Spatial and temporal distribution of shorebirds: predicting the effects of habitat change on the Forth Estuary

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Authors statement

This thesis and the data presented in it are the results of my own research except where collaborative work has been duly acknowledged. No part of this work has been submitted in any previous application for a higher degree.

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Rhys Bullman

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Firstly I would like to dedicate this thesis to my partner Gio and my long suffering children Amber and Rio who endured so many weekends without dad around and especially to Gio who never questioned my choice of career and has encouraged me all the way. Yve, Grandad and Mum gave essential financial support and have had nothing but confidence in my ability to complete this thesis.

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Chapter 1. Introduction

1.1 Overview

One of the many threats to coastal shorebirds globally is the loss or degradation of estuarine intertidal mudflats, a habitat that supports large concentrations of birds both on passage and throughout the winter months. British estuaries comprise 28% of the entire estuarine area of the Atlantic and North Sea coastal states (Atkinson *et al.* 2001), more than any other European country. Because of this, many UK estuaries are of great importance in both a European and international context for wintering birds (Pollitt *et al.* 2000). Furthermore, Britain's estuaries can be particularly important during periods of severe cold weather in continental Europe (Norman & Coffey 1994), when there may be influxes of waterfowl from other coastal regions or inland areas. Some sites also act as cold weather refuges where parts of the estuarine system freeze more slowly than other nearby coastal and inland wetlands and so can provide feeding habitat when other sites are unavailable.

Habitat change may not always mean habitat loss, even though large intertidal areas have been removed via landclaim (Evans 1979, McLusky *et al.* 1992) and engineering works (Schekkerman *et al.* 1994) or are threatened by the gradual rise in sea level (Austin *et al.* 2001). Determining the effects of habitat deterioration on shorebirds is often more difficult to predict (Sutherland 1998b) as, although the habitat remains intact, it may reduced in quality due to pollution events (McLusky 1982, McLusky & Martins 1998) or disturbance (Burger 1994, Burton 1996, West *et al.* 2002).

The consequences of habitat change on estuaries are so potentially threatening to shorebird populations that programs of managed realignment (Burd 1995) have been introduced at some sites in order to mitigate such alteration (Dixon *et al.* 1998, French 1999, Hackney 2000). Such management activity involves the breaching of existing sea walls to allow the land behind to gradually return to estuarine habitat. It has been shown that invertebrates will colonise suitable intertidal habitats and that birds are quick to adapt to such new habitats (Evans *et al.* 1998).

1.2 Estuaries

Estuaries have been variously defined in the past (Pritchard 1952, Cameron & Pritchard 1963, Prater 1981) but Day (1980) describes an estuary as:

> " ...a partially enclosed coastal body of water which is either permanently or periodically open to the sea and within which there is a measurable variation of salinity due to the mixture of sea water with fresh water derived from land drainage."

Fine sedimentary material is carried into the estuary from both the sea and rivers which then accumulates to form intertidal mudflats (McLusky 1989). This sediment load is constantly changing with respect to currents, wave conditions and the tidal state (McLusky 1989) and because of such stochasticity, estuaries can be harsh and difficult places to inhabit. However, estuarine intertidal areas are also relatively sheltered and can remain highly productive throughout the year. These sand and mudflats can be extensive and provide habitat for a range of invertebrate species which form an often abundant food source that attracts large numbers of shorebirds during migration and over the winter period, which forage on the exposed mudflats. At high tide when the flats are inundated, the coastal habitats above the high water mark and the open water of the estuary become important for continued feeding and as roosting places. Britain's intertidal areas form feeding, roosting and moulting grounds of considerable significance, especially during winter months, for western European wildfowl and waders (Davidson 1990).

1.3 The Forth Estuary

The Forth Estuary is defined as having its upper limit at Stirling and reaching its seaward limit at the Forth Road Bridge some 48km to the east (Wallis & Brockie 1997). The 'upper' estuary runs from Stirling to Alloa, the 'middle' estuary from Alloa to a line between Bo'ness and Crombie point: this section includes the largest mudflat areas at Skinflats, Kinneil and Torry Bay. The 'lower' estuary extends from Bo'ness/Crombie Point to the Queensferry road and rail bridges at the mouth of the estuary (Fig 1.1). Throughout this thesis 'Forth Estuary' refers to middle estuary area where all the study sites were located and 'Firth of Forth' refers to the whole Firth from Stirling to the open sea.

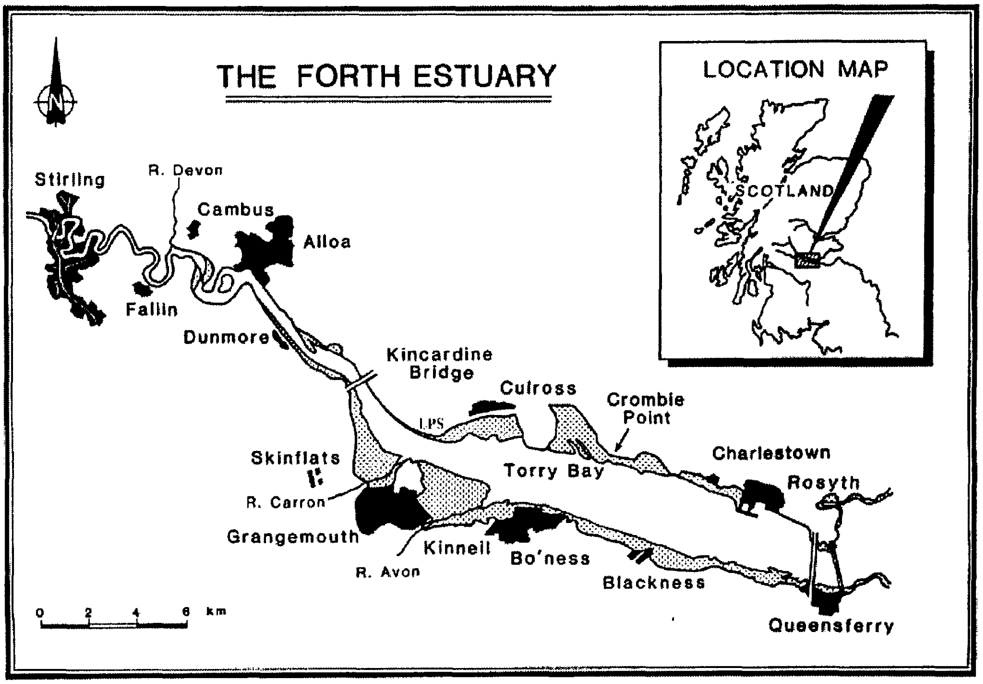


Fig 1.1: Map showing the location of the study areas within the Forth Estuary complex. The mudflat areas are hatched

The intertidal habitats throughout the middle Forth Estuary are dominated by fine grained muds (McLusky 1987). The two main study sites in this project, Kinneil and Skinflats have mean particle size diameters of 34.53µ (n = 220) and 26.66µ (n = 67) respectively; the third site at Torry Bay is mostly muddy-sand and has a mean particle size of 66.75µ (n = 40) (this study). In total, the estuary has 23.3 km^2 of mudflats, 15.1 km^2 of which are concentrated in the middle estuary 4.4 km^2 of which is at Skinflats and 6.5km^2 of which is at Kinneil (Bryant 1998). The tidal cycle within the estuary is semi-diurnal, with a mean spring tidal range of 5.0m and a mean neap range of 2.0m (Webb & Metcalfe 1987).

1.4 The importance of the Forth Estuary for birds

The estuaries of Scotland are of vital importance as staging posts for wintering migrants arriving from Greenland, north-eastern Canada, Iceland and Scandinavia. Evans (1968) in Prater (1981) identified the Forth Estuary as a major dispersal centre for waders using it to replace energy stores before moving on to other estuary complexes. Prater (1981) and Symonds & Langslow (1984) placed the Forth Estuary as one of the most important for birds in Scotland by virtue of its size, diversity of habitats and position. More recently the estuary has been ranked 12th out of 150 sites listed as the principal overwintering sites for shorebirds in the UK, all supporting over 10000 birds (Pollitt *et al.* 2001). For the Forth Estuary as a whole, Bryant (1998) identified four species of key importance: shelduck (*Tadorna tadorna*), redshank (*Tringa totanus*) and knot (*Calidris canutus*) with internationally important wintering populations and dunlin (*Calidris alpina*) with a nationally important wintering population. Shelduck also have an internationally important moulting flock on the Forth Estuary (Bryant & Waugh 1976, Bryant 1980). Curlew (*Numenius arquata*) and Oystercatcher (*Haematopus ostralegus*) also winter on the Forth Estuary in nationally important numbers. Table 1.1 shows the status of each of these species on the Forth Estuary and gives the estuary's position in the overall number of counted sites in terms of total numbers of birds. A site is considered internationally important if it regularly holds at least 1% of the NW European flyway population of a species or subspecies. In Britain an area is considered nationally important if it regularly holds 1% or more of the estimated British population (Pollitt *et al.* 2001). The mean maxima (November – March) from five winters is the measure adopted for qualification relative to this threshold.

Table1.1: This table shows the relative importance of the Forth Estuary as defined by the wetland bird survey for six species of shorebirds between 1995 and 2000 based on mean winter peak count data. The importance of the Forth Estuary for each species is ranked out of the 248 sites that are regularly counted around the UK. (from Pollitt *et al.* 2001)

Species	**International threshold**	**GB threshold**	**GB passage threshold**	**Importance**	**Mean peak count 1995-2000**	**The Forth Estuary's GB ranking for this species**
Shelduck	3000	750	-	International	4822	6
Redshank	1500	1100	1200	International	4311	5
Dunlin	14000	5300	2000	National	10900	16
Knot	3500	2900	-	International	8203	11
Curlew	3500	1500	-	National	2015	9
Oystercatcher	9000	3600	-	National	7203	8

From the early 1970s to the mid 1980s populations of some species declined on the Forth Estuary, with dunlin and knot being the most adversely affected shorebirds (Bryant 1987). Prater (1981) blamed the decrease in dunlin in the UK on poor breeding seasons in the Canadian Arctic and loss of wintering areas due to land claim schemes. Bryant (1987) also lists the following possible reasons:

- Land claim of intertidal habitats
- Changes in food accessibility, abundance or palatability.
- Changes in the flyway population.
- Movement away from the Forth Estuary due to poor weather conditions.
- Disturbance to feeding or roosting birds.
- The poisonous effects of toxic chemical inputs.

Bryant & McLusky (1997) considered long term population changes in waders (*Charadrii*) on the Forth Estuary over 22 years. Population changes at the whole estuary scale were largely reflected in changes at Kinneil and Skinflats highlighting the importance of these sites and their relevance to the present study. Knot declined at both sites and although fluctuations in the populations of other waders did occur they were partially explained by changes in the national index of abundance (Prys-Jones *et al.* 1994). Although it has been shown to have detrimental consequences on shorebird survival elsewhere (Mitchell *et al.* 2000, Stillman *et al.* 2001, Kelly *et al.* 2002), cold weather locally was found to have no significant effect and there was little evidence of density dependent site usage. Austin *et al.* (2001) however found that other aspects of the weather other than temperature also affected wader survival and noted that decreasing mean annual rainfall was beneficial to waders as high rainfall decreases prey availability. They also found that oystercatcher numbers increased at sites where mean wind speed was lowest. Bryant & McLusky (1997) also found that human disturbance and the effect of avian predators were unimportant but the main focus of the study, the effects of changing food densities showed that four species increased with increases in food abundance. At Kinneil, redshank and bar tailed godwit (*Limosa lapponica*) increased with favoured prey items as did numbers of knot and oystercatcher at Skinflats. For knot it was determined that local changes in food abundance were more important than changes in flyway populations. This study shows that changes in wader populations in winter are dependent on changes in food supply and it is consistent with an earlier study (McLusky & Bryant 1992) on the negative effect of land claim at Torry Bay and Kinneil. When populations at Torry Bay were considered five years before and two years after the loss of 20% of its intertidal area it was found that numbers of turnstone (*Arenaria interpres*), oystercatcher, bar tailed godwit, knot and dunlin all declined by >20%. The latter two species also declined with the national index. Wigeon (*Anas penelope*) and redshank remained stable, whereas curlew increased by 124%.

The prediction that species will decline in direct proportion to habitat loss was not upheld by this study, as there was no change in the numbers of redshank even though 44% of their preferred feeding areas had been in the land claim area. This suggests that the site may have been at a level below 'carrying capacity' for this species. However it may just be that they fed more intensively post-reclamation or switched prey. There may also be a time delay in any effect caused although numbers of redshank using the remains of the reclaimed area at Torry Bay were still broadly similar in 2000 compared to numbers pre-habitat loss. 'Carrying capacity' of estuaries has been defined in many ways and the term is still used to describe a range of situations (Dhont 1988). For overwintering shorebirds the carrying capacity of a site has been defined as either the maximum number of bird days it can support throughout the winter or the maximum number of birds that can survive to the end in good condition (Goss Custard & Charman 1976, Goss Custard 1985). A site is often deemed to have reached its carrying capacity when the addition of a further individual will result in the death or emigration of another (Goss Custard & Durell 1990, Sutherland & Goss Custard 1991). However the equilibrium population size at a site may be reached before the estimated value for carrying capacity (Sutherland 1996, Goss Custard *et al.* 2002), therefore it cannot be assumed that because carrying capacity was not reached a change in the size or condition of a site would not affect the birds using it.

1.5 The Avifauna of the Forth Estuary

The Forth Estuary is used as an overwintering area and passage stopover site for a wide variety of shorebirds and waterfowl. This study focuses on the four key species identified by Bryant (1998) that use the estuary in nationally or internationally important numbers. The following species were chosen as they were the most readily observed and regularly used all the sites included in the study.

1.5.1 Shelduck

The Forth Estuary has an important moulting flock of shelduck that were first noted at Kinneil by Bryant and Waugh (1976). Many shelduck migrate from the Forth in the autumn to moult on the German Wattenmeer, returning during the winter. Many of these birds breed locally (Symonds & Langslow 1984). Shelduck have been shown to use a sequence of estuaries during the non-breeding period (Evans & Pienkowski 1982).

1.5.2 Redshank

Two races of redshank overwinter on the Forth Estuary: *Tringa totanus totanus* from the Scottish breeding population and *T.t.robusta* which breeds in Iceland (Hale 1973). Proportions of the two races vary in mixed flocks throughout the winter and present work suggests that although some Scottish birds do stay throughout the winter, the majority of birds that overwinter on Scottish estuaries are of Icelandic origin (Summers *et al.* 1988a). Icelandic migrants start to appear on the coast as early as July and begin to return to their breeding grounds from March onwards. Colour marking of birds showed that they exhibit winter site fidelity and tend not to move around the estuary (Symonds *et al.* 1984).

1.5.3 Dunlin

The dunlin that overwinter on the Forth Estuary belong to the nominate race *Calidris alpina* which breed in Russia and Fenno-Scandia (Hardy & Minton 1980). Many of these birds use the Wash as a staging post before moving up to the Firth of Forth where they remain from November to March (Symonds & Langslow 1984). Marking studies within the estuary at Skinflats and Torry Bay show them to be site faithful throughout the winter, with 91% of marked birds remaining at Skinflats and 83% staying at Torry Bay; none of the marked birds moved to the outer estuary (Symonds *et al.* 1984). Most of the dunlin that winter on the inner estuary have left for their breeding grounds by late March.

1.5.4 Knot

The knot that winter on the estuary belong to the nominate race *Calidris canutus* that breeds in Arctic Canada and Greenland. Many birds move north to the Forth Estuary after staging on the Wash. Knot are a highly mobile species and move around the estuary from site to site such that numbers can fluctuate quite considerably within sites during the winter months (Symonds *et al.* 1984). Although fairly regular at the sites observed in this study they were occasionally absent from feeding areas and roosts for a number of days only to return as suddenly as they had disappeared. Knot may also move between estuaries during the course of the winter (Dugan 1981).

It is clear that populations of different species on the Forth Estuary may fluctuate on a year to year basis for many different reasons such as breeding performance, previous winter mortality, changes in local invertebrate abundance, habitat loss and disturbance (Fig 1.2.) Actual numbers will, of course, have a bearing on the way the birds distribute themselves and how great the effect of habitat loss might be in a given year, due to the increase or decrease in competition for resources and space.

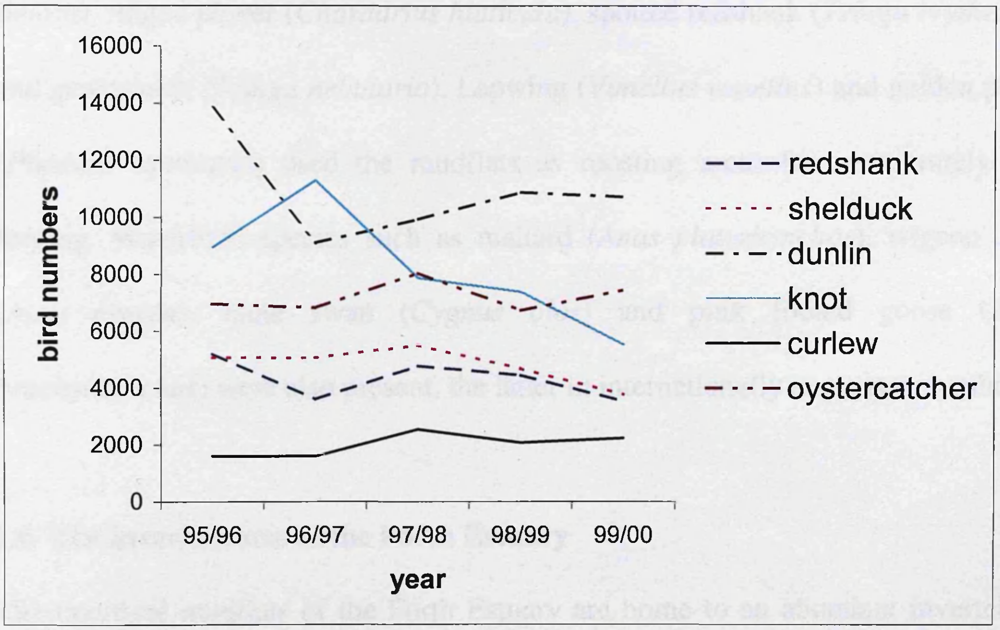


Fig 1.2: Wetland bird survey (WeBS) data for the Forth Estuary illustrating fluctuations in the winter maxima of redshank, shelduck, dunlin , knot, oystercatcher and curlew from 1995 to 2000 (data from Pollitt *et al.* 2000)

1.5.5 Other shorebird species

There are also nationally important numbers of curlew and oystercatcher on the Forth Estuary (Fig 1.2). These waders normally feed either as singletons or in small groups, often supplementing their diet by feeding inland away from the mudflats. Ringing recoveries on the Forth Estuary suggest that the overwintering population of oystercatcher come mostly from Scotland and in particular the Grampian region, Tayside and the Northern Isles (Symonds & Langslow 1984). There are also some recoveries showing birds from the Faeroes, Iceland and Norway also use the estuary. They are very site-faithful to feeding and roosting areas and return to the same sites year after year (Symonds *et al.* 1984). The majority of curlew on the estuary are likely to be local breeding birds although there is evidence of Swedish and Finnish birds also wintering (Bainbridge & Minton 1978). Other species seen feeding on the estuary during the study were bar tailed godwits and black tailed godwits (*Limosa limosa*), ringed plover (*Charadrius hiaticula*), spotted redshank (*Tringa erythropus*) and greenshank (*Tringa nebularia*). Lapwing (*Vanellus vanellus*) and golden plover (*Pluvialis apricaria*) used the mudflats as roosting areas but were rarely seen feeding. Waterfowl species such as mallard (*Anas platyrhynchos*), wigeon , teal (*Anas crecca*), mute swan (*Cygnus olor*) and pink footed goose (*Anser brachyrhynchus*) were also present, the latter in internationally important numbers.

1.6 The invertebrates of the Forth Estuary

The intertidal mudflats of the Forth Estuary are home to an abundant invertebrate fauna; which at Kinneil and Skinflats has for many years been subject to varying degrees of pollution via point sources from industrial activity adjacent to the mudflats (McLusky 1987, McLusky & Martins 1998). Invertebrate populations form the rich food source upon which overwintering shorebirds are so reliant for self-maintenance during this period. Numbers of individual species have been estimated at Kinneil on an annual basis over the last 25 years by McLusky *et al.* (2000) (Fig 4.34) and although populations appear to fluctuate the species composition has remained relatively stable. All the species that were commonly found in this study and were regarded as potentially important prey items for birds are listed in Table 1.2. See also Tables 4.5 and 4.6 for species found in other studies such as Bryant (1979) and Bryant & McLusky (1997). See also McLusky (1987), McLusky *et al.*

(2000) and Davis (2001) for other benthic invertebrate species present on the Forth Estuary.

Table 1.2. Invertebrate species commonly found at all study sites and during sampling in the winters of 1998/1999 and 1999/2000 (this study, Warnes 1981, Elliot 1979). Size ranges on the Forth Estuary are given where known.

Species	**Name given in the text**	**Common name**	**Details**	**Size range in the Forth Estuary (mm)**
Hydrobia ulvae	*Hydrobia*	laver spire shell	a small prosobranch mollusc	<1mm to 4mm
Macoma balthica	*Macoma*	Baltic Tellin	a deposit and suspension feeding bivalve mollusc	1 to 10mm.
Cerastoderma edule	*Cerastoderma*	Cockle	Principally a suspension feeding bivalve mollusc	5 to 30mm along the major axis.
Nereis diversicolor	*Nereis*	Ragworm	essentially a carnivorous polychaete worm which can exploit a wide range of foods. Also capable of suspension feeding	-
Manayunkia aestuarina	*Manayunkia*	-	small tube dwelling sabellid polychaete	c 2mm
Corophium volutator	*Corophium*	-	crawling and burrowing amphipod, chiefly a deposit feeder	up to 8mm
Pygospio elegans & Streblospio shrubsolii	Spionids	-	fairly ubiquitous spionid polychaetes	-
Tubificoides benedini	Oligochaetes	-	segmented oligochaete worm	-
Mytilus edulis	*Mytilus*	edible or blue mussel	a bivalve suspension feeder found in aggregations where the substrate is sandier	Up to 35mm
Nephtys hombergii	*Nephtys*	-	Carnivorous polychaete worm	-
Eteone longa	*Eteone*	-	Carnivorous polychaete worm	-

It might be expected that there will be some considerable variation in the diversity and density of macro-invertebrate species, on both a spatial and temporal scale, as their presence is highly dependent on their tolerance of the environmental variables that determine their ability to survive (McLusky 1992). The predominant factors on most estuaries controlling the intertidal community are exposure (i.e. tide height above mean chart datum) and salinity (McLusky 1989).

The spatial variation, abundance and temporal stability of invertebrate populations on the Forth Estuary are discussed in following chapters.

1.7 Threats to estuarine intertidal areas

Throughout the world estuarine habitats are being damaged and lost due, ostensibly, to anthropogenic activities (Goss Custard & Sutherland 1997). Table 1.3. lists a number of activities that can potentially cause or contribute to shorebird habitat loss on estuaries. Such activities may lead to a reduction in feeding or roosting areas causing birds to redistribute within the remaining mudflat, move to another mudflat or leave the estuary altogether.

Table 1.3. : Potential threats to the intertidal mudflats on the Forth Estuary (adapted from Elliot *et al* 1998)

Activity	**Impact**	**Affect of change on the physical environment**	**Affect on benthic community**	**Affect on birds**
Land-claim (Industry or Agriculture)	Can be high or low	Reduction of habitat integrity	Reduction due to loss of intertidal	Loss of feeding/roosting area and potential lowering of carrying capacity due to area loss
Industrial and domestic effluent	Can be high	May render areas devoid of invertebrate life and may act in tandem with other stressors	Can decrease the species richness via lethal and sub-lethal effects	May reduce or taint prey species and potentially make areas of the mudflat unusable
Organic enrichment	Can be high	May encourage anoxia in sediments	Can decrease or increase species richness depending on concentration	May be detrimental to shorebird prey species
Mining activity	Low	May cause subsidence of existing mudflat area	May change community structure due to changes in exposure time/salinity etc.	Potential loss of feeding time and feeding area
Recreational, engineering and other disturbance	Can be high	Some activities may scour the mud surface	Affects likely to be minimal	If persistent, disturbance can keep birds away from preferred feeding areas.
Sea level rise	Potentially very high	Reduction of habitat size	Reduction due to loss of intertidal	Loss of feeding/roosting area and potential lowering of carrying capacity due to area loss

1.7.1 Land Claim

Land claim has posed a significant threat, in terms of habitat loss, to overwintering shorebird populations on numerous UK and European estuarine sites (Evans 1979, Goss Custard *et al.* 1989, Goss Custard & Yates 1992, McLusky *et al.* 1992, Metzmacher & Reise 1994, Schekkermann *et al.* 1994, Burton *et al.* 1996, Yates *et al.* 1996, Percival *et al.* 1998). On the Forth Estuary land claim events have reduced the intertidal area by 22.8 km^2; almost 50%, over the past two centuries (McLusky 1987). Mudflat areas including the docks at Grangemouth and the Kincardine and Longannet power stations have been claimed for agriculture and industry. These developments include the fly ash lagoons at Torry Bay, which accounted for the loss of 2.41 km^2 at this site, with domestic refuse tipping accounting for the loss of 1.74 km^2 at Kinneil (McLusky *et al.* 1992). The main effect of land claim on the shorebirds of the Forth Estuary, apart from the immediate disturbance caused during construction work, is the potential loss of feeding and roosting areas that may lead to the reduction in the 'carrying capacity' of a site (Burton 2002). Birds may be forced to leave a favoured area due to increased competition resulting from area loss (but see Goss Custard *et al.* 2002)

1.7.2 Industrial effluent

Industrial effluents can have toxic effects on the populations of the benthic macrofauna upon which overwintering shorebirds depend for food (Chapman *et al.* 1994, Sherry *et al.* 1997) and such effects can be lethal (Garric *et al.* 1996) or sub-lethal (Conradi & Depledge 1999).

Much of the industrial effluent that finds its way onto the Forth Estuary intertidal originates from the petro-chemical works at Grangemouth. These effluents include heavy metals such as selenium, vanadium and zinc, also oils, greases, phenols, cyanides and nitrogen compounds (Cote 1976, Bleckmann *et al.* 1995, Siljeholm 1997, Davis 2001). During the last 30 years monitoring of these effluents has shown a considerable effect on the benthic macrofauna and hence the birds at this site (McLusky 1982, McLusky & McCrory 1989). Many pollutants can bio-accumulate in the food chain effecting both invertebrates (Krause 1994, Conradi & Depledge 1998, Conradi & Depledge 1999, Galloway & Depledge 2001) and birds (Ferns & Anderson 1994, Spahn & Sherry 1999, Hui *et al.* 2001). Intertidal mudflats which have a low energy environment and fine silt are very susceptible and may act as a sink for such pollutants (McLusky 1982). Some high level areas at Kinneil have been severely affected by effluent in the past with large areas of mudflat considerably depleted in invertebrate numbers (McLusky & Martins 1998). In recent years however, improvements to effluent discharge methods have seen the return of invertebrates to areas previously rendered unusable (McLusky *et al.* 2000).

1.7.3 Sewage and organic enrichment

Estuarine food webs may respond directly to organic enrichment (Riera *et al.* 2000) and such responses have been the subject of much study (Cloern 2001). Nutrient enrichment on the Forth Estuary, be it in particulate or dissolved form, is derived from a number of sources including sewage input and rivers and burns (for Kinneil see Fig 1.3.). The effect that this has on the macrobenthos is dependent on the level of this enrichment and whether or not it is discharged into the water column and thus diluted. A strong enrichment effect can reduce species richness and diversity

(Elliot *et al.* 1998, Mucha & Costa 1999) and encourage opportunistic species such as *Manayunkia.* Opportunists decrease with distance from the pollution source allowing species to finally reach a population level similar to an area of no pollution. Moderate increases in organic matter provide food and can increase abundance and diversity of organisms (Elliot 1994). This can have implications for the number of birds that a benthic site can support (Van Impe 1985, Hill *et al.* 1993) allowing increases in bird populations due to increased food supply (Harrison & Grant 1976, McKay *et al.* 1978). Sewage treatment can have the opposite effect and cause local declines in bird populations (Campbell 1984, Raven & Coulson 2001), especially if preferred invertebrate prey items are limited in their colonisation rate by levels of organic matter (Evans *et al.* 1998). Enrichment can also be accompanied by an increased coverage of green macroalgae such as *Enteromorpha sp.*, which can create anoxic conditions for the macrofauna (Martins *et al.* 1997, Lehvo & Back 2001), potentially inhibiting shorebird feeding activity. There is evidence of an algal mat at Torry Bay stretching approximately 300m out onto the mud from the shoreline and at Kinneil there is a 400m thick band along the seawall adjacent to the lagoon between the sewage works and Bo'ness bing. Both these areas of algal mats are however quite patchy and are currently well used by birds so there is no obvious detrimental effect. At Torry Bay the algal mat is fed on by wigeon at high tide.

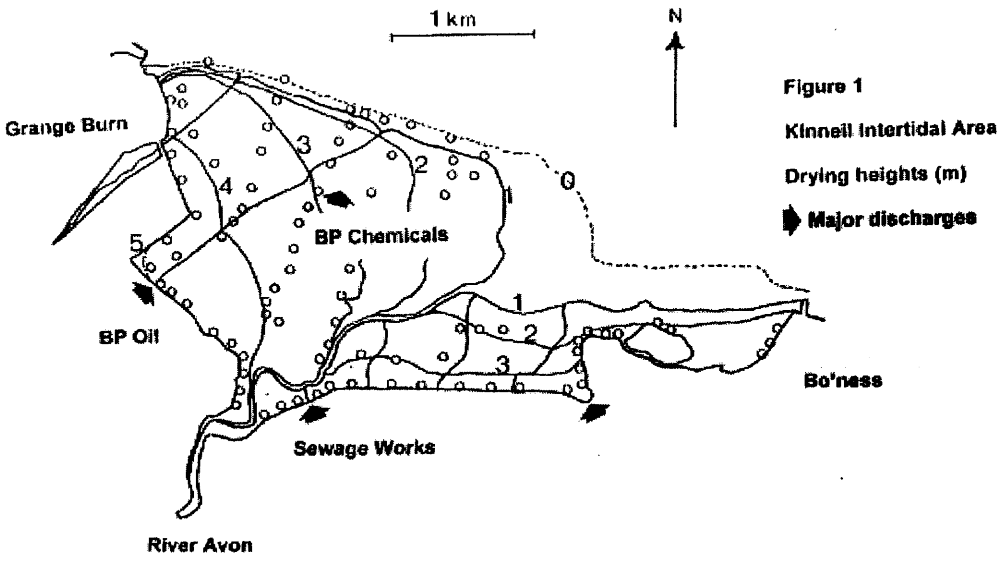


Fig 1.3: The major sources of effluent and organic input onto the Kinneil mudflat (from McLusky *et al.* 2000)

1.7.4 Mining activity

This is likely to be rare threat to intertidal mudflats in terms of direct mudflat damage or alteration. However until the recent flooding and subsequent closure of the Longannet coal mine opposite Skinflats, these workings did pose a potential threat. Extension of the coal mine under Skinflats could possibly have caused areas of the mudflat to subside allowing quicker inundation by the incoming tide therefore reducing the amount of feeding time available for shorebirds (Bryant 1998). Metals such as lead and zinc in mine leachates can also contaminate the estuarine mud and hence its macrofauna (Berry & Plater 1998, Warwick 2001, Ruiz 2001, Mol *et al.* 2001, Brown & McLachan 2002).

1.7.5 Recreational and other disturbance

Human disturbance does influence the spatial distribution and overwinter mortality of shorebirds (Burton *et al.* 2002) and even small disturbances can have a negative effect on the feeding behaviour of species such as the Oystercatcher (Goss Custard *et al.* 2002), turnstone and purple sandpiper (*Calidris maritima*) (Burton *et al.* 1996), semipalmated sandpipers (*Calidris pusilla*) (Shepherd & Boates 1999) and knot (Pfister *et al.* 1992, Burton *et al.* 1996). Although the potential consequences for birds are loss of feeding time and/or increased energy expenditure due to constant movement to avoid disturbance, this type of problem is not considered to be important on the Forth Estuary (Bryant 1998 & pers obs). This is mainly due to the fact that any human recreational disturbance would most likely occur during the summer months and because the mudflats are generally inaccessible to the public. The only human activity that may have a detrimental effect on the birds is shooting activity both legal and illegal, which can cause considerable disturbance to feeding waterfowl, particularly over high tide. The shooting pressure noted during this study (in the winters of 1998/1999 and 1999/2000) was focused mainly at Skinflats and Torry Bay. At Torry Bay, shooting mainly occurs near high tide as large rafts of wigeon move up the shore to feed on the *Enteromorpha* and as greylag geese (*Anser anser*) move in to roost on the water. At this site the concentration of guns is c 1-1.5km away from the main shorebird high water feeding areas and roosts and was never noted to cause any disturbance to them. At Skinflats shooting pressure was a little more intense as very large numbers of geese feed in the fields behind the mudflat and moved back and forth across the area whilst flying between feeding areas. Many of them also roost on the water over the mudflat as the tide rises. Shooting was observed all the way along the seawall within the bounds of the RSPB nature reserve area, often involving the shooters walking out on to the mud. There was also evidence of clay pigeon shooting as the remains of the clays were often found out on the mud (pers obs). Shooting pressure was apparently low and didn't appear to cause any major disturbance to the birds that fed on the mudflat areas. There was however some considerable disturbance to the birds feeding and roosting on the saline lagoons in the fields behind the intertidal. Shelduck, redshank, godwits and numerous species of duck that were the quarry of the shooters mostly used this area. Shooting was not observed at Kinneil although shooting hides were in position in the area adjacent to the main roost. Any shooting in this area at high tide would cause considerable disturbance to the roosting birds. Engineering works and heavy vehicles operating within the Grangemouth harbour and petrochemical works were not seen to disturb feeding birds at Kinneil or Skinflats and trains passing the mudflats at Torry Bay appeared to have no effect on bird distribution. However birds may have adjusted their feeding distribution to respond to low levels of constant disturbance. Where the disturbance was unexpected such as the ignition of gas flares adjacent to Kinneil, the birds would react by flying away from the disturbance but generally returned to their preferred feeding area within several minutes (pers obs).

1.7.6 Sea level rise

Sea level rise is another potential cause of habitat area loss which is most likely to occur if the rising sea level is contained by a sea wall (Austin *et al.* 2001, Galbraith *et al.* 2002). This would reduce the amount of time the mud was exposed for shorebirds to feed perhaps forcing them to feed for longer periods both during the day and night.

Projections of sea level rise in Scotland through the 21st Century, based on a regional climate change impact model using an emissions scenario, have been predicted by Hill *et al.* (1999) and Dawson *et al.* (2001) (Table 1.4.)

The relative sea level rise in Scotland will, however, in many parts be less than the values in Table 1.4, owing to continued isostatic rebound of the land mass. Since the country is experiencing differential rates of uplift, future sea level rise will vary according to locality.

Table 1.4: Projected relative sea level rises (mm) around Scotland to 2050: comparison of data of Hill *et al.* (1999) with those of Dawson *et al.* (2001).

Area	**Predicted rise in mm (Hill *et al.* 1999)**	**Predicted rise in mm (Dawson *et al.* 2001)**
Upper Forth Estuary	200 - 249	< 145

If these rates of uplift remain constant for the next 50 years, rises in land levels of 50-120 mm and 40-110 mm, respectively, are to be anticipated. However, if an eustatic sea level rise of *c.*300 mm is assumed over the next 50 years the net effect will be a rise in sea level of 180-250 mm at Stirling and 190-260 mm at Kincardine. The vulnerability of the Forth Estuary to coastal flooding upstream of Rosyth was referred to by Price & McInally (2001), but no site-specific figures for sea level rise were given.

1.8 Factors likely to influence the spatial distribution of birds : What determines how birds distribute themselves at the estuary and sub estuary scale ?

Due to the genetic and phenotypic variability between and within different species, variation is likely to exist in competitive and foraging abilities among the species that inhabit the Forth Estuary during the winter months. This is likely to lead to a degree of ecological segregation. Different species may choose to feed at different times of the day (McNeil *et al.* 1992) and stages of the tidal cycle (Piersma *et al.* 1993, DeVlas *et al.* 1996) depending on their choice of prey species and preferred size of the prey (Zwarts & Blomert 1992). They may also distribute themselves according to habitat characteristics such as sediment structure (Yates *et al.* 1993 & 1996, Scheiffarth *et al.* 1996), proximity to freshwater or creeks (Robertson 1997) or prefer to be a certain distance from their roost (Rehfisch *et al.* 1996) or areas of cover for potential predators (Cresswell & Whitfield 1994). A broad understanding of why and how birds distribute themselves around the estuarine complex, especially at the site (sub estuary) level is of importance when developing models to assess the relative importance of an area of mudflat to a given species. If the potential effect of land claim is to be predicted, then such a model should be developed using all relevant information on the potential preferences of that species when overwintering on the estuary.

1.8.1 Food : prey density and prey size

The presence of favoured invertebrate prey species has been shown to be a predictor of bird distributions within estuaries (Bryant 1979, Yates *et al.* 1993, Cummings *et al.* 1997) and between estuaries (Schnieder & Harrington 1981, Goss Custard *et al.* 1991). This is the case for a variety of different species: redshank (Goss Custard *et* *al.* 1977), curlew (Goss Custard *et al.* 1977), oystercatcher (Sutherland 1982, Goss Custard *et al.* 1992, Meire 1996 Triplet *et al.* 1999), western sandpiper (*Calidris mauri*) (Colwell & Landrum 1993), sanderling (*Calidris alba*) (Botton *et al.* 1994) and curlew sandpiper (*Calidris ferruginea*) (Kalejta & Hockey 1994). Spatial variation in the abundance of non-breeding shorebirds can be predicted to varying degrees by the density of their prey species (Colwell & Landrum 1993, Piersma *et al.* 1993, Botton *et al.* 1994, Weber & Haig 1997) and shorebirds may even have a role in structuring the invertebrate community (Thrush 1999) along with covariates such as salinity (McLusky 1989) and sediment structure (Warwick *et al.* 1991). Aggregative responses of predatory birds to their prey are stronger at some spatial scales than others. In waders feeding on benthic invertebrates, aggregative responses decrease in strength at scales less than 100m (Cummings *et al.* 1997). They determined that there was no response by waders to small-scale increases in prey patchiness, where larger scale changes in patchiness were controlled for. They hypothesised that a lower limit on the spatial scale of aggregative response is set by the mobility of prey relative to the predator and that the patch structure of a relatively immobile prey will change on a much smaller scale than that of a highly mobile prey. They also suggested that their respective predators become adapted accordingly. Although density of prey may initially attract birds to feed, the size of the invertebrates also has a bearing on where shorebirds choose to feed (Goss Custard *et al.* 1991, Rippe & Dierschke 1997, Weber & Haig 1997, Davis & Smith 2001).

When trying to establish a relationship between bird density (or time spent feeding) and the density or distribution of a particular invertebrate, it is important to have a good comprehension of the dietary flexibility of the species to understand the basis of any significant relationships. Bird abundance and diversity may be influenced more by the abundance and availability of specific prey items, than by species diversity. Estuarine birds are mostly able to switch prey depending on local circumstances (Bunskoeke *et al.* 1996) and therefore have dietary plasticity; so the presence of a particular taxa of prey is not necessarily going to be a good predictor of the bird community. This is because feeding density may be related to more than one invertebrate species. As the diversity of prey species is quite low on the Forth Estuary it is possible that prey size is just as important as invertebrate abundance in shorebird dietary segregation.

It is extremely difficult to observe accurately which invertebrate species shorebirds are selecting by observation alone. The birds mostly feed at some considerable distance from the observer and it is often impossible to identify what is being eaten. Probing birds such as the curlew may swallow the prey item before bringing it to the surface and although they sometimes wash their catch before swallowing (pers obs) it would be very difficult to distinguish the polychaete worm *Nereis* from *Nephtys* or *Eteone*. Even if the birds are picking prey items from the surface of the mud such as redshank feeding on *Hydrobia* or *Corophium* it can be hard to tell which pecks and probes are successful. Alternatives to field observations include gut analysis (Rundle 1982), the examination of faecal pellet contents (Warnes 1981, Dekinga & Piersma 1993) and video analysis (Wilson & Vogel 1997). Such investigations were not made in this study as work has already been done on the dietary preferences of birds feeding on the Forth Estuary (Bryant 1979, Warnes 1981) (Table1.5.).

Table 1.5: Prey items taken by the four key species of shorebirds at Skinflats, Kinneil and Torry Bay (Bryant 1979 & Warnes 1981). Selected size classes are given where known.

Bird species	**Selected invertebrate prey**	**Selected invertebrate size class**	**Site on the Forth Estuary**
Redshank	*Hydrobia*	>2.5mm	Skinflats and Kinneil
	Macoma	5 – 9mm	Skinflats and Kinneil
	Nereis	-	Skinflats and Kinneil
	Corophium	> 4mm	Skinflats and Kinneil
Knot	*Macoma*	$5.48^{+/-}$0.78mm	Skinflats and Kinniel
	Macoma	$8.45^{+/-}$1.42mm	Torry Bay
	Hydrobia	> 1.8mm	Skinflats
	Cerastoderma		Kinneil and whole estuary
Dunlin	*Hydrobia*	$2.2^{+/-}$0.77mm	Skinflats
	Nereis	-	Skinflats, Kinneil and whole estuary
	Macoma	-	Skinflats and Kinneil
	Oligochaetes	-	Skinflats
	Manayunkia	-	Skinflats
Shelduck	*Hydrobia*	0.6 – 4.4mm	Skinflats
	Oligochaetes	-	Skinflats
	Manayunkia	-	Skinflats

Although there is much correlative evidence linking bird distributions to their invertebrate prey, whether or not birds are limited by prey abundance is open to question. Difficulties may arise when trying to relate birds and invertebrates sampled at two spatial scales. High invertebrate variability at the small scale may make some bird/invertebrate correlative evidence questionable. Such potential problems are explored in chapter 5.

1.8.2 Substrate characteristics

1.8.2.1 Particle size and percentage of clay, silt and sand fractions

Intertidal mudflats, although apparently homogenous in character have been shown to exhibit considerable spatial heterogeneity in particle size (Mouritsen & Jensen 1992). Although many shorebirds have been shown to concentrate their foraging where densities of their prey have been found to be the highest (Bryant 1979, Goss Custard 1977a, Goss Custard *et al.* 1991), the differences in the physical characteristics of the sediment can influence the efficiency with which some birds detect and capture prey (Quammen 1982, Kelsey & Hassall 1989, Goss Custard & Yates 1992, Yates *et al.* 1993a, Nehls & Tiedemann 1993, Scheiffarth *et al.*1996). Quammen (1982) increased the sand content in study plots from 2 – 14 % and found that feeding time of shorebirds on these plots was significantly lower than on controls. However Winjsma *et al.* (1999) found that on a study of the benthic fauna of the Banc D'Arguin, Mauritania, that total density of invertebrates was not related to any of the sediment characteristics that they measured (median particle size, <16μm, 16μm - 2000μm). Although some correlations between invertebrate density and particle size were found, no causal explanation was given. In the same analysis they also found 'peculiar' results for some species suggesting that there was some element of chance involved in such correlative evidence and generally concluded that animal-sediment relationships are too variable to conclude that grain size alone is the best predictor of benthic invertebrate species distribution. Snelgrove & Butman (1985) also found very little evidence to suggest particle size was a good predictor of invertebrate densities.

1.8.2.2 Penetrability of sediment

Substrate penetrability can be an important factor in shorebird community structure (De Boer 2002). Mouritsen & Jensen (1992) suggested that an increase in sediment penetrability accounted for both the selection of micro-habitat by dunlin and their distribution on a larger scale and was a better predictor of their distribution on a mudflat than even invertebrate numbers. They suggested dunlin use areas of higher penetrability to allow deeper probing to increase the availability of prey whilst at the same time minimising foraging costs. They also found that penetrability could vary significantly between sites even though percentage of silt and sand and mean sediment particle size did not. Kelsey & Hassall (1989) found that patch selection by dunlin on the Wash was not just based on prey density but that they preferred wetter, softer substrates. They argued that increased penetrability would greatly enhance the prey encounter rate. However this advantage may well be offset by the fact that mud with a higher penetrability is also more difficult to walk through and that energetic advantages gained by easier feeding may be offset by increased energy expenditure whilst walking. This may be the case for larger heavier birds where the pace to peck ratio is high but probably not such a problem for smaller birds such as the dunlin whose 'stitching' feeding method reduces the amount of walking needed in order to encounter prey (Kelsey and Hassall 1989). Positive relationships between shorebirds and areas of comparatively high penetrability have also been found for Curlew Sandpipers (Kalejta & Hockey 1991). Quammen (1984) also found that the impact of shorebird and crab predation on the invertebrate community was affected by changes in sediment structure as depletion effects were detected in soft sediment but not at sandier sites (see also Quammen 1982).

1.8.2.3 Sediment organic matter content

The amount of organic matter present in estuarine sediment acts as a relative measure of the amount of food available to the benthic infauna (Parker 1983). It is, in itself, a potential predictive tool for the presence of the invertebrate fauna which may display clear responses to localised increases in organic matter e.g. around sewage outfalls (Li & Lee 1998). Organic matter is often measured as the quantity of carbon, nitrogen, phosphate or volatile substances, thus any measure of these fractions will give some idea of the amount of food available for consumption by sediment dwelling invertebrates (Elliot 1979), which are then predated by shorebirds (Goss Custard *et al.* 1991). Although the organic content of sediment can be accurately measured it does not follow that all of this is available as potential food for invertebrates as contaminants such as coal dust, hydrocarbons or calcium carbonate may also be included inadvertently in the measurement.

1.8.2.4 Tide height: mudflat exposure time

The length of time a particular area of mudflat is exposed (i.e. not covered by water) determines the time available for each species of shorebird to feed. This is in turn governed by the height of the mudflat above chart datum (ACD). Chart datum is approximately the lowest tidal level due to astronomical effects and excluding meteorological effects. Spring tides have higher high tides and lower low tides whereas neap tides have lower high tides and higher low tides. Hence, the range (difference in water level between high and low tide) is much larger in a spring tide than in a low tide. There are normally seven days between spring tides and neaps, in accordance with the phases of the moon. These differences in tidal range can affect the availability of certain areas of mudflat and restrict the feeding time in preferred areas or force birds to feed at night (see section 1.8.2.6).

1.8.2.5 Distance from shore

Birds may perceive proximity to the shoreline as a danger due to potential attack from avian predators or disturbance from human activity. Human disturbance can have a negative effect on the ability of birds to feed (Klein *et al.* 1995, Burton *et al.*

1996, De Boer 2002), especially if they are constantly being displaced to less preferred areas. Pfister *et al.* (1992) suggested that disturbance is implicated as a potential factor in long-term declines in shorebird abundance at Plymouth Beach, USA and West *et al.* (2002) concluded that for the oystercatcher on the Exe Estuary, disturbance could be more damaging in terms of potential mortality than permanent habitat loss.

Predation threat from *Falconidae, Accipitridae* and strigiformes may also have an effect on the distribution of birds on an intertidal area. Cresswell (1996) identified 'surprise' as the most important tactic for peregrine (*Falco peregrinus*), merlin (*Falco columbarius*) and sparrowhawk (*Accipter nisus*) hunting in winter, and for the two latter species this was achieved by attacking from a perch. The trade-off between resource access and relative tolerance to disturbance on various areas of high level mudflats may be measured by considering the amount of cover available for such attacks and how vigilance rates and bird feeding hours may relate to this (see Gill *et al.* 1996). It can be presumed that increased vigilance would mean reduced intake rates. Cresswell & Whitfield (1994) showed raptor predation to be the most significant cause of mortality in small wader species at a study site in south-east Scotland over the last 10 years (these two causes of mortality are however not incompatible as waders weakened by food shortage may be more vulnerable). They postulated that a single female sparrowhawk plus the effect of kleptoparasitism from crows (*Corvus corone*) could account for 154 redshank in a single winter (September - March). This figure if applied to the Forth population is 16.4% of the average winter population for this species between 1993 and 1998. Even without kleptoparasitism a single hawk could account for 106 birds or 11.3%.

It is also suggested on the basis of recent unpublished data collected at Boundary Bay, Canada that food availability is not as important as predation when it comes to the distribution of waders (Rob Butler pers com).

Increased night feeding may well be observed in response to increased human disturbance or avian predation. Human disturbance has been little studied but sanderlings increased their foraging at night in response to human disturbance (Burger & Gochfeld 1994). Rohweder & Baverstock (1996) noted that large species of wader were more sensitive to human approach than small ones. Some birds may choose to feed more at night to avoid daytime predators but owls are still a threat to night feeding waders (Whitfield 1985).

1.8.2.6 Temporal segregation

Nocturnal feeding was not studied in detail in this study (except three visits to Kinneil, Skinflats and Torry Bay after dark to confirm that there was indeed night feeding on the Forth Estuary). However, night feeding behaviour may affect the spatial distribution of the birds in a different manner to that of daytime feeding. If this is the case, areas of importance to the birds at night may be different to those of importance during the day and so will go undetected in this study. It is however thought unlikely that the differences would be so marked as to make the daytime model only partially valid. Nocturnal feeding at other sites is briefly considered here.

As food is a potentially limiting factor in the over-winter survival of shorebirds, the brevity of exposure time during neap tides or increased energy demand during particularly cold periods may necessitate night feeding. This temporal segregation of feeding shorebirds can reduce interference competition, interference being individual birds directly affecting the ability to forage of another bird by crowding, kleptoparasitism, and aggressive behaviour or even by altering the behaviour of the prey. The main activity that birds engage in during the hours of darkness other than roosting appears to be foraging (McNeil *et al.* 1992, Sitters 2000) and for shorebirds nocturnal foraging has mostly been interpreted as a way to gain more energy when foraging time during short winter days is not long enough (Goss Custard *et al.* 1977). It may be, however, that some species prefer to feed at night although none of the *Charadrii* has been reported as feeding exclusively nocturnally (McNeil *et al.* 1992). Physiological adaptations apparently aid night feeding in some species e.g. a high rod:cone ratio (Rojas *et al.* 1997). Rohweder & Baverstock (1996) found significant increases in densities of two sight feeding species, the pacific golden plover (*Pluvialis julva*) and greater sandplover (*Charadrius leschenaultii*) at plots which had increased light levels at night due to the presence of a town. It may be that light levels at Grangemouth from floodlights and gas flares are of importance to some sight feeders like redshank and grey plover (*Pluvialis squatarola*). Dodd & Colwell (1998), adopting a multi-species approach, suggested that interspecific variation in diurnal and nocturnal feeding patterns of shorebirds is associated mostly with tidal, seasonal and moonlight conditions and that foraging at night did not increase during periods of short day length. Robert & McNeil (1989) supports this final conclusion as they found that night foraging might not be entirely a consequence of short days and winter conditions as it also occurs in tropical environments.

Invertebrate capture rates may well be lower at night, therefore it might be expected that shorebirds would concentrate their feeding on the areas of greatest food abundance. Sutherland (1982) has shown that biomass intake rate in the oystercatcher feeding on cockles (*Cardium edule*) by sight during the day, halved when they adopted a tactile method at night. However, Zwarts *et al.* (1996a,b) showed that oystercatcher could not meet their energy requirements during one tidal cycle and when forced to feed at night their body weight increased with the duration of the available feeding time, irrespective of whether it was day or night. Few studies have recorded swallowing rates or the relative value of food at night therefore night sampling in this study may show that larger or more organisms are available at night. Evans (1987) for example reports changes in prey activity near the surface during the night in *Corophium, Hydrobia, Macoma* and *Nereis,* all important prey items for the birds on the Forth Estuary. McCurdy *et al.* (1997) counted droppings as they represent a cumulative amount of feeding over the tidal cycle. It was found however that there was no significant difference in the density of droppings between day and night but dropping density increased with distance from the shore. This does seem to highlight the relative importance of lower level mudflats at this site (Bay of Fundy, Canada) but in this instance the observations were made on just one day. The relative importance of habitat at night at any level of mudflat, mid, low or high, may lend weight to any conservation measures affecting an area that may be more intensively used at night by wintering shorebirds than during the day.

1.9 Modelling approaches previously used to predict the effects of habitat loss on wintering bird populations

1.9.1 Determining whether birds are limited by behavioural interactions

Predicting the consequences of estuarine habitat loss is a difficult problem when determining long term changes in bird populations because the losses may have occurred on breeding grounds, wintering grounds or both (Sutherland 1996b). If it is possible to understand the behavioural decisions made by individuals, it is possible to predict their behaviour in novel environments such as those resulting from environmental change (Sutherland 1998a). The generally theoretical 'Sutherland' approach to population modelling (e.g. Kokko & Sutherland 1998), considers the response of such individuals to environmental change in terms of 'density dependence'. The models aim to characterise the essential pressures that apply across many taxa, but the disadvantage of such an approach is that it is difficult to test and may not be appropriate in particular cases (Goss Custard *et al.* 1994). It is important to have an accurate knowledge of the nature of density dependence in both breeding and wintering grounds before habitat loss can be predicted. The buffer effect for instance (Kluijver &Tinbergen 1953 in Dolman & Sutherland 1995) predicts that a greater proportion of individuals breed in less productive territories as population density increases, possibly culminating in complete exclusion from breeding for some individuals. Loss of habitat either on breeding or wintering grounds should result in a local population decline and the consequences of this loss should be greatest where density dependence is greatest (Sutherland 1996a). Such behavioural models (Sutherland & Dolman 1994, Sutherland 1996b, Goss Custard & Sutherland 1997) also consider the individual interactions that underlie the descriptive parameters of vertebrate population models. To model the dynamics of a consumer population in a patchy environment, Sutherland & Dolman (1994) discuss two density dependent processes: *mutual interference*, defined as "a reversible decline in food intake rate with increasing bird density" (Goss Custard *et al.* 1994) and *depletion of resources.* Their model incorporates estimates of searching efficiency and competitive ability in an attempt to make the model more biologically realistic i.e. competitors are not assumed to be equal. In this model the initial removal of poor quality habitat has a negligible effect on population size but a crash occurs when the remaining habitat is lost. By assessing the relative importance of certain areas, as in this study of the Forth Estuary, it may be possible to assess those areas most at risk if threatened by environmental change. The Goss Custard *et al.* (1994) model also shows that where individuals from different migratory populations converge on the same wintering ground and compete for resources, effects of habitat loss may then affect breeding populations that do not use the damaged site. Here, knowledge of wintering bird origins would be an advantage. In an extension of this model, Dolman and Sutherland (1997) suggested that although a forager would wish to concentrate its feeding in areas of highest prey density (Bryant 1979) to maximise intake rate, when doing so it would often experience interference. This counters their ability to feed in the best areas and leads to a modified pattern of depletion. Because individuals differ in age, sex, dominance and parasite burden the magnitude of individual variation may effect the level of density dependent mortality amongst consumers, and ultimately population size.

Dolman and Sutherland (1995) have also considered the ability of migratory populations of birds to be flexible in their migration strategy in response to habitat loss. One argument used by potential 'developers' of tidal mudflats is that birds respond to change or loss of habitat by moving elsewhere but it is unclear just how flexible migratory populations are in this respect. Some populations are naturally mobile and opportunistic such as the knot (Davidson 1992), others like the redshank have a strong annual winter site fidelity (Burton 2000). At the extremes of this scale there may be genetic constraints but shorebirds do live in variable environments so they appear able to respond to change, this however is likely to depend upon the details of the genetic or behavioural system and this may be difficult to predict (Sutherland 1998b).

Depletion of prey late in winter could decrease the capacity of an estuary to support prey items even in one season. Bird density may become limited on an estuary as numbers increase and perceived habitat quality may fall due to competition for resources. If a bird is displaced from its feeding area due to habitat loss it cannot be assumed that it will be able to find another area of equal suitability (Goss Custard & Durell 1992). As competition for feeding areas increases less favoured areas of the estuary will be used in increased proportion; therefore the average bird will feed less well.

The work of Goss Custard and co-workers (Goss Custard 1985, Goss Custard *et al.* 1994, Goss Custard *et al.* 1995a, Goss Custard *et al.* 1995b, Goss Custard *et al.* 1998, Goss Custard 2002, Triplet *et al.* 1999, Durell *et al.* 2000, Durell *et al.* 2001), differs somewhat from that of Sutherland and colleagues and is mainly focused on a single species, the oystercatcher. Individual-based distribution models were developed, founded on empirical evidence relating bird numbers and winter mortality to environmental variables whose values in new circumstances can themselves be forecast (Goss Custard *et al.* 1994). Empirical studies can provide demographic parameter estimates for particular populations, often of one species at one locality. Thus ideas can be tested and the resulting models used to guide practical action (Goss Custard *et al.* 1994). The disadvantage is that they may take many years to build and test, therefore the principles that generally apply across many taxa may be slow to emerge. It may also be difficult to apply such models to a wide range of different sites and areas. Model structures are based on game theory i.e. the choices made by one bird reflect those made by others. Goss Custard *et al.* (1994) assumes that local carrying capacity is reached when numbers at a site reach a plateau even though other individuals keep arriving. Thus as one bird arrives another departs (Goss Custard 1985). It is assumed that feedback derives solely from interference and depletion competition for food although flexibility with regard to night feeding was not considered. This model, based on the oystercatcher, is appropriate for a large shorebird with low reproductive rates, high longevity and deferred breeding but it can be modified for other species. By setting the demographic parameters in the model to those appropriate for a smaller wader such as dunlin, and given the form of the density dependent winter emigration and mortality function, it is possible to see whether reduction in population due to habitat loss is proportional, supra proportional or sub-proportional (Goss Custard *et al.* 1994). The greatest advantage of the model is that it can predict the critical density dependent population functions in new environmental circumstances and is a means of predicting population change. However, although the carrying capacity of the food supply can be measured as either maximum number of bird days a site can support or maximum numbers that can survive the breeding season, some birds often emigrate or starve before carrying capacity is reached (Goss Custard *et al* 2002).

Goss Custard *et al.* (1995a) considered how the equilibrium population size of a subspecies population of oystercatcher might be affected by various levels of winter habitat loss, given different assumptions about the strengths of the density dependent functions operating in summer and winter. The model which was developed used parameters established from a review of oystercatcher field studies (Goss Custard *et al.* 1995b). Habitat loss simulations were run for 1000 years and the results of the model were tested against real data (Ens *et al.* 1992, Durell & Goss Custard 1995). Over a wide range of assumptions the model predictions fell within the observed range. By removing areas of average habitat quality in 10% increments it was found that at 60% winter habitat loss there was a 60% reduction in the autumn population size but a 69% reduction in breeding birds. This illustrates a non-linear relationship between winter habitat loss and population change (see also Sutherland 1996). It was also noted that winter habitat loss would be expected to affect population size sooner in populations of species where numbers fluctuated more widely. However variations in population fluctuations were to a large extent dependent on the various assumptions of the model.

All of these modelling approaches have their advantages and disadvantages. Wherever behavioural interactions are being modelled, good empirical data are essential and it is no coincidence that a large easy-to-observe wader such as the oystercatcher has been chosen as the model species for the majority of these studies. Much of this theoretical and empirical work lends its success to many years worth of data collected by a legion of fieldworkers; a luxury that this or few other studies have had. One of the main purposes of this study was to model the spatial distribution of a number of different species in relation to their habitat on the middle Forth Estuary. In this respect, a more site specific, rather than species specific approach was considered. The models do not take into consideration the behavioural interactions that determine distribution such as interference and dominance hierarchies but it is assumed that as these effects exist they are expressed in the actual numbers and densities of shorebirds present at sites throughout the winter.

1.9.2 British Trust for Ornithology (BTO) modelling approach: the effects of sea level rise on shorebird populations

The BTO have utilised the ESCAPE model (Hulme *et al.* 1995) that predicts the affects of sea level rise to allow estuarine shorebird densities on British estuaries to be predicted from estuary sediments, morphology and geographic location. Their models use a whole range of estuarine morphological variables such as width, length and fetch to predict how shorebird numbers may be affected by changes in the shape of estuaries with sea level rise. The model depends on work suggesting that it is the nature of sediments that dictates the number and species composition of invertebrates and in turn shorebirds that an estuary will hold (Austin *et al.* 1996, Holloway *et al.* 1996). Consequently as the shape of an estuary changes both the quality and quantity of habitat will change. Where intertidal flats are subjected to high wave action, typical of wide and open-mouthed estuaries, fine particles tend to remain in the water column and so are flushed out of the system leaving sandier sediments, except in sheltered areas such as the inner estuary. In estuaries, which are narrow or enclosed, finer particles are able to settle which allows muddier sediments to form (Austin *et al.* 2001). In two case studies the predictions for the effects on shorebirds follow a general pattern as sea level rises. As the estuaries become wider as land is claimed or reclaimed by the sea, sediments would be expected to become sandier (Yates *et al.*1996). Consequently they would support lower numbers of species such as redshank and dunlin, which are found at greatest densities on muddier sediments (Austin *et al.* 1996). In contrast they would be capable of supporting higher densities of species such as oystercatcher which tend to favour sandier sediments. For both of the studied sites, the increased area of intertidal habitat would offset any predicted decreases in density.

In broad terms the model suggests that where estuaries become more open to wave action without a substantial increase in area, the numbers of species favouring muddy sediments may decrease. The change in the nature of sediments brought about by an increased average estuary width or by the widening of the estuary mouth would be driven principally by increased fetch.

The output from the present study will identify areas of greatest importance for feeding birds so that the impacts of any planned land claim or other changes can be more accurately assessed. The models have been developed both at the whole estuary and sub-estuary scale using multiple regression analysis at plots of known character. These models of bird distribution at the sub-estuary level can feed into other models considering interactions between individual birds, parameters relevant to the whole estuary and density dependent effects on both breeding and wintering grounds (Fig 1.4). A hierarchy of modelling approaches that predict the effects of habitat loss are given in Fig 1.4.

KNOWLEDGE OF BIRD USAGE AND BEHAVIOUR AT THE MUDFLAT LEVEL
(Bryant 1979, McLusky *et al.* 1992, Bryant & McLusky 1997)

↓

PREDICTING THE CONSEQUENCES OF HABITAT LOSS AT VARYING SCALES, WITHIN AN ESTUARY
Individual based models using game theory to model effects of depletion and mutual interference
(Goss Custard *et al.1995a,b, Durell & Goss Custard 1995)*

↓

BETWEEN ESTUARY MODELS
Modelling between estuary bird densities using whole estuary parameters
(Austin *et al.* 1996, Holloway *et al.* 1996, Austin *et al.* 2001)

↓

THEORETICAL FLYWAY MODELS
Density dependent effects on wintering and breeding grounds
(Dolman & Sutherland 1995, Sutherland & Anderson 1993, Sutherland 1998)

Fig 1.4: Schematic diagram illustrating a model hierarchy. Each type of model seeks to predict the effects of habitat change on overwintering shorebird populations and distribution at different spatial scales.

1.10 Aims of the present study

- The present study attempts to map the spatial usage by overwintering shorebirds of the middle Forth Estuary mudflats, (primarily at the Kinneil site) and determine why certain areas are more important for feeding than others. The relative usage by birds of high-level mudflats is of specific interest as it is these areas that are normally at greater risk from land claim. Equally, it would be instructive to know more about usage of these high level areas when considering 'managed realignment' i.e. breaching the seawalls that bound the estuary to allow inland restoration of previously claimed mudflat areas.

- Using the data collected in this study, a series of predictive models will be developed at the whole estuary and sub estuary scale to quantify the affect of habitat loss and 'weighted area' maps are developed in a GIS. These maps relate the best predictor variables for a key species to the overall spatial usage of the mudflat by that species; in this way habitat areas of high importance to the species can be readily identified thus allowing some relative affects of habitat loss to be quantified. As each model is a snapshot of bird usage during one winter, the contemporary pattern at one site (Kinneil) is related to long term data collected at that site over 20+ years to see if spatial patterns of habitat use are variable or stable over time. Due to potential problems with spatial autocorrelation of data a separate comparative analysis was undertaken (using Kinneil as the model site) using a geostatistical methodology, which takes such spatial relationships into account.

- Food availability is of considerable importance for overwintering birds concerned primarily with self-maintenance, therefore a separate study was carried out to determine whether depletion of food might be a limiting factor. This study aims to discover just how spatially variable these food supplies might be. It also determines whether a depletion effect is detectable and suggests whether such an effect, if it exists, is likely to influence the spatial distribution of feeding effort on the Forth Estuary.

- Some species of shorebirds such as the redshank occur in mixed race populations in winter, these races are impossible to identify by field observation alone. As population sizes can fluctuate annually on the Forth Estuary an understanding the relative proportions of such populations can help to determine which race is more abundant. If the racial origins of species like the redshank are known then the overall effects of land-claim can be seen in the wider context of the whole population especially if one population is more vulnerable than another in response to habitat loss. This study attempts to test a methodology for identifying different races using $^{87}Sr/^{86}Sr$ isotopic ratios from the bones and feathers of Scottish and Icelandic shorebirds.

Chapter 2: Materials and methods: shorebird feeding effort distribution models

2.1 The modelling approach used in this study

In order to predict the consequences of habitat loss on bird numbers, feeding effort and spatial distribution on a Forth Estuary mudflat, it is first necessary to build a habitat model for each of the key species in this case shelduck, redshank, dunlin and knot. These four species were chosen for the following reasons:

- They are all regular overwintering species and occur in nationally or internationally important numbers.
- All the species rely heavily on the intertidal area for feeding and none of them spends significant periods of time feeding inland away from the estuary.
- Each species has been observed at all the study sites in previous years.

The modelling approach used here sets out to understand how each species distributes itself in relation to a number of predictor variables that in turn determine the relative attractiveness of any area of the intertidal. Significant predictor variables and bird feeding distributions were mapped to produce *'weighted area models'* (Bryant 1998) allowing the relative importance of a mudflat area to be quantified in an informed manner. Such visual information will allow planners to quantify the impact of potential habitat loss or alteration on the birds that inhabit the area during the winter months. The model can be treated as either of the following:

- **Closed system.** Where it is assumed that if a favourable sub-area is removed the displaced birds will either move to the next favoured area within the site or die.
- **Open system.** Allows the displaced birds to leave the site and look for suitable habitat at other sites within or outwith the estuary.

2.1.1 Why develop a spatially explicit model (SEM)?

The main aim of this study is to develop a model at the estuary/sub-estuary scale that is able to predict the effect of habitat change, be it land claim, pollution or sea level rise on the overwintering bird population. Spatially explicit models (Haig *et al.* 1998) can be useful tools when attempting to understand which ecological processes and variables are instrumental in determining the distribution of birds on an estuary. They also enable the estimation of possible responses of birds to changes in habitat quality (Moore *et al.* 2000, Marzluff *et al.* 2002). Such information is vital to land managers when considering likely impacts of habitat changes on waterfowl populations and is essential in the effective implementation of conservation measures. Such spatial models are intrinsically linked to landscape scale processes and characteristics as they seek to relate the population demographics and dispersal behaviour to areas of suitable habitat, in this case within the estuarine complex of the Forth Estuary. They can also be used to model the alteration of an area by allowing the reduction of useable habitat. The ability of a species to persist at the site can then be determined.

If the model is to be relevant to the population in question, the resolution of the information gathered must be appropriate to the scale of the habitat. In this study information was gathered from five mudflat areas on the Forth Estuary to identify model parameters. The sites ranged in size from 25ha (Bo'ness) to 750ha (Kinneil). The appropriate 'grain' of resolution for this information was set at 1ha (100m x 100m) for the bird distribution information, as this scale was considered relevant to the dispersion of the species being modelled. Other parameters such as sediment characteristics and invertebrate abundance were collected at two scales. Firstly, information was collected within random 1ha plots at the 125cm^2 scale (mean of five 25cm^2 samples) and related to the bird data using generalised linear models (GLMs). Secondly, some samples were taken at the 25cm^2 scale to facilitate estimates of sediment, invertebrate and bird distribution. This spatial model was designed to utilise the coefficients of the GLMs to generate predicted maps of bird dispersion. This kind of micro-scale model is appropriate in this context, as small changes in the quality of the habitat may have a large affect on the way in which the birds were able to use it.

It is important to point out that the model used in this study is a sub-population model and not an individual based model. Individual based models are capable of modelling variation among individuals, interactions between them and their population level consequences. Hence the scale of the modelling approach is appropriate to the scale of the estuary. Although an 'individual' may be represented by a number of organisms (e.g. a herd or a defined flock) the behavioural interactions between these organisms have to be regarded as uniform.

2.1.2 Advantages of spatially explicit models (SEMs)

Although habitat suitability models attempt to estimate a broad range of habitat conditions that will provide all the requirements of a particular species, they do not incorporate the spatial dynamics of species-habitat relationships (Turner *et al.* 1995). SEMs can consider both species-habitat relationships and the arrangement of the habitats in space and time (Dunning *et al.* 1995). The main advantage of SEMs is their ability to simulate the effect of landscape change on the subject of interest. The effects of this habitat change can then be modelled on a species by species basis.

2.1.3 Limitations of SEMs

As with all models, SEMs are simplifications of reality and it would be unwise to accept all model outputs literally. Keeping the model simple may be the best route to take when trying to understand the complex nature of bird dispersion on intertidal mudflats. Using this type of model though, it is possible to suggest likely responses of a sub-population of birds to notional changes in the quality of the environment that they rely on during the winter period. The predictive ability of a model is limited by the number of its parameters, but in this case extensive 'ground truth' data can be incorporated. The model can also be empirically tested at another site within the same or another estuary.

It has already been mentioned that spatial scale is important, and it is essential that the model operates at a resolution that is likely to reflect 'reality' as closely as possible. The scale chosen for this model (1ha) is more than adequate even at the smaller sites. It should be remembered however, that it might be difficult to apply the findings of this model to other sites if the data for that area are collected at a different spatial scale.

2.1.4 Parameter estimation

In this study parameters were chosen that were firstly of ecological relevance and secondly, logistically measurable, as it is important to make the model as biologically realistic as possible (Conroy *et al.* 1995). Guidance has been taken from previous literature on the variables most likely to be good predictors of bird distribution such as sediment structure (Quammen 1982, Yates *et al.* 1993a, Yates *et al.* 1993b, Yates *et al.* 1996, Scheiffarth *et al.* 1996, Botto *et al.* 2000) and prey density (Goss Custard 1977b, Bryant 1979, Mercier & McNeil 1994, Dolman & Sutherland 1997, Weber & Haig 1997a, Safran *et al.* 1997 and Brayton & Schneider 2000) but the sampling and analysis conducted in this study is specific to the Forth Estuary. The findings of the model may be generally applicable to other Scottish/ UK estuaries albeit with the caveat that this is a northern hemisphere, northern European, east coast estuary that may be affected by latitudinal and longitudinal factors (Fig 2.1). Differences in weather conditions; site characteristics and invertebrate density and diversity may all influence bird distribution in a site-specific way.

By determining the variables most likely to predict shorebird distribution an element of uncertainty has been removed for future research on the Forth Estuary. As these models are improved it should be easier to target the appropriate variables to measure in areas not included in this study, thus reducing both the physical effort of collecting and analysing data and the cost of such a venture.

2.1.5 Validating the model

Comparisons between predicted spatial patterns and actual data are required to evaluate spatially explicit models (Turner *et al.* 1989). The output from a given model scenario is testable if it is possible to compare it to changes that have occurred previously on the Forth Estuary. Such changes would include, pollution events, the removal of pollution sources and land claim events. It is also instructive to see how bird distribution responds to extended periods of relative stability where numbers of birds change on an annual basis. Caution must be exercised when assessing the accuracy of a model output, as there will always be an element of statistical uncertainty due to stochastic variation and sampling error. It may be appropriate to restrict the spatial resolution of the model so that movement assumptions are not made on too fine a scale. In doing so it may be reasonable to simply look at redistribution between tide height (mean above chart datum (MACD)) contours, rather than individual 1ha-grid squares. It is also possible to validate model predictions by continued observations of bird distribution, especially if it is known that an event likely to alter the character of the estuary is about to occur. For the model to remain relevant this constant updating and checking is a necessary undertaking. The results of any management (or lack of management) undertaken as a result of the model output can be used to improve future models and to enhance the validity of any predictions. It is envisaged that if the model is to be used, constant scrutiny should be a feature of its implementation.

An attempt is made to validate the contemporary models using long-term data on shorebird distribution and invertebrate abundance to look for stability in bird feeding distribution patterns and invertebrate populations at Kinneil. No long-term data exists for sediment characteristics.

It would be very difficult to manipulate the habitat in order to test the model predictions. It certainly would not be logistically possible or indeed desirable to remove areas of potential habitat, however it may be possible to alter habitat quality in test areas. In an attempt to encourage the proliferation of invertebrates it is possible to add an organic or inorganic substrate to the sediment (Gillon 1992) and on the small scale to alter sediment conditions e.g. increase the sediment particle size (Quammen 1984).

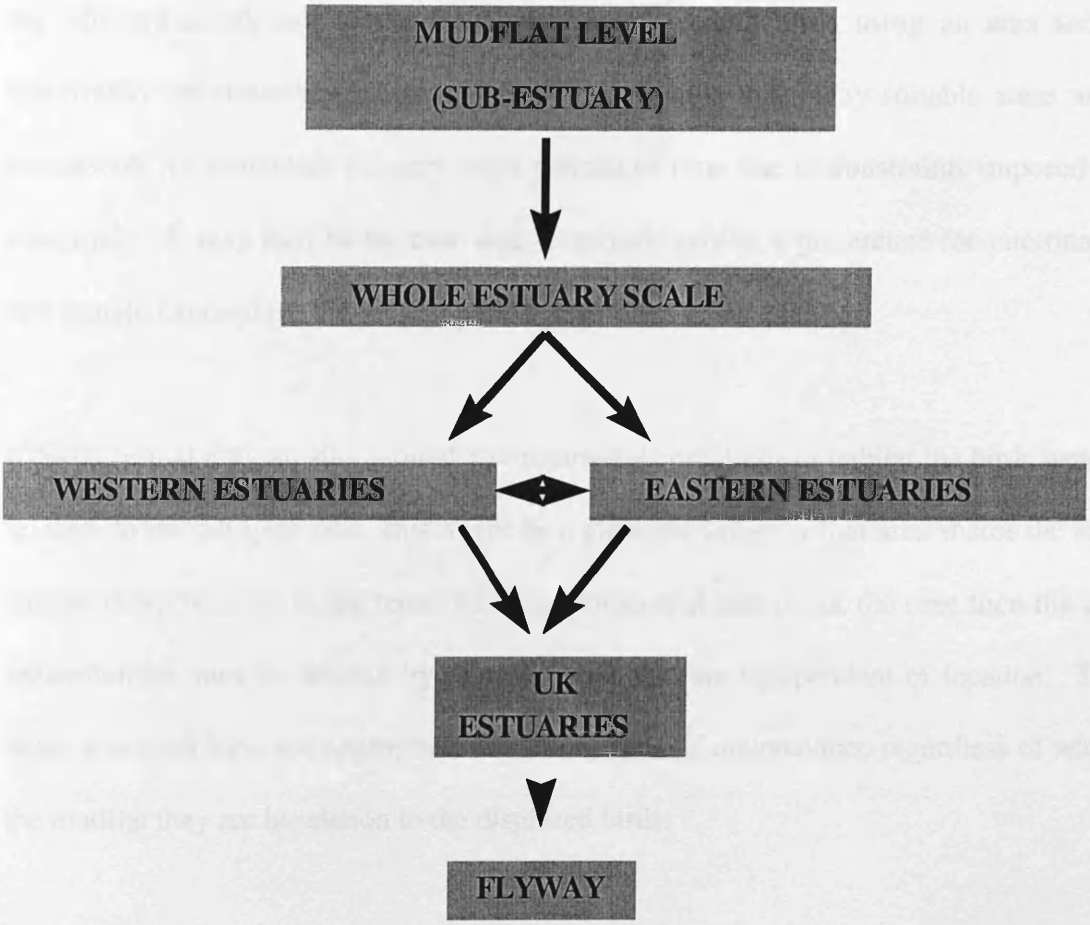


Fig 2.1: How information gathered at the sub-estuary level can feed into estuarine models at different scales

2.1.6 Modelling dispersal

One purpose of the model is to attempt to predict how birds will redistribute themselves within a mudflat area and also around the whole mudflat complex, in response to habitat change. It is however difficult to model the dispersal of any species accurately because robust assumptions must be made about the perceived dependence of a bird on the variables governing habitat suitability. Other factors such as awareness of predation and density dependence are more difficult to incorporate into the model. Estimated maps of variables most likely to predict shorebird feeding areas represent a snapshot of the whole mudflat at the time of sampling only. It is assumed that this picture is representative of the quality of the site and is relevant to the mean number of feeding birds using an area and more specifically the time they spend in there. It is possible that many suitable areas are only colonisable by shorebirds for very short periods of time due to constraints imposed by the tidal cycle. It may then be the case that shorebirds exhibit a preference for intertidal areas that remain exposed for the longest period, regardless of its quality.

It could be that after an alteration of environmental conditions or habitat the birds would just relocate to the adjacent area. This might be a plausible option if that area shares the same or similar characteristics to the removed area. However if this is not the case then the area of redistribution must be defined by characteristics that are independent of location. That is, those areas that have the appropriate conditions for self-maintenance regardless of where on the mudflat they are in relation to the displaced birds.

2.2 Study sites

In order to collect a data set representative of the Forth Estuary, five study sites were chosen for their range of substrate types, exposure times, aspect and area (Fig 1.1)

1. Dunmore to Kincardine Bridge
2. Skinflats
3. Kinneil
4. Bo'ness
5. Torry Bay

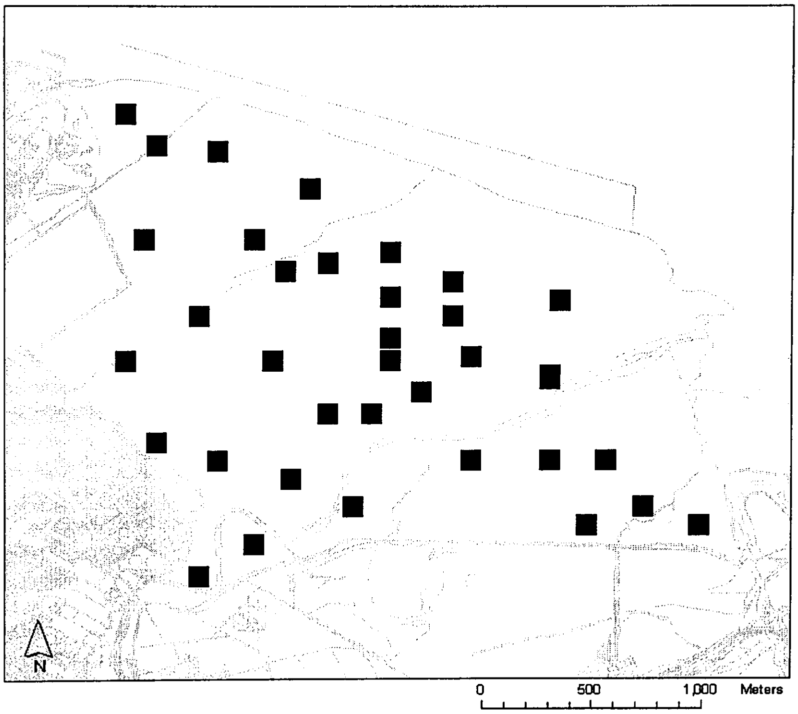
2.2.1 Distribution of study plots around the estuary

Sixty one, one hectare study plots (Table 2.1) were distributed between the sites, stratified by 1m tide height contours and spread randomly within them to cover the majority of the intertidal, taking in high, mid and low level areas. For a maps of the plots at all main sites see Fig 2.2.

Table 2.1: The number of one hectare study plots allotted to each of the study areas

Study Site	**Area of intertidal (ha)**	**Number of one hectare study plots**
Kinneil	750	30
Skinflats	370	17
Torry Bay	110	8
Boness	25	3
Dunmore to Kincardine Bridge	20	3

a)



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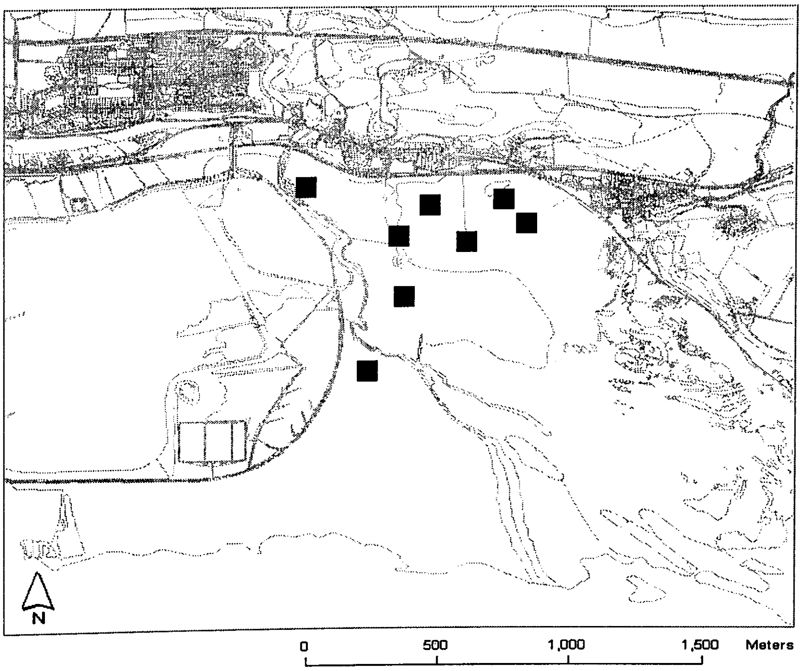

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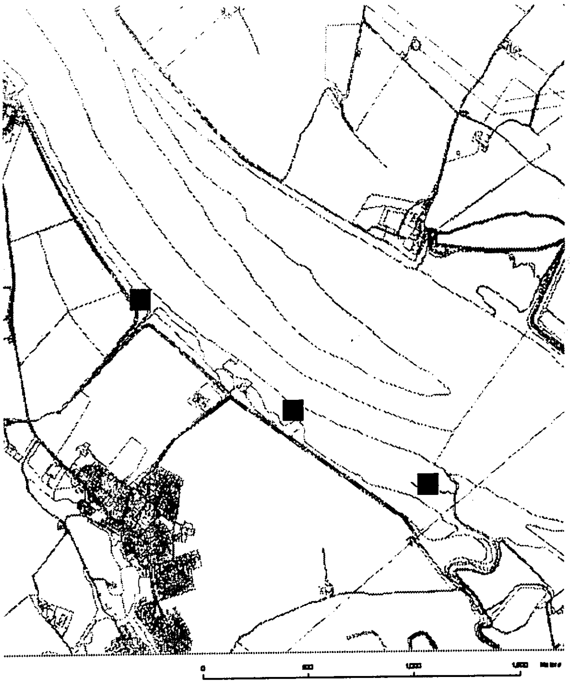

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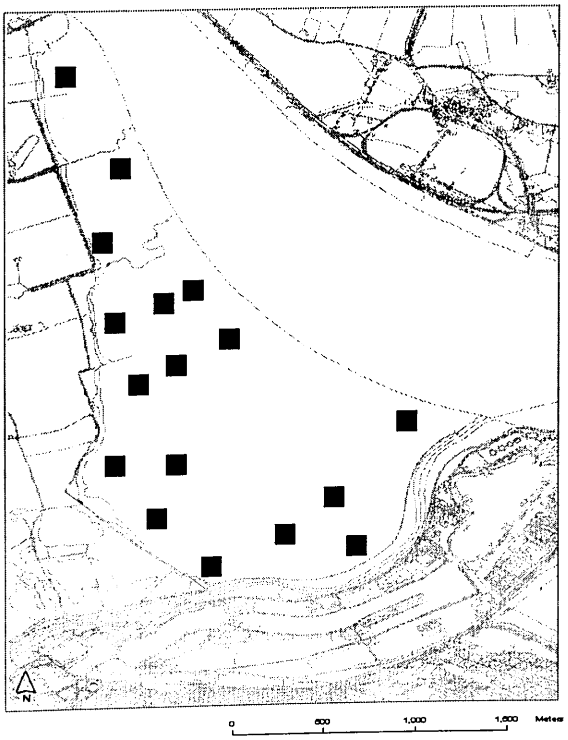


Fig 2.2: The location and distribution of one hectare study plots at a) Kinneil b) Torry Bay c) Dunmore to Kincardine Bridge and d) Skinflats

Each plot was marked out on the mud using 3m wooden posts painted with red and white markings for enhanced visibility at long range. The exact position of the corner of each square was determined using a Silva XL 1000 global positioning system and the post was then pushed into the mud leaving at least 2m still visible. These posts proved sufficient to mark the plot boundaries and could be easily seen from up to 3000m away with the aid of a spotting scope. At no time was their presence seen to affect the feeding behaviour of the shorebirds.

2.3 Bird observations

2.3.1 Counting methods for overwintering waterfowl

A major source of data detailing the numbers of waterfowl using UK estuaries in the winter is the 'Wetland Bird Survey' (WeBS), formerly known as the 'Birds of Estuaries Enquiry' (BOEE). This scheme already has a high quality long-term dataset and aims to monitor population sizes and trends and identify key sites for overwintering and staging waterfowl. These data form the basis for decisions on conservation or planning issues that may affect estuarine birds especially at sites of international importance where the UK is bound by international law (EU Birds Directive and EU Habitats and Species Directive) to maintain an efficient monitoring program. Shorebirds do not respect international boundaries and it is recognised that they are highly dependent on a network of sites during their migrations, often over long distances.

2.3.2 WeBS Methodology

The core counts are done using the 'look see' methodology (Bibby *et al.* 1992), where the observer records all birds seen or heard at a pre-defined site once a month at a specified date. Counts are made at or near high tide with the reasoning that this type of count should include all the birds that were using the area during that tidal period. This, however, only presents part of the picture, and does not collect data on how the birds may use a site through the tidal cycle. During the winter of 1992/1993 an additional 'low tide count' was instigated at a subset of sites and has continued since with a view to understand how the birds used the sites during the low tide period. Counts are normally made between November and February during the period two hours either side of low tide. These data provide an enhanced knowledge of the low tide distribution of birds, help to highlight regional variations in distribution and will help to plan for the effects of sea level rise (Pollitt *et al.* 1999)

2.3.3 How this study improves on the WeBS method

2.3.3.1 Collection of through the tide data

During the winters of 1998/1999 and 1999/2000 observations of the spatial distribution of shorebirds were undertaken at three main study sites in the upper Forth Estuary: Skinflats, Kinneil (including Bo'ness) and Torry Bay. In addition, some observations were also made above Kincardine Bridge where the intertidal area is relatively narrow. This study improves on the WeBS methods by employing through the tide counts (TTTC) made at half hourly intervals from low to high tide and *vice versa* or from the point at which the mud became inundated or exposed. This greatly increases the amount of information gained about the preferences of the birds for different areas of the mudflats and helps to provide an insight into how they are spatially constrained regardless of available resources. At each half-hourly observation interval the position of all the birds was noted on a map of the site (Fig 2.3). Each map was an enlarged photocopy taken from the Ordnance Survey Landranger 65 1:50000 series and was partitioned by a grid with each square equal to 100 x 100m or 1 hectare. Although it is accepted that the mean low water mark shown for the mudflat areas is the lowest possible annual low, and that the mapped areas were subject to subtle change over time (McLusky pers com), the mud area for each site with this map was deemed sufficiently accurate for present use.

Oystercatcher and curlew (pers obs), and to a lesser extent redshank (Masero & Perez-Hurtado 2001) and dunlin (Warnock *et al.* 1995, Sanzenbacher & Haig 2002), supplement their estuarine food intake by feeding inland. For oystercatcher and curlew this behaviour is common at all sites on the Forth Estuary, in the fields adjacent to the mudflats and may account for the observed fluctuations in the numbers of these species on the intertidal throughout the winter period. It was common at Torry Bay and Skinflats for these species to spend much if not all of the tidal cycle feeding (presumably on earthworms (*Lumbricus terrestris*)) in fields, when not frozen over. They only then returned to the mudflat as the tide neared the MHWM to feed briefly before roosting or resting at preferred sites depending on the light regime.

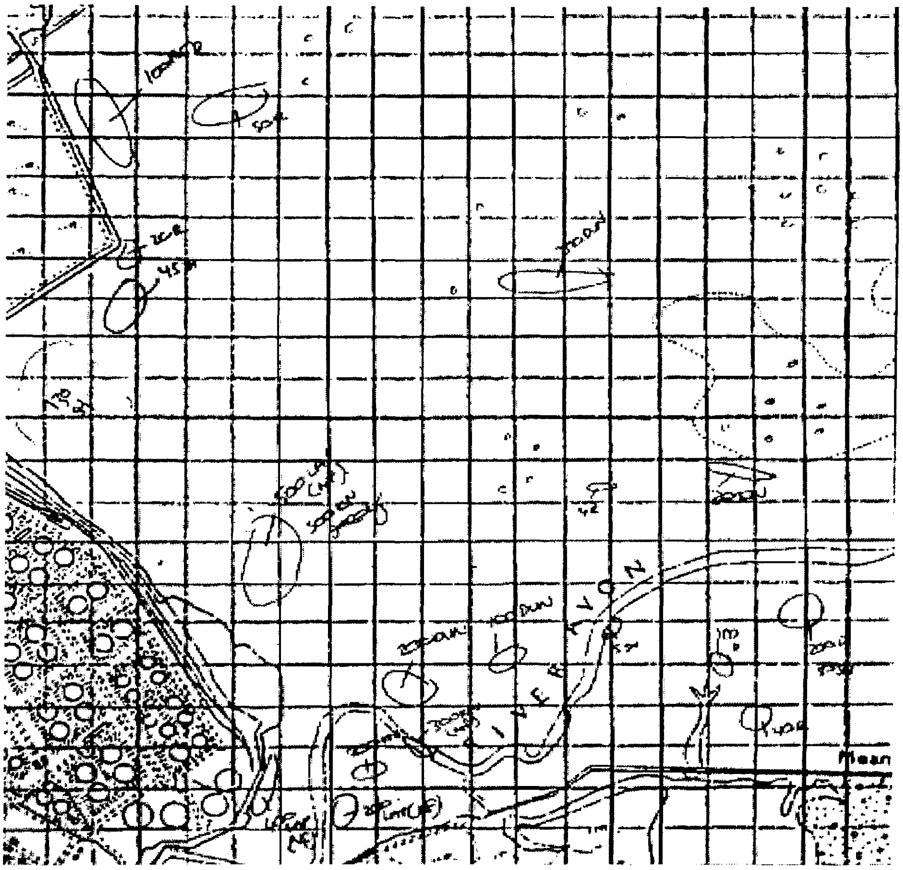


Fig 2.3: Example from a single half hourly observation made at Kinneil 29/11/99. Approximate positions and sizes of flocks are marked along with an estimate or head count of their number; a single letter denotes individual birds

Observations made during winter 1998/1999 were essentially a pilot study to determine the best way to sample the estuary and how best to collect the bird data. At this stage in the project it was assumed that GLMs only were going to be used to relate bird usage in randomly distributed plots to environmental variables. Thus the bulk of the spatial bird information collected just related to the study plots and the area in their immediate vicinity.

During the 1999/2000 winter, instead of concentrating the observations within and around the marked plots only, all the birds on the mudflat at each half hourly interval were located and their distribution mapped. Recorded flocks were all observed to be actively feeding (roosting flocks or non-feeding birds were recorded as such). Birds were identified to species and were counted using an Opticron HR60 spotting scope with a 22x eyepiece using the following groupings:

- up to 150 – counted singly
- >150 to 500 – counted in groups of 50
- >500 to 1000 –counted in groups of 100
- >1000 – counted in groups of 100 or 500 depending on flock size

As individual study plots were clearly marked it was often possible to count accurately every bird that fed within their confines at each observation interval.

2.3.4 Accuracy of bird mapping

As with all observational studies, the mapping of the birds on the mudflat will have been subject to some error. The main difficulty when positioning birds on a spatial grid is that the observer is viewing them from a low vantage point across large distances; in this case up to 1500m, making the distance from the observer to the subject difficult to judge. Accordingly, marker posts and features on the mudflat of known location were used to help position flocks of shorebirds. The features included the new effluent outfall at Kinneil and various creeks, freshwater inflows and semi-permanent flotsam. Many of the items of flotsam were positioned using a compass and a Bushnell Yardage Pro 1000 handheld laser rangefinder, which was able to give distance measurements accurate to 1m over a range of 1000m. This unit was of greatest use at Torry Bay where large numbers of rocky outcrops could be mapped. At Kinneil and Skinflats the rangefinder was of more use in calculating the distance and location of bird flocks at ranges up to 500m. To further reduce positioning error at Skinflats and Kinneil, observations were made at a number of different sites around the mudflat edge to obtain a variety of perspectives. In total, 70 visits were made to the study sites on 46 different days during the winter of 1999/2000. In total 397 half hour observations were made: 106 at Kinneil, 111 at Skinflats, 52 at upper Skinflats, 47 at Torry Bay, 38 at Boness and 43 from Kincardine Bridge to Dunmore. Error in the long-term data set for Kinneil was reduced by the use of two observers counting at the same time from different vantage points.

2.3.5 Calculation method for the spatial bird data relating to study plots

Mean bird numbers for all key species observed feeding (shelduck, redshank, dunlin, knot) were calculated for each grid square for each half-hourly observation map. Where the marked flock crossed more than one square the number of birds allotted to each square was directly proportional to the area of the flock in that square, thus if it was judged that one third of a flock was in a square then one third of the number of birds was assigned to it and so on.

2.3.6 Calculation of bird feeding effort for each grid square.

2.3.6.1 Mean feeding bird numbers per 1ha grid square

For each 1 ha grid square the total number of birds seen feeding in each square during the winter of 1999/2000 were summed. This figure was then divided by the total number of observation periods on all visits. An observation period lasted 30 minutes.

$$\textbf{Mean number of feeding birds} = \sum \frac{\textbf{birds per grid square}}{\textbf{number of observations}}$$

Observation time was different at each site so this calculation was used to measure feeding effort on a site specific basis.

2.3.7 Use of the long term bird distribution data set for Kinneil

Spatial feeding distribution data for the key species collected during this study represents just a snapshot of any long-term temporal pattern that may exist, so distribution maps from 2000 were compared to those generated for 1975, 1977, 1980, 1981 and 1986. For an example see Fig 2.4. These 'long-term' data were collected by Bryant *et al.* (1990) as part of an ongoing study of bird distribution at Kinneil. For the maps to be comparable slight adjustments were made to the data format. Bird data prior to 2000 were collected at the 200m x 200m scale compared to the 100m x 100m scale of the data collected in 2000, therefore the long term 4ha grids were superimposed onto the 2000 1ha grid and the values divided by four to give figures relevant to the single hectare scale. Another difference between the data was the actual values themselves; the long-term data referred to ***mean feeding hours/12.5 hour tidal cycle*** whereas the 2000 data referred to ***mean numbers of***

feeding birds/0.5 hour observation period. In this case the data for each grid were summed and the percentage of the total feeding effort each grid square value represented was calculated. This standardised the two counting methods in terms of 'relative bird usage' for each 1ha square and gave a percentage of the total feeding effort for each. Only data for January were available for all years so only this month was used.

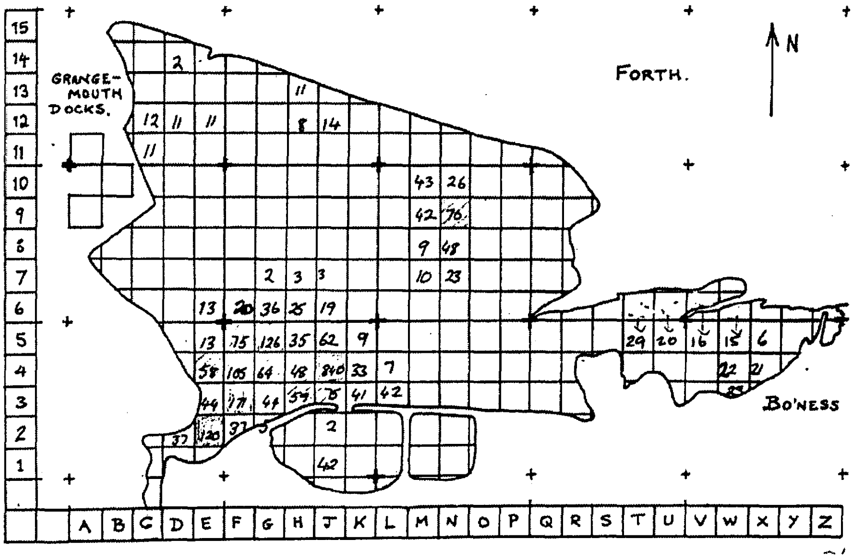


Fig 2.4: Spatial data for the January distribution of dunlin at Kinneil and Bo'ness in 1981. Data are collected at the 4ha scale (each square = 200m x 200m) and represent mean feeding hours/12.5 hour tidal cycle

2.4 Sampling methods for estuarine invertebrates and sediment

As each study plot was 100m x 100m it encompassed a considerable area within which to sample. Yates *et al.* (1993b) and Yates *et al.* (1996) sampled at the 1ha scale but took only one 25cm^2 sample assuming it to be representative of the plot. In this study it was assumed that a single sample of estuarine sediment for subsequent analysis was insufficient to give a reliable characterisation of the variability that was likely to exist within it. Sampling invertebrates from small cores and relating them to birds sampled at the one hectare scale does raise a scaling issue, as the total variation in the invertebrate densities at the hectare scale cannot be easily measured. Hence, five samples were collected, one from each corner of the plot and one from the centre with the mean of each measured parameter used in the statistical analysis (Fig 2.5). Although this number of samples is still small it was logistically impossible to increase the total number of samples beyond 250, for this part of the study due to sampling and analysis time constraints. Two methods were used to obtain the samples, depending on the accessibility of the study site.

2.4.1 Sampling by foot

Readily accessible plots were sampled on an ebbing tide by walking out onto the mud and taking 5x5x10cm cores from the mud. A purpose-built aluminium sleeve was utilised for this purpose which was inserted into the mud up to its neck, twisted to isolate a mud core, then withdrawn. The cores were removed from the aluminium sleeve with the aid of a wooden piston, placed into polythene 'ziploc' bags and labelled with the plot identification and the x-y co-ordinate of each sample. Two cores were taken within 10cm of each other at each sampling location, one for invertebrate counts and one for sediment analysis. The sediment was sampled to a depth of 10cm to cover the range of shorebird bill lengths likely to be found amongst the key species, but sampling at a fixed depth like this may result in the invertebrate counts not being relevant in terms of accessibility for all bird species due to their differing bill lengths and probe depths.

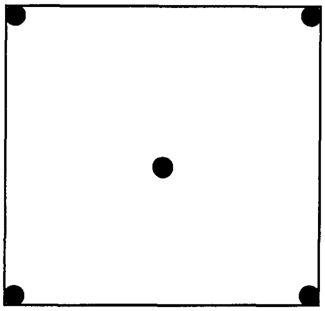


Fig 2.8 : The location of each of the five samples taken in every one hectare study plot

The aluminium sleeve and piston were washed or wiped clean before each sampling event to minimise cross contamination. All plots were approached from the bottom left hand corner (south to north) and the corner samples were taken in clockwise order to minimise any disturbance. The sample from the centre of the plot was taken last. Penetrability of the mudflats on the Forth Estuary can be locally variable making this type of sampling potentially dangerous due to the obvious risk of becoming 'stuck in the mud'. To help alleviate this risk an overshoe called a 'mud-shoe' (Merrimack, USA) was used. This device fits over the boot and acts to spread bodyweight over a large enough area to prevent sinking. This innovation enabled access to plots that would otherwise have been impossible to reach by foot and made walking on the mud considerably safer (see also George 1963). To further facilitate safety, samples were collected on the ebb tide, mobile phones were carried at all times and a co-worker remained on the shore should any difficulty arise. All mud cores were stored at -20°C prior to analysis. The samples for invertebrate analysis were all processed within 24 hours minimise the impact of predatory species.

2.4.2 Sampling by boat

Those plots that were too far out on the mudflats to reach safely were sampled from a small inflatable boat on the flow tide. The study plots were located using a hand-held satellite-assisted global positioning compass (Silva XL 1000). When the boat was in position over each sampling location a hand held Van Veen grab was lowered over the side and a 10x10x10 cm sample was hauled onboard. Before deployment over the side of the boat the grab is cocked open with a retaining latch, it is then hoisted over the side and lowered at *c*2m/sec. After contact with the bottom has been made (indicated by a slackening of the lowering rope) the tension on the rope is increased causing the lever arms to close the grab. The grab is then retrieved from the bottom and by opening the top doors the sample can be inspected.

2.4.3 Criteria for acceptable grab samples

To satisfy the needs of this study two important sample characteristics had to be met: sample condition and depth of penetration. An acceptable sample condition was judged to be one with an even surface and minimal disturbance. For infaunal sampling the sample depth should be at least 5cm but in this study it was decided to choose samples that were 10cm deep for the reason mentioned in 2.4.1.

Two 5x5x10cm cores were taken from this 10x10x10cm grab sample for examination using the aforementioned purpose-built aluminium corer, one for sediment analysis and the other for infaunal analysis. It was always ensured that this sample included surface sediments, and that the larger sample was not inverted or unnecessarily disturbed when deposited from the grab into a holding container. After each sample all the equipment was washed to prevent contamination of the next grab. After sampling each core was stored and labelled in the same fashion as the samples collected on foot. All the samples were gathered in late January to early February 2000.

2.5 Laboratory analysis of invertebrate samples

Each sediment sample was wet-sieved through a 250μm mesh to remove the entire sediment fraction so that subsequent counting and identification of the invertebrates could be undertaken as accurately as possible; all the infauna > 250μm in size were retained in the sieve. 250μm was chosen, firstly, so that the results of this study would be comparable to previous work (see McLusky *et al.* 2000) and secondly because Schlacher & Woolridge (1996) found that 45% of individuals sampled were lost when using a 500μm sieve and 92% with a 1000μm sieve. Crewe *et al.* (2001) also found that mesh size profoundly effected the retention of *Corophium* with more than 90% of *Corophium* less than 2 mm long passing through a 500mm sieve. Again this process was carried out for each sample within 24 hours to prevent loss of some species by predation. The retained invertebrates were then transferred to a labelled sample bottle where a solution of 4% formalin was added to preserve the animals. The formalin also contained rose bengal, a vital stain which coloured the animals aiding the counting and identifying process. Prior to counting, the formalin was washed off the sample, which was then placed in a petri dish in a small amount of water. As each sample is transferred from sieve to bottle then back into the sieve before transfer to the petri dish for counting, there is likely to be some loss of the sample. Great care was taken to avoid this, and as the same process was applied to each sample, any error was considered to be equal in all of them. All the invertebrates were identified to species and counted in each sample using a Wild M3Z observation microscope. The mean of the five samples was used in the final analysis. Some species were measured because it has been suggested that size or size class of animals, not just their density is an important factor in their choice as prey by shorebirds (Goss Custard *et al.* 1989). All bivalves (*Macoma, Mytilus* and *Cerastoderma*) and amphipods (*Corophium*) were measured using a mm scale taped to the base of a petri dish. To obtain accurate biometric measurements from *Hydrobia* a Polaroid DMC Ie digital microscope camera was used coupled to Image Pro Plus software. Measurements were obtained for major and minor axes, as well as longest and shortest length and total area. Measurements are initially given in pixels so the number of pixels in 1mm was first determined by measuring the distance between the mm marks on a metal rule. Ten measurements were made and the mean taken. In this case the mean was 67, therefore all initial pixel number measurements were divided by 67 to give dimensions in mm. As a 250μm sieve was used some of the smaller animals such as *Manayunkia* were retained. Only whole and undamaged animals were measured but worm species were excluded from the measuring process primarily due to time restrictions. Only the primary axis was measured on the bivalve molluscs as it was found that both the primary and secondary axes were highly correlated in a sub sample of measurements. *Corophium* were measured outstretched from the tail to head excluding the telson. As many of the animals such as *Corophium, Nereis* and *Eteone*, had become fragmented in the sieving process only heads were counted as representing whole bodies. Although nematodes were present in almost all the samples they were not counted. In retrospect this may have been a useful exercise as they are at least as large as *Manayunkia* quite abundant and rich in lipids so may be of some importance to species like the shelduck.

2.6 Laboratory analysis of sediment characteristics

2.6.1 Particle size

Many previous studies have used a combination of Bouyoucos hydrometry and dry sieving to determine particle sizes of estuarine sediments (Yates *et al.* 1993b, Goss Custard *et al.* 1989). Although this is normally a sufficiently accurate method it is very time consuming and provides only a limited amount of information about the characteristics of each sample. Sediment is commonly classified by their median particle diameters and is characterised accordingly (Table 2.2):

Table 2.2: Description of sediment particle size according to the Phi unit scale and micron ranges

Phi Units	**Microns**	**Character**
0-1	500-1000	Coarse sand
1-2	250-500	Medium sand
2-3	125-250	Fine sand
3-4	63-125	Muddy sand
>4	<63	Mud

As sediment structure is potentially an important predictor of shorebird spatial distribution, a more exact method of characterisation was adopted in this study. Instead of using traditional hydrometry techniques to size the sediment particles, a highly accurate laser diffractometry methodology was used. This method uses stream scanning to size and count individual particles in a suspension flowing past an array of sensors at rates of up to 10 000 per second (Coulter 1990). Its detection range is 0.04-2000μm with the instrument considering 116 sediment fractions, each being 1.098 times the size of the one before (Buurman *et al.* 1997).

Laser diffractometry collects information about individual sediment particles based on the principle that each one diffracts light through a given angle depending on its size. This angle decreases with increasing particle size (Beuselink *et al.* 1998). In order to gather the information two different diffraction theories can be used. The Fraunhofer theory is the default model operated by the particle sizing machine used in this study. This theory assumes that there is no diffraction of light only refraction. If there is any organic matter in the sample however, this may absorb some of the light so this assumption is not entirely accurate (Beuselink *et al.* 1998). The same authors noted that when they removed organic matter from silt/clay and sand fractions the grain sizes were not significantly affected when analysed with a Coulter LS 100. The lowest detection limit using this theory is 3.5 μm but Coulter suggests that it is inaccurate below 10um. Using the Mie theory in the detection algorithm the detection limit is lowered to 0.4μm. This theory assumes that all particles are spherical and have a homogenous refractive index so there is still room for error with particles < 10μm. For particles <0.4μm the Polarisation Intensity Differential of Scattered Light (PIDS) is used, lowering the detection limit again to 0.04μm. The PIDS measurements are added to the measurements obtained by diffraction sizing integrating the two analyses, so although two methods are used a single solution is obtained. In this study all the samples were analysed using a Coulter LS 230 Laser Grain Sizer with a 5-mW 750 nm laser beam and fluid module.

2.6.2 Sediment pre-treatment

In order to obtain a particle range representative of the whole sample it was manually homogenised by stirring for 30s before a sub-sample was removed for analysis. Although this action disturbs any micro strata that might exist within the sediment core it does allow the entire particle range to be examined. It is assumed that the invertebrates identified in the samples distribute themselves evenly throughout the core. Once homogenised the sample was placed in a glass vessel and oven-dried overnight to enable the sample weights for each plot to be kept to a standard. A sub-sample of *c*5g (mean = 5.25g +/- 0.44g, n = 272) was removed and placed into 100ml of hydrogen peroxide (100 volumes) to remove the organic matter. Although the detection range of the Coulter LS 230 is 0.04-2000μm, it is very difficult to obtain representative results if the sample is introduced into the machine in suspension. Even with small samples (*c*5g); when stirred they almost certainly contain suspended and non-suspended fractions making a truly accurate sub-sample difficult. In an attempt to avoid this each sample was passed through a 1000μm sieve to remove shell fragments, some invertebrates and other particles > 1000μm to reduce this coarse fraction (the fraction above 1000μm in all samples was negligible). The remainder was then retained in a sample jar for the final analysis. Sediment dispersant was used to help prevent any flocculation within the sample. To each sample, 10ml of Calgon (37g sodium hexametaphosphate and 7g sodium carbonate dissolved in 1l water) was added before it was placed on an automatic shaker for 1h to aid further particle dispersal. The sample was stirred using a magnetic stirrer before introduction to the Coulter Counter to evenly distribute the particles in solution. Typically a 10ml sub sample was introduced into the machines cuvette using a pipette. The sample was applied drop by drop until the PIDS registered about 40 – 50 % on the Coulter Counter. Each sample was run three times by the machine to account for any variation in the accuracy of the analysis. Where anomalous readings occurred that run was dropped from the analysis and the sample run again. The arithmetic mean values were taken for the output of these three runs.

One of the main difficulties in associating this kind of particle size evidence to invertebrate presence is that in preparing the samples for analysis (using any method) the samples become disaggregated and thus may not resemble the actual conditions that the invertebrates face when the mud is '*in situ*'. It may be that the majority of the invertebrates retained in the core are present only at a certain depth and ignore sediment structure below it. Alternatively they may be associated with the organic fraction, which may tend to bind the substrate or increase the range of particle sizes (Austen 1999).

2.6.3 Calculation of percentage (%) clay, silt and sand in each sample

The % volume of particle sizes was determined by the range of channel diameters through which the particles were able to pass and from this information the percentage of clay, silt and sand in each sample were calculated. Instead of using information derived from Phi units, as in the majority of shorebird sediment relationship studies, % clay, silt and sand were calculated using the size ranges defining these fractions as those recommended by the British Association for Soil Science (Table 2.3):

Table 2.3: Sediment character as described by micron range recommended by the British Association for Soil Science

Particle size (microns)	**Character**
< 2	Clay
> 2 and < 50	Silt
> 50 to 2000	Sand

It was decided to adopt these criteria for particle size classification (instead of those in Table 2.8) as it became obvious that the vast majority of the samples had a minimal amount of sand, making an irrelevance of sub-classifying this fraction any further. The % of clay, silt and sand in each sample was calculated using the run output data an example of which is shown in Table 2.10. % Clay was taken to be all values from measurement channels 0.04μm to 1.832μm, % silt was measured between 2.011μm and 47.94μm and % sand was measured between 52.62 and 1000μm.

Table 2.4: Example of the percentage volume of particles in one sample that were able to pass through channels of differing diameter. The % clay, silt and sand were calculated using such data output for each sample

Channel Diameter μm	Volume %	Channel Diameter μm	Volume %	Channel Diameter μm	Volume %	Channel Diameter μm	Volume %
0.040	0.000	0.656	0.397	10.780	3.410	176.900	0.000
0.044	0.000	0.721	0.515	11.830	3.830	194.200	0.000
0.048	0.000	0.791	0.639	12.990	3.600	213.200	0.000
0.053	0.000	0.868	0.760	14.260	3.150	234.100	0.000
0.058	0.000	0.953	0.867	15.650	2.910	256.900	0.000
0.064	0.000	1.047	0.947	17.180	3.010	282.100	0.000
0.070	0.000	1.149	0.984	18.860	3.300	309.600	0.000
0.077	0.000	1.261	0.970	20.700	3.610	339.900	0.000
0.084	0.000	1.385	0.895	22.730	3.730	373.100	0.000
0.093	0.000	1.520	0.765	24.950	3.570	409.600	0.000
0.102	0.000	1.668	0.582	27.390	3.290	449.700	0.000
0.112	0.000	1.832	0.380	30.070	3.120	493.600	0.000
0.122	0.000	2.011	0.151	33.010	3.080	541.900	0.000
0.134	0.000	2.207	0.014	36.240	3.070	594.800	0.000
0.148	0.000	2.423	0.000	39.780	2.950	653.000	0.000
0.162	0.000	2.660	0.000	43.670	2.590	716.800	0.000
0.178	0.000	2.920	0.023	47.940	2.060	786.900	0.000
0.195	0.000	3.205	0.312	52.620	1.710	863.900	0.000
0.214	0.000	3.519	1.020	57.770	1.750	948.300	0.000
0.235	0.000	3.863	1.890	63.410	1.870	1041.000	0.000
0.258	0.000	4.240	2.800	69.610	1.400	1143.000	0.000
0.284	0.000	4.655	3.480	76.420	0.757	1255.000	0.000
0.311	0.000	5.110	3.710	83.890	0.724	1377.000	0.000
0.342	0.001	5.610	3.380	92.090	1.060	1512.000	0.000
0.375	0.014	6.158	2.570	101.100	0.760	1660.000	0.000
0.412	0.039	6.760	1.580	111.000	0.155	1822.000	0.000
0.452	0.077	7.421	0.849	121.800	0.005	2000.000	0.000
0.496	0.131	8.147	0.708	133.700	0.000		
0.545	0.203	8.943	1.240	146.800	0.000		
0.598	0.292	9.818	2.350	161.200	0.000		

Mean and median particle size (μm) was also calculated from the Coulter output data. The mean of the five samples for each study plot was used in the final analysis for % clay, silt and sand and mean/median particle size.

2.6.4 Measurement of sediment penetrability

Numerous methods have been used to measure sediment penetrability: shorebird bill models (Kelsey & Hassall 1989) and compressive strength meters (Kalejta & Hockey 1991, Mouritsen & Jensen 1992, Sewell 1996) are examples. In the present study a measure of sediment shear strength and hence penetrability was taken using a shear vane. The shear vane was easy to transport to remote parts of the mudflats and simple to use. The shear vane consists of a vane of known dimensions attached to a 75cm rod, which is then screwed into the stress-measuring gauge. With the gauge set to zero the vane is pushed into the mud up to the required depth as marked on the metal rod and turned slowly in a clockwise fashion. When there is no longer any resistance to the vane and it spins freely in the sediment the shear stress can be recorded in ft lbs^{-1} in^{-2}. The gauge is then zeroed in readiness for the next reading. At each sampling station one measurement was taken at 5cm depth from the centre of each study plot. As it was impossible to access all the study plots by foot some were omitted from this part of the study. All measurements were taken during similar weather conditions (i.e. overcast), so that potential temporal variability in shear strength caused by increased drying on sunnier or windier days was reduced. Of the 50 plots around the estuary, shear vane readings were recorded for 34 of them. Caution should be given to penetrability measured at a given time because it can change significantly with length of exposure time to the air (Kalejta & Hockey 1991). Thus there is the possibility that the penetrability measurements obtained in this study were only valid at the time of measurement.

2.6.5 Calculation of % organic material in each sample

2.6.5.1 Methods of measuring organic matter

Parker (1983) compared the three most common ways of measuring the amount of organic matter in marine sediments using the following methods:

1. *Wet oxidation*: The carbon in the sediments is oxidised to carbon dioxide by excess potassium dichromate. The unused dichromate is then titrated against a reducing agent.
2. *Loss of volatile solids on ignition*: Samples are pre-treated with HCl, dried and then fired in a muffle furnace at 450°C and 600°C.
3. *Hydrogen peroxide treatment*: H_2O_2 is added to a sample of air dried sediment and the organic carbon is oxidised producing oxygen and carbon dioxide. Further aliquots of H_2O_2 are added until there are no further visible reactions.

It was concluded that all three of these methods were equally likely to provide an "adequate assessment" of organic matter levels in estuarine sediments. However, it is recognised that unless all workers use a standardised method, inter-study comparisons are difficult as estimations can vary widely. To compare the validity of these methods in this study, loss on ignition and hydrogen peroxide treatments were conducted on a subset of samples. This was done to see if significantly different estimates were reached using both methods, as the possibility of local sources of contamination on the estuary may lead to spurious results with loss on ignition.

2.6.6 Possible sources of carbon contamination

Local site characteristics around the Forth Estuary are variable and localised sewage, riverine organic inputs, oil wastes or contamination can bias results for percentage organic content of mud samples if such contamination is not considered. Coal dust derived from mine waste at Kinneil and power station ash at Torry Bay was observed in almost all the samples taken from Kinneil, Bo'ness and Torry Bay and ranged considerably in fraction. Often it was just a fine dust with particles < 500µm but many of the samples included large (>1cm) pieces. The inclusion of this fraction in any estimate of organic matter would seriously skew the results when using the loss on ignition method. Such coal particles were not digested during the H_2O_2 treatment therefore were not included in the estimate of organic matter content. Inclusion of the infauna in the sample to be tested is also a problem; unless each animal can be individually removed it is likely that an inaccurate figure for organic matter content will be obtained, however this would be an extremely time consuming task. Sieving of the sample down to 250um would remove some of the infauna but would most likely remove a proportion of the non-infaunal organics as well (Wolff pers com). Parker (1983) found that the density of estuarine invertebrates did not significantly affect the relative proportions of labile and refractory organic matter so in this study the infauna was included in the estimations and samples were taken as collected with no pre-sieving. This was considered reasonable, as the weight of the sediment sample taken for analysis was only 1g.

2.6.7 Comparison of methods of organic matter calculation

2.6.7.1 Loss on ignition

Loss on ignition is a commonly used method for estimating the amount of organic carbon in sediments, as it is essentially a rapid and economic way of doing so. The actual process employed by various workers however is highly varied and there is a considerable range of temperatures fired to, sample sizes used and lengths of time the sediment is heated. Luczak *et al.* (1987) attempted to standardise this variation in methods by working out the optimal temperature, time for ignition, and the influence of sample mass on the difference on ignition. Their results suggested that 500°C was the best ignition temperature although separation between organic and inorganic matter occurs between 500 °C and 550°C. Keeping the temperature at 500°C or below also prevents any error in the mass loss measured due to the combustion of calcium carbonate (Hirota & Szyper 1976). To avoid this error samples may be pre treated with 0.25M HCL (Buhl-Mortensen & Hoisaeter 1993) however this was not undertaken for this study as Roberts *et al.* (1973) found that HCl removed a significant fraction of the organic matter as well. Optimal combustion time was determined to be 6h as mass loss was significant until 4h in all tests after which it remained stable until 6h after which fluctuations in mass were attributed to loss of inorganic matter (Luczak *et al.*1987). In this study samples were combusted for 5h at 500°C in a Carbolite muffle furnace. Luczak *et al.* (1987) also found that sample size did not influence mass loss so in this study sample mass varied from 3.56 - 88.72g (x = 34.75g) depending on the availability of the sample.

2.6.7.2 Hydrogen peroxide (H_2O_2) treatment

Sediment samples were oven dried at 105°C overnight and a sub-sample of between 6.57 - 25g (x = 18.72g) was taken depending on the availability of the sample. The sediment was then lightly crushed with a rubber pestle and placed into a 500ml Erlenmeyer flask of known mass. Initially 100ml of 6% (20 volumes) hydrogen peroxide was added to the sample, which was then heated in a waterbath at 60°C overnight. If a visible reaction was still occurring after this time a further 100ml of $H_2 O_2$ was added and the sample was left until the reaction stopped. The samples were then oven dried again at 105°C and re-weighed. The percentage of organic matter was calculated by expressing any mass loss as a percentage of the original sample weight. The method used is a variation of those used by Buchanan & Longbottom (1970). Both these methods were compared on a subset of samples to determine whether coal dust contamination could be a potential problem for future studies. It was decided to use the data from the H_2O_2 treated samples in the final analysis using the mean figure from the five samples taken at each plot.

2.7 Tide height calculation (MACD)

For each study plot the height in metres above mean chart datum (MACD: the level of the lowest astronomical tide) was calculated (see Fig 4.1). This was used as a model parameter as it acted as a measure of mudflat exposure time with low values being exposed least, due to their proximity to the tidal channel. This measure was adopted as well as distance from shore as most of the mudflats have an uneven gradient so the rising tide can inundate the mud at one point on the shoreline before another. This is evident at Kinneil where the mud adjacent to the Bo'ness coal bing is covered about 45min before the last area of mud is inundated. At Kinneil, tide heights were calculated using data from a survey undertaken by Forth Ports Authority whilst information for all other sites was extrapolated from spot heights published on Admiralty chart for 'River Forth – Kincardine & Rosyth'.

2.8 Distance from shore calculation (m)

Distance from the centre of each study plot to the nearest shoreline was calculated using the appropriate function in the GIS package ARCVIEW. Distance to roost was not calculated as many of the species had multiple roosts at each site.

2.9 Site size calculation (ha)

Site size in hectares was extracted from the literature e.g. McLusky (1987) and Bryant & McLusky (1997)

2.10 Statistical analysis using generalised linear modelling

2.10.1 Assumptions made about the data

It was assumed that the birds were distributed evenly across each study plot, hence no sub plot level spatial variability was considered. It was also assumed that favoured prey do not vary spatially to such an extent that they may form dense aggregations at a scale less than 1ha. This is tested in chapter 5. It is also assumed that measured sediment characteristics are homogenous at the 1 ha scale. To account for some spatial variability, the mean value of five samples positioned around the plot (Fig 2.5) was used for invertebrate counts and sediment characteristics.

2.10.2 Models relating bird data to biotic and abiotic covariates for the four key species

Classical linear regression models make two important assumptions:

(i) Normal error distribution (i.e. Gaussian or bell-shaped)

(ii) Constant variance (i.e. independent of the mean)

Most of the data collected in this study however do not conform to these assumptions because they are count data, so *generalised* linear models were used. Such models do everything that a *general* linear regression model does, but also allows the construction of models with a range of different error distributions.

The object of this modelling process was to determine the *minimal adequate model* from the set of potential models with a view to usefully interpreting the data. The same process was followed for all models (Table 2.5)

Table 2.5: The stepwise deletion model fitting process for quasi likelihood using S-PLUS 2000 (Wilson 2001)

Step	**Procedure**	**Explanation**
1	Fit the maximal model	All the factors, interactions and covariates of interest were fitted and the residual deviance noted.
2	Begin model simplification	The parameter values were inspected and the least significant terms were removed first, starting with the highest order interactions, progressing on to lower order interaction terms and then main effects. Main effects that figure in significant interactions were not deleted.
3	If the stepwise deletion causes an insignificant increase in deviance	That term was left out of the model, then the parameter values were inspected again. The least significant term remaining was then removed.
4	If the deletion causes a significant increase in deviance	The term was put back in the model. This is a statistically significant term as assessed by deletion from the maximal model
5	Keep removing terms from the model	Steps 3 or 4 are repeated until the model contains nothing but significant terms. This is the minimal adequate model If none of the parameters is significant, then the minimal adequate model is the null model

A generalised linear model has three important properties:

1. *Error structure*: This essentially describes the shape of the distribution of residual values around the fitted model.

2. *Linear predictor*: The linear predictor is an equation predicting the value of y from various independent variables, but on the (transformed) scale determined by the link function.

3. *Link function*: The link function relates *the mean value of y,* μ, *to its linear predictor,* η and is essentially just a transformation. In all the models in this study this was set to 'Log'

2.10.3 Overdispersion

For a well fitting model, the residual deviance (rd) should be approximately the same as the residual degrees of freedom (df). The "empirical scale parameter" is the rd/df. Overdispersion means that there is more deviance than you would expect given the error structure, indicating that the underlying probability is not constant (randomly distributed data e.g. Poisson counts - require that there is a constant probability of an event happening in time or space). Overdispersion can occur if important factors have not been measured (so residuals are not randomly distributed but affected by the unmeasured variable) or if the underlying error structure is not correct.

Virtually none of the data collected in this study conformed to Gaussian, Poisson or negative binomial error structures so a 'quasi-likelihood' model was used in each case.

2.10.4 Correcting overdispersion using quasi-likelihood

Quasi-likelihood allows the data to specify the error distribution. Rather than supplying the error distribution and link, one specifies the variance and the link (in this case mu and log respectively). Because the empirical distribution is setting the scale parameter (rather than a theoretical distribution) the results from quasi-likelihood estimation are more approximate than a properly specified model. Because the empirical scale parameter is used, chi-squared tests are not appropriate to test the significance of terms, so F-tests were used instead.

2.10.5 The models

Minimum adequate models were calculated for each of the key species: shelduck, redshank, dunlin and knot. These data were modelled at two scales:

1. The whole estuary scale. This included data from Kinneil, Skinflats, Torry Bay, Boness and Kincardine Bridge combined.
2. The sub estuary or individual site scale. Only data from the two largest sites of Kinneil and Skinflats were modelled.

2.10.6 Model Parameters

The following data were used as covariates in the generalised linear models (Table 2.6):

Table 2.6: Covariates used in the quasi likelihood GLMs at the whole and sub estuary scale. For invertebrate size n was variable depending on the number of animals in the sample.

Data category	Data type
Invertebrates (mean count per plot, n = 5)	*Hydrobia* *Nereis* Oligochaetes *Manayunkia* Spionids *Nephtys* *Macoma* *Cerastoderma* *Corophium* *Eteone* *Mytilus*
Invertebrate length (mean (mm))	*Hydrobia* *Macoma* *Cerastoderma* *Corophium* *Mytilus*
Sediment characteristics (mean count per plot, n = 5)	Mean particle size % Clay % Silt % Sand % Organic matter Shear strength (ft lb^{-1} in^{2})
Other	Tide height (MACD) Distance from shore (m) Site size (ha)

2.11 Analysis of long-term data

If the models developed in this study, using data collected during one winter, are to be relevant in the future, it is important to be able to compare contemporary data on shorebird spatial distribution to that collected in previous years. Any long-term trends in mudflat usage by shorebirds may indicate a general temporal stability of spatial pattern. Statistical analyses of such spatial data however are difficult due to problems of spatial and temporal autocorrelation.

Physical (sediment characteristics) and biological (birds and invertebrates) variables in the estuarine environment often have well defined structures in time and space generated by spatio-temporal processes operating at a variety of spatial scales. For example the distribution of invertebrate species and densities are governed by salinity gradients, sediment structure and tide height among other things (McLusky 1989). This spatial structure will in turn influence the likely spatial configuration of the bird species that prey on them. Thus, the realisation of a variable at one location is dependent on its realisation at other locations close by (Simard *et al.* 1992). The data collected in this study is of a spatial nature locally and therefore exhibits spatial dependence as birds are present in adjacent grid cells (spatial autocorrelation), and temporal dependence due to stability of cell usage (temporal autocorrelation). This is due to the fact that most natural ecological phenomenon are geographically patchy at all spatial scales and don't exhibit large-scale homogeneity (Legendre 1993). Positive spatial autocorrelation is present in most spatial data in ecology (Lennon 2000) and is explained by Cliff & Ord (1973) in the following manner:

> 'If the presence of some quantity in a sampling unit makes its presence in neighbouring sampling units more or less likely, we say that the phenomenon exhibits spatial autocorrelation'.

2.11.1 Why is autocorrelated data a problem?

- Any measured variable of interest such as bird usage is likely to be influenced by the overall species assemblage structure at other locations. Because the value for usage at a grid square can be partially predicted by values in neighbouring squares the values cannot be considered independent therefore each new piece of data does not equal one full degree of freedom. The result of this is an artificial lowering of the P value inflating the estimate of the significance of an association. As independence of data points is one of the underlying assumptions of classical statistics then the results of any such tests should be treated with a great deal of caution (Roxburgh & Chesson 1998, Koenig 1999, Lennon 2000).

- Due to the non-independence of the data points (positive autocorrelation) the confidence interval around the correlation coefficient is narrower than it would be if calculated correctly, thus leading to an increased likelihood of a Type I error (Cliff & Ord 1981). This type of error occurs when there is an increase in the risk of concluding that a test statistic is significant where there is no association between variables (Dale *et al.* 1991) i.e. incorrect rejection of the null hypothesis.

Ignoring the problems listed above not only lead to difficulties in hypothesis testing but also to a bias towards a distorted understanding of ecological relationships. Lennon (2000) states:

‘ Past attempts to construct an importance hierarchy of explanatory factors influencing or explaining an ecological pattern may have only resulted in a ranking of these factors in order of their spatial autocorrelation strength.’

Scheiffarth *et al.* (1996) constructed a very promising model to predict the distribution of shorebirds on tidal flats in the Wadden Sea. Their model was constructed using the GIS package IDRISI and the coefficients of multiple regression models of bird usage against variables such as tide height and sediment particle size. All data were taken from 32 study plots arbitrarily placed in a small section of the mudflats and the results of the model extrapolated to the whole area. However spatial autocorrelation of these data was not considered.

In this thesis no statistical analyses were attempted on the long-term data. An attempt was made however to understand the temporal variation that exists in bird usage data between tide height contours. For each year the total percentage feeding effort of each of the key species was calculated for all the cells within the area bounded by two tidal contours, thus the mudflat area at Kinneil was partitioned in the following way (see Fig 4.1):

- 0.2-1 metres above chart datum
- >1-2 metres above chart datum
- >2-3 metres above chart datum
- >3-4 metres above chart datum
- > 4 metres above chart datum

The variation in the feeding effort within each area over time was then determined by calculating the coefficient of variation:

100 x standard deviation / mean (% feeding effort)

It would be expected that areas with low variance would display greater temporal stability of feeding effort than areas with high variance.

2.12 Spatially explicit study at Kinneil: GIS mapping and geostatistics

The Kinneil specific study was designed to use a spatially explicit statistical methodology to test the accuracy of the GLM approach when predicting the spatial distribution of overwintering shorebirds. It was also undertaken to determine whether the results of the GLM approach were likely to be compromised by the problems encountered with spatially autocorrelated data (see section 2.10.1). Increasingly GIS packages such as ARCVIEW (Austin *et al.* 1996) and IDRISI (Scheiffarth *et al.* 1996) have been used to model the spatial distribution of birds and to predict their distribution. These models have, however, relied on habitat data sourced from satellite information to create the base maps onto which bird spatial data was overlain. Such data are not readily available for the sites in this study at the small spatial scale required for accurate interpolated maps.

For the maps of bird distribution complete data was used. The Kriging interpolation was then applied to smooth the data map contours to give an even predicted distribution surface. All the maps were created in ArcMap and the Kriging carried out using the ArcMap spatial analyst extension. A brief overview of the geostatistical methodology is given below.

2.12.1 Geostatistics

In order to deal with some of the potential data autocorrelation problems already mentioned, geostatistical methods were incorporated into the analysis. Geostatistics is a set of tools used for characterising spatial variation, spatial prediction, spatial simulation and sampling design. In recent years geostatistics has been widely used in ecology as a way of mapping and estimating variation and pattern in spatially distributed data (Zirschky 1985, Rossi *et al.* 1992). Geostatistics is applicable to any spatial data and has been used to map distributions of plants (Donald 1994, Bellehumeur *et al.* 1997, Saetre 1999), insects (Gribko *et al.* 1995, Cesaroni *et al.* 1997, Crist 1998, Darnell *et al.* 1999, Dennis *et al.* 2002), marine invertebrates (Nicolajsen & Conan 1987, Gonzalez-Gurriaran *et al.* 1992, Simard *et al.* 1992, Bushek *et al.* 1998), fish (Pelletier & Parma 1994, Maravelius & Haralabous 1995, Patigas 1998, Rueda 2002) and birds (Villard & Maurer 1996, Carroll 1998, Pearson & Carroll 1999, Pereira *et al.* 1999, Linder *et al* 2000, Diniz *et al* 2002).

Geostatistics is based on the principle of spatial dependence (or spatial autocorrelation): observations that are close together in space tend to be more similar than those further apart. Therefore, if the spatial distribution of some variable is structured (as opposed to being random) geostatistics may be useful in some capacity. Such techniques provide quantitative tools for analysing spatial data and are generally centralised around the 'general regionalised variable model (GRVM)' (Matheron 1963, Haining 1990, Cressie 1991). The GRVM is a linear model of a spatial process that includes an explanatory component and a random component, which generally contains spatial correlation (Villard & Maurer 1996). It is therefore implicitly assumed that the predicted values are correlated with each other and the study of such a correlation is often referred to as variogram or semivariogram modelling

2.12.1.1 The variogram

The variogram underpins all of geostatistics. The variogram is used to model the way two values in space or time are correlated. It is likely that that two values in space that are close together tend to be more similar than two values farther apart and, as has already been mentioned, univariate statistics cannot take this into account. Two distributions might have the same mean and variance, but differ in the way they are correlated with each other. Geostatistics allows quantification of the correlation between any two values separated by a distance **h** (usually called the lag distance) and uses this information to make predictions at unsampled locations. Variogram modelling is a prerequisite for kriging, or making predictions.

2.12.1.1.1 How is a variogram calculated

Below is a brief description of the calculation method as described by Armstrong (1998), the software program GSLIB was used to automatically calculate all variograms. Firstly a lag increment (or spacing between any two points in the data) is defined. This distance may be for example 500m. All pairs of values separated by 500m are then taken and for each pair the difference between that number of pairs and the total number of pairs is calculated and squared. All the differences are summed and divided by twice the number of pairs. This gives the value of the variogram for that particular lag increment or distance. The same process is repeated for other lag distances e.g. 200m, 300m, 400m, and so on. The variogram value versus the lag distance is then plotted (Fig 2.6).

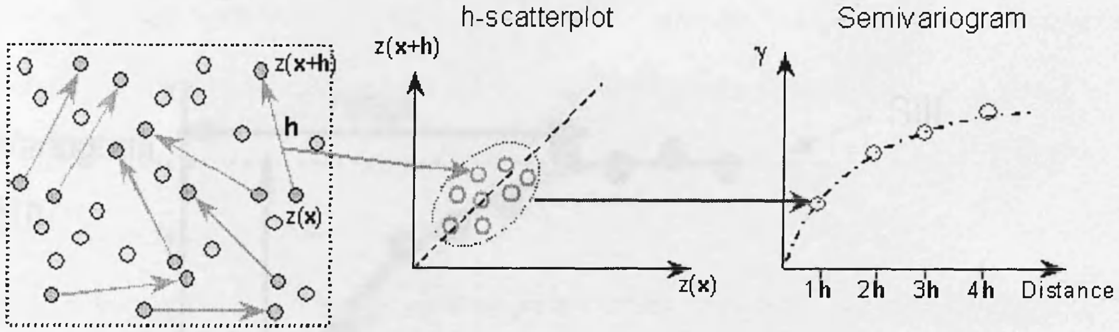


Fig 2.6: The calculation process illustrating how the experimental variogram is calculated from the initial sample map (from Wang *et al.* 1999)

In general, at smaller lag distances, the value of the variogram would also be smaller. For larger lag distances, the value of the variogram would be larger. This is because, values separated at small distances tend to be more similar compared to values separated at a larger distance. However, at a lag distance called the "range" the variogram would typically stabilise. The value of the variogram at this point is called the sill. At distances greater than the range, any two pairs of values are independent of each other

Variograms are usually described using three parameters (Fig 2.7):

- *The nugget*: this may indicate how much noise there is in the data, or the degree to which sampling has not been carried out at the smallest distance scales. In this study sample distances ranged from 50m to 3000m.
- *The range*: this is the lag distance at which all successive values are independent of each other i.e. it represents the distance beyond which the spatial autocorrelation being studied is effectively zero. All data up to this point are correlated.

- *The sill*: this is the variogram value corresponding to the range and measures the component of variance explained by that model.

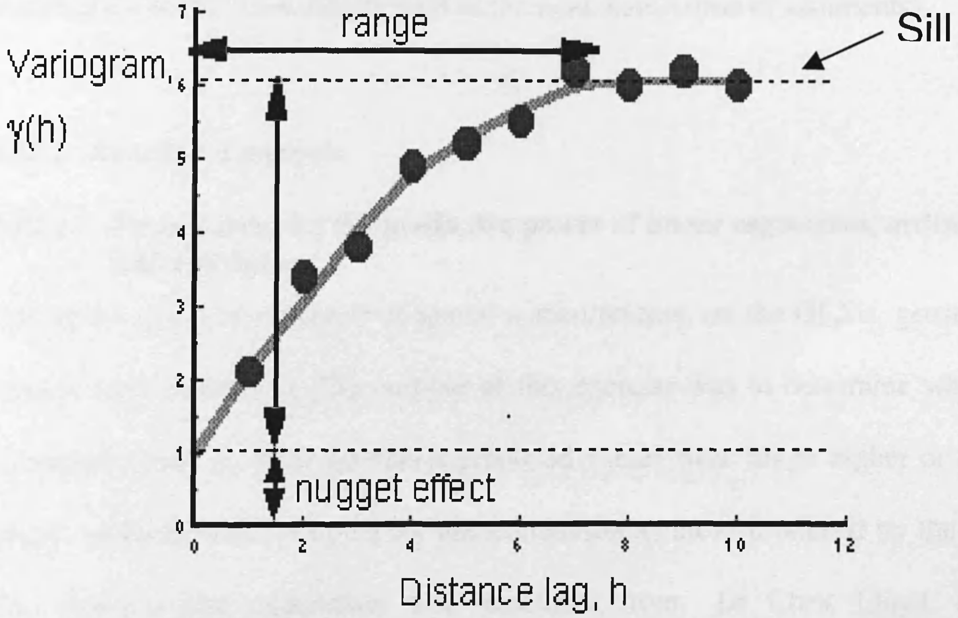


Fig 2.7: An example of a typical variogram illustrating the range sill and nugget effect components as described in 2.11.1.1 (from Wang *et al.* 1999)

2.12.1.2 Kriging

Once the variogram has been calculated predictions at unsampled locations are made using Kriging. This is a weighted average technique and can be used to assign an estimated value to a particular location (point kriging) or block (block kriging). The semivariance provides a method for developing maps of variation in abundance of for example invertebrate density or sediment characteristics using the data from the sampled locations and kriging interpolates abundances between these sample locations using the semivariance. As the semivariance represents the spatial covariation it contains information about what values are likely to be obtained for points within the neighbourhood of a sampled point. The estimation is a weighted combination of the sample values around the point to be estimated. The advantage of kriging is that it allows the observer to quantify the quality of the predictions via the kriging variance. Kriging also takes into account redundant data and possible anisotropies (directional effects such as the tidal distribution of sediments).

2.12.2 Structural analysis

2.12.2.1 Cross validating the predictive power of linear regression, ordinary kriging and cokriging

Due to the potential influence of spatial autocorrelation on the GLMs, geostatistical spatial models were developed. The purpose of this exercise was to determine whether the cross validation errors of observed versus predicted values were lower higher or the same using spatial methods which account for autocorrelation as those produced by the GLM method. This analysis was undertaken with assistance from Dr Chris Lloyd, Department of Geography, Queens University, Belfast.

Cross validation was used as a means of assessing the results obtained using each of the techniques. For both kriging methods the values were kriged, assuming that a particular sample was missing. The kriged values and the actual values were then compared. The difference between these values (the cross validated residual) was then assessed. Cross validation however does not prove that the variogram model is correct, just that it is not grossly incorrect (Cressie 1991). For the linear regression approach 30 data files were created each with a different data point missing, the coefficients of the minimal model were used to predict the location from which the data was extracted, i.e. (i) remove a data point (ii) estimate it using the other data (iii) put the data point back (iv) for another data point go to step (i). This is a standard procedure for assessing the performance of different interpolation procedures (Armstrong 1998). The summary statistics based on the cross validation errors were then calculated (e.g. summary of estimated values minus true values). These included the maximum negative error, the maximum positive error, the mean error and the root mean square error.

2.12.3 Constructing weighted area maps of actual and predicted bird feeding effort at Kinneil

Although shorebirds range widely around Kinneil during their feeding activities, inevitability some areas are preferred more than others due to locally important characteristics such as areas of high prey density or point sources of organic enrichment. A good knowledge of the spatial preferences of shorebirds at the sub site scale can be highly informative when making management decisions or determining the potential effects of habitat loss or change. With this objective in mind, *weighted area models* for each of the four key species at Kinneil were constructed and designed to highlight the most important feeding areas.

The coefficients from the *minimal adequate model* for each species were inputted into Arcview spatial analyst and acted on the spatial information contained in the kriged surfaces for each of the significant predictor variables. This extracted all the data relevant to those coefficients from each data surface and related it directly to bird feeding effort. This essentially 'lifts the veil' of the kriged 'actual' feeding effort surface and reveals only the areas of greatest importance to each species according to the model. It therefore identifies 'hotspots' and favoured areas within the whole general area that was used for feeding during the Winter of 1999/2000 and indicates whether feeding effort is likely to be spread widely throughout the entire area, focused locally, or a mixture of both. These weighted area maps were compared to kriged ‘actual’ feeding effort maps. Kriging was applied to complete data to create a smoothed distribution surface. This predicted bird feeding effort at observed and unobserved location and helped to account for the limited number of observation periods spent collecting spatial feeding effort data at this site (see McNeill 1991)

Chapter 3: Models predicting shorebird feeding effort on the Forth Estuary

3.1 Introduction

This chapter is divided into two sections. Section A describes the spatial variation of shorebird and invertebrate numbers and sediment characteristics, throughout the estuary and considers reasons why such variation, where it exists, may occur. Section B focuses on the results of the GLMs linking environmental variables to bird feeding effort at the whole estuary and sub estuary scale and presents the weighted area maps for bird feeding effort at Kinneil derived from the model coefficients.

3.2 Methods

The general methods describing sampling and analysis techniques for the bird observations and sediment and invertebrate sampling as well as the statistical analysis techniques used are given in chapter 2. The Kinneil specific model is tested using geostatistical methodology and the cross validations errors presented. Interpolated surfaces of all bird feeding distributions and all the key environmental variables were generated using ordinary kriging and Dr Sandy Winterbottom of the Department of Environmental Sciences, University of Stirling, constructed maps for these using ARCVIEW GIS. Coefficients from the GLMs were entered into the GIS and maps of the predicted distributions of key species were generated using information from the kriged maps of the relevant variables. These *weighted area maps* are then compared to actual distribution data. These maps act to summarise the statistical analysis in a visual manner and aim to highlight the areas of greatest conservation importance for each of the key species. Areas of high importance are weighted accordingly. Kinneil was chosen for this detailed analysis, as it is the largest and arguably the most important site for shorebirds on the Forth Estuary.

Section A: The variability of shorebird and invertebrate numbers and sediment characteristics at the main study sites of Kinneil, Skinflats and Torry Bay

3.3 Distribution, behaviour, density and roost sites of the four key bird species

3.3.1 Shelduck

The majority of shelduck using the Forth Estuary between December and February 1999/2000 were concentrated on the two largest mudflats: Skinflats (mean = 227 SD = 32) and Kinneil (mean = 178, SD = 64.5) with smaller numbers found at Torry Bay (mean = 21.7, SD = 15.4) (Figs 1-3). Birds tended to feed in loose flocks of up to 150 birds often keeping some distance from their nearest neighbour (up to 50m, as determined by a Bushnell Yardage pro 1000 laser rangefinder). Most of the feeding birds were observed scything their bill from side to side in the upper few centimetres of the sediment, this action left characteristic tracks in the mud thus making it possible to determine where birds had been feeding without actually being there to see them. This behaviour suggests that they prefer to feed in mud that would offer the least resistance.

Shelduck would often feed close to the shore at all sites but are easily disturbed and inclined to spend longer periods further out on the mudflats if disturbance is continued and prolonged (Burton *et al.* 2002, pers obs). During both winters 1998/1999 and 1999/2000 shelduck were observed out on the mudflats all the time that it was exposed although they were not always feeding. Feeding effort appeared to increase during periods of heavy rain possibly because of change in prey behaviour or maybe because the mud surface had become more fluid. The main roost at Kinneil was the lagoon adjacent to the refuse tip behind the seawall. This site was shared with the vast majority of the birds that fed at Kinneil. At Skinflats shelduck would feed at all distances from the shoreline but a marked preference was noticeable for high-level areas within 100m of the saltmarsh. Here birds would roost on the saltmarsh margins or on the small brackish lagoons in the fields behind the mudflats. Birds feeding at Torry Bay preferred to feed mostly on the very liquid mud (shear vane reading = 0.09 ft/lbs in^2) at the mouth of the Bluther Burn but singletons would feed wherever there was mud; sandier regions as determined by ground truth data, were noticeably avoided.

3.3.2 Redshank

Redshank were found at all study sites around the estuary and were seen feeding in widely dispersed loose flocks as well as much denser large flocks of up to 800 individuals. Birds generally began feeding as soon as the mud became exposed although sometimes, large roosts would remain for some considerable time before the birds dispersed to feed. This only occurred in the early morning as the tide was receding and it was assumed that these birds had been feeding at night. It was noted that groups of birds did not move very far from roost sites in order to feed and appeared to have some feeding site fidelity at the sub mudflat scale. Groups of birds similar in number could be seen feeding in exactly the same areas of mudflat on successive visits to each site both within and between winters. Although it was not determined whether these were the same birds it was possible that there was enough food close to the roost sites to sustain the populations of redshank at Kinneil, Skinflats and Torry Bay throughout the winter. Although some birds dispersed to lower shore areas of the mudflats, redshank mostly remained as a high level feeder throughout the study period, often feeding within 100m of a sea wall or the MHWM. At Torry Bay the vast majority of the birds fed throughout the tide near the Bluther Burn in the same area as the shelduck. Small groups of up to 20 birds were also seen feeding amongst the stonier substrates and in areas where algal mats were present. As has been found by Metzmacher & Reise (1994) and Lewis & Kelly (2001) these mats appeared not to deter or prevent redshank from feeding. Numbers remained fairly consistent throughout the winter of 1999/2000 (mean = 96.33, SD = 7.09). Not only is this area the most sheltered part of Torry Bay (redshank have been shown to be vulnerable to exposed conditions (Mitchell *et al.* 2000)) but it also had locally high densities of *Corophium*. *Corophium* is a favoured food item of the redshank (Goss Custard 1969, 1970, 1976, Bryant 1979, and Zwarts & Wanink 1993). The main roost for redshank at Torry Bay was also at the burn mouth.

At Kinneil, birds distributed themselves all around the mudflat but rarely fed more than 500m from the shore. High concentrations were noted around the freshwater inputs onto the mudflat, especially the Avon mouth, Grange Burn, and by the Bo'ness bing. Groups of up to 200 birds also fed on the banks of the Grange Burn up to 800m from the main mudflat. These birds would remain through the tide and were often joined by birds at high tide when the Kinneil intertidal was completely inundated, as the banks remained exposed for up to 30 min after the main site had been covered. These Grange Burn birds roosted on the saltmarsh on the banks of the river. Although *Corophium*, are associated with low salinity (Goss Custard 1969, Goss Custard 1970, Goss Custard & Jones 1976), none were found at sample stations adjacent to these areas. Birds would often utilise the mudflat creek although it was not clear whether this was for cover from predators, shelter from wind or because of higher densities of favoured prey items. Redshank fed throughout the tidal cycle as long as mud was exposed and often seemed reluctant to move to their roost sites. The main roosts were located on the seawall by the Avon mouth (up to 500 birds) and the main Lagoon. Various smaller roosts were located on the seawalls skirting the edge of the mudflat. Up to 80 birds also regularly used the small mudflat at Bo'ness feeding almost exclusively by the freshwater input at this site and almost always within 200m of the shore. These birds roosted at the old Bo'ness docks, which is infilled with mud and remains exposed for 40 minutes after the Bo'ness mudflat is covered. Birds moved to this site to continue feeding after the Bo'ness mud had become inundated by the tide.

The birds feeding at Skinflats roosted almost exclusively on the seawall piers next to the River Carron and at the saline lagoons in the fields opposite. They moved on to the mud to feed the moment it was exposed and remained mostly within 300m of the shore. Some birds dispersed downshore but these were generally singletons or loose flocks of up to 20 birds. Again extensive use was made of the creeks and large flocks were often seen feeding on the banks of the River Carron. Densities of birds declined towards the Kincardine Bridge where invertebrate density was markedly lower and the sediment more compacted. A secondary roost of up to 60 birds was sited on the saltmarsh by bridge. Birds were rarely observed moving far from their main roost to feed and they appeared able to satisfy their energetic needs within its vicinity. Short distances between high tide roosts and low tide foraging areas has been suggested as an important criterion for habitat selection (Swennen 1984, Scheiffarth & Nehls 1997).

Redshank were sparse above the Kincardine Bridge with only small loose flocks in the Airth and Dunmore areas. Most birds in this area fed on the mud at Kennet Pans.

At all the study sites on the estuary redshank fed by one of two methods:

1. *Sight feeding*: this involved slow deliberate pacing across the mud interspersed with short dashing runs to take items from the surface or just below it by pecking or probing, sometimes right up to the base of the bill.

2. *Touch feeding*: this usually occurred when the birds were in dense flocks and involved continuous deep probing, often moving the bill from side to side in more fluid mud.

The successful capture of a prey item was often accompanied with a backward jerking movement of the head indicating that it had been swallowed.

All the birds observed in this study were feeding in relatively dense flocks (although actual densities were not recorded) so it might be expected that an anti predator response was occurring (Selman & Goss Custard 1988) making it difficult for birds to feed in the same area. However, Yates *et al.* (2000) found that redshank would feed far less often than would be expected by chance in 1m^2 areas of mud that had recently been exploited by another redshank. By avoiding areas where prey would have been recently exploited, the feeding rate of redshank was up to three times faster than it would have been had they not avoided other foraging redshank. Interference through prey depression occurs because the proportion of vulnerable prey (and hence intake rate) decreases as predator density increases. However, Stillman *et al.* (2000) showed that, by adjusting its search path to avoid areas of depressed prey, a redshank can substantially reduce the amount of the interference it experiences. Speed of pacing was not recorded in this study but Speakman & Bryant (1994) predicted an inverse non-linear relationship between speed and prey encounter density such that in most circumstances predators will search at less than their maximum possible searching speeds.

Intake rates at Skinflats of 15.90 items/min compares closely to 14.74 items/ min calculated by Warnes (1981) and although this does not necessarily suggest that food availability now is similar to levels 10 years ago but it may indicate that spatial variability in invertebrate distribution is similar.

3.3.3 Dunlin

During the winter of 1999/2000 Kinneil supported the largest number of dunlin with a peak count of 5630 birds recorded in December 1999 (Fig 3.2). Skinflats was the second most important site with a peak count of 2176 birds between December and February 2000 (Fig 3.4). Torry Bay was virtually unused with just a single bird seen in February 2000. This is in marked contrast to previous studies (Elliot 1979, Bryant 1979), which found that dunlin used Torry Bay in reasonable numbers but loss of habitat at this site induced significant declines in the number of dunlin using the site (McLusky *et al.* 1992). Where it was more abundant the dunlin preferred to feed in large flocks of up to c 2500 birds although these flocks were rarely as large and as dense as those of knot. At Kinneil, many smaller flocks of up to 100 birds were scattered around the mudflat, often feeding very close (within 100m) to the seawall. These birds were at some considerable risk from predation from sparrowhawks, merlins and peregrines (Buchanan *et al.* 1988, Buchannan 1996, Cresswell 1996) and a number of attacks were observed. The larger flocks seldom came within

500m of the shore until forced to do so by the incoming tide. These dunlin were almost always observed feeding with hardly any loafing observed at all; their characteristic ‘stitching’ style of feeding was supplemented by careful individual probes, which were more noticeable when the flocks were smaller.

At Kinneil the main roost was the lagoon and they were almost always last in to roost, tending to feed longer in the >4m tidal contour than any other species. Equally, they were very prompt to begin feeding when the mud became exposed again on the ebb tide. At Skinflats, larger flocks were more inclined to feed closer to the shore (< 200m) and this may have had something to do with the location of their roosts which were almost exclusively on the stone training wall beside the River Carron allowing rapid access to the mudflats. Large flocks of dunlin were often noticed leaving for and coming from the mudflat at Kinneil (it was assumed), such interchange may be linked to density dependent pressures on feeding requirements. Flocks of dunlin were often restive at Skinflats when the tide inundated the mud and would often spend long periods in flight rather than settle down to roost, this may be a way of avoiding surprise attacks from raptors (Dekker 1998, Hotker 2000). Some of these dunlin, observed flying at high tide moved some distance inland before moving back to the mudflat area and may have used the pastures behind the seawall as foraging areas possibly as a trade off between food energy requirements and predation risk from falcons (Butler 1999). The lack of Dunlin at Torry Bay is surprising as potentially suitable feeding habitat exists there although factors such as site size and level of disturbance may now determine dunlin preference for this site.

3.3.4 Knot

Knot were present in large numbers at Kinneil throughout the winters of 1998/1999 and 1999/2000. They almost always fed in large dense flocks of up to 2000 birds and characteristically kept close to the waters edge rarely coming within 500m of the MHWM except when forced in by the tide. Their only roost at Kinneil was the main lagoon where all the birds would gather when the mud was completely inundated. Due to their highly mobile nature, the knot would occasionally be absent from the Kinneil site for successive visits, choosing to feed either at Skinflats or elsewhere on the estuary. When knot were driven together by the rising tide they would often form mixed flocks with dunlin and continue to feed until the mud was almost covered. They would then either head back to their lagoon roost or move around to Skinflats for another 45 minutes or so, until this site was covered. Large flocks of up to 3000 birds would also occasionally visit the small mudflat at Bo'ness probably due to the small size of the site these birds were invariably restless and rarely fed for very long. Like dunlin, the knot were probably undercounted on occasion as they wandered out of view into the numerous creeks out on the mud. This is especially a problem at Skinflats where the creek system is particularly dense when compared to Kinneil and Torry Bay (pers obs).

Knot usage at Skinflats was sporadic and flock sizes were never as large as they were at Kinneil reaching a maximum of 600 birds, the mean monthly peak count (December to February) here was 267 (SD = 306) (Fig 3.4). This large standard deviation reflects the fact that no birds were observed at Skinflats in December 1999. Visits would often only be relatively short with the flock moving on after an hour or so. No roost sites were located at Skinflats.

During the winters of 1998/1999 and 1999/2000 knot were completely absent from Torry Bay during the observation visits but it may be that birds did visit the site on occasion. Knot were never seen north of the Pow Burn on Skinflats or at any of the sites above Kincardine Bridge.

3.4 Bird count data from the three main study sites: Winter 1999/2000 (peak daily counts: November – March and peak monthly counts December to February)

Considerable variation exists in the count data for each site (Kinneil, Skinflats and Torry Bay) for each set of observations, as populations of the key species fluctuated with both within and between winter months. Figures 3.1, 3.4 and 3.7 show the variation in daily peak counts recorded throughout the 1999/2000 winter. Peak monthly counts are also given here in Figures 3.2, 3.5 and 3.8. Counts from December to February only are presented, as count data were only available for all the sites during these mid-winter months. Some of the variation in counts may be due to count error. Peak counts were recorded when the vast majority of the birds were most visible i.e. at their roosts or just as they began to feed on the ebb tide.

3.4.1 Kinneil

At Kinneil numbers of shelduck (mean daily peak count = 191.5, SD = 96.5) and redshank (mean daily peak count = 502, SD = 182.4) fluctuated only slightly within and between months indicating relatively stable populations at this site. The peak daily count of 720 birds was however in early November and probably contained numbers of passage birds moving to other sites or estuary complexes. Although there may have been interchange of birds between Kinneil and other sites this appears to have been fairly minimal. Dunlin (mean daily peak count = 2896, SD = 1362) and knot (mean daily peak count = 1681, SD = 1115) were highly variable in numbers throughout the winter months although their relative population sizes appear to follow a similar pattern (Fig 3.1).

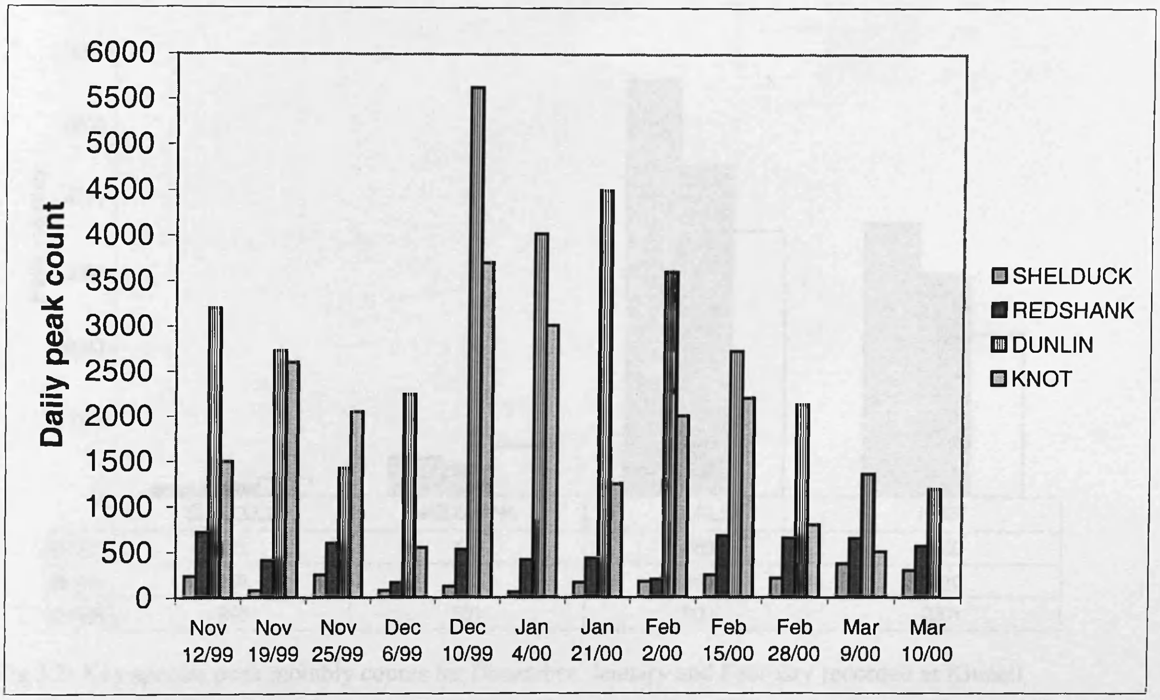
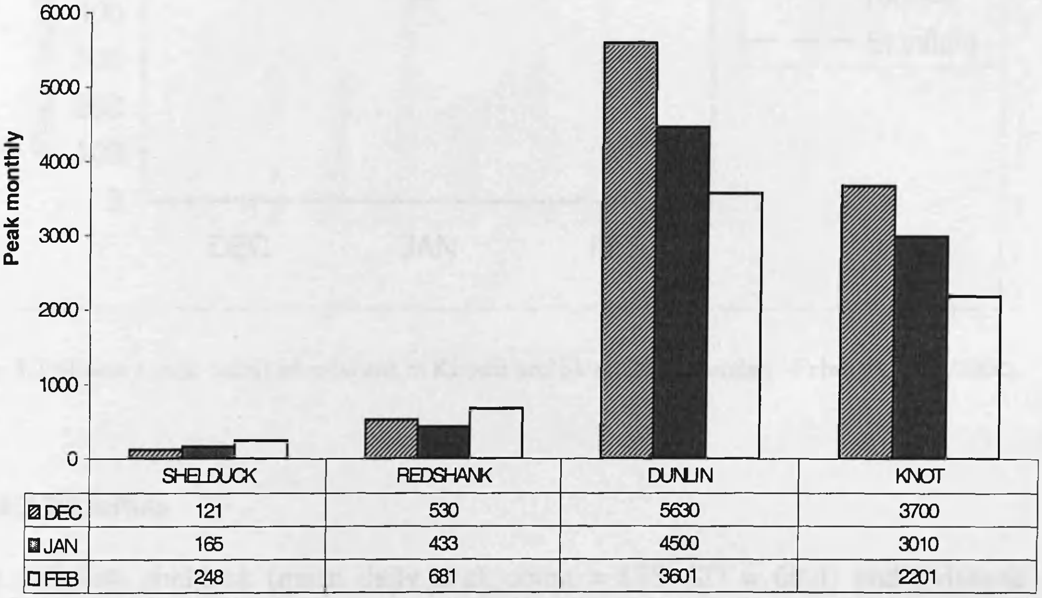


Fig 3.1: Daily peak counts of the key species recorded at Kinneil during the winter of 1999/2000

Figure 3.2 considers the peak monthly counts during the three main winter months, defined here as December, January and February. Shelduck numbers gradually increased at Kinneil as the months progressed peaking at 248 birds. These birds may have moved to Kinneil from Skinflats or from other sites around the Forth Estuary possibly in search of greater or more accessible food stocks. Redshank numbers dipped to 433 in January from a December peak of 530 and rose again to 681 in February, presumably due to interchange of birds between Kinneil and Skinflats as a similar pattern is observed in the population of redshank at Skinflats (Fig 3.3). Numbers of both dunlin and knot gradually declined between December and January possibly as birds dispersed themselves around other sites on the Forth

Estuary or because they were beginning to move north to their breeding grounds by late February.



	SHELDUCK	REDSHANK	DUNLIN	KNOT
▨ DEC	121	530	5630	3700
■ JAN	165	433	4500	3010
☐ FEB	248	681	3601	2201

Fig 3.2: Key species peak monthly counts for December, January and February recorded at Kinneil

Figure 3.3 shows that there was possibly a large movement of redshank from Kinneil to Skinflats during January and that by February these birds had moved back to Kinneil along with other birds that may have moved to this large site from other smaller areas. These peak counts are considered reasonably accurate as they were high tide feeding counts (not roost counts where birds from numerous sites could gather).

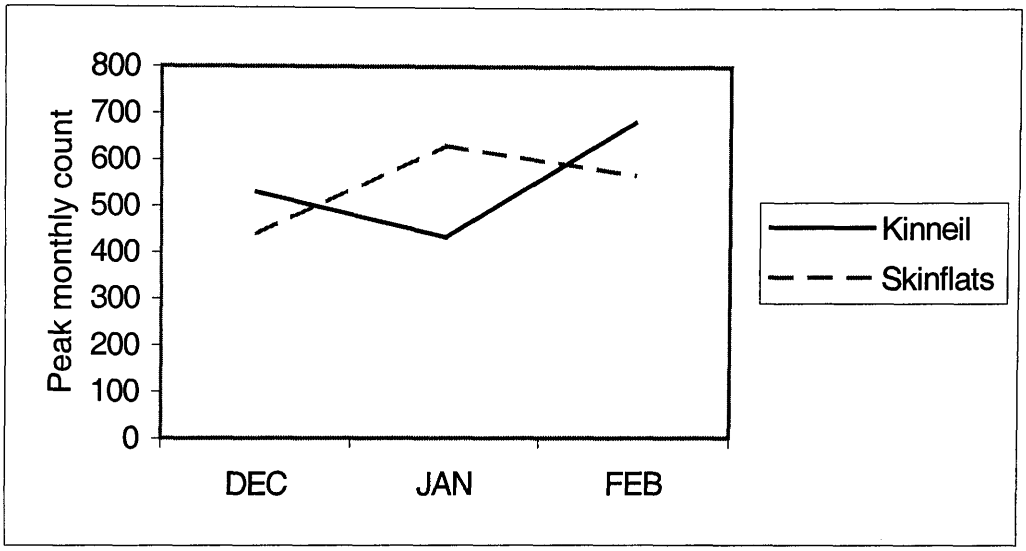


Fig 3.3 Monthly peak counts of redshank at Kinneil and Skinflats (December –February 1999/2000)

3.4.2 Skinflats

At Skinflats shelduck (mean daily peak count = 175, SD = 60.4) and redshank (mean daily peak count = 435, SD = 188.3) maintained fairly stable numbers of birds throughout the winter (Fig 3.4). Redshank numbers fluctuated at Skinflats somewhat more than they did at Kinneil (CV = 43.28 and 36.33 respectively) but much of this can probably be explained by occasional movements of birds to the upper area of Skinflats above Pow Burn on particularly cold days when the temperature approached 0°C (pers obs). Dunlin was the most ubiquitous bird at Skinflats and numbers, although lower than at Kinneil (mean daily peak count = 1606, SD = 690) gradually rose from December to February as numbers at Kinneil declined (see Fig 3.6). The sharp fluctuation in February may indicate more regular movements away from Skinflats. Knot were present sporadically and never in any great number (Fig 3.5)

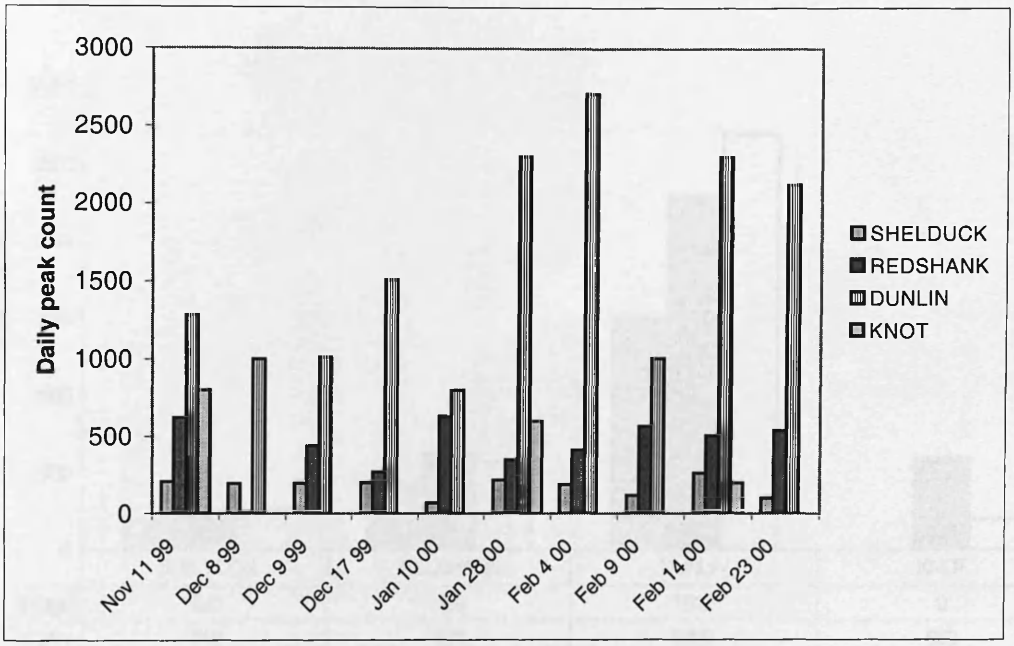
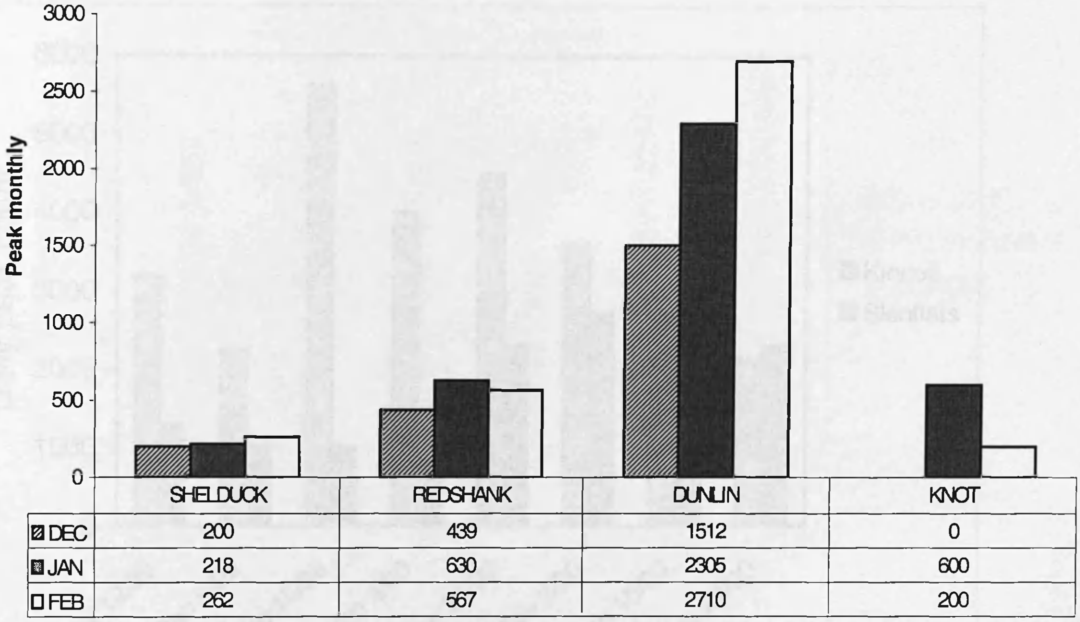


Fig 3.4: Daily peak counts of the key species recorded at Skinflats east of the Pow Burn during the winter of 1999/2000

Peak counts of shelduck at Skinflats also rose each month as they did at Kinneil, peaking in February with 262 birds. Overall there were more shelduck present at Skinflats than there were at Kinneil throughout the winter. Redshank numbers were similar to those at Kinneil and appeared to fluctuate in tandem with the Kinneil population as has already been mentioned (Fig 3.3). The dunlin peak of 2720 birds in February is still lower than the Kinneil low of 3601 birds, also in February. Knot only arrived at Skinflats in occasional flocks and never spent very long feeding. The largest of these groups (600 birds) arrived on February 4th 2000 and only fed for 2 hours before moving on.



	SHELDUCK	REDSHANK	DUNLIN	KNOT
▨ DEC	200	439	1512	0
■ JAN	218	630	2305	600
□ FEB	262	567	2710	200

Fig 3.5: Key species peak monthly counts for December, January and February recorded at Skinflats east of the Pow Burn

Figure 3.6 illustrates comparative counts of dunlin taken at the two sites (all pairs of counts are taken within one week of each other) and shows that numbers at Skinflats rose at about the same time as a decline in numbers at Kinneil. It may be that during February large numbers of birds moved from Kinneil to Skinflats, possibly in response to some density dependent pressure.

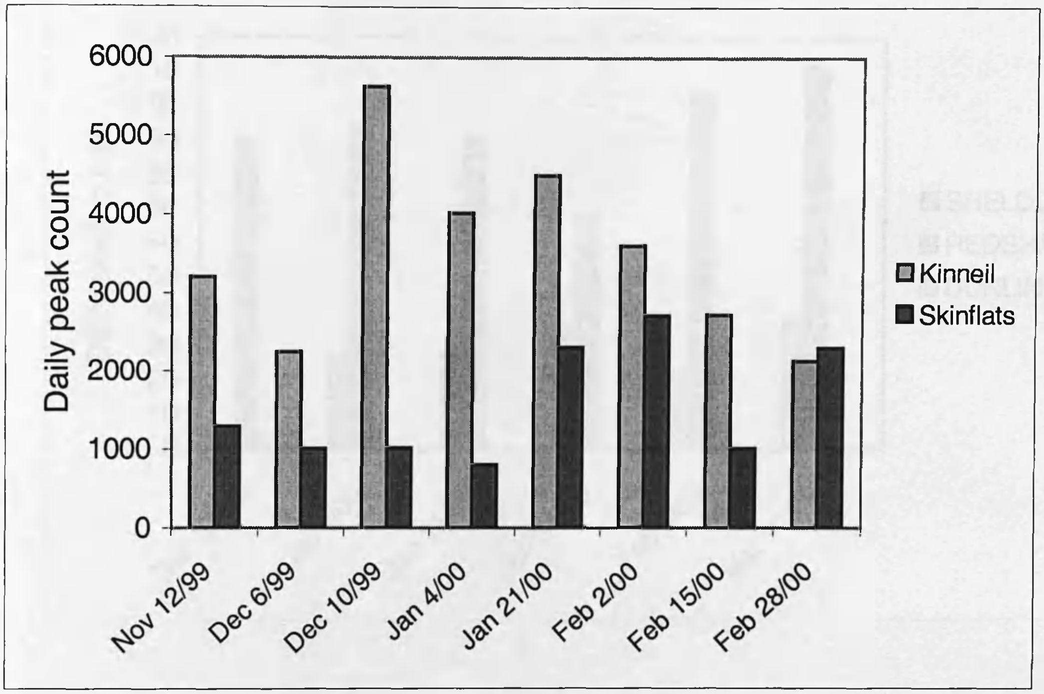


Fig 3.6: Comparative pairs of daily peak counts of dunlin from Skinflats and Kinneil taken between November and February 1999/2000. Counts taken within a week of each other.

3.4.3 Torry Bay

Torry Bay was the smallest of the main study sites and also supported the lowest numbers of the key species. Although there are nearly 200ha of soft sediment at this site only one dunlin was seen during the 1999/2000 winter and knot were completely absent. Neither species were seen at this site during the 1998/1999 winter either. As previously mentioned redshank (mean daily peak count = 93.3, SD = 15) fed throughout the winter in fairly stable numbers. The dip in numbers towards the end of February was almost certainly due to undercounting as drifting fog hampered observations at this time (Fig 3.7). Shelduck numbers (mean daily peak count = 26.3, SD = 11.3) were a little more variable but this species was undercounted as they had a tendency to move out of view, further along from Torry Bay towards Crombie Point or move across to the nearby mudflats at Culross.

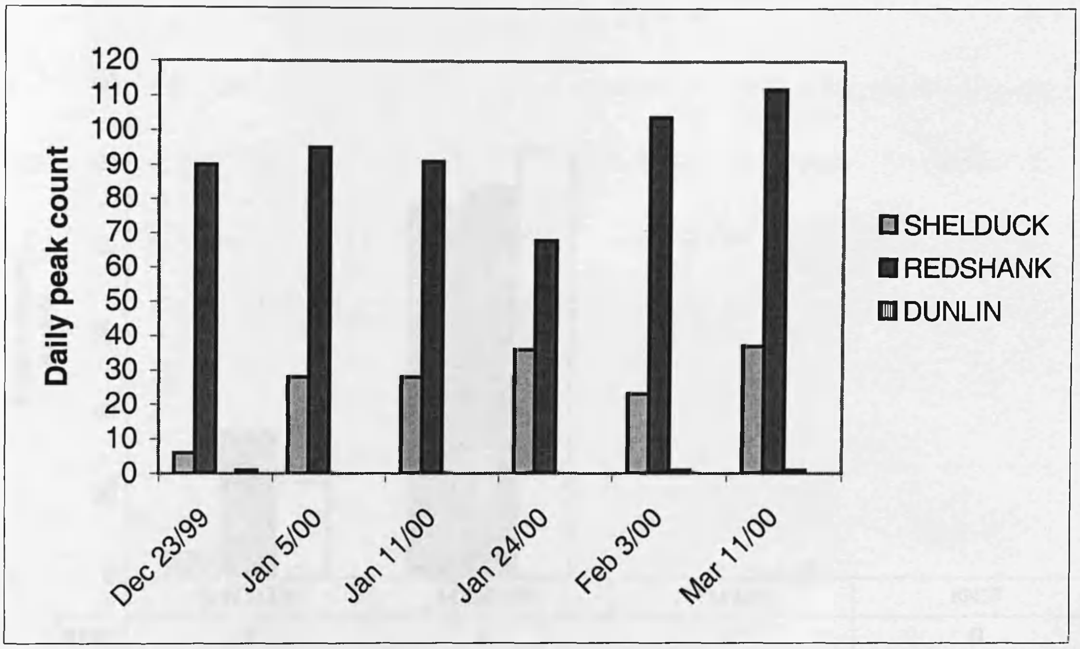
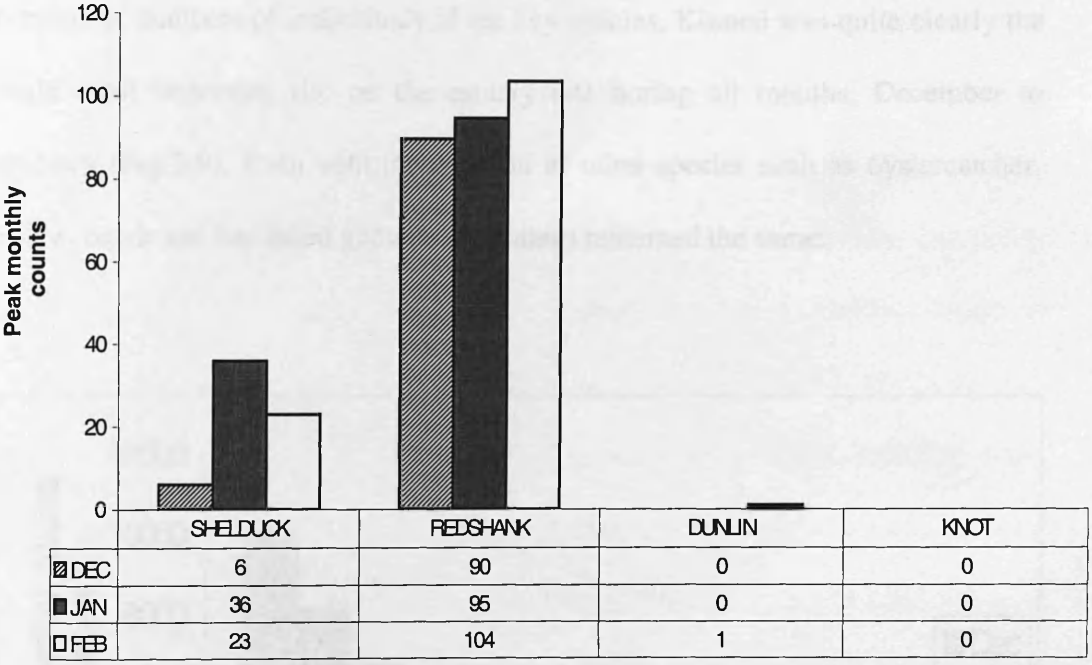


Fig 3.7: Daily peak counts of the key species recorded at Torry Bay during the winter of 1999/2000

Fig 3.8 Underlines the stability of the redshank population at Torry Bay, which hardly varied between December and February. It is quite likely that exactly the same number of birds resided here during these months (excepting natural mortality) and that some birds were just missed in the counts. Redshank were never seen to move away from the site or to move along the coast away from Torry Bay or across the estuary to Kinneil or Skinflats. Roost counts made here were consistent with this supposition and varied only by one or two birds each time.



	SHELDUCK	REDSHANK	DUNLIN	KNOT
▨ DEC	6	90	0	0
■ JAN	36	95	0	0
□ FEB	23	104	1	0

Fig 3.8: Key species peak monthly counts for December, January and February recorded at Torry Bay

3.5 Summary: bird distributions on the Forth Estuary

In terms of numbers of individuals of the key species, Kinneil was quite clearly the single most important site on the estuary site during all months, December to February (Fig 3.9). Even with the addition of other species such as oystercatcher, curlew, black and bar-tailed godwits the pattern remained the same.

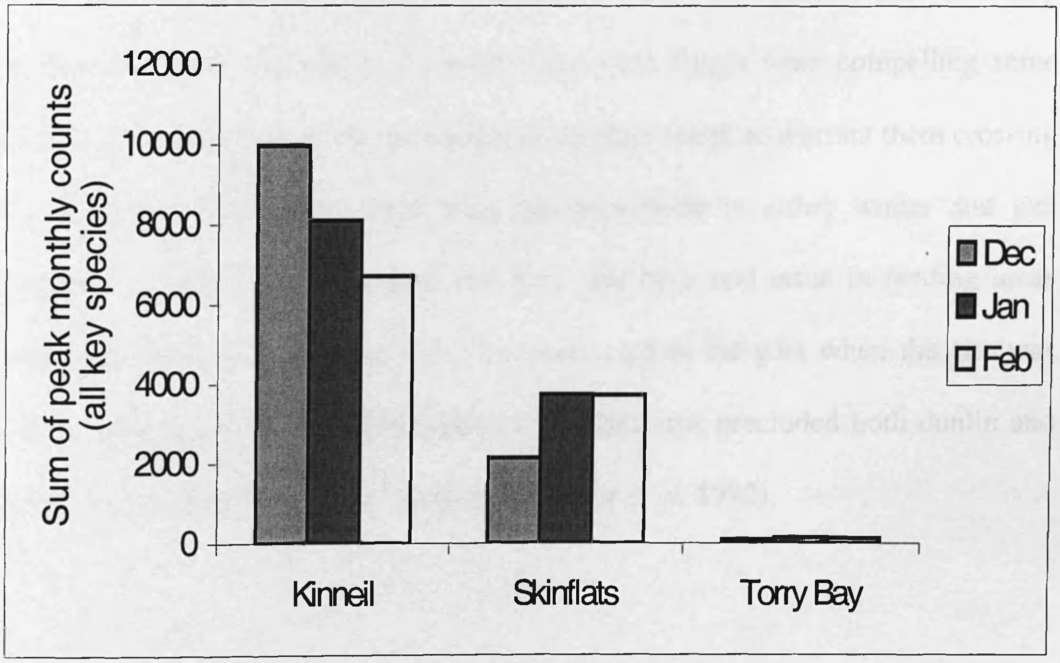


Fig 3.9: The sum of the monthly peak counts for shelduck, redshank, dunlin and knot during December, January and February at Kinneil, Skinflats and Torry Bay

It is evident that there is some variability in population size of all the species. Some of this variation is likely to be due to birds moving in from other areas and some of it seems to be movement between sites within the Forth Estuary complex. An element of this variation is also attributable to mortality. Shelduck numbers follow a similar pattern of gradual increase at both Skinflats and Kinneil whilst at Torry Bay numbers although few were fairly stable. Numbers of shelduck were greatest at Skinflats. Although there was some evidence of possible movement of redshank between Skinflats and Kinneil, they tended to exhibit strong winter site fidelity (see Burton 2000) choosing to feed regularly in the same areas in similar numbers at all the sites. Dunlin and to a greater extent knot were more mobile and their populations exhibited more fluctuation throughout the winter. Some dunlin appeared to move between Skinflats and Kinneil on occasion possibly in response to competitive pressure from other dunlin if food became a limiting factor in overwinter survival. Knot almost exclusively used the Kinneil site and only occasionally visited Skinflats. If density dependent forces were compelling some birds to move from site to site they were not strong enough to warrant them crossing the estuary to Torry Bay. Knot were not seen there in either winter and just occasional dunlin were seen. Site size then may be a real issue in feeding areas choice for these species. Torry Bay has been used in the past when the site was bigger but it seems that land reclamation here has now precluded both dunlin and knot from feeding there in any number (McLusky *et al.* 1992).

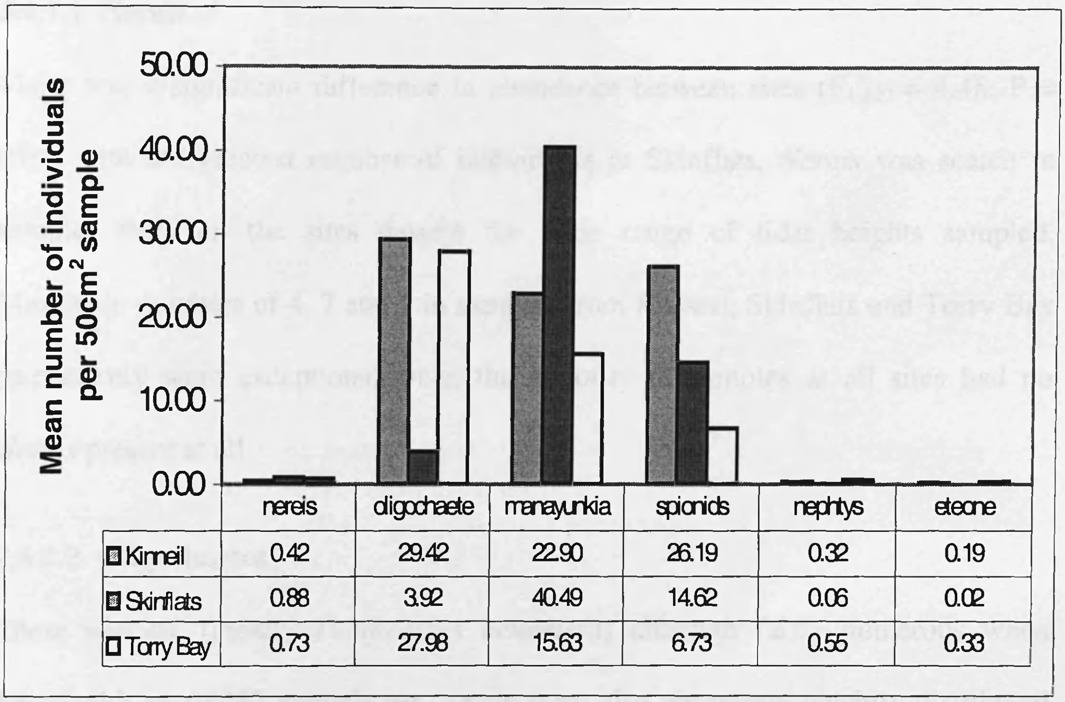
3.6 The distribution and abundance of Invertebrates on the Forth Estuary

In total, results are shown from 109 samples taken from the Kinneil and Bo'ness study plots, plus a further 67 additional samples taken for the purpose of kriging data surfaces for any species that proved to be significant predictors of key species feeding effort. The count results for 100 samples are given for Skinflats and Kincardine Bridge and 40 samples from Torry Bay. In total 316, $50cm^2$ samples of estuarine mud were analysed for invertebrate data.

3.6.1 The abundance of invertebrates at the main study sites

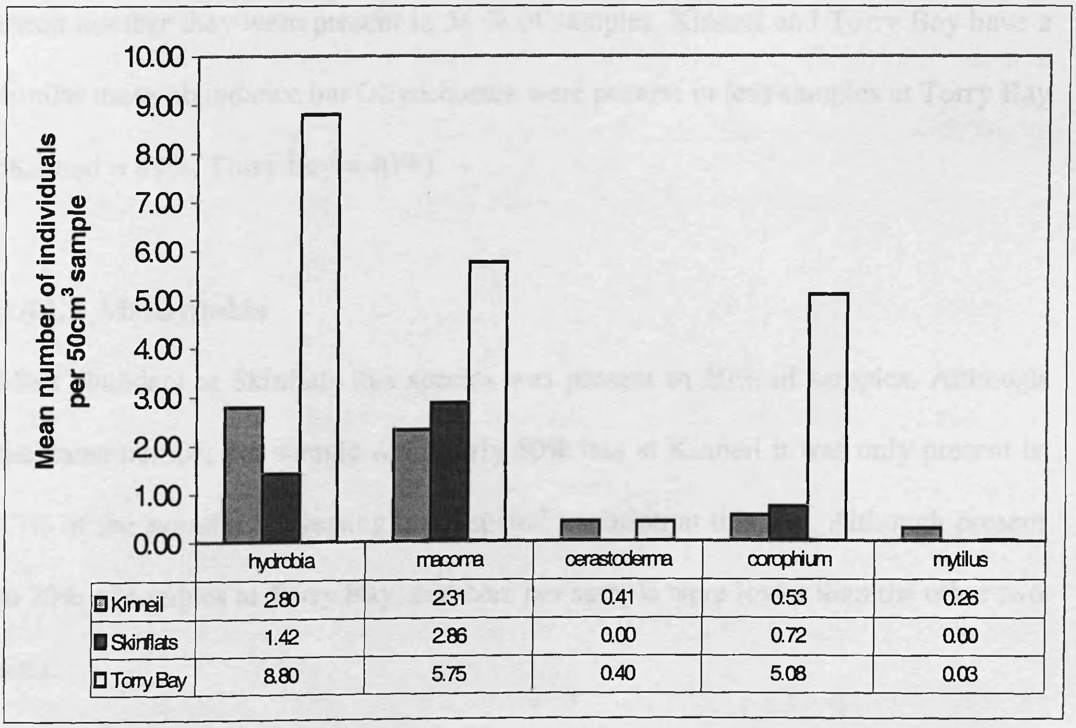
The mean number of each species from samples taken at Kinneil, Skinflats and Torry Bay are shown in Figure 3.10. Invertebrate species are grouped firstly by annelids (a) and secondly by bivalves, molluscs and arthropods (b). The difference between sites in invertebrate abundance was considered by putting all log10 transformed data invertebrate data into a GLM with site as a factor (all residuals were normally distributed) (Table 3.1)

a)



	nereis	oligochaete	manayunkia	spionids	nephtys	eteone
▨ Kinneil	0.42	29.42	22.90	26.19	0.32	0.19
■ Skinflats	0.88	3.92	40.49	14.62	0.06	0.02
□ Torry Bay	0.73	27.98	15.63	6.73	0.55	0.33

b)



	hydrobia	macoma	cerastoderma	corophium	mytilus
▨ Kinneil	2.80	2.31	0.41	0.53	0.26
■ Skinflats	1.42	2.86	0.00	0.72	0.00
□ Torry Bay	8.80	5.75	0.40	5.08	0.03

Fig 3.10: This figure illustrates the distribution of the mean number of individuals counted in all the samples collected at each of the main study sites. Kinneil, n = 176, Skinflats, n = 100, Torry Bay, n= 40. All the samples were collected in January/February 2000.

3.6.1.1 Nereis

There was a significant difference in abundance between sites ($F_{1,227} = 4.48$, $P = 0.01$) with the greatest number of individuals at Skinflats. *Nereis* was scarce in samples from all the sites despite the wide range of tidal heights sampled. Maximum numbers of 4, 7 and 5 in samples from Kinneil, Skinflats and Torry Bay respectively were exceptional when the majority of samples at all sites had no *Nereis* present at all.

3.6.1.2 Oligochaetes

These species, (mostly *Tubificoides benedictii*) although fairly numerous when found with up to 283 animals per sample were also apparently patchily distributed as they were not present at all in many samples. Although Skinflats had the lowest mean number they were present in 54 % of samples. Kinneil and Torry Bay have a similar mean abundance but Oligochaetes were present in less samples at Torry Bay (Kinneil = 88%, Torry Bay = 40%).

3.6.1.3 Manayunkia

Most abundant at Skinflats this species was present in 60% of samples. Although the mean number per sample was nearly 50% less at Kinneil it was only present in 43% of the samples suggesting more spatial variation at this site. Although present in 70% of samples at Torry Bay, numbers per sample were lower than the other two sites.

3.6.1.4 Spionids

Order of abundance, highest to lowest, of Kinneil>Skinflats>Torry Bay, is matched by the percentage of samples that contain Spionids with 85%, 69% and 62.5% respectively.

3.6.1.5 Nephtys and Eteone

Both these species were scarce at all sites although at Torry Bay they were both slightly more common. Maximum numbers found at this site were 7 for *Nephtys* and 5 for *Eteone*.

3.6.1.6 Hydrobia

As has already been found in previous work, (Elliot 1979, Berry 1994, Berry 1997) *Hydrobia* was most abundant at Torry Bay and only 3 of the 40 samples taken at this site failed to contain any. Kinneil was the next most important site with 66.5% of samples containing *Hydrobia*. At Skinflats only 50% contained *Hydrobia*.

3.6.1.7 Macoma

Kinneil and Skinflats had very similar densities of *Macoma* with 75% and 71% respectively of the samples having *Macoma* present. Skinflats though has a slightly higher mean number of individual samples and this is at odds with the results of previous long term work (Bryant & McLusky 1997) which found slightly more *Macoma* at Kinneil. Torry Bay had nearly twice as many animals as Kinneil or Skinflats per sample with 90% of them containing this bivalve.

3.6.1.8 Cerastoderma

Cerastoderma were only present at Kinneil and Torry Bay at very low density. In previous studies they have been found at Skinflats (Warnes 1981, Bryant & McLusky 1997) with Warnes (1981) finding on average 10 individuals per m^2 in December 1977. In this study not one of the 100 samples contained this species. This may be attributed to the fact that only the more accessible muddy regions were sampled. The more rocky and sandy area adjacent to the Carron mouth on the seaward edge of the mudflat, which would have been a likely habitat, was avoided due to the danger of being trapped by the incoming tide. It should be noted however that not one of Warnes (1981) samples came from this area so the present paucity of the species is evidence of a population decline.

Table 3.1: Results of a GLM determining whether there were significant differences in the abundance of invertebrate species between sites (Kinneil, Skinflats and Torry Bay). For relative abundance patterns see Figure 3.12.

Invertebrate	**$F_{1,227}$**	**P**
Nereis	4.48	0.01
Oligochaetes	14.07	<0.001
Manayunkia	9.35	<0.001
Spionids	4.53	0.01
Nephtys	6.48	0.002
Hydrobia	28.99	<0.001
Macoma	11.32	<0.001
Cerastoderma	7.35	0.001
Mytilus	1.84	0.16
Eteone	6.09	0.003
Corophium	12.54	<0.001

3.6.2 Invertebrate/sediment characteristic relationships

The relationship between invertebrate densities and sediment characteristics are given in Table 3.2. Results from this study are mixed at the whole estuary scale especially when controlling for tide height and distance from the shore. *Hydrobia*, *Mytilus*, *Nereis* and Spionids were all correlated to various aspects of grain size at the whole estuary scale. % clay fraction was not included in any of the models as it was strongly correlated to % silt. The percentage of particulate organic matter was only positively correlated to spionids, which was to be expected for this organic enrichment loving species.

Table 3.2 Relationships between mean invertebrate count (n=5) and mean sediment characteristics (n=5) based on information gathered at 50 study plots throughout the Forth Estuary. Tide height and distance from shore (m) are also included in the models.

Species	Variable	F	P	Relationship
Hydrobia	Median particle size	5.11	0.02	+ ve
Macoma	N/A	N/A	N/A	N/A
Cerastoderma	Distance from shore (m)	10.18	0.002	+ ve
Mytilus	Median particle size	6.65	0.01	- ve
	% silt	5.28	0.02	+ ve
	Distance from shore (m)	3.99	0.05	+ ve
Nereis	% silt	15.21	<0.001	+ ve
	Tide height (macd)	11.72	0.001	+ ve
Nephtys	Tide height (macd)	7.94	0.007	- ve
	Distance from shore (m)	4.13	0.04	+ ve
Eteone	Tide height (macd)	6.33	0.01	- ve
Oligochaetes	N/A	N/A	N/A	N/A
Manayunkia	Tide height (macd)	9.70	0.003	+ ve
Spionids	% organic matter	7.07	0.01	+ ve
	Median particle size	5.33	0.02	- ve
	Tide height (macd)	4.61	0.03	+ ve

3.6.3 Tide height and distance from the shore

Cerastoderma, Mytilus and *Nephtys* were all positively correlated to distance from shore and *Nephtys* and *Eteone* was also negatively correlated to tide height, thus higher densities of these species occurred further from the shore and at lower tide heights. *Nereis, Manayunkia* and Spionids were all positively related to tide height, preferring the high level areas.

3.7 The spatial distribution of invertebrate species at Kinneil

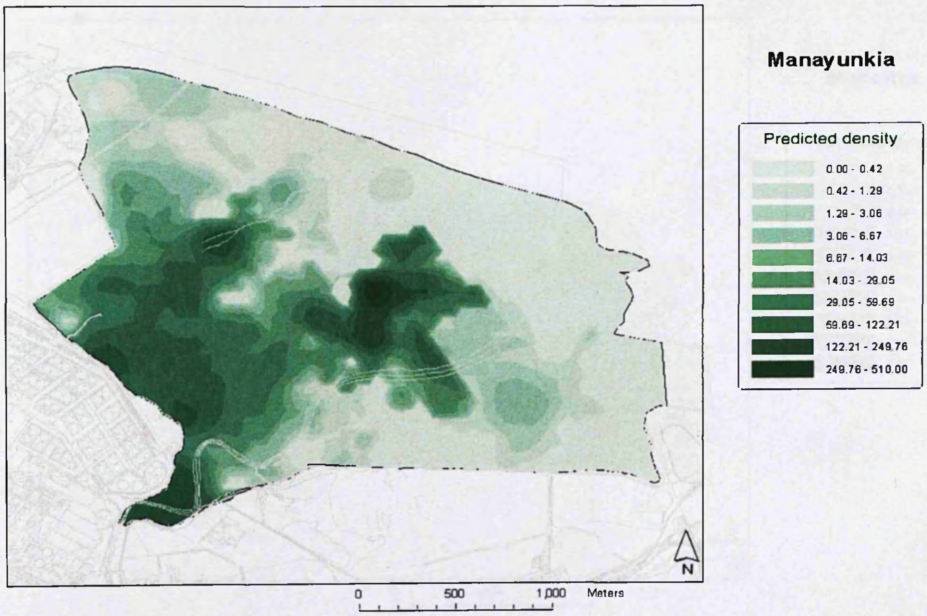
Davis (2001) concluded that there were some differences in the abundance and biomass of the invertebrate community at Kinneil between upper and lower shore areas in 1999/2000. The upper shore was richer in species such as *Manayunkia* and *Nereis* whereas the lower shore had a greater abundance and biomass of species like *Macoma*, *Cerastoderma*, Spionids, *Mytilus* and *Nephtys.* Samples collected in this study were taken from Kinneil during the same time period. Maps generated from the point samples taken at Kinneil indicate that there is some considerable spatial variability in the distribution of all the invertebrate species sampled in this study, with some species exhibiting marked preferences for upper or lower shore areas as well as more specific areas of the mudflats (Fig 3.11). *Manyunkia* are concentrated within the >3-4m and >4m contours. There is also a high density concentration roughly in the centre of the mudflat spanning into the >2-3m area. This central area is visible in the field as a region of boulders, small stones and seaweed interspersed with muddier areas of varying size. *Hydrobia* are dispersed widely across all of Kinneil with concentrations of higher density evident in the south eastern corner by the Bo'ness Bing, the top north western corner north of the Grange burn and the north central region within the >2-3m contours. *Macoma* are also broadly distributed and show a marked preference for the whole area within the >2-4m area. Localised concentrations in this area are visible. *Corophium* although present in low density throughout most of the site are mostly concentrated around the mouth of the River Avon and this may be linked to lower salinity levels in this area due to the freshwater input. Both *Eteone* and *Nephtys* show a marked preference for the margin of the mudflat and the lower tide height areas. High-level areas are mostly avoided or low densities are present. *Mytilus* and *Cerastoderma* share a similar distribution in terms of their areas of main concentration which fall mostly between the >1 – 3m contours. Local concentrations are present in the central region and along the southern seawall. *Nereis* density is apparently quite patchy but this is almost certainly due to the kriging process, which had attributed high concentrations to groups of samples close together within the study plots. This is not necessarily inaccurate but gives the appearance on the map of small islands of high density. It is more likely that with more sample points the whole region with high densities in it would appear more homogenous. Oligochaetes appear common at all tidal levels although there are marked areas of low density, namely the central region and the top northeastern corner. Spionid distribution is less patchy and covers the whole site. A broad band of higher density along the southern seawall and across the centre of the site closely matches the area within the >2-4m tide height contours. For most species patchiness in distribution is evident but this is to be expected (Thrush 1991) and can occur at a range of scales (Dayton 1984).

3.8 Summary: invertebrate distributions on the Forth Estuary

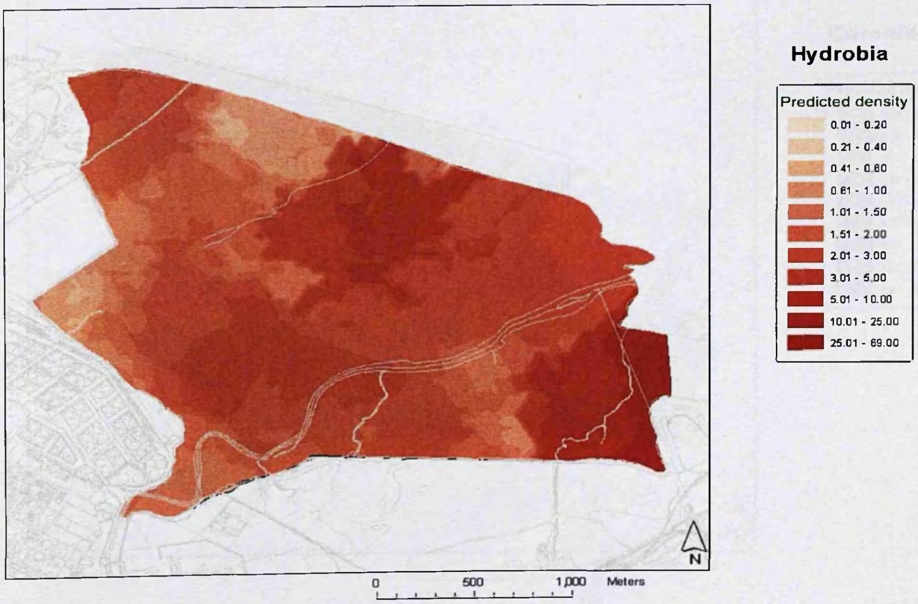
Invertebrate data collected at sites around the estuary show some variation. It is evident that some sites have higher concentrations of certain species than others do. If invertebrate densities have a significant influence on shorebird distribution then such spatial variation in invertebrates will help to determine how the birds distribute themselves round the estuary. Within-site variation is quite apparent (Fig 3.11a-k) and it is expected that concentrations of favoured prey items will have a profound effect on within site distribution of bird feeding effort.

Over the last few decades, many studies have correlated infaunal invertebrate distributions with sediment grain size, leading to the generalisation of distinct associations between animal distributions and specific sediment types. Examples of recent studies include Rizzo & Amoral (2001) who found strong relationships between annelid density and diversity, and sediment type, and Piersma *et al.* (2001) who noted that numbers of *Mytilus* and *Macoma* declined as the clay fraction of sediment was lost and median particle size increased in response to dredging works on the Waddensee. Animal/sediment relationships have been found both within (Arias & Drake 1994) and between estuaries (Engel & Summers 2000). Such animal particle size relationships can also affect the ability of species to recruit. Large grain size has been shown to have a negative affect on polychaete recruitment (Pinedo *et al.* 2000) and the larvae and adults of the surfclam (*Spisula solidissima*) are highly grain size specific (Snelgrove *et al.* 1998).

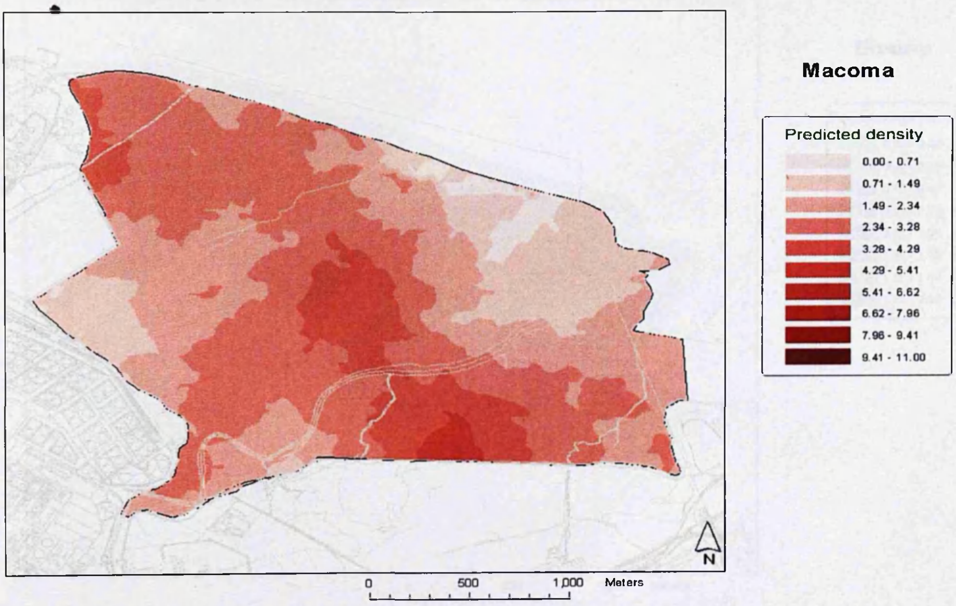
a)


Manayunkia
Predicted density
0.00 - 0.42
0.42 - 1.29
1.29 - 3.06
3.06 - 6.67
6.67 - 14.03
14.03 - 29.05
29.05 - 59.69
59.69 - 122.21
122.21 - 249.76
249.76 - 510.00
N
0
500
1,000
Meters

b)


Hydrobia
Predicted density
0.01 - 0.20
0.21 - 0.40
0.41 - 0.60
0.61 - 1.00
1.01 - 1.50
1.51 - 2.00
2.01 - 3.00
3.01 - 5.00
5.01 - 10.00
10.01 - 25.00
25.01 - 69.00
N
0
500
1,000
Meters

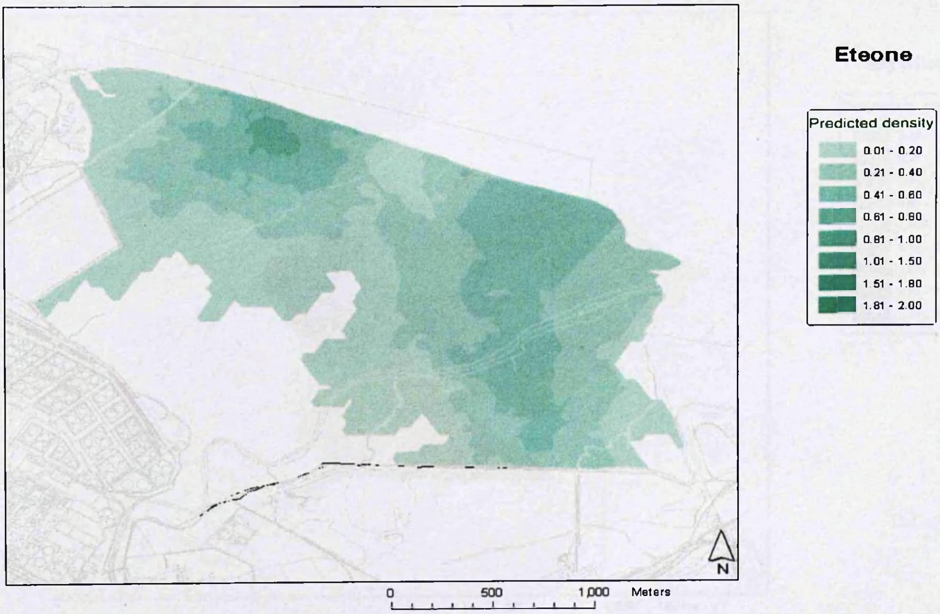
c)


Macoma
Predicted density
0.00 - 0.71
0.71 - 1.49
1.49 - 2.34
2.34 - 3.28
3.28 - 4.29
4.29 - 5.41
5.41 - 6.62
6.62 - 7.96
7.96 - 9.41
9.41 - 11.00
N
0
500
1,000
Meters

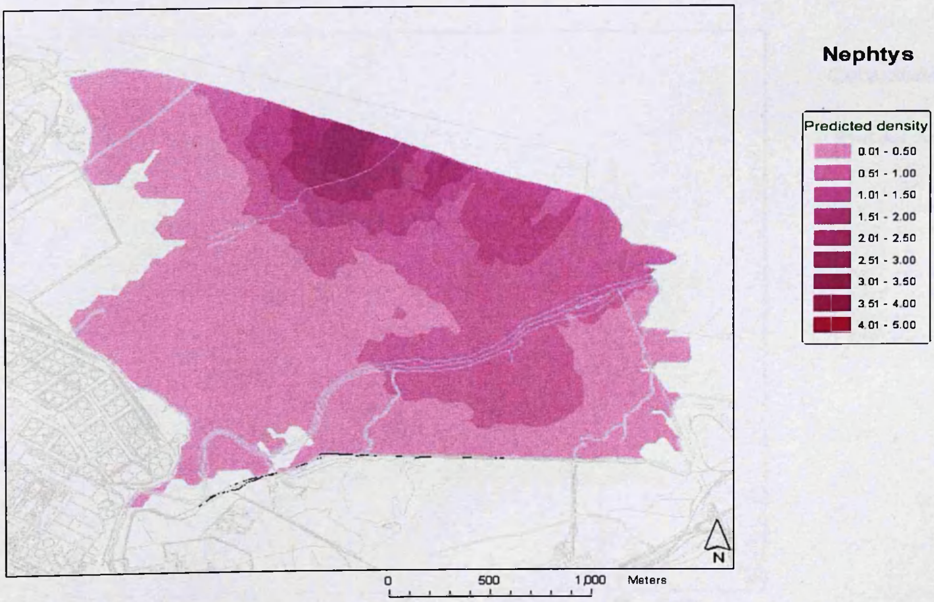
d)


Corophium
Predicted density
0.01 - 0.20
0.21 - 0.40
0.41 - 0.60
0.61 - 1.00
1.01 - 1.50
1.51 - 2.00
2.01 - 3.00
3.01 - 5.00
5.01 - 8.00
N
0
500
1,000
Meters

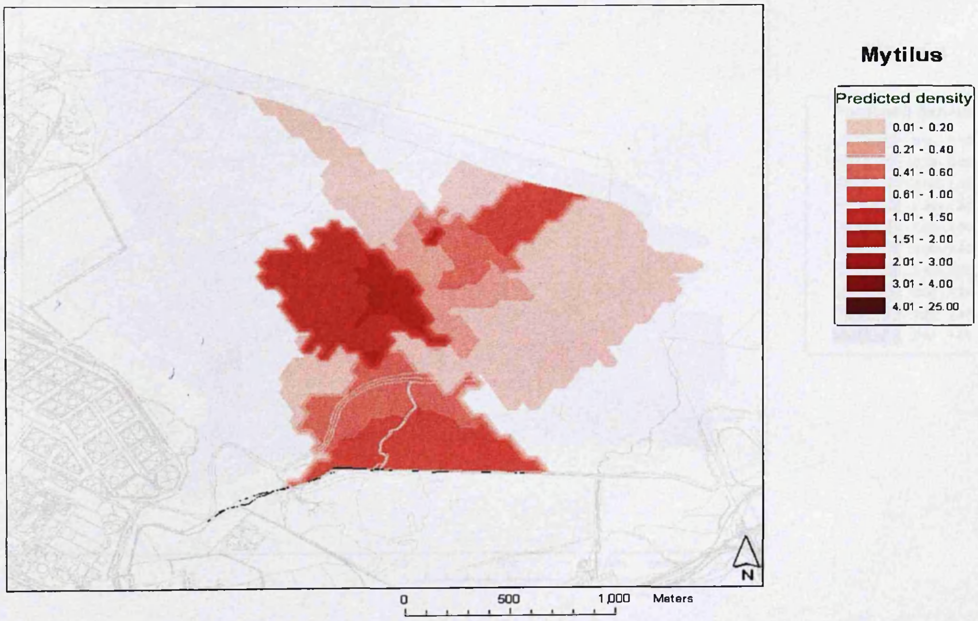
e)


Eteone
Predicted density
0.01 - 0.20
0.21 - 0.40
0.41 - 0.60
0.61 - 0.80
0.81 - 1.00
1.01 - 1.50
1.51 - 1.80
1.81 - 2.00
N
0
500
1,000
Meters

f)


Nephtys
Predicted density
0.01 - 0.50
0.51 - 1.00
1.01 - 1.50
1.51 - 2.00
2.01 - 2.50
2.51 - 3.00
3.01 - 3.50
3.51 - 4.00
4.01 - 5.00
N
0
500
1,000
Meters

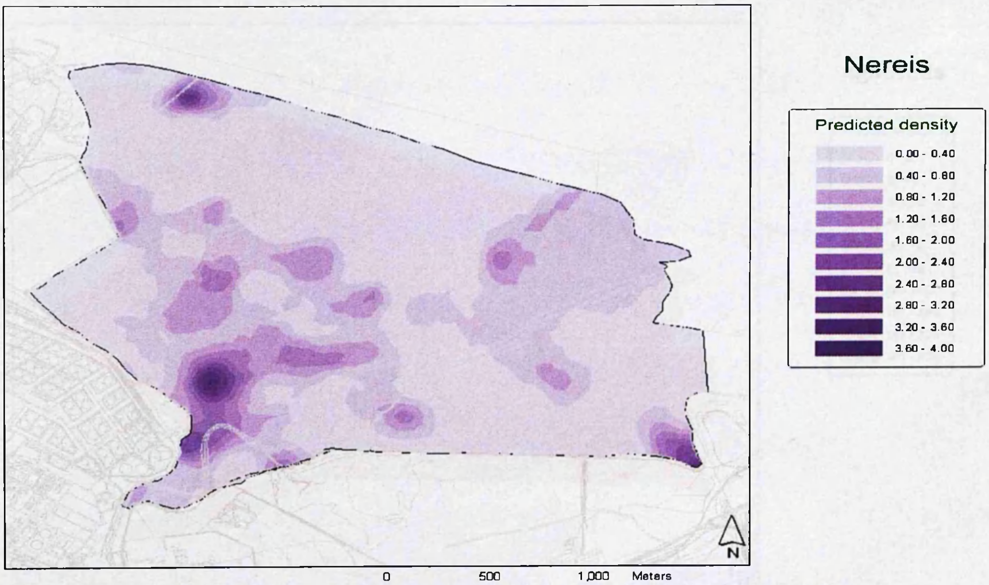
g)


Mytilus
Predicted density
0.01 - 0.20
0.21 - 0.40
0.41 - 0.60
0.61 - 1.00
1.01 - 1.50
1.51 - 2.00
2.01 - 3.00
3.01 - 4.00
4.01 - 25.00
N
0
500
1,000
Meters

h)


Cerastoderma
Predicted density
0.01 - 0.20
0.21 - 0.40
0.41 - 0.60
0.61 - 1.00
1.01 - 1.50
1.51 - 2.00
2.01 - 3.00
3.01 - 5.00
5.01 - 9.00
N
0
500
1,000
Meters

i)


Nereis
Predicted density
0.00 - 0.40
0.40 - 0.80
0.80 - 1.20
1.20 - 1.60
1.60 - 2.00
2.00 - 2.40
2.40 - 2.80
2.80 - 3.20
3.20 - 3.60
3.60 - 4.00
N
0
500
1,000
Meters

j)


Oligochaetes
Predicted density
1.0 - 2.5
2.6 - 5.0
5.1 - 10.0
10.1 - 15.0
15.1 - 20.0
20.1 - 30.0
30.1 - 50.0
50.1 - 100.0
100.1 - 150.0
150.1 - 200.0
200.1 - 245.0
N
0
500
1,000
Meters

k)

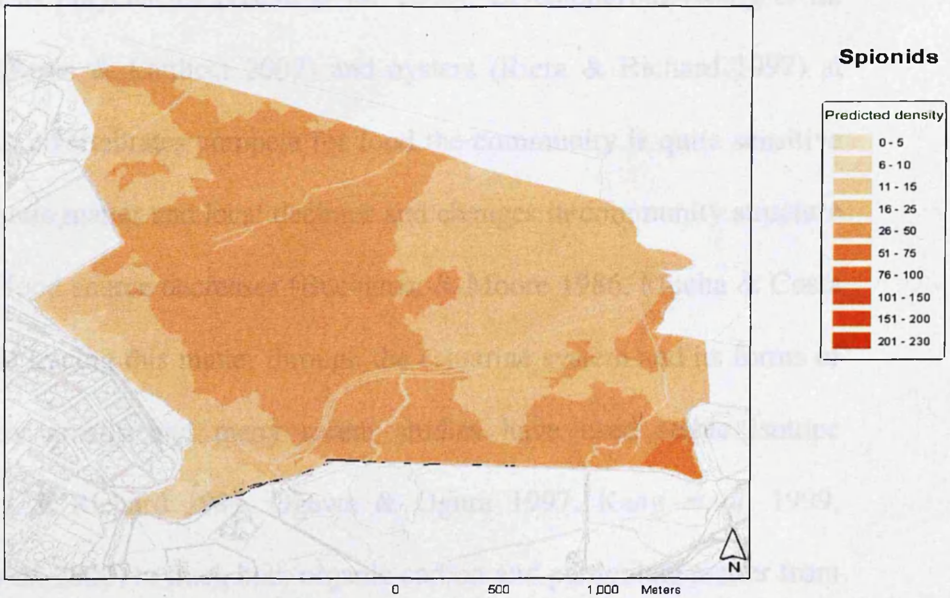


Fig 3.11: The predicted spatial distribution of all the invertebrates recorded at Kinneil during January/February 2000. The information surfaces are kriged from 160 randomly distributed sample points. The predicted density scale refers to numbers per 50cm^2 sample.

Particulate organic matter can be the most important form of nutrition for macrofauna such as polychaetes (Hseih *et al.* 2002), *Cerastoderma* (Kang *et al.* 1999), spionids (Rossi & Lardicci 2002) and oysters (Riera & Richard 1997) at estuarine sites. As invertebrates compete for food the community is quite sensitive to changes in organic matter and local declines and changes in community structure can occur as this food source decreases (Buchanan & Moore 1986, Mucha & Costa 1999). Methods of tracing this matter through the estuarine system and its forms of measurement vary greatly and many recent studies have used stable isotope techniques (Riera & Richard 1997, Ogawa & Ogura 1997, Kang *et al.* 1999, Maksymowska *et al.* 2000) to track both organic carbon and particulate matter from various terrestrial sources.

Tide or shore height has been shown to be an important factor in determining the spatial distribution of single species such as *Macoma* (Bouma *et al.* 2001a) and *Cerastoderma* (Bouma *et al.* 2001b). It has also been shown to be an important factor controlling community composition (Moore *et al.* 1987; Gonzalez-Oreja & Saiz Salinas 1999). The higher the organisms are up the shore the greater stress they are under in terms of exposure to the air, lower salinity and greater exposure to predation pressure from birds. Where invertebrate species are correlated with tide height or distance from shore these relationships are probably related to the salinity gradient as salinity is the dominant factor influencing the distribution of estuarine invertebrates and the gradients evident over intertidal areas produce a zonation in the fauna due to the physiological affects of salinity change upon them (McLusky 1989). Species such as *Macoma*, *Corophium*, *Nereis* and *Hydrobia* are all tolerant to a wide variation in the salinity of the surrounding water and may be found in the proximity of freshwater creek systems (Wolff 1983, Holland 1987). This is especially the case for *Corophium*, which is often associated with freshwater sources on the Forth Estuary (McLusky pers comm). Distinct zones of invertebrates are evident at Kinneil (McLusky *et al.* 2000) and these are linked almost entirely to tide height. Tide height determines the amount of time exposed to both sea and air and hence controls the level of salinity.

Although the relationships between invertebrates and tide height/distance from shore may have a broad affect on their spatial distribution, relationships with sediment particle size may be more spurious. Data from other studies showing correlative evidence between animals and sediment were compiled and reviewed critically by Snelgrove & Butman (1994). They found that animal-sediment relationships are much more variable than traditionally purported and concluded that there is little evidence that sedimentary grain size alone is the primary determinant of infaunal species distributions. In addition to observed variability in animal-sediment relationships, a clear mechanism by which grain size *per se* limits distributions has not been demonstrated. Sediment grain size is usually determined on completely disaggregated samples which may have little relevance to what an organism actually encounters in nature. Thus, the grain-size distributions described for a given habitat may be very different from those within the ambit of the organism. There is also the added dimension of the changing scale of relationships due to small-scale spatial variation in invertebrate densities. Although spatial structure of invertebrates may be readily explained at larger scales by biotic and abiotic variables, unknown phenomena operating at smaller spatial scales can be responsible for up to 90% of the variability in density (Legendre *et al.* 1997). The results of a study on the estuarine benthic community at Kinneil (Davis 2001) found no evidence that the level of organic matter or sediment composition played any major factor in determining the community structure at the single mudflat scale. Methods of analysis used however were different to those used in this study as they did not account for the error that loss on ignition methods introduce into organic matter estimation (see section 3.8.3).

In the past, chemical effluent from the petrochemical works at Grangemouth has had a profound effect on the spatial distribution of invertebrates at Kinneil (McLusky 1982 and McLusky & Martins 1998). However, an increase in diversity, eveness and species richness of the whole mudflat was found between 1976 and 1989 which can be attributed to the improved quality of these effluents and the increased water quality of the River Avon (Davis 2001).

Effects of pollutants at Skinflats may have had long-term consequences on the invertebrate populations but there is evidence that for some elements the situation is improving. Since 1983 the mercury concentration in *Mytilus* at Skinflats has declined from >5mg/kg to <0.5 mg/kg in 1997 (SEPA 1998), levels of lead however have varied more considerably over time.

There are no direct inputs of toxic wastes onto the mudflats at Torry Bay although there may be some incidental runoff from the fly ash pans adjacent to it. There is some methane gas seepage through the mud from abandoned coalworkings but this has been shown only to have a marginal effect on the intertidal fauna (Judd *et al.* 2002).

3.9 The distribution of sediment characteristics on the Forth Estuary

3.9.1 Differences in sediment characteristics between sites

When the sediment characteristics from each of the main study sites, derived from a series of point samples (Kinneil n = 87, Skinflats n = 67, Torry Bay n = 40), were analysed in a GLM, significant differences were found between the three sites for all the covariates: mean particle size, median particle size, % clay, % silt, % sand and % organic matter (Table 3.3, Fig 3.13) indicating that sediment structure is not homogenous throughout the estuary.

Table 3.3: Results of GLMs on log transformed sediment data indicting that all sedimentary characteristics measured in this study vary between the main three study sites of Skinflats, Kinneil and Torry Bay

Sediment characteristics	F-value	P-value
Mean particle size	13.43	<0.001
% sand	12.71	<0.001
% clay	10.87	<0.001
% silt	10.24	<0.001
Median particle size	9.11	<0.001
% organic matter	4.51	0.01

Torry Bay had by far the highest % sand in relation % clay and % silt where it scored the lowest of the three main sites. Kinneil had the next highest sand fraction with a mean value of 17.52% (n = 87) and Skinflats the lowest (11.15% n = 67). Significant negative correlation between % sand and % silt ensured that the converse was true for % silt content. Although Skinflats does have an strip of boulders, pebbles and sand c 100m broad stretching for about 500m along the tidal edge of the mudflat this area was not included in the sampling. Had it been so the results may well have been different. % organic matter was also highest at Skinflats and there is a weak relationship between organic matter and silt content at this site

($F_{1,53} = 3.73$, $P = 0.05$, R-sq = 6.6%). This weak relationship is reflected at Kinneil ($F_{1,85} = 4.59$, $P = 0.03$, R-sq = 5.1%) but not at Torry Bay where there was no significant relationship at all. When considering just an overall measure of sediment characteristic taking into account all size fractions i.e. mean particle size, Torry Bay still remains the site with the highest grain size, followed by Kinneil and finally Skinflats with the smallest overall particle sizes (Fig 3.12).

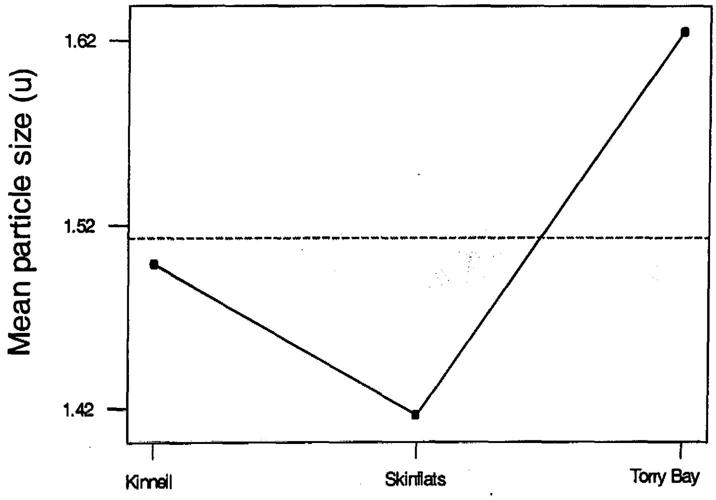


Fig 3.12: Main effect plot with mean particle size as the response where site is a factor indicating the relative overall measure of particle size at each of the three main study sites.

The spatial variability amongst the samples within each site is evident when the CV for each sediment fraction is calculated (Fig 3.13). For all measures of sediment character the CV is lowest at Skinflats indicating that although there is likely to be small scale variation in particle size it is generally more homogenous at this site and potentially stable. Torry Bay on the other hand has much more variability especially in the sand fraction and the overall measures of mean and median particle size, clay and silt fractions however are not markedly different from Skinflats or Kinneil. This may be attributed to its relatively high energy environment. Kinneil is has a very similar variation to Skinflats although it is slightly higher.

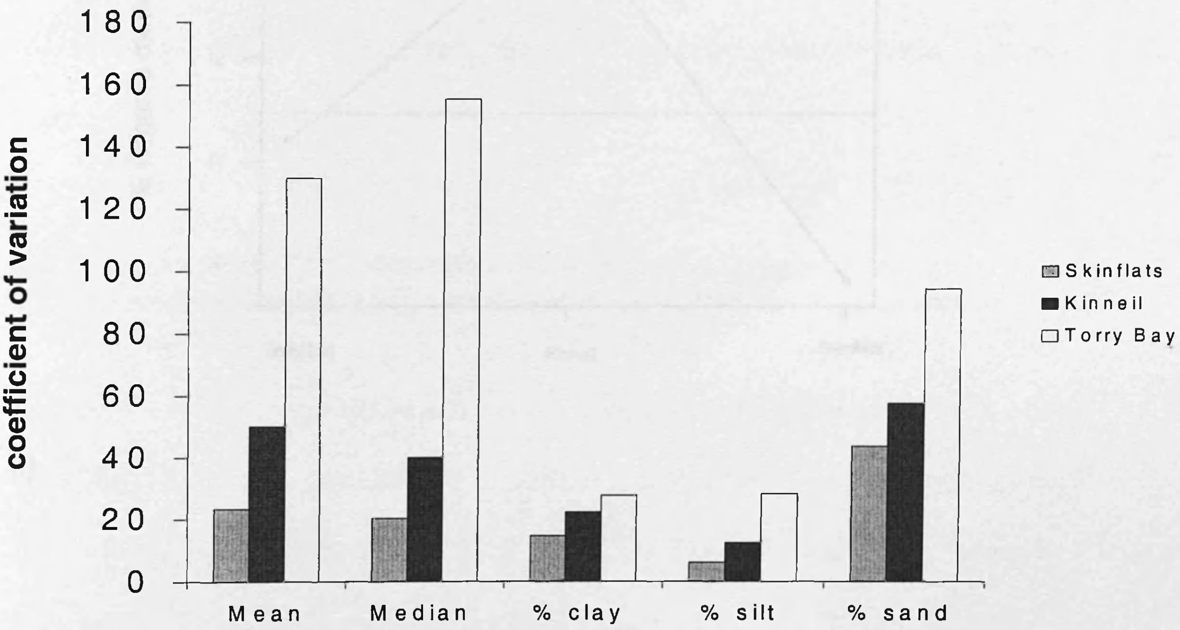
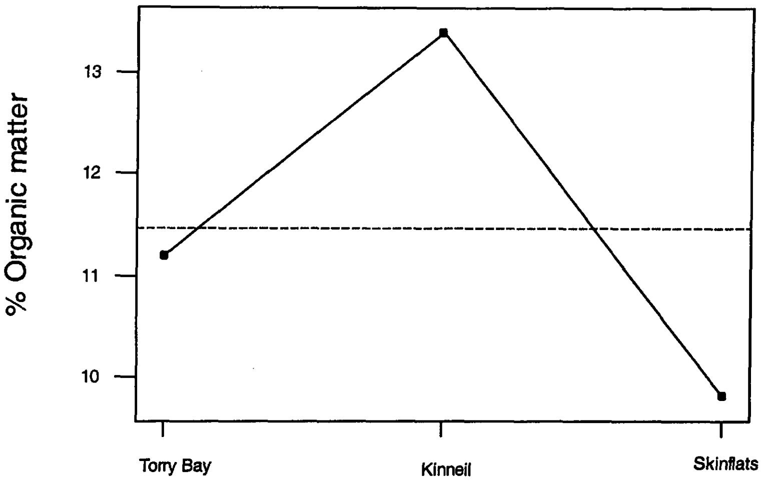


Fig 3.13: The CVs of sediment particle size characteristics calculated from the total sampling effort for each site and illustrating the spatial variability of each variable between the sites.

3.9.2 Differences in % organic matter between the sites

Both the loss on ignition (LOI) and the hydrogen peroxide (H_2O_2) methods indicate that there are significant differences in the mean % organic matter in the sediments between sites. LOI: $F_{1,116} = 14.97$, $P = < 0.001$ and H_2O_2: $F_{1,116} = 8.94$, $P = < 0.001$ however the main effects plots indicate that different conclusions may be drawn about these differences as each method gives a different site as having the greatest amount of organic matter (Figure 3.14)

a)



b)

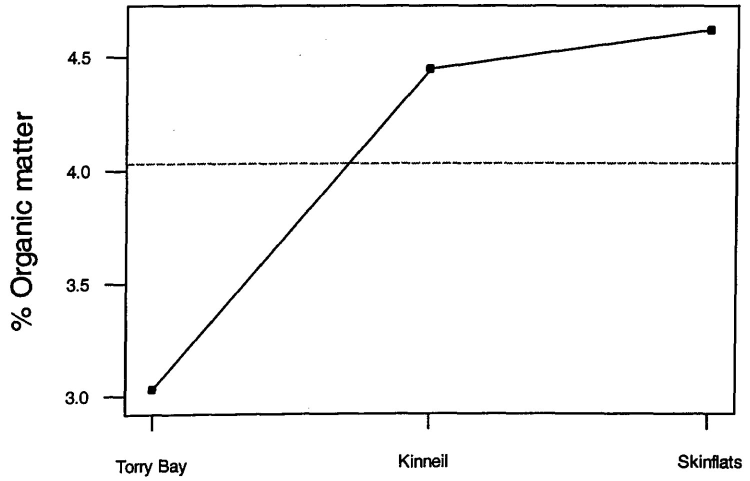


Fig 3.14: Main effects plot showing the differences in mean % organic matter between sites as derived by a) loss on ignition method and b) the hydrogen peroxide method

Clearly the method chosen has implications in terms of overall accuracy of results; in this case the LOI method gives Skinflats the highest mean % organic matter whereas the H_2O_2 method gives the site the lowest. There is, however, agreement in the ranking of the other two sites although the values are higher. This may imply that coal dust was not such a problem at Kinneil and instead that there was a contaminant at Skinflats which elevated values for organic matter when LOI was used.

3.9.3 Is there a significant difference between loss on ignition (LOI) and hydrogen peroxide (H_2O_2) treatment when measuring organic matter content?

In total 117 samples were tested using both methods, from 3 different sites, 38 from Torry Bay, 40 from Kinneil and 39 from Skinflats. A GLM was performed on the data with site and method as factors. Residuals from all tests were normally distributed and variances equal, no data were transformed.

There was a highly significant difference in the level of organic matter detected between the two methods: $F_{1, 233} = 446.52$, $P = <0.001$ with the loss on ignition method returning considerably higher values (LOI mean = 4.04% +/- 1.93, H^2O^2 mean = 11.45% +/- 3.26) Figure 3.15.

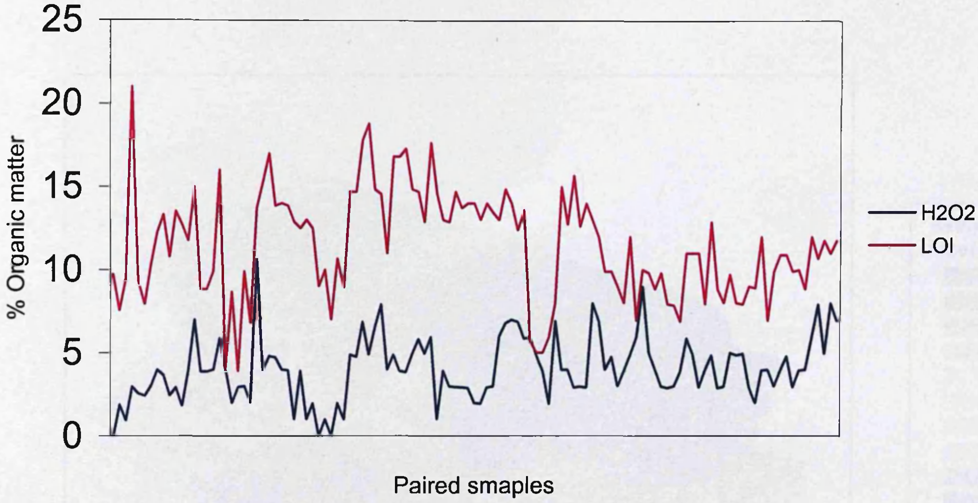


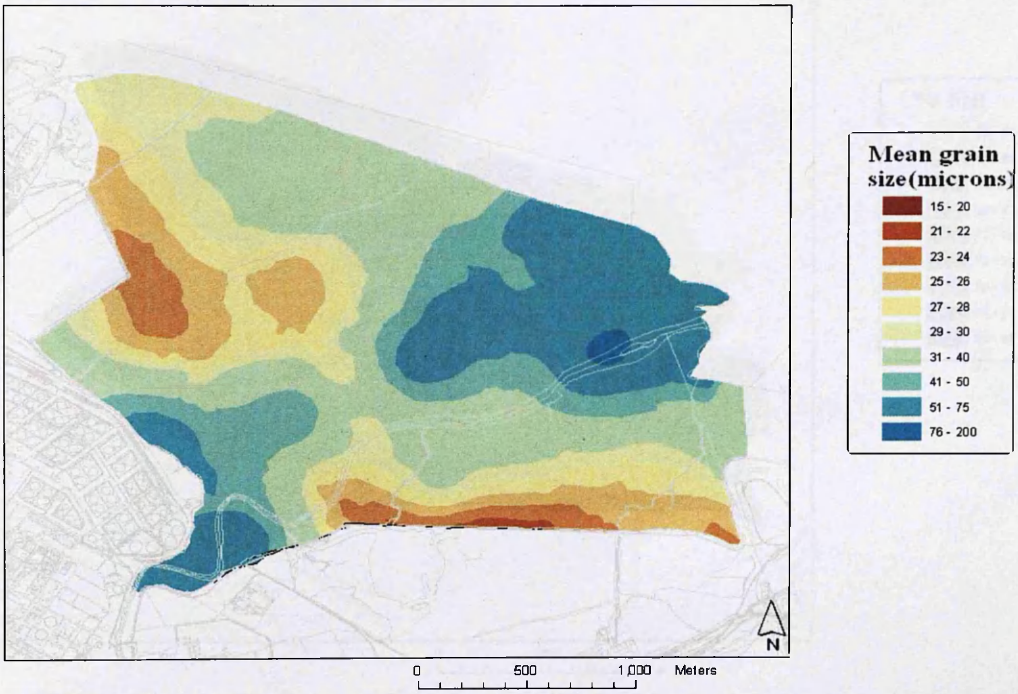
Figure 3.15: A comparison between LOI and H^2O^2 methods for determining % organic matter in estuarine sediment. The LOI method produces consistently higher results

In light of these results it was decided to use the measurement of % organic matter calculated using the H_2O_2 method, as a covariate in the modelling process.

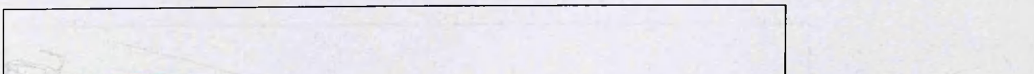
3.10 Spatial variation in sediment structure at Kinneil

The selection of maps shown (Fig 3.16) illustrates the spatial distribution of the sediment characteristics used as covariates in the GLMs for this site. Although other methods of visualising sediment structure are available such as satellite imagery (Yates *et al.* 1993) and airborne electromagnetic profiling (Pelletier & Holladay 1994) they do not provide the level of site specific accuracy that interpolated ground truth data can.

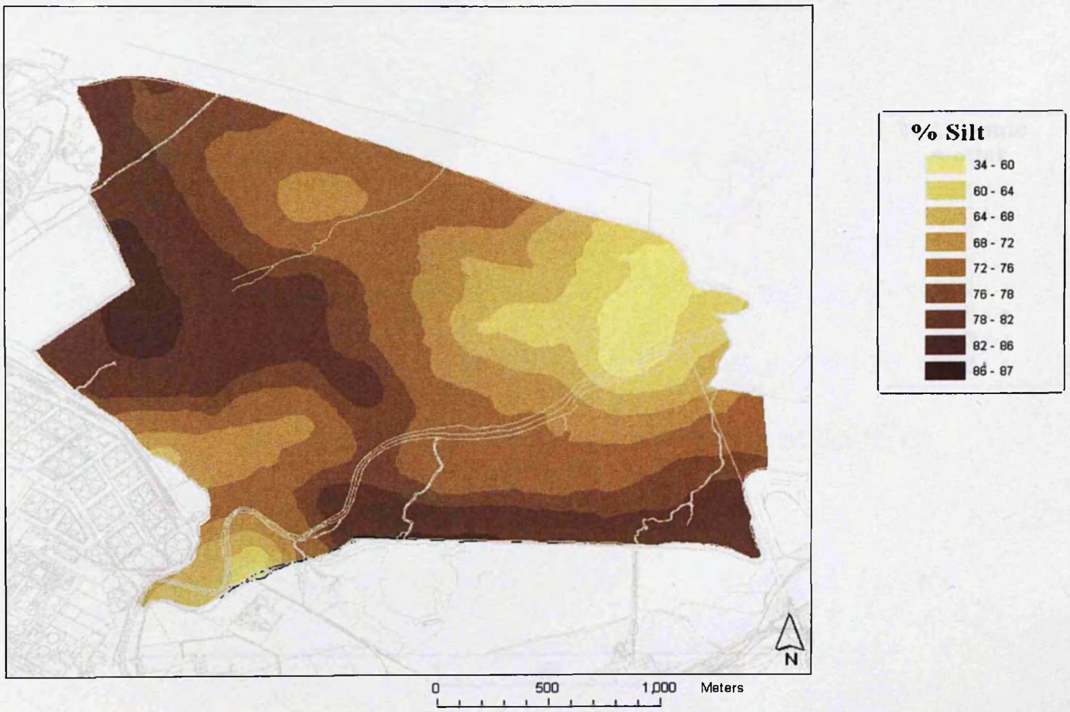
a)


Mean grain size(microns)
15 - 20
21 - 22
23 - 24
25 - 26
27 - 28
29 - 30
31 - 40
41 - 50
51 - 75
76 - 200
N
0
500
1,000
Meters

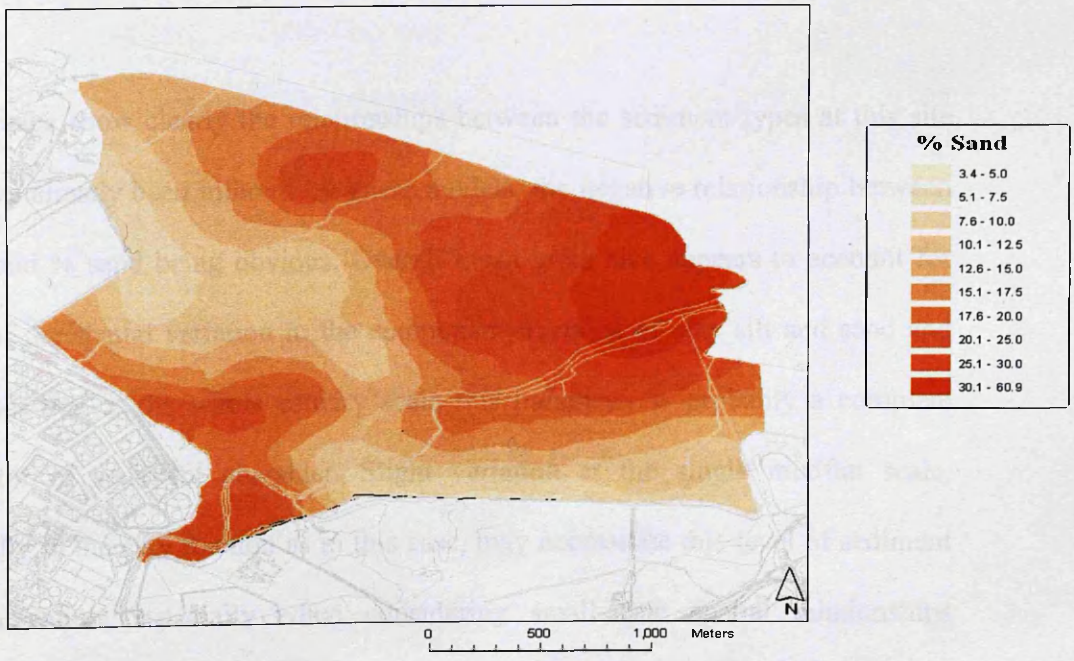
b)


% Clay
1.1 - 2.0
2.1 - 5.0
5.1 - 6.0
6.1 - 7.0
7.1 - 8.0
8.1 - 9.0
9.1 - 10.0
10.1 - 11.0
11.1 - 12.0
12.1 - 13.0
13.1 - 16.0
N
0
500
1,000
Meters

c)


% Silt
34 - 60
60 - 64
64 - 68
68 - 72
72 - 76
76 - 78
78 - 82
82 - 86
86 - 87
N
0
500
1,000
Meters

d)


% Sand
3.4 - 5.0
5.1 - 7.5
7.6 - 10.0
10.1 - 12.5
12.6 - 15.0
15.1 - 17.5
17.6 - 20.0
20.1 - 25.0
25.1 - 30.0
30.1 - 60.9
N
0
500
1,000
Meters

e)

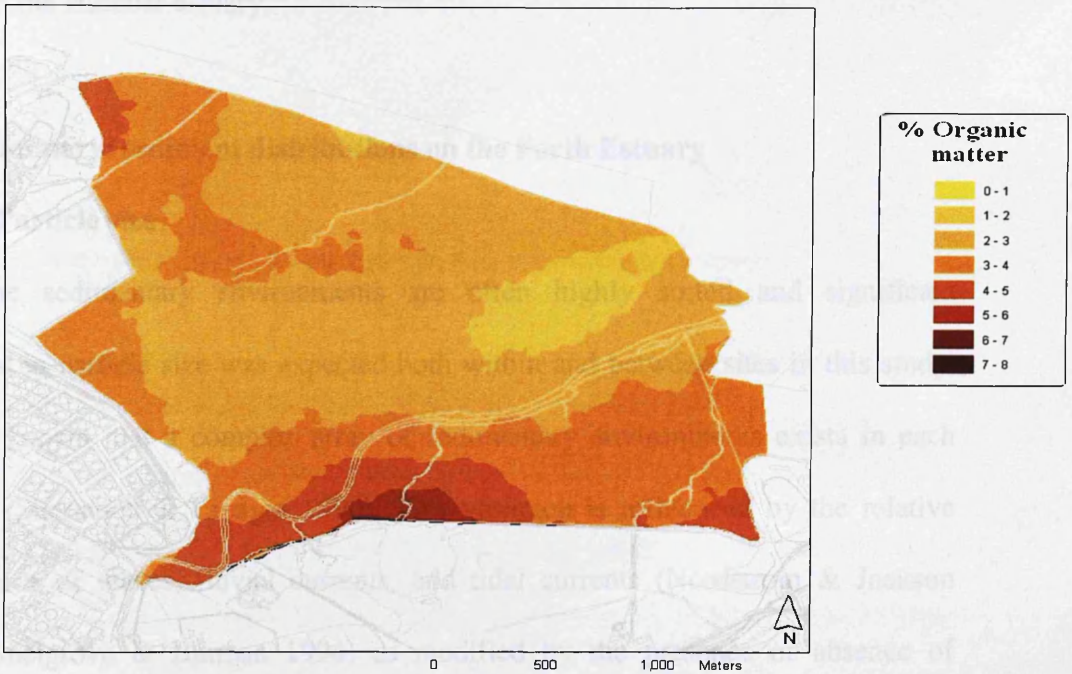


Fig 3.17: Distribution maps of predicted sediment characteristics (a: mean grain size (u), b: % clay, c: % silt, d: % sand and e: % organic matter) calculated for Kinneil using ordinary kriging (n = 221)

These maps show clearly the relationships between the sediment types at this site that have already been inferred by linear models, the negative relationship between % silt and % sand being obvious. Overall mean grain size appears to account for much of the spatial variation in the component fractions of clay silt and sand and illustrates that at the whole estuary scale this parameter is probably a complete descriptor of sediment character. Slight variation at the single mudflat scale, especially in the clay fraction as in this case, may necessitate this level of sediment characterisation, especially when considering small-scale spatial relationships between sediment and invertebrates/birds, if indeed they exist. Levels of organic matter are highest nearest the shore and appear to be related to point sources of organic input from streams and rivers. Galois *et al.* (2000) also found that there was preferential accumulation of particulate organic matter in sheltered sites close to the shore on the Humber estuary.

3.11 Summary: sediment distributions on the Forth Estuary

3.11.1 Particle size

Estuarine sedimentary environments are often highly sorted and significant variation in particle size was expected both within and between sites in this study, as it is known that a complex array of sedimentary environments exists in each estuary (Sherwood & Creager 1990). This variation is influenced by the relative importance of waves, fluvial currents, and tidal currents (Nordstrom & Jackson 1993; Snelgrove & Butman 1994) as modified by the presence or absence of estuarine circulation, vegetation, or human activity estuaries (Sherwood & Creager 1990). On the whole, spatial variation in sediment fractions although visually apparent, are only high at Torry Bay and this can be accounted for by the high energy environment at this site, which being situated on the north shore of the estuary, is exposed to the prevailing southwesterly winds.

3.11.2 Organic matter

A comparison of methods suggested that the loss on ignition method is not a useful or informative approach in this case. The higher estimates of particulate organic matter are almost certainly down to coal contamination and fragments of $CaCO_3$ that were not removed from the ignited samples and skewed the overall value upwards. It is safe to assume that the H_20_2 method is more representative of actual values as neither of these two fractions was removed in this treatment process. Variation in organic matter content between sites is apparent and may be an artefact of either sampling location i.e. some samples may have been taken closer to sources of organic input like rivers, than others or it may be linked in some way to variation in sediment structure.

Section B: The generalised linear models and weighted area maps

3.12 Results of the GLM analysis at the whole estuary and sub-estuary scale: What are the best predictors of shorebird feeding effort?

The generalised linear models: 'key species feeding effort v all measured parameters' were calculated at the whole estuary scale using data from all the study plots at Kinneil, Boness, Skinflats, Torry Bay and Dunmore to Kincardine Bridge. For a full list of measured parameters see Table 2.6. Models were also calculated to predict feeding effort at the single site scale using data collected at Kinneil/Boness and Skinflats. Only the two largest sites of Skinflats and Kinneil were used in the sub-estuary models as these areas had the greatest number of study plots within them (16 and 30 respectively). The aim of this two-tier approach was to determine which variables were important in predicting shorebird feeding effort at the sub estuary scale bearing in mind that sediment characteristics and invertebrate densities vary spatially around the estuary. The minimum models shown for each species at each scale are those that had the lowest residual deviance for the most biologically feasible model; residual degrees of freedom and residual deviance are given. The lower the residual deviance the closer the model fits the data. The model coefficients were extracted from the model output and in the case of the Kinneil models were used to generate the spatial maps of predicted bird feeding effort using the relevant kriged data surfaces in the GIS ARCVIEW. For each model the estimated relationship between the individual fitted terms and each of the corresponding predictors was plotted to cross validate the model accuracy. The size of each site varies and was controlled for in each model.

3.12.1 Shelduck

3.12.1.1 Shelduck: whole estuary scale

Table 3.4: Minimal model summary from shelduck feeding effort v all predictor variables at the whole estuary scale

Variable	F value	P value
Manayunkia count	14.12	< 0.001
% sand	8.60	< 0.001
Macoma size (mm, long axis)	4.75	0.03

Residual degrees of freedom = 47
Residual deviance = 100.48

3.12.1.1.1 Model coefficients for Shelduck feeding effort

Shelduck feeding effort = 3.12 + 0.01(*Manayunkia*) – 0.09 (%sand) – 0.23 (*Macoma* size (mm,long axis))

3.12.1.1.2 Predicted shelduck feeding effort values v actual feeding effort

Shelduck actual values = 0.107519 + 0.955481 shelduck predicted values, $F_{1,37}$ = 22.67, P = < 0.001, R-Sq = 54.8%

3.12.1.1.3 Summary: shelduck, whole estuary

At the whole estuary scale *Manayunkia* density is the most important predictor of shelduck feeding effort. A negative relationship with areas of high sand content suggests they prefer siltier areas, possibly with higher penetrability or greater fluidity. The negative relationship with *Macoma* size may suggest that shelduck are selecting some small (<1mm) individuals as some samples had high densities of very small *Macoma*.

3.12.1.2 Shelduck: Kinneil

Table 3.5: Minimal model summary from shelduck feeding effort v all predictor variables at Kinneil

Variable	**F value**	**P value**
Distance from shore (m)	11.46	0.002
Manayunkia	4.95	0.03

Residual degrees of freedom = 27
Residual deviance = 59.62

3.12.1.2.1 Model coefficients for shelduck feeding effort

Shelduck feeding effort = 1.29 + 0.01 (*Manayunkia*) – 0.003 (Distance from shore (m))

3.12.1.2.2 Predicted shelduck feeding effort v actual feeding effort

Shelduck actual feeding effort = 1.07222 + 0.371820 Shelduck predicted feeding effort, $F_{1,27}$, = 14.98, P = 0.001, R-Sq = 34.9%

3.12.1.2.3 Summary: shelduck, Kinneil

Again *Manayunkia* is important and is being preferentially selected over other invertebrate prey. Many of the other invertebrate species dropped out of this model early on including *Hydrobia* which has been shown to be a favoured prey item on the Forth Estuary (Bryant 1979; Warnes 1981) and elsewhere (Patterson 1982). *Hydrobia* size only just failed to be included in the minimal model returning a P-value of 0.06. The negative relationship to distance from the shore shows that shelduck prefer to feed in high-level mudflat areas. It is evident from Fig 3.17 that the most popular area at Kinneil during the period of this study was the triangular embayment adjacent to the Grangemouth petro-chemical works.

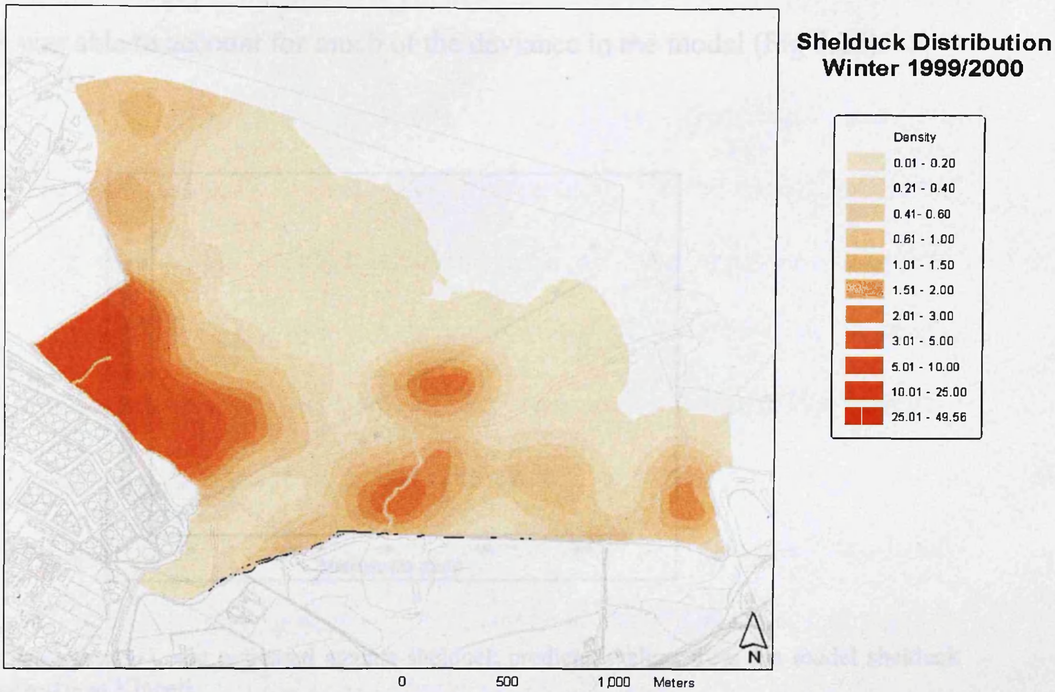


Fig 3.17: Shelduck feeding effort distribution at Kinneil based on complete spatial data on feeding birds collected between November 1999 and March 2000.

3.12.1.3 Shelduck : Skinflats

Table 3.6: Minimal model summary from shelduck feeding effort v all predictor variables at Skinflats

Variable	F value	P value
Manayunkia	5.91	0.02

Residual degrees of freedom = 15
Residual deviance = 52.61

3.12.1.3.1 Model coefficients for shelduck feeding effort

shelduck feeding effort = 0.57 + 0.008 (*Manayunkia*)

3.12.1.3.2 Predicted shelduck feeding effort v actual feeding effort

Shelduck predicted feeding effort = 1.90757 + 0.383468 shelduck actual feeding effort, $F_{1,15} = 9.82$, R-Sq = 35.5%, P = 0.007

3.12.1.3.3 Summary: shelduck, Skinflats

At Skinflats, only *Manayunkia* was positively related to shelduck and this lone variable was able to account for much of the deviance in the model (Fig 3.18).

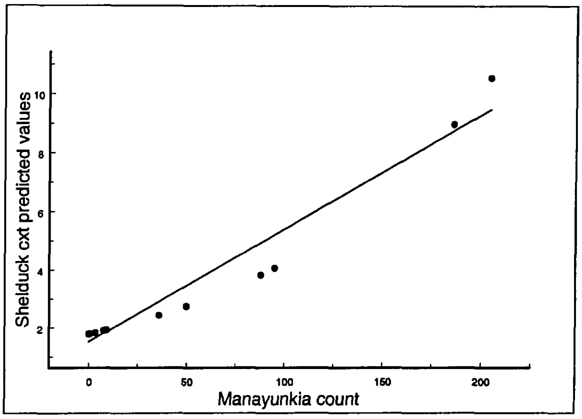


Fig 3.18: *Manayunkia* count regressed against shelduck predicted values from the model shelduck cxt~*Manayunkia* at Kinneil

In the Skinflats model, tide height just failed to make the minimal model $p = 0.07$.

3.12.1.4 Discussion: Shelduck

Density of *Manayunkia* is clearly the most important factor determining where shelduck are concentrating their feeding effort throughout the estuary. *Manayunkia* can reach a high abundance especially where there is high particulate organic matter content, with up to 50000m^2 recorded on an estuary in the southern Baltic (Bick 1996) It is often the dominant species in macrofauna assemblages (Horne *et al.* 1999, Angradi *et al.* 2001, Vitaliano 2002). On the Forth Estuary during the winter of 1999/2000 Skinflats had the highest density of *Manayunkia* (16197 m^2) and the greatest number of shelduck, feeding there. Mean number of shelduck declined with density of *Manayunkia* at Kinneil (mean number of shelduck at Skinflats December – February = 178, density of *Manayunkia* = 9160m^2) and Torry Bay (mean number of shelduck at Skinflats December – February = 21.7, density of *Manayunkia* = 6252m^2). The *Manayunkia* density recorded for Kinneil can be compared to another study at the site during the same winter (McLusky *et al.* 2000), which returned a density of 8462 m^2. Shelduck may be choosing other prey items and it is evident from the marginal failure of *Hydrobia* size to be included in the model for Kinneil that shelduck may prefer to select smaller individuals. The negative relationship between shelduck feeding effort and % sand at the whole estuary scale maybe because sandier substrates are likely to be less attractive to shelduck due to higher shear strength and larger particle size interfering with feeding. The negative relationship with distance from shore at Kinneil and the near positive relationship with tide height at Skinflats is likely to be linked to *Manayunkia* density as this has already been shown to positively correlate to tide height (Table 3.2)

3.12.2 Redshank

3.12.2.1 Redshank: whole estuary

Table 3.7: Minimal model summary from redshank feeding effort v all predictor variables at the whole estuary scale

Variable	F value	P value
Tide height (macd)	113.89	< 0.001
Distance from shore (m)	83.08	< 0.001
% Silt	51.95	< 0.001
Manayunkia	21.99	< 0.001
Nereis	21.63	< 0.001
% Organic matter	19.63	< 0.001
Median particle size (microns)	9.41	0.004
Hydrobia	5.47	0.02

Residual degrees of freedom = 42
Residual deviance = 50.61

3.12.2.1.1 Model coefficients for Redshank feeding effort

Redshank feeding effort = -5.09 + 4.74 (Median particle size) – 5.73 (distance from shore (m)) + 6.24 (% silt) + 4.19 (% organic matter) + 8.65 (Tide height) + 2.34 (*Hydrobia*) + 4.30 (*Nereis*) + 5.61 (*Manayunkia*)

3.12.2.1.2 Predicted redshank feeding effort v actual feeding effort

Redshank actual feeding effort = -0.434713 + 1.00743 redshank predicted feeding effort, $F_{1,42} = 5303.45$, P = < 0.001, R-Sq = 99.2%

3.12.2.1.3 Summary: redshank, whole estuary

At the whole estuary scale the minimal model for redshank retained a considerable number of variables and there were positive relationships with three species of invertebrate, *Hydrobia, Nereis* and *Manayunkia.* Of the sediment variables, redshank were positively related to % organic matter, % silt and median particle size. A negative relationship with distance from shore (m) and a positive one with tide height indicate that redshank strongly prefer high level mudflat areas.

3.12.2.2 Redshank: Kinneil

Table 3.7: Minimal model summary from redshank feeding effort v all predictor variables at Kinneil

Variable	F value	P value
Nereis	74.13	<0.0001
Manayunkia	47.66	<0.0001
Distance from shore (m)	40.89	<0.0001

Residual degrees of freedom = 27
Residual deviance = 17.71

3.12.2.2.1 Model coefficients for redshank feeding effort

Redshank feeding effort = 3.59 + 2.65 (*Nereis*) –0.04 (*Manayunkia*) – 0.009 (distance from shore (m))

3.12.2.2.2 Predicted values v actual values

Redshank predicted feeding effort = 0.136564 + 0.991427 redshank actual feeding effort, $F_{1,28} = 492.26$, $P = < 0.001$, R-Sq = 94.4 %

3.12.2.2.3 Summary: redshank, Kinneil

At the Kinneil site only, *Nereis* is again positively correlated to feeding effort but this time there is a negative relationship with *Manayunkia.* This may be because *Nereis* and *Manayunkia* are positively correlated. Again redshank are shown to prefer high level areas in which to feed with a significant negative relationship with distance from shore. The winter feeding effort distribution of redshank at Kinneil as given in Fig 3.20 illustrates this preference for feeding in upper mudflat areas.

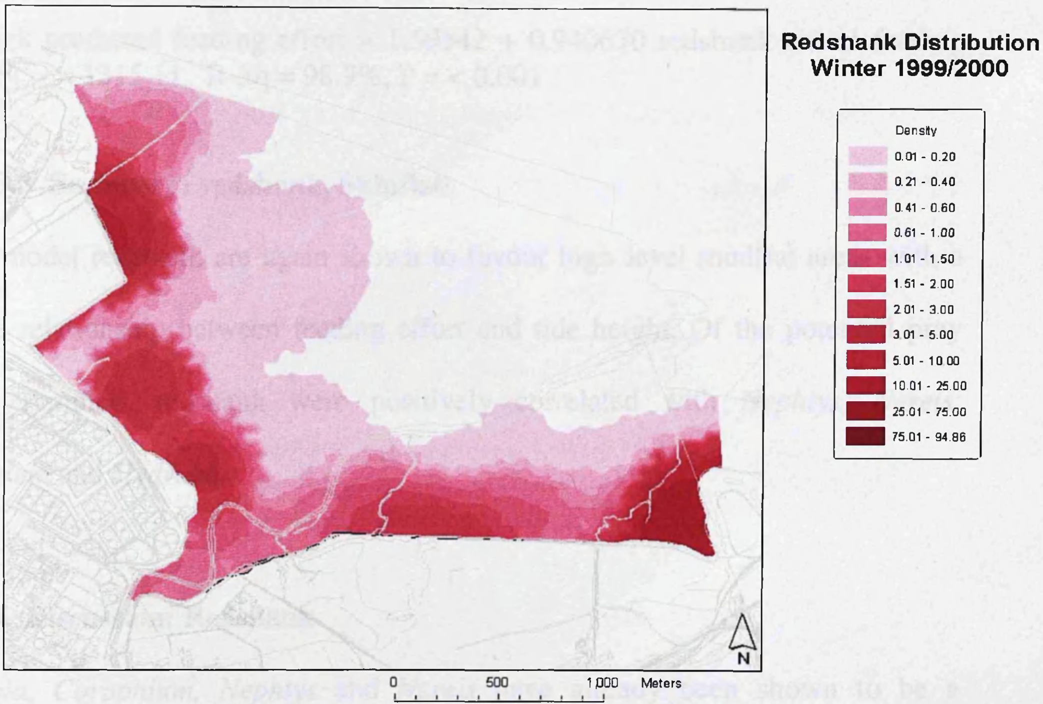


Fig 3.20: Redshank feeding effort distribution at Kinneil based on complete spatial data on feeding birds collected between November 1999 and March 2000.

3.12.2.3 Redshank: Skinflats

Table 3.8: Minimal model summary from redshank feeding effort v all predictor variables at Skinflats

Variable	F value	P value
Tide Height	29.23	<0.001
Corophium	16.64	0.001
Nephtys	8.68	0.01
Hydrobia	8.30	0.01
Nereis	5.94	0.03

Residual degrees of freedom = 11

Residual deviance = 46.69

3.12.2.3.1 Model coefficients for redshank feeding effort

Redshank feeding effort = -27.58 + 4.96 (Tide height (macd)) + 8.04 (*Nephtys*) + 2.95 (*Corophium*) + 1.20 (*Nereis*) + 2.14 (*Hydrobia*)

3.12.2.3.2 Predicted redshank feeding effort v actual feeding effort

Redshank predicted feeding effort = 1.59542 + 0.940670 redshank actual feeding effort, $F_{1,15} = 1315.11$, R-Sq = 98.9%, P = < 0.001

3.12.2.3.3 Summary: redshank, Skinflats

In this model redshank are again shown to favour high level mudflat areas with a positive relationship between feeding effort and tide height. Of the potential prey species sampled, redshank were positively correlated with *Nephtys*, *Nereis*, *Corophium* and *Hydrobia*

3.12.2.4 Discussion: Redshank

Hydrobia, Corophium, Nephtys and *Nereis* have already been shown to be a favoured food items of redshank on the Forth Estuary (see Table 1.5) and at other sites (Goss Custard 1976, 1977). *Manayunkia* however is not a recognised prey species in general but there is no reason to suggest that it not fed upon by redshank on the Forth Estuary at present. Although numbers of *Manayunkia* have declined in recent years (Fig 4.34d), they have only been noted on the estuary since 1979. The negative relationship with *Manayunkia* at Kinneil suggest that the link between redshank feeding effort and *Manayunkia* density may be more to do with the fact that they are both positively correlated to tide height at the whole estuary scale rather than selective choice by redshank of this prey item at different spatial scales. Positive relationships with median particle size and % silt were also evident. This may be linked to ease of feeding in certain sediment types or the relationship between sediment type and invertebrate species. *Nereis* is positively correlated to % silt and *Hydrobia* positively correlated to median particle size at the whole estuary scale (Table 3.2) so it is not surprising that all these variables are good predictors of redshank feeding effort. The positive relationship between redshank and organic matter may be linked to the redshanks preference for high level areas (positively correlated to tide height and negatively correlated to distance from shore) as % organic matter increases with tide height at the whole estuary scale, $F_{1,42} = 5.09$, $P = 0.02$ (Fig 3.20)

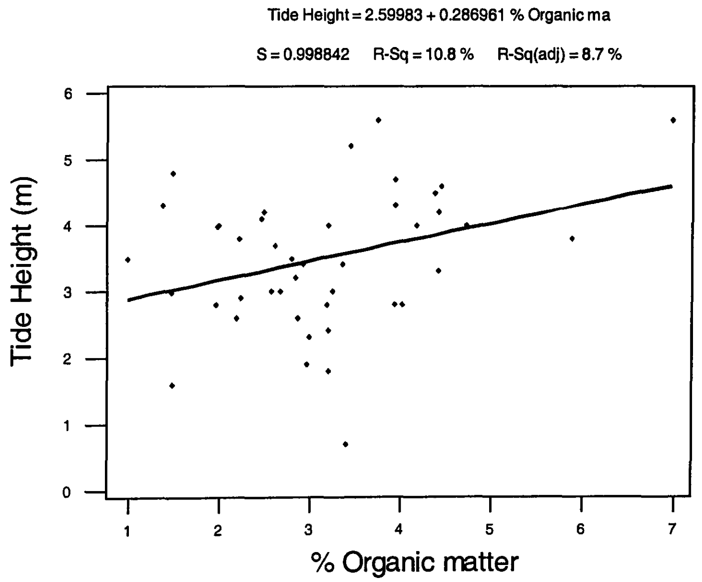


Fig 3.20: Tide height (m) regressed against % organic matter. Samples taken from Torry Bay, Kinneil and Skinflats

It is also clear from all the models that redshank strongly prefer high level areas of the mudflats at all spatial scales considered.

3.12.3 Dunlin

3.12.3.1 Dunlin: whole estuary

Table3.9: Minimal model summary from dunlin feeding effort v all predictor variables at the whole estuary scale

Variable	F value	P value
Site size (ha)	20.91	<0.001
Macoma size mm (long axis)	14.92	<0.001
% Silt	14.11	<0.001
% Sand	13.21	<0.001
Tide height (macd)	13.02	<0.001
Nereis	11.22	0.001
% Organic matter	6.04	0.01

Residual degrees of freedom = 43
Residual deviance = 63.06

3.12.3.1.1 Model coefficients for Dunlin feeding effort

Dunlin feeding effort = -3.82 – 3.08 (*Nereis*) + 3.57 (*Macoma* size mm (long axis)) + 3.49 (% silt) - 3.36 (% sand) + 2.47 (% organic matter) + 3.09 (tide height (macd)) + 3.57 (site size (ha))

3.12.3.1.2 Predicted dunlin feeding effort v actual feeding effort

Dunlin actual feeding effort = 0.0433353 + 0.998148 dunlin predicted feeding effort, $F_{1,41} = 245.40$, P = <0.001, R-Sq = 85.7%

3.12.3.1.3 Summary: dunlin, whole estuary

As with redshank, dunlin feeding effort was related to a wider range of variables at the whole estuary scale than it was at the single site scale. Site size was important, with feeding effort increasing with mudflat area. Of the abiotic variables % organic matter was positively significant and although the positive relationship with % silt and negative with % sand was probably due to multicolinearity the model collapsed with no significant variable left, when sand was left out of the model. Of the suite of prey items in the model only larger *Macoma* was positively related to feeding effort, as there was a negative relationship with *Nereis* density. Dunlin also preferred high tide level areas throughout the estuary.

3.12.3.2 Dunlin: Kinneil

Table 3.10: Minimal model summary from dunlin feeding effort v all predictor variables at Kinneil

Variable	F value	P value
Manayunkia	52.29	< 0.001
Nereis	15.53	< 0.001

Residual degrees of freedom = 28
Residual deviance = 57.81

3.12.3.2.1 Model coefficients for dunlin feeding effort

Dunlin feeding effort = 3.67 + 0.04 (*Manayunkia*) – 2.44 (*Nereis*)

3.12.3.2.2 Predicted dunlin feeding effort v actual feeding effort

Actual dunlin feeding effort = 40.4729 + 0.254230 predicted feeding effort,
$F_{1,28} = 15.10$, R-Sq = 32.7 %, P = < 0.001

3.12.3.2.3 Summary: dunlin, Kinneil

In this single site model, tide height dropped out with the dunlin showing no preference for high level areas, it was however nearly significant (P = 0.09). Again *Nereis* was negatively related to feeding effort but *Manayunkia* was strongly positively related to feeding effort. Fig 3.21 shows that dunlin ranged widely across Kinneil during the winter of 1999/2000.

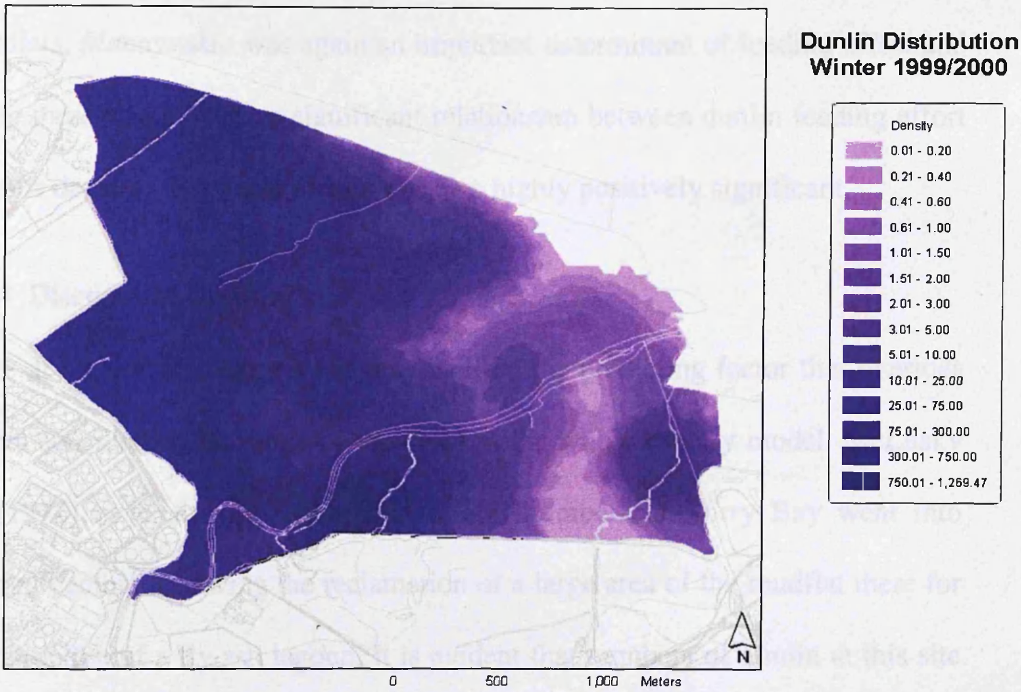


Fig 3.21: Dunlin feeding effort distribution at Kinneil based on complete spatial data on feeding birds collected between November 1999 and March 2000.

3.12.3.3 Dunlin: Skinflats

Table 3.11: Minimal model summary from dunlin feeding effort v all predictor variables at Skinflats

Variable	F value	P value
% Organic matter	95.47	<0.0001
Manayunkia	17.08	0.001
Nereis	9.53	0.008

Residual degrees of freedom = 13
Residual deviance = 12.12

3.12.3.3.1 Model coefficients for dunlin feeding effort

Dunlin feeding effort = -2.77 + 8.28 (% organic matter) + 4.18 (*Manayunkia*) + 3.04 (*Nereis*)

3.12.3.3.2 Predicted dunlin feeding effort v actual feeding effort

Dunlin predicted feeding effort= 12.1063 + 0.927518 dunlin actual feeding effort, $F_{1,15} = 663.88$, R- Sq = 97.6 %, P = < 0.001

3.12.3.3.3 Summary: dunlin, Skinflats

At Skinflats, *Manayunkia* was again an important determinant of feeding effort and this time there was a positive significant relationship between dunlin feeding effort and *Nereis* density. % organic matter was also highly positively significant.

3.10.3.4 Discussion: Dunlin

Site size at the whole estuary scale may well be the predicting factor that overides all others considering the range of variables in the whole estuary model. McLusky *et al.* (1992) have already shown that dunlin numbers at Torry Bay went into significant decline following the reclamation of a large area of the mudflat there for the construction of a fly ash lagoon. It is evident that numbers of dunlin at this site are still extremely low with only 3 birds seen in total during all the observations made here during the winters of 1998/1999 and 1999/2000. A muddy substrate with a high silt content is also preferred by dunlin and this has been shown elsewhere by Nehls & Tiedemann (1993). These workers however noted that dunlin moved to sandier areas in the late summer as their preference for prey items changed. Although such through the year changes place restrictions on the validity of the Forth Estuary dunlin model outside the winter months (November to February) numbers of dunlin present on the estuary in late summer and early spring are negligible. The negative relationship between *Nereis* density and dunlin feeding effort at the whole estuary scale and at Kinneil are in contradiction to previous work (Bryant 1979) and may be down to poor sample size or a lack of a good mixture of poor and rich sites for *Nereis* in the model. However at the Skinflats site the positive relationship here agrees with the findings of Warnes (1981) and may indicate that presently, *Nereis* is only important at this site. *Manayunkia* is also important at the single site scale although not at the whole estuary scale. Such a relationship, not noted before on the Forth Estuary, may be a new development as invertebrate populations recover on the estuary generally from previous pollution events (McLusky *et al.* 2000, Davis 2001)

3.12.4 Knot

3.12.4.1 Knot: whole estuary

Table 3.12: Minimal model summary from knot feeding effort v all predictor variables at the whole estuary scale

Variable	F value	P value
Site size (ha)	23.92	<0.001
Macoma size (mm,long axis)	14.75	<0.001
Cerastoderma	10.08	0.002
Nereis	8.03	0.007
Mytilus	7.33	0.01

Residual degrees of freedom = 45
Residual deviance = 22.40

3.12.4.1.1 Model coefficients for knot feeding effort

Knot feeding effort = -1.56 – 2.05 (*Cerastoderma*) + 2.01 (*Mytilus*) + 2.99 (*Macoma* size mm (long axis)) + 1.58 (Site size (ha)) – 2.03 (*Nereis*)

3.12.4.1.2 Predicted knot feeding effort v actual feeding effort

Knot actual feeding effort = -0.418220 + 1.09919 knot predicted feeding effort, $F_{1,42} = 56.18$, $P = < 0.001$, R-Sq = 57.2%

3.12.4.1.3 Summary: knot, whole estuary

At the whole estuary scale knot prefer to feed in larger sites where there are high densities of *Mytilus* and large *Macoma.* They also seem to be avoiding areas where there are large numbers of *Cerastoderma* and *Nereis.* None of the sediment characteristics was important for knot and these all fell out of the model first.

3.12.4.2 Knot: Kinneil

Table 3.13: Minimal model summary from dunlin feeding effort v all predictor variables at Kinneil

Variable	F value	P value
Tide height (macd)	12.25	0.001
Macoma	8.46	0.007
Nereis	6.85	0.01

Residual degrees of freedom = 27
Residual deviance = 32.54

3.12.4.2.1 Model coefficients for knot feeding effort

knot feeding effort = -2.27 + 0.62 (*Macoma*) +0.98 (tide height macd) – 1.62 (*Nereis*)

3.12.4.2.2 Predicted knot feeding effort v actual feeding effort

Knot actual feeding effort = -4.10816 + 2.41975 knot predicted feeding effort, $F_{1,28} = 5.13$, $P = < 0.01$, R-Sq = 31.4%

3.12.4.3.3 Summary: knot, Kinneil

At Kinneil feeding effort increased with tide height suggesting that birds preferred high level areas. Using this type of model though it is impossible to tell where in the higher tidal contours the birds tended to feed, as there is no spatial element that can identify this. Again *Macoma* is an important predictor of feeding effort but at this scale size of the animals was not significant, but only just (P=0.08). *Nereis* was also negatively related to knot as it was at the whole estuary scale. Figure 3.22 highlights a general preference for the >4m tide height contour in the embayment area and in the mouth of the River Avon at Kinneil.

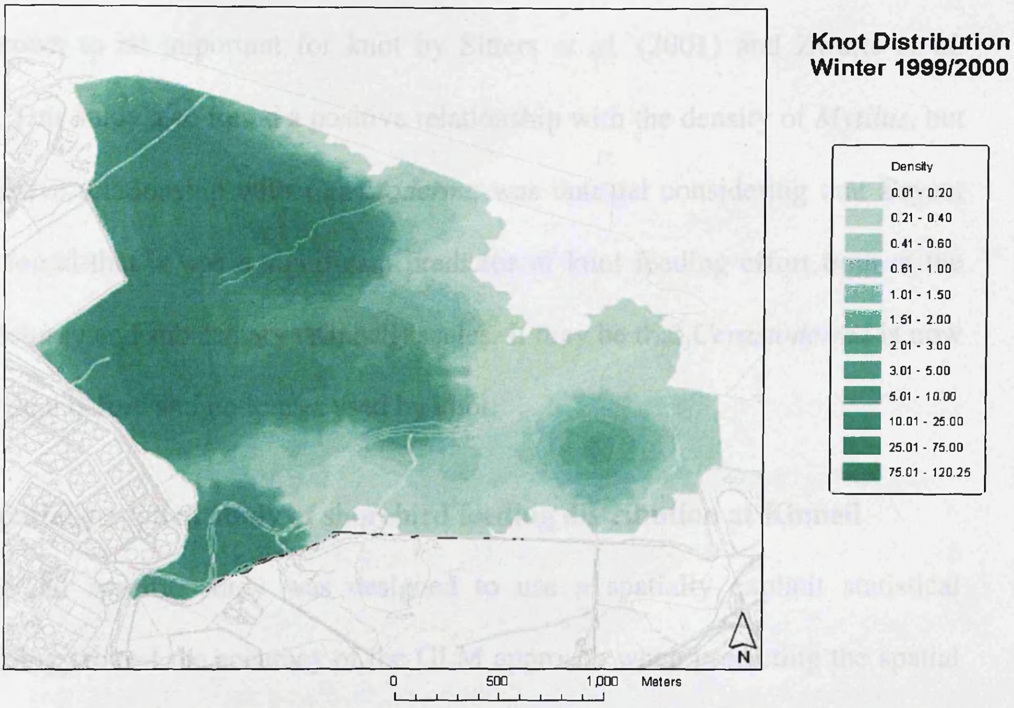


Fig 3.22: Knot feeding effort distribution at Kinneil based on complete spatial data on feeding birds collected between November 1999 and March 2000.

3.10.4.4 Discussion: Knot

Knot were only present in sufficient numbers at the whole estuary scale and at Kinneil for models to be calculated; their presence at Skinflats was too sporadic for any model to be constructed. It is unsurprising that *Macoma* have been shown to be important for knot on the Forth Estuary as this has been determined in previous studies (Bryant 1979, Warnes 1981). The positive relationship with *Macoma* size at the whole estuary scale suggests that knot prefer large *Macoma* although the size of chosen individuals is unlikely to exceed 10mm (Hulsher 1982). It is also clear from extensive work on the Dutch Waddensee that *Macoma* are normally the primary prey item choice in the diet of the knot (Zwarts & Blomert 1992, Dekinga & Piersma 1993, de Goeij & Luttikhuizen 1998). Piersma *et al.* 1993 found that although *Macoma* was the best predictor of the spatial distribution of knot on this site *Hydrobia*, *Mytilus* and *Cerastoderma* were also important. *Mytilus* has also been shown to be important for knot by Sitters *et al.* (2001) and Zwarts *et al.* (1992). This study also found a positive relationship with the density of *Mytilus*, but the negative relationship with *Cerastoderma* was unusual considering that Bryant (1979) found that it was a significant predictor of knot feeding effort both at the whole estuary and sub estuary (Kinneil) scales. It may be that *Cerastoderma* is now scarcer than before and no longer used by knot.

3.13 Spatially explicit study of shorebird feeding distribution at Kinneil

The Kinneil specific study was designed to use a spatially explicit statistical methodology to test the accuracy of the GLM approach when predicting the spatial distribution of overwintering shorebirds. It was also undertaken to determine whether the results of the GLM approach were likely to be compromised by the problems encountered with spatially autocorrelated data (see section 2.10.1). Data surface maps of all the variables that featured in the minimum models were estimated by kriging point samples distributed randomly around the mudflat with a view to visualising the spatial variability of all the measured characteristics. The sediment characteristic maps were based on 221 samples and the invertebrate maps on 161 samples. Tide height data were available for all 623 grid cells that covered the intertidal area. Distance from shore data for each grid cell was calculated using the relevant function in ARCVIEW. This process was undertaken to provide data surfaces to inform the predicted shorebird distribution maps generated using the model coefficients for each of the key species. All the maps of ‘observed’ versus ‘predicted’ feeding distribution are presented for shelduck, redshank, dunlin and knot and cross validation results from the comparison of linear regression, ordinary kriging and co-kriging are given for shelduck and redshank. The maps shown for actual distribution refer to the distribution in January when all the invertebrate and sediment data were collected.

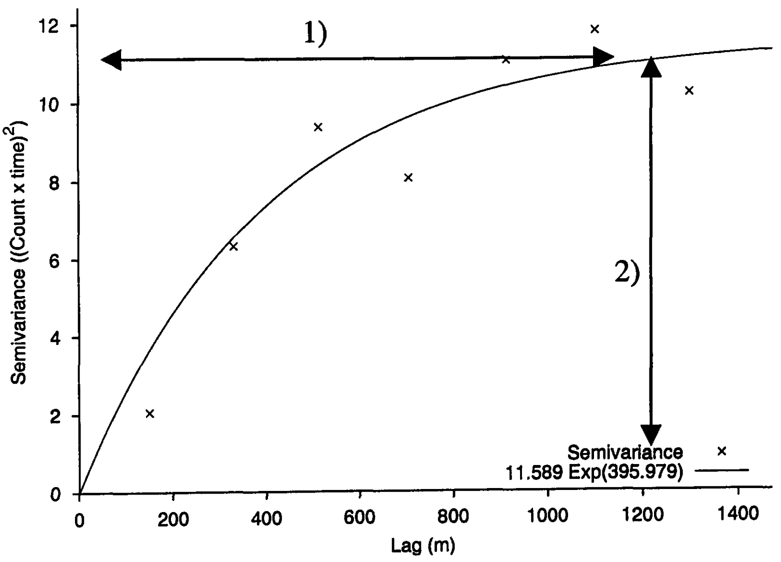
3.13.1 Predicting shorebird distribution using kriging

In this analysis, the variogram is used to characterise spatial variation in both shorebird feeding effort and secondary variables. The coefficients of models fitted to variograms are then used to make predictions at unsampled locations using kriging. Two varieties of kriging were used in this analysis. These are ordinary kriging (OK) and ordinary co-kriging (CK). OK uses information about one variable (e.g., shorebird feeding effort) while CK uses information about the primary variable and one or more secondary variables. If the secondary variable/s are linearly related to the primary variable then co-kriging may increase the accuracy of predictions.

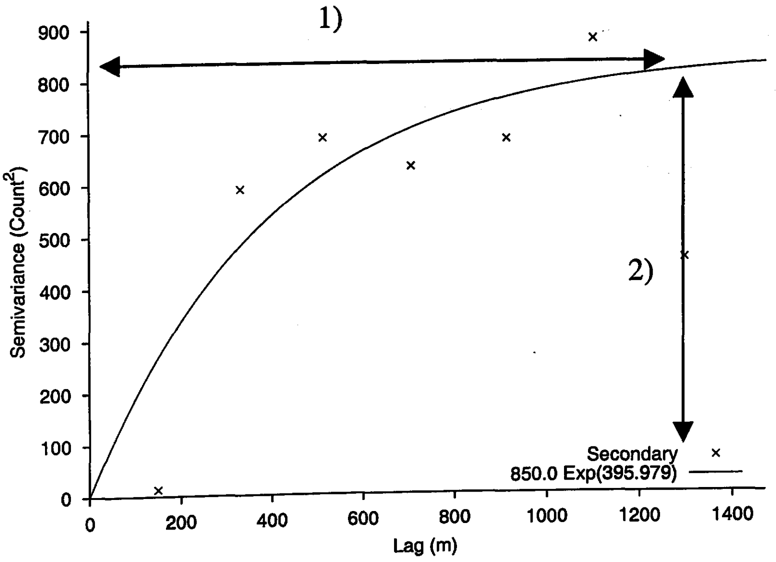
3.13.1.1 Variogram analysis

As the first stage of the geostatistical analysis, variograms were estimated for shelduck (Fig 3.23a) and redshank (Fig 3.24a) as they had the clearest spatial structure in their feeding distribution. Variograms were then estimated for invertebrate variables that had the highest correlation coefficient with the two shorebird species. For shelduck this was *Manayunkia* (Fig 3.23 b,c) and for redshank this was *Nereis* (Fig 3.24a,b).

a)


1)
2)
Semivariance ((Count x time)^2)
0
2
4
6
8
10
12
Lag (m)
0
200
400
600
800
1000
1200
1400
Semivariance ×
11.589 Exp(395.979)

b)


1)
2)
Semivariance (Count^2)
0
100
200
300
400
500
600
700
800
900
Lag (m)
0
200
400
600
800
1000
1200
1400
Secondary ×
850.0 Exp(395.979)

c)

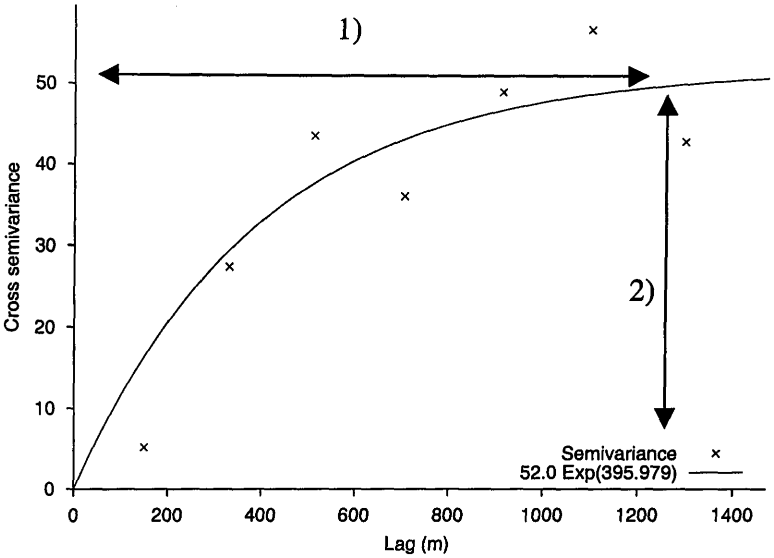
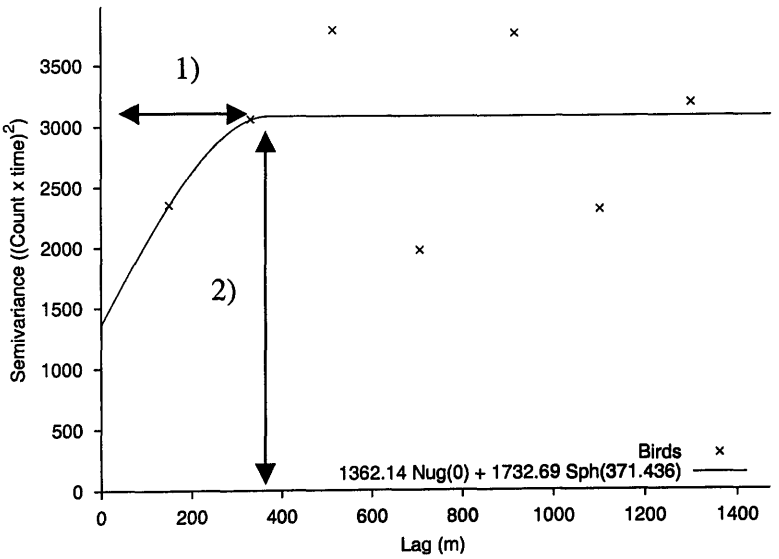


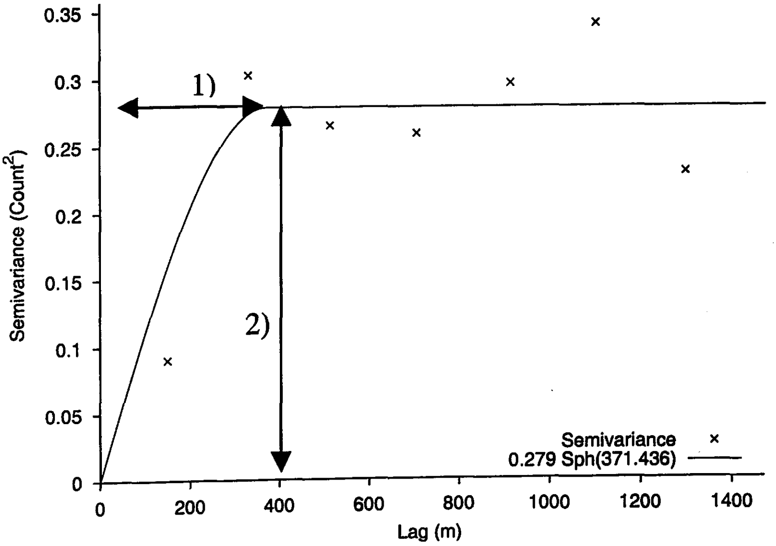
Fig 3.23: Variograms for shelduck feeding effort and *Manayunkia* count a) variogram for shelduck feeding effort b) variogram for *Manayunkia* count c) cross variogram shelduck feeding effort and *Manayunkia* count. The arrows indicate the range 1) and the sill 2) and allow the distance beyond which the data are no longer autocorrelated to be calculated.

In all the above variograms the quadratic behaviour near the origin indicates that the regionalised variables (shelduck feeding effort and *Manayunkia* count) are highly continuous. All sample data located within a distance of c1250m from each other are correlated, beyond this point autocorrelation disappears. There are no apparent changes in the curvature of the variogram therefore nested structures (i.e. processes operating at different scales are not evident).

a)


3500
3000
2500
2000
1500
1000
500
0
Semivariance ((Count x time)^2)
1)
2)
0
200
400
600
800
1000
1200
1400
Lag (m)
Birds ×
1362.14 Nug(0) + 1732.69 Sph(371.436)

b)


0.35
0.3
0.25
0.2
0.15
0.1
0.05
0
Semivariance (Count^2)
1)
2)
0
200
400
600
800
1000
1200
1400
Lag (m)
Semivariance ×
0.279 Sph(371.436)

c)

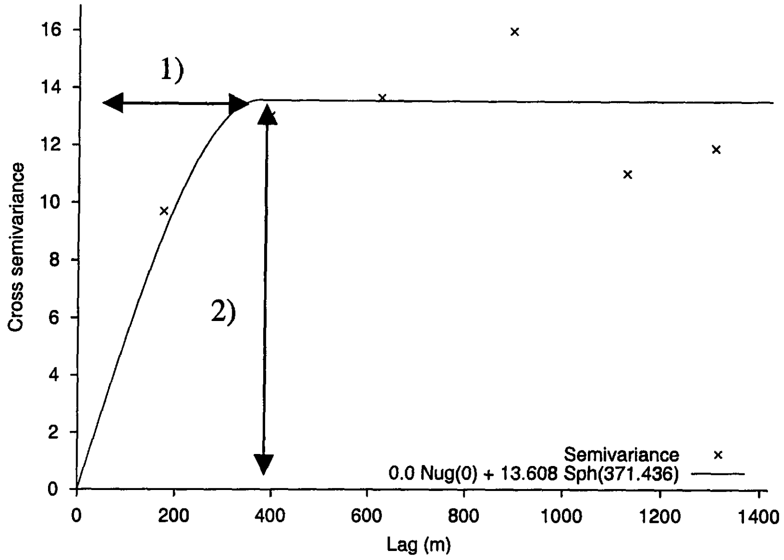


Fig 3.24: Variograms for redshank feeding effort and *Nereis* count a) variogram for redshank feeding effort b) variogram for *Nereis* count c) cross variogram redshank feeding effort and *Nereis* countThe arrows indicate the range 1) and the sill 2) and allows the distance beyond which the data are no longer autocorrelated to be calculated.

The variogram for redshank feeding effort Fig 3.24a shows a discontinuity near the origin i.e. the variogram does not tend to zero. This indicates that redshank feeding effort is highly irregular at short distances. Both the spatial distribution of redshank feeding effort and the distribution of *Nereis* are both highly correlated below about 380m and independent beyond this distance.

The coefficients of the models fitted to the variograms were used to inform spatial prediction with kriging. Firstly, cross-validation was used to assess the performance of linear regression (LR) using a range of covariates and then ordinary kriging and ordinary cokriging using the covariates specified above.

3.13.1.2 Cross validating the predictive power of linear regression (LR), ordinary kriging (OK)and co-kriging (CK)

Cross validation prediction error summary statistics are given in Table 3.14 (shelduck) and Table 3.15 (redshank). The mean value indicates whether the mean estimate over-estimates (positive value) or under-estimates (negative value). It is, therefore, a guide to bias in estimates. The standard deviation provides some indication of the magnitude (or more specifically, the precision) of the errors.

Table 3.14. Shelduck: cross-validation prediction error summary statistics.

Method	Minimum error	Median error	Maximum error	Mean error	Standard deviation	Root mean square error
LR	-15.12	-0.79	10.46	-1.39	4.48	0.005
OK	-14.53	0.41	6.16	-0.12	3.40	0.08
CK	-21.53	0.62	6.55	-0.21	4.98	-0.23

For shelduck, OK produced the smallest cross-validation prediction errors (judging by the mean and standard deviation). The largest errors were for CK.

Table 3.15. Redshank: cross-validation prediction error summary statistics

Method	Minimum error	Median error	Maximum error	Mean error	Standard deviation	Root mean square error
LR	-278.4	-2.55	2.77	-16.269	53.146	0.273
OK	-277.3	7.75	28.92	-1.734	56.51	-0.027
CK	-261.2	22.25	109.9	3.21	68.25	0.029

OK produced the least biased cross-validation prediction errors for redshank while the LR predictions were smaller (judging by the standard deviation).

3.13.1.1.1 Discussion: shelduck

The spatial structure of shelduck and its assumed principal prey item *Manayunkia* are very similar and it appears that although shelduck distribution is fairly continuous at Kinneil they show an aggregative response which coincides with that of *Manayunkia*, potentially optimising their forage rate success. The cross validation errors for the non-spatial and spatial methods (Table 3.14) although different are all similar enough to conclude that the linear regression method is as adequate as the spatial methods when it comes to predicting the spatial distribution of shelduck in response to various environmental variables. The fact that the co-kriging errors were the largest may indicate that the co-variation between shelduck feeding effort and *Manayunkia* count was not modelled well. LR prediction errors were only slightly greater than the other two methods.

3.13.1.1.2 Discussion: redshank

Redshank feeding effort is highly correlated at short range, in this case < 380m. This suggests a high level of aggregation when feeding. This is accompanied by their strong preference for high level areas (Table 3.7, Fig 3.19). Again the principal prey item of the redshank at Kinneil, *Nereis*, aggregates at the same spatial scale although it is apparent that such distributions are patchy around the site (Fig 3.11i). Linear regression had the smallest error standard deviation and although it had similar minimum error to the spatial methods, it had the lowest maximum error (Table 3.15). Again the predictive power of the GLM is comparable to that of kriging and co-kriging, so where a non spatial method has been used the results appear to be equally valid.

3.13.2 The weighted area models

3.13.2.1 Comparing the 'actual' January/February feeding effort of the key species to the feeding effort predicted by the minimal GLM for that species at Kinneil

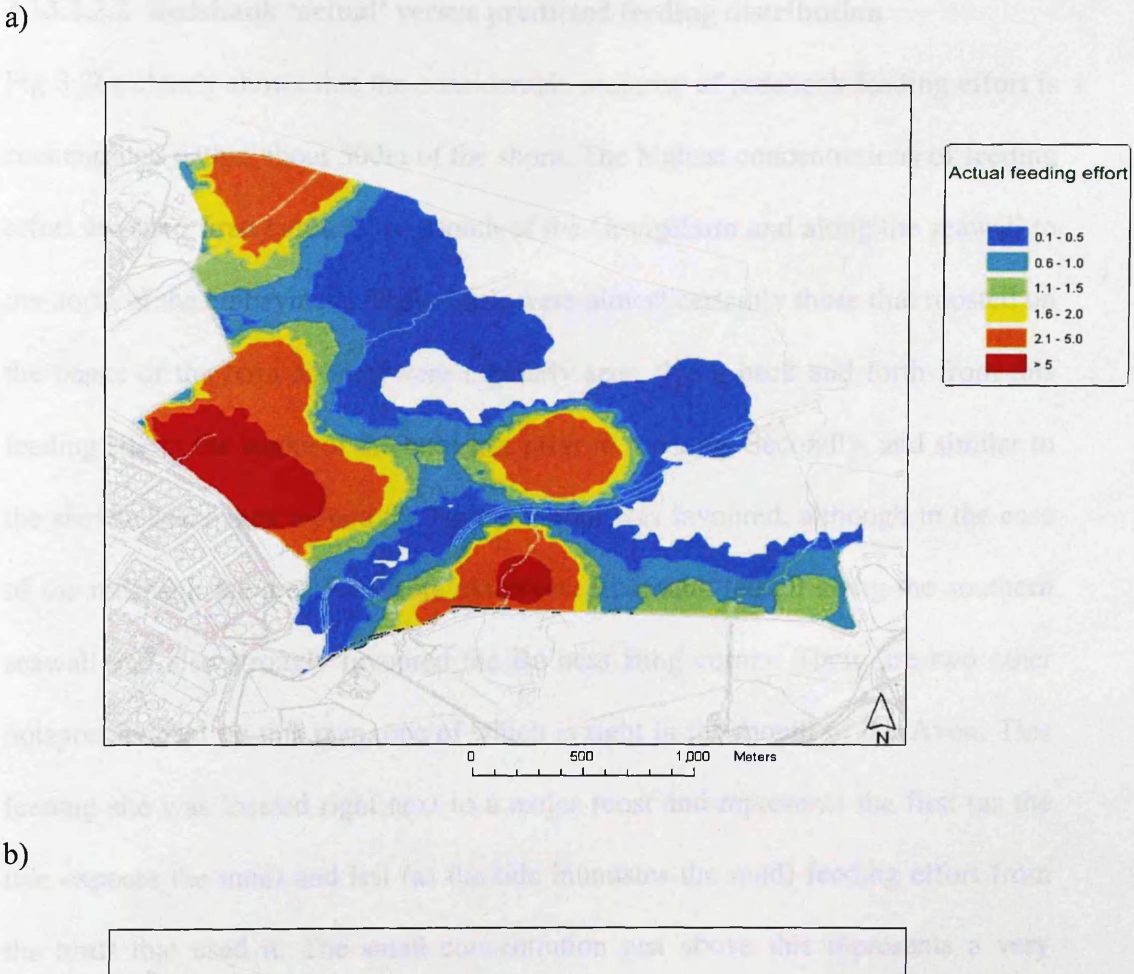
McLusky *et al.* (1992) concluded that the impact of land claim on the overwintering populations of different species of shorebirds at Torry Bay had affects varying from neutral to substantially negative. Although populations of some species like the dunlin and bar tailed godwit showed significant declines others like the redshank remained unchanged. Because of these variations in the effect of direct area loss they suggested that such a simple consideration was inadequate to describe the effects of land claim and the consequences it may have for the birds that use the area. In light of this work and that of Bryant (1998, 1999) at Skinflats, *weighted area models* for each of the four key species at Kinneil were constructed to highlight the most important feeding areas.

3.13.2.2 'Actua'l feeding effort v predicted feeding effort

The linear models for all the key species were produced using sample data based on just 30 randomly selected stations, but according to the model cross validation errors this method is still as good at predicting distribution of primary and secondary variables in space as kriging or co-kriging. The maps of actual feeding effort are the result of observations made between November 1999 and March 2000. The maps of 'actual' feeding effort are kriged complete data and represent the entire area where birds were both seen to feed and where they are likely to feed based on the interpolation weights. The maps are weighted on a scale of 0 - >5 or 0 - >10 depending on the range of values. The relationship between actual and predicted maps is considered.

3.13.2.2.1 Shelduck 'actual' versus predicted feeding distribution

The shelduck 'actual' feeding effort surface (Fig 3.25a) represents the interpolated complete data for this species and covers all the potential feeding areas as well. A strong preference for the embayment area and the low tide brackish water input to the mudflat from the lagoon are noticeable. The whole area within 500m of the southern seawall is favoured as is the central region north of the River Avon and the top northwestern corner. The minimal model for shelduck positively correlates feeding effort to the *Manayunkia* count and negatively correlates it to distance from shore (m). The map generated using the coefficients from this model (Fig 3.25b) highlight those areas that the model predicts to be most important for shelduck. The distance from shore weighting has included the vast majority of the area where actual feeding occurred in its greatest concentration and includes all the mud approximately 500m from the shoreline. The central area has also been picked out in the predicted map and this is related to the high *Manayunkia* density in this area (Fig 3.11a). With reference to Fig 3.11a it is possible to see how the actual feeding effort map relates generally to *Manayunkia* distribution. The area around the lagoon outfall however has lower densities of *Manayunkia* and some other, possibly unmeasured local conditions may be responsible for this preference. For instance this area is particularly high in organic matter with levels up to 7% per sample (Fig 3.16e), such conditions may be preferable to the shelduck on a local to micro scale. Such local factors influencing shelduck feeding behaviour may not be significant in a non-spatial model. Fig 3.25b successfully predicts a preference for the southern edge of the embayment, however this predicted feeding area continues around into the mouth of the River Avon, a prediction directly related to *Manayunkia* density once more (Fig 3.11a). Shelduck were not observed feeding in this river mouth area but this may be due to one of two reasons. Firstly, much of this area is quite compacted and sandy (up to 30% (Fig 3.16d)) potentially making conditions for shelduck feeding difficult as shelduck was negatively correlated to sand at the whole estuary scale (Table 3.4). This said, none of the sediment characteristics appeared to influence shelduck feeding effort at Kinneil. Secondly, the area in question in the Avon mouth was particularly hard to see from all counting positions, so undercounting of shelduck is a real possibility and it may be that more use was actually made of this part of the site. Shelduck feeding effort has often been linked to *Hydrobia* density (Bryant 1979, Patterson 1982, Cadee 1994) and although this was not a significant covariate in this shelduck model it is possible that this species may have some influence on shelduck feeding effort in another. Fig 3.11b shows that the area in the top northwestern corner of Kinneil has a high density of *Hydrobia*. When comparing this map to Fig 3.25a the presence of *Hydrobia* here may explain the high shelduck feeding effort here that is not apparently linked to *Manayunkia* density. Many such potential relationships may become apparent on closer examination when comparing the maps of covariates to those of bird feeding effort regardless of their significance in the whole site model.



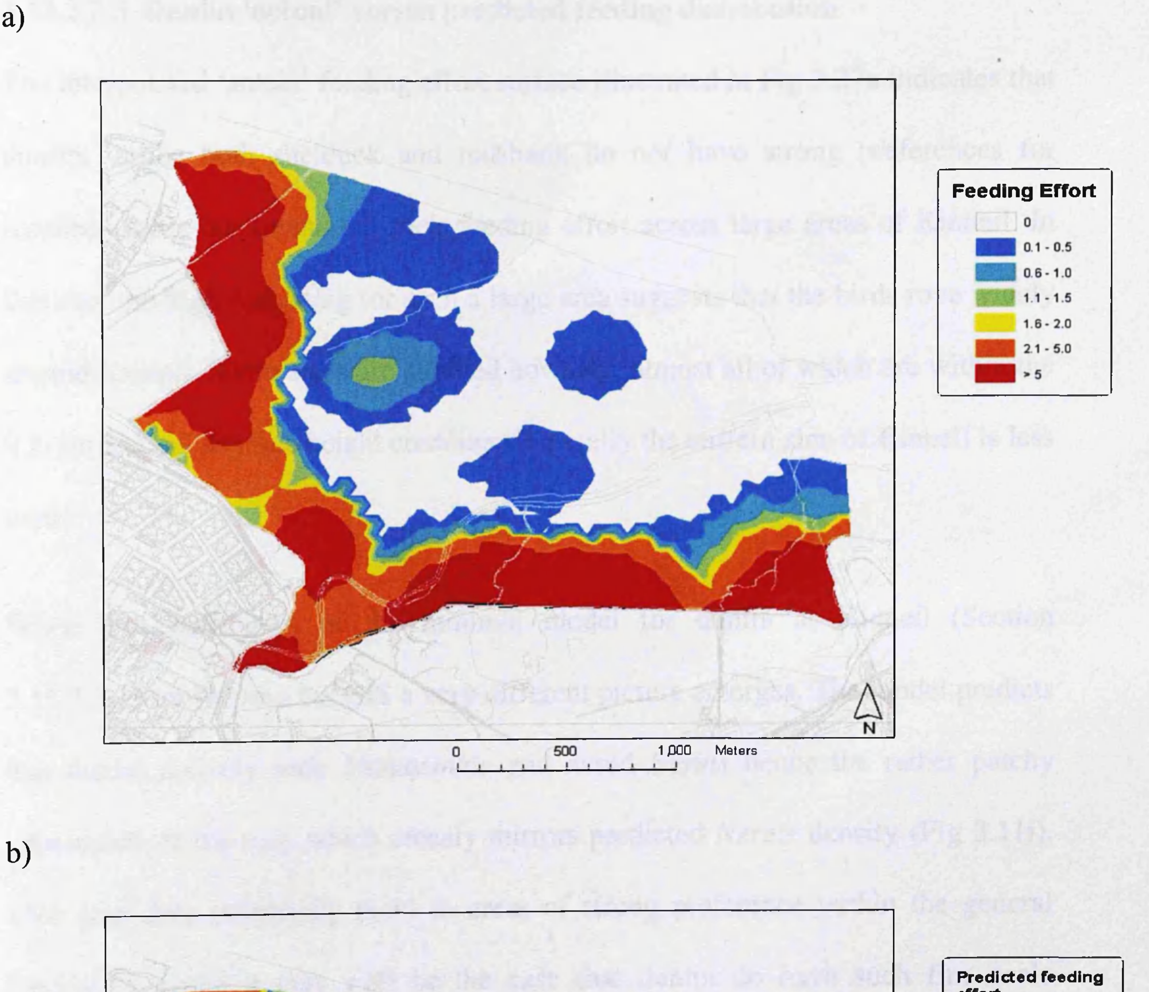
Prediction equation:
Shelduck = 1.29 + (0.01 * manayunkia) - (0.003 * distance from shore)

Fig 3.25: Maps illustrating a) kriged 'actual' shelduck feeding effort and b) predicted shelduck feeding effort based on the coefficients of the minimal model (see Table 3.5)

3.13.2.2.2 Redshank 'actual' versus predicted feeding distribution

Fig 3.26a clearly shows that the considerable majority of redshank feeding effort is concentrated within about 500m of the shore. The highest concentrations of feeding effort are sited firstly around the mouth of the Grangeburn and along the seawall to the north of the embayment. These birds were almost certainly those that roosted on the banks of the burn as they were regularly seen flying back and forth from this feeding site to the banks of the burn just prior to roosting. Secondly, and similar to the shelduck, the area around the lagoon outfall was favoured, although in the case of the redshank the area was more extensive. Redshank fed all along the southern seawall and also strongly favoured the Bo'ness Bing corner. There are two other hotspots evident on this map, one of which is right in the mouth of the Avon. This feeding site was located right next to a major roost and represents the first (as the tide exposes the mud) and last (as the tide inundates the mud) feeding effort from the birds that used it. The small concentration just above this represents a very localised concentration of feeding and it is likely that this is directly linked to one of the predicting variables.

The map predicting redshank feeding effort (Fig 3.26b) based on the coefficients of the minimal model for this species (Table 3.7) appears to fit the actual effort feeding effort quite closely. It does however lower the feeding effort weighting in some areas but highlights the most important spots within the more general feeding sites. Predicted feeding in the Bo'ness Bing corner has the same high weighting as the actual distribution and this is strongly linked to *Nereis* density (Fig 3.11i), *Nereis* density being the most important variable in the prediction equation (Section 3.10.2.2.1). It has already been mentioned that on a sub-mudflat level certain significant relationships between feeding effort and predictor variables will not show up in the whole site model. It is tempting in the case of the Bo'ness Bing area to suggest that *Hydrobia* are locally important for redshank as their density here, is also locally high (Fig 3.11b). Other variables may also be implicated in the redshanks' preference for the area by the mouth of the Avon, this prediction corresponds to actual feeding effort and also to a high density of *Nereis* (Fig 3.11i). Although not significant in the whole site model *Corophium* density is also high in this area (Fig 3.11d) and it might be expected that as it is a favoured food item at other sites, it might also be locally important at Kinneil at the sub mudflat scale. The predicted feeding effort distribution does not weight the Grange burn area quite as heavily as the actual distribution map but it acknowledges that within this general region, the most important area of it according to the linear model is the top corner of the embayment area, again this is linked to *Nereis* density.



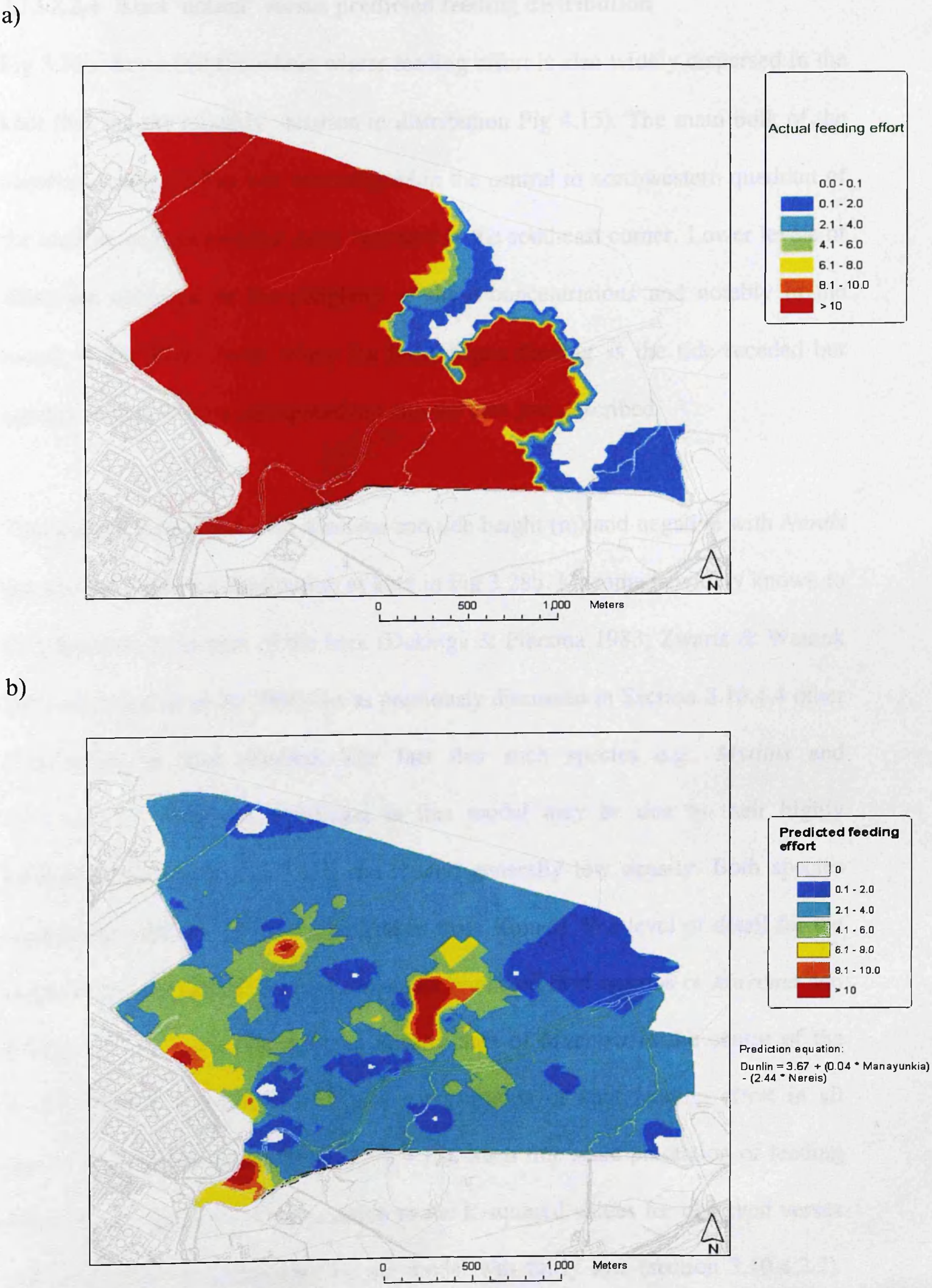
Prediction equation:
Redshank = 3.59 + (2.65 * nereis) - (0.004 * manayunkia) - (0.009 * distance from shore)

Fig 3.26: Maps illustrating a) kriged 'actual' redshank feeding effort and b) predicted redshank feeding effort based on the coefficients of the minimal model (see Table 3.7)

3.13.2.2.3 Dunlin 'actual' versus predicted feeding distribution

The interpolated 'actual' feeding effort surface illustrated in Fig 3.27a indicates that dunlin, unlike both shelduck and redshank do not have strong preferences for localised areas but spread out their feeding effort across large areas of Kinneil. In this case the high weighting for such a large area suggests that the birds rove widely around Kinneil. Some areas are avoided however, almost all of which are within the 0.2-1m and >1-2m tide height contours. Generally the eastern side of Kinneil is less used.

When the coefficients of the minimal model for dunlin at Kinneil (Section 3.10.3.2.1) are fed into the GIS a very different picture emerges. The model predicts that dunlin actively seek *Manayunkia* and avoid *Nereis* hence the rather patchy appearance of the map which closely mirrors predicted *Nereis* density (Fig 3.11i). This map does potentially point to areas of strong preference within the general feeding area and it may well be the case that dunlin do have such fine scale preferences that are difficult to pick up through general observation (Kelsey & Hassell 1989). Although this might be the case the model predictions for dunlin are unusual as *Nereis* has been shown to be a favoured food item for dunlin in many other studies at other sites, (Bryant 1979, Evans *et al.* 1979, Clark 1983 and Worrall 1984), and at Skinflats within the Forth Estuary (this study, Warnes 1981). Although this was the best minimal model for dunlin which left the least residual variance it is quite likely that there are other equally adequate models that would work for dunlin at Kinneil. A variety of models with different combinations of variables were tried in the model evaluation process but in none of them was *Nereis* density significant. As previously mentioned, *Nereis* may be important for dunlin at a scale finer than that of the whole site.



Prediction equation:
Dunlin = 3.67 + (0.04 * Manayunkia) - (2.44 * Nereis)

Fig 3.27: Maps illustrating a) kriged 'actual' dunlin feeding effort and b) predicted dunlin feeding effort based on the coefficients of the minimal model (see Table 3.10)

3.13.2.2.4 Knot 'actual' versus predicted feeding distribution

Fig 3.31a shows that the whole winter feeding effort is also widely dispersed in the knot (but see the monthly variation in distribution Fig 4.15). The main bulk of the observed feeding effort was concentrated in the central to northwestern quadrant of the mudflat with an isolated patch favoured in the southeast corner. Lower levels of effort are observed on the periphery of these concentrations and notably in the mouth of the River Avon where the birds began feeding as the tide receded but quickly dispersed from and spread out into the area just described.

The positive association with *Macoma* and tide height (m) and negative with *Nereis* governs the predicted distribution of knot in Fig 3.28b. Macoma is widely known to be a favoured food item of the knot (Dekinga & Piersma 1983, Zwarts & Wanink 1993 and Piersma *et al.* 1994) but as previously discussed in Section 3.10.4.4 other prey items are also selected. The fact that such species e.g., *Mytilus* and *Cerastoderma* were not significant in this model may be due to their highly localised distribution (Fig 3.11g and h) and generally low density. Both species occurred in very few of the samples taken from Kinneil. The level of detail for the predicted feeding effort closely follows the predicted distributions of *Macoma* and *Nereis* and it is clear that the high density area of *Macoma* in the centre of the mudflat (Fig 3.11c) is mirrored by a concentration of knot feeding effort in all observation months except March (Fig 4.15). Such fine scale prediction of feeding effort should be regarded with caution as the R-squared values for observed versus predicted values as determined by the model was fairly low (section 3.10.4.2.2). This model was however the most biologically realistic.

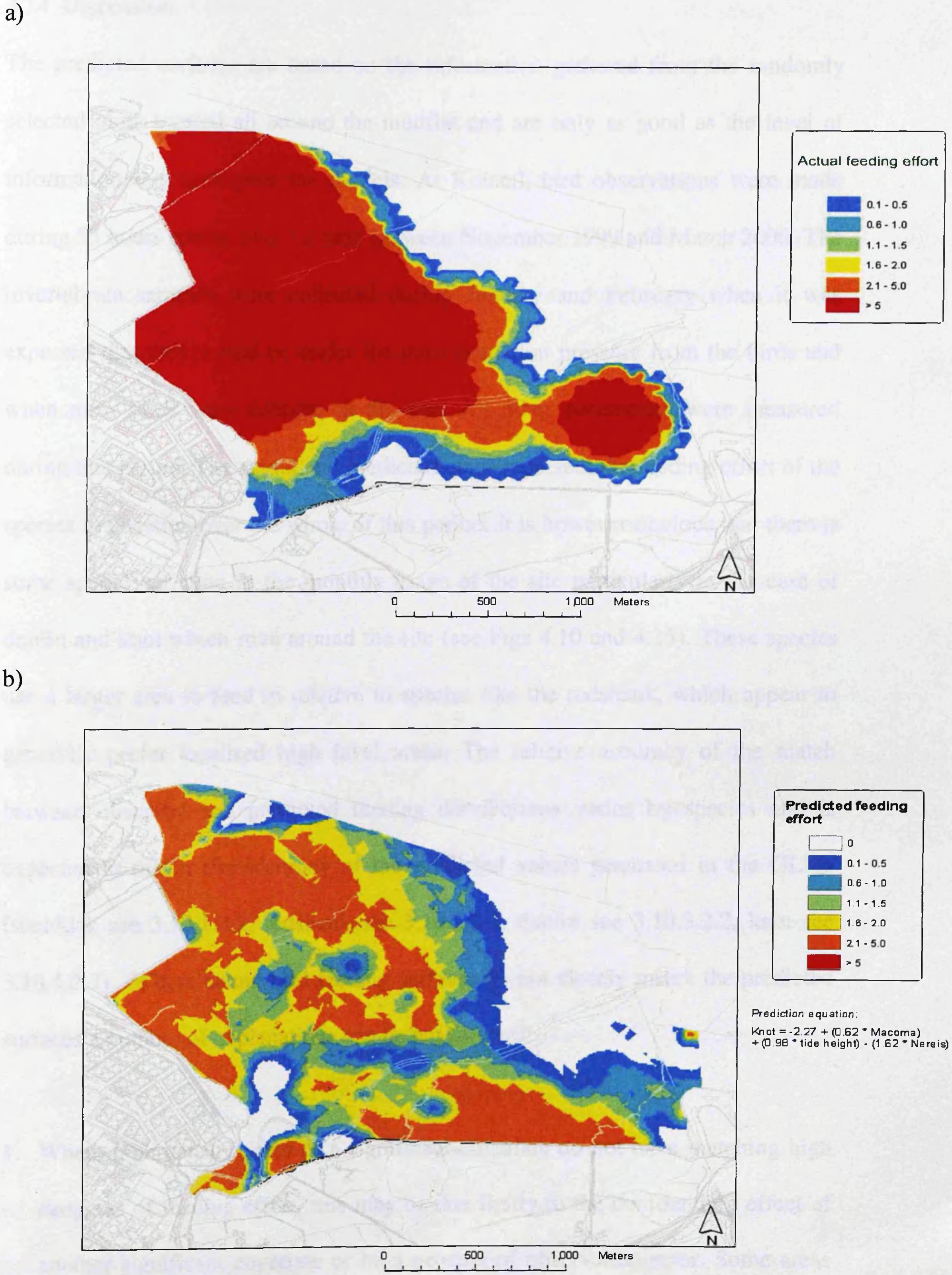


Fig 3.28: Maps illustrating a) kriged actual knot feeding effort and b) predicted knot feeding effort based on the coefficients of the minimal model (see Table 3.13)

3.14 Discussion

The predicted surfaces are based on the information gathered from the randomly selected plots located all around the mudflat and are only as good as the level of information that underpins the models. At Kinneil, bird observations were made during 53 hours spread over 12 days between November 1999 and March 2000. The invertebrate samples were collected during January and February when it was expected that they would be under the most predation pressure from the birds and when most birds were present on the site. All other parameters were measured during this period. The actual and predicted maps represent the feeding effort of the species in question over the whole of this period. It is however obvious that there is some spatial variation in the monthly usage of the site particularly in the case of dunlin and knot which rove around the site (see Figs 4.10 and 4.15). These species use a larger area to feed in relative to species like the redshank, which appear to generally prefer localised high level areas. The relative accuracy of the match between observed and predicted feeding distributions varies by species and is expected to match the accuracy of the predicted values generated in the GLMs (shelduck see 3.10.1.2.2, redshank see 3.10.2.2.2, dunlin see 3.10.3.2.2, knot see 3.10.4.2.2). Where actual bird feeding surfaces do not closely match the predicted surfaces a number of explanations can be put forward:

1. Where high-density areas of a significant covariate do not have matching high densities of feeding effort, this may be due firstly to the confounding effect of another significant covariate or be a product of observation error. Some areas will inevitably have been undercounted or overcounted due to the errors

associated with making such observations on estuarine mudflats. Such errors and the attempts made to mitigate them are discussed in section 2.3.4.

2. As any number of models may equally explain the feeding effort of a shorebird species, the prediction surfaces are only valid for the suite of variables in the chosen model. Therefore the influence of other potentially important measured covariates will be missing from the generated map.

3. With reference to point 2, many potentially important predictor variables may have gone unmeasured. For instance data were not collected on the nematodes present in each of the estuarine mud samples; these may be an important food source for some shorebirds.

4. As the models assume that the significant variables in the minimal adequate model apply equally to the entire area, locally important covariates may not have shown up as significant in the whole site model. The spatial variability of such covariates is evident (Fig 3.11a-k and Fig 3.16a-e) and it is likely that lack of bird feeding effort samples in certain areas did affect the outcome of the modelling process, i.e. some important information was either not used or not included in the model due to its random sampling element.

It has already been mentioned that the minimal adequate model adopted for each species was chosen from a large set of potential models that might usefully interpret the data. When conducting multiple regression analysis with many parameters, different combinations can result in the same probability of explanation (Gibbons *et* *al.* 1995) so the resultant distribution maps must be evaluated in the field (Sheiffarth *et al.* 1996).

The variation in the predicted surfaces for both dunlin and knot reflect the fact that although biologically reasonable models were chosen there were doubtless other models that would have been equally sound. The models chosen exhibited the least residual variance and gave the highest R-squared value when observed values were regressed against predicted values. Even so these values were still low (dunlin = 32.7% and knot = 31.4%). These surfaces predict how these species would respond to the covariates in the models chosen but it is likely that greater detail would be evident if other variables were included. It may be useful therefore to produce a series of equally reasonable surfaces based on the results of a number of models especially when aiming to assess the relative importance of a small area of the mudflat to these species. The fact that a number of models may be useful when predicting feeding effort in these species underlines that fact that they are both quite vagile species and roam considerably both within and between sites. Knot are especially mobile and as they are close to their metabolic maximum in North West Europe in winter (Wiersma & Piersma 1994) regular shifts in search of food may explain their high mobility even in milder winters when inter-estuary movements are common (Dick *et al.* 1976, Symonds *et al.* 1984, Davidson & Wilson 1992). Such variable site usage is considered in chapter 4. Shelduck also had a fairly low (34.9%) R-squared value as a result of the regression of observed versus predicted feeding effort values (section 3.10.1.2.2) and the generated surface only appears to explain certain elements of the observed feeding distribution. This is probably due to the influence of potentially important covariates dropping out of the minimal adequate model. This has been discussed in section 3.11.2.2.1. Of all the predicted feeding effort surfaces the results for redshank are the most promising although this is to be expected considering the good agreement between observed versus expected values as generated by the model (r-squared = 94.4%). Although it is likely that other covariates do have a bearing on redshank distribution, *Nereis* (+ve relationship), *Manayunkia* (-ve relationship) and distance from shore (m) (-ve relationship) are powerful predictors of redshank feeding effort at both coarse (whole site) and fine (sub site) scales. Such predictability of redshank distribution in this study coupled with good evidence of strong site fidelity elsewhere (Burton 2000) make this species and ideal candidate for future model testing. Such a test may compare the loss of an area of habitat at one site (e.g. Kinneil) with the loss of a similar area at another (e.g. Skinflats) on the assumption that all birds die. The variation of habitat importance weighting can be quantified and the relative proportion of the feeding effort/birds lost can be calculated. This allows the prioritisation of key *versus* other areas and enables such weighted area models to be used to inform practical management applications.

All of the above models refer to events occurring within only one winter. If the models are to be considered as valid for future studies on the Forth Estuary then an assessment must be made of their durability in the long term. The following chapter compares these contemporary results with data collected during selected winters over the last 25 years using Kinneil as the focal site. As well as this long-term variation in shorebird distribution invertebrate populations and sediment distribution, changes between and within winters are also considered.

Chapter 4. The long-term variability of shorebird distribution, invertebrate populations and sediment characteristics: How useful are the models in the long term?

4.1 Introduction

The models developed in Chapter 3 are based on the events occurring within a single winter and represent only a snapshot of the relationships between the spatial distribution of bird feeding effort and those variables that best predict it. What the models do not take into account are any short or long-term trends or fluctuations that might exist, either in bird numbers or in one or more of the predictor variables. Such temporal variation may mean that in the extreme case, the contemporary model is only valid during the winter it was developed. If so then just how valid are these models when predicting shorebird feeding effort in future winters? This chapter is divided into three sections. Section A considers temporal shorebird variation at Kinneil whilst sections B and C discuss variation in invertebrate populations and sediment characteristics respectively, both at Kinneil and at the wider estuary scale. Evidence of long term stability is discussed and implications for the relative validity of the models in the long term are indicated.

Section A: Shorebirds

4.2 Variation in the spatial distribution of the four key species of shorebird at Kinneil

Long term changes in the numbers of overwintering shorebirds in the UK have been well documented at the whole estuary scale (Moser 1987, Moser 1988, Prys Jones *et al.* 1994, Cayford & Waters 1996, Austin *et al.* 2000 and Pollitt *et al.* 2000) and it is evident that population numbers may both increase and decrease over time. The same is also the case for wildfowl (Kirby 1995, Pollitt *et al.* 2000). Bird community composition within an estuary may also change over time (Hill *et al.* 1993) although the vast majority of the 109 UK estuaries in this study showed little change in structure between the periods 1969-75 and 1981-85. Changing densities and spatial distributions of both birds and invertebrates and potential changes in sediment characteristics are considered at Kinneil for three different time scales: within winter, between two concurrent winters and between selected winters 1976 – 2000.

4.2.1. Results of variability within one winter, November 1999– March 2000

Certain levels (tide heights) and areas of the mudflat have already been shown to have higher weightings in terms of their relative importance for feeding birds. To determine whether or not the spatial distribution of each of the key species was consistent on a monthly basis throughout the winter, the percentage of the total monthly feeding effort for each species was calculated for the area between each 1m tide height contour (see Fig 4.1.). This broad level of spatial variation was chosen as it has been shown that the feeding effort of some species is significantly correlated with either tide height or distance from shore. Both shelduck and redshank were negatively correlated to distance from shore, preferring instead to feed closer to the shore and knot was positively correlated to tide height selecting the higher tide contour areas. For each species fluctuations in the monthly feeding effort is shown within each contour (Figs 4.4, 4.7, 4.10 and 4.15) and the relative stability of this feeding effort is shown by graphing the feeding effort CV for all winter months November to March. Spatial distribution maps illustrating feeding effort for each species were generated in ARCVIEW for each month to illustrate fine scale variations in shorebird feeding distribution within each tidal contour.

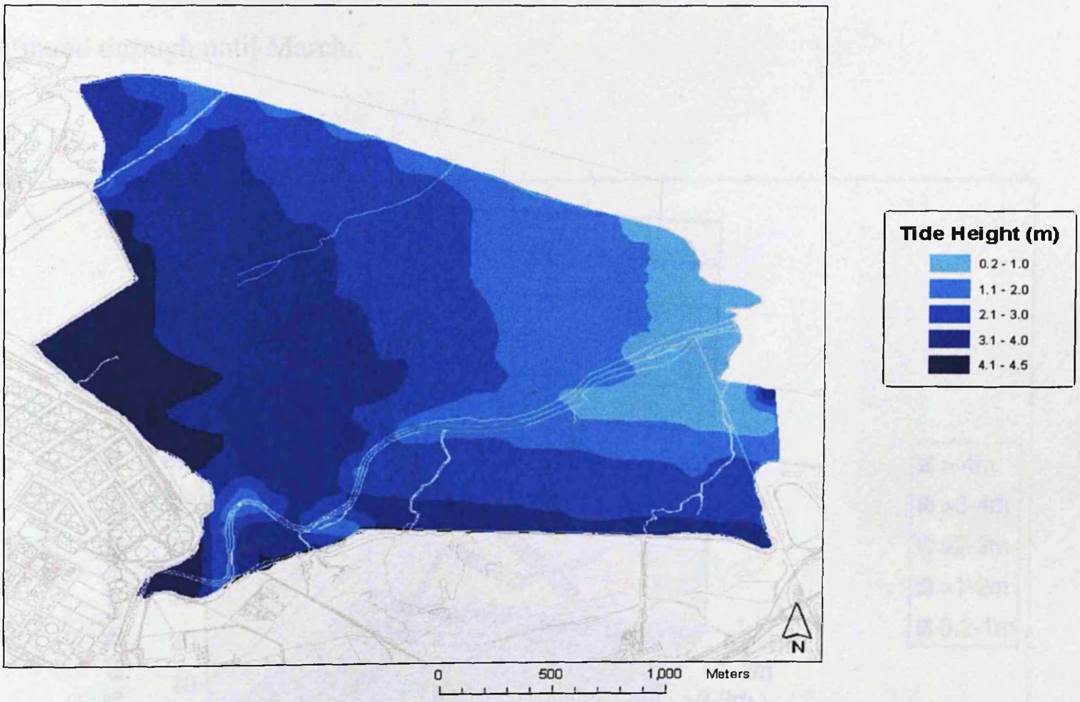


Fig 4.1: The area between each pair of 1m tide height contours is shown for Kinneil. The edge of the mudflat begins at 0.2m above chart datum and the highest recorded tide heights fall within the bounds of > 4.1m but < 4.5m. The contours were calculated using data from a survey undertaken by the Forth Ports Authority Nov/Dec 1986, drawing Nº 603/01 and from McLusky *et al.* 2000

4.2.1.1 Shelduck

In November and December, up to 93% of shelduck feeding effort was focused in the areas above the 4m tide height contour, especially in the triangular embayment on the left-hand side of Kinneil and the area at the mouth of the River Avon. Although there were some feeding shelduck in the Avon mouth area in November the vast majority of the birds were using the embayment throughout November and December and this concentration of feeding effort, albeit gradually declining, continued through until March.

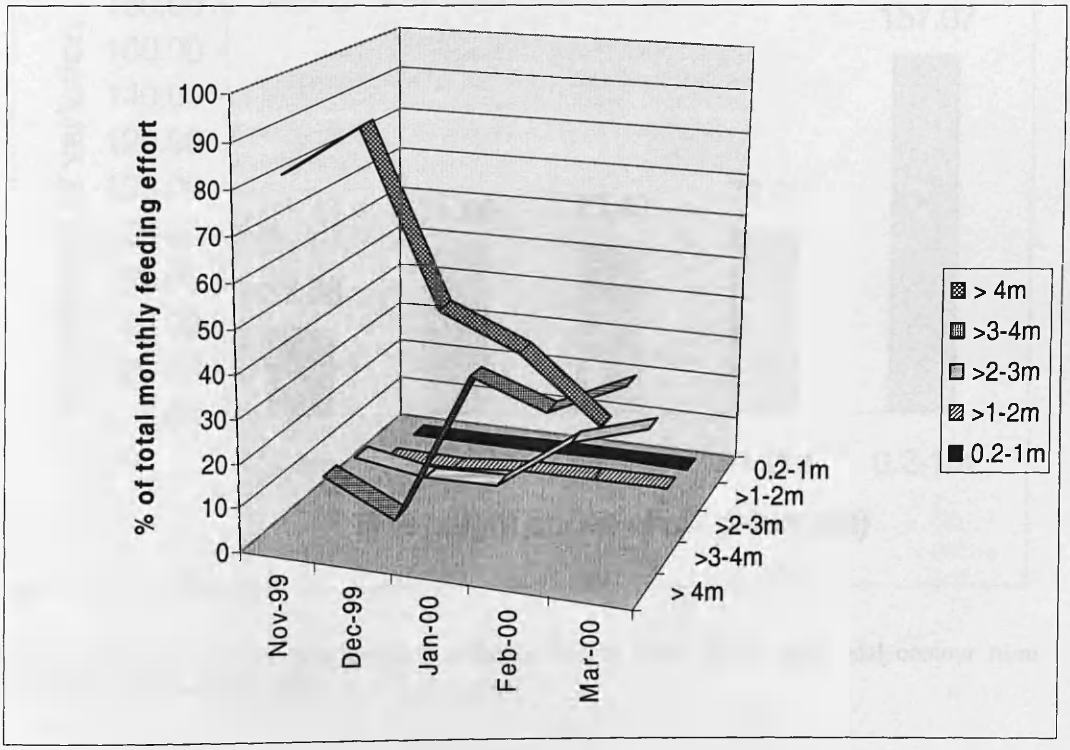


Fig 4.2: The percentage of the total shelduck feeding effort spent within each tidal contour each month from November 1999 to March 2000.

By March, usage of the >2-3 m and >3-4m areas had increased and was roughly on a par with feeding effort above 4m with 23%, 39% and 36% of shelduck feeding effort respectively concentrated in these areas. The intertidal below the 2m contour was barely used with a maximum of only 2.5% total feeding effort in March. The overall within winter pattern suggests a strong concentration on the highest level areas early in the winter with birds gradually spreading out to use all areas above 2m by the end of the winter. Fig 4.3 details the relative stability of each tidal area in terms of feeding effort and reiterates the fact that the most consistently used area was >4m. Feeding effort within the >2-3m and >3-4m areas were slightly more variable but this variation was almost the same in both areas. Although usage in the >1-2 m area was low, it was consistently low. The area below 1m was most variable due to the mix of very low to zero % feeding effort counts.

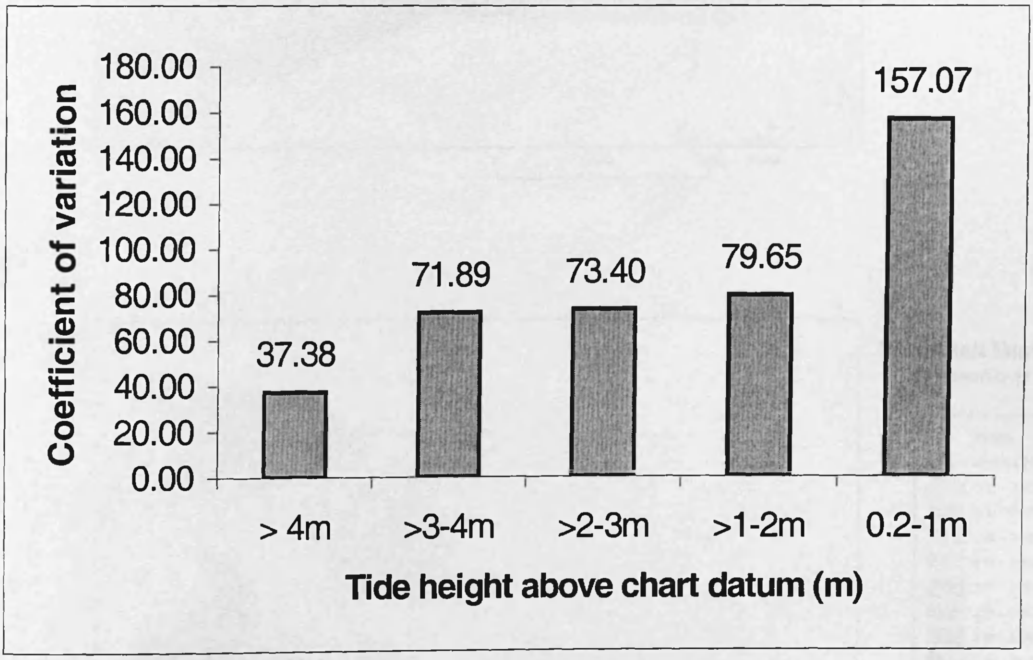
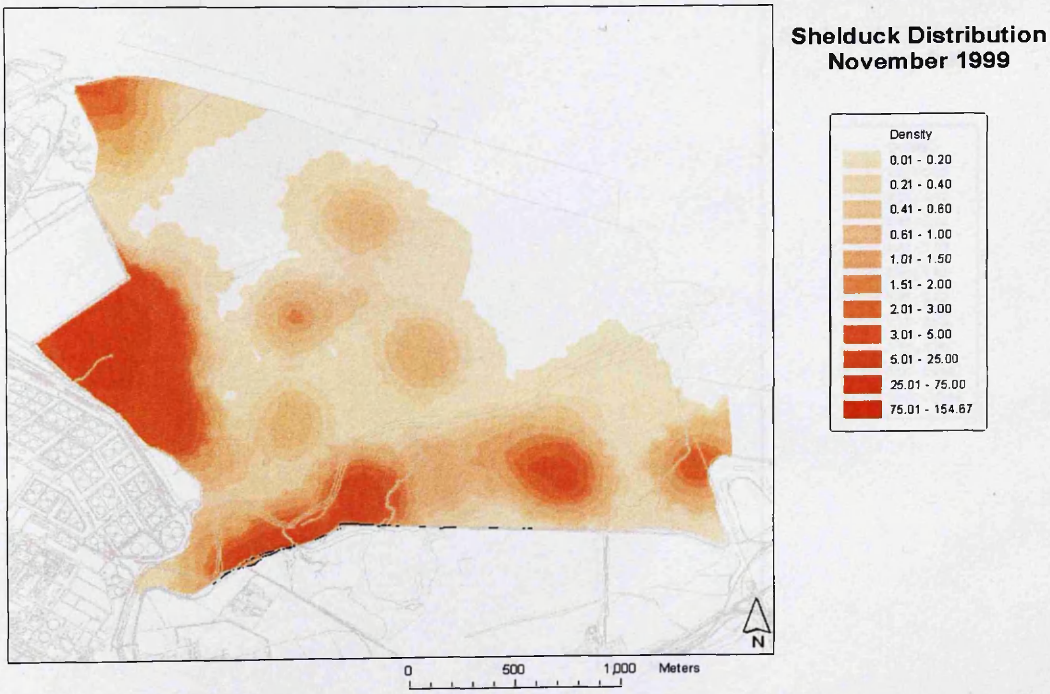


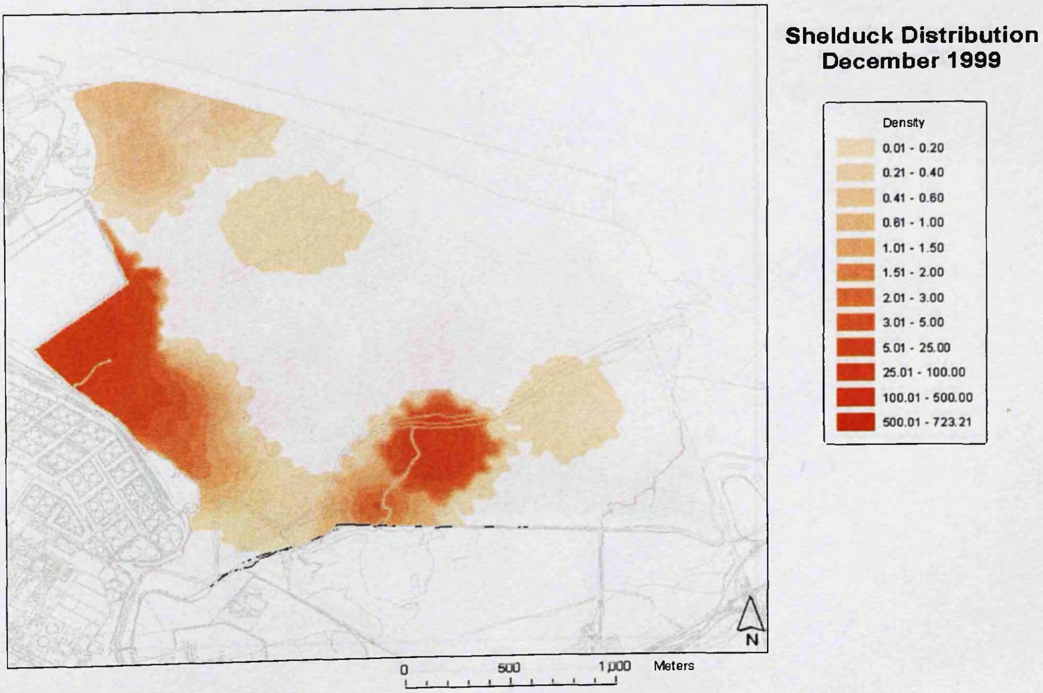
Fig 4.3: The CV of percentage monthly shelduck feeding effort within each tidal contour from November 1999 to March 2000

The maps (Fig 4.4) illustrate how the Kinneil intertidal was used spatially and show more graphically the dynamic movement of shelduck throughout the winter of 1999/2000. The final map removes the fine scale monthly detail and just considers total feeding effort for the whole winter; it clearly shows that the shelduck strongly prefer the embayment area.

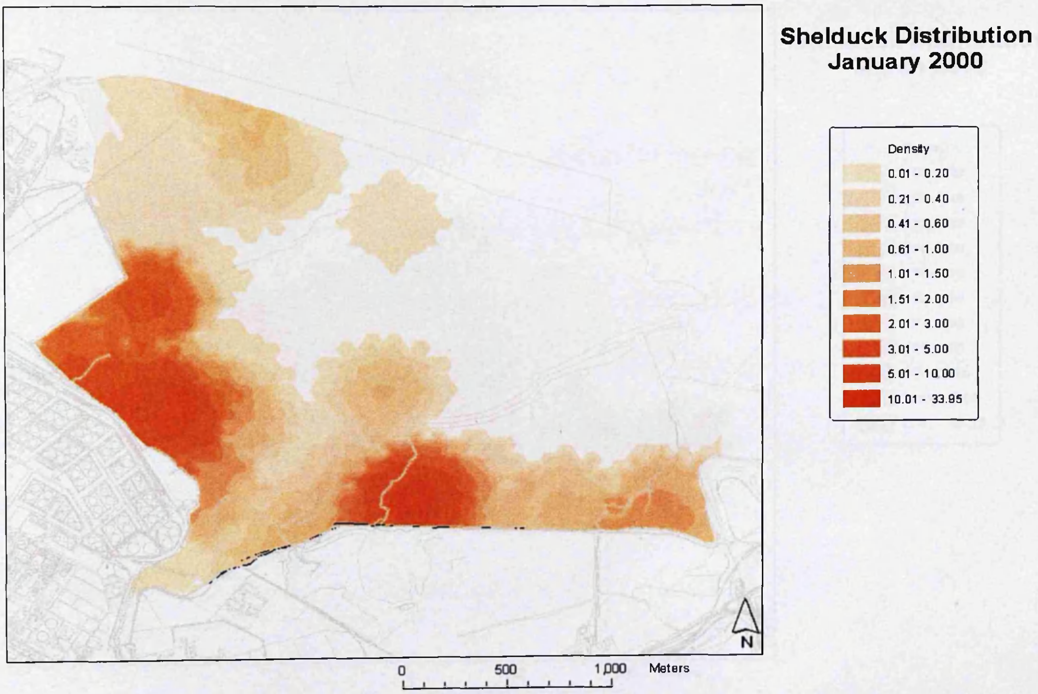
a)


Shelduck Distribution
November 1999
Density
0.01 - 0.20
0.21 - 0.40
0.41 - 0.60
0.61 - 1.00
1.01 - 1.50
1.51 - 2.00
2.01 - 3.00
3.01 - 5.00
5.01 - 25.00
25.01 - 75.00
75.01 - 154.67
N
0
500
1,000
Meters

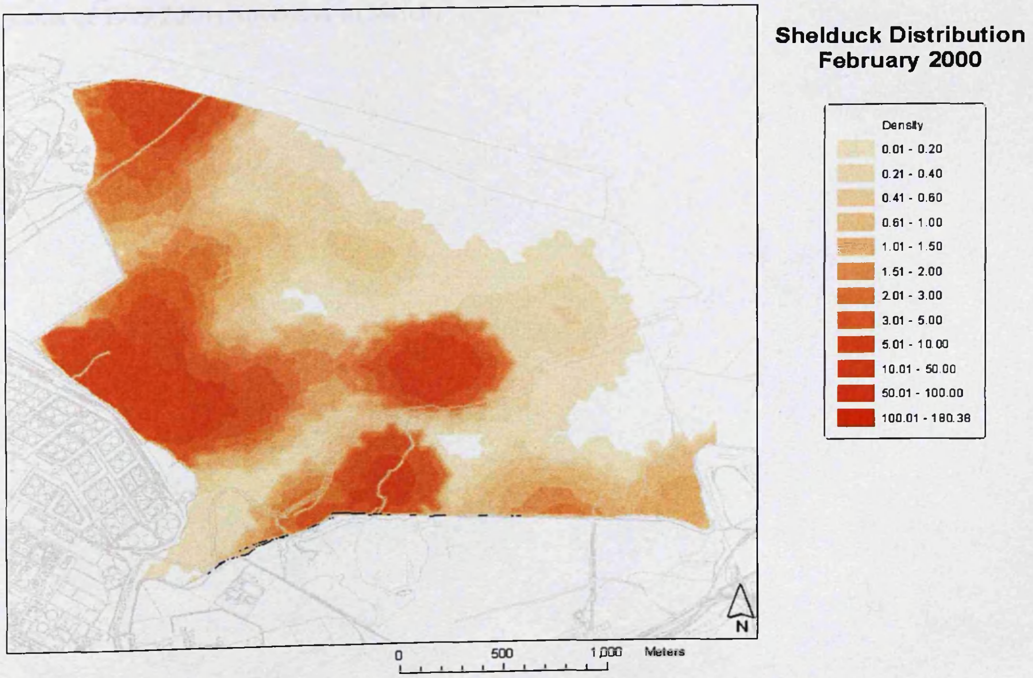
b)


Shelduck Distribution
December 1999
Density
0.01 - 0.20
0.21 - 0.40
0.41 - 0.60
0.61 - 1.00
1.01 - 1.50
1.51 - 2.00
2.01 - 3.00
3.01 - 5.00
5.01 - 25.00
25.01 - 100.00
100.01 - 500.00
500.01 - 723.21
N
0
500
1,000
Meters

c)


Shelduck Distribution
January 2000
Density
0.01 - 0.20
0.21 - 0.40
0.41 - 0.60
0.61 - 1.00
1.01 - 1.50
1.51 - 2.00
2.01 - 3.00
3.01 - 5.00
5.01 - 10.00
10.01 - 33.95
N
0
500
1,000
Meters

d)


Shelduck Distribution
February 2000
Density
0.01 - 0.20
0.21 - 0.40
0.41 - 0.60
0.61 - 1.00
1.01 - 1.50
1.51 - 2.00
2.01 - 3.00
3.01 - 5.00
5.01 - 10.00
10.01 - 50.00
50.01 - 100.00
100.01 - 180.38
N
0
500
1,000
Meters

e)

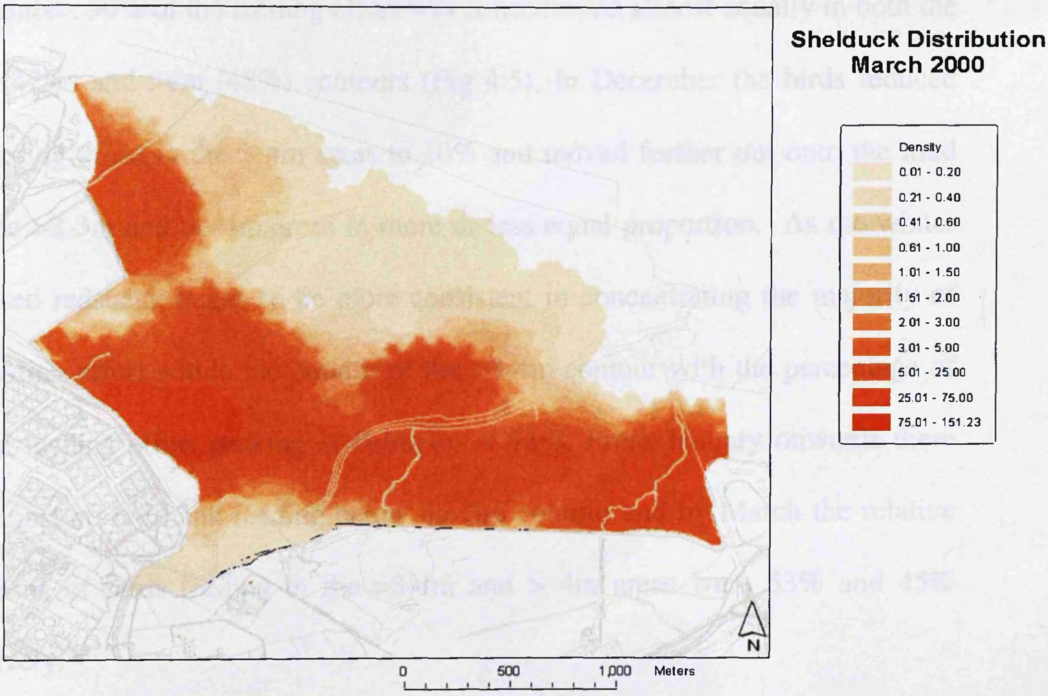


Fig 4.4. Spatial maps of the monthly distribution of feeding effort of shelduck during the winter of 1999/2000 (November to March)

4.2.1.2 Redshank

In November, 90% of the feeding effort was concentrated almost equally in both the >3-4m (42%) and >4m (48%) contours (Fig 4.5). In December the birds reduced their feeding effort in the > 4m areas to 10% and moved further out onto the mud using the >2-3m and >3-4m areas in more or less equal proportion. As the winter progressed redshank began to be more consistent in concentrating the majority of their feeding effort within the bounds of the >3-4m contour with the percentage of the total feeding effort peaking in February at 71%. From January onwards there were almost no redshank feeding below the 3m contour and by March the relative proportions of birds feeding in the >3-4m and > 4m areas were 53% and 45% respectively.

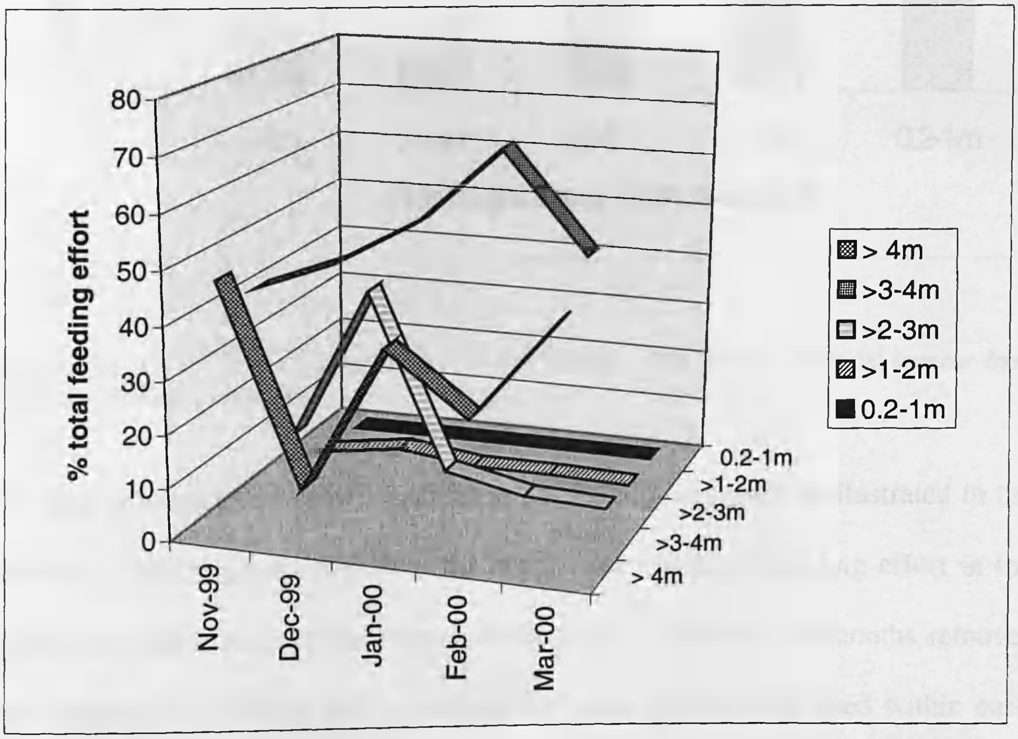


Fig 4.5: The percentage of the total redshank feeding effort spent within each tidal contour each month from November 1999 to March 2000.

The stability of the magnitude of this feeding effort is illustrated in Figure 4.6 and reiterates the fact that redshank were most consistently loyal to the >3-4m area first and then to the > 4m region. Far more variability of usage was evident in the area below 3m. The area below 1m was almost never used and only registered 0.0006% of total feeding effort in January when the redshank were most dispersed around the mudflat.

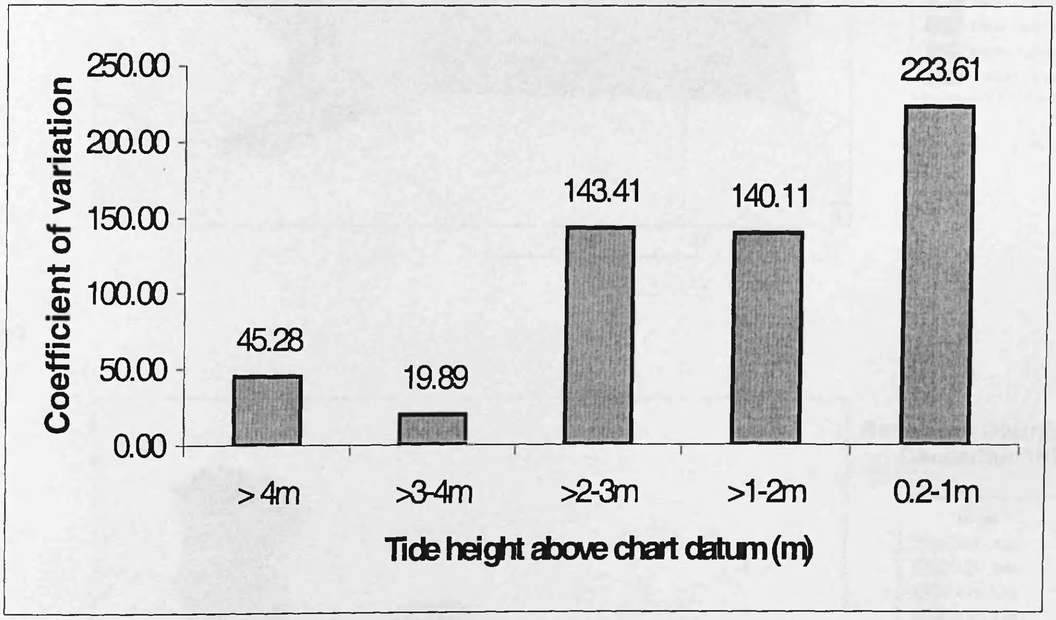
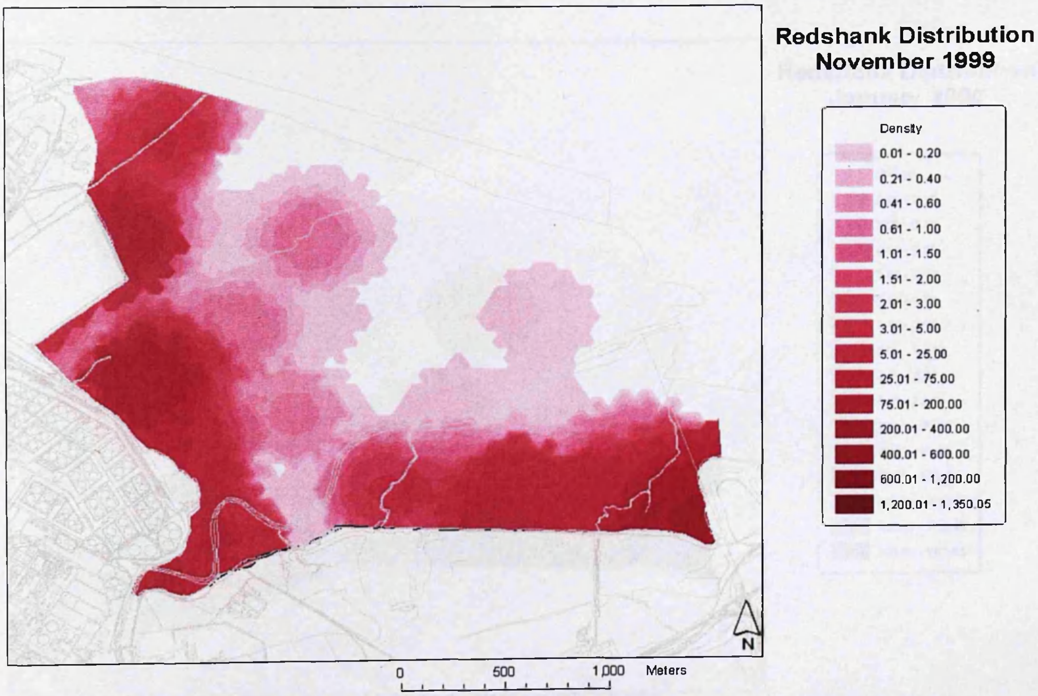


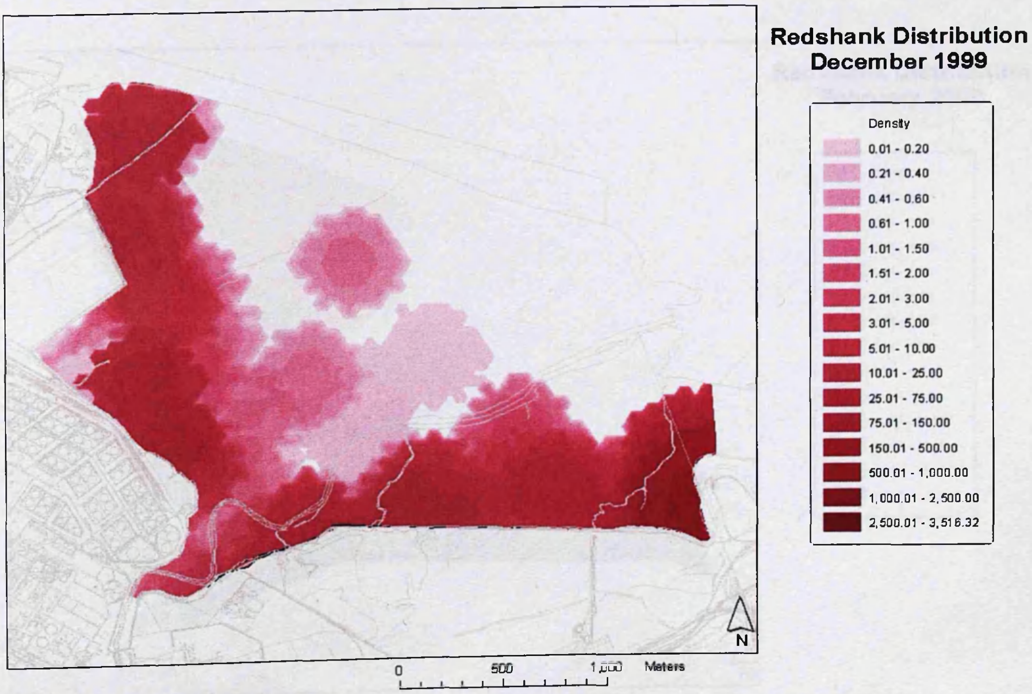
Fig 4.6: The CV of percentage monthly redshank feeding effort within each tidal contour from November 1999 to March 2000

The fine scale monthly spatial distribution of feeding redshank is illustrated in the GIS maps which graphically show the high concentration of feeding effort in the upper two tidal contours. The map showing feeding effort for all months removes the small-scale variability and highlights the areas most heavily used within each contour. The whole winter distribution is very similar to that of January and both these months show high concentrations of redshank in similar areas to those predicted by the GLM in Fig 4.7.

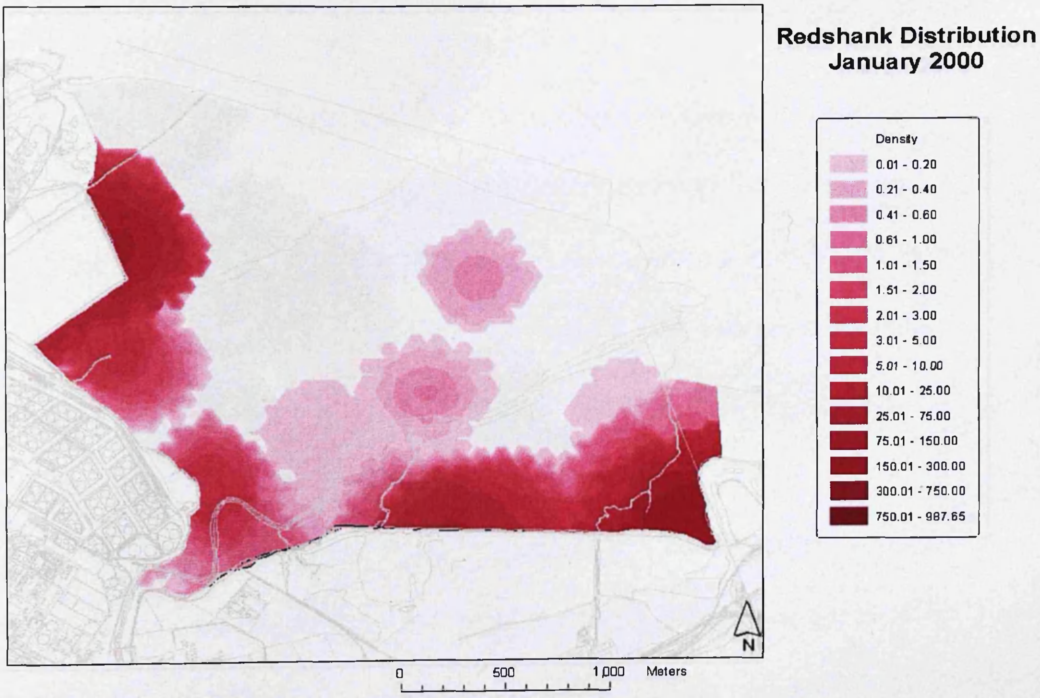
a)


Redshank Distribution
November 1999
Density
0.01 - 0.20
0.21 - 0.40
0.41 - 0.60
0.61 - 1.00
1.01 - 1.50
1.51 - 2.00
2.01 - 3.00
3.01 - 5.00
5.01 - 25.00
25.01 - 75.00
75.01 - 200.00
200.01 - 400.00
400.01 - 600.00
600.01 - 1,200.00
1,200.01 - 1,350.05
N
0
500
1,000
Meters

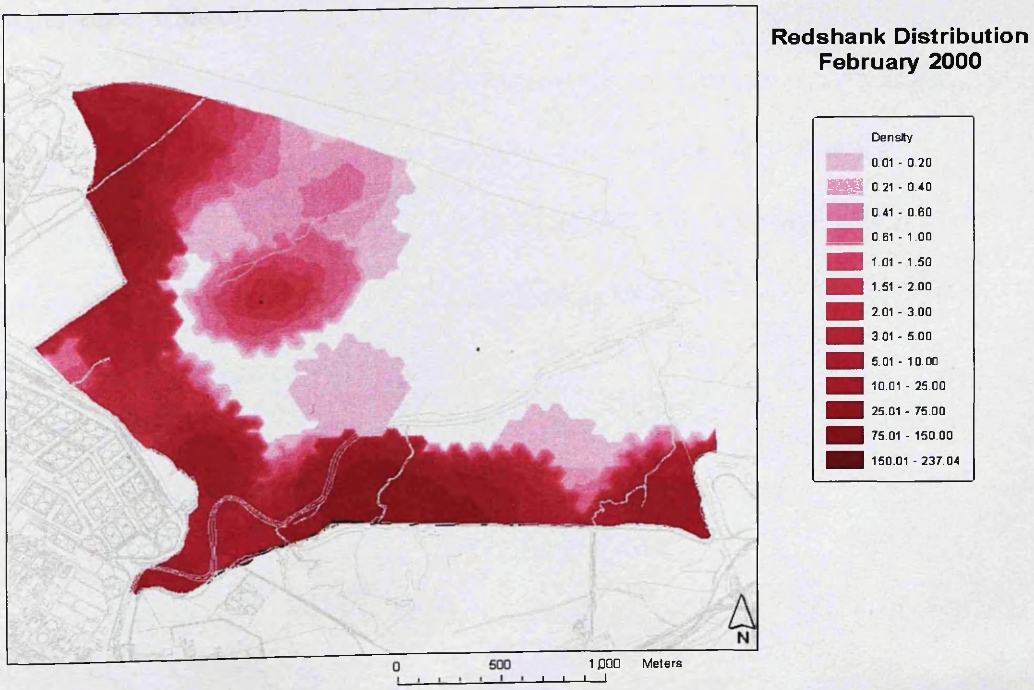
b)


Redshank Distribution
December 1999
Density
0.01 - 0.20
0.21 - 0.40
0.41 - 0.60
0.61 - 1.00
1.01 - 1.50
1.51 - 2.00
2.01 - 3.00
3.01 - 5.00
5.01 - 10.00
10.01 - 25.00
25.01 - 75.00
75.01 - 150.00
150.01 - 500.00
500.01 - 1,000.00
1,000.01 - 2,500.00
2,500.01 - 3,516.32
N
0
500
1,000
Meters

c)


Redshank Distribution
January 2000
Density
0.01 - 0.20
0.21 - 0.40
0.41 - 0.60
0.61 - 1.00
1.01 - 1.50
1.51 - 2.00
2.01 - 3.00
3.01 - 5.00
5.01 - 10.00
10.01 - 25.00
25.01 - 75.00
75.01 - 150.00
150.01 - 300.00
300.01 - 750.00
750.01 - 987.65
N
0
500
1,000
Meters

d)


Redshank Distribution
February 2000
Density
0.01 - 0.20
0.21 - 0.40
0.41 - 0.60
0.61 - 1.00
1.01 - 1.50
1.51 - 2.00
2.01 - 3.00
3.01 - 5.00
5.01 - 10.00
10.01 - 25.00
25.01 - 75.00
75.01 - 150.00
150.01 - 237.04
N
0
500
1,000
Meters

e)

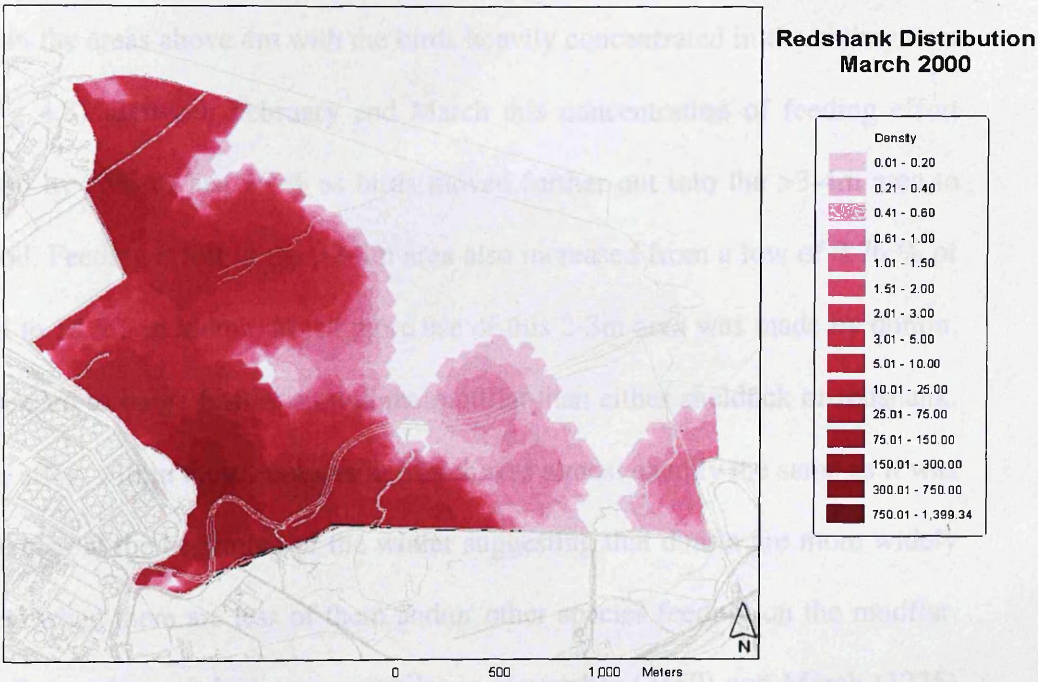


Fig 4.7. Spatial maps of the monthly distribution of feeding effort of redshank during the winter of 1999/2000 (November to March)

4.2.1.3 Dunlin

Between November 1999 and February 2000 dunlin feeding effort was consistently highest in the areas above 4m with the birds heavily concentrated in the embayment area (Fig 4.8). Between February and March this concentration of feeding effort decreased by 35% to just 15 % as birds moved further out into the >3-4m area to seek food. Feeding effort in the >2-3m area also increased from a low of 0.76 % of the total to 18.5% in March. Much more use of this 2-3m area was made by dunlin, which tended to range further around the mudflat than either shelduck or redshank. Feeding effort within these contours in March was almost exactly the same as it was in November at the beginning of the winter suggesting that dunlin are more widely dispersed when there are less of them and/or other species feeding on the mudflat. Peak daily numbers of dunlin were similar in November (2450) and March (1275) and considerably less than the winter maximum in January of 4260. However with reference to Figure 4.10 it is evident that birds are not so widely dispersed in March and the reason for this apparent similarity is a higher concentration of feeding effort in a smaller section of the >2-3m contour area (see also Fig 4.1). Very little use was made of the >1-2 m area with a peak of 4.5 % in November and there was almost no feeding in the 0.2- 1m area with just 1% of the feeding effort recorded in this area during November.

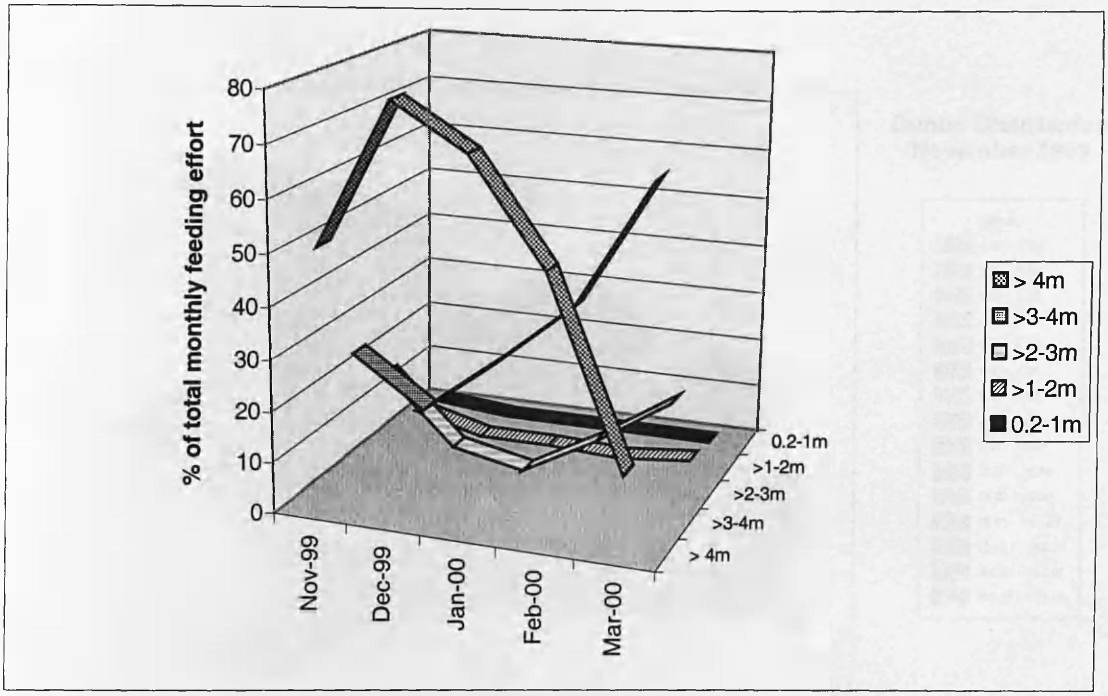


Fig 4.8: The percentage of the total dunlin feeding effort, spent within each tidal contour each month from November 1999 to March 2000.

Although the dunlin ranged around Kinneil in search of food considerably more than shelduck or redshank, their feeding effort was most stable in the > 4m area and became consistently more variable as shore height decreased.

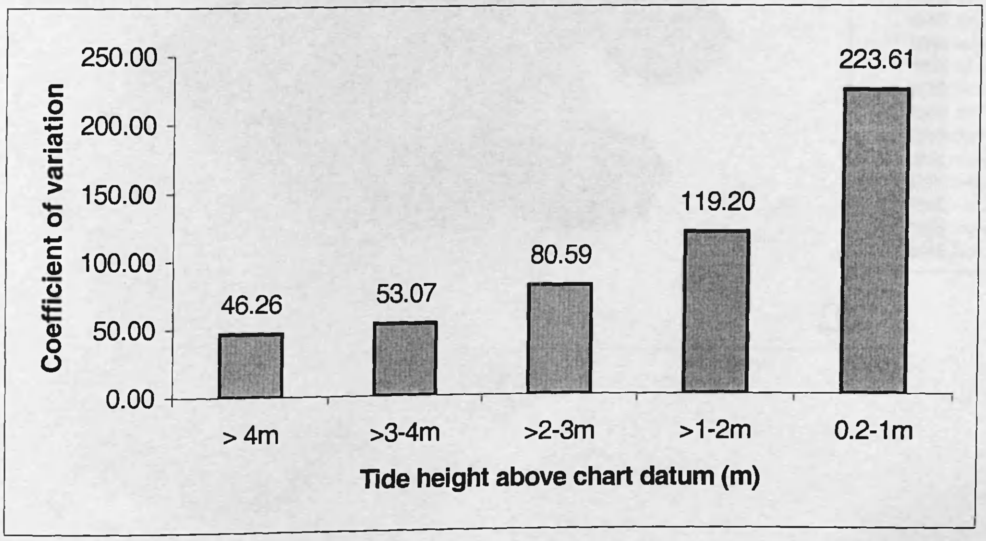
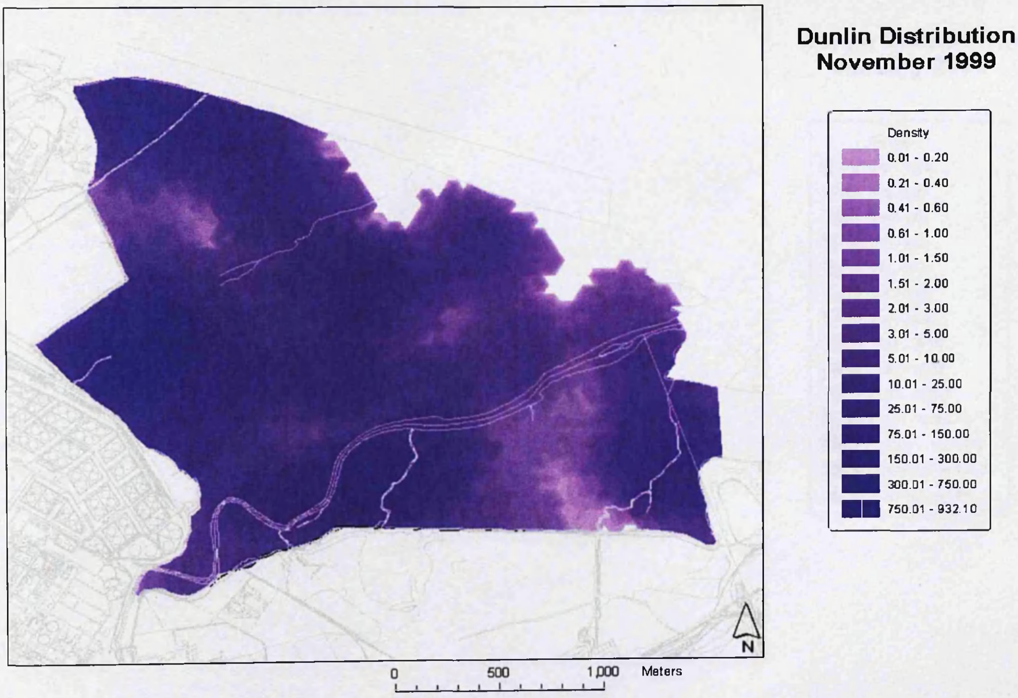
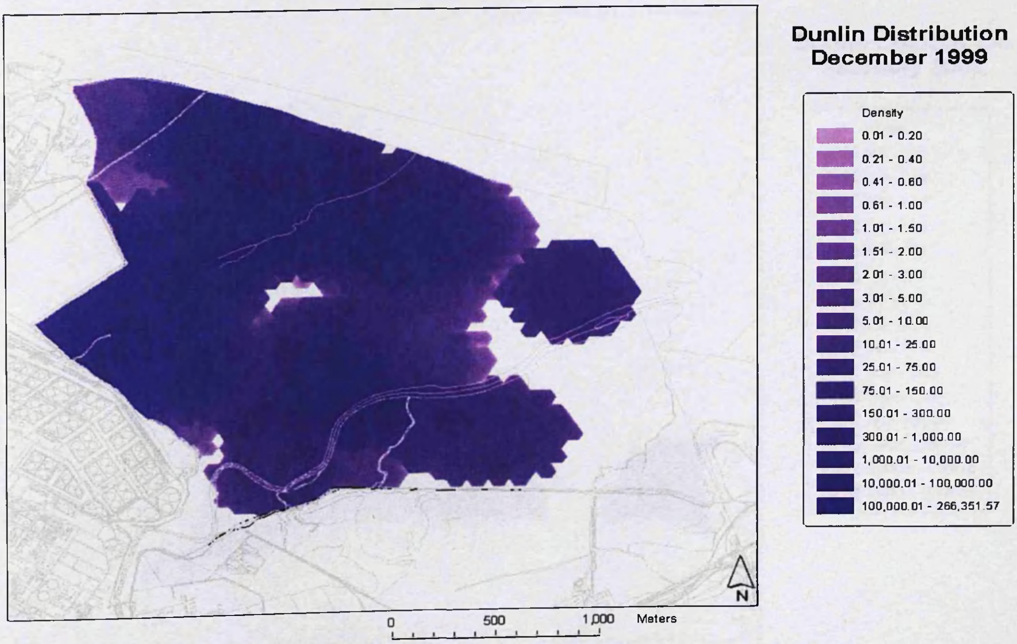


Fig 4.9: The CV of percentage monthly dunlin feeding effort within each tidal contour from November 1999 to March 2000

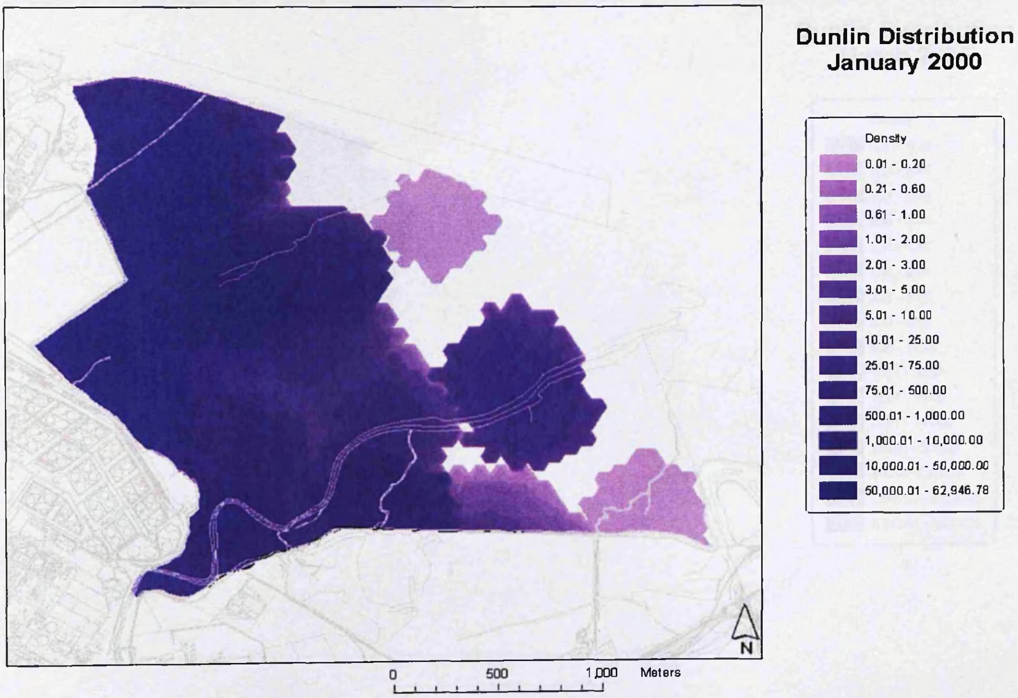
a)


Dunlin Distribution
November 1999
Density
0.01 - 0.20
0.21 - 0.40
0.41 - 0.60
0.61 - 1.00
1.01 - 1.50
1.51 - 2.00
2.01 - 3.00
3.01 - 5.00
5.01 - 10.00
10.01 - 25.00
25.01 - 75.00
75.01 - 150.00
150.01 - 300.00
300.01 - 750.00
750.01 - 932.10
N
0
500
1,000
Meters

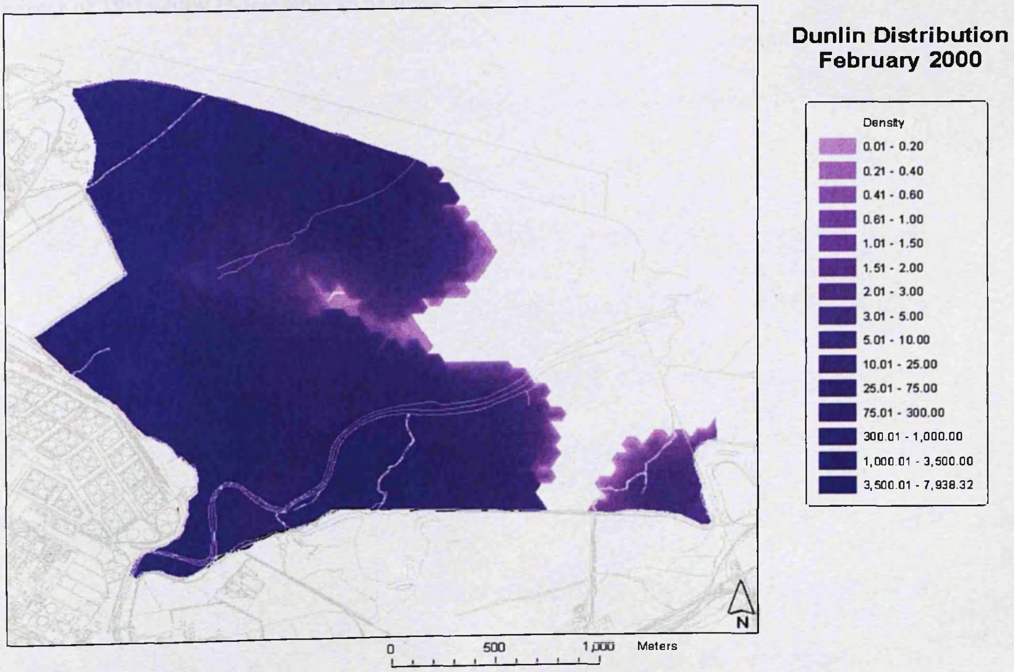
b)


Dunlin Distribution
December 1999
Density
0.01 - 0.20
0.21 - 0.40
0.41 - 0.60
0.61 - 1.00
1.01 - 1.50
1.51 - 2.00
2.01 - 3.00
3.01 - 5.00
5.01 - 10.00
10.01 - 25.00
25.01 - 75.00
75.01 - 150.00
150.01 - 300.00
300.01 - 1,000.00
1,000.01 - 10,000.00
10,000.01 - 100,000.00
100,000.01 - 266,351.57
N
0
500
1,000
Meters

c)


Dunlin Distribution
January 2000
Density
0.01 - 0.20
0.21 - 0.60
0.61 - 1.00
1.01 - 2.00
2.01 - 3.00
3.01 - 5.00
5.01 - 10.00
10.01 - 25.00
25.01 - 75.00
75.01 - 500.00
500.01 - 1,000.00
1,000.01 - 10,000.00
10,000.01 - 50,000.00
50,000.01 - 62,946.78
N
0
500
1,000
Meters

d)


Dunlin Distribution
February 2000
Density
0.01 - 0.20
0.21 - 0.40
0.41 - 0.60
0.61 - 1.00
1.01 - 1.50
1.51 - 2.00
2.01 - 3.00
3.01 - 5.00
5.01 - 10.00
10.01 - 25.00
25.01 - 75.00
75.01 - 300.00
300.01 - 1,000.00
1,000.01 - 3,500.00
3,500.01 - 7,938.32
N
0
500
1,000
Meters

e)

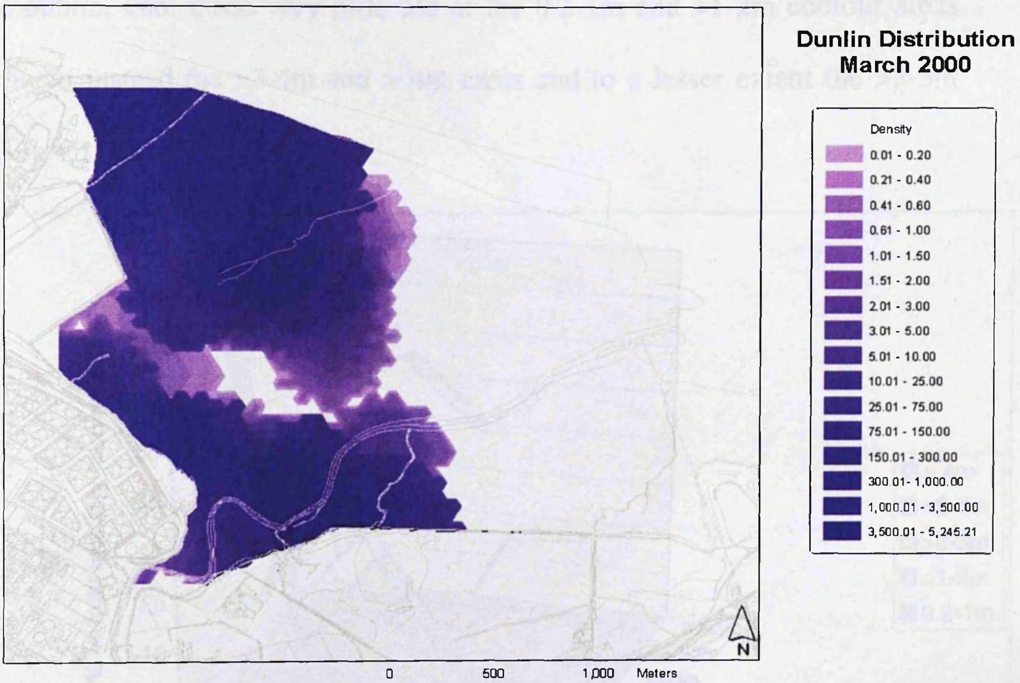


Fig 4.10. Spatial maps of the monthly distribution of feeding effort of dunlin during the winter of 1999/2000 (November to March)

4.2.1.4 Knot

Like the dunlin, knot made very little use of the 0.2-1m and >1-2m contour areas and favoured instead the >3-4m and > 4m areas and to a lesser extent the >2-3m region (Fig 4.11)

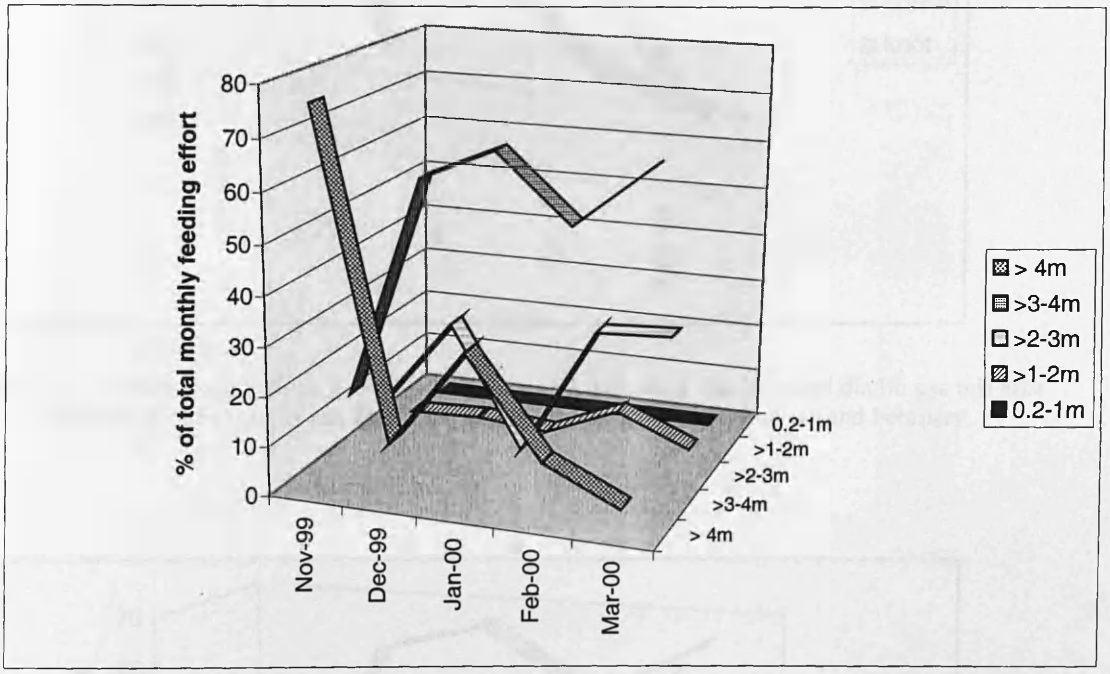


Fig 4.11: The percentage of the total knot feeding effort spent within each tidal contour each month from November 1999 to March 2000.

Knot utilised the upper two contour areas in an almost inverse way to dunlin throughout the winter (Figs 4.12 & 4.13) suggesting that they are actively choosing to feed in separate areas during the months of peak bird numbers (December, January and February). Although somewhat variable by month, feeding effort within the >2-3m contour is quite pronounced and higher than in the >4m area during December, February and March. Such variability in feeding effort around the mudflat suggests that knot are using most of the mudflat to varying degrees although the 0.2-1m areas are barely used with just 0.009% of the feeding effort occurring here in November.

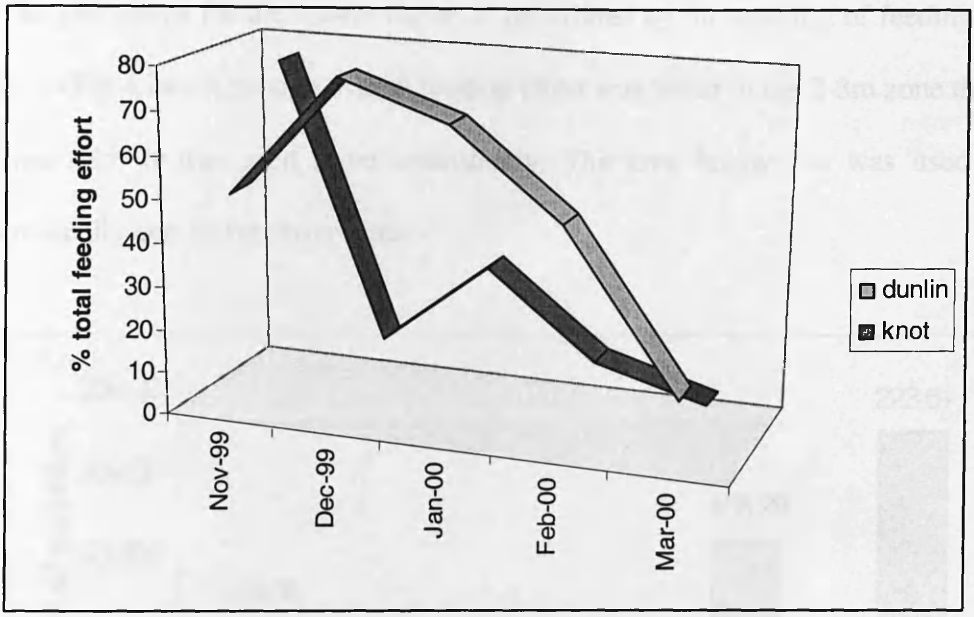


Fig 4.12: % total feeding effort in the > 4m contour area indicating that knot and dunlin use this area in a similar way in November and March but diverge during December, January and February

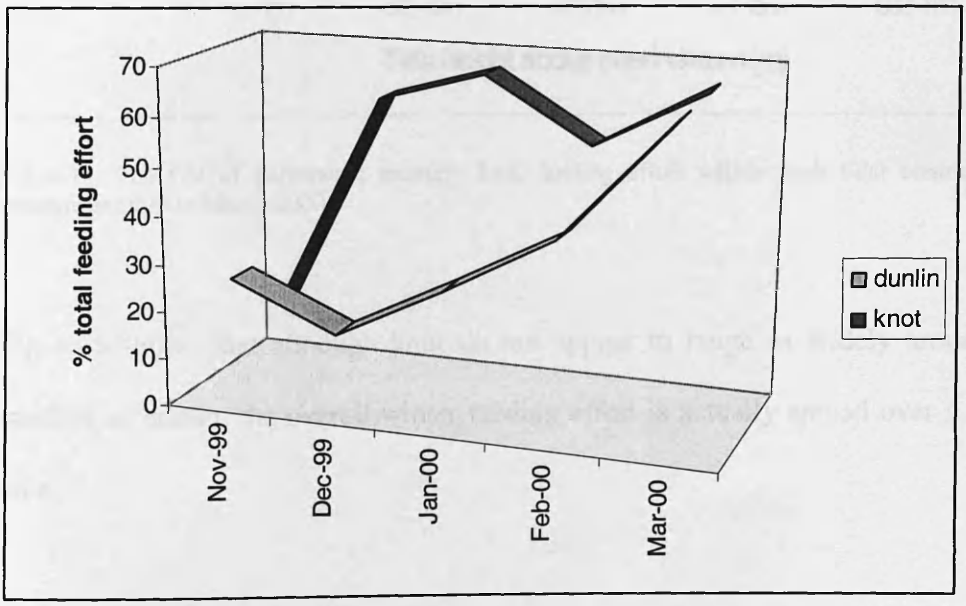


Fig 4.13: % total feeding effort in the >3-4m contour area indicating again that knot and dunlin use this area in a similar way in November and March but diverge during December, January and February.

The preference for the >3-4m region is underlined by the stability of feeding effort here (Fig 4.14). Although overall feeding effort was lower in the 2-3m zone than the area >4m it was used more consistently. The area below 1m was used more erratically and by far fewer birds.

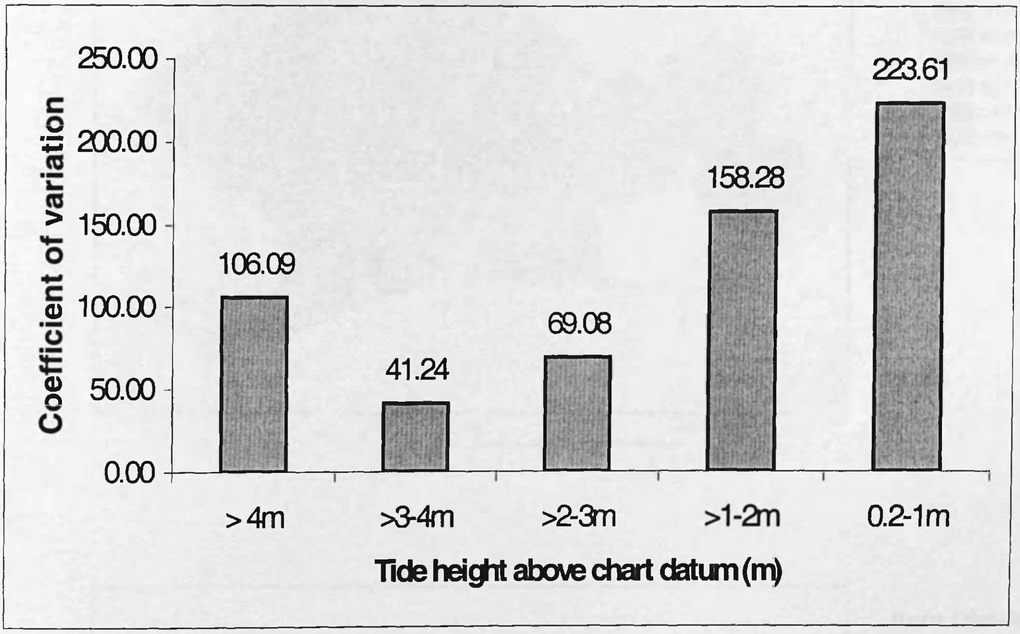
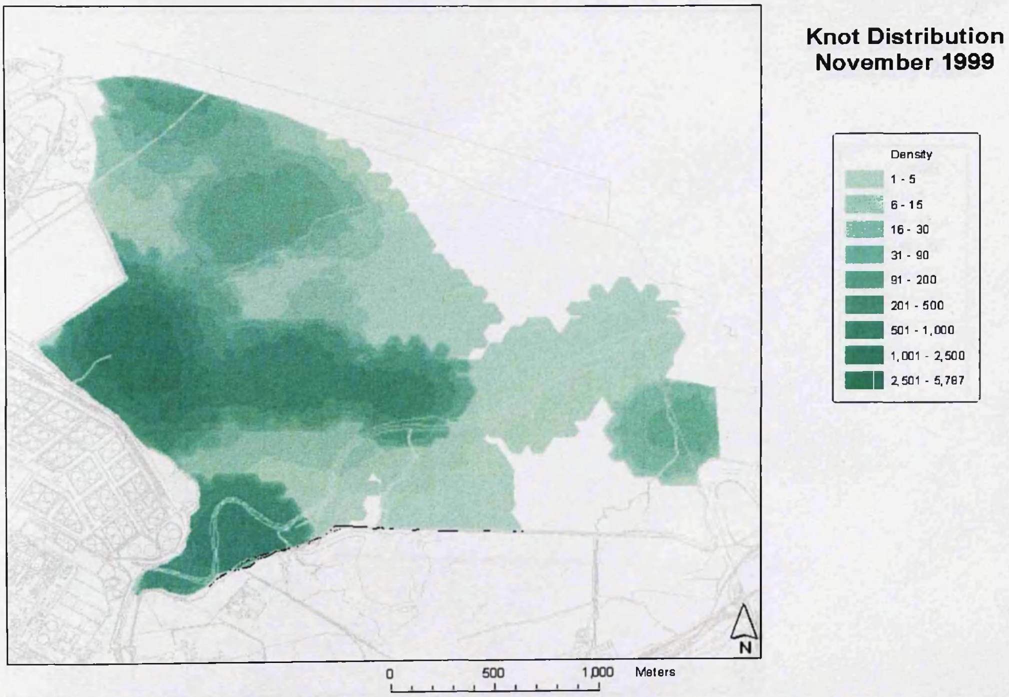


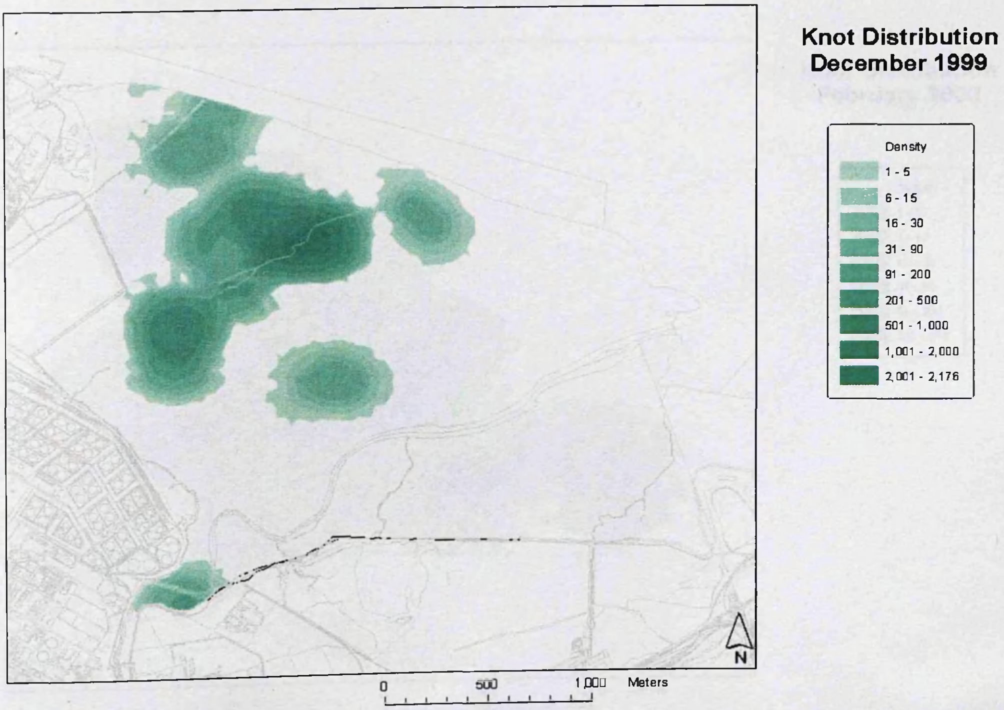
Fig 4.14: The CV of percentage monthly knot feeding effort within each tidal contour from November 1999 to March 2000

Fig 4.15 shows that although knot do not appear to range as widely around the mudflat as dunlin, the overall winter feeding effort is actually spread over a larger area.

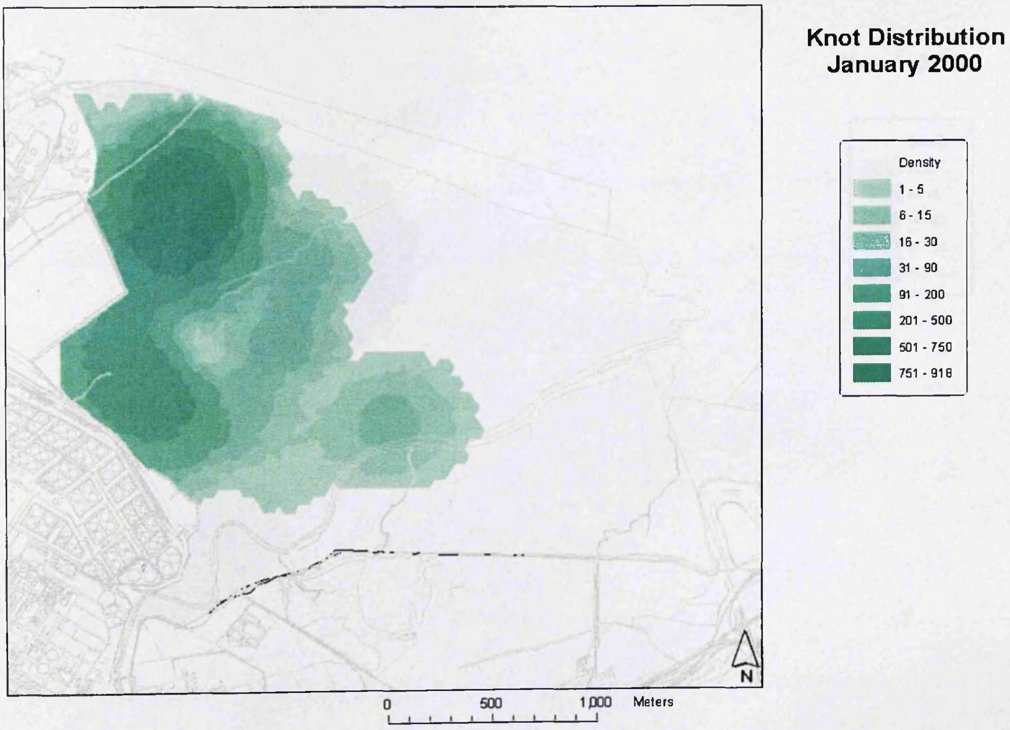
a)


Knot Distribution
November 1999
Density
1 - 5
6 - 15
16 - 30
31 - 90
91 - 200
201 - 500
501 - 1,000
1,001 - 2,500
2,501 - 5,787
N
0
500
1,000
Meters

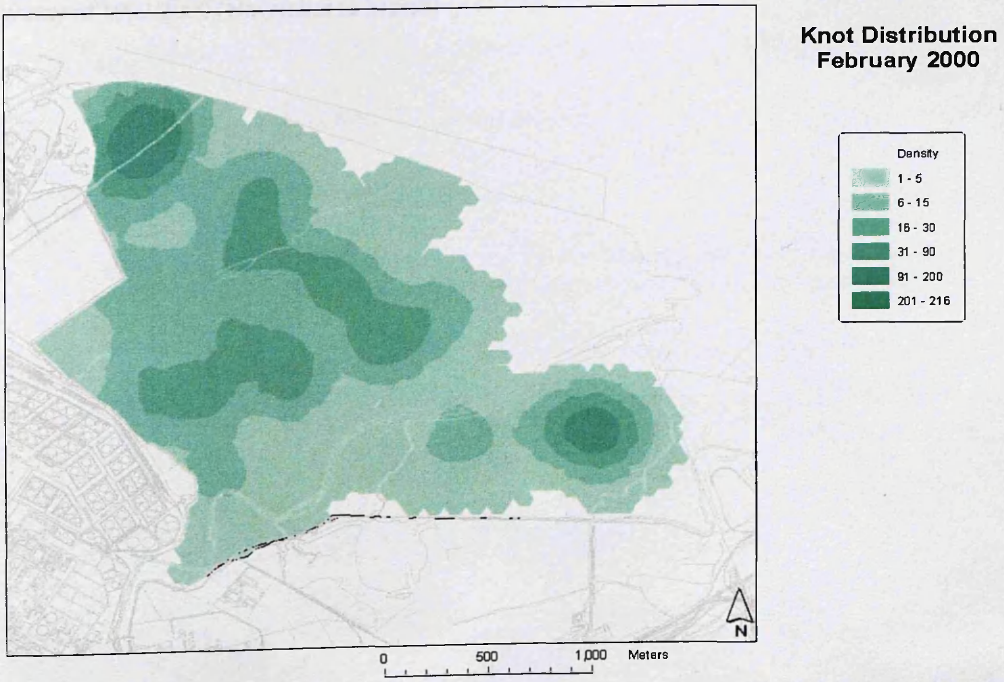
b)


Knot Distribution
December 1999
Density
1 - 5
6 - 15
16 - 30
31 - 90
91 - 200
201 - 500
501 - 1,000
1,001 - 2,000
2,001 - 2,176
N
0
500
1,000
Meters

c)


Knot Distribution
January 2000
Density
1 - 5
6 - 15
16 - 30
31 - 90
91 - 200
201 - 500
501 - 750
751 - 918
N
0
500
1,000
Meters

d)


Knot Distribution
February 2000
Density
1 - 5
6 - 15
16 - 30
31 - 90
91 - 200
201 - 216
N
0
500
1,000
Meters

e)

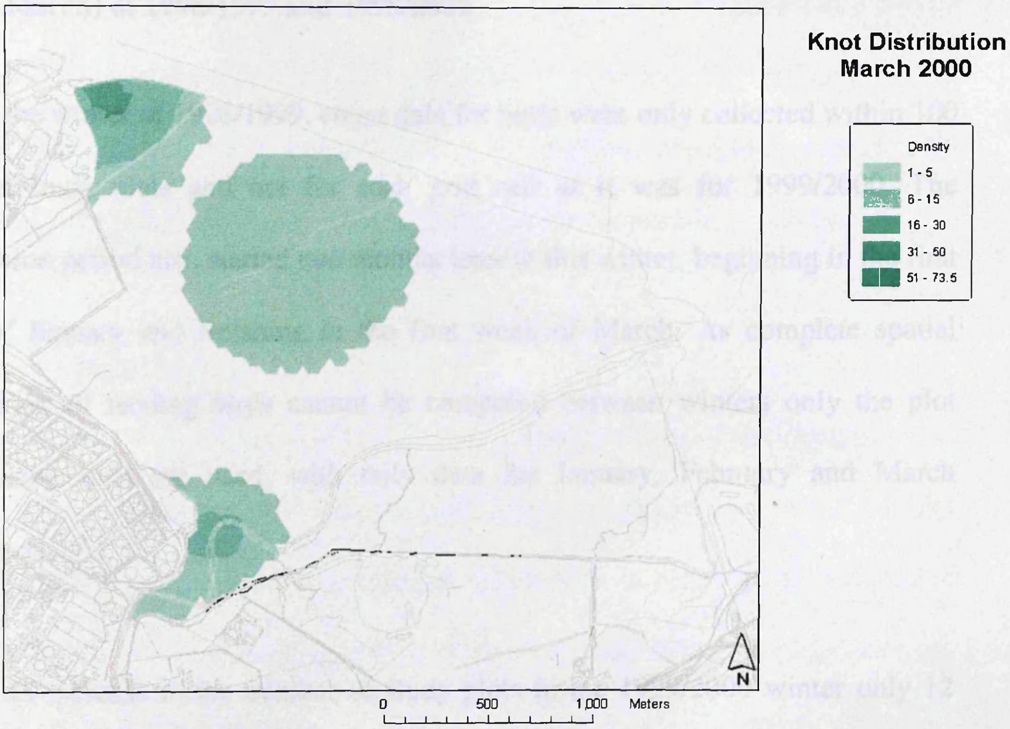


Fig 4.15. Spatial maps of the monthly distribution of feeding effort of knot during the winter of 1999/2000 (November to March)

4.2.2 Results of variability between winters: Comparison of mean bird count data from study plots at Kinneil between the winters (January – March) of 1998/1999 and 1999/2000

During the winter of 1998/1999, count data for birds were only collected within 100 x 100m study plots and not for each grid cell as it was for 1999/2000. The observation period also started two months later in this winter, beginning in the first week of January and finishing in the first week of March. As complete spatial distribution of feeding birds cannot be compared between winters only the plot mean count data are used, with only data for January, February and March considered.

Due to an increase in the number of study plots in the 1999/2000 winter only 12 plots are directly comparable between winters. Three of which were > 4m ACD, three in the >3-4m contour, two in the >2-3m, >1-2m and 0.2-1m contours respectively. For each of the key species, mean counts for plots within pair of tide height contours were compared between winters (Table 4.1)

Table 4.1.: GLM results for mean plot counts at Kinneil for the four key species comparing total counts between winters and tide height contour counts between winters for the study plots therein

Species	Difference between years	Difference between tide heights	Year * tide height interaction
Shelduck	F = 0.14, p= 0.71	F = 1.87, p = 0.17	F = 0.38, p = 0.82
Redshank	F = 0.54, p= 0.47	F = 1.58, p = 0.23	F = 0.41, p = 0.80
Dunlin	F = 1.32, p= 0.27	F = 1.24, p = 0.33	F = 0.63, p = 0.64
Knot	F = 3.29, p= 0.09	F = 0.96, p = 0.45	F = 0.62, p = 0.65

For each of the key species there were no significant differences in total mean counts of birds using the mudflats between January and March in each of the two successive winters. There were, however, fewer birds in total using all the plots in the winter of 1999/2000 but these differences were not significant for any of the key species. There were also no significant differences in the numbers of birds using mudflats of different heights between winters, suggesting that proportionally similar numbers of birds used the plots within each set of tidal contours in both winters pointing to possible stability of mudflat usage between two concurrent winters. Figs 4.17- 4.20. show the interaction plots from the GLMs for each key species.

4.2.2.1 Shelduck

Above the 4 m contour, there was a very similar mean number of shelduck per 0.5h in both winters suggesting that this is a consistently important area of the mudflat for them. Marked, although non significant differences in numbers of birds using the >2-3 m and >3-4 m areas suggest that in the 1999/2000 winter slightly more use was made of the lower tidal areas.

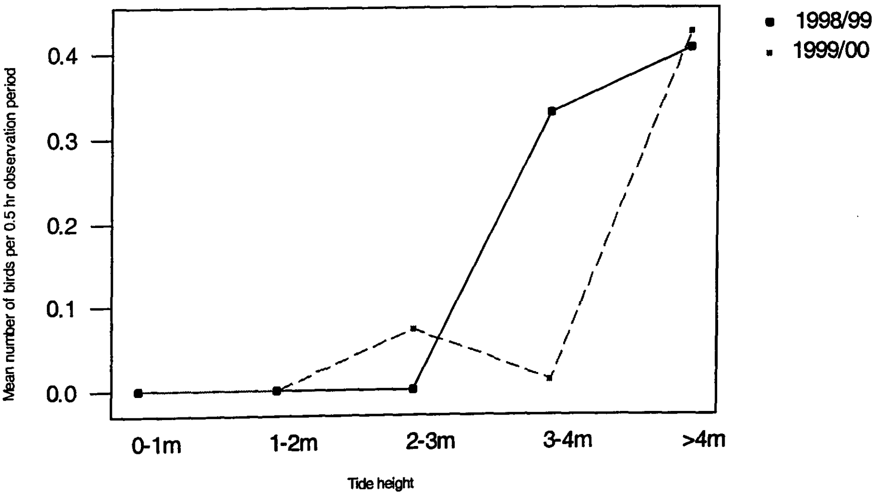


Fig 4.17: Interaction plots for the model: **shelduck** ~ year + tide height + year * tide height.

4.2.2.2 Redshank

Mudflat usage in both winters was almost the same for redshank, with this species strongly preferring the >3-4m area. Similar numbers of birds also used the area above the 4m contour.

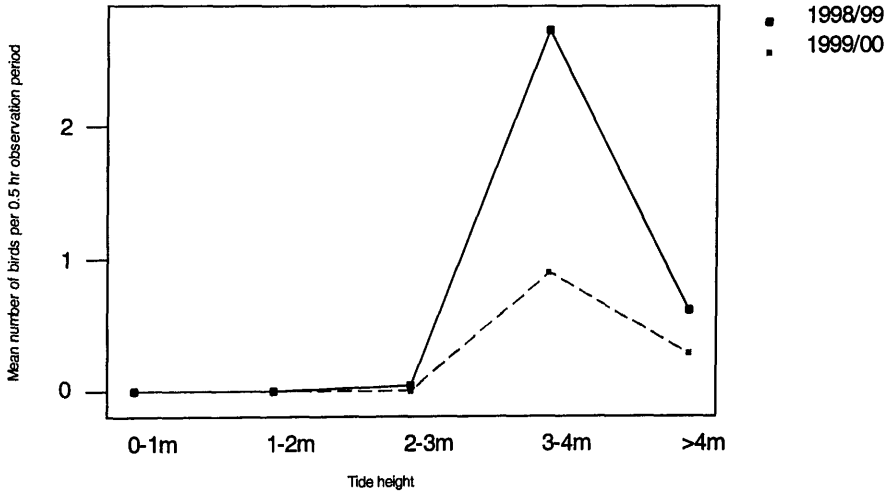


Fig 4.18.Interaction plots for the model: **redshank** ~ year + tide height + year * tide height.

4.2.2.3 Dunlin

In Figure 4.19. dunlin show very similar mudflat usage from 0.2m to 4m albeit more birds were present in the study plots during the winter of 1998/1999. Although fewer 1998/1999 birds used the area above the 4m contour the actual number was very similar to, but slightly lower than, the number using the area in 1999/2000.

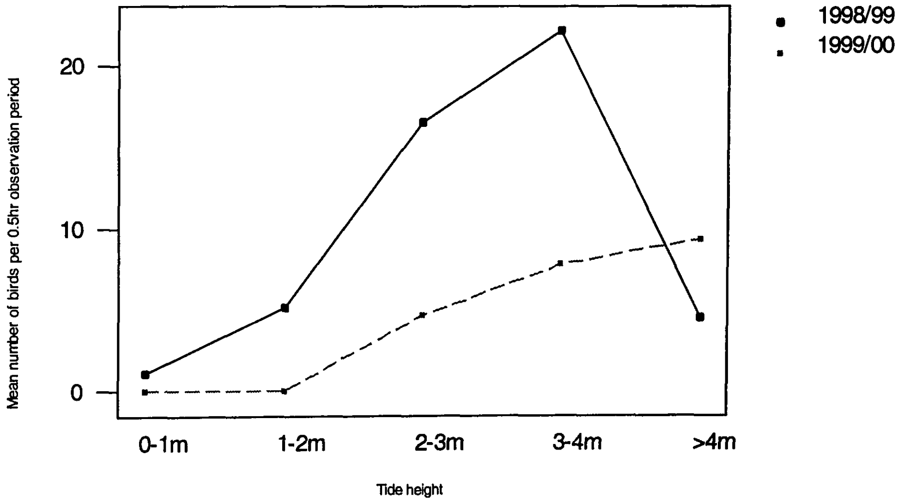


Fig 4.19 : Interaction plots for the model: **dunlin** ~ year + tide height + year * tide height.

4.2.2.4 Knot

Again knot displayed similar usage within tidal contours between winters although the 1-2m area was more important in 1998/1999. Usage of the >2-3m area was comparable but more marked in 1998/1999. Utilisation of the plots in the upper mudflat area between 3m and >4m was broadly the same although no birds were recorded in the 3-4m plots in 1999/2000.

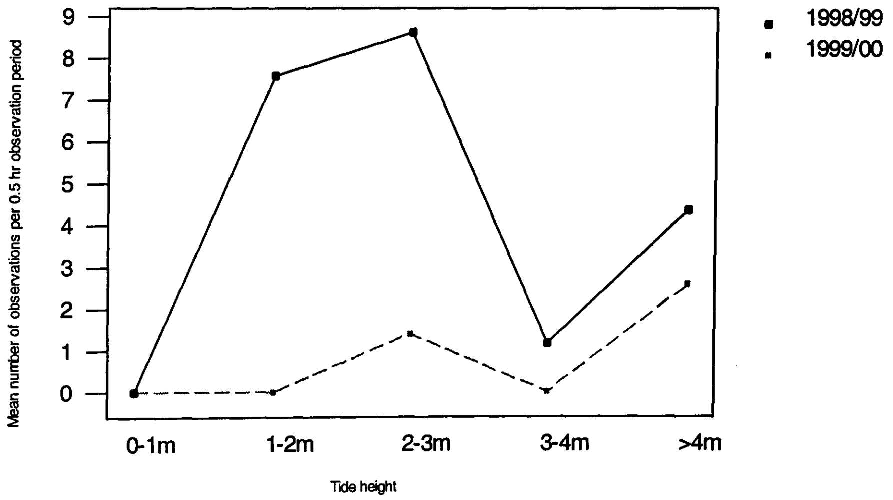


Fig 4.20: Interaction plots for the model: **knot** ~ year + tide height + year * tide height.

The results from the comparison of study plot data from two concurrent winters suggests that for all of the key species there is a relative stability of feeding effort within tidal contours between years. This is an encouraging result considering the fact that these are just random plot data and not complete spatial data.

4.2.3 Results of variability between selected winters (1976 – 2000)

All figures in this section show the temporal variation in January feeding effort (percentage of the total feeding effort) for each of the key species in selected winters from the last 25 years. Where the word 'winter' is mentioned it refers just to the January period (although including late December and early February in some years). Unfortunately years where complete spatial feeding effort data is available for Kinneil are limited and unevenly distributed during the 25-year study window. Data are regularly spread between 1975 and 1986 but there is a 14 year gap between 1986 and 2000 which make any large scale changes that have occurred since then appear on the Figures as if they have occurred instantaneously. Such changes where they have happened may indeed represent sudden change but they are more likely the result of long term increase or decrease in the preference of an area of the mudflat by one or more of the key species. Figures 4.21, 4.24, 4.27 & 4.30 show a fine scale analysis of how feeding effort is distributed within the whole area between each pair of tide height contours (Fig 4.1), these being 0.2-1m, >1-2m, >2-3m, >3-4m and >4m-shore. The remaining figures show the broad scale distribution of feeding effort across the entire mudflat. These maps allow the identification of 'hotspots' and favoured areas to be identified within tidal contour areas.

4.2.3.1 Shelduck

Between 1975 and 1986 shelduck barely used the area above 4m but by January 2000 this area was accounting for 58% of the shelduck feeding effort at Kinneil (Fig 4.21). Usage of the >3-4m area has declined where feeding effort in the >2-3m contour has fluctuated considerably. This suggests that since 1986 shelduck have switched the focus of their feeding effort to the high level area >4m tide height and moved closer to the shore, into the area of the embayment. Whereas the area below 2m had been used previously, no shelduck now chooses to feed there.

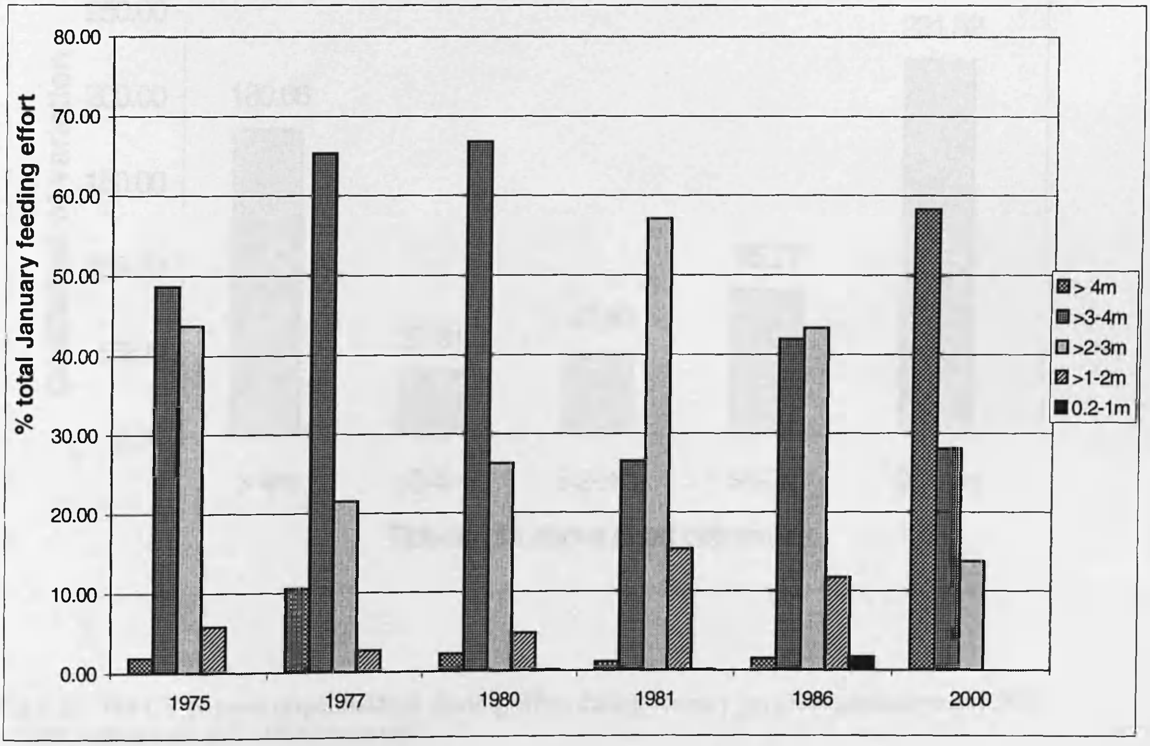


Fig 4.21: The percentage of the total shelduck feeding effort during January within each pair of tide height contours for selected winters 1975 –2000.

The area within the >3-4m contour had the least variance in January feeding effort over the study period, even though there has been a decline in usage there since the mid seventies (Fig 4.22). Usage by shelduck of this area over the last 20 years has varied between 26 % and 65% and it is the change between such high and low values that accounts for the low variance. The same is true for feeding effort in the

>2-3m contour where although the data exhibit a low variance usage of the area has fluctuated in almost an opposite way to the >3-4m contour. In 1975 usage of both these areas was almost equal, but between 1977 and 1986 preference was shown for either one area or the other. In 1986 usage of the two areas was again almost equal with 42% of the feeding effort within in the >3-4m contours and 44% in the >2-3m contours. Since 1986 shelduck feeding effort in both areas has declined as the birds have turned their attention to the area >4m.

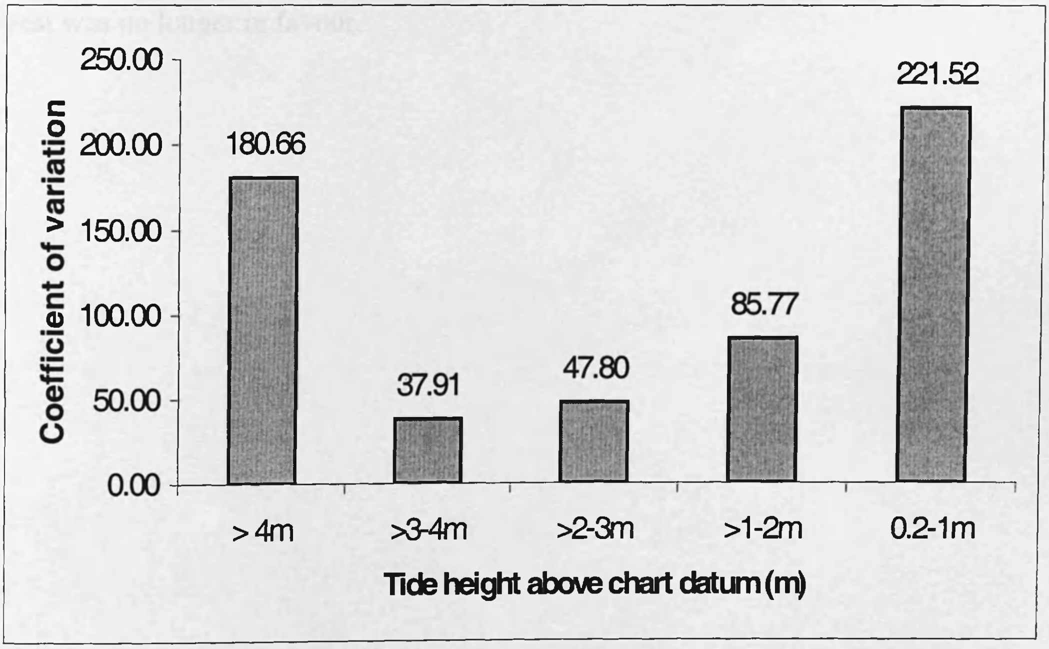
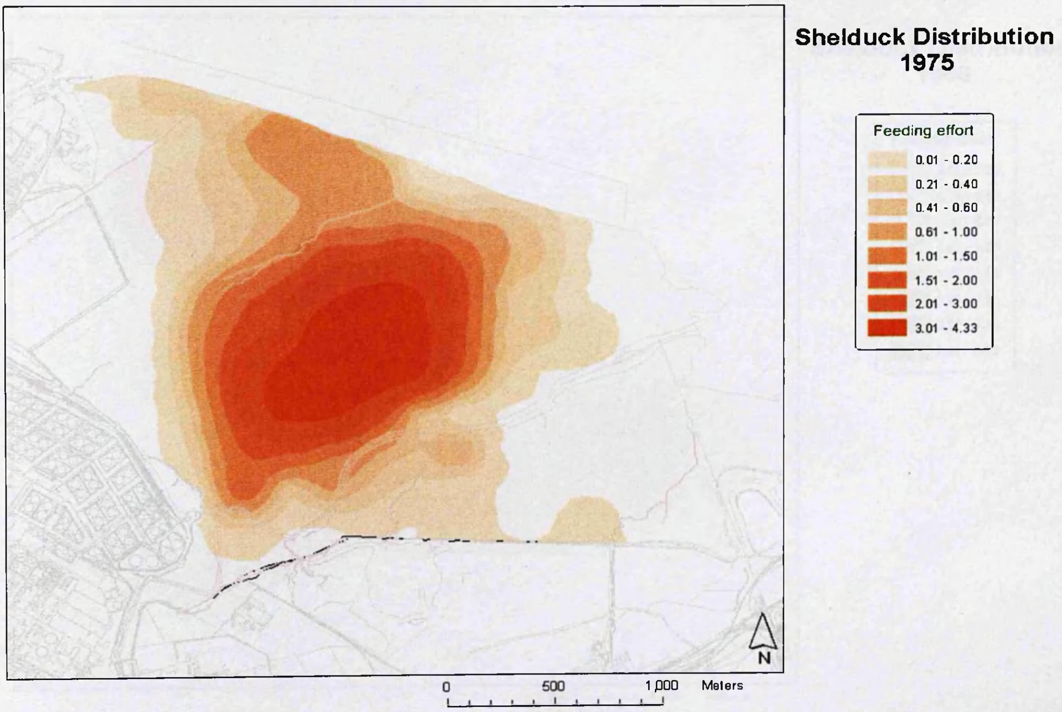


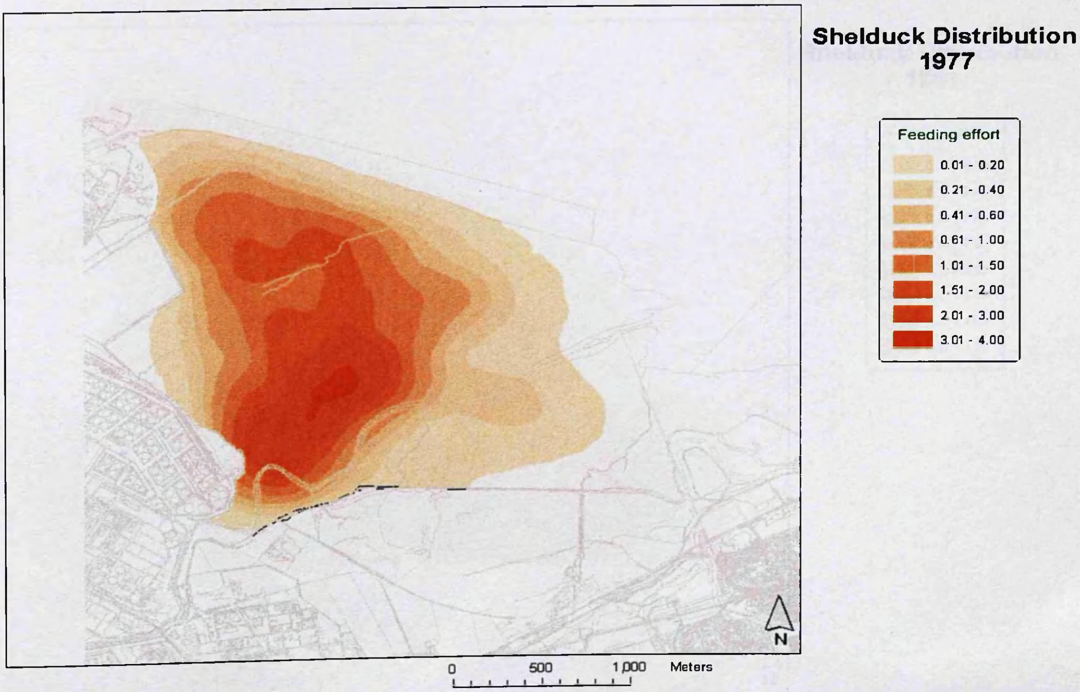
Fig 4.22: The CV of percentage shelduck feeding effort during January between selected years 1975 – 2000, within each pair of tidal contours

Figure 4.23 shows the complete spatial distribution of feeding shelduck across the entire mudflat across all tide heights for all selected winter 1975-2000. These maps clearly show that shelduck have consistently avoided the high level area > 4m within the triangular embayment (Fig 4.23a) adjacent to the Grangemouth petrochemical works between 1975 and 1986. It is quite clear that the recent rise in the use of this area has seen the shelduck preferentially feeding not only here by also in the > 4m area surrounding the brackish water output from the large lagoon behind the seawall. Distribution of feeding birds in 1975 was located quite centrally on the mudflat with birds radiating out from this most favoured point but by 1977 this central focus had shifted closer to the mouth of the River Avon and into the >3-4m contour area. This area was still favoured during January 1980 but now there was another heavily used area in the north-west corner of the mudflat between the Grange burn and the main effluent track. The following year the shelduck were using a broadly similar area in the south of the mudflat but the area to the north-west was no longer in favour.

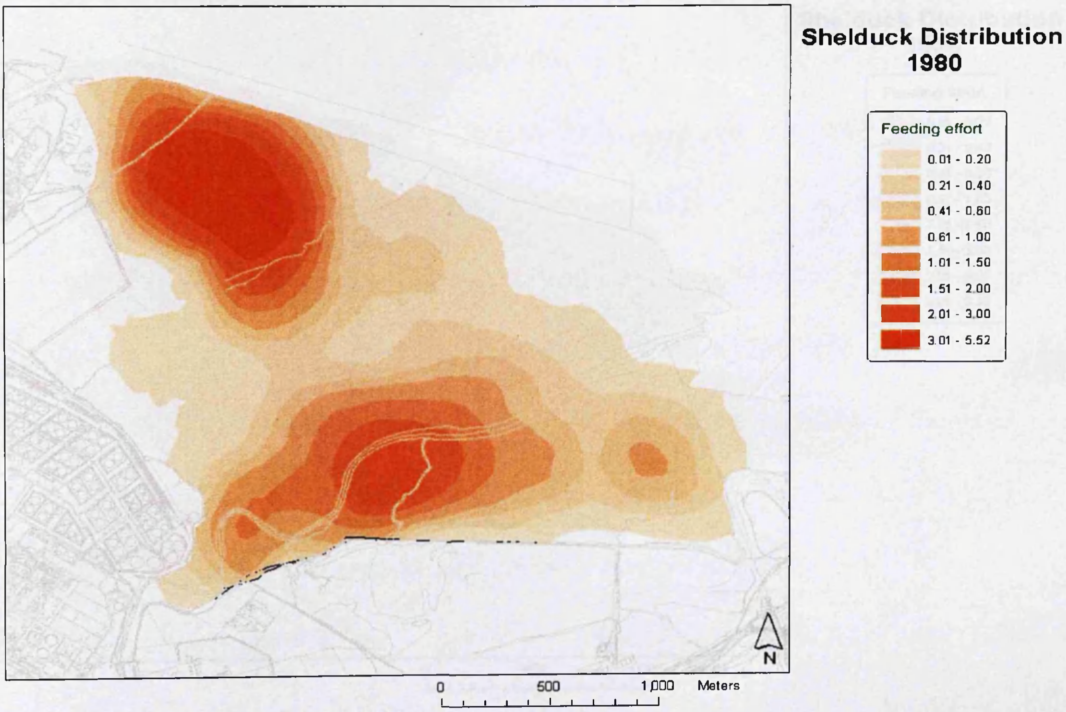
a)


Sheldúck Distribution
1975
Feeding effort
0.01 - 0.20
0.21 - 0.40
0.41 - 0.60
0.61 - 1.00
1.01 - 1.50
1.51 - 2.00
2.01 - 3.00
3.01 - 4.33
N
0
500
1,000
Meters

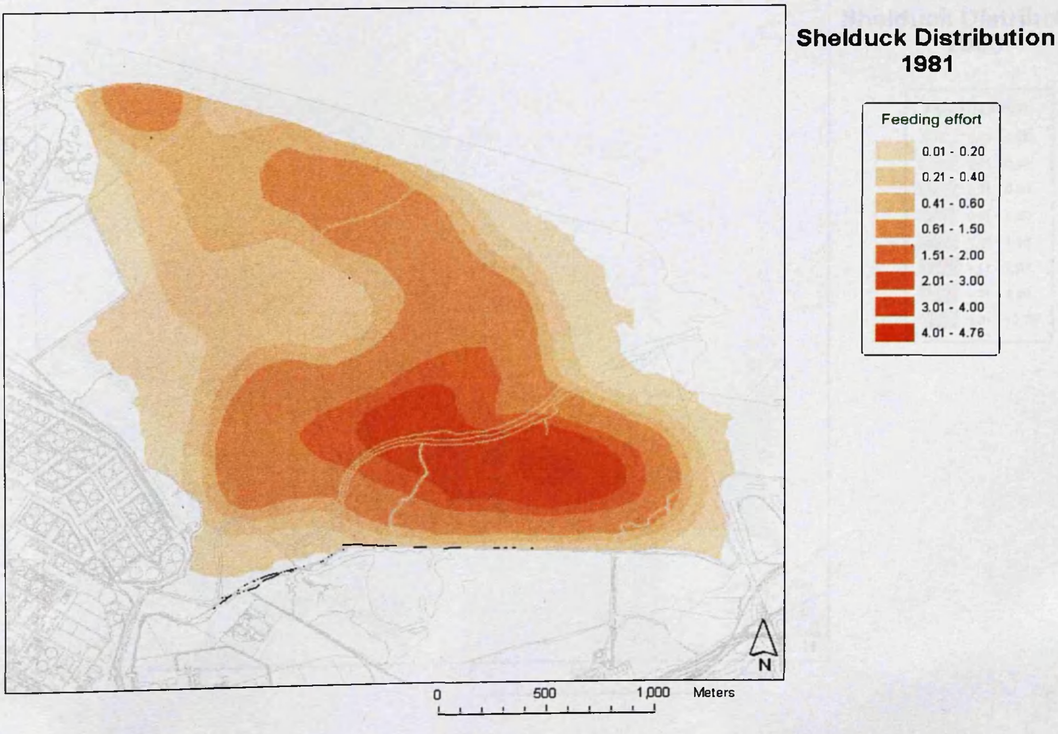
b)


Shelduck Distribution
1977
Feeding effort
0.01 - 0.20
0.21 - 0.40
0.41 - 0.60
0.61 - 1.00
1.01 - 1.50
1.51 - 2.00
2.01 - 3.00
3.01 - 4.00
N
0
500
1,000
Meters

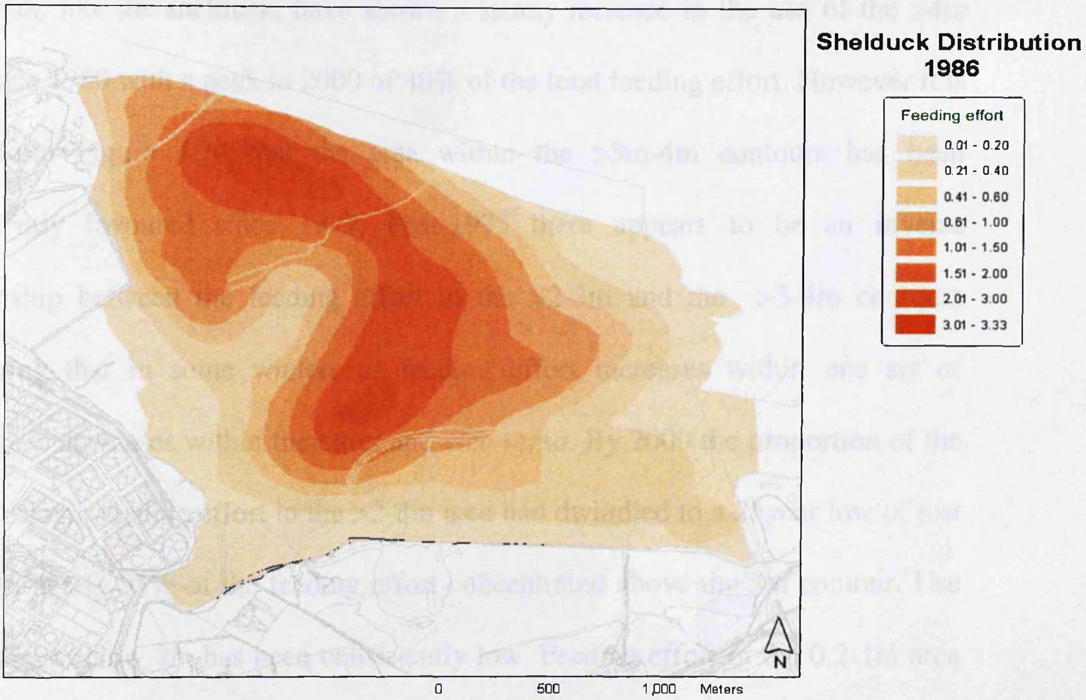
c)


Shelduck Distribution
1980
Feeding effort
0.01 - 0.20
0.21 - 0.40
0.41 - 0.60
0.61 - 1.00
1.01 - 1.50
1.51 - 2.00
2.01 - 3.00
3.01 - 5.52
N
0
500
1,000
Meters

d)


Shelduck Distribution
1981
Feeding effort
0.01 - 0.20
0.21 - 0.40
0.41 - 0.60
0.61 - 1.50
1.51 - 2.00
2.01 - 3.00
3.01 - 4.00
4.01 - 4.76
N
0
500
1,000
Meters

e)



f)

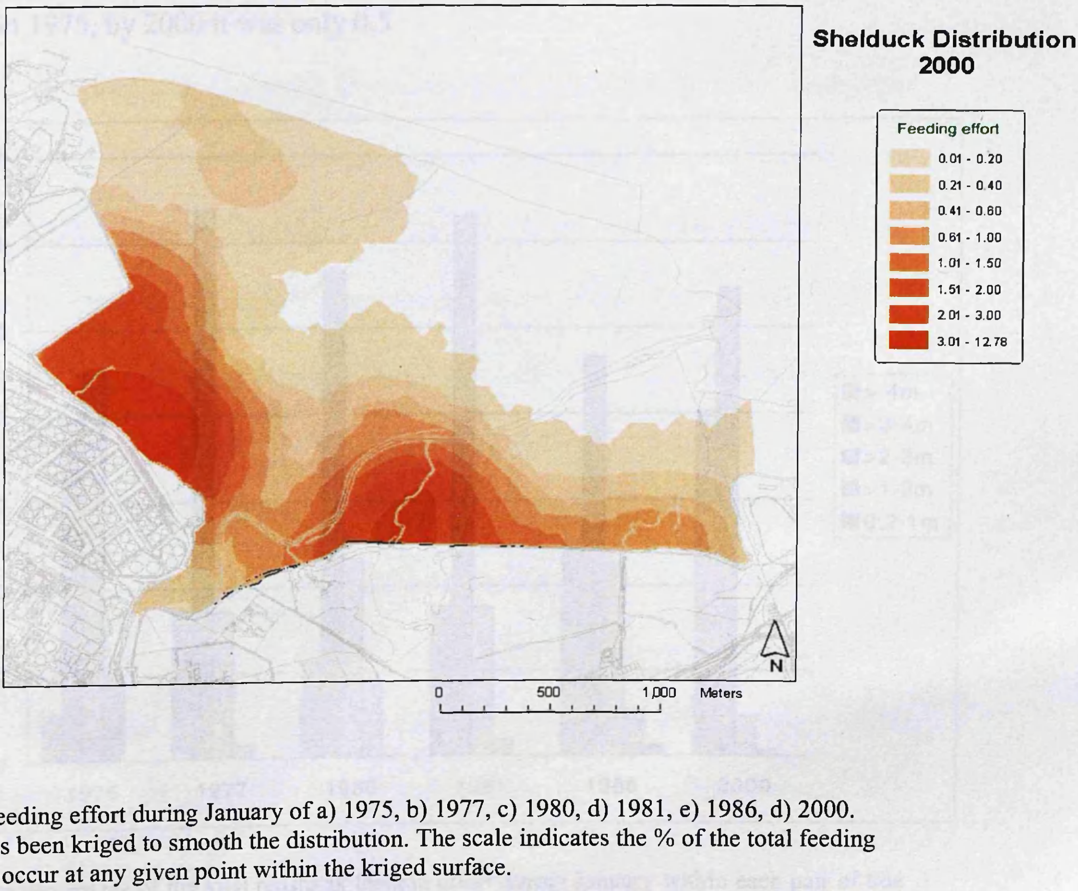


Fig 4.23.: Shelduck feeding effort during January of a) 1975, b) 1977, c) 1980, d) 1981, e) 1986, d) 2000. Actual spatial data has been kriged to smooth the distribution. The scale indicates the % of the total feeding effort that is likely to occur at any given point within the kriged surface.

4.2.3.2 Redshank

Redshank, like the shelduck, have shown a steady increase in the use of the >4m area since 1980 with a peak in 2000 of 40% of the total feeding effort. However it is clear from Figure 4.24 that the area within the >3m-4m contours has been consistently favoured since 1977. Post-1975 there appears to be an inverse relationship between the feeding effort in the >2-3m and the >3-4m contours suggesting that in some winters as feeding effort increases within one set of contours it decreases within the other and *vice versa.* By 2000 the proportion of the total redshank feeding effort in the >2-3m area had dwindled to a 25year low of just 5% with nearly 95% of the feeding effort concentrated above the 3m contour. Use of the areas below 2m has been consistently low. Feeding effort in the 0.2-1m area was zero in 1975,1977, 1981 and 2000 and peaked at only 1.2% in 1986. No more than 10% of the feeding effort was recorded in the >1-2m area with this peak value occurring in 1975, by 2000 it was only 0.5

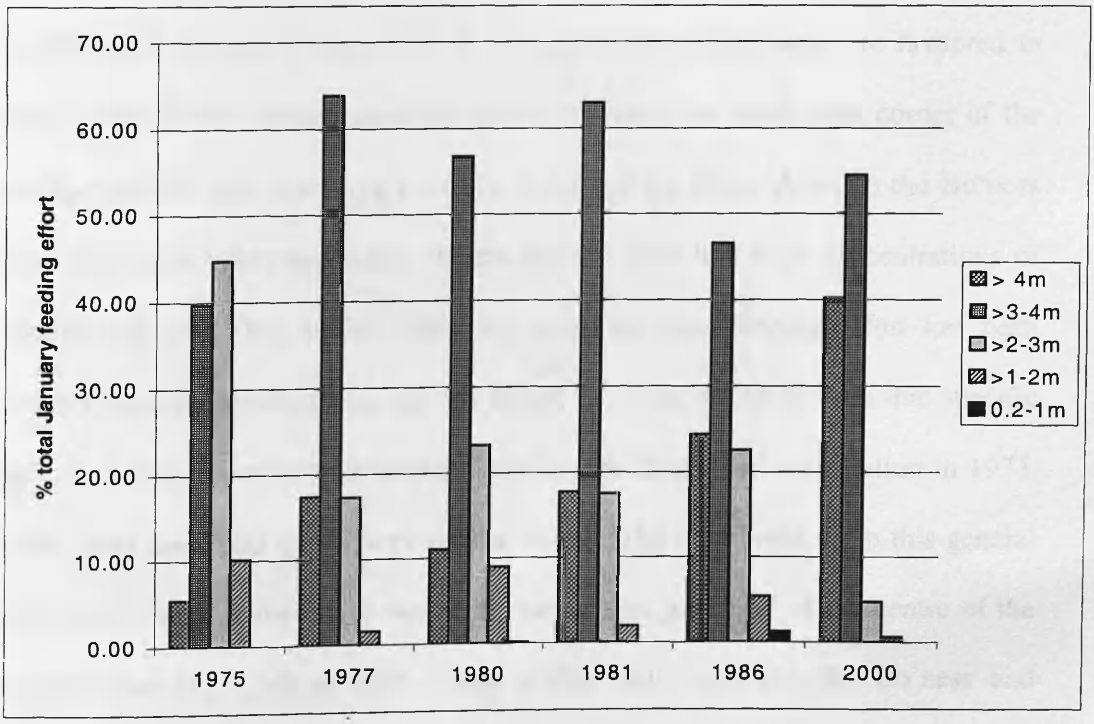


Fig: 4.24: The percentage of the total redshank feeding effort during January within each pair of tide height contours for selected winters 1975 –2000.

Feeding effort within the >3-4m contours has not only been consistently high but it also has the lowest variance highlighting the area's consistent favourability (Fig 4.25). Low variances in all areas above 1m indicate that redshank have been very constant in the way they have chosen to diperse their feeding effort by tide height.

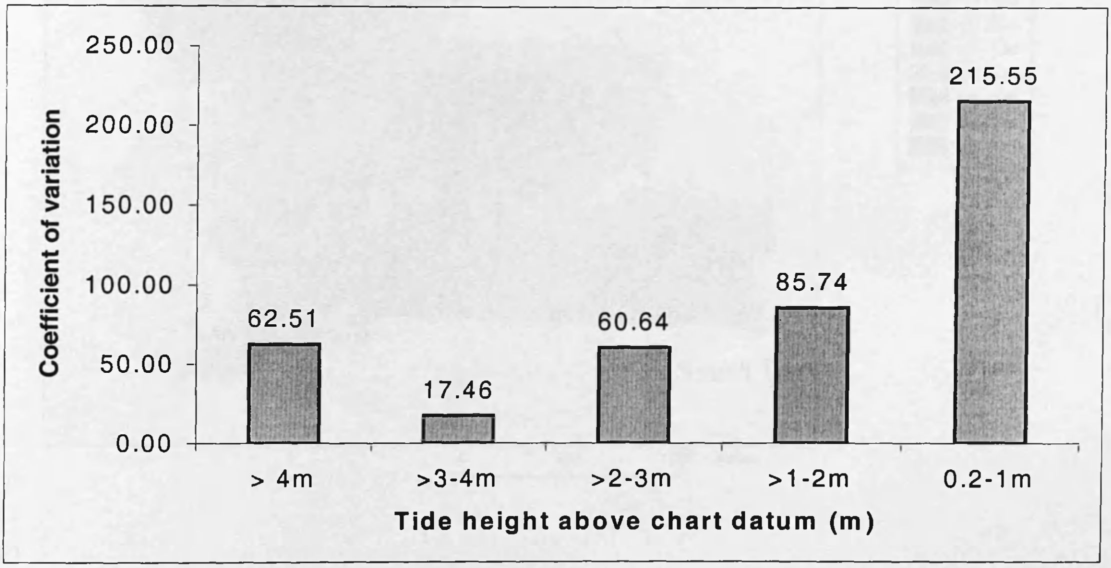
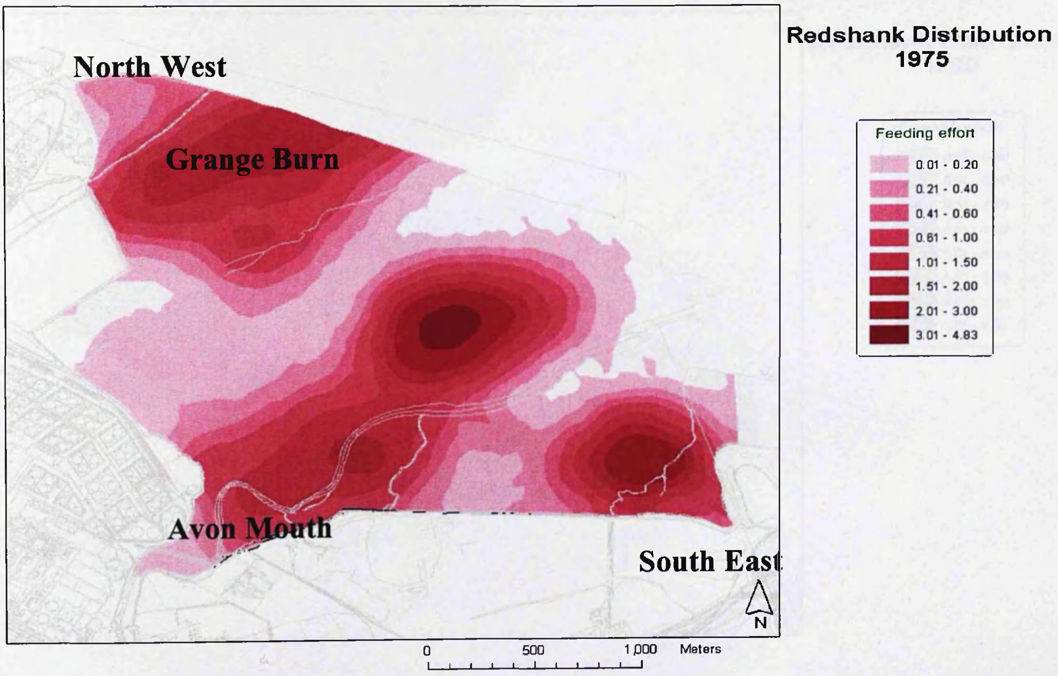


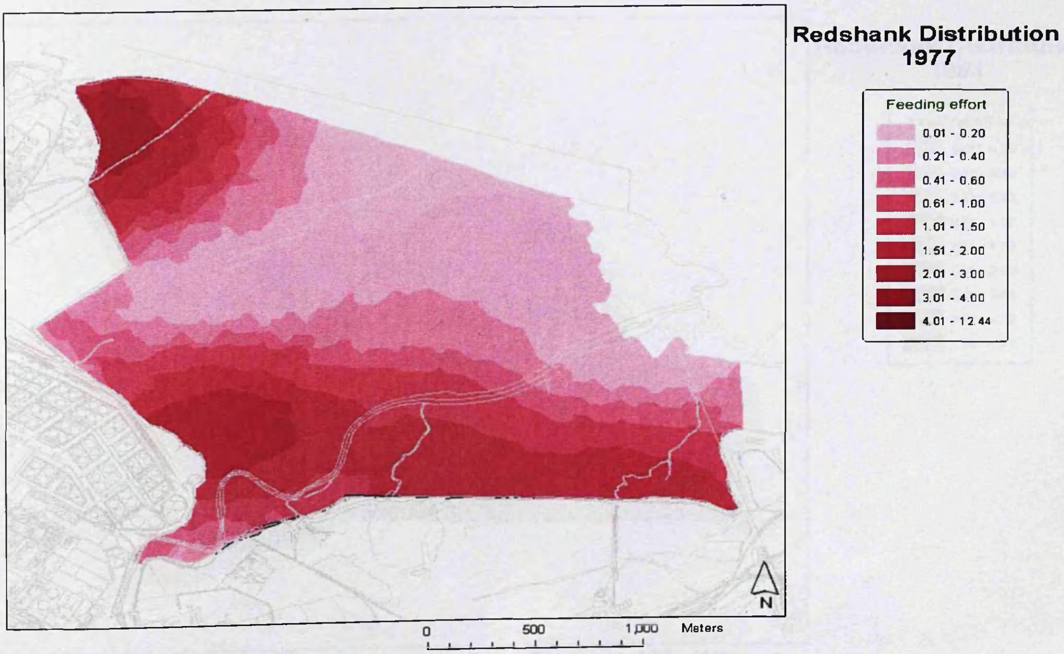
Fig 4.25 The CV of percentage redshank feeding effort during January between selected years 1975 – 2000, within each pair of tidal contours

Fig 4.26 illustrates how the redshank have positioned their feeding effort around the mudflat over the last 25 years and it is apparent that some areas are favoured in most or all of the selected years. In almost all years, the north west corner of the mudflat and an area stretching from the mouth of the River Avon to the Bo'ness bing (and particularly this south eastern corner) have had high concentrations of feeding redshank (Fig 4.26a). Although in some years feeding effort has been slightly more dispersed within the tide height contours, it can be seen that specific areas have been constantly favoured. Certainly, feeding effort distribution in 1977, 1980, 1981 and 2000 are all very similar indeed. The only break from this general distribution trend is the heavy use of the sandy area just right of the centre of the mudflat (see Fig 4.26) in 1975. Even in this year, however, the Bo'ness and Grangeburn areas were again popular.

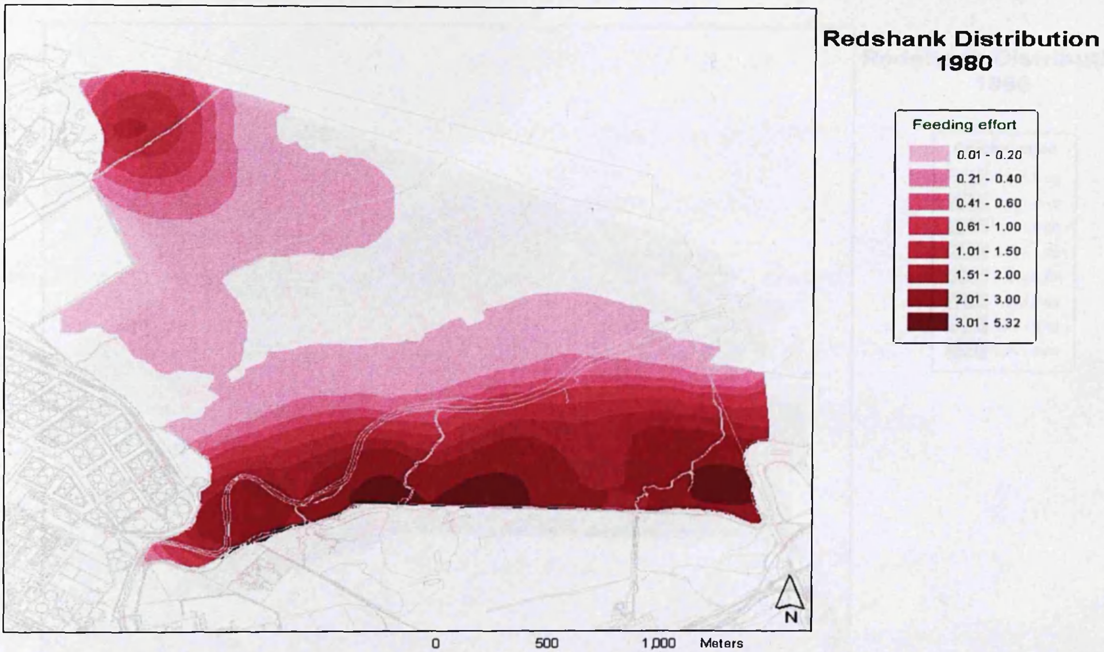
a)


North West
Grange Burn
Avon Mouth
South East
N
0
500
1,000
Meters
Redshank Distribution
1975
Feeding effort
0.01 - 0.20
0.21 - 0.40
0.41 - 0.60
0.61 - 1.00
1.01 - 1.50
1.51 - 2.00
2.01 - 3.00
3.01 - 4.83

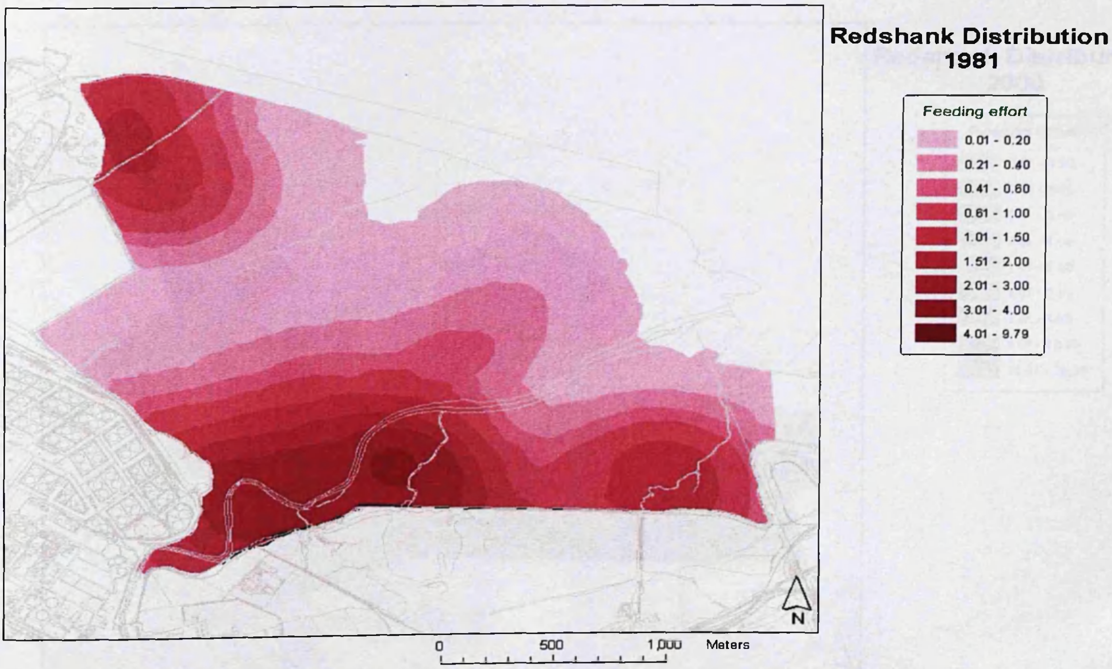
b)


N
0
500
1,000
Meters
Redshank Distribution
1977
Feeding effort
0.01 - 0.20
0.21 - 0.40
0.41 - 0.60
0.61 - 1.00
1.01 - 1.50
1.51 - 2.00
2.01 - 3.00
3.01 - 4.00
4.01 - 12.44

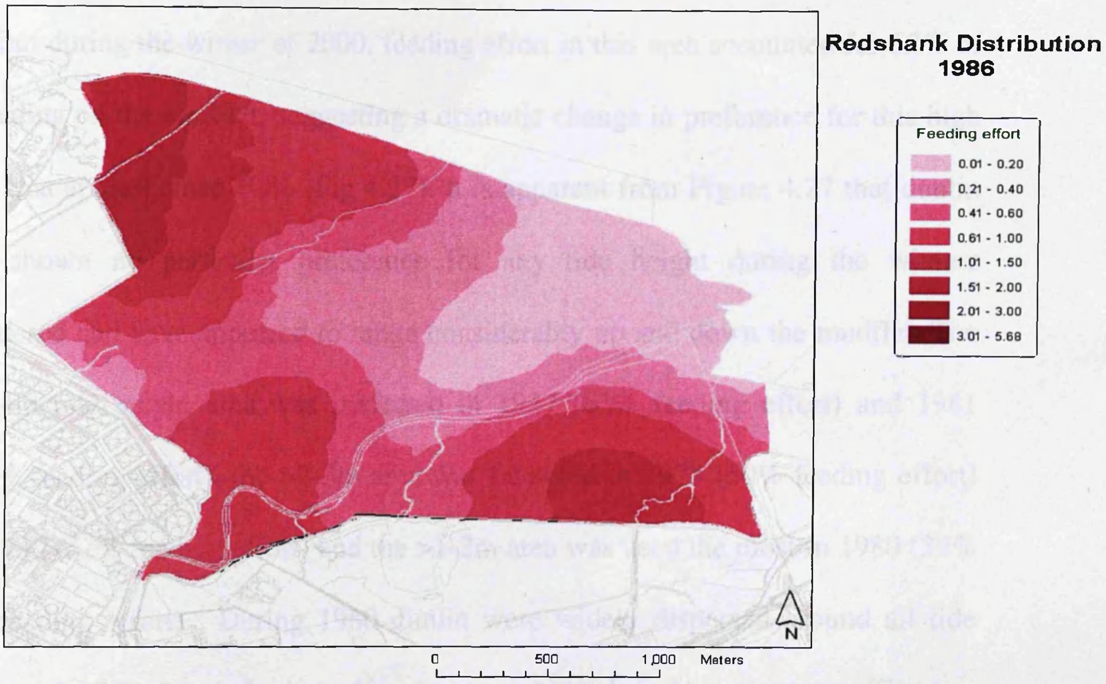
c)


Redshank Distribution
1980
Feeding effort
0.01 - 0.20
0.21 - 0.40
0.41 - 0.60
0.61 - 1.00
1.01 - 1.50
1.51 - 2.00
2.01 - 3.00
3.01 - 5.32
N
0
500
1,000
Meters

d)


Redshank Distribution
1981
Feeding effort
0.01 - 0.20
0.21 - 0.40
0.41 - 0.60
0.61 - 1.00
1.01 - 1.50
1.51 - 2.00
2.01 - 3.00
3.01 - 4.00
4.01 - 9.79
N
0
500
1,000
Meters

e)



f)

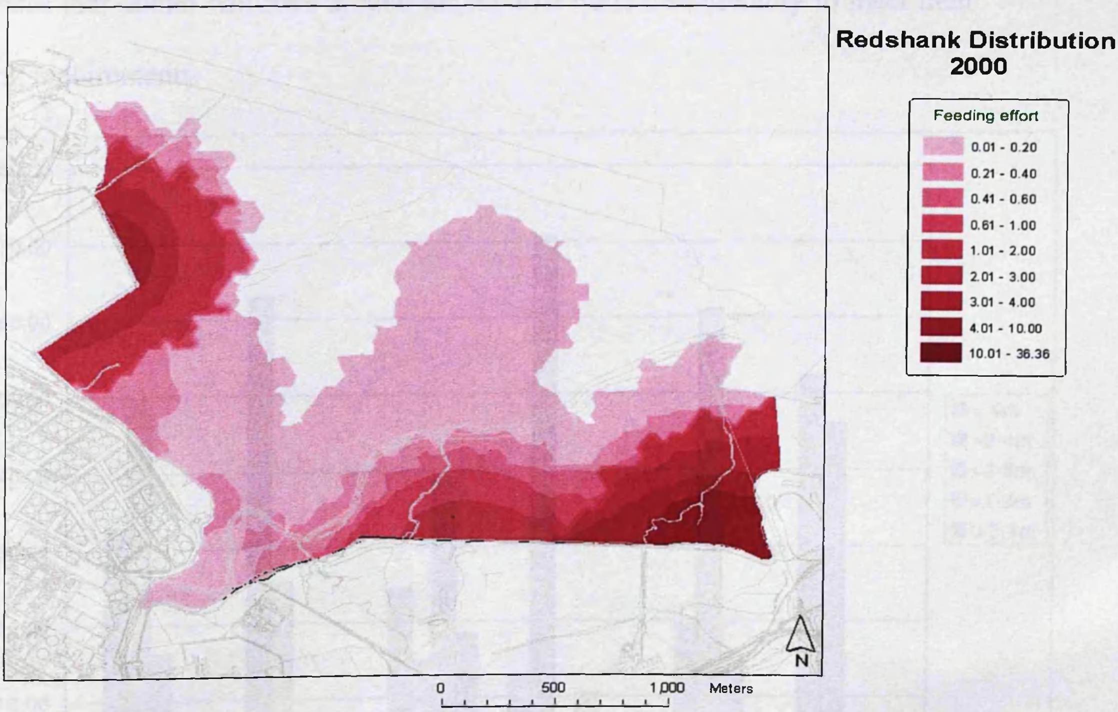
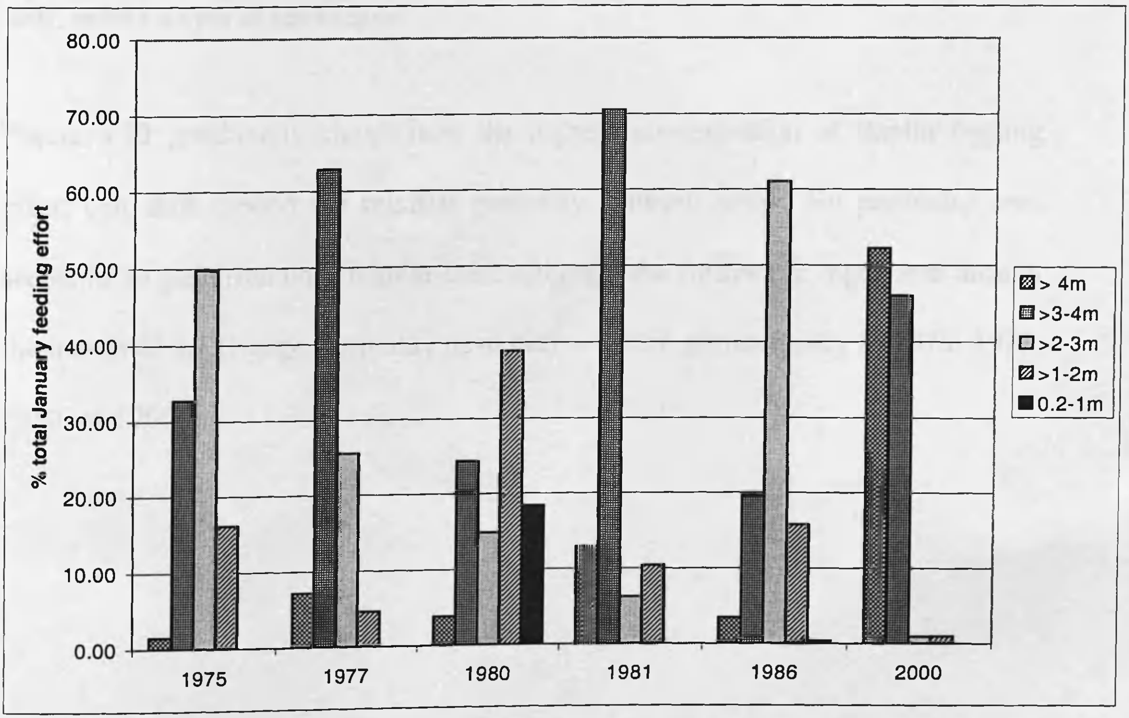


Fig 4.26: Redshank feeding effort during January of a) 1975, b) 1977, c) 1980, d) 1981, e) 1986, d) 2000. Actual spatial data has been kriged to smooth the distribution. The scale indicates the % of the total feeding effort that is likely to occur at any given point within the kriged surface.

4.2.3.3 Dunlin

Up until 2000, the embayment area above the 4m tide height contour had been little used but during the winter of 2000, feeding effort in this area accounted for 52% of all feeding on the mudflat, suggesting a dramatic change in preference for this high level area at least since 1986 (Fig 4.27). It is apparent from Figure 4.27 that dunlin have shown no particular preference for any tide height during the winters considered and have appeared to range considerably up and down the mudflat. The >3m-4m tide height area was preferred in 1977 (63% feeding effort) and 1981 (70.5% feeding effort), the >2-3m area was favoured in 1975 (50% feeding effort) and 1986 (61% feeding effort) and the >1-2m area was used the most in 1980 (39% total feeding effort). During 1980 dunlin were widely dispersed around all tide height with 18% of their feeding effort concentrated below the 1m contour. This is a marked difference to the high level preferences of the redshank and shelduck and illustrates that dunlin will rove around the mudflat quite considerably to meet their feeding requirements.



4.27: The percentage of the total dunlin feeding effort during January within each pair of tide height contours for selected winters 1975 –2000.

Figure 4.28 suggests that the whole area between 1m and 4m had the lowest variability in feeding effort over time although between year differences in relative feeding effort can vary considerably

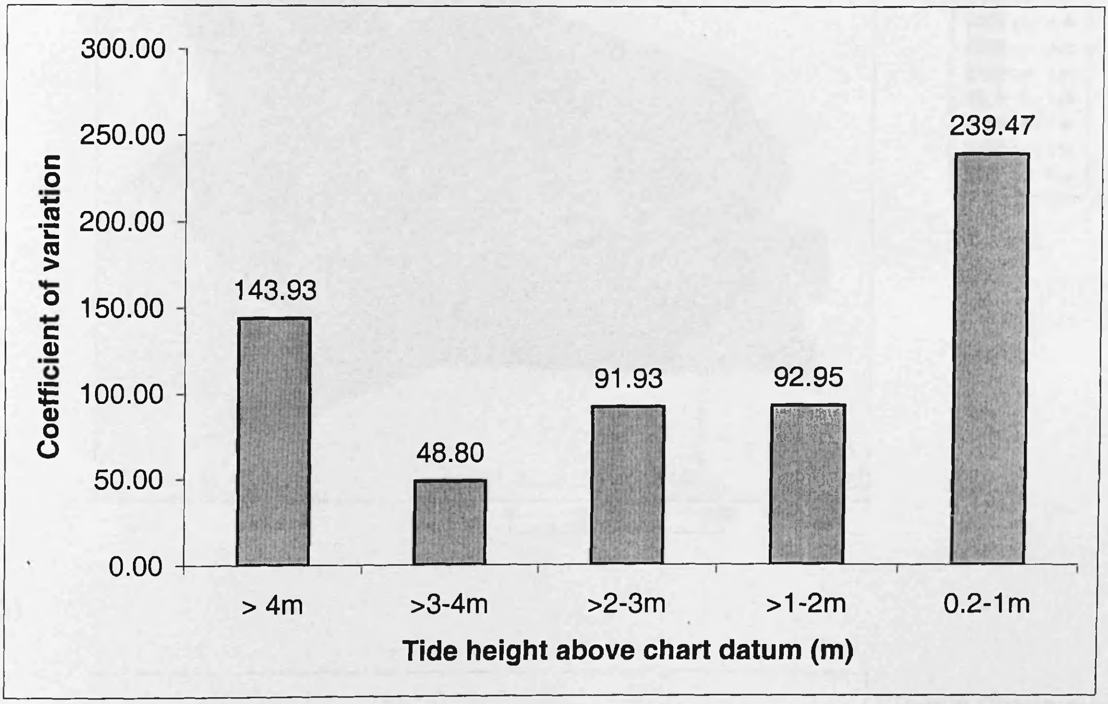
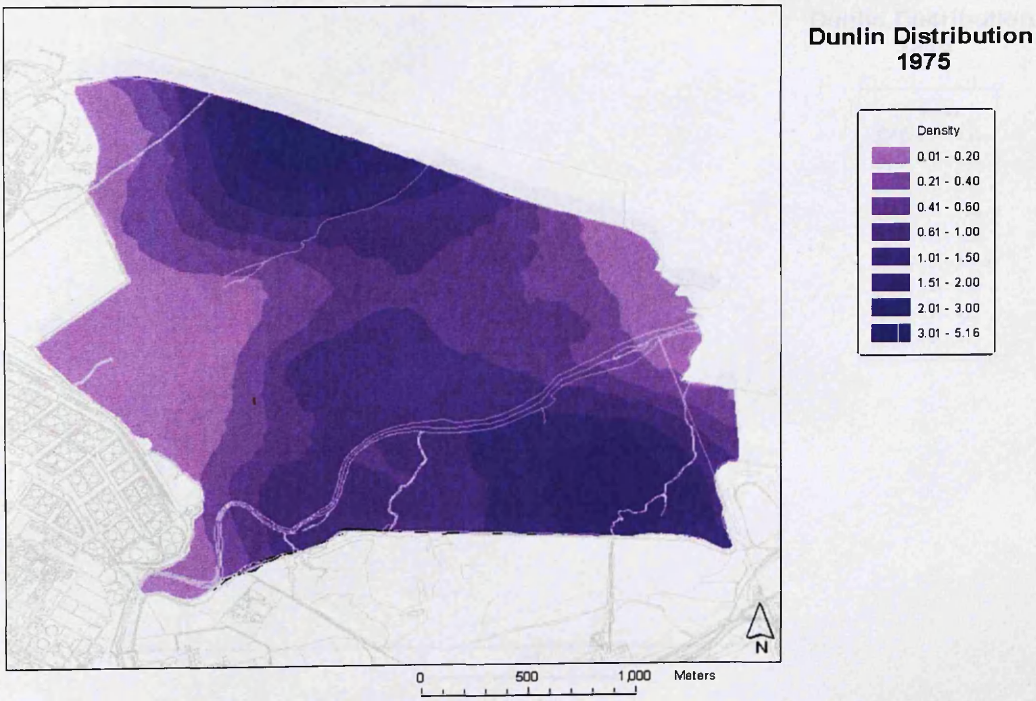


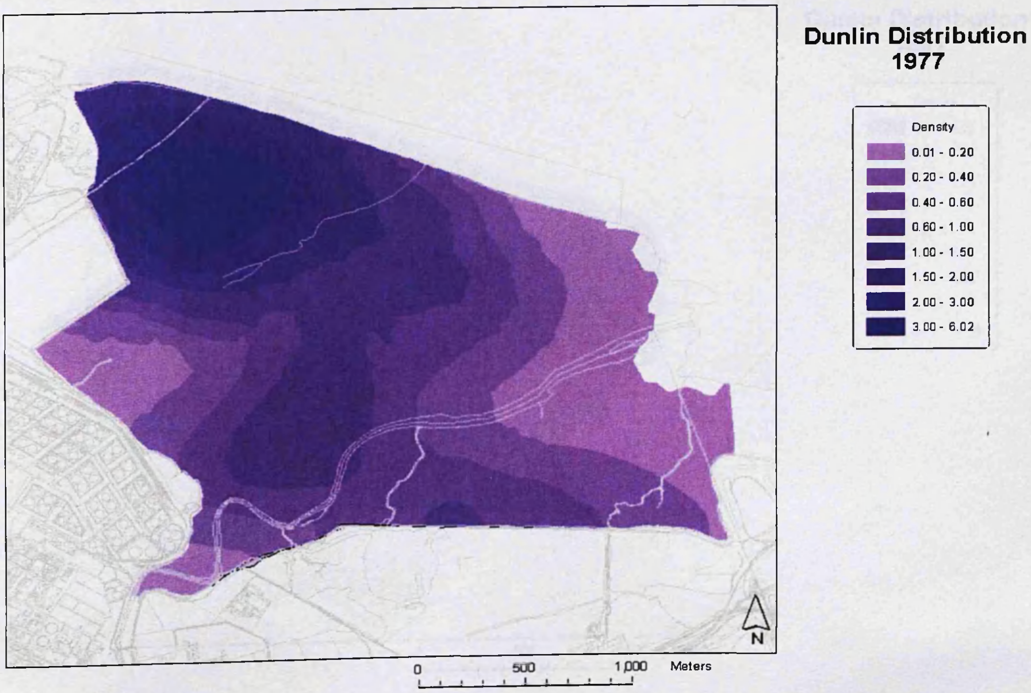
Fig 4.28 The CV of percentage dunlin feeding effort during January between selected years 1975 – 2000, within each pair of tidal contours

Figure 4.29 graphically shows how the highest concentration of dunlin feeding effort can shift around the mudflat generally between years. No particular area seems to be preferred on a regular basis although the freshwater input area around the mouth of the Grange Burn may have been selected preferentially in 1975, 1977, 1980, and 2000.

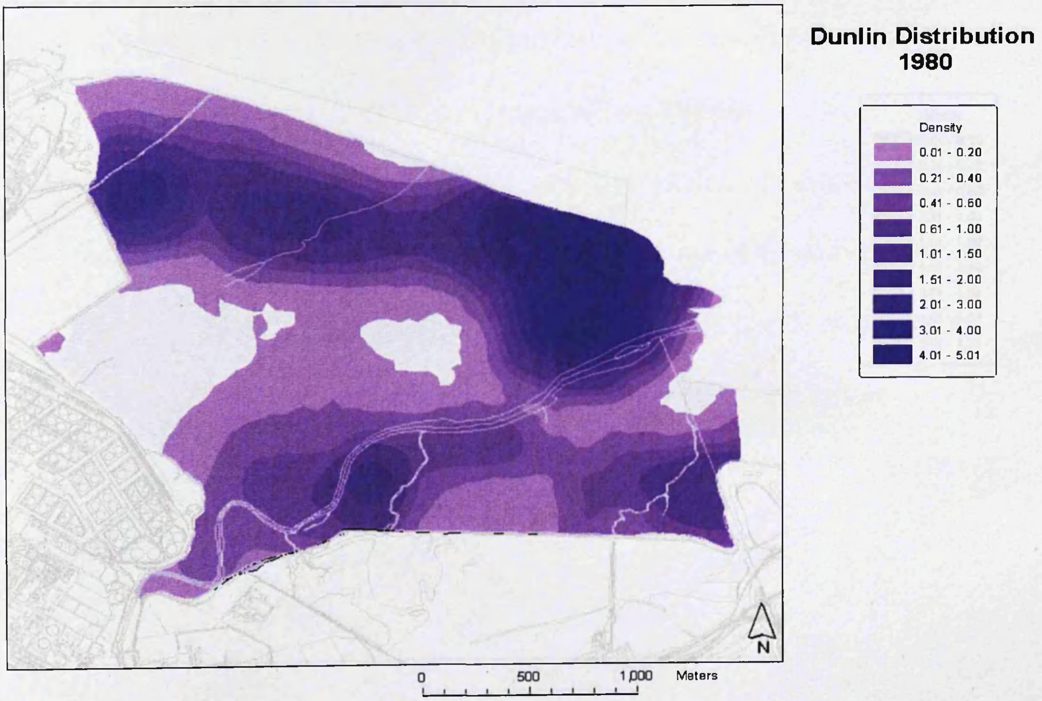
a)


Dunlin Distribution
1975
Density
0.01 - 0.20
0.21 - 0.40
0.41 - 0.60
0.61 - 1.00
1.01 - 1.50
1.51 - 2.00
2.01 - 3.00
3.01 - 5.16
N
0
500
1,000
Meters

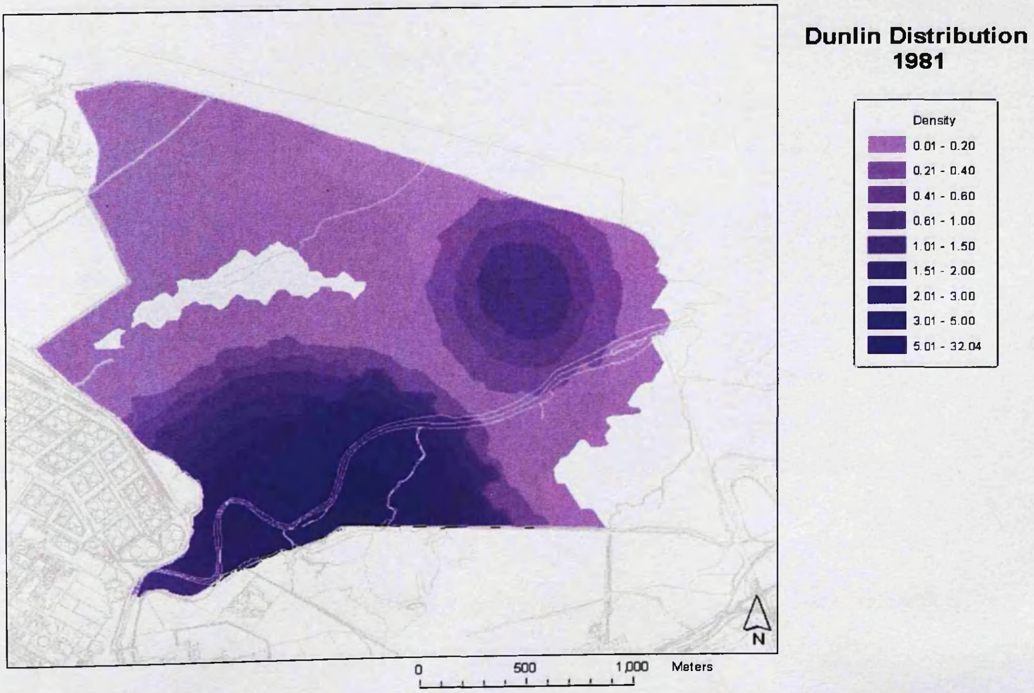
b)


Dunlin Distribution
1977
Density
0.01 - 0.20
0.20 - 0.40
0.40 - 0.60
0.60 - 1.00
1.00 - 1.50
1.50 - 2.00
2.00 - 3.00
3.00 - 6.02
N
0
500
1,000
Meters

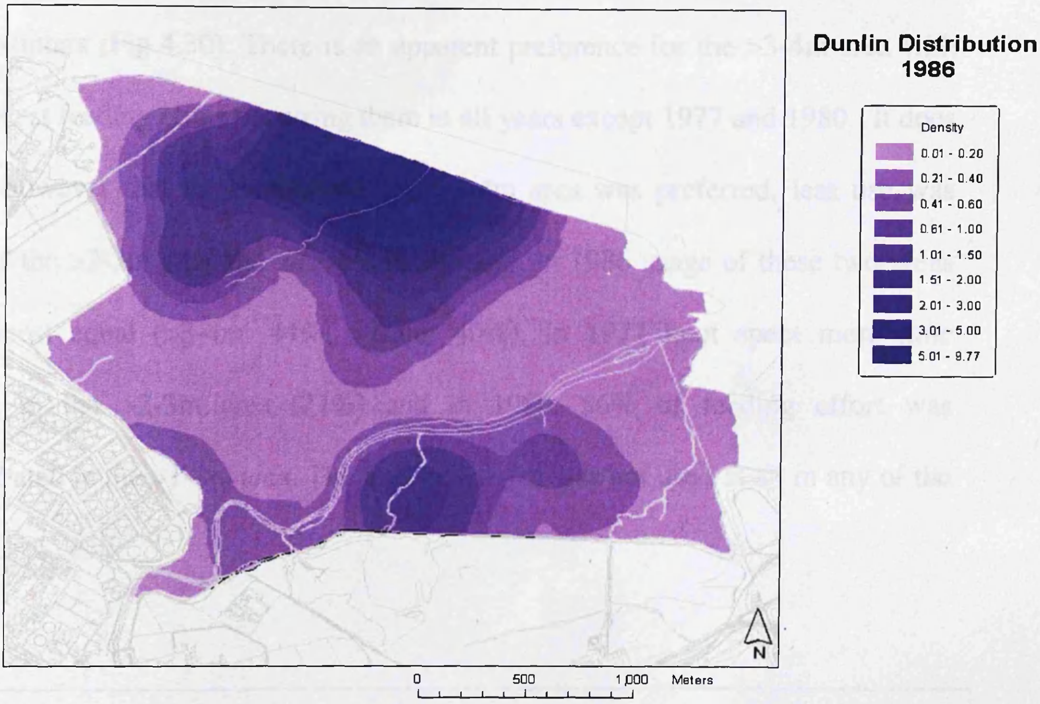
c)


Dunlin Distribution
1980
Density
0.01 - 0.20
0.21 - 0.40
0.41 - 0.60
0.61 - 1.00
1.01 - 1.50
1.51 - 2.00
2.01 - 3.00
3.01 - 4.00
4.01 - 5.01
N
0
500
1,000
Meters

d)


Dunlin Distribution
1981
Density
0.01 - 0.20
0.21 - 0.40
0.41 - 0.60
0.61 - 1.00
1.01 - 1.50
1.51 - 2.00
2.01 - 3.00
3.01 - 5.00
5.01 - 32.04
N
0
500
1,000
Meters

e)



f)

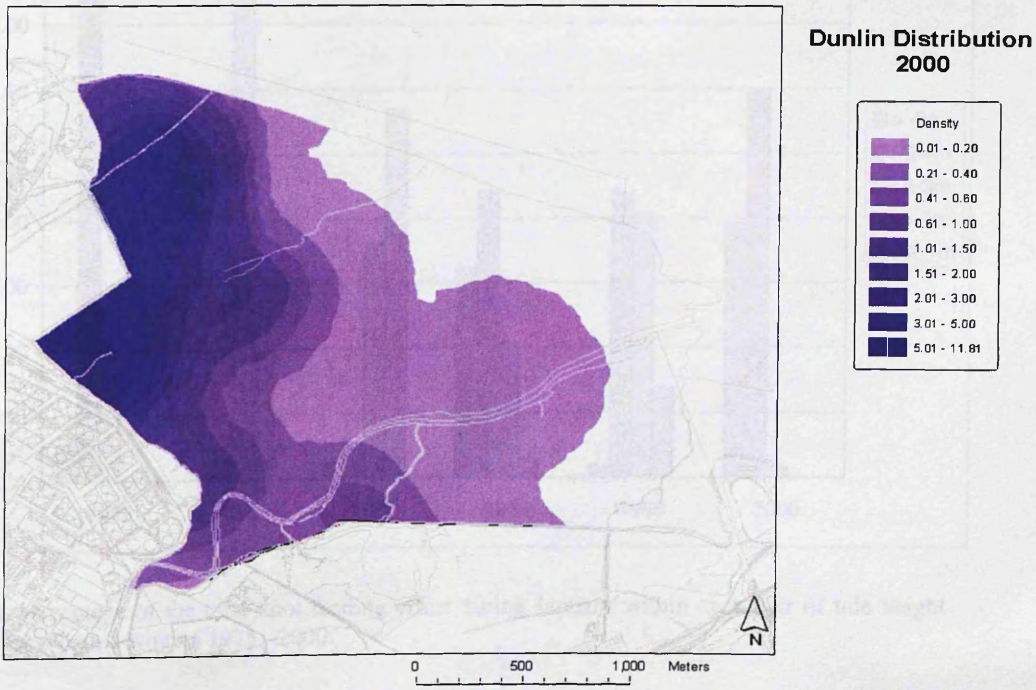
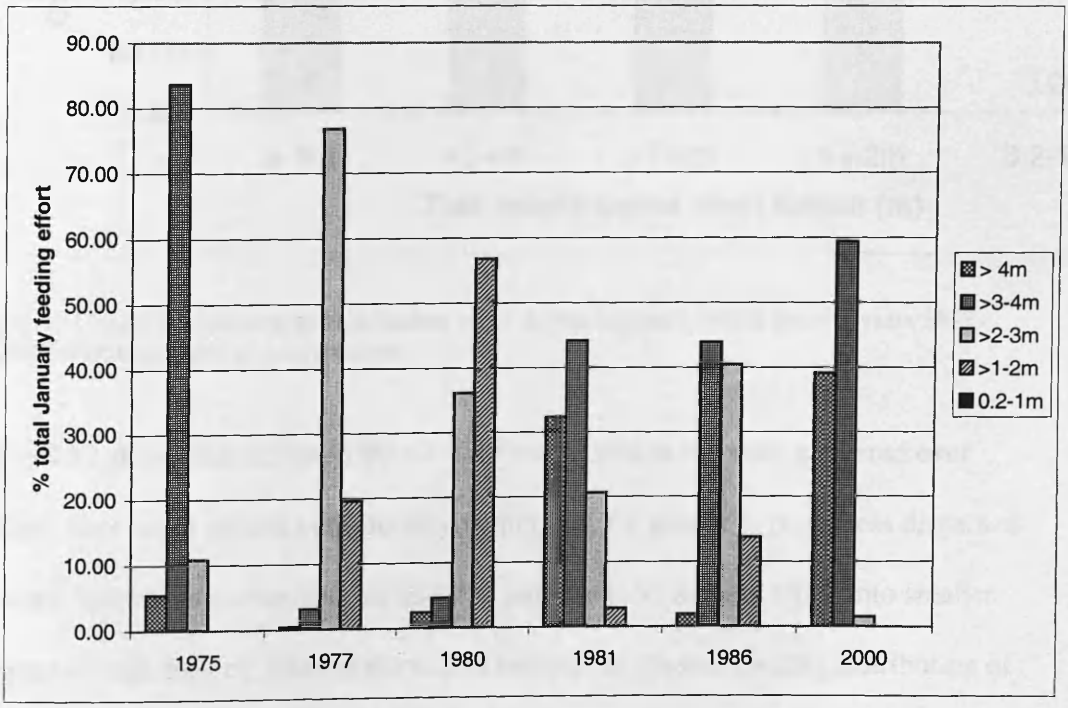


Fig 4.29.: Dunlin feeding effort during January of a) 1975, b) 1977, c) 1980, d) 1981, e) 1986, f) 2000. Actual spatial data has been kriged to smooth the distribution. The scale indicates the % of the total feeding effort that is likely to occur at any given point within the kriged surface.

4.2.3.4 Knot

Knot have shown considerable variability in their choice of feeding area throughout all the winters (Fig 4.30). There is an apparent preference for the >3-4m area with the greatest feeding effort occurring there in all years except 1977 and 1980. It does appear however that in years where the >3-4m area was preferred, less use was made of the >2-3m area and *vice versa*, although in 1986 usage of these two areas was almost equal (>3-4m: 44%, >2-3m: 40%). In 1977 knot spent more time feeding in the >2-3m area (77%) and in 1980, 56% of feeding effort was concentrated in the >1-2m area. The area below 1m was not used at all in any of the winters.



4.30: The percentage of the total knot feeding effort during January within each pair of tide height contours for selected winters 1975 –2000.

Relatively high variances in feeding effort within each set of tide height contours, between winters, indicates its considerable fluctuation between years (Fig 4.31). The preference for the >3-4m area is illustrated by the fact that it has the lowest feeding effort variance.

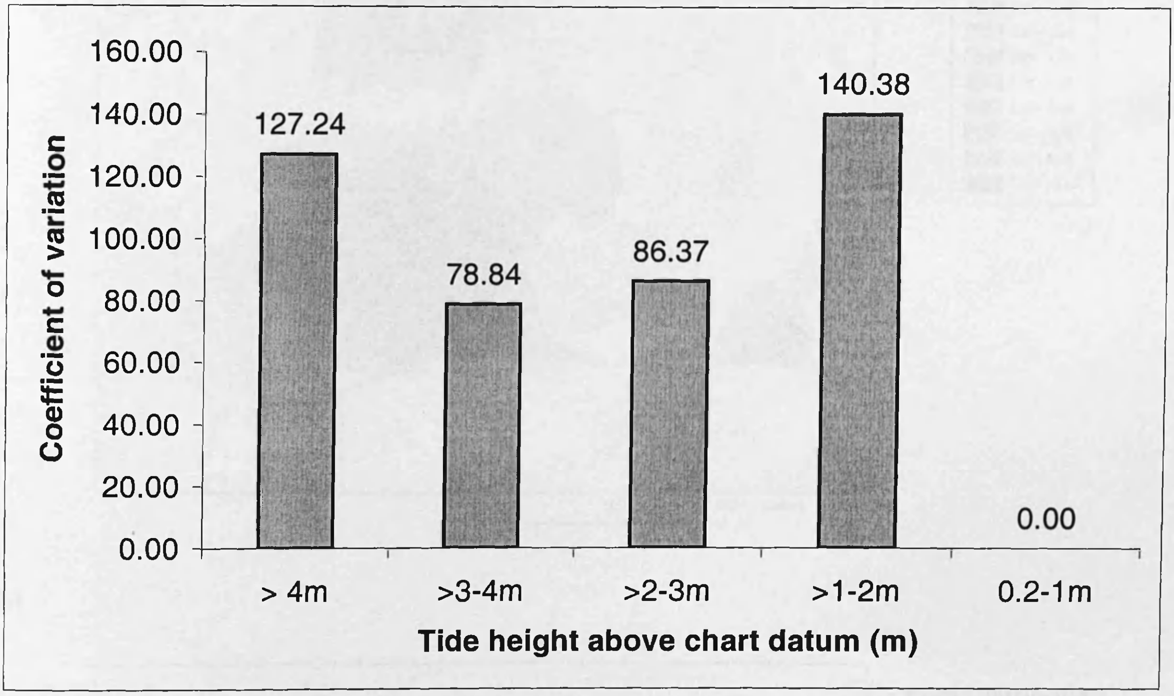
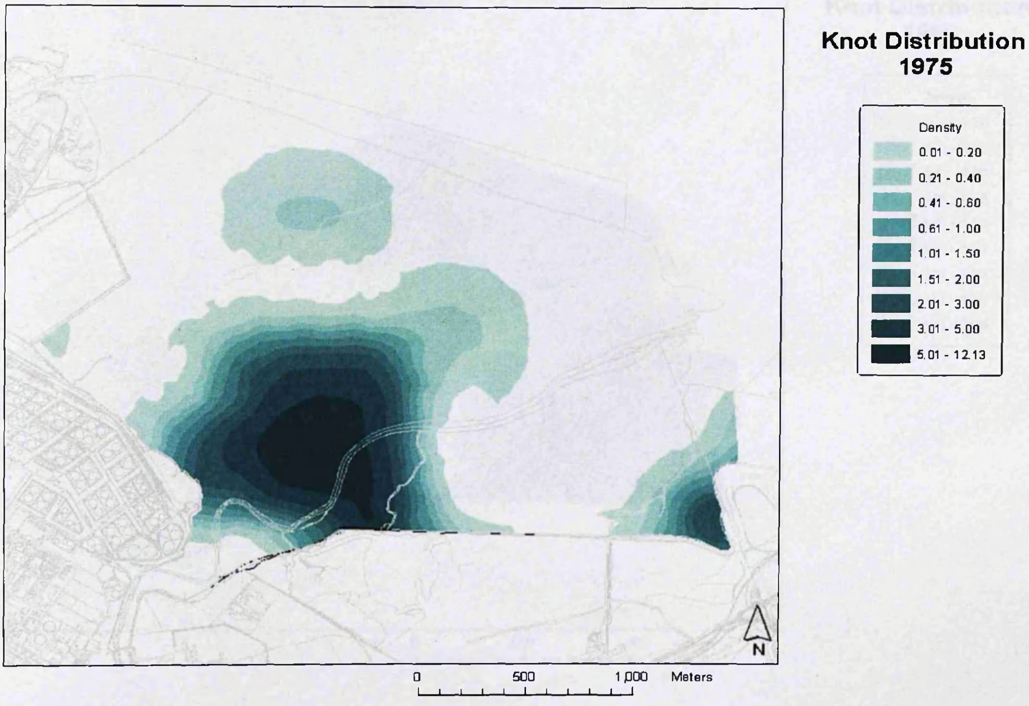


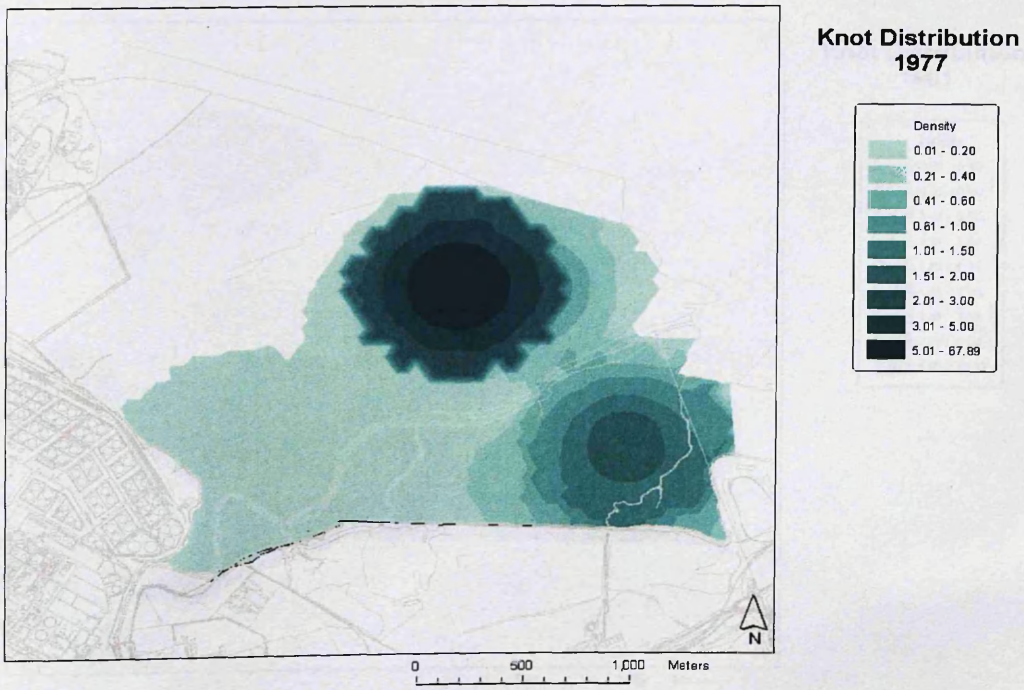
Fig 4.31 The CV of percentage knot feeding effort during January between selected years 1975 – 2000, within each pair of tidal contours

Fig 4.32 shows that although the >3-4m contour area is the most preferred over time, knot range around considerably within it. Knot appear to be far less dispersed when feeding than other species and will polarise their feeding effort into smaller areas of high feeding concentration. It is evident the present feeding distribution of knot and dunlin is extremely similar and they appear to be occupying almost identical areas of the mudflat. This does not appear to have been the case in past winters although there seemed to be a shared preference for the Avon mouth area in 1981. Redshank also shared a similar feeding distribution to knot in this year.

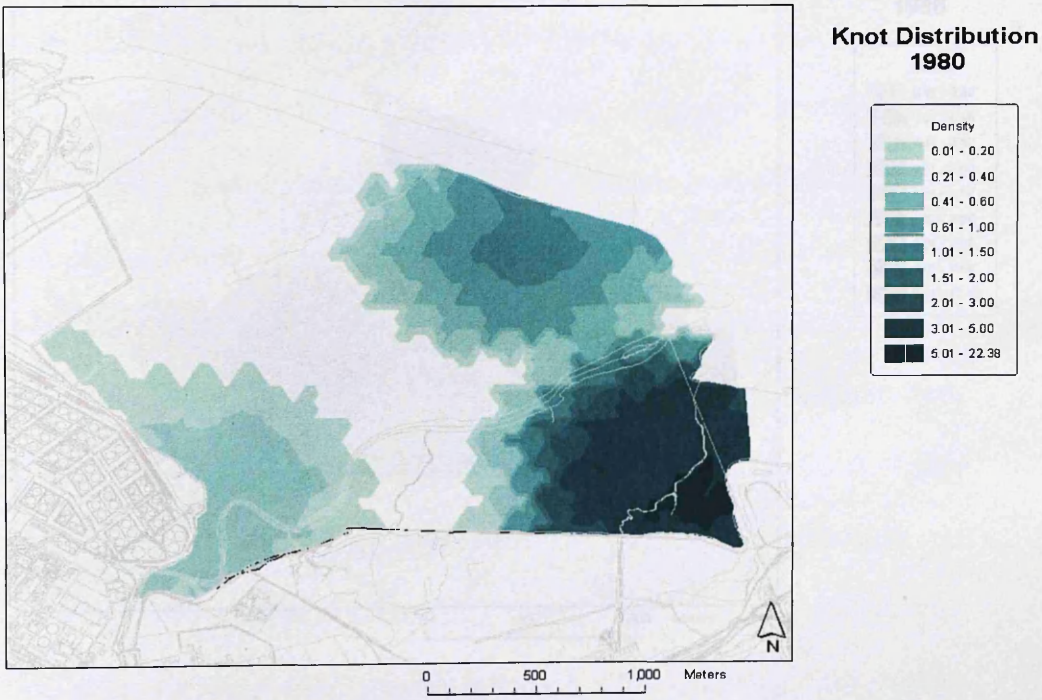
a)


Knot Distribution
1975
Density
0.01 - 0.20
0.21 - 0.40
0.41 - 0.60
0.61 - 1.00
1.01 - 1.50
1.51 - 2.00
2.01 - 3.00
3.01 - 5.00
5.01 - 12.13
N
0
500
1,000
Meters

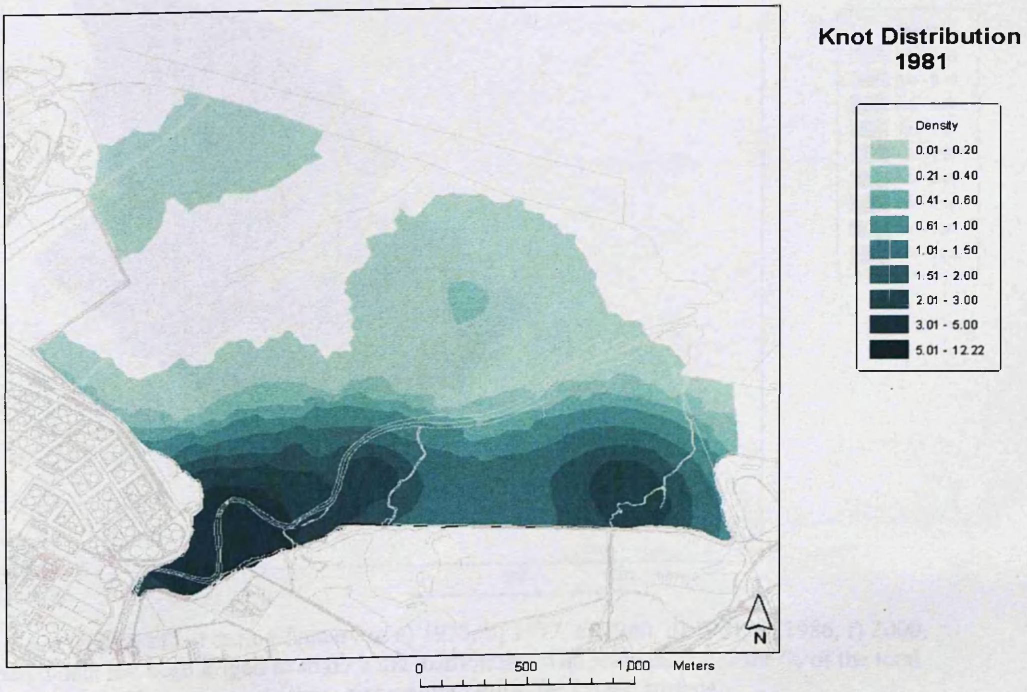
b)


Knot Distribution
1977
Density
0.01 - 0.20
0.21 - 0.40
0.41 - 0.60
0.61 - 1.00
1.01 - 1.50
1.51 - 2.00
2.01 - 3.00
3.01 - 5.00
5.01 - 67.89
N
0
500
1,000
Meters

c)


Knot Distribution
1980
Density
0.01 - 0.20
0.21 - 0.40
0.41 - 0.60
0.61 - 1.00
1.01 - 1.50
1.51 - 2.00
2.01 - 3.00
3.01 - 5.00
5.01 - 22.38
N
0
500
1,000
Meters

d)


Knot Distribution
1981
Density
0.01 - 0.20
0.21 - 0.40
0.41 - 0.60
0.61 - 1.00
1.01 - 1.50
1.51 - 2.00
2.01 - 3.00
3.01 - 5.00
5.01 - 12.22
N
0
500
1,000
Meters

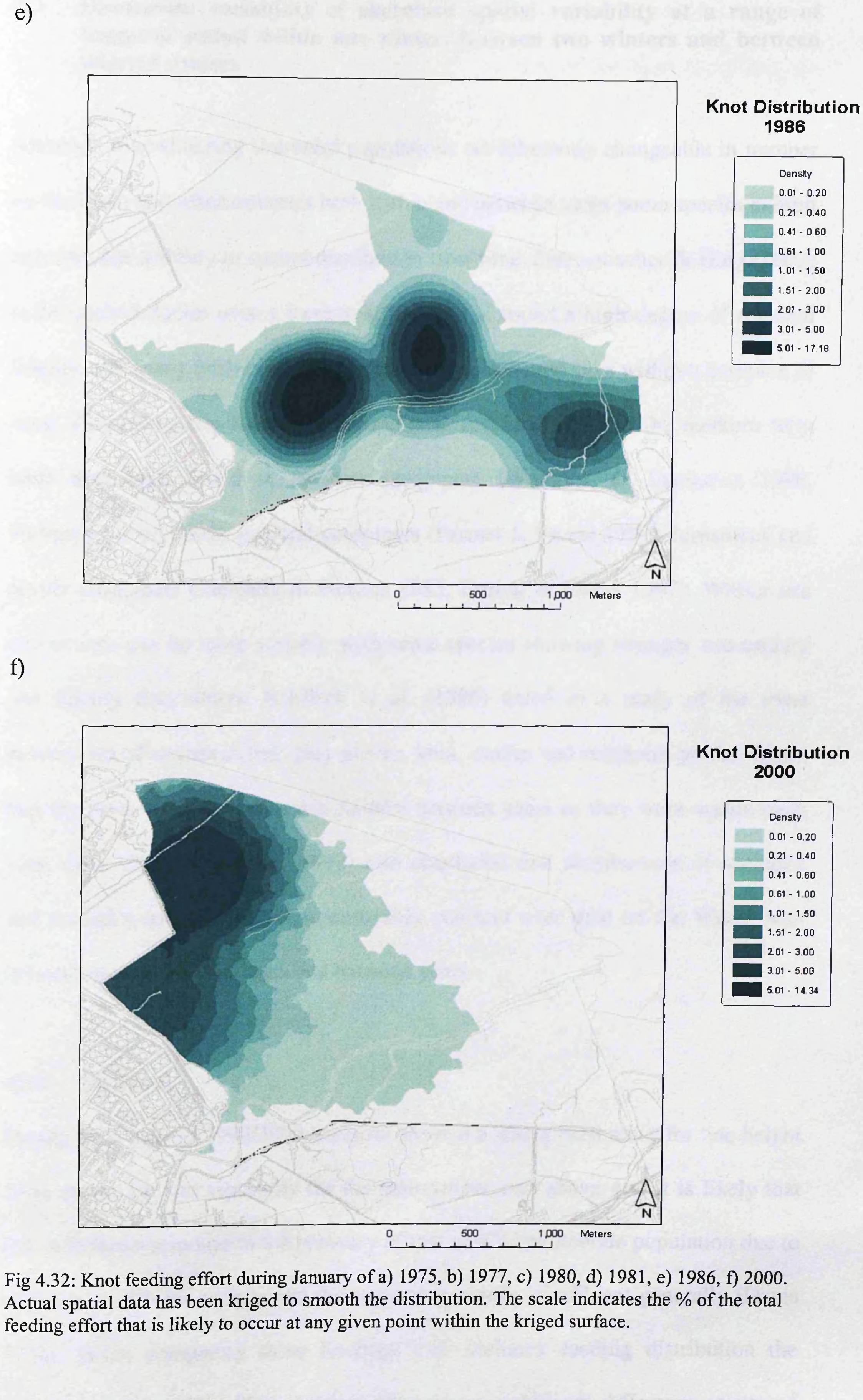


Fig 4.32: Knot feeding effort during January of a) 1975, b) 1977, c) 1980, d) 1981, e) 1986, f) 2000. Actual spatial data has been kriged to smooth the distribution. The scale indicates the % of the total feeding effort that is likely to occur at any given point within the kriged surface.

4.3 Discussion: variability of shorebird spatial variability at a range of temporal scales: within one winter, between two winters and between selected winters

Although overwintering shorebird populations are inherently changeable in number on the Forth and other estuaries both within and between years some species exhibit considerable stability in spatial distribution over time. Sanzenbacher & Haig (2002) radio tracked dunlin over a three-year period and found a high degree of regional fidelity with many birds consistently returning to favoured sites within a complex of sites. This strong site fidelity at the regional and local scale in the medium term have also been found in western sandpipers (Warnock & Takekawa 1996, Fernandez *et al.* 2002), pectoral sandpipers (Farmer & Parent 1997), turnstones and purple sandpipers (Metcalfe & Furness 1985, Burton & Evans 1997). Within site movements can be more variable with some species showing stronger sub-estuary site fidelity than others. Rehfisch *et al.* (1996) noted in a study of the roost movements of oystercatcher, grey plover, knot, dunlin and redshank on the Wash, that the birds were almost as site faithful between years as they were within each year. Goss Custard & Yates (1992) also concluded that distributions of shelduck and several wader species were reasonably constant over time on the Wash, both between seasons, within years and between years.

4.3.1 Shelduck

During the winter of 1999/2000 shelduck showed a strong preference for tide height areas above 3m and especially for the embayment area above 4m. It is likely that this is in direct response to the recovery of that area's invertebrate population due to re-siting of effluent outfalls and the improving quality of effluent generally (Davis 2001). When comparing these findings with shelduck feeding distribution the previous winter (1998/1999) shelduck showed no significant difference in use of tide height areas. Therefore it can be concluded that they used the mudflat in almost exactly the same way over these two winters. At least in the short term then the models developed for this species are likely to be valid.

By looking at the broad scale long term maps (Fig 4.23) it can be seen that although usage within a tide height contour area can be consistent over time the shelduck are ranging around quite considerably within them, apparently seeking out the best feeding conditions or avoiding disturbance (Burton *et al.* 2002). Although the shift to areas above the 4m tide height contour have been recent, the >2-3m and >3-4m areas have been consistently used over time. Although similar areas at Kinneil may be favoured in consecutive years it seems apparent that in the long term feeding amongst shelduck is spatially variable.

4.3.2 Redshank

Redshank consistently favoured the high level mudflats throughout the winter of 1999/2000, mostly in the >3-4m contour but also above 4m and this pattern was continued over two successive winters with redshank feeding distribution also not being significantly different between years. The weighted area model predicting redshank feeding effort, closely matched their actual feeding distribution and the fact that their spatial distribution is likely to be similar at least in successive years suggests that the model for redshank is likely to be valid in future years, especially considering that redshank exhibit strong site fidelity (Burton 1996). The findings of the long term study concur with this assumption as redshank showed the most stable long term use of tide height areas of all the species considered. High level mudflats, especially the >3-4m area has been consistently favoured over all other tide heights in all years and the recent increase in usage of the >4m area, possibly due to improvements in effluent quality, suggest that the trend in the use of high level areas is likely to continue.

4.3.3 Dunlin

During the single winter of 1999/2000 dunlin, like shelduck and redshank strongly favoured high level mudflats >4m although there was some dispersal to the >3-4m area as the winter progressed. This pattern of feeding distribution was also repeated between winters. Again the short-term use of the present model is most likely to be valid. Long term use of Kinneil is somewhat more variable suggesting that dunlin are able to range widely around the mudflat to meet their metabolic requirements. They may also have been responding to variations in disturbance levels or competition from other species such as knot. Such possible competition between knot and dunlin for feeding space are illustrated in Figures 4.12 and 4.13. Although long term variability in feeding distribution is evident the recent trend towards selecting high level areas and the similarity in usage in the short term lends weight to any future use of the dunlin model.

4.3.4 Knot

In the short-term knot distribution around Kinneil is quite variable with birds roving all around the mudflat but there was a strong preference for the >3-4m area, again emphasising the importance of high level mudflats. Knot also showed no significant difference in the way they used the mudflat in two successive winters. The long term picture illustrated in Figure 4.32 shows however that inter annual differences in mudflat usage can be high with CVs in all tide heights indicating some temporal variability. If the apparently recent trend for all species to spend longer feeding the high level mudflats is likely to continue for knot then the model may be useful in the medium term but of all the models the one for knot should be used with caution

Section B: Invertebrates

4.4 Is the spatial and temporal distribution and abundance of invertebrates on the Forth Estuary relatively stable over time ?

The abundance and spatial distribution of invertebrate species is subject to considerable change over time (Raffaelli *et al.* 1999, McLusky & Martins 1998) and such changes in distribution are consequently likely to affect the feeding distribution of shorebirds on an annual basis. Desmond *et al.* (2002) found that in an 11-year study on 3 Californian estuaries, invertebrates showed very little seasonal variation but a high degree of inter-annual variation. They also noted that irregular disturbances such as flooding events had a more important affect on invertebrate assemblages than more predictable seasonal cues like temperature. On the Dutch Wadden Sea, Beukema *et al.* (1983) found that the size of the food stocks shorebirds encounter varied from place to place and from year to year. They looked at the temporal variability of prey stocks, using a long-term data series of annual estimates of biomass of macro-benthic animals collected on tidal flats in various parts of the Dutch and German Wadden Sea. Year-to-year fluctuations were evident in nearly all invertebrate species. Various species differed significantly in their year-to-year variability. Throughout the whole site, *Macoma* was relatively stable, whereas species such as Cerastoderma and *Nephtys* fluctuated heavily and rapidly in all parts of the Wadden Sea where they were found. Within species, fluctuations in biomass of individual age or size classes were stronger than those in total biomass of the species. Several species showed minimal biomass values in the same years over large areas, possibly in response to harsh weather. Immediately after severe winters, cold-sensitive species as *Cerastoderma* and *Nephtys* were scarce all over the Wadden Sea limiting the possibilities for birds to switch to other areas to find their preferred prey in sufficient quantity.

Habitat loss on the Forth Estuary via mudflat removal (McLusky *et al.* 1992) and/or pollution (McLusky & Martins 1998) have had a negative effect on invertebrate population community structure over the long term. Such events and a diverse array of hydrodynamic regimes can affect the spatial dynamic of invertebrate populations over time (Snelgrove & Butman 1994). Populations of macrofauna, however, are able to persist due to 'diffusive dispersal' which allows a proportion of the population to reproduce close to their natal location (Spiers & Gurney 2001).

4.4.1 The short term

4.4.1.1 Within year changes in invertebrate abundance between summer and winter at Kinneil

Table 4.2 illustrates the overall percentage difference in mean numbers of invertebrates per m^2 between July 1999 and January 2000 at the Kinneil mudflat. Data for July was collected by McLusky *et al.* (1999). The January 2000 data was collected as part of this study. Although the need to convert data collected at the $50cm^2$ scale to the m^2 scale is questionable due to the inevitable introduction of error, it was necessary to do this to make these data comparable. Small scale spatial variation and species mobility aside, most species exhibit a varying decline in number which may or may not be due to shorebird predation (for a full study of the effects of predation on invertebrates see chapter 5). *Manayunkia, Mytilus* and spionids however have increased over this period. This is particularly unusual for *Manayunkia* as this species was found to be a good predictor of shelduck, redshank and dunlin feeding effort so if it were a favoured food item it might be expected to be considerably depleted in number. In order to determine whether this depletion pattern was repeatable in the short term the same exercise was undertaken for data collected in July 1998 and January 1999. (Table 4.3)

Table 4.2: The percentage change in mean invertebrate numbers (m^2) between Summer (n=90) and Winter (n=161) at Kinneil in 1999/2000. Means have been rounded to the nearest decimal place.

Invertebrates	**Mean number (m^2) in Summer 1999 (July)**	**Mean number (m^2) in Winter 2000 (January)**	**Percentage change 1999/2000**
Hydrobia	3908	1204	-69
Nereis	368	176	-52
Oligochaetes	13571	12830	-5
Manayunkia	4877	10007	+105
Spionids	6988	11282	+61
Nephtys	293	142	-51
Macoma	5444	1014	-81
Cerastoderma	182	129	-29
Corophium	915	231	-75
Eteone	802	57	-93
Mytilus	62	107	+71

The results in Table 4.3 suggest that apparent rates of depletion between July and January are broadly similar with *Manayunkia* again displaying an increase in number albeit a reduced one. Spionids however were much depleted in 1998/1999, quite the opposite to their 61% increase in 1999/2000. All the data presented in Tables 4.2 and 4.3 were from random samples and may not reflect actual changes in population sizes.

Table 4.3: The percentage change in mean invertebrate numbers (m^2) between Summer and Winter at Kinneil in 1999/2000. Means have been rounded to the nearest decimal place.

Invertebrates	**Mean number (m^2) in Summer 1998 (July)**	**Mean number (m^2) in Winter 1999 (January)**	**Percentage change 1998/1999**
Hydrobia	8898	207	-97.7
Nereis	993	40	-96.6
Oligochaetes	25575	17346	-32
Manayunkia	8591	8713	+1.4
Spionids	10235	367	-96.4
Nephtys	453	100	-78
Macoma	6617	1260	-81
Cerastoderma	207	113	-45.2
Corophium	900	320	-64.4
Eteone	935	133	-86
Mytilus	NA	NA	NA

4.4.1.2 Between year changes in invertebrate abundance at Kinneil and all study sites

Although the number of study plots on the Forth Estuary was increased from 30 in 1998/99 to 50 in 1999/2000, 23 plots were sampled in both years so it was possible to determine whether or not there were significant differences in the mean abundance of invertebrate species (Table 4.4)

Table 4.4: Results of GLMs comparing the difference in mean numbers of individuals in study plots (n=5 x 50cm^3 samples) between the winters of 1998/1999 and 1999/2000 at two spatial scales. Only study plots that were sampled in both years have been paired. 12 plots were coincident for Kinneil only (a) and 23 for the main study sites of Kinneil, Skinflats and Torry Bay (b). Winter and site were factors, all data Log^{10} + 1 transformed and Bonferroni corrections were applied. Significant differences in mean numbers between years and between sites are italicised and emboldened.

a)

Species	**Kinneil only**	
	F $_{1,11}$	***P***
Hydrobia	2.80	0.10
Nereis	2.36	0.13
Oligochaetes	4.23	***0.05***
Manayunkia	0.34	0.56
Spionids	11.80	***0.002***
Nephtys	0.24	0.62
Macoma	0.37	0.54
Cerastoderma	0.01	0.90
Corophium	1.36	0.25
Eteone	1.74	0.19
Mytilus	2.41	0.13

b)

Species	**Difference between winters**		**Difference between sites**	
	F $_{1,22}$	***P***	**F $_{1,45}$**	***P***
Hydrobia	6.84	***0.01***	0.66	0.52
Nereis	1.45	0.23	0.06	0.94
Oligochaetes	28.15	***<0.001***	0.04	0.95
Manayunkia	1.46	0.23	0.09	0.91
Spionids	18.21	***<0.001***	0.77	0.47
Nephtys	0.50	0.48	1.41	0.25
Macoma	0.52	0.47	0.27	0.76
Cerastoderma	0.06	0.80	2.52	0.09
Corophium	0.83	0.36	0.30	0.74
Eteone	0.79	0.38	4.69	***0.01***

At Kinneil, only Oligochaetes and Spionids showed significant changes in the mean number of invertebrates sampled (n=60) between winters. This signifies that in general there had been no major changes in species abundance in the short term at Kinneil. Although Oligochaetes were the most stable population in the long term it is clear that they are subject to short-term changes in abundance, in this case declining significantly. Spionids are the most highly variable species in the long term with a considerable increase in abundance in recent years, here it is evident that there is a significant increase in number between winters. *Eteone* was the only species to have significantly different numbers between sites with the greatest number at Torry Bay.

These findings were reflected at the Forth Estuary scale with both Oligochaetes and Spionids following the same trends as they did at Kinneil. There was also a significant increase in Hydrobia numbers between winters

4.4.2 The long term

4.4.2.1 Comparison of contemporary invertebrate densities on the Forth Estuary at Skinflats and Kinneil with data from with previous studies

Bryant & McLusky (1997) present data from these two study sites collected over comparable periods of time and Table 4.5 shows that for almost all the species with the exception of *Corophium*, densities were higher at Kinneil. Data collected in this study is mixed in its agreement with these data but only represent the findings of a single winter. Presently, Kinneil also has higher densities of *Hydrobia, Mytilus, Nephtys, Oligochaetes* and Spionids but now has lower densities of *Macoma, Nereis* and *Manayunkia. Corophium* numbers remained highest at Skinflats but *Cerastoderma* were not found at all here during the winter of 1999/2000. These results may however be confounded by the fact that the Bryant & McLusky (1997) data were collected between July and September as it has already been illustrated that invertebrate numbers can vary dramatically between summer and winter.

Table 4.5: Densities of invertebrates (m^{-2}) at both Kinneil and Skinflats. The Kinneil data is the mean of data collected annually between 1976 and 1994 (n = 100 per annum) and the Skinflats data is the mean of data collected between 1975 and 1992 (n = 18-31 per annum). Samples were collected between July and September. The highest figure for each species is emboldened and italicised. (After Bryant & McLusky 1997).

	Kinneil		**Skinflats**	
Species	**Mean**	**SD**	**Mean**	**SD**
Hydrobia	***6052***	3303	2377	1272
Macoma	***340***	180	303	202
Cerastoderma	***141***	151	39	86
Mytilus	***20***	46	0	-
Nereis	***611***	275	131	71
Nephtys	***262***	372	22	13
Eteone	***257***	234	20	24
Manayunkia	***36461***	29503	19	54
Oligochaetes	***26046***	9516	455	371
Spionids	***1466***	1780	0	-
Corophium	842	924	***891***	562

Data collected by Warnes (1981) during December and January 1977 is more directly comparable to the data gathered in this study during January 2000 (Table 4.6). Although the number of samples collected by Warnes (1981) was fairly low they were distributed widely and processed in a similar way. Numbers per m^2 of *Nereis, Manayunkia,* Spionids and *Corophium* are broadly similar despite the inevitable annual fluctuations in population size.

Table 4.6: A comparison of mean number of individual per m^2 collected at Skinflats by Warnes (1981) during December 1977 for *Macoma* and *Cerastoderma* and January 1977 for *Nereis* to *Corophium* (n=10) and counts undertaken in this study during January 2000 (n = 100)

	Mean number of individuals per m^2	
Invertebrate species	**Warnes (1981)**	**This study**
Macoma	239	1143 ± 1245
Cerastoderma	10	Not found
Nereis	233 ± 147	352.9 ± 574
Manayunkia	14080 ± 16530	16197 ± 353.65
Spionids	1040 ± 1070	5849 ± 8876
Oligochaetes	24440 ± 11236	1567 ± 2856
Corophium	100 ± 660	287 ± 889
Hydrobia	No data	569 ± 784
Nephtys	No data	23.52 ± 94.67
Eteone	No data	9.41 ± 60.99

4.4.2.2 Long term distribution of invertebrates at Kinneil

The biodiversity of a site and hence it's attractiveness to shorebirds as a potential source of food is strongly influenced by habitat stability as the physical hydrodynamics of an estuary controls the substratum type (Snelgrove & Butman 1994). If the substratum is complex then this is likely to increase the number of available niches and hence the diversity of the community. A long term study of invertebrates at Kinneil (McLusky 1982, Bagheri & McLusky 1982, McLusky 1987, McLusky & Martins 1998, McLusky *et al.* 2000) has collected annual data on invertebrate abundance at this site from 90 fixed sampling stations over a 25 year period from 1976 to 2000 (Table 4.7). Sample points were spread widely across the mudflat at all tidal heights and present a representative picture of the distribution of the infauna (Fig 4.32). All data were collected during July of each year, so it is not directly indicative of the food supply available to overwintering shorebirds over the long term. It is however, more than adequate to determine the stability of the invertebrate populations which form the potential winter food supply (for a comparison of July and January figures see Table 4.3).

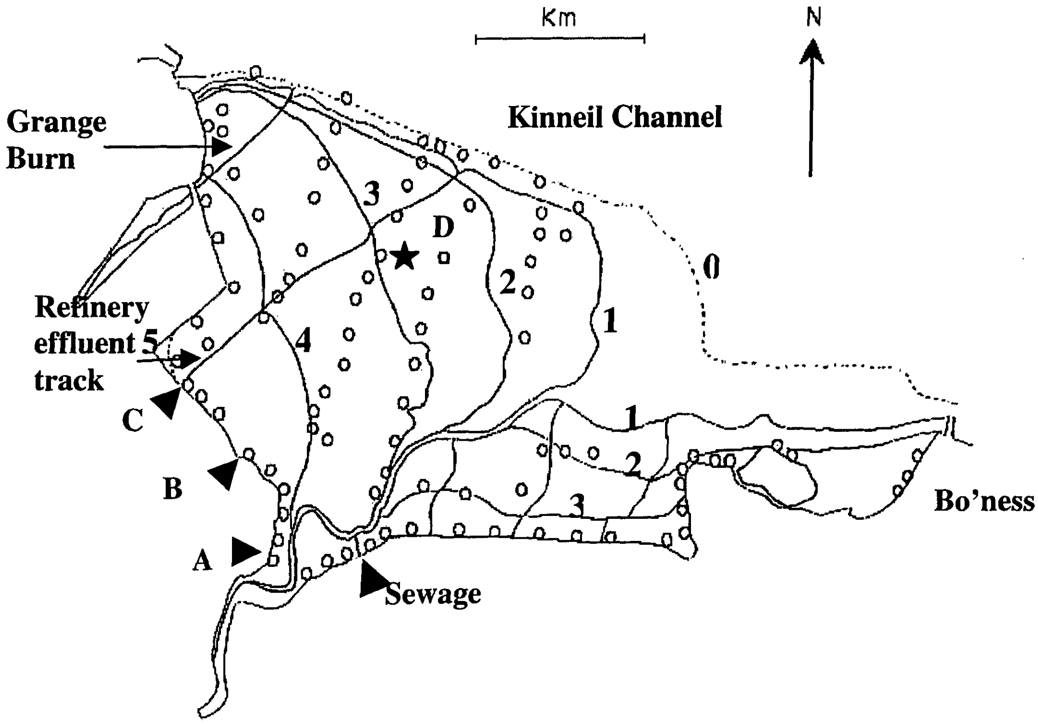


Fig 4.32: The open circles represent the sampling stations used by McLusky *et al.* in their long term study of invertebrates at Kinneil. Tidal contours are superimposed onto the mudflat area with each figure referring to the tide height (MACD). The black arrows indicate major discharges of effluent. A:Chemicals outfall until 1979, B:Chemicals outfall 1979-1999, C:Refinery + Ballast water outfall, D: Offshore chemicals outfall from 1999 (after Davis 2001)

The long-term data suggests that an increase in the diversity, evenness and richness of all invertebrate species over the whole of the Kinneil intertidal was found between 1976 and 1999 (Davis 2001).

Table 4.7: These data characterise the long-term abundance of invertebrates at 90 fixed sampling points at Kinneil over 25 years: 1976 –2000. Data was collected annually during August (McLusky *et al* 2000).

Species	Mean	Standard deviation	Coefficient of variation
Hydrobia	4818.17	3191.72	66.24
Nereis	606.86	327.35	53.94
Oligochaetes	24038.16	11248.79	46.80
Manayunkia	25210.75	23842.55	94.57
Spionids	3967.19	4149.71	104.60
Nephtys	346.07	340.30	98.33
Corophium	1212.70	854.32	70.45
Eteone	433.66	298.83	68.91
Macoma	2563.16	1935.00	75.49
Cerastoderma	185.91	139.59	75.09

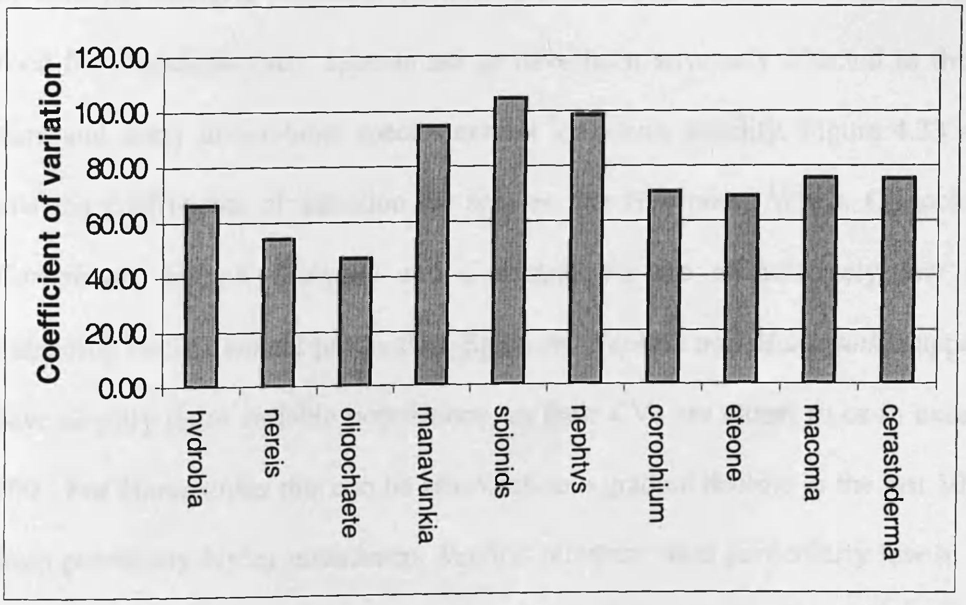


Fig 4.33: The coefficient of variation (see Table 4.7) for several invertebrate species at Kinneil indicating the relative stability of their populations over 25 years.

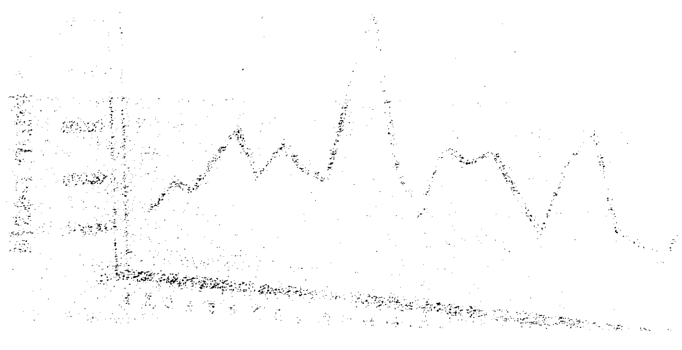
4.4.3 Discussion: variability of invertebrate population sizes and distribution

If positive or negative associations between shorebirds and invertebrate densities found in the models (Chapter 3) are assumed to be the same in future studies then it must also be assumed that where there is spatial variation in invertebrate populations, such variation is mirrored by the shorebird population. Although spatial variability is evident at Kinneil (Davis 2001) there was an increase in the diversity, evenness and species richness at this site. This has been attributed to the improved quality of the chemical and refinery effluents discharged onto the site from the Grangemouth petrochemical works effluent. BP Oil completed an effluent treatment system in 1994 and re-positioned an effluent outfall (operational in January 1999) that expelled effluent into the water column at high tide and not directly onto the mudflat. The arrival of two new species at the site, *Manayunkia aesturina* in 1979 and *Streblospii shrubsolii* in 1994 coincided with the movements of existing chemical discharge outfalls (Davis 2001). The general availability of food for shorebirds then, appears not to have been adversely affected in the long term and many invertebrate species exhibit long-term stability. Figure 4.33 shows that the coefficients of variation for species like *Hydrobia, Nereis,* Oligochaetes, *Corophium, Eteone, Macoma* and *Cerastoderma* are all relatively low (<80) indicating similar annual production. Spionids, *Nephtys* and *Manayunkia* appear to have slightly more variable populations, as their CVs are closer to or in excess of 100. For *Manayunkia* this can be attributed to a gradual decline in the last 10years from previously higher abundance. *Nephtys* numbers were particularly low in 1982 and 1983 and have seen periods where the mean abundance has been below 100 per m^2. Spionids have exhibited a marked increase in recent years after fairly low abundances between 1976 and 1991. For long term trends in invertebrate numbers at Kinneil see Fig 4.34.

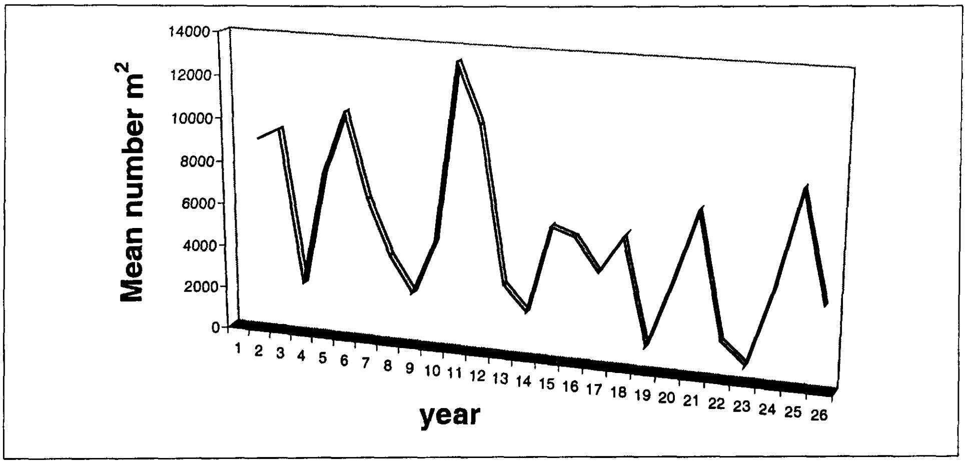
In conclusion it can be seen that invertebrate numbers on the Forth Estuary as on other estuaries are changeable at a range of temporal scales in terms of their abundance and spatial distribution. Invertebrate numbers at Kinneil have been partitioned into three phases of change during the period 1976-2000 by McLusky *et al.* (2000)

1. A period of chronic pollution, with diminished fauna from 1976-1984.
2. A period of steady recovery from 1985-1994.
3. Stable and generally consistent conditions from 1995 to the present day.

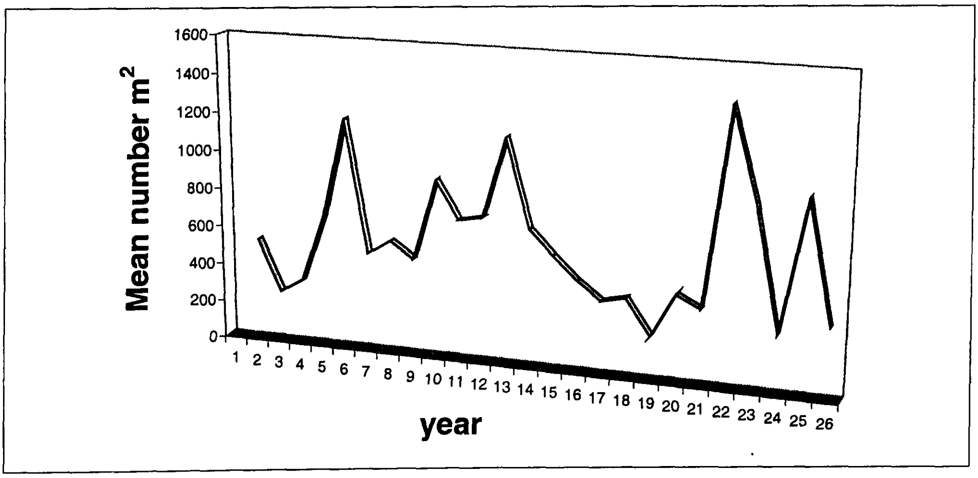
As intertidal areas are relatively stable anyway, any fluctuation in community numbers or distribution is likely to be only temporary (Elliot *et al.* 1998). It therefore seems reasonable to assume that the relationships determined in the GLMs are likely to be valid, at least in the short term.



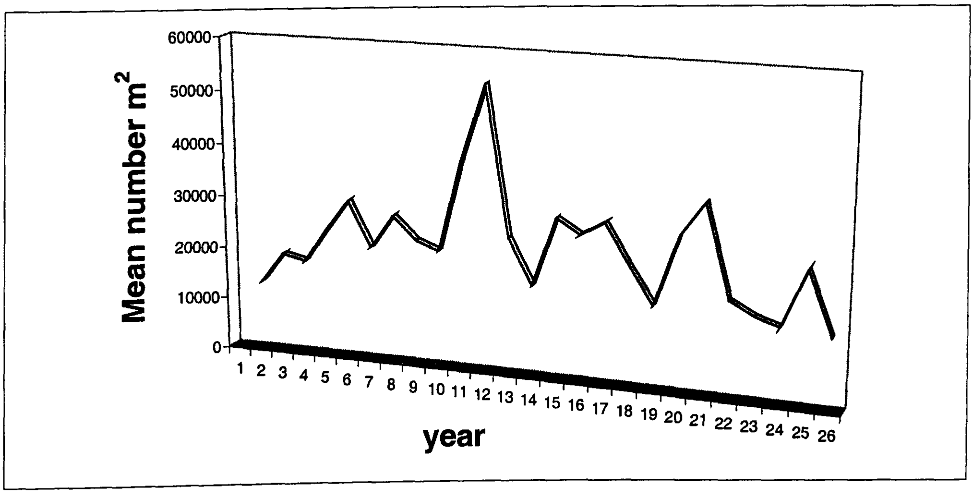
a) *Hydrobia*



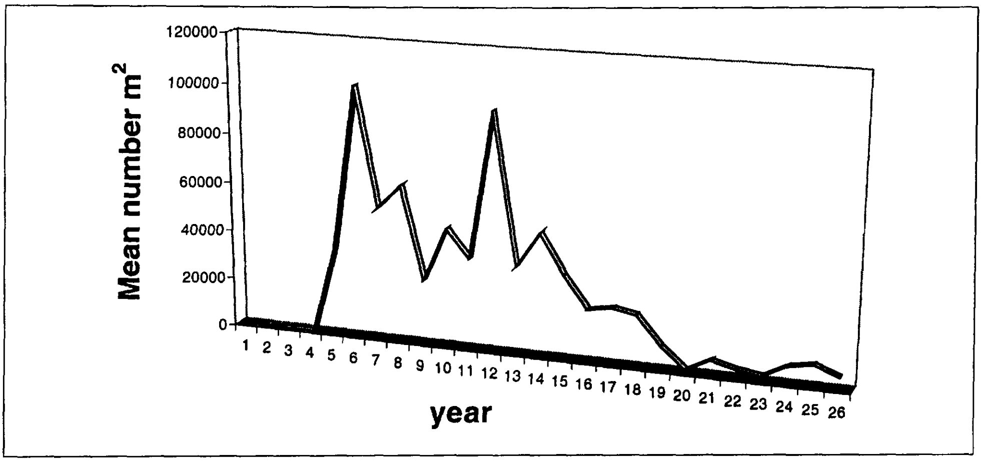
b) *Nereis*



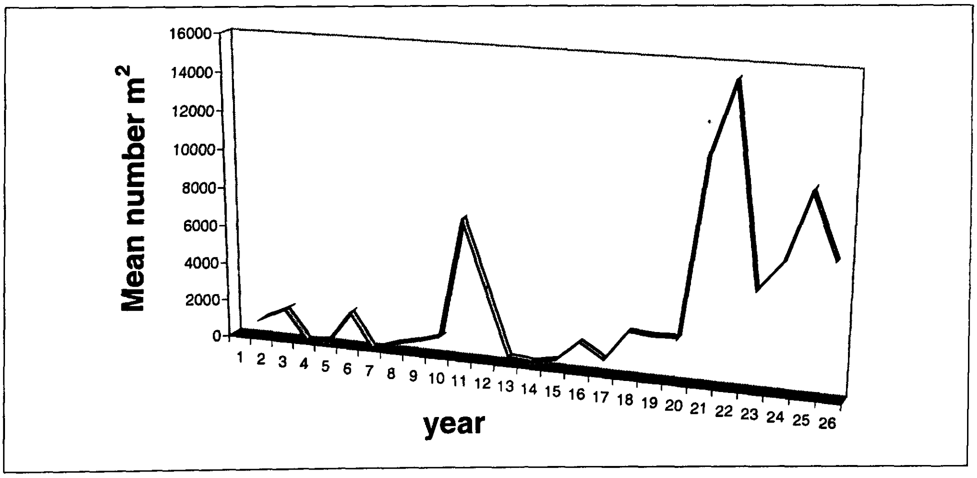
c) Oligochaetes



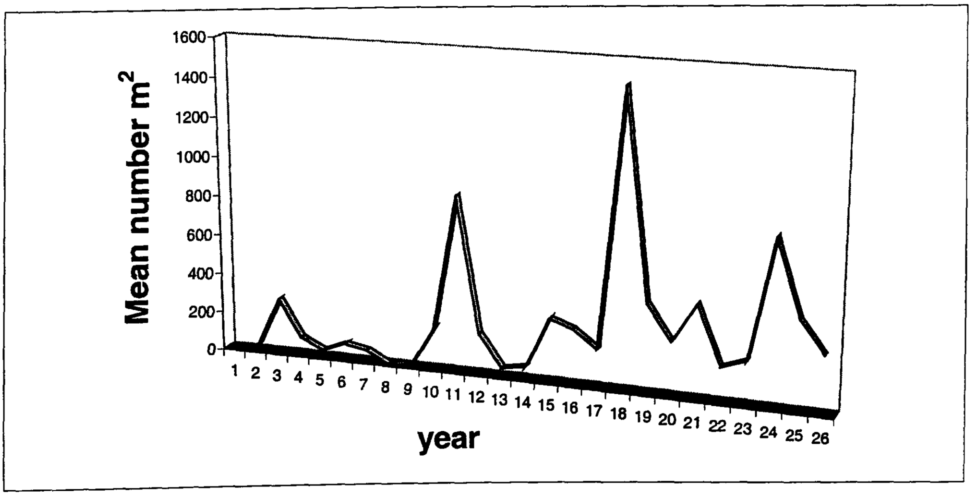
d) *Manayunkia*



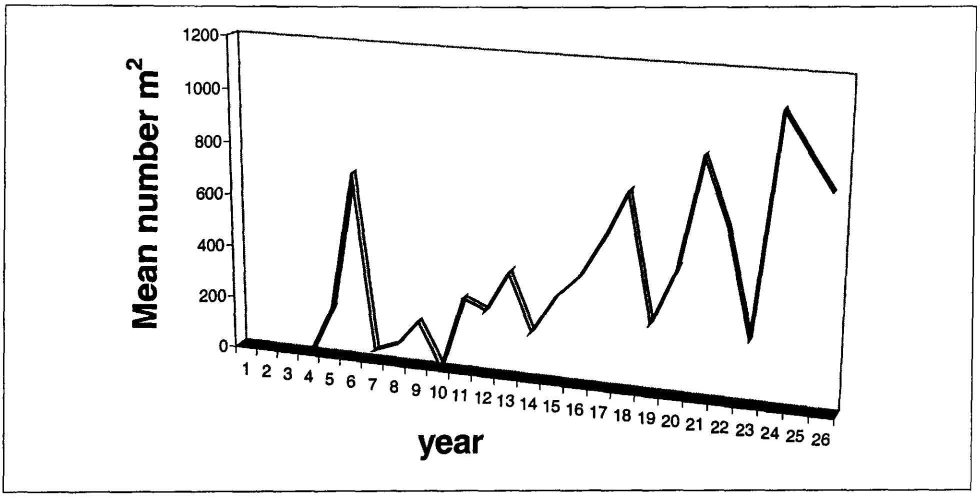
e) Spionids



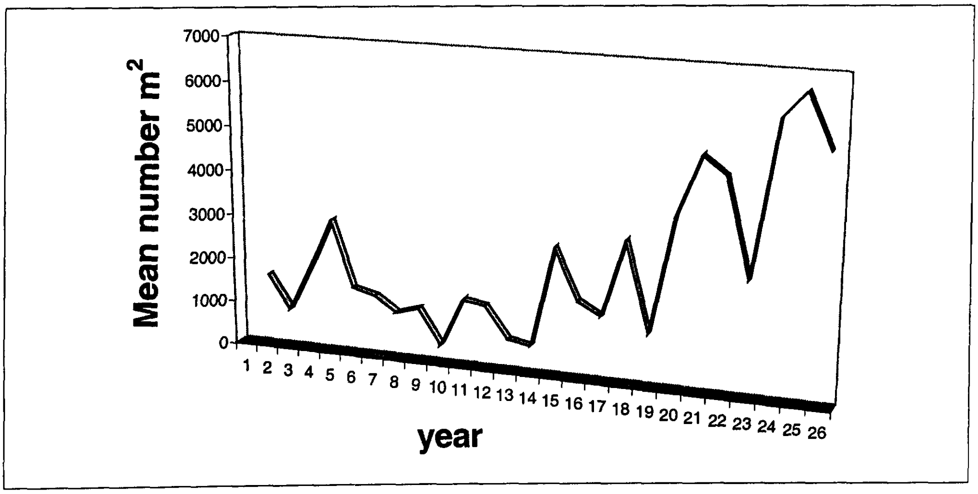
f) *Nephtys*



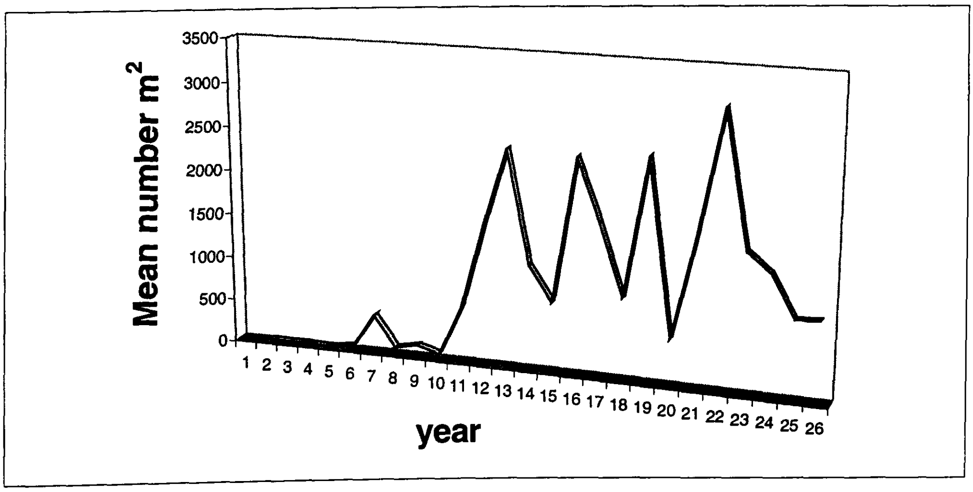
g) *Corophium*



h) *Eteone*



i) *Macoma*



j) *Cerastoderma*

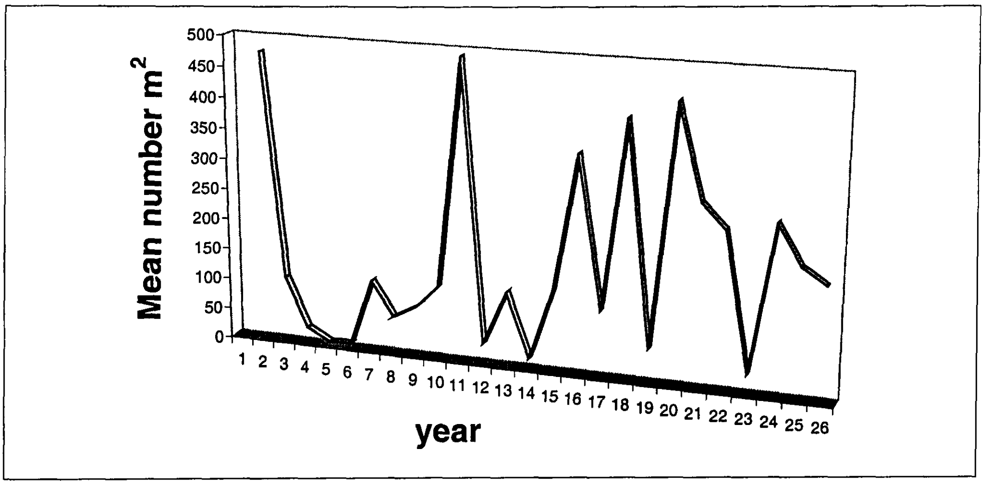


Fig 4.34: Long term trends in the mean number m^2 (n=90) of a) *Hydrobia*, b) *Nereis*, c) Oligochaetes, d) *Manayunkia*, e) Spionids, f) *Nephtys*, g) *Corophium*, h) *Eteone*, i) *Macoma*, j) *Cerastoderma*, sampled annually in July between 1976 and 2000 (McLusky *et al.* 2000)

Section C: Sediment

4.5 Long term stability of sediment structure

Sediment characteristics were important predictors of the feeding effort of some shorebird species both at the whole estuary and single site scales. Is it possible to assume that conditions are stable enough for such relationships to be valid in future seasons? Although no long-term data exists for sediment structure on the Forth Estuary it is assumed to be relatively stable (McLusky pers com). Evidence for this however is only anecdotal, based on site visits and the persistence of certain mudflat features (i.e. sandy and rocky areas) for extended periods of time. Warnes (1981) concluded that sediments at Skinflats were stable as they are generally fine deposits with small interstitial spaces and with a water content below the threshold of 70% (Green 1975), beyond which deposits become fluid enough to facilitate transportation. Although this general stability is likely to be affected by storm events, dredging and the overall shape of the estuary Raffaelli *et al.* (1999) concluded that a similar stability exists over time at the Ythan Estuary in Aberdeenshire. They compared contemporary sediment samples data taken in 1995 to data collected in the 1960s and concluded that 'the general pattern of sediment distribution in the Ythan has not changed greatly (if at all) over the last 30 years'. Their classification bands for mud, sand etc. were broad however and do not approach the small-scale accuracy of sediment analysis in this study. In the absence of any long term sediment data for the Forth Estuary there follows a general discussion on sediment stability.

4.5.1 The hydrophysical regime

The hydro physical regime can be very variable within an estuary and can have major affects on sediment structure and invertebrate abundance. Low energy areas such as Skinflats and Kinneil and the predominance there of silty mud (>2 and <

50μ) favours the establishment of mostly sessile polychaetes and bivalves, however many species are capable of surviving in a range of sediment types (Snelgrove & Butman 1994). Therefore it does not always follow that sediment structure is likely to be a good predictor of invertebrate fauna and hence shorebird distribution. Torry Bay is exposed to the prevailing SW winds and has a higher proportion of sandy sediments (50 - 2000μ) generally (this study). Storms and strong winds can have episodic effects on the invertebrate fauna at this site (Berry 1994) and can be the most important factor determining short term (<10yr) redistribution of sediments (Morton *et al.* 1995). The level of exposure probably also has an effect on the numbers of birds prepared to expose themselves to wind chill for extended periods of time. Wind chill can be especially problematic for redshank (Mitchell *et al.* 2000). With a following wind the tide comes in considerably faster at Torry Bay, inundating the mud up to one-hour earlier than on days with similar tides but low wind speed (pers obs). Such conditions decrease the amount of time available for shorebirds to feed.

The topography of the shore is important as flatter shores dissipate wave energy creating a more stable environment and consequently a more stable fauna (Elliot *et al.* 1998). All the mudflats on the Forth Estuary are relatively flat creating a low energy environment that does attract large numbers of shorebirds. However as previously mentioned Torry Bay lacks shelter for shorebirds and it is evident from the observations at this site that the favoured areas are those which are most sheltered from the wind e.g. the mouth of the Bluther Burn. There, large numbers of redshank and shelduck congregate through the tide feeding almost continuously. Storm events on the Forth may have contributed to shorebird redistribution in the past but if so they have gone unrecorded. Ferns (1983) found that gales and the high tidal range on the Severn Estuary removed large areas of surface mud prompting shorebirds to relocate to more sheltered areas.

4.5.2 Effect of invertebrates and birds on sediment cohesiveness

Sediment erodability varies spatially and temporally and is dependent on the interactions between physical processes, sediment properties and biological processes (Widdows & Brinsley 2002). Bio-stabilisers such as macroalgae (Sutherland *et al.* 1998 and Brouwer *et al.* 2000) and *Mytilus* (Wildish & Miyares 1990, Ragnarsson & Raffaelli 1999) can influence the hydrodynamics and provide some physical protection to the mud. In contrast, bio-destabilisers such as *Macoma* (Willows *et al.* 1998, Widdows *et al.* 2000 and Wood & Widdows 2002) and *Hydrobia* (Blanchard *et al.* 1997, Austen *et al.* 1999 and Andersen 2001) increase surface roughness, reduce the critical erosion threshold and enhance the erosion rate.

Austen *et al.* (1999) found that intertidal sites in the Danish Wadden Sea with higher numbers of *Hydrobia* eroded more quickly over the long term especially during warmer spells due to the grazing activity of these snails on the benthic micro algae. They also noted that the presence of *Hydrobia* faecal pellets in the sediment lowered the surface cohesion of the sediment. In a study of sediment erodability on the Humber, Widdows *et al.* (2000) found that although there was no evidence of a consistent seasonal cycle, long-term changes in sediment erodability correlated with the density of *Macoma.* These temporal changes in sediment erodability and biota were also apparent over a wider geographical scale and they concluded that parallel changes in benthic community structure and sediment erosion may be climate driven, probably via long-term biological cycles in 'stabilisers' and 'destabilisers'

Birds may also have a 'cascade effect' on sediment cohesiveness. In a comprehensive study of factors controlling the erodability of fine-grained intertidal sediments Daborn *et al.* (1993) found that sediment strength increased with the arrival of large numbers of migratory shorebirds. Before the birds came, sediment cohesion resulted in part from secretion of polysaccharides by benthic diatoms whose production was controlled mainly by a grazing amphipod, *Corophium volutator*. When the birds arrived, *Corophium* behaviour and abundance changed, bioturbation and grazing pressure on the diatoms decreased, and production of cohesion-inducing carbohydrates rose.

4.5.3 Conclusion: sediment stability

Some sediment characteristics have already been shown to predict bird feeding effort at the whole estuary (shelduck: % sand, redshank: % silt, % organic matter, median particle size and dunlin: % silt % sand, % organic matter) and sub estuary scale (Kinneil shelduck: % silt and Skinflats dunlin: % organic matter). Sherwood & Creager (1990) concluded that in any study attempting to quantify the relative stability of mudflats in the long term, variations in river flow, sediment supply, and tidal flow occurring over a range of time scales, make the study of modern processes, as they relate to long-term effects, particularly challenging. Whether the potential for long term changes in sediment character throughout the Forth Estuary may affect shorebird distribution in the future remains a question for future research but the validity of model output in the long term is unlikely to be affected by small scale changes in sediment character. Such changes are quite possibly one reason for the observed differences in the spatial distribution of some shorebird species during the last 25 years.

Chapter 5: Does shorebird predation significantly reduce invertebrate numbers during the winter months and can a depletion effect be measured ?

5.1 General Introduction

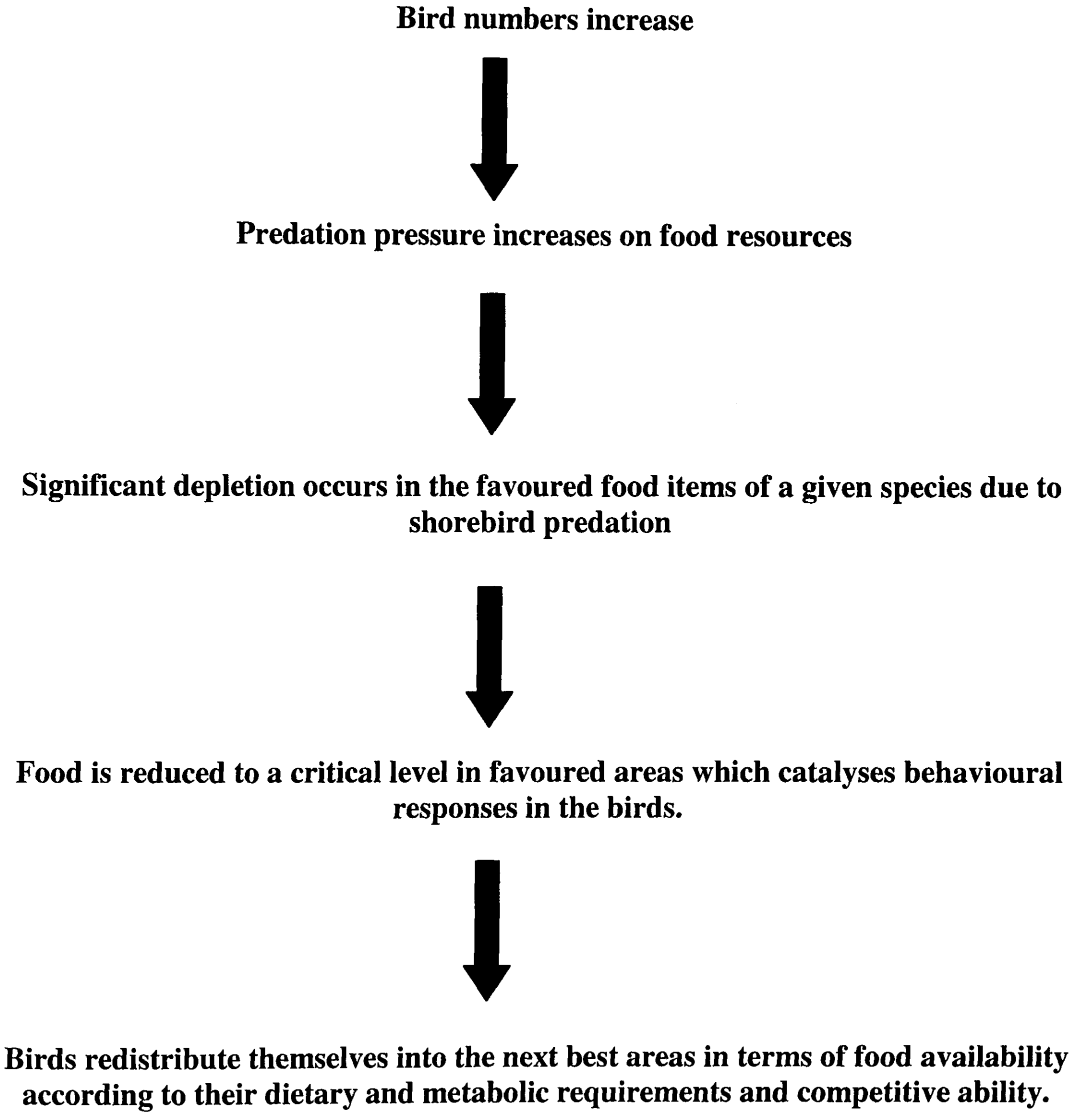
Depletion of food supply by overwintering shorebirds has often been cited as an important factor in determining their spatial distribution and intake rates (Goss Custard *et al.* 1995a, Sutherland 1996, Percival *et al.* 1996, Gill *et al.* 2001). This chapter considers whether it is possible to measure such an effect on the Forth Estuary and whether such an effect, if it exists, would have a bearing on the use of weighted area models described in chapter 3 in identifying priority sites for shorebirds. The more fundamental questions being addressed by this experiment are whether food levels on estuaries, may, in practice be reduced by shorebird predation to a level which may have consequences for food intake and foraging costs of shorebirds and whether as a result, there are population level responses to such reductions. If these occur, then there is a greater likelihood that food depletion or removal by anthropogenic means (i.e. landclaim/pollution) will lead to reductions in shorebird populations, at least locally.

Waders can have a considerable impact on the standing crop of their invertebrate prey over the winter period on estuarine mudflats (Table 5.1). In general, the majority of studies have found that 25-45% of prey is removed in one winter (Goss Custard 1984 in Szekely & Bamberger 1992). Consumption rates are, however, likely to vary both latitudinally (Wolff 1991) and within estuarine complexes (Scheiffarth & Nehls 1997), so any depletion detected on the Forth is likely to be site specific. Scheiffarth & Nehls (1997) found that the size and position of the intertidal area had a high impact on the consumption of invertebrates by birds, with depletion in a sub-area area of 4.32 km^2 being 50% higher than in the total intertidal area of 132km^2. To fully understand whether or not food resources limit bird numbers, detailed investigations need to be conducted as fluctuations in food resources affect different species of shorebird with potentially differing levels of sensitivity (Beukema *et al.* 1993).

Table 5.1: The impact of shorebirds on the standing crop of their invertebrate prey during the winter months

Author	**Bird species**	**Prey species**	**% standing crop removed**
Goss- Custard (1969)	Redshank	*Corophium volutator*	16-38
Goss-Custard (1977)	Bar tailed godwit Oystercatcher	*Arenicola marina* *Cerastoderma edule*	25 14
Warnes (1981)	Redshank Dunlin Knot Shelduck Curlew	Total invertebrate biomass	5.1 5.33 5.61 6.67 0.79
Scheiffarth & Nehls (1997)	Shorebirds	Total invertebrate biomass	15-25
Moreira (1997)	Shorebirds	Total invertebrate biomass	45

The significance of proportionate reductions in the standing crop is not clear; on one hand competition may increase, or on the other, prey may remain sufficiently abundant at the end of the winter that no increase in competition occurs. However, prey depletion by shorebirds may lead to their redistribution to areas with progressively lower abundance of food until bird density is proportional to prey density in all areas. Weber & Haig (1997) compared coefficients of variation (CVs) of prey and shorebird densities at the beginning and end of their experiment to determine whether there were positive correlations between shorebird and prey densities. They hypothesised that these CVs should decrease as relative densities of predators and prey approached equilibrium. Although they measured prey depletion in response to shorebird pressure they found no evidence of shorebird redistribution when prey were reduced, suggesting that at their study site food was not a limiting factor. Meltofte (1996) also argues that food is not a limiting factor for shorebirds on African Estuaries. Schekkerman *et al.* (1994) suggests that food is only limiting some of the time. Figure 5.1 illustrates the sequence of events leading to the redistribution of shorebirds where their food supply is depleted.



Bird numbers increase

Predation pressure increases on food resources

Significant depletion occurs in the favoured food items of a given species due to shorebird predation

Food is reduced to a critical level in favoured areas which catalyses behavioural responses in the birds.

Birds redistribute themselves into the next best areas in terms of food availability according to their dietary and metabolic requirements and competitive ability.

Fig 5.1 : Schematic sequence of events if food abundance is a factor which determines bird distribution on the Forth Estuary.

If a redistribution feedback loop is not observed i.e. birds do not respond to prey depletion by redistributing themselves spatially, it does not necessarily mean that food supplies are sufficient. It may just indicate a lack of ability to adapt to new circumstances in a particular species e.g. they avoid prey switching. Birds may well choose to stay in a low quality area if the energetic costs of moving to a new area are not worth the risk due to the threat of predation or territory loss for instance, even if it is within the same estuarine complex. In the past, exclosure experiments have been used when trying to determine whether there is a prey depletion effect due to shorebird predation. The mixed success of these experiments is primarily due to differing experimental designs. The duration of the experiment, the season, spatial layout, size and number of treatments and statistical analyses vary from study to study. There are also differences in invertebrate sampling strategies, sample core sizes, and mesh sizes through which the samples are sieved (see Schlacher & Woolridge (1996)). Assumptions about feeding behaviour of the birds can also vary. Szekely & Bamberger (1992) assume that intake rates are the same at night as during the day.

Some studies have shown statistical differences between treatments and controls before and after the experimental period (Schneider & Harrington 1981) but equally this is often significant for just a few species of invertebrates in a study area (Kent & Day 1983, Quammen 1981, 1984, Szekely & Bamberger 1992, Mercier & McNeil 1994, Weber & Haig 1997) or only at some sites and not at others (Quammen 1981, Botto *et al.* 1998). Other studies (Table 5.2) have shown little or no effect of shorebird predation on invertebrate depletion (Duffy *et al.* 1981, Raffaelli & Milne 1987, Kalejta 1993, Wilson 1994, Sewell 1996).

Authors	Treatments retain invertebrates	Fish excluded	Treatment size	Sample core size	Sieve size	Season	Experiment length	Cage effect	Invertebrate depletion effect
Quammen (1981)	No	Yes	1m x 1m	10 x 10 x 8cm	500µm	All Year	23 months	No	Yes
Schneider & Harrington (1981)	No	No	1m x 1m	10 x 10 x 10cm	1000µm	Summer to Autumn	3 months	N/A	Yes
Duffy *et al.* (1981)	No	No	1m x 1m	10 x 10 x 10cm	1000µm	Winter	25 days	N/A	No
Kent & Day (1983)	Yes	Yes	1.5m x 1.5m	8.5 x 8.5 x 10 cm	500µm	Spring to Autumn	6 months	No	Yes
Quammen (1984)	Yes	Yes	1m x 1m	10 x 10 x 8 cm	500µm	All Year	23 months	No	Yes/No
Raffaelli & Milne (1987)	No	Yes	2m x 2m	1.5 x1.5 x 5 cm	N/A	All Year	11 months and 5 months	No	No
Szekely & Bamburger (1992)	No	No	2m x 1m	10 x 10 x 12 cm	250µm	Summer	11 days	N/A	Yes
Wilson (1994)	No	No	0.8 x 0.6 m	10 x 10 x 10 cm	500µm	Spring	2 months	No	No
Sewell (1996)	No	Yes	0.8 x 0.6 m	10 x 10 x 10 cm	500µm	Spring	1 month	No	No
Weber & Haig (1997)	No	No	1.2m x 1.2m	5 x 5x 10 cm	500µm	Spring	2 months	N/A	Yes
Botto *et al.* (1998)	No	No	1m x 1m	20 x 20 x 15cm	500µm	Winter to Spring	38 – 60 days	No	Yes/No
Sutherland *et al.* (2000)	Yes	No	0.35 x 0.5 x 0.3 m	21.2 cm^3	1000µm500µm 63µm	Spring	22.5 minutes	No	Yes

Table 5.2: Results and methodology from previous exclosure experiment studies indicating the variety of different approaches and findings

One of the main problems with these studies is the failure to account for the immigration and emigration of the benthic infauna from the treatments, thus negating or confounding the detection of any potential depletion effects (Goss Custard 1977, Raffaelli & Milne 1987). If the population of invertebrates cannot be contained in the exclosures then they are of little use when measuring depletion of invertebrates. Some species are more mobile than others, although more sedentary polychaetes and oligochaetes may be less likely to move out of the exclosures. Kent & Day (1983) attempted to control invertebrate movements by using sub-surface boards on their exclosure cages but they were only studying one species of Nereid polychaete *Ceratonereis pseudoerythraeensis* so this device was sufficient. They found that 10cm deep boards retained a stocked population of this species for 6 months. Other taxa such as amphipods and molluscs would be able to crawl over such obstacles. Moreover *Hydrobia* can be transported around the mudflat due to tidal movement by floating and rolling and they are also very active crawlers. Also *Corophium* may move up into the water column (Raffaelli & Milne 1987).

In response to these problems of experimental design two exclosure experiments were carried out over two winters. Experiment 1, during winter 1998-1999 and Experiment 2 during winter 1999-2000 with a view to comparing different designs and to assess the validity of past approaches to measuring invertebrate depletion.

The models constructed in chapter 3 have shown that invertebrate densities are important predictors of shorebird distribution at the whole and sub estuary scale, therefore the aims of both experiments were to determine whether predators (shorebirds and fish/shrimps) depleted invertebrate numbers at Skinflats to a point where they become potentially limiting to shorebirds in terms of the numbers of birds the site can support in a given winter. If an effect was measurable at Skinflats it might be concluded that this bird density: invertebrate density ratio would also be relevant to other sites on the Forth Estuary where densities of feeding birds per unit area are roughly the same e.g. Torry Bay or higher as at Kinneil.

The aims of Experiment 1 were threefold:

1. To determine whether predators depleted invertebrate numbers during the winter period.
2. To ascertain whether birds or fish have the greatest effect, if a depletion effect exists.
3. To determine whether any effect varies with distance from mean high water springs (MHWS) i.e. is any effect greater with increased or decreased exposure time.

Point 3 has particular relevance in relation to species, which prefer high level mudflats for feeding. Cage effects on sediment structure were also monitored, as were differences in the penetrability of the sediment in the designated study plots.

The aims of Experiment 2 were to improve on the design of Experiment 1 by increasing the power of the experiment to detect any effects. To achieve this, treatments were greatly reduced in size to lower the confounding effects of invertebrate density variation, and the number of replicates was expanded to increase the power of the statistical tests. Also study sites were chosen for their variability in both sediment characteristics and bird predation pressure. Again the aim was to attempt to measure any depletion of invertebrate density due to predation but this time the potential effects of fish were not examined. The locations of all study plots are given in Fig 5.1.

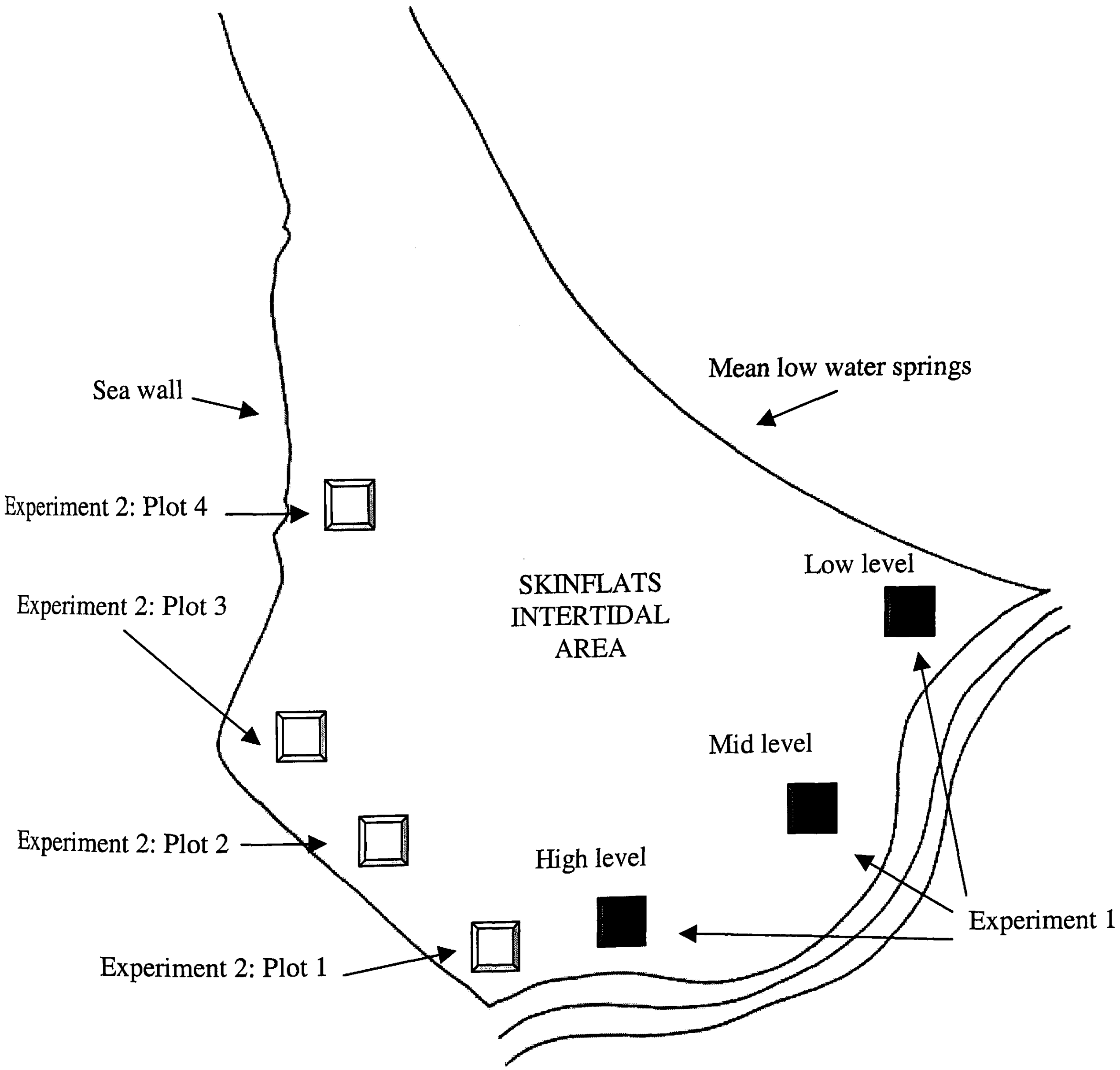


Fig 5.1 : Location of the study plots for experiment 1 and experiment 2 on the intertidal area at Skinflats

5.2 Experiment 1: 1998/99 exclosure study

5.2.1 Introduction

Skinflats inundates fairly rapidly (c1.5hrs) once the tidal level rises above the margin of the mudflat. The lower edge of the mud at Skinflats has a steep slope facing the tidal channel c3m in height, so much of the upper flat only begins to inundate during the late mid tide period although at the east end of the flat the tide comes in more gradually. Study plots were sited so that they differed in their exposure time. The plot closest to the mean high water mark was exposed the longest and hence was open to the greatest predation pressure from shorebirds; the plot closest to the mean low water mark with the least exposure time was most likely to have a greater predation pressure from fish species. The plot equidistant between the two was subject to predation from both fish and birds in varying measure depending on the tidal cycle.

5.2.2 Methods

This first experiment followed the much used method of utilising square wooden frame exclosure cages covered with galvanised wire netting with a mesh size of 10mm x 10mm (for sizes used in previous studies see Table 5.2).

The exclosure cages were set out at Skinflats within 1ha study plots at increments of 600m from MHWS with a view to ensuring that plots differed in their exposure time to predation from both fish and shorebirds (Table 5.3)

Table 5.3: Location of the study plots relative to the MHWS. The tide height is an indicator of exposure time and is given in metres above chart datum (MACD).

Plot	Distance from MHWS	Tide Height (MACD)
1 (High level)	600m	5.6
2 (Mid level)	1200m	4.3
3 (Low level)	1800m	3

Plots were accessed by walking out along a training wall adjacent to the Carron River and marked out with wooden posts. All plots were 100m away from the training wall. As Skinflats is largely a mid to high tide site, it was not possible to locate a study plot at an extreme low tide level but plots did differ in exposure time. All the plots were always covered by seawater at high tide regardless of whether they were neaps or springs. At each level 3 cages, 1m x 90cm in area, 10cm high and with 10cm subsurface boards were placed onto the mud approximately 20m apart (Figs 5.2 and 5.3).

Treatment cage 1 (TOTAL): This was designed to completely exclude both shorebirds and fish > 1cm in diameter and was totally enclosed with wire netting. The subsurface boards, although presumably not effective at preventing all invertebrate species from entering or leaving the treatments, were pushed into the mud to a depth of 10cm to minimise sub-surface movements. The boards were flush with the mud surface to help ensure that there was little potential for the retention of seawater within them and to reduce any turbulence effects that might cause scouring of the sediment inside the treatments. If a depletion effect was evident it would be expected that losses incurred within this treatment would only be due to natural mortality for those species deemed unlikely to emigrate or immigrate.

Treatment cage 2 (PARTIAL): This cage was only enclosed with a wire netting roof to exclude birds from feeding while allowing fish entry through the open sides. Sewell

(1996) suggests that exclosure cages with 15cm high roofs kept out western sandpipers. In this study the roof height was reduced to 10cm to help ensure that the similar sized species, dunlin, could not enter. Again subsurface boards were employed to retain invertebrates.

Treatment cage 3 (OPEN): This treatment was open to both fish and birds, lacking any netting. It still had the subsurface boards and was designed to measure the combined effect of the predators on the invertebrates contained within.

Control: Samples were taken randomly within the plots from the open mud. The point sample locations were marked with short bamboo canes to allow the 'after' sample to be taken at the same point. Invertebrate movements were not restricted in any way. The purpose of these samples was to determine whether any change in invertebrate numbers could be measured without the use of treatments.

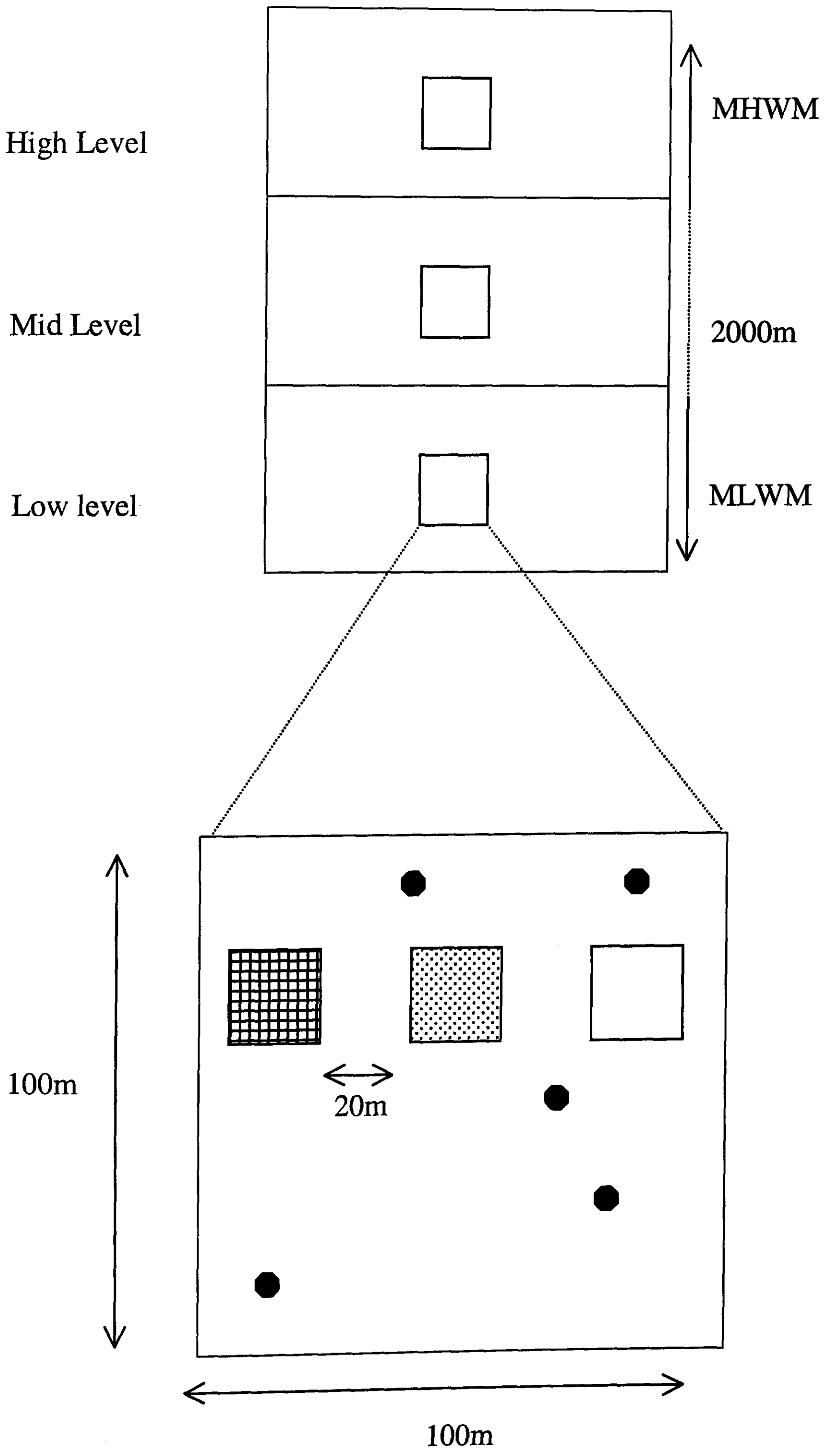
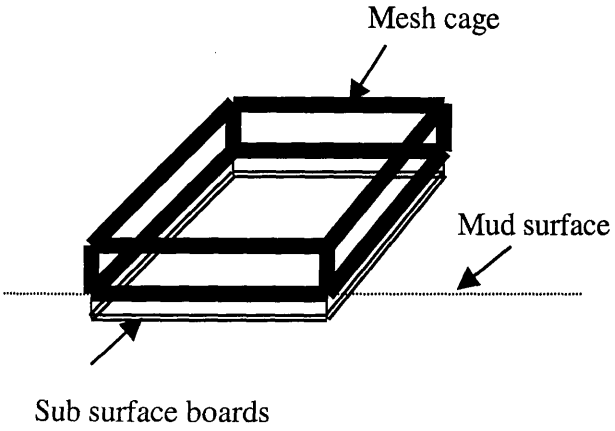
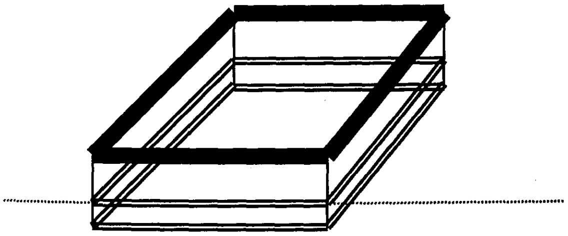


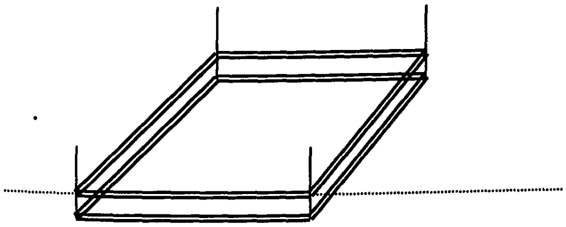
Fig 5.2: The spatial layout of the study plots at Skinflats for exclosure experiment 1. ⊞ = Totally enclosed cage excluding birds and fish. ⬚ = Partially enclosed cage excluding birds but allowing fish to feed. ☐ = Open, allowing birds and fish to feed but retaining sub-surface boards. ● = Control sample (random).



1. Total exclosure treatment with mesh roof and mesh walls to exclude feeding birds and most fish. It also has subsurface boards to retain invertebrates.



2. Partial exclosure treatment with a mesh roof to exclude feeding birds but allow fish and shrimps to feed. It also has subsurface boards.



3. Open treatment, allowing birds and fish to feed but with the sub surface boards to retain invertebrates

Fig 5.3: The three treatments used in the experiment. The bold lines indicate the extent of the mesh area and the double lines represent the subsurface boards.

5.2.2.1 Sampling: Invertebrates

Initial samples were taken at low tide in mid December 1998, at the time the cages were first laid out. At each treatment four 5cm x 5cm sample cores were taken, one at each corner, directly outside the caged area to determine the density of invertebrates at the beginning of the experiment (Fig 5.4). This sampling method assumes that the density and abundance of infauna are the same outside the cage as they are within and that sample variances are equal. In late January at the end of the study period (50 days) four more invertebrate samples were taken, this time within the cages directly opposite and within 20cm of the initial samples. The same invertebrate distribution assumptions were made. Five more samples were taken randomly within the study plots at the beginning and end of the experiment to determine whether any effects occurred without the use of the experimental treatments.

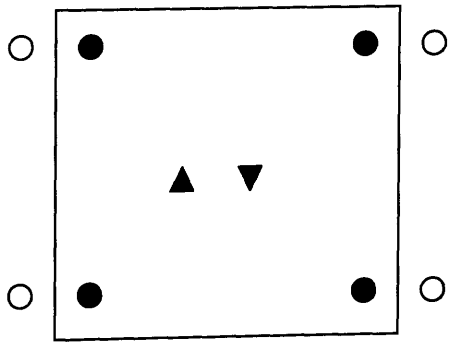


Fig 5.4 : Sample arrangement at each of the three treatments (total cover, partial cover and control). Invertebrate core sample = ○ (before) and ● (after). Sediment samples = ▲ (core, before/after), ▼ (surface, before/after).

5.2.2.2 Sampling: Sediment structure and cage effects

To assess whether the cage structure had any effects on sediment composition, one 5 x 5 x 5cm core was taken exactly in the centre of each cage. As it is more likely that the main effects would occur in the top 1cm, this being the most mobile layer at this site, a surface sample of 5 x 5 x 1cm was taken next to the core sample. The sediment samples were placed in polythene bags and returned to the laboratory where they were frozen at – 20°C prior to analysis. Particle size distributions were determined using a Coulter Counter (see methodology chapter). Sediment penetrability was measured on an arbitrary scale using a 1.5 m long steel rod, 0.75cm in diameter which was dropped down a 1m long plastic tube, 5cm in diameter placed on the mud surface. The rod was always dropped from the same height (1m) and the depth to which the rod penetrated the mud was measured in mm. This measurement was repeated at five random positions around the 1ha plot and the mean of the values used in the analysis. The mean penetration depth was taken to be representative of the penetrability of the mud at that site, with higher values indicating softer mud.

5.2.2.3 Bird observations

All birds seen feeding within the plots were counted at half hourly intervals through the tide. All plots could be observed at the same time. Eight visits were made during the winter of 1998/1999. Mean numbers of birds feeding per hour during the duration of the experiment were calculated to gauge the relative predation pressure on each plot.

5.2.2.4 Statistical analysis

All analyses were carried out using the generalised linear model function in S-Plus 2000. All response variables were log transformed and tested for normality. Where normality could not be achieved the error structure was determined and the relevant model used.

The minimum model in each case was determined by stepwise deletion of non-significant interactions and main effects and the residuals of the final model were tested for normality. Using a quasi-likelihood model (example for *Hydrobia*) the maximum model in each case was:

loghydrobia ~ plot + treatment + before/after + plot*treatment + plot*before/after + treatment*before/after + plot*treatment*before/after

5.2.3 Results

All the data were analysed on a per species basis to see if there was any measurable depletion effect which was potentially attributable to predators during the course of the experiment. For each species, the graphs show:

1. Changes within each treatment at each level relative to controls.
2. Changes for each treatment, across all levels combined relative to controls.

In each case: Plot 1 = high level, Plot 2 = mid level, Plot 3 = low level

Plot positions are given in **bold** and treatment types are given in CAPITALS throughout.

5.2.3.1 Hydrobia

No change occurred in any of the TOTAL exclosures (Figs 5.5 and 5.6). Significant changes were only evident at the **mid** level plot (Table 5.3) where there was a reduction of *Hydrobia* mostly in the PARTIAL exclosure, although there was some reduction in the OPEN treatment and CONTROL samples. The depletion in this plot alone accounts for the significance of the difference in invertebrate numbers at the end of the experiment.

Table 5.3: Results of a quasi likelihood model for loghydrobia.glm(loghydrobia ~ plot + treatment + before/after + plot * treatment + plot * before/after + treatment * before/after + plot * treatment * before/after)

Factor	Residual df	Residual deviance	F value	P value
Before/After	22	4.11	4.69	0.04

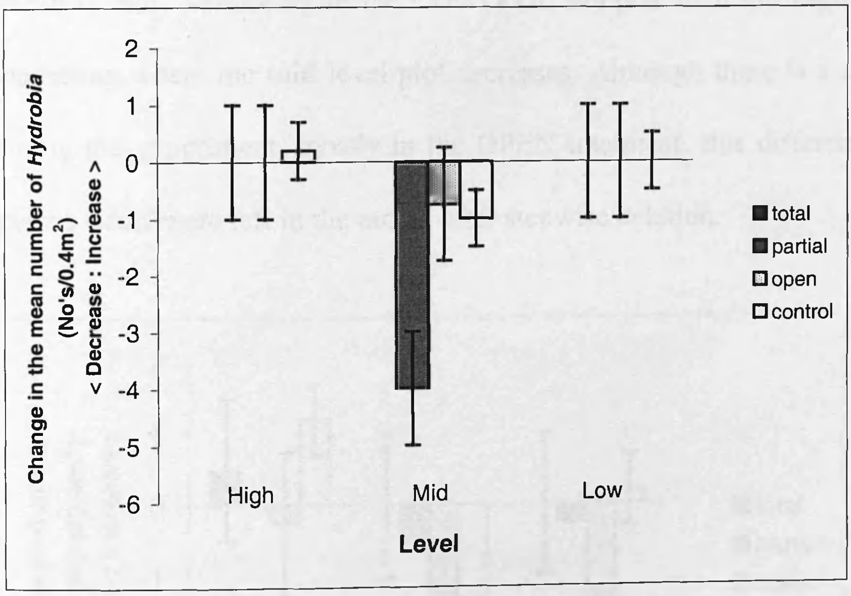


Fig 5.5: Change in the mean number of *Hydrobia* per treatment for each study plot

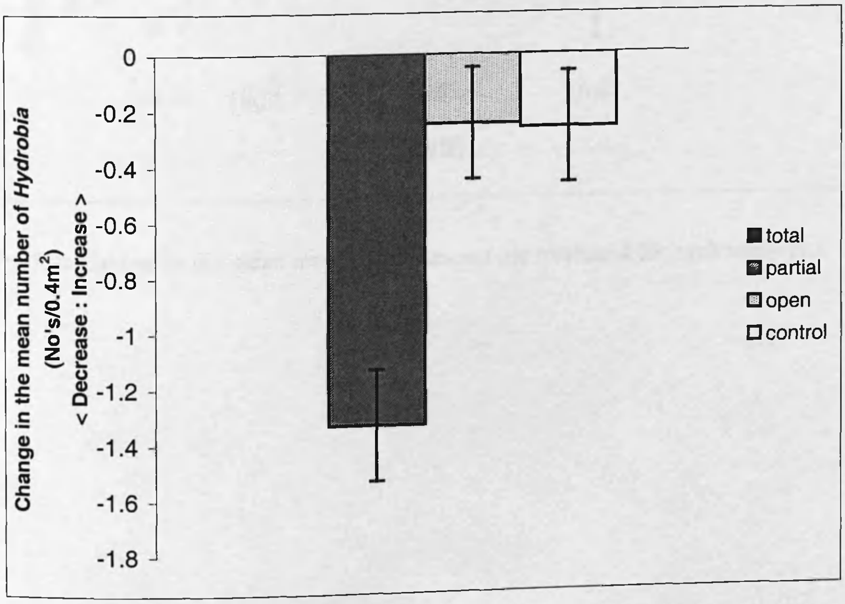


Fig 5.6: Mean overall change in *Hydrobia* numbers per treatment for all the plots.

5.2.3.2 Macoma

Numbers in the TOTAL exclosures remained virtually unchanged with only slight increases in the **high** level plot (Figs 5.7 and 5.8). The OPEN treatments show a decline in all the plots and the PARTIAL treatments have declines in the **mid** and **low** level plots. There is more variability in the CONTROL samples with the **high** and **low** level plots increasing where the **mid** level plot decreases. Although there is a reduction in *Macoma* during the experiment, mostly in the OPEN treatment, this difference is not significant and no terms were left in the model after stepwise deletion.

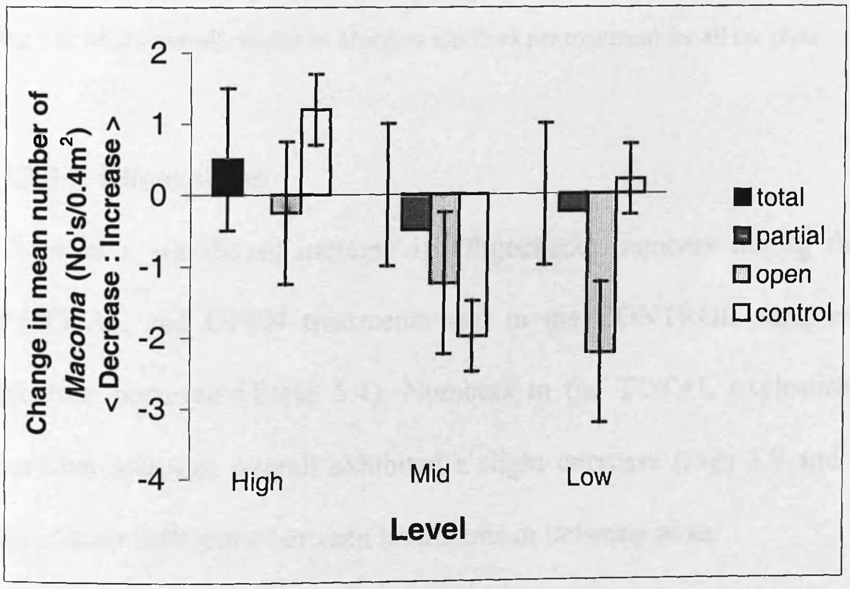


Fig 5.7: Change in the mean number of *Macoma* per treatment for each study plot.

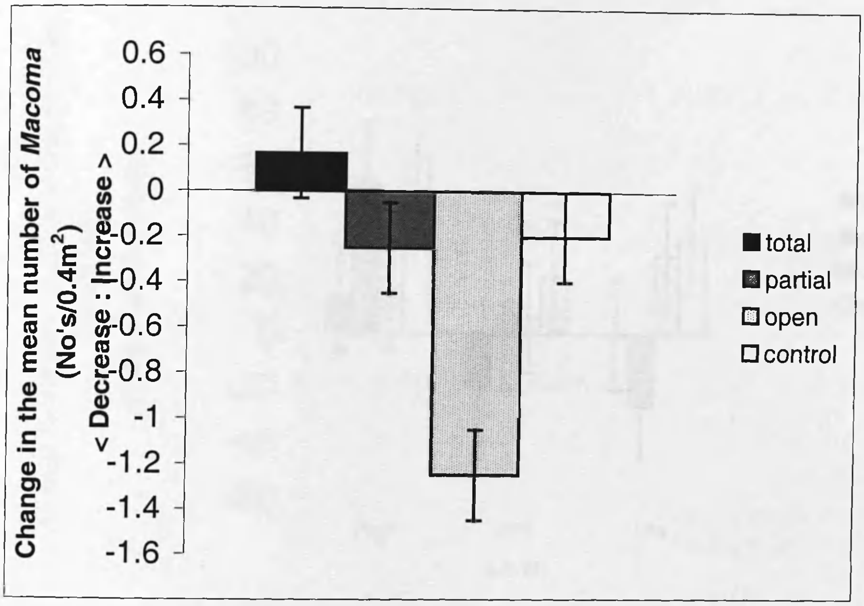


Fig 5.8: Mean overall change in *Macoma* numbers per treatment for all the plots

5.2.3.3 Oligochaetes

There is a significant increase in Oligochaete numbers during the experiment in the PARTIAL and OPEN treatments and in the CONTROL samples where the greatest increase occurred (Table 5.4). Numbers in the TOTAL exclosure remained relatively constant although overall exhibited a slight decrease (Figs 5.9 and 5.10). There was no significant difference between treatments or between plots.

Table 5.4: Results of a quasi likelihood model for logoligochaete ~ plot + treatment + before/after + plot * treatment + plot * before/after + treatment * before/after + plot * treatment * before/after

Factor	Residual df	Residual deviance	F value	P value
Before/After	20	0.73	4.06	0.05

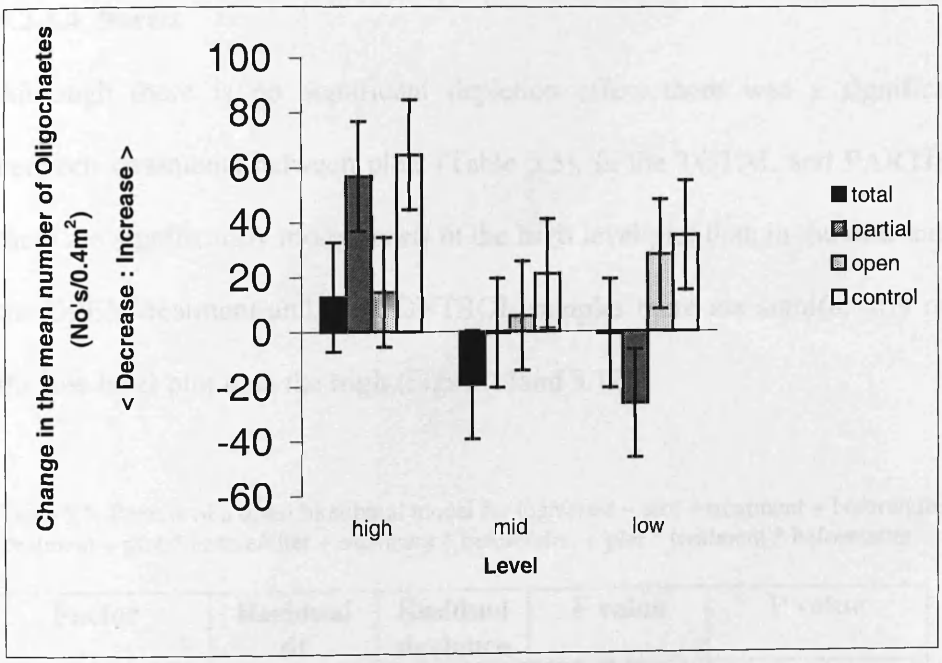


Fig 5.9: Change in the mean number of Oligochaetes per treatment for each study plot

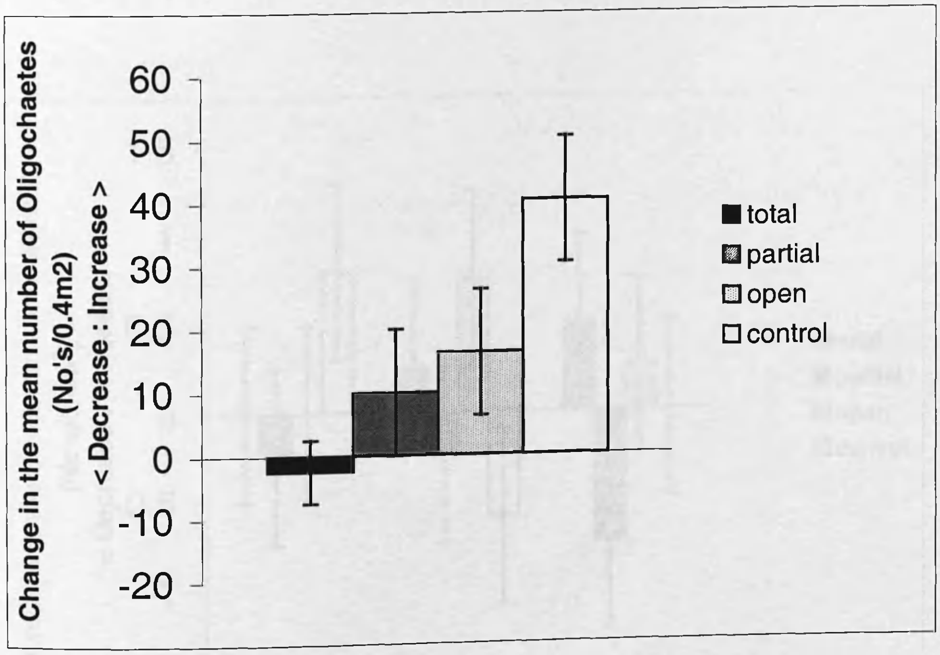


Fig 5.10: Mean overall change in Oligochaete numbers per treatment for all the plots

5.2.3.4 Nereis

Although there is no significant depletion effect there was a significant difference between treatments between plots (Table 5.5). In the TOTAL and PARTIAL treatments there are significantly more *Nereis* in the **high** level plot than in the **mid** and **low** plots. In the OPEN treatment and the CONTROL samples there are significantly more Nereis in the **low** level plot than the **high** (Figs 5.11and 5.12).

Table 5.5: Results of a quasi likelihood model for log*Nereis* ~ plot + treatment + before/after + plot * treatment + plot * before/after + treatment * before/after + plot * treatment * before/after

Factor	Residual df	Residual deviance	F value	P value
Plot	22	3.08	0.08	0.76
Treatment	21	3.07	0.10	0.74
Plot:Treatment	20	2.60	4.24	0.05

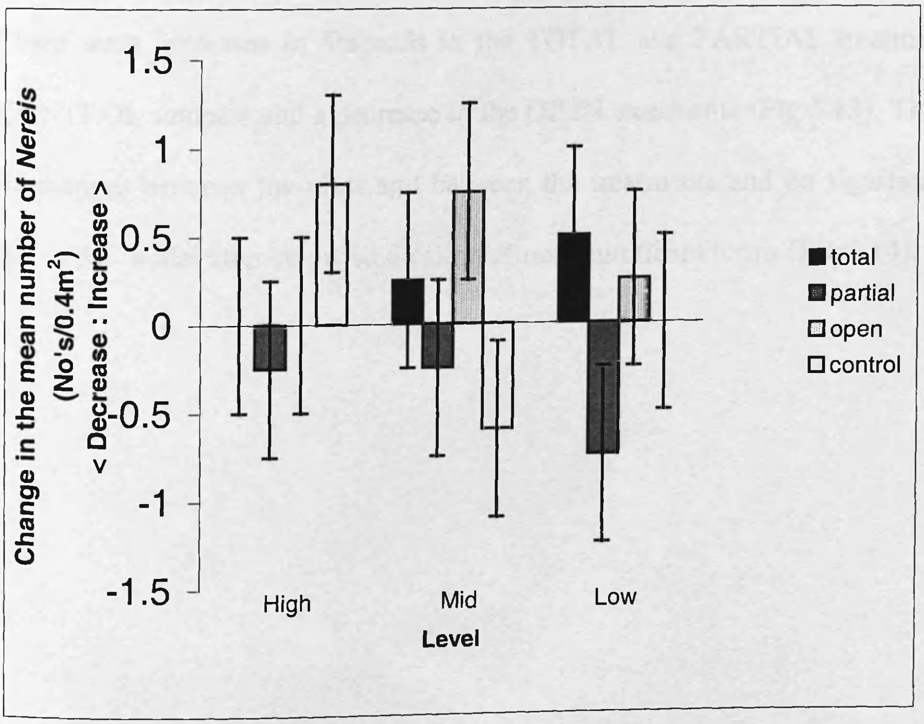


Fig 5.11: Change in the mean number of *Nereis* per treatment for each study plot

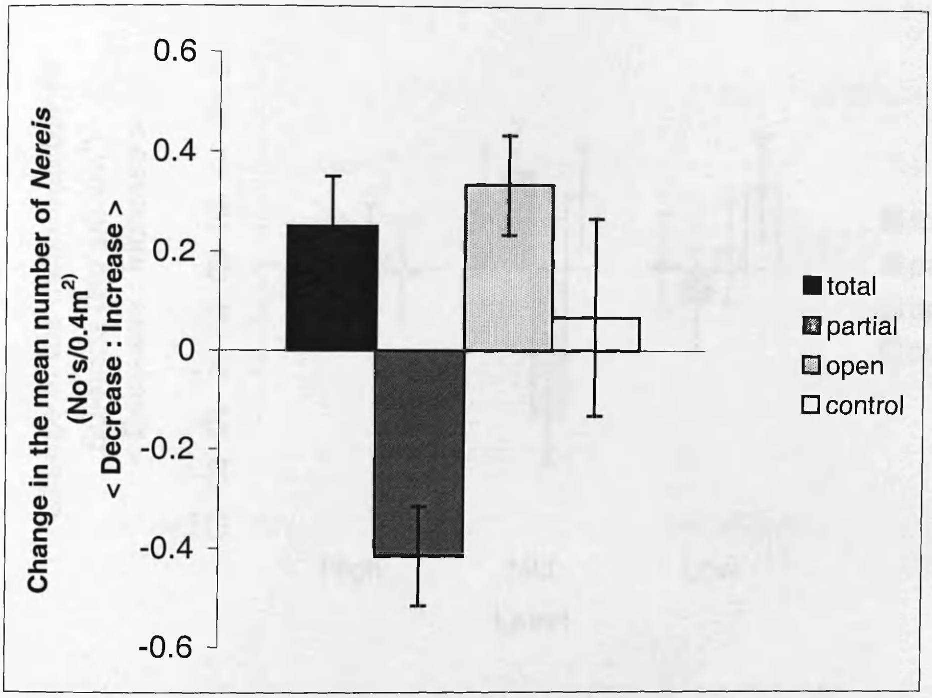


Fig 5.12: Mean overall change in *Nereis* numbers per treatment for all the plots

5.2.3.5 Spionids

There were increases in Spionids in the TOTAL and PARTIAL treatments and in the CONTROL samples and a decrease in the OPEN treatments (Fig 5.13). There is variation in changes between the plots and between the treatments and no significant terms were left in the model after stepwise deletion of non significant terms (Fig 5.14).

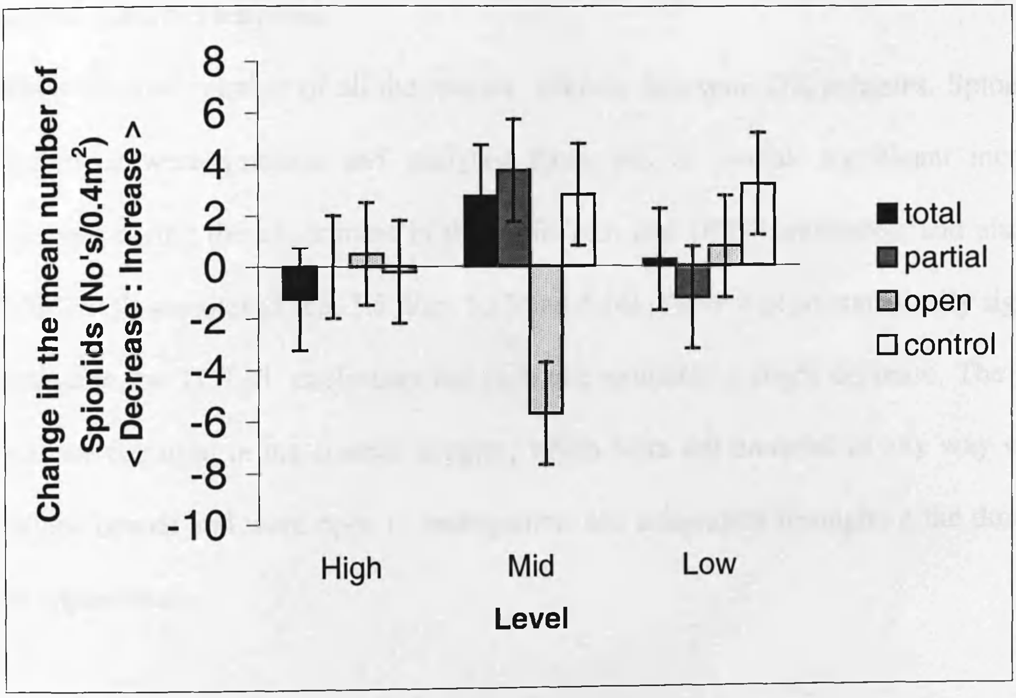


Fig 5.13: Change in the mean number of Spionids per treatment for each study plot

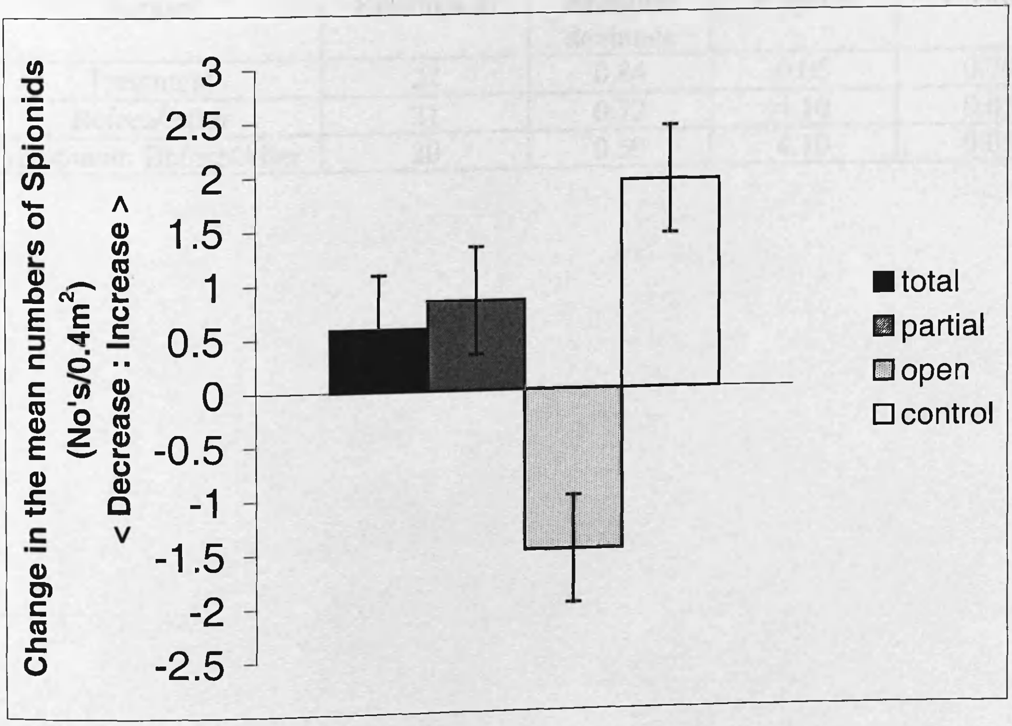


Fig 5.14: Mean overall change in Spionid numbers per treatment for all the plots

5.2.3.6 All invertebrates

When the total number of all the species (*Nereis, Macoma,* Oligochaetes, Spionids *and Hydrobia*) were summed and analysed there was an overall significant increase in numbers during the experiment in the PARTIAL and OPEN treatments and also in the CONTROL samples (Table 5.6, Figs 5.15 and 5.16). There was no statistically significant change in the TOTAL exclosures but each one exhibited a slight decrease. The greatest increase occurred in the control samples, which were not bounded in any way with sub surface boards and were open to immigration and emigration throughout the duration of the experiment.

Table 5.6: Results of a quasi likelihood model for log all invertebrates ~ plot + treatment + before/after + plot * treatment + plot * before/after + treatment * before/after + plot * treatment * before/after

Factor	Residual df	Residual deviance	F value	P value
Treatment	22	0.84	0.06	0.79
Before/After	21	0.72	4.10	0.05
Treatment: Before/After	20	0.59	4.10	0.05

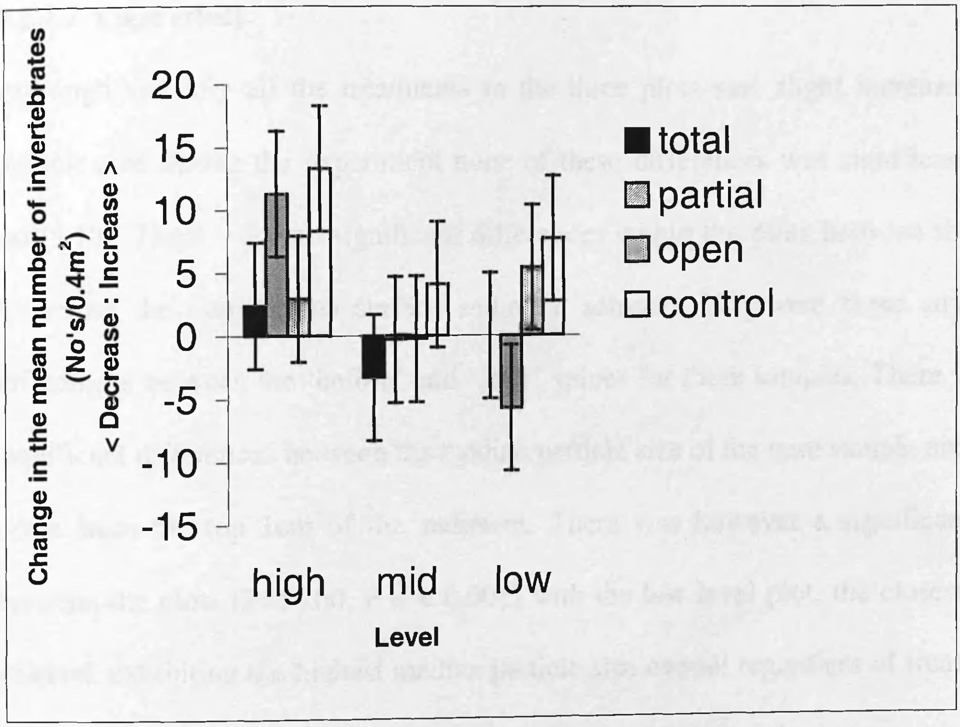


Fig 5.15: Change in the mean number of all invertebrates per treatment for each study plot

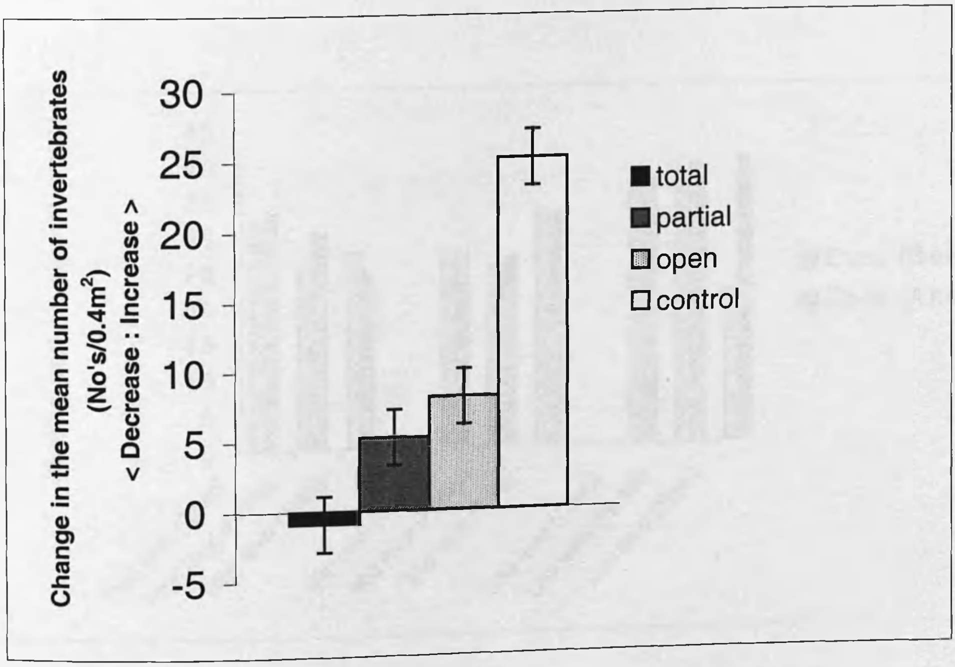


Fig 5.16: Mean overall change in all invertebrate numbers per treatment for all the plots

5.2.3.7 Cage effect

Although virtually all the treatments in the three plots saw slight increases in median particle size during the experiment none of these differences was significant (Figs 5.17 and 5.18). There were no significant differences within the plots between the treatments for either the core or the surface sediment samples. Nor were there any significant differences between the 'before' and 'after' values for these samples. There were also no significant differences between the median particle size of the core sample and the sample taken from the top 1cm of the sediment. There was however a significant difference between the plots (F=14.00, P = < 0.001) with the **low** level plot, the closest to the tidal channel, exhibiting the highest median particle size overall regardless of treatment. There were, however, no significant changes in sediment size during the experiment between the plots.

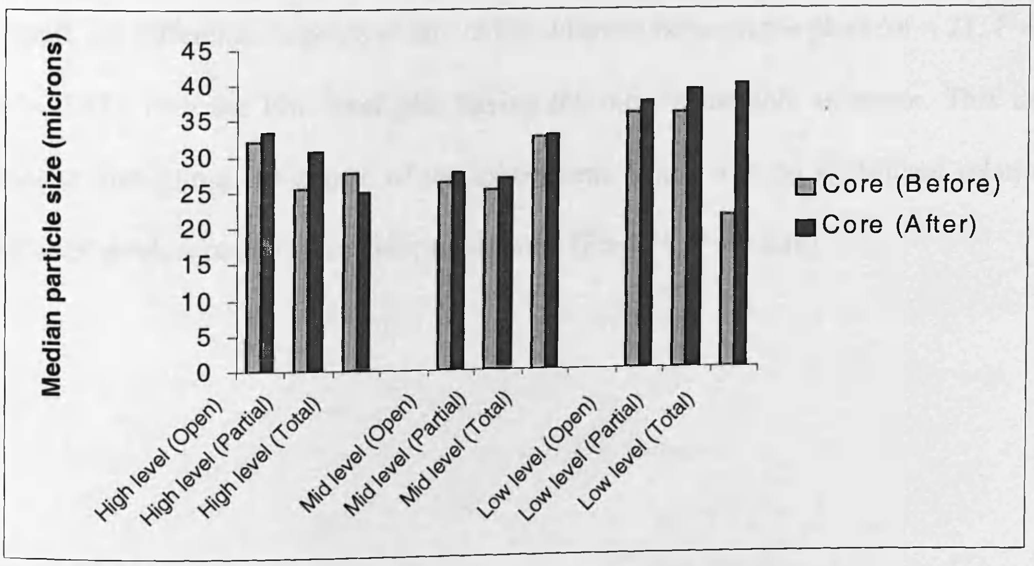


Fig 5.17: The change in median sediment particle size in the core samples during the experiment for the open, partial and total exclosures in all the study plots

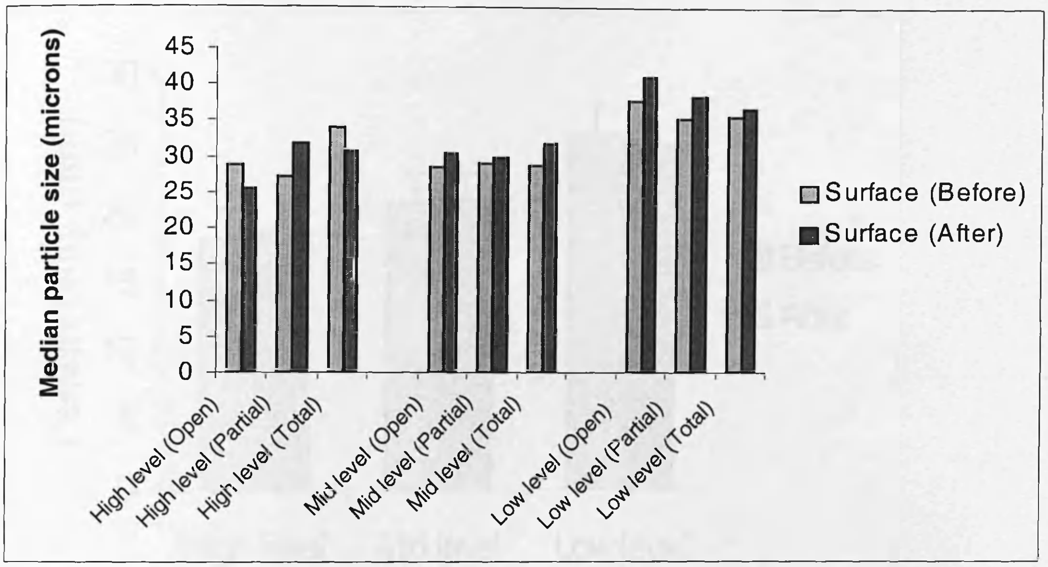


Fig 5.18: The change in median sediment particle size in the surface samples during the experiment for the open, partial and total exclosures in all the study plots

5.2.3.8 Penetrability

There was no significant difference in penetrability within plots (Fig 5.19) but there was a significant difference in penetrability of the substrate between the plots (df = 21, F = 5.55, P = 0.02), with the **low** level plot having the most penetrable substrate. This did not change throughout the course of the experiment. There was no significant relationship between median particle size and penetrability (F= 4.75, P = 0.838).

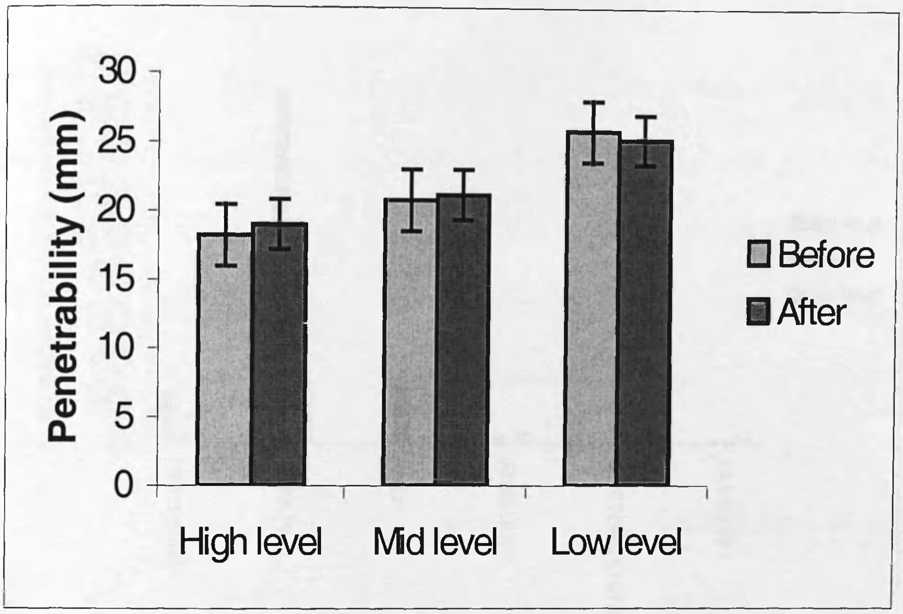


Fig 5.19: Mean penetrability (n=5) of each study plot before and after the experiment.

5.2.3.9 Bird numbers

The **high** level plot was the most intensively used area during the experiment, primarily because it was exposed to shorebird predation for the longest period (Fig 5.20). Redshank and dunlin were seen to feed in the plot throughout the tide but with numbers increasing considerably as birds were forced up the shore by the rising tide. The **low** level plot was the second most favoured site, mostly by redshank and dunlin. Birds were hardly ever seen feeding in the **mid** level plot hence the very low figures for this site. However only birds feeding within the confines of the plots were recorded. Many birds seen in the general vicinity of the plots but not actually within them went unrecorded.

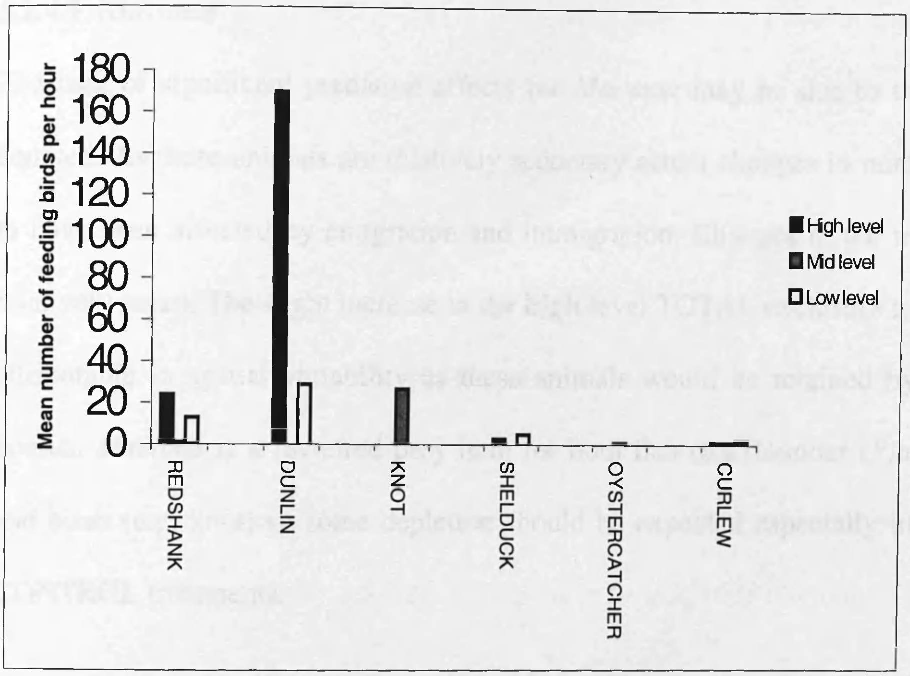


Fig 5.20: Mean number of birds feeding in each study plot per hour throughout the period of the experiment. Values are rounded to the nearest whole number and are displayed for each species

5.2.4 Discussion

5.2.4.1 Hydrobia

The lack of change under the TOTAL exclosures indicates that this treatment was effective in retaining this mollusc despite their potential mobility. Alternatively there may have been some movement in and out, so the density of this animal remained constant, indicating homogeneity of distribution over the 1m^2 spatial scale. There was a reduction under the PARTIAL treatment indicating either predation by fish or movement. With these treatments, it is impossible to infer, for surface dwelling animals such as *Hydrobia,* whether losses are attributable to predation, emigration or mortality. To a lesser extent there was also a change in the OPEN treatment and CONTROL. It may be that fish were attracted to feed under the partial exclosure as it offered them some shelter from predation.

5.2.4.2 Macoma

The lack of significant predation effects for *Macoma* may be due to the small number counted. As these animals are relatively sedentary actual changes in number are unlikely to have been affected by emigration and immigration. Changes in the mean number are relatively small. The slight increase in the **high** level TOTAL exclosure is just likely to be attributable to spatial variability as these animals would be retained by the subsurface boards. *Macoma* is a favoured prey item for both fish (e.g.flounder (*Platichthys flesus*)) and birds (e.g. knot) so some depletion should be expected especially in the OPEN and CONTROL treatments.

5.2.4.4 Oligochaetes

Oligochaetes were likely to fluctuate in number during the experiment due to their mobility (enabling them to potentially burrow under the retaining boards) and the results suggest that this type of experimental design is inefficient at measuring accurate changes in their number that might be due to predation. The overall slight decrease in Oligochaetes is a product of an increase at the **high** level site offset by a decrease at the **mid** level site. The significant change in numbers is positive, with increases after the experiment in the other treatments. The greatest increase in the CONTROL samples reflects the fact that even if invertebrates were to be locally depleted, others might move in from the surrounding mud to fill the vacant space. This suggests that it is very difficult to use just random samples when trying to measure predation effects.

5.2.4.5 Nereis

The results from this species are generally inconclusive partly again due to the low overall numbers of this normally carnivorous polychaete. In all the plots and all the treatments only 29 animals were found in total, 13 before and 16 after. Increases in the TOTAL and

OPEN treatments and the CONTROLS suggest again that movement into and out of the treatments occurred during the experiment even with the sub surface boards, indicating that this design is of little use in measuring predation effects on this species.

5.2.4.6 Spionids

Although a reasonable number of animals was found in the samples (37 before and 59 after) they were quite evenly distributed across the treatments and plots. Slight increases in the overall TOTAL, PARTIAL and CONTROL samples were offset by a decrease in the OPEN treatment leaving no convincing picture of depletion and no significant effects.

5.2.4.7 All invertebrates

Overall, although it is clear that there is only a slight decline in the TOTAL exclosures, suggesting that conditions remained relatively stable within them, changes did occur at the species level. It is also evident that there was some movement into and out of these exclosures regardless of the measures taken to retain invertebrates. The PARTIAL and OPEN treatments exhibited significant increases, and increases were especially evident in the CONTROL samples. As recruitment is not a possible cause of these increases as the experiment took place in the Winter the most likely explanation is spatial variation in invertebrate density or local movements during the course of the experiment. These small-scale movements completely confounded the aims of the experiment and showed that it is difficult to measure predation effects using such exclosure cage designs.

All the above results show few measurable effects on invertebrate densities within the treatments. Although the total exclosures exhibited either no change or in the case of spionids, an increase, there were no corresponding decreases in treatments exposed to predation i.e. within CONTROL samples and OPEN treatments.

5.2.4.8 Effect of cages

In concordance with other studies (Holland *et al.* 1980, Mahony & Livingstone 1982, Kent & Day 1983) there were no significant effects of cage structure on either the top 10cm of sediment, which might effect the burrowing polychaetes, or the top 1cm where the majority of the *Hydrobia* and *Macoma* dwelt. All these studies were undertaken on relatively sheltered tidal flats with similar conditions to those at Skinflats so it might be assumed that if exclosure cages of this design were to be used in future experiments they would not substantially alter the local sedimentary environment. Also it was noted at the Skinflats site that there was no build up of algae on the cages which might have some considerable effect on the sediment underneath it (Reise 1985). If such an accretion of algae had occurred it may have attracted amphipods and grazing gastropods, increasing numbers in the treatments. The TOTAL exclosures may have acted as refugia for small fish such as the sand goby (*Gobius minutus*) or *Crangon* which may in turn have biased the level of predation within the cages. Although the mesh size was small (10mm x 10mm) it probably would not have been able to keep such predators out and any future work using cages should consider a smaller mesh size (see Reise 1985).

5.2.4.9 Are fish likely to compete with birds for food?

The Forth estuary is an important habitat for a large number of fish, such as the flounder, which can utilise the benthic infauna of the intertidal during the inundation period. Just how much they may deplete the food supply available to the birds is open to debate. Schneider & Harrington (1981) considered it unlikely that flatfish utilize as much food as shorebirds due to their lower consumption rates, reported by Pearcy (1963) as being in the order of 2-3% of body mass /day. Quammen (1984) also regarded fish as less important predators due to their predominant sub tidal feeding habits at a site in southern California. However, numbers of flounder on the Ythan Estuary, Scotland, fluctuated between 0.05 m^{-2} in Winter to $0.24m^{-2}$ in Summer and their total food consumption was calculated at 58.1 kcal m^{-2} yr^{-1} which is three times the amount consumed by birds at the same site (Raffaelli & Milne 1987). Shrimps, mostly *Crangon crangon* are also present in large numbers during the winter on the Forth Estuary and feed on a wide variety of prey such as (in order of preference): *Nephtys,* Spionids, *Macoma, Corophium and Cerastoderma* (Jaymanne & McLusky (1997). They may not, however, be selecting the same size classes that would support the winter shorebird population.

Bryson (1997) considered the use of the Skinflats and Kinneil intertidal areas by fish. He found that only a proportion of the fish in the estuary such as plaice (*Pleuronectes platessa*) and flounder migrated to the intertidal and that these fish distributed themselves randomly, at a density of 0-10 per $1000m^{-2}$ for most species. Although the fish fed on the same animals as the shorebirds (i.e. oligochaetes, polychaetes, crustacea and molluscs), the numbers of fish feeding on the mudflat were at a minimum in the winter suggesting that competition between them during this season was lower that at any other time of the year. Bryson (1997) found no evidence linking fish abundance to prey abundance and concluded that the position of the feeding areas relative to the subtidal channels was an important predictor of fish presence. He states " high shore sites may be outside the distribution range of some fish species and may therefore be only accessible to species showing a widespread distribution with respect to height of the shore eg. adult flounder". He also notes that high-level sites have limited use for fish due to their long exposure time relative to sites closer to the MLWS and that although these areas are often rich in food they are too far from the sub tidal channel for all but the strongest swimmers. The fact that fish and birds are apparently present in inverse densities during the winter (with comparatively less fish and more birds when compared to the annual mean) and that fish prefer the lower tidal areas may suggest that there is a niche separation between them reducing any competition that may occur for food resources.

Although fish are important consumers of estuarine invertebrates throughout the year, they are probably less of a competitor to birds during the winter months when they are at their minimum density while shorebirds are at their maximum. The resource partitioning due to relative exposure times of high and low level mudflats also suggest that where competition for food does occur it is only likely to be important in lower shore areas (Fig 5.21).

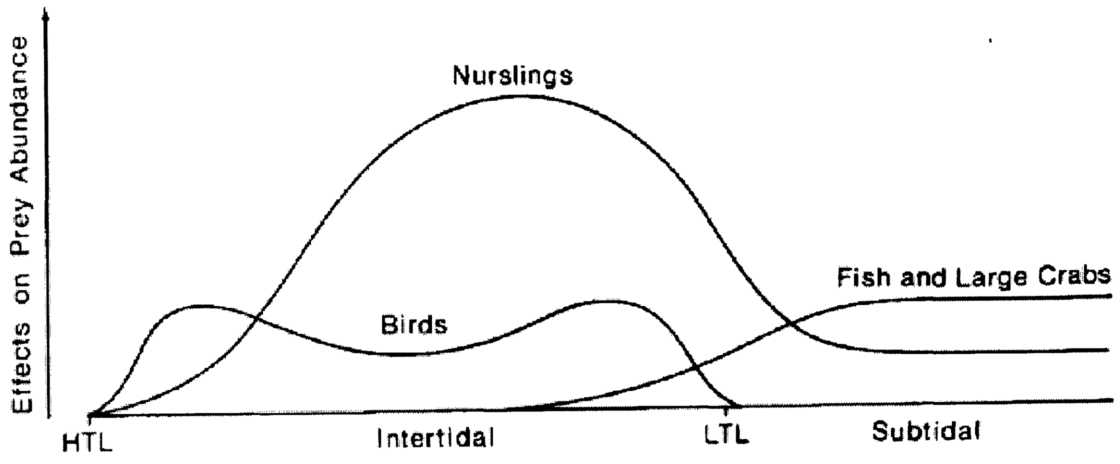


Fig 5.21: The hypothesised likely distribution of predator effects on intertidal invertebrate prey populations from the high tide line (HTL) to the low tide line (LTL) and the subtidal area. (from Reise 1985)

5.2.5 Conclusion

Even with the apparent inability of the exclosure cages to restrain invertebrate movements, the general lack of predation effects in this study may be partly due to the relatively low feeding density of birds at the study site. However although high tide densities are greater at Kinneil those at low tide are broadly similar on an area basis. Most birds at Skinflats were observed when only the high level plots were exposed because birds from Kinneil moved around to feed on Skinflats when mud at Kinneil became inundated. The expected depletion effect at this high tide site, however, was not noted.

Cage effects appeared to have no effect on the sediment structure although the possibility that the cages may have acted as refugia for shrimps and small fish cannot be ruled out. The latter is unlikely to be the case however, as invertebrate numbers increased in the all the treatments except the total exclosure and there were no significant decreases.

Overall the results were inconclusive, mostly due to the design of the experiment being insufficiently powerful to detect any small-scale effects. Even with the sub-surface boards, there were invertebrate movements, making it impossible to tell whether changes were due to predation, mortality or movement. The general increase in invertebrate numbers highlights this fundamental design problem. It can be concluded that either food may not be a limiting factor at this site or the treatments were ill placed and designed to detect any real affects. This experiment shows that previous work using similar exclosure cages was open to these kinds of errors, and their results should be viewed with considerable caution.

Further work on this experiment will focus on the area of greatest bird usage i.e. the margin near the MHWS, will involve a change in the design of the exclosures and increase statistical power by using a greater number of replicates of each treatment (see experiment 2).

5.3 Experiment 2: 1999-2000 exclosure study

5.3.1 Introduction

The previous experiment was undertaken specifically to determine just how effective traditional cage type exclosures were at measuring the impact of shorebirds and fish on estuarine invertebrates at this site. It was seen that the results were generally inconclusive and at best any positive declines were open to question due to problems of small-scale variability in invertebrate numbers and movement of animals in and out of the treatments, even though some effort was made to retain them. In experiment 2, scaling the size of the exclosures to this variability and increasing their number mitigated the potential error introduced by the inherent patchiness of sediment dwelling organisms.

5.3.2 Methods

5.3.2.1 Site and season choice

The high level area at Skinflats was chosen, firstly because of its easy accessibility for sampling and bird observations, and secondly because the site is heavily used by overwintering waders between November and February each year. The area where the plots were situated supports large numbers of feeding birds and in recent years has regularly had 3000 dunlin, 500 redshank, 250+ shelduck and 100+ curlew feeding throughout the winter months. This experiment was timed to coincide with peak numbers of birds at a time when their energetic needs were high. Thus predation levels on invertebrates would be expected to be high, especially in the high level margin near the MHWS where all the plots are sited. Although birds distributed themselves across the whole mudflat area throughout the tidal cycle, the thin high level strip where the plots were placed has the heaviest use as it is exposed to bird predation for the longest period. Often it remains exposed even at high tide, especially on neap cycles. Species like the redshank and shelduck show a preference for this high level area and concentrate their feeding efforts in this region throughout the tide (Pers Obs). As the experiment occurred in the winter months any problems of invertebrate recruitment confounding the results were avoided.

5.3.2.2 Experimental design

Four 100m x 100m study plots were marked out on the mud at Skinflats as before, but this time they were all placed in high level positions ensuring that exposure time for feeding by shorebirds was at a maximum. Conversely feeding time for potential competitors such as fish was at a minimum so a measured depletion effect might reasonably be attributed to shorebirds. The immersion sequence for the four plots is 4-3-1-2 but the time from immersion of plot 4 to immersion of plot 2 is on average only 0.5 h depending on the tide height and wind speed (Pers Obs). The plots were also positioned on the mud in areas known to vary in bird usage so that plots 1 and 2 were in 'high use' areas and plots 3 and 4 in 'low use' areas. This deliberate positioning of the study plots undermines any assumptions of random assignment but was considered a useful approach, as it can be hypothesised that depletion should be greater in 1 and 2. If the converse was correct then the underlying cause of any depletion might well be attributable to either mortality or high variation of invertebrate density on a small spatial scale, which is a potential confounding element in all such experiments. In order to try and reduce the error associated with assuming homogeneity of invertebrate density within a 1m^2 exclosure cage (as in experiment 1) the treatments were altered considerably to reduce their size and layout. Their small size also reduced their 'presence' on the mudflat as it was not desirable to have treatments that would affect the feeding behaviour of the shorebirds. No effect on bird behaviour was observed during this study and it was regarded as generally unlikely to occur. Kent & Day (1983) observed no effects on birds of much larger exclusion cages. The power of the experiment was also greatly improved by increasing the number of replicates per treatment from 3 to 20.

Treatment 1 (COVERED): This was a totally covered exclosure device designed to exclude feeding shorebirds and retain invertebrates so that immigration and emigration could not cause any measurable increase or decrease. It consisted of a section of light brown PVC drain pipe 20cm deep and 10cm in diameter. This was pushed into the mud to a depth of 18cm, it was assumed that any burrowing species would be unlikely to escape underneath it, considering that the majority of activity occurs in the top 5cm of sediment (McLusky pers comm). The 2cm of tube left protruding from the mud had a series of holes, 0.75cm in diameter drilled all the way round it to allow free flow of seawater on to the enclosed mud surface. This was done to help prevent any sedimentation within the cylinder, which may affect the animals held within. The whole pipe including the holes drilled to allow free flow of water was then covered with a plastic 250μ net to retain invertebrates within it and exclude those in the surrounding mud from entering. The pipe was topped with a 500μ steel mesh held on with a jubilee clip to protect the plastic mesh from rough weather and any other damage.

Treatment 2 (PARTIAL): This was a partial exclosure identical to treatment 1 except that it lacked a covering top. It allowed the potential free movement of all invertebrates that were able to crawl over the 2cm lip or move up into the water column. It also allowed birds to feed within them and was primarily there to determine whether there was any effect of the cylinder on the mud structure.

Treatment 3 (RANDOM): This was simply a randomly located control sample with no pipe at all.

Five replicate sets of these three treatments were randomly positioned within each of the study plots.

5.3.2.3 Sampling methods

5.3.2.3.1 Invertebrates

All the treatments were positioned at randomly assigned co-ordinates and the shortest possible route was taken when placing the treatments and taking the initial samples so as to minimise disturbance to the invertebrates and mud surface. It was observed that even deep footprints in the study area disappeared after about a week. With the treatment in place, a sample of mud was taken next to the cylinder and within 10 cm of the sample to be taken at the end of the experimental period. This approach reduces the chance of finding a significant difference between before and after samples that may be attributable to spatial variation of invertebrate densities instead of an actual depletion effect. Control samples were taken at their random co-ordinates and located using a Silva Global Positioning System. A small bamboo marker was left in the mud to aid relocation. The treatments were left for approximately 3 months (December 15th 2000 – March 21st 2001) before the 'after' set of samples was collected. These samples were collected from the centre of each treatment cylinder as it was removed from the mud. At the control locations the sampling procedure was the same as before.

5.3.2.3.2 Sediment

Sediment characteristics such as particle size, percentage organic matter and penetrability have been linked with different species of birds as good predictors of their spatial distribution on a mudflat e.g. shelduck (Yates *et al.* 1996), knot (Scheiffarth *et al.* 1996), dunlin (Kelsey & Hassall 1989, Mouritsen & Jensen 1992 & Nehls & Tiedemann 1993) and redshank (Yates *et al.* 1993). The results in Table 5.8 detail the mean (n=5) data extracted from the five randomly sampled cores in each plot. It is reasonable to assume, based on personal observations that changes in these characteristics are not abrupt and are unlikely to differ at the plot scale. Mean and median particle size measurements are complemented by the percentage breakdown of clay, silt and sand. Organic matter content was measured to indicate the potential amount of food available for invertebrates. Shear strength measurements indicate the relative penetrability of the mud. The lower the measurement, the lower the sediments shear strength and the higher its water content. It is likely that sediment with low shear strength is easier for birds to probe in for food and facilitates movement and burrowing for invertebrates.

Five sediment cores were taken randomly within each of the study plots to characterise the particle size distribution, % organic matter and shear stress (penetrability ft lb^{-1} in^{2})

5.3.2.4 Bird observations

Although previous observation data for these plots indicate that **3** and **4** had a lower bird predation pressure than **1** and **2**, complementary observations were made at the plots during the study period. Each plot was counted on 10 separate occasions throughout the winter (early January to early March 2000) over a range of tidal states (neap, ebb/flow and springs, ebb/flow). Through-the-tide counts of the birds that were feeding within the plots were made at 15min intervals; birds feeding outside the study plots were ignored.

5.3.2.5 Statistical analysis

The data was modelled using the generalised linear model (GLM) function in Splus 2000 using Quasi likelihood error structures. The maximum model employed for each species was:

response~plot + treatment + before/after + interactions

Non significant terms were dropped from each model until remaining terms were significant at the 0.05 level of probability.

5.3.3 Results

5.3.3.1 Sediment

The siltiest sites with the greatest penetrability and highest organic matter were plots 1 and 2, these sites also had the greatest number of birds feeding in them. The sediment at these plots is particularly mobile and can be difficult to walk on. Although potential changes in sediment structure were not measured within the treatments it was at least visually obvious that there was no sediment build up by the end of the experiment. It can be concluded that the holes drilled into the sides of the pipes allowed water circulation and helped to keep the sediment stable. Plots 3 and 4 were considerably more compacted with higher percentages of sand, less organic matter and higher shear strength indicating low penetrability. These harsher conditions were reflected in the fact that bird numbers were considerably lower at these sites for all the species counted. Percentage clay varied very little between sites but the sediment is best described by the negative correlation between percentage sand and percentage silt, the higher the amount of sand the lower the amount of silt. High percentages of sand were also positively correlated with higher shear strength and thus lower penetrability.

Table 5.8: Mean sediment characteristics (n=5) for each of the four study plots

	Mean particle size (μm)	Median particle size (μm)	% Clay	% Silt	% Sand	% Organic matter	Shear strength (ft^{-1} lb in^2)
Plot 1	22	16.57	9.54	84.06	6.78	6.76	0.41
Plot 2	18.41	13.03	11.05	84.10	4.84	3.20	0.66
Plot 3	35.3	20.79	9.97	73.87	16.16	4.13	1.25
Plot 4	28.91	23.17	9.82	76.90	13.29	1.30	3.56

5.3.3.2 Bird observations

Four species of bird were regularly observed feeding within the study plots throughout the duration of the experiment: shelduck, redshank, curlew and dunlin. These species are the commonest overwintering species at this site. Although they were not observed feeding within the plot areas, oystercatcher was also present on the mudflat as were knot. Knot are a frequent but unpredictable visitor to Skinflats and tend to visit at or near high tide or during periods of cold weather when conditions at their favoured site Kinneil become limiting

The ability to measure a depletion effect during the winter is also going to be influenced by the birds' capacity for accessing prey during the study period. Intensely cold weather can force invertebrates to burrow to greater depths making many of them difficult or impossible to catch, potentially reducing any measurable effects at the small scale of four 1 ha plots as in this study. The winter of 2001 was however relatively mild on the Forth Estuary with a mean midday temperature of 6.8°C between November 15th and March 20th.

Redshank and dunlin shared the same preferences for the plots, spending most of their time in plot **1** and then progressively less time in **2**, **3** and **4**. Table 5.9 shows that there were significant differences in the numbers of redshank and dunlin between the plots indicating that they preferred particular sites. Shelduck and curlew also had similar preferences for plots, both favouring plot **2** and then the others in about equal measure (Fig 5.22) there were however no significant differences in the numbers of curlew and shelduck between the plots (Table 5.9). Fig 5.23 illustrates the plot preferences when all birds are considered together and is broadly representative of total predation pressure. This graph is dominated by the two commonest species, dunlin and redshank. Although shelduck numbers were lower their food demands may be similar to several redshank for example, assuming energetic costs scale with mass. Therefore even small numbers of big shelduck may have a disproportionate effect on invertebrate depletion.

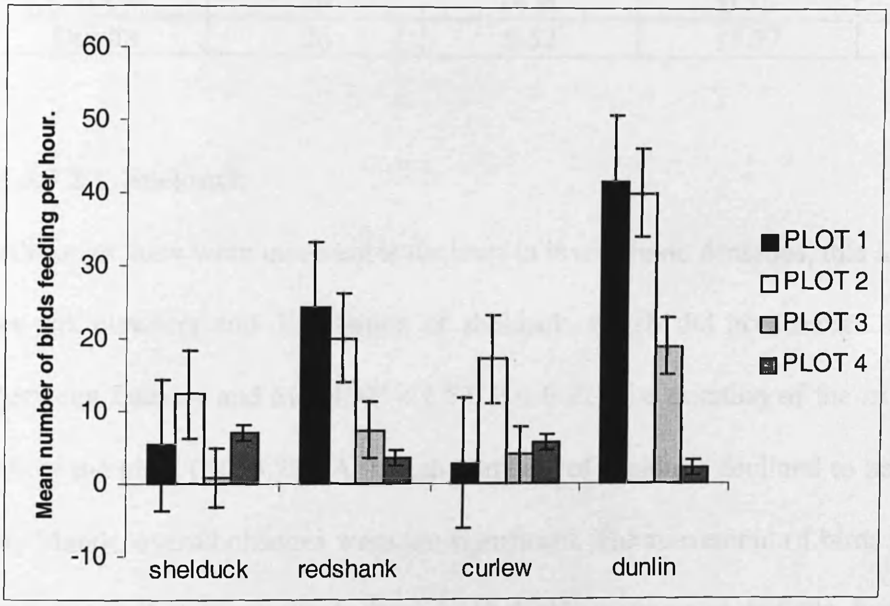


Fig 5.22: Mean density per hectare of shelduck, redshank, curlew and dunlin present feeding in each study plot per hour during the study period

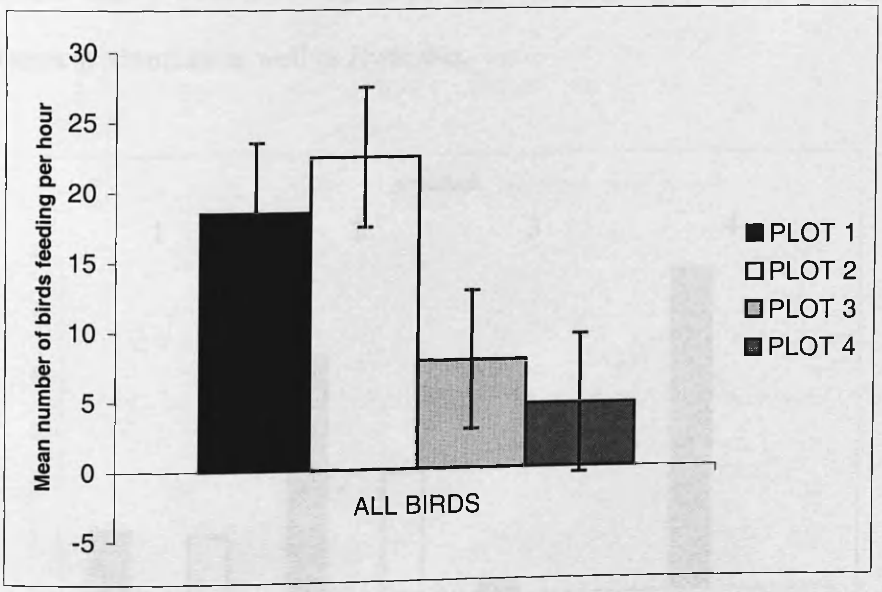


Fig 5.23: Mean number of all species present feeding in each study plot during the experiment

Table 5.9: Results of the GLMs for bird numbers v plot. The P values for redshank and dunlin show that there were significant differences in numbers between the plots whereas shelduck and curlew were more evenly distributed

Birds v plot	**Residual df**	**Residual deviance**	**F value**	**P value**
Shelduck	26	14.62	0.52	0.47
Redshank	26	12.18	6.22	0.01
Curlew	26	14.90	0.55	0.42
Dunlin	26	9.52	15.27	<0.001

5.3.3.2.1 Shelduck

Although there were measurable declines in invertebrate densities, this had no effect on the numbers and distribution of shelduck, which did not change significantly between January and March (F = 1.57, P = 0.22), the duration of the experiment in all of the plots (Fig 5.24). Although numbers of shelduck declined to zero in plot **4** by March, overall changes were not significant. The movement of birds from plot **4** may be attributable to the declines in *Hydrobia* numbers at this site, however there were still shelduck in plots **1** and **2** which had the lowest number of *Hydrobia* at the beginning of the experiment. This suggests that shelduck are choosing other prey items at Skinflats as well as *Hydrobia*.

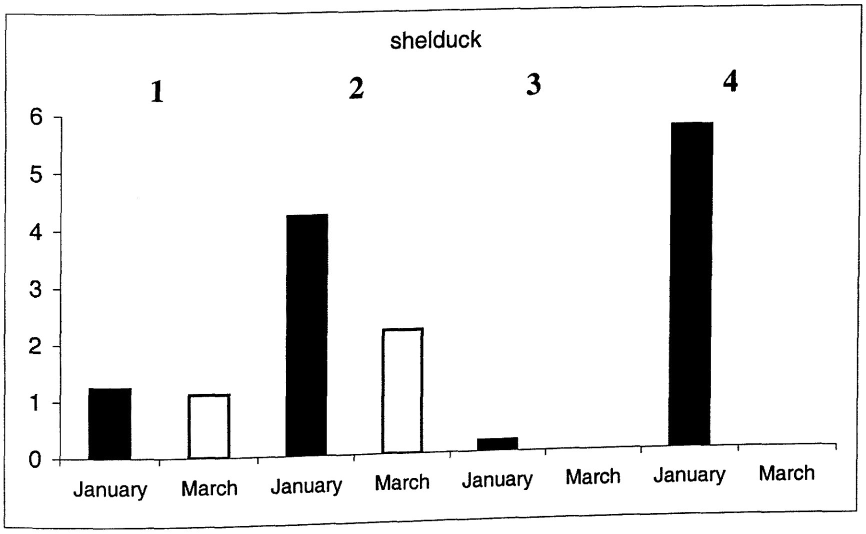


Fig 5.24: Mean number of shelduck feeding per hour during January and March in plots 1 to 4

5.3.3.2.2 Curlew

Numbers of curlew did not differ significantly before and after the experiment (F= 2.84 , P = 0.11) (Fig 5.25). Curlew showed minor non significant increases at plots **1** and **2** but their dependence on the mudflat for winter feeding is not as strong as other species and numbers can fluctuate considerably throughout the winter period. Curlew commonly supplement their diet of estuarine invertebrates by moving into wet fields at the estuary margin to prey on earthworms. Up to 80 birds used the fields adjacent to Skinflats throughout the study period.

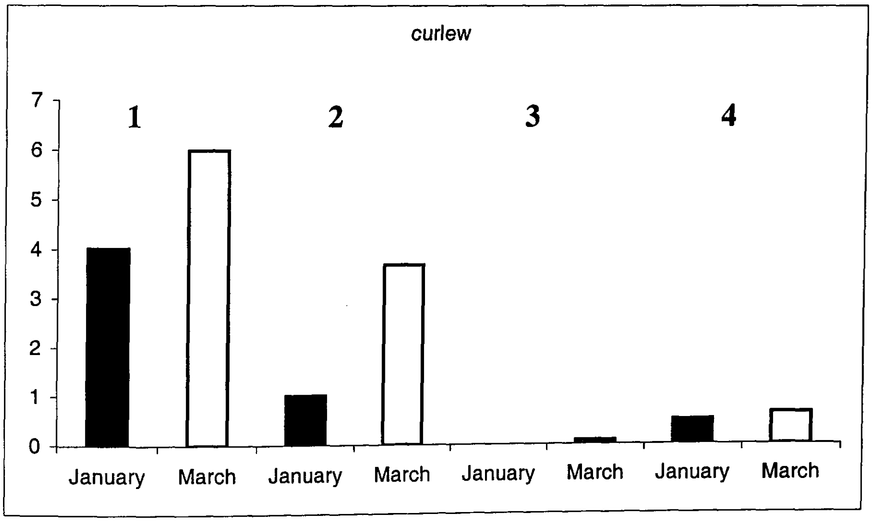


Fig 5.25: Mean number of curlew feeding per hour during January and March in plots 1 to 4

5.3.3.2.3 Redshank

Redshank showed significant differences in number between January and March (F = 5.27, P = 0.03) as well as differences between the plots (F = 5.34, P = 0.03). Numbers of redshank declined throughout this period in plots **1** and **2** but increased slightly in plot **4** (Fig 5.26). Such decreases in redshank numbers however may be nothing to do with declines in food supplies, as birds gradually leave the estuary from March onwards and head towards their breeding grounds in Scotland and Iceland.

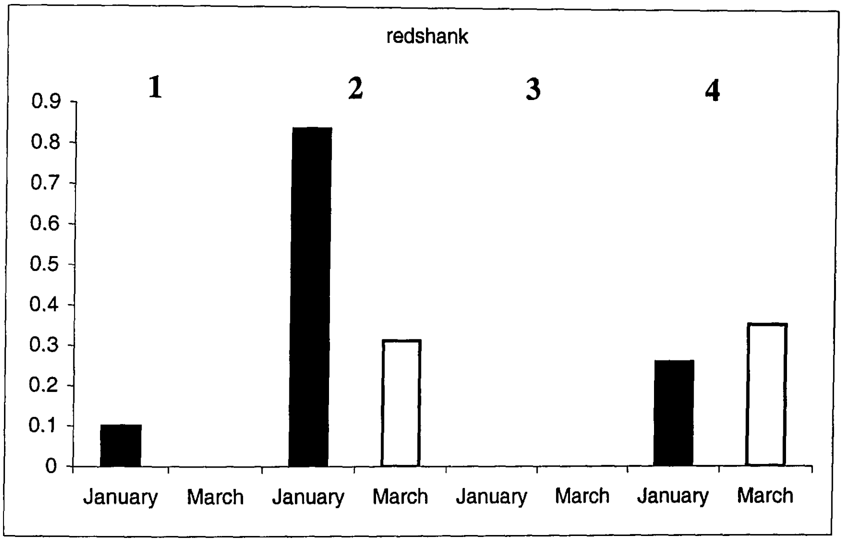


Fig 5.26: Mean number of redshank feeding per hour during January and March in plots 1 to 4

5.3.3.2.4 Dunlin

Dunlin numbers show a slight insignificant increase on plot **1**. Although not present in January birds were feeding in plot **2** in March (Fig 5.27). This appears to show that even with declines in food supplies plots **1** and **2**, Skinflats was able to support higher bird densities in March than it could in January.

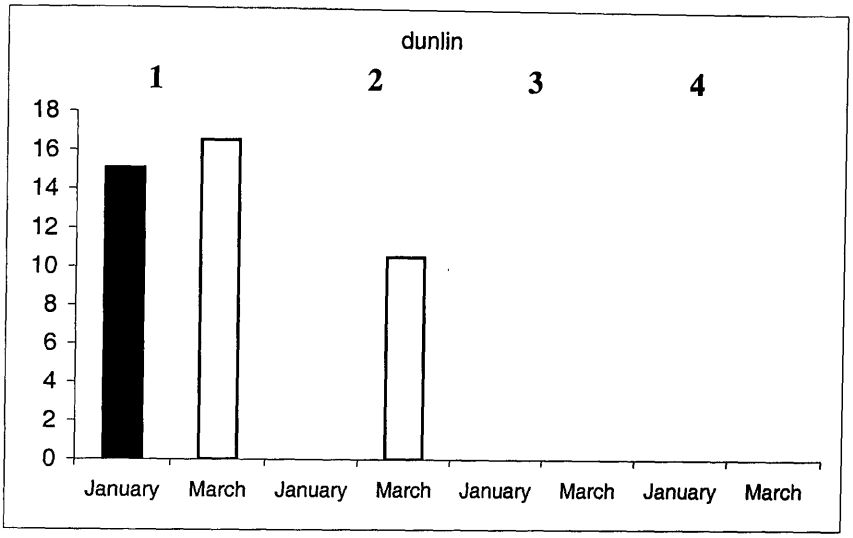


Fig 5.27: Mean number of dunlin feeding during January and March in plots 1 to 4

5.3.3.3 Invertebrates

5.3.3.3.1 Hydrobia

Overall there was a significant reduction in *Hydrobia* numbers during the experiment (F = 14.93, P = <0.001) however the greatest reductions did not occur where the greatest numbers of birds were feeding. There were also significant differences in *Hydrobia* numbers both between the plots and between the treatments (Table 5.10).

There was very little change in the mean number of *Hydrobia* in the COVERED exclosures apart from that in plot 4 where there was a large reduction. This was also evident in the other treatments at this site. In plots 1-3 the OPEN treatments remained relatively unchanged. Relative to the other treatments the RANDOM samples exhibited the most change over all and experienced a reduction in *Hydrobia* numbers in all the plots (Figs 5.28 and 5.29).

Table 5.10: Results of a quasi likelihood model for log*Hydrobia* ~ plot + treatment + before/after + plot * treatment + plot * before/after + treatment * before/after + plot * treatment * before/after

Factor	**Residual df**	**Residual deviance**	**F value**	**P value**
Before/After	118	40.94	14.93	<0.001
Plot	117	38.95	7.51	0.007
Treatment	116	37.69	4.80	0.03

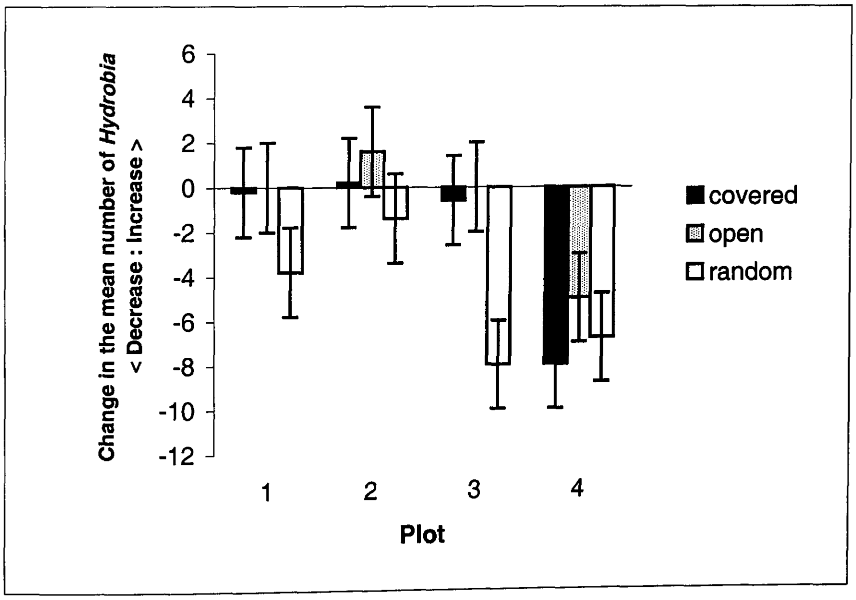


Fig 5.28: Change in the mean number of *Hydrobia* per treatment for each study plot

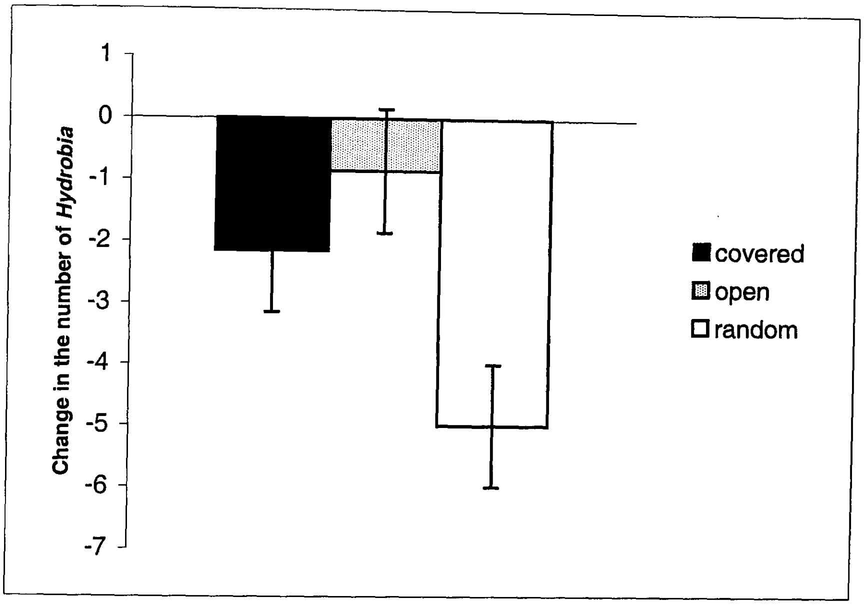


Fig 5.29: Change in the mean number of *Hydrobia* per treatment for all the study plots

5.3.3.3.2 Macoma

Changes in *Macoma* numbers were more uniform across the study plots with no significant differences between them. There was a significant difference between the treatments (F = 4.80. P = 0.03) with the RANDOM samples exhibiting the greatest reduction. Overall there was a significant reduction of *Macoma* during the experiment (F = 13.90, P = <0.001) (Table 5.11). Reductions in number occurred in all treatment types in all plots showing some variability with increases in plot **2** OPEN treatment and plot **3** COVERED treatment (Figs 5.30 and 5.31).

Table 5.11: Results of a quasi likelihood model for log*Macoma* ~ plot + treatment + before/after + plot * treatment + plot * before/after + treatment * before/after + plot *t reatment * before/after

Factor	Residual df	Residual deviance	F value	P value
Before/After	118	15.48	13.90	<0.001
Treatment	117	15.05	4.80	0.03

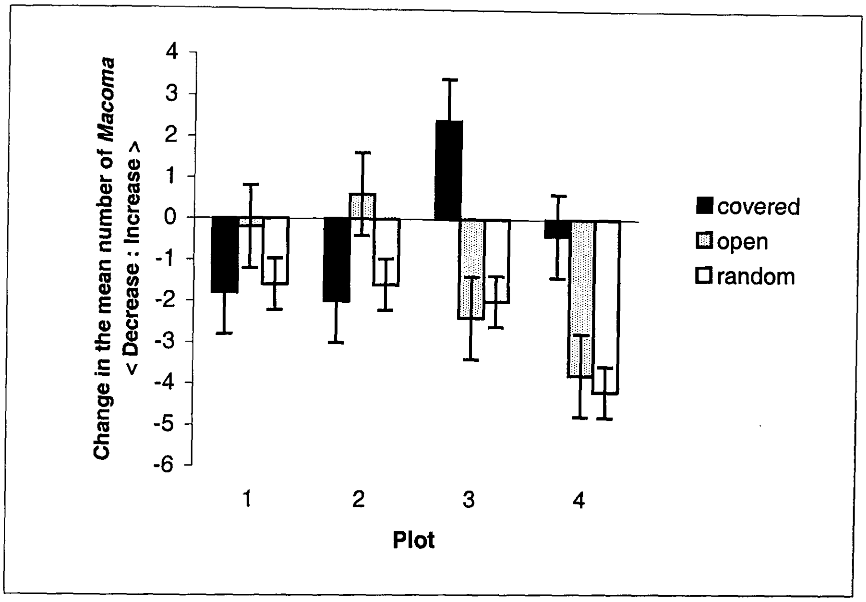


Fig 5.30: Change in the mean number of *Macoma* per treatment for each study plot

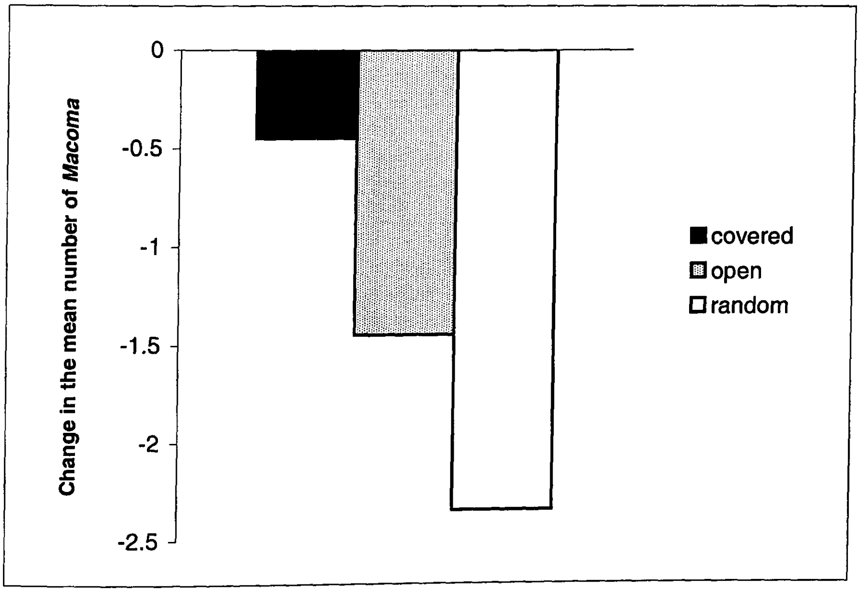


Fig 5.31: Change in the mean number of *Macoma* per treatment for all the study plots

5.3.3.3.3 Nereis

Considering the COVERED exclosures first there are increases in *Nereis* numbers in plots **1**,**2** and **4** and no change in **3**. All the RANDOM samples exhibited increases and the only decreases observed were in the OPEN treatments of plots **2** to

4. The OPEN treatment in plot 1 however shows the greatest increase of all the treatments in all the plots (Figs 5.32 and 5.33). There are significant differences in the change in *Nereis* numbers between the plots (F = 8.17, P = 0.005) with the overall change showing a significant increase in numbers across the plots (F = 6.00, P = 0.01) during the experiment (Table 5.12).

Table 5.12: Results of a quasi likelihood model for log*Nereis* ~ plot + treatment + before/after + plot * treatment + plot * before/after + treatment * before/after + plot * treatment * before/after

Factor	**Residual df**	**Residual deviance**	**F value**	**P value**
Plot	118	33.36	8.17	0.005
Before/After	117	31.53	6.00	0.01

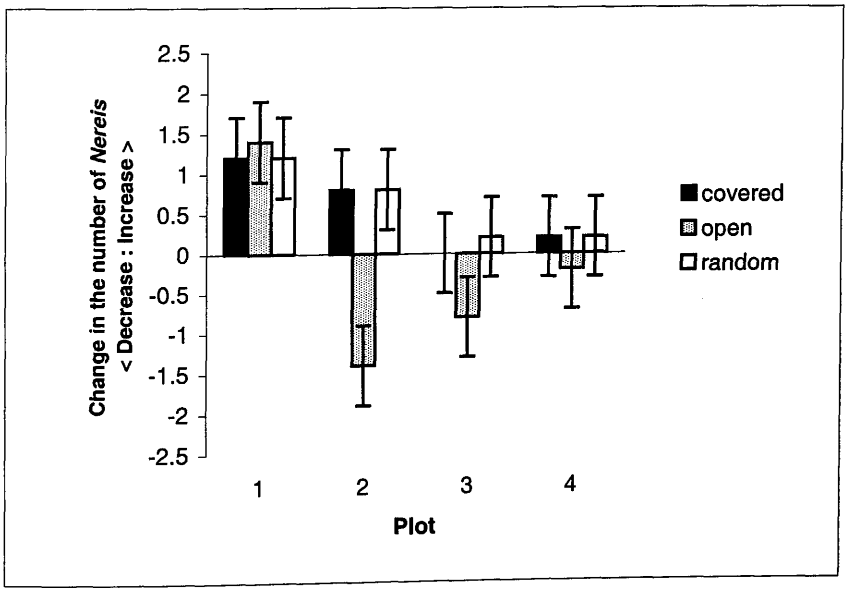


Fig 5.32: Change in the mean number of *Nereis* per treatment for each study plot

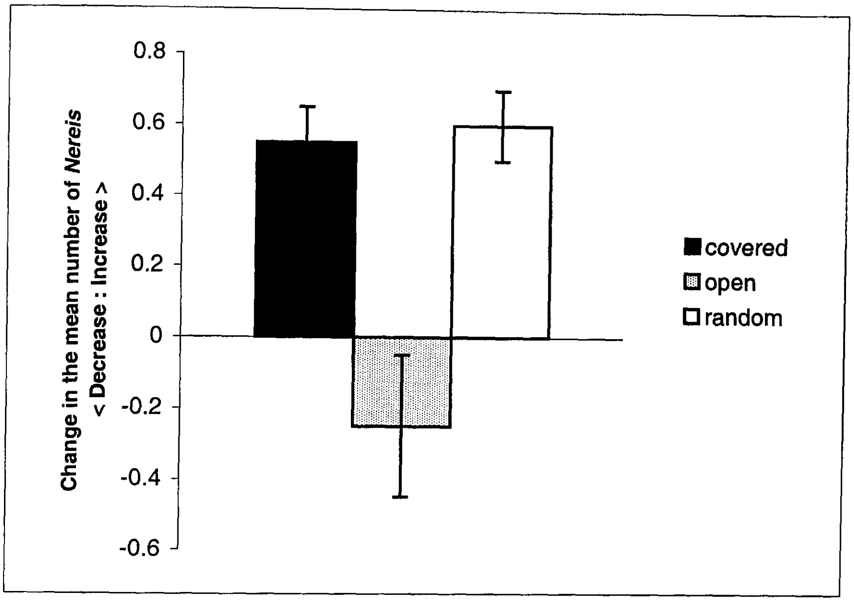


Fig 5.33: Change in the mean number of *Nereis* per treatment for all the study plots

5.3.3.3.4 Corophium

The significant interaction term, Treatment: Before/After (F = 16.29, P = <0.001) indicates that although there was a significant change in *Corophium* number (in this case a decline) it did not occur in all the treatments (Table 5.13). Declines were evident in the COVERED exclosures and the RANDOM samples but slight increases were seen in the OPEN treatments of plots **1** and **4** (Figs 5.34 and 5.35).

Table 5.13: Results of a quasi likelihood model for log*Corophium* ~ plot + treatment + before/after + plot * treatment + plot * before/after + treatment * before/after + plot * treatment * before/after

Factor	Residual df	Residual deviance	F value	P value
Before/After	118	36.27	14.65	<0.001
Treatment	117	35.41	3.31	0.07
Treatment:Before/After	116	31.16	16.29	<0.001

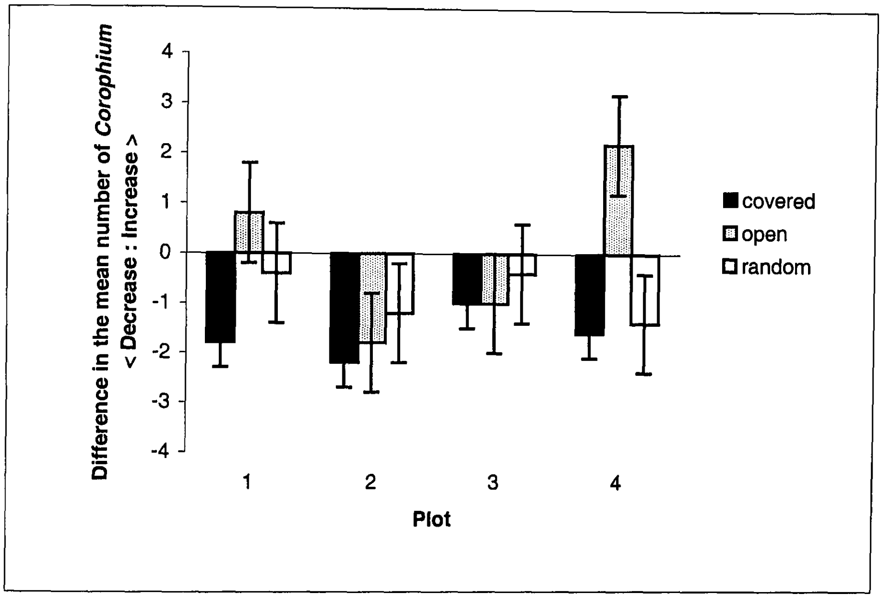


Fig 5.34: Change in the mean number of *Corophium* per treatment for each study plot

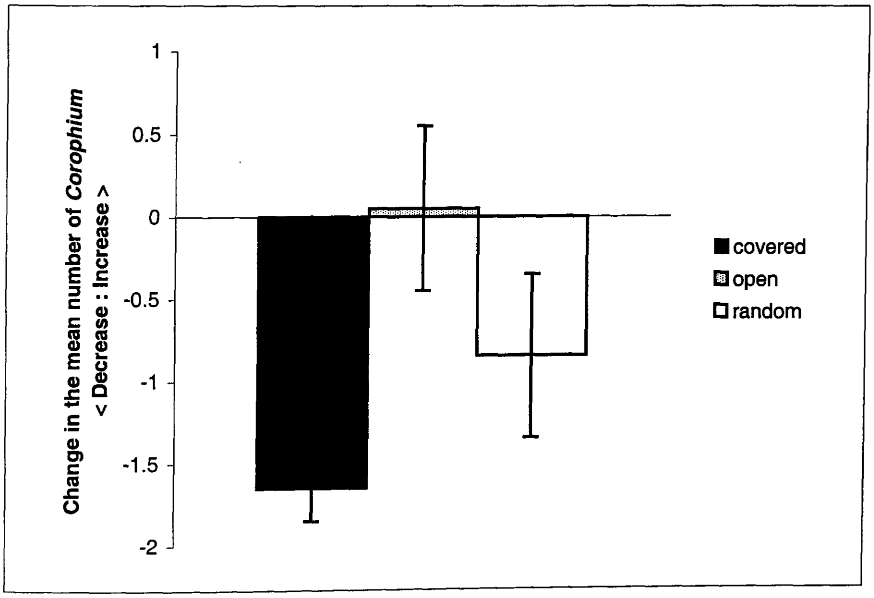


Fig 5.35: Change in the mean number of *Corophium* per treatment for all the study plots

5.3.3.3.5 All invertebrates

There was a significant decline in total invertebrate numbers during the experiment (Table 5.14) and this was greatest in the RANDOM samples in plot **3** and all treatments and RANDOM samples of plot **4**. Declines occurred to a lesser extent in all the treatments in plots 1 and 2 although there was a slight increase in the OPEN treatment of plot 1. When considering the all the plots, the RANDOM samples showed the greatest decline followed by COVERED treatment. The OPEN treatment declined in numbers the least (Figs 5.36 and 5.37).

Table 5.14: Results of a quasi likelihood model for log all invertebrates ~ plot + treatment + before/after + plot * treatment + plot * before/after + treatment * before/after + plot * treatment * before/after

Factor	Residual df	Residual deviance	F value	P value
Plot	118	10.20	0.99	0.32
Treatment	117	9.96	4.31	0.04
Before/After	116	8.46	26.53	<0.001
Plot: Before/After	115	7.82	11.50	<0.001

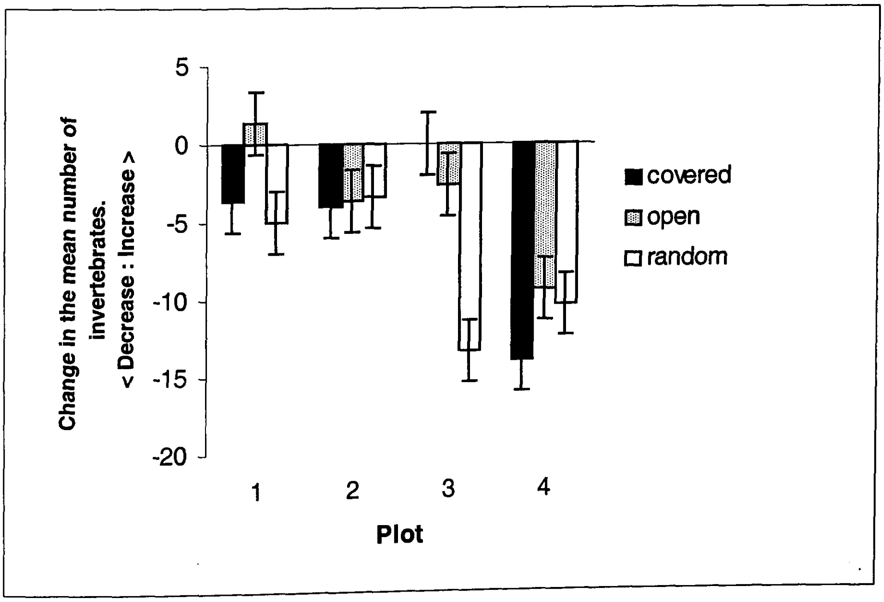


Fig 5.36: Change in the mean number of all invertebrates per treatment for each study plot

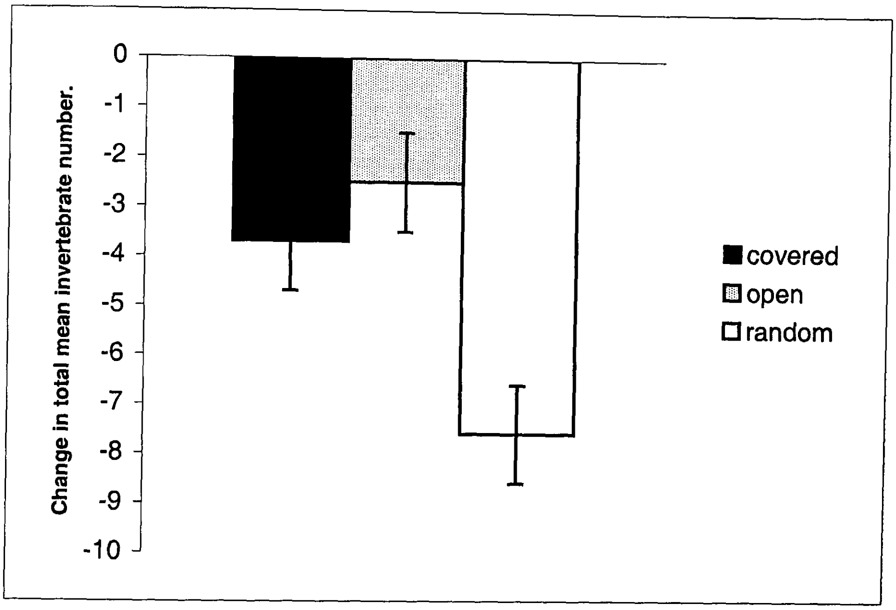


Fig 5.37: Change in the mean number of all invertebrates per treatment for all the study plots

The number of *Corophium, Macoma* and *Nereis* present in each plot at the start of the experiment were not significantly different but *Hydrobia* was (Table 5.15). Fig 5.38 shows the mean number (n=15) of invertebrates found in all the samples taken in each plot at the beginning of the experiment. As they were taken randomly within each plot they present a reasonable spread of data describing the densities of each invertebrate species. *Hydrobia* numbers were broadly similar in plots **1-3** but significantly higher in plot **4**.

Table 5.15: The difference in densities of invertebrates between the plots

Invertebrate species	**Residual df**	**Residual deviance**	**F value**	**P value**
Corophium	57	30.65	0.19	0.65
Hydrobia	57	27.24	7.81	<0.001
Macoma	57	29.90	1.71	0.19
Nereis	57	30.73	0.02	0.87

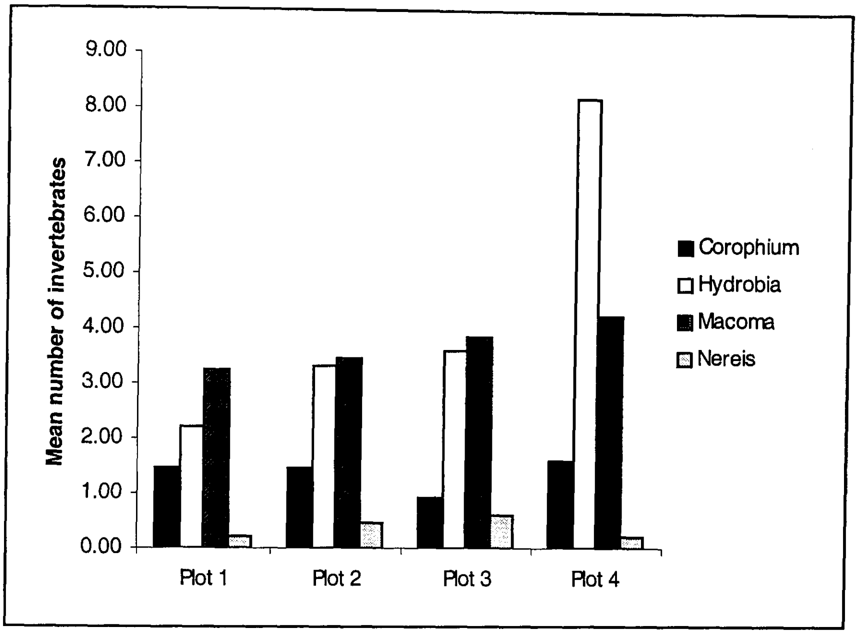


Fig 5.38: Mean number of each invertebrate species present at the beginning of the experiment in each study plot (n=15). The data used in this figure are taken from the initial samples collected from both treatments and the controls

5.3.4 Discussion

5.3.4.1 Did some plots have lower invertebrate densities at the end of the experiment ?

If the density of favoured food items was the main predictor of how a given species distributed itself at the 1 ha scale at Skinflats, then it would be reasonable to assume that bird numbers would be highest where prey numbers were highest (see Bryant 1979). The results in Table 5.15 show that there were no significant differences in the densities of *Corophium, Macoma* or *Nereis* between the plots therefore if food alone is the best determinant of bird density, those species that feed on these animals should be distributed evenly between the plots. This was not the case, Figs 5.22 & 5.23 clearly show that some species favour some plots over others. There is however a significant difference between the plots in *Hydrobia* density with much higher numbers of this mollusc at plot 4. Shelduck has been shown to favour *Hydrobia* in its diet on the Forth Estuary (Bryant 1979, Warnes 1981) therefore it might be expected that they would favour plot **4** over the other sites. Although the second most used site by shelduck, plot **4** was not the primary feeding site. The most numerous birds, redshank and dunlin clearly preferred plots **1** and **2** although there was no more food at these sites than at any other and depletion here was not the greatest.

5.3.4.2 Cage effects

Some authors have suggested that the very presence of an exclosure could have an effect that might bias any experiments by altering the physical environment (eg. sediment deposition, fouling, providing refuges both for predator and prey species of the invertebrates being studied (Virnstein 1978, Hulberg & Oliver 1980 and Olafsson *et al.* 1994, Sewell 1996). In this experiment, none of these potentially deleterious effects were observed around the pipe style exclosures. The fact that they were deliberately pushed into the mud so that only 2cm were protruding appears to have substantially reduced any potential changes in sediment structure. It is anyway debatable just how important such small-scale changes in sediment character might be to invertebrates (see Snelgrove & Butman 1994).

5.3.4.3 Hydrobia

The high mobility of *Hydrobia* would easily allow it to escape traditional exclosure cages such as those used in experiment 1. In this experiment however they should have remained confined in the COVERED exclosures. Small variation in plots **1– 3** was probably due to spatial heterogeneity and mortality but the dramatic significant reduction (F = 7.51, P = 0.007) in plot **4** is unexpected but not unsurprising considering the nature of the sediment at this site which is compacted and has the highest percentage of sand, lowest penetrability and lowest percentage of organic matter. It might be expected that *Hydrobia* would want to be able to range considerably wider than the bounds of the exclosure in such difficult conditions so it is likely that this reduction is attributable to treatment induced mortality. Significant differences between treatments (F = 4.80, P = 0.03) were evident as reduction was greatest in the RANDOM samples. If there was an overall depletion effect due to predation it should be detected here as birds have unhindered access to the invertebrate food stock. Although birds were not observed feeding within the OPEN treatments, possibly by choice, there still may have been some predation within them, although the shelduck which favours *Hydrobia* in its diet would have difficulty feeding within them due to their predominantly scything feeding action. The fact that the greatest reduction of *Hydrobia* occurred in the plots with the lowest bird predation pressure (**3** and **4**) suggests that either mortality is driving this depletion or predators other that shorebirds are responsible. Apparent predation effects on *Hydrobia* although measurable appear to be small.

5.3.4.4 Macoma

Of all the species considered *Macoma* is the most sedentary so any reductions in the OPEN treatments and RANDOM samples are likely to be the results of predation or mortality and not emigration and immigration. Although change was lowest in the COVERED exclosures, the low overall mean change was a product of decreases in plots **1**, **2** and **4** and an increase in plot **3**. This increase could only be due to spatial variability of Macoma within the small area inside the treatment. This indicates that even when potential for variability is reduced to this level it can still confound results especially when reductions are being measured on very small scales such as 1 or 2 individuals over the course of the experiment. Reductions were highest in the

OPEN treatments and RANDOM samples which might indicate a reduction due to bird predation. When all the variability in the data is considered there was a significant reduction of Macoma (F = 13.90, P = <0.001) and this reduction is lowest in the COVERED exclosures and highest in the RANDOM samples. This would concur with the expectation that areas open to predation will decline the greatest. However the greatest reductions occurred in the plots with the least birds so it remains unclear to what extent predation was driving the decline of *Macoma.*

5.3.4.5 Nereis

It is evident that there is a lot of variability in this data set. The overall increase in *Nereis* numbers in the COVERED exclosures and RANDOM samples is counter intuitive. In the COVERED exclosures, numbers would be expected to remain stable or decrease slightly due to mortality if the sub-surface walls of the treatment were indeed effective. These data suggest that they were not and that there was movement in and out of the treatments signifying that *Nereis* will freely burrow to depths of 18cm+ to remain mobile. Increases in the RANDOM samples do not suggest that *Nereis* were not being selected but only that, as some individuals are preyed upon, others move in making it very difficult to measure any predation effects whether they occur or not. The decrease in the open treatments is probably just due to density variability at the small spatial scale as well as movement of animals. This spatial variability could be responsible for the all the changes in this data set, as so few animals were found in all the samples in the first instance (n = 22). Smaller changes in plots 3 and 4 are probably due to the sandier, more compact nature of the sediment, which is likely to restrict *Nereis* movements.

5.3.4.6 Corophium

As with *Hydrobia* and *Macoma*, the decrease of *Corophium* in the COVERED exclosures (in this case all of them) was not expected but is probably not unusual. Possibly, spatial variability was confounding results but more likely, *Corophium* suffered natural mortality caused by entrapment within treatment itself. Declines are relatively uniform across the plots regardless of sediment structure, organic matter or shear strength so it seems likely that perhaps lack of light and consequent starvation due to retardation of the biofilm is a possible cause of mortality. Similar declines are evident in the RANDOM samples where the animals are free to move so this may be attributed to predation. Slight increases in the OPEN treatments in plots **1** and **4** are offset by decreases in **2** and **3** which might indicate that there is movement in and out of the treatments and that this movement accounts more for any changes in numbers than predation. *Corophium* may be preferentially moving into these treatments for shelter especially if birds are avoiding feeding within them (no birds were seen feeding within these treatments) which would account for the increases in **1** and **4** and the increase overall.

5.3.4.7 All invertebrates

The results for total invertebrate numbers show an almost universal decline across the treatments and present the most convincing evidence for a depletion effect. However, the cause of the depletion is less than clear. The COVERED exclosures were designed specifically to retain the invertebrates held within them at the start of the experiment and prevent any others from getting in. Any declines within these treatments should be almost entirely due to natural mortality (death or predation by another invertebrate) or treatment- induced mortality (death caused by the effects of the exclosure such as shading, feeding range restriction) and should be lower than any declines in the other treatments. It can be seen that in plots **2** and **4** declines were greatest in the COVERED treatment with that in plot **4** being the greatest overall decline of all the treatments. The high levels of mortality that occurred in this exclosure are problematic when trying to compare this decline against declines caused by predation. If mortality-induced declines are higher that those caused by predation then it will be very difficult to separate bird/fish induced depletion in the other treatments.

Significant declines were evident in both the OPEN treatments and the RANDOM samples, which do suggest an overall reduction in invertebrate numbers which, may be driven by predation. Results from the RANDOM samples in experiment 1 were inconclusive as it was assumed they were confounded by small scale local movements, however a larger sample size has revealed that depletion has occurred outside the treatments. Unusually, the greatest reductions of invertebrates have occurred in plots **3** and **4**, which had the lowest bird numbers. Plot **3** and **4** did not have any more invertebrates generally than the other plots at the beginning of the experiment but plot **4** did have considerably more *Hydrobia* than any other plot and there were significant declines of this species in this plot.

5.3.5 Conclusion

It is important to let biology underpin the interpretation of exclosure experiments such as this one and a good knowledge of the behaviour of the organisms involved, especially as regards their feeding ecology and relative mobility is required. Such knowledge can be applied when it is necessary to separate the direct effects of predation from the indirect effects of mortality, whatever its cause.

Although this experiment attempted to improve on some previous methods, it still failed to measure conclusively a reduction in the number of invertebrates that could be attributed to shorebird predation. Although invertebrate depletion appears to occur, factors other than predation, such as invertebrate movement and mortality may cause the observed local declines in invertebrate density. This experiment shows just how difficult this effect is to measure, even though it could be assumed that reduction of invertebrate numbers is likely to occur over the winter period. The failure to show any large-scale effects suggests that food supplies were not diminished to a point at which they became limiting for shorebirds, however birds are still limited by their competitive ability (Stillman *et al.* 2000). This moderate effect on the benthos may be explained in a number of ways. Firstly predation on the infauna does not always involve death, as regenerable parts such as siphons are often simply cropped (Peterson & Quammen 1982). Also birds and fish are limited in their access to prey by tidal exposure time and the burrowing behaviour of the prey in response to temperature. Large fish and birds can cause a change in the size composition of the infauna leaving many relatively small individuals and a few large ones in the presence of heavy predation pressure (Reise 1985).

Invertebrate densities and bird numbers have and will fluctuate on the Forth Estuary (McLusky *et al.* 2000). If there was a real predator-prey dynamic, these experiments were not powerful enough to detect it. The relationship between prey depletion, interference and carrying capacity and the affect that consequential food limitation constraints may have on shorebird distribution is discussed in chapter 7.

Chapter 6: Tracing the natal origins of the two races of redshank that overwinter on the Forth Estuary using ^{87}Sr/^{86}7Sr isotopic ratio fingerprints

6.1 Introduction

To understand the population dynamics of migratory shorebirds on a global scale it is often important to identify the breeding and wintering areas of different races of a single species. In Great Britain, for example the vast majority of redshank *Tringa totanus* belong to two races: *Tringa totanus robusta* that breeds in Britain and winters mostly in the UK and Ireland with some moving to France and the Netherlands (Cramp & Simmons 1993), and *T.t icelandica* that breeds in Iceland and winters in Britain (c60%) and Northern Europe. An understanding of the numbers of each of the races in an area allows the significance of any variation in breeding success of one race to be examined for its impact on the mixed-race wintering population as a whole and facilitates an effective conservation strategy to be developed on a site and species-specific basis. The redshank was chosen as the main study species not only because of its high conservation status on Scottish estuaries (Cranswick *et al.* 1999), but also because it is known that Icelandic birds winter in Scotland alongside Scottish birds (Hale 1973, Summers *et al.* 1988a).

Shorebird migration flyways in the Northern Hemisphere may cover thousands of kilometres, and involve non-stop flights between remote breeding grounds within the Arctic Circle and wintering areas in milder temperate regions. In order to ascertain natal or wintering origins of a shorebird species a number of mark- release – recapture / re-sighting methods have been employed. These include the use of metal or colour coded leg bands and flags, wing tags or plumage dyes. These methods can be both expensive and logistically demanding, however, and can also have low success rates. The use of radio transmitters and satellite tags is improving the level of understanding of migration routes (Johnson *et al.* 1997) but individual birds still have to be captured and the devices remain expensive. Other studies have inferred origin of species or races from biometric measurements (Summers *et al.* 1988a; Summers *et al.* 1988b; Atkinson 1996) and moult sequence (Furness & Baillie 1981 but see Mitchell *et al.* 1996). Morphological characteristics alone may not be enough to determine the exact location of a breeding area as there are often size differences between the sexes and clinal gradients in body size measurements (Wymenga *et al.* 1990). Problems of accuracy can also arise due to the variability introduced by large numbers of different individuals collecting biometric data (Barrett *et al.* 1989). DNA based approaches such as mDNA (Zink *et al.* 1996) and RAPD analysis (Haig *et al.* 1997) have also been used to distinguish between races and species of shorebirds and thus infer their geographical origins but these methods allocate individuals to populations and not to specific localities. In recent years the use of stable isotope analysis of bird tissue has proved to be a successful method for tracing the origins of migratory birds (Hobson 1999) because of large scale spatial variation of isotopic signatures that occur in food webs. If birds migrate between areas of distinct isotopic character and these signatures are reflected in tissues then it is possible to identify natal or wintering sites. The vast majority of the studies to date have concentrated on the use of $\delta^{13}C$, $\delta^{15}N$, $\delta^{34}S$ and δD (see Hobson (1999) for a review). In this study we explore the use of an alternative system, using strontium isotope ratios.

6.1.1 Strontium as a migratory tracer

Strontium isotopes have been used in a number of studies to trace the origins of migratory fish (Kennedy *et al.* 1997), mammals (van der Merwe *et al.* 1990; Vogel *et al.* 1990, Koch *et al.* 1995) and humans (Sillen *et al.* 1998, Price *et al.* 2000). Blum *et al.* (2000) and Blum *et al.* (2001) have used strontium ratios to determine sources of calcium in breeding black throated blue warblers (*Dendroica caerulescens*) but only Chamberlain *et al.* (1997) have explored the effectiveness of strontium isotope ratios as a migratory tracer for birds.

Strontium is a non-essential trace element and an 'analogue' of calcium, thus it is found wherever calcium occurs in animal tissues. Unlike other isotopes of lower mass such as carbon, nitrogen and sulphur, strontium is not affected by biological fractionation (Graustein 1989), hence the $^{87}Sr/^{86}Sr$ ratio in bone approaches a direct reflection of the underlying geology. The ratios in the birds' body tissue however will vary depending on their diet, the relative turnover rate of calcium in the tissue being tested and the relative concentrations of strontium in ingested rain water. The $^{87}Sr/^{86}Sr$ ratio in Scottish rain varies between 0.709 and 0.712 (Bain & Bacon 1994) and Iceland, although somewhat larger than Scotland, also has a maritime climate and is likely to have similar values (K.Grunvold pers com) The strontium ratio will also be affected by the mobility of the species being studied, as migratory birds will have differing proportions of strontium ingested at both their breeding and wintering areas. There is also the potential for strontium to enter the food chain via marine aerosols and this can have a marked influence on birds feeding near the coast. Vitousek *et al.* (1999) found that Sr ratios in the foliage of Hawaiian forests, and hence food chains more generally, was high close to the ocean but declined with distance from it (Andersson *et al.* 1990).

^{87}Sr is a decay product of ^{87}Rb. Thus its abundance relative to the stable ^{86}Sr is a product both of geological age as well as the amount of available rubidium in the environment. Hence the older the geology, the higher is the ^{87}Sr/^{86}Sr ratio. These differences in strontium ratios between areas of old and young geology were the main reason it was chosen for this study of the migration of shorebirds between Iceland and Scotland because Iceland is a geologically young area, strongly dominated by volcanism. The ^{87}Sr/^{86}Sr ratios in Icelandic rocks and soils are between 0.703 and 0.704 (Sin & Jahn 1975, Sigmarsson *et al.* 1992 and Hemond *et al.* 1993), which strongly contrast with the much older rocks (and consequently higher ^{87}Sr/^{86}Sr ratios) of the Scottish shield. In Scotland 0.711-0.723 has been recorded in the rocks and soils of Devonian andesites and 0.736-0.821 in Cambrian metamorphic areas (Bain & Bacon 1994).

6.1.2 The choice of tissue type for ^{87}Sr/^{86}Sr analysis

If strontium isotopes are to act as an effective migratory tracer, then whatever is incorporated into the tissue of a bird on its breeding or wintering areas must remain long enough for it to be identified at its destination without a level of mixing that might blur the signature of the two regions. Hobson & Clark (1992b) looked at turnover rates of carbon in the Japanese quail (*Coturnix japonica*) and found it to be fastest in the liver (half life = 2.6 days) and slowest in bone collagen (half life = 173 days).

6.1.2.1 Bone

The mineral matrix of bird bone is calcium phosphate hydroxyapatite [$Ca_{10}(PO_4)6(OH)_2$] and as strontium is substituted for calcium in this mineral it can be used for Sr ratio analysis. Bone tissue turns over rapidly in young birds at a rate much faster than in mammals (Gay 1988), and even hatchlings possess well-mineralised bones (Dacke 1998). Isotopic ratios are expected to be weighted to the signature of the diet during this initial rapid growth (Hobson & Clark 1992b). Different parts of the skeleton remodel at different rates, however, especially in juvenile animals, and caution must be exercised when choosing the type of bone for analysis and it location in the body. For instance bone types with a high ratio of trabecular bone such as vertebrae and the heads of long bones have higher turnover rates than the long bone cortex and skull (C.Dacke pers comm.) The greatest turnover rates are likely to be in medullary bone in adult females so it may be important to ascertain whether the bird is an egg-laying female. Wing bones such as the humerus, radius and ulna are all likely to contain some medullary bone, therefore the sex of the bird can have a considerable effect on the residence time of Sr in a particular bone type. As medullary bone is cycled rapidly during egg production (10-15 times faster than cortical bone (Dacke *et al.* 1993) $^{87}Sr/^{86}Sr$ ratios in it should be closer to the local signature. However, Blum *et al.* (2001) have shown that values in the femurs of black throated blue warblers (which contain medullary bone) were significantly lower than those in their food.

The most heavily remodelled bones are the long bone metaphyses; where the proximal tibia is likely to turnover its calcium in a few weeks with long bone diaphyses being slightly slower. The skull roof calvariae are usually not remodelled at all as they are designed not to erode and thus protect the cranium, so calcium residence time is likely to be much longer in this tissue (C.Farquharson pers comm.). The dermal bones of the mandible also have a very slow turnover rate (J.Skulan pers comm).

The choice of bone for analysis must therefore be relevant to the study in question. As migratory adults will have ingested strontium on both breeding and wintering grounds it will be present in their bones in varying proportions depending on the turnover rate of the bone isotope ingestion rates and the time spent feeding at each site. In this study we tested the appropriateness of the ulna as a bone for analysis in natal tracing studies. Although it is a lightly remodelled bone that contains some medullary bone we aimed to test the hypothesis that it would retain enough of its natal signal to allow Scottish and Icelandic birds to be distinguished in spite of the inevitable mixing of signatures. It was also chosen as wings are convenient to collect from corpses and are quite often all that is left of a raptor kill as the more suitable skull bones are rarely recovered. In this regard, the bone tissues could be obtained without capture or killing of the study species.

6.1.2.2 Feather

The use of feather tissue in migratory tracing studies using stable isotope ratios δC, δN and δD has proved to be very successful (Hobson & Wassenaar 1997; Cherel *et al.* 2000 and Hobson *et al.* 2001). In this study we show that there is enough measurable strontium in feathers to be able to use $^{87}Sr/^{86}Sr$ ratios from them. Apart from having a non-destructive sampling method the advantage of using feathers is that once they are fully grown they cease to exchange materials with the body and so only reflect the isotopic character of the diet ingested during their period of growth (Hobson & Clark 1992b). This means that the mixing effect from two or more strontium pools found in active tissue such as bone does not occur to the same degree, so feathers grown on breeding or wintering grounds should directly reflect the strontium signature of that area. The moult sequence of many species of birds is often well understood. If it is known when and where moult occurs and how long it takes for each feather type to grow it is possible to use feathers as a temporal scale to gain a better understanding of what a bird ate or where it had been during the growth phase of a particular feather (Mizutani *et al.* 1992, Thompson *et al.* 1998, Bearhop *et al.* 1999).

In this study we test the hypothesis that geologically derived strontium in the bone of Icelandic and Scottish shorebirds, particularly redshank, would be sufficiently different to allow the natal origin of species and races wintering in Scotland to be identified. We also test the use of feathers as a non-destructive alternative to bone and discuss the potential for application of this technique in future work.

6.2 Materials and Methods

All the shorebirds used in this study were collected in the field by volunteers and were either raptor kills or road kills. Icelandic birds (n=21) of 6 species were collected at sites in the southern lowlands (20° 21' W, 63° 50' – 64°10' N) or from the Lake Myvatn area (17° 00' W, 65° 35' N) during the spring/summer of 2000 (with the exception of

WAD 9 which was collected in summer 1999) (Table 6.1). Although redshank made up the bulk of the sample, other species included in the study were snipe (*Gallinago gallinago*), golden plover, whimbrel (*Numenius phaeopus*), ringed plover and dunlin. In order to characterise the Icelandic natal signal it was important to have a number of juvenile birds in the sample (n= 10) to ensure only the Icelandic strontium signature was present in the tissue. The $^{87}Sr/^{86}Sr$ ratios in the bones of Icelandic adults (n=11) would most likely be a mixture of both Scottish and Icelandic strontium but it is probable that a few individuals of some of these species such as the snipe (Cramp & Simmons 1993) overwinter in Iceland, even if most migrate. The wings were removed from all the birds found and imported to Scotland under licenses from the Icelandic Institute of Natural History and the Scottish Executive Rural Affairs Department license number IAPPPO/2000/136. Scottish birds (n=8) of 3 species, redshank, curlew and lapwing were collected at various sites around Scotland (Table 6.1) during the spring/summer of 2000 except Red 2, Cur 1 (summer 1999) and Lap 1 (summer 1991). Where possible a soil sample was collected from next to the corpse and in one instance insect material was collected from the vicinity of the bird for strontium ratio analysis. Although no significant difference between Scottish juveniles and adults was expected due to the lack of significant volcanic geology in their normal winter range, juvenile birds were included in the sample (n=3). The ulna was removed from each bird and manually cleaned after drying at 90°C for 12 hours. Claw material was also removed from one bird (RED 7). All samples were stored at –20°C before preparation for analysis. The feathers taken for analysis were all primaries.

6.2.1 Sample preparation

Bone was cut from the ulna (0.1-0.2 gm) and weighed. The bone was then ultra-soniced in de-ionised water for 5 minutes to remove any surface contamination. This process was repeated three times for each sample. The bone was then placed in a pre cleaned Savillex beaker and spiked with ^{84}Sr tracer solution. Samples were weighed before washing to avoid having to re-dry the sample. As the bone masses, and hence concentrations, are approximate (because the calculations are dependent upon the amount of fluids and organic matter in the bone), this procedure was considered expedient and acceptable. The concentrations should not be taken as more than guidelines i.e. ± 10% for the bone, whereas feather, nail, and insect should be close to the normal reproducibility for spiked analysis, i.e. ± 0.1% 1σ (Dicken 1995).

The samples were transferred to a class 100 laminar flow hood and dissolved in Teflon distilled, 16M HNO_3. The residue was converted to chloride using quartz-distilled 6M HCl and then taken up in 1 cm^3 of quartz-distilled 2.5M HCl. This was then centrifuged. Sr was separated from the solution using standard Dowex AG50W X12 cation exchange resin in a quartz column. Samples were then dried in clean Savillex beakers. The first samples to be run on the mass spectrometer did not run as well as expected i.e. they did not achieve desired precision. This was attributed to calcium interference and organic material causing instability. Two adaptations to normal procedures were made in the subsequent batches to address the problem:

1) An extra 1cm^3 of 2.5M HCl was washed through the column before the Sr was collected, to improve the removal of calcium.
2) The Sr residue was re-dissolved and dried down in 1 cm^3 of Teflon distilled 16M HNO_3 to remove any organic material that had passed though the column.

6.2.2 Isotope analysis

Sr was loaded onto an outgassed single Ta filament in a class 100HEPA-filtered cupboard. The sample was taken up in 8M Teflon distilled HNO_3 then loaded onto the filament with 1 microlitre of 1M H_3PO_4 (Suprapure) and dried down. Feather, claw, and insect samples were run using TaF method, (Birck 1986, Evans & Nowell 1986) which enhances the Sr emission of small samples. Samples were run using a Finnigan Mat 262 automated multicollector mass spectrometer. Unspiked samples were run in dynamic mode and spiked samples were run using static mode. $^{87}Sr/^{86}Sr$ was normalised during run time to $^{86}Sr/^{88}Sr = 0.1194$.

The majority of samples achieved an internal run precision of better that ± 0.000010 (1 SE). Some of the samples, especially the small samples from wing and feathers did not achieve this level of internal precision. Of these, all achieved between ± .000030-0.000010 internal precision with the exception of one sample, RED 13 which only achieved ± 0.000040.

6.2.2.1 Standards

A single run of the mass spectrometer comprises 13 samples of which between 1-3 are usually standards. The sample data are normalised to values for the international Sr standard NBS 987 of 0.710235 using the values of the NBS 987 standard for that particular run. This will be the average result if more than one standard was run. The standard values vary through time and between static and dynamic mode. Data associated with the samples in this study were as follows.

0.710271 ± 24 (2σ), n=12 static mode

0.710301 ± 36 (2σ), n=8 static mode

0.710255 ± 22 (2σ), n=6 dynamic mode

0.710252 ± 40 (2σ), n=12 dynamic mode

0.710318 ± 28 (2s); n=5 static mode

6.2.2.2 Blanks

All sample preparation procedures result in a mixing of the analyte in the sample with the same element in the reagents and the laboratory environment. The level of contamination can be determined by performing the entire chemical procedure in the absence of a sample: i.e. a blank run. During this study six blank determinations were made.

1. (P219:6)	190 picograms
2. (P219:13)	44 picograms
3. (P219:14)	41 picograms
4. (S89:14)	199 picograms
5 (S90:15)	277 picograms
6. (S90:16)	110 picograms

These values average 143 picograms, which is well within the expected range of values of c 100 picograms for acetic acid carbonate dissolution and high quality silicate dissolution of c. 250 picograms. The best result of 41 picograms is not far from the best value achieved in the laboratory of 31 picograms. All isotope analysis work was undertaken at the NERC Isotope Geosciences Laboratory, Keyworth, UK by Dr Jane Evans.

6.3 Results

6.3.1 All shorebird species

$^{87}Sr/^{86}Sr$ ratio values for bone samples of all species are presented in Table 6.1.

Table 6.1. $^{87}Sr/^{86}Sr$ ratio values for Icelandic (I) and Scottish (S) shorebirds of all species.

Sample number	Species	Location	Age	$^{87}Sr/^{86}Sr$ ratio
ICE 7	Redshank	S.Lowlands (I)	Adult	0.708314
ICE 6	Redshank	S.Lowlands (I)	Adult	0.708362
ICE 11	Redshank	Myvatn (I)	Adult	0.708475
ICE 10	Redshank	S.Lowlands (I)	Adult	0.708620
ICE 9	Redshank	Myvatn (I)	Adult	0.708713
ICE 8	Redshank	Myvatn (I)	Adult	0.708784
ICE 2	Redshank	S.Lowlands (I)	Juvenile	0.704531
ICE 3	Redshank	S.Lowlands (I)	Juvenile	0.705669
ICE 1	Redshank	S.Lowlands (I)	Juvenile	0.705684
ICE 5	Redshank	S.Lowlands (I)	Juvenile	0.706080
ICE 4	Redshank	S.Lowlands (I)	Juvenile	0.706665
ICE 12	Redshank	S.Lowlands (I)	Juvenile	0.708659
WAD 3	Snipe	S.Lowlands (I)	1st Summer	0.706207
WAD 2	Snipe	S.Lowlands (I)	1st Summer	0.706751
WAD 1	Snipe	S.Lowlands (I)	1st Summer	0.707797
WAD 4	Whimbrel	S.Lowlands (I)	Juvenile	0.705143
WAD 5	Whimbrel	S.Lowlands (I)	Juvenile	0.705622
WAD 6	Whimbrel	S.Lowlands (I)	Juvenile	0.706167
WAD 9	Dunlin	S.Lowlands (I)	Adult	0.705897
WAD 7	Golden plover	Reykjavik (I)	Adult	0.707135
WAD 8	Ringed plover	S.Lowlands (I)	Juvenile	0.708729
RED 7	Redshank	S.Uist (S)	Adult	0.709268
RED 1	Redshank	Orkney (S)	Adult	0.709361
RED 2	Redshank	Orkney (S)	Adult	0.709395
RED 5	Redshank	N.Uist (S)	Adult	0.710070
RED 4	Redshank	Islay (S)	Juvenile	0.708580
RED 6	Redshank	N.Uist (S)	Juvenile	0.709710
LAP 1	Lapwing	Perthshire (S)	Adult	0.709017
CUR 1	Curlew	Stirlingshire (S)	Juvenile	0.710515

The initial GLM for these data included all the adult and juvenile shore birds from both Scotland and Iceland to see if this technique may be applicable to other shorebird species. After stepwise deletion of non-significant factors there was a highly significant difference in the $^{87}Sr/^{86}Sr$ ratios of Scottish and Icelandic birds (F=23.65, P=<0.001) and a significant difference in these ratios between adults and juveniles (F=5.34, P=0.02). Two outliers had a marked affect on the fit of the model and involved two Icelandic juvenile birds with relatively high Sr ratios compared to adults (redshank (WAD 8) = 0.70859 and ringed plover (ICE 12) = 0.708729 where the mean for Icelandic juveniles is 0.706316 +/- 0.001380 see Fig 6.1). With these two outliers included in the model the best r^2 value attainable was 0.55.

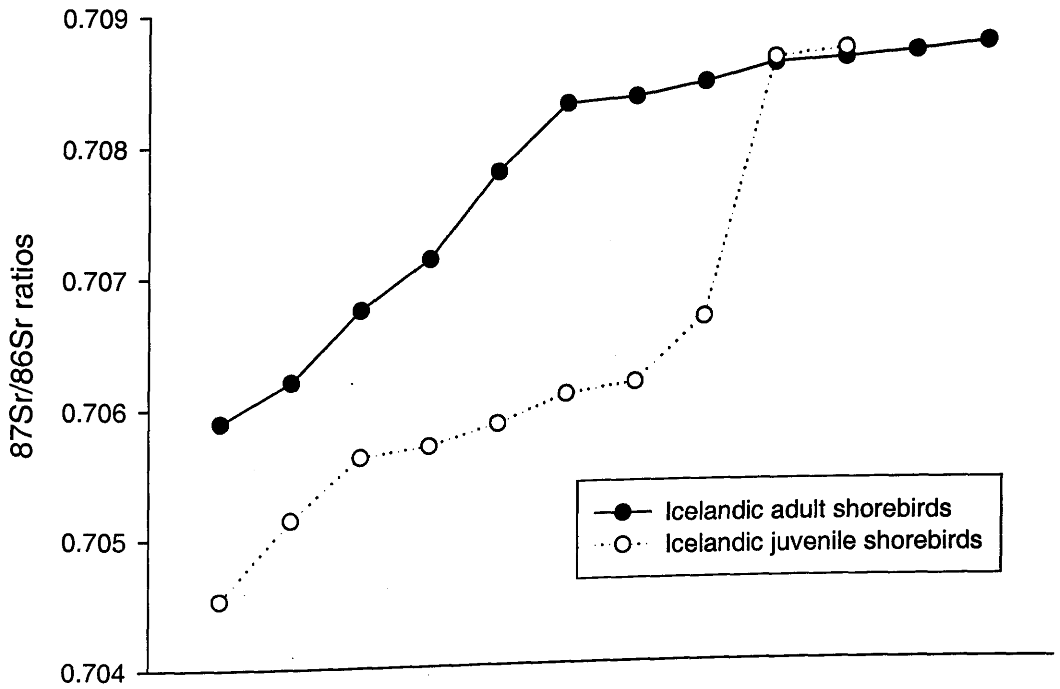


Fig 6.1: Isotope values for juvenile and adult Icelandic shorebirds ranked in ascending order illustrating the two Icelandic juvenile outliers with high $^{87}Sr/^{86}Sr$ ratios.

When the two outliers were excluded from the model its power to explain the variation in the data increased markedly (r^2=0.91). The highly significant difference between Scottish and Icelandic birds also remained, (F=111.95, P=<0.001) and the difference between adults and juvenile birds was also significant (F=7.45, P=<0.01). The difference in ^{87}Sr/^{86}Sr ratios between redshank and other species is location-dependent with the greatest difference occurring on the Icelandic breeding grounds (F=6.48, P=0.01) where redshank had the highest values. In Scotland this difference was much smaller and with other species having marginally higher values than redshank.

The difference in strontium ratios between adults and juveniles was also strongly dependent on location (F=24.17, P=<0.001) with the greatest difference evident in Iceland with Icelandic juveniles having considerably lower values than adults. In Scotland this difference was much smaller although juveniles had slightly higher strontium ratio values than adults did. The difference between adults and juveniles was greater in redshank than in other species which only displayed a small decrease from adults to juveniles (F=13.41, P= 0.002) but the difference between redshank and other species was less in Scotland with other species being slightly higher. The interaction plot (see Fig 6.2) illustrates the differences between birds of known Scottish and Icelandic provenance, adults and juveniles and between redshank and other species.

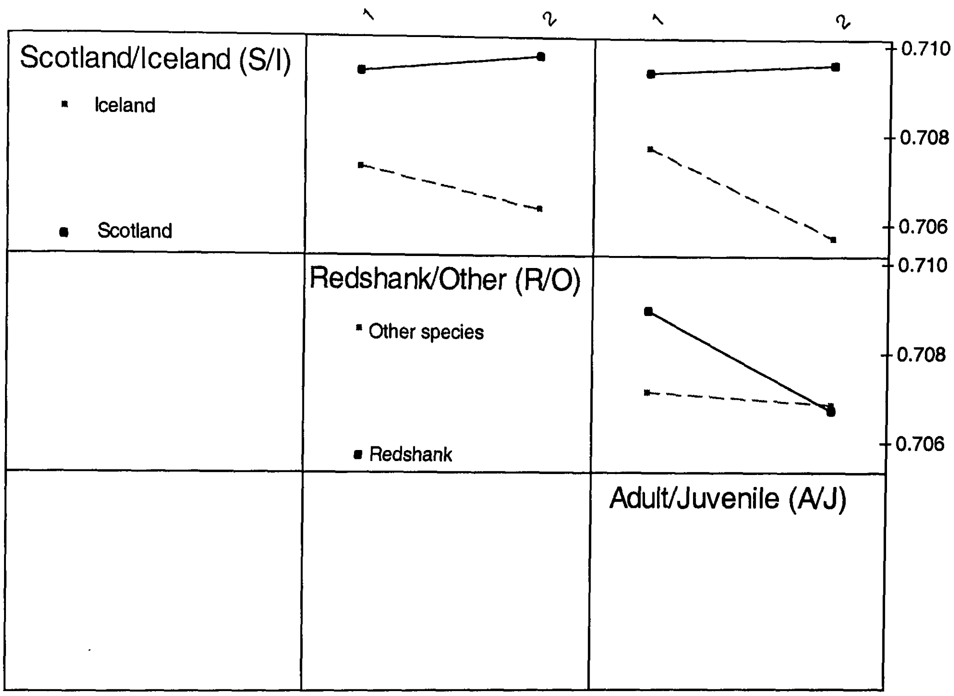


Fig 6.2: Interaction plots for Scotland/Iceland * Adult/Juvenile, Scotland/Iceland*Redshank/Other and Adult/Juvenile*Redshank/Other (all outliers excluded)

The three-way interaction Scotland*Iceland + redshank*other species + adult*juvenile was not significant (F = 0.04, P = 0.85).

6.3.2 Redshank

When just the ^{87}Sr/^{86}Sr ratios from redshank bone alone were considered the difference between Scottish and Icelandic birds was significant regardless of age (F = 60.11, P = <0.001), (the outlier ICE 12 was excluded). There was also a significant difference between adults and juveniles within each country (F = 31.54, P = <0.001), although this was only significant in Iceland (F = 18.22, P = 0.001). The interaction plot (Fig 6.3) illustrates the differences between Scottish and Icelandic and adult and juvenile redshank. The difference in the data means 'A' for Scottish adults and juveniles is considerably lower than that for their Icelandic counterparts 'B'. This suggests that even though the Scottish adults may have wintered much further south in northern

Europe or the Iberian Peninsula, the range of Sr values was not significantly different from those in Scotland.

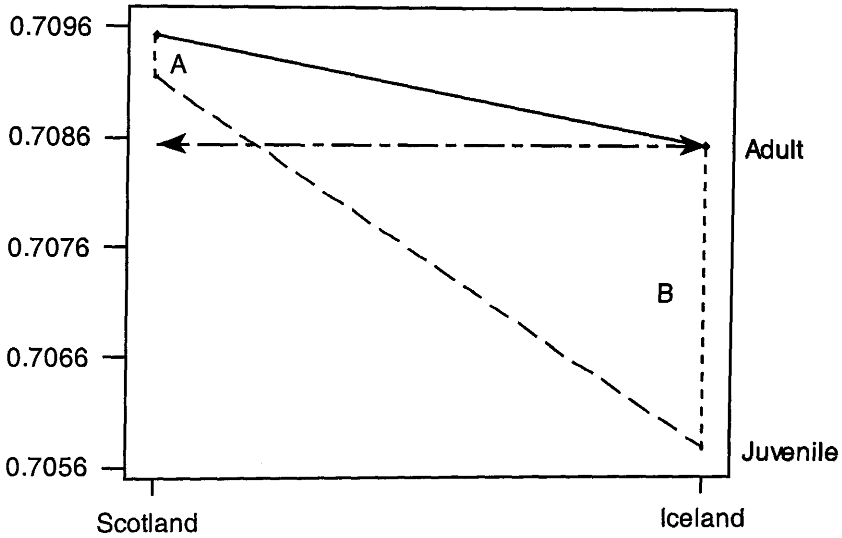


Fig 6.2: Interaction plot of redshank adult (solid line) and juvenile (dashed line) data means in Scotland and Iceland. The arrowed line indicated the hypothesised minimum value for Scottish birds.

This shows that the difference in Sr ratios between the breeding and wintering areas of Scottish redshank are trivial compared to the Icelandic birds, exemplifying how distinct was the range of Sr values for Icelandic birds.

6.3.3 Feather, claw and soil

Feather and claw materials were analysed to determine whether it was possible to obtain a reliable $^{87}Sr/^{86}Sr$ signature from it. Soil samples were also analysed from some to see if these values corresponded to those in the bones and feathers. For RED14 (north Uist chick), feathers and bone had very similar values (Fig 6.3) suggesting a close correspondence between these two tissues if a bird has remained at one site. This relationship is to be expected, as RED 14 had not yet fledged so would have had a limited foraging range. The soil ratio at this site was the same as seawater, probably due to the effect of sea spray on North Uist, a small island off the west coast of Scotland exposed to strong onshore winds from the Atlantic Ocean. Although the soil Sr ratio was the same as seawater, dietary Sr in bone and feather is somewhat lower suggesting that invertebrate prey have lower signatures than the soil or that there is some considerable geological variation in Sr levels at this site.

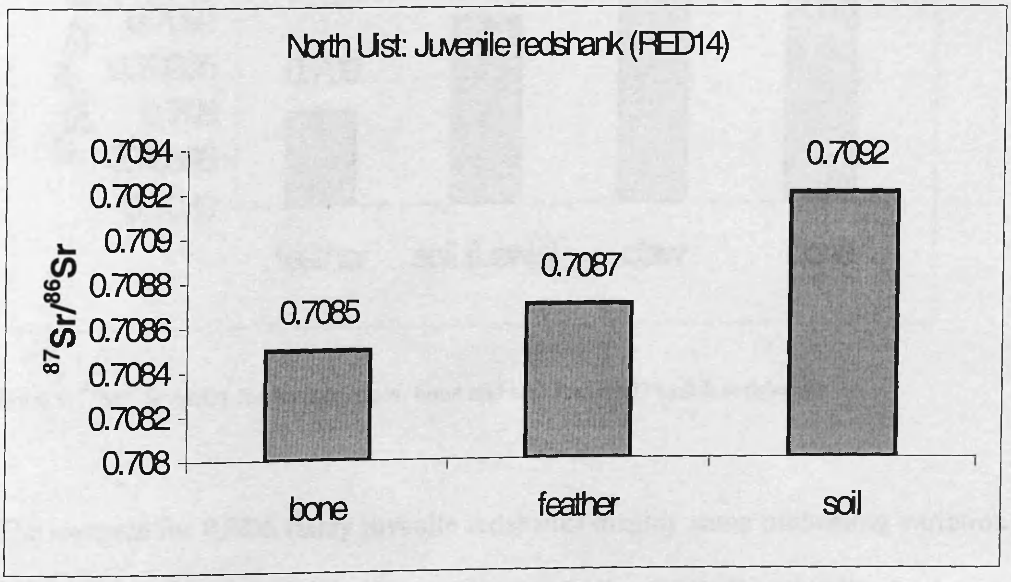


Fig 6.3: $^{87}Sr/^{86}Sr$ values for bone, feather and soil for RED 14 (redshank chick)

In the adult South Uist redshank, RED 7, feather, soil and bone values are very similar (Fig 6.4). The value for soil on south Uist was inferred from the mean of four samples taken from the Isle of Lewis Machair, which has very similar dry soils, it is also very similar to the value obtained for soil on North Uist. The similarity between bone and claw material for RED 7 suggests that claw clipping may be a non-destructive source of tissue when sampling from large birds such as geese. The claw is a small bone covered with a keratin sheath and although the sample in this analysis was < 0.01g it yielded enough strontium to measure the ^{87}Sr/^{86}Sr ratio.

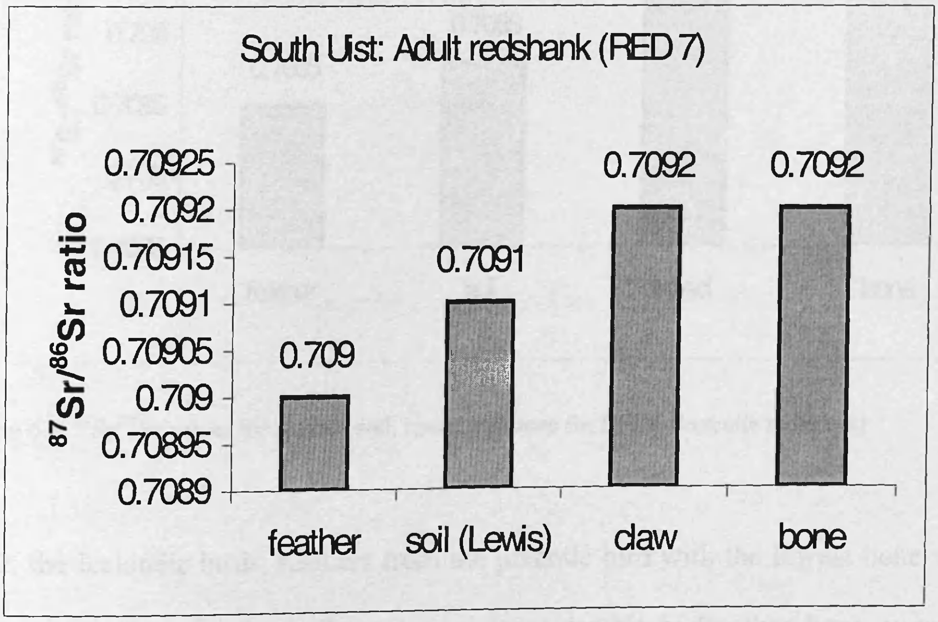


Fig 6.4: ^{87}Sr/^{86}Sr ratios for feather, claw, bone and soil for RED7 (adult redshank)

The samples for RED6 (Islay juvenile redshank) display some interesting variation (see Fig 6.5). Values for feather and soil are very similar suggesting that the feathers tested were grown in the area the bird was found. The bone value for this bird is somewhat higher suggesting that the bird was hatched at another site with greater $^{87}Sr/^{86}Sr$ values. The value for the insect (a noctuid moth) suggests that there may be some considerable variation on Islay as it is different from the feather value. Its $^{87}Sr/^{86}Sr$ value was very similar to the bone for redshank however suggesting that it was of local origin and had not immigrated.

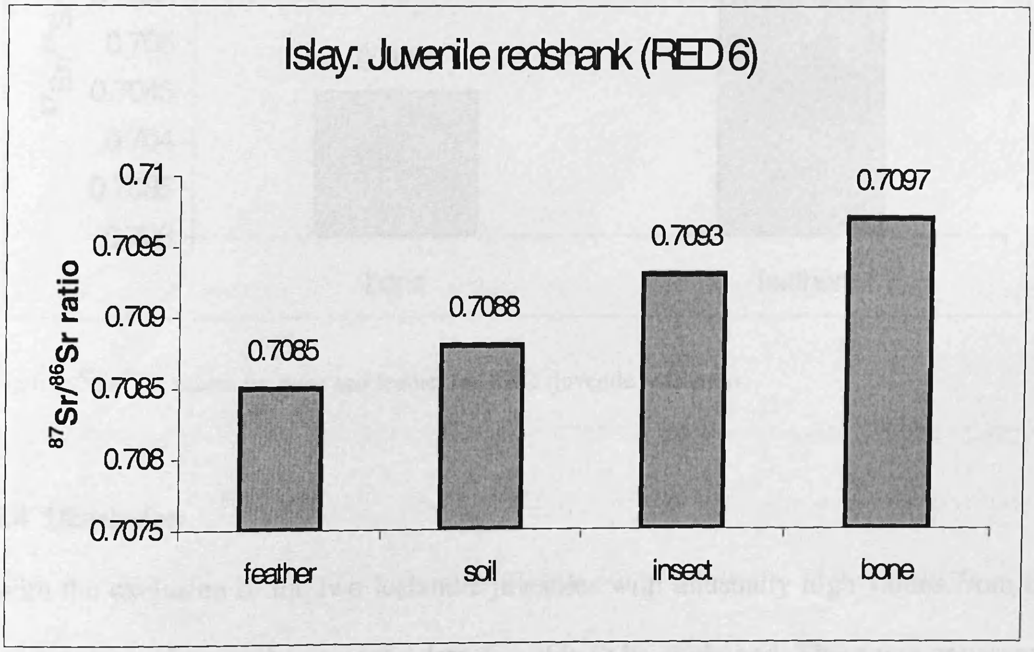


Fig 6.5: $^{87}Sr/^{86}Sr$ values for feather, soil, insect and bone for RED6 (juvenile redshank)

Of the Icelandic birds, feathers from the juvenile bird with the lowest bone value were chosen. In this case the feather value was considerably higher than bone, suggesting that it developed at a more coastal site, but it was still lower than all Scottish values (see Fig 6.6).

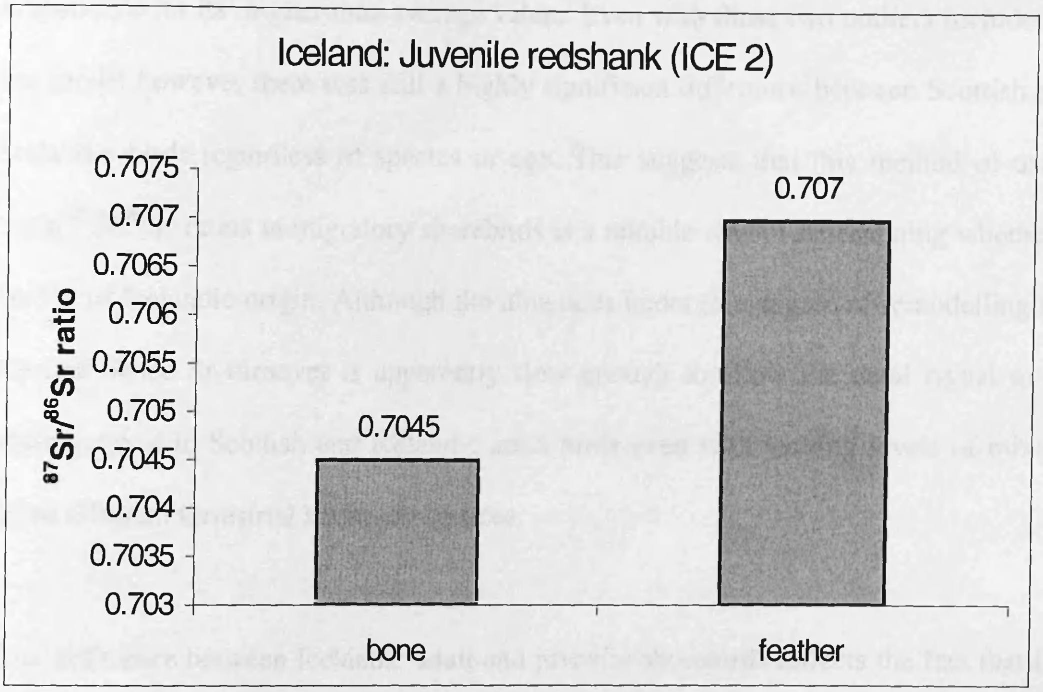


Fig 6.6: ^{87}Sr/^{86}Sr values for bone and feather for ICE2 (juvenile redshank)

6.4 Discussion

With the exclusion of the two Icelandic juveniles with unusually high values from the model more of the variation in the data was able to be explained. There was apparently a confounding factor which raised the outlier Sr values above the mean juvenile value (redshank (ICE 12) = 0.70859 and ringed plover (WAD 8) = 0.70872 where the mean for Icelandic juveniles is 0.70631 +/- 0.00138). This was likely due to the effect of strontium from a marine source in the diets of these birds, elevating the ^{87}Sr/^{86}Sr ratio in their bones towards that of seawater (0.7092). Ringed plover mostly nest at coastal sites and generally have a dominant marine component in their diet although they also breed at suitable inland sites in Iceland. The redshank (ICE12) was also found at a coastal site and it is likely that the influence of marine derived strontium was responsible for its' higher than average value. Even with these two outliers included in the model however there was still a highly significant difference between Scottish and Icelandic birds regardless of species or age. This suggests that this method of using bone $^{87}Sr/^{86}Sr$ ratios in migratory shorebirds is a reliable way of determining whether a bird is of Icelandic origin. Although the ulna does undergo a degree of remodelling the Ca and hence Sr turnover is apparently slow enough to allow the natal signal to be distinguished in Scottish and Icelandic adult birds even with varying levels of mixing from different terrestrial strontium sources.

The difference between Icelandic adult and juvenile shorebirds reflects the fact that the adult birds for the most part have spent the winter on estuaries and coastal sites in the UK and northern Europe. In winter the diet of shorebirds such as redshank and dunlin are essentially marine, involving mainly estuarine invertebrates, however some species like the lapwing, golden plover, curlew and snipe often have a considerable or dominant terrestrial component to their diet and habits, due to feeding in arable fields or largely fresh water environments. The ingestion of either marine derived strontium or strontium from an underlying geology with considerably higher $^{87}Sr/^{86}Sr$ ratios than the Icelandic volcanism has evidently raised their Sr isotope signatures above the natal mean.

Even allowing for the fact that Icelandic birds do migrate to Scotland, their $^{87}Sr/^{86}Sr$ ratios remain highly significantly different from Scottish birds. Icelandic juveniles, however, have much lower $^{87}Sr/^{86}Sr$ ratios because they are only representative of the

Icelandic dietary signal, having not yet migrated to wintering grounds further south. The small difference between Scottish adult and juvenile birds is to be expected, even though many of the adults may have wintered further south in the UK or northern Europe. It is highly unlikely that any of the birds will have visited an area with $^{87}Sr/^{86}Sr$ ratios low enough to significantly alter their natal signature, as there are no other areas in their winter range with $^{87}Sr/^{86}Sr$ ratios known to be as low as those of Icelandic volcanism. The fact that Scottish Juveniles have slightly higher values than adult birds may be due to the fact that the adults have been wintering on sites with lower bioavailable $^{87}Sr/^{86}Sr$ ratios or that a more marine dominated diet is lowering the adult signature.

The difference in $^{87}Sr/^{86}Sr$ between adults and juveniles is considerably greater in redshank than all the other species and this may either be a product of diet, differential rates of calcium cycling, wintering site choice or time spent on wintering grounds. This difference is surprising however as the adult redshank appear to have retained a large amount of their winter strontium well into the summer (all birds were collected between mid June and late July) and appear to be returning to Icelandic dietary levels at a much slower rate than the other species. Using the mass balance equation below given by Blum *et al.* (2001) a rough calculation can be made of the amount of winter-derived strontium that still remains in the Icelandic adults on their breeding grounds.

$$_{\text{winter Sr in bone}} = [(^{87}\text{Sr}/^{86}\text{Sr})_{\text{bone}} - (^{87}\text{Sr}/^{86}\text{Sr})_{\text{summer}}] / [(^{87}\text{Sr}/^{86}\text{Sr})_{\text{winter}} - (^{87}\text{Sr}/^{86}\text{Sr})_{\text{summer}}]$$

Theoretically an adult redshank should have an average strontium value that represents the time it spends in both Iceland and its wintering grounds in Scotland. Redshanks generally arrive on wintering areas in mid July and return to their breeding areas around mid April (Cramp & Simmons 1993). This is proportional to c 70% winter strontium and 30% summer strontium. Although food samples were not analysed for Iceland it is possible to estimate their likely value by taking the mean of the bone strontium for the all the Icelandic juvenile waders. With no fractionation expected up the food chain (Graustein 1989), the value of food and water ingested by these birds should be directly reflected in their bone signatures. This value should be somewhere between the value for Icelandic soils (0.703) and that of rain/seawater (0.709) depending on the relative concentrations of Sr in the two components; in fact the mean value for the Icelandic juveniles is 0.706 (+/- 0.00138). This figure concurs with the findings of Åberg (1995) who obtained a value of 0.706 from the bone of an Icelandic reindeer. As the adult redshank mostly feed on estuarine invertebrates in the winter it can be assumed that the winter food value is going to be close to or the same as seawater. Using this equation for all six Icelandic adults the proportion of winter strontium in their bones was calculated at 72-87% but even with such high levels of Scottish strontium in their bones there was enough Icelandic strontium to enable differentiation between Scottish and Icelandic birds. Although the bulk of the Icelandic redshank arrive in August with 45% Icelandic birds on Scottish estuaries by September (Summers *et al.* 1988a), some arrive as early as late June and this would increase the winter strontium input for these individuals. As none of the adult Icelandic redshank had Sr values approaching that of the juveniles (and the natal signal) it can be tentatively concluded that they were all migratory and that none of them wintered in Iceland. Some birds however do winter on Icelandic estuaries and shores so it would be instructive to determine the Sr ratios in the bones of these birds to see if there is overlap with the migratory population.

Of the other species, snipe are mostly migratory, although some birds do winter in Iceland; therefore it may be expected that the average amount of winter strontium in this species could be lower than redshank. For this species the Summer food value was estimated to be the same as redshank but the winter value is probably likely to be higher due to the terrestrial component in the diet of the snipe. Because of this it was expected to be higher than seawater.

The mean of the Scottish juveniles of all species was taken to reflect the likely range of bio-available strontium values (0.7096 +/- 0.0006, n=3), but due to the low sample size it was prudent to add one standard deviation to the mean thereby raising the critical value to 0.7101. When the mass balance equation was applied to the three Icelandic adult snipe, a range of 0-37% winter strontium was estimated. This is an anomalous result as it would be expected that snipe should have similar if not higher values than redshank, reflecting their more terrestrial habits in the winter. It is of course possible that any or all of these birds spent the winter in Iceland and it is possible that this is the norm rather than the exception. The snipes respective values of 0.7077, 0.7067 and 0.7062 are all very similar to the value estimated for the Icelandic diet. If they had migrated to Scotland some mixing would have been expected. Two of the snipe were first summer birds, which would have only left Iceland once unlike the adults who have migrated least twice. These younger birds may have $^{87}Sr/^{86}Sr$ ratios closer to their natal value. Alternatively all the birds may have similar values, suggesting that there is a relatively seasonal shift in strontium values between summer and winter for the Icelandic migratory population. The difference was found not to be significant (F=0.39, P=0.578) when just species other than redshank were considered, however this does assume that all the birds are migratory and that none of them wintered in Iceland. It is possible that calcium cycling in this species is considerably slower than in the redshank.

The Icelandic golden plover population is wholly migratory, spending their winters mostly in Ireland and the west coast of Britain and also France and NW Iberia. As they too share a similar diet to the snipe in that it is potentially a mix of both marine and terrestrial, the winter food value of 0.7101 was used. In this instance a single adult bird (0.7071) was estimated to have 21% winter strontium, another low value. This is indicative of a largely terrestrial diet in Iceland as is likely to be the case.

These lower values for the snipe and golden plover may relate to the amount of time that these species spend on breeding and wintering grounds. Both species leave Iceland in October and return in April giving them six months at each site. This equates to 50% summer Sr and 50% winter Sr. It would be expected that adult values could be solved by the following equation:

$$\mathbf{(^{87}Sr/^{86}Sr)_{winter} - (^{87}Sr/^{86}Sr)_{summer}/100(50)}$$

giving an average value of 0.7079. The values for the adult snipe and adult golden plover are 0.7077 and 0.7071 respectively. Using a similar equation for adult redshank with their estimated vales of 70% winter strontium and 30% summer strontium.

$$(^{87}\mathrm{Sr}/^{86}\mathrm{Sr})_{\text{winter}} - (^{87}\mathrm{Sr}/^{86}\mathrm{Sr})_{\text{summer}} / 100(70)$$

This gives an average value of 0.7080, which is virtually the same, as the value for the snipe and golden plover, therefore the time spent on wintering grounds does not seem to have an influence. The failure of these equations to account for the differences in redshank and the other species is probably most likely due to either low sample size or the variability in the geology in wintering areas. It is of course possible that Sr levels in winter Icelandic redshank either never reach seawater or are elevated well above it due to high Strontium ratios in the estuarine mud. The vast majority of Icelandic redshank are thought to winter in Scotland (Summers *et al.* 1988[a]) so it follows that winter strontium levels in the diet of the redshank should be a minimum of 0.7092.

As the snipe were collected mid to late summer, like the redshank it might be expected that their values would be similar but this is not the case. These differences depend on the residence time of Sr in bird bones, which is not yet understood and needs more research. Hobson (1992a) calculated that carbon in bone collagen would completely turnover in 346 days, therefore if calcium behaves in the same way as carbon it might be expected that the mixture of summer and winter strontium would be approximately 50/50. The species with winter strontium values lower than 50% such as the snipe and the golden plover suggest that their values are returning to that of the Icelandic diet. Adult redshank however are higher at 72-87 %. As this appears to have nothing to do with time spent on wintering and breeding grounds it suggests that the redshank in this analysis are ingesting a relatively high marine component in their Icelandic diet as well as terrestrial invertebrates with values likely to be close to that of the soil (see Blum (2001)). This would raise their potential Icelandic Sr input range above 0.706, thus the proportion of winter Sr calculated in the above equation may not be all from the previous winter but may be partially derived from coastal sources in Iceland.

This uncertainty about Sr residence time in bone and the potential for mixing of the Scottish and Icelandic Sr pools in individuals lend weight towards the use of feathers in future work.

6.4.1 Feathers

The Sr variation in shorebird feathers suggests caution should be exercised when choosing which type of feather to analyse. It is important to use feathers that are grown at the natal area and not those that may incorporate isotope signals from other sites. All wing feathers are grown at the same time and in redshank this takes about 60-90days (I. Mitchell pers com). As birds move to the coast after fledging the marine component of their diet may serve to raise Sr levels in feather tissue if the feathers are still growing. Conversely values in feathers may be lower than bone if the bird moves to an area of lower Sr values. Although this doubtless elevated the Sr value in feathers of the juvenile Icelandic redshank, the mixing did not occur fast enough to equilibrate the feather value with that of seawater. A larger sample size will be needed to determine whether the variation is Sr ratios is greater between rather than within Icelandic and Scottish breeding grounds.

The fact that the best model excluded those juvenile birds whose Sr ratios had been influenced by the marine environment suggests that this technique would be highly suited to tracing more terrestrial waterbirds or passerines e.g. pinkfooted goose, meadow pipit (*Anthus pratensis*) or redwing (*Turdus iliacus*) where the influence of a marine diet will not be a complicating factor.

6.5 Conclusion

This work tested the hypothesis that the stable isotopes of strontium in the bones and feathers of migratory shorebirds could be used to identify the natal origins of shorebirds in mixed race populations on Scottish estuaries and found that there were significant differences in the bone $^{87}Sr/^{86}Sr$ ratio between Icelandic and Scottish birds of all species tested. There were also differences between adults and juveniles but this was location - dependent and only evident in the Icelandic birds, the adults of which had apparently ingested strontium of non-Icelandic origin whilst in Scotland. Differences in strontium isotope ratios were directly related to the contrasting geology of the two countries, with Icelandic juvenile birds displaying much lower $^{87}Sr/^{86}Sr$ ratios than their Scottish counterparts. Similar but less marked differences were apparent between adults and juveniles in spite of dietary mixing between breeding and wintering grounds amongst

Icelandic birds and the effect of marine aerosols on coastal birds that tended to push the background geological signal towards that of seawater.

This work shows strontium isotope ratios in the bones and feathers of birds can discriminate those hatched in Scotland and Iceland and can potentially determine the crude proportions of different races of the same species in mixed wintering populations. Such an analytical tool may be of some considerable use in studies determining the spatial distribution and density of shorebirds especially when such work is informed by events on breeding grounds. If Icelandic birds are known to have had a particularly poor breeding season it might be expected that the proportion of that race using a Scottish estuary would be depressed allowing their Scottish counterparts to colonise winter feeding territories without the level of competition usually experienced from incoming migrants. The implications of this work and recommendations for improvements and future study are discussed in chapter 7.

Chapter 7: General Discussion

7.1 Introduction

The purpose of this study was to predict the potential effects of habitat change on the distribution and feeding effort of the shorebirds that overwinter on the Forth Estuary. To this end, *weighted area models* were developed at the sub-estuary scale using a GIS format, which utilised Generalised Linear Models relating shorebird feeding effort to a suite of predictor variables.

The findings of these models varied between the whole-estuary scale and the single site scale although some covariates were common to all models for each species. Throughout this study attempts were made to improve on previous work, for example by greater accuracy of the methodological approaches. It is with this in mind that a laser diffraction technique was employed to measure sediment characteristics and careful thought was given to the best way to measure the organic fraction within it. Sampling regimes for invertebrates were designed to give a broad representation of density within the study plots and shorebirds were monitored on a through-the-tide basis and spatially mapped, avoiding problems arising from shorebird censuses at high tide roosts or at low water. Innovative geo-statistical approaches were employed to account for the spatial structure of the data and comparisons were made to a more conventional linear approach.

The *weighted area models* indicated a preference for high-level mudflats throughout the estuary, which was often linked to locally variable densities of preferred invertebrate prey species and sediment characteristics. The output from the contemporary models was then compared to long term data for both bird feeding effort and invertebrate densities at a single well studied intertidal site, Kinneil. To provide a wider context for this work, an attempt was also made to determine whether or not the food supply available to the shorebirds was limiting, with the aim of exploring the concept of 'carrying capacity' as applied to estuaries (Sutherland 1996, Goss Custard *et al.* 2002). Also isotopic techniques were employed to see whether it was possible to characterise the geographical origin of shorebirds using the estuary.

7.2 The weighted area models

It was evident from integrated studies of shorebird feeding effort, invertebrate densities and sediment characteristics, that there was some variation both within and between sites on the Forth Estuary and this was emphasised by the range of predictor variables, which explained shorebird feeding effort at these sites. Nevertheless, while shorebird feeding effort was linked to the density of a variety of invertebrate species (for shelduck, the density of *Manayunkia* was the most important predictor at all scales) and sediment characteristics, the most striking feature of the models was that for all the key shorebird species there were either negative relationships with distance from the shore, or positive relationships with tide height. This finding emphasises the importance of high level mudflats. This has implications for any habitat change that may occur around the mudflat edges such as land-claim or increased disturbance from anthropogenic sources, as these high level areas are clearly important for the majority of the birds that use the Forth Estuary. The management implications then are clear, high level mudflat areas have, in general, a high 'feeding effort' weighting and are relatively more important to the key species feeding on the Forth Estuary than other areas more distant from the shore. Piecemeal landclaim around the edges of a mudflat or changes in landuse that may cause disturbance to feeding or roosting birds (e.g. building new developments close to the edge of the intertidal) are likely then, to have a disproportionately negative effect on birds feeding in these high level areas.

7.2.1 Proposed Improvements to the *weighted area* models and maps

Numerous methods have been used to construct habitat suitability models for a wide variety of bird species at a range of different scales (Naugle *et al.* 2000, Uhmann *et al.* 2001, Storch 2002). Such models have been used to design and plan nature reserves (Van Langevelde *et al.* 2000), predict the effects on bird distribution of successional habitat change (Hunt 1998) or determine the effects of anthropogenic habitat alteration at the site and landscape scale (Green & Stowe 1993, Hansen *et al.* 1993, Roseberry & Sudkamp 1998).

Some of these models have used parameters suitable for large scale habitat attributes such as the presence or absence of wooded areas (Dettmers *et al.* 2002, Lauver & Busby 2002) or finer scale information like detailed woodland structure (Nelson & Beuch 1996). Often such model input is limited to presence/absence data (Buckland *et al.* 1998, Lenton *et al.* 2000) or on limited habitat factors chosen by 'expert judgement' only (Hansen *et al.* 1993, Tucker *et al.* 1997, Tamis & Van't Zelfde 1998).

This study incorporates various aspects of many of the above models, but attempts also to improve on some of them, as the habitat suitability model is strictly quantitative and constructed at the single site scale (750ha). It uses fine scale observational evidence of feeding effort, linked to interpolated spatial information of the variables that best predict this effort based on ground truth measurements. This approach has the advantage of being able to combine the results of robust statistical models predicting feeding effort with geostatistical interpolation and GIS mapping techniques to create *weighted area maps* that can be used to inform management decisions at the sub-site scale.

For all the species of shorebird on the Forth Estuary there was more than one *minimum adequate model* that could be used to explain distribution of feeding effort at all scales considered. The criteria for model acceptance in this study was that the model be biologically credible and have the least residual deviance. Obviously the first of these two criteria is open to debate where it might be suggested that only the 'best looking' model was chosen. This was mitigated to some degree by opting for the lowest deviance but there are improvements that can be made to this approach by considering more than one model. In some of the models shown in chapter 3, covariates that might have expected to be retained in the models such as *Hydrobia* density for the shelduck model (Bryant 1979), narrowly failed to reach the 0.05 probability level. Two or more models therefore, can be considered together using this mapping approach described in section 2.11.3 as long as the residual deviance is within a predetermined maximum acceptable limit. It is likely that the use of more than one model will still see the retention of covariates common to both or all models. The coefficients of these models can be inputted into a GIS along with the relevant kriged information for the covariates and weighted in the same way using the same scale. The resultant maps can then be overlain and compared firstly to each other and then to the actual shorebird feeding effort. To get a quantitative measure of the association or dissociation between any two sets of mapped data 'spatial analysis by distance indices' (SADIE) methodology can be used (Perry 1995, 1997, 1998, Holland *et al.* 1999, Perry & Dixon 2002)

7.2.2 Spatial analysis by distance indices (SADIE)

SADIE operates by comparing the spatial arrangement of the observed sample with other arrangements derived from it to determine whether counts of two variables are associated or not. The SADIE approach contrasts with geostatistics for the following reasons.

- SADIE is designed for situations where species are distributed in discrete aggregations ('patches') with relatively well-defined boundaries. In this instance each weighted class has such boundaries.

- SADIE is more concerned with the measurement and testing of spatial pattern, rather than the geostatistical goal of estimation of density in unsampled areas.

The method assesses similarity on the basis of clustering indices, down-weighting outlying density values.

Spatial association might also be used to quantify temporal change, for example when the same shorebird species is counted at the same area on successive occasions. This could be applied to within or between winter data and measures spatial instability or the rate of change of spatial distribution. The example below considers the spatial patterns of a beetle *Pterosticus melanarius* and an aphid

Metapolophium dirhodum, sampled on a 12m x 12m grid (Winder *et al.* 1999) and determines whether two populations may be spatially positively associated, negatively dissociated or occur at random with respect to one another. At each sample unit, the cluster indices of beetle and aphid are measures of their local spatial pattern and the extent to which the cluster indices 'agree' at each point provides a measure of spatial association. The results of this experiment indicate strong negative dissociation between beetles and aphids (Fig 7.1)

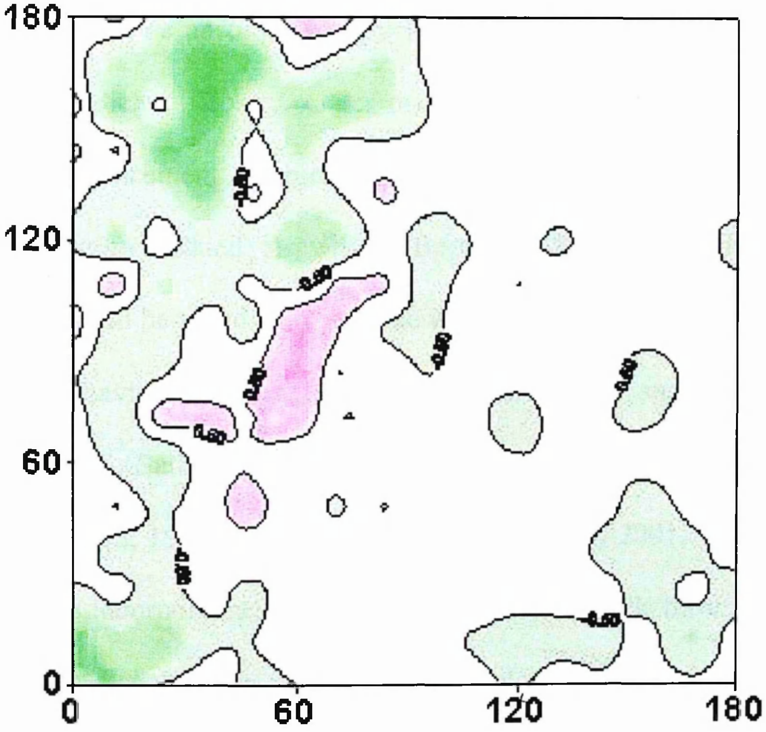


Fig 7.1: The map illustrates the measure of association between a population of predatory beetles and their aphid prey in an experimental area. Areas of strongly positive association are shown in plum, and strongly negative dissociation in green. On the whole, it is the green areas that predominate, indicating overall dissociation (From Winder *et al.* 2001)

Such methods could also be used to look at the association between the feeding effort of pairs of species to determine areas of feeding effort overlap. This might be especially useful when making management decisions that may affect more than one species. An example would be managing for teal by increasing or not reducing organic inputs. This might have a negative effect on dunlin which are known to be at low density when teal are high (Bryant & McLusky 1991). Such associations may also reveal evidence of competition between species e.g. dunlin and knot.

7.2.3 Giving dynamism to the weighted area model using cellular automata

The effects of localised habitat change are simple to quantify in terms of displaced or lost feeding effort, but in order to give the model an element of dynamism it would be an improvement if the spatial redistribution of displaced birds could be predicted. Clearly, under many scenarios, habitat degradation or loss will lead to displacement of birds in the first instance, at least some of which may be accommodated elsewhere (Burton 2000). To predict patterns of redistribution would be an advantage if the results of models that considered the consequences of behavioural interactions between individual shorebirds (Sutherland & Anderson 1993, Sutherland & Dolman 1994, Goss Custard *et al.* 1994, Goss Custard *et al.* 1995a, 1995b, Sutherland 1996b, Gill *et al.* 2001, Goss Custard *et al.* 2002) could be incorporated. While individual based models have much potential with regard to predicting losses at the scale of whole estuaries, the need to incorporate information at the sub-estuary scale will commonly be required. This is because degradation of estuaries (e.g. landclaim for industry) often occurs at this scale. Combining the benefits of the weighted area approach (which identifies areas of particular value), and the individual based modelling approach is therefore more appealing and potentially valuable. The use of cellular automata may represent a useful move in this direction.

Cellular automata are computer simulations of dynamic systems where space, time, and the states of the system are discrete (Adamatzky 1994). Each point in a regular spatial lattice, called a cell, can have any one of a finite number of states. The states of the cells in the lattice can be updated according to a local rule. That is, the state of a cell at a given time depends only on its own state one time step previously and the states of its nearby neighbours at the previous time step. All cells on the lattice are updated synchronously. Thus the state of the entire lattice advances in discrete time steps. Some examples of previous models include those that seek to predict schooling behaviour in fish (Vabo & Nottestad 1997, Stocker 1999, Schonfisch 2001) and spatial aggregation behaviour in ant colonies (Cole & Cheshire 1996, Morale 2001).

Bahr & Bekoff (1999) developed a cellular automata that was designed to predict vigilance behaviour in feeding birds using a set of simple rules. This model, however, did not incorporate the effects of bird gender, age or dominance, nor did it allow the birds to move. Such a model could be developed to include such properties and adapted to predict the response of feeding birds to habitat change. Rules governing individual behaviour in response to depletion and interference (see Sutherland (1996a) could be incorporated, as could hierachical elements such as dominance versus subordinate interactions (Bahr & Passerini 1998a, b). As an area of intertidal mudflat can be spatially *weighted* in terms of its relative importance for feeding shorebirds (this study) the strength of such interactions can be weighted accordingly, depending on the population size attributed to the model area. As chosen portions of the weighted area map are 'removed' or 'adjusted' (i.e. by the effects of pollution) to simulate habitat change, the behavioural rules written into the model will determine which birds will move to the next most suitable area. The 'social temperature' (Callen & Shapiro 1974) can also be raised or lowered in relation to density or simulated environmental factors. The type of collective behaviour observed in a group can depend on the group's social temperature with 'consensus' more likely at higher temperatures and fragmented pockets of 'majority' and 'minority' opinions at lower social temperatures (Bahr & Passerini 1998a,b). In the case of this proposed model, negative pressure on feeding rate and intake due to depletion and disturbance will convince more birds to move from an area of good feeding quality to a less favoured area when this 'social temperature' is high. It would also be possible to manipulate food resource abundance and to set a maximum 'carrying capacity' for the model site which if exceeded would determine what proportion of the birds being modelled would have to leave the site. The carrying capacity of a site may be changed in response to disturbance (Burton *et al.* 2002a,b), variation in food abundance (Colwell & Mathis 2001, Goss Custard *et al.* 2001) or habitat loss such as sea level rise (Austin *et al.* 1996, Holloway *et al.* 1996, Colwell & Mathis 2001) or engineering works (Schekkerman *et al.* 1994). It would also be possible to consider a similar mirror image model to see if overspill of birds could be accommodated in a less favoured area (based on food availability etc.).

7.2.4 Application of these weighted area models to other estuaries

There is potential to use the models developed on the Forth Estuary at other estuaries. This must be attempted with caution, however. It has been shown in chapter 3, that there is some variability in the significant variables that predict shorebird feeding effort at the sub-estuary scale. The methodology, however, is transferable regardless of the character or location of the estuary and it would be instructive to test this approach at another site. The preference for high level mudflats by shelduck, dunlin and especially redshank has been shown for the Forth Estuary, and if it can be assumed that such preferences are generalisable to other estuaries, then the findings of the Forth Estuary models may be of use when making management decisions elsewhere. The most appropriate sites for such tests would be those on the east coast of Scotland, which have a broadly similar character to those on the Forth.

7.2.5 The use of other GIS platforms

Although the *weighted area models* were developed using ARCVIEW, there are more flexible GIS packages which have habitat suitability models already developed for them. One such model is the VVF (Valutazione della Vocazionalita Faunistica) designed by Ranci Ortigosa *et al.* (2000) which is linked to the GIS Grassland (LAS 1996). This computer program has been developed to assess the suitability of a territory as habitat for a species. It integrates several types of habitat suitability models into the GIS and allows a user to create, modify and store new habitat suitability models for different species. This could be applied to estuarine sites where a wide range of physical conditions exist i.e. variations in substrate and levels of disturbance at the sub-estuary scale.

7.3 The validity of the weighted area approach in the long term: testing the long-term stability of the estuarine community at Kinneil

The estuarine environment is in a constant state of flux, yet intertidal areas can be remarkably stable in the long term (Elliot *et al.* 1998). Habitat change events such as pollution, disturbance or land claim may affect the estuarine community and determine the numbers of animals a site can support and how they distribute themselves in space. The models described in chapter 3 were developed to predict the spatial feeding distribution of shorebirds on the Forth Estuary with a view to assessing the potential effects of such habitat change. They were, however, completed during one winter. Chapter 4 considered the stability of the distribution and density of shorebirds and invertebrates and the nature of the estuarine in the short to long term with a view to justifying use of the current models in future years. Long-term (1976-2000) changes in the number and spatial distribution of shorebirds at Kinneil were evident. Nevertheless some species were more consistent in their use of certain areas of the mudflat than others. Redshank strongly favoured high level (>3m ACD) areas of the mudflat in all years emphasising the importance of such areas and the vulnerability of this species to any increase in disturbance from the shore or upper shore land claim events (land claim is most likely to affect high level areas). Shelduck also favoured the area between the >3-4m contours and in recent years have greatly increased in the >4m area probably as a result of pollution mitigation. This suggests that high level flats are also preferred feeding sites for shelduck. Knot and dunlin were more variable in their distribution over the long term but all species have increased their use of high level mudflats since 1980. The evidence for preferential use of high level areas in the short term is more convincing, with no significant differences in the way all species used the mudflat between the winters of 1998/1999 and 1999/2000. During a single winter shelduck, redshank and dunlin all consistently favoured the area >3m ACD in all months from November to March, whereas knot were more widely dispersed.

Invertebrate densities have also fluctuated in the long term (1976-2000) (McLusky *et al.* 2000) and although some species such as *Manayunkia* have declined in recent years most of the species excepting *Manayunkia*, Spionids and *Nephtys* exhibit a similar long-term stability (Fig 4.33). In the short term (single year) there are apparent declines in densities of almost all species between summer and winter but it was found that between years the winter densities of all species except *Oligochaetes* and Spionids were not significantly different suggesting that populations may remain relatively stable during the winter months.

Changes in sediment structure were also considered but with a lack of any long term data for the Forth Estuary evidence from the literature was examined. It is known that invertebrates can influence the cohesiveness of sediment structure (Austen *et al.* 1999, Widdows 2000) and that shorebirds can also do so by feeding on the invertebrates that graze on the diatoms which produce cohesive carbohydrates. Excepting storm events and major anthropogenic change, any fluctuations in sediment structure are likely to be mirrored by fluctuations in the invertebrate population and the shorebirds that feed on them. It is concluded that sediment structure characteristics are stable in the long term.

Overall, long term fluctuations in shorebirds and invertebrates are evident but there is still evidence of considerable stability. This stability is most noticeable in the short-term and it may be that the estuarine community at Kinneil has now adjusted to recent changes in the way industrial effluents are disposed of at this site. The implications of long-term patterns described here for the models developed in this study are that they are likely to be valid at least in the short term and for species like shelduck and redshank which display more predictable distributions over time they are likely to be useful for some years, or likely decades, to come. It is proposed however that they be updated on a regular basis by limited complementary fieldwork to test these assumptions.

7.4 The further use of geostatistical methods in characterising and predicting the spatial distribution of regionalised variables.

Geostatistics has been defined by Matheron (1963, 1984) as "the application of probabilistic methods to regionalised variables", a regionalised variable being, any variable distributed in space (or time). The values of such variables are implicitly assumed to be correlated with one another. As has already been explained in more detail in section 2.11.1, geostatistics differs from conventional statistics in that it searches to reveal the structure of spatial correlation (Armstrong 1998). This accounts for the intuitive idea that points close in the space are likely to have similar values. In other words randomness does not mean independence. What makes geostatistics powerful is its capability to characterise that spatial structure by means of a consistent probabilistic model. Therefore the predictions made using the geostatistical methods are tailored to the intrinsic structure of the variable and not only to the samples numbers and sampling patterns. This spatial structure is characterised by the variogram.

In this study geostatistics has been used to estimate the spatial structure of biotic (benthic invertebrates and shorebirds) and abiotic (sediment characteristics) variables at the whole mudflat scale from random point samples and complete data collected at the 1ha scale. These data were then used to construct the *weighted area models* (section 2.11.3) based on the coefficients of the GLMs. Further potential uses of geostatistics are described below.

7.4.1 Determining the optimal sampling design for mapping over-wintering shorebirds

This study has illustrated that the estimation of the spatial distribution of estuarine bird feeding effort based on visual assessment can be an extremely time consuming process. However, the need to derive detailed maps of the distribution of these birds necessitates representative counts of birds. A random sampling procedure is unlikely to be appropriate since the distribution of shorebirds is clearly conditioned by a range of localised factors. In addition, the sample spacing must be sufficiently fine to ensure that the variation of interest is captured. Conversely, more samples than is necessary to resolve variation of interest are not desirable. The variogram can be used to characterise spatial variation in shorebirds where the birds have been mapped exhaustively over 1ha plots. The model fitted to the variogram can then used in conjunction with kriging to ascertain the sample spacings required to achieve different degrees of precision i.e. will allow the researcher to design an experiment with the optimum number of study plots at optimum distances apart. If spatial variation in shorebirds can be considered similar at other sites, the results of a study of this kind offers a powerful tool for ecologists and other researchers who are concerned with mapping a range of different species.

7.4.2 The application of conditional simulation for assessing the sensitivity of inputs to models of estuarine shorebird distribution

It is important to quantify the sensitivity of a model to its inputs. For example, if a map of shorebird distribution is derived through interpolation from sparse observations then the interpolation algorithm employed will affect both the output map and the results of the model into which the map is inputted. One way to assess the fit of a model in such a case is to employ conditional simulation to generate several equally-probable realisations of the property of interest. Each of the realisations can then be inputted into the model in turn and the impact of using different realisations on the model output can be assessed. A sequential Gaussian simulation can be employed for this purpose. Pereira *et al.* (1999) used this approach to characterise the spatial distribution of shorebirds on the Tagus Estuary, Portugal. A number of realisations of shorebird distributions were generated and input into a predictive model. The results provided an indication of the confidence in which model outputs could be held and were used to inform land managers of the potential bird displacement effects that the construction of a bridge across the site might have.

7.4.3 Characterising spatial variation in the distribution of estuarine invertebrates: assessing the validity of scaling up count measurements

It is often the case that concentrations of shorebirds are estimated visually over study areas of 1ha or more (Scheiffarth *et al.* 1996, Yates *et al.* 1993). The mapping of these birds is often informed by their relationship with the invertebrate food resource on which they feed. The invertebrate concentrations are measured through extraction of small volumes of sediment (typically 5 cm^2). In usual practice, these small invertebrate samples are considered to be representative of much larger areas than covered by the sample itself. Typically, invertebrates are counted both within the areas where shorebirds are and at other locations. Therefore, linear regression is employed to estimate shorebird numbers at locations where invertebrates only are sampled. Clearly, if the assumption that spatial variation of invertebrates is homogenous over larger areas than that over which they are sampled is unfounded, then the mapping procedure is flawed. To test this assumption, a grid of 10 by 10, 5 cm^3 observations could obtained with a sample-spacing of 10 m within a one hectare block. The spatial distribution of invertebrate counts can then examined using a range of approaches including moving window statistics and the variogram. This will determine the spatial variation of invertebrates across the block and inform the validity of using a 5cm^2 core to represent the invertebrate density contained within 1ha.

7.5 Does the carrying capacity of a site have to be reached before birds are at risk of starvation or displacement?

Carrying capacity has been defined in section 1.3, where it was mentioned that equilibrium population size at a site may be reached before the estimated value for carrying capacity (Sutherland 1996, Goss Custard *et al.* 2002). It cannot therefore be assumed that simply because carrying capacity may not be reached as on the Exe Estuary (Goss Custard *et al.* 1998), a change in the size or condition of a site would not affect the birds using it. Goss Custard *et al.* (2002) developed a model, which indicated that birds could starve or emigrate at population sizes below that required to reach the 'maximum' carrying capacity for a site.

If the carrying capacity of a site is reduced, due to habitat loss or change, then it is possible that a number of shorebirds will either starve or be permanently displaced. Equally such habitat changes, regardless of the importance weighting given in the models described in chapter 3, (i.e. as per the scale on each map), will have no affect on displaced shorebirds as long as their chances of survival and reproduction are unaffected. Evidence suggesting that a site does not have to be at 'carrying capacity' before birds are displaced or excluded, however, means that birds emigrating from one site due to density dependent processes may find it hard or impossible to settle at another, because competition throughout its winter range is likely to increase with loss of any habitat, thereby increasing mortality. (Pettifor *et al.* 2000). Goss Custard *et al.* (2002) suggests, therefore, that as carrying capacity does not have to be reached before birds will emigrate, it is important to determine whether reduction in food supply or intake rate via permanent or temporary habitat loss or disturbance is density dependent. If this is the case, any proposed changes to an estuary are likely to increase mortality rates and reduce the proportion of birds that are in good condition prior to migration to breeding grounds, thereby compromising survival or reproductive success. If there is no evidence of such density dependent effects, then habitat loss may only have a local effect, with displaced birds being accommodated elsewhere.

7.6 How important is habitat change induced prey depletion for shorebird survival?

The purposes of the exclosure experiments described in chapter 5 were twofold. Firstly they set out to test and improve upon methods used in previous experiments and secondly they sought to measure any depletion effect that predatory shorebirds might have on their invertebrate prey.

Depletion of food resources has been shown affect the distribution of shorebirds (Goss Custard 1980, Sutherland & Anderson 1993). Equally, it can be expected that where habitat change removes a proportion of the food available to the birds it may force the redistribution or emigration of some of them depending on their competitive abilities (Sutherland & Dolman 1994, Goss Custard *et al.* 1994, Sutherland 1996). Hence evidence of depletion would imply that redistribution is likely. Equally, however, an absence of depletion does not rule out redistribution as a key process as other factors may influence prey availability or the demands of predators, and these could induce a competitive pressure analogous to that caused by prey depletion.

This study like others before it (Duffy *et al.* 1981, Raffaelli & Milne 1987, Kalejta 1993, Wilson 1994, Sewell 1996) failed to detect a depletion effect within the winter study period in Experiment 1. However this does not necessarily mean that there was no measurable depletion, only that this study may have failed to find it. Even if there is no measured effect it does not mean that food is not limiting as only a small fraction of the prey are harvestable (Zwarts & Blomert 1992). Also many accessible prey are ignored due to low profitability, while some profitable prey are inaccessible (Zwarts & Wanink 1992). Changes in prey availability may also be due to changes in the risk taking strategies of the prey (Ens *et al.* 1992). Piersma *et al.* (1994) found that although the harvestable biomass of *Macoma* was of comparable magnitude between two sites on the Dutch Waddensee, knot always left one of the sites earlier. It was concluded that this was not a direct response to prey depletion but to some unknown factor.

Density dependent starvation in shorebirds can occur without significant depletion. Stillman *et al.* (2000a) have concluded that individual variation in intake rate depends on foraging efficiency and susceptibility to interference and that foraging efficiency and search pattern (Stillman et al. 2000b) is of greatest importance for determining intake rate in the oystercatcher and other shorebirds. Goss Custard *et al.* (2001) found that starvation occurred in oystercatchers due to interference, without prey depletion having a significant influence. At the population size studied, intake rate was reduced as population density increased only through increased interference. This led to starvation in not only the sub dominant birds but also the least efficient ones. Even without prey depletion occurring, shorebirds would have an increased risk of mortality should the areas, which they prefer to feed in, be subject to disturbance or change.

7.6.1 Improvements for future work measuring shorebird prey depletion

Experiment 2 improved on the experimental design of experiment 1 and increased the number of replicates. Significant depletion of invertebrate numbers was found for some species and overall when all species were considered. However, doubts still exist about whether such apparent effects were real or just artefacts of small scale variability of invertebrate density, invertebrate mortality or invertebrate mobility. Small scale variability in density has been found in invertebrates living on beaches (Colombini *et al.* 2002), in hedges (Maudsley *et al.* 2002) on the sea bed (Wahl 2001) and on intertidal areas where Lawrie *et al.* (2000) found that *Corophium* formed random high density patches up to 6cm in diameter on the Ythan Estuary during the winter months. Underwood & Chapman (1996) also found spatial variability at the cm scale in estuarine molluscs and concluded that this was linked to small scale changes in micro habitat.

It would be useful to continue this study using the methods outlined in Experiment 2 by further increasing the number of replicates. The OPEN treatment can be omitted as it is just as instructive to have the COVERED exclosures and the RANDOM controls only. In an attempt to completely reduce the potential error introduced by small-scale variation of invertebrate density within the treatments, two approaches could be taken:

1. The diameter of the treatment could be exactly the same size as the sample.

2. If the treatments are to remain 10cm in diameter then the whole surface area within the treatment should be sampled to a depth of 10cm.

Finer scale sampling might also be employed to look at the vertical stratification of invertebrate densities (Soumille & Thiery 1997). Before/after sampling however is still an inefficient way of determining whether changes in invertebrate numbers is due to mortality, shorebird predation or emigration and immigration. This study only sampled twice (before and after) due to logistic constraints but it would be better to sample at regular intervals during the experiment. This might give a clearer picture of the temporal fluctuations in invertebrate numbers, always assuming that bird predation is significant.

7.7 The importance of determining the relative proportions of sub-populations of overwintering shorebirds.

In a study of two breeding sub-populations of oystercatcher that shared the same winter habitat, Goss Custard *et al.* (1995b) suggested that each population might be affected in different ways by gradual loss of habitat. In simulations of habitat loss both populations initially decreased in tandem with decrease in habitat, but as habitat continued to be lost the sub-population with the lowest fledgling success began to be disproportionately affected. Durell *et al.* (1997) simplified this model and tested it on four notional sub-populations of oystercatcher over a simulated 100 year period. All these populations declined at the point when all adult birds were able to attain a breeding territory. The sub-population with the lowest breeding success (A) reached this point of decline first. Prior to this there were always non-breeders competing for the breeding territories vacated by those breeders that died during a winter. Winter mortality in populations with higher reproductive rates (B) slowed temporarily as they profited from the rapid decline of (A). This divergence of sub-populations occurred after 50% of the winter habitat had been lost. Before this point all populations declined in parallel as the affects of increased competition on wintering areas was equal. In arriving at these conclusions, there were some assumptions made about the birds. Firstly, that they competed for winter and breeding territories at an equal rate. For oystercatchers this may not be the case (Hulsher *et al.* 1996), however, nor need it be true for the redshank considered in this study. Indeed, the competitive ability of the Icelandic race of redshank may exceed that of their Scottish counterparts as they have been reported to be larger birds (Hale 1973, Furness & Baillie 1981, Summers *et al.* 1988a, Mitchell *et al.* 2000). It was such differences in biometric measurements that underpinned the model of Summers *et al.* (1988a) that was used to differentiate these races and it was found that that Icelandic birds tended to replace Scottish birds in Scottish estuaries as the winter progressed, suggesting that Icelandic birds are stronger competitors. However, evidence from this study and from D.P. Whitfield (pers com) suggests that Icelandic birds can easily be misclassified as Scottish and *vice versa* and that large numbers of Scottish birds do remain on Scottish estuaries. The second assumption made in the Durell *et al.* (1997) model is that as sub-populations decline a point will be reached where all birds will find a breeding territory regardless of competition from other sub-populations. In the case of the redshank wintering on

Scottish estuaries it is unlikely that Icelandic birds will compete with Scottish ones for breeding sites but other more localised sub-populations within the same country may not be so philopatric. It can be seen from the Durell *et al.* (1997) study that declines in local breeding sub-populations may not just be a product of breeding habitat decline but also be due to a reduction in the quality of their shared wintering areas. Therefore, the methods for defining the relative proportions of two races of redshank wintering on Scottish estuaries are potentially very useful, in detecting the early effects winter habitat loss on population size, because below average rates of reproduction in one or another race will affect this ratio.

7.7.1 Improvements and potential applications of strontium isotope ratios in bird tissue

In future studies of migratory tracing using strontium isotope ratios in bone tissue, ratios in the skull could be compared with those of the ulna, radius and humerus. It is expected that due to a much slower turnover the bias towards the natal signal will be much higher in the skull calvariae. This variation of residence time of strontium in different bones increases the amount of information that can be extracted from whole skeletons.

It has been shown in this study that the use of $^{87}Sr/^{86}Sr$ ratios in avian bone can be used to identify birds of Icelandic origin. This can have implications for validating previous studies that have attempted to work out the relative proportions of Icelandic and British races of birds that winter in mixed flocks in Britain. Little is known about the relative proportions of the two races of redshank that occur in Scotland throughout the winter months. Differences in body measurements of wing, tarsus/toe and bill length have all been used to separate the two races

(Summers *et al.* 1988a) Although it is acknowledged that inter-observer error and uneven sex ratios may bias results and that the standard deviations of all the predictors overlap it was concluded by Summers *et al.* (1988a) using a discriminant function that the vast majority of redshank wintering on Scottish estuaries from December each winter are of Icelandic origin and that Scottish breeding birds winter further south in the UK and northern Europe. Mitchell *et al.* (2000) tested this discriminant function and were able to assign a race to 77% of a sample of redshank caught at Teesmouth in northern England. Of this 77%, they assigned race if the probability of a bird being Icelandic was > 0.7 Mitchell (1996a) also looked at the impact of observer error on measurements and out of 46 birds, which were captured, measured and subsequently recaptured only 3 (7%) changed race as a result of error. Although this level of accuracy may be adequate to work our relative proportions of the two races in large sample sizes, there is scope for error where sample size is small and where the effect of the mis-attribution of one or two individuals would have a greater overall effect. To test this potential error in the discriminant function analysis using biometrics, it could be established using strontium analysis whether birds were of Icelandic origin or not. With the race identified using strontium ratios it would be possible to cross check the race assignment derived from tarsus-toe, wing and bill measurements to see if there was agreement. For this it would be prudent to use the same level of race probability (0.7) with the biometric method as that used by previous studies (see Mitchell *et al.* (2000)). This type of comparison is only possible when all three biometric predictors are available, so if bone is being analysed the corpse of the redshank must be relatively intact. This is not often the case as sparrowhawks and peregrines generally remove the head before eating the flesh from the body cavity. There is also the problem of finding the remains of raptor kills as corvids and rats are quick to remove and consume corpses left by raptors. Strontium analysis of feathers would be a simpler alternative to bone and would allow biometric measurements to be taken from live birds caught for migration study purposes. Icelandic redshank adults moult and replace their feathers on their wintering grounds before returning to Iceland to breed, so adults only incorporate the Sr signature of their winter quarters into their feathers. Therefore only the feathers from juvenile birds can be used in any study that needs to determine the natal origin of a bird especially if it is from feather material alone.

When collecting corpses for this type of analysis there is the possibility of racial bias in the sample if one race or the other was more susceptible to either raptor attack or cold weather. However Whitfield *et al.* (1999) found no evidence for sparrowhawks selecting redshank according to size (Icelandic redshank have longer wings and tarsus toe length (Summers *et al.* 1988a)) or body condition. Mitchell *et al.* (2000) also found no likelihood of one race being more prone to die from prolonged periods of cold weather, as they found no differences in seasonal patterns of body mass changes in relation to temperature.

7.7.2 The potential uses of tissues other than bone and feather in isotopic studies for tracing natal origins of birds

7.7.2.1 Eggshell

Hobson (1995) found the C and N ratios in eggshell reflected the diet over the past 3-5 days and Blum *et al.* (2001) found that $^{87}Sr/^{86}Sr$ ratios in local food sources almost exactly mirrored those in eggshell even though up to 30-40% of eggshell calcium could be mobilised from medullary bone (Dacke 2000). They concluded that eggshells refected the strontium in the food of the adult which was ingested one day before laying. Therefore eggshells should mirror the geology of the foraging area of the adult birds and should act as a reliable measure of the local bioavailable strontium signature. This would be a desirable non destructive way of assertaining the natal signature.

7.7.2.2 Blood

Hobson and Clark (1993) determined that for ^{13}C the plasma fraction of blood has a rapid turnover time with a half-life of about 3 days, whereas the cellular fraction is about 30 days. The value for whole blood is intermediate between the values for these two fractions (Hobson and Clarke 1992a). Samples taken from chicks at the nest would give the amount of ^{87}Sr ingested over the previous few days, would directly reflect the signature of the natal environment and would not be subject to significant mixing. As the cellular fraction reflects Sr in the diet over about two months this may be useful when determining breeding origins of newly arrived wintering adults in a non-destructive way.

7.8 Summary

- The approach taken to predict the effects of habitat change taken in this thesis indicates that it is possible to identify specific areas within a mudflat or mudflat complex and weight them according to there relative importance to the feeding effort of a shorebird species during the winter months. It is also possible to quantify such effects to make informed management decisions.

- The models used to predict shorebird feeding effort were compared to other models which specifically took into account the spatial structure of the data and the prediction errors were found to be comparable.

- All the key species showed a marked preference for high level mudflats suggesting that caution should be observed when considering events, which may impact upon these sensitive area of mudflats. It was concluded that the increase in the use of these areas at Kinneil was in part, due to the recovery of the invertebrate fauna in these areas, after recent improvements in the quality effluent discharged onto the mudflat.

- Spatial variability of shorebird numbers, invertebrate densities and sediment characteristics was evident both at the whole estuary and sub-estuary scale. This was reflected in the range of predictor variables for each shorebird species at each of the main study sites and the number of potential *minimum adequate models* at each scale.

- Temporal variability in shorebird feeding distribution was tested at the sub-estuary scale and found to be stable in the short term for all key species and relatively stable in the long term for redshank and shelduck. Invertebrate densities also remained stable in the short term but fluctuated in the long term. However, there was evidence of long term stability in these invertebrate populations. It was concluded that sediment characteristics were stable at all temporal scales although subject to abrupt changes in the short term.

- Due to the overall temporal stability in the majority of the significant variables used to predict shorebird feeding effort, the models are valid for use in future work on the Forth Estuary. The models may also be applicable to other estuaries on the east coast of Scotland if only in terms of methodology.

- Where habitat change removes a proportion of the food available to shorebirds it may force the redistribution or emigration of some of them depending on their competitive abilities hence evidence of depletion would imply that redistribution is likely. Evidence of depletion was found in this study but a number of confounding factors other than shorebird predation may have accounted for it. Shorebirds can however be forced to redistribute or leave a site in the absence of depletion.

- Habitat changes that affect the food supply or mudflat area on the Forth Estuary may also have consequences for the number of birds that the estuary is able to support regardless of whether carrying capacity has been reached. Such affects may also impact on sub-populations of shorebirds that share the estuary to differing degrees. The technique tested in this study shows that it is possible to identify sub-populations of redshank on the Forth Estuary allowing the relative effects of habitat loss to be considered for both the Scottish and Icelandic races.

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