The ecology of Dunlin (*Calidris alpina* L.) wintering on the Severn Estuary

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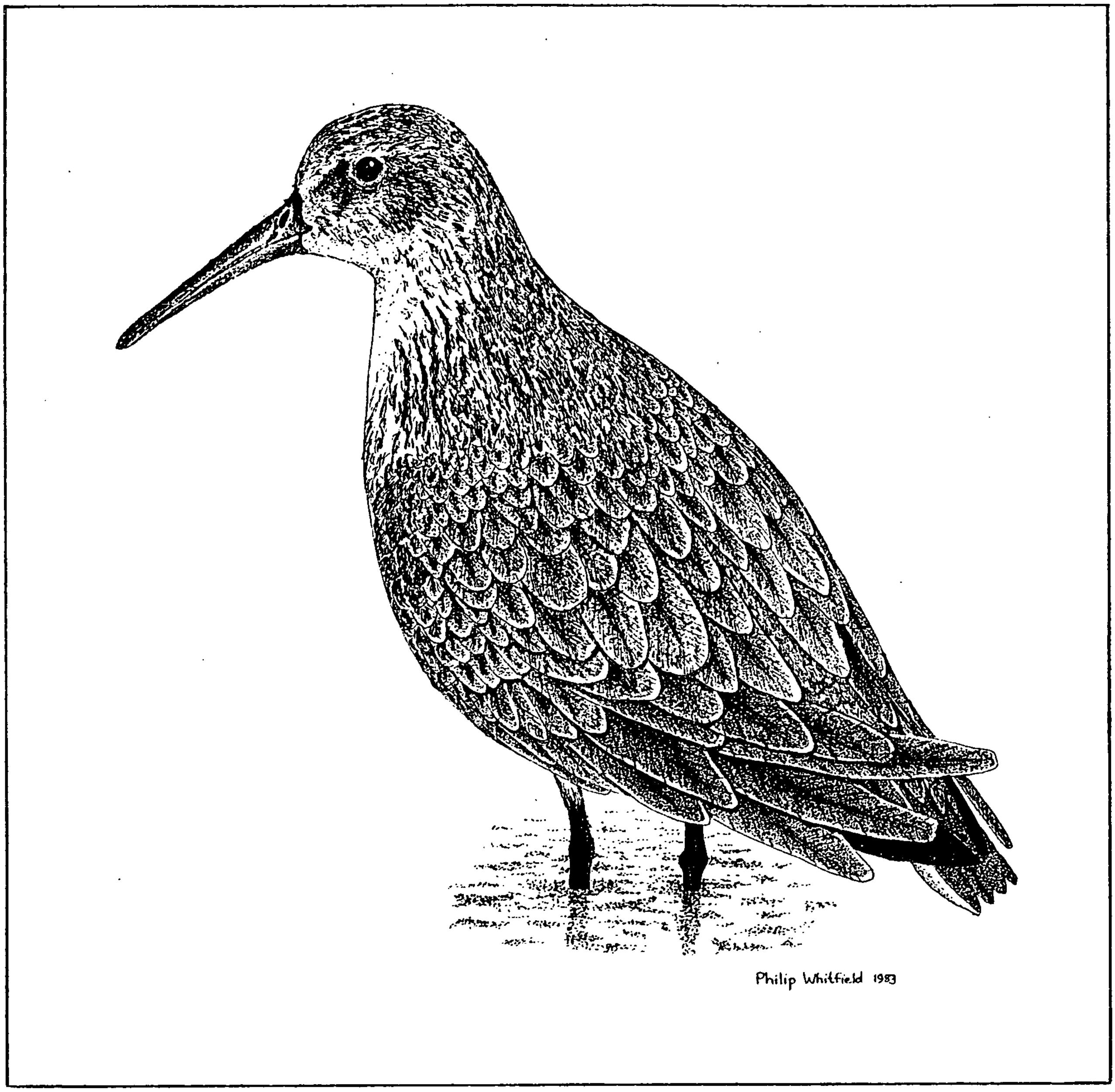
Philip Whitfield 1983

To my wife, Jacquie

I hereby declare that this thesis has been composed by myself, and that the all the work it describes was carried out by myself alone except where otherwise stated.

Nigel A. Clark

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ABSTRACT

The winter ecology of the Dunlin *Calidris alpina* was studied over a period of three years. The study area consisted of four bays on the south shore of the Severn Estuary. Large numbers of Dunlin were caught during the study and were sexed using discriminant analysis based on total head length and wing length. Total head length (which is highly correlated with bill length) was the most important variable; males have short bills and females long bills.

Movements of Dunlin within the study area showed a standard pattern each year. The birds arrived on the Severn Estuary during October and November; during this period there was some movement between bays. Between 1 December and 20 February, a few birds moved between adjacent bays, but no further. After 20 February, birds again became more mobile before leaving the area in early March.

In mid winter there was a higher sex ratio (number of males divided by number of females) at Berrow than at Clevedon. At Berrow the substrate in the main feeding area was liquid mud and the the main prey species were *Hydrobia ulvae* and *Nephtys hombergi*. At Clevedon the substrate in the main feeding area was firm mud and the main prey species were *Nereis diversicolor*, *Macoma balthica* and *Hydrobia ulvae*. After a hard frost at Clevedon, some males and juveniles continued to feed when most of the flock was roosting. At this site females showed little diurnal variation in weight, but males lost weight during the day and gained weight at night. *Nereis* were shown to respond to lower daytime temperatures by retreating into the mud. Below 10 degrees Centigrade, only small *Nereis* were available to short-billed Dunlin in the daytime.

In Sand Bay there was a high percentage of juveniles feeding on the sand where the main prey was Corophium arenarium; here, the sex ratio among juveniles was high. Among juveniles feeding on firm mud (where the main prey species were Nereis, Hydrobia and Macoma) the sex ratio was lower. In this bay juveniles fed for longer than adults.

Males tended to moult on the Wadden Sea and females on the Wash; there were, however, very few females from Clevedon and Sand Bay moulting on the Wash and their moulting site is unknown. Birds from these bays tended to move through migration sites in Finland and Ottenby, Sweden, later than birds wintering in Weston Bay and at Berrow.

There were slight differences in the measurements of birds of known sex (sexed by dissection) from different sites within the Severn. This may suggest different breeding areas for birds wintering in different bays.

In two winters of the study, Dunlin increased weight after arrival until January, after which they lost weight until they left in March. In the other winter, there was no evidence for a mid-winter peak in weights. Birds wintering at Clevedon had consistently lower weights in mid winter than birds wintering elsewhere in the study area. In the severe winter of 1978/79 birds attained the highest mid-winter peak weights of the study. Juveniles had higher estimated fat levels than adults at the beginning of the winter, but lower fat levels by the end of February. Studies on captive birds showed that with an unlimited food supply, weights increased to a peak in January, declining until March, before increasing rapidly prior to migration.

ACKNOWLEDGEMENTS

I would like to thank my parents, who indulged my interest in animals in the belief that I would grow out of it, not even complaining when my crocodiles frightened their guests away. John McMeeking introduced me to bird ringing and first took me to the Wash, where I was inspired by Clive Minton's enthusiasm for studying waders.

This study was only made possible by the many ringers who gave up their weekends and evenings to help catch Dunlin, whatever the weather. I would like to thank the Wash Wader Ringing Group for the loan of cannon netting equipment, and the many members who followed it to the Severn. Members of the Chew Valley Ringing Group spent most of their winter weekends catching Dunlin. I am especially grateful to Alan Ashman, Geoff Pudney and Bob Webber, who were never put off by the many cold, and often wet, occasions when they barely saw a bird - let alone caught any; without their support the study would have been much less successful. Graham Appleton, Peter Ferns, Christine Johnson and Phil Ireland's unrestricted cannon net licences were useful on some of the large catches. My best man, Graham Appleton, and his wife, Janet, helped on many catches on the Severn. Ironically, they followed me to Edinburgh where they continued to provide moral, and in Graham's case, mathematical support.

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CHAPTER 1

INTRODUCTION

1.1 General introduction

Wading birds, which occupy estuarine environments throughout the winter months, have become threatened either through environmental pollution or habitat loss, caused by drainage schemes, water storage schemes and tidal barrages. Virtually all the major estuaries in Britain have had some form of reclamation. This reclamation has been considerable in the Wadden Sea during the course of this century; large areas of the Netherlands Delta are at the moment in the process of being reclaimed. Some of these schemes have suddenly changed the available feeding area within an estuary by reclamation of large sections at a single time. On other estuaries (eg The Wash) the salt marshes have been reclaimed in small sections every few years and this has slowly reduced the feeding area as the mean low water mark has not changed substantially.

The growing realisation that the habitats which wading birds occupy in the non breeding season are threatened has stimulated a large number of studies. Some of these have been directly related to reclamation proposals (eg The Wash - Goss-Custard et al., 1977a,b; Morecambe Bay - Prater, 1972; Teesmouth - Evans et al., 1979, Davidson, 1980; The Dee - Buxton et al., 1977). Others have concerned the ecology of a single species (eg Oystercatcher Haematopus ostralegus - Norton-Griffiths, 1967, Heppleston, 1971, Hulscher, 1976, Goss-Custard et al., 1982,83; Redshank Tringa totanus - Goss-Custard, 1966,69,70a,b,76,77a,b; Dunlin Calidris alpina - Worrall, 1981; Sanderling Calidris alba - Myers et al., 1979, Myers, 1980, Brearey, 1981; Ringed Plover Charadrius hiaticula - Pienkowski, 1980; Grey Plover, Pluvialis squatarola - Pienkowski, 1980, Dugan, 1982; Curlew Numenius arquata - Townshend, 1981a,b; Bar-tailed Godwit Limosa lapponica - Smith, 1975; Turnstone Arenaria interpres - Harris, 1979, Brearey, 1981).

These studies fall into two groups:

i) those concerned with individual colour marked birds (eg Townshend, 1981a,b; Dugan, 1982) and

2) those concerned with the general ecology of a species rather than with individual variation within that species (eg Goss-Custard, 1966; Worrall, 1981);

A few studies have concentrated on differences in feeding ecology between the sexes (eg Smith, 1975; Puttick, 1981; Townshend, 1981b).

Many waders have been shown to undergo cyclical variations in weight levels through the year (eg Branson, 1979; Pienkowski et al., 1979) and several studies have been undertaken to assess the importance of fat and protein reserves during the winter and before migration (eg Evans & Smith, 1975; Prater, 1975; Davidson, 1981).

The advent of cannon netting in the early sixties brought about a tremendous increase in wader ringing. The analysis of the subsequent ringing recoveries has led to a better understanding of the migration routes and breeding areas of some species of waders which winter in western Europe (eg Grey Plover - Branson & Minton, 1976; Curlew - Bainbridge & Minton, 1978; Dunlin - Hardy & Minton, 1980; Knot - Dick et al., 1976; Turnstone - Branson et al., 1978,79; Sanderling - Clark et al., 1982; Purple Sandpiper - Calidris maritima - Atkinson et al., 1981).

Information on breeding grounds has also been obtained from the study of museum specimens (Redshank - Hale, 1971,73; Ringed Plover - Taylor, 1978; Dunlin - Greenwood, 1979).

Further information about breeding areas and migration routes has been gained from expeditions to areas where little ringing had previously been carried out (Greenland - Green & Greenwood, 1978; Iceland - Morrison, 1971; Norway - Lessells & Leslie, 1974; Morocco - Pienkowski, 1972; Mauritania - Dick, 1976).

Attention has recently been focused on wader movements within the winter both within a single estuary (Pienkowski & Clark, 1979) and between estuaries (eg Dugan, 1981b; Pienkowski & Pienkowski, 1983).

It was against this background of previous ecological research that the present study on the wintering ecology of Dunlin of the Severn Estuary was undertaken.

1.2 The study area

The main study area was between Clevedon (Avon) and Burnham-on-Sea (Somerset) on the south shore of the Severn Estuary, England (figures 1.1 and 1.2); additional information was gathered from Severn Beach (to the north) and from Bridgwater Bay National Nature Reserve (to the south of the study area).

The Severn Estuary has been defined as extending from Upton-on-Severn to Steep Holm (NERC, 1972) a distance of 150 km. It drains nearly one sixth of the land area of England and Wales. Its funnel shape amplifies the tidal range to 12.3 m at Avonmouth giving it the third highest tidal range in the world. As a consequence of the large water movements the water in the Severn is very turbid, limiting the invertebrate fauna of the intertidal areas. There are

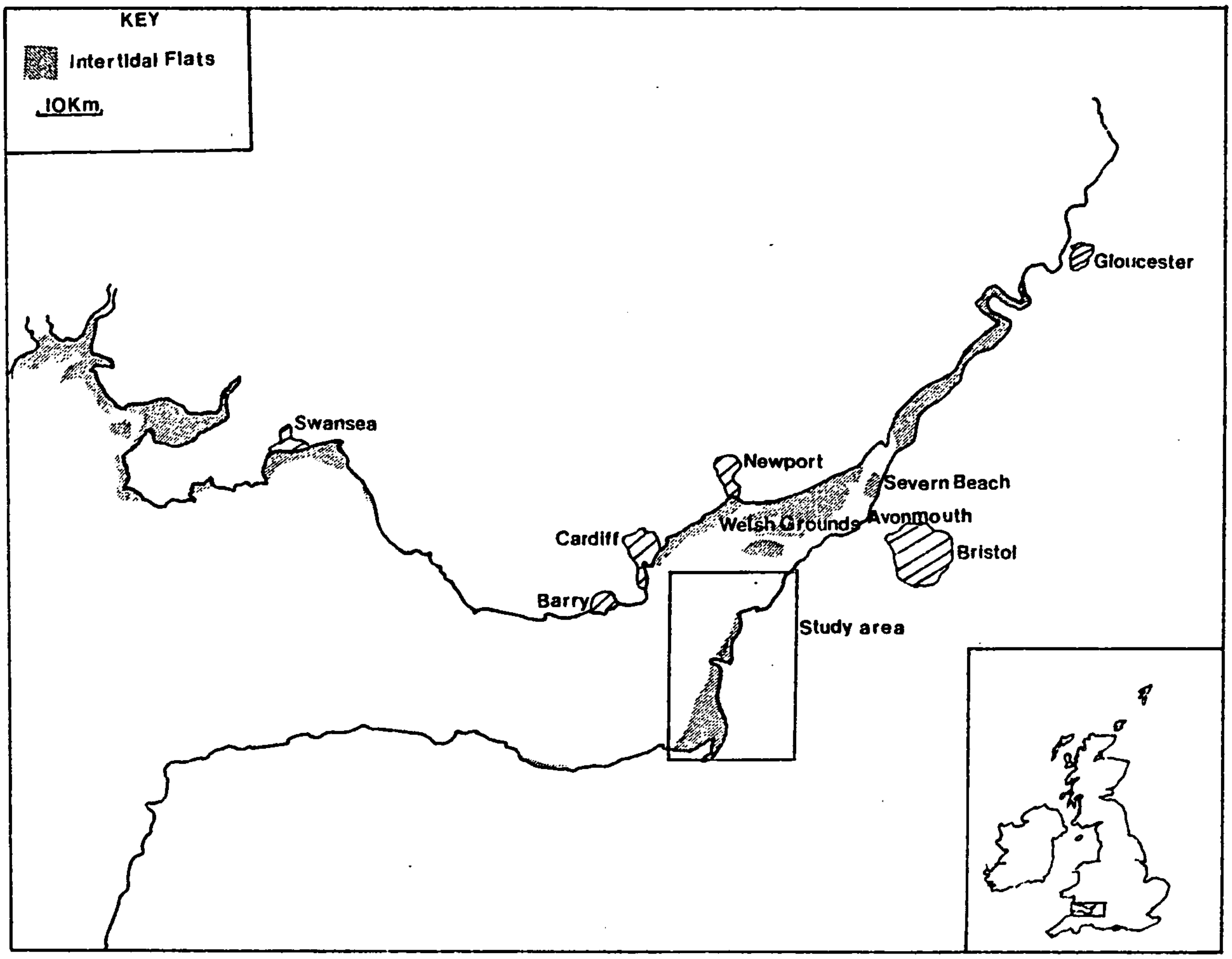


FIGURE 1.1

The Severn Estuary showing the position of the study area

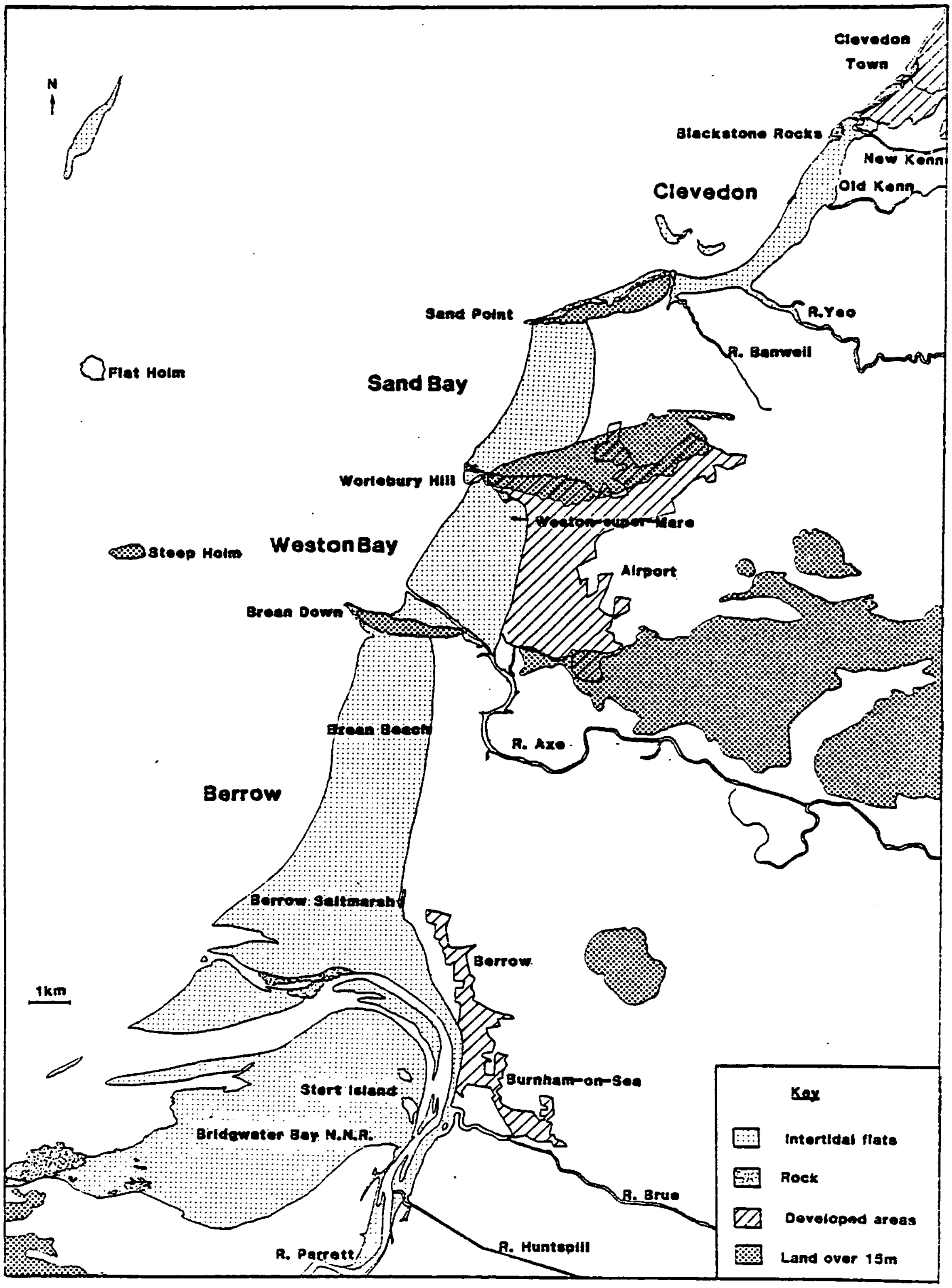


FIGURE 1.2

The study area

also large unstable sand banks in the centre of the estuary which are largely devoid of invertebrate fauna.

There are, on average, 63,000 waders wintering on the Severn (Ferns, 1983); 70 percent of these (43,500) are Dunlin and on the south shore of the Severn an even higher proportion of the wintering waders are Dunlin. This made the area ideal for a study of Dunlin which involved catching large numbers as very few birds of other species were caught incidentally.

The main study area consisted of four bays (Clevedon, Sand Bay, Weston Bay and Berrow) bounded by the rock outcrops of Sand Point, Worlebury Hill and Brean Down.

1.2.1 Clevedon

This bay is in fact the intertidal area between Clevedon town and Sand Point. Three rivers drain into this bay: the Kenn, the Congresbury Yeo and the Bradwell. By far the largest of these is the Congresbury Yeo. The substrate near the extreme low tide mark is liquid mud, there is then a relatively steep area of firm clay and on the higher levels this is covered by mud with frequent runnels. Above the neap high tide mark there is an area of *Spartina anglica* (C. E. Hubbard) and in places there is a narrow band of short grazed saltmarsh just in front of the sea wall.

At low tide Dunlin tended to feed in one or two large flocks and these flocks regularly moved up and down the bay, although they spent most of their time feeding on the areas of runnelled mud. As the rising tide covered the feeding area, the Dunlin formed pre roosts at the mouth of the Yeo, the mouth of the old Kenn and on

Blackstone Rocks. They sometimes remained on Blackstone Rocks on neap tides. On spring tides they often roosted on the saltmarsh just north of Blackstone Rocks, but if this area was covered they would sometimes (especially around dawn) fly throughout the high tide period two or three kilometres out into the estuary; on other occasions they would roost on the fields just behind the sea wall. If there was a lot of disturbance they would sometimes fly two or three kilometres inland, presumably roosting on Kenn Moor, and on other occasions they would move south and occasionally roosted in the Yeo estuary.

1.2.2 Sand Bay

As at Clevedon, there is liquid mud at the lowest reaches; above this there is a large area of runnelled mud and the top 400 m consists of sand. At the north end of the bay there is an area of *Spartina* marsh.

At low tide the majority of the Dunlin fed on the runnelled mud, although there was normally a small flock (less than 500) on the sand. When the birds feeding on the runnelled mud were forced off by the rising tide, they formed a pre roost on the sand before moving to the saltmarsh to roost. On high spring tides they would occasionally remain at the north end of the bay, being forced onto a small sand beach behind the saltmarsh. There was a lot of disturbance in this bay, mainly from people exercising their dogs; this meant that the birds often left the bay completely at high tide, sometimes moving to the Yeo (four kilometres away) or flying south over Worlebury Hill and roosting on Weston airport (three and a half kilometres south of the bay). On other occasions they would join the Weston Bay roost, returning on the falling tide.

1.2.3 Weston Bay

The river Axe drains into the south end of Weston Bay. The predominant substrate in this bay is liquid mud, only the higher levels being sand. There is a small area of runnelled mud just north of Black Rock.

At low tide the birds nearly always fed on the liquid mud, and mainly at the south end of the bay. When this area was covered on the rising tide, the birds normally moved to a pre roost on the edge of the saltmarsh just south of Brean Down before moving to the shingle beach behind or to Black Rock. These sites were often used by fishermen at high tide and then the birds would move up the Axe and roost on its banks or move to Weston airport.

1.2.4 Berrow

This bay consists of the area from Brean Down in the north to the river Parrett in the south. Like Weston Bay the major substrate is liquid mud, although there is a very small area of runnelled mud just south of Brean Down. The upper beach consists of sand forming sand dunes behind the high tide mark. There is a small saltmarsh in front of the sand dunes just north of Berrow village.

At low tide the birds normally split into four or five flocks. On neap tides these birds would gather into two flocks to roost, one on Brean Beach about two kilometres south of Brean Down and the other at the small Berrow saltmarsh. If the birds on Brean Beach were disturbed, some would go down to the Berrow saltmarsh, while others would go to the Weston Bay roost. On spring tides the situation was rather different. As the tide rose the majority of birds would move south, normally forming a pre roost off the Berrow saltmarsh, but often they would move straight across the Parrett to roost in Bridgwater Bay. The few birds that remained at the north end of the Berrow flats would move across to Weston Bay as soon as the liquid mud was covered.

1.3 Catching methods

Catching operations were undertaken in the four winters between autumn 1977 and spring 1981. Two methods were used: mist netting and cannon netting.

1.3.1 Mist netting

In the autumn of 1977 mist netting was started using wader nets with a one and a half inch mesh size and thick braided shelf strings. These nets caught very few birds, probably because it never gets very dark on the Severn due to the lights from all the nearby towns. In 1978 I changed to using Gundry superfine mist nets which had thicker than normal shelf strings; this was possible only because I rarely caught large waders on the mist netting sites. These nets proved much more effective than the wader nets previously used. Some forty foot mist nets were made later that winter out of standard Gundry mesh and thick twisted shelf strings; it was easier to extract birds from these nets; this allowed me to put up more mist nets on my own, but there was a slight reduction in the number of birds caught per net. The nets used were again changed in January 1980 when some very fine two inch mesh material became available. These were spectacularly more successful than any nets used previously; however, it was much more difficult to extract birds from them and whenever Curlew were caught, they made large holes. These nets are therefore not be suitable for sites where many large waders were present. A tape lure with the calls of a mixed flock of roosting waders proved effective on sites where the nets were set over small pools; but they had a very much stronger attraction for Redshank (Tringa totanus) than Dunlin and so were used only when it was necessary to increase the size of the catch.

Clevedon was the only site which had an obvious place to mist net: some pools on a high saltmarsh where the birds came regularly on night time spring tides but where they were never seen in the daytime. On the lower tides it was possible to mist net near Blackstone Rocks. In Sand Bay there were large numbers of birds present at night, except on high spring tides. It was only from the late autumn of 1979 that it was possible to catch successfully. In the daytime the birds moved into the saltmarsh from the south to the north but at night on the rising tide they moved to the outer portion of the saltmarsh and then eastward as the tide came in; there was a tenfold increase in the number of birds caught when the direction of the nets was changed to take account of this. The Weston Bay saltmarsh had large numbers of birds on it at night but they were always very spread out and never more than a dozen birds were caught even when as many as twenty nets were used. In spring

1980 some pools on the narrow saltmarsh at the side of the Axe were found and these proved moderately successful, but this was the only site where Dunlin made up less than fifty percent of the total catch. Many attempts at mist netting birds at Berrow were made, but I obtained a catch of more than 30 birds on only one occasion: 120 birds were caught in February 1981 by placing nets along the outer sand ridge in a north-west - south-east direction instead of over the small pools that the birds were coming on to at high tide.

During the course of the study it became apparent that it would be valuable to catch a sample of birds on Bridgwater Bay National Nature Reserve. Although over 2,000 man hours were spent trying to catch only 23 birds were trapped; unfortunately the study came to an end before we could finally work out how to mist net or cannon net birds on this site.

1.3.2 Cannon netting

Cannon netting operations started in February 1978 when a team from the Wash Wader Ringing Group came to Somerset to try to find out whether Dunlin ringed on the Wash in autumn moved to the Severn in winter. The weekend was spectacularly successful with a catch of over 1,000 birds in Weston Bay; a month later another team caught a further 250 birds at Clevedon. During the the next three years cannon netting operations were undertaken frequently throughout the winter, but it was often only possible to assemble a small team of people. For this reason special methods were devised to catch birds as efficiently and safely as possible. On many occasions a half size cannon net (13 yards x 13 yards) with two cannons was used;

this made it easy for a team of five or six people to move a net. There were major problems in cannon netting at most sites as the beaches are flat and with the enormous tidal range of the Severn it is very difficult to predict where the tide will come. To combat this problem a large stretcher was made that enabled the small cannon net to be moved easily (Clark, 1982b - Appendix 1). This also had the advantage that it was possible to move the net and catch on the falling tide on sites where birds would not land on the rising tide but would on the falling tide. It seemed that under these conditions they were not put off by a cannon net on a stretcher (even though it was very obvious).

In the summer of 1979 the university obtained material for one and a half cannon nets. Before making these nets, the positioning of the ropes was redesigned (Appendix 2) and these nets proved much more effective than the nets which had been loaned by the Wash Wader Ringing Group for the first year of the study. It was also possible to adjust the length of the jump ropes from one metre to four metres, which meant that the effective catching area in front of the net was increased from nine metres to 12 metres. One final refinement to the equipment was made in 1980: the weight of two projectiles was increased from 3.6 kilos to 6.8 kilos. These projectiles were placed in the two central positions on the large net with the effect that the whole front edge of the net went the same distance, as opposed to the previous situation, in which the corners went out further than the centre.

As the team was often small it was not possible to have a large number of people just moving birds after extraction from the net to the keeping cages; to solve this problem keeping boxes were made.

These were plastic five gallon water containers with a hole cut in the side (to put the birds through), the hole then being covered with a rubber flap; a large number of small ventilation holes were then drilled in the side. Although the boxes proved excellent to keep birds in for a short time the birds feathers tended to get damp due to condensation if they were left in them for long; the boxes were therefore used only for holding birds temporarily.

Attempts were made to cannon net birds at all the major roost sites with the exception of Black Rock in Weston Bay. Only at Clevedon did birds go onto fields; on all the other sites birds had to be caught on the tide edge. There were very few sites where there were well defined roost points; so decoys were nearly always used. By far the most effective decoys proved to be a small mixed flock in a non alert posture; one or two Lapwing Vanellus vanellus, about five Redshank and a couple of Dunlin. Appendix 3 describes the method used for making decoys.

1.4 The weather during the study period

Figures 1.3 to 1.6 give mean daily wind speed (in knots) and mean daily temperature (in degrees Centigrade) and also note air frosts for Rhoose airport on the north shore of the Severn in the four winters of the study.

In the 1977/78 winter catching started in late winter and coincided with a short spell of severe weather during which wind speeds were near average.

The 1978/79 winter was the severest since 1962/63. There were spells of severe weather both in January and February, the period in

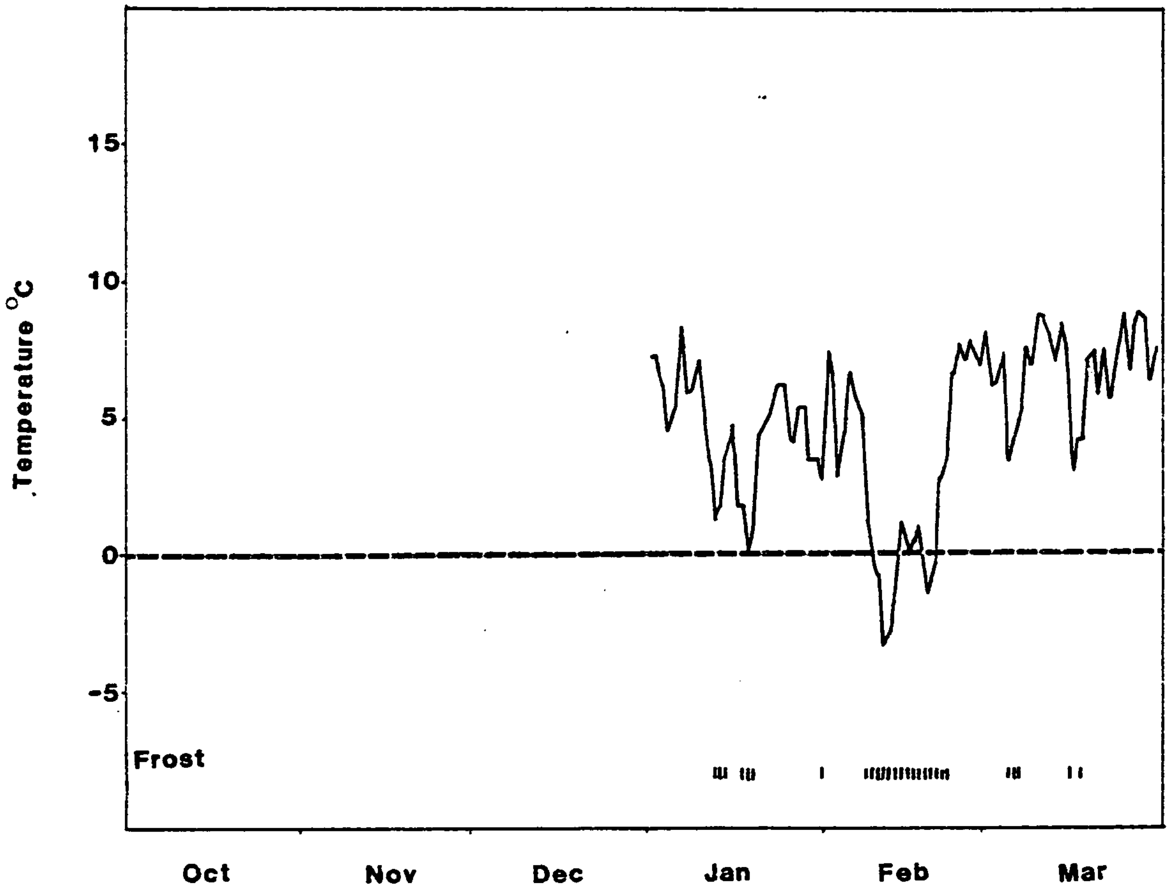


FIGURE 1.3a

Mean daily temperature at Rhoose airport (Cardiff) in late winter 1978

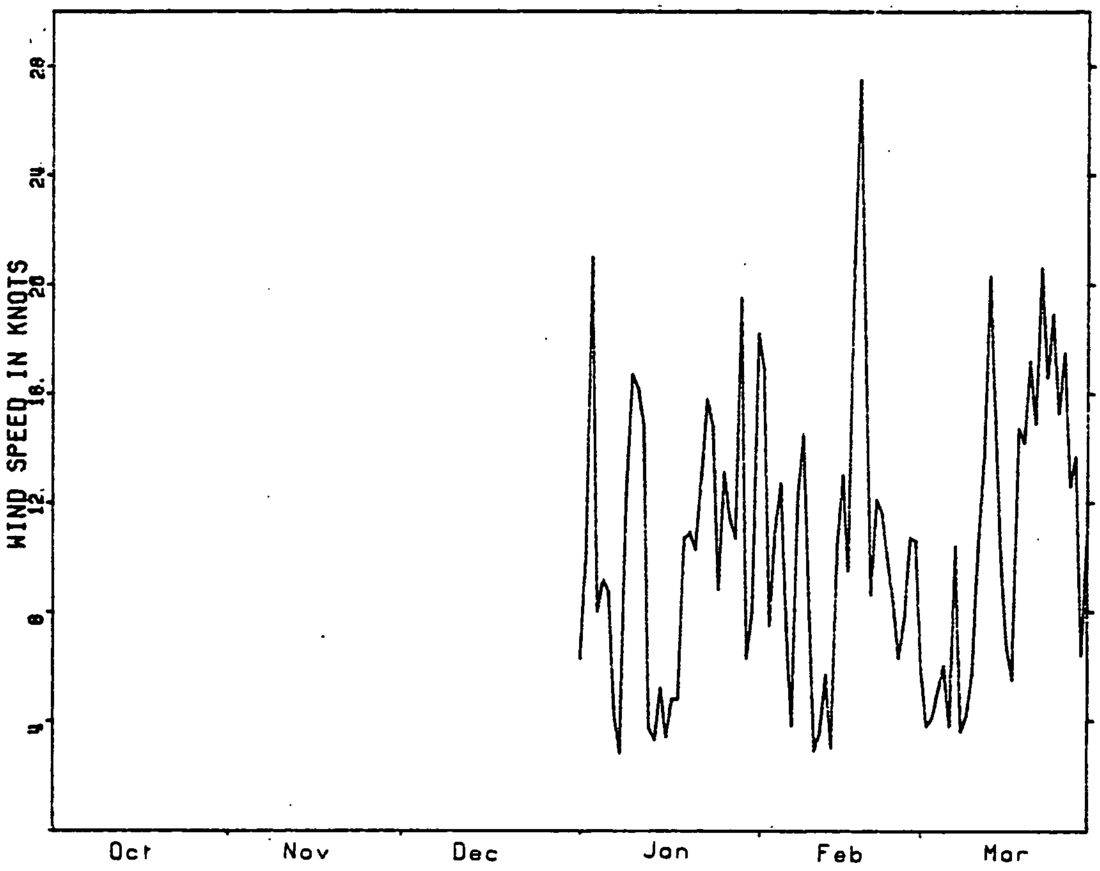


FIGURE 1.3b

Mean daily wind speed at Rhoose airport (Cardiff) in late winter 1978

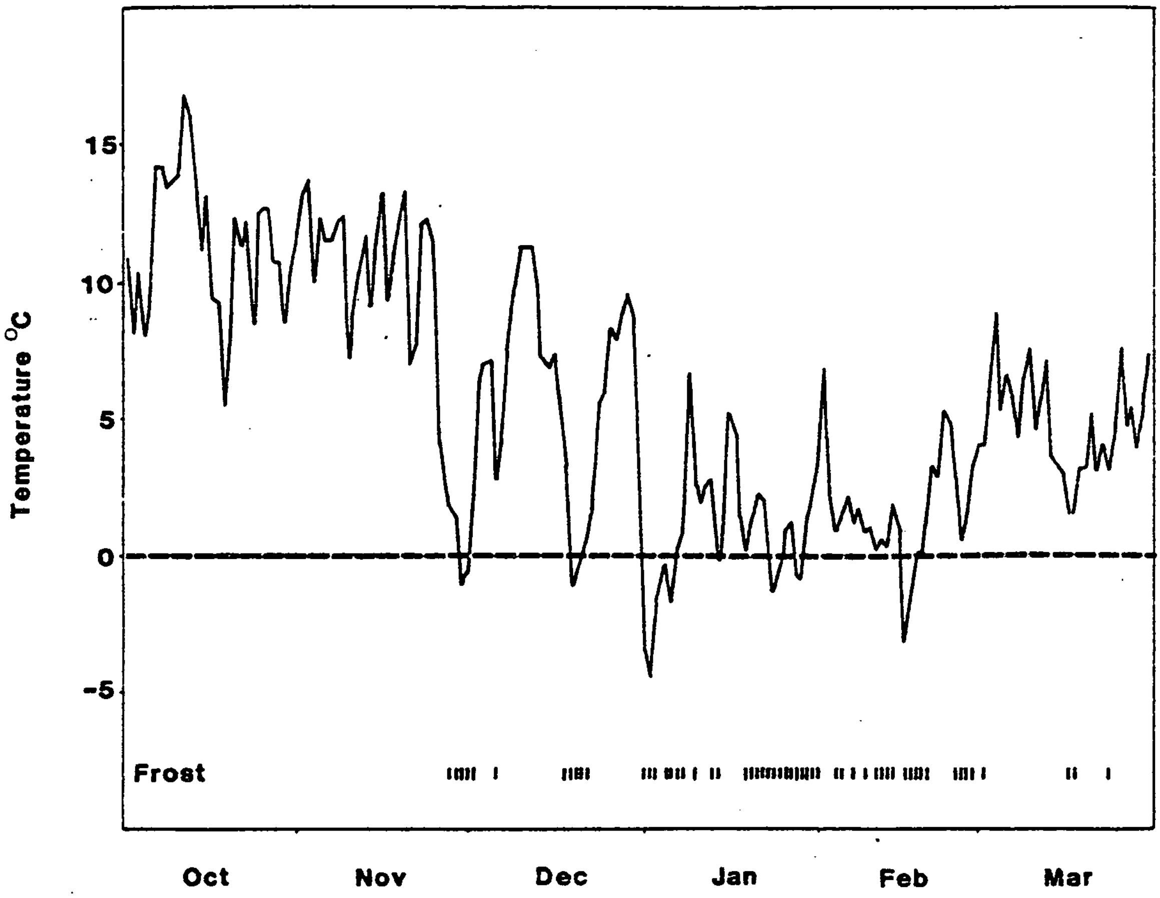


FIGURE 1.4a

Mean daily temperature at Rhoose airport (Cardiff) in winter 1978/79

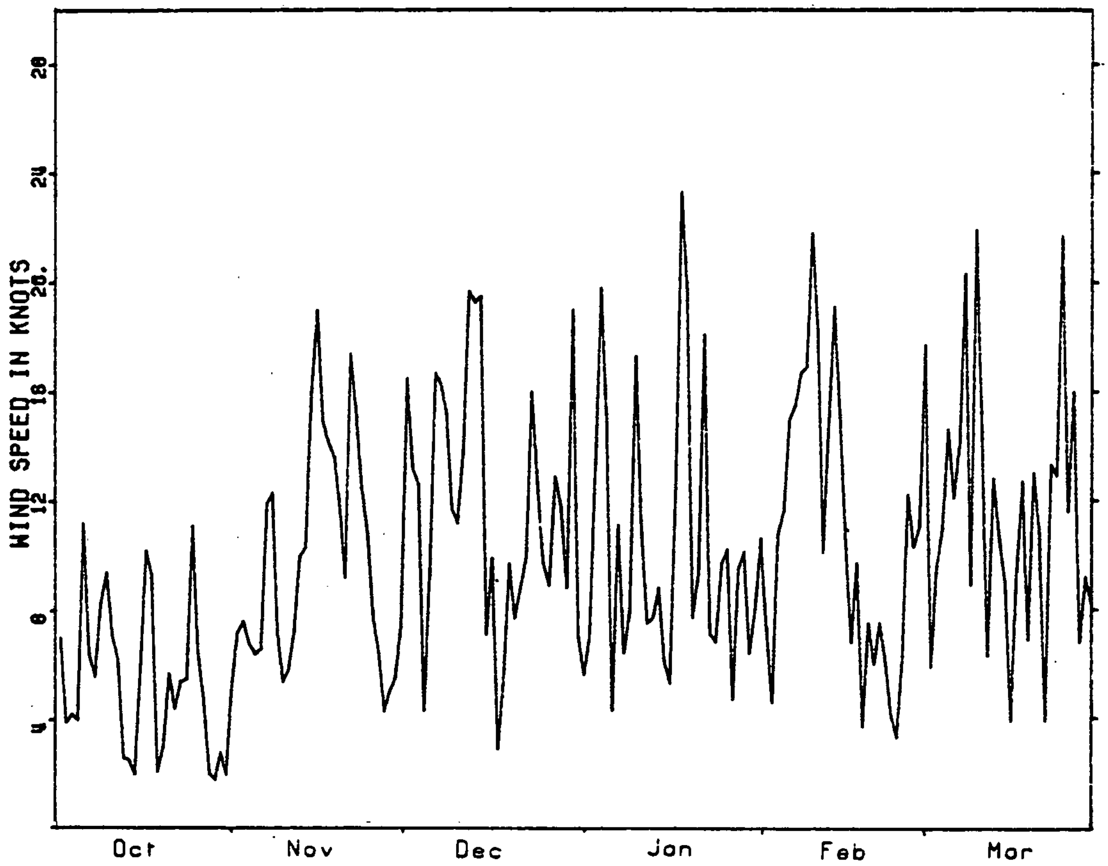


FIGURE 1.4b

Mean daily wind speed at Rhoose airport (Cardiff) in winter 1978/79

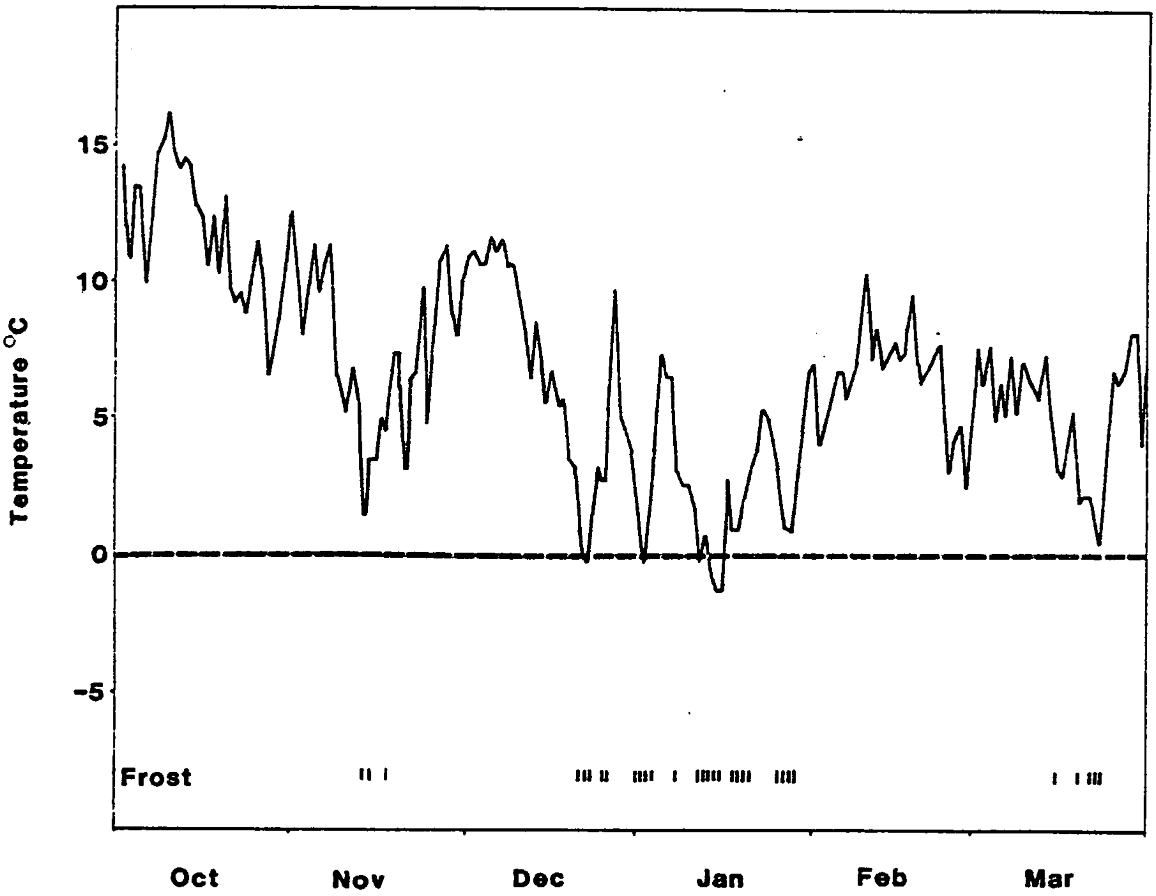


FIGURE 1.5a

Mean daily temperature at Rhoose airport (Cardiff) in winter 1979/80

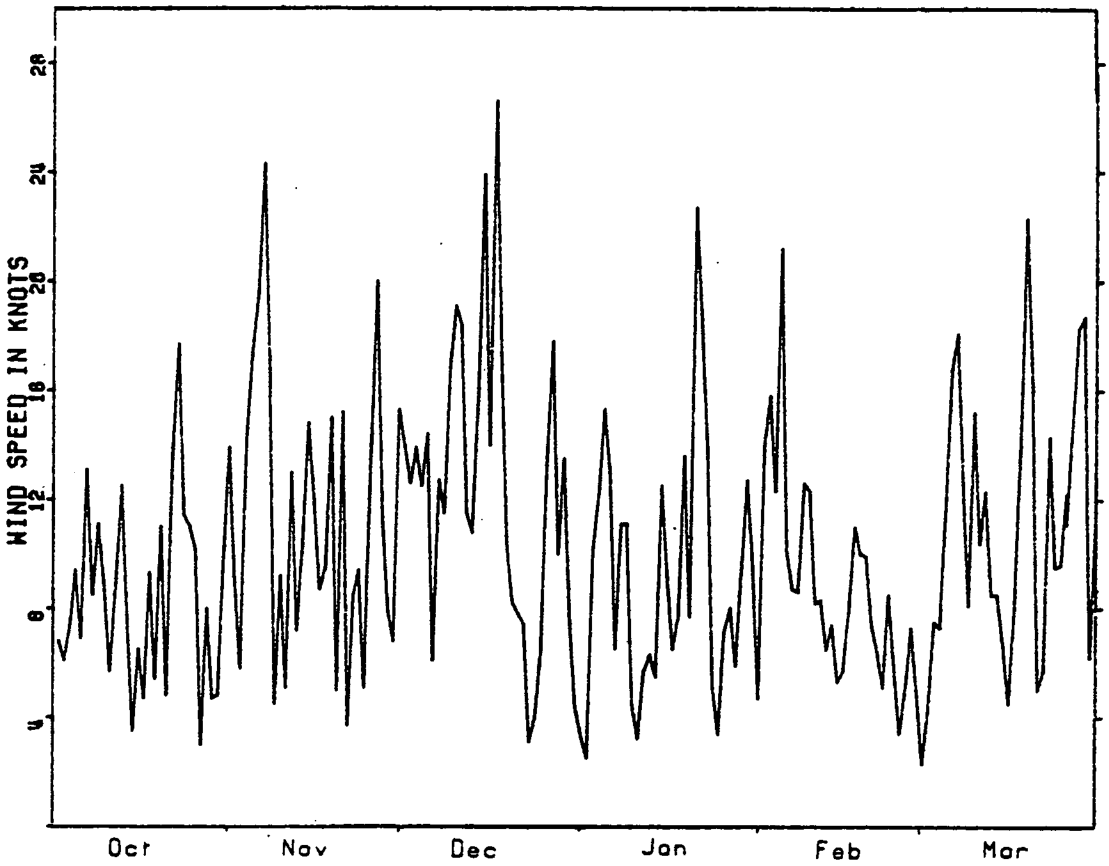


FIGURE 1.5b

Mean daily wind speed at Rhoose airport (Cardiff) in winter 1979/80

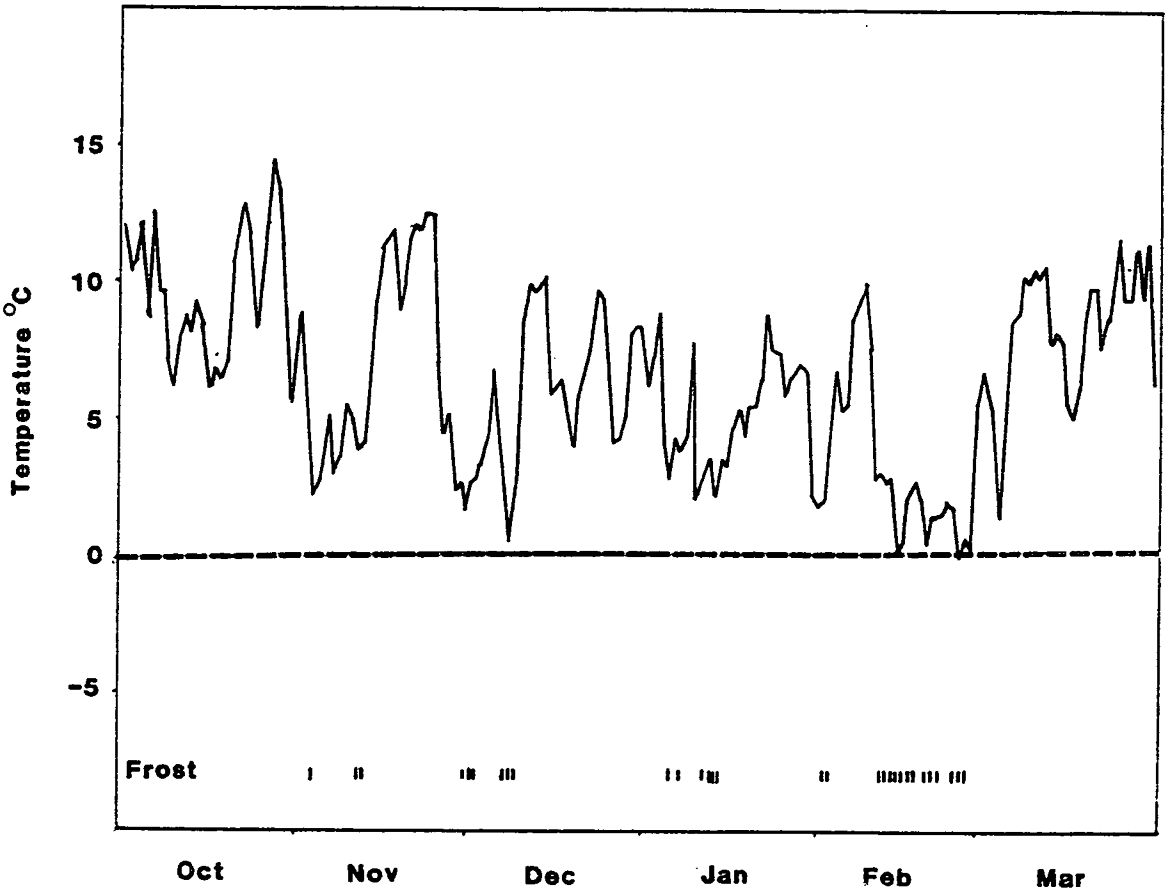


FIGURE 1.6a

Mean daily temperature at Rhoose airport (Cardiff) in winter 1980/81

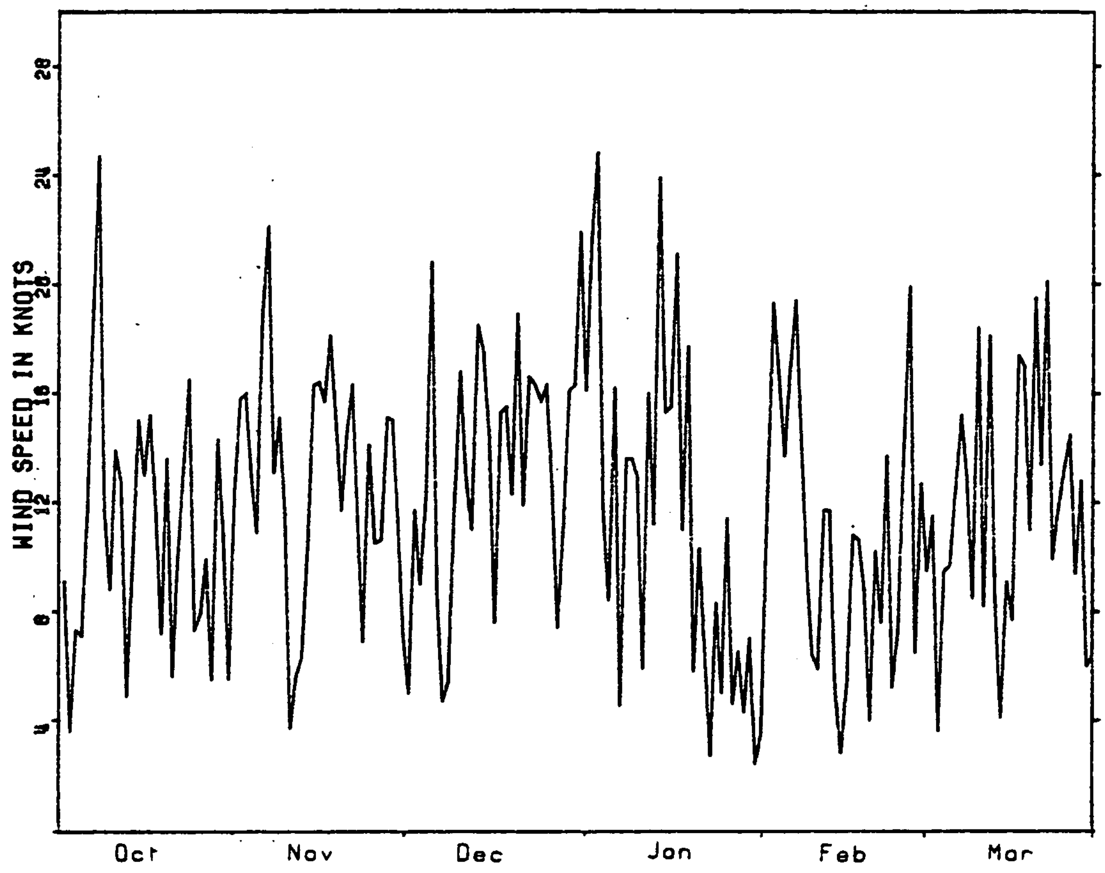


FIGURE 1.6b

Mean daily wind speed at Rhoose airport (Cardiff) in winter 1980/81

February coinciding with a period of high winds.

The 1979/80 winter was mild, although there was a period of high winds in early December. These were mainly north westerly and caused considerable sediment erosion (Ferns, 1983; Chapter 5).

The 1980/81 winter was exceptionally mild, the only period of cold weather being in mid February, but this coincided with a period of low wind speeds.

The study, therefore, covered a variety of winter weather conditions and the effects of this on the birds and their prey will be discussed later.

CHAPTER 2

STUDIES ON THE PREY AVAILABLE TO DUNLIN

2.1 Introduction

There have been several studies on the marine invertebrates of the intertidal area of the Severn Estuary. Bassindale (1942, 1943) undertook studies on the fauna of the rocky shore promontories of the Bristol Channel and showed that the most important factors affecting the distribution of estuarine rocky shore invertebrates are salinity, current velocity and turbidity. Faunal distributions in soft sediments within the Severn have been studied by Rees (1940), Haderlie and Clark (1959), Boyden and Little (1973) and Withers (1977). Withers (1977) examined the sand dwelling macrofauna on the north shore of the Bristol Channel between Swansea Bay and Milford Haven. Boyden and Little (1973) studied the distribution of invertebrates at seventeen sites on the southern shore of the Severn, including four of the five sites investigated in the present study. Their work was undertaken during the summer months and does not necessarily reflect the prey available to Dunlin in the winter. Subsequently Little and Boyden (1976) turned their attention to seasonal variations in invertebrate numbers at four sites on the south shore of the Severn, including Weston Bay which was also covered in the present study. They sampled in July/August and February/March, thus providing valuable baseline information on the prey available to wading birds on the south shore of the Severn.

More detailed studies of the seasonal population changes of _Nereis diversicolor_ (O. F. Muller) on the north shore of the Severn have been undertaken by Mettam (1979) and Worrall (1981). In the light of these previous studies, information on total invertebrate numbers (or biomass) within each of the bays would not have added very much information to the present study. A sampling programme was devised to assess which prey were available to Dunlin at the beginning, middle and end of the 1979/80 winter.

As well as obtaining an understanding of which prey were available to Dunlin on different sites it was considered important to obtain more information as to how the highly mobile prey species were affected by different environmental conditions. Previous work by Goss-Custard (1969) has shown that *Corophium volutator* (Pallas) appear less frequently at the surface as the mud temperature decreases. Holmstrom and Morgan (1979) have demonstrated an inherent tidal activity rhythm in *Corophium*. Vader (1964) showed that *Nereis* taken into the laboratory from a tidal environment also showed an inherent tidal activity rhythm; however individuals obtained from a non-tidal saline pond did not show any such rhythm. He also found no inherent tidal rhythm in the gastropod mollusc *Hydrobia ulvae* (Pennant) but he was able to demonstrate that in the Dutch Wadden Sea the animals were active on the surface when the mudflat was submerged and burrowed when it became exposed. Little and Nix (1976) found no evidence for rhythmic behaviour patterns in *Hydrobia*. More recently Dugan (1981a) showed that many species of invertebrates are more active on the surface at night than in the daytime. The aim of my behavioural study of *Nereis* was to ascertain the importance of temperature in influencing their vertical height distribution within the substrate and thus their availability to Dunlin.

2.2 Study sites

To determine general food availability transects were taken in each bay on the study site. In each case the transect was as near as possible to the middle of the bay. (For exact locations see table 2.1). The study site for the temperature/depth sampling programme was on an area of flat mud at the neap high tide mark (9.5 - 9.8m above Newlyn Datum) at Clevedon (grid ref. 385 696). Care was taken not to sample in exactly the same place on successive sampling days as footprints remained obvious for several weeks or even months.

2.3 Prey availability in different bays

2.3.1 Methods

Samples were taken on all transects in October 1979, January 1980 and March 1980. Stations were established at regular intervals down the shore (as shown in fig 2.1) although it was difficult to be precise. The stations were marked by posts in October, and in December and April samples were taken within ten metres of the posts. Unfortunately some posts were washed away, this became apparent only when samples were being taken and it was not possible to re-establish the stations accurately. The lowest stations on the shore could not always be reached due to the presence of large amounts of liquid mud or very soft sand. In April the highest station at Severn Beach had extremely hard packed mud which was impossible to sieve; a careful search over a large area showed no *Nereis* to be present but information could not be obtained on other

TABLE 2.1

Grid references of transects used for mud sampling

Severn Beach	ST 538 843	ST 527 844
Clevedon	ST 385 694	ST 380 696
Sand Bay	ST 332 646	ST 313 646
Weston Bay	ST 314 594	ST 308 595
Brean Beach	ST 296 562	ST 286 563

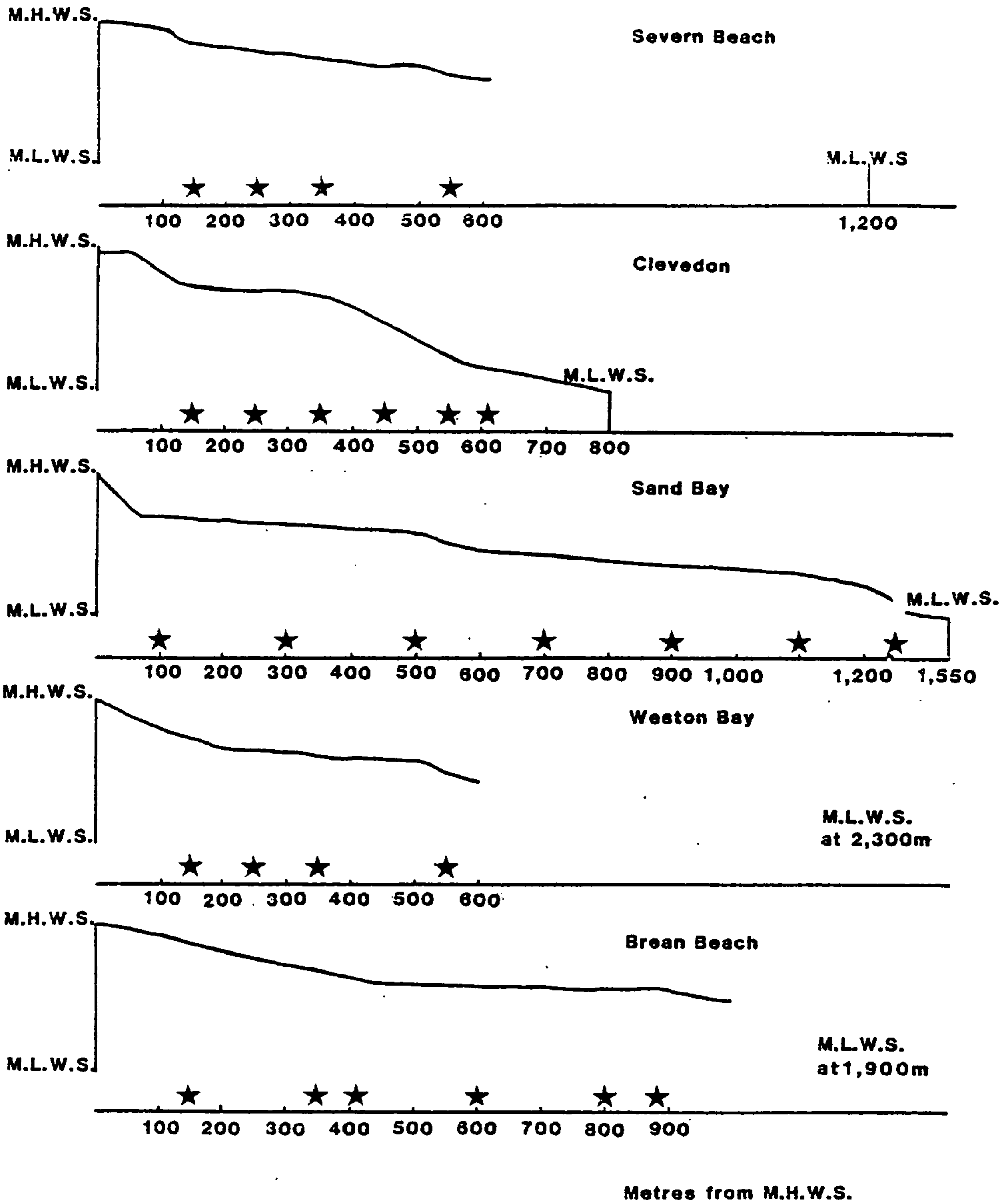


FIGURE 2.1

Beach profiles along transects

species.

At each station down the shore four samples were taken. Mud samples were obtained only under stable weather conditions, with temperatures above five degrees Celsius (except in January at Sand Bay and Weston Bay) and when no rain had fallen since the last high tide. Mud temperatures (to the nearest 0.5 degrees Celsius) were taken at the highest station on the shore at 20 mm depth and are given in table 2.2.

All samples were taken using a sledge sampler (figs 2.2 and 2.3). The sampler consists of a 450 mm square "sledge" made out of thin steel. At the front of the sledge is a 60 mm high baffle angled at 45 degrees, on the other three sides there is a 20 mm high lip. In the centre there is a 150 mm square hole through which a stainless steel shovel protrudes to a given depth. The shovel can be moved to give different sample depths, but for this study the shovel was set at 42 mm. 100 mm above the sledge a rigid tube is fixed transversely at a 10 degrees angle to the horizontal. The sledge is attached to two bamboo poles as shown in figure 2.2b. The upright pole is held as high up as possible and pulled towards the operator to lift the sledge off the mud. The cross pole is then swung round 90 degrees to bring the sledge over undisturbed mud where the sledge is allowed to fall onto the surface, its forward motion forcing a "strip" of mud into the shovel. There is no back to the shovel so any excess mud falls off. A 150 x 150 mm sample at the front of the shovel is then delineated and any excess mud removed. A polythene bag is attached to the back of the shovel and the sample slid in to it. On most muddy substrates this is easily achieved, but on some substrates the mud in the sledge tends to

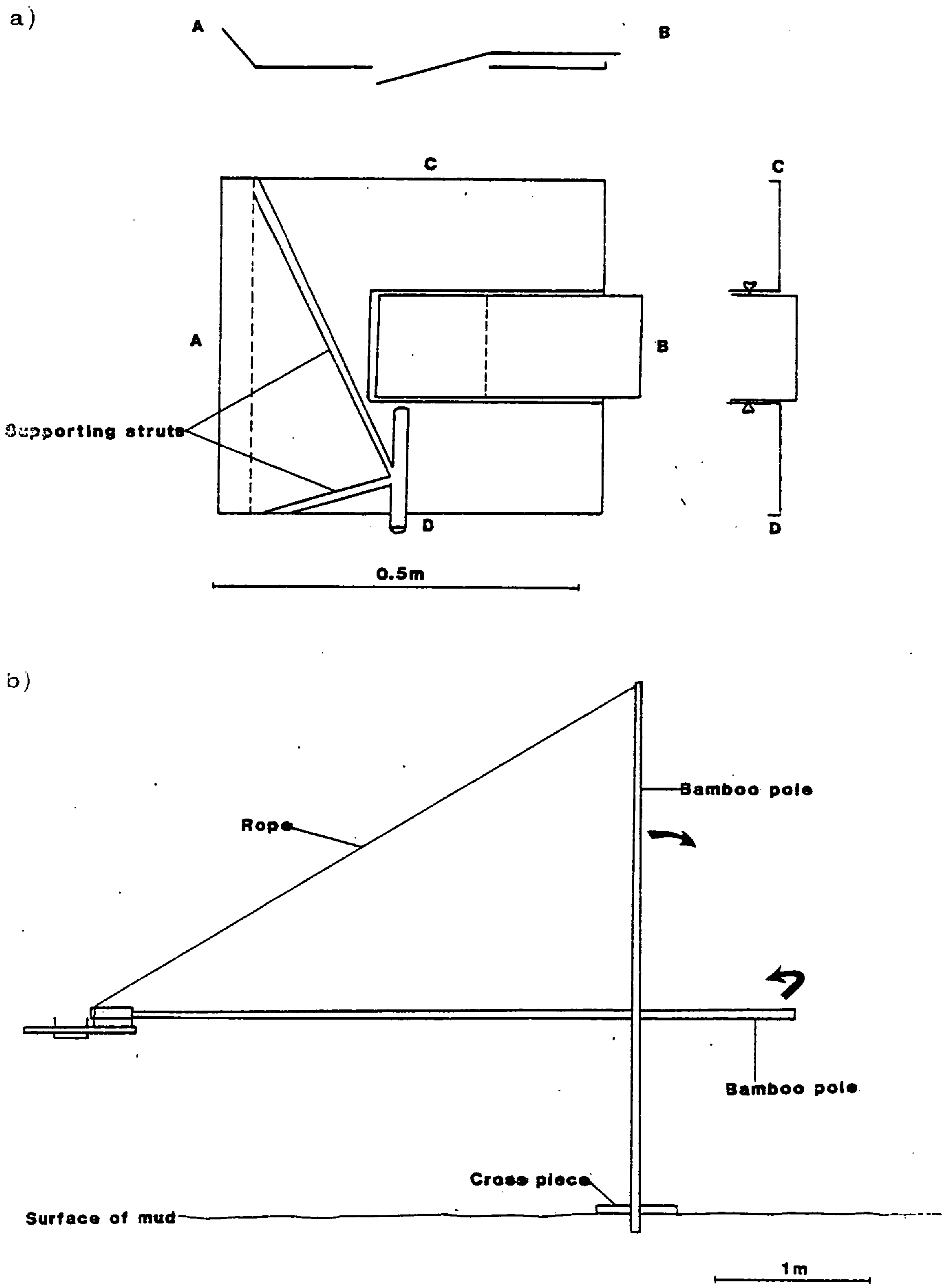


FIGURE 2.2

a) Diagram of sledge, b) diagram of sledge sampler

FIGURE 2.3a

The sledge sampler in operation

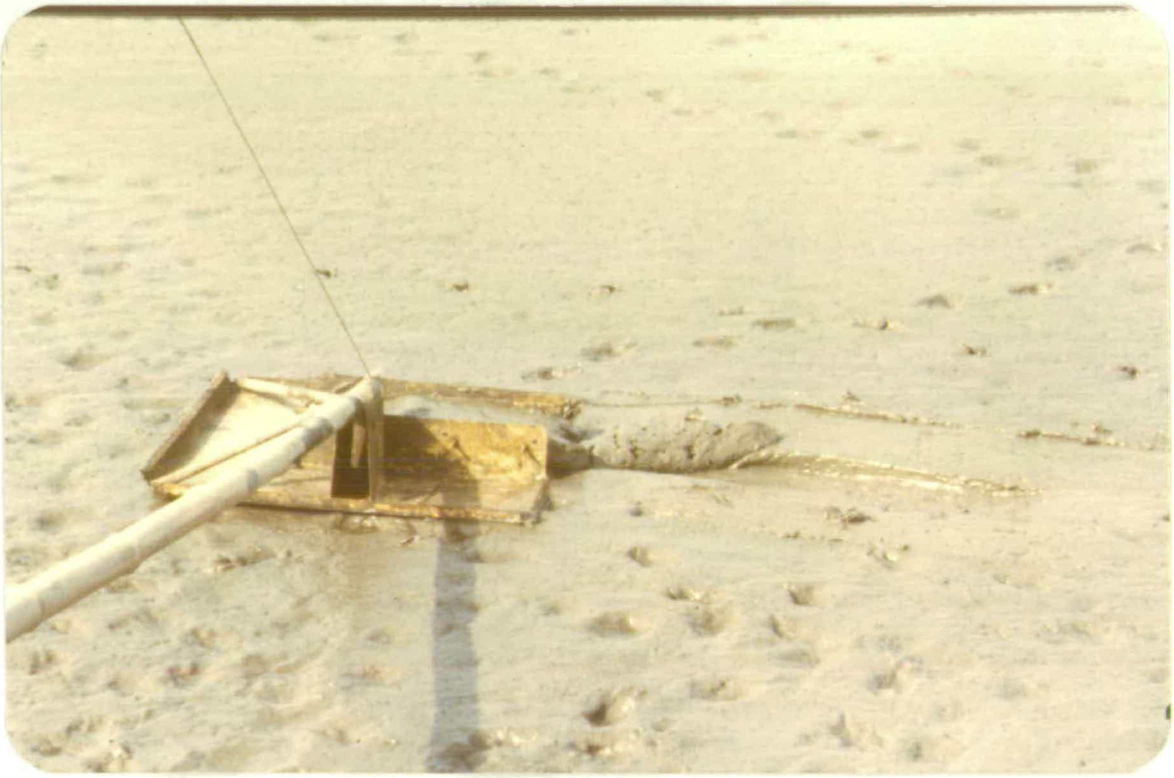


FIGURE 2.3b

The sledge with a skim

FIGURE 2.3c

The mud after the skim has been removed; note the Nereis burrows

TABLE 2.2

Mud temperatures in degrees Celsius on each sampling day

Bay	October 1979	January 1980	April 1980
Severn Beach	8.0	9.0	12.0
Clevedon	9.0	8.5	13.0
Sand Bay	12.0	3.5	11.0
Weston Bay	8.0	2.0	9.5
Brean Beach	7.0	5.0	9.0

"concertina" making it difficult to judge a 150 x 150 mm square. On substrates which were totally sand it was impossible to use the sampler as the friction between sledge and sand was too great. On these sites the sledge was taken off the poles and a sample was taken by placing the sledge on the surface and pushing it by hand across the surface as quickly as possible. A small plastic tube containing an individually numbered label was placed in each sample and sample numbers were recorded on a tape recorder which was operated from a remote microphone covered in polythene.

The samples were taken starting at the top of the transect three hours after high tide, so that the samples near the low tide point were obtained near low water; this meant that it was normally possible to leave the shore by two hours after low tide which is very important for safety on flat beaches and where soft mud occurs (McGrorty, 1973). A smoke canister and two flares were carried on the first sampling day at any site, and always on sites where soft mud occurred.

The samples were stored in a cool place and sieved within two days. Before sieving all samples were weighed. The sieving procedure for muddy substrates was as follows: the weighed sample was placed in a bucket of cold fresh water and agitated carefully by hand until the mud was in suspension; the liquid mud was then poured through a 0.5 mm sieve, this procedure often taking twenty minutes per sample. Samples from sandy substrates were placed in the sieve and shaken with the bottom of the sieve approximately 25 mm below water level. As the sand was agitated it liquefied and easily passed through the sieve. The organisms were then washed into a labelled sample bottle and relaxed in a 50 percent solution of magnesium chloride before being preserved in formalin.

All specimens were assigned to size categories using a binocular microscope with an eyepiece graticule measuring to the nearest 0.2 mm. Table 2.3 gives the measurements for different size classes for each species. Nereid worms were classed by body width at the third pair of legs as many worms were cut in two by the sampler and this proved a quick and easy method of assigning individuals to size classes. Any part of a worm without a head was not measured as it may have been broken during extraction.

2.3.2 Results and Discussion

Figures 2.4 to 2.8 give information on invertebrate densities (per square metre) found in each bay, for each species which occurred at a high enough density to be significant as a food source for Dunlin. For each site the ranges are given and a line is plotted through the median. The surface substrates occurring at each station at each sampling time are indicated.

Several other species of invertebrate were recorded. The most abundant of these were small Nemertines which were present at Severn Beach (all stations, density up to 5,000 per square metre), Clevedon (all stations, density up to 10,000 per square metre) and in Sand Bay (700 m from M.H.W.S. at very low density and 1,200 m from M.H.W.S. at a density of 70,000 per square metre). Nephtys caeca (O. F. Muller) was present at Clevedon in the soft mud below 550 m from M.H.W.S. in October at densities up to 750 per square metre, but was not found later in the winter; a few individuals were also found in Sand Bay. Small numbers of Dipteran larvae were found wherever firm

TABLE 2.3

Measurements (in millimetres) used in assigning individuals to size classes

Species (dimension used)	Small	Medium	Large
Macoma balthica (max. shell length)	<5.0	5.0<10.0	>10.0
Retusa obtusa (max. shell length)	<2.0	2.0< 4.0	> 4.0
Hydrobia ulvae (max. shell length)	<2.0	2.0< 3.0	> 3.0
Nereis diversicolor (width at third pair of legs)	<0.8	0.8< 1.4	> 1.4
Nepthys hombergi (width at third pair of legs)	<0.8	0.8< 1.6	> 1.6
Corophium spp (total body length)	<2.0	2.0< 4.0	> 4.0
Bathyporeia pilosa (total body length)	<2.0	2.0< 4.0	> 4.0

Key for figures 2.4 to 2.8

☆	Not sampled
M	Mud
C	Clay
L	Liquid mud
S	Sand
L/C	Thin layer of liquid mud over clay
L/M	Thin layer of liquid mud over mud
S/M	Multiple thin layers of sand and mud

At each site the range is given and a line is plotted through the median

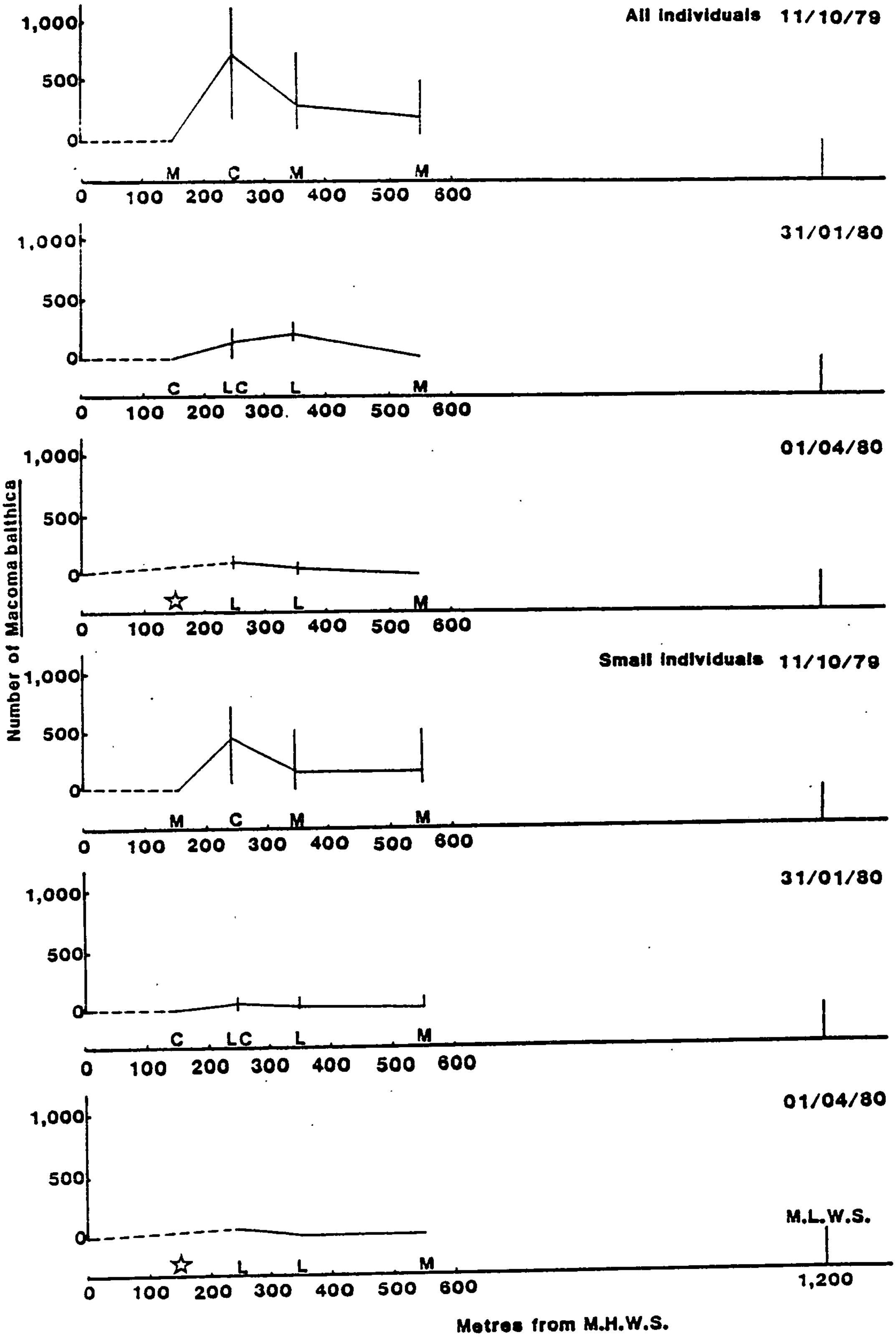


FIGURE 2.4a

Number of Macoma balthica per square metre at Severn Beach

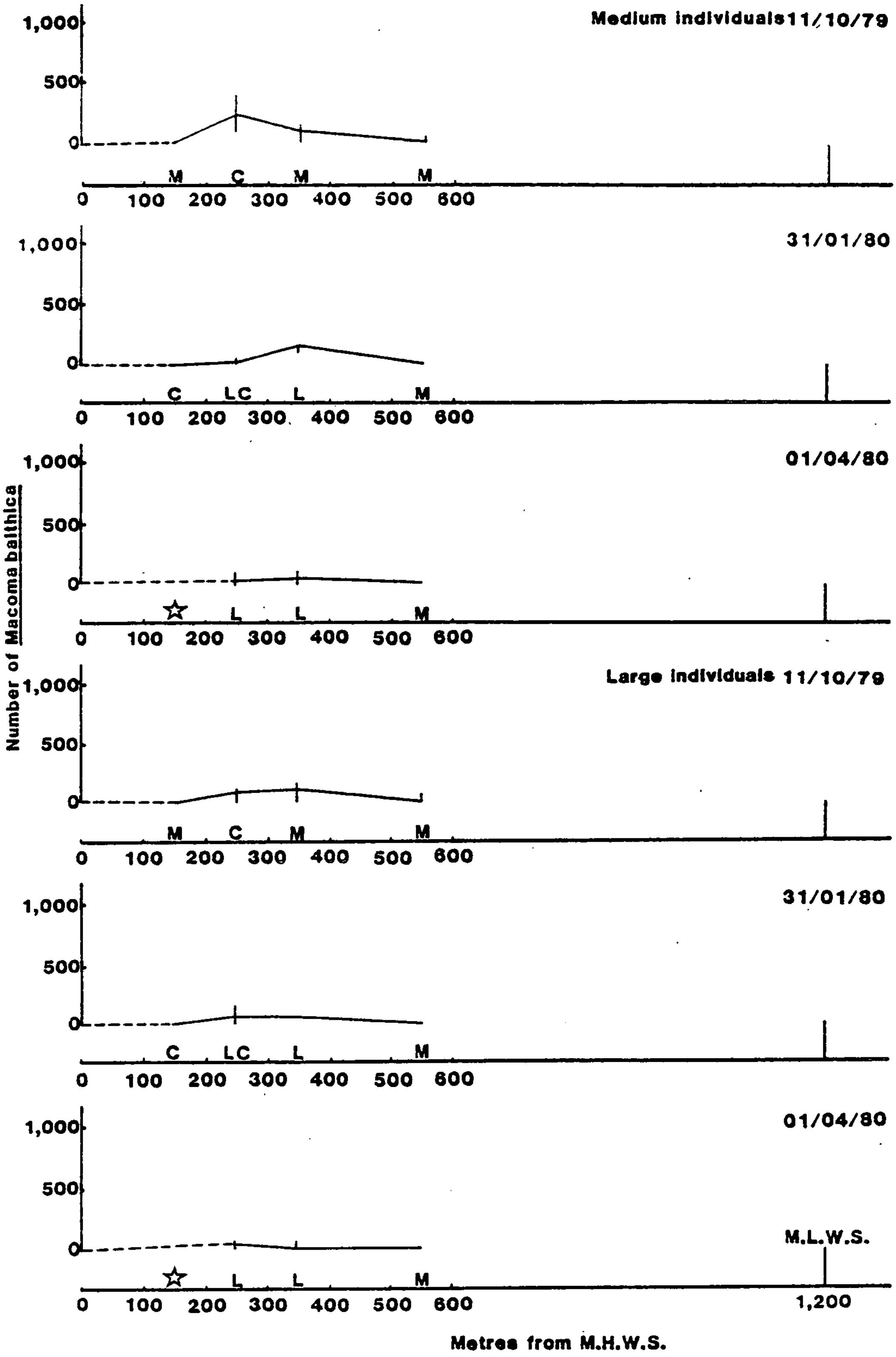


FIGURE 2.4b

Number of *Macoma balthica* per square metre at Severn Beach

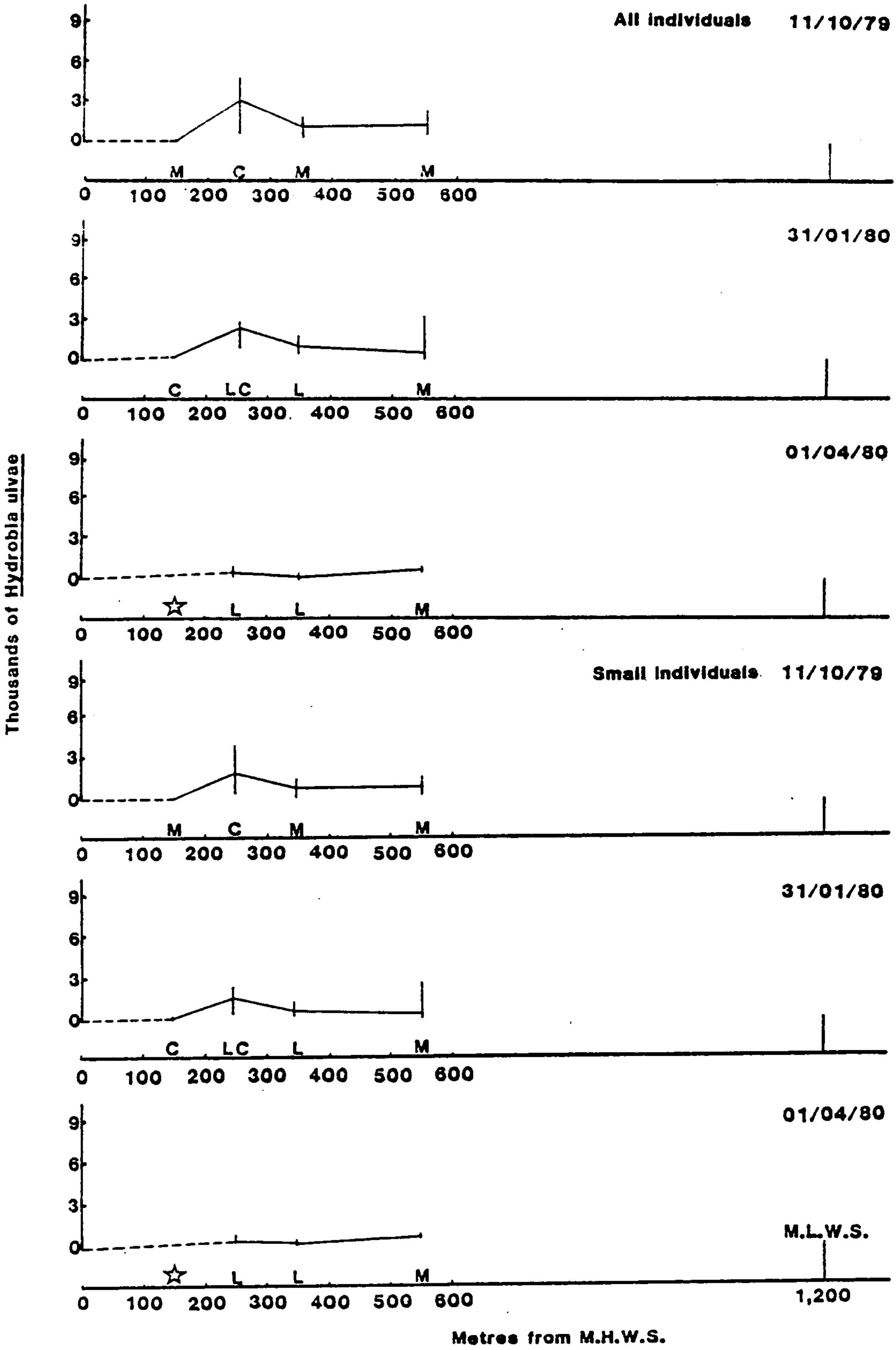


FIGURE 2.4c

Number of Hydrobia ulvae per square metre at Severn Beach

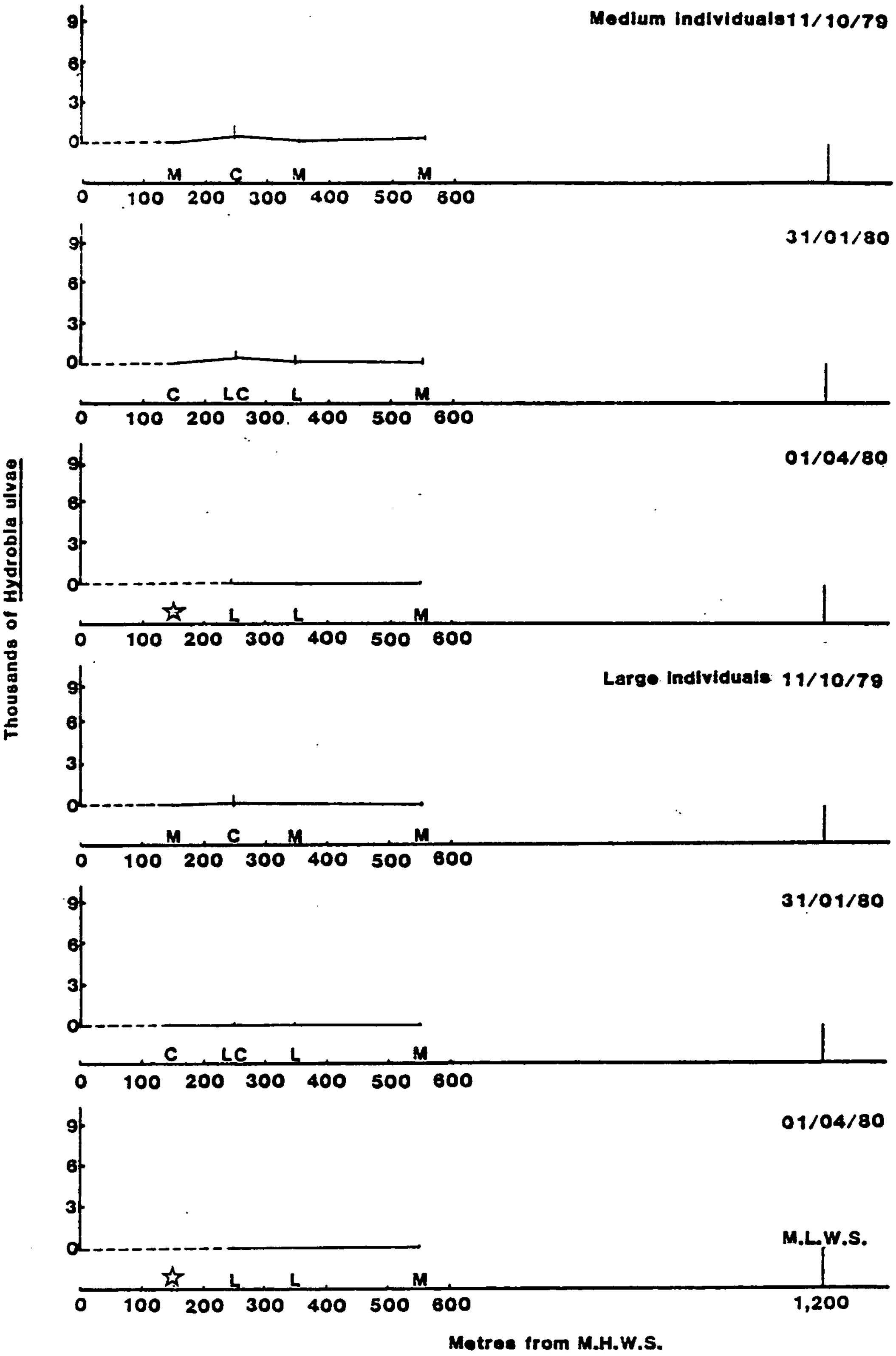


FIGURE 2.4d

Number of Hydrobia ulvae per square metre at Severn Beach

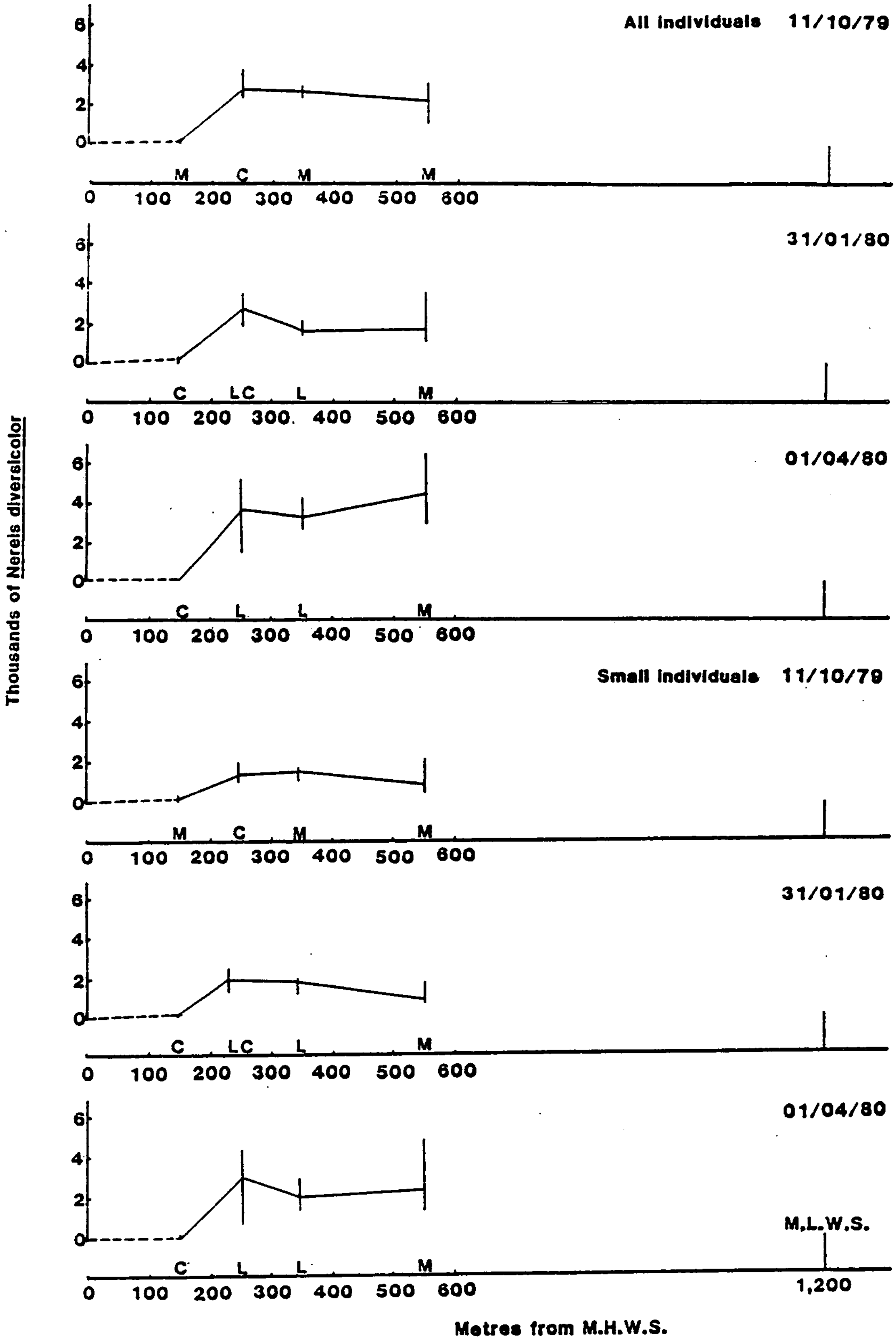


FIGURE 2.4e

Number of *Nereis diversicolor* per square metre at Severn Beach

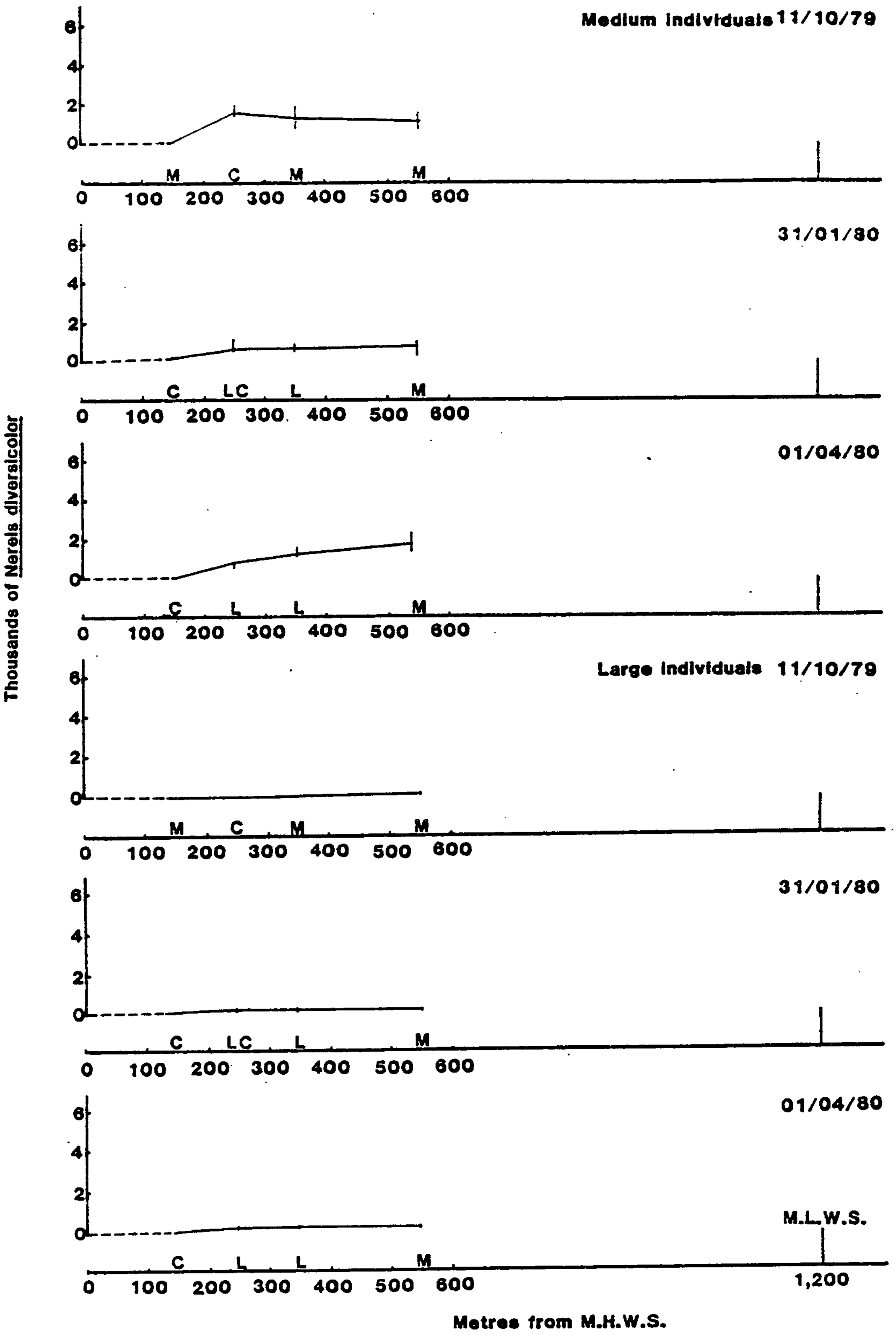


FIGURE 2.4f

Number of Nereis diversicolor per square metre at Severn Beach

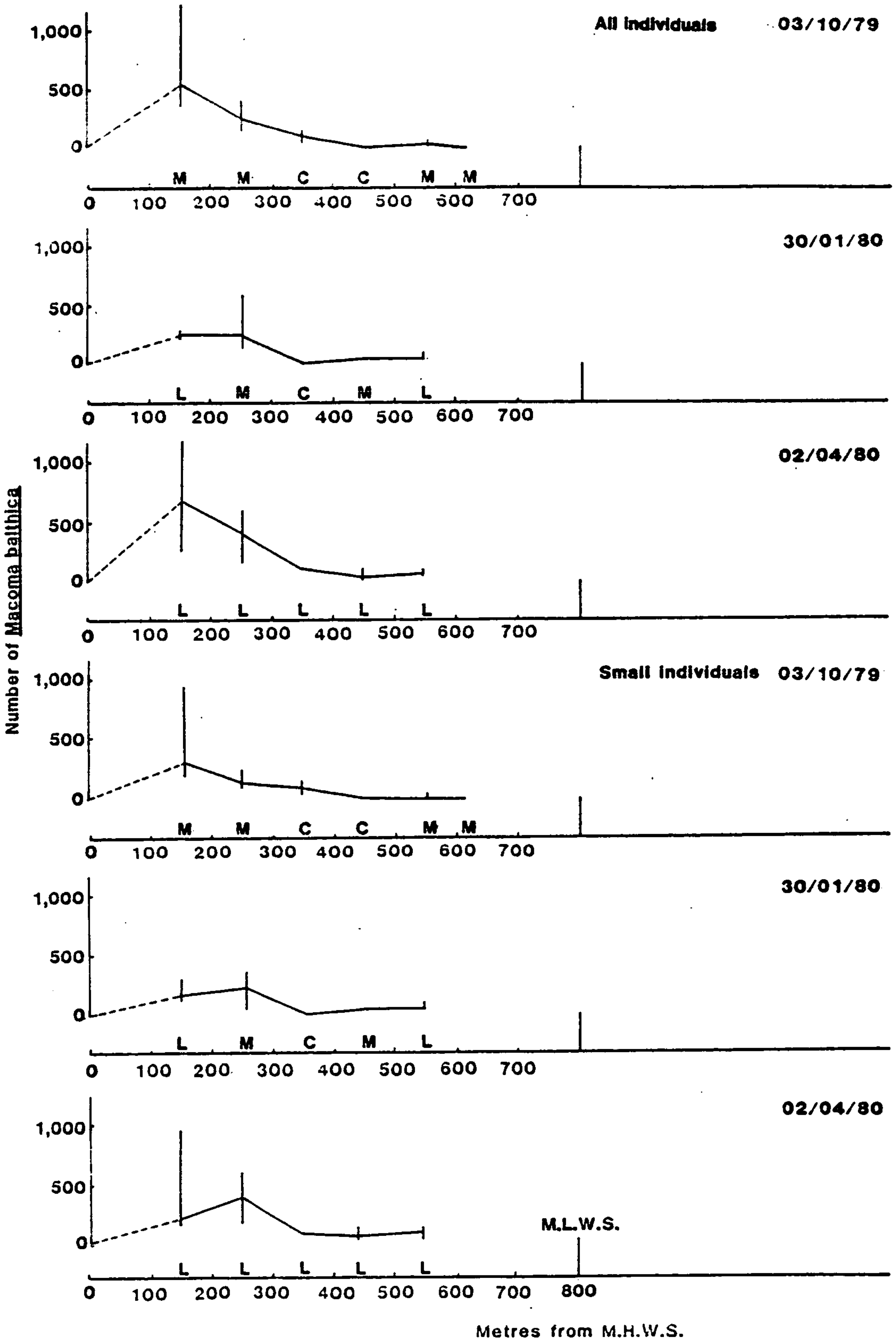


FIGURE 2.5a

Number of Macoma balthica per square metre at Clevedon

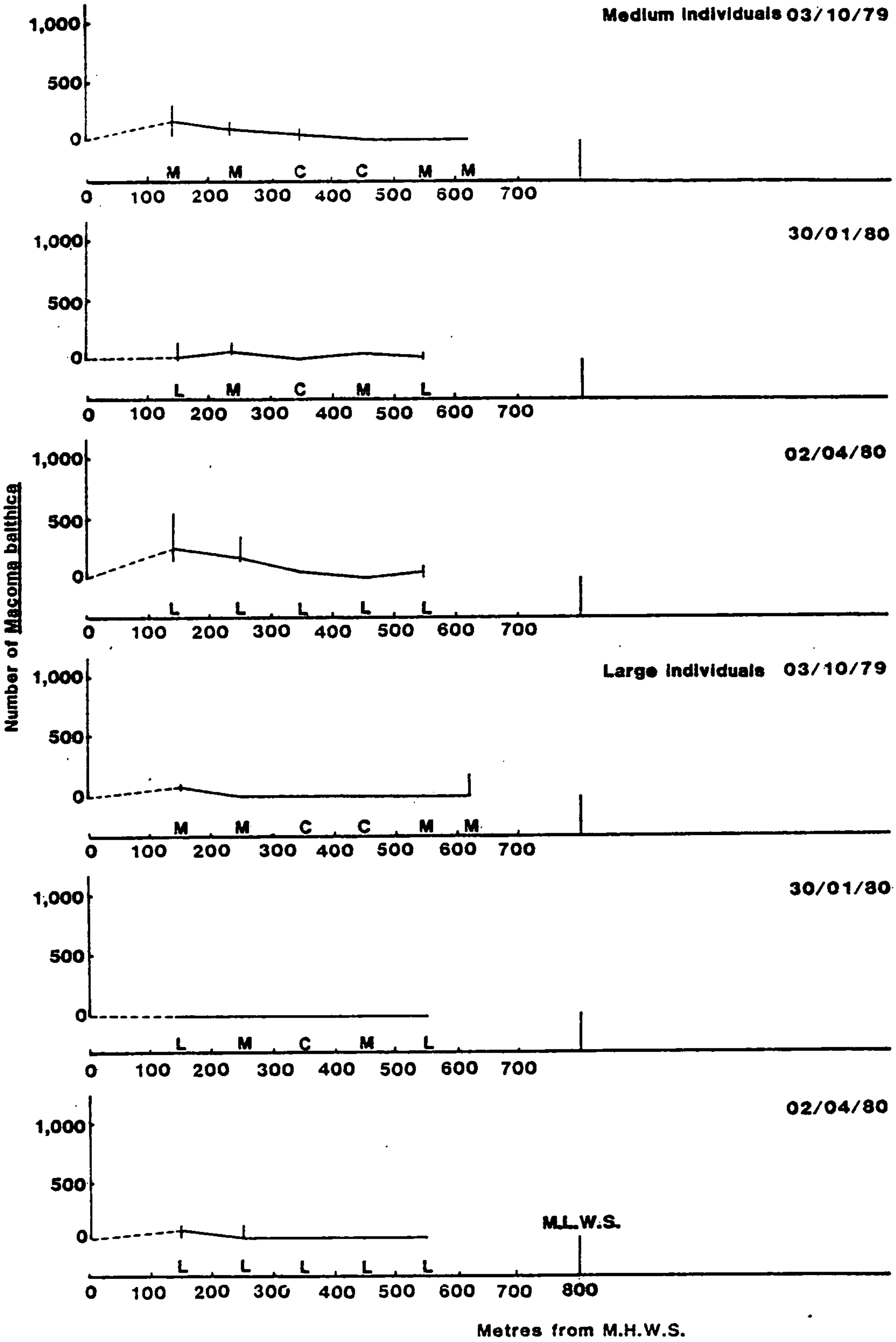


FIGURE 2.5b

Number of Macoma balthica per square metre at Clevedon

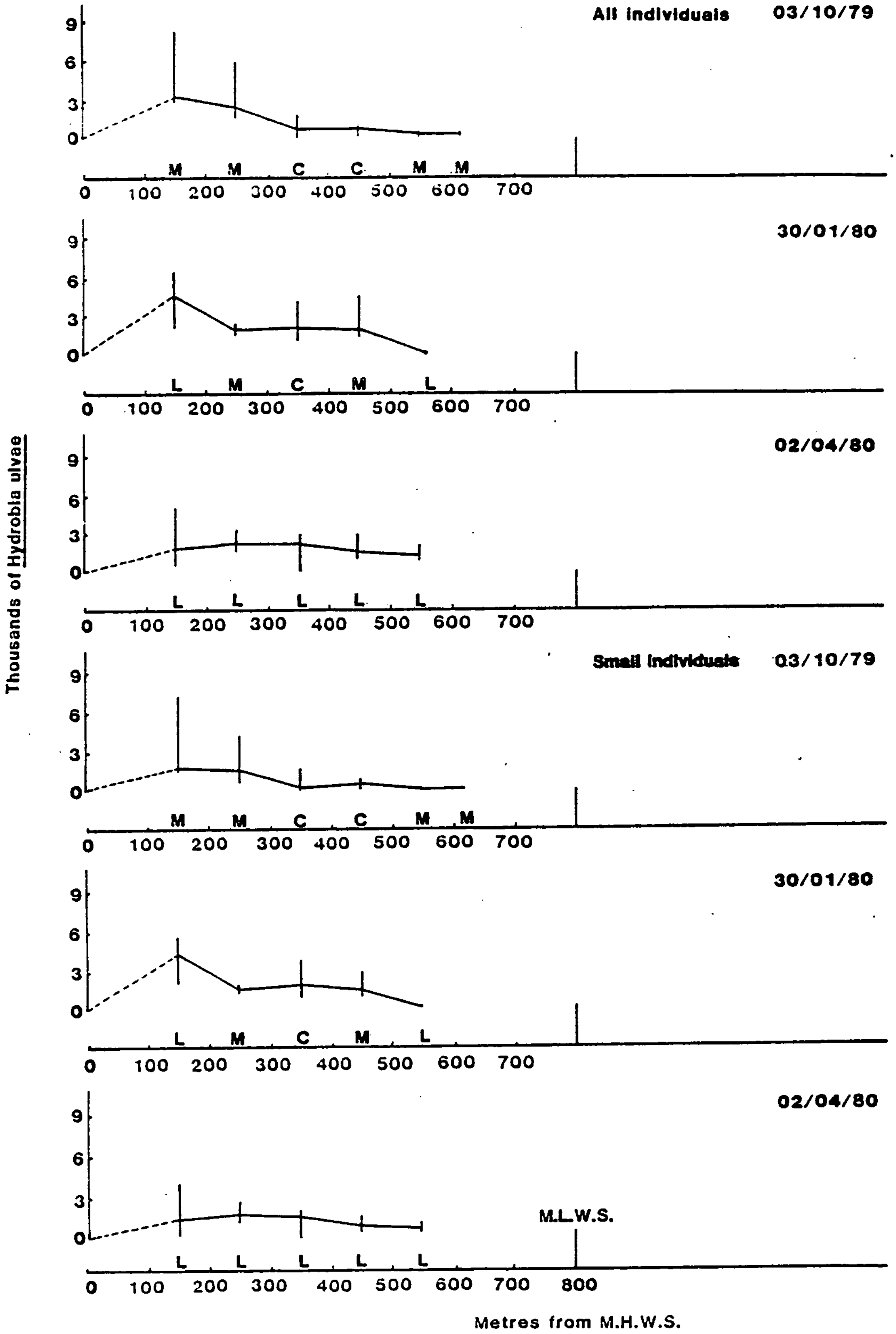


FIGURE 2.5c

Number of Hydrobia ulvae per square metre at Clevedon

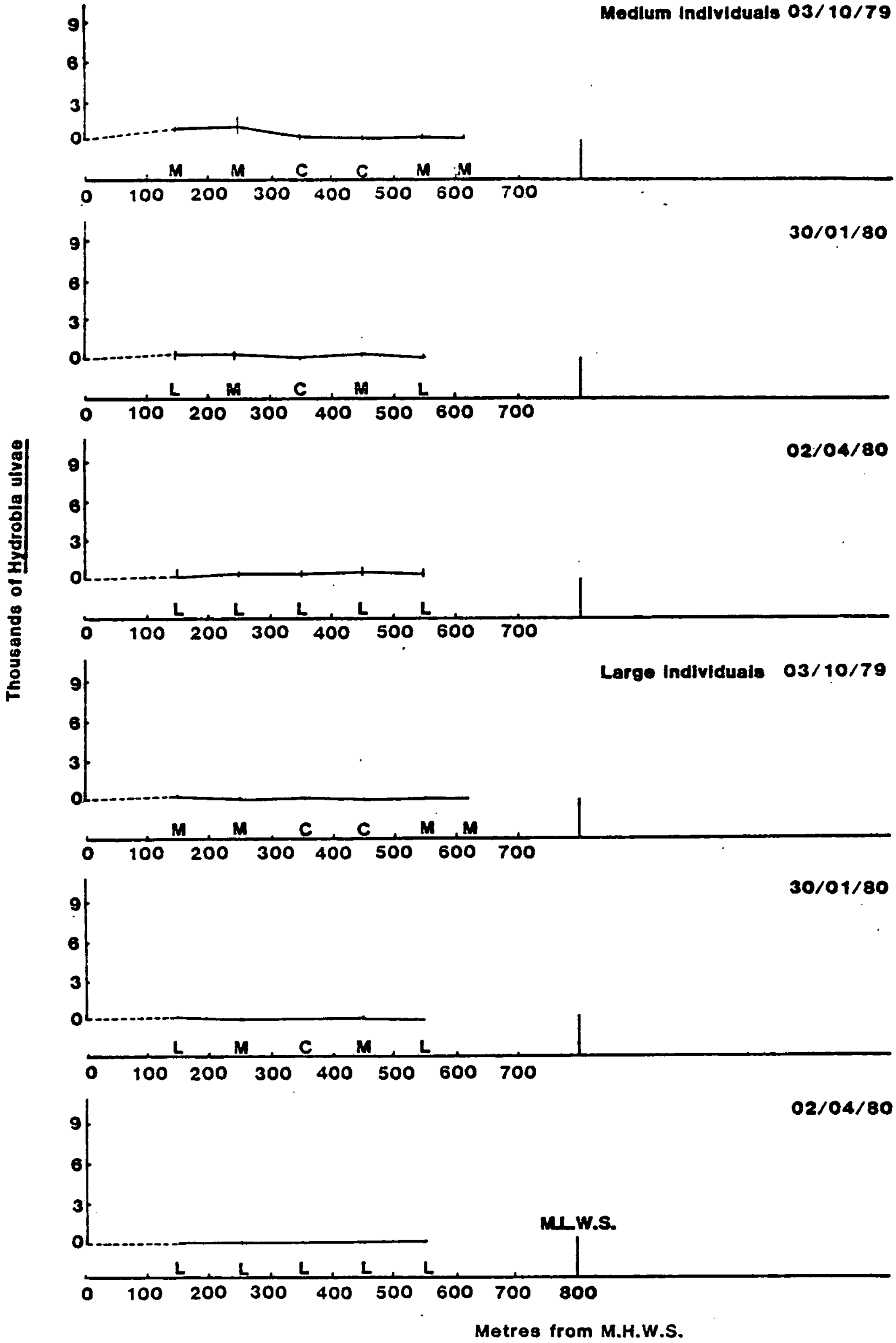


FIGURE 2.5d

Number of Hydrobia ulvae per square metre at Clevedon

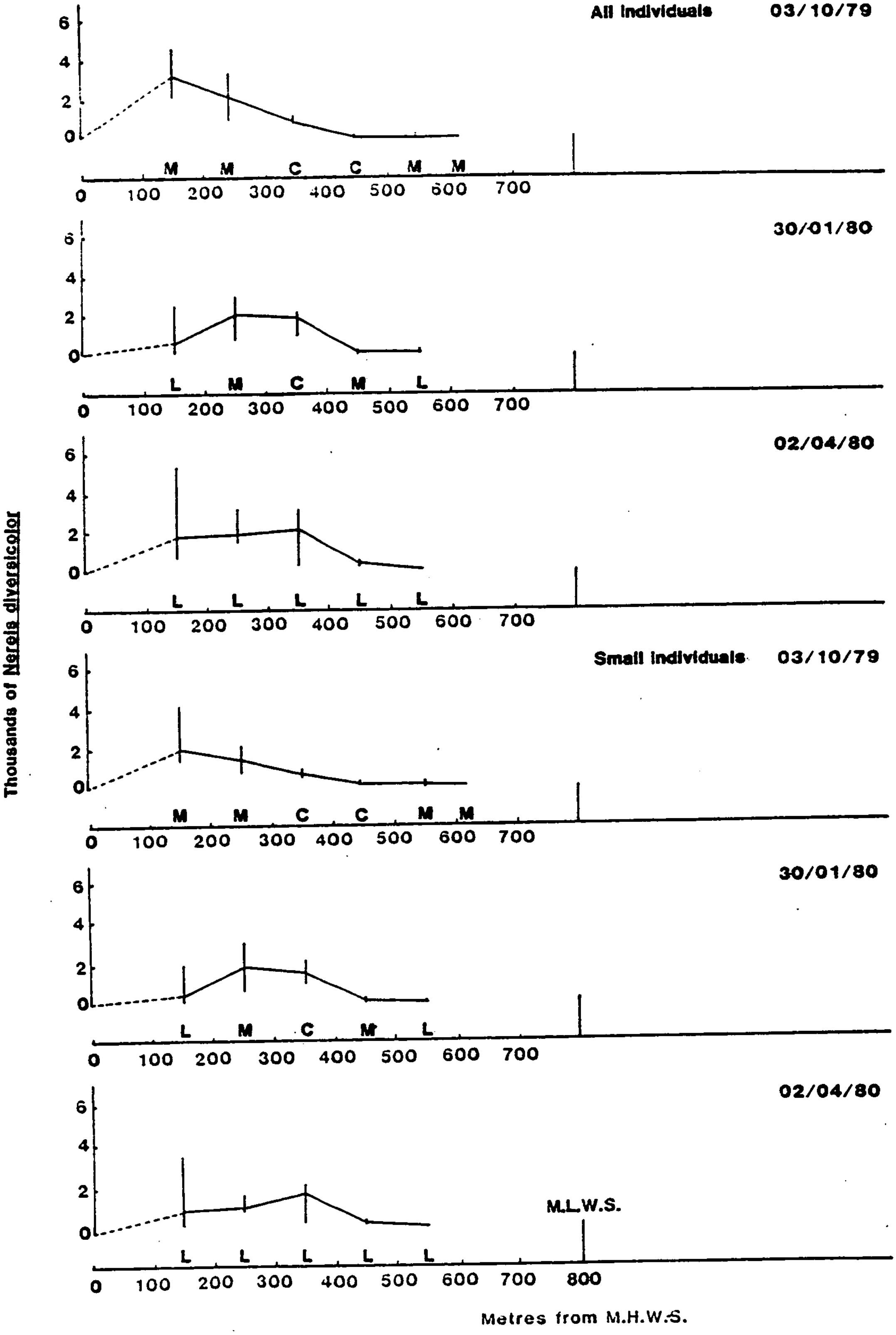


FIGURE 2.5e

Number of Nereis diversicolor per square metre at Clevedon

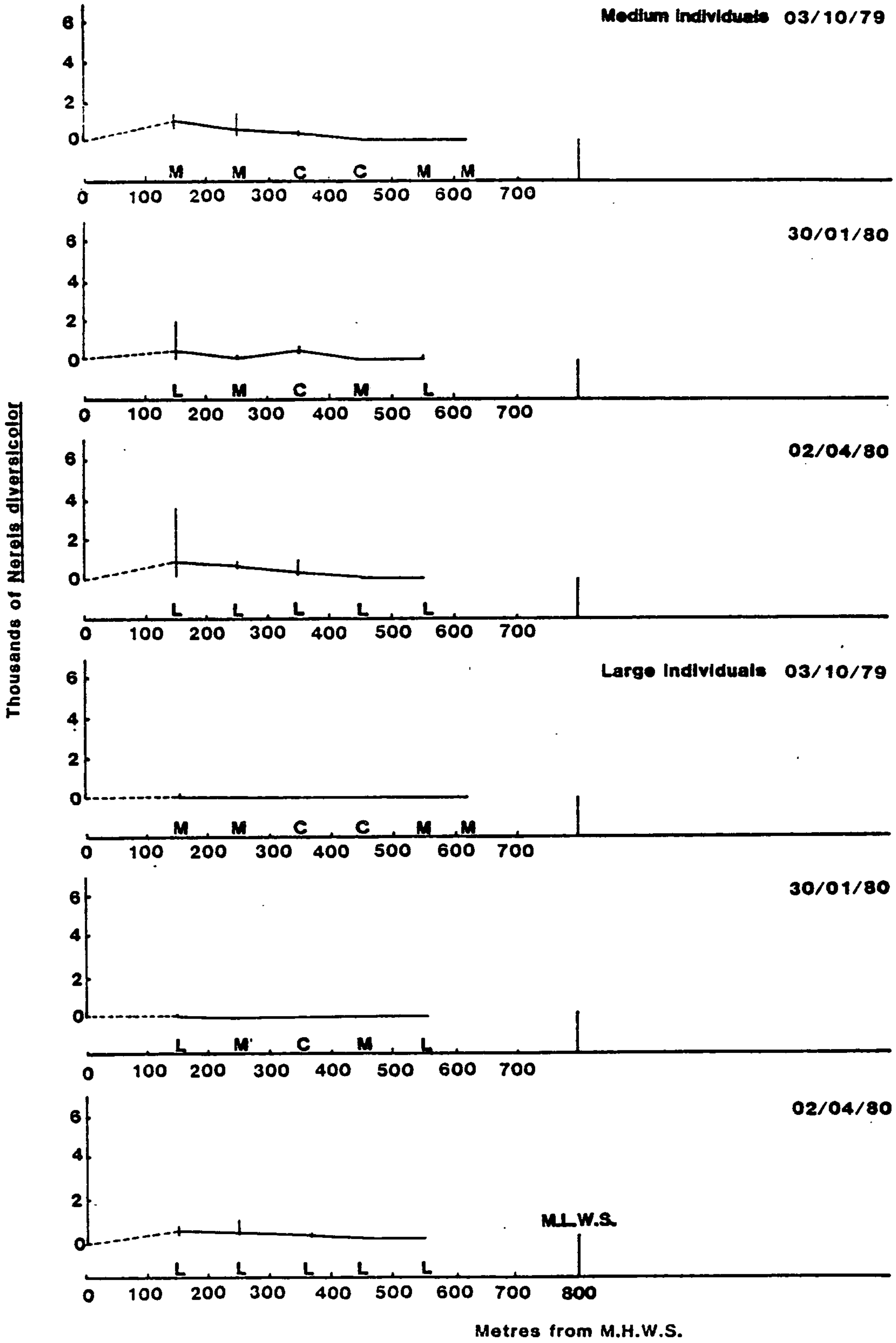


FIGURE 2.5f

Number of Nereis diversicolor per square metre at Clevedon

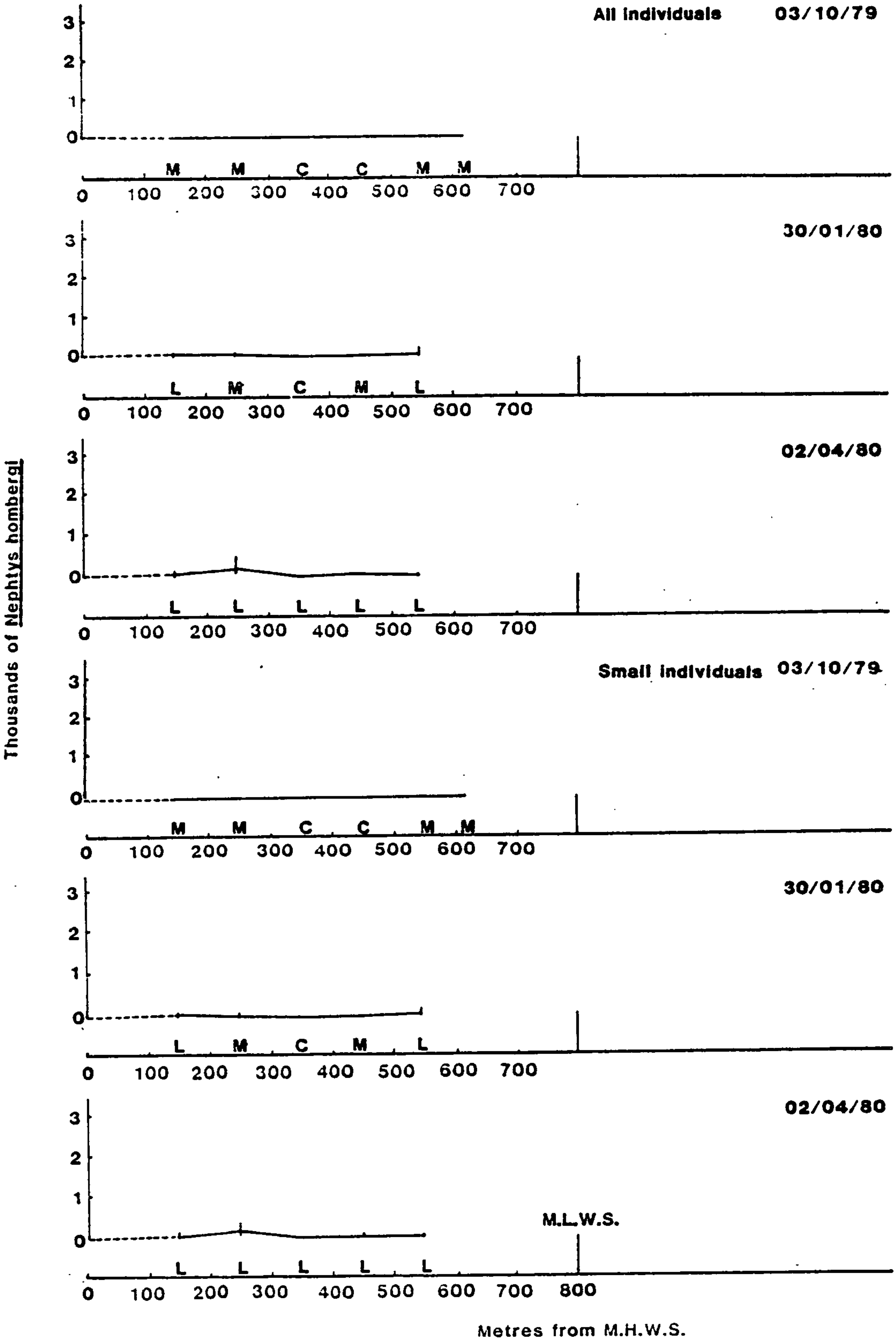


FIGURE 2.5g

Number of Nepthys hombergi per square metre at Clevedon

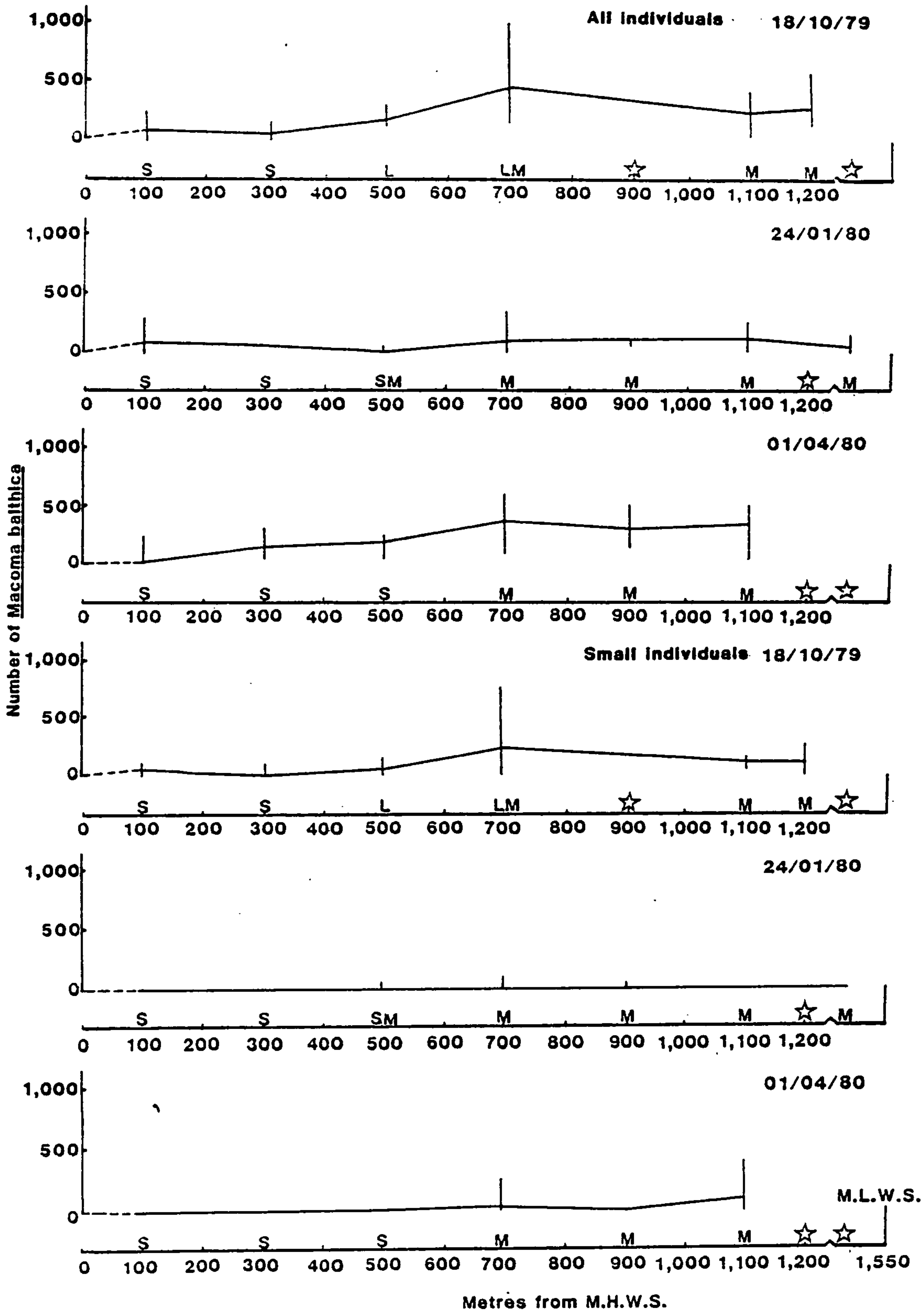


FIGURE 2.6a

Number of Macoma balthica per square metre in Sand Bay

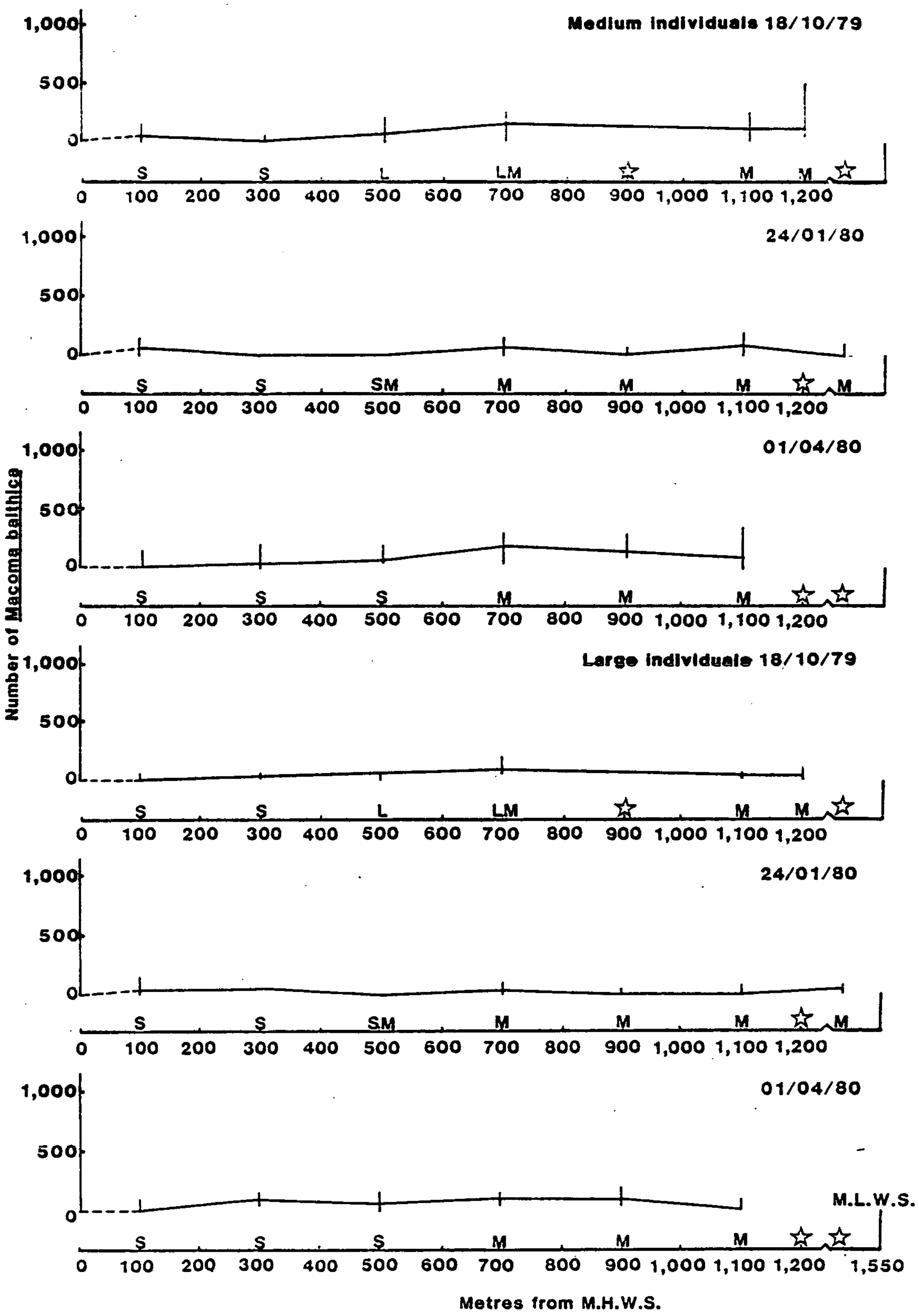


FIGURE 2.6b

Number of Macoma balthica per square metre in Sand Bay

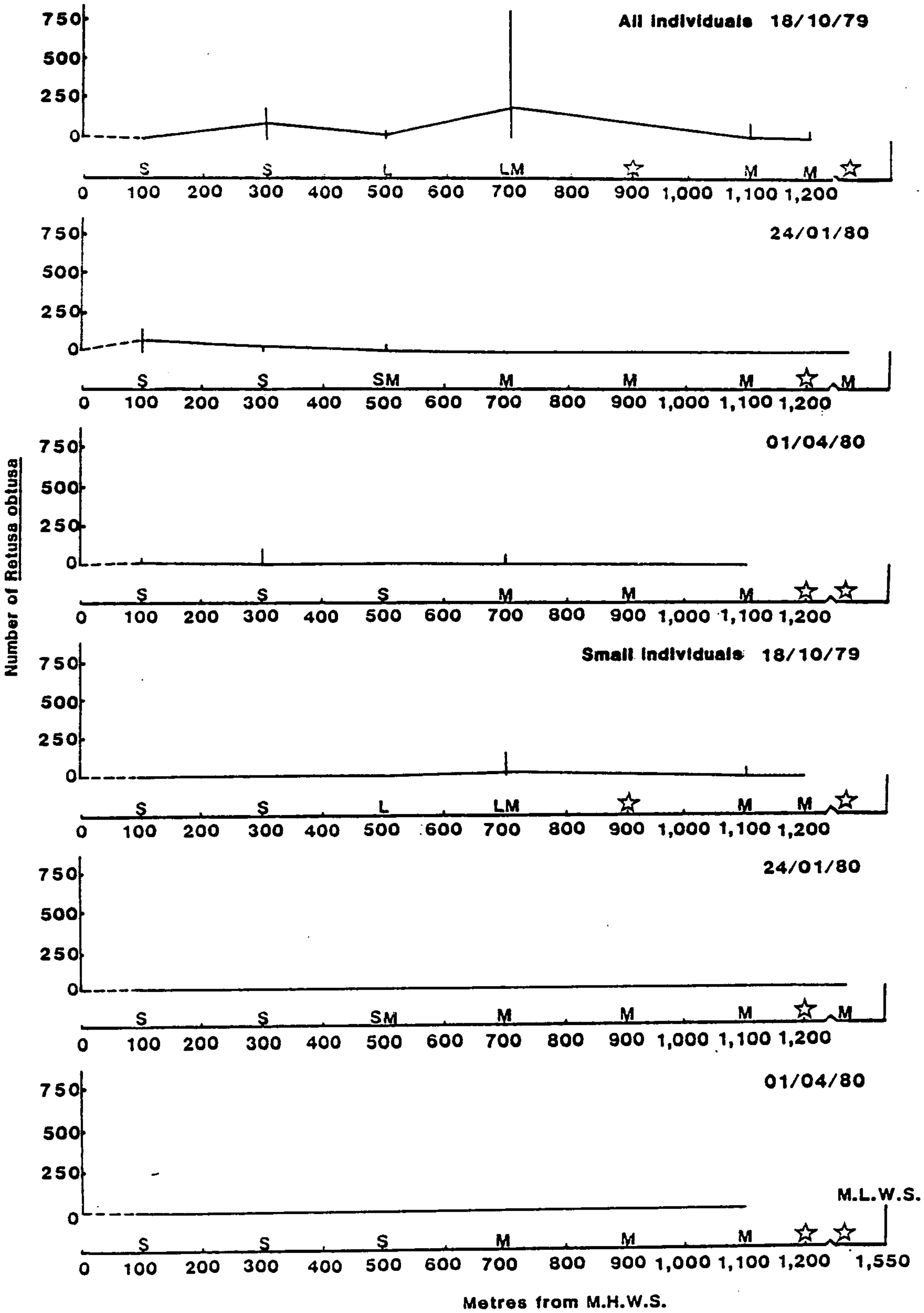


FIGURE 2.6c

Number of Retusa obtusa per square metre in Sand Bay

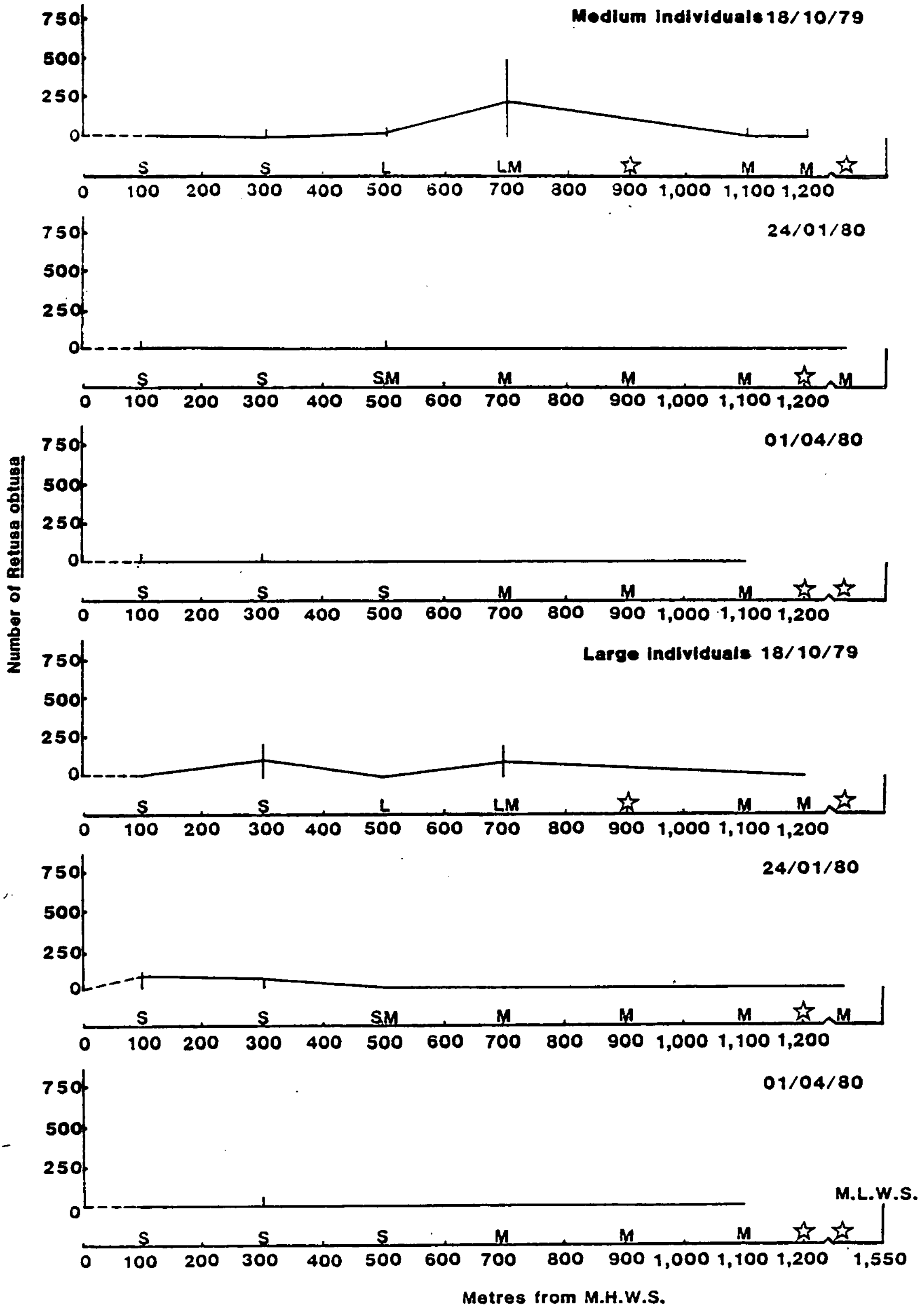


FIGURE 2.6d

Number of Retusa obtusa per square metre in Sand Bay

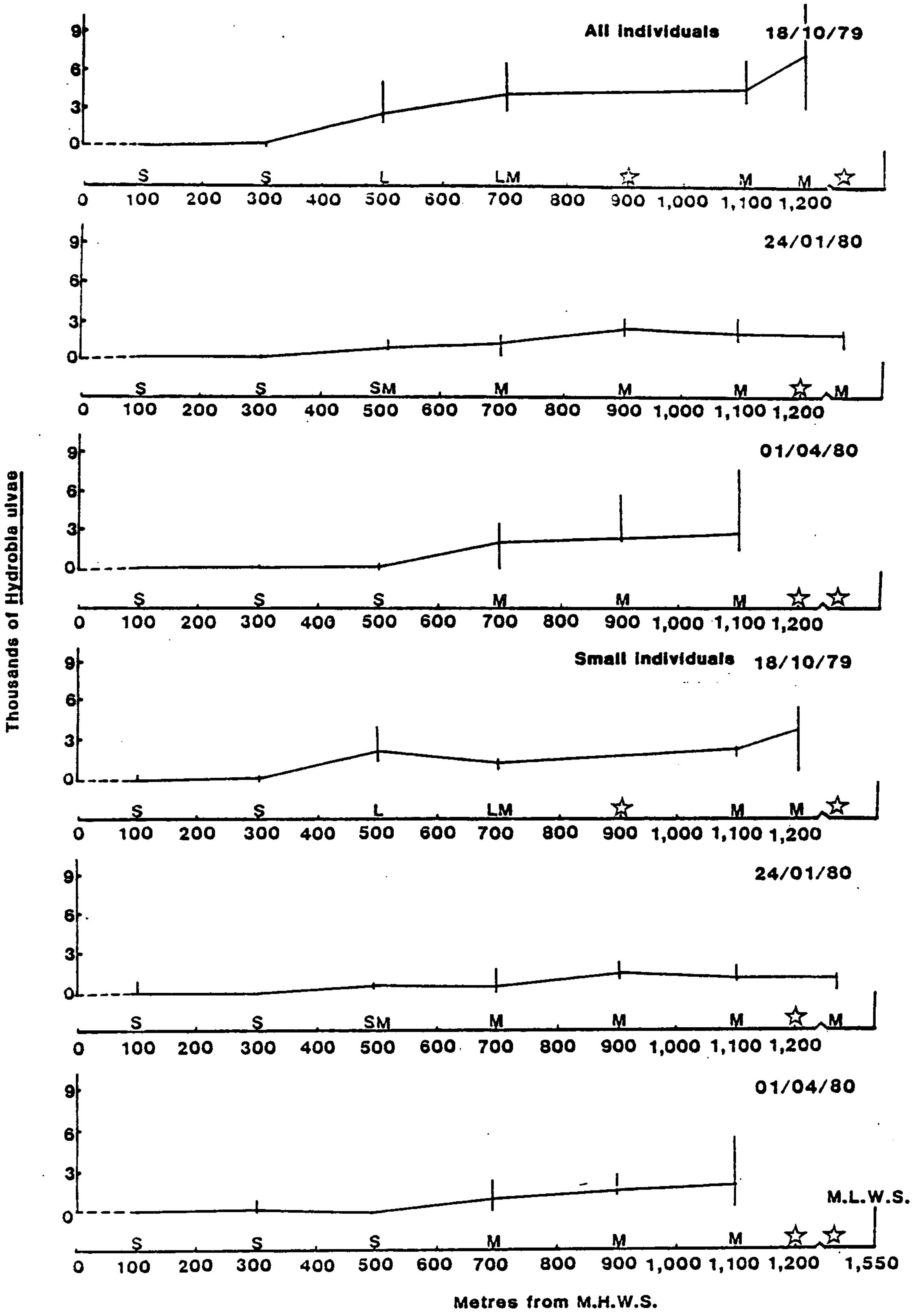


FIGURE 2.6e

Number of Hydrobia ulvae per square metre in Sand Bay

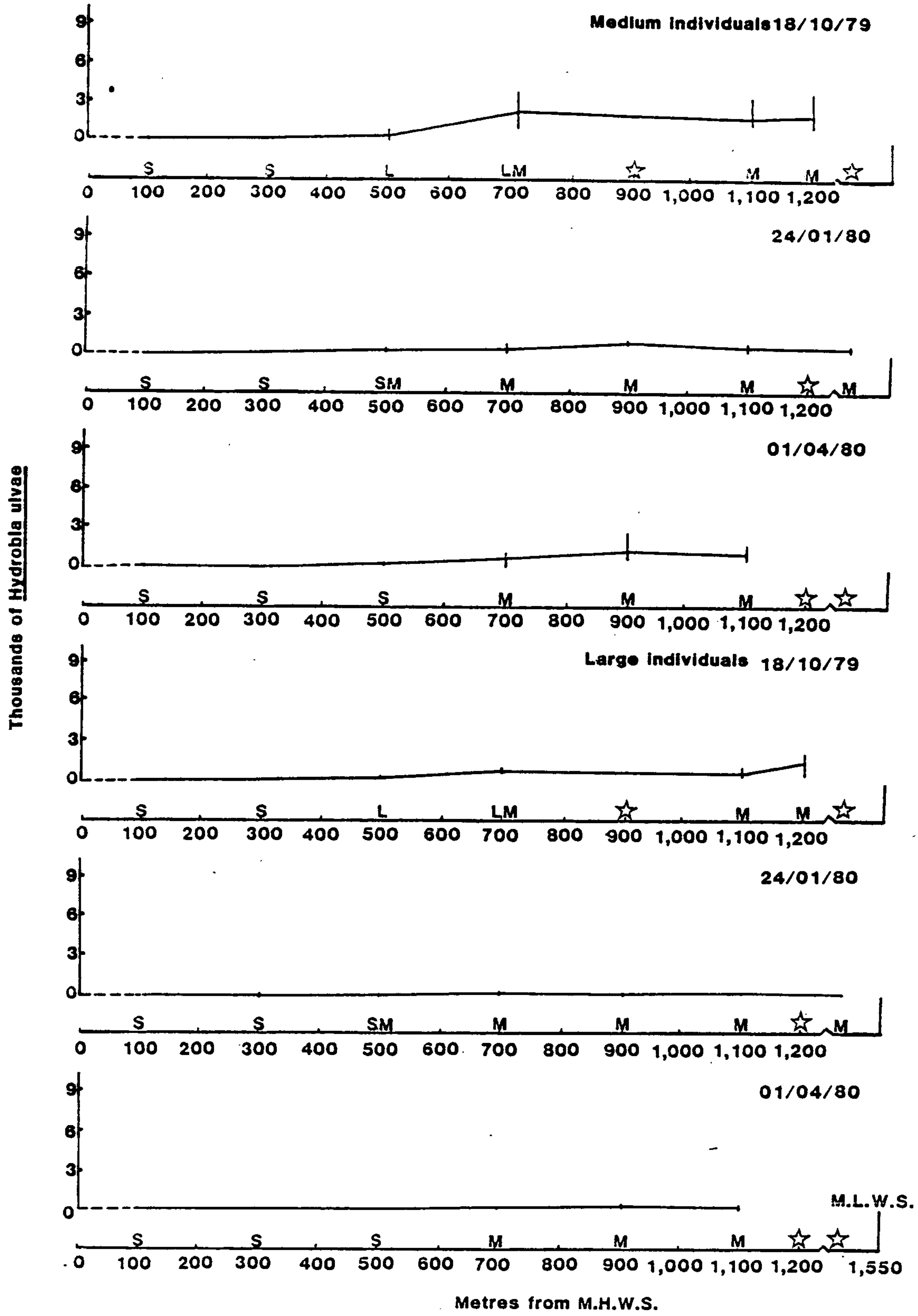


FIGURE 2.6f

Number of *Hydrobia ulvae* per square metre in Sand Bay

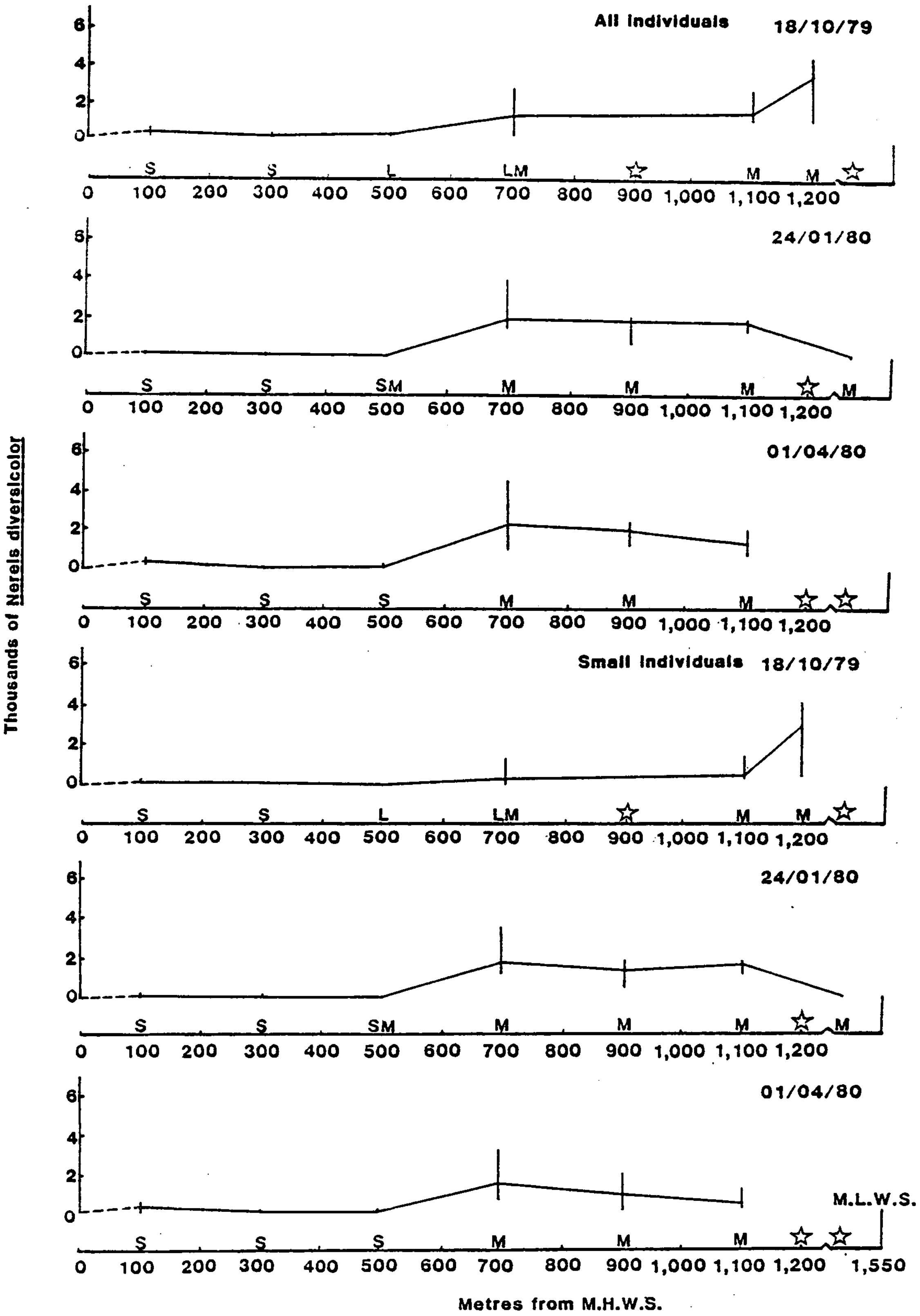


FIGURE 2.6g

Number of Nereis diversicolor per square metre in Sand Bay

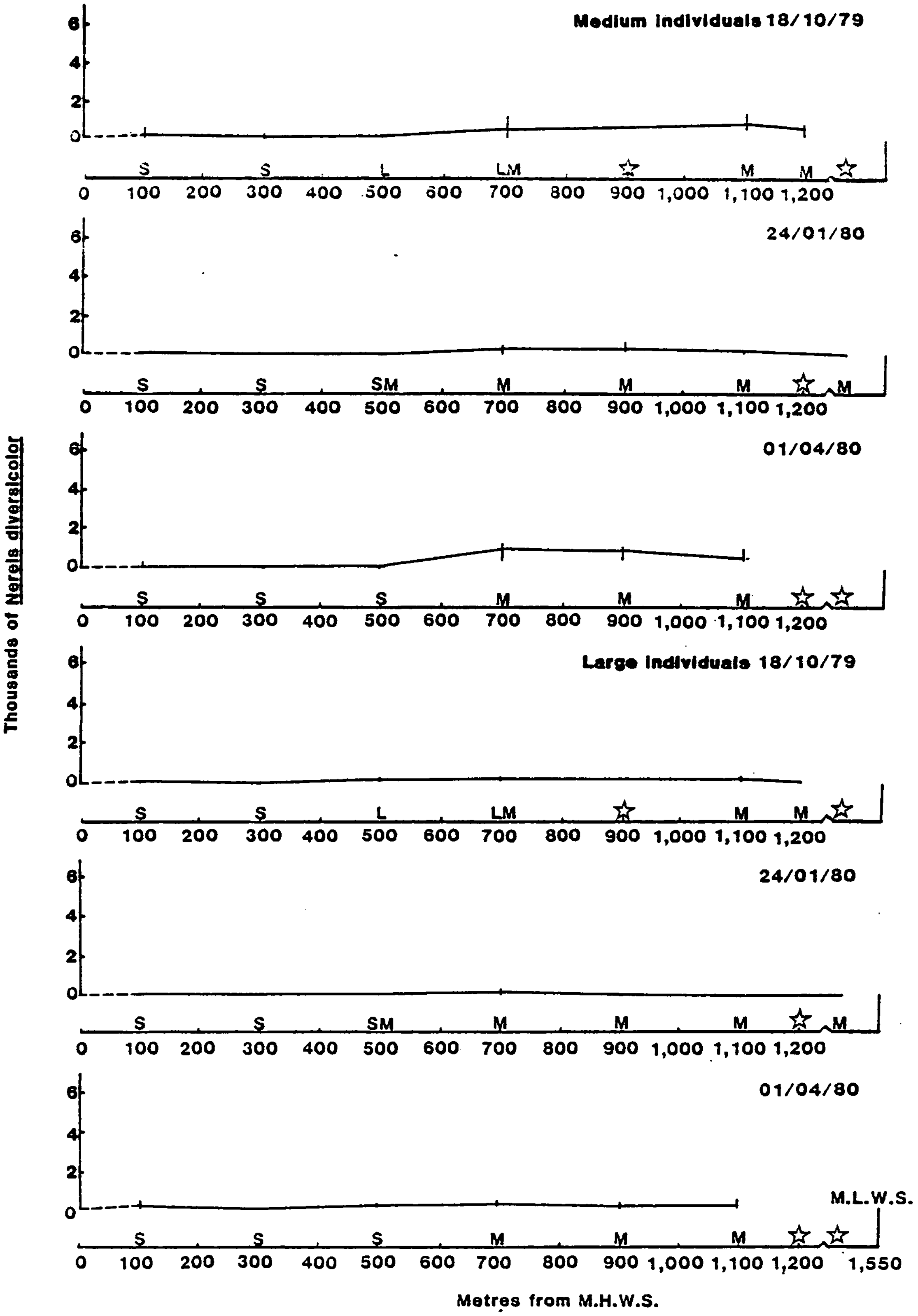


FIGURE 2.6h

Number of Nereis diversicolor per square metre in Sand Bay

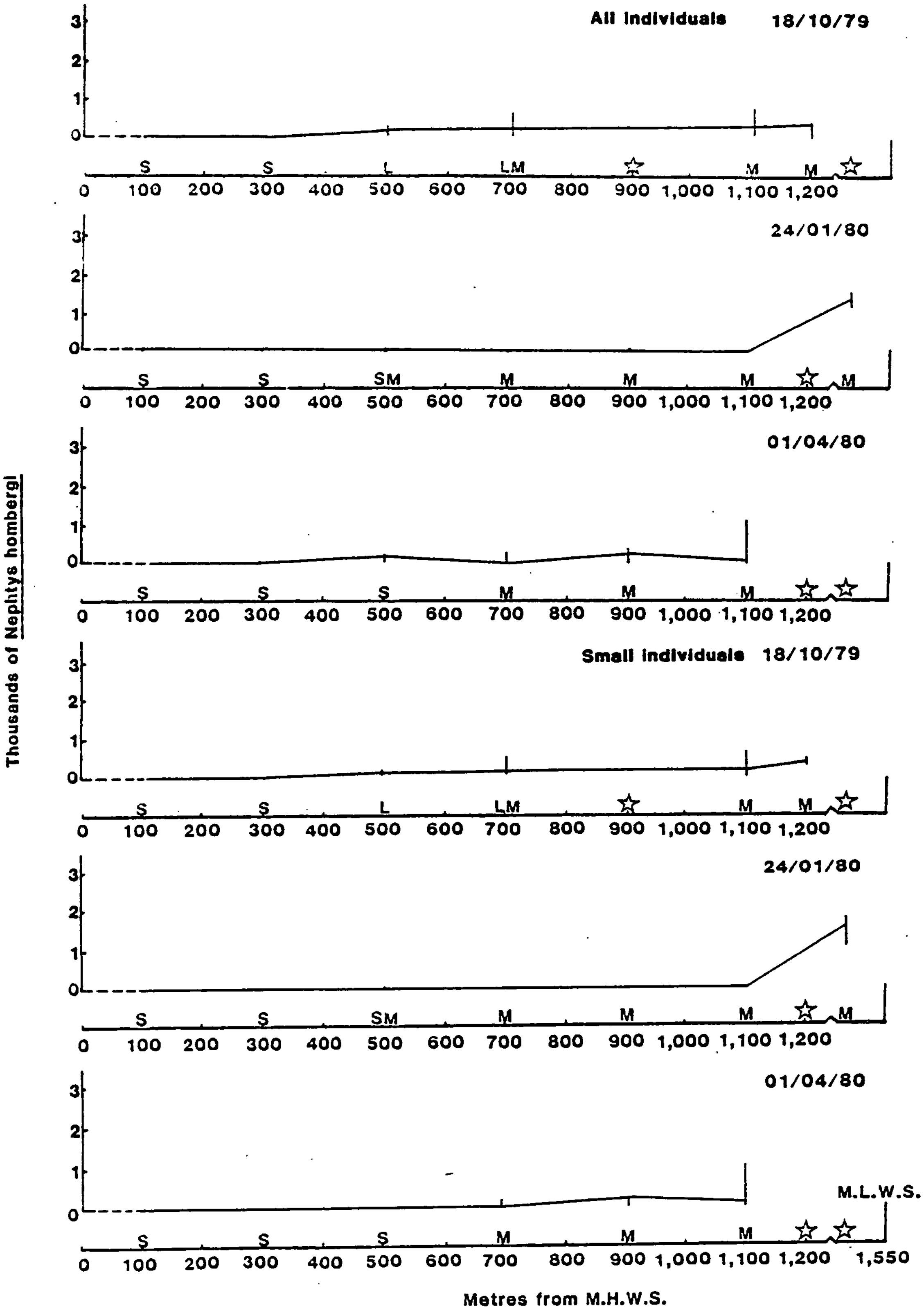


FIGURE 2.6i

Number of Nepthys hombergi per square metre in Sand Bay

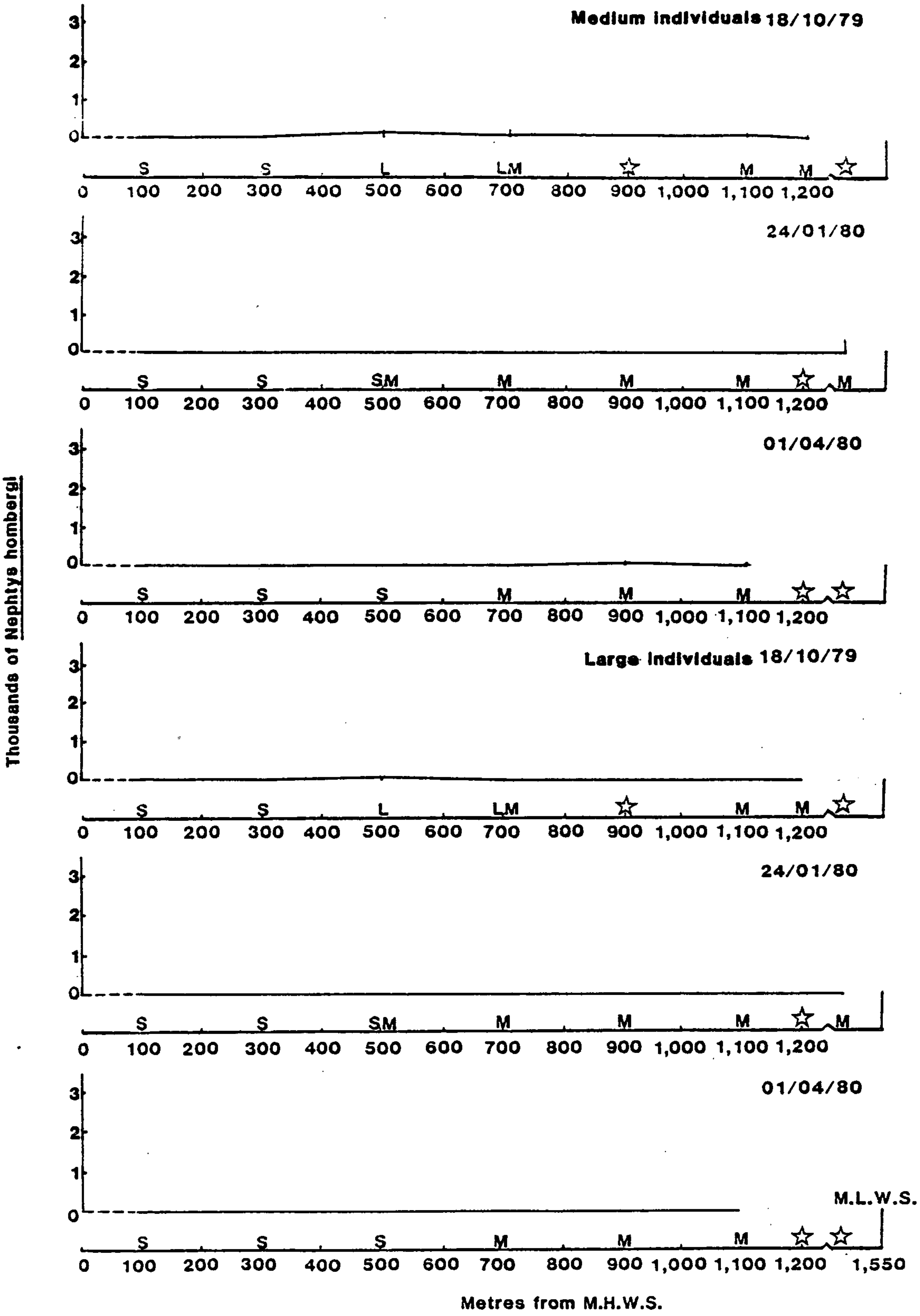


FIGURE 2.6j

Number of Nepthys homgbergi per square metre in Sand Bay

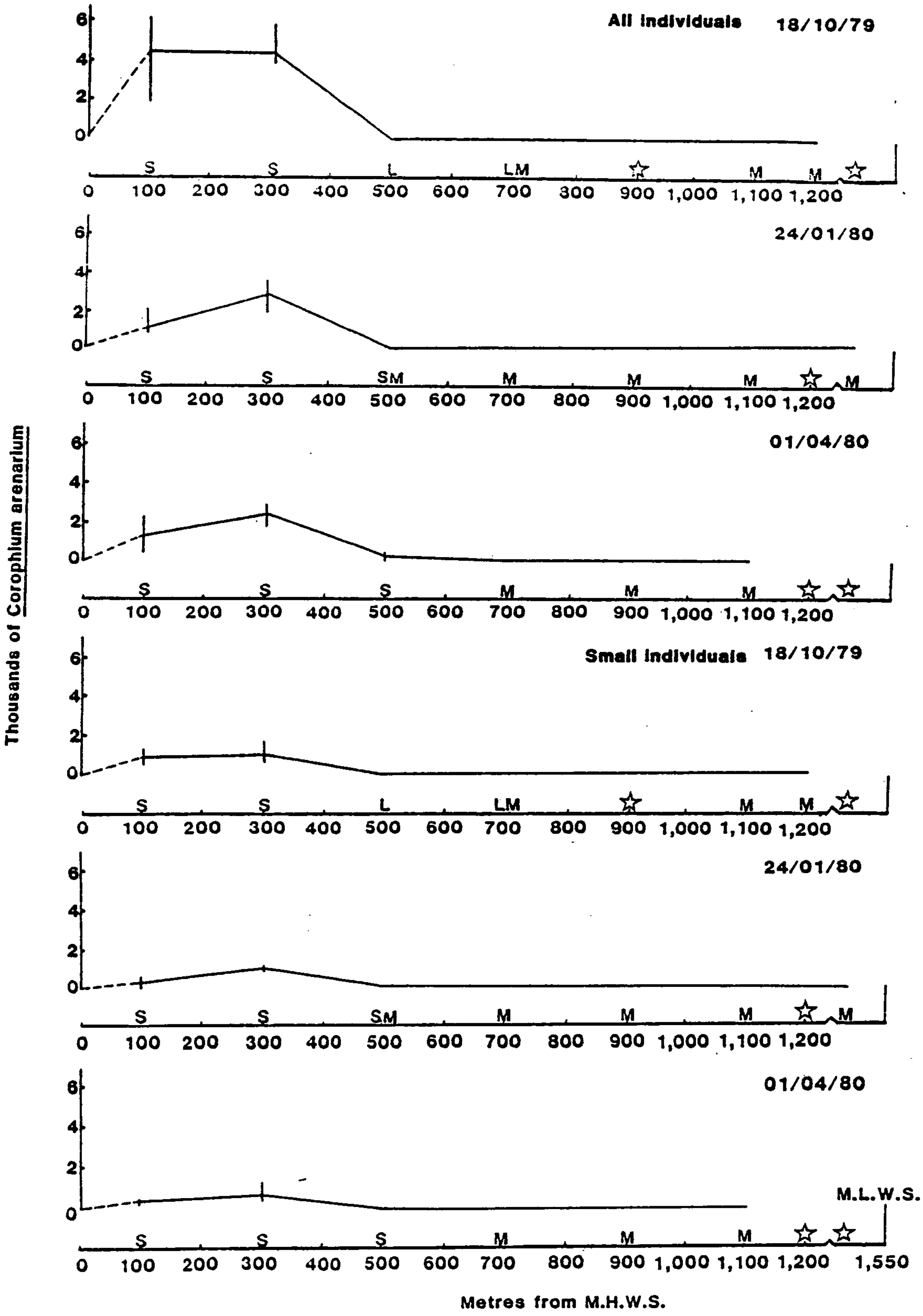


FIGURE 2.6k

Number of Corophium arenarium per square metre in Sand Bay

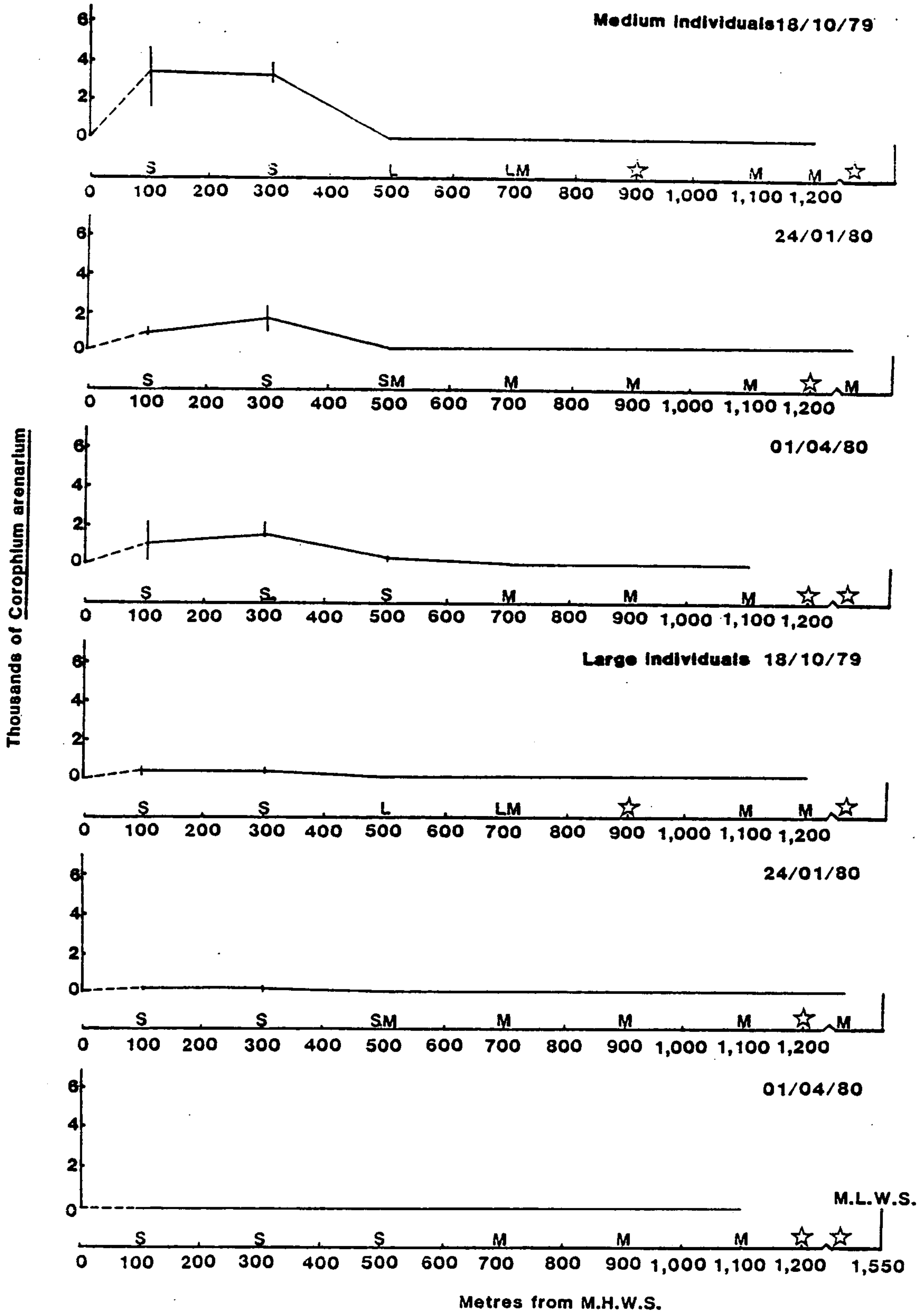


FIGURE 2.61

Number of Corophium arenarium per square metre in Sand Bay

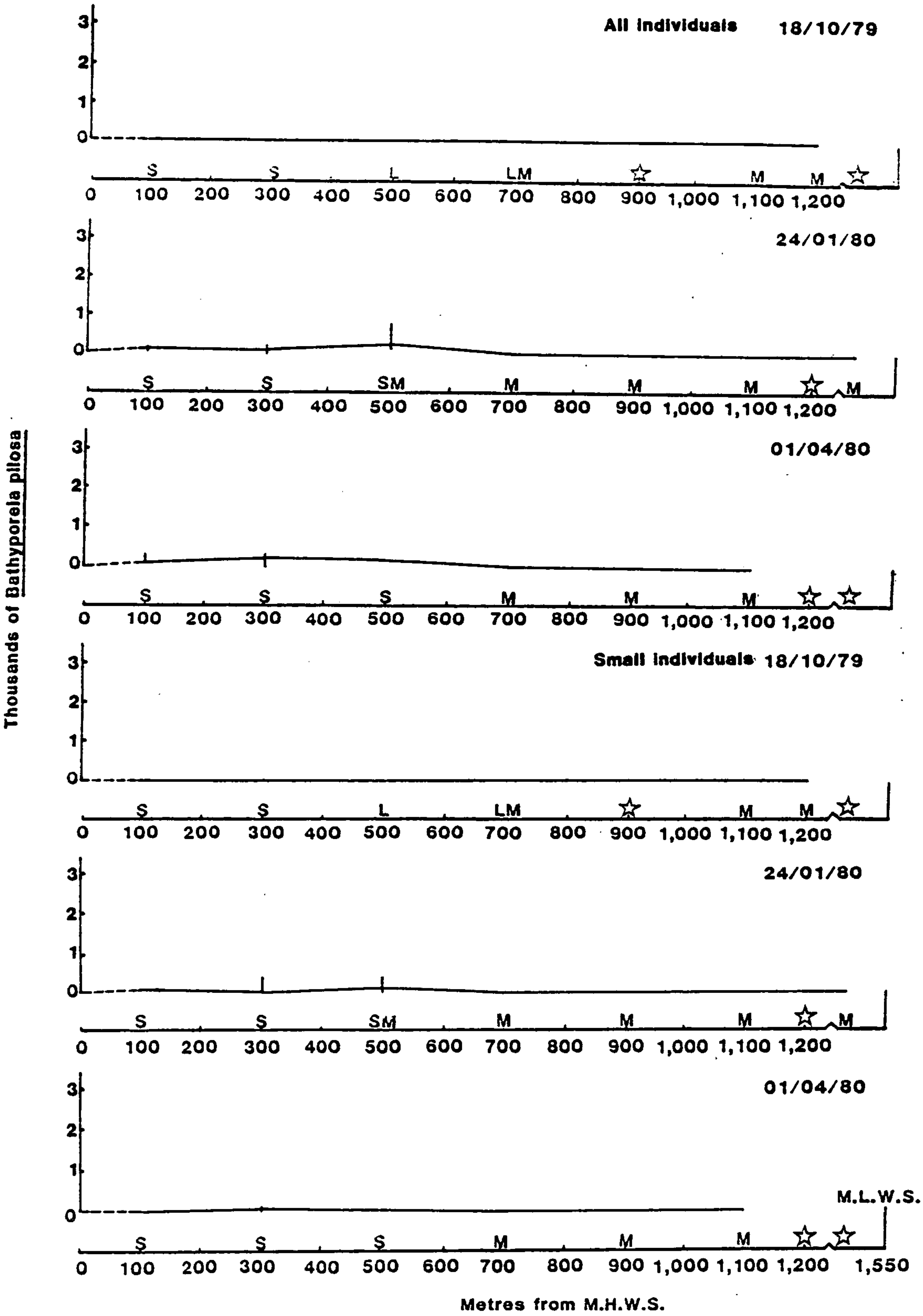


FIGURE 2.6m

Number of Bathyporeia pilosa per square metre in Sand Bay

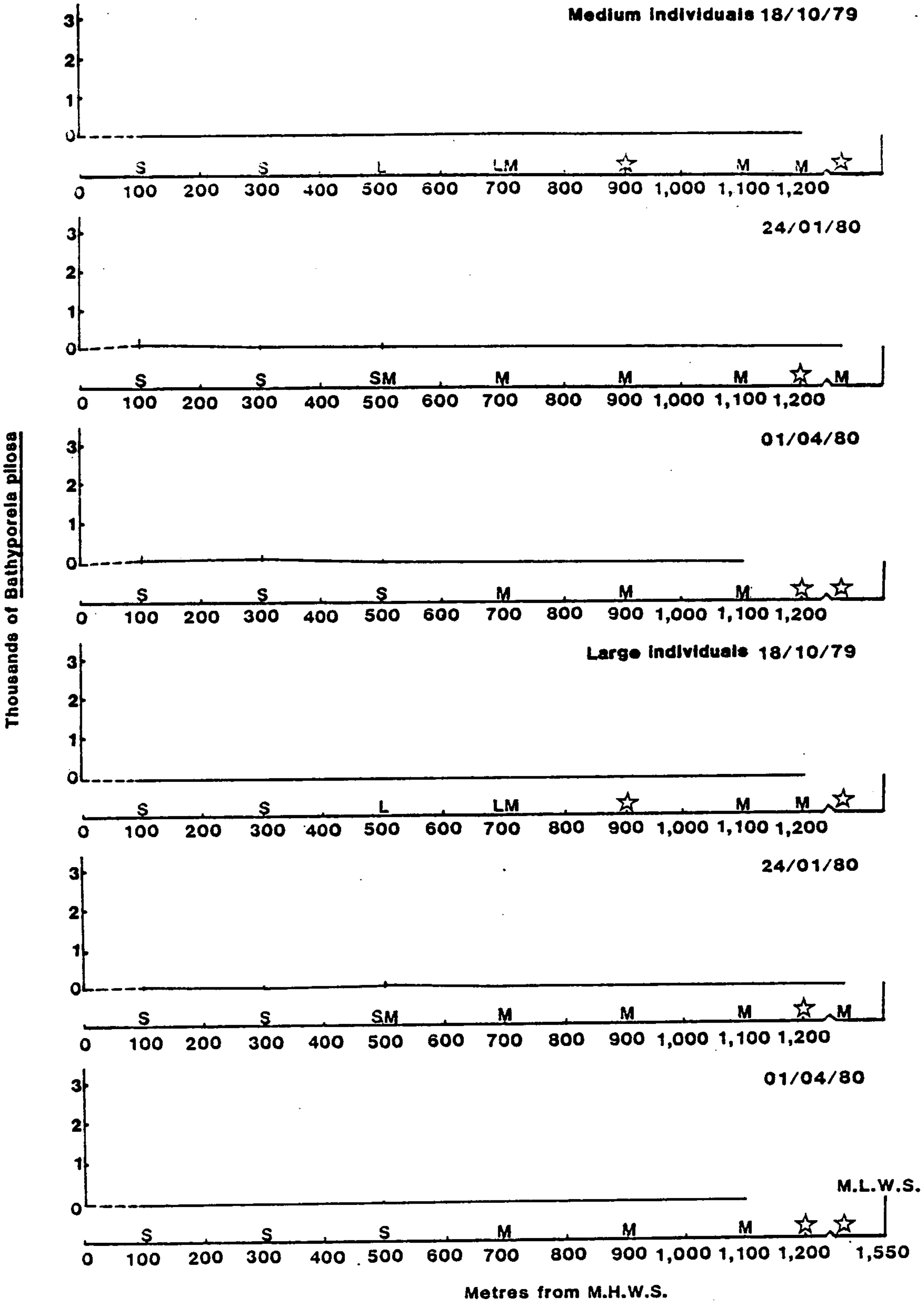


FIGURE 2.6n

Number of Bathyporeia pilosa per square metre in Sand Bay

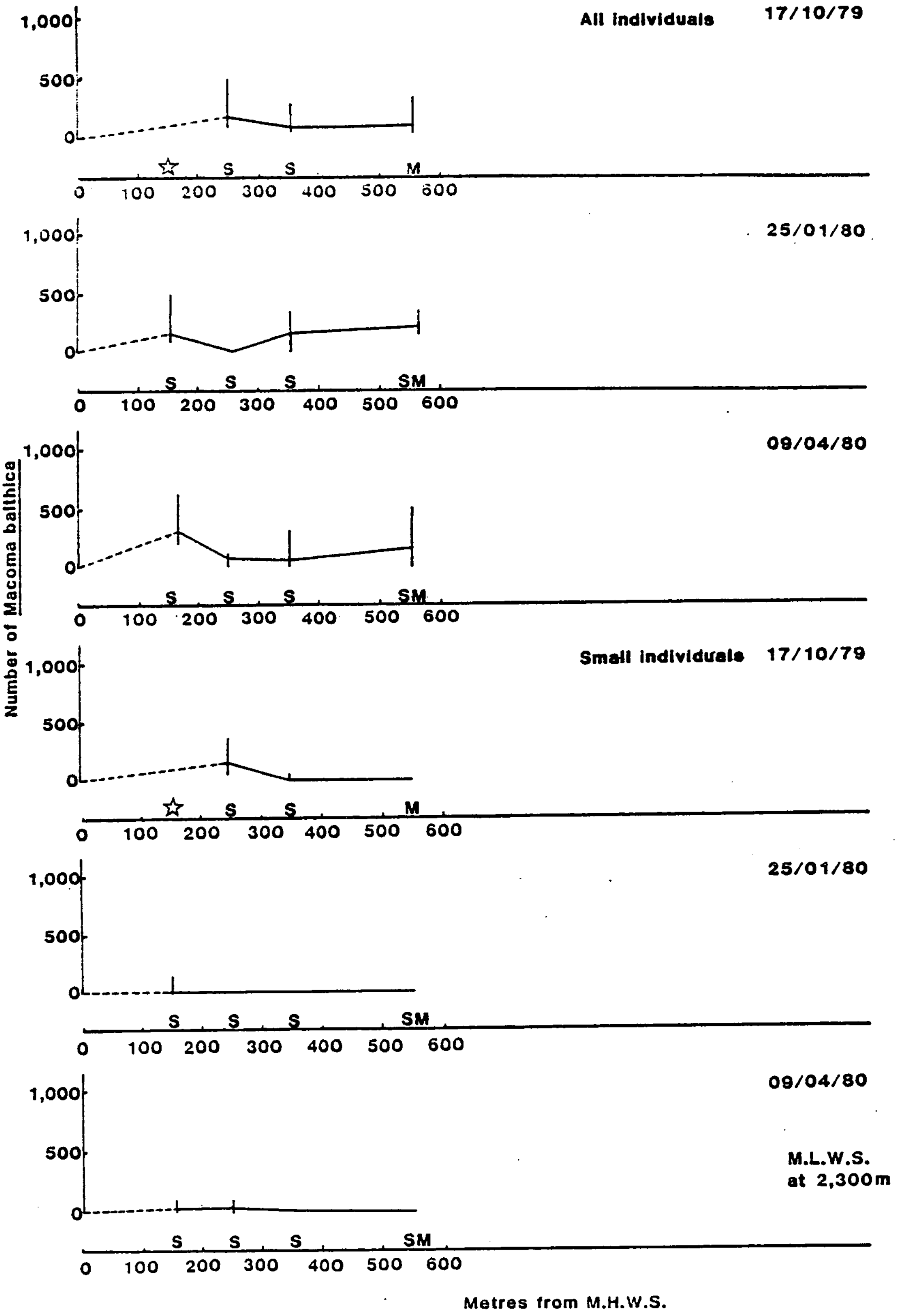


FIGURE 2.7a

Number of Macoma balthica per square metre in Weston Bay

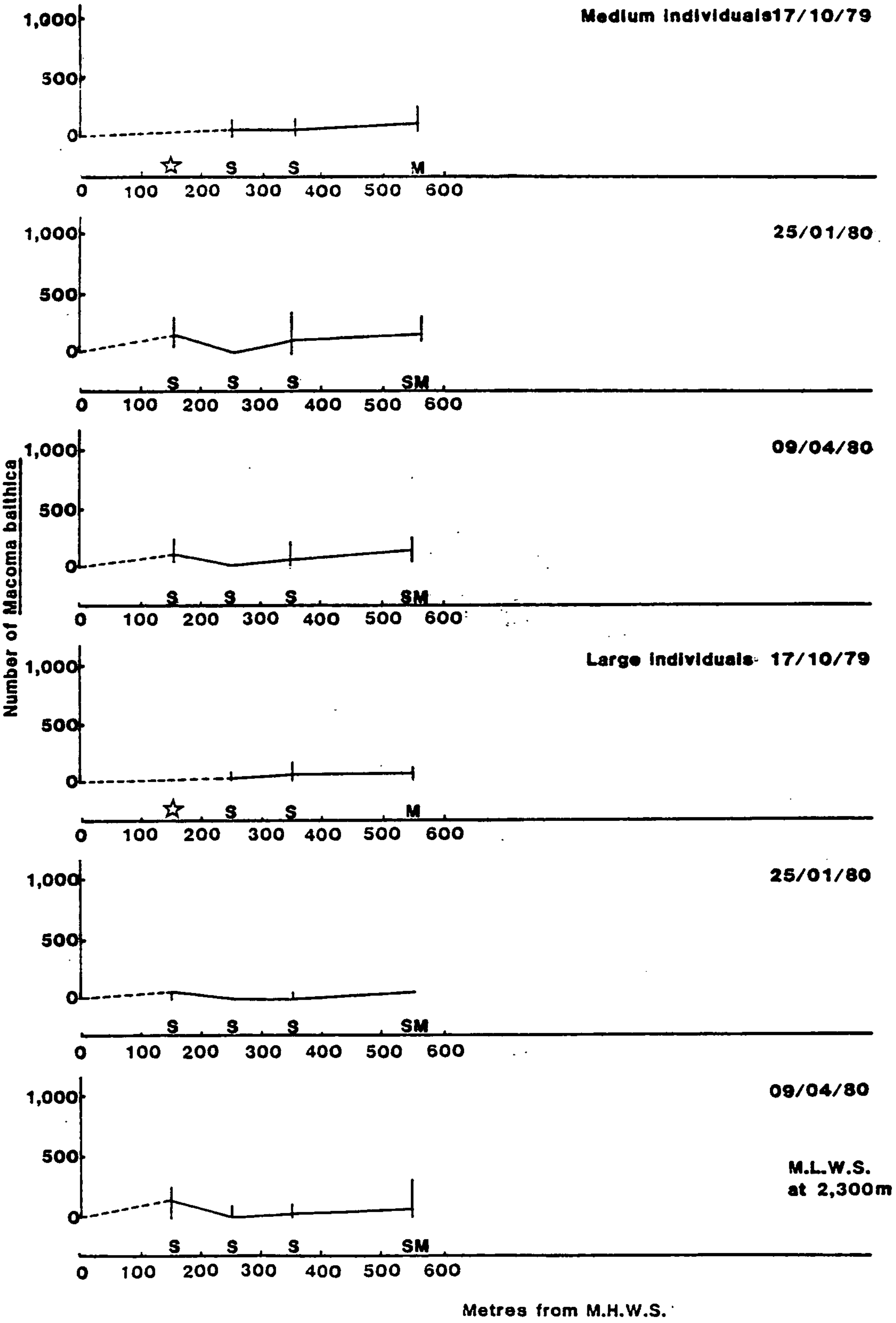


FIGURE 2.7b

Number of Macoma balthica per square metre in Weston Bay

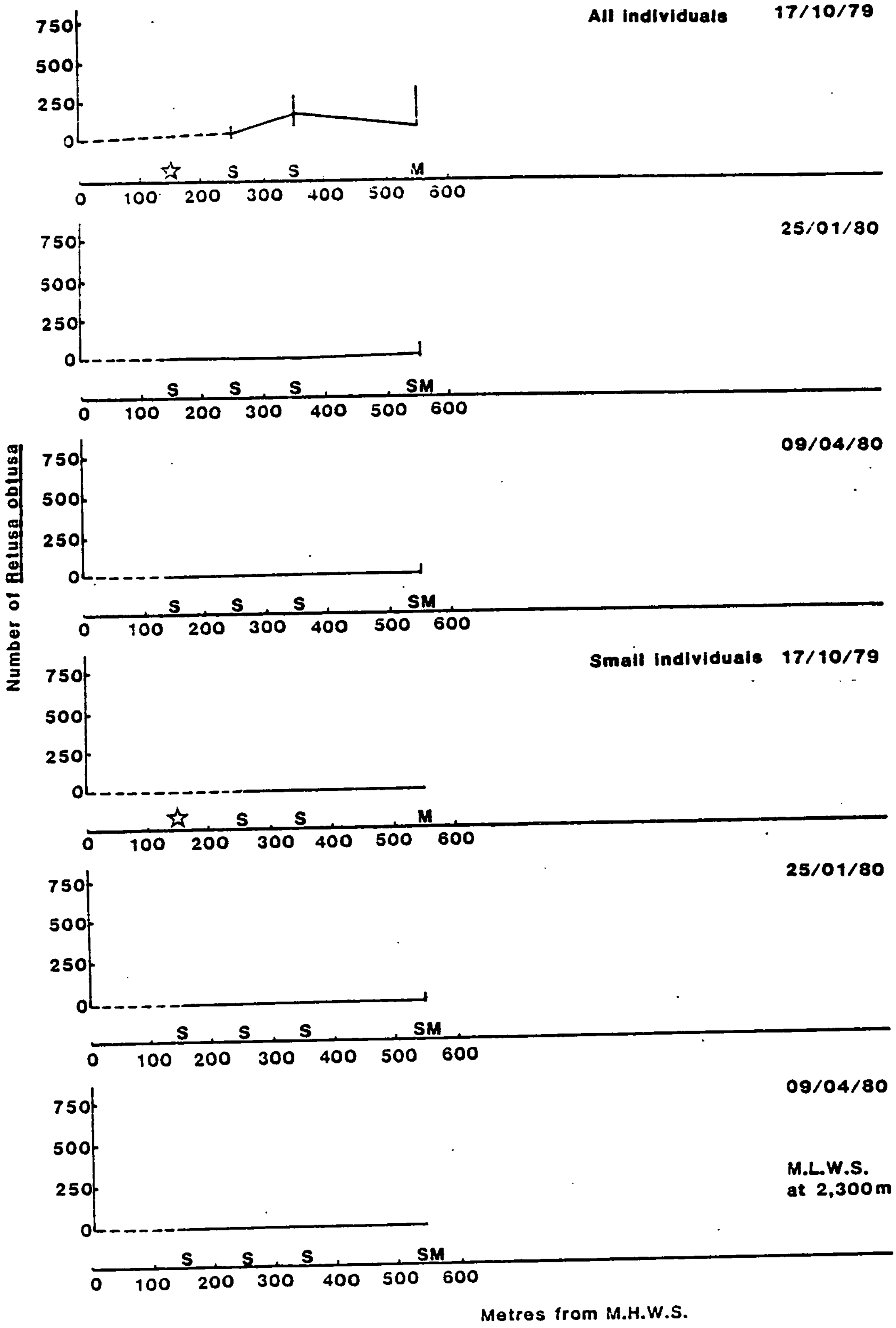


FIGURE 2.7c

Number of Retusa obtusa per square metre in Weston Bay

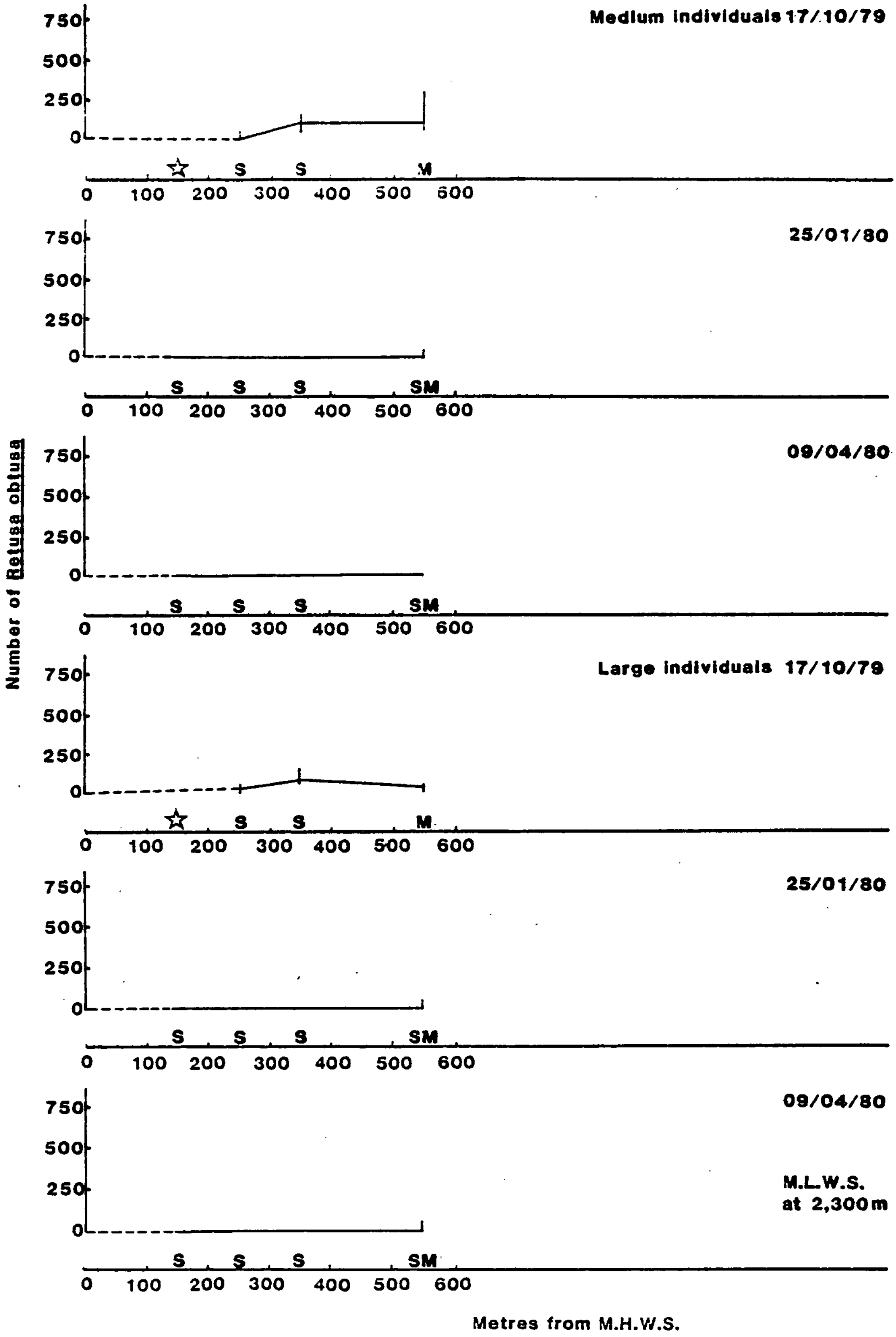


FIGURE 2.7d

Number of Retusa obtusa per square metre in Weston Bay

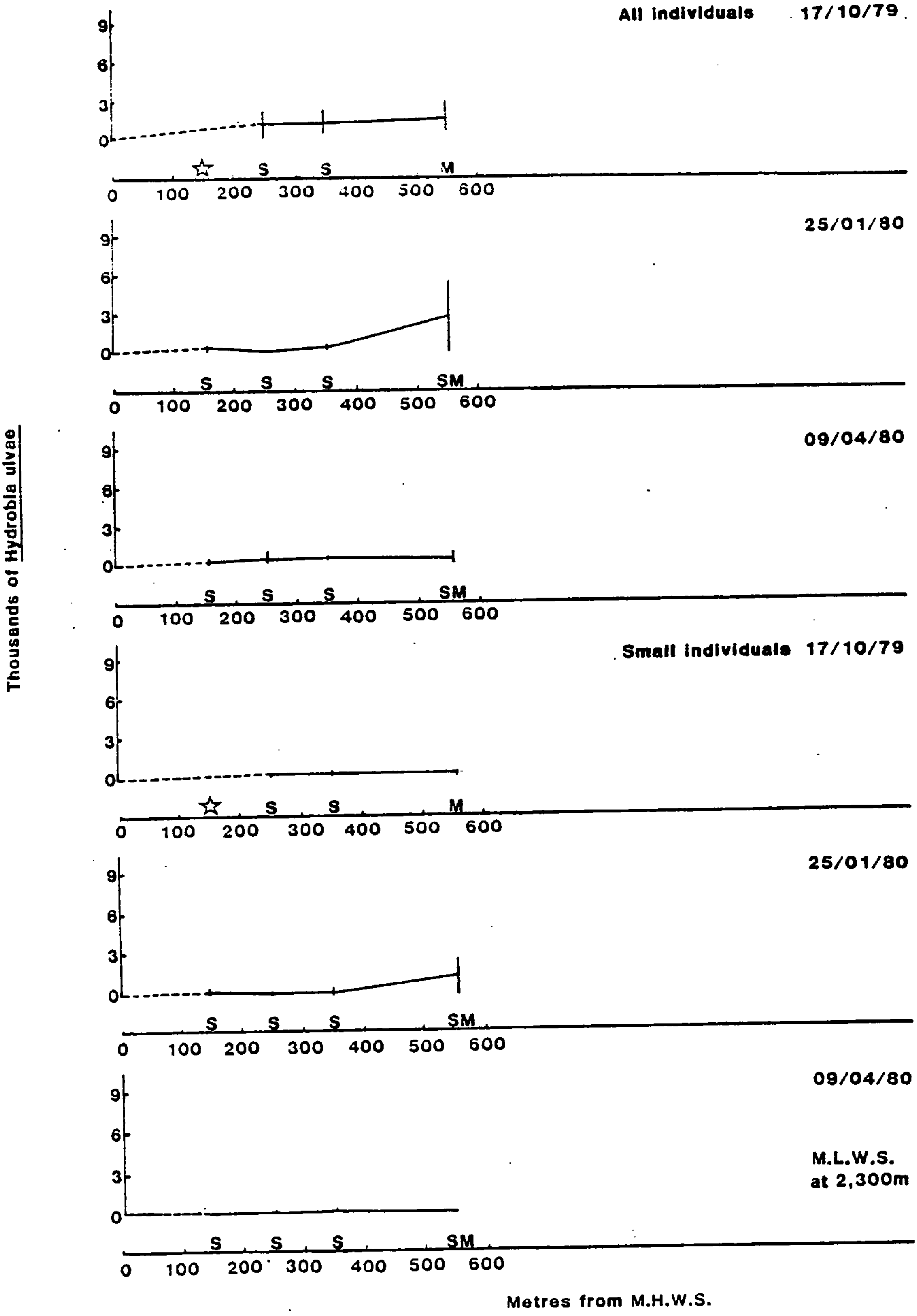


FIGURE 2.7e

Number of *Hydrobia ulvae* per square metre in Weston Bay

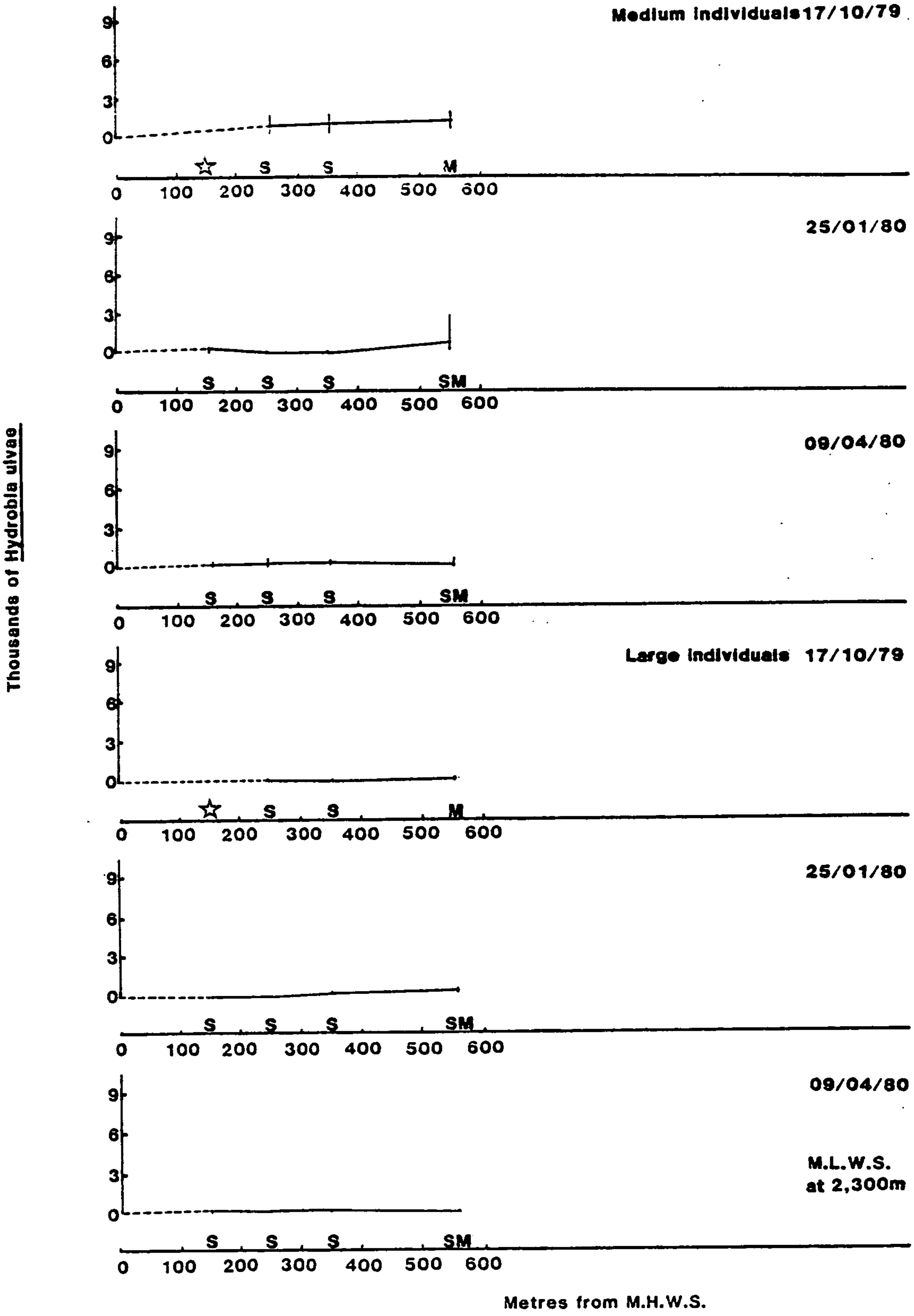


FIGURE 2.7f

Number of *Hydrobia ulvae* per square metre in Weston Bay

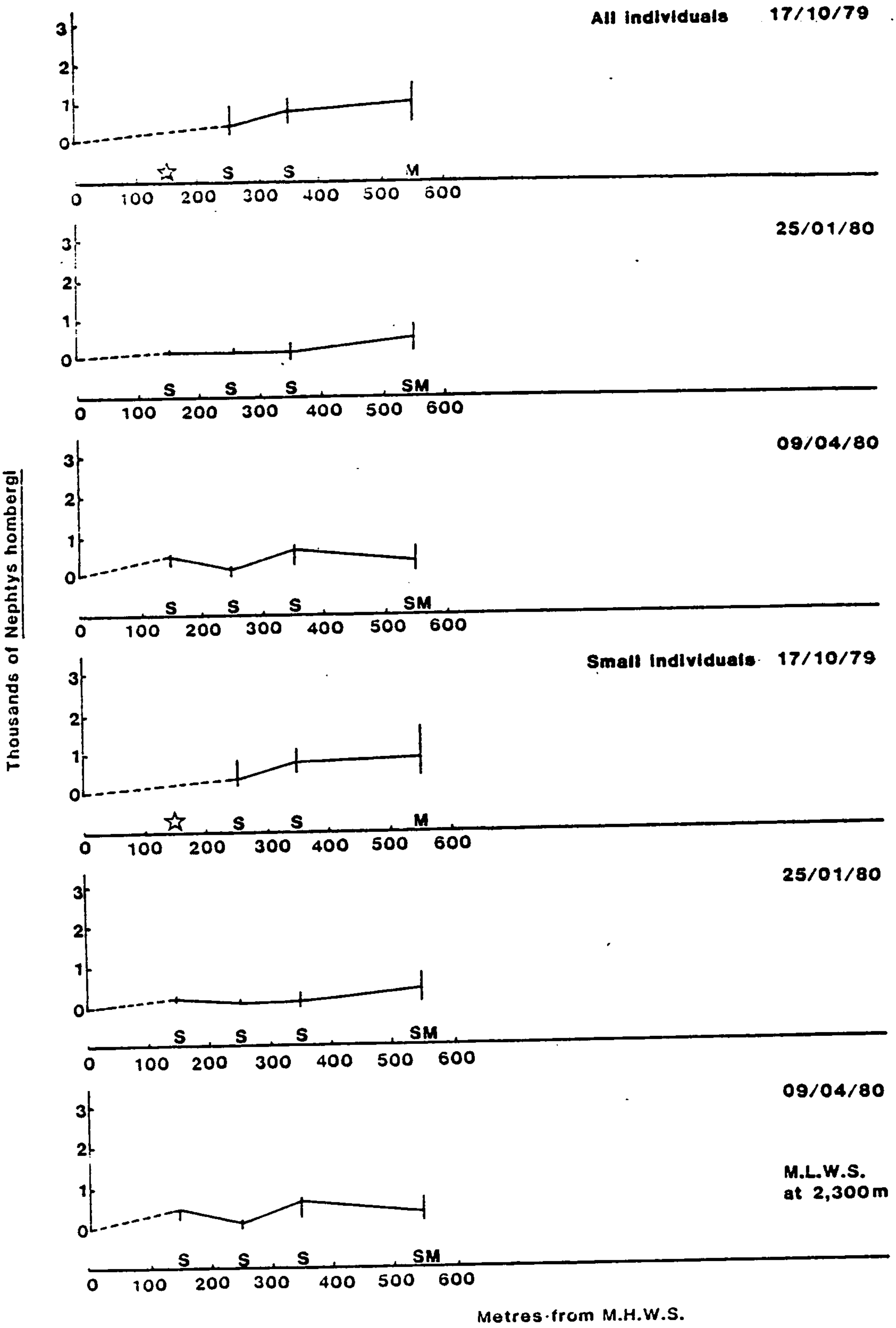


FIGURE 2.7g

Number of Nepthys hombergi per square metre in Weston Bay

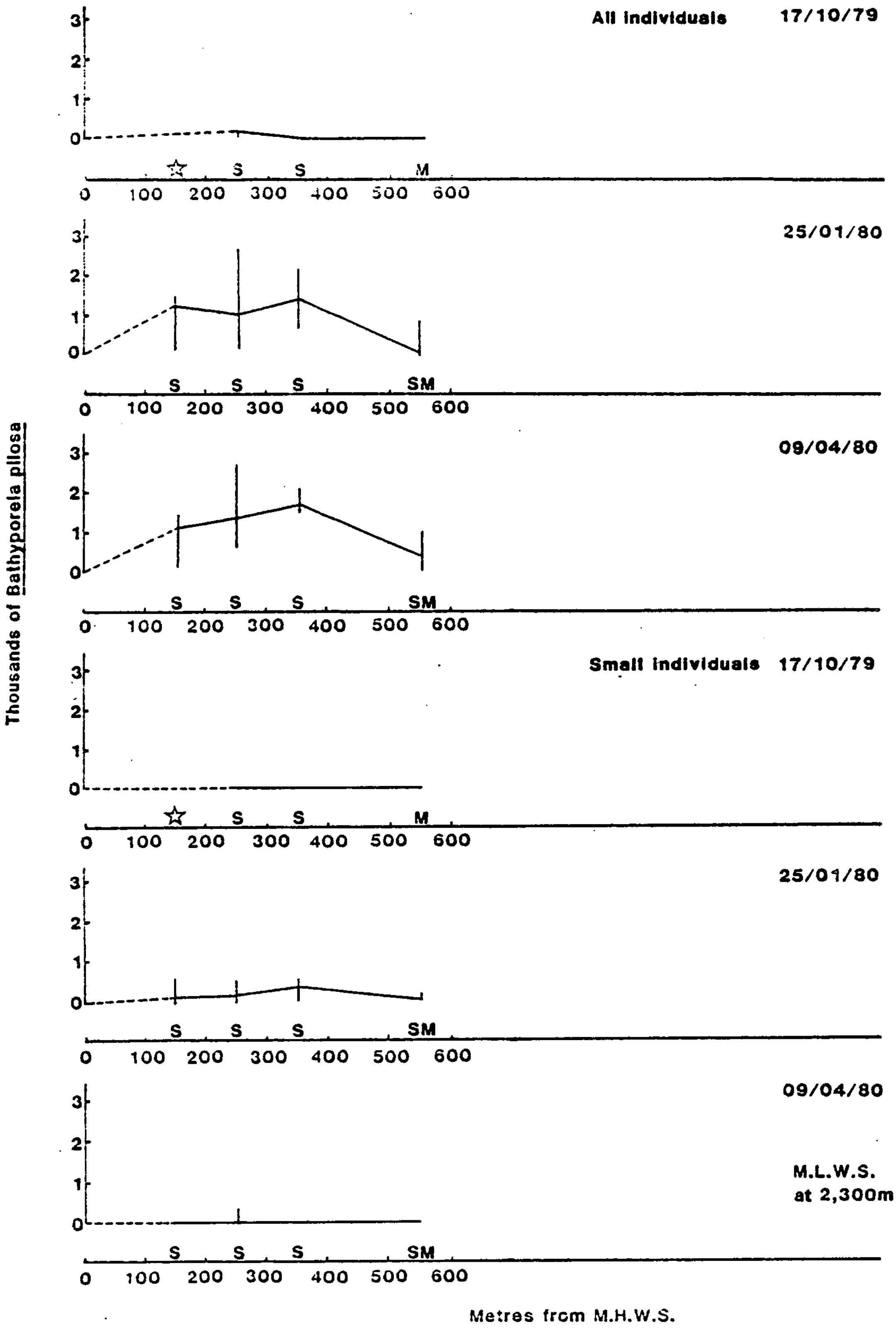


FIGURE 2.7h

Number of Bathyporeia pilosa per square metre in Weston Bay

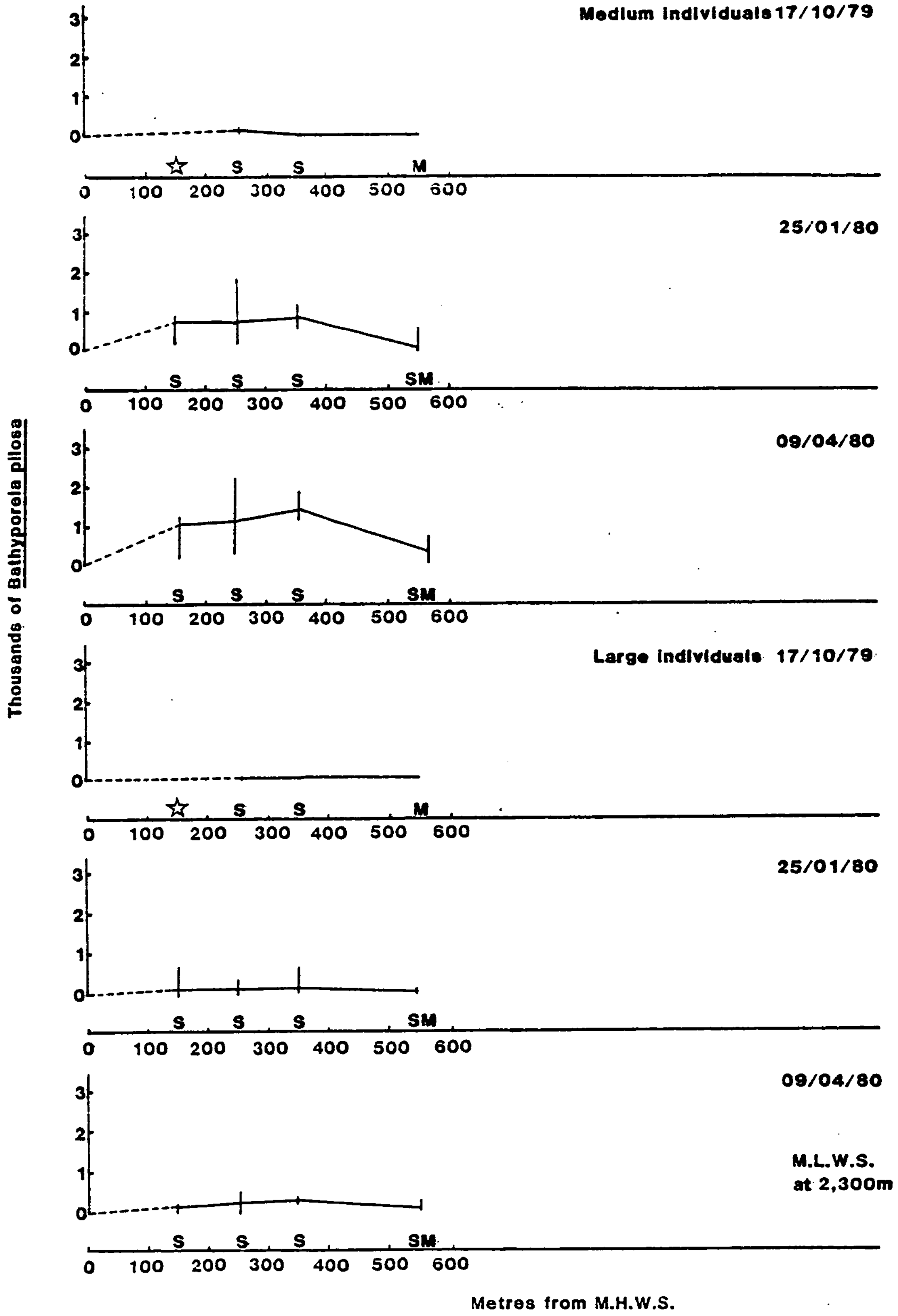


FIGURE 2.7i

Number of *Bathyporeia pilosa* per square metre in Weston Bay

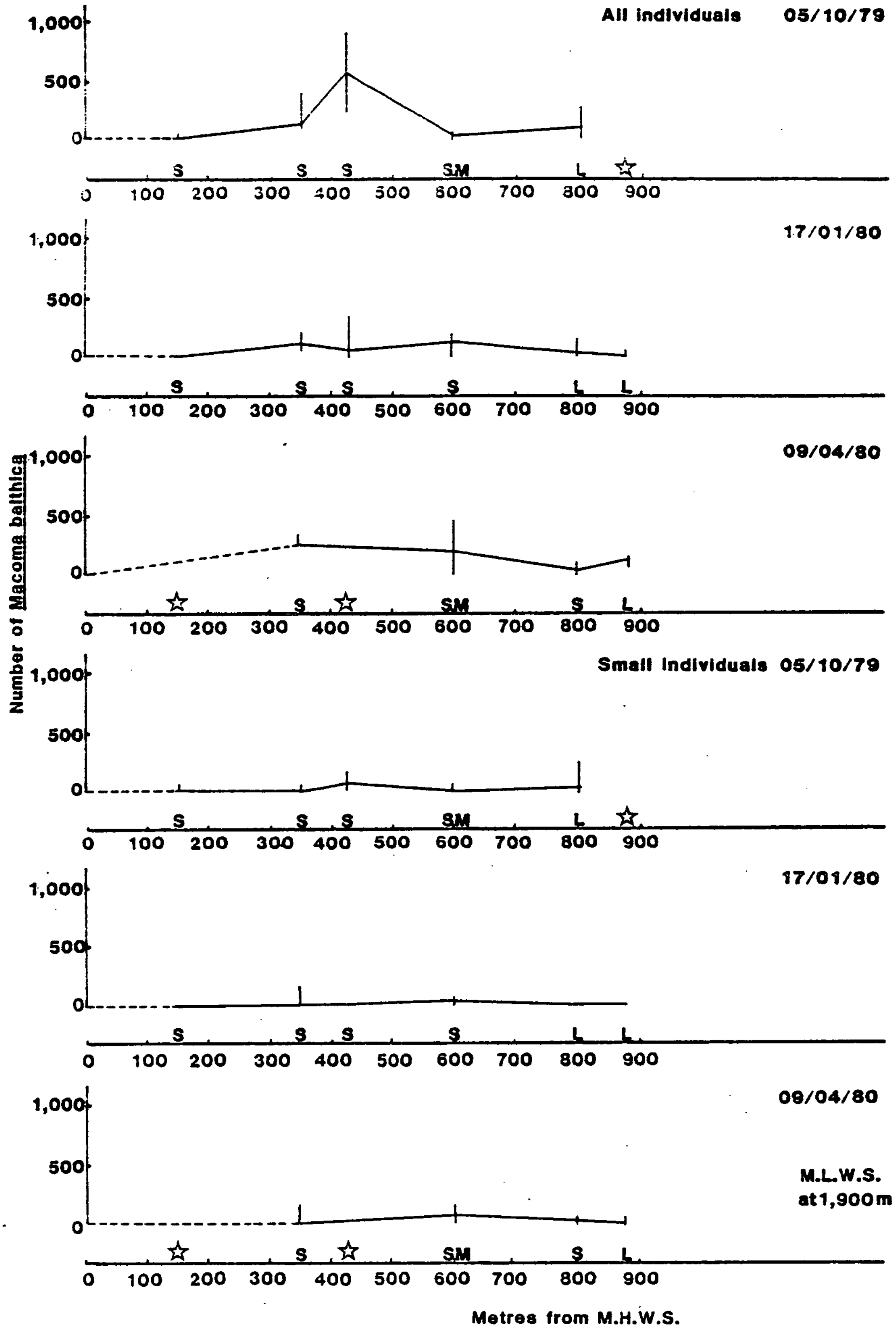


FIGURE 2.8a

Number of *Macoma balthica* per square metre at Brean Beach

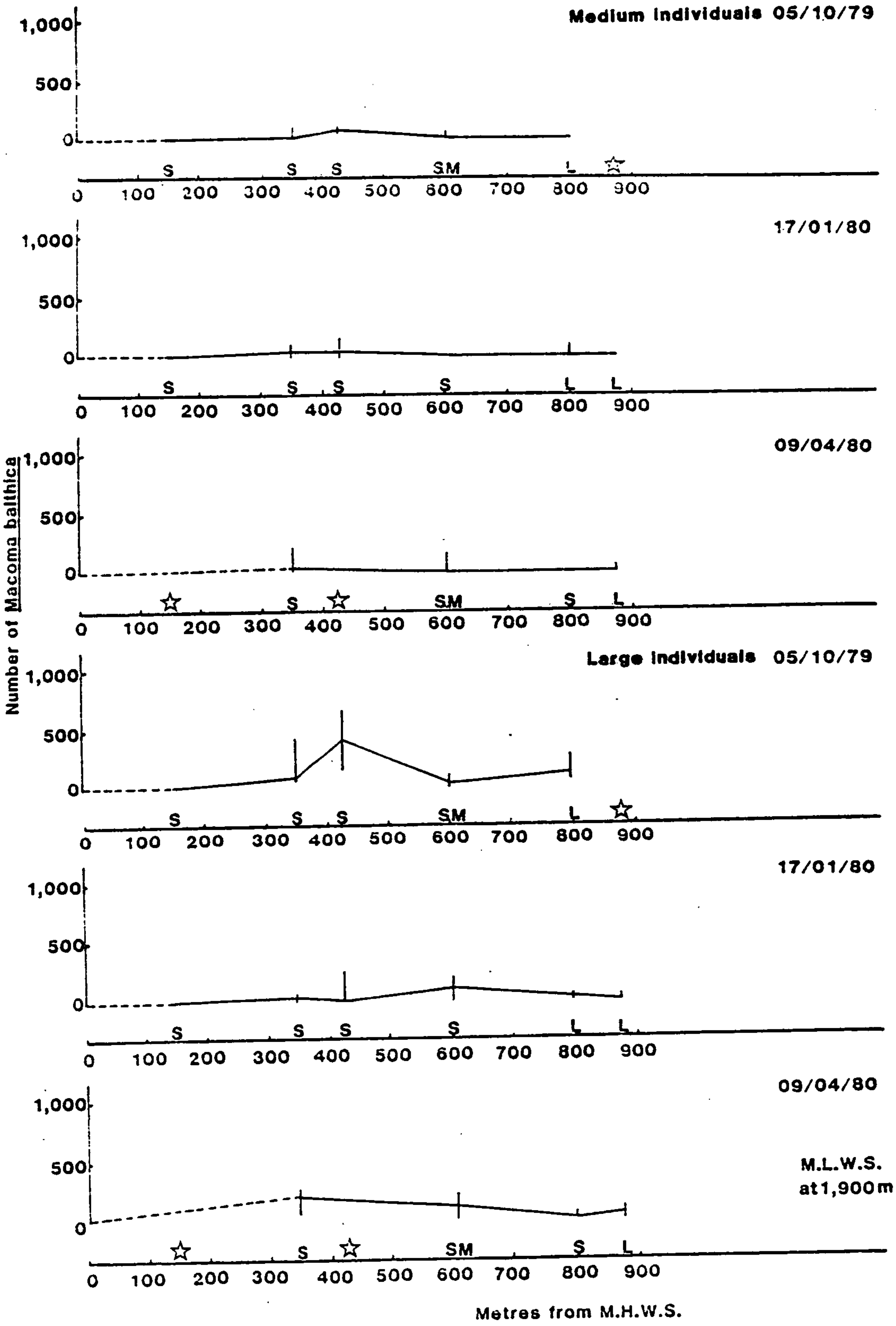


FIGURE 2.8b

Number of Macoma balthica per square metre at Brean Beach

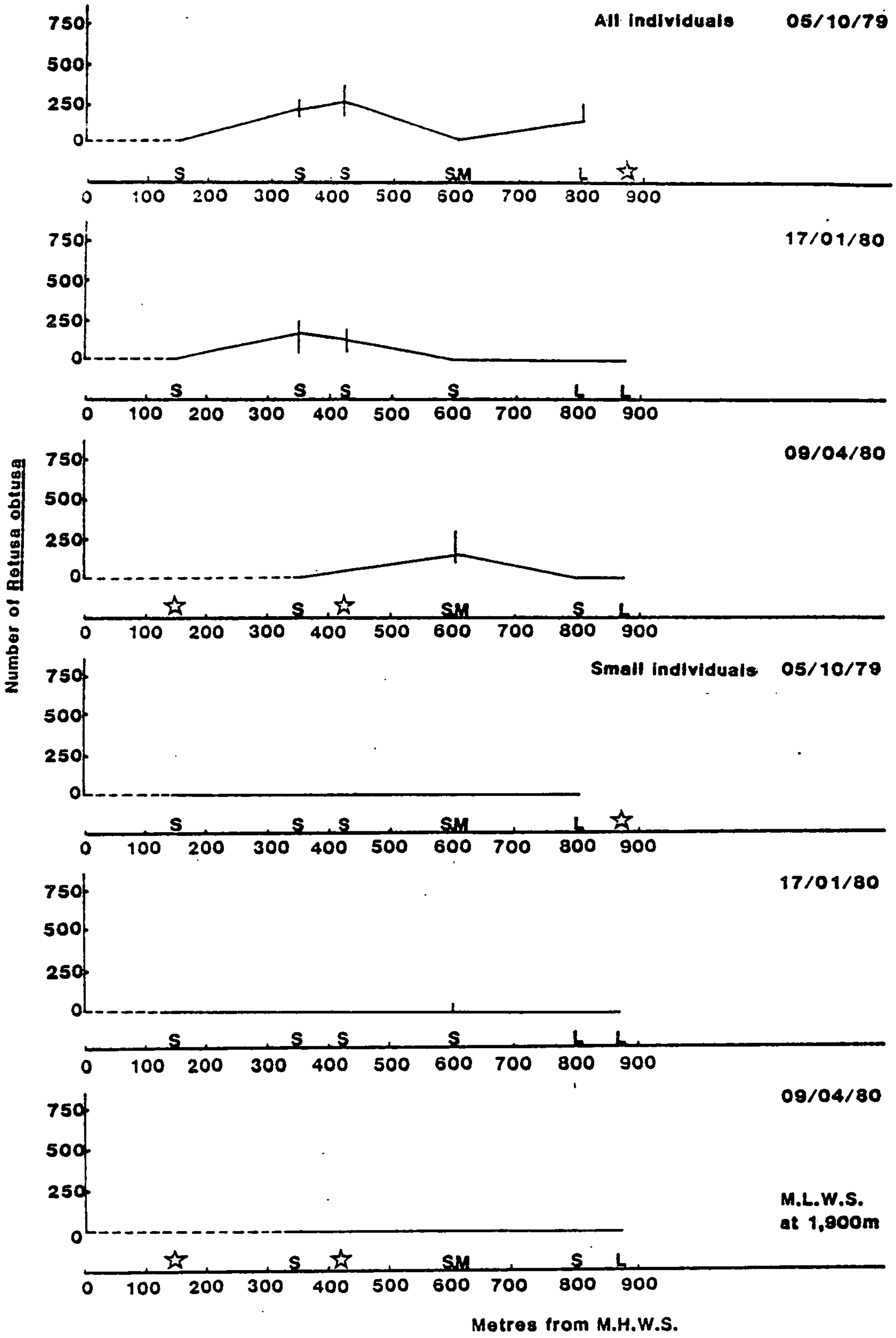


FIGURE 2.8c

Number of Retusa obtusa per square metre at Brean Beach

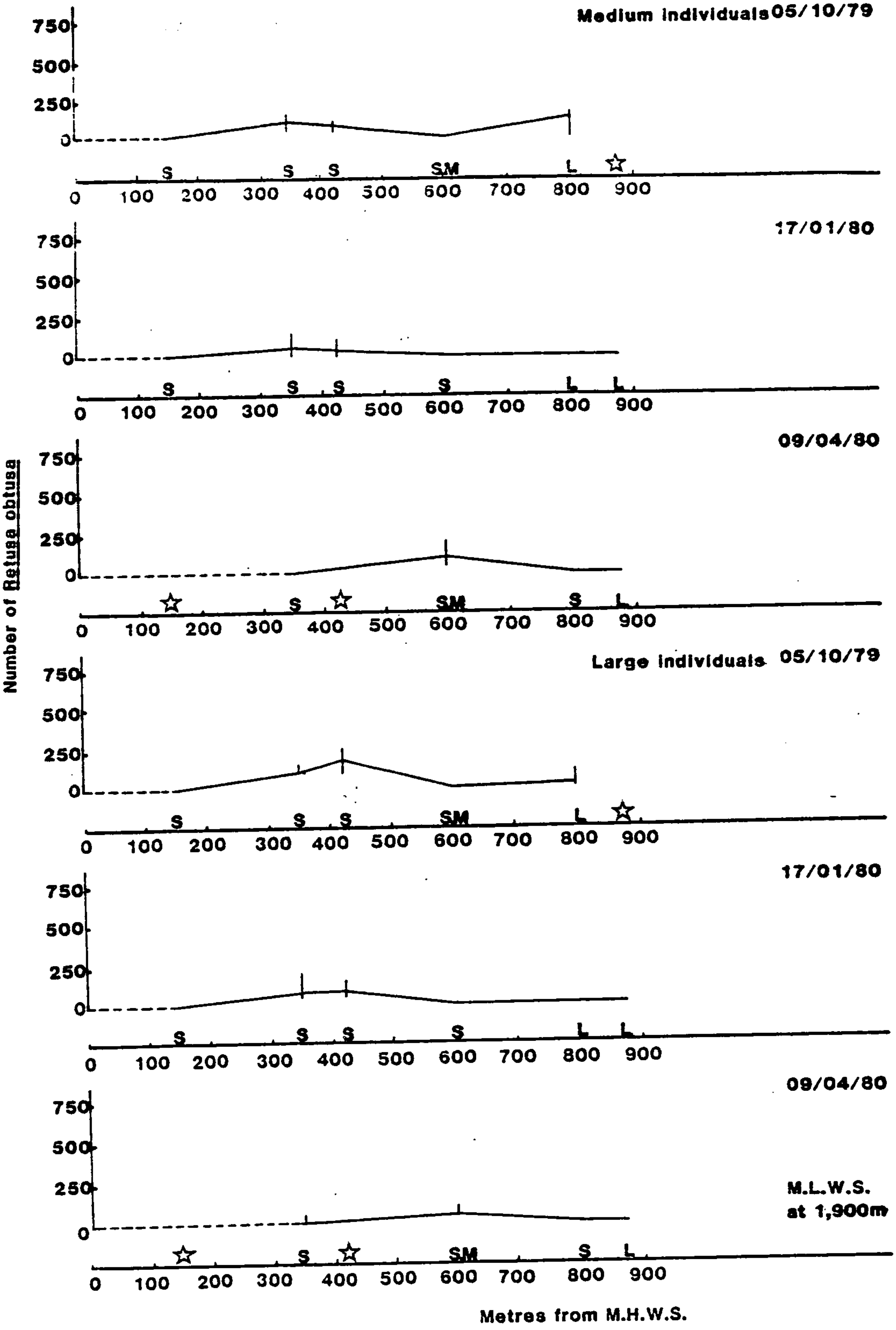


FIGURE 2.8d

Number of *Retusa obtusa* per square metre at Brean Beach

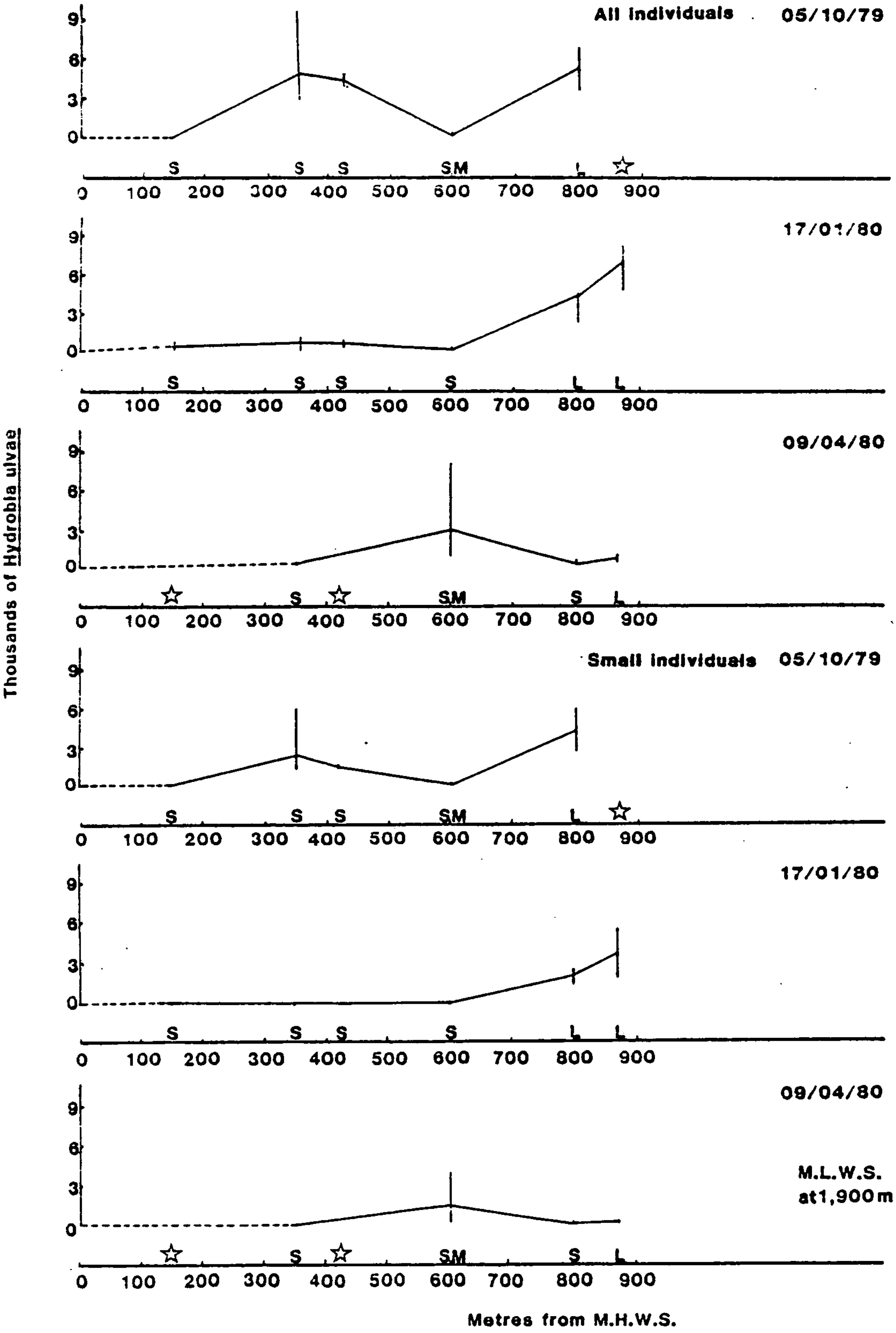


FIGURE 2.8e

Number of Hydrobia ulvae per square metre at Brean Beach

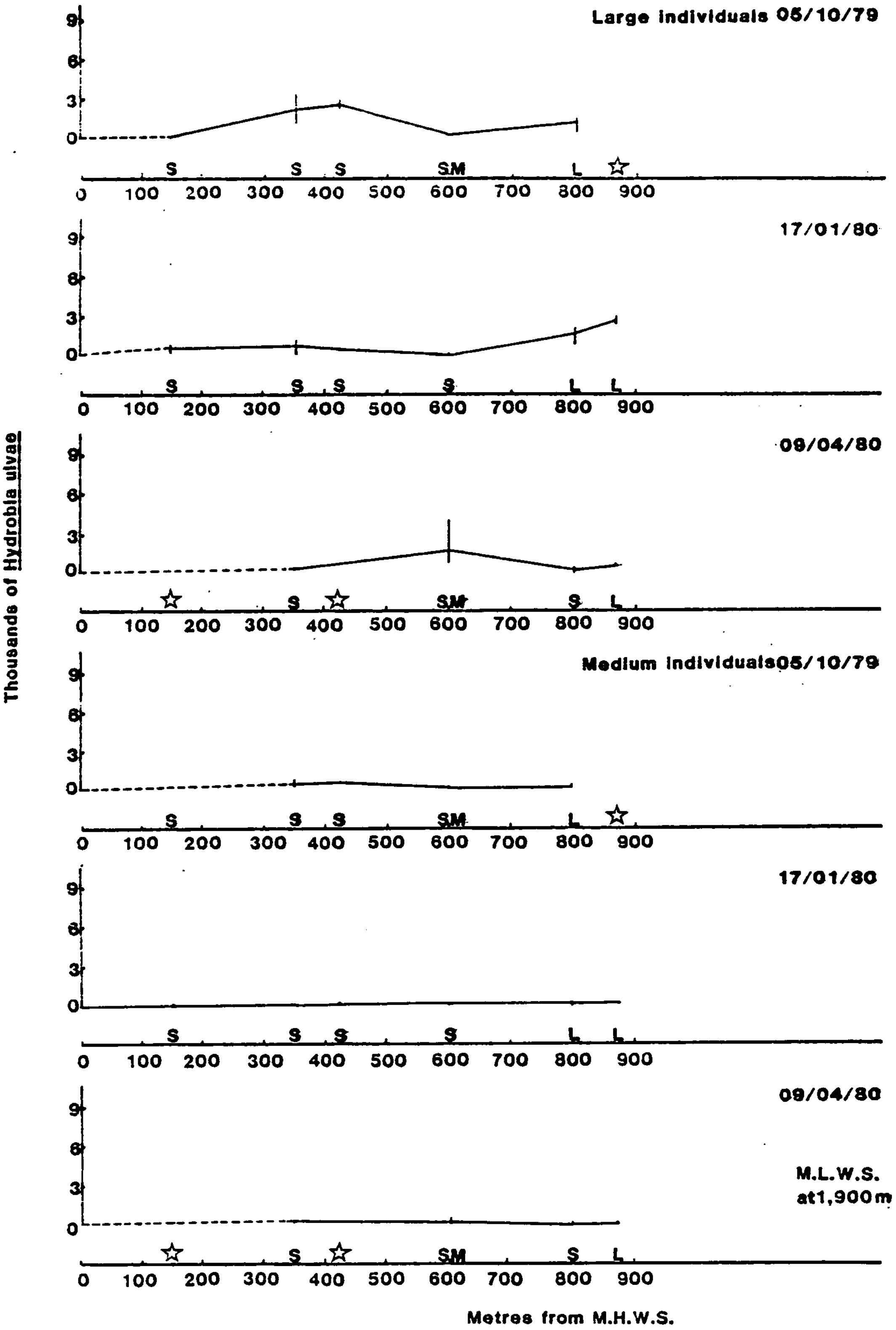


FIGURE 2.8f

Number of Hydrobia ulvae per square metre at Brean Beach

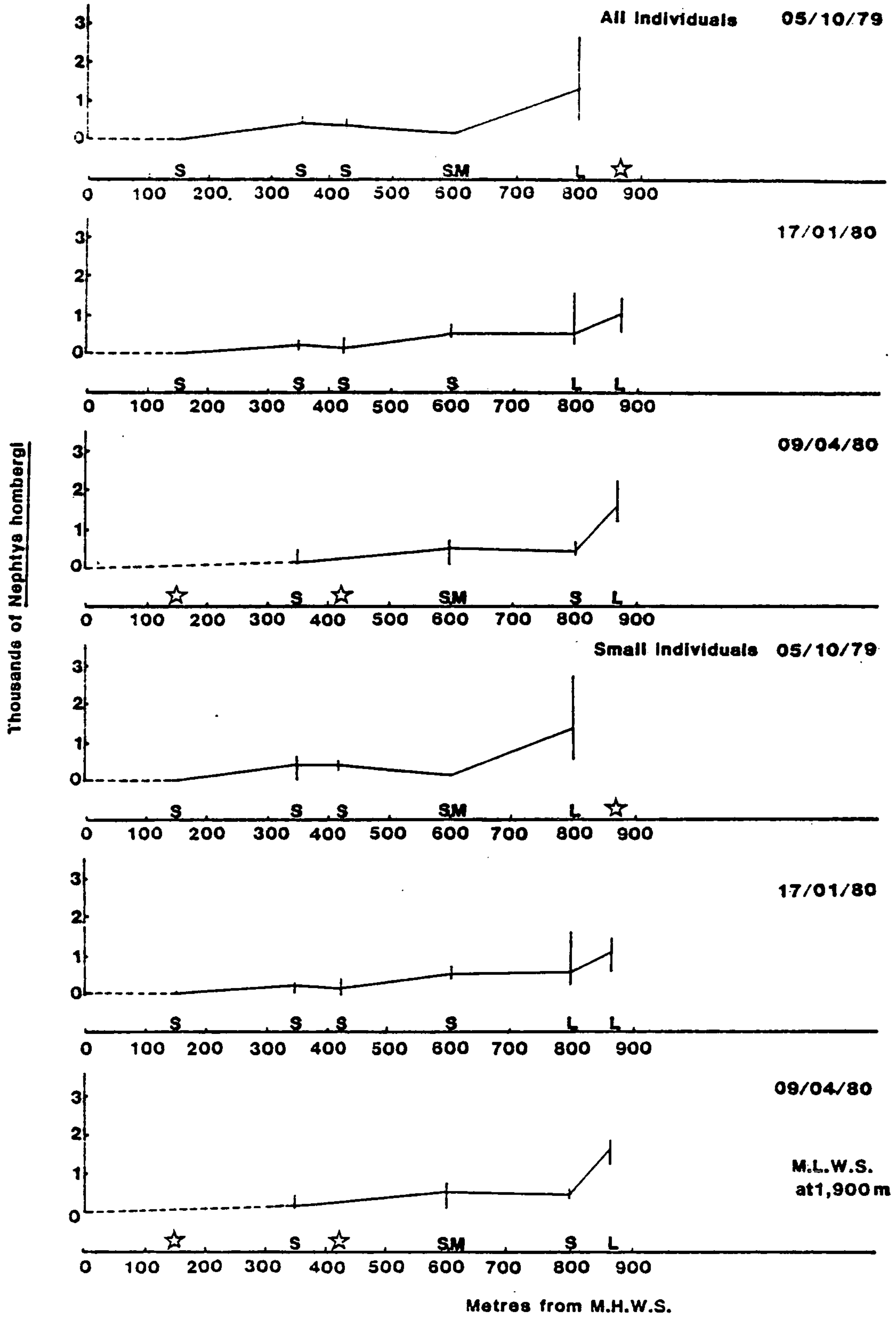


FIGURE 2.8g

Number of Nepthys hombergi per square metre at Brean Beach

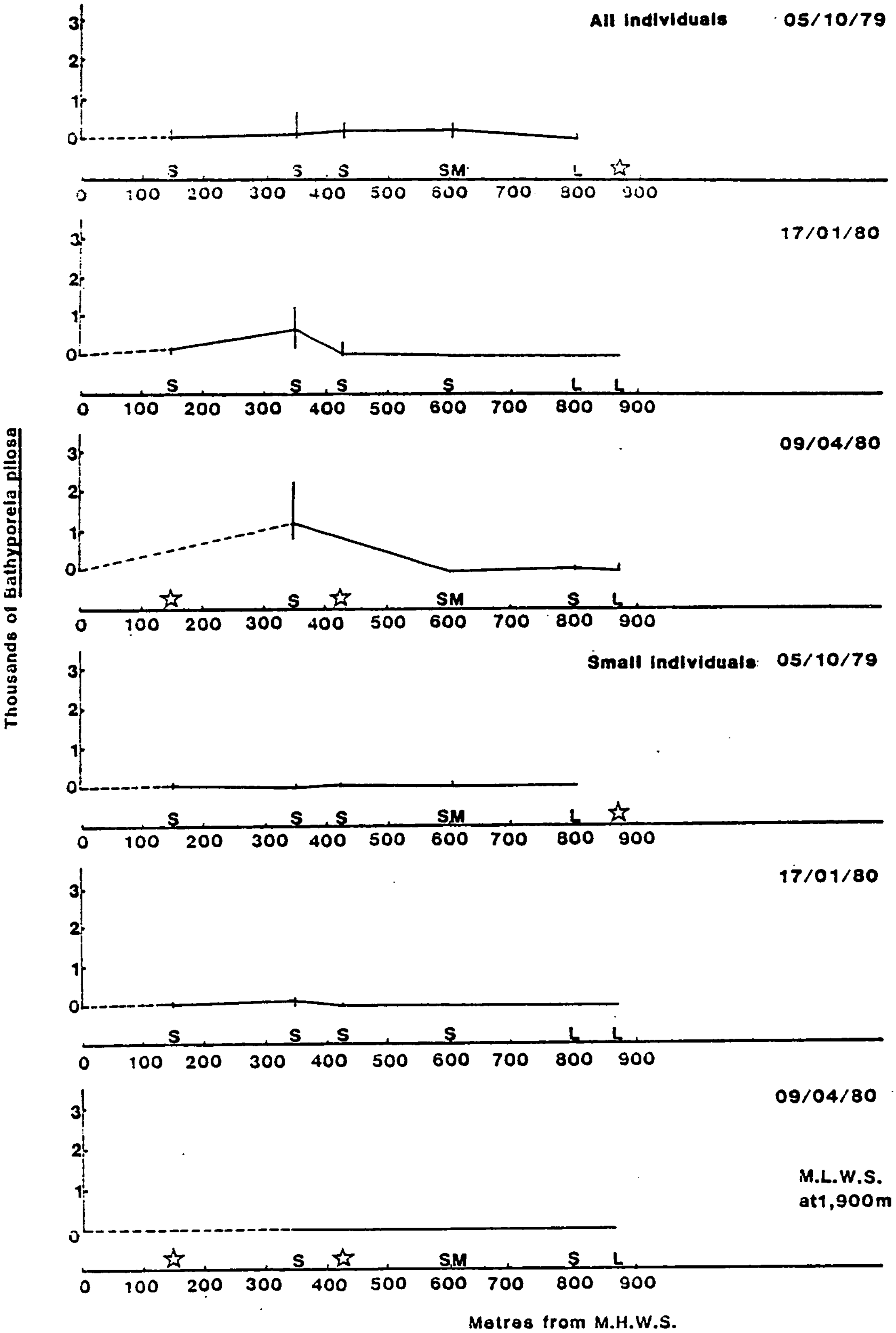


FIGURE 2.8h

Number of Bathyporeia pilosa per square metre at Brean Beach

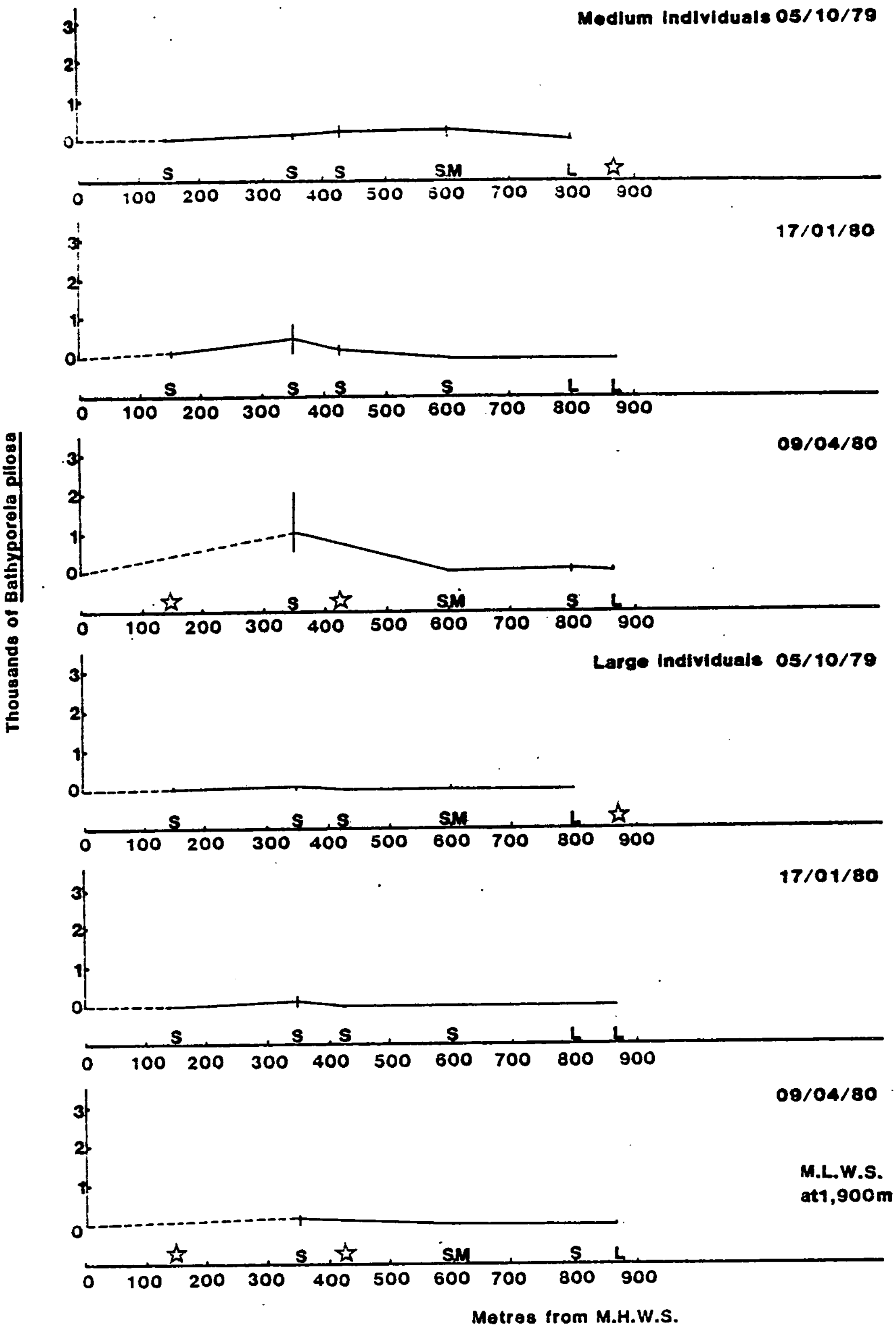


FIGURE 2.8i

Number of Bathyporeia pilosa per square metre at Brean Beach

TABLE 2.4

Maximum median densities of invertebrates in each bay on the south Severn

(distance from M.H.W.S. in metres and month are given in brackets)
(O = October; J = January; A = April)

Species	Severn Beach	Clevedon	Sand Bay	Weston Bay	Brean Beach
Macoma balthica	725 (250,O)	675 (150,O)	450 (700,O)	300 (150,A)	555 (425,A)
Retusa obtusa			325 (700,O)	175 (350,O)	250 (425,O)
Hydrobia ulvae	3,200 (250,O)	4,700 (150,J)	7,325 (1,200,O)	1,575 (550,O)	6,975 (600,J)
Nereis diversicolor	4,375 (550,A)	3,375 (150,O)	3,575 (1,200,O)	-	-
Nepthys hombergi	-	175 (250,A)	1,325 (1,450,J)	925 (550,O)	1,350 (800,O)
Corophium arenarium	-	-	4,500 (100,O)	-	-
Bathyporeia pilosa	-	-	275 (500,J)	1,725 (350,A)	1,200 (350,A)

TABLE 2.5

Maximum densities of invertebrates recovered in the Severn compared with elsewhere

Species	This Study	Boyden & Little	Worrall	Other Estuaries	Ref
Macoma balthica	725	844	5,645	7,227 Dovey	(1)
Retusa obtusa	325	56	-	75 Dovey	(1)
Hydrobia ulvae	7,325	9,600	11,470	80,000 Ythan	(2)
Nereis diversicolor	4,375	6,800	15,034	3,030 Tamar	(3)
Nepthys hombergi	1,350	432	-	500 Tamar	(3)
Nepthys cirrosa	750	20	-	8 Exe	(4)
Corophium arenarium	4,500	1,600	-	10,000 Dee	(5)
Bathyporeia pilosa	1,725	14,400	-	8,576 Towy	(6)

(1) Beanland, 1939; (2) Goss-Custard, 1970b; (3) Spooner & Moore, 1940; (4) Holme, 1949; (5) Stopford, 1951; (6) Howells, 1965.

mud occurred. In the liquid mud in Weston Bay and at Brean Beach Eurydice pulchra (Leach), Crangon vulgaris (Fabricus) and unidentified Cumaceans were all found at densities not exceeding 100 per square metre. Arenicola marina (Linnaeus) casts were seen on the sand in Sand Bay, Weston Bay and at Brean Beach but no worms were found in the samples.

Maximum densities of prey species

The maximum densities at any station within each bay are given in table 2.4. When these figures are compared with table 2.5 it can be seen that the maximum densities of some invertebrate species are noticeably different from data given by Boyden and Little (1973).

For Macoma balthica (Linnaeus) my study showed zonation down the shore similar to that which they found, and the maximum densities between bays varied from 300 per square metre to 725 per square metre; the data they gave suggested that densities at Clevedon and Sand Bay were about twenty percent of those at Brean, while I found the density at Clevedon to be greater than at Brean and detected little difference between Sand Bay and Brean. However, the maximum density found within the estuary was similar in the two studies (884 per square metre).

Retusa obtusa (Montagu) was the species for which my data contrasted most strongly with those of Boyden and Little: they found the species in Sand Bay, Weston Bay and at Stert with a maximum density of 56 per square metre and remarked on its absence from Brean Beach and Berrow. In this study it was present in significant numbers in Sand Bay (325 per square metre), Weston Bay (175 per square metre) and at Brean Beach (250 per square metre). It seems unlikely that sampling errors in either study could have accounted for the staggering difference in numbers and the most likely explanation is that Retusa has become much more numerous between 1972 and 1980. The only other British estuary in which the density of Retusa has been recorded is the Dovey (Wales) where it occurred at a density of 75 per square metre, thus the densities found in this study are apparently the highest recorded for any estuary in Britain to date. Although Retusa was not present in such high densities as many other species it is easy to detect on the surface as it leaves very obvious trails through the sand which birds could easily use as visual cues.

The maximum density of Hydrobia found by Boyden and Little (9,600 per square metre) was only slightly greater than in the present study (7,325 per square metre). Its maximum density in Sand Bay was found to be higher in this study; in contrast its maximum density in Weston Bay was lower than that found by Boyden and Little the latter may well be accounted for by the fact that I was not able to sample in the lower area of Weston Bay.

Nereis was present in significant numbers only at Severn Beach, Clevedon and Sand Bay. In all these bays Nereis was found at higher densities during 1979/80 than it had been in 1972; this could be due to the sampling procedures adopted in the two studies. As it will be seen from 2.4, sieving can easily destroy smaller Nereids and Boyden and Little also remark that Nereis densities could only be considered relative as many individuals burrowed deeper than their sample depth of 100 mm.

The densities of Nephtys hombergi (Lamarck) were much greater in this study than in Boyden and Littles′ in all bays in which the species occurred, perhaps partly because of different sampling procedures. However, as the difference is so large it seems more likely that there has been a substantial increase in density.

In both studies Corophium arenarium (Crawford) occurred in significant numbers only in Sand Bay on the high sand area. However, its density in this area was three times as great in 1979/80 as in 1972. Bathyporeia pilosa (Lindstrom) on the other hand was only at a third of the density in Weston Bay in 1979/80 when compared to 1972; however, it′s density had increased at Brean.

High densities of Nemertines were recorded in some bays, but most were very small and I suspect that they are not a major food source for Dunlin.

Invertebrates found in each bay

Each bay was strikingly different from all the others and each will be discussed separately.

Severn Beach

It was only possible to sample the upper shore at Severn Beach as there was a large area of shingle between 600 m and M.L.W.S. at 1,200 m. Cursory observation showed that large numbers of Littorina littorea (Linnaeus) were present in the shingle, but no other species was found which could be an important food source for Dunlin. The area of mudflat which was sampled showed marked seasonal changes in the surface substrate, mainly due to the large amount of mud worn away in early winter and the subsequent deposition of liquid mud. The most numerous prey species was Nereis which was abundant at stations between 250 m and 550 m down the shore. Macoma occurred at densities up to a median of 725 per square metre at station two in October, but the densities in January were very much lower and it is questionable whether Macoma was present at high enough densities to be a major food source. The third prey species available was Hydrobia which was present in reasonable numbers in October and January although by April the numbers were very low. It must be noted however that there were very few medium or large Hydrobia present at any station.

When sampling in April it was noticed that there were a large number of small (less than 10 mm diameter) globules of oil in the surface layer of the mud. A small stick was used to probe randomly at the surface and this made contact with a globule of oil about once in twenty probes. The oil could have had detrimental effects on both the invertebrate populations and the wading birds wintering on the site.

Clevedon

There were marked changes in the surface substrates at Clevedon through the winter; these are detailed in Chapter 5.

Four prey species occurred at Clevedon. Again the most important species was Nereis which was present at high densities on the upper mud flat; on the steep middle area and the lower liquid mud area it was present at much lower densities. Macoma was also present at reasonable densities in the upper mud flat and in contrast to Severn Beach its density did not change markedly through the winter. In October Hydrobia was present at high densities only on the upper mud flat but as the winter progressed it became more evenly distributed throughout all stations. A fourth species, Nephtys hombergi, although absent in October was present at very low densities in January and at slightly higher levels in April: it is possible that its occurrence was related to the large sediment changes in that winter.

Sand Bay

In contrast to Clevedon and Severn Beach, Sand Bay has two different major substrates, the top 500 m being predominantly flat sand and the lower 1,000 m being mud. Different invertebrate species were present in the two substrates: the upper sand area was dominated by Corophium arenarium with small numbers of Retusa and a few Bathyporeia; the lower mud area had high densities of Nereis, Macoma and Hydrobia. Nephtys hombergi occurred at high densities only at the station nearest low water mark.

Weston Bay

Due to the treacherous nature of the outer reaches of this bay it was only possible to sample the top 600 m. This area was mainly sand with mud at the outermost station. The most important species in the area was Bathyporeia. Macoma occurred irregularly throughout the sampling area. In contrast Hydrobia occurred at low densities in October and April, but in January was present at high densities (over 3,000 per square metre) at the lowest sampling point: concentration in this area could be due to individuals being washed up the shore from lower reaches. Nephtys hombergi was the only Nereid present and did not exceed 1,000 per square metre. Retusa was found only in October, except at the lowest station.

I was not able to sample the major Dunlin feeding areas in Weston Bay, but this is a bay which Little and Boyden (1977) studied intensively using a "mud horse". Although their sample transect was not in the same position as mine they obtained broadly similar results in the sand portion of their transect except for Nephtys hombergi which they barely encountered in the sand area. The main species that they found in the lower portion of Weston Bay were Hydrobia, Nephtys hombergi and Macoma: it is unlikely that the prey available in this bay have changed drastically since their study.

Brean Beach

For the same reason as in Weston Bay it was only possible to sample the upper sand area at Brean Beach. This is the only site at which my data on vertical distribution differed noticeably from those obtained by Boyden and Little (1973). The latter authors commented that Retusa was absent even though its prey (Hydrobia) was at its highest density here. I found Retusa at up to 250 per square metre, which is considerably higher than the highest density that they recorded for this species anywhere on the Severn (56 per square metre).

The upper, steep, portion of the sand beach had extremely few invertebrates of any kind; further down the beach invertebrate prey were more abundant. Densities of large Macoma (which are too big for Dunlin to feed on) were erratic, but densities of medium and small individuals were more uniform. Hydrobia was also unevenly distributed although present at high densities in places. In October and April (but not in January) there was a strong correlation between the density of Hydrobia and that of Retusa. The density of Nephtys hombergi steadily increased towards the lower levels, in contrast Bathyporeia tended to occur in the middle of the sandy area.

From the comparison of the two studies on the invertebrate distribution on the south side of the Severn it can be seen that although the major prey species have not changed significantly between 1972 and 1979/80 the relative importance of each species has changed. This could have important repercussions for the Dunlin populations in each bay; these will be discussed later.

2.4 Temperature/depth sampling

2.4.1 Methods

Samples were taken using the sledge sampler as described in 2.3. In the 1979/80 season each sample set consisted of a 0.02 square metre skim sample (32 mm deep) and a 0.0082 square metre core sample (150 mm deep), the core sample always being taken not more than 250 mm away from the skim sample. In the 1980/81 season a skim sample was taken as previously described (either 25 mm or 40 mm deep), but a 0.0082 square metre core sample was taken from the skim. The sledge was then carefully removed from the surface and a 0.0082 square metre core sample (150 mm deep) was taken from underneath it so as to match the sample taken from the sledge. In practice the match was not exact but the centres of the two samples were normally within 20 mm of one another. On each day the mud temperature (to the nearest 0.5 degrees Celsius) was taken at 20 mm below the surface. Sieving and measuring procedures were as described in 2.3.

The following equations were used to calculate the percentage of *Nereis* at the surface:

1979/80

$$\text{Percentage at surface} = \frac{\text{Number of } \textit{Nereis} \text{ heads in the skim}}{\text{Number of } \textit{Nereis} \text{ heads in the core}} \times 100$$

1980/81

$$\text{Percentage at surface} = \frac{\text{Number of } \textit{Nereis} \text{ heads in the skim}}{\text{Number of } \textit{Nereis} \text{ heads in the skim} + \text{core}} \times 100$$

The data were transformed using an arcsin transformation before analysis.

2.4.2 Results

In the 1979/80 season the data obtained did not show the expected correlation between temperature and proportion of *Nereis* near the surface (figs 2.9 and 2.10); this was probably due to the enormous variation in density of *Nereis* between skim samples and nearby core samples and was exacerbated by problems in sieving (see

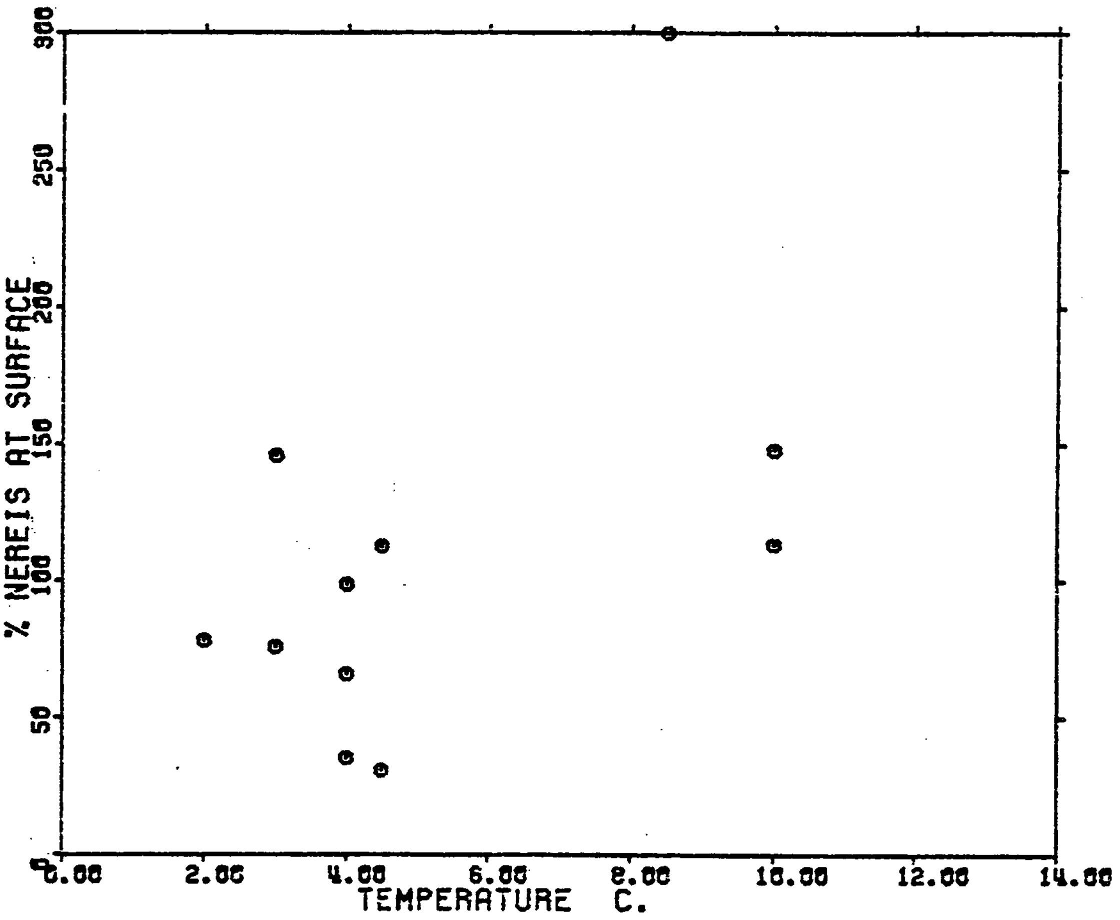


FIGURE 2.9

Percentage of small Nereis in the top 32 mm of mud against temperature (data collected in 1979/80; each point represents the mean of 4 samples)

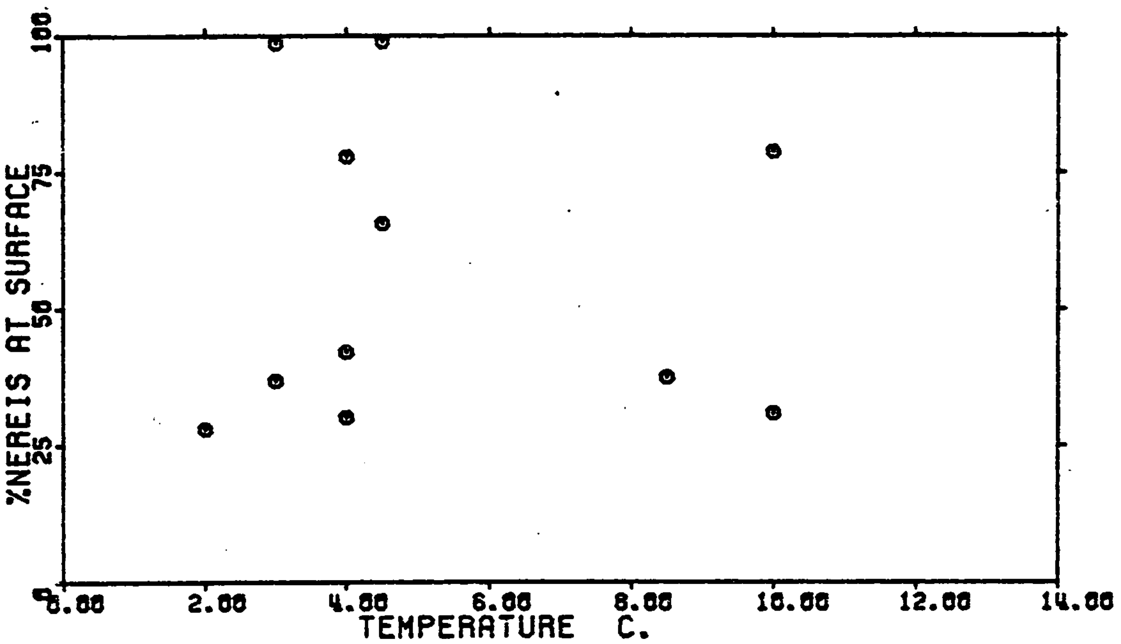


FIGURE 2.10

Percentage of medium <u>Nereis</u> in the top 32 mm of mud against temperature (data collected in 1979/80; each point represents the mean of 4 samples) later). The method was revised for the 1980/81 season as detailed in methods. Figures 2.11 and 2.12 plot the proportion of small Nereis at different levels against date for 1980/81. There appears to be a gradual reduction in the proportion above 25 mm depth until February, but with virtually all Nereis at the surface in March. However, the vast proportion remained above 43 mm except in late February when the temperature was very low.

The situation for medium size Nereis appears very different (figures 2.13 and 2.14). Between the beginning of December and the end of February there were virtually none in the upper 25 mm and usually less than half in the top 43 mm.

When the proportion near the surface is plotted against the mud temperature (figures 2.15 to 2.18) a strong positive correlation is found in all cases.

There is evidence to suggest that a significant proportion of the small Nereis were destroyed during sieving of the core samples. There was a significantly larger number of Nereis in the 43 mm skim plus core set than in the 25 mm skim plus core set ($t = 2.88$, $p>0.05$). The mud in the core samples was often very difficult to get into suspension to pour through the sieve and on these occasions small individuals would probably be destroyed. This will tend to distort the true values as it would appear that there was a higher percentage at the surface when the actual percentage at the surface was near 50 percent; the effect diminishes towards zero and one hundred percent. The data were not sufficient to obtain a correction factor but it is likely that in the order of thirty to fifty percent of the small Nereis were destroyed in the core samples; this effect may have exaggerated the anomalous results in

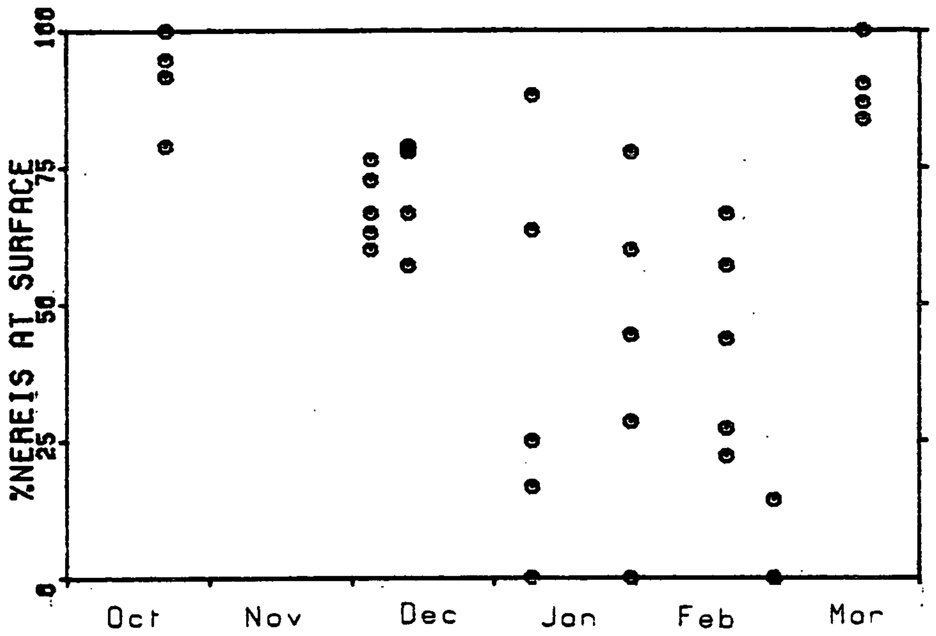


FIGURE 2.11

Percentage of small Nereis in the top 25 mm of mud against date

(data collected in 1980/81)

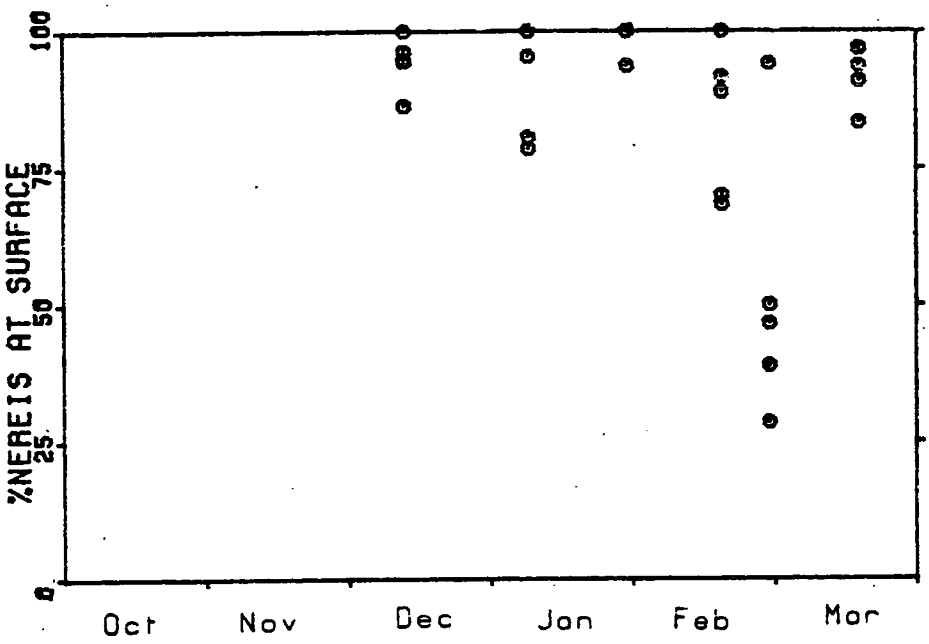


FIGURE 2.12

Percentage of small Nereis in the top 43 mm of mud against date

(data collected in 1980/81)

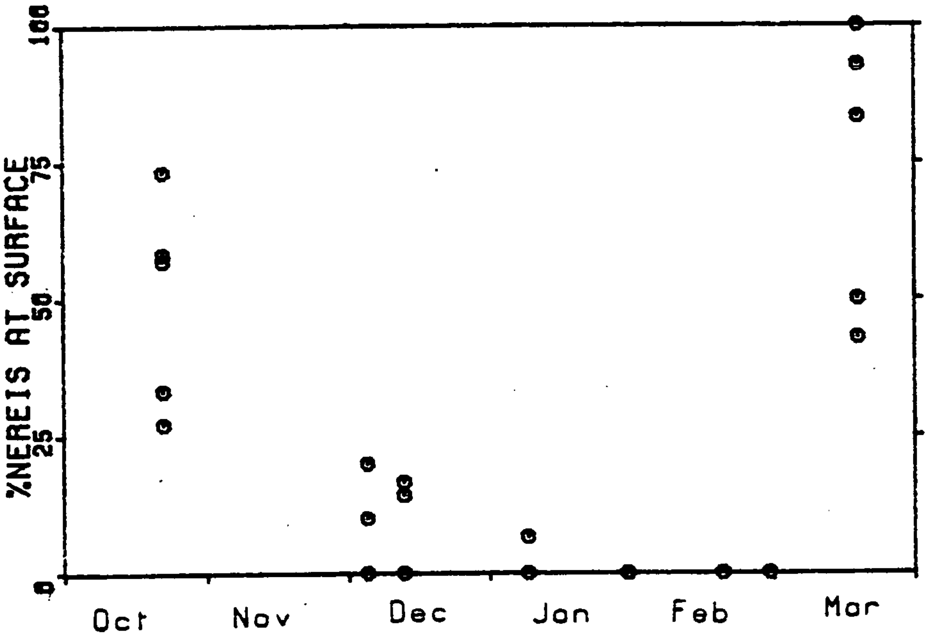


FIGURE 2.13

Percentage of medium Nereis in the top 25 mm of mud against date

(data collected in 1980/81)

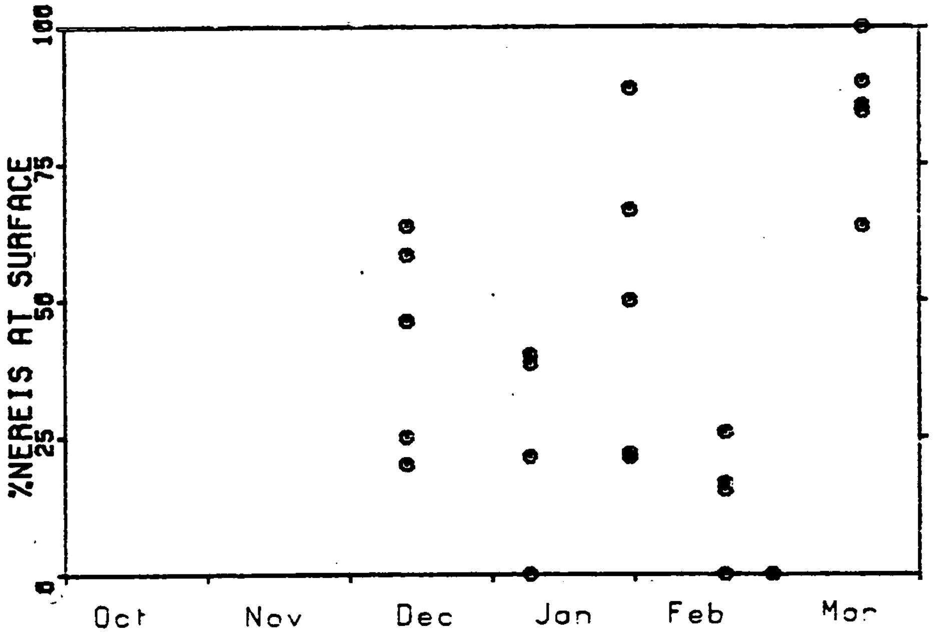


FIGURE 2.14

Percentage of medium Nereis in the top 43 mm of mud against date

(data collected in 1980/81)

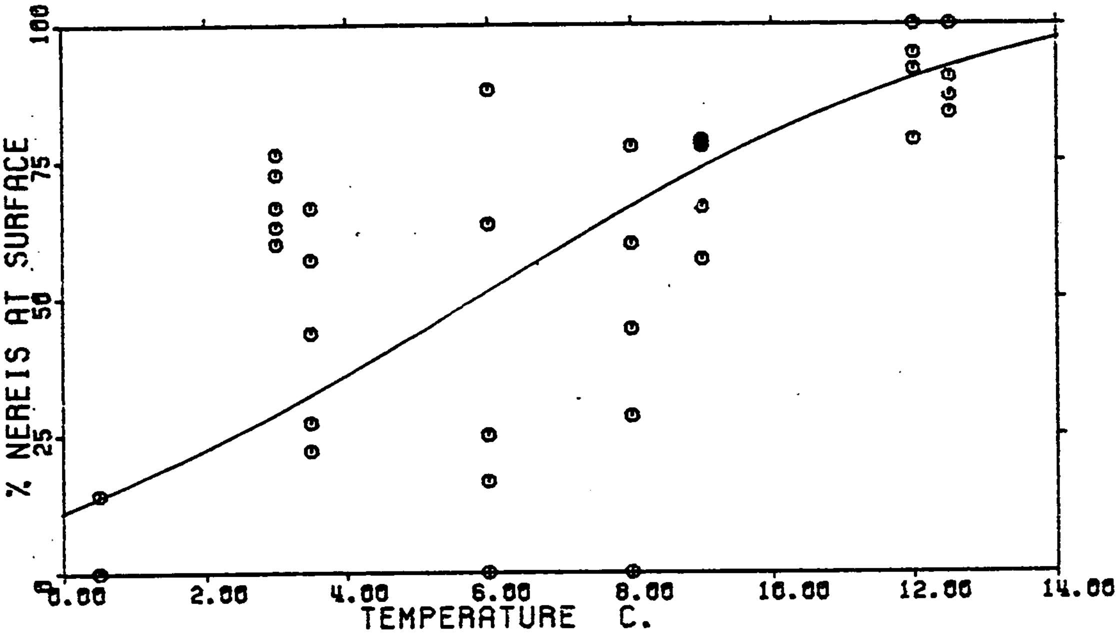


FIGURE 2.15

Percentage of small Nereis in the top 25 mm of mud against temperature

(data collected in 1980/81;
$\arcsin \sqrt{\text{proportion}} = 4.61 \times \text{temperature} + 18.4$, $r = 0.756$, $p<0.001$)

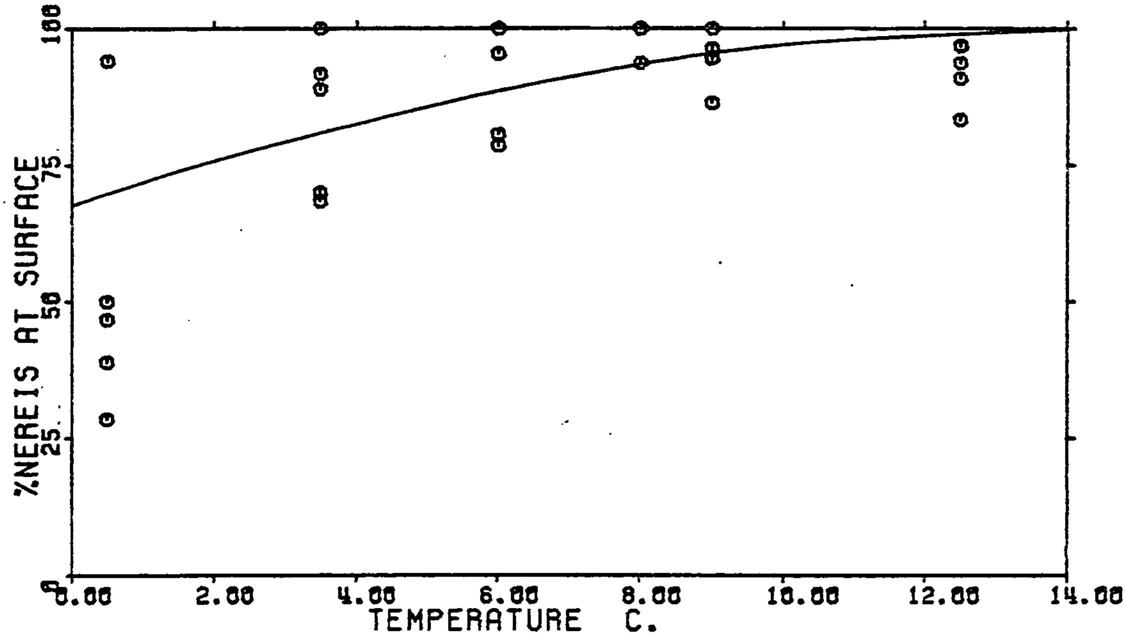


FIGURE 2.16

Percentage of small Nereis in the top 43 mm of mud against temperature

(data collected in 1980/81;
arcsin $\sqrt{\text{proportion}}$ = 2.3 x temperature + 56.8, r = 0.559, $p<0.001$)

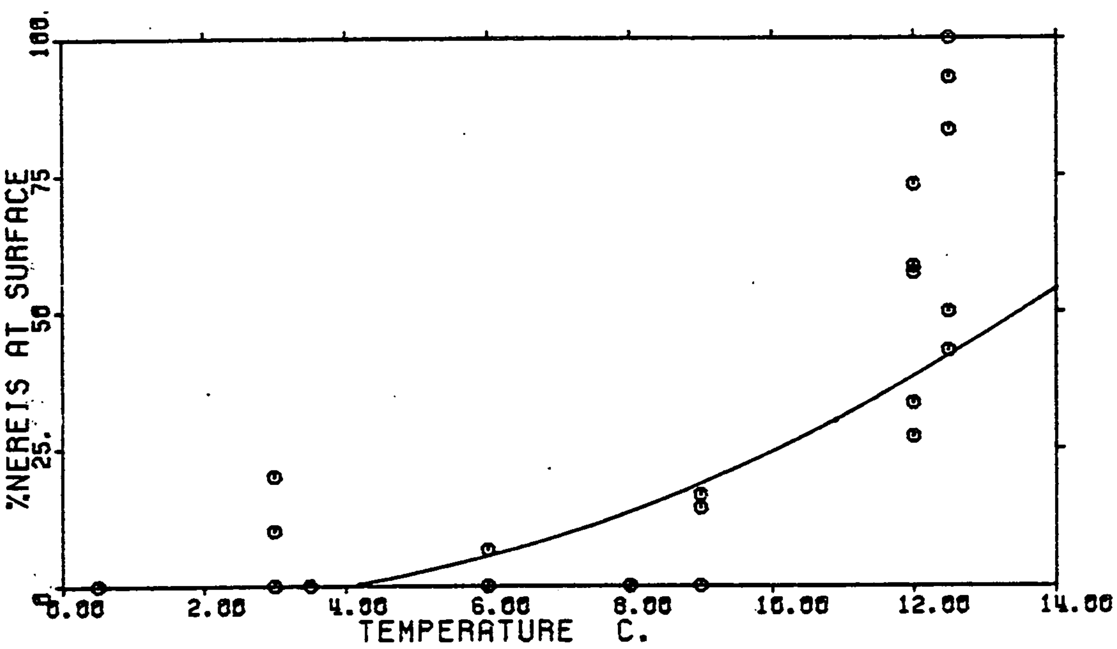


FIGURE 2.17

Percentage of medium Nereis in the top 25 mm of mud against temperature

(data collected in 1980/81;
arcsin $\sqrt{\text{proportion}}$ = 4.4 x temperature - 13.7, r = 0.723, $p<0.001$)

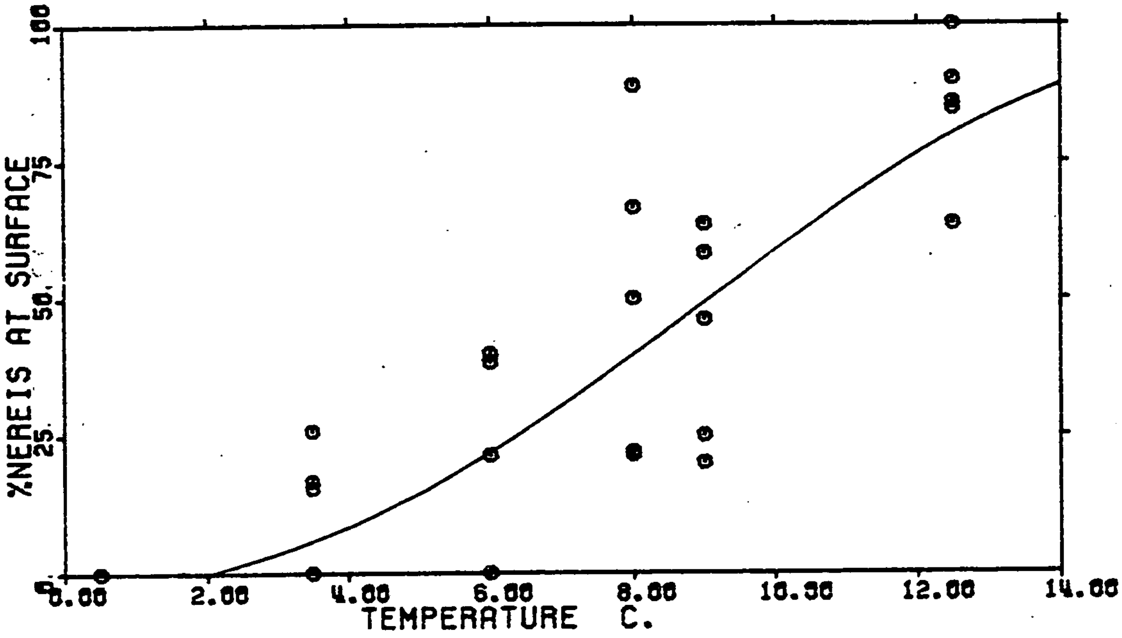


FIGURE 2.18

Percentage of medium Nereis in the top 43 mm of mud against temperature

(data collected in 1980/81;
arcsin $\sqrt{\text{proportion}}$ = 5.7 x temperature - 5.8, r = 0.85, $p<0.001$)

the 1979/80 season.

2.4.3 Discussion

It can be seen from figure 2.15 that the percentage of small Nereis that are within the top 25 mm of mud declines as the temperature decreases, however figure 2.16 shows that it is only at the coldest temperature sampled that there is a significant reduction in the numbers of small Nereids above 43 mm. For medium Nereis on the other hand there are only very few in the top 25 mm until the mud temperature gets above 10 degrees Celsius. The number above 43 mm decreases as temperature drops, there being only a few present at temperatures below six degrees Celsius.

The bill lengths of most Dunlin wintering on the Severn are between 27 mm and 39 mm. The data presented here suggest that those Dunlin with short bills would have less prey available to them than those with the longest bills; furthermore, the prey available to short billed birds would include less medium and small Nereis than the prey available to long billed birds. The difference in prey availability becoming greater as the temperature drops. However, the food requirements of Dunlin increase as the temperature decreases, and on sites where Nereis is the main prey species longer billed Dunlin are likely to be able to obtain more prey than short billed birds in the mid winter period when temperatures are lowest. Dugan (1981a) has shown that Nereis are more active at the surface at night than in the day time. In this study no samples were taken at night. It is possible that night time samples would reveal a different picture, and my results (Chapter 6) suggest that night feeding in Dunlin may be more important than suggested by Worrall (1981).

CHAPTER 3

FACTORS AFFECTING FORAGING

3.1 Introduction

Many studies have been carried out on the feeding ecology of wading birds in an attempt to obtain a better understanding of the factors which affect winter survival. There have been several previous studies on Dunlin (eg Dewar, 1909; Bengtson & Svensson, 1968; Burton, 1974; Worrall, 1981). The aim of my study was to look at some of the factors which affect feeding rate of Dunlin on the Severn. Worrall (1981) has already looked in great detail at Dunlin feeding on the north shore of the Severn, at two sites which have broadly similar substrates and prey available. Within my study site, however, there are many different types of habitat and prey available.

The first part of this chapter shows that adult, juvenile, male and female Dunlin exhibit different patterns of dispersion and feed for different lengths of time during the tidal cycle.

The second part of this chapter assesses the different feeding methods which are used and relates their use to the age and sex of the bird and the habitat in which it is feeding. It is rarely possible to see the small prey items which Dunlin feed on and on some of my sites it was never possible; here the birds must have been taking very small prey. With these constraints it is not possible to make accurate measurements of success rates and calorific intakes

3.2 Methods

Birds were observed using a 15-60 x 60 zoom telescope, the feeding actions being recorded on a portable cassette tape recorder. Whenever possible observations were taken from a vehicle, but in some situations a portable hide (fig 3.1) was used. At the beginning of each day's observations the weather conditions were recorded and a note was made of any changes throughout the day. Air temperature was measured to the nearest degree Celsius, wind was recorded using the Beaufort scale, rain using a scale of 0-5 (table 3.1) and cloud cover in octaves.

Observations were taken on individual birds which were marked with permanent leg flags (Clark, 1979) or dye. Conventional colour rings on the tarso-metatarsus were not used, since Dunlin legs often get covered in mud and it was felt that the rings would not be visible. Colour rings placed on the tibio-tarsus are very close to the body feathers and would not stand out; leg flags were designed to overcome these problems. Adult birds carried one leg flag on the left leg, the colour denoting the total head length category of the individual. Total head length was used as this is a repeatable skeletal measurement and correlates very well with bill length (see chapter 4). Birds hatched in 1979 were marked with a permanent leg flag on the right leg and those hatched in 1980 were dyed pink with Rhodamine B; short billed birds (with a total head length of less than 56 mm) being marked above and below the tail; long billed birds (with a total head length of more than 56.5 mm) on the breast; and intermediate birds (with a total head length between 56 and 56.5 mm) not at all.

For the analysis of results leg flag sightings were split into three groups:

1. Those denoting a total head length of less than 56 mm

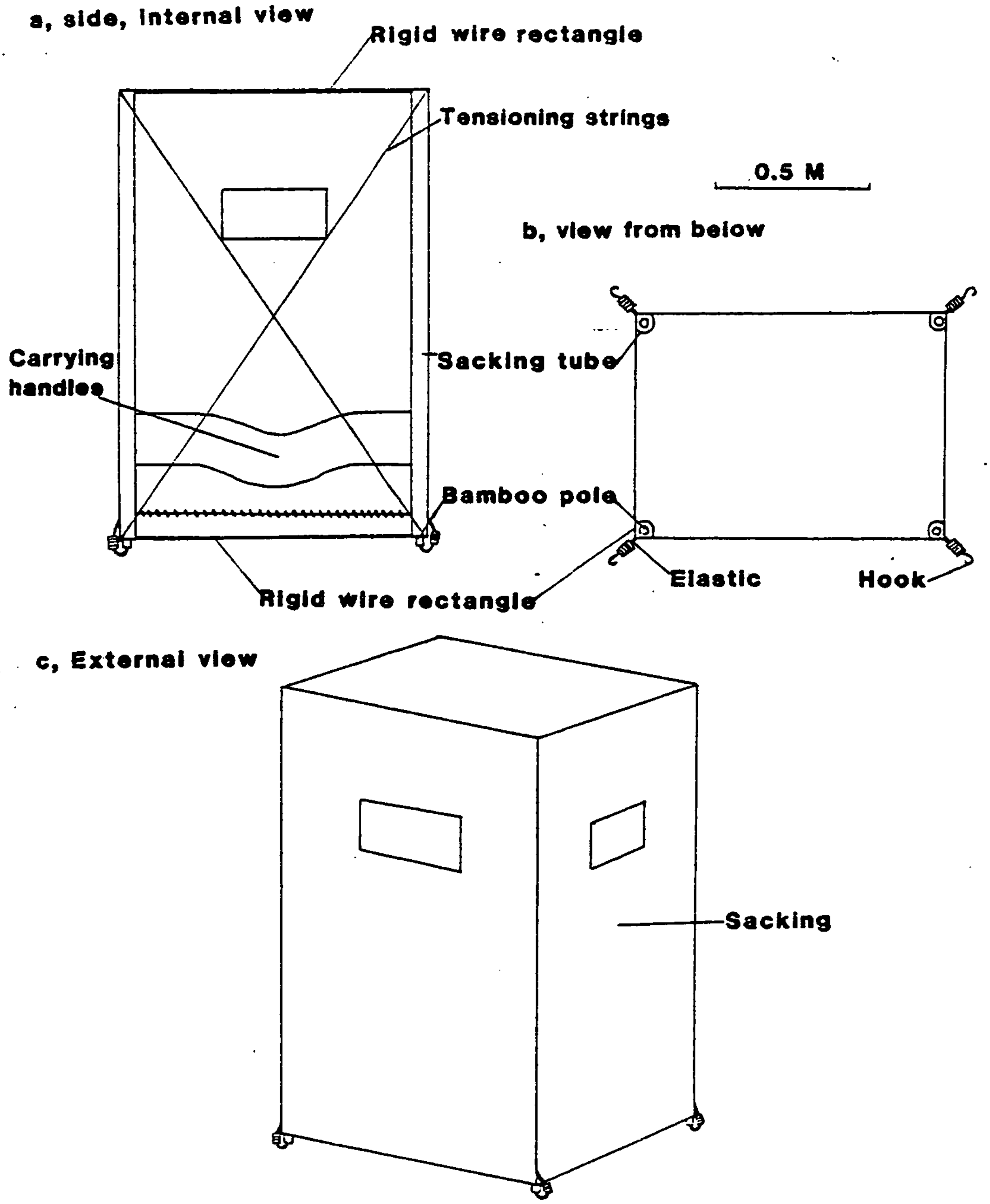


FIGURE 3.1

Portable hide used for feeding observations

TABLE 3.1

Scale	
0	No rain since last high tide
1	Rain since last high tide but no rain in the last hour
2	Rain in the last hour but not in last 10 minutes
3	Rain in the last 10 minutes but not raining at present
4	Light rain
5	Heavy rain

(white, lime, yellow and orange flags); these birds were almost certainly males and will be referred to as such.

2. Those denoting a total head length of more than 57.5 mm (green, blue and black flags); these birds were almost certainly females and will be referred to as such.

3. Those denoting a total head length of 56-57.5 mm (red flags), some of these birds were in the overlap zone. They were excluded from any analyses in which sex differences were considered.

When a flock was encountered in a position in which it was possible to see colour marks, a scan through the flock was first undertaken and the number of birds in the flock and all marked birds that could be seen were noted; then focal animal samples were taken. Initially it was hoped to work only on observation periods of a minute or more, but most Dunlin flocks on the study site, especially those of under 1,000 birds, normally alighted for just one or two minutes at a time before lifting off and moving to another feeding area. Only 20 percent of the observations were of 60 seconds or longer, therefore to maximise the number of bird observations (while maintaining a fixed observation length) only the first 30 seconds of each observation was used in the analysis. At the end of each bird observation the flock size and substrate on which the bird was feeding were noted.

Dunlin used three main feeding actions on my study area, as follows:

1. Pecks - these were defined as quick movements of the head such that the bill touched the surface or only entered the substrate by one or two millimetres.

2. Probes:

a. Shallow Probes - these consisted of the bill being inserted into the substrate more than two millimetres but less than a third of the bird's bill length. In practice the vast majority of shallow probes entered the substrate about 10 mm and there was virtually never any doubt whether a peck or a shallow probe had occurred.

b. Deep Probes - a deep probe occurred when more than one third of the bird's bill entered the substrate. The bill was usually inserted and vibrated once or twice and then removed, but on occasions a bird would put its bill in the substrate and move it up and down several times as if having difficulty in extracting a prey item; unless the bird removed its bill from the substrate this was considered to be one action.

In some analyses shallow and deep probes were combined to give probe rate as deep probes were comparatively rare.

3. Ploughing - this was when about a third of the bill was placed in the substrate and vibrated up and down, the bird walking slowly forward: this is similar to the action described by Worrall as sifting.

Pecking and probing were combined to give "activity" rates, as both have visual components; ploughing, however, is probably a purely tactile form of feeding. An individual which spent a lot of time ploughing automatically had low peck and probe rates even though it may have been pecking or probing very actively when not ploughing; an actual peck or probe rate is therefore dependant on the amount of time spent ploughing so both actual rates and adjusted rates are given. Adjusted rates are calculated using the following equation:

$$\text{adjusted rate} = \frac{\text{number of actions recorded in 30 seconds}}{30 - \text{number of seconds of ploughing}}$$

Data are only used when the denominator is more than 10 as only the adjusted rate showed a very high variance when the denominator was small.

In addition to the four common feeding actions birds would occasionally run; the bird would stop feeding and run for at least 10 paces before resuming feeding. One other feeding action that occurred regularly on the study site is stitching. This involves a rapid series of probes and always occurred on the tide edge. Stitching has been recorded by other authors but only Worrall (1981) has previously stated that it is confined to the tide edge. As stitching never occurred on the exposed feeding area (where all my feeding observations were taken) it was not recorded during focal animal sampling. Aggressive interactions and short preening bouts were also noted, although these were very rare events. On the occasions when a prey item was seen to be taken this was noted and the species recorded if possible.

3.3 Results

3.3.1 Sightings of marked birds in Sand Bay

In Sand Bay there are two main feeding areas available to Dunlin at low tide, a wet sand area at the top of the bay and a large area of runnelled mud further out. It was only rarely possible to look at the birds which fed on the mud, but most birds on the sand could normally be seen and any marked birds recorded. In the 1979/80 winter there were normally less than 100 birds feeding on this area at low tide, but in the 1980/81 winter the flock on the sand typically consisted of about 400 birds. During the 1979/80 winter I thought that the flock consisted mainly of juveniles and that most of these were males, but as comparatively small numbers of birds were marked it was not possible to test this. Data for the 1980/81 winter were much more substantial but it was still difficult to test whether age and sex composition was as predicted. The reasons for this were as follows:

1. Although there were quite a lot of marked adults present at the beginning of the winter (marked previous year) there were very few marked juveniles.
2. Some of the juveniles marked in the early autumn moved out of the bay after marking (Chapter 5).
3. Dyemarked birds (juveniles) were very much more obvious than the leg flagged adults. Occasions when it was thought likely that a significant number of flagged birds had been missed (in high winds or poor light conditions) were noted and the data were excluded from the analyses.

It is not possible in any one test to prove conclusively that there is a biased sex or age ratio feeding on the wet sand but several pieces of evidence suggest that this is the case.

First, it can be seen from table 3.2 that in the early autumn when it was possible to age birds in the field there was always a very high percentage of juveniles on the sand.

Second, later in the winter the proportion of marked juveniles out of total marked birds was always over 60 percent for flocks feeding on the sand; this compares with the much lower percentages in samples of birds caught in late winter (table 3.3). The only exception was one flock of 600 birds seen feeding on the sand on 24 December when only 16 percent of the marked birds were juveniles (table 3.2). Shortly after this count was made the flock moved out onto the recently exposed runnelled mud, while another flock of 400 birds continued feeding on the sand until low tide (in this flock 93 percent of marked birds were juveniles). The proportion of marked birds that were juvenile in the flock that moved onto the runnelled mud was significantly lower than the proportion in the flock that stayed on the sand (Fisher's exact test $p < 0.0001$).

Third, two flocks which were observed roosting on the sand shortly after being forced off the runnelled mud on the rising tide had very few juvenile marked birds in them, in contrast to the flocks that continued feeding on the sand (table 3.2). On both these occasions the roosting flock was spaced out in a way that made it possible to check most, if not all, of the birds for dye (juveniles), but it was not possible to check for leg flags (adults) as these sometimes get covered by feathers when the bird is roosting or are covered when the bird roosts on one leg.

TABLE 3.2

The proportion of juveniles seen in flocks in Sand Bay throughout the 1980/81 winter

(- represents an occasion when the relevant data are not obtainable)

Date	Site	Act (1)	Flock size	Number of birds marked as Adult	Number of birds marked as Juv.	Percentage of marked birds Juv.	Percentage of flock marked as Juv.	Percentage of juvenile birds in flock (2)
16 Oct	sand	F	17	0	-	-	-	94
"	sand	F	50	0	-	-	-	50
17 Oct	mud	F	300	18+	-	-	-	-
"	sand	F	300	2	-	-	-	82
07 Nov	sand	F	213	2	8	80	3.7	95
18 Nov	sand	F	400	3	6	66	1.5	-
"	sand	R	300	-	0	-	0	-
01 Dec	sand	F	500	-	10+	-	-	-
"	sand	R	3000	-	0	-	-	-
24 Dec	sand	F	400	1	14	93	3.5	-
"	sand	F(3)	600	18	4	16	0.6	-
04 Jan	sand	F	350	15	34	69	9.7	-
19 Jan	sand	F	150	2	11	84	7.3	-
05 Feb	sand	F	150	4	23	85	15.3	-
17 Feb	sand	F	115	8	13	61	11.3	-

(1) Activity: F = Feeding; R = Roosting
(2) Birds aged on plumage characteristics
(3) Flock feeding on sand then moved to mud

Fourth, it can be seen by comparing tables 3.2 and 3.3 that 10 percent of birds in late winter feeding flocks were marked juvenile whereas less than four percent of the birds in catches at the end of the winter were previously marked juveniles.

Fifth, very often when it rained during the low tide period the birds feeding on the mud moved onto the sand to feed. For instance, on 17 December 1980 the ratio of marked juveniles to marked adults among birds feeding on the sand was significantly higher before it rained when only 400 birds were present than when it was raining and 2,000 birds were feeding (table 3.4).

All this evidence suggests that there tends to be a higher proportion of juveniles feeding on the sand than on the mud when the tide is out. If this is the case one would expect that the percentage of marked juveniles out of all marked birds would be lower near high tide when all feeding birds are forced onto the sand. Between zero and three hours from high tide, if the sand was uncovered, there was normally a flock of birds feeding and another flock roosting. It can be seen from figure 3.2 that there was no decrease in the percentage of juveniles in feeding flocks near high tide (the data are plotted in three sets as the proportion of marked birds changed through the winter). This strongly suggests that juveniles feed for longer than adults. Mist net catches provide evidence that this is also the case at night. When birds were mist netted whilst the mud was still exposed the first net round normally contained a very small percentage of juveniles, but later on when the feeding area was covered there was a much higher proportion of juveniles (Chapter 6).

There was no apparent difference in the sex ratio of the few

TABLE 3.3

Proportion of previously marked birds in catches in Sand Bay at the end of the winter 1980/81

Date	10 02 81	21 02 81
Method	Mist netted	Cannon netted
Total caught	102	187
Number of juveniles caught	30	30
Number of juveniles previously marked	4	6
Number of adults previously marked	9	35
Percentage of previously marked birds that were juveniles	30.7	17.1
Percentage previously marked juveniles in catch	3.9	3.2

TABLE 3.4

The effect of rain on the proportion of marked adults and juveniles on the wet sand on 17 December 1980

	Number present	Marked birds seen Adult	Juvenile
Before rain (1)	400	2	27
During rain (2)	2,000	14	28

Chi squared = 5.44 with 1 degree of freedom $p<0.05$

(1) Whole flock scanned for marked birds
(2) Only a portion of flock scanned for marked birds

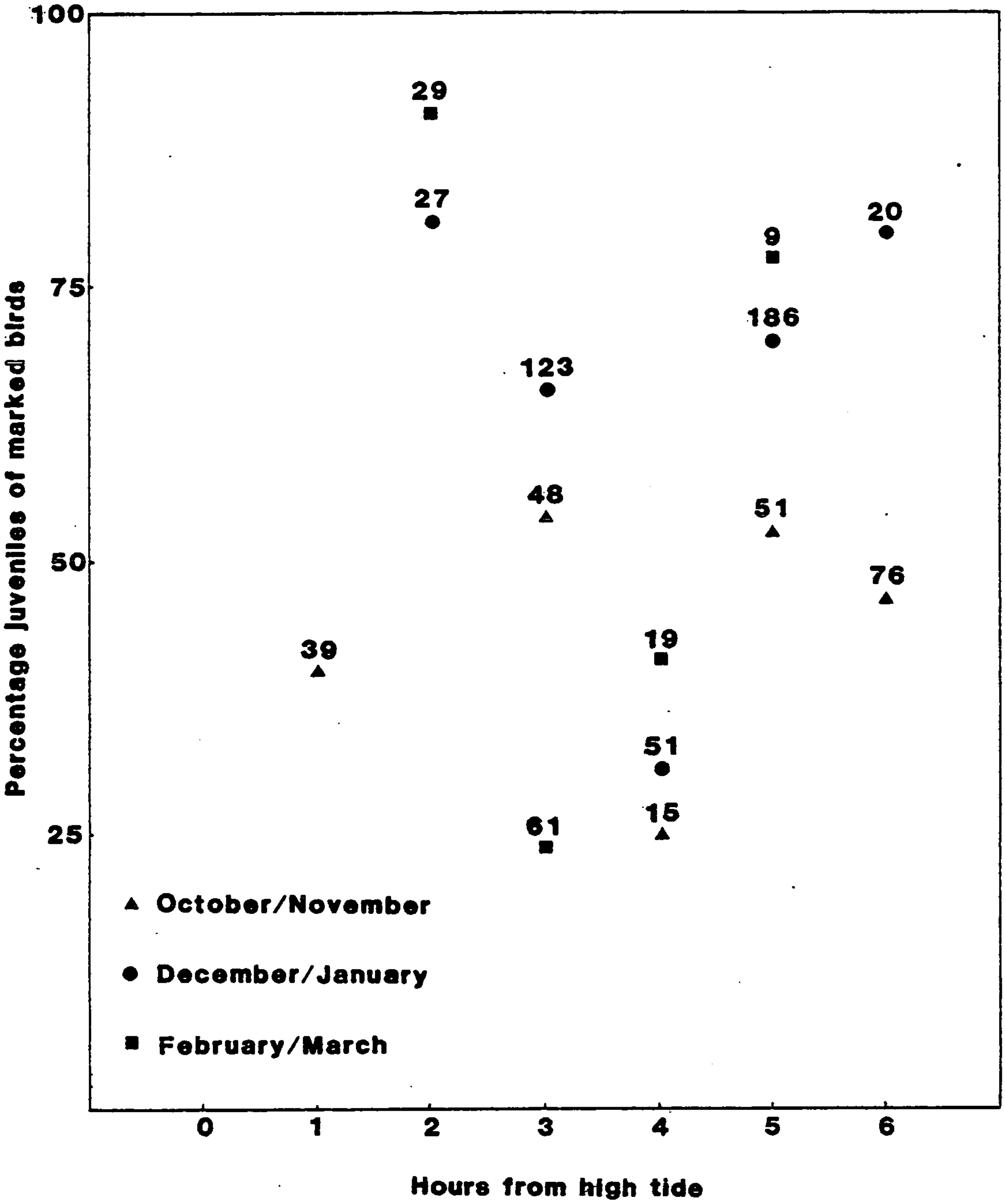


FIGURE 3.2

Percentage of juveniles (of all marked birds) in feeding flocks at different times from high tide on the wet sand in Sand Bay adult Dunlin that fed on the wet sand but among the juveniles there was a higher proportion of males than would be expected. There was normally only 400 birds feeding on the sand, most of the birds feeding further out on the runnelled mud. Large flocks were seen on the sand only during rain or occasionally when they had been disturbed by predators out on the mud. Table 3.5 shows that in flocks of up to 600 birds feeding on the wet sand there was a tendency for there to be more males than in flocks of over 600; it was not significant but I believe this was due to the small sample size of marked birds in the large flocks. Figure 3.3 shows that among marked juveniles the sex ratio was around 50 percent near high tide but the proportion of males significantly increased to between 60 and 70 percent near low tide (Chi-squared = 4.14,$P<0.05$). This suggests that either some juvenile males which normally fed on the wet sand joined the roosting flock when it was forced off the mud or that juvenile females which normally fed on the mud joined the feeding flock on the sand near high tide. As the number of birds feeding on the sand near high tide tended to increase the second hypothesis is more likely to be correct. Table 3.6 shows that among the juveniles feeding on the wet sand around low tide the proportion of males was significantly higher than the proportion among all juveniles caught and marked there during the winter. On one occasion it was possible to check the proportion of males to females among juveniles when the flock that had been feeding on the mud first left it to come to roost; at that time the proportion of males was significantly lower than in a flock feeding on the wet sand at low tide two days later (table 3.7).

The evidence from Sand Bay thus points to more juvenile males

TABLE 3.5

The proportion of male and female juvenile Dunlin in small and large flocks on wet sand in sand bay

	Male	Female
Flocks up to 600	272	149
Flocks over 600	13	16

Chi squared = 3.76 with 1 degree of freedom $0.1>p>0.05$

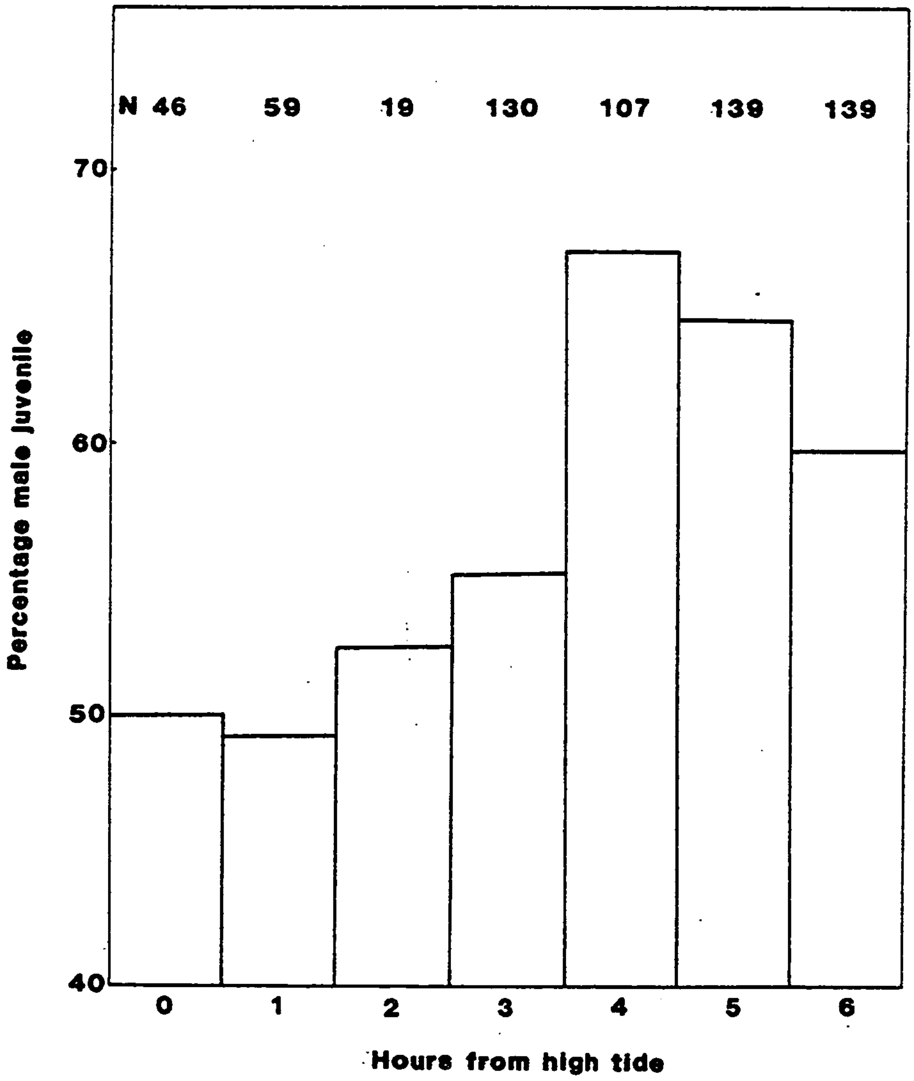


FIGURE 3.3

Percentage of males out of all marked juveniles at different times from high tide on the wet sand in Sand Bay

TABLE 3.6

The ratio of male to female juvenile Dunlin observed on the wet sand compared to those marked, in the 1980/81 winter

	Male	Female
caught during winter	118	98
on wet sand	272	149

Chi squared = 5.57 with 1 degree of freedom $p<0.05$

(Flock size less than 600, no rain, less than three hours from low tide)

TABLE 3.7

The proportion of male and female juvenile Dunlin in two flocks in Sand Bay during January 1981

	Male	Female
Flock of 350 feeding on wet sand 04 01 81	29	5
Flock roosting on sand after coming off mud on rising tide on 06 01 81	28	32

Chi squared =11.99 with 1 degree of freedom $p<0.01$

than juvenile females feeding on the wet sand and shows that juveniles in general tend to feed for longer than adults.

3.3.2 Differences in the amount of time spent feeding at Clevedon

During the first winter of the study, it was very noticeable that when the weather was severe some birds would feed whenever possible whereas others would roost from long before high tide until long after high tide. I hoped to be able to test whether one section of the population was having to feed for longer than the rest of the birds, but the subsequent two winters were very mild and during these winters all the birds tended to roost for the same length of time. However, on one occasion it appeared that a frost had different effects on different sections of the population. On the night of 18 February 1981 there was a severe frost: on the following day most of the birds started to roost three hours before high tide but 200 continued to feed. The flock of 200 birds included a higher ratio of juveniles to adults - and of males to females among the adults - than flocks observed on 25 February and 3 March when all birds were feeding (table 3.8):this suggests that some adult males and juveniles were more severely affected by cold weather at Clevedon than were adult females.

3.3.3 Factors affecting feeding behaviour

A total of 803 individual 30 second observation periods on colour marked Dunlin were recorded. It will be seen from chapter 5 that Dunlin within the Severn are non-randomly distributed with

TABLE 3.8

The composition of the flock of 200 Dunlin which continued to feed on the rising tide at Clevedon when most of the birds were roosting after a hard frost on 19 02 81, compared with that of feeding flocks on 25 02 81 and 02 03 81

	MALE		FEMALE	
	Ad.	Juv.	Ad.	Juv.
25 02 81 + 02 03 81	16	2	19	3
19 02 81	9	6	1	3

Fisher's exact test for the difference in the proportions of males and females (adults only) p = 0.027

Fisher's exact test for the difference in the proportions of adults and juveniles (sexes combined) p = 0.005

respect to both age and bill length. It was thought likely that adults and juveniles and possibly males and females would feed in different ways within the same flock; the largest data set (from the upper wet sand area in Sand Bay) was used to investigate this. Unfortunately it was rarely possible to obtain feeding data during heavy rain, and when the air temperature was below four degrees Celsius all birds fed on the runnelled mud further out in the bay, where detailed observations could not be made.

Age related effects

Although my data set was small there was no suggestion of any differences between adults and second winter birds, so they were both classed as adults for comparison with first winter (juvenile) birds. Table 3.9 shows that juveniles peck significantly more than adults, but there was no difference in probe or activity rates.

Table 3.10 compares the proportion of adults and juveniles which spent any time during a feeding bout ploughing. It can be seen that significantly more adults spent some time ploughing than juveniles; this may be because large numbers of adults fed on the sand only when the outer runnelled mud was covered or when there was heavy rain (which may limit visual feeding). It is possible that feeding observations tended to be taken on adults in different weather conditions to those on juveniles (even though I could not detect any difference); this may also account for the differences in peck rate between adults and juveniles.

TABLE 3.9

Variation in feeding rate due to age on wet sand area in Sand Bay (adjusted rates give results when ploughing is removed from the calculations)

Action		N	Mean	Significance (1)
Peck rate	Ad.	97	0.394	P <0.05
	Juv.	160	0.515	
Probe rate	Ad.	97	0.271	N.S.
	Juv.	160	0.231	
Activity rate	Ad.	97	0.665	N.S.
	Juv.	160	0.746	
Adjusted Peck rate	Ad.	71	0.586	N.S.
	Juv.	123	0.735	
Adjusted Probe rate	Ad.	71	0.411	N.S.
	Juv.	123	0.319	
Adjusted Activity rate	Ad.	71	0.997	N.S.
	Juv.	123	1.055	

(1) Student's t-test

TABLE 3.10

The effect of age on the proportion of adults and juveniles which spend some time ploughing

	Adult	Juvenile
No ploughing	41	108
Some ploughing	92	102

Chi squared = 13.24 with 1 degree of freedom $p<0.001$

Sex related effects

Since there are only slight differences between juveniles and adults the data are combined in table 3.11 which gives the peck, probe and activity rates. This shows that there was no difference between the sexes. The non-normal frequency distribution of the amount of time individuals spent ploughing meant that it was not possible to test for sex differences using a t-test. Figure 3.4 gives the distribution for the amount of time spent ploughing for the two sexes and suggests that there may be differences between males and females. The cumulative frequency distribution for the data set can be plotted (Figure 3.5). If there was an equal likelihood of an individual spending a given amount of time ploughing during an observation period a straight line would be produced. If on the other hand the data were normally distributed a sigmoid curve would be produced. This is certainly not the case for males. This suggests that at least some individuals may switch from visual feeding techniques to tactile feeding and, in the short term, specialize in ploughing. For females the plot produced is almost a straight line with a steeper angle when the amount of time spent ploughing is less than five seconds. These sex differences were tested using Chi-squared, males and females were significantly different (Table 3.12). The data have also been split into age classes; these all follow the same trend.

TABLE 3.11

Variation in feeding rate due to sex on wet sand area in Sand Bay (adjusted rates give results when ploughing is removed from the calculations)

Action	Sex	N	Mean	Significance (1)
Peck rate	M	128	0.473	N.S.
	F	102	0.517	
Probe rate	M	128	0.219	N.S.
	F	102	0.259	
Activity rate	M	128	0.691	N.S.
	F	128	0.776	
Adjusted Peck rate	M	92	0.696	N.S.
	F	83	0.723	
Adjusted Probe rate	M	92	0.330	N.S.
	F	83	0.339	
Adjusted Activity rate	M	92	1.026	N.S.
	F	83	1.062	

(1) Student's t-test

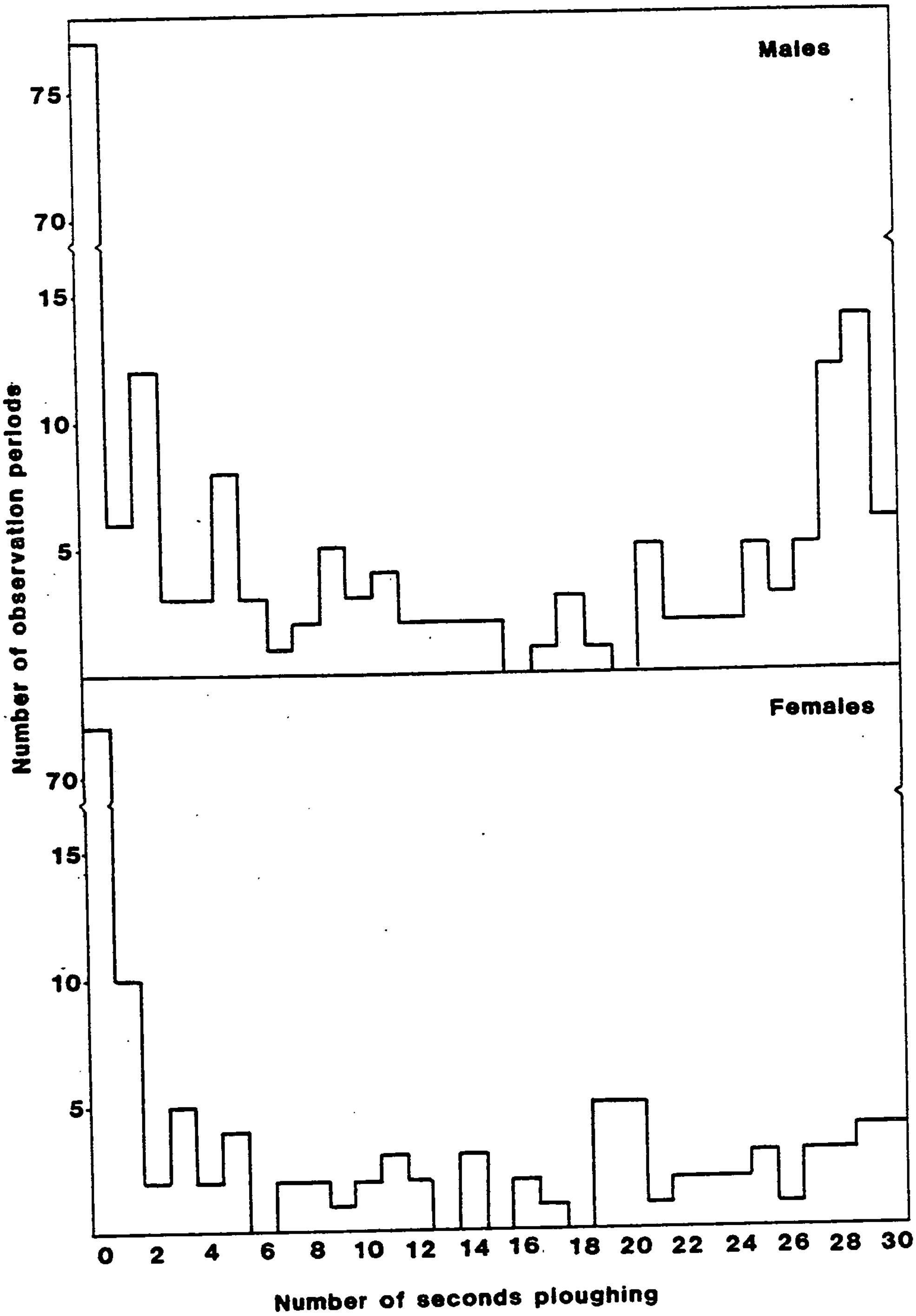


FIGURE 3.4

Frequency of observation periods with different amounts of time spent ploughing for males and females on the wet sand in Sand Bay

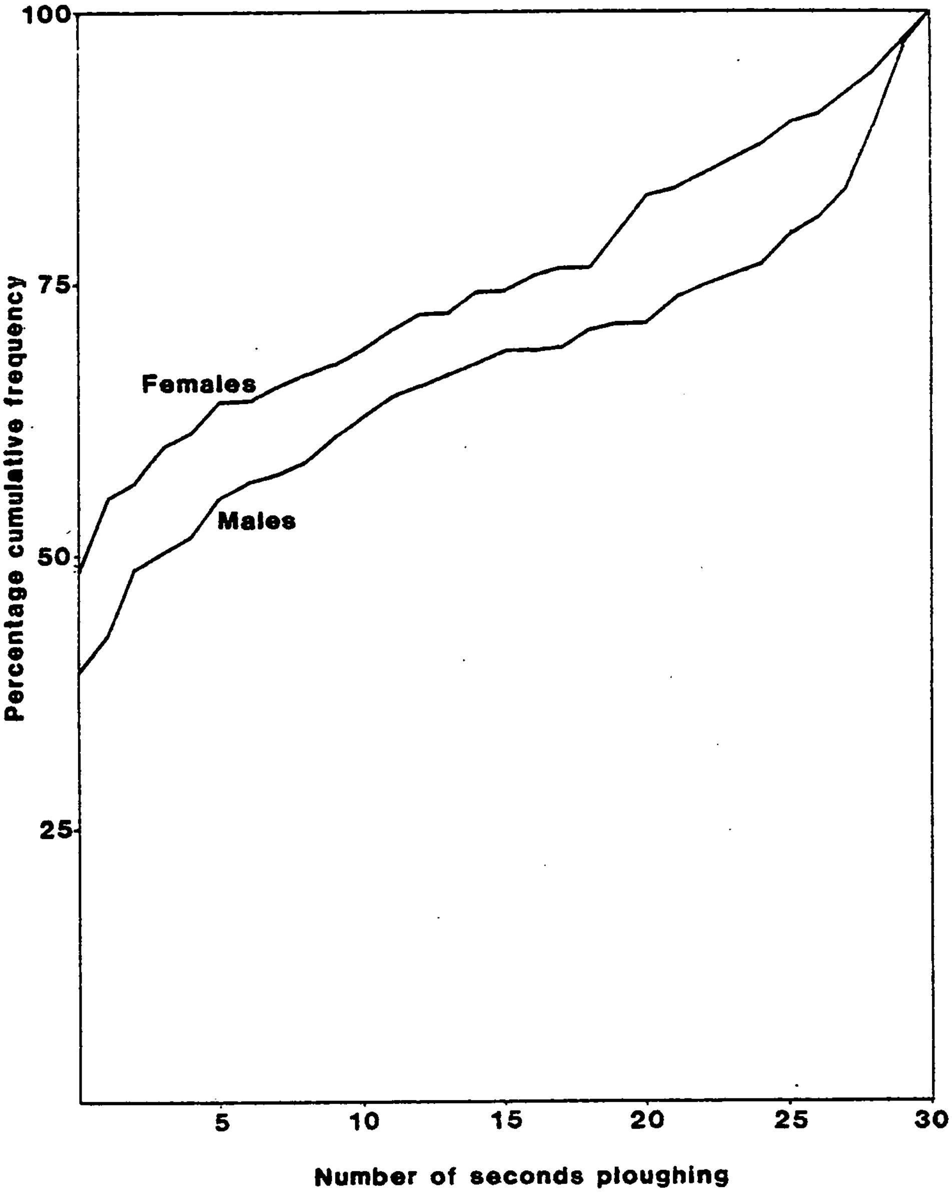


FIGURE 3.5

Percentage cumulative frequency for the amount of time spent ploughing for males and females on the wet sand in Sand Bay

TABLE 3.12

Time spent ploughing by males and females (Number of adult, second winter and juvenile birds are given in brackets)

Time spent ploughing	Number of observations Males	 Females
0 sec	77 (21,3,53)	72 (13,4,55)
1-10 secs	45 (20,3,22)	30 (13,1,16)
11-20 secs	17 (8,1,8)	21 (7,1,13)
21-30 secs	56 (25,5,26)	25 (7,1,17)

Chi squared = 9.18 with 3 degrees of freedom $p<0.05$

Effect of environmental factors

It has already been shown that with the exception of ploughing there were no differences between males and females or adults and juveniles. As the data set was insufficient to undertake a multiple analysis of variance, four individual analyses (rain, temperature, tidal state and wind) were undertaken to assess their effects on feeding rate on the wet sand area in Sand Bay. The four variables were looked at to see if there were correlations between any of them. The only significant correlation was between rain and temperature; a subsequent analysis showed that the reduction in feeding rate was not due to the drop in temperature when it rained.

The main prey species on the wet sand is known to be affected by rain: Goss-Custard (1970c) found that *Corophium* were less active when water was sprinkled on the substrate. This factor was looked at first and it can be seen from table 3.13 that peck rates and activity rates declined when it rained. As it was easy to eliminate the effect of rain all subsequent analyses were undertaken using data when it had not rained.

Corophium is known to be affected by mud temperature (Goss-Custard, 1969) which in turn correlates with air temperature. Peck, probe and activity rates were found to be positively correlated with temperature (table 3.14), but when the effect of ploughing was removed only the activity rate was found to positively correlate with temperature. This was because the amount of time spent ploughing by the individuals which undertook ploughing significantly declined with increasing temperature. There was also

TABLE 3.13

The effect of rain on feeding actions on the wet sand area in Sand Bay (adjusted rates give results when time spent ploughing is removed from the calculations)

Action	N	Y = a + bX (1)		Correlation	Significance
		a	b	R	P<
Peck rate	386	0.505	-0.0425	-0.1661	0.001
Probe rate	386	-	-	-	N.S.
Activity rate	386	0.7422	-0.0495	-0.1910	0.001
Adjusted Peck rate	289	0.722	0.0457	-0.1635	0.01
Adjusted Probe rate	289	-	-	-	N.S.
Adjusted Activity rate	289	1.0564	-0.0564	0.2654	0.00001

(1) Y = feeding actions per second, X = arbitary rain scale

TABLE 3.14

The relationship between feeding actions and temperature when not raining

(adjusted rates give results when time spent ploughing is removed from the calculations)

Action	N	Y = a + bX (1) a	 b	Correlation R	Significance P<
Peck rate	257	0.228	0.026	0.167	0.01
Probe rate	257	0.077	0.016	0.179	0.01
Activity rate	257	0.323	0.043	0.274	0.00001
Adjusted Peck rate	194	-	-	-	N.S.
Adjusted Probe rate	194	-	-	-	N.S.
Adjusted Activity rate	194	0.856	0.018	0.163	0.05
Ploughing (2)	148	-	-	-0.182	0.05 (3)

(1) Y = feeding actions per second, X = temperature in degrees Celsius
(2) observations of less than one second ploughing omitted
(3) data not normally distributed, tested using Spearman Rank Correlation

a tendency for the proportion of individuals that spent some time ploughing to decrease as temperature increased (table 3.15) although this was not significant.

The length of time the mudflats have been exposed is likely to have an effect on invertebrate activity due to drying of the substrate. Although there were noticeable differences in the feeding of Dunlin at the tide edge all observations were undertaken on birds feeding 10 m or more from the tide edge. Initial examination of the data suggested that the peck rate and activity rate were positively correlated with the length of time from high tide, but there seemed to be a decline on the rising tide, even though no observations were taken less than an hour before the rising tide reached the wet sand area. The data was thus split into two sets: up to seven hours after high tide and more than six hours after high tide; the data from low tide were used in both analyses. It was found that peck rate significantly increased with time from high tide until low tide and then started to decline (table 3.16). There was a weak fall in probe rate until low tide but no significant effect on the rising tide. The activity rate followed the same pattern as peck rate. There was no significant correlation in the amount of time spent ploughing or the number of birds that spent some time ploughing.

The fourth environmental factor which it was thought might be important in affecting the way Dunlin forage was the wind speed. Birds were observed at a a wide variety of wind speeds but no effect of wind speed on feeding rate was found.

TABLE 3.15

The effect of temperature on the proportion of birds which spend some time ploughing when it has not rained since high tide

Temperature (degrees C)	3 - 5	6 - 8	9 - 11	12 - 13
No time spent ploughing in 30 second time period	12	37	16	44
Some time spent ploughing in 30 second time period	32	57	17	42

Chi squared = 7.68 with 3 degree of freedom $0.01>p>0.05$

TABLE 3.16

The relationship between feeding actions and tide
when it has not rained
(adjusted rates give results when time spent ploughing is removed
fron the calculations)

Action	N	Y = a + bx (1)		Correlation	Significance
		a	b	R	P<
Falling tide					
Peck rate	197	0.238	0.066	0.276	0.0001
Probe rate	197	-	-	-	N.S.
Activity rate	197	0.543	0.048	0.202	0.01
Adjusted Peck rate	149	0.407	0.079	0.331	0.0001
Adjusted Probe rate	149	0.455	-0.030	-0.198	0.05
Adjusted Activity rate	149	0.8625	0.050	0.322	0.0001
Rising tide					
Peck rate	118	1.538	-0.135	-0.263	0.01
Probe rate	118	-	-	-	N.S.
Activity rate	118	1.668	-0.119	-0.257	0.01
Adjusted Peck rate	95	1.648	-0.121	-0.219	0.05
Adjusted Probe rate	95	-	-	-	N.S.
Adjusted Activity rate	95	1.698	-0.083	-0.241	0.05

(1) Y = feeding rate per second, X = hours from previous high tide

The effect of bay and substrate on feeding actions

Unfortunately it was not possible to obtain large data sets in many situations. However, the feeding observations were split into substrates and bays giving eight areas. Mean values and significant differences between different areas for the different feeding actions are given in tables 3.17 to 3.19 and the mean values are displayed as histograms in figures 3.6 and 3.7. As can be seen from chapter 2 there are differences in the prey that are present in different substrates and differences in the prey available in the same substrate in different bays. It is possible that the feeding activity of Dunlin is determined by the substrate on which they are feeding, but it is also possible that the available prey may determine the feeding behaviour. The tables show that there are significant differences both between substrates and between the same substrate in different bays, suggesting that both the substrate available and the prey are important in determining the feeding actions used by Dunlin; this will be discussed fully later.

3.4 Discussion

3.4.1 Age related effects

In recent years there have been a number of studies on the feeding ecology of birds which have shown that juveniles are less efficient foragers than adults: Brown Pelican Pelecanus occidentalis - Orians, 1969; Little Blue Heron Florida caerulea - Recher &

TABLE 3.17

Differences in peck rate in different bays and on different substrates

Bay		CL LM	BB LM	CL RM	SB RM	CL CL	SB WS	WB WS	N	Mean Rate
Clevedon	Liquid Mud								35	0.2076
Brean Beach	Liquid Mud								40	0.3667
Clevedon	Runneled Mud								68	0.3167
Sand Bay	Runneled Mud	XXX		XXX					40	0.6867
Clevedon	Clay				XX				79	0.4108
Sand Bay	Wet Sand	XX	XX			X			257	0.4695
Weston Bay	Wet Sand	XXX		XXX		X			22	0.7030
Brean Beach	Wet Sand	XXX		XXX		XX	XX		41	0.6870

Adjusted rates

Bay		CL LM	BB LM	CL RM	SB RM	CL CL	SB WS	WB WS	N	Mean Rate
Clevedon	Liquid Mud								30	0.2860
Brean Beach	Liquid Mud								40	0.3919
Clevedon	Runneled Mud								68	0.3224
Sand Bay	Runneled Mud	XXX	XXX	XXX					37	0.7513
Clevedon	Clay				XXX				79	0.4186
Sand Bay	Wet Sand	XXX	XXX	XXX		XXX			194	0.6809
Weston Bay	Wet Sand	XXX	XXX	XXX		XXX			20	0.8388
Brean Beach	Wet Sand	XXX	XX	XXX		XXX			40	0.7317

Tested using modified Least Significant Difference test
X = P<0.05 XX = P<0.01 XXX = P<0.001

TABLE 3.18

Differences in probe rate in different bays and on different substrates

Bay	Substrate	CL LM	BB LM	CL RM	SB RM	CL CL	SB WS	WB WS	N	Mean Value
Clevedon	Liquid Mud								35	0.3886
Brean Beach	Liquid Mud								40	0.3875
Clevedon	Runneled Mud								68	0.3574
Sand Bay	Runnneled Mud	XXX	XXX	XXX					40	0.1200
Clevedon	Clay	X	XX	X					79	0.2152
Sand Bay	Wet Sand	X	X	X					257	0.2462
Weston Bay	Wet Sand	XXX	XXX	XXX					22	0.1106
Brean Beach	Wet Sand	XX	XX	XX					41	0.1691
<u>Adjusted rates</u>										
Clevedon	Liquid Mud								30	0.4661
Brean Beach	Liquid Mud								40	0.4130
Clevedon	Runneled Mud								68	0.3609
Sand Bay	Runneled Mud	XXX	XXX	XXX					37	0.1317
Clevedon	Clay	XXX	XX	X					79	0.2249
Sand Bay	Wet Sand				XXX	XX			194	0.3529
Weston Bay	Wet Sand	XXX	XX	X			X		20	0.1425
Brean Beach	Wet Sand	XXX	XXX	XX			XX		40	0.1791

Tested using modified Least Significant Difference test
X = P<0.05 XX = P<0.01 XXX = P<0.001

TABLE 3.19

Differences in activity rate in different bays and on different substrates

Bay	Substrate	CL LM	BB LM	CL RM	SB RM	CL CL	SB WS	WB WS	N	Mean Value
Clevedon	Liquid Mud								35	0.5962
Brean Beach	Liquid Mud								40	0.7542
Clevedon	Runneled Mud								68	0.6740
Sand Bay	Runneled Mud								40	0.8067
Clevedon	Clay								79	0.6257
Sand Bay	Wet Sand								257	0.7157
Weston Bay	Wet Sand								22	0.8136
Brean Beach	Wet Sand	X				X			41	0.8561

Adjusted rates

Bay	Substrate	CL LM	BB LM	CL RM	SB RM	CL CL	SB WS	WB WS	N	Mean Value
Clevedon	Liquid Mud								30	0.7497
Brean Beach	Liquid Mud								40	0.8049
Clevedon	Runneled Mud								68	0.6833
Sand Bay	Runneled Mud			XX					37	0.8819
Clevedon	Clay		X		XXX				79	0.6435
Sand Bay	Wet Sand	XXX	XXX	XXX		XXX			194	1.0339
Weston Bay	Wet Sand	X		XXX		XXX			20	0.9809
Brean Beach	Wet Sand			XXX		XXX			40	0.9162

Tested using modified Least Significant Difference test
X = P<0.05 XX = P<0.01 XXX = P<0.001

Key for figures 3.6 and 3.7

▓ **Deep probe**

▨ **Shallow probe**

░ **Shallow + deep probe**

□ **Peck**

▩ **Activity**

▒ **Ploughing**

▥ **Stitching**

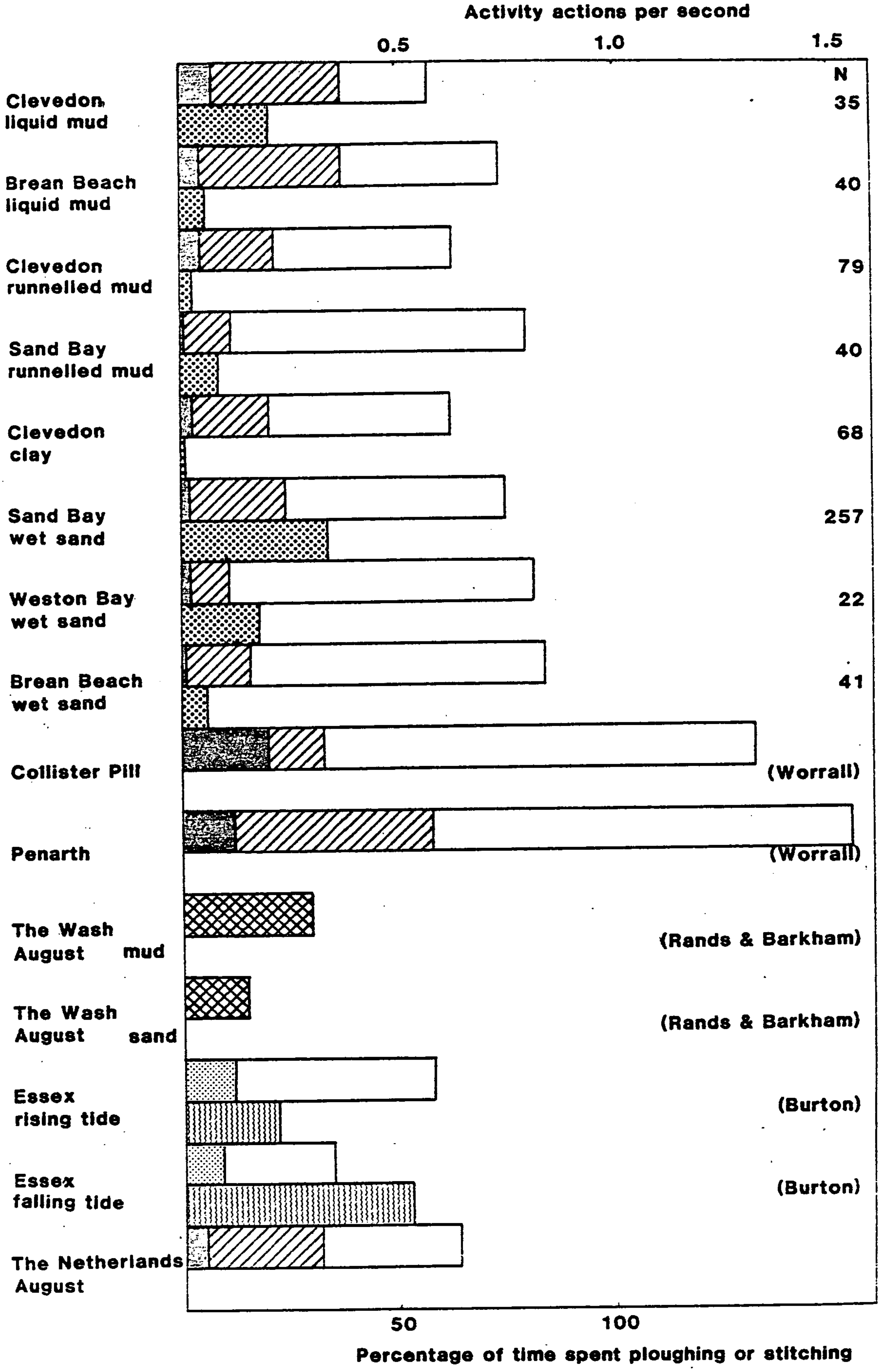


FIGURE 3.6

Mean values for different feeding actions on different sites sampled during the study compared with published data

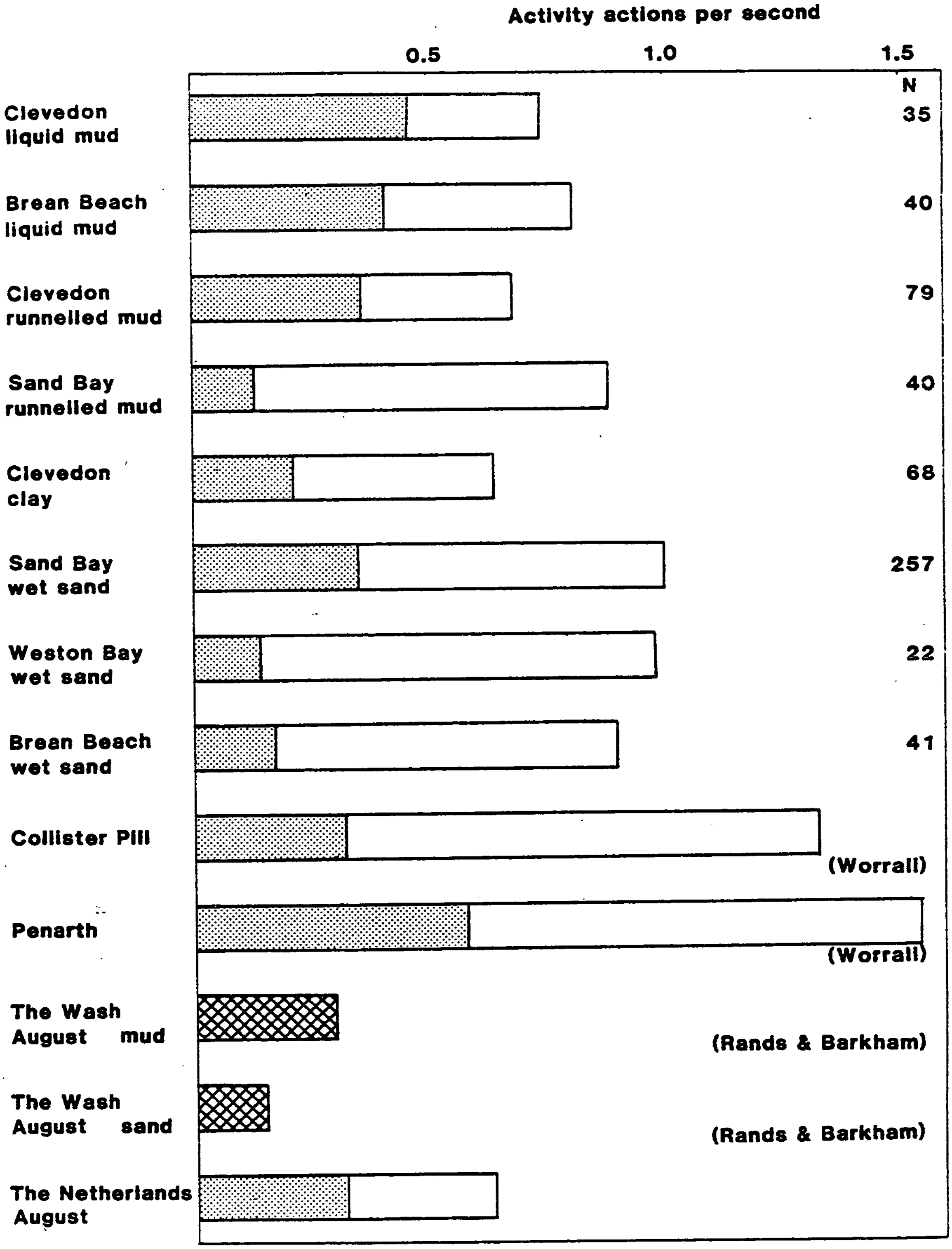


FIGURE 3.7

Adjusted activity rates on different sites sampled during the study compared with published data

Recher, 1969; Sandwich Tern *Sterna sandvicensis* - Dunn, 1972; Royal Tern *Sterna maxima* - Buckley & Buckley, 1974; Turnstone *Arenaria interpres* - Groves, 1978; Oystercatcher *Haematopus ostralegus* - Goss-Custard *et al.*, 1982,83.

Groves showed that juvenile Turnstone had a slower foraging rate than adults, but the same frequency of success per foraging action as adults, and so took longer to obtain an individual prey item. Goss-Custard et al (1982,83) showed that juvenile Oystercatchers are excluded from the mussel beds which are the preferred habitat, only feeding on the best mussel beds in the summer months when the adults are on the breeding grounds. They also showed that most juveniles during their first winter feed on *Nereis* and *Scorbicularia* and a higher proportion of juveniles move into the fields and continue to feed at high tide than adults. As the juveniles mature they are found feeding on the preferred mussel beds but this takes several years. Clark (1982b) showed that juvenile Redshank *Tringa totanus* had a much higher mortality rate during a period of severe weather than adults.

Against this background it was expected that juvenile Dunlin would be found to feed in different ways to adults. With the possible exception of tactile feeding in which there may be differences between adults and juveniles the feeding actions used by both adults and juveniles were the same although they feed in different areas. There are three possible explanations for this finding:

1. Although adults and juveniles were using the same feeding methods the success rate might have been significantly different. As already noted it was not

possible to obtain success rates as the prey taken in this area were too small to be seen.

2. Juveniles specialize in feeding on the wet sand area, and since they are feeding there all the time they are as efficient as the adults feeding in this area.

3. There is no difference in feeding actions between juveniles and adults.

It has been shown that there is a higher percentage of juveniles on the wet sand area than on the runnelled mud further out in Sand Bay; this could be accounted for in three different ways:

1) competitive exclusion of juveniles by adults;

2) inability of juveniles to forage efficiently on the runnelled mud;

3) inability of juveniles to learn to feed efficiently in two separate habitats.

I find the first possibility hard to accept as the Dunlin that fed on the runnelled mud normally did so in one or two large flocks which covered less than five percent of the total runnelled mud at any one time. It was often not possible to see the feeding Dunlin from any one position on the mud so juveniles could have fed on this habitat undetected by the adults. Thus I do not believe that in this situation competitive exclusion through interference such as Goss-Custard _et al._ (1982) have shown for Oystercatchers could occur.

It seems unlikely that juveniles are unable to forage efficiently on runnelled mud as this area in Sand Bay was very similar to the runnelled mud at Clevedon and the same prey were available in the two sites. Although juveniles in Sand Bay had the option of feeding on sand or mud there was no such option available at Clevedon; at this site juveniles were seen feeding on the runnelled mud in the same proportions as in flocks at high tide roosts, suggesting that they did not avoid feeding on runnelled mud at Clevedon as no juveniles were seen to leave the bay to feed.

It is possible that due to a low success rate juveniles need to feed for longer during the tidal cycle than adults; this appeared to be the case in Sand Bay. On the falling tide it was noticeable that juveniles were the first to start feeding and on the rising tide when the adults came off the runnelled mud they tended to roost in a large flock on the sand; the juveniles continued to feed on the sand often until just before it was covered, thus the juveniles fed for longer than the adults. It may be that if an individual is learning to feed on two substrates simultaneously its net food intake will be less than if it specializes in learning the most efficient feeding method for one substrate at a time; if this is the case it would be best for a juvenile to utilize the habitat which is available for longest. This may explain why the juveniles at Sand Bay are selecting the wet sand area on which to feed.

Although it is not possible to show which of the above hypotheses is correct the third hypothesis seems the most likely to be the reason for juveniles feeding on the wet sand. Recent experiments by L. Partridge and P. Green (pers. comm.) have shown that hand reared Jackdaws Corvus monedula forced to feed using three different techniques are less efficient than birds forced to specialize in one of these techniques.

3.4.2 Sex related effects

Many species of waders show a degree of sexual dimorphism in bill length. It has been suggested by Jehl (1970) that sexual dimorphism is an adaptation to promote rapid pairing in a short arctic summer. He argues that there is no reason to postulate that dimorphism has evolved as a means of reducing intraspecific competition for food. This may be true in the breeding season but in the non breeding season it has been shown that for species which have a high degree of sexual dimorphism males and females often feed in different places (eg Bar-Tailed Godwit *Limosa lapponica* - Smith, 1975; Curlew *Numenius arquata* - Townshend, 1981b; Curlew Sandpiper *Calidris ferruginea* - Puttick, 1981) this could result in reduced competition.

I found that there were different percentages of males and females wintering in the different bays on my study site (Chapter 5). Furthermore there was segregation between habitats in Sand Bay, there being a higher proportion of juvenile males on the wet sand area than on the runnelled mud. I have previously stated that I find it difficult to accept that competitive exclusion could account for juveniles feeding on the wet sand area; the same argument applies for the possibility that juvenile males are competitively excluded from the runnelled mud.

As birds of different sex are selecting different habitats I thought it possible that they are doing so because males are more effective at obtaining prey from sand than runnelled mud; this could be the case for one of three reasons:

1. Male and female Dunlin may show differences in feeding behaviour and some of the feeding techniques used may be more efficient at obtaining prey from sand and others from mud.

2. All may use the same feeding method on any given substrate but males may be more effective at obtaining prey on the sand than they are on the mud (possibly because with a shorter bill they are more efficient at taking prey from near the surface (as suggested by Maude-Roxby, 1983) or that they are more effective at handling the small Corophium that are available in the sand).

3. Females may be more effective at obtaining prey on the runnelled mud than on the sand.

As can be seen from table 3.11 there were no significant differences in the feeding rates between males and females when employing visual feeding techniques. There were only differences when tactile feeding which suggests that the first hypothesis is unlikely. The data given in table 3.8 suggest, however, that some males were having to feed for longer after a severe frost on mud at Clevedon (a site where there is a high percentage of females). It is interesting that eight of the 12 marked adults that were feeding had total head lengths of less than 54.5 mm and that only 24 percent of all birds marked at Clevedon were in this category. There is a larger number of short billed birds present in the autumn than in winter (Chapter 5). It would appear then that it was the males that were having to feed; this may be because their main prey (Nereis) had burrowed too deep for them to capture (Chapter 2). It appears, therefore, that females are more efficient at obtaining prey from the runnelled mud than males. This suggests that the third hypothesis is correct possibly with the second also being true. The suggestion from the data presented in table 3.12 and figure 3.4 is that males are actively switching between visual and tactile feeding techniques whereas the females exhibit a graded response.

Evans (1976) suggests that if there are two possible methods of obtaining food, one of which is more costly than the other but more effective at high availability levels of prey, and the other being more effective for obtaining prey when availability is low; then birds should switch from using one technique to the other when prey density changes. They may however change to the less costly technique when their net energy gain is reduced if the lowering in metabolic rate is more than the difference in energy intake between the two methods. This could explain the males switching, the females reaching this situation only rarely.

3.4.3 The effect of environmental factors

Various environmental factors are known to have effects on the feeding behaviour of several species of wading birds (eg Redshank - Goss-Custard, 1969,70c; Grey Plover - Pienkowski, 1981). The data presented in this chapter cannot be considered to show the way in which environmental factors influence feeding behaviour on all the study sites on the south shore of the Severn as the analyses were carried out only for birds feeding on one substrate (the wet sand area in Sand Bay where the major prey species was Corophium). Worrall (1981) made assessments of the factors affecting Dunlin feeding behaviour on the north shore of the Severn. His analyses may be relevant to the areas of mud in Sand Bay and Clevedon which hold similar prey species to those on his study site. Direct comparison between Worrall's data and the data presented in this chapter cannot be made but some of the differences between the two studies shed light on the different ways environmental factors affect the prey species and hence Dunlin feeding behaviour.

My data show a strong negative correlation between rain and peck and activity rates. The reduction in feeding rate could be for a combination of two reasons: first, a reduction in prey activity as has been shown by Goss-Custard (1970c) who reduced the activity rate of *Corophium* by sprinkling water on the surface; and second, the obliteration of any visual cues by the rain. It may be that the reduction in peck rate is due to there being few cues available to the birds; this does not automatically mean that there is a reduction in the success rate as the only cues available at the surface would be those very recently produced. The lower activity rate could be coupled with a higher success rate per feeding action so that the actual success rate may be higher than when it is not raining. Metcalfe (pers. comm.) has recently suggested that an increased success rate for Lapwing *Vanellus vanellus* feeding on *Corophium* in heavy rain may be because *Corophium* are forced to the surface by heavy rain and are therefore both more available and more visible to predators. This at first sight contradicts Goss-Custard's findings but it is possible that *Corophium* become less active when there is disturbance at the surface (ie during light rain) but during heavy rain their burrows may be flooded with fresh water causing increased activity as they move in an attempt to find their normal saline environment.

The increase in peck, probe and activity rates with temperature differs from the findings of Worrall (1981) who found that both peck and probe rates increased at low temperatures. This difference, although possibly partly due to the amount of time spent ploughing, can certainly not be entirely accounted for in this way as even my adjusted activity rates showed a significant positive correlation with temperature. It could be that the differences are directly related to the prey species available in the two study sites, as I have shown that a higher percentage of Nereis (one of the major food sources of the birds studied by Worrall) are available to Dunlin at higher temperatures than at low temperatures (especially larger individuals - Chapter 2). If the increase in availability at high temperatures means that Nereis becomes a superabundant food resource then it might result in decreased activity rate as there would be fewer abortive feeding actions.

The increased activity rate of Dunlin feeding on Corophium in Sand Bay would thus not be expected (unless it never becomes superabundant) as it has been shown that Corophium are more active at the surface as temperature rises (Goss-Custard, 1969); this suggests that there is no simple explanation for the differences in results between the two studies. The fact that the proportion of birds that spent some time ploughing decreased as temperature increased suggests that Dunlin were changing from tactile feeding to visual feeding as temperature increased, as would be expected if prey activity increased with temperature.

Worrall (1981) showed that there was a consistent fall in the peck rate when the tide was rising but when the feeding area was exposed for more than one tidal cycle peck rate tended to increase.

I found that both peck and probe rate significantly increased until low tide and then decreased on the rising tide. It is difficult to know whether these changes in activity rates occur in response to a change in the substrate (possibly drying out) or a change in prey availability or a combination of these two factors. Vader (1964) showed changes in the activity of Nereis through the tidal cycle, there being a reduction in activity the longer the substrate had been exposed. Evans (1983) has recently shown similar responses in several other prey species. A tidal activity rhythm has been shown for Corophium (Holmstrom & Morgan, 1979) although its relevance to the likelihood of predation by wading birds has not been assessed.

Worrall (1981) found several other factors important on the north shore. There was a strong seasonal effect, although much of this could be explained by his work at one site (Collister Pill), which carried on right through the spring passage period when large numbers of migrant birds were present. Although there were still seasonal effects when only the winter was considered these were nowhere near as strong. I could find no such seasonal variation although this could be due to my smaller sample sizes. Worrall also found significant differences in activity which were related to flock density. It was not possible to assess within flock density as the size of Sand Bay made a complete staked grid impractical and the Dunlin flock showed no consistent preference for one area of the Bay. I did, however, gain the impression that there was little seasonal variation in flock size or density.

3.4.4 Differences in feeding rate between different bays and different substrates

There have been several studies of the feeding behaviour of Dunlin (eg Burton, 1974; Rands & Barkham, 1981; Worrall, 1981). There are striking differences among the feeding rates found in these studies, ranging from 0.15 actions per second (Rands & Barkham) to 1.5 actions per second (Worrall). Rands & Barkham's study was carried out on the Wash in August and it may be that Dunlin feeding at this time of year were taking only large prey available at the surface. I am still rather surprised by their extremely low feeding rate as I have watched many flocks of Dunlin feeding on the Wash at different times of year and although I believe that feeding rate is lower in the summer time I have never been aware of rates approaching those that they recorded. Observations I carried out on the Wadden Sea in several sites during August lead me to believe that the situation they observed was very abnormal. For a very small sample of Dunlin observed at random on one site on the Wadden Sea (Zwartehaan, The Netherlands) where they were feeding mainly on *Nereis* I found an activity rate of 0.64 actions per second.

The differences found between my study and Worrall's, although not as striking as the differences with Rands & Barkham's work, are surprising as he was working on the other side of the same estuary at the same time of year. I have tried to work out whether differences between observers could account for this but I believe that although this possibility cannot be excluded it is much more likely that the feeding rate on the north shore is higher than on the south shore. Unfortunately I have not undertaken any observations on Worrall's study area and to be certain that the difference is real and not a result of the different observer technique this would have to be carried out.

Rands & Barkham (1981) showed differences in feeding and feeding behaviour on two different substrates; they found that on mud over 80 percent of feeding actions were pecks whereas on sand more than 70 percent were deep probes. I did not find such large differences between substrates but I did find significant differences between substrates and between similar substrates in different bays. The most striking difference was between the runnelled mud at Clevedon and in Sand Bay (figure 3.6). As previously mentioned it was extremely difficult to obtain observations on Dunlin feeding on the mud in Sand Bay and most of the observations were in fact taken on an area of runnelled mud just below the salt marsh. In this area the substrate was rather firmer than the major areas of runnelled mud in the bay (somewhere between the runnelled mud and clay substrates at Clevedon), but the feeding rates were unlike those found for birds feeding on clay at Clevedon, suggesting that either Dunlin only fed on this area under certain rather abnormal conditions (although there was no apparent difference in the weather conditions under which birds fed on this area) or that the birds were taking a large number of prey items off the surface. I did not sample this area but there appeared to be larger numbers of Hydrobia on the surface here than further out on the runnelled mud where they tended to be found in the rather softer mud in the bottom of the runnels.

The differences found between the wet sand areas in Sand Bay, Weston Bay and at Brean Beach are almost certainly related to the different prey available, there being *Corophium* available in Sand Bay, mainly *Bathyporeia* in Weston Bay and *Bathyporeia* and *Hydrobia* at Brean Beach. As it will be seen from Chapter 5 the Dunlin at Brean Beach are mainly males (short billed birds); I predicted that they would be feeding on prey available close to the surface and so would have high peck rates and low probe rates; this was in fact the case for birds feeding on the wet sand, but on the liquid mud at Brean Beach there was a high probe rate and low peck rate. This may in part be due to the nature of liquid mud and although half the feeding actions were probes even the deep probes might have been obtaining prey only 20 to 25 mm below the surface. It would have been useful to have obtained observations on the prey activity on this substrate but this was not possible because of its treacherous nature. I also predicted that birds would probe more on the sites where there were more long billed birds; although this is the case the differences are not very striking. All the feeding observations were carried out in the daytime and no very severe weather was encountered when feeding observations were being taken. It may well be that Dunlin would tend to probe much more on the runnelled mud sites during very cold weather when as I have shown there would be very few *Nereis* at the surface; under these conditions bill length may be a critical factor affecting survival but it was not possible to test this hypothesis.

Although I have shown that there are differences in feeding behaviour between different bays and substrates I am not convinced that I observed Dunlin under any conditions in which they were likely to be at serious risk from starvation; for this reason I feel the differences I found may not be relevant to a full understanding of why female Dunlin tend to winter in some bays and male Dunlin tend to choose others. It would only be possible to satisfactorily test whether there are different survival rates attributable to bill length on the different parts of the study site if an intensive study was carried out during a spell of severe weather.

CHAPTER 4

THE BIOMETRICS OF THE POPULATION

4.1 Introduction

Many studies of birds have involved catching for marking and often a number of measurements have been taken at the same time, as a method of finding out the skeletal body size (eg Davidson, 1983), the origins of populations (eg Furness & Baillie, 1981), and to aid sexing individuals (eg Green, 1982b). Comparatively little work has been undertaken to ascertain how accurate these measurements are when taken in the field. There have been a number of previous studies on variation in bill length (eg Davis, 1951; White & Gittins, 1964; Pienkowski, 1976; Green, 1981) and wing length (eg Pienkowski & Minton, 1973) over time. Differences between juveniles and adults have been studied by Flegg & Cox (1977).

The first part of this chapter assesses measurement accuracy and variability in measurements over time for Dunlin. The second part of the chapter considers two different methods of sexing birds by discriminant analysis; it also gives simple equations as there is no easily followed publication of these methods for biologists. The comparison of these two methods shows that in some situations individuals may be considered to have a very high probability of being one sex using one method, and a lower probability if the other method is used.

4.2 Methods

In studies of this kind it has not been possible for one observer to take all the measurements on every bird, as on all large catches the amount of time for which it is reasonable to keep birds does not allow this luxury. In the present study the observer's name was noted at the top of each field sheet so that this could be coded later.

Wing length was taken using maximum chord method 3 of Svensson (1975). Bill length was measured from the tip of the upper mandible to the base of the feathers on the top of the upper mandible. Total head length was taken by measuring from the tip of the upper mandible to the back of the skull, pressing the feathers flat against the skull so that the measurement consisted of the skull, rhampotheca and skin and feathers over the back of the head. The skeletal portion was by far the largest component.

Wing lengths were taken to the nearest millimetre using a stopped wing rule. Bill length was measured to the nearest millimetre using a wing rule in late winter 1977/78. During the 1978/79 winter a pair of adapted stainless steel dial calipers (figure 4.1 & Green, 1980b) were used to take bill length and total head length. These are better than vernier calipers as the scale is much quicker and easier to read but they do have one drawback: the dial rotates once every five millimetres and can only be interpreted by reference to the main scale. This would be no problem under laboratory conditions but in a field situation when observers were often cold and tired some mistakes were made. It was possible to estimate the rate of mistakes by looking at retraps. This was less than one percent, but when looking for differences between individuals in weight cycles, movements, etc this could bias the data. In the summer of 1979 some comparatively cheap plastic calipers manufactured by CAMLAB (Reference number AR/CAL6921 Model C) were obtained. CAMLAB calipers have two advantages: first, one

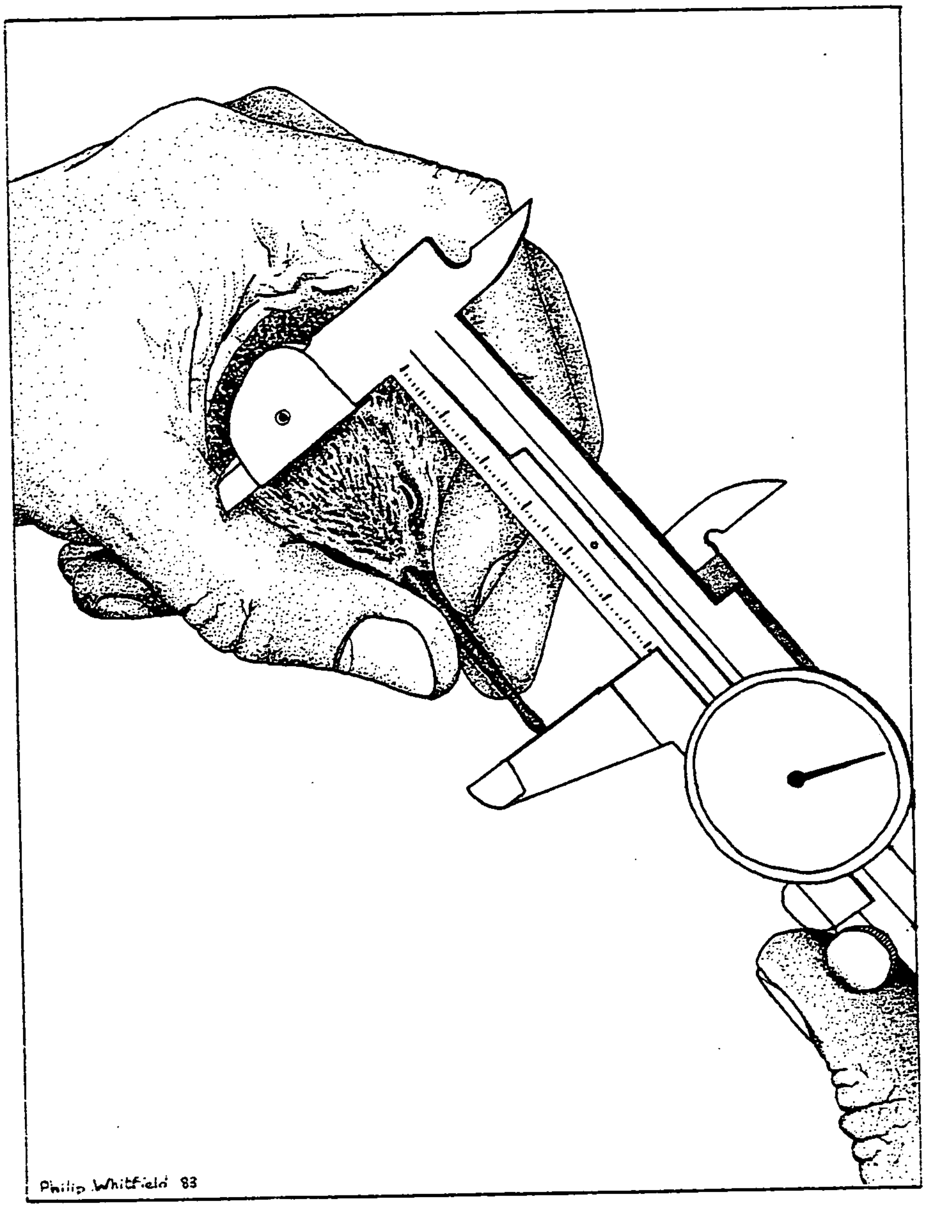


FIGURE 4.1

Adapted calipers used to measure total head length revolution of the dial occurred every 10 mm and, as the span of bill lengths and total head lengths is not much over 10 mm, few mistakes in reading the main scale were made; second, the cog and groove system turning the dial is much larger and therefore is not affected by sand.

On 18 March 1979 total head lengths of birds were measured to the nearest 0.5 mm using a wing rule as two teams were operating and I had only one pair of dial calipers; retraps of birds measured on this day show how this method compares with using adapted calipers.

Over 1,300 birds were caught more than once, the maximum number of captures of a single bird was six but no bird was measured more than four times (as on a few very large catches there was not enough time even to measure all retraps). To analyse measurement accuracy and seasonal variation two sets of measurements for each bird were treated as one unit; thus a bird that was only measured twice had one line in the data set but a bird that was measured three times had three lines in the data set (first and second time measured, second and third time measured and first and third time measured). This could potentially have caused problems with an inflated sample size but it did not occur often enough to cause any serious problem. In this section data were used only when the observer was the same on both occasions, in practice this meant that the vast majority of measurements were taken by myself.

For part of the analysis the winter was split into two portions: October, November and December were termed early winter and January, February and March were termed late winter.

Although Dunlin are sexually dimorphic there is overlap between the sexes in all measurements. In winter it is not possible to sex individuals by any external criteria. For this reason measurements of all British wintering Dunlin that had been sexed by dissection were gathered together in an attempt to find a method of assigning sex to an individual of given measurement by discriminant analysis. The birds came from several sources: birds taken under licence for other studies (eg heavy metal analysis); birds found freshly dead after severe weather and casualties from catching operations. This produced a large sample, and for the analysis only birds from the Severn Estuary were used with one large sample from North Wales for comparison. I measured all birds used in the analysis apart from those obtained from the North Shore of the Severn.

An SPSS discriminant analysis programme (Nie et al., 1975)was run on a small amount of data in the summer of 1979 but it was not possible to produce sensible contour lines. After consulting Dr C. M. Theobald of Edinburgh University Statistics Department, equations were derived for: 1. determining the probability that a bird is male or female; and 2. producing probability contours on a graph. This is termed the "estimative method" (Aitchison et al., 1977). After further discussions with Dr Theobald it became clear that the "estimative" method has serious drawbacks and that a different method, the "predictive method" may give better results. The two methods were compared by Aitchison et al., (1977). Again with the help of Dr Theobald it was possible to produce equations for assigning the probability of an individual being male; however, the probability contours are not straight lines using this method so an equation could not be derived for them. The equations for both methods are given below.

4.2.1 The Estimative Method

This is the method used by SPSS (Nie *et al.*, 1975) which can only be used when a large sexed sample is available and when the sex ratio of that sample is approximately equal. The probability of group membership of an individual and the probability contours of group membership are found by solving equation (1)

$$\log_e \left(\frac{1 - P}{P} \right) = \left(\underline{X}^{(2)} - \underline{X}^{(1)} \right)^{T} S^{-1} \left\{ \underline{X} - \frac{1}{2} \left(\underline{X}^{(1)} + \underline{X}^{(2)} \right) \right\} \qquad (1)$$

Where P = Probability of being male

S = The pooled within-groups covariance matrix

$\underline{X}^{(j)}$ = The sample mean of group j

$\underline{X}$ = The individuals' values

When two variables (wing and bill) are used the following data is needed:

$\overline{Wm}$ = The mean wing length for males

$\overline{Bm}$ = The mean bill length for males

$\overline{Wf}$ = The mean wing length for females

$\overline{Bf}$ = The mean bill length for females

From the pooled within groups covariance matrix:

	Wing	Bill
Wing	WW	
Bill	WB	BB

All these values may be obtained from the SPSS discriminant package.

First solve equations (2) and (3)

$$Y = \frac{BB(\,\overline{Wf} - \overline{Wm}\,) - WB(\,\overline{Bf} - \overline{Bm}\,)}{(\,WW \times BB\,) - WB^{2}} \qquad (2)$$

$$Z = \frac{WW(\,\overline{Bf} - \overline{Bm}\,) - WB(\,\overline{Wf} - \overline{Wm}\,)}{(\,WW \times BB\,) - WB^{2}} \qquad (3)$$

To find the probability p of an individual, with a wing length Wa and bill length Ba, being a male, solve (4).

$$p = \frac{1}{1 + e^{\left[\,Y\left\{\,Wa - \left(\,\frac{\overline{Wf} + \overline{Wm}}{2}\,\right)\right\} + Z\left\{\,Ba - \left(\,\frac{\overline{Bf} + \overline{Bm}}{2}\,\right)\right\}\right]}} \qquad (4)$$

To find the probability contours for given values of p, solve (5) inserting three values for bill length (Ba) and finding the corresponding wing length for each value of p. The contour is a straight line through these points and when p = 0.5 the best discriminating line is given.

$$Wa = \frac{(\overline{Wf} + \overline{Wm})}{2} + \frac{\left[\mathrm{Log}\ e\left\{ \frac{1 - p}{p} \right\} - Z\left\{ Ba - \left(\frac{\overline{Bf} + \overline{Bm}}{2} \right)\right\}\right]}{Y} \qquad (5)$$

4.2.2 The Predictive Method

This method uses similar information to the estimative method, but also needs additional information to take the size of the sexed sample into account. The probability of group membership of an individual is found by solving the general equations 6 to 9.

$$P = \frac{1}{1 + A} \qquad (6)$$

$$A = \left(\frac{1 + \left(\frac{1}{Nm}\right)}{1 + \left(\frac{1}{Nf}\right)} \right)^{0.5C} \times \left(\frac{D}{E} \right)^{0.5(Nm + Nf - 1)} \qquad (7)$$

Where Nm = Number of males

Nf = Number of females

C = Number of variables used

$$D = \frac{1 + (\underline{X} - \underline{X}^{(1)})^{T} \; S^{-1} \; (\underline{X} - \underline{X}^{(1)})}{(Nm + Nf - 2)\;(1 + \frac{1}{Nm})} \qquad (8)$$

$$E = \frac{1 + (\underline{X} - \underline{X}^{(2)})^{T} \; S^{-1} \; (\underline{X} - \underline{X}^{(2)})}{(Nm + Nf - 2)\;(1 + \frac{1}{Nf})} \qquad (9)$$

When two variables are used, the same data are needed as for the Estimative Method with the addition of:

Nm = number of males

Nf = number of females

First solve equations 10 to 14.

$$F = \{[BB(Wa - \overline{W}m) - WB(Ba - \overline{B}m)] \times (Wa - Wm)\} + \{[WW(Ba - \overline{B}m) - WB(Wa - \overline{W}m)] \times (Ba - \overline{B}m)\} \qquad (10)$$

$$G = [(BB \times WW) - (WB \times WB)] \times [(Nm + Nf) \times (1 + \frac{1}{Nm})] \qquad (11)$$

$$H = \{[BB(Wa - \overline{W}f) - WB(Ba - \overline{B}f)] \times (Wa - \overline{W}f)\} + \{[WW)Ba - \overline{B}f) - WB(Wa - \overline{W}f)] \times (Ba - \overline{B}f)\} \qquad (12)$$

$$J = [(BB \times WW) - (WB \times WB)] \times [(Nm + Nf) \times (1 + \frac{1}{Nf})] \qquad (13)$$

$$K = \frac{1 + \frac{1}{Nm}}{1 + \frac{1}{Nf}} \qquad (14)$$

Now to find the probability of the individual (with wing length Wa and bill length Ba) being male solve equation 15.

$$P = \frac{1}{1 + K\left(\frac{(1 + \frac{F}{G})}{(1 + \frac{H}{J})}\right)^{0.5(Nm + Nf - 1)}} \qquad (15)$$

Initially it was hoped that by taking a series of measurements it would be possible to sex all individuals with a high degree of certainty. So for one sample of birds (from Berrow) the following measurements were taken: wing; bill; total head length; tarsus + toe; 'knee' joint width (joint between tibio-tarsus and tarso-metatarsus) and external keel length. The measurements which discriminate best between the sexes were: wing; bill and total head length. Although there was a significant ($F = 4.91$, $0.025<P<0.05$) improvement in discrimination ability with using three measurements rather than using just wing and total head length, the problems of taking bill length in the field convinced me that bill length should not be used whenever total head length was available. To produce the predictive contours a "fake" data set was created containing all the possible combinations of wing (from 110 to 130 mm) and total head length (from 48.0 to 66.0 mm). The predictive programme for each site was then run assigning the probability of being male to each individual in the "fake" data set. The birds close to the probability of the predictive contours to be plotted were then selected to give narrow bands of individuals. When these individuals were plotted they gave narrow bands of points through which contour lines could be drawn. Although the lines were not exact they were close enough to be able to compare graphically the effect of the two different methods when sexing Dunlin.

4.3 Results and Discussion

4.3.1 Wing length - adults

In order to ascertain the repeatability of this measurement the variance in the difference between two measurements for each bird was assessed. A total of 119 birds were measured twice in the same late winter; the data are plotted in figure 4.2a. Of the 119 birds 51 percent had the same measurement on both occasions and over 90 percent varied by less than one millimetre; only 2.5 percent varied by more than two millimetres. Thirty-four birds were measured in both early and late winter in the same season; although the sample size is small there is no significant reduction in wing length through the winter (figure 4.2b). As there is no difference in Dunlin wing lengths through the winter, measurements from the different periods in one season can be combined in order to look for differences between years. There is a significant positive correlation ($R = 0.119$, $p<0.05$, $y = 0.059 + 0.0155x$) between difference in wing length and years between capture, the variance

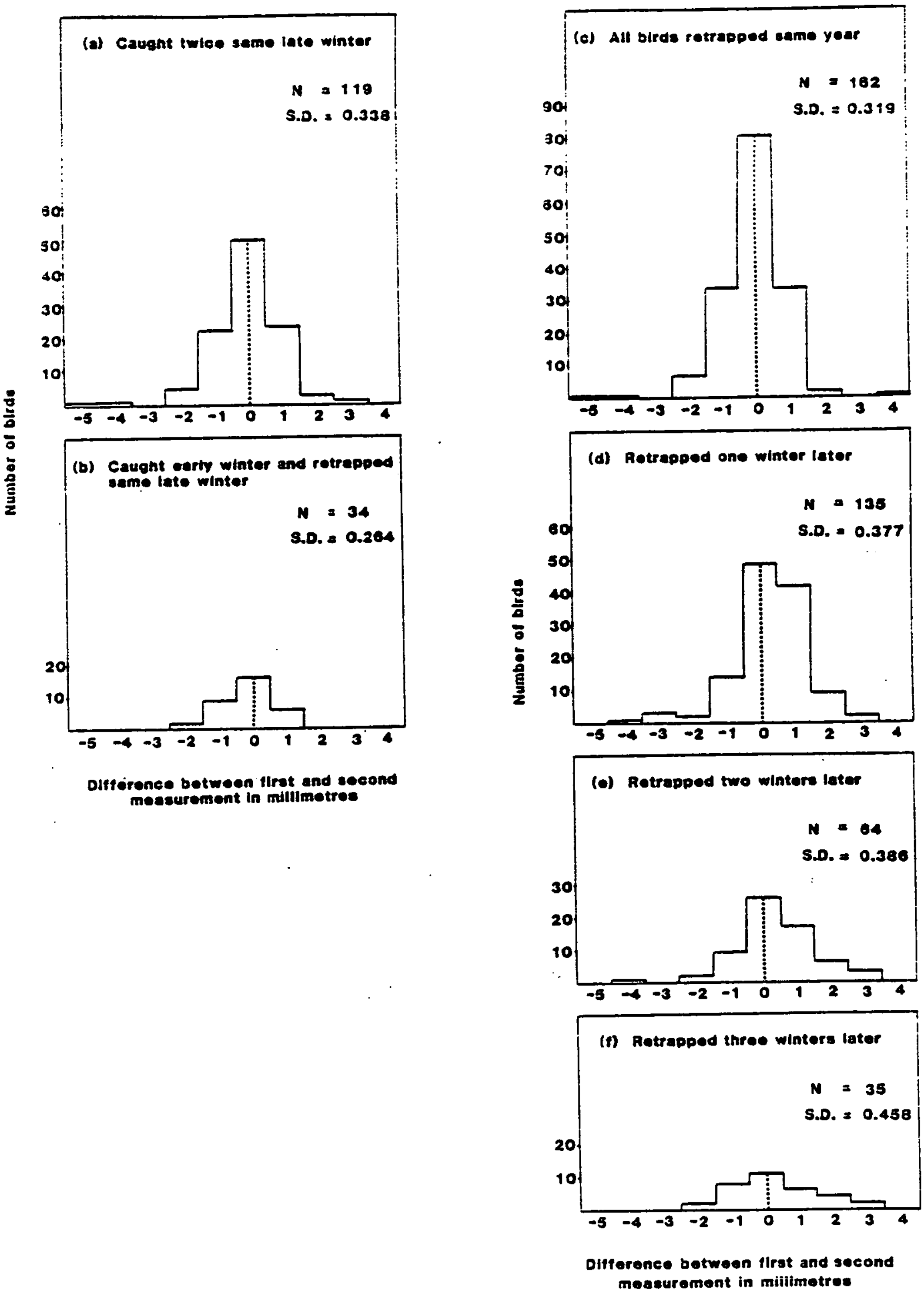


FIGURE 4.2

Differences in wing length for individual adult Dunlin with various time intervals between measurements also significantly increased with measurements one year apart ($F = 1.39$, $P<0.05$); two years apart ($F = 1.49$, $P<0.05$); and three years apart ($F = 2.062$, $P<0.01$). These data are plotted as histograms in figure 4.2c-f).

Most previous studies of wader wing lengths have suggested that wing length declines linearly during an inter-moult period (eg Pienkowski & Minton, 1973). I find no evidence for a decline in wing length during the winter months in adult Dunlin and it was noticeable in the field that the wing tips of most individuals looked in perfect condition even in late winter. The data presented by Pienkowski and Minton to show wing length reduction in Knot Calidris canutus suggest a smaller decline in wing length over the winter months than in spring and summer, although they treat the decline as a linear relationship. Wing feathers on adult birds normally last for only one year and it would not be at all surprising if the rate of wear on the feathers increased as the feathers aged. Thus a linear decline throughout the year seems unlikely and it is not justifiable to calculate an average wing length reduction per month. The increase between years in adult birds agrees with Pienkowski & Minton's findings but is very much smaller (ca 0.2 mm; 0.16% per annum) than the one percent per year in Knot.

4.3.2 Wing length - juveniles

The data set for juveniles is very small in comparison to that for adults. Juvenile Dunlin measured twice in the same late winter follow the same pattern as for adults (figure 4.3a) but there is a

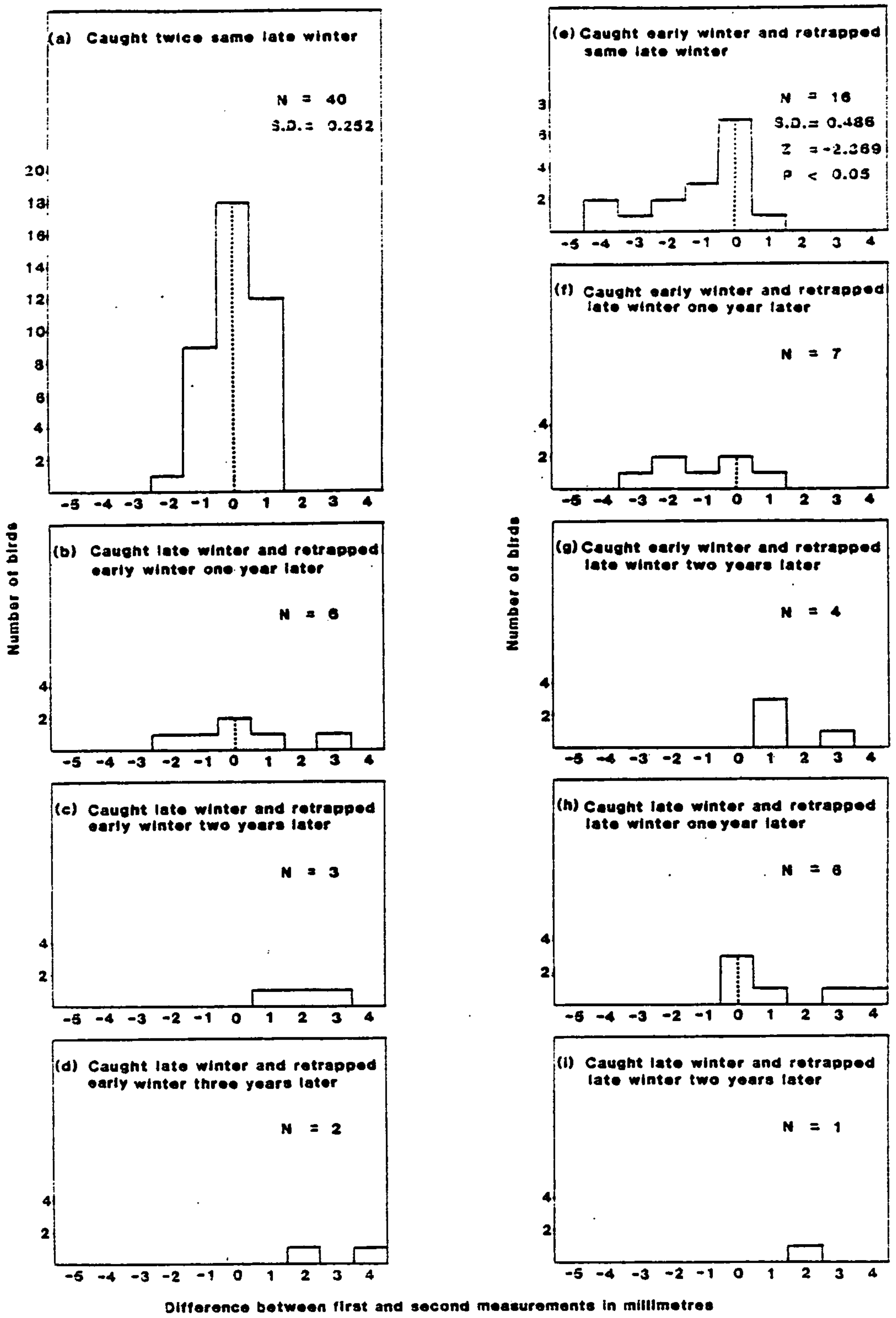


FIGURE 4.3

Differences in wing length for individual juvenile Dunlin with various time intervals between measurements significant decline in wing length between early winter and late winter (figure 4.3e). This means that it is not possible to combine data when looking for between year differences. I have therefore plotted separately in figure 4.3 the data for birds caught between early winter and late winter, late winter and early winter and late winter and late winter. All three sets of data, although meagre, show the same trend. They indicate a decline in wing length during the second winter as well as the first winter but the sample sizes are too small to test for significance. Although the data set is very small it suggests that between the second and third winter of a Dunlin's life there is an increase in wing length.

The decline in juvenile wing length during the first winter may be expected as the primaries are grown before the birds leave the breeding grounds and the juvenile feathers are beginning to show signs of wear by the end of the winter. The pattern of change in wing length of juvenile birds retrapped in subsequent winters appears to be different to that found in previous studies which have shown for a wide variety of species that wing length increases substantially between the first and second winters of a bird's life (eg Great tit _Parus major_ and Blackbird _Turdus merula_ - Kluijver, 1939; House Sparrow _Passer domesticus_ - Lohrl & Bohringer, 1957; Blue tit _Parus caeruleus_ - Stewart, 1963; Knot - Pienkowski & Minton, 1973). My data provide no evidence for an increase in wing length between the first and second winter of a Dunlin's life, but there is an indication of an increase between the second and third winters.

There is no obvious reason why Dunlin should differ from other birds; but they differ in their biology from Knot (and other large waders) in that individuals in their first summer migrate at least part of the way to the breeding grounds and some breed (Soikelli, 1967) whereas juvenile Knot stay on the wintering grounds throughout the summer (Prater, 1981). One year old Dunlin may thus be stressed whilst going through their first moult and this could possibly account for the difference between these two closely related species. The increase in wing length of birds between their second and third year could have significant implications for the use of discriminant analysis to sex Dunlin, but although the wing length may be one or two millimetres shorter than when fully adult it would not change the sex of any bird outside the 0.75 and 0.25 confidence limits when all Severn data are used (see later).

4.3.3 Total head length

Experience in taking bill length measurements on waders prior to the start of this project led me to be concerned about the use of this measure in biometric studies. Bill length is variable, when it is measured from the tip of the upper mandible to the margin of the feathers on the upper mandible, as the feather margin is liable to change if feathers get worn away at the top of the bill (this is often very noticeable when the birds are in moult) and also because these feathers, being bedded in skin, can move as the rhampotheca on the top of the bill moves. On waders it is not possible to measure bill length to the base of the skull as there is no sharp divide. I undertook preliminary tests to find an alternative measure by measuring bill length to the front of the nares as suggested by Pienkowski (1976) and by using total head length (as has been successfully used with other species (eg Gulls - Coulson et al., 1981). I found it possible to take accurate repeatable measurements in both these ways but total head length proved to be easier to measure as it was possible to hook the calipers around the back of the skull and then close the other arm until it touched the tip of the bill. In contrast, when measuring to the nares it was easy to overshoot the front of the nares when moving the calipers into position and thus more errors were made. Wherever possible throughout the project both bill length and total head length were taken but when time was limited only total head length was measured.

Figure 4.4 shows bill length plotted against total head length for a sample of birds caught during the study. It can be seen that there is a very high degree of correlation between these two measures and that they are linearly related. On average total head length increases by one millimetre for every 0.9 mm increase in bill length.

To check that total head length accurately predicts bill length, accurate measurements were taken on a sample of 17 Dunlin skulls. It was not possible to measure bill length in the same way as in live individuals as the skin had been removed, therefore, a measurement was taken with calipers from the back of the lachrymal bone (front of eye socket) to the tip of the bill. It can be seen from figure 4.5 that there is a very high degree of correlation between this measurement and total head length (R = 0.99). Head length (total head length minus bill length) significantly correlated with head width (R = 0.58) showing that birds with a greater head length (and therefore greater total head length) also had wider skulls. This would be expected as it is already known

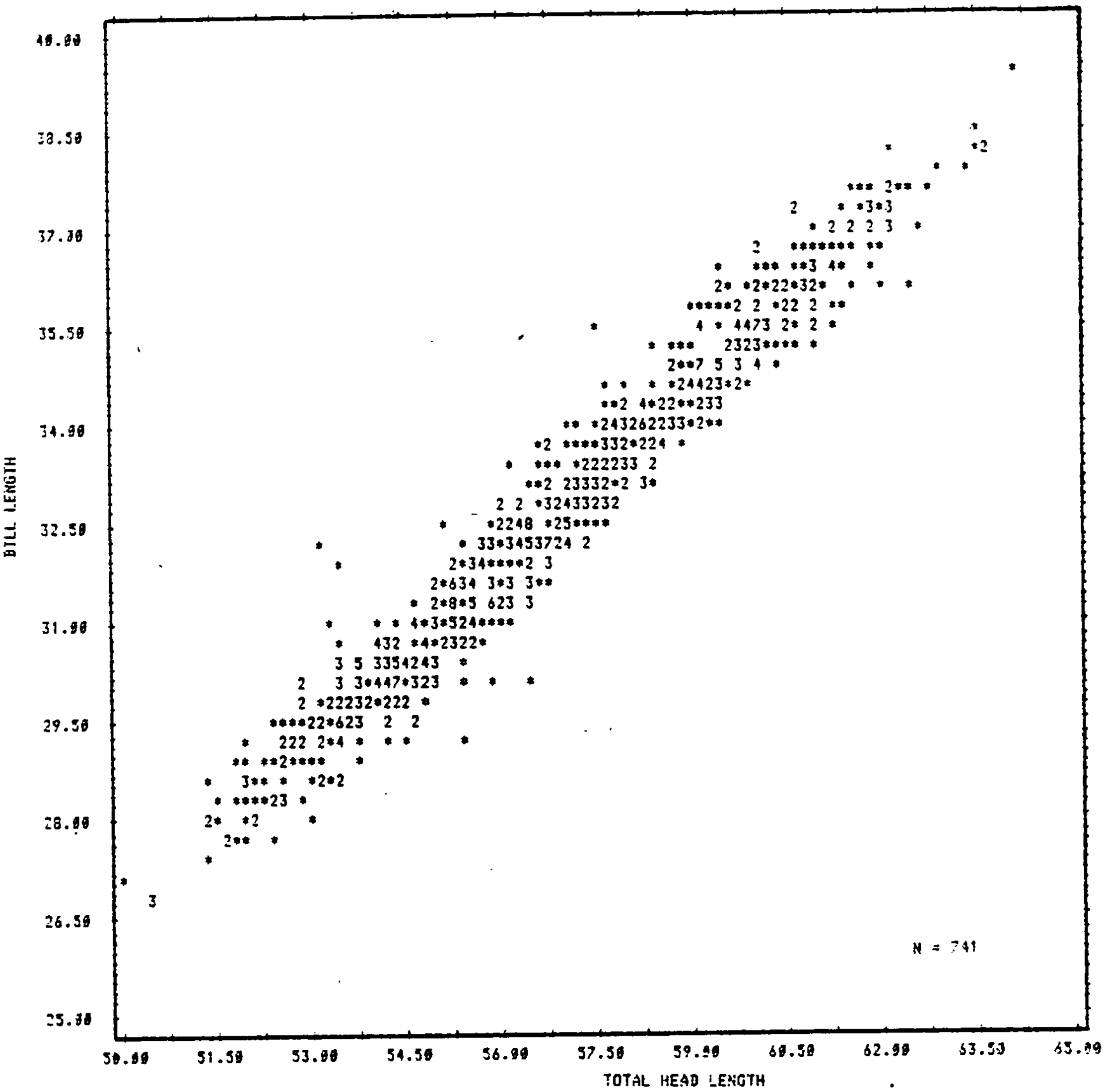


FIGURE 4.4

The relationship between bill length and total head length for a sample of adult Dunlin wintering on the Severn

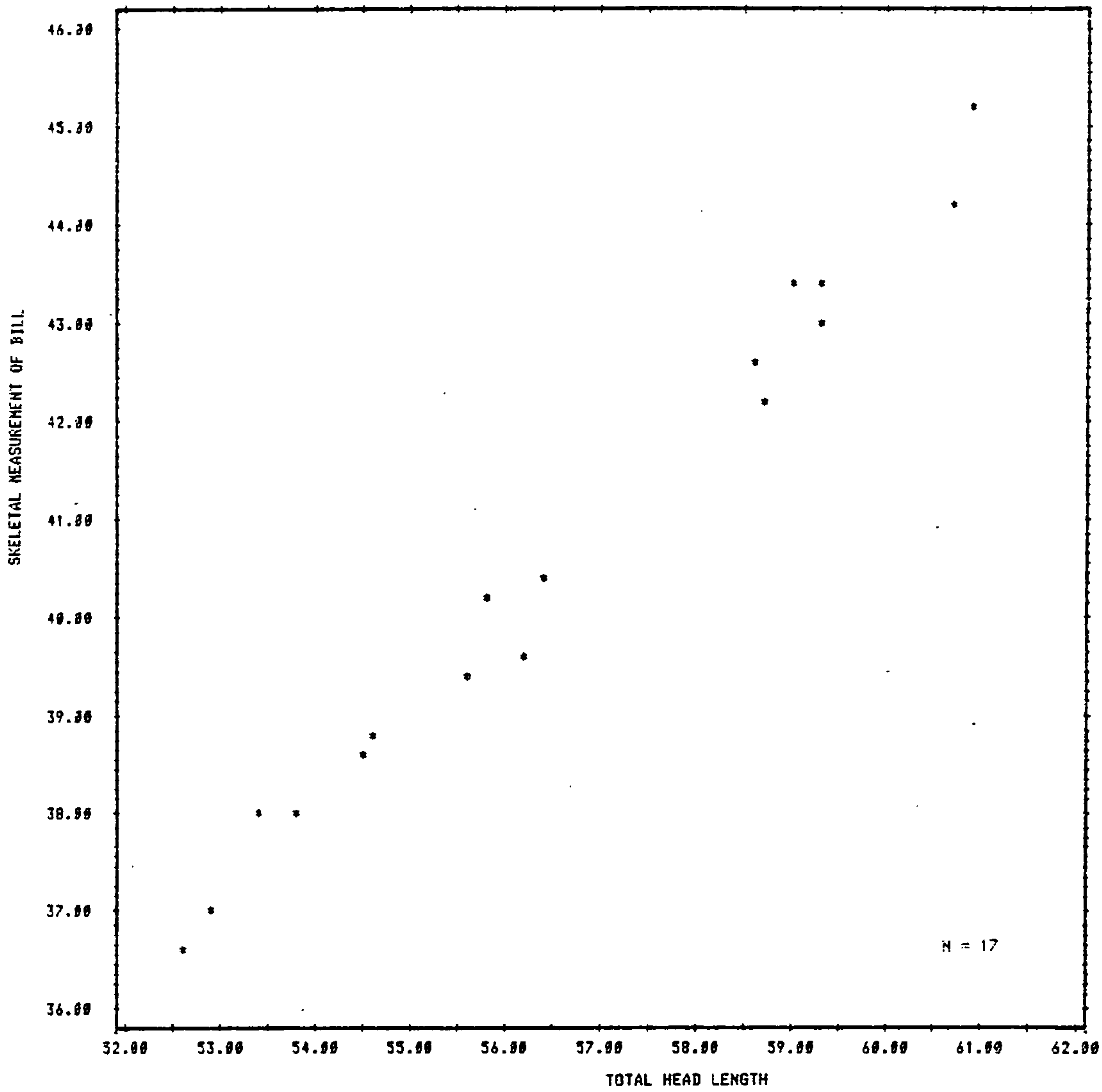


FIGURE 4.5

The relationship between a skeletal measurement of the bill and total head length for a sample of Dunlin skulls Obtained on the Severn in winter that females have a larger body size than males, as well as longer bills.

4.3.4 Total head length - adults

The data were treated in the same way as those for wing length. No within winter differences were found (figures 4.6a & 4.6b) but there is strong evidence for a reduction in total head length between years (figure 4.6c-e). I have shown that total head length and bill length are very strongly correlated (figure 4.4), so it is initially surprising that similar results are not obtained for both measurements when looking for within and between year variation. The decline in total head length with age is highly significant and it is probable that the reason this is not found in bill length is that with a less repeatable measurement and a smaller sample size small effects like this will not show up. As the bill in Dunlin consists of bone covered with a rhampotheca this decline in a skeletal measurement over time seems surprising.

A series of Dunlin skulls were stained using Mallory's triple stain to show up the presence of bone and cartilage. It was found that although most of the bill consists of bone the section of the dorsal bar of the premaxilla between 0.5 and 1.0 mm from the bill tip had a substantial portion of cartilage. There was a similar area on the ventral bars but this was from 0.5 to 1.5 mm from the bill tip. It was noticeable that when the bill tip was flexed the bending occurred solely in this portion (figure 4.22). Mammalian cartilage ossifies with age and may shrink as a result (Prof. R. A. Stockwell, pers. comm.) it is possible that this could be happening

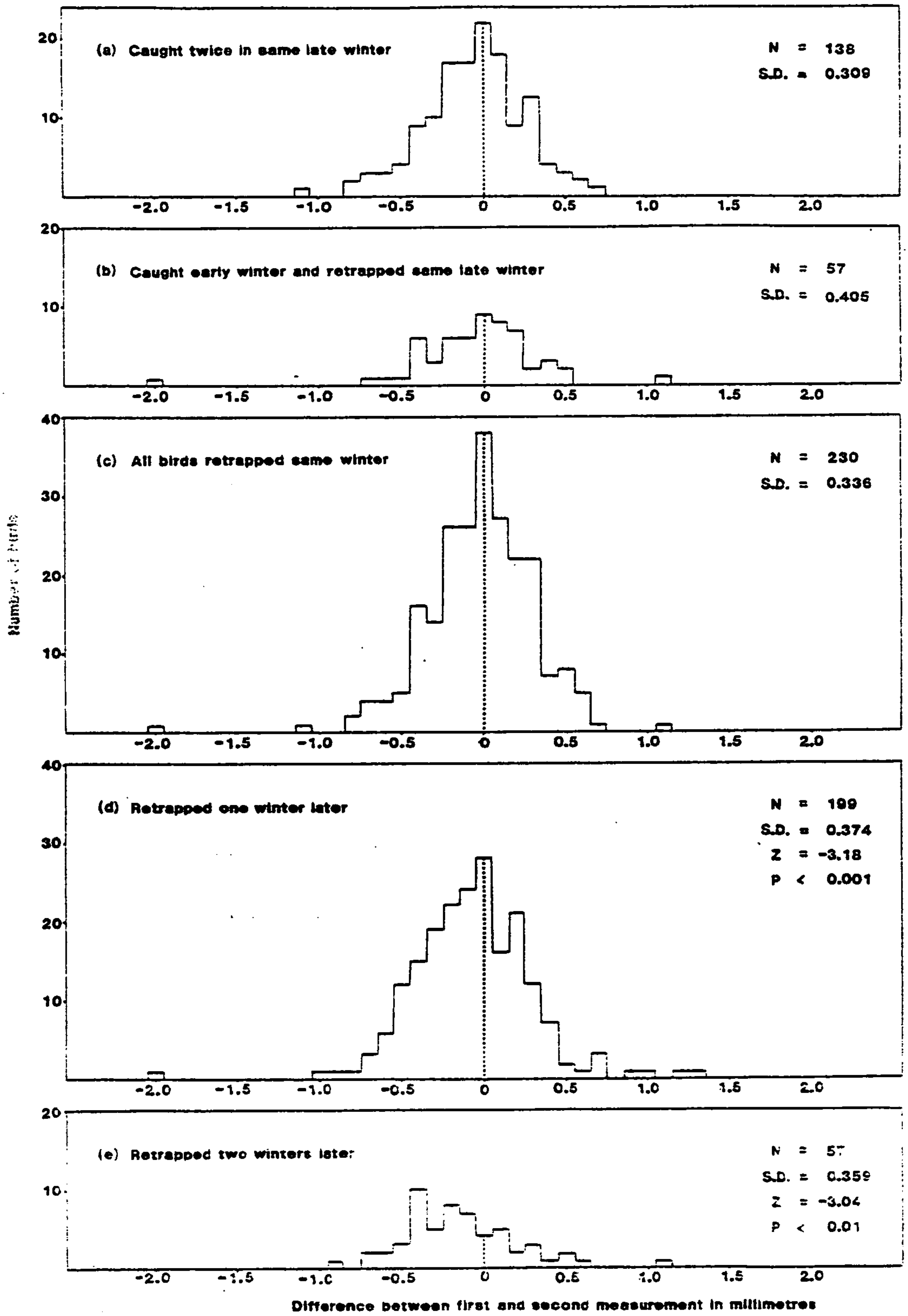


FIGURE 4.6

Differences in total head length for individual adult Dunlin with various time intervals between measurements

Where the difference between the two measurements differed significantly from zero using Wilcoxon's matched pairs sign test Z and P are given

in Dunlin.

4.3.5 Total head length - juveniles

There was no decline in total head length of juvenile birds in fact there was a slight suggestion of an increase and there was a significant increase in bill length, this suggests that growth might not be quite completed during the first winter and that the shrinkage may only occur in older birds.

4.3.6 Bill length - adults

Figure 4.8a shows that there is a significantly higher variance in the difference in bill length on retrap than that for total head length ($F = 1.97$, $P<0.001$). Figure 4.8b shows that there is a significant decline in bill length between early and late winter; this means that it is not possible to combine data to look at year to year differences so only data obtained in late winter (when most birds were measured) were used. There is no year to year decline in bill length (figure 4.8c-e). The reduction in bill length over the winter in adult Dunlin suggests either that new feathers grow down the bill or that there is a slight shrinkage in the rhampotheca through the winter causing the feather margin to move towards the tip. The possibility that the bill is being worn away has been discounted as, if this was the case, total head length would show a significant decline through the winter. I find it unlikely that there is any significant feather growth through the winter as I have never observed this in the field. Pienkowski (1976) showed in adult

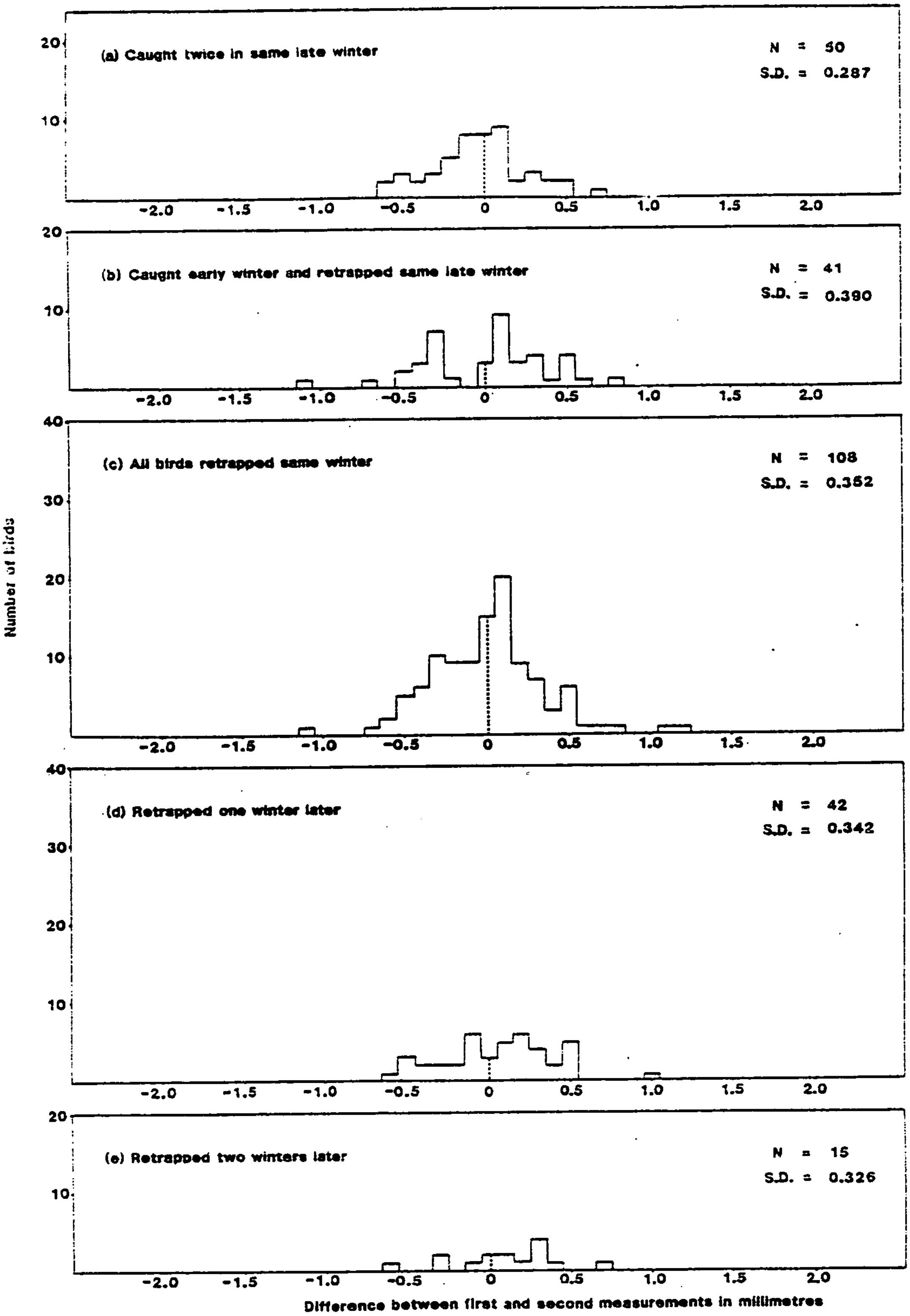


FIGURE 4.7

Differences in total head length for individual juvenile Dunlin with various time intervals between measurements

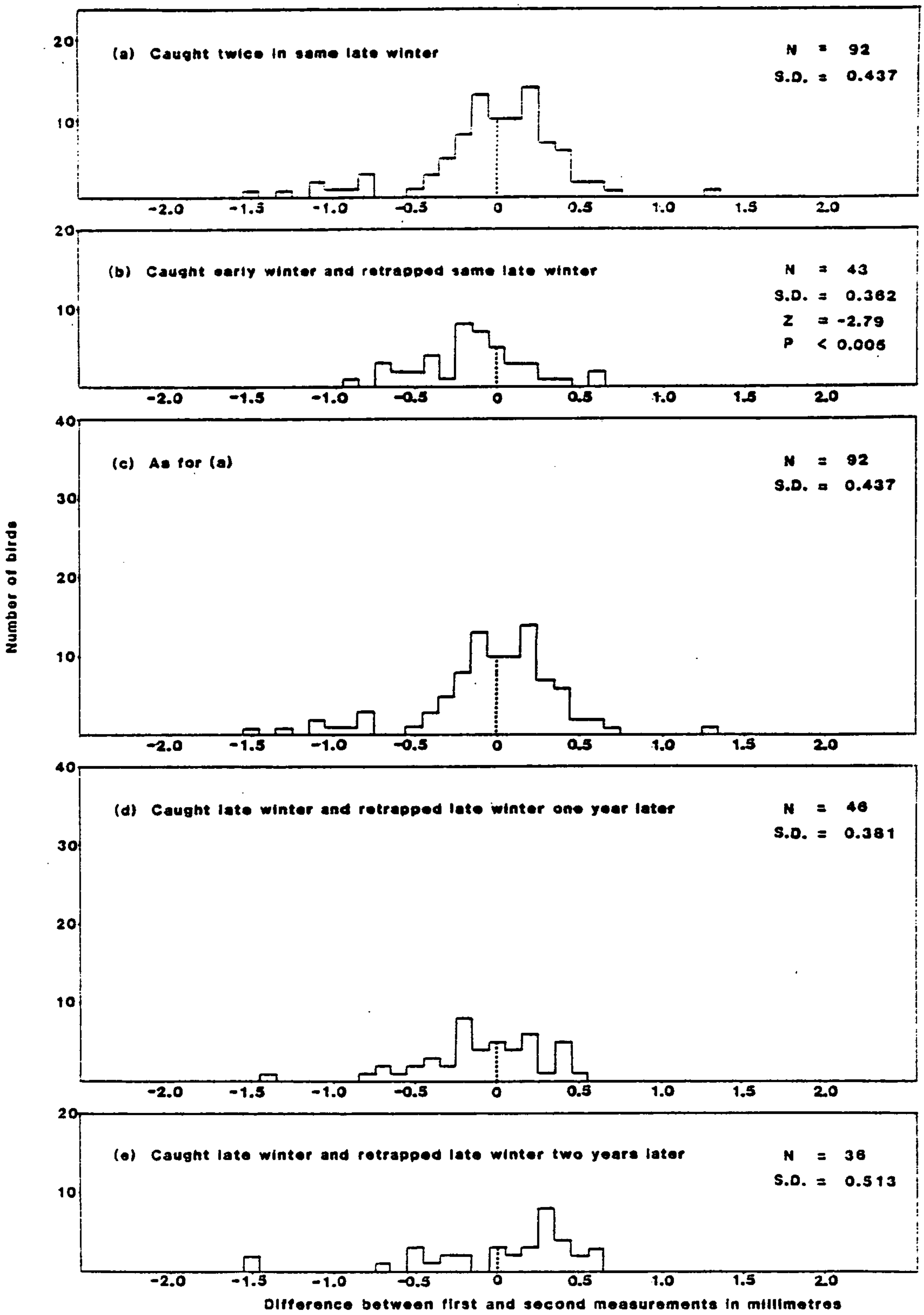


FIGURE 4.8

Differences in bill length for individual adult Dunlin with various time intervals between measurements

Knot bill length increases by about 0.6 mm between December and February. The increase in Knot (with similar bill length and rhampotheca to Dunlin) contrasts with the 0.2 mm reduction in Dunlin.

4.3.7 Bill length - juveniles

Unlike the adults there is no evidence of a decline in bill length from early to late winter (figure 4.9b), so all data can be combined to look at year to year differences. There is a significant increase in bill length between the first and second winter (Wilcoxon's matched pairs sign test $z = -2.14$, $p<0.05$) (figure 4.9c-e). This result could occur if most second captures were in early winter (there was no such bias in the data). The data set is too small to test for significant differences between first and third winter.

4.3.8 Measurement techniques

Bill length measured by wing rule versus dial calipers

The bill lengths of seventeen birds caught twice during late winter in 1978 were measured each time using a wing rule (figure 4.10a). Eleven birds had the same bill length, five differed by one millimetre and one differed by two millimetres. The variance was significantly higher than that for birds measured twice in late winter of the same year (figure 4.8) using dial calipers ($F = 2.80$, $P<0.01$). The bill lengths of 95 birds were measured with a wing

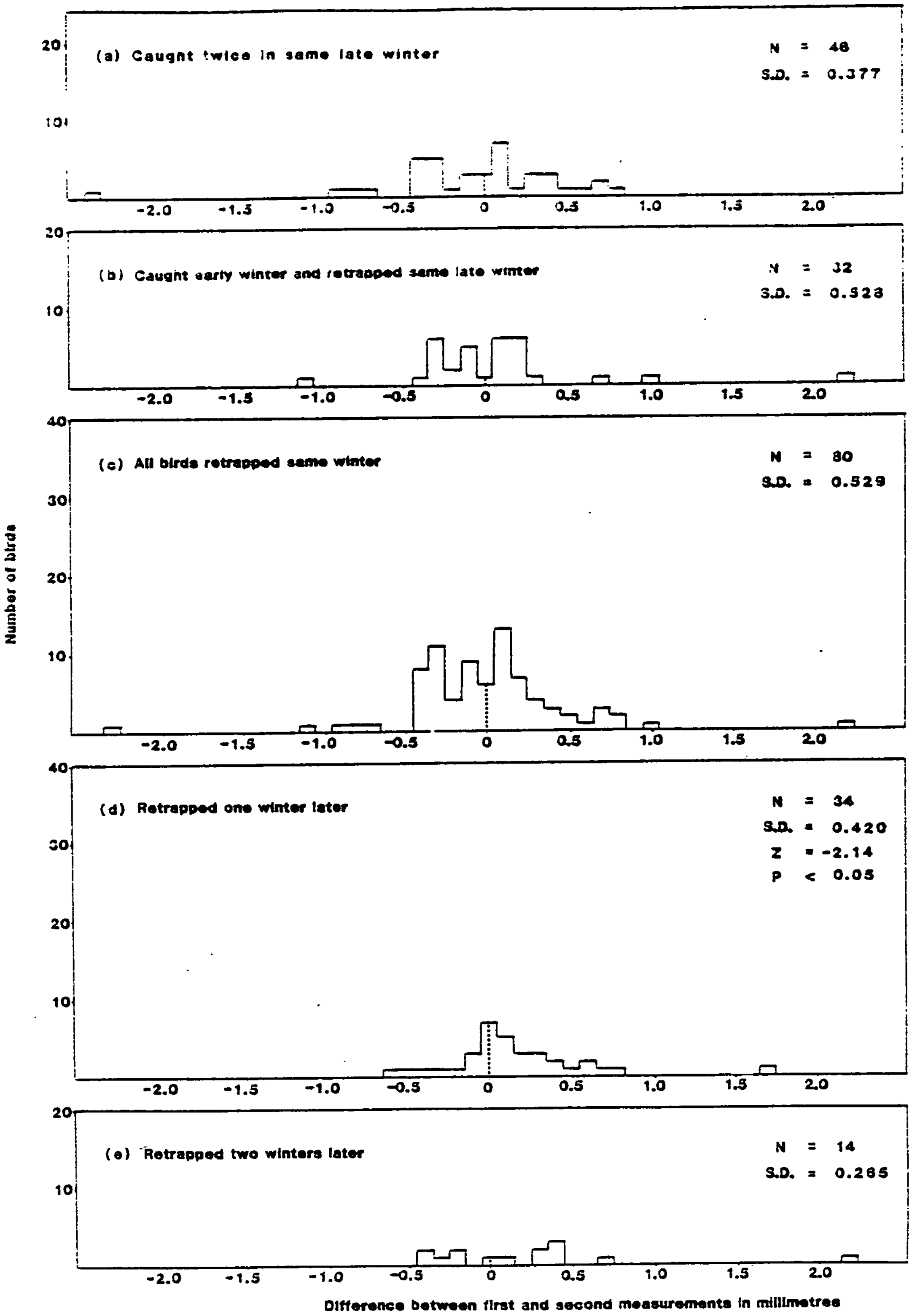
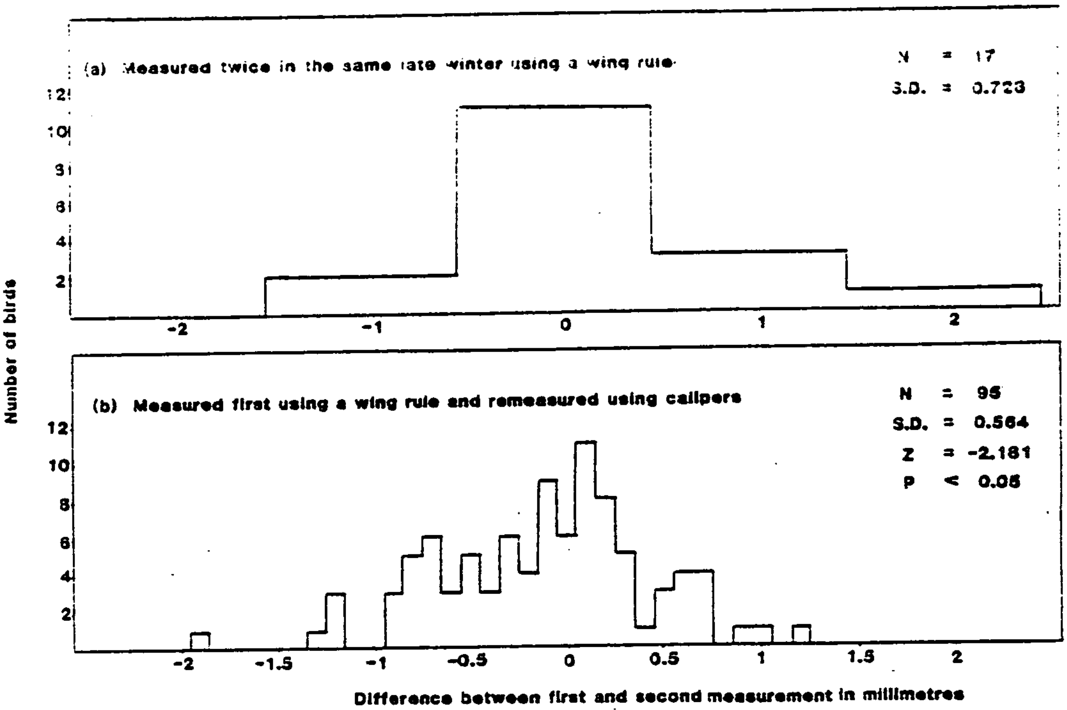


FIGURE 4.9

Differences in bill length for individual juvenile Dunlin

with various time intervals between measurements

Where the difference between the two measurements differed significantly from zero using Wilcoxon's matched pairs sign test Z and P are given


(a) Measured twice in the same late winter using a wing rule

(b) Measured first using a wing rule and remeasured using callipers

FIGURE 4.10

Comparison of bill length measured by two different methods:

wing rule, measured to the nearest millimetre;

calipers, measured to the nearest 0.1 millimetres

Where the difference between the two measurements differed significantly from zero using Wilcoxon's matched pairs sign test Z and P are given

rule in late winter 1978 and subsequently remeasured in late winter using dial calipers. All three years showed the same pattern so the data are combined in figure 4.10b. This shows that bill length measured to the nearest millimetre with a wing rule overestimates the actual bill length by about 0.2 mm (Wilcoxon's matched pairs sign test $z = -2.18$, $p<0.05$).

Total head length measured by wing rule versus dial calipers

Fourteen birds were measured first using calipers and then, later in the same late winter period, with a wing rule to the nearest 0.5 mm (figure 4.11a). The difference between the two measurements on these birds was significantly higher than that for birds measured on two separate occasions with calipers ($F = 2.85$, $P<0.01$) (figure 4.7a). Nineteen birds were caught in subsequent winters and although the data set was small there was a significant reduction in total head length with time (Wilcoxon's matched pairs sign test $z = -2.58$, $p<0.01$) (figure 4.11b). This reduction with time has been discussed earlier.

4.3.9 Discriminant analysis

The small variation in wing, bill and total head length measurements over time has no significance in this study, as they are highly variable in Dunlin. In a species which shows much less sexual dimorphism such differences could cause significant biases in the use of discriminant analysis.

Figures 4.12 to 4.14 show the total head lengths and wing

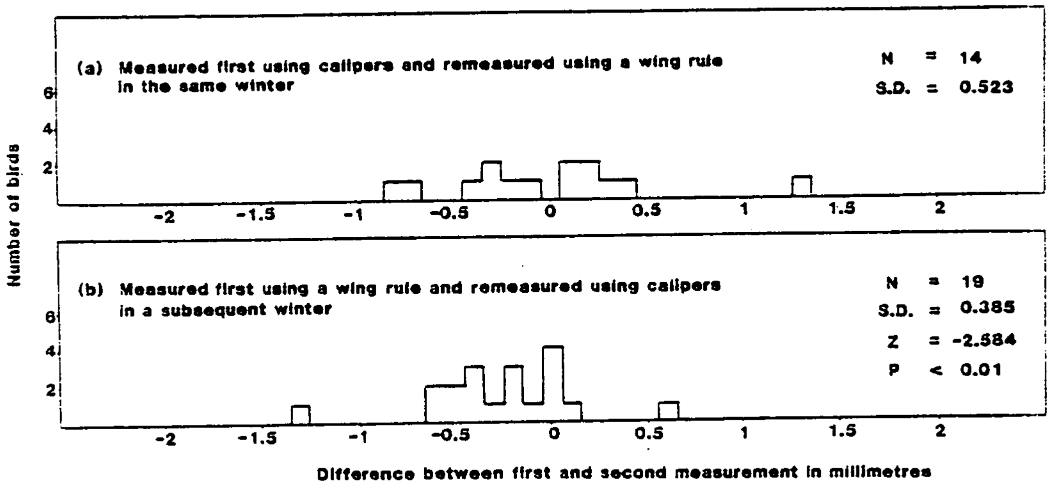


FIGURE 4.11

Comparison of total head length measured by two different methods:

wing rule, to the nearest 0.5 millimetres

Calipers, to the nearest 0.1 millimetres

Where the difference between the two measurements differed significantly from zero using Wilcoxon's matched pairs sign test Z and P are given

FIGURE 4.12

The correlation between wing length and total head length for male (+) and female (O) adult Dunlin from Berrow, with probability contours for individuals being male:

solid lines = estimative method; broken lines = predictive method

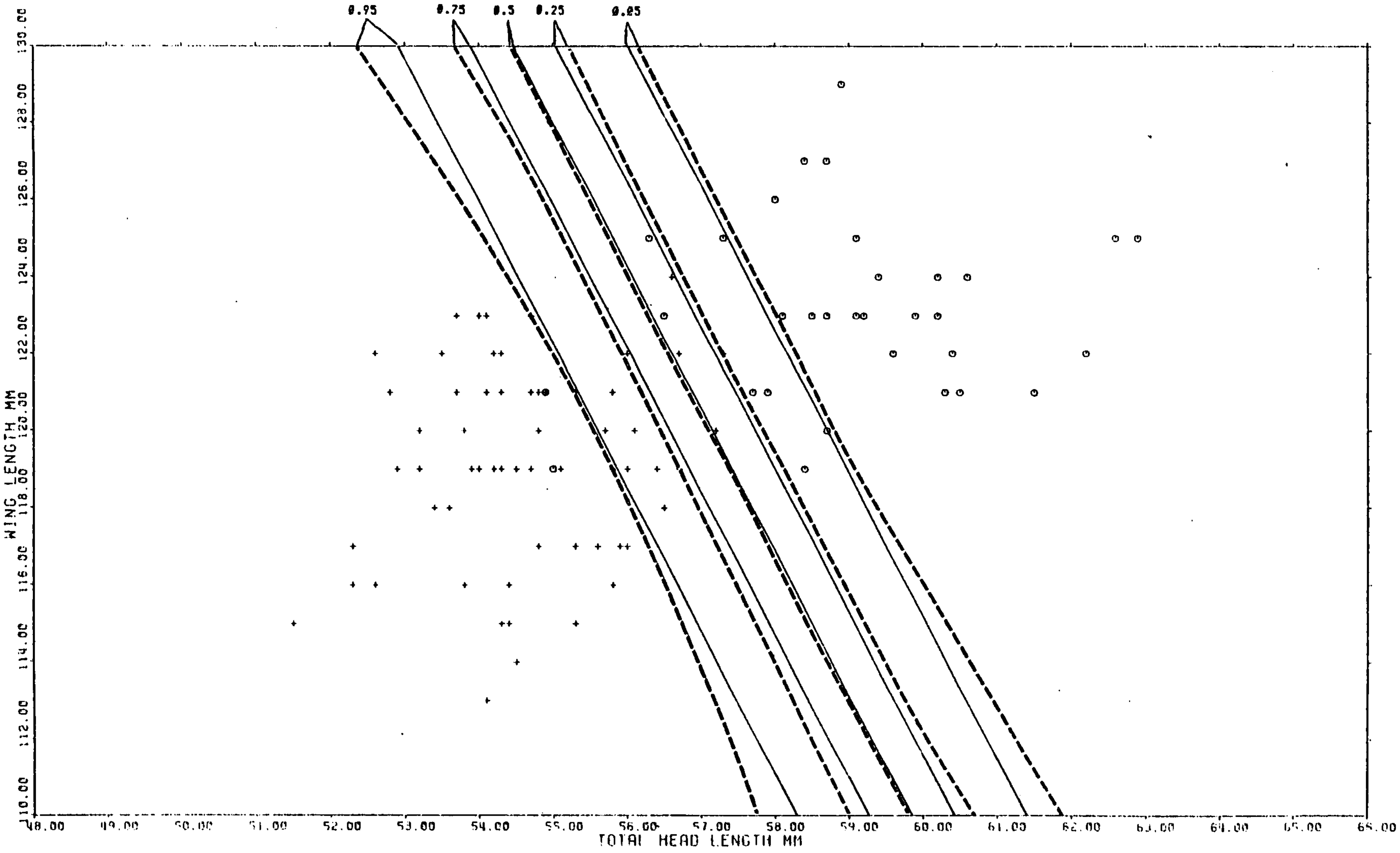
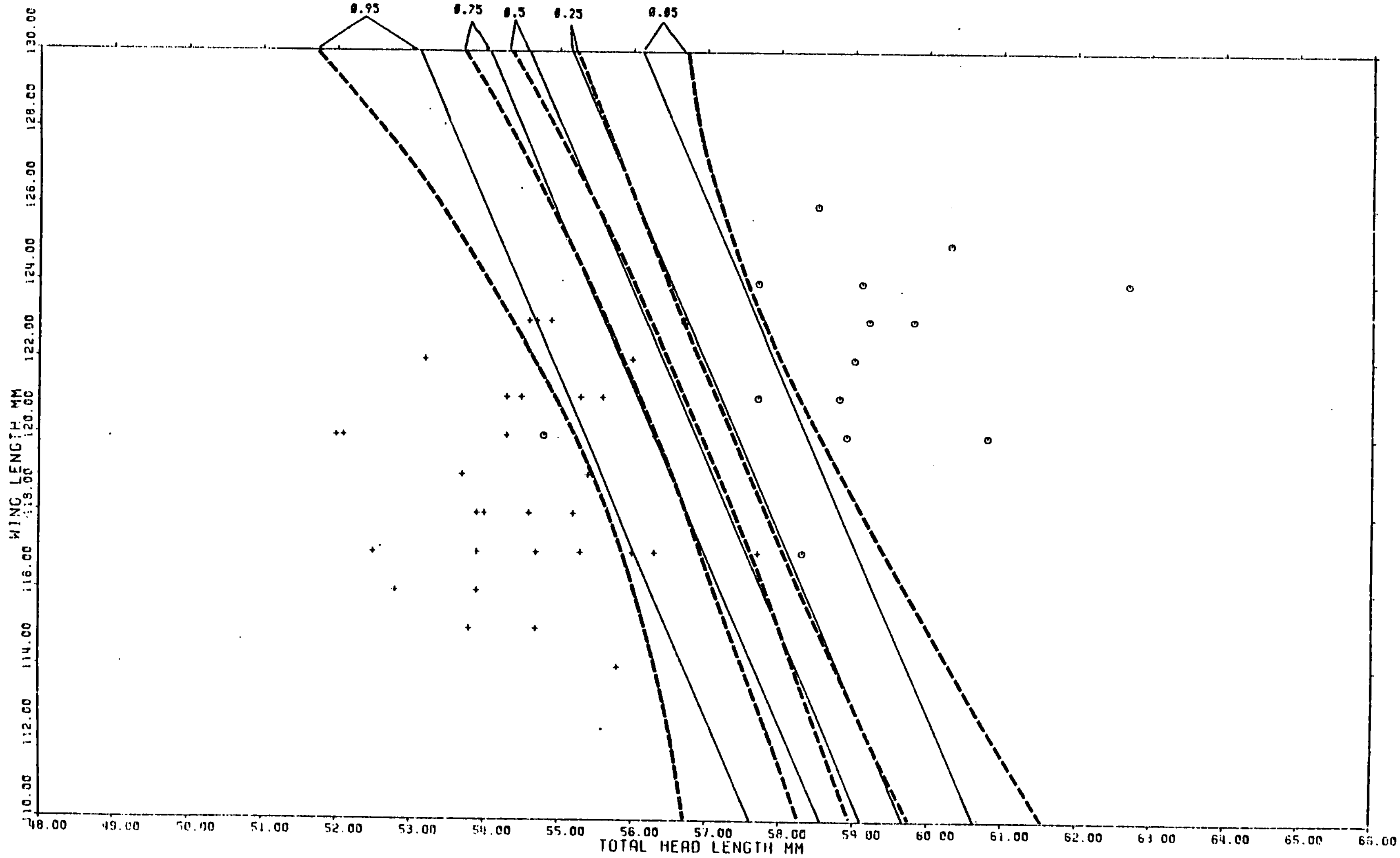

0.95
0.75
0.5
0.25
0.05
WING LENGTH MM
130.00
128.00
126.00
124.00
122.00
120.00
118.00
116.00
114.00
112.00
110.00
48.00
49.00
50.00
51.00
52.00
53.00
54.00
55.00
56.00
57.00
58.00
59.00
60.00
61.00
62.00
63.00
64.00
65.00
66.00
TOTAL HEAD LENGTH MM

FIGURE 4.13

The correlation between wing length and total head length for
male (+) and female (O) adult Dunlin
from the South Shore of the Severn (except Berrow),
with probability contours for individuals being male:
solid lines = estimative method; broken lines = predictive method


0.95
0.75
0.5
0.25
0.05
WING LENGTH MM
130.00
128.00
126.00
124.00
122.00
120.00
118.00
116.00
114.00
112.00
110.00
48.00
49.00
50.00
51.00
52.00
53.00
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55.00
56.00
57.00
58.00
59.00
60.00
61.00
62.00
63.00
64.00
65.00
66.00
TOTAL HEAD LENGTH MM

FIGURE 4.14

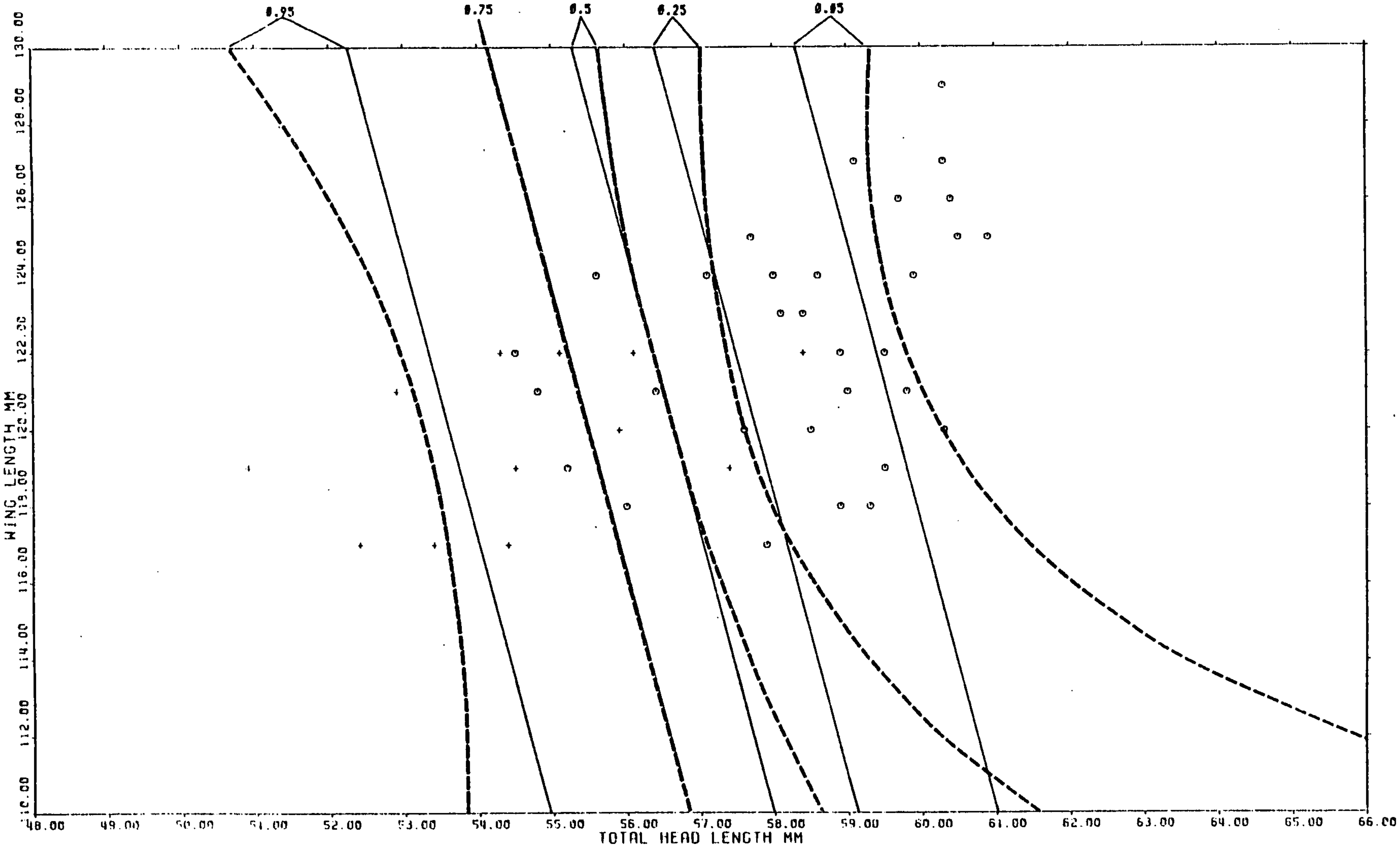
The correlation between wing length and total head length for

male (+) and female (O) adult Dunlin

from the North Shore of the Severn,

with probability contours for individuals being male:

solid lines = estimative method; broken lines = predictive method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0.75
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WING LENGTH MM
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118.00
116.00
114.00
112.00
110.00
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51.00
52.00
53.00
54.00
55.00
56.00
57.00
58.00
59.00
60.00
61.00
62.00
63.00
64.00
65.00
66.00
TOTAL HEAD LENGTH MM

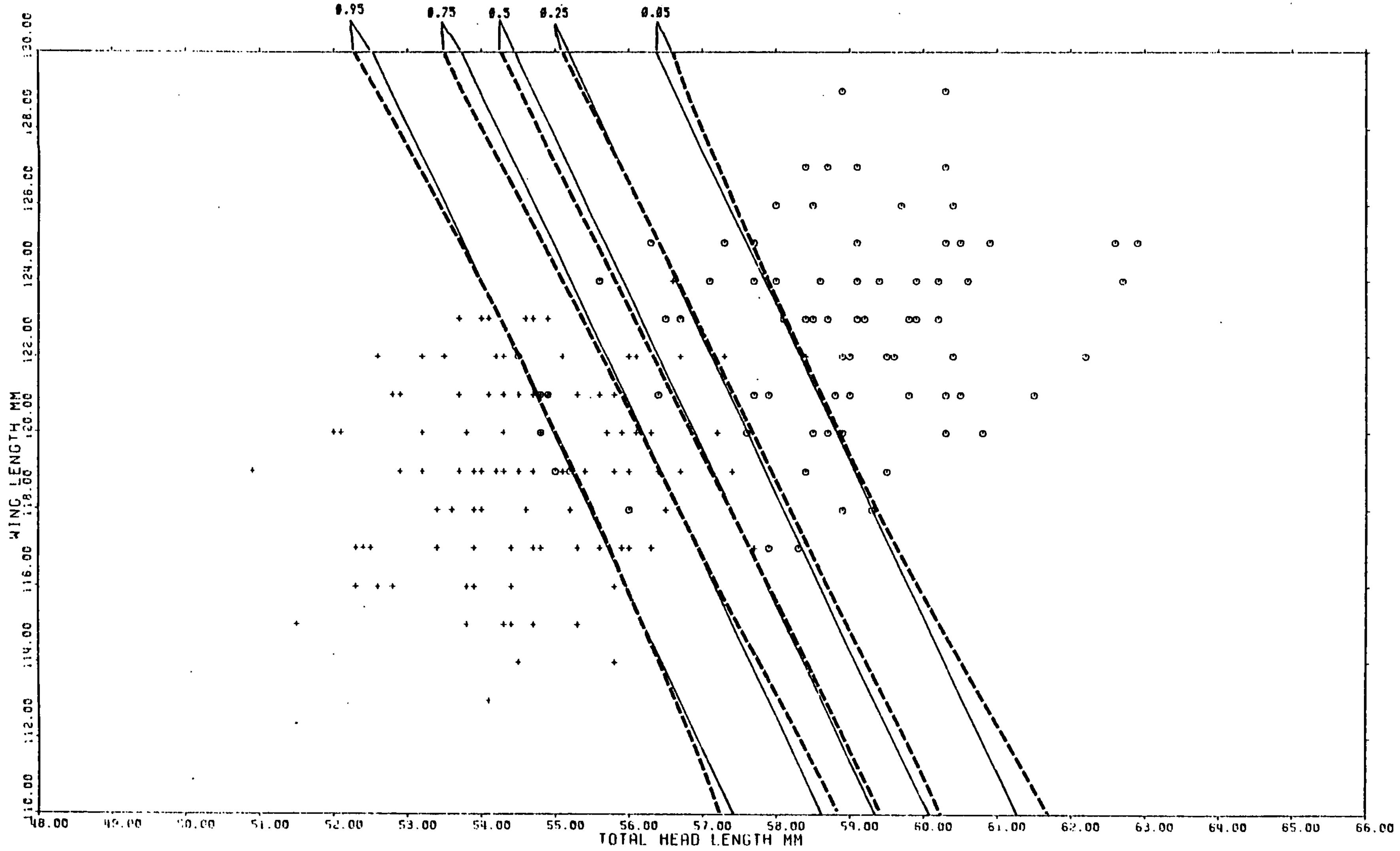
lengths of birds from three different sections of the Severn. It was initially expected that a similar discriminant analysis would be produced from any site within the Severn, but it is apparent that there is a very much better discrimination between the sexes in the sample of birds from Berrow, than in samples from other sites within the Severn. When the data for all the sites on the Severn are combined (figure 4.15) they give similar numbers of males and females for the analysis and a reasonable discrimination is achieved. The data set from Anglesey (figure 4.16) on the other hand shows a considerably greater overlap and fewer birds can be assigned with a high degree of confidence. All the information needed to sex individuals by discriminant analysis (using either method) is given in appendix 4 (Severn data) and appendix 5 (other wintering populations in Britain). Data are given for wing, bill and total head lengths so that discriminant analysis can be used on populations where only wing and bill length have been taken.

Figures 4.12 to 4.16 also give confidence limits (chance of being male; $p=0.05$, 0.25, 0.5, 0.75 and 0.95) for both the estimative and predictive methods. It can be seen that there is very little difference between the two methods when the sample size is large, the only substantial difference arises when the data for the North Shore are considered: here the sample size for males is only 12. If the sample sizes were smaller then the differences would become larger.

The two methods for producing confidence limits and individual probabilities used here give very similar results, mainly due to the fact that the sample sizes are large, but for many analyses on other species the number of internally sexed birds is much smaller and the

FIGURE 4.15

The correlation between wing length and total head length for male (+) and female (O) adult Dunlin from all sites on the Severn, with probability contours for individuals being male: solid lines = estimative method; broken lines = predictive method


0.95
0.75
0.5
0.25
0.05
WING LENGTH MM
130.00
128.00
126.00
124.00
122.00
120.00
118.00
116.00
114.00
112.00
110.00
48.00
49.00
50.00
51.00
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53.00
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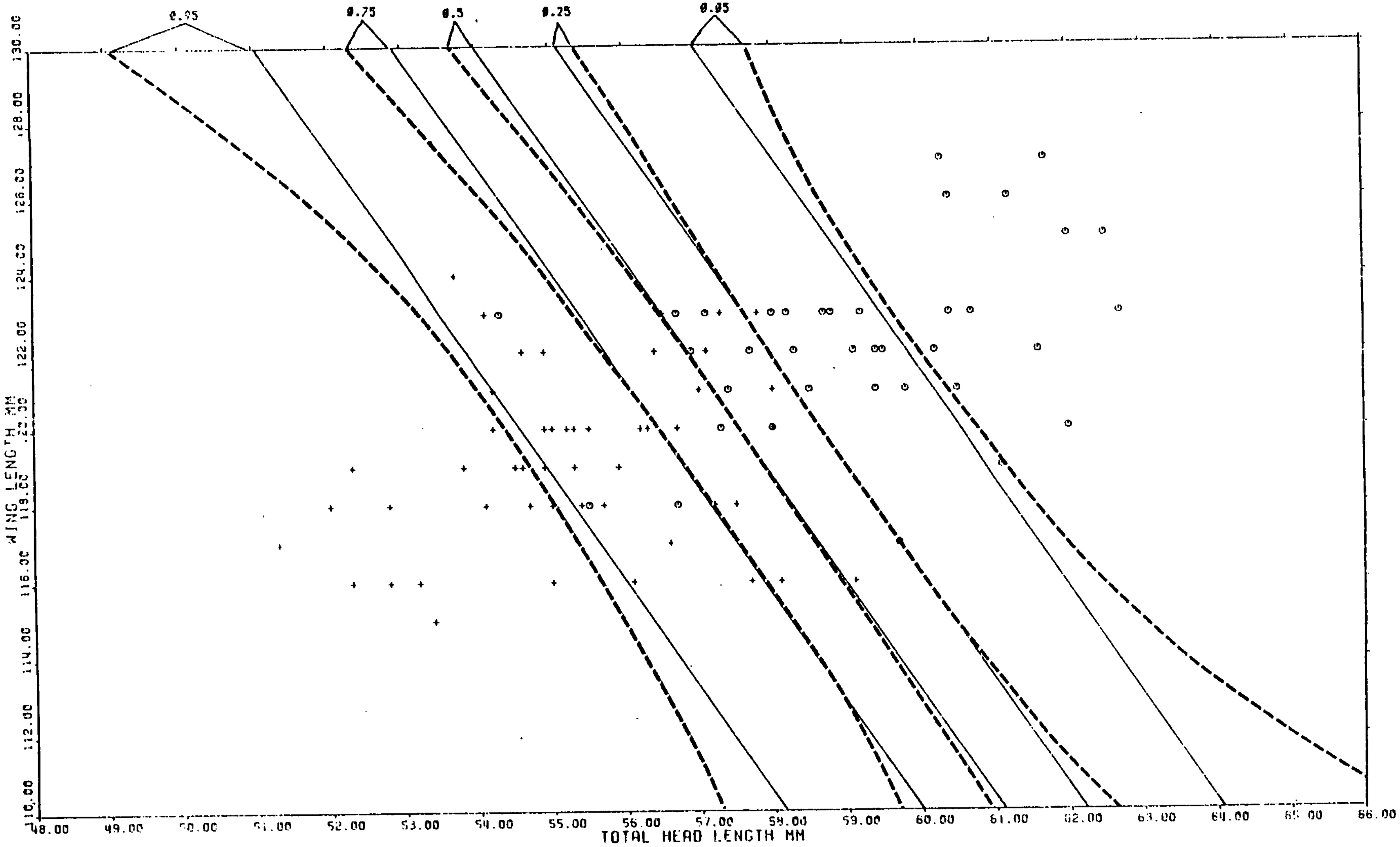
58.00
59.00
60.00
61.00
62.00
63.00
64.00
65.00
66.00
TOTAL HEAD LENGTH MM

FIGURE 4.16

Correlation between wing length and total head length for male (+) and female (O) adult Dunlin from Anglesey, with probability contours for individuals being male: solid lines = estimative method; broken lines = predictive method


0.95
0.75
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0.25
0.05
WING LENGTH MM
130.00
128.00
126.00
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120.00
118.00
116.00
114.00
112.00
110.00
48.00
49.00
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65.00
66.00
TOTAL HEAD LENGTH MM

smaller the sample size the greater the difference in the results between the two methods. The results of previous studies may have been different if the predictive method had been used. Dunnet & Anderson (1961) used sample sizes of 12 male and nine female Fulmars Fulmarus glacialis, here there would be significant differences in the probability assessment between the two methods. Sample sizes in a study of Moorhens Gallinula chloropus (Anderson, 1975) were larger but no group exceeded 23 and there were only nine sub-adult females. On the other hand studies of the Herring Gull Larus argentatus and the Lesser Black-backed Gull L. fuscus by Harris & Hope-Jones (1969) and a study of Puffins Fratercula arctica by Corkhill (1972) used samples sizes which would be large enough for the different methods to have little effect on the probability assessment of an individual. There can, however, be little justification in using the estimative method for assigning the sex of birds using biometrics.

For all further analyses the predictive method was used. A test was undertaken using measured retraps (as a random sample of Dunlin wintering on the Severn) to see what effect different predictive discriminant analyses would have on the percentage of predicted males and females from different sites. Figure 4.17 plots the probability of an individual being a male using the Berrow sexed sample against that same individual's probability of being a male using the North Shore sexed sample. It can be seen that the vast majority of individuals are assigned the same sex on both data sets, but 70 individuals (about five percent) predicted as being male using the Berrow sexed sample would be classed as females using the data from the North Shore sexed sample.

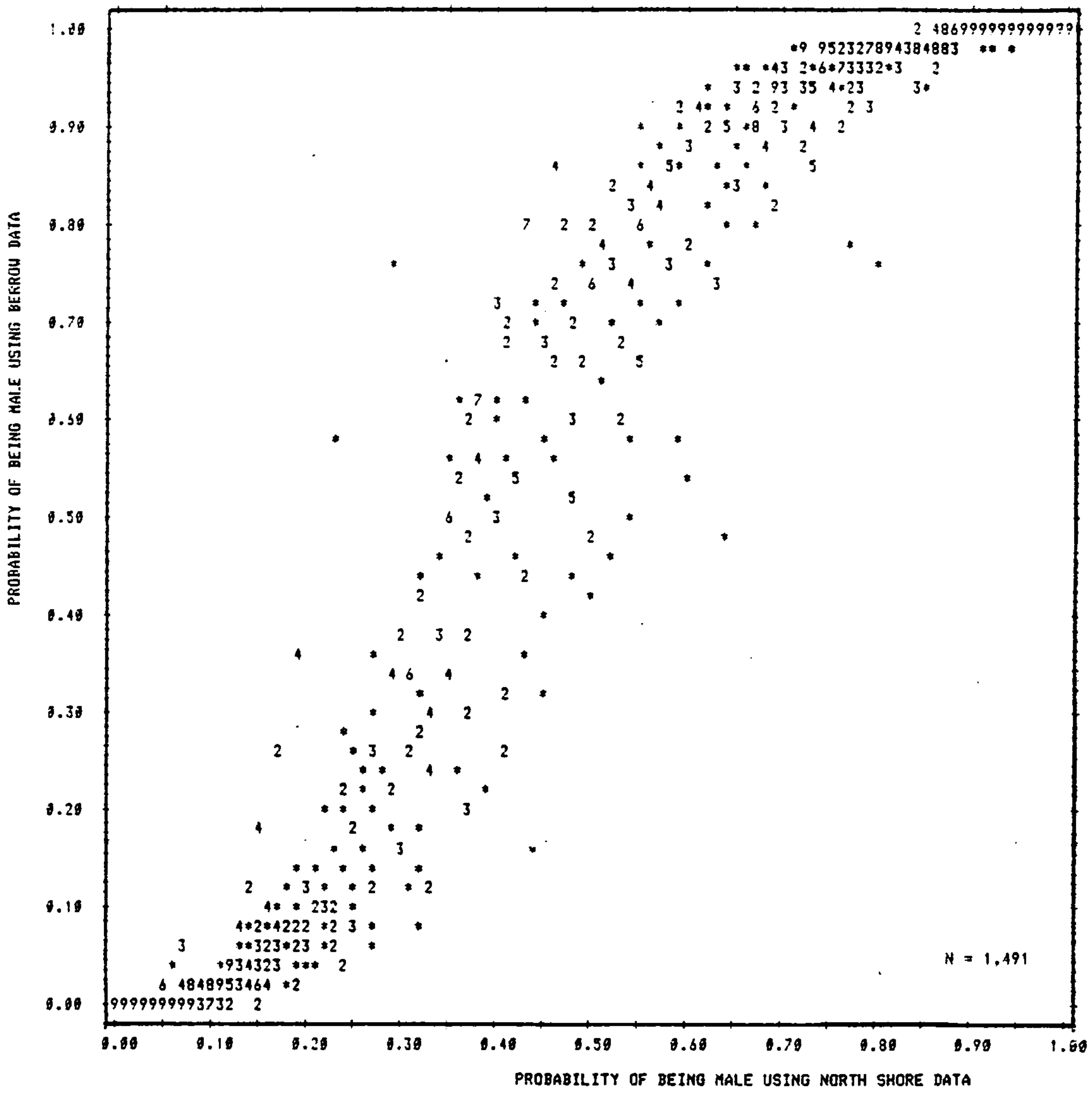

FIGURE 4.17

Probability assessment for individual Dunlin using discriminant analyses from Berrow and the North Shore of the Severn

Figure 4.18 compares the predictive probability using the Berrow sexed sample and that using the sexed sample from the rest of the South Shore. It shows that there is less difference between the South Shore and Berrow than between the North Shore and Berrow. In contrast 25 more males were predicted using the Angelsey sexed sample than the Berrow sexed sample (figure 4.19). With the amount of information available it is not possible to decide whether internally sexed birds from a given site should be used to sex birds on that site and if so, whether a different set of data should be used to sex autumn, winter and spring birds. A conservative approach has been used, all sexed samples from within the Severn being combined in one discriminant analysis and used for all birds within the Severn. It must be noted however that this will be inclined to underestimate the differences in sex ratio found between different sites.

One final analysis was carried out to look at whether a bird was assigned the same sex on each occasion that it was measured. Eight hundred and seventy birds were measured twice during the study, figure 4.20 plots the probability of being male, on the first occasion against the probability of being male on the second occasion. As expected there was a high degree of correlation between each sexing with no bird changing predicted sex which was sexed on either occasion with 95 percent certainty and only two that were predicted with 75 percent certainty. Figure 4.21 plots the 343 birds that were measured twice by the same observer, as expected, there is a higher degree of correlation between these birds than those in the previous data set.

If all birds wintering on the Severn bred in the same area and

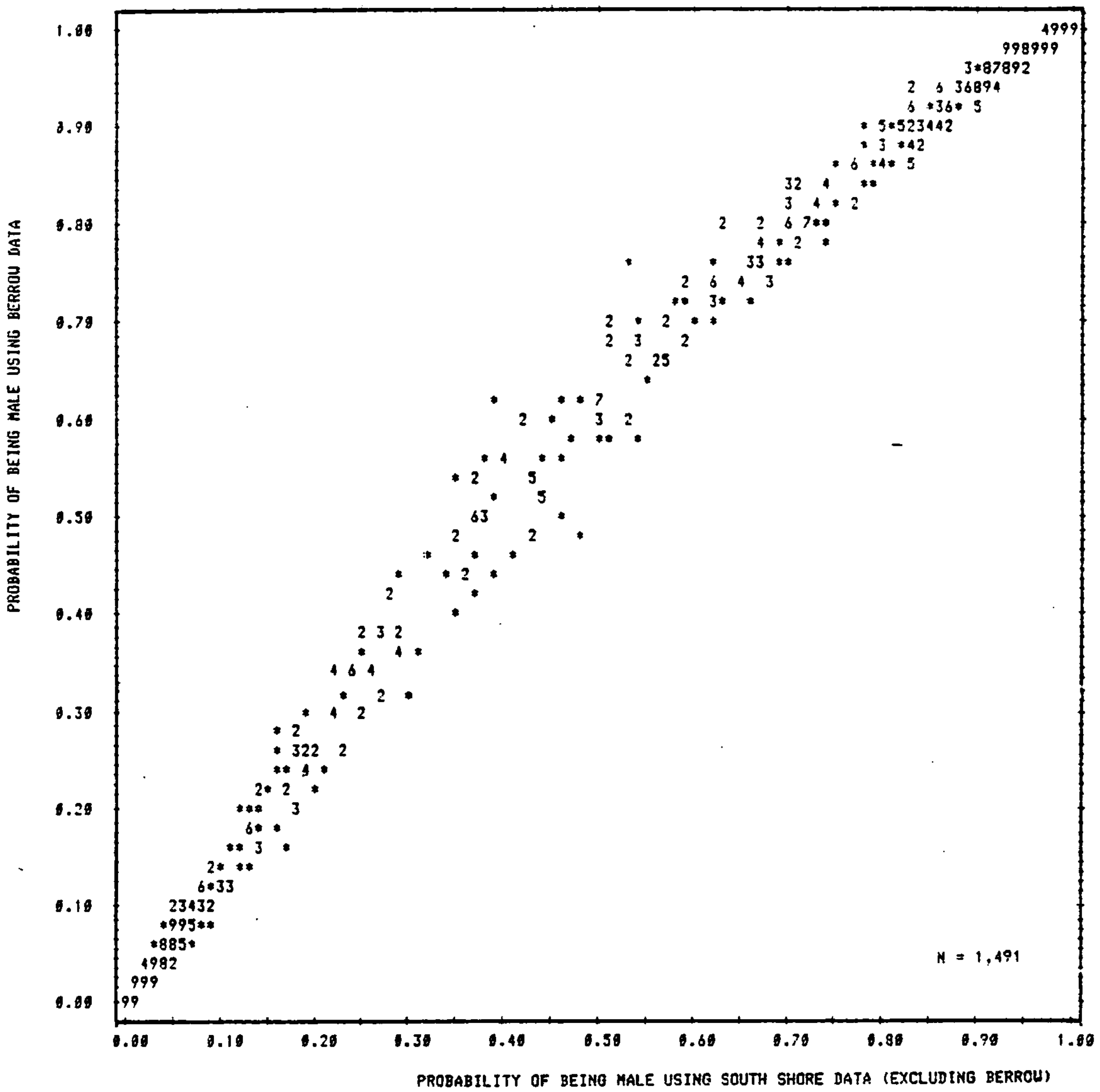

FIGURE 4.18

Probability assessment for individual Dunlin using discriminant analyses from Berrow and the rest of the South Shore of the Severn

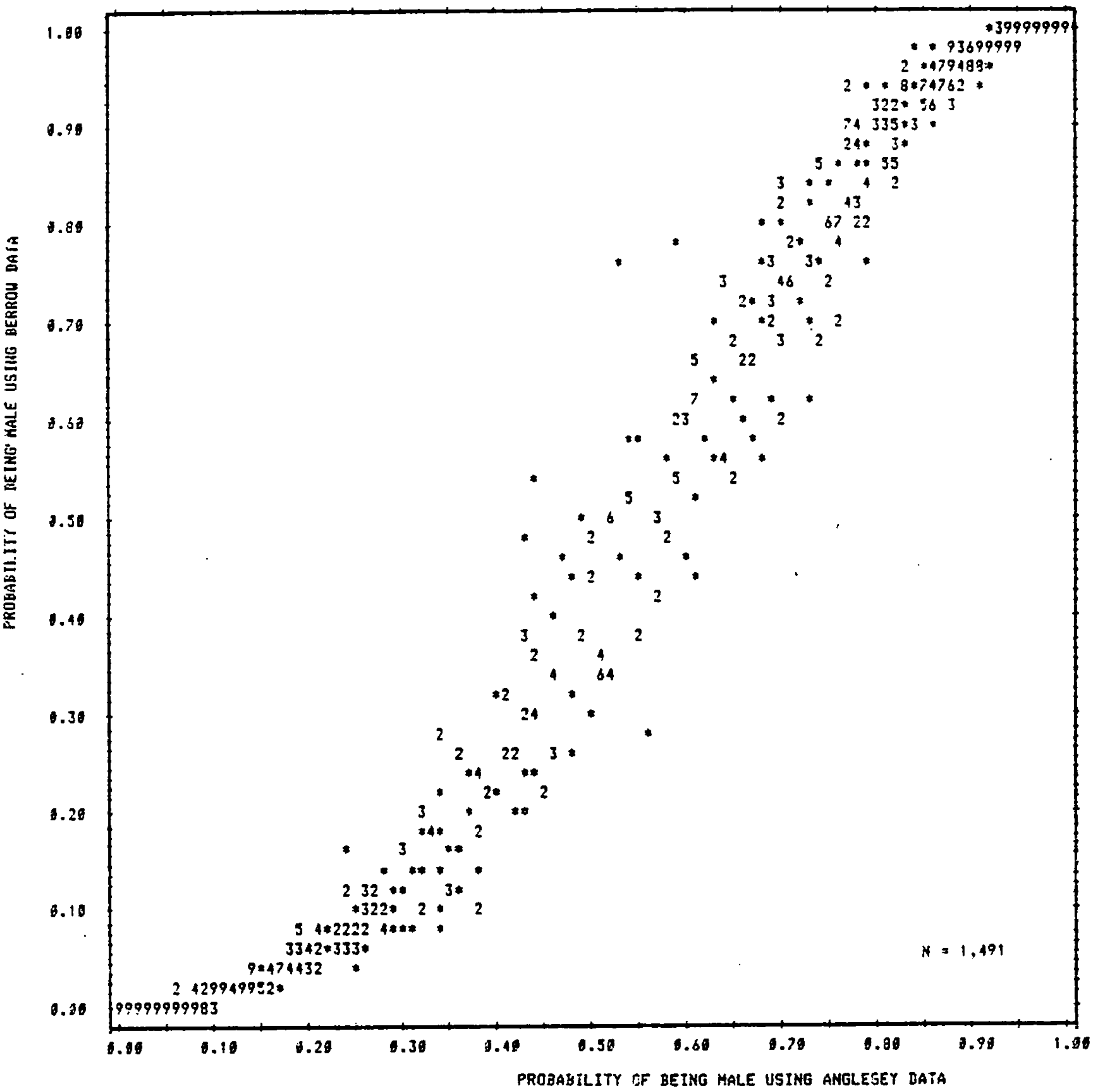

FIGURE 4.19

Probability assessment for individual Dunlin using discriminant analyses from Berrow and Anglesey

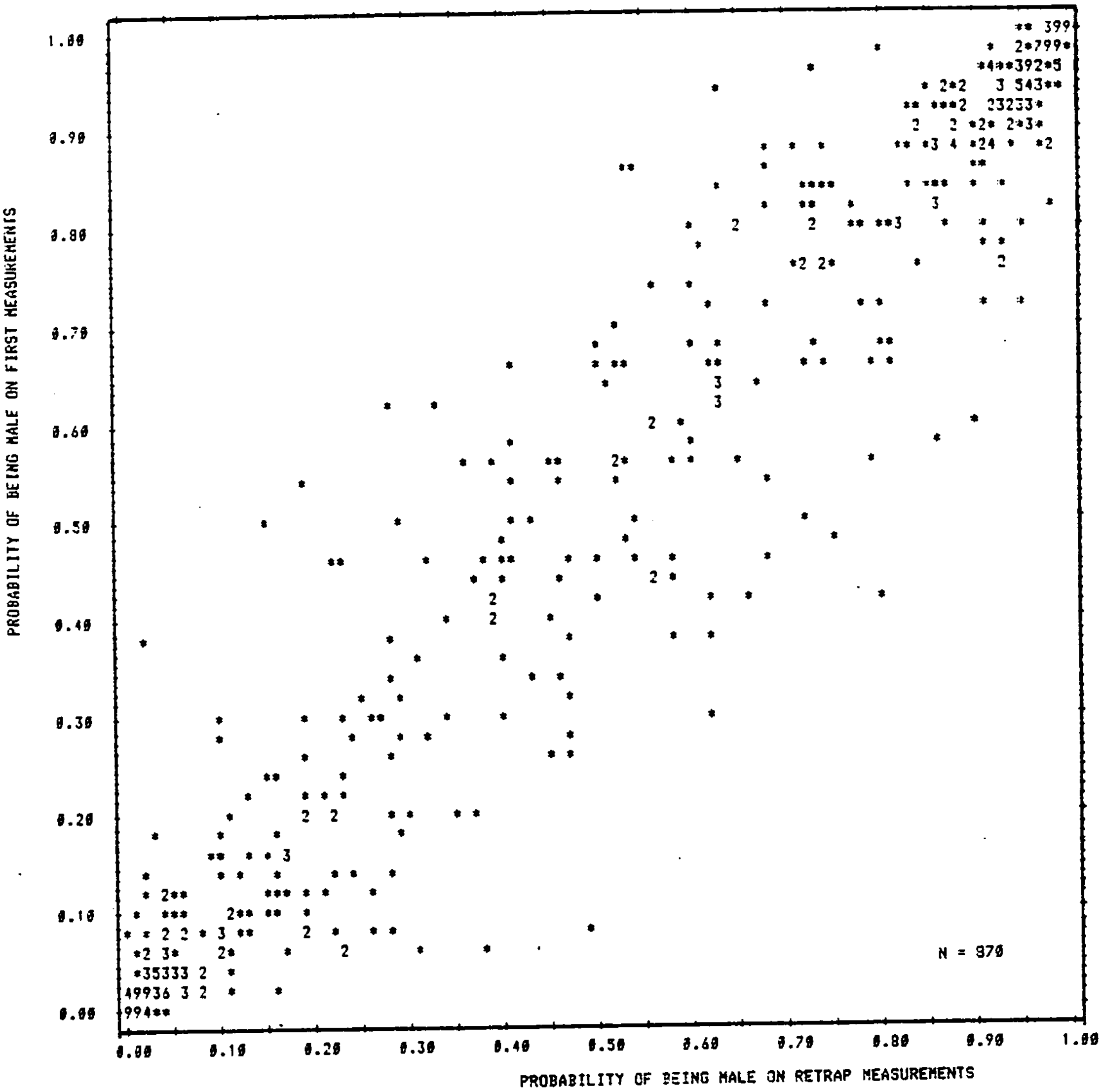

FIGURE 4.20

The correlation between the probability of an individual being male on first measurements against retrap measurements (all observers).

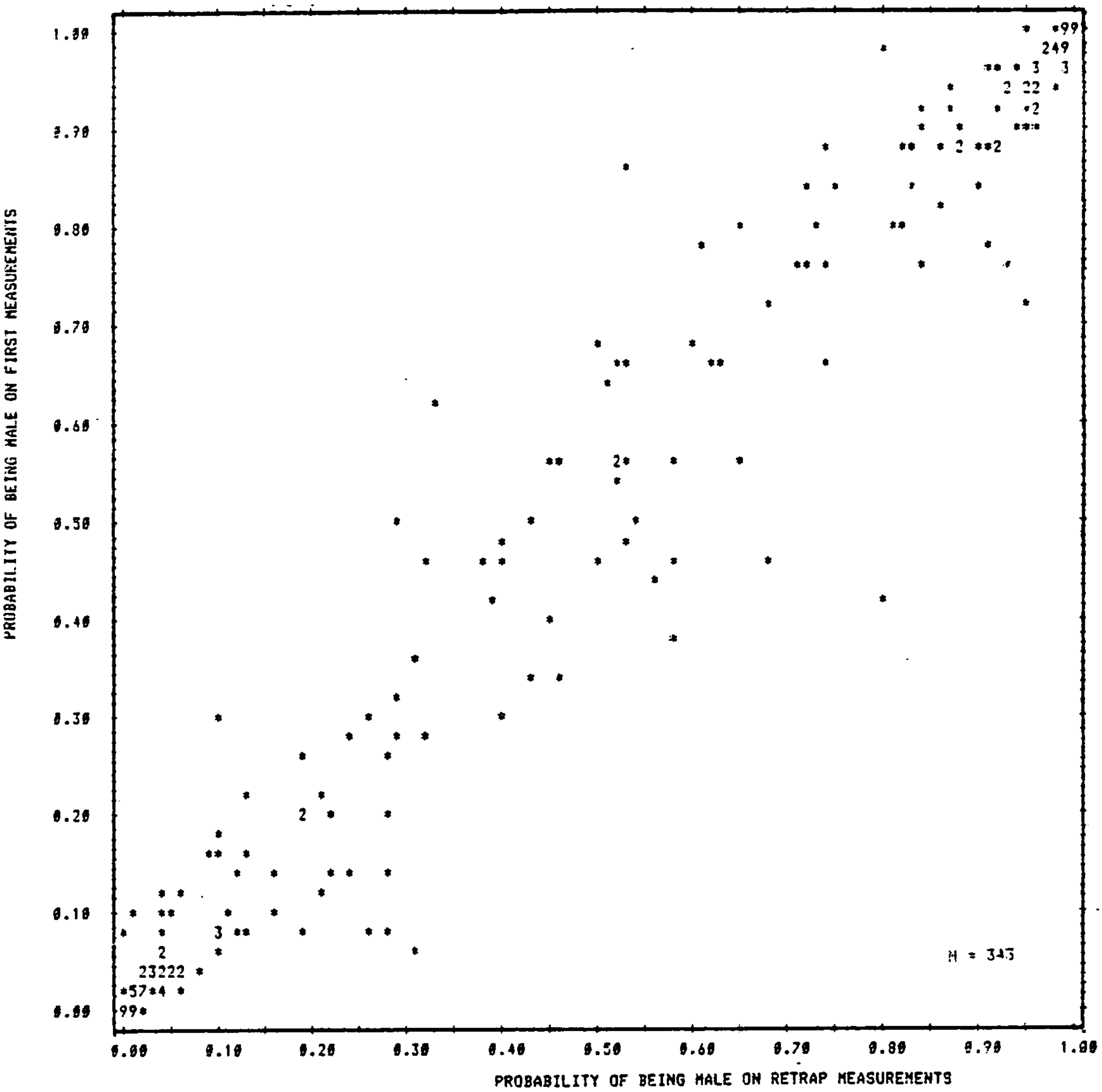

FIGURE 4.21

The correlation between the probability of an individual being male on first measurements against retrap measurements (same observer)

FIGURE 4.22

Dunlin skulls showing zone of bending

were distributed randomly from that area throughout the Severn one would expect to get the same discriminant analysis using internally sexed birds from any site within the Severn: this was not the case, and the implications are discussed in Chapters 5 and 7.

The high degree of correlation between the sexing of a bird the first time it was measured and subsequent occasions was made possible by the accuracy to which the measurements were taken. In the past many wader bill measurements were taken only to the nearest millimetre and if data taken in this way had been used it would have significantly reduced the accuracy of sexing. There seems no justification for researchers to take bill and total head length measurements to the nearest millimetre when it is as quick and easy to measure to the nearest 0.1 mm.

CHAPTER 5

BREEDING AREAS, MIGRATION ROUTES AND WINTER SITE FIDELITY

5.1 Introduction

During the course of my study I hoped to get a clear understanding of the way in which Dunlin utilize the south shore of the Severn. It was initially expected that birds would regularly move up and down the whole study area and that the numbers in each bay would be directly related to food resources, or to some other factor such as roost sites.

This chapter aims to show how much movement there is between the different bays on the study site and whether there are age and sex differences. It also looks at movements of birds away from the study site and assesses differences between the birds that winter in different bays.

5.2 Methods

Whenever a bay was visited on the study area an attempt was made to assess the number of birds present. It quickly became apparent that the state of tide strongly influenced the number of birds that could be counted on each site; at low tide it was easy to count birds at Clevedon but in the other bays it was easy to miss large sections of the population unless the visibility was very good. Near high tide there were also problems, as when the birds were disturbed they would often move between bays to roost, returning as the tide fell (Chapter 1). For this reason counts were only included in the analysis when they were taken around mid tide and when there was little disturbance and good visibility; all these constraints meant that counts could not be undertaken on a regular basis.

It was originally hoped to catch a large sample of birds in each bay in every month throughout the winter period, so as to be able to assess movements of birds within the study area. From these catches it would have been possible to assess the proportions of juveniles and adults, and males and females, on the different sites. Unfortunately it was not possible to catch on every site in midwinter, as when the days were short, the highest spring tides occurred at dawn and dusk. Attempts were also made to catch on the same sites in different years to see if within winter movements were the same as between winter movements.

Analyses were first carried out splitting the winter into five time periods: 1) October; 2) November; 3) 1 December to 10 January; 4) 11 January to 20 February and 5) 21 February to the end of March. With the aid of a series of computer programmes, matrices were produced to show both within year movements and between year movements, for different categories of birds. It was not possible to test for differences within years and between years, as the chance of a bird moving between any given sites was related to both the number of birds caught on one site in one winter, and the other sites in the other winters. The matrices are given in full in appendix 6. The differences between the within year and between year matrices can be accounted for by reference to the numbers of birds caught in each time period in each year given in table 5.1. The similarity was so striking that no further tests were carried out.

A further programme was then run which assigned an individual only once to a given box within the matrix, whether it was caught

TABLE 5.1

Numbers of birds caught at different sites in each year of study

Site	Time Period	Adults				Juveniles			
		77/78	78/79	79/80	80/81	77/78	78/79	79/80	80/81
Clevedon	1		8	94			11	43	2
	2		55	167	921		10	95	62
	3		61	121	304		31	25	74
	4	43	113	69	142	7	55	24	61
	5	314	274	11	49	43	53	4	19
Sand Bay	1	12	3		34	21	4		32
	2		4	43	100		7	15	39
	3			68	59			40	51
	4		26	185	175		7	35	116
	5		32	199	151		7	20	40
Weston Bay	1					2	1		
	2		2		10	1	4		43
	3	8	92	1	29	13	57	4	13
	4	1,016	105	64	53	126	4	30	31
	5			203				134	
Berrow	1			67				4	
	2			232	337			37	49
	3		39		26		2		4
	4	9	132	14	221	4	6	7	18
	5		5		1,267				36

within the same winter, between winters, or both. Even with 10,000 birds caught this did not give large enough numbers in many boxes to undertake a detailed analysis. The data were therefore grouped into two time periods: autumn/spring (before 1 December and after 20 February) and winter (1 December to 20 February). The results are given in tables 5.2 to 5.5. The final analysis was undertaken solely on these data sets. In these analyses no account was taken of mortality rates as, at present, there is no accepted annual mortality rate for Dunlin. The mortality rate of Dunlin in Finland was considered to be 25 percent with a first year mortality of 70-74 percent (Soikelli, 1970). Recent studies of waders wintering in Britain have produced lower annual mortality rates for several species of waders which have been colour ringed (Evans, 1981). This problem will be discussed further later. However, as mortality will tend to bias some of the data, statistical tests giving probability levels greater than 0.01 should be treated with caution.

Large numbers of birds which were caught were also colour marked for feeding studies. There were a number of reports of these birds away from the study area which show the extent of movements of birds within the winter. During the final year of the study large numbers of Dunlin were marked in two main moulting areas, the Wash and the Wadden Sea, as part of a European Economic Community project on the movements of waders in Western Europe. I observed a considerable number of these birds on my study site throughout the winter. Sightings of these colour marked birds, in conjunction with the ringing recoveries, were used to see if there are differences in the moulting areas of birds wintering in different bays. A recovery is considered to be any bird whether ringed on the south shore of the

TABLE 5.2

Movements of adult Dunlin within the study area

Figures in matrix are numbers of birds recaptured (both within and between years) in the various bays in spring/autumn (1) and winter (2)

		CLEVEDON		SAND BAY		WESTON BAY		BERROW		NUMBER CAUGHT
		1	2	1	2	1	2	1	2	
CLEVEDON										
	1	-								1,755
	2	298	-							760
SAND BAY										
	1	35	2	-						567
	2	23	2	53	-					493
WESTON BAY										
	1	13	4	40	20	-				215
	2	23	0	17	17	39	-			1,302
BERROW										
	1	1	0	1	1	6	25	-		1,809
	2	3	0	2	1	2	22	69	-	436

TABLE 5.3

Movements of juvenile Dunlin within the study area

(see figure 5.2 for explanation)

		CLEVEDON		SAND BAY		WESTON BAY		BERROW		NUMBER CAUGHT
		1	2	1	2	1	2	1	2	
CLEVEDON										
	1	-								272
	2	63	-							180
SAND BAY										
	1	8	1	-						150
	2	5	1	24	-					190
WESTON BAY										
	1	7	1	5	8	-				151
	2	6	0	7	4	17	-			232
BERROW										
	1	0	1	0	0	3	5	-		117
	2	0	0	1	0	2	2	8	-	31

TABLE 5.4

Movements of adult male Dunlin within the study area

(see figure 5.2 for explanation)

		CLEVEDON		SAND BAY		WESTON BAY		BERROW		
		1	2	1	2	1	2	1	2	
CLEVEDON										
	1	-								860
	2	130	-							349
SAND BAY										
	1	20	1	-						317
	2	14	2	21	-					255
WESTON BAY										
	1	8	3	21	9	-				121
	2	11	0	6	8	17	-			657
BERROW										
	1	1	0	0	1	3	8	-		1,166
	2	2	0	3	0	2	11	40	-	258

TABLE 5.5

Movements of adult female Dunlin within the study area

(see figure 5.2 for explanation)

		CLEVEDON		SAND BAY		WESTON BAY		BERROW		NUMBER CAUGHT
		1	2	1	2	1	2	1	2	
CLEVEDON										
	1	-								895
	2	152	-							411
SAND BAY										
	1	12	1	-						250
	2	6	0	30	-					238
WESTON BAY										
	1	5	1	17	9	-				94
	2	12	0	9	8	20	-			645
BERROW										
	1	0	0	4	0	3	15	-		643
	2	1	0	3	0	0	10	27	-	178

Severn and subsequently recovered elsewhere or vice versa.

To facilitate the analysis of the recoveries of Severn wintering Dunlin that were recovered in July, August and September, they were split into three main areas:

1) birds caught at the migration sites in Fenno-Scandia, Poland, East Germany and Denmark;

2) birds caught on the German and Dutch Wadden Sea;

3) birds caught on the Wash.

5.3 Results

5.3.1 Counts

Counts made during the winters 1979/80 and 1980/81 are displayed for each bay in figures 5.1 to 5.4. Roughly similar patterns are followed between the two years in each bay although there are noticeable differences between bays.

At Clevedon (figure 5.1) the first birds arrive in October and there is a steady increase until the end of November when the numbers decrease. There was often a considerable difference between my counts and those made at high tide by Dr. H. E. Rose (Birds of the Estuaries Enquiry - BoEE - counts) and K. Fox; high counts were probably due to birds moving to the Yeo from Sand Bay at high tide (Chapter 1) and low counts were made when the birds went inland or flew out to sea during the high tide period. In the 1979/80 winter the numbers declined steadily until the end of January before rising again in mid February. In 1980/81 the numbers were stable between mid December and mid February and there was then an influx at the

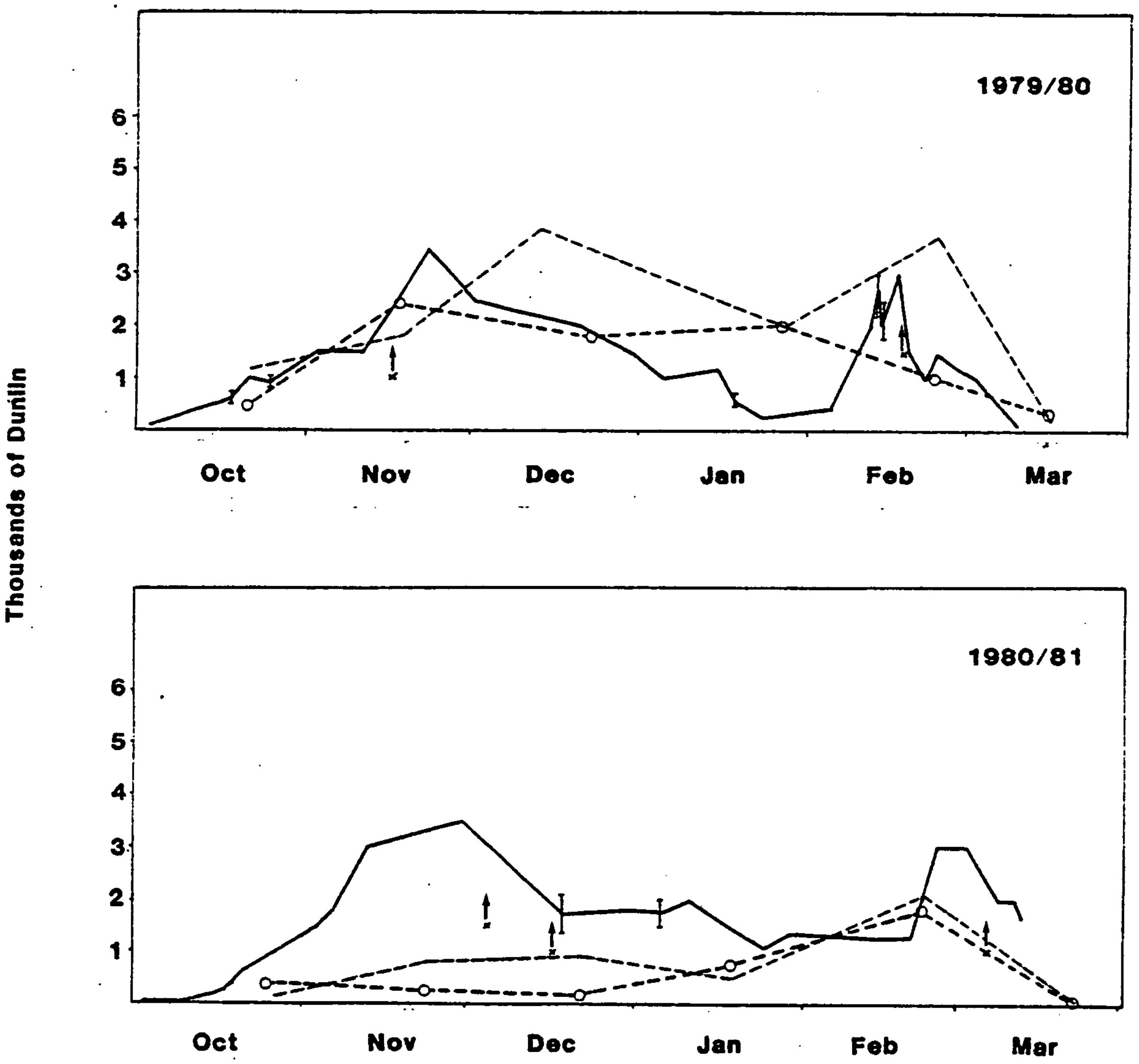

FIGURE 5.1

Counts of Dunlin at Clevedon

(crosses indicate minimum estimates of numbers present;
O----O represent BoEE counts; ---- represent counts by K. Fox)

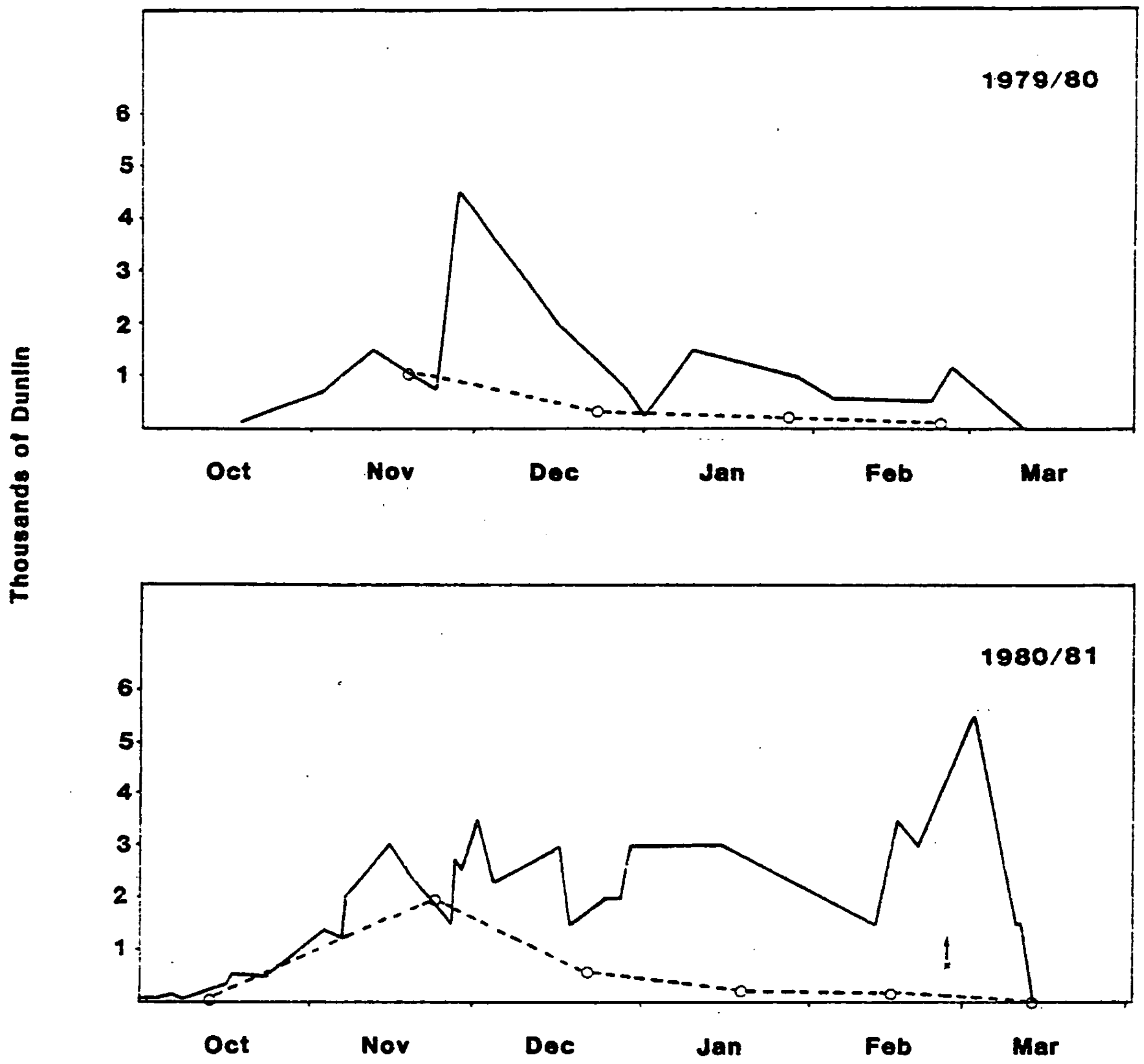

FIGURE 5.2

Counts of Dunlin in Sand Bay

(crosses indicate minimum estimates of numbers present;

0----0 represent BoEE counts)

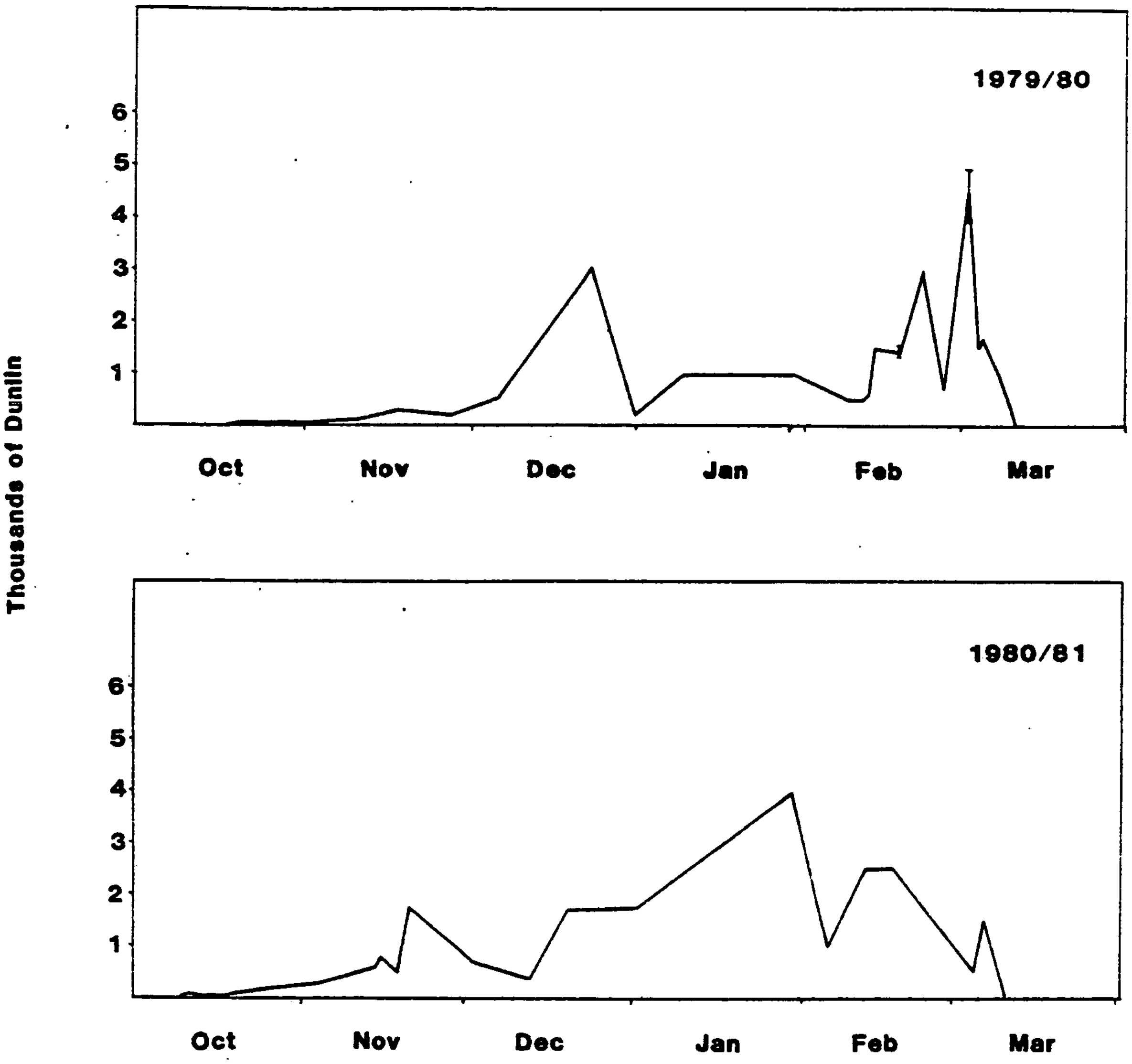

FIGURE 5.3

Counts of Dunlin in Weston Bay

(crosses indicate minimum estimates of numbers present)

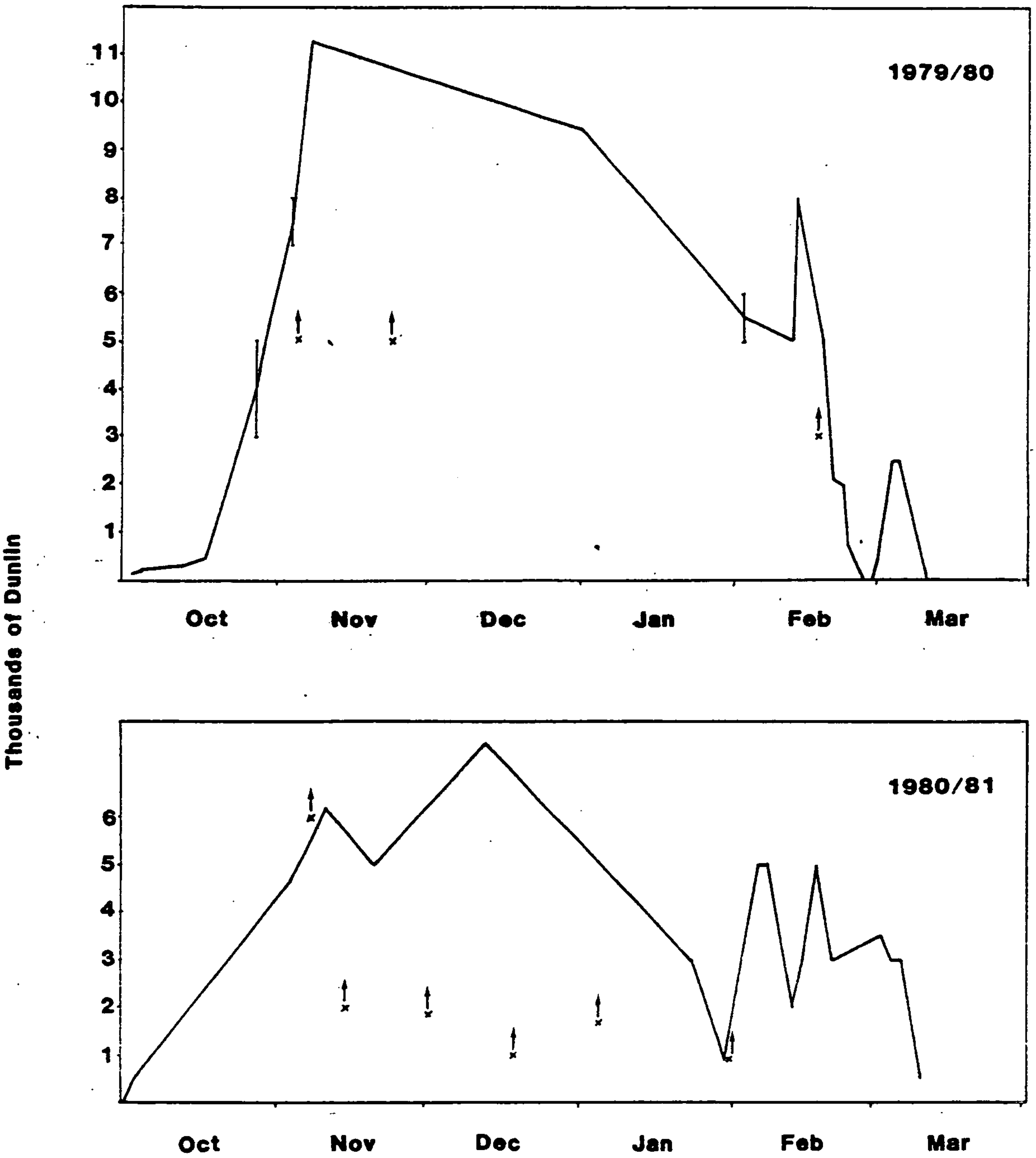

FIGURE 5.4

Counts of Dunlin at Berrow

(crosses indicate minimum estimates of numbers present) end of February.

Figure 5.5 gives the estimated numbers of males and females present in the 1979/80 winter. These were obtained from two sources: 1) samples of birds caught; 2) sightings of colour marked birds. The proportions of the sexes in the samples was then used to estimate the numbers of males and females present on the nearest day on which there was an accurate count of the numbers of birds at Clevedon. As birds were colour marked according to their total head length the sex ratios were computed using only this measurement, to make sure that the results from the two sources were comparable.

Sand Bay and Weston Bay pose the greatest problems for counting, as in Sand Bay there was often considerable disturbance and then the birds would move to Weston Bay or to the airport, sometimes only two and a half hours after low tide. For this reason BoEE counts (made by J. Barbour at high tide) were normally very low in comparison to my counts. The 1979/80 counts for both Sand Bay and Weston Bay are very erratic and I believe that this reflected the real situation in these bays. The 1980/81 winter showed a rather more stable situation with the numbers steadily increasing to mid November in Sand Bay and then being roughly constant through the winter with a peak at the end of the winter. This contrasts with the low numbers present in Sand Bay in 1979/80 at the end of the winter; but in that year a catch in Weston Bay on the first of March had a very large number of Sand Bay wintering birds. I would suggest that some birds may regularly switch between Sand Bay and Weston Bay towards the end of the winter depending on the amount of disturbance at each site.

Counts at Berrow were extremely difficult through the winter as birds often did not return to the feeding site until three hours

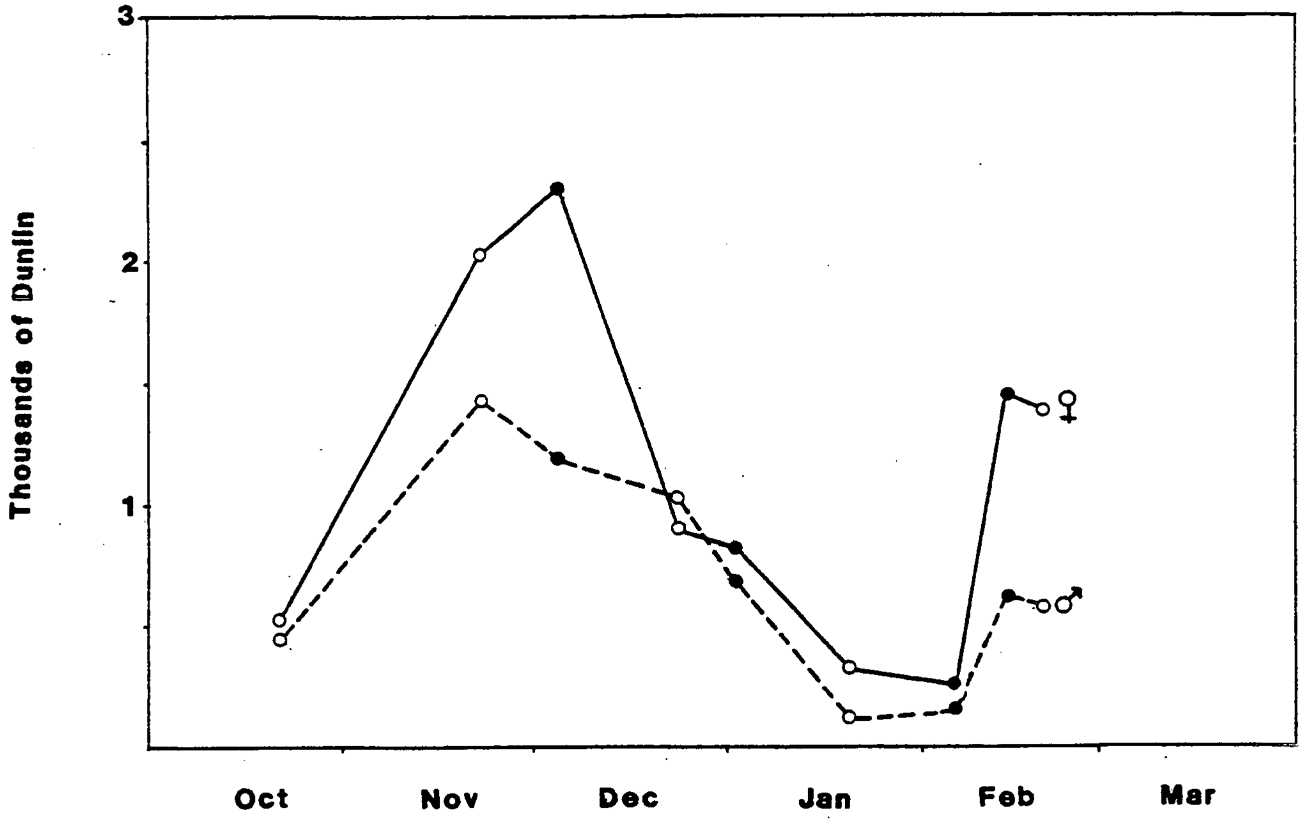

FIGURE 5.5

Estimated numbers of male and female Dunlin at Clevedon

in winter 1979/80

(open circles represent estimates from samples caught; closed circles represent estimates from leg flag sightings) after high tide, when the tide edge was often one to two kilometres away from the high tide mark. Peak numbers are reached in November and then numbers are comparatively stable until the end of January when counts become erratic. This may be due to a decline in numbers, the occasional high counts could have been birds from the NNR although I have no evidence for this.

5.3.2 Sex Ratios

Sex ratio is here defined as number of males divided by number of females. Figure 5.6 gives sex ratios of birds caught in different time periods in different years at Clevedon and Berrow. At both sites the sex ratio is similar in different years with the exception of one small catch in period three at Berrow which had a very low sex ratio (see below). The Berrow samples appear to be more variable; this is because birds caught on Brean Beach tended to have a lower sex ratio than those caught at the Berrow salt marsh. Figure 5.7 gives the sex ratio of birds caught in different bays in each time period, with data for all years combined. Although the sample sizes are small there is no indication of any differences between the bays in time period one; there were, however, highly significant differences ($p<0.001$) in the sex ratio between the different bays in time period two. There is a reduction in sex ratio in period three at Berrow, but there seems to be no special reason for this. The total number of birds caught is only 65 made up of two catches and one of these was made on Brean Beach on a day when only about 200 birds were present. These birds were seen feeding on an area of firm mud just below Brean Down on the rising

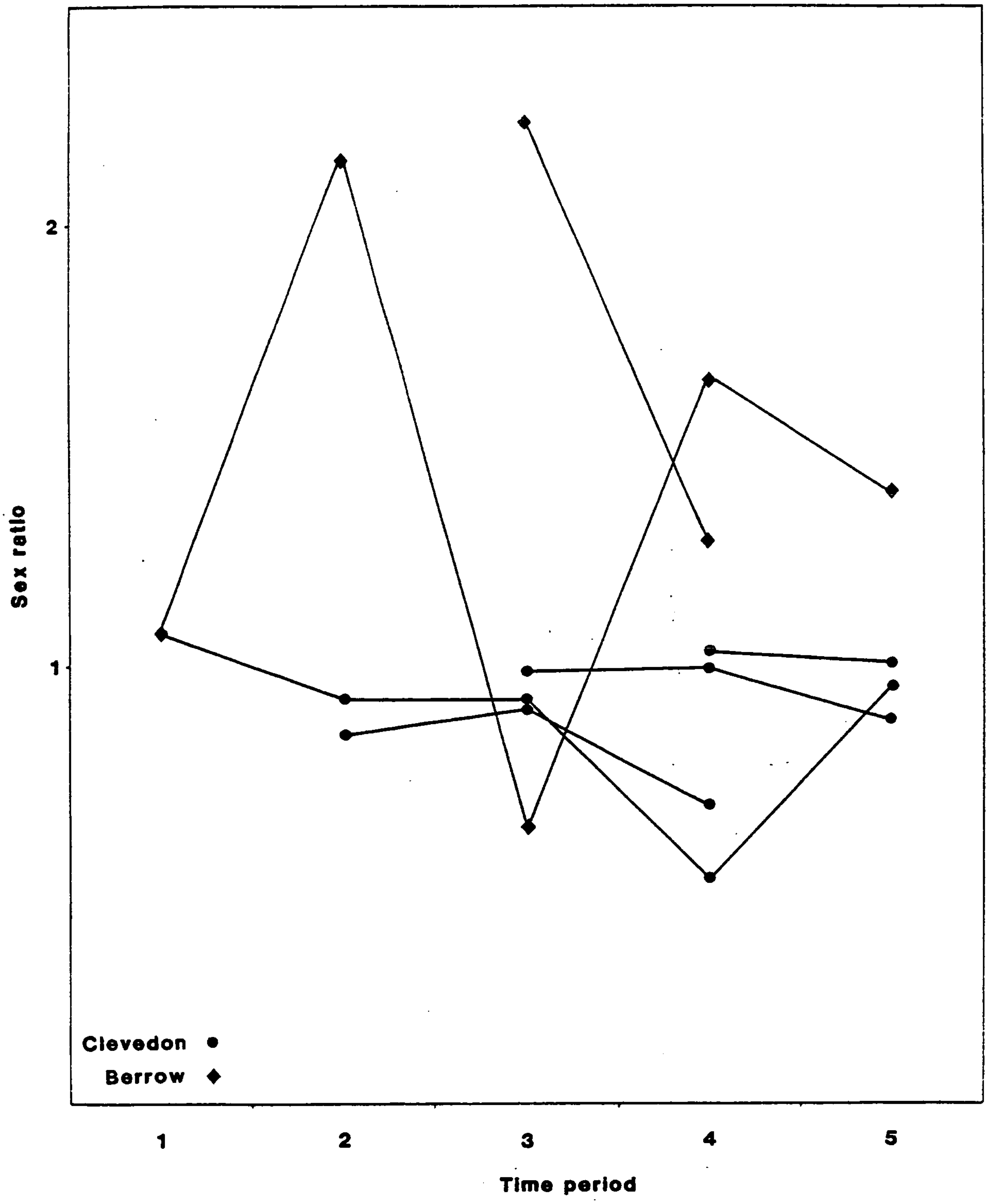

FIGURE 5.6

Sex ratios (males/females) of adult Dunlin in different time periods at Clevedon and Berrow (lines join catches within one year)

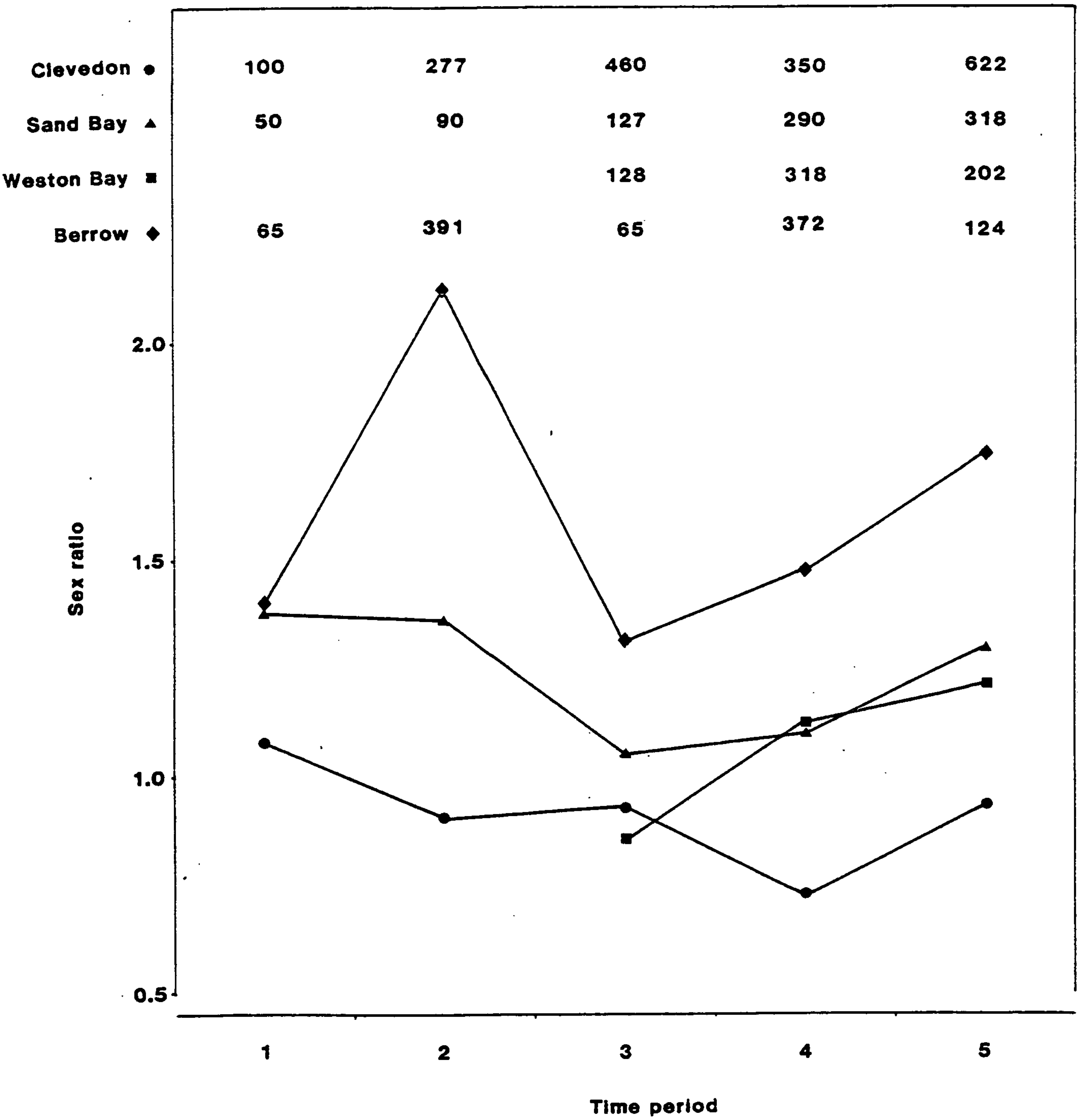

FIGURE 5.7

Sex ratios (male/female) of adult Dunlin in different bays

(all years combined; sample sizes given above) tide (there were no birds that day feeding on the liquid mud off Brean Beach, where the vast majority of birds normally fed). This sample was significantly different (adjusted Chi-squared = 4.8, $p<0.05$) from the other sample in the time period which was also caught on Brean Beach, but under normal conditions. In time period four there were highly significant differences between sites and this difference was maintained in time period five ($p<0.01$) although in all sites the sex ratio increased.

5.3.3 Age

Figure 5.8 gives the percentage of juveniles in the different bays. Data for all years have been combined as there are similar percentages of juveniles in different years (table 5.8); this is probably because there were no bad breeding seasons in the arctic during the course of this study. Two large catches were excluded from figure 5.8. The first was one in Weston Bay in February 1978: on this occasion the catch was made during a period of cold weather; there had been about 3,000 birds roosting in the catching area at high tide, but the catch was made on the receding tide when 2,000 birds had left the roosting flock to feed. It is probable that there a was higher percentage of juveniles in the feeding flock than in the whole flock, a situation which has been shown for Sand Bay. The second catch to be excluded was one in November 1982 when a flock was caught on a field at Clevedon on the rising tide when many birds were still feeding on the mudflats; again, this probably meant that there was a smaller percentage of juveniles in the catch than in the population as a whole. There appears to be little difference

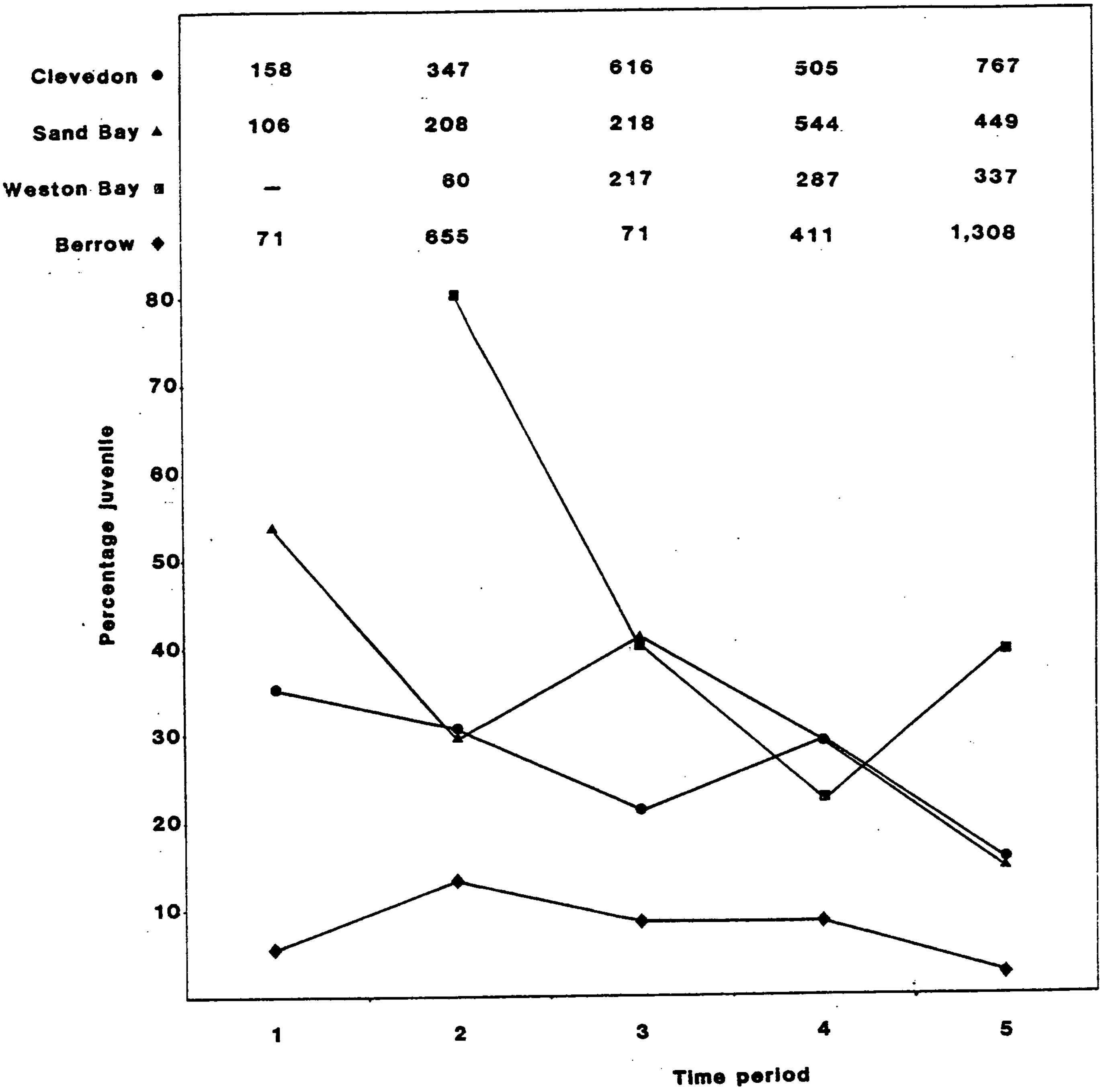

FIGURE 5.8

Percentage of juvenile Dunlin in different bays

(all years combined; sample sizes given above) between Clevedon, Sand Bay and Weston Bay but Berrow had a consistently lower percentage of juveniles; this is discussed later.

5.3.4 Local Movements

The movements between sites for adult birds are given in table 5.2. Birds caught at Clevedon in autumn/spring (period 1) were significantly more likely to be caught in winter (period 2) in another bay than were birds caught at Clevedon in winter (adjusted Chi-squared = 15.2, $p<0.001$). In fact out of the 760 birds caught in mid winter at Clevedon only two were recaptured in any other bay in mid winter and only six in the autumn/spring period; this suggests that birds wintering at Clevedon did not move to any other bay within the study site.

There was no such significant difference for Sand Bay, there being an equal likelihood of birds in both autumn/spring and winter being caught in Weston Bay. However, birds present in Sand Bay in the autumn/spring were much more likely to be present there in mid winter (53 caught in autumn/spring out of 493 caught in winter) than to move to Weston Bay (17 caught in autumn out of 1,302 caught in winter) (adjusted Chi-squared = 82.1, $p<0.001$). Very few birds were caught in the autumn/spring period in Weston Bay; in fact virtually all were caught in one catch on 1 March 1980 and thus the difference between the autumn/spring and winter periods in the likelihood of birds moving to Sand Bay reflects the fact that in the spring of 1980 there were a large number of Sand Bay wintering birds in Weston Bay. Birds caught in Weston Bay in winter were significantly more likely to be caught at Berrow in mid winter than at Berrow in autumn/spring (adjusted Chi-squared = 21.2, p<0.001). This is probably because almost 300 of the 436 birds caught at Berrow in winter were caught on Brean Beach on neap tides; these birds often roosted in Weston Bay on spring tides or when disturbed. Birds caught at Berrow in mid winter were significantly more likely to be caught in Weston Bay in midwinter than in Sand Bay (adjusted Chi-squared = 5.16, p<0.05); they were also more likely to be caught at Berrow in the autumn/spring than in Weston Bay in the winter (adjusted Chi-squared = 10.54, p<0.01).

Tables 5.4 and 5.5 give matrices for movements of adult male and female Dunlin and the numbers caught. There was no significant difference between the proportions of males (130 caught in winter out of 860 caught in autumn) and of females (152 caught in winter out of 895 caught in autumn) which were present in the autumn/spring period at Clevedon and those that were present there in the winter. Furthermore, the same proportions of males and of females present at Clevedon in the autumn/spring period moved further south within the study area during the winter. However, males present there in autumn were more likely to be caught in another bay in the autumn/spring period than females (adjusted Chi-squared = 5.07, p<0.05). There were also no sex differences between those staying and those moving between Sand Bay and Weston Bay. Of those birds present at Berrow in autumn/spring females were significantly more likely to have changed bay in midwinter than males (adjusted Chi-squared = 6.56, p<0.01).

It was expected that juveniles would be much more mobile in their first winter than adults; in fact it can be seen from appendix 6 that there was no difference between the movements of juveniles and those of adults; for comparison the reduced data set is given in table 5.3. In addition to the data given two juveniles caught at Severn Beach in October were subsequently caught in the study site in winter: one at Clevedon and one in Weston Bay.

During the final year of the study juveniles were marked with Rhodamine B dye (females on the breast; males on the undertail coverts and rump). Since each animal had a temporary leg flag (Goodyer et al., 1979) denoting the bay where it was caught, it was possible to study their movements across the area. The number of juveniles marked in each bay and the number of birds seen in each bay are given in table 5.6. Some leg flags were lost but field observations suggested that these were only few and would be unlikely to affect the results obtained. There was strikingly little movement between bays, even of birds marked in October. Only one bird was seen to have moved further than one bay away from site of marking (this bird was marked on 15 October at Severn Beach and moved to Weston Bay; it was probably the bird caught in this bay referred to earlier). Of the fourteen sightings of birds that had moved from Weston Bay to Berrow all but one were seen on Brean Beach on neap tides, or on the feeding areas off Brean Beach.

Many casual observers saw and recorded colour marked Dunlin within the study site and some were seen away from the study site but in the local area (table 5.7). There were very few sightings of colour marked birds at Severn Beach by mid winter, although birds were marked there on 15 October. Although the dye would have faded by then, the individuals that moved from Severn Beach still had visible dye; this suggests that most of the marked birds left the area and probably left the Severn. A few leg flagged adults were

TABLE 5.6

Sightings of dye-marked juvenile Dunlin in 1980/81

Site marked	Number marked	Number of sightings at:				
		Severn Beach(1)	Clevedon	Sand Bay	Weston Bay	Berrow
Severn Beach	60	9	1		1	
Clevedon	111		90			
Sand Bay	216		1	881	3	
Weston Bay	79			3	24	14
Berrow	45				4	42

(1) For numbers seen by casual observers see table 5.7

TABLE 5.7

Local movements of colour marked Dunlin (away from main study site)

(adults, leg flag sightings; juveniles both leg flag and dye mark sightings; various casual observers)

Site	Time Period	Adults			Juveniles		
		M	?	F	M	?	F
North Shore of Severn	1	1					
	2					1	
	3	1		1	1		
	4	2	2				
	5						
Upper Severn (above Severn Bridge)	1				2		1
	2						
	3						
	4	1			3		
	5				1		
Severn Beach - Avonmouth (1)	1	1	1	2	26		18
	2				4		3
	3				2		
	4						3
	5	2	1				
Stert	1				1		2
	2	1	5		3		
	3						
	4	1	2	2	2		3
	5	1	1				
Chew Valley Lake (2)	1				1		
	2	3			4		
	3	2	3		6	3	
	4	3	2		5		11
	5				1		

(1) Juveniles, all leg tags seen were local, except for one female in time period 4 which was from Clevedon.

(2) Minimum number of juveniles 8:

Site marked	Male	Female
Severn Beach	1	1
Clevedon	2	2
No flag	2	-

seen at this site in October and March, although none were marked here.

Marked birds were observed at two other sites: Chew Valley Lake and Stert (Bridgwater Bay National Nature Reserve). Both these sites are frequented by large numbers of birdwatchers. At Chew Valley Lake I expect that virtually every colour marked bird present was noted; the minimum number of juvenile birds seen is likely to be near to the maximum number present. Personal observations at Stert suggested that there was a much smaller proportion of colour marked birds there than at Berrow. The small number of sightings from the north shore of the Severn is remarkable as D. H. Worrall was studying Dunlin on the north shore in the winter 1979/80 in which year over 1,700 adults were leg flagged.

5.3.5 Movements relating to Moulting and Migration

Tables 5.8 and 5.9 summarise the recovery rates for birds caught away from the Severn in July, August and September. Figure 5.9 shows the sites at which these birds were caught. There were no significant differences in the recovery rates from migration sites between bays within my study area or between the two time periods. There were also no significant differences between the two sexes. However, there was a suggestion that birds caught at Clevedon tended to be caught later in Finland and at Ottenby, Sweden; this did not result from the fact that females migrate first (Ingolfsson _et al._, 1955; Boere, 1973) as both males and females show the same pattern.

Recoveries from the Wadden Sea also showed no significant difference between bays in the autumn/spring or winter, but birds

TABLE 5.8

Recovery rates for different sites in autumn/spring

(for definition of recovery see 5.2)

Site		Number caught	Europe migrating	Wadden Sea moulting	Wash moulting
Clevedon	All	1,755	22 (1.3)	9 (0.5)	11 (0.6)
	Male	850	12 (1.4)	6 (0.7)	7 (0.8)
	Female	895	7 (0.8)	3 (0.3)	3 (0.3)
Sand Bay	All	567	10 (1.8)	4 (0.7)	6 (1.1)
	Male	317	8 (2.5)	3 (1.0)	3 (1.0)
	Female	250	2 (0.8)	1 (0.4)	2 (0.8)
Weston Bay	All	215	4	1	4
	Male	121	3	0	2
	Female	94	1	1	2
Berrow	All	1,809	24 (1.3)	10 (0.6)	14 (0.8)
	Male	1,166	13 (1.1)	4 (0.3)	7 (0.6)
	Female	643	11 (1.7)	6 (0.9)	5 (0.8)

TABLE 5.9

Recovery rates for different sites in winter

(for definition of recovery see 5.2)

Site		Number caught	Europe migrating	Wadden Sea moulting	Wash moulting
Clevedon	All	760	7 (0.9)	2 (0.3)	1 (0.1)
	Male	349	4 (1.2)	2 (0.6)	0
	Female	411	3 (0.7)	0	1 (0.2)
Sand Bay	All	493	13 (2.6)	3 (0.6)	2 (0.4)
	Male	255	4 (1.6)	2 (0.8)	0
	Female	238	9 (3.8)	1 (0.4)	2 (0.8)
Weston Bay	All	1,302	19 (1.5)	3 (0.2)	14 (1.1)
	Male	657	7 (1.1)	1 (0.2)	1 (0.2)
	Female	645	10 (1.6)	0	12 (1.9)
Berrow	All	436	8 (0.2)	3 (0.7)	5 (1.2)
	Male	258	3 (1.2)	3 (1.2)	4 (1.6)
	Female	178	5 (2.8)	0	1 (0.6)

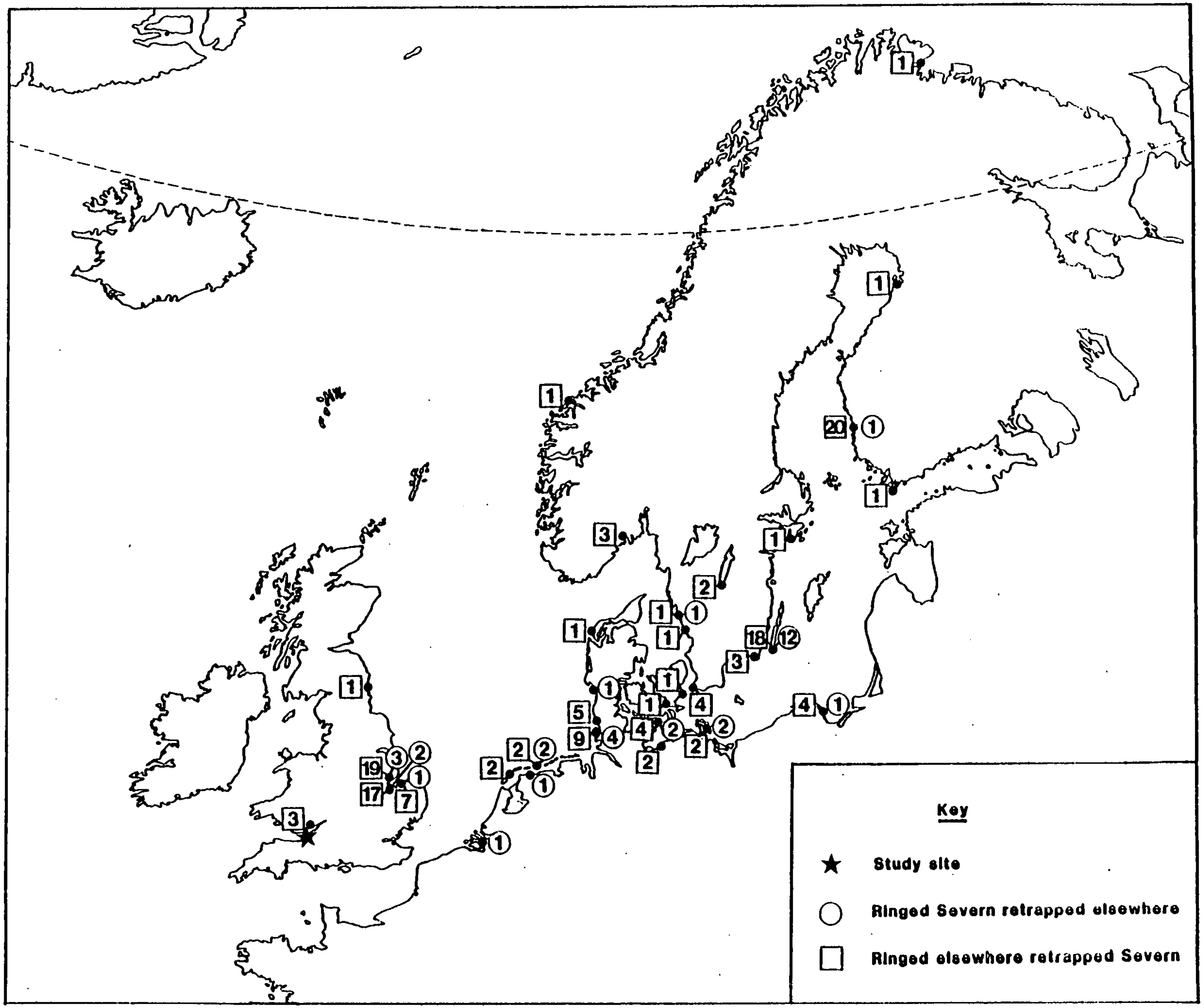

FIGURE 5.9

Trapping sites of adult Dunlin caught away from the Severn in July, August and September moulting on the Wash were more likely to winter at Berrow and in Weston Bay than at Clevedon or in Sand Bay (table 5.9). Of the birds wintering in Weston Bay there were significantly more females recovered while moulting on the Wash than males (adjusted Chi-squared = 7.85, $p<0.01$). There is a hint of a reversed trend at Berrow with males moulting on the Wash, but the sample of birds caught in winter is much too small to test. Within the study site as a whole males were more likely to moult on the Wadden Sea and females on the Wash (Fisher's exact test $p = 0.0015$).

Figure 5.10 gives the recoveries of birds in March, April and May showing large numbers of birds caught in the German Wadden Sea and on the north shore of the Severn. Although only small numbers of _C_. _a_. _alpina_ Dunlin are present on the north shore of the Severn, the intensive spring catching operations there produced many recoveries. The high number of recoveries in the German Wadden Sea is to be expected as there are very large numbers of Dunlin in this area in the spring (Smit & Wolff, 1981).

There are also some winter recoveries away from the study site (figure 5.11). Almost all are in October, early November or at the end of February (ie in a period when birds are still arriving on the study site or have already started to leave).

Figure 5.12 shows the recoveries of birds first ringed as juveniles (all but two of these were first caught away from the Severn). Although these show a very similar pattern to the adults, there are three important differences:

1) there are a considerable number of recoveries in Norway and this follows the pattern of juveniles migrating down the west coast of Norway suggested by Lesley & Lessells (1978);

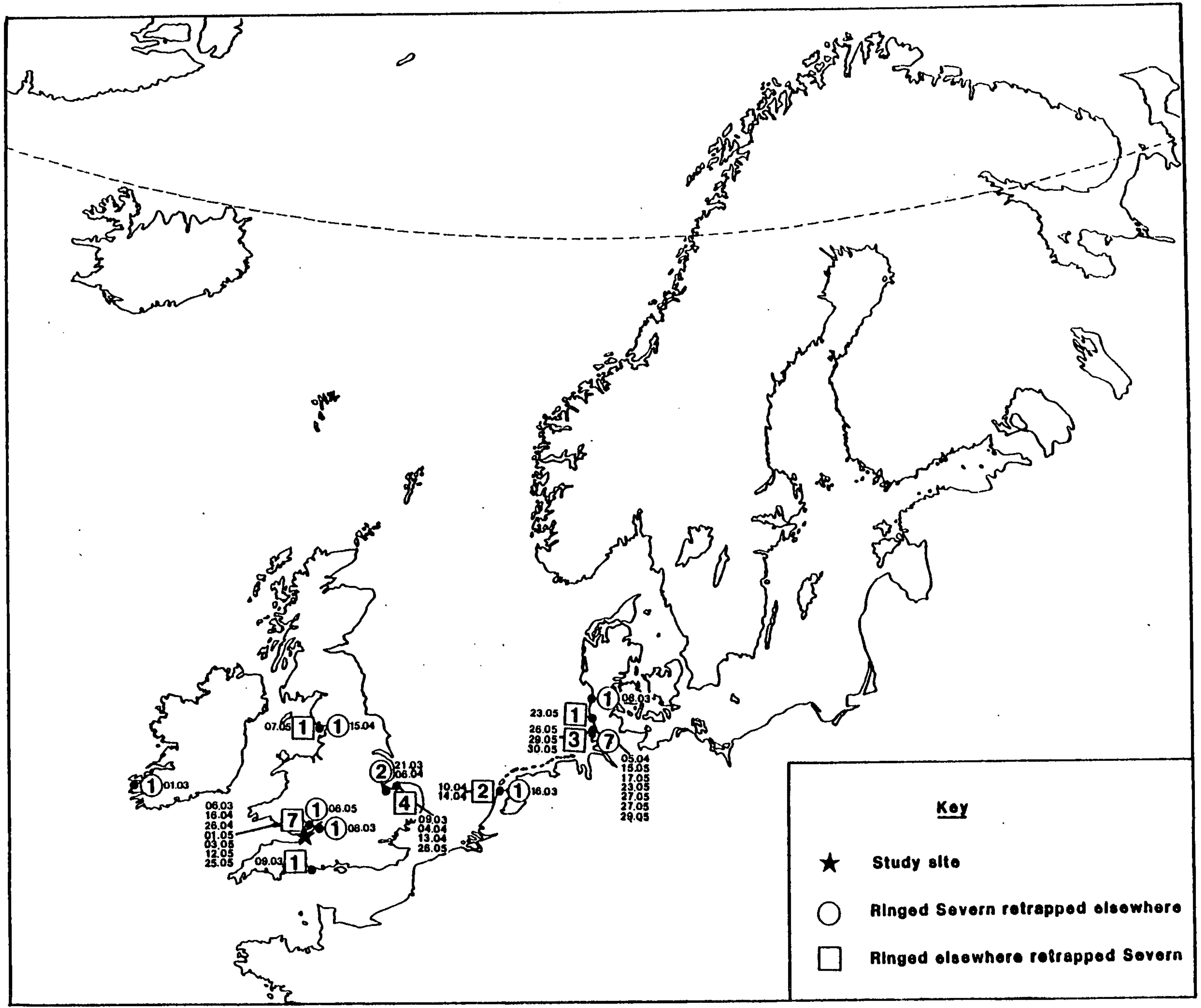

FIGURE 5.10

Trapping sites of adult Dunlin caught away from the Severn in March, April and May (day and month of recovery away from the Severn are given)

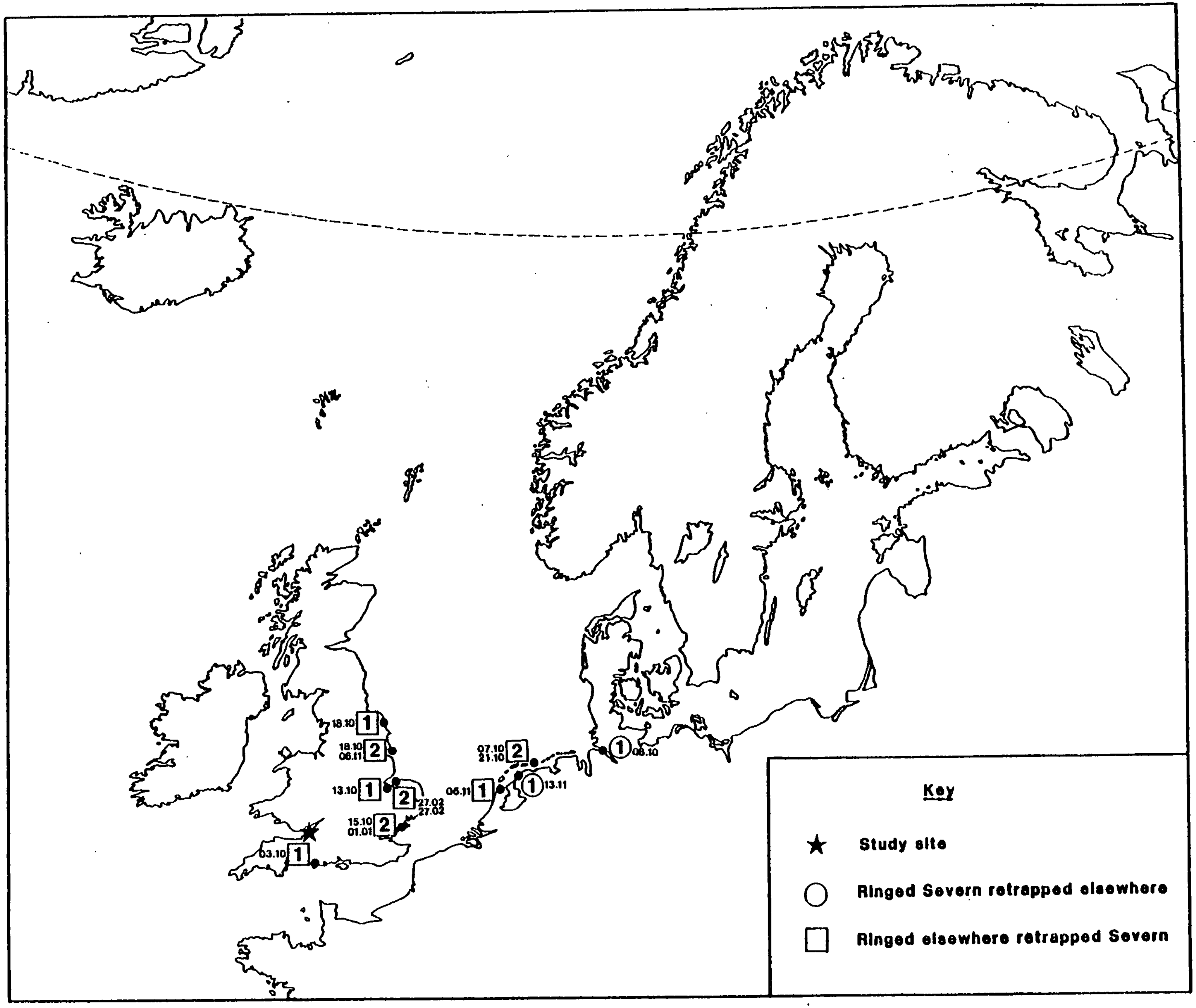

FIGURE 5.11

Trapping sites of adult Dunlin caught away from the Severn between October and February (day and month of recovery away from the Severn are given)

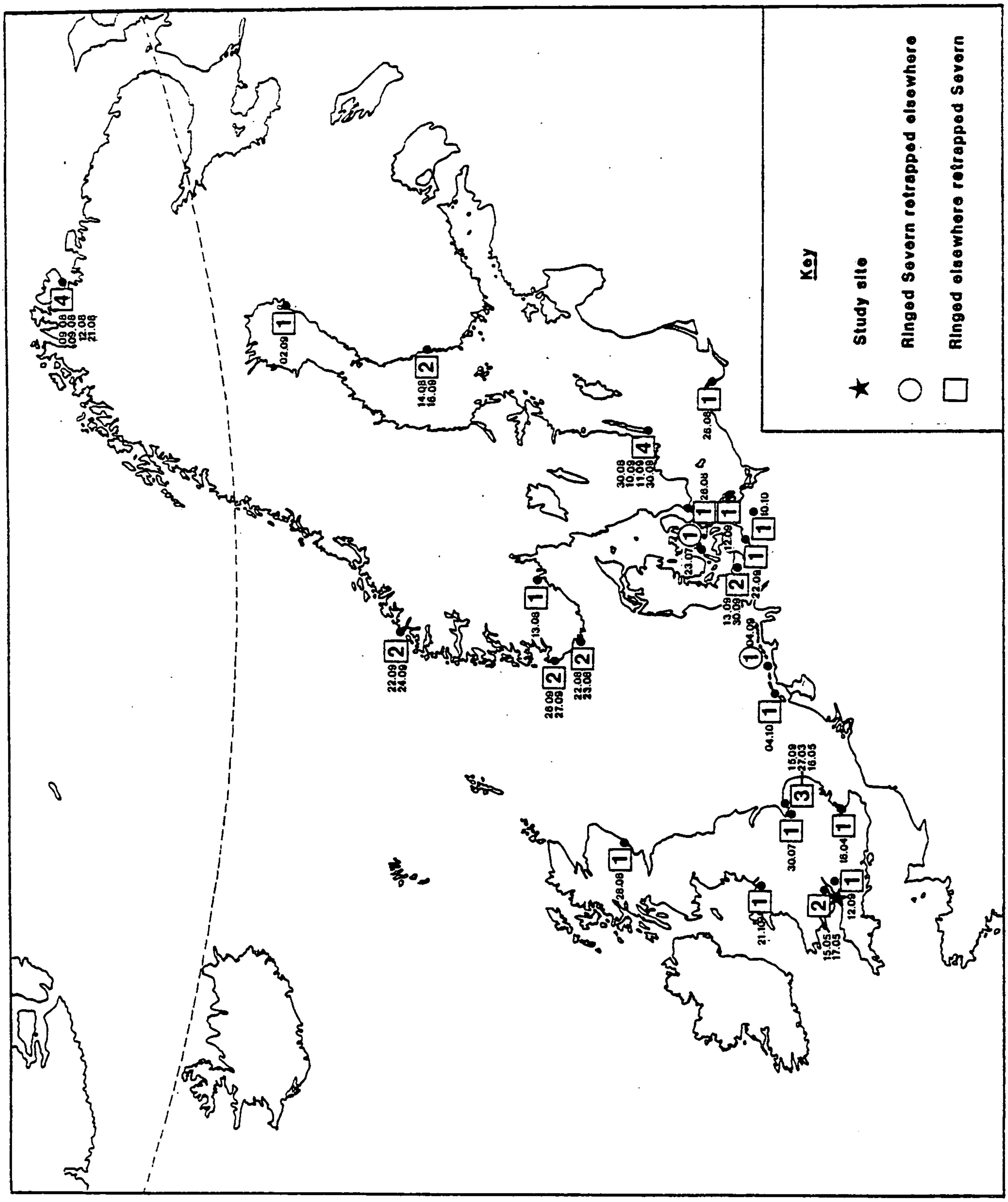

FIGURE 5.12

Trapping sites of juvenile Dunlin (birds aged as juvenile on first capture) caught away from the Severn (day and month of recovery away from the Severn are given)

2) there is a complete lack of recoveries from the German Wadden Sea. This is not surprising as juveniles are less than one percent of the large moulting flocks (pers. obs.) which have been extensively caught in the area.

3) The juveniles in general show a much wider spread of recoveries than the adults.

A number of colour marked individuals were seen away from the Severn (tables 5.10 and 5.11 and figure 5.13). I found more leg flagged birds at Terrington on the south shore of the Wash in March than at Heacham on the east Wash. Although this difference was not significant (Fisher's exact test p = 0.067), I strongly suspect that the effect was real as many more birds were seen at Heacham in tight flocks on the rising tide. These birds were not counted due to the difficulty of assessing the number actually checked in dense flocks, but no more leg flags were seen. There were, however, significantly fewer leg flagged birds present at Terrington in April than in March (adjusted Chi-squared = 9.059, p<0.01).

Most of the leg flagged birds seen by other observers follow the pattern of ringing recoveries. However, some birds were seen in the mid-winter period away from the Severn, these had all moved in a south to south westerly direction and may have been birds marked on passage in October or March. The only exception (two females seen on the Wash on 20 February) could have been birds leaving the Severn very early. Most sightings were of males or red flagged birds; this is at first surprising, but to the casual observer the yellow and orange (male) and red (unsexable) flags stand out much more than the green, blue and black (female) ones.

There were a number of sightings of colour marked juveniles

TABLE 5.10

Sightings of adult Dunlin away from the Severn

(Personal observations)

Date	Place	Sex (1)	Number checked
24 July 80	Den Helder, Netherlands	R	1,000
31 July + 1 Aug 80	Schiermonnikoog, Netherlands	M	3,717
6 Aug 80	Terschelling, Netherlands		553
11 Aug - 22 Aug 80	Schleswig-Holstein, FR Germany		5,001
17 Mar 80	Heacham, The Wash	M	1,014
20 Mar + 21 Mar 80	Terrington, The Wash	3M,6R 2F	2,321
15 Apr 80	Morecambe Bay		4,396
17 Apr 80	Heacham, The Wash		483
17 Apr + 18 Apr 80	Terrington, The Wash	1M,2F	4,065
19 Apr 80	Friskney, The Wash		176

(1) M = male; F = female; R = sex unknown

TABLE 5.11

Sightings of adult Dunlin away from the Severn and local sightings between April and September (various casual observers)

Date	Place	Sex (1)	Number checked
28 July + 8 Aug 80	Ufshale, Nordstrand, N.E. Denmark	R	-
3 Aug 81	Het Zwin, Belgium	M	27
14 Aug 80	Romo Bank, Denmark	R	6,000
17 Aug 80	Severn Beach	R	90
30 Aug 79	Hamburger Hallig, F.R. Germany	M	-
2 Sept 81	Severn Beach	R	150
6 Oct 80	Westerhever, F.R. Germany	R	300
7 Oct 80	Westerhever, F.R. Germany	R	1,200
10 Jan 81	Exe Estuary, Devon	M	-
28 Jan 82	Wyke Regis, Portland, Dorset	M	97
29 Jan 82	Wyke Regis, Portland, Dorset	M	200
20 Feb 83	Snettisham, The Wash	2F	-
15 Feb 81	River Penze Estuary, Brittany, France	R	200
26 Feb 81	River Penze Estuary, Brittany, France	R	300
14 Mar 80	L'anse d'Yffinac, Brittany, France	R	-
16 Mar - 24 Apr 80	Spurn Point, Yorkshire	M	450
2 Apr 82	Tipperne, Jylland, Denmark	R	330
3 Apr 80	Ager Tange, Jylland, Denmark	M	431
10 Apr 80	Deventer, Netherlands	R	-
20 Apr 80	Westerhever, F.R. Germany	R	200

(1) M = male; F = female; R = sex unknown

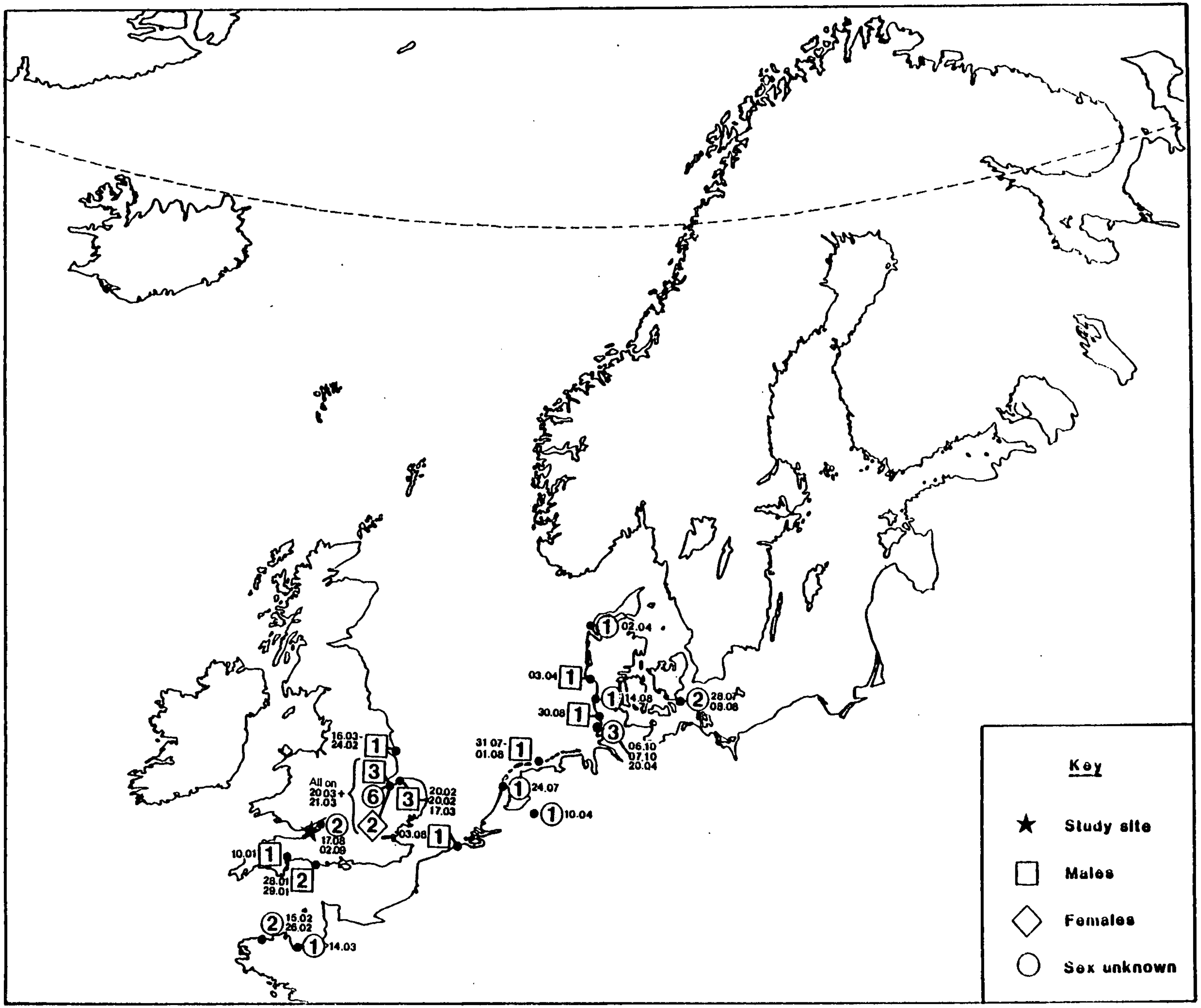

FIGURE 5.13

Sightings of colour marked adult Dunlin away from the Severn

(day and month of sighting are given)

(table 5.12 and figure 5.14) and in this case there are some noticeable differences from the recovery data. Three birds moved to the north of Britain, and one of these was known to have been marked on 9 November at Berrow: this shows that some juveniles may move a considerable distance after their arrival on the Severn in autumn. Two birds showed a westward movement from the study site during the winter, one of these again being marked early in the winter. The spring movements follow those of adults very closely.

The sightings of dye marked birds from the Wadden Sea and Wash (table 5.13) are difficult to interpret as one bird may be seen on many occasions; for instance: all eight Wadden Sea sightings in Weston Bay were attributable to one individual marked in the Netherlands which had a distinctive pattern of dye. There appeared to be a reduction in the number of Wash marked birds at Clevedon and Sand Bay in the mid-winter period: all the sightings at Clevedon refer to one dyemarked bird, which was caught and also gave the only wintering recovery of a Wash moulting bird at Clevedon. It is interesting to note that there were roughly similar numbers of Wadden Sea and Wash birds seen on the Severn although two and a half times as many birds were marked on the Wash (2183) than the Wadden Sea (855); this suggests that a much greater proportion of birds moulting on the Wadden Sea move to the Severn than Wash birds, but the data are not suitable to test this.

5.4 Discussion

The counts presented in figures 5.1 to 5.4 appear at first sight to show wild and almost random fluctuations. There are considerable

TABLE 5.12

Sightings of juvenile Dunlin away from the Severn

(various casual observers)

Date	Place	Sex (1)	Site marked
4 Nov 80	Kidwelly Quay, Dyfed	M	Sand Bay
15 Dec + 19 Dec 80	Caron Mouth, Firth of Forth	F	Berrow
19 Dec 80	Caron Mouth, Firth of Forth	M	?
27 Dec 80	Belfast Lough, County Down	F	?
18 Jan 81	RAF Chivenor, Taw Torridge, Devon	?	?
25 Mar 81	Fano, Denmark	F	?
30 Mar 80	Fano, Denmark	M	(2)
6 Apr 81	Terrington, The Wash	F	?
15 Apr 81	Schiermonnikoog, Netherlands	?	?
1 May 80	Breyden Water, Norfolk	M	(2)
4 May 80	Cotswold Park, Gloucestershire	M	?

(1) M = male, F = female; ? = sex or site marked unknown
(2) Bird marked with permanent leg flag in winter 1979/80

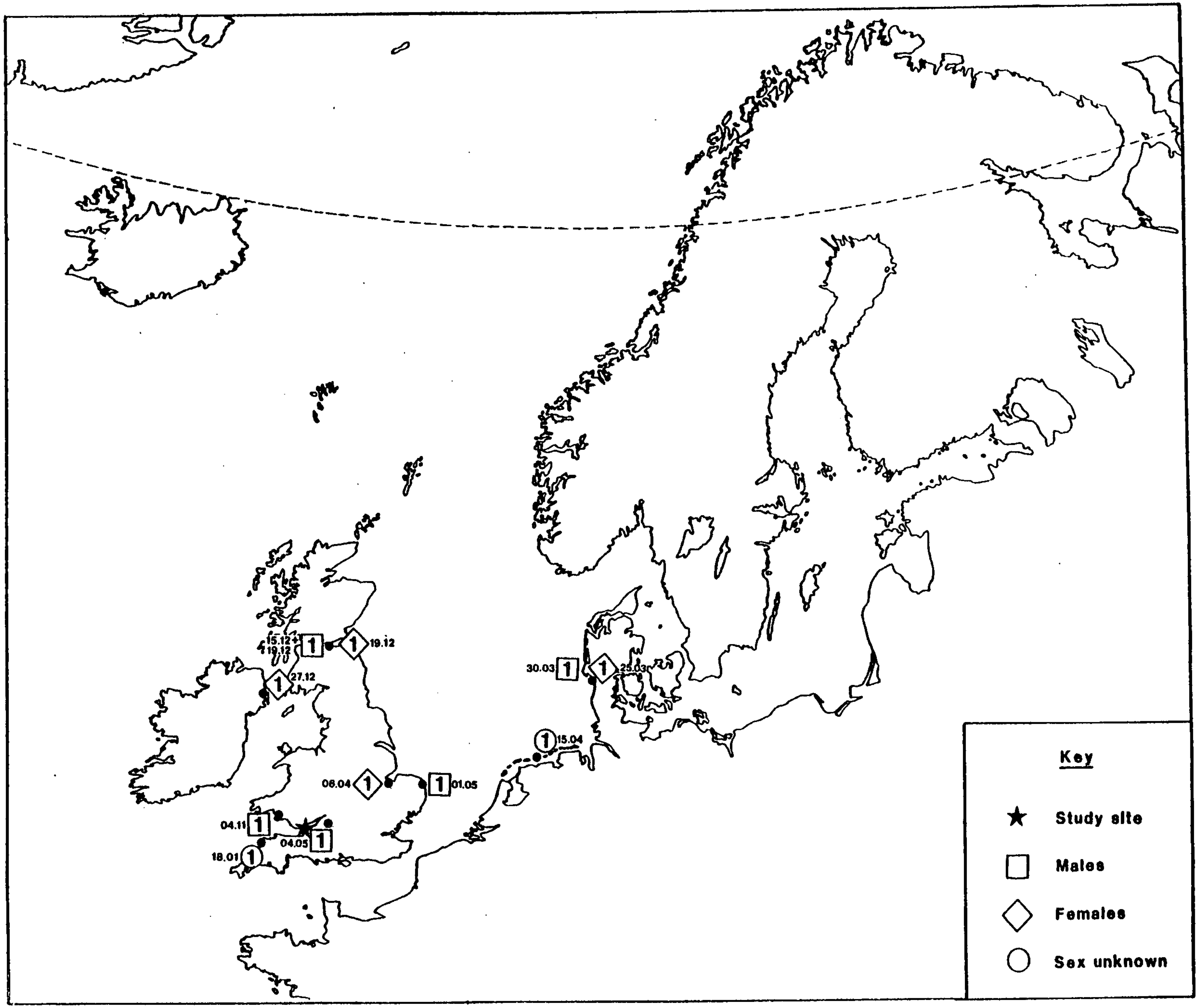

FIGURE 5.14

Sightings of colour marked juvenile Dunlin away from the Severn

(day and month of sighting are given)

TABLE 5.13

Sightings of Dunlin on the Severn which were colour marked on the Wash or on the Wadden Sea

(Personal observations)

Site	Time Period	Bird days	Wash Ads.	Wadden Ads.	Percent marked	Wash Juvs.
Severn Beach	October	645				
	1 Dec - 10 Jan	90				1(1)
Clevedon	October	1,210	3(1)	2(2)	0.41	
	November	3,000	2(2)	3(2)	0.17	
	1 Dec - 10 Jan	3,320	2(1)	1(1)	0.09	
	11 Jan - 20 Feb	920	1(1)		0.11	
	21 Feb - 30 Mar	800				
	WINTER TOTAL		(2)	(3)		
Sand Bay	October	2,295	5(2)		0.22	
	November	14,260	13(4)	4(2)	0.12	
	1 Dec - 10 Jan	7,350	5(1)	5(2)	0.14	4(1)
	11 Jan - 20 Feb	3,200			0.00	3(1)
	21 Feb - 30 Mar	182				
	WINTER TOTAL		(4)	(3)		
Weston Bay	October	175			0.00	
	November	3,100		4(1)	0.13	
	1 Dec - 10 Jan	3,000		3(1)	0.10	1(1)
	11 Jan - 20 Feb	0				
	20 Feb - 30 Mar	1,500		1(1)	0.07	
	WINTER TOTAL			(1)		(1)
Berrow	October	66			0.00	
	November	11,500	6(3)	1(1)	0.06	
	1 Dec - 10 Jan	3,200	3(1)	1(1)	0.12	
	11 Jan - 20 Feb	6,300	3(1)	4(2)	0.11	
	21 Feb - 30 Mar	1,800	1(1)		0.05	
	WINTER TOTAL		(3)	(2)		

Numbers in brackets show absolute minimum number of individuals present.

problems in counting (see earlier) and it is particularly interesting to note the large differences between my counts and the Birds of the Estuaries Enquiry (BoEE) counts. The BoEE counts are undertaken on spring tides when there is considerable movement between bays (Chapter 1). The high counts at Clevedon in December 1979 and January 1980 could be birds moving from Sand Bay to the Yeo Estuary (at the southern end of Clevedon Bay), as these numbers of birds were certainly not feeding in the area. The BoEE counts for the 1980/81 winter were consistently lower than my feeding counts. During that winter there was considerable disturbance as the sea wall was being raised along a large section; this meant that the birds often went to fields far inland to roost at high tide.

Prater (1981) gives mean monthly counts for the south and west of Britain and Ireland averaged over a number of years. These show low numbers in July, August and September with a large increase through October and November. December, January and February show very similar figures although there is a slight peak in January. Half the birds have left by March and virtually all by April. This general pattern fits very well with that of the Severn.

Ferns (1982) considered the counts of many species of waders and waterfowl in the Severn Estuary and split the year into four periods. Ferns' autumn period covers August, September and October. It encompasses both the autumn passage (which occurs in August and early September and on the south shore of the estuary is entirely of the races *C. a. schinzii* and *C. a. arctica*) and also the first arrivals of the wintering *C. a. alpina*. Ferns suggested slight differences between the sites on the south shore (Sand Bay and Weston bay increasing and Bridgwater Bay and Clevedon decreasing) in the two winter periods (November/December and January/February). Ferns' spring period (March, April and May) covers the tail end of the wintering population (all of which have left the south shore by the end of March) and the spring passage of *C. a. schinzii* and *C. a. arctica* northwards.

The counts for both Sand Bay and Weston Bay are extremely difficult to interpret except for the fact that in Weston Bay there are normally only small numbers of birds until the beginning of December. Those birds present in October and November normally had a very high percentage of juveniles amongst them.

The counts for Berrow suggest a big difference in the population size between years; I am uncertain whether this is a real effect or an artefact. During the winter of 1980/81 the birds appeared to move across the Parrett and feed on the northern part of the Stert flats as the tide was coming in, and to stay there to roost. All the really high counts at Berrow in 1979/80 were made when the birds were carefully watched on the rising tide and counted before they moved across the Parrett or as they were coming up to roost at the Berrow saltmarsh. In 1980/81, however, many birds moved across the Parrett when they were still very far out. This meant that it was very difficult to get accurate estimates and I suspect that I seriously undercounted the numbers present.

The situation during the third year of the study (1979/80) was seriously complicated by some severe gales which washed away the upper layers of mud on the south shore beaches at the beginning of December. The most serious effect was at Clevedon. Figure 5.15 shows the situation in November 1979 (this is the same as it had been for the whole winter of 1978/79) and figure 5.16 shows the

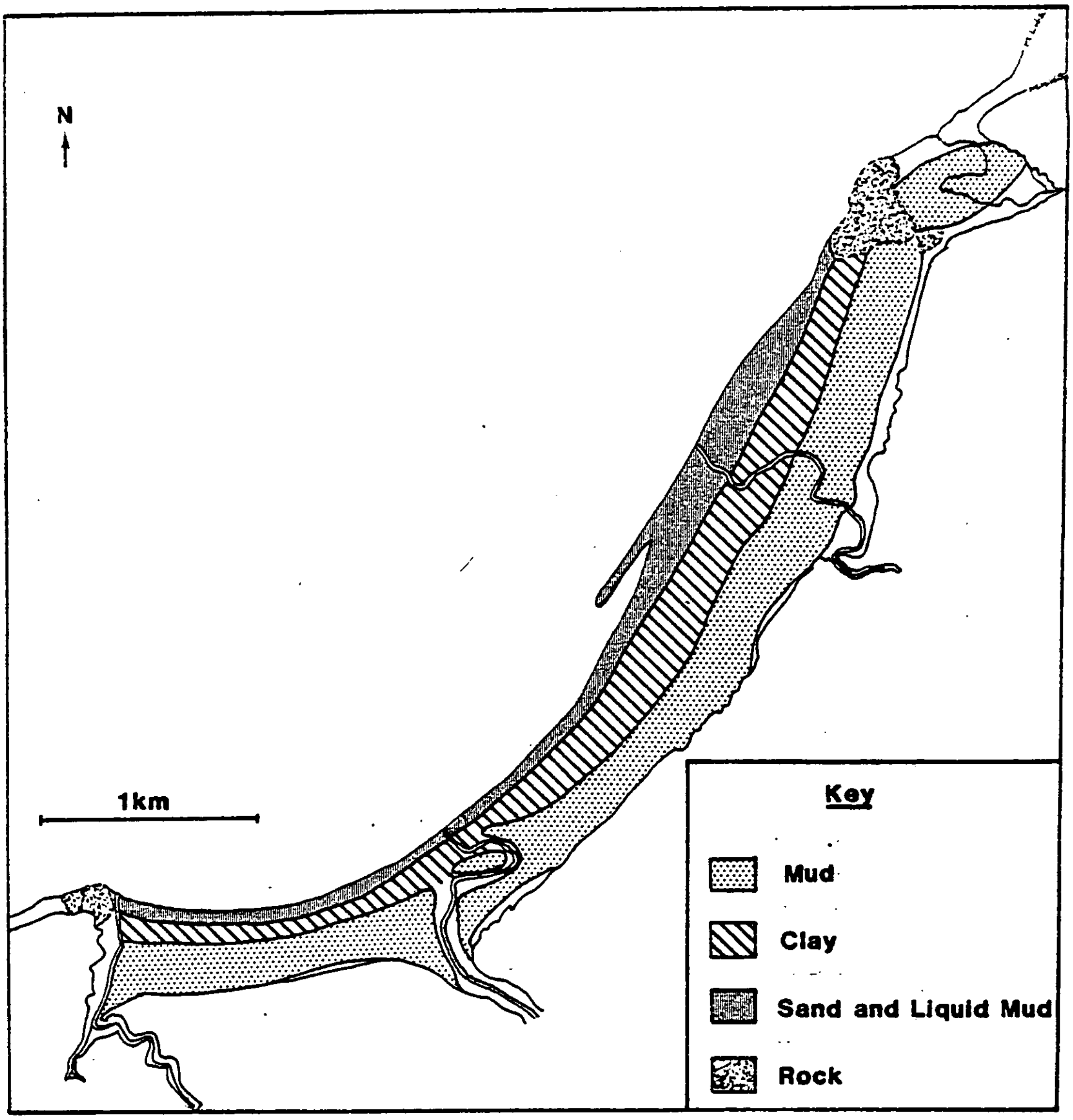

FIGURE 5.15

Surface substrates at Clevedon in November 1979

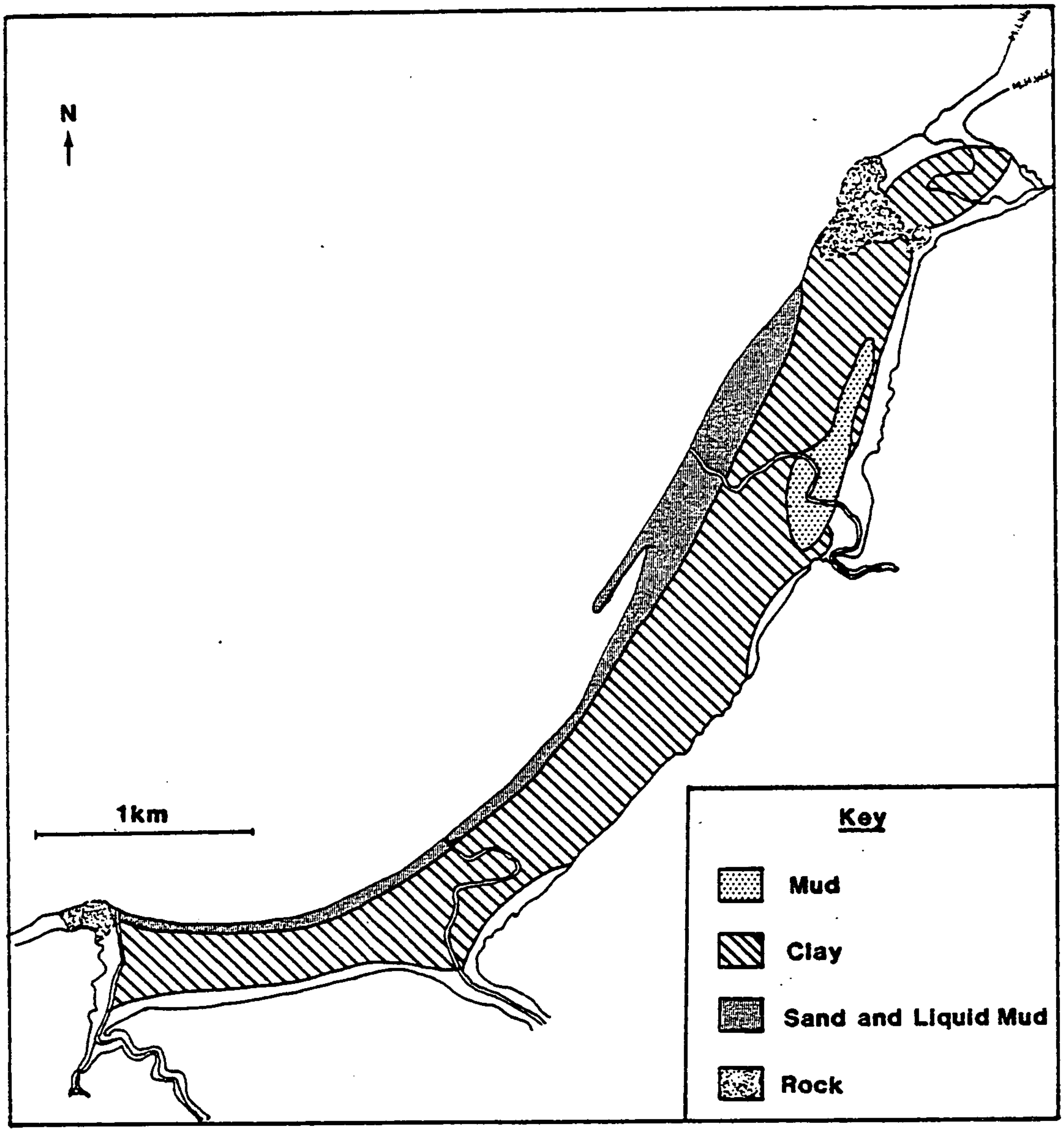

FIGURE 5.16

Surface substrates at Clevedon on 15 December 1979 situation on 15 December 1979, after severe gales had eroded the mud area on the upper shore, leaving hard clay exposed. Ferns (1983) analysed the effect this had on the whole estuary, the counts showing a decrease on all of the southern shore sites. The figures were, however, very different from mine and I suspect that this is partly due to the BoEE counts being taken on spring tides where there was often considerable movement between bays. In December, January and February the BoEE counts in Sand Bay were 400; 200 and 100. Mine were considerably higher, there being only one occasion when I found less than 500 birds in the bay. The BoEE for Bridgwater Bay (this area equates to the Berrow roost plus that at Stert) were considerably lower than mine, except for the 12,000 birds counted in December. I believe this area has been consistently undercounted as the birds roost in very large flocks which tend to be undercounted (Prater, 1979). This is a problem which I feel to be widespread amongst observers who are not experienced in cannon netting, as estimates of large flocks are sometimes only half the number of birds that are caught.

The situation at Clevedon bears further examination as it became apparent that the birds that left Clevedon were predominantly the females. When one looks at the numbers of males and females present (figure 5.5) it can be seen that soon after the mud was lost (at the beginning of December), a high percentage of the females left. In the next period (up to mid January) both males and females left Clevedon and in mid February the returning birds were predominantly females.

When the mud had been lost the birds were only able to peck over the surface except in the bottom of the runnels where small amounts

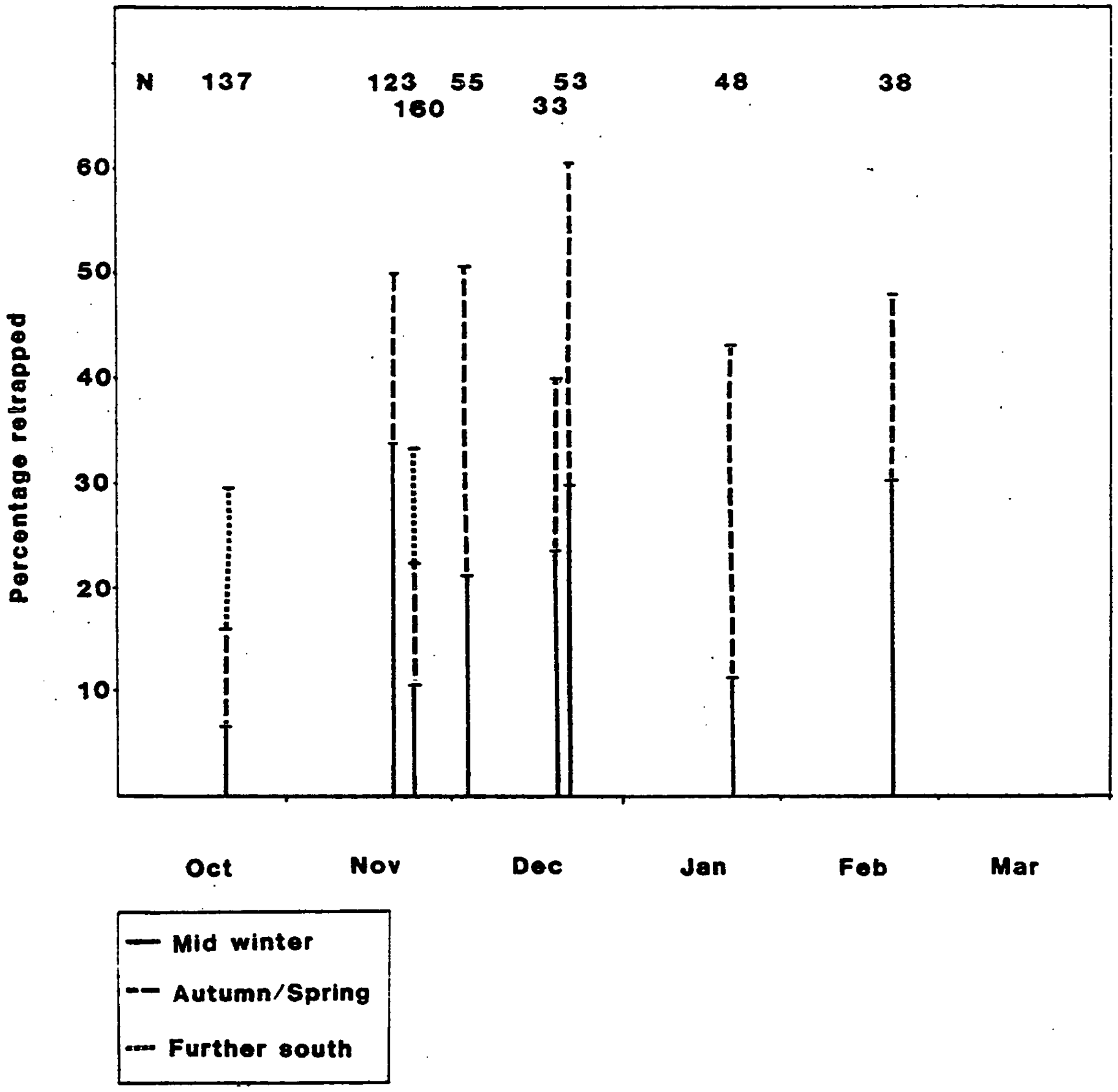

FIGURE 5.17

Percentage of retraps in catches of Dunlin at Clevedon

in winter 1979/80

(here a retrap is considered as a bird either previously or subsequently caught) of mud were present; it was my impression that females tended to feed in these runnels. However, because these areas of mud were not well defined, it was not possible to gather relevant data. The catches right through winter 1979/80 at Clevedon, though small (around 50), always had a similar percentage of retraps of birds originally ringed at Clevedon or ringed there at these times and subsequently retrapped there (figure 5.17). It can also be seen that birds which moved to (or had come from) further south than Clevedon were only present in October and November. The increase in numbers shown by Ferns (1983) on the north shore of the estuary in January and February 1980, together with the ringing information from the south shore, suggests that birds went to the north shore (even though there were very few leg flag sightings there). A few birds were caught on the north shore during that winter and on 19 February 1980 a female, originally ringed at Clevedon on 21 November 1979, was caught at Collister Pill; this bird was subsequently caught back at Clevedon on 10 January 1981.

The variation in sex ratio followed a similar pattern in each winter in all bays, except Clevedon in 1979/80 (figures 5.6 and 5.7). The data for the 1979/80 winter at Clevedon were very different from the general trends, probably because of the sediment removal at that site. The catches were comparatively small, so they did not seriously bias the total data set.

The increased sex ratio (figure 5.7) at all sites in period five (20 February onwards) is of interest as it suggests that birds are arriving on the study area from outside. The recovery in south west Ireland on 1 March 1980 of a bird ringed at Clevedon on 11 March 1978, may give a clue to where the birds are coming from.

The percentage of juveniles (figure 5.8) in different catches has to be treated with caution; it has been shown that mist net samples tend to contain more juveniles and cannon net catches more moulting adults (Pienkowski & Dick, 1976). For this reason it is likely that Sand Bay would show more juveniles as most birds were mist netted there. Most of the birds caught at Berrow were cannon netted, so a lower percentage of juveniles could be expected, but even the mist net catches here had a very low percentage of juveniles in them. Furthermore, although only 47 juveniles were caught in November, 6 were retrapped among the 36 caught on 21 February together with 1,267 adults. This would suggest about 300 juveniles (5%) in the 6-9,000 birds wintering at Berrow. It was thought that the juveniles might winter in Bridgwater Bay and of the 19 birds caught there, four were adult males, 11 juvenile males and four juvenile females. As we were failing to sample the main roost, I would expect a high percentage of juveniles, but it is interesting to note that there were very few females present, as at Berrow.

To date there has been very little work done on movements of waders within a single estuary. Pienkowski and Clark (1979) looked at movements of waders within the Firth of Forth; their data suggested that Dunlin only moved short distances, and this result was consistent with the lack of roost sites available on the Forth, although some birds moved several miles.

The data I present suggest that within the south shore of the Severn there is a regular pattern of movements schematically shown in figure 5.18. The data presented in tables 5.2 to 5.5 and appendix 6, suggests that in the autumn period birds would first arrive at Clevedon, some of them then drifting south to Sand and

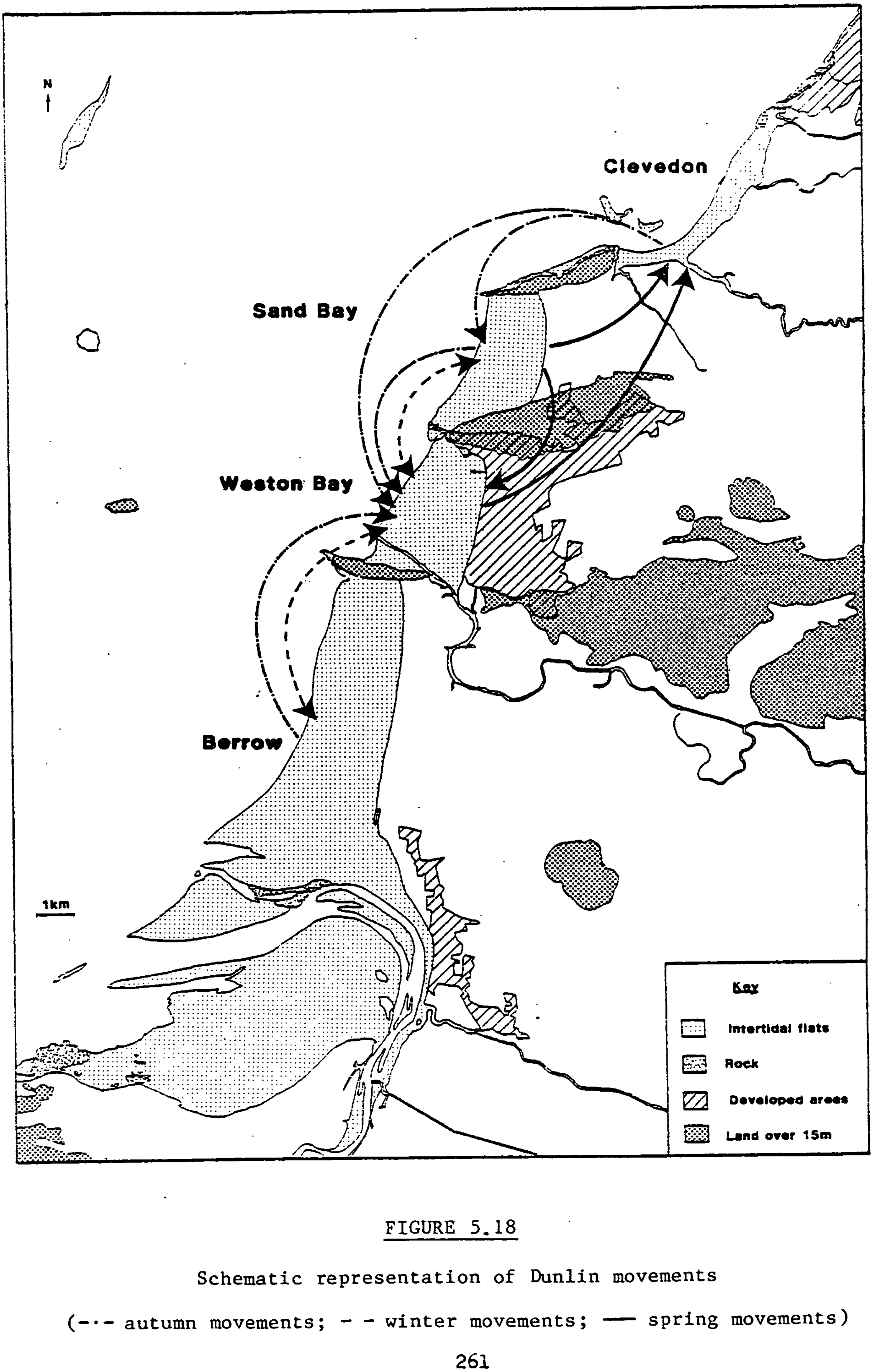

FIGURE 5.18

Schematic representation of Dunlin movements

(–·– autumn movements; – – winter movements; —— spring movements)

Weston Bays, but birds would not move from Clevedon to Berrow. Some birds arriving originally at Berrow and Sand Bay moved to Weston Bay in winter: this interpretation agrees with the count data which suggest autumn peaks at Clevedon and possibly Berrow with very few birds in Weston Bay.

Within the mid winter period birds would move between Sand Bay and Weston Bay and Berrow and Weston Bay but they would not move between Berrow and Sand Bay. However, the data also suggest that birds present at Clevedon, Sand Bay or Berrow in the autumn were more likely to remain there throughout the winter rather than move. Spring movements were the reverse of autumn movements.

These data suggest that during the midwinter period and probably also during the autumn and spring period the majority of birds would remain in the same bay, but some would use two adjacent bays. It must be remembered, however, that all these birds were caught roosting and that the midwinter movements found between adjacent bays may be purely movements to and from roost and not movements between different feeding areas. In any case, Clevedon appears to be isolated from the other bays on the south shore in winter.

The patterns of recoveries for the whole of the south shore of the Severn follow closely those from other sites in winter time (Steventon, 1977; Hardy & Minton, 1980; Branson, 1983) showing a migration route through the Baltic for adults with large numbers of birds moulting on the Wash and the Wadden Sea. The sightings of birds dye marked on the Wash and the Wadden Sea strongly suggest that only a small proportion of birds wintering on the Severn moult on the Wash. Recovery rates on the Severn of birds moulting on the Wash average less than one percent; approximately ten percent of the Dunlin moulting on the Wash (at the sites where catching operations occur) carry rings. This would suggest that a maximum of ten percent of birds wintering on the Severn moult on the Wash. The wader catching effort on the Wadden Sea has been very much less until recent years and even though many thousands have now been ringed, still only a very small percentage of the moulting population carries rings. The data presented for the different sites strongly suggest that Severn wintering males tend to moult on the Wadden Sea and some Severn wintering females moult on the Wash. Boere <u>et al</u>.(1973) showed that females start moulting before males on the Wadden Sea. Females also tend to migrate through Ottenby before males, but I do not believe that these small differences in the timing of moult could account for the different recovery rates obtained. Within the Severn I have shown differences in the percentage of recoveries from different sites. The data suggest that in Weston Bay and at Berrow about ten percent of birds come from the Wash and of these birds from the Wash the females are more likely to go to Weston Bay and the males to Berrow. Very few birds from the Wash, however, winter in Sand Bay or at Clevedon. The recoveries of Wadden Sea moulters during the winter period are few but there is a suggestion that the pattern may not be straightforward. The problem remaining is: where do the females wintering in Sand Bay and at Clevedon (the sites where females predominate) undergo their annual moult? Several possibilities arise:

1) the birds are moulting in part of the Wadden Sea where very little ringing is carried out (large numbers of birds have been ringed only in Schleswig-Holstein and the Netherlands); or

2) the birds moult in a completely unknown site; or

3) the birds start moulting on their breeding grounds and moult as they move south.

Each one of these suggestions poses considerable problems. If they were moulting as they were migrating, it is likely that they would migrate more slowly and therefore be more likely to be caught on the migration sites. In fact, they tend to have a lower recovery rate than birds from further south within the Severn. Kozlova (1962) showed that many Dunlin in central USSR (east of 70 degrees east) start moulting on the breeding grounds or nearby. If these birds are moulting on the breeding grounds, one would expect them to be caught at the migration sites in August and September, when the juveniles are caught. It is possible that they could be migrating via another route, possibly on a more southerly line across Europe. There is a late autumn passage of Dunlin through Germany and Switzerland (Harengerd _et al_., 1973; Baula & Sermet, 1975), but these are mainly juveniles (H. Hotker pers. comm.). In an attempt to check whether Severn wintering Dunlin were moulting in the Wadden Sea, in areas where they are not trapped, I visited a series of sites in the Netherlands and Germany during the summer of 1980. Unfortunately, it was only possible to visit a few sites. Out of a total of 11,000 birds checked, only two leg flagged birds were seen. Since the European wintering population of Dunlin is about 1.2 million (Prater, 1981) and 1,700 had been flagged prior to summer 1980, one would expect to find more than one in a thousand birds in the area as a whole, if Dunlin were randomly distributed as to moulting and wintering area. There are in the region of 900,000 Dunlin on the Wadden Sea in autumn (Smit & Wolff, 1981). Therefore, unless the females wintering at Clevedon are part of a very small population, some of them must moult on the Wadden Sea. The most likely areas are either the Niedersachsen region or Denmark, both of which hold 200,000 moulting Dunlin (Smit & Wolff, 1981).

The data presented in chapter 4 show that males and females have slightly different measurements in different sites within the Severn and away from the Severn. This information, together with the information on recovery rates, strongly suggests that Dunlin wintering in different bays within the study site have different migration routes and possibly different moulting areas. The sex differences between bays in winter time might then be related partly to birds of different size preferring to feed on different substrates and partly to different populations wintering in different bays. There is no special reason to suppose that the different sexes from one population should both winter on the same site. Ketterson & Nolan (1976) showed that female Dark-eyed Juncos _Junco hyemalis_ winter further south than males and Boere (1976) has shown that male Dunlin arrive on the moulting grounds before females.

Neither the bill lengths nor wing lengths of Dunlin wintering on the Severn correlate exactly with the breeding ground data for the nominate race in western USSR (Greenwood, 1979), even taking into account _post mortem_ changes in museum skins (Green, 1980a; Engelmoer _et al._, in press) It is possible that many of the birds wintering on the Severn come from further east than the Yamal Penisula which Cramp & Simmons (1983) have suggested as the farthest east that western European wintering Dunlin breed. Even for birds breeding as far east as the Taymyr Penisula, western Europe (5,000 km away) is closer than the coast of the Indian sub-continent (the great circle route between the Taymyr Penisula and western Europe goes across northern Norway and the North Sea).

From the combination of recoveries and sightings of marked birds it is possible to obtain a good understanding of movements of the Severn wintering Dunlin in early spring. Birds were never seen migrating in Spring; but on a very calm night on 24 February 1981 large numbers were heard migrating in an easterly direction from Sand Bay on the rising tide; this would take them straight towards the Dutch Wadden Sea and not the Wash. The recoveries suggest a build up in the Dutch Wadden Sea in spring but some birds from the Severn do go to the Wash, mainly to Terrington on the south Wash where there are very large numbers in March. By April most of these birds have moved on, probably to the Wadden Sea. The birds which go straight to the Wadden Sea appear to congregate in the Dutch Wadden Sea (this fits with the visible migration at Scheveningen - Jansen, 1979), moving on to the German Wadden Sea in April. The juveniles seem to follow the same pattern as the adults.

A few wintering birds stay on the Severn in spring as the ringing recoveries on the north shore show. All these recoveries were _C. a. alpina_, even though only about two percent of the 4,000 Dunlin present on the north shore in spring belong to this race (P. N. Ferns, pers. comm.). Three recoveries on the north shore of the Severn on 21 August, however, were either _C. a. schinzii_ or _C. a. schinzii/arctica_; two of them were in moult but the third was in full summer plumage. This suggests that there are not only _C. a. alpina_ wintering on the south shore of the Severn; the sexed samples suggest that a few _C. a. schinzii_ winter on the Severn, but they must comprise much less than five percent of the population.

CHAPTER 6

SEASONAL WEIGHT CHANGES IN DUNLIN

6.1 Introduction

In recent years several studies have shown that waders wintering in Europe go through an annual weight cycle (eg Morecambe Bay - Prater, 1975, Dare, 1977, Clapham, 1978; Wash - Branson, 1979; Wadden Sea - Smit & Wolff, 1981), whereas waders wintering in equatorial regions maintain stable weights throughout the winter (eg Pearson et al., 1970; Elliot et al., 1976; Dick & Pienkowski, 1979). There has been much speculation about the reasons for midwinter peak weights in temperate areas. Two main hypotheses have been put forward:

1. Birds put on weight in autumn and early winter, when feeding conditions are good, and subsequently lose weight in January, February and March when feeding conditions are poor.
2. Waders maintain a fat reserve in relation to the likelihood of them encountering severe weather and, as this likelihood is reduced in late winter, so they reduce the fat reserve they carry.

This chapter aims to assess these two hypotheses and suggests how Dunlin cope with the problems encountered during winter time.

6.2 Methods

Samples of Dunlin were caught in each winter of the study using both cannon netting and mist netting techniques. As far as possible birds caught by both methods were treated in the same manner after capture. Whenever birds had to be kept for any length of time they were always held in keeping cages as described in Chapter 1. Whenever possible all birds were both weighed and measured but when this was not the case, only random samples were used for the analysis of weight patterns. Weights of birds were measured to the nearest 0.5 g using a 100 g Pesola balance. The time of capture was recorded as were the times at the start and end of each field sheet which contained data on 25 birds. Later this information was used to calculate the length of time taken to finish the sheet. For each sheet a computer programme was run to calculate the length of time each bird was kept between capture and weighing. To assess weight loss during this period I weighed a sample of 10 birds just after capture and again after 5.2 hours. The average weight loss was 0.75 g per hour. Weight loss has been shown to be highest in the first hour after capture. The vast majority of birds were weighed between two and four hours after capture; over this range 0.75 g per hour gives a similar value to those obtained by Pienkowski _et al._ (1979) and Davidson (1981) but is higher than found by O.A.G. Munster (1976). All weights were therefore corrected for the length of time the birds were kept before processing (which was measured to the nearest 0.1 hours) by the following equation:

$$\text{Corrected Weight} = \text{Weight at processing} + (0.75 \times \text{time after capture})$$

Birds of different body size have different lean weights. I have shown that the sex ratio varies between the different bays and also within a given bay through the winter. For this reason direct comparison of the weight of birds caught at different sites and different times of the year can not be made. There are no published formulae for estimating the lean weight of Dunlin on the Severn in winter so I have used the equation produced by Davidson (1981) for the Tees to calculate the lean weight of each individual bird. Wintering birds on the Tees and Severn are predominantly of the race _C. a. alpina_. The numbers of _C. a. schinzii_ present on the Severn in winter are too small to seriously affect the lean weights of samples. The equation which is given in Davidson (1983) gives inaccurate results as it is given to only two decimal places and four decimal places are needed to give an accurate prediction. The more precise 1981 equation gave average lean weights for the Severn of 51 g. This is, however, three grams heavier than the lean weight for Dunlin wintering on the Severn suggested by Worrall (1981) on the basis of carcass analysis. I have therefore computed an estimated fat level for each individual by using the equation:

$$\text{estimated fat} = \text{weight} - (\text{computed lean weight} - 3\text{ g})$$

Although individual fat levels were calculated, only information on samples of birds caught were used, as the computation of lean weight for individual birds is not reliable (Davidson, 1981). As expected the variance was lower for fat levels than for weight levels, the reduction being about a third in most cases.

Although lean weights of adults and juveniles were computed using different equations, three grams were removed from the computed lean weights in both cases, as there are no published data for lean weights of juveniles on the Severn and it is likely that they vary in a similar way to the adults. Due to the uncertainty as to lean weights of Dunlin on the Severn it was not considered justifiable to compute lipid indices; therefore in the analyses just the "estimated fat levels" (in grams) were used.

6.3 Results

6.3.1 Mean weights through the winter on the south shore

Figure 6.1 gives mean weights of birds caught on the south shore of the Severn (all winters and all sites combined). It can be seen that peak weights for adults occur in the second half of January and not in December as on the Wash (Branson, 1979) and thus in December and the first half of January adults on the Severn are lighter than those on the Wash, while from late January onwards they are heavier. It must be remembered, however, that these data are not exactly comparable as weights of birds on the Wash are not corrected for time after capture. Real Wash weights are probably, therefore, one or two grams higher than those given in Branson (1979).

The pattern for juveniles on the Wash follows closely that for adults, but juveniles are approximately one gram lighter. The situation on the Severn appears rather different: juveniles and adults have roughly similar weights through the first half of December, after which juveniles are lighter relative to adults. Juveniles gain little or no weight between early December and early January, and then decline steadily until they leave in March.

There are considerable problems with the use of crude weight data (see above). Figure 6.2 plots the estimated average weight of fat carried by Dunlin through the winter and indicates that, among adults, there might be a slightly stronger peak in late January than suggested by crude weight data. When juveniles are compared to

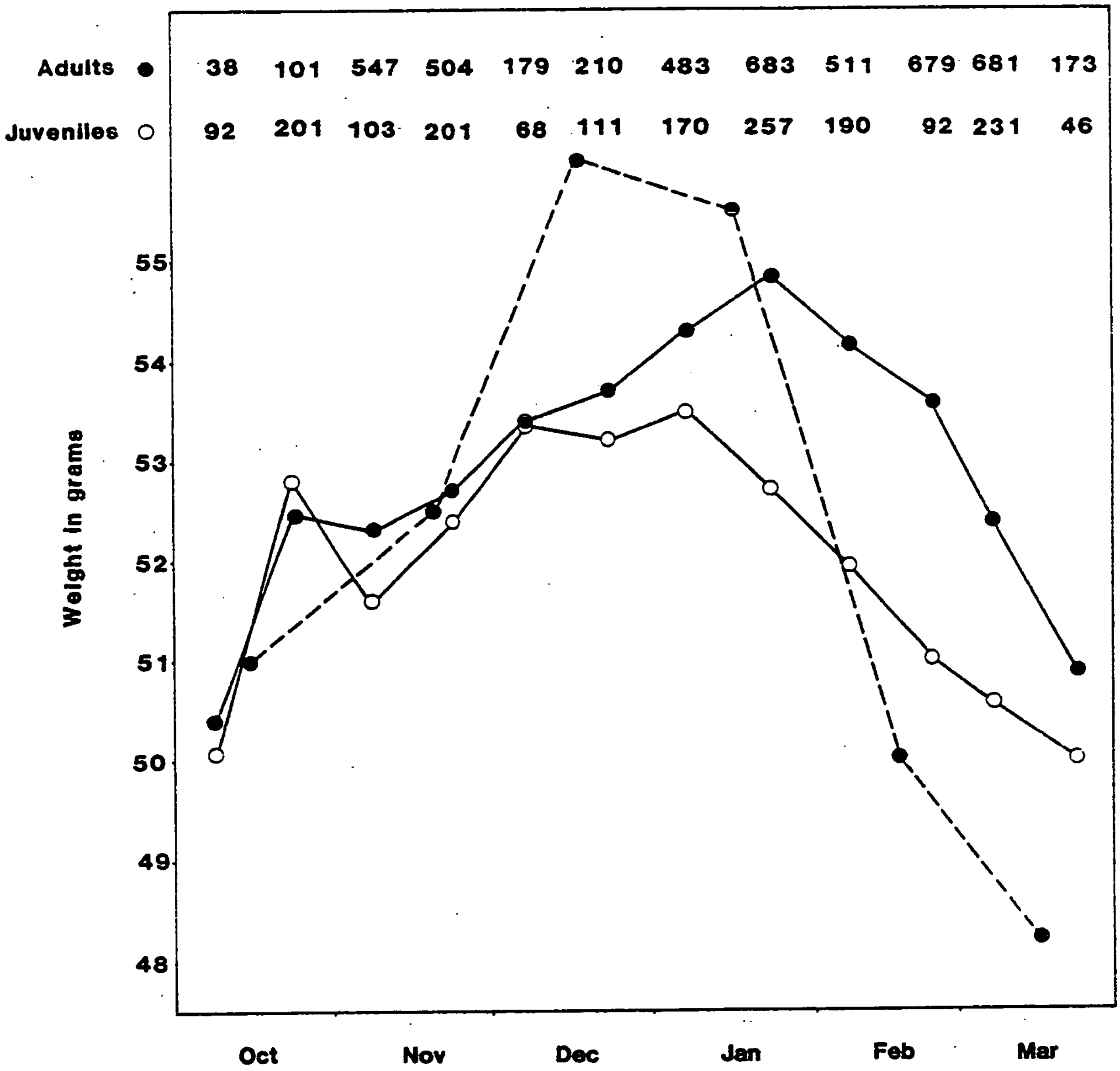

FIGURE 6.1

Mean weights of Dunlin caught on the south shore of the Severn between 1977 and 1981

(sample sizes given above;
dashed line indicates mean weights of adults on the Wash)

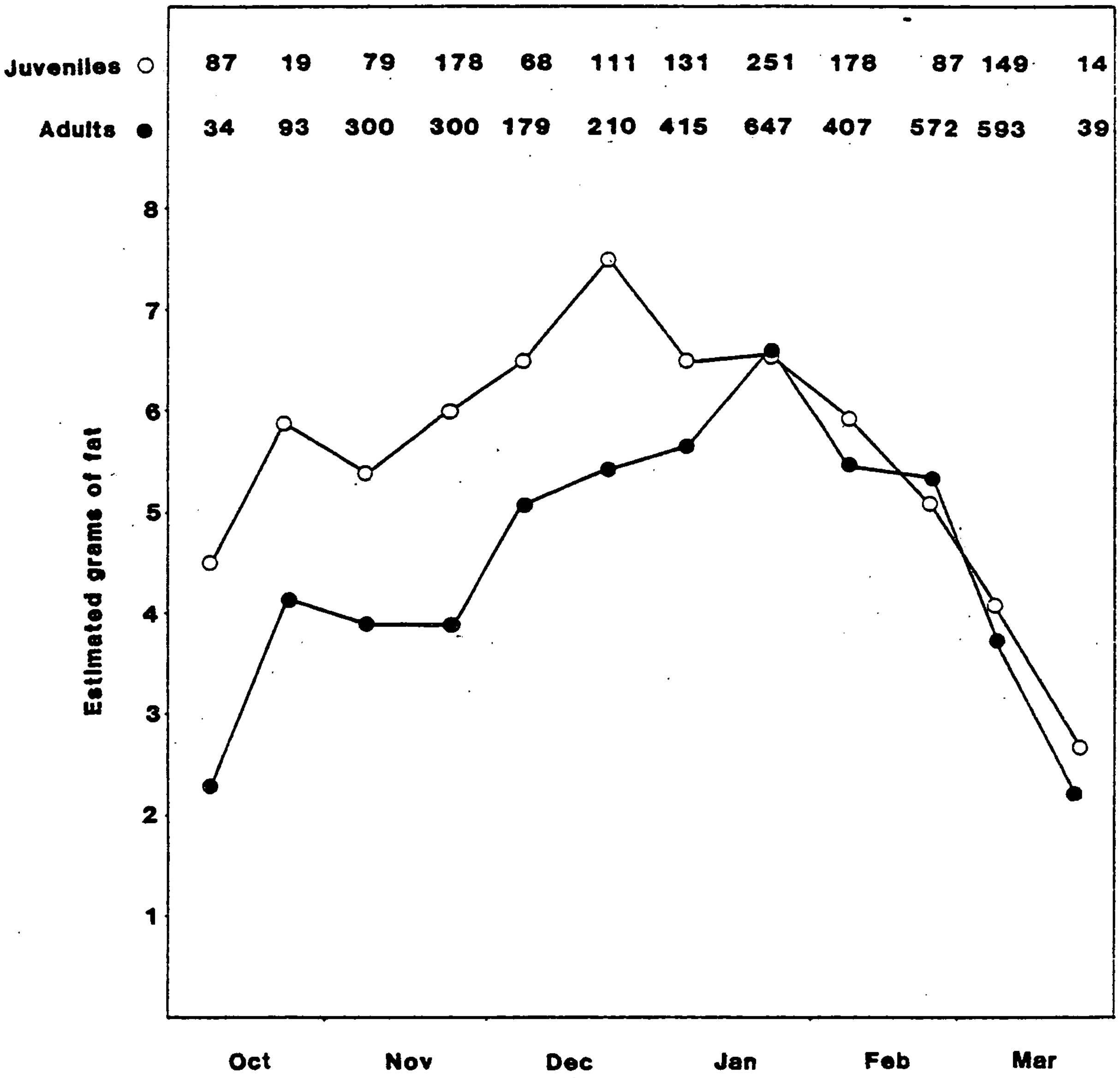

FIGURE 6.2

Fat levels of Dunlin caught on the south shore of the Severn between 1977 and 1981

(sample sizes are given above)

adults a different pattern to that found with crude weight data emerges. It appears that juveniles carry more fat than adults until late January but then follow the same pattern as adults until the end of the winter.

6.3.2 Weights of adult Dunlin

Figures 6.1 and 6.2 have shown the crude pattern throughout the winter, but there were very noticeable differences both between bays and the years of the study. Figures 6.3 to 6.6 give fat levels of adults, for all catches on the south shore of the Severn during the study (samples of less than 10 have been excluded). It is apparent from the three main years of the study that fat levels of birds at Clevedon tended to be lower than those on other sites. This was especially true in the mid winter period. I believe the pattern of weight change shown in figures 6.4 to 6.6 shows the following points:

1. Dunlin at Clevedon tend to have lower fat levels in mid winter than those in other bays.
2. Dunlin in Sand Bay, Weston Bay and at Berrow maintain similar fat levels in any one year (with the possible exception of 1979/80).
3. There are large differences in the fat levels carried at any given date in different years.
4. There are often large differences in the fat levels carried within a few days, especially in late winter.

It was hoped to be able to gain a clear understanding of weight variations through the winter in a given bay both through a single

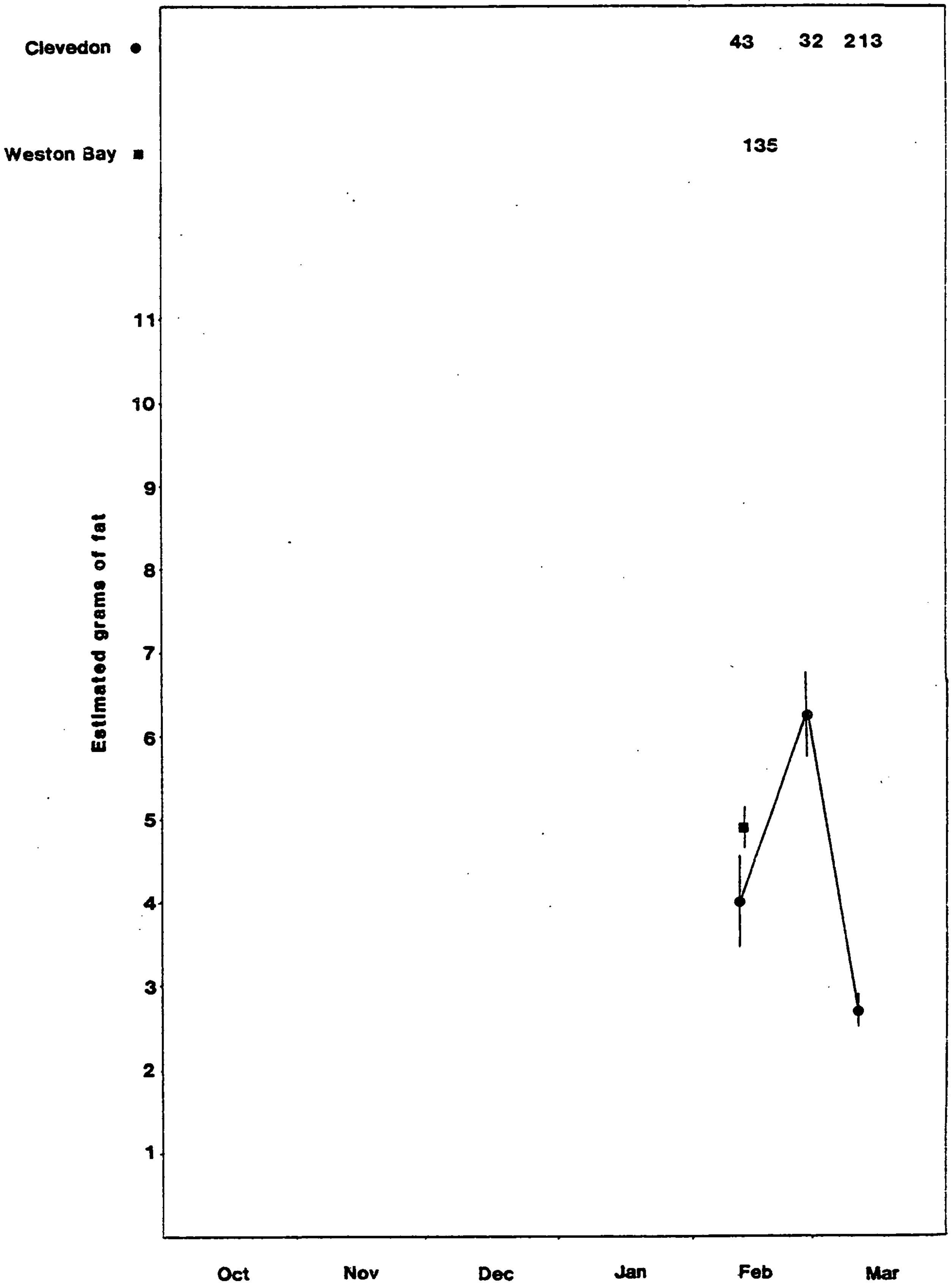

FIGURE 6.3

Fat levels of samples of Dunlin caught in the 1977/78 winter (mean and standard error are given)

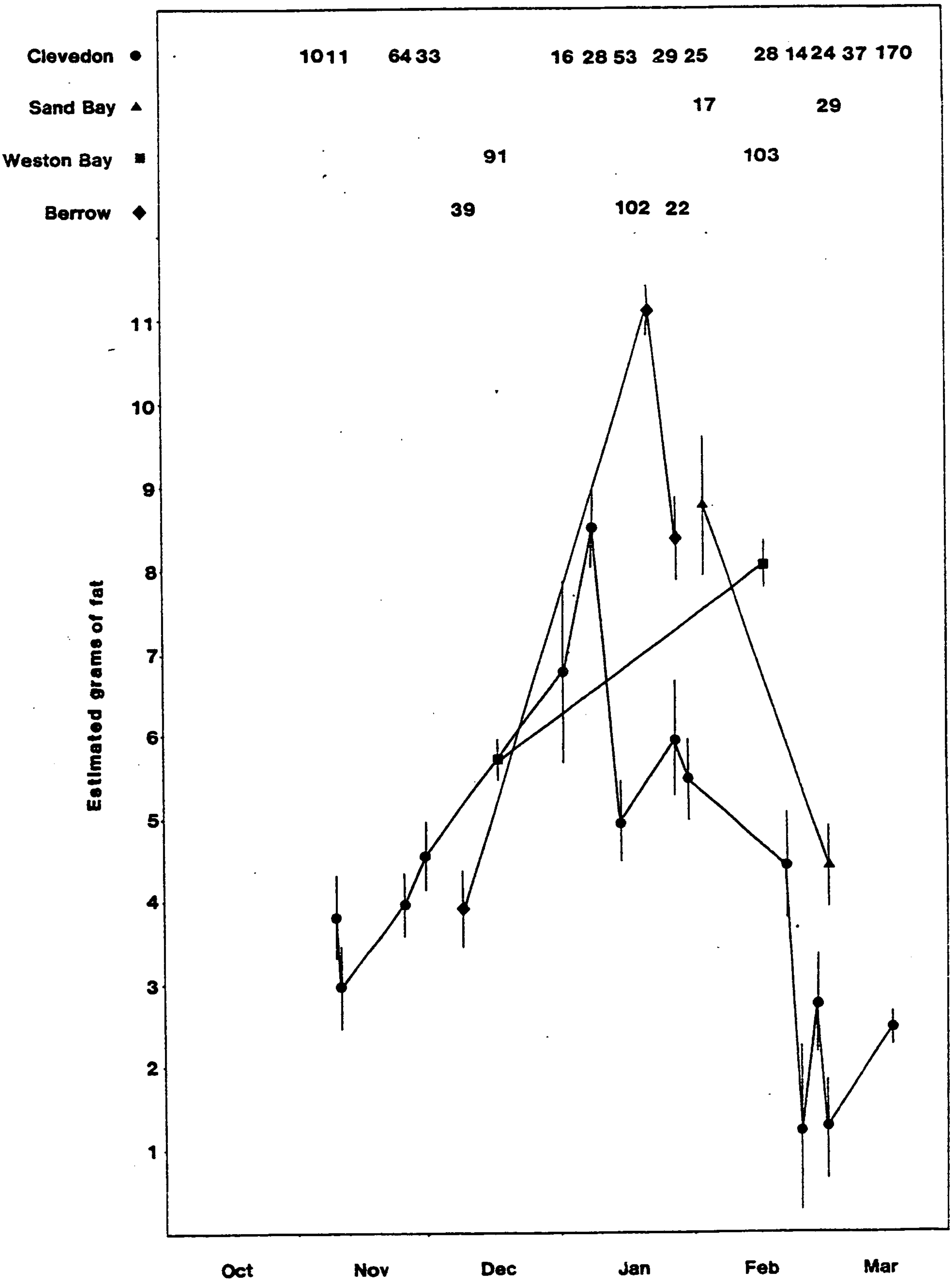

FIGURE 6.4

Fat levels of samples of Dunlin caught in the 1978/79 winter (mean and standard error are given)

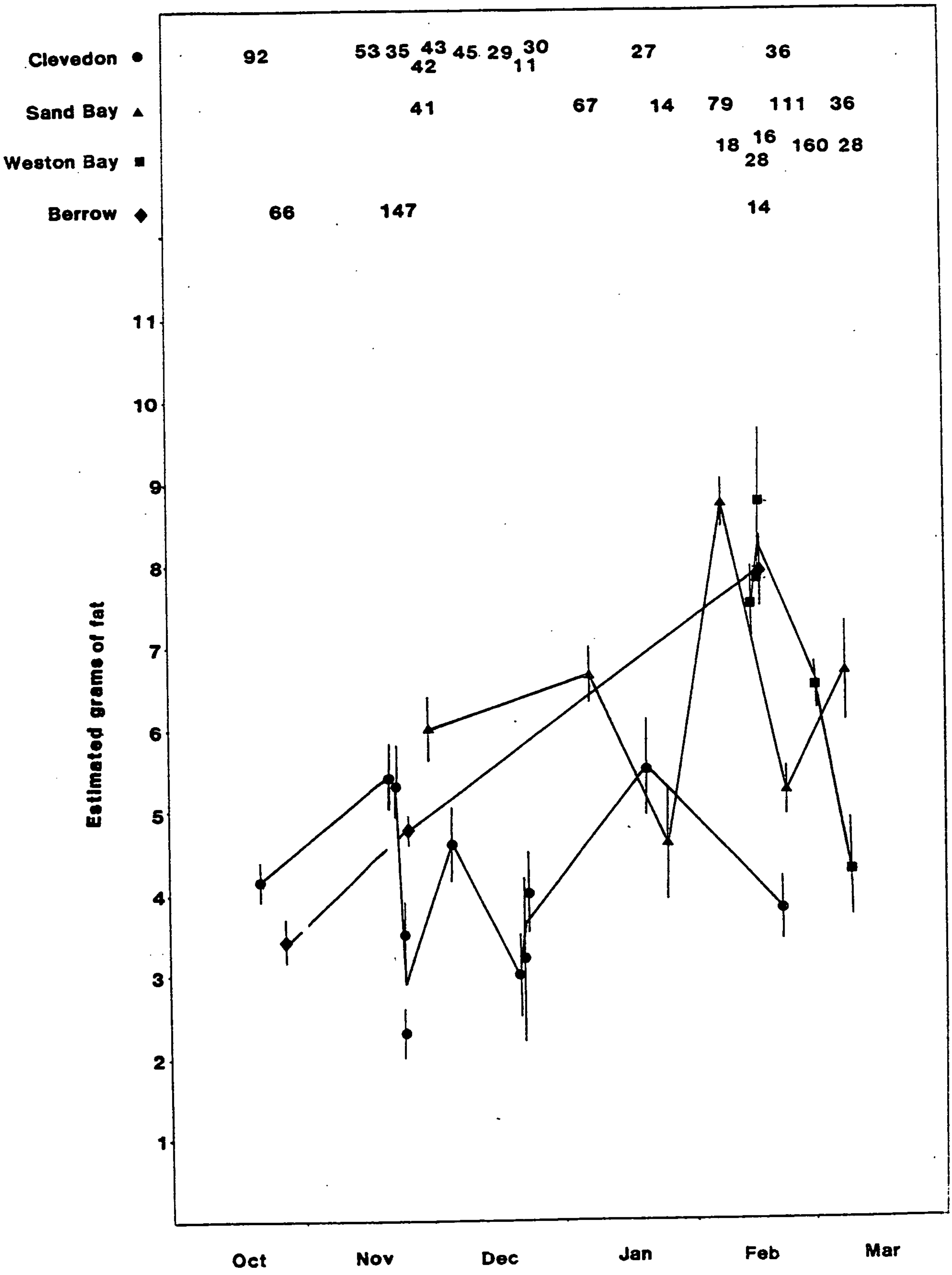

FIGURE 6.5

Fat levels of samples of Dunlin caught in the 1979/80 winter

(mean and standard error are given; when two catches are made at the same site on one day the line is drawn through the mean of the two points)

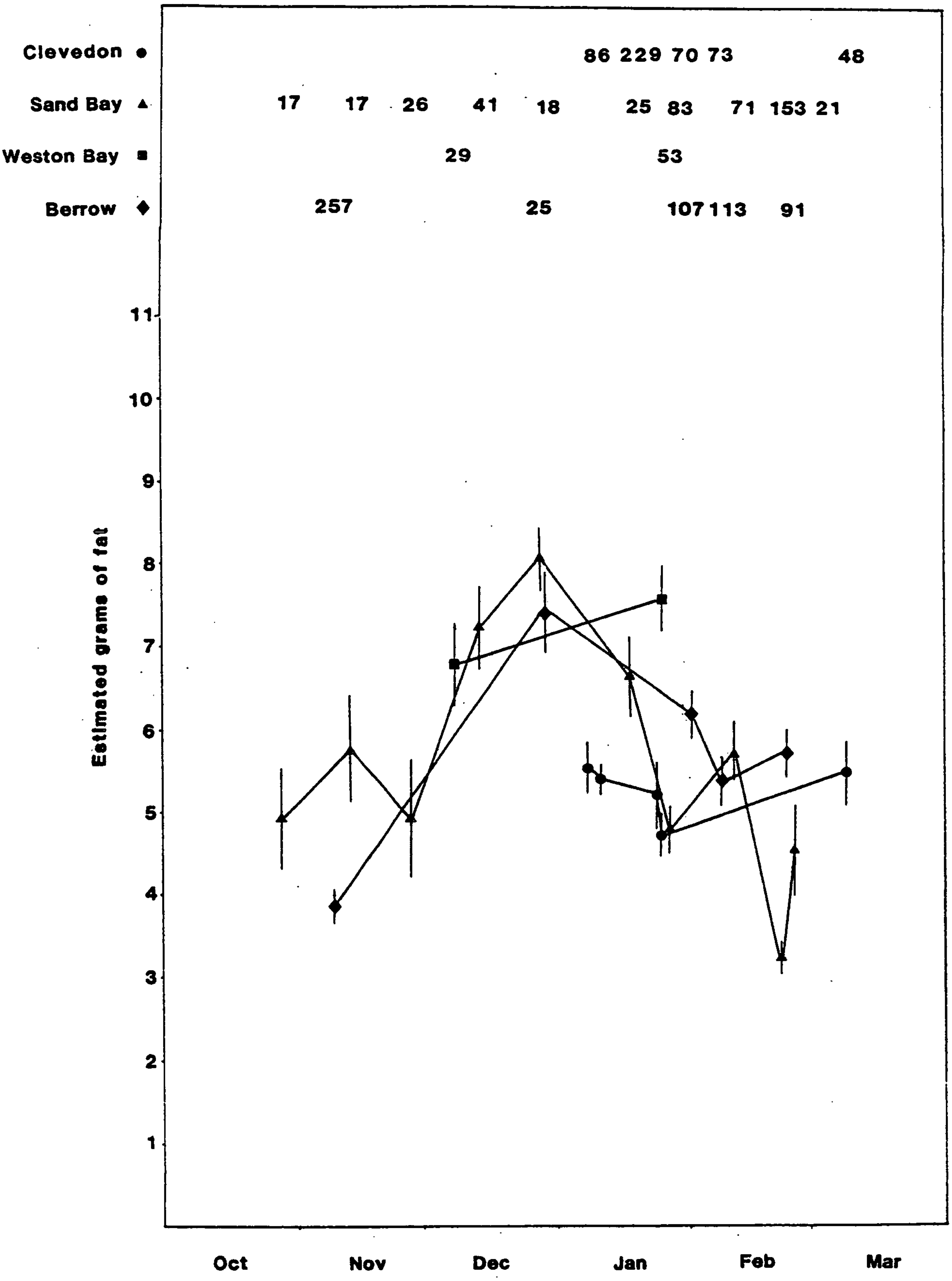

FIGURE 6.6

Fat levels of samples of Dunlin caught in the 1980/81 winter

(mean and standard error are given)

winter and between winters by looking at retraps. I quickly realised that when a bird was caught twice in the space of a few days there was a considerable weight loss due to stress caused by the first capture. When the data for all retraps within 40 days were plotted there was a significant negative correlation between the days between the capture and the number of grams of weight loss. There was no such correlation when retraps of birds with a time interval of between 10 and 40 days were plotted. It was clear from the data that the amount of weight lost due to capture varied substantially between catches; this was not related to the length of time birds were held after capture nor to the method of capture. Birds that were caught twice within three days were about three grams lighter on second capture than on first capture, but they had regained their original weight within 10 days. To remove this affect only retraps of birds more than 10 days apart were plotted. Figures 6.7 to 6.9 plot retraps of adults at Clevedon in the different years.

The retraps of birds at Clevedon in 1978/79 (figure 6.7) show three features:

1) birds caught from January onwards tended to show a decline in weight;

2) birds caught before mid December and in late winter were at similar weights on both occasions; and

3) although there are only a few retraps in January and early February of birds caught in mid December, five increased and only one showed a decline.

The data for retraps at Clevedon in 1979/80 (figure 6.8) although sparse suggest that birds tended to lose weight through the

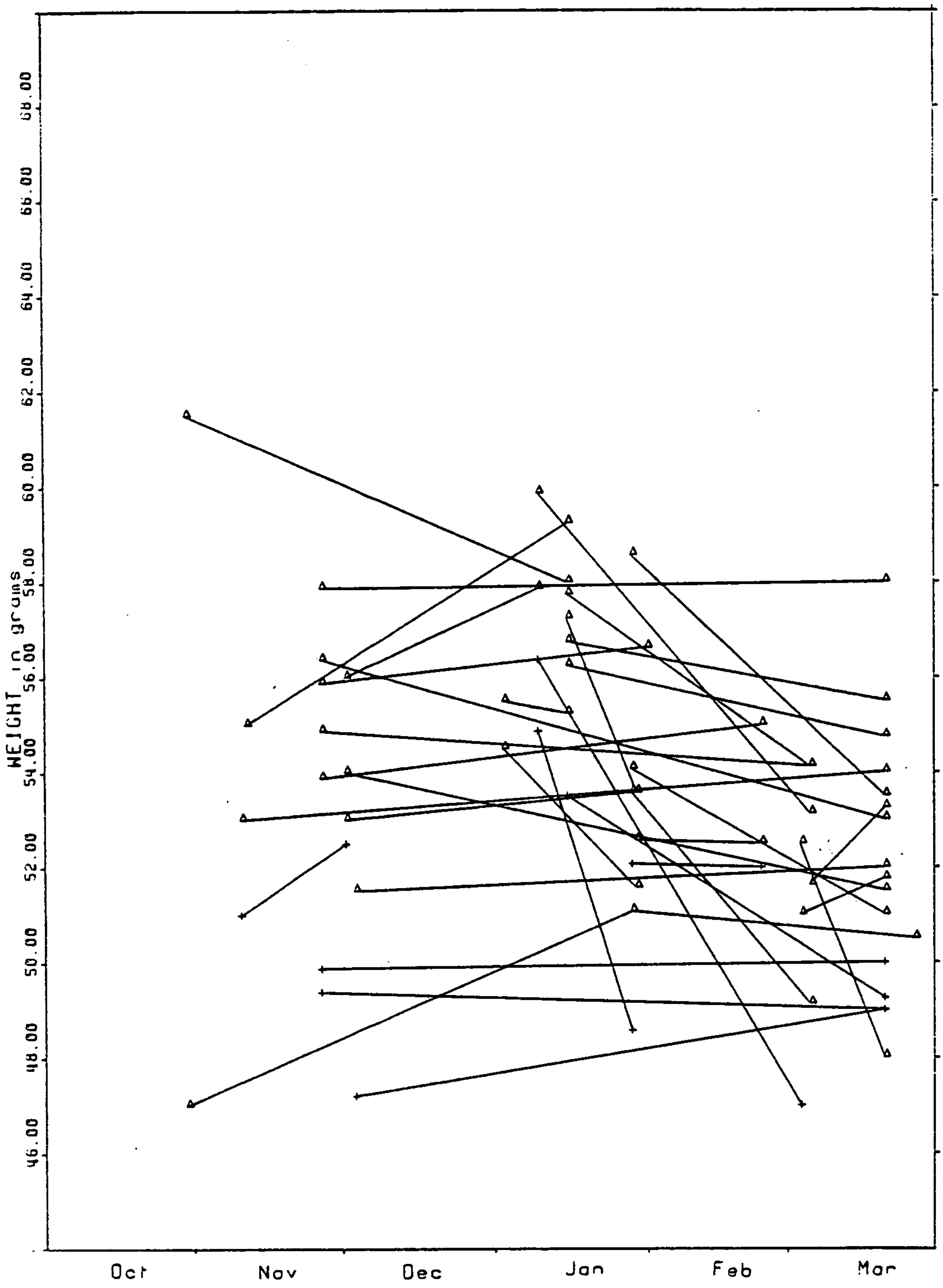

FIGURE 6.7

Weights of adult Dunlin caught twice in the 1978/79 winter

at Clevedon

(birds caught twice within 10 days are omitted;
▲ = females, + = males)

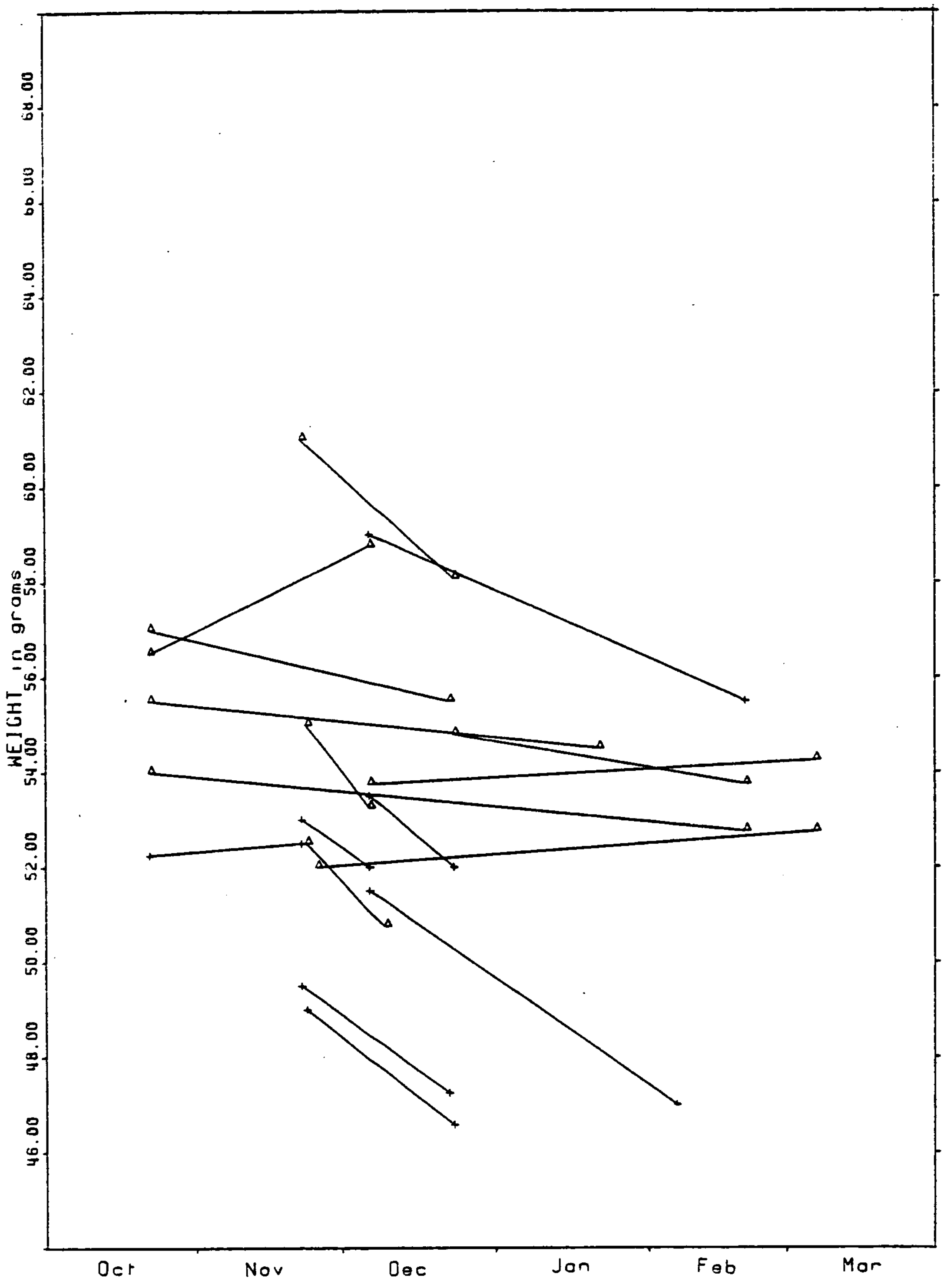

FIGURE 6.8

Weights of adult Dunlin caught twice in the 1979/80 winter at Clevedon

(birds caught twice within 10 days are omitted;
△ = females, + = males)

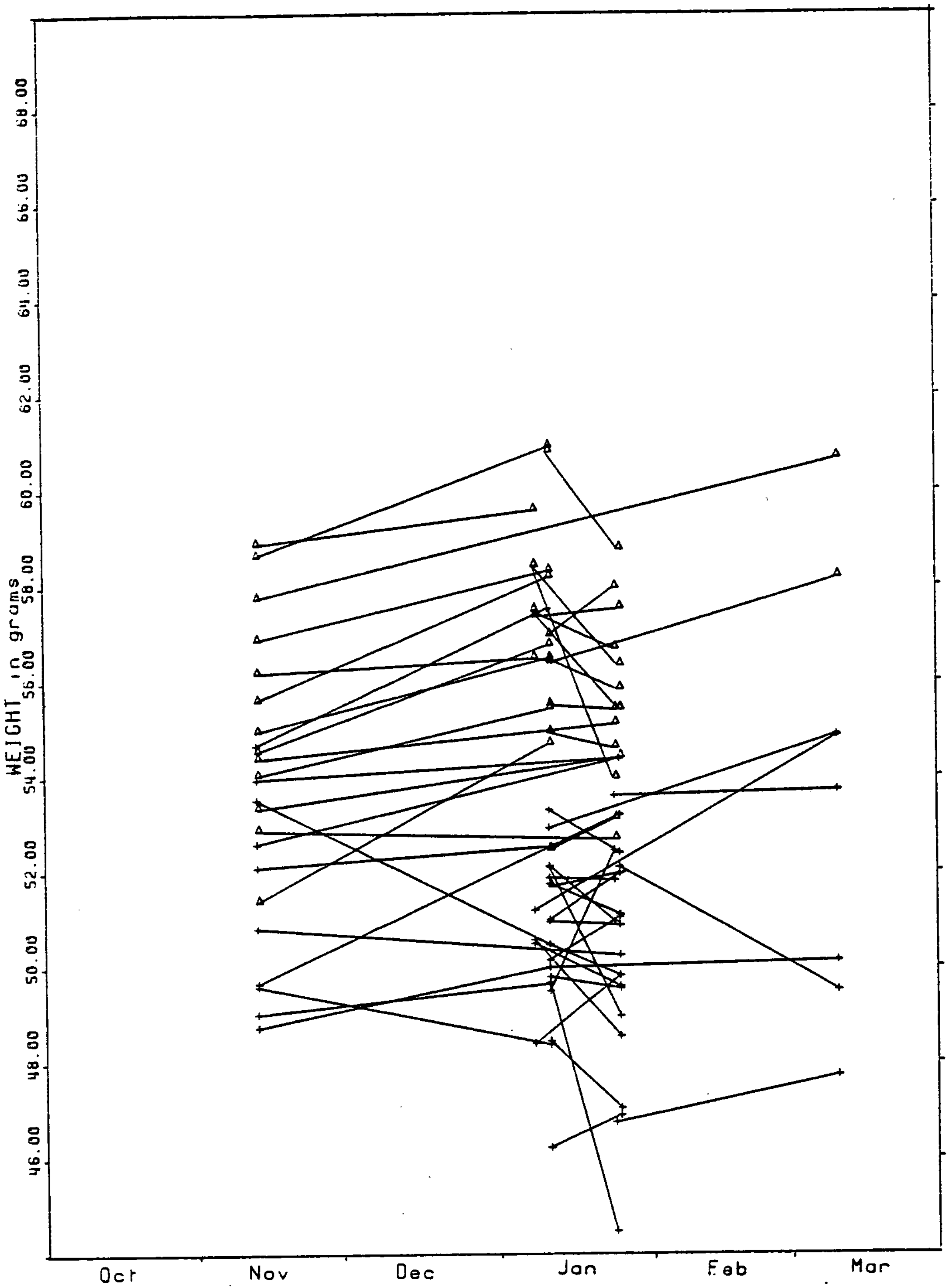

FIGURE 6.9

Weights of adult Dunlin caught twice in the 1980/81 winter at Clevedon

(birds caught twice within 10 days are omitted; △ = females, + = males) winter. There were only four birds that put on weight and thirteen that lost weight. These data in conjunction with the graphs of mean weights throughout the winter (figure 6.5) suggest that there was no mid winter peak in weight at Clevedon in that winter.

In 1980/81 there were good numbers of birds caught at Clevedon on 11 November and again in January, these tended to show an increase in weight (figure 6.9). There are no obvious differences between males and females.

Figures 6.10 and 6.11 plot similar data for Sand and Weston Bays. Figure 6.10 suggests that birds caught in late November 1979 and again at the end of the winter were at similar weights on both occasions. Birds caught twice in late winter, however, showed a very steep decline in weight. Figure 6.11 suggests a slight decline in weights from November to February; unfortunately there are no retraps in early winter when mean fat levels were increasing. There is considerable variation in the weights of individual retraps (figures 6.7 to 6.11), but most follow a similar pattern to mean fat levels.

6.3.3 Weights of juvenile Dunlin through the winter

Figure 6.12 plots the difference (juvenile - adult) in mean fat levels between adults and juveniles for all samples in which more than 10 adults and 10 juveniles were weighed. There is a significant decline in the difference in fat levels through the winter ($N = 35$, $r = -0.666$, $p<0.001$). This pattern would be expected from the data presented in figure 6.2 but it does show that there is considerable consistency between different samples. There

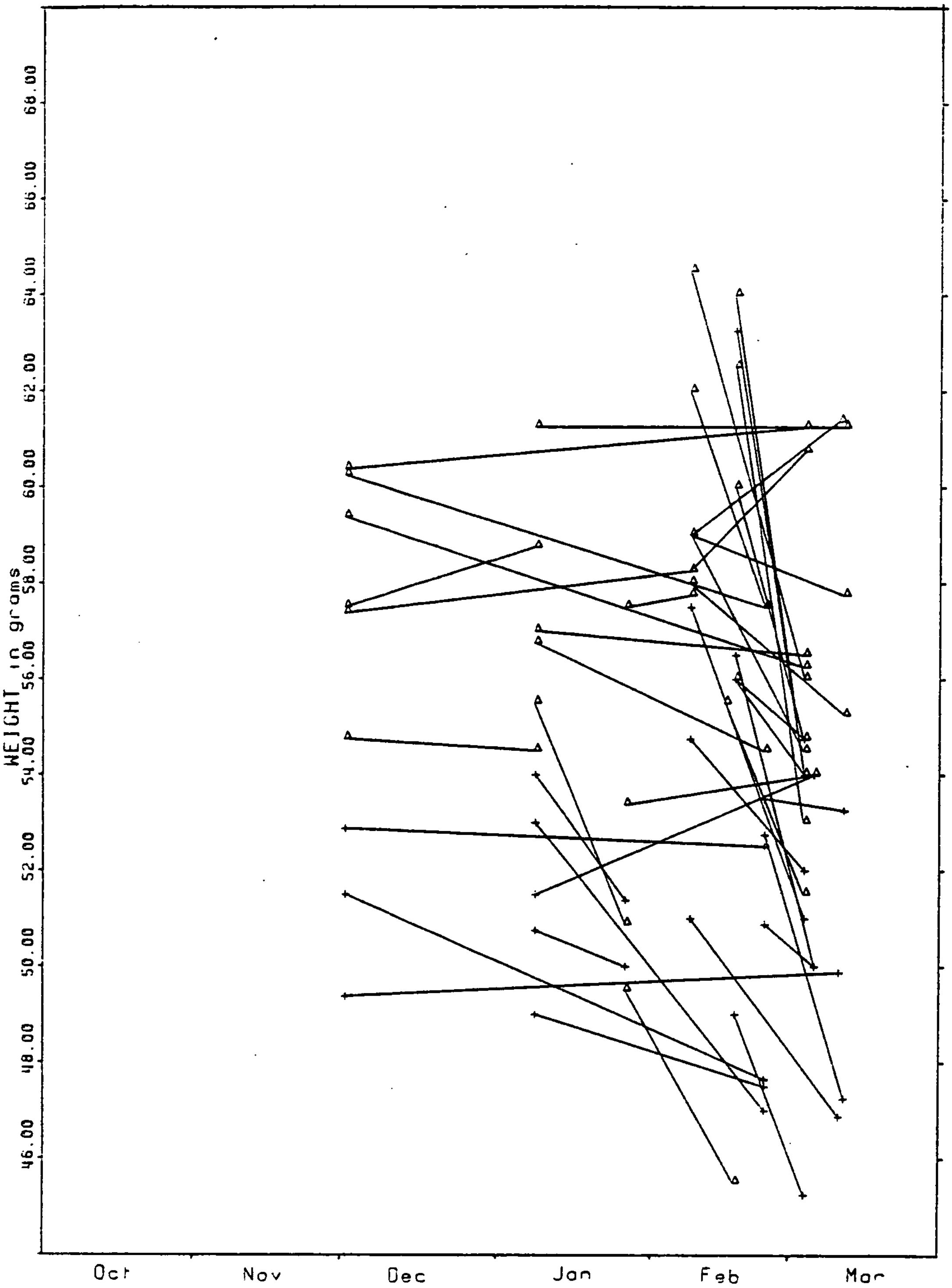

FIGURE 6.10

Weights of adult Dunlin caught twice in the 1979/80 winter in Sand and Weston Bays

(birds caught twice within 10 days are omitted;

△ = females, + = males)

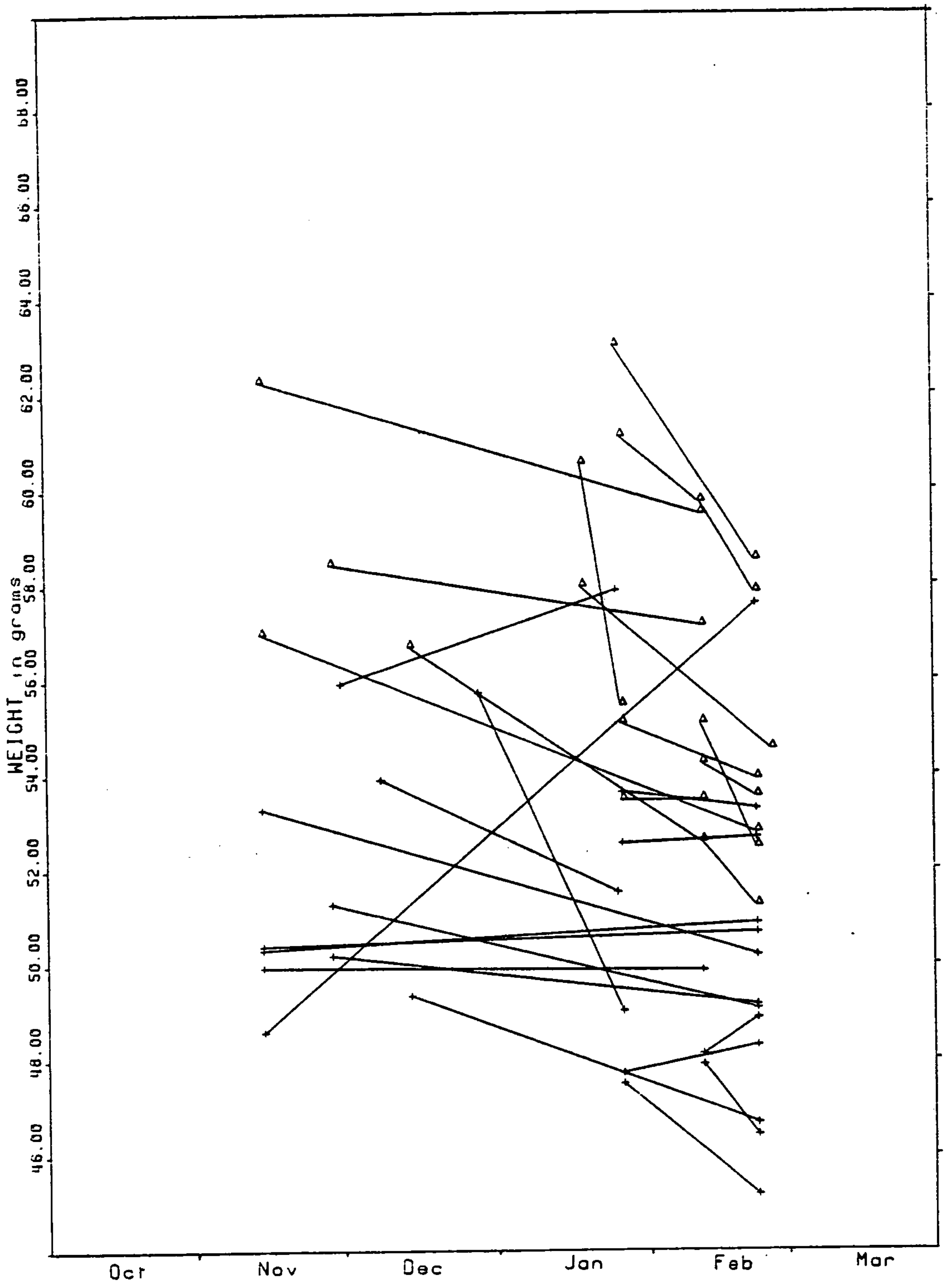

FIGURE 6.11

Weights of adult Dunlin caught twice in the 1980/81 winter in Sand and Weston Bays

(birds caught twice within 10 days are omitted;

△ = females, + = males)

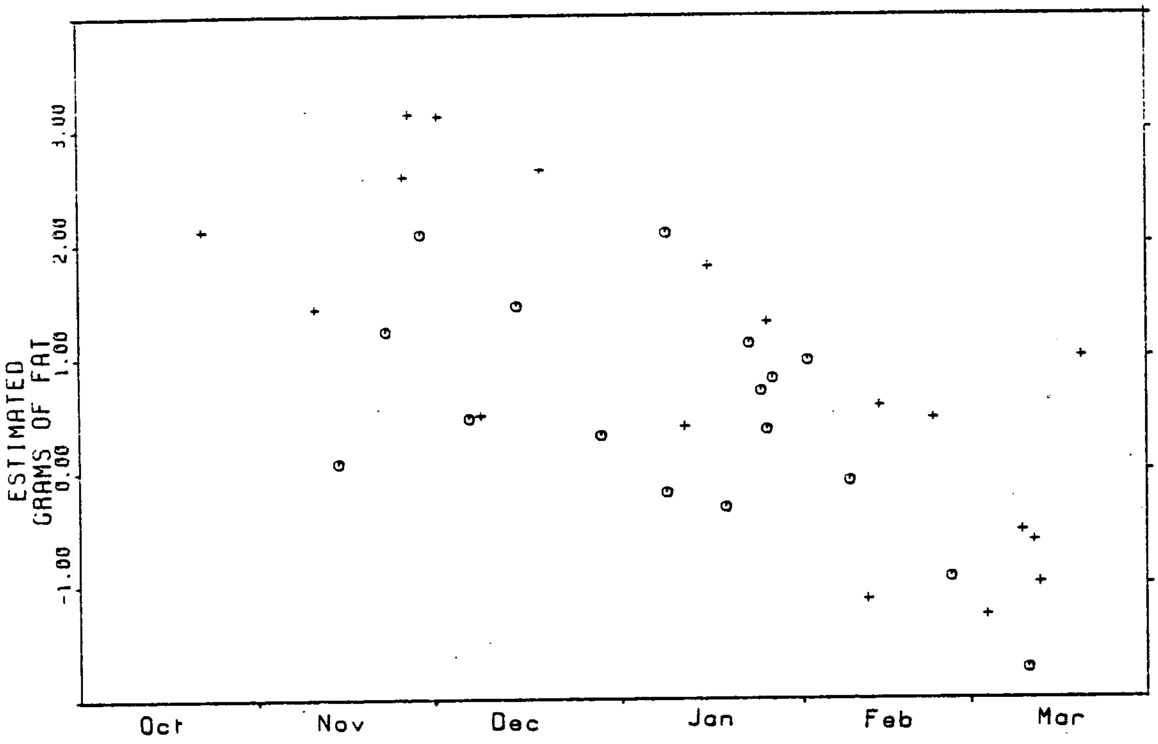

FIGURE 6.12

Difference in fat levels between adults and juveniles

in different catches throughout the winter

(samples of less than 10 birds of each age are excluded;
+ = morning tides; o = evening tides)

is an apparent anomaly between the late winter data given in figures 6.2 and 6.12. Figure 6.2 suggests that juveniles have slightly higher fat levels in early March but, figure 6.12 shows adults as heavier than juveniles in all five samples. The difference between the two data sets arises because of two large samples of adults caught at Clevedon in 1978 (over 300 birds in all) which had very low fat levels (there were less than 10 juveniles in each of these catches) which reduced the mean value of adults to below that for juveniles. This anomaly shows how misleading weight graphs can be when the mean of all birds caught over a number of years is plotted (eg Branson, 1979, figures 6.1 and 6.2).

Juveniles in morning catches tended to be heavier in relation to adults than juveniles in evening catches, but the difference was not significant.

Figure 6.13 plots retraps of juvenile Dunlin within one winter at Clevedon and figure 6.14 plots similar data for the other bays combined. The data follow broadly similar patterns to that for adults although there is a tendency for individuals to be losing weight from an earlier point in the winter, there also appears to be greater variation between individual juveniles than adults.

6.3.4 Differences between the weights of male and female Dunlin

Figure 6.15 plots the difference (males - females) between mean fat levels for males and females for samples in which more than ten birds of each sex were weighed; there is no significant change in the relationship through the winter, although there appears to be greater variability between the two groups in any given catch in

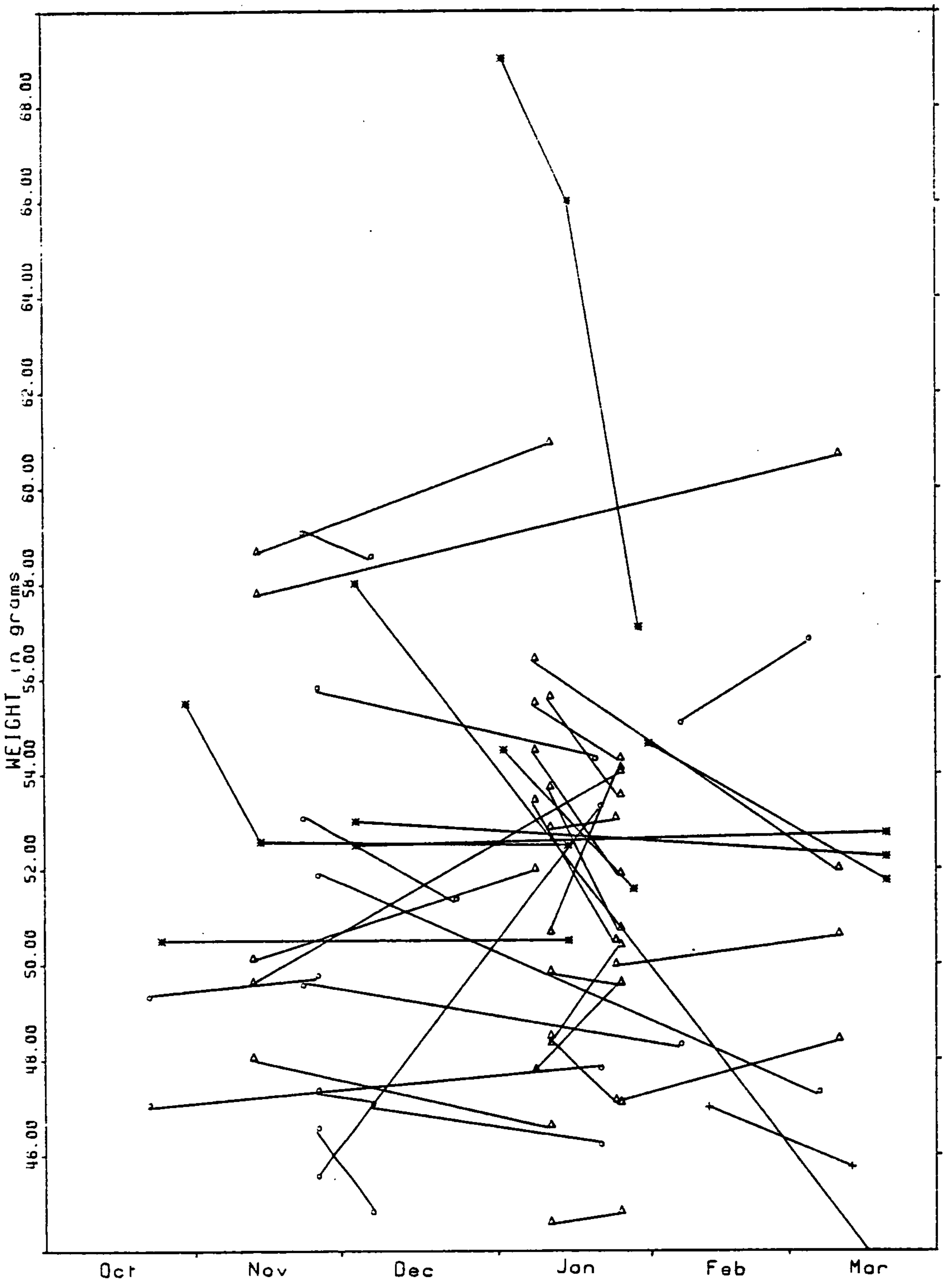

FIGURE 6.13

Weights of juvenile Dunlin caught twice in one winter at Clevedon

(+ = 1977/78; * = 1978/79; o = 1979/80; △ = 1980/81)

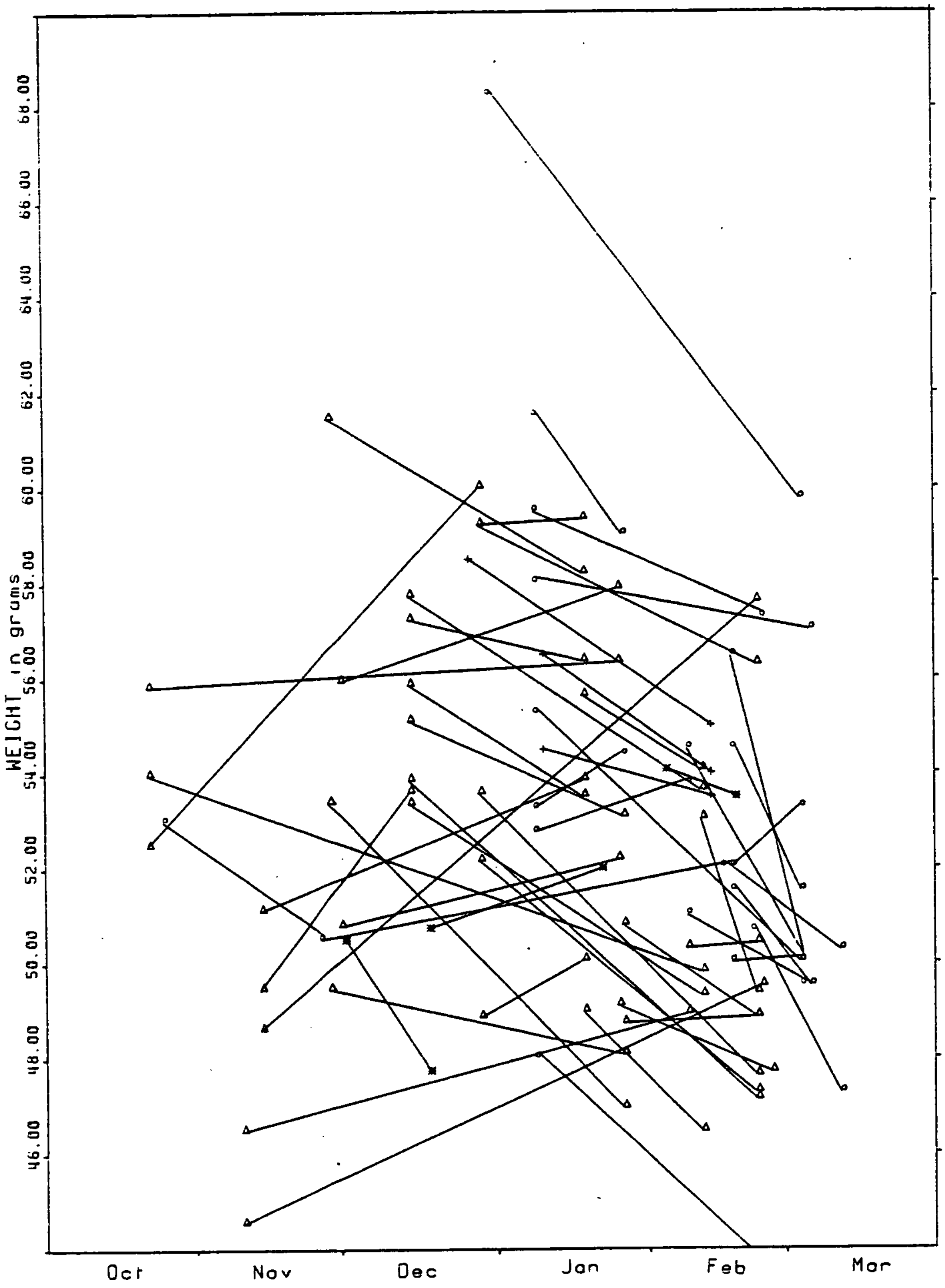

FIGURE 6.14

Weights of juvenile Dunlin caught twice in one winter in the southern bays (Sand Bay; Weston Bay; Berrow)

(+ = 1977/78; * = 1978/79; o = 1979/80; ▲ = 1980/81)

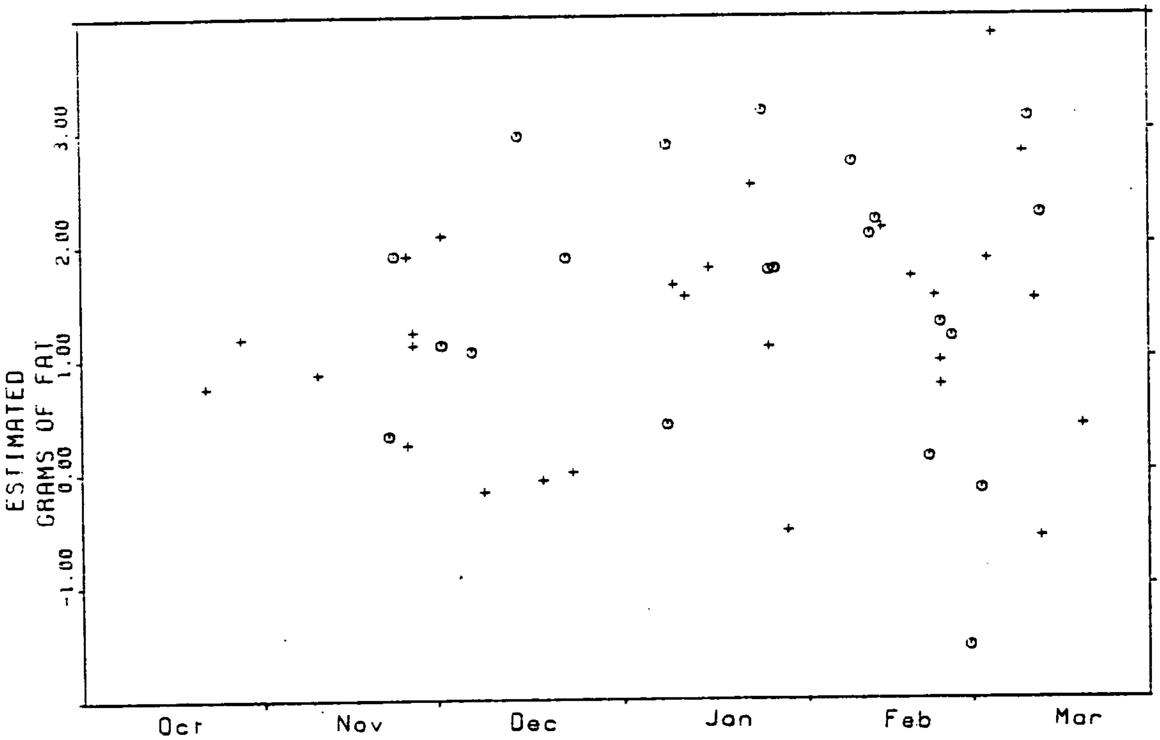

FIGURE 6.15

Difference in fat levels between male and female adult Dunlin in different catches throughout the winter

(samples of less than ten birds of each sex are excluded; + = morning tides; o = evening tides) late winter than early winter. There were three occasions on which samples were caught on both morning and evening tides at one site; all three of these were at Clevedon. The data are given in table 6.1. A two way analysis of variance was used to assess whether fat levels in males and females varied in different ways between morning and evening tides. It can be seen that only one of the data sets was significant on its own but when the three tests were combined (using the method shown by Sokal and Rohlf, 1981) the data were found to be significant at the 0.01 level (Chi-squared = 17.128).

6.3.5 Weights of Dunlin during severe weather

During the winter of 1981/82, I obtained some data on weight levels of waders in eastern Scotland during severe weather, which sheds light on the weights of Dunlin found on the Severn. A preliminary report of my findings was submitted to the Nature Conservancy Council and appears in appendix 7. Figure 6.16 reproduces figure 5 from appendix 7 with the addition of one data point obtained on 3 February 1983. The results are contained in the appendix but a reappraisal of this work in the light of new data will form a part of the discussion.

During this same spell of severe weather a sample of Dunlin was caught on the Wash by P. N. Watts who kindly made the data available (table 6.2). A sign test was carried out to see if these weights were significantly higher than those normally found on the Wash at this time of year as standard deviations are not available for the weight data given in Branson (1979) The weights were found to be significantly higher than predicted ($z = 3.71$, $p<0.001$). These

TABLE 6.1

Fat levels of male and female Dunlin in catches made on successive tides at Clevedon

Date	Time of catch	Males Mean fat (g)	N	Females Mean fat (g)	N
11 03 78	08	2.44	128	3.02	89
11 03 78	20	1.16	28	3.41	48
Interaction between sex and time f = 3.59, p = 0.059					
21 12 79	22	2.12	14	3.99	15
22 12 79	10	3.99	18	4.01	12
Interaction between sex and time f = 2.08, p = 0.15					
23 01 81	21	3.37	30	6.54	40
24 01 81	09	4.23	41	5.33	32
Interaction between sex and time f = 5.43, p = 0.021					

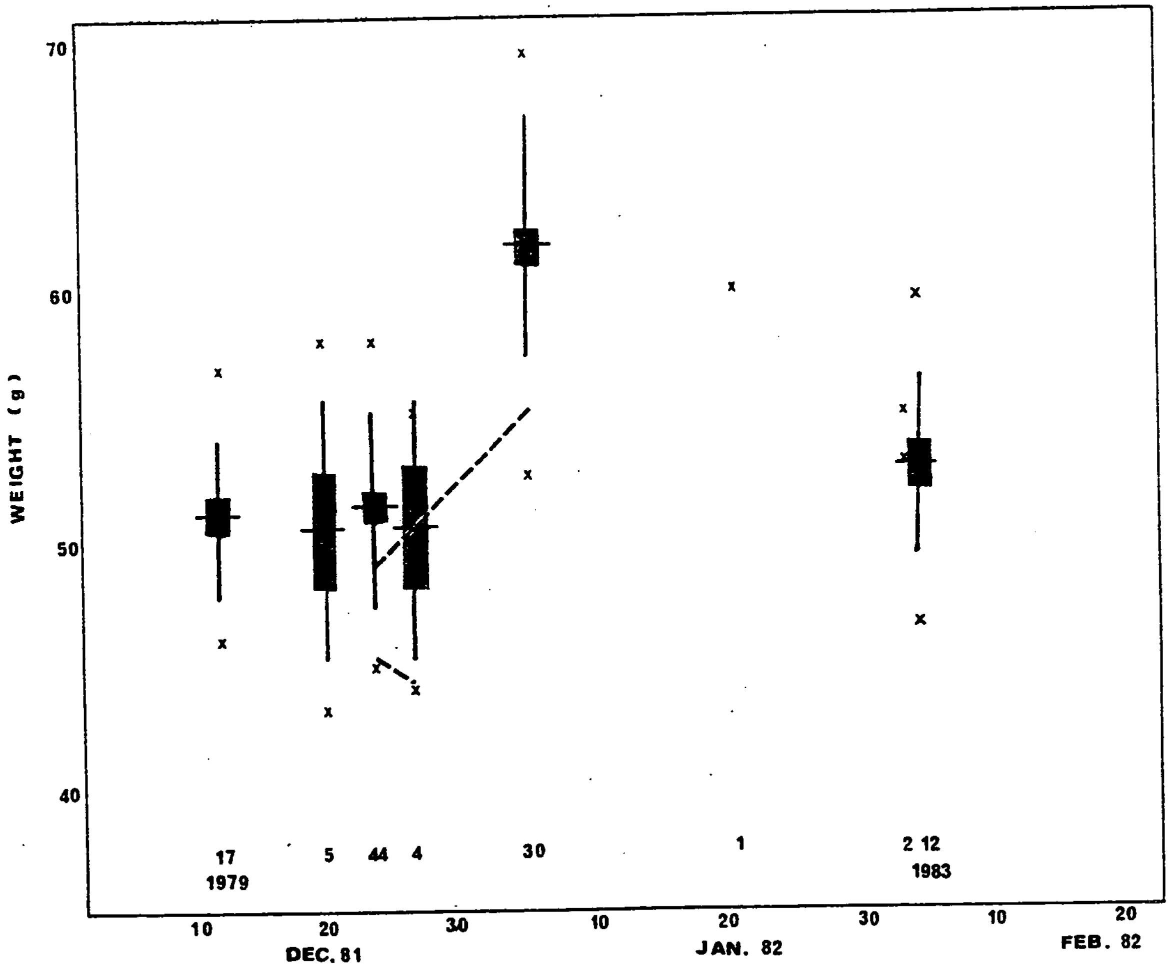

FIGURE 6.16

Weights of adult Dunlin on the Firth of Forth in the 1981/82 winter

(reproduced from appendix 7 with one additional point)

TABLE 6.2

Weights of waders caught at Benington, the Wash on 28/29 12 1981

Species		N	Mean	Range	Sd
DUNLIN					
	Adults	29	61.3	51.0-70.5	5.4
	Juveniles	9	64.4	58.5-71.5	3.7
GREY PLOVER					
	Adults	4	213.0	192.0-252.0	26.8
KNOT					
	Adult	1	173.0		
	Juveniles	3	158.0	142.0-182.0	21.2
REDSHANK					
	Adults	2	163.0	150.0-176.0	

birds were caught after three weeks of severe weather in which the temperature barely rose above freezing (P. N. Watts, pers. comm.). This shows that after three weeks of severe weather Dunlin on the Wash had increased their fat reserves well above "normal" winter levels; this was not the case for the Grey Plover Pluvialis squatarola caught at the same time.

6.4 Weights of Dunlin in captivity

6.4.1 Introduction and Methods

The first part of this chapter attempted to answer the question posed in the introduction, but it soon became clear that a study of weight variation of captive Dunlin could test the two hypotheses. The experiment planned to test three questions:

1. Do Dunlin have a seasonal weight cycle, even if food is superabundant?
2. Is this seasonal weight cycle temperature dependent?
3. Do birds wintering in different sites have different mid-winter peak weights if kept under the same environmental conditions?

I hoped to catch 10 birds known to winter on the west coast of Britain and 20 birds known to winter on the Wash for the experiment, but due to poor catching success at Wolferton (The Wash) in August 1981 only four birds of known wintering area were obtained.

All birds were obtained under licence by cannon netting whilst undergoing primary moult on the Wash. Those whose wintering site was not known were all birds that had been previously caught on the

Wash undergoing moult (all these birds were selected from one catch and were at approximately the same stage of moult). When first taken into captivity the birds were kept in a room in which the window had been covered with thin sacking and were fed on the same diet (table 6.3) as was provided throughout the winter, with the addition of large numbers of maggots sprinkled on the surface of the food pots to entice the birds to feed.

The birds were transported to Edinburgh in keeping boxes with food and water; a maximum of ten birds was put in each box. On arrival all birds were placed in the outside aviaries and left undisturbed, except when feeding, for the first nine days. After nine days all the birds were caught and weighed for the first time. For individual recognition each bird had two coloured temporary leg flags attached: one taped around the ring (Goodyer et al., 1979) and one on the unringed leg with a small piece of backing tape to prevent it adhering to the leg. Most of the flags remained attached for four or five months, but a few lasted only two or three weeks. The flags placed around the ring tended to last for longer than those with backing tape. Any flags that were lost were replaced on the next capture date.

The birds were housed in two outside aviaries, each initially holding ten birds; and one aviary inside, also holding ten birds (figure 6.17). The inside aviary measured 4 m by 4 m and each outdoor aviary was 10.7 m by 4 m. The floor of the inside aviary was covered with a thin layer of sand which was changed approximately once a month; water was provided in two shallow metal trays measuring 0.75 m by 0.75 m with sloping pieces of concrete on both the inside and outside so that birds could easily run in and

TABLE 6.3

Diet for Dunlin kept in captivity

MIX

Half litre	Dry mixture *
1	hardboiled egg
1 tablespoon	Cod-liver oil
5 drops	Abidec multi vitamins
Enough water to	make mixture moist, but not liquid

* Dry mixture

6 parts	Dog biscuit (puppy mash)
2 parts	Layers mash (poultry feed)
1 part	Wheatgerm
1 part	Ground dried meat
1 part	Mixed small seed

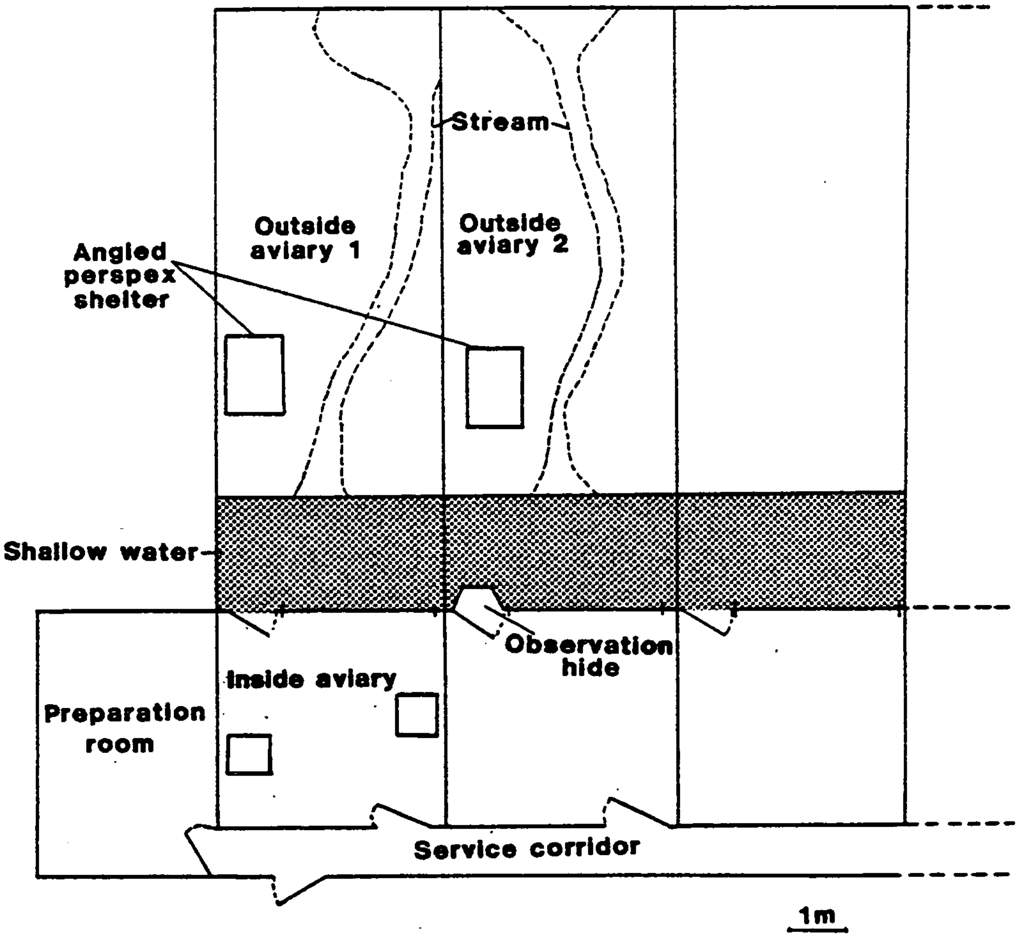

FIGURE 6.17

Plan of aviaries used to house captive Dunlin out of the water. The water was changed daily. The windows were half a metre off the floor and measured 3 m by 2 m; they were covered with soft stretch netting (manufactured by Mallardworth Limited) stretched taut about 100 mm from the glass, to prevent the birds from flying into the glass. Below the windows were some slatting shelves on which the birds regularly sat; they were then in visual as well as vocal contact with the birds in the outside aviaries.

The floor of the outside aviaries was covered with loose gravel which was occasionally raked. Each aviary had a large shallow pool of continually running water which drained through the gravel forming a small stream in each cage. Half inch (12 mm) chicken wire (1 m high) was placed around the outside of the aviaries and cemented to the concrete surround; above this a 200 mm wide continuous strip of hardboard was attached to try to stop weasels <u>Mustela nivalis</u> entering the cage. The inside of the aviaries above 1 m was lined with stretch netting which was stretched taut. This stopped the birds flying straight into the ends of the aviaries. Half of the roof of the aviary was covered with polythene sandwiched between two layers of chicken wire giving an area of the aviary which was sheltered from heavy rain.

The birds were fed at approximately 0900 hours each day on the diet given in table 6.3. Towards the end of the winter the meat portion of the diet was changed from dried meat to live maggots as these became easily obtainable. All maggots that were fed were fully grown larvae which had stopped feeding and were about to pupate; this meant that there was no risk of the problems of maggots boring through the crop. The food for each aviary was split into five plastic flower pot holders (140 mm diameter, 20 mm deep) which were spread out in the aviary so that no one bird could dominate the feeding area. The birds were always fed to excess. Before the start of the experiment I weighed six captive Dunlin three times in the same day to see if they showed a weight loss after handling as wild Dunlin do (6.3.2); these birds all put on weight through the day.

The birds in the inside aviary were easily caught by hand but it was much more difficult to catch the birds in the outside aviaries so a small mist net of the same dimensions as the cage was made to catch them. The birds were always weighed to the nearest 0.5 g using a pesola balance at 1600 hours to reduce the effect of any daily variation in weight. In the first nine days after capture all birds lost weight but by their second weighing (22 days after capture) their weights had started to increase again.

The birds never became completely habituated to humans, normally taking flight when anybody entered their cages. When observed the birds tended to flock and act in a similar way to Dunlin in the wild, except that they spent a very small proportion of their time feeding. When the ground was not frozen they would often probe in the substrate and occasionally caught and ate worms.

One of the major problems encountered through the study was that of Sparrowhawks Accipiter nisus trying to attack birds in the aviary. On some days a Sparrowhawk perched on the end of the cage for two or three hours. Whenever a Sparrowhawk arrived all the Dunlin would take flight for ten or twenty seconds before landing at the top of the cage where they remained until the Sparrowhawk had gone. Even the presence of a person in the cage would not deter a

Sparrowhawk from flying at the netting and attempting to catch the Dunlin. One bird was found dead half pulled through the wire of the cage; from the marks on it, it appeared that a Sparrowhawk had caught it. Due to this disturbance and that caused when people entered the cage the tips of the primaries on the group of birds kept outside became considerably abraded in the course of the winter.

On two occasions during the winter a Weasel got into the cages; on the first occasion the animal was seen before it had attacked the Dunlin and was caught in a Longworth trap. On the second occasion a Weasel killed a Dunlin before it was captured. Both Weasels entered the cages via the holes made by Bank Voles *Clethrionomys glareolus* which had burrowed underneath the concrete foundations of the cages.

At the onset of the severe weather there was a considerable snow fall. Most of the snow accumulated on the roof of the cages, this had to be removed as it made the cages very dark. Much of the snow fell into the cages whilst it was being cleared from the roof and although it was shovelled up into piles the birds only used the area which was completely free of snow. The water was kept running continually and some of the food pots were floated on it in an attempt to stop the food freezing. This meant that there was a considerable build up of ice down the streams further reducing the area which the birds used.

Some birds seriously lost condition during the severe weather and none of these survived. The reasons for birds losing condition are unclear but there are two main possibilities:

1. A number of birds suffered from frostbite on the toes and lost joints as a result; some of these birds also lost

condition and died although others seemed unaffected.

2. It is possible that some birds were effectively excluded from the food pots as these had to be grouped at the top of the cage where they would not be affected by snow.

Post mortem examinations were carried out (by J. W. MacDonald, MAFF Veterinary Laboratory, Lasswade, Midlothian) on three individuals which died during the severe weather but they were inconclusive. They all showed that the birds had died in very poor condition and had inflamed kidneys, although the kidney inflamation may not have been the cause of the initial loss of condition.

6.4.2 Results

Figure 6.18 plots the mean weights for the two groups of birds as well as mean weights for Wash Dunlin in the wild. It can be seen that both groups of birds showed a mid-winter peak, although in the group kept inside there was comparatively little variation in weight through the winter. The group kept outside significantly increased in weight between 20 October and 18 December (paired sample test: $t = 4.24$, $p<0.01$) and then declined in weight to 29 March ($t = 5.66$, $p<0.001$) and subsequently increased again to 2 June when they were released ($t = 4.97$, $p<0.001$). The weights of the birds outside followed the Wash weights until 20 December; they then fell steadily until the end of January during which time they were well below Wash weights. Between mid-December and mid-January the weather was very severe, during the first cold spell (7 December to 26 December) both the outside and inside groups attained peak winter weights (on 20 December). The steady decline in weights occurred irrespective of a

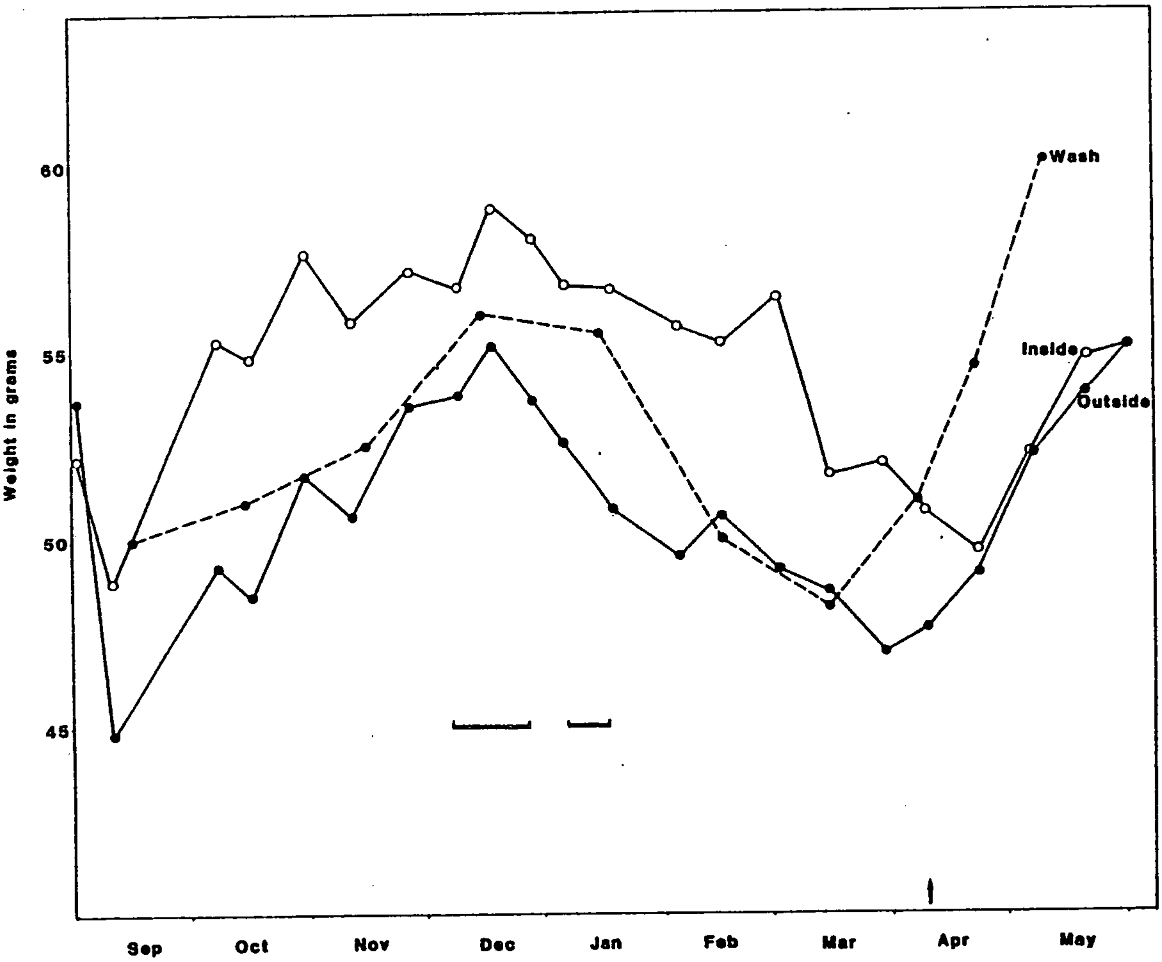

FIGURE 6.18

Mean weights of Dunlin kept in captivity between

September 1981 and June 1982

(arrow indicates date inside birds were moved outside;
thick lines indicate periods of severe weather)

mild period (27 December to 5 January) or the second cold spell (6 January to 16 January). The birds lost weight until the end of March (by which time on the Wash birds were already beginning to gain weight), but when they started to put on weight they increased at a similar rate to birds on the Wash at least until 20 May when they seemed to stop putting on weight.

One interesting point to emerge was that between two weighings the vast majority of birds (both inside and outside) changed weight in the same direction, as can be seen from figures 6.19 and 6.20. Actual weights were not plotted but the deviation from the individual's own mean weight was used in an attempt to remove the effect of different body sizes. For clarity the outside and inside groups have each been split into birds that put on large amounts of weight in spring and those that did not. One possible reason for all birds changing weight in the same direction between weighings could be a response to temperature variation. It can be seen from figure 6.21 that birds kept inside never encountered temperatures below freezing, but they also encountered much less variation in daily temperatures. However, temperatures were somewhat lower inside during cold periods thus the possibility that they were responding to temperature can not be completely excluded.

One bird (yellow, yellow) in the outside aviary did not follow the pattern of the others. This bird was one of the group studied by Bradley (1982) who was looking at social dominance in Dunlin. This bird tended to stay on it's own most of the time and spent a considerable amount of time running up and down the edge of the cage. It is likely that this bird never adjusted to captivity and it should, perhaps, therefore have been excluded from the analysis.

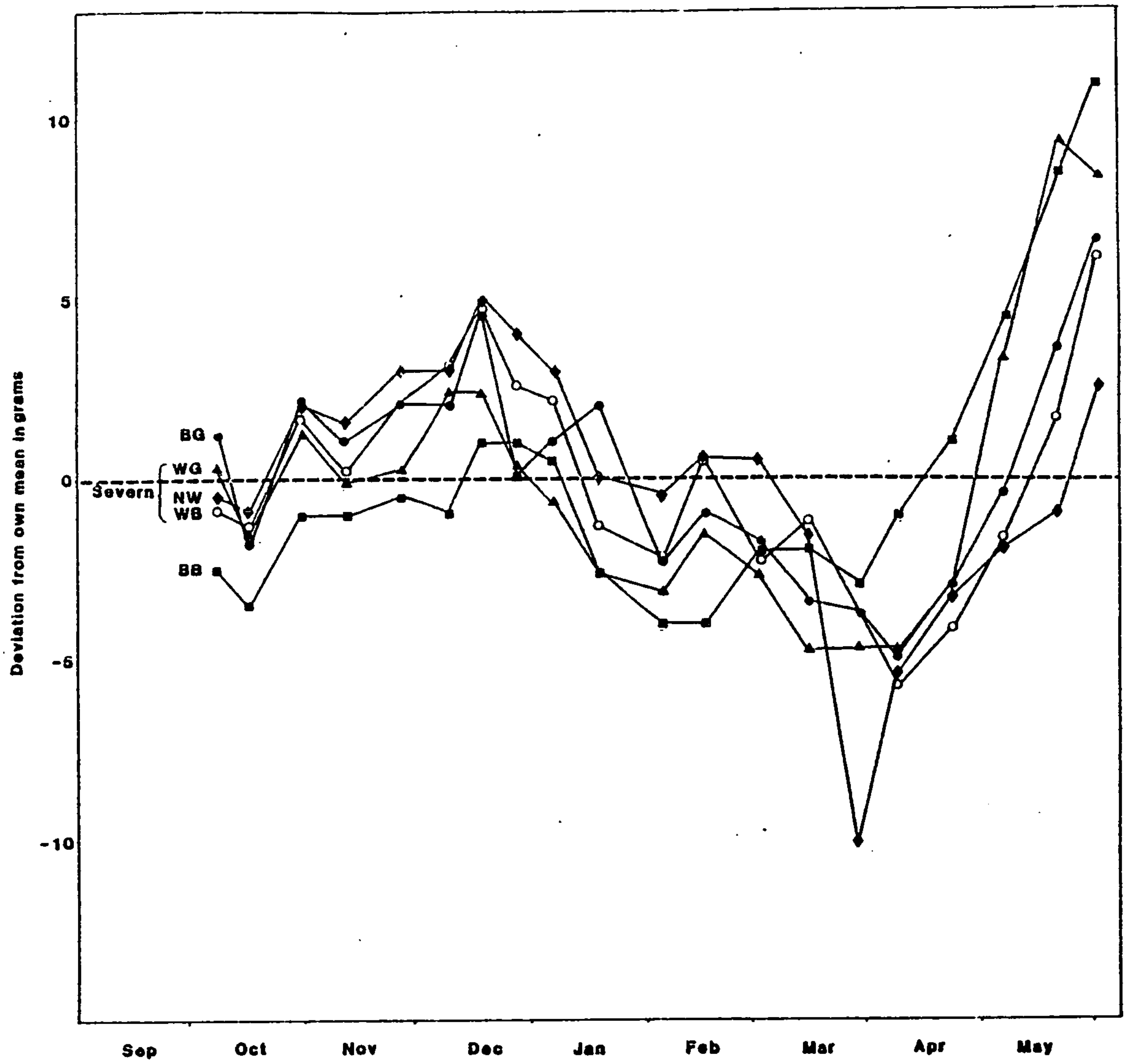

FIGURE 6.19a

Change in weight of individual Dunlin kept outside between September 1981 and June 1982

(the deviation from the individual's own mean weight is plotted)

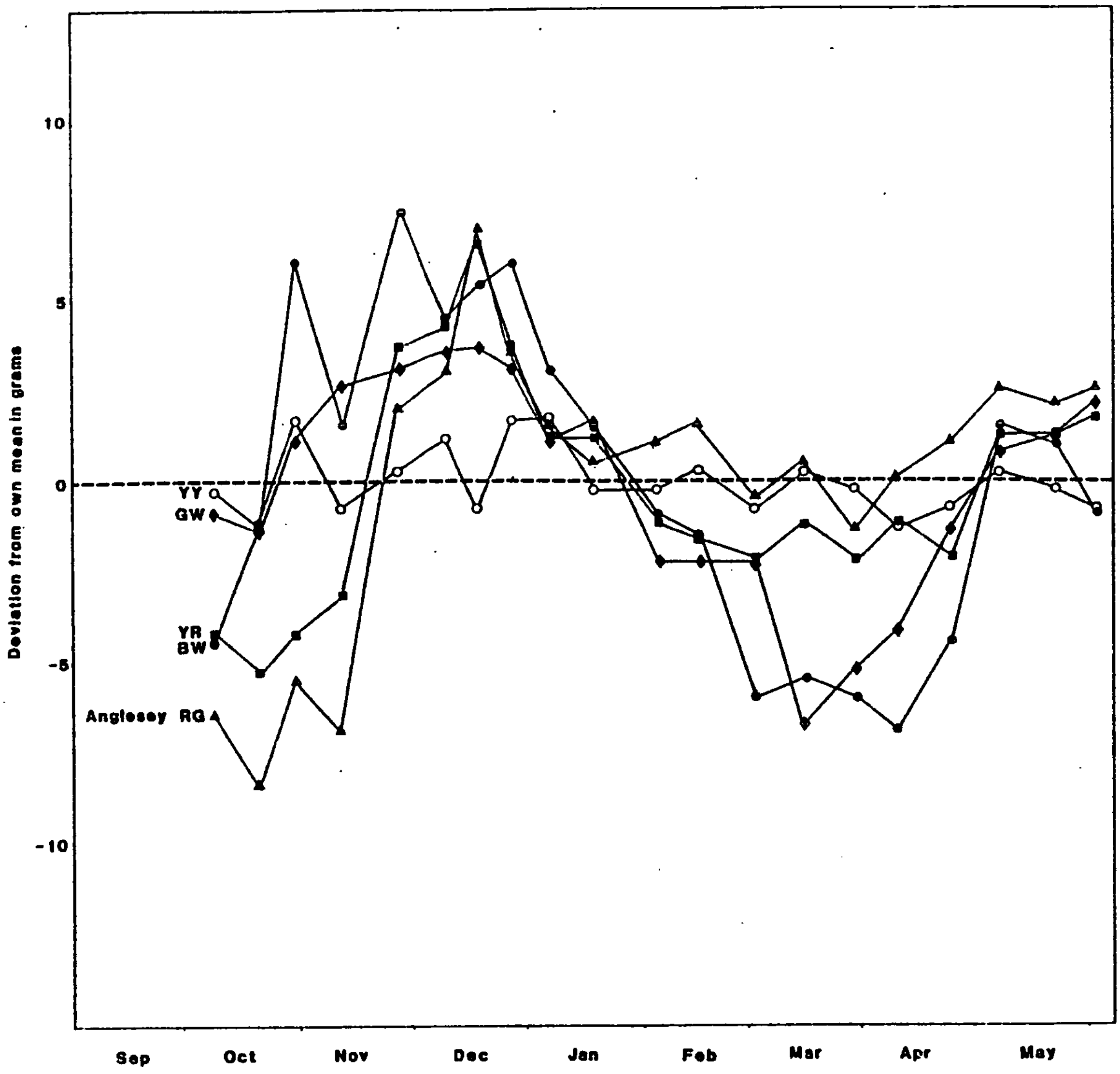

FIGURE 6.19b

Change in weight of individual Dunlin kept outside between

September 1981 and June 1982

(the deviation from the individual's own mean weight is plotted)

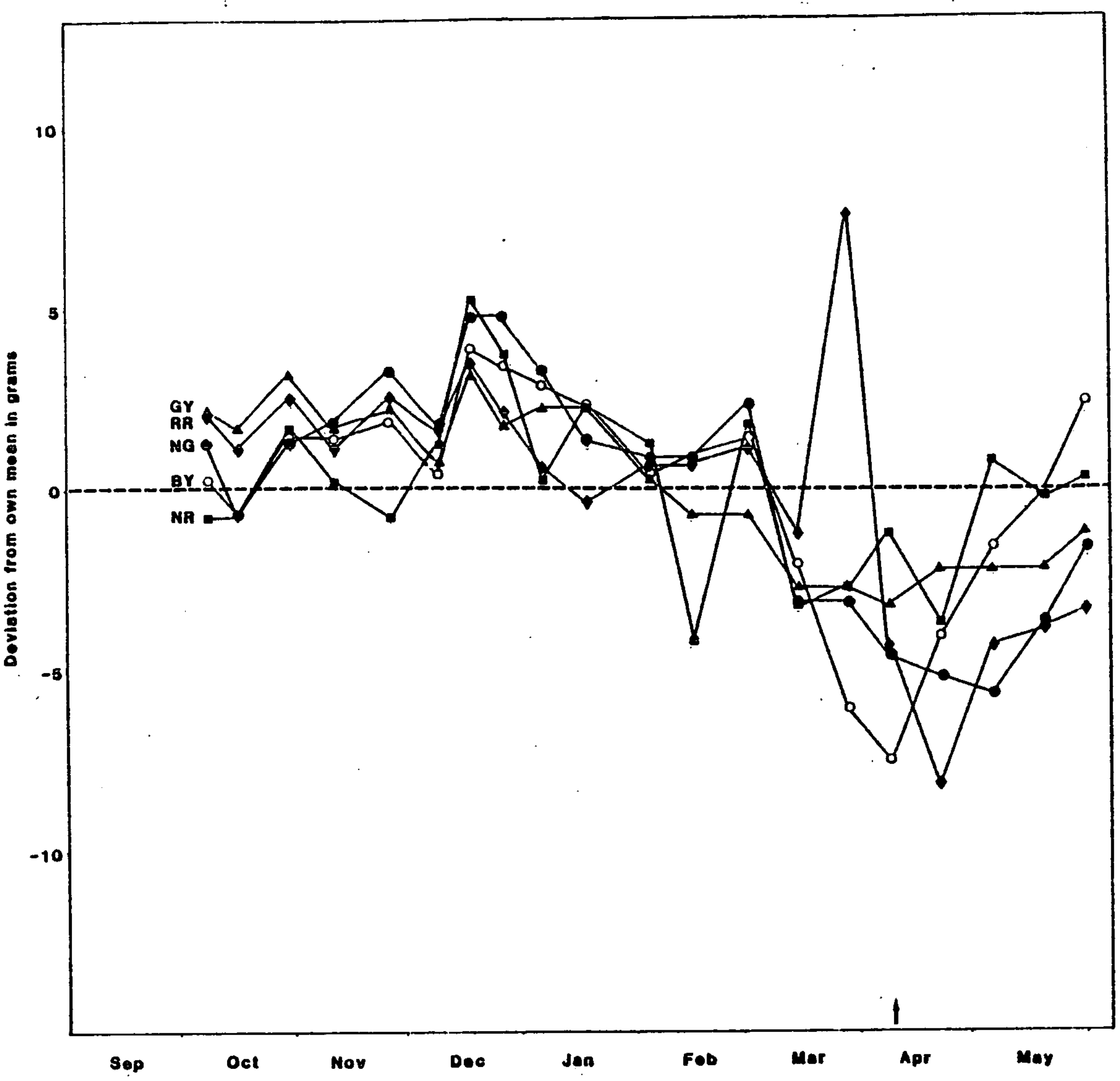

FIGURE 6.20a

Change in weight of individual Dunlin kept inside between

September 1981 and June 1982

(the deviation from the individual's own mean weight is plotted;
arrow indicates date birds were moved outside)

FIGURE 6.20b

Change in weight of individual Dunlin kept inside between

September 1981 and June 1982

(the deviation from the individual's own mean weight is plotted; arrow indicates date birds were moved outside)

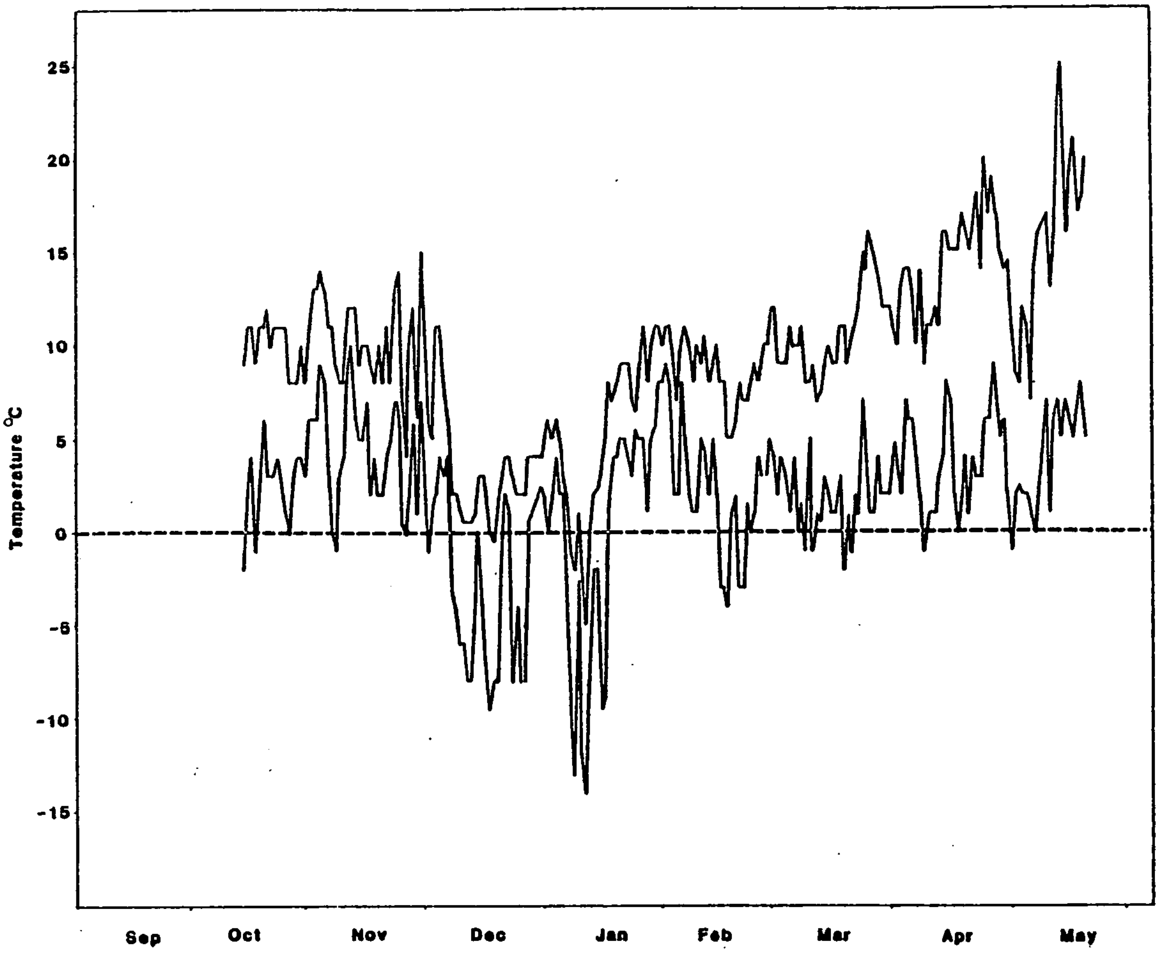

FIGURE 6.21a

Maximum and minimum temperatures recorded in the outside aviaries

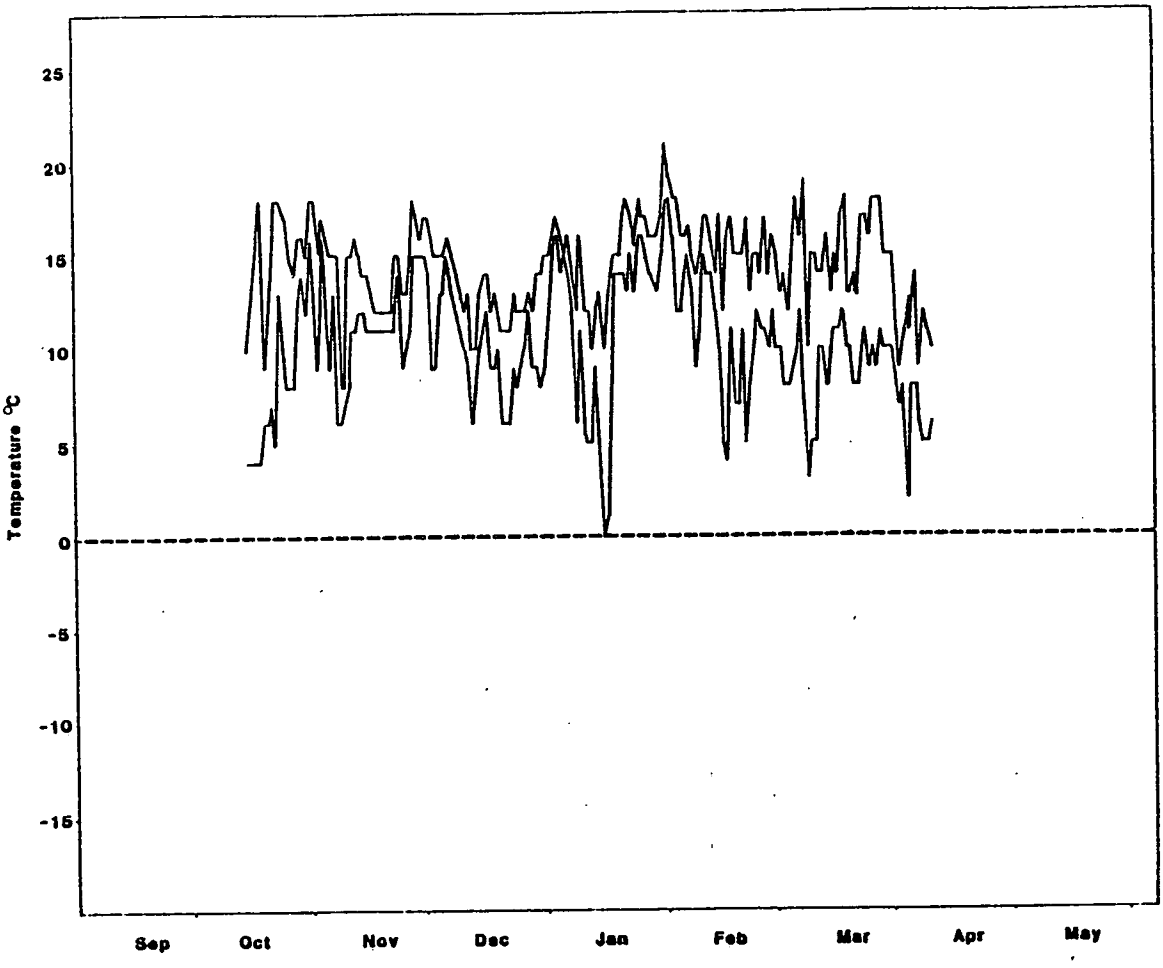

FIGURE 6.21b

Maximum and minimum temperature recorded in the inside aviaries

It was hoped that a sample of birds known to winter on the west coast estuaries could be caught, but as already stated this was not possible. It is interesting to note, however, that the three Severn and the one Anglesey wintering Dunlin all attained mid-winter peak weights.

6.5 Discussion

Of the two current hypotheses which have been suggested for weight cycles in wading bird populations of temperate regions (Pienkowski et al., 1979; Davidson, 1981) my data support the view that, at least in Dunlin, fat is stored as an "insurance policy" against the likelihood of severe weather. This is clearly shown by the birds kept in captivity, which approximately followed the weight cycle of birds on the Wash even though they always had food in excess. Goss-Custard et al. (1981) kept small numbers of Knot Calidris canutus in captivity for the second half of the winter. These birds appeared to take a long time to adjust to captivity; although, in the spring, they deposited fat at a similar rate to wild Knot on the Wash. The field data collected in mid winter 1981/82 show that in response to that cold spell Dunlin on the Wash increased the fat that they were carrying.

It has been suggested that an increase in weight in severe weather could be due to the lighter birds in the population dying; in this instance this possibility can be discounted as many of the birds were several grams heavier than the weights of the heaviest Dunlin on the Wash in most winters; furthermore, there was no significant mortality in Dunlin on the Wash during that period

(Clark, 1982a). The data from the Forth given in appendix 7 and figure 6.16 are more difficult to interpret. There is not sufficient data from previous years to be certain of "normal" winter weights, although one or two recent small samples suggest that Dunlin may maintain very low fat levels in normal winter conditions; this contrasts with data obtained in the early seventies which suggested that Dunlin on the Forth had very high winter weights (Pienkowski _et al._, 1979). If this is the case then Dunlin either: maintained their normal fat level throughout the severe weather; or showed only a slight reduction (presumably by increased food intake to counteract the increased energy loss through thermoregulation at cold temperatures - Gessamann, 1973) and then after the severe weather increased weight rapidly. This could be explained if they increased their food intake rate in response to the severe weather but did not reduce their food intake when the weather became milder; the overshooting would cause the net energy gain. It is possible that something similar could have happened on the Wash, in that during the severe weather the birds maximised their food intake rate and overshot even during the severe weather.

The data presented in figure 6.16 suggest that the majority of the Dunlin population may not have been under stress through food shortage in this winter although Redshank _Tringa totanus_ on the Forth certainly were (appendix 7) and Grey Plovers on the Wash probably were (table 6.1). Davidson (1982) has suggested that Redshank are unable to regulate their fat reserves on the Forth even in mild winters. In 1981/82 Redshank were able to put on weight between the two cold spells, when the weather was still bad (when compared to mild winters). It seems surprising that they can not regulate their weight in mild winters when weight gains of this magnitude are possible in mid winter, the period when Davidson suggests that Redshank are losing condition through an inability to regulate reserves. It is possible that Redshank are not maintaining high fat levels through the winter for some other reason. Dick & Pienkowski (1979) have suggested that there are several costs to maintaining high weights, for instance higher energy expenditure in movement in carrying the extra weight and an increased rate of predation. Page and Whitacre, (1975) have shown that predation can be severe in wintering waders and on the East coast of Scotland mortality, in certain populations, through raptor predation can be almost 20 percent (Whitfield, pers. comm.). Mortality in the 1981/82 winter at some sites in eastern Scotland was possibly as high as 30 percent. Redshank may sacrifice the need to maintain high weight levels for the need to be quick and agile in flight when avoiding predators; thus, selection may be acting to reduce overall mortality rates to a minimum level.

Dunlin weights on the Severn have been analysed in terms of grams of fat to overcome problems of body size. Grams of fat in this context can really be considered as weight of a standard bird minus computed lean weight; it signifies both changes in fat and protein reserves, although most of this change is of fat (Evans & Smith, 1975; Davidson, 1981). Throughout this discussion the term weight is used in descriptions of variations in fat and protein reserves. The weather on the Severn during the study was never as severe as during the 1980/81 winter on the Forth and the Wash (Chapter 1). The weather conditions on the Severn in the three main winters of the study were very different. The 1978/79 winter was the severest since 1962/63 but in this winter the highest weights were encountered. These high weights occurred on the southern bays after several weeks of severe weather. None of the sharp declines in weight occurred during severe spells of cold weather. After the beginning of January weights at Clevedon tended to be lower than those in the southern bays. There are three main possible explanations for this:

1. Birds at Clevedon never encountered severe food shortage and therefore there was no need for individuals to increase food intake, whereas those birds in the southern bays encountered short periods of food shortage and increased intake rates and therefore "overshot".
2. All birds encountered food shortage and as a result increased food intake rates but at Clevedon food availability was never high enough to allow substantial weight gain.
3. All birds increased weight over their "normal" winter weights but "normal" winter weights at Clevedon are lower than at other sites and therefore birds there never attained as high weights as birds in the southern bays.

The data available for the subsequent winters may shed some light on this. In the winter of 1979/80 there was no evidence for a mid-winter peak weight. The winter was very mild; the only high weights recorded were in February which was extremely warm. There was, however, serious erosion of sediments along the south shore of the Severn as documented in Chapter 5 and Ferns (1983). The mud that was lost in early December was only redeposited in late January; it could be that birds were unable to attain their normal mid-winter peak weights due to reduction in food availability; the samples from Clevedon certainly suggest that this was the case. The retraps of birds at Clevedon also suggested a decline rather than a peak in weights in mid winter. The data from retraps in Sand and Weston Bays of birds caught in mid and late winter suggest comparatively stable weights through the winter with a sudden reduction in weight at the end of the winter. Unfortunately there are not enough retraps between December and the middle of February to be sure whether birds increased weight then, as suggested by the mean weights of the samples.

The final winter of the study was an exceptionally mild one. Regular samples were obtained at both Berrow and Sand Bay; these suggest a mid winter peak in fat level at the end of December. Unfortunately there are no random samples of birds weighed at Clevedon before January, but from January through to March weight levels remained static. The birds weighed in November and again in January suggest an increase in weight between the two periods thus it is likely that weights at Clevedon increased to January and then remained steady; they were, however, lower than fat levels in other bays.

From these data I would tentatively suggest that under "normal" winter conditions Dunlin attain peak weights in either late December or January and that Dunlin wintering at Clevedon attain lower mid winter peak weights than those wintering further south within the estuary. I would suggest that the third hypothesis put forward above is most likely to be correct for the Severn.

Dugan _et al._ (1981) have shown that Grey Plovers lost condition during severe weather and had used both protein and fat reserves;

but after the severe weather they recovered to near normal weights for that time of year.

Pienkowski et al. (1979) suggested that mid-winter peak weights in Dunlin were correlated with minimum January temperature. My data suggest that mid winter peak weights may vary considerably within one estuary; although the general hypothesis put forward may be true, I would suggest that other factors such as types of food available are important in determining mid winter peak weights. Pienkowski et al. presented a small amount of data on Dunlin caught in severe weather on the Wash in 1976 and stated that although the birds caught during the severe weather were at lower than normal weights, shortly afterwards they attained weights slightly higher than normal for that time of year. The data for severe weather that I have presented have all been from December and January; while the data which Pienkowski et al. presented were from a spell of severe weather in late February. It is possible that although Dunlin are able to increase their food intake during periods of severe weather in early winter, they may not be able to increase food intake during similar spells of severe weather in late winter. Further information is needed to clarify this. The picture suggested by Pienkowski et al. is that the same mid-winter peak weights occur each year; my data do not support this.

Davidson (1981) documents the effects of two spells of severe weather: during the first, in February 1978, adult Dunlin showed no loss in lipid or protein reserves, but some juveniles did. The second period of severe weather was in the 1978/79 winter when weather conditions on the Tees were more severe than on the Severn. Here both adult and juvenile Dunlin had consistently lower lipid indices than samples caught in the following winter. On the Tees the severe weather came in two main spells: Davidson suggests that Dunlin lost condition during the first cold spell (or the birds had never attained mid-winter peak weights); adults then maintained a steady lipid index until the second spell, when there was evidence for a reduction in lipid index to near lean weights. Juveniles, on the other hand, had low lipid indices at the end of the first cold spell and then put on fat before the beginning of the next cold spell (so that lipid indices were only slightly below those found in the following winter) and then lost condition in the second cold spell. There is no evidence from these data for Dunlin on Tees overshooting their normal winter weights during or after severe weather. The feeding grounds on the Tees are only exposed for about seven hours during each tidal cycle, there being no feeding areas above mid tide because of the extensive reclamation of the estuary. It is possible that on the Tees feeding conditions may not have been good enough to allow birds to increase their lipid indices after the first spell of severe weather It could be that non-random samples of juveniles were caught (all the samples were less than 15) or that different sections of the population were trapped in the different catches.

From my own work and other studies it is possible to predict the rules that govern weight levels in Dunlin through the winter:

1. Dunlin on any given estuary attain a mid-winter peak which is related to the likelihood of severe weather.
2. When weather conditions deteriorate Dunlin respond by increasing (possibly maximising) their food intake; this means that on some occasions, especially during severe

weather in early winter, Dunlin increase weight above the "normal" weight for that time of year (this may result in a rapid change in weight).

3. Dunlin reduce weight after mid winter as the likelihood of severe weather diminishes.

4. When severe weather occurs in late winter Dunlin may not be able to increase food intake rates to increase their weight level either during or after severe weather.

There may be a strong selective advantage in putting on extra weight during severe weather (obeying rule 2); as the weather conditions may deteriorate still further and then any birds which have low fat levels are likely to starve. On the Forth in the 1981/82 winter Redshank started the second cold spell at below normal weights and suffered high mortality. Dunlin, however, put on weight between the two cold spells (entering the second cold spell at extremely high weights) and were able to survive with very little mortality.

The relationship between juvenile and adult weights suggests that after their arrival in the autumn juveniles increase weight to a higher level than that attained by adults. The juveniles have no previous experience of the wintering site, but adults have; by mid winter juveniles have assessed the severity of weather conditions and food availability and respond on the Severn by reducing their fat levels. It is interesting that juveniles show a consistent relationship to adults both in different bays and in different winters.

The differences between juveniles and adults were similar in the 1978/79 winter to those in other winters; thus in the periods of severe weather juveniles, as well as adults, tended to put on weight. This result is surprising in view of the large number of studies which suggest that juveniles have lower feeding efficiencies than adults (eg Recher & Recher, 1969; Quinney & Smith, 1980). Siegfried (1971,72) showed that juvenile Cattle Egrets Bubulcus ibis were less efficient during periods of food shortage than adults and Pienkowski (1980) showed that juvenile Ringed Plovers Charadrius hiaticula had similar feeding rates to adults in early autumn, but had a lower feeding rate in late autumn and winter. My data (Chapter 3) showed that juvenile Dunlin tended to feed for longer and in different places than adults. When mist netting at night the majority of birds are caught in a short period of time; and normally all birds are extracted from the nets at the same time. Occasionally the birds are extracted in two stages. Table 6.4 gives data for two occasions when this happened. It shows that juveniles came on to the roost later than adults at night and therefore probably fed for longer at night than adults; this is similar to the situation in day time (Chapter 3).

I have suggested that weights of adults vary between bays (6.3.2). The consistent difference between juveniles and adults in all the bays suggests that juveniles must be quickly assessing the environmental factors and food availability in the bay they are wintering in, or that birds from different bays come from different breeding areas and therefore possibly have different programmed winter fat levels.

The difference between males and females at Clevedon is at first perplexing. It has been shown, however, that Nereis diversicolor are more active at the surface at night (Dugan,1981a) than in the

TABLE 6.4

The proportion of juveniles mist netted at different stages of the tide in Sand Bay

30 11 79	Juveniles	Adults
up to 1 hour before high tide	3	16
after 1 hour before high tide	13	25

Adjusted Chi-squared = 1.31 N.S.

07 01 80	Juveniles	Adults
up to 1 hour before high tide	11	50
after 1 hour before high tide	31	17

Adjusted Chi-squared = 21.62 $p<0.001$

daytime. I have shown that in the day time Nereis are at deeper levels at lower temperatures (Chapter 2). It is possible that although females are able to maintain a nearly steady fat level by maintaining similar intake rates in the day time and at night, males may not be able to balance their energy requirements during the day time and so have to feed for longer at night, when they are able to make up the deficit in daily energy requirements. If this is the case, it would be predicted that females would arrive on the roost at night before males. Table 6.5 gives data for the two occasions when it was possible to test this. Neither showed a significant difference, although on both occasions a smaller portion of males were caught in the first catch than the second. Further work should be undertaken to test this hypothesis.

Worrall (1981) suggested that Dunlin can obtain most of their daily intake during the day; if this was the case there should be a consistent difference in the weights of samples caught in the morning and evening. I found no such difference on the south shore of the Severn. From this analysis of weight variation in Dunlin it has become clear that many factors influence their weight on any given day; I have suggested a few. Future work with captive Dunlin in a controlled environment may give a better understanding of other factors affecting weight levels, especially if regular monitoring of weights of undisturbed individuals can be carried out.

TABLE 6.5

The proportion of males (amongst adults) mist netted at different stages of the tide

30 11 79	Males	Females
up to 1 hour before high tide	7	9
after 1 hour before high tide	14	11

Chi-squared = 0.2 N.S.

07 01 80	Males	Females
up to 1 hour before high tide	23	27
after 1 hour before high tide	11	6

Chi-squared = 1.106 N.S.

CHAPTER 7

CONCLUSION

The preceding chapters have focused on many different aspects of the wintering ecology of Dunlin. There have, however, been two main themes which relate to most of these aspects:

1) differences between the sexes; and

2) differences between adults and juveniles.

During this study Dunlin were sexed by discriminant analysis using wing length and total head length which is highly correlated with bill length. Total head length was, however, a much more important variable than wing length, so males can be considered as short-billed birds and females as long-billed birds. Thus any conclusions on sexual differences could equally well refer to differences between long-billed and short-billed birds. For convenience, throughout this discussion birds are referred to as males and females.

A few *C. a. schinzii* winter on the Severn. Since *schinzii* have shorter bills than *C. a. alpina*, *schinzii* females will have been considered as *alpina* males and *schinzii* males as very short-billed *alpina* males.

It has been suggested that the niche width that a species can occupy is at least partly related to the morphological variability within the population (Van Valen, 1965; Davidson 1978). There is evidence that sexual dimorphism tends to be greatest when species diversity is low (Woodpeckers *Centurus* - Selander, 1966; Lizards *Anolis* - Schoener, 1977; Lizards *Lieocephalus* - Schoener *et al.*, 1982). Maude-Roxby (1983) has shown that in Dunlin, males (short-billed birds) are able to take small prey at a faster rate than females (long-billed birds). Females, however, can obtain prey from deeper than males. Schoener (1965) found less difference in bill size between sympatric species in studies where food was abundant. In shorebirds on their arctic breeding grounds it has been stressed that bill size is the most important factor in determining prey size (Holmes and Pitelka, 1968; Connors _et al_., 1979). Bill size has also been suggested as being important in habitat partitioning away from the breeding grounds, both within a species (Smith, 1975; Puttick, 1981) and between species (Bengtson and Svensson, 1968; Thomas and Dartnall, 1971).

I found significant differences in the feeding ecology of males (short-billed birds) and females (long-billed birds). In Chapter 3 I showed that males feeding on one substrate (wet sand) tended to spend a larger amount of time ploughing than females. Amongst the juveniles males tended to feed on the wet sand and females on the runnelled mud. Furthermore, at Clevedon after a severe frost, it was some males that continued to feed when the rest of the flock had started roosting. Clevedon is the site where, in mid winter, there is the lowest sex ratio (lowest proportion of males) and the fact that males were feeding after a frost suggests that at least on that night they had had difficulty in balancing their energy requirements whereas the females had not. At Clevedon males were shown to lose weight during the day and gain weight at night, whereas females showed little diurnal variation. Dugan (1981a) showed that _Nereis_, the main prey species available at Clevedon, was more active at night. Evans (1983) found that prey availability at night was the same, or higher, than in the day time. However, he also found a higher correlation between activity rate of all invertebrates and temperature in the day time than at night. Temperature may be a less significant factor in determining prey availability at night than in the day time; this may be why males are able to put on weight at night in winter even though they lose weight on the cold winter days. It is unfortunate that I have no comparable data from other bays but one might suspect that in sites where there is a high sex ratio it would be the females that would have to feed for longer when conditions deteriorated.

The evidence from Chapter 6 shows that the difference between the fat levels of males and females is not related to the bay in which the birds are wintering. It might be expected that the section of the population which was most likely to experience food shortage would carry most fat. However, males and females at Clevedon have lower fat levels than birds in other bays. This suggests either:

1) a very finely adjusted response to the likelihood of poor feeding conditions; or

2) different populations wintering in the different bays and having either different "programmed" winter fat levels or different lean weights relative to bill and wing lengths.

If the first hypothesis was true one would also expect differences between the sexes at Clevedon; this was not the case and the data from Chapter 5 suggest that there may be differences in the origins of birds wintering in different bays.

In the light of previous work, which has shown that in many species juveniles have lower feeding efficiencies than adults, I expected to obtain similar results. I did find that juveniles fed for longer than adults, although they did not show any differences in feeding actions. However, it was not possible to assess foraging efficiency. In the severe weather in 1978/79 I expected to find juveniles at very low weights but the difference between juveniles and adults followed the same seasonal pattern as in subsequent winters. This suggests that juveniles were able to respond to periods of severe weather by increasing weight and presumably they, like adults, did not encounter any periods that were so severe that they could not at least balance their daily energy needs. It is still possible, however, that juveniles have slightly lower feeding efficiencies than adults.

In the early part of the winter juveniles had higher fat levels than adults; as the winter progressed the difference between them showed a linear decline so that in late February and early March juveniles tended to be lighter than adults. There are three possible explanations for this:

1) juveniles, being less efficient feeders, had high fat levels as they were more likely to encounter periods of food shortage;

2) juveniles, having no previous knowledge of the weather conditions on the Severn, carried higher levels of fat in early winter, which would enable them to survive much harsher conditions than they did in fact encounter;

3) juveniles increase weight shortly after arrival when the conditions are still good and then steadily lose weight due to an inability to feed as efficiently as the adults in late winter.

The facts that juvenile weights vary in direct relation to adult weights, and that I could not detect differences in foraging efficiencies, suggest that the third hypothesis is incorrect, but my data do not shed any light on the other two hypotheses.

I have shown that birds first caught as juveniles in mid-winter are likely to be retrapped in subsequent winters in the same bay. This means that it is as a juvenile that a bird "decides" where it is going to winter for the rest of its life. How does a bird make this decision? Juveniles leave the breeding grounds after the adults (Cramp and Symonds, 1982) so they can not migrate with them and learn the wintering area from them. Juveniles take a more westerly route than adults, some moving across northern Scandinavia and then down the coast of Norway (Leslie & Lessells, 1978) while others move through the Baltic. There must be a genetic component to the determination of the area in which a juvenile will winter. I have shown that three juveniles moved a considerable distance north in autumn after arriving on the Severn, these may have "overshot" their genetically "programmed" wintering area. Most of the juveniles arriving on the Severn in autumn stay there to winter and return every year, probably for the rest of their lives. These birds must be quickly assessing the suitability of the bay they are in and, presumably, move on if feeding conditions are not good enough for their own feeding abilities. There are differences in the proportions of male (short-billed) and female (long-billed) birds in the wintering population between the bays on the south side of the Severn. From this it appears that more juvenile male than juvenile female Dunlin arriving at Clevedon "decide" not to stay, because they encounter unsuitable feeding conditions. At Berrow the converse is true with females more likely to move than males.

This explanation does not take any account of differences in recovery rates and in discriminant analyses found between different bays. These suggest that birds wintering at Clevedon have different timing of migration and possibly come from a different breeding area. One possible solution is that the juveniles from certain breeding areas have either previously encountered, or have a genetically determined preference for, substrates or types of prey which are similar to those that they encounter at Clevedon. These birds would be more likely to stay there than juveniles from other breeding areas which would tend to move to other bays. It has recently been shown that there is a genetic basis to the migratory response in partial migrant passerines (Berthold & Querner, 1981,82a,b). There is likely to be a genetic basis to the habitat preferred on the wintering grounds. Partridge (1974) showed that young hand-reared Blue tits Parus caeruleus preferred oak branches whereas young hand-reared Coal tits Parus ater preferred pine branches, even though they had never encountered them before. This clearly shows a genetic preference in habitat selection and such preferences could account for the differences in the biometrics of Dunlin wintering in different bays.

Numbers of Dunlin wintering on the Severn vary from year to year (Ferns, 1981). Part of this variation will be due to variations in the breeding success but in some winters (eg 1979/80) there is considerable movement within the estuary due to environmental factors (Ferns,1983; Chapter 5). It is interesting to note that there was no increase in movement between bays on the south shore in such winters. If the birds from Clevedon and Sand Bay had moved to Weston Bay or Berrow they would have encountered very different feeding conditions. However, on the north shore they would have found similar feeding conditions to those at Clevedon and Sand Bay.

I found that the invertebrate fauna of the south shore of the

Severn had changed in the eight years between the study of Boyden and Little (1973) in 1972 and my study. Although there were changes in the relative abundance of individual species the main prey species available to Dunlin in each bay did not change. It seems unlikely that these variations in prey density will have substantially changed the sex ratios in the Dunlin populations which winter on the south shore.

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APPENDIX 1

A SIMPLE RAPID METHOD OF MOVING A SET CANNON NET WITH MINIMAL DISRUPTION

by Nigel A. Clark

In response to the cannon-netter's nightmare of unpredictable tides a new method of setting or re-setting a cannon net was sought. This has now been developed to the point at which a two-cannon net can be set or re-set by five experienced people in less than five minutes.

The method involves the use of a "stretcher" made of hessian or polyester sacks, 13 metres long and ½ metre wide. Three 5½ metre-long bamboo mist-net poles are threaded through channels on each side, and these poles must overlap to make the entire structure rigid.

The net, which is 13 metres long, is set in the usual way, on top of the stretcher. If it becomes necessary to move the net, the cannons and projectiles are lifted and placed on top of the net on the stretcher with the electrics still connected. (N.B. see 1, below). The pegs connected to the jump ropes are also placed on the net, as are spade, mallet, decoys, etc. The five people are spaced out at regular intervals along the stretcher to move the net.

There are several very important points to be remembered:-

1. As loaded cannon are being moved with cables attached, THE FIRING BOX MUST BE DISCONNECTED before the team starts the move. It is NOT sufficient only to switch off.
2. Each person must be allotted a particular job before starting the operation, so that it can be carried out as quickly and quietly as possible.
3. When cannons and pegs are lifted off the net, care should be taken to ensure that the net is not twisted.
4. New cannon holes must be dug and the cannon weighted down properly so they are not displaced when fired.
5. All normal safety precautions must be taken when positioning cannon, and all members of the team must be behind the net when circuit-testing.
6. The stretcher poles in front of the net must be below the trajectory of the net, otherwise the net will not extend properly.

We have found this method extremely successful. It has proved very useful for catching on sites which are exposed on the falling tide; birds seem to have no hesitation in landing with the decoys, in front of the very obvious stretcher, perhaps as they have learned that cannon nets cannot be set below high tide!

This method may also prove useful for catching species such as Sanderling *Calidris alba* and Turnstone *Arenaria interpres* on sites where it is possible to make several catches over the high-tide period.

If any further information is required, I shall be happy to provide it.

Nigel A. Clark, Department of Zoology, University of Edinburgh, Scotland.

APPENDIX 2

A method of roping a cannon net

The rope positions for the full net (13 x 26 m) and for the half net (13 x 13 m) used in the study are shown in figures A.1.1 and A.1.2 respectively.

The roping is carried out as follows:

Thread 4 mm rope along the sides and the back. Thread 8 mm rope through the front of the net, 0.5 m from the front edge, leaving three metres at one end (this will form an end trace rope) and 10 m at the other end (this leaves slack rope which will be used when tying in the 12 centre trace ropes and will form the other end trace rope). Tie the centre trace ropes to the front edge of the net starting near the short end rope (leave two metres spare to form a tethering rope which will later be tied into the netting). To tie the centre trace ropes to the front edge rope, loosely tie a clove hitch around a small stick, carefully remove the stick and tie another clove hitch through the clove hitch in the front rope. Gently tighten all four ends. When all the trace ropes are attached there should be some slack netting along the front edge. Cut the long end of the front edge to three metres to form an end trace rope. Fold the 0.5 metres of loose netting under the front edge to form a flap. Thread 0.5 m of each tethering rope back through both the net and flap. Untwist the remaining 1.5 m of each tethering rope so that one strand can go to one side and two strands to the other. Thread the strands through the netting (remember to leave

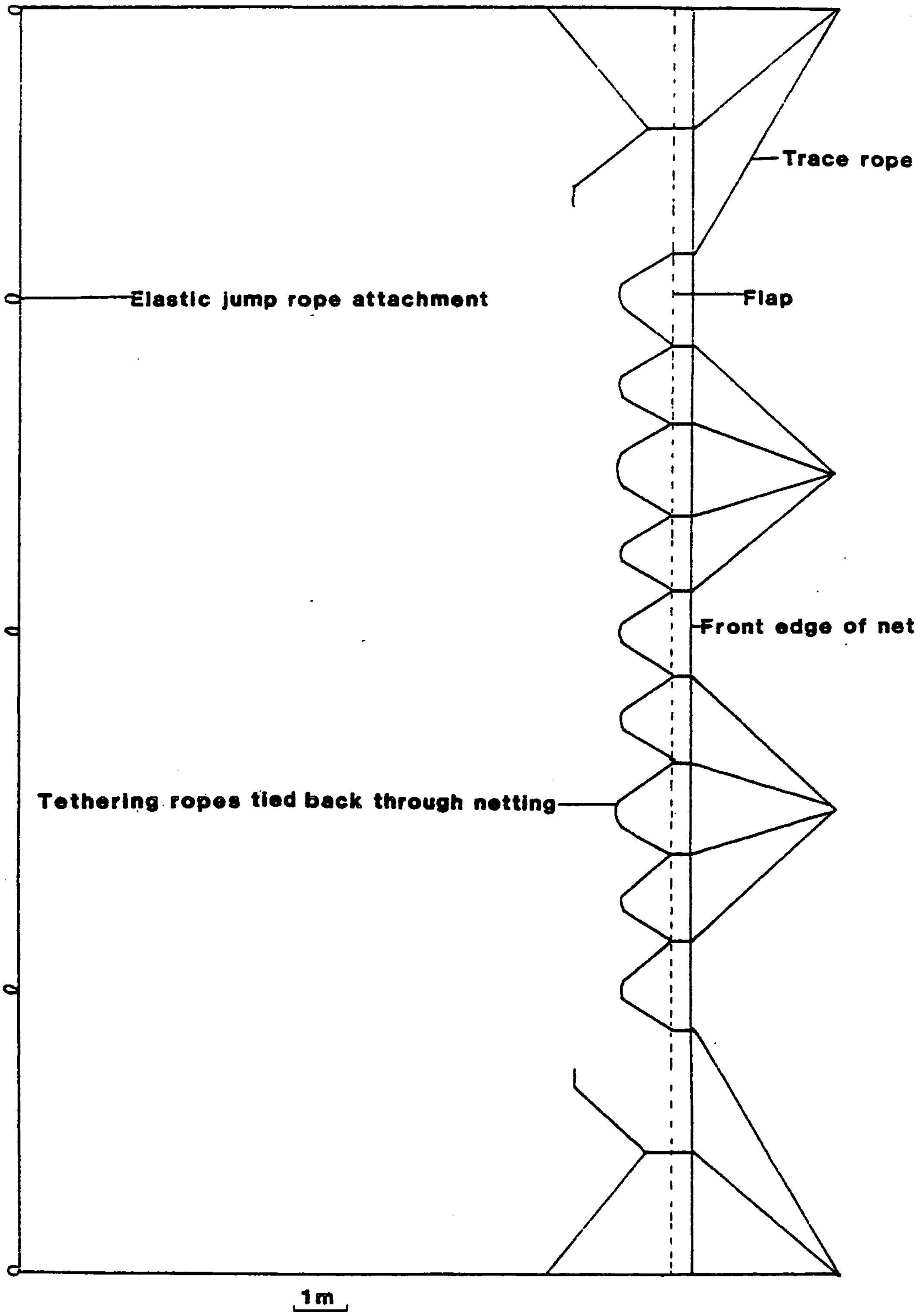

FIGURE A.2.1

Rope positions for full net

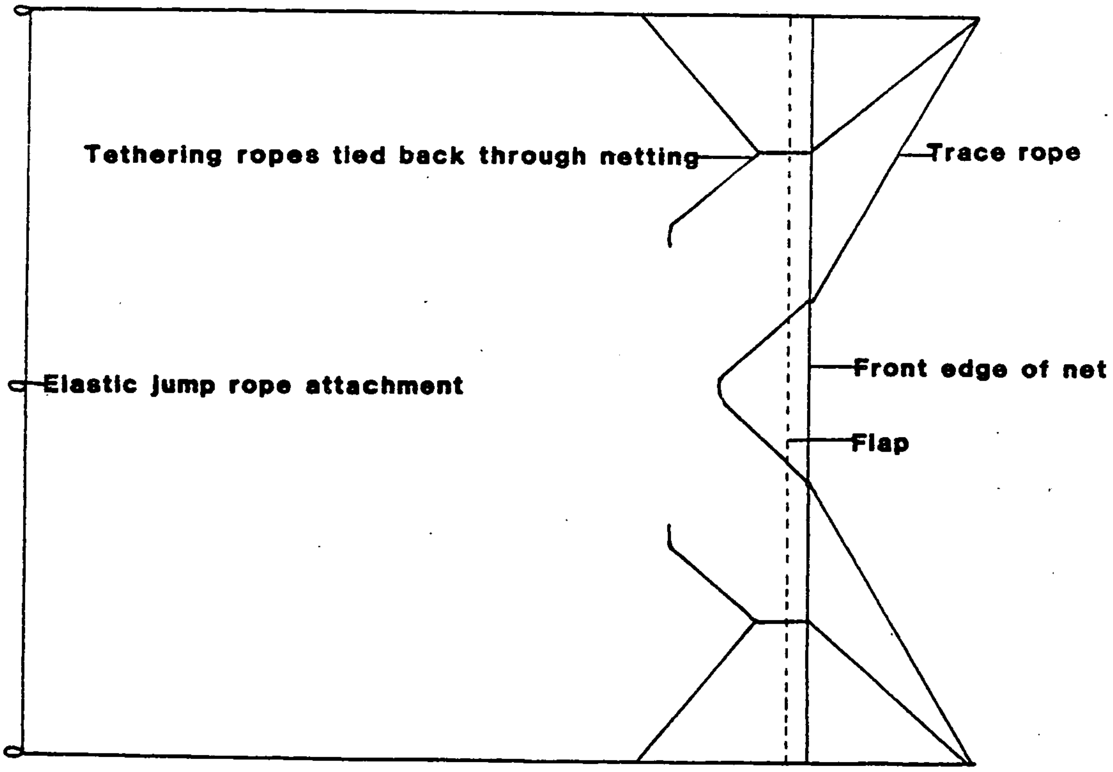

FIGURE A.2.2

Rope positions for half net

slack netting) so that each meets the tethering rope from the next trace.

With thread of the same dernier as the netting, tie all ropes (ropes around the edge of the net first, then tethering ropes) to the net using clove hitches or camel hitches (Ashley, 1944) at regular intervals. When the roping is finished there should be no points of stress on the netting as these will cause tears when the net is fired.

APPENDIX 3

A method of making wader decoys

The method of making wader decoys outlined here is a modified version of Bainbridge (1976).

Safety note

When using formalin or latex, always wear safety spectacles and work near a supply of running water.

Materials

Cotton wool; stout needle; button thread; sharp-pointed scissors; strong blunt seeker; forceps; galvanised wire (1 - 2 mm gauge, depending on the size of the bird); syringe; hypodermic needle; commercial formalin (40 percent formaldehyde); Revoltex (a form of latex manufactured by Dunlop Ltd); glass eyes or map pins; enamel paint; hardboard; awl; long pins; wire cutters; toothbrush; safety goggles.

Method

Only fresh, undamaged birds which do not have a large amount of fat should be used. If the birds must be stored they should be frozen flat, wrapped in soft tissue, so that the plumage is undisturbed. Birds should be defrosted before treatment. I make a full set of measurements of the bird.

1. First, remove the gut. Part the feathers of the stomach centrally, and slit the body wall from the end of the sternum to the cloaca. Remove the gut (at this point the bird can be sexed) and then fill the gut cavity with cotton wool. Sew up the body wall and replace the feathers over the stitching.

2. Slit the pad of the foot, insert a blunt seeker under the tendons and remove them (figure A.3a). Insert a suitable gauge of galvanised wire up the tarsi and thighs in place of the tendons. Lay the legs back at an angle to the body and push the wire diagonally through the rib cage and out through the skin (figure A.3b). Bend the protruding wire about 20 mm from the end to form a hook and pull the wire back into the bird so that the hook secures the wire to the rib cage. Cut off the ends of the wires about 200 mm from the feet. Carefully bend the legs into the standing position. Using mist net mending twine or strong cotton tie a series of half hitches around the legs about every 5 mm to strengthen them. This is best done by using a series of half hitches.

3. Thread a piece of wire down the back of the throat and push it right through the abdomen and out through the skin near the top of one of the legs. Bend the wire round the top of the leg so that the end lies flat along the underside of the bird and extends past the tip of the tail. Bend the wire in the mouth, about half way along the bill, to form an eyelet. Figure A.3c shows the final position of the wire. Sew the wire to the upper mandible through the nares, and then sew the lower mandible to the upper mandible. This wire can later be bent into a realistic position.

4. Lay the bird on its back and push a piece of thin wire, one

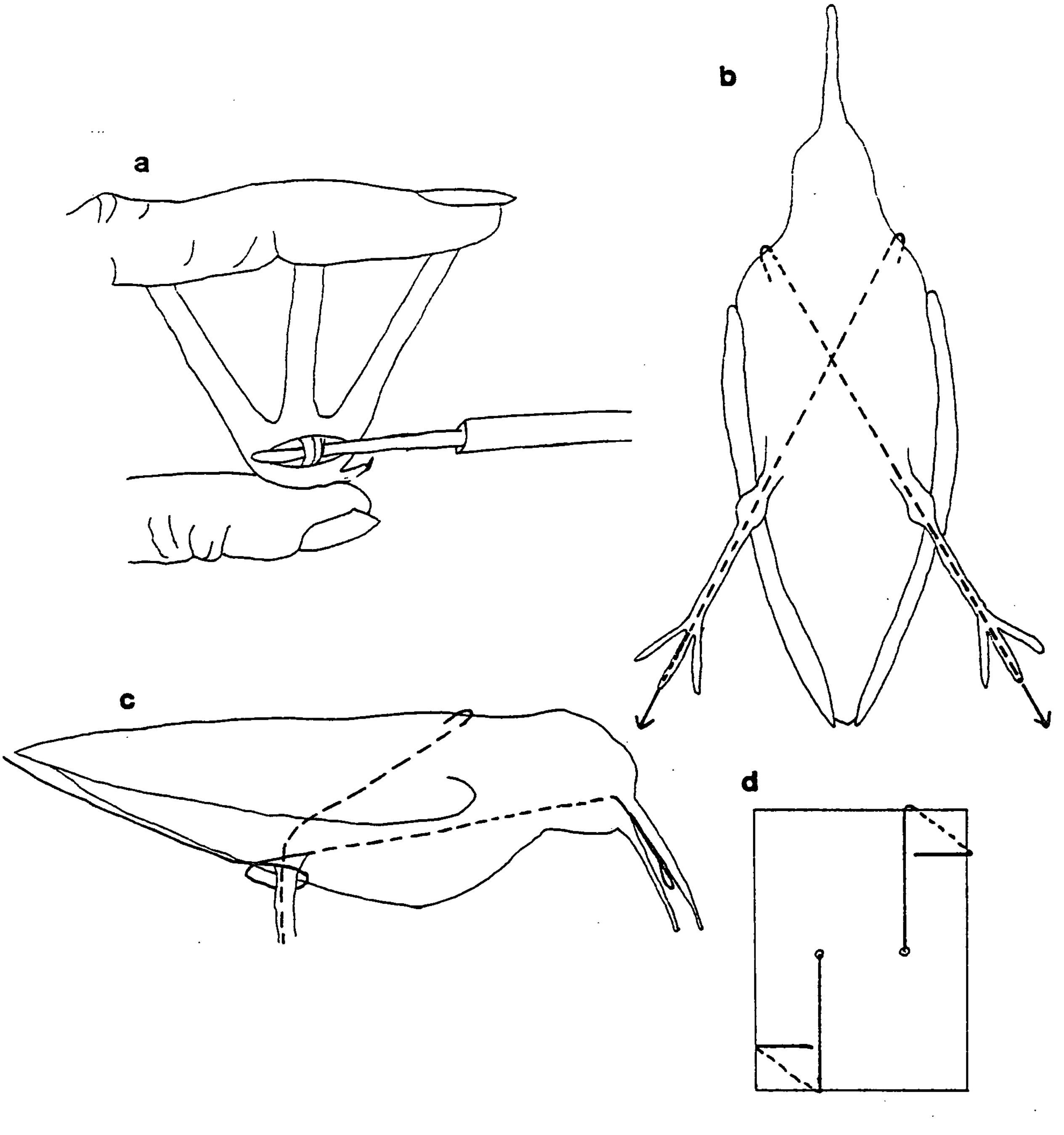

FIGURE A.3

a) Removal of tendons, b) position of leg wires when fully inserted, c) position of head wire, d) mounting board as seen from below.

millimetre in diameter, through the wing near the carpal joint, through the body, and out through the carpal joint of the other wing. Now bend one end so that it forms an eyelet round the radius. Cut the other end 20 mm from the wing and repeat the procedure. This sets the wings at a fixed distance apart.

5. Cut an oblong of hardboard (1 x 1.5 "bird widths") and make two holes in it. Thread the wire through the hardboard and bend it into the position shown in figure A.3d. Use a pair of pliers to pull the wire tight and flatten it off. Bend the body and legs into a realistic position.

6. Carefully remove the eye balls (try not to puncture them as the aqueous humour badly stains the feathers). Insert glass eyes (for small birds use map pins). Using forceps, bring the eyelids over the eyes to hold them in place. If using map pins, insert them at an angle away from the bill, so that they do not push against each other inside the head.

7. Bend the head into a realistic roosting position, bill tucked into wing, or head up. If necessary, stick a pin through the top of the skull and use cotton tied to drawing pins on the hardboard to keep the head in the correct position. The posture of the bird is very important. If the decoy is in an alert position it will act as an excellent bird-scarer. I find the best position is "head-up roosting posture", where the head is nestled close to the body, showing very little neck. It is always best to have pictures of roosting waders to refer to when setting your decoy.

8. If the primaries are not lying flat to the body and the upper tail coverts are showing, bend a piece of thin wire around the body and wings just behind the legs. With a piece of cotton, attach the

wire to a pin in the skull to stop it slipping towards the tail (this is often necessary for large birds).

9. Inject Revoltex into the pectoral muscles, the front of the neck and a small amount under the skin over the skull. This will minimize the effects of shrinkage. If any latex oozes out leave it until it starts to set, as it can then be pulled away from the feathers.

10. Inject the bird with commercial formalin, into the abdomen, thorax and through the foramen magnum into the brain. For a small bird, inject between five and ten millilitres; for bigger birds increase the amount of formalin proportionally (in general use too much rather than too little). The thighs and wings of bigger birds may also need injecting (inject one or two millilitres into the fleshy part of the limbs). If the formalin causes the eyes to swell, firm but gentle pressure should relieve this. As well as preserving the bird, the formalin acts as a setting agent for Revoltex.

11. Make sure all the feathers are in place. A small, stiff brush (toothbrush) will help.

12. Set the decoy in the finished posture, taking care that it is in a natural position and that all the feathers are in place. Put in a warm, dry, fly-free place for two or three weeks. When the decoy has dried cut off the threads and the wire which protrudes from the tip of the tail and, if necessary, paint the bill and legs. Finally, cover the bill and legs liberally with Araldite or fibreglass resin, to strengthen them and stop them rotting so quickly.

If the bird is left on the board the legs are strengthened. In the field the hardboard can be covered with sand or soil. This is often easier, for both ringer and decoy, than sticking galvanised wire into the ground. To maintain decoys in good condition they should always be stored dry and never left with the feathers flattened. If decoys do get wet, use a hair dryer to dry them, gently rubbing the feathers so that they do not stick together.

APPENDIX 4

Data required to predict the sex of Dunlin
from different sites within the Severn

	Berrow	South Shore ex. Berrow	N. Severn	All Severn
Number of males	66	35	12	113
Number of females	33	15	33	81
Data from covariance matrix				
Wing - Wing	5.952671	5.940476	7.685870	6.309018
THL - THL	2.227572	2.058559	3.545342	2.485314
Wing - THL	0.5002813	0.3417267	1.770634	0.7732335
Bill - Bill	1.840619	1.800144	2.668115	2.020935
Bill - Wing	0.4463618	0.0510119	1.484179	0.5972685
Mean values				
Male wing	119.16667	118.91429	119.7500	119.15044
Male bill	30.85758	31.00286	30.6500	30.88053
Male THL	54.60303	54.65429	54.6416	54.62301
Female wing	123.15152	122.200	122.48485	122.70370
Female bill	35.09394	34.6866	34.4394	34.75185
Female THL	59.08788	58.8200	58.3242	58.72716

APPENDIX 5

Data required to predict the sex of Dunlin

from different sites within Britain

	Anglesey	The Wash	The Tees
Number of males	54	16	24
Number of females	37	17	19
Data from covariance matrix			
Wing - Wing	5.141614	6.066414	7.816217
THL - THL	3.478266	5.068349	-
Wing - THL	1.196953	1.234157	-
Bill - Bill	2.711886	6.10843	2.693263
Bill - Wing	0.9003101	1.178558	0.7586115
Mean values			
Male wing	119.2222	118.25	118.0833
Male bill	31.39815	31.05	30.145
Male THL	55.36111	54.80	-
Female wing	122.21622	121.235	122.579
Female bill	34.92432	34.641	34.7368
Female THL	59.22973	58.235	-

APPENDIX 6

Matrices of Dunlin movements

This appendix gives information on retraps of Dunlin both within the same winter (tables A.6a,d,g and j) and between winters (tables A.6b,e,h and k). These data are then combined in tables A.6c,f,i and 1 to give movements both within and between years. Figures 5.2 to 5.5 give these data in simplified form. This appendix should be looked at with reference to table 5.1 which gives the number of birds caught at each site in each year of the study.

Explanation of tables

The numbers under the name of each bay refer to the five winter time periods: 1) October; 2) November; 3) 1 December to 10 January; 4) 11 January to 20 February and 5) 21 February to 31 March.

The figure at each position in the matrix is the number of individuals which were caught in both the column and the row which identify that box. The row does not necessarily refer to the first capture; it is only in the tables which show within winter movements that direction of movement can be found (as the first capture of the bird has to be in the earlier time period) and then only if the movement is between different time periods.

A bird can only be counted once in any given position but can be counted at more than one position if it has been caught on more than two occasions.

- signifies the positions at which the data would be meaningless as the figures would depend on the number of catches at any given site in a given time period.

. signifies no individuals recorded at that position.

The positions which show mid-winter movements between bays are enclosed in boxes.

TABLE A.6a

RETRAPS OF ADULT DUNLIN WITHIN THE SAME WINTER

	CLEVEDON					SAND BAY					WESTON BAY					BERROW				
	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5
CL																				
1	-																			
2	1	-																		
3	2	106	-																	
4	5	53	39	-																
5	1	28	?	18	-															
SB																				
1	.	1	.	.	.	-														
2	.	1	.	.	.	1	-													
3	1	1	.	.	1	.	2	-												
4	1	5	1	.	.	2	4	8	-											
5	3	4	1	.	5	1	10	5	15	-										
WB																				
1	.	.	.	.	.	.	.	.	.	.	-									
2	.	.	.	.	.	.	.	.	.	.	.	-								
3	.	.	.	.	.	.	.	.	.	.	.	.	-							
4	.	2	.	.	6	.	.	.	2	1	.	1	5	-						
5	2	3	.	.	1	.	2	3	10	29	.	.	.	10	-					
BE																				
1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	-				
2	.	.	.	.	.	.	.	1	.	1	.	1	1	4	2	.	-			
3	.	.	.	.	.	.	.	.	.	.	.	.	3	.	.	.	1	-		
4	.	.	.	.	1	1	.	.	.	2	.	.	2	5	1	.	6	1	-	
5	.	.	.	.	.	.	.	.	.	1	.	.	.	2	.	.	54	2	32	-

TABLE A.6b

RETRAPS OF ADULT DUNLIN BETWEEN WINTERS

	CLEVEDON					SAND BAY					WESTON BAY					BERROW				
	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5
CL																				
1	.																			
2	29	80																		
3	12	62	26																	
4	3	87	48	14																
5	14	127	70	67	26															
SB																				
1	1	1	.	.	.	.														
2	.	3	.	.	3	.	1													
3	1	1	.	.	4	2	2	.												
4	.	5	1	.	6	2	9	5	11											
5	2	8	1	1	7	3	4	4	18	9										
WB																				
1	.	.	.	.	.	.	.	.	.	.	.									
2	.	.	.	.	.	.	.	.	2	.	.	.								
3	.	.	.	.	.	.	.	.	.	.	.	.	1							
4	3	7	.	.	7	1	5	3	12	15	.	2	29	39						
5	..	6	3	2	2	.	3	2	7	12	.	.	6	22	5					
BE																				
1	.	.	.	.	.	.	.	.	.	.	.	.	.	5	.	.				
2	.	1	.	.	.	1	.	.	.	2	.	.	1	9	3	6	27			
3	.	.	.	.	.	.	.	.	.	1	.	.	.	3	.	.	4	.		
4	.	1	.	.	2	.	.	.	.	1	.	.	.	11	1	2	17	2	2	
5	.	.	.	.	.	.	.	.	.	.	.	.	.	6	.	13	25	1	12	.

TABLE A.6c

RETRAPS OF ADULT DUNLIN BOTH BETWEEN AND WITHIN WINTERS

	CLEVEDON					SAND BAY					WESTON BAY					BERROW					NUMBER CAUGHT
	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5	
CL																					
1	-																				102
2	19	-																			1,143
3	7	144	-																		463
4	8	110	64	-																	350
5	15	129	67	28	-																623
SB																					
1	1	2	.	.	.	-															66
2	.	4	.	.	3	1	-														146
3	2	2	.	.	5	2	4	-													127
4	1	9	2	.	6	4	13	11	-												372
5	5	10	1	1	13	4	14	9	27	-											139
WB																					
1	.	.	.	.	.	.	.	.	.	.	-										0
2	.	.	.	.	.	.	.	.	2	.	.	-									12
3	.	.	.	.	.	.	.	.	.	.	.	1	-								129
4	3	9	.	.	13	1	5	3	14	13	.	1	32	-							1,199
5	2	3	2	2	3	.	5	4	15	35	.	.	4	36	-						203
BE																					
1	.	.	.	.	.	.	.	.	.	.	.	.	.	4	2	-					66
2	.	1	.	.	.	1	.	1	.	2	.	1	2	8	3	6	-				548
3	.	.	.	.	.	.	.	.	.	1	.	.	3	3	.	.	5	-			65
4	.	1	.	.	2	1	.	.	1	4	.	.	4	16	2	2	23	3	-		373
5	.	.	.	.	.	.	.	.	.	1	.	.	.	8	.	13	75	3	44	-	1,269

TABLE A.6d

RETRAPS OF ADULT MALE DUNLIN WITHIN THE SAME WINTER

	CLEVEDON					SAND BAY					WESTON BAY					BERROW				
	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5
CL																				
1	-																			
2	1	-																		
3	.	55	-																	
4	.	24	21	-																
5	.	7	5	5	-															
SB																				
1	.	1	.	.	.	-														
2	.	.	.	.	.	1	-													
3	1	1	.	.	.	.	.	-												
4	1	3	1	.	.	.	1	3	-											
5	.	1	1	.	3	.	3	3	7	-										
WB																				
1	.	.	.	.	.	.	.	.	.	.	-									
2	.	.	.	.	.	.	.	.	.	.	.	-								
3	.	.	.	.	.	.	.	.	.	.	.	.	-							
4	.	1	.	.	1	.	.	.	1	.	.	1	3	-						
5	1	3	.	.	.	.	.	1	2	18	.	.	.	4	-					
BE																				
1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	-				
2	.	.	.	.	.	.	.	1	.	.	.	1	.	1	1	.	-			
3	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	1	-		
4	.	.	.	.	1	1	.	.	.	1	.	.	1	1	1	.	3	1	-	
5	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	32	1	18	-

TABLE A.6e

RETRAPS OF ADULT MALE DUNLIN BETWEEN WINTERS

	CLEVEDON					SAND BAY					WESTON BAY					BERROW				
	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5
CL																				
1	.																			
2	12	31																		
3	2	25	16																	
4	1	28	19	7																
5	7	61	36	32	12															
SB																				
1	1	.	.	.	.	.														
2	.	4	.	.	2	1	1													
3	1	1	.	.	2	1	1	.												
4	2	3	1	.	2	.	2	2	3											
5	1	5	2	1	5	2	4	3	5	6										
WB																				
1	.	.	.	.	.	.	.	.	.	.	.									
2	.	.	.	.	.	.	.	.	2	.	.	.								
3	.	.	.	.	.	.	.	.	.	.	.	.	1							
4	.	4	.	.	3	1	1	1	6	6	.	2	17	13						
5	.	3	4	.	2	.	1	.	4	10	.	.	2	15	.					
BE																				
1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.				
2	.	1	.	.	.	.	.	.	.	.	.	1	.	5	1	5	16			
3	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	2	.		
4	.	1	.	.	.	.	.	.	.	1	.	.	2	7	1	1	7	2	2	
5	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	5	11	1	10	.

TABLE A.6f

RETRAPS OF ADULT MALE DUNLIN BOTH BETWEEN AND WITHIN WINTERS

	CLEVEDON					SAND BAY					WESTON BAY					BERROW					NUMBER CAUGHT
	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5	
CL																					
1	-																				53
2	8	-																			541
3	2	71	-																		224
4	1	46	30	-																	148
5	7	55	34	21	-																303
SB																					
1	1	1	.	.	.	-															38
2	.	4	.	.	2	1	-														84
3	2	2	.	.	2	2	1	-													65
4	2	7	2	.	2	.	3	5	-												203
5	1	4	1	.	7	2	12	6	12	-											209
WB																					
1	.	.	.	.	.	.	.	.	.	.	-										0
2	.	.	.	.	.	.	.	.	2	.	.	-									9
3	.	.	.	.	.	.	.	.	.	.	.	.	-								59
4	.	5	.	.	4	1	1	1	7	4	.	1	18	-							633
5	1	5	3	1	2	.	1	1	6	22	.	.	1	16	-						112
BE																					
1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	-					38
2	.	1	.	.	.	.	.	1	.	.	.	.	.	5	2	5	-				373
3	.	.	.	.	.	.	.	.	.	.	.	.	2	2	.	.	3	-			37
4	.	1	.	.	1	1	.	.	.	2	.	.	3	8	2	1	10	3	-		223
5	.	.	.	.	.	.	.	.	.	.	.	.	.	3	.	5	41	2	28	-	736

TABLE A.6g

RETRAPS OF ADULT FEMALE DUNLIN WITHIN THE SAME WINTER

	CLEVEDON					SAND BAY					WESTON BAY					BERROW				
	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5
CL																				
1	-																			
2	.	-																		
3	2	48	-																	
4	5	26	16	-																
5	1	19	4	11	-															
SB																				
1	.	1	.	.	.	-														
2	.	.	.	.	.	.	-													
3	.	.	.	.	1	.	2	-												
4	.	.	.	.	.	2	3	5	-											
5	2	3	.	.	2	.	2	2	7	-										
WB																				
1	.	.	.	.	.	.	.	.	.	.	-									
2	.	.	.	.	.	.	.	.	.	.	.	-								
3	.	.	.	.	.	.	.	.	.	.	.	.	-							
4	.	1	.	.	5	.	.	.	1	1	.	.	2	-						
5	1	.	.	.	1	.	2	2	7	11	.	.	.	6	-					
BE																				
1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	-				
2	.	.	.	.	.	.	.	.	.	1	.	.	1	3	1	.	-			
3	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	-		
4	.	.	.	.	.	.	.	.	.	1	.	.	1	3	.	.	3	.	-	
5	.	.	.	.	.	.	.	.	.	1	.	.	.	1	.	.	14	1	14	-

TABLE A.6h

RETRAPS OF ADULT FEMALE DUNLIN BETWEEN WINTERS

	CLEVEDON					SAND BAY					WESTON BAY					BERROW				
	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5
CL																				
1	.																			
2	15	46																		
3	5	44	8																	
4	1	48	27	6																
5	3	61	26	35	12															
SB																				
1	.	.	.	.	.	.														
2	.	.	.	.	1	.	.													
3	.	.	.	.	1	.	1	.												
4	1	1	.	.	3	2	7	3	6											
5	.	2	.	1	2	1	.	1	8	2										
WB																				
1	.	.	.	.	.	.	.	.	.	.	.									
2	.	.	.	.	.	.	.	.	.	.	.	.								
3	.	.	.	.	.	.	.	.	.	.	.	.	.							
4	.	4	.	.	6	.	.	1	6	9	.	.	12	26						
5	.	2	.	1	1	.	4	1	1	2	.	.	2	17	.					
BE																				
1	.	.	.	.	.	.	.	.	.	.	.	.	.	5	.	.				
2	.	.	.	.	.	1	.	.	.	2	.	.	1	4	2	1	10			
3	.	.	.	.	.	.	.	.	.	1	.	.	.	1	.	.	1	.		
4	.	.	.	.	.	.	.	.	.	1	.	.	.	4	.	1	9	.	.	
5	.	.	.	.	.	.	.	.	.	.	.	.	.	3	.	8	6	.	2	.

TABLE A.6i

RETRAPS OF ADULT FEMALE DUNLIN BOTH BETWEEN AND WITHIN WINTERS

	CLEVEDON					SAND BAY					WESTON BAY					BERROW					NUMBER CAUGHT
	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5	
CL																					
1	-																				49
2	9	-																			602
3	4	68	-																		238
4	6	60	32	-																	202
5	4	67	26	39	-																320
SB																					
1	.	1	.	.	.	-															28
2	.	.	.	.	1	.	-														62
3	.	.	.	.	2	.	3	-													62
4	1	1	.	.	3	4	10	6	-												169
5	2	5	.	1	4	1	2	3	13	-											163
WB																					
1	.	.	.	.	.	.	.	.	.	.	-										0
2	.	.	.	.	.	.	.	.	.	.	.	-									3
3	.	.	.	.	.	.	.	.	.	.	.	.	-								70
4	.	4	.	.	9	.	2	1	7	9	.	.	14	-							566
5	1	3	.	1	1	.	4	2	8	13	.	.	2	20	-						91
BE																					
1	.	.	.	.	.	.	.	.	.	.	.	.	.	4	2	-					27
2	.	.	.	.	.	1	.	.	.	2	.	.	2	5	1	1	-				175
3	.	.	.	.	.	.	.	.	.	1	.	.	1	1	.	.	1	-			28
4	.	.	.	.	1	.	.	.	1	2	.	.	1	7	.	1	10	.	-		150
5	.	.	.	.	.	.	.	.	.	1	.	.	.	4	.	8	18	1	16	-	533

TABLE A.6j

RETRAPS OF JUVENILE DUNLIN WITHIN THE SAME WINTER

	CLEVEDON					SAND BAY					WESTON BAY					BERROW				
	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5
CL																				
1	-																			
2	3	-																		
3	.	19	-																	
4	3	12	16	-																
5	.	3	4	5	-															
SB																				
1	1	.	.	.	1	-														
2	2	.	.	.	1	.	-													
3	.	.	.	.	.	1	1	-												
4	1	2	.	.	.	1	4	10	-											
5	.	.	.	.	.	.	1	7	3	-										
WB																				
1	.	.	.	.	.	.	.	.	.	.	-									
2	.	.	.	.	.	.	.	.	.	.	.	-								
3	.	2	.	.	.	.	1	.	.	.	.	1	-							
4	1	.	.	.	1	1	.	.	1	2	.	2	3	-						
5	1	3	.	.	.	.	.	3	3	3	.	.	2	6	-					
BE																				
1	.	.	.	.	.	.	.	.	.	.	.	.	.	2	1	-				
2	.	.	.	.	.	.	.	.	.	.	.	.	.	2	1	3	-			
3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	-		
4	.	.	.	.	.	.	.	.	.	1	.	.	1	.	.	.	1	.	-	
5	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	5	.	3	-

TABLE A.6k

RETRAPS OF JUVENILE DUNLIN BETWEEN WINTERS

	CLEVEDON					SAND BAY					WESTON BAY					BERROW				
	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5
CL																				
1	.																			
2	1	8																		
3	1	14	2																	
4	1	17	13	7																
5	.	18	5	12	2															
SB																				
1	.	.	.	.	.	.														
2	2	2	.	1	3	1	.													
3	.	1	.	.	.	.	1	.												
4	.	.	1	.	2	3	.	1	3											
5	1	.	.	.	.	.	.	2	1	.										
WB																				
1	.	.	.	.	.	.	.	.	.	.	.									
2	.	.	.	.	.	.	.	.	.	.	.	.								
3	.	1	.	.	.	.	.	.	.	1	.	2	.							
4	.	1	.	.	2	1	.	.	3	1	.	3	7	6						
5	.	1	1	.	2	.	1	1	1	1	.	.	2	3	.					
BE																				
1	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.				
2	.	.	.	.	.	.	.	.	.	.	.	.	2	.	1	.	.			
3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.		
4	.	.	.	.	.	.	.	.	.	.	.	.	1	.	1	.	2	.	1	
5	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	6	.	2	.

TABLE A.6l

RETRAPS OF JUVENILE DUNLIN BOTH BETWEEN AND WITHIN WINTERS

	CLEVEDON					SAND BAY					WESTON BAY					BERROW					NUMBER CAUGHT
	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5	
CL																					
1	-																				56
2	4	-																			167
3	1	32	-																		130
4	4	25	23	-																	146
5	.	19	9	15	-																119
SB																					
1	1	.	.	.	1	-															58
2	4	2	.	1	4	1	-														61
3	.	1	.	.	.	1	2	-													91
4	1	2	1	.	2	4	4	11	-												158
5	1	.	.	.	.	.	1	9	4	-											67
WB																					
1	.	.	.	.	.	.	.	.	.	.	-										2
2	.	.	.	.	.	.	.	.	.	.	.	-									48
3	.	3	.	.	.	.	1	.	.	1	.	2	-								37
4	1	1	.	.	1	2	.	.	4	3	.	3	8	-							191
5	1	4	1	.	2	.	1	4	4	4	.	.	4	9	-						124
BE																					
1	.	.	.	.	.	.	.	.	.	.	.	.	.	3	1	-					17
2	.	.	.	.	.	.	.	.	.	.	.	.	2	2	2	3	-				36
3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	-			6
4	.	.	.	.	.	.	.	.	.	1	.	.	2	.	1	.	3	.	-		35
5	.	.	1	.	.	.	.	.	.	.	.	.	.	.	1	.	11	.	5	-	36

APPENDIX 7

The effect of the severe weather in December 1981 and January 1982 on waders in Eastern Scotland

A preliminary report to the Nature Conservancy Council

by Nigel A. Clark

Introduction

Studies on waders have shown that different species carry varying amounts of fat through the winter months (Branson, 1981; Davidson 1979) and that Dunlin (*Calidris alpina*) achieve different midwinter peak weights at different estuaries around Britain (Pienkowski, Lloyd & Minton, 1979). However, little is known about the ability of waders to survive periods of severe weather or their ability to recover body condition afterwards (Dugan *et al* 1981).

Data from the 1962/63 and 1978/79 winters have suggested that Redshank (*Tringa totanus*) have the highest mortality (Baillie 1980; Pilcher 1974). This was again found to be the case in the 1981/82 winter with Oystercatchers (*Haemotopus ostralegus*) also having a high mortality. The kills in 1981/82 occurred in three main areas on the East coast of Britain: The Moray Firth, Montrose Basin and the Wash (Clark 1982).

This paper is a preliminary analysis of the results of work carried out in Eastern Scotland during the cold weather in 1981/82. A detailed analysis of all the corpses collected is being undertaken. The measurements of dead birds are being compared with those of birds that survived, in Edinburgh; body composition analysis is being undertaken at Durham University.

The Weather

Figure 1 gives the mean daily temperatures at the Firth of Forth (measured at the Royal Botanic Garden) and Montrose (measured two miles north of the Basin).

The timing and severity of the cold weather can be seen clearly. It/

It took the form of two cold spells with a milder period in between. The first cold spell started on 7 December and continued until 27 December. During this period it was colder on the Forth than at Montrose. There were then 8 days of mild weather followed by 11 days of very cold weather; in contrast to the first cold spell it was much colder at Montrose than on the Forth. Figure 2 gives the mean daily wind speed for the Forth (Turnhouse Airport) and Montrose (the nearest site being Leuchars which is 50 km south of Montrose).Leuchars'measurements are similar to those found in Aberdeen which is 50 km north of Montrose. From these data it can be seen that it was in general less windy on the Forth than at Montrose. It can also be seen that it was very windy between the two periods of cold weather. During the second cold spell it was much windier at Montrose than on the Forth.

Dugan <u>et al</u> (1981) used a hypothetical wind chill factor:- the number of °C below 10°C x the square root of the wind velocity in knots. This is plotted in Figure 3, and suggests that conditions were much more severe in Montrose than the Forth and that the second cold spell was extremely severe at Montrose.

The Firth of Forth

After three weeks of severe weather an intensive catching programme was started at Musselburgh on the Firth of Forth. The first catch was made on 20 December with further catches on 23rd and 28 December 1981, and 5th and 22 January 1982.

Redshank

Redshank caught on 20th and 23 December were close to lean weights (Figure 4) with lipid index 0.95 as calculated from Davidson (pers. comm.); some birds being near to death weights. Between 23 December and 5 January both juveniles and adults had put on an average of 10 grams giving a lipid index of 9.6, with 3 juvenile retraps gaining 8, 10 and 21 grams respectively.

Due to licensing restrictions no catches were made in the second period of severe weather between 5th and 16 January. The final catch was made on 22 January after 5 days of very mild weather; the Redshank caught on this date were near their normal winter weight levels, lipid index 12.2%. Observations during the second cold spell suggested that some Redshank were losing condition, however tideline searches revealed only two corpses.

Dunlin

The samples caught between 20th and 27 December were 53 adults and 18 juveniles. Data for adults is plotted in Figure 5. All the adult birds caught in this period were close to lean weight (lipid index 1.2%). The only comparable sample available from a mild winter is of 17 adults on 12 December 1979. These birds were also near lean weight, with the lowest weight 46.5 grams. Birds would be expected to put on weight rapidly after that date as many would only recently have arrived from the Waddensee. 8 out of 53 birds caught between 20 and 28 December 1981 were below 46.5 grams, the lowest being 42.5. These are extremely low weights for Dunlin under normal conditions. By 5 January, when 30 adults were caught, they had put on weight rapidly (lipid index 17%) and were at a very high weight, possibly higher than expected for that time of year. The lowest weight was 51 grams and one adult retrap had put on 7 grams in two weeks. The small number of juveniles caught follow a similar pattern to the adults.

Turnstone (*Arenaria interpres*)

Two small catches were made of this species, 29 adults on 23 December 198 and 15 on 5 January 1982. The mean weight on the 23rd was 118.5 grams and on 5 January 113 grams. There were 4 retraps which lost over the period 4.25 grams on average. This weight change is small, and for this species and both these samples are expected weights at this time of year.

Grey Plover

One juvenile was caught on 20 December and had a normal weight for this time of year.

Bar-tailed Godwit

Three juveniles were caught on 20 December. These were at normal weights.

Montrose Basin, Tayside

The first reports of dead birds were received on 12 January. On that day, a search of the tideline by the roost site at the south-east corner of the basin found corpses of 122 Redshank, 19 Oystercatcher, 5 Dunlin, 1 Curlew and 13 Wildfowl. There were also many corpses floating in the water. At this time, all the Redshank at Montrose were using the south-east roost, as the other roost site, in the north-west corner of the basin, was completely covered by ice. The roost consisted of 300 Redshank, all of which were reluctant to fly: 100 would fly only 5 to 10 metres when disturbed, and 20 seemed incapable of flight. Other waders seemed less seriously affected. On 14 January large numbers of corpses were collected and no birds were seen in very poor condition. Some further Redshanks were found freshly dead, or dying, on 16 January, after another two nights of severe frost. All the tideline of the basin was searched between 17th and 23 January, as the ice melted. This revealed additional corpses, bringing the total found to 341 Redshanks, 104 Oystercatcher, 16 Dunlin, 3 Knot (*Calidris canutus*) and 5 Curlew.

However, these figures underestimate the total mortality for several reasons. Firstly, most deaths probably occurred at the south-east roost, less than 300 metres from the exit of the basin to the sea, so many corpses will have been washed out to sea. There is some corroborative evidence for this: on the north side of the entrance, where little tide-wrack is normally deposited because of steep banks, only 4 Oystercatchers, 1 Dunlin and 1 Redshank were found dead, but these corpses formed most of the tide-wrack; also, 6 Oystercatchers and 4 Redshank were found dead on the beach just to the north of the entrance, where few Oystercatchers and no Redshanks fed or roosted. Secondly, many birds were washed up in large ice-fields, and were seen to be eaten by scavengers as the ice thawed. The remains of these corpses were not found during tideline searches. Thirdly, many birds died on fields near the basin, but only a few corpses were recovered from these areas.

Redshank

By 23 January the population had increased to 600 from the 300 which were present on 12 January. Two cannon net catches were made on 24th and 28 January totalling 173 birds. It can be seen from Figure 6 that the adult birds that died had a mean weight of 109 grams, the two common net samples had mean weights of 157 and 158 grams. The 14 retraps between the two catches had not changed weight significantly.

These weights of live birds are possibly slightly lower than one would expect in a normal winter, but data from previous winters are sparse. It must be remembered that most of the birds that survived from the basin population had moved out during the severe weather. The rate at which birds returned suggested that they had not moved large distances but there is no information as to where they went.

Table 1 shows the proportion of juveniles in the different categories of corpses.

State of decay	Juvenile	Adult	Not aged
Very bad	23	55	11
Partly eaten	17	84	0
Perfect	6	75	0
Caught alive	0	173	0
Total	46	387	11

($X^2 = 54.56$ $P < 0.0001$)

Table 1. Proportion of juveniles in different samples from Montrose

The corpses found in the worst condition almost certainly died first and were buried under ice. They were then eaten as they became exposed by the melting ice. The data strongly suggests that most if not all of the juveniles died on the Basin.

As large numbers of birds have been ringed on the Basin in autumn, ringing recoveries can be used to see which birds died.

Date of ringing	Found dead	Caught 24/28 Jan. 1982
1979-1981	18	21
Before 1979	22	11

($X^2 = 3.0008$ $p < 0.05$)

Table 2. Age of Redshank from Montrose

A significantly higher proportion of birds ringed before the last severe winter (1978-79) were present in the sample found dead than in the sample later caught alive (Table 2).

This is a surprising result as it would be expected that the better adapted birds would have survived the 1978-79 winter and would therefore be more likely to survive another severe winter.

Dunlin

The 67 adults weighed on 24 January had a mean weight of 54.7 gms and 10 juveniles had a mean weight of 52.7 gms. There is little comparable data from previous winters, but these weights are probably normal for this time of year. These data, when taken in conjunction with the fact that only 16 Dunlin were found dead out of a winter population of about 3,000 suggest that Dunlin were not as seriously affected by the cold weather as Redshank.

Oystercatcher

No oystercatchers were caught after the severe weather and the 104 found dead represent only a 3% mortality out of a population of 3,500.

Discussion

The data collected on the Firth of Forth suggested that Redshank were more seriously affected than Dunlin, and that Turnstone were unaffected at least in the first cold spell.

Furthermore, although Dunlin went into the second cold spell with a high lipid index and therefore in good condition, Redshank were at lower than normal weights.

This may help to explain why large numbers of Redshank died at Montrose and only very few Dunlin.

It took only 5 days of very mild weather for Redshank to recover body condition after the second cold spell. This shows clearly that the ability of Redshank to regain body condition after severe weather is greatest on warm windless days, and that on windy days or when the temperature is only just above freezing they may only be able to maintain the status quo or may even lose condition.

A fuller analysis of the effect of wind and temperature on the weight of Redshank is in progress. I would like to thank the Nature Conservancy Council for field expenses incurred during this project. I am also grateful for the help given by members of the Wader Study Group, Edinburgh and Tay ringing groups for their help in catching waders, often in severe weather. I would like to thank Dr. N.P. Ashmole and Mrs. J.A. Clark for helpful comments on discussion on an earlier draft of this paper.

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FIG: 1 MEAN DAILY TEMPERATURE

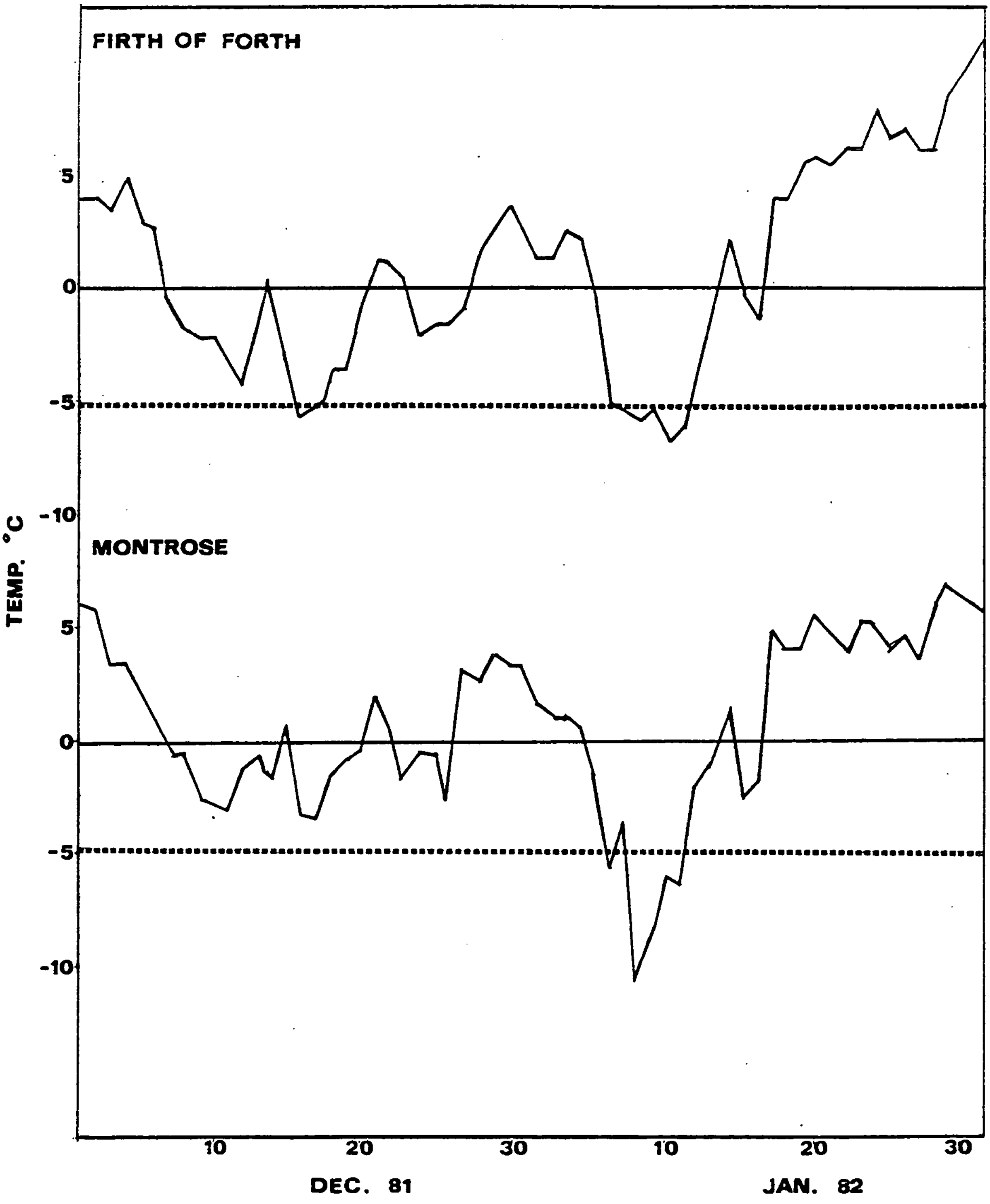


FIG. 2 MEAN DAILY WIND SPEED

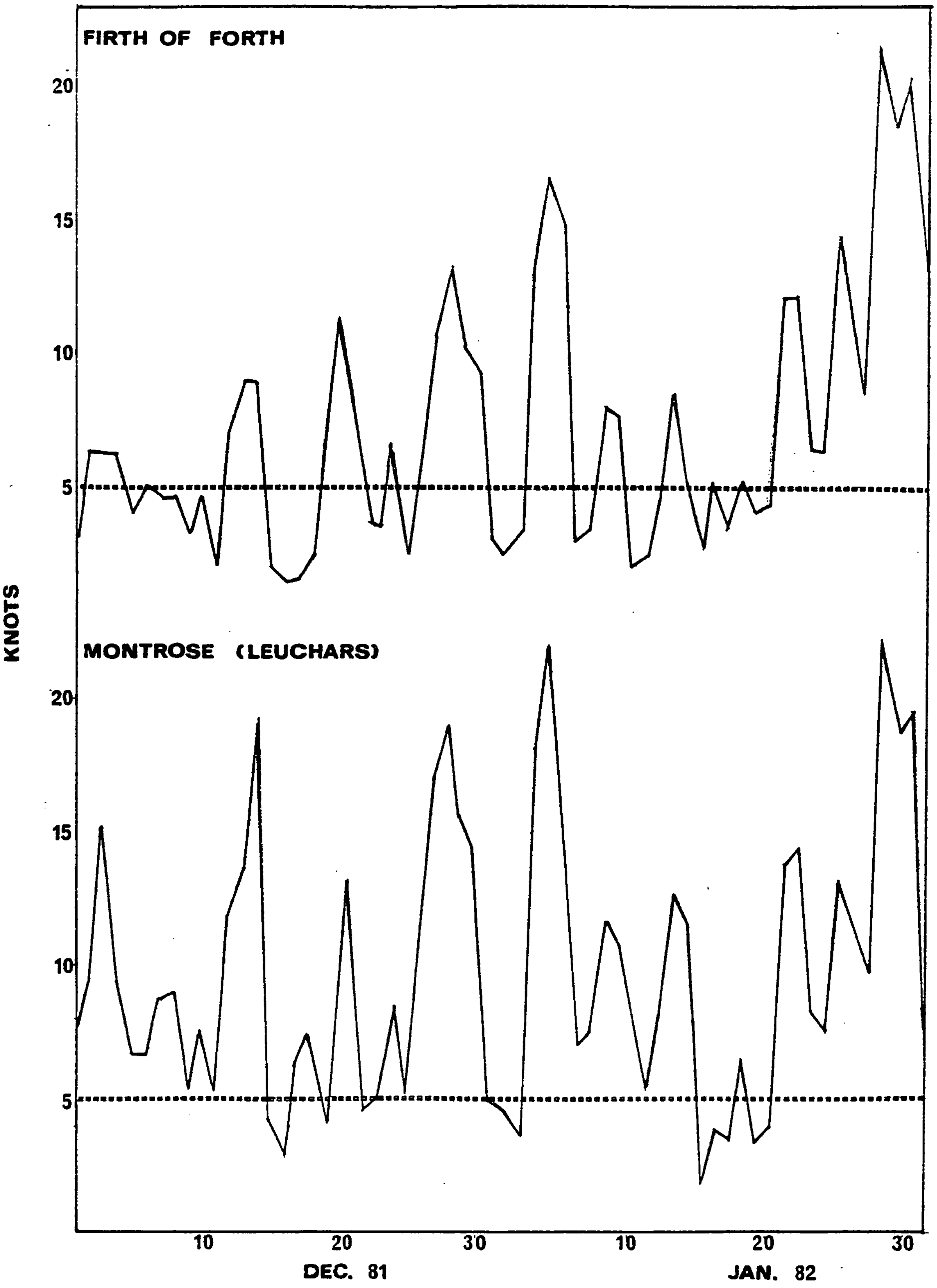
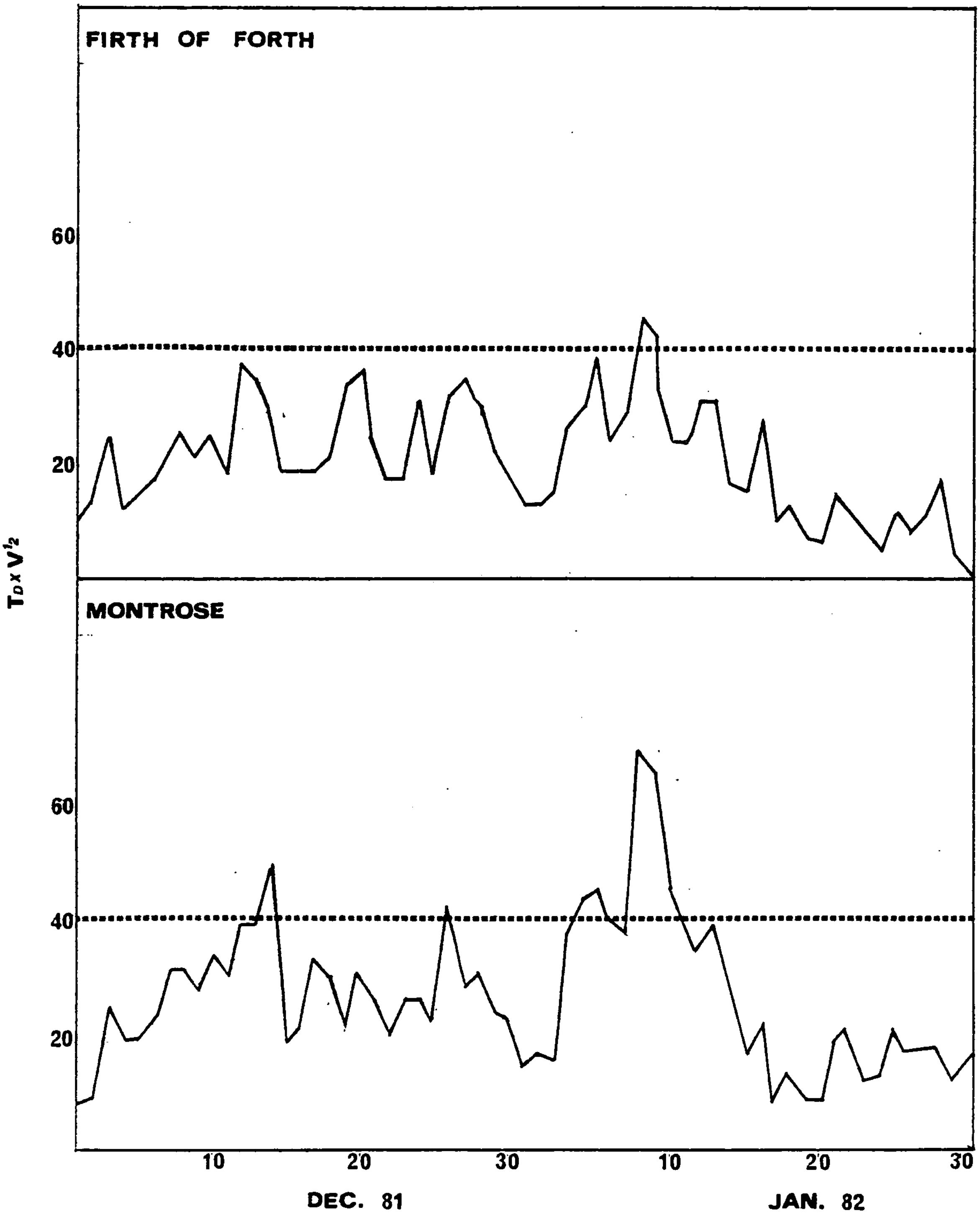


FIG. 3 $T_D \times V^{\frac{1}{2}}$ WINDCHILL INDEX



Legend for Figs. 4, 5 and 6

■	Standard error	Adults
░	Standard error	Juveniles
x	Range	
❘	Standard deviation	
⋮	Retrap	Adults
¦	Retrap	Juveniles

The year is given below the sample size for samples not caught in December 1981 or 1982.

FIG. 4 REDSHANK WEIGHTS ON THE FIRTH OF FORTH

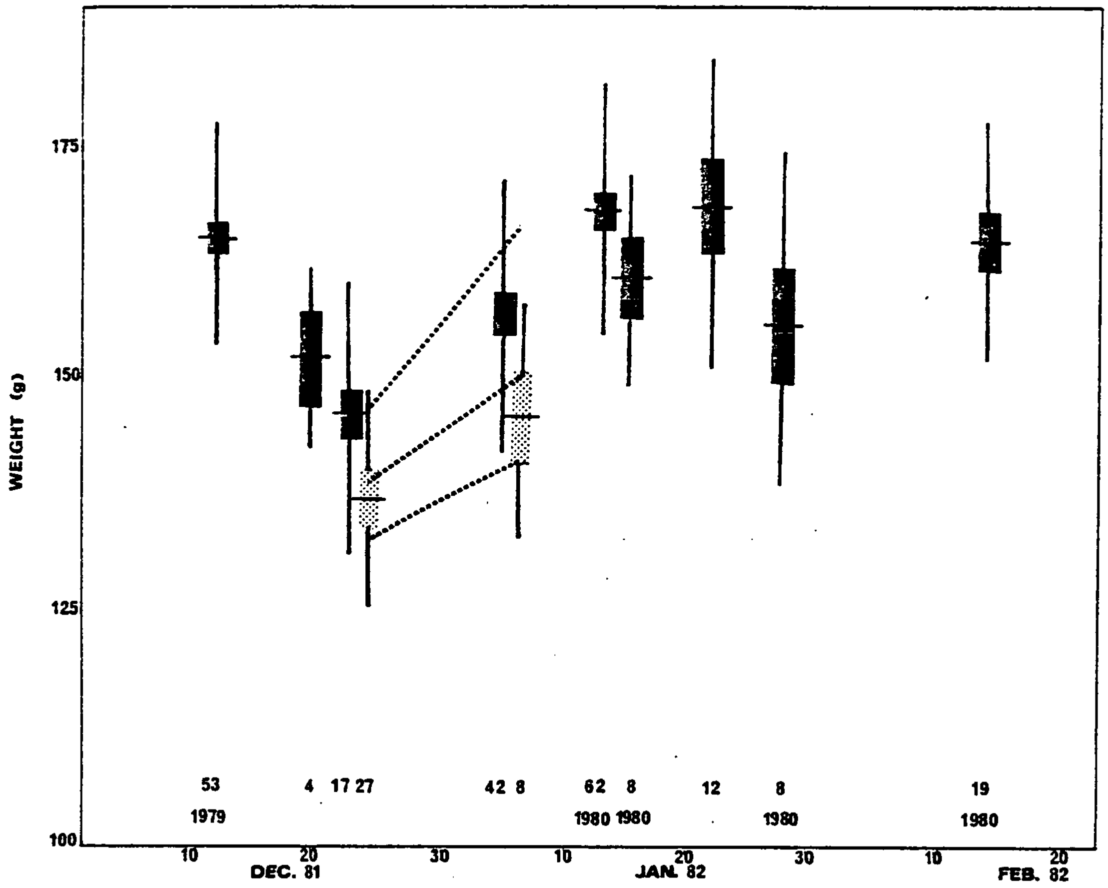


FIG. 5 WEIGHTS OF ADULT DUNLIN ON THE FIRTH OF FORTH

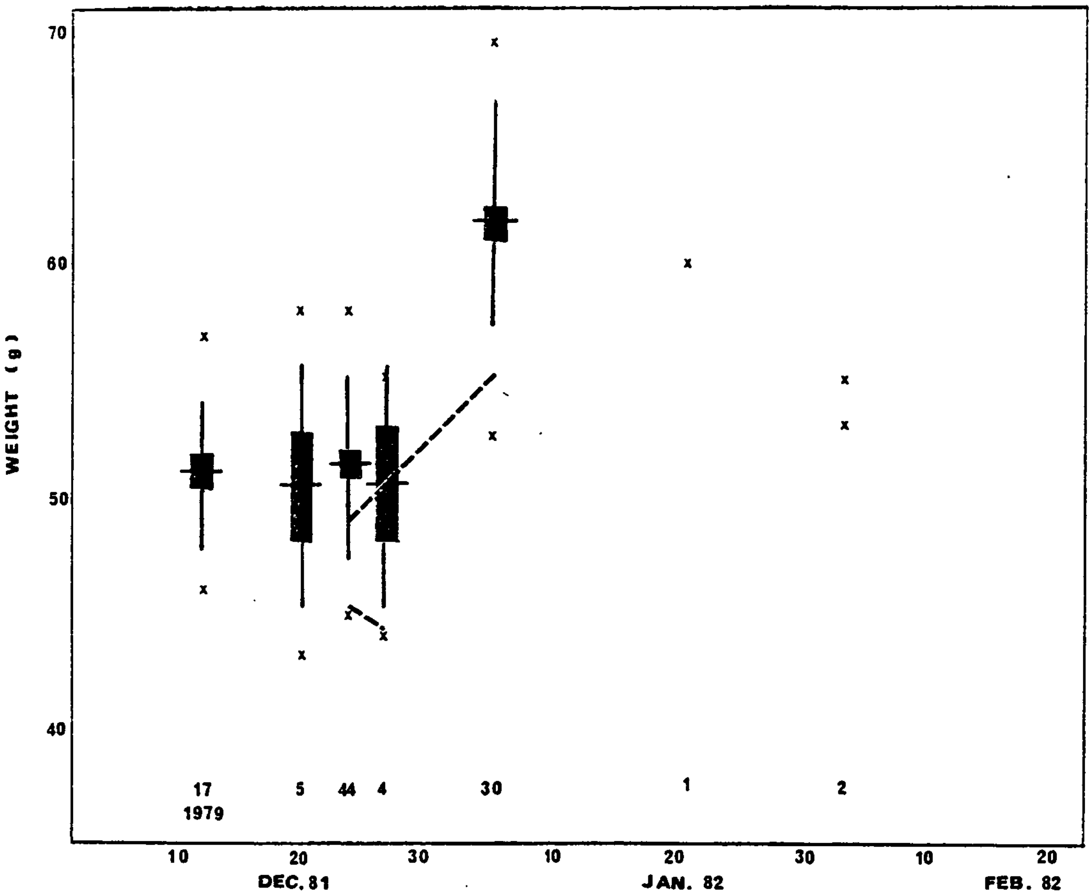


FIG. 6 REDSHANK WEIGHTS AT MONTROSE