The feeding ecology and foraging behaviour of sanderling calidris alba and turnstone arenaria interpres at Teesmouth N. E. England

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To my parents,

Jack & Olga Brearey

The Feeding Ecology and Foraging Behaviour of Sanderling Calidris alba and Turnstone Arenaria interpres at Teesmouth, N.E. England

by

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ABSTRACT

The distributions of Sanderling and Turnstone were determined for the south side of the Tees Estuary. Location of roosting sites and the movement of the tide were the major factors affecting movement patterns of these two species. The invertebrate species Nerine, Bathyporeia and Eurydice, were observed to comprise virtually all of the Sanderling's open-beach diet. Extensive sampling of these three prey species showed a predictable occurrence along the beach with each species most common at a particular transect and distance below the High Water Mark, (e.g., Nerine was most abundant at 50 to 90 metres below the HWM). The times when these bands became available to foraging Sanderling helped to determine the movement patterns of the birds.

Detailed studies of the feeding behaviour of Sanderling showed three main foraging techniques: probe feeding, water-column feeding and stitch feeding. The first two of these techniques have a visual component, (the Pause position). Switching occurred between these two techniques but was uncommon between the water column and stitch technique (which was a tactile feeding method). When feeding, Sanderling oriented themselves so that they could watch the progress of the waves.

Colour-marked individuals of both Sanderling and Turnstone helped to determine movement patterns, fidelity to site within a season and survival and fidelity between seasons. Mortality rates for Turnstone were especially low; fidelity was high for both species.

Feeding observations on winter Turnstone showed both dispersed and concentrated situations. While aggression was seldom observed for Sanderling, it was common for Turnstone. Two main types of aggressive encounters were observed for the Turnstone and were determined mainly by the potential 'payoff' of the encounter. The suggestion is advanced that aggressive patterns may help to determine the dispersion of the Turnstone. Aggression may also help to determine the feeding location of the juveniles.

Observations of breeding Turnstone (Finland) present a picture of communal feeding (aiding in predator awareness), high nesting concentrations and numerous interactions with the larid species present. The latter include extensive robbing of larid eggs by Turnstone. Although the summer and winter Turnstone populations have different wintering grounds, there are valuable comparisons to be made.

CONTENTS

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CHAPTER 1. INTRODUCTION

The basic problem of ecology is determining the causes of distribution and abundance of organisms (Krebs 1972). Within the feeding areas, the distribution of birds may be affected by the density of both the prey and the birds themselves (Cody 1974, Goss-Custard 1977a). A scarcity of food may cause certain wader species to leave an estuary (Davidson 1966). Distributions of birds amongst neighbouring estuaries have been correlated with food density (for Curlew and Redshank see Goss-Custard et. al. 1977a). A similar process may be detect~~i~~able within a single estuary.

This thesis concerns the feeding ecology and foraging behaviour of Turnstone, Arenaria interpres (L.) and Sanderling, Calidris alba (Pallas), primarily at Teesmouth, northeast England, an important wintering site for both species. Of special concern are two major problems: how the bird populations distribute themselves in space and time in relation to their prey; and, by what methods they exploit their prey. Most attention is paid to Sanderling, since the range of prey they take is limited and observational accessibility was greater. Additional information is presented from Turnstone, particularly in relation to the influence of social behaviour of the birds in modifying their own distribution. A comparison of the two species helps to draw conclusions of the benefits birds obtain from their social habits. Studies of Turnstone on their breeding grounds in Finland add further information to the effects social behaviour has on modifying distribution. Behaviour must be viewed in both its social and environmental context (Smith 1977), and year-round studies help clarify the role played by social behaviour.

Although prolonged cold periods may bring large winter mortalities (Pilcher et. al. 1974) there is little evidence to support the idea that waders face heavy losses during most winters (Goss-Custard 1980). Competition, if it is more acute on the winter grounds, may make this season a focal point for intense selection, leading to increased prey restriction (Schoener 1971, Baker & Baker 1973). (Increased competition has not been found for wintering waders in a tropical area, Duffy et. al 1981.) While Sanderling and Turnstone seldom have exclusive use of any particular feeding area, their foraging mechanisms isolate them from most other species. This simplifies any field approach and allows the observer to concentrate on intraspecific interactions. The major difficulty then, is in dissociating behavioural interactions of conspecifics from the effects of the environment and prey populations of the birds.

Sanderling, normally considered a bird of sandy beaches, breed in Siberia and Greenland and winter in Europe and Africa (Prater & Davies 1978). The average winter population in Europe (believed to be of the Siberian population) has been estimated at 14,300, of which, 10,300 winter in Britain (Prater & Davies). Up to c. 1200 Sanderling may occur at Teesmouth. As there is an appreciable turnover of the population during the autumn, winter and spring, more individuals use Teesmouth than are indicated by the peak counts. The area serves as a stopping point and a moulting and fattening ground for birds continuing further south in autumn.

Turnstone occurring in Britain belong to two populations; British wintering birds which breed in Greenland and north-east Canada, and British passage birds which breed mainly in Finland and elsewhere in northern Europe (Branson et. al. 1979). Compared with Sanderling, much less precise estimates are available for population sizes, but at least 12,000 Turnstone winter around the British Isles (Branson et. al. 1978) of which c. 350 winter at Teesmouth. Turnstone are normally considered a bird of rocky shores.

Study Sites

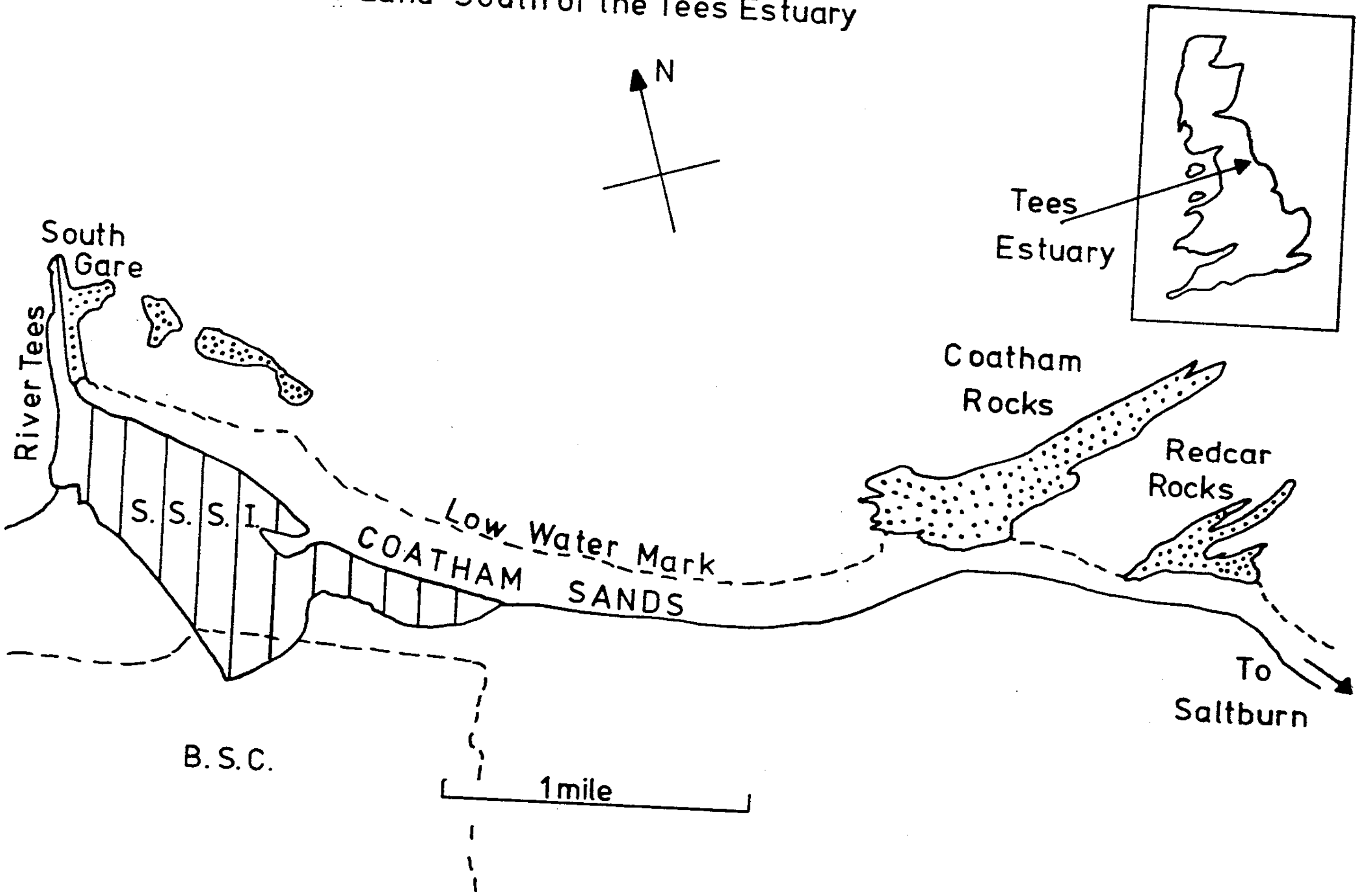
Two main habitats are utilized by Sanderling and Turnstone along the coast south of the River Tees (Fig. 1.1). The calcareaous sandstone outcrops, Coatham Rocks and Redcar Rocks, form the main low water feeding zones, along with the slag-piles or "German Charlies",

Figure 1.1. The coastal rock and beach areas south of the River Tees. Insert in right hand corner shows the location of the estuary in northeast England.

S.S.S.I.- Site of Special Scientific Interest

B.S.C.- British Steel Corporation

Intertidal Land South of the Tees Estuary



adjoining South Gare. The other main habitat is the sand beach area of Coatham Sands and Redcar Beach. Additional habitats are the outcrops of Saltburn, approximately 8 km south of the main feeding area and Bran Sands, the only remaining intertidal flats on the south side of the estuary. The most productive area of the "German Charlies" and the rock outcrops are exposed for about two hours either side of low water on spring tides and somewhat less on neaps. The coastal sands, while being available for most of the tidal cycle are generally considered 'exposed' only when wave-washed.

Contents of the Thesis

In Chapters 2 and 3, I explore, respectively, the distributions of the main invertebrate prey of Sanderling and of the birds themselves, and discuss the relations between predator and prey. I ask first what would be the expected distribution of Sanderling and then, what is the observed distribution of the birds. If differences occur, what are the possible reasons to account for the differences?

Chapter 4 presents a detailed analysis of the foraging methods and behaviours used by Sanderling when feeding on invertebrates on sandy beaches. What are the factors affecting the foraging patterns of Sanderling and how are constraints incorporated into their feeding strategy? Chapter 4 is the most important of the thesis. The results of this chapter are used to discuss the importance of social behaviour in modifying feeding dispersion patterns. I discuss the disparity between laboratory studies and field-based studies, and the need to guard against careless extrapolation.

Additional information on movement of Sanderling between feeding sites north and south of the River Tees, and on year-to-year survival of Sanderling, collected during the study, are presented in a special Appendix (3.1).

Chapter 5 considers aspects of social behaviour of foraging Turnstone at Teesmouth. A look at aggressive patterns helps to understand the mechanisms leading to their observed distribution. In a special Appendix (5.1), I consider foraging behaviour on Turnstone breeding grounds in Finland, where foraging is set in the context not only of individual survival but of increasing survival chances of chicks. The discussion which closes this Appendix, compares Turnstone behaviour in the very different contexts of winter survival and the breeding season.

Finally, in Chapter 6, I discuss similarities and differences between the foraging of Sanderling and Turnstone in the light of their degree of opportunism shown in exploitation of new food sources and the extent to which social behaviour functions in allowing birds to successfully utilize their habitats.

CHAPTER 2. DISTRIBUTION AND DENSITIES OF THE INVERTEBRATE PREY OF SANDERLING ALONG COATHAM SANDS

2.1 Introduction

Studies on intertidal zonation have centred on rocky shores, where the distribution of the macrofauna is an obvious feature (Eltinghham 1971). Although particulate shores have a shallower gradient than those of rocky shores, the fauna inhabiting them show zonal patterns (Newell 1970). Beach-inhabiting species can occur over very wide ranges of tidal heights (Watkin 1940). The zonation of beach macrofauna have important consequences on their predators' feeding strategies.

A series of sampling programmes was undertaken to determine the distribution and abundance of the potential beach prey of Sanderling. Three main questions are posed: i) what are the distributions of the macrofauna on Coatham Sands; ii) what is the predictability of the prey species (how do the distributions change from one sampling date to the next); and iii) do the prey exhibit regular, random or clumped dispersion patterns.

Although all invertebrate macrofauna were retained during sampling, the study focused on the three species of greatest importance; the polychate Nerine Cirratulus (Delle Chiaje), the amphipod Bathyporeia pelagica (Bate) and the isopod Eurydice pulchra (Leach).

These species have been studied throughout the British coast and each has been shown to occur in rather well defined zones. Brady (1943) found that *Nerine* favoured prolonged periods of exposure between tides and thrived on clean sand, occurring to a depth of 22.5 cm. At the very exposed beach of Stoupe Beck (Gray and Rieger 1971), *Nerine* was the dominant polychaete. *Eurydice* prefers the upper beach and occurs in the top 5 cm of sand (Brady 1943). Scott (1960) reported *Eurydice* being found over the entire beach at Village Bay, St. Kilda, with a maximum distribution around mid-tide level. Four species of *Bathyporeia* are usually mentioned in intertidal studies (McIntyre 1968, Newell 1970). All four species show a definite zonation, with one species replacing the next from high-tide mark to low-tide mark (Watkin 1939). While the species found in the coastal sands at Teesmouth is mainly *B. Pelagica*, some *B. pilosa* probably occur. On exposed shores, *B. pelagica* is the dominant amphipod (McIntyre 1968, Gray & Rieger 1971). No major behavioural differences occur between these two species and all further reference is made to *B. pelagica*. Behavioural and seasonal patterns of the three main prey species are discussed when considering the possible constraints the prey place on the Sanderling.

2.2 Methods

Sampling was done on Coatham Sands (the major feeding area of the Sanderling) during the winters of 1977-78 and 1978-79. All samples were returned to Durham in labelled polytheme bags and washed through a 20 mesh per inch (mpi) sieve over a 30 mpi sieve. The 20 mpi sieve retained the larger crustaceans and polychaetes. Polychaetes as small as 4 mm were retained in the 30 mpi sieve. After preliminary extraction of animals from each sieve, the remaining contents were washed, from the opposite side, into a large metal pan. All animals on the bottom of the pan were collected and the water, which contained the swimming individuals, was poured into a 100 mpi sieve and the animals extracted. If much coarse material remained, a few drops of 10% formalin were added to make the crustaceans active, aiding in their collection. All animals were preserved in 70% alcohol. Extraction was done on the day of collection or the samples kept in a 10^{o} C. temperature-controlled room until extraction, during the following 48 hours.

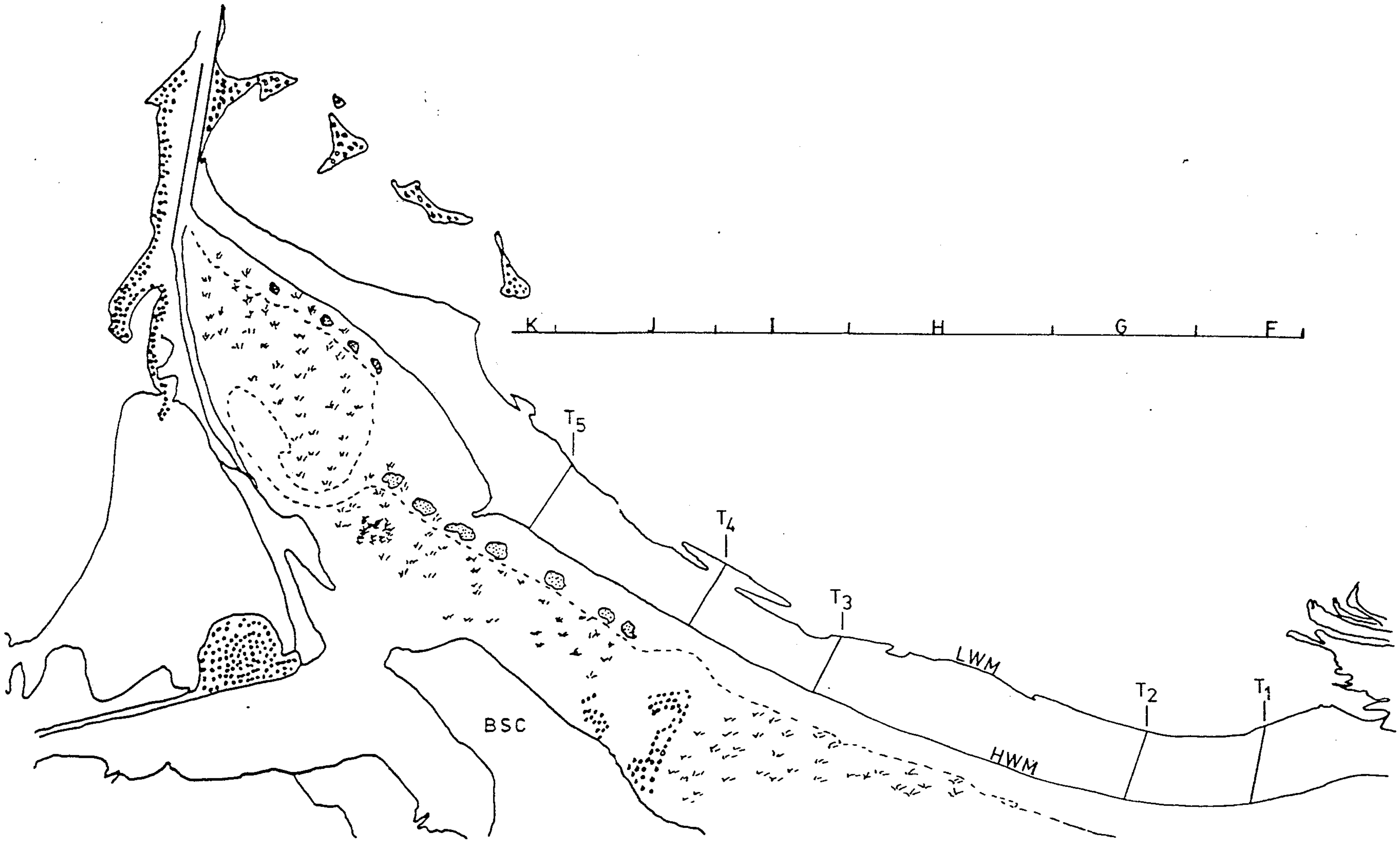
Three sampling programmes were undertaken: i) five major transects were sampled (Fig. 2.1) with stations from 20 m to 190 m below the High Water Mark (HWM) to examine zonation of invertebrate prey (sampling stations were 20 m, 30 m, 40 m, 50 m, 60 m, 70 m, 80 m,

Figure 2.1.

The five transects along Coatham Sands. High Water Mark (HWM) and Low Water Mark (LWM) are labelled. The extent of the beach above the HWM is also shown. Beyond transect 5 is located the Ducky, the raised area of beach where flocks of roosting Sanderling gathered.

Areas along Coatham Sands were labelled F through K with the transects occurring as follows:

F - Transect 1
G - Transect 2
H - Transect 3
I - Transect 4
J - Transect 5
K - Beyond Transect 5, including the Ducky.


K
J
I
H
G
F
T5
T4
T3
T2
T1
LWM
HWM
BSC

90 m, 100 m, 130 m, 160 m and 190 m below the HWM); ii) alongshore sampling (parallel to the tide) in the zones of highest prey densities; and iii) intensive local sampling to determine prey dispersion. The HWM was set as the level reached by a mid-level tide (5.0 m). The five major transects were chosen in the two areas of beach of greatest physical differences; slope, sand grain size and wave action. Transects were sampled in November 1977, January, February, March, August, November and December 1978, and February 1979. Size distribution of all major prey were determined from preserved specimens collected in February, March, August and November of 1978. For Bathyporeia and Eurydice, the length of individuals from 1.5mm to 6.5 mm were measured on a calibrated dissecting microscope to the nearest 0.5 mm. Lengths of Nerine were measured to the nearest 1.0mm by laying worms on a plate of glass placed over graph paper.

The five transects also formed the reference points for recording the feeding observations on Sanderling. Counts of the birds were made in reference to these transects.

To determine alongshore distribution, a sample (1/128 m^2) was taken every twenty metres from transect 3 to 150 metres past transect 5 at 70 m below the HWM on 10/4/1978 (75 samples). On 11/5/1978 the above procedure was repeated for three beach levels; 50m, 70 m, and 90 m below the HWM (225 samples). Samples collected on 11/5/1978 were used to examine size distribution of Nerine.

Determination of dispersion patterns was carried out in November and December of 1977 and March of 1978. On 26/11/1977, 64 samples (corer diameter of 3.7 cm, depth of 6 cm) were taken at 50 m and 60 m below the HWM at transect 5. A sample was taken in the centre of each 10 cm x 10 cm square in an 80 cm x 80 cm grip (64 equal sections). On 3/12/1977 the November procedure was repeated, at transect 3, 50 m below the HWM, with a corer of diameter 2.3 cm. Each sample was taken to a depth of 12 cm and divided into two 6 cm sections. Two additional sets of samples were taken on 12/3/1978; the first at transect 3 (50 m below the HWM). Samples were taken in three twenty-sample rows (60 samples). Each sampling site was one metre from adjacent sites. Each sample was divided into two 6 cm sections (corer diameter of 2.6 cm). The second set of samples was at transect 5, 90 m below the HWM where three fifteen-sample rows were taken (45 samples). Each sampling site was one metre from adjacent sites. Samples were taken with a corer of diameter of 6.2 cm.

2.3 Results

2.3a Transect sampling

Data for main transect sampling are presented in Appendix 2.1. Nerine contributed the majority of individuals on all eight days (Fig. 2.2) The general distribution pattern of the three main invertebrate species is presented for 2/1978 in Fig. 2.3. The widespread distribution of Nerine, with upper-beach peak density and down-the-beach shift at transect 5, was the dominant pattern. Bathyporeia and Eurydice reached their highest densities at transect 5.

In analyzing patterns of Nerine distribution, transect 5 has been separated from transects 1 to 4 on the basis of major differences, as tested by the Spearman rank coefficient and the Kendall coefficient of concordance (Siegel 1956).

Sampling stations of transects 1 to 4 were ranked according to their Nerine density and tested by the Spearman rank coefficient and the Kendall coefficient of concordance. When the density pattern of each transect is compared with each other transect, there were 45 within-sampling date comparisons; 20 were significantly similar by the Spearman coefficient (rho) with one negative correlation (Table 2.1). In the Spearman test, the ranks of case values of two variables (transects) are

Figure 2.2.

The proportion of individuals contributed by each species on the eight days of transect sampling (1977-79). *Nerine* (Open boxes), *Bathyporeia* (Diagonals) and *Eurydice* (Solid boxes).

All species collected considered. Total percentages for each day need not equal 100%.

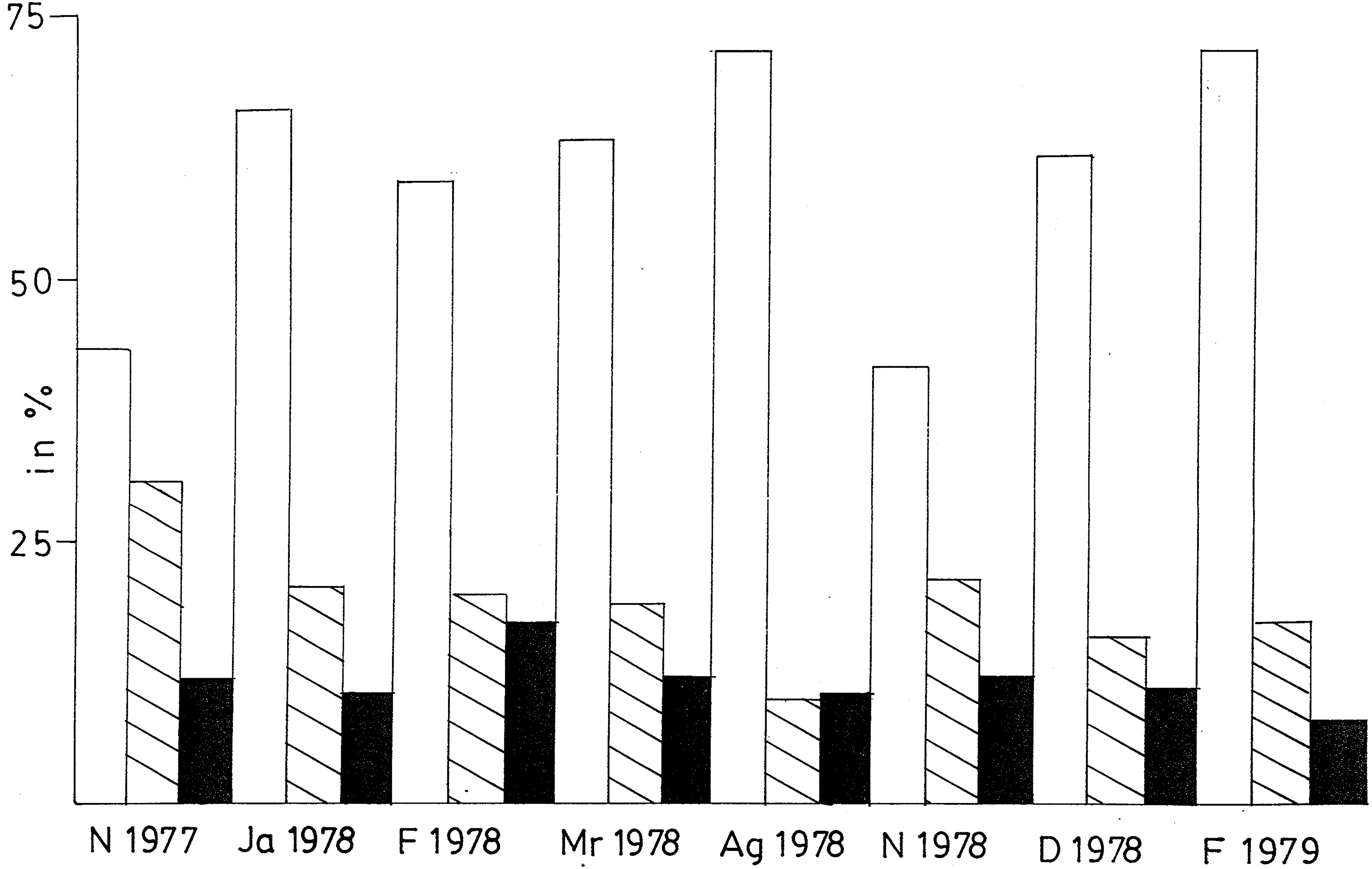

75
50
25
in %
N 1977
Ja 1978
F 1978
Mr 1978
Ag 1978
N 1978
D 1978
F 1979

Figure 2.3

The general distribution patterns for the three main prey of Sanderling from main sampling February 1978. Figure shows densities in relation to metres below the HWM. Patterns are shown for transect 2 and transect 5.

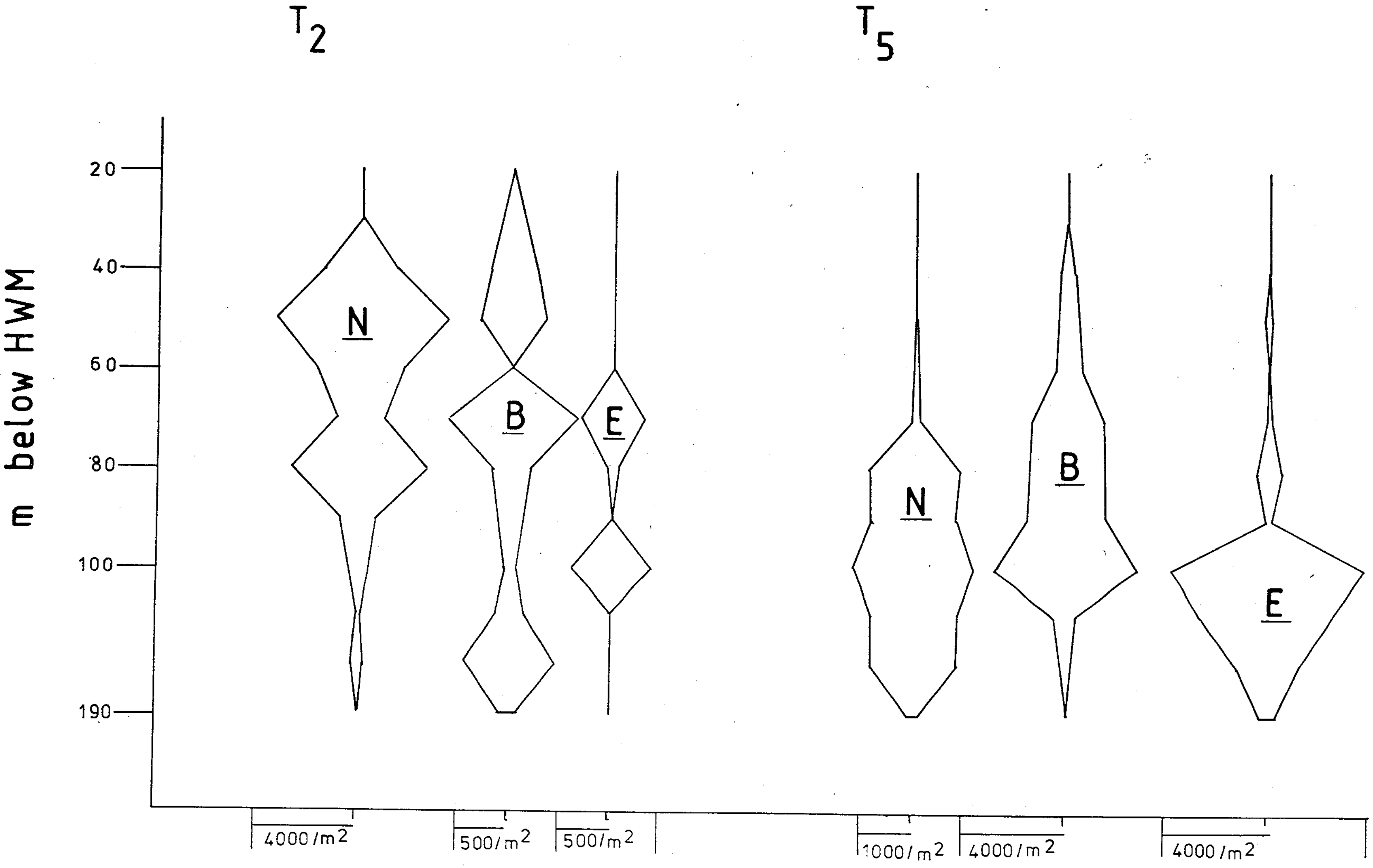

T2
T5
m below HWM
20
40
60
80
100
190
N
B
E
N
B
E
4000/m2
500/m2
500/m2
1000/m2
4000/m2
4000/m2

TABLE 2.1

Within sampling date comparison for Nerine distribution patterns, transects 1 to 4. Significant levels based on the Spearman coefficient (rho).

November 1977

T_1	---		
T_2	0.01	---	
T_3	0.001	0.01	---
T_4	0.05	0.01	0.05
	T_1	T_2	T_3

January 1978*

T_2	---	
T_3	0.05	---
T_4	0.01	0.05
	T_2	T_3

February 1978

T_1	---		
T_2	0.05	---	
T_3	N.S.	0.01	---
T_4	0.01	N.S.	N.S.
	T_1	T_2	T_3

March 1978

T_1	---		
T_2	0.05	---	
T_3	N.S.	N.S.	---
T_4	N.S	N.S.	N.S.
	T_1	T_2	T_3

August 1978

T_1	---		
T_2	N.S.	---	
T_3	N.S.	0.001	---
T_4	N.S.	N.S.	N.S.
	T_1	T_2	T_3

November 1978

T_1	---		
T_2	0.05	---	
T_3	N.S.	0.05	---
T_4	N.S.	0.05	N.S.
	T_1	T_2	T_3

December 1978

T_1	---		
T_2	N.S.	---	
T_3	0.05	0.05	---
T_4	0.05**	N.S.	N.S.
	T_1	T_2	T_3

February 1979

T_1	---		
T_2	0.01	---	
T_3	N.S.	N.S.	---
T_4	N.S.	N.S.	N.S.
	T_1	T_2	T_3

* T_1 not sampled

** Negative correlation

tested, with +1 for two identical rankings and -1 for exactly opposite rankings (MIDAS operational manual 1980). Transects 1 and 2 showed similar distribution patterns on five of seven days and transects 2 and 3 showed similar patterns on six of eight days (Table 2.2). Analysis by the Kendall rank correlation coefficient (tau) gave very similar results.

The similarity of distribution patterns in *Nerine* was also measured by Kendall's coefficient of concordance (W). This is a linear function of the arithm~~a~~etic mean of all the pairwise Spearman's rho coefficients, expressing the degree of association among a number of varibles (transects) (Siegel 1956). The measure of concordance and their levels of significance for each sampling date are given in Table 2.3. Values for W range from 0 to 1, with 0 signifying no agreement and 1 signifying complete agreement with the set of rankings. December 1978 was the only sampling month lacking a significant level of concordance. Distribution patterns in transects 1 to 4 were similar.

Figure 2.4 shows the distribution of *Nerine* at the five transects for November 1977 and 1978. Analytical techniques used to compare within-sampling date were again used to compare between-sampling date patterns. Each transect was compared with its replicates for the eight sampling days (seven for transect 1). Of 133 possible comparisons (28 for transects 2 to 5 and 21

TABLE 2.2

The number of sampling days for which the following pairs of transects were significantly correlated (showed a similar distribution of Nerine). Levels of significance at least $P < 0.05$.

Comparison	Number of days correlated
Transects 1 and 2	5*
Transects 1 and 3	2*
Transects 1 and 4	2*
Transects 2 and 3	6
Transects 2 and 4	3
Transects 3 and 4	2

* As transect 1 was not sampled during January 1978, only seven comparisons are possible with this transect.

TABLE 2.3

Concordance values (w) and their significance levels for the eight main sampling days, representing the overall agreement in distribution of Nerine for all transects considered- for a single day. All significance levels refer to transects 1 to 4.

	Comparison		Level of significance
	Transect 1 to 5	Transect 1 to 4	
November 1977	0.4181	0.8079	$P < 0.001$
January 1978	0.5677	0.8313	$P < 0.001$
February 1978	0.4835	0.680	$P < 0.001$
March 1978	0.3775	0.5221	$P < 0.01$
August 1978	0.4021	0.4217	$P < 0.05$
November 1978	0.490	0.7126	$P < 0.001$
December 1978	0.1646	0.4008	n.s.
February 1978	0.5181	0.5867	$P < 0.01$

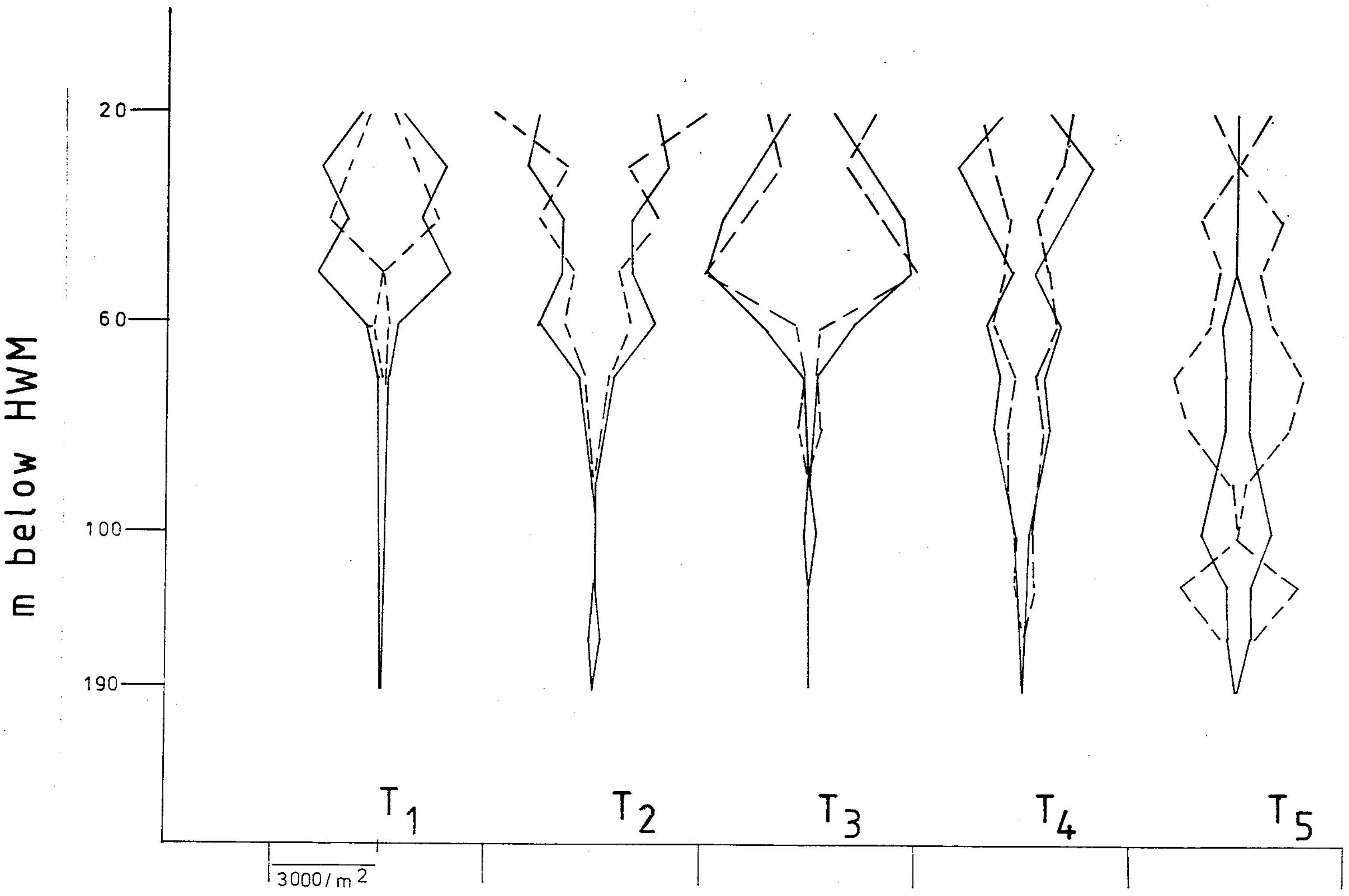
Figure 2.4

The distribution of <u>Nerine</u> at the five transects for November 1977 and 1978.

Solid line- 1977

Broken line- 1978

All densities are shown in relation to metres below the HWM.


m below HWM
20
60
100
190
T1
T2
T3
T4
T5
3000/m2

for transect 1), 30 showed significant levels for their distribution patterns (with one negative correlation), as judged by the Spearman rank correlation (rho) (Table 2.4). Concordance levels (W) were significant for each transect in a between sampling date comparison (Table 2.5). For between-date comparisons of distribution there is no suggestion of a seasonal shift in Nerine (Table 2.6).

The mean density of Nerine within a transect can serve as a measure of potential food availability of that area. The pattern of mean density (Table 2.7, as determined from Appendix 2.2) suggests a high level of predictability, in regards Nerine along Coatham Sands. Nerine numbers in transects 1 and 5 were consistently lower than those of transects 2, 3 and 4, though concordance level of the pattern shown in Table 2.7 was not significant.

As each transect represents a feeding potential for the Sanderling, so too will the levels (metres below the HWM) of the beach. Six levels of the beach were compared (20-30 m, 40-50 m, 60-70 m, 80-90 m, 100-130 m and 160-190 m below the HWM). When densities were averaged for the eight sampling days, there was no significant difference between 40-50 m and 60-70 m below the HWM. Both of these levels, however, were significantly greater than the other four levels (Table 2.8).

TABLE 2.4

Between-sampling date comparisons. Each transect is compared with replicates from all sampling dates. All significant values at $P < 0.05$ or greater.

Transect	Number of significant occurrences (based on rho)
1	0
2	7
3	7
4	8*
5	9

* This includes one negative correlation- August 1978 and November 1978.

TABLE 2.5

Concordance values (W) for each set of transect replicates and their levels of significance.

Transect	(W)	Level of significance
1	0.3390	$P < 0.05$
2	0.4840	$P < 0.001$
3	0.4877	$P < 0.001$
4	0.3204	$P < 0.01$
5	0.3956	$P < 0.001$

TABLE 2.6

The number of pair-combinations of transect replicates between sampling months showing similar distribution patterns for Nerine ($P < 0.05$ or greater).

	Nov. 1977	Jan. 1978	Feb. 1978	March 1978	April 1978	Nov. 1978	Dec. 1978
Nov. 1977	---						
Jan. 1978	0	---					
Feb. 1978	2	3	---				
March 1978	1	2	2	---			
Aug. 1978	0	0	2	0	---		
Nov. 1978	3	0	1	0	2*	---	
Dec. 1978	3	0	1	1	0	1	---
Feb. 1979	1	0	2	2	0	0	1

* With one negative correlation.

TABLE 2.7

Rank ordering of transects as determined by mean densities of *Nerine* (Appendix 2.2).

November 1977	3	2	4	1	5
January 1978*	2	4	3	5	
February 1978	3	2	1	4	5
March 1978	2	4	3	1	5
August 1978	4	2	3	1	5
November 1978	5	3	2	4	1
December 1978	2	4	3	5	1
February 1979	2	4	3	1	5

* Transect 1 was not sampled.

TABLE 2.8

Comparisons between six beach levels (metres below the HWM) for mean densities ($\bar{X}$) of *Nerine*.

Level	N	$\bar{X}$	S.E.
20-30 m	58	749.2	126.6
40-50 m	61	1535.5	191.5
60-70 m	62	1366.7	168.5
80-90 m	62	641.6	90.5
100-130 m	59	331.9	61.7
160-190 m	34	72.5	18.1

Comparisons showing significant differences.*

	t	d.f.	P <
40-50 m vs. 20-30 m	3.4	117	0.001
40-50 m vs. 80-90 m	4.2	121	0.001
40-50 m vs. 100-130 m	6.0	118	0.001
40-50 m vs. 160-190 m	7.6	93	0.001
60-70 m vs. 20-30 m	2.9	118	0.005
60-70 m vs. 80-90 m	3.8	122	0.001
80-90 m vs. 100-130 m	2.8	119	0.01
80-90 m vs. 160-190 m	6.2	94	0.001
100-130 m vs. 160-190 m	4.0	91	0.001
20-30 vs. 100-130 m	3.0	118	0.005

* All comparisons show the greater level on the left.

Bathyporeia occurred in all five transects but densities were too low and too variable to make detailed analysis possible except at transect 5. Where *Bathyporeia* did occur at transects 1 to 4, the numbers were highly localized. *Bathyporeia* exhibited a down-the-beach shift in mid-winter, 1977-78 (Fig. 2.5). An upper-brach level (20-70 m below the HWM) and a lower-beach level (80-190 m below the HWM) were designated to test whether a significant shift occurred in *Bathyporeia* during the 1977-78 winter; the relevant comparisons are presented in Table 2.9. The shift in distribution was tested as significant ($P < 0.05$).

Numbers of *Bathyporeia* showed a significant decrease in 1978-79 over 1977-78 (Fig. 2.5). When densities in November 1977, January and February 1978 are compared with November and December 1978 and February 1979, a significant decrease is shown ($t=2.5$ with 68 d.f., $P < 0.025$). For the eight sampling days, *Bathyporeia* showed significant concordance between rankings of mean densities for the five transects ($W= 0.4531$, $P < 0.01$).

Figure 2.5

Densities of Bathyporeia from seven main sampling days.

Data are paired to provide a comparison of numbers between years.

Broken line- first sampling year

Solid line- second sampling year

All densities are shown in relation to metres below the HWM.

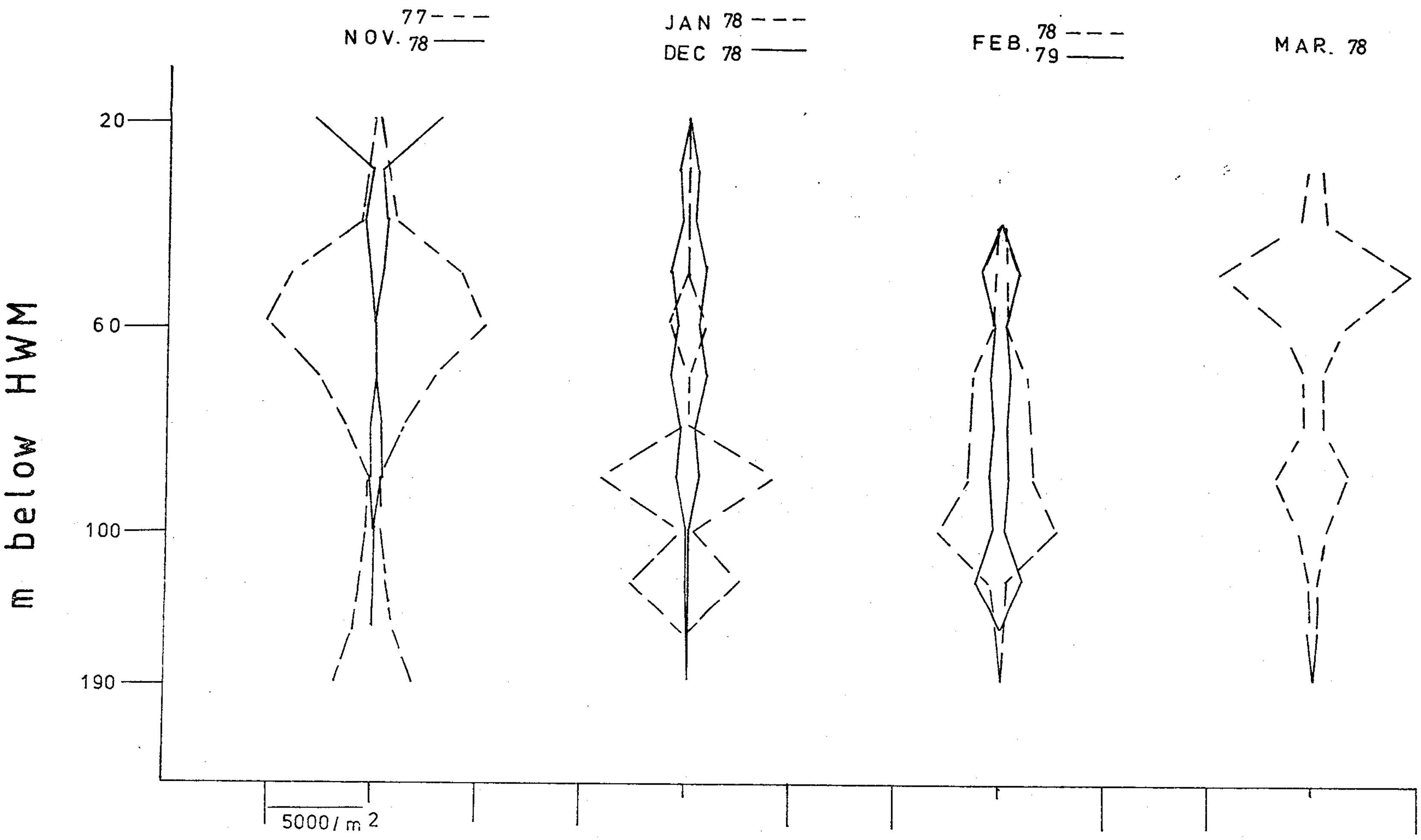

NOV. 77 - - -
NOV. 78 ——
JAN 78 - - -
DEC 78 ——
FEB. 78 - - -
FEB. 79 ——
MAR. 78
m below HWM
20
60
100
190
5000/m 2

Table 2.9

Test of distribution shift for Bathyporeia, 1977-78.

Upper beach = 20-70 m below the HWM.

Lower beach = 80-190 m below the HWM.

Upper beach			
November 1977	vs.	March 1978	N.S.
January 1978	vs.	February 1978	N.S.
Lower beach			
November 1977	vs.	March 1978	N.S.
January 1978	vs.	February 1978	N.S.

To compare upper and lower beach distributions, November 1977 and March 1978 are combined and January 1978 and February 1978 are combined.

a. November 1977 and March 1978 combined:

Densities in upper beach significantly greater than in lower beach,

$t = 2.2$ $\quad$ $d.f. = 21$ $\quad$ $P < 0.05$.

b. January 1978 and February 1978 combined:

Densities in lower beach significantly greater than in upper beach,

$t = 2.1$ $\quad$ $d.f. = 22$ $\quad$ $P < 0.05$.

2.3b Size distribution

Size distribution was examined for all the main prey species collected on February, March, August and November of 1978. *Bathyporeia* and *Eurydice* were separated into size classes of 0.5 mm intervals. Class sizes for *Bathyporeia* ranged from 1.5 mm to 6.5 mm and for *Eurydice*, from 2.0 mm to 5.5 mm. As 80 percent of all *Bathyporeia* measured were in size classes 2.5 mm, 3.0 mm and 3.5 mm, and 81 percent of all *Eurydice* measured were in size classes 2.0 mm or 2.5 mm, no further analysis as to the distribution of the size classes were made for these two species.

Nerine as small as 4 mm were measured. It is possible that *Nerine* smaller than 4 mm were missed. As there was no simple pattern in size class distribution of *Nerine*, probability paper (showing cumulative frequencies) was used to plot the population (Fig. 2.6).

A greater proportion of very large *Nerine* (greater than 18 mm) was present in August and November 1978 compared to March and February 1978. The smallest size classes were poorly represented in August compared to other months. For the three smallest size classes (4 mm, 5 mm and 6 mm) the cumulative percentages for February, March, August and November were: 30.5%, 40.2%, 12.5% and 26.5% respectively. The increase in the percentage contribution of these smallest classes, between August and November, was probably due to growth of very small worms (smaller than 4 mm),

Figure 2.6.

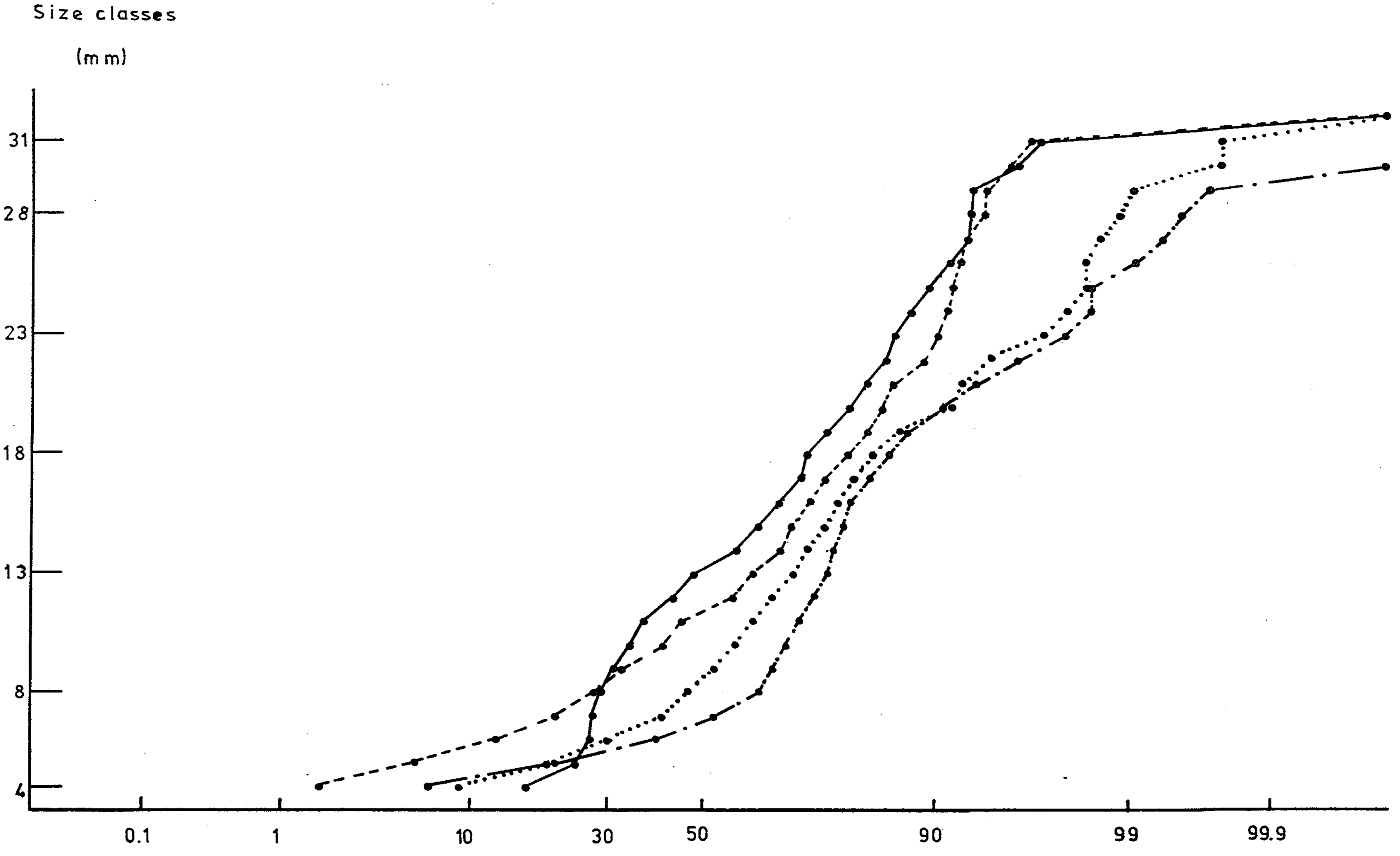
Size class distribution for *Nerine*, plotted on probability paper, showing cumulative frequencies.

.... February 1978,

_._._ March 1978

----- August 1978

_____ November 1978


Size classes
(mm)
31
28
23
18
13
8
4
0.1
1
10
30
50
90
99
99.9

which were not retained during the August sampling. Joyner (1962) found that the reproductive period of Nerine began early in the year and was of a long duration. Pelagic stages existed between March and October and lasted in excess of 30 days.

Size distribution of Nerine was analyzed to test whether the densities in different months were adequate measures of the prey biomass present. The difference in biomass between a Nerine of 4 mm and one of 30 mm is considerable. Therefore, location of large Nerine may have a large effect on where birds choose to feed. The relationship between size distribution and tidal height was tested. Any analysis using mean values will be highly influenced by the large numbers of small worms. For this reason I looked at worms greater than 10 mm and those less than, or equal to, 10 mm.

I looked first at the relationship between the proportion of Nerine greater than 10 mm at each station against the density there. For this analysis there were 215 samples from which 1782 Nerine were measured. There was no significant trend between size (proportion of large worms) and density.

I then looked at size distribution with respect to tidal height. As the Nerine band was displaced down the beach at transect 5, only transects 1 to 4 were considered. As no seasonal trend was noted for Nerine, the four days were lumped. A 2 x n contingency table was used to test any relationship between tidal height and size distribution (Table 2.10). There was a significant increase in the proportion of large Nerine at lower tidal heights. Figure 2.7 presents a histogram of the percentage of large worms (greater than 10 mm) at each of the tidal heights. Sanderling rarely fed at 20 m, 160 m and 190 m below the HWM. Few size data were available for these three tidal heights. To insure that these three tidal heights did not affect the results, they were excluded from a second 2 x n contingency table. The results were again highly significant ($X^2 = 110.8$, d.f.= 8, $P < 0.001$).

2.3c Alongshore sampling

As determined by the two alongshore sampling days (Appendix 2.3), Nerine was widely distributed throughout, with Bathyporeia and Eurydice very localized (Fig. 2.8a-c). Some sites held high densities of all three prey species. The shift in densities from transect 3 to transect 5 was clarified by these alongshore samplings. For Nerine, 50 m below the HWM held significantly greater densities than 70 m or 90 m below the HWM for samples 1-35 (Table 2.11). In this same region, 70 m below the HWM held significantly greater densities than 90 m below the HWM. No significant differences were evident for samples 36-75. Densities

TABLE 2.10

Contingency table testing the relationship between tidal height and the distribution of large (greater than 10mm) *Nerine*.

Size of *Nerine*	Metres below the High Water Mark 20	30	40	50	60	70	80	90	100	130	160	190	Totals
> 10mm	23	55	85	99	102	66	94	67	51	30	10	3	685
≤ 10mm	6	70	148	234	146	130	73	33	29	6	5	3	883
Totals	29	125	233	333	248	196	167	100	80	36	15	6	1568

$X^2 = 124.8$

11 degrees of freedom

$P < 0.001$

Figure 2.7.

Percentage of Nerine greater than 10 mm at different tidal heights from transects 1 to 4. Data taken from same four sampling dates, (February, March, August and November 1978). as used in Table 2.10.

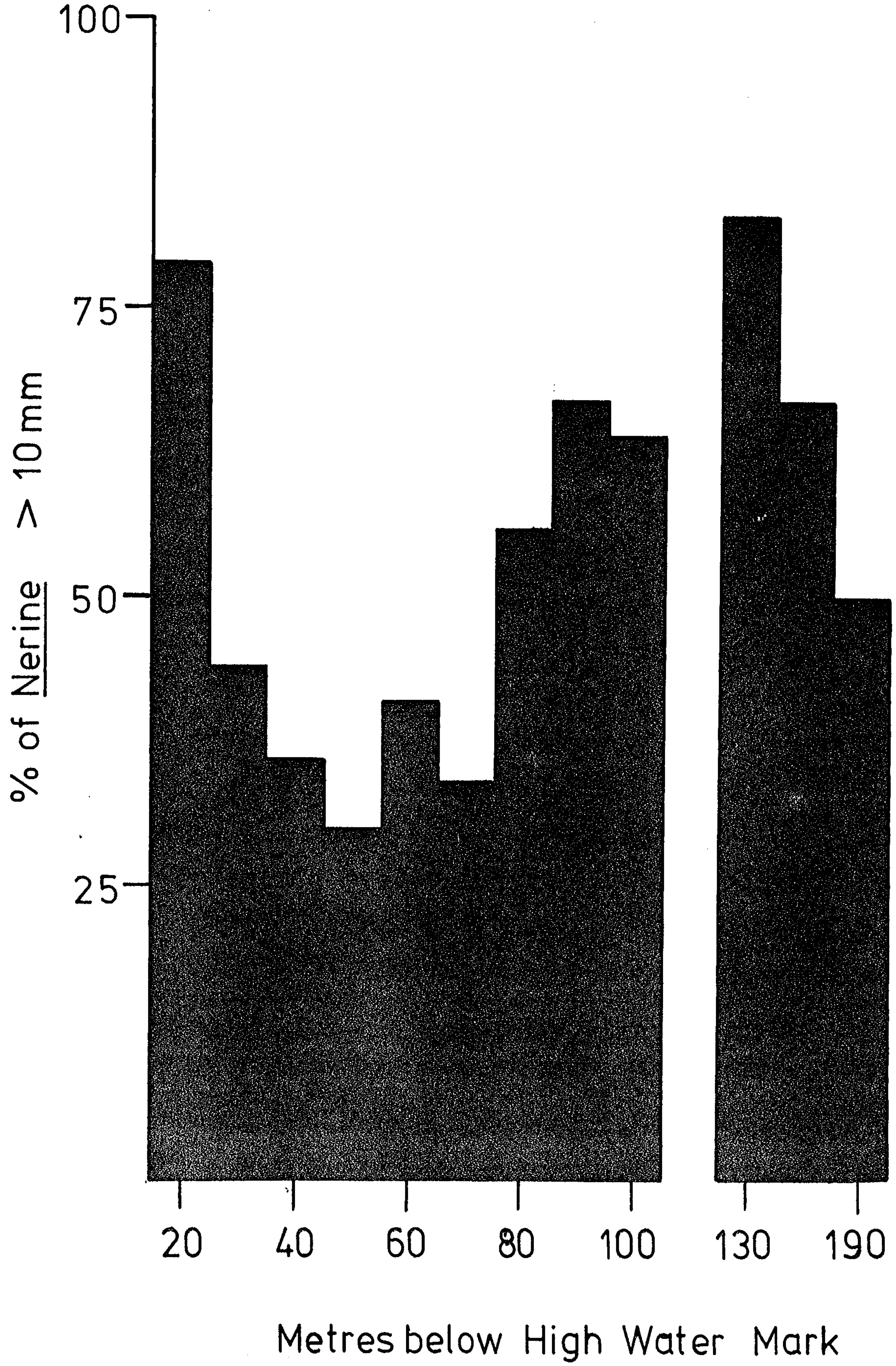
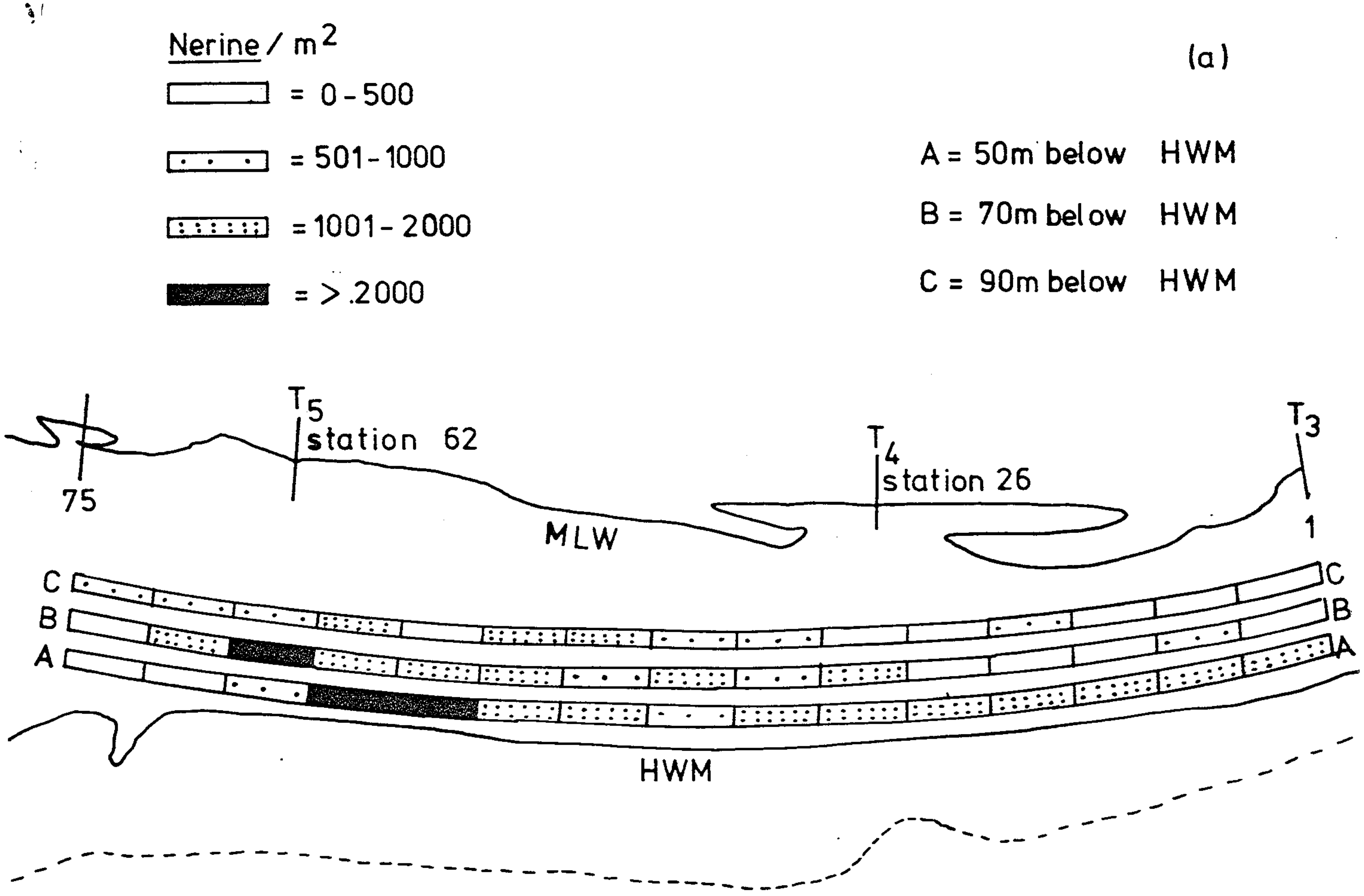

100
75
50
25
% of Nerine > 10 mm
20
40
60
80
100
130
190
Metres below High Water Mark

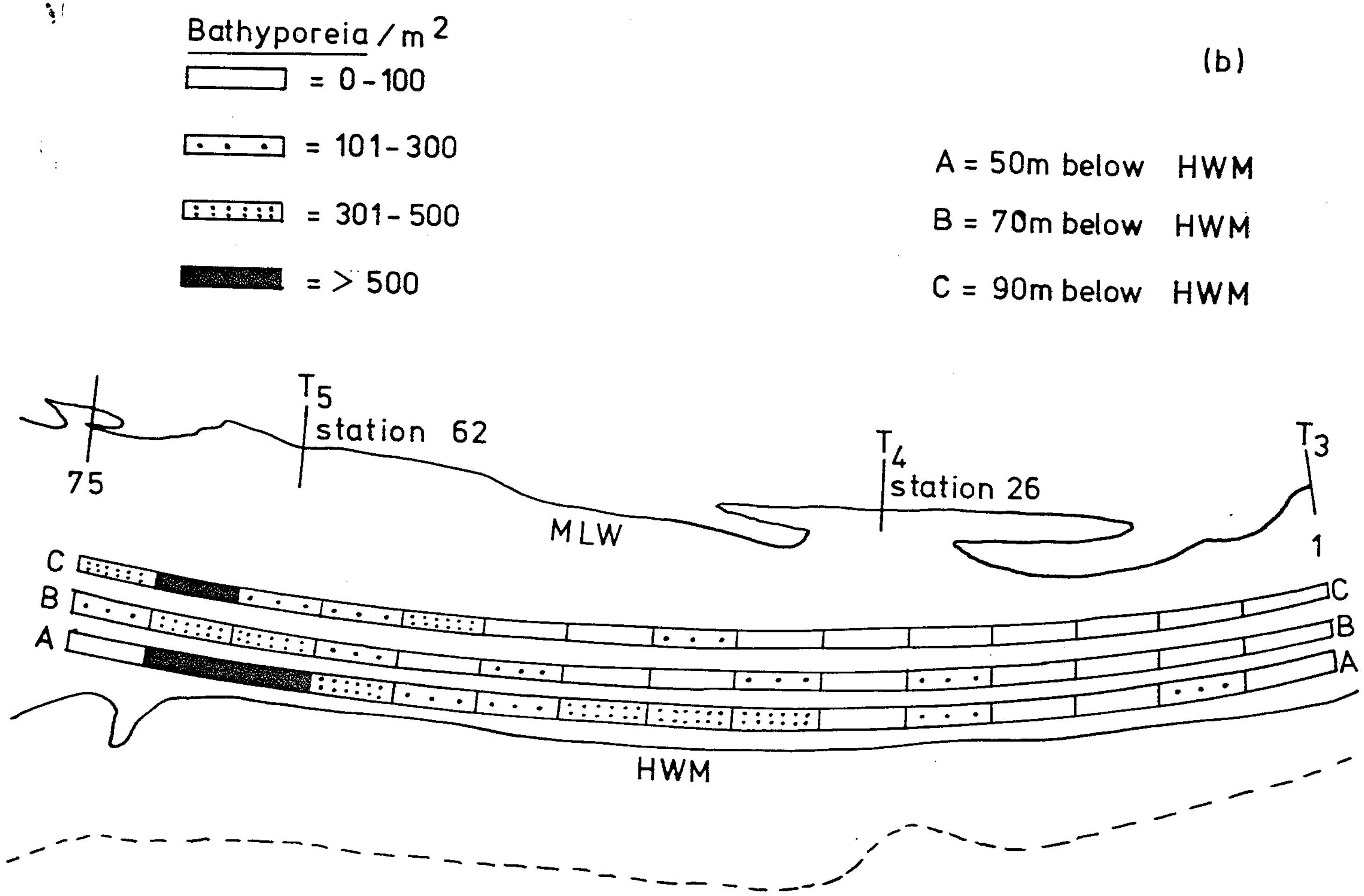
Figure 2.8a-c.

Summaries for alongshore sampling, May 1978. The 75 samples at each level (one sample taken every 20 m) are divided into 15 5-sample segments, with each successive segment averaged: 2.8a *Nerine*

2.8b *Bathyporeia*

2.8c *Eurydice*


Nerine / m^2
= 0 - 500
= 501-1000
= 1001 - 2000
= > .2000
(a)
A = 50m below HWM
B = 70m below HWM
C = 90m below HWM
T_5
station 62
T_4
station 26
T_3
75
1
MLW
HWM
C
B
A


(b)
Bathyporeia / m^2
= 0-100
= 101-300
= 301-500
= > 500
A = 50m below HWM
B = 70m below HWM
C = 90m below HWM
T_5
station 62
T_4
station 26
T_3
75
1
MLW
HWM
C
B
A

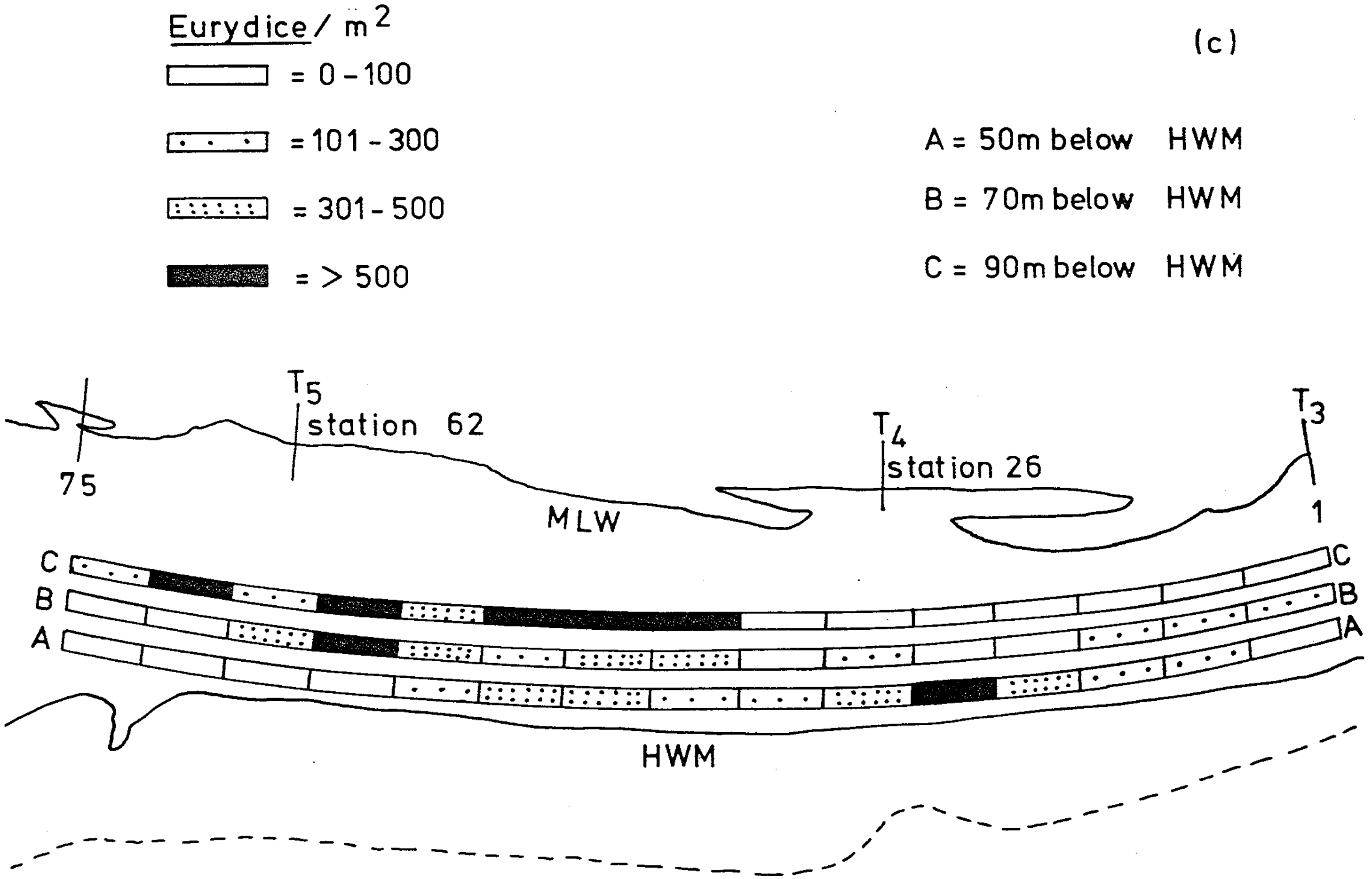

(c)
Eurydice / m²
= 0 - 100
= 101 - 300
= 301 - 500
= > 500
A = 50m below HWM
B = 70m below HWM
C = 90m below HWM
T5
station 62
75
T4
station 26
T3
1
MLW
HWM
A
B
C

TABLE 2.11

Average density for Nerine along Coatham Sands, from transect 3 to beyond transect 5. Sampling from parallel procedure of May 11th, 1978 (Appendix 2.3); 50 m below HWM (A), 70 m below HWM (B) and 90 m below HWM (C).

	$\bar{X}$	S.E.	
Samples 1-35			
A	$1426.3/m^2$	142.3	A > B, $P < 0.001$
B	$625.4/m^2$	93.1	A > C, $P < 0.001$
C	$201.1/m^2$	53.6	B > C, $P < 0.001$
Samples 36-75			
A	$1270.4/m^2$	232.9	N.S.
B	$1264.0/m^2$	140.9	N.S.
C	$1146.0/m^2$	254.6	N.S.

of Bathyporeia increased significantly at samples 36-73 (Table 2.12). Numerical distribution showed no pattern for Bathyporeia in samples 1-35. For Bathyporeia, numbers were greatest at 50 m below the HWM at 36-73 (significantly greater than 70 m below the HWM, $P < 0.025$, with no significant difference with 90 m below the HWM). Eurydice was most abundant at 50 m below the HWM for samples 1-35, although not significantly so with 70 m below the HWM (Table 2.13). For samples 36-73 significanly higher densities were located at 90 m below the HWM.

Very small Nerine (4 mm, 5 mm and 6 mm) comprised a very high percentage of the total densities at 50 m below the HWM (51.1%). At 70 m and 90 m below the HWM these size classes contributed 26.9% and 17.4% respectively. A highly significant increase in the proportion of large worms (greater than 10 mm) occurred at the lower tidal levels (data from alongshore sampling, Table 2.14). At 50 m below the HWM the highest Nerine densities were located, with the area most abundant in large Nerine at 70 m below the HWM.

2.3d Dispersion patterns

Sampling for dispersion patterns was carried out on 26/11/1977 (Appendix 2.4). At 50 m below the HWM (transect 5) no Nerine were found and at 60 m below the

TABLE 2.12

Average density for Bathyporeia along Coatham Sands, from transect 3 to beyond transect 5. Sampling from parallel procedure of May 11th, 1978 (Appendix 2.3); 50 m below HWM (A), 70 m below HWM (B) and 90 m below HWM (C).

	$\bar{X}$	S.E.	
Samples 1-35			
A	98.7/m^2	34.0	n.s.
B	65.8/m^2	21.9	n.s.
C	25.6/m^2	13.7	n.s.
Samples 36-73			
A	609.7/m^2	169.5	A $>$ B, $P < 0.025$
B	171.8/m^2	47.4	
C	299.8/m^2	71.3	

TABLE 2.13

Average density for Eurydice along Coatham Sands, from transect 3 to beyond transect 5. Sampling from parallel procedure of May 11th, 1978 (Appendix 2.3); 50 m below the HWM (A), 70 m below HWM (B) and 90 m below HWM (C).

	$\bar{X}$	S.E.		
Samples 1-35				
A	307.2/m^2	60.6	$A > C$,	$P < 0.001$
B	256.0/m^2	82.6	$B > C$,	$P < 0.025$
C	62.2/m^2	16.9		
Samples 36-73				
A	158.3/m^2	58.5	$C > A$,	$P < 0.001$
B	294.0/m^2	48.1	$C > B$,	$P < 0.001$
C	728.5/m^2	105.5		

TABLE 2.14

Table showing numbers of large (greater than 10 mm) and smaller *Nerine* at three tidal heights (metres below the HWM).

	Tidal Height			Totals
	50 m	70 m	90 m	
Size category				
> 10 mm	83	213	128	424
< 10 mm	346	318	165	829
Totals	429	531	293	1253

$X^2 = 62.2$

d.f. = 2

$P < 0.001$

HWM only two Nerine were found (depth of 6 cm). The more extensive data for Bathyporeia were subjected to analysis by the Index of Dispersion measure (Southwood 1966). Using X^2, the extent to which the distribution conforms to a Poisson model can be tested.

$X^2 = \frac{S^2\ (N-1)}{\bar{x}}$ where S^2 = variance, N = number of samples and $\bar{x}$ = mean. If the distribution is Poisson the value of X^2 will not lie outside the limits of X^2 for N-1. Where X^2 does conform, the Index of Dispersion, $X^2 \div (N-1)$, will approximate to unity. An index value of zero implies a regularly distributed population and a value significantly greater than 1 implies aggregation. Samples taken at both tidal heights, (dispersion indicies were 1.8, $X^2 = 113.2$ with N = 64 and 4.1, $X^2 = 255.1$ with N = 64, respectively), were significantly greater than 1 ($P < 0.001$), indicating a clumped dispersion for Bathyporeia. A second stage of analysis lumped the 64 samples, at each tidal height, into 16 four-square samples. The dispersion index at 50 m below the HWM (0.93, $X^2 = 14.0$ with N = 16) was no longer significantly different from 1 and the index for the 60 m site was reduced to 1.5 ($X^2 = 80.9$, with P still < 0.001). Although the sample size was small (16) these results suggest that the clumps of Bathyporeia were also small in size. In situations where Bathyporeia are being taken from the sand by Sanderling, both the dispersion patterns and the actual size of the patches of prey are important.

Analysis of the Index of Dispersion for the 64 samples collected on 3/12/1977 (Appendix 2.5) showed no clumping for Nerine. Of the 205 Nerine collected, 155 (77.6%) were in the bottom half of the samples (lower 6 cm).

On 12/3/1978 the Index of Dispersion for Nerine (transect 3 at 50 m below the HWM) was 2.2 ($X^2 = 125.7$ with $N = 60$), significantly greater than 1 ($P < 0.001$), indicating a degree of clumping (Appendix 2.6). Of the 136 Nerine extracted, 122 (89.7%) were in the bottom section of the samples (lower 6 cm). Only six Bathyporeia and eleven Eurydice were found. Also on 12/3, sampling was undertaken at transect 5, 90 m below the HWM (Appendix 2.7). For both Bathyporeia and Eurydice the indicies were significantly greater than 1 (2.1, $X^2 = 96.3$ with $N = 45$ and $P < 0.001$, and 7.3, $X^2 = 312.3$ with $N = 45$ and $P < 0.001$, respectively) indicating clumped distributions. The index for Nerine, 1.9 ($X^2 = 76.3$ with $N = 45$) was also significantly greater than 1 ($P < 0.01$).

2.4 Discussion

A major constraint of any predator is the distribution and population dynamics of its prey. For Sanderling at Teesmouth, the study of its invertebrate prey provides the basis for an understanding of the birds' observed distribution (Chapter 3) and may help to account for the large number of Sanderling that winter at Teesmouth.

Nerine has been shown to have a very wide distribution (McIntyre 1968). It is generally abundant only in the upper half of the tidal range (Pierrie et. al. 1932 and Rees 1939). Maximum densities of Nerine at Stoupe Beck were only 160/m^2 (Colman and Segrove 1955); at Kames Bay, 464/m^2 (Watkin 1940); and at Firemore, 1184/m^2 (McIntyre 1968). At Firemore, only three samples (from 80 stations) held densities greater than 500/m^2 (mean density was 107/m^2 ± 19.2). The alongshore data at Coatham Sands showed both the widespread distribution of Nerine and its consistently high densities (147 of 300 samples had a density of 1000/m^2 or greater, with the highest density at 10,240/m^2).

The pattern of distribution of Nerine was similar in transects 1 to 4 throughout the year and between sampling years. Brady (1943) found that the zoning of Nerine was similar in March and November with a "general increase to seaward in the density of Nerine". At Coatham Sands the band of Nerine density was highest at a beach level of 40 m to 70 m below the HWM.

The increase in the proportion of large Nerine at lower beach levels suggests (from the alongshore data) that Sanderling should concentrate feeding efforts at

70 m below the HWM around transect 5. Although *Nerine* densities at transect 3 were highest at 50 m below the HWM they were low at 70 m and 90 m below the HWM. This meant that although feeding could occur at lower levels birds should either feed on *Bathyporeia*/*Eurydice* (when available) or proceed to transects 4 and 5. Transects 2 and 4 consistently held the highest densities of *Nerine*. With nearly 50% of *Nerine* in the three smallest size classes at 50 m below the HWM (alongshore data) movement to transect 4 and beyond should be an advantageous strategy for Sanderling, if : i) transect 2 is unavailable because of density-dependent factors arising from conspecifics, or, ii) if the tide has risen to 50 m below the HWM or higher.

The transect data showed that although patterns were similar throughout Coatham Sands, there was a choice in potential availability of prey amongst the transects. Both from previously sited literature and from the samples of 3/12/1977 and 12/3/1978 it is clear that a large proportion of *Nerine* were beyond the foraging depth of Sanderling. As sampling was done some hours after the tide had receded, worms may have moved vertically downward to avoid desiccation. The availability of *Nerine* may approximate recorded density much closer as the beach becomes wave-washed. The ability of *Nerine* to withdraw to deeper layers on the retreating tide (Watkin 1940) allows it to survive several hours of exposure to drying.

The percentage of very small size classes (Fig. 2.6) throughout the year suggests a constant recruitment of *Nerine*. Despite heavy Sanderling predation (Chapter 4) there is no indication of even partial depletion of *Nerine* over the winter. Even with very conservative estimates, the *Nerine* population can be set at well over 100 million for the area of the five transects along Coatham Sands. Joyner's observations (1962) suggest that the first pelagic individuals should begin settling in April-May. This could account for the small proportion of very small *Nerine* in August. The lengthy reproductive period of *Nerine* may provide the Sanderling with an important renewable food source.

Although highly localized, the densities of *Eurydice* were considerably higher than those reported for other studies (Watkin 1942 and McIntyre 1968). The activity patterns of *Eurydice* have been the subject of several studies. *Eurydice* has been shown to rely on wave action to wash them into the sand (Jones & Naylor 1970). As predacious animals, they seek their prey within the tide. Fish (1970) states that they are synchronized by wave action and that their activity pattern is reinforced by hydrostatic pressure changes. They have been found to be photonegative when well-fed, entering the water only when necessary (Jones & Naylor 1970). The swimming behaviour of *Eurydice* has been correlated with the time of high water of spring tides (Fish 1970); this may help insure that the animals are not stranded. In the laboratory, *Eurydice* has been entrained to an endogenous circa-tidal activity rhythm of emergence and swimming by being stimulated at periods of high water on spring tides (Hastings 1981). Enright (1963) has shown entrainment for another isopod, *Excirolana*. In the field, *Eurydice*, "swim at the water"s edge in surf and breaking waves where turbulence is greatest. This shallow area offers some protection from marine predators and will also be a region of high food availability whether such food is suspended infauna or flotsam" (Hastings 1981). Protection from predation is likely to play an important role in the activity patterns of *Eurydice*. Studies on the food of Plaice off the Cumberland coast in the Irish Sea showed that of the isopods taken, they were almost exclusively *Eurydice pulchra* (Pentreath and Jefferies 1971). *Bathyporeia* sp. were the principle amphipods taken. Such activity patterns of *Eurydice* may have important implications on Sanderling feeding in the area of the waves.

Unlike *Eurydice*, *Bathyporeia* feeds on sand particles and need not come into the water (Watkin 1939), although they were found to be common on the edge of the incoming water. Experiments in the laboratory showed a peak activity in the darkness on the early ebb and a smaller peak prior to high water. Knight-Jones and Morgan (1966) referred to this type of activity pattern as "ebb-transport", where falling pressure promotes swimming. However, as *Bathyporeia* showed a similar zonal distribution in the sand as in the water (Watkin 1939) one might expect more activity prior to high water if resettlement is to be possible. Light has been found to have an inhibiting effect on the swimming activity of *Bathyporeia* and may account for greater night activity (Fincham 1970). McGrorty (1972) observed that *Bathyporeia* left "tracks" on the surface of the sand. These "tracks" were also observed on Coatham Sands and may have provided a valuable visual cue for Sanderling. Sanderling would congregate in areas of high *Bathyporeia* densities and feed in areas of "tracks" just prior to the area being covered by the tide. The rising pressure of the interstitial water might have been activating *Bathyporeia*. Watkin (1939) suggested that movement into the water aided *Bathyporeia* in its double breeding cycle in each month.

Although Coatham Sands is very limited in its species composition, those species present occur in high densities, either throughout or in localized areas. If density is any indication of availability, we can expect *Nerine* to form the basis of the Sanderling's foraging efforts. Any environment contains a number of constraints for animals inhabiting it. While Nerine is widespread and abundant throughout Coatham Sands, Bathyporeia and Eurydice are highly clumped and extremely localized. Vertical tide-controlled movements have been found to be common amongst Polychaeta, Amphipoda and Mollusca (Vader 1964). Movement and cycles of the tide affect activity of the prey and their subsequent availability. Myers et. al. (1980) have shown (for laboratory-tested Sanderling) that prey size, prey depth, microdistribution of prey and substrate penetration can all affect the feeding performance of birds.

From this general invertebrate survey it is clear that without such a base, numerous assumptions would be forced upon the observer. This chapter has dealt with some of the most considerable constraints encountered by the Sanderling. In subsequent chapters I will discuss other constraints and show how these constraints help shape the actual patterns of the Sanderling's foraging behaviour.

CHAPTER 3. THE DISTRIBUTION OF FORAGING SANDERLING IN RELATION TO THE DISTRIBUTION OF THEIR FOODS

3.1 Introduction

Little is known about the feeding habits of Sanderling. Probing in wet sand, feeding in the wave body and foraging along the strand line, left by receding waves, are the main foraging occupations. Townsend (1920) recorded Sanderling probing for sand fleas and other crustaceans and stated, "I have a record of one I shot in 1884, whose stomach was stuffed with small specimens of the common mussel, *Mytilus edulis*". Bent (1962) records Sanderling taking, "sand fleas, shrimps, and other small crustaceans, small mollusks, marine worms, flies, fly larvae, and other insects, and sometimes a few seeds". Observations on feeding individuals at Bodega Bay, California, have shown Sanderling to be taking megalops of *Emerita analoga* and the isopods *Excirolana linguifrons* and *E. kincaidii* (Myers et. al. 1980). Sanderling take these isopods by probing in the substrate (tactile method) or as the isopods rise out of the substrate and swim in the wave wash (visual method).

The feeding activity of waders is partly determined by tide time (Burger et. al. 1977 and Myers et. al. 1981). This sets constraints on feeding, influences foraging strategies and brings birds into close contact, thus increasing the likelihood of aggression (Recher & Recher 1969).

The location of the tide can affect prey activity, and thus availability, as well as the birds' ability to penetrate the feeding substrate (Myers et. al. 1980). Burger et. al. (1977) found that on the outer beach (ocean side) of Cape May , Sanderling reached peak abundance after low tide with a secondary peak after high tide. Much roosting occurred between these times. In this area, Sanderling fed exclusively on water-covered sand. On the inner beach, where there was negligible surf action Sanderling fed on the water's edge.

This chapter describes the general movement of Sanderling within their south-side habitats, including an analysis of roosting location and patterns. Having provided an overview, I then give a more detailed analysis of the correlation of prey density with bird location. The tide determines where the birds can feed by altering prey availability and activity, and substrate penetrability. The question of where the birds are feeding when the major prey is made available is addressed. I then describe factors which alter the general pattern and analyze data on group size in foraging Sanderling. Finally, I discuss the ways in which movement of the birds affect their general ecology.

3.2 Methods

Counts of Sanderling were made from a Landrover driven along the upper beach. All counts were taken with reference to the five sampling transects. After high water the upper beach often held enough water to make driving there dangerous, so that more counts were made on rising than falling tides. Counts were taken throughout the winter period (late September to early May) with as even a month-by-month distribution as possible. Several counts were occasionally made on a single day. This was not possible on most days. All roosting and colour-marked Sanderling were noted.

During 1977-78 the size of feeding groups was determined along with the total number of birds within the five transect areas of Coatham Sands. Group size was determined by means of a commentary, spoken into a tape recorder while driving along the beach. Closeness (not exceeding five metres) and observable directional coordination in movement were used to define the limits of a foraging group.

3.3 Results

3.3a General distribution

During each tidal cycle Sanderling changed their feeding sites progressively along a 3 km stretch of beach, spending the low water hours at Coatham Rocks, Redcar Rocks or Redcar Beach, then moving northwards, reaching the bay at transect 5 one or two hours before high water. On the ebbing tide the pattern was reversed (Fig. 3.1).

Sanderling made their first appearance on Coatham Sands one hour after low water but did not occur in appreciable numbers until two hours after low water, when the flood tide began to cover the main zone of *Nerine*. Transects 1 and 2 (F-G) were the initial feeding areas for a large proportion of the birds, with a gradual movement of Sanderling continuing along Coatham Sands (Fig. 3.2). By low water plus 4.5 hours the main *Nerine* zone was covered at transects 1 to 4 and the birds concentrated in the limited areas of beach where *Bathyporeia* and *Eurydice* were available, namely at transect 5 and further north. The birds remained in this area until high water plus one hour, either roosting or feeding.

During the period between HW + 1 and HW + 2, the birds began moving back towards Redcar Rocks. Birds flew back in groups of 5 to 30 birds or fed along the beach while moving south. By HW + 3 few Sanderling, if any, remained on Coatham Sands.

Sanderling at the Redcar area could be separated into three groups: birds foraging on the rocks, birds foraging on Redcar Beach and roosting individuals. Fig. 3.3 shows the number of Sanderling feeding at Redcar Rocks during spring tides and neap tides. Sanderling were present on the rocks between HW + 3 and LW + 2.

Figure 3.1.

Average numbers of Sanderling on Redcar Rocks (○) and Coatham Sands (●) throughout the tidal cycle during the 1977-78 winter (late September to early May). Broken line shows numbers of roosting individuals on Coatham Sands.

Figures for Redcar Rocks and Coatham Sands based on 56 and 84 counts, respectively.

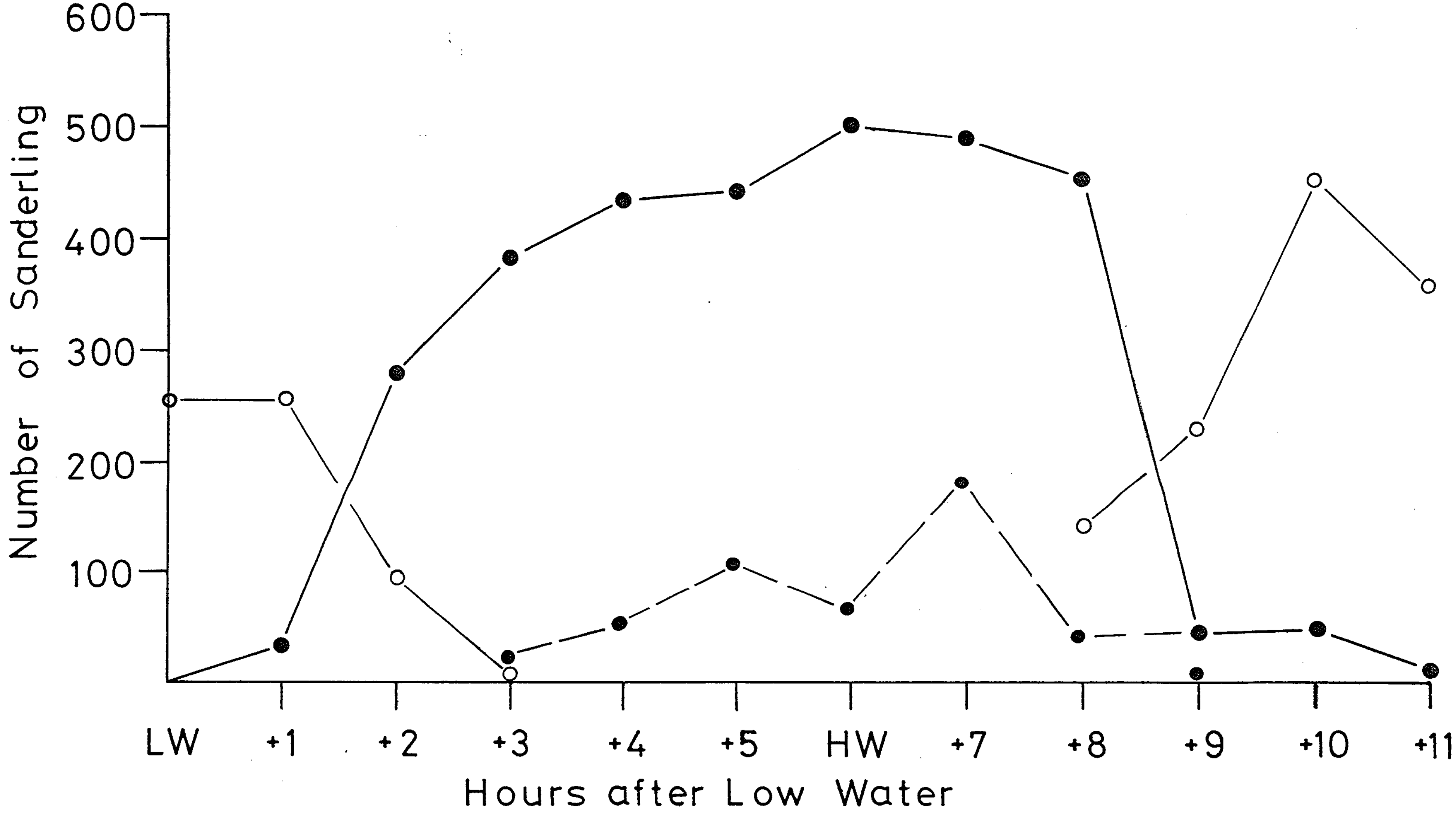

Number of Sanderling
600
500
400
300
200
100
LW
+1
+2
+3
+4
+5
HW
+7
+8
+9
+10
+11
Hours after Low Water

Figure 3.2.

Percentages of total Sanderling (Ordinate) on Coatham Sands in the five areas at different times after low water. Only feeding individuals were considered. This data is taken only from counts during neap and mid-tide days, (tide not greater than 5.3 m). Counts were based on neap-tide levels (thus low water plus five hours on a neap tide and low water plus four hours on a mid-tide were equivalent).

See Figure 2.1 for description of areas F to K.

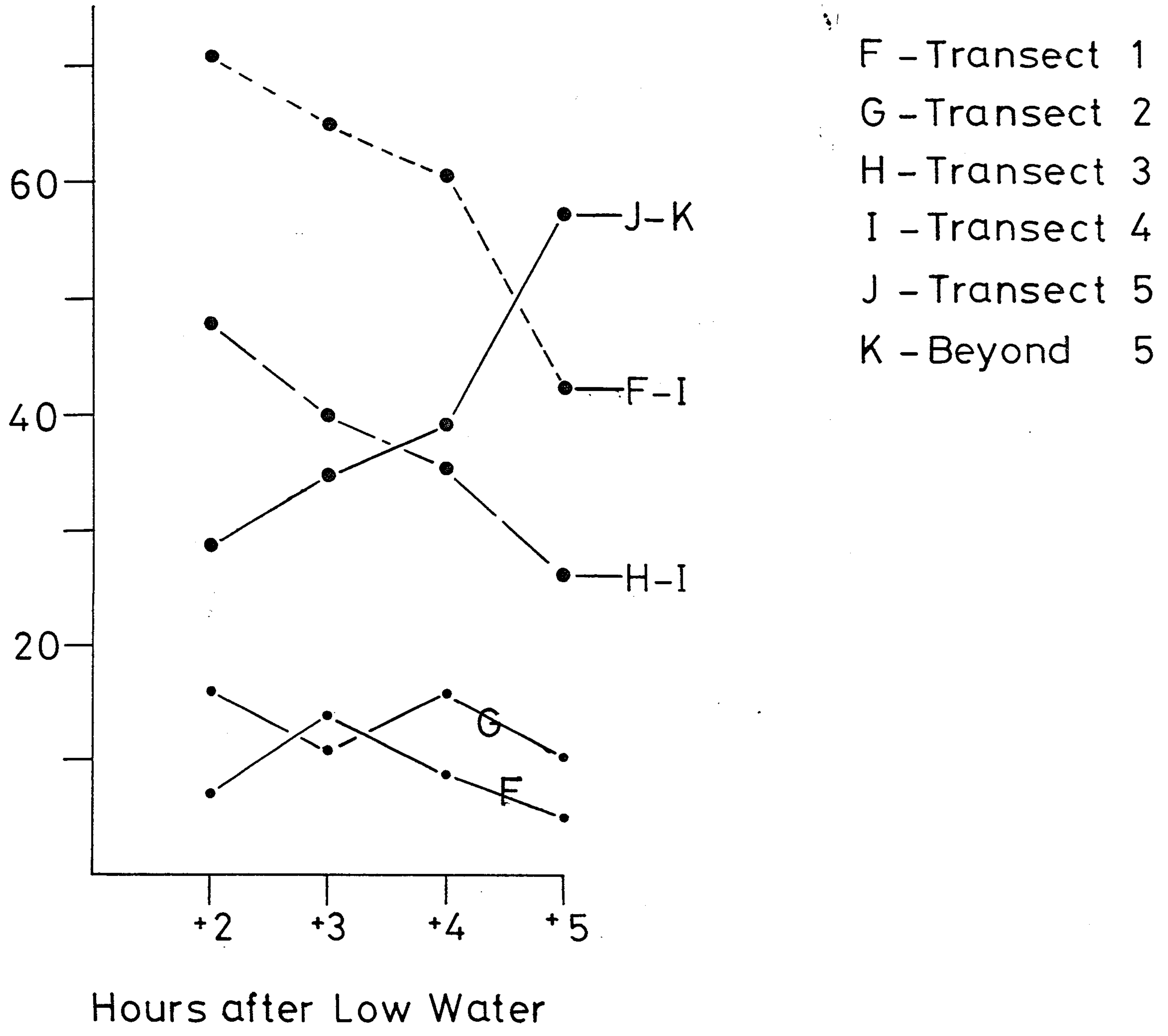
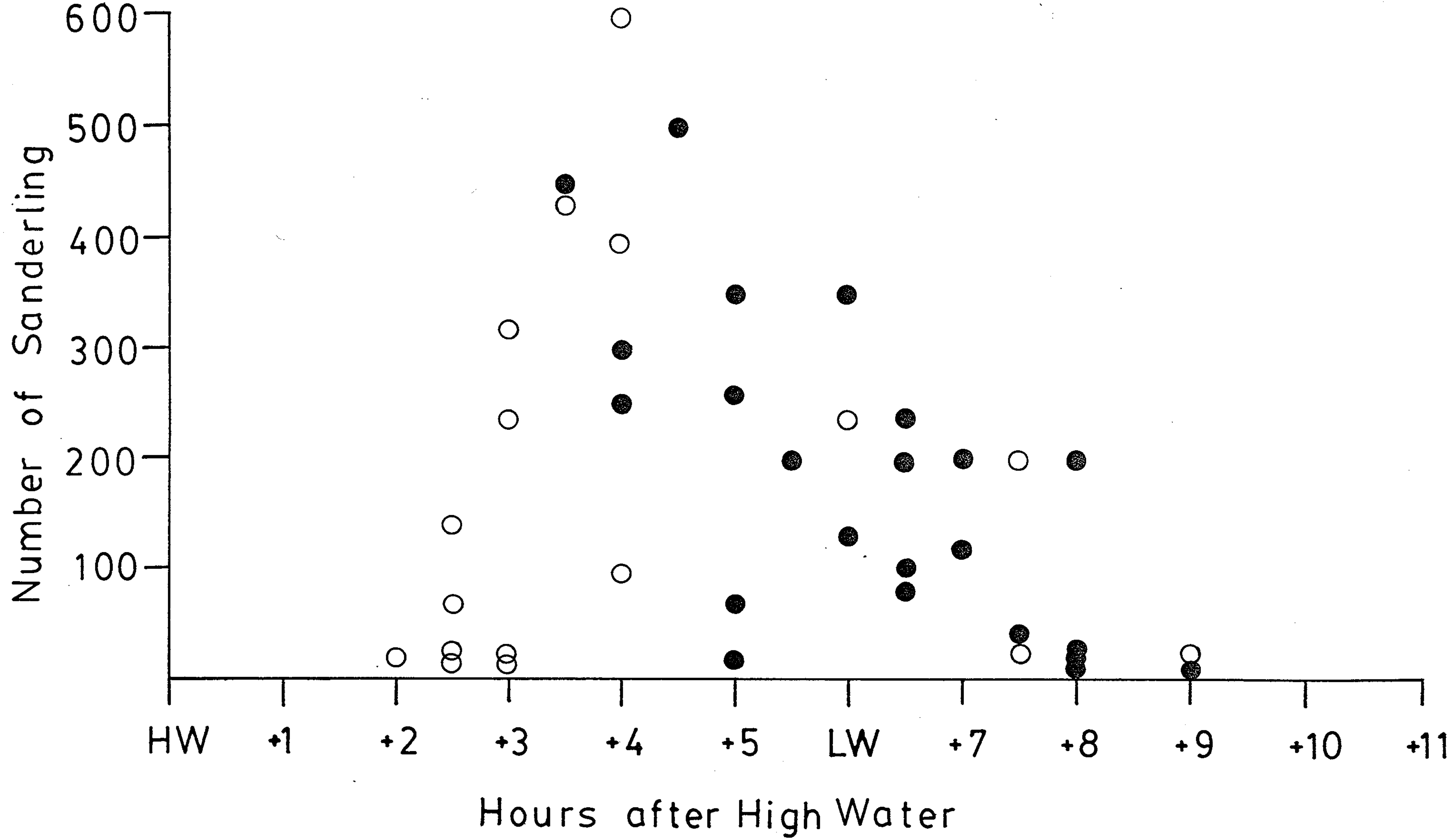

60
40
20
+2
+3
+4
+5
Hours after Low Water
J-K
F-I
H-I
G
F
F - Transect 1
G - Transect 2
H - Transect 3
I - Transect 4
J - Transect 5
K - Beyond 5

Figure 3.3.

Numbers of Sanderling feeding on Redcar Rocks (1977-78). Solid symbols represent counts on spring tides and open symbols represent counts for neap tides. Each symbol represents a single count.


Number of Sanderling
600
500
400
300
200
100
HW
+1
+2
+3
+4
+5
LW
+7
+8
+9
+10
+11
Hours after High Water

3.3b Roosting patterns

Roosting at Redcar Rocks showed a seasonal trend, being frequent during September-November and becoming less frequent in early December, as beach feeding was becoming more frequent. This pattern was similar for the two years, 1976-77 and 1977-78. Roosting at Redcar Rocks again became more frequent in early April. Roosting was more frequent before low water.

The second main area used by Sanderling for roosting was Coatham Sands, mainly in the area beyond transect 5, where a large expanse of upper beach remained uncovered at high water (Fig. 3.4). Roosting along Coatham Sands varied with the season. Throughout August and September of 1977,most birds roosted there over high water. By November few Sanderling were roosting and with less regularity, not becoming frequent again until March of 1978. On spring tides, birds began roosting at LW + 4 and left the roost at HW + 2. Most of the roosting on neap tides occurred after high water. Table 3.1 summarizes the general patterns of Sanderling movement.

Figure 3.4.

Numbers of Sanderling roosting on Coatham Sands. Open symbols represent spring-tide roosting and solid symbols represent roosting during all other tidal heights. Each symbol represents a single count. Counts are taken from 1976-77 and 1977-78.

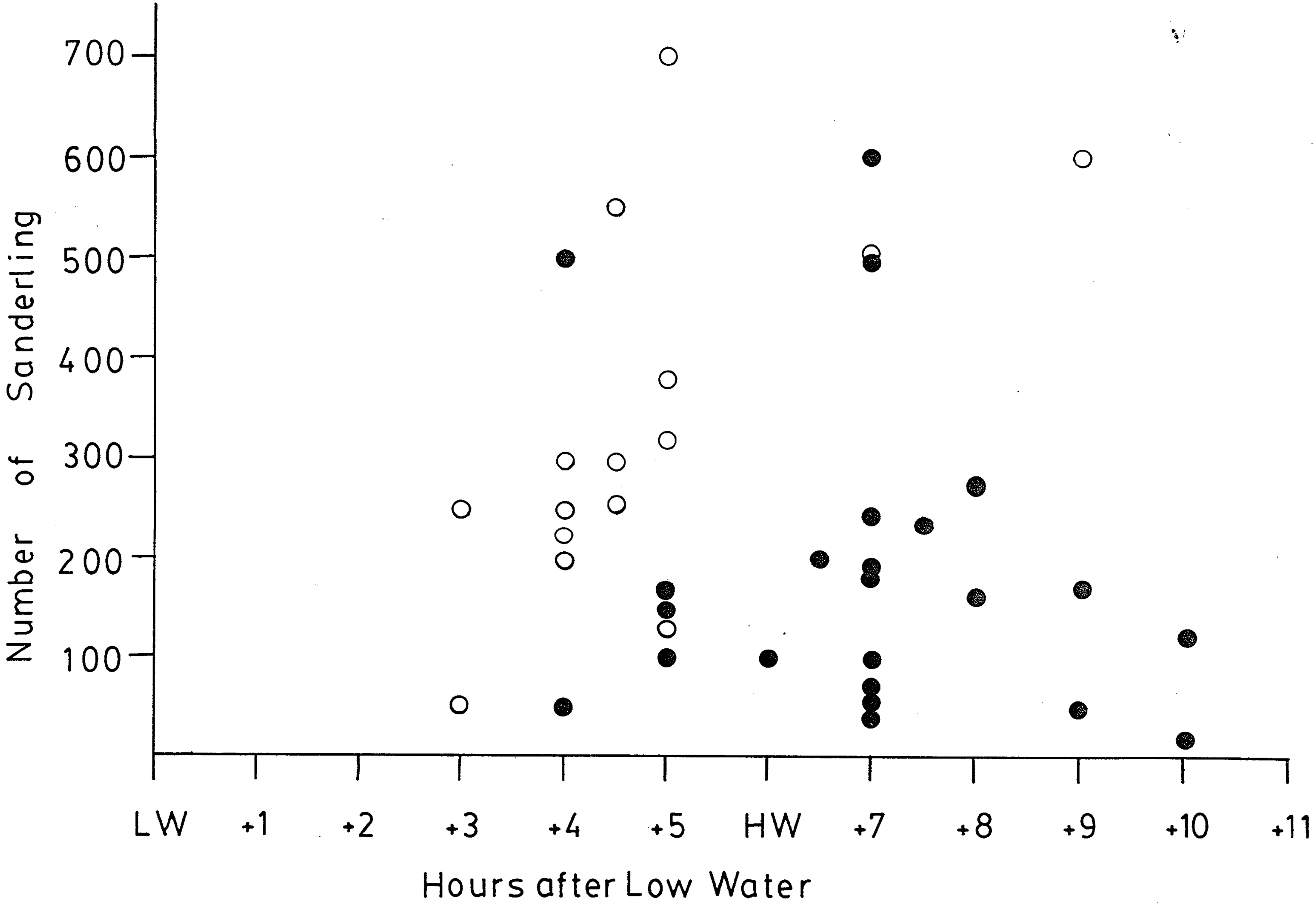

Number of Sanderling
700
600
500
400
300
200
100
LW
+1
+2
+3
+4
+5
HW
+7
+8
+9
+10
+11
Hours after Low Water

TABLE 3.1

Summary of Sanderling movement along coastal rocks and beaches.

HW	- Roost at Coatham Sands.
	- On neap tides may feed on Coatham Sands over HW.
HW+1	- Movement south begins at Coatham Sands.
	- First arrivals at Redcar Rocks.
	- Some individuals continue to roost at Coatham Sands, (neap tides).
HW+2	- Continued appearance at Redcar Rocks.
HW+3	- Rapid increase of numbers at Redcar Rocks.
	- Almost complete disappearance from Coatham Sands.
HW+4	- Most birds at Redcar Rocks and feeding.
HW+5	- Pronounced roosting at Redcar Rocks.
	- Few birds moving to Redcar Beach and some individuals radiating further south.
LW	- Birds continue to move onto the beach at Redcar.
	- Some birds moving onto beach and out of the area.
LW+1	- Birds continue to move to Redcar Beach.
	- First appearance of birds on Coatham Sands.
LW+2	- Rapid decrease of birds at Redcar Beach and Rocks.
	- Spring tides- few birds may remain at Redcar.
	- Areas F-I heavily used at Coatham Sands.
LW+3	- Rapid increase of birds on Coatham Sands.
	- Slow build-up at areas J-K.
	-Main band of <u>Nerine</u> exposed.
LW+4	- <u>Nerine</u> band exposed; soon to be covered.
	- Large shift from F-I to J-K occurs.
	- Roosting begins on Coatham Sands, (spring tides).
LW+5	- Almost 60 percent of the birds in J-K.
	- Roosting continues at Coatham Sands, (spring and neap tides).

3.3c *Nerine* densities at Coatham Sands and the location of foraging Sanderling-the test of some field data

In Figs. 3.5 and 3.6, the location of the tide (metres below the HWM) at each hour after high water and the *Nerine* densities at each location are presented. Can these be used to predict the location of foraging Sanderling? Fig. 3.6 suggests that if *Nerine* densities are the main determinant of Sanderling foraging location (given the location of the tide), Sanderling should be most numerous at transects 1 to 4 at 20 m to 90 m below the HWM (HW + 1 to HW + 3 and, LW + 3 to LW + 5; see Fig. 3.2). I tested, by regression analysis, for a relationship between the number of foraging Sanderling at points along Coatham Sands and *Nerine* densities. No correlation existed. Thus *Nerine* densities alone can not predict the location of foraging Sanderling. Due to the high patchiness of the crustacean prey, a similar analysis could not be performed. The constraints which determine the distribution of foraging Sanderling will be fully detailed in the discussions of Chapters 3 and 4.

3.3d Factors altering general patterns

Deviations from the distributions described in 3.3a occurred occasionally during the winter period. During a severe cold spell in January and February 1978,

Figure 3.5.

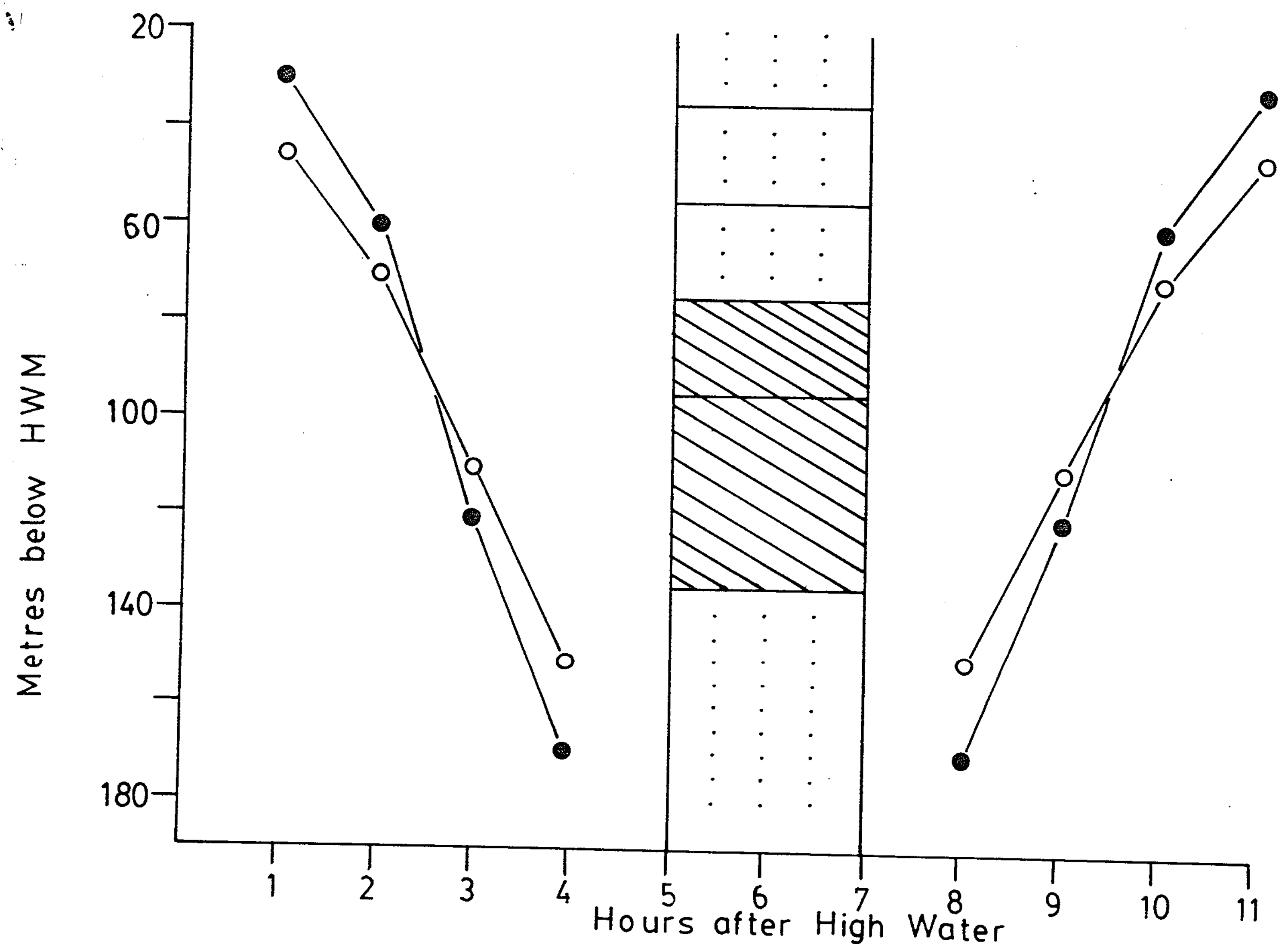
The location of the tide and the density of *Nerine* at transect 5 for each hour after high water.

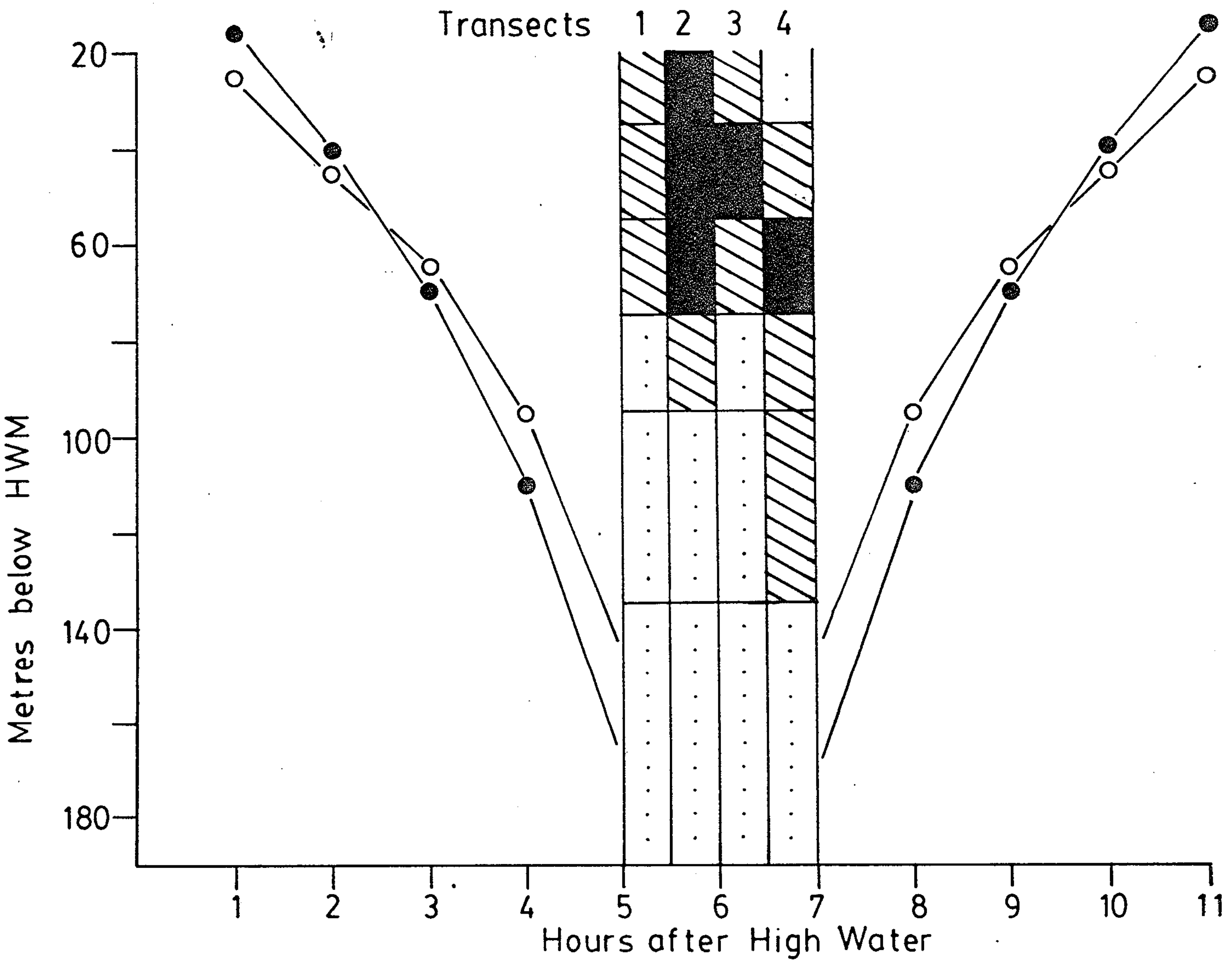
Figure 3.6.

The location of the tide and the density of *Nerine* at transects 1 to 4 for each hour after high water.

Legend for Figures 3.5 and 3.6:

(○) Neap tide
(●) Spring tide
▨ 0-500 *Nerine*/m^2
⬚ 501-1000 *Nerine*/m^2
■ greater than 1000 *Nerine*/m^2


Metres below HWM
20
60
100
140
180
1
2
3
4
5
6
7
8
9
10
11
Hours after High Water


Transects
1
2
3
4
20
60
100
140
180
Metres below HWM
1
2
3
4
5
6
7
8
9
10
11
Hours after High Water

Coatham Sands was inundated by thousands of roosting gulls. Sanderling avoided feeding in these areas for several tidal cycles. On January 25th, thousands of gulls were loafing on Coatham Sands and Redcar Rocks. At low water, only 20 Sanderling were at Redcar Rocks, while a flock in excess of 300 were seen at the tip of Saltburn Rocks, some 8 km further south. On February 8, LW + 1, 120 Sanderling were feeding on Redcar Rocks. By LW + 2, more than 200 Sanderling were feeding on the beach at Redcar. By LW + 3, Redcar Rocks were covered, yet only 15 Sanderling had moved to Coatham Sands. Several thousand gulls were still present on Coatham Sands. At LW + 4.5, no Sanderling were to be found on Coatham Sands. At this time, 319 Sanderling were reported roosting at Crimdon Dene, to the north of the estuary. Common Gulls were sometimes seen in pursuit of feeding Sanderling at Redcar Rocks and areas along Coatham Sands.

Three additional factors which modified the expected routine of foraging Sanderling were: i) the occurrence of wrack or coal dust along Coatham Sands; ii) the occurrence of opened bivalves, either through their detachment and death during cold spells or those left opened and partly eaten by Oystercatchers; and iii) very strong winds, especially those blowing off the shore.

Wrack and coal dust concentrated the birds in very limited areas, although they did not become noticeably more aggressive. Large flocks of Knot, often in excess of 2000 birds, also fed on the coal dust (which contained much Mytilus spat) and Sanderling tended to keep to the outside of these flocks. Sanderling mixed much more freely with Dunlin. They would often avoid Turnstone, as the Turnstone were often aggressive towards Sanderling, robbing them of both bivalves and crabs.

Wrack and coal dust on Coatham Sands delayed the time of the birds' departure so that they did not move to Redcar Beach before the Rocks were exposed. Under such conditions, Sanderling returned to Coatham Sands after low water earlier than normal and reduced the time spent roosting at high water at transect 5. Indeed, they often failed to reach the area of transect 5 at any time during the tidal cycle.

There was much fluctuation in the total numbers of Sanderling using the south side of the estuary from one day to the next. As with the Turnstone, Sanderling were quick to locate large and 'unusual' food sources. On January 22 and February 1 of 1977, enormous wrack beds were present on Coatham Sands and on those days the numbers of Sanderling using the area increased markedly (to 1024 on January 22 and to 1200 on February 1).

It was difficult to know whether the numbers of Oystercatchers present on Coatham Sands affected the numbers of Sanderling. By opening large mussels but not eating all the flesh they provided an additional source of food for Sanderling but probably did not actually change the distribution. Exploring the shells left by Oystercatchers was a common practice for both Sanderling and Turnstone. In most shells some parts of the abductor muscles as well as mantle tissue were left. Sanderling actively searched for these shells while Turnstone waited impatiently by a feeding Oystercatcher, remaining close until it left the bivalve. This behaviour of the Turnstone has also been noted by Campbell (1966).

Strong winds created severe problems for feeding Sanderling, especially offshore winds which blew dry sand from the upper beach. Sanderling feeding out into the waves experienced difficulties as the wind blew their feathers about. When running up from the waves the dry sand being blown impaired their vision. It became difficult for the birds to maintain their very precise spacing within the groups. On 27/4/1977 very strong winds occurred; at HW + 1.5, 400 Sanderling were roosting on Bran Sands. At HW + 3, 160 Sanderling had moved to Redcar Rocks and were roosting there. No Sanderling were seen on any part of Coatham Sands on that day.

Information regarding the distribution of Sanderling within all of the estuary can be found in Appendix 3.1. This information will be discussed in Chapter 4.

3.3e Group size in foraging Sanderling

Sanderling moved along the beach in groups of two or more. The move from Redcar and Coatham Rocks to transect 5 and beyond was achieved by flying to transects 1 and 2 and moving north, feeding as they did so. Sanderling concentrated in stretches of tide edge 20 m to 50 m long; probably due to local concentrations of prey and behavioural interactions. Where waves occurred in rapid succession (e.g., no flattened area behind the wave edge) the birds could not venture far beyond the edge and were forced into higher concentrations.

Fig. 3.7 shows the increase in group size with increasing numbers of birds foraging in each section of Coatham Sands. In all five cases (areas F through J) regression analysis showed a significant relationship between group size and number of birds in the areas. There were no significant differences amongst the five slopes (group size increased in much the same rate in each section). The composition of group sizes along Coatham Sands is shown in Fig. 3.8.

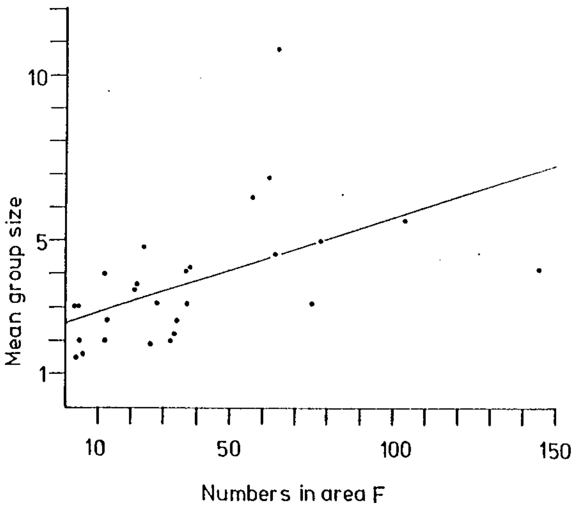
3.4 Discussion

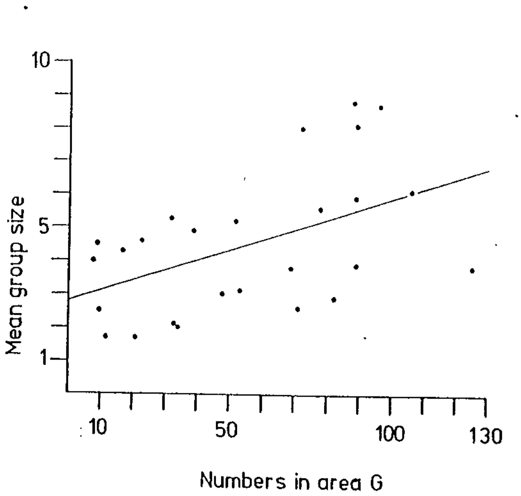
Waders have been shown to respond to spatial variations in the density of their prey and to the profitability of foraging at different sites (Goss-Custard,

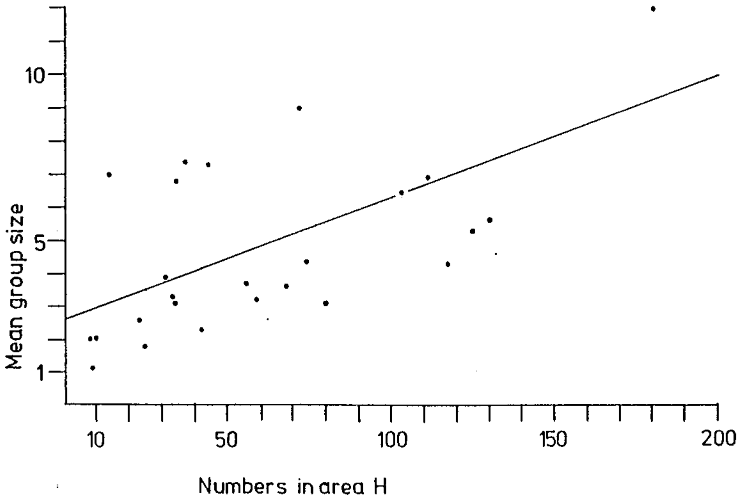
Figure 3.7 (a-e).

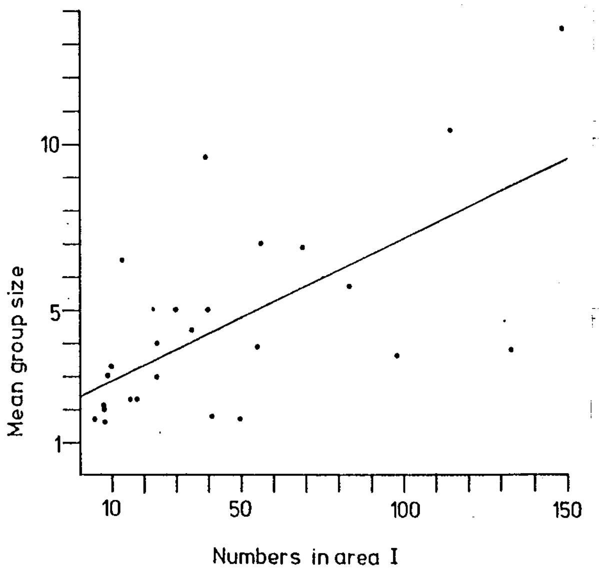
The relationship between the number of foraging Sanderling in an area and the mean group size. The abcissa represents the total number of foraging Sanderling, for any one count in the specified area. The ordinate represents the mean group size, for any one count. (For example, in area F, on 20/9, 62 Sanderling were in the area in feeding groups of: 1,1, 2,2,3,3,10,16 and 24 individuals, giving a mean group size of 6.9.) All counts are from the 1977-78 winter.

a-	Area F		
	Slope	0.03098	
	r	0.52185	
	P	< 0.01	with 25 degrees of freedom
b-	Area G		
	Slope	0.03113	
	r	0.51246	
	P	< 0.01	with 24 degrees of freedom
c-	Area H		
	Slope	0.03452	
	r	0.59638	
	P	< 0.01	with 23 degrees of freedom
d-	Area I		
	Slope	0.04712	
	r	0.63553	
	P	< 0.001	with 23 degrees of freedom
e-	Area J		
	Slope	0.02248	
	r	0.84350	
	P	< 0.001	with 21 degrees of freedom


10
5
1
Mean group size
10
50
100
150
Numbers in area F


10
5
1
Mean group size
10
50
100
130
Numbers in area G


10
5
1
Mean group size
10
50
100
150
200
Numbers in area H


10
5
1
Mean group size
10
50
100
150
Numbers in area I

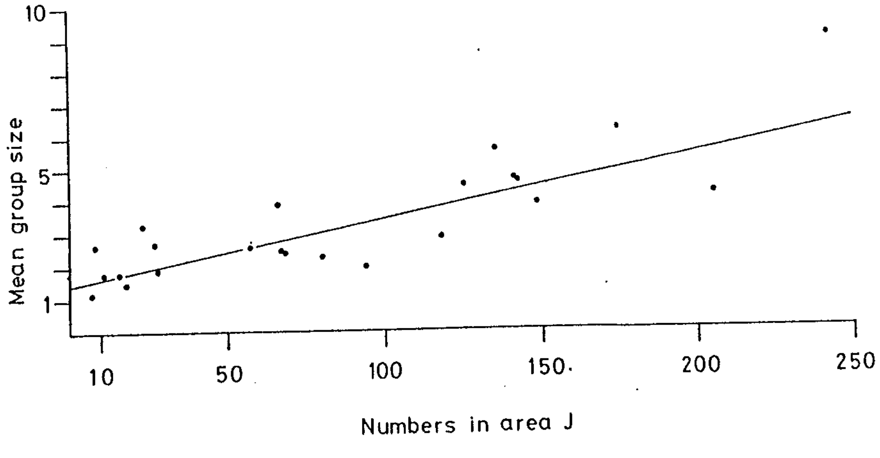
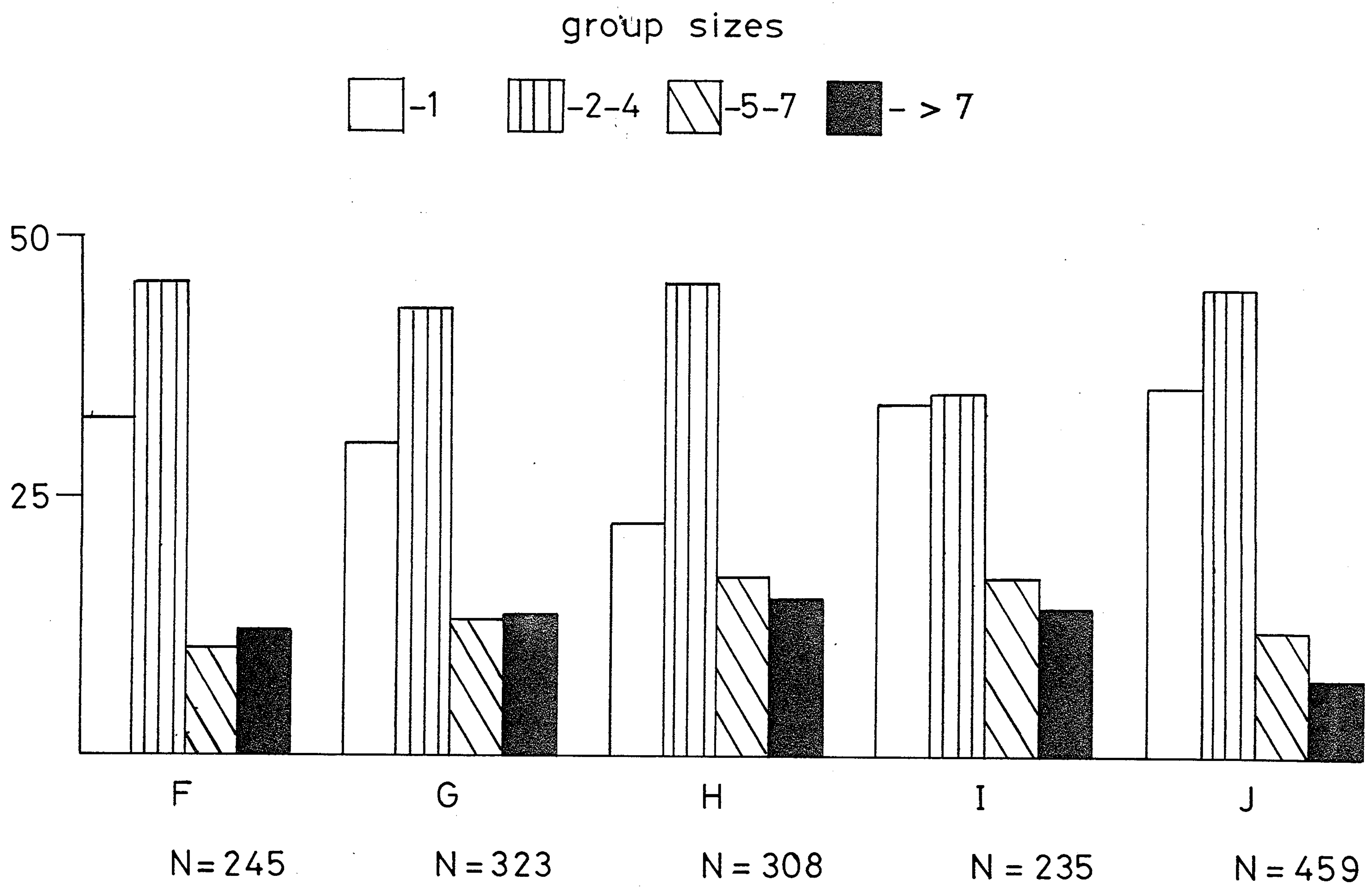

10
5
1
Mean group size
10
50
100
150
200
250
Numbers in area J

Figure 3.8.

Groups size structure for foraging Sanderling in the five areas along Coatham Sands. Ordinate shows the percentage of groups represented by the four size classes: 1, 2-4, 5-7 and groups with more than 7 individuals. N is the number of groups studied in each area. All data are from 1977-78 winter. See text for the criteria used to define a group.


group sizes
-1
-2-4
-5-7
- > 7
50
25
F
G
H
I
J
N=245
N=323
N=308
N=235
N=459

1970, 1979; Myers et. al. 1979). Where tidal exposure differs in a set of habitats, waders may forage sequentially in order to increase available foraging time (Goss-Custard 1969 and Heppleston 1971). Connors et. al. (1981) found that Sanderling foraged amongst tidal flats and beach areas, exploiting the most profitable locations. Along the south side of the Tees Estuary, the rock outcrops and the beach areas (Coatham Sands and Redcar Beach) comprise the major foraging habitats of the Sanderling. The switch in foraging locations between Redcar Rocks (Beach) and Coatham Sands (Fig. 3.1) is tide-determined. At low water the rocks are uncovered and the invertebrate prey are not available at Coatham Sands; approaching high water, the rocks are covered and the main bands of invertebrate prey are available at Coatham Sands.

To understand the movement of Sanderling along the beach at Coatham Sands, both the environmental constraints placed on the Sanderling and their general ecology (e.g., roosting patterns) must be discussed. The tide is the major constraint of foraging Sanderling, for it determines where the birds are able to feed. If Sanderling can only feed on Nerine and the crustacean prey when an area is wave-washed, the tide becomes the indicator of availability. Additional constraints could be space or behavioural constraints, physical features of the beach or actual foraging techniques (see Chapter 4), proximity of suitable roosting sites or behaviour of the prey species.

The major change in Sanderling distribution along Coatham Sands occurs at LW + 4 (two hours before high water- HW + 10) (Fig. 3.2). At this time there is a shift from transects 1 - 4 to transect 5. At LW + 4 a spring tide at transect 5 is at 70 m to 80 m below the HWM. During the autumn and spring, this was the area of the main Bathyporeia band. From HW + 10 to HW + 11, the most productive areas of transects 1 to 4 (40m to 70 m below the HWM, Table 2.8) are being covered (Fig. 3.6). At this time extensive areas of transect 5 are still open for feeding, however, the Nerine concentrations are low. On a spring tide the tide edge is pushed to 10m to 20m below the HWM at transects 1 to 4 and most foraging Sanderling are at transect 5, where the tide still has 40 m to travel before reaching the HWM. The majority of the birds may not be 'choosing' transect 5, but rather, they may be pushed from transects 1 to 4 by the tide. When the tide is at HW + 9 to HW + 10 (LW+ 3 to LW +4) Nerine densities are at their highest at transects 1 to 4 and few birds are moving into transect 5. No relationship could be established between the location of Sanderling and the densities of Nerine. The situation is obviously far more complicated. Nerine greater than 10 mm were in significantly greater proportion at lower tidal heights at transects 1 to 4 (Table 2.10 and Fig 2.7). At transects

1 to 4 the greatest proportion of large Nerine occurred at LW + 2. From the alongshore data, more than 50% of all Nerine at 50 m below the HWM, belonged to the three smallest size classes (4 mm, 5 mm and 6 mmm). This may be a factor in the shift of birds from transects 1 to 4 to transect 5 at LW + 4.

Group size was shown to increase with the number of Sanderling in an area (Fig. 3.7). There was no noticeable increase in aggression with increasing group size. Birds in groups moved together and adding individuals to this movement did not cause a breakdown in feeding patterns. Where waves occurred in rapid succession (the upper beach at transects 1 to 4) no flattened area behind the wave was available for birds to feed in. This helped to limit the number of birds in an area by concentrating them in a single dimension, increasing the opportunity for interference. The beach area at transect 5 has a shallow slope where flattened areas for feeding are extensive.

Birds moved progressively from transect 1 to transect 5, seldom stopping to feed in any one area and rarely moving south to north (along the beach). This pattern of movement helped to mask any possible relationship with the birds' location and prey density.

One way in which birds can increase their foraging time is to reduce roosting during daylight hours (Goss-Custard et. al. 1977b). During mid-winter Sanderling seldom roosted during the tidal cycle. If roosting did occur it was only when no foraging habitat remained. During neap tides (4.1 m to 4.3 m) birds were able to feed even at high water, as the upper beach was not covered and many Sanderling never reached transect 5. With foraging time at a premium (birds foraged during available time and did not fit the category of "time minimizers"), Sanderling should carefully select the areas in which they forage. Because of the number of factors which ultimately affect the Sanderling's choice of foraging location, it is difficult to say if they are "optimally" dispersed, or overdispersed. Sanderling forage in groups. Benefits of group foraging include protection from predation, assessment of conspecifics' foraging success and location of clumped prey. Benefits of group feeding on the one hand, and the reduction of time spent feeding through interference on the other, may have determined the "optimal" group size in areas along the beach. Such a regulatory mechanism, by partially dispersing feeding individuals, may have helped to determine the numbers of Sanderling found in any area.

The area in which Sanderling roost at high water is directly up from the first area to become exposed, transect 5. Are roosts just a function of the tide and the availability of feeding areas? The area beyond transect 5 is raised beyond the tide in a protected pocket with a good view of the beach and overhead. Roost locations may thus help determine the feeding pattern.

Sanderling have a great ability to put on large stores of fat prior to migration in May (Prater and Davies 1978 and Les Goodyer, pers. com.). This may suggest that Sanderling need not carry large fat stores during mid-winter, but rather live on the "edge". This would be especially adaptive considering their foraging methods and the distances covered by a Sanderling while feeding. If birds do live on the "edge", there is a need for flexibility to balance the daily energy needs. This is also reflected in the use of unusual food sources (wrack and mussle spat) and seasonal changes in roosting patterns. (Further evidence for daily changes in feeding patterns can be found in Appendix 3.1 and in Chapter 4).

CHAPTER 4 FORAGING METHODS OF SANDERLING

4.1 Introduction

A large body of literature has grown up around the ideas of optimal foraging strategies during the past fifteen years (for a review, see Krebs & Davies 1978). Much of this literature has its origins in the early work of MacArthur and Pianka (1966). What a bird is trying to optimize may depend on the risk of predation or on the choice between maximizing; i) the rate of food intake; and ii) the rate of net energy gains (Evans 1976). Evans points out some of the possible effects which different feeding techniques (assuming they represent different energetic costs) may have on both the preference and choice of a feeding individual. Factors such as handling time, differences in the rates of locomotion and net calorific assimilation are all important.

The main objective of this chapter is to arrive at an understanding of the factors controlling the feeding of Sanderling on the south side of the Tees estuary. An understanding of these factors will help to explain how Sanderling are able to winter so successfully at Teesmouth.

The analysis of Sanderling foraging begins with a description of the individual components of foraging, using film and taped commentaries, the basis of the field observations. This is followed by a summary of the general findings, after which the three foraging methods are analyzed in detail. I consider the implications of social feeding and discuss features of the foraging behaviour which are not explained by density or availability of the prey. In the discussion I use the observations mentioned in the chapter to comment on some of the current trends in studying optimal foraging.

The Sanderling feeding along the open coast are presented with alternatives in foraging techniques, plus a range of invertebrate prey species of varying densities. Along this coastal area Sanderling have been observed to obtain prey by four main methods: i) feeding on prey items on the surface of the sand (surface feeding); ii) penetrating the top of the sand in a single location (probing); iii) penetrating the top of the sand while making forward progress (stitching); and iv) feeding on prey which have been washed into the water (water-column feeding). The birds take Nerine from the substrate and small crustaceans from the substrate and the water. The distributions of the three main invertebrate prey species along Coatham Sands were highly predictable (Chapter 2). Nerine occurred in greater densities than Bathyporeia or Eurydice and were therefore expected to be the most important prey item for Sanderling. At almost all levels of the beach (metres below the HWM, see Chapter 2), and in most areas along the beach, Nerine were present, although the majority occurred within a narrow zone of high density (40 m to 70 m below the HWM).

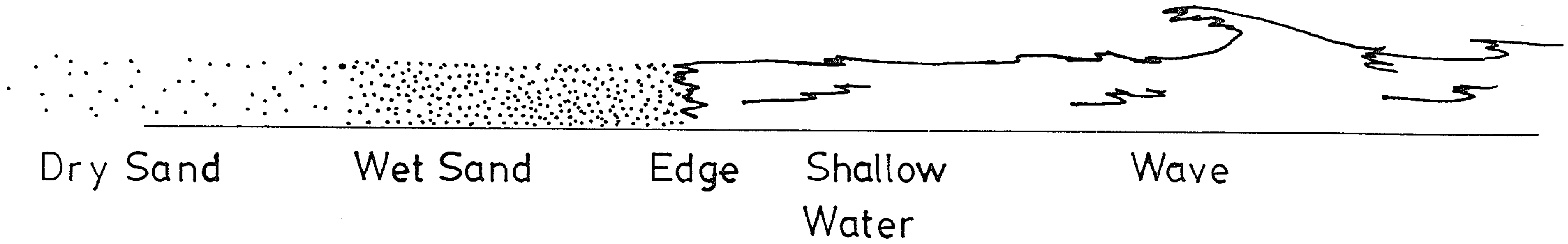
Energy expenditure during prey capture has been largely ignored in much of the avian foraging literature. Smith (1975) was able to show that Godwit, in cold weather, searched smaller areas and thus reduced foraging costs by walking less. The possibility that energy expenditure by a Sanderling in obtaining food represented a major demand on the energy thus acquired, prompted me to measure a bird's running distance (measured in units of time) and direction, over short feeding bouts. Longer periods of observations were used to determine a Sanderling's time allocation.

4.2 Methods

The data collected for the foraging Sanderling measures the effects of several variables on foraging behaviour and performance. The variables included were: i) the three areas of beach south of the estuary's mouth (transect 5, transects 1 to 4, and Redcar Beach, see Chapter 2); ii) the three main foraging methods (see above); iii) the five beach positions (in relation to the location of the tide edge- dry sand, wet sand, tide edge, shallow water, and wave (Fig. 4.1)); iv) the

Figure 4.1.

The five feeding positions in relation to the location of the wave and the moisture of the sand. See text for further description.


Dry Sand
Wet Sand
Edge
Shallow Water
Wave

two prey types (polychaetes and crustaceans); v) the flood tide and ebb tide periods; and vi) the successful and unsuccessful feeding attempts.

Detailed analysis of Sanderling feeding techniques was possible only through the use of cine film. This was supplemented by taped commentaries to provide a more extensive and accurate description of the ways in which Sanderling forage along the beach. Observations were recorded by both film and tapes at all main transects along Coatham Sands and at Redcar Beach.

4.2a Film

Filming was done with a Bolex H16 cine camera. Lenses used included a Vivitar 85mm-205mm zoom, Vivitar 2x multiplier and a Soligor 400mm telephoto. Kodachrome-25 cine film was used. Filming was carried out during the winters of 1976-77 and 1977-78. I analyzed 59 sequences, representing c. 38,000 frames, or about 30 minutes of feeding observations. All film was analyzed frame by frame. Only those sequences in which most movements and the majority of foraging successes could be detected were used. These 59 sequences were selected from over 250 sequences. Film was analyzed on a Singer Mark III Motion Analysis Projector. All sequences were shot at either 16 frames/second or at 24 frames/second, depending on the area and the type of feeding being filmed. All data taken from the film were made in reference to the specific frame number (i.e., all activity was sequenced). Information extracted from the film included:

(1). the frame at which each pace was initiated.

(2). the frame when the bird's bill entered the sand or water, and the frame when it was withdrawn (giving the duration of each feeding attempt).

(3). the method of foraging;

- surface, no penetration of sand substrate,

-probe, penetration of the sand, either in a single feeding movement or in multiple up-and-down penetrations, all in the same location (i.e., bill not leaving the substrate and extracted in the same position at which it entered),

-stitch feeding, once the bill had penetrated the substrate, the bird would move the bill up and down while walking forward. This is a similar "sewing" stitch to that made by Oystercatchers feeding on *Cardium edule* (Hulscher 1976) and by the North American Dowitcher (Burton 1972).

-water-column feeding, with the bill in the water without penetrating the sand.

(4). all successful attempts.

(5). the type of prey taken. Successful prey captures were often made without any noticeable movement. *Nerine* were often visible, extending beyond the tip of a bird's bill. When feeding in the water the bill was often gaped after successful prey captures (perhaps owing to the bird holding the exoskeleton of Bathyporeia and Eurydice). The birds would often shake their heads vigorously after these captures. These were interpretated as crustacean captures. When feeding for crustaceans in the water, very characteristic movements and postures were adopted by the Sanderling; these are fully described in a later section. No attempt was made to distinguish whether the birds were feeding on Bathyporeia or Eurydice. Both occurred in the top centimetres of the sand and both were found when sampling the water by means of a drag-net. Henceforth, any reference to Bathyporeia includes both these prey species. If the prey could not be determined from a characteristic type of head movement or by its being visible on the film, it was not included in the analysis.

(6). the handling time, which was measured as the number of frames a bird spent in the injestion of the prey once the bill had left the feeding substrate. Prey handling also occurred while the bill was still in the substrate, although it was not possible to separate prey handling (while in the substrate) from locating the prey. (Handling time is often treated as a separate component of foraging (Schoener 1971, Charnov 1973 and 1976), usually to simplify the feeding model being constructed. As it was obvious that Sanderling could either move off towards their next prey item or begin to search while handling prey, complete separation of handling time from other components of foraging may not be justified).

(7). the size of the group in which the subject bird was feeding. (For the method of determining the group size, see Chapter 3).

(8). any interactions with other birds.

(9). the bird's position with respect to the wave.

(10). the direction of the bird's visual orientation, as determined by the direction of the bill. The direction of the bill was based on a 360° grid with 0° (or 360°) facing the tide, 180° facing directly away from the tide, 90° facing south and parallel to the tide and 270° facing north and parallel to the tide.

(11). every change in visual orientation greater than 10° and the frame when the change occurred.

An example of how the cine data was recorded is given in Appendix 4.1.

After the above data had been extracted from each sequence, notes were made on the behaviour of the subject bird and of any conspecifics which might have affected the direction of movement or reaction of the subject bird. As the birds often foraged in groups, there was much potential for interaction. An attempt was made to determine how much of the search path of each individual resulted from the behaviour of conspecifics, by displacement due to the waves and from the bird seeking a new 'patch'.

To look at the possible effects of social interactions during feeding, the follow information was taken from the film during a second analysis of each sequence:

(1). the number of paces between one feeding attempt and the next.

(2). whether the bird fed in the same place after a feeding attempt.

(3). if the bird did move away from an area after feeding, and for what reason.

(4). all non-contact "interactions" with conspecifics. These were low intensity and non-threat behaviours such as stopping to watch the subject bird feed, moving towards another feeding individual or any investigation of the area where another bird was, or had been feeding. All distances between individuals were estimated in 'bird lenghts' (bill to tail).

For details of computer analysis of the film data see Appendix 4.2.

4.2b Tapes

The film sequences were not of sufficient duration to investigate a bird's time allocation. Taped commentaries were made to complement the film data. Zeiss 10 x 50 binoculars and a Swift variable telescope were used from a hide (Landrover). These commentaries covered continuous periods of up to five minutes. Of observations carried out in 1977-78, 201 observations were described by tape, totaling 490 minutes. When possible, success was noted. Recorded information included:

(1). the bird's position with respect to the wave.

(2). the direction of movement, which corresponded to 0^{o}, 90^{o}, 180^{o} and 270^{o} of the film data.

(3). all major changes in the direction of movement.

(4). the time spent running up from, and down into the tide edge and the time spent running parallel to the waves. Running was recorded as time, not distance.

(5). all periods of Pause, which were defined as momentary stops during prey searching.

(6). any interactions with conspecifics.

See Appendix 4.3 for examples of taped data.

Foraging rates were affected by the state of the tide and the area in which the foraging occurred. The film analyzed does not equally represent each area of the beach, or tide conditions. The amount of film and taped commentaries analyzed for each area of the beach under different conditions of the tide is shown in Table 4.1. Feeding in the waves meant that birds were feeding further out from the tide edge, making both filming and analysis of the film, more difficult.

4.3 Results

4.3a Foraging patterns

Feeding attempts by Sanderling were filmed at Redcar Beach, and on two sections of Coatham Sands. In order to analyze the distribution of foraging techniques and to allow for the bias introduced by the greater number of attempts filmed at Redcar Beach, the three areas were considered independently (Table 4.2). Comparisons between ebb and flood tide foraging show that the proportions of stitch to probe feeding was significantly greater on the ebb tide in the two areas in which both techniques were used commonly ($X^2 = 17.1$, $P < 0.001$ for transect 5; $X^2 = 31.6$, $P < 0.001$ for Redcar Beach).

TABLE 4.1

Total time, (in minutes), of film and taped commentaries analyzed for areas along the south-side beaches.

Film

	Ebb tide*	Flood tide**	Total time
Redcar Beach	9.07	2.92	12.0
Transects 1-4	8.73	4.65	13.38
Transect 5	2.1	5.7	7.8

Taped Commentaries

	Ebb tide	Flood tide	Total time
Redcar Beach	80.4	98.03	178.43
Transects 1-3	41.34	135.96	177.3
Transect 4	49.85	31.16	81.01
Transect 5	27.18	84.68	111.86

* Period covering High Water to Low Water.

** Period covering Low Water to High Water.

TABLE 4.2

Number of feeding attempts, on ebb and flood tides, filmed on three sections of beach.

	Ebb Tide				Flood Tide			
	Probe	Stitch	Water-Column	total	Probe	Stitch	Water-Column	total
Redcar Beach	109	202	11	322	57	25	0	82
% of attempts	34%	63%	3%	100%	70%	30%	0	100%
Coatham Sands T 1-4	76	4	84	164	67	14	37	118
% of attempts	47%	2%	51%	100%	57%	12%	31%	100%
Coatham Sands T 5	53	55	4	112	81	25	15	121
% of attempts	47%	49%	4%	100%	67%	21%	12%	100%

Of all stitch attempts analyzed, 69.8% were filmed at Redcar Beach, and comparatively few along Coatham Sands. On the otherhand, only 7.3% of all water column feeding attempts were filmed at Redcar Beach. These figures are representative of the differences in feeding behaviour to be seen on the different areas. The differences were associated with different proportions of prey being taken in each area (Fig. 4.2). Of the three foraging methods, only probing resulted in the capture of both prey types. Water-column feeding yielded only *Bathyporeia*, whilst stitching (with one exception), yielded only *Nerine*.

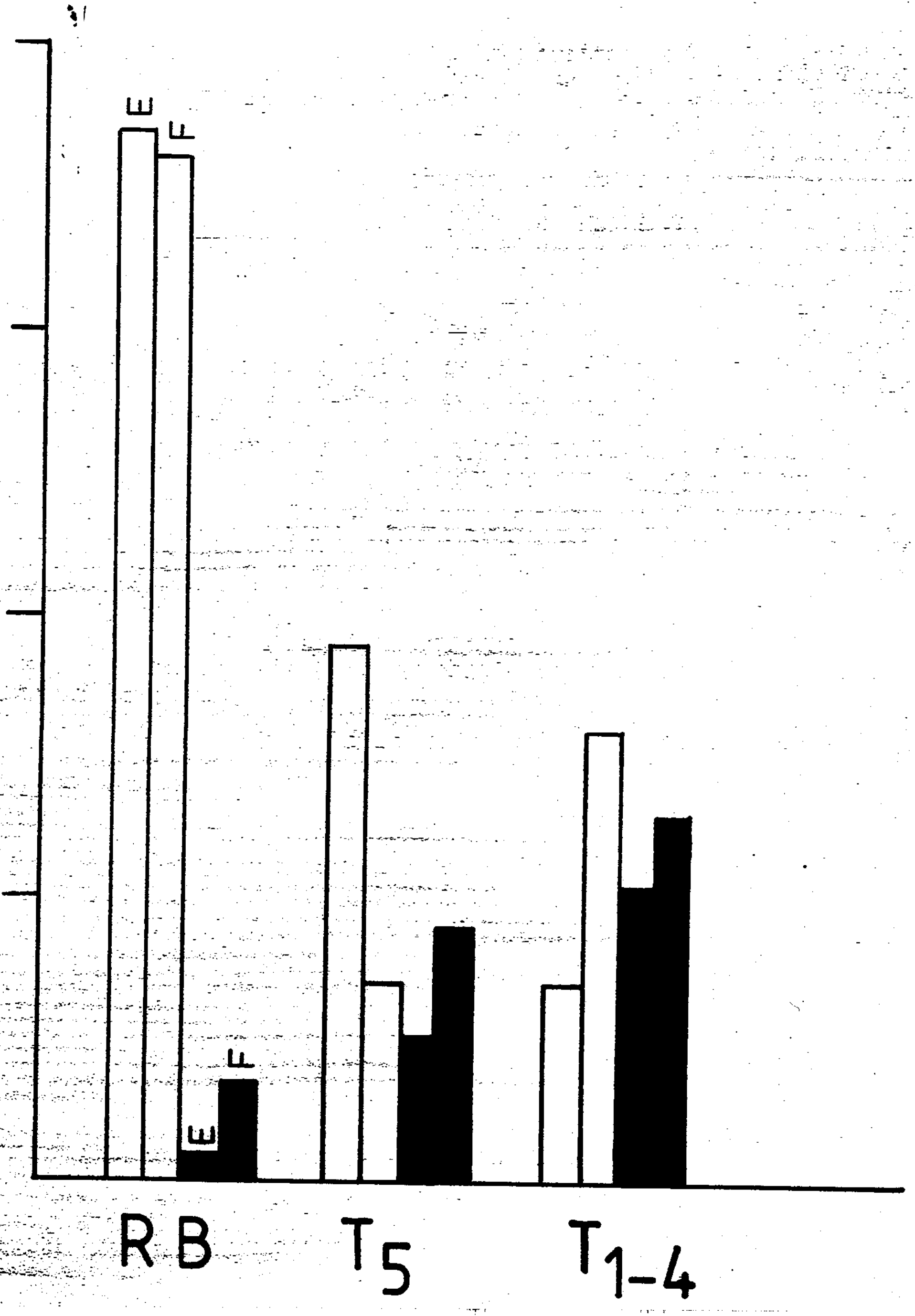
Figure 4.2 shows that the mean rate at which *Bathyporeia* were taken was less at transect 5 than at transects 1-4, a surprising result considering the higher densities of both *Bathyporeia* and *Eurydice* on transect 5 (see Chapter 2). Figure 4.2 also shows that mean rates of prey capture differed between ebb and flood tides (e.g., for *Nerine* at transect 5). However, sample size was not large enough ~~[illegible]~~ for statistical significance ~~[illegible]~~ at the 5% level. Redcar Beach was clearly the most important feeding area for *Nerine* (in terms of prey capture rate) and the least important for *Bathyporeia*. (It must be mentioned that Redcar Beach was, however, available for feeding for only relatively short periods in each tidal cycle, during low water.)

Figure 4.2

Prey taken, in numbers per minute, in the three areas; Redcar Beach (RB), Transect 5 (T_5), and Transects 1-4 (T_{1-4}). Open columns for Nerine, solid columns for Bathyporeia, separated into ebb (E) and flood (F) tide.

Standard errors for Figure 4.2:

	Nerine		Bathyporeia	
	ebb	flood	ebb	flood
Redcar Beach	1.0	3.1	0.3	1.3
T_5	0.8	0.5	0.5	0.8
T_{1-4}	0.6	1.1	0.6	0.8


E
F
E
F
R B
T_5
T_{1-4}

Success rates (expressed as the percentage of attempts that yielded prey) for the three foraging methods at the various beach levels are shown for the three sections of the beach in Table 4.3a-c. These data show many differences between areas and between beach levels. For example, the success rate for stitching in the waves was very low. This foraging technique, which was used to obtain Nerine, was much more successful at Redcar Beach than elsewhere. Success rates for water-column feeding were high in all three areas and greatest at transect 5; however, success for probing was low at that transect. These differences arise in part from differences in the proportions of the different prey taken at the various sites.

Sanderling feeding on Bathyporeia were most successful when foraging by the water-column method in the waves. There were 46 Bathyporeia captures recorded on film: 30 of these were from transects 1 to 4, including 6 taken by probing and 24 by water-column feeding. They were taken from all zones of the beach on both ebb and flood tides. Success rates are summarized in Table 4.3.

TABLE 4.3

Rates of success (expressed as the percentage of total attempts that yielded prey) for three foraging methods at various beach levels.

a. Redcar Beach

	Wet sand	Edge	Shallow water	Waves	Overall
Probe	33.3%	17.4%	20.3%	21.4%	22.9%
	n=36	n=23	n=79	n=28	n=166
Stitch	27.3%	22.0%	25.6%	0%	22.9%
	n=33	n=59	n=117	n=18	n=227
Water Column	0%	0%	0%	40.0%	18.2%
	n=0	n=5	n=1	n=5	n=11

b. Transects 1-4

	Wet sand	Edge	Shallow water	Waves	Overall
Probe	20.0%	10.3%	25.0%	22.6%	20.6%
	n=20	n=29	n=56	n=31	n=136
Stitch	0%	50.0%	8.3%	0%	11.1%
	n=1	n=2	n=12	n=3	n=18
Water Column	100%	26.7%	16.7%	19.0%	20.5%
	n=2	n=15	n=42	n=58	n=117

c. Transect 5

	Wet sand	Edge	Shallow water	Waves	Overall
Probe	4.9%	66.7%	11.1%	11.4%	9.3%
	n=82	n=3	n=9	n=35	n=129
Stitch	9.4%	0%	60.0%	14.3%	12.5%
	n=58	n=3	n=5	n=14	n=19
Water Column	20.0%	0%	22.2%	60.0%	31.6%
	n=5	n=0	n=9	n=5	n=19

4.3b Running time

Sanderling spent considerable time running along the shore and up and down the beach foraging. Birds would regularly run into and beyond the wave edge, often many metres past it and into the shallow water zone. Running represents a large portion of the Sanderling's energy expenditure while feeding. As the duration of the film sequences was not sufficient to measure the proportion of time spent running, taped commentaries were used.

Brief bursts of paces formed part of the birds' prey capture (rather than searching) technique and were not included in the running time measured. Table 4.4 presents the percentages of time spent in running in the areas considered. The time commitment to running was very large, between 33.7% and 48.3% of a bird's foraging time. Significant differences occurred between the different areas in the amount of running parallel to the tide edge (see Table 4.4).

The movement of the tide edge limited the effectiveness of the particular feeding method used. Tidal movement dictated the time available for the birds to feed and helped determine whether they would probe or stitch feed. Birds spent different amounts of time in running into and away from the tide in different areas of the beach and at different times of the tide

TABLE 4.4

The proportion of observed time spent running.

This is the same table as that sent with the last Chapter 4, with the addition of the following t-distributions.

a. Parallel running.

T_{1-3} vs T_4	n.s.
Redcar Beach vs T_{1-3}	$t = 4.50$, $P < 0.001$
Redcar Beach vs T_4	$t = 2.31$, $P < 0.02$
Redcar Beach vs T_5	n.s.
T_5 vs T_4	$t = 2.09$, $P < 0.05$
T_5 vs T_{1-3}	$t = 4.38$, $P < 0.001$

All other comparisons are n.s.

cycle (Table 4.5). The running time associated with feeding in an area must have affected the profitability (net rate of assimilation of energy) of that particular area.

4.3c. Detailed consideration of foraging techniques

The mean times for successful and unsuccessful bouts of stitching and probing in the three different feeding areas are given in Table 4.6. For all six categories, the mean length of time for stitching was significantly greater than for probing ($P < 0.001$).

Discounting the only two successes recorded for stitching at transects 1 to 4, there were no significant differences between areas in the duration of successful stitching attempts; nor were there between-area differences in the duration of failed stitching attempts. However, for probing, the duration of failed attempts was significantly shorter at transects 1 to 4 than at Redcar Beach and transect 5 ($P < 0.001$) and the duration at transect 5 was shorter than that at Redcar Beach ($P < 0.001$). Similarly, successful probe attempts were of shorter duration at transects 1 to 4 than at Redcar Beach ($P < 0.001$).

No significant differences occurred between the duration of successful and failed attempts at probing in any of the three areas. However, successful

TABLE 4.5

The percentage of time spent running into and away from the tide in two areas at different times of the tide. All data from taped commentaries.

This is the same table as that sent with the last Chapter 4, with the addition of the following t-distributions.

Transects 1-3:

LW+5-HW vs LW-LW+3	$t=4.02$, $P < 0.001$
L+5-HW vs L+3-L+4	$t=5.37$, $P < 0.001$
L+5-HW vs L+4-L+5	$t=3.33$, $P < 0.01$
HW-H+3 vs LW-L+3	$t=2.13$, $P < 0.005$
HW-H+3 vs L+3-L+4	$t=3.46$, $P < 0.01$

All other comparisons for T_{1-3} n.s.

Transect 5:

L+5-HW vs L+3-L+4	$t=2.82$, $P < 0.05$
HW-H+3 vs L+3-L+4	$t=2.46$, $P < 0.05$

All other comparisons for T_{1-3} n.s.

TABLE 4.6

The mean duration (in sec.) of stitch and probe feeding attempts by Sanderling.

Stitch attempts

	Failed attempts			Successful attempts		
	N	$\bar{x}$	± 1 S.E.	N	$\bar{x}$	± 1 S.E.
Redcar Beach	175	1.14	0.06	52	1.67	0.16
Transects 1-4	16	1.59	0.22	2	0.86	0.07
Transect 5	70	1.25	0.09	10	1.53	0.21

Probe attempts

	Failed attempts			Successful attempts		
	N	$\bar{x}$	± 1 S.E.	N	$\bar{x}$	± 1 S.E.
Redcar Beach	128	0.61	0.04	38	0.70	0.06
Transects 1-4	112	0.31	0.02	30	0.36	0.06
Transect 5	122	0.43	0.03	12	0.56	0.08

TABLE 4.6 cont.

Summary of comparisons

i) Stitch vs. Probe

	"t"	d.f.	P
Success			
Redcar Beach	5.7	88	< 0.001
Transects 1-4	5.5	30	< 0.001
Transect 5	4.2	20	< 0.001
Failure			
Redcar Beach	8.1	301	< 0.001
Transects 1-4	5.7	126	< 0.001
Transect 5	8.7	190	< 0.001

ii) Failure vs, Success

	"t"	d.f.	P
Stitch			
Redcar Beach	3.1	225	< 0.005

iii) Probe- failures compared and successes compared

Failure

Redcar Beach is longer than transects 1-4

$t = 7.6$, d.f. = 238, $P < 0.001$

Transect 5 is longer than transects 1-4

$t = 3.4$, d.f. = 232, $P < 0.001$

Redcar Beach is longer than transect 5

$t = 4.1$, d.f. = 248, $P < 0.001$

Success

Redcar Beach is longer than transects 1-4

$t = 4.3$, d.f. = 66. $P < 0.001$

attempts at stitching were significantly longer ($P < 0.001$) than failures at Redcar Beach, and except for the two quick successful stitches at transects 1 to 4, the average duration of successful attempts were longer (though not significantly so) than failures for both stitching and probing in each area.

The duration of a single unsuccessful attempt represents the persistence time for that particular foraging attempt. During a successful attempt, handling of the prey began before the bill was withdrawn from the substrate. This was one reason for successful attempts taking longer than failures and explains why very little of the prey was seen. No attempt was made to separate handling from the tactile search elements of stitching and probing. Several additional factors may also explain why failed attempts were shorter than successful ones. A bird could, while feeding, visually obtain a cue near where it was feeding. This might account for some of the switching which occurred in foraging methods Also, birds were constantly being pushed up shore by the waves, particularly on the flood tide, often having to interrupt a feeding attempt. A final factor was the influence of other individuals, such as birds flying overhead, running past a feeding individual or coming close to a feeding individual. In such cases, feeding attempts were often abandoned before prey had been captured.

The mean duration of failed attempts at different levels of the beach are shown in Table 4.7 for stitch foraging at Redcar Beach and probe attempts at all three beach areas. For stitching, failed attempts lasted longer in shallow water than at the tide edge. For probing, within a single beach area, the only significant difference in duration of failed attempts occurred at transect 5, where birds probed for longer before giving up in the waves than on wet sand. Comparisons between areas show that failed probe attempts were longest at Redcar Beach. Four of six possible comparisons at equivalent beach levels are significantly different (Table 4.7). At all beach levels, failed stitch attempts were longer than failed probe attempts.

Analysis of those film sequences in which stitching was the major method used (and therefore in which water column feeding was uncommon) showed a significant inverse relationship ($P < 0.05$, $r = -0.5381$, with d.f. = 15) between the duration of unsuccessful stitching attempts and the rate of capture of Nerine, the only prey obtained by this foraging technique (Fig. 4.3, data from all three beach areas). This result accords with the idea that, with a greater capture rate, an individual bird should have a reduced persistence time, as expectation of success elsewhere increases.

TABLE 4.7

Duration of failed stitch and probe attempts at different positions of the beach. All times in seconds. N is the number of attempts analyzed.

a. Stitch- Redcar Beach

	N	Range	$\bar{x}$	± 1 S.E.
Wet Sand	19	0.42 - 2.04	0.93	0.10
Edge	46	0.24 - 2.88	1.02	0.09
Shallow Water	72	0.30 - 4.62	1.32	0.09
Waves	8	0.52 - 2.32	0.97	0.18

b. Probe

Redcar Beach

	N	Range	$\bar{x}$	± 1 S.E.
Wet Sand	27	0.12 - 1.68	0.61	0.07
Edge	26	0.24 - 1.36	0.57	0.06
Shallow Water	56	0.12 - 1.64	0.59	0.05
Waves	13	0.16 - 1.38	0.91	0.19

Transects 1 to 4

Wet Sand	17	0.08 - 1.74	0.47	0.10
Edge	23	0.12 - 0.84	0.35	0.04
Shallow Water	33	0.08 - 1.32	0.30	0.04
Waves	23	0.24 - 0.84	0.39	0.04

Transect 5

Wet Sand	83	0.12 - 1.14	0.39	0.02
Waves	31	0.20 - 1.50	0.59	0.06

TABLE 4.7 cont.

Summary

a. Stitch

i) Shallow water vs. Edge $t = 2.3$ $P < 0.02$

b. Probe

Redcar Beach n.s.

Transects 1-4 n.s.

Transect 5

i) Wet sand vs. Waves $t = 3.0$ $P < 0.01$

c. Comparisons of areas (Probe)

i) Wet Sand

Redcar Beach vs. Transect 5 $t = 2.8$ $P < 0.01$

ii) Edge

Redcar Beach vs. Transects 1-4 $t = 3.1$ $P < 0.01$

iii) Shallow water

Redcar Beach vs. Transects 1-4 $t = 4.6$ $P < 0.001$

iv) Waves

Redcar Beach vs. Transects 1-4 $t = 2.7$ $P < 0.01$

Figure 4.3

The relationship between the duration of unsuccessful stitch attempts and the rate of capture of *Nerine* by Sanderling.

Ordinate- The duration of stitch attempts in seconds.

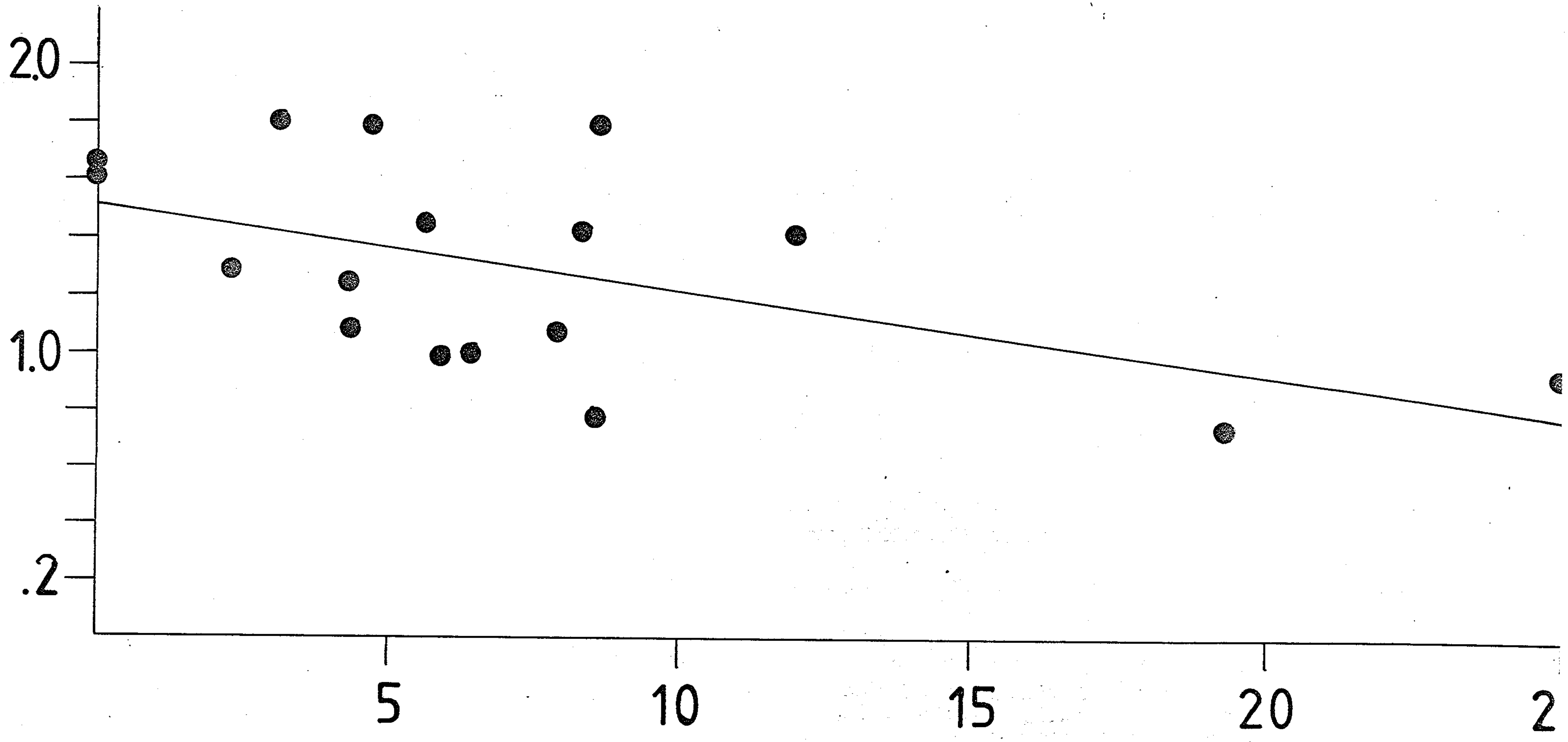
Abscissa- The number of *Nerine* capture per minute.

Slope- -0.0298.

r- -0.5381.

P- 0.05.

15 degrees of freedom.


2.0
1.0
.2
5
10
15
20
2

In Fig. 4.4, typical feeding maps (from film sequences 8 and 42, Reccar Beach) are presented. In sequences 8 there was a rate of capture of 21.4 *Nerine*/minute and a persistence time of 0.93 seconds (S.D. = 0.188). In sequence 42, with a much lower success rate of 3.1 *Nerine*/minute, the persistence time was 1.8 seconds (S.D. = 1.64).

There was no relationship between persistence time and the rate of prey capture by probe feeding, during which both prey types might be taken.

To further compare the three foraging methods, the number of paces and also the direction of the paces prior to the actual feeding attempt were analyzed. The components of movement analyzed were: paces running into or towards the waves (340° to 20°), paces running away from the waves (160° to 200°), paces running parallel to the waves (250° to 290° and 70° to 110°), and paces running in a diagonal direction. The mean number of paces taken before stitching and probing attempts at the different beach positions are presented in Tables 4.8 and 4.9 respectively. The mean number of paces taken prior to a stitch attempt did not differ significantly between the two areas tested. There were also no significant differences between areas in the mean number of paces before probing or within areas between probing and stitching. Differences did occur amongst the various beach positions, however, but there

Figure 4.4.

Sanderling feeding maps for cine sequences 8 (a) and 42 (b). See Appendix 4.4 for details of individual sequences.

Symbols:

■ - starting point
▬ - prey capture
● - probe attempt
X - stitch attempt
B- <u>Bathyporeia</u> capture
N- <u>Nerine</u> capture

a)

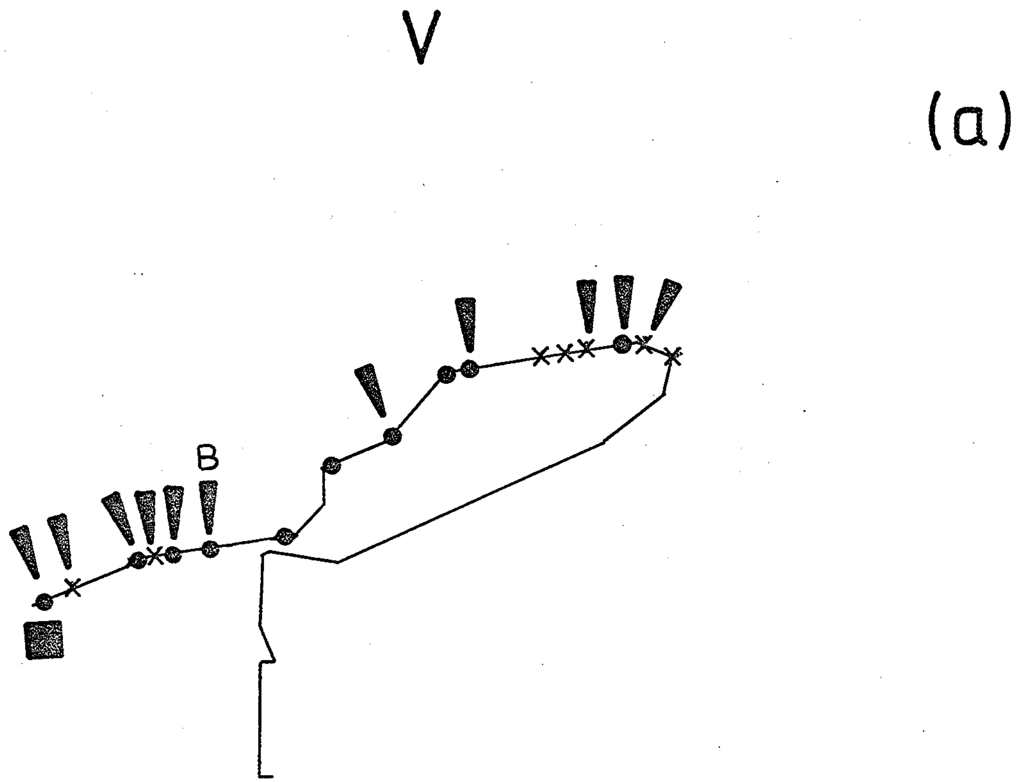
All prey captures <u>Nerine</u> except one <u>Bathyporeia</u> capture (labelled).

Attempts 1-6 in wet sand.
Attempts 7-17 in shallow water.

b)

Attempts 1-4 in wet sand.
Attempts 5-8 in shallow water.
Attempt 9 in wave edge.
Attempts 10-15 in shallow water.

Arrows identify direction of the waves.


V
(a)
B

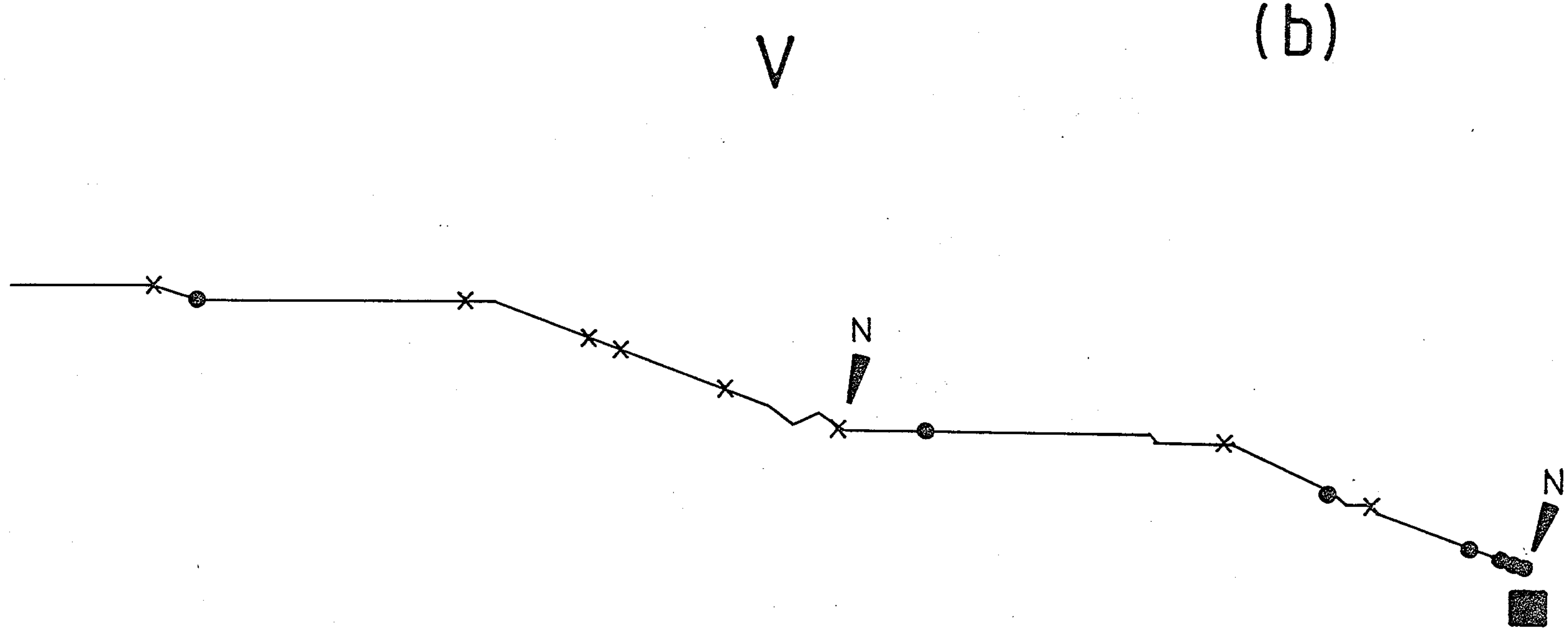

V
(b)
N
N

TABLE 4.8

The mean number of paces before stitch feeding attempts at the different beach positions at Redcar Beach and transect 5.

Redcar Beach

	Parallel	Into	Away	Diagonal	Total	N*
Wet Sand	3.1	0	0.7	6.4	10.2	33
Edge	3.0	0.3	0.6	2.0	5.9	59
Shallow Water	4.8	0.1	0.1	3.3	8.3	117
Waves	2.7	0.7	0	4.5	7.9	18
$\bar{x}$ **	7.9 1 S.E. = 0.9					

Transect 5

	Parallel	Into	Away	Diagonal	Total	N*
Wet Sand	1.6	0	0.6	2.6	4.8	58
Edge	2.7	0	0.4	0	3.1	3
Shallow Water	4.8	0	0	3.5	8.3	5
Waves	3.0	0	0	4.2	7.2	14
$\bar{x}$ **	5.4 1 S.E. = 1.2					

* Number of observations. ** Value for all observations (mean).

TABLE 4.9

The mean number of paces before probe attempts at the different beach positions along south side areas.

Redcar Beach

	Parallel	Into	Away	Diagonal	Total	N*
Wet Sand	5.9	3.7	0	3.9	13.5	36
Edge	1.8	0	0.3	3.6	5.7	23
Shallow Water	2.8	0	0.7	2.9	6.4	79
Waves	1.2	0	0.9	5.2	7.3	28
$\overline{x}$	8.0 1 S.E. = 0.9					

Transects 1 to 4

	Parallel	Into	Away	Diagonal	Total	N*
Wet Sand	7.3	0.2	0.1	6.9	14.5	19
Edge	6.3	2.7	0.2	1.4	10.6	25
Shallow Water	1.5	2.0	0.4	3.2	7.1	56
Waves	5.7	0.5	1.3	0	7.5	29
$\overline{x}$	9.0 1 S.E. = 1.1					

* Number of observations. ** Value for all observations (mean).

TABLE 4.9 cont.

Transect 5

	Parallel	Into	Away	Diagonal	Total	N*
Wet Sand	2.5	0.7	0	0.4	3.6	79
Edge	17.6	0.4	0	17.7	35.7	3
Shallow Water	17.8	0.1	0	7.1	25.0	6
Waves	1.5	0.1	2.0	2.8	6.4	35
$\bar{x}$**	6.2 1 S.E. = 0.9					

* Number of observations. ** Value for all observations (mean).

was no trend to suggest an effect of a particular position. Before a stitch attempt, very few paces were taken and therefore very little time was spent running into the waves. The large number of parallel and diagonal paces allowed the birds to maintain their position with respect to the waves or tide edge, while keeping within a particular intertidal zone, and therefore within a particular prey zone.

The search paths for stitch feeding showed no concentration of searching efforts. Of those sequences where stitch feeding was a main foraging method, only three showed concentration in searching efforts (18 and 57 are presented in Fig. 4.5). Rate of prey capture in sequence 57 was 4.3 <u>Nerine</u>/minute and for sequence 18, success rate was 8.6 <u>Nerine</u>/minute. The "typical" search path for stitching has already been shown in Fig. 4.4b.. For probe feeding, the pattern of forward progression while feeding and the lack of restricted search were similar to those of stitch feeding.

The visual orientation of each bird before it put its bill into the substrate was also taken from the film. Figure 4.6 shows the visual orientation for all feeding methods combined in the three areas. A bimodal distribution of visual orientation, corresponding to the two orientations parallel to the waves, was most pronounced at Redcar Beach but almost absent at transect 5. These differences could have been due to a basic

Figure 4.5.

Sanderling feeding maps for cine sequences 18 (a) and 57 (b). See Appendix 4.4 for details of individual sequences.

Symbols:

■ - starting point
▬ - prey capture
● - probe attempt
x - stitch attempt

a)

All prey captures *Nerine*.

Attempts 1-6 in waves.
Attempts 7-12 in shallow water.
Attempts 13-15 in wave edge.
Attempts 16-17 in shallow water.

b)

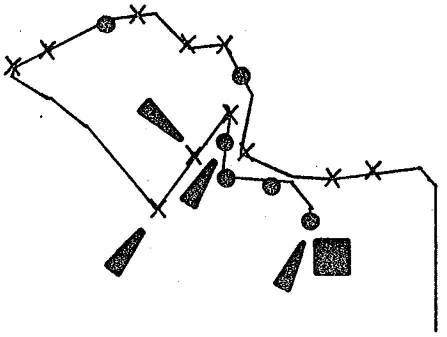
All captures *Nerine*.

Attempts 1-5 in wet sand.
Attempt 6 in waves.
Attempts 7-16 in wet sand.
Attempt 17 in wave edge.
Attempts 18-33 in wet sand.

Arrow identifies direction of the waves.

V

(a)



(b)

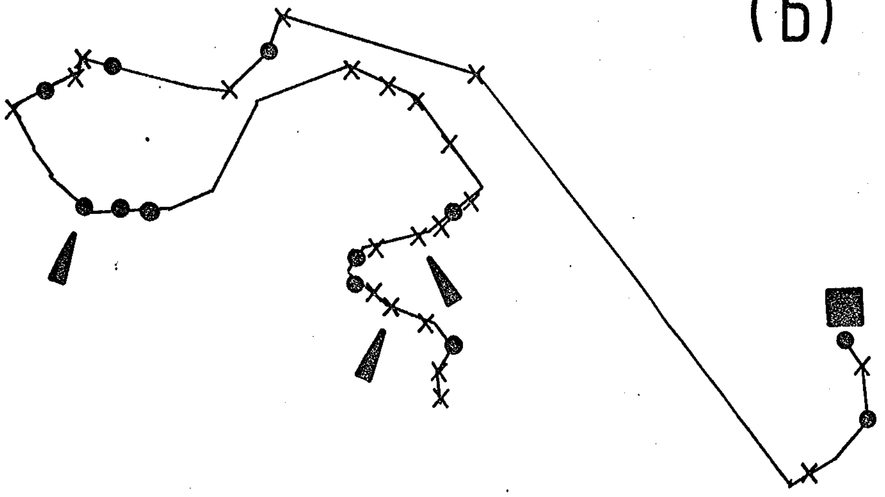


Figure 4.6.

Visual orientation of foraging Sanderling in the three areas of the southside beaches.

a. Transect 5.

b. Transects 1-4.

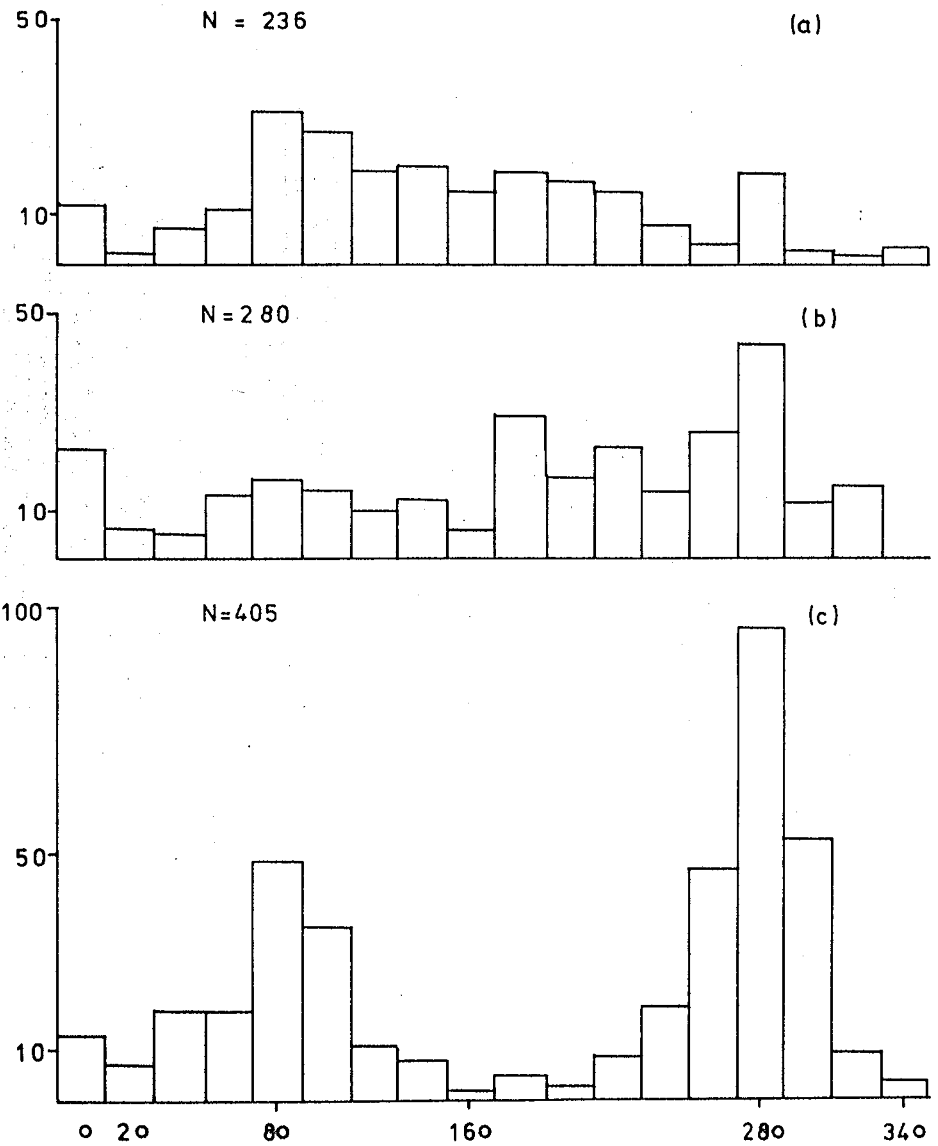
c. Redcar Beach.

All foraging attempts are included.

Abscissa- the visual orientation of foraging birds before feeding attempt. See text for directional explanation.

Ordinate- the number of times each orientation occurred.

N- the total number of attempts analyzed in each area.


50
N = 236
(a)
10
50
N=280
(b)
10
100
N=405
(c)
50
10
0
20
80
160
280
340

physical difference in the areas (e.g., in slope of the beach) or to differences in the proportion of the different foraging methods used in the areas. In Fig. 4.7 the visual orientations are shown for the three foraging methods separately. Of all attempts, 51.2% of the probes, 62.5% of the stitch attempts and 41.1% of the water column feeding methods were preceded by an orientation parallel to the waves (60° to 120° or 240° to 300°).

Water column feeding was visual, brief, and did not at any time involve the loss of sight since only the bill penetrated the water. The orientation of a bird before a water feeding attempt may not have been important to its subsequent success. At Redcar Beach, parallel orientation before stitch feeding was not as evident on the wet sand as it was for positions closer to the wave edge (Fig. 4.8). Clearly, both feeding method and beach position were important in determining the orientation of a bird before it attempted to capture prey.

The search path from film sequence 49 is shown divided into two sections, to demonstrate the effects of the waves on the birds' feeding behaviour and success (Fig.4.9). The sequence began with very long stitch feeding bouts, with little movement between each bout and a high success rate, the bird maintaining itself in the same beach zone (parallel region). At frame 321 the

Figure 4.7.

Visual orientation of Sanderling before each of the three foraging methods.

a. Probe.

b. Stitch.

c. Water Column.

Abscissa- the visual orientation of foraging birds before feeding attempts.

Ordinate- the number of times each orientation occurred.

N- the total number of each method analyzed.

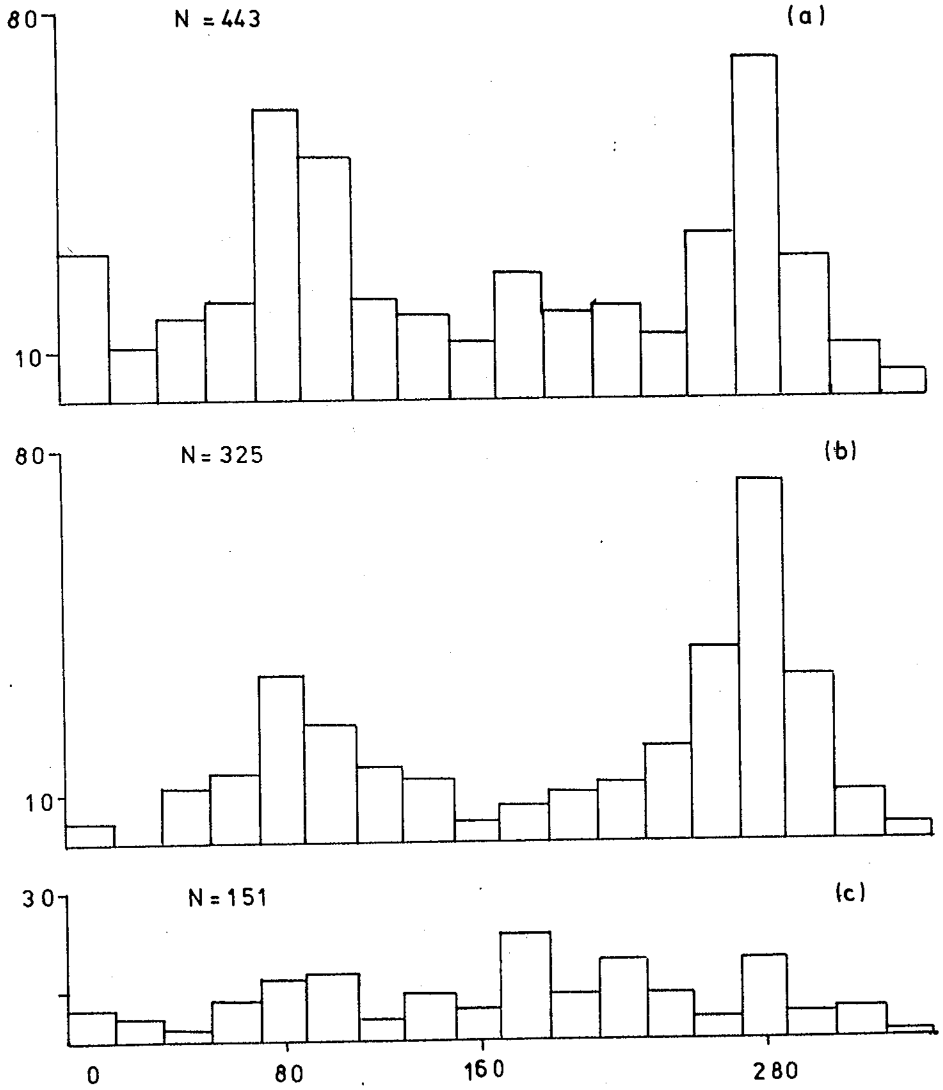

80
N = 443
(a)
10
80
N = 325
(b)
10
30
N = 151
(c)
0
80
160
280

Figure 4.8.

Visual orientation of Sanderling at Redcar Beach for stitch feeding at different levels of the beach.

a. wet sand.
b. shallow water.
c. edge.
d. waves.

Abscissa- the visual orientation of foraging birds before feeding attempts.

Ordinate- the number of times each orientation occurred.

N- the total number of orientations analyzed at each level.

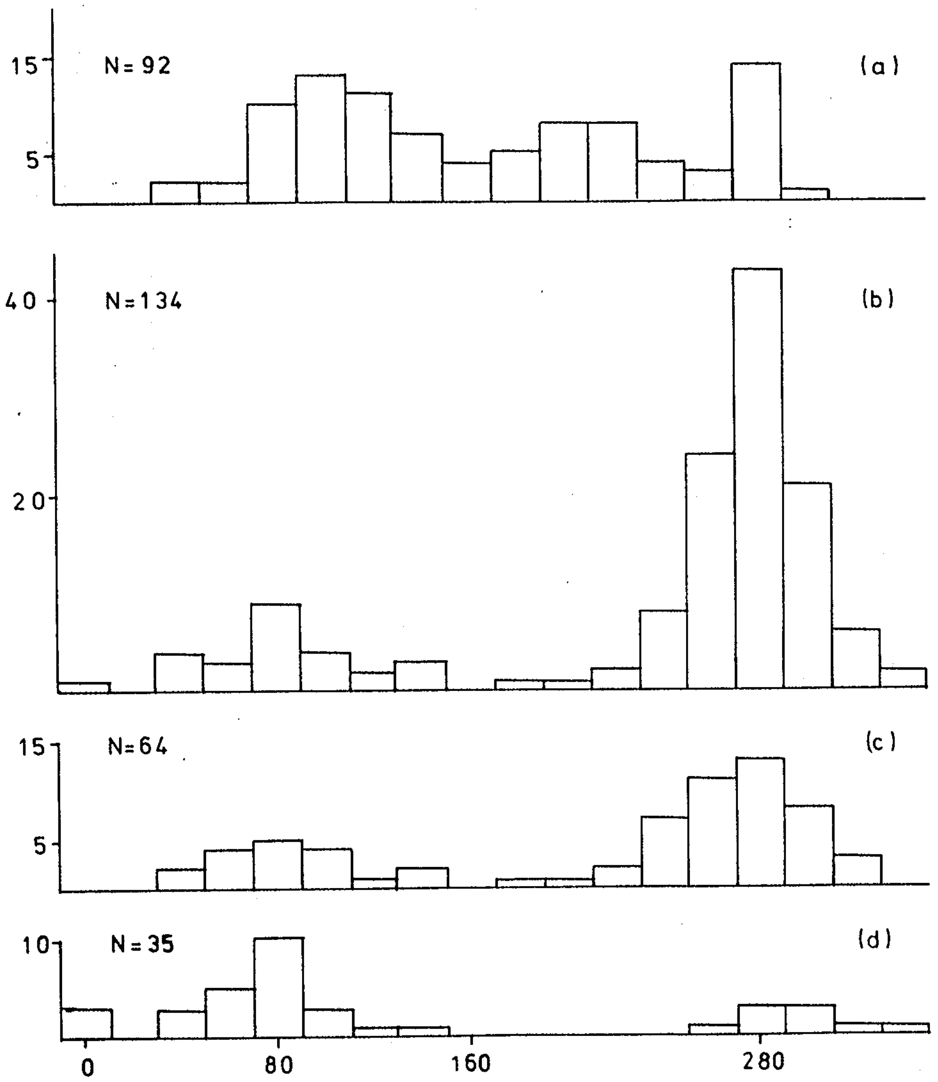

15
5
N=92
(a)
40
20
N=134
(b)
15
5
N=64
(c)
10
N=35
(d)
0
80
160
280

Figure 4.9

Cine sequence 49 divided into two segments, the first (a) of frames 1 to 320, and the second (b) of frames 321 to 635. Feeding bout refers only to the time the bill is in the substrate. The length of the feeding bout is indicated (in number of frames- each frame represents 1/16 of a second) along with the symbol for the foraging method.

Symbols:

● - probe attempt

X - stitch attempt

➡ - success

h - handling time (in number of frames)

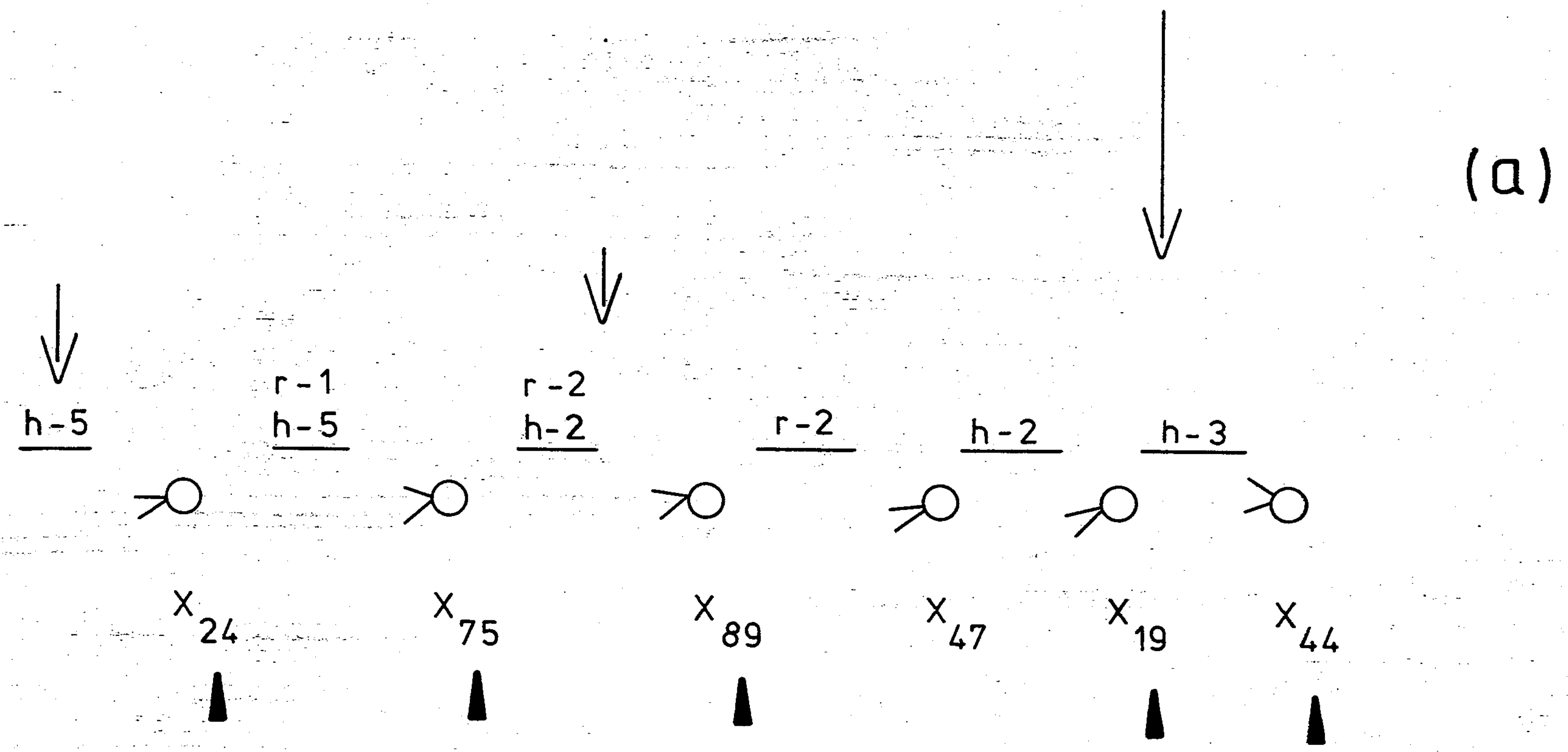
r - number of frames between attempts

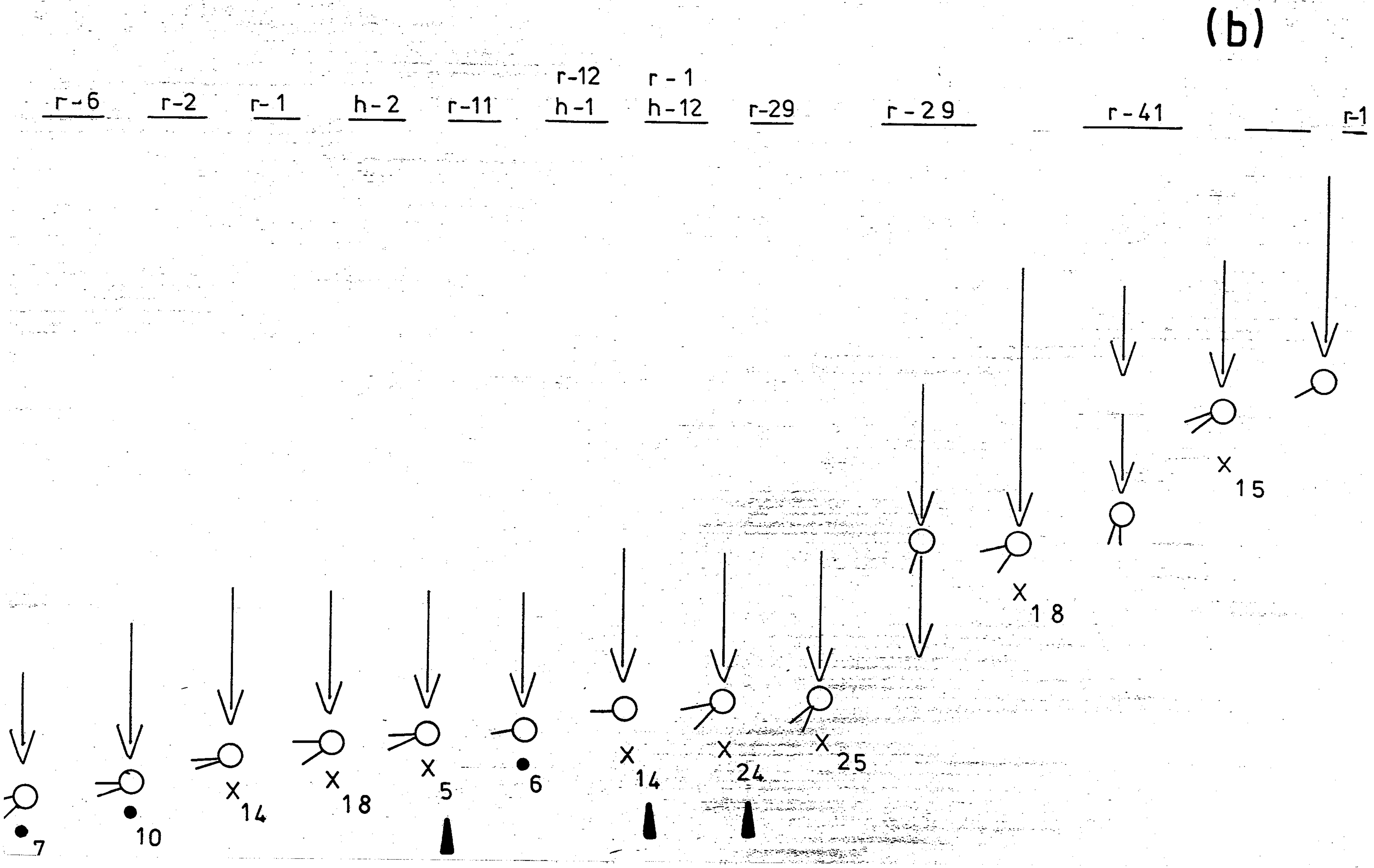
a) total of 20 seconds, 6 feeding bouts
average bout- 49.7 frames (3.1 sec.)
success rate- 83.3%
bill in substrate- 93.1% of the time

b) total of 19.8 seconds, 11 feeding bouts
average bout- 14.2 frames (0.9 sec.)
success rate- 27.3%
bill in substrate- 49.5% of the time

All successes are <u>Nerine</u>

α - gives the limits of visual orientation prior to the feeding attempt.


(a)
h-5
r-1
h-5
r-2
h-2
r-2
h-2
h-3
X24
X75
X89
X47
X19
X44


(b)
r-6
r-2
r-1
h-2
r-11
r-12
h-1
r-1
h-12
r-29
r-29
r-41
r-1
7
10
X 14
X 18
X 5
6
X 14
X 24
X 25
X 18
X 15

bird was pushed up by the tide. The bird kept ahead of the wave and, when far enough from the wave, turned parallel to the wave, feeding by the stitch method. There was then a sudden decrease of feeding bout length and a dramatic drop in the bird's success, most of which was attributed to the interruption caused by the location of the waves.

The water-column feeding method involved a very characteristic stance of the bird, which was easily recognizable. When feeding on crustaceans in the water, a bird would extend its neck so that its head was at maximum distance from the water. Such birds fed with great intensity and with rapid pacing rates and rapid changes in visual orientation. This feeding stance allowed the bird to scan a considerable area and may have also allowed it to counteract parallax effects. During feeding by this method, the carpals (of some individuals) and areas about the birds' ear often flashed black. The black was noticeable to a human observer and contrasted sharply with the rest of the plumage. These contrasting black regions might have served as some cue to conspecifics as to foraging success.

The number of paces preceding an attempt at prey capture by water-column feeding was significantly greater than for the other two methods (Table 4.10). Search paths for water-column feeding are shown in Fig. 4.10.

TABLE 4.10

The mean number of paces before water-column feeding attempts at transects 1 to 4 and transect 5. Data averaged for all beach levels.

Transects 1 to 4	
Number of Observations	113
$\bar{x}$	14.7
± 1 S.E.	2.2
Transect 5	
Number of Observations	19
$\bar{x}$	17.6
± 1 S.E.	3.8

Comparisons with the number of paces before stitching and probing attempts for similar areas. Mean values for all levels used for each method. (See Tables 4.8 and 4.9.)

Water-Column vs. Stitching

Transect 5
d.f. = 244
$t = 3.1$
$P < 0.005$

Water-Column vs. Probing

Transects 1-4
d.f. = 240
$t = 2.3$
$P < 0.025$

Transect 5
d.f. = 140
$t = 2.9$
$P < 0.005$

Figure 4.10.

Sanderling feeding maps for cine sequences 10 (a), 20 (b), 30 (c) and 32 (d). See Appendix 4.4 for details of individual sequences.

Symbols:

■ - starting point

▶ - prey capture

● - probe attempt

/ - water column attempt

N- Nerine

All unmarked captures are Bathyporeia.

a)

Attempts 1-21 in waves.

Attempt 22 in wave edge.

b)

Attempts 1-2 in shallow water.

Attempts 3-15 in waves.

Attempt 16 in wave edge.

Attempts 17-18 in shallow water.

c)

Attempts 1-4 in waves.

Attempts 5-8 in wave edge.

Attempts 9-17 in waves.

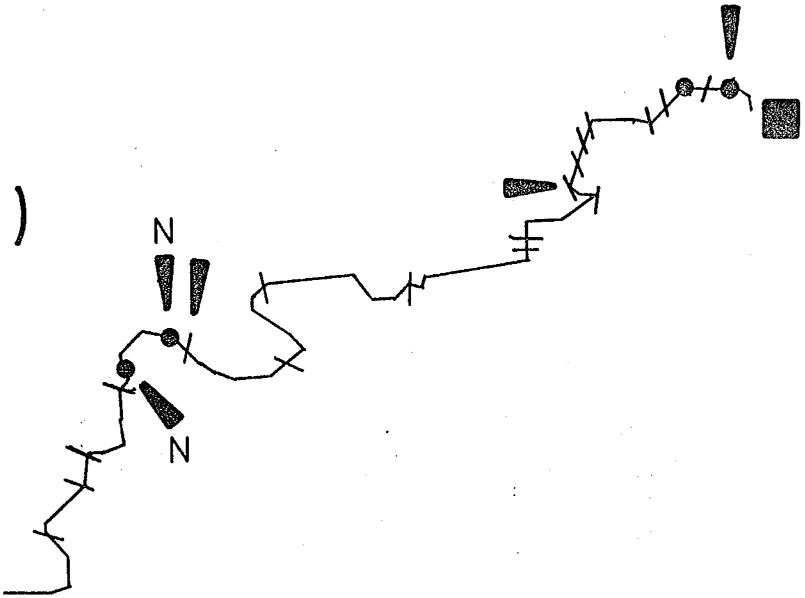
Attempts 18-20 in shallow water.

d)

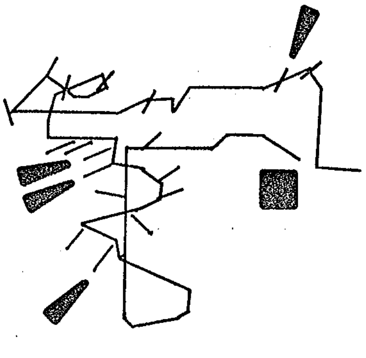
Attempts 1-3 in shallow water

Attempts 4-8 in waves.

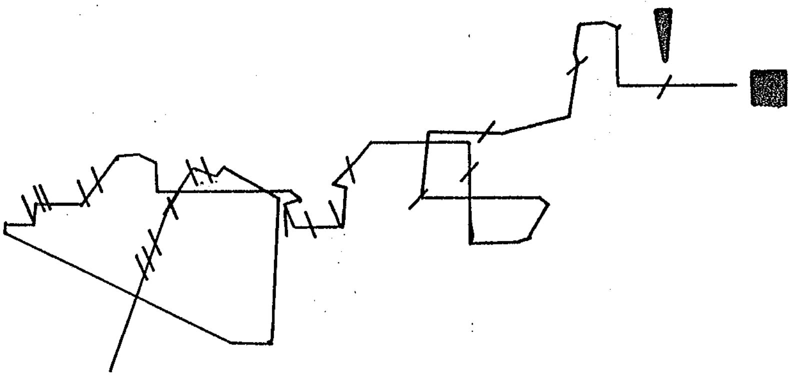
(a)



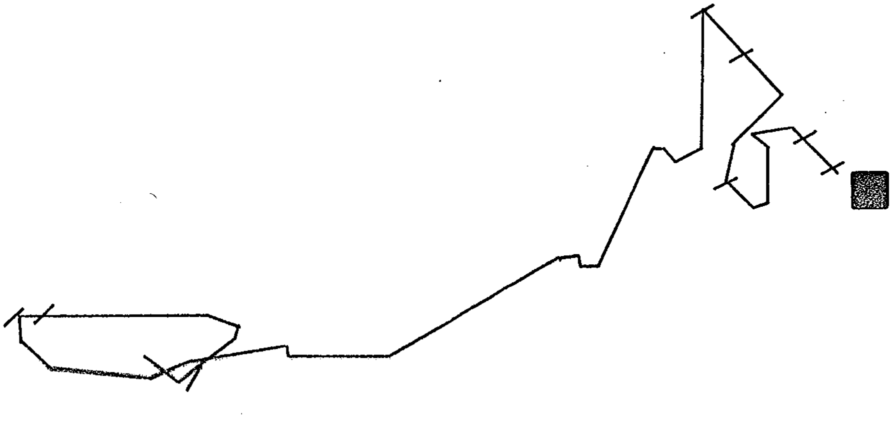
(b)



(c)



(d)



4.3d. Pause position

The Pause position refers to the brief and downward searching movement made by a bird when it came to a momentary stop. This behaviour was interpreted as a visual component of foraging. A main difference between probing and stitching was the lack of the Pause position before a stitch attempt. Table 4.11 shows the distribution of behaviours that followed the Pause position (data from taped commentaries). If a Pause was followed by a brief run and then another Pause, this was treated as two separate Pause positions. Of the Pauses recorded, 45.2% were not followed by a feeding attempt, presumably because an appropriate stimulus did not occur during the Pause. The scarcity of the Pause position before stitch feeding (o.7%) suggested that this method did not rely on a visual cue (apart from the choosing of a general area or feature such as the ripples).

4.3e. Switching in foraging method

Table 4.12 presents a summary of information on switching in foraging methods after both successes and failures. Only 2.1% of failed stitch attempts but 5.2% of failed probe attempts were followed by water column attempts. (While these proportions might vary,

TABLE 4.11

The distribution of behaviours following 2079 recorded Pauses, from taped commentaries, 1977-78.

<u>Behaviour Recorded</u>

	Pause	Direction Change	Surface Feed	Water-Column	Probe	Stitch
Total Recorded	2079	4121	3622	1198	4293	3076
Number preceded by a Pause	412	529	95	181	840	22
Percentage preceded by a Pause	19.8%	12.8%	2.6%	15.1%	19.6%	0.7%

TABLE 4.12

Two-way cross-tabulation; feeding method used following successful and unsuccessful attempts.

Unsuccessful attempts:

Foraging method after failure	Unsuccessful attempt: Probe	Stitch	Water-Column
Probe	247	76	12
Stitch	80	162	5
Water-Column	18	5	92
Totals	345	243	109

Successful attempts, Nerine:

Foraging method after success	Successful attempt: Probe	Stitch
Probe	44	14
Stitch	16	43
Totals	60	57

Successful attempts, Bathyporeia:

Foraging method after success	Successful attempt: Probe	Water-Column
Probe	10	6
Water-Column	0	22
Totals	10	28

depending on the proportion of Bathyporeia to Nerine present, the difference is mainly a function of visual vs. tactile feeding.) Both water-column and probe attempts have visual components; hence the switch from one to the other does not require a change in the sensory system involved. For feeding on Nerine by both stitching and probing, the chosen method was followed by a similar foraging method more often when the first attempt was successful than when unsuccessful (75.4% vs. 66.6% for stitching and 73.3% vs. 71.5% for probing), although neither difference was significant at the 5% level.

Switching between probing and stitching which involved a change from at least partly visual to chiefly tactile feeding, was noted when birds were forced up the beach by a series of waves. One example of switching is seen in film sequence 22 (Fig. 4.11). This bird began by feeding on the wet sand and was continually pushed up the beach by the waves. The repeated pattern of movement upshore followed by turning parallel to the tide edge is clearly seen in this sequence. It suggests that birds would have fed more in this location by stitching if sufficient time had been available before the tide covered the area.

Figure 4.11

Sanderling feeding map for cine sequence 22. See Appendix 4.4 for details of individual sequences.

Symbols:

■ - starting point

► - prey capture

● - probe attempt

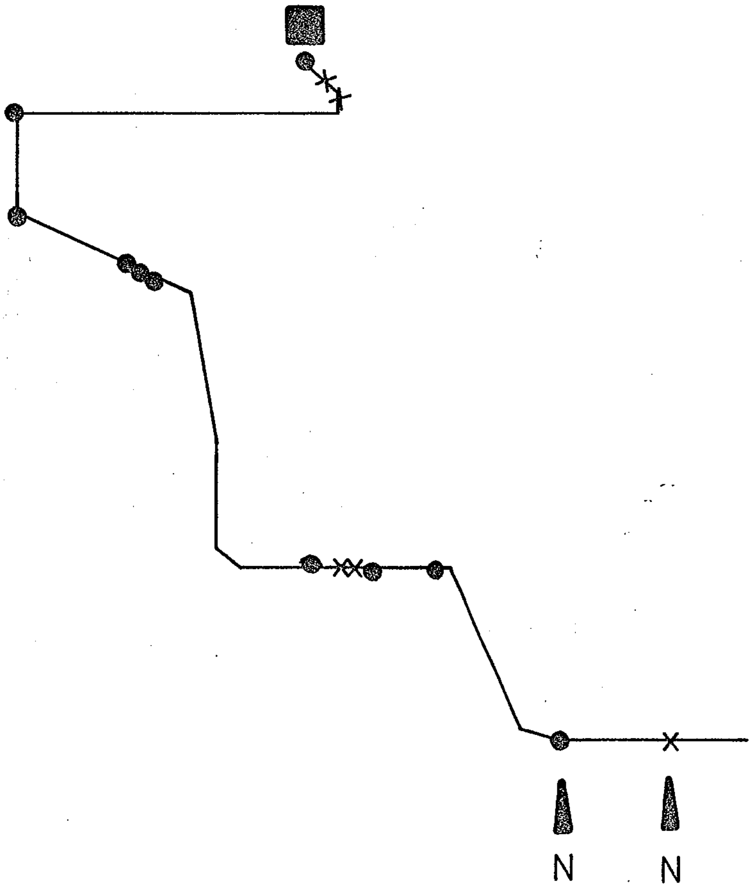
X - stitch attempt

N - *Nerine* capture

Arrow indicates direction of waves.

Attempts 1-5 in wet sand.
Attempts 6-8 in wave edge.
Attempts 9-14 in wet sand.
Attempt 15 in wave edge.

V



4.3f. Social feeding

No detailed analysis was carried out on the patterns and effects of social feeding in Sanderling, since such information was not collected systematically. However, the following observations are instructive.

Figure 4.12 shows the search path of four individuals feeding together at Redcar Beach. All birds were feeding by the stitch or probe method, feeding together as a group, and moving parallel to the tide edge. This film sequence suggests that as birds may feed very close together the opportunity for assessing each other's foraging succes is present. It also suggests, from the location of successes, that the birds may take advantage of clumped prey.

I looked at 14 film sequences in which birds were feeding in groups of two or more (totalling 166 feeding attempts). (These sequences were taken from areas with different proportions of Nerine and Bathyporeia.) I noted the type of feeding attempt, the number of paces taken after the attempt, the success or failure of the attempt and, where possible, the reasons for any movement away from a feeding site. Table 4.13 summarizes the 166 feeding attempts. In 23 cases, the bird either turned away from another individual, joined another individual, or searched the area in which another individual had fed. Three changes

Figure 4.12.

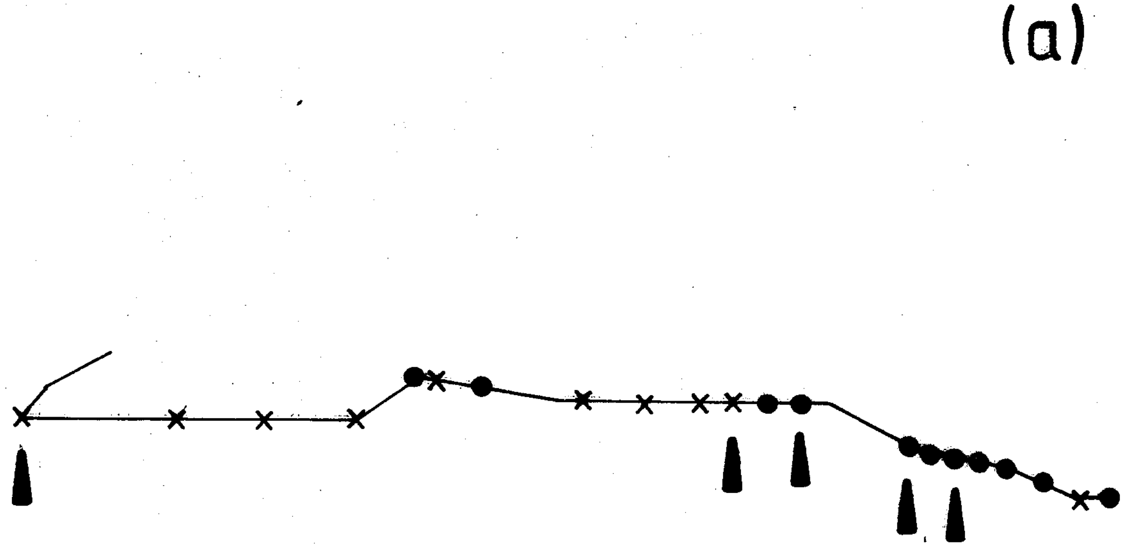
The search maps of four individuals feeding together. Although these maps have been extracted from the same piece of film, each has been treated as a separate sequence: (a) sequence 50, (b) sequence 51, (c) sequence 52 and (d) sequence 53. See Appendix 4.4 for details on individual sequences. All four individuals had the same starting point, moving from the right to the left.

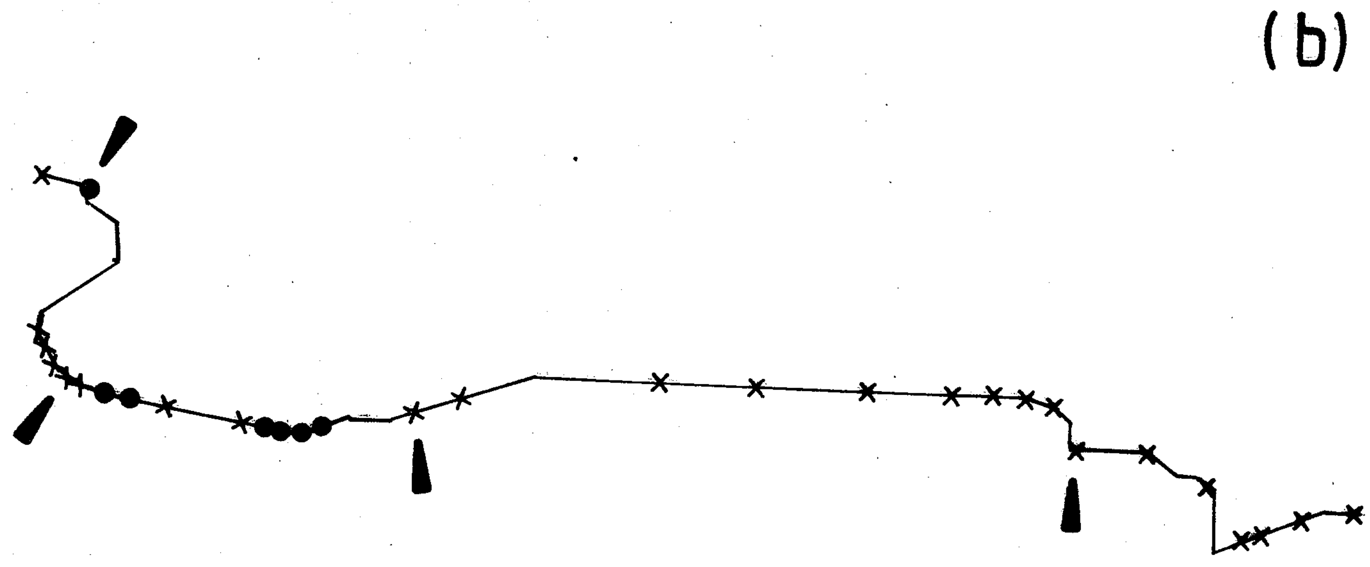
Symbols:

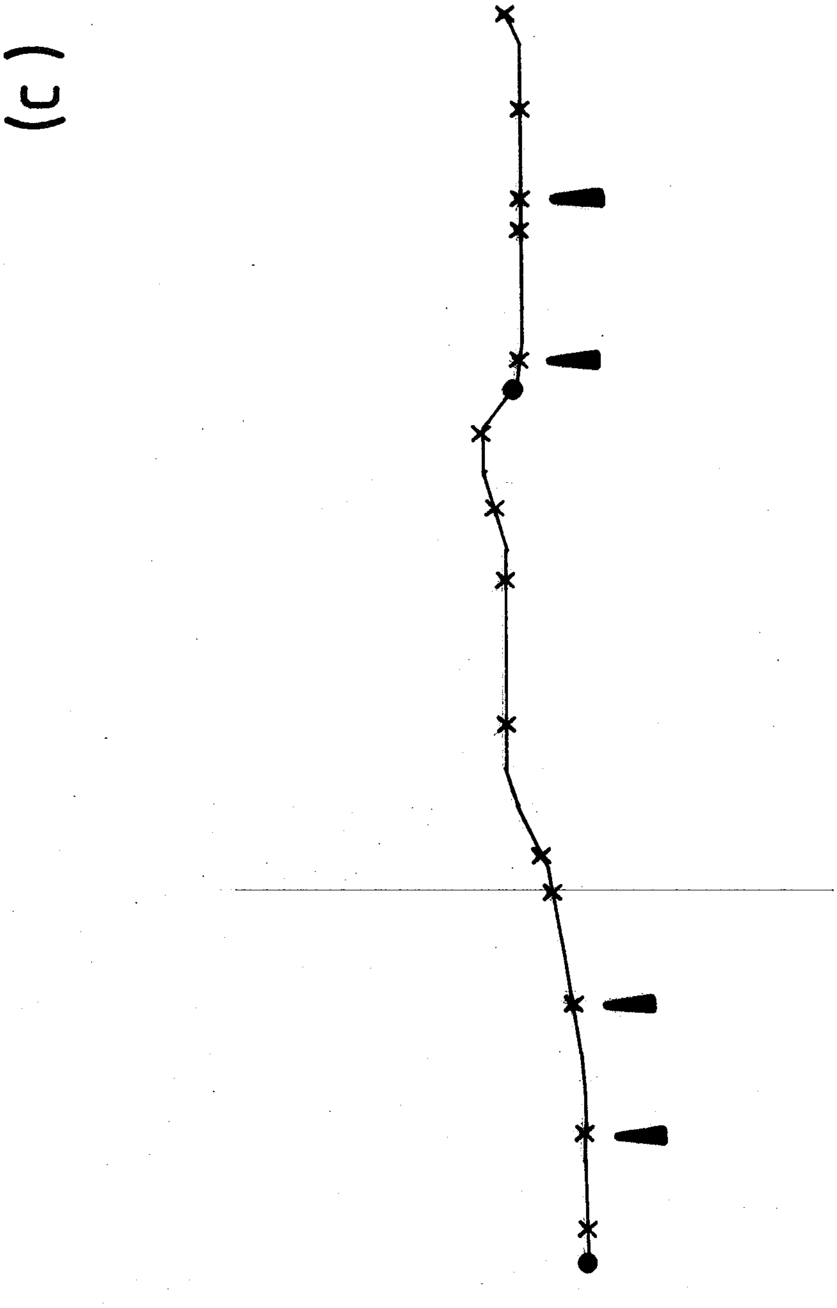
● - probe attempt.
X - stitch attempt
➤ - prey capture.

All prey captures Nerine.

(a) Attempts 1-8 in wave edge.
Attempts 9-13 in shallow water.
Attempt 14 in wave edge.
Attempts 15-21 in shallow water.
(b) Attempts 1-11 in wave edge.
Attempts 12-32 in shallow water.
(c) Attempt 1 in wave edge.
Attempts 1-12 in shallow water.
Attempts 13-16 in wave edge.
(d) Attempts 1-4 in wave edge.
Attempts 5-21 in shallow water.
Attempts 22-32 in wave edge.


(a)


(b)


(c)

(d)

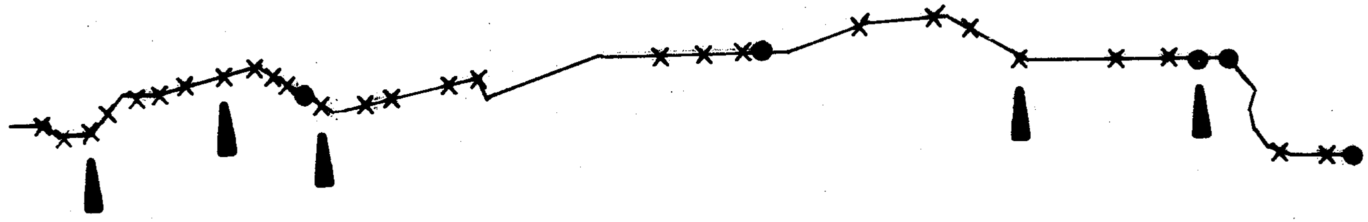


TABLE 4.13.

Reasons for moving from a feeding site after successful and unsuccessful stitch, probe and water column attempts.

Reason for moving from area	Stitch		Probe		Water Column	
	Success	Fail	Success	Fail	Success	Fail
Running from tide	1	5		7		5
Running into tide	2		1		2	1
Visual Search	1	3		6	3	6
Inspection of another bird	1	1		11		2
Turning from another			1	2	1	3
Site change			2	4	1	6
Another bird running by						1
Visual Cue				1	2	

Paces ($\overline{X}$) after foraging attempts-

	After Success	After Failure
Stitch	7.1	9.8
Probe	8.4	12.6
Water Col.	9.1	14.9

in feeding site resulted from noticing a visual cue. Birds rarely inspected others while feeding by the water column method (only 3 of 53 cases). When foraging by this method the birds acted independently with long searching periods and very high pacing rates between attempts. Similarly, birds rarely investigated other Sanderling stitch feeding (2 of 40 instances). However, during probing, birds inspected other birds on 11 of 73 attempts, all of them after the inspecting bird had failed to capture prey. After many of the feeding attempts, a bird either fed again directly and thus did not appear to be affected by the presence of others (72 cases), or some noticeable change in feeding site occurred (82 cases), or it could not be established why the bird moved (12 cases). On 24 occasions the bird moved from a feeding area to run into or away from the tide edge. Location changes (e.g., going from tide edge to shallow water etc.) accounted for 13 zone changes; and intensive prey searching (several paces with visual orientation directed towards the substrate) accounted for 19 area changes. For all three foraging methods, the number of paces moved after failed attempts was, on average, greater than after successful attempts. (Because of small sample sizes and large S.E., thses results can not be tested for statistical significance.)

Birds did not follow one another only in order to investigate a feeding site. For example, birds passing overhead or running past could bring others out of a feeding position.

This brief analysis shows the potential for, and the occurrence of, social interactions while foraging. More detailed studies would be rewarding.

4.4 Discussion

In Tinbergen's detailed study of Starling foraging (1980), he considers three main questions: 1) what are the constraints on a foraging bird; 2) what are its foraging goals, and; 3) what is the time scale over which the goal-directed behaviours are maximized. In the design of experimental or field research on foraging behaviour, these questions determine the approach and scope of the researcher. For my study of foraging Sanderling, the first of these questions was the central one. Before one can attempt to answer the remaining questions, one must have considerable understanding of the constraints.

In order to detail the constraints on the foraging individual in its natural environment, the animal must be observed there and not solely in a laboratory, or in a highly modified situation. For example, Tinbergen's finding, that the prey chosen by parent Starlings is affected by the nesting demand, which in turn is affected by the hunger state and number of the young, argues for measuring the constraints in a natural environment. Maximization of the rate of caloric intake alone, which might have been predicted as the foraging goal on the basis of laboratory studies, did not explain prey choice by the adults when feeding young in the field.

It is necessary to decide when observations are to be made. Does the observer collect data only when the weather creates a greater demand on feeding efficiencies (rate of energy intake) and time allocation or does he try and record the foraging of the animal under a wide variety of conditions? The object then is to determine how an individual achieves a given strategy, or set of strategies. Cody's comment (1974) that, "populations spend more time tracking moving fitness optima (that is, climbing the sides of shifting adaptive peaks on Sewall Wright's adaptive landscape) than they do sitting the summit optima", points out that we really need not find a single solution for a given situation, but rather, need to measure the animal's attempt to make correct decisions regarding its foraging environment. The degree to which this correctness is possible has been of central importance to the idea of stability and predictability in different environments.

The Sanderling at Teesmouth are feeding in a "coarse-grained" environment (Levins 1968), giving them an opportunity to choose which prey to take and also at which time of the tide to concentrate on the different prey species in the different areas. The occurrence of alternative foraging methods, a variety of metereological variables, and numerous physical constraints (e.g., the waves), makes prediction of their foraging behaviour complex. An important question could be, "How should a Sanderling forage in order to minimize the time from one prey capture to the next ?" (In this consideration, attention to size selection of prey should also be important.) This requires that the Sanderling make the correct choices as to where, when and how to feed.

Sanderling in mid-winter feed for a large part of each tidal cycle. Roosting by Sanderling at Teesmouth was in response to high water and outside of this time the birds choose mainly to feed. The birds have a well defined pattern of feeding locations and times of feeding (Chapter 3) suggesting that they are "pushed" to feed with great efficiency (i.e., it takes virtually all of the time available to obtain sufficient energy). This included flying to the north side of the estuary once the available feeding areas of Coatham Sands had been covered (see Appendix 3.1). Sanderling do not store much fat in autumn (Les Goodyer, pers. com.); they must balance their energy budget daily. In severe weather, Sanderling suffer increased mortality (Evans 1981). Therefore, one would expect them to try to maximize the rate of energy intake.

At Teesmouth, Sanderling feed on three main prey: Nerine, Bathyporeia sp, and Eurydice. In terms of numbers and biomass, Nerine is the most profitable. Nerine are obtained by the tactile foraging method of stitching and by probing, which includes a visual and tactile component. Nerine is distributed patchily alongshore, although found throughout Coatham Sands. Hence, the foraging methods of the Sanderling are not evenly distributed in the beach areas. Nerine occur in distinct zones. (The zones are defined by their distance below the HWM.) One strategy might be to concentrate feeding efforts in the zones of highest Nerine numbers. (Size distribution of Nerine should also be accounted for.) Continued feeding in these zones is not possible on two accounts: i) each zone is rapidly covered by the flooding tide, and ii)availability is related to the wetness of the sand and hence to the position of the tide. For the latter, either Nerine in drying sand retreat out of the range of the Sanderling's 25 mm bill or stitching is not possible in dry sand (although probing may still be possible). Once out of the main Nerine zone, Sanderling should feed on whatever prey is most profitable. For a major portion of their foraging, Sanderling are dependent on the location of the waves.

The duration of stitching (for both successful and unsuccessful attempts) was significantly longer than probing. Birds were constantly being pushed up the beach by incoming waves, feeding by stitching chiefly on the ebb tide or where wave frequency was reduced (transect 5) or showed little movement (such as Redcar Beach at the low water period). While stitching, birds have a limited search area, with heads buried in the sand, thus confining them to reduced foraging areas. Thus, coupled with the fact that they had to orient parallel to the waves, Sanderling maintained themselves in the zones of high Nerine numbers (Fig. 4.12).

The Sanderling's response to their major constraint, the waves, is shown in their visual orientation prior to feeding. A bimodal distribution of visual orientation (corresponding to directions parallel to the waves) was especially well defined for stitching, and most pronounced while stitching in beach positions closest to the waves (Figs. 4.7 and 4.8).

Proximity to the waves and the available foraging time helped determine if stitching or probing occurred (see Fig. 4.11). The frequency of probing was greater on the flood tide, however, this may have been due to an inability to forage by stitching (because of available time) rather than a preference for probing. Probing resulted in the capture of Nerine and Bathyporeia/Eurydice.

When the Nerine zone is covered by the tide (prior to high water, see Fig. 3.2), or when birds are feeding in an area where *Bathyporeia* are more numerous (Coatham Sands) the feeding method is determined by the state of the tide, which also affects the activity of the prey. Once covered by the tide, both *Bathyporeia* and *Eurydice* come into the water column. Waves were the preferred beach position when foraging by the water-column method (and the least preferred when stitching). When foraging by the water-column method, birds only submerged their bill, reducing the need to orient to the waves. This made foraging in the waves by this method possible.

The invertebrate data alone cannot determine how and where the birds will feed. The constraints found in each area must be considered at all times. With the uncovering of the first *Nerine* at transects 1 and 2, the Sanderling begin to appear on Coatham Sands; stitching was virtually absent, with the birds concentrating in the shallow zone, feeding by probing and the water-column method. At transect 5 the incidence of the water-column method was reduced, with the birds concentrating efforts in the wet sand. During a rising tide, waves breaking in rapid succession made the time-consuming stitch method inappropriate. It was at transects 1 to 4 where the greatest amount of time was spent in running. With rapidly successive waves, there was also a reduced wet sand area, the birds being forced to probe and feed by the water-column method. That Sanderling continued to feed mainly by stitching and probing at transect 5 with little success (on *Nerine*), suggests that *Nerine* was the preferred prey, despite large *Bathyporeia* concentrations in this area.

If *Nerine* is the preferred prey of Sanderling (at transect 5 and Redcar Beach), what determines how long birds will continue to search? If the duration of a single unsuccessful attempt represents the "persistence time", then there was a significant inverse relationship between persistence time and the success rate of *Nerine* captures (when stitching). While stitching, birds did not show area-concentrated search, but maintained a forward movement, parallel to the waves and within a particular feeding zone (when possible). Contraction of the predator's search path after success in prey capture has been suggested by several authors (Banks 1957, Cody 1971, Smith 1974a, 1974b, and Pyke et. al. 1977). As the foraging areas of the Sanderling were rapidly covered, such contraction was seldom possible.

For probing, no relationship existed between persistence time and success rate with *Nerine*. This was perhaps due to a visual component present while probing. As with stitching, no area-concentrated search was evident while probing. Birds moved from an area to avoid another foraging Sanderling, because of the waves, to move to a new foraging "patch" or to inspect another individual. Most investigations occurred by birds that were probing and when the investigating bird had been unsuccessful. While probing, birds orient parallel to the waves and continue moving forward maintaining itself in a particular zone, thus responding to the same constraints encountered while stitching.

Sanderling must adapt to the constraints of the ebbing and flooding tides. They can choose where to feed alongshore at each state of the tide, all in relation to the density and availability of alternative prey. The foraging method, in part, is determined by prey availability which itself is determined by the state of tide and conditions of the substrate.

In a series of laboratory experiments, Myers et. al. (1980) studied the role of prey size, prey depth, prey microdistribution and substrate penetrability in affecting prey availability to Sanderling. All factors affected prey risk, and thus Sanderling feeding habits. In simulating the upper portions of the wave-washed area (the area where the wave had receded) the researchers constructed an optimal situation (in terms of time available for feeding), where social interactions were no longer a factor.

It could have been stated apriori that the above four factors would affect both prey risk and the resulting foraging of the Sanderling. The extrapolation of these test results onto the natural situation, however, must be cautioned (especially in terms of the amount of affect resulting from each factor). In their experiments, the prey was "frozen", thus there was no possibility of Sanderling detecting any movement. Because little time is available for Sanderling to feed in specific areas (where waves are a factor), the birds may not be able to feed optimally; rather, they may be making the best use of available time. Although the strand line may not represent a high caloric area, there may be more actual feeding time there and a greater probability of obtaining at least some energy.

If different prey species live in different "patches" of the predator's hunting range, the problem for the hunter is to allocate its time between them in the most productive way (Curio 1975). A series of spatial problems confront the Sanderling which forage along the open beaches of Teesmouth. To locate prey economically the birds must decide first on their feeding location. The choice of foraging method and position of beach in which to feed is at least partially determined by the environmental constraints. Areas are rapidly opened and closed by the waves, and a limited amount of time is available on most feeding attempts. Social effects may also help determine spatial requirements and limitations. Smith (1971) referred to 'rules' which birds should follow to achieve success while foraging (e.g., making alternate left and right turns when unsuccessful in a feeding attempt). Similar results have been reported for goldfish (Kleerekoper et. al. 1970), herring larvae (Rosenthal & Hempel 1970), and sticklebacks (Thomas 1974). The option of left and right turns is not often available for birds feeding along the wave's expanse. Although Nerine have been shown to exhibit some clumping in their distribution, they are usually available throughout the band of highest density. If densities are high enough it may not be necessary for birds to alter a search path, but rather, to maintain their location within the invertebrate band and feed by the most appropriate method on the most available prey.

The value of a given foraging strategy comes from its integration with the ecology of the individual. Field studies such as Cody's (1971) suggest that foraging strategies should be seen as long term processes, and not limited to any particular segment of time. In order to reduce foraging studies to manageable levels, two trends occur: simplification of the components of foraging and the simplification of environmental factors (reduction of complicating constraints). Both of these lead to false impressions regarding the operation of foraging mechanisms.

Interactions with conspecifics manifest effects in both obvious and subtle ways. A most notable example has been provided by Goss-Custard (1976) in describing the effects of interference in feeding success in Redshank and their main prey (Corophium). Where optimal models are tested in a manipulated situation (such as Krebs et. al. (1977), external factors such as competing species, behaviour of the prey and physical conditions are eliminated. This is not an argument against proposing theoretical models, or models based on laboratory studies, for they often provide the framework on which the views of the fieldworker are based. However, a feeding strategy can be seen realistically only when placed in the context of the field situation.

In the Charnov model (1973 page 14), "the prey items are handled one at a time and this handling time is unavailable for searching (i.e., no new prey may be encountered during the handling of a prey item)". Sanderling do not remain inactive while handling prey. In 37 of 177 analyzed foraging successes, the bird took two paces or more while handling prey. There was also much head turning during this period. Handling time has often been designed as a distinct phase of feeding in which no other activity takes place. Such assumptions are misleading and may have an effect on how the observer measures time allocation of the birds and how the observer's understands the foraging mechanisms.

It is perhaps prudent for the researcher to invest time in understanding the constraints (physical and environmental) rather than just building models which result from laboratory situations (not actually experienced by the birds). The constraints present at

Teesmouth are such that they shape the structure of the Sanderling's foraging mechanisms (e.g., turning parallel to the waves). Laboratory observations in the absence of detailed field observations may lead to dangerous conclusions as to the nature of the Sanderling's feeding strategies.

CHAPTER 5 TURNSTONE ECOLOGY AND MOVEMENT PATTERNS ON TEESMOUTH"S SOUTH SIDE.

5.1 Introduction

Turnstone, like Sanderling, are social feeders. As a winter visitor in Europe and the Pacific North American coast, Turnstone occur in rather tightly packed groups while feeding and roosting, seldom solitary (pers. obs.). At high tide at the Wash, as many as 1000 may roost together (Minton, 1970). In winter Turnstone are mainly inhabitant of coastal regions where they feed on wrack flies, mollucs, annelids and crustaceans. The most common winter habitat is rock outcrops with mussels (Mytilidae). Turnstone are known to scaveng on cockles on the Wash (Jones 1975). Also on the Wash, Turnstone were observed digging systematically through mud extracting Corophium (Jones 1974). This is similar to the Turnstone at Teesmouth which dig for Nerine in piles of sand left by bait diggers. (See Jones, 1974, for a list of foods found in Turnstone pellets on the Wash.) As is a common practice of Sanderling, Turnstone will remain close to Oystercatchers, feeding on the final scraps of meat left in mussels (pers. obs.).

Turnstone are seen in connection with Sanderling, Dunlin, Knot and Redshank on open coastal areas. Along with Purple Sandpipers, Turnstone may be the first to appear on rocky areas following high tide periods.

A main difference between the Sanderling's and the Turnstone's social organization is the large number of aggressive displays within Turnstone groups. In this chapter I discuss the observations on the Turnstone, during the winter, how repulsion (via aggression) and attraction towards conspecifics, helped to determine the distribution patterns seen on the south side of the estuary. Aggression may be a main factor in providing distribution patterns and may restrict the number of individuals using the set of habitats contained within the estuary.

The detailed feeding observations carried out on Sanderling left relatively little time for observations on Turnstone. It was difficult determining what food Turnstone were taking during each individual feeding movement. Birds were often obscured by rocks, making them difficult to count. This species does, however, provide a valuable comparison to the Sanderling.

5.2 Methods

Throughout the winter season at Teesmouth, (September to May), Turnstone were counted at roosting and feeding localities to determine movement patterns and the distribution of the birds. Taped commentaries were made to determine aggressive levels, the reasons aggression occurred, and the outcome of intraspecific aggression. Colour-marking of individuals facilitated individual recognition. Birds were colour-marked for several reasons: i) to understand the habitat utilization, feeding and movement patterns along the south side of the estuary; ii) to look at the mortality and site fidelity between years, thus providing an estimate of total Turnstone pressure on the resources of the south side; iii) to study the pattern of roost locations with available food sources; and, iv) to see if there was any positive associations amongst individuals within the populations. Observations on colour-marked birds provided the best indications as to movement patterns, consistency of area use, the difference between adult and juvenile birds and the survival and return rates over the course of the study. (See Appendix 5.1 for a summary on survival rates of Turnstone at Teesmouth.)

In the first year of the study, 34 Turnstone were individually marked. In the second and third years of the study, 48 and 8 additional Turnstone were colour-marked. Of the marked birds, 17 were ringed as juveniles and 73 as adults. In addition to the above birds, 20 Turnstone, (7 juveniles), were colour-marked on 5/5/1977. As this was a "passage" period these birds were not included in the return rates.

5.3 Dispersal from the roost and general movement patterns

More than other wader species utilizing the south side of the estuary, Turnstone confined their feeding activity to the area between South Gare and Saltburn. Birds roosted on two main sites (Fig. 5.1). Two hours after high water the Turnstone left the roost and dispersed along the beach from South Gare to Saltburn (Fig. 5.2). As the rocks adjoining South Gare became exposed the Turnstone began to leave the roost and started foraging on small crabs, limpets, barnacles, amphipods and polychaetes within the _Fucus_ along the "German Charlies" at South Gare, (see Fig. 5.1). From South Gare the birds would move south in successive waves of two to twenty birds, flying towards Coatham and Redcar Rocks and further south, or to the adjoining Coatham Sands. After low water, the pattern was reversed (Fig. 5.3). The roosting pattern of the Turnstone was modified by gales and wrack beds which tended to be localized according to wind direction. The time at which the birds returned to the roost depended on the state of the tide, (neap or spring), what food was available and the prevailing weather conditions.

Turnstone are extremely opportunistic in their feeding habits (Jones 1975, MacDonald & Parmelee 1962, Mercer 1966 and Prater 1972). During the emergence

Figure 5.1.

The main roosts for Turnstone feeding along the Tees' south side. The main roosts were located in Bran Sands and the small adjoing harbour. See text for the pattern of birds radiating out along the coast after the High Water period.

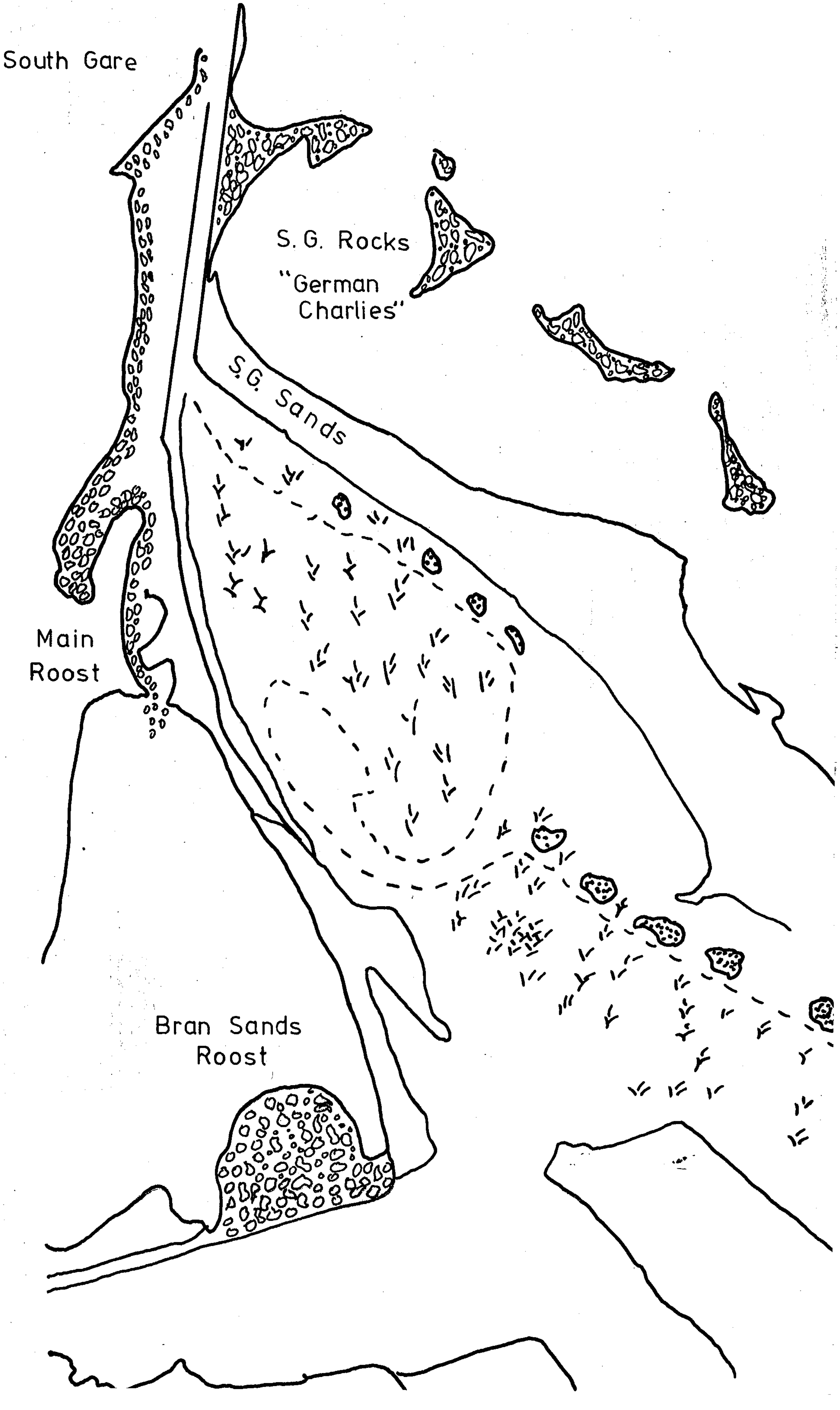

South Gare
S.G. Rocks
"German Charlies"
S.G. Sands
Main Roost
Bran Sands Roost

Figure 5.2.

The average number of Turnstone using the main roost during the 1976-77 and 1977-78 winters, (late September to mid-April).

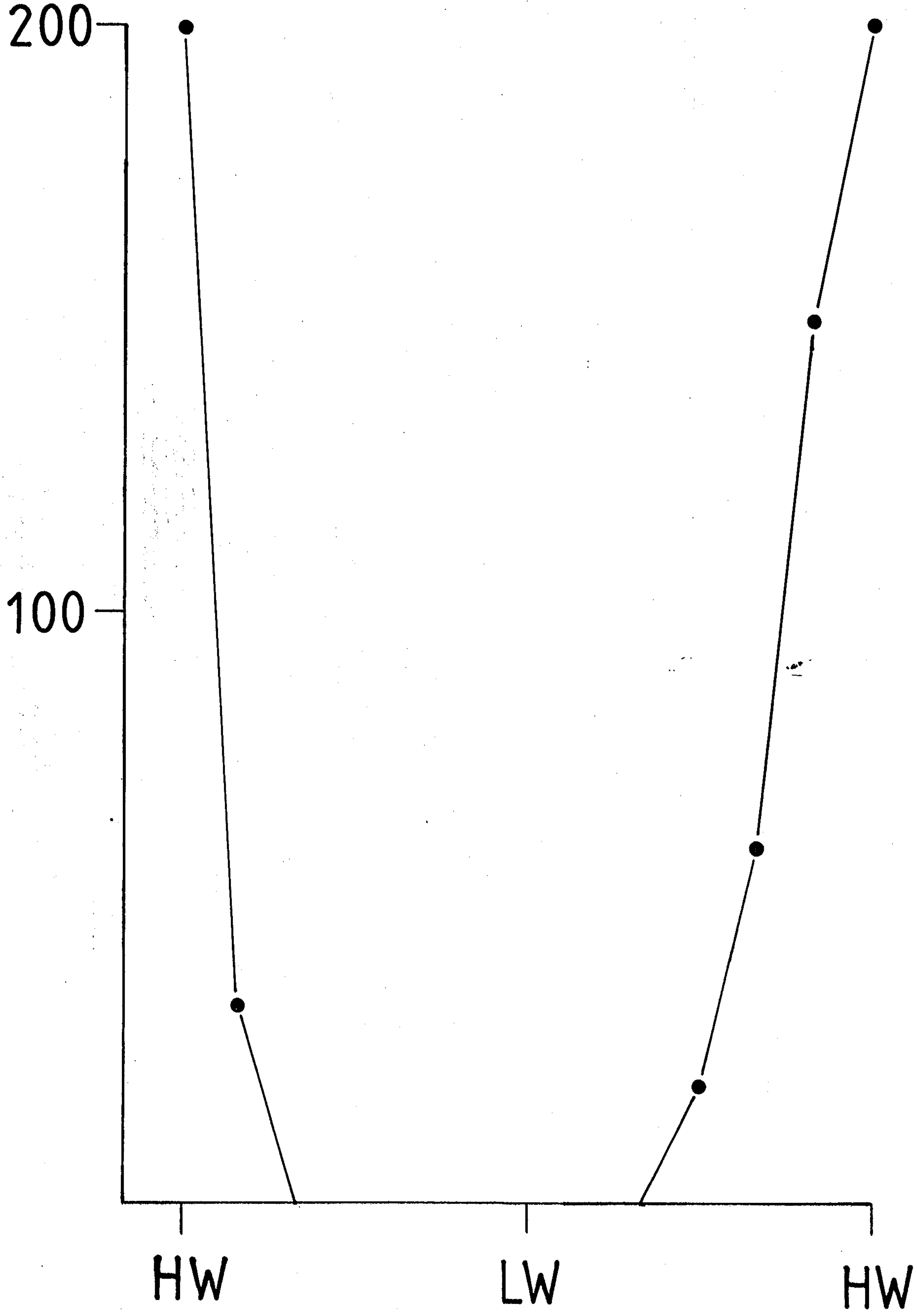

200
100
HW
LW
HW

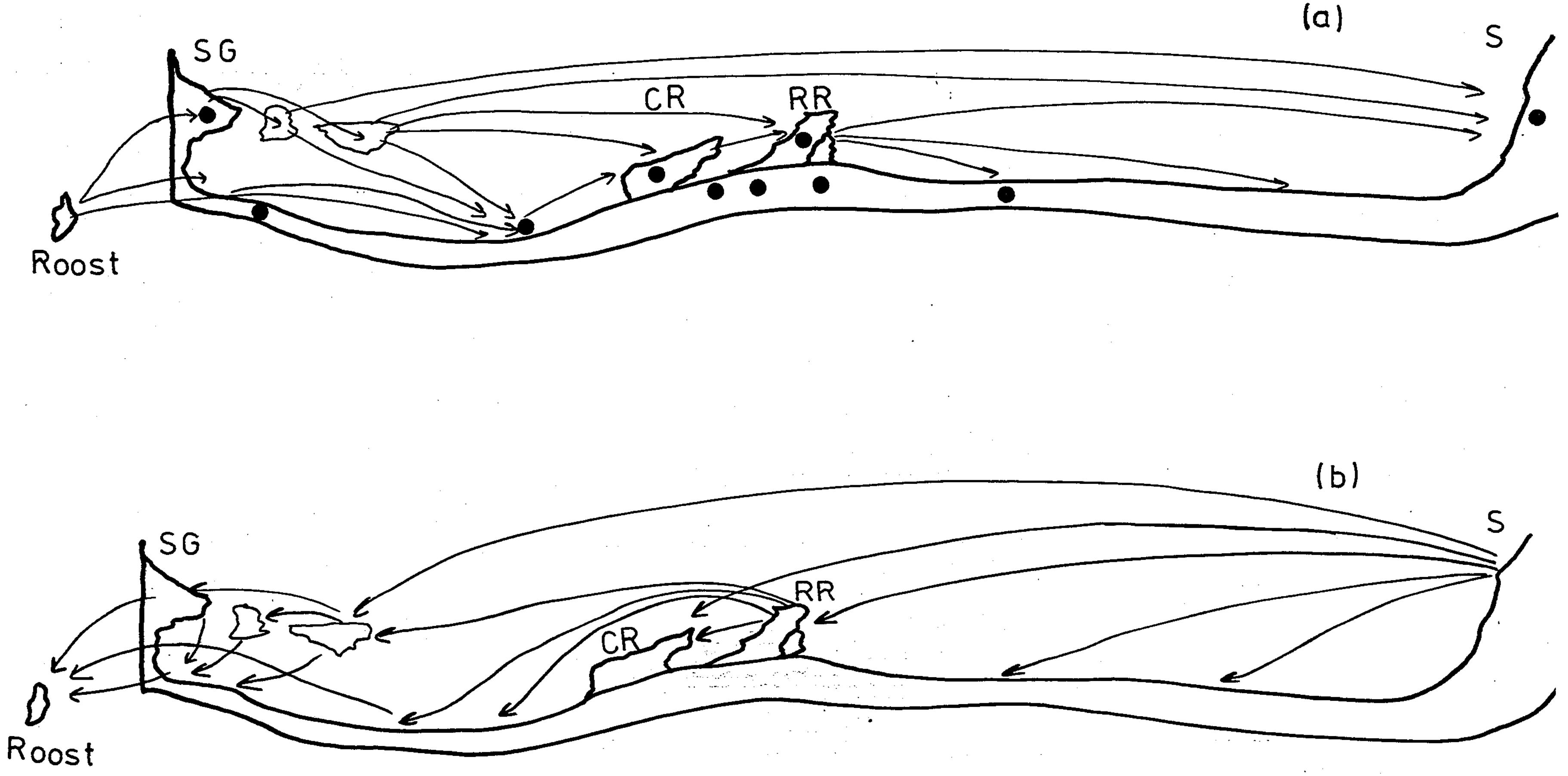
Figure 5.3.

A summary of movement patterns of Turnstone on the Tees' south side.

(a) The period following high water. Circles (solid) represent areas where Turnstone might stay to feed during low water.

(b) The period following low water when Turnstone begin moving north on their return to the Main Roost.

S G- South Gare.
C R- Coatham Rocks.
R R- Redcar Rocks.
S - Saltburn.


(a)
S
SG
CR
RR
Roost
(b)
S
SG
RR
CR
Roost

of wrack flies or the sudden availability of other rich food sources on the beach even those individuals which utilized certain rocks with great regularity would move to the beach. The appearance of such sporadic food sources affected the birds roosting habits. It was not uncommon for the majority of the Turnstone to begin to roost, (along Coatham Sands or South Gare Sands), two or three hours before a midday high water period. During the emergence of wrack flies the birds would sometimes not go to the roost over high water but would continue to feed, or roost, on the beach. There was no indication that the birds were stressed in terms of energy procurement; more data on weight changes over the winter period might provide some proof for this statement.

The main roosts provided a sheltered location where birds had easy and rapid access to the first exposed rocks, (South Gare Rocks). On days of heavy gales, birds had access to rock and beach areas without having to fly as far south as they normally did. The beach at South Gare often held large wrack beds and when thrown up on a spring tide provided suitable habitat for the breeding of wrack flies.

The main roost was used as a place for birds to collect before or after the main feeding periods. No aggression was evident at the roost. On several occasions Turnstone roosting on smaller roosts within Bran Sands were seen flying as a group to the main roost, just before the time of roost departure, and then seen landing and departing with birds already on the roost. This suggests that the main roost may have served as a place of information transfer, as has been proposed by Krebs (1974) and Zahavi (1971). I also observed birds spending the high water period along South Gare Sands, and flying to the main roost just before the time of the birds' departure from the roost. Even on days when the tide would completely cover the main roost, birds would collect on the roost before flying to another roost. The movement both to and from the main roost occurred in stages with groups of ten birds or less, although larger groups occasionally flew to and from the roost. If winds retarded the movement of the tide up the beach, allowing birds to remain longer, they would still fly to the roost on schedule.

Turnstone collected at South Gare Rocks after their departure from the main roost. The utilization of South Gare Rocks dropped to its lowest about the time of low water (Fig. 5.4). Not all birds that collected on South Gare Rocks fed there. For many it was a further roosting period, apparently waiting for more productive areas to become available. There was no suggestion that aggression was causing birds to leave South Gare Rocks. It did not represent a preferred feeding area.

The southward movement and the returning northward movement are best shown by counts at Redcar Rocks (Fig. 5.5). Outside of the main period of

Figure 5.4.

The average number of Turnstone at South Gare Rocks, (solid line- based on 56 counts), and at South Gare Beach, (broken line- based on 46 counts), during the 1977-78 winter, (late September to early May). Counts are for all individuals, roosting or feeding. The left hand scale is for South Gare Rocks and the right hand scale for South Gare Beach.

HW- High Water.

LW- Low Water.

Arrows show the direction of Turnstone movement.

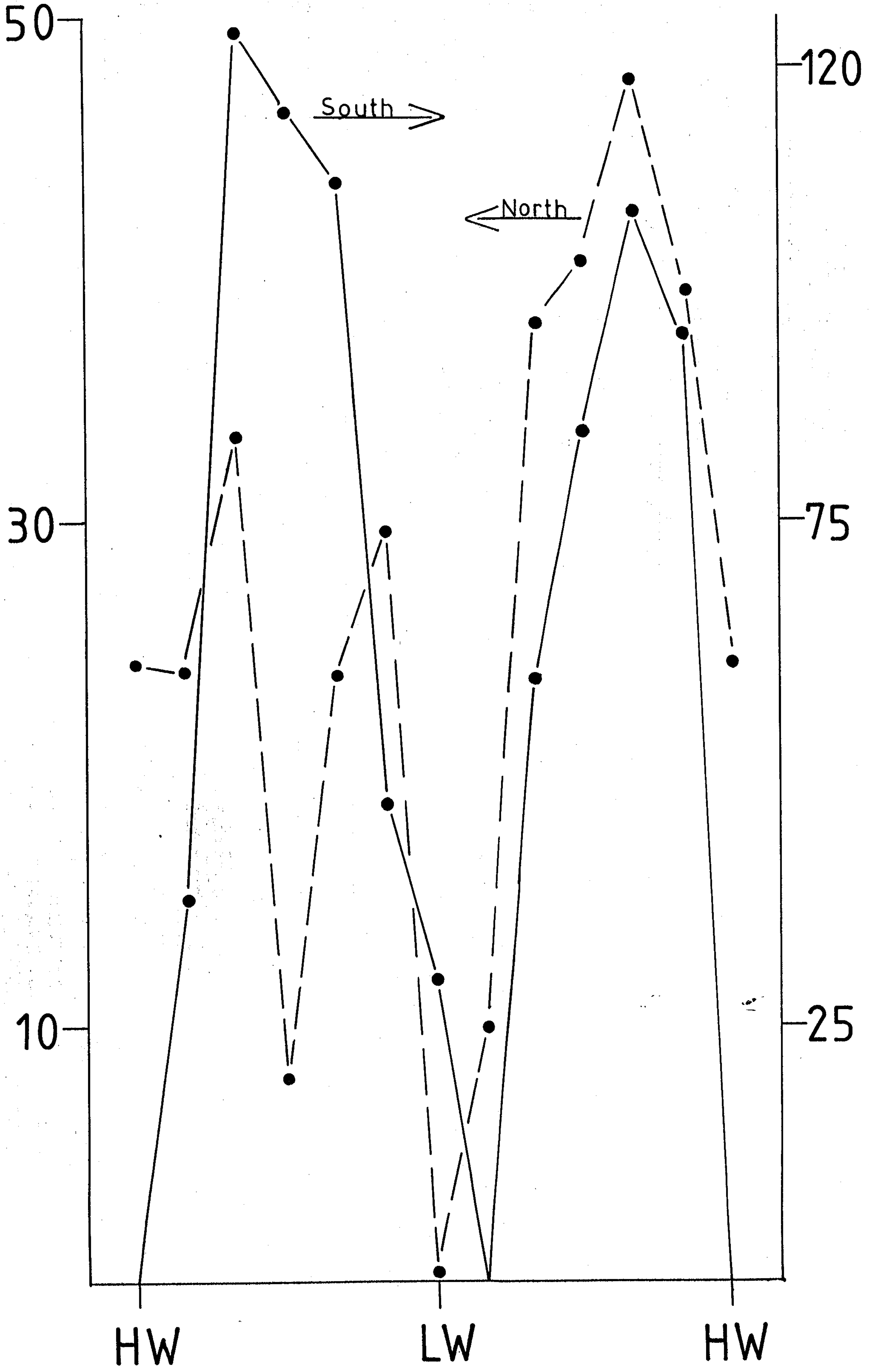

50
30
10
120
75
25
South
North
HW
LW
HW

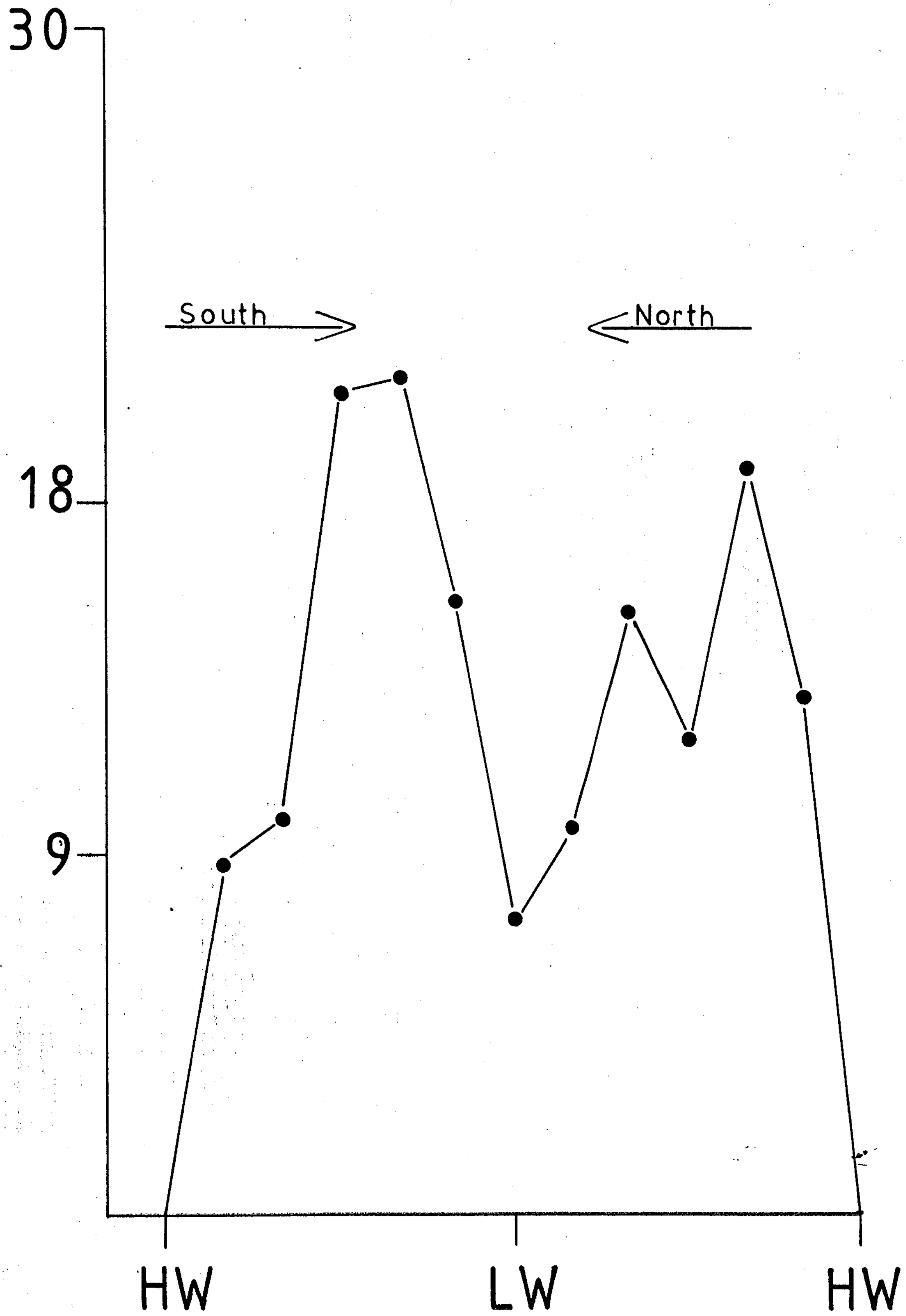
Figure 5.5.

The average number of Turnstone at Redcar Rocks during the 1977-78 winter, (late September to early May). Counts are for all individuals, roosting or feeding. This figure is based on 54 counts.

HW- High Water.

LW- Low Water.

Arrows show the direction of Turnstone movement.



30
18
9
South
North
HW
LW
HW

utilization at Redcar Rocks there was a Turnstone population of five to twenty birds. Although not preferred by most of the Turnstone population, some individuals fed at Redcar Rocks consistently. Birds could be seen flying south towards Saltburn without stopping at Redcar Rocks. Others would collect as the rocks were becoming exposed, flying south during the time before low water. As with South Gare Rocks, birds appeared to leave by choice as opposed to being pushed out by aggression. Individuals may have selected Redcar Rocks because of the reduced concentration of birds and thus reduced aggression. When bait diggers left mounds of sand, and made Nerine available, more Turnstone remained and increased the likelihood of aggressive encounters.

5.4 Site fidelity

There was a strong predictability as to the location of colour-marked individuals. (See Appendix 5.2 for a summary of the use of the estuary by colour-marked birds.) In all patterns of site fidelity mentioned below, appearance of wrack or weather conditions could alter a bird's location.

As expected, there was much individual variation in the birds' use of the various habitats. Certain individuals showed attachment to specific areas while others were more difficult to track during observations.

Redcar Rocks was a preferred feeding site by relatively few individuals. One such bird was Y/O R. Ringed as a juvenile on 23/11/1976, this bird showed consistent use of Redcar Rocks in its first year (Appendix 5.3). During this first year, (a juvenile), Y/O R was only seen at Redcar Rocks, and once on Coatham Sands. This bird was often seen alone, which was unusual for this species. During its second year on the Tees, (1977-78, its first year as an adult bird), it was seen several times on the beach at South Gare as well as the South Gare Rocks ("German Charlies"). The few taped commentaries of this bird as a juvenile showed it to be extremely wary and unsuccessful in aggressive encounters. If there was a definite difference in the aggressive outcome of adult and juveniles (as suggested by Groves 1978), this may have helped to determine where the bird fed (i.e., choosing a location such as Redcar Rocks where few other birds fed). Familiarity with the Tees and a possible change in status with adulthood may help explain the additional location sightings of the bird in its second year.

A second juvenile, L/R Y, ringed on 5/2/1977, was absent from South Gare (the area near the main roost), preferring Redcar Rocks and Coatham Sands (Appendix 5.4). In contrast to L/R Y and Y/O R, R L (an adult) showed a preference to South Gare for all years of observations (Appendix 5.5). Although juvenile Turnstone were seen roosting with adults along Coatham Sands they were rarely seen on the main Turnstone roost. For the 1976-77 observations, of 45 sightings of colour-marked Turnstone on the main roost, only one was a juvenile. (The marked population during these obserbations consisted of 19 juveniles and 79 adults.) Juveniles may have avoided the roost to continue feeding elsewhere over high water. Their inexperience at foraging may have caused them to feed for a longer period than the adults. Alternatively, juveniles may not have been as tolerated by the adults on the main roost.

5.5 Association between birds

All sightings for the 1977-78 winter were put on to computer cards to test for positive associations. For all sightings, the following data were collected:

- the location of the individual (South Gare Rocks, Redcar Rocks etc.);
- the time of day and the state of the tide;
- the size of the group in which the subject bird occurred;
- the number of Turnstone in the area;
- whether the bird was roosting or feeding;
- the number of Turnstone roosting in the area;
- the number of colour-marked birds present and the 'status' of each colour-marked bird. The 'status' of these birds was determined by their relationship with the subject bird and placed into one of four

> categories: 1) associated and feeding together; 2) associated and roosting together; 3) not associated and feeding; and, 4) not associated and roosting. Association depended on the birds being in the same group.

The difficulty in testing such associations is in trying to insure that the choice of habitats made by the birds do not simply coincide with another individual (i.e., that similar choice of site does not lead to the definition of the group). The occurrence of large wrack piles attracted a high percentage of the Turnstone population, sightings in these areas had to be approached with caution.

Using the computer to sort out sightings of the individuals, two main clusters were identified: birds Y/R Y, L Y, Y G; and, L B, W Y, R L, L O and L/W Y. Birds G/W Y and O L also showed relationships within the groups. The connections between some of these birds are shown in Fig. 5.6. The strength of relatedness (defined as those birds most often seen with a particular individual) are shown by the width of the connecting lines. These relationships were determined from sightings at all points along the south side and not only from the major gathering areas. The sightings of two sets of birds, Y G & Y/R Y and W Y & L B, are shown in Table 5.1a-b. The most important similarities will be those sightings when relatively few birds were in the area, as

Figure 5.6.

The relationships amongst several colour-marked Turnstone. Relationships are suggested by the width of connecting bars. Relationships were derived from the number of times birds were seen foraging or roosting together. For an example of sightings, see Table 5.1.

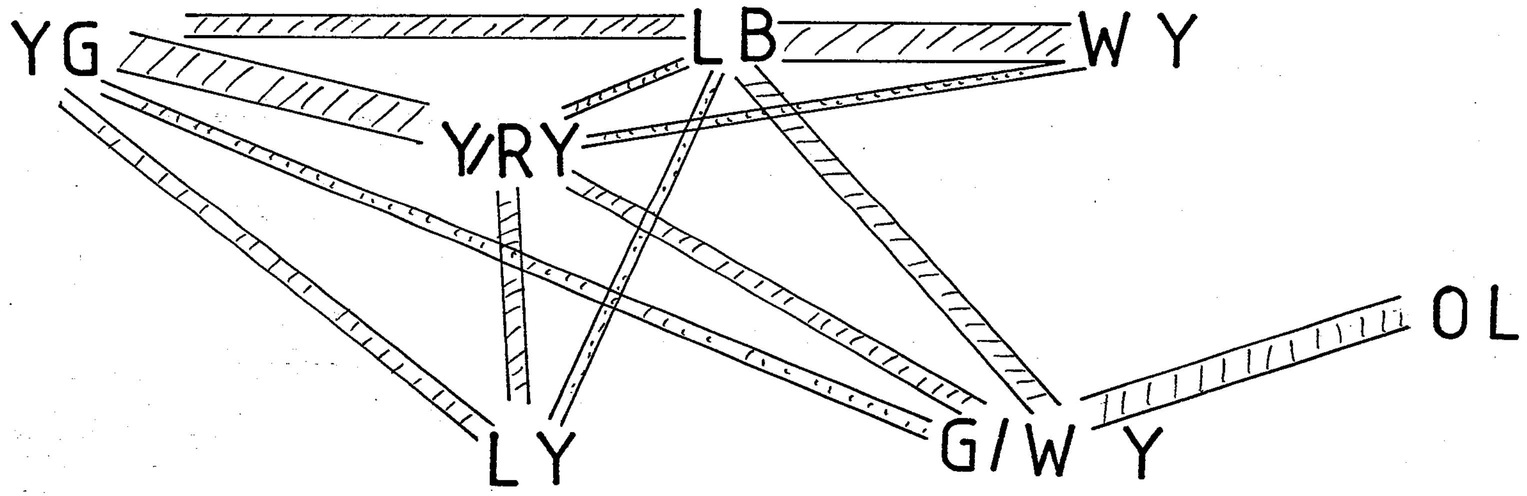

YG
LB
W Y
Y/RY
L Y
G/W Y
OL

TABLE 5.1 a,b.

Sightings of birds feeding together: a, (Y G & Y/R Y), and b, (W Y & L B).

(a) Y G & Y/R Y

Date	State of tide	Location	Turnstone present
20/9/77	LW+520	Redcar Rocks	13
8/11/77	LW+245	Redcar Rocks	15
15/11/77	HW+400	Redcar Rocks	15
18/1/78	HW+115	S G Rocks	
20/2/78	HW+215	S G Rocks	14
1/4/78	LW+140	S G Rocks	40
3/4/78	HW+:50	Transect 5 (Coatham Sands)	45
18/4/78	HW+300	Transect 4 (Coatham Sands)	
20/4/78	LW+345	Transect 3 (Coatham Sands)	20
20/4/78	LW+530	Transect 5 (Coatham Sands)	20

Total sightings: Y G- 21
Y/R Y- 25

Index of association = 45%

TABLE 5.1 cont.

(b) W Y & L B

Date	State of tide	Location	Turnstone present
27/1/77	HW+500	Redcar Rocks	10
1/2/77	HW+100	Transect 5 (Coatham Sands)	
15/2/77	LW+350	Transect 5 (Coatham Sands)	35
21/3/77	LW+320	Redcar Rocks	36
22/3/77	LW+300	Redcar Rocks	30
25/4/77	LW+130	Redcar Rocks	3
8/11/77	LW+245	S G Sands	140
18/1/78	HW+110	S G Rocks	55
22/1/78	LW+245	S G Rocks	
11/2/78	LW+145	Redcar Rocks	14
1/4/78	HW+400	Redcar Rocks	30
3/4/78	HW+:50	Transect 5 (Coatham Sands)	45
20/4/78	LW+300	Redcar Rocks	16
25/4/78	LW+200	Redcar Rocks	3

Total sightings: W Y- 34

L B- 31

Index of association = 43%

opposed to a large portion of the Turnstone population. More information on specific interactions between individuals is necessary to say if pairs are showing cohesive tendencies or if they are showing similar feeding patterns.

5.6 Aggression

Aggression amongst foraging Turnstone was common. It appeared that aggression helped to limit the number of birds in an area (except for those times when an overly abundant wrack was present). Aggression helped to space the individuals. In the case of Y/O R it may have also set its pattern for choice in foraging sites (at least while it was a juvenile). In a recent article, Groves (1978), looked at age-related aggressive behaviour in Turnstone. She found that juveniles lost in all confrontations with adults, and that the dropped tail posture was a sign of eventual success. During my feeding observations on Turnstone I noticed two very different types of aggressive encounters. The first was "rear-ending" (Type A); during these encounters, one bird displaced another by attacking another bird from behind. The bird that was attacked was unprepared and in 95 of 95 encounters, the 'victory' went to the attacking bird. Type A aggression often occurred when there were high concentrations of feeding birds and when food was abundant. This might explain why birds did not make an attempt to defend a site once displaced. In the second type of aggression (Type B) a face-off or eye contact battle occurred. Aggression increased an individual's feeding space, by displacing another bird. Displacement may have resulted over a feeding site or a feeding object (these were often very difficult to separate). Table 5.2 shows the outcome of the two types of aggressive encounters. It appears that in Type A, birds were both gaining access to a site and increasing their feeding space. Type B was more common when there was the possibility of gaining a specific food item. More energy expenditure and potential conflict occurred with Type B aggression. Although difficult to prove, it would appear that aggression played a role in the resulting distribution of the Turnstone on the south side. Affecting the distribution on a very local scale may have also affected the overall distribution of the birds.

More will be said about the use of aggressive signals and how Turnstone use and communicate the information (within the context of the situation) when I compare aggressive signaling and defence signaling in the summer and winter situation (Appendix 5.6).

TABLE 5.2

The outcome of Type A and Type B aggressive encounters in the Turnstone population. See text for description of Types A and B aggression.

Type A Aggression

95 encounters

In 100% of the encounters, the aggressor was the victor.

Behaviour of victor immediately following encounter:

-Leaves area	4.2% (4)
-Stays to feed	85.3% (81)
-Stays, doesn't feed	10.5% (10)

Type B Aggression

36 encounters

In 75% (27) of the encounters, feeding individual was the victor.

In 25% (9) of the encounters, non-feeding individual was the victor.

Behaviour of birds immediately following encounter:

Feeding individual as victor-

-Stays to feed	100% (27)

Non-feeding individual as victor-

-Stays to feed	100% (9)

CHAPTER 6. SOCIAL FEEDING IN SANDERLING AND TURNSTONE.

Sanderling and Turnstone are highly social during major feeding periods and while roosting. The winter ecology of both species is based on open coastal beaches and rock outcroppings. Both species face little interspecific competition at Teesmouth. For the Sanderling, Knot and Dunlin do present possible competition, but this only when the birds are feeding on the rocks, or on the mussel spat which collects along Coatham Sands after gales. Turnstone compete to varying degrees with Knot, Redshank, Oystercatchers and Purple Sandpipers. Turnstone are extremely opportunistic in foods taken and habitats explored. Their specialized habits of rock-turning and algae-flipping, plus their strong stout bill, make food sources available which are open to few other species. In comparison to Turnstone, Sanderling can be regarded as food specialists, although their range of feeding techniques suggest rather flexible foraging patterns.

The main daytime constraint for both species is the tide (especially for the Sanderling). The effects of the tide is clearly shown in roosting and feeding patterns of the two species. The movements of the birds in their search for feeding areas at each stage of the tidal cycle make certain areas more likely to be chosen for roosting. Transect 5 (Coatham Sands) is one of the last profitable Sanderling feeding areas to be covered by the tide. The nearest area to transect 5 which is a suitable high water roosting location (and indeed the main Sanderling roost) is the raised beach known as the Ducky. South Gare Beach and South Gare Rocks are not covered until late in the tidal cycle and are exposed again soon after high water. The nearest rocks suitable for the Turnstone to roost on are along South Gare. This is the main Turnstone roost and is well protected from the cold and the strong onshore winds.

Sanderling and Turnstone are quick to identify and exploit new and temporary food sources. There is both the possibility and opportunity for the transfer of information regarding these food sources amongst conspecifics. The foraging patterns of colour-marked birds are well defined, however, there are frequent deviations which suggests "testing" of different patches. Although all birds may not come together each day for roosting purposes, enough mixing occurs that information can be transferred over a two or three day period (for a review see Ward & Zahavi 1973). Individuals might follow one another while radiating out from their roosts, or they may simply land where other conspecifics are already feeding. This would be a major advantage for "testing" different foraging areas and is not peculiar to these two species, but rather, is widespread throughout the Charadrii.

There are several factors which lead to the formation of social groups; protected roosts, close to main feeding sites were limited; possible social attraction; benefits from conspecifics such as imitation of feeding behaviour or the locating of food sources; and protection from predation.

The distribution of the food source may be affecting the size and cohesion of foraging groups of Sanderling and Turnstone. The food of the Turnstone is especially patchy. Wrack beds and rock outcroppings form discrete habitats, separated from one another by considerable distances. Birds are thus forced to use the same areas. The food source of the Sanderling has greater continuity, being available along the entire length of Coatham Sands. Both _Nerine_ and _Bathyporeia_ occur in clumps, which should affect the size of Sanderling groups feeding on them. Aggression and interference amongst conspecifics, the size of the clumps of prey, the threat of predation and the behavioural effect of increased numbers of predators on the prey, could help establish the foraging group size of Sanderling.

Silliman et. al. (1977) found that increased flock size resulted in increased aggression for Sanderling. In another set of observations, Barash (1974) found that solitary Black-Capped Chickadees (_Parus atricapillus_) were more likely to experience aggression from other solitary birds than an individual which was in a flock. He suggested that flocking may result in a degree of social immunity. Social learning has been cited as a main advantage of flocking (Krebs 1972).

Page and Whitacre (1975) showed that single waders were at a greater risk than those feeding as a flock. In their study, the number of Sanderling taken by predators represented 13.5% (18) of the total Sanderling population; furthermore, the likelihood of a wader being preyed upon as a single bird compared with a bird in a flock was 3.2:1. (See Powell 1974 for experimental data on predator detection in Starlings.) Lazarus (1972) states that feeding dispersion results from two main pressures, predation (feeding dispersion should minimize this) and feeding efficiency (feeding dispersion should maximize this). Predation need not be common to make flock feeding advantageous (Buskirk 1976). Stinson (1980) suggested that predation was the key to the distribution of waders on a "uniform" stretch of beach.

Sanderling rely on several foraging techniques, both tactile and visual. An individual might benefit from the feeding information gained from conspecifics (location of the prey clumps). Spacing should not be so reduced that significant interference of foraging occurs. Group size, acting in response to prey availability, may help to determine the numbers feeding in a particular area on any given day. Over an entire season, this may have a major effect on the overall distribution of Sanderling on the south and north sides of the estuary.

Turnstone are mainly surface feeders, using visual cues for the location of their prey items. Their feeding areas are available for relatively long time periods (hours vs. seconds or minutes as is the case with Sanderling). From observations on Turnstone in winter, it appears that, like the situation for breeding Turnstone (see Appendix 5.6), birds gain in potential feeding time, by a reduction in wariness, when feeding near conspecifics. Despite this attraction for conspecifics, Turnstone often try to maintain a larger feeding space than the concentration of birds would allow, which often leads to prolonged aggressive encounters. This aggression appears to have the effect of dispersing individuals. It is still unclear what determines whether a bird will stop at a given estuary. The effects I have listed will help to determine the birds' distribution once they have arrived. These effects may have even greater long term results (e.g., juveniles may not successfully compete in an area).

For these two social species, the determinants and outcomes of sociality can best be understood by observing movement patterns and interactions with conspecifics. Perhaps the major outcome of sociality is the resultant distribution along their feeding habitats and within the estuary as a whole. It must be remembered that the main causes of sociality are the distribution of the food sources and possible predation.

Appendix 2.1

Invertebrate densities along the five sampling transects (Fig.2.1) for the eight main sampling days.

All numbers are in individuals/m^2. All distances refer to the number of metres below the mean HWM. When two samples were taken at one station on any one day, densities were averaged.

N - *Nerine*
B - *Bathyporeia*
E - *Eurydice*

NOVEMBER 1977

Transect 1

	20m	30m	40m	50m	60m	70m	80m	90m	100m	130m	160m	190m
N	640	1728	992	1856	384	128	64	96	128	64	0	0
B	64	160	64	32	32	32	0	0	0	32	0	0
E	0	0	0	32	32	0	32	32	0	64	0	0

Transect 2

	20m	30m	40m	50m	60m	70m	80m	90m	100m	130m	160m	190m
N	1728	2048	992	1024	1600	544	384	128	32	32	128	64
B	0	224	96	96	128	64	256	896	64	352	32	192
E	0	0	256	128	64	64	0	32	32	32	0	0

Transect 3

	20m	30m	40m	50m	60m	70m	80m	90m	100m	130m	160m	190m
N	672	1632	2496	2784	1184	96	32	0	96	0	0	32
B	32	288	256	160	128	64	128	128	64	32	96	0
E	320	352	992	256	32	96	0	0	0	32	0	0

Transect 4

NOVEMBER 1977

	20m	30m	40m	50m	60m	70m	80m	90m	100m	130m	160m	190m
N	672	1952	1248	352	1088	608	832	480	192	160	32	32
B	96	608	384	352	192	192	32	128	64	32	0	0
E	288	1120	416	128	128	512	32	64	32	0	0	0

Transect 5

	20m	30m	40m	50m	60m	70m	80m	90m	100m	130m	160m	190
N	0	32	0	32	416	352	384	768	928	288	352	64
B	128	480	864	4096	5152	2784	1248	256	256	608	928	1728
E	0	0	0	0	0	32	128	96	1216	1056	864	192

JANUARY 1978

Transect 2

	20m	30m	40m	50m	60m	70m	80m	90m	100m	130m		
N	128	128	384	5248	5760	3456	2304	2304	256	256		
B	0	384	0	0	0	128	0	128	256	128		
E	0	0	0	0	0	256	0	256	896	0		

Transect 3

	20m	30m	40m	50m	60m	70m	80m	90m	100m	130m		
N	0	0	1024	512	768	3328	384	1920	0	128		
B	0	0	512	0	0	768	0	512	128	128		
E	0	0	0	0	0	0	128	256	384	0		

JANUARY 1978

Transect 4

	20m	30m	40m	50m	60m	70m	80m	90m	100m	130m		
N	0	0	128	512	1536	5888	768	1152	384	768		
B	0	128	128	0	0	384	1280	256	128	0		
E	0	0	0	0	0	256	2432	768	640	0		

Transect 5

	20m	30m	40m	50m	60m	70m	80m	90m	100m	130m	160m	190m
N	0	0	0	0	0	128	768	256	384	1152	1152	896
B	0	0	0	0	896	128	128	4096	384	2688	128	128
E	0	0	0	0	0	0	0	0	0	128	256	128

FEBRUARY 1978

Transect 1

	20m	30m	40m	50m	60m	70m	80m	90m	100m	130m	160m	
N	384	0	640	1664	2112	1792	384	512	768	64	320	
B	0	0	0	0	896	64	0	0	64	64	0	
E	0	0	0	0	128	0	0	64	0	0	0	

Transect 2

	20m	30m	40m	50m	60m	70m	80m	90m	100m	130m	160m	190m
N	0	0	1408	3392	1728	960	2752	704	448	64	256	0
B	0	128	256	320	0	640	192	128	64	128	448	64
E	0	0	0	0	0	320	64	0	384	0	0	0

Transect 3

	20m	30m	40m	50m	60m	70m	80m	90m	100m	130m	160m	190m
N	0	1024	2624	2880	2816	704	1024	512	448	192	0	320
B	0	0	256	0	0	64	0	192	0	320	256	192
E	0	0	64	64	128	320	128	448	64	0	0	0

FEBRUARY 1978

Transect 4

	20m	30m	40m	50m	60m	70m	80m	90m	100m	130m	160m	190m
N	0	0	0	576	1472	3904	256	704	1088	64	64	192
B	0	0	64	576	192	256	512	320	0	0	128	0
E	0	0	0	0	64	128	1728	576	0	0	64	0

Transect 5

	20m	30m	40m	50m	60m	70m	80m	90m	100m	130m	160m	190m
N	0	0	0	0	64	64	896	832	1216	832	832	128
B	0	0	256	320	448	1408	1472	1600	2816	448	64	0
E	0	0	0	64	0	64	512	128	3840	2560	1216	320

MARCH 1978

Transect 1

		30m	40m	50m	60m	70m	80m	90m	100m	130m	160m	190m
N		1024	1152	1856	512	448	704	1216	320	384	0	0
B		64	0	0	0	64	256	0	0	0	0	0
E		64	64	64	0	0	0	0	0	0	0	0

Transect 2

		30m	40m	50m	60m	70m	80m	90m	100m	130m	160m	190m
N		192	2240	8640	2752	1344	2432	1088	192	64	64	0
B		320	320	0	192	128	0	0	64	512	256	0
E		0	0	64	64	64	128	0	0	128	0	0

Transect 3

		30m	40m	50m	60m	70m	80m	90m	100m	130m	160m	190m
N		1920	320	1600	1664	1472	128	512	448	0	0	128
B		0	64	0	0	0	192	0	192	0	128	64
E		64	128	256	0	0	448	0	128	0	0	0

MARCH 1978

Transect 4

	30m	40m	50m	60m	70m	80m	90m	100m	130m	160m	190m
N	0	0	128	3520	3904	2304	576	1216	192	64	128
B	576	448	256	64	0	128	128	64	64	0	64
E	64	64	384	1472	64	640	256	0	64	0	0

Transect 5

	30m	40m	50m	60m	70m	80m	90m	100m	130m	160m	190m
N	0	64	0	64	896	832	448	832	0	192	448
B	320	704	4544	1536	448	448	1728	704	128	128	0
E	0	0	0	0	64	704	2624	704	512	128	64

AUGUST 1978

Transect 1

	20m	30m	40m	50m	60m	70m	80m	90m	100m	130m	160m	190m
N	0	768	128	640	1280	128	0	2176	0	640	384	0
B	0	0	128	0	0	0	0	128	0	0	0	0
E	0	0	0	0	0	0	0	0	0	0	0	0

Transect 2

	20m	30m	40m	50m	60m	70m	80m	90m	100m	130m	160m	190m
N	0	1536	4480	1152	128	0	256	0	0	1408	0	0
B	0	0	0	0	0	0	0	0	0	0	1024	0
E	0	0	0	0	0	256	128	128	128	0	0	0

Transect 3

	20m	30m	40m	50m	60m	70m	80m	90m	100m	130m	160m	190m
N	0	2432	1024	1408	512	256	1280	256	0	384	0	0
B	128	0	256	0	0	0	0	0	0	0	512	0
E	0	0	128	128	0	1280	0	0	256	640	128	0

AUGUST 1978

Transect 4

	20m	30m	40m	50m	60m	70m	80m	90m	100m	130m	160m	190m
N	0	0	1024	0	1408	2688	1152	256	2048	1280	128	0
B	0	1280	0	0	0	0	0	0	0	0	0	0
E	0	128	128	128	0	640	128	0	128	128	128	128

Transect 5

	20m	30m	40m	50m	60m	70m	80m	90m	100m	130m	160m	190m
N	0	768	640	128	384	0	1664	0	1408	640	384	0
B	128	1024	0	256	0	0	0	0	0	0	0	512
E	0	0	128	128	0	128	0	384	256	640	0	256

NOVEMBER 1978

Transect 1

	20m	30m	40m	50m	60m	70m	80m	90m	100m		
N	512	896	1536	0	256	0	0	256	0		
B	0	0	0	0	0	128	0	0	128		
E	128	0	0	0	128	0	0	0	0		

Transect 2

	20m	30m	40m	50m	60m	70m	80m	90m	100m	130m	
N	2816	896	1664	640	896	256	128	128	0	128	
B	128	256	0	128	128	0	512	384	128	1280	
E	512	128	256	128	0	0	0	0	0	0	

Transect 3

	20m	30m	40m	50m	60m	70m	80m	90m	100m	130m	
N	1408	896	1792	2944	256	128	256	0	128	0	
B	256	256	0	256	1024	0	1408	1280	1280	768	
E	512	128	256	0	128	0	0	0	0	0	

NOVEMBER 1978

Transect 4

	20m	30m	40m	50m	60m	70m	80m	90m	100m	130m	160m	
N	1280	1024	512	640	896	256	512	512	128	256	0	
B	384	128	0	128	256	256	128	256	1024	512	0	
E	0	384	768	0	0	256	384	0	128	0	0	

Transect 5

	20m	30m	40m	50m	60m	70m	80m	90m	100m	130m	160m	
N	640	0	1408	640	896	1792	1408	128	0	1664	512	
B	3072	256	640	256	0	0	256	256	0	0	0	
E	128	0	128	0	512	128	512	2432	1536	384	0	

DECEMBER 1978

Transect 1

	20m	30m	40m	50m	60m	70m	80m	90m	100m	130m		
N	896	2432	384	128	128	256	0	128	0	768		
B	0	128	0	128	128	0	384	0	128	0		
E	256	0	256	128	256	0	0	0	0	0		

Transect 2

	20m	30m	40m	50m	60m	70m	80m	90m	100m	130m		
N	1920	4864	1280	4096	1664	2048	0	128	128	0		
B	0	0	256	0	128	0	0	512	0	128		
E	0	0	128	0	128	384	128	0	0	128		

Transect 3

	20m	30m	40m	50m	60m	70m	80m	90m	100m	130m	160m	190m
N	1408	1472	2752	512	448	448	128	192	128	192	64	64
B	64	64	0	64	128	64	512	64	0	384	64	64
E	0	0	0	256	128	64	128	128	0	0	0	0

DECEMBER 1978

Transect 4

	20m	30m	40m	50m	60m	70m	80m	90m	100m	130m		
N	0	0	384	1792	2176	1152	1408	128	128	0		
B	128	128	512	1536	640	0	384	0	128	128		
E	0	0	256	128	128	0	256	128	256	128		

Transect 5

	20m	30m	40m	50m	60m	70m	80m	90m	100m	130m	160m	190m
N	0	0	128	64	640	960	512	1088	2176	576	256	0
B	0	448	256	896	576	960	256	576	192	0	0	0
E	0	0	192	64	0	768	128	2240	192	0	64	128

FEBRUARY 1979

Transect 1

	20m	30m	40m	50m	60m	70m	80m	90m	100m	130m		
N	0	128	1024	1536	1024	512	512	384	384	0		
B	0	256	128	128	0	256	384	128	0	128		
E	0	0	0	0	0	0	0	0	0	0		

Transect 2

	20m	30m	40m	50m	60m	70m	80m	90m	100m	130m		
N	128	0	3072	3328	1536	2944	512	0	256	128		
B	0	512	0	128	0	128	0	256	128	384		
E	0	0	0	256	0	0	256	128	256	0		

Transect 3

	20m	30m	40m	50m	60m	70m	80m	90m	100m	130m		
N	896	128	2432	512	768	128	0	256	896	0		
B	0	0	128	128	0	128	128	0	384	0		
E	128	0	0	256	0	0	0	0	0	0		

FEBRUARY 1979

Transect 4

	20m	30m	40m	50m	60m	70m	80m	90m	100m	130m		
N	0	0	512	1792	1280	1408	768	1280	2048	0		
B	128	384	0	0	128	640	256	0	0	0		
E	0	0	0	0	0	1792	0	384	128	0		

Transect 5

	20m	30m	40m	50m	60m	70m	80m	90m	100m	130m	160m	190m
N	0	0	128	64	64	896	320	2432	1024	0	896	128
B	64	128	0	960	384	512	384	448	256	1152	0	
E	0	0	0	0	0	64	0	512	256	0	0	128

Appendix 2.2

Densities of Nerine at transects 1 to 5, Coatham Sands, for the eight main sampling days.

November 1977

Transect	$\bar{x}$	S.E.
1	506.7	202.1
2	725.3	221.6
3	752.0	1311.4
4	637.3	172.7
5	301.3	91.8

January 1978

Transect	$\bar{x}$	S.E.
1	not sampled	
2	2022.4	726.0
3	806.4	357.0
4	1113.6	583.4
5	394.7	141.1

February 1978

Transect	$\bar{x}$	S.E.
1	785.5	230.5
2	976.0	343.8
3	1045.3	330.2
4	693.3	337.3
5	405.3	141.2

March 1978

Transect	$\bar{x}$	S.E.
1	692	179.8
2	1728.0	796.0
3	744.7	238.3
4	1093.8	140.3
5	343.3	115.9

August 1979

Transect	$\bar{x}$	S.E.
1	512.0	199.5
2	746.7	397.6
3	629.3	229.5
4	832.0	275.6
5	501.3	169.0

November 1978

Transect	$\bar{x}$	S.E.
1	384.0	186.6
2	755.2	296.6
3	780.8	328.3
4	546.9	124.2
5	826.2	208.2

December 1978

Transect	$\bar{x}$	S.E.
1	512.0	247.2
2	1612.8	574.7
3	650.7	247.7
4	716.8	278.9
5	533.3	193.2

February 1979

Transect	$\bar{x}$	S.E.
1	550.4	167.2
2	1190.4	467.9
3	601.6	244.8
4	908.8	254.8
5	496.0	227.9

Appendix 2.3a

Alongshore sampling for April 10, 1978

One sample was taken every 20 m from transect 3 to 150 m past transect 5 at 70 m below the HWM. Corer used was the same as that used for the main sampling days.

Appendix 2.3a

Site number	Densities of prey species in numbers/m^2		
	Nerine	Bathyporeia	Eurydice
1	640	0	384
2	384	0	128
3	4992	0	384
4	128	0	128
5	1152	0	0
6	1664	128	128
7	768	0	0
8	4224	0	128
9	896	0	256
10	1920	0	128
11	3456	0	0
12	640	0	128
13	2048	0	128
14	2048	0	0
15	4480	0	0
16	1408	0	128
17	2432	128	256
18	2176	0	0
19	1792	0	0
20	1664	0	128
21	1536	128	256
22	2816	0	0
23	2432	128	0
24	4864	0	256
25	4864	0	256
26	2688	128	384
27	4480	0	0
28	1664	0	256
29	2816	0	128
30	3712	0	256

Site number	Nerine	Bathyporeia	Eurydice
31	3584	0	768
32	2176	0	9088
33	1664	128	5504
34	4736	128	640
35	1792	384	384
36	2048	256	0
37	1920	2048	1664
38	640	256	128
39	1664	1920	2688
40	896	512	5504
41	384	256	0
42	2048	128	128
43	2432	128	128
44	1664	512	1152
45	512	896	0
46	512	128	384
47	256	384	0
48	640	1024	2048
49	384	128	128
50	1280	640	384
51	0	384	0
52	2304	0	0
53	2688	0	384
54	4096	512	2816
55	4096	128	1792
56	2048	0	640
57	3200	128	384
58	2816	0	1280
59	2560	0	896
60	4864	128	1280
61	1920	512	1152
62	2816	128	128
63	4224	512	896
64	1280	1408	256

Site number	Nerine	Bathyporeia	Eurydice
65	1920	2944	5888
66	1664	2048	2688
67	2560	1280	2048
68	384	896	896
69	896	768	2048
70	2432	384	640
71	0	256	640
72	512	896	1664
73	1280	512	768
74	0	128	256
75	0	0	0

Appendix 2.3b

Alongshore sampling for May 11, 1978.

One sample was taken every 20 m from transect 3 to 150 m past transect 5.

(A) -50 m below the HWM.

(B) -70 m below the HWM.

(C) -90 m below the HWM.

Appendix 2.3b

(A)	Densities of prey species in numbers/m^2		
Site number	Nerine	Bathyporeia	Eurydice
1	1792	128	0
2	1024	0	256
3	2944	0	0
4	896	0	0
5	1792	0	128
6	3200	128	128
7	2560	128	256
8	1792	0	256
9	1408	128	0
10	128	128	512
11	2304	0	128
12	896	0	128
13	1536	128	384
14	1152	0	0
15	640	128	512
16	1920	0	256
17	1152	0	128
18	384	0	256
19	1792	128	0
20	1280	0	1408
21	1536	128	1152
22	1664	256	1280
23	2304	0	128
24	1024	0	640
25	1792	128	128
26	1792	0	256
27	384	0	0
28	2176	128	256
29	640	0	256
30	512	0	768

(A)	Densities of prey species in numbers/m^2		
Site number	Nerine	Bathyporeia	Eurydice
31	0	0	256
32	2688	256	128
33	256	128	512
34	2304	256	0
35	256	1152	256
36	2432	128	768
37	0	640	0
38	0	0	0
39	0	384	0
40	2048	384	0
41	384	1408	1664
42	3712	256	0
43	0	128	0
44	896	384	0
45	128	0	0
46	1152	512	0
47	768	512	256
48	3072	128	0
49	768	128	256
50	640	128	1280
51	2560	0	640
52	2560	256	384
53	3712	0	256
54	4352	256	128
55	5120	0	0
56	3968	128	0
57	2176	0	128
58	3584	256	128
59	896	640	0
60	1536	512	128
61	384	5632	0
62	0	1664	0
63	1408	2304	0

(A) Site number	Densities of prey species in numbers $/m^2$ Nerine	 Bathyporeia	 Eurydice
64	128	2432	0
65	896	768	0
66	512	1536	0
67	0	640	0
68	256	1024	0
69	128	0	0
70	256	0	0
71	256	0	0
72	128	0	0
73	0	0	0
74	0	0	0
75	0	0	0

(B)

Site number	Densities of prey species in numbers/m^2		
	Nerine	Bathyporeia	Eurydice
1	256	0	0
2	256	128	256
3	1024	0	0
4	128	256	384
5	128	0	512
6	384	0	0
7	1152	0	0
8	512	128	512
9	640	128	384
10	768	0	512
11	384	0	256
12	128	0	0
13	768	0	384
14	384	0	128
15	0	0	128
16	128	384	128
17	1152	0	0
18	128	0	0
19	256	0	0
20	128	0	0
21	384	128	0
22	128	0	128
23	512	128	128
24	384	384	0
25	896	0	0
26	2560	0	128
27	1408	128	1024
28	1024	0	0
29	512	0	0
30	512	0	0
31	896	0	0
32	512	0	128

(B)	Densities of prey species in numbers/m^2		
Site number	Nerine	Bathyporeia	Eurydice
33	1152	0	0
34	1920	0	1408
35	384	512	2432
36	896	0	512
37	128	128	256
38	2560	128	256
39	1664	128	512
40	1280	0	128
41	2304	0	128
42	1152	0	256
43	128	0	640
44	256	0	384
45	256	256	128
46	1280	384	256
47	1792	0	256
48	1664	128	128
49	256	128	128
50	1024	0	384
51	640	0	128
52	1408	0	256
53	896	0	512
54	2304	128	640
55	768	0	384
56	1280	128	256
57	2432	128	256
58	1664	128	768
59	2816	128	384
60	1792	0	1280
61	2304	128	1152
62	1408	256	0
63	1664	256	128
64	1408	896	256
65	3840	512	0

(B) Site number	Densities of prey species in numbers/m^2 Nerine	 Bathyporeia	 Eurydice
66	1152	128	256
67	1408	0	128
68	2304	128	0
69	896	0	0
70	384	1536	0
71	768	384	0
72	256	384	0
73	128	0	0
74	0	0	0
75	0	0	0

(C)	Densities of prey species in numbers/m^2		
Site number	Nerine	Bathyporeia	Eurydice
1	0	0	128
2	0	0	0
3	0	0	0
4	128	0	0
5	256	0	384
6	0	0	0
7	256	256	0
8	0	0	0
9	0	0	128
10	0	0	128
11	512	0	128
12	0	0	128
13	0	0	0
14	0	0	0
15	0	0	128
16	256	0	0
17	128	128	128
18	256	0	0
19	1536	0	128
20	384	0	0
21	128	384	0
22	128	0	0
23	0	0	384
24	128	0	0
25	0	0	0
26	0	0	0
27	0	0	0
28	0	0	0
29	256	0	128
30	128	0	0
31	128	128	0
32	640	0	128
33	512	0	128

(c)

Densities of prey species in numbers/m^2

Site number	Nerine	Bathyporeia	Eurydice
34	896	0	0
35	384	0	0
36	384	0	512
37	0	128	640
38	896	128	1152
39	10280	384	512
40	1024	128	640
41	1152	0	0
42	2048	0	0
43	1280	0	1664
44	512	0	2432
45	768	0	2340
46	1536	0	2048
47	2944	128	1920
48	1408	0	256
49	512	128	1408
50	1664	0	256
51	128	1024	0
52	1152	128	1024
53	384	384	384
54	512	384	512
55	0	512	640
56	256	384	896
57	384	384	1280
58	1920	0	256
59	1536	128	384
60	1280	0	256
61	1024	128	128
62	128	0	0
63	768	0	128
64	1152	512	384
65	128	256	512
66	1408	512	1152

(C) Site number	Densities of prey species in numbers/m^2 Nerine	 Bathyporeia	 Eurydice
67	512	256	896
68	256	2304	640
69	1024	384	896
70	1280	896	384
71	512	640	384
72	1280	1024	512
73	1024	128	256
74	1152	0	0
75	256	0	0

Appendix 2.4

Sampling results for November 26th 1977. Sampling stations at 50m and 60m below the HWM at transect 5. All results for Bathyporeia. One sample taken, (diameter of corer, 3.7 cm), in the centre of each 10cm x 10cm square. Grid consisted of 80cm sides partitioned into 8 sections, yielding 64 samples. Samples are numbered consecutively with row, eg.

1 8
9 16 etc.

Sample site	50m	60m
1	930	0
2	1860	1860
3	930	2790
4	2790	930
5	930	4650
6	0	9300
7	930	11160
8	0	2790
9	0	1860
10	930	930
11	0	2790
12	5580	0
13	4650	1860
14	2790	10230
15	3720	3720
16	0	10230
17	0	930
18	0	0
19	0	930
20	1860	0
21	1860	19530
22	930	4650
23	1860	12090
24	0	11160
25	4650	10230
26	930	3720
27	930	4650

Sample site	50m	60m
28	2790	2790
29	3720	930
30	1860	2790
31	0	1860
32	3720	8370
33	0	1860
34	930	1860
35	0	1860
36	0	930
37	0	930
38	0	10230
39	0	0
40	930	12090
41	0	4650
42	930	2790
43	930	2790
44	2790	5580
45	4650	930
46	4650	4650
47	1860	7440
48	2790	13020
49	1860	2790
50	0	6510
51	0	3720
52	3720	930
53	930	930
54	0	4650
55	1860	2790
56	4650	8370
57	2790	6510
58	1860	3720
59	0	930
60	0	4650
61	930	930
62	930	930
63	0	3720
64	930	7440

Appendix 2.5

Sampling results for December 3rd 1977. Sampling was carried out at 50m below the HWM on transect 3. All results for Nerine. Grid used was identical to that used on November 26th 1977 (Appendix 2.4) Each sample was divided into 2 layers, (diameter of corer was 2.25cm, each layer was 6cm deep). 64 samples were taken, consecutively with row, as in Appendix 2.4. All results in numbers/m^2.

Sample site	Upper layer	layer	Total
1	0	629	629
2	1258	1258	2516
3	0	1258	1258
4	0	0	0
5	0	1887	1887
6	0	0	0
7	0	3774	3774
8	0	629	629
9	0	629	629
10	3145	0	3145
11	0	1258	1258
12	0	1258	1258
13	0	1258	1258
14	629	2516	3145
15	0	1887	1887
16	1258	0	1258
17	0	1258	1258
18	0	629	629
19	0	0	0
20	629	1258	1887
21	0	1887	1887
22	0	2516	2516
23	629	629	1258
24	0	1258	1258
25	629	629	1258
26	1258	2516	3774

Sample site	Upper layer	Lower layer	Total
27	1887	3774	5661
28	0	1887	1887
29	629	1887	2516
30	3145	1258	4403
31	0	1258	1258
32	0	3145	3145
33	1258	1258	2516
34	0	1258	1258
35	0	1258	1258
36	0	629	629
37	629	629	1258
38	0	5661	5661
39	0	1258	1258
40	0	629	629
41	1887	1887	3774
42	0	629	629
43	1887	629	2516
44	629	2516	3145
45	1258	1258	2516
46	0	3145	3145
47	629	1258	1887
48	0	3145	3145
49	0	629	629
50	1258	0	1258
51	1258	629	1887
52	629	1258	1887
53	1258	1258	2516
54	1258	1887	3145
55	629	3774	4403
56	0	1258	1258
57	629	3145	3774
58	0	629	629
59	0	0	0
60	0	3774	3774
61	0	1887	1887
62	0	1258	1258
63	1258	1258	2516
64	0	3774	3774

Appendix 2.6

Sampling results for March 12th 1978. Sampling was carried out at 50m below the HWM on transect 3. The grid was as follows:

3 6...60
2 5...59
1 4...58

with each sampling site 1 metre from adjacent sites. As with samples taken on December 3rd (Appendix 2.5) each was divided into 2 layers, (corer same as that used on December 3rd). All results are for *Nerine* and are expressed as numbers/m^2.

Sample site	Upper layer	Lower layer	Total
1	0	629	629
2	0	0	0
3	0	0	0
4	0	1258	1258
5	0	2516	2516
6	0	0	0
7	0	0	0
8	0	629	629
9	0	1258	1258
10	0	629	629
11	0	0	0
12	629	1887	2516
13	0	0	0
14	0	2516	2516
15	0	5032	5032
16	0	0	0
17	0	0	0
18	0	0	0
19	0	0	0
20	0	1887	1887
21	0	1258	1258
22	0	629	629
23	0	0	0
24	629	3145	3774
25	0	1887	1887

Sample site	Upper layer	Lower layer	Total
26	0	0	0
27	0	629	629
28	629	1258	1887
29	0	1887	1887
30	0	2516	2516
31	0	1258	1258
32	0	0	0
33	1258	1258	2516
34	0	0	0
35	0	1258	1258
36	0	3145	3145
37	0	2516	2516
38	0	1887	1887
39	0	0	0
40	629	1887	2516
41	629	0	629
42	0	2516	2516
43	0	2516	2516
44	0	629	629
45	629	6919	7548
46	0	1258	1258
47	1258	629	1887
48	629	629	1258
49	0	1887	1887
50	0	629	629
51	629	1887	2516
52	629	1887	2516
53	629	1887	2516
54	0	0	0
55	0	1887	1887
56	0	2516	2516
57	0	1258	1258
58	0	629	629
59	0	1258	1258
60	0	1258	1258

Appendix 2.7

Sampling results for March 12th 1978 on transect 5, 90 metres below the HWM. The grid was as follows:

3 6...60

2 5...59

1 4...58

with each sampling site 1 metre from adjacent sites, (diameter of corer being 6.2cm). Results given in numbers/m^2.

Site number	Nerine	Bathyporeia	Eurydice
1	0	2317	662
2	662	2317	1655
3	1655	662	2979
4	662	662	662
5	0	1986	993
6	331	993	1655
7	0	5296	1324
8	0	993	8937
9	662	2648	3310
10	331	993	6951
11	331	3972	3310
12	0	1324	1986
13	0	1655	662
14	0	1655	3641
15	993	993	993
16	662	993	1655
17	0	2317	2648
18	331	1324	4303
19	0	3641	1986
20	0	1655	1324
21	0	2975	5296
22	0	662	993
23	0	1986	1986
24	993	1986	6620

Site number	Nerine	Bathyporeia	Eurydice
25	331	331	1324
26	662	331	662
27	331	2317	1324
28	0	993	1324
29	331	1324	1324
30	0	662	331
31	331	1655	1986
32	0	1655	662
33	331	331	1655
34	993	3310	1324
35	993	331	3972
36	0	1986	1655
37	331	1324	993
38	662	1655	3972
39	331	993	1986
40	331	1655	1324
41	2317	3972	5958
42	1324	3641	13240
43	662	993	2317
44	331	2648	1986
45	662	331	662

Appendix 3.1 Movement and survival of Sanderling at Teesmouth

The habitats available to foraging and roosting Sanderling and the invertebrate prey contained in these habitats have now been thoroughly documented. The Sanderling's movements are governed by the tidal cycle, which alters the availability of habitats, and by the densities of prey at the different locations. The precise foraging techniques of Sanderling feeding on Coatham Sands, the allocation of time to the various components of foraging and the birds' search paths and success rates will be discussed, with reference to environmental and social factors, in Chapter 4. One environmental factor was the position of the wave edge, in relation to the foraging individual's time spent running. A possible social factor was interference during feeding, causing potential overlap of area-concentrated search, resulting in the birds moving away from the "group" after a success. The utilization of the north and south sides of the estuary, both by birds spending the entire winter and those using it for only a portion of the non-breeding season (e.g., those Sanderling on passage to the breeding grounds) will now be examined.

Most of the analysis of the north-south distribution of the birds is based on counts. Some of the fluctuation in these counts may have been due to inaccuracies in counting (such as missing a large number of roosting individuals). To insure that these counts represented the situation as closely as possible, great care was taken to include only complete counts, counts relatively free from disturbance, counts undertaken during the times when the rocks were covered and often when birds were about to roost. A single value for any one day was frequently checked by taking two or three counts within one or two hours of one another. This insured that birds were not missed. Although counts were not made from Saltburn to the end of Coatham Sands each time, frequent visits to the beach south of Redcar Rocks were made to insure that birds were not being constantly overlooked.

During the 1978-79 winter, systematic counting of the Sanderling's use of the north side of the estuary was begun. Simultaneous counts of the north and south sides are available for the entire 1978-79 season. Simultaneous counts were necessary in determining the relative importance of the two sides to the Sanderling. Even if one side was heavily preferred, the other side might have helped to ease the pressure of habitat utilization on the preferred side. By 1978, enough colour-marked Sanderling were present to observe the different patterns of area preference in the estuary. Counting continued the same on the south side with Nick Davidson and Simon Fraser counting the north during the time around High Water.

Fig. 1 shows the highest count for each month for Sanderling on the south side for the 1976-77 winter. Figs. 2 and 3 show the number of Sanderling on the south side during the 1977-78 winter. In Fig. 2 the highest monthly counts are presented, while in Fig. 3 all counts, (not just the highest of each month), are presented, with spring, neap and mid-tidal heights indicated. Some of the anomalies, (presence of gulls in 1977-78 and the presence of the large wrack beds in 1976-77), have already been mentioned and clearly stand out. There was heavy use of the area in August which was due, in part, to birds on passage, returning from the breeding grounds, (see Prater & Davies 1978). The large increase during March did not follow the expected trend, based on the 1976-77 figures, but it will become clear that increases could occur in almost any month of the winter. The numbers between autumn 1977 and spring 1978 fluctuated between about 550 and 700 in most months. Fig. 3 has been included to demonstrate the erratic fluctuations that occurred in a single year.

The counts from 1978-79 (simultaneous counts of the north and south sides) are presented in Fig. 4. The total number of Sanderling using the Tees was difficult to determine, as daily fluctuations appeared to be large. Evidence from colour-marked individuals (discussed below) points to both a high degree of feeding site fidelity in certain individuals and mixing

Figure 1

Monthly peak counts of Sanderling for 1976-77.

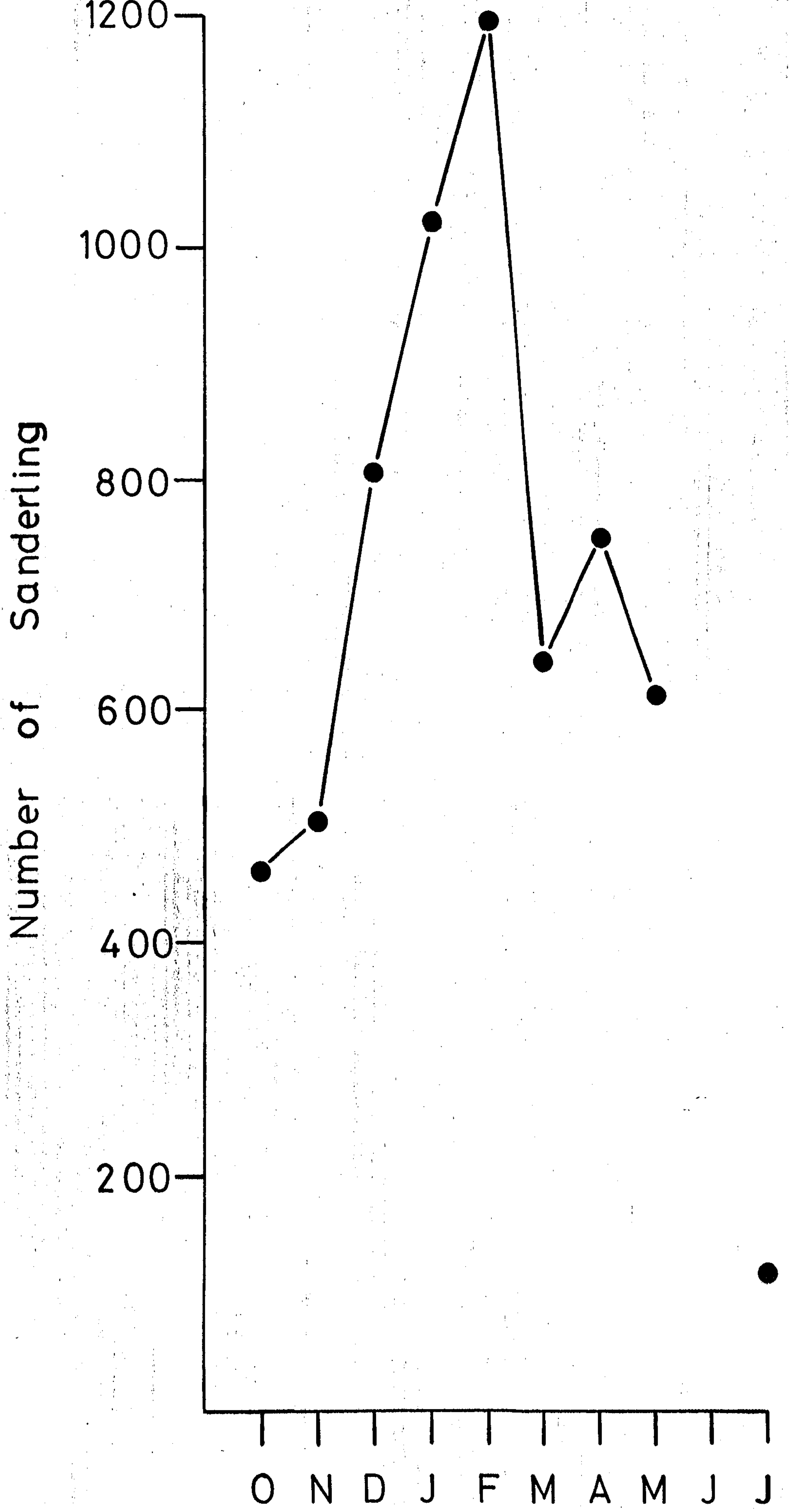

1200
1000
800
600
400
200
Number of Sanderling
O
N
D
J
F
M
A
M
J
J

Figure 2

High Water counts for the south side 1977-78. These counts are the monthly highs, regardless of tidal height, (spring or neap). High Water counts were made one to two hours before the High Water, when most birds were feeding on Coatham Sands.

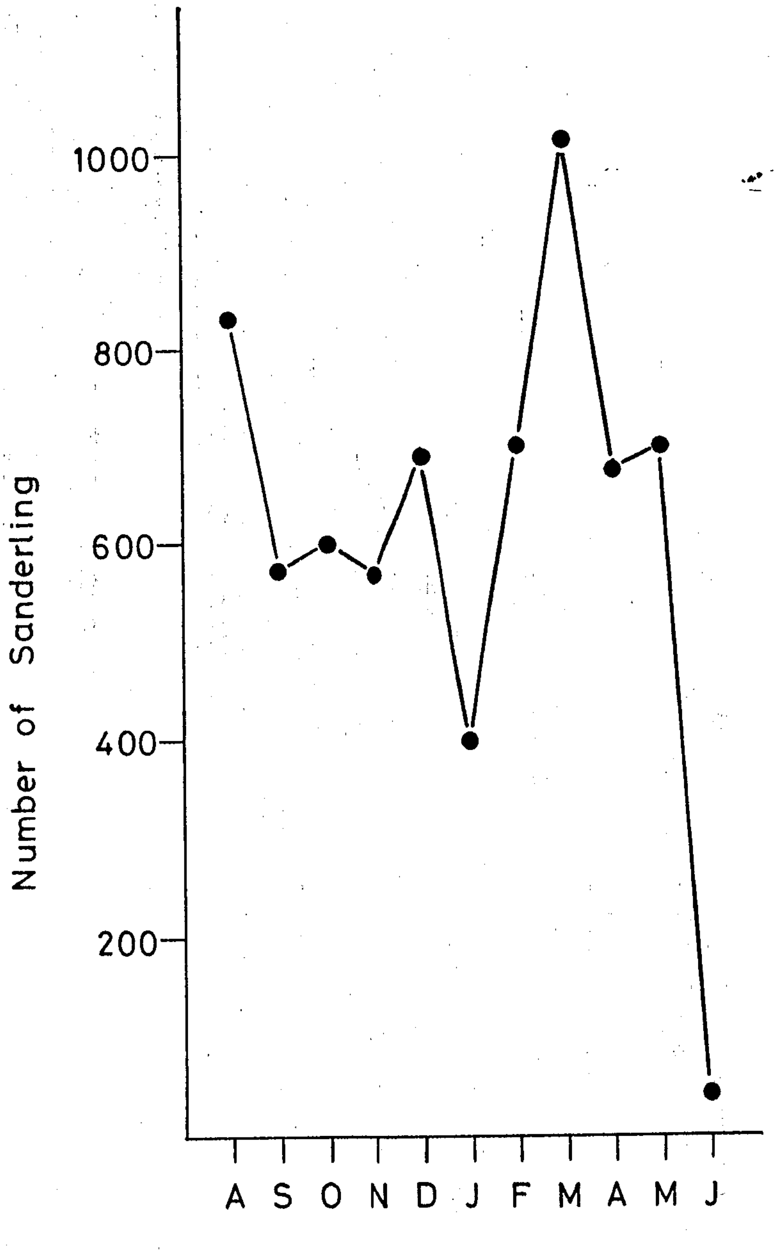

Number of Sanderling
1000
800
600
400
200
A
S
O
N
D
J
F
M
A
M
J

Figure 3

Counts of Sanderling on the south side for 1977-78. (●) spring tides, (■) neap tides, (x) mid-level tides and (⊙) notes the counts during large gull presence.

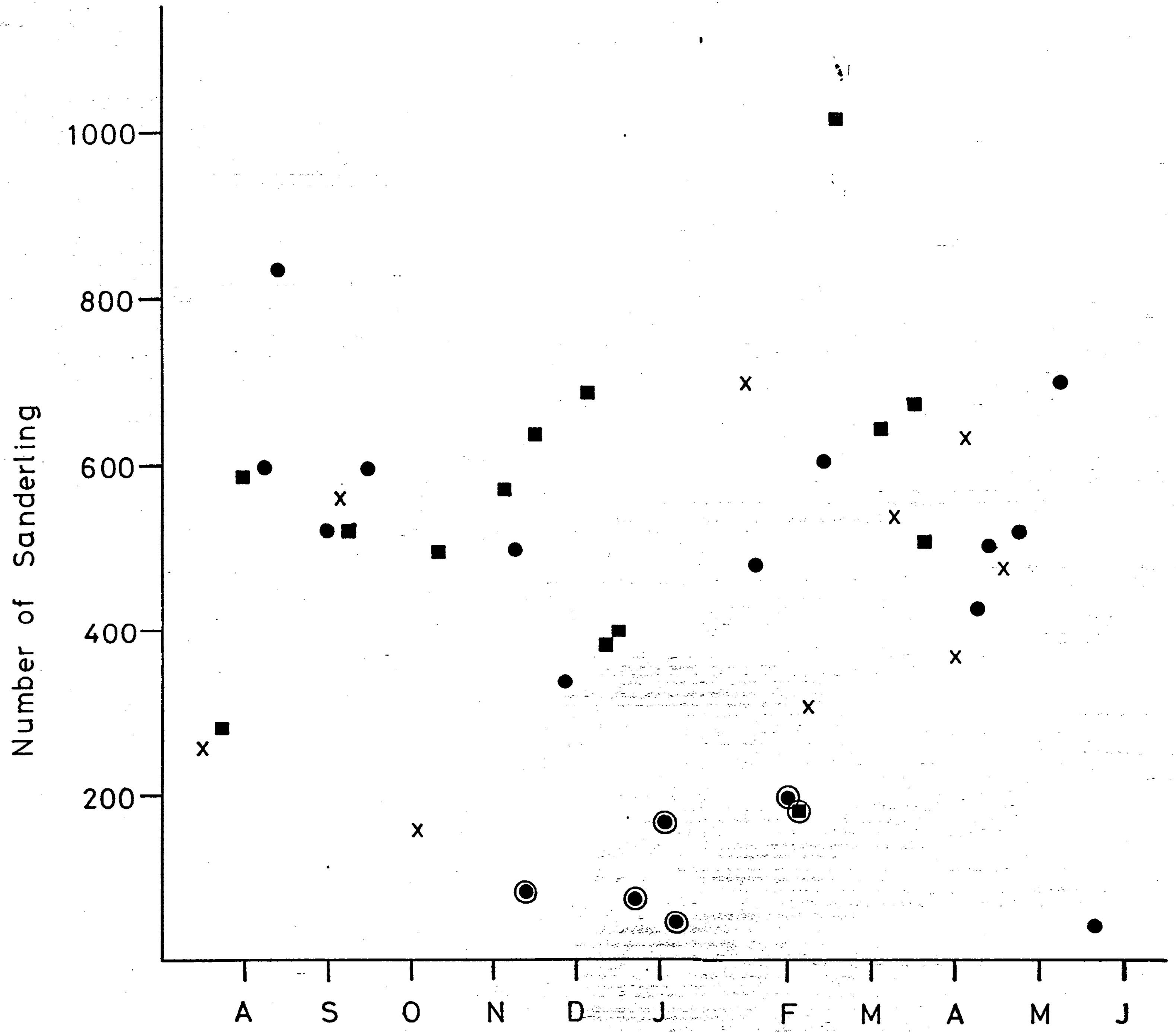
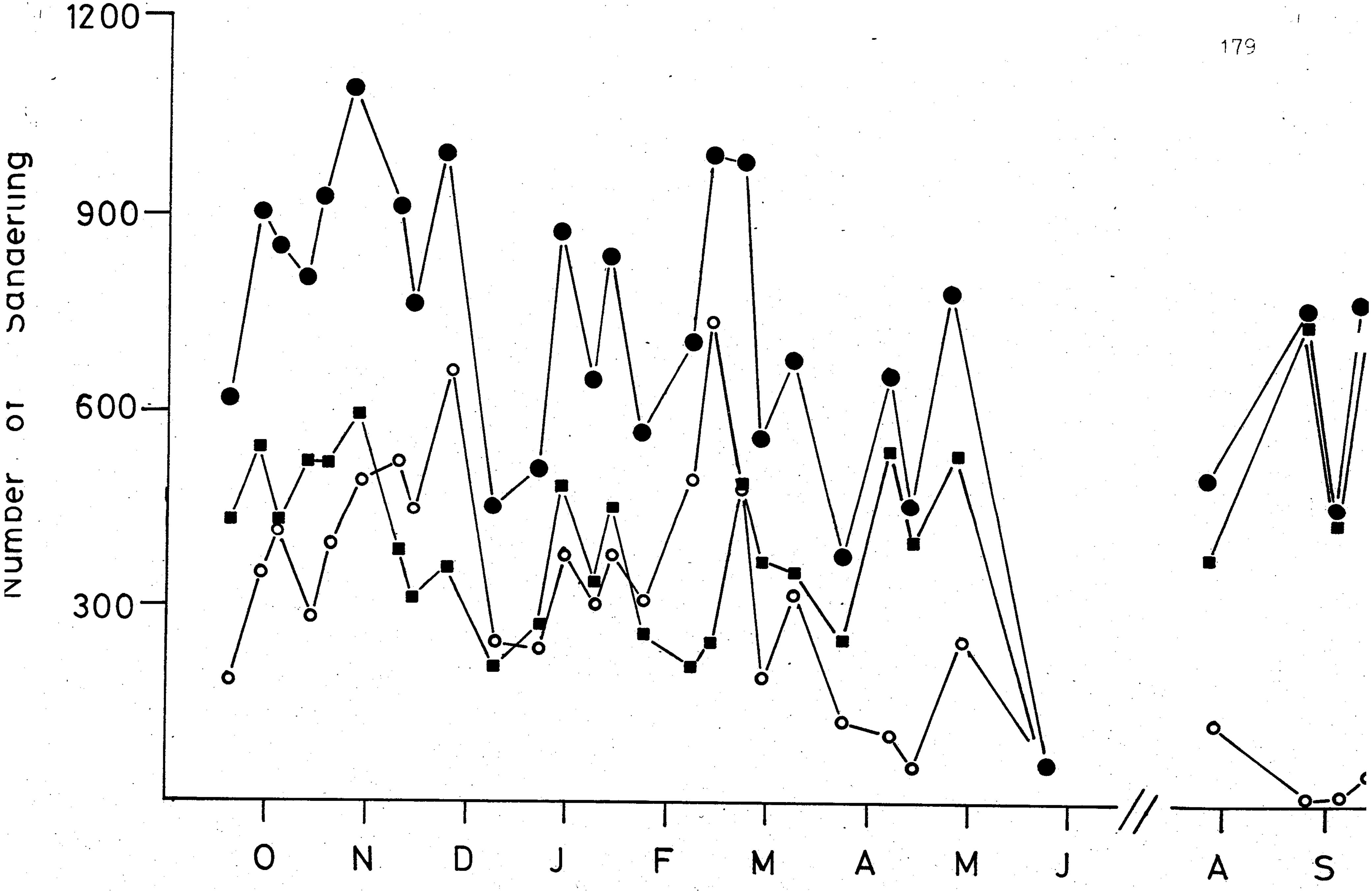

Number of Sanderling
1000
800
600
400
200
A
S
O
N
D
J
F
M
A
M
J

Figure 4

Simultaneous counts for Sanderling, 1978-79. (●) total numbers, (■) Sanderling on the south side and (○) Sanderling on the north side.


Number of Sanderling
1200
900
600
300
O
N
D
J
F
M
A
M
J
A
S

of feeding areas in others. This lessens any idea of a single cohesive Sanderling population. The occurrence of unusual food sources, and the birds' ability to locate them, provides evidence that different segments of the Tees Sanderling are mixing, and that there is the possibility that informatin is being transferred. Just how far north or south along the eastern coast Sanderling utilizing Teesmouth range is not at all clear. Rapid build-up of numbers, (as seen on 15/1 and 21/1, 1977), suggest that not all birds which use the estuary at any one time are necessarily permanent winter residents, (i.e., that they inhabit only Teesmouth during the entire winter). If information regarding food sources was being obtained through exploratory flights or through information transfer at roosting centres (see Ward & Zahavi 1973), then mixing of the Teesmouth Sanderling must have been occurring over considerable distances.

The large fluctuations in numbers mean that trying to ascribe the number of permanent winter residents using the estuary may give a considerable underestimation of its importance in providing suitable habitat for Sanderling. It might be the case that although the Tees could not support the very large population, (shown by the largest of the annual counts), throughout the winter period, its ability to provide suitable habitat at crucial stress periods during the birds' annual cycle might be a more important consideration.

During the 1978-79 winter, lower Bathyporeia densities were reported. This may have affected the capacity of Teesmouth to supply Sanderling with suitable habitats during stressed periods. When one looks at the numbers of birds using the north side and the poor invertebrate availability there, (as determined by Andrew Wood, 2H project), compared to the south side, it seems unlikely that all Sanderling on the estuary could have been where the best, (most profitable), food conditions were. One mechanism for determining the distribution of Sanderling in an area may be the behavioural interactions while foraging. Behavioural interactions may be a direct result of the changing conditions in the invertebrate profitability. This would make the birds responsive to the constraints placed on their foraging potential and affect group size and number. During periods of lowered food sources, crowding could be especially damaging to energy intake.

How do birds, upon their arrival in autumn, or on any particular day, decide whether they will feed on Coatham Sands, south of the estuary, or Seaton Sands, north of the estuary? Fig.s 5 and 6 show the relationship between total numbers of Sanderling in the estuary and numbers in the south and north side

Figure 5

Regression showing the relationship between total Sanderling count on the estuary and numbers on the south side.

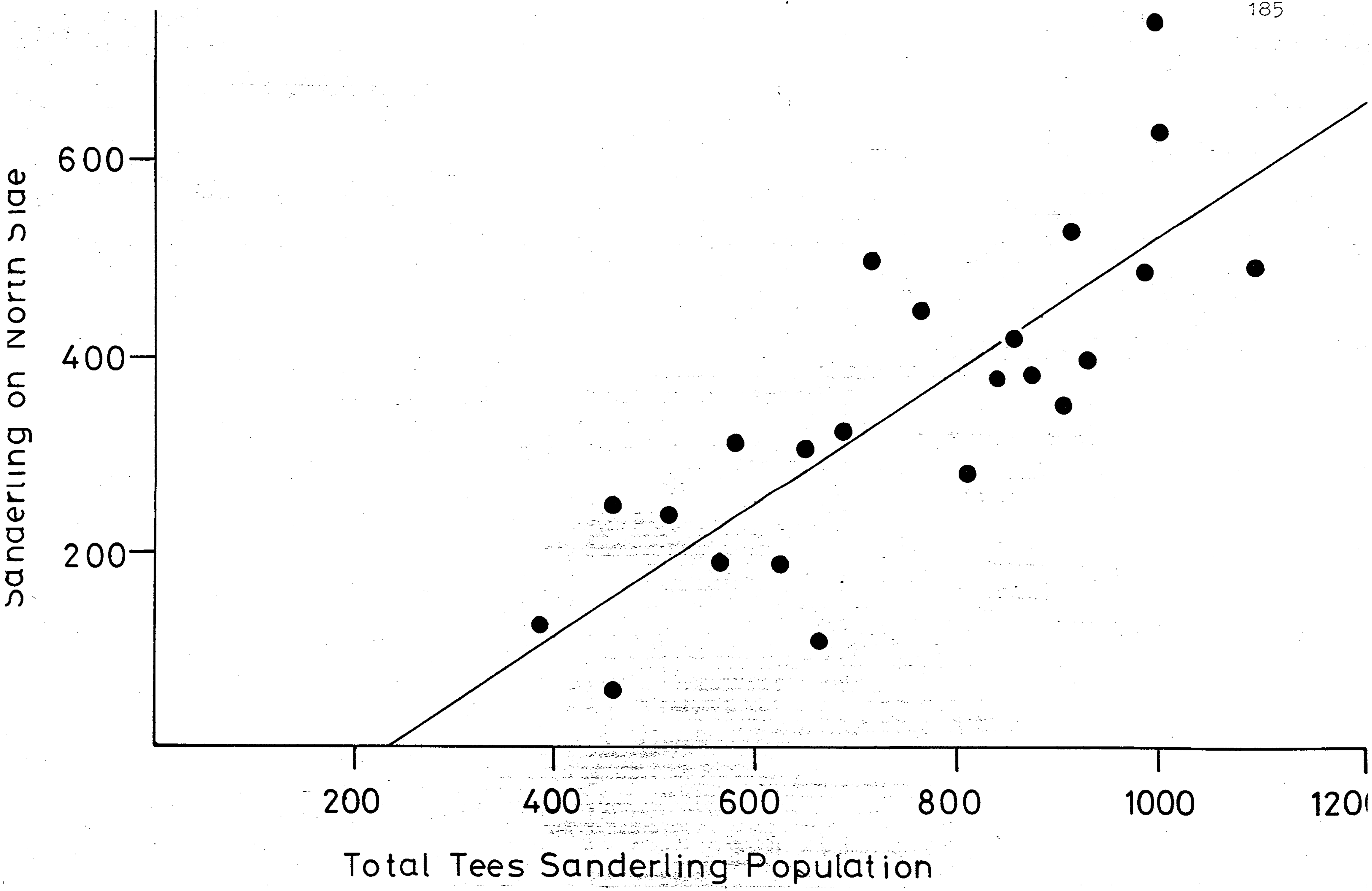
Slope	0.3898	
r	0.55736	
P	<0.01	with 21 degrees of freedom


Sanderling on South Side
600
400
200
200
400
600
800
1000
120
Total Tees Sanderling Population

Figure 6

Regression showing the relationship between total Sanderling counts on the estuary and numbers using the north side.

Slope	0.68226	
r	0.8098	
P	< 0.001	with 21 degrees of freedom


Sanderling on North Side
600
400
200
200
400
600
800
1000
120
Total Tees Sanderling Population

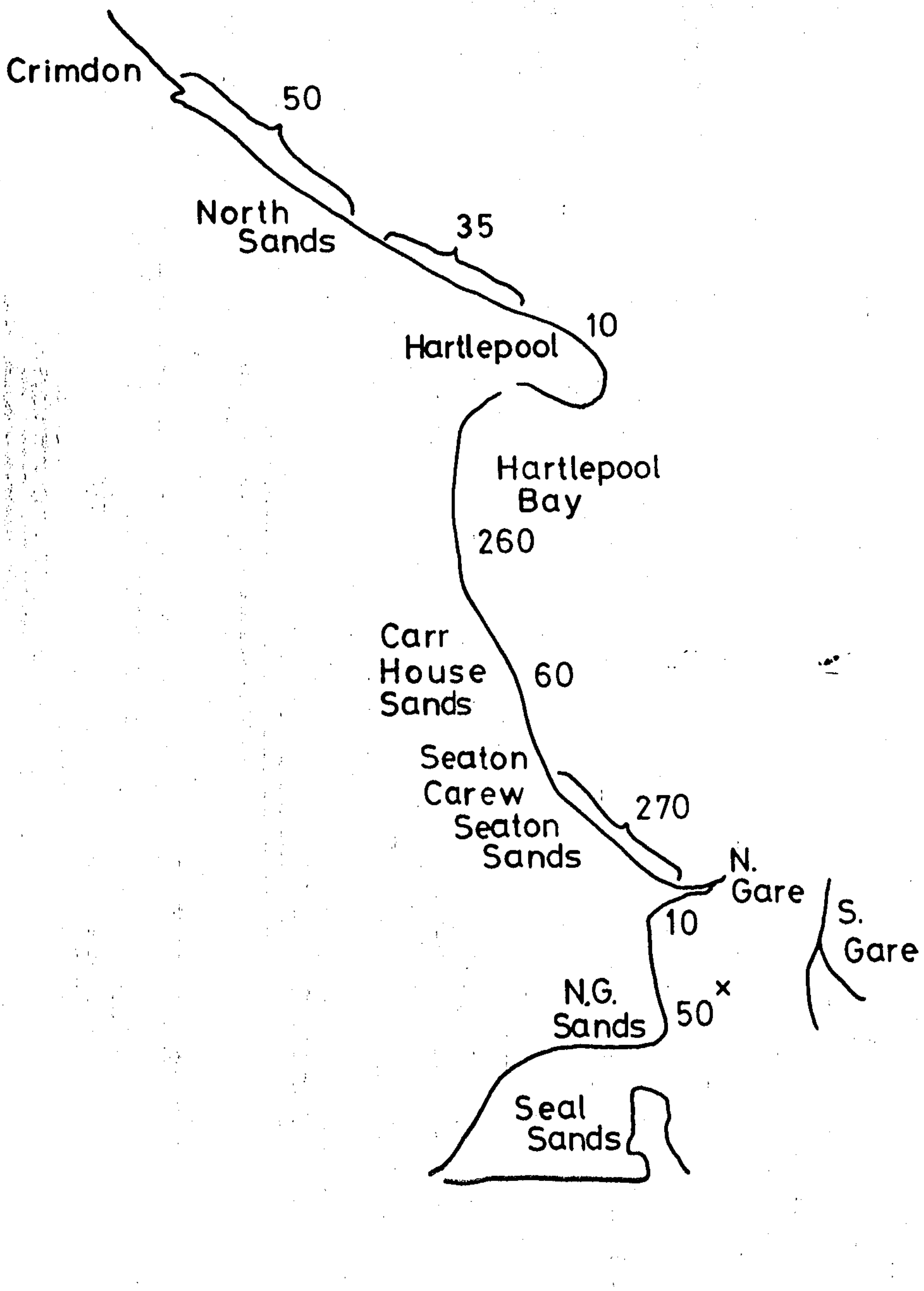
respectively. Significant relationships between total numbers in the estuary and numbers at each side suggest that there might be no preference by birds. The relationship for the north (Fig. 6) is highly significant at $P < 0.001$, and shows that when total numbers are low, north side numbers are very low. The relationship on the south side, although also significant at $P < 0.01$, seems less responsive to total numbers in that its increase is slower in relation to total number increase than on the norh side. This suggests a more constant or stable population level.

The decline in Bathyporeia and Eurydice populations at transect 5, between 1977-78 and 1978-79 could have caused the decline of Sanderling numbers on the south side between the two years. Birds reaching transect 5 one to two hours before High Water might not have satisfied their daily energy needs, and if other habitats were available they could take advantage of additional resources. Even at High Water, Sanderling are able to feed, (e.g., on wrack beds, north side, N. Davidson, pers. comm.). Sanderling often continued to feed on Coatham Sands over High Water on neap tides during the winter. During the 1977-78 winter, Sanderling were seen flying from the Ducky area towards the north side either before going to roost or after the roost had formed, (L. Goodyer, pers comm.). Thus, not all Sanderling roosted over the High Water period. On January 30th, 1979 at 1500 hours, (Low Water plus one hour), Sanderling feeding at transect 5 were beginning to fly to the pool at the Ducky to bathe and preen. About 60 individuals were present at the roost. By 1520 hours, 160 Sanderling were present. (A very high spring tide, 6.0m, accounted for the early roost.) At 1525 hours, 25 Sanderling rose and flew from the roost toward Bran Sands, in the direction of the north side. These flights occasionally accompanied Knot flocks, also returning to the north side. These observations suggest that some of the birds using the north side might be partly comprised of individuals unable to meet their daily requirements on the south side.

The above observations are not meant to suggest that Sanderling only began using the north side in the 1977-78 season. R. T. McAndrew (pers. comm.) reported that 400 or more Sanderling fed regularly on the north side. A summary of his counts (1975-77)is presented in Fig. 7. Although individual birds did in fact use both sides of the estuary, the constancy of location in sightings of colour-marked birds suggested a fairly stable situation. This does not explain, however, the erratic fluctuations in numbers using the south side. There may have been a transitory segment of the Teesmouth birds, (perhaps those not using the estuary everyday and thus including few of the colour-marked individuals), and other segments which were consitent in their choice of sides.

Figure 7

High counts of Sanderling using different areas of Teesmouth's north side during 1975-77.


Crimdon
50
North Sands
35
10
Hartlepool
Hartlepool Bay
260
Carr House Sands
60
Seaton Carew Seaton Sands
270
N. Gare
10
S. Gare
N.G. Sands
50
×
Seal Sands

The areas used by Sanderling on the north side are shown in Fig. 8. Some invertebrate data are available for the north side, at Seaton Sands. (Andrew Wood, 2H project). The data were collected to determine potential prey for Sanderling feeding at Seaton Sands and as a comparison with prey found on Coatham Sands. Sampling at Seaton Sands showed extremely low densities of the three most important invertebrate species: Nerine, Bathyporeia and Eurydice. There was no clear dominance of Nerine in the contribution to the overall invertebrate populations. The results were surprising as this area held the highest numbers of Sanderling on the north side, often with over 300 birds. Of the 27 counts from October 5th to May 9th, Seaton Sands held over 50% of the Sanderling counted on 15 of the counts. The invertebrate data suggest that the Sanderling should indeed have actively selected the south side for feeding in 1978-79. Sampling on Coatham Sands was carried out on 15/5, 21/5, 28/5, 4/6 and 11/6 1979 (Andrew Wood). The results found on the south side were strikingly similar to earlier sampling, Nerine being the most important prey, occurring in its greatest densities at transect 2, in the zone between 50m and 70m below the HWM. However, Bathyporeia and Eurydice were more evenly distributed along Coatham Sands, than in previous samplings.

Fig. 9 shows the fidelity to the north and south sides for colour-marked Sanderling present in 1978-79. These results are summarized in Table 1. Seven birds ringed on the south side spent the majority of their time on the north side. The birds ringed on

Figure 8

Location of areas used by Sanderling on the north side of the river Tees.

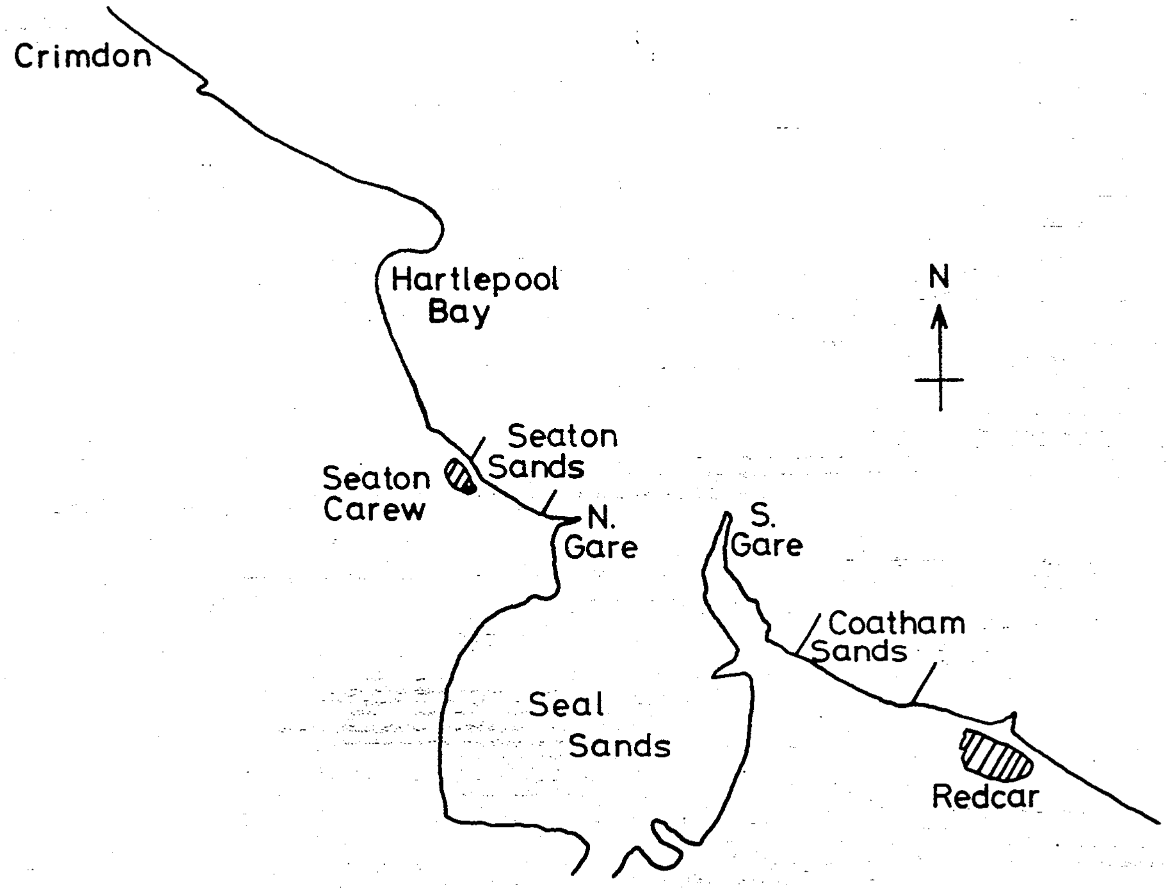
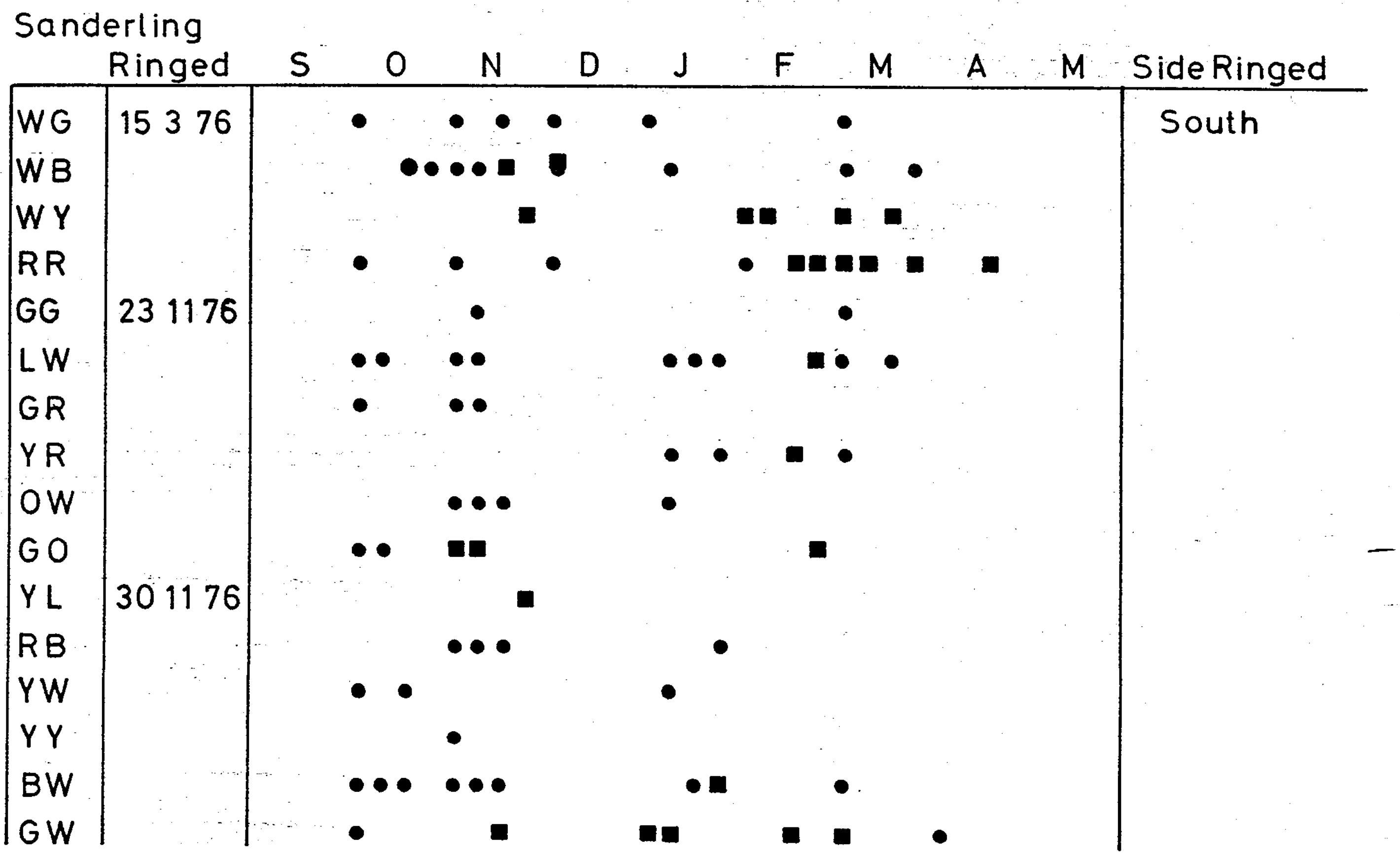
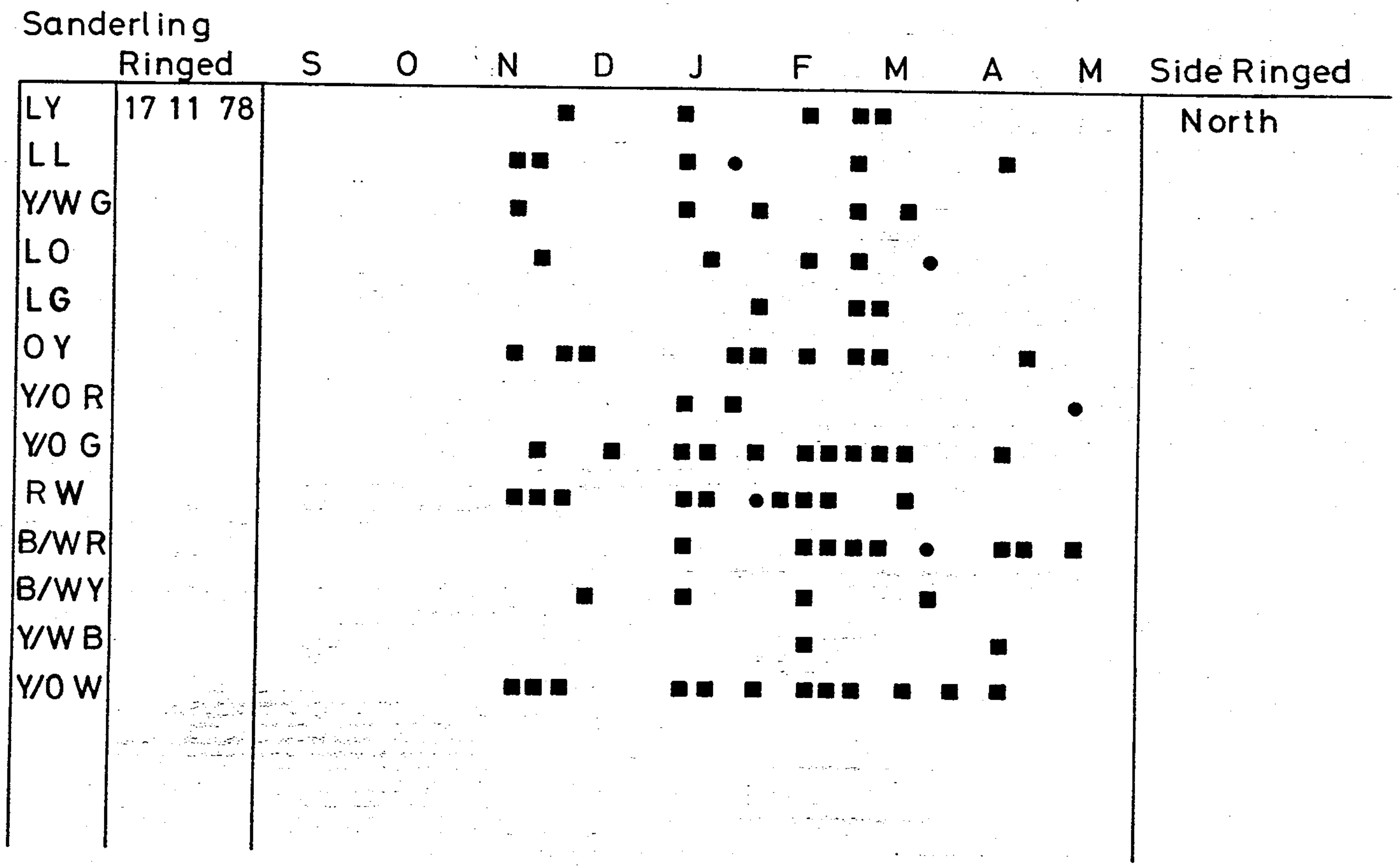

Crimdon
Hartlepool Bay
N
Seaton Sands
Seaton Carew
N. Gare
S. Gare
Coatham Sands
Seal Sands
Redcar

Figure 9

Site fidelity for ringed Sanderling. Ringing date and side on which bird was ringed are given. All sightings are for the autumn-spring of 1978-79.


Sanderling
Ringed
S
O
N
D
J
F
M
A
M
Side Ringed
WG
15 3 76
South
WB
WY
RR
GG
23 11 76
LW
GR
YR
OW
GO
YL
30 11 76
RB
YW
YY
BW
GW


Sanderling
Ringed
S
O
N
D
J
F
M
A
M
Side Ringed
LY
L L
Y/W G
L O
L G
O Y
Y/0 R
Y/0 G
R W
B/W R
B/W Y
Y/W B
Y/0 W
17 11 78
North

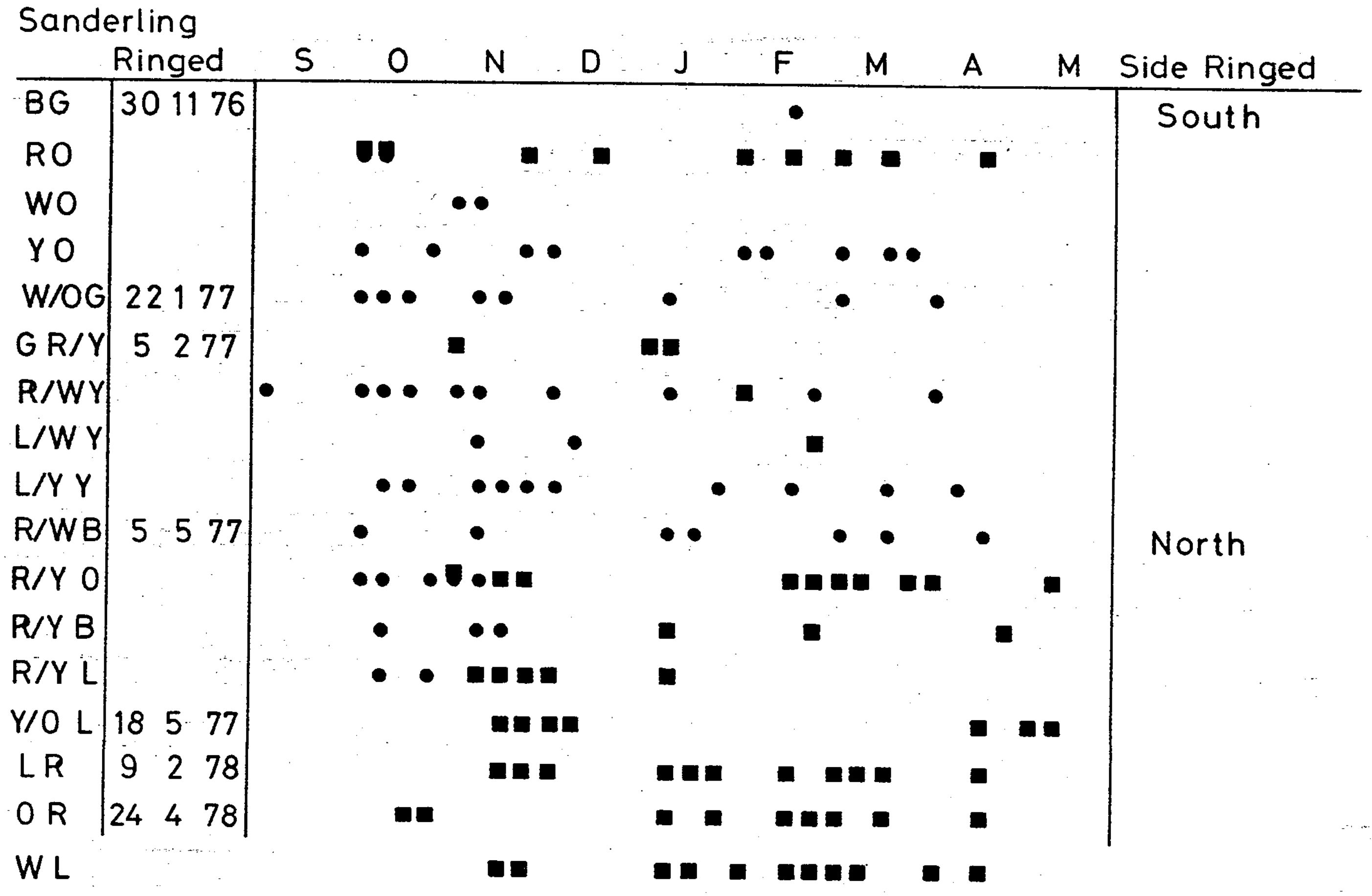

Sanderling
Ringed
S
O
N
D
J
F
M
A
M
Side Ringed
South
North
BG
30 11 76
RO
WO
Y O
W/OG
22 1 77
G R/Y
5 2 77
R/WY
L/W Y
L/Y Y
R/WB
5 5 77
R/Y 0
R/Y B
R/Y L
Y/0 L
18 5 77
L R
9 2 78
0 R
24 4 78
W L

TABLE 1

Colour-ringed Sanderling present at Teesmouth during the 1978-79 winter (total of 45 birds).

Birds ringed on the south side (24).

Seen only on south side	Seen only on north side	Seen once on north side	Seen more than once on north
10	4	6	4

Birds ringed on the north side (21).

Seen only on north side	Seen only on south side	Seen once on south side	Seen more than once on south
8	1	9	3

17/11/1978 (north) were extremely instructive as very few south-sightings of them were made. Most south-ringed birds remained faithful to the side they were ringed on. Various types of movements occurred. Three south-ringed birds switched sides, one in early November and two in mid-February. All north-ringed birds which made their first appearance (upon their return to the estuary in autumn) on the north side remained faithful to the north. Four north-ringed birds made their first autumn appearance on the south side, one never being reported on the north and three switching back to the north side and remaining faithful after that. For some birds, either one or several visits were made to the other side, mainly in late January, February and in March (often attributable to the presence of wrack beds).

On three occasions a single bird was sighted on both sides of the estuary on the same day (Table 2). On 24/1/1979 three counts were made on the south side: at 1110 hours (LW plus five hours) there were 342 Sanderling, at 1300 hours (HW plus one hour) there were 321 Sanderling and at 1415 hours (HW plus two hours) there were 199 Sanderling. Multiple counts on the same day on the north side showed an increase of birds at these times. This was another suggestion that birds used the north side when High Water had covered the feeding areas on the south side.

In additiona to site fidelity, associations of individuals were common. This suggested that several

TABLE 2

Birds seen on both sides of the estuary on a single day.

Individual	Date ringed	Side ringed	Sighted	South side	North side
R/Y O	5.5.77	north	2.11.78	Coatham Sands Transect 4 LW + 4	Seaton Carew
W B	15.5.76	south	7.12.78	Redcar Rocks HW + 5	Seaton Sands LW + 1
B/W Y	17.11.78	north	29.10.79	Redcar Rocks HW + 3	Seaton Rocks HW + 5

separate segments might have existed at Teesmouth. Mixing, however, did occur throughout the year. For birds which used the same habitat consistently, (such as those on Redcar Rocks), their associations with others doing the same could have been coincidental. However, not only were Sanderling seen feeding together at Redcar Rocks, they were also reported together at various areas along Coatham Sands. In the case of W/O G, L/Y Y, YW and R/W Y, no northside sightings were made from the time of their capture up to, and including, the 1979-80 season, (123 total sightings). The areas they foraged in became very predictable, showing the typical movement of Sanderling as described.

Table 3 shows the return and departure dates for the colour-marked individuals. The data are summarized in Table 4, which shows the minimum survival of the marked individuals. Sanderling are highly faithful, at some time during each winter, to Teesmouth. Caution must be exercised, however, in using these dates and sightings for determining survival and turnover of the population. As in the case of BB and RL, (and the absence of RL in 1977-78), could have been taken for mortality, whereas they could have either used Teesmouth only occasionally and not have been seen, or wintered at another estuary. A check of Table 4 will show much lower survival rates after the hard winter of 1978-79. In this year Bathyporeia densities were lower and the weather was very cold and windy.

TABLE 3

		1977-78		1978-79		1979-80	
		1st sighting	last sighting	1st sighting	last sighting	1st sighting	last sighting
Ringed	15.3.1976						
	W G *	28.2.78	22.3.78	5.10.78	7.3.79	8.8.79	
	W W *						
	W B *	16.10.77	25.4.78	18.10.78	30.3.79	4.10.79	
	W Y *	20.9.77	14.10.77	29.11.78	22.3.79		
	R R *	18.9.77	22.3.78	5.10.78	18.4.79	5.9.79	
Ringed	23.11.1976						
	G G	18.10.77	6.5.78	9.11.78	7.3.79	29.10.79	
	L W	31.8.77	4.5.78	5.10.78	22.3.79	5.9.79	
	G R	22.9.77	12.4.78	5.10.78	9.11.78	27.8.79	
	Y R	5.12.77	18.4.78	11.1.79	8.3.79	16.10.79	
	O W	7.11.77	6.3.78	2.11.78	11.1.79		
	G O	5.12.77	4.5.78	5.10.78	26.2.79	4.3.79-DEAD	

		1977-78 1st sighting	last sighting	1978-79 1st sighting	last sighting	1979-80 1st sighting	last sighting
Ringed	30.11.76						
	Y/B G	1.9.77	9.1.78				
	Y L	18.10.77	25.4.78	24.11.78			
	R Y	20.9.77	12.4.78				
	R G	9.3.78					
	R B	20.9.77	18.4.77	2.11.78	30.1.79		
	Y W	31.8.77	2.3.78	5.10.78	11.1.79	12.10.79	
	Y Y			2.11.78			
	B W	20.9.77	25.4.78	5.10.78	7.3.79	12.10.79	
	B B	17.11.77	12.4.78			5.9.79	
	G W	24.8.77	19.12.77	5.10.78	8.4.79	18.10.79	
	B G	13.12.77	25.4.78	21.2.79		5.9.79	
	R O	23.10.77	6.3.78	3.10.78	26.4.79	5.9.79	
	W O	6.10.77	12.4.78	2.11.78	9.11.78	13.12.79	
	Y O	22.9.77	9.5.78	15.8.78	20.3.79		
	R L					6.9.79	

		1977-78 1st sighting	last sighting	1978-79 1st sighting	last sighting	1979-80 1st sighting	last sighting
Ringed	19.1.77						
	W/Y G	11.12.77	22.3.78				
Ringed	22.1.77						
	W/O G	20.9.77	9.5.78	5.10.78	6.4.79	9.8.79	
	W/B G					22.11.79	
	W/O R	17.12.77					
Ringed	5.2.77						
	G R/Y	18.9.77		8.11.78	11.1.79		
	O R/W						
	R/W Y	1.10.77	12.4.78	4.9.78	6.4.79		
	L/W Y	28.2.78	2.3.78	9.11.78	26.2.79	26.10.79	
	L/Y Y	18.9.77	1.4.78	15.8.78	22.3.79	4.10.79	
	L/Y G						
Ringed	5.5.77						
	R/W B	19.12.77	6.3.78	5.10.78	18.4.79	5.9.79	
	R/W R						
	R/Y O	20.11.77		5.10.78	9.5.79		

		1977-78 1st sighting	last sighting	1978-79 1st sighting	last sighting	1979-80 1st sighting	last sighting
Ringed	5.5.77 con't						
	R/Y B	8.10.77	12.4.78	12.10.78	25.4.79	17.9.79	
	R/Y L	19.11.77	9.5.78	12.10.78	11.1.79		
Ringed	18.5.77						
	Y/O L			17.11.78	9.5.79	5.9.79	
Ringed	9.2.78						
	L R			17.11.78	18.4.79		
Ringed	24.4.78						
	O R				18.4.79	10.9.79	
	[illegible] L				18.4.79	5.9.79	
Ringed	17.11,78						
	L Y				14.3.79	29.10.79	
	L L				18.4.79	5.11.79	
	Y/W G			21.2.79-DEAD			
	L O				30.3.79	29.10.79	
	L G				8.3.79	20.12.79	

		1978-79 1st sighting	last sighting	1979-80 1st sighting	last sighting
Ringed	17.11.78 con't				
	O Y		25.4.79		
	Y/O R		9.5.79	12.10.79	
	Y/O G		18.4.79	6.8.79	
	O G				
	R W		22.3.79	5.9.79	
	B/W R		9.5.79	5.9.79	
	B/W Y		28.5.79	29.10.79	
	Y/W O				
	W/R R				
	Y/W B		18.4.79	5.9.79	
	Y/O W		18.4.	10.9.79	

TABLE 4

Survival rates of colour-marked Sanderling. Upper figure for each date gives survival of birds seen the year prior; lower figure gives survival of original number of ringed birds for that date. All figures in percentage

Date ringed	Number ringed	1975-76 to 1976-77	1976-77 to 1977-78	1977-78 to 1978-79	1978-79 to 1979-80
3.1976	5	100	80 80	100 80	75 60
11.1976	21		95.2	90 85.7	66.7 57.1
1.1977 and 2.1977	10		80	75 60	66.7 40
5.1977	6		83.3	100 83.3	60 50
2.1978 and 4.1978	3			100 100	
11.1978	16				68.8

This may have been a stress period for the Sanderling.

Teesmouth may play an important roll for birds on passage, both northward in the spring and southward in the autumn. An adult bird, presumably on its return from breeding and ringed on the Waddenzee on 9/8/75, was netted on Coatham Sands on 22/5/78. Several controls have been netted on the Tees, many from the Wash. An individual ringed on the Wash on 15/9/77 was caught on North Gare Sands (Teesmouth) on 9/2/78. The bird had presumably migrated south to the Wash and had then come north to the Tees for the winter. One controlled bird was caught for the first time on the Wash in 1970 and again in 1971-72-73 and 1974. It was caught on the Tees on 23/11/76. These observations suggest that movement between estuaries does exist, although the mechanism or pressures leading to the movements are not at all clear.

Population turnover and the number of birds which use the Tees on passage are difficult to assess- mainly due to the mixing of individuals on the north and south sides. In 1977 and 1978, a large flock of c. 800 Sanderling spent the months of August and September on Coatham Sands moulting their flight feathers (L. Goodyer, pers, comm.). 178 birds from the flock were caught and ringed in September 1977. Of these 178 birds, 25 were netted at Teesmouth either before or after this date (Table 5). Two of the birds were found dead (31/5/78 and 21/1/79). These data show how difficult it is to

TABLE 5

Number of Sanderling from the 1.9.1977 catch which were netted in previous or subsequent catches.*

Date of catch	Area	Number of Sanderling from 1.9.1977 catch
23.11.76	Coatham Sands	2
30.11.76	Coatham Sands	3
5.2.77	Coatham Sands	1
25.3.77	Redcar Rocks	1
18.5.77	North Gare	3**
9.2.78	North Gare	2***
24.4.78	North Gare	4***
22.5.78	Coatham Sands	2
24.11.78	Seaton Sands	1***
8.3.79	Seaton Sands	2***
6.9.79	Coatham Sands	7
5.10.79	Coatham Sands	1

* Four individuals were controlled twice. In addition, two birds from the 1.9.77 catch were found dead on the Tees, (31.5.78 and 21.1.79). The 1/9/77 catch was on the south side.

**Caught on the north side prior to the 1/9/77 catch.

***North side.

determine numbers of passage birds unless very accurate counts can be consistently obtained, as it is not clear which birds counted on passage use Teesmouth all winter, and which individuals move on.

Appendix 4.1

Example of data taken from film sequences. Sequence 8, see Appendix 4.4. All references to frame number.

Bill In	Out	Forage method	Prey	Handling time
1	6	probe	Nerine	2 frames
12	27	stitch	Nerine	2 frames
46	55	probe	Nerine	1 frame
57	70	stitch	Nerine	1 frame
72	75	probe	Nerine	1 frame
77	107	probe	Bathy.	9 frames
122	156	probe	fail	
177	203	probe	fail	
220	246	probe	Nerine	2 frames
268	283	probe	fail	
284	301	probe	Nerine	11 frames
306	333	stitch	fail	
336	354	stitch	fail	
355	376	stitch	Nerine	2 frames
384	397	probe	Nerine	2 frames
399	416	stitch	Nerine	2 frames
422	444	stitch	fail	

Each frame in which a pace occurred.

Appendix 4.1 cont.

Position and visual orientation (degrees) of Sanderling in sequence 8. See text for explanation of visual orientation.

Frame number	Position	Visual orientation
1	Wet sand	70
31		65
46		75
70		85
120	Shallow water	80
158		50
160		40
169		0
180		65
240		40
280		80
417		120
435		155
444		185
452		230
470		245
549		240
551	Wet sand	280
565		20
567		65
570		275
584		250
589		185
603		160
629		270
634		190
640		125
648		180

Appendix 4.2

Analysis of Sanderling behaviour

In order to evaluate the behavioural patterns recorded on the film it was necessary to break the information down into the smallest time intervals and into units of action which can best be termed as "behavioural primitives". This generates a large amount of data, as the smallest time interval is either 1/16 or 1/24 of a second, determined by the film speed. Moreover, the primitives can be such characteristics as individual paces, visual orientation, prey handling, surface pecks, etc. The combination and order of occurrence of behaviour primitives constitute the overall behaviour pattern of a bird. It was necessary with this amount and complexity of data to use computer techniques for effective analysis; these and their development will now be described.

The nature of the topic and the desire to evaluate the characteristics of all behavioural responses in optimal feeding strategies made appropriate, and almost essential, the use of graphical display as a 'data-exploration' tool. Foraging strategy of waders cannot be simply evaluated as many parameters will affect the way in which the behavioural primitives will occur, such as the state of the tide, proximity of other birds, or degree of sand saturation. Thus, in attempting to understand and explain the processes, an overall perspective must compliment any in-depth studies of individual feeding attempts. This was achieved by performing two modes of parallel analysis and data exploration. This first mode was an enquiry into the overall movement pattern and the relative occurrences of characteristic events, (e.g., prey capture). The method of representing this data was to display the movements of a graphics terminal (Tektronics 4013) as a series of vectors whose direction and length were determined by the recorded visual orientation on the one hand, and occurrence of paces on the other. This gave a bird's eye view (!) of beach movement and an immediate indication of any commonly occurring patterns. Onto these simple vector images were superimposed the location and characteristics of the feeding attempts. Symbols were added representing a sub-set of the behavioural primitives, indicating searching and prey capture or failure. A picture of movement and relative feeding positions was thus simply created. Any particular film or section of interest was reproduced on a hard copy graph plotter (Hewlett Packard HP7221). This form of data exploration proved to be very valuable and has led to further study, again taking advantage of interactive graphical facilities which will be discussed at some future date. The technical details of the computing proceedures are as follows: the data were entered into the computer in a sparse matrix form using a "key to disc" system (MDS), which produced 25 single density floppy discs of information. These were transferred into permanent disc files under the Michaigan Terminal Operating System (MTS) on the IBM370/168, which is the mainframe at the core of the NUMAC organisation. (NUMAC: Northumbrian Universities Multiple Access Computer, a cooperative of Durham and Newcastle Universities and Newcastle Polytechnic.) Data manipulation programmes were written in the MTS dialect of FORTRAN, as were the graphical programmes which used the GHOST and IG (1) graphical subroutine libraries. The parallel stage of analysis was to evaluate the characteristics of each feeding attempt. The primitives were processed to extract summary information for each feeding attempt to give such details as; number of paces whilst searching and handling, changes in visual orientation, length of search, etc. A matrix of cases (feeding attempts) and variables (feeding characteristics) was created in this manner, allowing input into any standard statistical analysis package. In this instance the choice of an interactive package system, MIDAS, was made to allow flexibility in data exploration.

Appendix 4.3.

Description of data taken from taped observations.

Symbols:

p- probe attempt.

st- stitch attempt

wc- water column attempt.

P- Pause position

B- *Bathyporeia*

N- *Nerine*

→ bird runs right, 90°, parallel to the waves

← bird runs left, 270°, parallel to the waves.

↑ bird runs away from the waves, 180°

↓ bird runs towards the waves, 0°

The above degrees refer to the visual orientation of the foraging bird. See text for explanation of visual orientation.

S- Sanderling, when coming in close contact with subject bird, refers to individuals which are within two body lengths.

→ P P p P p → P p → P p P p p P ↑ p P
p p p ↑ P p P p st (edge) st p ↑ (edge) p p
p P p ← P p ← P p P p P p p(B) P p P p
← P p P p ← P p p P p P p P p ↑ (above tide)
p(B) p p p → p p st st st → st (in the tide) p
st → p → P P P p P p P p P p P p P p P
p P p P p P p P p P p P p P → p p → P
p ↑ P p P p P p p p p P p p(N) P p ↑ (edge)
(dry sand) (wet sand) p(N) p p (in the tide) p(N) p
st → st st st(N) p(N) ↓ p(N) ← st p(N) ← st
P → p(N) p p p p p → p p(N) ← ↓ → p p
p p(N) p → p p(N) p(N) p ← → p p p p →
p p → p p ← p(N) ← p p p p p → p (edge)
p p → p p p p p → p p ↓ ← P P p p ←
p P p (edge) p(N) p (wing stretch) ← p ↑ p st
(edge) st st st → (above tide) P p p p P p →
P P p P st p ← ↓ (ripples) p p p ↓ st ↑ st
↑ st ↑ → (out of view)...........

4.8 observation time.
19.3.1978.
Transect 5.
1320 hours.
Low Water + 4 hours.
Alongshore running- 0.8 minutes.
Up-and-down-beach running- 0.5 minutes.
Prey captures, 12 Nerine and 4 Bathyporeia.
Single bird.

<- ↑ st p(B) ↓ st st st ← st (edge) st ↓ (1-s)
p p p(N) p p(N) st p <- p (waves) p ↑ p p p
(edge) p ↑ p p (edge) p ↓ (waves) p p p p(N) p
p ↓ p (ripples) p st st st ← st ← st(N) p(N)
p p(N) p p ↑ p p ↑ p(N) p st st ↑ (above wave) p
p p p → (edge) p st st p → p (edge) ↓ st p
↑ p st ↑ p → p(N) p(N) p ↓ p p p p ↑ p p
(edge) p ↓ p p p p(N) p p → p p p st ← st
↑ (above tide) → st ↑ → (edge) ↓ p p p p ↓
p st → st st p st → ↓ p p p p (ripples) p
p st ← st ↑ st st ← ↑ (edge) p ↓ p(N) wc(B)
p p p p(N) p ← p st st ↑ p (Preen) st ← →
(edge) (2-s) st st st → st st ↓ p(N) p p p
p(N) p(N) → st p(N) ↑ p P (edge) p ↓ p p st
(ripples) p st st ← st st ← st st st ← (edge)
↓ (kany birds overhead, subject bird takes flight and
joins birds overhead)....................

4.5 minutes, observation time.
12.4.1978.
Redcar Beach.
1130 hours.
High Water 4 hours.
Alongshore running- 0.42 minutes.
Up-and-down-beach running- 0.88 minutes.
Prey captures, 16 Nerine and 2 Bathyporeia.
Group size- 3 Sanderling.

Appendix 4.4

Data on individual cine sequences for foraging Sanderling.

Explanation of listed categories:

Area- RB- Redcar Beach

T - identifies the transect and its number

Time- the length of the given sequence

Tide- the state of the tide- H- High Water

L- Low Water

Success- this is the number of prey (*Nerine* and *Bathyporeia* combined) taken per minute, regardless of the number of prey attmepts.

Sequence	Area	Time (in sec.)	Tide	Nerine	Bathy.	Probe	Stitch	WC	Success per min.
1	RB	28.1	H+ :20	6	0	12	4	0	12.8
2	RB	26.0	H+ :20	3	2	8	5	2	11.4
3	T3	28.0	L+4:50	0	2	2	0	3	4.3
4	T3	28.0	L+5:50	0	2	0	0	2	4.3
5	T1	28.0	L+3:40	4	0	20	0	3	8.6
6	RB	28.0	LW	4	0	17	2	0	8.6
7	RB	28.0	L+ :40	4	0	8	5	0	8.6
8	RB	28.0	L+2	10	1	10	7	0	24.6
9	T5	42.0	L+4	1	0	8	0	0	1.4
10	T3	28.0	L+4	2	3	3	0	19	10.7
11	T3	42.0	L+4	1	4	4	0	10	7.1
12	T3	42.0	L+4	1	0	5	2	0	1.4
13	T2	42.0	HW	2	2	3	0	7	5.7
14	T2	42,0	HW	3	0	26	0	0	4.3
15	T3	41.0	H+1	1	3	2	0	8	5.9
16	T5	42.0	H+1	1	1	36	21	1	2.9
17	T3	28.0	H+3	0	1	2	2	1	2.1
18	RB	28.0	H+4	4	0	6	11	0	8.6
19	RB	28.0	H+4	3	0	6	8	0	6.4
20	T3	42.0	H+5	0	4	0	0	18	5.7
21	T1	42.0	L+4	3	1	22	1	0	5.7
22	RB	28.0	L+1	2	0	10	5	0	4.3
23	RB	21.0	L+2	0	0	0	6	0	0

Sequence	Area	Time (in sec.)	Tide	Nerine	Bathy.	Probe	Stitch	WC	Success per min.
24	RB	42.0	H+5	5	0	4	15	3	7.1
25	RB	42.0	L+3	1	1	12	0	0	2.9
26	T5	42.0	L+3	2	0	20	2	0	2.9
27	T5	28.0	L+3	0	2	0	0	3	4.3
28	T5	42.0	L+3	0	3	1	0	12	4.3
29	T3	28.0	H+1	3	3	10	0	16	12.9
30	T3	28.0	H+4	0	1	0	0	20	2.1
31	T3	42.0	H+4	1	1	11	0	4	2.9
32	T3	42.0	H+4	0	0	0	0	8	0
33	T4	28.0	H+2	0	0	1	0	1	0
34	T3	28.0	H+3	0	0	1	0	1	0
35	T3	22.6	H+3	2	1	8	1	0	8.0
36	RB	26.3	H+4	3	0	11	4	0	6.8
37	RB	28.0	H+4	3	0	6	6	0	6.4
38	T1	28.0	L+1	4	0	5	7	0	8.6
39	T1	27.0	L+1	0	0	0	3	0	0
40	T1	26.0	HW	0	0	6	0	0	0
41	RB	42.0	H+4	2	0	8	14	6	2.9
42	RB	39.0	H+5	2	0	7	8	0	3.1
43	RB	28.0	H+5	9	0	7	12	0	19.3
44	T5	25.0	L+4	1	0	12	1	0	2.4
45	T5	42.0	L+4	3	2	13	13	0	7.1

Sequence	Area	Time (in sec.)	Tide	Nerine	Bathy	Probe	Stitch	WC	Success per min.
46	T5	42.0	L+3	0	0	6	0	0	0
47	T5	42.0	H+1	4	1	5	13	3	7.1
48	T1	28.0	L+4	0	0	6	1	0	0
49	RB	40.0	H+5	8	0	3	14	0	12.0
50	RB	36.0	H+5	5	0	11	10	0	8.3
51	RB	42.0	H+5	4	0	7	24	0	5.7
52	RB	32.0	H+5	4	0	2	14	0	7.5
53	RB	38.0	H+5	5	0	5	27	0	7.9
54	RB	41.0	H+5	4	0	7	26	0	5.9
55	T5	26.0	L+4	0	0	8	0	0	0
56	T5	28.0	L+3	0	3	10	4	0	6.4
57	T5	42.0	H+1	3	0	12	21	0	4.3
58	T5	26.0	L+4	1	0	3	5	0	2.3
59	T3	42.0	H+3	0	2	6	1	0	2.9

Appendix 5.1

Survival rates of Turnstone at Teesmouth

A summary of the Turnstone survival rates is given in Table 1. This can serve only as an approximation of survival and will be an underestimate, as birds may have returned to other estuaries. In Table 2 all return and departure information of the colour-marked birds is given. It can be seen from Table 2 that on several occasions, birds were not seen for an entire year, being recorded the following year, or a subsequent year. This may have been due to missing a bird (not observing the area of that particular individual), the bird using an alternate coastal area, or it being a passage bird and tkus at the Tees for a relatively short period. Birds may have also changed estuaries on a permanent basis, such as R/Y O which was absent after 27/3/1978, but reported in Liverpool on 9/4/1978.

TABLE 1

Losses of marked Turnstone.*

34 Ringed during winter of 1975/76

Losses between	No. lost	No. died at Tees	No. left	
75/76 - 76/77	1	1	33	97.1%
76/77 - 77/78	5	1	28	82.4%
77/78 - 78/79	4	0	24	70.6%

48 Ringed during winter of 1976/77

Losses between	No. lost	No. died at Tees	No. left	
76/77 - 77/78	5	0	43	89.6%
77/78 - 78/79	7	1	36	75.0%

8 Ringed during winter of 1977/78

Losses between	No. lost	No. died at Tees	No. left	
77/78 - 78/79	2	1	6	75.0%

* Percentages refer to year-to-year survival.

TABLE 2.

Ringing data, first sighting and last sighting for each winter of colour-marked Turnstone.

Birds ringed 14/11/1975

	1976-77		1977-78		1978-79
W/Y B	Nov.	April	Sep.	March	....
W/Y R	Oct.	Feb.	Oct.	April	....
W G	Jan.	March	Oct. only		Oct. only
W O	Nov.	March	Sep.	April	March-Oct.
W W	Oct.	Feb.	Nov.	Jan.	April-Oct.
W L	Dead 17/1/1976				
W R	Oct.	May	Oct.	April	.......Subsequent report
W B	Oct.	Dead 18/3/1977			
W Y	Oct.	April	Sep.	May	March only
Y Y	Oct.	March	....		April only
Y O	Nov.	May	Oct.	April	.... Subsequent report
Y R	Oct.	May	Sep.	Feb.	Feb.-Dec.
Y L	Oct.	April	Sep.	April	April-Oct.
Y G	Oct.	April	Sep.	April	March-Oct.
Y B	Oct.	April	Sep.	March	Feb.-Oct.
O O	....		Oct.	Jan.	....
O R	Nov.	March	....		....
O G	Oct.	Dec.	Jan.	Feb.	Feb. only
O L	Oct.	March	Aug.	April	March-Nov.
O B	Oct.	March	Sep.	April	April-Oct.
R R	Nov.	March	....		....
R G	Oct.	March	....		....
R L	Oct.	May	Sep.	April	Feb.-Oct.
R B	Oct.	Nov.	April only		....
G G	....				.. Subsequent report
G L	Dec.	Jan.	....		....
G B	Oct.	May	Nov.	April	Jan. only
L L	Oct.	May	Oct. only		May only

TABLE 2

Birds ringed 14/11/1975 cont.

L B	Oct.	April	Sep.	May	Nov-Feb.	
B B	Dec. only		Feb.	March	Jan.	Feb.
Y W	Oct.	Jan.	Oct.	Feb.	Nov.	Jan.
O Y	Dec. only		....		Nov. only	

Birds ringed 15/3/1976

L W	Nov.	April	Oct. only		.... Subsequent report	
L Y	Oct.	May	Sep.	May	Dec.	April

Birds ringed 23/11/1976

	1977-78		1978-79	
L R	Sep.	April	Nov.	Feb.
L O	Oct.	April	April only	
L G	March	April	... Subsequent report	
O W	Aug.	April	Oct. only	
G W	Dead 7/10/1977			
G R	Oct.	March	Nov.	March
G O	Sep.	Dec.	......	
G Y	Jan.	March	Nov.	Jan.
R Y	Oct.	Dec.	Oct. only	
R W	Oct.	March	Oct.	Dec.
R O	Oct. only		...... Subsequent report	
B W	Aug. only		Nov.	Jan.
B G	Jan.	April	Jan.	Feb.
B O	Oct.	March	Jan.	Feb.
B R	Oct.	April	Nov.	March
Y/O O	Oct.	May	Nov.	Jan.
Y/W W	Oct.	April	Oct.	Nov.
Y/R W	Sep.	March	Nov.	April
Y/L W	...		.... Subsequent report	
Y/L G	Oct.	Feb.	Jan.	March
Y/O L	Oct.	March	..... Subsequent report	
Y/R R	....		..... Subsequent report	
Y/O R	Oct.	May	Oct.	March
Y/O W	Sep.	May	Oct.	March
Y/L Y	Nov. only		Jan. only	

Birds ringed 23/11/1976 cont.

	1977-78		1978-79	
Y/G Y	....		....	
Y/B Y	Oct.	March	....	
L/O O	....		....	
L/Y Y	Sep.	April	....	
L/W Y	Oct.	April	Nov.	Feb.
L/O Y	Oct.	March	....	
L/O W	....		....	
L/W G	....		....	
L/B G	Oct. only		....	Subsequent report
L/B L	Oct.	Feb.	....	
L/R W	Oct.	April	....	Subsequent report
R/W L	....		Jan.	Feb.

Birds ringed 9/12/1976

	1977-78		1978-79	
Y/G L	Nov.	April	....	Subsequent report
Y/G W	Feb, only		....	Dec. only
R/Y L	Oct.	March	Jan. only	

Birds ringed 5/2/1977

	1977-78		1978-79	
L/R Y	....		Jan.	April
L/R L	Oct.	May	Nov.	April
Y/W Y	Sep.	Feb.	Nov.	March
Y/R Y	Sep.	April	Oct.	Feb.
R/G B	Oct.	Nov.	....	
R L/Y	March	April	......	Subsequent report
G/W Y	Sep.	April	....	Subsequent report

Birds ringed 5/5/1977

	1977-78		1978-79	
R/Y O	Reported in Liverpool March/April 1978 and April 1980			
R/Y B	April only		April	May
W/G L	....		Nov.	Jan.
W/Y G	Feb. only		....	
W/G O	March only		....	Subsequent report
W/L L	Sep.	Jan.	Oct.	Feb.
W/B Y	Oct. only		Jan.	April

TABLE 2

Birds ringed 5/5/1977 cont.

	1977-78		1978-79		
W/O B	March only		....		Subsequent report
L/G G	Oct. only		....		
L/G O	....		....		
L/G B	Oct. only		....		
L/Y R		April	....		Subsequent report
L/Y O	March only		....		
L/Y L	Dec.	March	Nov.	Jan.	
L/W R	March only		....		
L/W G	....		....		
L/W O	Oct.	Jan.	....		Subsequent report
L/W B	....		Feb.	March	
L/Y B	Oct only		Feb. only		
L/Y W	Oct. only		....		

Appendix 5.2

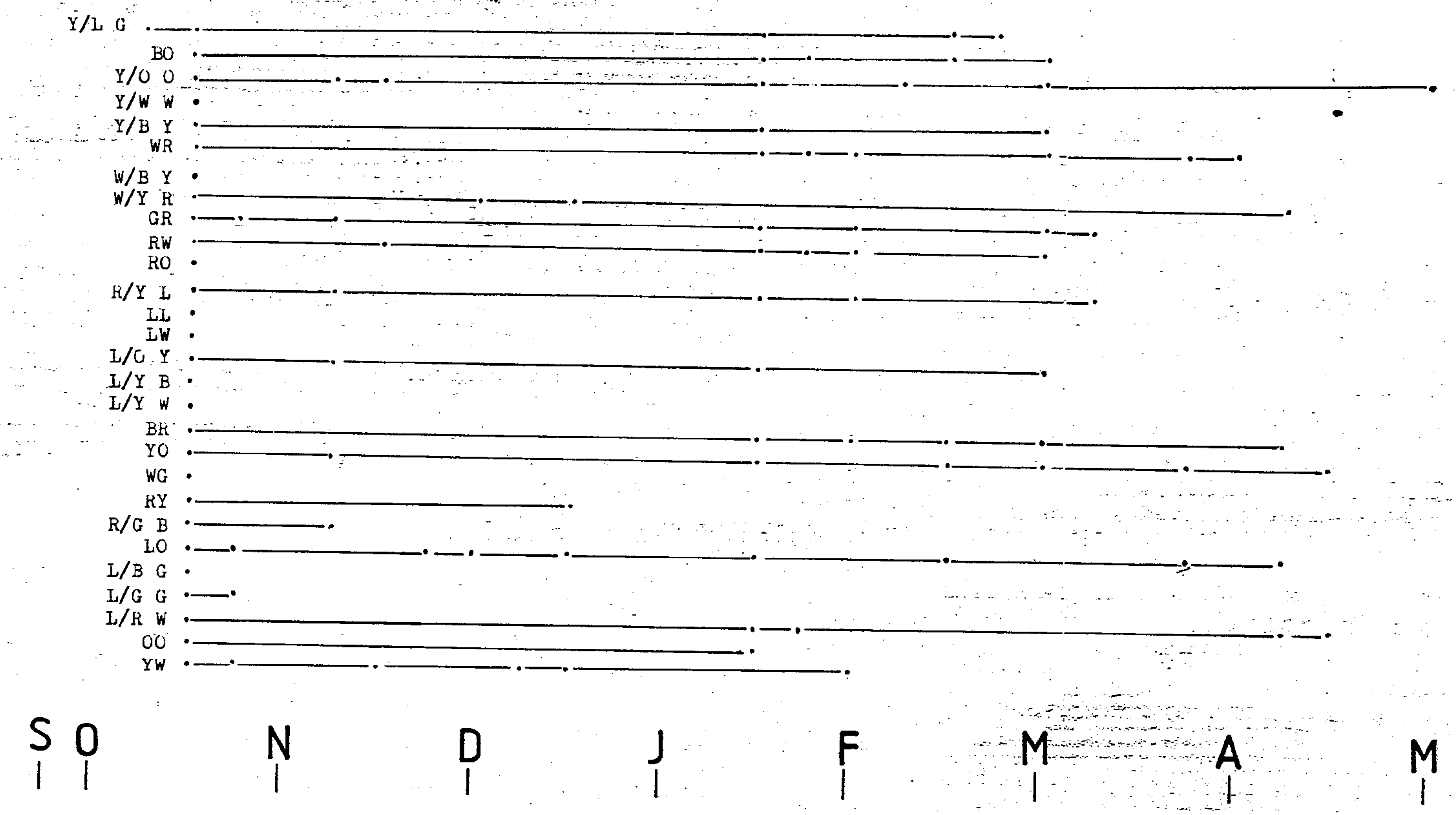
Use of the Tees by colour-marked Turnstone

The use of the Tees by colour-marked Turnstone for the winter of 1977-78 is shown in Fig. 1. Most colour-marked birds used Teesmouth throughout the entire winter period. Other individuals appeared to use Teesmouth as migrants on passage in autumn as well as in spring. Referring to Table 2-Appendix 5.1, it can be seen that R B and L L are two such examples. For L L, the bird was seen on the Tees in October 1976, May 1977, October 1977 and May 1979. R B was seen in October and November of 1976 and April of 1978. It is instructive to look at the catch of 20 birds on 5/5/1977 (Table 2, Appendix 5.1). May was a time of departure for many of the resident Turnstone. It was also a time of passage, presumable of birds coming from further south. There was a very high percentage of juveniles in this particular catch (7 of 20). The fate of these 20 birds is shown in Table 1. It is apparent that these birds did not form part of the resident Turnstone population. It is possible that they may have formed a cohesive population of their own (i.e., they may have originated from the same estuary, and may have been migrating as a group). It is interesting to note that three birds of this 5/5/1977 catch were seen in the same area at South Gare on October 18th 1977, presumably on their return from their breeding grounds in the north. For L/Y W and W/B Y, they were sighted only on the 18th that entire winter. L/Y B was seen on October 18th and on the 20th but not later in the season. On 20/10/ 1977 three of these twenty birds were seen feeding together at South Gare Sands (W/Y G, L/G G and L/Y B). Mid to late October was an important return time for many of the resident Turnstone. In 1977 16 colour-marked birds made their first appearance on October 18th (at South Gare). An additional eight birds made their first appearance on the 20th of October. Several of these birds appeared for the first time and together in mid to late October in 1978 as well. Some of these birds had been colour-marked in the same catch in 1975.

On the Wash, the average counts of Turnstone (1970-1974) were highest in September (780) tappering rapidly in October and November (560 and 420 respectively) (Branson et. al. 1979). Following a low in December, the numbers remain constant until a slight increase and second peak in March and April (530 and 510 respectively).

Figure 1.

The use of the south side habitats by colour-marked Turnstone for the 1977-78 winter. Each dot represents a single sighting. See Table 2 of Appendia 5.1 for ringing data, departure and return dates for marked birds.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Y/O O
Y/W W
Y/B Y
WR
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W/Y R
GR
RW
RO
R/Y L
LL
LW
L/O Y
L/Y B
L/Y W
BR
YO
WG
RY
R/G B
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L/B G
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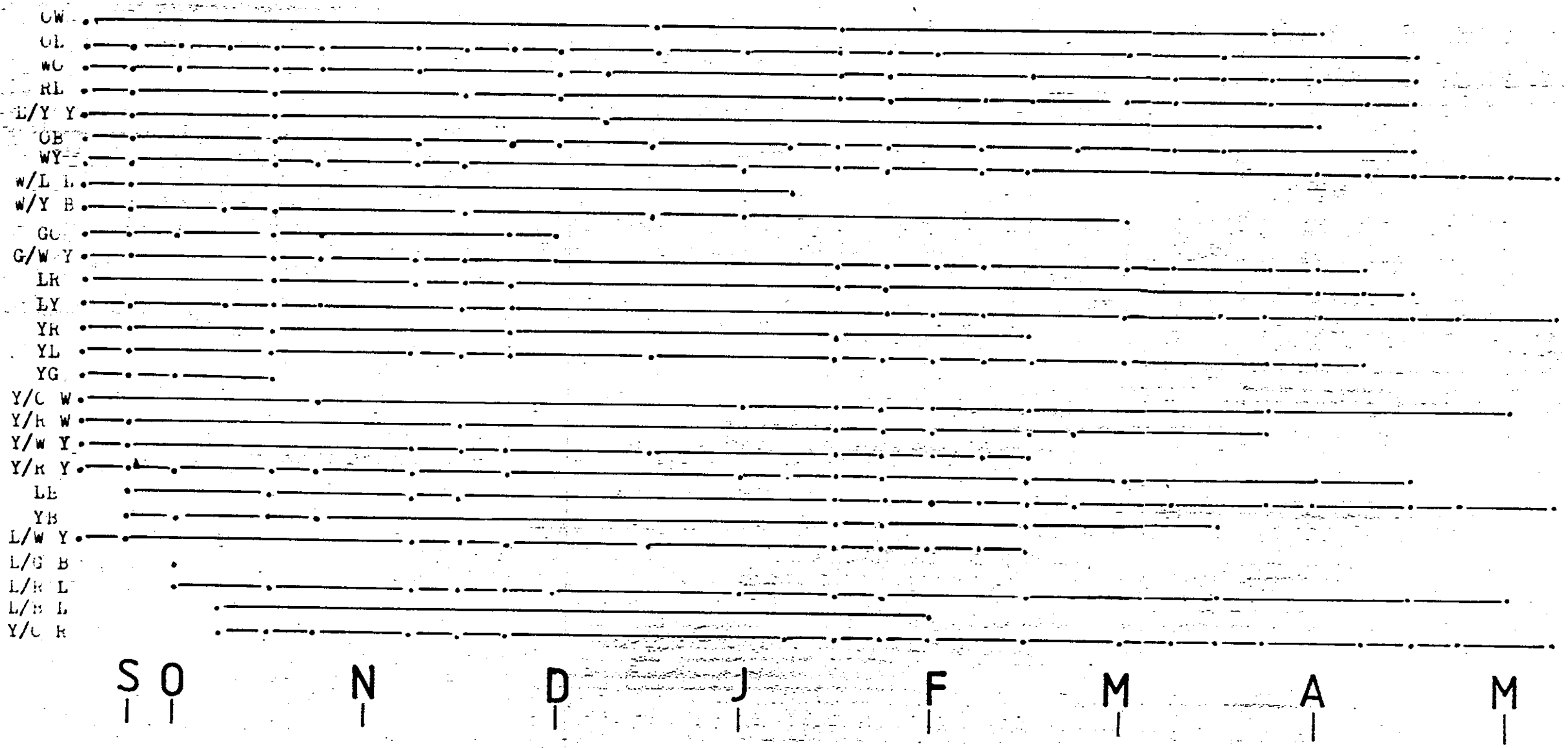
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OL
WO
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GO
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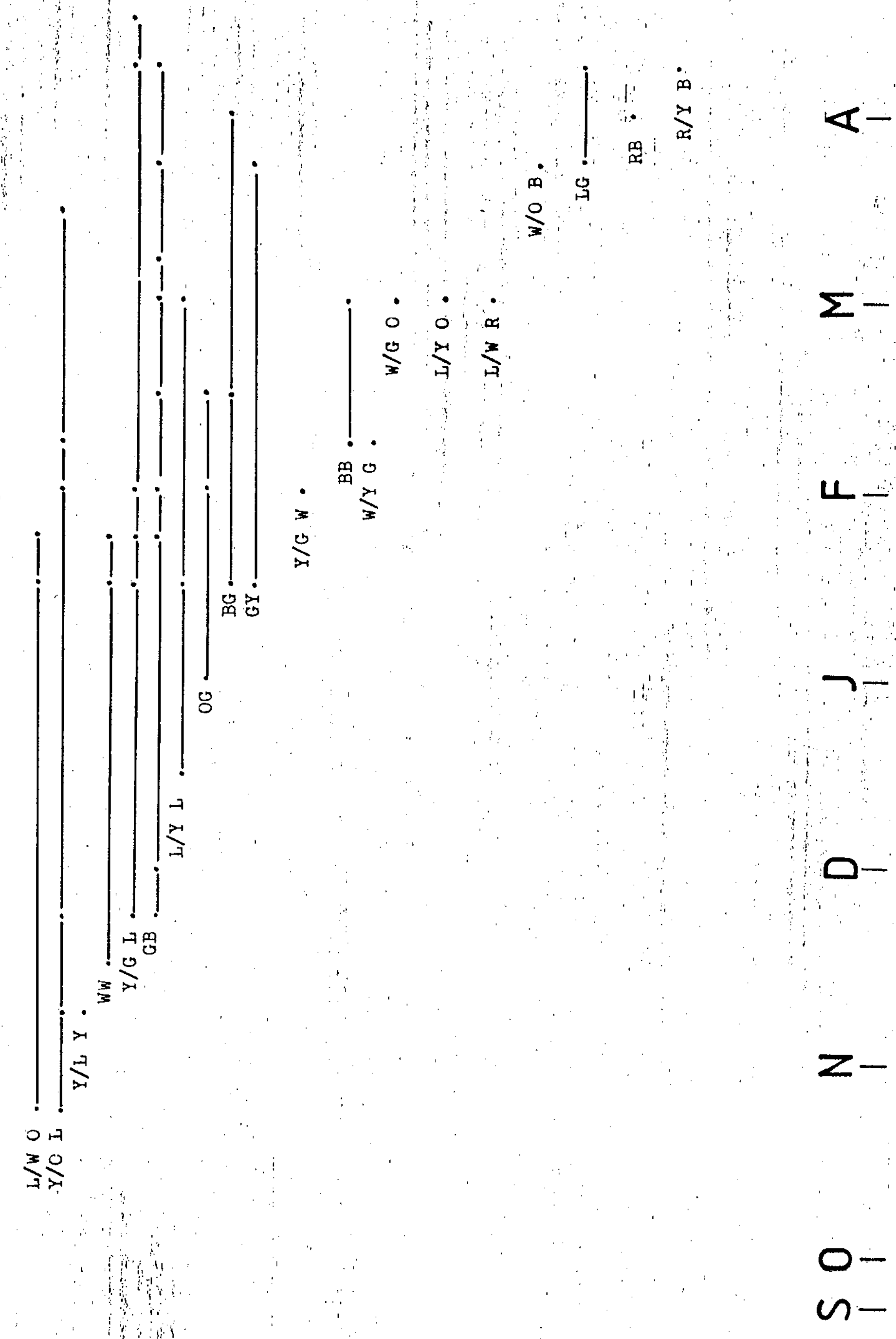
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Y/L Y
WW
Y/G L
GB
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OG
BG
GY
Y/G W
BB
W/Y G
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L/Y O
L/W R
W/O B
LG
RB
R/Y B
S
O
N
D
J
F
M
A
M

TABLE 1

Fate of the 20 Turnstone colour-marked on 5/5/77.

R/Y O	Adult	Reported in Liverpool in the fall.
R/Y B	Adult	Seen April 1978 and 1979.
W/G L	Adult	Seen November 1978, January 1979.
W/Y G	Juvenile	Seen February 1978.
W/G O	Juvenile	Seen March 1978.
W/L L	Juvenile	Seen September 1977, January 1978, October 1978 and February 1979.
W/B Y	Juvenile	Seen October 1977 and January and April 1979.
W/O B	Adult	Seen March 1977.
L/G G	Adult	Seen October 1977.
L/G O	Juvenile	Not seen again.
L/G B	Adult	Seen October 1977.
L/Y R	Adult	Seen April 1978.
L/Y O	Juvenile	Seen March 1978.
L/Y L	Adult	Seen December 1977, March 1978, November 1978 and January 1979.
L/W R	Adult	Seen March 1978.
L/W G	Adult	Not seen again.
L/W O	Adult	Seen October 1977 and January 1978.
L/W B	Juvenile	Seen February and March 1979.
L/Y B	Adult	Seen October 1977 and February 1979.
L/Y W	Adult	Seen October 1977.

3 birds not seen again on the Tees.

9 birds with only a single sighting after ringing.

Appendix 5.3

Sightings for Y/O R during the 1976-77 and 1977-78 winters.

Date	State of tide	Location	Group size
1976-77			
8/12	LW+540	Redcar Rocks	5
11/12	LW+115	Redcar Rocks	9
22/12	LW+110	Redcar Beach	
23/12	LW+235	Redcar Rocks	Single
17/2/77	LW+130	Redcar Rocks	Single
9/3	HW+440	Redcar Rocks	9
11/3	HW+545	Redcar Rocks	4
19/3	LW+210	Redcar Rocks	10
22/3	HW+430	Redcar Rocks	Single
5/4	LW+215	Redcar Rocks	Single
12/4	HW+300	Redcar Rocks	Single
18/4	LW+230	Redcar Rocks	3
25/4	LW	Redcar Rocks	Single
1977-78			
14/10	LW	Redcar Rocks	2
16/10	HW+330	Redcar Rocks	3
18/10	HW+545	Redcar Rocks	Single
20/10	LW+:30	South Gare Sands	40
27/10	LW+:20	Redcar Rocks	7
10/11	LW+135	Redcar Rocks	2
15/11	LW+215	Redcar Beach	25
17/11	HW+420	Redcar Beach	

Appendix 5.3 cont.

Date	State of tide	Location	Group size
1977-78	cont.		
29/11	LW+140	Redcar Rocks	15
9/1/78	LW+200	Redcar Rocks	4
18/1	HW+115	South Gare Rocks	
22/1	LW+245	South Gare Rocks	
7/2	LW+140	Redcar Rocks	5
18/2	LW+445	Coatham Sands (Ducky)	14
20/2	LW+215	South Gare Sands	24
	HW+215	South Gare Rocks	
2/3	HW+400	South Gare Sands	84
6/3	LW+320	South Gare Sands	150
9/3	LW+200	South Gare Rocks	
19/3	LW+330	Redcar Rocks	10
	HW+330	Transect 4 (Coatham Sands)	13
25/3	LW+200	Redcar Rocks	10
12/4	HW+330	Redcar Rocks	10
18/4	HW+300	Transect 4 (Coatham Sands)	
25/4	LW+200	Redcar Rocks	3
9/5	HW+500	Redcar Rocks	15

Appendix 5.4

Sightings for L/R Y during the 1976-77 winter (ringed as a juvenile on 5/2/1977).

Date	State of tide	Location	Group size
11/2	HW+445	Redcar Rocks	35
15/2	LW+400	Transect 5 (Coatham Sands)	35
17/2	HW+540	Transect 5 (Coatham Sands)	5
22/2	LW+200	Transect 5 (Coatham Sands)	30
24/2		Redcar Rocks	5
3/3	LW+440	Transect 5 (Coatham Sands)	10
15/3	LW+300	Redcar Rocks	20
	LW+410	Main Roost	200
22/3	LW+300	Redcar Rocks	10
5/4	LW+215	Redcar Rocks	15
25/4	LW+130	Redcar Rocks	
27/4	HW+200	Redcar Rocks	10

Appendix 5.5

Sightings for R L during 1975-76, 1976-77 and 1977-78 winters. S G- South Gare.

Date	State of tide	Location	Group size
1975-76			
19/1	LW+315	S G Rocks	
1/21	LW+300	S G Rocks	
1/26	HW+130	S G Rocks	
2/10	LW+530		
1976-77			
7/10	LW+230	S G Sands	45
8/2	HW+340	S G Rocks	
9/2	HW+345	S G Rocks	
17/2	LW+315	S G Rocks	
22/2	LW+340	Transect 5 (Coatham Sands)	77
26/2	HW+120	S G Rocks	
	HW+400	S G Rocks	
3/3	LW+315	Main Roost	70
15/3	LW+410	Main Roost	200
1977-78			
24/8	LW+530	Transect 5 (Coatham Sands)	73
8/9	LW+440	Transect 5 (Coatham Sands)	14
20/9	HW+210	S G Rocks	
16/10	HW+330	Redcar Rocks	25
20/10	HW+435	S G Sands	77
17/11	HW+300	S G Rocks	

Appendix 5.5 cont.

Date	State of tide	Location	Group size
1977-78 cont.			
5/12	HW+130	S G Rocks	
16/1	HW+130	S G Rocks	
22/1	LW+245	S G Rocks	
25/1	LW+250	S G Rocks	
28/1	HW+435	S G Rocks	
	LW+135	S G Rocks	
8/2	LW+110	Redcar Rocks	10
20/2	LW+215	S G Sands	24
2/3	HW+130	S G Sands	37
	HW+145	S G Rocks	
9/3	LW+205	S G Rocks	
22/3	LW+430	S G Sands	46
12/4	HW+220	S G Rocks	
18/4	LW+345	S G Rocks	

Appendix 5.6 Aspects of Turnstone breeding ecology at Valassaaret, Finland.

1. Introduction

Studies of the breeding ecology/biology of waders have led to an understanding of factors determining laying schedules (Pitelka 1959 [redacted], Parmelee 1970, Holmes 1971 and 1972, [redacted] and Norton 1972), the choice of nesting habitat and nest sites (Hildén 1965, Burger et. al. 1978) and the mortality which occurs on the breeding grounds (Soikkeli 1967, 1970 and 1973 and Parmelee 1970). Some emphasis has been given to the foraging behaviour of breeding wader populations with regard to the use of space (territoriality, communal grounds for foraging etc.) (Holmes and Pitelka 1968). Detailing the foraging behaviour should help clarify the pressures (e.g., predation, food distribution etc.) which ultimately determine spacing and the 'social system' of the breeding population.

Turnstone nest in arctic Canada, Greenland, northern Alaska, Northern Europe and Siberia (Terres 1981). Birds occurring in Britain belong to two different groups (Branson et. al. 1979). Those Turnstone which stop to accumulate fat reserves on their way to Africa's west coast (autumn passage) breed in Finland and elsewhere in Northern Europe. Birds which winter in Britain and along the Atlantic coast of sout-west Europe breed in Greenland and north-east Canada. Studies of Turnstone breeding ecology have not been extensive; the most thorough account being provided by Nettleship (1973). Turnstone on their breeding grounds, as well as on the wintering grounds, have a large selection of food stuffs included in their diet (Beven & England 1977). The number of food stuffs and the techniques with which their food is gathered greatly reduces potential competition with other wader species.

My studies of breeding Turnstone on the Archipelago of Valassaaret, Finland, focused on the foraging behaviour social interactions and the distribution of nesting individuals. The very different behavioural and ecological contexts of winter survival and summer breeding discloses information regarding patterns of social behaviour and the pressures responsible for such behaviour. Here I describe the summer situation and close with a comparison of summer and winter pressures and the effects they have on the dispersion of the birds.

2. Description of the Archipelago

During the summers of 1976 (26/5 to 13/7) and 1977 (18/5 to 24/7) I studied a Turnstone population breeding on the Archipelago of Valassaaret (lat. $63^{o}25$'N and long.$21^{0}4'$E). The archipelago is situated beyond the coastal town of Björkoby, in the middle of the Quark, the narrowest portion of the Gulf of Bothnia (Fig. 1). Except for the southeast side, the archipelago is surrounded by open sea. A detailed description of the archipelago is provided by Hildén (1964), who also made extensive studies of the avifauna (1964, 1966 ~~and~~ [illegible]). Valassaaret's avifauna has been protected since 1948 and the first account of breeding birds was published by Taxell in 1934.

The archipelago consists of seven main islands and approximately 60 scattered islets, suitable for nesting birds. Most pre-laying feeding activity took place on the main islands of Storskär and Ebbskär (see Fig. 1). The sheltered coves of Törmeokroken, Antonskroken and Käringsund (Fig. 2) provide suitable feeding habitat for Turnstone during this pre-laying period. These coves, being shallow, protected, and with mud-ooze bottoms, serve as breeding areas for the considerable chironomid (Diptera) populations (Passivirta 1972).

3. Methods

During the summer of 1976 a general survey of the archipelago was made. A census area was chosen on the west side of the island group. The majority of

Figure 1

A. The island group of Valassaaret. Important islands and islets of the study:

1. Ljusgrund
2. Norderstören
3. Ebbskär
4. Storskär
5. Tuorelarev
6. Käringbåda
7. Yttre Oxgrynna
8. Långgrynna
9. Bullergrynna
10. Bredbåda

b. Location of the island group of Valassaaret (boxed area) within the Gulf of Bothnia.

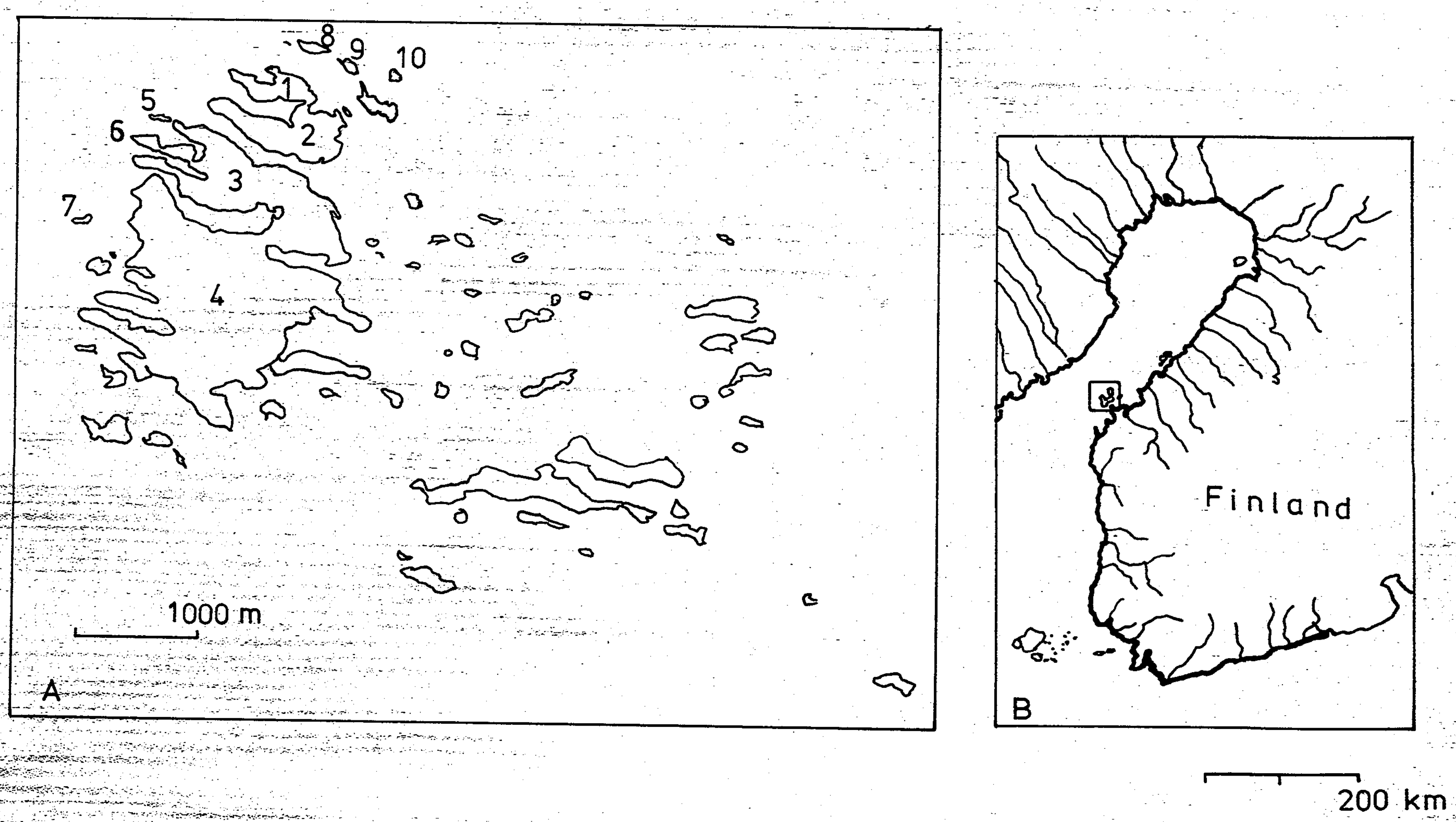
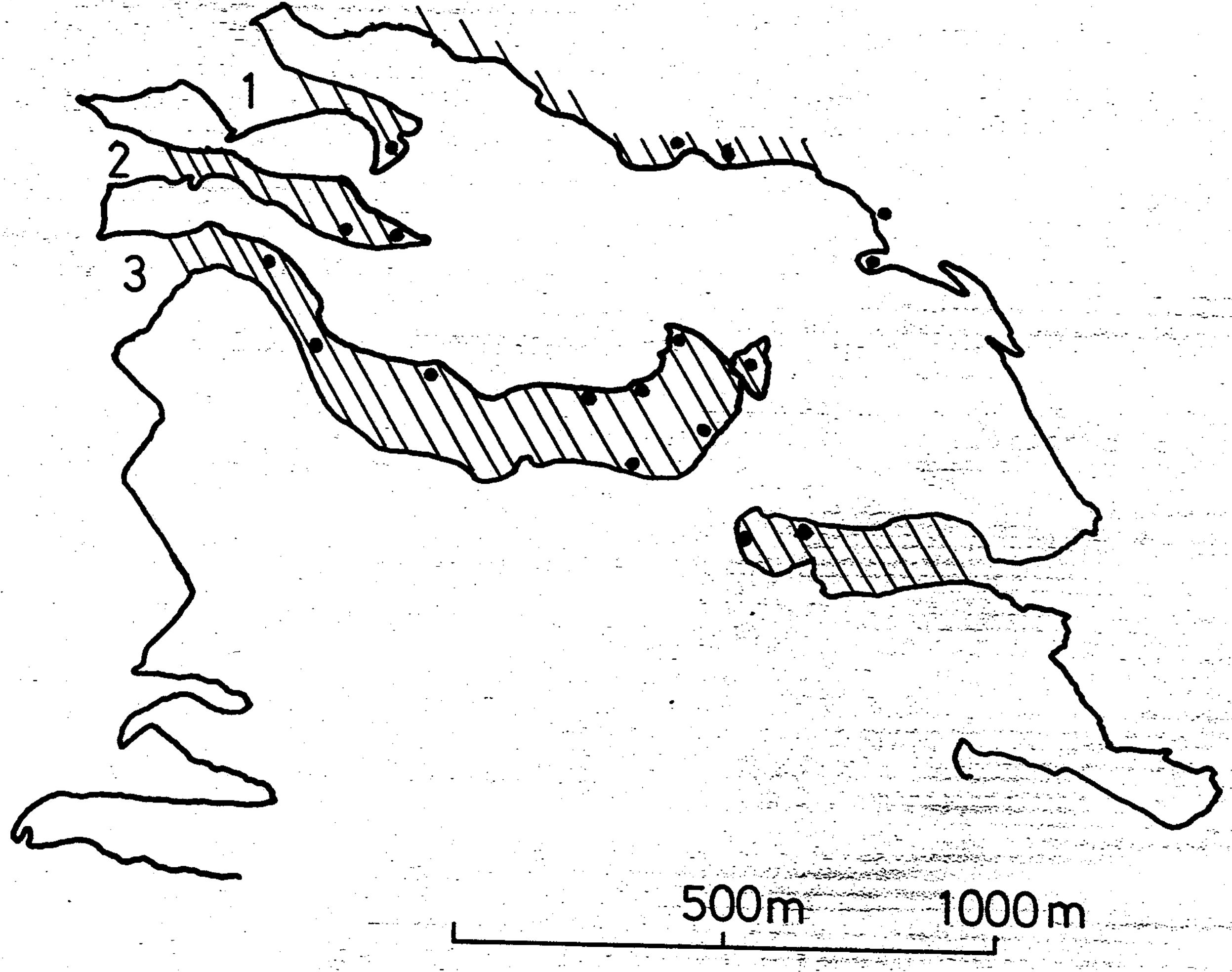

8
9
10
1
5
2
6
3
7
4
1000 m
A
Finland
B
200 km

Figure 2

Location of feeding observations. Lined areas show location of *Tanytarsus gracilentus*, Holmgr, after Paasivirta (1972).

Coves: (1) Törmeokroken,
(2) Antonskroken,
(3) Käringsund.


1
2
3
500m
1000m

data presented here are from the observations during the summer of 1977.

On each visit to the census area (several daily) one of two circuits was followed (Fig. 3). Observations were made along the circuits to determine the activity patterns and location of feeding individuals. Sightings of all predators were noted.

Observations on feeding rate and time spent in activities other than feeding (e.g., surveillance and aggression etc.) were designed to distinguish any difference in the feeding behaivour of males and females. Observations quantifying feeding substrate and feeding rates were made. As it was not possible to determine each success or the specific food items taken, the rate of contact (pecks, probes or rock-turning/minute) with the feeding substrate was measured. To determine advantages gained from feeding with a bird's mate or near conspecifics, I measured the postural behaviour of the foraging individual. Six movements (of varying intensity, and used to determine "wariness" of the bird) were selected (Table 1), and their frequency measured. Taped commentaries were made on foraging individuals, noting the frequency of each of the six position and the feeding rates. Interactions amongst conspecifics were also noted. These commentaries were suspended on 26/6 1977.

Census work determined changes in distribution

Figure 3

Main circuits for census and distribution studies, 1977.

Coves: (1) Törmeokroken,
(2) Antonskroken,
(3) Käringsund.

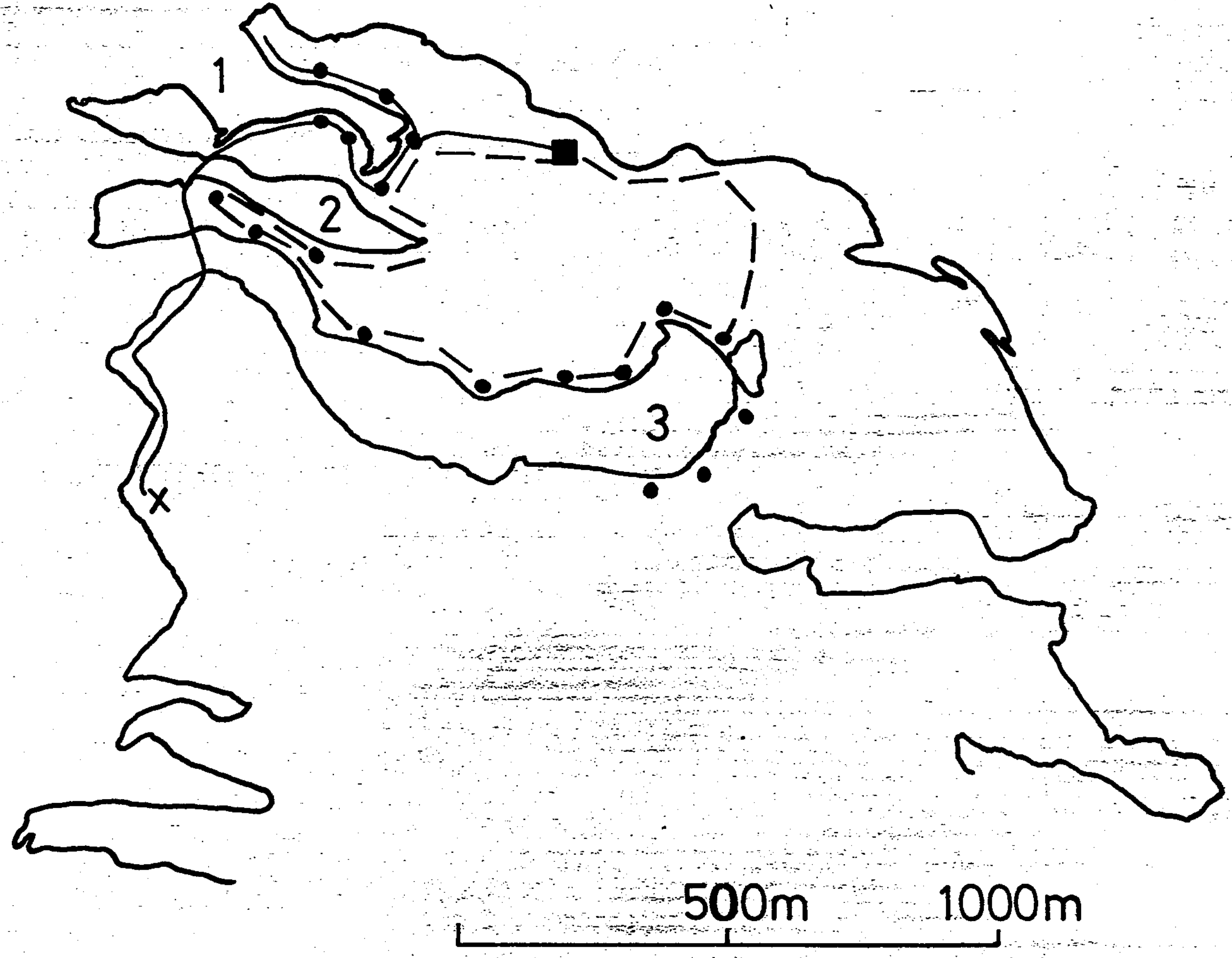

1
2
3
500m
1000m

TABLE 1

Description of six positions, measured during feeding observations.

Position*	Abbreviation	Description
Head-Up	HU	The bird brings its head up to a horizontal position, not in threat, and clearly away from the feeding surface.
Pause	P	The bird brings its head up and remains stationary.
Look-Around	LA	The bird brings the head up and turns the neck through 90° or more.
Head-Tilt	HT	The bird brings the head up and then tilts the neck so that one eye is looking up into the sky.
Neck-Stretch	NS	The bird stretches the body and neck upwards. Most common when feeding behind rocks or in rushes.
Crouch	C	Similar to an aggressive posture but in the context acts as a flight intention movement.

* Positions represent an increasing degree of wariness,

at Valassaaret during the pre-laying period and the laying and incubating periods.

Aspects of breeding biology were studied on the main islands and on several surrounding islets. On Yttre Oxgrynna (see Fig. 1), extended periods of observations were made from a portable hide. A total of 250 observation hours were made on Yttre Oxgrynna in 1977 of which 50 hours were spent observing parental care and attention of eggs and fledglings. Of the 20 territorial Turnstone on Yttre Oxgrynna, 15 were easily recognized by coloured rings or head patterns (see Ferns 1978).

The location of nests, laying and hatching schedules, territory size and defence behaviour were monitored. Observations were made to establish the territorial boundaries of nesting Turnstone. The behaviour of defending individuals was observed. After each observational session, all points of territorial contact and display were placed on a map of the area and used to determine size of territories and location of shared boundaries.

4. Results

4a. Feeding behaviour

The 1977 observations on feeding behaviour are presented in Table 2. Observations are divided into

TABLE 2 .

Feeding results from 1977 observations.

	Female solo	Female others	Female pair	Male solo	Male others	Male pair	Yttre Oxggrynna
Total time in minutes	6.7	11.9	80.8	36.0	81.5	126.8	30.2
Number of observations	3	7	34	6	22	37	14
Pause per/min	1.98 ±0.7	0.5 ±0.3	0.8 ±0.1	1.6 ±0.4	0.7 ±0.1	1.2 ±0.2	0.3 ±0.1
Head-Up per/min	22.6 ±3.0	2.6 ±1.3	5.3 ±0.7	19.4 ±2.0	6.0 ±0.5	9.6 ±0.8	2.7 ±0.6
Look-Around etc. per/min	4.2 ±0.5	1.1 ±1.1	1.6 ±0.3	4.0 ±1.0	1.5 ±0.2	2.9 ±0.4	1.0 ±0.2
Pause* % of time	9.7	5.3	3.6	5.6	2.8	8.2	0
Pause total time	0.6	0.6	2.9	2.0	2.2	10.4	0
Aggression % of time	0	0	0	0	3.7	4.5	0
Aggression total time	0	0	0	0	2.9	5.7	0

* As the Pause is only a momentary movement, not each Pause contributes to Pause-% of time, (i.e., the time contributed varies with each Pause movement).

seven categories, three each for males and females and a seventh, taken solely from Yttre Oxgrynna (males and females combined and representing birds feeding within their breeding territory). Apart from this final category, all observations are of birds feeding in the communal coves and off their breeding territories. The Head-Up and Pause positions, are analyzed independently in Table 2 while the Look-Around, Head-Tilt, Neck-Stretch and Crouch behaviours have been grouped. Although comparisons between categories for a given behaviour are not all statistically significant (due to a lack of data), trends are present. For females, the percentage of time spent feeding is greater when feeding with conspecifics or with their mates than when feeding alone. In all rows, the male's disruption during feeding is greater when feeding with its mate or in the absence of conspecifics. Due to the small sample sizes I have not attempted to separate the observations into those where only the pair was present from those where a pair was feeding near other conspecifics. (Some of the male's wariness may be associated with protection of the female from other males.) Females are only very rarely seen feeding on their own.

Table 3 presents a similar analysis as that shown in Table 2 but refers to members of three feeding pairs. Again, these observations were on individuals feeding in the communal coves. For all three sets of

TABLE 3

Feeding performance for pairs, 1977 observations.

	Female	Male	Female	Male	Female	Male
Observation time-min	4.0	14.8	14.2	12.5	5.1	10.8
Pause per/min	0.4	0.8	0.6	1.3	1.4	3.5
Head Up per/min	3.6	4.5	5.7	7.2	5.6	15.0
Look-Around etc. per/min	0.8	1.6	0.8	3.0	0.6	4.4
Pause % of time	0.1	7.2	0.3	2.0	10.0	27.0
Aggression % of time	0	0	0	0	0	10.1
Feeding rate per/min	55	42	79	64	28	15
Time feeding % of total	99.1	92.8	99.7	98.0	90.0	62.9

observations both male and female were feeding on chironomids. Although there is no statistical support for the conclusions, the trends are clear in each case. The female spent more time on feeding, as opposed to aggression or in the Pause position, than the male. Potential predators were seen throughout the study period (Table 4) and elicited strong responses from the Turnstone.

4b. Chironomid swarms-effects on Turnstone distribution and breeding behaviour

Chironomid are the dominant group within the macroscopic bottom fauna of the coves at Valassaaret (Passivirta 1972). Within five days after the beginning of emergence, 91% of the total number of Tanytarsus gracilentus (Holmgr) had emerged in one trap and 59% in another (data for 1968, Passivirta 1972). Passivirta found that in 1968, the swarming of this species occurred from 30/5 to 4/6. The species has a very distinct peak of availability. The large number of Turnstone which fed in the coves during the pre-laying season did so in response to the increase in chironomid numbers. These dipterans comprised a transient food source, localized in the coves. Sexual and territorial behaviour attributed to birds about to breed nearly ceased when the swarms were at their peak. There was a general suspension of breeding behaviour with many

TABLE 4

Potential predators present on the Archipelago of Valassaaret.

The predators listed here are for adult Turnstone or their eggs and young. Sightings concentrated on Yttre Oxgrynna and the protection the Turnstone received from tern and gulls (althougk gulls are also seen as potential predators of Turnstone eggs and young).

18/5	1815 White-tailed Eagle above Storskar.
19/5	Osprey and female Kestrel seen.
20/5	0600 Hawk Owl near Käringsund.
	0700 Hooded Crow at Antonskroken, chased by terns.
21/5	2000 Hawk Owl at Törmeokroken, no Turnstone present.
22/5	1400 Yttre Oxgrynna, two Hooded Crows, chased by gulls and terns.
	1720 Hawk Owl hunting at Käringsund, no Turnstone present.
26/5	1130 Ten Hooded Crows at Käringsund.
27/5	1000 Hawk Owl at Antonskroken, Redshank not bothered.
29/5	0900 Hobby hunting at Käringsund, driven away by several terns.
1/6	1200 Harrier (Marsh ?) over Törmeokroken, chased by terns.
2/6	Honey Buzzard seen, few on migration until 10/6.
3/6	1230 Hawk Owl feeding at Törmeokroken.
	Osprey over Käringsund.
	Short-eared Owl and two Kestrels.
	Goshawk seen by Lighthouse.
7/6	0830 Hawk Owl and Merlin seen at Törmeokroken, no Turnstone seen. Both birds being chased by terns and gulls.
	1600 Great Black-backed Gull at Törmeokroken, being chased by terns.
10/6	1630 Hooded Crow at Käringsund, being chased by Turnstone, the first time of the season.
19/6	Short-eared Owl off Käringsund (nest is near), being chased relentlessly by gulls and terns.
26/6	2400 Yttre Oxgrynna, Arctic Skua causing commotion.
8/7	2100 Yttre Oxgrynna, Arctic Skua over islet, put off by two terns.

9/7 1100 Yttre Oxgrynna, Arctic Skua at the end of the islet, by Eider chicks, driven off by several terns.

2100 Yttre Oxgrynna, Common Gull being attacked by terns.

10/7 1000 Osprey over Yttre Oxgrynna, Common Gulls and terns drive it away.

11/7 1130 Yttre Oxgrynna, Common Gull overhead, terns all rise up.

1230 Three Common Gulls loafing on Yttre Oxgrynna, put off by terns.

2200 Osprey above Yttre Oxgrynna, driven off by a single tern and a single Common Gull.

12/7 1300 Yttre Oxgrynna, three Common Gulls overhead, driven off by terns.

1400 Yttre Oxgrynna, Common Gull overhead, terns rise and attack.

13/7 1030 Yttre Oxgrynna, Hooded Crow overhead, driven off by several terns.

14/7 0700 Yttre Oxgrynna, Great Black-backed Gull overhead, driven off by several terns.

16/7 0700 Young Hawk Owl over Yttre Oxgrynna, driven off by terns.

1100 Great Black-backed Gull over Yttre Oxgrynna, driven off by terns.

1400 Arctic Skua over Yttre Oxgrynna, driven off by terns and Common Gulls.

1700 Herring Gull takes young Scaup from the water at Tormeokroken.

Female Kestrel found dead and eaten, hanging from an Alder tree.

17/7 1700 Yttre Oxgrynna, terns chase Common Gull.

1800 Yttre Oxgrynna, Hooded Crow chased by terns and Redshank.

21/7 1200 Yttre Oxgrynna, two Hooded Crows chased by terns.

23/7 1800 Yttre Oxgrynna, Hooded Crow chased by Common Gulls.

territories left deserted.

The advent of the chironomid swarms in late May to early June altered the foraging behaviour of the Turnstone. At the time of the swarms, Turnstone switched from feeding in tight protected pairs to feeding in concentrated groups. The greatest feeding activity was at Käringsund. There was an influx of Turnstone feeding in the communal coves with the increase in the swarms (Fig. 4). The first day of major chironomid activity, was May 26, 1977. By June 1st enormous swarms were present. Inclement weather reduced the chironomid's activity on June 3, and on the 4th of June the entire archipelago was engulfed by heavy downpours. The largest numbers of Turnstone in the coves appeared on June 5. A marked decrease in the presence of chironomid swarms occurred on the 6th of June. At this time, Turnstone using the coves also decreased and continued to do so until June 12th when virtually no Turnstone were found in Käringsund. Despite the occurrence of large swarms of 13/6, few Turnstone foraged in the coves. By 2/7 there was a near-total disappearance of Turnstone from Käringsund (19/6 for Antonskroken and 22/6 for Törmeokroken).

In Fig. 5 the use of Käringsund by single males, single females and pairs is shown. At no time were single females common. Single males may represent unmated individuals, mates of females who are at the nest,

Figure 4

Numbers of Turnstone feeding in the coves, 1977. Solid line- birds feeding in Käringsund. Broken line- total for Törmeokroken, Antonskroken, and Käringsund. All numbers are averages for all counts of any particular day.

Arrows:

⤈ Moderate chironomid activity

↓ Heavy chironomid activity

R Rain

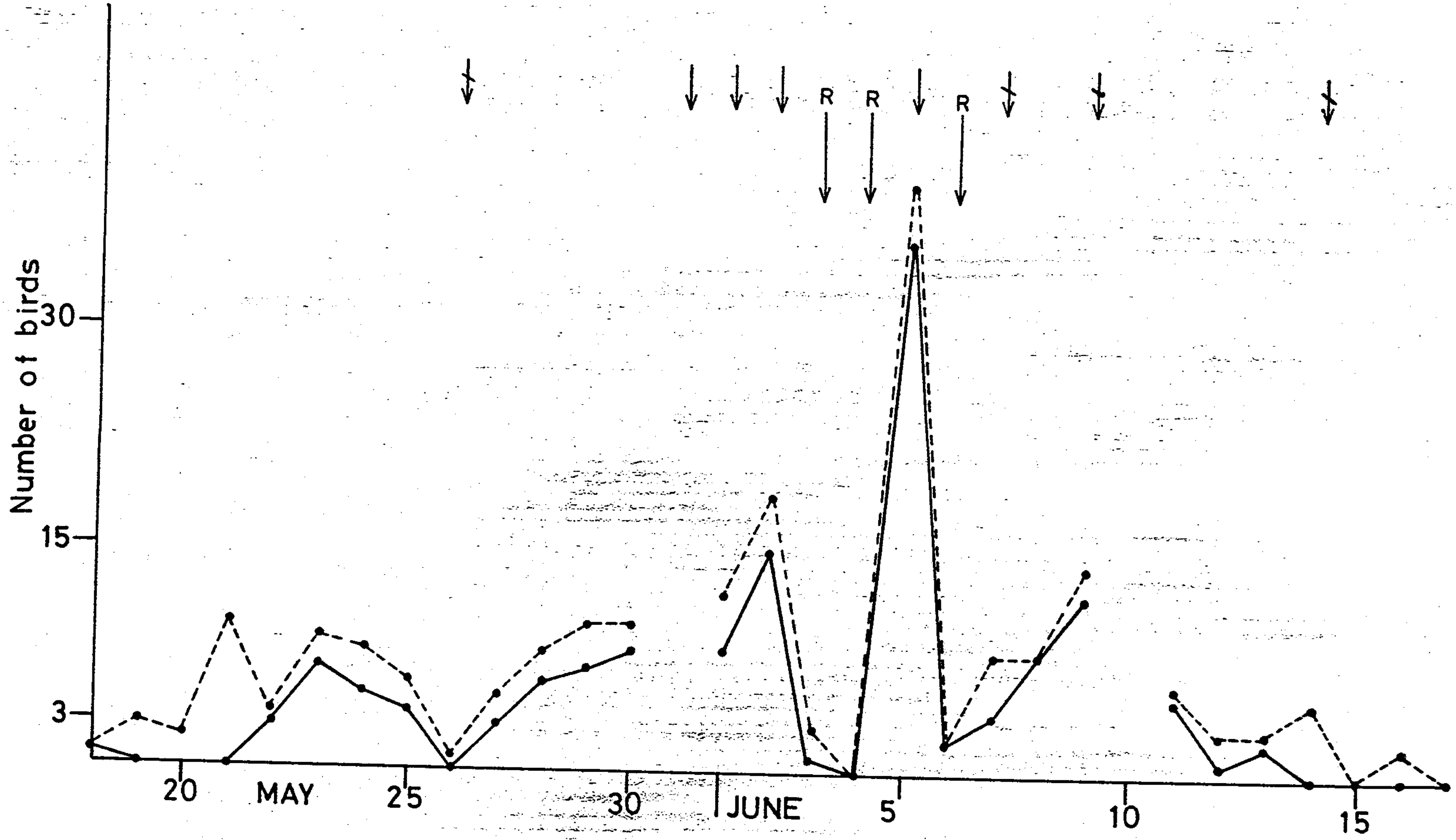
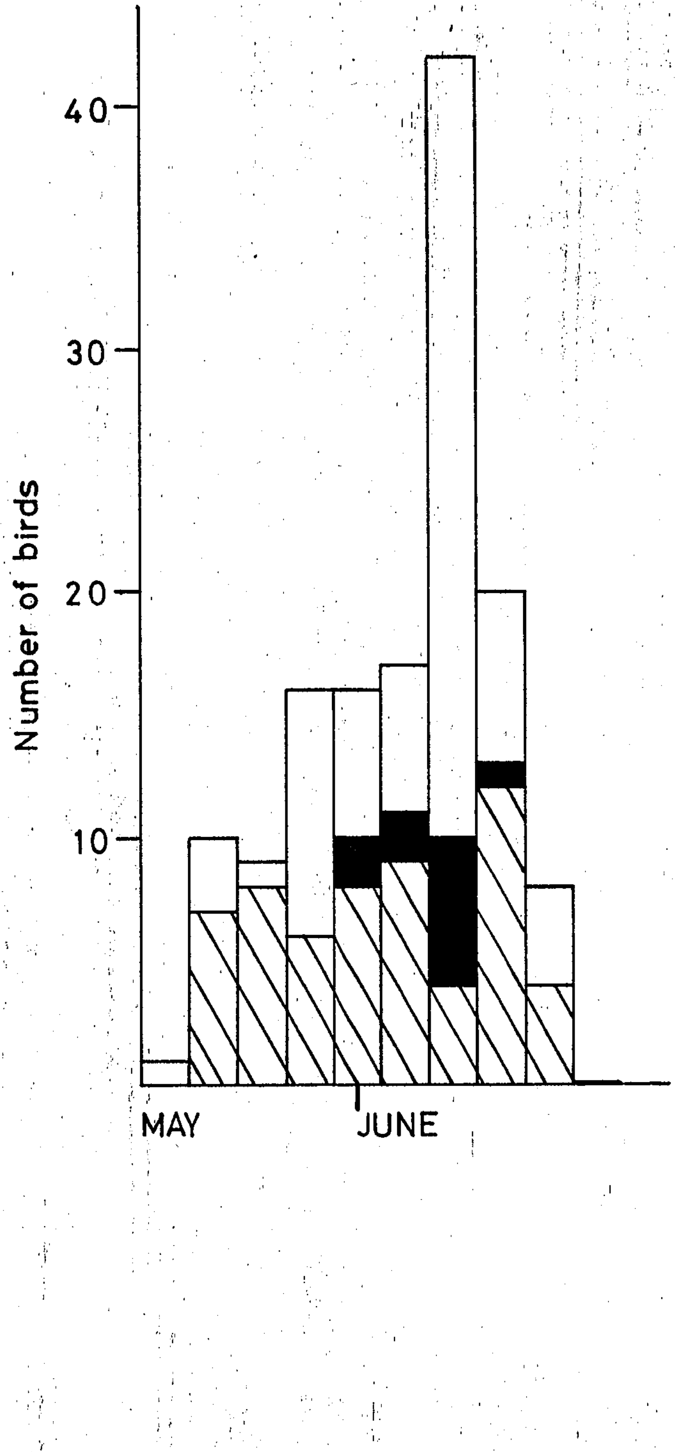

Number of birds
3
15
30
20
MAY
25
30
JUNE
5
10
15
R
R
R

Figure 5

Numbers of Turnstone feeding in Käringsund, 1977. Numbers are averages for counts over three day periods, the first being 18/5 to 20/5. Open area of the histogram- single males, solid area- single females, and diagonals- birds in pairs.


Number of birds
40
30
20
10
MAY
JUNE

or members of pairs who nested unsuccessfully. On 30/5 1977 most of the Turnstone present on Yttre Oxgrynna were females. It is likely that most of the males were still feeding in the coves. Within the larid colonies of Yttre Oxgrynna the females could feed and still have protection from predators, near the larids. Turnstone from Yttre could be seen flying in the direction of the coves (Fig. 6) There was no pattern to the birds' leaving. Birds ceased leaving the islet once laying began. The date of the first egg for clutches on Yttre Oxgrynna was from June 1 to June 9 (Table 5). Once laying began the birds spent all their time on Yttre Oxgrynna.

4c. Main islands vs. islet nesters

Basic differences occurred between birds nesting on the main islands and those nesting on the islets. Differences included the amount of separation tolerated (distance) within a pair, the feeding area used by the non-incubating parent and the Turnstone's predation on larid eggs. These differences were due, in part, to necessary vocal contact and the food resources available in the different areas.

For those individuals nesting on the main islands the coves were still available for feeding once laying began. Birds could feed in the coves and still communicate with the sitting mate. The opportunity for

Figure 6

Numbers of Turnstone leaving Yttre, per hour.

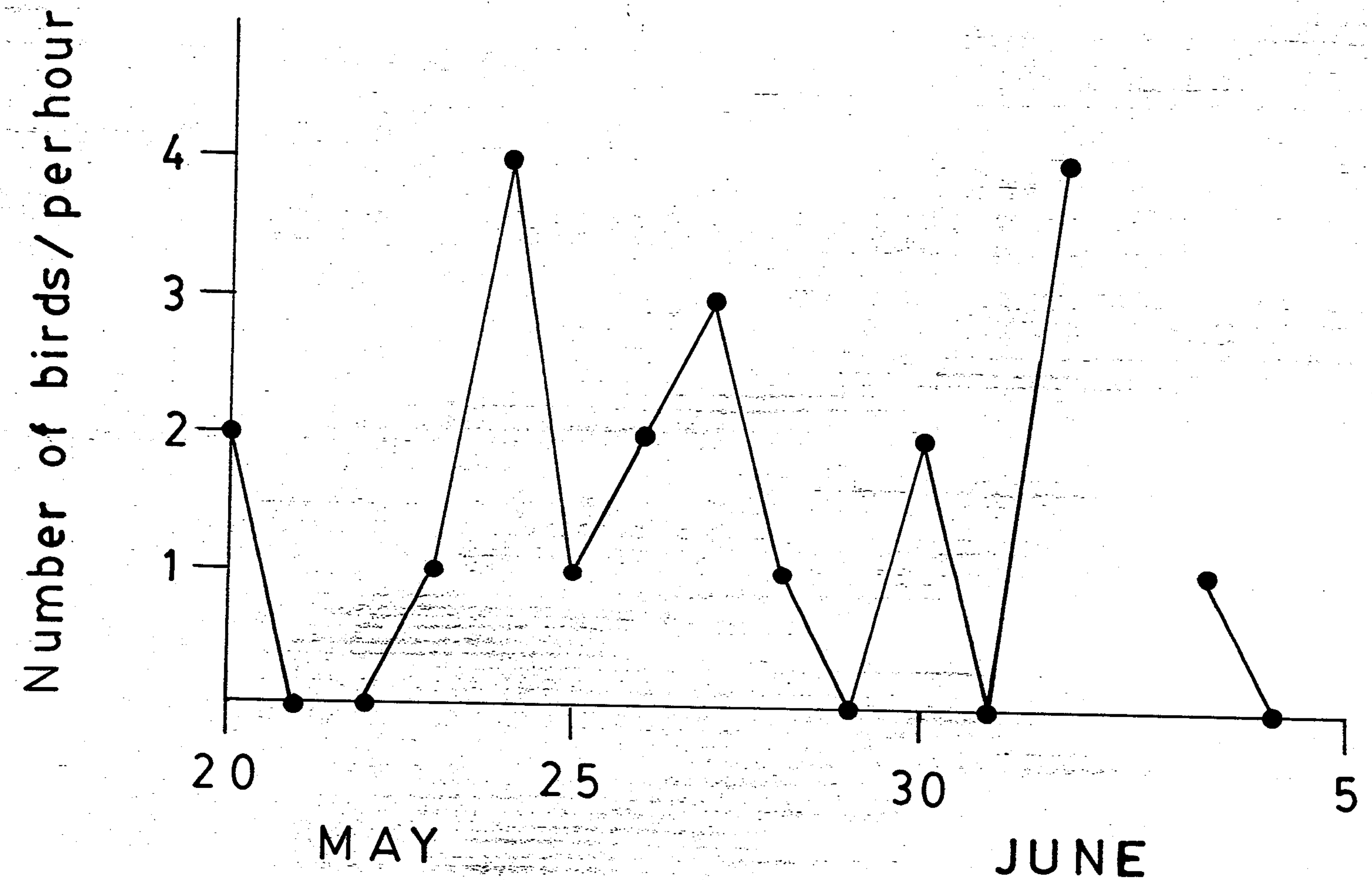

Number of birds/ per hour
4
3
2
1
20
25
30
5
MAY
JUNE

TABLE 5

Laying data for 1977.

Nest Site	First Egg	Hatching Begun	Hatching
Yttre Oxgrynna#			
1	7/6	30/6	4/7
2	4/6	29/6	1/7
3*	2/6	--	28/6
4	6/6	29/6	3/7
6	9/6	29/6	6/7
8	8/6	--	5/7
9	1/6	27/6	28/6
10	3/6	--	30/6
Tuorelarev**	7/6	29/6	2/7
Prior to Tuorelarev	2/6	27/6	28/6
Käringbada	14/6	9/7	11/7
Prior to Käringbada **	16/6	--	8/7
Bredbådagrynna	11/6	--	--

Numbers refer to the territory in which these pairs were found, on Yttre.

* Three egg nests.

** Two egg nests.

All other nests had complete clutches of four eggs.

visual or auditory communication between members of a pair helps to determine the amount of spatial separation that is tolerated. Care of the nest and of the young is done jointly and necessitates constant communication.

Birds nesting on the main island continued to utilize the cove areas of Törmeokroken and Antonskroken, although they did not penetrate as far as during the pre-nesting period. These birds maintained feeding territories along the opening of the coves. The coloured-marked birds of these areas (Table 6) were frequently seen within the coves adjacent to their nesting areas. When I approached a nest, the incubating individual flew several metres from the nest, calling in territorial defence. This caused the mate feeding in the cove to return. The distances from islets to coves were too great for communication to be possible between an incubating and cove-feeding individual.

Laying data for 1977 has been presented in Table 5. It should be noted that the time spread in laying and hatching on Yttre Oxgrynna (1/6 to 9/6 for the first egg and 28/6 to 6/7 for hatching) was considerably shorter than for all thirteen nests followed (1/6 to 16/6 for the first egg and 28/6 to 11/7 for hatching). Data on individually marked birds are presented in Tables 5 and 6.

TABLE 6.

Location and biometrics of ringed Turnstone.

Nest location	Date Ringed	Sex	Weight,g	Bill (mm)	Wing (mm)
Yttre Oxgrunna					
1	22/6	F	100	25	157
2	17/6	F	103.5	22	157
2	26/6	M	116	24	159
3	24/6	F	104	24	157
4	23/6	M	110	24	161
5	14/6	M	108	23	155
6	25/6	F	108	24	160
7	22/6	M	102	23	153
8	24/6	M	106	23	153
9	25/6	M	104	23	154
10	26/6	M	108	23	159
Tuorelarev	16/6	M	96.5	25	153
Prior to Tuorelarev	13/6	M	94	25	159
Käringbada	22/6	F	94	23	152
	Females				
	Average		102	23.6	156.6
	Range		94-108	22-25	152-160
	Males				
	Average		105	23.7	156.2
	Range		94-116	23-25	153-161

4d. Territory size, territorial behaviour and the Head-Bob

Considering the total area used for nesting territories at Valassaaret (4.4 km^2) and a Turnstone population of approximately 160 pairs, breeding densities were 36.8 pairs/km^2. (Compare this with the 3.04 pairs/km^2 found by Nettleship (1973) at Camp Hazen, N.W.T., Canada.)

The location of all nesting species on Yttre Oxgrynna is shown in Fig. 7. The average size of Turnstone territory on Yttre Oxgrynna was 769 m^2 (1306 pairs/km^2) with a range of 142 m^2 to 1939 m^2. Vegetation maps for two Turnstone territories on Yttre Oxgrynna are shown in Fig. 8. The entire area of the islet was encorporated into the ten Turnstone territories. This appeared to be the situation on all islets which I visited. Territorial defence was very strict. Intruding Turnstone were immediately recognized and driven from the islet. Relatively little aerial chasing of avian predators by the Turnstone occurred, due to the larids' efficiency in driving predators off.

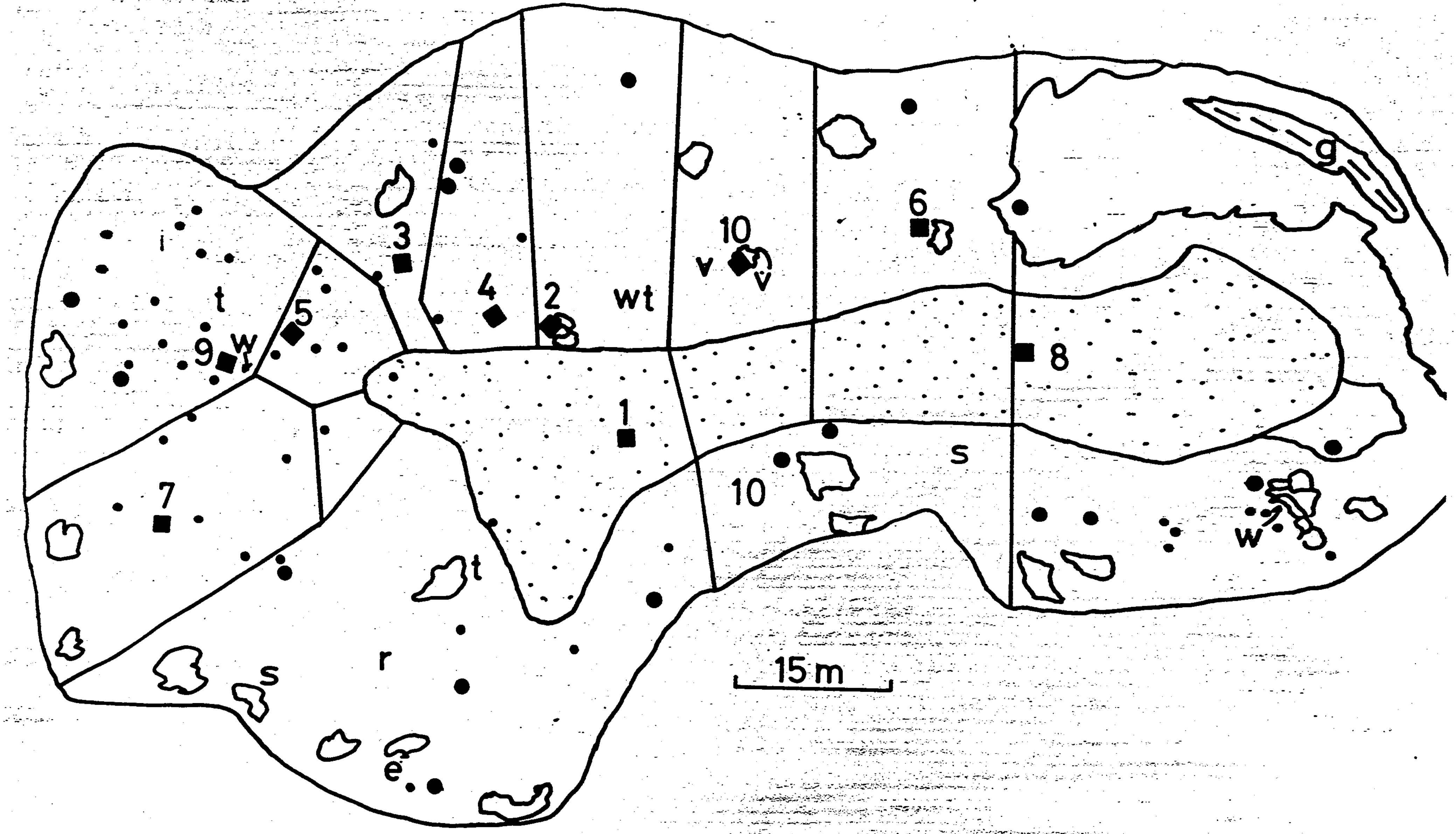
Both members of the pair engaged in the defence of the territory. Throughout this period there continued to be much communication between the male and female. The call of the guarding or incubating member immediately retrieved its mate. Although the female engaged in aerial attacks against both predators and other Turnstone,

Figure 7

Location of all nests on Yttre.

Squares-	Turnstone
Small dots-	Tern (Arctic and Common)
Large dots-	Common Gulls
g-	Black Guillemot
t-	Tufted Duck
s-	Scaup
e-	Eider
w-	Wagtail
r-	Redshank
v-	Velvet Scoter
wt-	Wheatear

Numbers refer to Turnstone territories.


i
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9
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wt
10
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10
6
8
g
s
w
t
r
s
e
15 m

Figure 8 (a,b).

Vegetation and nest location on Turnstone territories, 1(a) and 6(b), on Yttre.

Legend:

R- *Rubus*

H- *Hippophaë*

// - *Chrysanthemum*

≡ - *Scirpus*

||| - *Chamaenerion*

☁ - rocks

∴ - sand

GR- Guard Rock

X- Turnstone nest

s- Scaup

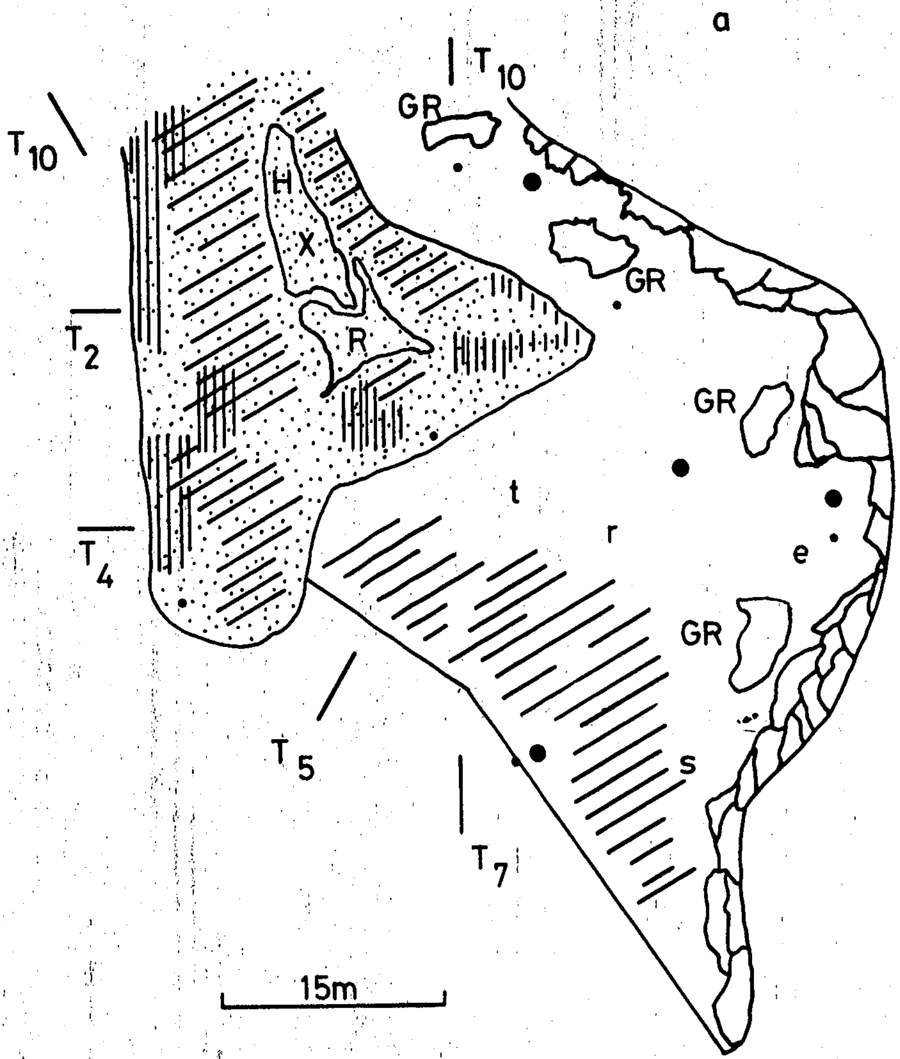
t- Tufted Duck

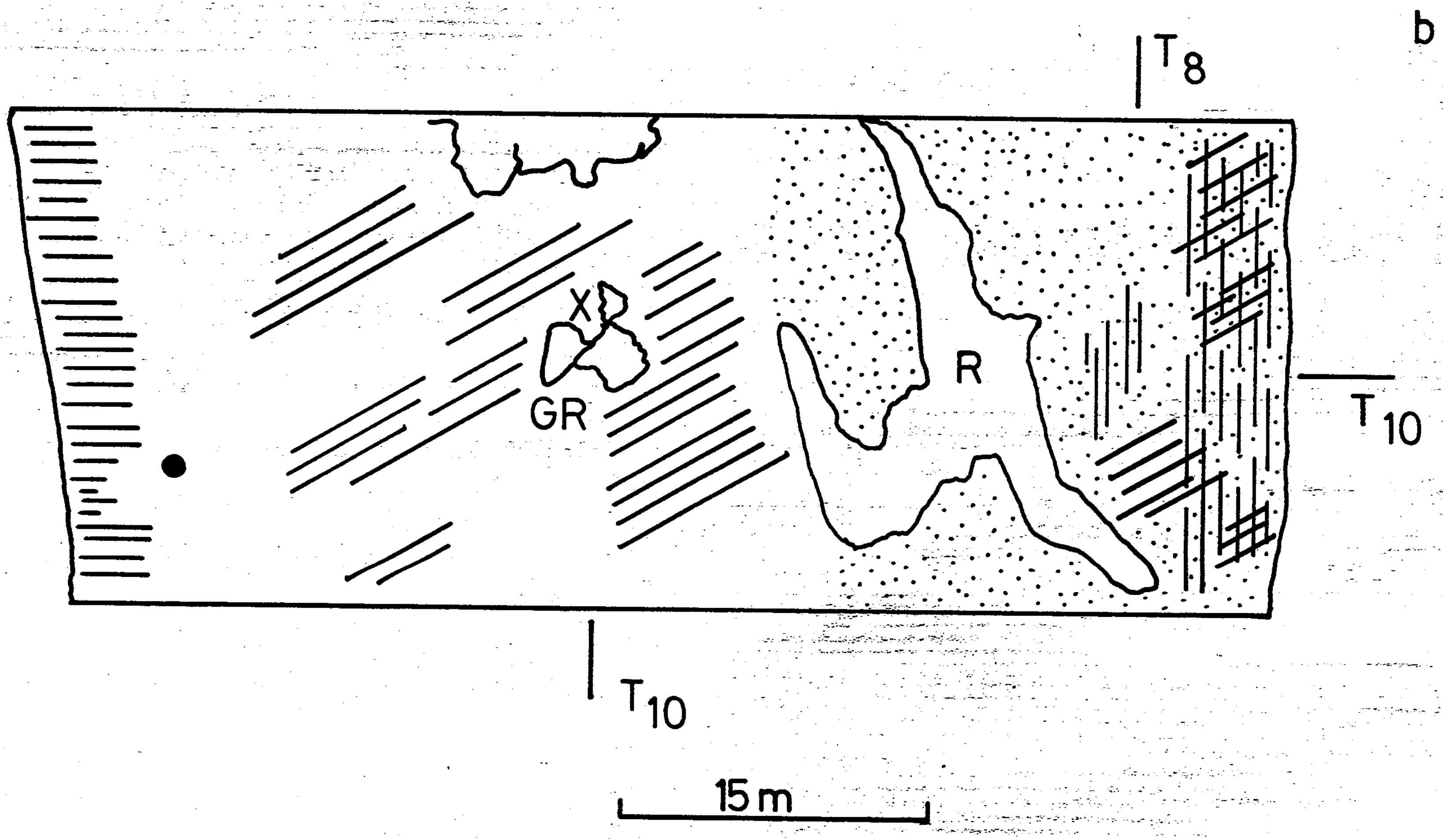
r- Redshank

e- Eider

● - Common Gull

• - Tern (Arctic and Common)


a
T$_{10}$
T$_{10}$
GR
H
X
GR
R
T$_2$
GR
t
r
e
T$_4$
GR
T$_5$
s
T$_7$
15m


b
T_8
T_{10}
R
X
GR
T_{10}
15 m

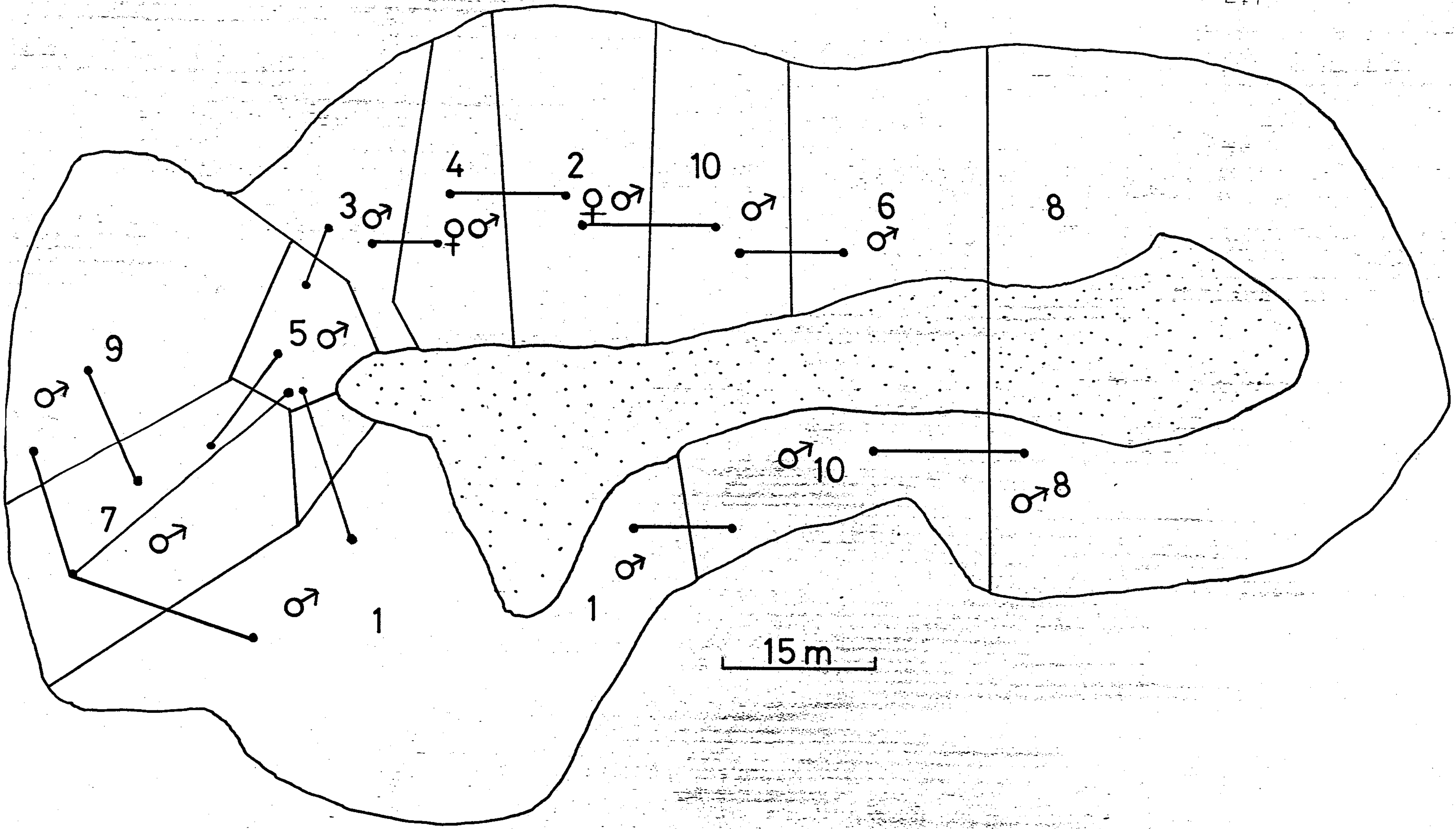
she often incited the male to attack while she remained guarding the nest. During 19.7 hours of observations, 19 aerial attacks were recorded. Of these attacks, four were directed towards larids (two by each a male and female Turnstone) and fifteen were directed towards intruding Turnstone (six by the territorial female and thirteen by the territorial male).

Activities such as territorial warning were centred about the guard rocks. These were large rocks which provided good vantage points. The young were often kept close to these rocks. In territories 2,3,4, 6, and 10 (see Fig. 7) the nest sites and guard rocks were the same.

The particular display of Head-Bob (Bergman 1946) greatly mollified potentially harmful aggression. Head-Bobbing occurred between two males, two females or with as many as five individuals at the boundaries of territories and on the communal feeding areas. The behaviour also occurred between members of a pair, as a greeting following an aggressive encounter with an intruder or larid. Neighbouring pairs would Head-Bob together when off their territory (not so when non-neighbouring memebers met). Those sets of pairs which engaged in the Head-Bob display are shown in Fig. 9. On several occasions when two males, sharing territorial borders, put off an intruding Turnstone, they returned to their borders and began Head-Bobbing together. There were many instances when two or three neighbouring

Figure. 99

Combinations of territorial birds participating in Head-Bobbing. Lines connect territories that engaged in the Head-Bob display. Sex of participating member is indicated.


4
2
10
3 ♂
♀ ♂
♀ ♂
♂
6
♂
8
5 ♂
9
♂
7
♂
♂
1
♂
1
♂ 10
♂ 8
15 m

males would jointly drive an intruding individual from the islet. Upon their return they would often Head-Bob together.

4e. Clutch size and hatching success

Eighteen nests were found in 1977 (Table 7). Three nests had two eggs. At Yttre Oxgrynna, nest number 5 was destroyed on 14/5; it is not known if it was completed or not.

All the young of any one nest hatched on the same day. On Yttre Oxgrynna, nest 6 had hatching times of 1420 to 2100 hours and nest 9 had hatching times of 1000 to 2100 hours. The cracking of shells was extremely variable. Of the 31 eggs followed, 23 began cracking two to four days before hatching. Once clutch of four showed no signs of cracking 24 hours before they hatched and another clutch of four began cracking seven days before hatching!

4f. Incubation

Not much data were collected on the incubating roles of male and female. For eleven nests, 71 spot records were made, mainly between the hours of 0800 and 2300. Of these sightings, 46 were of the female at the nest. During the first seven days of incubation there were only eight sightings, four for each male and female.

TABLE 7

Clutch size and hatching success.

Location	Clutch Size- 2	3	4	Total Eggs	Hatching Success
Yttre Oxgynna	1	1	8	37	(30) 81%
Main Islands	2		2	12	(11) 92%
Other Islets		1	3		
Total	3	2	13		

For days 8 to 14, 18 of the 24 sightings were for females. During the period of the 15th day until hatching, 24 of the 39 sightings were of females. Contrary to the suggestion that females incubate from sunrise to 1500 or 1700 hours and males the rest of the day and night (Bergman 1946), no differences could be detected for various times of the day. Differences were seen in individual nests. At no nest did the male do the majority of the incubating. At nest 1 (Yttre Oxgrynna) the male was never seen on the nest, although it was seldom absent from the territroy. The male was very rearely seen at nest 3 (Yttre Oxgrynna) although seldom absent from the area.

4g. The young and the effects of vegetation

Weights, growth and bill length of the young are presented in Table 8. The young were capable of leaving the nest on the day of hatching. On Yttre Oxgrynna the nest was used for much of the fledging period. The young were taken to areas where they could feed on chironomids. They usually first ventured out to feed with the male, who pecked at their feet while they imitated. From all observations, chironomids were the main food source for the young birds. This had a great influence on where the adults took the young and on the overall use of the territory. Chironomids were active on/about _Rubus_ and _Chrysanthemum_, even during

TABLE 8

Growth of colour-marked Turnstone young, 1977.

Age, in days	Weight, in g	Bill length, in cm	Number measured
Day of hatch	11.8	1.10	22
1	11.8	1.14	9
2	13.0	1.22	2
3	14.5	1.33	2
4	21.0	1.43	3
6	28.0	1.61	1
7	31.2	1.62	3
8	38.0	1.62	1
11	39.3	1.78	2
12	40.2	1.78	3
14	45.0	1.83	4
16	56.0	1.85	1
17	57.5	1.90	2
18	58.0	1.94	2
19	60.5	1.97	2

inclement weather. During the first days after hatching, the young had to rely on taking food from the ground. Within three to five days they were taking food from plant stems and leaves. At this time they still had some difficulty in obtaining moving chironomids. It was thus important to have an area where the young could feed on stationary dipterans. In the more dense vegetation where enough warmth was trapped and protection provided for the chironomid, young birds could feed even on rainy days.

4h. Breakdown in territories and territorial behaviour

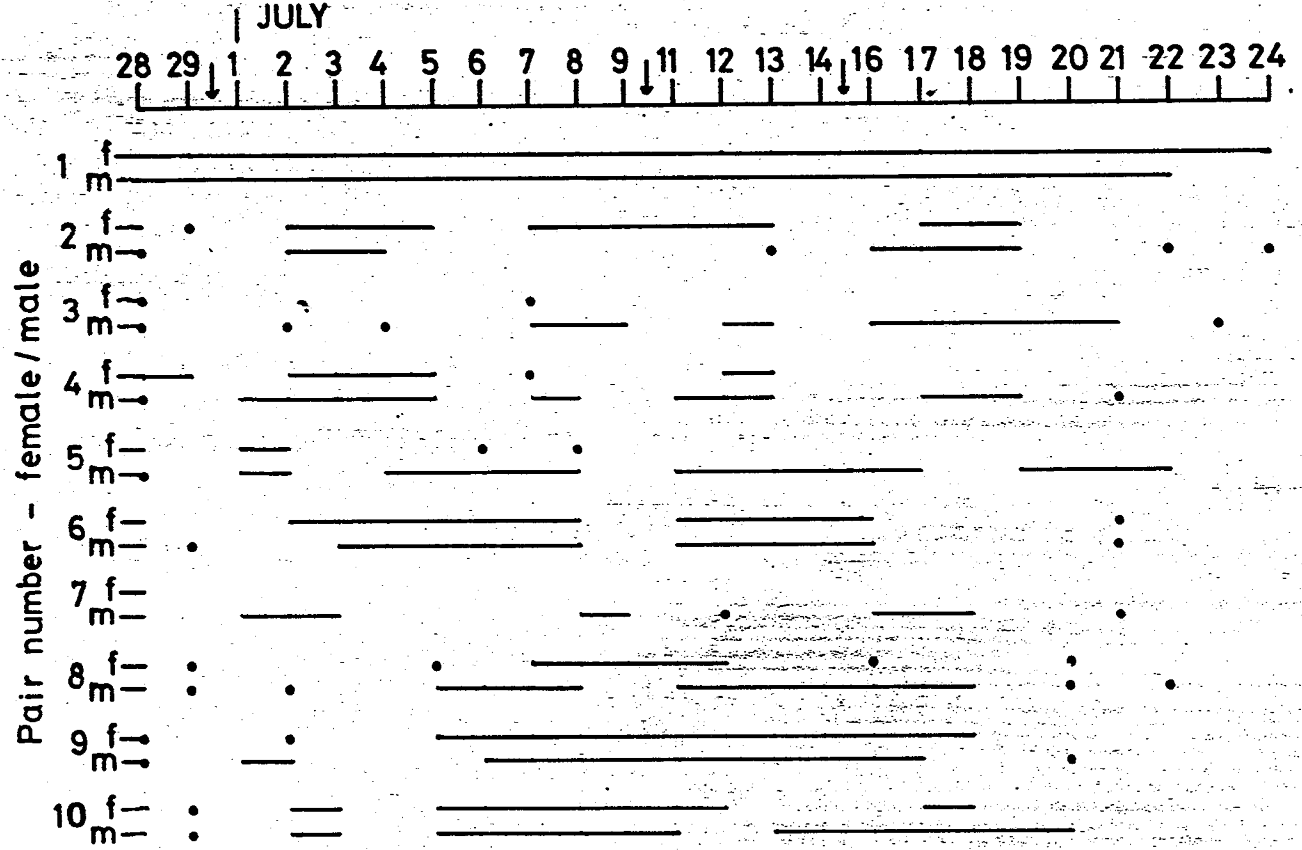
Territorial behaviour of Turnstone is known to decline with the onset of incubation (Nettleship 1973) and during the fledging period (Beven & England 1977). The situation is markedly different on the islets. As the birds are confined to the territory after hatching has occurred, territorial behaviour continued. It has also been stated (Nettleship 1973 and Beven & England 1977) that the female leaves early on during the fledging period. This was not the situation at Valassaaret. The pair nesting beyond Törmeokroken was intact 19 days after its two young had hatched. In many territories the female played an active roll in caring for and protecting the young. At nest 1 (Yttre Oxgrynna) it was the female that remained last with the young, the male being seen last on 23/7, 19 days after the young had hatched.

The situation on Yttre Oxgrynna was greatly disrupted by a series of severe storms (1/7 to 4/7) which flooded much of the islet and probably destroyed many of the young. The disappearance of territory holders on Yttre Oxgrynna is shown in Fig. 10. Nest 5 was destroyed (predated) on 15/6. It was the last territory to be established and the smallest. Nest 7 was destroyed by floods on 1/7. Male 5 remained until 22/7, defending his territory with the strictest territorial behaviour. His mate remained until 8/7, although she spent much time off the islet. Male 7 remained until 21/7, showing far less territorial defence and sporadic attendance. His mate was not seen after the destruction of the nest. Several birds showed sporadic attendance, especially after the storms.

Only pairs 1 and 8 had any remaining young (two and one respectively) on Yttre Oxgrynna on 16/7. Bergman (1946) reported that young Turnstone are able to swim after ten days and thus could move to other islets. Given the weather at the time, the currents and the distance needed to reach the main island, this seems unlikely for Yttre Oxgrynna. By the end of the study, 24/7, only two territroy holders remained on Yttre Oxgrynna. On this day, male 4 was seen on the main island in a group of four Turnstone. At this time, Turnstone groups of fifteen or more were forming in

Figure 10

Daily attendance of territorial Turnstone on Yttre. Any two consecutive days of attendance have been connected.


JULY
28
29
1
2
3
4
5
6
7
8
9
11
12
13
14
16
17
18
19
20
21
22
23
24
Pair number - female / male
1 f
m
2 f
m
3 f
m
4 f
m
5 f
m
6 f
m
7 f
m
8 f
m
9 f
m
10 f
m

many areas.

On 12/6, the first of the intruding Turnstone began to appear on Yttre. Their presence resulted in aggressive encounters. By 4/7 the number of intruders, mainly males, had greatly increased. Territory holders countered by 'co-operating' in putting these birds off. One intruder, identified by a metal ring, first appeared at territory 2 on 7/7. The male of territory 2 was absent from 5/7 to 12/7. The intruder was very submissive and spent most of the time at the water-edge, where territorial defence was not so intense. Over the next seven days the intruder had moved to territroy 9, remaining submissive and feeding in taller vegetation. Even though not completely tolerated by male 9, the intruder would put other Turnstone off the territory. Male 9 was not seen on Yttre Oxgrynna on the July 18 or 19. During this period the intruder took to the guard rock and began defending the territory. On my last visit to Yttre Oxgrynna, July 24, the intruder was still present and defending the territory.

4i. Turnstone interactions with larids

Turnstone only nested in areas where larids also nested. Turnstone and larids had many similar nesting requirements. Larids provided protection to birds nesting within their colonies. Turnstone are very aggressive towards the larids, especially gulls. Both gulls and terns offer protection from predators. Gull, however, pose a threat as potential predators of eggs and young. (In 1976 I witnessed a Common Gull carry off a Redshank chick from Yttre Oxgrynna.) Turnstone are capable of putting gulls off their territories.

At Valassaaret, Turnstone exploit the eggs of larids. Ample opportunity exists for Turnstone to destroy larid nests. Larids do not react to Turnstone as an enemy, as they would crows, skuas etc. Terns would occasionally bomb a Turnstone if it approached its nest, but this was uncommon and not a prolonged attack. Turnstone spent time walking about their territory and they appear to know where larid nests are located. Turnstone would fly directly to a nest that was to be exploited. I witnessed one Turnstone put a tern off its nest when the tern returned to its half-eaten eggs. Turnstone will take eggs of all ages. One Turnstone destroyed an egg from the nest of a Common Gull, severed the head of the 14 to 16 day-old embryo and removed the body. The male Turnstone initiated the original destruction of the nest (of all those witnessed). It would often stand guard while the female would continue to feed. Gulls' nests suffered heavy destruction from Turnstone, often lossing an entire three-egg clutch at one time.

The degree to which Turnstone exploit larid eggs is highly variable at Valassaaret. Of areas visited, exploitation on Yttre Oxgrynna and Långgrynna was particularly heavy. Laying data and egg disappearance for larids on Yttre Oxgrynna are presented in Table 9. Table 10a-c summarizes the predation on tern and gull eggs at Yttre Oxgrynna, and a comparison for these two groups, respectively. There is not evidence to suggest preferential robbing (between tern and gull nests) by Turnstone (Figs. 11 and 12). No single laying period provided a greater chance of success for tern nests (i.e., swamping the predator in time was not successful, Fig. 13). Of those tern nests whcih successfully produced young, 67% (8 of 12) were located in a single Turnstone territory (Fig. 14). Table 11 provides a summary for successful tern nests on Yttre Oxgrynna.

To insure that my presence did not create a situation in which the Turnstone could easily exploit the larids, I set the islet of Långgrynna aside as a control. Relatively few visits were made to the islet during the early season. Originally, 22 gull nests were marked. Of these, four produced young, nine were completely destroyed and the fate of the remaining nine nests could not be determined. Of these final nine nests, at least two had one egg destroyed. Of the original ten tern nests marked, nine were destroyed and the fate of one could not be determined. Later in the season, six additional nests were marked; none of

TABLE 9

Laying data of terns (a) and gulls (b) on Yttre Oxgrynna.

Each nest is identified to its location on Yttre Oxgrynna. The number of eggs found in each nest for each day observed is given. If the nest ended in no eggs or young it is indicated by O. Young are represented by Y. It was not always possible to determine the outcome of each nest (e.g., Table 9a, nest 9).

(a)

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43
M-27	1	1																																									
28	2	1	1																																								
29	0	2	1	1	1	1																																					
30		0	1	1	0	0																																					
31			1	2																																							
J-1			0	2			1	1																																			
2			0	2			2	1																																			
3				2			1	1	1	1	1																																
4				2			1	1	1	1	1																																
5				2			0	1	1	2	2																																
6				2				2	2	2	2																																
7				2				2	2	0	3	1						1																									
8			1	2				2	2		3	1				1	1	1					1		1																		
9			1	2				2	2		3	1				1	1	2	1		1		1	1	1																		
10			2	2				2	2		3	2	1	1	1	2	2	2	1	1	2		2	1	1	1																	
11			2	2				2	2		3	2	1	1	0	2	0	2	1	0	2		2	1	2	2	1	1		1				1		1							
12			2	2				2	2		3	2	2	0		1		2	2		2		2	2	2	2	2	2	1	1	1			1		1							
13			2	2				2	2		3	2	2			1		2	2		2		2	2	2	2	2	2	0	2	1	1	1	2	1	1							
14			2	2				2	2		3	2	2			0		2	2		2		2	2	2	2	2	2		2	1	0	1	2	1	2							
15			2	2				2	2		3	2	2					2	2		2		2	2	2	2	2	2		2	1		2	2	1	2		1					
16			2	2				2	2		3	2	1					2	2		2		1	2	2	2	2	2		2	1		2	2	0	2		1					
17			2	2				2	2		3	2	1					2	2		2		1	2	2	2	2	2		2	1		1	0		2	1	2					
18			2	1				2	2		3	2	1					2	2		2		1	2	2	2	2	2		2	1		1			2	1	2	1				
19			2	1				2	2		3	2	1					0	2		2		1	2	2	2	2	2		2	1		1			2	2	2	1				
20			2	1				2	2		3	2	1						2		2		1	2	2	2	2	2		2	1		1			2	2	2	2	1		1	
21			2	1				2	2		3	2	1						2		1		1	2	2	2	2	2		2	1		1			2	2	2	2	1		1	
22			2	0				2	2		3	1	2						2		2		1	2	2	2	2	2		2	1		1			2	2	2	2	2	1	2	1
23			2					2	2		3	1	2						2		2		1	2	2	2	2	0		2	1		1			2	0	2	2	1	1	1	1
24			2					2	2		3	1	2						2		2		1	2	2	2	2			2	1		1			2		2	2	0	1	1	0
25			2					2	2		3	2	0						2		2		1	2	2	2	2			2	1		0			2		2	2		1	1	
26			2					2Y	2		2Y	2							2		1		1	2	2	2				2	1					2		2	2		1	1	
27									2			1Y							2		0		1	2	2	2				2	1					2		2	0			1	
28																			2				1	2	2					2	1					2		2				1	
29			1Y																2				1Y	2	1Y					2	1					2		2				1	
30																			1					2						2	1					2		0				1	
J-1																			0					1Y						2	1					2							
2																														1Y	1					2							
3																															1					1Y							
4																															1					2Y							
5																															1												
																															1Y												

(b)

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
M-23	1			1													
24	1	1		1	1												
25	2	1		2	1												
26	3	2	1	3	2	1											
27	3	2	1	3	3	1											
28	3	3	0	3	0	2											
29	3	3		3		0	1	1									
30	3	3		3			1	1	1								
31	3	3		3			2	1	1								
J-1	2	3		3			2	1	2	1	1	1	1				
2	2	3		3			2	0	2	1	1	1	0				
3	0	2		3			0		1	1	1	2					
4		0		3					0	0	0	2					
5				3								3					
6				3								3					
7				3								0					
8				3										1			
9				3										1			
10				3										2			
11				0										0			
12																	
13																	
14																	
15																	
16																	
17																	
18															1		
19															2		
20															2		
21															2	1	
22															2	0	
23															2		
24															2		
25															0		
26																	1
27																	0

TABLE 10a-c

Summaries of hatching and breeding success for terns(a), and gulls (b) on Yttre Oxgrynna, and a comparison of the two groups (c).

(Egg days provide a measure of egg availability.)

Periods-	Date-
0	May 23-26
1	May 27-30
2	May 31-June 3
3	June 4-7
4	June 8-11
5	June 12-15
6	June 16-19
7	June 20-23
8	June 24-27

Turnstone began to lay in period.

a

Period	Nests Begun	Nests Destroyed	Eggs Laid	Eggs Destroyed	Egg Days	Eggs Laid/Total	% Nests Successful of those Begun
0	0	0	0	0	0	0	0
1	6	4	8	6	14	9.9	16.7
2	5	0	7	2	23	8.6	60.0
3	2	2	7	3	36	8.6	50.0
4	18	3	28	4	103	34.6	33.3
5	6	5	15	6	168	18.5	16.7
6	2	3	4	9	160	4.9	0
7	4	3	9	9	161	11.1	0
8	0	5	3	7	125	3.7	0
9	0	2	0	4	49	0	0
Total	43	27	81	50	835	99.9	

b

Period	Nests Begun	Nests Destroyed	Eggs Laid	Eggs Destroyed	Egg Days	Eggs Laid / Total	% Nests Successful of those Begun
0	6	0	12	0	24	37.5	0
1	3	3	6	6	47	18.8	0
2	4	4	7	9	55	21.9	0
3	0	5	1	8	20	3.1	0
4	1	2	2	5	13	6.3	0
5	0	0	0	0	0	0	0
6	1	0	2	0	3	6.3	0
7	1	1	1	1	9	3.1	0
8	1	2	1	3	3	3.1	0
Total	17	17	32	32	174	100.1	

C

Period	Total Eggs Laid	Total Eggs Taken	Tern Eggs Available Beginning of Period	Gull Eggs Available Beginning of Period	Total Eggs Available	Gull Eggs Taken / Total Available in %	Tern Eggs Taken / Total Available in %	Egg Days (Gulls) / Total Egg Days in %
0	12	0	0	0	0	0	0	100
1	14	12	0	12	12	50.0	50.0	77.0
2	14	11	2	12	14	64.3	14.3	74.3
3	8	11	7	10	17	47.5	17.6	35.7
4	30	9	11	3	14	35.7	28.6	11.2
5	15	6	35	0	35	0	17.1	0
6	6	9	42	0	42	0	21.4	1.8
7	10	10	39	2	41	2.4	22.0	5.3
8	4	10	39	2	41	7.3	17.1	2.3
9	0	4	23	0	23	0	17.4	0

Figure 11

The relationship of tern (Arctic and Common) eggs taken compared to the total larid eggs available and the availability of tern eggs (expressed in egg days). The solid line is the ratio (expressed in percent) of tern eggs taken to total larid eggs taken. The broken line represents the ratio of tern egg days to the total larid egg days.

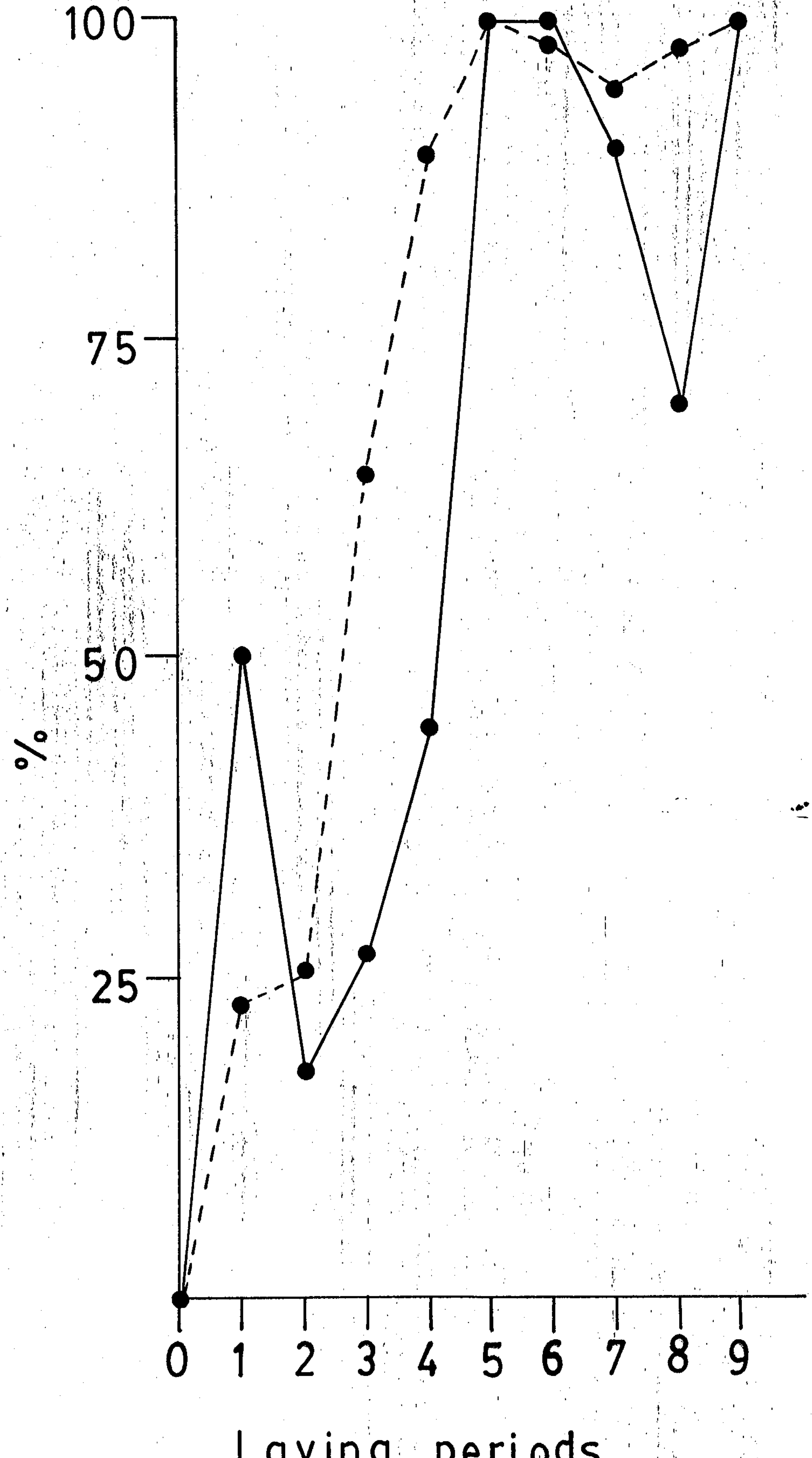

100
75
50
25
%
0
1
2
3
4
5
6
7
8
9
Laying periods

Figure 12

The relationship of Common Gull eggs taken, compared to the total larid eggs available and the availability of gull eggs (expressed in egg days). The solid line is the ratio (expressed in percent)of gull eggs taken to total larid eggs taken. The broken line represents the ratio of tern egg days to the total larid egg days.

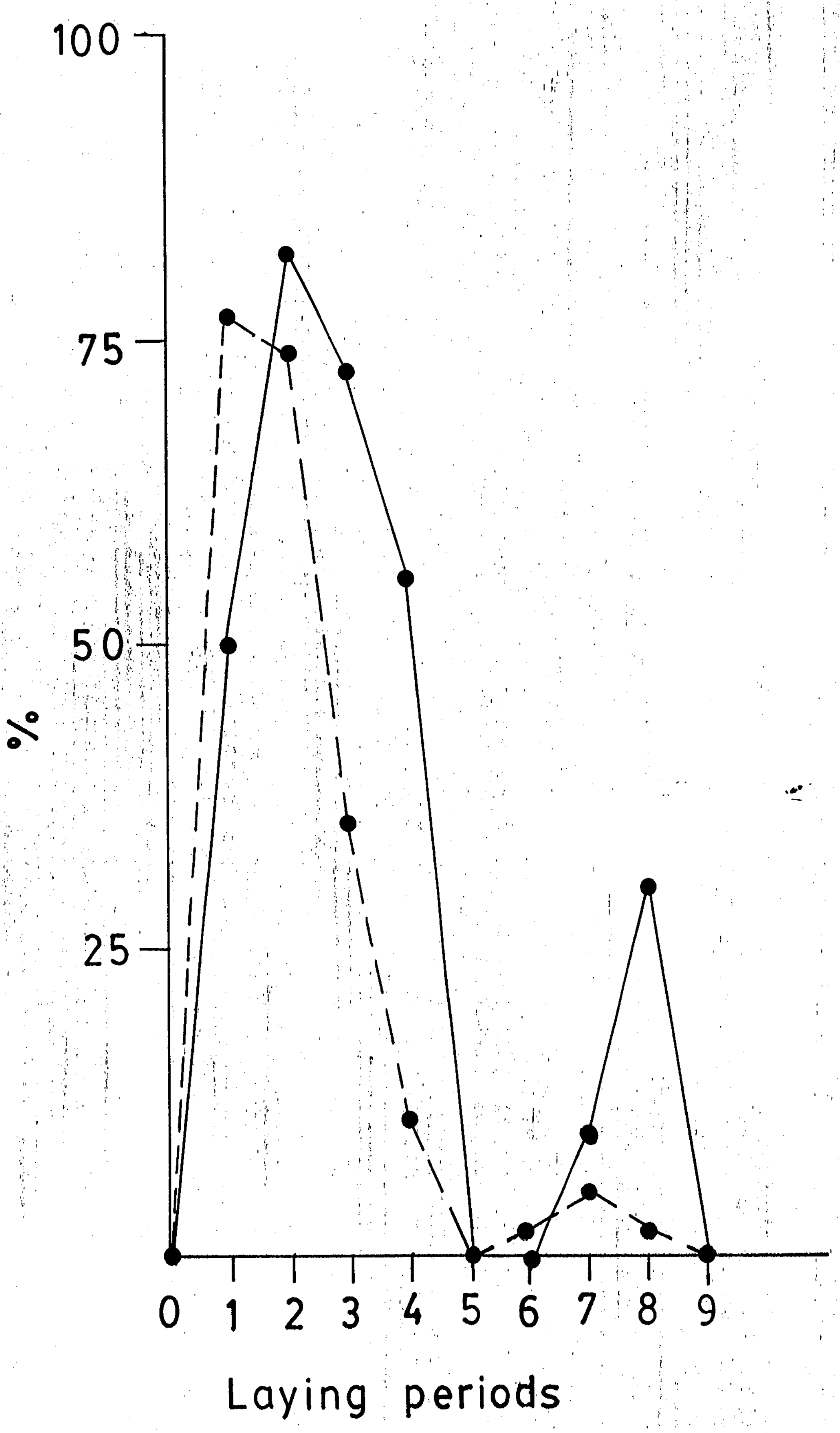

100
75
50
25
%
0
1
2
3
4
5
6
7
8
9
Laying periods

Figure 13

The total number of successful tern nests for each laying period (broken line) and the total number of tern nests started in each laying period. (solid line).

For dates of the laying periods, see Table 10.

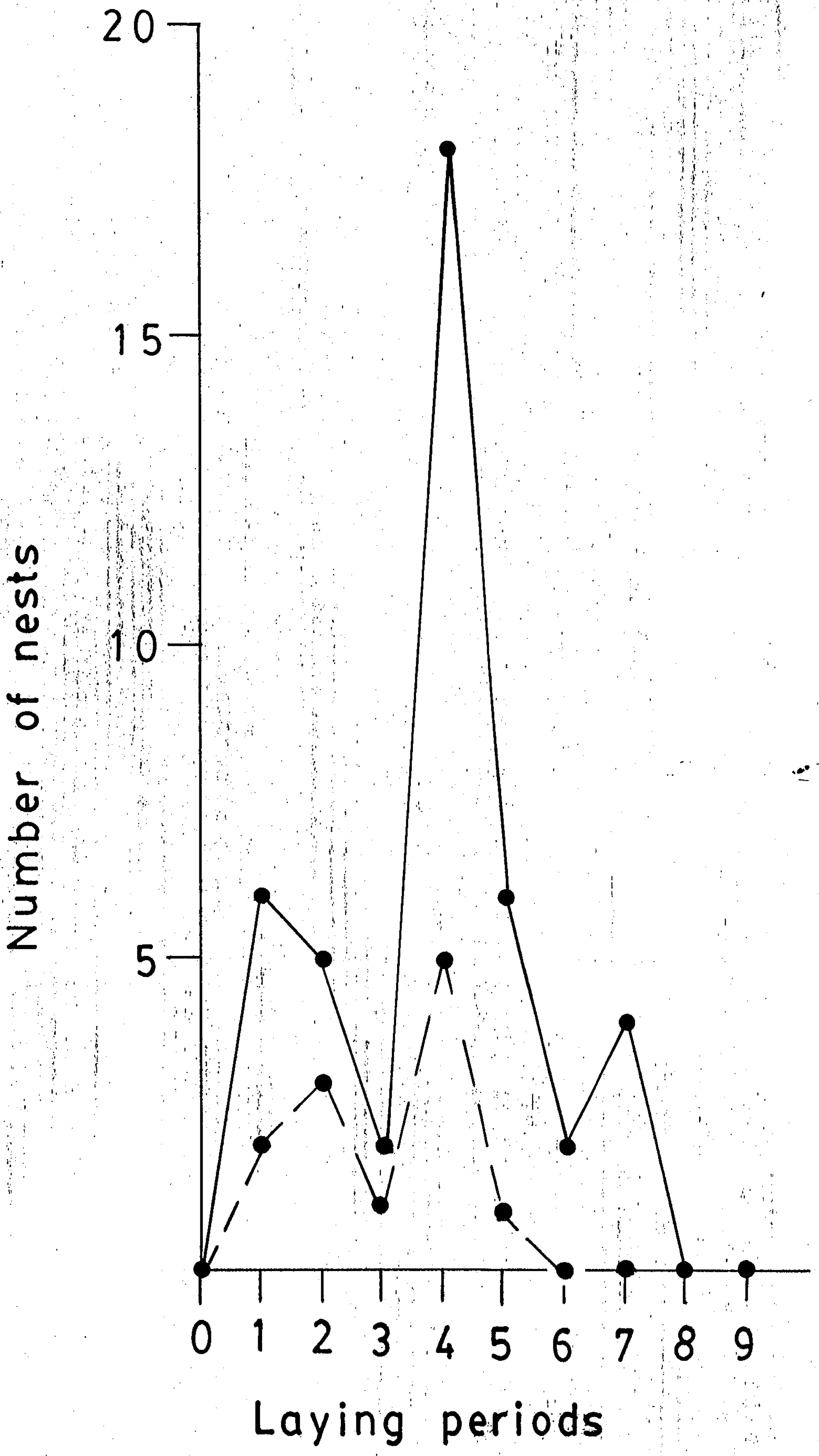

Number of nests
20
15
10
5
0
1
2
3
4
5
6
7
8
9
Laying periods

Figure 14

The location of tern nests on Yttre. Circled nests represent tern nests which were successful.

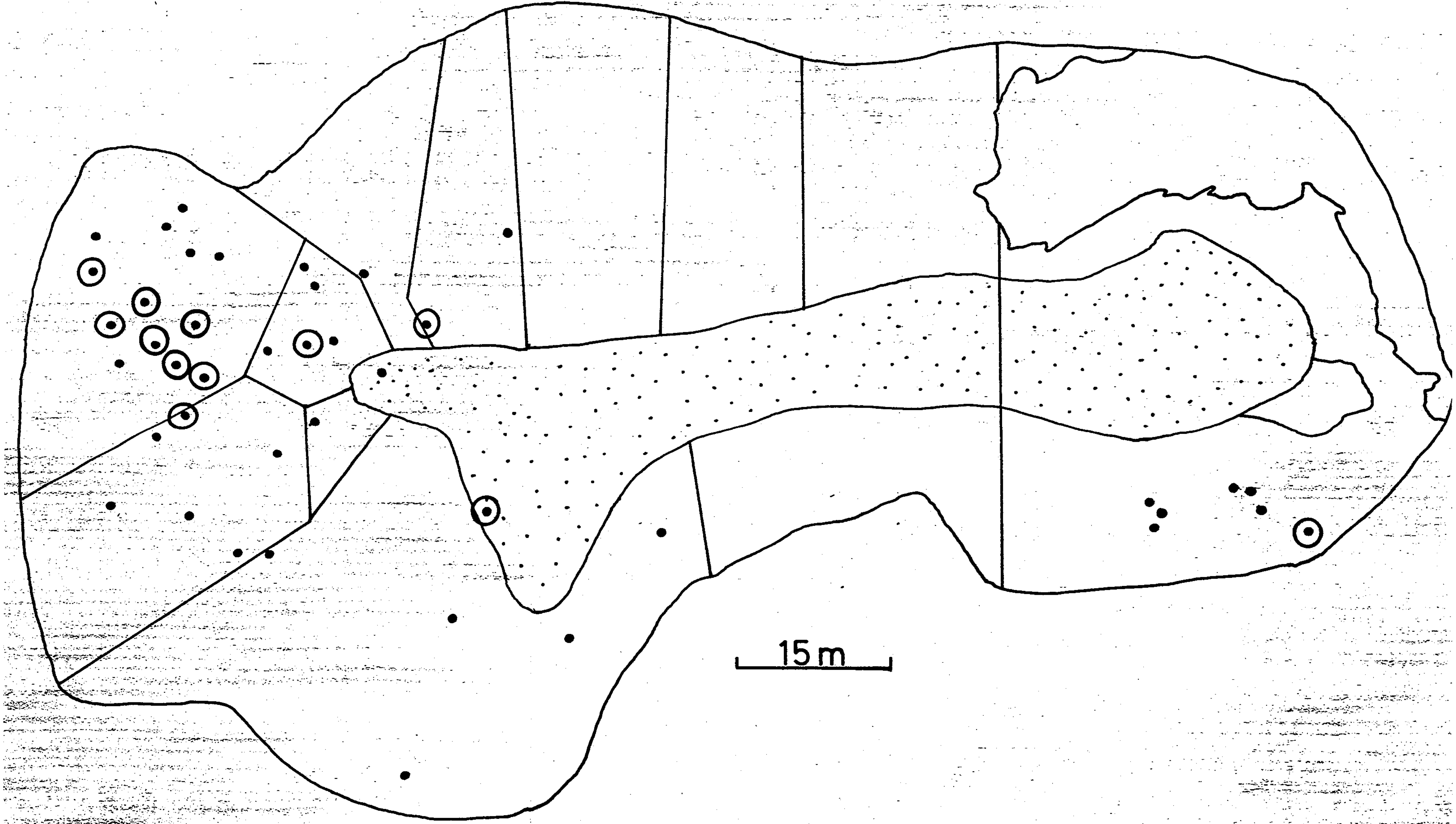

15 m

TABLE 11

Summary of successful tern nests on Yttre.

Successful Tern Nests	Period Nests Begun *	Found in which Territory **
3	1st	9
8	2nd	1
9	2nd	9
11	2nd	7
12	3rd	8
23	4th	9
24	4th	9
25	4th	9
26	4th	9
30	4th	9
31	5th	5
36	4th	4

Total Nests	43
Nests Bird-Destroyed	27
Nests covered by Storm	2
Nests Hatched	12
?	2

* Periods 2-3-4 yielded 58.1% of the total nests and 83.3% of the successful nests.

** Turnstone territory number 9 yielded 58.3% of nests which hatched. 30.8% of the Tern nests hatched on Yttre. (This final figure does not include the 2 nests destroyed by storms or the 2 nests for which the outcome was not known.)

these nests produced young.

On Tuorelarev (considered as part of the main island, Ebbskär) 23 tern nests and one gull nest were marked. Of the tern nests, eight were destroyed, three failed to hatch, five produced young and the outcome was not determined for seven nests. The single gull nest produced one young (24/6).

On Karingbåda, six tern nests were marked and all produced young. Of the sixteen gull nests marked, three were destroyed by rising water (during heavy storms) and only one showed signs of predation. Two Turnstone nests were marked in this area, with as many as four pairs nesting on Käringbåda. Turnstone nesting in this area had access to Antonskroken and did feed in this cove. That Turnstone had a marked effect on the tern population is shown by the dates of the first observed flight in young tern, 19/7 on Yttre Oxgrynna and 13/7 on the main islands. The first tern egg laid for four areas was: Yttre Oxgrynna 27/5, Långgrynna 27/5, Tuorelarev 28/5 and Käringbåda 29/5.

The adult Turnstone continued to exploit the tern population once the tern eggs had hatched. When adult tern returned with fish for the young, male Turnstone would take fish either from the adults or often from the defenceless chicks. The male Turnstone would fly to a rock to feed on the fish. The female Turnstone would occasionally fly to join the male, and, after slight chattering and a 'submissive' posture, would be allowed to feed on the fish.

5. Discussion

At Valassaaret, the Turnstone breeding population utilize a few highly concentrated food sources. The occurrence of the chironomid swarms represented a peak in food abundance. These swarms were localised in three coves. Territories were not held, many established behavioural patterns broke down (at the height of the swarms), and most indications that the population was indeed breeding (protection of the mate, defence on the breeding territory) were absent. Prior to this, however, two weeks of foraging in these communal coves provided adequate foraging, with a minimum of aggressive disturbance. The presence of conspecifics had a positive effect on the foraging behaviour of the Turnstone; allowing birds to feed with less disruption. Potential predators were numerous and birds reacted to their presence. When feeding as pairs, females benefited from the vigilance of its mate. The male's constant scanning, limited it to surface feeding. Freed from this scanning, the female could feed behind large rocks, in the thicker vegetation and on prey within the mud. It has been shown that birds benefit from group size in avoiding predation (Page & Whitacre 1975 and Kenwood 1978). (Predation of a Turnstone by a female Kestrel, one of the most common avian predators at Valassaaret, has been reported by McCullock (1960).) When flying into a cove, Turnstone landed within several yards of a conspecific. This was followed by spacing, which reduced aggressive encounters. When males of two pairs came into contact with one another they would Head-Bob (often incited by the female) and aggression would seldom occur. One stylized behaviour, with body low and neck extended forward (similar to the Nod-Swim in Mallards and also activated by an inciting mate (see Lorenz (1951)), would also stop potential aggression. Birds were thus provided with the benefit of conspecifics in the detection of possible predators and utilized behavioural mechanisms that maintained spacing and reduced aggression.

There appeared to be space restrictions in the choice of nest sites (the lower rocky-sand areas where larids also nested). Here, breeding densities of Turnstone reached their highest recorded levels (in the available literature). On the islets, a single territory served for both breeding and feeding. One territory on Yttre Øxgrynn a shared borders with four other Turnstone territories. In these areas, the Head-Bob display was the msot common behaviour and greatly reduced potential aggression. Aggression not only decreased the time available for maintenance activites, but also exposed the nest and young to possible predation from gulls.

It is typical for wintering Turnstone to feed on open coastal areas, as in the situation at the Tees estuary (Bent 1929, Bannerman 1960, and Beven & England 1977). The situation at Valassaaret, where birds are often confined to very small islets with high nesting densities, may not be as representative for this species. Nettleship (1973) reported a total of thirteen or fourteen pairs in a cnesus area of 240 hectare at Camp Hazen, Ellesmere Island, N.W.T. This is in sharp contrast to the very high concentration of nests at Valassaaret. Turnstone breeding at Valassaaret, winter in Africa, while Turnstone wintering on the Tees breed in Greenland. However, it is still informative to discuss the different "groups" in their different settings.

Due to the localized nature of the Turnstone's food sources (highly concentrated) during winter and summer, and the limited preferred nesting sites at Valassaaret, some means of reducing potential aggression is necessary. The ability of Turnstone to exploit temporary food sources and the rapidity with which information of feed sources travels through the population has been discussed in Chapter 6. This may be due, in part, to social roosting and the attraction towards conspecifics when searching out feeding areas. Because of the distribution of the Turnstone's food source, exclusive defence of an area is seldom possible. In both winter and summer, several factors force Turnstone into concentrated associations.

Within the behavioural repertoire of the Turnstone (postures and calls), a single component can have different meanings under differnt situations. Individual components of the Head-Bob display occurred during other displays. The Crouch position was an exaggeration of the down phase of the Head-Bob display. On the communal feeding coves, the Crouch was a flight intention movement; on Yttre Oxgrynna it acted as an appeasement gesture. During the up phase of the Head-Bob, with neck fully extended, the Neck-Stretch was used (see Table 1). The tail is in the dropped position, which is associated with chasing and aggression when feeding (Groves 1978). The mock-preen is another component of the Head-Bob. Associated with the Head-Bob, mock-preening approximated appeasement. On the feeding grounds (winter and summer), mock-preening aided in spacing without resulting to aggressive contact. Mock-feeding was also associated with the Head-Bob display, with one or both birds pecking repeatedly at the ground or grass in this redirected behaviour. At the communal coves of Valassaaret and the wrack beds of Teesmouth, mock-feeding occurred after an aggressive encounter and asserted the victor's dominance. Although Groves does not mention the Tail-Up posture during aggressive encounters, I found that when associated with the Crouch position, that this was an aggressive posture of the highest intensity, both in the summer and winter. Social stability is aided by behavioural displays, which bring about a dispersal pattern that limits the number of birds in any one area.

It appears that by a combination of social context and posturing that Turnstone are able to accurately convey a social message. Social stability ((in the form of reduced aggression) is aided by a widespread dispersal pattern, when possible, during the winter feeding period. One additonal factor in reducing the amount of aggression is the possibility of individual recognition. Bordering male territorial holders at Valassaaret appeared to recognize one another (in that they did not become aggressively involved with one another), even off their territories. Territorial birds may have behaved differently but this could not account for the fact that this tolerance did not extend to birds from a territory beyond a bird's borders.

The factors which seem most important for Turnstone selection of breeding habitat are: i) the geomorphological type of island; ii) the vegetation type of the island; and iii) the occurrence of larids. During the past 30 years, land upheaval at Valassaaret has resulted in an increase of 50 hectares. The area has also seen a large increase in both larids and Turnstone. In Bergman's 1946 monograph, he states that the Turnstone's preference for sparse vegetation is due to their short legs and locomotion techniques.

Turnstone are amongst the first species to inhabit rising islets.

Several species are known to nest within larid colonies. Whether it is a casual relationship or one of similar nesting requirements, has not been well established. At Valassaardt, Hildén (1964) has shown that for several species, especially _Aythya_ _fuligula_ and _A_. _marila_, strong attractions to nest amongst larids existed. Koskimies (1957) has suggested that terns and gulls might act as a positive attraction to an area (a feature of habitat recognition for other species). Bourget (1973) was not able to show the ultimate factors which influence eiders in selecting breeding sites; he did show that all known eider colonies in Maine are on islands where gulls also nest. Olsson (1951) has shown that in Finland, when eiders nested on islands where gulls nested, the percentage of nests destroyed by Hooded Crows was less than where no gulls nested.

Turnstone at Valassaaret exploit the larids' abiltiy to drive off potential predators. They rapidly learned to distinguish larid alarm calls from larids aggressive calls; for the latter, birds would not even come off their nest to mount their guard rocks. Turnstone did extensive damage to larid eggs at Valassaaret. They did not show signs of selective predation between terns and gulls. Egg damage was greater on islets than on the main islands, as were the densities of nesting Turnstone. Turnstone are extreme generalists and are known to exploit unusual food sources. Turnstone have been shown to cause large scale destruction of Royal Tern (Sterna maxima) eggs in Florida (Loftin & Sutton 1979). The authors were of the opinion that the Turnstone were attracted to the "densely packed mass of adult Royal Terns standing in the colony, rather than to the eggs themselves". Turnstone predation on Common Tern eggs has been noted by Parkes et. al. (1971). They reported that the movements of the Turnstone did not appear to be random, but, "seemed to be following a definte itinerary". Crossin and Huber (1970) reported that several Turnstone attacked the nest of an incubating Sooty Tern (S. fuscata). The incubating bird was able to ward the Turnstone off. Terns in the colony made at most a feeble attempt to expel the Turnstone from their colony.

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