Resource partitioning and competition in shorebirds at Teesmouth, with particular reference to grey plover pluvialis squatarola. curlew numenius arquata and bar-tailed godwit limosa lapponica

Parsons, Matthew

How to cite:

Parsons, Matthew (1994) *Resource partitioning and competition in shorebirds at Teesmouth, with particular reference to grey plover pluvialis squatarola. curlew numenius arquata and bar-tailed godwit limosa lapponica*, Durham theses, Durham University. Available at Durham E-Theses Online: http://etheses.dur.ac.uk/5556/

Resource Partitioning and Competition in Shorebirds at Teesmouth, with Particular Reference to Grey Plover *Pluvialis squatarola*, Curlew *Numenius arquata* and Bar-tailed godwit *Limosa lapponica*

by

Matthew Parsons, B.Sc. Hons. (Southampton)

**This thesis is presented in candidature for
the degree of Doctor of Philosophy**

Department of Biological Sciences

University of Durham

1994

ABSTRACT

Resource Partitioning and Competition in Shorebirds at Teesmouth, with Particular Reference to Grey Plover *Pluvialis squatarola*, Curlew *Numenius arquata* and Bar-tailed Godwit *Limosa lapponica*

Two shorebird assemblages were identified as providing high potential for interspecific competition - sanderling, knot, oystercatcher and turnstone on a rocky shore, and curlew, bar-tailed godwit and grey plover on soft substrates. Observations were concentrated on the latter group which all fed chiefly on ragworm *Nereis diversicolor.*

Sizes of prey taken by the three species were estimated by two independent methods. Sexual and age differences in diet within species were examined. Dietary overlap between species was high only between certain age/sex classes.

Depletion of prey by each species was estimated. Between 44 and 77 percent of the larger size class of *Nereis* was consumed in a favoured feeding area over one winter. Implications for competition are discussed.

Interspecific aggression rates were very low compared to rates within species.

All three species were present on Seal Sands, Teesmouth, in high densities in mid-winter, but temporal segregation between grey plover and curlew occurred on a favoured feeding site within a low water period. Segregation resulted from different micro-habitat choice by the two species, rather than avoidance, since grey plovers exhibited identical behaviour at times of year when densities of curlews were low.

Within a period of exposure, grey plovers moved feeding site when their energy intake rate decreased due to drying of the sediments. Energy intake rate of grey plovers was not reduced in proportion to the density of curlew surrounding them, except at very high curlew densities.

Competition between the three large species during the study was not important. Partitioning of prey size, temporal partitioning of feeding areas, and use of different sediment types enabled their coexistence. Competition may occur during years of high shorebird populations and low densities of available prey. Evidence from the rocky shore assemblage showed significant avoidance of knot by sanderling when feeding area was limited.

CONTENTS

CHAPTER SEVEN A SEARCH FOR COMPETITIVE INTERACTIONS BETWEEN KNOT, SANDERLING, TURNSTONE AND OYSTERCATCHER ON REDCAR AND COATHAM ROCKS

No part of this thesis has previously been submitted for a degree in this or any other university. The work described is my own except where duly acknowledged

ACKNOWLEDGEMENTS

I am grateful to Professor Peter Evans for his help, criticism and patience during my period of study and in the preparation of the thesis.

Thanks are due to Michael Bone for the help and encouragement he has given me.

Robin Ward supplied me with additional count data and information on invertebrate densities, and for these I am grateful.

Cannon-netting expeditions would not have been possible without a team of dedicated helpers, and for this I thank Robin Ward, Ian Scott, Niall Burton, Andrew Hoodless and others who from time to time were persuaded to spent a day at beautiful Teesmouth.

Tom Dewdney and Jack Green were kind enough to mist-net sanderling and turnstone for my studies.

Steve Percival must be applauded for his heroic attempts, albeit in vain, to rescue landrover "FUP" from the North Sea in March.

This thesis was funded by the Natural Environment Research Council.

To my parents

CHAPTER ONE

GENERAL INTRODUCTION.

The theoretical framework for the study of competition was established several decades ago, yet demonstrating its existence and importance in the field situation challenges community ecologists to this day. Work in the past has concentrated upon types of organisms that are relatively immobile and small and therefore amenable to laboratory studies and field manipulations. Studies on birds have tended to focus on the outcome of possible competition in the past, rather than on present interactions. Rather little literature exists on the role and importance of interspecific competition in shorebirds, even though it may be an important force in the structuring of these assemblages and have implications for the effects of habitat loss in coastal areas.

Before introducing the particular case of shorebirds I will define what I mean by "competition" and by "resource partitioning" in the context of general ecological theory. Modern definitions of competition (in this thesis "competition" will be synonymous with interspecific competition, unless otherwise stated) differ in the main as to whether the emphasis is placed on effect or on process. Of the former group Odum (1953) and Williamson (1972) are the main proponents. Williamson (*op. cit.*) for example, provides a definition based on a demonstrable effect of the population size of one species on the population size of another, or *vice versa*. In contrast Milne (1961) favours a definition by process, namely "the endeavour of two (or more) animals to gain the same particular thing, or to gain the measure each wants from the supply of a thing when that supply is not sufficient for both (or all)." I believe a definition by process to be a more precise tool for the study of competition. The definition by effect (*sensu* Williamson 1972) is unhelpful because the observed "effect" may simply be a result of, for example, predation or physical perturbation, and may have little or nothing to do with competition. The definition by process (*sensu* Milne 1961) on the other hand encourages a comprehension of the mechanisms behind any observed changes in abundances.

Elton and Miller (1954) and Park (1954) distinguished between *interference* competition and *exploitation* competition. Interference in foraging is the process in which one species adversely affects the prey intake of the other by means of spatial exclusion, aggression and food stealing or by means of disturbance of its foraging method, even if the resource itself is not limiting. Exploitation is the utilisation of a resource once access to it has been achieved. Nicholson (1955) termed this latter type "scramble competition", in the sense that the successful competitor removes part of the resource and deprives the other species of part of its share.

The subject of "resource partitioning" is inexorably linked with the theory of competition. Put simply, resource partitioning is a mechanism by which species avoid competition when resources are limiting. If we view the ecological niche in a Hutchinsonian sense, then the degree of niche overlap between two (or more) species can be used as a measure of strength of potential competition (MacArthur and Levins, 1967); the more ecologically similar two or more species are the more they potentially compete. A logical progression of this idea means that competition can be avoided if the resource on which the potential competitors depend is partitioned, such that each species "specialises" in utilising a particular range along a resource continuum. In this way all species in a given assemblage could become "ecologically segregated" and competition is avoided. The role of resource availability is an important one, especially in terms of the amount of niche overlap that is acceptable before competition occurs. By definition, if resources are super-abundant then no matter how high the niche overlap between species, competition will not occur. However, rather little overlap would be expected to persist if the resource is in short supply; in such cases each species would partition the resource so that the number of individuals utilising each fraction of it is reduced (Pianka 1972).

Compared with other taxa, competition among shorebirds has received rather little attention. The sparse literature is divided between studies on the breeding grounds, during migration, and on the wintering grounds. In the former category it is likely that intraspecific effects override interspecific ones because on the breeding grounds shorebirds tend to be widely dispersed and regulation of density of many species occurs via intraspecific territorial behaviour (Holmes 1966, 1970, Recher, 1966), although this is not always the case. Hale (1980) admits that the factor which limits the densities of those species which do not hold territories during the breeding season, such as redshank *Tringa totanus* (Hale 1956), is unknown, but is likely to be food limitation. During migration shorebird densities are often very high, and although the assemblages are transitory, food depletion has been demonstrated which could lead to competitive interactions between individuals and species (Schneider and Harrington 1981). However, it is perhaps on the wintering grounds that shorebirds are most likely to experience competition, because it is during this period that they encounter high densities of heterospecifics for an extended period (usually at least five months) at a time when food may become scarce through depletion and/or lowered availability caused by adverse weather conditions (Evans 1976). Food depletion is important because it could lead to there being insufficient prey biomass to meet an individual's daily energy requirements. This, coupled with a possible increase in food stealing and aggression during such periods, could result in a reduction in body condition of the inferior competitor, its emigration to a more favourable area or even, if migration is not an option, to its death.

In an important early paper Recher (1966) investigated the ways in which shorebirds migrating through coastal California and New Jersey during spring and autumn coexist in dense aggregations. Recher showed that within a species for a given season birds pass through a feeding area in pulses, thereby staggering the times of peak densities and reducing the potential for interference competition between individuals. Furthermore, he showed that each species tends to migrate at slightly different times within a season, reducing the likelihood of excessive densities at which processes such as prey depletion and interference may operate. Studies by Busche (1980) and Drenckhahn (1980) suggested that observed differences in the times of migration of shorebird species passing through the Schleswig-Holstein region of the German Wadden Sea were a way of reducing interspecific competition. Even different populations of the same species have been shown to pass through refuelling sites in Schleswig-Holstein at different times. When populations of knot *Calidris canutus* which breed in Greenland and Canada are leaving the area in mid May Siberian breeders (wintering in Africa) are only starting to arrive (Prokosch 1988). It is hypothesised that excessive densities of shorebirds at this important refuelling site would result in interference in foraging and prevent competitively inferior individuals from building sufficient energy reserves to complete the migration to the breeding grounds. Baker and Baker (1973) investigated resource use by six species of shorebird that were studied both on the breeding grounds (in the eastern Canadian Arctic) and during winter (in the United States Gulf Coast). These authors showed a higher degree of behavioural and microhabitat diversity (broader niche and higher niche overlap) of species on the breeding grounds than for the same suite of species in winter, and suggested that this was largely a result of superabundant food resources during summer. Similarly the observed small niche breadth of each species on the wintering grounds was, the authors argue, probably a response to food limitation, so that niche overlap, and therefore competition, is kept to a minimum in times of food shortage.

Evidence that competition may occur among wintering shorebirds was provided by Zwarts (1978), who studied the assemblages on a mudflat in North-Ventjager, Netherlands. He showed that curlew *Numenius arquata* and avocets *Recurvirostra avosetta,* which both fed on the same prey and preferred the same feeding area, each day occupied different areas, but always mutually exclusive. For example, if large numbers of curlew were present on the preferred feeding area, relatively few avocet fed there. Conversely when large numbers of avocet were present, relatively few curlew fed there. A rather different situation was revealed by Thompson *et al.* (1986) on the Clyde Estuary, Scotland who, using stepwise multiple regression, evaluated the relationship between the density of each species of shorebird, the density of each species of benthic prey, and the density of each bird species in a series of 0.2 x 0.2 km square sample cells. These workers found no significant inverse relationships between the density of a shorebird species and the density of any other species. However, as these authors point out, if there *were* inverse relationships these would not necessarily indicate that competition is occurring, because negative correlations in numbers could simply be a reflection of an innate sediment preference of each shorebird species. For competition to be shown there would need to be observations of displacement from a feeding area of one species by another and/or the demonstration of high levels of interspecific aggression or food stealing. Myers and McCaffery (1984), in a rather brief study of shorebirds wintering in coastal Peru, identified the mechanism for interference competition in that assemblage, namely the existence of intra- and interspecific territoriality, but were unable to make any quanitative measurements of competitive interactions. Pienkowski (1979) provided evidence to show that plovers may experience interference competition from other species. He showed that at Lindisfarne, N.E England there existed a negative correlation between the numbers of plovers and the numbers of other shorebirds in a study area, and that at Teesmouth, also in N.E. England, as the tide rose, reducing feeding area, grey plovers *Pluvialis squatarola* were apparently forced off by incoming curlew and bar-tailed godwit *Limosa lapponica* which continued to feed there. Furthermore, at Lindisfarne he observed that, after the departure of most bar-tailed godwits in April, grey plovers, which remain until May, continued to feed on their main feeding areas until these were reached by the tide, whereas earlier in the season they were apparently forced off by the godwits which moved ahead of the tide.

Competition may be difficult to detect in the field if it occurs, as is likely, only intermittently, or at unpredictable times of the year, or is manifested in subtle ways. For example, Evans *et al.* (1979) suggested a mechanism of "indirect competition" for food among shorebirds on the Tees estuary. They argued that the population densities of small 0-1 year old ragworm *Nereis diversicolor*, which were the preferred prey of small shorebird species could be depleted by these predators to such an extent that recruitment of this cohort into the large 1+ age class is reduced. In this way the large shorebirds which fed on the large 1+ age class may experience food shortage in the following winter.

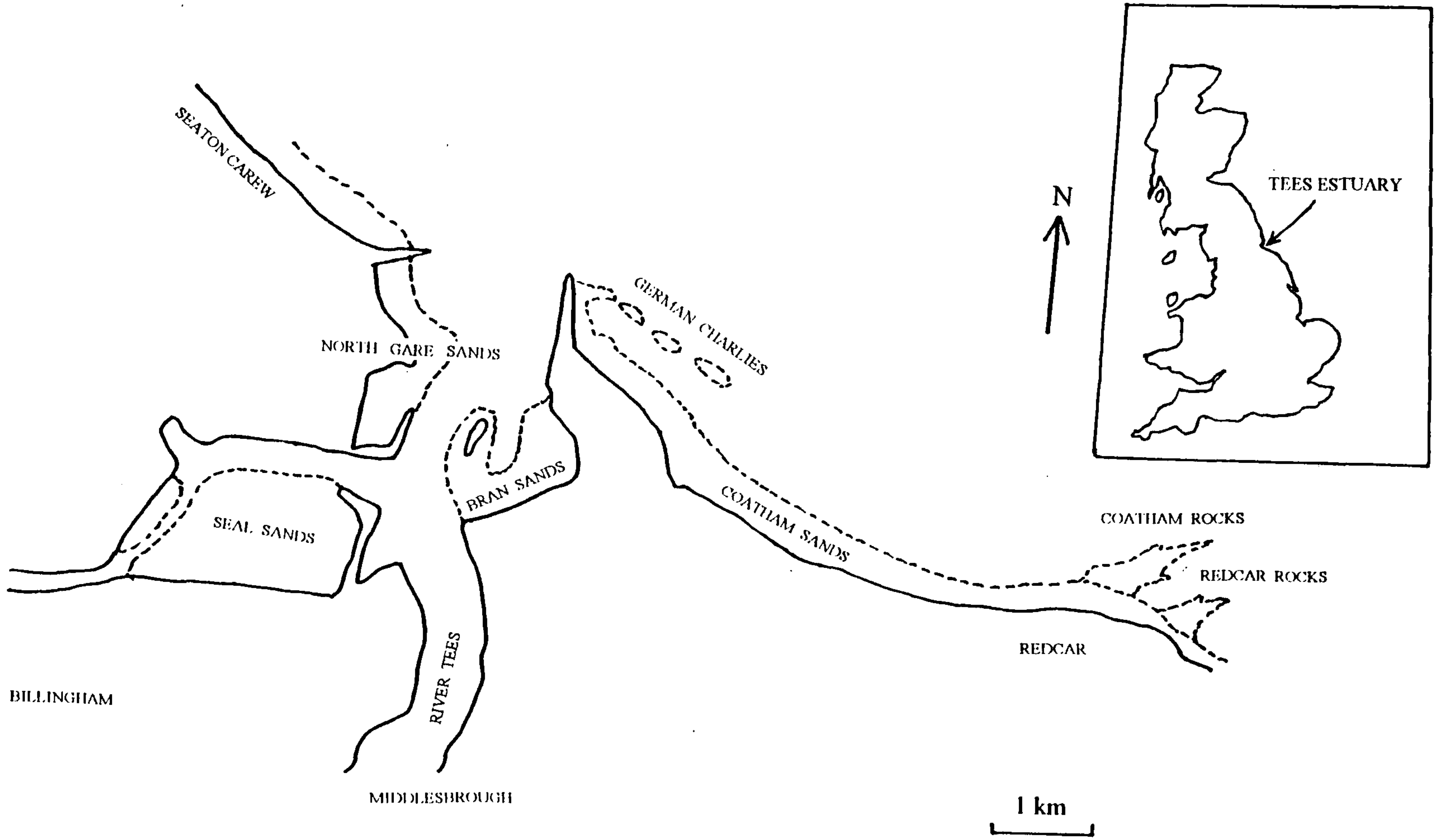
Detailed studies on the Tees estuary have been in progress since 1971, when invertebrate sampling of the intertidal areas was first undertaken (Gray, 1976). In response to major intertidal reclamation of Seal Sands in 1973 Pienkowski (1973) investigated whether the estuary could continue to support the high numbers of shorebirds following a reduction of the intertidal area. Pienkowski (*op. cit.*) investigated the parameters which may control the densities of shorebirds that can be sustained by an area, namely minimum required feeding duration of individuals, densities of invertebrate prey, and aggressive interactions between and within species. This work, and the observations of Evans (1979) that there may be displacement of dunlin *Calidris alpina* by feeding flocks of shelduck *Tadorna tadorna*, resulting in a low wintering population of dunlin in those years when shelduck are numerous, are the few instances when the notion of interspecific competition has been addressed on the Tees Estuary. The majority of shorebird studies on the Tees (and indeed elsewhere) have been largely autecological. These have, in many cases, provided crucial background information to 'set the scene' for the present study of interactions between species of shorebird. Dugan (1981) and Townshend *et al.* (1984) investigated the ways in which shorebirds, and in particular grey plovers, respond spatially to environmental variables and prey availability; Townsend (1981a) studied in detail the use of space made by curlew and grey plover (and to a lesser extent, bar-tailed godwits) and Townshend (1981b) discussed the importance of inland feeding to the population of curlew on the Tees. Wood (1984) and Dugan (1981) looked at time and energy budgets of grey plovers and Wood (1984) carried out radio telemetry to throw light on the movements and distribution of this species at night; Woodford (1981) studied the feeding ecology of a summering population of curlew; Brearey (1982) studied the feeding behaviour and ecology of sanderlings *Calidris alba* and turnstones *Arenaria interpres* on the sandy beaches and mussel beds to the south of the estuary, while Cooper (1987) and Roberts (1990) looked at migration strategies and flocking behaviour respectively in the sanderling.

Aims of the study.

In this thesis I will describe work aimed to investigate the ways in which shorebirds partition resources, and whether present-day interspecific competition occurs among shorebirds on the Tees Estuary. I began work on one group of potential competitors, namely sanderling knot, oystercatcher *Haematopus ostralegus* and turnstone which occurred together on Redcar and Coatham Rocks (Fig 1.1). The idea was to test if the arrival of large flocks of knot at Teesmouth in November displaced sanderling or other species that had been present on the feeding area for the previous three months, given that the same area was prefered by all species. Also, given that they fed largely on the same prey species, *Mytilus edulis,* was there overt aggression and food stealing between the species? This work, however was abandoned after one winter because increased human disturbance on the study site led to a redistribution of the study species within the estuary. The results of this study are reported in Chapter 7.

Most of the thesis will concern a detailed study of the interactions between three large species of shorebird; grey plover, bar-tailed godwit and curlew, on Seal Sands (Fig 1.1). Previous studies (Pienkowski 1973, Evans *et al.* 1979) showed that these species overlapped broadly in their preferred prey, in the period of their peak abundance and in their spatial distribution - criteria making them possible competitors and therefore interesting subjects for study.

Figure 1.1 The main feeding sites of shorebirds on and around the Tees estuary. The "south side" comprises the German Charlies, Coatham Sands and Coatham and Redcar rocks.



Structure of the thesis.

Chapter two details the study area, its invertebrate fauna and introduces the three study species. Details of bird count methodology and methods used to estimate prey size of each of the shorebirds are given.

Chapter three looks at the shorebird assemblage of the Tees estuary as a whole and establishes which species, among the suite of eleven present in large numbers, are most likely to compete with each other.

Chapter four concerns trophic relationships between the species, and is in three main sections. Firstly the degree of overlap in prey size between the species is determined, and sexual and age differences within the species are investigated. Secondly, calculations are presented that estimate the proportion of the September prey stock that is depleted by the shorebirds over the course of one winter, and the implications of this for competition are discussed. Thirdly data are presented on rates of aggressive interaction between the species, and whether rates are affected by changes in bird density and prey availability.

Chapter five investigates temporal and spatial relationships between the species, and asks whether species avoid one another or whether differences in the distribution of species on Seal Sands is a result of habitat selection.

Chapter six examines in closer detail a pattern of apparent avoidance by grey plovers of concentrations of curlew and godwit on a favoured low-water feeding site. Estimates of energy intake rate of grey plovers on different feeding areas, and the effect of different curlew densities on intake rates of grey plovers are used to explain the pattern of apparent avoidance in the context of a competition hypothesis.

Chapter seven presents the results of searches for competitive interactions between sanderling knot, turnstone and oystercatcher on Redcar Rocks.

Chapter eight provides a synthesis of the conclusions of the preceding chapters and assesses the evidence for and against competitive interactions between shorebirds on the Tees estuary. Some of the wider aspects and implications of the findings are explored, and topics for further study discussed.

Appendix one holds the raw data used in chapter three, and Appendix two gives workings of the calculation of energy intake requirements and prey depletion rates of Chapter four.

CHAPTER TWO

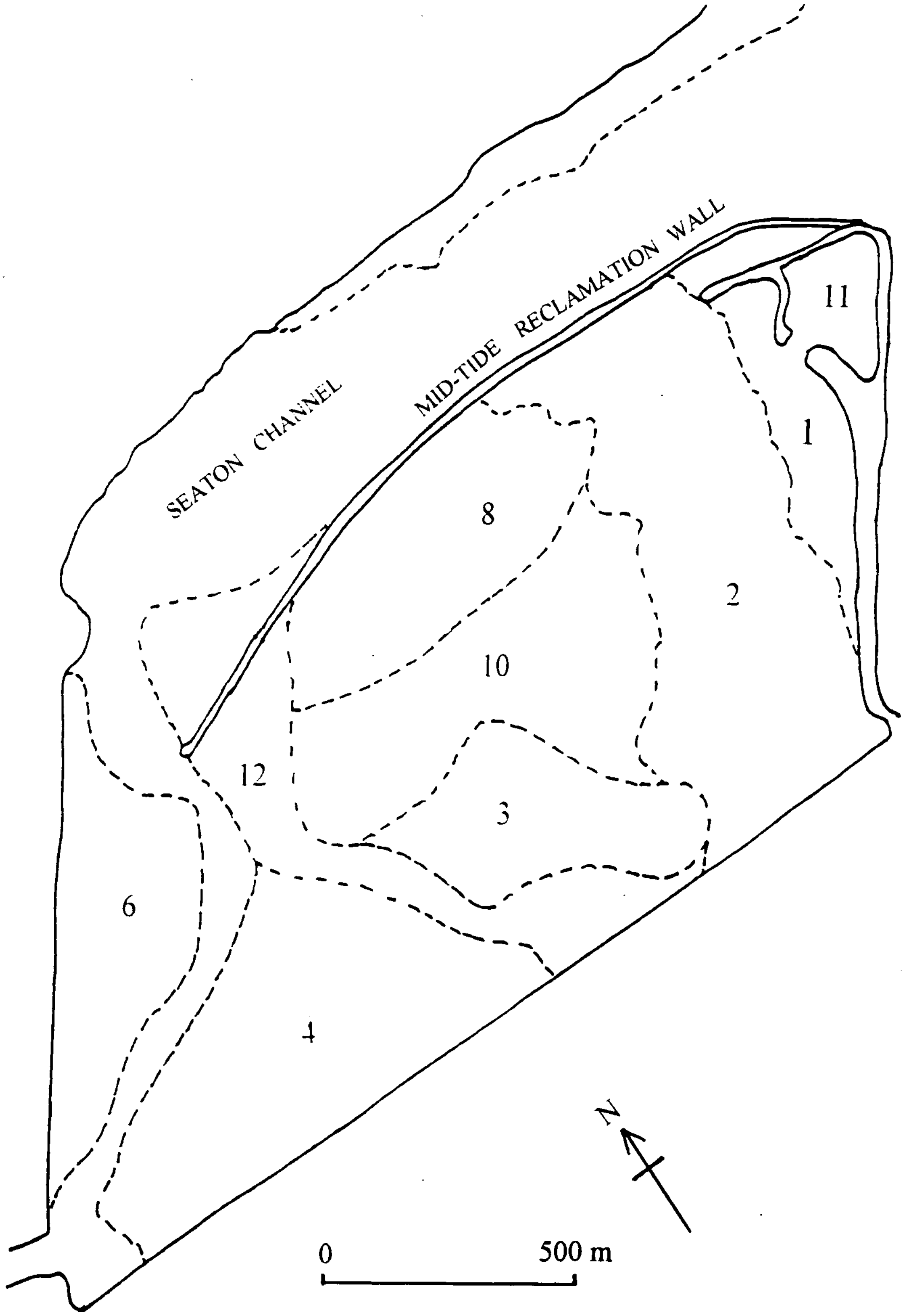
STUDY AREA, STUDY SPECIES AND GENERAL METHODS

2.1 The study area.

Seal Sands is the largest intertidal area in the Tees estuary, comprising 140 hectares of mud and sand. Other shorebird feeding sites on and around the estuary (Figure 1.1) support lower numbers of all species, except for bar-tailed godwits, which occasionally move from Seal Sands to Bran Sands, and curlew, which use Bran Sands especially during times of migration. Sandy beaches to the north and to the south of the estuary proper, and rocks at Redcar support a variable population of sanderling, knot, turnstone and oystercatcher, with lower numbers of redshank, dunlin, ringed plover *Charadrius hiaticula* and curlew.

Seal Sands (Fig. 2.1), bordered on three sides by slag walls constructed during the extensive reclamation in the 1970's, comprises a range of sediment types. In the west is Greenabella Bank, an important feeding site for the three study species. It lies at a low tidal level, is exposed only for three to four hours in each tidal cycle and consists of rather soft mud with a high central area of firmer sandy mud. To the south of this is Scalloped Mud, most of which is at a higher level than Greenabella Bank and consists of medium to soft muds. Central Bank, separated from Scalloped Mud by a channel of very soft mud (Central Channel), is the other main feeding site for shorebirds. It is comprised of a range of sediment types and in summer is partly covered by algae *Enteromorpha* spp. Peninsula Sands is not important as a feeding area but is frequently used as a high water roost site during neap tides. When the tide covers this area birds roost either in the Peninsula Enclosure, on Seaton Snook, on the Bran Sands Islands or in Greenabella Marsh.

Figure 2.1 Seal Sands and its constituent shorebird feeding areas. Key to numbered areas; 1 Peninsula Sands, 2 Eastern Channel, 4 Scalloped Mud , 3, 8 and 10 Central Bank, 11 Enclosure, 12 Central Channel, 6 Greenabella Bank



2.2 The invertebrate fauna.

The invertebrate fauna of Seal Sands is abundant but relatively species-poor. The larger species of invertebrate important in the diet of shorebirds are restricted in number. Table 2.1 shows the densities of the more numerous macrofaunal species on Seal Sands. The nereid polychaete *Nereis diversicolor* ("ragworm") is widespread over Seal Sands and in patches highly abundant; the larger *Nereis virens* ("king ragworm") is much less numerous and locally distributed on the lower shore. The shore crab *Carcinus maenas* appears on Seal Sands during the spring and summer, and is taken by curlews, and various gulls *Larus* spp. Bivalve molluscs are rather scarce and are represented by the cockle *Cerastoderma edule* and the Baltic tellin *Macoma balthica*. The small gastropod *Hydrobia ulvae* which is present at high densities on the softer substrates, and *Corophium volutator*, an amphipod occurring in sandier sediments, are important food for the smaller shorebirds. Polychaetes of the family Capitellidae are locally numerous and also of importance, mainly to small shorebirds. Other species recorded in low numbers include the polychaetes *Eteone longa, Nephtys spp.* and *Phyllodoce spp.* and the isopod *Eurydice pulchra*.

2.3 The study species.

In the large order Charadriiformes, shorebirds (suborder Charadrii) comprise two families, the Charadriidae (plovers and lapwings) and the Scolopacidae (sandpipers and their relatives).

The grey plover *Pluvialis squatarola* is the largest member of the subfamily Charadriinae in the Western Palearctic, with a length of 27-30 cm and a wingspan of 71-83 cm (Cramp and Simmons 1983). Its breeding range is confined to the high Arctic but it winters in Europe, South America, Africa, southern Asia and Australia. The estimated

Table 2.1 The densities of the more numerous invertebrate macrofauna of Seal Sands in September 1991. From sieving 2 x 10 cm diameter cores of sediment from 100 sampling stations over Seal Sands. Invertebrates identified and counted by R.M. Ward.

Species/group	Mean number m^{-2}	Standard Error
Capitellidae	202	80
Corophium colutator	814	113
Carcinus maenas	9	3.3
Eteone longa	30	6.3
Eurydice pulchra	6	4.4
Hydrobia ulvae	6200	664
Macoma balthica	20	4.8
Phyllodoce sp.	12	3.9
Nereis diversicolor	960	90

population size in western Europe is 30,000-40,000, of which about 21,000 occur in Britain (Moser 1987) and about 200 on the Tees estuary. In winter it is almost exclusively coastal, preferring open mud or sand flats. Sexes are very similar in size and plumage in winter, but in breeding plumage some dimorphism occurs. Juveniles can be aged in the field by plumage characteristics until at least late winter. Feeding behaviour in the wintering grounds is well documented (see Dugan 1980, Pienkowski 1980, Townshend 1980). Unlike sandpipers, plovers feed largely using visual cues to detect the presence of their prey at the sediment surface, adopting the typical run - stop - peck method of the Charadriinae. The grey plover's short bill (27-31 mm) relative to its overall size restricts the depth to which it can probe into the sediments. A proportion of individuals may hold feeding territories on the wintering grounds (Michael 1935; Dugan 1980). On Seal Sands Townshend *et al.* (1984) found that about 40% of the population defended at least short-term territories from conspecifics.

The curlew is the largest representative of the subfamily Tringinae, indeed the largest of all shorebirds in the western Palearctic, with a length of 50-60 cm, a wing span of 80-100 cm and a bill length of 10-17 cm. (Cramp and Simmons 1983). The breeding grounds extend from northern and central Europe to Russia and Siberia. In winter the species is more widespread, migrating as far south as South Africa, favouring extensive sand and mudflats but also rocky coasts and coastal pastures. Townshend (1981) found that some curlews from the Tees estuary frequently fed in fields at high and low water. The west European winter population of curlew probably numbers around 300,000, of which around 91,000 occur in Britain (Moser 1987) and 100,000 in Ireland (Prater 1981). The Tees estuary supports a variable population of from 300 to over 1000. Sexual dimorphism is marked; females generally being larger in tarsus length, wing length, and especially bill length. Juveniles, given a good view, can be identified using plumage characteristics (feather edging) in the field until mid-late winter. Feeding methods on the wintering grounds are quite diverse, but generally use exploratory probes to locate prey buried in sediments. Surface dwelling prey such as crabs are located by sight. On Seal

Sands most prey is taken by probing to at least half the bill length (Knights 1979). Like the grey plover, curlews may defend winter feeding territories (Ens and Zwarts 1980; Townshend 1981; Evans 1987). Townshend (1981) estimated that about 10% of wintering individuals defended feeding territories on the Tees (see also review in Townshend *et al.* 1984).

The bar-tailed godwit (in this thesis the species shall be referred to simply as "godwit") is midway in size between grey plover and curlew, being 37-39 cm long with a wingspan of 70-90 cm and a bill of 6.9-10.8 cm. (Cramp and Simmons 1983). The breeding range is restricted to the sub- and low Arctic from Norway east to Alaska, where it frequents low-lying coastal tundra. Outside of the breeding season it ranges widely and utilises a range of coastal habitats. About 115,000 bar-tailed godwits winter around southern North Sea and Irish Sea estuaries (Drent and Piersma 1990) of which about 61,000 occur in Britain (Moser 1987) and 18,000 in Ireland (Prater 1981). The Tees estuary supports a population of between 100 and 250. The species exhibits marked sexual dimorphism, the females having on average a 20% longer bill than males (Prater *et al.* 1977). Differentiating larger females from smaller males is possible in the field, based on overall size and bill length. Identifying juveniles is possible in the field using plumage characteristics (Marchant *et al.* 1984). Feeding method is fairly variable; Smith (1973) found that godwits at Lindisfarne, N.E. England used both visual and tactile methods of prey detection. In the former category the appearance of faecal casts of lugworms *Arenicola marina* on the sand surface was used to detect the animal buried below. In the latter category, bivalves were detected by a series of probes into the sediment. Godwits on the Tees tend to rely on tactile prey location, firstly making shallow test probes and then inserting the bill more deeply when an item is located. Unlike the grey plover and the curlew the godwit is not known to defend feeding territories in the wintering grounds. The species is highly gregarious in winter and the Seal Sands population often behaves as a single flock (pers. obs.).

2.4 General Methods.

2.4.1 Shorebird counts

Data on the distribution and numbers of each species within Seal Sands were obtained from counts of mudflat sub-areas, each of which corresponds to broad sediment types (Figure 2.1). These areas were identified using the different appearance of each substrate, aided by natural features such as creeks. An extensive grid of squares 100 m by 100 m formed by colour-coded wooden marker posts covers all but the most inaccessible parts of Seal Sands, and facilitated bird counting and provided consistent sampling sites for a program of invertebrate monitoring which was conducted twice per year - in the early autumn before significant predation by shorebirds had started, and in the early spring when most predation by wintering shorebirds had occurred but just before invertebrate reproduction started.

Bird counts were conducted using a 30x80 telescope, and the distribution and numbers of feeding and roosting individuals of the three study species on the whole of Seal Sands could be recorded in an half hour period during good light and calm wind conditions.

2.4.2 Estimations of prey size.

Two methods were used to estimate the size of *Nereis* that each species fed upon: faecal analysis in which the indigestible jaws of *Nereis* ingested by shorebirds pass into faeces and the length of *Nereis* ingested is estimated from a jaw-length worm-length relationship, and direct observation of length of worms taken in relation to the length of each bird species' bill.

i) Faecal analysis.

Faecal samples of each species were collected from roost sites and feeding sites, and could be assigned to species, given knowledge of feeding distribution, footprint size and shape, and peck marks on the feeding grounds, and species composition and distribution at roost sites. Individual faecal samples were collected with a knife and placed in labelled bottles of 70% alcohol. In the laboratory the contents of each bottle were emptied into a petri dish and examined under a binocular microscope fitted with a graticule. The chitinous jaws of *Nereis* were located in the samples and their maximum lengths were measured to the nearest one hundredth of a mm. It is unlikely that small jaws were overlooked, as scrutiny of samples at high magnification after the initial search revealed no more jaws. A sample of *Nereis* of a range of sizes were taken from Seal Sands, kept in estuarine water at about 5°C and their live un-stretched length measured to the nearest mm. Each worm measured was then dissected to obtain the jaws and these were measured to the nearest one hundredth of a mm. In this way a regression equation of worm length against jaw length was obtained;

worm length (mm.)= -44.5 + 61.1 (jaw length, mm.), where $P<0.0001$

The relationship is shown graphically in Figure 2.2. Worm lengths taken by shorebirds were estimated from the lengths of worm jaws found in their faeces using this equation.

ii) Direct observation.

Estimates of worm length taken by each species were made by comparing the length of a worm being held by a bird prior to ingestion with the (known) length of the bill of the shorebird in question. The categories into which a worm was assigned is given in Table 2.2.

Table 2.2 Categories used in the estimation of worm size in relation to the bill length of curlew, godwit and grey plover.

curlew; mean bill length=120mm.

size category as proportion of bill length	size category (mm.)
0 - 0.25	0 - 30
0.26 - 0.50	31 - 60
0.51 - 0.75	61 - 90
0.76 - 1.00	91 - 120
1.01 - 1.25	121 - 150

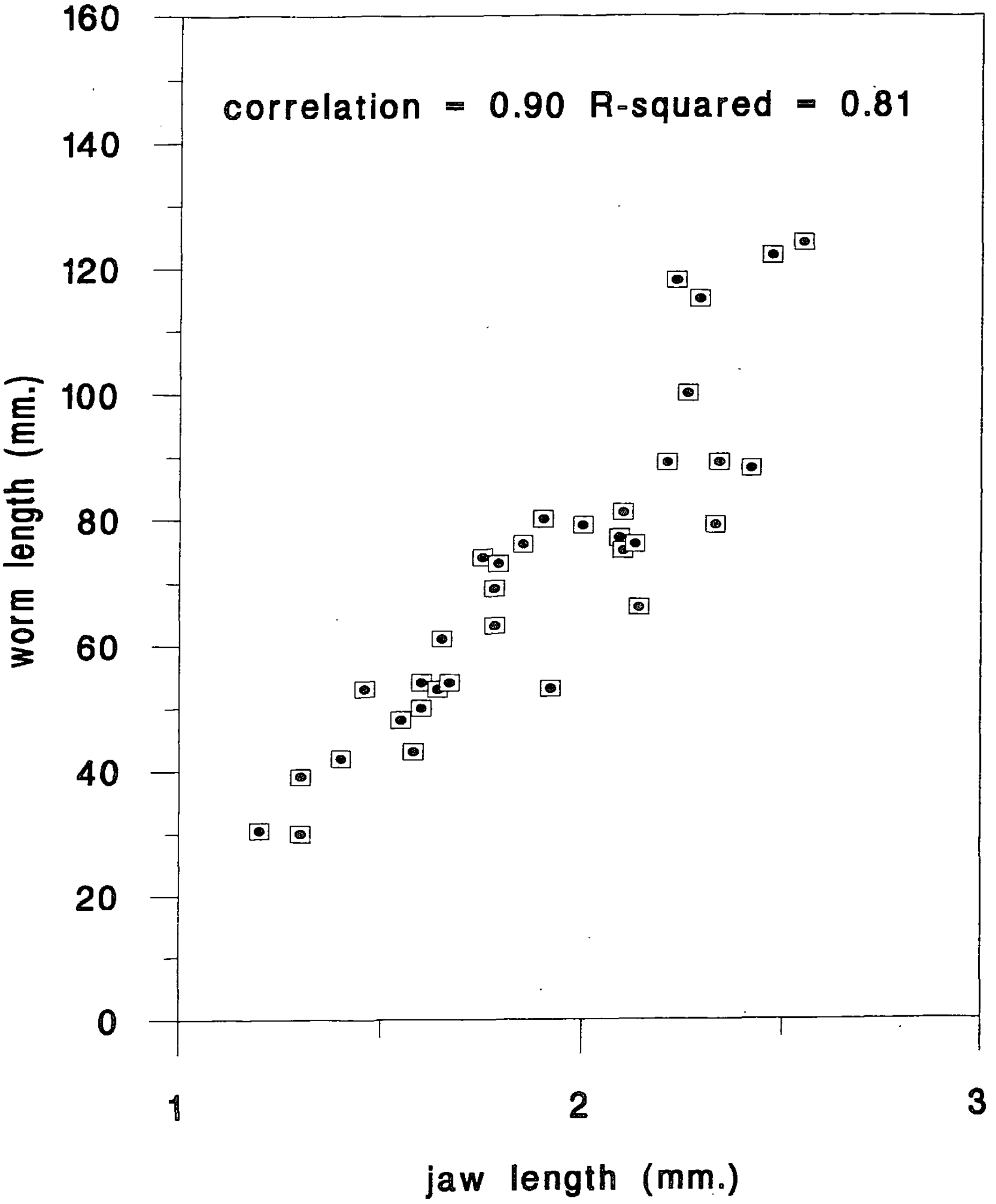
godwit ; mean bill length=92mm.

size category as proportion of bill length	size category (mm.)
0 - 0.25	0 - 23
0.26 - 0.50	24 - 46
0.51 - 0.75	47 - 69
0.76 - 1.00	70 - 92
1.01 - 1.25	93 - 115
1.26 - 1.50	116 - 138

grey plover; mean bill length=30mm.

size category as proportion of bill length	size category (mm.)
0 -0.50	0 - 15
0.51-1.00	16 - 30
1.01 - 1.50	31 - 45
1.51 - 2.00	46 - 60
2.01 - 2.50	61 - 75
2.51 - 3.00	76 - 90

Figure 2.2 The relationship between the maximum jaw length and the total unstretched body length of *Nereis diversicolor*.



In order to test the reliability of the method of estimating worm lengths in relation to bill length, 30 *Nereis* of known length were held with forceps at the tip of the bill of a model curlew by an assistant while I observed from a distance of two hundred metres with the telescope and estimated the length of each worm. This distance is comparable to those encountered in the field. To test reliability of the method for godwit, a pair of forceps 90mm long were used to simulate the birds bill, with each worm held by the "bill" between 45° and 180° to the level of the ground to simulate the angle at whch worms are removed from the substrate. To simulate the bill of grey plover, the forceps were covered by the assistants hand, leaving 30mm protruding - the length of a grey plover's bill. Worms were held in the same way as for the godwit simulation. My estimates of the size class of each worm were later compared to the measured length.

The results for simulated curlew (Table 2.3) indicate that the method gives a reliable estimate of worm size class in the field, with about 83% of worms being categorised successfully. There was no consistent over- or underestimate of worm size (2 underestimates and three overestimates). For simulated godwit, the results were similar (Table 2.4), with 80% of worms being assigned to the correct category, but with the suggestion of a bias towards over-estimation of worm length (4 over-estimates, 2 under-estimates). The sinulated grey plover results (Table 2.5) show the direct observation method was generally reliable (80% correct), but that there was failure to correctly assign some of the largest worms. This is not considered a serious fault, because in practice grey plovers rarely took these large items.

Further tests of the reliability and biases of direct observation are given in chapter four, in which the results of faecal analysis and direct observation are compared

Table 2.3 Reliability of the method of estimating *Nereis* lengths in relation to bill length of curlew. The results of each of 30 comparisons are given in order of presentation to the observer. A tick denotes correct size classification. In cases where the category was miss-classified, the estimated category is given.

actual size category as proportion of bill length	estimated size category as proportion of bill length
0.5 - 0.75	✓
0.5 - 0.75	0.25 - 0.5
0 - 0.25	✓
0.5 - 0.75	✓
0.75 - 1.0	✓
0.5 - 0.75	✓
0 - 0.25	✓
0.75 - 1.0	1.0 - 1.25
0.25 - 0.50	✓
0.25 - 0.50	✓
0 - 0.25	✓
1.0 - 1.25	✓
0.50 - 0.75	✓
0 - 0.25	✓
0.75 - 1.0	✓
0 - 0.25	0.25 - 0.5
0.25 - 0.50	✓
0 - 0.25	✓
0.75 - 1.0	0.5 - 0.75
0.25 - 0.5	✓
0 - 0.25	✓
0.25 - 0.50	✓
0.50 - 0.75	✓
0 - 0.25	✓
0.50 - 0.75	✓
0.25 - 0.5	✓
0.75 - 1.0	✓
0.25 - 0.5	✓
0 - 0.25	✓
0 - 0.25	0.25 - 0.5

Table 2.4 Reliability of the method of estimating *Nereis* lengths in relation to bill length of godwit. The results of each of 30 comparisons are given in order of presentation to the observer. A tick denotes correct size classification. In cases where the category was miss-classified, the estimated category is given.

actual size category as proportion of bill length	estimated size category as proportion of bill length
0.75 - 1.0	✓
0.25 - 0.50	✓
1.0 - 1.25	✓
0.25 - 0.50	✓
0.75 - 1.0	0.50 - 0.75
0 - 0.25	✓
1.0 - 1.25	✓
0.25 - 0.5	✓
0 - 0.25	✓
0.75 - 1.0	1.0 - 1.25
0.50 - 0.75	✓
1.0 - 1.25	✓
1.25 - 1.5	✓
0 - 0.25	✓
0.25 - 0.50	✓
0.50 - 0.75	✓
0.50 - 0.75	0.25 - 0.5
1.0 - 1.25	✓
0.25 - 0.50	0.50 - 0.75
0.50 - 0.75	✓
0.50 - 0.75	✓
0.25 - 0.50	✓
0.50 - 0.75	✓
0.75 - 1.0	✓
0.75 - 1.0	✓
0 - 0.25	0.25 - 0.5
1.0 - 1.25	✓
0.50 - 0.75	0.75 - 1.0
0.25 - 0.50	✓
0.25 - 0.50	✓

Table 2.5 Reliability of the method of estimating *Nereis* lengths in relation to bill length of grey plover. The results of each of 30 comparisons are given in order of presentation to the observer. A tick denotes correct size classification. In cases where the category was miss-classified, the estimated category is given.

actual size category as proportion of bill length	estimated size category as proportion of bill length
0 - 0.50	✓
3.5 - 4.0	✓
1.0 - 1.5	✓
0.5 - 1.0	✓
1.0 - 1.5	0.5 - 1.0
0.5 - 1.0	✓
1.5 - 2.0	1.0 - 1.5
0 - 0.5	✓
3.0 - 3.5	2.5 - 3.0
1.5 - 2.0	✓
2.0 - 2.5	✓
0 - 0.5	✓
2.0 - 2.5	✓
4.0 - 4.5	3.5 - 4.0
0.5 - 1.0	✓
0.5 - 1.0	✓
2.5 - 3.0	✓
2.0 - 2.5	✓
1.5 - 2.0	✓
2.0 - 2.5	3.0 - 3.5
0.5 - 1.0	✓
1.0 - 1.5	✓
0.5 - 1.0	✓
3.0 - 3.5	✓
1.5 - 2.0	✓
3.0 - 3.5	✓
2.5 - 3.0	✓
2.0 - 2.5	✓
3.5 - 4.0	4.0 - 4.5
0.5 - 1.0	✓

2.4.3 Duration of observations for estimating energy intake rates.

It was expected that estimates of mean intake rates of *Nereis* by grey plovers would be heavily dependent on the length of observation period used to obtain the estimate. In order to establish a suitable duration of observation, a "time-true" audio tape recording of pecks, successful prey captures and duration of pacing of foraging grey plovers in the field was made. Six individuals were watched for between 10 and 27 minutes. In the laboratory, the tapes were played back and the number of pecks, prey captures, and duration of pacing were recorded after each minute, until each observation was concluded. For each of the six sample observations, a running mean of each of the variables plotted against time of observation was calculated and graphed. The mean of each of the variables after 0-1min, 0-2 min, 0-3 min and so on was compared to the mean obtained after the whole period of observation. After between five and seven minutes the estimate of each of the variables stabilised to within about ± 10% of the mean obtained after the whole period of observation, and therefore seven minutes was used in all observations of intake rates.

CHAPTER THREE

THE SHOREBIRD ASSEMBLAGE - POTENTIALLY COMPETING SPECIES

3.1 Introduction.

Coastal and estuarine shorebird assemblages in winter in Britain generally comprise ten or so species that co-occur regularly in significant numbers. Certain species are commonly found together in the same broad habitat, for example sandy shore or mudflat, while other combinations of species are rarely encountered, at least on their feeding grounds. Certain species, although occupying the same habitats, do so at different times of year. A further dimension which can segregate species in an ecological sense is the prey species they select.

In the search for competitive interactions among shorebird species it is helpful to concentrate on those species that have the most similar ecologies. In this chapter pairs or groups of potential competitors are identified to provide a focus for more detailed investigations of competitive interactions between species on the Tees Estuary.

3.2 Methods.

The analyses in this chapter can be viewed as a series of "filters" that, from the whole suite of species commonly found on the estuary, sequentially remove from further consideration those pairs of species that are completely segregated or show little overlap along each of 4 resource dimensions. These are, in order; i) timing of use of the Tees estuary by each species through the year; ii) which of the major intertidal areas within and around the estuary are used for foraging; iii) on which different substrates within these areas foraging takes place, and iv) the preferred prey species/taxa of each shorebird species. Of course, this method does not comprehensively describe the multidimensional niche (*sensu* Hutchinson 1957) of each species. Rather, it is intended to focus attention on species pairs which are most similar with respect to the more detailed aspects of winter shorebird ecology. At the end of this "screening" process there will remain groups of species that have the greater potential to compete with each other.

The methods for determining the degree of overlap along each of the dimensions are given below;

1) Degree of temporal overlap of peak numbers on the Tees estuary

High water roost counts from the British Trust for Ornithology's "Birds of Estuaries Enquiry" (BoEE) for the years 1985-91 were used to assess the timing of peak use by eleven shorebird species on the estuary. An objective threshold of abundance was used to establish which species were present at the same time in densities likely to provide opportunities for competitive interactions. For each species of shorebird, the seven-year mean for each month was calculated, and those months in which the mean number exceeded 60% of the year-round maximum were designated "peak months". For species that were present in exceptionally high numbers in only a few months, namely knot, redshank, shelduck and dunlin, the 60% criterion would have eliminated many months in which the numbers of birds were high in absolute terms, and in these species a seven year mean of greater than 500 birds was used to designate months of peak abundance.

The months of peak abundance were compared for pairs of species. Those pairs which had no months in common were assigned an overlap score of 0, while pairs which had one or more months in common were assigned scores thus; 1-2 months shared, score =1; 3-4 months shared, score =2; 5-6 months shared, score =3, and 7-8 months shared, score =4. Pairs which scored 0 were considered to be temporally segregated and therefore the potential for direct interspecific interactions was considered very low; these pairs were eliminated from the following analyses. Pairs which scored 1 or above were overlapping in their use of the estuary, which allows the potential for competitive interactions. The overlap scores between 1 and 4 should not be viewed as a measure of the potential *intensity* of competition, but give an indication of the *duration* of potential interactions between two species on the estuary.

2) Overlap in use of major intertidal areas on and around the estuary.

Overlap in use of broad geographical areas was calculated from monthly low water counts of each species on the four main areas of the estuary; Seal Sands, Bran Sands, the "south side" of the estuary (excluding Bran Sands), and North Gare Sands (see Figure 1.1). The counts (provided by R.M. Ward and L.B. Muirhead) covered the period July 1991 to June 1992, as co-ordinated low-water counts for the whole estuary were available for this year only. Knot, which generally feed at low water on intertidal rocks to the south of the estuary, and move to feed on Seal Sands at mid tide, were generally missed during the low water counts of Seal Sands. In this case it was assumed that all the birds counted on the south side at low tide were present at mid tide on Seal Sands. Counts were transformed to overall density of each shorebird species on each of the sites, using surface area of each site at mean low water, calculated from large scale Ordnance Survey maps. In each site, the combined density of each species pair was calculated (=density of species x plus density of species y) for each of the months of peak abundance, and the highest combined density, D_{max}, used for further analysis Where only one month of overlap occurred, the single figure was used. A threshold combined density, D_{thr}, above which there is greater potential for competitive interactions, was selected as 2 birds/ha. In many cases, although the combined density was well above the threshold, a very large component of that density came from just one species in the pair ; interspecific competitive interactions are less likely in such cases. With this in mind a further restriction was imposed, such that the potential for competitive interactions was considered significant only in pairs in which the density of each species was greater than 1/ha. (and in which the combined density was therefore greater than D_{thr}).

Different criteria were used for species pairs involving ringed or grey plovers, because these visual feeders might suffer from interference in foraging at densities of heterospecifics well below those at which tactilely-foraging species (such as sandpipers) experience interference. To this end, where either of the plovers was one of a species pair, the threshold density for the other (non-plover) species was taken as 0.5/ha., i.e. half that for species in which both members of the pair were tactile feeders. Thus in such cases it was deemed that the potential for competitive interactions was significant in pairs in which the density of the plover species was greater than 1/ha. and in which the density of the non-plover species was greater than 0.5/ha..

Within each of the four sites, species pairs were assigned density overlap scores based on the combined density of birds. Pairs which did not meet the density criteria detailed above scored 0; where the combined density of a pair was 1.6 -4.0/ha., the overlap score was 1; 4.1-7.0/ha., score=2; 7.1-10.0/ha., score=3; >10.0/ha., score=4.

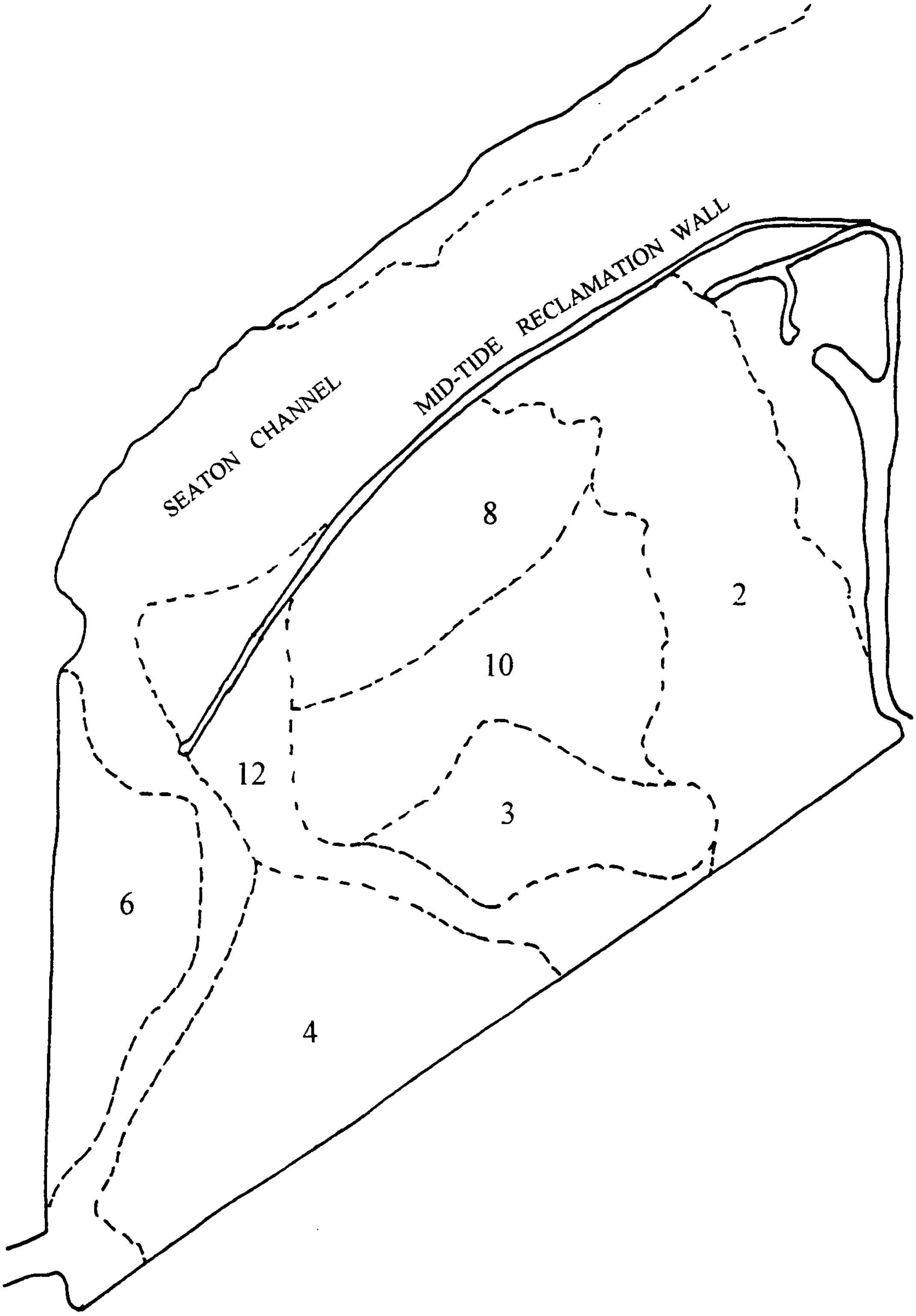
3) Overlap in use of substrate types

Overlap in use of substrate types within the main feeding sites was estimated in two ways. The first method aimed to establish sediment preference and avoidance by each of the species that used Seal Sands as their main feeding site. The other method was less quantitative, but was probably adequate since it concerned four species that used other sites in addition to, or instead of, Seal Sands for feeding; the variety of substrate types on these other sites was much more limited.

On Seal Sands, count areas were chosen that reflect the major sediment types - some areas are predominantly soft or liquid mud, others firmer sandy mud, and others sand with varying small admixtures of mud (Figure 3.1). Sediments were classified using i) results of particle-size analysis from ground sampling of count areas (data supplied by

Figure 3.1 The sediment types of the main shorebird feeding areas of Seal Sands.

The areas consist largely of the following sediment types; 2, 4 and 10 = firm mud; 3 = sand; 6 = soft mud; 8 = sandy mud; 12 = liquid mud.



D.M.N. Donoghue, Y. Zong and R.M. Ward) and ii) judgements gained from walking over count areas. Monthly low water count data between June 1990 and February 1994, collected by R.M. Ward, were analysed, and count area preference indices calculated in the following way :

For each month in each year, the percentage of the Seal Sands total of each species on each of the count areas was calculated. The mean percentage for each month was then calculated for the whole of the survey period.

The percentage of the total surface area of Seal Sands occupied by each count area was then calculated from a map. Finally a preference index, $(O_P - E_P) / E_P$ was calculated for each month, where O_P = observed mean percentage of Seal Sands total for that species that was on the area, and E_P = expected percentage of total on area, given an even density of individuals over the whole of Seal Sands. Values between $^{-}1.0$ and $^{-}0.5$ were taken to indicate avoidance of the area, values between $^{-}0.4$ and +0.5 were taken to indicate use of area in accordance with that expected from random distribution, and values of +0.6 and above were taken to indicate preference for the area.

The area preference indices were then translated into substrate preferences by categorising each of the count areas into a substrate type. The seven count areas were grouped into five substrate types; sand (with various small admixtures of mud), sandy mud, firm mud, soft mud, liquid mud (Figure 3.1). For each of the months of overlap in peak numbers in a species pair, the number of preferred substrate types that were common to both species was determined, and expressed as a proportion of the total number of different preferred substrate types used by the pair. The table below gives an example of this procedure for the pair knot-curlew.

month of overlap in peak numbers	knots' preferred sediments	curlews' preferred sediments	shared ÷ total
December	sandy mud	soft mud, liquid mud	0
January	sandy mud, firm mud	liquid mud firm mud	0.33
February	sandy mud, firm mud	soft mud	0
March	sandy mud	soft mud, liquid mud	0

The mean of the figures in column four of the above table gives a measure of the overlap of preferred substrates of the two species of shorebird during the periods when each species is most numerous. This mean was then assigned an overlap index thus; 0-0.20, score=0; 0.21-0.30, score=1; 0.31-0.40, score=2; 0.41-0.50, score=3; >0.50, score=4. Hence in the above example, the pair knot-curlew, with a mean in column four of 0.08, had an overlap score of 0.

Substrate preferences for species using North Gare Sands or Bran Sands were inferred from the preferences that the species in question showed on Seal Sands.

The substrate preferences of the four species that also used areas other than Seal Sands for feeding (turnstone, sanderling, oystercatcher and knot) were assessed chiefly from anecdotal evidence.

4) Overlap in main prey species consumed.

Overlap indices of main prey species consumed were based on information on the diets of shorebirds and shelduck at Teesmouth published in Brearey (1981), Evans *et al.*

(1979), Pienkowski (1973), and from personal observations of feeding behaviour. Overlap was determined in the following way. An estimate of the proportion of the total number of individuals of each shorebird species that fed to some extent on each prey species was obtained from the literature. A prey species was considered to be "important" in the diet of each shorebird if more than 50% of the total number of individuals examined fed on it. The number of prey species/taxa common to both shorebird species in a pair was then divided by the total number of prey species/taxa important to the pair. If no "important" prey species was common to both shorebird species in a pair, a dietary overlap index of 0 was assigned to the pair. An overlap index of 1 was assigned when the ratio of common prey : total prey was 0.1-0.3; an overlap of 2 when the ratio was 0.4-0.5; an overlap of 3 when the ratio was 0.6-0.7 and an overlap of 4 for a ratio of greater than 0.7.

3.3 Results and discussion.

Table 3.1 gives the species of shorebird that occur regularly in large numbers on the intertidal land between North Gare Breakwater in the N.W and Redcar in the S.E. (Figure 1.1). These species were entered into the analysis to determine pairs of potentially competing species.

The first stage in the analysis compared the temporal use of Teesmouth by each of the shorebird species. Figure 3.2 gives the scores for temporal overlap between pairs of species, and the abundance of each species in each month is summarised in Appendix 1.1. Species pairs that scored zero were eliminated from subsequent analyses, since there was no overlap in the months in which peak numbers occurred. Species pairs that scored from one to four were all entered into subsequent analyses. Certain species pairs involving ringed plover showed low temporal overlap. This is because this plover is abundant only briefly, during spring and autumn passage periods, which are times when

Table 3.1. Commonly-occurring shorebird species of the Tees Estuary and mean number of each during the month of peak abundance†.

COMMON NAME	SCIENTIFIC NAME	MEAN COUNT DURING MONTH OF PEAK ABUNDANCE	STANDARD ERROR
dunlin	*Calidris alpina*	1200 (Aug)	314
knot	*Calidris canutus*	3200 (Jan)	862
sanderling	*Calidris alba*	270 (May)	59
redshank	*Tringa totanus*	1300 (Aug)	115
curlew	*Numenius arquata*	490 (Jan)	83
bar-tailed godwit	*Limosa lapponica*	240 (Jan)	59
ringed plover	*Charadrius hiaticula*	310 (May)	52
grey plover	*Pluvialis squatarola*	125 (Mar)	32
turnstone	*Arenaria interpres*	175 (Nov)	54
oystercatcher	*Haematopus ostralegus*	750 (Nov)	161
shelduck*	*Tadorna tadorna*	1300 (Jan)	106

† Mean shorebird numbers from "Birds of Estuaries" counts 1985-91.

* Shelduck has been included because it is ecologically similar to shorebirds.

Figure 3.2 Temporal overlap in peak numbers of eleven species of shorebirds on the Tees Estuary.

Two letter codes for species are as follows; OC oystercatcher; RP ringed plover; GV grey plover; KN knot; SA sanderling; DN dunlin; TN turnstone; SH shelduck; BA bar-tailed godwit; CU curlew; RK redshank. 0 and 4 indicate no overlap and maximum overlap, respectively. For details, see text.

RP	1									
GV	2	0								
KN	3	0	2							
SA	2	1	1	1						
DN	4	1	2	2	2					
TN	2	0	1	1	1	2				
SH	3	0	2	3	1	3	1			
BA	2	0	2	2	0	2	1	2		
CU	3	1	2	3	2	4	2	3	2	
RK	3	1	2	2	2	4	1	2	1	4
	OC	RP	GV	KN	SA	DN	TN	SH	BA	CU

species such as grey plover, knot, shelduck and godwit are not usually abundant (see Appendix 1.1). Most other species showed at least some degree of overlap in the months of their peak abundance, which is the first necessary condition for interspecific interactions.

Forty-nine (out of the total of 55) pairs of species were entered into the next stage of the analysis, which identified, for species pairs, the degree of spatial overlap in use of major intertidal areas on and around the estuary (Figure 3.3a-d). The densities of each species on each of the feeding sites is given in Appendix 1.2.

Certain species, such as curlew, grey plover and shelduck, fed away from Seal Sands on other intertidal areas only occasionally, while others, such as sanderling, turnstone and oystercatcher, fed mainly on the intertidal areas outside the estuary to the south of the river Tees. Seal Sands held the highest densities of many species of waders, as reflected by the number of species pairs that exceeded the density threshold (Figure 3.3a). Turnstone, sanderling and oystercatcher were present usually in low densities on Seal Sands, but the latter two species occurred at much higher densities on Bran Sands (Figure 3.3c) and the area to the south of the estuary (Figure 3.3d). Bran sands held moderate densities of ringed plovers but (unlike Seal Sands) only low densities of grey plovers.

Although the density of turnstone on the south side was below the threshold used to identify potential competitors (see Appendix 1.2), this species often shows a localised distribution, with temporary concentrations on the intertidal rocks and on the strand line. In view of this, the pairs knot-turnstone, sanderling-turnstone and oystercatcher-turnstone have been assigned an overlap score of 2.

Figure 3.3a Spatial overlap between eleven species of shorebirds on Seal Sands.

Shaded cells show pairs of species that were eliminated in the previous analysis. Two letter codes for species are as follows; OC oystercatcher; RP ringed plover; GV grey plover; KN knot; SA sanderling; DN dunlin; TN turnstone; SH shelduck; BA bar-tailed godwit; CU curlew; RK redshank. 0 = no overlap. For definitions of other degrees of overlap, see text.

	OC	RP	GV	KN	SA	DN	TN	SH	BA	CU
RP	1									
GV	1	▨								
KN	0	▨	2							
SA	0	0	0	0						
DN	0	4	4	4	0					
TN	0	▨	0	0	0	0				
SH	0	▨	3	3	0	4	0			
BA	0	▨	1	2	▨	4	0	3		
CU	0	2	2	3	0	4	0	3	1	
RK	0	3	1	3	0	4	0	3	1	4

Figure 3.3b Spatial overlap between eleven species of shorebirds on North Gare.

For key see Figure3.3a.

	OC	RP	GV	KN	SA	DN	TN	SH	BA	CU
RP	0									
GV	0	▨								
KN	0	▨	0							
SA	0	0	0	0						
DN	0	1	0	0	2					
TN	0	▨	0	0	0	0				
SH	0	▨	0	0	0	0	0			
BA	0	▨	0	0	▨	0	0	0		
CU	0	0	0	0	0	0	0	0	0	
RK	0	0	0	0	2	1	0	0	0	0

Figure 3.3c Spatial overlap between eleven species of shorebirds on Bran Sands.

For key see Figure 3.3a.

RP	0									
GV	0	▨								
KN	0	▨	0							
SA	0	2	0	0						
DN	0	2	0	0	2					
TN	0	▨	0	0	0	0				
SH	0	▨	0	0	0	0	0			
BA	3	▨	0	0	▨	0	0	0		
CU	0	1	0	0	1	2	0	0	0	
RK	1	2	0	0	1	2	0	0	0	1
	OC	RP	GV	KN	SA	DN	TN	SH	BA	CU

Figure 3.3d Spatial overlap between eleven species of shorebirds on the South Side.

For key see Figure 3.3a.

RP	0									
GV	0	▨								
KN	2	▨	0							
SA	1	0	0	2						
DN	0	0	0	0	0					
TN	2	▨	0	2	2	0				
SH	0	▨	0	0	0	0	0			
BA	0	▨	0	0	▨	0	0	0		
CU	0	0	0	0	0	0	0	0	0	
RK	0	0	0	0	0	0	0	0	0	0
	OC	RP	GV	KN	SA	DN	TN	SH	BA	CU

The number of species pairs that exceeded the density threshold was relatively low on North Gare Sands (Figure 3.3b), reflecting the marginality of this area as a low-water feeding site for shorebirds.

The feeding distribution of knot on the Tees needs special mention, because most individuals use two main feeding areas during a single period of exposure. Between about two hours before and two hours after low water, knot feed on the rocks and sea beaches to the south of the estuary to take advantage of food resources exposed only when the tide approaches its lowest ebb. The remainder of the period of exposure is spent feeding on Seal Sands. Flocks of knot fly between these two feeding sites at about mid tide. Spatial overlap involving knot on Seal Sands and on the south side is therefore high at certain states of the tide but low at others. This partial overlap would have the effect of reducing the duration of competitive interactions between such species, although the intensity of interactions could be high.

The next stage of the analysis assessed the degree of overlap in use of different substrate types within particular geographical areas of the estuary (Figure 3.4a-d, and Appendix 1.3 for individual preference indices).

Many species showed preferences for certain substrate types within a site, although some species, such as shelduck, grey plover and godwit used both soft and firmer/sandier substrate types (Table 3.2). Dunlin, redshank, shelduck, godwit and curlew showed preferences for the softer muds, and overlap occurred between these species. Ringed and grey plovers and knot (when present on Seal Sands) generally preferred firmer muds and sandy muds, as also did shelduck when they fed on invertebrates associated with areas of the alga *Enteromorpha*, which occurs on some of the more sandy substrates. Note that although the counts did not indicate a preference by grey plover for area 6 (soft mud) at low water during some months (Appendix 1.3), this substrate was favoured on the rising tide, and therefore has been categorised as "preferred" (Table 3.2). Since

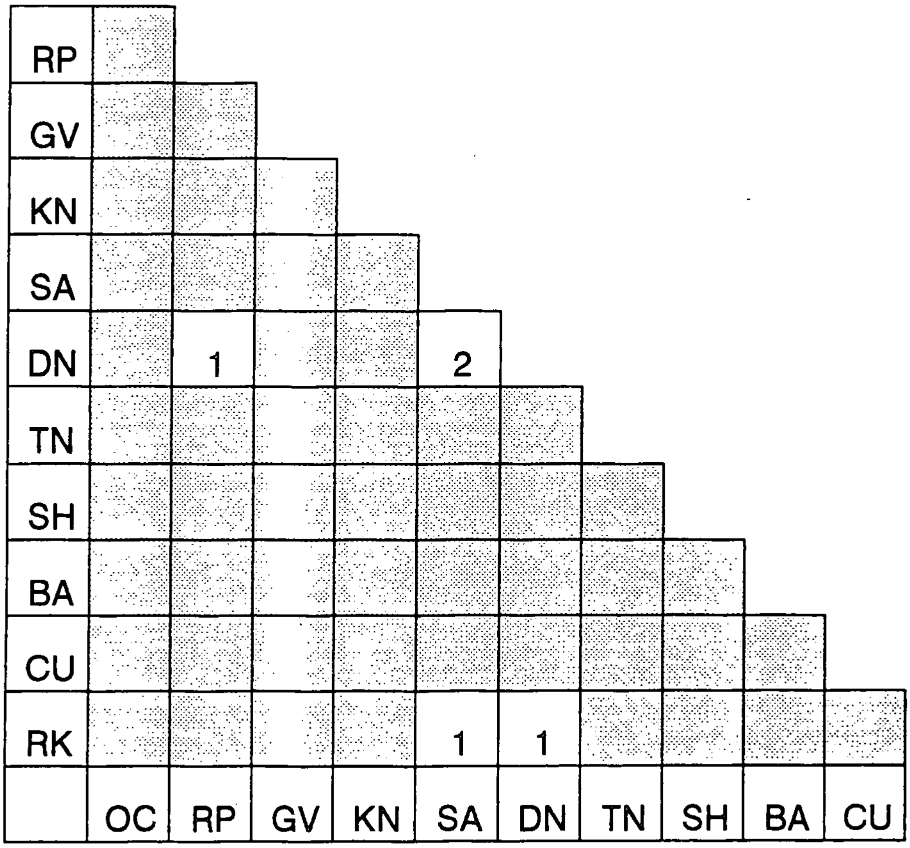
Figure 3.4a Overlap in the use of substrate types between eleven species of shorebirds on Seal Sands.

Shaded cells show pairs of species that were eliminated in the previous analysis. Two letter codes for species are as follows; OC oystercatcher; RP ringed plover; GV grey plover; KN knot; SA sanderling; DN dunlin; TN turnstone; SH shelduck; BA bar-tailed godwit; CU curlew; RK redshank. 0 = no overlap. For definitions of other degrees of overlap, see text.

RP	0									
GV	2	▨								
KN	▨	▨	3							
SA	▨	▨	▨	▨						
DN	▨	0	1	1	▨					
TN	▨	▨	▨	▨	▨	▨				
SH	▨	▨	1	4	▨	1	▨			
BA	▨	▨	1	0	▨	2	▨	4		
CU	▨	0	2	0	▨	4	▨	1	4	
RK	▨	0	2	1	▨	1	▨	0	2	4
	OC	RP	GV	KN	SA	DN	TN	SH	BA	CU

Figure 3.4b Overlap in the use of substrate types between eleven species of shorebirds on North Gare Sands.

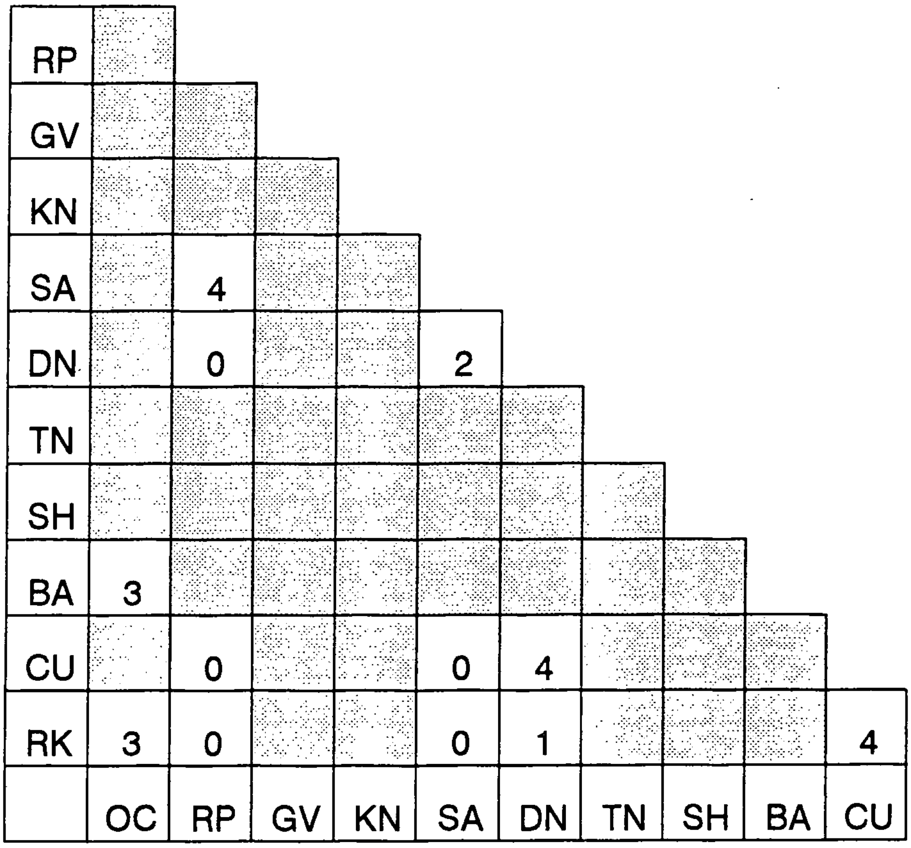
For key see Figure 3.4a.



	OC	RP	GV	KN	SA	DN	TN	SH	BA	CU
RP										
GV										
KN										
SA										
DN		1			2					
TN										
SH										
BA										
CU										
RK					1	1				

Figure 3.4c <u>Overlap in the use of substrate types between eleven species of shorebirds on Bran Sands</u>.

For key see Figure 3.4a.



RP	▨									
GV	▨	▨								
KN	▨	▨	▨							
SA	▨	4	▨	▨						
DN	▨	0	▨	▨	2					
TN	▨	▨	▨	▨	▨	▨				
SH	▨	▨	▨	▨	▨	▨	▨			
BA	3	▨	▨	▨	▨	▨	▨	▨		
CU	▨	0	▨	▨	0	4	▨	▨	▨	
RK	3	0	▨	▨	0	1	▨	▨	▨	4
	OC	RP	GV	KN	SA	DN	TN	SH	BA	CU

Figure 3.4d Overlap in the use of substrate types between eleven species of shorebirds on the South Side.

For key see Figure 3.4a.

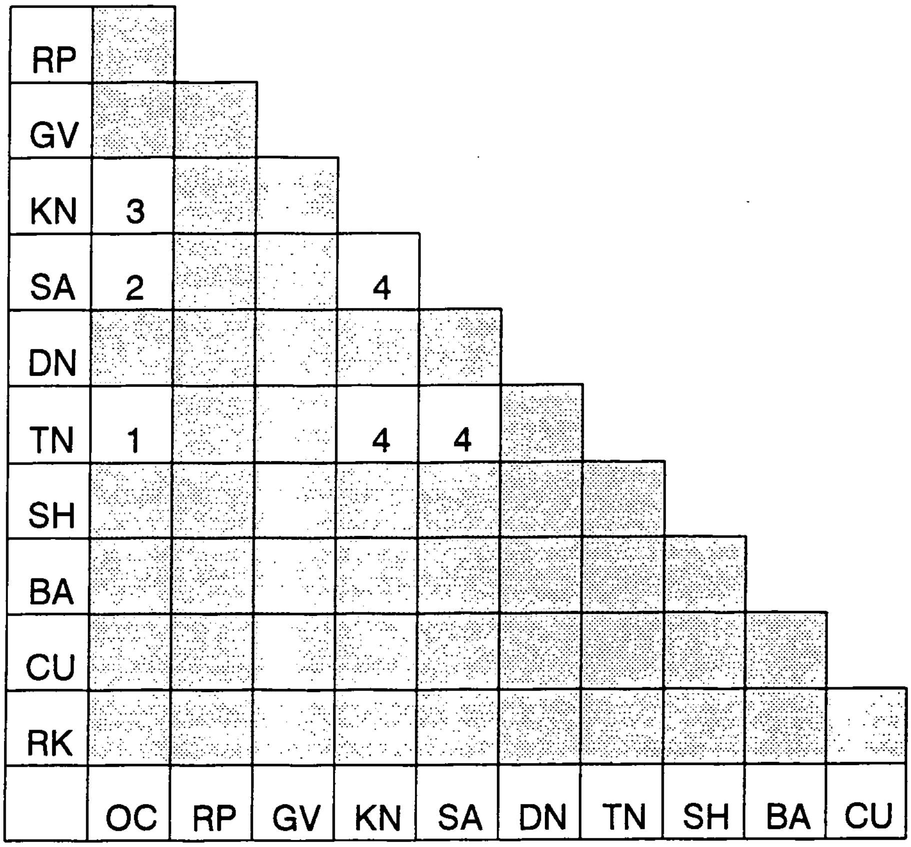


Table 3.2 The preferred substrate types of shorebirds on and around the Tees estuary.

Most species were concentrated on Seal Sands, and for these species substrate preferences for this and additonal feeding sites were based on distributional data from Seal Sands. Some species were found in high densities on the south side (which consisted of substrates unique to that site) as well as on other sites, and this is indicated in the table.

SPECIES	PREFERRED SUBSTRATES
ringed plover	sand, sandy mud
grey plover	sandy mud, firm mud, soft mud
knot	sandy mud, firm mud (Seal Sands) strand line, intertidal rocks (south Tees)
sanderling	sand, sandy mud, firm mud (Seal Sands) open sandy beach, intertidal rocks, strand line (south Tees)
dunlin	firm mud, soft mud, liquid mud,
turnstone	intertidal rocks, strand line (south Tees)
shelduck	liquid mud, sandy mud with *Enteromorpha* cover
godwit	sandy mud, soft mud, liquid mud
curlew	soft mud, liquid mud
redshank	firm mud, soft mud, liquid mud
oystercatcher	sand, sandy mud, firm mud (Seal Sands) intertidal rocks (south Tees)

the pairs ringed plover-grey plover and ringed plover-knot are segregated temporally (Figure 3.2), there is little potential for competition between these species. However knot, shelduck and grey plover are found on the estuary in high numbers in similar months and show overlap in the substrates on which they prefer to feed on Seal Sands (Figure 3.4a), which indicates the potential for competitive interactions between these species. Grey plover also overlap with curlew, dunlin, oystercatcher, godwit and redshank in their preferred substrates on Seal Sands (Figure 3.4a). There is therefore the potential for competitive interactions between grey plovers and these species.

On North Gare Sands substrate overlap occurred between the pairs dunlin-sanderling and dunlin-redshank, but both dunlin-ringed plover and sanderling-redshank were scored 0 on the basis of their substrate preference on Seal Sands. However, since in reality there is little opportunity for segregation of species by substrate type on North Gare Sands - a rather homogeneous site, it is still possible that competition could occur in these two pairs of species, which were assigned an overlap score of 1 (Figure 3.4b).

On Bran Sands, during certain times of year, sanderling are present with curlew, dunlin and redshank in densities that might be thought high enough to elicit competition. However, sanderling overlap only with dunlin in their preferred substrate types (Figure 3.4c).

On the south side of the estuary there is substrate overlap between the species pairs that occur in densities above the threshold, namely knot-oystercatcher, knot-sanderling, knot-turnstone, turnstone-oystercatcher, turnstone-sanderling and sanderling-oystercatcher (Figure 3.4d). Knot, turnstone and sanderling commonly used more than one substrate type during any one low water period. Knot spent most of their feeding time while on the south side of the estuary on the mussel beds of Redcar and Coatham Rocks, but also fed among the strand line when this habitat was available. Turnstones are opportunists and fed wherever there was suitable food - on the mussel beds (often taking the scraps of mussels left over by oystercatchers), among the strand line, or on sparsely distributed items washed up on the sea beaches. Sanderling, while specialists of open wave-washed beaches, also fed on invertebrates among the mussel beds as well as on the strand line. Oystercatchers are specialist mussel-feeders and therefore were largely restricted to the mussel beds of Redcar and Coatham Rocks.

The final stage of the analysis determined the degree of dietary overlap between species, based on the major prey taxa taken. Table 3.3 summarises the preferred prey of each species of shorebird, and Figures 3.5a-d show the overlap scores for each feeding site. Because the invertebrate macrofauna of the Tees estuary is fairly poor in species, particularly on Seal Sands where the only common large species is *Nereis diversicolor*, there is little opportunity for segregation of similarly sized shorebird species by prey taken. Most segregation, therefore, was a result of the tendency for differently sized shorebirds to feed on different sized prey species. For example, the dunlin (mean mass about 50 g) forages on small prey items, whereas the much larger curlew (mean mass about 800 g) feeds exclusively on large prey species. On Seal Sands the three large shorebirds (curlew, godwit and grey plover) took mainly *Nereis*, and high overlap occurred between these species (Figure 3.5a). The distinctly smaller species (dunlin, ringed plover, knot and redshank) fed on a range of small prey taxa such as small oligochaetes, the gastropod *Hydrobia*, and the amphipod *Corophium* ; a relatively small proportion of their diet consisted of *Nereis* (Evans *et al.* 1979). The shelduck, although a heavier bird than even the curlew, fed generally on small invertebrates such as oligochaetes and *Hydrobia* and took relatively few large species such as *Nereis*. It is able to attain a sufficient rate of energy intake from these small items because its "sieving" method of feeding in mud allows very large numbers of prey items to be ingested per unit of time. Its dietary overlap was therefore high with relatively small shorebirds such as dunlin, knot and grey plover (Figure 3.5a).

Table 3.3 The preferred prey taxa of shorebirds on and around the Tees Estuary.

Information on diets obtained from Evans *et al.* (1979), Brearey (1981), Pienkowski (1973) and from personal observations of feeding behaviour. N.B. Where the prey "*Nereis*" is mentioned in the table, the species is *diversicolor*, unless otherwise stated.

SHOREBIRD	PREFERRED PREY
ringed plover	*Corophium, Nereis*
grey plover	*Nereis, Hydrobia*
knot	*Hydbrobia, Macoma balthica* (Seal Sands) *Mytilus, Talitrus/Orchestia,* wrack flies (south Tees)
sanderling	*Corophium, Nereis* (Seal Sands) *Nerine, Bathyporeia/Eurydice, Mytilus, Talitrus/Orchestia,* wrack flies (south Tees)
dunlin	*Hydrobia, Nereis,* small oligochates
turnstone	*Mytilus, Balanus, Talitrus/Orchestia,* wrack flies
shelduck	small oligochates, *Hydrobia, Macoma*
godwit	*Nereis, Macoma*
curlew	*Nereis*
redshank	*Nereis, Hydrobia, Macoma*
oystercatcher	*Nereis, Macoma* (Seal Sands) *Mytilus, Nereis virens* (south Tees)

Figure 3.5a Overlap in main prey species consumed between eleven species of shorebirds on Seal Sands.

Shaded cells show pairs of species that were eliminated in the previous analysis. Two letter codes for species are as follows; OC oystercatcher; RP ringed plover; GV grey plover; KN knot; SA sanderling; DN dunlin; TN turnstone; SH shellduck; BA bar-tailed godwit; CU curlew; RK redshank. 0 = no overlap. For definitions of other degrees of overlap, see text.

RP	▨									
GV	1	▨								
KN	▨	▨	2							
SA	▨	▨	▨	▨						
DN	▨	▨	4	1	▨					
TN	▨	▨	▨	▨	▨	▨				
SH	▨	▨	1	4	▨	3	▨			
BA	▨	▨	1	▨	▨	1	▨	1		
CU	▨	▨	3	▨	▨	2	▨	0	2	
RK	▨	▨	▨	4	▨	3	▨	▨	3	2
	OC	RP	GV	KN	SA	DN	TN	SH	BA	CU

Figure 3.5b Overlap in main prey species consumed between eleven species of shorebirds on North Gare Sands.

For key see Figure 3.5a

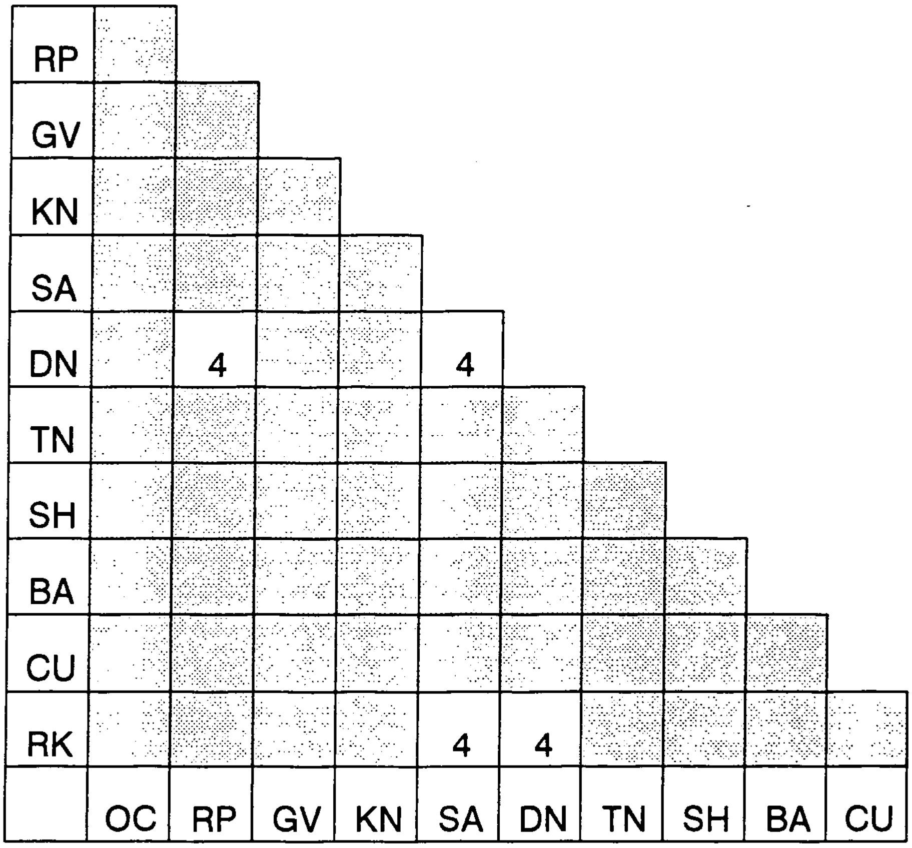


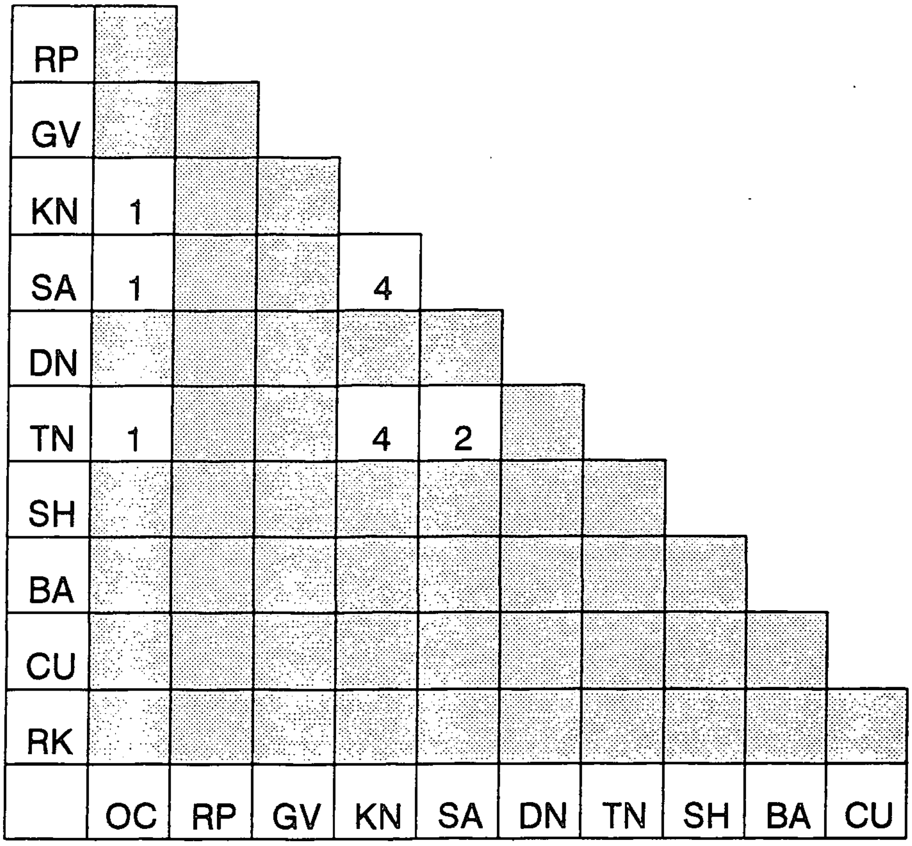
Figure 3.5c Overlap in main prey species consumed between eleven species of shorebirds on Bran Sands.

For key see Figure 3.5a

RP	▨									
GV	▨	▨								
KN	▨	▨	▨							
SA	▨	4	▨	▨						
DN	▨	▨	▨	▨	1					
TN	▨	▨	▨	▨	▨	▨				
SH	▨	▨	▨	▨	▨	▨	▨			
BA	4	▨	▨	▨	▨	▨	▨	▨		
CU	▨	▨	▨	▨	▨	2	▨	▨	▨	
RK	4	▨	▨	▨	▨	3	▨	▨	▨	2
	OC	RP	GV	KN	SA	DN	TN	SH	BA	CU

Figure 3.5d Overlap in main prey species consumed between eleven species of shorebirds on the South Side.

For key see Figure 3.5a



RP	▨									
GV	▨	▨								
KN	1	▨	▨							
SA	1	▨	▨	4						
DN	▨	▨	▨	▨	▨					
TN	1	▨	▨	4	2	▨				
SH	▨	▨	▨	▨	▨	▨	▨			
BA	▨	▨	▨	▨	▨	▨	▨	▨		
CU	▨	▨	▨	▨	▨	▨	▨	▨	▨	
RK	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨
	OC	RP	GV	KN	SA	DN	TN	SH	BA	CU

Dietary overlap occurred between all the species that occurred on similar substrates on the south side of the estuary (Figure 3.5d).

Knot feeding on Seal Sands overlap with grey plover because the diet of both these species includes *Hydrobia* and *Nereis* - knot largely the former, grey plover largely the latter. However, they are present together only at around mid-tide on Seal Sands.

The four stages of analysis have therefore identified 29 pairs of species for which further study may be warranted (Table 3.4). However, it is unlikely that competitive interactions could occur within all these pairs of species, since the criteria for inclusion were probably conservative. Three groups of species are considered of particular interest, and corroborative evidence for the potential for competition within these groups was added from personal observations not formally integrated into the 4-stage analysis, as well as evidence from published studies;

1) Knot, turnstone, sanderling and oystercatcher on the rocks on the south side of the estuary. These four species, although distributed widely and at varying densities over the whole of the south side, occur at particularly high densities on the intertidal rocks, where the abundance of *Mytilus* attracts all four species. In particular, combined densities of birds may be especially high during neap low waters, when the area of rocks exposed is greatly reduced. It is possible that the arrival of large flocks of knot from Seal Sands at around mid-tide on the ebb could displace feeding sanderling and turnstone from the rocks (interference competition) and force them onto less favoured feeding areas. Although it is unlikely that flocks of knot could displace the much larger oystercatcher from the mussel beds, both species feed predominantly on *Mytilus,* which could lead to depletion competition.

2) Grey plover, godwit and curlew on Seal Sands. This group is of special interest because; a) all three species rely on *Nereis* for the majority of their energy intake on the

Table 3.4. Potentially competing shorebird species on the Tees estuary.

Only those species found to be potential competitors are shown. An asterisk denotes the site(s) in which interactions are most likely. SS=Seal Sands; NG=North Gare Sands; BS=Bran Sands; ST=south Tees.

POTENTIALLY COMPETING PAIR	SS	NG	BS	ST
knot - oystercatcher				*
sanderling - oystercatcher				*
sanderling - knot				*
turnstone - oystercatcher				*
godwit - oystercatcher			*	
redshank - oystercatcher			*	
sanderling - ringed plover			*	
dunlin - ringed plover		*		
knot - grey plover	*			
dunlin - grey plover	*			
shelduck - grey plover	*			
curlew - grey plover	*			
dunlin - knot	*			
grey plover - oystercatcher	*			
godwit - grey plover	*			
godwit - dunlin	*			
godwit - shelduck	*			
curlew - godwit	*			
redshank - godwit	*			

Table 3.4 (continued).

POTENTIALLY COMPETING PAIR	SS	NG	BS	ST
turnstone - knot				*
shelduck - knot	*			
redshank - knot	*			
dunlin - sanderling		*	*	
turnstone - sanderling				*
redshank - sanderling		*		
shelduck - dunlin	*			
curlew - dunlin	*		*	
redshank - dunlin	*	*	*	
redshank - curlew	*		*	

Tees estuary and past work (Evans *et al* 1979) suggested that each concentrated upon the large size class, suggesting the potential for depletion of the preferred prey stock, and b) grey plovers detect their prey largely by visual means that requires them to be free from disturbance while foraging; they may therefore experience interference from species (curlew and godwit) that occur on their feeding sites in denser aggregations.

3) Dunlin, redshank and shelduck on Seal Sands. The species of this group are of interest because of their distinct preference for areas of soft mud, especially near the receding tide edge. Past work suggested that competitive interactions might occur between shelduck and dunlin, because influxes of shelduck coincided with reductions in the numbers of dunlin on Seal Sands (Evans 1979). Also, Moumoutzi (1977) showed that widely-dispersed feeding redshank may be displaced by compact feeding flocks of dunlin on Seal Sands.

3.4 Conclusions.

This semi-quantitative analysis has highlighted groups of species which are most similar with respect to the more detailed aspects of their ecologies, but no conclusions about the prevalence or the intensity of competitive interactions between the highlighted species should be inferred. The analysis, because of its approach in describing the general, may in some cases overlook important subtleties. For example, even shorebird species which feed on entirely different species of prey may interfere with the detection and capture of each other's prey if the two species occur on the same feeding sites at the same time. Conversely two shorebird species that feed exclusively on the same prey species taken from the same areas may avoid direct competition if one species feeds largely on a small size class and the other feeds predominantly on the large size class, but in this case indirect (asymmetric) competition could occur if the species taking the small worms so deplete that size class in one winter that the abundance of large worms - the preferred prey of other species - in the following winter is reduced. However, such details are beyond the scope of the above analyses; they are dealt with more fully in the following chapters, which investigate interactions between curlew, godwit and grey plover on Seal Sands. Interactions between knot, turnstone, sanderling and oystercatcher on Redcar and Coatham Rocks are described in Chapter 7.

CHAPTER FOUR

COMPETITION FOR FOOD

4.1 Introduction.

Competition for food can occur in two broad ways; by interference, where an individual's access to a food resource is limited, or when its feeding efficiency is hindered by the presence of other individuals; and by depletion when one individual removes part of the resource itself and deprives another of its needs.

If several shorebird species feed largely on the same prey species then depletion could limit the population densities of some or all of the predator species at levels below those which could be sustained if each shorebird species fed on different prey species. However, if each species concentrated its feeding on different *sizes* of that common prey, then such resource partitioning would allow direct competition to be avoided. But even if different shorebird species take different and discrete sizes of a single prey species, indirect competition might not be avoided because *successive* depletion of the food stock could occur over a period of a few years. Zwarts and Wanink (1984) studied this phenomenon on mudflats of the Fresian coast of the Netherlands and showed that clams *Mya arenaria* in their first winter were below the acceptance size threshold of oystercatchers. Only during their second winter did they become suitable for oystercatchers and only in the following year did they become profitable for curlews. This resulted in the successive depletion of clams over two winters; in the first winter of predation oystercatchers fed on the cohort and in the second winter curlew fed on the remaining animals. The authors suggested that oystercatchers could so deplete the stocks of *Mya* in one winter that in the following winter curlew experienced a shortage of the size class suitable for them.

If prey depletion is not important, competition could still occur if the presence of one species adversely affects the prey intake rate of another species. For example, it has been postulated (Pienkowski 1979) that grey plovers may avoid high concentrations of other shorebirds because they rely largely on visual methods of prey location and require a relatively large open space to scan for prey movements on the sediment surface. Food stealing (kleptoparasitism) and fighting over food items are other forms of such interference competition and could lead to a decrease in the prey biomass intake rate of the "victim", although stealing and fighting may be detrimental to both parties if the energy expended in being aggressive exceeds energy gained in a certain time period (Kushlan 1979).

There is a great deal of literature that documents the ways in which differences in morphology between closely related bird species affect the type and size of food items that they eat. Perhaps the most obvious and frequently studied feature in this respect is the size of mouthparts, as this is thought to directly limit the size of prey item that can be handled efficiently. The classic work of Lack (1947), for example, showed how marked differences in the beak morphology of Darwin's finches were strongly correlated with differences in their feeding habits. Recher (1966) and Baker and Baker (1973) provided some of the earlier considerations of how bill morphology relates to foraging behaviour and resource partitioning in shorebirds.

This chapter examines the importance of the processes described in the preceding paragraphs, in curlew, godwit and grey plover feeding on a diet dominated by the polychaete worm *Nereis diversicolor*. On Seal Sands this animal has a two year life-cycle, with spawning occurring in May and early June, but with few juveniles settling in the substratum before September. Growth of 0-1 year old animals is rapid until October but then ceases until April when further growth occurs through the summer. The following spring the 1+ year old animals reproduce and then die (Evans *et al.*1979).

Firstly in this chapter I shall describe observations I undertook to determine the size classes of prey taken by each shorebird species in order to see if resource partitioning was occurring. Secondly I estimate the extent of depletion of the prey stock. Finally I shall present data on aggressive interactions between the three shorebird species.

4.2 METHODS

The sizes of ragworms *Nereis diversicolor* taken by each shorebird species were estimated by two methods; i) faecal analysis, whereby the indigestible jaws of the worms recovered in faeces were measured and translated into worm length using a jaw size - worm length equation, and ii) direct estimation in the field, by assessing the length of a captured worm in relation to the (known) length of the bird's bill. Details of each of these methods were given in chapter 2. Although the direct method of observation has the advantage over faecal analysis in that estimates of the size of prey of age/sex groups within species can be obtained, the method is prone to errors resulting from missing very small prey items as they are taken by birds, which can lead to an under-estimation of the importance of these sizes in the diet. Pienkowski (1982) used detailed analysis of cine film of feeding grey plovers and found that when the film was analysed frame by frame, behaviours that he attributed to unsuccessful attempts at prey capture at normal speed were actually captures of very small worms. In order to investigate whether my observations were under-estimating the proportion of small worms in the diet, faecal analysis was undertaken for each shorebird species and the results obtained by the two methods were compared. Note that for the direct observation method, one "observation" means one worm taken, although number of worms taken by the individual being watched varied from one to twelve, depending on the frequency of capture (which was variable) and length of observation of the individual (which was generally about five minutes). Whilst there are insufficient data per individual to test for any variation between individuals of a given species/sex/age group in the size of *Nereis* taken, variation in morphological and behavioural traits (which are thought to largely control the size of prey taken) is likely to be far less between individuals within an age and/or sex group than between groups, which is the feature of interest here.

Faecal samples were collected both from roost sites and feeding sites. I was careful to ensure that I did not mistakenly collect faeces of other species of shorebirds. This was possible because i) samples were collected from roosts that were watched during roost formation and ii) samples were taken from roosts that contained only the species of interest. Collection of faeces from the feeding grounds was more problematic, but with practice and knowledge of the size, shape, stride length, and peck marks of the trails of each shorebird, their faeces could be identified with confidence.

Estimates of rates of aggression were made using Focal Animal Sampling (Altmann 1974) whereby I focused on a randomly chosen animal and followed it for a minimum of five minutes, during which the number and type of any encounters - whether territorial aggression, non-territorial aggression, or food stealing - and the species identity of the aggressor and victim were noted. Clearly, during a period of sampling the focal animal could be both the giver and receiver of aggressive behaviours. If the focal animal was lost from sight before five minutes had elapsed, data collected from it were discarded and another individual was selected for observation.

4.3 Does each species of shorebird feed on the same size of ragworm or is there partitioning of the food resource?

4.3.1 Introduction.

The advantage of the direct observation method over faecal analysis is that the age and sex of the bird being watched can often be identified. This enables a more revealing analysis to be undertaken, for there are good reasons to expect differences in foraging behaviour within species (see below). In addition, when samples have been divided into age/sex groups within species, possible seasonal changes in the size of *Nereis* taken can be looked for. This analysis is necessary before species comparisons are made using the whole data set for a species, because one might expect seasonal changes in the density of available prey of each size class. Firstly, there is the possibility that selective depletion of certain size classes of worm by shorebirds (not just the three study species) during the first part of the winter (September to December) will result in a paucity of those sizes of worm later in the winter (January to March) since very little body growth or recruitment of *Nereis* occurs during the winter (Evans *et al.* 1979). Significant depletion of the infaunal food stock can occur, as has been shown by several workers (e.g. Goss-Custard 1969; Smit 1981; Zwarts and Drent 1981; Zwarts and Wanink 1984). Secondly there are thought to be temperature dependent effects on prey availability, which increase the burrowing depth of polychaete worms at low temperatures and reduce surface activity, especially of the larger individuals (Evans 1976, Pienkowski 1983). These would lead to a reduction in the proportion of large worms that are available to all three shorebird species during the part of the winter when air and sea temperatures are expected to be lowest (January to March).

When considering interspecific differences in morphology and hence foraging behaviour it is necessary to be aware that differences may also exist within a species. This has an important bearing on interspecific competition, for overlap in prey sizes taken (and therefore competition) may occur only between certain age or sex categories within the population of two species.

Sexual dimorphism within species often has implications for the type and size of food items that can be handled by the sexes, even if the difference between sexes might appear to be slight. For example, Newton (1967) showed that the bill of the male goldfinch *Carduelis carduelis* averaged about one millimetre longer than that of the female, a difference that was sufficient to allow males to successfully exploit the seeds of the teasel *Dipsacus fullonum* but prevent females from doing so. Selander (1966) showed how marked sexual dimorphism in the woodpecker *Centurus striatus* (the bill of the male averages 21% longer, and the tongue 34% longer, than that of the female) led to distinct differences in the foraging behaviour of the sexes. The males tended to probe into tree crevices while the females picked from the bark surface. Similarly, Holyoak (1970) found that male carrion crows *Corvus corone,* which had bills about 8% longer than the females, probed more deeply into soil and caught larger prey items than did females. Some groups of birds, such as shorebirds (Charadrii) and birds of prey (Falconiformes), exhibit so-called reversed sexual dimorphism, in which the female is larger than the male in most species. Apart from plumage, dimorphism is often most marked in bill length. Zwarts and Wanink (1984) showed that female curlews, whose bill averages about 20% longer than the males', were able to reach large clams *Mya arenaria* buried deep in sandflats, whilst males were able to reach only the small clams that lay nearer the surface. In the closely related bar-tailed godwit, which shows marked sexual dimorphism in leg and bill length, Smith (1973) found that females tended to wade in shallow water when foraging whilst males usually fed at the tide edge. The ability to wade became advantageous during very cold weather because the lugworm *Arenicola,* which was the major prey species of both sexes, was more active in such cold conditions when covered by seawater and hence more available.

In the present study some predictions were made about expected differences in the size of prey taken by male and female curlew, godwit and grey plover;

i) females have greatly and significantly longer bills than males in curlew and godwit (Prater *et al.* 1977), so females can probe deeper into the substrate. It has been shown for molluscs (Reading and McGrorty 1978; Zwarts and Wanink 1984) and polychaete worms (Muus1967), that larger individuals lie deeper in the sediment than small ones. I would predict therefore, that larger worms would be less frequent in the males' diet than in the females' diet.

ii) there is very little sexual dimorphism in the grey plover, and especially little in bill length (Prater *et al.* 1977), so I would predict that males and females take similar size prey items. In any case, this species does not probe into the sediment when feeding on *Nereis,* so any differences in bill length would be of little relevance.

Differences in foraging abilities between adults and juveniles have been demonstrated in a wide variety of bird groups (review by Marchetti and Price 1989), and may be the result of morphological or learning constraints. Kear (1962) found that juveniles of seven species of finch (family Fringillidae), when presented with a range of seed sizes, took mainly the small seeds but after twelve days in captivity had switched to feeding mainly on large seeds, like the adult birds. Furthermore, some immatures, probably older juveniles, took large seeds. Kear (*op. cit.*) argued that small seeds are easier to husk than large seeds and that juveniles develop the musculature necessary to husk larger - and more energetically profitable - seeds during the first few weeks after fledging. Juvenile bills are often slightly shorter than those of adults. Heppleston (1970) found that the shorter bill of juvenile oystercatchers *Haematopus ostralegus* prevented them from probing deeply enough into the mudflat to reach the prey available to adults. Oystercatcher bills take about nine weeks to reach the length of adults (Heppleston, 1970), and Townshend (1981) provided some data to suggest that measurable bill growth in curlews may last until March - a period of over thirty weeks. Given this prolonged development period it is reasonable to expect that differences in foraging between juveniles and adults may last a similar time, a result of morphological differences alone. In addition, the development of foraging skills through learning early in life is thought to play an important role in explaining observed adult-juvenile differences. For example, Recher and Recher (1969) found that juvenile little blue herons *Florida caerulea* were less successful at catching fish than adults, and caught fewer large prey than the more experienced birds, even though the age groups were morphologically similar. The authors concluded that the learning process in these birds took at least nine months to complete, for differences between adults and juveniles persisted at least until adult plumage was acquired and the exact age of a bird became indeterminate. Studies on passerines show that even in relatively short-lived species, juveniles learn foraging skills only gradually. For example, Gochfeld and Burger (1984), studying the American robin *Turdus migratorius*, showed that juveniles caught fewer large prey than adults and found that the difference persisted at least until the birds were three to five months old. Desrocher (1992) showed that one- year-old blackbirds *Turdus merula* were half as successful at catching large worms as two-year-olds, which in turn were less successful than adults.

If specialised food handling (and indeed detection) skills need to be learned, it is likely that juveniles of many shorebird species will catch the prey that is most easily caught and not necessarily that which is most profitable. Studies have shown that shorebirds select certain sizes of prey when a range of sizes is available (for example Goss-Custard 1977; Norton Griffiths 1967) and it is thought that the chosen size of prey represents a compromise between maximising the size of a single prey item and minimising the time and effort needed to capture and handle it. In the present study, one can predict that juveniles of curlew, godwit and grey plover will take smaller *Nereis* than will the adults of each species, for the following reasons;

i) juveniles may be limited by the length of their bills as to the maximum size of prey they can reach, for it has been shown for some benthic invertebrates that larger individuals of a species live at greater depths in the sediment than do smaller ones. This effect is likely only in the curlew, because there is little age difference in bill length of adult and juvenile grey plovers or of godwits by the time they reach their winter feeding grounds.

ii) that larger worms are more profitable prey than smaller worms (they afford greater net energy intake rate) but juveniles are less skilled than adults at identifying the presence of large worms. If active selection is occurring, in other words if individuals are ignoring some small prey and accepting most large prey, then there must be a mechanism by which the foraging bird can perceive the size of *Nereis* when they are encountered. The precise cue that each species uses to detect prey is uncertain, but it is believed that curlew and godwit use tactile probing in the sediment to locate the worm in its burrow, while grey plovers are thought to rely on movements of the worm at the sediment surface. It is predicted that acquisition of the skills of detection, and, more importantly here, the skills of selection of prey, require a period of learning. If selection of worm size is poor then we would predict that worms are taken more or less in proportion to the sizes present in the substrate.

iii) if large worms, once detected, are more difficult to handle than small worms, or if they are able to take evasive action more rapidly, it is likely that juveniles will be less skilled in dealing with them and therefore large worms are likely to be captured less frequently, or broken more frequently during extraction from burrows.

iv) juveniles may feed in different areas to adults, perhaps forced to an inferior feeding site by more dominant adults. If different areas contain different availabilities or proportions of large worms, then this could lead to differences in the size of worms taken by adults and juveniles. Age-related separation of feeding sites has been demonstrated in dunlin (van der Have *et al* 1984), and oystercatcher (Goss-Custard and Durell 1984).

Bringing together the predictions from considerations of a) foraging differences related to bill length, based on species, sex and age criteria, and b) age-related foraging differences based on acquisition of skills through learning, the following predictions are made. (Note that since it is not straightforward to predict on theoretical grounds the size of *Nereis* taken by grey plovers, comparisons between this species and the other two shall be made *a posteriori*).

i) Adult female curlews will take the highest proportion of large worms;

ii) Juvenile male godwits will take the lowest proportion of large worms;

iii) highest potential overlap in prey size will occur between juvenile male curlew and adult female godwits.

4.3.2 Results and discussion.

4.3.2.1 Validation of the technique of direct observation.

A detailed comparison of the two methods is not realistic, as the faecal analysis can tell us nothing about the age or sex of the individual which produced the sample, yet we know that there are likely to be intraspecific differences in the size of worms taken (see above). Indeed the large amount of variation in size composition between faecal samples within the species (for curlew and godwit, but not grey plover) reflect this (Tables 4.1-4.3). Nevertheless a useful general comparison can be made to test whether the direct observation method underestimated the proportion of small worms in the diet, as predicted. Figure 4.1a-c shows the results of the two methods, with the data from the faecal analysis recoded into the size classes used for the direct observations, to facilitate comparison. The direct observations consistently under-estimated the proportion of small worms in the diet of all three species - curlew, godwit and grey plover. There was particular discrepancy in the 24-46 mm size class of the godwits', and the smallest three size classes of the grey plovers' diet. The former was probably caused by the fact that

Table 4.1 Variation in mean estimated worm length (mm) between curlew faecal samples. N= total number of jaws found in each sample/2.

SAMPLE NUMBER	MEAN (ranked)	S.E	N
1	53.5	8.1	8
2	61.8	1.7	65
3	64.4	4.0	14
4	64.7	4.9	9
5	65.1	4.8	8
6	71.4	9.8	16
7	72.9	6.6	16
8	73.0	2.0	28
9	73.1	6.6	20
10	73.2	3.3	21
11	74.2	6.0	16
12	75.8	2.6	20
13	77.2	2.3	21
14	78.0	6.3	22
15	78.2	2.3	51
16	81.1	4.9	13
17	83.4	3.5	7
18	88.1	8.5	18
19	89.0	4.3	21
20	90.7	13.0	12
21	110.1	12.8	10
22	141.3	21.9	8

Table 4.2 Variation in mean estimated worm length (mm) between grey plover faecal samples. N=total number of jaws found in each sample/2.

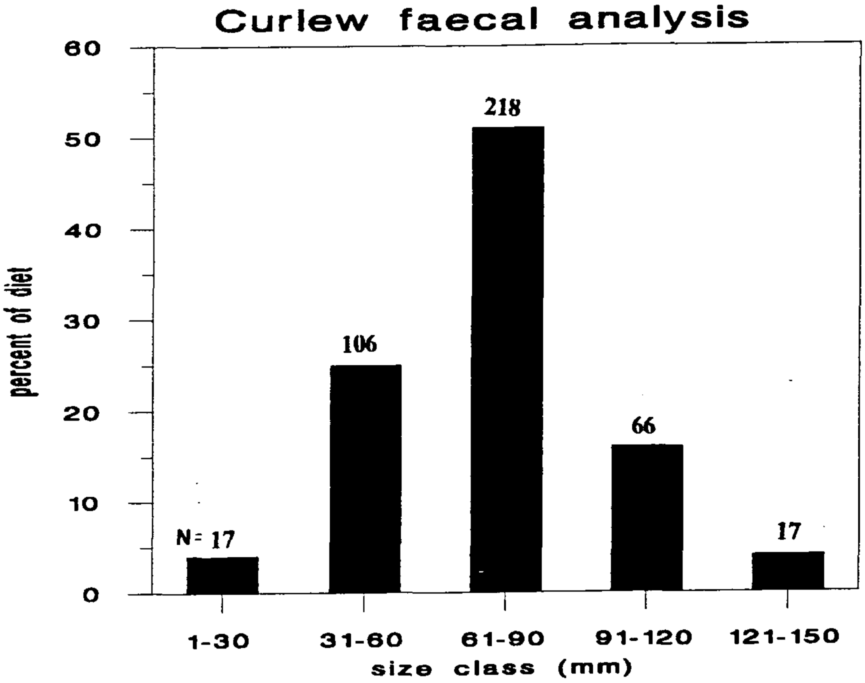
SAMPLE NUMBER	MEAN (ranked)	S.E.	N
1	24.8	5.5	8
2	31.9	7.0	8
3	33.5	5.3	11
4	34.0	4.9	10
5	34.3	8.3	11
6	35.0	5.9	6
7	35.9	5.7	8
8	37.4	6.2	8
9	37.8	6.3	9
10	38.5	5.4	13
11	38.9	4.2	12
12	40.3	5.8	9
13	40.9	3.9	16
14	47.2	5.8	11
15	51.7	7.3	14

Table 4.3 Variation in mean estimated worm length (mm) between godwit faecal samples. N=total number of jaws found in each sample/2.

SAMPLE NUMBER	MEAN	S.E.	N
1	36.6	9.1	7
2	40.1	4.1	14
3	43.1	6.2	
4	44.1	6.7	9
5	53.8	5.9	8
6	55.2	5.2	9
7	61.8	6.9	8
8	65.0	5.5	14
9	65.0	3.5	19
10	67.7	4.3	6
11	69.2	5.3	9
12	69.9	11.1	9

Figure 4.1a Comparison of estimates of lengths of *Nereis* in curlew diets from faecal analysis and from direct observation.

Numbers of observations used in faecal analysis and direct observation are given in Tables 4.1 and 4.4, respectively.



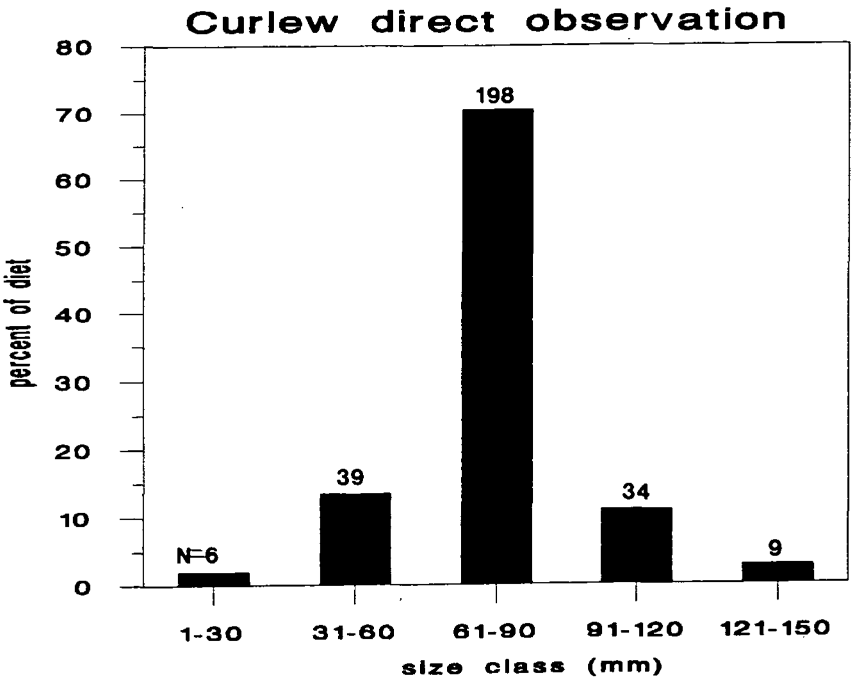
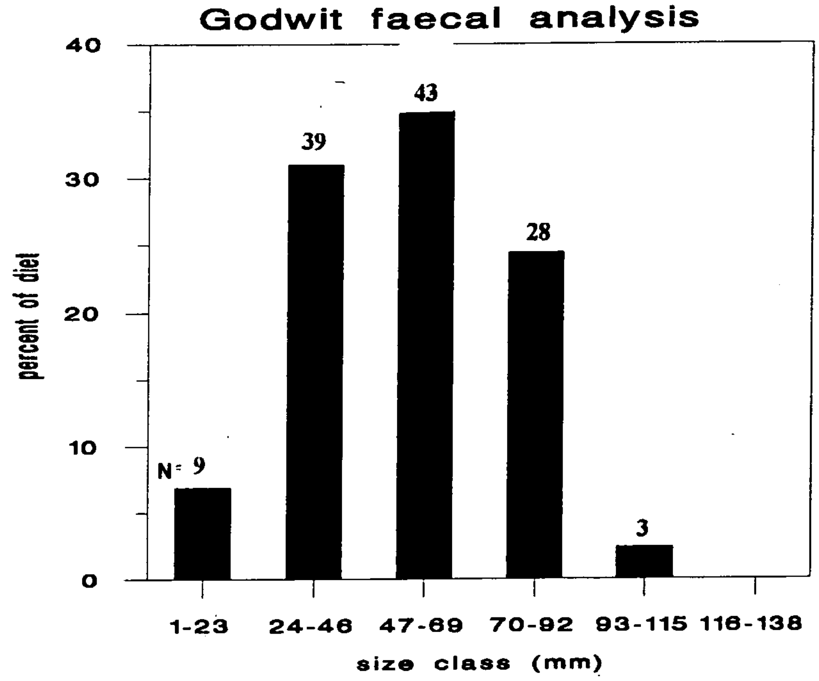


Figure 4.1b Comparison of estimates of lengths of *Nereis* in godwit diets from faecal analysis and from direct observation.

Numbers of observations used in faecal analysis and direct observation are given in Tables 4.2 and 4.4, respectively.



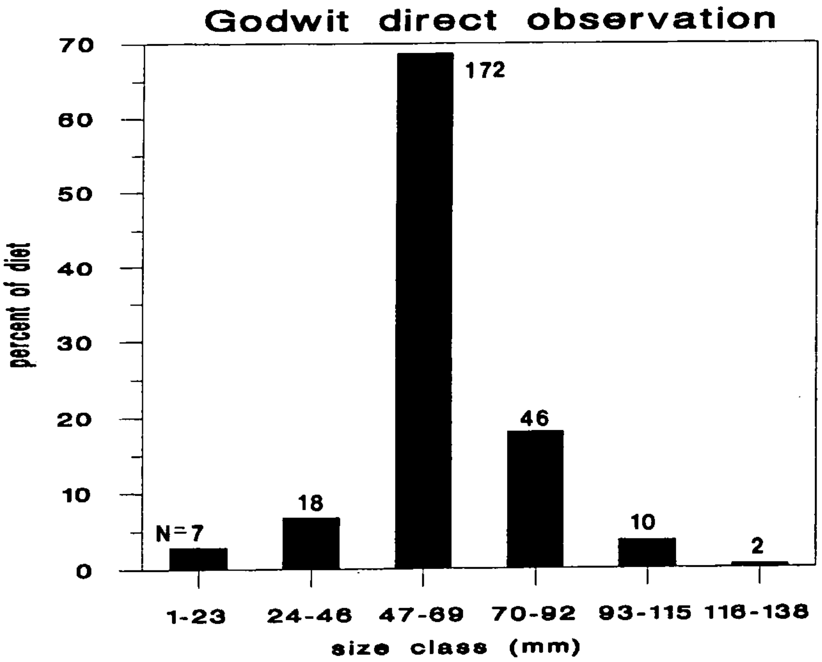
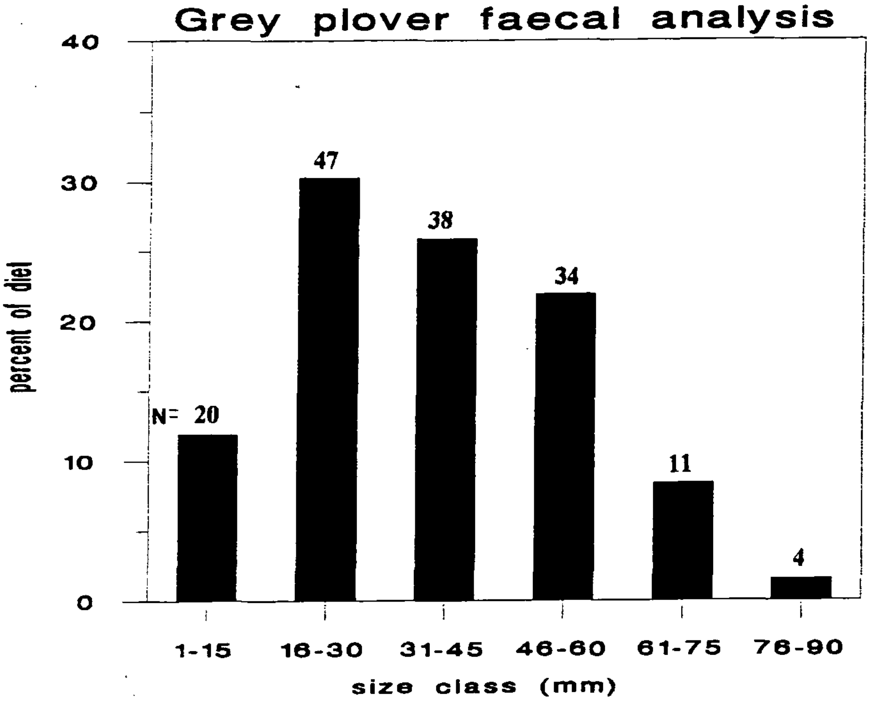
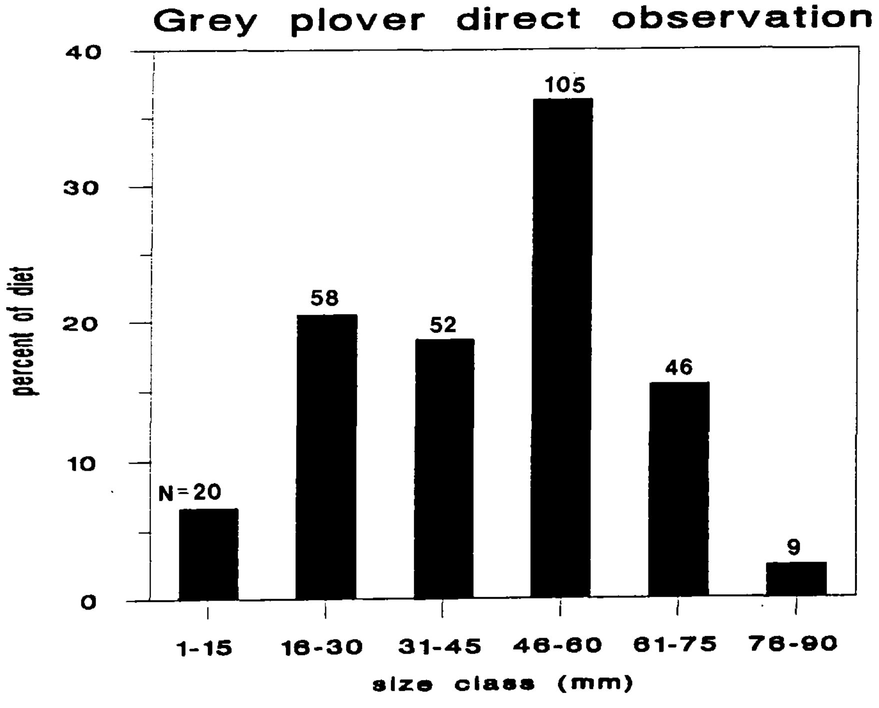


Figure 4.1c Comparison of estimates of lengths of *Nereis* in grey plover diets from faecal analysis and from direct observation.

Numbers of observations used in faecal analysis and direct observation are given in Tables 4.3 and 4.4, respectively.





the godwits habitually swallowed some prey (probably the small worms) while their bills were still in the sediment or in water, which would result in many of the small worms being missed. The discrepancy in the methods when applied to grey plover was likely to be caused by a) failure to detect some small worms in some light conditions and b) the fact that small worms are handled very rapidly which precludes comparison with the length of the bill. A further source of error could have arisen if small jaws were excreted in faeces, and large jaws in pellets, which would bias the estimates obtained from faecal analysis. A sample of pellets obtained from curlews showed no evidence for this, although I could not find pellets from godwits or grey plovers. The nine curlew pellets examined contained mostly bivalve shell fragments (probably *Macoma*) and pieces of exoskeleton of shore crabs *Carcinus maenas*, with large proportions of sand grains, and one pellet contained a single *Nereis* jaw. This suggested that the great majority of jaws were excreted in faeces rather than pellets, so the discrepancy between the results from the two methods can be attributed to factors a) and b) above.

Since we do not know the age or sex of the individual that produced each faecal sample and because there are likely to be age- and sex-related differences in prey size, it is not possible to produce a reliable correction factor for the direct observations based on the faecal samples. However the faecal analysis was useful in highlighting the biases of the direct observation technique, and therefore the "best estimate" of true size classes of *Nereis* taken by each species will encompass a range, the minimum of which is derived from the faecal analysis and the maximum from the direct observations. This will be incorporated into the estimates of prey size overlap later in this chapter.

4.3.2.2 Evidence for seasonal change in prey size.

Table 4.4 gives a summary of the number of observations, divided by date, age and sex where these have been determined.

Table 4.4 The number of samples taken using the direct observation method, broken down into time, age and sex classes for the winter1991-92.

"Observation" refers to one worm taken.

a) curlew and godwit, where each individual could be aged and sexed

AGE/SEX/TIME CLASS	CURLEW, NUMBER OF OBSERVATIONS	GODWIT, NUMBER OF OBSERVATIONS
ad. male sep-dec	18	38
ad. male jan-mar	28	37
ad. female sep-dec	16	23
ad. female jan-mar	39	40
juv. male sep-dec	18	7
juv. male jan-mar	0	48
juv. fem. sep-dec	15	11
juv. fem jan-mar	0	27
species total	134	231

b) curlew and godwit, where individuals could not be assigned a sex or an age, or both.

AGE/SEX/TIME CLASS	CURLEW, NUMBER OF OBSERVATIONS	GODWIT, NUMBER OF OBSERVATIONS
no age/sex sep-dec	13	0
no age/sex jan-mar	0	0
male sep-dec	12	3
male jan-mar	25	6
fem. sep-dec	17	0
fem. jan-mar	85	7
juv sep-dec	0	8
total	152	24

c) grey plover - in all cases individuals could be aged but not sexed.

AGE/TIME CLASS	NUMBER OF OBSERVATIONS
adult sep-dec	46
adult jan-mar	125
juvenile sep-dec	56
juvenile jan-mar	108
species total	290

Figure 4.2 shows the size classes taken by adult male and adult female curlew in early and late winter. In both sexes, the most frequently taken size class (61-90 mm) was the same in the two periods and this is reflected by the non-significance of the Kolmogrov-Smirnov test between periods (for adult males $Z_{18,28}$ =0.828, one-tailed P=0.25; for adult females $Z_{16,39}$ =0.356, one-tailed P=0.5). This is a test which is sensitive mainly to changes in median value between groups (Sokal and Rohlf 1981). However, there are differences in the proportion of the other size classes through the winter. In the adult males the very small worms (1-30 mm) are absent in late winter and the large worms in the 91-120mm class are absent in the early winter. It is important to remember that I showed in the previous section that the direct observation method is prone to underestimate the proportion of small worms in the diet, hence the accuracy of the left hand tail of the statistical distribution is questionable. It is therefore unwise to draw substantial inferences based on differences in the left-hand tails of the distributions. No juvenile curlews could be identified in the second winter period, as ageing characters become unreliable with feather wear and the few juveniles that were colour marked did not appear on the feeding grounds that winter, so comparison of this group through the season was not possible.

Figure 4.3 shows a comparison of the size classes taken by adult male and adult female godwits between the two periods. In both sexes, the size class most frequently taken (47-69 mm) did not change from early to late winter, reflected in the non-significance of the Kolmogrov-Smirnov test (for adult males $Z_{38,37}$ =1.133, one-tailed P=0.077; for adult females $Z_{23,40}$ =0.665, one-tailed P=0.385). However there are more subtle changes in the diets of both males and females over the winter. In the first winter period the adult males took significantly more of the small worms than did the adult males in the late winter (Mann-Whitney test $U_{38,37}$ =520.5, one-tailed P=0.009), whilst adult females took a slightly higher proportion of large worms early in the winter than they did later on, although the difference is not significant (Mann-Whitney test $U_{23,40}$ =442.0, one-tailed P=0.377). The same caution concerning interpretation of differences in the left hand tail

Figure 4.2 Seasonal change in prey size of adult male and adult female curlews as revealed by direct observation.

Number of observations is given in Table 4.4.

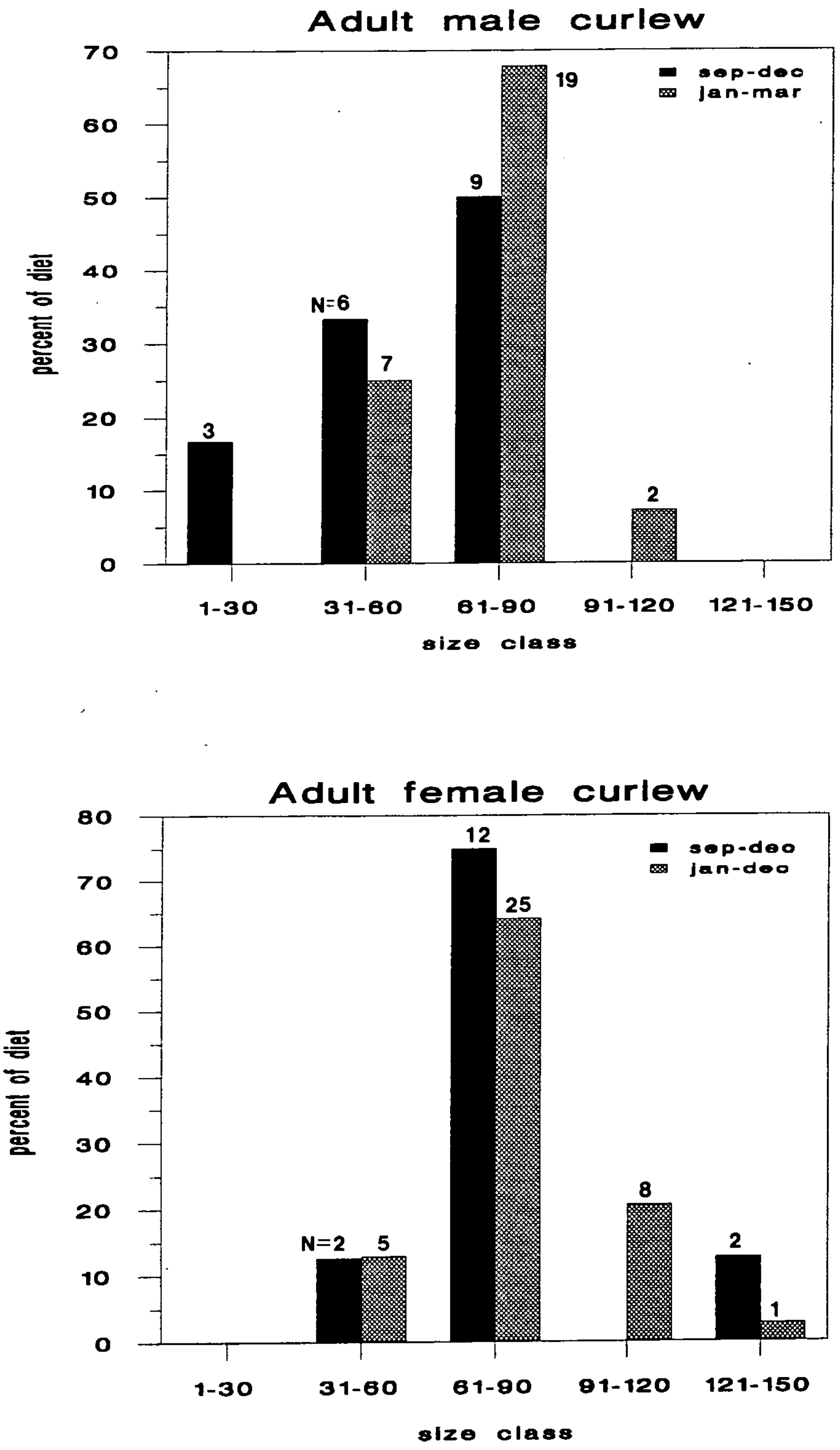
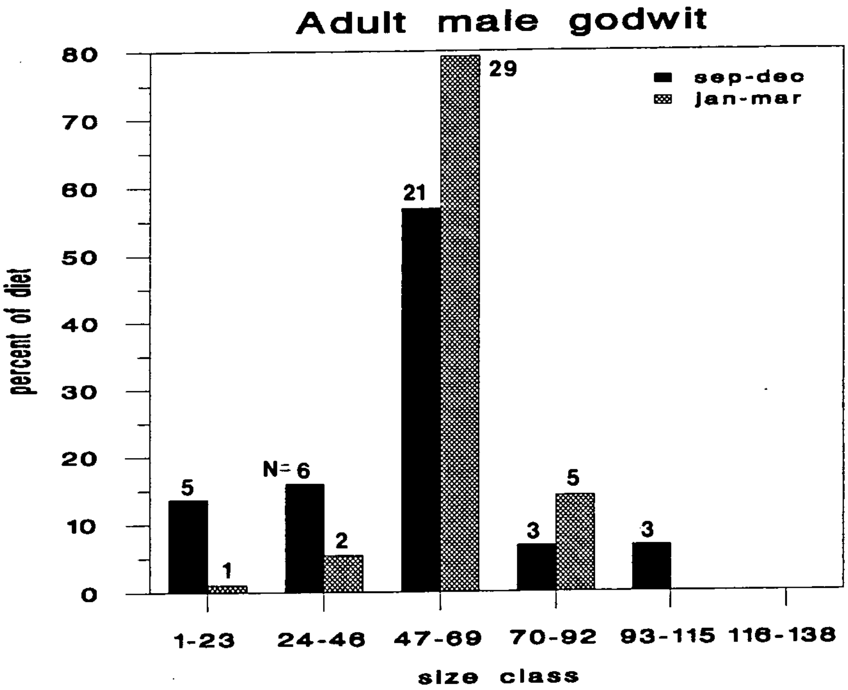


Figure 4.3 Seasonal change in prey size of adult male and adult female godwits as revealed by direct observation.

Number of observations is given in Table 4.4.



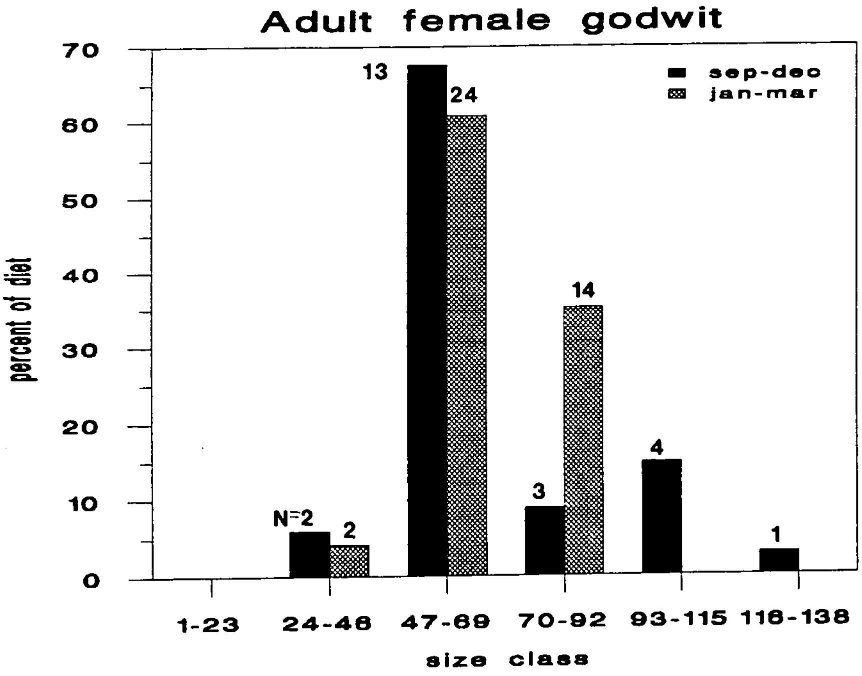
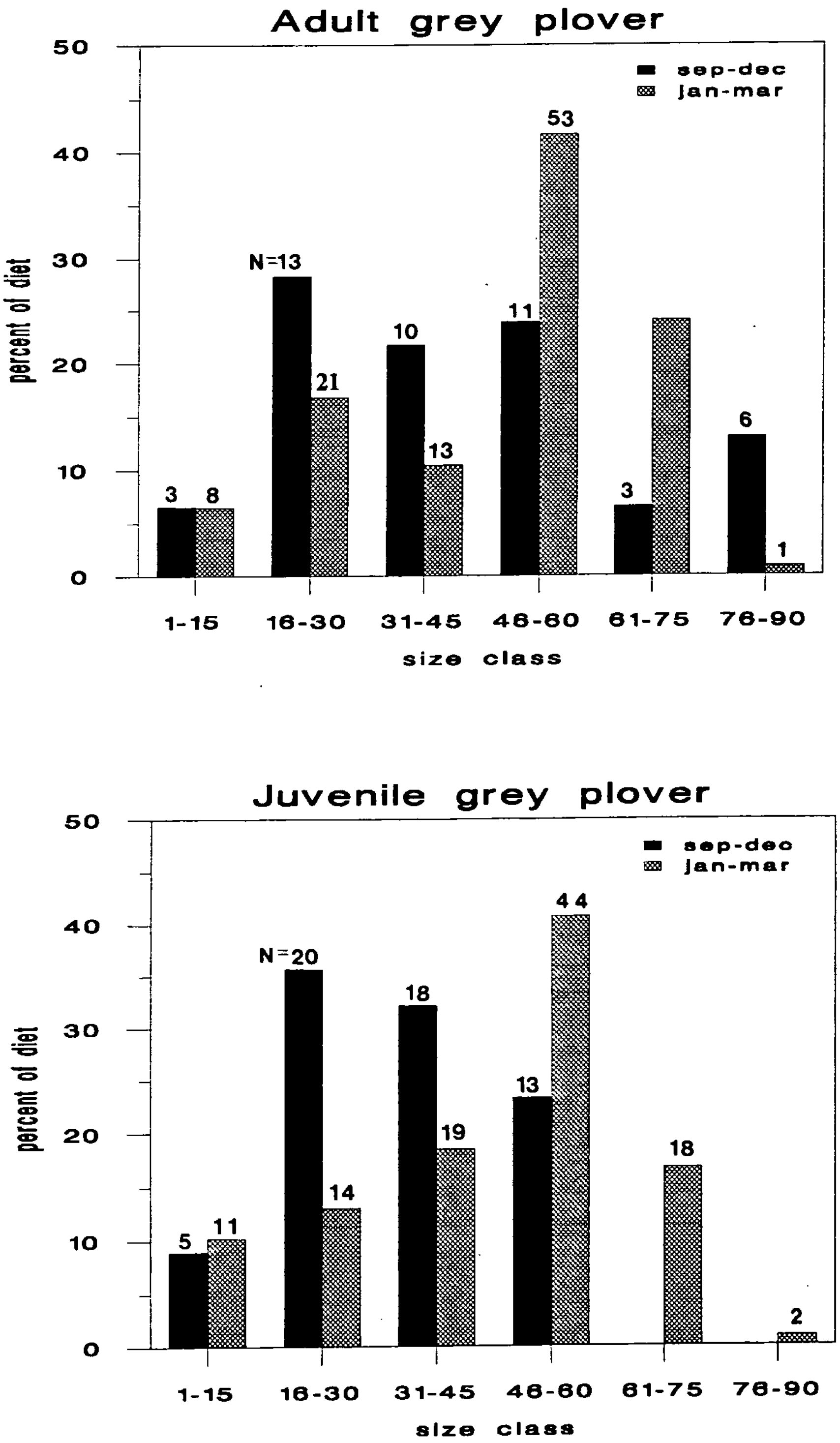


Figure 4.4 Seasonal change in prey size of adult and juvenile grey plovers as revealed by direct observation.

Number of observations is given in Table 4.4.



of the distribution that was applied to the curlew data is relevant here. Unfortunately, insufficient samples were obtained from juvenile males and juvenile female godwits to make a meaningful seasonal comparison (see Table 4.4 for sample sizes).

Figure 4.4 shows a comparison of the size classes taken by adult and juvenile grey plovers between the two periods. The first point to note is that there is far less emphasis on any single size class than was seen in curlews and godwits. For the adult grey plovers there is a higher proportion of small worms in the diet early in the winter (especially in the 16-30 and 31-45 mm classes), while the proportion of worms in the 46-60 mm classes and above increases through the winter. These changes are significant as tested by the Kolmogrov-Smirnov test ($Z_{46,\,125} = 1.329$, one-tailed $P=0.029$) which points to a shift to the right of the size frequency distribution during the winter, but non-significant as tested by the Mann-Whitney U test (one-tailed $P=0.27$) which is a result of broader scatter of the data. The changes shown by juvenile grey plovers through the winter are more striking, however. The juveniles showed a marked decrease in the proportion of small worms in the diet between the two periods, and an increase in the proportion of large worms taken; worms in the 46-60 mm class and above more than doubled in frequency between early and late winter. These differences are highly significant (Mann-Whitney $U_{56,\,108}$, one-tailed $P<0.0001$; Kolmogrov-Smirnov test $Z=2.133$, one-tailed $P<0.0001$).

In summary, the seasonal changes in prey size were generally rather subtle and the modal size class of the diet did not change, except in the grey plover. The most marked change was shown by juvenile grey plovers, and this is perhaps partly a reflection of increased skills in selection of large worms over the course of the winter, although adults also showed a slight increase in worm size. In view of the relatively small change in median worm size between early and late winter, it is reasonable to combine the data for the whole winter for adult male and adult females of curlew and godwit in subsequent analyses, but treat each winter period separately for grey plovers.

4.3.2.3 Evidence for sexual and age differences within the species.

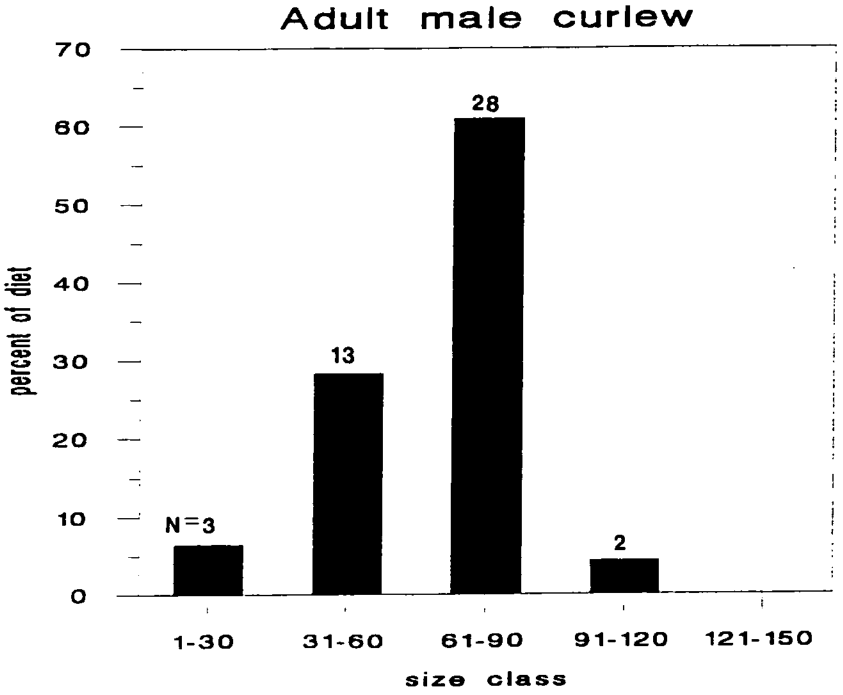
A summary of the number of observations for each age/sex class of each species is given in Table 4.4, but note that for the analysis in this section data from September-December and January-March are combined, except for adult and juvenile grey plovers, which showed a large seasonal difference.

Figure 4.5 compares the size classes of *Nereis* taken by adult male and adult female curlews. Although the proportion of the modal size class (61-90mm) is similar for each sex, the females took significantly more large worms and the males took significantly more small worms than the other sex (Mann-Whitney test $U_{46, 55}$ =856, one-tailed P<0.001). This is the result that was predicted, since the female's longer bill enables her to reach the larger worms that tend to be buried deeper in the sediment than the small worms.

Figure 4.6 compares the sizes classes of *Nereis* taken by adult male and juvenile male curlews. The proportions taken of the modal size class (61-90 mm) were similar (Kolmogrov-Smirnov test one-tailed test P=0.395), but adults took less large worms than juveniles, and juveniles took less small worms than adults (Mann-Whitney test, $U_{46, 18}$ =290, one tailed P=0.016). This is somewhat surprising since I predicted that adults would catch larger prey than juveniles due to the former's longer bill and greater experience. It should be borne in mind, however that the observations of juvenile males are rather few and are based on samples from September to December only, since no juvenile curlew could be identified in the second winter period. It is possible then that there may have been a seasonal difference in prey size in juveniles (as predicted) but this could not be tested. In view of this, subsequent analyses will pool data of adult and juvenile male curlew.

Figure 4.5 The size classes of *Nereis* taken by adult male and adult female curlews as revealed by direct observation.

Number of observations is given in Table 4.4. Size classes in millimetres



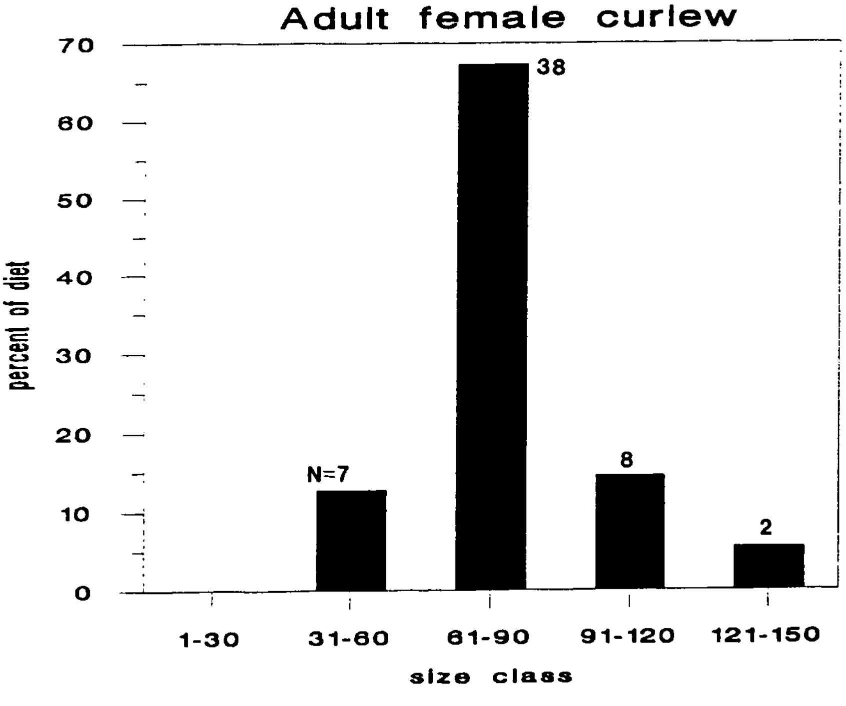
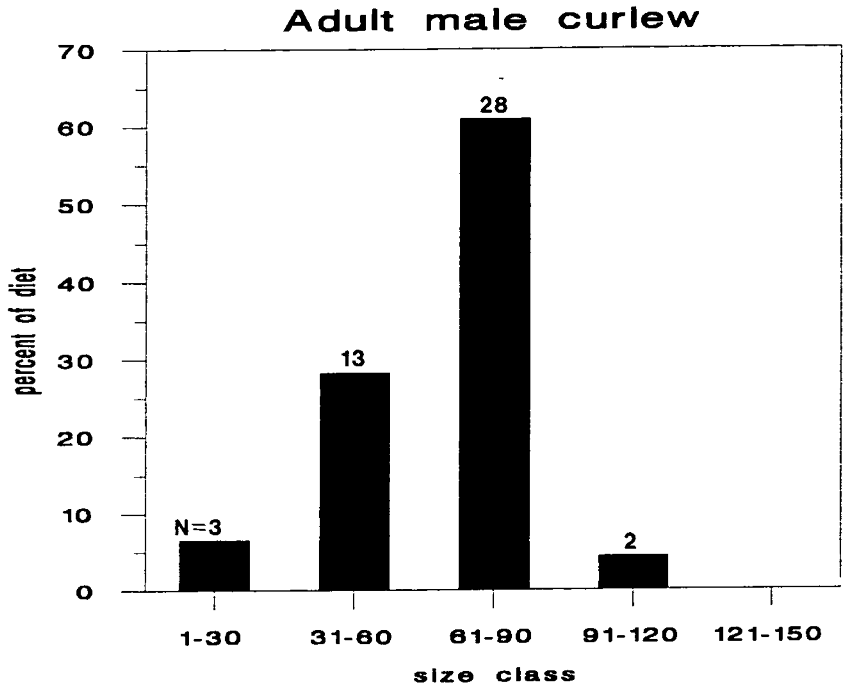


Figure 4.6 The size classes of *Nereis* taken by adult male and juvenile male curlews as revealed by direct observation.

Number of observations is given in Table 4.4. Size classes in millimetres



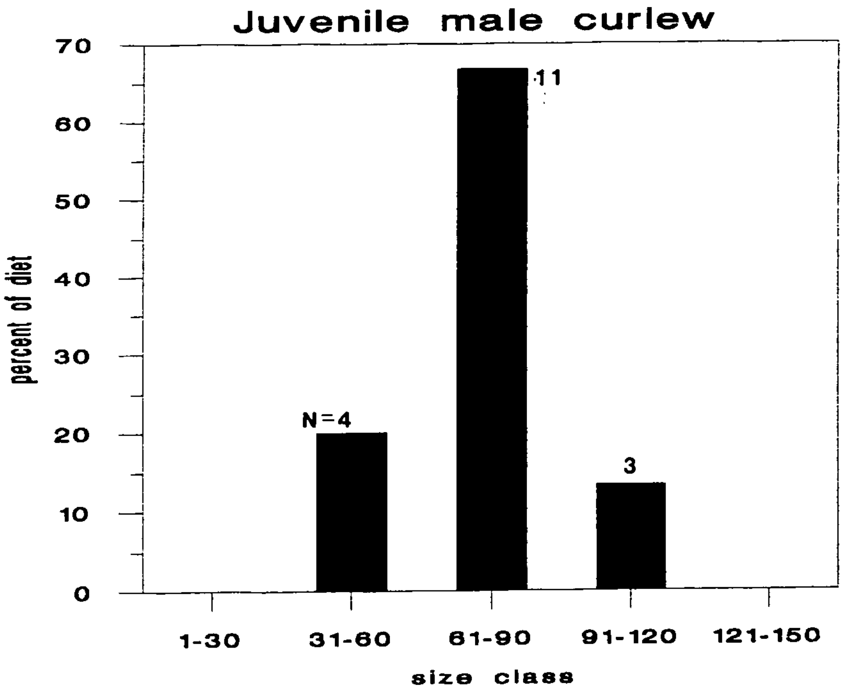


Figure 4.7 compares the size classes of *Nereis* taken by juvenile male and juvenile female curlews. The data reveal no significant difference between the two sexes (Mann-Whitney test $U_{18,15}$ =122, one-tailed P=0.284).

Figure 4.8 show the size classes of *Nereis* taken by adult female and juvenile female curlews. The proportion of the modal size class (61-90 mm) is similar in both ages, and the sample from females showed more of the very large worms (121-150mm), but this was not statistically significant (Mann-Whitney test, $U_{55,15}$=362, one tailed P=0.190). It should be borne in mind that the sample from juvenile females may not be representative of the whole season as juveniles could not be identified in the late winter.

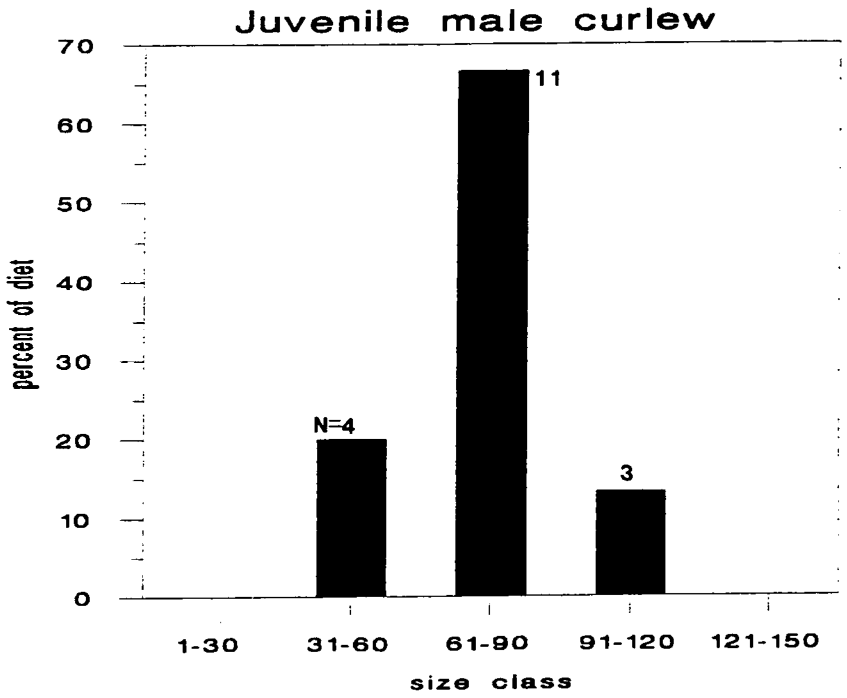
In summary of the age/sex comparisons for curlews, it has been shown that females took significantly more large worms than males, but this was statistically proven only in adults. The effect of bird age on the sizes of worms taken is less clear, since juvenile males took larger worms than adult males, while no difference was shown between juvenile females and adult females. Clearly, further data from the whole winter are needed to resolve any possible seasonal differences in prey size that juveniles may exhibit.

Figure 4.9 shows the size classes of *Nereis* taken by adult male and adult female godwits. The proportion taken of the modal size class (47-69mm) is similar, but adult females took more large worms than males and adult males took more small worms than females (Mann-Whitney test $U_{75,63}$ =1767, one tailed $P<0.001$).

Figure 4.10 shows the size classes of *Nereis* taken by adult male and juvenile male godwits. The proportions taken of the modal size class (47-69 mm) are similar, and there are no significant differences in the proportion of large and small worms taken (Mann-Whitney test $U_{75,55}$ =1803, one-tailed P=0.062).

Figure 4.7 The size classes of *Nereis* taken by juvenile male and juvenile female curlews as revealed by direct observation.

Number of observations is given in Table 4.4. Size classes in millimetres



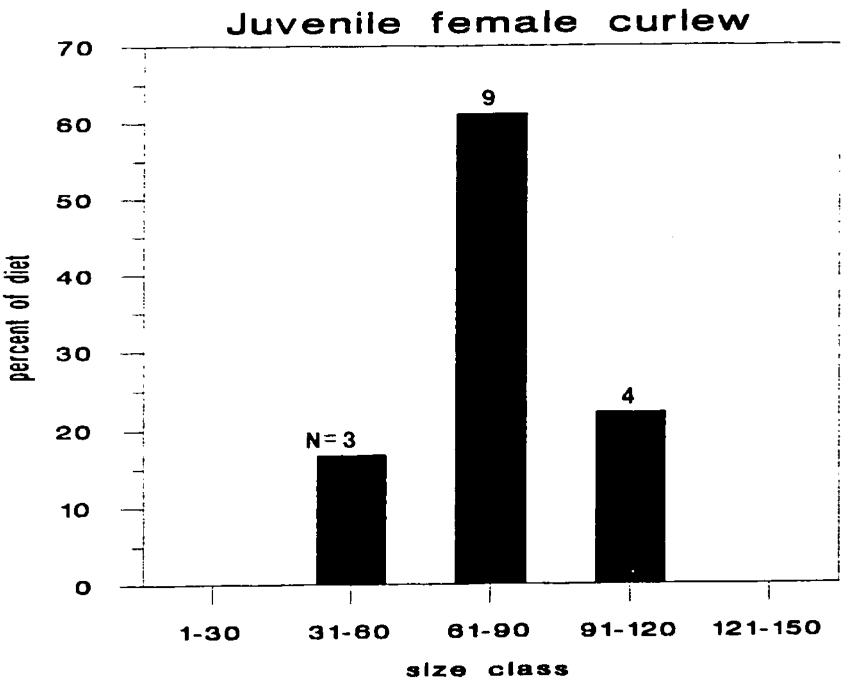
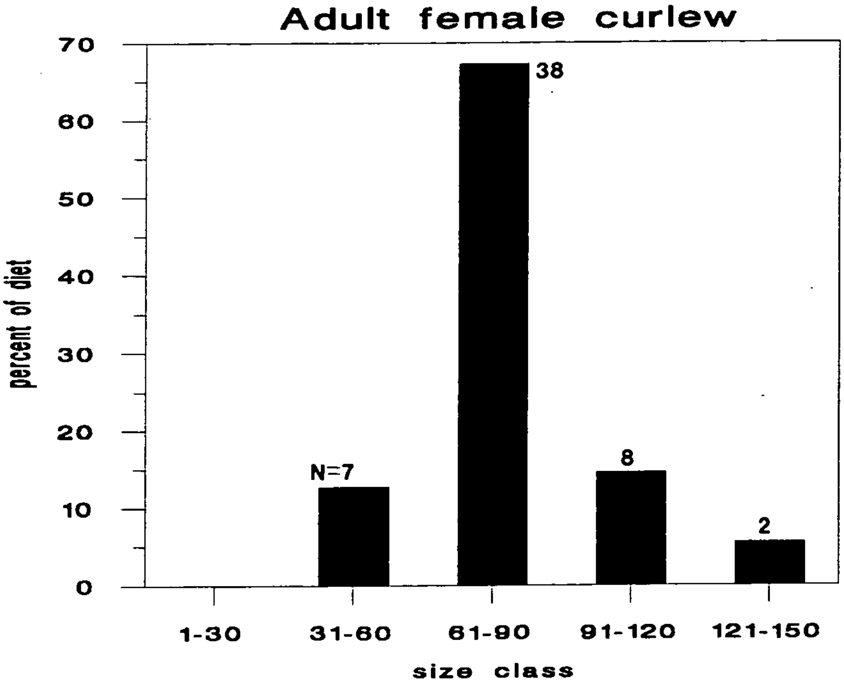


Figure 4.8 The size classes of *Nereis* taken by adult female and juvenile female curlews as revealed by direct observation.

Number of observations is given in Table 4.4. Size classes in millimetres



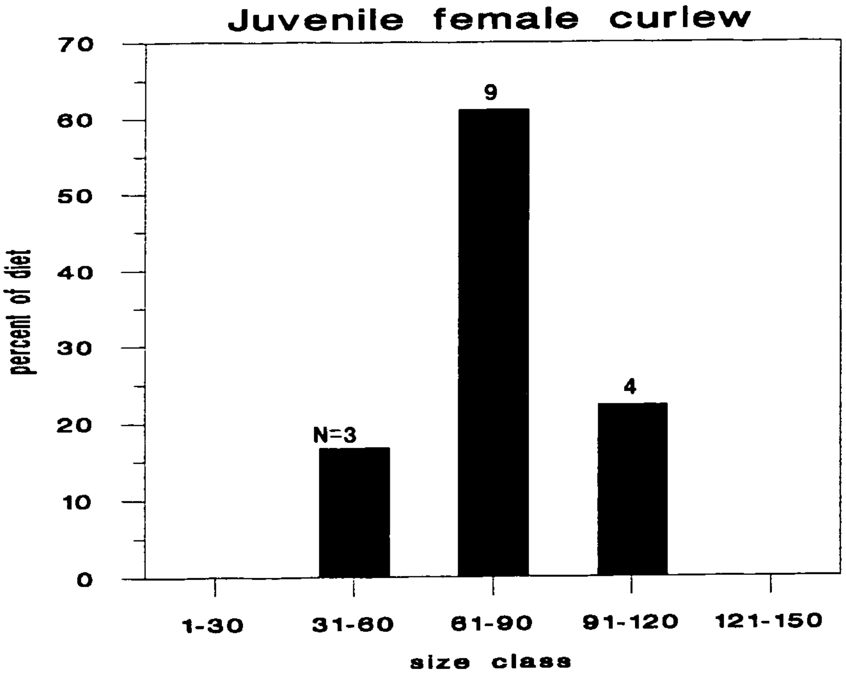
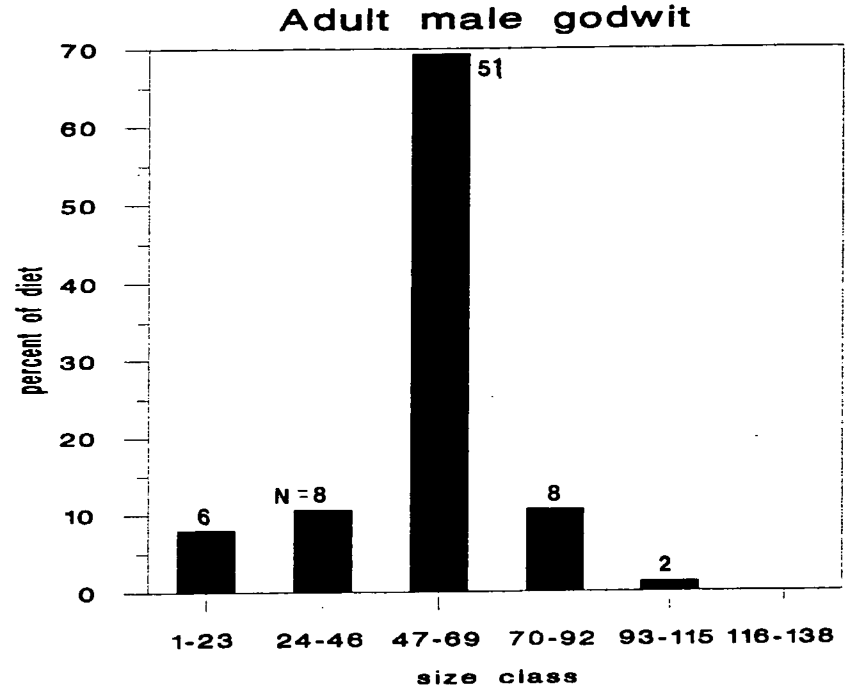


Figure 4.9 The size classes of *Nereis* taken by adult male and adult female godwits as revealed by direct observation.

Number of observations is given in Table 4.4. Size classes in millimetres



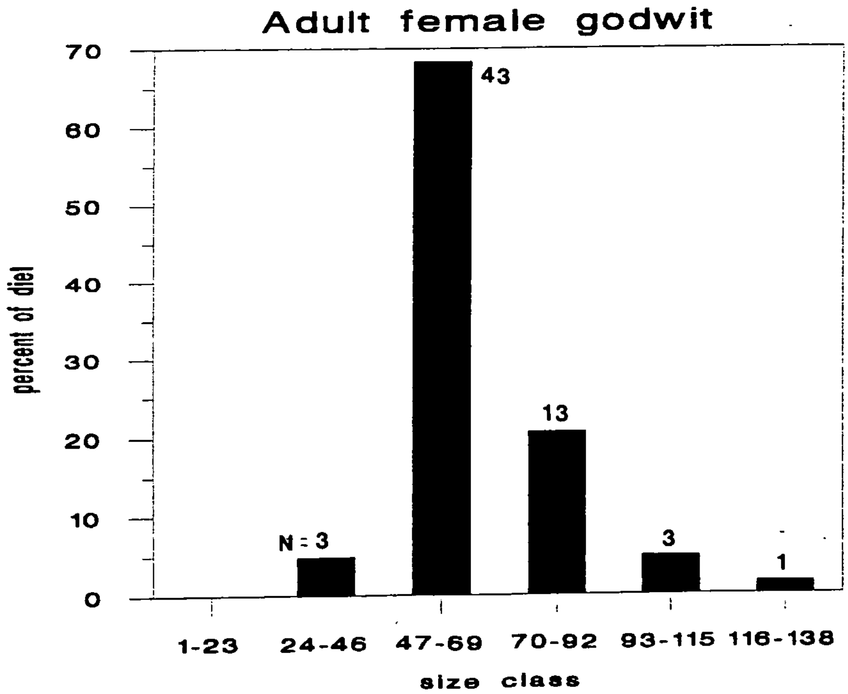
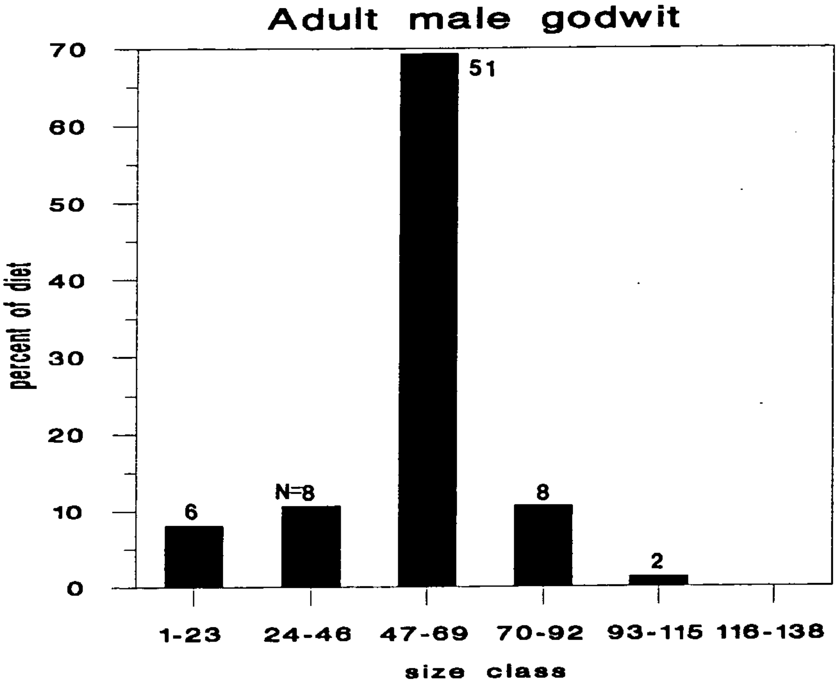


Figure 4.10 The size classes of *Nereis* taken by adult male and juvenile male godwits as revealed by direct observation.

Number of observations is given in Table 4.4. Size classes in millimetres



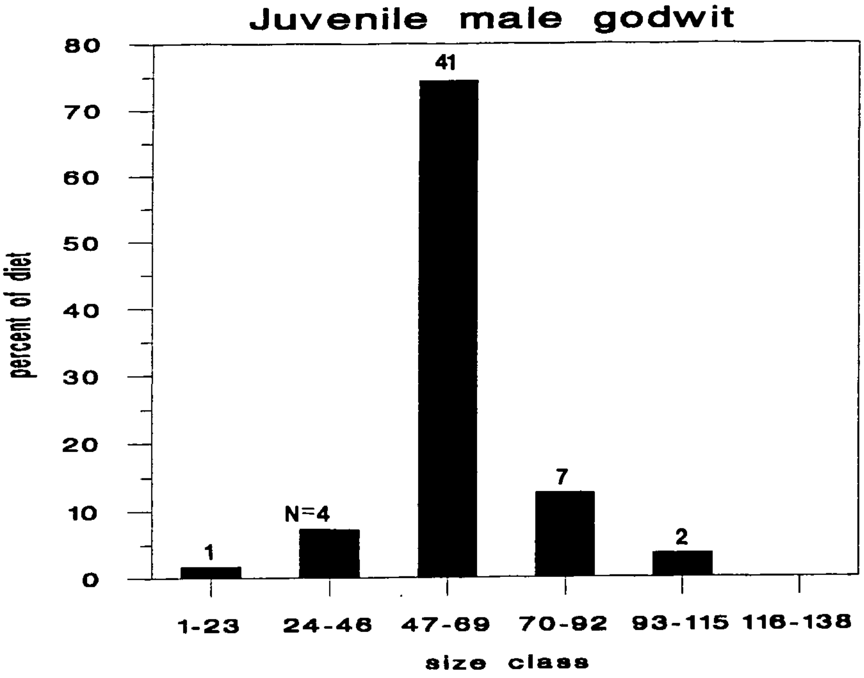


Figure 4.11 compares the size classes taken by juvenile male and juvenile female godwits. While the proportions of the modal size class (47-69 mm) are similar, the females took significantly more large worms than males, especially in the 70-92 mm class (Mann-Whitney test $U_{55,\ 38}$ =727, one tailed P<0.01). The difference is also significant with the Kolmogrov-Smirnov test (one-tailed P<0.05), which identifies a more general difference in distribution.

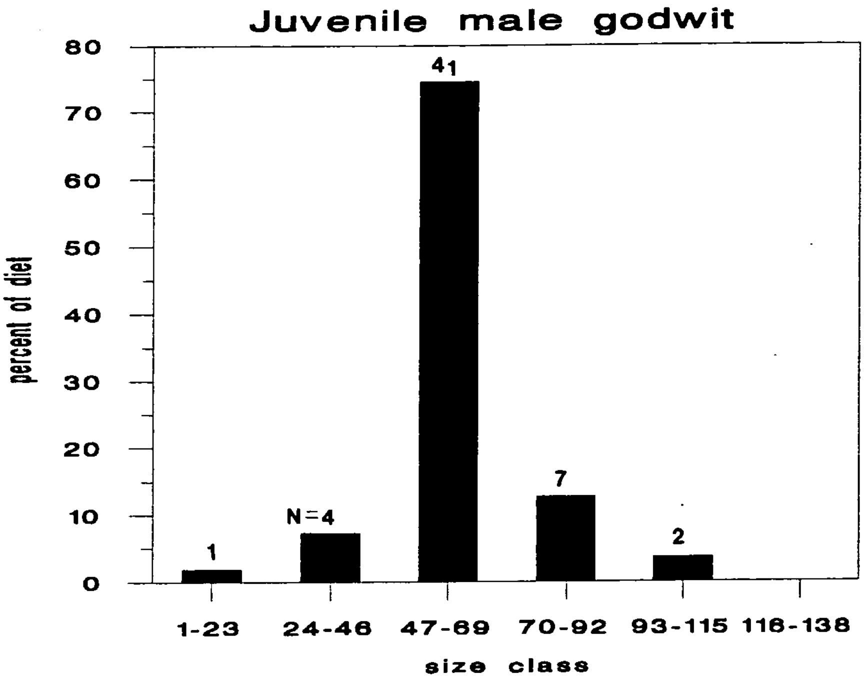
Figure 4.12 compares the size classes taken by adult female and juvenile female godwits. Again, the proportions of the modal size class are similar, but juveniles took more worms in the 70-92 mm class than did adults; the difference only just reaches conventional significance (Mann-Whitney test $U_{63,\ 38}$=994, one-tailed P=0.049). Whilst one would not expect any difference between adults and juvenile godwits based on bill length alone, it was predicted that juveniles may be less adept at detecting and handling large worms. The data presented here suggest that the reverse may be true for worms in the 70-92 mm class, but there is some evidence to show that juveniles were unable to capture the very largest worms.

In summary of the age/sex comparisons for godwits, I have shown that there is a significant sex difference in diet of both adults and juveniles, with females taking larger worms than males, as predicted. The age comparisons were less clear, for in males there was no age difference, but in females juveniles apparently caught larger worms than adults. Why this was so is unclear, and requires further study - the result would not have been significant if a two-tailed test had been used and may represent the one occasion in 20 in which such a result would have occurred by chance.

Figure 4.13 compares adult and juvenile grey plovers for the first winter period. There is a clear effect of age; adults took significantly more large worms than juveniles, and juveniles took more small worms than adults (Mann-Whitney test $U_{46,\ 56}$ =988, one-tailed P=0.018). Indeed the two largest size classes are absent from the juveniles' diet. The

Figure 4.11 The size classes of *Nereis* taken by juvenile male and juvenile female godwits as revealed by direct observation.

Number of observations is given in Table 4.4. Size classes in millimetres



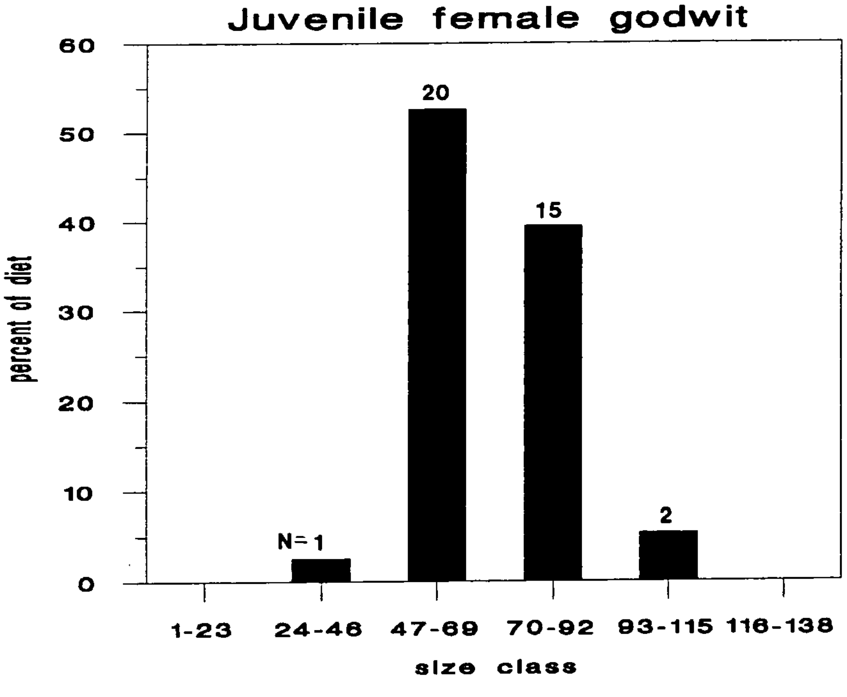
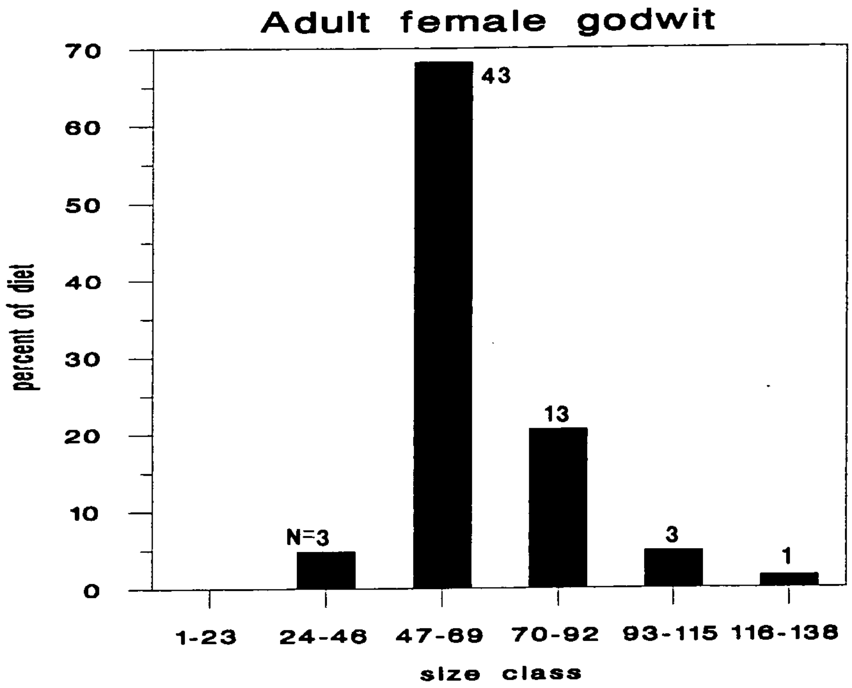


Figure 4.12 The size classes of *Nereis* taken by adult female and juvenile female godwits as revealed by direct observation.

Number of observations is given in Table 4.4. Size classes in millimetres



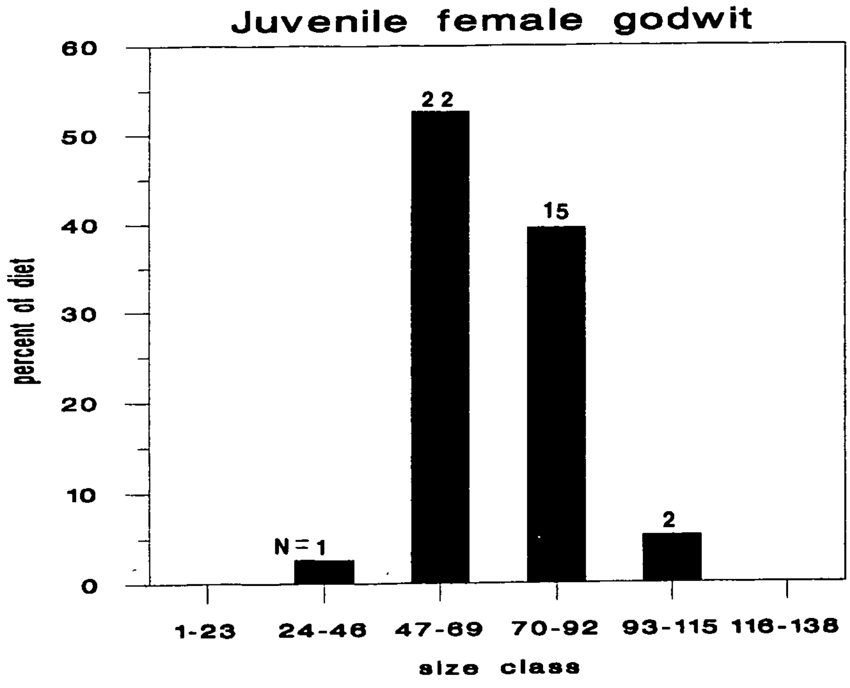
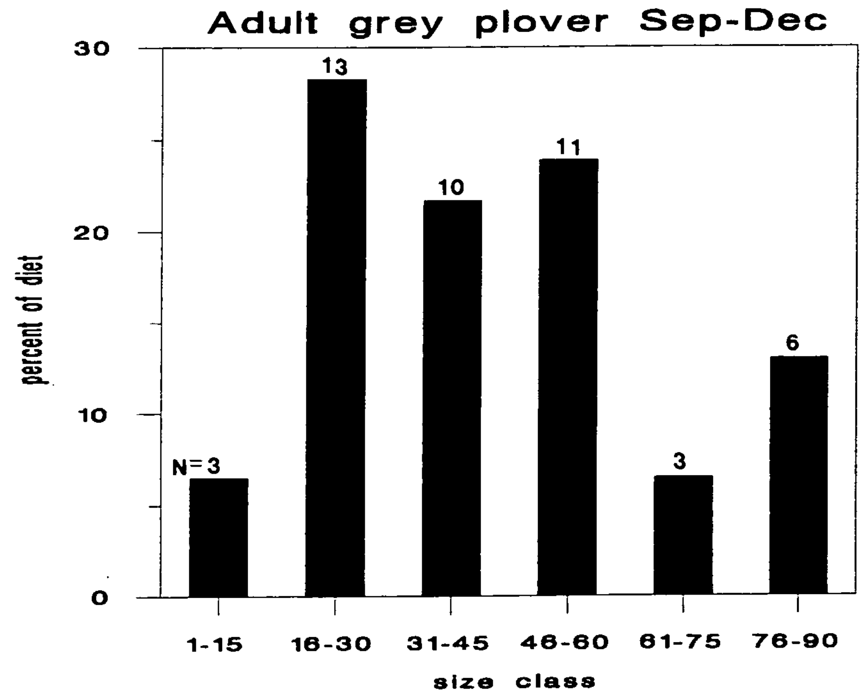


Figure 4.13 The size classes of *Nereis* taken by adult and juvenile grey plovers during September to December as revealed by direct observation.

Number of observations is given in Table 4.4. Size classes in millimetres



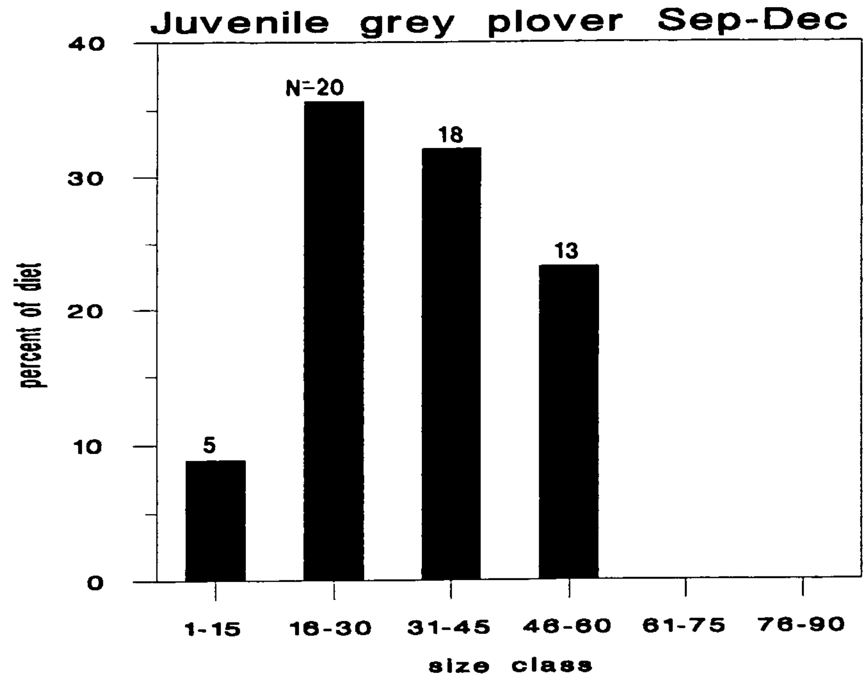
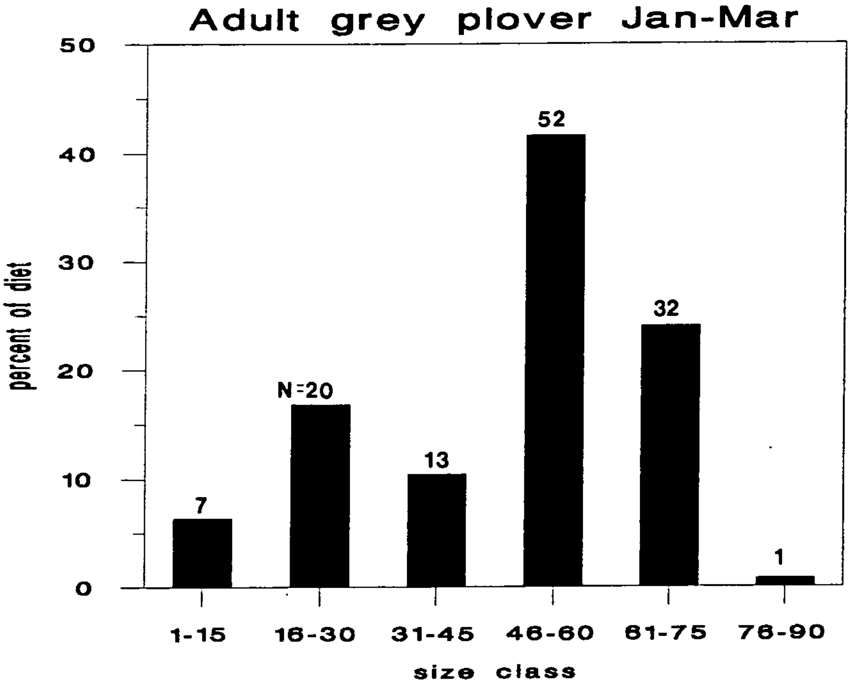
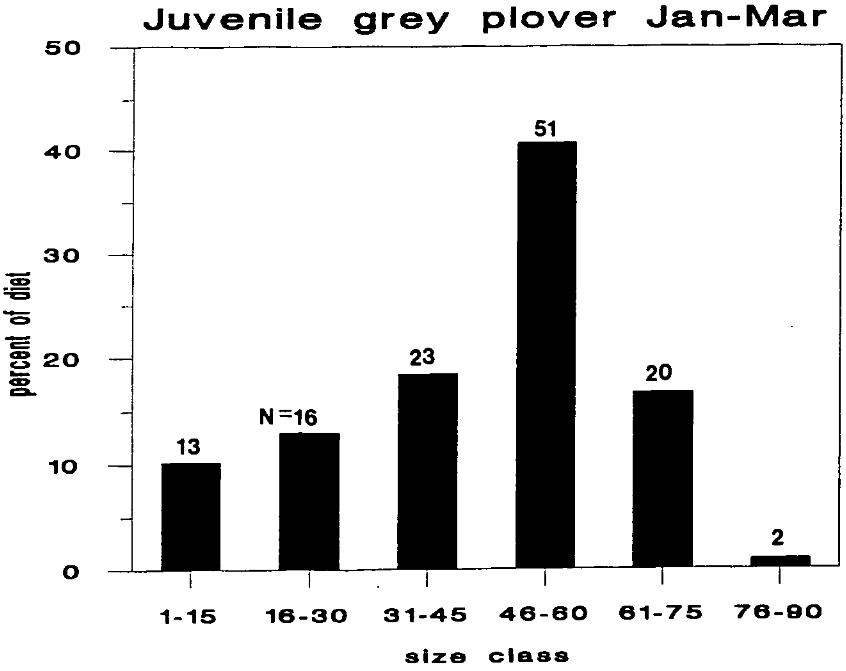


Figure 4.14 The size classes of *Nereis* taken by adult and juvenile grey plovers during January to March as revealed by direct observation.

Number of observations is given in Table 4.4. Size classes in millimetres.





reason for this age-related difference may due to the extra experience of adults in detecting and handling large prey, or due to different distribution on the feeding grounds, for which there is no evidence. The results for adult and juveniles in the second winter period lend credence to the experience hypothesis (Figure 4.14). Here there is very much less age difference, except that adults took slightly more worms of 46mm and above, and the difference is not statistically significant (Mann-Whitney test $U_{125, 108} = 6095$, one-tailed P=0.093). If juveniles improved in their foraging skills over the winter, we would expect to see an increase in the proportion of large worms taken.

4.3.2.4 Between which species is overlap in prey size highest?

The preceding section identified that significant intraspecific differences occurred in grey plover, godwit and curlew. In which species and age/sex groups between species do we observe greatest overlap, and which groups least overlap? Since the size-classes to which worms were assigned were different for each species (because worm length was estimated in relation to the overall length of the bird's bill), it is not so easy to compare the observational data between species directly. Nevertheless, the important patterns of size distribution can be resolved. From the results of the previous section we can rank each group within the species and between species in increasing order of size of *Nereis* that is most important in the diet :

juvenile grey plover Sep-Dec < juvenile grey plover Jan-Mar < adult grey plover Sep-Dec < adult grey plover Jan-Mar < male godwits (of all ages) < adult female godwit < juvenile female godwit < male curlew < female curlew.

Whilst interspecific differences are likely to be greater than intraspecific differences, the degree of overlap between species will depend on the age/sex group that is used in the comparison. Hence the greatest interspecific overlap in prey size is expected between juvenile female godwits and male curlews (of all ages), and between adult grey plover (Jan-Mar) and male godwit (of all ages). The least amount of overlap is expected between juvenile grey plovers in September-December and female curlews. It is necessary to modify the estimates of worm size for males and females of godwit and curlew for estimates of dietary overlap between species, because in the direct observations it was assumed that bill length in the sexes in curlew and godwit were similar and a mean bill length for the species was used in the comparisons of worm length with bill length. We know that there are sexual differences in bill length in godwit (Smith 1975) and curlew (Townshend 1981), and hence estimates of worm length in relation to males' bills (which are smaller than the species mean) were slight overestimates of worm length and estimates of worm length in relation to females' bills (which are larger than the species mean) were slight underestimates of worm length. Table 4.5 shows the original size categories used for curlew and godwits and the categories allowing for the sexual difference in bill length. These adjustments are necessary in order to establish the degree of overlap between species, which is the primary reason for this investigation.

The dietary overlap equation of Pianka (1973) gives a measure that can be used to make prey size comparisons between pairs of species :

$$\text{Overlap} = \Sigma\, p_i\, q_i \,/\, (\,\Sigma\, p_i^{2}\ \ \Sigma\, q_i^{2})^{1/2}$$

where p_i and q_i are the relative occurrences of each prey size category i in the diets of the two predators respectively. The prey-size categories used in the calculations of overlap are given in Appendix 2.1.

Table 4.6 shows the prey size overlap indices for all pairs of species. Although the indices should be viewed only as a guide to the degree of dietary overlap (since the prey size categories for each species were not precisely the same), interspecific depletion

Table 4.5 The size-classes (mm) used in the direct estimations of *Nereis* length taken by curlew and godwit, allowing for sexual difference in bill length within these two species.

a) curlew

UNCORRECTED SIZE CLASS	CORRECTED FOR MALES	CORRECTED FOR FEMALES
1-30	1-28	1-35
31-60	29-55	36-70
61-90	56-83	71-105
91-120	84-110	106-140
121-150	111-138	141-175

b) godwit

UNCORRECTED SIZE CLASS	CORRECTED FOR MALES	CORRECTED FOR FEMALES
1-23	1-20	1-25
24-46	21-40	26-50
47-69	41-60	51-75
70-92	61-80	76-100
93-115	81-100	101-125
116-138	101-120	126-150

Table 4.6 Prey size overlap indices (percent) within and between species for curlew, grey plover and godwit.

Abbreviations used: juv=juvenile, ad=adult, fem=female, GV=grey plover, BA=godwit, CU=curlew.

	juv GV Sep-Dec	juv GV Jan-Mar	ad GV Sep-Dec	ad GV Jan-Mar	male BA	ad fem BA	juv fem BA	male CU
juv GV Jan-Mar	89							
ad GV Sep-Dec	94	83						
ad GV Jan-Mar	69	97	79					
male BA	46	84	55	86				
ad fem. BA	41	88	67	90	96			
juv fem. BA	33	74	62	75	80	95		
male CU	34	48	47	69	58	93	76	
fem CU	16	22	37	22	39	49	75	98

competition is potentially important only between certain ages/sexes, and particularly high dietary overlap occurred between male curlew and adult female and juvenile female godwit (Figure 4.15), between adult grey plover (Jan-Mar) and adult female and male godwit (Figure 4.16), and between juvenile grey plover (Jan-Mar) and male and adult female godwit (Figure 4.17). Direct depletion competition is unlikely to occur between curlew and grey plover, since overlap in the sizes of *Nereis* between these species is very low (Figure 4.18). The implication, for interspecific depletion competition, of intraspecific differences in prey size taken is that the number of individuals of each species that share the same size of prey will be lower than if all individuals of each species fed on the same size of prey. This reduces the potential for interspecific depletion of each size of prey. The following section examines the extent to which each shorebird predator can deplete the prey stock over the course of a winter.

4.4 Depletion of the prey stock.

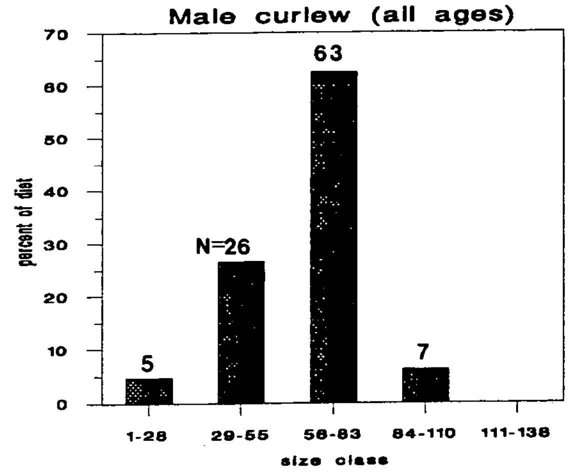
4.4.1 Introduction.

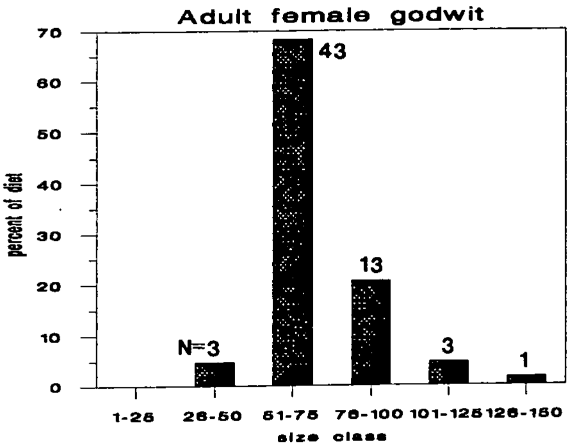
Competition can occur if individuals of one species eat so much of the available prey stock that individuals of other species experience a decrease in their prey intake rate due to reduced prey densities. Whilst it is difficult to predict or measure a level of prey abundance below which food supply affects intake rate, it is possible to determine the proportion of the standing crop present at the start of the season that is consumed by each shorebird species during the course of the season and hence to evaluate the likelihood of competition occurring. There are three methods for estimating total benthic food consumption by each species of predator;

i) direct field observations of feeding rates and estimates of the duration of feeding during a 24 hour period.

Figure 4.15 The degree of overlap in the size classes of *Nereis* taken by male curlew, adult female godwit and juvenile female godwit.

Number of observations is given in Table 4.4. Size classes in millimetres. Size classes have been corrected for differences in bill length between male and females (see text).





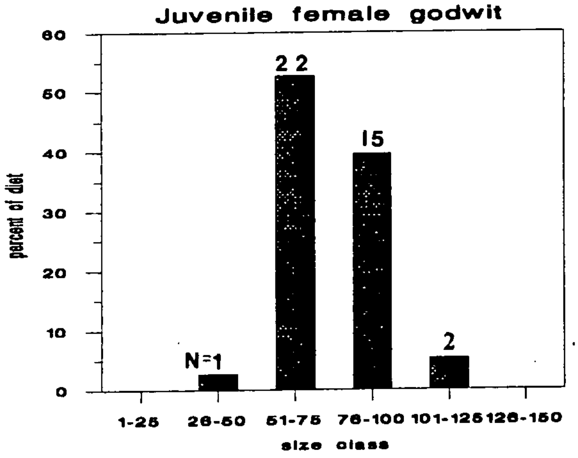


Figure 4.16 The degree of overlap in the size classes of *Nereis* taken by adult grey plover in January to March and adult female and male godwit.

Number of observations is given in Table 4.4. Size classes in millimetres. Size classes have been corrected for differences in bill length between male and female godwits (see text).

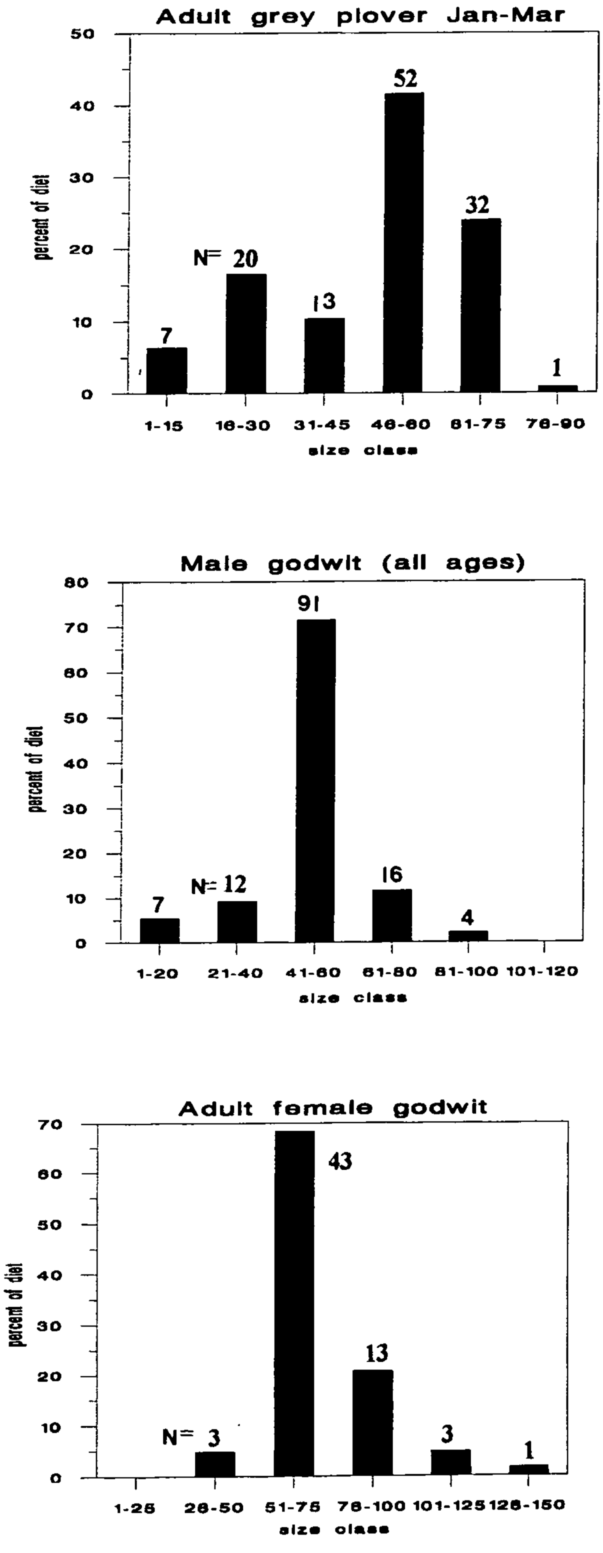


Figure 4.17 The degree of overlap in the size classes of *Nereis* taken by juvenile grey plover in January to March and male and adult female godwit.

Number of observations is given in Table 4.4. Size classes in millimetres. Size classes have been corrected for differences in bill length between male and female godwits (see text).

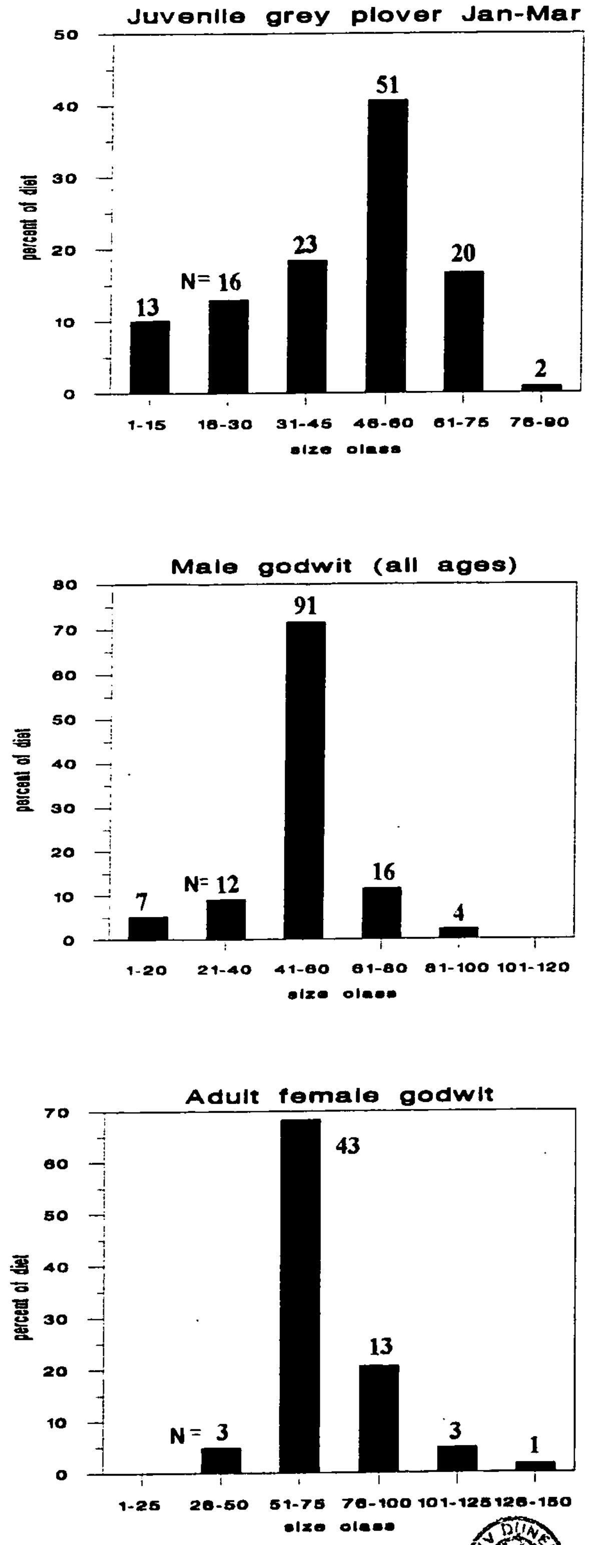
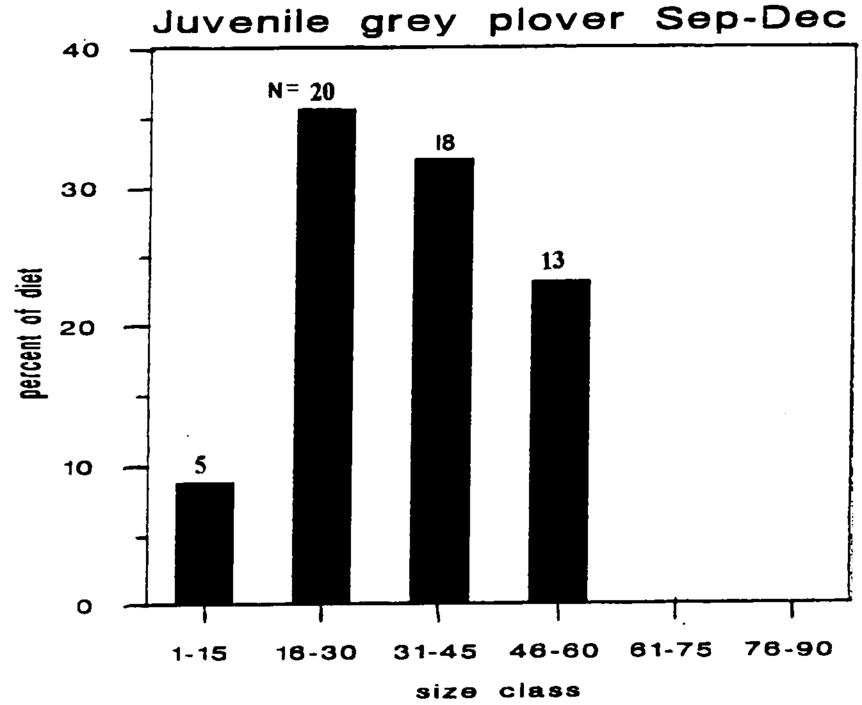
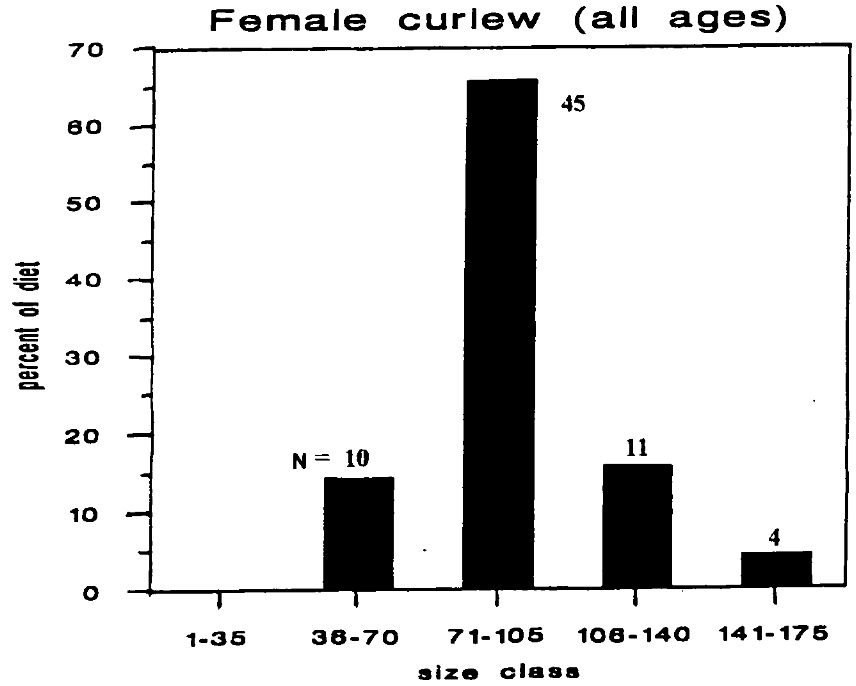


Figure 4.18 The degree of overlap in the size classes of *Nereis* taken by juvenile grey plover in September to December and female curlew.

Number of observations is given in Table 4.4. Size classes in millimetres. Size classes have been corrected for differences in bill length between male and female curlews (see text).





ii) from comparison of measured prey densities before and after a period of predation. Predator exclosure devices may be used to exclude only the relevant predators and to allow in others, such as bottom- feeding fish and invertebrate predators.

iii) from estimates of the metabolic requirements of each species coupled with estimates of the energy content of prey items and estimates of prey stock at the start of the period of predation.

The first method can generally provide reliable estimates of food intake during daylight hours only, due to difficulties of measuring prey size and intake rate during darkness. Since we know that shorebirds feed at night as well as by day, and that some species may acquire at least 50% of their daily energy requirements during darkness (Dugan 1981*b*; Pienkowski *et al.* 1984), it is an imperfect method. The second method carries with it problems of accurate sampling of prey that is known to be very patchily distributed, and cannot attribute loss of worms to any particular predator or to non-predator mortality. Even with the use of exclosures, which aim to circumvent the latter problem, there are difficulties of interpretation, in that the physical presence of the exclosure may alter patterns of water-flow and sedimentation inside the exclosure. This in turn may artificially change the relative and absolute densities of invertebrates inside the exclosure (Millard 1975; Pienkowski 1980), or may decrease invertebrate densities inside relative to outside if invertebrates move into the low density predated area to avoid the possible effects of intraspecific competition in the less predated area (Baird *et al.* 1985).

The third method probably provides the best single estimate of overall prey intake since the energetic requirements of a shorebird can be calculated over a whole 24 hour period - to include predation by both day and night.

4.4.2 Methods and calculations.

The method I have used employs a set of predictive equations and assumptions to calculate an individual bird's total daily energy consumption (note that values of energy are given in kcal, as predictive equations from the literature used this measurement. To convert kcal into kJ, multiply by 4.187) :

i) Basal Metabolic Rate (BMR), that is the rate of energy expenditure of an inactive, post-absorptive animal in a thermoneutral environment during the resting phase of its daily cycle. Estimates were taken from values in Evans *et al.* (1979) who used allometric equations derived by Kendeigh *et al.* (1977) from a range of non-passerine species;

BMR $(\text{kcal day}^{-1}) = 0.5224\ W^{0.7347}$ where W= mass in grams

More recent work however, suggests that shorebirds maintain BMRs higher than the average for non-passerines (Castro 1987; Kersten and Piersma 1987; Scott 1991). With this in mind, BMR calculated from the equation of Kendeigh *et al.* (1977) should probably be considered a minimum estimate for shorebirds.

ii) Daily Energy Budget (DEB). This is the total energy requirements of a free-living bird and includes the energy required in foraging, flying to and from roost sites, avoiding predators, roosting and any social behavour such as territorial defence. DEB is usually expressed in terms of a multiple of BMR. Ebbinge *et al.* (1975) suggested that DEB for a range of free-living birds generally falls between 2 and 4 times BMR. However, Smith (1975) estimated the DEB of free-living bar-tailed godwits to equal about 5.0 times BMR. In the present study the assumption made by Evans *et al.* (1979) of 4X BMR for curlew and godwit and 3X BMR for grey plover was used, since it is believed that grey plovers use a less energy-demanding method of foraging. (The multiples of BMR used were derived from field studies of DEBs which were then related to BMRs calculated from the equation of Kendeigh *et al. op. cit.*).

iii) average energetic values of prey. Dugan (1981) calculated the calorific value for *Nereis* (the main prey of the three predators) and calculated a relaxed body length - mass equation;-

$$\log(\text{dry flesh weight in mg}) = a + b \log(\text{body length in cm})$$

where $a = {}^{-}0.462 \pm 0.039$ (S.E.)

$b = 2.47 \pm 0.0037$ (S.E.) $n=22$

mean calorific value for *Nereis* (from bomb-calorimetry) = 4.7 cal mg^{-1} (Dugan 1981).

iv) Digestive efficiencies. Shorebirds assimilate about 80-90% of the food they ingest (Ashkenazie and Safriel 1979; Evans *et al.* 1979). This means that the multiple of BMR to estimate energy intake as food should be increased to about 4.5 for curlew and godwit and to about 3.5 for grey plover.

The estimate of DEB for an individual of each species is therefore;

SPECIES	BODY MASS (g)	BMR (kcal day $^{-1}$)	MULTIPLE	DEB (kcal day $^{-1}$)
CURLEW	790	70	4.5	315
GODWIT	280	33	4.5	149
GREY PLOVER	240	29	3.5	102

The DEB values above are estimates of the total energy required as food for an individual per 24 hours. In order to calculate the total energy requirements of the whole population of each species during the main period of predation on *Nereis* (September to March), the DEB is multiplied by the number of bird days, where ;

Bird Days = population size x number of days that population is present (Appendix 2.2).

Total energy requirements as food of the curlew population of Seal Sands September 1991 to March 1992= DEB x bird days

= 315 kcals x 77280 bird days = 24.34 million kcal

Total energy requirements as food of the godwit population of Seal Sands September 1991 to March 1992= DEB x bird days

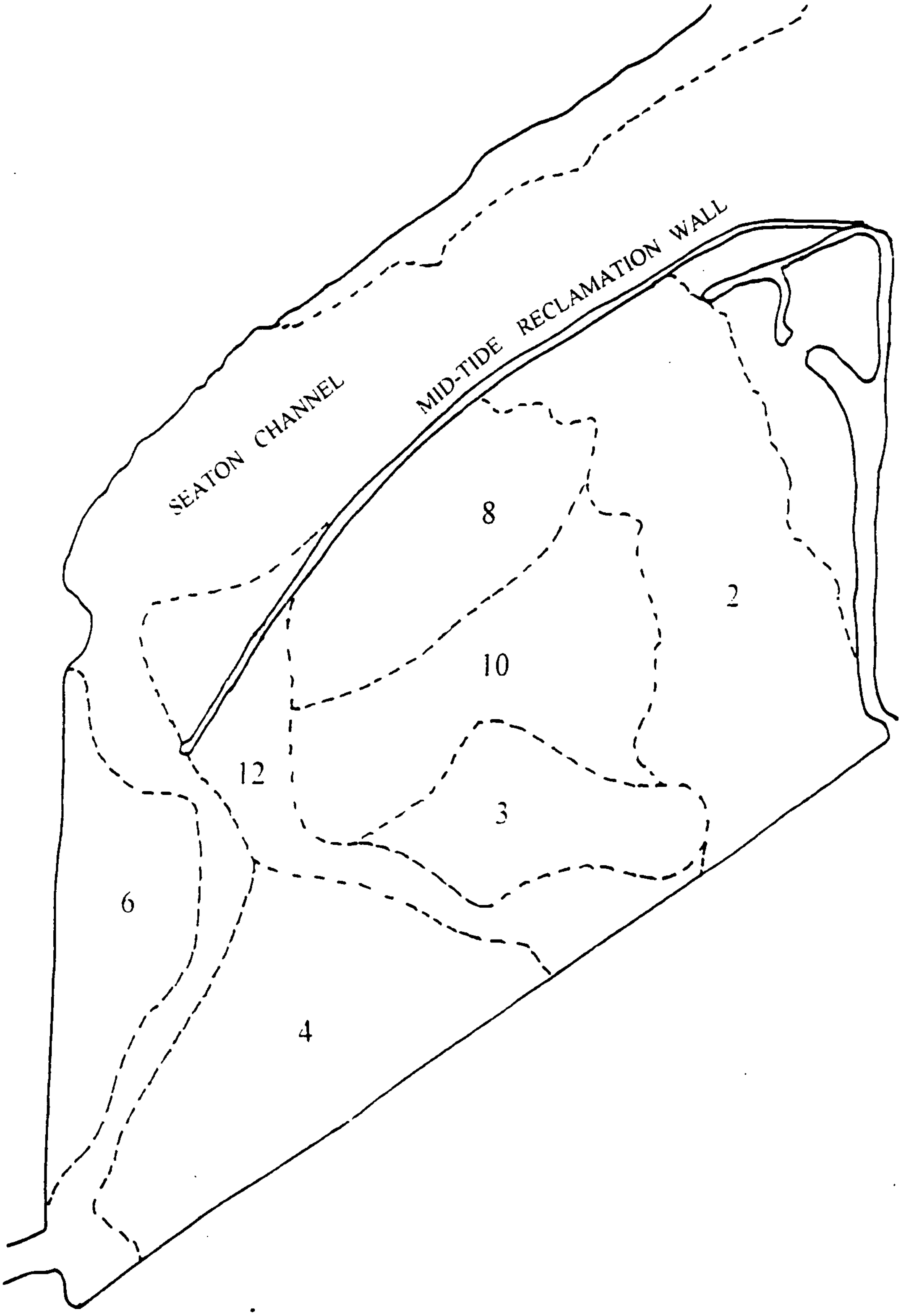
= 149 kcals x 26345 bird days = 3.93 million kcal

Total energy requirements as food of the grey plover population of Seal Sands September 1991 to March 1992 = DEB x bird days

= 102 kcals x 25805 bird days = 2.63 million kcal

Since spatial heterogeneity exists with respect to prey density and density of shorebird predators over Seal Sands, spatial variation in depletion is expected. Estimates of depletion were therefore made for seven mudflat areas (Figure 4.19). In order to calculate the depletion of the September standing crop of *Nereis* over the winter in the different feeding areas, we firstly need to estimate the number of worms taken by each species. To estimate this, the total feeding duration for each species on Seal Sands is calculated, which will equal the amount of feeding time that the population of each of the predators uses to acquire its required energy intake. Since shorebirds change their distribution over the feeding areas through the tidal cycle, it is necessary to calculate bird feeding hours for each stage of the tidal cycle and sum the results to get an estimate of the total bird feeding hours for each area (see below). All feeding by the three large shorebird species generally occurred between five hours before low water and 4 hours

Figure 4.19 Shorebird feeding areas of Seal Sands used for calculations of prey depletion rates.



after low water, although particular feeding areas are exposed for less time than this, especially at lower tidal elevations.

Monthly (at least) counts of feeding birds of each species were made through the tidal cycle to estimate bird feeding hours on each of the main feeding areas per day. These counts were then multiplied by the number of days in each month to provide estimates of the monthly bird feeding duration on each area. Counts were occasionally missed for a particular segment of the tidal cycle, and in these cases a value was interpolated from adjoining counts. Although it is known that nocturnal foraging occurs in shorebirds on Seal Sands (Dugan 1981; Wood 1984), for the purposes of these calculations none is assumed, since as long as the proportion of bird feeding hours on each area was the same by day as by night the proportion of total energy intake that each area provides remains the same.

The duration of feeding in each month on each area in hours was transformed to days by dividing by 24 (see Appendix 2.3 for details of bird feeding hours).

The energy intake of each species on area *a*, $EIR_a = BFD_a / BFD_t \times EIR_s$

where BFD_a is bird feeding days of each species on area *a* between September and March; BFD_t is bird feeding days of each species on the whole of Seal Sands, September to March; and EIR_s is the energy intake requirement (million kcal) for each species population September to March (see Appendix 2.3 for workings of calculations).

The energy requirements of each species of shorebird on the main feeding areas of Seal Sands are summarised in Table 4.7.

Now that we have estimates of the total energy intake of each population of predator on each feeding area, we can convert this energy into worm equivalents, given a knowledge

Table 4.7 Summary of the estimated energy requirements (in million kcal) of three shorebird species between September '91 and March '92 on the main feeding areas of Seal Sands.

FEEDING AREA	**ENERGY REQUIREMENTS OF CURLEW**	**ENERGY REQUIREMENTS OF GODWIT**	**ENERGY REQUIREMENTS OF GREY PLOVER**
2	1.28	0.18	0.29
3	1.20	0.08	0.18
4	6.46	1.31	0.22
6	8.04	1.41	0.85
8	2.52	0.30	0.55
10	2.50	0.43	0.41
12	2.34	0.22	0.12
TOTAL (EIRs)	24.34	3.93	2.63

of the mean sizes of prey taken and the calorific content of that prey. For these purposes it is assumed that all energy that each species ingests on Seal Sands is derived from *Nereis*, which is present on Seal Sands as 0-1 year old animals of mean length 25 mm, and as 1+ year old animals of mean length 65 mm, (Evans *et al.* 1979). This assumption is valid since *Nereis* is the only abundant large prey species on Seal Sands. From the length-mass equation of Dugan (1981) the energy content of each age-class of *Nereis* was calculated as 6.30 mg for 0-1 year old animals and 42.89 mg for 1+ year old animals, equivalent to energy contents of 29.6 cal and 202 cal respectively.

The observations of favoured size classes of *Nereis* taken by each shorebird (see earlier in this chapter) were used to summarize the diet of each shorebird species;

curlew; 10% 0-1 yr. worms by number, 90% 1+ yr. worms by number
godwit; 30% 0-1 yr. worms by number, 70% 1+ yr. worms by number
grey plover; 50% 0-1 yr. worms by number, 50% 1+ yr. worms by number

The proportion P of total energy requirement supplied to each species by 0-1 yr. worms
$= E_s \times P_s / (E_s \times P_s) + (E_l \times P_l)$
where E_s and E_l is the energy content of small and large worms respectively
and P_s and P_l is the proportion in the diet of small and large worms respectively

The proportion of total energy requirement supplied to each species by 1+ worms is (1-P). See Appendix 2.4 for these calculations.

The estimated energy supplied by each size class of *Nereis* = the proportion of total energy requirement supplied by size class x total energy requirement (see Appendix 2.5). The worm equivalent that these amounts of energy represent was calculated by dividing the estimates of energy from small worms by 0.0296 kcal (i.e. the energy content of 0-1 yr. worm), and by dividing the estimates from large worms by 0.202 kcal (i.e. the energy content of 1+ yr. worm). See Appendix 2.5 for calculations.

Now that we have estimates of the total worm consumption by each species of predator for the main feeding sites, we need to estimate the total worm stock of each of these areas at the begining of the autumn of 1991. Work by Gray (1976) and Evans *et al.*(1979) showed that the 0-1 yr. *Nereis* on Seal Sands constituted about 60% by number of the total population, and the 1+ yr. worms about 40% by number. Total worm stock of each area = mean worm density (obtained from invertebrate sampling) x surface area, and the number of 0-1 yr. worms and 1+ yr. worms = 60% and 40% of this total, respectively (Appendix 2.6).

The depletion of each of the two size classes of *Nereis* = the number of worms consumed divided by the number of worms in the sediment of each area. The percentage depletion of each size class of *Nereis* by each of the shorebird predators is summarized in Table 4.8.

4.4.2.1 The effect of ambient temperatures on the daily energy requirements of shorebirds.

The energy requirements estimated in the previous calculations were based on those of an individual shorebird within its "thermo-neutral zone"; that is, in ambient temperatures in which body temperature is maintained by adjusting the effectiveness of body insulation, rather than by using metabolic energy. With decreasing temperatures however, there comes a point, the "lower critical temperature", when insulation reaches its maximum capacity and further heat production becomes necessary in order to maintain a constant body temperature. Kendeigh (1969) showed, in a range of non-passerines species, that lower critical temperature (T_{lc}) varies with body mass , such that;

Table 4.8 The percentage depletion of each size class of *Nereis* on the main feeding areas of Seal Sands by three large shorebird species between September 1991and March 1992.

a) Curlew

FEEDING AREA	% DEPLETION OF 0-1 YR. WORMS	% DEPLETION OF 1+ YR. WORMS
2	0.42	5.75
3	0.62	8.44
4	1.95	24.37
6	2.68	35.83
8	0.93	12.68
10	1.81	24.55
12	1.88	25.65

b) Godwit

FEEDING AREA	% DEPLETION OF 0-1 YR. WORMS	% DEPLETION OF 1+ YR. WORMS
2	0.23	0.77
3	0.15	0.53
4	1.34	4.71
6	1.73	6.02
8	0.42	1.43
10	1.13	3.99
12	0.66	2.34

c) Grey plover

FEEDING AREA	% DEPLETION OF 0-1 YR. WORMS	% DEPLETION OF 1+ YR. WORMS
2	0.79	1.14
3	0.75	1.14
4	0.51	0.73
6	2.27	3.35
8	1.67	2.46
10	2.40	3.59
12	0.81	1.13

that:

$T_{lc} = 47.17\ W^{-0.1809} \pm 1.382$ (S.E.)

At ambient temperatures below the respective T_{lc} for each species, the rate of heat production (temperature coefficient, *b*) can be described by a rising line representing the regression of standard metabolism (SM) at decreasing ambient temperature. The temperature coefficient *b* for non-passerines during winter was calculated by Kendeigh *et al.* (1977) to be : $b = 0.0457\ W^{0.5886} \pm 1.33$ (S.E.) N=12

The estimated lower critical temperature and temperature coefficient for each species are;

SPECIES	MEAN WINTER BODY MASS (g)	LOWER CRITICAL TEMPERATURE °C	TEMPERATURE COEFICIENT (kcal per °C)
CURLEW	830	14.0	2.39
GODWIT	300	17.0	1.31
GREY PLOVER	240	17.5	1.15

Mean ambient temperature over a 24 hr period (sampled hourly) was calculated from meteorological data (supplied by Hartlepool Borough Council), to produce an estimate of mean monthly temperature (MMT) between September 1991 and March 1992;

MONTH	MEAN TEMPERATURE (°C)
SEPTEMBER	13.4
OCTOBER	9.6
NOVEMBER	5.4
DECEMBER	3.2
JANUARY	3.0
FEBRUARY	4.9
MARCH	6.2

In order to calculate the temperature-adjusted energy consumption of each species, the differences between the mean ambient temperature (MMT) for each month and the lower critical temperature are calculated first. These values are then multiplied by the respective temperature coefficients for each species to estimate the extra energy required for thermoregulation, and the product added to the estimate of BMR. The rate of energy intake as food required per bird day is equal to ;

$[(T_{lc} - \mathrm{MMT})\, b + \mathrm{BMR}]$ x multiple to estimate energy required for feeding and flying (4.5 for curlew and godwit, 3.5 for grey plover). See Appendix 2.7 for workings of calculations.

Now that the temperature-adjusted daily energy intake (DEI) has been calculated for an individual of each species of shorebird in each month, this rate can be multiplied by the monthly population size of each species feeding on Seal Sands, and by the number of days in each month. (see Appendix 2.8 for workings of calculations).

Comparison of the temperature-adjusted total energy requirements with the non-adjusted totals reveals the extent to which ambient temperature is likely to affect intake requirements (Table 4.9).

The ambient temperature-adjusted depletion estimate for each of the feeding areas of Seal Sands is obtained from estimates of the energy that was obtained each month on each of the feeding areas=

$\mathrm{BFD}_{a\,m} / \mathrm{BFD}_{t\,m} \times \mathrm{EIR}_{s\,m}$

where $\mathrm{BFD}_{a\,m}$ is bird feeding days of each species on area *a* in month *m*, and $\mathrm{BFD}_{t\,m}$ is bird feeding days of each species on the whole of Seal Sands for month *m* (from Appendix 2.3), and $\mathrm{EIR}_{s\,m}$ is the energy intake requirements (million kcal) for each species population in month *m* (from Appendix 2.8). These estimates were summed to obtain an estimate of the temperature-adjusted energy consumption on each area for

Table 4.9 The effect of adjusting estimates of energy requirement of shorebirds to ambient temperature over the winter 1991/92.

SPECIES	NON-ADJUSTED ESTIMATE OF POPULATION ENERGY REQUIREMENTS (Million kcal)	TEMP.-ADJUSTED ESTIMATE OF POPULATION ENERGY REQUIREMENTS (Million kcal)	FACTOR OF INCREASE OF ENERGY REQUIREMENT
CURLEW	24.34	30.12	1.24
GODWIT	3.93	5.64	1.44
GREY PLOVER	2.63	3.82	1.45

Table 4.10 The temperature-adjusted percentage depletion of each size class of *Nereis* on the main feeding areas of Seal Sands by three large shorebird species between September1991and March 1992.

a) Curlew

FEEDING AREA	% DEPLETION OF 0-1 YR. WORMS	% DEPLETION OF 1+ YR. WORMS
2	0.5	7.2
3	0.8	10.6
4	2.3	30.9
6	3.2	43.7
8	1.2	15.6
10	2.3	30.4
12	2.4	32.9

b) Godwit

FEEDING AREA	% DEPLETION OF 0-1 YR. WORMS	% DEPLETION OF 1+ YR. WORMS
2	0.3	0.9
3	0.2	0.7
4	1.6	5.5
6	2.6	9.3
8	0.7	2.4
10	2.1	7.5
12	0.9	3.2

c) Grey plover

FEEDING AREA	% DEPLETION OF 0-1 YR. WORMS	% DEPLETION OF 1+ YR. WORMS
2	1.1	1.7
3	1.1	1.6
4	0.7	1.0
6	3.3	4.9
8	2.5	3.7
10	3.4	5.1
12	1.2	1.9

September 1991 to March 1992, and the worm equivalents and depletion percentages were calculated in the usual way (Appendix 2.9). Table 4.10 shows the temperature-adjusted depletion percentages of each size class of *Nereis* in each of the main feeding areas of Seal Sands.

4.4.2.2 Adjustment for changes in assumptions of worm size and DEB.

The estimates of percentage depletion of *Nereis* on each of the main feeding areas presented above were based on the following assumptions;-

1) The daily energy requirement for curlew = 4.5 x BMR
" " " " " godwit = 4.5 x BMR
" " " " grey plover = 3.5 x BMR

2) The mean length of a 1+ age worm = 65 mm
" " " " " 0-1 age worm = 25 mm

These assumptions may not be wholly accurate. To test the sensitivity of the depletion rate calculations to the values of worm length and DEB listed above, calculations were repeated with different values as follows;

A) Worm length assumptions

Different values of worm length used in repeat calculations were substituted into the equations used in the previous analyses to calculate the percentage depletion of each size class of *Nereis* for each of the main feeding areas of Seal Sands;

i) 0-1 yr. worm = 20 mm., 1+ yr. worm = 60 mm. (i.e 20% decrease in length over original estimate of 0-1 worm; 8% decrease in length of 1+worm).

Table 4.11 shows the adjusted depletion percentages based on the assumption of worm 0-1 yr.=20mm and 1+ yr.=60mm. Appendix 2.10 gives the calculations of the adjusted levels of depletion.

A decrease in the assumed length of 0-1 age *Nereis* from 25mm. to 20mm.(20% decrease) and a decrease in the assumed length of 1+ age *Nereis* from 65mm. to 60mm. (8% decrease) increased the number of worms eaten by each species and therefore the percent depletion (since the worm stock is held constant) by an average of 15% in curlew, 16% in godwit, and 17% in grey plover, compared to original estimates.

ii) 0-1 yr. worm = 30 mm., 1+ yr. worm = 70 mm. (i.e. 17% increase in length over original estimate for 0-1 worm; 7% increase in length of 1+ worm).

Table 4.11 shows the adjusted depletion percentages based on the assumption of worm 0-1 yr.=30mm. and 1+ yr. worm=70 mm.. Appendix 2.11 gives the calculations of the adjusted levels of depletion.

An increase in the assumed length of 0-1 age *Nereis* from 25mm. to 30mm.(17% increase) and an increase in the assumed length of 1+ age Nereis from 65 to 70 mm. (7% increase) decreased the number of worms eaten by each species and therefore the percent depletion (since the worm stock is held constant) by a mean of 14% in curlew, 15% in godwit, and 17% in grey plover, compared to original estimates.

Table 4.11 Estimated percentage depletion of each size class of *Nereis* in each of the main feeding areas of Seal Sands between September 1991 and March 1992.

Depletion "A" is based on age 0-1 worms of 30mm and age 1+ worms of 70mm
Depletion "B" is based on age 0-1 worms of 25mm and age 1+ worms of 65 mm
Depletion "C" is based on age 0-1 worms of 20mm and age 1+ worms of 60mm

curlew

i) 0-1 yr. worms

AREA NUMBER	DEPLETION"A"(%)	DEPLETION"B"(%)	DEPLETION"C"(%)
2	0.5	0.5	0.6
3	0.7	0.8	0.9
4	2.0	2.3	2.7
6	2.8	3.2	3.8
8	1.0	1.2	1.4
10	2.0	2.3	2.6
12	2.1	2.4	2.9

ii) 1+ yr. worms

AREA NUMBER	DEPLETION"A"(%)	DEPLETION"B"(%)	DEPLETION"C"(%)
2	6.2	7.2	8.5
3	9.2	10.6	12.4
4	26.6	30.9	36.4
6	37.6	43.7	51.5
8	13.4	15.6	18.4
10	26.2	30.4	35.9
12	28.3	32.9	38.9

godwit

i) 0-1 yr worms

AREA NUMBER	DEPLETION"A"(%)	DEPLETION"B"(%)	DEPLETION"C"(%)
2	0.2	0.3	0.3
3	0.2	0.2	0.3
4	1.4	1.6	1.9
6	2.3	2.6	3.1
8	0.6	0.7	0.8
10	1.9	2.1	2.5
12	0.8	0.9	1.1

ii) 1+ yr. worms

AREA NUMBER	DEPLETION"A"(%)	DEPLETION"B"(%)	DEPLETION"C"(%)
2	0.8	0.9	1.1
3	0.6	0.7	0.9
4	4.7	5.5	6.6
6	7.9	9.3	11.0
8	2.1	2.4	2.9
10	6.5	7.5	8.9
12	2.8	3.2	3.9

Table 4.11 (continued).

grey plover

i) 0-1 yr. worms

AREA NUMBER	DEPLETION"A"(%)	DEPLETION"B"(%)	DEPLETION"C"(%)
2	1.0	1.1	1.4
3	0.9	1.1	1.1
4	0.6	0.7	0.8
6	2.7	3.3	3.9
8	2.0	2.5	3.0
10	2.8	3.4	4.1
12	1.0	1.2	1.5

ii) 1+ yr. worms

AREA NUMBER	DEPLETION"A"(%)	DEPLETION"B"(%)	DEPLETION"C"(%)
2	1.5	1.7	2.1
3	1.4	1.6	1.9
4	0.8	1.0	1.2
6	4.1	4.9	6.0
8	3.1	3.7	4.5
10	4.3	5.1	6.2
12	1.5	1.9	2.2

B) Change in the values of DEB used.

In addition to the adjustments of worm length used in the calculations, different values of DEB were substituted into the equations to allow for inaccuracies in its estimation, since the precise multiple of BMR to use is the subject of debate. The values of depletion calculated above (those adjusted for likely extremes in worm size) were themselves adjusted to different values of DEB. In the original calculations the multiples of BMR used to represent the daily energetic requirements of each shorebird were; curlew = 4.5 x BMR; godwit = 4.5 x BMR; grey plover 3.5 x BMR. In the adjusted estimates of depletion, a chosen maximum and minimum multiple of BMR was used that probably encompassed the true energy requirements of each species; curlew and godwit minimum multiple 4.0, maximum multiple 5.0; grey plover minimum multiple 3.0, maximum multiple 4.0.

The adjusted depletion percentage = adjusted multiple of BMR / original multiple of BMR x estimate of depletion. This provides us with a likely minimum and maximum depletion percentage. Clearly, a 10% (for example) change in the multiple used will give a 10% change in estimated depletion.

4.4.2.3 Final estimates of percentage depletion of foodstock.

Three estimates of percentage depletion are made, which incorporate adjustments for ambient temperature, and low, high and standard values of worm length and BMR;

The "minimum" estimate of depletion was obtained by assuming that the energetic requirements of curlews and godwits equal 4.0 times BMR and that of grey plovers equal 3.0 times BMR, and that the mean length of a 0-1 yr. *Nereis* is 30 mm and that of a 1+ yr. *Nereis* is 70 mm.

The "maximum" estimate of depletion was obtained by assuming that the energetic requirements of curlews and godwits equal 5.0 times BMR, and that of grey plovers equal 4.0 times BMR, and that the mean length of a 0-1 yr. *Nereis* is 20 mm and that of a 1+ yr. *Nereis* is 60 mm.

The "standard" estimate of depletion was obtained by assuming that the energetic requirements of curlews and godwits equal 4.5 times BMR, and that of grey plovers equal 3.5 times BMR, and that the mean length of a 0-1 yr. *Nereis* is 25 mm and that of a 1+ yr. *Nereis* is 65 mm.

Tables 4.12-4.14 give the final estimates of minimum, maximum and standard percentage depletion of *Nereis* numbers by the three large shorebird species on the main feeding areas of Seal Sands.

4.4.3 Implications of food depletion.

Are the degrees of depletion seen here high enough to elicit food shortage, here defined as a decrease in rate of net energy intake caused by a decrease in the density of available prey? Since depletion of the small size class of *Nereis* by the three large shorebird species in all sites was less than 6% it seems unlikely that the available density of small worms becomes low enough to reduce the rate of net energy intake. However, other shorebirds which feed on small *Nereis* and which are abundant during the winter, such as redshank and dunlin (Evans *et al.* 1979), may consume a considerable amount of the small size class, although this has not been estimated in the present study. The great majority (87%) of energy intake of grey plovers came from the large worms, so it is possible that this species could experience food shortage in the areas where depletion of large worms was high. Indeed, the grey plover may be more susceptible than other species to lowered prey densities, since the density of available prey (that is the density

Table 4.12 The minimum, standard and maximum estimates of percentage depletion of *Nereis* by curlew on the main feeding areas of Seal Sands, September '91 to March '92. See text for definitions of minimum, standard and maximum.

a) 0-1 yr.worms

AREA NUMBER	MINIMUM ESTIMATE	STANDARD ESTIMATE	MAXIMUM ESTIMATE
2	0.41	0.53	0.70
3	0.60	0.78	1.02
4	1.77	2.29	2.99
6	2.50	3.23	4.23
8	0.88	1.16	1.50
10	1.73	2.26	2.93
12	1.88	2.43	3.19

b) 1+ yr. worms

AREA NUMBER	MINIMUM ESTIMATE	STANDARD ESTIMATE	MAXIMUM ESTIMATE
2	5.49	7.18	9.41
3	8.07	10.57	13.82
4	23.63	30.91	40.49
6	33.39	43.69	57.23
8	11.93	15.59	20.42
10	23.29	30.43	39.86
12	25.15	32.91	43.22

Table 4.13 The minimum, standard and maximum estimates of percentage depletion of *Nereis* by godwit on the main feeding areas of Seal Sands, September '91 to March '92. See text for definitions of minimum, standard and maximum.

a) 0-1 yr. worms

AREA NUMBER	MINIMUM ESTIMATE	STANDARD ESTIMATE	MAXIMUM ESTIMATE
2	0.20	0.27	0.37
3	0.16	0.21	0.29
4	1.22	1.57	2.09
6	2.04	2.64	3.48
8	0.52	0.69	0.90
10	1.65	2.14	2.81
12	0.69	0.93	1.20

b) 1+ yr. worms

AREA NUMBER	MINIMUM ESTIMATE	STANDARD ESTIMATE	MAXIMUM ESTIMATE
2	0.71	0.94	1.26
3	0.55	0.74	0.96
4	4.16	5.52	7.33
6	6.98	9.25	12.26
8	1.83	2.41	3.19
10	5.73	7.52	9.90
12	2.48	3.24	4.36

Table 4.14 The minimum, standard and maximum estimates of percentage depletion of *Nereis* by grey plover on the main feeding areas of Seal Sands, September '91 to March '92. See text for definitions of minimum, standard and maximum.

a) 0-1 yr.worms

AREA NUMBER	MINIMUM ESTIMATE	STANDARD ESTIMATE	MAXIMUM ESTIMATE
2	0.82	1.14	1.55
3	0.78	1.08	1.52
4	0.48	0.67	0.93
6	2.35	3.27	4.46
8	1.72	2.47	3.42
10	2.43	3.43	4.72
12	0.87	1.23	1.74

b) 1+ yr. worms

AREA NUMBER	MINIMUM ESTIMATE	STANDARD ESTIMATE	MAXIMUM ESTIMATE
2	1.24	1.71	2.38
3	1.17	1.62	2.22
4	0.72	1.01	1.41
6	3.51	4.90	6.81
8	2.67	3.70	5.14
10	3.69	5.14	7.12
12	1.29	1.85	2.50

of prey that is active and near the sediment surface) becomes depressed at low temperatures (Pienkowski 1980). Whilst it is as yet impossible to calculate the density of available prey, it is certainly lower than the absolute density calculated from sediment samples, since not all prey are available at any given time. If grey plovers were suffering food shortage by late winter, then the most important competitor is the species removing the most worms. In each case curlews were responsible for consuming the largest number of large worms, and depleted on each of the main feeding areas between 5.2 times and 17 times (median 7.3 times) the proportion of large worms that godwits depleted, and between 4.8 times and 34.9 times (median 7.7 times) the proportion of large worms that grey plovers depleted. Whilst about half of the prey items caught by grey plovers were large worms (the preferred size of curlew and godwit), their low level of depletion of the large *Nereis* was probably unlikely to reduce prey densities to levels that reduced intake rates of curlews or godwits. The possibility exists that curlews and godwits were competing for large worms, since 98 and 94% of their respective energy intake came from this size class. I have shown above that curlews depleted a far greater proportion of the food stock than did godwits, so curlews were responsible for any food shortage that godwit may have experienced. Because godwits are largely tactile feeders and can reach worms buried in sediment up to at least 10cm, the density of prey available to them is higher than that available to grey plovers, at a given absolute worm density. Therefore, under similar environmental conditions and at a given absolute prey density, godwits are likely to be able to attain a higher rate of energy intake than grey plovers. However, since plovers probably expend less energy in foraging than godwits and because grey plovers require less energy per day than do godwits, it is unlikely that grey plovers experience greater food shortage than godwits.

The intraspecific partial segregation of prey size that was demonstrated earlier in this chapter doubtless plays a part in reducing interspecific depletion competition, because the number of individual shorebirds sharing a given size class of prey is reduced, which in turn reduces the magnitude of depletion of a given size class.

It is possible that the percentage depletion of the standing crop is of little relevance to shorebirds if densities of available prey were very much greater than the level at which prey availability affects the rate of net energy intake. If however depletion of the large size class of *Nereis* in certain areas was severe enough to reduce densities of prey to such levels, we would expect to observe some or all of the following to occur during the latter part of the winter:-

i) reduced bird usage late in the season on those feeding areas that held low densities of prey, because there may a limit to the density of predators that a given density of prey can support.

ii) a reduction of net energy intake rate in late winter, at least in some individuals.

iii) migration of part of the population away from Seal Sands.

iv) poor condition or mortality of individuals.

v) switch to more abundant prey type.

I shall deal with the evidence for each in turn.

i) If the density of large *Nereis* in a particular area became too low to provide shorebirds with a rate of energy intake greater than the rate of energy expenditure, one would expect that the predators would abandon the depleted areas and move into less depleted ones. However, the situation is complicated by the fact that prey density alone may not explain most of the variation in bird density; factors such as the height of the feeding area above the water table, sediment type, and distance to roost sites are likely to play important roles in determining the feeding site chosen by shorebirds, especially if the minimum prey density encountered on

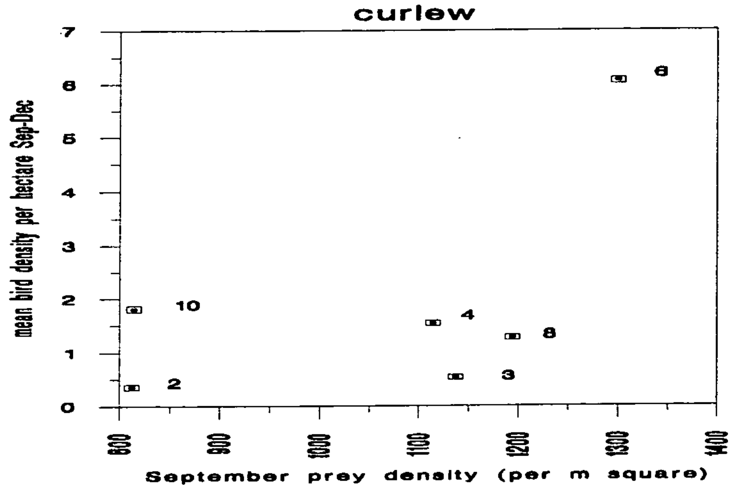
Seal Sands is well above the level at which prey density starts to limit energy intake rates. Notwithstanding these caveats, it is legitimate to compare firstly bird density with prey density for the main feeding sites, and then to see whether areas which held low densities of prey by late winter were less preferred by shorebirds late in the season. Figure 4.20 and Table 4.15 show that the relationship between prey density on a feeding area and low-water shorebird density is rather weak, but that area 6, which had the highest density of *Nereis,* consistently supported the highest low-water shorebird densities. Note that Figure 4.20a shows data from the autumn (using prey density sampled in September and bird counts from September to December) and Figure 4.20b shows data from the spring (using prey density sampled in March and bird counts from January to March). The generally weak correlations between absolute prey density and lowwater bird density of an area (Table 4.15) suggests that factors other than absolute prey density- such as the relative availability of prey - are important in determining low- water bird usage at given sites. However, there is evidence that there was a decrease in use through the winter by curlew and grey plover of those areas that held low densities of prey by March, namely areas 10 and 2 (Figure 4.21). This suggests that densities of prey limited the number of bird-hours that could be sustained on these areas. It should be emphasised, however, that without estimates of the density of available prey in each area, conclusions about the effect of absolute prey density on bird use should be tentative.

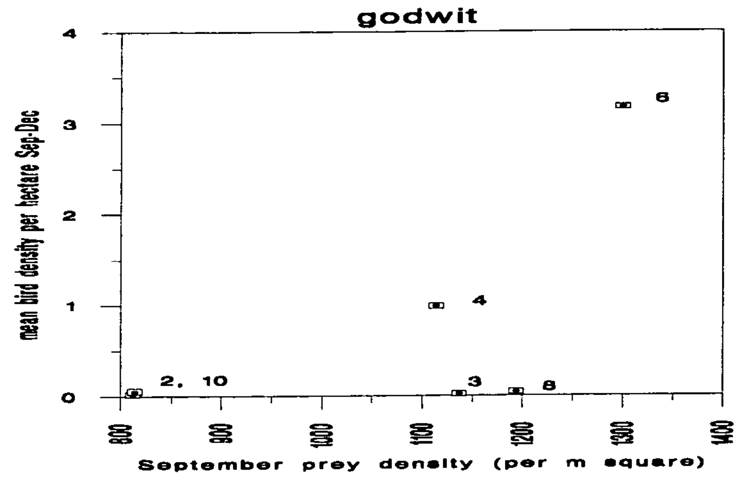
ii) There are insufficient data to test the prediction that lowered prey density can cause lowered energy intake rates of each shorebird species.

iii) It is true that the numbers of all three of the study species start to decline in late winter/early spring, although that this is in any way related to lowered food densities at this time of the year is doubtful. The numbers of godwit and grey plover generally reach a yearly maximum in February so it seems unlikely that prey stocks during this time of the year are insufficient to support large numbers of

Figure 4.20a The relationship between the September prey density and the mean low-water bird density (September to December) on six areas of Seal Sands.

Data from 1991. Numbered points refer to the feeding sites shown in Figure 4.19. Correlation coefficients given in Table 4.15.





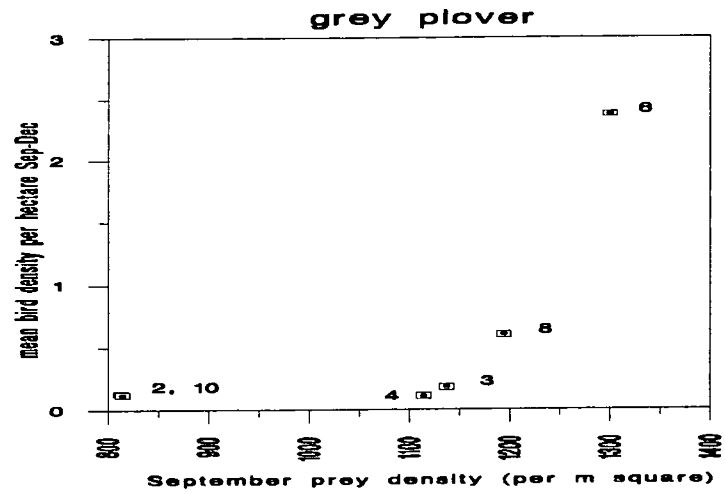


Figure 4.20b <u>The relationship between the March prey density and the mean low-water bird density (January to March) on six areas of Seal Sands.</u>

Data from 1992. Numbered points refer to the feeding sites shown in Figure 4.19. Correlation coefficients given in Table 4.15.

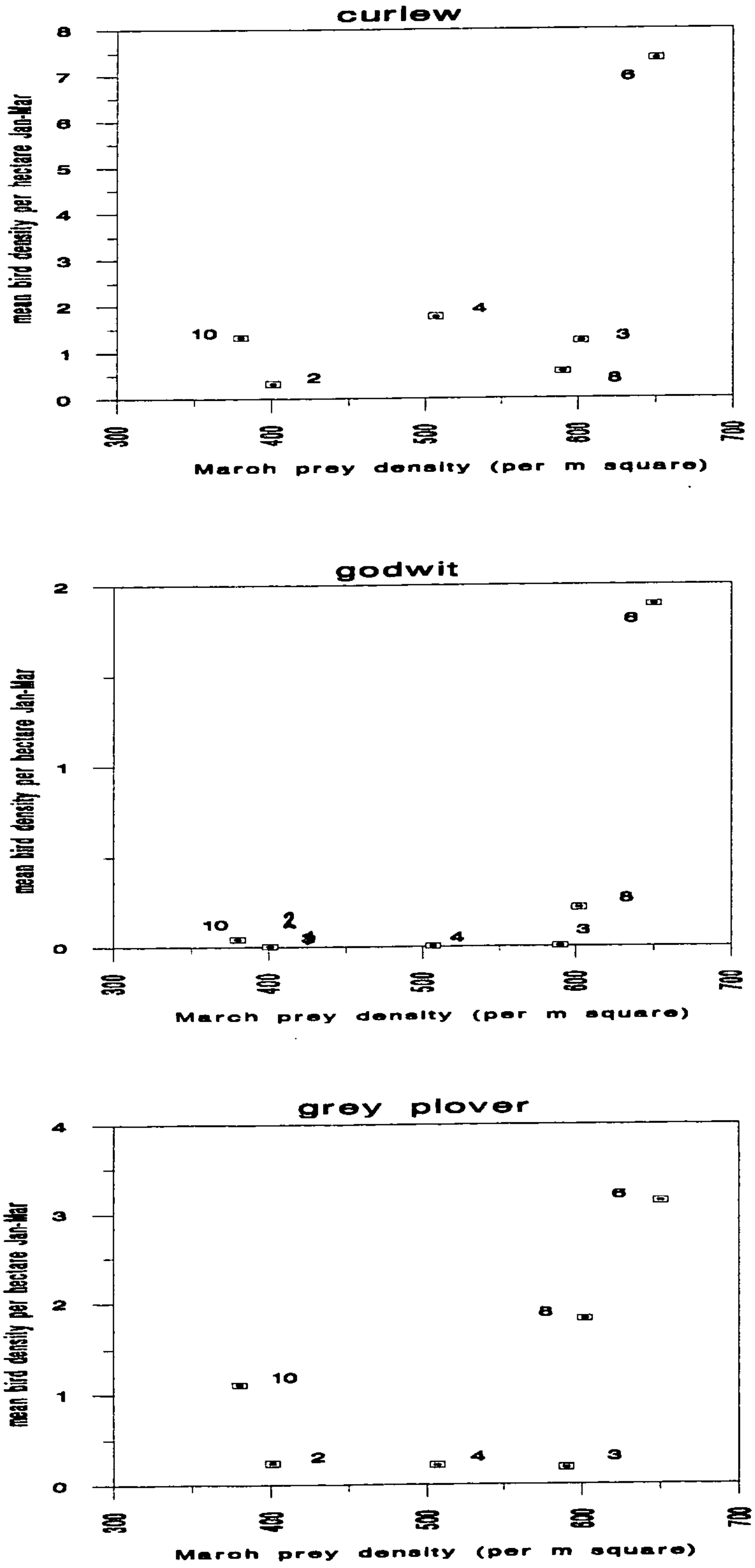


Figure 4.21a Monthly percentage of the Seal Sands total of curlew present on each site at low water during the winter 1991/92.

From low water counts in the middle of each month..

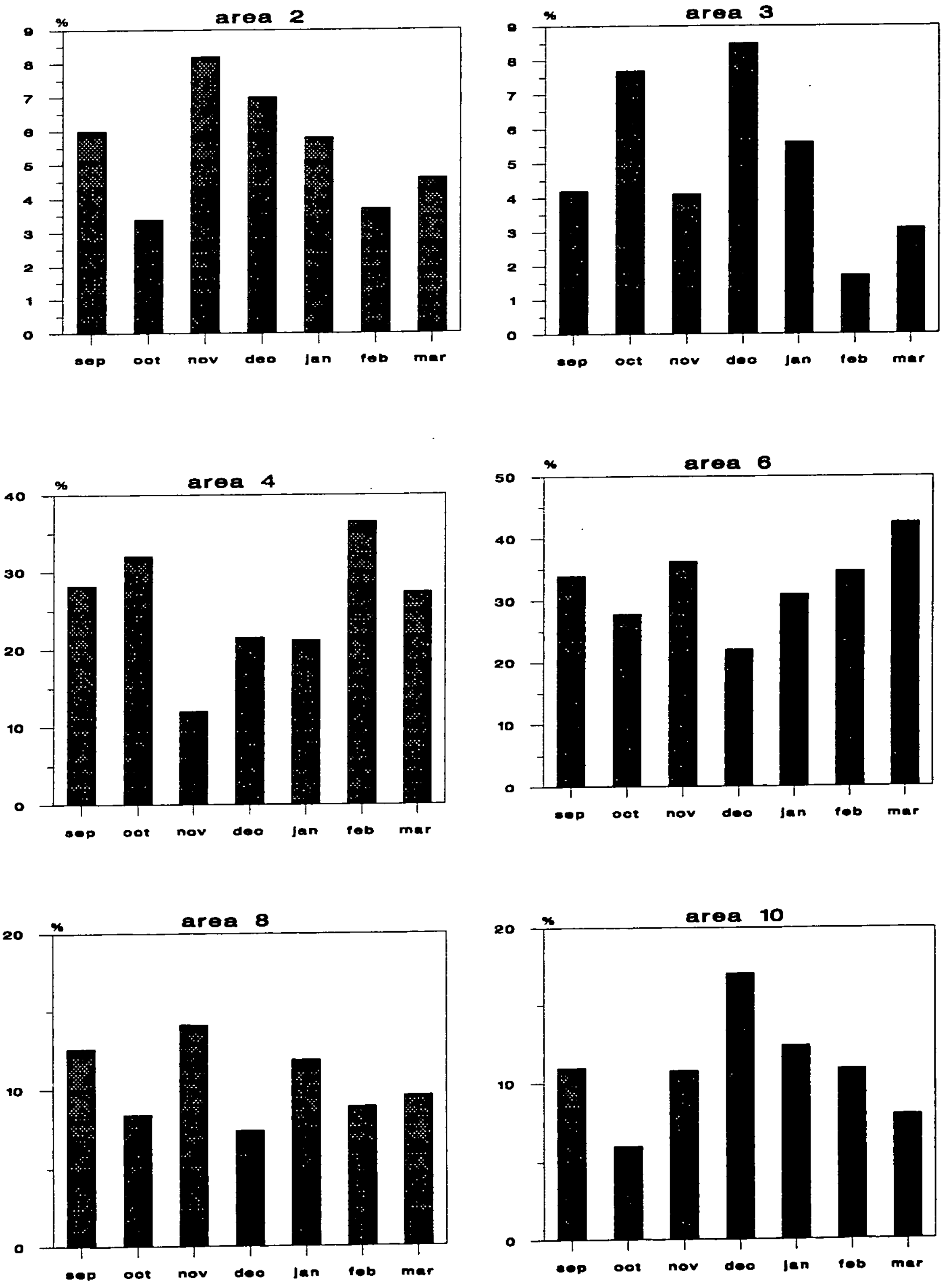


Figure 4.21b Monthly percentage of the Seal Sands total of godwit present on each site at low water during the winter 1991/92.

From low water counts in the middle of each month..

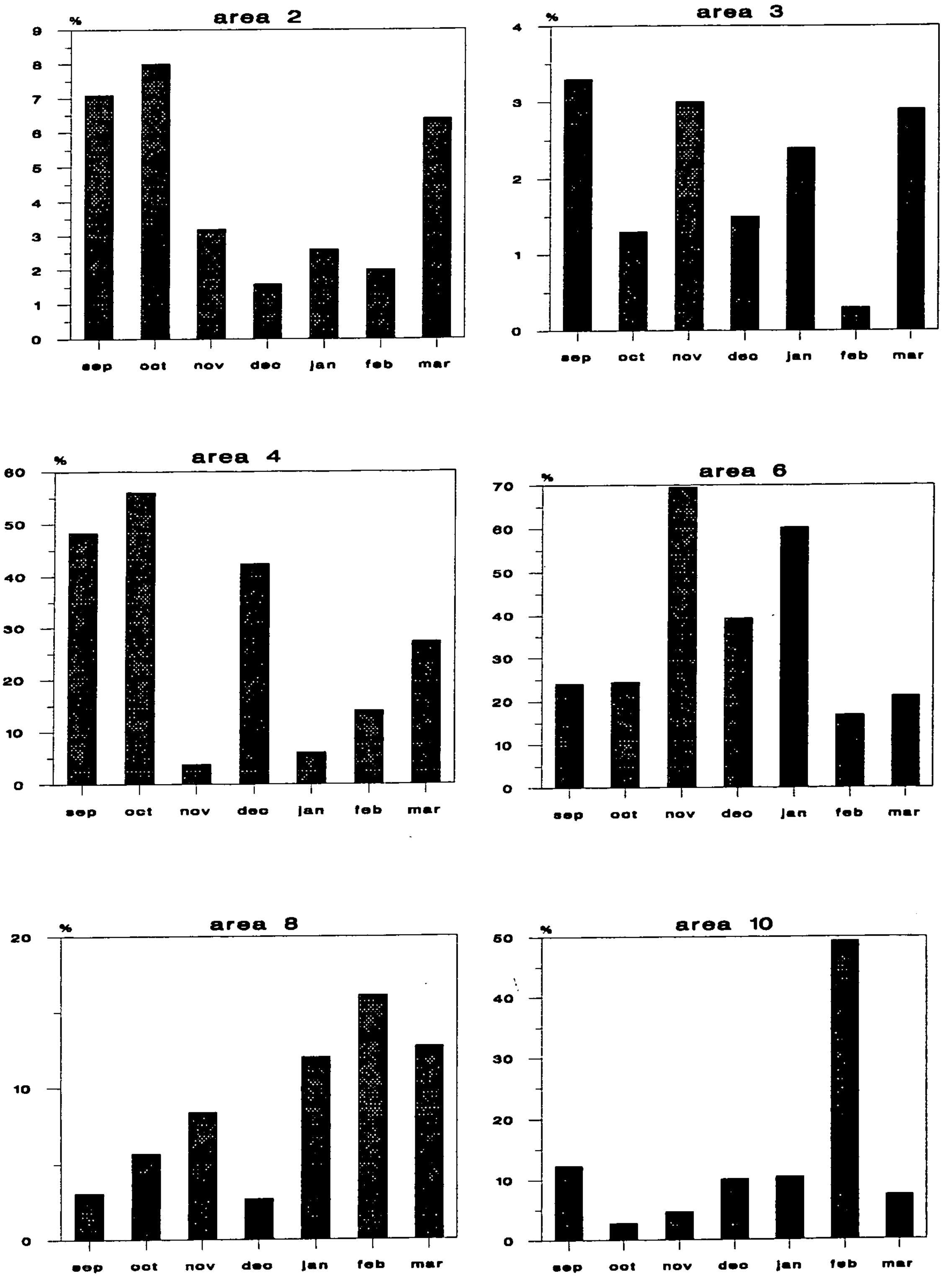


Figure 4.21c Monthly percentage of the Seal Sands total of grey plover present on each site at low water during the winter 1991/92.

From low water counts in the middle of each month..

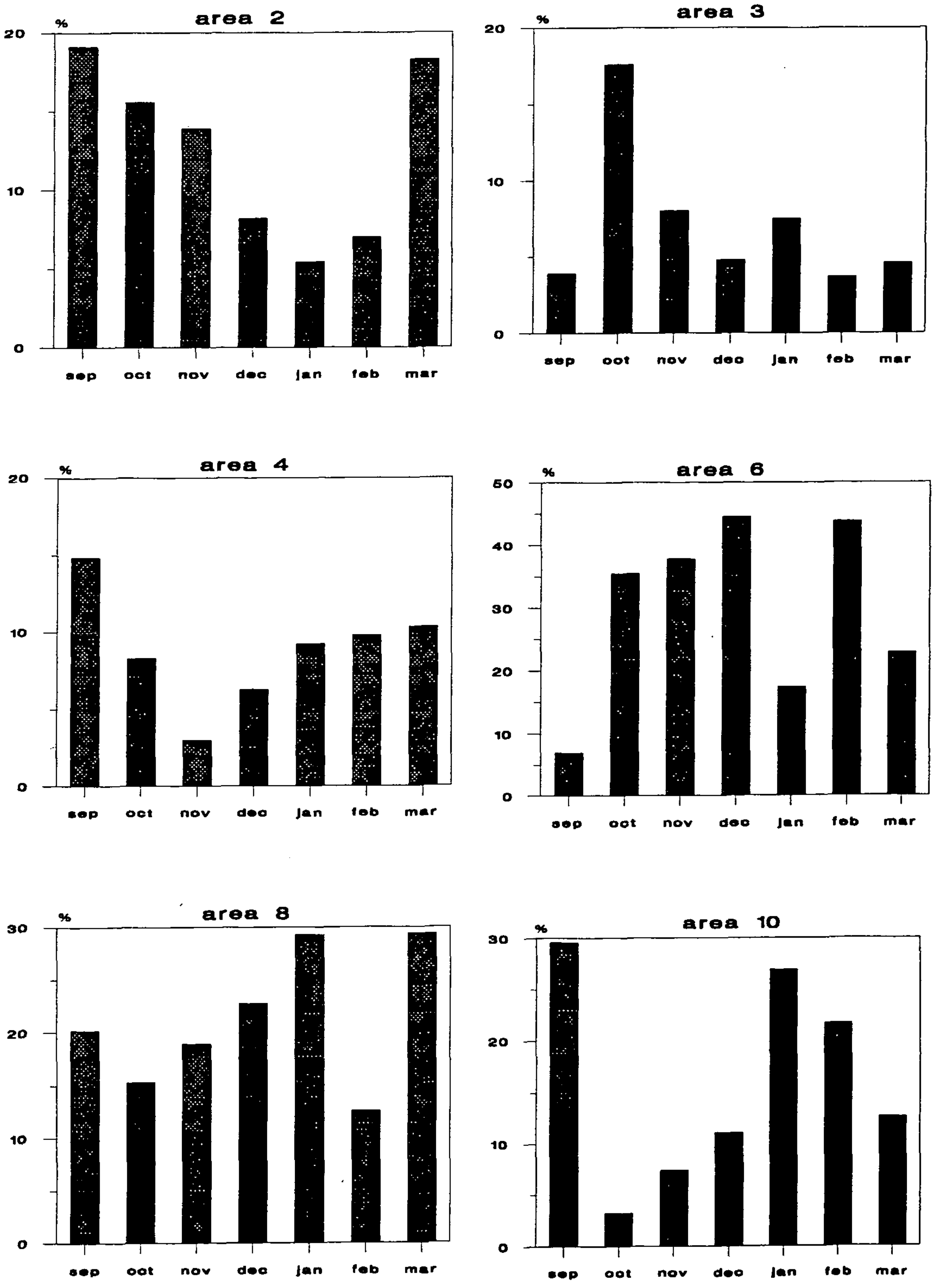


Figure 4.15 Spearman rank correlation coefficients of prey density and density of curlew, godwit and grey plover at low water on six feeding areas of Seal Sands over the winter 1991/92.

Separate analyses were performed on data from September-December (using invertebrate density sampled in September) and from January-March (using invertebrate density sampled in March). Low water bird density was sampled in the middle of each month.

September to December			January to march		
species	Rs	P	species	Rs	P
curlew	0.49	0.164	curlew	o.37	0.234
godwit	0.46	0.177	godwit	0.58	0.115
grey plover	0.77	0.036	grey plover	0.43	0.198

birds. Certainly, migration to the breeding areas is the main reason for the decrease in population size on Seal Sands, and adequate food supply is presumably a necessary precondition to migration. Indeed one would expect migration to be delayed during years when food was considered to be limiting because of poor settlement of juvenile prey in the previous autumn and/or high levels of prey depletion through the winter. Low densities of available prey may protract the period of pre-migratory fattening if these densities reduce the rate of energy intake that shorebirds can achieve. Grey plovers have been shown by ringing studies to make an initial migration away from Teesmouth in early spring to the Danish Wadden Sea, where they lay down fat reserves for the long journey to their Siberian breeding grounds. It is possible that the prey densities on Seal Sands at this time of year are insufficient to allow the migrants to amass the reserves that would allow them a direct journey to the north-east. However, this is not to say that prey densities on Seal Sands are limiting food intake rates since the initial migration these birds undertake -a journey of several hundred km - requires shorebirds to carry sufficiently large reserves of fat before departure, although it is possible that reserves built up over the winter may be used for this purpose.

iv) Although mean body mass of grey plovers has been shown to decline from a peak in December (when birds maintain a very large fat load as insurance against bad feeding conditions and high energy demands in winter) to a minimum in May (Scott 1991), body condition of birds in late winter and spring is good, and grey plovers are unlikely to need a large fat load at this time of year, even to fuel their migration to the Wadden Sea. No corpses of the three species were recovered during the 1991/92 winter, which suggests that winter mortality was low.

v) There is no evidence to suggest that any of the three shorebirds changed prey species late in the season, except that curlews took advantage of the arrival of shore crabs when they became available from May onwards. Since *Nereis* was by far the most abundant large prey item available, there was little opportunity for switching prey species.

4.5 Aggressive interactions.

4.5.1 Introduction.

Competition can occur if the prey intake rate of a species is adversely affected by aggressive interactions with individuals of another species. Aggression can take three main forms;

i) food stealing (kleptoparasitism)

ii) defence of an individual's feeding space

iii) defence of territory

The latter two forms are distinct because on Seal Sands territoriality involves defence of a fixed and usually large area of feeding ground, whereas defence of an individual's feeding space is not site-specific and is elicited only when individuals are in close proximity to each other. Territoriality within a species occurs in curlews and grey plovers on Seal Sands (about 10% and 40% of individuals of each species respectively hold territories), but interspecific territoriality has not been recorded there and is generally rare in shorebirds (Myers *et al.* 1979). Aggressive interactions between shorebird species have been observed on a casual basis in the past on Seal Sands and in the present study field observations were undertaken to estimate the frequency of such aggression and to determine whether these frequencies were likely to affect food intake rates. It was hypothesised that interactions would be most frequent at times of the year when the density of shorebirds on Seal Sands was highest (greater likelihood of random encounters) and when the availability of prey was lowest (prey items at a premium). On this premise the data set was divided into a predicted period of lower aggression rates (September to December), and a predicted period of higher aggression rates (January to March).

4.5.2 Results and discussion.

Table 4.16 shows the rates of interspecific aggression of three species of shorebirds during the winter September 1991 to March 1992. Firstly it is important to note that the frequency of interactions between species was extremely low. Secondly, there was a doubling of the rate between early and late winter, but since the rates were at all times so low, there was no statistically significant difference (median test). Six of the observed interactions were of curlews attacking godwits in a brief "lunge" when the former's individual feeding space was invaded. One interaction consisted of a godwit briefly chasing a grey plover. None of the observed interactions involved squabbles over food items. Whilst the increase in the late winter period may have been a product of increased bird densities and/or reduced availability of prey at this time of year, the low frequency of interactions was unlikely to have significantly reduced the mean net energy intake rate of any species. The conclusion is that interference competition mediated by overt aggression was not strong between the three study species during the winter 1991/92.

Quite intense interspecific aggression was observed during a period of sub-zero temperatures on 28 and 29 January 1992, when large numbers of golden plovers *Pluvialis apricaria* moved from their usual inland habitat, which was frozen over, to the intertidal flats of Seal Sands. Aggressive interactions were most common between grey plovers and golden plovers, when the former generally initiated the conflict, but also occurred between golden plovers and ringed plovers *Charadrius hiaticula*, the former

Table 4.16 Rates of interspecific aggression during the winter 1991/92.

Bird-minutes of observation for each species as follows; curlew Sept-Dec 410, Jan-Mar 428; grey plover Sep-Dec 350, Jan-Mar 488; Godwit Sep-Dec 215, Jan-Mar 209.

September-December			January-March		
number of interactions	bird-minutes	rate (interactions per bird-minute)	number of interactions	bird-minutes	rate (interactions per bird-minute)
2	975	0.002	5	1125	0.004

Difference in rate of interaction between winter periods not significant (Median test) being apparently dominant. It is important to note that interactions were frequent only for a period of about two hours during the ebb tide when intertidal feeding area was restricted and hence bird density very high. On the 28 January, during a 24 minute period of continuous observation, 10 attacks on golden plovers by grey plovers were noted and on 29 January during a 16 minute period of continuous observation, 6 attacks on golden plovers by grey plovers, one attack on grey plover by golden plover, one attack on dunlin by grey plover, and one attack on ringed plover by golden plover were recorded. These rates of interaction are clearly far higher than those normally encountered on Seal Sands. It seems that the presence of high densities of golden plovers at a time of year when this species is usually absent from Seal Sands and when grey plovers are very numerous, was a peculiar situation which led to this unusual level of interspecific aggression. In addition, it is also likely that low ambient temperatures (mean daily temperature for 23-29 January $=^{-}0.8$ °C) depressed the density of *available* prey so that feeding space was at a premium. Plovers require an undisturbed space around them to search for prey, which needs to be increased when prey density is low.

The discussion so far has referred to interactions over feeding space, rather than the acquisition of prey items. Food-stealing was not observed between species of shorebird during the study. However in late May 1992 large flocks of gulls, mostly common gulls *Larus canus* were present on Seal Sands and kleptoparasitised curlews feeding on shore crabs, which were a large and profitable prey of the curlew at that time of year. A gull would associate loosely with foraging curlews and once a crab was caught would pursue the curlew, initially on foot and then in flight (often for thirty seconds or more) until the curlew relinquished its food, or rarely, until the gull abandoned the chase. Although curlews at this time also caught *Nereis,* on no occasion did I see gulls chasing curlews for this prey. Curlew's handling time when feeding on crabs is much greater than when feeding on worms. Curlews generally spend several seconds shaking the crab to remove its legs before swallowing the body and this action probably alerts the gull to the opportunity of a meal and allows the gull time to attack before the crab is swallowed.

The handling time when feeding on worms, even large ones, is generally far less than for crabs, and does not give a potential pirate time to attack. In addition, the energy value of a single worm is likely to be far less than a crab, so stealing is only profitable if the booty is worth the effort of its acquisition.

CHAPTER FIVE

SPATIAL AND TEMPORAL RELATIONSHIPS BETWEEN SPECIES

5.1 Introduction

Space is one of the fundamental resources, as heterotrophs require space in which to feed. In assemblages of wintering shorebirds, adequate feeding space is essential if individuals are to obtain sufficient food to survive. It is thought that individual grey plovers require a relatively large undisturbed space in which to feed efficiently (Pienkowski 1979). Since it appears that plovers detect prey visually by responding to prey movements on the sediment surface - events that are well dispersed in space - the individual needs undisturbed access to an expanse of sediment to attain sufficient prey intake rates. Tactile probers such as curlew and godwit have a far higher proportion of prey available to them at any one time (within the reach of their bills), and so can forage successfully without access to such large undisturbed expanses. With this in mind it is postulated that grey plovers avoid concentrations of curlews and godwits in order to escape interference with detection and capture of their prey. It is much less likely that curlew and godwit experience this kind of interference from either each other or grey plovers. If other forms of interference are considered, such as displacement from a feeding site or food stealing, the small size of grey plovers and godwit makes these species more susceptible to interference competition than the larger curlew. This means that interspecific competition, if it occurs, is likely to be asymmetric.

It is important to consider the phenomenon both in terms of present day competition and in terms of interactions that may have occurred at some time in the past. One reason why we may not detect interspecific competition today is if strong competition in the past acted as a kind of sieve which left behind communities composed of species with different niches. Connell (1980) called this the "ghost of competition past". However, even if competition has been strong in the past it may still occur now but be detectable only in certain seasons or years when resources are particularly restricted (Wiens 1977). How then are we to interpret patterns of coexistence that are observed in natural communities today? Persistent segregation of species in space into separate micro-habitats may be the result of niche differentiation driven by past competition. Segregation may, however, be indicative of present day competition if, in the absence of one species, another moves into that previously occupied physical space. Such a situation was observed by Pienkowski (1979), who showed that when the population of wintering godwits of Lindisfarne, N.E. England migrated in April, the grey plovers that remained there increased their feeding range to include sites previously used by godwits. Another situation that is indicative of present-day competition is if species segregate themselves spatially, but not according to (detectably) different microhabitats. On a mudflat in North-Ventjager, Netherlands, Zwartz (1980) found that curlew and avocets, which both preferred the same feeding area, used these areas at mutually exclusive times - when large numbers of curlews were present on the feeding area few avocets fed there, and *vice versa.*

This chapter investigates the inter-relationships between the distributions of curlew, grey plover and godwits on Seal Sands. Firstly I will present data to establish the degree of temporal overlap of species on Seal Sands on a gross scale and then investigate spatial and temporal relationships on finer scales.

5.2 Results

5.2.1 The timing of peak numbers of curlew, grey plover and godwit on Seal Sands.

Figure 5.1 shows that the timing of peak numbers of each of the three large species of shorebirds of Seal Sands was rather similar in 1991/92 and 1992/93, with maximum

Figure 5.1a The timing of peak numbers of curlew, godwit and grey plover on Seal Sands during 1991/92.

From low water counts in the middle of each month.

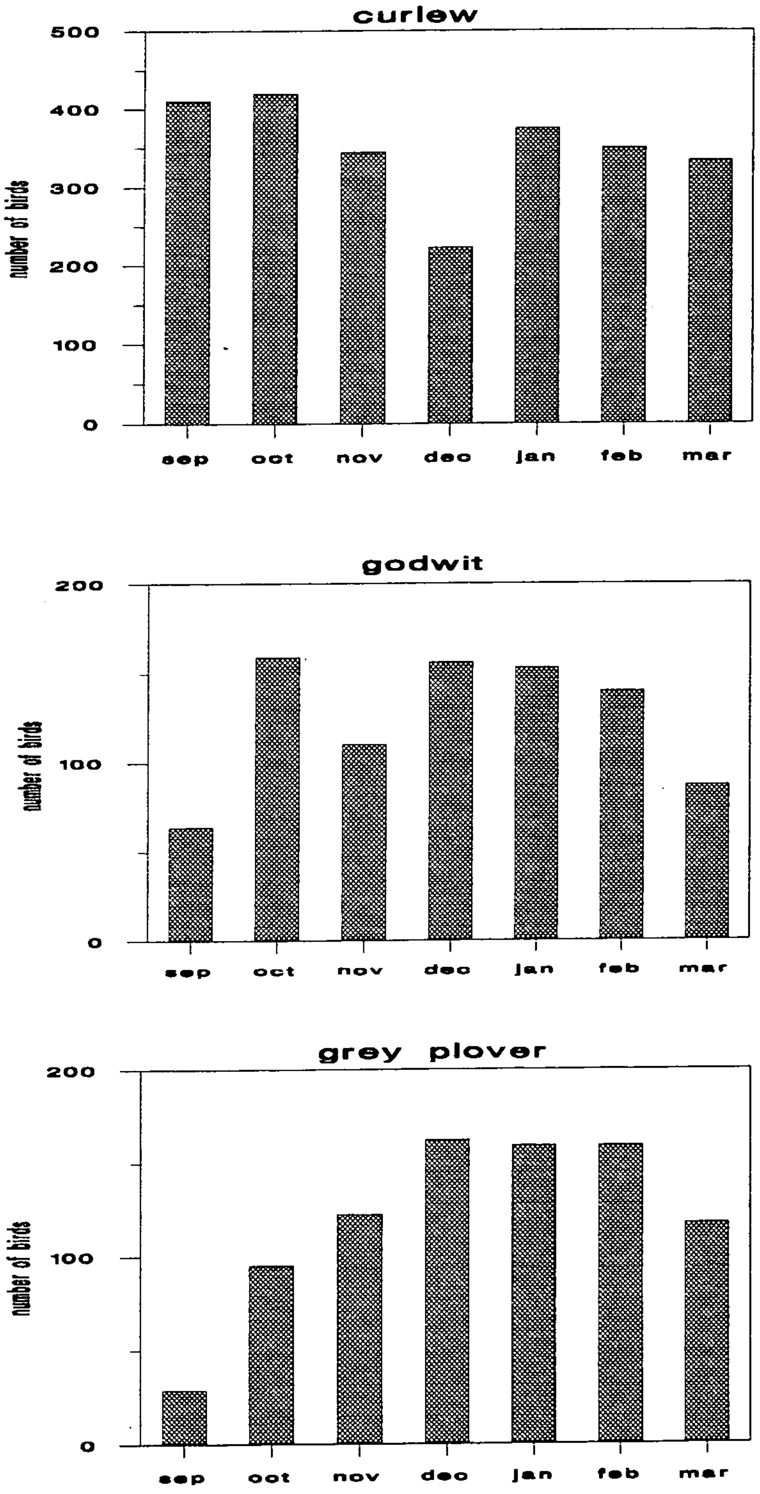
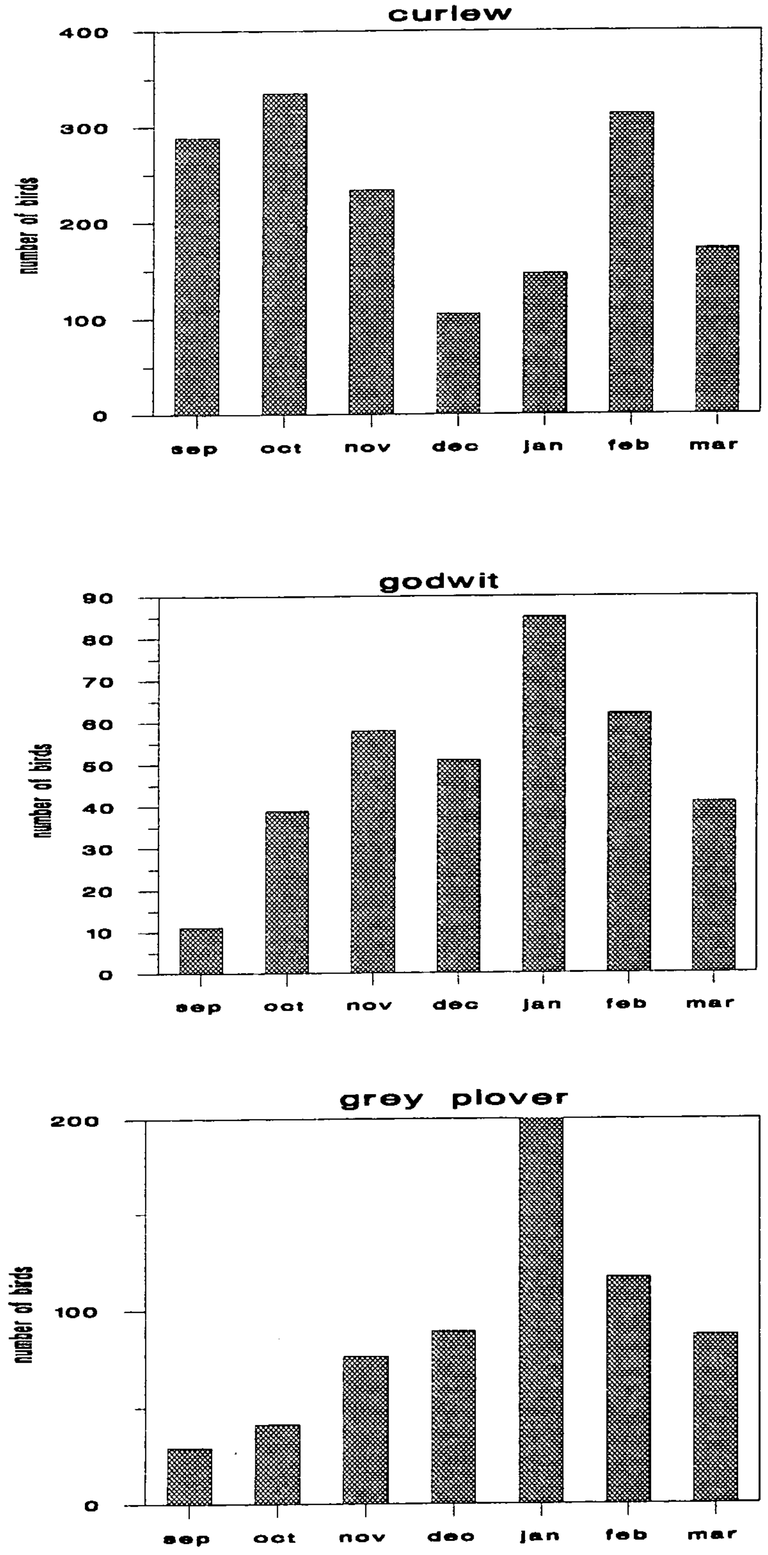


Figure 5.1b The timing of peak numbers of curlew, godwit and grey plover on Seal Sands during 1992/93.

From low water counts in the middle of each month.



numbers occurring in late winter. There is thus potential for interspecific competition to occur, since the three species co-occur in high numbers. Also of note is the mid-winter drop in the number of curlews feeding on Seal Sands and a subsequent rise in late winter. This phenomenon will be discussed in a later section as it provides opportunity for investigating the response of the other species to a reduction in the density of this potential (and larger) competitor. Figure 5.2 shows that there are no strong negative correlations between the monthly numbers of species pairs on Seal Sands, which indicates that each species did not time its use of Seal Sands in order to avoid high numbers of other species. The weak negative correlations between the numbers of curlew and grey plover in winters 1991/92 and 1992/93 and between the numbers of curlew and godwit in 1992/3 resulted largely from the mid-winter fall in numbers of curlew using Seal Sands at a time of year when numbers of grey plovers and godwits were high. Since Figure 5.1a shows that numbers of grey plover and godwit did not fall in January 1992 when curlew numbers increased after the December minimum, it seems unlikely that the negative correlations between curlew and grey plover and curlew and godwit on the gross spatial scale of the whole of Seal Sands were the result of a causal relationship.

5.2.2 Use of Greenabella Bank by curlew, grey plover and godwit

Greenabella Bank is a mudflat at a low tidal level with an area of 21 ha., the higher parts of which are exposed for about four hours per low water period, although the lowest parts are exposed only on spring tides. Sediment sampling showed the mudflat to consist largely of poorly drained unconsolidated mud, but with a central area of firmer sandy-mud that is higher than the surrounding sediments (Figure 5.3). The boundary of these two major sediment types was established with reference to a grid of marker posts which was set up over the whole of Seal Sands. The mudflat is a preferred feeding site for all three of the study species over the low water period (Figure 5.4).

Figure 5.2a <u>The relationship between total numbers of curlew, godwit and grey plover on Seal Sands at low water during 1991/92</u>. Plotted points are the Seal Sands total low-water count in the middle of each month from September 1991 to March 1992. The Spearman rank correlation coefficient and its significance level are indicated.

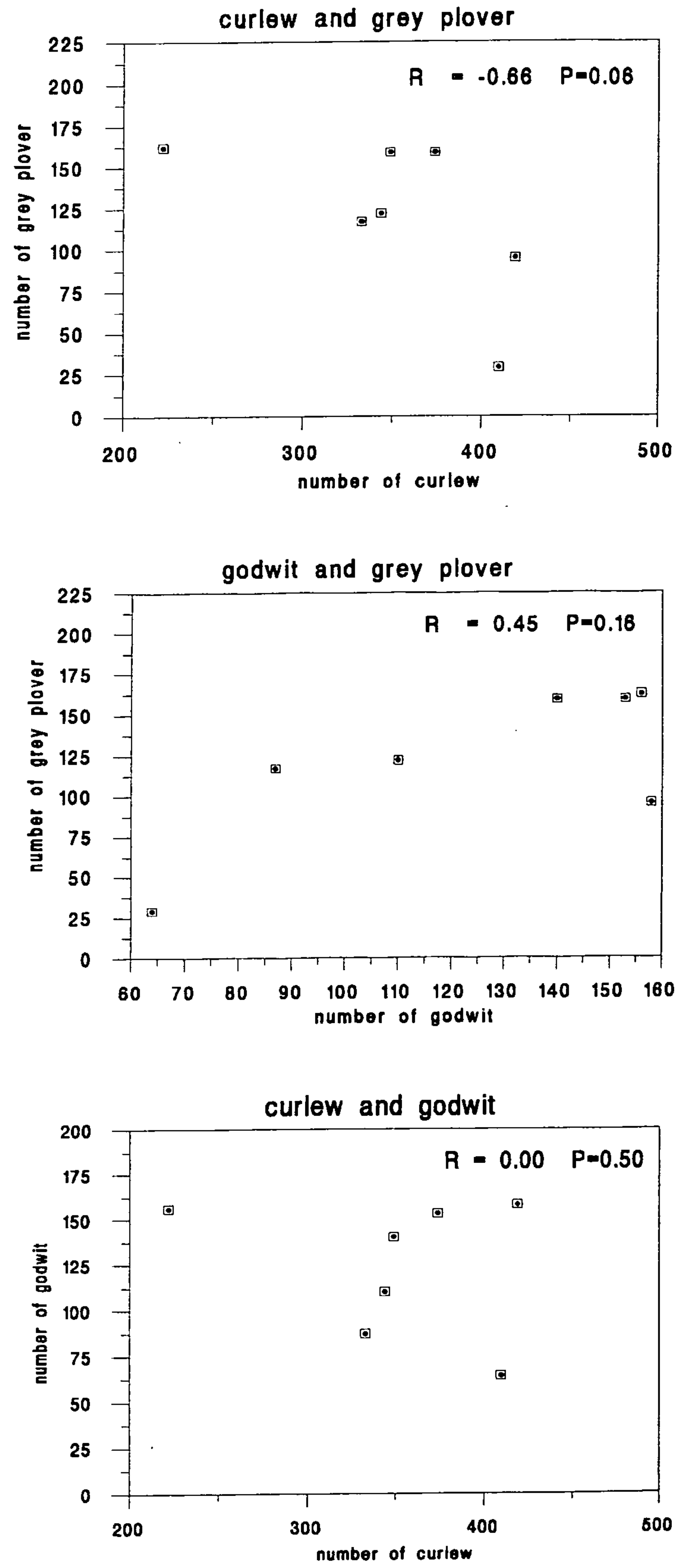


Figure 5.2b The relationship between total numbers of curlew, godwit and grey plover on Seal Sands at low water during 1992/93. Plotted points are the Seal Sands total low-water count in the middle of each month from September 1992 to March 1993. The Spearman rank correlation coefficient and its significance level are indicated.

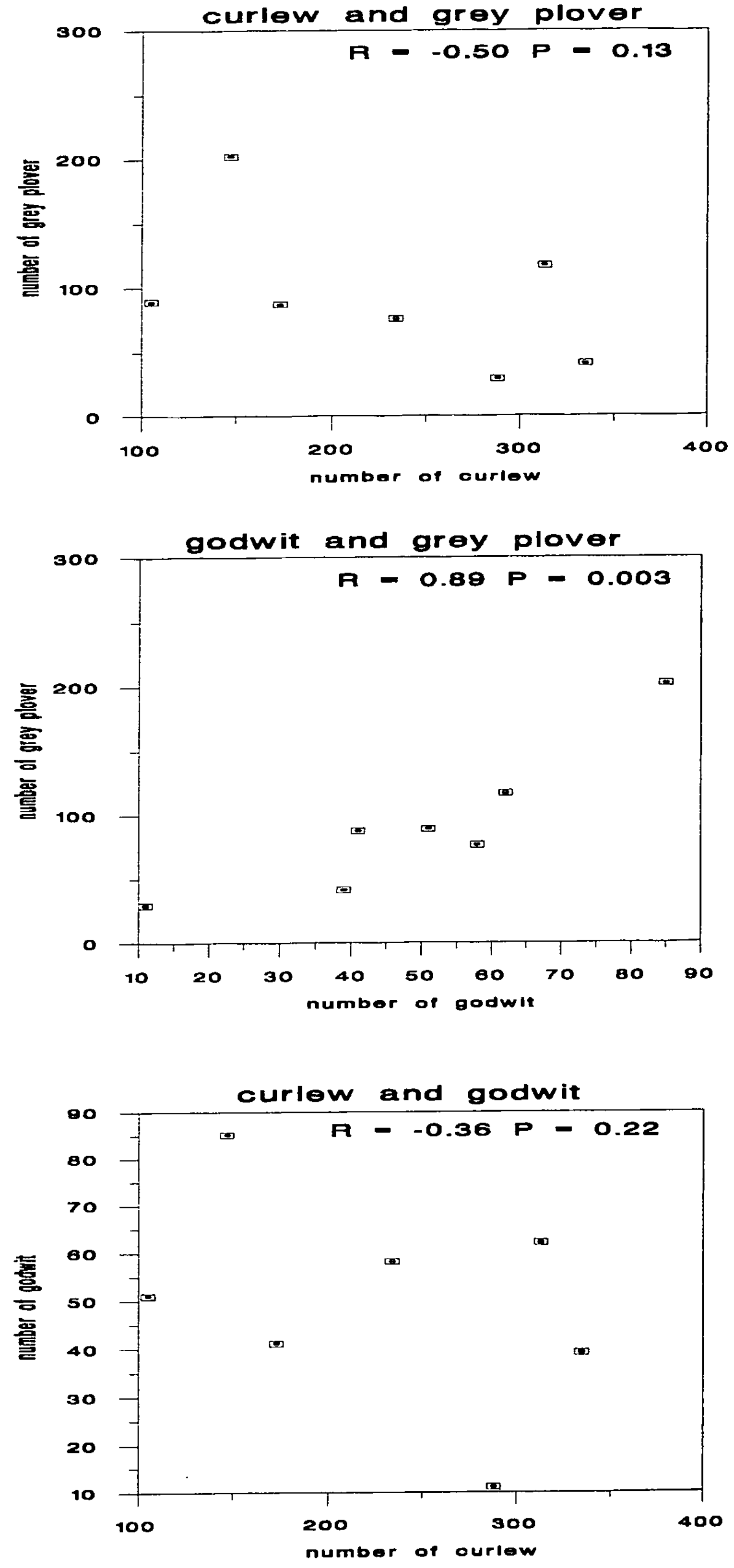


Figure 5.3 The sediments of Greenabella Bank and the grid of reference stakes. Soft muddy sediments at a low tidal level are shown shaded grey, surrounding the central area of firmer sandy mud at a higher tidal level. The reference stakes are 100m apart; the study plot is outlined by a broken line.

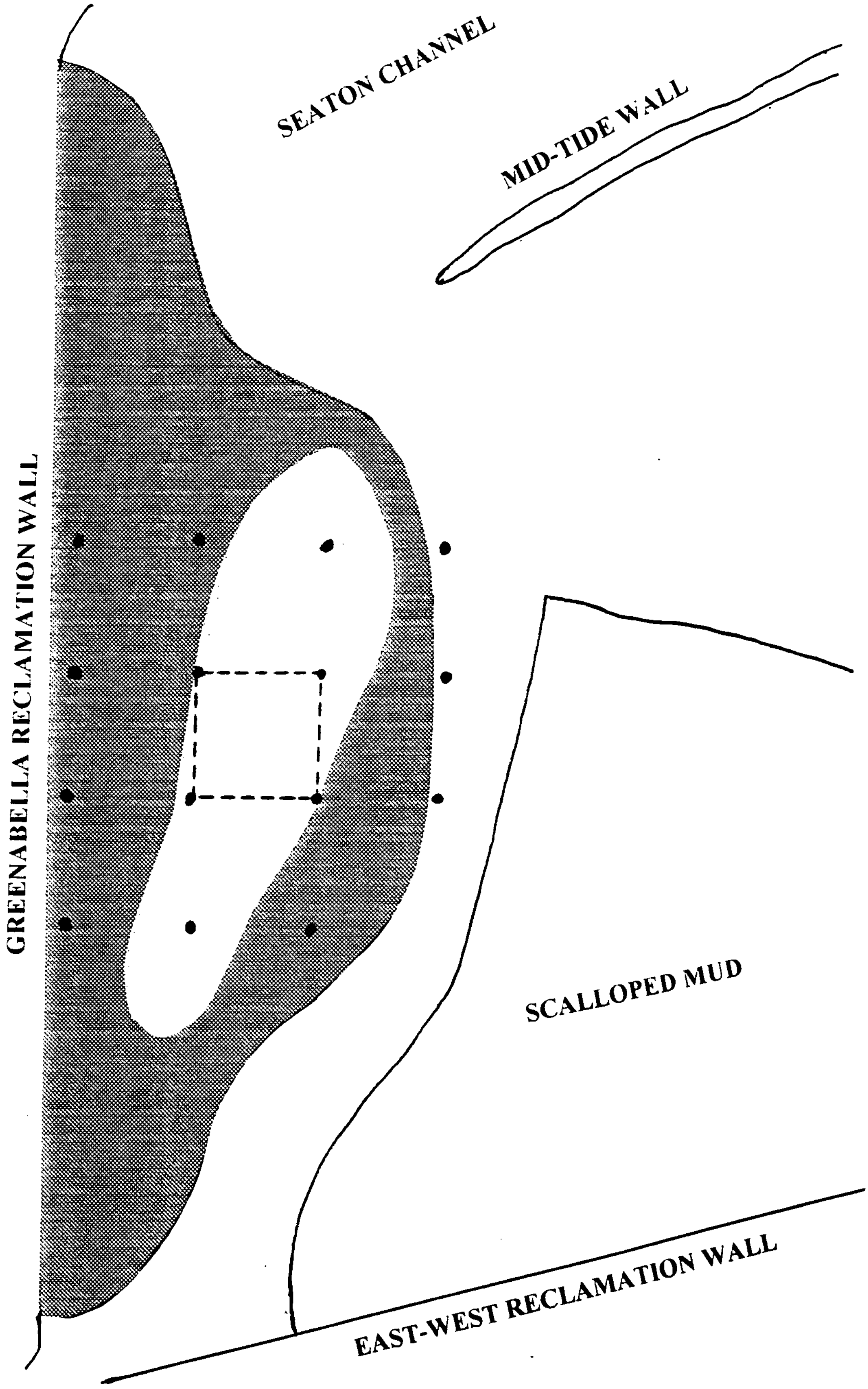
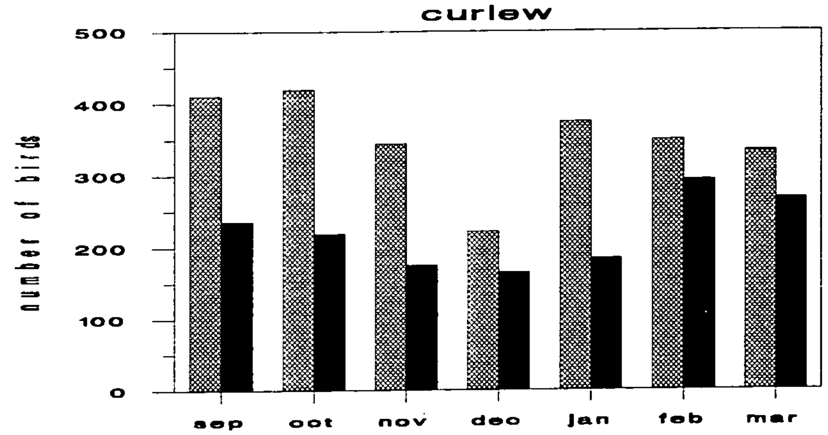
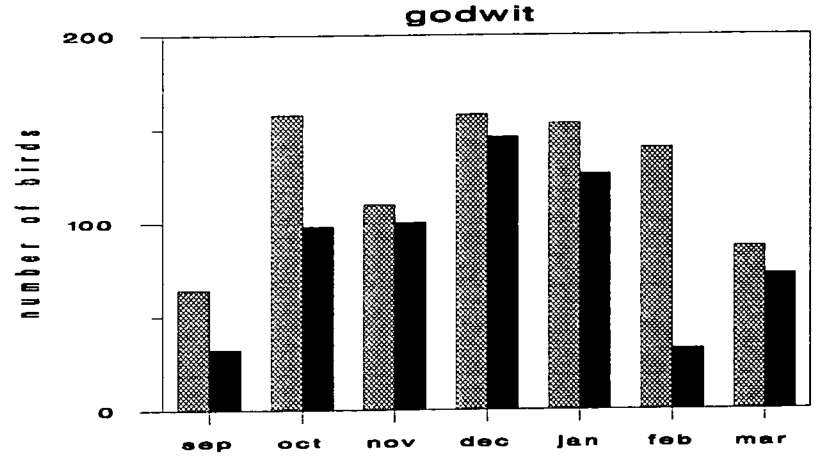


Figure 5.4a The importance of Greenabella Bank as a feeding site for curlew, godwit and grey plover during 1991/92.

The pale bars represent the total Seal Sands count of each species at low water in the middle of each month, and the dark bars represent the maximum count of each species on Greenebella Bank during the period of exposure.





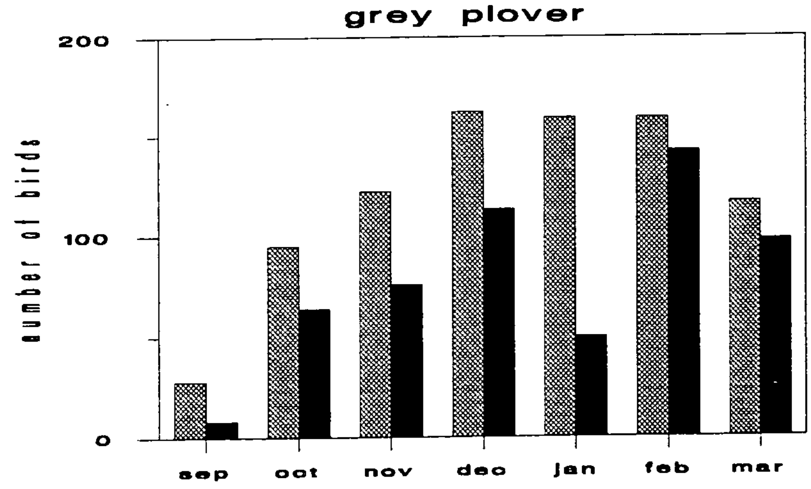
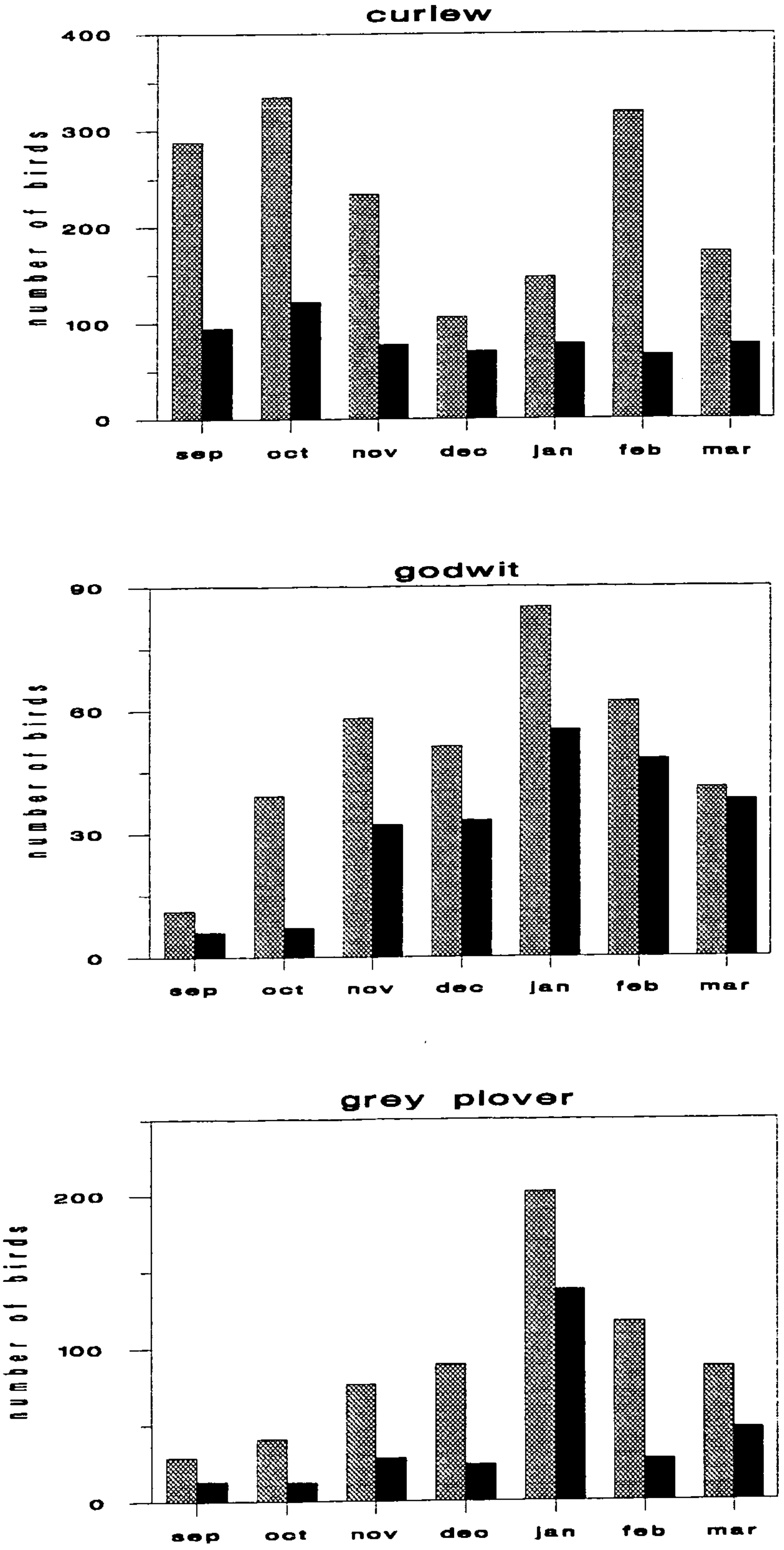


Figure 5.4b The importance of Greenabella Bank as a feeding site for curlew, godwit and grey plover during 1992/93.

The pale bars represent the total Seal Sands count of each species at low water in the middle of each month, and the dark bars represent the maximum count of each species on Greenebella Bank during the period of exposure.



5.2.2.1 Timing of arrival during the tidal cycle.

Greenabella Bank was used by each of the study species at predictable times of the tidal cycle (Figure 5.5). Curlews moved from other feeding sites onto Greenabella Bank as soon as the central area became exposed on the falling tide, whereas grey plovers did not arrive until later in the tidal cycle and increased in number until the rising tide forced them off. Godwits showed a pattern of use similar to curlews. If grey plovers were experiencing interference from curlews (and/or godwits) one might have expected negative correlations to exist between numbers of these species, yet the mean number of grey plovers increased through the low water period whilst the numbers of curlew and godwit varied rather little throughout that period.

5.2.2.2 Changes in location of the three shorebird species on Greenabella Bank during the tidal cycle.

It was noted that rather than feeding in mixed species flocks, segregation in feeding location occurred. Curlews and godwits followed the tide edge on the ebb from the central sandy mud down on to the unconsolidated mud. They concentrated on areas recently uncovered, whereas grey plovers concentrated on the higher areas in the centre of Greenabella Bank, areas that had been exposed for the longest period of time. To quantify the temporal changes in the distribution of these shorebirds on a finer scale, a representative area on the high central part of Greenabella Bank was marked out with wooden posts to form a plot 100 m by 100 m square (Figure 5.3). Figure 5.6 shows that early in the low water period, when the highest sediments become exposed, curlew were present at high densities but these decreased thereafter as the sediments of the study plot dried out (sediments lost the surface film of water and became dull in appearance). No grey plovers were present on the study plot during the first hour of exposure but arrived thereafter and increased in number rapidly.

Figure 5.5 Numbers of curlew, godwit and grey plover on the whole of Greenabella Bank through the period of exposure. Plotted points are the mean (± S.E.) of nine low water periods during March and December 1992 and February and March 1993.

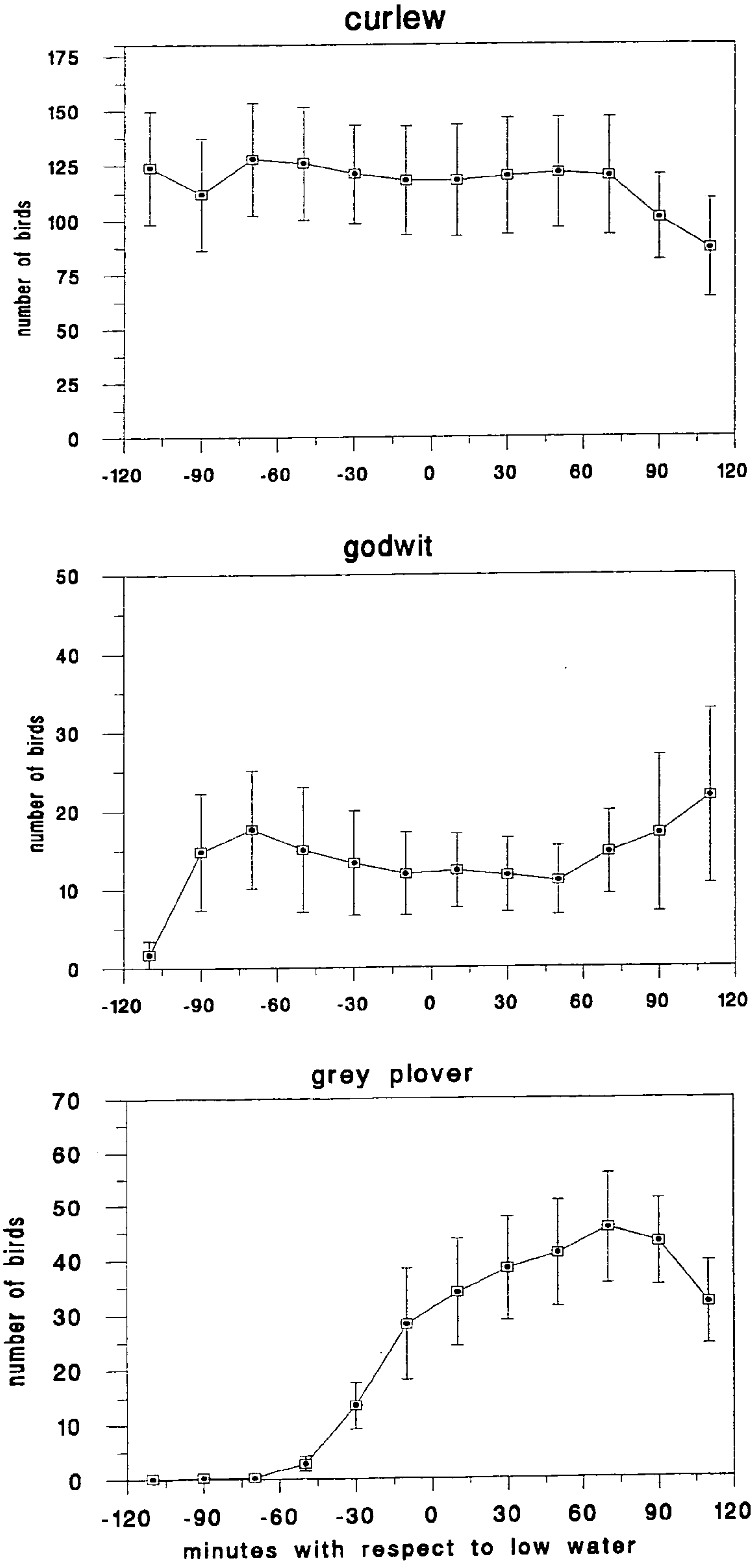


Figure 5.6 Temporal use of the central part of Greenabella Bank by curlew and grey plover through the period of exposure. Plotted points are the mean number (± S.E.)of each species on a 100 x 100m grid (see Fig. 5.3) for nine low water periods during March and December 1992 and February and March 1993.

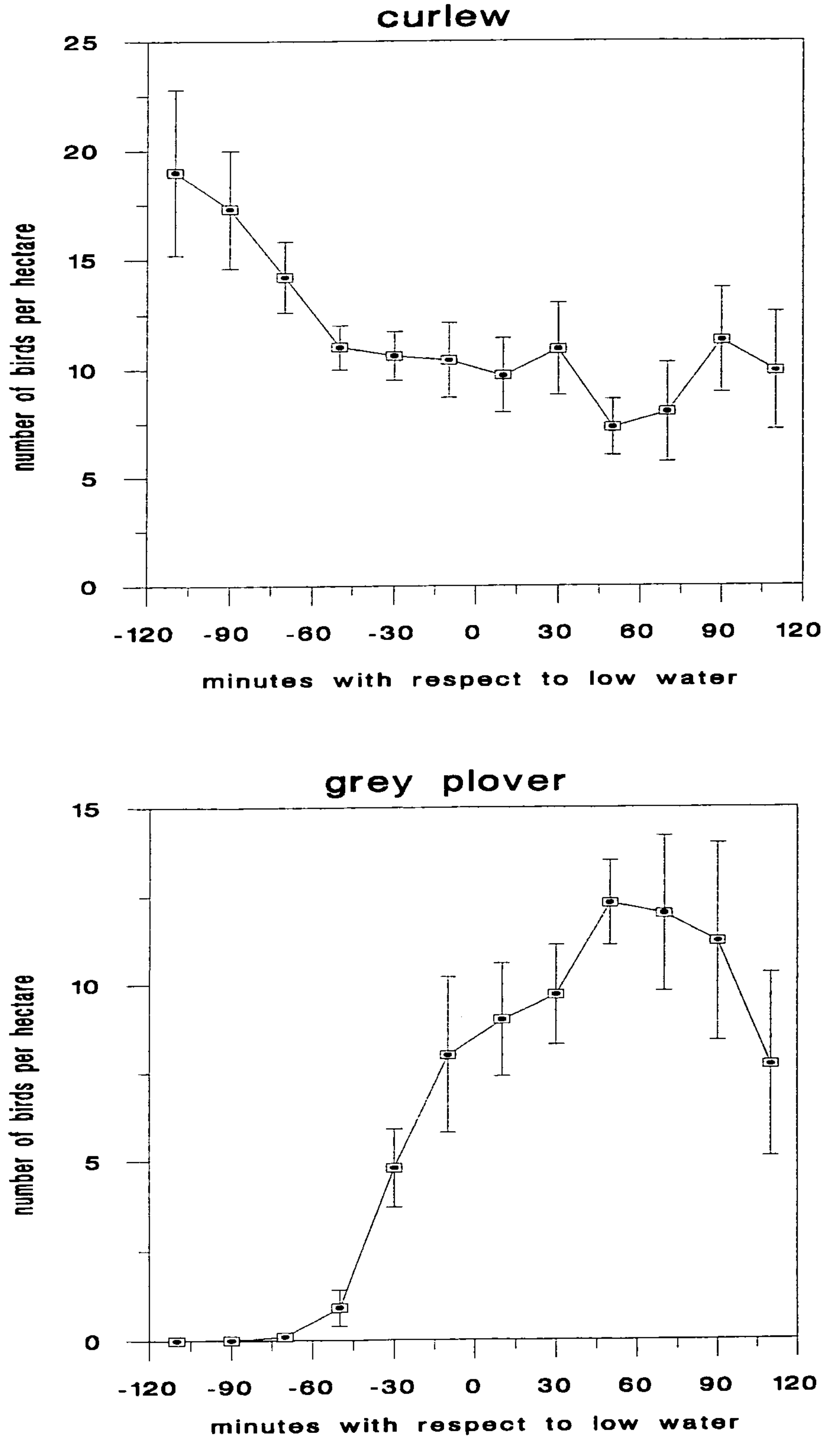


Figure 5.7 shows that there were negative correlations between the density of curlews and that of grey plovers measured at 20 minute intervals on the study plot during separate periods in late winter 1992 (Spearman Rank R_s =$^-$0.34 $P<0.05$ n=47) and late winter 1993 (R_S =-0.36 $P< 0.01$ n=45). However, competition is not necessarily implicated. Two hypotheses can be put forward to explain the observed pattern, only the first of which involves competition (by interference) :

1. Grey plovers avoided high densities of curlews, since it is believed that the former species cannot forage efficiently when crowded.

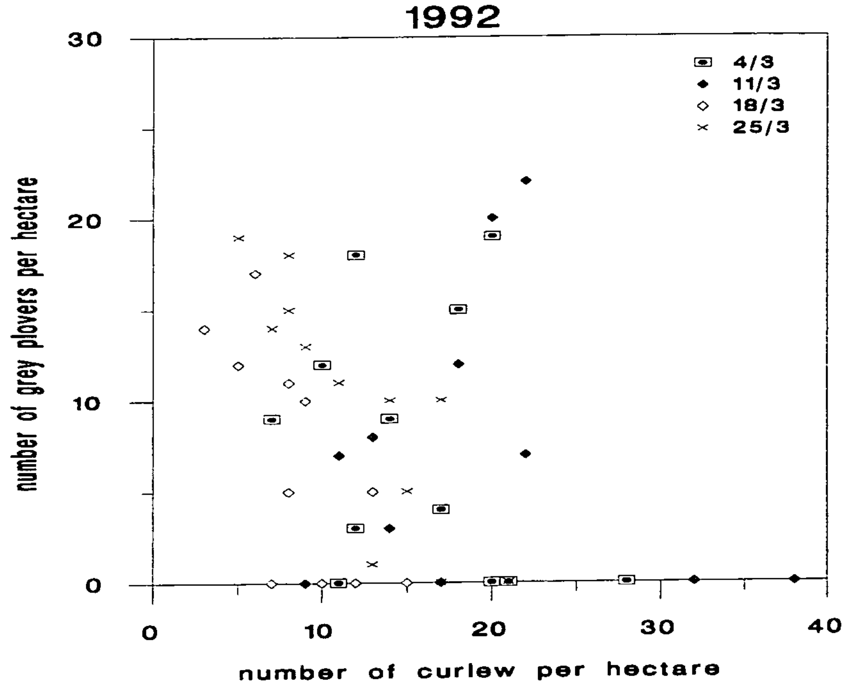
2. The grey plovers' movement onto Greenabella was independent of the density of curlew there. Two possible reasons why the plovers delayed the movement for an hour after first exposure are : i) They detect surface movements of prey (e.g. water outflows from a worm burrow) better on a sediment that has been exposed to the air for a period of time. Distracting reflections from the surface might be reduced once the film of water that is left by the falling tide has soaked into the sediment; ii) *Nereis* comes to the surface of the sediment more frequently when the water table has fallen. This would increase the density of *available* prey later in the low water period and therefore the area could sustain an increasing density of grey plovers.

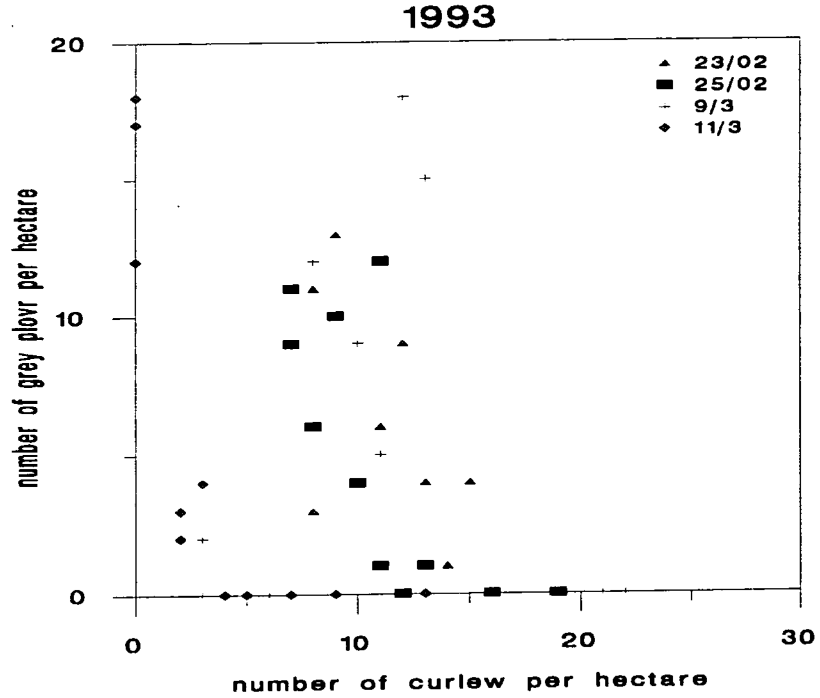
These hypotheses are examined in the following section.

5.2.3 <u>Seasonal changes in the timing of use of Greenabella Bank during the tidal cycle.</u>

The data presented above were obtained from counts at times of year when each species was abundant. However, a way of testing whether grey plovers were actually avoiding high densities of curlews or were simply responding to changes in sediment dryness with

Figure 5.7 Scatter plots of the densities of grey plovers against the densities of curlews on the central part of Greenabella Bank during two periods in March 1992 and late February/early March 1993 Each low water period is coded by a different symbol and each point represents a separate time during the period of exposure (from -110 minutes to + 110 minutes, at 20 minute intervals).





time after emersion, is to observe the spatial and temporal distribution of grey plovers when numbers of curlews on the estuary are low.

As was shown in Figure 5.1, curlew numbers fell in mid-winter during each of the two years of study. This pattern occurs annually on Seal Sands and Townshend (1981) demonstrated that a proportion of curlews abandon the mudflats at this time of year to feed on earthworms and other invertebrates in coastal fields bordering the estuary.

Figure 5.8 shows the numbers and time of arrival of each species on the whole of Greenabella Bank during two low water periods when total number of curlews on Greenabella Bank (and Seal Sands as a whole) were particularly low. On both days grey plovers exhibited the same temporal pattern of arrival as they did when numbers of curlews were very much higher (compare with Figure 5.5).

5.2.4 Seasonal changes in the intensity of use of Greenabella Bank.

Even if the timing of the arrival of grey plovers on Greenabella Bank during the low water period was independent of the number of curlews on the feeding site, interference might still have occurred during those particular times of year when curlews were most abundant there. Figure 5.9 shows that the number of grey plovers on Greeenabella Bank an hour after low water (when peak numbers tend to occur) during spring tides changed little from month to month and was not affected by the large seasonal fluctuations in the abundance of curlews there (Spearman Rank Correlation $R_s = {}^{-}0.357$ $P=0.47$). This indicates that the number of grey plovers using Greenabella Bank was independent of the number of curlews using the site.

Figure 5.8a The timing of arrival of curlew, godwit and grey plover onto Greenabella Bank on 14/12/92 during a period when total numbers of curlew on Seal Sands were particularly low. Numbers of each species on the whole of Greenabella Bank are given.

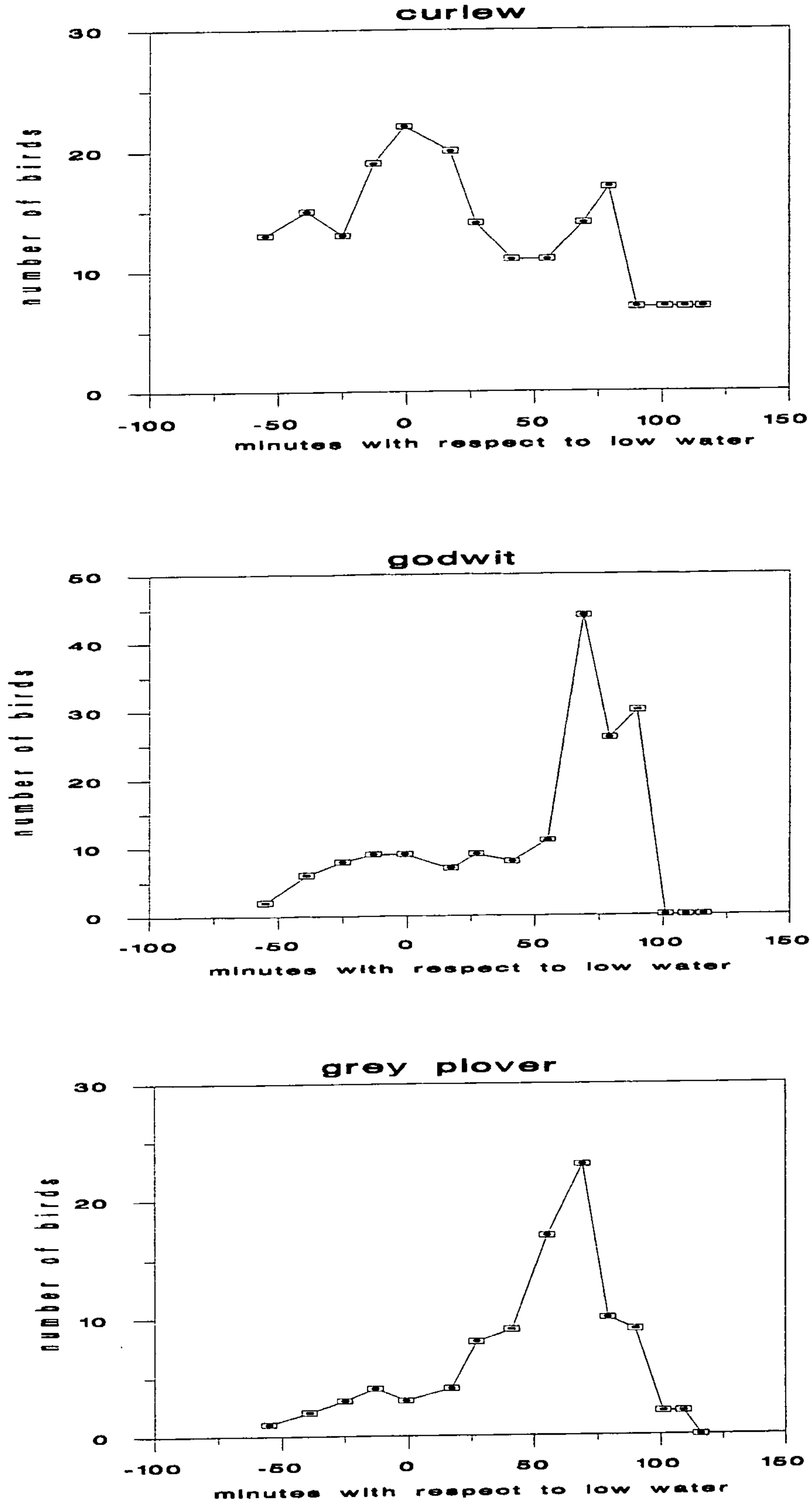


Figure 5.8b The timing of arrival of curlew, godwit and grey plover onto Greenabella Bank on 12/1/93. See legend of Fig. 5.8a.

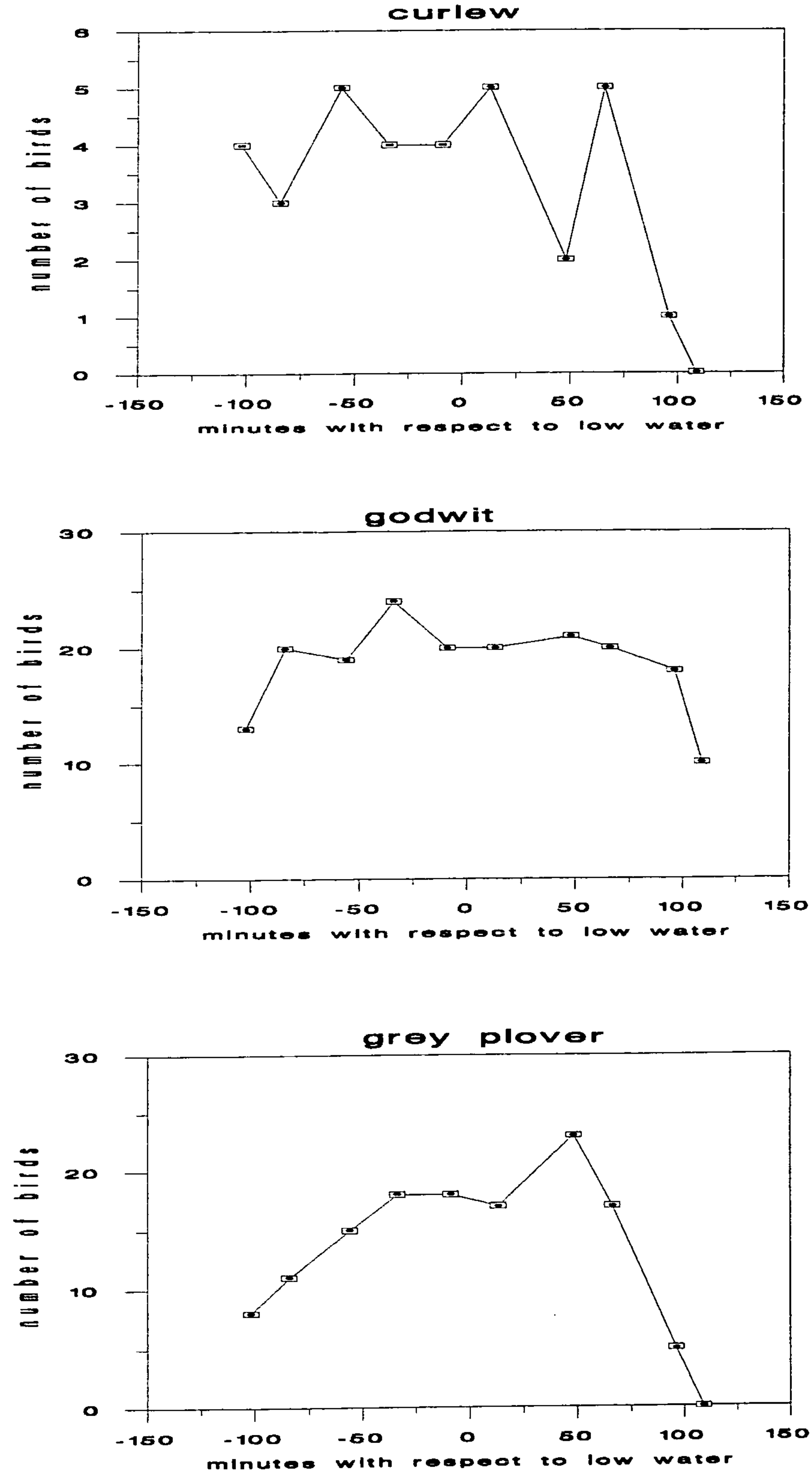
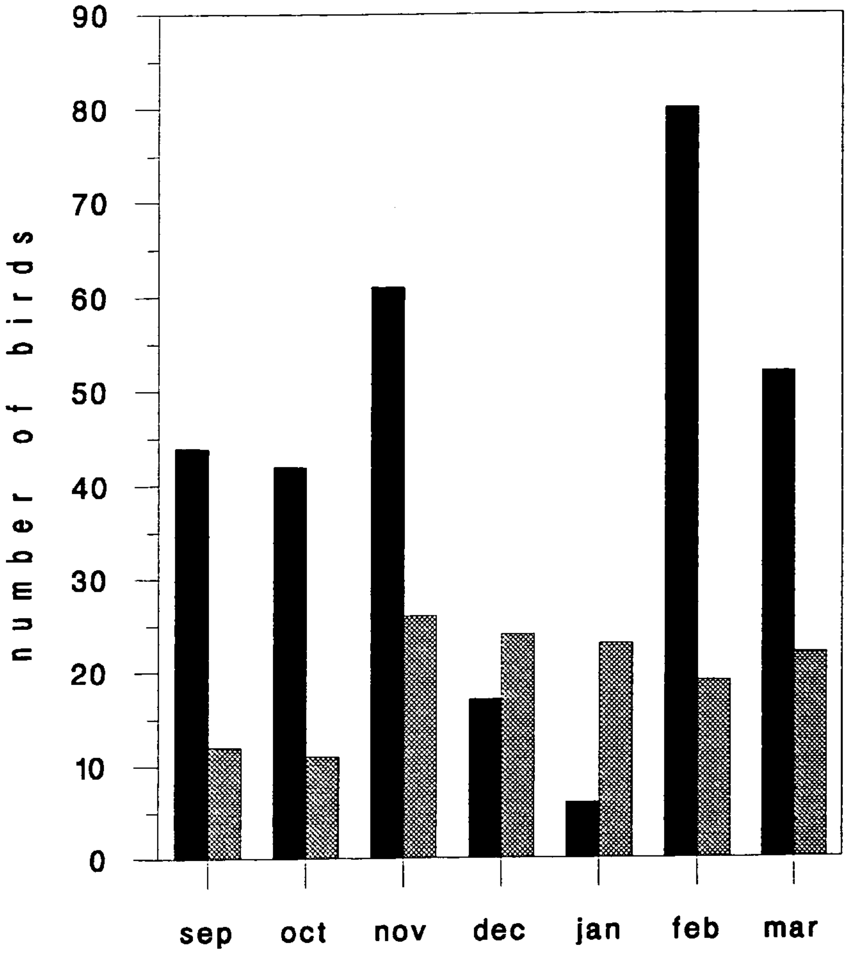


Figure 5.9 The use of Greenabella Bank by grey plovers during times of fluctuating use by curlews.

Dark and light bars represent the number of curlews and grey plovers respectively on the whole of Greenabella Bank at low water in the middle of each month from September 1992 to March 1993.



5.2.5 The effect of tidal height on the use of Greenabella Bank.

During low water of neap tides (defined here as 1.6 m O.D. and above) the intertidal area exposed is less than during spring tide low water (less than 1.4 m O.D.). Because of this, for a given number of birds on Greenabella Bank their density would be heightened during neap tides. One might expect that the number of grey plovers on Greenabella Bank during neap tides would be lower than the number that occur there at low water during springs, since it is believed that crowding by heterospecifics (and conspecifics) can reduce their foraging efficiency. In contrast, because curlew and godwit habitually forage in denser aggregations than grey plovers, one might expect that the numbers of these two species would be similar on neap and spring tides. Eight pairs of data were obtained to test these ideas for grey plovers, and seven pairs were obtained for curlew and godwit. A "pair" consisted of a count of each species of shorebird on two dates as close to each other as was possible to control for possible changes in the overall population of each species; one during a neap tide and one during a spring tide. In addition, the two counts were directly comparable because the time with respect to low water was synchronised as closely as possible (Table 5.1). Although there was no significant difference between numbers using Greenabella Bank on neap and spring tides for curlew (Wilcoxon matched pairs test Z= $^{-}$1.18, one-tailed P=0.12) or godwit (Z=$^{-}$0.85, one-tailed P=0.20), numbers of grey plovers on Greenabella Bank during neap tides were significantly lower than numbers on spring tides (Z=-2.52, one-tailed P=0.006). When the *densities* of each species on the 100 x 100 m grid in the centre of Greenabella Bank during neap and spring tides are compared (Table 5.2), there was again no significant difference for curlews (Wilcoxon matched pairs test Z= $^{-}$0.11, one-tailed P=0.46), but a significantly lower density of grey plovers on neap tides (Z= $^{-}$2.20, one-tailed P=0.014). This indicates that grey plovers were responding to some factor that changed between neap and spring tides, other than curlew densities.

Table 5.1 <u>The difference in abundance of the three shorebird species on Greenabella Bank during neap and spring low water</u>.

Each row contains one "pair" of data; N/C stands for "no count".

Date of neap	date of spring	height of neap at low water	height of spring at low water	minutes after low water neap	minutes after low water spring	curlew neap	curlew spring	plover neap	plover spring	godwit neap	godwit spring
151091	211091	2.4 m	1.3 m	53	47	125	207	1	64	30	063
110392	180392	1.6 m	0.9 m	27	31	211	186	26	67	14	13
250392	180392	1.8 m	0.9 m	64	57	131	203	28	69	36	13
191092	011092	2.2 m	1.3 m	72	73	57	124	1	12	5	3
171192	141192	2.0 m	1.4 m	61	70	33	61	0	26	0	36
300193	270193	1.9 m	1.4 m	67	78	88	37	21	119	176	71
160393	110393	2.0 m	0.6 m	71	66	29	23	22	31	51	5
170194	130194	1.9 m	1.0 m	00	00	N/C	N/C	8	20	N/C	N/C

Table 5.2 <u>Comparison of the density of curlew and grey plover during neap and spring tides on the central area of Greenabella Bank.</u>

Densities are presented as counts from a 100 x 100 m grid (see text). Each row contains one pair of data.

Date of neap	date of spring	height of neap at low water	height of spring at low water	minutes after low water neap	minutes after low water spring	curlew neap	curlew spring	plover neap	plover spring
110392	180392	1.6 m	0.9 m	22	27	27	8	4	5
250392	180392	1.8 m	0.9 m	66	66	11	3	6	16
191092	011092	2.2 m	1.3 m	70	70	5	28	1	6
171192	141192	2.0 m	1.4 m	60	64	3	16	0	11
300193	270193	1.9 m	1.4 m	61	72	11	4	8	17
160393	110393	2.0 m	0.6 m	81	80	6	2	7	13

5.3 Discussion and conclusions

As was demonstrated in Figure 5.5, although grey plovers were numerous on Greenabella Bank only during the latter part of the period of exposure, this coincided with high numbers of curlew and godwit, since these two species were numerous for most of the period of exposure. Looking at Greenabella Bank as a whole, there was broad overlap in the timing of use of this preferred low water feeding site, which indicates that grey plovers did not attempt to avoid curlew. However, when the pattern of distribution of each species on Greenabella Bank through the tidal cycle was investigated on a more local scale, a negative association between the density of curlews and the density of grey plovers on the central area of the mudflat was revealed (Figures 5.6 and 5.7). It therefore appears that grey plovers moved onto Greenabella Bank only when the density of curlews on their preferred feeding areas was low. This observation begs two questions: firstly, why did curlews move from the study plot in such a predictable way towards low water, and secondly, is the negative correlation between densities of these two species (Figure 5.7) based on a causal relationship, or is there an alternative explanation? The answer to the first question probably lies in the tendency of curlews to follow the tide edge when foraging. It is suggested (e.g. Vader 1964) that intertidal invertebrates move near to the substrate surface when covered by sea water, but burrow more deeply after the tide exposes the sediment and the water table falls. Given this, the density of prey available to a foraging curlew (within reach of its bill) is greatest when the substrate is shallowly covered and soon after it is exposed. This probably explains why curlew are present on the study plot soon after the area is uncovered by the ebb tide (high prey availability), but abandon the site later in the low water period (lower prey availability) to feed on areas more recently uncovered.

If grey plovers were indeed discouraged from feeding on Greenabella Bank for the first hour of its exposure period by high densities of foraging curlews, one would expect that during times of year when curlew densities on Greenabella Bank were low, grey plovers would move onto the feeding area soon after the ebb tide had exposed it. This holds only if most grey plovers were free to make a new choice on each tidal cycle; since information from colour-marked individuals indicated that the grey plovers using Greenabella were not territorial, the supposition is probably valid. However it was demonstrated that grey plovers showed the same temporal pattern of arrival on the Bank whether curlew numbers were high or low (Figure 5.8). Further evidence against the avoidance hypothesis comes from the comparison of the intensity of use of Greenabella Bank during months of curlew abundance and scarcity (Figure 5.9). This revealed that even on those dates in December and January when the numbers of curlew on Greenabella Bank were very low, the number of grey plovers did not increase.

One more piece of evidence suggests that the density of grey plovers was not determined by the density of curlews on the preferred feeding site, namely that although the density of curlew on the central area of Greenabella Bank did not change significantly between neap and spring tides, the density of grey plovers there was significantly lower on neap tides (Table 5.2). Possibly the grey plovers reacted to differences in prey availability during neap and spring low waters. I suggested earlier that grey plovers may detect surface prey movements more readily, and/or that *Nereis* come to the surface more frequently, on a partly dried out sediment than on a wet sediment. During low water of neap tides, the sediments on the central area of Greenabella Bank are closer to the water table than during low water of spring tides. It follows therefore, that if grey plovers prefer to feed on partly dried out sediments (for whatever reason), then they could occur at higher density during spring tides than during neap tides. The cue that grey plovers use to detect the presence of their prey may well be the water outflow produced by a surfacing worm, and these can be discerned more readily on a dry surface. When human foot pressure is applied to the partly dried sediments of the feeding areas preferred by grey plovers, water outflows from burrows of *Nereis* were very conspicuous. In contrast, outflows were obscure on the poorly-drained sediments.

These observations also suggest that the negative correlations between the density of curlews and the density of grey plovers on the central part of Greenabella Bank through the low water period (Figures 5.6 and 5.7) are the result of the two species responding in opposite ways to drying out of the sediments after the ebbing tide had exposed the feeding area. Curlews moved *away* from the central area during the low water period to follow the highest availability of prey, while grey plovers moved *into* the area when the drying sediments provided increased prey availability for this species.

CHAPTER SIX

DO GREY PLOVERS ACTIVELY AVOID CONCENTRATIONS OF LARGE SHOREBIRDS TO REDUCE INTERFERENCE COMPETITION?

6.1 Introduction.

As I showed in the last chapter, many grey plovers move onto the Greenabella Bank to feed at or after low water, having previously fed on Central Bank. The question that is posed is why do the grey plovers move at all and why do they not move until they do?

Let us assume that under non-extreme weather conditions shorebirds move from one mudflat to another, or from patch to patch within a mudflat, primarily to maintain or increase food intake rates, with an unchanging risk of predation. In this case, shorebirds must assess the quality of the environment in some way related to the rate of energy intake they can achieve in a particular place. This will depend both on the density of suitable and available prey in the sediment and on any depression of intake rate by interference from competitors. Where different foraging methods or strategies have different energy *costs* associated with them, then *net* rate of energy intake is the most useful "currency" to use because a higher rate of energy expenditure will reduce the benefits of a higher gross energy intake rate (Evans 1976).

One possible explanation for the observed pattern of use of Greenabella Bank is that it is the preferred feeding site for all of the three study species, but that grey plovers chose not to feed on this site before low water in the tidal cycle because of the high densities of curlew and godwit (and possibly other species) there which might interfere with the plovers' feeding method because they require an undisturbed area in which to locate (visually) and then capture their prey (see Pienkowski 1979). For convenience I will refer to this as the "competition hypothesis". This explanation is feasible because, towards low water, and especially on the rising tide, curlew and godwits concentrate near to the tide edge leaving sediments near the centre of the mudflat relatively free from these two species, whereas early in the tidal cycle these species are more evenly distributed (for details see previous section). The alternative explanation (the "no-competition hypothesis") is that the grey plovers are simply moving onto Greenabella Bank in response to a decreased rate of prey intake on Central Bank and that they can achieve a higher net energy intake when they arrive on Greenabella. The supposition is that this coincides in time with the reduction in use of the higher parts of Greenabella Bank by curlews and godwits.

In order to test between these two hypotheses, observations were carried out to answer three specific questions:

i) Do some of the grey plovers foraging on Central Bank experience a decrease in prey biomass intake before the move to Greenabella Bank? If they do, then this is evidence to suggest that the observed movements are not a response to lowered curlew densities on the area of Greenabella Bank favoured by grey plovers.

ii) Do they achieve a higher net rate of prey biomass intake once they arrive? If they do, then this is consistent with the competition hypothesis because it suggests that they may have been prevented from using this more profitable area earlier in the tidal cycle.

iii) Once on Greenabella does intake rate increase with time as curlews and godwits concentrate at the tide edge and leave the plovers less crowded so that the overall density of large shorebirds on the plovers' feeding area decreases? If it does, then this is also is consistent with the competition hypothesis.

6.2 Methods.

Details of the methodology of estimating prey intake rates and prey size in the field is given in the general methods section in chapter two. Conversion of estimated lengths of *Nereis* into calorific content was achieved using Dugan's (1981) equation, obtained from bomb calorimetry of a range of sizes of *Nereis;*

log (dry flesh weight in mg.) = a + b (body length in cm.)

where a= -0.642 ± 0.039 (S.E.)

b= 2.47 ± 0.0037 (S.E.) n=22

and mean calorific value for Nereis = 4.7 cal mg $^{-1}$.

Observations were carried out; i) from one hour before low water to low water, and ii) from low water to low water plus one hour. This enabled, given a seven minute observation period per individual (see Chapter two), a maximum of eight individuals to be observed in each of these two test periods. The time periods i) and ii) were chosen to represent, in the first case the period of the tide before most grey plovers on Central Bank move to Greenabella Bank and, in the second case, the time period when most of the grey plovers abandon Central Bank and move onto Greenabella Bank. Unfortunately, it was not possible to measure the prey biomass intake of individuals immediately prior to their departure, and hence impossible to determine a threshold intake below which the bird changes feeding site, because: a) very few colour-ringed individuals were available for observation, b) precise time of departure was variable and therefore unpredictable, and c) an individual would need to be watched until it departed. Because sample time for that individual would have to be indefinite, very few samples would have been obtained on any one day.

To see if grey plovers achieve a higher rate of prey biomass intake once they arrive on Greenabella Bank, individuals were watched as soon as they arrived and foraging information gathered for seven minutes after this. Thereafter, individuals were chosen at random until they moved off Greenabella Bank during the rising tide.

In order to see if intake rate of grey plovers on Greenabella Bank was affected by the density of heterospecifics, curlew and godwit were counted immediately after an individual grey plover was sampled for intake rate. These counts could be converted into densities because the area in which foraging grey plovers were monitored was bounded by marker posts into a 100 x 100m square.

6.3 Results.

6.3.1 Do grey plovers experience a decrease in energy intake before they move to Greenabella Bank?

Table 6.1 shows the intake rate of worms of various size classes by grey plovers for five tidal cycles over the period January-March 1993. These data were converted into gross energy intake rates, presented in Table 6.2. Independent-sample t-tests were conducted on the data for each tidal cycle, and the results show that on each day a significant decrease in gross energy intake occurred between the periods one hour before low water and one hour after low water. In order to investigate whether, in addition to a *gross* decrease in energy intake, the costs of foraging changed between the two time periods, the rate of pacing was compared. Table 6.2 shows the results of this analysis. Pacing rate decreased on one day, remained the same on one day and decreased on the other three days of observations, but none of these changes were significant. This indicates that the energy expended during foraging was similar between the periods.

Table 6.1 Rate of intake of *Nereis* of estimated size classes by grey plovers foraging on Central Bank between the hour before low water and the hour after low water, for five tidal cycles (tables a-e) during late winter 1993.

"Mean" refers to mean for a seven minute period of observation, for each size class represented. Where particular size classes are not tabulated they were absent from the diet.

a) 26/01/93

PERIOD	MEAN WORMS 0.25 BILL L'GTH	S.E.	MEAN WORMS 0.5 BILL L'GTH	S.E.	N
LW -1HR	6.1	1.2	6.7	1.3	7
L +1HR	6.8	0.8	7.5	0.9	4

b) 10/02/93

PERIOD	MEAN WORMS 0.25 BILL L'GTH	S.E.	MEAN WORMS 0.5 BILL L'GTH	S.E.	N
LW -1HR	2.8	0.6	5.2	0.9	5
LW+1HR	1.4	0.5	2.0	0.6	5

c) 23/02/93

PERIOD	MEAN WORMS 0.25 BILL L'GTH	S.E.	MEAN WORMS 0.5 BILL L'GTH	S.E.	MEAN WORMS 1 BILL L'GTH	S.E.	N
LW -1HR	3.3	0.8	3.6	0.9	0.1	0.1	7
LW+1 HR	1.6	0.7	0.2	0.2	0	-	5

PERIOD	MEAN WORMS 1.5 BILL L'GTHS	S.E.	N
LW -1 HR	0.1	0.1	7
LW+1 HR	0	-	5

Table 6.1 (continued).

d) 25/02/93

PERIOD	**MEAN WORMS 0.25 BILL L'GTH**	**S.E.**	**MEAN WORMS 0.5 BILL L'GTH**	**S.E.**	**MEAN WORMS 1 BILL L'GTH**	**S.E.**	**N**
LW -1HR	3.3	0.9	3.3	0.5	0	-	4
LW+1 HR	2.1	0.6	1.6	0.5	0.1	0.1	8

PERIOD	**MEAN WORMS 2 BILL L'GTHS**	**S.E.**	**N**
LW -1 HR	0.3	0.3	4
LW+1 HR	0	-	8

e) 08/03/93

PERIOD	**MEAN WORMS 0.25 BILL L'GTH**	**S.E.**	**MEAN WORMS 0.5 BILL L'GTH**	**S.E.**	**MEAN WORMS 1 BILL L'GTH**	**S.E.**	**N**
LW -1HR	4.1	0.3	3.0	0.6	0.4	0.2	8
LW+1 HR	2.1	0.6	1.4	0.3	0	-	8

PERIOD	**MEAN WORMS 1.5 BILL L'GTHS**	**S.E**	**MEAN WORMS 2 BILL L'GTHS**	**S.E**	**N**
LW -1 HR	0.3	0.1	0.1	0.1	8
LW+1 HR	0.1	0.1	0	-	8

Table 6.2 Change in energy intake rate and pacing rate of grey plovers foraging on Central Bank Between the hour before low water and the hour after low water, for five tidal cycles(a-e) during late winter 1993.

a) 26/01/93

PERIOD	MEAN CALS PER 7 MINS	S.E.	MEAN PACES PER 7 MINS	S.E.	N
LW -1HR	211.0	17.1	292	36.5	7
LW+1 HR	124.5	39.5	261	52.6	4

POOLED VARIANCE t-TEST FOR CALORIE INTAKE BETWEEN PERIODS

t=3.17 d.f.=9 P=0.011

POOLED VARIANCE t-TEST FOR PACE RATE BETWEEN PERIODS

t=0.51 d.f.=9 P=0.622

b) 10/02/93

PERIOD	MEAN CALS PER 7 MINS	S.E.	MEAN PACES PER 7 MINS	S.E.	N
LW -1HR	121.0	18.8	249	18.6	5
LW+1 HR	48.4	8.3	305	27.4	5

POOLED VARIANCE t-TEST FOR CALORIE INTAKE BETWEEN PERIODS

t=3.54 d.f.=8 P=0.008

POOLED VARIANCE t-TEST FOR PACE RATE BETWEEN PERIODS

t=1.70 d.f.=8 P=0.128

c) 23/02/93

PERIOD	MEAN CALS PER 7 MINS	S.E.	MEAN PACES PER 7 MINS	S.E.	N
LW -1HR	139.1	23.2	303	7.6	7
LW+1 HR	44.2	24.8	300	18.9	5

POOLED VARIANCE t-TEST FOR CALORIE INTAKE BETWEEN PERIODS

t=2.74 d.f.=10 P=0.021

POOLED VARIANCE t-TEST FOR PACE RATE BETWEEN PERIODS

t=0.20 d.f.=10 P=0.843

Table 6.2 (continued).

d) 25/02/93

PERIOD	MEAN CALS PER 7 MINS	S.E.	MEAN PACES PER 7 MINS	S.E.	N
LW -1HR	121.5	29.9	223	7.9	4
LW+1 HR	56.6	13.6	259	15.4	8

POOLED VARIANCE t-TEST FOR CALORIE INTAKE BETWEEN PERIODS

t=2.31 d.f.=10 P=0.04

POOLED VARIANCE t-TEST FOR PACE RATE BETWEEN PERIODS

t=1.55 d.f.=10 P=0.151

e) 08/03/93

PERIOD	MEAN CALS PER 7 MINS	S.E.	MEAN PACES PER 7 MINS	S.E.	N
LW -1HR	157.9	30.5	308	24.0	8
LW+1 HR	57.1	11.7	317	24.0	8

SEPARATE VARIANCE t-TEST FOR CALORIE INTAKE BETWEEN PERIODS

t=3.09 d.f.=9.01 P=0.013

POOLED VARIANCE t-TEST FOR PACE RATE BETWEEN PERIODS

t=0.27 d.f.=14 P=0.792

6.3.2 Do grey plovers achieve higher energy intake rates on Greenabella Bank than they do on Central Bank?

Table 6.3 shows the results of observations for three tidal cycles during late winter 1993. Data are in two groups - the first corresponding to observations of grey plovers on Central Bank from low water to low water plus one hour, and the second corresponding to observations of grey plovers on Greenabella from one hour after low water until about two hours after low water. For reasons detailed in the methods section it was not possible to obtain observations from the same individual on each of the feeding areas.

The results show that grey plovers achieved a higher gross energy intake during the hour after leaving Central Bank than they did when foraging on Central Bank, but on 23/02/93 this was not quite statistically significant (t=2.07 d.f.=10 P=0.065) due to the large amount of variation between the intake rate of the individuals that were sampled. Table 6.3 also gives details of pace rates of grey plovers on the two mudflat areas. There was no significant difference between the pace rates of grey plovers on Central Bank and those on Greenabella, indicating that the *costs* of foraging were likely to be rather similar on the two areas.

Grey plovers feeding on Greenabella Bank achieve between 2.6 and 2.9 times the gross energy intake of grey plovers feeding on Central Bank in the previous hour. The high energy intake rate on Greenabella was achieved largely because the frequency of capture of large worms (greater than one bill length) there was higher than on Central Bank; large worms contribute a disproportionately high amount to overall energy intake (Table 6.4).

Table 6.3 Difference in net energy intake rate and pace rate of grey plovers between Central Bank and Greenabella Bank for three low water periods (a-c) during late winter 1993.

a) 10/02/93

AREA	MEAN CALS PER 7 MINS	S.E.	MEAN PACES PER 7 MINS	S.E.	N
CENTRAL BANK	48.4	8.3	305	27.4	5
G ' BELLA BANK	136.8	22.3	260	23.4	6

SEPARATE VARIANCE t-TEST BETWEEN AREAS FOR CALORIE INTAKE RATE :

t=3.72 d.f. =6.32 P=0.009

POOLED VARIANCE t-TEST BETWEEN AREAS FOR PACE RATE :

t=1.25 d.f.=9 P=0.243

b) 23/02/93

AREA	MEAN CALS PER 7 MINS	S.E.	MEAN PACES PER 7 MINS	S.E.	N
CENTRAL BANK	44.2	24.8	300	42.4	5
G ' BELLA BANK	113.6	22.1	266	47.7	7

POOLED VARIANCE t-TEST BETWEEN AREAS FOR CALORIE INTAKE RATE :

t=2.07 d.f. =10 P=0.065

POOLED VARIANCE t-TEST BETWEEN AREAS FOR PACE RATE :

t=1.26 d.f.=10 P=0.236

Table 6.3 (continued).

c) 25/02/93

AREA	MEAN CALS PER 7 MINS	S.E.	MEAN PACES PER 7 MINS	S.E.	N
CENTRAL BANK	56.6	13.6	259	14.4	8
G ' BELLA BANK	162.3	24.3	264	20.6	6

POOLED VARIANCE t-TEST BETWEEN AREAS FOR CALORIE INTAKE RATE :

t=4.05 d.f. =12 P=0.002

POOLED VARIANCE t-TEST BETWEEN AREAS FOR PACE RATE :

t=0.19 d.f.=12 P=0.86

Table 6.4 Contingency table to show the association between the size of worms captured by grey plovers and the mudflat on which they were caught. "Cases" refers to the seven minute observation period of grey plovers; "Large" worms are those estimated to be 30 mm.or longer, which corresponds to the 1+ age class.

	CENTRAL BANK	G ' BELLA BANK	TOTALS
CASES WITH "LARGE" WORMS	13	21	34
CASES WITHOUT "LARGE" WORMS	50	20	70
TOTALS	63	41	104

CHI-SQUARE TEST (WITH YATES' CORRECTION)

$\chi^2 = 9.23$ $P < 0.01$ d.f.=1.

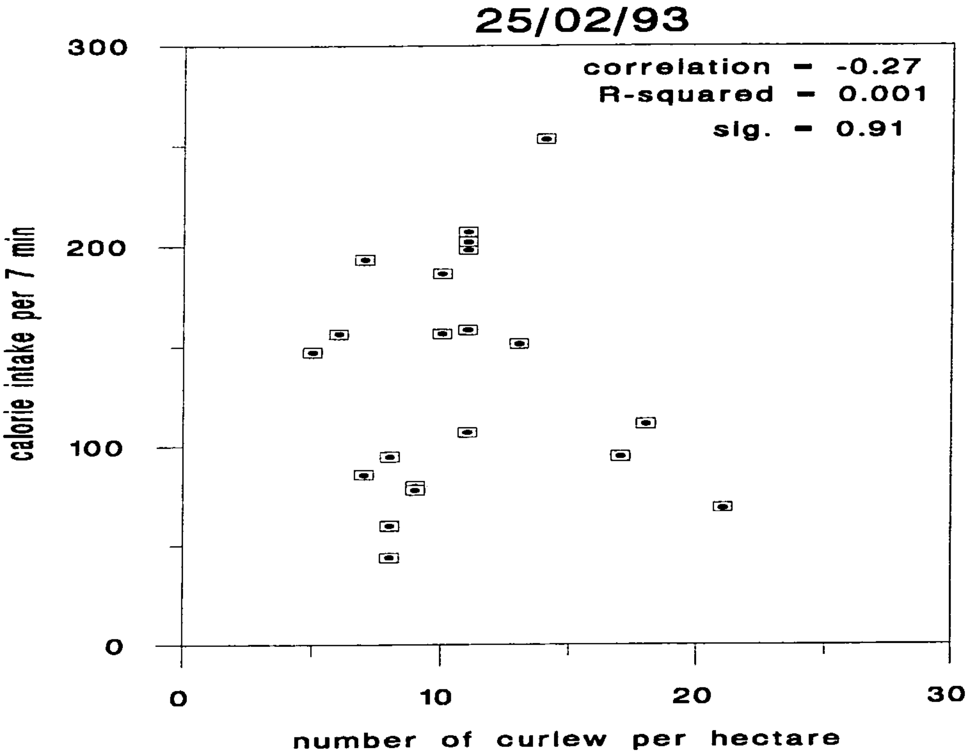
6.3.3 Does the density of curlews affect the energy intake rate of grey plovers on Greenabella Bank?

Figure 6.1 shows the results of observations comparing energy intake of grey plovers with the density of curlews in a 0.1 x 0.1 km square on the high flats of Greenabella Bank for two low water periods in late winter 1993. The regression statistics for the two graphs indicate that there is no significant linear relationship between the two variables, and there is a large amount of "scatter" of the data points, reflected by low r^2 values. On both dates there was a depression of grey plover intake rate at curlew densities above about 15 curlew per hectare, though this was not significant. Even when the data for both days were combined, the decrease was not quite significant at the five percent level (Table 6.5; χ^2=2.09 d.f.=1 P<0.25). If the value of about 15 curlews per ha. represents a threshold density above which grey plovers experience interference in foraging, then we would predict that grey plovers would tend to avoid feeding on areas which support such high densities. Table 6.6 shows that at densities of 16 curlews per ha. and above, grey plovers were absent significantly more often from the 1 hectare grid than when curlew densities were less than 16 per hectare. The difference is a real one because all the counts were made at times of year (October to March) when both species were present on the estuary in high numbers, so that the "supply" of birds was not limited. This indicates that most grey plovers may be delaying their arrival on Greenabella to avoid the highest concentrations of curlew, but there are times when, even though the density of curlew is above 15 per hectare, grey plovers are present (Table 6.6).

6.4 Discussion.

I shall discuss the results from each of the three sets of field observations in turn and then synthesise the evidence for competitive interactions on Greenabella Bank.

Figure 6.1 The relationship between the rate of energy intake of grey plovers on Greenabella Bank and the density of curlews surrounding them.



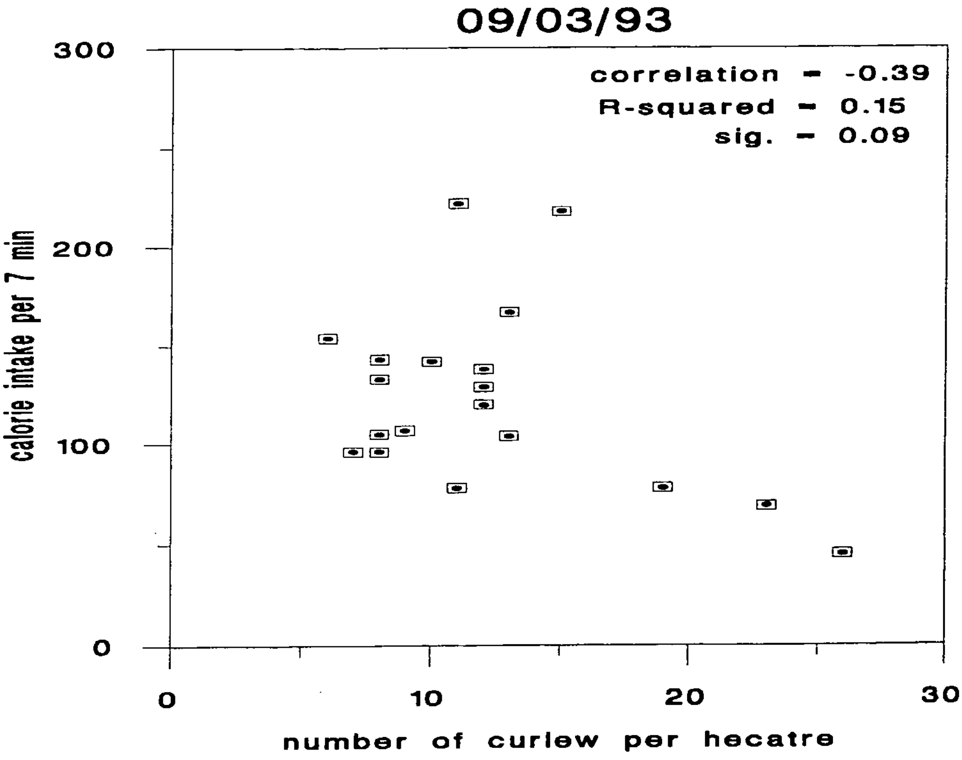


Table 6.5 Contingency table to show the association between calorie intake of grey plovers and the density of curlews surrounding them.

The categories for the cells were chosen because a decrease in intake rate occurred at about 15 curlew per ha. and when intake rate was about 150 cals per 7 minutes.

	CASES WHERE DENSITY <15 CURLEW PER HA.	**CASES WHERE DENSITY >15 CURLEW PER HA.**	**TOTALS**
CASES WHERE CALORIE INTAKE <150 PER 7 MINS.	21	6	27
CASES WHERE CALORIE INTAKE >150 PER 7 MINS.	14	0	14
TOTALS	35	6	41

CHI-SQUARE TEST (WITH YATES' CORRECTION)

$\chi^2 = 2.085$ $P < 0.25$ d.f.=1

Table 6.6 Contingency table to show the association between the occurrence of high densities of curlew and the absence of grey plovers from a 1ha. plot on the grey plovers' prefered feeding site on Greenabella Bank.

Each case represents one count. Counts were conducted on 20 days from October to March, throughout the period of exposure.

	CASES WHERE GREY PLOVERS ABSENT	CASES WHERE GREY PLOVERS PRESENT	TOTALS
CASES WHERE CURLEW <16	43 χ^2=3.5	101 χ^2=2.4	144
CASES WHERE CURLEW >15	30 χ^2=13.3	8 χ^2=9.0	38
TOTALS	73	109	182

CHI-SQAURE TEST (WITH YATES' CORRECTION)

$\chi^2 = 28.2$ $P<<0.001$ d.f.=1

The results contained in Tables 6.1 and 6.2 demonstrate that grey plovers experienced a decrease in energy intake rate and no saving in the rate of energy expenditure between the periods one hour before low water and one hour after low water. This is the period during which, as I showed in the previous chapter, most grey plovers that had been feeding on Central Bank as the tide ebbed abandoned the site and moved to Greenabella Bank to feed. Although I was unable to show that only those *individuals* which experience a decrease in energy intake subsequently depart (not all grey plovers move feeding site), the observations I obtained strongly suggest that the grey plovers moved when their energy intake rate fell to a level at or below which it was unprofitable to stay. Why *does* energy intake rate fall in such a predictable way? One possible explanation is that grey plovers become satiated after low water and therefore feed less intensively. This is unlikely for two reasons: i) because searching rate as expressed by pacing rate did not vary significantly between the two observation periods (see Table 6.2), and ii) because individuals moved to Greenabella Bank where a higher rate of energy intake was obtained (see Table 6.3). A more likely explanation for the decrease in intake rate on Central Bank is a decrease in the availability of their prey with the progression of the tidal cycle. "Availability" comprises two components - accessibility (important for probing species such as sandpipers) and detectability/activity (important for shorebirds that forage visually, such as plovers). For example, no matter how high the absolute density of a particular prey species in the sediment, availability will be low if most of the animals are buried beyond the reach of the bill of the shorebird in question or if prey are inactive so as to make them undetectable. For a given density of invertebrate prey, the density of available prey may change in relation to a variety of parameters, such as sediment temperature (Pienkowski 1980) and the time after emersion by the falling tide (Vader 1964). The latter factor may be responsible for controlling the availability of *Nereis* at the sediment surface during the tidal cycle because it is thought that grey plovers rely on prey movements or water outflows at the surface from the worm moving in its burrow to detect their prey (Pienkowski 1980). These surface cues will become less frequent if an increasing proportion of worms in the sediment burrow deeper or come to the surface less often as the tidal cycle proceeds (Townshend 1980). As the sediment surface dries by evaporation and lowering of the water table after being uncovered by the falling tide, it is postulated that worms burrow deeper down towards the water table to ensure the continued irrigation of their burrows. The higher energy intake rates achieved by grey plovers on Greenabella Bank as compared to Central Bank (see Table 6.3) may in part be explained in terms of different levels of activity of *Nereis* in these two sites. Greenabella Bank lies at a lower tidal level than Central Bank and the highest parts of it become exposed about two hours before low water whereas the favoured feeding areas for grey plovers on Central Bank are exposed about four hours before low water. If absolute densities of *Nereis* on Central Bank and Greenabella Bank are similar then the density of *available* prey at a given time of tidal cycle will be greater on Greenabella Bank than on Central Bank. This is because the water table is nearer the surface on Greenabella and the surface sediments there will have had less time in which to become dry and therefore worms will be nearer the surface. In fact invertebrate sampling during March 1993 showed that mean density of *Nereis* on Greenabella Bank was 480 m^{-2} (S.E.=109 n=13) while the mean density on Central Bank was 199 m^{-2} (S.E.=97 n=11), so densities of available prey were probably a good deal higher on Greenabella Bank at a given time in the tidal cycle. Another reason why energy intake rates may be higher on Greenabella Bank is if the sizes of the prey items caught are larger there. The calculations of Dugan (1981b) showed that large worms have disproportionately higher energy contents than small worms; in other words even rather few large worms will provide a bird with more energy than many small ones. Table 6.4 shows that the proportion of seven minute samples containing "large" worms was significantly higher for birds on Greenabella Bank compared to the proportion on Central Bank.

Whilst I have established that *gross* energy intake was higher on Greenabella Bank than on Central Bank, it is important to attempt to make an estimate of *net* energy intake rates by considering the relative costs of foraging in the two areas, as well as the energetic cost of flying between them. The latter can be considered negligible because the flight time of one journey is less than ten seconds and observations of colour marked grey plovers showed that once on Greenabella Bank individuals normally did not change feeding sites until the tide pushed them off. However foraging costs between the two sites could differ if the foraging method changes between sites or if locomotion on one site is impeded by soft sediments. Both these factors are similar on the two sites; the typical run-stop-peck feeding method was employed throughout, the pacing rate between sites was similar (see Table 6.3) and sediment viscosity seemed, using a subjective judgement, to be similar between sites. With these factors taken into account, it appears that grey plovers did achieve a net increase in energy intake rate by moving to Greenabella Bank and the reason seems to be combination of increased availability of all prey and/or a higher abundance of large worms on Greenabella Bank.

An important test in the study of possible competitive effects is to determine if the co-occurrence of species leads to a depression in the energy intake rate of one or more of the species concerned. In the situation which I have been describing, the "competition hypothesis" predicts that a close association between grey plovers and concentrations of other large shorebirds such as curlew and bar-tailed godwit will result in a decrease in the prey capture rate, and hence energy intake rate, of grey plovers. Field observations showed that energy intake of grey plovers on Greenabella Bank was not reduced in proportion to the density of curlews surrounding them (see Figure 6.1). There is however evidence from both dates that at curlew densities above about 15 per hectare there was a reduction in the energy intake of grey plovers. Whilst this was not shown to be statistically significant, if it does represent a real decrease then there is evidence that interference in foraging is operating when densities of curlew are high. However, in order to assess the potential importance of these effects it is necessary to determine how frequently such densities occur on Seal Sands. For Greenabella Bank, which is the mudflat supporting among the highest densities of curlews, as well as being an area of suitable substrate for grey plovers, densities of curlews at times exceed those that were encountered at the time of my foraging observations, but generally only at times when either the falling tide had recently exposed the highest parts of the mudflat or when the rising tide concentrated birds just before they were forced off the area. With this in mind it seems that for the greater part of the tidal cycle curlew densities are too low to cause interference to the foraging of grey plovers.

To summarise the evidence for competitive interactions provided by the field observations discussed above, the first two pieces suggest that grey plovers delayed their arrival on Greenabella Bank, not to actively avoid potential interference by high densities of feeding curlews and godwits, but in response to falling prey availability on Central Bank. I have established that after about one hour after low water grey plovers can achieve a higher net rate of energy intake on Greenabella Bank than they can on Central Bank. This poses the question why, if prey availability is much higher on Greenabella Bank, do grey plovers feed on Central Bank at all and not go onto Greenabella as soon as it becomes exposed? The reason may be because grey plovers move only when they have to in order to maintain a threshold rate of energy intake. Another possible explanation for the delay in moving is that early in the tidal cycle the surface sediment on Greenabella may be too wet for grey plovers to detect prey effectively. Thus if they *had* moved earlier they might not have achieved the higher rates if intake that they were seen to achieve when they did move. A film of water on the sediment surface, which is left by the falling tide and remains for a period after emersion, will reflect light and may prevent grey plovers from seeing as many prey movements as they might when the sediment is drier. This may be especially relevant if the plovers use water outflows from worms moving in their burrows to detect their prey; tiny trickles of water will be difficult to detect against a background of water, but relatively easy to detect against a background of rather drier mud. Anyone who has walked over a mudflat containing high densities of *Nereis* will confirm that outflows from the worm burrows when the mud is compressed by footsteps are strikingly apparent on firm slightly dry mud but less so on softer wet sediments.

In the last set of field observations I investigated the effect of curlew density on energy intake rates of grey plovers on Greenabella Bank. If depression of intake rate does occur it seems to arise only at densities which occur for a short period in the tidal cycle. It seems unlikely that the arrival of grey plovers from Central Bank is timed to avoid such densities because grey plovers exhibit very similar patterns of arrival at times (of year) when curlew densities are low (Chapter 5).

CHAPTER SEVEN

A SEARCH FOR COMPETITIVE INTERACTIONS BETWEEN KNOT, SANDERLING, TURNSTONE AND OYSTERCATCHER ON REDCAR AND COATHAM ROCKS

7.1 Introduction.

Chapter three identified groups of species that were potential competitors; the above species were one such group, on the basis that they occurred together in high densities on the same feeding areas on the south of the estuary, favoured similar substrates, and overlapped in their favoured prey species. They were the group first chosen for study (in winter 1990/91) but numbers of knot were unexpectedly low and the main focus of research was changed in subsequent winters to the shorebird species feeding on *Nereis* on Seal Sands.

The original study aimed to answer the following questions;

1) Do sanderling, turnstone or oystercatcher change feeding site when large flocks of knot arrive on the estuary in November, several months after the other species had established feeding routines on Redcar Rocks? If the other species remain feeding on Redcar Rocks, does the arrival of large flocks of knot from their mid-tide feeding site (Seal Sands), onto Redcar Rocks cause displacement of sanderling (and perhaps turnstone) onto another part of the rocks? Since knot habitually feed in large closely packed flocks, which can "carpet" substantial areas of intertidal feeding space, and since knot have a larger body size than sanderling and turnstone, displacement might have been anticipated.

2) Are there negative correlations between the number of knot and the number of other species using the rocks at times when all species are potentially numerous (i.e. between November and March)? If there is no correlation on spring tides (when feeding area is large and bird densities low) are there negative correlations when feeding area is reduced and bird densities high, during neap tides?

3) Is there overt aggression between species? Do aggressive interactions between species occur more frequently when the density of birds is high? If interactions occur, do they take the form of food-stealing or of aggressive displacement from a feeding site?

7.2 Study area and methods.

While sanderling, and to a lesser extent turnstone and knot, use the open sea beaches in addition to the rocks, it is on the rocks that highest concentrations of all species occur. A substantially greater area of rocks is exposed at spring low water when, in addition to Redcar Rocks, Coatham Rocks also become exposed and available to shorebirds for about two hours. However, because of high levels of human and canine disturbance on Coatham Rocks, most data were collected from Redcar Rocks. These rocks have in places a dense cover of molluscs, dominated by the mussel *Mytilus edulis*, together with smaller proportions of littorinids, and the limpet *Patella vulgata*. Among the Crustacea, barnacles and the shore crab are also available to shorebirds. In between ridges of rocks, sand has accumulated to various depths, creating alternate strips of rock and sand. Coatham Sands (and the beaches adjacent to and within Coatham and Redcar rocks) contain the polychaete worm *Nerine cirratulus*, the amphipods *Bathyoreia* spp. and the isopod *Eurydice pulchra*.

Counts and feeding observations of birds on Redcar Rocks were made from a landrover, which enabled close approach to birds without causing disturbance. Thirty-one counts of birds were made at low water, on both spring and neap tides, and eight days of behavioural observations were undertaken, between 22/10/90 and 10/04/91. Focal animal sampling (Altman 1974) was used; randomly chosen individuals were watched for 5 minutes, and the number and nature of any interactions between individuals noted. In order to test whether bird density affected rates of aggression, records were classified as to whether the focal bird fed in a "flock" - where inter-individual distance was less than one metre - or "singly" - where inter-individual distance remained greater than one metre for the duration of the observation period. In most cases the distinction between the two was immediately apparent because the average nearest-neighbour distances were about 60 cm in sanderling and about 30cm in knot.

7.3 Results and discussion.

Rates of intraspecific aggression amongst sanderling were more than twice the rate of aggression involving sanderling and another species (Tables 1 and 2). Most interspecific interactions with flocking sanderling were disputes over food items, in which turnstones attempted to steal food (7 out of eight interactions), although in one case in which a knot directed aggression towards a sanderling, no food item was apparent and it was probably a dispute over feeding space. Rates of interspecific interactions were higher with those sanderling that were sparsely distributed over the feeding area than with those that fed in flocks (Table 2), although the difference was not significant at the 5% level (Wilcoxon matched pairs test, one tailed P=0.103 N=8). An increased rate of interaction with single sanderling is probably because it is energetically profitable for an aggressor to steal only large food items, and it was only sparsely-distributed sanderling that took large food items such as scraps of mussel flesh left by oystercatchers (also commonly taken by individual turnstone). When sanderling fed in flocks, small food items were most common, and these are handled much more rapidly than large items; this presents a potential thief with little opportunity to steal.

Table 7.1 Rates of intra-specific aggressive interactions in sanderling on Redcar Rocks during the winter 1990/91.

These tables summarise observations taken on eight days over the winter (1 day in October, 1 day in November, 1 day in December, 3 days in January, 1 day in February, and 1 day in March).

	minutes of observations	total number of interactions	of which over food items	of which over space/other	overall rate (per minute)
single	185	28	23	5	0.15
flocks	245	16	5	11	0.07

Table 7.2 Rates of inter-specific aggressive interactions involving sanderling on Redcar Rocks during the winter 1990/91.

	minutes of observations	total number of interactions	of which over food items	of which over space/other	overall rate (per minute)
single	185	11	11	0	0.059
flocks	245	8	7	1	0.033

The average rate of interspecific aggression, between sanderling and another species, was calculated for each of the eight days of observation. There was no significant correlation between this (daily) rate and the numbers present on that day of any one of the four species involved - sanderling or knot or turnstone or oystercatcher (Table 7.3). However the (daily) rate of aggression was positively correlated with the combined total numbers of the three smaller species present on that day (Spearman rank correlation $R_s = 0.64$ $P<0.05$ $N=8$; Figure 7.1). One might have expected to see a positive correlation between aggression rate and the abundance of turnstone - the species that was involved in the majority of interactions with sanderling. Although the correlation coefficient of 0.35 (Table 3) was the highest recorded, it was not significant at the 5% level.

In summary, although overt interspecific aggression did occur, it was relatively infrequent during the period of my study and intraspecific interactions were more prevalent. Other studies (e.g. Recher and Recher 1969) have also shown that direct intraspecific interactions in shorebirds are generally far more frequent than interspecific ones.

Territoriality is one way in which competition for feeding space can be resolved but which may involve aggressive interactions at certain times. However, no territoriality - intra- or interspecific - was observed in any species on Redcar Rocks, unlike in coastal Peru, where Myers (1979) found that sanderlings defended territories against semipalmated plovers *Charadrius semipalmatus*. The reason for this difference may result from the unprofitability of defending a territory on Redcar Rocks, an area that supports very high densities of birds and that is exposed for only a few hours per low water period.

Competition can occur even if there is little overt aggression between species; one species can prevent another from occupying its preferred feeding area if the inferior

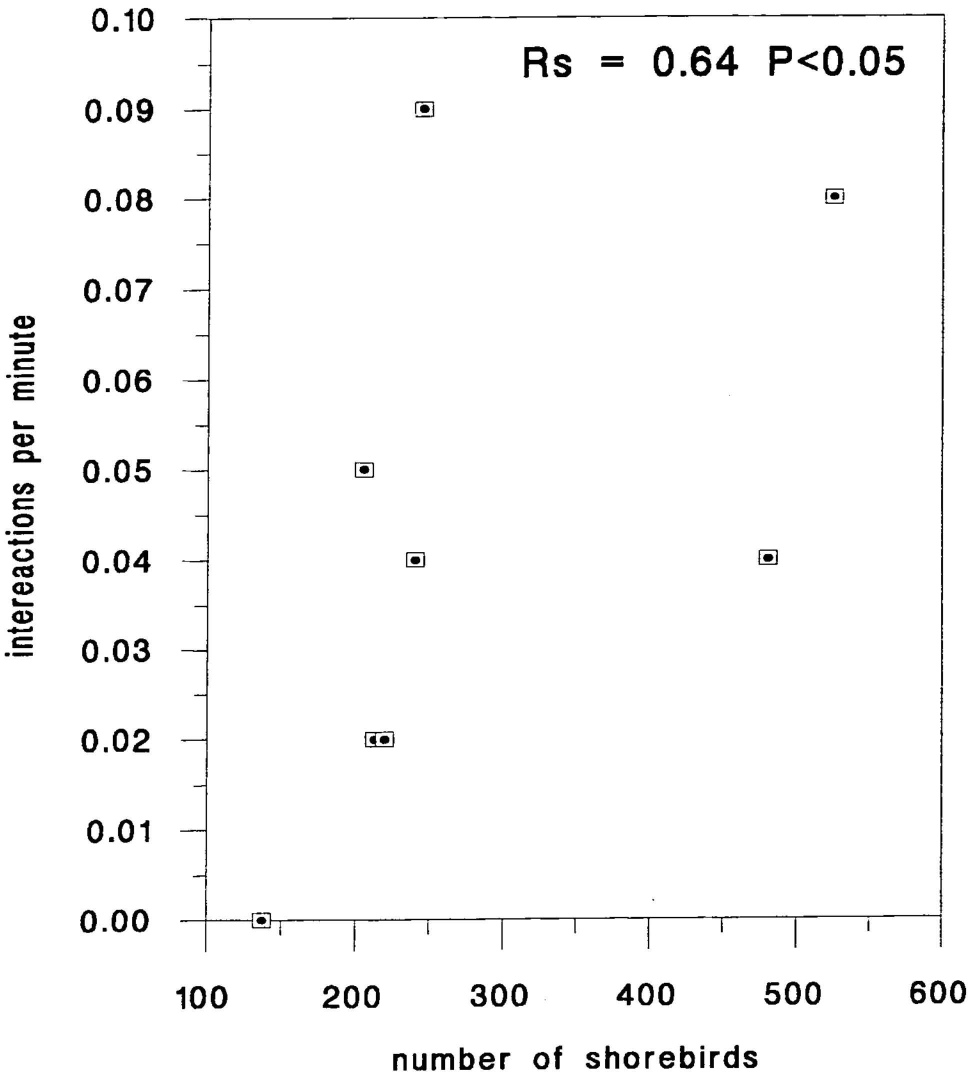
Table 7.3 The relationship between the average daily rate of interspecific aggression and the number of four species of shorebird on Redcar Rocks on those days

Species	Spearman rank correlation coefficient	Probability level
sanderling	-0.04	0.47
knot	0.19	0.32
turnstone	0.35	0.20
oystercatcher	0.012	0.49

N.B. Number of cases in each correlation is 8.

Figure 7.1 The relationship between the total number of shorebirds* and the rate of interspecific interactions on Redcar Rocks between October 1990 and March 1991

* The sum of the numbers of knot, sanderling and turnstone.

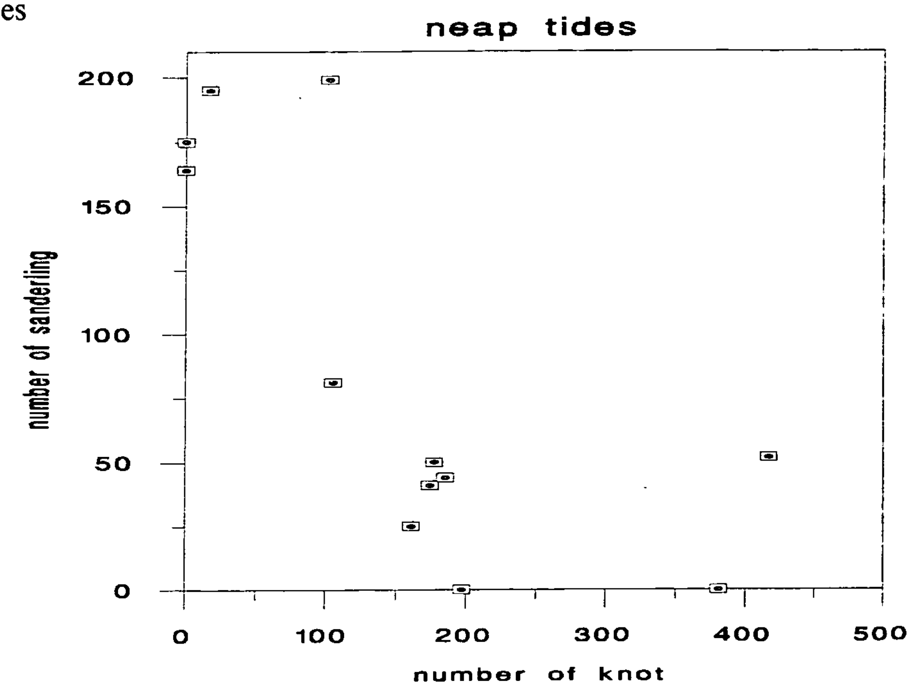


competitor suffers from interference in foraging with another species and therefore avoids it. No displacement of species was observed on Redcar Rocks, but there was a negative correlation between numbers of knot and sanderling using Redcar Rocks on different dates at low water ($R_S = -0.52$ $P<.0.05$ $N=23$). Furthermore, when neap and spring low waters were analysed separately, there was a markedly stronger relationship during neap tides ($R_S = -0.74$ $P< 0.01$ $N=12$; Figure 7.2a) than during spring tides ($R_S = +0.254$ $P=0.45$ $N=11$; Figure 7.2b). The number of knot and oystercatcher on Redcar Rocks also showed a negative correlation during neap tides ($Rs = -0.57$ $P<0.05$ $N=12$; Figure 7.3a) but no correlation on spring tides ($Rs = -0.15$ $P=0.30$ $N=15$; Figure 7.3b). During neap low water periods the intertidal area of Redcar Rocks available to shorebirds is greatly reduced, to an estimated 60% of the area exposed on spring tides. This resulted in increased densities of shorebirds, since there were no systematic differences in the numbers of birds using Redcar rocks (allowing for seasonal changes in numbers) between neap and spring tides in sanderling (Wilcoxon matched pairs test $P=0.87$; Figure 7.4), knot (Wilcoxon matched pairs test $P=0.13$; Figure 7.5) or oystercatcher (Wilcoxon matched pairs test $P=0.74$; Figure 7.6). The negative correlation between numbers of knot and sanderling on neap but not on spring tides suggests that knot may have discouraged sanderling from using Redcar Rocks when densities of knot were particularly high. I suggest that the larger knot have the potential to interfere with the ability of sanderling to gain access to food on the rocks. It seems unlikely that knot could affect the distribution of oystercatcher, especially because no really large knot flocks were present and because the oystercatcher is considerably heavier than the knot. High densities of oystercatchers on neap tides may have discouraged knot from feeding on the mussel beds, as both species' distributions on the rocks are closely associated with this food source, although the species undoubtedly take different size classes of mussels.

These negative correlations were apparent even though numbers of knot during the winter in which the data were collected were unusually low. Figure 7.7 compares the

Figure 7.2 The relationship between the number of knot and the number of sanderling on Redcar Rocks at low water between October 1990 and April 1991 on a) neap tides and on b) spring tides.

a) Neap tides



b) Spring tides

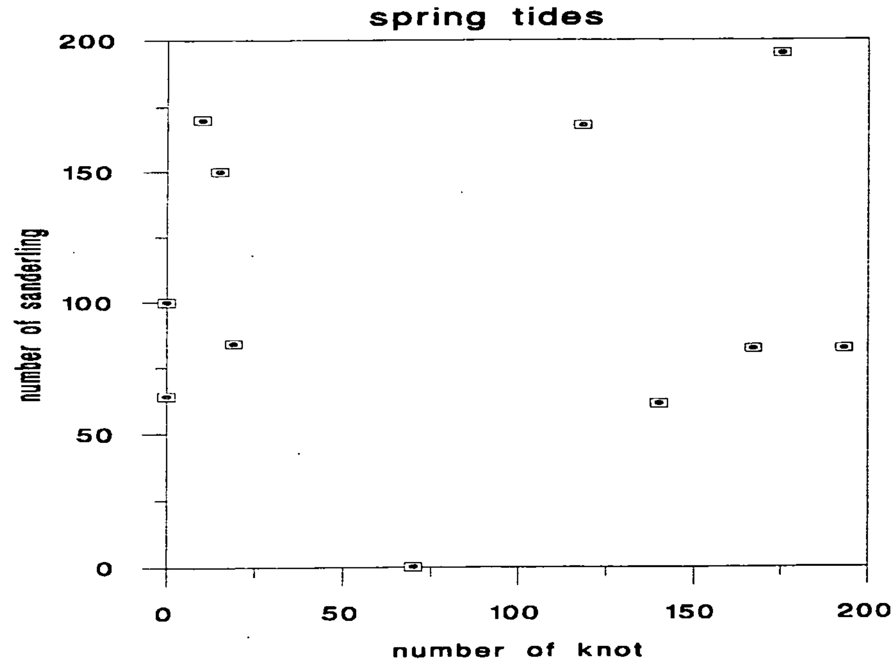
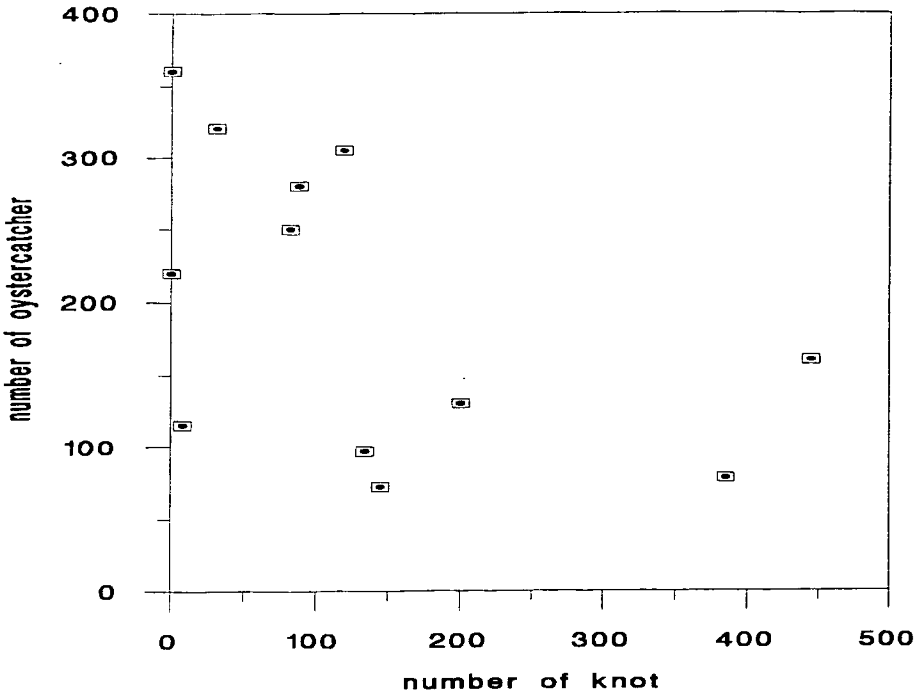


Figure 7.3 The relationship between the number of knot and the number of oystercatcher on Redcar Rocks at low water between October 1990 and April 1991 on a) neap tides and on b) spring tides.

a) Neap tides



b) Spring tides

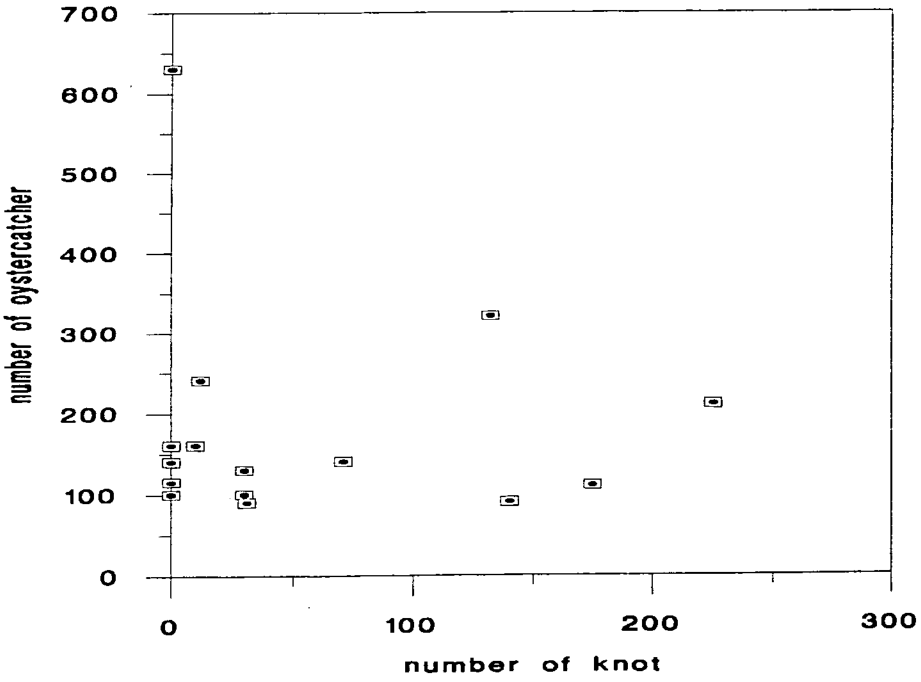


Figure 7.4 The number of sanderling on Redcar Rocks at low water between October 1990 and April 1991 on neap and spring tides.

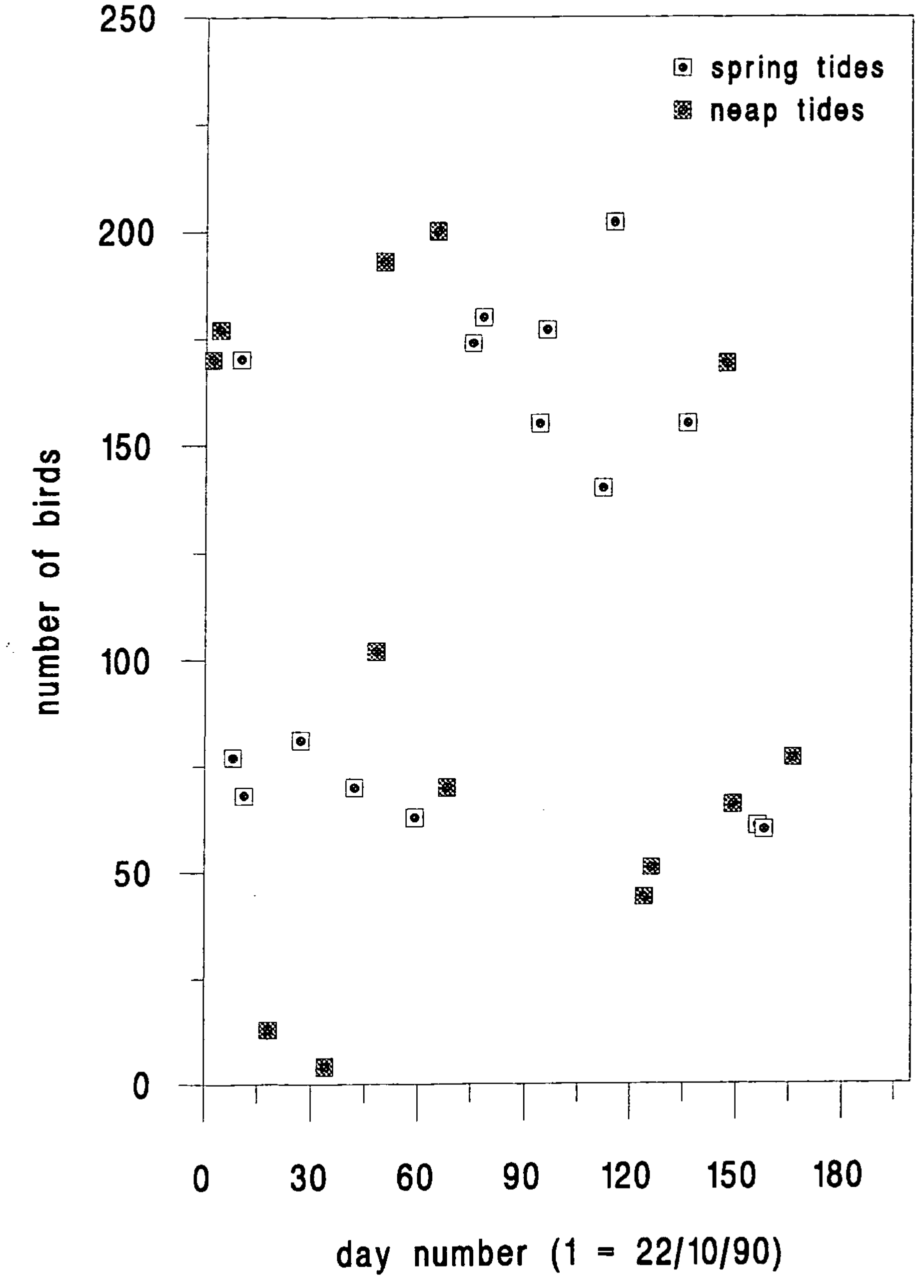


Figure 7.5 The number of knot on Redcar Rocks at low water between October 1990 and April 1991 on neap and spring tides.

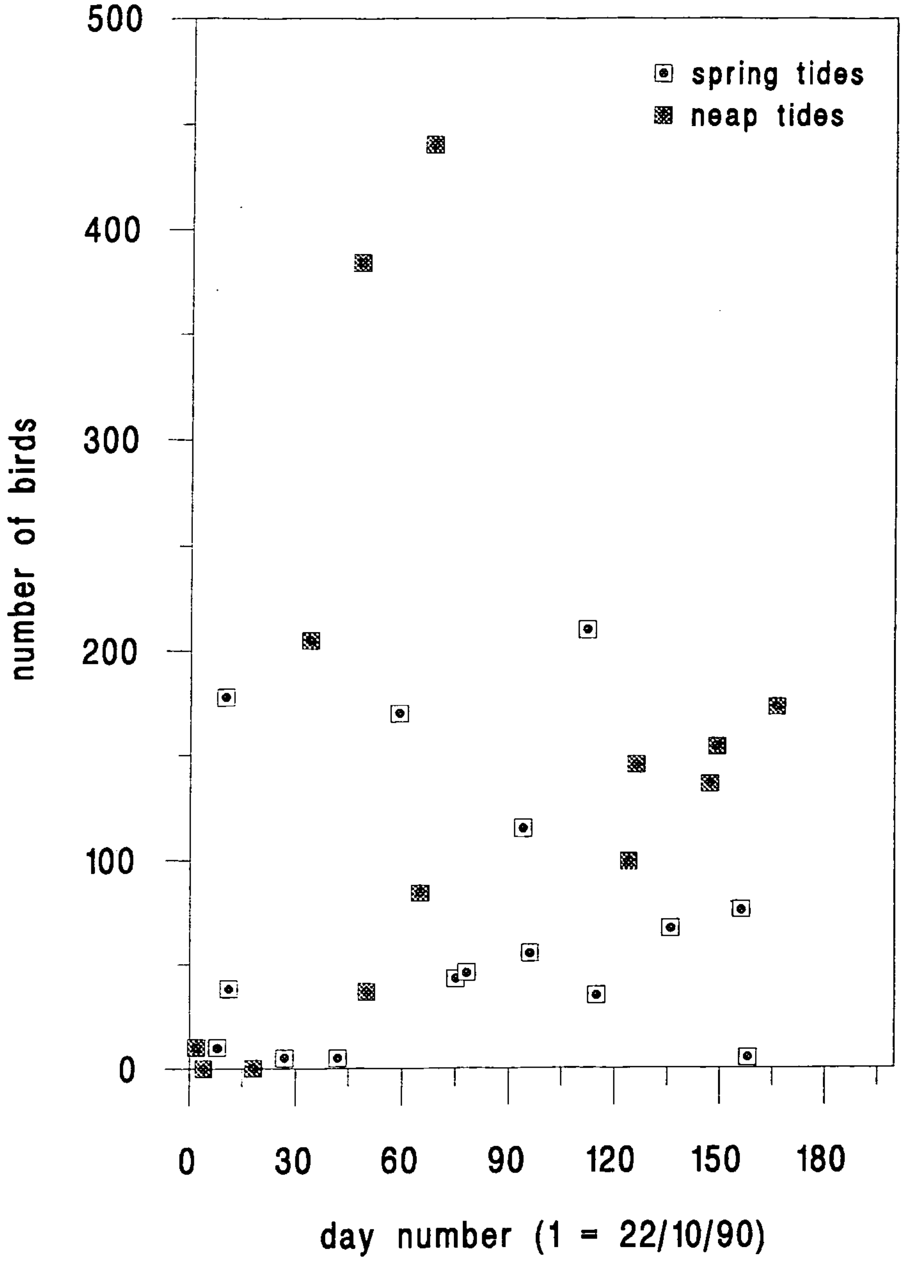


Figure 7.6 The number of oystercatcher on Redcar Rocks at low water between October 1990 and April 1991 on neap and spring tides.

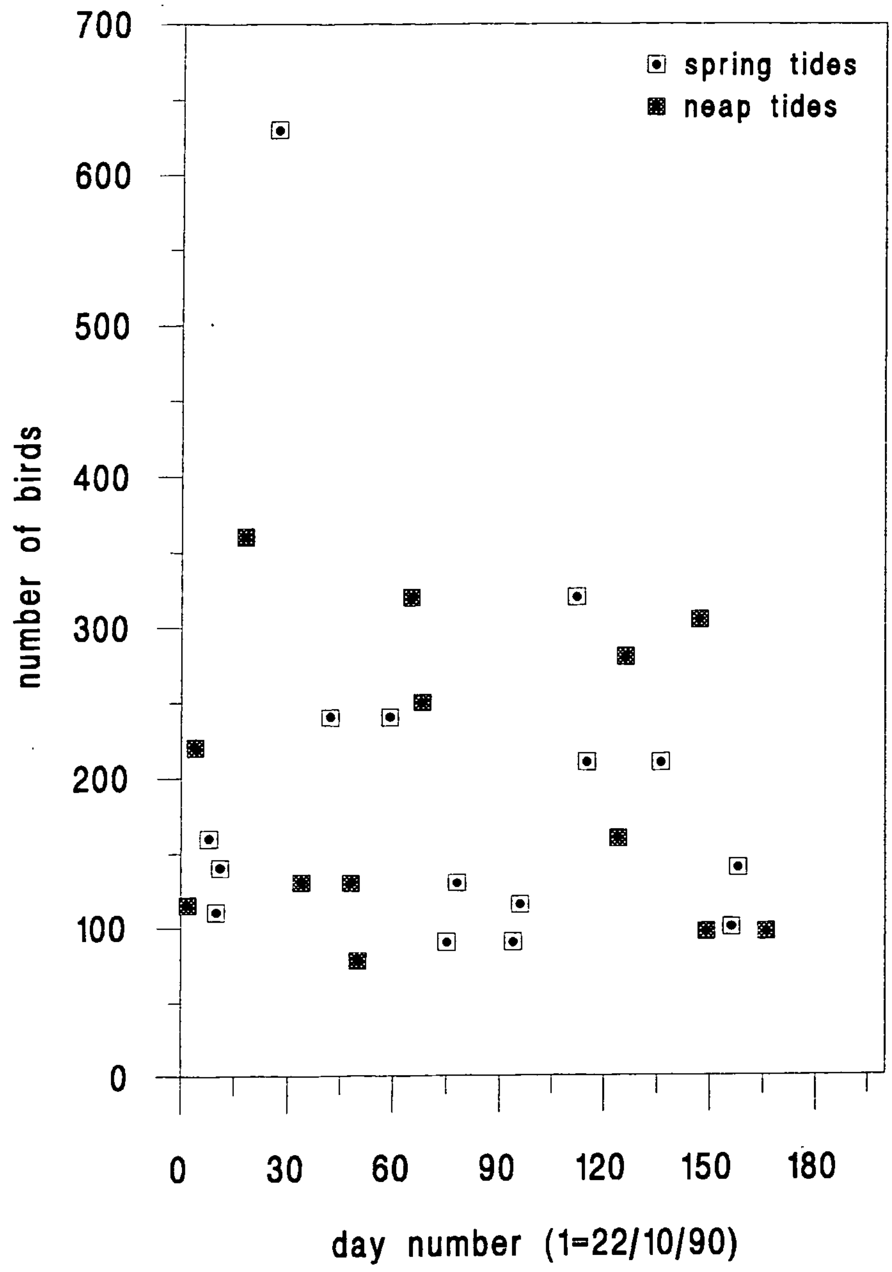
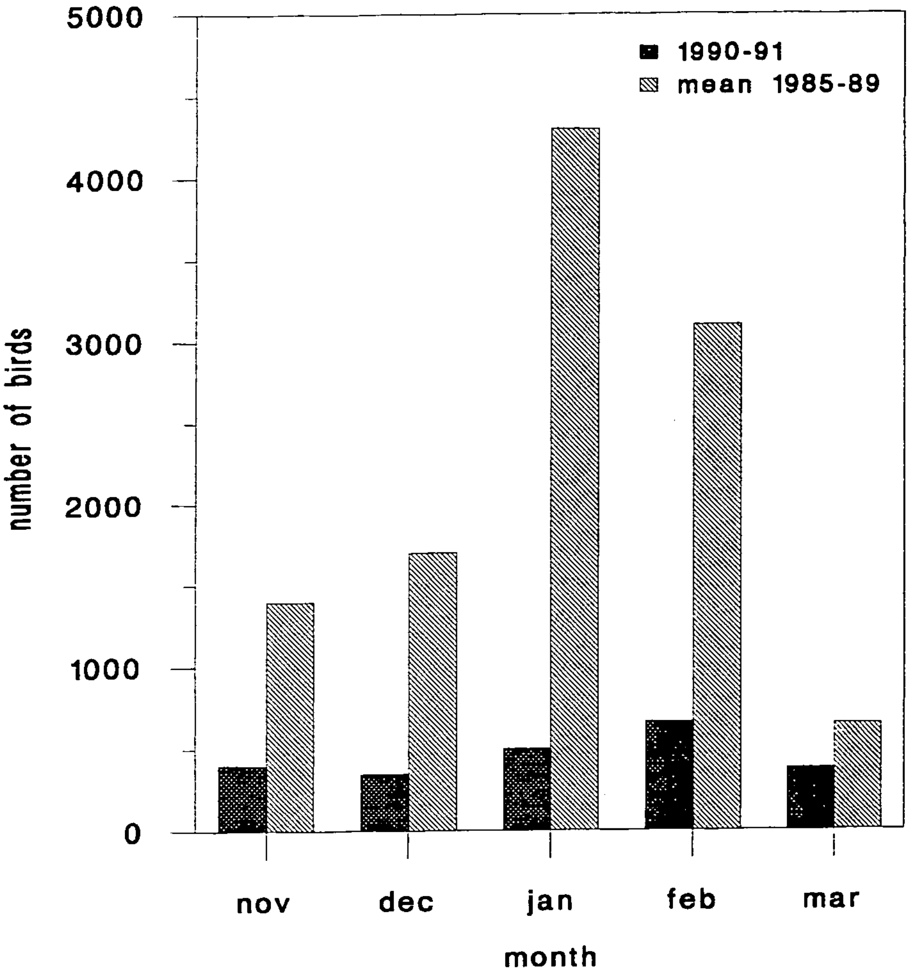


Figure 7.7 The number of knot on the Tees estuary during the winter 1990/91 and the mean of winters 1985/86 to 1989/90.

Counts made at high water roosts in the middle of the month by the "Birds of Estuaries Enquiry" (British Trust for Ornithology).



mean count of knot for the Tees over the period 1985/86 to 1989/90 with 1990/91 count (data from "Birds of Estuaries" counts, B.T.O.). This suggests therefore, that given more usual numbers of knot on Redcar rocks - thousands rather than hundreds - competitive interactions would be more intense than revealed in this study. It was decided not to pursue study of this group of potentially competing species in case numbers of knot fell again in the winter 1991/92.

7.4 Conclusions.

1. Rates of overt interspecific aggression were low in relation to rates of aggression within the species, but when they did occur the most common form of interaction was turnstone stealing large food items from sanderling. Direct interaction between sanderling and knot was scarce.

2. There was a positive correlation between the rate of interspecific aggression in sanderling and the total number of shorebirds present on Redcar Rocks.

3. No active displacements of sanderling by the arrival of flocks of knot were observed.

4. There was a negative correlation between the number of knot and the number of sanderling that used Redcar Rocks over the winter during neap tides but not during spring tides. It is suggested that high densities of knot on neap tides discourage many sanderling from using Redcar Rocks. There was a negative correlation between the number of knot and the number of oystercatcher on neap tides. High densities of oystercatcher may have discouraged knot from using the mussel beds. It was not possible to test whether shorebirds changed their use of Redcar Rocks in response to the arrival of knot in November, because the study started when knot were already present and only one winter of field-work was undertaken.

5. Numbers of knot during the period of study were unusually low. It is predicted that competitive interactions between knot and sanderling may be important at times of higher knot abundance. This highlights the need for long term studies of competition in systems in which the densities of species fluctuate from year to year.

CHAPTER EIGHT

GENERAL DISCUSSION

The preceding chapters reported investigations, using several lines of enquiry, of the importance of interspecific competition between species of shorebirds on the Tees estuary. In this chapter I discuss the important findings and their wider implications in the study of communities and outline the areas for which further work is needed.

The general conclusion from studies of the three large shorebird species on Seal Sands is that competition could not be detected. There is evidence, however, that for the more tightly-packing rocky shore species, avoidance of one species by another did occur.

Limits to similarity, mechanisms of coexistence and ghosts of competition past.

How can these three large species of shorebird, which winter together on the same general feeding areas, coexist? Competition theory (MacArthur 1968) says that species with "similar" niches will compete, but that at a certain niche separation, competition will be reduced to a level at which coexistence is allowed. This begs the question how "similar" two species have to be to compete with each other? Hutchinson (1959) was the first to show that when measurements of mouthparts of species in a community were ranked in order of size, there is an apparently regular ratio of the mouthpart size of the larger species to that of the smaller species of about 1.3. Hutchinson suggested that his ratio was an indication of the minimum difference between species to enable them to coexist, and this notion was mathematically formalised into the theory of limiting similarity by MacArthur and Levins in 1967. Several further comparisons of sizes of mouthparts of species within communities were made; some studies confirming the pattern of regular and minimum size ratios, and some refuting the pattern. However, it is necessary to compare the observed pattern against null models of the ratios that would be expected if species sizes were randomly distributed in an assemblage (Harvey *et al.* 1983). In addition, there is no theoretical reason to expect a single ratio of limiting similarity that applies to all communities, or even a given community at different levels of population or resource density (Abrams 1983). Notwithstanding such caveats, the balance of evidence today suggest that there *are* limits to the ecological similarity of species in communities. In shorebirds, Holmes and Pitelka (1968) found bill length ratios of sympatric calidrine sandpipers breeding around Barrow, Alaska of 1.23, 1.26 and 1.23, and Eldridge and Johnson (1988) found ratios of bill size between 1.2 and 1.3 between at least eight pairs of sympatric sandpiper species at a migration stop-over site in North Dakota. A limiting level of similarity is also evident within species that show sexual dimorphism; for example in two separate studies, Dayan (1989,1990) measured the diameter of the upper canines in mustelids and felids, which show marked sexual size dimorphism, and found an even spacing of "morphospecies" (each sex of each species) along this size gradient.

What are the bill length ratios between curlew and godwit (which show marked sexual dimorphism) if we treat the sexes as separate "morphospecies"? Measurements from large samples of each species caught with cannon nets on the Tees show that the average bill lengths of male godwit, female godwit, male curlew, female curlew are, respectively, 80 mm, 100 mm, 120 mm and 145 mm, which produces the ratios of larger to smaller of 1.25, 1.20 and 1.21. These ratios are close to those of Hutchinson (1959), and it is tempting to believe that these morphological differences allow sufficient size partitioning of the *Nereis* resource to allow godwit and curlew to share the same prey species. However, it should be borne in mind that selection for sexual dimorphism may have acted on the breeding grounds in relation to some aspect of breeding biology, but the difference in the size of the bill in males and females may have the subsidiary effect of reducing intra- and interspecific competition for food on the wintering grounds. One criticism of the so-called "adaptionist programme" made by Gould and Lewontin (1979) is "its failure to distinguish current utility from reasons for origin", and we should be mindful of this when seeking explanations for the morphological differences in shorebirds.

There are intriguing aspects to differences in the size of *Nereis* taken by males and female in curlews and godwits that I demonstrated in chapter four. These differences arise from the sexual dimorphism in bill length in these species, that allows the longer-billed females to reach deeper into the substrate to catch the large worms that are buried deeper than the small worms. The differences in diet between the sexes has implications for intra- and interspecific competition. Within a species the implication is that there is low depletion competition between males and females because the niche overlap is reduced, resulting in reduced intraspecific competition (MacArthur and Levins 1967). The implication for interspecific competition is that while overall overlap between *species* as a whole is unaffected by sexual differences within the species, overlap is high only between certain sexes of species. In chapter four I showed that there was an increase in the average size of *Nereis* taken, from male godwit (smallest worms) to female godwit to male curlew to female curlew (largest worms). If prey resources at times become limiting, depletion competition would be expected to be highest between female godwits and male curlews, but rather lower between male godwits and female curlews. The likely result of strong depletion competition is spatial segregation of male curlews and female godwit - either within Seal Sands (different feeding areas) or on a larger spatial scale (different wintering areas). Information on the sex ratios of curlew and godwit (obtained from biometrics of large samples of birds caught with cannon nets) suggests that there is no bias in sex ratios of either species at Teesmouth. However, there is evidence that curlew and godwit are partially segregated in their use of different substrate types within Seal Sands (see below), so although there is overlap between male curlew and female godwit in the sizes of *Nereis* that each takes, the prey is taken from different areas.

Prey size is just one dimension along which species may be ecologically segregated. I have also shown temporal separation between grey plovers and curlew (and godwit) in their use of a favoured low water feeding site with respect to time after exposure, which I suggest is a consequence of the different foraging methods of each species (see chapter five for a detailed explanation). This temporal segregation greatly reduced the potential for interference competition between grey plovers and both curlew and godwit. Burger *et al.* (1977) showed similar temporal segregation in the use of a mudflat in New Jersey between semipalmated plover *Charadrius semipalmatus* and several species of shorebirds (plovers, including grey plover, and sandpipers). In fact the temporal pattern that these workers found with semipalmated plover - a steady increase in use of the mudflat from low water until low water plus one hour - is strikingly similar to the pattern I observed in grey plover on Seal Sands. Other studies (e.g. Recher 1966, Baker and Baker 1973, Pienkowski 1979) have shown segregation between plovers and sandpipers in feeding position with respect to the tide edge. That the specialised strategy of use of feeding areas away from the tide edge was employed by a plover in the above and present studies suggests that it is a general way in which plovers avoid interference competition with other taxa of shorebirds, notably sandpipers.

The degree of segregation of the three large shorebird species on Seal Sands with respect to sediment type requires further investigation, but the differences in bill morphology between curlew and godwit have interesting implications for the type of substrate that these species utilise, and therefore the degree of ecological segregation of these potentially competing species. Davidson *et al.* (1986) suggested that the long decurved bill of the curlew restricted this species to rather soft sediments in which the bill can be quickly inserted without the risk of bill damage. The bar-tailed godwit, in contrast, possesses a straight bill which, these authors point out, enables the godwit to exploit areas of firm substrate in addition to soft muds. My observations of substrate use of these two species substantiate this observation. In addition to mudflats, curlews search for crabs and molluscs on rocky substrates (a habitat provided by a tidal reclamation wall in my study area on Seal Sands). Unlike the straight bill of the godwit, which rarely forages on rocks, the decurved bill of the curlew may enable this species to "feel around corners" with only slight movements of the head and neck. This allows the curlew to efficiently locate and capture prey items in an environment for which the godwit is poorly equipped (Davidson *et al.* 1986). Such partial segregation of micro-habitat may well lessen the potential for depletion and interference competition between curlew and godwit.

In summary, the partitioning of prey size between curlew, godwit and grey plover, together with temporal partitioning of use of feeding areas between grey plovers and the other two species, and the partial partitioning of use of sediment types between curlew and godwit is sufficient to enable the coexistence of these three shorebirds on the wintering grounds. The co-occurrence of species that we observe today may be the result of niche divergence driven by competitive interactions at some time during evolutionary history, which Connell (1980) called "the ghost of competition past". However this theory is impossible to test because we have no information on the existence or strength of interactions between species in evolutionary history. Indeed one might expect at least *some* niche differences between species in a community by chance alone, in the absence of competitive interactions between species (Connell 1980).

Morphological and behavioural differences between species; selection on the breeding grounds or the non-breeding grounds?

One explanation why sympatric species differ morphologically and behaviourally is that such differences prevent hybridisation which can confer reduced fitness on the progeny (Dobzhansky 1937). This may apply when considering characters such as plumage pattern and colour, which would enable quick and correct identification of species identity on the breeding grounds, but the evolution of differences in bill length and foraging behaviour between species is less convincingly explained in such terms. If we accept that the morphological and behavioural differences between shorebirds are the result of selection and adaptation, and not chance events (see Gould and Lewontin 1979 for a critique of the "adaptionist programme"), this leaves us with the explanation that morphological and behavioural differences between sympatric species have evolved in relation to feeding, since food is the main factor that ultimately limits bird population density (Lack 1947). Whether in shorebirds these differences have evolved in response to selection for behavioural and morphological traits on the breeding grounds or on the wintering grounds has been the subject of much debate, and Owens (1984) suggests the possibility that differences in morphology between shorebird species as seen on the wintering grounds may be "exaptations", that is, traits that perform a certain function, but not one for which the character was selected.

Much of the past uncertainty about where selective pressures were most strongly exerted stemmed from the lack of information on the relative mortality (that associated with starvation but not predation) of shorebirds on the breeding and wintering grounds. Recently such studies have suggested that most mortality of shorebirds takes place on the wintering grounds (Evans and Pienkowski 1984), because it is during winter that energy demands are high and food is scarce (Evans 1976, Davidson 1981). The great abundance of insect prey on the Arctic and subarctic breeding grounds, together with 18 hours or more of daylight for feeding (Baker and Baker 1973) constitute conditions of high food availability, and most of the mortality that occurs on the breeding grounds is probably exerted on young chicks as a result of periods of cold and wet weather, or predation. The brief period of residency of shorebirds on their northern breeding grounds (late May to mid August) probably does not allow densities of prey to be reduced substantially by depletion (Holmes and Pitelka 1968). Since the availability of food in winter may be decreased by prey becoming inactive or buried deeply in the sediment in response to low sea and air temperatures, morphological and behavioural differences between species (and indeed within species) that allow feeding specialisation, will separate niches and therefore reduce competition for scarce food. Schoener (1982), in a review of case studies of niche overlap, tested the theoretical expectation that niche overlap between co-occurring species would be greater during times of resource abundance than during times of shortage. In the majority of cases overlap was indeed less during the relatively lean times, usually the winter. This lends support to the hypothesis that morphological and behavioural differences between shorebird species (as they relate to resource use) were selected for on their wintering grounds. Further evidence comes from the relative lack on the breeding grounds of feeding specialisation of shorebirds with very different bills, as compared to observed feeding specialisations of the same species on the wintering grounds (e.g. Baker 1977).

The grey plover, curlew and godwit that winter on Seal Sands are unlikely to interact on their breeding grounds because their summer ranges do not overlap; grey plover breed in high Arctic Russia, curlew in subarctic, boreal and temperate Finland, Norway and Sweden, and bar-tailed godwit in low-arctic or sub-arctic Finland and Russia, and only locally overlap with the high arctic (Cramp and Simmonds 1983). Therefore these species occur together only at migration stop-overs - when associations are relatively brief and food availability is probably high due to moderate air and sea temperatures - and during the winter months. Indeed grey plover, godwit and curlew spend about half of the year together on Seal Sands (from October until March) and it is this time of year that, even though prey densities are often high, availability may be low due to sub-zero air temperatures, and the birds' energy demands are high (Evans 1976). Hence competitive interactions between grey plover, godwit and curlew are most likely to occur on their wintering grounds.

Competitive interactions between shorebird species at Teesmouth in the context of other studies.

Many studies have claimed to demonstrate present day interspecific competition, and the most convincing of these have involved field experiments (see Connell 1983 and Schoener 1983). It has been pointed out by these authors that no conclusions about the general prevalence of competition in communities can be drawn from their reviews because ecologists are more likely to select for study groups of organisms in which they suspect *a priori* competition to be found, and because studies that find no competition are less likely to be put forward for publication than studies that do detect competition. Without discussing the general prevalence of competition in communities, I will briefly discuss the conclusions of some of the more interesting published studies of competition in animals in relation to my findings. Perhaps the most convincing test of present-day competition is the response of species to the absence of the presumed competitor - usually the superior in systems in which asymmetric competition is suspected. This may take the form of experimental removal from, or introduction of a competitor to, a field situation, or use of "natural" fluctuations in the presence/absence of one species, or changes in its distribution. Of the first kind of test, most studies have been conducted on easily manipulated animals such as songbirds or small mammals. These studies showed a variety of outcomes ; that the removal of a superior competitor either increased the weight of young of the inferior competitor (Minot 1981 with blue and great tits *Parus caeruleus* and *P. major*), allowed a greater number of breeding territories to be established (Garcia 1983 with *Sylvia* warblers, Reed 1982 with chaffinch *Fringilla coelebs* and great tit *Parus major*), allowed an expansion of foraging location into the most profitable microhabitat (Alatalo *et al.* 1985 with tits and goldcrest *Regulus regulus*, Thompson and Fox 1993 with Australian heathland rodents), allowed an increase in the area searched in foraging (Williams and Batzli 1979 with a bark-foraging guild of birds), or allowed an increase in the densities of one species when the other was removed (Brown and Davidson 1977 with granivorous ants and rodents). Roughgarden *et* *al.*(1984), in a thorough set of experiments, showed that introduction of one species of *Anolis* lizard onto an island of the Antilles resulted in lowered survival of the resident species. In one of the relatively few published studies on interspecific competition not to invoke the phenomenon, Fonstad (1983) showed that removal of territorial brambling *Fringilla montifringilla* did not result in the establishment of territory by willow warbler *Phylloscopus trochilus.* Instead of competition, different habitat preference of each species explained the pattern of non-overlapping territories. The second kind of test, so-called "natural experiments", do not rely on the difficult task of removal of competitors from the environment. Williams and Batzli (1979) provided additional evidence for competition to support their removal experiments (see above) and showed that in one winter in which the superior competitor was absent from the study site the inferior competitors expanded their foraging area. Minot (1981) showed that in areas of high blue tit density, the weights of great tit young were reduced as compared to sites in which blue tits were at low density. Shealer and Burger (1993) showed that flock-feeding roseate terns *Sterna dougallii* had significantly lower feeding success in the presence of brown noddies than they did in single species flocks. In two species of gerbil, Ziv *et al.* (1992) showed that both species prefer the same microhabitat, but where the species occurred together, the inferior competitor used a less-preferred habitat in which to forage, but was able to coexist with its congener because it was a more efficient forager. In my study the species were not amenable to experimental removal, but a "natural experiment" was used to test the competition hypothesis. I showed in chapter five that the number of curlew (the suspected superior competitor) that used Seal Sands decreased markedly in mid-winter, but grey plovers did not expand their feeding range, occupy additional habitats or use the preferred feeding sites at an earlier state of tide, even in the near-absence of curlew from the mudflat. This is good evidence that interference competition did not occur between these two species during the period of study, but that the observed temporal and habitat partitioning was a consequence of innate species-specific preferences, possibly shaped by past competitive interactions. Experimental disturbance of grey plovers was attempted on Seal Sands by placing

In late winter, when large numbers of golden plovers were present on Seal Sands (they were prevented from feeding on their usual inland sites, by frozen ground), there were frequent, and at times intense, non-territorial interactions with grey plovers. It seems that overt interspecific aggression in the grey plover is most likely to be directed towards another plover species, which have space-demanding methods of foraging. Interspecific aggression may be expected only when populations of two species come together for the first time, as was first suggested by Orians and Willson (1964) in relation to the breeding situation. Certainly, grey and golden plovers do not usually come into contact with each other while wintering at Teesmouth, due to the different habitats used by each. An additional reason why intense interspecific aggression was seen only between these two species may be the similarity of their appearance. Aggression amongst grey plovers is at times frequent, and grey plovers may have mistaken golden plovers for juveniles of their own species, although I believe that the morphological differences, together with the different call-notes of each species make confusion unlikely.

Zwarts (1978) demonstrated avoidance between species; avocet and black-headed gull *Larus ridibundus* preferred the same feeding areas on an intertidal mudflat in Holland, but each day occupied different, mutually exclusive areas. On Seal Sands segregation was a consequence of differences in the habitat preferences and no avoidance was shown. However, there is evidence that sanderling avoided knot on intertidal mussel beds of the south Tees during neap tides when feeding area was restricted (Chapter Seven), and further work is needed on these species.

Several studies have measured invertebrate prey depletion by shorebirds over the winter (Goss-Custard 1969, Prater 1972, Smith 1975, Goss-Custard 1977, Horwood and Goss-Custard 1977, Evans *et al.* 1979, Zwarts and Drent 1981, Zwarts and Wanink 1984, Piersma 1986), but the effect of depletion on intake rates have not been investigated thoroughly. Goss-Custard (1980) calculated that, for redshank feeding on *Nereis* *diversicolor*, depletion of 25-45% of the standing crop (a range found by Goss-Custard in his review of depletion rates from several studies) of prey could lead to a 15-30% reduction in the rate of biomass ingested over the winter. Of crucial importance to the effect of prey depletion on shorebird intake rates is the initial density of prey in the substrate, which is highly variable both between sites and within sites from year to year. The proximate effects of a reduction in energy intake rate of species in the present study were discussed in chapter four, which suggested that there were no adverse effects of the estimated 24-57% reduction in standing crop during the winter of my study. Effects of decreased energy intake on the wintering grounds or migration refuelling sites may be felt in the longer term if females in poor body condition suffer from reduced reproductive output. This has been demonstrated in geese (Cabot and West 1973, Ankney and MacInnes 1978, and Davies and Cooke 1983), but similar evidence from shorebirds is lacking, because arctic-breeding shorebirds, unlike geese, generally have large and ill-defined breeding areas and nests are widely dispersed in space, preventing the success of nests and broods of individuals from known wintering/migration grounds being monitored. Indirect evidence that poor body condition can lead to poor reproductive success of shorebirds is provided by Davidson and Wilson (submitted), who showed that knots that were known to survive the exceptionally harsh Arctic summer of 1972 and 1974 had better than average body condition when they were caught on their late spring staging area in Iceland in 1970-72 than the average condition of all knot caught there. Knots that survived the mild Arctic summer of 1985 were of average condition when leaving their staging site in north Norway. Davidson and Wilson's data detected the extreme case of individuals dying due to poor body condition; presumably many more birds than those that died may have suffered from poor breeding success. If an individual shorebird that left the wintering grounds in poor body condition is able to improve its body condition by the time it leaves the last spring staging area, deleterious effects of competition on the wintering ground will be ameliorated. However an individual in poor body condition will build up nutrient reserves needed for the journey to the breeding ground and for breeding itself more slowly than an individual that arrives in good condition, arrival on the breeding grounds may be delayed, and could result in failure to obtain a good territory or allow insufficient time to raise a brood in the short Arctic summer.

In my calculations of depletion over the winter, I assumed that grey plover, godwit and curlew were the only avian predators of *Nereis*. Other shorebirds, in particular the redshank, have been shown to take the large size class of *Nereis* as an important part of their diet (Evans *et al.* 1979). The effect of additional depletion by such species has not been determined, but may be considerable because of the high abundance of these predators (Appendix 1).

Final conclusions.

I have demonstrated that present day competition between species of shorebirds on Seal Sands is avoided by partitioning by prey size taken, sediment type and position in relation to the tide edge, and temporal segregation within a tidal cycle. Kotler and Brown (1988) propose that a mechanism of coexistence is composed of two essential features; a resource axis of environmental heterogeneity and an evolutionary trade-off between the abilities of the co-existing species to utilise various parts of the axis. Certainly the first and possibly the second of these requirements have been identified in the study of the three large shorebird species on Seal Sands. For the species that used the mussel beds to the south of the estuary, I showed avoidance of knot by sanderling, but coexistence of sanderling with knot is allowed because additional feeding habitats, such as the sandy beach, are available to the sanderling if they suffer from interference competition on the mussel beds on neap tides.

It may be unwise to make generalisations about the importance of competitive interactions based on just two winters of study, because the major determinants of the intensity of competition are the abundance of resource and the density of shorebirds at a given time, and these are likely to fluctuate considerably from year to year (Wiens 1993). For example, densities of shorebirds may be elevated following a successful breeding season in which many juveniles are produced. If this coincided with a low prey densities after a year of poor invertebrate reproduction, competitive interactions could be intense. There is therefore a need to conduct longer term studies, in which the same indices of the intensity of competition (e.g. rate of aggressive interactions, the effect of heterospecific density on energy intake rate) are compared between years of varying resource levels, weather conditions, which affect availability of prey, and shorebird densities.

Suggestions for further work

Certain important questions about competitive interactions between shorebird species on the Tees estuary remain unanswered;

1. The extent to which each species forages at night is important to establish because, even if one species prevents another from occupying the best feeding sites during the day, the effects of competition over a 24 hour period could be ameliorated if the superior competitor is absent from the feeding grounds at night. If the proximate effect of any competitive interactions is a depression of the energy intake rate of the inferior competitor, then competition could be reduced if any shortfall in energy intake during the day is compensated for at night. Indeed increased availability of prey may enable greater rates of energy intake to be achieved at night (Dugan 1981).

2. There is a gap in our understanding of how densities of available prey affect the densities of their shorebird predators; we do not know the minimum density of available

prey that can sustain an individual, and in particular we have little idea of what proportion of prey in the sediment is available (detectable and accessible) to shorebirds under different conditions of temperature and windspeed. Although Smith (1975) was able to obtain a measure of the availability of lugworms *Arenicola marina* to bar-tailed godwits, because the birds used casts on the sediment surface to indicate the presence of buried prey, and these could be counted by the observer, *Nereis* produces no easily measured cues.

3. I obtained some evidence to show that at high densities of curlews (above about 15 per hectare), the energy intake rate of grey plovers was depressed, presumably by interference with detection, or depression of the activity, of their prey. Such densities were generally infrequent but occurred when the rising tide pushed feeding shorebirds into a restricted area. More data is needed to show how energy intake is affected by different densities of heterospecifics.

REFERENCES.

Abrams, P.A. (1983) The theory of limiting similarity. *Ann. Rev. Ecol. Syst.*, 14, 359-376.

Alatalo, R.V., Gustafsson, L., Linden, M. and Lundberg A. (1985) Interspecific competition and niche shifts in tits and the goldcrest : an experiment. *J. Anim. Ecol.*, 54, 977-984.

Altmann, J. (1974) Observational study of behavior : sampling methods. *Behaviour*, 49, 227-267.

Ankney, C.D. and MacInnes, C.D. (1978) Nutritional resources and reproductive performance of female lesser snow geese. *Auk*, 95, 459-471.

Ashkenazie, S. and Safriel, U.N. (1979) Time-energy budget of the semipalmated sandpiper *Calidris pusilla* at Barrow, Alaska. *Ecology*, 60, 783-799.

Baird, D., Evans, P.R., Milne, H. and Pienkowski, M.W. (1985) Utilisation by shorebirds of benthic invertebrate production in intertidal areas. *Oceanography and Marine Biology: an Annual Review*, 23, 573-597.

Baker, M.C. (1977) Shorebird food habits in the Eastern Canadian Arctic. *Condor*, 79, 56-68.

Baker, M.C. and Baker, A.E.M. (1973) Niche relationships among six species of shorebirds on their wintering and breeding ranges. *Ecological Monographs*, 43, 191-212.

Boere, G.C. and Smit, C.J. (1983) Ecological data on bird species of the Wadden Sea. In : Smit, C.J. and Wolff, W.J (Eds.) *Birds of the Wadden Sea*. Balkema, Rotterdam.

Brearey, D.M. (1981) *Feeding ecology and foraging behaviour of sanderling (Crocethia alba) and turnstone (Arenaria interpres) at Teesmouth, N.E. England.* Ph.D thesis, University of Durham.

Brown, J.H. and Davidson, D.W. (1977) Competition between seed-eating rodents and ants in desert ecosystems. *Science*, 196, 880-882.

Burger, J., Howe, M.A., Hahn, D.C. and Chase, J. (1977) Effects of tidal cycles on habitat selection and habitat partitioning by migrant shorebirds. *Auk*, 94, 743-758.

Busche, G. (1980) *Vogelbestände des Wattenmeers von Schleswig-Holstein*. Greven.

Cabot and West (1973) Population dynamics of barnacle geese *Branta leucopsis* in Ireland. *Proc. R. Irish Acad.*, 73B, 415-443.

Castro, G. (1987) High basal metabolic rate in sanderling *Calidris alba*. *Wilson Bulletin*, 99(2).

Connell, J.H. (1980) Diversity and the coevolution of competitors, or the ghost of competition past. *Oikos*, 35, 131-138.

Connell, J.H. (1983) On the prevalence and relative importance of interspecific competition : evidence from field experiments. *Am. Nat.*, 122, 661-696.

Cooper, R.H.W. (1987) *Migration strategies of shorebirds during the non-breeding season , with particular reference to the sanderling* (*Calidris alba*). Ph.D thesis, University of Durham.

Cramp, S. and Simmons, K.E.L. (ed.) (1982) *The birds of the western Palearctic*, Vol. III. Oxford University Press, Oxford.

Davidson, N.C. (1981) *Seasonal changes in nutritional conditions of shorebirds during the non-breeding season*. Ph.D. thesis, University of Durham.

Davidson, N.C., Townshend, D.J., Pienkowski, M.W. and Speakman, J.R. (1986) Why do curlews *Numenius arquata* have curved bills? *Bird Study*, 33, 61-69.

Davidson, N.C. and Wilson J.R. (submitted) Journal of Avian Biology.

Davies, J.C. and Cooke, F. (1983) Annual nesting productivity in snow geese - praire droughts and arctic springs. *J. Wildlife Management*, 47, 291-296.

Dayan, T., Simberloff, D., Tchernov, E., and Yom-Tov, Y. (1989) Inter- and intra-specific character-displacement in mustelids. *Ecology*, 70, 1526-1539.

Dayan, T., Simberloff, D., Tchernov, E., and Yom-Tov, Y. (1990) Feline canines : community-wide character-displacement among the small cats of Israel. *Am. Nat.*, 136, 39-60.

Desrochers, A. (1992) Age and foraging success in European blackbirds : variation between and within individuals. *Animal Behaviour*, 43, 885-894.

Dobzhansky, Th. (1937) *Genetics and the origin of species*. Columbia University Press, New York.

Drenckhahn, D. (1980) Nahrungsökologishe Aspekte zum Vorkomnen der Watund wasservögel im schleswig-holsteinischen Wattenmeer. In Busche, G. (1980) *Vogelbestände des Wattenmeers von Schleswig-Holstein*. Greven.

Drent, R. and Piersma, T. (1990) An exploration of the energetics of leap-frog migration in arctic breeding waders. In: Gwinner, E. (ed.) *Bird migration*. Springer-Verlag, Berlin Heidelberg.

Dugan, P.J. (1981) *Seasonal movements of shorebirds in relation to spacing behaviour and prey availability.* Ph.D thesis, University of Durham.

Dunbrack, R.L. (1979) A re-examination of robbing behaviour in foraging egrets. *Ecology*, 60, 644-645.

Ebbinge, B., Canters, K. and Drent, R.M. (1975) Foraging routines and estimated daily food intake in barnacle geese wintering in the northern Netherlands. *Wildfowl*, 26, 5-19.

Eldridge, J.L. and Johnson, D.H. (1988) Size difference in migrant sandpiper flocks : ghosts in ephemeral guilds. *Oecologia*, 77, 433-444.

Elton, C.S. and Miller, R.S. (1954) The ecological survey of animal comminities : With a practical system of classifying habitats by structural characters. *Journal of Ecology*, 42, 460-496.

Ens, B., Esselink, P. and Zwarts, L. (1990) Kleptoparasitism as a problem of prey choice: a study on mudflat-feeding curlews. *Anim. Behav.*, 39, 219-230.

Ens, B. and Zwarts, L. (1980) Wulpen op het wad van Moddergat. *Waterwögels*, 5, 108-120.

Evans, A.D. (1987) *Individual difference in foraging behaviour, habitat selection and bill morphology of wintering curlew, Numenius arquata.* Ph.D. thesis, University of Edinburgh.

Evans, P.R. (1976) Energy balance and optimal foraging strategies in shorebirds: some implications for their distributions and movements in the non-breeding season. *Ardea*, 64, 117-139.

Evans, P.R. (1979) Adaptations shown by foraging shorebirds to cyclical variations in the activity and availability of their intertidal invertebrate prey. In: Naylor, E. and Hartnoll, R.G. (ed.) *Cyclic phenomena in marine plants and animals.* Pergamon Press, Oxford.

Evans, P.R., Herdson, D.M., Knights, P.J. and Pienkowski, M.W. (1979) Short-term effects of reclamation of part of Seal Sands, Teesmouth, on wintering waders and shellduck. I. Shorebird diets, invertebrate densities, and the impact of predation on the invertebrates. *Oecologia*, 41, 183-206.

Evans, P.R., and Pienkowski, M.W. (1984) Population dynamics of shorebirds. In : Burger, J. and Olla, B.L. (Eds.) *Behaviour of marine animals.* Plenum, New York.

Fonstad, T (1983) Reduced territory overlap between the willow warbler and the brambling in heath birch forest : competition or different habitat preference. *Oikos*, 42, 314-322.

Garcia, E.F.J. (1983) An experimental test of competition for space between blackcaps and garden warblers in the breeding season. *J. Anim. Ecol.*, 52, 795-805.

Gochfeld, M. and Burger, J. (1984) Age differences in foraging behaviour of the American robin (*Turdus migratorius*). *Behaviour*, 88, 227-239.

Goss-Custard, J.D. (1969) The winter feeding ecology of the redshank *Tringa totanus*. *Ibis*, 111, 338-356.

Goss-Custard, J.D. (1977) The ecology of the Wash.III Density-related behaviour and the possible effects of a loss of feeding grounds on wading birds (Charadrii). *Journal of Applied Ecology*, 14, 721-739.

Goss-Custard, J.D. (1980) Competition for food and interference among waders. *Ardea*, 61, 31-52.

Goss-Custard, J.D. and Le V. Dit Durell, S.E.A. (1984) Feeding ecology, winter mortality and the population dynamics of oystercatchers on the Exe estuary. In: Evans, P.R., Goss-Custard, J.D. and Hale, W.G. (eds.) *Coastal waders and wildfowl in winter*. Cambridge University Press, Cambridge.

Gould, S.J. and Lewontin, R.C. (1979) The Spandrels of San Marco and the Panglossian Paradigm : a critique of the adaptionist programme. *Proc. R. Soc. Lond. B*, 205, 581-598.

Gray, J.S. (1976) The fauna of the polluted River Tees Estuary. *Estuarine Coastal Marine Science*, 4, 653-676.

Hale, W.G. (1956) The lack of territory in the redshank. *Ibis*, 98, 398-400.

Hale, W.G. (1980) *Waders*. Collins, London.

Harvey, P.H., Colwell, R.K., Silvertown, J.W. and May, R.M. (1983) Null models in ecology. *Ann. Rev. Ecol.Syst.*, 14, 189-211.

Hayman, P., Marchant, J.H. and Prater, A.J. (1980) *Shorebirds : an identification guide to the waders of the world.* Croom Helm, London.

Heppleston, P.B. (1970) Anatomical observations on the bill of the oystercatcher (*Haematopus ostralegus*) in relation to feeding behaviour. *Journal of the Zoological Society of London*, 161, 519-524.

Holmes, R.T. (1966) Breeding ecology and annual cycle adaptations of the red-backed sandpiper (*Calidris alpina*) in northern Alaska. *Condor*, 68, 3-46.

Holmes, R.T. and Pitelka, F.A. (1968) Food overlap among coexisting sandpipers on Northern Alaskan Tundra. *Syst. Zool.*, 17, 305-318.

Holyoak, D.T. (1970) Sex differences in feeding behaviour and size in the carrion crow. *Ibis*, 112, 397-400.

Horwood, J.W. and Goss-Custard, J.D. (1977) Predation by the the oystercatcher *Haematopus ostralegus* in relation to the cockle *Cerastoderma edule* fishery in the Bury inlet, South Wales. *J. Appl. Ecol.*, 14, 139-158.

Hutchinson, G.E. (1957) Concluding remarks. *Cold Spring Harbour Symposia on Quantitative Biology*, 22, 415-427.

Hutchinson, G.E. (1959) Homage to Santa Rosalia, or why are there so many kinds of animals? *Amer. Nat.*, 93, 145-159.

Kear, J. (1962) Food selection in finches with special reference to interspecific differences. *Proceedings of the Zoological Society of London*, 138, 163-204.

Kendeigh, S.C. (1969) Energy responses of birds to their thermal environments. *Wilson Bulletin*, 81, 441-9.

Kendeigh, S.C., Dol'nik, U.R. and Gavrilov, U.M. (1977) Avian Energetics. In: Pinowski, J. and Kendeigh, S.C. (eds.) *Granivorous birds in ecosystems.*

Kersten, M. and Piersma, T. (1987) High levels of energy expenditure in shorebirds : Metabolic adaptations to an energetically expensive way of life. *Ardea*, 75, 175-187.

Knights, P.J. (1979) *Effects of changes of land use on some animal populations.* Ph.D thesis, University of Durham.

Kotler, B.P. and Brown, J.S. (1988) Environmental heterogeneity and the coexistance of desert rodents. *Ann. Rev. Ecol. Syst.*, 19, 281-307.

Kushlan, J.A. (1979) Short-term energy maximisation of egret foraging. *Ecology*, 60, 645-646.

Lack, D. (1947) Darwin's Finches. Cambridge University Press, Cambridge.

Lack, D. (1966) *Population studies of birds.* Clarendon, Oxford.

MacArthur, R.H. (1968) The theory of the niche. In : Lewontin, R.C. (Ed.) *Population Biology and Evolution.* Syracuse University Press, Syracuse, New York.

MacArthur, R.H. and Levins, R. (1967) The limiting similarity, convergence and divergence of coexisting species. *American Naturalist*, 101, 377-385.

Marchetti , K. and Price, T. (1989) Differences in the foraging of juvenile and adult birds : the influence of developmental constraints. *Biological Revues*, 64, 51-70.

Michael,C.W. (1935) Feeding habits of the black-bellied plover in winter. *Condor*, 37, 169.

Millard, A.V. (1976) *The invertebrate faunas of Spartina marshes and their utilisation by shorebirds at Lindisfarne, Northumberland.* Ph.D thesis, University of Durham.

Milne, A. (1961) Deffinitions of competition among animals. *Symposia for the Society for Experimental Biology*, 15, 40-61.

Minot, E.O. (1981) Effects of interspecific competition for food in breeding blue and great tits. *J. Anim. Ecol.*, 50, 375-385.

Moser, M. (1987) Limits to the number of grey plovers wintering on British Estuaries. Journal of Applied Ecology, 25, 473-485.

Moumoutzi, L. (1977) *A study of the feeding distribution of the dunlin on Seal Sands during the spring and late summer.* M.Sc. dissertation, University of Durham.

Muus, B.J. (1967) The fauna of Danish estuaries and lagoons : distribution and ecology of dominating species in the shallow reaches of the mesohaline zone. *Medd. Danmarks Fisk og Havunders*, 5, 1-34.

Myers, J.P., Connors, P.G. and Pitelka, F.A. (1979) Territoriality in non-breeding shorebirds. *Studies in Avian Biology*, 2, 231-246.

Myers, J.P. and McCaffery, B.J. (1984) Paracas Revisited : Do shorebirds compete on their wintering ground? *Auk*, 101, 197-199.

Myers, J.P. and Myers, L.P. (1979) Shorebirds of Coastal Buenos Aires Province, Argentina. *Ibis*, 121, 186-200.

Newton, I (1967) The adaptive radiation and feeding ecology of some British finches. *Ibis*, 109, 33-98.

Nicholson (1955) An outline of the dynamics of animal populations. Australian *Journal of Zoology*, 2, 9-65.

Norton-Griffiths, M. (1967) Some ecological aspects of the feeding behaviour of the oystercatcher, *Haematopus ostralegus*, on the edible mussel, *Mytilus edulis*. *Ibis*, 109, 412-424.

Odum, E.P.(1953) *Fundamentals of Ecology.* W.B. Sanders, New York.

Orians, G.H. and Wilson, M.F. (1964) Interspecific territories of birds. *Ecology*, 45, 736-745.

Owens, N.W. (1984) Why do curlews have curved beaks? *Bird Study*, 31, 230-231.

Park, T. (1954) Experimental studies of interspecific competition :II. Temperature, humidity and competition in two species of *Tribolium*. *Physiological Zoology*, 27, 177-238.

Persson. L. (1985) Asymmetrical competition : are larger animals competitively superior? *Am. Nat.*, 126, 261-266.

Pianka, E.R. (1972) r and k selection or b and d selection. *American Naturalist*, 106, 581-588.

Pianka, E.R. (1973) The structure of lizard communities. *Annual Review of Ecology and Systematics*, 4, 53-74.

Pienkowski, M.W. (1973) *Feeding activities of wading birds and shellducks at Teesmouth and some possible effects of further loss of habitat*. Report to the Coastal Ecology Research Station (The Nature Conservancy).

Pienkowski, M.W. (1979) Differences in habitat requirements and distribution patterns of plovers and sandpipers as investigated by studies of feeding behaviour. *Verh Ornithol. Ges. Bayern*, 23, 105-124.

Pienkowski, M.W. (1980) *Aspects of the ecology and behaviour of ringed and grey plovers Charadrius hiaticula* and *Pluvialis squatarola*. Ph.D thesis, University of Durham.

Pienkowski, M.W. (1982) Diet and energy intake of grey and ringed plovers, *Pluvialis squatarola* and *Charadrius hiaticula*, in the non-breeding season. *Journal of Zoology of London*, 197 511-549.

Pienkowski, M.W. (1983) The effect of environmental conditions on feeding rates and prey-selection of shore plovers. *Ornis. Scand.*, 14, 227-238.

Pienkowski, M.W., Ferns, P.N., Davidson, N.C. and Worrall, D.H. (1984). Balancing the budget : measuring the energy intake and requirements of shorebirds in the field. In: Evans, P.R., Goss-Custard, J.D. and Hale, W.G. (eds.) *Coastal waders and wildfowl in winter*. Cambridge University Press, Cambridge.

Piersma, T. (1986) Wader foraging and benthic food production at a spring migration staging site in Morocco. *Wader study group Bull.*, 47, 10.

Prater, A.J. (1972) The ecology of Morecambe Bay. The food and feeding habits of knot (*Calidris canutus*) in Morecambe Bay. *J. Appl. Ecol.*, 9, 179-194.

Prater, A.J. (1981) *Estuary birds of Britain and Ireland*. T & A.D. Poyser, Calton.

Prater, A.J., Marchant, J.H. and Vuorinen, J. (1977) *Guide to the identification and ageing of Holarctic waders.* B.T.O. Guide 17.

Prokosch, P. (1988) Arktische watvogel im Wattenmeer. *Corax,* 12.

Reading, C.J. and McGrorty, S (1978) Seasonal variations in the burrying depth of *Macoma balthica* and its accessibility to wading birds. *Estuarine Coastal Marine Science,* 6, 135-144.

Recher, H.F. (1966) Some aspects of the ecology of migrant shorebirds. *Ecology,* 47, 393-407.

Recher, H.F. and Recher, J.A. (1969a) Comparative foraging efficiency of adult and immature little blue herons (*Florida caerulea*) . *Animal Behaviour,* 17, 320-322.

Recher, H.F. and Recher, J.A. (1969b) Some aspects of the ecology of migrant shorebirds. II. Aggression. *Wilson Bull.,* 81, 140-154.

Reed, T.M. (1982) Interspecific territoriality in the chaffinch and great tit on islands and the mainland of Scotland : playback and removal experiments. *Anim. Behav,* 30, 171-181.

Roberts, J.G. (1990) *Studies of the flocking behaviour of sanderlings (Calidris alba).* Ph.D thesis, University of Durham.

Roughgarden, J.D., Pacala, S.W. and Rummel J.D. (1984) Strong present-day competition between the *Anolis* lizard populations of St. Maarten (Neth. Antilles). In : Shorrocks, B. (Ed.) *Evolutionary Ecology.* Blackwell Scientific Publications, Oxford.

Schneider, D.C. and Harrington, B.A. (1981) Timing of shorebird migration in relation to prey depletion. *Auk,* 98, 81-84.

Schoener, T.W. (1982) The controversy over interspecific competition. *Amer. Sci.,* 70, 586-595.

Schoener, T.W. (1983) Field experiments on interspecific competition. *Am. Nat.,* 122, 240-285.

Scott, I.A. (1991) *Studies on seasonal variation in metabolic rate, related to changes in body composition, with particular reference to shorebirds (Charadrii).* Ph.D thesis, University of Durham.

Selander, R.K. (1966) Sexual dimorphism and differential niche utilization in birds. *Condor,* 68, 113-151.

Shealer, D.A. and Burger, J. (1993) Effects of interference competition on the foraging activity of tropical roseate terns. *Condor,* 95, 322-329.

Smit, C.J. (1981) Production of biomass by invertebrates and consumption by birds in the Dutch Wadden Sea area. In: Smit, C.J. and Wolff, W.J (eds.) *Birds of the Wadden Sea*. Balkema, Rotterdam.

Smith, P.C. (1975) *A study of the winter feeding ecology and behaviour of the bar-tailed godwit (Limosa lapponica)*. Ph.D thesis, University of Durham.

Sokal, R.R. and Rohlf, F.J. (1981) *Biometry*. W.H. Freeman, New York.

Thompson, D.B.A., Curtis, D.J. and Smyth, J.C. (1986) Patterns of association between birds and invertebrates in the Clyde Estuary. *Proceedings of the Royal Society of Edinburgh*, 90B. 185-201.

Thompson, P. and Fox, B.J. (1993) Asymmetric competition in Austalian heathland rodents:a reciprocal removal experiment demonstrating the influence of size-class structure. *Oikos*, 67, 264-278.

Townshend, D.J. (1981a) *The use of intertidal habitats by shorebird populations, with special reference to grey plover (Pluvialis squatarola) and curlew (Numenius arquata)*. Ph.D thesis, University of Durham.

Townshend, D.J. (1981b) The importance of field feeding to the suvival of wintering male and female curlews *Numenius arquata* on the Tees estuary. In : Jones, N.V. and Wolff, W.J. (Eds.) *Feeding and suvival strategies of estuarine organisms*. Plenum Press, New York.

Townshend, D.J., Dugan, P.J. and Pienkowski, M.W. (1984) The unsociable plover : use of intertidal areas by grey plovers. In: Evans, P.R., Goss-Custard, J.D. and Hale, W.G. (eds.) *Coastal waders and wildfowl in winter*. Cambridge University Press, Cambridge.

Vader, W.J.M. (1964) A preliminary investigation into the reaction of the infauna of tidal flats to tidal fluctuations in water level. *Netherlands Journal of Sea Research*, 2, 189-222.

Van der Have, T.M.E., Nieboer, M.E. and Boer, G.C. (1984) Age-related distribution of dunlin in the Dutch Wadden Sea. In: Evans, P.R., Goss-Custard, J.D. and Hale, W.G. (eds.) *Coastal waders and wildfowl in winter*. Cambridge University Press, Cambridge.

Wiens, J.A. (1977) On competition and variable environments. *Amer. Sci.*, 65, 590-597.

Wiens, J.A. (1993) Fat times, lean times and competition among predators. *Trends in Ecology and Evolution*, 8, 348-349.

Williams, J.B. and Batzli, G.O. (1979) Competition among bark-foraging birds in central Illinois : experimental evidence. *Condor*, 81, 122-132.

Williamson, M. (1972) *The analysis of Biological Populations.* Arnold, London.

Wood, E.G. (1984) *Time and energy budgets of the grey plover (Pluvialis squatarola) at Teesmouth.* Ph.D thesis, University of Durham.

Woodford, W.J. (1981) *Aspects of the summer feeding ecology of a coastal population of curlew (Numenius arquata).* M.Sc. thesis, University of Durham.

Ziv,Y., Abramsky, Z., Kotler, B.P. and Subach, A.. (1992) Interference competition and temporal and habitat partitioning in two gerbil species. *Oikos*, 66, 237-244.

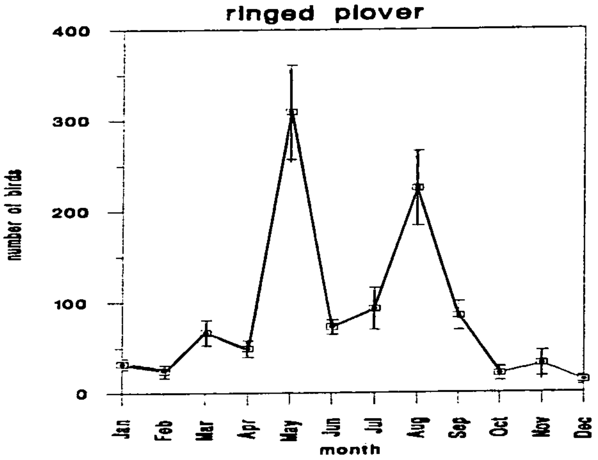
Zwarts, L. (1978) Intra- and interspecific competition for space in estuarine bird species in a one-prey situation. *Proceedings of the XVII International Ornithological Congress* (Berlin).

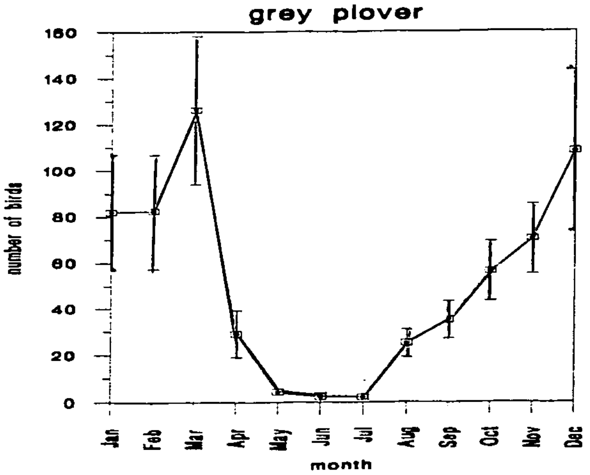
Zwarts, L. and Wanink, J. (1984) How oystercatchers and curlews successively deplete clams. In: P.R. Evans, J.D. Goss-Custard and W.G. Hale (eds.) *Coastal waders and wildfowl in winter.* Cambridge University Press, Cambridge.

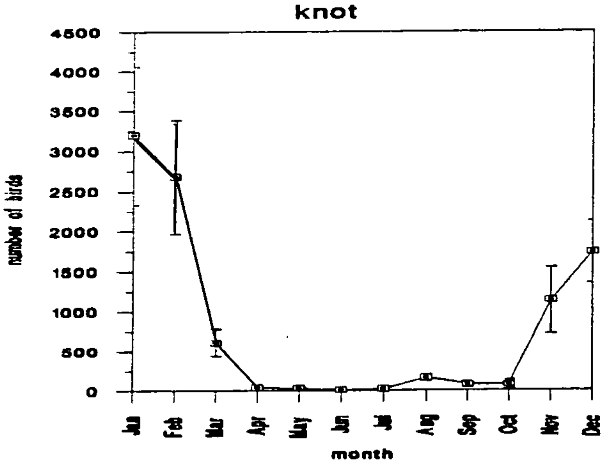
Zwarts. L. and Drent, R.H. (1981) Prey depletion and the regulation of predator density : Oystercatchers (*Haematopus ostralegus*) feeding on mussels (*Mytilus edulis*). In: Jones, N. V. and Wolff, J. (eds.) *Feeding and survival strategies of estuarine organisms.* Plenum Press, New York.

Appendix 1.1 The abundance of eleven species of shorebirds on the Tees estuary through the year.

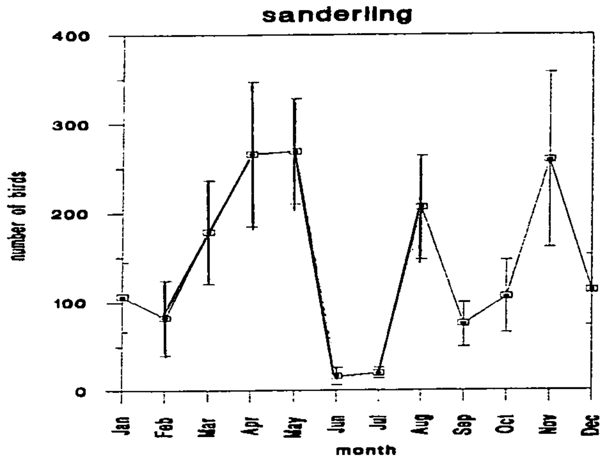
Plotted points are the monthly seven year mean (± S.E.) from B.T.O.'s "Birds of Estuaries" counts between 1985 and 1991. Counts taken in the middle of each month.

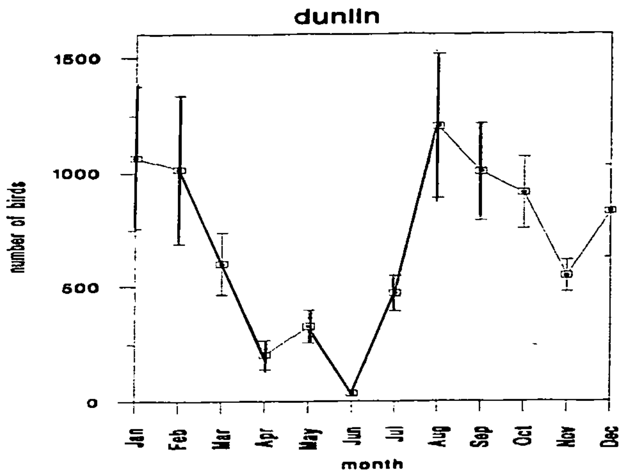


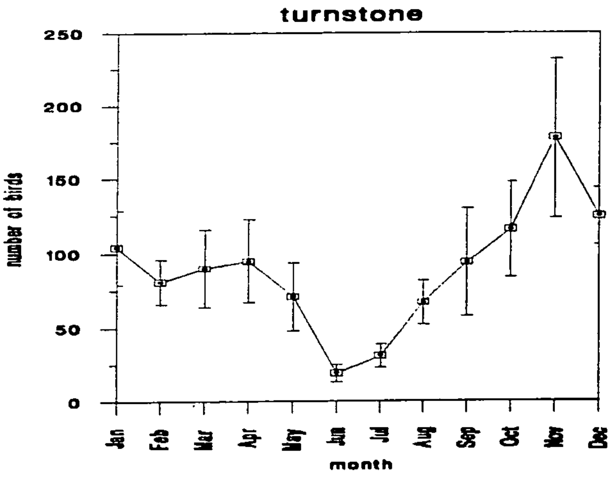




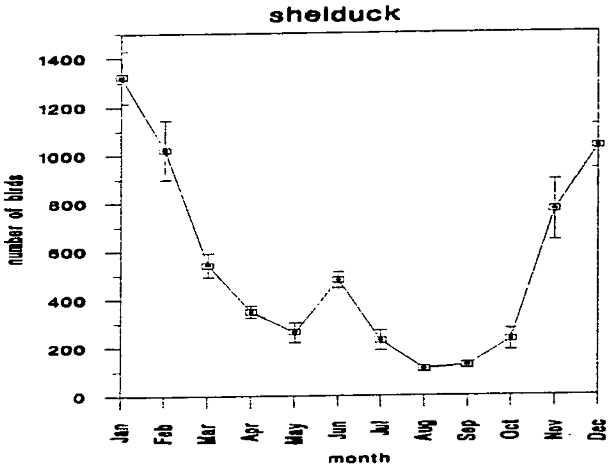
Appendix 1.1 (continued).

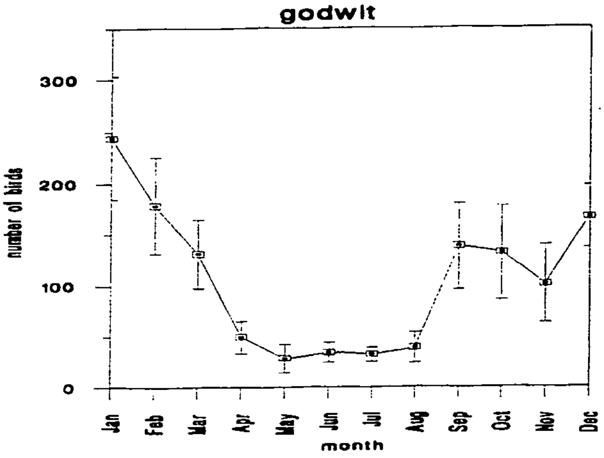


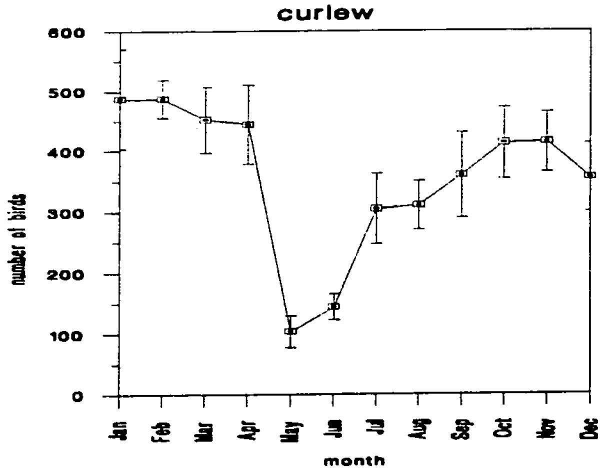




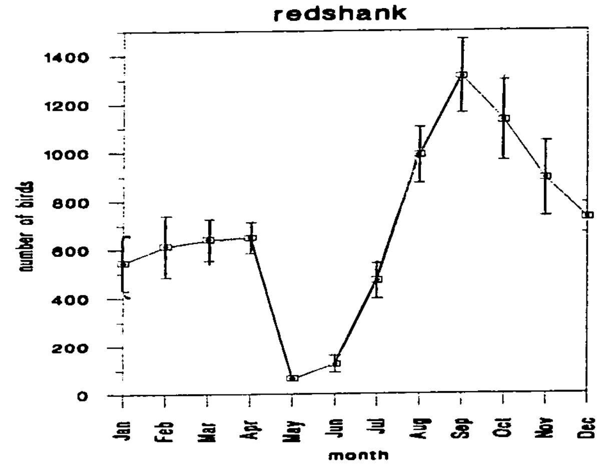
Appendix 1.1 (continued).

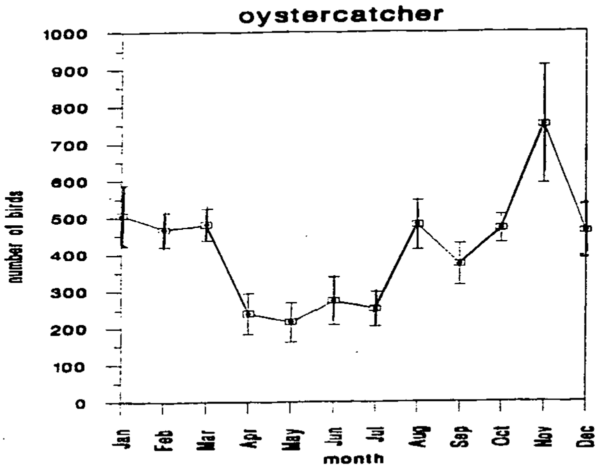






Appendix 1.1 (continued).





Appendix 1.2 The densities per hectare of eleven species of shorebirds on four feeding areas of the Tees Estuary. From monthly low water counts between July 1991 and June 1992.

ringed plover

Month	Seal Sands	N.Gare	Bran Sands	South Side
July	0.09	0.02	0.18	0.03
August	1.87	0.27	2.78	0.13
September	0.70	0.22	0.13	0.21
October	0.38	0.64	0	0.21
November	0.20	1.11	0	0.24
December	0.14	0	0	0.04
January	0.09	0	0	0.18
February	0.56	0.02	0.04	0.11
March	0.26	0	0.29	0.03
April	0.66	0.09	0.36	0.05
May	1.57	0.02	0.51	0.01
June	0.14	0	0.04	0

grey plover

Month	Seal Sands	N.Gare	Bran Sands	South Side
July	0.04	0	0	0
August	0.10	0	0	0
September	0.19	0	0.13	0
October	0.67	0.09	0.16	0
November	0.76	0.02	0.16	0
December	1.01	0	0.07	0
January	0.99	0	0.18	0
February	1.14	0	0.22	0
March	0.62	0	0	0
April	0.15	0	0	0
May	0.05	0	0	0
June	0.04	0	0	0

knot

Month	Seal Sands	N.Gare	Bran Sands	South Side
July	0	0	0.20	0
August	0.04	0	1.33	0.03
September	0.03	0	0.09	0.02
October	0.09	0	0.11	0.07
November	3.1	0	0	2.37
December	3.2	2.44	0	2.48
January	4.4	0	0	3.38
February	4.3	0	0	3.27
March	0.9	0	0	0.72
April	0	0	0	0
May	0	0	0	0
June	0	0	0	0

Appendix 1.2 (continued).

sanderling

Month	Seal Sands	N.Gare	Bran Sands	South Side
July	0.04	0.09	0.20	0.03
August	0.03	0.11	1.78	0.66
September	0	0.02	0	1.07
October	0	2.91	0.07	0.39
November	0	0.16	0	0.58
December	0	0.11	0	0.21
January	0	1.89	0	0.15
February	0	1.56	0	1.25
March	0.01	0.76	0	0.41
April	0.01	0.40	1.18	0.19
May	0.16	0.71	1.58	0.21
June	0	0.20	1.02	0

dunlin

Month	Seal Sands	N.Gare	Bran Sands	South Side
July	3.36	0	0.62	0.03
August	7.66	0	3.84	0.09
September	10.63	5.91	0.98	0.43
October	5.04	1.51	3.62	0.53
November	10.96	0.84	0.27	0.39
December	8.74	0.27	0.24	0.20
January	13.63	0	0.07	0.37
February	8.82	0	0.18	0.15
March	3.86	0	0.11	0.03
April	2.44	0	0	0
May	2.15	0	0.07	0
June	0.05	0	0.02	0

turnstone

Month	Seal Sands	N.Gare	Bran Sands	South Side
July	0.21	0	0.07	0.02
August	0.07	0.02	0.07	0.33
September	0.01	0	0.02	0.27
October	0	0.58	0	0.27
November	0	0.13	0.02	0.27
December	0	0.96	0.02	0.19
January	0	0.02	0	0.13
February	0	0	0.07	0.08
March	0	0	0.02	0.18
April	0.43	0.40	0.36	0.07
May	0.19	0.11	0.02	0.05
June	0.09	0	0	0

Appendix 1.2 (continued).

shelduck

Month	Seal Sands	N.Gare	Bran Sands	South Side
July	0.88	0	0.07	0
August	0.05	0	0	0
September	0.28	0	0.02	0
October	2.66	0	0.16	0
November	5.41	0	0.47	0
December	5.51	0	0.89	0
January	3.55	0	0.22	0
February	3.14	0	0.42	0
March	1.68	0	0.98	0
April	0.78	0	0.42	0
May	0.28	0	0.31	0
June	0.34	0.02	0.27	0

godwit

Month	Seal Sands	N.Gare	Bran Sands	South Side
July	0.08	0	0.13	0.01
August	0.08	0	0.22	0.03
September	0.34	0.04	0.89	0.04
October	0.51	0	0.51	0.03
November	0.69	0	0.53	0
December	0.94	0	0.53	0
January	0.96	0	4.87	0
February	0.15	0	6.07	0
March	0.66	0	1.04	0
April	0.25	0	0.02	0
May	0.32	0	0.02	0
June	0.24	0.02	0.02	0

curlew

Month	Seal Sands	N.Gare	Bran Sands	South Side
July	2.51	0	0.87	0.01
August	3.20	0	1.11	0.02
September	2.70	0	0.93	0.04
October	3.00	0.02	0.78	0.01
November	2.15	0	0.56	0.04
December	1.39	0	0.42	0.04
January	2.34	0.02	0.49	0.03
February	2.64	0	0.80	0.03
March	1.14	0	0.69	0.01
April	0.74	0	0.09	0
May	0.44	0	0.16	0
June	0.59	0	0.13	0

Appendix 1.2 (continued).

redshank

Month	Seal Sands	N.Gare	Bran Sands	South Side
July	2.45	0	0.87	0
August	6.81	0	2.24	0.02
September	9.87	0.04	2.53	0.03
October	7.12	1.58	1.33	0.22
November	3.66	1.47	0.47	0.42
December	2.52	0.31	0	0.33
January	1.91	1.73	0.67	0.24
February	2.15	1.13	0.96	0.18
March	3.60	0.07	1/62	0.11
April	5.24	0.04	1.89	0.01
May	0.44	0	0.11	0
June	0.29	0	0	0

oystercatcher

Month	Seal Sands	N.Gare	Bran Sands	South Side
July	0.52	0.16	0.44	0.26
August	0.52	0.20	0.31	1.09
September	0.80	0	0.56	1.59
October	0.39	0	0.27	3.26
November	0.55	0.04	0.22	2.81
December	0.40	0	0.02	1.86
January	0.74	0.18	0.60	1.81
February	0.53	0.04	1.09	1.28
March	0.33	0.02	0.42	1.41
April	0.51	0	1.13	0.54
May	0.51	0.29	0.80	0.35
June	0.82	0.91	0.33	0.29

Appendix 1.3 Substrate preference indices of shorebirds on Seal Sands.

Areas correspond to substrate types; 2, 4, 10=firm mud; 3=sand; 6=soft mud; 8=sandy mud; 12=liquid mud.

ringed plover

Month	Area 2	Area 3	Area 4	Area 6	Area 8	Area 10	Area 12
Jul	-1	-1	-1	-0.70	-1	-1	-1
Aug	-0.48	+1.20	-0.45	+0.20	0.79	-0.20	-0.50
Sep	-0.96	-1	-0.90	-0.50	+2.29	+1.30	+2.0
Oct	-1	-1	-0.65	-0.70	+5.64	-1	-1
Nov	-1	-1	+2.15	-0.70	+0.14	+1.20	-1
Dec	-1	-1	-1	-0.70	-1	-1	-1
Jan	-1	-1	-1	-0.70	-1	-1	-1
Feb	-0.87	+3.9	+0.35	-0.7-	+0.43	-1	-1
Mar	-1	-0.70	+1.25	-0.70	+2.71	-1	-1
Apr	-0.91	+2.30	+0.70	-0.65	+0.57	-0.50	-0.50
May	-0.70	-1	+0.95	-	+1.57	-0.70	-1
Jun	-0.91	+2.00	-0.45	-0.70	+2.93	-0.80	-1

grey plover

Month	Area 2	Area 3	Area 4	Area 6	Area 8	Area 10	Area 12
Jul	-1	-1	-1	-0.70	-1	-1	-1
Aug	-1	-1	-1	-0.70	-1	-1	-1
Sep	-0.74	-1	-1	+0.05	+0.70	-1	+6.0
Oct	+0.3	-	-0.80	+1.10	+0.29	-0.90	-0/75
Nov	-0.30	-0.60	-0.75	+1.00	-0.07	+1.20	-0.25
Dec	-0.39	-0.60	-0.70	+0.60	+1.14	0	+0.25
Jan	-0.61	-0.40	+0.55	+0.10	+0.07	+0.80	-0.25
Feb	-0.65	-0.50	-0.70	+0.25	+0.56	+2.30	-0.13
Mar	-0.96	+0.60	-1	+0.20	+2.79	-0.80	+0.25
Apr	-0.91	-0.10	-0.80	+0.45	+1.14	+2.10	-1
May	-1	-1	-1	-0.70	-1	-1	-1
Jun	-1	-1	-1	-0.70	-1	-1	-1

knot

Month	Area 2	Area 3	Area 4	Area 6	Area 8	Area 10	Area 12
Jul	-1	-1	-1	-0.70	-1	-1	-1
Aug	+1.61	+0.10	-1	-0.70	+1.07	-1	-1
Sep	-1	-1	-1	-0.70	-1	-1	-1
Oct	-1	-1	-1	-0.70	-1	-1	-1
Nov	-1	-1	-1	-0.70	-1	-1	-1
Dec	-1	+0.50	-1	-0.70	+5.07	-1	-1
Jan	-0.83	-0.90	+0.75	-0.70	+0.93	+2.20	-1
Feb	+0.35	-0.80	-0.70	-0.70	+1.00	+1.70	-0.25
Mar	-1	-1	-1	-0.70	+6.07	-1	-1
Apr	-1	-1	-1	-0.70	-1	-1	-1
May	-1	-1	-1	-0.70	-1	-1	-1
Jun	-1	-1	-1	-0.70	-1	-1	-1

Appendix 1.3 (continued).

sanderling

Month	Area 2	Area 3	Area 4	Area 6	Area 8	Area 10	Area 12
Jul	-1	-1	-1	-0.70	-1	-1	-1
Aug	-0.91	+2.30	-1	-0.70	+0.71	+3.00	-1
Sep	-1	-1	-1	-0.70	-1	-1	-1
Oct	-1	-1	-1	-0.70	-1	-1	-1
Nov	-1	-1	-1	-0.70	-1	-1	-1
Dec	-1	-1	-1	-0.70	-1	-1	-1
Jan	-1	-1	-1	-0.70	-1	-1	-1
Feb	-1	-1	-1	-0.70	-1	-1	-1
Mar	-1	-1	-1	-0.70	-1	-1	-1
Apr	-1	-1	-1	-0.70	-1	-1	-1
May	-0.96	-1	-0.80	+1.65	-	+2.50	-1
Jun	-1	-1	-1	-0.70	-1	-1	-1

dunlin

Month	Area 2	Area 3	Area 4	Area 6	Area 8	Area 10	Area 12
Jul	-0.78	-1	-0.85	+1.40	+0.86	-0.80	+1.75
Aug	-0.65	-0.90	-0.35	+0.40	+0.14	+2.40	-0.13
Sep	-0.74	-1	-0.15	+1.75	-0.50	-0.20	+0.75
Oct	-0.83	-0.90	0	+2.10	-0.79	-1	+1.00
Nov	-0.91	-1	+0.15	+1.10	-0.64	+0.10	+1.88
Dec	-0.91	-0.90	+0.15	+0.60	-0.57	+1.40	+1.38
Jan	-0.83	-0.50	+0.65	+0.40	-0.29	0	+1.00
Feb	-0.65	+0.50	+1.15	-0.10	-0.43	-0.60	+0.25
Mar	-1	-0.40	+0.90	-0.25	-0.29	-1	+3.63
Apr	-0.52	-0.10	+0.50	-0.45	+1.93	-0.70	-1
May	-0.61	-1	+0.30	+0.95	+0.36	-0.60	+0.13
Jun	-1	-1	-1	-0.70	-1	-1	-1

shelduck

Month	Area 2	Area 3	Area 4	Area 6	Area 8	Area 10	Area 12
Jul	-0.43	-1	+0.45	-0.70	-1	-1	+6.25
Aug	-1	-1	-1	-0.70	-1	-1	-1
Sep	-1	-1	-1	-0.70	-1	-1	-1
Oct	-0.83	-1	-1	+0.45	-0.21	-1	+6.75
Nov	+0.26	-0.90	-0.40	+0.20	+0.50	-0.80	+1.38
Dec	-0.39	-0.50	-0.05	+0.30	+0.57	-0.60	+1.00
Jan	-0.65	-1	-0.30	+0.20	+1.50	-0.70	+1.75
Feb	-0.57	-0.90	-0.50	+0.5	+1.36	-0.70	+1.50
Mar	+0.30	-0.60	-0.10	-0.35	+1.07	-0.50	-0.13
Apr	-0.48	0	-0.30	-0.70	+0.36	+0.80	+2.50
May	-1	-1	-0.30	-0.20	+0.21	0	+5.25
Jun	-0.78	+0.70	+0.85	+0.15	-1	-1	+1.88

Appendix 1.3 (continued).

godwit

Month	Area 2	Area 3	Area 4	Area 6	Area 8	Area 10	Area 12
Jul	-1	-1	-1	-0.70	-1	-1	-1
Aug	-1	-1	-1	-0.70	-1	-1	-1
Sep	-0.87	-1	+2.40	-0.70	+0.21	-0.90	+0.38
Oct	-0.96	-1	-0.80	+3.80	-0.93	-1	-0.63
Nov	-0.96	-1	-0.80	+3.50	-0.93	-1	+0.25
Dec	-0.96	-1	-1	+3.60	-1	-0.90	+0.63
Jan	-0.78	-0.50	-0.45	+1.20	-0.07	-0.50	+1.88
Feb	-0.48	-0.70	-0.95	-0.15	+2.29	+0.10	1.00
Mar	-1	-1	-1	+2.65	-0.86	-1	+2.88
Apr	-0.87	-0.70	-1	-0.65	-0.43	-1	+9.75
May	-0.26	-1	+0.95	+0.65	+0.07	-1	-0.75
Jun	-1	-1	-1	-0.70	-1	-1	-1

curlew

Month	Area 2	Area 3	Area 4	Area 6	Area 8	Area 10	Area 12
Jul	-0.74	-0.50	-0.50	+0.80	+0.86	-0.20	+1.00
Aug	-0.70	-0.40	-0.35	+0.95	+0.50	0.00	+0.13
Sep	-0.78	-0.50	+0.10	+0.75	-0.07	+0.10	+0.75
Oct	-0.74	-0.30	-0.10	+1.10	-0.21	-0.20	+0.63
Nov	-0.65	-0.80	-0.40	+1.00	-0.21	0.00	+1.75
Dec	-0.74	-0.70	-0.25	+0.65	-0.14	+0.30	+2.00
Jan	-0.78	-0.60	-0.15	+0.25	-0.14	+0.80	+2.00
Feb	-0.83	-0.70	-0.20	+1.55	-0.43	+0.20	+0.50
Mar	-0.78	-0.60	+0.30	+0.50	+0.07	-0.30	+1.50
Apr	-0.83	-0.60	+0.20	+1.65	-0.57	-0.50	+0.25
May	-0.04	-0.90	-1	-0.25	+2.07	+0.80	0.00
Jun	-0.30	-1	-0.85	-0.25	+1.57	+0.10	+2.25

redshank

Month	Area 2	Area 3	Area 4	Area 6	Area 8	Area 10	Area 12
Jul	-0.70	-0.90	-0.20	+1.60	-0.57	-0.40	+1.13
Aug	-0.65	-0.80	+0.15	+1.60	-0.71	-0.40	+0.38
Sep	-0.65	-0.90	+1.75	+0.05	-0.57	-0.50	+0.25
Oct	-0.61	-0.20	+0.65	-0.05	+0.29	+0.30	-0.13
Nov	-0.26	-0.80	-0.15	+0.30	+1.07	-0.20	-0.13
Dec	-0.30	-0.40	+0.30	+0.35	+0.29	-0.30	-0.25
Jan	-0.30	-0.50	+1.00	-0.60	-0.21	-0.60	+1.75
Feb	-0.52	-1	+0.65	+0.30	+0.14	-0.70	+1.13
Mar	-0.87	-1	+1.25	+0.95	-0.43	-0.40	-0.38
Apr	-0.78	-0.30	+0.40	+0.75	0.00	-0.30	+0.13
May	-1	-1	-1	-0.70	-1	-1	-1
Jun	-1	-1	-1	+3.15	-0.21	-0.60	+0.13

Appendix 1.3 (continued).

oystercatcher

Month	Area 2	Area 3	Area 4	Area 6	Area 8	Area 10	Area 12
Jul	-1	-1	-1	-0.70	-1	-1	-1
Aug	+0.70	+0.30	-0.60	-0.70	+0.14	+1.30	-0.88
Sep	+0.78	-0.80	-0.05	-0.50	+1.00	+1.50	-0.25
Oct	-0.39	+0.60	-0.40	-0.70	+1.21	+2.40	-1
Nov	+0.13	-0.20	-0.95	-0.70	+1.21	+2.40	-1
Dec	+0.09	-0.10	-0.85	-0.65	+0.93	+2.20	-0.63
Jan	-0.13	-0.20	-0.05	-0.55	-1	+1.50	+4.63
Feb	-0.65	+0.90	-0.85	-0.70	+0.79	+3.50	-0.88
Mar	-1	+1.30	+1.35	-0.70	-0.71	+1.60	-1
Apr	-1	-1	-1	-0.70	-1	-1	-1
May	-0.74	-1	-1	+0.60	-0.14	+1.50	-1
Jun	-1	-1	-1	+2.00	-0.43	-1	-1

Appendix 2.1 <u>Prey size categories (mm) used in determination of prey size overlap indices.</u>

Categories used are deonoted by the cells, and categories for curlew and godwit have been adjusted for sexual differences in bill length in these species.

grey plover	1-15 16-30 31-45	46-60	61-75	76-90	
male godwit	1-20 21-40	41-60	61-80	81-100	101-120

grey plover	1-15 16-30	31-45	46-60 61-75	76-90		
female godwit	1-25	26-50	51-75	76-100	101-125	126-150

grey plover	1-15 16.30	31-45 46-60	61-75	76-90	
male curlew	1-28	29-55	56-83	84-110	111-138

grey plover	1-15 16-30	31-45 46-60 61-75	76-90		
female curlew	1-35	36-70	71-105	106-140	141-175

male godwit	1-20	21-40	41-60 61-80	81-100	101-120	
female godwit	1-25	26-50	51-75	76-100	101-125	126-150

Appendix 2.1 (continued).

male curlew	1-28	29-55 56-83 84-110	111-138	
female curlew	1-35	35-70 71-105	106-140	141-175

female godwit	1-25 26-50 51-75	76-100	101-125 126-150	
female curlew	1-35 36-70	71-105	106-140	141-175

grey plover	1-20 21-40 41-60	61-80	81-100	101-120
male godwit	1-28 29-55	56-83	84-110	111-138

female godwit	1-25	26-50	51-75	76-100	101-125	126-150
male curlew	1-28	29-55	56-83	84-110	111-138	

grey plover	1-20 21-40	41-60	61-80 81-100		
female godwit	1-35	36-70	71-105	106-140	141-175

Appendix 2.2

Number of bird days spent by curlew, godwit and grey plover on Seal Sands between September 1991 and March 1992.

a) curlew

MONTH	POPULATION SIZE	NUMBER OF DAYS	BIRD DAYS
SEPTEMBER	410	30	12300
OCTOBER	519	31	16089
NOVEMBER	344	30	10320
DECEMBER	222	31	6882
JANUARY	374	31	11594
FEBRUARY	349	28	9772
MARCH	333	31	10323
TOTAL	-	-	77280

b) godwit

MONTH	POPULATION SIZE	NUMBER OF DAYS	BIRD DAYS
SEPTEMBER	64	30	1920
OCTOBER	159	31	4929
NOVEMBER	110	30	3300
DECEMBER	156	31	4836
JANUARY	153	31	4743
FEBRUARY	140	28	3920
MARCH	87	31	2697
TOTAL			26345

c) grey plover

MONTH	POPULATION SIZE	NUMBER OF DAYS	BIRD DAYS
SEPTEMBER	29	30	1170
OCTOBER	95	31	2945
NOVEMBER	122	30	3660
DECEMBER	162	31	5022
JANUARY	159	31	4929
FEBRUARY	159	28	4452
MARCH	117	31	3627
TOTAL			25805

Appendix 2.3 Bird feeding time (BFD$_a$, days) and energy intake requrements (EIR $_a$) of three shorebird species on each of the main feeding sites of Seal Sands 1991/92. (see text for method of calculation).

Curlew.

MONTH	AREA 2	AREA 3	AREA 4	AREA 6	AREA 8	AREA 10	AREA 12	TOTAL
SEP	150	105	703	848	314	275	102	2497
OCT	127	291	1205	1047	318	225	552	3765
NOV	191	95	278	840	328	252	338	2322
DEC	124	150	379	390	131	300	290	1764
JAN	156	150	567	832	319	334	323	2681
FEB	106	49	1058	1006	257	318	126	2920
MAR	141	93	833	1296	293	244	95	2995
TOTAL (BFD$_a$)	995	933	5023	6259	1959	1948	1826	18944 (BFD$_t$)

EIR$_a$	1.28	1.20	6.46	8.04	2.52	2.50	2.34	24.34 (EIR$_s$)

Godwit

MONTH	AREA 2	AREA 3	AREA 4	AREA 6	AREA 8	AREA 10	AREA 12	TOTAL
SEP	32	15	216	108	14	55	9	449
OCT	98	16	689	300	70	57	22	1252
NOV	16	15	19	350	43	24	38	505
DEC	16	14	413	383	26	98	25	975
JAN	17	16	39	388	78	67	40	645
FEB	7	1	49	59	56	172	5	349
MAR	37	17	160	124	75	44	131	588
TOTAL (BFD$_a$)	223	94	1585	1712	362	517	270	4763 (BFD$_t$)

EIR$_a$	0.18	0.08	1.31	1.41	0.30	0.43	0.22	3.93 (EIR$_s$)

Grey plover

MONTH	AREA 2	AREA 3	AREA 4	AREA 6	AREA 8	AREA 10	AREA 12	TOTAL
SEP	31	6	24	12	33	48	9	163
OCT	121	137	65	277	119	25	35	779
NOV	118	50	19	235	118	47	69	656
DEC	72	43	56	393	200	98	67	929
JAN	59	81	101	191	321	293	45	1091
FEB	88	47	124	551	159	273	17	1259
MAR	165	41	93	206	265	114	18	902
TOTAL	654	405	482	1865	1215	898	260	5779 (BFD$_t$)

EIR$_a$	0.29	0.18	0.22	0.85	0.55	0.41	0.12	2.63 (EIR$_s$)

Appendix 2.4

The proportion of total energy requirement supplied to curlew, godwit and grey plovers by 0-1 yr. and 1+ yr. *Nereis.*

curlew, 0-1 yr. worms = 29.6 x 0.1 / (29.6 x 0.1) + (202 x 0.9) = **0.016**

" 1+ yr. worms = 202 x 0.9 / (202 x 0.9) + (29.6 x 0.1)= **0.984**

godwit 0-1 yr. worms = 29.6 x 0.3 / (29.6 x 0.3) + (202 x 0.7) = **0.059**

" 1+ yr. worms = 202 x 0.7 / (202 x 0.7) + (29.6 x 0.3)= **0.941**

grey plover 0-1 yr. worms = 29.6 x 0.5 / (29.6 x 0.5) + (202 x 0.5) = **0.1278**

" 1+ yr. worms = 202 x 0.5 / (202 x 0.5) + (29.6 x 0.5)= **0.8722**

Appendix 2.5 The estimated number of *Nereis* of each size class consumed by curlew, godwit and grey plover between September 1991 and March 1992.

curlew

i) 0-1 year old worms

	AREA 2	AREA 3	AREA 4	AREA 6	AREA 8	AREA 10	AREA 12
ENERGY REQUIREMENT IN MILLION KCAL (EIR$_a$)	1.28	1.20	6.46	8.04	2.52	2.50	2.34
ENERGY FROM 0-1 YR. WORMS (MILLION KCAL)	0.020	0.019	0.10	0.13	0.04	0.04	0.037
NUMBER OF 0-1 YR. WORMS (MILLIONS)	0.68	0.64	3.78	4.39	1.35	1.35	1.25

ii) 1+ year old worms

	AREA 2	AREA 3	AREA 4	AREA 6	AREA 8	AREA 10	AREA 12
ENERGY REQUIREMENT IN MILLION KCAL (EIR$_a$)	1.28	1.20	6.46	8.04	2.52	2.50	2.34
ENERGY FROM 1+ YR. WORMS (MILLION KCAL)	1.26	1.18	6.36	7.91	2.48	2.46	2.30
NUMBER OF 1+ YR. WORMS (MILLIONS)	6.24	5.84	31.49	39.16	12.28	12.18	11.39

Appendix 2.5 (continued).

godwit

i) 0-1 year old worms

	AREA 2	AREA 3	AREA 4	AREA 6	AREA 8	AREA 10	AREA 12
ENERGY REQUIREMENT IN MILLION KCAL (EIR_a)	0.18	0.08	1.31	1.41	0.30	0.43	0.22
ENERGY FROM 0-1 YR. WORMS (MILLION KCAL)	0.011	0.0047	0.077	0.083	0.018	0.025	0.013
NUMBER OF 0-1 YR. WORMS (MILLIONS)	0.37	0.16	2.60	2.84	0.61	0.84	0.44

ii) 1+ year old worms

	AREA 2	AREA 3	AREA 4	AREA 6	AREA 8	AREA 10	AREA 12
ENERGY REQUIREMENT IN MILLION KCAL (EIR_a)	0.18	0.08	1.31	1.41	0.30	0.43	0.22
ENERGY FROM 1+ YR. WORMS (MILLION KCAL)	0.17	0.075	1.23	1.33	0.28	0.40	0.21
NUMBER OF 1+ YR. WORMS (MILLIONS)	0.84	0.37	6.09	6.58	1.39	1.98	1.04

Appendix 2.5 (continued).

grey plover

i) 0-1 year old worms

	AREA 2	AREA 3	AREA 4	AREA 6	AREA 8	AREA 10	AREA 12
ENERGY REQUIREMENT IN MILLION KCAL (EIR_a)	0.29	0.18	0.22	0.85	0.55	0.41	0.12
ENERGY FROM 0-1 YR. WORMS (MILLION KCAL)	0.038	0.023	0.029	0.11	0.072	0.053	0.016
NUMBER OF 0-1 YR. WORMS (MILLIONS)	1.28	0.78	0.98	3.72	2.43	1.79	0.54

ii) 1+ year old worms

	AREA 2	AREA 3	AREA 4	AREA 6	AREA 8	AREA 10	AREA 12
ENERGY REQUIREMENT IN MILLION KCAL (EIR_a)	0.29	0.18	0.22	0.85	0.55	0.41	0.12
ENERGY FROM 1+ YR. WORMS (MILLION KCAL)	0.25	0.16	0.19	0.74	0.48	0.36	0.10
NUMBER OF 1+ YR. WORMS (MILLIONS)	1.24	0.79	0.94	3.66	2.38	1.78	0.50

Appendix 2.6 The estimated number of *Nereis* of each size class in each of the main feeding areas of Seal Sands, September 1991.

FEEDING AREA	MEAN WORM DENSITY (M^{-2})	SURFACE AREA (M^2)	TOTAL WORM STOCK (MILLIONS)	STOCK OF 0-1 YR. WORMS (MILLIONS)	STOCK OF 1+ YR. WORMS (MILLIONS)
2	805	33700	271.29	162.77	108.52
3	1135	152400	172.97	103.78	69.19
4	1114	290000	323.06	193.84	129.22
6	1301	210000	273.21	163.93	109.28
8	1192	203200	242.21	145.33	96.88
10	814	152400	124.05	74.43	49.62
12	957	116000	111.01	66.61	44.40

Appendix 2.7 Ambient temperature adjusted daily energy requirements per individual curlew, godwit and grey plover on Seal Sands between September 1991 and March 1992.

curlew

MONTH	Tlc - MMT	(Tlc - MMT) *b*	(Tlc - MMT) *b* + BMR	TOTAL DAILY ENERGY INGESTION (kcal)
SEPTEMBER	0.6	1.43	71.43	321.4
OCTOBER	4.4	10.52	80.52	362.3
NOVEMBER	8.6	20.55	90.55	407.5
DECEMBER	10.8	25.81	95.81	430.0
JANUARY	11.0	26.29	96.29	433.3
FEBRUARY	9.1	21.75	91.75	412.9
MARCH	7.8	18.64	88.64	398.9

godwit

MONTH	Tlc - MMT	(Tlc - MMT) *b*	(Tlc - MMT) *b* + BMR	TOTAL DAILY ENERGY INGESTION (kcal)
SEPTEMBER	3.6	4.72	37.72	169.7
OCTOBER	7.4	9.69	42.69	192.1
NOVEMBER	11.6	15.20	48.20	216.9
DECEMBER	13.8	18.08	51.08	229.9
JANUARY	14.0	18.34	51.34	231.0
FEBRUARY	12.1	15.85	48.85	219.8
MARCH	10.8	14.15	47.15	212.3

grey plover

MONTH	Tlc - MMT	(Tlc - MMT) *b*	(Tlc - MMT) *b* + BMR	TOTAL DAILY ENERGY INGESTION (kcal)
SEPTEMBER	4.1	4.72	33.72	118.0
OCTOBER	7.9	9.09	38.09	133.3
NOVEMBER	12.1	13.92	42.92	150.2
DECEMBER	14.3	16.45	45.45	159.1
JANUARY	14.5	16.68	45.68	159.9
FEBRUARY	12.6	14.49	43.49	152.2
MARCH	11.3	13.00	42.00	147.0

Appendix 2.8 Ambient temperature-adjusted energy requirement of the populations of curlew, godwit and grey plover on Seal Sands between September 1991and March 1992.

curlew

MONTH	DEI (KCAL)	POPULATION	NUMBER OF DAYS	REQUIREMENT OF POP^{N} (MILLIONS KCAL)
SEPTEMBER	321.4	410	30	3.95
OCTOBER	362.3	519	31	5.83
NOVEMBER	407.5	344	30	4.21
DECEMBER	430.0	222	31	2.96
JANUARY	433.3	374	31	5.02
FEBRUARY	412.9	349	28	4.03
MARCH	398.9	333	31	4.12
TOTAL	-	-	-	**30.12**

godwit

MONTH	DEI (KCAL)	POPULATION	NUMBER OF DAYS	REQUIREMENT OF POP^{N} (MILLIONS KCAL)
SEPTEMBER	169.7	64	30	0.33
OCTOBER	192.1	159	31	0.95
NOVEMBER	216.9	110	30	0.72
DECEMBER	229.9	156	31	1.11
JANUARY	231.0	153	31	1.10
FEBRUARY	219.8	140	28	0.86
MARCH	212.3	87	31	0.57
TOTAL	-	-	-	**5.64**

grey plover

MONTH	DEI (KCAL)	POPULATION	NUMBER OF DAYS	REQUIREMENT OF POP^{N} (MILLIONS KCAL)
SEPTEMBER	118.0	29	30	0.10
OCTOBER	133.3	95	31	0.39
NOVEMBER	150.2	122	30	0.55
DECEMBER	159.1	162	31	0.78
JANUARY	159.9	159	31	0.79
FEBRUARY	152.2	159	28	0.68
MARCH	147.0	117	31	0.53
TOTAL	-	-	-	**3.82**

Appendix 2.9 <u>Temperature-adjusted estimates of percentage depletion of *Nereis* of each size class in each of the main feeding areas of Seal Sands</u>.

<u>curlew</u>

AREA NUMBER	ENERGY INTAKE REQUIREMENT SEPTEMBER-MARCH (MILLION kcal)	NUMBER OF 0-1 WORMS CONSUMED (MILLIONS)	NUMBER OF 1+ WORMS CONSUMED (MILLIONS)	DEPLETION OF 0-1 WORMS (%)	DEPLETION OF 1+ WORMS (%)
2	1.6	0.86	7.79	0.53	7.18
3	1.5	0.81	7.31	0.78	10.57
4	8.2	4.43	39.94	2.29	30.91
6	9.8	5.30	47.74	3.23	43.69
8	3.1	1.68	15.10	1.16	15.59
10	3.1	1.68	15.10	2.26	30.43
12	3.0	1.62	14.61	2.43	32.91
TOTAL	30.30	16.38	147.59	-	-

<u>godwit</u>

AREA NUMBER	ENERGY INTAKE REQUIREMENT SEPTEMBER-MARCH (MILLION kcal)	NUMBER OF 0-1 WORMS CONSUMED (MILLIONS)	NUMBER OF 1+ WORMS CONSUMED (MILLIONS)	DEPLETION OF 0-1 WORMS (%)	DEPLETION OF 1+ WORMS (%)
2	0.22	0.44	1.02	0.27	0.94
3	0.11	0.22	0.51	0.21	0.74
4	1.53	3.05	7.13	1.57	5.52
6	2.17	4.33	10.11	2.64	9.25
8	0.50	1.00	2.33	0.69	2.41
10	0.80	1.59	3.73	2.14	7.52
12	0.31	0.62	1.44	0.93	3.24
TOTAL	5.64	11.25	26.27	-	-

Appendix 2.9 (continued).

<u>grey plover</u>

AREA NUMBER	ENERGY INTAKE REQUIREMENT SEPTEMBER-MARCH (MILLION kcal)	NUMBER OF 0-1 WORMS CONSUMED (MILLIONS)	NUMBER OF 1+ WORMS CONSUMED (MILLIONS)	DEPLETION OF 0-1 WORMS (%)	DEPLETION OF 1+ WORMS (%)
2	0.43	1.86	1.86	1.14	1.71
3	0.26	1.12	1.12	1.08	1.62
4	0.30	1.30	1.30	0.67	1.01
6	1.24	5.36	5.35	3.27	4.90
8	0.83	3.59	3.58	2.47	3.70
10	0.59	2.55	2.55	3.43	5.14
12	0.19	0.82	0.82	1.23	1.85
TOTAL	3.84	16.60	16.58	-	-

Appendix 2.10 Estimated percentage depletion of *Nereis* of each size class in each of the main feeding areas of Seal Sands assuming 0-1 yr. worms=20 mm and 1+ yr. worms =60mm.

Parenthesised figure in the "D adjusted" row is the percent difference between size-adjusted and non-adjusted depletion.

curlew

i) 0-1 year worms

	AREA 2	AREA 3	AREA 4	AREA 6	AREA 8	AREA 10	AREA 12
Na (MILLIONS)	1.02	0.96	5.20	6.25	1.95	1.96	1.91
No (MILLIONS)	0.86	0.81	4.43	5.30	1.68	1.68	1.62
Do (PERCENT	0.53	0.78	2.29	3.23	1.16	2.26	2.43
D ADJUSTED (PERCENT)	0.63 (+16)	0.92 (+15)	2.69 (+15)	3.81 (+15)	1.35 (+14)	2.64 (+14)	2.87 (+15)

ii) 1+ year worms

	AREA 2	AREA 3	AREA 4	AREA 6	AREA 8	AREA 10	AREA 12
Na (MILLIONS)	9.19	8.60	47.08	56.29	17.80	17.80	17.27
No (MILLIONS)	7.79	7.31	39.94	47.74	15.10	15.10	14.61
Do (PERCENT	7.18	10.57	30.91	43.69	15.59	30.43	32.91
D ADJUSTED (PERCENT)	8.47 (+15)	12.44 (+15)	36.44 (+15)	51.51 (+15)	18.38	35.87 (+15)	38.90 (+15)

godwit

i) 0-1 year worms

	AREA 2	AREA 3	AREA 4	AREA 6	AREA 8	AREA 10	AREA 12
Na (MILLIONS)	0.53	0.27	3.66	5.14	1.17	1.88	0.72
No (MILLIONS)	0.44	0.22	3.05	4.33	1.00	1.59	0.62
Do (PERCENT	0.27	0.21	1.57	2.64	0.69	2.14	0.93
D ADJUSTED (PERCENT)	0.33 (+18)	0.26 (+19)	1.88 (+16)	3.13 (+16)	0.81 (+15)	2.53 (+15)	1.08 (+14)

Appendix 2.10 (continued).

ii) 1+ year worms

	AREA 2	AREA 3	AREA 4	AREA 6	AREA 8	AREA 10	AREA 12
Na (MILLIONS)	1.23	0.59	8.52	12.06	2.77	4.42	1.74
No (MILLIONS)	1.02	0.51	7.13	10.11	2.33	3.73	1.44
Do (PERCENT	0.94	0.74	5.52	9.25	2.41	7.52	3.24
D ADJUSTED (PERCENT)	1.13 (+17)	0.86 (+14)	6.60 (+16)	11.03 (+16)	2.87 (+16)	8.91 (+16)	3.92 (+17)

<u>grey plover</u>

i) 0-1 year worms

	AREA 2	AREA 3	AREA 4	AREA 6	AREA 8	AREA 10	AREA 12
Na (MILLIONS)	2.22	1.38	1.58	6.40	4.34	3.07	1.01
No (MILLIONS)	1.86	1.12	1.30	5.36	3.59	2.55	0.82
Do (PERCENT	1.14	1.08	0.67	3.27	2.47	3.43	1.23
D ADJUSTED (PERCENT)	1.36 (+16)	1.33 (+19)	0.81 (+17)	3.90 (+16)	2.99 (+17)	4.13 (+17)	1.52 (+19)

ii) 1+ year worms

	AREA 2	AREA 3	AREA 4	AREA 6	AREA 8	AREA 10	AREA 12
Na (MILLIONS)	2.26	1.34	1.58	6.50	4.35	3.09	0.97
No (MILLIONS)	1.86	1.12	1.30	5.35	3.58	2.55	0.82
Do (PERCENT	1.71	1.62	1.01	4.90	3.70	5.14	1.85
D ADJUSTED (PERCENT)	2.08 (+18)	1.94 (+16)	1.23 (+18)	5.95 (+18)	4.50 (+18)	6.23 (+17)	2.19 (+16)

Appendix 2.11 Estimated depletion of *Nereis* of each size class in each of the main feeding areas of Seal Sands assuming 0-1 yr. worm=30mm and 1+ yr. worms=70mm.

The parenthesised figure in the "D adjusted" row is the percent difference between size-adjusted and non-adjusted depletion.

curlew

i) 0-1 year worms

	AREA 2	AREA 3	AREA 4	AREA 6	AREA 8	AREA 10	AREA 12
Na (MILLIONS)	0.75	0.71	3.84	4.61	1.44	1.45	1.41
No (MILLIONS)	0.86	0.81	4.43	5.30	1.68	1.68	1.62
Do (PERCENT	0.53	0.78	2.29	3.23	1.16	2.26	2.43
D ADJUSTED (PERCENT)	0.46 (-13)	0.68 (-12)	1.99 (-13)	2.81 (-13)	0.99 (-14)	1.95 (-14)	2.12 (-13)

ii) 1+ year worms

	AREA 2	AREA 3	AREA 4	AREA 6	AREA 8	AREA 10	AREA 12
Na (MILLIONS)	6.71	6.28	34.35	41.04	13.00	13.00	12.56
No (MILLIONS)	7.79	7.31	39.94	47.74	15.10	15.10	14.61
Do (PERCENT	7.18	10.57	30.91	43.69	15.59	30.43	32.91
D ADJUSTED (PERCENT)	6.18 (-14)	9.08 (-14)	26.58 (-14)	37.56 (-14)	13.42 (-14)	26.20 (-14)	28.29 (-14)

godwit

i) 0-1 year worms

	AREA 2	AREA 3	AREA 4	AREA 6	AREA 8	AREA 10	AREA 12
Na (MILLIONS)	0.37	0.19	2.67	3.75	0.85	1.38	0.52
No (MILLIONS)	0.44	0.22	3.05	4.33	1.00	1.59	0.62
Do (PERCENT	0.27	0.21	1.57	2.64	0.69	2.14	0.93
D ADJUSTED (PERCENT)	0.23 (-15)	0.18 (-14)	1.37 (-13)	2.29 (-13)	0.59 (-15)	1.86 (-13)	0.78 (-16)

Appendix 2.11 (continued).

ii) 1+ year worms

	AREA 2	AREA 3	AREA 4	AREA 6	AREA 8	AREA 10	AREA 12
Na (MILLIONS)	0.87	0.43	6.05	8.58	1.99	3.20	1.24
No (MILLIONS)	1.02	0.51	7.13	10.11	2.33	3.73	1.44
Do (PERCENT	0.94	0.74	5.52	9.25	2.41	7.52	3.24
D ADJUSTED (PERCENT)	0.80 (-15)	0.62 (-16)	4.68 (-15)	7.85 (-15)	2.06 (-15)	6.45 (-14)	2.79 (-14)

grey plover

i) 0-1 year worms

	AREA 2	AREA 3	AREA 4	AREA 6	AREA 8	AREA 10	AREA 12
Na (MILLIONS)	1.56	0.94	1.08	4.49	2.92	2.11	0.68
No (MILLIONS)	1.86	1.12	1.30	5.36	3.59	2.55	0.82
Do (PERCENT	1.14	1.08	0.67	3.27	2.47	3.43	1.23
D ADJUSTED (PERCENT)	0.96 (-16)	0.91 (-16)	0.56 (-16)	2.74 (-16)	2.01 (-19)	2.84 (-17)	1.02 (-17)

ii) 1+ year worms

	AREA 2	AREA 3	AREA 4	AREA 6	AREA 8	AREA 10	AREA 12
Na (MILLIONS)	1.58	0.94	1.08	4.48	3.02	2.14	0.67
No (MILLIONS)	1.86	1.12	1.30	5.35	3.58	2.55	0.82
Do (PERCENT	1.71	1.62	1.01	4.90	3.70	5.14	1.85
D ADJUSTED (PERCENT)	1.45 (-15)	1.36 (-16)	0.84 (-17)	4.10 (-16)	3.12 (-16)	4.31 (-16)	1.51 (-18)