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Reclamation of intertidal land: some effects on Shelduck and wader populations in the Tees estuary

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Introduction

In many parts of the developed and developing world, intertidal land in estuaries is disappearing rapidly at present, usually under a permanent cover of industrial or domestic waste, in reclamation schemes, or under water, following the construction of storage reservoirs. Further loss of intertidal land often accompanies reclamation, when river channels are deepened by dredging, to allow the entry of ever larger vessels into sheltered harbours. As estuaries become more heavily industrialized, the locations of major new industrial developments are often on reclaimed land near the river mouths, where deeper-water anchorages can be provided. This is particularly true if the industries rely on imported raw materials or export of their products. Examples are given by Porter (1973).

Estuarine sand and mud-flats, particularly near river mouths, are highly productive habitats. The invertebrates they support provide the food for many species of wading birds (Charadriidae and Scolopacidae) and a few species of wildfowl, notably among the Shelducks, Tadornidae. Although shorebirds confine their use of estuaries chiefly to their non-breeding seasons, these comprise most of the year in temperate regions. Hence the disappearance of estuarine intertidal areas is a matter for considerable concern to scientific conservation organizations. However, little is known of the quantitative effects of loss of intertidal land on the populations of shorebirds which use particular estuaries during the northern winters, or as refuelling areas, on spring and autumn migration.

This paper documents the effects of the loss of about 60 % of the most important intertidal mudflat in the estuary of the River Tees, north-east England (54°37′ N 1°12′ W), on the numbers of Shelduck *Tadorna tadorna* and waders to be found there in winter. Because land at the highest tidal levels was reclaimed preferentially, the birds suffered a reduction not only in the size of their feeding grounds but also in the time for which the mudflats were uncovered. Their potential feeding time was cut from about 12 to about 8 hours in each tidal cycle of $12^1/_2$ hours. In this paper, it will be shown that the severity of changes in numbers of different shorebirds after the reclamation differed markedly between the species. For each species, the effects of reclamation depended on its diet, on the time for which it required to feed each day, on the presence of suitable additional feeding sites for use when the intertidal flats were covered during high water, and on interactions with other species. (In no case did the numbers of any shorebird species decrease by exactly 60 %, in proportion to the loss of feeding habitat, as had been confidently expected by many industrialists and planners.)

The time-course of reclamation in the Tees estuary

In the first half of the nineteenth century, the Tees estuary contained about 6000 acres (2500 ha) of intertidal sand and mudflats (Fig. 1). At the end of that century, the river mouth was narrowed by the construction of two large breakwaters, North and South Gares, composed chiefly of slag waste from nearby steelworks. Another slag bank was laid at that time near South Gare, running southeastwards for over one km, parallel to the beach. This bank, the "German Charlies", is uncovered only at low tide. Within the estuary, areas of intertidal land have been reduced steadily by reclamation, particularly during this century. By 1969 no more than about 1000 acres of Seal Sands, the major intertidal area on the north bank of the river, remained. In Autumn 1970, a porous slag wall was built across the middle of what was left of Seal Sands, dividing the higher from the lower tidal level flats. This wall retarded, but did

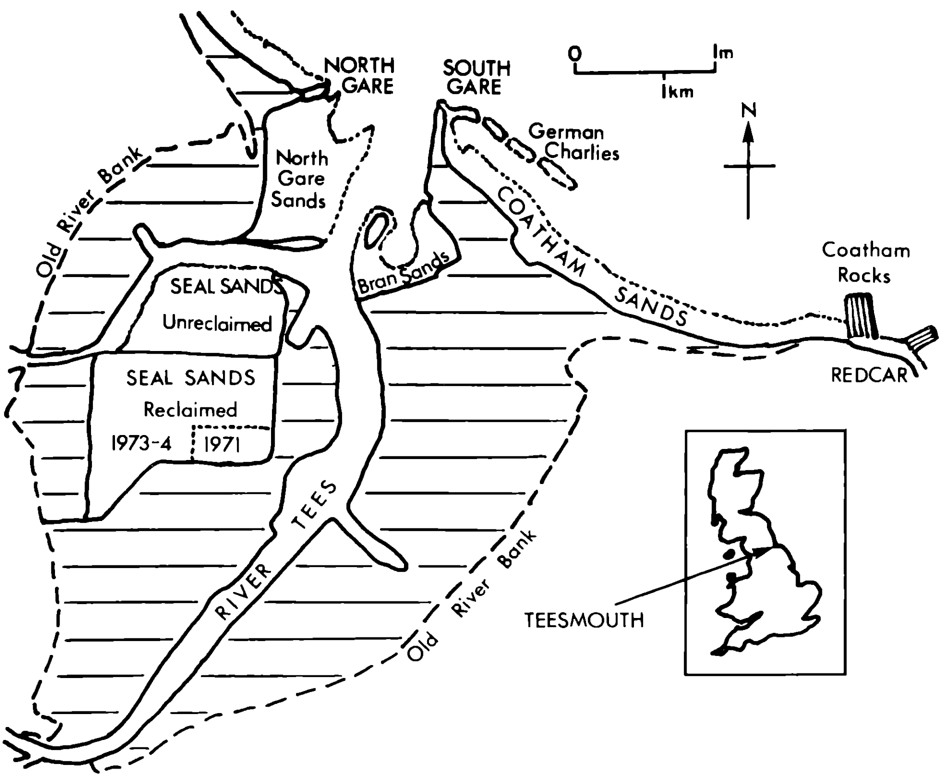

Fig. 1.
The estuary of the River Tees.

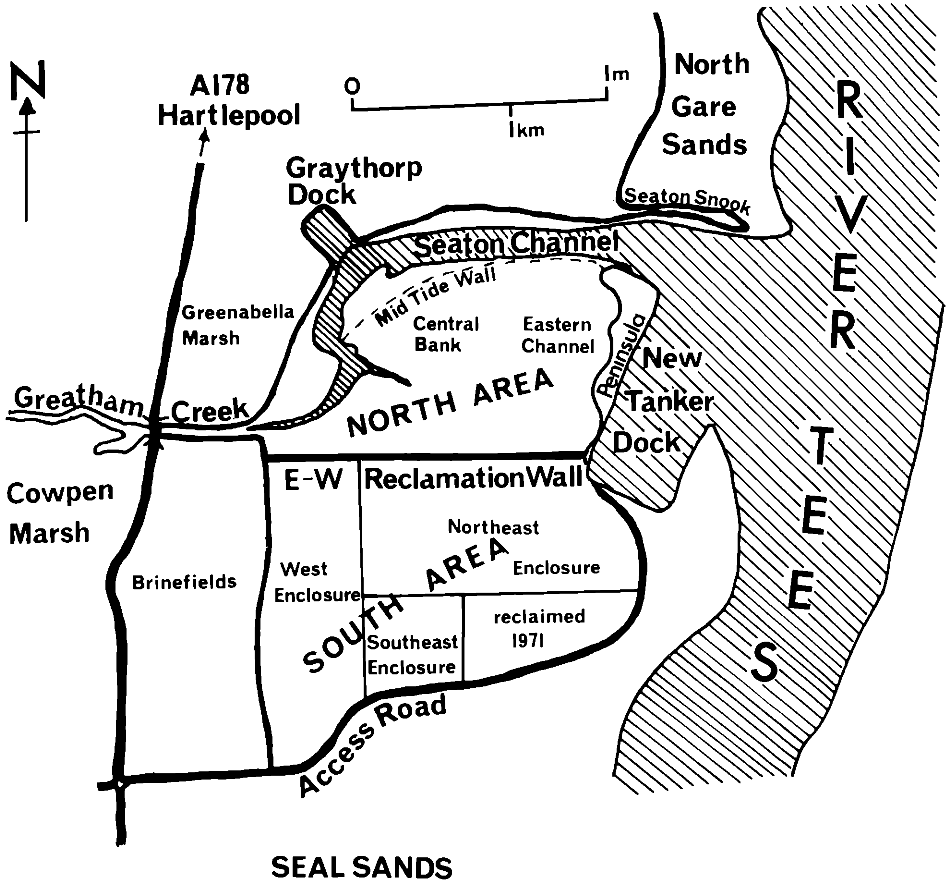

Fig. 2.
Seal Sands, showing the main intertidal areas described in the text.

not prevent, the ebb and flow of the tide over the enclosed "South Area" of the Sands (Fig. 2). High tide occurred about 2 hours later within the enclosure than on the open "North Area" About 100 acres (40 ha) of land at the extreme southeast corner of the South Area was filled in and built upon in 1971.

Reclamation of the rest of the South Area, by infilling with dredgings pumped from the river, took place by stages during 1973. Additional slag walls were built within the first enclosure and sections filled sequentially. The North-east Enclosure of 250 acres (100 ha) was filled in April and May, so that by the time birds returned in late summer 1973, only 650 acres (260 ha) of intertidal feeding grounds remained. These were reduced to 410 acres (165 ha) by December by partial filling of the West Enclosure. After a few weeks' delay, reclamation of the South Area was completed by infilling of the Southeast Enclosure, so that from early February 1974 onwards only 350 acres (140 ha) of intertidal land remained, all on North Area.

The shorebird and invertebrate populations of Seal Sands

In the five years before the reclamation of South Area, Seal Sands provided the feeding grounds for many thousand Dunlin *Calidris alpina* and (at certain stages of the tide) Knot *Calidris canutus,* for a few thousand Shelduck and Redshank *Tringa totanus,* for many hundred Curlew *Numenius arquata* and Bar-tailed Godwit *Limosa lapponica,* and for a few hundred Ringed Plover *Charadrius hiaticula* and Grey Plover *Pluvialis squatarola.*

The range of invertebrate prey available to these birds on Seal Sands was (and is) very restricted. The ragworm *Nereis diversicolor* is by far the largest species present, at densities of a few hundred/m^2. The gastropod *Hydrobia ulvae* is the commonest element of the macrofauna, reaching densities of several tens of thousands/m^2. The bivalve *Macoma balthica* is widely distributed but scarce, usually at densities of only a few tens/m^2, as is the shore crab *Carcinus maenas,* but this is present only in autumn. On the other hand, the amphipod *Corophium volutator* has a very restricted distribution but is locally common (Evans et al., 1979). In contrast, the meiofauna of this heavily polluted estuary is abundant and more diverse in species. Six species of small estuarine polychaetes and oligochaetes are common, and are present at combined densities of 1-2 million/m^2, equivalent to a biomass of 20–40 gm ash-free dry material/m^2 (Gray, 1976).

The three largest waders, Curlew, Godwit and Grey Plover, obtain most of their daily food intake on Seal Sands from the larger size-classes of *Nereis.* Knot take chiefly large *Hydrobia* from Seal Sands, but mussels *Mytilus edulis* from the other, more important, feeding sites at Teesmouth. Dunlin and Shelduck feed, by very different methods, chiefly upon the abundant small polychaetes and oligochaetes, while Redshank take a wide variety of sizes and species of possible prey. Detailed information on the diets and on invertebrate densities before and after reclamation of South Area is presented elsewhere (Evans et al., 1979).

Background to research and methods

Some 200 acres (80 ha) of the West Enclosure of South Area had been part of the Seal Sands Site of Special Scientific Interest (SSSI), declared by the Nature Conservancy Council in 1965. Their loss by reclamation left about 450 acres of SSSI intact, comprising 350 acres (140 ha) of land, the North Area, and almost 100 acres (40 ha) of water in Seaton Channel and Greatham Creek. The Nature Conservancy had agreed in January 1969 not to oppose reclamation of the South Area provided that the effects of the developments on the wildfowl and wader feeding areas were monitored. At their request, and that of the Teesmouth Bird Club, a research programme was begun by the Zoology Department of Durham University in January 1971. At that time it was not known when reclamation of South Area was to take place, and the initial aim of the work was to predict how many Shelduck and waders could be supported by North Area alone, once South Area had been infilled. The emphasis of the research in 1971 and 1972 was placed on surveys of invertebrates and on shorebird diets and foraging patterns. Although monthly counts of shorebirds had been made at Teesmouth since 1968, these had been confined to counts at roost sites. Counts of birds feeding on Seal

Sands, within two hours of low water, were started as part of the research programme at the beginning of 1973, and were made at monthly intervals or more frequently thereafter. Birds were counted with the aid of a 15-60 × telescope from a vehicle, from suitable vantage points on the reclamation walls. Birds on each enclosure within South Area were recorded separately.

Because roosts moved frequently, in response to disturbance, tidal height (spring or neap), wind direction and other factors, less weight is placed on roost counts in the discussion of the results presented below. Counts of feeding birds are available for the later part of the winter of 1972/73, before reclamation of South Area; for the winter of 1973/74, during reclamation; and for the winters of 1974/75 and 1975/76, after South Area had been completely infilled. The area of intertidal feeding grounds available in these last two winters was identical. Seasonal and year-to-year changes in the numbers of each shorebird species are examined in relation to changes in (i) the area of feeding grounds available, (ii) the time for which they were uncovered by the tide, (iii) the abundance of food, and (iv) the total numbers of that species present in the British Isles during each winter. These last figures have been taken from the reports of the 'Birds of Estuaries' Enquiry by PRATER (1974, 1975, 1976 and in prep.).

Results

Counts for the months of October to March inclusive are shown for Shelduck in Fig. 3, Grey Plover in Fig. 4, Curlew and Bar-tailed Godwit in Fig. 5, and Redshank and Dunlin in Fig. 6. For all species, counts cover the four successive winters of 1972/73 to 1975/76 inclusive. Counts of Shelduck are also available for the winter of 1976/77.

The patterns of use of the Enclosures of South Area and of the North Area during the winter of 1973/74, whilst reclamation was actively taking place, are shown for Grey Plover and Godwit in Fig. 7 and for Redshank and Dunlin in Fig. 8.

Discussion

1. What happened during the winter of active reclamation?

Shorebirds returning to Seal Sands in the autumn of 1973 were faced with a smaller feeding area and, from December onwards, a reduction in feeding time. Also, the total biomass of *Nereis* and *Hydrobia* present on North Area in early autumn 1973 was less than that which had been taken by Curlew, Godwit, Grey Plover, Redshank and Knot from the whole of Seal Sands in the previous winter of 1972/73. Therefore the number of bird-days for which these species could be supported in the winter of 1973/74 on North Area alone was necessarily less than in the previous winter, when food stocks on North and South Areas combined were greater (EVANS et al., 1979). A reduction in bird-days could have occurred in one of three ways (i) a reduction in the numbers of birds settling in autumn and early winter, but no reduction in the time for which they stayed, (ii) a reduction in the period for which each species used Seal Sands, but no reduction in the numbers settling (this would have led to death or emigration of birds earlier than usual in winter or spring), or (iii) a reduction both in numbers settling and in their duration of stay.

2. Seasonal patterns of use of Teesmouth by shorebirds: did birds stay for shorter periods than usual after reclamation?

Data from the 'Birds of Estuaries' monthly counts, from winter 1 969/70 to 1972/73 inclusive, have been used to identify the normal patterns of change in numbers of each species during the winter and spring. It would be misleading to present these as diagrams, which would invite direct quantitative comparison with the seasonal changes summarized in Figs. 3-6, because the 'Birds of Estuaries' data comprise counts for the whole of Teesmouth, whereas Figs. 3-6 refer only to birds feeding on Seal Sands. As will be discussed later, the numbers of birds feeding elsewhere on and around the Tees estuary often fluctuate seasonally much more than the numbers feeding on Seal Sands. The following general pictures emerge of the normal seasonal patterns.

Shelduck: Numbers exceed 1000 from October onwards in most years. Counts separated by only a few days often fluctuate by several hundreds, indicating that 'waves' of migrants pass though continually. Numbers fall rapidly through February and March.

Grey Plover: Autumn arrivals and passage take place in October and November. Spring departures occur chiefly in late March.

Curlew: Numbers fall steadily from an early autumn peak in August or September to minima in December and January, before rising again to a second peak in March. Most birds depart in April, as has been recorded elsewhere in northeast England (Evans, 1966).

Bar-tailed Godwit: Autumn numbers are high in September, and further arrivals take place in November, as found also at Lindisfarne, 150 km further north. The late arrivals are adults which have moulted elsewhere (Evans and Smith, 1975). Spring departures occur in February and March. Early departures from Lindisfarne, in mid-February, have occurred after recent mild winters (Smith and Evans, 1973).

Redshank: Peak numbers occur in September or October, but then fall sharply until December or early January. Numbers decline further in February, but may be increased by passage migrants in late March in some years. The picture for this species is much less consistent than for the other shorebirds.

Knot: Birds arrive in large numbers in late October or November and depart in late February or early March.

Dunlin: Potential wintering birds arrive in September and October; most leave in February or March. Passage migrants are seen in late April and May. Birds leave earlier after mild winters, as is true also at Lindisfarne; Brady (1949) recorded departures in March after cold winters, whereas in recent mild years numbers have fallen in February.

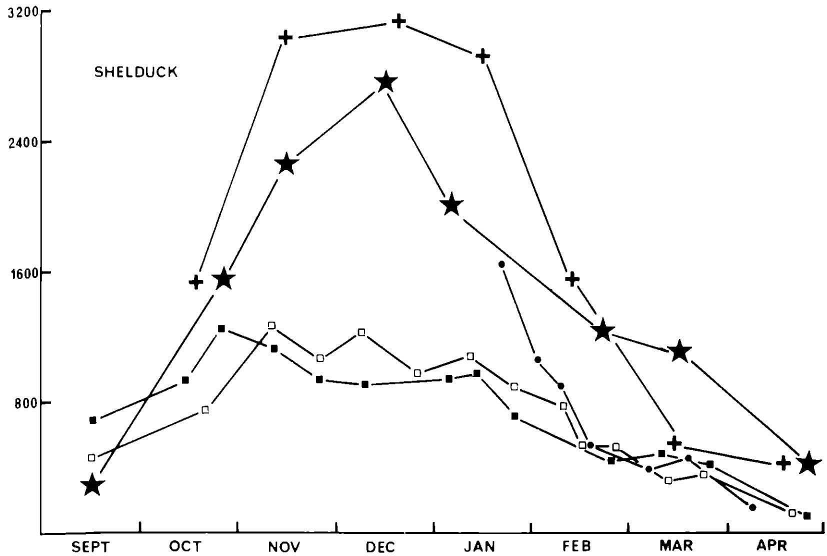

Fig. 3.
Counts of *Tadorna tadorna* feeding on Seal Sands in five winters. Key: filled circle – winter 1972/73; filled square – winter 1973/74; open square – winter 1974/75; star – winter 1975/76; cross – winter 1976/77.

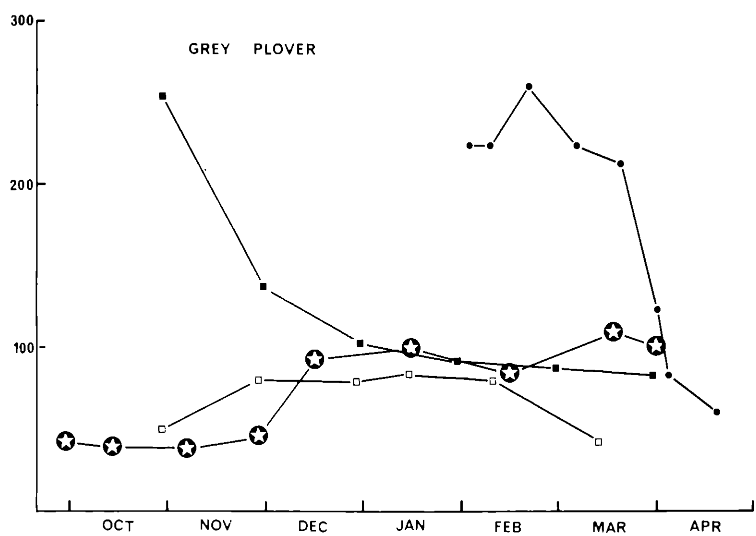

Fig. 4.
Counts of *Pluvialis squatarola* feeding on Seal Sands in four winters. Key: as in Fig. 3.

Against this background of information, inspection of Figs. 3-6 indicates that numbers of Shelduck, Grey Plover, Curlew and Bar-tailed Godwit fell no earlier than usual, either in the winter of active reclamation, or in subsequent winters. For Redshank the pattern is less consistent between winters. Numbers fell in March in 1974, immediately after reclamation finished, and in 1976, but rose in March in 1973 (before reclamation) and again in 1975. March 1973 was milder than usual and this may have stimulated an unusually early influx of passage migrants. Thus the fall in numbers in March 1974 cannot be attributed with any conviction to food shortage associated with loss of

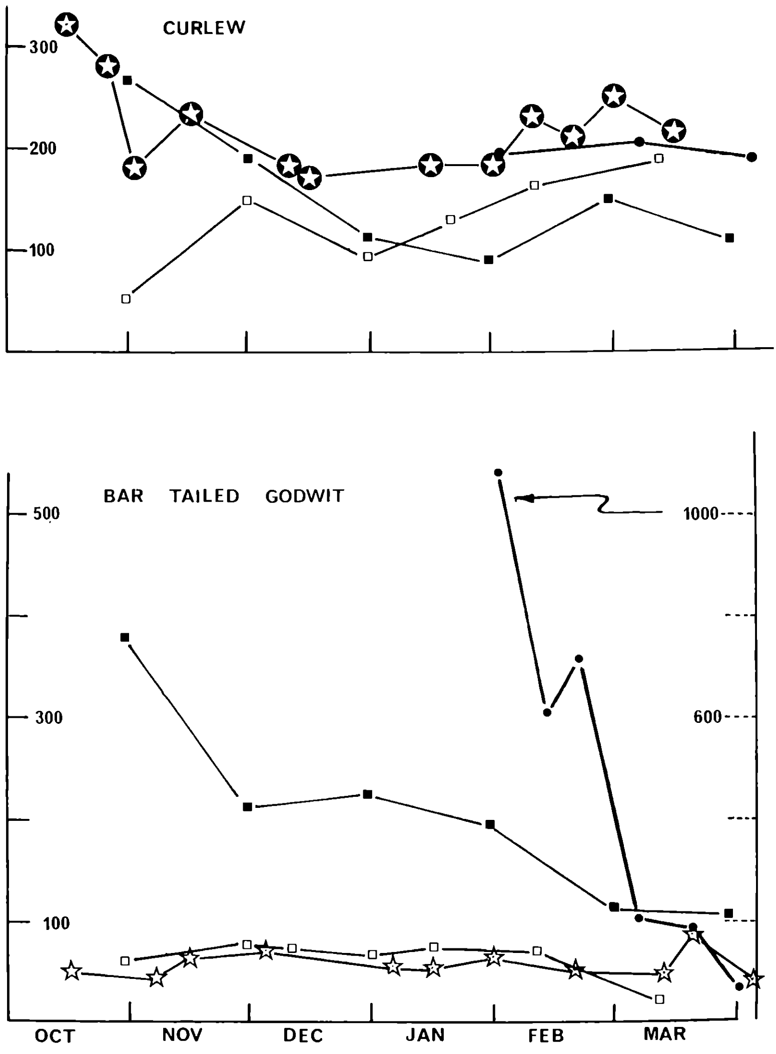

Fig. 5.
Counts of *Numenius arquata* (above) and *Limosa lapponica* (below) feeding on Seal Sands in four winters. Key as in Fig. 3.

feeding area. Only for Dunlin is there an indication that birds emigrated earlier than usual during the winter of reclamation. The sharp drop in numbers from about 8000 to about 4000 between late December 1973 and late January 1974 spanned a cold period at the beginning of January in which temperatures remained at or below freezing point for three days. It seems probable that a temporary reduction in food availability, caused by low mud temperatures, rather than a continuing decline in total food resources, caused by bird predation, provoked the Dunlin to depart. In support of this interpretation, two observations are relevant: (a) although numbers of Dunlin feeding on Seal Sands fell further in February and March 1974 (as expected), they rose again in April to 3600, even though the densities of five of the six common

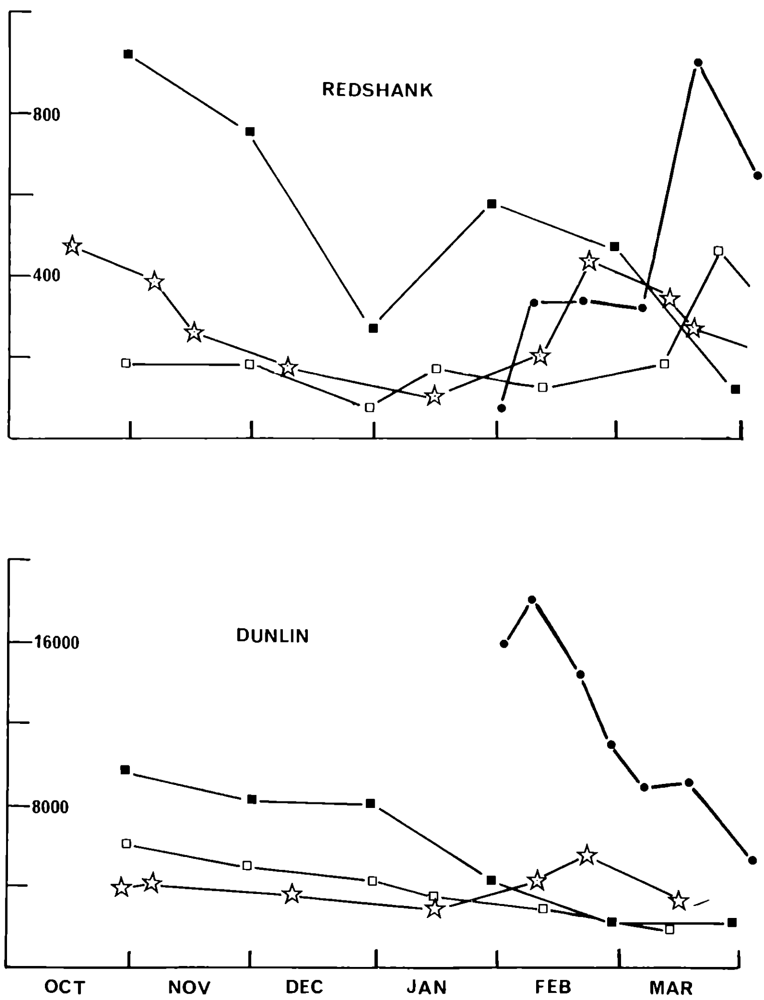

Fig. 6.
Counts of *Tringa totanus* (above) and *Calidris alpina* (below) feeding on Seal Sands in four winters. Key as in Fig. 3.

small annelids, which form their chief prey, continued to decline. (Reproduction of the sixth species, the polychaete *Manayunkia aestuarina,* took place by April [Gray, 1976], but presumably these recruits to the prey population did not provide much extra biomass.) (b) shortly after the period of cold weather, most of those Dunlin which remained on Seal Sands (3250 out of about 4000) fed in flooded fields over high water, probably to regain fat reserves used up during the cold spell, rather than because they were having extreme difficulty in obtaining their basic daily food requirements by feeding on the intertidal areas alone. The evidence for this is that the use of fields for feeding declined later in January even though the daily temperatures remained much the same. Hence it is probable that the Dunlin had difficulties in feeding only during the short cold spell at the beginning of January, when adequate food stocks on North Area became temporarily unavailable.

To summarize, for no species was there convincing evidence, in the winter of active reclamation of South Area, of premature departure of birds from North Area caused by depletion of food stocks earlier in the winter than usual. This implies that bird numbers were adjusted somehow to the food resources in autumn or early winter, before the most difficult feeding conditions were to be expected. Similar suggestions were made for Curlew and Redshank in south-east England by Goss-Custard, Kay and Blindell (1977), who found that these species distributed themselves amongst estuaries in relation to the food resources of each in autumn, before feeding conditions deteriorated.

3. The effects of reduction in potential feeding time during the period of active reclamation

When birds returned to Seal Sands in autumn 1973, although their feeding areas had been reduced by loss of the North-east Enclosure, the time for which they could feed was unaffected. The remaining Enclosures of South Area offered suitable feeding conditions at all stages of the tidal cycle, even when North Area was covered, just as they had done in the previous winter. It was not until December, during the pause in reclamation of the Enclosures, that these no longer offered suitable alternative or additional feeding areas. Thus, in December, the birds which had settled on Seal Sands in the autumn found their potential feeding time on the intertidal areas cut to about 8 hours in every tidal cycle. As documented in detail elsewhere (Goss-Custard et al., 1979), the average feeding times of the various species during a daylight tidal cycle were approximately as follows: Shelduck 5 hours; Curlew 5-6; Bar-tailed Godwit 6-8; Grey Plover 6 $^1/_2$-10; Redshank 9-11; and Dunlin 9$^1/_2$-11. (The range of values given for each species covers measurements in different months.) The reduction in feeding time was thus not expected to affect Shelduck and Curlew; nor did it. Very few Shelduck fed on the Enclosures in the autumn of 1973, and those Curlew which fed on North Area did not have to move to the Enclosures to obtain additional feeding time over high water, but instead flew directly to their high-water roosts.

The other four wader species, with longer feeding times, behaved differently. In October and November, the majority of Grey Plover, Godwit and Redshank fed only on the Enclosures, whereas the majority of Dunlin spent the low-water feeding period on North Area (Figs. 7 and 8). Almost all those birds, of all four species, which had fed on North Area at low water, moved to the Enclosures before high water and continued to

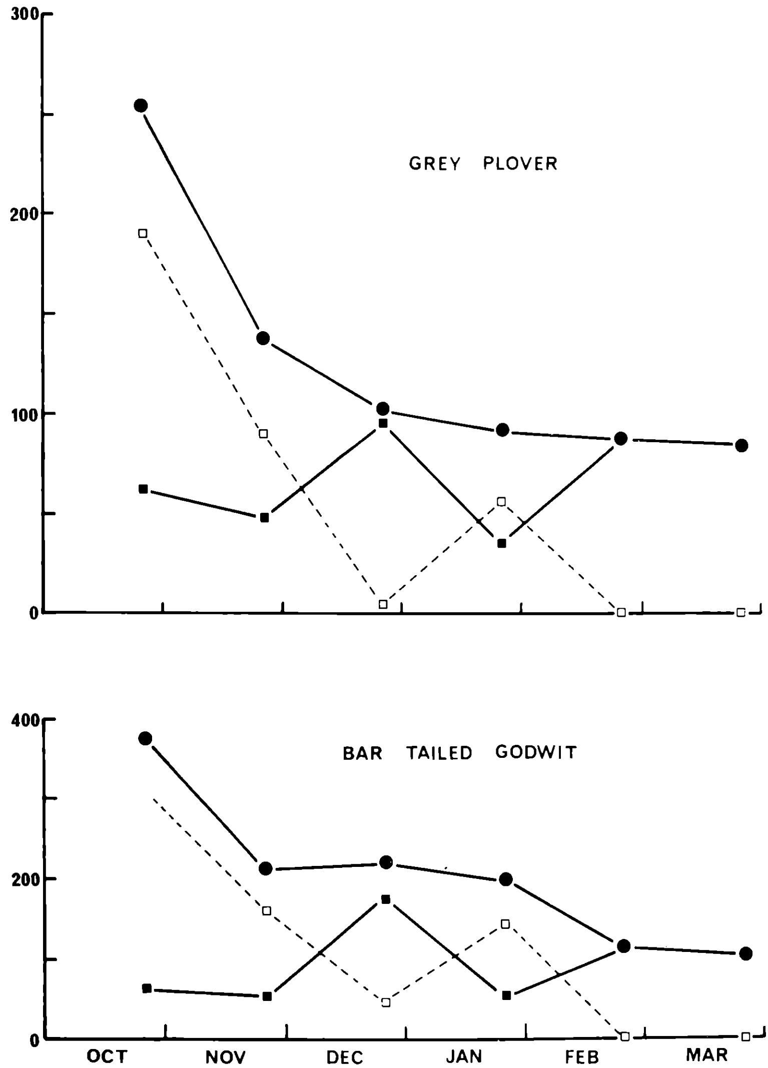

Fig. 7.
Counts of *Pluvialis squatarola* (above) and *Limosa lapponica* (below) feeding on different parts of Seal Sands in the winter of 1973/74, during reclamation. Key: solid circle – total numbers; filled square – North Area; open square – Enclosures of South Area.

feed there for as long as necessary. If they had moved to the Enclosures at the times when their feeding grounds on North Area became covered by the tide, rather than when the profitability of feeding on North Area became less than on the Enclosures, then all four species should have encountered difficulties in gaining their daily food requirements in December 1973, when the Enclosures no longer offered suitable feeding conditions. Unless they were able to exploit other feeding areas over the high wa-

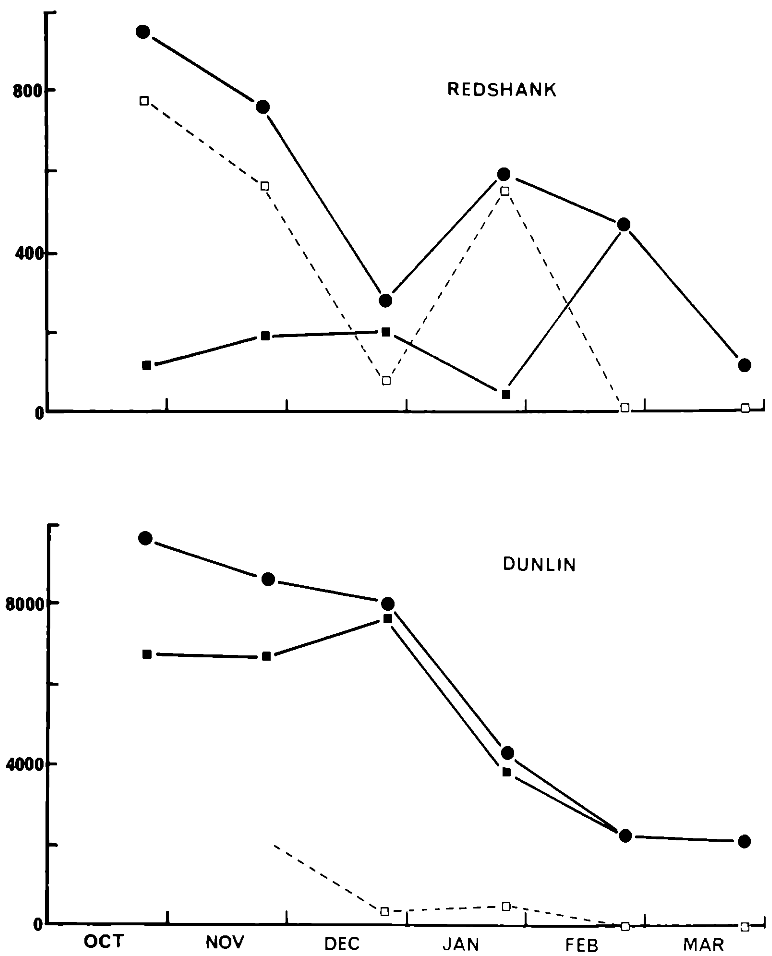

Fig. 8.
Counts of *Tringa totanus* (above) and *Calidris alpina* (below) feeding on different parts of Seal Sands in the winter of 1973/74, during reclamation. Key: as in Fig. 7.

ter period (or increase the amount of feeding at night), numbers would have been expected to fall through emigration or death.

In the event, the numbers of Dunlin supported by Seal Sands fell only slightly in December (Fig. 8); almost all of these fed on North Area while this was uncovered by the tide, and many then flew to brackish-water feeding areas, on the Brinefields and near Cowpen Marsh, at high water. Numbers of Redshank on Seal Sands fell markedly in December (Fig. 8). North Area was used at low water by approximately the same numbers of birds as in the previous month. Since many Redshank returned to feed in the Enclosures in January, it seems probable that they had not left the estuary in December, but had moved to freshwater marshes or other non-tidal feeding areas, where they spent the entire day in preference to feeding on North Area when it was uncovered. Bar-tailed Godwit numbers did not change between November and December (Fig. 7). All the birds which had fed on the Enclosures of South Area managed to obtain their daily food requirements from North Area alone in December. Nor did they use additional feeding sites over high water. In January, when reclamation of the South-east Enclosure recommenced, many Godwits returned to feed there (Fig. 7). This supports the conclusion that feeding was more profitable on the Enclosures than on North Area during at least some of the time for which possible feeding areas on the latter were uncovered by the tide. Numbers of Grey Plover (Fig. 7) fell slightly in December, though North Area was able to provide adequate feeding conditions for most of the birds displaced from the West Enclosure. Almost all the Grey Plover which fed on North Area at low water in December did not use additional feeding sites at high water, but a few individuals fed regularly on brackish pools in the Brinefields, sometimes staying throughout the day. In January, when feeding became possible in the South-east Enclosure, many Grey Plover fed there in preference to feeding on North Area.

In summary, of the shorebirds which settled on Seal Sands in autumn 1973, only Dunlin and Redshank were affected by the reduction in feeding time in December. These two species apparently could not satisfy their daily food requirements from North Area alone, in the 8-hour period for which this was uncovered in each tidal cycle.

4. The effect of reduction in feeding area during the winter of active reclamation

The temporary halt in reclamation of South Area in December 1973 provided not only the first test of the effects of a reduction in potential feeding time in the intertidal habitats, but also a test of the effect of reduction in feeding area after birds had settled on Seal Sands for the winter. Figs. 7 and 8 show that the numbers and therefore densities, of Grey Plover, Godwit and Dunlin feeding on North Area rose, in some cases appreciably, in December, when they could no longer feed on South Area. On the other hand, numbers of Redshank and Curlew feeding on North Area were very similar in November and December 1973. Numbers of birds equivalent to those which had been feeding on the Enclosures in November must have moved to feed elsewhere when they could no longer use West Enclosure. The changes (or otherwise) in density of birds feeding on North Area will be discussed further in a later section.

5. Year to year changes in numbers settling on Seal Sands

Because the numbers of birds settling on North Area appeared to be adjusted to food resources before feeding conditions were most difficult, year to year comparisons are made only of numbers present in the months of October, November and, for some species, December.

(a) shorebird populations in 1974/75 and 1975/76 winters: no change in feeding area or potential feeding time

In the two winters after reclamation of South Area had been completed, shorebirds were limited to the use of North Area alone as intertidal feeding grounds, and to about 8 hours feeding, at maximum, in every tidal cycle. Differences in numbers of birds settling between the two years must therefore have been related to differences (i) in the numbers of birds arriving in eastern England, (ii) in the abundance of their preferred foods on North Area, and (iii) to any changes in the importance of feeding interactions between species.

Of the two species which fed chiefly on the abundant small polychaetes and oligochaetes, Shelduck numbers in autumn 1975 were about double those recorded in the same month of autumn 1974, whereas numbers of Dunlin were about 1000 birds (20 %) less in November and December 1975 than in the previous autumn (Figs. 2, 6). The winter counts for the whole of Britain indicate that the Shelduck population in winter 1975/76 was about 70 % above that in the previous winter, while the Dunlin population was only slightly higher, by 1 % (Atkinson-Willes; Prater, in prep.) Possibly, therefore, the higher numbers of Shelduck feeding on North Area in autumn 1975 displaced some of the Dunlin which might otherwise have wintered there.

The relation of Shelduck numbers to food resources in the two years is not known, however, and would be difficult to interpret anyway, since, unlike the behaviour of most of the shorebirds, there is a continual turnover of the Shelduck present at Teesmouth in autumn and winter, as birds arrive from further south and depart northwards to other migration staging posts. Therefore, although comparisons are possible of the numbers present at any chosen date in two years, the relation between such counts and the total numbers of birds passing through the estuary in the two years is not necessarily identical. It is quite possible that the Shelduck which pass through later in the winter may react to the feeding conditions in a quantitatively different way from those which pass through earlier in the autumn. Certainly the total biomass of suitable food will be less for those ducks which arrive in mid-winter than for those which come earlier.

Of the three wader species which rely chiefly on *Nereis diversicolor* to provide their daily food requirements, numbers of Curlew feeding on North Area (Fig. 5) were about 75 birds (50 %) higher in autumn 1975 than in the equivalent months of 1973 (excepting October 1974, when the count was unusually low for reasons not understood). In contrast, counts of Bar-tailed Godwits feeding on North Area (Fig. 5) were slightly lower in the winter of 1975/76 than in 1974/75. From November 1974 onwards, numbers fluctuated only slightly around the 75 mark, whereas from mid-November 1975 onwards, only about 60 birds fed regularly on North Area. Numbers of Grey Plover feeding on North Area (Fig. 4) also showed only small fluctuations from late autumn onwards. In 1974/75, the relatively stable winter population was about 80 birds, whereas in 1975/76, it rose to about 100. Thus the reactions of these three shorebird species to any (unmeasured) changes in their prey populations between the two winters were not consistent: two species increased in numbers, one decreased. Counts of these species in the whole of the British Isles in these two years revealed that the Curlew population in winter 1975 was 5 % lower than in 1974, but that Grey Plover and Godwit winter numbers were unchanged in 1975. Hence, the fall in the Godwit population feeding on North Area in 1975 may well be related to the increase in the Curlew population in that winter. Curlew and Godwits use very similar feeding methods to obtain *Nereis* on Seal Sands (Goss-Custard et al. 1979), whereas Grey Plover, whose numbers increased in 1975 despite the increase in Curlew, forage for *Nereis* by a different technique and often on much firmer sandier substrates.

Numbers of Redshank, the species with the widest range of prey in its diet, in early autumn 1975 were almost double those counted in October and November 1974 (Fig. 6). This may be linked with the decrease in Dunlin feeding on North Area in 1975, as a recent study (Moumoutzi, 1977) found evidence of displacement of Redshank from preferred feeding areas by the arrival of Dunlin flocks.

(b) changes in shorebird numbers between the winters of 1972/73 and 1973/74: reduction in feeding area.

As mentioned earlier, counts of birds feeding on Seal Sands were not begun until early in 1973, so figures for autumn 1972 can only be estimated (often roughly) from the counts of roosting birds made for the 'Birds of Estuaries' Enquiry. Yet, for reasons discussed earlier, it is the counts of birds settling in autumn which need to be compared, rather than the late winter counts.

Counts of roosting Shelduck are reliable, and it may be assumed that almost all of these fed on Seal Sands. There was also reasonable agreement between the counts of feeding Redshank in February and March 1973 and the roost counts in those months, so roost counts have been used for autumn 1972. For all other species, more birds were counted while feeding on Seal Sands in the early months of 1973 than were found on the roosts, i. e. some roost sites had been overlooked. Therefore guesses are made of the size of the autumn 1972 populations by extrapolation from the February 1973 feeding counts, using the normal pattern of fluctuations in winter numbers as a guide. The estimates and guesses are listed in Table 1, where they are compared with accurate counts of feeding birds from the autumns of 1973 and 1974. (No comparison is included for Curlew, for which both roost and feeding counts were highly erratic in two of the three autumns concerned, because of irregular use of feeding areas a few kms inland.) Also included in Table 1 are population indices for the British Isles for the five species, the waders from Prater (in prep.), the Shelduck from figures supplied by Atkinson-Willes (in litt.).

Changes from 1972 to 1973 in the numbers of birds settling on Seal Sands might have arisen from changes in the numbers of birds reaching the estuary or from changes in the prey density, and size of feeding areas, on Seal Sands. (Potential feeding time was not reduced until after the birds had settled in 1973.) Even though the 1972 data for species other than Shelduck and Redshank are numerically uncertain, it is clear that the numbers of all five species were lower in 1973 than 1972, even though the numbers present in the whole of the British Isles were higher in 1973. Hence the decreases must have arisen through the responses of birds to the more restricted feeding conditions.

If similar numbers of birds had attempted to settle in 1973 as in 1972, but on a feeding area only 72 % of the former size, the average densities of each species would have risen by 100:72 = 1.4 times. Now bird density can affect feeding rate. Goss-Custard (1976) showed that Redshank searching for prey by sight fed more slowly when they were

Table 1 Estimates and counts of birds settling and feeding on Seal Sands in three autumns

	1972	1973	1974
Feeding area available	900 acres	650 acres	350 acres
	360 ha	260 ha	140 ha
Area Index	100 %	72	39
Shelduck			
Numbers	1 900	1300	1280
Index	100 %	69	68
National Index	100 %	122	114
Grey Plover			
Numbers	* 200	100	80
Index	100 %	45	36
National Index	100 %	140	160
Bar-tailed Godwit			
Numbers	** 600 (+)	220	75
Index	100 %	35 (—)	12 (—)
National Index	100 %	119	107
Redshank			
Numbers	1 000	900	190
Index	100 %	90	19
National Index	100 %	103	111
Dunlin			
Numbers	** 15 000 (+)	9700	5000
Index	100 %	65 (—)	33 (—)
National Index	100 %	125	112

Notes: * = estimate; ** = guess; all others are counts

close together. He also found evidence (Goss-Custard 1977) of a reduction in feeding rate of Knot, possibly as a result of increased encounter rates when they moved closer together. Thus an increase in bird density may make it necessary for each bird to feed for a longer time to obtain its daily food requirements. Incoming birds may therefore avoid settling in areas of existing high densities of birds. However, several species of wader have been shown to concentrate their feeding in those parts of an intertidal area where their preferred prey are most abundant and where the birds achieve their highest rates of biomass intake (Goss-Custard 1970, 1977). Therefore immigrant birds attempting to settle in an estuary may be able to avoid areas of high bird density only by settling in less rich feeding areas, where, once again, they may need to feed for a longer time to obtain their daily requirements. For these reasons, one might have expected a reduction in the numbers of birds settling on Seal Sands when their feeding areas were reduced in size in 1973, unless the average prey densities were higher in that year than in autumn 1972.

Table 1 shows that the percentage decreases in numbers of all species (except Redshank) were greater than, or equal to, the percentage reduction in total feeding area.

Therefore, the average densities of birds settling on North Area and the West Enclosure in autumn 1973 were generally less than on the whole of Seal Sands in 1972, even though, in Britain as a whole, the average settling densities of all species (except Redshank) must have been higher in autumn 1973, as indicated by the National Indices in Table 1. It will be remembered that, when the total feeding area on Seal Sands was decreased again in December 1973, by loss of use of the Enclosures, the densities of Grey Plover, Godwit and Dunlin feeding on North Area rose and remained higher for several weeks. Thus the densities when the birds of these three species settled on North Area in autumn 1973 were not the highest the food supplies of that area could support. Of course, it is not certain that these higher densities could have been supported there for the whole winter.

Reasons for the reductions in densities from 1972 to 1973 of most species settling on Seal Sands cannot be identified with certainty. Some species may have been affected by changes in prey density. Limited information on *Nereis* densities in 1972 suggests that these were higher on South Area than on North Area, and were also higher than those found on North Area in autumn 1973 (Evans et al. 1979). Thus the percentage reductions in numbers of Curlew, Grey Plover and Godwits resulting from the loss of part of South Area (the richer feeding grounds) might have been expected to exceed the value of 28 % calculated solely on the basis of the reduction in size of the total feeding areas available. While this was true for Grey Plover and Godwit, it is difficult to be sure of the exact size of the change in the Curlew population between autumn 1972 and autumn 1973. In both years, September counts are available of birds roosting on Seal Sands and adjacent marshlands; there were 377 Curlew in 1972 and 293 in 1973, a 21 % decrease. By the following springs, counts of Curlew feeding regularly on Seal Sands indicated 27% fewer in late February and early March in 1974 than in 1973 (Fig. 5). Both estimates of the size of the reduction in the Curlew population, associated with reclamation, are less than those for Grey Plover and Godwit, so the numbers of Curlew present in autumn 1973 may have affected the numbers of the other two species settling on Seal Sands, as was suggested earlier to explain the changes in numbers of these three species between the winters of 1974/75 and 1975/76.

Since Dunlin had fed chiefly on North Area before reclamation, it is perhaps surprising that their numbers were appreciably reduced in autumn 1973 from those present in the previous winter. However, linked with their decline was the increased use of North Area by Shelduck in autumn 1973; before reclamation Shelduck had fed chiefly on the North-east Enclosure of South Area. Numbers of Redshank settling in autumn 1973 were only slightly less than in autumn 1972, in spite of the 28 % reduction in total feeding area. The feeding conditions during reclamation of South Area were particularly good for this species, which used a variety of feeding methods (Goss-Custard et al. 1979) and was able to forage in deeper soft mud than the Dunlin flocks. These therefore had little opportunity to influence the Redshank feeding areas in autumn 1973, although they probably did so in other autumns.

(c) changes in shorebird numbers between the winters of 1973/74 and 1974/75: reduction in feeding area and in potential feeding time

As shown in Fig. 2 and Table 1, Shelduck numbers were very similar in the two years, in spite of the reduction in potential feeding area; however, the ducks had not used the Enclosures often in autumn 1973. The reduction in feeding time was not expected to affect this species (Goss-Custard et al. 1979). Numbers of Dunlin settling in autumn 1974 were, however, only about half as many as in autumn 1973. Although the small annelids which form their main food, and that of the Shelduck, might have been less abundant in 1974, the Shelduck were apparently unaffected. This suggests that at least part of the decrease in the Dunlin numbers was associated with the reduction in potential feeding time. Perhaps only the more experienced or adept foragers settled and stayed in 1974. The suggestion is that these individuals might have been capable of higher-than-average rates of food intake, and so managed to obtain their daily requirements in spite of the shorter intertidal feeding hours. Alternatively or additionally, the capacity of nontidal feeding sites to hold Dunlin over the high-water period, and thus provide them with additional feeding time, may have been important in affecting the numbers which settled.

Total numbers of Redshank were much lower in autumn 1974, when birds were restricted to North Area, than in 1973 when the Enclosures were also available for feeding (Table 1). However, the numbers using North Area alone were in fact higher in early autumn 1974 than in 1973. The reasons for this are not clear, but may be associated with the lower numbers of Dunlin on North Area in 1974.

Of the three species which rely chiefly on *Nereis* for food, numbers of Curlew in November and December 1974 were about 15 % less than in the corresponding months of 1973 (Fig. 5). The numbers counted in October 1974 were exceptionally low, and as they refer to only one day, it is possible that birds may have been feeding elsewhere temporarily. The stable winter numbers of Grey Plover were only 20 % less in 1974/75 than in the previous winter, but numbers of Godwits were almost 70 % less. From the estimates of the times required by these species to feed during the daylight tidal cycle, the reduction in potential feeding time had not been expected to affect them directly. The total feeding area had been reduced by autumn 1974 to just over half of that available in autumn 1973, so the average densities of Curlew and Grey Plover were higher in the second winter, but that of Godwits much lower. Again, the possibility arises that fewer Godwits settled in 1974 because of the increase in the density of Curlew on the feeding areas available. To this should be added the effects of a lower density of *Nereis* on North Area in autumn 1974 (Evans et al. 1979).

6. Changes in the wintering populations of Ringed Plover and Knot

Although several hundred Ringed Plover fed on Seal Sands during the migration seasons, only about 50 birds wintered there before reclamation. Most fed either on the Central Bank of North Area, or on the North-east Enclosure of South Area. In the winter of 1973/74, during reclamation of South Area, only occasional individuals were seen on North Area, and the situation has not improved in the following winters. It is possible that Ringed Plover suffered directly from the loss of potential feeding time, since many birds appeared to feed for most of the tidal cycle in the spring of 1972. However, they may also have reacted adversely to the increased densities of other species in later winters on their one feeding site on North Area.

Numbers of Knot using Seal Sands have also declined following the reclamation of South Area. Although the main feeding areas for this species, throughout the study period, were on the south side of the estuary (on Coatham and Redcar Rocks and on the "German Charlies"), these are available only for 4-5 hours over low water. Hence, most Knot used Seal Sands only for additional feeding, at about mid-tide, if this was needed. However, in February 1973 at least 500 birds stayed on South Area to feed throughout the tidal cycle, with perhaps 5000 commuting to and from the south side of the estuary. In the following winters few birds remained on North Area during low water, but several thousand fed there at mid-tide, at least in October and November in both 1973 and 1974. Their feeding sites on North Area coincided with the areas of highest densities of *Hydrobia* (Evans et al. 1979).

Table 2 Maximum counts of Knot at Teesmouth roost sites in different winters

Winter	1972/73	1973/74	1974/75	1975/76
Month of highest count	February	February	December	February
Numbers	4500	5600	3600	2900
Index	100 %	124	80	65
National Index	100 %	121	74	83

Since counts of Knot at roosts are likely to be less accurate than on their feeding grounds, where they are less closely packed, it is difficult to obtain exact measures of the year-to-year changes in population from roost counts. However, these are all that are available (Table 2), since the topography of the rocky intertidal feeding areas makes counts there most difficult. As may be seen, the changes in the numbers of Knot at Teesmouth have closely parallelled the changes in the total numbers of Knot in the British Isles. However, because of the recent mild winters, many of the Knot at Teesmouth have not needed to use the additional feeding time which Seal Sands could provide, so the true effects of the reclamation of South Area may not have been tested.

7. Conclusions

The information and arguments presented in this paper suggest that, at least in the mild and wet winters studied, the numbers of shorebirds settling on the Tees estuary were determined in autumn, before feeding conditions became most difficult. Environmental conditions leading to reductions in food availability and difficulties in feeding have been reviewed elsewhere (Evans 1976).

Probably only two species, the Dunlin and the Redshank, decreased in numbers after the reclamation of the South Area of Seal Sands as a direct result of the shorter time for which intertidal feeding areas are now exposed. But even these species were not lost completely, as a result of the use by some birds of alternative non-tidal feeding areas over high water. Both species were reduced in numbers by somewhat greater percentages than the 60 % loss in feeding area, whereas numbers of Shelduck rose in autumns 1975 and 1976 to levels much higher than the pre-reclamation counts (Fig. 3). These increases parallelled, but were greater than, the increases in the total British Shelduck population in the winters of 1975/76 and 1976/77. It is not known, however, whether these numbers of Shelduck on Seal Sands represented maximum sustainable densities, in relation to the total resources and density of their prey, in the two winters. As mentioned earlier, the numbers present on any date depended on the balance between continual immigration and emigration, and the control of these two processes is unknown at present. Whatever the factors affecting Shelduck densities, these were associated inversely with the densities of Dunlin settling on Seal Sands. Since both species took chiefly the same foods and used similar feeding sites, it seems probable that some form of interaction took place between them. The mechanisms have not been investigated. In their turn, the numbers of Dunlin settling on North Area have been inversely related to the numbers of Redshank which stayed to winter there. Redshank populations on Seal Sands reach a peak before the main influx of wintering Dunlin in October, and no investigation was made of the factors affecting the size of that peak. From the work of Goss-Custard, Kay and Blindell (1977), it seems probable that it is related at least in part to the density of potential prey in the available feeding areas.

Of all the species which fed throughout the tidal cycle on Seal Sands before reclamation of South Area, the Bar-tailed Godwit has suffered the greatest percentage decrease in numbers. This has occurred despite a slight increase in the numbers wintering in the whole of the British Isles (Table 1). The other species feeding chiefly on *Nereis,* the Curlew, has decreased only slightly (Fig. 5), despite the 60 % decrease in feeding area. Numbers of Curlew reach their peak in August or September, at a level presumably related at least in part to the density of potential prey (Goss-Custard, Kay and Blindell 1977), but the reasons for the decline in numbers during the autumn are not known at present. By the time the main influx of Godwits occurs, in November, the density of Godwits settling is inversely related to the density of Curlew present on Seal Sands, but the precise nature of any interactions which lead to this relationship is unknown. In turn, the density of Grey Plover which settle for the winter has often been related inversely to the density of Godwits, but whether there is a direct causal link is uncertain. Although numbers of both Godwit and Grey Plover feeding on Seal Sands remain fairly steady through a winter, unless spells of cold weather occur, numbers of both species on the whole estuary rise to a peak in January or February. This implies that Seal Sands is normally the most profitable feeding ground, and is filled first in autumn, in a manner similar to that described for Teal *Anas crecca* on tidal mudflats in Holland by Zwarts (1976).

Finally, it may be remarked that the monthly counts of shorebirds in the whole of the British Isles (Prater 1974, 1975, 1976) parallel the situation on the Tees in two interesting ways. First, the seasonal patterns of change in Redshank and wintering Dunlin numbers are almost mirror images, Redshank numbers reaching their lowest levels when Dunlin numbers are highest; and second, the seasonal pattern of change in Curlew numbers is the mirror image of the changes in numbers of Grey Plover and Bar-tailed Godwit. What emerges from the Tees study is the possibility that Redshank are pushed out by immigrant Dunlin, but that only if Curlew choose to leave are additional feeding opportunities provided for Grey Plover and Godwit.

Summary

This paper documents the effects of loss of about 60 % of an important shorebird feeding area in the estuary of the River Tees, north-east England. The maximum feeding time in the intertidal zone was also cut, from 12 to 8 hours in every tidal cycle.

Between spring and autumn 1973, the area available for feeding was cut by nearly 30 %, but the feeding time was unaltered. Numbers of *Tadorna tadorna, Pluvialis squatarola, Numenius arquata, Limosa lapponica, Tringa totanus* and *Calidris alpina* which stayed to winter in 1973 were less than in 1972, but there was no evidence of emigration in spring 1974 earlier than usual. Thus numbers were adjusted to the reduced feeding area and food resources in autumn, before the feeding conditions were most difficult.

In December 1973, the feeding time was cut. *Calidris alpina* and *Tringa totanus* were then unable to obtain their daily food requirements from the intertidal zone alone, and had to use supplementary non-tidal feeding areas over high water. When these areas froze for three days, many *Calidris alpina* left the estuary (or died).

The area of intertidal land and its period of exposure did not alter between autumn 1974 and autumn 1975. However, numbers of *Tadorna tadorna* in the second autumn were double those in the first. Increases were also recorded in *Numenius* (50 %), *Pluvialis* (25 %), and *Tringa* (100 %), but decreases in *Limosa* (20 %) and *Calidris* (20 %).

In general, increases in the density/ha of *Tadorna* were associated with decreases in the density of *Calidris* settling on the estuary. Both fed chiefly on small annelids. *Tringa* densities also varied inversely with *Calidris* densities in some years. The other three species fed chiefly on *Nereis diversicolor*. Increases in the density of *Numenius* between years were associated with decreases in density of *Limosa*. *Pluvialis* densities also varied inversely with *Limosa* densities in some years.

Factors affecting the numbers of birds settling in autumn include the total size of the population wintering in Britain, the prey density, the density of other bird species and the area of intertidal land available, which affects the density of birds.

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