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ASPECTS OF PRE-MIGRATORY FEEDING ECOLOGY OF SANDERLING (*Calidris alba* Pallas) AT TEESMOUTH, NE ENGLAND

by

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ABSTRACT

Sanderlings (Calidris alba) like other long distance migrating waders accumulate fat reserves for migration. Feeding ecology of Sanderling was studied during a 8 week period before spring migration, at Teesmouth, NE-England (54°37'N 1°12'W), an important wintering site, to establish how they achieve increased energy. Indications were found of a prolonged feeding-period during daylight hours within each tidal cycle and for less time spent roosting, but nocturnal feeding was not studied. A shift in foraging methods was observed which suggests that they changed to utilizing another prey. A slight increase in rate of feeding attempts and a marked increase in foraging costs were observed which suggests that an increase in prey availability had occurred or that more valuable prey was being taken. Neither suggestion could be tested. Sanderlings foraged in areas where one of their main prey species, the polychaete Nerine cirratulus, was most abundant. Environmental factors which can affect the energy balance of waders in temperate regions in spring are discussed.

ACKNOWLEDGEMENTS

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Chapter 1 INTRODUCTION

The amount of fat carried by most waders wintering in western Europe varies seasonally. Fat reserves are accumulated in autumn and early winter, but used up from mid-winter onwards. As early as March in some species fat reserves are built up rapidly before migration, often to levels much higher than those carried in mid-winter (for discussion see Evans & Smith 1975, Davidson 1982, Pienkowski *et al*. 1984). Many waders are long distance migrants, breeding in arctic or northern temperate regions, but wintering as far south as South Africa. Fat is the main energy source used for these migratory flights (Davidson 1984).

The aim of my study was to find out by what methods Sanderlings (*Calidris alba* Pallas) increase their daily energy intake, when depositing pre-migratory fat reserves. This problem has been studied in only one wader species the Turnstone, *Arenaria interpres*, (Metcalfe & Furness 1984) and certainly not in Sanderling. I carried out my study at Teesmouth, NE England, an important wintering site for Sanderlings in Great Britain. Out of an estimated wintering population of 10,300 Sanderlings in Britain, belived to be of the Siberian breeding population (Prater & Davies 1978), up to c.1200 may occur at Teesmouth (Evans *et al*. 1980) although the average number of individuals present during the winter months of most years is much lower at c.600 (P.R.Evans pers. comm.). During late April and May there is a great turnover in the population, with an influx of passage birds which use the site as a refuelling station on the way to Greenland, at the same time as the wintering birds gradually leave the area to return to Siberia.

There are several possible ways in which birds could increase their daily energy consumption. The following questions were asked and thereafter answers sought in a field study:

i) Do Sanderlings change the proportion of time allocated to different behaviours, within their normal activity period, so that they forage more? Increased foraging time could be achieved by decreasing the time spent in other behavioural states such as vigilance, preening and resting. I found no evidence to support this hyphothesis (see result section 4.3).

ii) Do Sanderlings extend their activity period and thereby their total foraging time? Sanderlings at Teesmouth were known, in the winter, to roost for few hours over the high water period (Brearey 1982), so one possibility was that time formerly allocated to roosting might be decreased so that foraging over high water could thereby be increased. I found some indications that this happened (see results section 4.3 and Appendix 1). I was unable to explore another possibility: whether feeding at night occurs in Sanderling and if so whether it was increased. Many wader species feed at night as well as by day, using primarily tactile search methods (Evans 1976, Wood 1984, Pienkowski _et al._ 1984).

iii) Do Sanderlings increase their foraging rates during the period of pre-migratory fattening? Foraging costs and benefits need to be considered in order to calculate the net rate of energy gain. As long as success rate (successful prey captures per unit of time) increases with an increase in the rate at which attempts are made to capture prey; and if the additional cost of foraging faster is less than the gain from increased success, such a method could be used. I observed a slight increase in foraging rates and a distinct increase in foraging costs before migration but unfortunately I could not measure success rate (see result section 4.4).

Other alternatives by which Sanderling might increase their fat deposits by responses to physical and environmental factors are discussed at the end of the dissertation (Chapter 5).

Intertidal invertebrates are often unevenly distributed (e.g. in patches and clumps) and therefore the quality of feeding sites for their bird predators varies. Data from several field studies have suggested that birds may usually feed where they obtain food at the fastest rate (Goss-Custard 1970, 1977a, 1977b, Connors et al. 1981). Rands & Barkham (1981) found a relationship between within-flock feeding densities of Dunlin (Calidris alpina (L)) and total prey density. To examine whether Sanderlings at Teesside responded to spatial variations in prey densities when foraging, distributions of foraging Sanderlings and their main prey species were studied, though prey availability, which may be more important than absolute density in determining feeding success, was not measured. Prey distribution was far from uniform but I shall show that Sanderlings foraged in areas where one of their main prey species was most abundant (see result section 4.2).

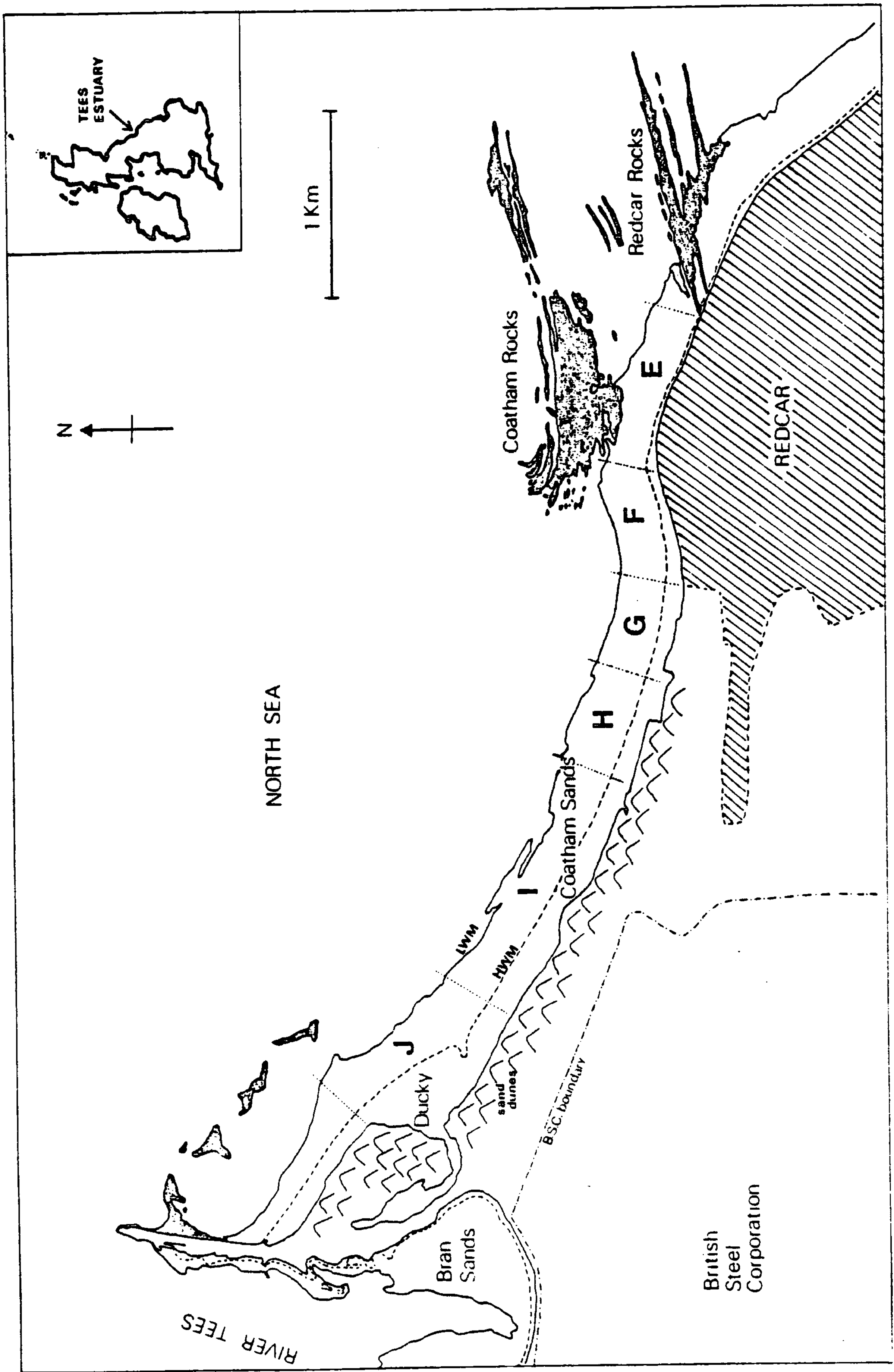
Chapter 2 STUDY AREA

South east of the River Tees estuary (Teesmouth), Co. Cleveland NE England (approx. 54°37'N 1°12'W) lie Coatham Sands, which were the main part of my study area (fig.2.1). Coatham Sands are approximately 5 km long, a stretch of gently sloping beach with fairly fine-grained sand. Coatham Sands face the open sea and there can be considerable wave action during north and easterly winds. At spring tides up to 250 m width of the beach is exposed at low water. East of Coatham Sands opposite the town of Redcar are two limestone outcrops, Coatham- and Redcar Rocks which are exposed for only a few hours of each tidal cycle. Coatham Rocks, which are exposed only at low water of spring tides were not included in the study, but Redcar Rocks were censused regularly. In addition some observations were obtained from a tidal flat within the Tees Estuary called Bran Sands. All previously mentioned sites are used by foraging Sanderlings to a greater or lesser extent, depending on the stage of tide. Over high water in late winter and spring, from March to June (Evans et al. 1980), Sanderling roost at the "Ducky" which is a high part of Coatham Sands, seldom covered except by extreme tides (Fig. 2.1).

Coatham Sands were divided into six sections or sites, labelled E, F, G, H, I and J from east to west respectively, for the the study of bird and invertebrate distributions. These are the divisions which recent and current students of Sanderling ecology at Teesmouth have been using.

The beach and the rocks are much used by people for a variety of outdoor activities during late spring and increasingly so towards the summer. Utilization of the area depends upon the weather and varies between days of the week. People walk dogs, ride horses, bicycles, motorcycles and even tanks along the beach, collect crabs and mussels from the rocks and dig for bait in sand and mud. Off- and onshore are fishing boats and scuba-divers. All this can cause considerable disturbance to birds and thereby for those studying them.

Figure 2.1 A map of the study area. The sites used to locate birds along Coatham Sands are shown, labelled E, F, G, H, I and J.



Chapter 3 METHODS

3.1 General

All field observations on Sanderling were made using a telescope (22x magnification) on a stable tripod. On most days birds were followed along the beach and between sites on foot and approached without using a hide. On 5 occasions observations were made from a vehicle. Observation distance was kept as short as possible without causing obvious disturbance. Observations were either written down in a field-notebook or tape recorded and transcribed later. Locations of birds observed along the beach were allocated to a site (see fig 2.1), their approximate distance from the tide edge and the time of the day were recorded.

Data were collected on 25 days between 17th April and 7th June 1984, during a total of 153 hours of observation. The study period was divided into eight weeks and each of them considered as a sampling unit (Table 3.1). The number of days of observation varied between weeks, ranging from 2 to 4 because of limitations imposed by weather (mainly rain and sea-fog) and transport between Durham City and Teesmouth. Each week spanned a period of either spring- or neaptides.

Table 3.1 Division of the study period into weeks.

week	date	No. of obs. days	tide
1	15.04.-21.04.	3	Spring
2	22.04.-28.04.	3	Neap
3	29.04.-05.05.	3	S
4	06.05.-12.05.	2	N
5	13.05.-19.05.	4	S
6	20.05.-26.05.	4	N
7	27.05.-02.06.	4	S
8	03.06.-09.06.	2	N

The behaviour of a bird was allocated to one of thirteen categories, 1. walking, 2. running, 3. pecking, 4. probing, 5. standing, 6. eating, 7. preening, 8. bathing, 9. stretching wing, 10. roosting, 11. flying, 12. aggression and 13. vigilance. Most of these categories are self-explanatory, although the divisions between some are arbitrary, for example, walking and running, since there is a gradual increase in speed from walking slowly to running fast. Pecks are feeding attempts in which the bill penetrates the sand surface only slightly, whereas in probing at least 1/3 of the bill penetrates the surface. The probing category includes what sometimes has been called "stitching" (Puttick 1979, Brearey 1982). Stitching differs from normal probing in that the bird penetrates the surface while walking forward (in contrast to doing so in a single location). Standing is a rather imprecise category because standing birds can either be foraging or resting. When birds were standing still on both legs, alongside roosting individuals (on one leg or lying down), they were categorised as roosting; otherwise it was assumed that they were foraging (i.e. waiting for a cue). Birds were termed "vigilant" if they stood and stretched their necks, obviously looking out for danger. Under "aggression" were included all aggressive interactions between two individuals (scored as one interaction for the pair).

For many years Sanderlings have been caught in all months in which they have been present at Teesmouth (i.e. from August to June), using mist and cannon-nets, and then ringed and released. Many birds have been colour-ringed using unique combinations of rings which makes identification of individuals possible. I tried to identify as many as possible of those individuals present on each visit, to identify their departure dates.

All analysis of data was carried out on the main-frame computer at the University of Durham using the Michigan Terminal System with either the new SPSSx package (Statistical Package for Social Science) (Nie *et al*. 1983) or a locally devised statistical package for zoologists.

3.2 Distribution of Sanderlings

The ideal method to obtain information on distribution of Sanderlings within the study area would have been to count birds on predefined sectors, from a vehicle driven along the beach at different tidal stages throughout each of several days. A vehicle was nor available and because my study area was approx. 5 km long I was not able to cover the whole area fast enough on foot to make total counts. Therefore I had to apply other methods to obtain information on bird distribution.

By identifying as many colour-ringed individuals as possible throughout the period of study and making a few assumptions I managed to obtain distributional data for the Sanderling. The assumptions were the following: i) colour-ringed individuals were randomly distributed in the population, ii) there was the same chance of seeing the colour-ringed birds in all sites if they were present somewhere at Teesmouth. Also, because I stood to benefit most by making observations where many birds were within range of the telescope I tended to spend most time where the highest densities were; thus iii) I assumed that the distribution of sightings of colour-ringed birds was representative of the population distribution.

3.3 Invertebrate sampling

Transect were taken on Coatham Sands both along- and downshore on 15th of June (and a few to complete the survey a week later). 36 downshore transects were taken at 100 and 200 m intervals along 4 km stretch of the beach, taking samples 0, 20, 30, 40, 50, 60, 80, 100 and 140 meters below high water mark of spring tide (MHWS). Because of an incoming tide, some of the lowest stations on many transects had to be left out (see Fig. 4.5). Height was measured for most sampling stations on 22nd of June using a surveyor's level. The MHWS (5.2 m) was used as the zero level.

The sediment samples were taken using a corer of dimensions 10x10x10 cm (1000 cm^3) and put into labelled polythene bags. All samples were brought to the MSc Ecology laboratory in Durham, where invertebrates were extracted by sieving within 5 days of collection. Samples were kept in a coolroom (5°C). Sieving was done in 37‰ salt solution to avoid osmotic shock for the animals, using a sieve with 20 meshes per inch (mesh size approx. 1 mm). Animals which did not pass through the sieve in about half a minute sifting time were collected. All species apart from Nerine cirratulus were killed in 70% alcohol and then identified and counted. Nerine, a polychaete, curls up when killed in alcohol and therefore they were put in a very dilute Formaldehyde solution to make length measurements easier.

The lengths of all undamaged Nerine specimens were measured to the nearest millimeter.

All data for counts were transformed using a logarithmic transformation (log(x+1) (Elliott 1977). Analysis was then carried out on the transformed data using Student's t-test for comparison between tidal height zones and longshore positions (sites). Kendall rank coefficient of concordance (Siegel 1956) was used on untransformed data to test for zonation of the prey animals.

3.4 Population timebudgets

Time budgets were measured by using near-instantaneous sampling on groups, a technique often referred to as scan sampling (Altmann 1974). At regular intervals throughout the day a group of individuals was scanned in rapid succession and each individual's current activity recorded. Time spent watching each individual was kept constant. Scan sampling data give the time distribution of behavioural states and behavioural synchrony in the the group observed (Altmann 1974).

Foraging flocks of Sanderlings (more than 20) were scanned in three different habitats i) on Redcar Rocks, ii) on Coatham Sands and iii) on Bran Sands, though mainly on the first two. Scans were taken at 15 minute intervals when possible, but movements of flocks out of observation range, due to disturbance or other reasons, often led to irregularity. Care was taken to avoid including the same individual more than once in each scan. Activity of each individual was categorised as described above and tape recorded as soon as the bird was spotted. Each scan took less than 5 minutes, depending on flock size and distribution, so that only few seconds were spent on each individual. I tried to divide the observation periods as evenly as possible throughout the tidal cycle and the 8 week study period, but planning in advance was often negated by bad weather.

To allow for differences in sample size all data were transformed into proportions (each behaviour as a percentage of all observed behavioural events) to make the scan samples comparable. Investigation of these proportions, otherwise untreated, showed that for all behavioural states the distribution of the data was significantly skewed. All attempts to correct the skewness by transformations of the data failed and therefore non-parametric statistics were applied (Siegel 1956).

To simplify analysis, the data were pooled when possible. The Kruskal-Wallis one-way anova was used to test whether data could legitimately be pooled. Chi-square tests (on observed numbers) were used to test for differences.

3.5 Foraging rates

When monitoring feeding rates and other behaviours, I obtained data primarily from colour-ringed Sanderlings. I began by selecting individuals which were known from previous years' records to leave late in May or in June, to be able to follow them throughout the pre-migratory period, taking series of measurements. However I spent valuable time looking for these birds without finding them. Later, when the number of colour-marked birds decreased, I began to take measurements on all available birds, regardless of their departure dates in previous years. The last sightings of individuals were assumed to be the result of departure rather than death (many of the individuals have again returned to Teesmouth after the 1984 breeding season (D.Townshend, pers.comm.)).

Foraging rates were measured by observing a selected foraging individual (i.e. a colour-ringed bird) for 5 minutes and describing and counting all its movements on a tape recorder. The 5 minutes duration time was selected having regard to other studies on waders using similar methods. Townshend (1982) in his study of Grey Plovers (Pluvialis squatarola) and Curlew (Numenius arquata) came to the conclusion that 4 minutes was a sufficient time-period and that longer measurements did not decrease the variation. Dugan (1981) who also tested for optimal duration of observation in his study on Grey Plover used more than 3 minutes. As the Sanderlings move in all respects faster than Grey Plovers, 5 minutes was taken as sufficient duration. The observation period was measured using a stopwatch with a bleeper. Actual timing of separate behavioural events was impossible because of the fast movements of Sanderlings. (Some observations were less than 5 minutes due to departure of the individual, caused by disturbance or other reasons. These measurements were used in the analyses provided that observations lasted more than 60 seconds.)

To check the validity of field measurements and in the hope that it might solve the problem of measuring feeding success rate, video films of foraging Sanderlings were taken the 24th of May. A Sony videocamera was used, provided with a 25-300 mm manual zoom lens and attached to a Hitachi video-recorder. The film was later analysed (using a JVC video-projector); i) by taking repeated measurements in selected parts (1 - 2 ½ min.) played at normal speed, using the same methods as in the field and ii) slowing the film sufficiently to allow accurate counting of each behavioural event.

Data analyses were carried out using rates per minute. Only foraging rates were analysed, because other events which could be presented as rates were too infrequent. Data distribution were tested for skewness and transformed where appropriate. Transformations used to stabilize the variance included square root transformation (x+1) and logarithmic transformations (log x) (Snedecor & Cochran 1967). The transformed data were then analysed using regression and correlation techniques. Comparisons between groups were made using Student's t-test.

Chapter 4 RESULTS

4.1 Distribution of Sanderlings

The distribution of Sanderlings was studied to answer the question whether utilization of the feeding areas lying to the south of South Gare, Teesmouth, varied with tidal stage (cf. Brearey 1982) and whether it related to densities of the main prey species of Sanderling (see section 4.2). I also examined whether the utilization pattern changed during the 8 week period of study.

Out of a total of 711 sightings of colour-ringed Sanderlings, 636 from Redcar Rocks and Coatham Sands were used for analysis. The remaining sightings were from (i) the "Ducky", which was not a feeding area, (ii) site E on Coatham Sands which was not included in the invertebrate survey and (iii) from Bran Sands which were only rarely visited.

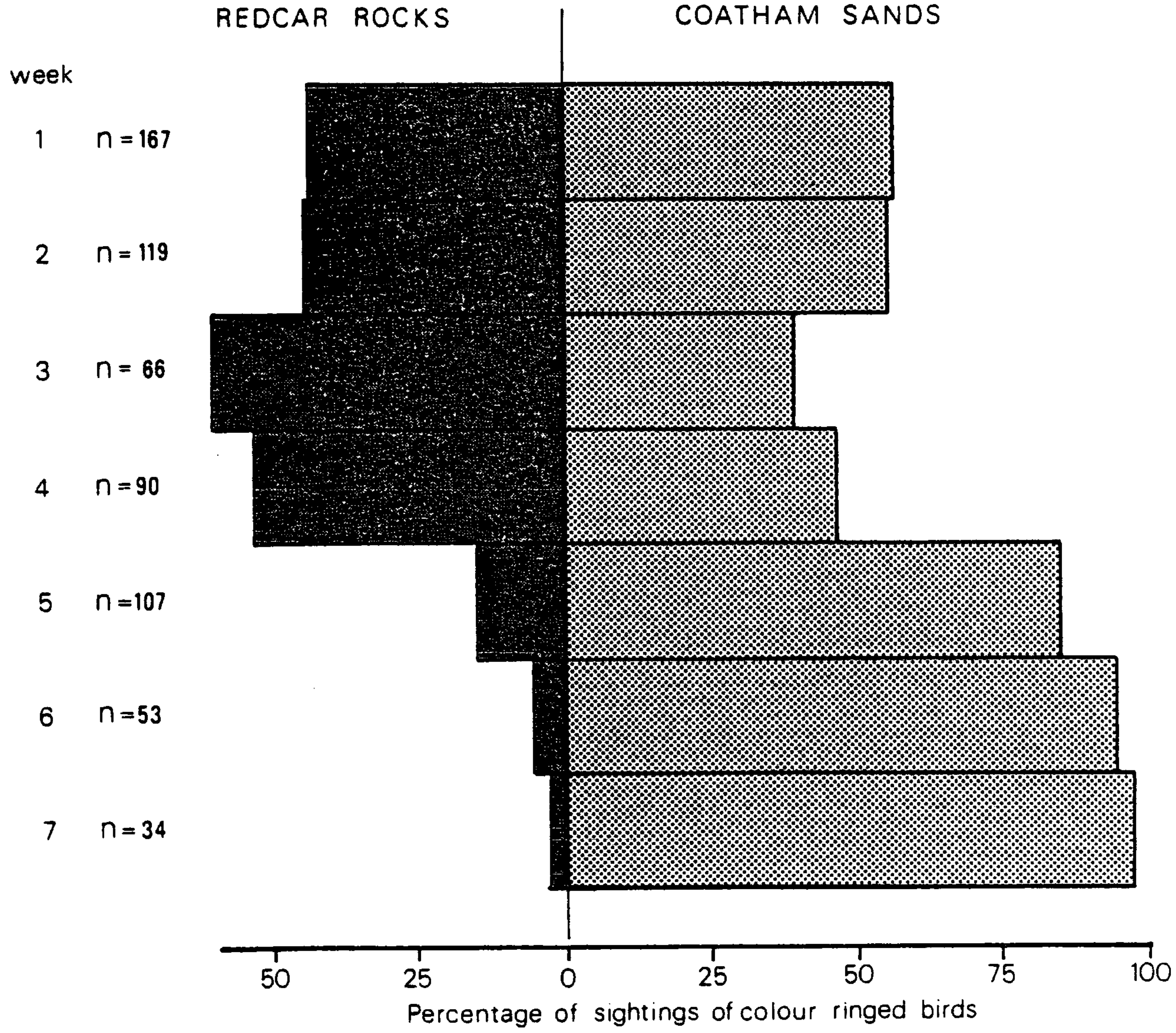
Two analyses were made; (i) a comparison between numbers of sightings on Redcar Rocks on the one hand and the whole of Coatham Sands (sites F to J pooled) on the other, regardless of tidal stages. This was done to see how these two habitats were utilized in different weeks; (ii) a comparison amongst sites (F to J) on Coatham Sands at different tidal stages, using pooled data from all weeks. This was done to see whether there was a relationship between distribution of foraging Sanderlings on the beach and measured densities of their main prey animals, at each stage of the tidal cycle.

The results from the first part are shown in Figure 4.1. For the first four weeks the proportions of sightings in the two areas were similar (40-60%) (n x m chi-square test on raw data for weeks 1 - 4 gave $\chi^2_3 = 6.99$, $p > 0.05$). For the remaining three weeks (5 - 7) the proportions between sites diverged but did not differ significantly amongst the weeks ($\chi^2_2 = 5.71$, $p > 0.05$). However when all the weeks were compared the results were highly significantly inhomogenous ($\chi^2_6 = 93.98$, $p < 0.001$). This suggests that around the middle of May the birds behaviour changed. Sanderlings almost gave up using Redcar Rocks over the low water period, and began using Coatham Sands throughout the entire tidal cycle. I kept on censusing Redcar Rocks throughout the study period, but was unable to obtain any data there in the last three weeks because of low number of birds present. I can only guess that this shift was due to increased disturbance by holiday makers at Redcar. Unfortunately, no quantitative data were obtained on magnitude of disturbance.

Until mid May the utilization of the area followed the same patterns as noted by Brearey (1982) for the period August to April. The main features were that on the ebbing tide, after high water, birds that had been roosting on the Ducky moved gradually along the beach towards Redcar Rocks, where a great proportion spent the low water period (when the rocks were exposed). The reverse happened on the flooding tide.

The second analysis was conducted as follows. First I compared the use of the different sites on Coatham Sands by Sanderlings between the two previously mentioned time

Figure 4.1 Utilization of Coatham Sands and Redcar Rocks by Sanderlings in different weeks, presented as proportions of all observations of colour ringed birds within sites.



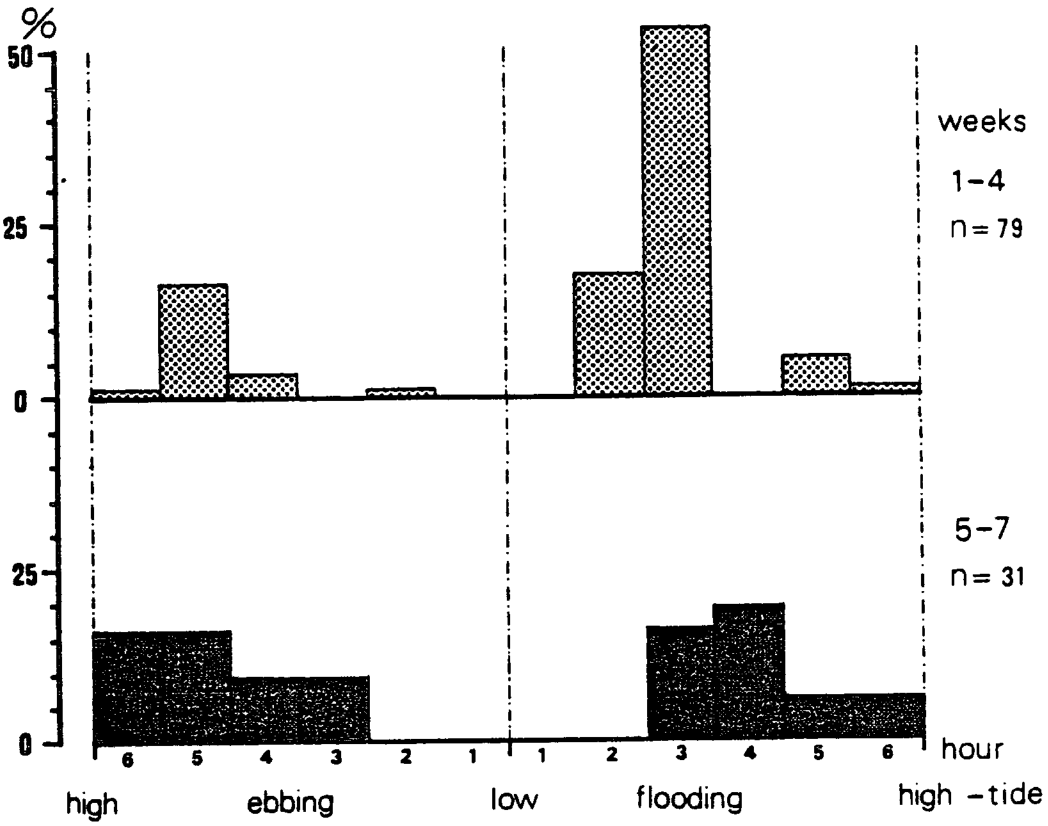
periods (weeks 1-4 and 5-8) at different stages of the tidal cycle. During the period until mid May not a single sighting of colour-ringed individual was made on the ebbing tide on site J and only a few on site I. These sites were primarily used one to two hours after LW. After mid May the utilization of sites I to J changed markedly. Site I was used particularly on the ebbing and flooding tides but not over the period LW ± 2h. Site J was primarily use over the low water period (see Figure 4.2). For other sites on Coatham Sands no obvious change in use occurred between the periods before and after mid May. I therefore pooled observations from all weeks to obtain an overall picture of utilization of different sites along the beach at different tidal stages. Data were corrected for differences in the size of each site by ajusting the number observed in each according to the length of beach involved. The results are presented in Figures 4.3 and 4.4. Figure 4.3 shows the corrected proportion of sightings at the different sites (F to J) at eleven tidal stages (approx. one hour each). Figure 4.4 shows the proportions of Sanderlings within each site using it at six different tidal heights which correspond roughly to the height zones used in the invertebrate analysis (see section 4.2). These results will be discussed jointly with the results from the invertebrate survey.

4.2 Distribution of the Sanderlings main prey

Although all macro-invertebrates present in the samples were extracted, the study focussed on the dominant prey species. Those species and groups which were left out (e.g.

Figure 4.2 Percentage of sightings of colour ringed Sanderlings within sites J and I on Coatham Sands at different hours of tide. The observations are split into two periods, weeks 1 to 4 and 5 to 7, which are compared.

Site I on Coatham Sands



Site J on Coatham Sands

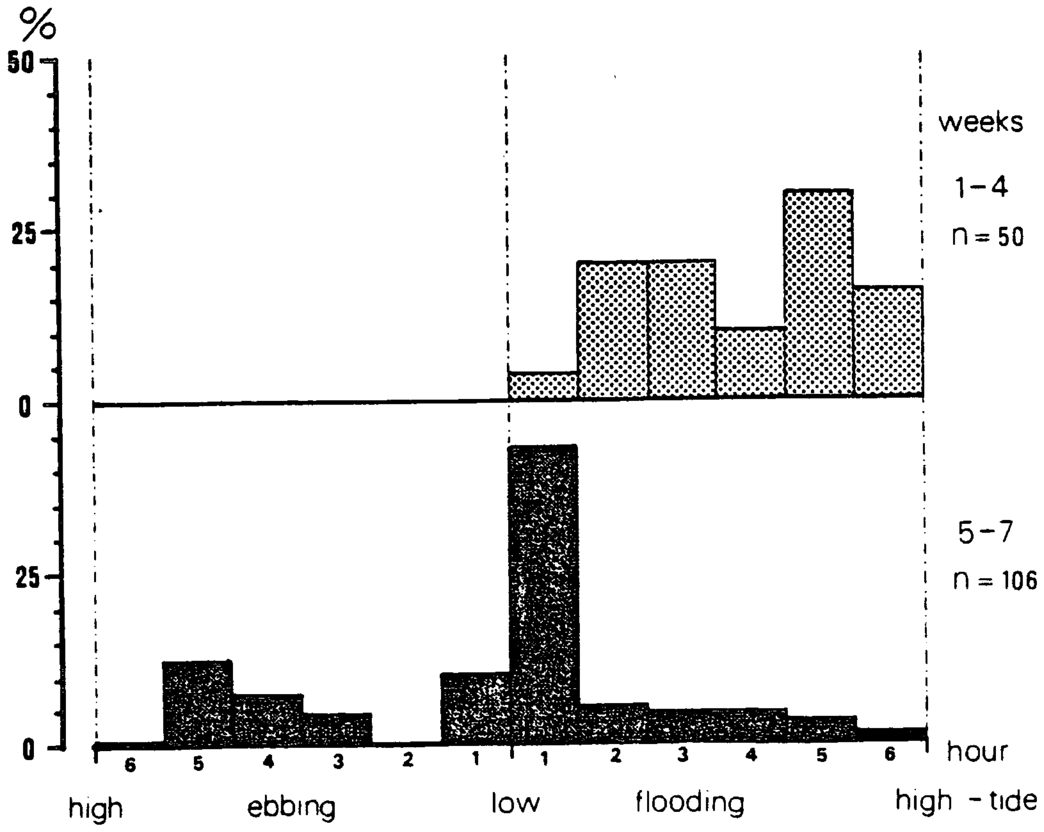


Figure 4.3 Distribution of feeding Sanderlings along Coatham Sands in relation to time of tide. The proportion of sightings of colour ringed birds at each site and at each hour of tide is shown (n=402). The numbers were adjusted for length of the sites. Data from all weeks (1-8) pooled.

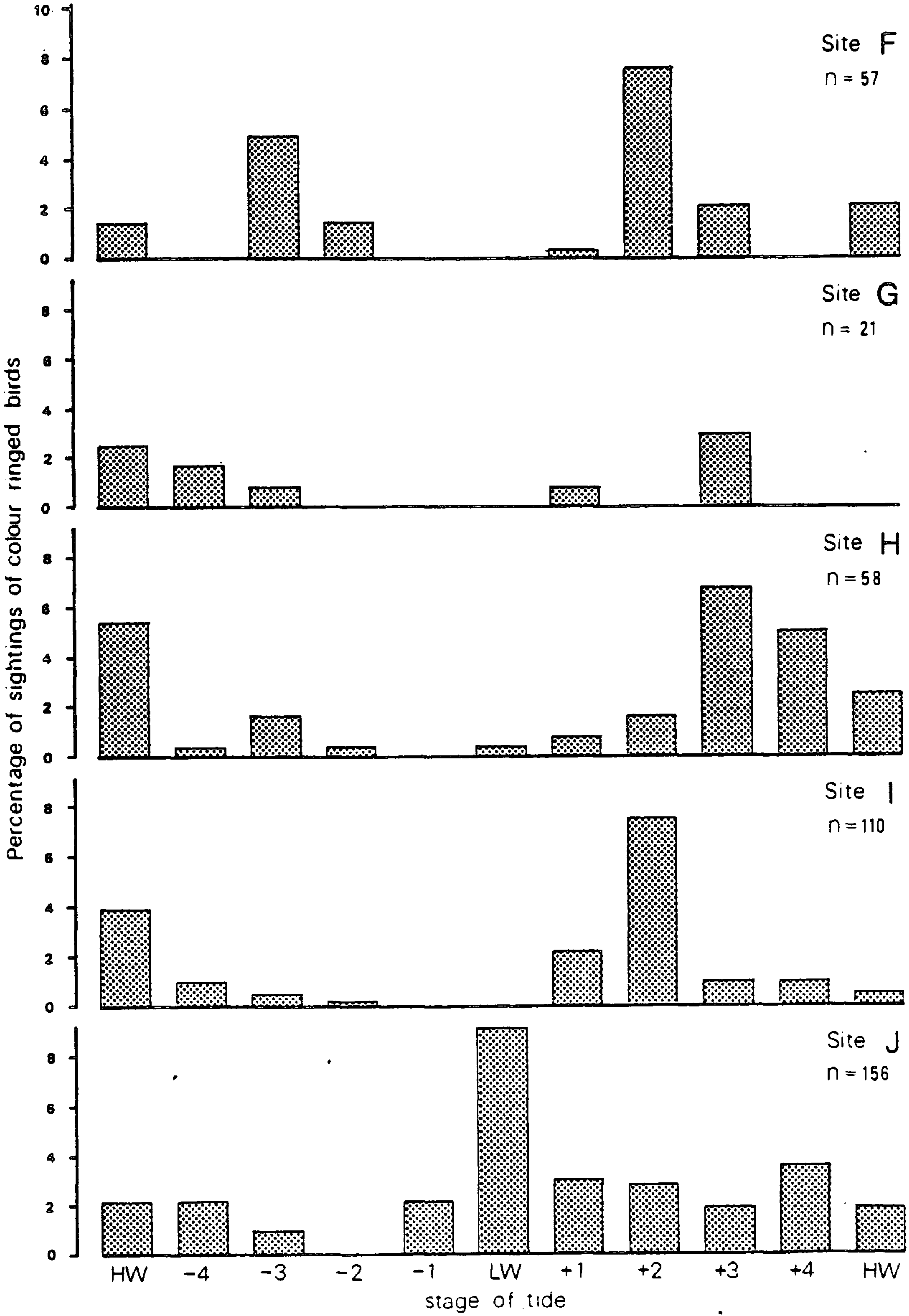
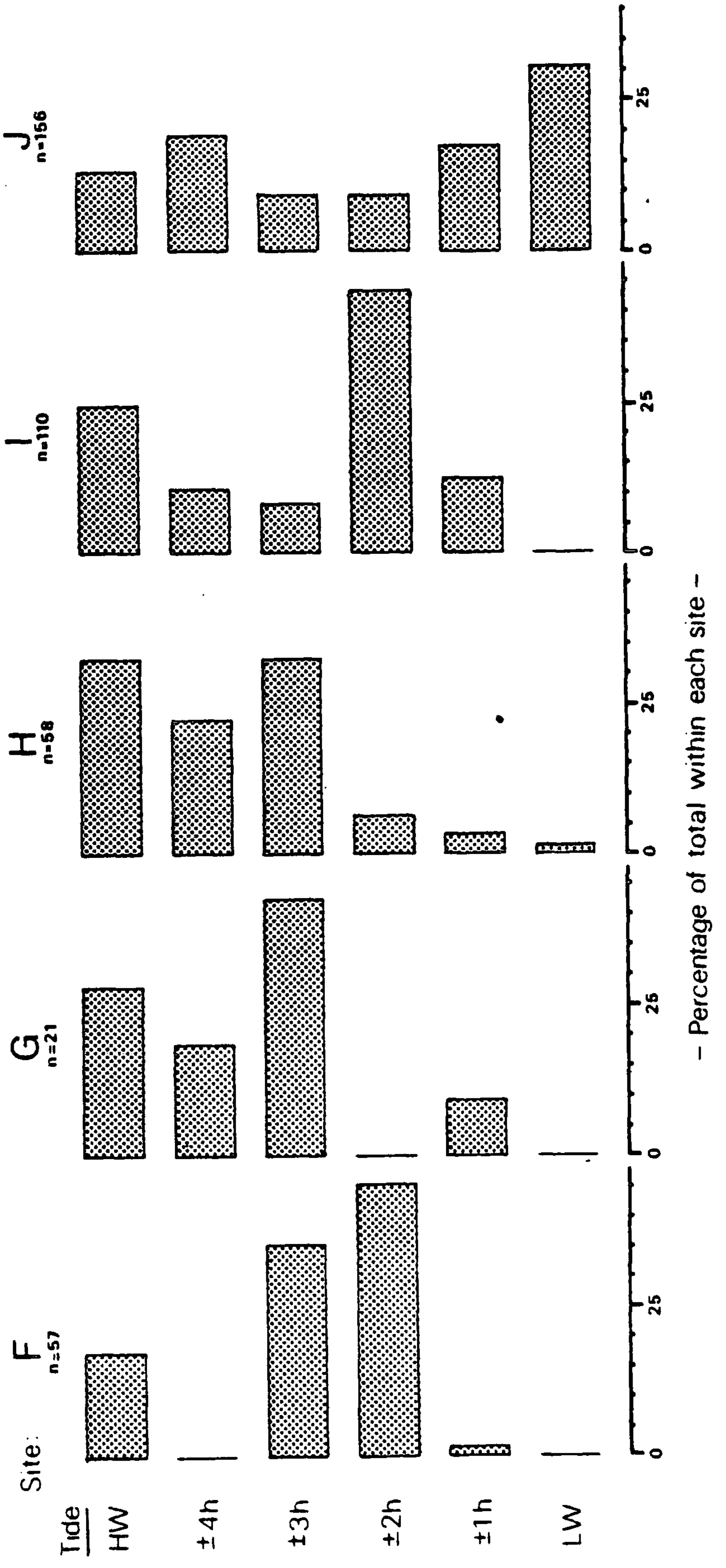


Figure 4.4 Utilization of Coatham Sands by feeding Sanderlings. Percentage of total sightings within each site at six tidal stages is shown.



polychaete species *Nephthys* spp., the crustaceans *Talitrus saltator* and *Haustorius arenarius*) were represented by only a few individuals and often in very restricted areas. They were assumed to be of little importance to foraging Sanderlings.

The three groups of importance were the polychaete species *Nerine cirratulus* (Delle Chiaja), the amphipod genus *Bathyporeia* (primarily *B. pelagica* (Bate) but also *B.*cf.*pilosa* (Lindström), which was much less frequent) and the isopod species *Eurydice pulchra* (Leach). The decision was taken not to separate the *Bathyporeia* species in the analysis but to treat them as one group.

Data were pooled for transects within each site along Coatham Sands but divided into six height-zones, as illustrated in Figure 4.5. The data were grouped into five sites (F to J) to obtain information which could be compared directly to the distributional data of Sanderlings, rather than dealing with each transect independently. The height-zones covered 0.5 m height ranges as follows, counting up the shore: zone 5 = 2.2 to 2.7 m, zone 4 = 2.7 to 3.2 m, zone 3 = 3.2 to 3.7 m, zone 2 3.7 to 4.2 m, zone 1 = 4.2 to 4.7 m and zone 0 = 4.7 to 5.2 m. Height-zone 0 was not included in the analysis because no *Nerine* and very small numbers of other main prey species were found there. The average counts (presented as numbers m^{-2}) for the three most important groups of prey are shown in Table 4.1. Weighted column averages (derived from all samples in zones 1 to 4 within each site) and weighted row averages (derived from all samples from each height-zone in all transects) are also given.

Figure 4.5 Sampling stations and the height zones in the invertebrate survey on Coatham Sands. Each height zone covers 0.5m height difference.

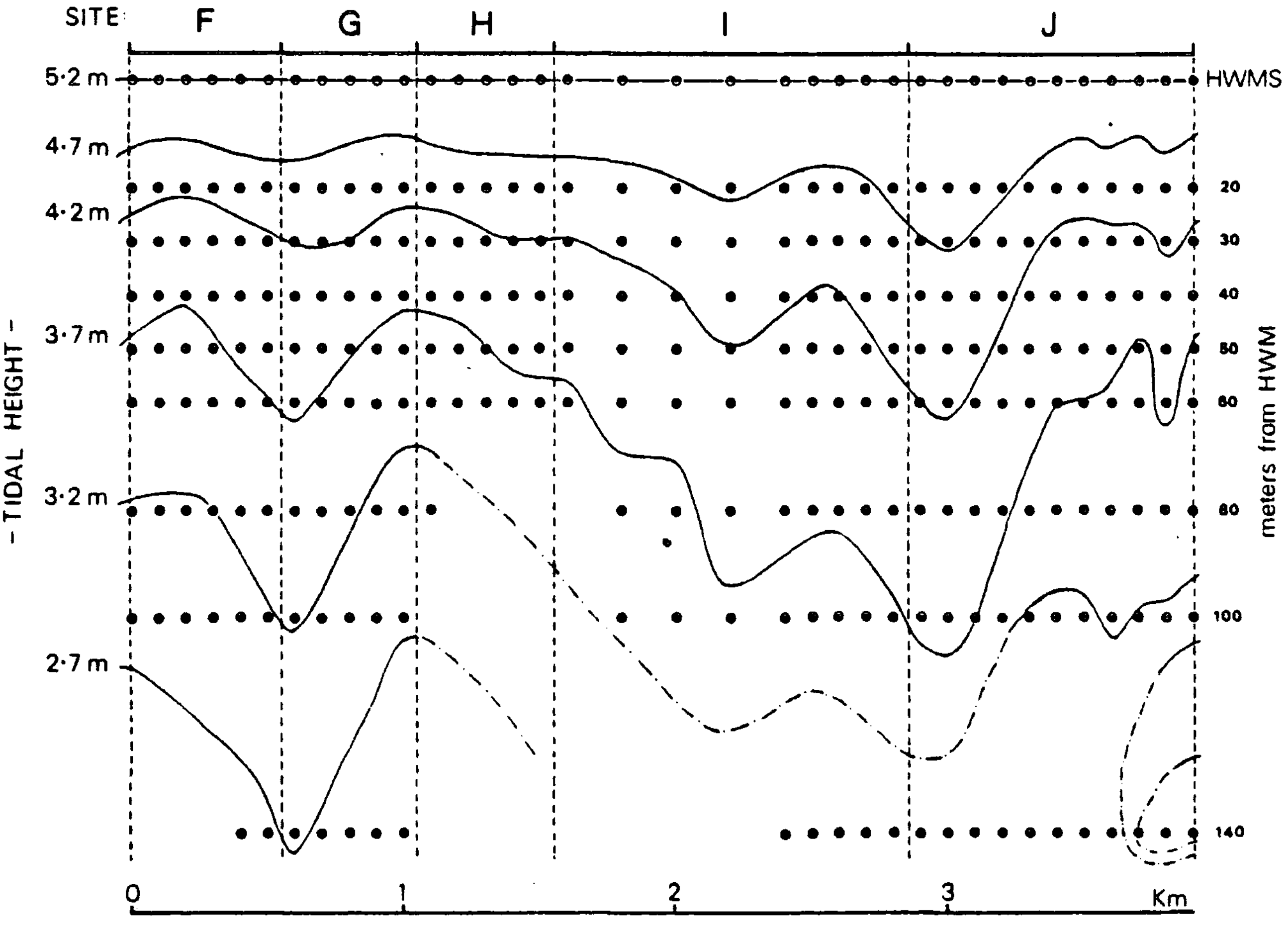


Table 4.1 PREY DENSITIES, (nos. m^{-2})

Average densities of Sanderling's three main prey invertebrates, in different height-zones at various sites along Coatham Sands. The height-zones cover 0.5 m height range, going from 0 (near HW) to 5 (near LW).

a) Number of samples within sites and zones from which mean densities were calculated.

Height -zone	Site: F	G	H	I	J	n
0	6	5	5	11	16	43
1	6	7	7	21	20	61
2	14	12	10	27	29	92
3	12	10	8	13	17	60
4	10	7	1	5	14	37
5	2	4	0	0	0	6
m	50	45	31	77	96	299

b) *Nerine cirratulus*

Height -zone	Site: F	G	H	I	J	weighted mean
0	0	0	0	0	0	0
1	333	971	557	133	10	257
2	236	475	340	63	79	178
3	100	120	113	154	71	108
4	140	0	0	60	128	94
5	(0)	(50)	-	-	-	-
weighted mean	188	334	315	103	69	(141.5)

c) *Eurydice pulchra*

Height -zone	Site: F	G	H	I	J	weighted mean
0	17	0	0	0	0	2
1	83	14	14	48	490	189
2	36	8	40	85	317	136
3	58	10	13	62	100	57
4	40	43	0	0	107	59
5	(0)	(25)	-	-	-	-
weighted mean	50	17	23	62	278	(99.7)

d) *Bathyporeia* spp.

Height -zone	Site: F	G	H	I	J	weighted mean
0	0	0	0	9	6	5
1	67	29	14	181	455	223
2	179	25	40	626	338	325
3	292	120	163	77	82	140
4	350	86	0	80	71	149
5	(250)	(125)	-	-	-	-
weighted mean	236	64	69	335	266	(196.0)

The downshore distribution of the prey species was examined by using ranking techniques (Kendall coefficient of concordance, W (Siegel 1956)), ranking the zones within each site using mean densities (Table 4.1). The highest density was ranked as 1, the second highest as 2 etc. The ranks were then added for each site giving the values x_F to x_J. The formula for calculating concordance

$$W = \frac{12\ S}{m^2 n(n-1)}$$

was then applied where m = no. of sites, n = no. of zones and $S = (x_{\text{for site}} - x)^2$, where x = mean of x_F to x_J. The significance of W was tested using the variance ratio test statistic F, where

$$F = \frac{(m-1)\ W}{1 - W}$$

with calculated degrees of freedom

$$P_1 = n-1-2/m \quad \text{and} \quad P_2 = (m - 1)P_1$$

Comparisons for both *Nerine* and *Eurydice* gave W-values which were significant on the 0.01 probability level (see Table 4.2). Such a high probability suggests that there is an agreement amongst the sites as to which zone has highest density. The sum of ranks within zones indicates the order of relative density, the smallest sum indicating the zone of highest density.

These results show: i) that *Nerine* is most abundant at height zone 1 and numbers decrease down the shore, ii) that *Eurydice* ia also most abundant high on the shore and that numbers decrease down the shore, and iii) that *Bathyporeia* showed no significant zonation. When the absolute abundances of each prey species within each zone, at each

Table 4.2

"DOMINANCE". Ranks of mean densities of Sanderling's three main prey invertebrates, for different height-zones within a site, used to calculate the order of dominance of the zones.

a) *Nerine cirratulus*

Height -zone	Site: F	G	H	I	J	sum of ranks
1	1	1	1	2	4	9
2	2	2	2	3	2	11
3	4	3	3	1	3	14
4	3	4	4	4	1	16

Calculated W = 1.16
Calculated F = 29.0, $(p < 0.01)$ Significant.

b) *Eurydice pulchra*

Height -zone	Site: F	G	H	I	J	sum of ranks
1	1	2	2	3	1	9
2	4	4	1	1	2	12
3	2	3	3	2	4	14
4	3	1	4	4	3	15

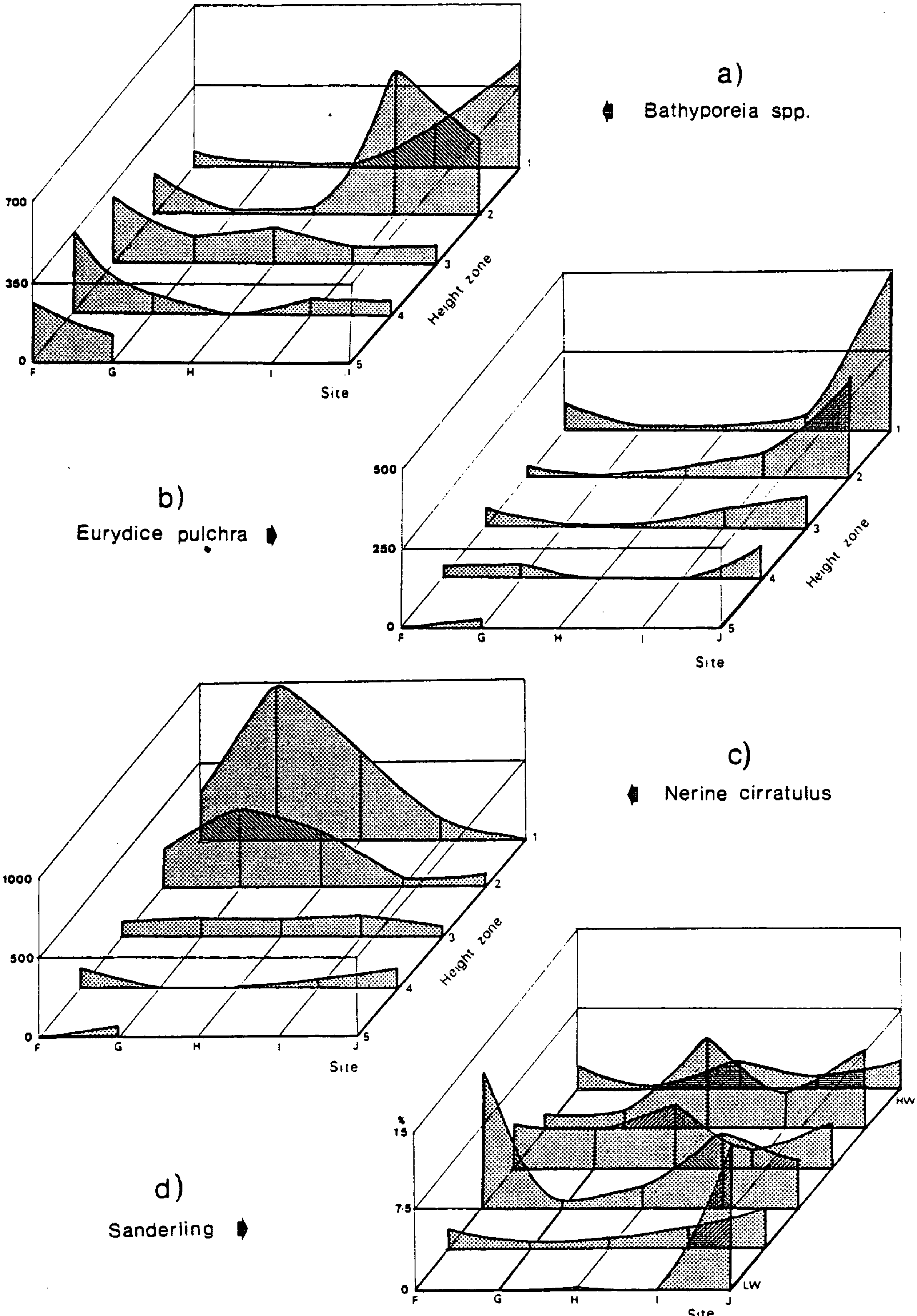
Calculated W = 0.84
calculated F = 21.0, $(p < 0.01)$ Significant.

c) *Bathyporeia* spp.

Height -zone	Site: F	G	H	I	J	sum of ranks
1	4	3	3	2	1	13
2	3	4	2	1	2	12
3	2	1	1	4	3	11
4	1	2	4	3	4	14

Calculated W = 0.20
Calculated F = 1.0 $(p > 0.05)$ Not significant.

Figure 4.6 a) to c) Mean densities (No.of indiv.m^{-2}) of Sanderling's three main prey invertebrates within sites and height zones on Coatham Sands compared with d) The distribution of foraging Sanderlings at six tidal heights presented as proportions of all sightings, ajusted for length of sites.



site, are plotted (Figure 4.6) it is clear that Nerine and Eurydice show marked zonation.

When height zonations within sites were examined, using Kendall rank correlation coefficient, τ (tau) (Siegel 1956), it became clear that the failure to find a consistent zonation of Bathyporeia was caused by differences between sites. The test showed that within sites F and G Bathyporeia density increased significantly down the shore (τ negative) but vice versa on J (τ positive) (Table 4.3 a). Nerine also showed irregularities in zonation which were not detected in the concordance test. Nerine abundance decreased significantly down the shore in sites F, G and H but increased in J where it was scarce. For Eurydice densities two significant correlations were found between abundance and zone, in sites F and J, where Eurydice became less abundant down the shore (Table 4.3 a).

To examine the alongshore distribution of the prey animals, the Kendall rank correlation coefficient was used again. I tested for correlations between densities and sites within height-zones (see Table 4.3 b, for numerical results). The Nerine density decreased significantly along the beach from east (G) to west (J) within height-zones 1 and 2 (τ negative). However, within height-zones 3 to 5 the correlation was positive, but not significant at the 5% level. Eurydice density increased significantly along the beach from east to west within height-zones 1, 2 and 3; Bathyporeia increased significantly from east to west within height-zone 1 but vice versa within zones 3 and 4.

When variations in invertebrate density are examined (both within site and within zone, Figs. 4.6 and 4.7) the

Table 4.3

Correlation matrices examining a) trends in densities of invertebrates with height-zone within each site b) trends in densities of invertebrates alongshore within each height-zone. Number of samples = 256. (1)Kendalls rank correlation coefficent, (2) Probability, (3) Significance.
NER. = *Nerine cirratulus*, EUR. = *Eurydice pulchra*, BAT.= *Bathyporeia* spp.

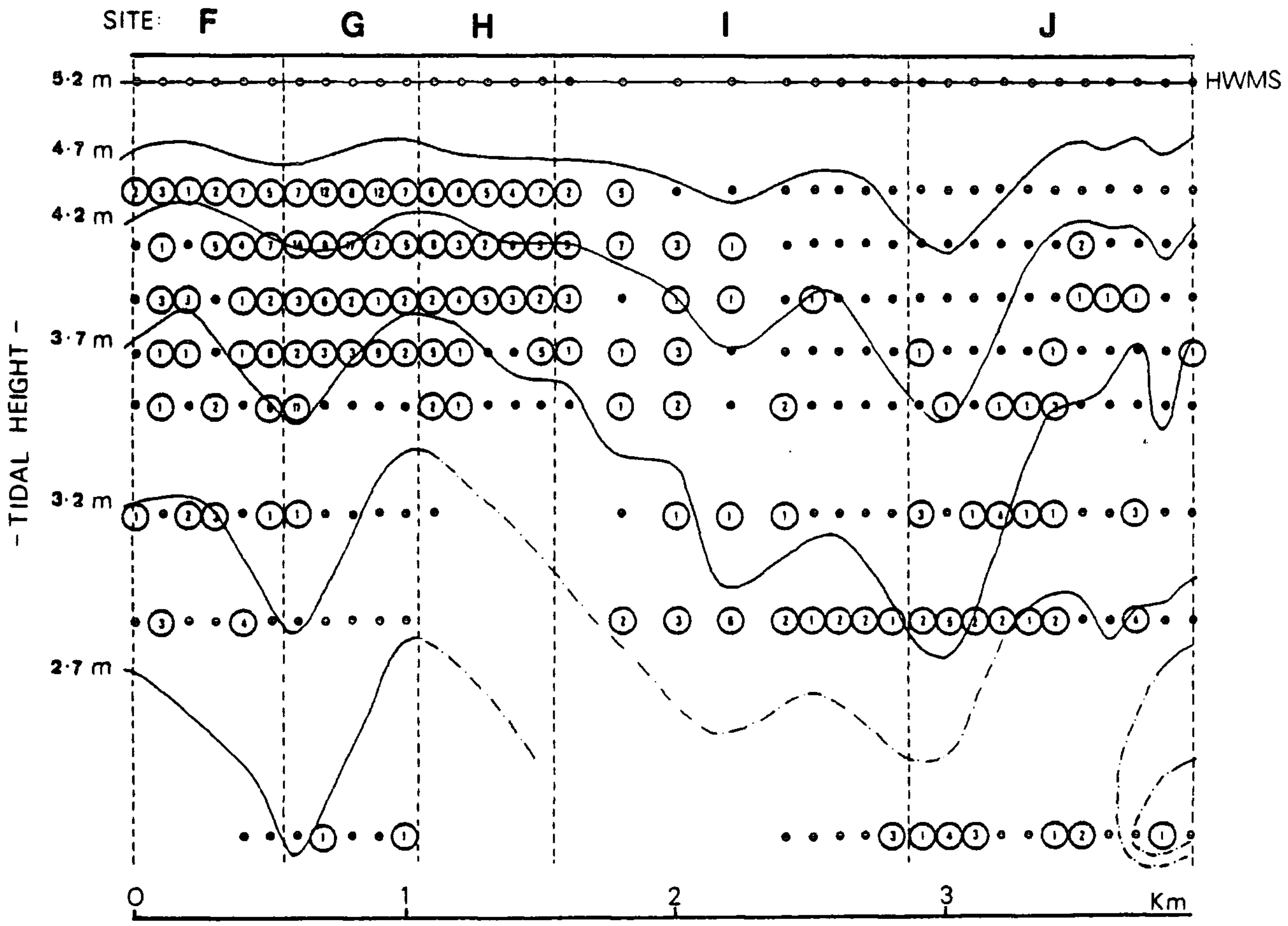
a) Within site

	F	G	H	I	J	
	-0.32	-0.68	-0.66	+0.11	+0.29	(1)
NER.	0.006	0.000	0.000	0.162	0.002	(2)
	**	***	***	n.s	**	(3)
	-0.24	+0.19	-0.06	-0.02	-0.18	(1)
EUR.	0.035	0.094	0.379	0.412	0.030	(2)
	*	n.s.	n.s.	n.s.	*	(3)
	+0.24	+0.30	+0.28	-0.04	-0.19	(1)
BAT.	0.023	0.014	0.062	0.366	0.021	(2)
	*	*	n.s.	n.s.	*	(3)

b) Within zone

	0	1	2	3	4	5	
	-	-0.62	-0.38	+0.03	+0.05	+0.50	(1)
NER.	-	0.000	0.000	0.404	0.361	0.132	(2)
	-	***	***	n.s.	n.s.	n.s.	(3)
	-0.22	+0.26	+0.33	+0.23	+0.18	+0.32	(1)
EUR.	0.061	0.009	0.000	0.021	0.110	0.204	(2)
	n.s.	**	***	*	n.s.	n.s.	(3)
	+0.11	+0.27	+0.10	-0.28	-0.32	-0.20	(1)
BAT.	0.209	0.006	0.134	0.005	0.012	0.311	(2)
	n.s.	**	n.s.	**	*	n.s.	(3)

Figure 4.7 Numbers of *Nerine cirratulus* found in each 10x10x10 cm sample in the invertebrate survey on Coatham Sands 15th and 22nd June 1984. A dot indicates stations where no *Nerine* were found.



distribution of Nerine rather than other species, correlates most closely with the observed distribution of foraging Sanderlings along the beach. The birds use sites F, G and H mainly at times when only the upper shore is exposed (see Figs 4.4 and 4.6). This is shown quantitatively in Table 4.4 in which observations of Sanderlings have been divided according to location along the beach and tidal level. (Because the birds feed mainly close to the waters edge this division was possible). Sanderlings utilized the two halves of the beach to significantly different extents between the two tidal stages ($\chi^2_1 = 32.79$, $p < 0.001$). Amongst the invertebrates, only the distribution of Nerine, considered in relation to half of beach and tidal stage, corresponds to that of Sanderling. I am aware of that the validity of the following comparison, where Sanderling distribution based on observations over a period of 8 weeks is compared to the distribution of the prey invertebrates measured when the birds had left the area, might be limited. There is a possibility that the predation by Sanderlings might have altered the apparent distribution of their prey. However this is the closest I can get. I confirmed this similarity statistically by the following method. The mean densities of the prey species within the two height levels (zones 1 to 3 pooled (upper shore) and zones 4 to 5 pooled (lower shore)) and two areas of the beach (sites F to H pooled (eastern half) and I and J pooled (western half)) were compared using Student's t-tests The results are shown in Table 4.5. Within the upper half of the shore there were significant alongshore differences in density for all three invertebrates with Nerine density higher in site F to H than

Table 4.4

Observations of colour-ringed Sanderlings on Coatham Sands divided into four groups according to location along the beach and tidal level. The division assumes that the birds fed close to the waters edge. 2x2 contingency table (observations are the main entries; expectations are in brackets). Upper shore = observations 3 to 6 h before or after LW, lower shore = observations at LW ± 3 h.

	Sites F to H	Sites I & J	Totals
Upper shore	100 (72.4)	114 (141.6)	214
Lower shore	36 (63.60)	152 (124.39)	188
Totals:	136	266	402

$\chi^2_1 = 32.79, \quad p < 0.001$

Table 4.5

Comparisons of densities of invertebrates between two beach levels (upper and lower) and between the eastern and western halves of Coatham Sands. a) Number of samples in each location, b) Student's t-test results, with t-values as the main entries and probabilities in brackets.

a)

	eastern half	western half
upper level	86	127
lower level	24	19

b)

	Nerine	*Eurydice*	*Bathyporeia*	df.
east vs west upper shore	+7.65 (0.000)	-4.68 (0.000)	-2.28 (0.024)	211
east vs west lower shore	-1.09 (0.281)	-1.12 (0.276)	+1.88 (0.067)	41
upper vs lower eastern half	+4.36 (0.000)	-0.15 (0.881)	-1.85 (0.067)	108
upper vs lower western half	-1.05 (0.294)	+1.31 (0.194)	+1.61 (0.109)	144

on I and J but with both Eurydice and Bathyporeia higher on the western half (I and J): Only for Nerine was a significant difference found between height levels, such that density was higher on the upper part of the shore within the eastern half of the beach. This agrees with the use of the beach by Sanderlings. Nerine is larger than the crustaceans and forms the bulk of invertebrate biomass available to Sanderlings on Coatham Sands, where it is known to be their chief prey (Brearey 1982).

The length of all undamaged Nerine, found in the samples taken, was measured. The length distribution was not uniform within the beach. Nerine tended to be smallest high on the shore and longer lower on the shore (Fig. 4.8). This trend was significant at sites H, I and J (for Kendall's rank correlation coefficient see Table 4.6). This means that although Nerine abundance generally decreases downshore, their individual sizes increases. How much this effects the distribution of biomass available to Sanderlings I cannot say, because no data were obtained on length/weight ratio.

4.3 Population timebudgets

During a total of 201 scan samples, 16,849 behavioural states were recorded (see Table 4.7 for the distribution of sampling effort in time). Due to decrease in the number of Sanderling present at Teesmouth late in the study period, no scan samples involving the necessary minimum number (20) of individuals could be obtained at Redcar Rocks in the last two weeks and only five at Coatham Sands in the last week.

Figure 4.8 Mean length (mm) of *Nerine cirratulus* in different height zones. Indications of the sites are following: F= ○ , G= △ , H= □ , I= △ and J= ⊡ .

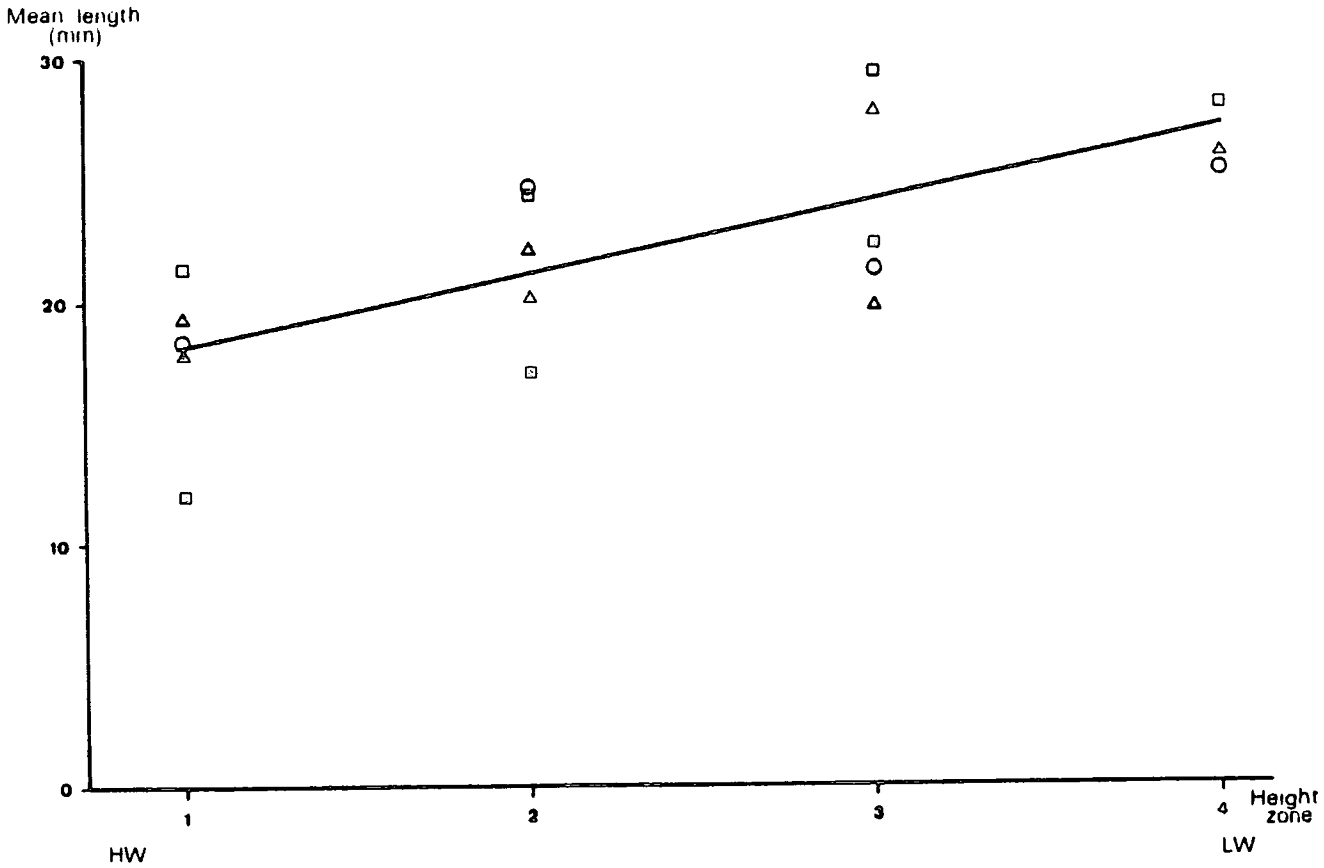


Table 4.6

Length distribution of _Nerine_ at Coatham Sands.
Mean of means within stations are presented with s.e. of the mean. Number of stations are shown in brackets. A total of 357 individuals were measured.

Height -zone	Site: F	G	H	I	J	all sites
1	18.4 ± 2.0 (6)	19.3 ± 0.4 (7)	21.4 ± 2.2 (7)	17.8 ± 1.7 (7)	12.0 (2)	18.8 ± 0.8 (29)
2	24.7 ± 2.7 (10)	22.1 ± 1.7 (12)	24.4 ± 1.4 (8)	20.1 ± 2.3 (10)	17.1 ± 2.1 (10)	21.6 ± 1.0 (50)
3	21.3 ± 2.3 (5)	19.8 ± 3.0 (3)	29.4 ± 1.3 (3)	27.8 ± 3.4 (9)	22.3 ± 3.7 (6)	24.5 ± 1.6 (26)
4	25.4 ± 3.3 (5)	-	-	26.0 (1)	28.0 ± 1.4 (7)	26.9 ± 1.4 (13)
Kendall coeff(τ):	+0.2182	-0.0297	+0.4697	+0.4105	+0.4898	+0.2775
Probability:	0.158	0.861	0.016	0.007	0.002	0.000
significance:	n.s.	n.s.	*	**	**	***

Table 4.7

Distribution of scan-sampling effort between sites, weeks and tidal stages. The number of scans and the number of behavioural states recorded are shown. E = ebbing tide, L = low water, F = flooding tide, H = high water.

Site	Weeks:	1	2	3	4	5	6	7	8
Redcar Rocks	E	-	9 642	3 461	-	6 487	-	-	-
	L	6 461	1 102	10 1907	3 248	5 215	1 43	-	-
	F	2 123	-	8 702	-	-	1 24	-	-
	H	-	-	-	-	-	-	-	-
Coatham Sands	E	1 24	-	3 326	3 106	6 185	1 59	2 207	1 21
	L	1 45	-	-	11 924	16 2377	-	-	-
	F	6 228	3 85	-	10 441	11 1447	2 110	5 403	-
	H	6 711	1 197	-	12 522	1 84	4 230	8 961	4 123
Bran Sands	E	6 541	-	-	-	-	-	2 109	-
	L	-	-	8 167	-	-	-	-	-
	F	-	-	12 744	-	-	-	-	-
	H	-	-	-	-	-	-	-	-

Sanderlings which are depositing fat reserves for migration might use either or both of the following strategies, both of which involve changes in their daytime budgets; i) they might devote a higher proportion of their normal activity period to foraging (instead of resting, preening or vigilance) and thereby gain more energy each day without increasing their instantaneous feeding rate (section 4.4); or ii) they might extend the duration of their activity period during each tidal cycle. In the case of Sanderling at Teesmouth this would be achieved by increasing time spent foraging over the high water period at the expense of roosting. To check whether Sanderlings used the first method, I used the scan-sampling data. To simplify analysis of the scan-sampling data and to concentrate on time spent foraging versus other behaviours, the categories of walking, running pecking probing, eating and standing were summed and called "foraging". The behavioural states of preening, bathing and stretching wing became "preening etc". The remaining four categories, roosting, flying aggression and vigilance were treated separately.

A Kruskal-Wallis one-way anova was used to test whether data obtained at different stages of the tidal cycle could be pooled. When data from all three sites pooled were compared from different hours of the tidal cycle no significant differences were detected for any of the six behavioural categories. Therefore the tidal cycle was arbitrarily divided into four blocks as detailed below.

When scan-sampling is used, the assumption has to be made that the sample is representative of the whole population. Because samples were taken only on the beach and it was known that a high proportion of the population roosted elsewhere over high water, that tidal period had to be excluded from the analysis. By examining the timings of arrival of birds at the high water roost throughout the study period, it was decided to define the high water period as 4½h after LW to 4½h before LW (approx. HW ± 2½h) (All timings are presented as hours before or after LW = 0). The period that remained was split into three blocks, 4½h to 1½h before LW - termed the ebbing tide, 1½h before to 1½h after LW - termed low water - and 1½h to 4½h after LW - termed flooding tide.

A Kruskal-Wallis one-way anova was also used to examine whether data from different sites could be pooled. The proportion of time allocated to most categories of behaviour differed significantly amongst the three habitats previously mentioned (Redcar Rocks, Coatham Sands and Bran Sands), but not within Coatham Sands, which was divided into six sites (E to J) when sampled. These sites were therefore pooled into one area.

An initial examination of the data showed that Sanderlings spent most of their time (60-98%) foraging (the period HW ± 2½h was excluded, see above). Other behaviours, apart from preening and roosting occupied relatively little time. The relative frequencies of behavioural states were similar between tidal stages (ebbing, flooding and LW) and between weeks. However, when the proportions of each behavioural state were examined separately there was a tremendous variation. The results are presented in Table 4.8 and Figures 4.9 to 4.11.

Table 4.8

Proportions of behavioural states measured by scan-sampling at two sites, a) Redcar Rocks and b) Coatham Sands in different tidal stages and weeks.
FOR = foraging, PRE = preening, ROO = roosting, VIG = vigilance, FLY = flying, AGG = aggression, N = number of behavioural states recorded.
E = ebbing tide, L = low water, F = flooding tide.

a) Redcar Rocks

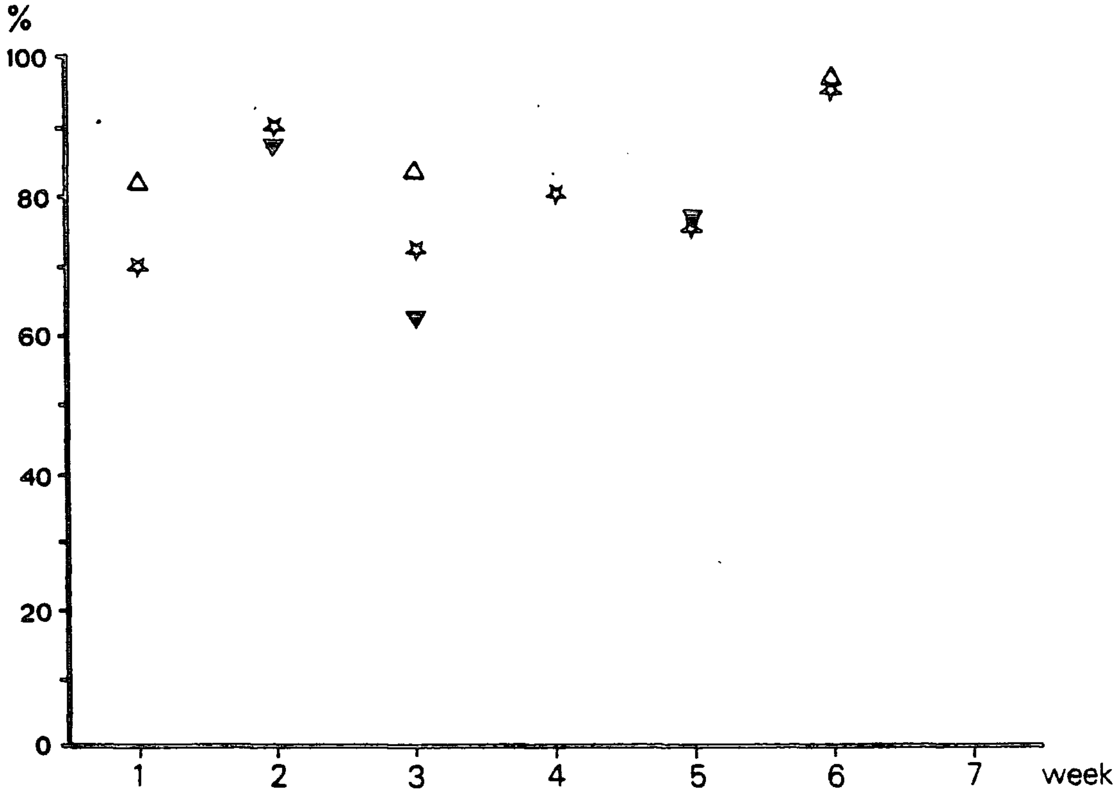
		FOR	PRE	ROO	VIG	FLY	AGG	N
Week 1	E	-	-	-	-	-	-	0
	L	70.2	14.8	9.0	2.8	3.3	0	461
	F	87.8	8.1	0	2.5	1.6	0	123
Week 2	E	87.7	4.9	0.9	2.3	3.8	0.3	642
	L	90.2	2.0	1.0	4.9	2.0	0	102
	F	-	-	-	-	-	-	0
Week 3	E	62.3	21.5	13.5	0.2	2.2	0.2	461
	L	72.0	12.7	9.1	0.6	4.9	0.7	1907
	F	83.8	8.2	2.7	0	5.2	0.1	702
Week 4	E	-	-	-	-	-	-	0
	L	80.6	7.6	5.7	0.5	5.7	0	248
	F	-	-	-	-	-	-	0
Week 5	E	76.2	12.1	8.1	0.6	3.1	0	487
	L	75.4	13.3	4.6	1.1	4.2	1.3	215
	F	-	-	-	-	-	-	0
Week 6	E	-	-	-	-	-	-	0
	L	95.3	4.7	0	0	0	0	43
	F	95.8	0	0	0	4.2	0	24

b) Coatham Sands

		FOR	PRE	ROO	VIG	FLY	AGG	N
Week 1	E	70.8	12.5	16.7	0	0	0	24
	L	91.1	4.4	2.2	0	0	2.2	45
	F	94.2	4.6	0	0.9	0.4	0	228
Week 2	E	-	-	-	-	-	-	0
	L	-	-	-	-	-	-	0
	F	98.9	0	0	0	1.1	0	85
Week 3	E	84.7	7.1	5.1	0	2.5	0	326
	L	-	-	-	-	-	-	0
	F	-	-	-	-	-	-	0
Week 4	E	95.1	1.9	0	0	3.0	0	106
	L	87.2	7.6	2.1	0.2	2.5	0.4	924
	F	79.4	15.2	2.2	0.3	1.4	0	441
Week 5	E	68.1	17.4	7.4	0.3	6.7	0	185
	L	58.4	20.6	16.3	0.1	2.8	1.7	2377
	F	57.7	10.5	30.4	0	1.4	0.1	1447
Week 6	E	84.7	13.6	0	0	1.7	0	59
	L	-	-	-	-	-	-	0
	F	91.3	2.9	1.6	0	4.2	0	110
Week 7	E	74.2	15.9	7.4	0	2.4	0	207
	L	-	-	-	-	-	-	0
	F	84.1	3.8	10.0	0	2.1	0	403
Week 8	E	71.4	23.8	4.8	0	0	0	21
	L	-	-	-	-	-	-	0
	F	-	-	-	-	-	-	0

Figure 4.9 The weekly mean proportion of Sanderlings, allocated in foraging at Redcar Rocks and Coatham Sands at three tidal stages (flooding tide △ , ebbing tide ▼ and low water ✡) measured by scan-sampling.

REDCAR ROCKS



COATHAM SANDS

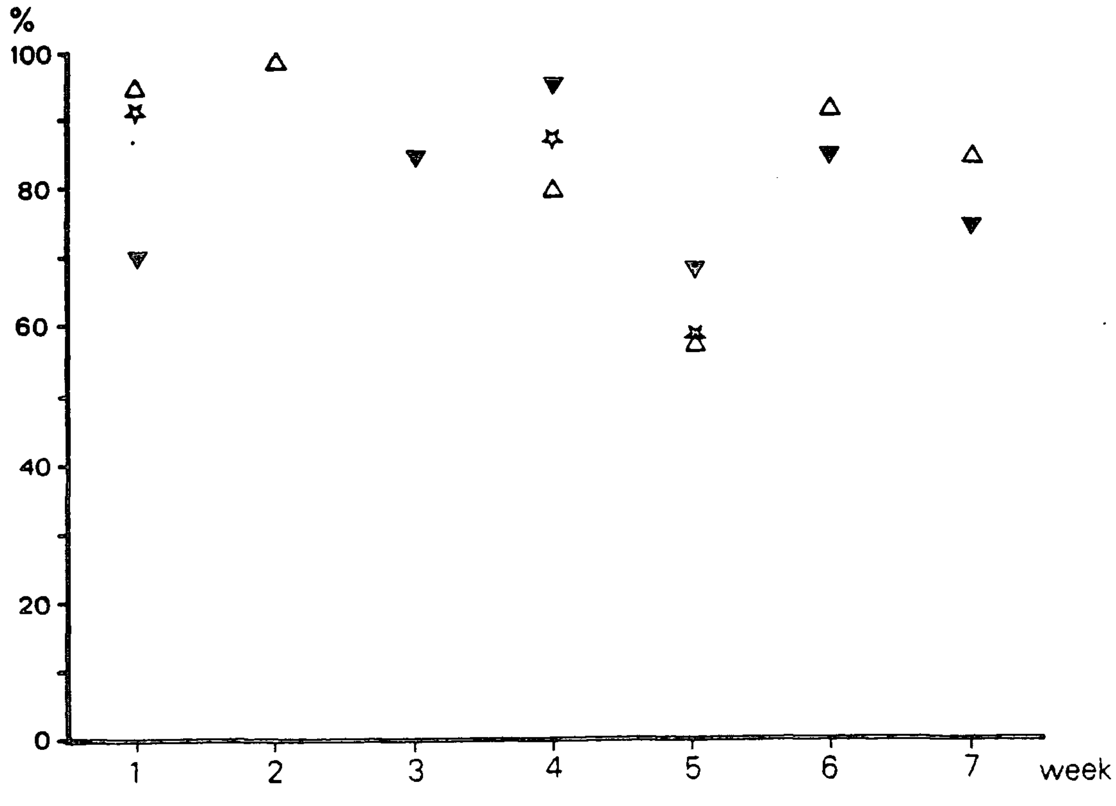


Figure 4.10 The time allocation by Sanderling in various behavioural states a) at Redcar Rocks and b) on Coatham Sands. Weekly means are shown where scan-sampling results from all tidal stages have been pooled (HW ± 2 ½h is excluded).

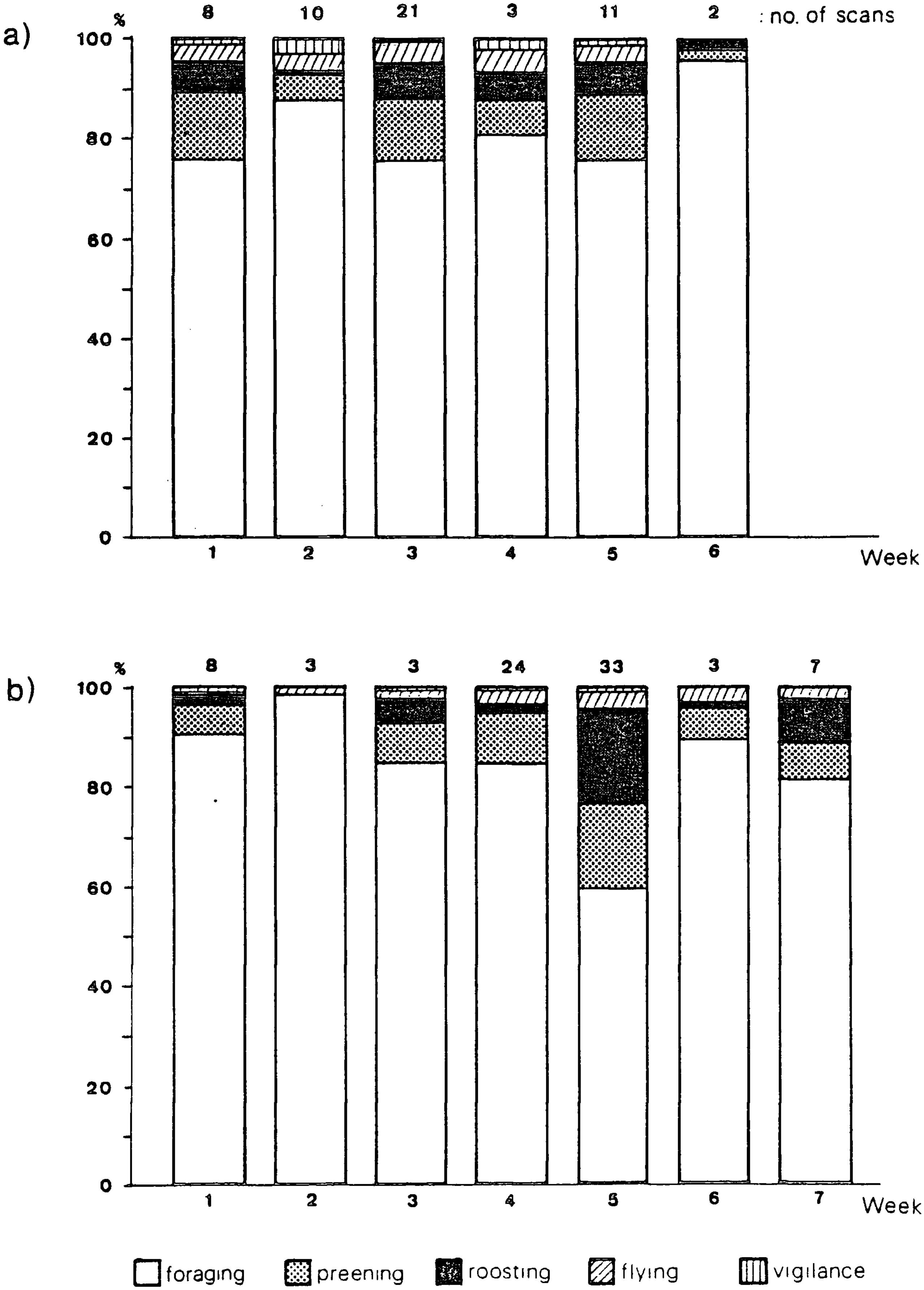
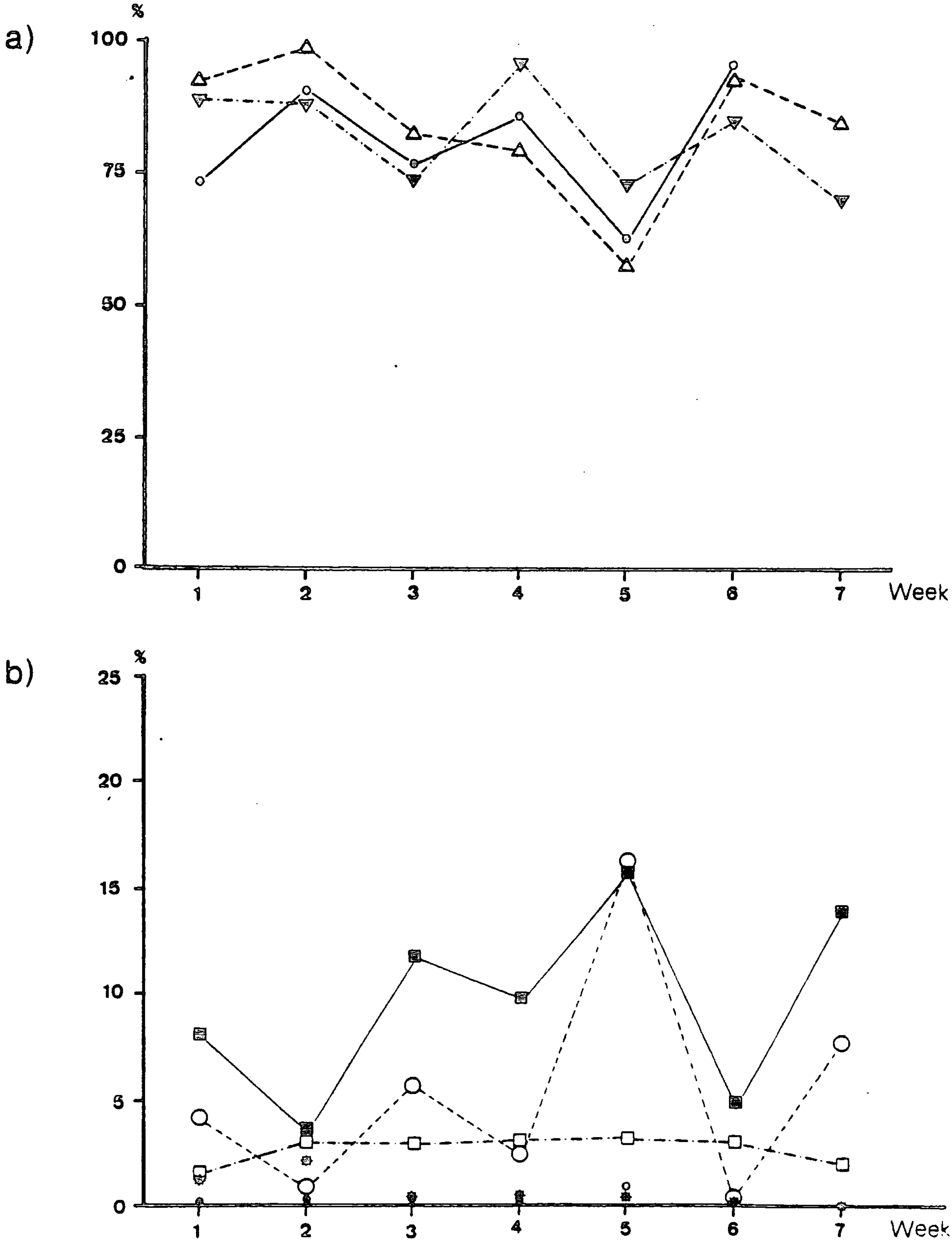


Figure 4.11 Scan-sampling results:
a) Percentage of Sanderlings allocated in foraging behaviour at three tidal stages (flooding tide △ , ebbing tide ▽ and low water ○). Data from all sites were pooled.
b) Proportions of Sanderlings allocated in various behavioural states other than foraging; preening ▤ , roosting ◯ , flying ☐ , aggression ✲ and vigilance ○ . Weekly means where data from all sites and tidal stages have been pooled (HW ± 2 ½h is excluded).



It is obvious that no trend can be detected, with season, in the proportion of activity time spent foraging. This applies both to Redcar Rocks (Fig. 4.9a) and Coatham Sands (Fig. 4.9b), for each tidal stage and for the three tidal stages pooled (Figs. 4.10a and 410.b).

For other behavioural states, similar problems arise. The variation is great and no marked tidal or seasonal trends can be found (Fig. 4.11). Sanderlings tend to roost more frequently on the ebbing tide than the flooding at Redcar Rocks during their 'active period', but vice versa on Coatham Sands. This agrees with Brearey's (1982) results from the same area. Vigilance occured significantly more often on Redcar Rocks than on Coatham Sands ($\chi^2_1 = 39.09$, $p < 0.001$); based on numbers of observations of vigilant and non-vigilant birds, summed over all 8 weeks of study). Such differences in vigilance between habitats where visibility is not the same (e.g. open sand in contrast to rocks covered with sea-weed), has been found in other wader species, Turnstone (Arenaria interpres) and Purple Sandpiper (Calidris maritima) (Metcalfe 1984). Both at Redcar Rocks and Coatham Sands the frequency of vigilance decreased throughout the study period.

Several tests were carried out using n x m contingency tables to examine four of the six behavioural states (foraging, preening etc., roosting and flying) for differences between weeks. Differences between tidal stages within weeks were also tested. Vigilance and aggression were left out because of low frequencies (many zeroes). Almost all comparisons which fulfilled the conditions of the test came out as highly significant. Because of lack of trends these tests do not tell us much else than confirming how great the variability is in the time allocation.

It is therefore clear that the scan-sampling results did not suggest any increase in proportion of time spent foraging, during daylight hours at any tidal stage, towards the departure of the Sanderlings from Teesmouth. Though such increase might have been true for individuals, instantaneous samplings on groups failed to detect it for reasons discussed later (see Chapter 5, Discussion).

To examine the second possible way in which Sanderlings might have changed their daylight timebudgets, i.e. by extending the duration of their activity period when building up fat loads, I timed arrivals of birds at high water roost. The time at which birds left the beach and flew to the roosting site ("The Ducky") or were seen arriving there were recorded. The number of Sanderlings roosting were counted and the proportions of birds still feeding on the beach at high water was estimated.

Although data on roosting time are limited (see Appendix 1) some patterns could be detected. Birds began roosting earlier on spring tides than neap tides and the overall trend throughout the study period was that duration of the high water roost shortened through April and May. Higher proportions of birds fed over high water later in the study period. My data indicate that the activity period during daylight, and thereby feeding time, was extended before migration, although they are insufficient to allow statistical analysis to support this conclusion.

4.4 Foraging rates

111 observations in which rates of behavioural events were measured, were obtained from all sites during the whole period of study. Most of the observations lasted 5 minutes and referred to colour-ringed individuals.

As the main aim of my study was to find out what strategies Sanderlings are using to increase their reserves of fat before spring migration, I focused primarily on foraging. All movements of Sanderlings are so fast that it is impossible to make any direct field measurements of foraging behaviour apart from counting behavioural events. For Sanderling such timing would be possible only by applying techniques of filming and frame-by-frame analysis (cf. Brearey 1982).

All behavioural events (13 categories) were recorded in the field but some could not be measured as rates, as in case of "standing". Standing is in many cases a part of foraging behaviour when birds are waiting for visual (or other) cues for location of prey. Because of the variable duration of that state, this category had to be excluded from analysis. However, the remaining five behavioural events which counted as foraging (pecking, probing, feeding success, running and walking) can all be presented as rates per minute. Again, the high speed of Sanderling movements and the small size of most of their prey, created difficulties in obtaining data on feeding success. I could be sure that something was being eaten only when very big Nerine and possible Nephthys sp. were taken. Sometimes I also saw Sanderlings making obvious swallowing movements although I could not see the prey items. Knowing that the success rates were severely underestimated I did not use them in the analysis.

Videofilming was used to evaluate the reliability of field measurements. Foraging Sanderlings were filmed and data recorded from the films later by the same methods as used in the field. These data were then compared with accurate estimates of rates of behaviours obtained by running the film at slow speed. Recording of data from the film at normal speed using the field methods, was very consistent. Reruns of the film produced variation of less than 10%. Comparisons between "field-counts" and accurate counts from the slowed-down film showed that nearly all rates were underestimated and increasingly so with increased speed of the behavioural events (Table 4.9 and Figure 4.12).

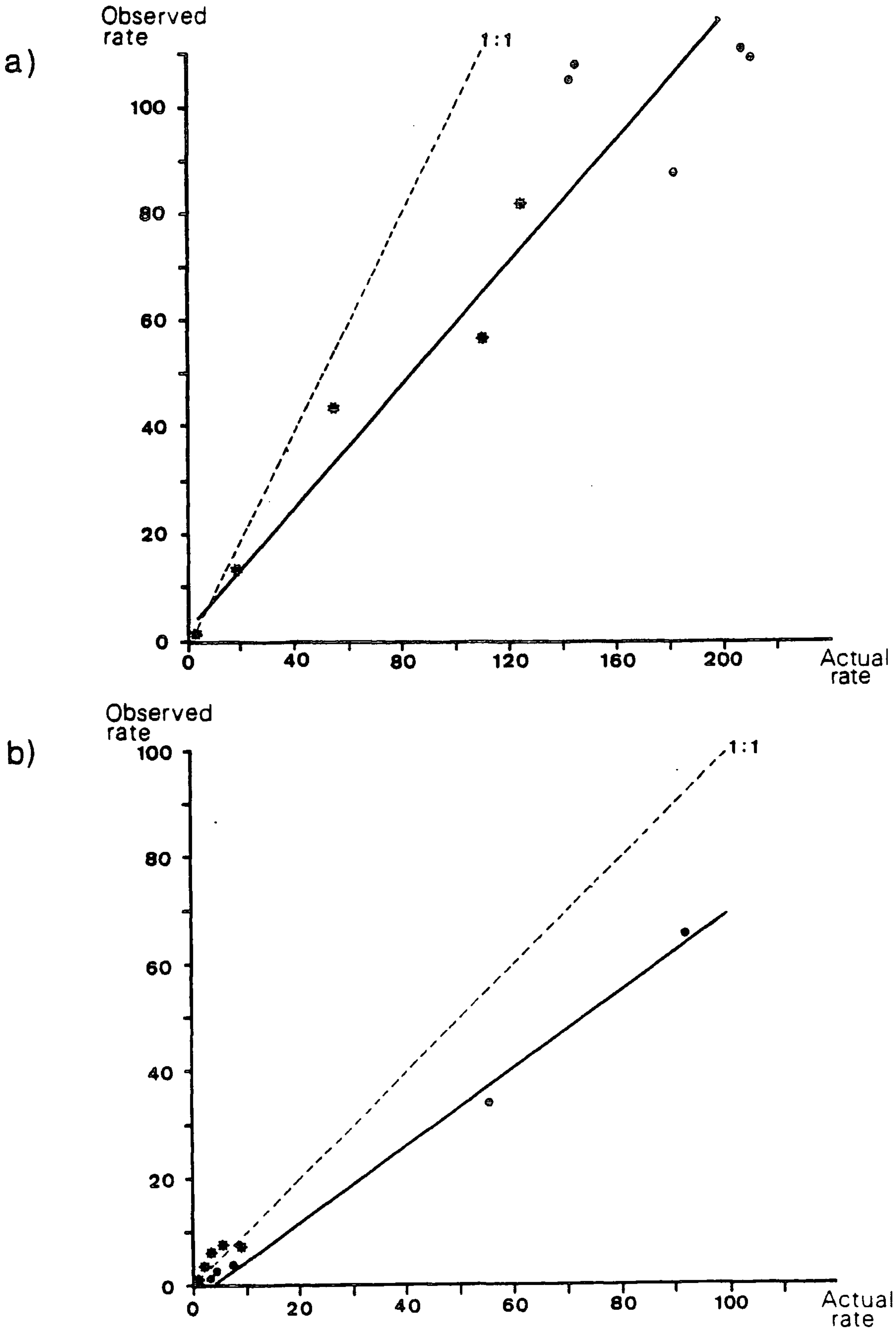
Differences in foraging rates between two out of the three habitats where measurements were obtained, were examined using the t-test. When data were pooled for all weeks and tidal stages, significant differences in rates of most behavioural events occured between Coatham Sands (n=85) and Redcar Rocks (n=15). The rate of probing was higher on Coatham Sands than Redcar Rocks (t=2.00, df=98, p=0.048) as expected considering the habitat types. The pecking rate was also somewhat higher but not significantly so, (t=1.39, df=98, p=0.168). Sanderlings walked significantly more on Coatham Sands (t=3.41, df=98, p=0.01) and also ran more (t=2.82, df=98, p=0.06) than on Redcar Rocks. This was not unexpected because the method by which Sanderlings tend to feed on sandy shores involves following the retreating waves and avoiding the incoming ones, particularly on the ebbing

Table 4.9

Comparison of observed and actual rates of behavioural events measured from a video film taken of foraging Sanderlings on Coatham Sands the 24th May 1984. Observed rates were measured by running the film on normal speed and using the field-methods. N = number of re-runs. Actual rate was measured by slowing the film to allow accurate counting.

	Shot no.	Duration (in sec)	N	Observed rate min.	Actual rate min.
Walking	1	144	3	107.2	145.4
	2	170	2	104.8	143.3
	3	134	4	110.5	207.8
	4	73	3	108.5	210.4
	5	255	3	87.9	191.1
Running	1	144	3	43.3	55.4
	2	170	2	0.9	2.5
	3	134	4	13.4	18.8
	4	73	3	57.5	110.1
	5	255	3	81.2	125.9
Pecking	1	144	3	3.2	2.9
	2	170	2	0.9	0.7
	3	134	4	6.2	4.5
	4	73	3	7.7	6.6
	5	255	3	7.1	9.4
Probing	1	144	3	34.2	55.8
	2	170	2	65.7	92.5
	3	134	4	3.7	8.1
	4	73	3	1.1	4.1
	5	255	3	2.3	4.7

Figure 4.12 Validity of field measurements tested using video-films of foraging Sanderlings. Observed rate (measured using field methods) compared to actual rate.
a) Pacing rate (min^{-1}); walking ⊛ , running ✱ . b) Rate of feeding attempts (min^{-1}); probing ○ , pecking ✱ .



tide. The mean number of paces walked and run on Coatham Sands pr minute was 96.7 ± 3.4 s.e. of the mean in contrast to 60.1 ± 5.2 on Redcar Rocks (Table 4.10).

Student's t-test were used to check whether there were differences in the various foraging rates between ebbing and flooding tide. Data from Coatham Sands only, were used because of the differences between sites. Data from all weeks were pooled giving 28 observations on the ebbing tide and 57 on the flooding. Only the probing- and pecking rates differed between the two tidal stages but not significantly so (see Table 4.11). The probing rate was higher on the ebbing tide than the flooding but vice versa for the pecking rate. These compensating differences caused the total of feeding attempts per minute to be almost identical for both tidal stages (see Table 4.11 and Figure 4.13).

Because of the marked differences between the three habitats, only the data from Coatham Sands could be used for comparisons amongst groups of birds which left the area at similar times in the spring. Three groups were compared; i) Sanderlings which left Teesmouth between 1st and 15th May (n=10), ii) Sanderlings which left between 15th and 31st May (n=44) and iii) Sanderlings with unknown departure dates (n=31). The results are shown in Figure 4.14a and 4.14b. For earlier departing birds no relationship was found between rate of feeding attempts and date but pecking rate decreased significantly (r=0.55, df=8, p=0.05) and probing rate increased (r=0.64, df=8, p=0.022). The late departing Sanderlings showed the same pattern, with significant decrease in pecking (r=0.26, df=42, p=0.043) and an increase in probing rate (r=0.26, df=42, p=0.044). The third group

Table 4.10

Foraging rates $\min^{-1}$ (means derived from transformed data) compared between two sites, Coatham Sands (n=85) and Redcar Rocks (n=15), using Student's t-test. Observations from all weeks and tidal stages are pooled.

	Coatham Sands	Redcar Rocks	Student's t-value	probability
Pecking rate	16.0	19.2	1.39	0.168
Probing rate	8.2	1.5	2.00	0.048
Feeding attempts	24.1	21.1	0.45	0.657
Walking (no.of paces)	66.3	46.2	3.41	0.001
Running (no.of paces)	30.5	14.1	2.82	0.006
Sum of paces	96.7	60.1	4.42	0.000

Table 4.11

Foraging rates min^{-1} (means derived from transformed data) compared between ebbing- (n=28) and flooding tide (n=57), using Student's t-test. Observations from all weeks were pooled. 'Feeding attempts' is the sum of pecking and probing rates.

	ebbing tide	flooding tide	Student's t-value	Probab-ility
Pecking rate	13.9	17.0	1.70	0.092
Probing rate	12.9	6.0	1.83	0.071
Feeding attempts	27.3	22.8	0.03	0.975
Walking (no.of paces)	65.8	66.5	0.16	0.872
Running (no.of paces)	33.3	29.2	0.89	0.377
Sum of paces	98.9	95.6	0.45	0.652

Figure 4.13 a) Weekly mean feeding attempt rate min^{-1} (pecks and probes) and pacing rate (running and walking) at two tidal stages (flooding △ and ebbing ▼). b) Weekly mean probing(○), pecking(●), running( ) and walking(✱) rates (min^{-1}). All tidal stages are pooled.

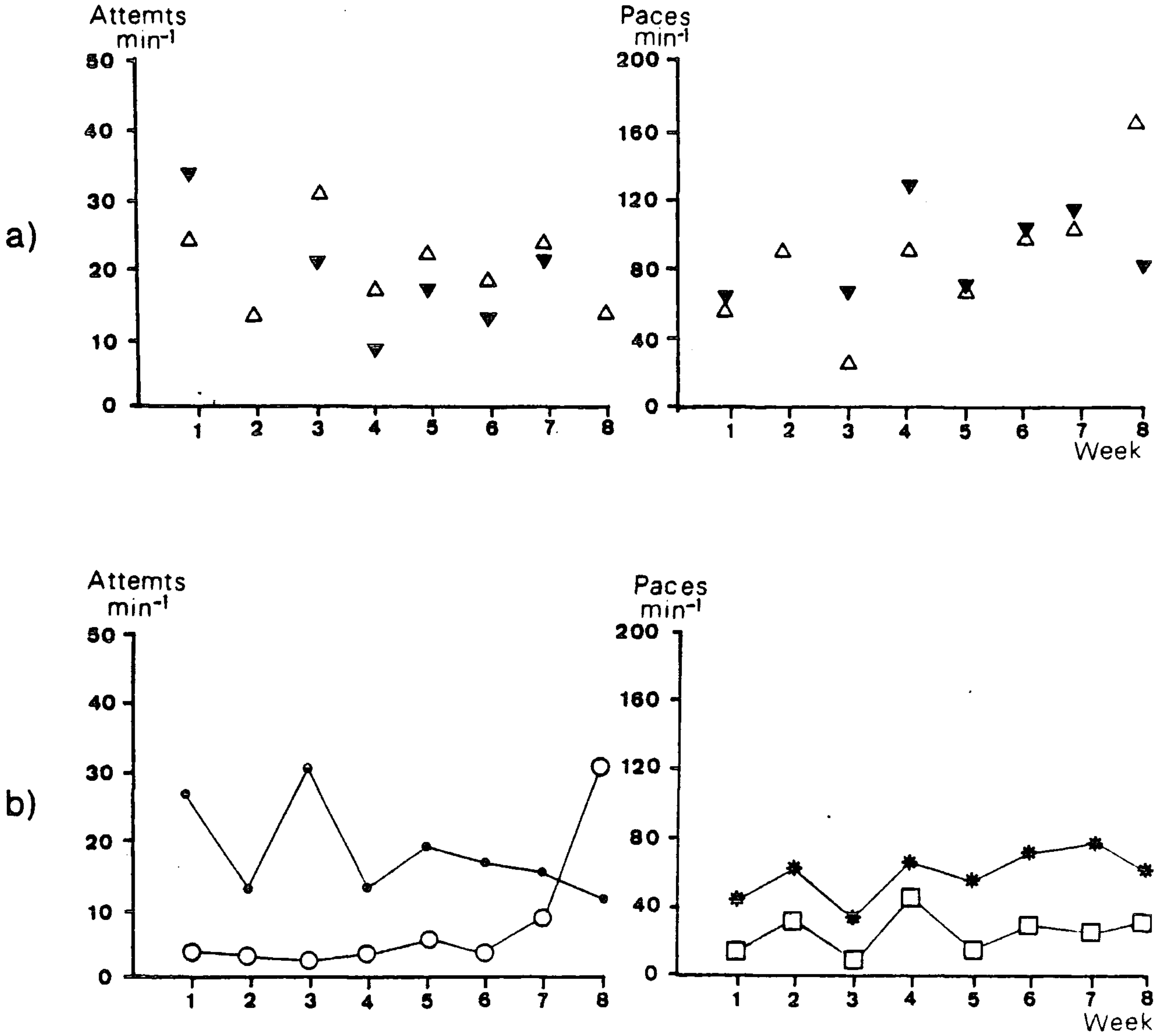
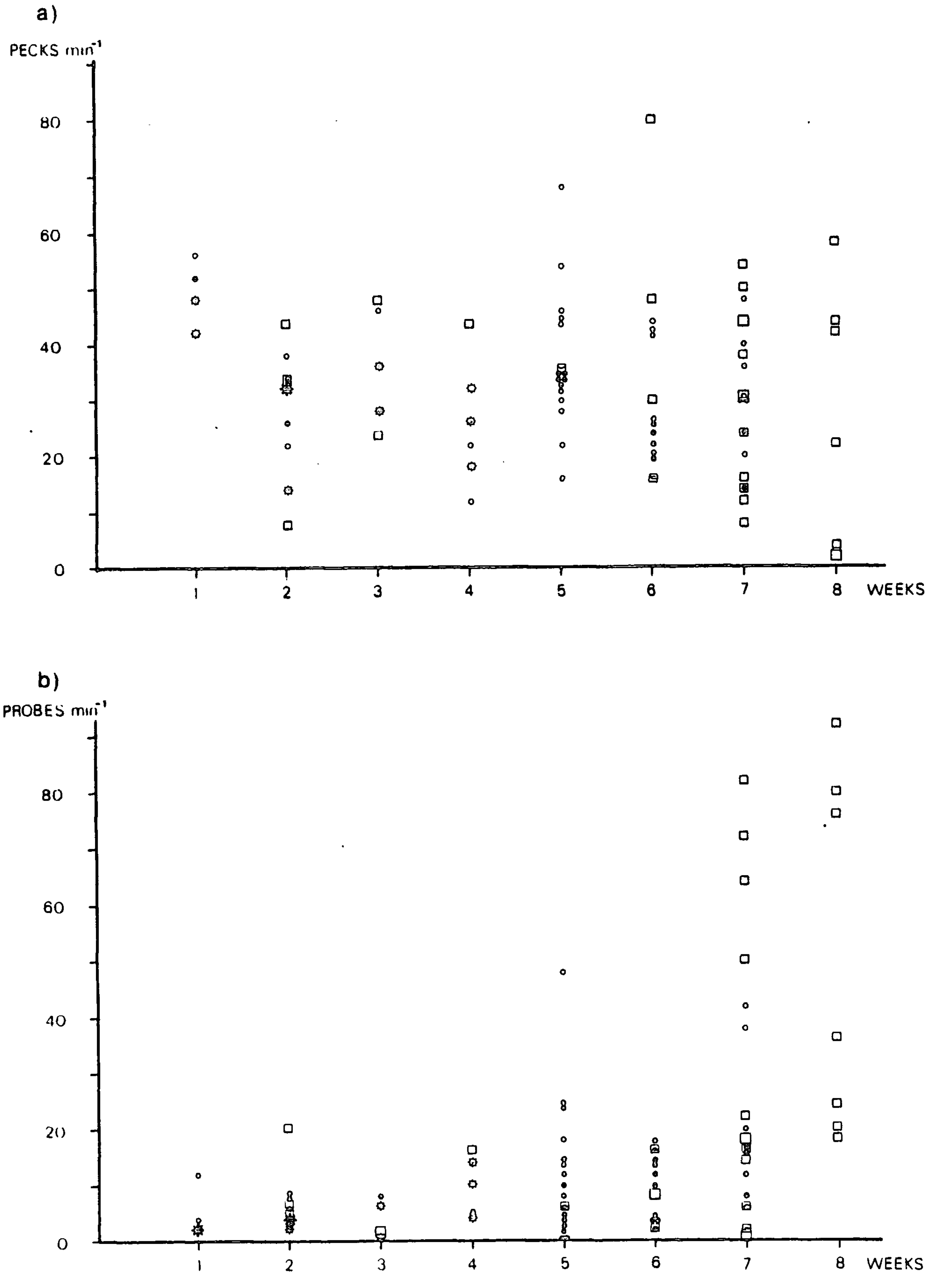


Figure 4.14 The feeding attempt rates of three groups of Sanderlings. Birds which left Teesmouth between 1st and 15th May (❋) n=10, between 15th and 31st May (○) n=44, and birds with unknown departure date (□) n=31. a) Pecking rate. b) Probing rate.

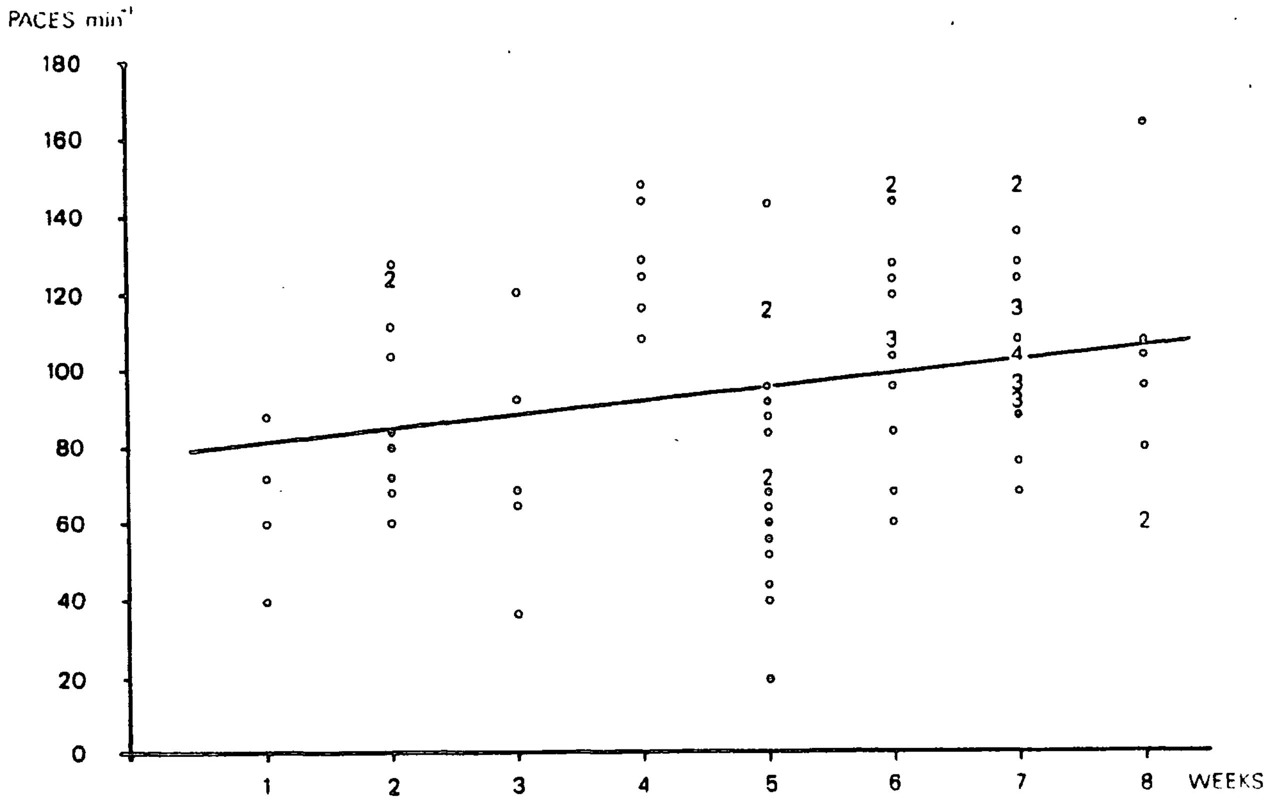


(unknown departure date) behaved similarly. An overall increase in the rate of feeding attempts occured throughout the period (r=0.49, df=29, p=0.005). To summarize these results the pecking rate decreased with season in all three groups (significantly in two) whereas the probing rates significantly increased in all three groups.

The results in respect of attempt rates are different from those I had expected, i.e. that attempt rate would increase towards the the time of departure. The explanation might lie in the observed shift in foraging methods used (an increase in probing and a decrease in pecking). The observed increase in probing arose primarily because in late May (around the 20th) the Sanderlings began using tactile search methods when probing (stitching), instead of looking for visual cues and probing once or twice at each spot. What caused this shift in behaviour is not known. It is possible that this shift arose because a new and more valuable prey became available to the Sanderlings, but I have no evidence to support this.

The cost of foraging (number of paces walked or run per minute) was studied for all three groups pooled, within Coatham Sands (n=85). A significant increase was found in the total number of paces taken per minute with season (r=0.23, df=83, p=0.018, Fig. 4.15). Number of paces run increased slightly but not significantly whereas number of paces walked per minute increased significantly with season (r=0.22, df=83, p=0.021). This indicates that more energy was spent while foraging before migration. Therefore, if the Sanderlings were to gain extra energy, their energy consumption must have increased, either by increased success

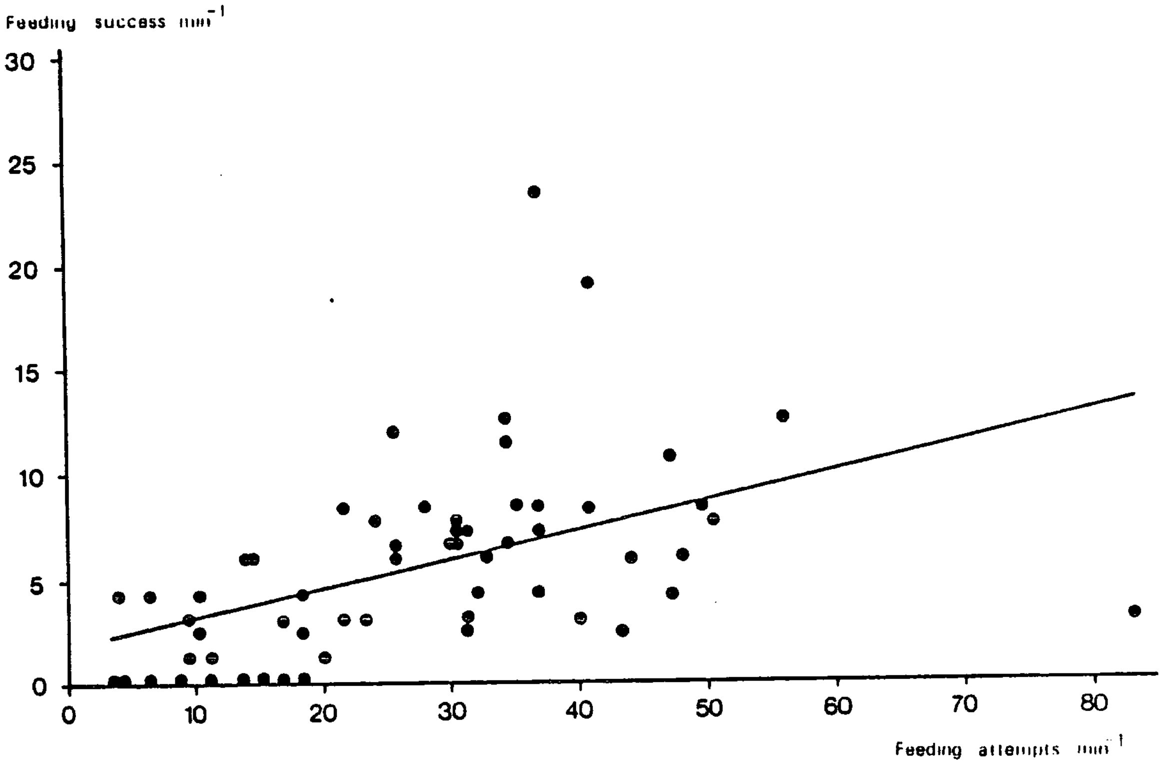
Figure 4.15 The pacing rate (both paces walked and ran) of Sanderlings on Coatham Sands. Data from all sites and tidal stages are pooled.



rate or that larger food items became available to them, as suggested above.

I could not measure success rates in the field but data which D. Brearey obtained from films of foraging Sanderlings at Teesmouth (Brearey 1982) showed that there is a significant positive correlation between attempt rates and success rates ($r=0.47$, $df=57$, $p<0.001$, Fig. 4.16). The mean proportion of successful attempts estimated from the films, was 21% (ranging from 0 - 100). For Sanderlings to increase their net rate of energy gain the most obvious way would be to increase foraging rates as long as the cost increases more slowly than the gain. My data does not support this hypothesis except if the possibility of increased prey availability is considered. That might allow Sanderling to forage with the same or even a lower rate and although increasing its success at the same time.

Figure 4.16 Success rate vs feeding attempt rate of foraging Sanderlings at Teesmouth. This data was gathered by David Brearey (Brearey 1982) by frame-by-frame analysis of cine-film.



Chapter 5 DISCUSSION

In this study I focussed on two ways which Sanderlings might have used when building up fat loads during the spring pre-migration period: (i) an increase in foraging rates (feeding attempts per minute) and (ii) an increase in time spent foraging, by decreasing time spent roosting over the high water period and/or decreasing time spent in other behavioural states such as vigilance and aggression. These were the methods I thought most likely to be used, and were easiest to measure. (I was unable to study whether birds foraged at night; nor could I measure whether birds increased the percent success of their feeding attempts). However, because of day-to-day variability in behaviour, I obtained few firm conclusions. This variability was caused by many factors, some of which will be discussed here.

Weather, acting directly on birds or undirectly on their food supply is without doubt one of the main factors affecting the foraging behaviour of shorebirds. Sanderlings forage mainly on open sandy beaches close to the water's edge and are therefore highly sensitive to wave action. Large waves can prevent them from utilizing their main feeding sites at the tide-edge and force them to forage elsewhere, e.g. higher on the beach where availability of food is less or more difficult to obtain it. Little wave action reduces the area of wet sand in which the birds can probe for prey at the tide edge, though it also reduces the distance birds have to run up and down shore between successive waves. Thus the degree of wave action will affect many components of the time activity budget.

During and after onshore gales mussel, *Mytilus edulis*, spat is often washed on shore and utilized by waders. I investigated the gizzard contents of ten Sanderlings, collected under licence at Teesside in May 1983 by other students of Sanderling biology, and found remains of small mussels in four of them. The unpredictable occurrence of a food source of this kind can obviously cause day- to-day variability in time spent feeding and it also leads to changes in the normal foraging pattern of the birds. When foraging under normal circumstances on the beach during ebbing tide, Sanderlings usually feed by probing in the wet area of sand, left by the retreating tide, where polychaetes are active or close to the surface. During the flooding tide the birds tend to stay close to the water's edge, following each wave and picking up what lies on the sand surface or floats in shallow water. A wreck of mussels deposited upshore of the tide edge attracts birds and they often spend much time foraging there. It is likely that by doing so they can gain much more energy per unit of time than by foraging by the above described methods, which involve much more movement.

As well as causing waves, wind can also affect foraging directly. It has been shown that Grey Plovers (*Pluvialis squatarola*), which rely almost entirely on visual detection of prey at surface of the mud, are less able to do so in strong winds, and that in windspeed of more than 25-30 knots they stop feeding altogether (Townshend *et al.* 1984). Foraging of Sanderlings may also be affected if dry sand is blown over their feeding areas. Foraging costs are also likely to increase in strong winds because the birds suffer increased heat loss (Evans 1976).

Severe disturbance often forces the birds to move from one feeding site to another. Flight between sites is both time and energy consuming and continual disturbance, particularly by people, might force the birds to forage in areas which are not as good in terms of density of available food as the area of first choice. Disturbance, which varied between days, is therefore likely to be one of the sources of variation in Sanderling activity budgets in my study. Indeed, the reason why Sanderlings stopped using Redcar Rocks during low water in the latter half of my study period was most likely increased disturbance by people and their dogs visiting the beach (cf. Fig 4.1). The same explanation might apply to the distribution of Sanderling on Coatham Sands (cf. Fig. 4.6), i.e. that they did not use the area of highest Nerine density (site G) as much as other areas with lower densities lying further away from the town of Redcar. On the other hand, many other explanations can be found to explain the distribution of Nerine and Sanderlings. The invertebrates were not studied until two weeks after the Sanderlings had left the area, and during that period the distribution of the prey animals could have changed. One explanation might be that Sanderlings had depleted Nerine in other areas than G, where they foraged less because of much disturbance. Still another explanation might be that the areas of highest prey density were not the same as those of highest prey availability. A predator optimizing its foraging would be expected to be in the most profitable area. It has been shown that Oystercatchers (Haematopus ostralegus) feeding on cockles (Cerastoderma edule) do not choose areas of highest densities for feeding but areas where their food intake is highest (Sutherland 1982).

Another problem arising in my attempts to use results of scan-sampling to obtain statistically significant changes on foraging behaviour related to preparation for migration was that I was dealing with several populations of Sanderlings which were not distinguishable. These populations were firstly the Sanderlings which winter at Teesmouth and secondly at least two waves of birds using Teesmouth as a refuelling site. The wintering population started to leave in mid-April, but individuals continued to depart at intervals until early June (cf. Appendix 2b). Therefore birds within flocks that I scanned were at various stages of migratory readiness from "just arrived" to "about to leave".

The foraging patterns of shorebirds are highly dependent upon the tidal cycle. The tidal cycle and its continually changing timing with respect to the hours of daylight lead to variability in the birds environment which is reflected in their behaviour. This variability is great, especially when spring- and neap tides are born in mind. To be able to quantify differences between days, which had for example two high water periods during the daylight hours in contrast to a day with only one, I would have needed much more data.

The effectiveness of the approach used in this study was limited by lack of a vehicle. By using a vehicle there would have been better chance to follow certain individuals throughout the 2-month period. A better methodology I think, would have been to measure time-activity budgets during winter conditions, e.g. in February or March when passage birds have not arrived, and compare it to the pre-migration conditions, e.g. in May, rather than trying to measure a gradual change.

In spite of all these difficulties, which meant that statistical confirmation of trends was difficult to obtain, I concluded that there was no change in the time allocation to different activities during the pre-migration period. In particular, vigilance seemed to be very infrequent behavioural state and no significant decrease was detected during the study period. Purple Sandpiper (Calidris maritima) and Turnstone (Arenaria interpres), showed a marked decrease in vigilance during the pre-migration period and allowed the birds to spend more time foraging (Metcalfe 1984). Aggression was also rarely seen in my Sanderlings, and no significant change were observed. Little aggression might be due to the fact that the Sanderlings did not defend territories during spring at Teesside, although this has been observed elsewhere during the winter months (Myers et al. 1979). At Teesmouth Sanderlings were rarely seen defending resources and, if so, only for a very short time, for example, on three occasions they were seen defending dead shore crabs, presumably left by gulls, while eating them. Time spent preening varied much between days but no patterns were detected. Foraging time during the normal activity period was not increased, at the expense of other behaviours, nor would this have provided more than about another 10% (i.e. 3/4h) feeding time during each tidal cycle.

Indications for longer activity period, instead of high water roosting, and thereby increasing time spent foraging, were found (Appendix 1a), though statistical confirmation could not be provided. A combination of this, and increased feeding success due to increased prey availability I now think are the methods used by Sanderlings to gain more energy each day during their pre-migratory fattening in spring.

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APPENDIX 1 Some notes on Sanderlings roosting on the Ducky, or feeding during HW. The observations were made from 17th April to 6th June 1984. Time is given in hours ± LW (LW = 0).

date	time	
1st week		
17.04.1984	+3.45	A roost already established.
	+3.75	490 Sanderlings counted roosting.
21.04.1984	-5.33	A flock of 300 Sanderlings came and joined a group of 400 feeding on site J. Later many roosted on the beach (possibly caused by disturbance on Ducky)
	-4.45	No Sanderlings seen on the Ducky.
	-4.00	A flock of 14 and later (-3.83h) other 15 began roosting on Ducky.
	-3.25	No Sanderlings seen on the Ducky.
	+4.50	The first Sanderlings came to Ducky.
	+4.92	Many also roosting on the beach.
	+5.37	50 out of 470 still feeding at tide edge.
2nd week		
26.04.1984	+4.61	A roost already established on the Ducky.
	+4.70	A flock of 100 arrived; a total of 460 counted roosting.
	+6.28	(=HW) The roost is still increasing, 555 Sanderlings counted. At the same time, 193 Sanderlings counted on C.S. either feeding or flying to Ducky
3rd week		
29.04.1984	+4.00	30 Sanderlings flew from B.S. to Ducky.
	+4.17	10 more left B.S. and vent to Ducky.
	+4.25	About 400 Sanderlings roosting on Ducky.
	+4.87	Roost now stable, counting 7-800 indiv.
	+6.25	(=HW) About 900 Sanderlings roosting.
	-5.15	The birds began to leave the roost.
	-3.52	The last Sanderling left (see graph,p.)
04.05.1984	+3.57	A roost already established, 280 counted. Increasing fast; birds coming from C.S.
	+4.47	Approx. 150 Sanderlings feeding on J & I.
5th week		
16.05.1984	+4.82	The last Sanderling left J and joined the roost on Ducky.
	+5.57	Only 3 Sanderlings seen feeding on C.S. from F to J.
17.05.1984	+5.65	Several Sanderlings vent to Ducky.
	+5.73	A group came to Ducky (direction Rc.R.).
	+5.82	≥300 Sanderlings in a roost on Ducky.
	-5.83	196 Sanderlings roosting on Ducky.
	-5.47	Only 10 still left roosting.

6th week

24.05.1984	-5.75	About 200 Sanderlings roosting on Ducky.
	-5.25	65 still left roosting.
26.05.1984	-	During HW 150-250 Sanderlings were feeding at HWM and higher on the beach. Number on Ducky unknown.

7th week

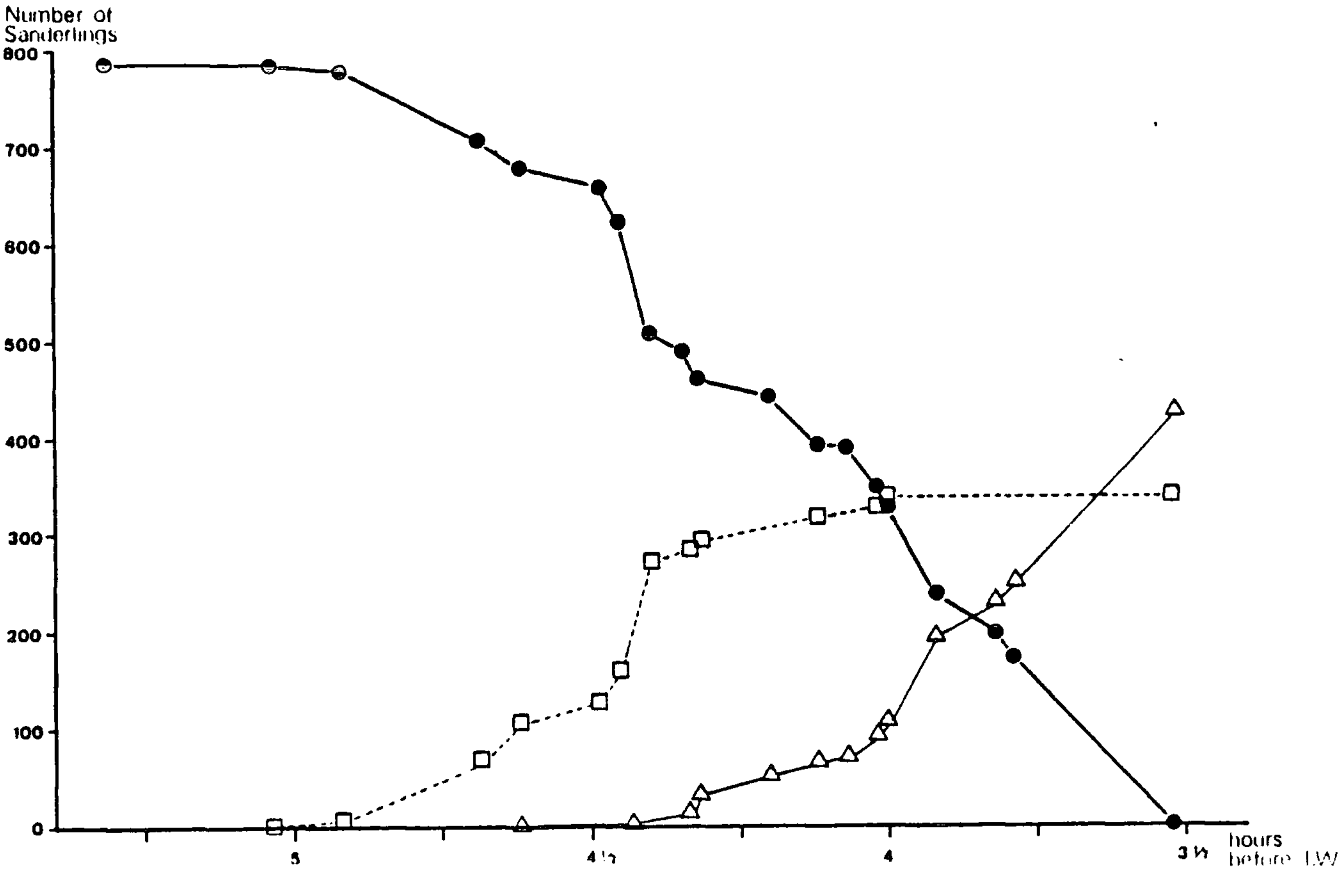
28.05.1984	+6.25	About 50 Sanderlings trying to roost on Ducky, but much disturbance at the time.
	-5.70	15 Sanderlings roosting on Bran Sands.
29.05.1984	+4.53	Sanderlings moved from the tide edge higher on the shore and began roosting.
	+4.65	The group vent to Ducky; about 200 birds. At the same time only 5 feeding on I & J.
	+4.75	Sanderlings feeding on the Ducky!
	+5.53	95 in a dense roost on the Ducky.
	+6.12	160 Sanderlings feeding at tide edge near Ducky. At the same time 70 roosting and 30-40 feeding on Ducky.
01.06.1984	+4.68	31 out of a estimated total of 100 indiv. still feeding on I.

8th week

06.06.1984	-6.12	No Sanderlings roosting on the Ducky. All birds feeding, scattered along C.S.
	-5.87	33 Sanderlings flew to the edge of Ducky and stood there.
07.06.1984	+5.38	Already established roost of 33 indiv. on Ducky (approx. half of total on C.S.).
	-6.45	All roosting birds left the Ducky and went to the beach feeding.

APPENDIX 1 b)

Departure of Sanderling from the roost on Ducky 29.04.1984. Birds present at Ducky (●), cumulative number which left in direction to Redcar Rocks (△) and cumulative number which left in direction to Bran Sands (□).



APPENDIX 2

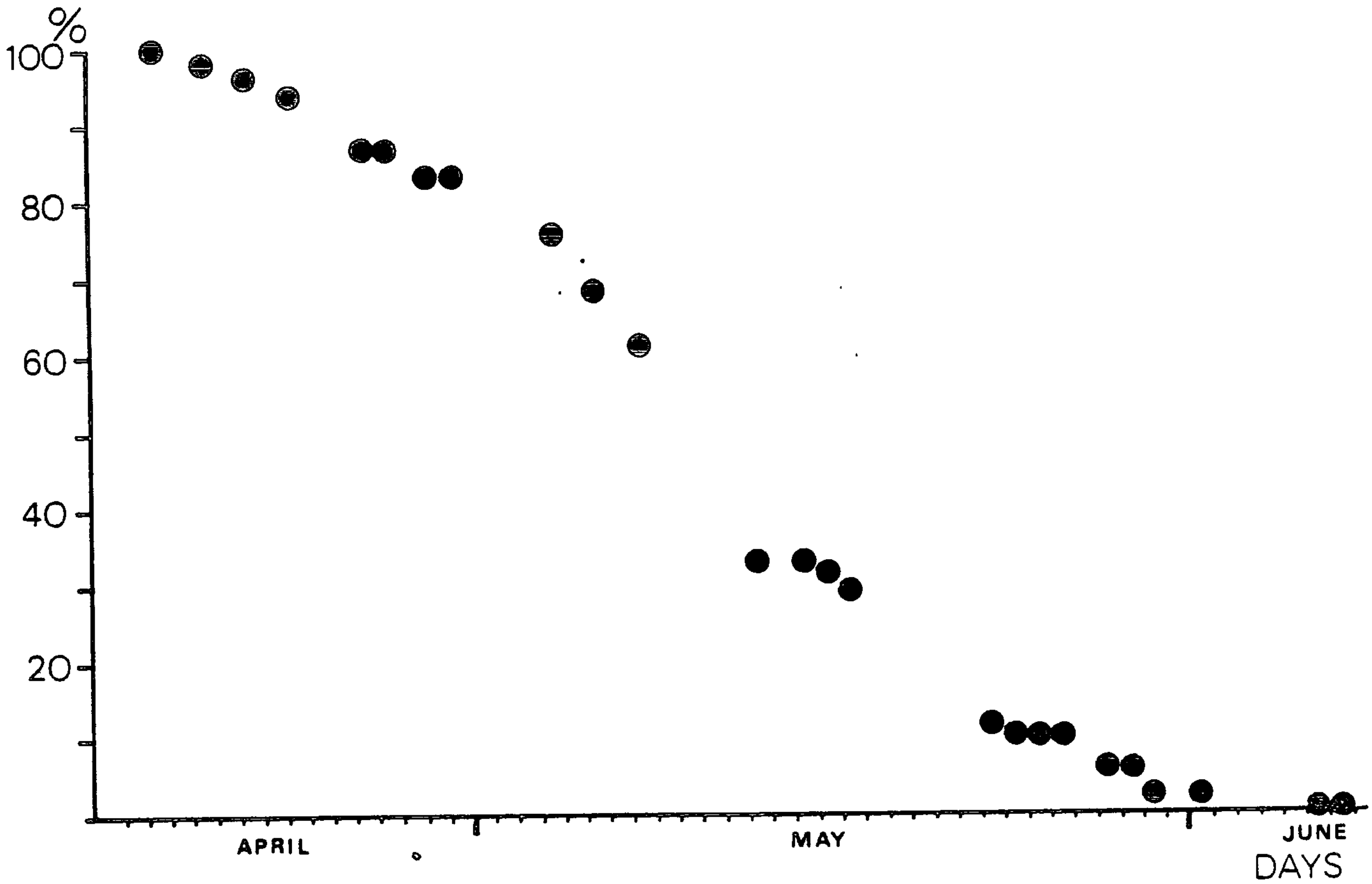
a) Most of the colour ringing of Sanderlings at Teesside has been carried out during the winter months. Therefore most colour ringed individuals are members of the wintering population. To find out when, and at what rate the wintering population of Sanderlings at Teesside left the area in spring 1984, I used the colour ringed birds as a sample. It was assumed that the date of last sighting of each colour marked individual was its actual departure date. By plotting the proportion of colour ringed individuals (N=54), which were not seen again, for each day of fieldwork, the graph (overleaf) was achieved. This graph shows the proportion of the wintering population present each day.

b) When the total number of Sanderlings, present at Teesside during the study period, is examined, two distinctive peaks in numbers can be detected. These peaks, one in late April and another around mid May, can be explained as major influxes of passage birds passing quickly through the area.

T = A total count for the whole study area.
R = A total count at the main roosting site (Ducky).
☐ = A estimated total.
● = The maximum number seen away from the roosting site.

APPENDIX 2

a)



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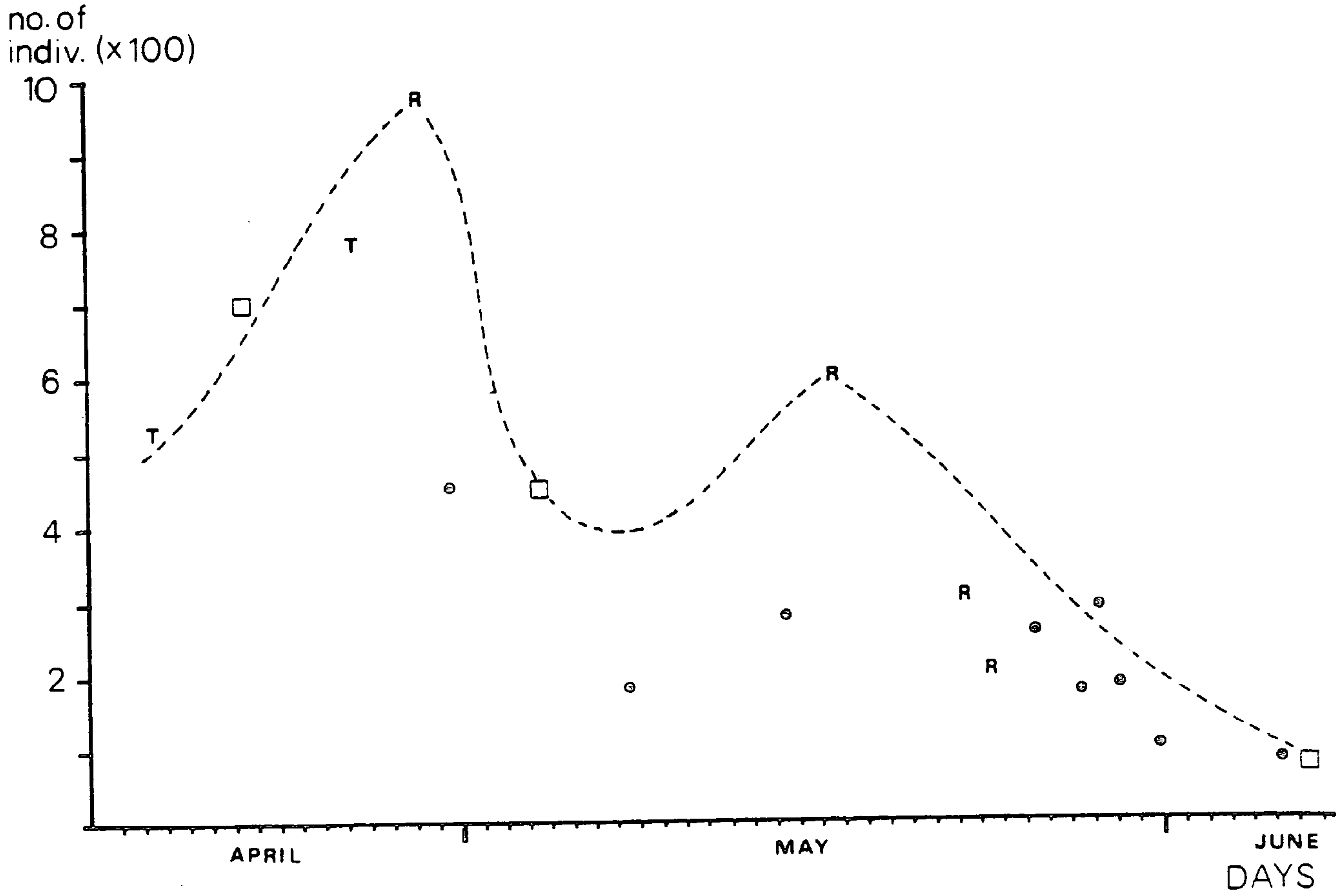


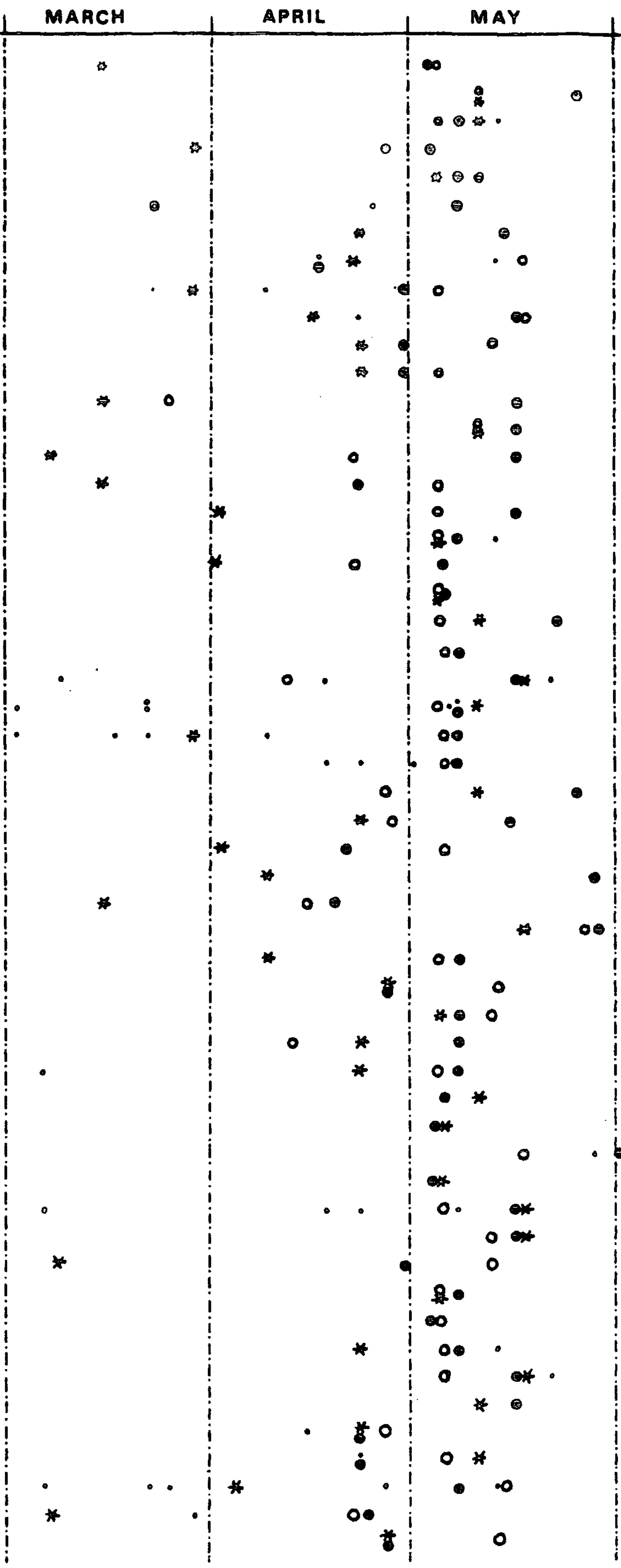
APPENDIX 3

a) Last sightings in spring of a series of colour-ringed Sanderlings wintering at Teesside, in the years 1982 (○), 1983 (✱) and 1984 (●) with several additional sightings from 1977 - 1981 (•).

b) The graph shows the departure of the wintering population of Sanderlings from Teesmouth, during spring in four successive years, 1981 - 1984. As in Appendix 2 this is based on the last sightings of colour-ringed individuals each spring, presented as the weekly cumulative percentage of the sample that has left the area.

I intended to link the departure time to meterological factors, e.g. temperature and wind, to see whether they had any influence on the birds. It has been shown that most migrant birds depart in peak numbers in calm following winds and avoid strong opposing winds (Richardson 1978) and that the optimal conditions for migration occur under very specific circumstances (Rappole & Warner 1976). The data turned out to be insufficient, because the number of observation dates, used to establish the presumed departure dates, varied amongst years.

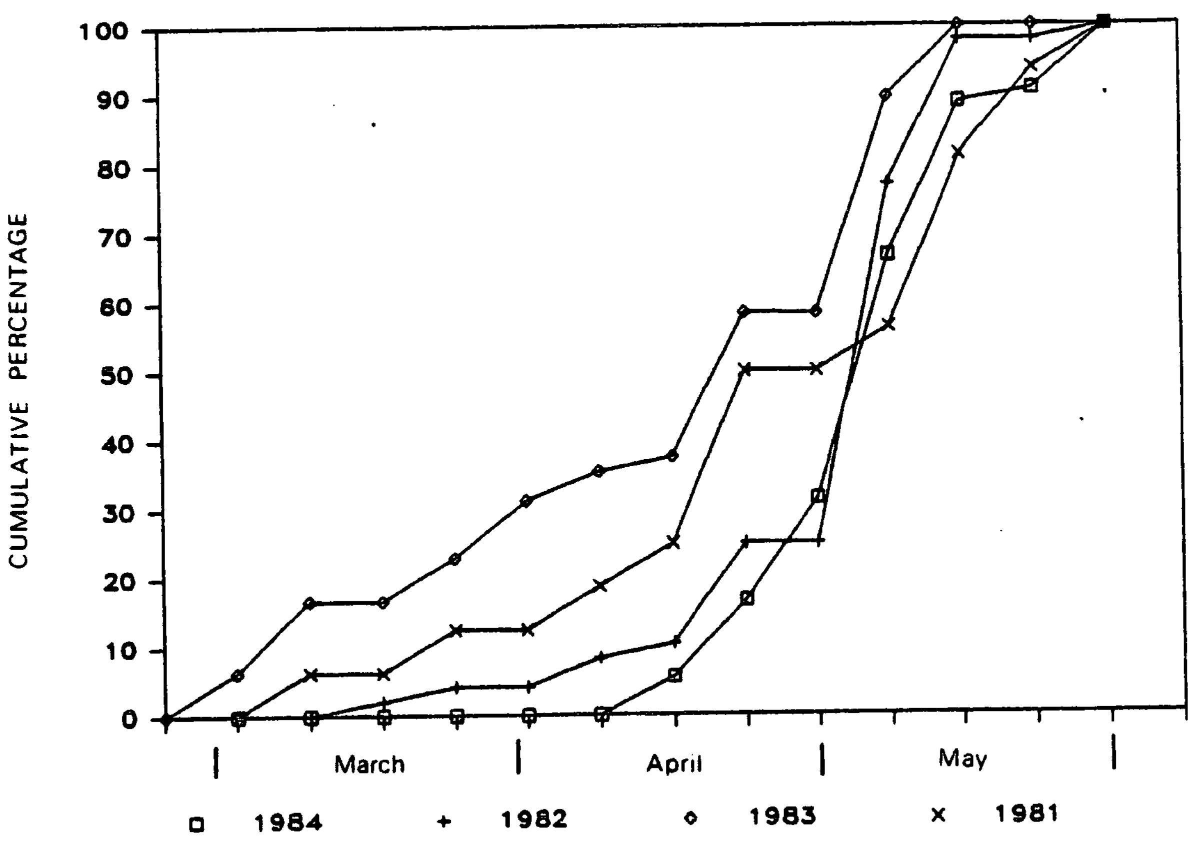
APPENDIX 3 a)



Sanderling	N	DEPARTURE PERIOD	DURATION	
BO G				
BO Y	3	11.-26/5	15	
BY RY	4	06.-14/5	9	
GO R				
GG Y	3	06.-11/5	5	
B G				*
BO O				
BW --	5	17/4-18/5	32	
BY GO				
BY WR	4	16/4-18/5	33	
GG R	3	23/4-13/5	21	
GO W	3	23/4-05/5	13	
GO Y				
GR R	3	11.-17/5	7	
GR W				
GW GO				
GW GR				
GW RW	4	05.-14/5	10	
GW YG				
GW YR	3	05.-06/5	2	
GW WY	3	05.-23/5	19	
L B				**
L L				
L W	5	05.-11/5	7	
LW Y				
O R	5	18/4-08/5	21	*
O WR	3	27/4-26/5	30	
OG G	3	23/4-16/5	24	
OG O				
OR G				
OR O				
OR Y	3	18.-29/5	12	
OW G	3	10/4-08/5	30	
OW W	3	27/4-14/5	17	
OY G	3	05.-13/5	9	
OY R	3	13/4-08/5	26	
RB RY				
RG G				
RG O				
RG RY	3	17/5-01/6	15	*
RG W				
RW B				
WB GR	3	13.-18/5	6	
WB GW				
WB OG	3	05.-08/5	4	
WB WG				**
WB WY	4	23/4-14/5	22	
WW B	4	06.-22/5	17	
Y RO				
YB RB	4	15.-27/4	13	
YR RB	3	23/4-11/5	19	
YR W				
YY W				***
OW W	3	27/4-15/5	18	

* not seen 1983,neither late winter nor spring
**not seen in spring 1983 but once in mid-winter
*** 1981 in Saltburn, 1983 in Hart Warren

APPENDIX 3 b)


CUMULATIVE PERCENTAGE
100
90
80
70
60
50
40
30
20
10
0
March
April
May
□ 1984
+ 1982
◇ 1983
× 1981

APPENDIX 4 Site fidelity.

Sightings of colour-ringed individuals at Teesmouth (South Gare) from mid April throughout May 1984 at different sites and tidal stages. Individuals selected which were seen on seven or more occasions. Sightings from same day used providing that more than one hour had passed or that the bird had moved between sites. ● = Redcar Rocks, ✱ = site J on C.S., ☐ = Ducky, ☆ = Bran Sands; letters E, F, G, H & I refer to other sites on Coatham Sands.