Distribution and feeding ecology of dunlin on seal sands

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DISTRIBUTION AND FEEDING ECOLOGY OF DUNLIN ON SEAL SANDS

Monica Cristina Chanca Calado

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ACKNOWLEDGEMENTS

I would like to thank my supervisers, Prof. P. R. Evans and Dr. J. C. Coulson, for the help and advice throughout the completion of this thesis; R. Ward and M. Bone for their valuable help during the fieldwork; and finally, R. J. Wilson for his constructive criticisms and support in the preparation of this manuscript.

CONTENTS

ABSTRACT

This study describes patch selection by Dunlin, a small, shallow feeding wader, observed feeding on physically heterogeneous intertidal mudflats at Seal Sands, Teesmouth in N. E. England.

Seal Sands was not viewed as a homogeneous feeding ground by the dunlin population. The dunlin showed a tendency to congregate on certain subareas, namely Greenabella (A), and Central (C), Banks.

The feeding distribution of the dunlin was examined with respect to the substratum characteristics, and it was shown that dunlin concentrated on the soft, wet, muddy substrata. Thus, their feeding distribution was influenced by the stage of the tidal cycle. The tide can affect the dunlins' distribution both directly, by restricting the space in which they can feed, and indirectly, by affecting the substratum's texture (wetness) and hence the availability of prey within it.

In general, the feeding dunlins' microdistribution revealed a preference for the "Film" microhabitat. Hence the birds' feeding activity showed a tidal rather than a diurnal periodicity. The feeding behaviour of dunlin was also influenced by the wetness of the substratum, and thereby the tidal situation.

Final conclusions with regard to the Bill length differences between sexes, and the seasonal change in Body Weight, due primarily to the accumulation and depletion of fat reserves are not presented here in order to emphasize

their tentative nature, resulting from small sample size. For the same reason, this data was simply presented in appendix IV rather than in the body of the text.

The two commonest races of Dunlin on the Teesmouth estuary, *Calidris alpina alpina* and *Calidris alpina schinzii*, were both captured during both the spring and autumn migrations. In the latter period, juveniles were in the majority in the captured samples.

INTRODUCTION

It is typical of many long distance migratory birds to spend more than three-fourths of the year in migration and on their wintering grounds (Recher, 1966). Even so, little attention has been paid to the ecology of birds during migration, as most studies refer to the inter or intraspecific interations involving breeding or wintering populations.

During the long non-breeding period, many shorebirds from breeding areas in both palaearctic and nearctic regions, for example northern Canada, Greenland, northern Siberia, Scandinavia and Iceland, concentrate in coastal areas during their autumn and spring migrations to and from Africa (Pienkowski, 1984; Fuller, 1982).

Many species of birds use the estuaries of Britain throughout the year. These intertidal areas form feeding, resting and moulting grounds of considerable significance for Western European wildfowl and wader populations (Prater, 1981; Fuller, 1982). Most estuaries are highly productive of benthic invertebrates and are used as staging posts at which the waders feed to gain weight, chiefly by accumulation of fat, before proceeding further on their migration (Prater, 1981; Evans & Davidson, 1990).

Delays in reaching any of these staging posts may cause either late arrival at the breeding grounds, or in autumn, force birds to use an extra staging post if food has been depleted by earlier migrants. Along the North West

African coast suitable refuelling sites are few and separated by many hundreds of kilometres, and birds sometimes arrive without adequate reserves at their wintering grounds (Evans in press, 1990; Dick & Pienkowski, 1979; Evans & Davidson, 1990). On the other hand, delays during spring migration might affect the success of arctic breeding species, as the timing of the breeding season is an important factor affecting the chances of survival of the chicks (Holmes, 1966; Evans in press, 1990; Morrison & Davidson, 1989). The start of the breeding season in the arctic is controlled by weather conditions, therefore in years in which the thaw is later than normal, or the spring weather is bad, birds might have to survive mainly off their stored reserves until conditions improve (Davidson & Evans, 1989). Moreover, not only are large fat reserves essential both for the northward flight (especially if it is to be non-stop) and also for survival for a few days after arrival, but for females an increase in weight associated with breeding is necessary (O'Connor, 1972). In the arctic, females must be able to lay as soon as possible due to the very restricted period they have in which to breed successfully.

Many European shorebird populations tend to be faithful in successive years to their breeding sites, migration staging posts and wintering grounds (Pienkowski, 1976). For this reason, the loss of refuelling areas could seriously affect the populations involved. Thus, the removal of any major link, or of several less important links, in the chain of estuaries used during migration could have consequences far greater than apparent at first sight.

Many of Britain's estuarine systems face significant threats, which could, and indeed do, affect birds (Prater, 1981; Fuller, 1982). These systems are subjected to a large number of proposals for land reclamation, mainly for industry and agriculture (Prater, 1981; Fuller, 1982). These types of developments in estuarine areas normally lead to a reduction of intertidal land available and usable as feeding grounds by shorebirds, and sometimes also to a reduction in the time for which intertidal land is uncovered during each tidal cycle, and this means a reduction in maximum feeding time each day (Evans in press, 1990; Evans & Pienkowski, 1983; Pienkowski, 1984).

Like any other part of our environment used by man, estuaries are subjected to many types of pollution, such as organic nutrients, heavy metals, oil and hot water. Their potential impact on the intertidal invertebrate fauna is considerable (Prater, 1981).If the density and availability of invertebrates are reduced, shorebirds' rates of fat deposition may be reduced (Piersma, 1987).This would require an increase in the time spent on a staging ground.

Teesmouth (54°73'N, 1°12'W), in North-East England, is one of the best documented British examples of industrial reclamation of an estuary and its impact on wildlife (Prater, 1981). The recent history of its reclamation is shown in figure 1.

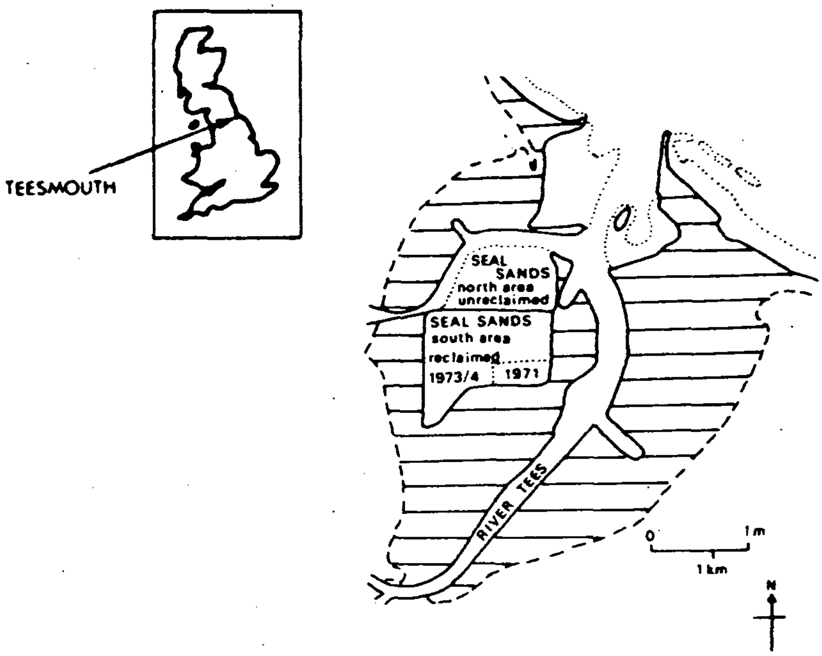


Figure 1: The estuaty of the River Tees showing the area of Seal Sands in 1973/74. The hatched area bounded by the dashed lines indicates land reclaimed in the 19th and 20th centuries. The dotted lines enclose areas exposed at low water. Redrawn from Evans et al (1979).
(Source: Prater, 1981)

Since the first half of the nineteenth century, the intertidal mudflats of the Tees estuary have been reduced from approximately 2500 ha, to about 140 ha in 1974 (Evans, 1978-1979; Evans & Pienkowski, 1983). Nowadays, the North area of Seal Sands is the main feeding area remaining available to shorebirds. During the most recent reclamation (1973/74) these birds not only suffered a loss of feeding grounds, but also a reduction in potential feeding time, from about 12 to about 8 hours in each tidal cycle, because the upper tidal zones were entirely covered (Evans, 1978-1979; Evans & Pienkowski, 1983).

Consequently, after reclamation the numbers of most of the main species of waders at Teesmouth decreased

(Evans, 1978-1979). Dunlin, *Calidris alpina*, was seriously affected, as it usually fed for 90-95% of each tidal cycle, but after reclamation its feeding area was available for only 70% of this time (Evans & Pienkowski, 1983).

Many shorebirds, especially Scolopacidae, are gregarious, normally feeding in flocks rather than as scattered individuals (Goss-Custard, 1970a). During migration they may be forced to form aggregations in restricted areas where, although food might not be a limiting factor relative to the individual demands of the birds, space and time are. This situation occurs at Seal Sands and is ideal for the study of behavioural and ecological interactions within migrant species.

The Dunlin, a small Scolopacid wader (Cramp *et al.*, 1983) was the species chosen for this study, because it is a regular visitor using Seal Sands as a feeding ground during spring and autumn migration as well as in winter (Evans, 1978-1979). It is very easily observed in open intertidal habitats in spring due to its black ventral mark in breeding plumage (see Cramp *et al.* (1983) for a fuller description).

Being a circumpolar breeder (Holmes, 1966; Cramp *et al.*, 1983), with a restricted breeding period, it needs to achieve a certain level of fat reserves in a very short period during its stay in Seal Sands, before migrating to Iceland and Western Russia, if it is to breed successfully, and this in part dependent on density and availability of the invertebrate fauna on the feeding grounds.

This project analysed the macro and microhabitat distribution of Dunlin on Seal Sands in conjunction with studies of its feeding ecology. Measurements of the Dunlin's fat deposition during spring and autumn migrations were also taken.

Together, these provide information about Seal Sands' importance as a feeding habitat and therefore an essential staging post for migrating Dunlin, thus helping towards Teesmouth's conservation. The conservation of these migratory birds is obviously linked with the conservation of the habitats used during their spring and autumn migrations, so the environmental quality of the staging posts must be maintained, as recognised by the Ramsar Convention on the conservation of wetlands of international importance. If not, the adult mortality rate will increase, and consequently, affect the size of the Dunlin's European populations in the long run.

STUDY AREA and METHODS

The study area, Seal Sands (fig. 1), is situated at Teesmouth in North-East England (54°73'N, 1°12'W).

Seal Sands is an area (140ha) of intertidal mudflats extensively used by migrant waders as a staging post and also a wintering ground.

All 3 races of Dunlin, *Calidris alpina*, which breed in the Western Palearctic have been recorded at Seal Sands (Evans, pers. comm.; Goodyer & Evans, 1979; South Cleveland Ringing Group, 1985; Evans & Davidson, 1990):

- *Calidris alpina alpina*, from Northern Europe, Western Russia;
- *Calidris alpina schinzii*, from Iceland, Southern Scandinavia, Britain;
- *Calidris alpina arctica*, from North- East Greenland.

The first two are very common at the Teesmouth. However, only the former winters at Seal Sands. Juvenile alpina begin to arrive in mid-September and are followed by the adults from October to November, both groups leave the site in March and May (Evans, pers. comm.; South Cleveland Ringing Group, 1985). The other two races have been recorded only as spring and autumn passage migrants. *C.a. schinzii* passes northwards through Seal Sands between April and May. During its southward migration in late summer, adults predominate in July and early August and juveniles later in August and in early September. A few adults of *C.a. arctica* have been recorded in late July and early August (Evans, pers. comm.).

To examine the macro-distribution and feeding behaviour of Dunlin on Seal Sands, the study area was divided into five subareas (fig. 2), distinguishable by tidal level and substrate type:

- Greenabella Bank, area A, a soft muddy area, exposed at low water;
- Scalloped Bank, area B, a firm muddy area;
- Central Bank, area C, a soft muddy area with patches of *Enteromorpha spp.*, exposed below mid-tide;
- Eastern Channel, area D, a sandy muddy area;
- Eastern Channel, area E, a sandy area with patches of *Enteromorpha spp.*, covered only towards high water.

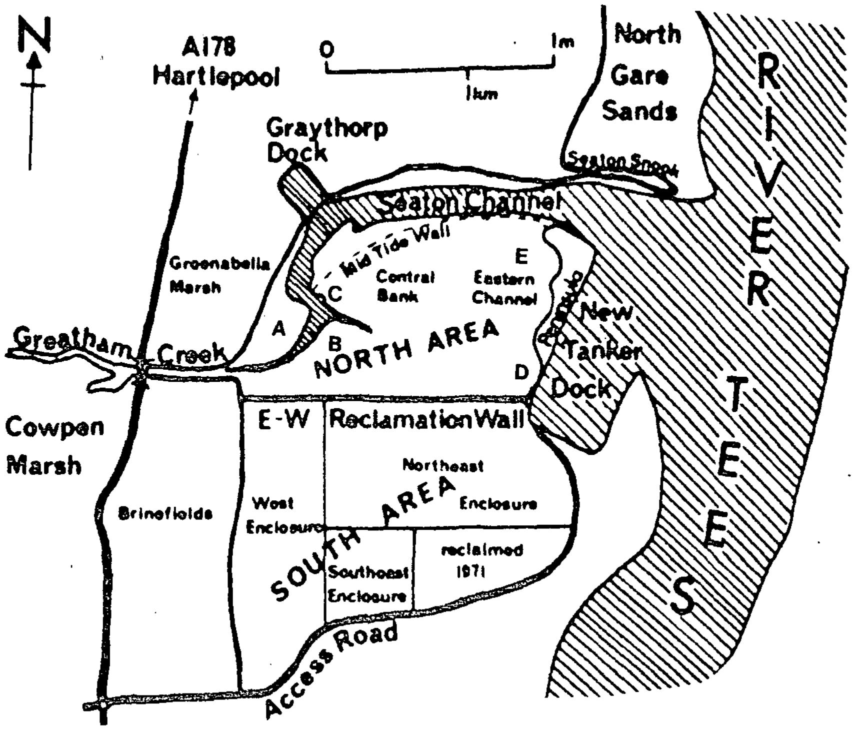


Figure 2: Seal Sands, showing the main intertidal mudflats and the study's subareas. (Source: Evans et al., 1979)

To record feeding positions of birds, five microhabitats were distinguished, roughly parallel to the water's edge. These are described below and shown in the following figure.

In Water - "T"
In Water - "H"
-------------------- Water's edge
Film
/////// Dry ////////

Figure 3: Microhabitats.

The area beyond the water's edge was divided into two microhabitats dependent on the depth of the water relative to the bird's legs:

- "H", legs half covered;
- "T", legs totally covered.

Above the water's edge, the first zone was recognized as the microhabitat on which a surface film of water remained visible, and this was followed by a second zone which lacked a surface film of water. The water's edge itself was considered also a microhabitat.

The fieldwork was conducted between May and September 1990. Birds were watched without disturbance from a permanent hide or from a car.

During May, the Dunlin's distribution, movements and feeding behaviour on Seal Sands were studied with the use of a telescope (Swift-Telemaster, 15-60x60), binocular (Carl Zeiss 10x50), and a counter (Handy Tally). During each tidal cycle and approximately at hour and a half intervals, observations were made that recorded the activity of the Dunlin on the site (whether feeding or not), and in the case of a feeding bird, its position relative to the subareas and their microhabitats. No quantitative distinction was made of the foraging methods used by the birds in the different subareas or microhabitats. It was also not possible by direct observation to determine the degree of feeding success and what prey organisms birds were taking, as the observation distances were too great.

During July and September, during the ebb and flood tides, measurements were made of the feeding rate by counting, in alternate minutes, the number of paces a Dunlin made and the number of times it completely withdrew its bill from the mud or water (hereafter termed the number of head lifts) although not necessarrily changing its posture from the feeding to the upright position. The neighbour to neighbour distance was also recorded on these occasions, and was defined as the distance, in bird lengths, between adjacent feeding birds.

During the fieldwork several attempts were made to catch Dunlin on diurnal roosting sites during high tide, using cannon-nets, but only on two occasions were they successful. Birds were caught for ringing, morphometric analysis and measurements of total body electrical conductivity (TOBEC index). The latter was used for the estimation of the bird's total lean mass. Only dry unringed birds were used for measurement of the TOBEC index, as contamination of plumage with salt or metals would increase the TOBEC index obtained. Birds were wrapped in a soft plastic jacket with velcro fastenings before being placed into the apparatus, known as the SA-1 Small Animal Body Composition Analyser. For each bird, three readings were taken with the bird in the chamber of the apparatus (X), alternating with three readings with an empty chamber (Y). Before and after each set of six readings a reference number was recorded (R). The TOBEC index was then calculated using the following formula (See Scott et al., in press 1990 for a fuller description of the method used):

$$I = \frac{\sum_{1}^{3} (Yi-Xi)/3}{0.9883\ R};$$

- R : mean of R data;
- 0.9883 : constant for the instrument (supplied by manufacturer).

Bills were measured to the nearest millimetre from the feathers to the tip along the upper mandible. Wings were measured to the nearest millimetre from the carpal joint to the tip of the longest primary by the maximum extension method (Evans, 1964). Birds were weighed to the nearest gram using a Salter spring balance. Age and race were determined by plumage characteristics, the former using particularly the wing coverts, and the latter using the feathering of the upper parts (mantle, scapulars and tertiaries) (Prater, Marchant & Vuorinen, 1977).

RESULTS

TIMING OF MIGRATION (CENSUS)

Counts of Dunlin during April and May at Seal Sands are presented in figures, 4 and 5. They give an approximate indication of when birds began to arrive and how long they stayed and used Seal Sands as a staging-post during their spring migration. The data of the first arrivers was not recorded as the project only started in May.

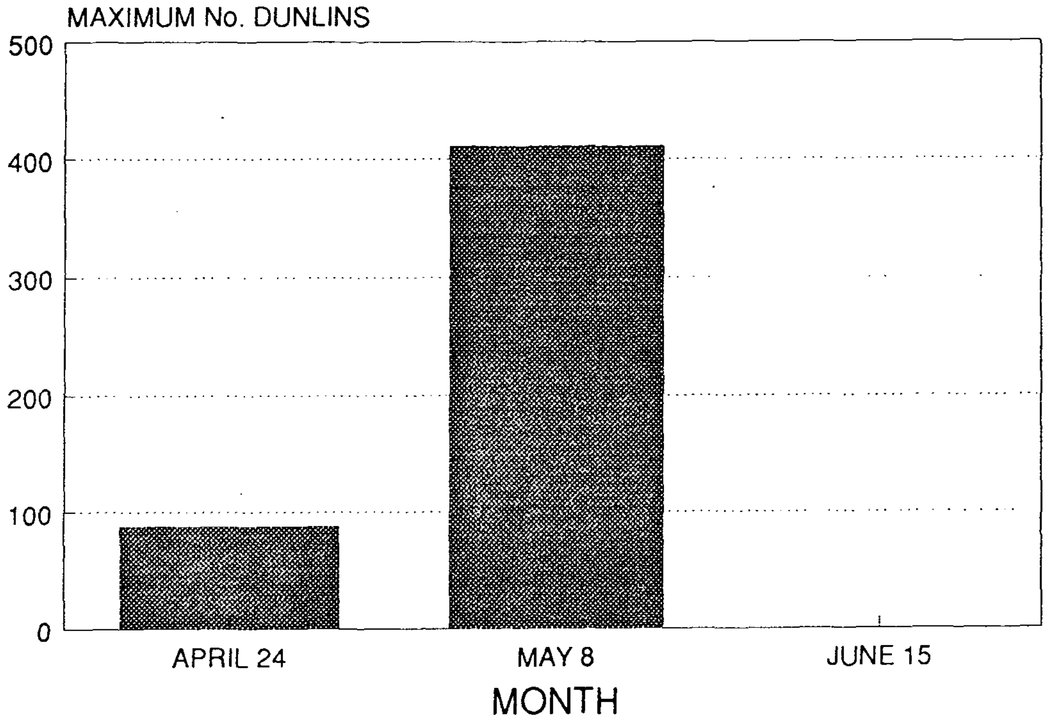


Figure 4: Monthly maxima of Dunlin at Seal Sands. (April - June).

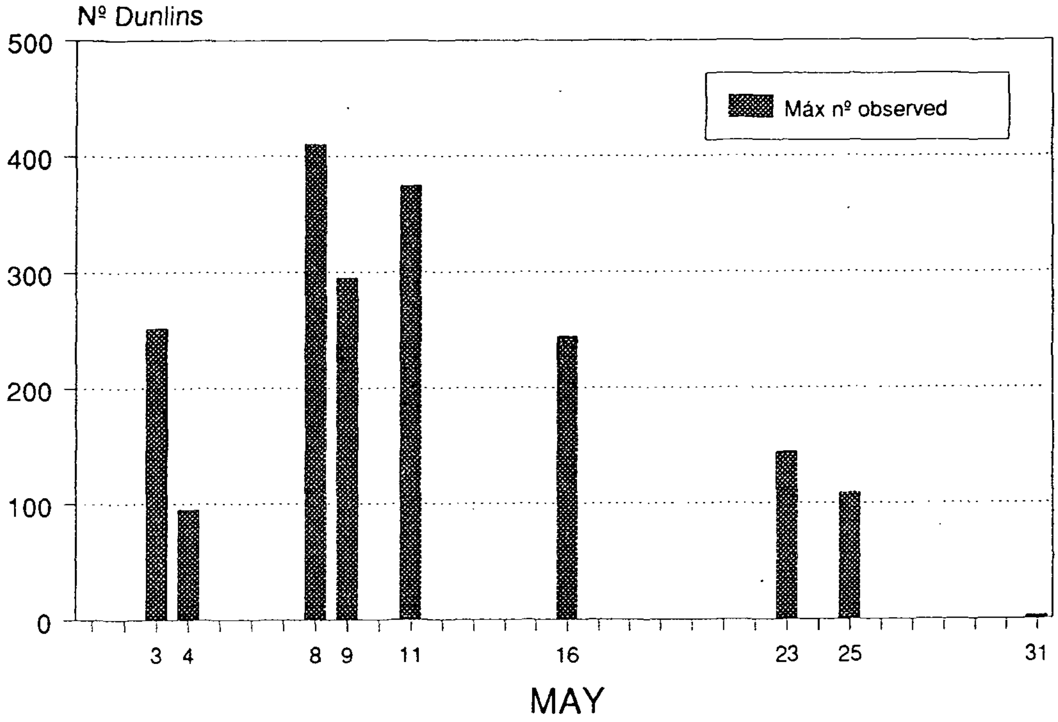


Figure 5: Maximum number of Dunlin observed during May on Seal Sands.

The maximum numbers of Dunlin seen on each day were chosen to show Seal Sands importance as a feeding habitat during May. The fluctuations observed (fig. 5) might be a consequence of the time of the tide when the respective counts were done, or be due to waves of immigration and emigration, thus suggesting different individual times of arrival and departure as Seal Sands is just a "temporary site" on the birds' flight path. From mid-May Dunlin numbers declined steadily; the last spring departure was observed at about 1.30 pm on 25 May. Similar dates of departure have been recorded in previous springs.

FEEDING PATTERN ON SEAL SANDS DURING A TIDAL CYCLE

Figure 6 summarizes the proportions of Dunlin present on each day that were seen to feed before and after low water.

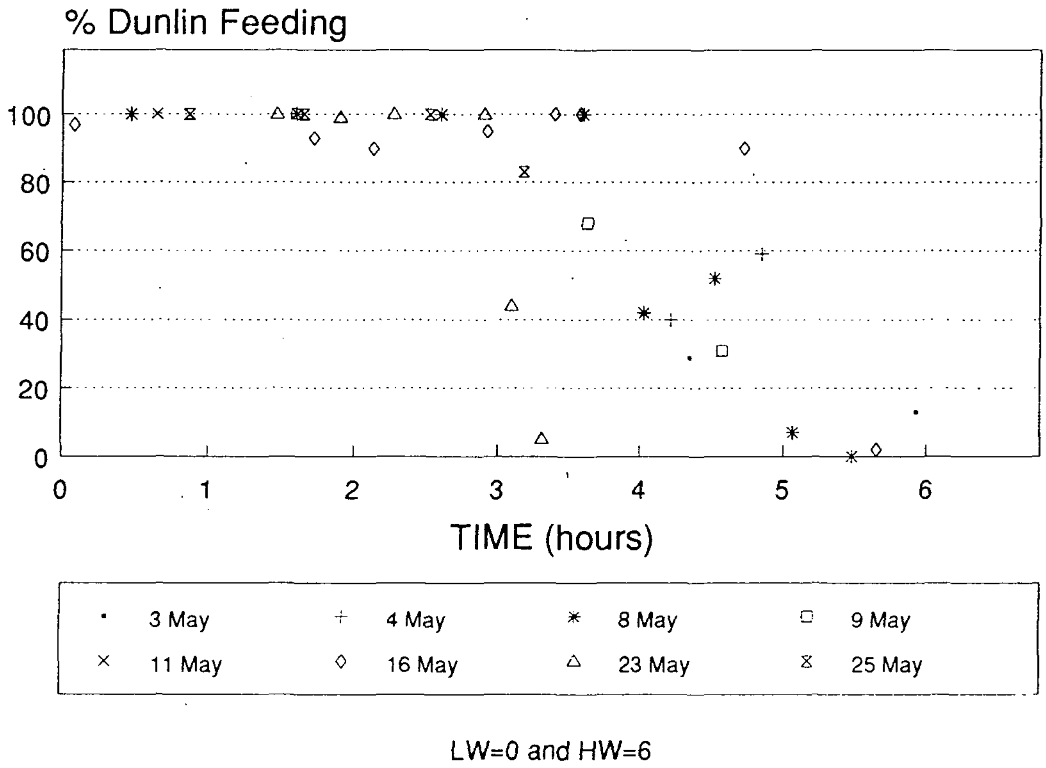


Figure 6: Percentage of Dunlin feeding during May versus tidal cycle.

Independent of the area uncovered by the tide and therefore available for feeding, the main activity of the birds was feeding from low water till low water plus 3 hours. After this the percentage of Dunlin feeding on Seal Sands decreased, reaching a minimum at high water.

If we divide the data of figure 6 into two by date, before and after the 15th of May, (figures 7 and 8 respectively), we can observe that in the first half of the month some birds tended to feed till almost high water, but on 23 May, two days before spring migration, birds stopped feeding earlier, i.e. approximately three hours after low water.

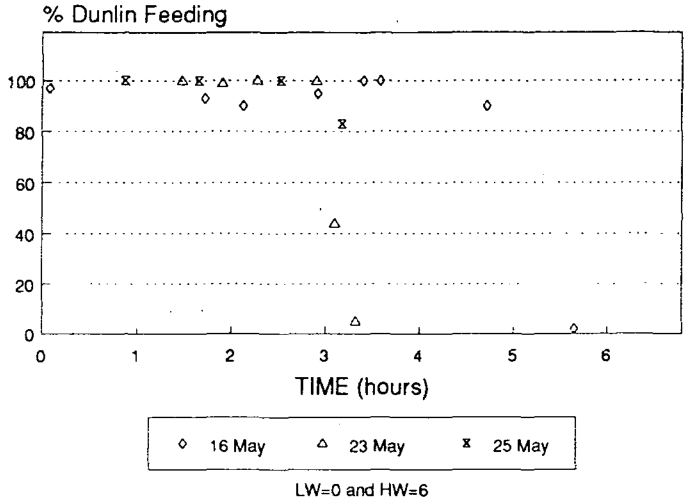


Figure 7: Percentage of Dunlin feeding, versus the tidal cycle, during the first half of May.

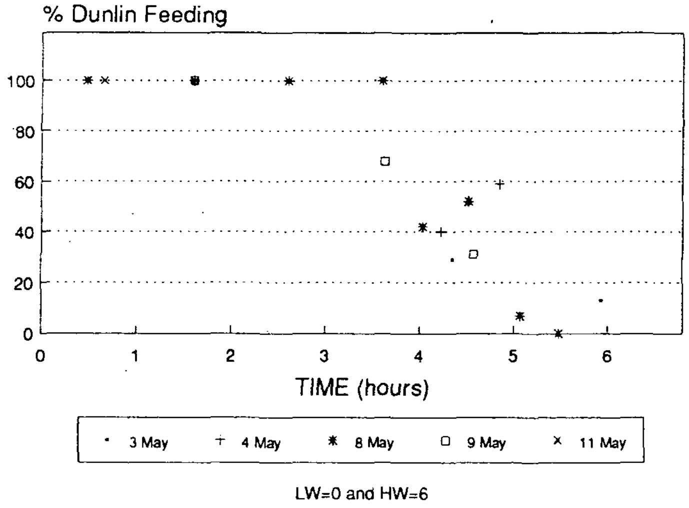


Figure 8: Percentage of Dunlin feeding, versus the tidal cycle, during the second half of May.

MACRO DISTRIBUTION ON SEAL SANDS DURING A TIDAL CYCLE

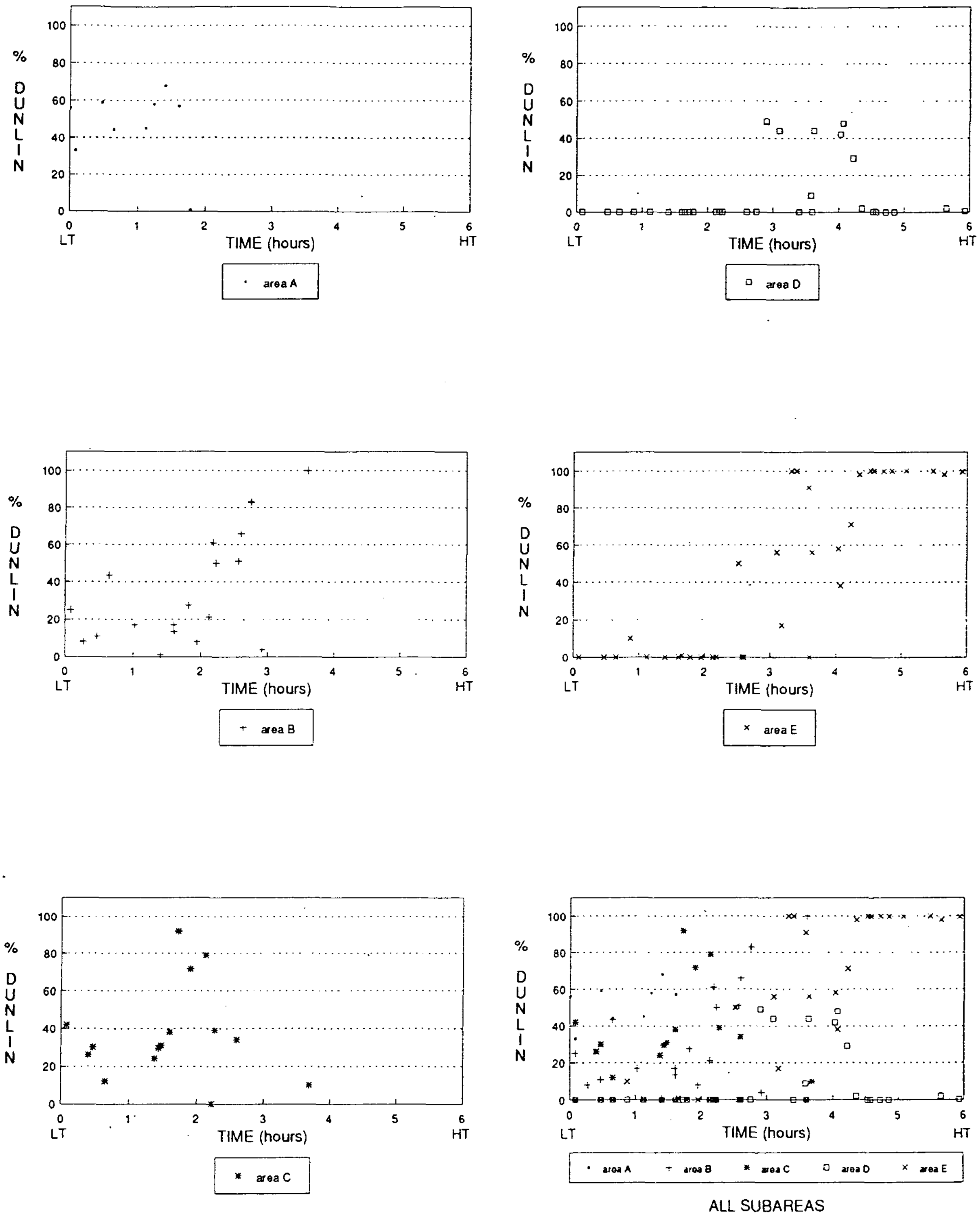
TIDAL PERIOD	SUBAREAS AVAILABLE
LW -> LW±2	A B C D E
LW±2 -> LW±3	B C D E
LW±3 -> LW±4	B D E
LW±4 -> LW±5	D E
LW±5 -> HW	"E"

Table 1: Availability of subareas through the tidal cycle ("E"= subarea E partly covered)

Figure 9 summarizes as six graphs the relative use of each subarea of Seal Sands (A, B, C, D and E) when they are available to the birds (see table 1). Indicating the sequential pattern of subarea usage over the tidal cycle, it shows the concurrent movement of Dunlin with the tide . The figure does not distinguish between feeding and non-feeding birds.

When all the subareas were available (during approximately low water ± 2 hours, depending upon the type of tide, neap or spring), the preferred subarea, defined as that with the greatest number of Dunlin, was subarea A, followed by subarea C. When these were unavailable, within approximately three hours of high tide, the birds moved to subareas B, D, and E. Finally, from about low water ± 4 hours, when only subareas D and E were available, the birds used mainly subarea E. That such preferences were real, and did not simply reflect differences in the size of the subareas, was evidenced by the preference for subarea A over its neighbours B and C. Furthermore, when all subareas were available, from low water to low water ± 2 hours, subarea D

Figure 9: Percentage of Dunlin recorded in each subarea during May versus the tidal cycle. (LT=Low Tide; HT=High Tide).



ALL SUBAREAS

was not used at all and subarea E, the largest of all subareas, was only used to a minimal extent (fig. 9).

The only exception is from low water ± 3 hours to low water ± 4 hours, when although area E is presented as the most preferred one, area B is also indicated (fig. 9) as being a prefered subarea for the birds, however the latter is due to a single data point and so such preference is open to question.

Figure 10 indicates the relative usage of each subarea, during May, independent of the tidal situation. To calculate this, each day's data was taken in turn and the percentage of the Dunlin present in each subarea was calculated. Then each subarea's daily percentages were averaged - A (30.2%), B (23%), C (20.5%), D (6.1%) and E (33%). Finally, each of these figures was expressed as a percentage of their collective total, as shown in the pie chart. Furthermore, the percentage of Dunlin feeding and roosting within each subarea, over the same period and again independent of the tide, is shown in the encircling bars.

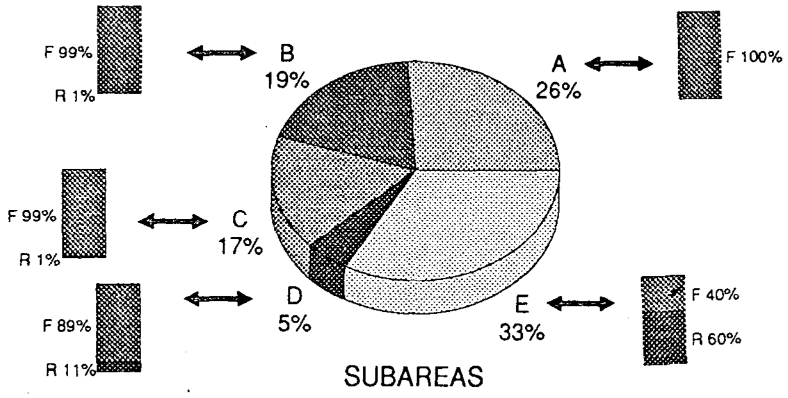


Figure 10: The percentage of the average percentage of Dunlin present in each subarea and the percentage of Dunlin feeding and roosting within each subarea, during May, independent of the tidal cycle. (F=Feeding; R=Roosting).

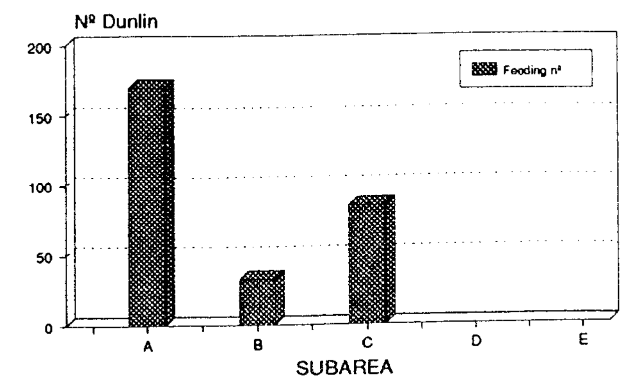
Figure 10 indicates that subarea E is used mainly as a roosting habitat during high tide when no other subarea is available, whereas subarea A was used chiefly as a feeding habitat.

Figure 11 shows the change of use and activity of the Dunlin in relation to the tidal cycle on the 8, 16 and 23 May. As the tide progressed from low water to high water the subareas were successively covered by water (table 1), and became unavailable to the birds. When all subareas were exposed, the birds were present on subareas A, B and C, although a marked preference for subareas A and C was evident. The birds moved from subareas A and C to subarea B, when the former two were not flooded. Subsequently, when subarea B became covered with water, the birds were forced to move to subareas D and E. Finally when subarea D was also covered they were confined to subarea E, this one being partially available even at high water. Again, it can be said that on each day the subareas A, B, C and D were used chiefly as feeding sites by the birds, but subarea E was mainly used as a roosting ground. The order of use of the subareas on the outgoing tide was almost the same of that on the incoming tide, as illustrated by the graphs for 16 May.

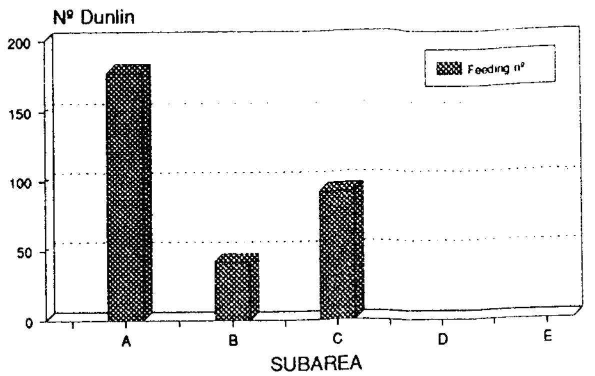
The pattern of use of Seal Sands by Dunlin described above was shown on all days when observations that covered a complete tidal cycle were made (8, 16 and 23 May).

8th

MAY



LW (0.04-0.28)
n=288



LW (1.10-1.36)
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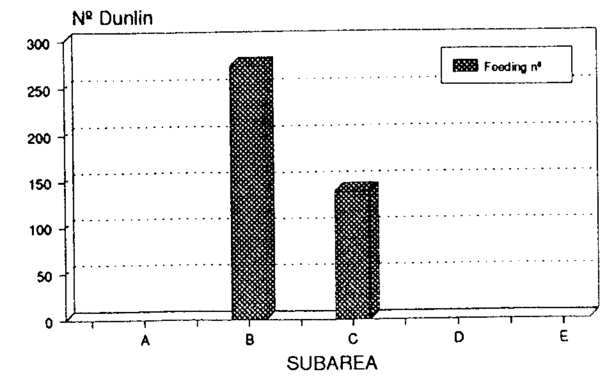

LW (2.16-2.36)
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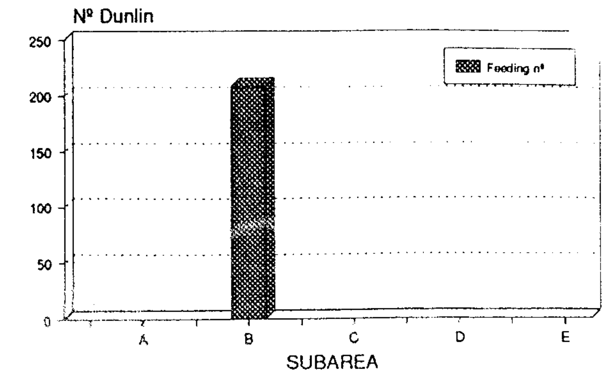

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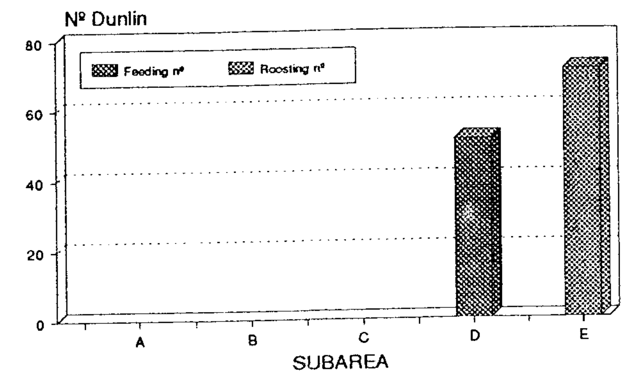

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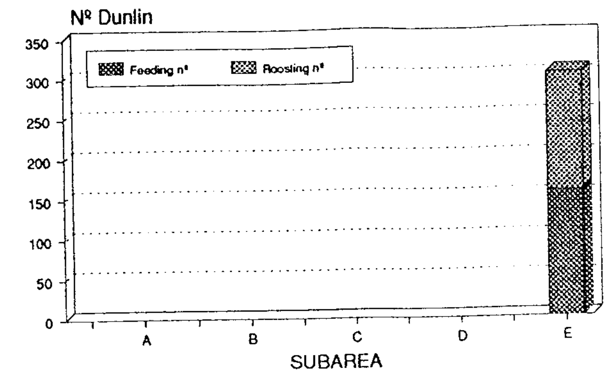

LW (4.31)
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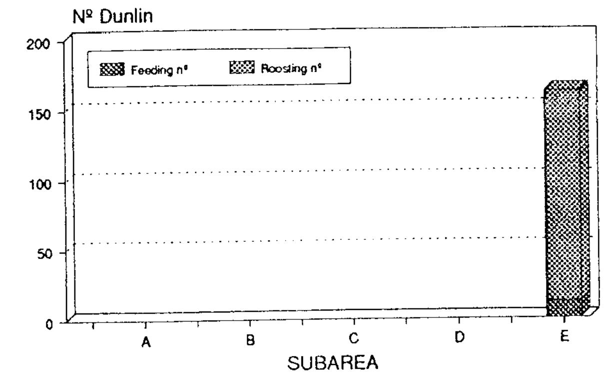

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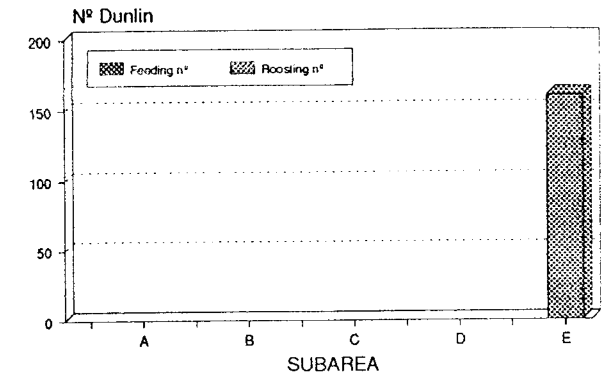
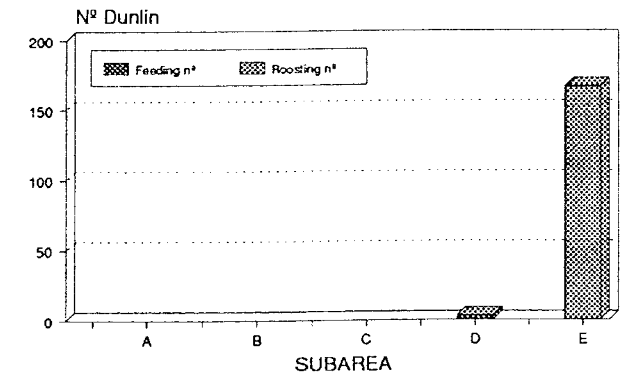


LW (5.29)
n=160

16 th

MAY



HW (0.21)
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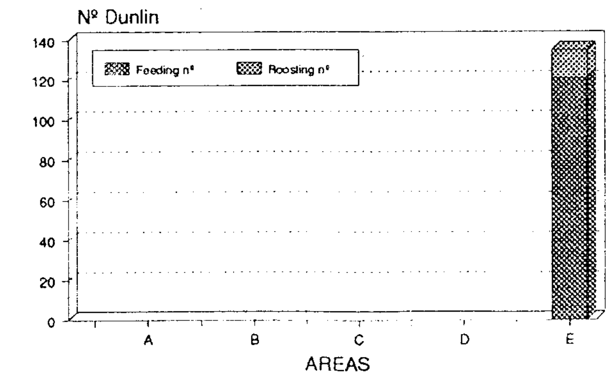

HW (1.17)
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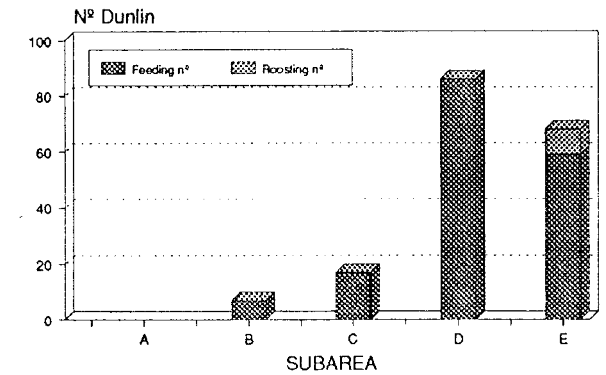

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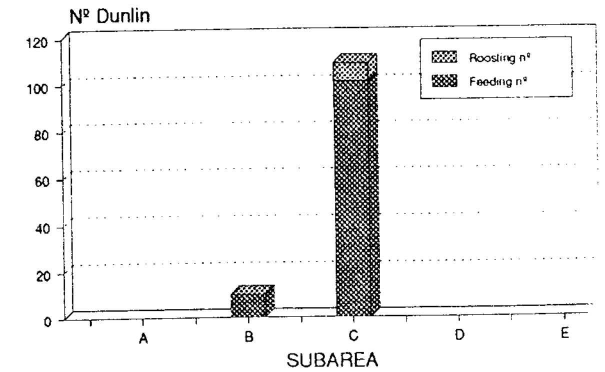

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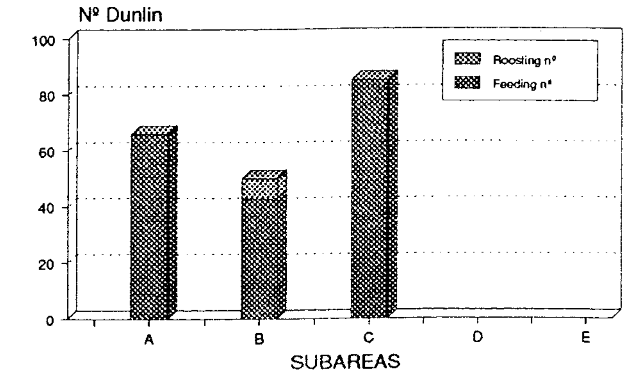

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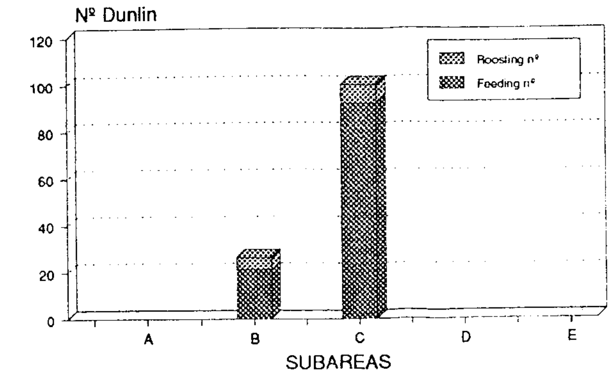

LW (2.08-2.38)
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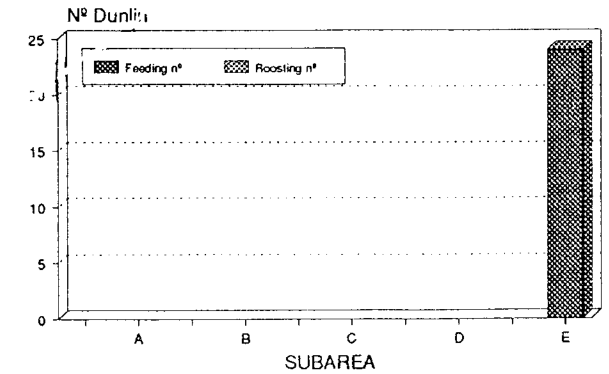
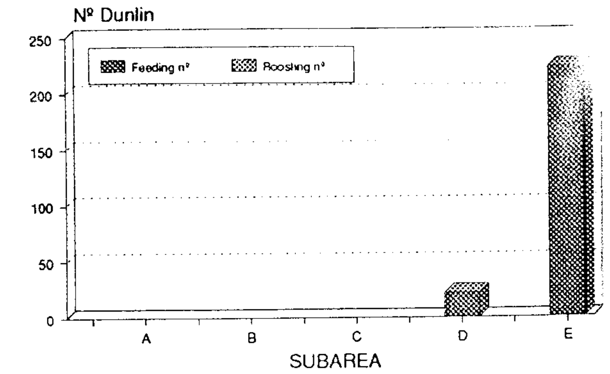


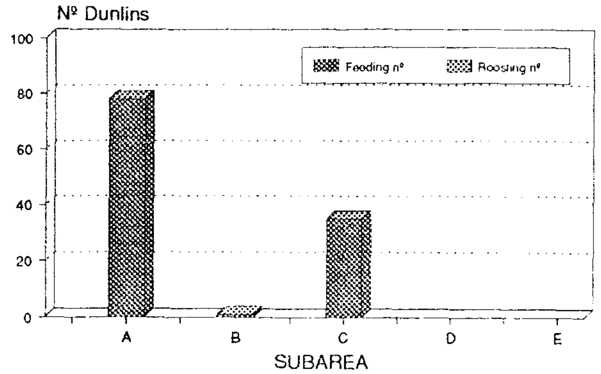
LW (3.24)
n=24



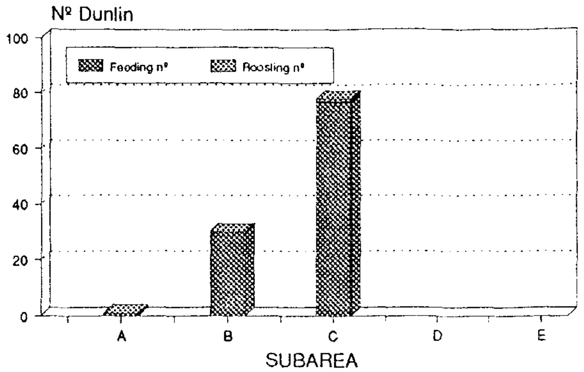
LW (3.35)
n=245

23th

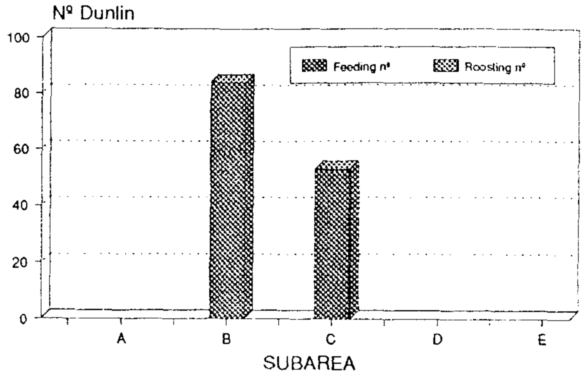
MAY



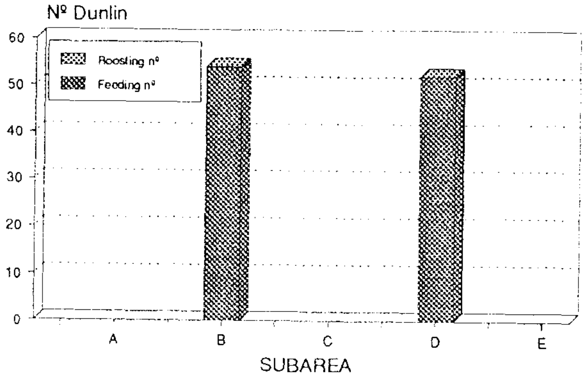
LW (1.14-1.28)
n=114



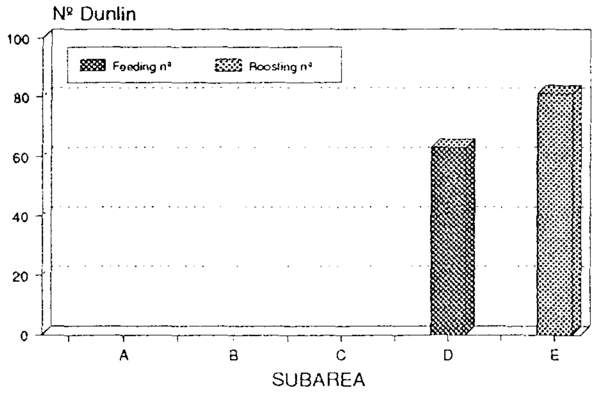
LW (1.47-1.59)
n=109



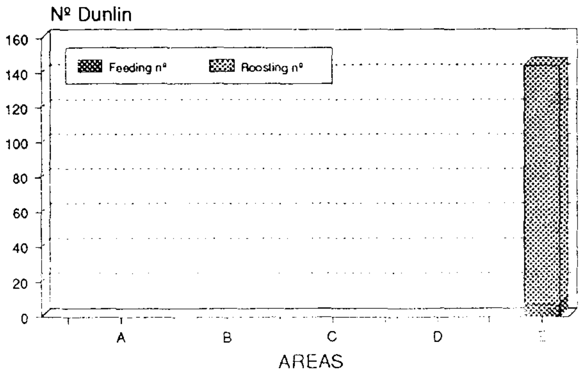
LW (2.06-2.19)
n=137



LW (2.34-2.54)
n=106



LW (3.06)
n=144



LW (3.19)
n=144

Figure 11: Number of Dunlin present in each subarea during the tidal cycle on 8, 16, and 23 May. The interval of time (hours.minutes - hours.minutes) after Low Water (LW) or High Water (HW) at which the count was carried out, and the total number of Dunlin observed (n), are also shown.

MICRO DISTRIBUTION OF FEEDING DUNLIN DURING A TIDAL CYCLE

The main purpose of Figures 12, 13, 14 and 15 is to show the importance of different microhabitats to feeding Dunlins. They summarize where the birds were feeding in each subarea in relation to the tide edge at different times during the tidal cycle. Figure 12 refers to 8 and 23 May, and Figure 13 to 16 May. On 8 and 23 May observations were only made during the flood tide.

In subarea A, birds fed mainly on the "Film" and only a small proportion used the "Water's edge" (8th and 16th) and the "Dry" (16th).

Within subarea B, from low water to high water (fig. 12 and 13), birds fed mainly on the "Film" with the exception of single counts on the 16th and 23rd, when the "Water's edge" was the preferred microhabitat.

From high water to low water on subarea B on 16 May the "Film" was the only microhabitat used by the birds (fig. 13).

In subarea C, during the flood tide (figures 12 and 13), the "Film" was the dominant microhabitat used on all occasions. However,in common with subarea B on the 16th other microhabitats, namely the "Dry" and to a lesser extent "T" and the "Water's edge" were also used. The latter was the only microhabitat, other than the "Film", used on the 8th and 23rd. Furthermore no birds fed on microhabitat "H" during this period. During the ebb tide (fig. 13) the "Film" was still the dominant microhabitat, but in this case all the other microhabitats were used, although again to a minor degree.

8th . MAY 23th

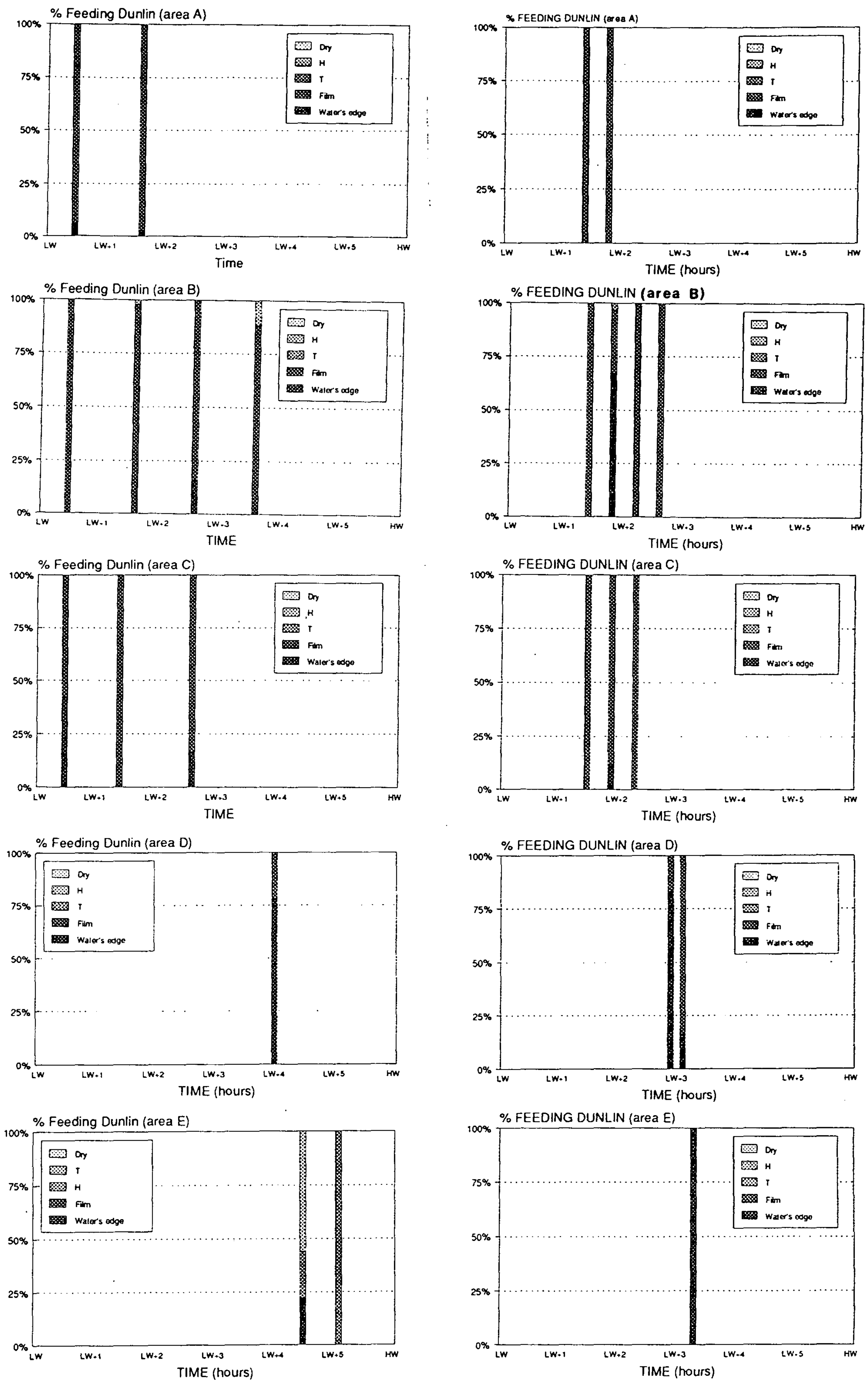


Figure 12: Percentage of Feeding Dunlin in each subarea's microhabitat during the flood tide (LW - HW) for 8 and 23 May. (LW=Low Water; HW=High Water)

16 th

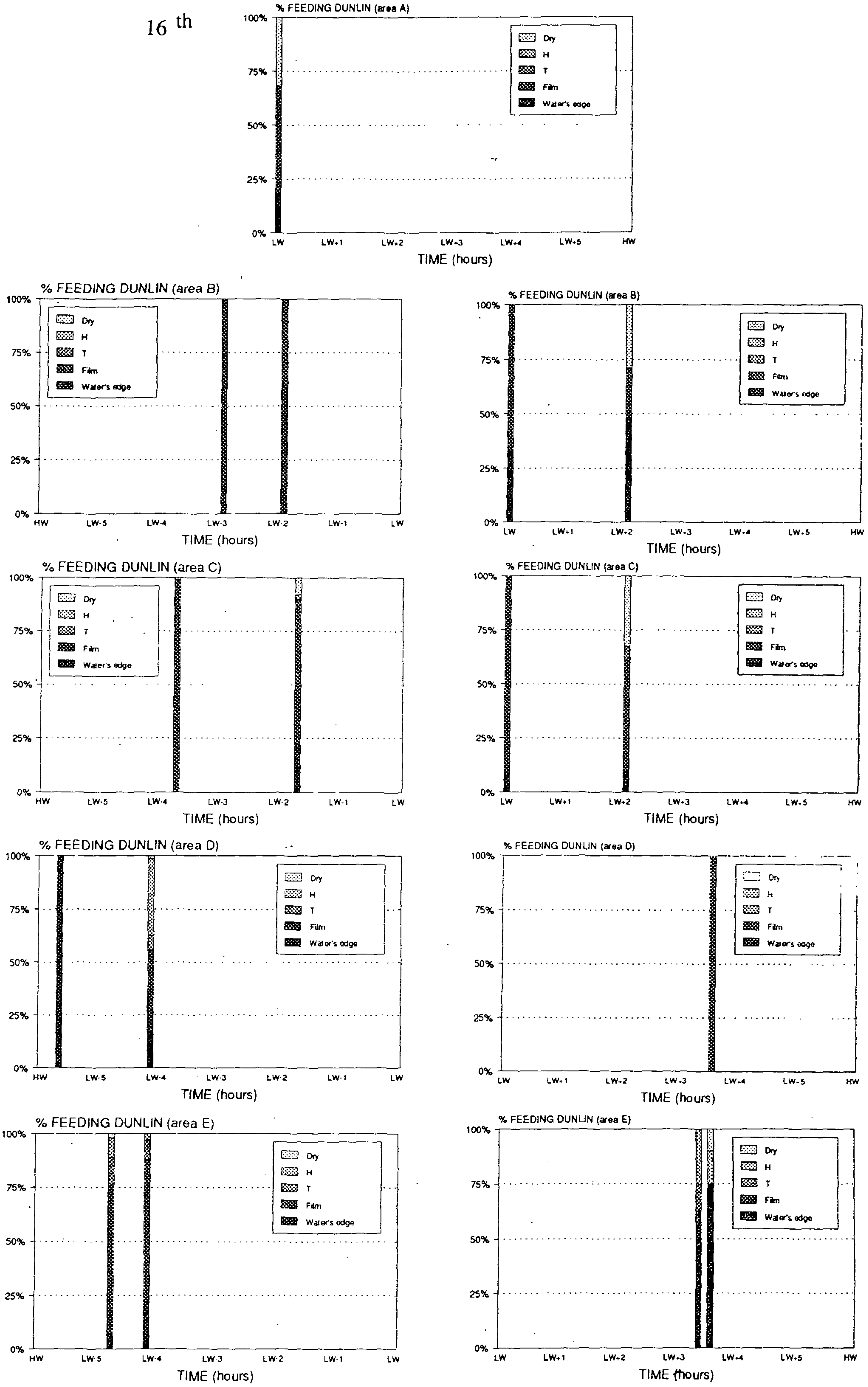


Figure 13: Percentage of feeding Dunlin in each subarea's microhabitat during the ebb (HW - LW) and flood (LW - HW) tides for 16 May. (LW=Low Water; HW=High Water).

With reference to subarea D, on all three days during the flood tide (figures 12 and 13), the "Water's edge" and the "Film" were the only microhabitats used and were approximately of equal importance, but on the ebb tide (fig. 13), although initially the "Water's edge" was the dominant microhabitat as the tide receded the "Film" and the "H" began to be used as feeding grounds more than the "Water's edge".

Finally in subarea E, a trend was discernable through time (figures 12 and 13), namely a decrease in the use of the "Water's edge" from low water plus 3 hours (100%) to low water plus 5 hours (0%) with a concurrent increase in the use of "T" (0% to 100%). Microhabitat "H" was also used especially in the middle of this period. At 4 hours after low water, on the 8th, it held 56% of all the feeding Dunlin. During the ebb tide (fig. 13), the "Film" was the microhabitat with the highest percentage of feeding Dunlin, followed by the "Water's edge". The other microhabitats were also used but only to a minor degree.

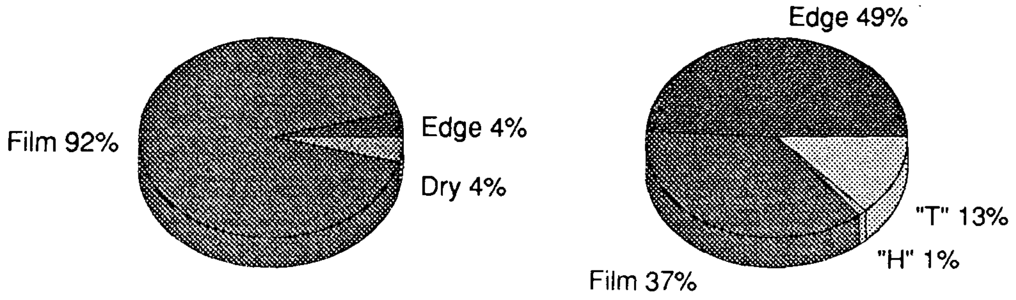
Figure 14 shows a comparison between the ebb and the flood tide for the 16th, the only day when a complete tidal cycle was followed.

A marked difference in microhabitat used by the feeding Dunlins was apparent between the ebb and flood tide for subareas B and E. During the receding tide, the "Film" was the dominant microhabitat; in contrast, the "Water's edge" was most used during the incoming tide. In subarea D, due to lack of data, no conclusions can be drawn, and for the subareas A and C no difference was observed between microhabitat use on ebb and flood tides.

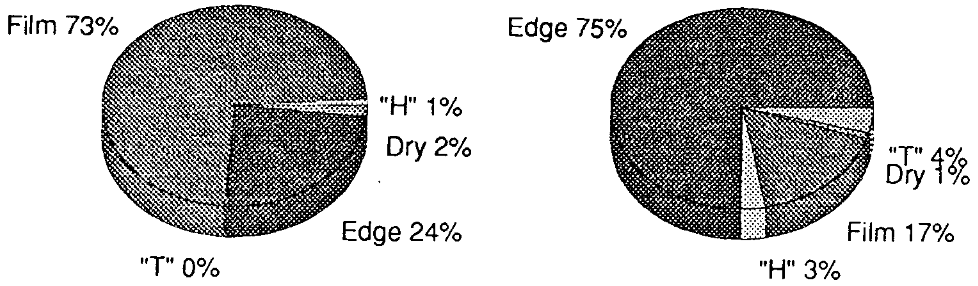
DOMINANT	FEEDING	MICROHABITAT							SUBAREA
<--------- N.A. ------->				film	<-------- N.A. ----->				A
<-- N.A. -->		film	film	film	edge	<---- N.A. --->			B
<-- N.A. -->		film	film	film	film	<---- N.A. --->			C
edge	0	film	0	0	0	0	film	?	D
0	film	film	0	0	0	edge	edge	?	E
HW				LW				HW	

Figure 14: Dominant feeding microhabitat in each subarea during the ebb (HW - LW) and flood (LW - HW) tides for 16 May. (N.A. = subarea not available to the birds).

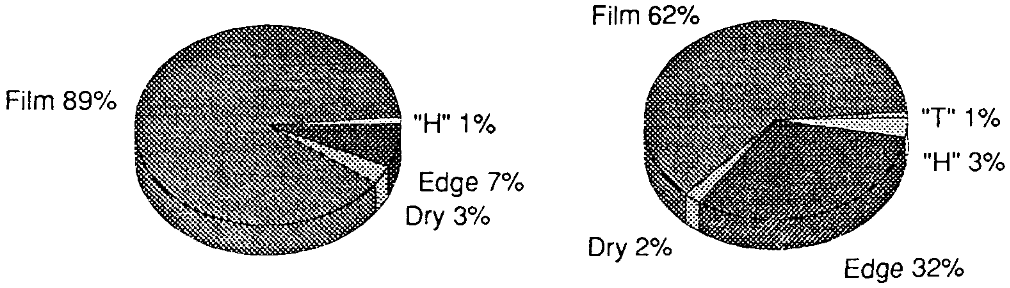
In order to obtain a more complete picture of the importance of each microhabitat in each subarea, all the days of May when counts were made from low water to high water were combined to produce figure 15.



AREA A AREA D



AREA B AREA E



AREA C MEAN ALL AREAS

Figure 15: Mean percentage of feeding Dunlin in each microhabitat for each individual subarea, and overall, during the flood tide in May. (E=Water's edge).

On the muddy subareas, A, B and C (fig. 15), independent of the time of the tidal cycle, the "Film" was the dominant microhabitat, holding over 70% of the percentage of feeding Dunlin. The "Water's edge" was more important in subarea B (24%) than in subareas A (4%) and C (7%). In contrast, in subareas D and E, the "Film" had less than 40% of the percentage of feeding Dunlin, 37% and 17% respectively. In these more sandy subareas, use of the "Water's edge" was more important than in the muddy subareas. In subarea E, the sandiest of all subareas, the percentage of feeding Dunlins present on the "Water's edge was the highest.

In figure 15, is shown, in the pie chart entitled "Mean all areas", the general importance of each microhabitat in Seal Sands, independently of the subarea and tidal situation, this was obtained by doing a mean of the data of all the other five charts. In general on Seal Sands the "Film" was the most frequented microhabitat by the feeding Dunlins, followed by the "Water's edge". There was a marked preference for wet substrata, "in water", "water's edge" and "Film" (98%) then for the "Dry" substratum (2%).

FORAGING BEHAVIOUR

The three statistics, head lift rate, pace rate and nearest neighbour distance, were recorded in order to analyse changes in feeding behaviour between microhabitats at the intra-subarea level with the tidal cycle. These measurements should also give an indication of the availability of prey within each microhabitat.

In subarea A (fig. 16), on both the ebb and flood tides, there was an increase in the head lift rate and a decrease in the pace rate as the degree of wetness of the substratum rose, from the "Film" to "in water". During the flood tide, both rates, in every microhabitat, were significantly different from each other (see appendix I). On the ebb tide the "Water's edge" and "in water" were not significantly different either for head lift rate (p=0.47) or for pace rate (p=0.98). On both parts of the tidal cycle, the neighbour to neighbour distance was greater on the "Film" than on the two wetter substrata, the latter two not being significantly different from each other (see appendix I). Although the trend was similar, the birds fed faster on the ebb tide than on the flood tide in the less wet substrata and the pace rate was also greater. But the distance between feeding Dunlins was shorter on the ebb tide than on the flood tide.

Figure 16: Head lift rate, pace rate and neighbour to neighbour distance during ebb and flood tides for each microhabitat in subarea A. (In Water = microhabitat "H" and "T").

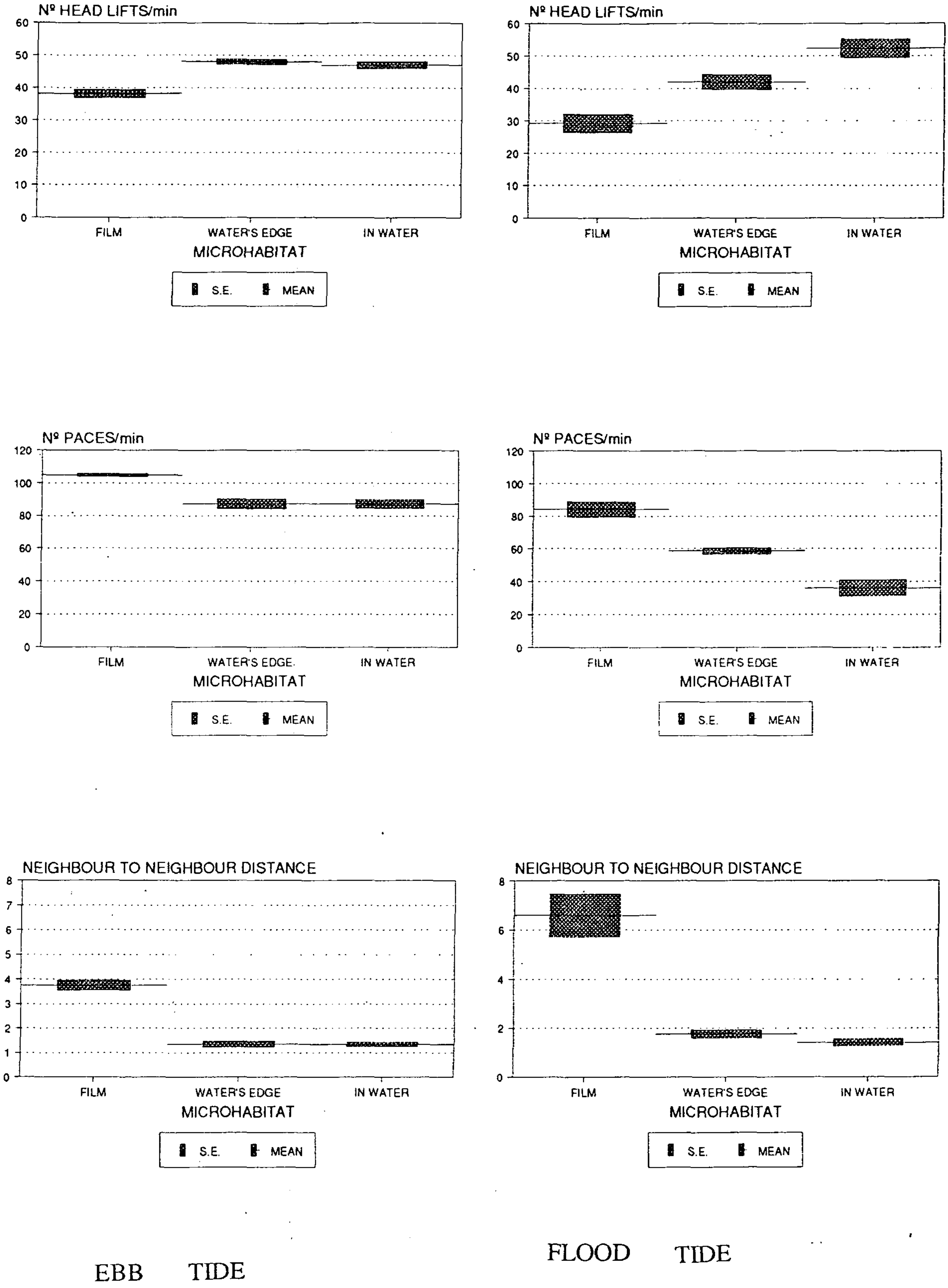


Figure 17: Head lift rate, pace rate and neighbour to neighbour distance during ebb and flood tides for each microhabitat in subarea B. (In Water = microhabitat "H" and "T").

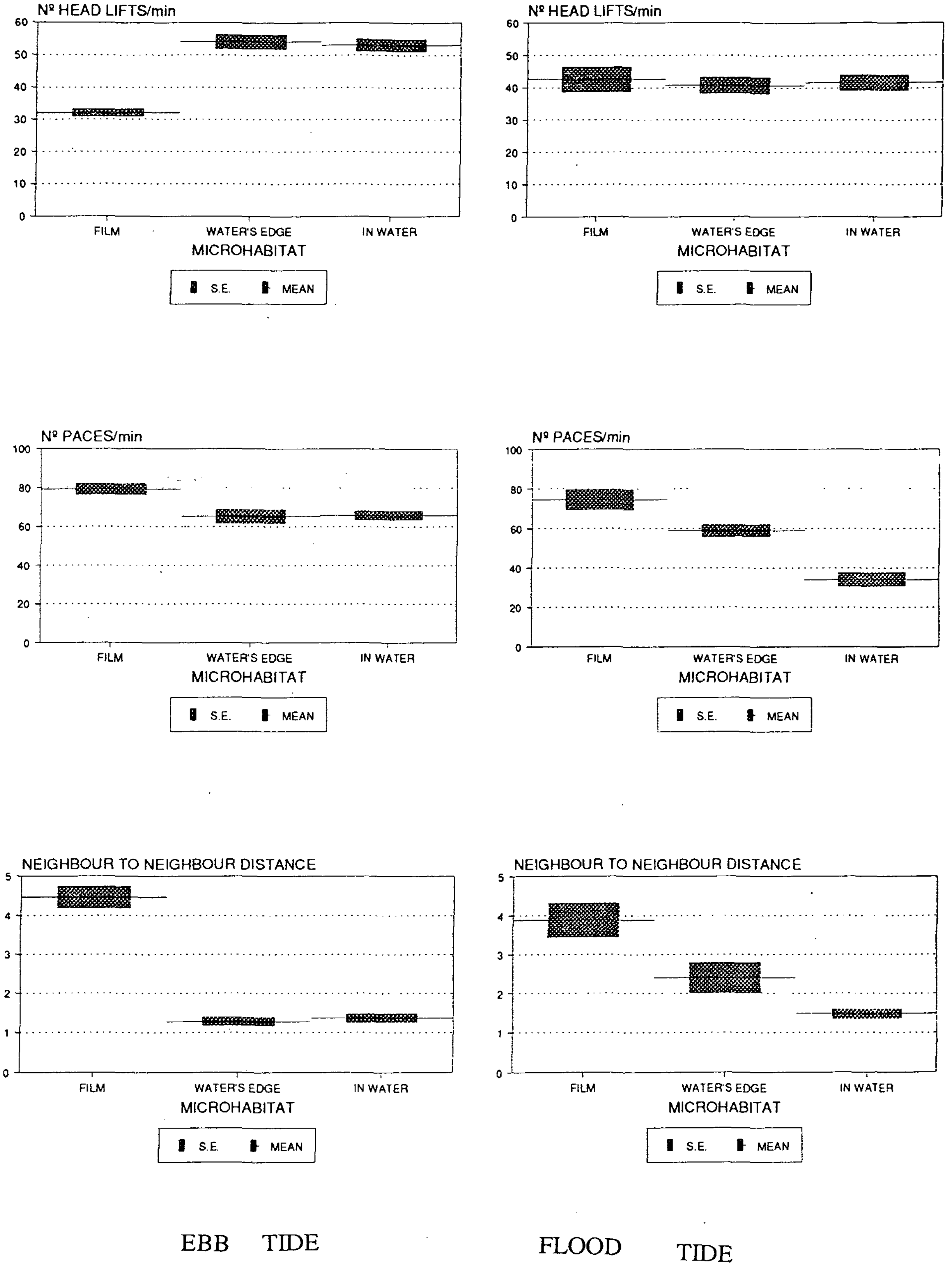


Figure 18: Head lift rate, pace rate and neighbour to neighbour distance during ebb and flood tides for each microhabitat in subarea C. (In Water = microhabitat "H" and "T").

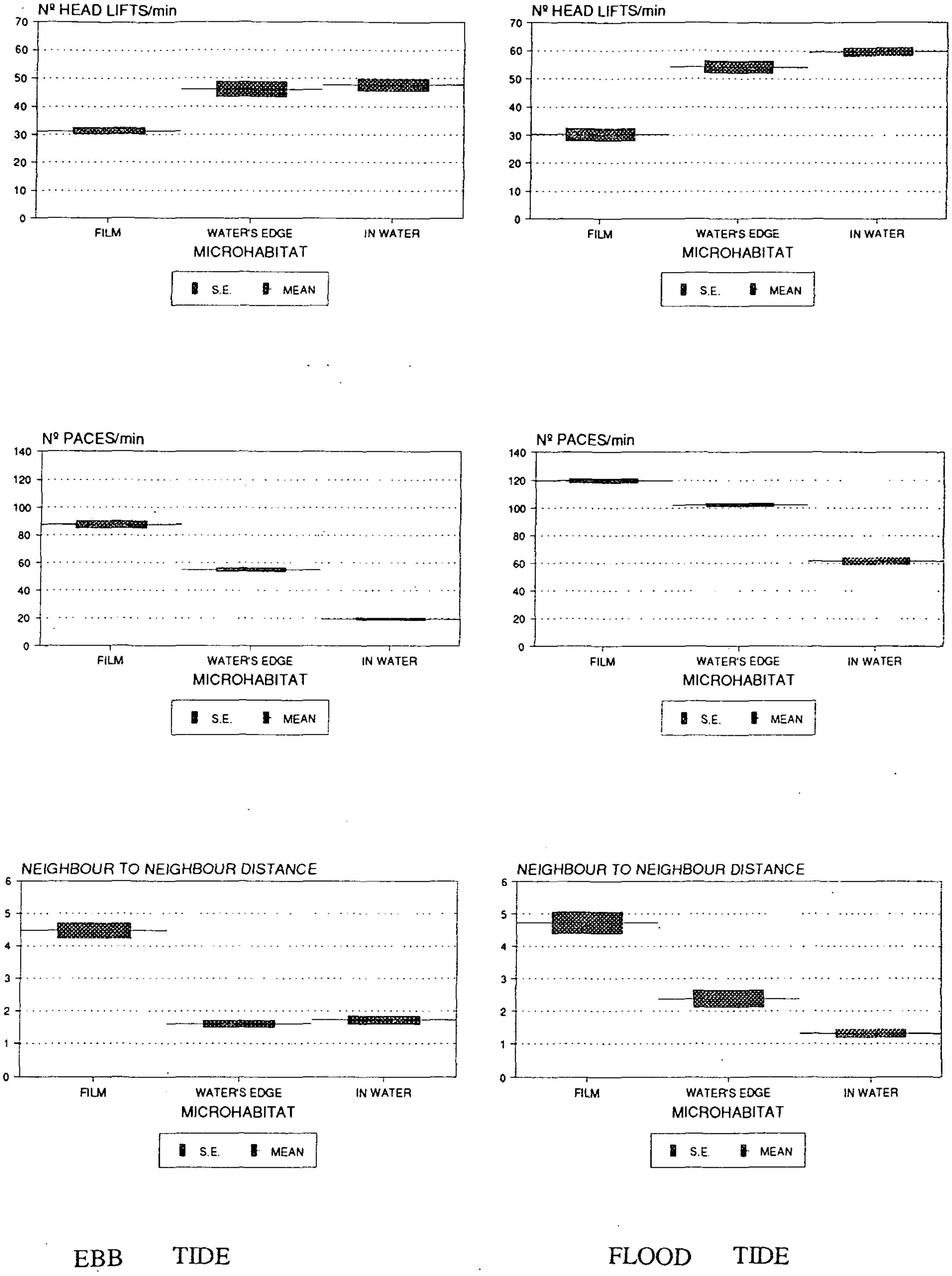
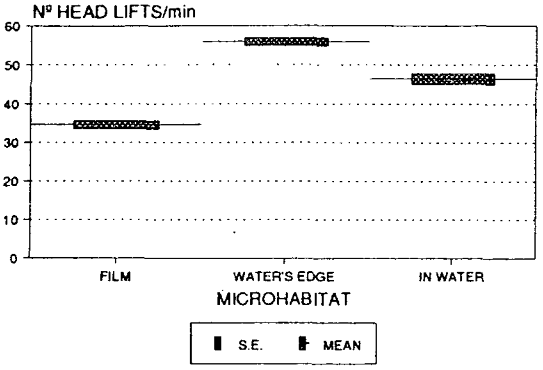
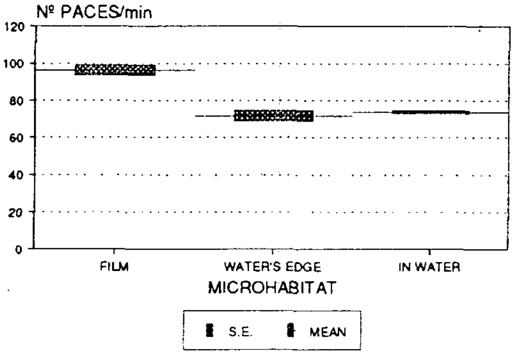


Figure 19: Head lift rate, pace rate and neighbour to neighbour distance during the ebb tide for each microhabitat in subarea D. (In Water = microhabitat "H" and "T").





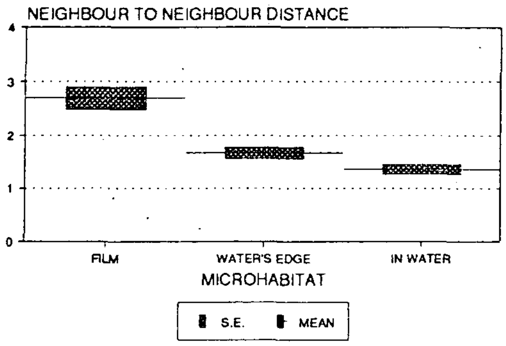
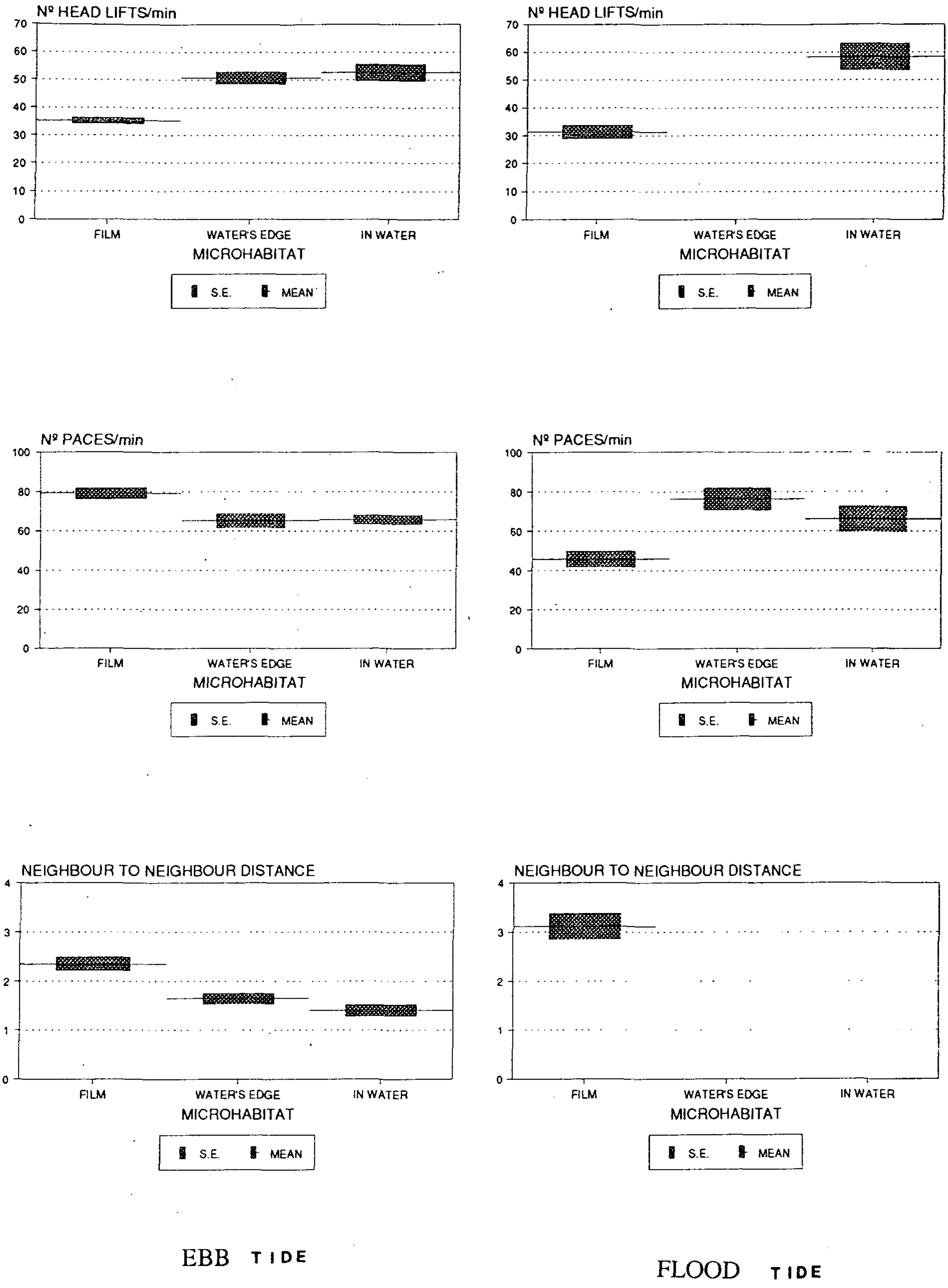


Figure 20: Head lift rate, pace rate and neighbour to neighbour distance during ebb and flood tides for each microhabitat in subarea E. (In Water = microhabitat "H" and "T").



In relation to subarea B (fig. 17), during the ebb tide the same pattern with regard to the head lifts was observed as in subarea A. With the "Film"'s head lift rate, pace rate and neighbour to neighbour distance being significantly different from both those observed on the "Water's edge" or "in water" (see appendix I), between the latter two no diference was found (see appendix I). During the flood tide, although the pace rate had a similar trend as in subarea A, there was no diference between the substrata in terms of head lift rate (see appendix I). The neighbour to neighbour distance showed a similar trend to the pace rate, decreasing with the increasing wetness of the substratum, and again all substrata were significantly different (see appendix I) from each other.

Again in subarea C (fig. 18), the general pattern revealed in subarea A was found, although with two exceptions, in both pace rate ($p<0.0001$) and neighbour to neighbour distance ($p<0.002$) the "Water's edge" was significantly different from "in water". The former on the ebb tide and the latter on the flood tide.

In subarea D (fig. 19), during the ebb tide the "Water's edge" had the highest head lift rate and the lowest pace rate, in contrast with the "Film", which recorded the opposite pattern. In relation to the neighbour to neighbour distance all microhabitats were significantly different (see appendix I), with the "Film" presenting the greatest dispersion of birds and "in water" the least. The data refering to the flood tide was not collected due to lack of time.

With respect to subarea E (fig. 20), during the ebb tide , the trend was the same as found on subareas A and B, with an increase on the head lift rate and a simultaneous decrease on the pace rate and neighbour to neighbour distance associated with the increasing degree of wetness of the microhabitat. From low water to high water, the data was not completed due to lack of time, nevertheless the "Film" presented the lowest head lift and pace rates. Furthermore, the birds' head lift rate was higher in the flood tide "in water" and lower on the "Film" by comparison with the results for the same microhabitat on the ebb tide. The birds, during the incoming tide, walked less on the "Film" and more on the "Water's edge", but no significant change was observed "in water" (p=0.26). Still refering to the "Film" the birds fed further away from their nearest neighbour on the flood tide than on the ebb tide.

It was found, on the basis of the head lift/pace ratio (table 2), that the "Film" was in all cases the poorest microhabitat (few head lifts/ many paces). During the ebb tide there was no apparent difference between the "Water's edge" and "in water" with the exception of the subarea C, where the "in water" ratio was three times higher than for the "water's edge" ratio. In contrast, during the flood tide the ratio was consistently higher (approximatly two times) "in water" than in the edge.

HEAD LIFT/PACE RATIO

SUBAREA A:	**HW -> LW**	**LW -> HW**
FILM	0.36	0.35
WATER'S EDGE	0.55	0.72
IN WATER	0.54	1.45
SUBAREA B:		
FILM	0.41	0.57
WATER'S EDGE	0.83	0.69
IN WATER	0.81	1.22
SUBAREA C:		
FILM	0.36	0.25
WATER'S EDGE	0.84	0.53
IN WATER	2.47	0.97
SUBAREA D:		
FILM	0.36	
WATER'S EDGE	0.78	
IN WATER	0.63	
SUBAREA E:		
FILM	0.40	0.68
WATER'S EDGE	0.82	
IN WATER	0.90	0.88

Table 2: Head lift/pace ratios for each microhabitat (Film, Water's edge, In water) within each subarea during ebb (HW->LW) and flood (LW->HW) tides.
(In water = microhabitats "H" and "T")

DISCUSSION

TIMING OF MIGRATION (CENSUS)

The Dunlins using Seal Sands as a staging-post during their spring migration began to arrive in April and the last departure occurred on 25th May (figs. 4 & 5). During this northwards passage, a mixture of two subspecies, *Calidris alpina alpina* and *C. a. schinzii* were present. This pattern of spring passage at Teesmouth has been noted by other authors, namely Goodyer and Evans (1979), South Cleveland Ringing Group (1985) and Evans (pers. comm.).

FEEDING PATTERN ON SEAL SANDS DURING A TIDAL CYCLE

During their stay at Seal Sands, the Dunlins' primary aim is to increase their reserves of fat in order to be able to migrate to their breeding grounds; consequently they spend most of their time feeding.

The general decrease in percentage of Dunlin feeding between the periods low water to low water   3 hours and low water 3hours to high water, was related to the fact that around low water all subareas were available, but as the tide advanced to high water, they progressively became unavailable to the birds (The exception was subarea E, which was always partly exposed (table 1); the relative lack of usage of subarea E for feeding purposes will be discussed later). Thus the birds' feeding activity tended to follow a tidal rather than diurnal periodicity, as also suggested by

Pienkowski *et al.* (1979).

To explain the difference in the birds' feeding behaviour between the first and second half of May, it may be hypothesised that when the birds first arrive they needed to restore body reserves quickly in order to continue their migration as soon as possible. This is necessary because of the very restricted period for breeding in the arctic. Consequently, they need to feed for as long as the tide permites, a situation represented e.g. by the data of 16th May. Once they had reached the necessary level of fat reserves, and were just waiting for the right wind/weather in which to depart, i.e. after 23rd May, they stopped feeding when subareas A, B and C were covered, at approximately low water ± 3 hours. Later it will be shown that these three subareas were the most heavily used and thus probably the most profitable ones.

MACRO DISTRIBUTION ON SEAL SANDS DURING A TIDAL CYCLE

Many birds are knwon to concentrate their feeding in areas which have the highest densities of available prey (Goss-Custard, 1970b, 1977a, 1981; Goss-Custard *et al.*, 1981; Bryant, 1979; Wolff, 1989). In habitats where the physical characteristics of the prey patches are similar, an efficient predator would forage in areas where prey density or biomass is greatest. However, many feeding areas are physically heterogeneous and these differences in physical characteristics of the sediment can influence the efficiency with which birds can detect and/or capture their prey.

Instead of having a random distribution, as would be expected while feeding, the Dunlin on Seal Sands showed a preference for certain subareas over others (figures 9 and 10). Thus, when all subareas were available, between low water and low water ± 3 hours, the birds fed mainly on subareas A and C (fig. 9). This preference suggests differences in the quality of each subarea as feeding grounds at that stage of the tide. These differences may persist as only a small proportion of Dunlin used subarea E for feeding at any time (fig. 10). Roosting in this latter subarea represented the optimal behaviour during the high water period, while the birds waited for better subareas for foraging to be uncovered.

Dunlins' activity and distribution at Seal Sands were highly correlated with the tidal cycle (fig. 11). As the tide fell, the birds followed the receding water, moving to each subarea in turn as it became available. At low tide, the birds were concentrated in subareas A, B and C, the former holding the most birds. With the rising tide, the birds were forced off (low water +2 hours to low water +3 hours) their apparently favoured subareas, and it was during this period that a change in their activity, from feeding to roosting, was observed. A similar tide-dependent activity pattern was found in California by Recher (1966).

As the tide retreated the substratum became drier and the wet areas holding surface water became more restricted within subareas D and E. Being sandier, they retained less water than the muddy subareas A, B and C.

It is probable that the presence of feeding

Dunlin in a subarea is related to both the density and the availability of prey in that subarea. This latter is a function of the wetness of the substratum, as the activity of many invertebrates increases with the substratum wetness (Pienkowski, 1981), thus producing more visible cues to feeding shorebirds (Goss-Custard, 1977b). The benthic fauna tends to bury deeper, following the water level, as the tide falls in order to prevent desiccation, hence becoming unavailable to the feeding birds. This explains why birds moved as the tide fell, the first subareas to be exposed to the wind and sunshine becoming drier sonner than those exposed later.

Myers *et al.* (1980) and Quammen (1982) showed that substratum penetrability strongly influenced the availability of prey to birds such as sanderling *Calidris alba* and Dunlin *Calidris alpina*. The maximum depth at which the prey are found is probably limited by the depth they can penetrate into the anaerobic layer. This lies deeper in a sandy substratum than in a muddy substratum, due to the latter's lower permeability. Woodin (1974) has shown that most invertebrates in muddy anaerobic sediments occur in the top 2 cm. This may explain the Dunlins' marked preference for the muddy subareas A, B and C, over the sandier subareas D and E. By choosing to feed in such muddier subareas, even if the absoute density of prey was equal in all subareas, they would be able to maximize the net rate of energy gain. Gerritsen & Heezik (1985), Kelsey & Hassal (1989) and Moumoutzi (1977), the latter of whom worked at Seal Sands, concur with these findings.

Quammen (1982) also suggested that sand

interfered with the feeding success of the birds because the individual grains, being of similar diameter to the prey items, impeded both the detection and capture of the latter. Such differential success in prey capture between muddy and sandy substrata may be invoked as another explanation for the observed preferences in subareas used at Seal Sands.

Myers *et al.* (1980) also showed that prey availability is increased when the substratum is made softer by adding water. This may explain why birds prefered subareas A and C, to subarea B. Subarea A was flat and was the last to be exposed and the first to be covered by the ebbing and flooding tides respectively. Subarea C had a concave profile and was the last but one to be exposed and the second subarea to be covered. In contrast, subarea B, although being a muddy area like A and C, had a convex profile, and so dried more quickly. Furthermore,during a tidal cycle, subarea B was exposed for longer than either subareas A and C . Consequently, it seems probable that it would have had a small proportion of prey available than subareas A and C late in the low water period.

To summarize, the tide affected the feeding distribution of the Dunlin, both directly by restricting the space in which they could feed, and indirectly, by affecting the availability of the prey items through altering the wetness of the substrate.

MICRO DISTRIBUTION OF FEEDING DUNLIN DURING A TIDAL CYCLE

The distribution of the birds feeding within each subarea (figures 12, 13 and 14) was similary non-uniform and varied with the tidal cycle. This is again related to the degree of wetness of the microhabitats, this increasing from the "Film" to "In water".

The flatness of subarea A and the fact that it was only exposed at low water, meant that it was always heavily waterlogged; thus the "Film" microhabitat constituted a large part of its area. This probably explains why the "Film" was always the dominant microhabitat for feeding in subarea A, during the short period of the tidal cycle when it was exposed.

The same can be said for subarea C, but in this case it was its concave profile that was responsible for the dominance of the area of "Film" microhabitat.

In subarea B, during the ebb tide the "Film" also represented a extensive zone, hence the preference for it by the birds. However, with the exposure to the wind and/or sunshine this subarea began to dry and the "Film" became more restricted to the area near the "Water's edge". This probably explains the two occasions on which the latter microhabitat was seen to be the most important. During the flood tide, the preference for the "Water's edge" was maintained, the prolonged exposure and hence drying out of that part of the subarea above the "Water's edge" again being the likely explanation.

The same can be said for subareas D and E. As long as the "Film" persisted as a extensive zone during the ebb tide, it was the microhabitat most used for feeding, but as it became more restricted in area, due to prolonged exposure, the other wetter microhabitats increased in their importance as feeding sites. The importance of the "Water's edge" just after high water, in subarea D, was probably due to lack of space, no extensive area of "Film" having had the chance to form. Also in the subarea D, during the flood tide the "Film" was highly restricted to a zone near the "Water's edge". Most probably these two microhabitats had similar characteristics in terms of prey availability, both having been exposed for similar period of time and both being innundated virtually contemporaneously. This may explain the equal importance of these two microhabitats in this period of the tidal cycle.

Subarea E was exposed for the longest period, and being the sandiest subarea it was, therefore, the driest during the flood tide. This explains why most birds used the "Water's edge" at low water plus 3 hours, a time at which subareas A, B and C were covered and subarea E was being covered. As the tide rose it would take some time for the invertebrates to move up to the surface of the sediment. This explains the increasing importance of microhabitats "H" (legs Half covered) and "T" (legs Totally covered) and the decreasing importance of the "Water's edge" in terms of usage for feeding.

Excluding the differences between subareas, and thinking only in general terms, it would be expected that the wetter microhabitats, namely the "T" and the "H", would be the most frequented ones.

The head lift/pace ratio was used as an indicator of microhabitat richness. To reiterate, in this study, a headlift was defined as simply the removal of the bill from the substratum and not necessarily a change in posture from the feeding to the upright position. Thus in a poor habitat we would expect few head lifts and many paces, giving a low ratio; and vice versa for a rich habitat.

On this basis it was found that the "Film" was the poorest microhabitat, in contrast to the "In water" microhabitats that presented the highest ratio (table 2). Moreover, Myers *et al.* (1980) and Quammen (1982) showed that the wetter substrata were the ones with higher percentage of prey available. Nevertheless,the "Film" was the dominant microhabitat, in terms of numbers of Dunlin using it, followed by the "Water's edge", and only in a minor extent were "T" and "H" used (fig. 15).

What seems an apparent contradiction in the results is due to the attempt to explain the distribution of feeding birds by taking into account only the percentage of prey available in relation to the wetness of the substratum. Meanwhile, if the following concepts are also taken in account it might be possible to prove that the "contradiction" is only apparent. The "Film" was a more stable microhabitat than either the "Water's edge" or "In water". In the latter two, the movement of the water, due to wind and tide, may cause movement of the substratum. Consequently, it would be more difficult for a bird to locate and capture prey in these circumstances even if a higher proportion were available; hence the higher head lift rate. That is to say that on a rich and stable substratum, the birds would have a high head lift rate in order to take maximum advantage of the food available, similarly however, on a rich and unstable substratum the birds may make several near misses before achieving success, this again leading to a high head lift rate. Furthermore the expected higher costs, in terms of thermal energy spent to keep warm a bird feeding in cold water, should be taken in consideration. Another reason for the apparent importance of the "Film", could be that this microhabitat, of all microhabitats, accounted for the highest proportion of Seal Sands, both overall and within each subarea, in terms of area (Unfortunately this was impossible to measure accurately as it varied with the tidal situation).

FORAGING BEHAVIOUR

Changes in physical characteristics of the substratum, related to its wetness, resulted not only in changes in the Dunlin's distribution, but also in their foraging behaviour. The foraging methods used by the Dunlins in this study were defined on the basis of Holmes' (1966) descriptions. When a bird picked on the surface of the ground, and the beak did not entered the substratum, the bird was described as pecking. Conversely, when insertion of the beak into the ground occurred the bird was said to be probing. The definition of probing also requires that several paces are taken between probes, the prey being detected by both visual and tactile clues. A variation on this is stitching, where prey is detected solely by touch and the birds probe repeatedly with only minimal pacing.

Different foraging methods may indicate that different prey species are being taken, and the birds may feed in specific areas where the preferred prey species are more abundant (Worral, 1984). Gerritsen & Heezik (1985) showed that Calidris species, when confronted with substrata of different firmness, will show a shift towards eye-hunting on the firmer substrata, but towards touch-hunting on the softer substrata. This was also observed in this study even though no quantitative data was collected.

Generally, the birds fed on the "Film" by pecking on the surface with occasional single probes, walking more than pecking, but when "In water" they used mainly continual probing (stitching). This difference in feeding behaviour, depending on the distance to the "Water's edge", might very well be, as Gerritsen & Heezik (1985) also suggested, a gradual shift in foraging technique forced on the birds by the decreasing penetrability of the substratum as it dried.

Dunlins when foraging by eye-hunting use visual cues to locate prey items within the substratum, thereby appreciably increasing their foraging success (Evans, 1986). Visual cues include surface tracks made by prey, siphons of buried molluscs, and prey movements associated with respiration and feeding (Van Heezik *et al.*, 1983). Thus, although the "Film" was at first sight a less favourable microhabitat for birds that needed to achieve a certain weight in a limited period of time, it seems possible that its poverty in terms of percentage of prey available could be compensated for by the foraging strategy used.

However, when hunting by touch, the continual probing of the bill into the sediment surface implies the use of chemosenses in the localization of hidden prey. As Van Heezik *et al.* (1983) suggested, not only is the bird able to taste, but information on taste had a direct effect on the length of time spent in searching for food.

It was observed that the number of head lifts, number of paces and the neighbour to neighbour distance between feeding birds varied within each subarea and between ebb and flood tides.

In general, in all subareas, during the ebb tide birds feeding on the "Film" registered the lowest head lift rates, the highest pace rates and the longest neighbour to neighbour distances in contrast with the wetter substrata. The "Film", being less wet, would have less prey available, so the birds would search more and so walk more to reach the amount of food that provided the energy required.

Even though flocking behaviour may confer an advantage to individuals in providing protection against predation, to feed in close proximity to other birds might not always be advantageous. Besides the competition, if the birds are feeding by sight, disturbances caused by other birds on the sediment surface may cause invertebrates to burrow deeper, thereby becoming unavailable, and thus reducing the chances of success of the foraging bird. This might explain the observation that the highest neighbour to neighbour distance between feeding birds was on the "Film", a microhabitat in which the foraging technique most commonly used was eye-hunting. In contrast, if a bird used a probing or stitching method of feeding in which it hunted by touch, its feeding success would be less affected by the disturbances of prey, at the surface, by other birds. This might explain why the distance between feeding birds was considerably lower in the wetter microhabitats, namely "Water's edge" and "In water".

During the flood tide, although with two exceptions, in relation to the "Film"'s head lift and pace rates the subareas presented the same pattern observed during the receding tide. The "Film", the driest of the wet microhabitats, once again presented the highest head lift rate and the lowest pace rate.

During the ebb tide in most subareas, the ratio head lifts/paces (table 2) was very similar between the "Water's edge" and "In water", due to the similar physical characteristics in terms of wetness of the substratum. But in contrast with the ebb tide, during the incomimg tide, the "In water"'s head lift and pace rates were greater than those observed for the "Water's edge". This might be due to the fact that as the substratum became wetter the prey's activity increased, hence giving more visual cues. Due to the richness of the microhabitat the birds did not need to search as much and hunted more.

Of the two exceptions, one occured in subarea B, where all the microhabitats revealed head lift rates that were not significantly different from each other, this might have been caused by subarea B's profile, with several channels/ridges in which the "Film" was a very narrow zone near to the shallow water in the channels. Hence the "Film", "Water's edge" and "In water" had, very similar physical characteristics, which in turn led to similar bird behaviour in terms of head lift rates.

The second exception, relates to the pace rate in subarea E, in which there is no significant difference between the "Water's edge" and "In water" and in which the "Film" had a lower pace rate than either of the two wetter microhabitats. The former discrepancy could be attributed to their approximately equal time of immersion. The latter result has no apparently obvious explanation. Given the "Film"'s highly restricted spatial extent we may have expected an non-significantly different result, but for the "Film" to have a lower pace rate defies obvious explanation.

In relation to the distance between feeding birds observed during the flood tide, for the same reasons presented previously, the "Film" recorded the highest neighbour to neighbour distance and was also significantly different from the wetter subatrata, namely the "Water's edge" and "In water". The latter two, in subarea A, were not significantly different probably due to the similarity of wetness between the microhabitats, thus inducing a similar percentage of prey available. But in subareas B and C, these microhabitats were significantly different, the "In water" microhabitat presenting, in both subareas, the shortest neighbour to neighbour distance. Again this may be attributed to the fact that as the substratum became wetter the prey availability increased, and so the birds would shift to touch-hunting, mainly continual probing (stitching), and so the disturbance on the sediment surface caused by other birds would have less effect on foraging success, thereby reducing the distance between feeding birds. During the flood tide the "In water" microhabitat became the richest, as the activity of the invertebrates increased with the increasing wetness of the substratum.

At Seal Sands Dunlins fed mainly on the open mudflats. It was observed that Dunlin exploited most of the intertidal area for feeding, though at varying densities, but they apparently tended to avoid areas with a dense crop of algae, i.e. *Enteromorpha spp.*. Although, especially during the flood tide, small numbers of Dunlin were seen feeding in areas with dense algal mats, close observation showed that most individuals were following intricate paths over mud, either lightly covered or totally free from algae. Nicholls *et al.* (1981) referred to the same feeding behaviour. He suggested that it was either the algal mats or the associated high levels of hydrogen sulphide that acted as a deterrent, because the Dunlins' main prey items were abundant.

It was very difficult to obtain a complete picture of the diet of Dunlins using only field observations, due to the latter's rapid movements, diverse foraging methods and distance from the observer. Therefore from a survey of which invertebrates were in the sediment surface at Seal Sands, and also by observing the prey items taken by the birds, it was presumed that the diet of the Dunlins consisted mainly of polychaetes, olygochaetes and *Hydrobia ulvae*. This concurs with the findings of other authors (Evans *et al.*, 1979; Nicholls *et al.*, 1981; Quammen, 1982; Lifjeld, 1983; Worral, 1984; Buchanan *et al.*, 1985; Kelsey & Hassal, 1989). It was, however, difficult to identify successful prey captures and even when swallowing was visible it could have been associated with more than one prey item.

Normally a study of diet is based upon analysis of the gut contents, regurgitated pellets and also by direct observations. However, Lifjeld (1983) showed that the analysis of stomach contents should not be used to provide any quantitative assessments of the Dunlins' diet, due to the differential digestability of the prey items. He found that data obtained from oesophagus samples were not biassed as these had not been digested. Nevertheless, the rapidity of transference of the contents of the stomach makes rapid sampling of actually feeding birds essential. Thus, great circumspection should be applied when the size or proportions of the prey items of a bird's diet are suggested.

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APPENDIX I

DATA OF EBB TIDE

No. HEAD LIFT/min

SUBAREA A

Film: 32 32 38 40 42 39 39 41 42 46 32 35

Water's Edge: 50 44 50 46 45 48 51 48 43 52 51 49

In Water: 44 40 43 53 46 48 48 47 50 50 51 45

SUBAREA B

Film: 38 28 33 40 30 36 28 28 33 36 28 28 26 26 34 36 38

Water's Edge: 54 54 60 43 44 64 63 62 51 49 52

In Water: 52 50 44 48 60 51 64 63 56 47 46 56

SUBAREA C

Film: 28 40 28 30 26 28 30 38 36 26 28 42 26 36 28 30 32

Water's Edge: 40 40 28 40 48 46 46 40 80 40 46 52 60 48 46 42 40

In Water: 48 46 54 50 73 32 48 33 50 48 48 40 60 48 46 40 40 54

SUBAREA D

Film: 40 36 40 34 28 30 35 36 33 30 36 38

Water's Edge: 60 64 56 58 53 56 50 56 58 53 52 56

In Water: 42 48 42 47 43 50 42 54 45 52

SUBAREA E

Film: 40 36 36 36 38 38 33 30 28 33 32 40 38

Water's Edge: 48 52 52 40 49 40 45 43 48 56 48 66 60 64

In Water: 52 40 40 46 45 66 66 60 42 63 64 48

No. PACES/min

SUBAREA A

Film: 108 106 105 108 100 107 104 106 107 102 101

Water's Edge: 82 80 92 105 101 76 76 80 84 92 93

In Water: 80 86 93 84 91 82 90 102 76 100 76

SUBAREA B

Film: 96 80 80 88 74 74 74 70 64 90 76 68 96

Water's Edge: 54 76 73 68 72 70 68 76 40 56

In Water: 74 56 56 64 66 71 55 74 72 70

SUBAREA C

Film: 78 78 93 96 88 98 93 80 96 76 76 64 96 100 94 96

Water's Edge: 52 64 60 40 48 53 64 56 55 56 58 54 53 56 54

In Water: 20 18 16 16 23 24 8 16 20 18 18 16 24 20 22 25 18 26

SUBAREA D

Film: 104 98 103 108 108 98 76 98 73 86 98 96 98 100 103

Water's Edge: 76 66 56 56 71 65 77 86 67 73 77 90

In Water: 74 75 76 72 70 70 68 76 77 74 76 75 72 72 80

SUBAREA E

Film: 88 93 95 80 102 80 90 74 76 87 91 89

Water's Edge: 56 57 52 56 66 70 66 70 64 60 62 63

In Water: 60 56 53 64 63 60 55 61 60 58 55

NEIGHBOUR TO NEIGHBOUR DISTANCE

SUBAREA A

Film: 2 2 2 2 2 2 2 2 3 3 3 3 3 3 3 3 4 4 4 4 4 4 4 4 4 4 4 4 5 5 5 5 5 6 6 6 6 6 6

Water's Edge: 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 2 2 2 2 2 2 3

In Water: 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 2 2 2 2 2 2 2 2

SUBAREA B

Film: 2 2 3 3 3 3 3 3 4 4 4 4 4 4 4 4 4 5 5 5 5 5 5 6 6 6 7 7 7 7

Water's Edge: 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 2 2 2 2 2 3

In Water: 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 2 2 2 2 2 2 2 2 3

SUBAREA C

Film: 2 2 2 2 2 3 3 3 3 3 3 3 4 4 4 4 4 4 4 4 4 4 4 4 5 5 5 5 5 5 6 6 6 6 6 6 6 6 7 7 7 7 7

Water's Edge: 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 2 2 2 2 2 2 2 2 2 2 2 2 2 2 3 3 3 3 3 3

In Water: 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 2 2 2 2 2 2 2 2 2 2 2 2 3 3 3 3 3 3 3 3

SUBAREA D

Film: 1 1 2 2 2 2 2 2 2 2 2 2 3 3 3 3 4 4 4 4 4 4 4

Water's Edge: 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 3 3 3 3

In Water: 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 2 2 2 2 2 2 2 2 2

SUBAREA E

Film: 1 1 1 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 3 3 3 3 3 3 3 3 3 3 4 4

Water's Edge: 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 3 3 3 3

In Water: 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 2 2 2 2 2 2 3 3 3

DATA OF FLOOD TIDE

No. HEAD LIFT/min

SUBAREA A

Film: 38 22 10 26 34 30 28 32 44 28

Water's Edge: 36 30 36 38 40 52 40 40 50 58 40 44

In Water: 38 50 60 46 52 52 32 52 68 60 58 60

SUBAREA B

Film: 24 54 46 48 32 62 54 40 36 30

Water's Edge: 38 38 40 42 34 34 40 52 40 58 52 32 46 24

In Water: 40 20 41 38 46 40 52 48 46 48 36 44

SUBAREA C

Film: 23 32 34 16 34 30 32 36 40 26

Water's Edge: 64 42 56 46 44 52 68 60 52 52 52 56 60

In Water: 56 56 50 64 56 58 58 56 60 62 60 70 68

SUBAREA D

Film: no data

Water's Edge: no data

In Water: no data

SUBAREA E

Film: 30 46 34 30 26 24 22 28 34 38

Water's Edge: no data

In Water: 82 36 60 46 62 80 52 68 42 56

No.PACES/min

SUBAREA A

Film: 46 64 104 74 68 78 86 88 74 88 106 104 98 100

Water's Edge:56 52 52 60 48 72 58 66 64 58 58 60

In Water:44 22 24 12 50 38 28 28 54 60

SUBAREA B

Film: 70 112 78 80 52 76 40 80 78 80 76 72

Water's Edge: 64 80 56 58 52 62 64 40 60 52 60

In Water: 36 16 16 24 64 36 24 24 34 32 40 48 42 42

SUBAREA C

Film: 108 120 132 120 120 122 122 118 117 123 119 116

Water's Edge: 108 104 100 101 111 104 102 101 103 102 100 99 96

In Water: 52 56 50 51 63 72 73 67 72 70 56 57

SUBAREA D

Film: no data

Water's Edge: no data

In Water: no data

SUBAREA E

Film: 40 34 30 32 54 54 58 40 46 70

Water's Edge: 56 68 100 58 100 84 58 64 96 80

In Water: 28 66 84 40 64 56 76 96 84 68

NEIGHBOUR TO NEIGHBOUR DISTANCE

SUBAREA A

Film: 3 3 4 6 6 7 7 9 10 11

Water's Edge: 1 1 1 1 1 1 1 2 2 2 2 2 2 2 3 3 3

In Water: 1 1 1 1 1 1 1 1 1 1 1 2 2 2 2 2 3

SUBAREA B

Film: 1 2 2 3 3 3 3 4 4 4 4 4 5 5 5 5 9

Water's Edge: 1 1 1 1 1 1 1 1 2 2 2 2 2 3 3 3 4 4 6 7

In Water: 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 2 2 2 2 2 2 2 2 3 3

SUBAREA C

Film: 2 2 3 3 4 4 4 4 4 4 4 4 4 4 5 5 5 5 6 6 6 6 7 7 10

Water'Edge:1 1 1 1 2 2 2 2 2 3 3 3 3 4 4 4

In Water: 1 1 1 1 1 1 1 1 1 2 2 2 2

SUBAREA D

Film: no data

Water's Edge: no data

In Water: no data

SUBAREA E

Film: 2 2 2 2 2 2 2 2 2 2 2 3 3 3 3 3 3 4 4 4 4 5 5 6 6

Water's Edge: no data

In Water: no data

RESULTS OF STUDENT-T TEST OF EBB TIDE

No. HEAD LIFTS/min

SUBAREA A

	MEAN	S.E.	n	
Film	38.17	1.3	12	T=-6.32
Water's Edge	48.08	2.97	12	p=0.0000
				Df=18.9
Film				T=-5.27
In Water	47.08	3.70	12	p=0.0000
				Df=21.1
Water's Edge				T=-0.73
In Water				p=0.47
				Df=21.0

SUBAREA B

	MEAN	S.E.	n	
Film	32.12	1.1	17	T=-8.88
Water's Edge	54.18	2.2	11	p=0.0000
				Df=15.2
Film				T=-9.37
In Water	53.08	1.9	12	p=0.0000
				Df=18.3
Water's Edge				T=-0.37
In Water				p=0.71
				Df=20.3

SUBAREA C

	MEAN	S.E.	n	
Film	31.29	1.2	17	T=-4.98
Water's Edge	46.0	2.7	17	p=0.0000
				Df=22.6
Film				T=-6.40
In Water	47.67	9.48	18	p=0.0000
				Df=26.5

Water's Edge	T=0.48
In Water	p=0.64
	Df=31.6

SUBAREA D

	MEAN	S.E.	n	
Film	34.67	1.1	12	T=-13.64
Water's Edge	56.0	1.1	12	p=0.0000
				Df=22
Film				T=-6.61
In Water	46.50	1.4	10	p=0.0000
				Df=18.1
Water's Edge				T=-5.35
In Water				p=0.0000
				Df=17.9

SUBAREA E

	MEAN	S.E.	n	
Film	35.23	1.0	13	T=-6.41
Water's Edge	50.79	2.2	14	p=0.0000
				Df=18.5
Film				T=-5.45
In Water	52.7	3.0	12	p=0.0000
				Df=13.6
Water's Edge				T=0.50
In water				p=0.62
				Df=20.8

No. PACES/min

SUBAREA A

	MEAN	S.E.	n	
Film	104.91	0.85	11	T=5.66
Water's Edge	87.36	3.0	11	p=0.0000
				Df=11.6
Film				T=6.24
In Water	87.27	2.7	11	p=0.0000
				Df=12.0
Water's Edge				T=-0.02

In Water				p=0.98
				Df=19.8

SUBAREA B

	MEAN	S.E.	n	
Film	79.2	2.9	13	T=2.98
Water's Edge	65.3	3.7	10	p=0.0081
				Df=18.2
Film				T=3.57
In Water	65.80	2.4	10	p=0.0019
				Df=21.0
Water's Edge				T=0.11
In Water				p=0.91
				Df=15.6

SUBAREA C

	MEAN	S.E.	n	
Film	87.6	2.7	16	T=10.64
Water's Edge	54.87	1.5	15	p=0.0000
				Df=23.7
Film				T=23.87
In Water	19.33	1.0	18	p=0.0000
				Df=19.4
Water's Edge				T=-19.29
In Water				p=0.0000
				Df=25.2

SUBAREA D

	MEAN	S.E.	n	
Film	96.5	2.7	15	T=6.13
Water's Edge	71.7	3.0	12	p=0.0000
				Df=23.6
Film				T=8.09
In Water	73.80	0.81	15	p=0.0000
				Df=16.5
Water's Edge				T=0.68
In Water				p=0.51
				Df=12.6

SUBAREA E

	MEAN	S.E.	n	
Film	87.08	2.4	11	T=8.71
Water's Edge	61.83	1.7	12	p=0.0000
				Df=19.7
Film				T=10.94
In Water	58.64	1.1	11	p=0.0000
				Df=15.2
Water's edge				T=-1.62
In Water				p=0.12
				Df=18.4

NEIGHBOUR TO NEIGHBOUR DISTANCE

SUBAREA A

	MEAN	S.E.	n	
Film	3.76	0.21	38	T=9.95
Water's Edge	1.348	0.12	23	p=0.0000
				Df=55.0
Film				T=10.42
In Water	1.333	0.098	24	p=0.0000
				Df=50.9
Water's Edge				T=0.09
In Water				p=0.93
				Df=43.0

SUBAREA B

	MEAN	S.E.	n	
Film	4.47	0.27	30	T=11.10
Water's Edge	1.28	0.11	25	p=0.0000
				Df=38.2
Film				T=10.78
In Water	1.37	0.11	27	p=0.0000
				Df=38.3
Water's Edge				T=0.59
In Water				p=0.56
				Df=49.9

SUBAREA C

	MEAN	S.E.	n	
Film	4.47	0.24	43	T=11.04
Water's Edge	1.59	0.11	44	p=0.0000
				Df=59.3
Film				T=10.25
In Water	1.72	0.13	39	p=0.0000
				Df=63.9
Water's Edge				T=0.76
In Water				p=0.45
				Df=77.6

SUBAREA D

	MEAM	S.E.	n	
Film	2.70	0.21	23	T=4.28
Water's Edge	1.67	0.11	36	p=0.0001
				Df=34.4
Film				T=5.71
In Water	1.36	0.10	25	p=0.0000
				Df=31.1
Water's Edge				T=-2.05
In Water				p=0.045
				Df=58.9

SUBAREA E

	MEAN	S.E.	n	
Film	2.36	0.14	31	T=4.03
Water's Edge	1.65	0.11	37	p=0.0002
				Df=60.9
Film				T=5.21
In Water	1.40	0.12	30	p=0.0000
				Df=58.6
Water's Edge				T=-1.50
In Water				p=0.14
				Df=62.2

RESULTS OF STUDENT-T TEST OF FLOOD TIDE

No. HEAD LIFTS/min

SUBAREA A

	MEAN	S.E	n	
Film	29.2	2.9	10	T=-3.48
Water's Edge	42.0	2.3	12	p=0.0029
				Df=17.8
Film				T=-5.62
In Water	52.3	2.9	12	p=0.0000
				Df=19.8
Water's Edge				T=2.81
In Water				p=0.011
				Df=20.7

SUBAREA B

	MEAN	S.E	n	
Film	42.6	3.9	10	T=0.41
Water's Edge	40.71	2.4	14	p=0.68
				Df=15.6
Film				T=0.22
In Water	41.58	2.4	12	p=0.83
				Df=15.3
Water's Edge				T=0.26
In Water				p=0.80
				Df=23.9

SUBAREA C

	MEAN	S.E.	n	
Film	30.30	2.2	10	T=-7.81
Water's Edge	54.15	2.1	13	p=0.0000
				Df=20.3
Film				T=-10.97
In Water	59.54	1.5	13	p=0.0000
				Df=16.6
Water's Edge				T=2.07
In Water				p=0.051
				Df=21.7

SUBAREA E

	MEAN	S.E.	n	
Film	31.2	2.3	10	T=-5.10
In Water	58.40	4.8	10	p=0.0000
				Df=12.7

No. PACES/min

SUBAREA A

	MEAN	S.E.	n	
Film	84.1	4.8	14	T=4.98
Water's Edge	58.67	1.9	12	p=0.0000
				Df=17.0
Film				T=7.01
In Water	36.0	5.0	10	p=0.0000
				Df=20.9
Water's Edge				T=-4.27
In Water				p=0.0013
				Df=11.6

SUBAREA B

	MEAN	S.E.	n	
Film	74.5	5.0	12	T=2.70
Water's Edge	58.91	3.0	11	p=0.015
				Df=17.8
Film				T=6.65
In Water	34.1	3.5	14	p=0.0000
				Df=20.4
Water's Edge				T=-5.40
In Water				p=0.0000
				Df=23.0

SUBAREA C

	MEAN	S.E.	n	
Film	119.75	1.6	12	T=9.05
Water's Edge	102.38	1.1	13	p=0.0000
				Df=19.6
Film				T=19.25
In Water	61.58	2.6	12	p=0.0000
				Df=18.4

Water's Edge				T=-14.66
In Water				p=0.0000
				Df=14.8

SUBAREA E

	MEAN	S.E.	n	
Film	45.8	4.1	10	T=-4.38
Water's Edge	76.4	5.7	10	p=0.0005
				Df=16.4
Film				T=-2.64
In Water	66.2	6.6	10	p=0.019
				df=15.1
Water's Edge				T=-1.18
In Water				p=0.26
				Df=17.6

RESULTS STUDENT-T TEST of NEIGHBOUR TO NEIGHBOUR DISTANCE

SUBAREA A

	MEAN	S.E.	n	
Film	6.6	0.88	10	T=5.35
Water's Edge	1.77	0.18	17	p=0.0000
				Df=9.8
Film				T=5.78
IN Water	1.412	0.15	17	p=0.0000
				Df=9.5
Water's Edge				T=-1.49
In Water				P=0.15
				Df=30.8

SUBAREA B

	MEAN	S.E.	n	
Film	3.88	0.43	17	T=2.57
Water's Edge	2.40	0.39	20	p=0.015
				Df=33.8
Film				T=5.37
In Water	1.48	0.13	25	p=0.0000
				Df=19.0
Water's Edge				T=-2.25
In Water				p=0.034
				Df=23.3

SUBAREA C

	MEAN	S.E.	n	
Film	4.72	0.34	25	T=5.35
Water's Edge	2.37	0.27	16	P=0.0000
				Df=39.0
Film				T=9.25
In Water	1.31	0.13	13	p=0.0000
				Df=30.4
Water's Edge				T=-3.52
In Water				p=0.002
				Df=21.5

APPENDIX II

MAY CAPTURE

RING Nº	RACE	WEIGTH	BILL LENGTH	WING LENGTH
NR 06000	ALP	69	33.3	120
NR 05999	ALP	64	36.5	118
NR 05998	ALP	60	36.9	119
NR 44503	ALP	62	37.1	122
NR 44508	ALP	53.5	34.2	117
NR 44507	ALP	58.5	35.2	116
NR 44504	ALP	62.5	35.2	117
NR 05997	ALP	57	31	117
NR 05993	ALP	61	30.6	120
NR 05990	ALP	60	30.7	115
NR 05996	ALP	56	31.5	113
NR 44506	SCH	54	26.5	115
NR 44505	SCH	60	34.7	118
NR 44509	SCH	52	34.6	116
NR 05991	SCH	47	33.2	113
NR 44501	SCH	47.5	30.9	115
NR 05994	SCH	46.5	34.9	117
NR 44502	SCH	53.5	28.1	113
NR 05992	SCH	58	33.5	119
NR 05995	SCH	56.5	27.5	114

AUGUST CAPTURE

RING Nº	RACE	WEIGHT	BILL LENGTH	WING LENGTH
NR 44533		40	26.5	118
NR 44532		46	33.1	123

TOBEC INDEX	TOTAL LEAN M	TOTAL FAT MAS	LIPID INDEX
57.2	51.7	17.3	25.1
58.6	52.5	11.5	18.0
70.9	59.0	1.0	1.7
60.2	53.3	8.7	14.1
59.7	53.0	0.5	0.9
54.3	50.2	8.3	14.3
62.6	54.6	7.9	12.7
56.2	51.2	5.8	10.2
57.6	51.9	9.1	14.9
52.6	49.3	10.7	17.8
49.3	47.5	8.5	15.2
41.4	43.4	10.6	19.7
69.1	58.0	2.0	3.3
47.3	46.5	5.5	10.6
47.7	46.7	0.3	0.6
46.3	46.0	1.5	3.2
45.3	45.4	1.1	2.3
41.9	43.6	9.9	18.5
63	54.8	3.2	5.5
50.2	48.0	8.5	15.0

TOBEC INDEX	TOTAL LEAN M	TOTAL FAT MAS	LIPID INDEX	AGE
43.3	39.1	0.92	2.3	3
33.4	44.4	1.64	3.6	3

APPENDIX III

SPRING MIGRATION

On 10 May, 27 adult Dunlins were captured, of which 17 were from the subspecies alpina (9 females, 5 males and 3 not sexed) and 10 from subspecies schinzii (5 females and 5 males).

SUBSPECIES	n	BODY WEIGHT	
		(x	S.E.)
Alpina-f	9	61.0	1.48
Alpina-m	5	58.5	1.40
Schinzii-f	5	52.7	2.76
Schinzii-m	5	53.4	1.57

Table 3: Body weight (g) of different subspecies and sexes of Dunlin (f-female, m-male).

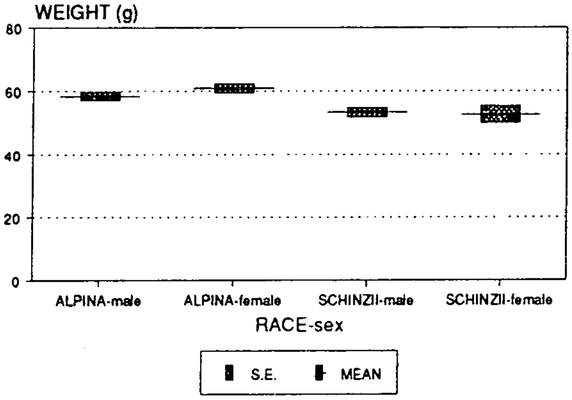

Figure 21: Weight against subspecies and sex (f-female, m-male).

Figure 21 and Table 3, show that, within each subspecies, the difference in mean body weight between the two sexes was no significant. Thus data from the two sexes of each subspecies was combined (fig. 22 and table 4) in order to permit comparisons with data obtained in Ausgust.

SUBSPECIES	n	BODY WEIGHT	
		(x	S.E.)
Alpina	17	59.4	0.98
Schinzii	10	53.1	1.50

Table 4: Body weight (g) of subspecies of Dunlin.

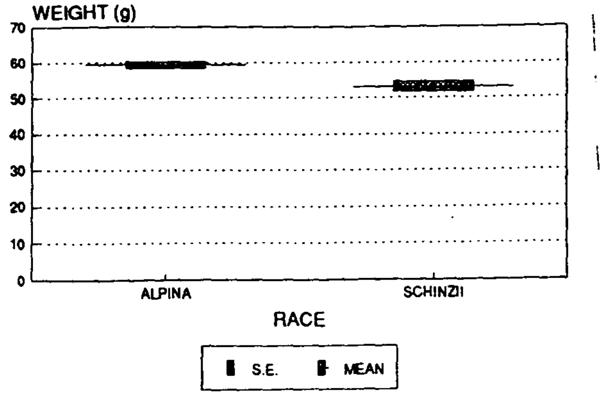

Figure 22: Weight against subspecies.

The two subspecies differed significantly in body weight, alpina (the larger race) being heavier than schinzii.

SUBSPECIES	n	T.L.M.	
		(x	S.E.)
Alpina-f	8	53.2	0.96
Alpina-m	3	49.6	1.28
Schinzii-f	5	50.3	2.56
Schinzii-m	4	45.3	1.09

Table 5: Total Lean Mass (g) of subspecies and sexes (f-female, m-male).

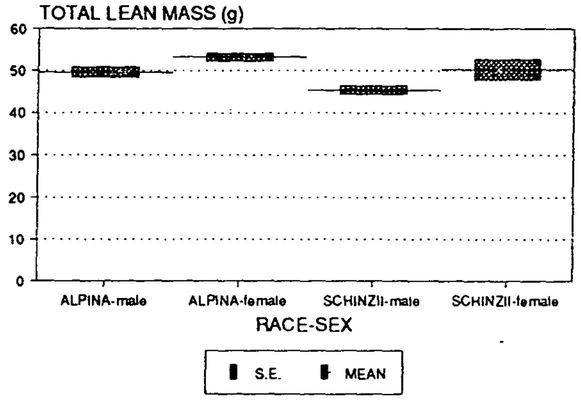

Figure 23: Total lean mass against race and sex (f-female, m-male).

Figure 23 and Table 4 indicate that for both subspecies the Total Lean Mass (calculated from the TOBEC INDEX values) of the males was significantly lower than the females.

SUBSPECIES	n	FAT (x S.E.)
Alpina-f	8	7.6 1.93
Alpina-m	3	9.4 0.66
Schinzii-f	5	2.4 0.91
Schinzii-m	4	7.6 2.09

Table 6: Fat reserves (g) of subspecies and sexes of Dunlin (f-female, m-male).

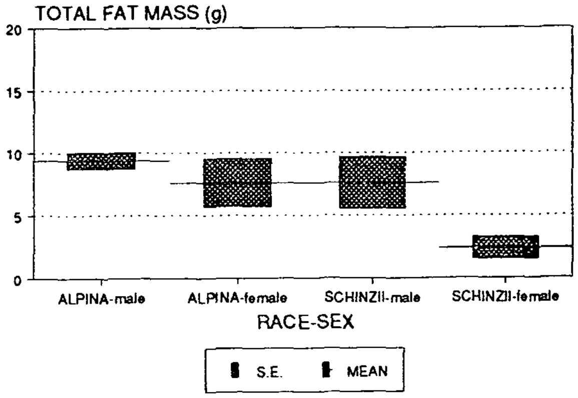

Figure 24: Fat reserves against race and sex.

Figure 24 and Table 6 show that within the subspecies alpina, the amounts of fat reserves (calculated as Body Weight minus Total Lean Mass) carried by the two sexes on the 10 May were not significantly different. In contrast, within the subspecies schinzii, males carried significantly more than females. The fat reserves of male schinzii were similar to those of male alpina, but female alpina carried significantly more than female schinzii.

ANALYSIS OF WING LENGTH

SUBSPECIES	n	WING LENGTH (x S.E.)
Alpina-f	9	118.2 0.62
Alpina-m	5	117.4 1.12
Schinzii-f	5	116.6 1.03
Schinzii-m	5	113.8 0.58

Table 7: Wing Length (mm) of subspecies and sexes (f-female, m-male).

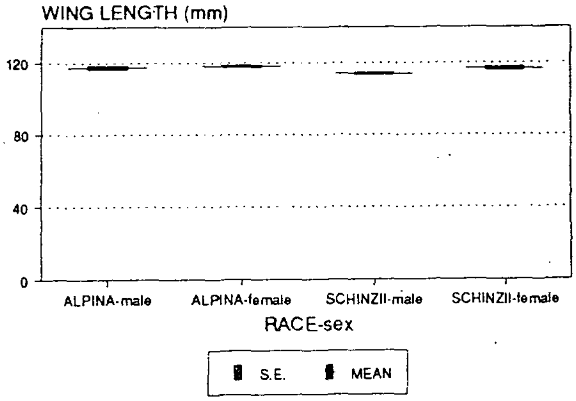

Figure 25: Wing length againts race and sex.

Figure 25 and Table 7, show that although for the subspecies alpina the females' wing length was not significantly longer than that of the males, for the subspecies schinzii a difference was found. An overall tendency, for alpina to be bigger than schinzii was confirmed, although the wing lengths of females for both subspecies was found to be not significantly different.

AUTUMN MIGRATION

On the 21 August, 33 Dunlin were captured of which 13 were adults and 20 were juveniles. The birds were not sexed and only 12 adults (11 schinzii and 1 alpina) could be assigned to subspecies.

AGE GROUP	n	BODY WEIGHT (x	 S.E.)
Adults	11	48.6	1.84
Juveniles	20	45.1	0.92

Table 8: Body Weight (g) by age category (only schinzii adults).

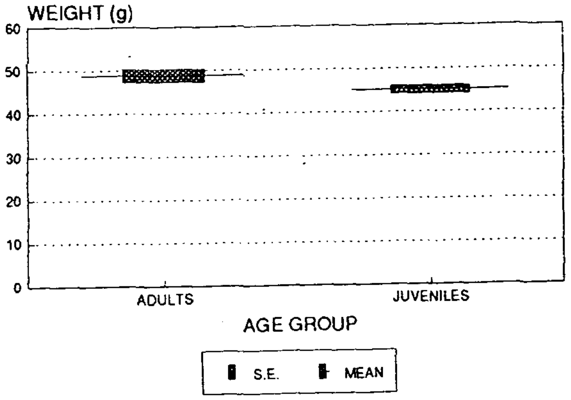

Figure 26: Weight against age group (only schinzii adults).

Figure 26 and Table 8, show the relationship between body weight and age. The adult birds were found to be significantly heavier than the juveniles, all of which were probably Icelandic schinzii.

As contamination by salt increases the Tobec Index, and only 2 of the 33 Dunlin captured were dry, it was not possible to infer useful information about Total Lean Mass and fat reserves during this period (see appendix II for results on dry birds).

SPRING AND AUTUMN MIGRATION

Female Dunlin have longer bills than the males (Snyder, 1957; Brennan *et al.*, 1984; Evans, 1986). A longer bill may allow females to feed more deeply than males and thus to obtain prey that would be unavailable to males. Furthermore, it may help avoid intersexual competion during migration, when shorebird densities on the feeding grounds can be very high.

Pienkwoski *et al.* (1979) found that, during the autumn migration, female schinzii Dunlins were on average, about 6 g heavier than males and that adults were significantly (4g) heavier than first-year birds. This was also found in this study.

It was shown by several authors (Pienkowski & Dick, 1975; Mascher & Marcstrom, 1976; Goodyer & Evans, 1979; Pienkowski *et al.*, 1979; Davidson, 1980) that Dunlins increase in weigth rapidly while pausing during their spring migration, a requirement for long flights and perhaps preparation for the breeding season. However there is no evidence that adult alpina put on large quantities of fat at any time during the early autumn, and this is consistent with the lack of a need for a single long, non-stop migration when moving southwards.

It was shown in this study that there was a difference between subspecies's weight during spring migration. However as the birds of the August capture were not sexed, comparisons cannot be made, as this would assume that during the autumn migration males and females, of the subspecies schinzii, were of similar weight and Pienkowski *et al.* (1979), although not for Seal Sands, showed that a significant difference existed. In relation to the subspecies alpina we only had data available for May, so again comparisons are not possible.

Several authors (Mascher & Marcstrom, 1976; Pienkowski *et al.*, 1979) have found correlation between the total lean mass of a bird and its wing length during the winter, in Sweden and in the Wash, respectively. However in this study, due to small data sets, in no case larger than eight, and also because the wing length was significantly different between males and females of the subspecies schinzii, and also between the two subspecies, the alpina males having longer wings than the schinzii males, no meaningful analysis could be attempted.

The equation calculated by Brennan *et al.* (1984) to predict the sex of individual birds using specific body measurements, namely bill length, wing length and body weight, was not used in this study to sex the birds of the August capture, because these authors applied it to a different subspecies (*C.a.pacifica*) in N.America. Furthermore, no significant difference was detected between immature and adult weights in the case of *C.a.pacifica*, the converse being true in this study. Moreover, Brennan *et al.* (1984) actually advise other researcher to test their predictive model with morphometric data collected from other Dunlin populations or subspecies and if necessary produce area-specific sex determination models.