirements can be obtained and under suitable conditions these daily amounts might be obtained:

	S. M. R.	S. M. R. x 5
Oystercatcher	47.6 Kcals	238
Curlew	44.0	220
Black-tailed Godwit		
male	37.4	187
female	40.2	201
Bar-tailed Godwit	34.3	172
Redshank	22.6	113
Knot	21.0	105
Dunlin	10.2	51

These amounts would have to be ingested if the birds were to remain in an area over a long period otherwise they would be utilizing fat stores or in danger of dying from starvation.

Even if the errors discussed in the last section were added to the calculations of the amounts of food taken by waders presented in Chapter VIII, some species do not ingest these amounts. Curlew, Black-tailed Godwit, Redshank and winter Knot have daily calorie intakes well below these levels. Oystercatchers, except possibly those feeding on Macoma, Bar-tailed Godwits, autumn Knot and Dunlin might take these amounts. In all these cases, however, the conclusions of Chapter VIII still apply.

(c) The calculations of total amounts of food taken

This was calculated by multiplying the mean daily intake for one bird by the monthly population of each species of wader and then by adding together the monthly totals to give annual totals. As was outlined earlier, it is impossible to obtain an estimate of the error involved in monthly counts. Thus the maximum error on daily food intake (60%) applied to the figures of Table 74 and p. 236.

However, from field work in autumn 1975 (described above), there appears little evidence that mean ingestion rates are as much as 60% too low.

A further series of computations has been made of the amounts of food which would be taken from the Ribble Estuary if every wader were obtaining the equivalent of standard metabolic rate multiplied by five. This has not been done for Mytilus as Oystercatchers take the vast majority of these at a rate equivalent to at least five time standard metabolic rate.

The mean intake of prey over the estuary (in terms of Kcals per m^2 per annum) might thus be as follows:

	Original Calculation	Allowing for 60% maximum error	Amount of intake x 5 S.M.R.
Nereis	1.57 Kcal/m^2/year	2.76	2.91
Corophium	0.91	1.50	1.83
Hydrobia	3.74	6.15	6.21
Macoma	14.26	23.53	28.44
Mytilus	4.89	8.05	-

It is of note that the hypothetical amounts consumed on the basis of five times standard metabolic rate are in excess of the means plus 60% maximum error.

It seems unlikely that the true figure biomass removed by waders is lower than that originally calculated.

(d) The effects of predation by waders on the invertebrate populations

It was decided to use productivity (the amounts of biomass produced over the year) of the invertebrate populations rather than simply biomass measurements in assessing the effects of predation on the prey species. Thus a measure of production had to be obtained and this was done initially as minimum positive biomass increase through the year using monthly samples. This gives a measure of production lower than those which have been shown to occur in other studies (see page 233 for example). Thus a Production/Biomass ratio of 1.5 was adopted in this study rather than ratios of between 1.37 obtained from minimum positive biomass increase. These latter ratios did not take into account prey losses during each month to predators other than waders, nor mortality of the 'rey by non-biotic factors such as erosion, dessication, or freezing of the mudflats. This figure of 1.5 is still possibly low, judging from published studies of productivity in Neanthes virens (P/B = 1.63), Scrobicularia, Littorina irrorata and Mytilus (discussed in pp. 233-234).

Thus, whereas measures of food intake by waders may be too low by a factor of up to 60%, the estimate of productivity is likely also to be too low by a factor (using the N. virens figure)of

$$\frac{1.63 - 1.50}{1.5} = 0.85$$

Thus the estimate of productivity presented on p. 234 may be up to 10% below the real value:

	Original Calculation	Allowing for 10% underestimate
Nereis	27.9 Kcal/m^2/year	30.6
Corophium	41.7	45.8
Hydrobia	22.1	24.3
Macoma	82.5	90.9
Mytilus	1053.0	1158.0

Now it is likely that all errors are additive. The data derived from the original calculations were low; that the mean daily food intake estimate was probablu also low is suggested from comparison with expected energy requirements (S.M.R. x 5); that the P/B ratio used as 1.5 was probably too low judging from other measures of productivity (see above).

Thus, the possible values of percentage productivity taken by waders can be recalculated (Table 80).

If it is accepted that the figure in column A are the minimum proportions of productivity taken by waders, then columns C, D, E, F and G give possible values of the maximum proportions taken by waders. On this basis waders would appear to remove at most about 10% of Nereis, 5% of Corophium, 30% of Hydrobia, 35% of Macoma and 1% of Mytilus production. The remainder of the invertebrate production must therefore be removed by other predators, or die as a consequence of non-biotic factors or possibly competition for space or food in the mudflat.

Table 80 Percentage of productivity of major prey species taken by waders

	Original Calculations	Allowing 20% error on food intake but no error on P/B ratio	Allowing 60% error on food intake but no error on P/B ratio	Allowing 20% error on food intake and 10% error on P/B ratio	Allowing 60% error on food intake and 10% error on P/B ratio	Food intake 5 x S. M. R. but no error on P/B ratio	Food intake 5 x S. M. R. and 10% error on P/B ratio
Nereis	5.6%	7.1	9.9	6.5	9.0	10.2	9.5
Corophium	2.1	2.6	3.6	2.3	3.2	4.4	4.0
Hydrobia	16.8	20.3	27.8	18.4	25.3	28.1	25.6
Macoma	17.3	20.7	28.5	18.8	25.9	34.4	31.3
Mytilus	0.5	0.6	0.8	0.5	0.7	-	-
Column	A	B	C	D	E	F	G

Food as a limiting factor of bird populations

It has been suggested that in most bird species population densities are controlled by density dependant factors which operate by exerting in increaing influence as the population grows and vice versa (reviewed by Lark, 1954, 1966).

In the breeding season the availability of nest sites or territories may be limiting, providing a ceiling to the population as in the Red Grouse *Lagopus lagopus scotius* and Pied Flycatcher *Fidicula hypoleuca* (discussed by Lack 1966). However, in winter, when territories are not generally maintained then the only pressure on the birds is to obtain sufficient food. Hence it is supposed that in winter food is the major limiting factor: as Lack (1954) stated, "outside the breeding season, food shortage might be an important density dependant cause of adult mortality".

There is little evidence from the available studies that food is a limiting factor, that is 'limiting' in a density dependant manner, for as Lack (1954) pointed out "the main evidence as to whether food shortage limits bird numbers is indirect". As evidence Lack suggested four lines of arguement:

1. Few adults appear to die from predation or disease, a negative arguement "Leaving food shortage as the likliest cause of density dependant loss".
2. Birds are "more numerous where their food is more abundant".
3. Each bird species "living in the same region depends upon primarily different foods". In a later book Lack (1971) attempted to demonstrate this for many bird groups, though many data he summarized were inconclusive, especially for sympatric waders and wildfowl (pp. 315-320).
4. Fighting frequently occurs in winter flocks of birds suggesting food shortage, for example tits *Parpus* spp. (Hinde 1952) and crows *Corvus* spp. (Lockie 1955). Presumably Lack considered that such fighting was over food which was short in supply relative to the birds "requirements".

However, if food was the main limiting factor one would as Lack pointed out expect to find starving individuals and a declining mean weight through the winter. Lack suggested that the reason for not finding many birds dead through food deficiency was that mortality due to starvation affected a few individuals at any one time and hence these might be overlooked. This tends to make nonsense of his first piece of evidence. Furthermore, waders appear to reach a peak in terms of weight and fat content in mid-winter (e.g. Prater 1975).

For waders the third line of evidence does not follow, though different species do appear to feed on different mean sizes of prey. Point number four also does not hold for most species of waders which, in the period September - February, spend only up to 2% of the time available for feeding in display of any sort whether sexual or antagonistic (see Table 16).

Lack's second line of arguement was extended by Wynne-Edwards (1962) who suggested that an inherent factor acting in a social fashion tends to maintain the population at a level lower than food supplies can actually support. Hence, one would not expect to find much mortality due to starvation. According to Wynne-Edwards food does not limit bird population size through mortality but regulates the dispersion of birds, i.e. they distribute according to their food distribution.

To summarize, if food limits bird populations then it may do so by either

a) density dependant means, through mortality, or

b) dispersive means, bird dispersion correlating to food dispersion and the bird populations in an area being maintained at a level below that which would be affected by density dependant checks on the populations.

Is food limiting the wader populations on the Ribble?

Firstly, the decline in food stocks on the Ribble through the winter does not result in a decline of feeding rates. As was described in Chapter VIII most waders feed at similar rates in spring to the rates in autumn, when food density was at a peak. This would suggest strongly that food density is not a limiting factor: otherwise the decline in food stocks would be paralleled by a decrease of the rate of food intake (following Holling, 1959, 1966).

Both these observations suggest that the wader populations are maintained at a level below which they have an impact on the prey density. it might be considered therefore that the wader populations were not being controlled in a density dependant manner by the food populations.

However, though food intake in terms of numbers per unit time remains high through the winter, biomass ingested per day declines through the winter as the daylight period is reduced and the waders have to feed more in the dark when feeding success is probably lower. Mid-winter intake is also affected by the lower energy value at this season comapred to autumn, certainly of some, and possibly all prey. Thus, although the wader can take in prey items at the same rate in mid-winter as it did in autumn, the prey item size for size may be of less energy value than in autumn. The birds will also have less time for feeding. It may be therefore that the amount of prey biomass which can be ingested per day provides a control in some way on the wader populations.

Each wader requires a certain energy intake per day, this requirement increasing during colder weather (normally mid-winter). Most species can easily obtain the basic requirements in autumn and spring when higher temperatures reduce the energy demands and long light periods permit prolonged feeding. However, with the halving of daylength and lower temperatures, many waders cannot obtain sufficient foods in winter from the shore. Hence they must turn to other, more energy-rich foods, migrate or starve. Apparently, only the Dunlin, of the abundant mudflat-feeding waders and Mytilus-feeding Oystercatchers can obtain sufficient food on the shore in mid-winter to meet its expected energy requirements. The Dunlin is the one species which has a peak population in winter.

A variable proportion of other species emigrate. Oystercatcher (especially those feeding on Macoma), Curlew and Redshank move onto the fields at high water to supplement their shore foods with earthworms, tipulids and other land invertebrates. In the Oystercatcher field-feeding was a relatively rare occurrence in winter in North-west England (Dare 1966) up to the hard winter of 1962-3. In the years preceeding this winter their main food was Cardium edule (Drinnan 1958) and it seems likely from Drinnan's figures that their intake was sufficient to meet their needs. Following the catastrophic decline of Cardium, Macoma took its place as a main invertebrate prey. However, probably because of its smaller biomass and the limitation of time, in winter Oystercatchers cannot obtain their requirements from Macoma. Hence the swing, especially in mid-winter, to field invertebrates which can be taken throughout high water when Macoma beds are covered by the tide. For some birds these now provide the whole of the food, except possibly at night when they return to the shore. If hard weather excludes them from the fields then fat stores may be sufficient for them to survive short periods, though a prolonged hard spell would necessitate emigration or result in death (c.f. 1962-3 in Dobinson and Richards 1964).

Black-tailed Godwits can probably not obtain in winter sufficient food on the small restricted feeding areas they use on the Ribble in autumn, so they move, probably to the Dee. Many Bar-tailed Godwits likewise move away, possibly to Morecambe Bay where they feed on Nereis and a high proportion of Macoma (pers. obs.). Those that remain also appear to take a higher proportion of Macoma in winter which overall yields more energy per unit time. This probably brings winter intake up to requirements, especially during mild winters. Most Knot emigrate, either to Morecambe Bay, where they take larger Macoma than they do on the Ribble (Prater 1972, pers. obs.) or abroad where daylength is greater. Again, it probably depends on mild winter conditions, as experienced in recent years, for others to remain in winter on the Ribble as generally their food intake here barely covers their requirements.

The biomass of the prey would appear to be the factor which exerts pressure on the waders in winter though in autumn and spring this does not apply since the extended light feeding period enables requirements to be obtained.

Two problems remain to be answered. Firstly what do most waders achieve by migrating in mid-winter from the Ribble to other estuaries in Britain or southern Europe and west Africa. Until these have been adequately studied it must be presumed that these areas provide food resources which enable the waders to obtain their energy requirements. Morecambe Bay certainly provides Bar-tailed Godwits and Knot with prey, Nereis and Macoma, of a biomass much greater than those on the Ribble can obtain (Prater 1972, pers. obs.). Similarly, the area on the Dee Estuary where Black-tailed Godwits winter contains much larger Nereis than their feeding areas on the Ribble (Stopford 1951, pers. obs.). Waders wintering further south would also have the advantage of a longer daylight period than they have on the Ribble.

Secondly, if food is so poor on the Ribble to warrant emigration of most individuals of all wader species expect the Mytilus-feeding Oystercatcher and Dunlin, how do those which remain manage? In Macoma-feeding Oystercatcher, Curlew, Redshank food from fields at high water provides sufficient in most instances for daily requirements to be attained. Bar-tailed Godwits tend to take more Macoma in winter which privides more energy than Nereis, the staple diet in autumn. Thus there appears to be some change of diet and feeding habits in winter of some remaining waders (see also Feare 1966, Goss-Custard 1969, Hepplestone 1971). This is, however, a point worthy of further study.

In conclusion, the wader-food relationship does not suggest that the food supplies provide a density dependant limitation on the wader populations. On the Ribble individual prey biomass is the prime constraint in mid-winter for although the rate of intake of prey items is as high as in autumn and spring, the reduction of daylight feeding makes it hard for waders to obtain their energy requirements. At this season the autumn Ribble waders mostly disperse to areas where they can presumably obtain their energy requirements more easily.

It may therefore be that the Ribble could hold more waders in autumn and spring when daylength linked with the feeding rate and prey biomass yields sufficient food. In winter however, most would have to move elsewhere, as they do now.

SUMMARY

This thesis describes the results of research carried out on the Ribble Estuary through the years 1964-74, including a concentrated programme of work in the years 1971-74, on the populations, foods and feeding ecology of waders (Aves : Charadrii). Censuses of waders both on feeding areas and at high water roosts were made at regular intervals, in recent years including counts for the *British Trust for Ornithology* Estuaries Enquiry.

Forty-eight species of wader have been recorded on the Ribble, six of those species occurring mainly on the inter-tidal zone having populations on the Ribble of major importance: Grey Plover *Pluvialis squatarola*, Black-tailed Godwit *Limosa limosa*, Bar-tailed Godwit *L. limosa*, Knot *Calidris canutus*, Sanderling *C. alba* and Dunlin *C. alipina*. In the Grey Plover and Sanderling the annual peak has occurred in spring, with rather erratic numbers in autumn sometimes resulting in a clear peak. In the Black-tailed Godwit and Knot the well-defined peak occurs in autumn, whilst in the Bar-tailed Godwit an autumn peak is later followed by a smaller peak in mid-winter. Cnly in the Dunlin is the main peak in mid-winter.

Likewise for other shore-waders important on the Ribble peak numbers follow clear patterns. Curlew *Numenius arquata* and Redshank *Tringa totanus* have very clear autumn peaks, the Ringed Plover *Charadrius hiaticula* having distinct autumn and spring peaks. The Turnstone *Arenaria interpres* has a clear autumn peak though the spring peak occurs early, in January-February. The Oystercatcher has the most complex population fluctuations through the year, and it is possible that within the whole Ribble area numbers fluctuate little from autumn to early spring.

Food availability was studied by taking regular samples at monthly intervals at five census points, transects across the intertidal zone and other samples at irregular intervals to tie in with observations of feeding rate or gut content analysis. From these samples were obtained

measurements of the prey which could be used to give indications of the annual variation in biomass of the main prey. Factors affecting the distribution of the fauna of the intertidal zone were measured.

On the inner-mid estuary (areas of greatest variation in salinity, with substrates of medium particle size usually in the median particle diameter range 60 - 100μ) the bulk of the invertebrate biomass is composed of the four species Nereis diversicolor, Corophium volutator, Hydrobia ulvae and Macoma balthica with smaller but significant amounts of Arenicola marina, Cardium edule and Scrobicularia plana. These are largely replaced in the higher salinity sandy shores of the outer estuary by Scoloplos armiger, Nephthys caeca and other polychaetes, Bathyporeia pelagica, Eurydice pulchra, Haustorius arenarius and Tellina tenuis.

Most species show very clear zonation in relation to shore-level with Corophium on the upper shore (mainly between 2-5 m above O.D.), Hydrobia on a similar range though with peak density lower than that of Corophium (Hydrobia peak density about 3m above C.D., Corophium at about 4m above O.D.). Macoma occurs over a much wider range (generally O.D. to 5m above O.D.) with a peak density zone at about 2-3 m above O.D. Such distributions appear to be related to gradient of shore, substrate particle size, salinity and tidal range.

The mean sizes of some major invertebrates varies to some extent according to height on the shore. Mean size of Corophium increases with height on the shore whilst mean size in Macoma tends to decrease up the shore. Several factors, including tidal range, exposure of the substrate and different mortality factors at different shore levels, contribute to these variations. In the more mobile Nereis and Hydrobia size does not appear to vary with shore level.

Within the substrate the main prey show characteristic depth distribution. For examples, Corophium occurs closest to the substrate surface around high water, burrowing down into the mud so that over the low water period most Corophium occur at or below 3cm of the surface. Few Corophium occur at below 10 cm deep. In Macoma spat fall results in the bulk of the population occurring in the surface 1 cm of substrate from June whilst during the following twelve months the mean depth of this population steadily increases. This is presumably due to the burrowing of the spat and higher mortality in those *Macoma* occurring closer to the substrate surface. In *Hydrobia* there is no significant variation depth distribution through the year though variation with the tide does occur, burrowing occurring, in 30% of the population to a depth greater than 1 cm, over the low water period.

Food intake of waders was studied by gut analysis, pellet analysis and direct observation.

Oystercatchers feeding on the intertidal zone do so either on *Mytilus edulis* at Fairhaven (Table 4 gives the population), or *Macoma* with some *Cardium*, *Scrobicularia* and *Mactra corallina* (all the birds other than those given on Table 4). Up to 25% of the Oystercatchers on the Ribble may feed inland through the daylight period and these are joined at high water by some birds which spend the low tide period feeding on the shore and using the fields as a source of food (oligochaetes) over high water (see Chapter II).

About 50-60% of the Curlew diet on the shore is composed of *Nereis*, 20% of *Macoma* and the remainder of miscellaneous items including *Arenicola* (5-10%). The majority (70-80%) of the Black-tailed Godwit diet is composed of *Nereis* whilst lamellibranchs comprise the remainder. The diet of the Bar-tailed Godwit appears to vary through the year in the proportions of its main constituents. In autumn and early winter *Nereis* comprises about 60% and *Macoma* 20% whilst in late winter and spring *Nereis* comprises only 25% and *Macoma* 70%. Between 5-10% of the diet is composed of *Arenicola* through the year.

Redshank diet is related to feeding area. Most feed on the upper shore where *Corophium* predominates (between 80-95% of the whole diet) with *Nereis*, *Hydrobia* and *Macoma* comprising most of the remainder. At night the *Hydrobia* proportion increases as the others decrease. Those Redshanks feeding lower on the shore take a higher proportion of *Nereis* and *Macoma* whilst the saltmarsh feeders have a very mixed diet.

Knot generally feed on Hydrobia, with very small amounts of Corophium, around high water and Macoma, with small quantities of Cardium, Tellina and other lower shore fauna, over the low water period. A high proportion of Knot, however, probably miss out the Hydrobia component, either altogether or at least before high water.

Sanderling, the one species feeding almost exclusively on the sandy shores, takes a wide cross-section of the available prey, though Bathyporeia pelagica and is associate crustaceans provide the bulk (80%).

Dunlin mostly feed on Corophium around high water with a swing to Hydrobia (70 - 85% of the diet) on the mid-shore, the species main feeding range. The populations feeding on the lower shores do so mainly on Macoma or nereids.

The rate of food intake was calculated for the major prey of the main waders in terms of peck rate (pecks per minute), percentage of successful pecks or simply ingestion rate (number of prey taken per minute). In some cases (e.g. Sanderling or Dunlin feeding on tiny amphipods or Hydrobia) no good estimate of ingestion rate was possible as it was often impossible to see clearly whether a food item had been ingested.

For the calculations of daily food intake the time spent roosting, the proportion of time on the feeding grounds actually involved in catching food, the effects of various factors on feeding rate, daylength and the extent of night feeding had to be ascertained. The expected requirement was estimated by calculating standard metabolic rate (Lasiewski and Dawson 1967) and multiplying this by a factor of three to allow for the birds being in the wild. There are doubts as to this factor, some authors considering a factor less than three would be suggicient.

The ingestion rate of Oystercatchers on Mytilus increases to mid-winter, thereafter decreasing in late winter due to loss of young mussels. An Cystercatcher feeding on mussels takes 30-40% less on spring tides than neap tides. Those Cystercatchers taking Macoma have a decreasing daily food intake from September due mainly to the reduction of light hours.

It was concluded that most Oystercatchers can obtain sufficient food to meet energy requirements, possibly with the exception of those feeding on Macoma which supplement their shore-food with earthworms at high water. This latter compensates for the low Macoma ingestion.

From a comparison of observations of food intake with movements of birds to and from inland feeding grounds and the estuary it appears that Curlews take only about 30% of their daily requirements from the shore.

In the Black-tailed Godwit (which occurs to a significant extent only in autumn) highest feeding rate was recorded in the main feeding area. The overall daily intake was less than that expected requirement based on standard metabolic rate. In autumn the requirement will be less than mid-winter, so the autumn intake may be sufficient for then, but not for the harder winter weather.

The Bar-tailed Godwit, however, obtains only slightly less than the expected requirement if it feeds entirely on Nereis and thus the Macoma and Arenicola obtained will make-up the intake to the requirement. The more Macoma the higher the energy intake and thus it will be an advantage in late winter to concentrate more on Macoma . This is what this species appears to do in January-March.

In spring-autumn the Redshank can obtain 67% of its daily requirements on the shore at low water and probably easily make up the rest at high water on saltmarsh or fields or at night. In winter, however, the daylight intake on the shore is only about 40% of the requirement. This is, of course, also in the time when requirements are greatest due to hard weather.

In the Knot (and Dunlin) ingestion rate on Hydrobia was counted as 80% of pecks. This may not be unreasonable in that the prey are easily observed and have only to be picked up. In autumn and early winter Knot appear to have little difficulty in obtaining their energy requirements but in mid-winter (December-February) with the hardest weather and short days their intake is reduced to barely half the requirements.

Dunlin feeding on Corophium and Hydrobia, when the daylight intake is supplemented by night feeding, can obtain sufficient energy from food to meet expected requirements. When a small proportion of Nereis and Macoma is included then the intake is certainly sufficient to meet requirements.

Other points emerged from this aspect of the study: feeding success is generally higher on wet than dry substrates, feeding success in flocks is generally higher than in solitary or small groups of birds, in the Black-tailed Godwit females have higher feeding rates than males. These are outside the main theme of the study and will be dwelt on elsewhere.

It appears that main population fluctuations may be related to food density and intake. Thus the Black-tailed Godwit, Redshank and Knot can obtain enough food in autumn but not in mid-winter so most of them leave for the winter. Oystercatcher, Bar-tailed Godwits and Dunlins, however, can obtain their daily energy requirements in mid-winter so they over winter.

The overall effect of the wader populations on the main prey was ascertained. The annual intake by the wader populations was estimated as 3-5% of the Nereis production, 10-15% of the Corophium production, up to about 47% of the Hydrobia production and 25% of the Macoma production. The reduction of prey densities over the main wader feeding ranges did not appear to result in a significant decrease of ingestion rate.

In a discussion, the sizes and fluctuations of the wader populations were related to food requirements and the ability of the Ribble to provide these requirements.

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APPENDIX

The use of correction factors in assessing proportions of prey in the diet.

Goss-Custard (1969) showed that in assessing the actual diets of Redshank from gizzard contents it is necessary to apply a correction factor to the counts of fragments of each food species in the gizzard in order to calculate the amounts taken otherwise hard-bodied prey (e.g. *Hydrobia*) would be overestimated compared with soft-bodied prey (e.g. *Corophium*).

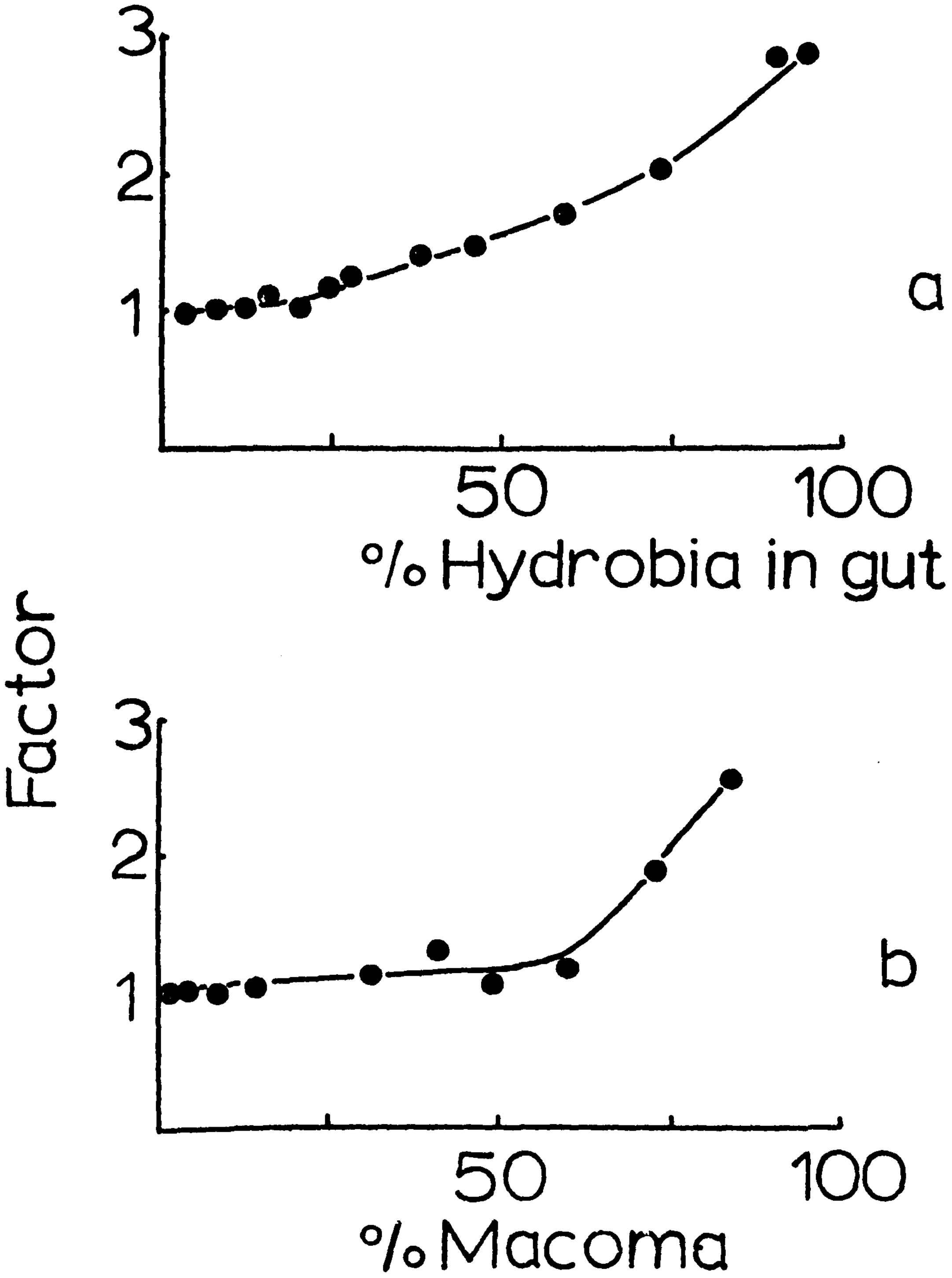
In order to obtain the necessary correction factor it is necessary to count the number of each prey species in the oesophagus (where little or no digestion occurs) and divide the proportion of soft-bodied prey in the oesophagus by the proportion present in the gizzard. If the gizzard contents truly reflected the diet then a correction factor of one would be obtained.

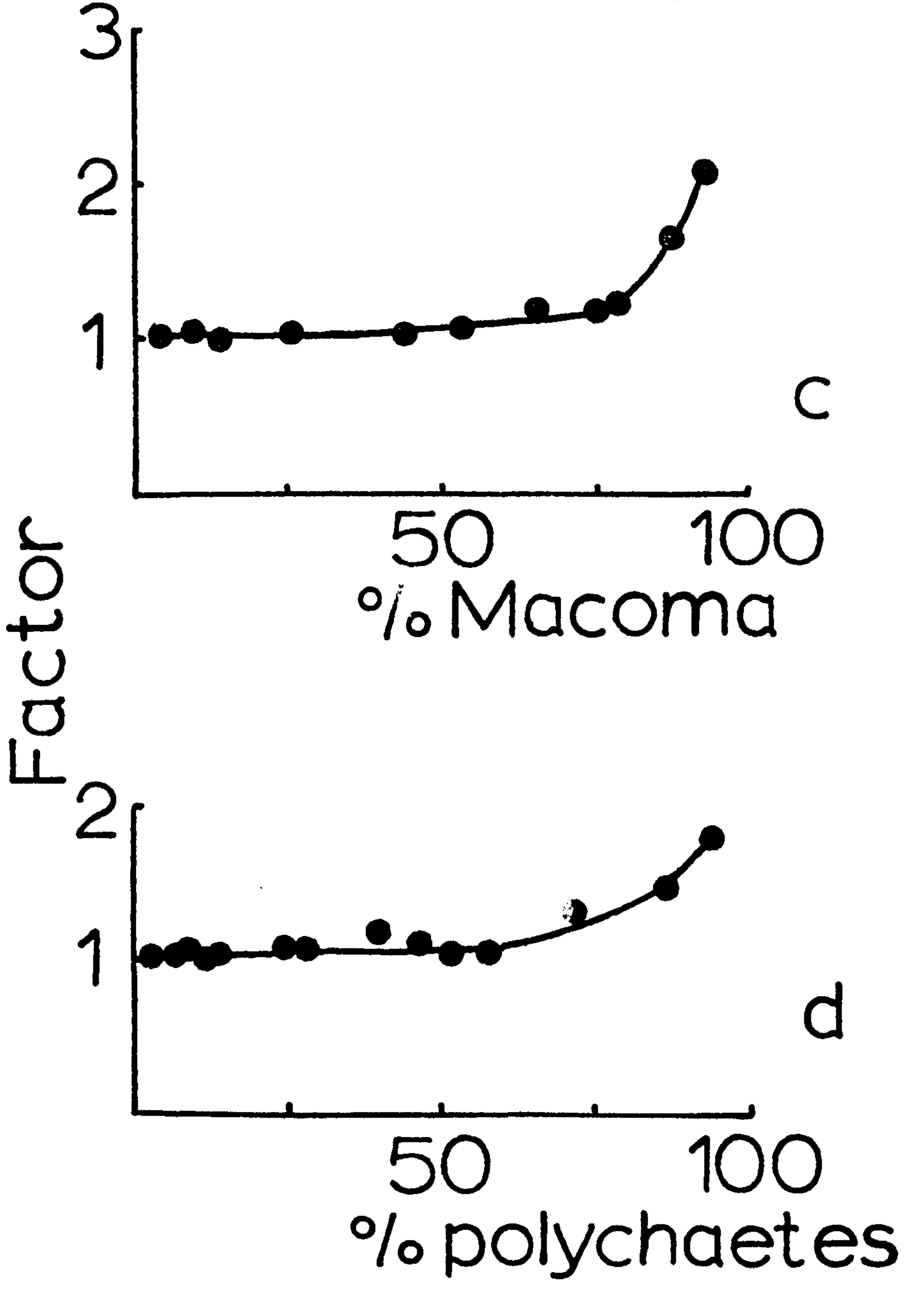
Correction factors were obtained for Redshank and Dunlin feeding on *Hydrobia*, *Macoma* and *Corophium*, Bar-tailed Godwits feeding on *Macoma* and *Nereis*, and Sanderling feeding on *Bathyporeia* and polychaetes. These are presented in graph form in Figure 44.

When a wader is collected with no food in the oesophagus, its gizzard content can be estimated by multiplying the proportion of the relatively soft-bodied prey (the one probably underestimated in the gizzard) by the appropriate correction factor and modifying the proportion(s) of other prey accordingly. For example, if a Dunlin is collected with 85% *Hydrobia* and 15% *Corophium* in the gizzard, the correction factor for *Corophium* would be 2.7 and this multiplied by the observed proportion of *Corophium* to give a corrected *Corophium* fraction of 41%. The *Hydrobia* proportion would thus be taken as 59%.

Figure 44

Correction factor curves for a. Redshank feeding on Hydrobia and Corophium. b. Redshank feeding on Macoma and Corophium, c. Bar-tailed Godwit feeding on Macoma and Nereis, d. Sanderling feeding on Bathyporeia and polychaetes. Curves fitted by eye.


Factor
3
2
1
50
100
% Hydrobia in gut
a
3
2
1
50
100
% Macoma
b


3
2
1
c
50
100
% Macoma
Factor
2
1
d
50
100
% polychaetes