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HABITAT UTILISATION BY DUNLIN ON BRITISH ESTUARIES

by

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EXECUTIVE SUMMARY

Previous barrage-related studies on the Severn have concentrated on the origins and current distributions of waders and Shelduck in relation to the proposed tidal power barrage and the ability of estuaries to absorb waders displaced by this development (Clark 1989, 1990). Arising from these studies has been a need for better understanding of determinants of bird distribution, particularly in relation to predicting the likely impacts of a barrage. In particular, anticipated changes in sedimentology post-barrage may have implications for bird distribution and a better understanding of the relationship between the two is fundamental. This study investigates this relationship for one species of wader, the Dunlin.

This project had three main objectives. First, to assess the densities of Dunlin throughout British estuaries in relation to their likelihood of being at carrying capacity. Second, to assess the main sediment types used by Dunlin and relate this to their dispersion patterns on British estuaries. Third, to predict the likely effect of changes in substrate type on the numbers of Dunlin that the Severn could accommodate post-barrage.

The study consisted of a detailed analysis of the long term Birds of Estuaries Enquiry data for Dunlin in relation to various physical and environmental characteristics of estuaries

throughout Britain and secondly collection of new data on sediment composition and the dispersion patterns of Dunlin, on a sample of estuaries with tidal ranges similar to those predicted for the post-barrage Severn.

Section 1 of this report assesses the role of physical and environmental factors influencing the likelihood of estuaries being at capacity for Dunlin. Four parameters of Dunlin populations on British estuaries were used to indicate the status of each site. These were: the rate of change in numbers over time, the ranked estimate of the likelihood of the site being at capacity, the coefficient of variation in peak counts between winters and the mean density of Dunlin on the site. Multiple regression analyses indicated that these parameters were related to a number of environmental variables. However, not all environmental variables were available for all sites. The environmental variables that were found to be significant for one or more of these parameters were: area, longitude, rainfall, windspeed, tidal range, temperature, mean concentration of orthophosphate, mean biochemical oxygen demand, maximum biochemical oxygen demand and two sediment parameters which reflect the proportion of silt and fine sand. Analysis of variance revealed that sites at capacity had, on average, larger intertidal areas, more westerly location, lower rainfall and higher biochemical oxygen demand than sites where numbers were below capacity. In order to select the suite of variables which were most likely to affect Dunlin populations, the mean value of each environmental variable for sites that were at capacity were compared with the mean values for sites not at capacity. This gave five environmental variables for which there were significant differences between the two groups. These were area, rainfall, average biochemical oxygen demand, maximum biochemical oxygen demand and longitude. Unfortunately, there were only twenty sites for which there were measures of all these five variables. However, these environmental variables accounted for some 55% of the variance in carrying capacity score and some 65% of the variance in density.

Section 2 considers the role of sediments in determining the distribution and density of Dunlin on estuaries of similar tidal range to those of the post barrage Severn. Fifteen estuaries were surveyed on five occasions through the winter at low tide and the mean number of birds on each intertidal area was calculated. One site, the Swale, had poor bird data due to bad weather conditions and so was excluded from the analysis. For the remaining fourteen sites, sediment samples were taken on representative substrates occurring throughout the estuary. The percentages of sand, silt and clay and fine clay were recorded for each area as well as the yield shear stress. On some estuaries there was insufficient variability in substrate type to obtain any relationship between Dunlin density and sediment composition. However, there was a general relationship on many sites for increasing Dunlin density on areas which had a higher percentage of silt/clay. This relationship was significant for

Leigh-Canvey, the Blackwater and the Colne and for all estuaries combined. There was also a negative relationship with yield shear stress; higher densities of Dunlin occurring on softer muds, this was most marked when data were combined for all estuaries.

It was clear that on many soft muddy sites there were very few Dunlin, although high densities of Dunlin only occurred on such sites. It was considered likely that this apparent anomaly was related mainly to low tide counts for this study inevitably providing a 'snapshot' of feeding distribution for only part of the tidal cycle. Consequently, those muddy sites with low densities of Dunlin may have been used mainly either during the rising and/or falling tide, but not at low tide, or at night rather than in the day, although this could not be proven without all-day and night time fieldwork.

There was a highly significant relationship between the mean silt and clay content within an estuary and the mean density of Dunlin on that estuary, with 75% of the variance in Dunlin density being explained by sediment type. This was a curvilinear relationship with low densities of Dunlin on estuaries which had less than 50% of silt and clay, but for sites that had over 50% of silt and clay there was an increase of approximately 2 Dunlin per hectare for every 10% increase in the proportion of silt and clay. This gives considerable scope for altering the density of Dunlin that an estuary can support if the sediment regime can be modified.

Section 3 of this report assesses the results from Sections 1 and 2 and considers the implications for predicting post-barrage densities of Dunlin. It was found that there was no significant correlation between the proportion of an estuary holding either half or 90% of the Dunlin and the density of Dunlin on that site, showing that there is no direct limit to the proportion of an estuary that can be utilised by Dunlin. It was considered that further studies should be undertaken to investigate the relationship between sediments and birds to assess the general applicability of the relationships found in this sample of 15 estuaries. It was also considered that there should be further sediment studies which should concentrate on predicting the proportion of areas of high silt and clay content within the post-barrage Severn, since Dunlin is the most important species likely to be affected by changes in the post-barrage sediment regime. It is also suggested that studies should be undertaken to assess whether additional engineering measures could be undertaken in order to increase the proportion of silt and clay and so maintain the existing Dunlin population of the Severn post-barrage.

GENERAL INTRODUCTION

The populations of waterfowl which winter on the Severn are of considerable international importance and originate from breeding areas as far apart as northern Canada and the Taimyr peninsula of the Soviet Union. Dunlin are numerically the most important species on the Severn, comprising over three quarters of the fifty thousand-plus birds wintering there (Kirby et al. 1990). Consequently, it is critically important to understand the effects that construction of a tidal barrage across the Severn might have on this species. A barrage would modify the estuarine environment in a number of ways. Perhaps the most obvious of these would be a reduction in intertidal area to approximately half of its present 20,000 hectares. There would, however, be a number of other changes to water quality and the characteristics of the intertidal sediments which could have substantial effects in changing the attractiveness of the Severn to wintering waterfowl.

It is not possible at present to predict with any accuracy the numbers of waterfowl that may be accommodated on the Severn post-barrage. Neither is it possible to predict the number of waders which a given habitat type can support. This study aims to address this problem of prediction for one species, Dunlin, by studying it on several sites which have tidal ranges akin to that predicted for the post-barrage Severn. Once the predictions for sediment types in this changed environment are available, it will be possible to determine the likely effects on Dunlin from comparison with the results of this study.

In order to predict the density of Dunlin which a given environment will be able to accommodate, it is likely that there will be two main types of factors of importance. The first is overall environmental variables, e.g. geographical location, winter temperatures and the nutrient status of the estuary. The second is the sediment characteristics of the estuary; for instance, Dunlin are known to prefer muddier areas on the Severn (Clark 1989).

Section 1 of this report assesses the role of environmental variables in determining the carrying capacity status of British estuaries for Dunlin (after Clark 1989), with the aim of ascertaining whether estuaries which are at capacity can be defined by any particular set of environmental variables. Further, it assesses whether these environmental variables can be used to predict the density of Dunlin on British estuaries. Environmental data were assembled from several sources and were not collected specifically for this study. Consequently, not all variables were available for all sites, leading to a relatively poor dataset. Section 2 reports on the role of sediment characteristics in determining the density of Dunlin both within and between estuaries. Section 3 then considers the relevance of these two analyses to the problem of predicting post-barrage densities of Dunlin and considers the scope for further work on this subject.

Here, carrying capacity is defined as the population level at which for every additional bird that arrives on a site, on average one bird either dies or emigrates (Goss-Custard 1985). This could be due either to feeding interference as a result of high bird density or, because of poor competitive ability over limited food resources.

SECTION 1:SITE PREFERENCE BY DUNLIN

1.1INTRODUCTION

The overwinter survival of Dunlin depends on their being able to minimise metabolic stress. This depends largely on the quality of their winter environment in terms of food availability and climatic conditions. However, environmental quality varies between estuaries, so not all estuaries will be equally attractive to Dunlin.

Fretwell and Lucas (1970) have proposed that, in times of population increase, the occupancy of habitat available to a species should occur in a hierarchical fashion. At low population levels, all birds should be concentrated on the highest quality (preferred) sites. As the population increases, the number of individuals able to use the preferred areas and obtain adequate resources for survival will be limited by density-dependent processes such as intra-specific aggression and territoriality, depletion of food supply and reduction of food intake due to interference between individuals. Eventually, an upper limit will be reached whereby additional individuals can only utilise the habitat profitably if there is a compensatory loss of residents through death or emigration. This upper limit is referred to as the "carrying capacity" of the area (Goss-Custard 1985). When the carrying capacity of an areas is reached, the numbers of birds on that area will remain stable despite any further increase in the population as a whole. As a result, birds excluded from areas at carrying capacity will sequentially occupy areas of progressively lower environmental quality. The bird density at which carrying capacity is reached on these areas will decline with quality. There is now a substantial body of field evidence for such sequential site occupancy in birds (O'Connor 1980, 1982, 1985, Moser 1988, Clark 1989).

Several studies of wintering waders and wildfowl have shown a similar pattern of distribution within individual estuaries. As increasing numbers of birds arrive in autumn, those parts of the estuary providing the best feeding conditions are filled first while later arriving and subordinate birds (often juveniles) occupy poorer quality areas at reduced density (Goss-Custard et al. 1982, van der Have et al. 1984, Goss-Custard and Durell 1990). In single-site studies, however, it is difficult to ascertain whether the maximum observed overall density on a particular estuary is a ceiling density, resulting from limitation by density-dependent processes or because all potential occupants have been accommodated on a suite of estuaries (Moser 1988).

In this study, an attempt has been made to identify British estuaries and other coastal sites at which Dunlin numbers are currently at carrying capacity and to examine relationships between site preference by Dunlin and a range of geographical, physical, climatic and chemical variables with a view to characterising preferred sites in terms of these variables. This would allow predictions to be made of the effect on Dunlin of major environmental changes, such as those brought about by the construction of tidal barrages.

1.2METHODS

The Birds of Estuaries Enquiry (BoEE), organised by the British Trust for Ornithology, has collected monthly counts of waders throughout the year on most British estuaries since 1969. Counts are synchronised nationally and within each estuary, being made around high tide on a specified weekend in the middle of each month. The counts are computerised each year on a site basis. Most estuaries are considered as single sites. However some, mainly large estuaries, are split into a number of sub-sites. Many non-estuarine coastal areas are also covered by the Enquiry. Not all sites are counted in every month or every year.

In this study, the peak winter BoEE count was used as the measure of annual Dunlin abundance at each site. For each site, a winter was only included if there had been at least three complete counts between November and March. Only sites which had data for at least 10 winters were used in the analysis.

Because some sites are not counted in all months or in all years, it is not possible to compare the size of the British Dunlin population in different years simply by considering the sums of counts for each estuary. This problem has been circumvented by the calculation of an index of national population size that is independent of coverage. Indices are based on the sums of the peak winter counts for consecutive years and are calculated from the formula:

New Index = Old Index x (2nd Winter Total/1st Winter Total)

A total of 115 estuarine and non-estuarine sites were used in the analysis (Appendix 1). Where sub-sites of an estuary had sufficient data, these were used in preference to summed data for the whole estuary.

The model of Fretwell and Lucas (1970) makes it possible to predict how numbers of birds wintering on an estuary should increase as the national population increases. The increase should follow a sigmoid curve in all but the most preferred sites (Figure 1.1). When the national population is low all birds will be on the highest quality estuaries and most estuaries will be unoccupied (ie at position 1 in

Figure 1.1). As the national population rises, birds will begin to use less preferred sites at which, this time, initial increase will describe a concave curve (2). With further increase nationally, numbers of birds using these estuaries will show near linear increase (3) until they reach levels at which density-dependent processes induce negative feedback. This stage will first result in a regression line with a slope at less than 1 (4) and then a convex curvature of the line (5). When carrying capacity is reached the numbers of birds using the estuary will remain stable, irrespective of any further increase in the national population (6).

For each of the 115 sites, the log-transformed annual peak count was regressed on the log-transformed national index. Log-transformation of data is a standard manipulation which allows investigations of the rate of change in numbers in a population. Both linear and curvilinear regressions, with the addition of a quadratic term, were carried out as per Clark 1989 which expands on the methodology given here. The resultant regression slopes provided a measure of the rate of population change and allowed sites to be categorised according to their position on the site occupancy curve (Figure 1.1).

If it is assumed that bird numbers on estuaries are not limited, then the numbers of Dunlin at individual sites should vary proportionately with the national index and the slope should be equal to 1. If numbers have reached carrying capacity on an estuary then numbers should be unrelated to the index (slope = 0). All slopes were tested for significant deviation from these hypotheses.

For sites that showed no significant relationship between Dunlin numbers and the national index, it was possible that either the sites were at capacity or, alternatively, the variation in counts may have been so high that a large number of years of data will be necessary to reveal a relationship. It may be possible to distinguish between these two possibilities: if a site is at carrying capacity, it should have a relatively low coefficient of variation between the counts; on the other hand, if counts are highly variable, the site is less likely to be at capacity. Coefficient of variation was therefore used as a means of distinguishing sites that were at capacity from those which were highly variable.

Sites were allocated a carrying capacity score as follows (after Clark 1989):

1. No relationship to national index. Maximum peak count less than 50.
2. Significant concave curvilinear relationship with index or no significant relationship and high coefficient of variation (>1.0).
3. Significant positive linear relationship with index, slope >1.

4. Significant positive linear relationship with index, slope between 0 and 1.
5. Significant convex curvilinear relationship with index.
6. No relationship to national index, coefficient of variation between 0.5 and 1.
7. No relationship to national index, coefficient of variation <0.5.

Sites with scores of 5 and 7 were taken to be at carrying capacity.

To identify environmental factors influencing site preference by Dunlin, four measures of preference were used in separate stepwise regressions on a range of 36 geographical, physical, climatic, chemical and sedimentological variables (see Appendix 2). The four preference indicators were:

a) the slope of regression of peak count on national index (= rate of change);
b) carrying capacity score;
c) coefficient of variation of peak counts;
d) mean Dunlin density.

Mean density was calculated for each estuary by first calculating the number of Dunlin coinciding with the mean index value, for each site, for the period 1970-1990 from the regression of the peak counts on the index. This figure was then divided by the total intertidal area in hectares (measurement of area follows the estuary limits used by the former Nature Conservancy Council in their Sites Review). This is, however, a relatively poor measure of site preference, particularly for large estuaries, as the environment is likely to show considerable heterogeneity and consequently birds will not be evenly distributed throughout.

Data on water chemistry and sediments were obtained principally from River Purification Boards and the National Rivers Authority. Additional material was provided by universities, polytechnics and publications commissioned by the Nature Conservancy Council (Green et al. 1991). The data on water quality used here are the best available at the present time but, in interpreting the results, it should be borne in mind that these were not systematically collected for this purpose. They were also available for only relatively few sites.

No single site had data for all 36 variables listed in Appendix 2, therefore two separate stepwise regressions were initially carried out. The first of these used only the five variables for which data were available for all 115 sites (AREA, TIDR, JTMP, LAT, LNG). The second regression maximised the number of both sites (89) and variables (12) that could be included. The variables used were: AREA, TIDR, JTMP, LAT, LNG, ELNG, WENTR, WMAX, RFL, TAV, TMIN, WS. This was repeated after excluding sites with highly variable counts (carrying capacity scores 2 and 6). The four measures of site-preference were individually regressed on each of the remaining variables, none of which was available for more than 50 sites.

In an alternative approach to identifying key environmental factors, the mean values of each variable were compared for sites at carrying capacity with those below carrying capacity by single classification analysis of variance. The analysis of variance was repeated after allocating sites to four geographical groups in order to investigate whether factors affecting site-preference differed regionally. The four regions were:

1. Nyfer - Rye Bay
2. Pegwell Bay - Humber
3. Tees - Moray Firth
4. Clyde - Dyfi

The large geographical spread represented by each region was necessary to provide large enough sample sizes for comparison of regional effects.

A similar comparison was also made between west (Regions 1 and 4) and east (Regions 2 and 3).

Those factors which showed significant differences in mean values between sites at carrying capacity and less preferred sites were used as independent variables in multiple regressions with each of the four preference indicators.

1.3 RESULTS

The number of sites in each carrying capacity category is presented in Table 1.1.

Initial stepwise regression of the four preference indicators on the five variables with complete data sets revealed significant relationships with only two factors: area and longitude, with larger estuaries and more westerly estuaries being more likely to be at carrying capacity. They are however more likely to hold lower densities of Dunlin. None of the environmental variables or combinations of variables explained more than 10% of the variance in the preference indicators (Table 1.2).

Repetition of the regression utilising the maximum number of sites and variables indicated further influences of tidal range, rainfall and minimum temperature, but in all cases less than 20% of the variance was explained (Table 1.3a). Exclusion of variable sites (carrying capacity score 2 and 6) produced only a modest improvement in the proportion of variance explained by the regression, but rainfall was a correlate of all four preference indicators (Table 1.3b). Rainfall is a potentially important variable in terms of its potential impact on birds. It may interfere with feeding behaviour by disturbing visual cues or it may enhance food availability for other birds by flooding the burrows of some intertidal invertebrates which, having a low freshwater tolerance, are forced to the surface.

Individual regression of preference indicators on variables with small sample sizes revealed only six significant relationships: mean phosphate concentration with rate of change (negative); mean percentage of dissolved oxygen with carrying capacity score; mean biochemical oxygen demand with carrying capacity score; mean ammonia concentration with mean Dunlin density and two measures of how muddy the estuary is (PMDS and PSTF) with mean Dunlin density, (Table 1.4).

Analysis of variance revealed that sites at carrying capacity had, on average, larger intertidal areas, more westerly location, lower rainfall and higher biochemical oxygen demand than sites where Dunlin numbers are below carrying capacity (Table 1.5).

When sites were grouped regionally, no differences in mean values were found between carrying capacity categories for any variable in regions 1 and 3. In region 2, mean biochemical oxygen demand was significantly higher in sites at carrying capacity indicating that these sites were more likely to have high organic inputs. In region 4, there were significant differences in area, minimum temperature (January-March) and minimum concentration of dissolved oxygen (Table 1.6). When sites were divided between east and west no significant differences were found between categories in the eastern group. In the western group, the only variables to differ between categories were mean percentage dissolved oxygen and mean biochemical oxygen demand (Table 1.6).

There were five variables which had mean values which were significantly different between sites considered to be at capacity and those not at capacity. One last analysis was undertaken on the 20 sites for which all five of these variables were recorded. A step-wise multiple regression was undertaken for each of the preference indicators. These multiple regressions were found to be significant for carrying capacity and density (Table 1.7). Thus estuaries were more likely to be at carrying capacity if they were larger but had lower rainfall, higher biochemical oxygen demand and were in the west. The mean density of Dunlin was high on small estuaries in the east with lower rainfall and a low average biochemical oxygen demand, but with a high maximum biochemical oxygen demand. This analysis explained 69% of the variance in density. However, it must be stressed that only 20 sites were included, and it would be advantageous if data for these variables could be obtained for a number of other estuaries.

1.4DISCUSSION

The results of this analysis indicate that environmental factors are likely to have considerable influence in determining site preference by Dunlin. Many of these variables are highly inter-correlated so the relative importance of one may be partly masked by another. As a result, all the variables which were found to have a significant effect on Dunlin populations are discussed in turn.

1.4.1. Winter Temperature

Dunlin occur throughout the range of winter temperatures in Britain. However, in this study Dunlin were found to be at higher densities on sites with higher average minimum winter temperatures (TMIN). There is considerable evidence that lower temperatures within a site increase the environmental stress on waders. Low winter temperatures result in an increasing energy demand in birds simply to maintain body heat. Additional energy requirements include those for flight between roost sites and feeding areas and for feeding activity. The costs of maintaining body temperature and of feeding are also most likely to be subject to short-term variations during winter (Evans 1976, Evans and Dugan 1984, Pienkowski et al. 1984). Loss of body heat will tend to be most acute when low temperatures are accompanied by high windspeeds. Hart and Berger (1972) have shown in wind-tunnel experiments that heat loss through skin and feathers is approximately doubled at windspeeds similar to those encountered in normal flight. Most waders are able to survive all but the most severe weather because of their ability to store fat, but extended periods of low temperatures and high winds are likely to result in a general loss of body condition (Goss-Custard *et al*. 1977b, Davidson 1981, Clark 1982).

Low temperatures can also affect the availability to Dunlin of prey organisms. During such conditions, many invertebrate species such as *Corophium*, *Arenicola*, *Nereis* and *Macoma* burrow deeper into the sediments and become less active, thus reducing the probability of their being detected by waders (Goss-Custard 1970, Evans 1976, Reading and McGrorty 1978). In extreme conditions, sediments may freeze, limiting the area available and limiting the time available for foraging to the falling tide. Prey intake by Redshank and Grey Plover has been shown to decline as temperature decreases (Goss-Custard 1970, Pienkowski 1980). Worrall (1981) found that the probe rate of Dunlin on the Severn increased at low temperatures but Clark (1983) has suggested that, as the diet of the population studied by Worrall contained a high proportion of Nereis, the reduced activity near the sediment surface by this species would result in a lower capture rate per unit effort than in warmer conditions. Clark's (1983) observations on Dunlin feeding on Corophium at another Severn site indicated a change from visual to tactile feeding methods as temperature and prey activity decreased.

1.4.2 Wind Speed

At times of increasing national population of Dunlin, their numbers were likely to increase more rapidly on sites with higher wind speeds than when the national population was stable or decreasing. This result indicates that sites with higher wind speed were less likely to be at capacity. However, densities were on average found to be higher on windier sites. High winds have been shown to reduce the detectability of buried prey by suppressing indicators of their presence at the surface (Dugan et al. 1981). Winds also dry out the upper layers of sediments, causing deeper burrowing by invertebrates. As a result, prey availability in windy conditions will tend to be greatest in moist sediments near the tideline and birds might be expected to congregate in this zone (Evans 1976) with consequent higher densities. This has been observed in Bar-tailed Godwits Limosa *lapponica* feeding on *Arenicola* (Smith 1975). Increased density of birds at the tideline in such circumstances may, however, result in reduced feeding efficiency because of increased competition, in the form of a higher rate of prey depletion and interference and aggressive interactions between birds resulting in a loss of feeding time. It is thus surprising that wind was positively correlated with Dunlin density and it may be that is the effect of a covariate or that wind may have an effect on the productivity of the site rather than a direct effect. However, exposure to prevailing winds has been shown to affect the productivity of intertidal areas (Emerson 1989). The direction of prevailing winds and the orientation of each estuary were not considered in detail for this study.

1.4.3 Rainfall

Rainfall was found to be a significant factor, with sites with lower rainfall tending to higher densities and being more likely to be at capacity. Rainfall is unlikely to have a major effect on the energy balance of Dunlin. There is, however, some evidence of the behaviour of prey organisms being influenced by rain. Experiments carried out by Goss-Custard (1970) showed that the activity of *Corophium* was reduced while water was falling on the surface of the substrate. Clark (1983) found that the feeding rate of Dunlin on the Severn was negatively correlated with rainfall. However, Metcalfe (quoted by Clark 1983) observed that the success rate of Lapwing Vanellus vanellus feeding on Corophium increased during heavy rain. This has been attributed to the burrows of the crustaceans becoming flooded with fresh water, resulting in increased activity at the surface as the Corophium seek more saline conditions.

1.4.4 Tidal range

Coefficients of Variation for peak counts of Dunlin at sites with a high tidal range tended to be less variable than those for sites with a low tidal range. Tidal range may be a significant factor in determining the suitability of an estuary as a wintering site for Dunlin because of its interaction with windspeed. Where tidal amplitude is small, high winds may hold back the falling tide thus restricting the feeding area available to birds. Under the most severe conditions of this kind, the feeding grounds of short-legged species, such as Dunlin, may be totally inaccessible (Evans and Dugan 1984).

The combination of wind and tide may also make feeding conditions at the tideline difficult because of wave action. Regular, severe wave action results in shorelines with coarse-grained sediments in which the resident invertebrates are predominantly very mobile and exhibit morphology or behaviour that make them unsuitable prey for Dunlin. On otherwise suitable shores, avoidance of breaking waves is likely to reduce the energetic efficiency of birds feeding at the water's edge (Evans 1976).

Many invertebrates are distributed according to the length of time for which the sediments they inhabit are exposed at low tide. As a result of this, the number of prey species, prey density and biomass available to birds foraging on neap tides may be restricted (Evans 1976). This effect will be most marked at sites with a large tidal range but is probably of relatively minor importance unless compounded by other factors such as severe weather. A large tidal range may, however, have a greater effect on birds through disturbance of the sediments by the tidal flow, thus creating an unstable environment for prey organisms which would, as a result, tend to be less abundant than on estuaries with a smaller tidal range.

1.4.5 Geographic factors

Longitude emerged as a significant factor in a number of analyses. However, the results were contradictory. This is almost certainly due to auto-correlation between factors. It has been suggested that the west coast of Britain should be relatively less attractive to Dunlin than the east (Furness et al. 1986) although west coast temperatures are, on average, higher. Thus it might be expected that the majority of sites at which Dunlin numbers have reached carrying capacity would be in the south and east. Eastern sites are also the first to be encountered by the majority of alpina Dunlin migrating into Britain in autumn from Fenno Scandinavia and the Soviet Union, which may be of importance in the selection of wintering areas (Hardy and Minton 1980).

An analysis by logistic regression of the relationship between Dunlin abundance and similar physical and water chemistry variables to those used here also found that high Dunlin numbers were associated with high temperatures and low rainfall (Hill et al., in prep.). However, windspeed and tidal range were also found to be positively associated with Dunlin numbers. Intertidal area appears as a significant variable in some of the analyses carried out in this study. Area is negatively correlated with rate of change, coefficient of variation and mean density but positively correlated with carrying capacity score. Thus increasing estuary size is associated with more stable Dunlin populations, at carrying capacity, but with a lower density of Dunlin overall. This might be because substantial parts of large estuaries may be unsuitable for Dunlin (Clark 1989).

1.4.6 Water chemistry

Several components of water chemistry also play an important role in determining the quality of estuarine environments for birds through their effects on the distribution and abundance of prey species. Salinity, organic input and oxygen content are particularly important in this respect (Anderson 1972, Goss-Custard et al. 1988, review by Green et al. 1991). In this analysis, site preference by Dunlin showed little relationship to concentrations of chloride ions, although rate of change decreased with increasing phosphate concentration and density increased with ammonia concentration. The oxygen regime of estuaries does, however, appear to be of importance to Dunlin. The limited data available indicate that sites where Dunlin numbers are at carrying capacity tend to have relatively high concentrations of dissolved oxygen (Table 1.6). The strongest correlate of carrying capacity score amongst water chemistry variables was, however, mean biochemical oxygen demand.

Large biochemical oxygen demands are commonly associated with high levels of microbial decomposition of organic detritus and nocturnal respiration by phytoplankton (Maskell 1985, Griffiths 1987). Thus they may be taken as being indicative of areas of high natural productivity and areas subject to anthropogenic organic input (Wharfe et al. 1986). The former would obviously be attractive to waders as feeding areas, but there is also some evidence to suggest that moderate levels of organic pollution may benefit birds by supporting increased invertebrate biomass (eg Mudge 1972, Van Impe 1985, Meire and Dereu 1990). Mean biochemical oxygen demand was found to be the most important factor when all variables showing significant differences in mean values between carrying capacity categories were used in a multiple regression. This suggests that it may have considerable capacity to predict the attractiveness of particular sites to Dunlin.

1.4.7 Sediment factors

Data on the sediment variables used in this analysis were available only for a few sites and little evidence of relationship with site preference by Dunlin was found, although it was found to have an effect on mean density. The nature of sediments in terms of structure, grain size, organic content and oxygen regime is of considerable importance to waders as this will determine the composition of the intertidal invertebrate community and its productivity (Anderson et al. 1970, Anderson 1972, Goss-Custard et al. 1977a, 1988). The significance of sediment character in determining Dunlin distribution will be discussed in detail in the following chapter.

It is clear from this discussion that a wide range of environmental variables act together to influence the density and site preference of Dunlin wintering on British estuaries. These variables could be used to predict both the likelihood of a site being at capacity and the density of Dunlin wintering on the site with an encouraging degree of precision (R^2 of 55% and 69% respectively). However, the sample size for the number of sites with the relevant data was only small. For this reason it is necessary to be cautious about predicting Dunlin density from the five variables that were found to be important (intertidal area, annual rainfall average, mean and maximum biochemical oxygen demand and longitude). This does, however, show that there is considerable value in pursuing this type of approach to predict the populations of Dunlin that will occur on a site after it has been modified in a particular way. One area where there was very poor information available was on sediment type. It was found to be significant for Dunlin density but the values that were available were only very crude assessments of sediment type within estuaries. This factor will be considered in detail in Section 2 of this report.

SECTION 2:THE EFFECT OF SEDIMENT TYPE ON DUNLIN DENSITY

2.1INTRODUCTION

A number of studies have shown that the feeding distribution of wading birds can be influenced by variation in the characteristics of sediments within estuaries (Prater 1972, Tjallingii 1972, Clark 1983, Rands and Barkham 1981, Goss-Custard et al. 1988, Kelsey and Hassall 1989). This is primarily a response to variation in the feeding conditions prevailing in sediments of differing composition. The physical structure of sediments can determine their suitability as habitats for prey organisms, and it is the abundance of these and the efficiency with which they can be harvested that determines the value of particular sediments as environments for birds (Wolff 1969, Goss-Custard 1970, 1977, Evans 1976, Goss-Custard et al. 1988).

The main characteristics of sediments that determine their suitability as feeding environments are grain size, cohesion and organic content. Sediments with small mean grain-size generally support the greatest abundance of invertebrates (Anderson 1972, Prater 1972, Goss-Custard et al. 1988). Such sediments are often called "muds" and consist of silts and clays. Silts are classified as being composed of particles of less than 63µm, and clays less than 2µm (Leeder 1982). These fine-grained sediments support high densities of many species of intertidal invertebrates, in part as a result of their generally high organic content. The organic content of sediments in several British estuaries has been found to show a strong inverse relationship with grain-size (Goss-Custard et al. 1988, Ravensrodd 1989, Warwick et al. 1991). The cohesiveness of sediments generally decreases with grain-size and provides better burrowing conditions for invertebrates (Ravensrodd 1989). In certain circumstances very fine-grained sediments may become highly cohesive (overconsolidated) and these tend to have a relatively low organic content. Such sediments occur in areas of the Severn estuary (Ravensrodd 1989).

The physical composition of sediments may affect the feeding efficiency of wading birds both through the productivity of particular sediment types, as determined by their organic content, and through the cost incurred by birds in extracting prey organisms. The degree of consolidation of sediments may determine the feeding method employed. Rands and Barkham (1981) found that Dunlin feeding in mud on the Wash took over 80% of prey by pecks at the surface, while on sand 70% of feeding actions were deep probes. Similar but less pronounced differences were found by Clark (1983) on the Severn. Probing is likely to become more costly in energetic terms as sediments become more consolidated (Myers et al. 1980, Kelsey and Hassall 1989).

Although Dunlin are the most numerous of the species of waders wintering on the Severn, they only occur on part of the intertidal area which is available to them (Clark 1989). Similarly, patchy distributions have been recorded from other British estuaries, and these indicate that Dunlin tend to concentrate on muddier substrates (Prater 1972, Goss-Custard et al. 1988). It has also been shown in experiments with captive Dunlin that increasing the sand content of substrates caused a reduction in time spent by the birds on manipulated areas (Quammen 1982).

This study attempts to assess the importance of sediment composition and physical properties in determining the distribution and density of feeding Dunlin in a number of British estuaries which have tidal regimes broadly similar to those predicted for the Severn post-barrage. A better understanding of Dunlins' requirements in terms of feeding substrates may allow some manipulation of environmental conditions within the area affected by any barrage to offset the reduction in intertidal area. The maintenance of high quality feeding areas for Dunlin within the Severn is likely to be of particular importance in view of the fact that birds displaced by the barrage would be unlikely to be absorbed by other estuaries in southwest Britain as Dunlin numbers at many of these appear to be at carrying capacity (Clark 1989).

2.2 METHODS

2.2.1 Site Selection

Sites for sediment studies were selected on the basis of their having a tidal range similar to that predicted for the Severn post-barrage (3.5m - 5.5m) and an average peak winter count of at least 1000 Dunlin. Examination of Birds of Estuaries Enquiry data identified 20 estuaries as potentially suitable. All of these sites were visited during October and early November 1990. As a result of those visits, five sites were rejected because numbers of Dunlin were below the threshold 1000, or there were problems of access to the main feeding areas. The sites included in the study were: Tamar, Plym, Exe, Chichester Harbour, Pagham Harbour, Adur, Pegwell Bay, Swale, Leigh-Canvey, Blackwater (Essex), Colne, Lindisfarne, Tyninghame, Eden (Fife) and Montrose Basin (see Figure 2.1).

2.2.2 Counts

It was hoped to carry out five low-tide counts of Dunlin at each of the above sites between November 1990 and March 1991, before the onset of the main period of northward passage for Dunlin populations that winter to the south of Britain. This was achieved at all but one site, the Swale, where only four counts were possible. In addition, sediment data were considered to be suspect from the Swale and so it was excluded from the analyses. Coverage was incomplete on two counts at Chichester Harbour because of military restrictions on access to Thorney Island during the Gulf crisis.

Counts were made for each section using 10 x 40 binoculars or 20-60 x 60 telescope. The numbers of feeding and roosting Dunlin were recorded, but only numbers feeding were used in the analysis. Sites were sub-divided on the basis of clearly visible transitions between sediment types or, where large areas of similar sediments occurred, by topographical features.

At the largest estuaries (Chichester Harbour, Blackwater, Colne, Lindisfarne) only a representative sample area could be covered during a single visit. Estuary configuration required visits to be divided between north and south shores at Leigh-Canvey and Blackwater. At each of these sites, three visits were made to the north shore and two to the south shore.

Dunlin feeding at low density could be counted individually, but it was often necessary to estimate the size of large flocks. The accuracy of estimation attempted was determined by the behaviour of the flock, climatic conditions and topography, but in no case was it less precise than to the nearest 100 birds.

2.2.3 Sediment Sampling

Two 7.5cm diameter core samples of 5cm depth were taken at 15 points within each estuary except Chichester Harbour, where only 9 samples were collected because of the restrictions on access mentioned above. The sampling points were equally divided among: a) sections on which Dunlin consistently fed at high density b) sections where feeding occurred consistently at relatively low density, c) areas used for feeding only occasionally, or not at all. Where there were more than five sections in any of the above categories, selection of those to be sampled was randomised. If there were insufficient sections in any category, more than one sample was taken from some sections. Whenever possible, the position of the sampling point(s) within a section was randomised. From an approximately central point in the section, the direction and distance moved to the sampling point were determined by reference to a table of random numbers. A number from 1-12 was obtained corresponding to direction in terms of a horizontal clock-face. A limit was set to the number of paces moved in the selected direction; this varied according to the dimensions of the section. Samples were placed in polythene bags and were frozen within 24 hours of collection to kill any invertebrates present.

The cohesion of sediments was investigated by measurement of yield stress using a shear vane (Pilcon DRI-240). This has the capacity to measure yield stresses in the range 0-120 kPa. A vane of 5cm depth was used, fully inserted into the sediment. Three stress readings were obtained within a 1m radius of each core sampling point. Algal mats on the sediment surface were avoided, as were buried shell and gravel that would distort the measurement.

2.2.4 Sediment Composition

Frozen sediment samples were allowed to defrost at room temperature prior to preparation for analysis. Each sample was then mixed thoroughly to ensure that sub-samples were fully representative of all layers within the sediment. Approximately 50g of each sample was passed through a 1mm mesh sieve after addition of a deflocculant ("Calgon", Benckiser Ltd, Swindon). This was made up to 1 litre with water and mixed thoroughly by magnetic stirrer for 10 minutes. The percentage total volume comprising particles too large to pass through the sieve was estimated. The suspension of fine particles was then decanted into a 1 litre capacity perspex cylinder and left for three weeks to settle. Particles of various sizes segregated during settlement to form, in most cases, well defined bands. These allowed the proportions of the total volume, comprising sand, total silt and clay, and fine clay to be visually identified and measured directly. In some samples, it was possible to distinguish fine clay and silt and clay bands while in others this proved impossible. For this reason, all analyses of silt and clay also included the fine clay band if it was present. Where possible, fine clays were also analysed separately. However, these should be considered as minimum estimates.

2.2.5 Data Analysis

The area of each estuary section, together with shore width, was measured from 1:50000 Ordnance Survey maps and the mean Dunlin density for each section was calculated by dividing the mean count within the section by the section area in hectares. The sections within each estuary holding 50% and 90% of feeding Dunlin were mapped and the proportions of the intertidal areas in which this occurred were calculated.

Mean Dunlin density was regressed on percentage silt/clay content of sediments (arcsine transformed Sokal & Rohlf 1969), within individual estuaries. Similar regressions were also carried out in which percentage clay and mean yield stress were the independent variables. Sediments with a high sand content tend to produce unreliable yield stress measurements because of variability in interstitial water content, therefore data from all sections where sediments had a sand content greater than 50% were excluded from all analyses of yield stress. It is important to predict the total Dunlin population which can winter on an estuary so the overall Dunlin density was regressed on the overall percentage of silt/clay within each estuary.

A series of multiple regressions of mean density on all possible combinations of the above variables and shore width were undertaken to investigate whether interactions between these factors contributed significantly to variation in Dunlin density.

The strength of the overall relationship between Dunlin density and sediment composition, based on differences between sections, may be affected by small-scale spatial variation in sediment characteristics within sections because of the small number of samples taken at each estuary. The mean percentage of silt and clay across all sampled sections within an estuary may, therefore, be a better indicator of the general sedimentological character of the site. Overall mean Dunlin density was calculated for the area of each estuary covered by the counts, and this was regressed on the mean percentage of silt and clay to determine whether average sediment character could be used to predict the attractiveness of estuaries to Dunlin. In calculating the mean percentage of silt and clay for each estuary, the percentage for each sampled section was weighted by the section area.

2.3RESULTS

Patterns of Dunlin feeding distribution were found to be generally consistent within individual estuaries throughout the winter. Areas of each estuary holding 50% and 90% of feeding Dunlin are shown in Figures 2.2 - 2.15. Figures 2.16 and 2.17 present these areas as proportions of each estuary. Information from all species on the Severn is also given for comparison. It was thought possible that Dunlin may tend to favour either the upper or the lower reaches of estuaries. However, it is clear that there is no simple means of predicting the distribution of Dunlin from maps, and that a combination of variables may need to be considered.

The proportion of each estuary holding 50% of the Dunlin feeding at low tide varies between about 12% on the Severn and Colne and 35% on Pegwell Bay (Figure 2.16). On all estuaries over 35% of the area is utilised by 90% of the Dunlin population Figure 2.17. Two sites, The Plym and Pegwell Bay, had 75% and over 90%, respectively, of the area being utilised by Dunlin. From these two figures it is clear that the dispersion patterns of Dunlin vary markedly between estuaries, a feature which is investigated in Section 3.

Figures 2.18 - 2.31 show variations between sections in mean feeding density of Dunlin for each estuary and Figures 2.32 - 2.45 show spatial variation in percentage silt and clay content of sediments. In general terms it can be seen that areas of high Dunlin density occur where there is a high proportion of silt and clay. However, not all areas with high silt and clay content contain large numbers of Dunlin, often for no immediately obvious reason.

The relationships between mean Dunlin density and the percentage of silt/clay are given for each estuary in Figures 2.46 to 2.59. Significant correlations between mean density and percentage silt/clay were only found for three sites: Leigh-Canvey, Blackwater and Colne (Figures 2.53, 2.54 and 2.55 respectively). Density was correlated with percentage fine clay for Blackwater and Colne. It was not expected that there would be a significant relationship within some estuaries as there was not sufficient variation in the amount of silt and clay between different sampling sites.

When the data for all sites are combined (Table 2.1, Figure 2.60), it is clear that sites with a high percentage of silt and clay tend to have high densities of Dunlin. However, it is obvious that there are also large numbers of sites with a high percentage of silt and clay which have very low Dunlin densities at low tide. Several possible factors could explain this apparent anomaly:

1. Dunlin density was sampled only at low tide and it may be that some of these areas were used on the rising and falling tides but not at low tide, because of the timing of prey availability coinciding with these states of tide.
2. It is possible that these areas were used extensively at night rather than in the day to avoid possible sources of disturbance.
3. It is possible that there were not enough bird counts to enable us to pick up all the important sites where Dunlin feed within an estuary.
4. It is possible that Dunlin feed on different sites in different winters within most estuaries as a result of changes in substrate composition or even changes in spatfall between years. This type of response has been recorded on the Severn (Clark 1990) for Dunlin.
5. The final possibility is that Dunlin were only utilising substrates with both a high silt and clay content and some other factor that is as yet unidentified.

It is possible that Dunlin were only favouring areas with a certain type of cohesive sediment. In order to test for this possibility, the yield stress was taken for each area sampled for sediment. The relationships between mean Dunlin density and yield stress are given for each estuary in Figures 2.61 - 2.74. For many estuaries there was comparatively little variation in yield stress between sampling sites. Consequently, only two estuaries displayed sufficient variation in yield stress readings to show a significant relationship with Dunlin density; the Exe and the Adur (Figures 2.63 and 2.66). When the data for all sites were combined, Dunlin densities tended to be highest where yield stress was low (Figure 2.75).

A multiple regression was undertaken of mean Dunlin density with combinations of the proportion of silt and clay, yield stress and shore width. However this failed to improve significantly the proportion of the variation in Dunlin density that could be explained.

Part of the reason why there were comparatively poor relationships between Dunlin densities and sediment variables was due to insufficient data being available to locate all Dunlin feeding areas with accuracy. It is likely that there is a relationship between the overall density of Dunlin on each estuary and the mean silt and clay content of that estuary. It was found that there was a highly significant ($P<0.001$) relationship between mean

Dunlin density and mean silt and clay content, explaining 65% of the variation in Dunlin density between estuaries. Adding a quadratic term increased the explained variance to 75% (Figure 2.76). It is clear from the figure that the density of Dunlin is independent of sediment type until the site has a mean silt/clay content of over 50%. At higher mean silt/clay content the density of Dunlin rises rapidly.

2.4DISCUSSION

The results obtained in this study indicate that the average silt/clay content of estuarine sediments is the most important physical determinant of differences in overall Dunlin density between estuaries. The 75% of variance in density explained by the relationship far exceeds that explained by any of the physical and chemical variables considered in the previous sections. Although invertebrate abundance was not investigated at the study sites, the strong correlation between prey density and grain size reported elsewhere (Warwick et al. 1991) indicates that food availability is likely to be the ultimate factor determining Dunlin distribution. On the Wash, the density of 11 out of 24 invertebrate species commonly preyed upon by waders increased significantly as mean grain size of sediments declined (Goss-Custard et al. 1988). These species included Hydrobia ulvae and Nereis diversicolor, both extremely important prey of Dunlin. Data from this study indicate that sites with a mean silt/clay content of surface sediments less than 50% are relatively unattractive to Dunlin, but at "muddier" sites Dunlin density increases at a rate of approximately 2 birds/ha per 10% increase in mean silt/clay content.

Within individual estuaries, the percentage of sediments consisting of silt/clay was a less effective predictor of Dunlin density on individual areas. Only large sites with a broad spectrum of sediment types produced significant correlations. This may be due to deficiencies in the sampling of sediments. As only relatively few samples were taken this undoubtedly reduced sensitivity to small-scale spatial variation in sediment composition and structure within superficially homogenous mudflats. Dunlin have been shown to be sensitive to such variations in selecting feeding areas. Kelsey and Hassall (1989) found that Dunlin feeding on a mudflat in the Wash, comprising a series of ridges and runnels of mud of essentially similar composition but differing in degree of consolidation, attained significantly higher density in the less consolidated runnels where prey organisms were more easily captured.

Kelsey and Hassall's (1989) results and those obtained for Sanderling _Calidris alba_ by Myers _et al_. (1980) indicate that the degree of consolidation of sediments is an important factor in determining the feeding distribution of waders, because of its effect on the energetic costs of obtaining food by tactile means i.e. probing. Such sediments may also constitute a difficult physical and chemical environment for many invertebrate species (Kirby and Parker 1977). The feeding densities might therefore be expected to be relatively low in such areas. This is supported by the relationship between Dunlin density and yield stress, as measured by shear vane, across all estuaries, which indicates that muddy sediments with a mean yield stress greater than 6kPa are little used by Dunlin. The proportion of variation in density explained by this relationship is, however, small. This may be because either an insufficient number of measurements were obtained from each section and or due to the exclusion of several measurements because of the unreliability of this method in predominantly sandy substrates. It is unlikely, however, that the correlation between Dunlin density and sediment cohesion is a simple, direct one. There is some evidence to suggest that even small waders may have difficulty in moving around and feeding efficiently in extremely underconsolidated sediments.

The relationship between Dunlin density and sediment composition, demonstrated here, indicates that sedimentological changes engendered by developments such as the proposed Severn barrage have the potential to alter profoundly the ability of estuaries to support wintering

Dunlin. These results do, however, suggest that it may be possible to manipulate sedimentation patterns to provide substrates fulfilling the environmental requirements of waders and thus ameliorate the effects of loss of a proportion of intertidal feeding areas through inundation post-barrage.

SECTION 3: IMPLICATIONS FOR PREDICTING POST-BARRAGE DENSITIES OF DUNLIN

Section 1 of this report showed that Dunlin occurred at higher densities on small estuaries, with lower rainfall, lower average biochemical oxygen demand, although a higher maximum biochemical oxygen demand, as well as being in the east of the country. Section 2 found that sites with a high silt and clay content had higher mean Dunlin densities. It is unfortunate that most of the sites, where the fieldwork was carried out, did not have adequate environmental data available for the analyses in Section 1. Otherwise it would have been possible to undertake a multiple regression analysis to assess the amount of variation that can be explained by all these factors.

It may well be that some of the geographic factors (e.g. exposure) that were found in Section 1 to be important in predicting Dunlin density were actually important predictors of the proportion of silt and clay in the estuary. Therefore, there may not be a significant increase in the predictability of Dunlin densities if all the variables were available for each estuary. If a barrage is built across an estuary, it will not change the actual size of the estuary unless it effectively splits the estuary into a number of smaller estuarine units and it will certainly not change the rainfall or its location. This means that in order to modify the estuarine environment to improve it for Dunlin post-barrage, it will be necessary to affect the average and maximum biochemical oxygen demand and the proportion of silt and clay within the intertidal sediments.

It is likely that there will be constraints on the water quality in the post-barrage environment which would override any possibility for modifying the manmade organic inputs in order to increase the maximum biochemical oxygen demand. Indeed, it is likely that the general principle to which statutory bodies will work to is that, if anything, there should be a reduction in organic inputs to estuaries.

This leaves only the possibility of engineering the mudflats to trap increased levels of silt and clay in order to increase the densities of Dunlin that can winter within an estuary post-barrage. Techniques for trapping sediments have been widely used in order to reclaim land over the centuries and are especially important in areas like the Wadden Sea. Fine sediments are encouraged to settle on the upper mudflats by the extensive use of brushwood walls which reduce water flow and wave action.

It is clear from Figures 2.16 and 2.17 that there is no fixed proportion of an estuary which holds 50% or 90% of the wintering population. It might be expected that the higher proportion of the estuary would be utilised by Dunlin if the overall density on that site was higher. This was, however, not found to be the case for either the areas holding 50% of the Dunlin (Figure 3.1) or the areas holding 90% of Dunlin (Figure 3.2). This again indicates the variability in quality of estuaries for Dunlin and shows that there is scope for increasing the density of Dunlin if suitable conditions can be engineered. This is further emphasised by the very strong relationship between the mean Dunlin density of an estuary and its mean silt and clay content (Figure 2.76). Thus it appears, from the sites that have been studied so far, that for every 10% increase in the mean silt and clay content over 50% then there should be a corresponding increase in Dunlin density of approximately two birds per hectare. There is clearly a considerable degree of variation between estuaries and from this study it would be unwise to produce confidence limits for these predictions as there was only a small number of estuaries with really high silt and clay content.

Further studies should be undertaken to investigate this relationship further before safe predictions can be made. This study does, however, suggest that it might be possible to maintain the existing Dunlin populations within the Severn by increasing the mean silt and clay content by approximately 10% within the estuary as a whole. This would only be true, however, if the majority of the sediments remain unconsolidated and is unlikely to hold if the Severn moved to an even more erosional regime with large areas of hard clay platforms. Further studies predicting the sediment regime of the estuary should therefore concentrate on predicting the proportion of soft areas with a high silt and clay content. Only when these predictions can be made will it be possible to make a firm prediction of the expected post-barrage Dunlin density and then assess whether additional engineering measures would be required in order to maintain the existing Dunlin population.

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Table 1.1 Definition of carrying capacity categories derived from regression of log peak winter Dunlin count on log national index of Dunlin abundance

Score	Definition	No. sites
1	Peak Dunlin count <50	3
2	a) Concave curvilinear regression	0
	b) No significant relationship, coefficient of variation >1	7
3	Significant positive linear regression slope ≥1	35
4	Significant positive linear regression slope <1	0
5	Convex curvilinear regression	1
6	No significant relationship, coefficient of variation 0.5 - 1.0	24
7	No significant relationship, coefficient of variation <0.5	45
		115

Table 1.2 Results of stepwise regression of indicators of site preference by Dunlin on variables with data for all sites (AREA, TIDR, JTMP, LAT, LNG). For key to environmental variables see Table 2.2.

Indicator variable	Environmental variables selected	r^2	P
b	LNG (-)	0.077	0.003
cc	AREA (+)	0.033	0.056
CV	AREA (-), LNG (-)	0.089	0.009
MD	LNG (+), AREA (-)	0.094	0.009

(-) = negative relationship   (+) = positive relationship

b = regression slope (rate of change of peak numbers)

cc = carrying capacity score

CV = coefficient of variation of peak numbers

MD = mean Dunlin density

Table 1.3 Results of stepwise regression of indicators of site preference by Dunlin on variables allowing the maximum number (89) of sites to be analysed (AREA, TIDR, JTMP, LAT, LNG, WENTR, WMAX, RFL, TAV, TMIN, WS). For key to environmental variables see Appendix 2.

a) 89 sites

Indicator variable	Environmental variables selected	r^2	P
b	LNG (-), WS (-)	0.164	0.001
cc	RFL (-)	0.044	0.048
CV	AREA (-), RFL (+), TIDR (-) TMIN (-)	0.159	0.006
MD	AREA (+), TMIN (+), WS (+)	0.181	0.001

b) As above after exclusion of variable sites (cc=2 and cc=6)

Indicator variable	Environmental variables selected	r^2	P
b	RFL (+), WS (-)	0.249	0.000
cc	RFL (-)	0.122	0.004
CV	RFL (+), TIDR (-)	0.221	0.003
MD	TMIN (+), RFL (-), WS (+)	0.181	0.001

(-) = negative relationship (+) = positive relationship

b = regression slope (rate of change of peak numbers)

cc = carrying capacity score

CV = coefficient of variation of peak numbers

MD = mean Dunlin density

Table 1.4 Results of regression of indicators of site preference by Dunlin on environmental variables with small sample sizes (50 sites or less). Only significant (P<0.05) relationships are listed.

Indicator variable	Environmental variable	n	slope	r^2
b	AVP	27	-0.734	0.193
cc	AVPDOX	36	0.027	0.132
cc	AVBOD	28	0.593	0.307
MD	AVAM	35	1.394	0.129
MD	PSTF	13	0.917	0.307
MD	PMDS	20	1.849	0.281

Table 1.5 Results of comparison of mean values of environmental variables between sites where Dunlin numbers are at carrying capacity and other sites by single-classification analysis of variance. Only significant (P<0.05) differences are listed, df = degrees of freedom, F = variance ratio.

	Mean values				
Environmental variable	**At capacity**	**Other**	**df**	**F**	**P**
AREA	2755.1	993.0	1,113	7.22	0.008
RFL	221.4	260.7	1,87	5.06	0.027
LNG	-2.1	-3.1	1,113	6.18	0.014
AVBOD	9.7	8.1	1,26	7.41	0.011
MXBOD	2.8	1.8	1,35	5.55	0.040

Table 1.6 Results of comparison of mean values of environmental variables between sites where Dunlin numbers are at carrying capacity and other sites, within geographical regions. Only significant differences (P<0.05) are listed. Region 1 = Nyfer - Rye Bay; Region 2 = Pegwell Bay - Humber; Region 3 = Tees - Moray Firth; Region 4 = Clyde - Dyfi; West = Region 1 + Region 4; East = Region 2 + Region 3, df = degrees of freedom, F = variance ratio.

		Mean values				
Region	**Environmental variable**	**At capacity**	**Other**	**df**	**F**	**P**
1	none	-	-	-	-	-
2	AVBOD	9.2	7.5	1,6	9.50	0.022
3	none	-	-	-	-	-
4	AREA	3873.3	1386.4	1,34	4.55	0.040
4	TMIN	2.3	2.0	1,19	6.79	0.017
4	MNDO	8.3	3.2	1,9	6.61	0.033
West	AVPDOX	107.9	79.6	1,15	6.24	0.026
West	AVBOD	10.1	7.8	1,14	6.67	0.022
East	none	-	-	-	-	-

Table 1.7 Results of multiple regressions of indicators of site preference by Dunlin on environmental variables showing significant differences in mean values between sites where Dunlin numbers are at carrying capacity and other sites (highly variable sites, c = 2 and c = 6 excluded).

Indicator variable	**Environmental variable**	**Slope**	**individual p**	**overall r^2**	**overall p**
b(n=20)	AREA	-0.0000181	0.740	0.379	0.141
	RFL	-0.00546	0.801		
	AVBOD	-0.840	0.034		
	MXBOD	0.0868	0.865		
	LNG	-0.545	0.503		
cc(n=20)	AREA	0.0000542	0.358	0.553	0.016
	RFL	-0.00743	0.741		
	AVBOD	1.03	0.014		
	MXBOD	0.163	0.758		
	LNG	0.0293	0.971		
CV(n=20)	AREA	-0.00000448	0.621	0.265	0.373
	RFL	-0.00182	0.603		
	AVBOD	-0.102	0.097		
	MXBOD	0.0824	0.325		
	LNG	-0.115	0.380		
MD(n=20)	AREA	-0.000324	0.016	0.692	0.003
	RFL	-0.0950	0.057		
	AVBOD	-0.770	0.335		
	MXBOD	1.99	0.086		
	LNG	-2.23	0.212		

b= regression slope (rate of change of peak numbers)

cc= carrying capacity score

CV= coefficient of variation of peak numbers

MD= mean Dunlin density

Table 2.1 Results of regression of mean Dunlin feeding density on percentage silt/clay content of sediments, percentage fine clay (percentages arcsine transformed) and mean yield stress of sediments for all estuaries combined and individual estuaries. Probability levels: ns = not significant; * = P<0.05; ** = P<0.01; *** = P<0.001

	% silt/clay			**% fine clay**			**yield stress**		
	slope	**r^2**	**P**	**slope**	**r^2**	**P**	**slope**	**r^2**	**P**
All estuaries	10.992	0.175	***	14.674	0.113	***	-2.840	0.124	***
Tamar	-22.071	0.116	ns	14.037	0.169	ns	1.064	0.001	ns
Plym	4.263	0.024	ns	-0.213	0.000	ns	-0.700	0.010	ns
Exe	4.326	0.267	ns	12.503	0.248	ns	-6.644	0.524	*
Chichester H	-11.468	0.010	ns	101.278	0.255	ns	-2.095	0.007	ns
Pagham H	-19.170	0.108	ns	71.504	0.048	ns	-4.157	0.349	ns
Adur	27.506	0.118	ns	-33.793	0.002	ns	-5.243	0.529	*
Pegwell B	-0.920	0.028	ns	6.338	0.054	ns	-	-	-
Leigh-Canvey	25.971	0.453	*	354.045	0.196	ns	-5.076	0.274	ns
Blackwater	14.267	0.403	**	22.087	0.510	**	-0.625	0.022	ns
Colne	28.567	0.414	**	28.567	0.414	**	-3.124	0.066	ns
Lindisfarne	0.415	0.004	ns	8.124	0.154	ns	-	-	-
Tyninghame	1.509	0.152	ns	8.519	0.226	ns	-	-	-
Eden	-2.171	0.012	ns	-1.057	0.003	ns	-2.599	0.243	ns
Montrose B	2.458	0.047	ns	-3.920	0.055	ns	-0.689	0.090	ns

Appendix 1. Estuaries, coastal areas and sub-sites used in analysis of site preference by Dunlin.

1. Severn (Glos.)
2. Severn (Somerset & Avon)
3. Bridgwater Bay
4. Taw/Torridge
5 Hayle
6. Tamar (St John's Lake)
7. Tamar (Upper)
8. Tavy
9. Plym
10. Yealm
11. Erme
12. Avon (Devon)
13. Kingsbridge
14. Dart
15. Teign
16. Exe
17. Otter
18. Axe
19. Weymouth area
20. Poole Harbour
21. Christchurch Harbour
22. N.W. Solent
23. Beaulieu
24. Southampton Water
25. Newtown
26. Brading Harbour
27. Guernsey
28. Portsmouth Harbour
29. Langstone Harbour
30. Chichester Harbour
31. Pagham Harbour
32. Rye Harbour
33. Pett Levels
34. Pegwell Bay
35. Medway
36. Inner Thames
37. Leigh/Canvey
38. Foulness
39. Crouch
40. Dengie Flats
41. Blackwater
42. Colne
43. Hamford Water
44. Stour
45. Orwell
46. Deben
47. Ore
48. Havergate Island
49. Butley
50. Blyth (Suffolk)
51. Breydon Water
52. Wash
53. Humber (North)
54. Tees
55. Whitburn Coast
56. Boulmer-Howick
57. Howick-Beadnell
58. Beadnell-Seahouses
59. Seahouses-Budle Pt.
60. Lindisfarne
61. Tweed
62. Tyninghame
63. Forth (South)
64. Forth (Inner)
65. Eden
66. Tay (Outer, South)
67. Tay (Inner)
68. Montrose Basin
69. Ythan
70. Rosehearty-Fraserburgh
71. Lossie
72. S.Kessock-Alturlie
73. Inner Moray Firth
74. Cromarty Firth
75. Loch Fleet
76. Inner Clyde
77. Hunterston
78. Ardrossan/Seamill
79. Irvine
80. Ayr/Prestwick
81. Doon
82. Maidens Harbour
83. Turnberry/Dipple
84. Loch Ryan
85. Wigtown Sands
86. N.Solway
87. S.Solway (Inner)
88. S.Solway (Outer)
89. Irt/Mite/Esk
90. Duddon
91. Ribble
92. Alt
93. Mersey
94. Dee (England/Wales)
95. Clwyd
96. Conwy
97. Lavan Sands
98. Menai
99. Red Wharf Bay
100. Inland Sea
101. Pwllheli Harbour
102. Traeth Bach
103. Dyfi
104. Nyfer
105. Gann
106. Sandy Haven
107. W.Cleddau
108. Burry (South)
109. Blackpill
110. Taff/Ely

Appendix 1. (continued)

111. Dundrum Bay
112. Strangford Lough
113. Larne Lough
114. Bann
115. Lough Foyle

Appendix 2 Name, units and source of the physical and environmental data used in the analyses. There are five groups of variables - physical, climatic, geographic, chemical and sediment types.

Variable	Description/Units	Source
Physical		
AREA	Total area intertidal feeding zone (hectares)	BTO & Peter (1981)
ELNG	Estuary or inlet length (km)	1:50000 OS maps
WENTR	Estuary width at entrance (km)	1:50000 OS maps
WMAX	Maximum width of estuary (km)	1:50000 OS maps
TIDR	Tidal range (difference between mean high water and mean low water), (m)	Admiralty Tide Tables, Volume 1
MXDP	Maximum depth of estuary (m)	Admiralty charts
SPRT	*(Spartina)* score	Goss-Custard & Moser 1988
Climatic		
RFL	Mean total rainfall for Jan-Mar (mm)	ITE Land Characteristics Data Bank
JTMP	Mean January air temperature (°C)	Met Office Memo No 73 (1975)
TAV	Mean air temperature Jan-Mar (°C)	ITE Land Characteristics Data Bank
TMIN	Mean minimum air temperature Jan-Mar (°C)	ITE Land Characteristics Data Bank
WS	Mean windspeed Jan-Mar (km h^{-1})	ITE Land Characteristics Data Bank
LWT	Minimum water temperature during the year (°C)	RPB's & NRA's
HWT	Maximum water temperature during the year (°C)	RPB's & NRA's

Geographic

EA	Easterly bearing of 10-km square containing the site	OS Atlas of the British Isles
NO	Northerly bearing of 10-km square containing the site	OS Atlas of the British Isles
LAT	Latitude	Phillips University Atlas
LNG	Longitude	Phillips University Atlas

Chemical

LCL	Minimum concentration of chloride ions in estuarine water (mg 1^{-1} Cl). Related to salinity, where salinity = 1.80655 x chlorinity	RPB's & NRA's
HCL	Maximum concentration of chloride ions (mg 1^{-1} Cl)	RPB's & NRA's
AVCON	Mean conductivity of estuarine water. (USIE.cm^{-1})	RPB's & NRA's
MXCON	Maximum conductivity of estuarine water (USIE.cm^{-1})	RPB's & NRA's
AVAM	Mean concentration of ammonia (mg 1^{-1}N)	RPB's & NRA's
MXAM	Maximum concentration of ammonia (mg 1^{-1}N)	RPB's & NRA's
AVP	Mean concentration of orthophosphate (mg.l^{-1}P)	RPB's & NRA's
MXP	Maximum concentration of orthophosphate (mg.l^{-1}P)	RPB's & NRA's
MNPDOX	Minimum percentage dissolved oxygen (%O_2)	RPB's & NRA's
AVPDOX	Mean percentage dissolved oxygen (%O_2)	RPB's & NRA's
MINDO	Minimum concentration of dissolved oxygen (mg $1^{-1}O_2$)	RPB's & NRA's
AVBOD	Mean biochemical oxygen demand (mg $1^{-1}O_2$)	RPB's & NRA's
MXBOD	Maximum biochemical oxygen	RPB's & NRA's

demand (mg l^{-1} O_2)

Sediment

MDPHI	Median sediment particle size (phi)	RPB's & NRA's
PSTF	Percentage of particles <125 microns, fine sand or finer	RPB's & NRA's
PSLT	Percentage of particles <62.5 microns, silt/clay fraction	RPB's & NRA's
AVPHI	Mean particle size (phi)	RPB's & NRA's
PMDS	Percentage of sites sampled where mean particle size <63 microns, "muddy sites".	RPB's & NRA's