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Determinants of habitat and site use by Turnstones and Purple Sandpipers in N.E. England, and possible effects of the removal of coastal nutrients

by

Mark A. Eaton, M.Sc (Durham)

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

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2001

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Abstract

Determinants of habitat and site use by Turnstones and Purple Sandpipers in N.E. England, and possible effects of the removal of coastal nutrients

PhD. thesis by Mark Eaton, 2001

Purple Sandpipers and Turnstones were studied on the coast of south Northumberland, with regard to the possible effects of reductions in sewage inputs into inshore waters along the Northumberland coast as a result of new European legislation. Multivariate analysis of bird density in relation to 33 habitat variables indicated that Purple Sandpiper distribution was positively correlated with the abundance of intertidal musselbeds, but negatively correlated with raptor density. Turnstone density was positively correlated with several intertidal habitats such as bare and barnacle-covered rock, as well as the amount of detached wrack deposited on the strandline. Analysis of stable carbon and nitrogen isotopes in particulate organic matter in inshore waters indicated that sewage contributed up to 60% of the total organic matter in the immediate vicinity of outfalls, and hence probably supported increased intertidal invertebrate densities.

Purple Sandpiper numbers were unlikely to be limited by food resources, but birds sought to feed in areas that offered the highest food intake rates, in order to reduce the time spent feeding and therefore minimise the risk of predation by raptors. Social status determined where birds could feed, with larger and older birds excluding subordinates to poorer feeding areas. Social status in Turnstones was determined by sex and age. By feeding on the richest intertidal food resources, dominant individuals (males and adults) minimised the time spent foraging on ephemeral deposits of strandline wrack over high water, which carried a greater risk of predation. Dominant individuals of both species were able to carry less stored fat and hence improved their chances of escaping attacks by raptors. While both species are unlikely to decline in numbers as a direct response to lower food densities, subsequent changes in foraging behaviour and distribution could result in greater mortality.

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

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Dedicated to my parents, Kit and Tricia Eaton, to my wife, Nicola Eaton, and to Peter Evans.

Chapter 1

General introduction, study area and species

1.1 Introduction

This thesis describes studies undertaken to understand, model and predict habitat use by populations of Purple Sandpipers *Calidris maritima* and Turnstones *Arenaria interpres* on the Northumberland coast in Northeast England. The possible impact on these populations of reductions in their food supplies resulting from reductions in sewage inputs to inshore waters was also investigated. These birds occur in internationally important numbers at present in this part of Britain, which has recently been designated a Special Protection Area by the European Union.

Northumbrian Water plc. is currently undertaking a major programme of improvements in the treatment and disposal of sewage along the coast of Northeast England in order to meet the requirements of E.C. Urban Waste Water Directive 91/271. This work will involve the building of additional treatment facilities (in most cases to secondary sedimentation level) and/or longer seaoutfalls. Recent changes in government policy, such as ceasing to recognise "Areas of High Natural Dispersion" designations, may result in further levels of treatment being applied above and beyond those required by E.C. legislation. The aim of the E.C. Directive is to reduce the level of sewage-derived materials introduced into inshore waters. While this policy may have the benefits of a reduction in inputs of soluble nutrients and suspended solids, as well as a possible reduction in public health risks, it may have a negative impact on some aspects of the natural environment. In particular, a reduced total (soluble plus particulates) nutrient input could result in reduced productivity in inshore ecosystems.



1.2 The effects of sewage inputs on coastal ecosystems

Sewage can have a major impact on all aquatic ecosystems and can be a major pollutant (defined as an artificially introduced substance liable to cause hazards to human health and/or harm living resources and ecological systems, (Holdgate 1979)). Such waste is very rich in organic matter, and influences water quality in three main ways:

- The bacterial degradation of organic compounds to stable inorganic compounds requires oxygen. This can cause a reduction of the oxygen content of water bodies if the rate of uptake of atmospheric oxygen is not sufficient to replace the rate at which it is used in the oxidation of organic molecules. The oxygen needed for breakdown is measured as Biochemical Oxygen Demand (BOD). A high BOD can result in severely deoxygenated water.
- 2. By causing nutrient enrichment. The breakdown of organic matter releases large quantities of inorganic nutrients, including nitrogen and phosphorus. The uptake of these nutrients by algae and phytoplankton leads to increased productivity that may have repercussions elsewhere in the ecosystems.
- 3. Sewage, depending on the level of treatment it has received, may contain a high level of suspended solids. At very high levels, this suspended material may increase the turbidity of water and decrease light availability for benthic algae. However it may increase populations of filter-feeding fauna.

The effect of sewage often depends on the dilution it receives after discharge. In small or slow-moving water bodies, sewage may remain at a relatively high concentration whereas sewage discharged into a large volume of water, such as the sea, will be rapidly diluted and any effects less severe. In the case of offshore sewage outfalls, the extent of their effects on local ecosystems will depend on currents.

Unlike other pollution types, organic waste can have a beneficial effect on aquatic ecosystems, particularly when at a moderate level. Bird populations may increase if greater algal productivity increases invertebrate populations, even though this increase in productivity may cause a change in community composition of invertebrates (often a decrease in diversity). Green *et al.* (1992) reviewed the impact of organic nutrients on bird populations in estuaries (but not on open coasts). There are instances with harmful consequences; in Langstone Harbour, Hampshire, nutrient enrichment resulted in *Enteromorpha* growth that covered large areas of mudflat and killed the benthic invertebrate populations, which are essential foods of some wintering birds. However in some cases, high organic input has been correlated with increases in wintering bird populations.

The impact of organic materials put directly into the sea has been the subject of less research but has indicated that any harmful effects are often limited to deposition of particulate matter in the immediate vicinity of outfalls (Topping 1976). There is little doubt that certain types of sewage discharge have allowed affected coastal areas to support increased bird populations (see Green *et al.* 1992).

The changes in sewage treatment and disposal that Northumbrian Water plans to complete by 2001 are outlined in section 1.4.2, below. In all cases sewage will undergo primary and secondary treatment. Primary treatment involves the use of settlement tanks to remove suspended solids, although a proportion will remain and BOD and nutrient levels will remain high. Secondary treatment uses filter beds of rock or coke to allow bacterial decomposition of organic matter. At some sites longer sea outfalls will be constructed. These new longer outfalls will mean that sewage will be less likely to be carried inshore by currents, and even if it is, dilution will be increased.

Within the study area, it seems likely that reductions in nutrients from sewage could result in a decrease in algal productivity. Algae such as *Enteromorpha*, *Fucus* and *Ulvae* are consumed by grazing molluscs which include species that are important prey to Purple Sandpipers, Turnstones and other waders on rocky shores. Furthermore, the abundance of filter feeders such as *Mytilus edulis* could

decrease due to lower levels of suspended solids. This decline could affect species such as Eiders, Oystercatchers *Haematopus ostralegus* and Knot *Calidris canutus* by reducing their prey resources. Invertebrate densities may also be reduced along soft-shores and could lead to a reduction in waders including Sanderling *Calidris alba* and Ringed Plover *Charadrius hiaticula*.

1.3 Objectives

The research detailed in this thesis was conducted with a number of objectives:

- 1. To create a "baseline" through monitoring of the bird populations (and their invertebrate food resources) that currently utilise the study area to enable comparisons to be made with those observed after the installation of new sewage treatment works and sea outfalls.
- 2. To discover what factors currently influence the distribution of Turnstones and Purple Sandpipers by using multivariate analysis to examine relationships between bird density and a large number of environmental variables thought to be possible influences (Chapter 2). Predictive models were created to allow the testing of whether similar relationships between birds and variables occurred in another coastal area.
- 3. To assess the current importance of sewage inputs to inshore ecosystems at sites within the study area, using analysis of stable isotope ratios (Chapter 3) to determine what proportion of suspended particulate matter comes from sewage inputs.
- 4. To consider how any changes in food resources will effect Purple Sandpiper and Turnstone populations within the study area, by studying the habitat use by the wintering populations at each site within the study area, along with the stability and movements of these populations (Chapters 4 and 5).

5. To determine what factors control/influence the considerable variation in habitat and site use by individual birds of both species (Chapters 6 and 7).

1.4.1 The study area

The study area covers a 36 km stretch of coast-line from St. Mary's Island to the Coquet Estuary (Figure 1.1). This region has several distinct coastal habitats. Rocky shores are found on the headlands at Amble-Hauxley, Cresswell, Newbiggin, North Blyth and Seaton Sluice-St. Mary's Island. These stretches have extensive areas of wave-cut rock platforms and are backed by low cliffs or dunes, except at North Blyth where natural conditions have been altered by seadefences and the mile-long East Pier. Coquet Island, a low island of approximately 8 Ha, lies one mile offshore from the rocky headland at Hauxley.

Between these headlands lie the sweeping sand beaches of Druridge Bay, Cambois and South Blyth Valley. The industrial legacy of mining at Lynemouth has left the beach there covered with spoil and of very little interest to ornithologists. Both Lynemouth and the sandy beaches are little used by Purple Sandpipers and Turnstones, and so separate the coast into distinct stretches of rocky shore habitat suitable for both species. In addition there are three rivers large enough to produce estuaries; the Coquet, Wansbeck and Blyth.

For fieldwork purposes the study area was sub-divided into a number of sites, given in Table 1.1.

The study area lies within the recently notified Northumberland Shore SSSI that covers the Northumberland coast from the Scottish border to Tynemouth, excluding Lindisfarne. Notification of this SSSI was justified on the basis of the wintering bird populations. In 1999 this area was designated as the Northumberland Coast Special Protection Area due to the wintering populations of Purple Sandpiper and Turnstone (as well as breeding Little terns *Sterna albifrons*), and also qualifies as a Ramsar site (see Robinson *et al.* 1996).

Figure 1.1: South Northumberland study area

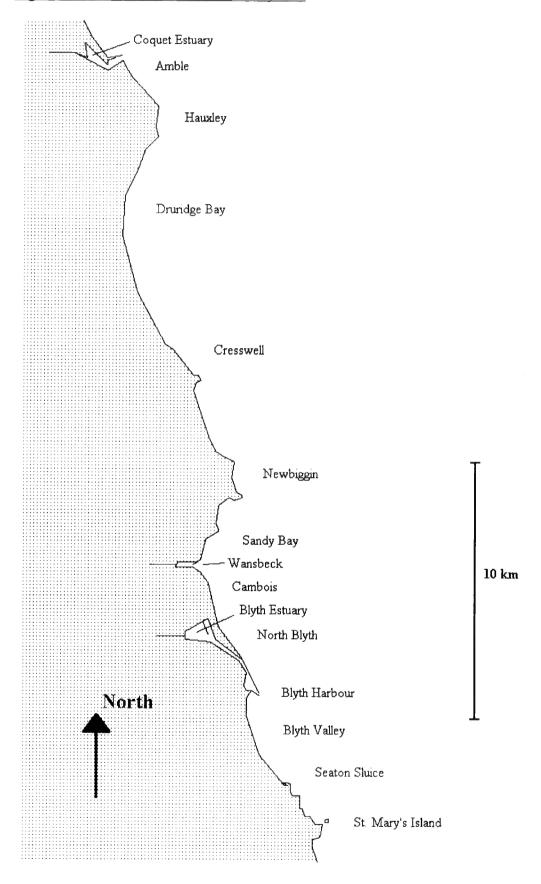


Table 1.1: Sites within the south Northumberland Study Area

Site	Principal habitat	Length (open coast sites)
Coquet Estuary	Estuary	
Amble	Rocky shore	2.1 km
Coquet Island	Rocky shore	
Hauxley	Rocky shore	3.1 km
North Druridge Bay	Sandy shore	2.9 km
South Druridge Bay	Sandy shore	4.7 km
Cresswell	Rocky shore	2.9 km
Newbiggin	Rocky shore	4.0 km
Wansbeck Estuary	Estuary	
Cambois	Sandy shore	1.7 km
North Blyth	Rocky shore	2.0 km
Blyth Estuary	Estuary	
Blyth Harbour	Piers, breakwaters	
South Blyth Beach	Sandy shore	4.4 km
St. Mary's Island	Rocky shore	4.6 km

The south Northumberland coast was chosen for study for several reasons. The coast holds large numbers of wintering shorebirds. Five species have populations of designated conservation importance within the Northumberland Coast SSSI: Purple Sandpiper, Turnstone, Ringed Plover, Eurasian Golden Plover *Pluvialis apricaria* and Sanderling. In addition there are large numbers of other species such as Redshank *Tringa totanus*, Knot and Dunlin *Calidris alpina*. The presence of large stretches of both rocky and soft shores means that the environmental impact of changes in sewage inputs on two distinct ecosystems could be monitored, although research was mainly concentrated on rocky shores.

Several sites within the study area, such as Amble and North Blyth, are located near sewage discharges that will receive extra treatment after 2000. Additionally there will be increased dilution of sewage material in the cases where outfalls are being lengthened i.e. at Cambois. These sites will experience a reduction in the sewage input to the inshore ecosystem. Conversely, sites such as Cresswell and

St. Mary's Island are several miles from any discharge point and are highly unlikely to experience any change. This combination of potentially affected sites and unaffected sites in relatively close proximity provides the equivalent of "experimental" and "control" sites for comparison.

1.4.2 Changes in treatment levels and locations of sewage discharges

The changes in sewage treatment and disposal conducted by Northumbrian Water north of the river Tyne to comply with the Urban Waste Water Directive by 2001 are as follows:

Amble

There will be no change in the location of the outfall (between the mainland and Coquet Island). A new sewage works providing primary and secondary treatment is due for completion by April 2001.

Newbiggin

Primary and secondary treatment will be added to the existing outfall by March 2001; the outfall was constructed in 1993 to replace the previous shorter pipe.

Cambois

Construction of a new 1 km long outfall pipe was completed in September 1997. Sewage will be diverted through it in March 2001 after a secondary treatment plant has been built.

Blyth

The sewage currently discharged untreated into the river will be diverted to the Blyth sewage works, where it will receive secondary treatment before discharge into the river.

The Northumberland coast experiences a net southward flow of currents over the tidal cycle. These currents, coupled with frequent strong winds, result in strong dispersive forces on the sewage from inshore discharges. The study area was part of an area designated as a "region of high natural dispersion" under E.C.

legislation until such status was abolished. The net southward movement of currents means that the greatest impact on the environment is likely to be south of discharge points, while the high dispersion suggests that any impacts are likely to restricted to a relatively small area.

1.5 The study species

Two main study species were chosen for detailed research into bird populations and individual behaviour for several reasons.

- Both species are present in internationally important numbers (defined as 1% or more of the western flyway population) within the Northumberland Coast SPA. Significant proportions of these wintering populations are found between St. Mary's Island and Amble.
- 2. Both Purple Sandpipers and Turnstones have relatively stable wintering populations and are not prone to large cold-weather movements during the winter, unlike species such as Knot. These habits reduce (but do not eliminate) the impact of external factors on population levels within the study area.
- 3. If the decrease in organic inputs from sewage does have a significant impact on intertidal ecosystems, populations of both species may be affected through changes in prey densities, making them suitable species to assess ecological impacts of the Urban Waste Water Directive.
- 4. Purple Sandpipers and Turnstones show high site-fidelity and hence low mortality, and have high between-year return rates (Evans & Pienkowski 1984, Burton 1995). These habits mean that the behaviour of the same individuals could be studied in more than one winter.
- 5. Nearly all research on shorebirds, and the factors that control their distribution and behaviour, has been conducted on soft-shore feeders. Comparatively little research has been focussed on rocky shore species despite the use of this habitat by a number of shorebird species and the common occurrence of rocky shores on western European coasts.

1.5.1 Purple Sandpiper

Purple Sandpipers breed on Canadian arctic islands, Greenland, Iceland, Scandinavia (chiefly Norway) and Siberia (Cramp & Simmons 1983). In many regions breeding is mainly coastal, but in low arctic and subarctic sites such as Sweden breeding may be inland and at altitudes up to 1300 m (Swanberg 1945). In recent years birds have successfully bred in the Scottish uplands (Dennis 1983, Ogilvie 1996).

Most sandpipers (Charadrii) winter south of the Arctic Circle. Purple Sandpipers are the only species that regularly winter farther north with substantial numbers wintering along the coasts of Greenland and Norway. Whether these birds are truly resident or are high Arctic breeders is not known, although some wintering birds on Iceland are thought to be resident. The Purple Sandpiper is not as commonly ringed as other species of wader (Atkinson *et al.* 1981) and geographical variation in appearance is limited (see below), hence knowledge of its migratory movements is still incomplete.

The British population of Purple Sandpipers is in the southern half of the wintering range. The numbers are probably relatively insignificant, being estimated at 14,000-23,000 (Atkinson *et al.* 1978) although probably near the upper limit of that range (Lack 1986). The most recent survey of non-estuarine shorebirds, the 1997-98 non-estuarine waterbird survey (NEWS), produced an estimate of 17,041 Purple Sandpipers in Britain (M. Rehfisch pers. comm.). Within Britain, the Purple Sandpiper is chiefly concentrated in the northeast; in Shetland, Orkney, eastern Scotland and Northeast England. Although Buxton *et al.* (1985) found at least 2575 birds wintering in the Outer Hebrides, numbers elsewhere on the west coast are low. Small numbers are found in a few localities south of Yorkshire in England and in Wales.

Wintering Purple Sandpipers are rarely found away from rocky shores where they feed in the littoral zone. The main prey species are molluscs; small first-year Winkles *Littorina* (edible periwinkle *L. littorea*, rough periwinkle *L. saxatilis*, flat periwinkle *L. littoralis*) were the main species taken by a wintering

population studied in North Yorkshire (Feare 1966) along with the dog whelk *Nucellus lapillus. Hydrobia* spp. and mussels *Mytilus edulis* were also taken along with small crabs, and algae were found in most faeces examined. In studies done in other parts of the wintering range, *Littorina* were also the principal prey with various other molluscs (*M. edulis, Lacuna, Margarites*) and crustaceans (*Gammarus, Idotea*) (Strann & Summers 1990) being taken. Birds in some areas may feed on strand-line wrack deposits, often accompanying Turnstones and feeding on the larvae, pupae and adults of the wrack fly *Coelopa frigida* (Lack 1986).

Feare (1966) stated that Purple Sandpipers did not feed at night time. However more recent studies (Atkinson 1981, Strann & Summers 1990, Summers 1994) have indicated that they do, although it is not known to what extent, on what prey species and with what efficiency. McKee (1982) suggested that Purple Sandpipers are highly tactile feeders, which would mean that they might be able to feed efficiently even on dark nights. Night-time feeding would be a further aid to winter survival, especially in mid-winter and at high latitudes where daylight hours are very limited.

Purple Sandpipers are sexually dimorphic, with females larger and heavier than males (Cramp & Simmons 1983). This size difference is particularly obvious in bill length. Size variation also occurs between populations, again most apparent in bill length. Birds from Greenland, Svalbard, Scandinavia and north-west Russia have shorter bills (adult male mean 27.5 mm, range 26-29 mm, female mean 32.0 mm, range 29-34 mm, Cramp & Simmons 1983) than those from Iceland (adult male mean 29.9 mm, range 27-35 mm, female mean 34.3 mm, range 32-37 mm, Cramp & Simmons 1983), Canada and Siberia. Although the situation is confused by the overlap between male 'long-billed' and female 'short-billed' birds, British studies of the biometrics of wintering birds have given an indication of the origins of wintering birds.

Nicoll *et al.* (1988) collected the biometrics of birds from all wintering areas in Britain. They found a predominance of 'long-billed' birds in western and northeast Scotland, and an increasingly large proportion of 'short-billed' birds in

south-eastern Scotland (77% in Fife, n = 190) and north-east England (62% 'short-billed' in Northumberland, n = 49, 60% in Yorkshire, n = 92). However a study of a Purple Sandpiper population at Hartlepool Headland, 45 km south of St. Mary's Island, estimated that only 36% (of 65 birds caught) were from the 'short-billed' population (Burton 1995). Populations in western England are mixed while the tiny numbers in south-east England are long-billed.

The numbers of wintering birds of the two types, based on a total population of 19,000, are 15,000 'long-billed' and 4,000 'short-billed' (Nicoll *et al.* 1988). A Norwegian origin for 'short-billed' Purple Sandpipers is supported by the ringing or recovery in Norway of six birds recovered or ringed in eastern Scotland. The identity of the 'long-billed' population remains unclear. Ringing recoveries have linked 'long-billed' birds with Iceland (as has the 'long-billed' population in the Netherlands, Boere *et al.* 1984) and with Greenland. It is also possible that some or all of the 'long-billed' birds in southern England are from the Siberian population. The arrival dates in Britain differ significantly for the two populations; Norwegian 'short-billed' birds begin arriving in July, while the 'long-billed' population does not arrive until late October. Biometric studies have also shown that in Britain there is an unequal sex ratio among wintering birds, estimated by Nicoll *et al.* (1988) at 1:2.11 female:male ratio in the 'long-billed' population and 1:1.34 in the 'short-billed' population.

Counts of Purple Sandpipers in the Northumberland shore SPA regularly exceed 600 (English Nature 1992). Two locations hold the majority of birds: Stag Rocks at Bamburgh, and Blyth. The situation within the study area has changed somewhat since the 1980s as the major roost has moved from St. Mary's Island to Blyth East Pier (possibly due to increased disturbance by the public at St. Mary's Island). Most birds from the Blyth roost feed on North Blyth Rocks. Maximum roost counts at Blyth have been over 300 in recent years and have not been affected by the installation of a wind farm in 1992 (Little 1996). Elsewhere, birds are found at Newbiggin, Cresswell and Amble-Hauxley with an unknown number on Coquet Island.

1.5.2 Turnstone

The breeding range of the Turnstone is circumpolar, with populations at high latitudes of Europe, Asia and North America. The birds found in Europe are of the nominate race *Arenaria interpres interpres*, which breeds on Ellesmere and Axel Heiberg Islands in Canada, Greenland, Spitsbergen, along the coasts of Fenno-Scandia and as far east as Siberia (Kamchatka) (Branson *et al.* 1978). The nominate race can be divided into three populations with different wintering ranges and migratory routes. The Canadian-Greenland population is the principal source of wintering Turnstones in north-west Europe and is estimated at a minimum of 50,000 breeding individuals.

The British wintering population of Turnstones has been estimated at close to 50,000 (Lack 1986); 38,500 were counted wintering on non-estuarine coast in 1984-85 (Moser & Summers 1987) and 38,416 by the 1997-98 non-estuarine waterbird survey (M. Rehfisch pers. comm.). This population arrives in Britain from August onwards, adults first, and remains until May. First-year birds may migrate to the breeding grounds while others summer in Iceland or remain on the wintering grounds (Summers *et al.* 1989).

The British wintering population is spread relatively evenly around the coastline except for the Inner Hebrides and north-west mainland Scotland where they are scarcer (Lack 1986). As with the Purple Sandpiper and unlike most other waders Turnstones do not occur in major congregations in estuaries, which means that distribution is not as well documented as for estuarine waders. Morecambe Bay does hold over 1,000 wintering birds and other estuaries may have several hundred during migration but otherwise Turnstones are thinly spread along rocky coastline. Scotland has most of the British population, with over 5,000 Turnstones on both Shetland and Orkney, 4,000 on the Outer Hebrides and 5,000 down the east coast (Moser & Summers 1987).

Turnstones are often found in the same rocky shore habitats as Purple Sandpipers. However their diet is significantly different and they take a wide range of food and feed in a wider variety of habitats. McKee (1982) compared

the distribution of feeding Purple Sandpipers and Turnstones and found the former to be much more conservative in their choice of substrate. The main part of the diet of Turnstones is made up of rocky shore species. These include barnacles *Balanus*, which are hammered off rocks and shore crabs *Carcinus maenas*, *Corophium*, *Gammarus*, *M. edulis* and *Littorina* (Cramp & Simmons 1983). Turnstones often feed amongst live wrack, pushing aside fronds to expose prey.

A wide variety of other prey species have been recorded (see Cramp & Simmons 1983) of which some is taken when feeding away from rocky shores. Turnstones feed on sandy beaches, forage on inland fields and scavenge in docks when opportunities present themselves. They often feed on strand-line wrack deposits taking *Talitrus saltator* and *Coelopa frigida*.

Studies on the return rates of Turnstones in Britain indicate that it is amongst the longest lived of waders. Evans & Pienkowski (1984) found an autumn to autumn return rate in colour-ringed birds of 85% at Teesmouth, while Metcalfe & Furness (1985) had an adult return rate of at least 86% in birds on the Firth of Clyde. These figures also indicate that Turnstones are site-faithful, with most birds rarely moving more than a few miles (Lack 1986). A high degree of site fidelity may be an indicator of temporal stability in food resources (Evans 1981).

The wintering population within the Northumberland Shore SPA is of international importance with peak counts often exceeding 1,300 birds (English Nature 1992). WeBS (Wetland Bird Survey) counts show that the largest concentrations are found in the northern half of the county. Mean maximum annual counts for 1983/84 - 1987/88 exceeded 300 at Lindisfarne and Seahouses-Beadnell, and exceeded 200 at Budle Pt.-Seahouses and Boulmer-Alnmouth. Numbers on the Farne Islands in the winter may also be substantial; certainly, large concentrations of up to 600 are found in August during passage and moult (Kerr & Johnston 1996). Within the study area, winter concentrations of over 100 are frequently found at Amble-Hauxley, Newbiggin-North Blyth and St. Mary's Island with smaller numbers spread in between. As elsewhere in

Northumberland, variable (small) numbers of first-year birds may be found throughout the summer (Galloway & Meek 1980).

Chapter 2

Relationships between bird density and environmental variables.

2.1 Introduction

2.1.1 Factors determining the distributions of Purple Sandpipers and Turnstones

Two principal approaches can be used to reveal the factors that influence the distribution and abundance of biological populations. Firstly, observations of the behaviour of individuals within a population will reveal what resources these individuals, and hence the population as a whole, exploit. For wintering shorebird populations, for example, such observations would allow the determination of food resources, roost-site requirements and so on. These studies were conducted on Purple Sandpipers and Turnstones within the south Northumberland study area and are detailed in Chapter 4 and 5. This approach does not, however, give any indications of what resources are the most important in controlling the size and geographical distribution of the population.

The other approach is to use multivariate analysis to discover what environmental factors are correlated with the distribution and density of the study population. A relationship between bird abundance and a particular habitat variable may arise from an ecological association between the two. If a model can be created and used to accurately predict the occurrence or density (depending on the modelling approach used) of the study species in a previously unstudied area, a more convincing case can be made for causation, rather than merely correlation.

In order to predict how the forthcoming changes in sewage treatment and discharge may affect wintering shorebird populations, it is essential to know what factors currently determine the distribution and abundance of these birds.

Only if the density of a particular species were related to the abundance of a food

source that may be adversely affected by the sewage "clean-up", would a subsequent decline in numbers of this species be expected.

The distribution of the Purple Sandpiper and Turnstone populations in south Northumberland is determined by the decisions made by each individual bird. On their arrival in the study area in the autumn, each Purple Sandpiper and Turnstone settles at a site (or sites, as some individuals move between sites regularly, Chapters 6 and 7) that affects its chances of surviving the winter, and thus returning to the breeding ground to reproduce in the following summer. For some individuals, particularly first-years that are visiting the area for the first time, settlement is preceded by an exploratory period during which they sample different sites in order to assess where to settle (Whitfield 1985a). For adult birds, settlement location may be based on experience of the conditions in previous winters.

A number of different environmental factors influence where each individual bird decides to settle. The principal amongst these may be food; a site must have sufficient food for an individual to obtain a certain (net) energy intake per day (Burger & Olla 1984). As well as absolute abundance (density), the availability of such prey is relevant; prey must be accessible, of the right sizes and not require too great an expenditure of energy during searching and handling (Zwarts et al. 1996). In intertidal areas, the period for which prey is exposed by the tide is an important consideration, and whether alternative sources of food are available over the high water period if the required intake can not be obtained over low water alone (Burger et al. 1977).

A significant consideration for wintering shorebirds may be the avoidance of predation by raptors, which may be a significant cause of mortality (Whitfield 1985b, Cresswell 1994). Areas that offer the greatest rate of energetic return for foraging birds may not be preferred if birds that feed there suffer a higher risk of predation. The effect of raptors may not only be to increase the risk of predation, but also to reduce food intake rates as birds spend more time in vigilance behaviour (Metcalfe 1984).

A third important consideration for shorebirds is the availability of suitable roost sites. Preferred roost sites offer shelter from wind and protection from predation and disturbance (Furness 1973, Burton 1995). By roosting close to low water feeding grounds, birds can reduce the energy expended in travel to and from the roost (Caccamise & Morrison 1986). If there is no suitable roost site near a profitable low water feeding location, this may deter shorebirds from foraging there because of the high energetic costs of travelling to and from a high water roost site twice in every 24 hours, (although not necessarily so, Rehfisch *et al.* 1996).

Many researchers have tried modelling the decisions made by individual birds and their impacts on overall population distribution. The "ideal free distribution" (IFD) model (Fretwell & Lucas 1970, Fretwell 1972) describes a situation where animals are able to measure the fitness benefits of settling at all available sites and choose the most profitable site. The fitness benefits of settling at any given site are determined by the resources available and the density of animals already present; at a certain density threshold, it becomes more profitable for an individual to settle at a site with lower resources but less competition. This approach is over simplistic for many ecological situations, not least because most organisms do not meet the criteria necessary for IFD to apply, and the "ideal despotic distribution", which allows for variation in the quality of individual animals, is probably more appropriate for describing the distribution of bird populations (Bernstein *et al.* 1991).

Such a situation is likely to exist amongst Purple Sandpipers and Turnstones within the study area; the decision each bird makes on where to settle is not only influenced by the benefits of each site as influenced by food resources, predation and roost sites, but also by the density of birds already present at a site.

This study was faced in a potential problem in that the number of sites was low, so any multivariate analysis would be forced to work on comparatively few cases. This meant that few explanatory variables could be used in any regression analysis. To cope with this problem Principal Component Analysis was used — this is a technique that allows information on many variables to be "compressed"

into a few "principal components" describing most of the variation in the dataset (Tabachnick & Fidell 1996).

2.1.2 Spatial scales

This study considered the distribution of Purple Sandpipers and Turnstone and the environmental factors that determined these distributions, at two spatial scales. One, the larger scale, was based on the separate rocky shore sites within the study area in order to determine why, for example, a higher density of Turnstones wintered on the rocky shore at Amble rather than that at Cresswell. The second smaller scale divided these sites up so as to study the distribution within sites as well as between them to determine why, for example, did Turnstones prefer some areas of the Amble foreshore to others. Of course, Purple Sandpipers and Turnstones have to make decisions on spatial scales both larger and smaller than the two considered in the present study. Even within the same feeding location the foraging location of birds may be influence by prey patchiness, substrate type, visibility and microclimate. The degree of exposure and shelter from wave action can vary, both between and within rocky shores. This aspect of rocky shore physiography can have a major impact on the density and growth of invertebrate prey of shorebirds. It can also influence the availability of prey, and the energetic costs of foraging there for shorebirds. On a larger scale, the wintering region may be determined by climate and migration costs; birds seek to winter in a suitable climate while minimising the distance migrated from the breeding grounds.

2.1.3. Temporal scales

The suitability of wintering sites (and hence their desirability to wintering individuals) may vary on a number of different temporal scales. Sites may become more or less attractive over the course of the lunar tidal cycle, as principal feeding areas (e.g. mussel-beds) may remain uncovered on neap low waters at some sites but not others (Goss-Custard & Durell 1987). Short-term fluctuations in the attractiveness of sites could also be caused by weather events, as some sites may be more sheltered than others during storm conditions and

hence provide better feeding and/or roosting conditions. Harsh weather conditions may also increase the energy requirements of birds, forcing them to feed in areas that provide high food intake rates but are otherwise avoided due to higher predation risks (Hilton *et al.* 1999). The occurrence of ephemeral food resources, such as mussel spat on rocky shores and detached wrack deposits on sandy beaches, may also cause temporary changes in distribution. In addition, other, competing, predators will also prey upon shorebird food resources. Starfish, crabs, fish and other bird species can all have major impacts on the density, distribution and behaviour of invertebrate prey.

Longer-term variation may occur as the foraging of shorebirds through the autumn and winter depletes food resources. Sites with plentiful food resources may initially attract a high density of shorebirds, which then deplete this resource. As a consequence, birds may redistribute to other sites where foraging pressure had previously been lower, or possibly switch to a different food resource (Goss-Custard *et al.*1996). Factors other than predation pressure may cause changes in food density; of particular relevance to shorebirds is the ability of winter storms to scour rocky shores of barnacles and mussel-beds (Dayton 1971, Levin & Paine 1974).

On an even longer temporal scale the distribution of birds may change between years. Total numbers in a region (and hence at sites within that region) may vary due to fluctuations in breeding success or adult and juvenile survival.

Alternatively, conditions within the wintering area may persuade more or fewer shorebirds to settle at each site in different winters. The abundance of larval mussels *Mytilus edulis* (spat) can vary massively between years according to local climate conditions during both the breeding season and larval settlement period (Suchanek 1985).

2.2 Methods

2.2.1. Environmental variables

Bird densities were calculated from the counts made weekly over the 1996-97 winter and fortnightly in 1997-98 and 1998-99. "Mid-winter" means were calculated for each winter, and an overall mean for each species calculated from these three values. For Turnstones the "mid-winter" period included counts from October to February, for Purple Sandpipers from November to February (due the later arrival of part of this wintering population).

Only low water counts were used for the calculation of means which were defined as counts made at tide levels below 3.7m O.D. (Ordnance Datum), levels interpolated from tide tables and tidal curves. This height-based approach was more appropriate than that of a fixed time-period around low water, which would have been affected by large variations in tidal exposure (and hence size and location of feeding areas) between extreme neap and spring tides. 3.7m O.D. was selected as the median value between the mean high and low tide levels (for both spring and neap tides.)

Bird counts were expressed as densities (birds per km of coastline) to allow for the differing length of coastline of sites. The independent variables were therefore also expressed as means per km of coastline when appropriate.





An example of the 1:10,000 aerial photographs used for data extraction. Several substrate types can be seen; the bright green areas are rocks encrusted with *Enteromorpha*, the darker green/brown is *Fucus*. Bare/barnacle-covered rocks show as a pale straw colour, and sand is paler still. With care, dark mussel-beds can be picked out near the low tide mark, below the *Fucus* zone.

33 variables were measured for each study site within the study region (Table 2.1). They included variables measured in mid-winter (e.g. raptor density, strandline wrack), during invertebrate sampling (e.g. invertebrate density, shore topography measures) and from aerial photographs (e.g. mussel-bed area, total intertidal wrack). As the bird density values used in the multivariate analysis were from the mid-winter period only, values for variables such as raptor density were calculated only from data collected in the same period in all three years.

1:10,000 colour photographs, (e.g. Figure 2.1) taken by ADAS Aerial Photography Unit at low water on 17th July 1996, show extents of different types of shore cover similar to those present in the mid-winter period, with one exception. Green algae, *Enteromorpha* spp. cover large areas of the intertidal zone in mid-summer, but this cover is greatly reduced by mid-winter. Much of the area covered by *Enteromorpha* is mussel-beds on the lower intertidal levels. All photographs were taken on this date: none were available for the winter period, and no effort was made to adjust the measurements taken from this summer photographs to the winter situation:

Area coverage values were extracted from the photographs by overlaying a transparent grid of 1.58 mm squares: at a scale of 1:10,000, each square corresponds to a real area of 250 m². Each square was recorded as containing whatever substrate type was most abundant within it. This method may have been biased against those substrate types, such as rock pools, that tend to occur as a low proportion of the coverage in a lot of squares. In particular, the underestimation of rock pool area, a popular micro-habitat for feeding shorebirds (see Chapter 4), might lead to an underestimation of the importance of this cover type in determining shorebird distribution.

The accuracy of identification of substrates was checked in the field at low tide in December 1997. In addition, the assessment of cover type using aerial photographs was repeated at Cresswell and the two sets of results compared (see Appendix 1). The greatest variation for any substrate between the two assessments was 4%.

Most invertebrate densities were calculated from ten 1 m² quadrats sampled at regular intervals along three transects between mean high water level and mean low water level per site, to give a mean value for the whole intertidal area. At each site the transects were located across the areas of shore most used by foraging Purple Sandpipers and Turnstones. Mussel data were collected only from mussel-beds. Percentage cover was measured within these beds and ten 0.01 m² samples were taken to calculate mean density of the various size classes of mussels. For the multivariate analysis, an estimate of numbers of mussels per km was derived by multiplying density within mussel beds by the area of mussel bed per km.

2.2.2 Spatial scales

Analysis of bird density with regard to habitat variables was conducted on two spatial scales. For the "large" spatial scale the study area was sub-divided into nine sites (Figure 2.2 and Appendix 1) with a mean shoreline length of 3.8 km. For the "small" spatial scale these sites were further sub-divided to produce 28 sites (Appendix 1), with a mean length of 1.2 km. In all cases the sites were divided along distinct topographical lines such as boundaries between rocky shores and sandy bays. The large spatial scale enabled the choice of birds for separate sites to be examined, while the smaller scale enabled some investigation into what determines the distribution of birds within sites.

Some of the 33 environmental variables were measured at both spatial scales. However others, such as raptor presence, were measured only at the larger spatial scale. For these variables, when the large sites were sub-divided for the small spatial scale analysis, each small site received the same value for a variable as the larger site it lay within. In addition, measuring invertebrate abundance and shore topography for each of the 28 small-scale sites would have been too time-consuming; these variables were omitted from the analysis, so reducing the number of variables entered to 13.

2.2.3 Statistical techniques

All variables were transformed before analysis. Area variables were converted by $\sqrt{\ }$, percentages by Arcsine transformation, and counts by $(\ln + 1)$.

For the larger spatial scale analysis (which had nine sites only), multiple regression was unsuitable: the working rule of a 5:1 ratio for data points: variables meant that only two variables could be entered into regression analysis at any one time. Even for the smaller scale analysis a limited number of the many predictor variables could be entered into regressions. To overcome this problem without grossly simplifying the environmental data, principal component analysis was used. Principal component analysis (PCA) is a method of condensing a data set of many variables into a few "factors" while still retaining as much information as possible (Tabachnick & Fidell 1996, Fowler *et al.* 1998). The dependant variable (in this case bird density) can then be regressed against these condensed factors to detect any significant relationships.

2.2.4 Testing models

The models generated from the south Northumberland study area were tested on the north Northumberland coastline between Warkworth Beach and Budle Bay, a distance of 40 km. This study area was sub-divided on both a "large" and "small" spatial scale to allow the testing of both scales of model. The coastline was divided into 10 sites (Figure 2.3 and Appendix 1), mean length 3.9 km, for the testing of the large scale models. These sites were further divided into 24 sites (Appendix 1), mean length 1.6 km, for the testing of the small-scale models.

Bird counts were provided by English Nature. They were conducted as part of research into the designation of the Northumberland coast as a Special Protection Area. These counts were made between October 1998 and March 1999 with one high and one low tide count each month. Bird densities were calculated using only the low tide counts from October-February for Turnstones and November-February for Purple Sandpipers. In addition, the length of strandline wrack

deposits for each site on every visit was estimated, allowing a mean to be calculated from 12 estimates. Substrate cover data were again extracted from the ADAS 1:10,000 aerial photographs, from the same flight run as for the south Northumberland coast (on 17th July 1996).

Table 2.1: Variables used in multivariate analysis

Variable	Abbreviation in analysis	Source	Units	Notes
Total intertidal area	TOTINTER	1	m ² per km	1:10,000 maps used where photographs not available
Total rock area	ROCKAREA	_	m ² per km	As above
Total sand area	SAND	-	m ² per km	As above
Rock pool area	ROCKPOOL	2	m ² per km	
Fucus covered rock	FUCUS	2	m ² per km	
Bare or barnacle covered rock	BARE	2	m ² per km	
Mussel-bed rock	MUSSELS	2	m ² per km	
Green algae covered rock	ALGAE	7	m ² per km	All chlorophyceae, e.g. Ulva, Enteromorpha
Non-Fucus covered rock	NONFUCUS	2	m ² per km	Total rock area minus Fucus covered rock.
Mean slope	SLOPE	1	gradient - no units	Drop in height (m)/horizontal distance (m), measured
				over 5 m distance. Calculated from mean of 20
				MHWM to MLWM measurements.
Littorinids < 4 mm	LIT<4	3	individuals per m ²	From minimum of 30 0.25m ² quadrats spread
				between all shore levels.
Littorinids < 8 mm	LIT<8	3	individuals per m ²	As above.
All littorinids	LITTORIN	3	individuals per m ²	As above.
Dog whelks < 5 mm	THAIS<5	3	individuals per m ²	As above.
Dog whelks < 8 mm	THAIS<8	3	individuals per m ²	As above.
All dog whelks	THAIS	3	individuals per m ²	As above.
Littorinids and dog whelks < 8 mg GAST<8	I GAST<8	3	individuals per m ²	As above.
All littorinids and dog whelks	GAST	3	individuals per m ²	As above.
Mussels, all < 2 mm	MUSS<2	3	individuals per km	Mean density from sampling × mussel-bed area.
Mussels $> 2 \text{ mm}, < 4 \text{ mm}$	MUSS2-4	4	individuals per km	As above.

Table 2.1 continued

Variable	Abbreviation	Source	Units	Notes
	in PCA			
Mussels, all < 4 mm	MUSS<4	4	individuals per km	As above.
Mussels > 4 mm, < 6 mm	MUSS4-6	4	individuals per km	As above.
Mussels, all < 6 mm	9>SSNW	4	individuals per km	As above.
Mussels $> 6 \text{ mm}, < 10 \text{ mm}$	MUSS6-10	4	individuals per km	As above.
Mussels, all < 10 mm	MUSS<10	4	individuals per km	As above.
Mean crevicing	CREVICES	5	cm crevicing per	Total length of crevices within 0.25 m ² quadrat;
			$0.25 \mathrm{m}^2$	minimum of 30 samples spread between shore levels.
Mean roughness	ROUGHNES	. 5	ratio - no units	(See p192 in Baker & Wolff 1987).
Mean stones	STONES	5	%	Minimum 30 samples from all shore levels.
Rock pool area 2	ROCKPO02	5	%	As above.
Distance to nearest roost	ROOST		km	Mean distance to nearest regularly used roost site
				from 10 evenly spaced points along coast within site
Raptors	RAPTORS	9	Birds per km per field	Sparrowhawk, Merlin and Peregrines within 100 m of
			visit	intertidal area.
Strand-line wrack	STRAND	9	m per km	Wrack deposits >0.5m in width. From >20 visits.
Human/dog disturbance	HUMAN	9	Individuals per km	Counted once at start of each site visit: minimum of
				20 visits.

aerial photographs and maps
 aerial photographs
 invertebrate surveying Jan-Feb 1998
 invertebrate sampling and aerial photographs
 surveying Jan-Feb 1998
 feldwork, midwinter 1996-97 and 1997-98

Figure 2.2: Subdivisions of south Northumberland study area for multivariate analysis at the larger spatial scale

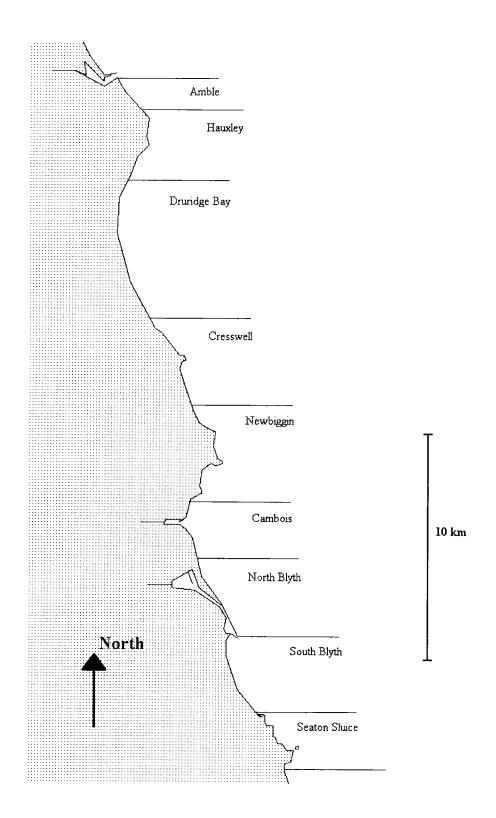
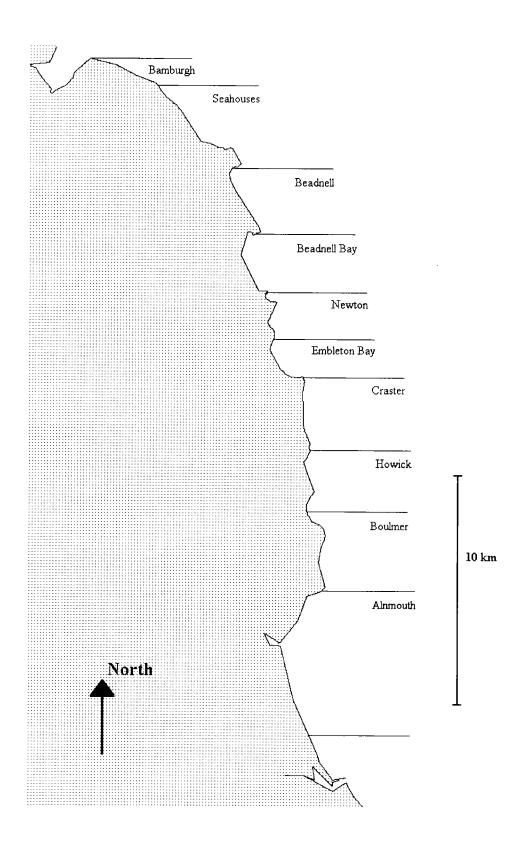


Figure 2.3: Subdivisions of north Northumberland coast used to test predictions generated by multivariate analysis at the larger spatial scale



2.3 Results

2.3.1. Purple Sandpiper principal component regression at the larger spatial scale

Principal component analysis was conducted on the 33 variables measured on the large spatial scale. Variables that were highly inter-correlated with others were eliminated from the analysis. Although it is important to reduce the correlation between variables entered into PCA (Kline 1994), several inter-correlated substrate variables were retained in the analysis as it was felt that each was biologically important. The aim of this analysis was to produce a model that could be tested with data from the north Northumberland coast which meant that several variables were excluded from the analysis as data for them were not available from north Northumberland e.g. raptor density.

Principal component analysis was performed with an unrotated matrix which produced two principal components with eigenvalues greater than one, together describing 86% of the total variation in the variables. Table 2.2 gives the eigenvalues of these two components and Table 2.3 the factor loadings.

Table 2.2: Variance explained by principal components at the larger spatial scale

Component	Eigenvalue	% of variance	Cumulative %
1	4.169	59.56	59.56
2	1.839	26.27	85.83

Table 2.3: Component matrix from PCA at the larger spatial scale

	Factor number		
Variable	1	2	
BARE	0.4600	0.2078	
ALGAE	0.4315	-0.2902	
FUCUS	0.1928	0.5939	
MUSSELS	0.4138	-0.2508	
ROCKPOOL	0.4222	-0.2037	
SAND	-0.4408	-0.1391	
STRAND	0.0763	0.6293	

These two principal components lend themselves well to interpretation. The first factor has high loading for those variables associated with areas of rocky shores: bare & barnacle covered rock, mussel-bed, encrusting algae. Strand-line has an almost negligible loading while sand area is strongly negatively loaded. This component could be interpreted as a measure of "rockiness". The second factor has low or negative loadings for these variables, but high loadings for the area of *Fucus* covered rock and, in particular, the amount of wrack deposited on the strandline. This component could be interpreted as a measure of "strand".

Purple Sandpiper densities, transformed by $\ln(\text{density} + 1)$, were regressed against these principal components. There was no statistical relationship between bird density and the second principal component ($r^2 = 0.009$, F = 0.66, not significant) but there was with the first principal component ($r^2 = 0.714$, F = 17.49, P < 0.01):

Purple Sandpiper density = $(0.4922 \times PC1) + 1.22$

Where Purple Sandpiper density and PC1 transformed by ln(variable + 1).

When both principal components were entered into a multiple regression with Purple Sandpiper density the resulting regression, although statistically significant ($r^2 = 0.63$, F = 7.83, P < 0.01), was weaker than that found with the first principal component alone.

2.3.2. Purple Sandpiper principal component regression at the small spatial scale

The same seven variables were retained in principal component analysis as were entered into the larger spatial scale analysis. Three principal factors with eigenvalues greater than one were derived from this analysis. Eigenvalues and factor loadings are given in Tables 2.4 and 2.5.

Table 2.4: Variance explained by principal components at the small spatial scale

Component	Eigenvalue	% of variance	Cumulative %
1	2.3933	34.2	34.2
2	1.3062	18.7	52.8
3	1.1557	16.5	69.4

Table 2.5: Factor loadings from PCA at the small spatial scale

	Factor number				
Variable	1	2	3		
BARE	0.5059	0.0784	-0.3497		
ALGAE	0.3443	-0.2091	0.3262		
FUCUS	0.4126	0.4722	0.2183		
MUSSELS	0.1849	-0.7089	-0.2187		
ROCKPOOL	0.3303	-0.1074	0.7014		
SAND	-0.4357	0.2831	0.1882		
STRAND	0.3495	0.3645	-0.3852		

Interpretation of the "meaning" of these three principal components is rather more difficult than for the larger spatial scale analysis. The use of these components in a regression analysis may produce accurate descriptive models. However, without a biological explanation for what the principal components actually describe, even the most accurate model would not help in determining

what environmental variables might define bird density. This part of the analysis was not pursued further.

2.4.1 Turnstone principal component regression at the larger spatial scale

The first two principal components from the larger spatial scale PCA, detailed in Tables 2.2 and 2.3, were univariately regressed against (transformed) Turnstone density. There was no significant relationship between the second principal component and Turnstone density (r2 = 0.31, F = 3.08 (8 d.f.), not significant). Turnstone density was, however, significantly correlated with the first principal component, interpreted as "rockiness". This relationship was described by the equation:

Turnstone density = $(0.4246 \times PC1) + 2.058$

Where Turnstone density and PC1 were transformed by ln(variable + 1). F = 12.72 (8 d.f.), P < 0.01, r^2 = 0.645.

Turnstone density was then regressed against both principal components giving a highly significant regression, which explained over 93% of variation in Turnstone density.

Turnstone density = $(0.4246 \times PC1) + (0.44 \times PC2) + 2.0585$

Where Turnstone density, PC1 and PC2 were transformed by ln(variable + 1). F = 57.85, 8 d.f., P < 0.001, $r^2 = 0.934$.

2.4.2 Turnstone principal component regression at the small spatial scale

As with the analysis of Purple Sandpiper data (Section 2.3.6, Tables 2.4 and 2.5), the principal components generated by PCA at the small spatial scale did not relate to any discrete environmental "characteristics" of the coastline. No attempt was made to regress Turnstone density against the results of this PCA.

2.5.1 Testing the accuracy of model predictions

Three models predicting Purple Sandpiper (one) and Turnstone (two) distribution were produced. These models were used to generate predictions of bird density for the north Northumberland coast. Tables 2.6 - 2.8 give the predictions and 95% confidence intervals for each site. These tables allow comparison with the actual densities derived from counts made by English Nature, also given in these tables.

2.5.2 Accuracy of models of Purple Sandpiper density

<u>Table 2.6: Testing of Purple Sandpiper density predictions from larger spatial</u> <u>scale principal component regression model</u>

Site	Mean	Predicted	Lower	Upper	Within	Error
	density	density	95% C.I.	95% C.I.	C.I.?	
Bamburgh	75.39	10.56	-0.42	125.89	Yes	-64.83
Seahouses	5.88	5.40	-0.45	74.73	Yes	-0.48
Beadnell	4.02	3.72	-0.49	43.15	Yes	-0.30
B'dnell Bay	0.85	0.09	-0.63	2.26	Yes	-0.76
Newton	2.38	1.31	-0.69	3.76	Yes	-1.07
Embleton B	0.95	0.45	-0.47	4.45	Yes	-0.50
Craster	6.36	5.34	-0.59	22.11	Yes	-1.02
Howick	0.32	0.10	-0.63	2.08	Yes	-0.22
Boulmer	2.39	3.95	-0.48	47.05	Yes	+1.56
Alnmouth	1.81	4.59	-0.47	58.54	Yes	-2.78

Nine of the ten Purple Sandpiper densities predicted using the model derived from PCA at the larger spatial scale were lower than the actual recorded density. In the case of Bamburgh, which had the highest density of any site (by a very large margin) this underestimation was considerable. However, in all cases the measured densities fell within the 955% confidence limits of the predicted values.

2.5.3 Accuracy of models of Turnstone density

Both models derived using the components from the PCA for south Northumberland were very poor at predicting Turnstone density in north Northumberland at the large spatial scale (Tables 2.7 and 2.8). The first model (incorporating the first principal component) produced predictions that erred from the actual densities by a mean of 125%. The predictions produced by the second model, using both principal components, had a low margin of error, but no actual Turnstone densities lay within the 95% confidence intervals of the predicted densities. In both models the predicted densities were mostly below the actual values.

<u>Table 2.7: Testing of Turnstone density predictions from univariate principal</u> <u>component regression model at the larger spatial scale</u>

Site	Mean	Predicted	Lower	Upper	Within	Error
	density	density	95% C.I.	95% C.I.	C.I.?	
Bamburgh	12.42	4.80	4.01	5.69	No	-7.62
Seahouses	19.35	5.49	4.44	6.73	No	-13.86
Beadnell	18.33	6.17	4.84	7.77	No	-12.16
B'dnell Bay	4.53	2.28	2.22	2.32	No	-2.25
Newton	27.29	7.22	5.45	9.45	No	-20.07
Embleton B	4.44	4.21	3.64	4.84	Yes	-0.23
Craster	5.55	6.61	5.10	8.48	Yes	+1.06
Howick	2.37	7.19	5.43	9.40	No	+4.82
Boulmer	27.19	17.02	10.35	27.58	Yes	-10.17
Alnmouth	9.04	3.42	3.12	3.72	No	-5.62

<u>Table 2.8: Testing of Turnstone density predictions from multiple principal</u> component regression model at the larger spatial scale

Site	Mean	Predicted	Lower	Upper	Within	Error
	density	density	95% C.I.	95% C.I.	C.I.?	
Bamburgh	12.42	2.36	2.26	2.47	No	-10.06
Seahouses	19.35	5.94	5.39	6.53	No	-13.41
Beadnell	18.33	11.09	9.22	13.31	No	-7.24
B'dnell Bay	4.53	1.34	1.21	1.49	No	-3.19
Newton	27.29	14.71	11.81	18.26	No	-12.58
Embleton B	4.44	3.84	3.68	4.01	No	-0.60
Craster	5.55	7.82	6.88	8.88	No	+2.27
Howick	2.37	9.23	7.95	10.69	No	+6.86
Boulmer	27.19	129.26	77.20	215.99	No	+102.07
Alnmouth	9.04	3.09	3.03	3.16	No	-5.95

2.6 Discussion

2.6.1 Purple Sandpiper

The predictive model developed for Purple Sandpipers was based on a positive relationship between Purple Sandpiper density and the principal component describing "rockiness". This factor had high loadings for habitat types, such as mussel-bed and bare rock, commonly associated with Purple Sandpipers, and shown to be used by them later in this thesis. This model gave a good fit to the data from sites in South Northumberland. When used to generate predictions for the North Northumberland coast it consistently underestimated bird densities, especially at the site with by far the highest density of overwintering Purple Sandpipers, Bamburgh.

Underestimation by a predictive model suggests that the area that predictions are made for has a higher density of birds per resource unit than the area from which the data used to generate the model was collected – that a site with a certain

value of "rockiness" in North Northumberland has more Purple Sandpipers than an equivalent site in South Northumberland. This might be expected for a species, such as Purple Sandpiper, that migrates to Britain from the north and fills up wintering sites from the north, with progressively fewer birds wintering the further south they have to travel (Summer *et al.* 1992). However, it seems extremely unlikely that such a small distance as between the two contiguous lengths of Northumberland coastline would be sufficient to cause such a difference. Instead it appears that although giving a good fit to data in South Northumberland the model was poor at predicting in other regions, probably because using a single predictor, albeit one that combined data from many variables, was not sufficient to encompass the factors that actually control Purple Sandpiper variation.

A number of the variables used in the PCA may have been instrumental in determining Purple Sandpiper density. Mussels are an important component of the diet of wintering Purple Sandpipers (Feare 1966, Summers *et al.* 1990a, Dierschke 1994), along with rocky shore invertebrates such as littorinids, which may be found within mussel-beds and on other rocky shore substrates, such as encrusting algae, *Fucus* and bare/barnacle-covered rock which had high loadings in the first principal component factor with which Purple Sandpiper density was significantly correlated.

The availability of roost sites may have been important for Purple Sandpipers, although all rocky shore sites within the south Northumberland study area had suitable roost sites. However, the roost site at Cresswell was not available for birds on some spring tides (the main site is covered by tides higher than 4.8 m O.D. and the alternative site in Lynemouth is subject to frequent disturbance). The single roost-site variable used in the analysis did not reflect this periodic unavailability and hence may not have been appropriate for this analysis.

As discussed in Section 2.1.3, the distribution of Purple Sandpiper changes on a number of temporal scales. By using data (e.g. bird density, human disturbance, frequency of raptor sightings) collected over the course of the wintering period it was hoped to encompass some of this variation, such as that between neap and

spring tides. However, by seeking to find a relationship with an "average" distribution, the accuracy of the models produced may have been diminished. Perhaps more importantly, the analysis made no attempt to encompass betweenyear variation in Purple Sandpiper distribution, as many of the most important variables required for the analysis were not available for each winter separately. These included those obtained from aerial photographs, and invertebrate densities (the intensive fieldwork necessary to accurately measure invertebrate densities was only conducted in one winter). For example, between-year fluctuations in wintering Purple Sandpiper numbers due to e.g. variation in breeding success would result in changes in bird density unrelated to any environmental variables within the wintering area. Fluctuations in the number of birds arriving in the autumn could also change the proportion of the total settling at each site; if wintering sites vary in quality, preferred sites fill up first and if reduced numbers mean "vacancies" at these sites, individuals could move from other, poorer, sites to fill them. Thus the highest quality ("primary") sites may retain a relatively constant density of birds while poorer quality ("secondary") sites act as "buffers" and show more fluctuations in density from year to year (Brown 1969, Fretwell 1972).

In addition, the fitness benefits of wintering at each site may have varied between years due to variation in mussel spat settlement. Unfortunately, as data on substrate cover were available from aerial photographs taken on only one date (and that not in any of the three winters from which the other data were collected), it was not possible to measure many variables for each winter separately. Such an approach very likely would be to produce models that had a better fit with the data used to generate them, and subsequently might be better at predicting densities in other regions.

Although the lack of raptor data from north Northumberland meant it was not possible to test the relationship between Purple Sandpiper density and raptors density, this factor may have been important in restricting distribution. Purple Sandpipers are taken by raptors along the Northumberland coast; one colourringed bird was observed being taken by a Sparrowhawk (*Accipiter nisus*), while a radio-tagged individual was taken by an unknown raptor. Dierschke (1998)

believed that raptor predation was the biggest cause of winter mortality of Purple Sandpipers on Helgoland (Germany). The direct effect of raptor presence on Purple Sandpiper density was observed in early 1999 when a female Merlin (*Falco columbarius*) frequently roosted on the East Pier at Blyth, within 20 m of the usual Purple Sandpiper roost site. Her presence resulted in a 95% decrease in the number of birds using the roost and, as a consequence, the North Blyth feeding areas. Burton *et al.* (1996) found that disturbance by a Merlin caused a decrease in the number of Purple Sandpipers using a roost site at Hartlepool. In addition, on several occasions, hunting Peregrines (*Falco peregrinus*) have been seen to cause all Purple Sandpiper to leave a study site. Cresswell (1994) found that adult Redshank (*Tringa totanus*) used suboptimal foraging areas to minimise predation risk, and some Purple Sandpipers may react to raptor predation risk in a similar manner.

In recent years the numbers of raptors wintering on the Northumberland coast have steadily increased (Galloway & Meek 1980, Kerr & Johnston 1996, 1997, 1998). A particularly significant increase has been in the number of Peregrines, as the population has recovered nationally from the impact of organochloride insecticide poisoning (Gibbons *et al.* 1993). At present, Peregrine distribution along the Northumberland coast is patchy, with birds maintaining wintering territories at some sites (Coquet Island/Amble, Blyth and St. Mary's Island) but not others. With any further increases in numbers the "gaps" in Peregrine distribution may be filled which could have the effect of reducing the impact of raptor density on Purple Sandpiper distribution: if all sites had hunting Peregrines, then birds would not be able to choose feeding sites to avoid them. Alternatively, the result could be a decline in the number of Purple Sandpipers using the area as a whole, although it is unlikely that other regions on the coast of Northeast England would offer any respite from raptor predation for these birds.

Levels of disturbance from humans and dogs were reasonably uniform between the nine sites on the larger spatial scale. On the smaller spatial scale there was greater variation, with certain parts of the foreshore being preferred by dogwalkers and, maybe more importantly, sea-anglers choosing certain rocky promontories. The separate recording of these different forms of use (dogwalkers cause temporary disturbance while anglers may exclude birds from a feeding location for several hours) at the small spatial scale might have resulted in a stronger relationship of bird density to environmental variables.

The substrate variables used in modelling were all measured as area per km. This measurement may not have been appropriate for assessing the relationships with Purple Sandpiper distribution, as birds spend almost all of their time feeding within a very short distance of the tide's edge (Chapter 4 in this thesis, Feare 1966). At any instant it is not the total area of substrate exposed but the amount along the tideline that may determine the attractiveness to Purple Sandpipers. Although superficially similar to the south Northumberland study area. geological differences mean that the north Northumberland coast in general has steeper sloping shores and so less intertidal area. Using the area-based approach resulted in lower predictions of Purple Sandpiper density in north Northumberland due to smaller mussel-bed area. However, these mussel-beds may be exposed on the tide's edge for a similar time as at the larger, shallower sloping, south Northumberland sites. If Purple Sandpiper density is so great that prey depletion over the course of the winter is a limiting factor then the absolute area (and hence prey population size) may be important. But if this explanation were false then the absolute area of substrate types would not be relevant to accurate modelling. Invertebrate surveying before and after the winter (Appendix 2) found no evidence of major decline in the densities of the dominant species.

The British wintering population of Purple Sandpipers is only a small fraction of the total European population. The large numbers of birds that winter in Norway (Summers *et al.* 1990b) are present at a higher density (birds per km of coastline) than in Britain despite a harsher climate and the greater daily food intake that each bird therefore requires (Summers *et al.* 1998). It seems unlikely that the relatively lower densities in Britain, and Northumberland in particular, are restrained by food density or availability. In addition, sites within the study area held considerably larger populations in the 1980s and the early 1990s (data from WeBS counts). The drop in numbers appears to be related to a national decline (Cranswick *et al.* 1999). It is possible that this decline might be related to a decline in food resources, caused by reductions in sewage inputs in many areas in

recent decades, but there is no evidence to prove that this is the case. Although Purple Sandpipers within the study area do appear to be distributed in relation to mussel-bed area, it may require very large reductions in either mussel-bed area, or the density of mussels of suitable size-class within these mussel-beds, to cause birds to winter elsewhere. The abundance of suitable prey means that other factors, such as predation risk from raptors, could be a major influence on Purple Sandpiper distribution.

2.6.2 Turnstone

The principal components derived by the larger spatial scale PCA appeared to be relevant to Turnstone ecology, describing as they do the amount of low water foraging area (first component) and the availability of strand-line wrack for high water foraging (second component). The model generated with these components provided a good fit to Turnstone densities ($\mathbf{r}^2 = 0.93$) on the south Northumberland coast, but then produced highly inaccurate predictions of Turnstone density on the north Northumberland coast. Most predictions were below the actual observed density, and outside the 95% confidence limits. Due to the much better fit of the model to the data used to generate it, these confidence limits were considerably smaller than for the Purple Sandpiper model. It should be noted that despite the poor performance, the highest predictions made by the model were for the sites with the highest Turnstone density (Newton and Boulmer). The same was true for the second Turnstone model, that generated on the small spatial scale.

The relationship with habitat variables, albeit condensed into PCA factors, concurs with Turnstone foraging habitat choice (McKee 1982, Whitfield 1985a, 1990). If it had been possible to test for a relationship between Turnstone abundance and invertebrate abundance a relationship between Turnstone and prey density may have been found. Such relationships have been demonstrated in a number of shorebird species such as Curlew Sandpipers *Calidris ferruginea* (Kalejta & Hockey 1994), Dunlin *Calidris alpina* (Rands & Barkham 1981) and Oystercatchers *Haemotopus ostralegus* (Goss-Custard *et al.* 1995). However,

such a relationship may be hard to detect in Turnstones due to the many types of prey that they take (Cramp & Simmons 1983).

Raptor predation certainly occurred (corpses of Turnstones killed by raptors were found at three sites) and, as with Purple Sandpiper, is probably the most significant cause of winter mortality. Whitfield (1985b) found predation by Sparrowhawks to be the most important source of winter mortality in Southeast Scotland.

The models constructed to describe Turnstone density produced more accurate predictions of bird distribution on the north Northumberland coast than those for Purple Sandpipers. This accuracy was maintained at the smaller spatial scale. As Turnstone do not use tide-edge foraging to the same extent as Purple Sandpipers (Chapters 4 and 5), the use of variables measuring the area rather than the proportion of substrates may have been more appropriate. The single variable used to express roost availability was probably not an accurate measure, but may have been less critical for Turnstones than for Purple Sandpipers. Turnstones in the south Northumberland study area utilise a wider range of roost sites, are more tolerant of disturbance and are more likely to feed over the high water period than are Purple Sandpipers.

Turnstone densities are affected by the abundance of the substrates used for foraging at low water and high water. At both low and high water the relationship is likely to be with the availability of prey within these habitats. The strongly despotic behaviour of Turnstones (although possibly not all individuals, Chapter 7) means that as the density of birds on both intertidal feeding grounds and strand-line wrack deposits increases, the profitability of doing so for each individual decreases (to different extents) due to competition and interference. Individual birds make a decision regarding where to settle based on a trade-off between the quality of a foraging area and the density of birds feeding there. Although raptor predation was not found to be an important model component, it seems likely that the risk of being preyed upon has an effect on the decisions

made by individual Turnstones on where to winter. A more accurate measure of the risk of predation may enable such a relationship to be revealed.

Recent winter surveys have shown that Turnstone numbers have declined nationally by 36% between 1984-85 and 1998 (Cranswick *et al.* 1999) and by up to 46% in Northumberland (Rehfisch *et al.* 1999). There is no evidence of a change in local food resources that might have caused this decline, although changes such as the building of a longer sea outfall at Newbiggin and removing the discharge at Seaton Sluice may have caused declines in intertidal invertebrates (Rehfisch *et al.* 1999 suggest recent mild winters have caused a distribution shift nationally). If food availability has remained constant and Turnstone numbers have declined, the population in Northumberland would not presently be limited by food resources.

Chapter 3

Measuring the relative inputs of particulate organic matter from sewage outfalls and from dead macroalgae using stable isotopes

3.1 Introduction

The removal of a large proportion of suspended solids and, to a lesser extent, dissolved nutrients from sewage discharged along the Northumberland coast may have a significant impact on the inshore ecosystem, as described in Chapter 1. In order to be able to predict what impacts may occur, to monitor the environment for changes and then to establish a causal link between the two, it is necessary to know how important these inputs are at present. Table 3.1 gives details of all the sewage inputs into inshore waters within the study area (before the ongoing programme of upgrades in treatment and discharge). Somewhere in the region of seven tonnes of materials which give rise to B.O.D. and eight and a half tonnes of suspended solids are discharged into inshore waters along the south Northumberland study area every day. The Northumberland coast is subject to strong southerly offshore currents, which aid the rapid dispersal of much of this sewage (the region was formerly designated as an "Area of High Natural Dispersion" under E.C. legislation). However, it seems highly likely that some is swept inshore, leading to local concentrations of sewage constituents to the south of discharge points. This chapter describes the use of stable isotope analysis to quantify the relative contribution of sewage to the particulate organic matter (POM) in the water column of inshore waters.

Table 3.1: Coastal sewage discharges in the south Northumberland study area

No.	Name	Equiv. Pop.	Distance of	Treatment
			discharge	
			beyond MLW	
1	Amble	24981	300 m	Maceration,
				screening
2	Hadston/Broomhill	4171	50 m	Screening
3	Cresswell	$164^2, 1200^3$	15 m	Septic tank
4	Newbiggin	38062	1350 m	Screening, grit
				removal
5	Cambois	42884	90 m	Maceration

Sewage output as equivalent of human population. Calculated by Northumbrian Water with assumed COD:BOD ratio of 2:1 and a BOD loading of 60g BOD/person/day.

Several constituents of sewage sludge can be used to trace sewage inputs in inshore waters. Micro-organisms commonly associated with sewage include bacteria, viruses, protozoa and helminths (Alderslade 1981), but most use has been made of measurements of faecal bacteria such as *Escherichia coli* (e.g. Kaye & Haddad 1992, Ghinsberg *et al.* 1994, Obiridanso & Jones 1999). More recently molecular tracers (substances persistent after discharge and not found naturally in the receiving waters) have become a popular tool for tracing sewage. Tracers have included sterols associated with human faeces (Bachtiar *et al.* 1996, Chan *et al.* 1998), bile acids (Elhmmali *et al.* 1997), linear alkylbenzenes (Zeng *et al.* 1997) and detergents (Aboulkassim 1992).

Although these techniques may allow the dispersal and dilution of sewage to be traced after input, they cannot in themselves provide an estimation of the amount of sewage relative to naturally occurring organic matter. One technique that does allow this comparison, and hence was used in this study, is stable isotope analysis.

Typically the ratio of 13 C to 12 C (known as δ^{13} C) is higher in marine plants and algae than in terrestrial plants, because of the higher δ^{13} C found in bicarbonate

²Winter, ³summer.

(the source of carbon fixed by marine algae) than in carbon dioxide (the source of carbon fixed by terrestrial plants) (Lajtha & Michener 1994). Samples enriched in 13 C or 15 N are referred to as being "heavier" than non-enriched samples. Sewage particulates result from the consumption by man of plants of predominantly terrestrial origin, which are not digested and have a relatively low δ^{13} C value. A difference in the ratio of the two stable isotopes of nitrogen (15 N to 14 N, referred to as δ^{15} N) may also be found between marine and terrestrial sources, as may differences in the ratios of stable isotopes of sulphur and hydrogen. By comparing the stable isotope ratios of a sample with that of its potential sources, it is possible to identify and quantify its origin.

A number of studies have successfully used stable isotopes to demonstrate the dispersal and uptake of sewage in marine ecosystems, using carbon (Burnett & Schaeffer, 1980), nitrogen (Sweeney et al. 1980), sulphur (Sweeney & Kaplan 1980) and hydrogen (Rau et al. 1981). Some studies have used stable isotopes to trace sewage inputs through food chains, as the stable isotope composition of an organism reflects that of its diet (although some fractionation of isotopes normally occur during assimilation). For example, by measuring carbon and nitrogen stable isotopes, Spies et al. (1989) calculated that 15-20% of the diet of fish (such as Dover sole Microstomus pacificus) near an outfall in California was derived from sewage particulates. Other studies have also found evidence for the uptake of sewage particulates by marine organisms e.g. Gearing et al. (1991), Van Dover et al. (1992) and Moore et al. (1996).

The present study aimed to determine the proportion of the suspended POM in inshore waters that originated from sewage. This approach was used by Tucker *et al.* (1999) to trace sewage through Boston Harbour and Massachusetts Bay (using nitrogen stable isotopes).

In the present study a range of intertidal seaweeds were sampled in order to measure $\delta^{13}C$ and $\delta^{15}N$ values for this major natural source of POM in inshore waters. In addition, sewage samples were taken from the coastal outfalls at Amble and Blyth in order to measure the isotope ratios for the sewage particulate matter. With the knowledge of isotope ratios of these two sources of particulate

matter the contribution of each to the particulate matter sampled at a number of sandy beaches and rocky shores along the south Northumberland coast could be estimated. An attempt was made to measure the ratios of carbon and nitrogen isotopes in the Coquet River. Such data would have allowed a three-source mixing model to have been used, in order to quantify the relative input to organic particulates in inshore waters from freshwater sources. Unfortunately the results from this analysis were ambiguous; details are given in Appendix 2.

The percentage of particulate matter that originates from sewage inputs was calculated using a mixing model:

$$F_{sewage} = (\delta_{sample} - \delta_{algae})/(\delta_{sewage} - \delta_{algae}) \times 100$$

Where F_{sewage} = the percentage of particulates in a given sample that are derived from sewage.

With a net southwards tidal flow along the Northumberland coast, sewage would be expected to disperse southwards from outfalls. Therefore a sampling program was devised to include sampling stations at increasing distances southward from the two outfalls investigated. Sampling was conducted in spring and autumn 1999 as it was thought likely that there would be seasonal variation in the abundance of algal-derived particulate matter in coastal waters. However, all sampling design was constrained by the high cost of stable isotope analysis; in some ways work and results detailed herein should be regarded

3.2 Methods

3.2.1 Sampling locations

Sewage samples were collected in the first week of April and the second week of September 1999; coastal water samples and algae were collected within a week either side of these dates. Sewage samples were taken at the pumping stations prior to discharge from major outfalls at Amble and Cambois (Figure 3.1, Table 3.1). Water samples (for the extraction of particulate matter) were collected from

a total of 12 sites (Figure 3.1, Table 3.2). The sampling regime differed between the two seasons, as analysis of samples taken in the spring revealed that variation between replicates was far less than between different samples from a site. Thus fewer replicates of more samples were analysed in the autumn.

Table 3.2: Water sampling stations in the south Northumberland study area

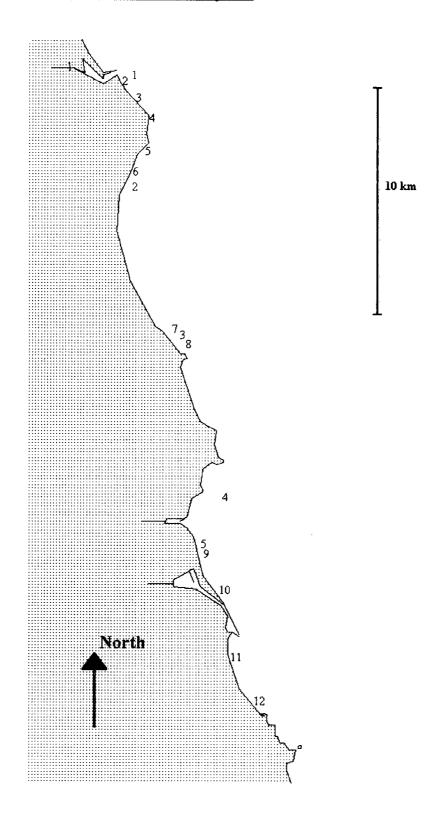
No.	Site	Habitat	When sampled
1	Coquet Estuary	Tidal river	Autumn
2	North Amble	Rocky shore	Spring & autumn
3	South Amble	Sandy shore	Spring & autumn
4	North Hauxley	Rocky shore	Spring & autumn
5	South Hauxley	Sandy shore	Spring & autumn
6	North Druridge	Sandy shore	Spring
7	North Cresswell	Rocky shore	Spring & autumn
8	Cresswell Beach	Sandy shore	Spring
9	Cambois	Sandy shore	Spring
10	North Blyth	Rocky shore	Spring & autumn
11	South Blyth	Sandy shore	Spring
12	Seaton Sluice	Rocky shore	Spring & autumn

The numbers given for sites refer to Figure 3.1

Algae were sampled from five rocky shore sites in the spring – Amble, Hauxley, Cresswell, North Blyth and Seaton Sluice. The same sites, minus Hauxley, were sampled in the autumn.

The sampling sites effectively formed two transects running south (down current) from sewage outfalls: one of five sites to the south of Amble outfall and another of four sites to the south of the Cambois sea outfall. In addition, two locations near the much smaller outfall at Cresswell were sampled.

Figure 3.1: Locations of sewage discharges (red) and water sampling sites (blue) in the south Northumberland study area



3.2.2 Sampling methods

Sewage samples were collected in 1 litre bottles. These samples were filtered using a hand-operated vacuum pump through pre-ashed 47 mm diameter Whatman GF/F filters, which retained particulates above 0.6 mm in size. Approximately 200 ml was filtered from each sewage sample at which point the filters tended to become completely clogged (samples were well mixed and screened through a 2mm mesh before filtering to prevent any large particles biasing the analysis). Filter papers were subsequently air-dried at 60°C. Initial analysis used half of a single filter paper for each sample (approximately 8.7 cm²), but these proved too large for the combustion chamber. Subsequent trials using a quarter of a filter paper did not provide enough sample (particularly nitrogen) for accurate analysis. Eventually a technique was developed where the top layer of the filter paper was scraped off with a sharp blade so that all particulates were retained but most of the filter paper could be discarded to keep the bulk of the sample down. Use of this method allowed half of a single filter paper to be analysed, equivalent to the POM from 100 ml of water sample.

In the spring, two replicates were analysed from three effluent samples from each of the two discharges. In the autumn, eight non-replicated samples were analysed from each discharge.

Water samples were collected at half-tide on the rising tide, by wading out to approximately 0.5 m water depth and collecting water from below the surface in one-litre bottles. Care was taken to avoid areas with high wave action as such samples contained large amounts of sand. This method insured that samples represented water that flowed over intertidal rock on the incoming tides and was filtered for food by feeding mussels and other invertebrates. Samples were sieved in the same manner as sewage effluent samples; approximately 500 ml of each sample was sieved.

Whole, healthy-looking specimens of three algal species were collected from rocky shore sites, washed thoroughly in de-ionised water and dried at 60 °C. These samples were then finely ground with a pestle and mortar. The algae

collected were *Laminaria hyperborea* (lower shore), *Fucus vesiculosus* (midshore) and *Enteromorpha linza* (uppershore). *E. linza* was sampled only in the autumn as very little is present in the spring. Samples for analysis consisted of 1 ml of ground and homogenised algae.

In the spring two replicate samples were analysed from one stolon (*L. hyperborea* and *F. vesiculosus*) from each of the five sites. As little variation in isotope ratios was found between replicates in the spring (see below), in the autumn one non-replicated sample was analysed from two individuals at each of the four sites sampled. For *E. linza* replicate pairs were taken from two individuals at each site.

Measurements of stable isotope ratios were determined using continous flow isotope ratio mass spectrometry, ANCA SL 20/20 (PDZ Europa Ltd, Crewe, UK) at the Biomedical Mass Spectrometry Unit at the Medical School, University of Newcastle-upon-Tyne. Samples were weighed into tin capsules prior to analysis and referenced to a cod standard; the cod standard had been previously referenced against IAEA standards. Isotopic values for the standard were 16.45 δ air and -16.50 δ PDB for N and C respectively (see below).

Isotope values are expressed as

$$\delta$$
 (‰) = (R_{sa}/R_{std} - 1) × 1000

Where R_{sa} = isotopic ratio of the sample and R_{std} = isotopic ratio of the standard. The standard used for carbon analysis is Pee Dee Belemnite (a marine limestone fossil) (PDB) (Craig 1953) and for nitrogen analysis is atmospheric air (Mariotti 1983).

Samples were analysed in batches of eight, preceded and followed by a reference sample, which allowed correction for instrumental drift.

3.3 Results

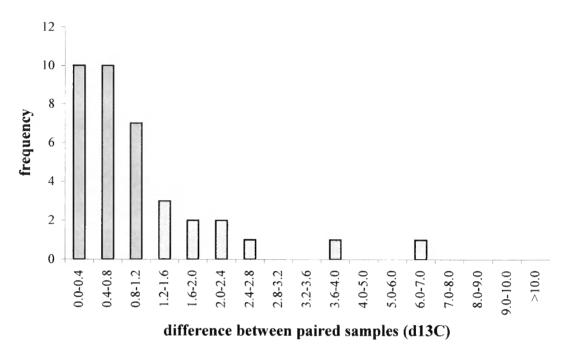
3.3.1 Variation between replicated samples

In the spring replicates were successfully analysed for sewage (five samples), particulates (15), *Fucus* (15) and *Laminaria* (15). There was no significant difference in the variation in δ^{13} C values between replicates in these four different sample-classes (one-way ANOVA, F = 0.13, d.f. = 3, not significant) However, variation between replicates in δ^{15} N values did differ significantly between sample classes (F = 5.16, d.f. = 3, P < 0.01), with particulate samples showing the greatest disparity between replicates and the two algal sources the least (mean variation between replicates for sewage = 0.49 ± 0.16, for particulates = 0.63 ± 0.32, for *Fucus* = 0.32 ± 0.17, for *Laminaria* = 0.37 ± 0.25).

In the autumn replicate pairs were analysed for samples of river particulates, seawater particulates and *Enteromorpha*. There was a significance difference in the within pair variation in δ^{13} C values between the sample types (F = 5.62, d.f. = 2, P < 0.01) with sea particulates showing the greatest variation (mean difference between replicate pairs for marine POM = 0.92 ± 0.14, for freshwater POM = 0.12 ± 0.05, for *E. linza* = 0.17 ± 0.05).

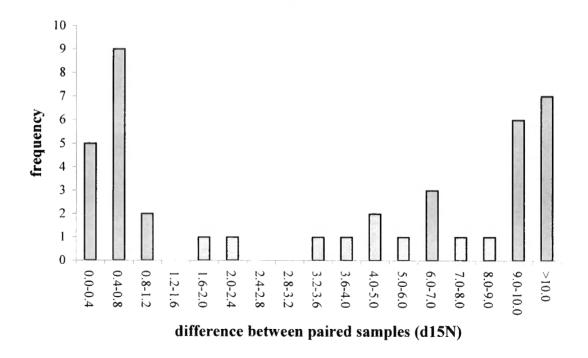
Particularly with respect to δ^{15} N, a large number of erroneous results were obtained during the analysis of samples, mostly for samples of POM. A number of these were easily identifiable, as there had been mechanical problems during the combustion or the amount of material analysed (total beam area) was insufficient for accurate analysis. However, a number of obviously wayward results occurred for no discernible reason. It was decided to include in the discussion of results only pairs of replicates that were within an "acceptable distance" of each other, identified by plotting the differences between replicate pairs (Figures 3.2 & 3.3).

Figure 3.2: Variation in δ^{13} C values (‰) between paired samples of POM



Most replicates showed similar $\delta^{13}C$ values, but pairs that differed by more than 2.8% have been eliminated from the following discussion.

Figure 3.3: Variation in δ^{15} N values (‰) between paired samples of POM



The variation between replicate pairs was much greater for $\delta^{15}N$ than $\delta^{13}C$, with many samples showing a large difference between replicates. Samples with a difference of less than 2.4% between replicates were retained for further discussion.

3.3.2 Isotope ratios for sources of inshore POM

3.3.2.1 Sewage

Table 3.3: Mean and S.E. δ^{13} C values (‰) for sewage effluent from Amble and Cambois

	Amble			Cambois		
	mean	S.E.	n	mean	S.E.	n
Spring	-26.63	0.17	3	-26.81	0.13	3
Autumn	-25.37	0.10	8	-26.09	0.07	8

The δ^{13} C value of sewage from the Cambois outfall was significantly heavier (less negative) in autumn than in spring (two-tailed t-test, d.f. = 6, t = 4.523, P < 0.01). Similarly, the δ^{13} C of sewage sampled at Amble was significantly heavier in autumn than in spring (d.f. = 8, t = 6.409, P < 0.01).

There was no difference in δ^{13} C values between sewage samples from Amble and Cambois in the spring (d.f. = 9, t = 0.836, not significant), but in autumn the Amble samples had a significantly heavier δ^{13} C than those from Cambois (d.f. = 12, t = 5.859, P < 0.01).

Table 3.4: Mean δ¹⁵N values (‰) for sewage effluent from Amble and Cambois

	Amble			Cambois		
	mean	S.E.	n	mean	S.E.	n
Spring	4.04	0.29	3	1.12	0.93	3
Autumn	2.35	0.24	8	2.23	0.22	8

There was no significant difference in $\delta^{15}N$ between the sewage samples collected in spring and autumn at Cambois (d.f. = 4, t = 1.144). The sewage samples collected at Amble in the spring had a significantly heavier mean $\delta^{15}N$ than those collected in the autumn (d.f. = 11, t = 4.527, P < 0.01).

In the spring, sewage samples from Amble had a significantly higher mean $\delta^{15}N$ than those from Cambois (d.f. = 5, t = 2.977,P < 0.05). There was no significant difference in sewage from the two discharges in the autumn (d.f. = 14, t = 0.395).

3.3.2.2 Macroalgae

The samples collected in spring revealed considerable variation in isotope ratios between plants from different sites (Tables 3.5 and 3.6). This variation was significant for both $\delta^{15}N$ (one-way ANOVA, d.f. = 4, F = 22.49, P < 0.01) and $\delta^{13}C$ (d.f. = 4, F = 8.08, P < 0.05) values in L. hyperborea and $\delta^{15}N$ (d.f. = 4, F = 16.08, P < 0.01) values in F. vesiculosus. In comparison with between-plant variation, between-replicate variation was very small and indicated that the isotopic analysis of algal samples was satisfactorily accurate. However the sampling regime employed in the spring did not reveal whether variation was chiefly between sites or between individual plants as it sampled only one plant from each site.

<u>Table 3.5: Mean isotope ratios for *L hyperborea* from five south</u>

Northumberland sites sampled in spring

	δ ¹³ C (‰)			δ ¹⁵ N (‰)		
	mean	s.e.	n	mean	s.e.	n
Amble	-14.88	0.11	1	4.17	0.16	1
Hauxley	-14.06	0.23	1	6.93	0.22	1
Cresswell	-16.85	0.22	1	4.76	0.36	1
Blyth	-15.83	0.77	1	4.81	0.18	1
S. Sluice	-16.05	0.10	1	5.40	0.06	1
All sites	-15.53	0.34	5	5.25	0.32	5

<u>Table 3.6: Mean isotope ratios for *F. vesiculosus* from five south</u>

Northumberland sites sampled in spring

		δ ¹³ C (‰)			$\delta^{15}N$ (‰)		
	mean	S.E.	n	mean	S.E.	n	
Amble	-17.46	0.12	1	6.16	0.12	1	
Hauxley	-17.74	0.16	1	6.37	0.10	1	
Cresswell	-16.82	0.02	1	6.72	0.12	1	
Blyth	-17.05	0.03	1	5.45	0.13	1	
S. Sluice	-17.05	0.49	1	6.12	0.10	1	
All sites	-15.53	0.34	5	5.25	0.32	5	

In the autumn two individual algae were sampled from each site, but without replicate isotope analysis (Tables 3.7-3.9). Statistical analysis found no difference between sites (one-way ANOVAs) and variation (sum of squares) within sites exceeded that between sites, which strongly suggests that the between-site differences in the spring were due to only one alga being sampled from each site and that a major source of variation is between individuals.

<u>Table 3.7: Mean isotope ratios for *L. hyperborea* at four south Northumberland sites sampled in autumn</u>

	δ ¹³ C (‰)				δ ¹⁵ N (‰)		
	mean	S.E.	n	mean	S.E.	n	
Amble	-14.91	0.39	2	5.97	0.11	2	
Cresswell	-15.65	1.55	2	4.92	1.89	2	
Blyth	-11.45	0.19	2	6.16	0.32	2	
S. Sluice	-13.40	0.14	2	6.16	0.72	2	
All sites	-13.85	0.68	8	5.80	0.43	8	

<u>Table 3.8: Mean isotope ratios for *F. vesiculosus* at four south Northumberland sites sampled in autumn</u>

- ''		δ ¹³ C (‰)			δ ¹⁵ N (‰)		
	mean	S.E.	n	mean	S.E.	n	
Amble	-16.34	0.73	2	7.63	0.19	2	
Cresswell	-17.31	0.77	2	7.47	0.47	2	
Blyth	-15.58	0.24	2	6.50	0.47	2	
S. Sluice	-16.86	1.13	2	8.17	0.27	2	
All sites	-16.52	0.38	8	7.44	0.26	8	

<u>Table 3.9: Mean isotope ratios for *E. linza* at four south Northumberland sites sampled in autumn</u>

	δ ¹³ C (‰)				δ ¹⁵ N (‰)		
	mean	S.E.	n	mean	S.E.	n	
Amble	-15.22	0.04	2	8.60	0.21	2	
Cresswell	-13.85	0.10	2	8.75	0.08	2	
Blyth	-15.35	0.06	2	6.78	0.06	2	
S. Sluice	-18.58	0.11	2	7.77	0.13	2	
All sites	-15.75	0.45	8	7.97	0.21	8	

3.3.3 Sewage and algae values used in calculations of input to POM in the inshore water column

Calculations of the percentage of total POM in the water column that originated from sewage were performed using the δ values for sewage from the outfall nearest to each sampling location; Amble for Amble, Hauxley and Cresswell and Cambois for Blyth and Seaton Sluice (Tables 3.10-3.13). As variation in algal δ values between sites was probably chiefly due to variation between individuals (Section 3.3.2 above), averaged values for algae from all sites combined were used in the analysis. For both sewage and algal inputs, only the values from the appropriate sampling period (spring or autumn) were used.

The relative importance of the different types of algae sampled, in terms of volume of input into inshore waters, is not known. Therefore, the overall values for algae used in calculations were derived giving equal importance to each type -F. vesiculosus and L. hyperborea in spring, and plus E. linza in autumn.

Table 3.10: δ^{13} C values (‰) used in calculations for spring sampling

	Amble	Hauxley	Cresswell	Blyth	S.Sluice
Sewage	-26.633	-26.633	-26.633	-26.811	-26.811
Combined algae	-16.44	-16.44	-16.44	-16.44	-16.44

Table 3.11: δ^{13} C values (‰) used in calculations for autumn sampling

	Amble	Hauxley	Cresswell	Blyth	S.Sluice
Sewage	-25.375	-25.375	-25.375	-26.087	-26.087
Combined algae	-15.376	-15.376	-15.376	-15.376	-15.376

Table 3.12: δ^{15} N values (‰) used in calculations for spring sampling

	Amble	Hauxley	Cresswell	Blyth	S.Sluice
Sewage	4.044	4.044	4.044	1.125	1.125
Combined algae	5.705	5.705	5.705	5.705	5.705

Table 3.13: δ¹⁵N values (‰) used in calculations for autumn sampling

	Amble	Hauxley	Cresswell	Blyth	S.Sluice
Sewage	2.355	2.355	2.355	2.227	2.227
Combined algae	7.072	7.072	7.072	7.072	7.072

3.3.4 The relative contribution of sewage to particulates in inshore waters

The δ values for POM samples were calculated using only the paired replicates which showed acceptable consistency, chosen as described earlier (Section 3.3.1). Tables 3.14-17 give the δ values for particulate samples and the estimates of the % of POM originating from sewage.

3.3.4.1 Spring sampling

Table 3.14: Estimates of % of organic particulates derived from sewage calculated using $\delta^{13}C$ values from spring sampling

Site	No.	Mean δ ¹³ C	S.E.	% sewage
	samples	(‰)		
North Amble	4	-20.054	0.246	35.35
South Amble	2	-19.247	0.227	27.46
North Hauxley	2	-18.534	0.058	20.48
South Hauxley	2	-19.455	0.001	29.49
North Druridge	2	-19.454	0.008	29.48
North Cresswell	4	-21.641	0.089	50.88
Cresswell Beach	2	-21.571	0.024	50.19
Cambois	2	-20.122	0.005	35.50
North Blyth	4	-19.572	0.124	30.20
South Blyth	2	-18.577	0.373	20.61
Seaton Sluice	2	-19.743	0.109	31.85

Table 3.15: Estimates of % of organic particulates derived from sewage calculated using δ^{15} N values from spring sampling

Site	No.	Mean δ ¹⁵ N	S.E.	% sewage
	samples	(‰)		
North Amble	-	-	-	-
South Amble	2	6.941	0.252	*
North Hauxley	2	6.542	0.058	*
South Hauxley	-	-	-	-
North Druridge	-	-	-	-
North Cresswell	2	4.607	0.568	66.105
Cresswell Beach	-	-	-	-
Cambois	-	-	-	-
North Blyth	2	5.470	0.547	*
South Blyth	-	-	**	-
Seaton Sluice	-			

^{*} In these cases, the $\delta^{15}N$ value for POM lies outside the range between sewage and algae. It seems likely that most of the measurements of $\delta^{15}N$ in the spring analysis were inaccurate.

Figure 3.4 maps the results given in Table 3.14. As would be expected, there is a relationship between the percentage of particulates from sewage and proximity to the relevant outfall. The percentage of POM derived from sewage is relatively high near the Amble outfall, and then decreases with distance to the south. It then increases again near the (comparatively small) Hadston/Broomhill outflow. The percentage of sewage contribution is highest at Cresswell, and also relatively high near the Cambois outfall. As at Amble, the proportion of POM from sewage then declines with increasing distance south from Cambois.

Key to Figures 3.4 and 3.7:

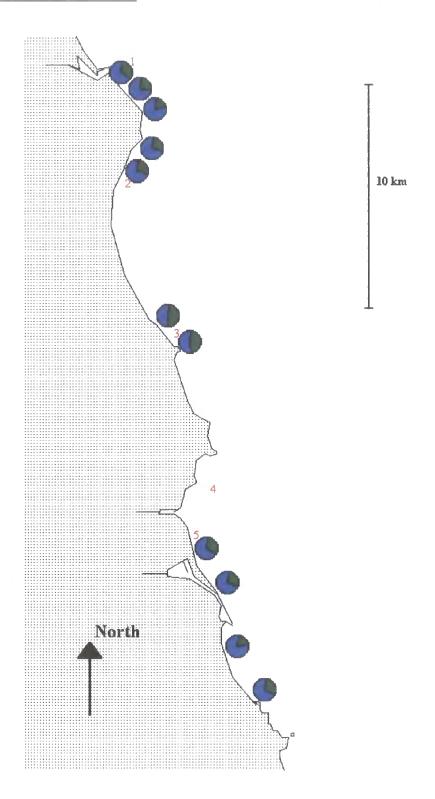
Pie charts represent sampling locations.

Green = % of POM originating from sewage.

Blue = % of POM originating from algae.

Sewage discharges given by numbers (see Table 3.1).

Figure 3.4: % of organic particulates originating from sewage at 11 sampling sites along the south Northumberland coast, as estimated from spring measurements of $\delta^{13}C$



3.3.4.2 Autumn sampling

<u>Table 3.16</u>: Estimates of % of organic particulates derived from sewage calculated using δ^{13} C values from autumn sampling

Site	No.	Mean δ ¹³ C	s.e.	% sewage
	samples	(‰)		
North Amble	6	-19.053	0.368	36.77
South Amble	8	-16.854	0.343	14.78
North Hauxley	10	-20.062	0.253	46.86
South Hauxley	12	-17.849	0.198	24.73
North Cresswell	12	-20.417	0.193	50.41
North Blyth	12	-21.879	0.259	60.71
Seaton Sluice	12	-20.565	0.185	48.44

Table 3.17: Estimates of % of organic particulates derived from sewage calculated using δ^{15} N values from autumn sampling

Site	No.	Mean δ ¹⁵ N	s.e.	% sewage
	samples	(‰)		
North Amble	6	6.540	0.380	11.28
South Amble	8	4.491	0.475	54.72
North Hauxley	6*	5.614	0.296	30.91
South Hauxley	6	4.737	0.301	49.50
North Cresswell	10	5.069	0.930	42.46
North Blyth	4	4.111	0.222	61.11
Seaton Sluice	4	6.376	0.600	14.36

^{*} All replicates failed in analysis so this value is based on single samples.

The technique used to prepare samples for analysis had been refined by the time that samples collected in the autumn were analysed (Section 3.2) which resulted in fewer inaccuracies in the analysis of the nitrogen isotope ratios of POM samples. However, there was no agreement in the estimates of percentage of POM originating from sewage calculated using $\delta^{13}C$ and $\delta^{15}N$ values ($r_s = -0.125$, n = 7, not significant).

Figure 3.5: Percentages of POM originating from sewage at seven locations in autumn 1999; calculations using carbon and nitrogen stable isotopes

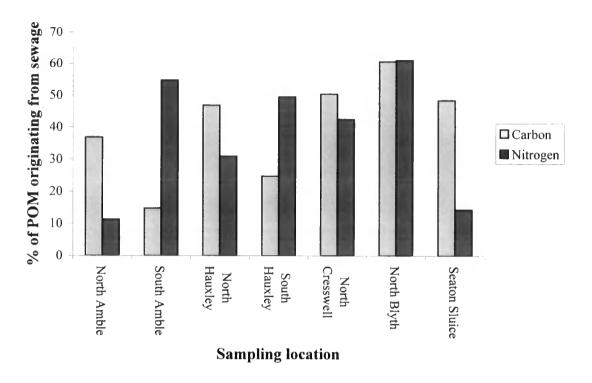


Figure 3.6: Percentages of POM originating from sewage at seven locations in spring and autumn 1999; calculations using δ^{13} C values only

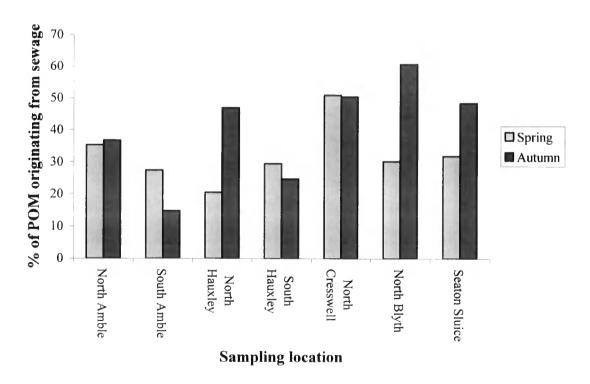
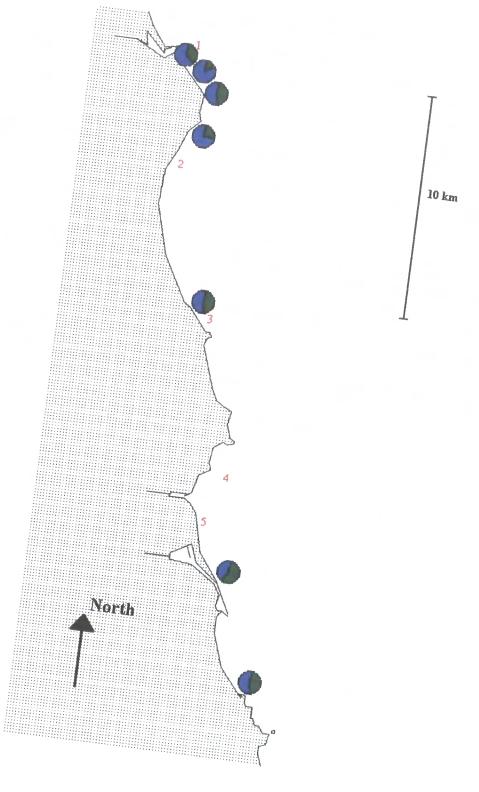


Figure 3.7: % of organic particulates originating from sewage at 11 sampling sites along the south Northumberland coast, as derived from autumn measurements of δ^{13} C



There was no significant difference between the percentage of POM originating from sewage in spring and in autumn (Wilcoxon ranked pairs, z = 1.01, n = 7, not significant) (Figure 3.6). Figure 3.7 illustrates the differences in the contribution of sewage to POM at the seven different sampling locations used in the autumn (calculated using δ^{13} C values).

3.4 Discussion

3.4.1. Errors, problems and possible solutions

The present study suffered from two main sources of error, which means that the accuracy of the results presented in Section 3.3 needs to be treated with caution. Firstly, the measurement of isotopes of samples did not always appear to be satisfactorily accurate, particularly with respect to nitrogen. Many previous studies have managed to record a mean discrepancy in δ^{15} N values between replicate samples of less than 0.5% (e.g. Kwak & Zedler 1997, Hansson et al. 1997 and Tucker et al. 1999). The mean discrepancy between replicates for the present study was 4.7% for samples collected in the autumn (when analysis accuracy had been improved from that in the spring). With many samples excluded from discussion because of the obvious inaccuracy in $\delta^{15}N$ for one or both replicates, the mean error between replicates was still 0.68%, perhaps because of insufficient nitrogen in the sample. Although analysis of a greater amount of sample would have been possible, it would have resulted in "overloading" of carbon, and hence an inaccurate δ^{13} C measurement. Any future studies would be advised to extract separate samples of particulates from the same water sample for the analysis of carbon and nitrogen stable isotopes.

The second cause of inaccuracy could have been the sampling regime itself. Samples of sewage were taken on only one occasion, both in the spring and the autumn. Stable isotope ratios might vary considerably in sewage over the diel cycle as the diet of humans producing the sewage changes. This variation would

be more marked if sewage has not undergone a treatment stage that would allow mixing of sewage from different periods of the day.

POM samples from inshore waters were also taken on only one occasion in each season. Although samples were taken at the same tidal stage at each site, in order to minimise variation due to tidal movements, it is inevitable that samples taken on only one occasion amidst the tidal action on Northumberland rocky shores may not provide representative values on analysis.

3.4.2 Isotope ratios of POM and its sources

A number of studies have found carbon isotopes unsuitable for detecting sewage inputs to marine ecosystems because the δ^{13} C values for marine detritus and sewage inputs were too similar (Myers 1974, Sweeney *et al.* 1980). That was not a problem in the present study, which found a difference of 10% between macroalgae and sewage effluent. The values of -25.4 to -26.8% δ^{13} C for sewage found by the present study are similar to the value of -26.2% found in sewage sludge in New York Bight by Burnett & Schaeffer (1980). Other studies have found slightly heavier (richer in 13 C) values; -23.5% (Spies *et al.* 1997) and -23.7% (Kwak & Zedler 1997) for sewage discharges on the Californian coast and a mean of -22.8% for nine sources in the USA (Van Dover *et al.* 1992).

The mean δ^{13} C values of three species of macroalgae sampled by the present study varied between -13.85 and -17.35‰. These values are heavier than those found by the few studies that have analysed stable isotope ratios in macroalgae, such as that by Kwak & Zedler (1997) who found δ^{13} C values of between -18.6 and -20.2‰ for various macroalgae species in southern California.

There has been considerable variation in the $\delta^{15}N$ of sewage found by previous studies. While Tucker *et al.* (1999) found a value of 3.3% for sewage in Massachusetts and Hunt *et al.* (1996) a value of 3.2% for sewage sludge dumped off New York, Van Dover *et al.* (1992) found a range of values from -1.1% to 7.2% for sewage at a number of sites in Northeast USA. The values found by the

present study varied from 1.1 to 4‰ and hence seem in keeping with previous studies. Unfortunately there was only a relatively small difference between these values and those calculated for macroalgae (spring mean = 5.7‰, autumn mean = 7.1‰). These δ^{15} N values for macroalgae are considerably lighter than those found by previous studies e.g. values for *Enteromorpha* of 8.1 and 14.4‰ by Tucker *et al.* (1999) and 11.9 and 11.4‰ by Kwak & Zedler (1997), compared with 7.9‰ found by the present study.

3.4.3. Estimates of the percentage of sewage in POM

Although possibly flawed, the values calculated for the percentage of POM originating from sewage do show the expected pattern of decline with increasing distance southward from outfalls. There are notable exceptions to this generalisation, such as the low sewage contributions to POM at South Amble and South Hauxley in the autumn. It is possible that this discrepancy could be related to the tendency for detached wrack to accumulate on the beaches at these sites (Chapter 2). The microbial decomposition of this wrack may result in local increases in the amount of marine POM in the water column, thereby reducing the relative input of sewage at these locations (but not the absolute amount of POM originating from sewage).

Given the lack of any major outfall at Cresswell, the high contribution of sewage towards total POM at this site was unexpected. The outfall at Cresswell mainly carries untreated sewage from a nearby caravan park, and so the volume of sewage discharged varies seasonally. The spring sampling period overlapped with Easter, when large numbers of holidaymakers were present at the caravan park and sewage outflow would have been at its maximum. Similarly large numbers of holidaymakers were still present when POM was sampled in the autumn. Had this study also been conducted in the winter, it is likely that it would have recorded a considerably lower % contribution to POM from sewage at Cresswell.

POM from rivers may have contributed to POM in inshore waters, particularly at those sites south of the mouths of the Coquet and Blyth rivers. Although this study failed to measure the stable isotope ratios of freshwater POM accurately, it is terrestrial in origin and hence probably has similar isotope ratios to those measured in sewage. This input may have led to an overestimation of the proportion of sewage in inshore waters. However, POM from freshwater sources is unlikely to have been a major contribution to overall POM at sites such as North Druridge Bay and Cresswell, where the estimated contribution to POM from sewage was still as high as between 30 and 50%. Additionally, while the influence of freshwater POM at locations such as North Amble may have caused an overestimation of sewage contribution, this potential error may have been offset by the use of macroalgae alone as the source of naturally occurring POM. Marine phytoplankton contributes to POM in inshore waters to an unknown extent (possibly relatively insignificantly). Previous studies have found δ^{13} C values for phytoplankton to be heavier than for macroalgae (e.g. Gearing et al. 1984 and Rau et al. 1990), and so any contribution from phytoplankton to POM would have led to an underestimate of the relative input from sewage.

Analysis of carbon stable isotopes gave values of between 20 and 60% for the contribution of sewage towards the total POM in inshore waters. The same results using nitrogen stable isotopes gave values between 11 and 66%. Despite the shortcomings of this investigation it seems clear that the relative inputs from sewage of POM into inshore waters within the study area are substantial.

The program of improvements being implemented by Northumbrian Water means that sewage will undergo secondary treatment before discharge at Amble and Cambois. In addition, a new sea outfall at Cambois will mean that the sewage will be discharged considerably further out to sea. Secondary treatment may remove up to 95% of POM before discharge, and longer outfalls result in greater dilution of sewage. The result could be a considerable reduction in the total POM available in inshore waters (possibly as much as 60% at some locations) and subsequent impacts on the intertidal ecosystem (Chapter 1).

Chapter 4

Use of the south Northumberland coast by Purple Sandpipers.

4.1 Introduction

The work described in this chapter served three purposes:

- To provide a baseline of the current use of the south Northumberland coast by Purple Sandpipers, to allow the comparison of numbers and spatial distribution in 1996-99 with those after the new sewage treatment and disposal facilities have been installed.
- By examining the use of sites, foraging habitats and diet of the populations of
 Purple Sandpipers to indicate what ecosystem components are important to
 the birds wintering on the Northumberland coast. This information, together
 with that derived from the multivariate analysis (Chapter 2) and knowledge of
 the likely reduction in sewage inputs (Chapter 3) allow informed predictions
 of the impact of the improvements in sewage treatment and disposal along the
 south Northumberland coast.
- To describe the behaviour of the study population as a whole to provide a background against which variation in behaviour of individual birds can be assessed (Chapter 6). Understanding variations in behaviour between individual organisms is increasingly being recognised as vital to a good understanding of how a population as a whole reacts to changes in its environment (e.g. Ens *et al.* 1994, Goss-Custard 1996: Sutherland 1996).

The first two points above fulfil the definition of biological monitoring given by Furness *et al.* (1993) as basic surveillance plus (i) assessment of changes against some standard or target, (ii) gathering of data in order that the reason(s) for change(s) from the standard may be explained, and (iii) clear understanding of the objectives of the programme.

Basic surveying of shorebird numbers along the Northumberland coast is not sufficient to establish that any changes that may occur in the future are attributable to reductions in sewage outputs. To make such predictions it is necessary to assess *how* Purple Sandpipers use the study area, and how their activities vary with tidal height and seasons (and between years), as well as where the birds are within the area. Their presence and activities change over the tidal cycle, and sometimes in different ways at different sites within the study area, possibly related to food distribution. It thus seemed important to assess the birds' diet within the study area, and the availability of prey species found to be important to Purple Sandpipers. If any of the important prey were to decline in abundance in future, then the birds could react in a number of different ways:

- i. No change. Bird numbers would not be affected if their densities are not limited by food at present and if densities of prey species (though reduced) remain above levels at which they limit bird densities.
- ii. **Behavioural change**. If a significant decrease occurs in the density of one or more preferred prey items, Purple Sandpipers may be able to compensate by increasing their intake of another prey, and show no change in overall numbers or distribution. This factor might lead to a change in behaviour over the tidal cycle. For example, birds might increase their foraging time over the high water period at the expense of time spent roosting.
- iii. Change in distribution. Purple Sandpiper numbers in the whole study area might remain constant, but the distribution of these birds between sites might change if some sites no longer hold sufficient food densities to maintain the present Purple Sandpiper densities. Not all sites used by Purple Sandpipers in south Northumberland are likely to experience reductions in enrichment from sewage and so some should retain the same levels of food resources while food densities at other sites may decrease.

iv. Change in numbers. If the decline in food resources is sufficiently large, and birds cannot adjust by changing their diets, behaviour or distribution to compensate, then a reduction may occur in the number of birds using the study area, or in the time birds stay in the study area. These effects may be detectable only in years when food densities fall below a certain threshold due to e.g. poor reproductive success of prey organisms or severe weather conditions and/or numbers of birds arriving from the breeding grounds are particularly high.

4.2 Methods

4.2.1 Counts

The study region was divided into nine coastal stretches, plus three estuaries. Six of these sites consisted of predominantly rocky shore and held all of the Purple Sandpipers; Amble, Hauxley, Cresswell, Newbiggin, Blyth and St. Mary's Island (see Figure 2.2). These sites were surveyed at least once a fortnight from September to May inclusive. Counts were made on a monthly basis over the summer.

Over the 1996-97 winter, counts were made alternately between high and low water at each site, which led to some variation in counts as, for example, on spring high tides Purple Sandpipers from Amble would leave to roost on Coquet Island and so escape counting. Therefore in 1997-98 and 1998-99 counts of birds were made to provide estimates of numbers using each site at low tide. In many cases rising or high tide counts provided such estimates, as it was known that all birds remained at the site throughout the tidal cycle. Indeed, at some sites (e.g. North Blyth) roost counts provided a more accurate measure of Purple Sandpiper numbers as the inconspicuousness and tide-hugging nature of this species can make it hard to census at low tide.

For the analysis of faecal samples, "winter" was defined as the period from November to March inclusive, and "spring" as April-May. Tidal state was defined by tidal height, not the time from high or low water, as I felt that this definition was more relevant to food availability, since many sessile invertebrates show marked zonation up/down-shore. Low water was defined as below 3.7 m O.D., high water as at or above this height, when most or all intertidal rocks were covered at all six rocky shore sites. Mean high water for the nearest major port (Tynemouth) is 4.7 m O.D.; tides above this height were classified as spring tides, those below as neaps.

In addition to the count data collected as part of this study, Wetland Bird Survey (WeBS) counts for winters from 1984-85 to 1994-95 were obtained from the British Trust for Ornithology to provide information on trends in Purple Sandpiper numbers along the Northumberland coast before the onset of this study. WeBS count sections (defined stretches of coastline) were frequently not counted in every month. Therefore mean winter numbers for the whole study area were derived not from the mean of monthly totals for the whole area but by summing the mean count for each count section; in all years at least three counts per winter were available for each count section. Counts made by the present study showed that Purple Sandpiper numbers were relatively stable from November to March, so this period was defined as winter for the comparison of counts between years. Although WeBS count sections were not the same as the sections used during my fieldwork (some sections matched, but other WeBS sections were considerable longer, subsuming two or three of my count sections), WeBS count sections did end at the north and south of study region allowing totals for the whole study area to be calculated from WeBS data.

4.2.2 Habitat use and behaviour

Over the 1996-97 and 1997-98 winters, data were collected on the locations (microhabitat and distance from the tide's edge) of all Purple Sandpipers observed. (In the 1998-99 winter, these data were collected only for colour-ringed individuals and are presented in Chapter 6.)

Data on behaviour and location were recorded by scan sampling (Altmann 1974) of individuals or groups of birds when first sighted. Repeat scans were made at fifteen minute intervals. Observations were made throughout the tidal cycle on

more than 30 occasions at all six rocky shore sites from November to March in both winters, and classified using the categories listed in Table 4.1.

Table 4.1: Data classes and categories if bird activity for habitat use data

Bird activity	Distance from tide	Substrate
	edge	
roosting	<1 m	strand-line ²
feeding	1-2 m	wrack deposit ³
preening/bathing	2-5 m	mud
vigilance	5-10 m	sand
other	10-20 m	bare rock
	20-50 m	barnacles
	>50 m	mussels
		Fucus
		Chlorophyta
		Rhodophyta
		Enteromorpha

Predominant cover type within 1 m of a bird

4.2.3 Faecal samples

Faeces from feeding Purple Sandpipers were collected at North Blyth, Amble, Hauxley and St. Mary's Island by waiting for feeding birds to move from an area, or flushing them deliberately, and then collecting the faeces that were stored in 70% alcohol. In addition some were collected from high tide roost sites at Amble, Cresswell, Newbiggin and Seaton Sluice.

During microscopic examination, the species present were identified and the length of any intact shells measured to the nearest 0.1 mm. Although specific identification of intact shells was usually possible, many faeces contained only highly fragmented shell remains and so could not be identified further than "gastropod spp." or *M. edulis* with any certainty.

²Small amounts of debris deposited on tide's edge.

³Large deposits of seaweed (*Fucus* and *Laminaria*) along high-water mark.

4.3 Results

4.3.1 Counts of Purple Sandpipers

4.3.1.1 Variation in total numbers

Figure 4.1: Purple Sandpiper numbers in the study area, 1996-99

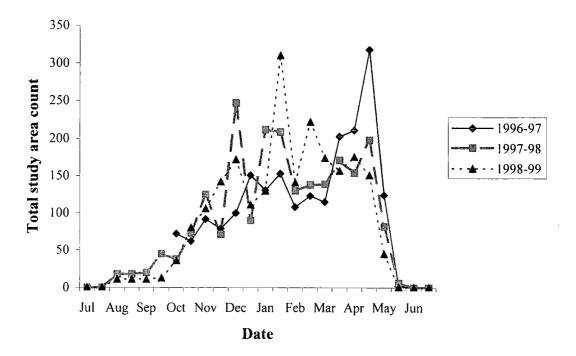


Figure 4.1 shows that there were considerable fluctuations in Purple Sandpipers numbers over the main November – March wintering period. In part these fluctuations may have been due to the difficulty in obtaining accurate counts at Blyth, the principal wintering site. Weather conditions and disturbance influenced the roosting locations of birds within the Blyth Harbour area. In easterly winds, birds were easily visible on the west side of the East Pier wavetrap, whereas in westerly winds birds could be on the east side or within the wavetrap and hence very difficult to count. Late afternoon or evening counts may have been more accurate, as birds seemed more inclined to roost on the west side of the pier if it was warmed by sun at this time of day. In calm conditions, some or all of the birds roosted on the South Pier, but only if it was not being used by large numbers of fisherman.

Purple Sandpipers arrived in the study area in small numbers from August, with a slow increase until November when larger numbers arrived. There was no significant difference between numbers present in the five months from November to March (Kruskal-Wallis, $\chi^2 = 6.8$, d.f. = 4, not significant). Therefore in all subsequent analyses in this chapter, winter is defined as November to March inclusive. In 1996-97 and 1997-98, this period was followed by a rise in numbers, presumably as migrant birds passed through, peaking in early May before a rapid decline. No such peak was found in 1998-99.

Although variability in count accuracy may have contributed to variation in estimates of numbers within winters, influxes of Purple Sandpipers did occur, e.g. in late January 1999 when 310 birds were counted within the study area, a sharp increase on the 130 birds counted two weeks before. This peak was followed by a rapid decline to 108 birds by early February.

When count-to-count variation is ignored and emphasis placed on annual means and winter peaks (Table 4.2), it is obvious that there was considerable variation in the total numbers of Purple Sandpipers using the study area between years.

Table 4.2: Mean and peak Purple Sandpiper counts for each winter (Nov-Mar)

Winter	Mean	S.E.	Peak winter count
1996-97	125.5	11.4	203
1997-98	153.2	17.7	247
1998-99	166.5	19.2	310

Figures 4.1 and 4.2 and Table 4.2 indicate that there was some variation in Purple Sandpiper numbers using the study area between years. Analysis of the WeBS counts obtained for the ten winters from 1985-86 to 1994-95 showed that this variation could in fact be far greater than that shown by my counts.

Both mean WeBS counts over the ten years preceding the fieldwork period for this thesis, and the fieldwork itself, show fluctuations in the numbers wintering in the study area. Winter means varied from 67 to 346 and winter peaks from 101 to

487 (Figure 4.3); in both measures there was over four-fold variation between years.

Figure 4.2: Mean winter (Nov-Mar) counts of Purple Sandpipers from WeBS (1985-95) and my fieldwork (1996-99)

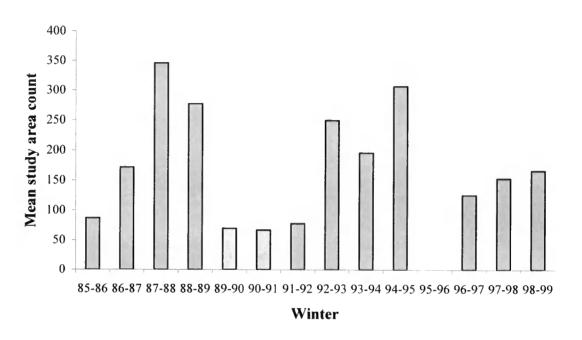
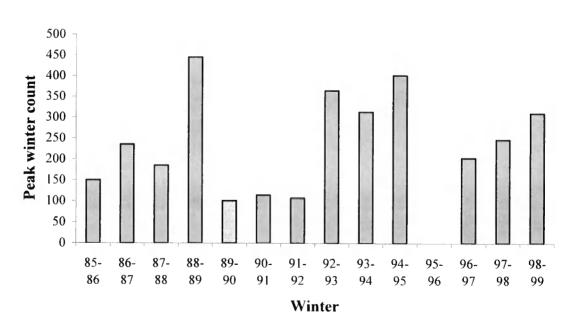
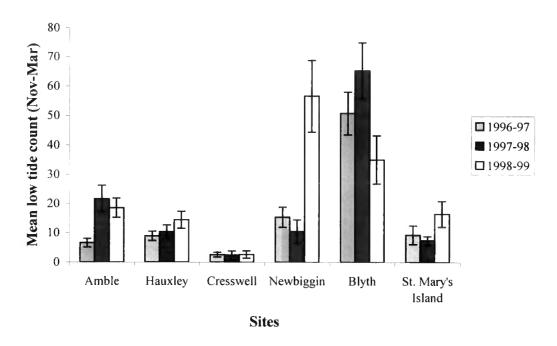


Figure 4.3: Peak winter (Nov-Mar) counts of Purple Sandpipers from WeBS (1985-95) and my fieldwork (1996-99)



4.3.1.2 Distribution between sites

Figure 4.4: Mean counts of Purple Sandpipers at low water at rocky shore sites, 1996-99



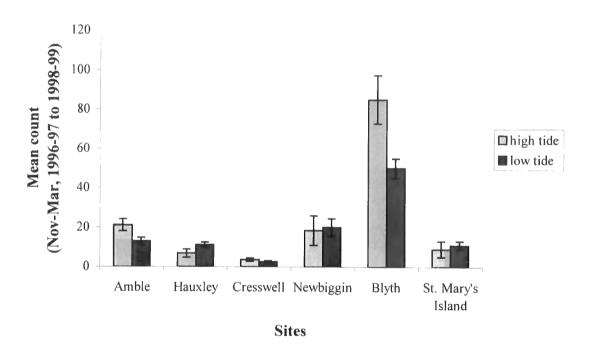
Error bars show one standard error either side of the mean.

Figure 4.4 illustrates the importance of Blyth as the principal wintering site for Purple Sandpipers within the south Northumberland study area, with a mean of 50.3% of the total numbers at this site over the three study winters. However, numbers at Blyth were not significantly lower in the 1998-99 winter (Kruskall-Wallis, $\chi^2 = 5.74$, d.f. = 2, n.s.).

Significant between-year variation in winter low tide counts occurred at two of the six sites, Amble (Kruskall-Wallis test, $\chi^2 = 14.39$, d.f. = 2, P < 0.01) and Newbiggin ($\chi^2 = 8.11$, d.f. = 2, P < 0.05). The increase in numbers at Newbiggin in the 1998-99 was associated with the reduction in the number of birds at North Blyth mentioned above; birds were observed leaving North Blyth and flying to Newbiggin during visits by hunting raptors. This conclusion was confirmed by sightings of the same colour-ringed and radio-tagged birds at both Newbiggin and Blyth (see Chapter 6).

The increase in birds at Amble in 1997-98 and 1998-99 compared with 1996-97 may have been related to feeding opportunities on the foreshore. Casual observations of the Amble foreshore suggested that settlement of mussel spat was higher in 1997-98 than in the previous winter. As a very important component of Purple Sandpiper diet (see Section 4.3.3), the availability of a large supply of prey in the right size class may have attracted the larger number of birds feeding at Amble. This increase may have been due to birds that fed on Coquet Island during the previous winter moving to the mainland to feed.

Figure 4.5: Comparison between counts of Purple Sandpipers made at low and high water, 1996-99

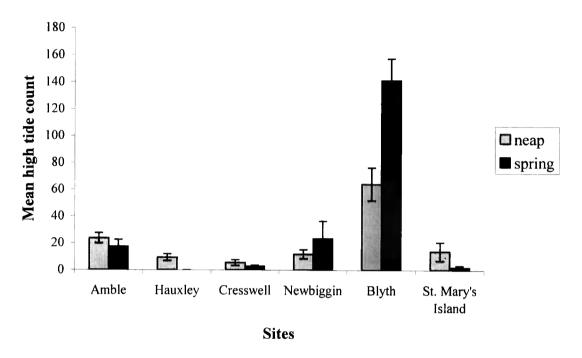


Error bars show one standard error either side of the mean.

At two sites the numbers of birds present at high and low tides were significantly different (Figure 4.5); Hauxley (Mann-Whitney 2-tailed z = 2.27, P < 0.05) and Blyth (z = 2.43, P < 0.05, 2-tailed). On spring high tides (see Figure 4.6), Purple Sandpipers were not able to roost at Hauxley and so flew north to Coquet Island or the Amble foreshore. Therefore Amble had swollen numbers at high tide, with birds roosting inside a large crack in the north pier of Amble Harbour mouth on spring tides. The insignificant (z = 1.59, not significant) difference between high and low tide counts at Amble may have been due to birds being undercounted in

the hard-to-view Harbour Pier. The large discrepancy between high and low tide counts at Blyth is believed to result from the difficulty of counting birds on the extensive North Blyth intertidal area, particularly because some birds fed out of view on offshore scars.

Figure 4.6: Comparison between counts of Purple Sandpipers made at spring and neap high waters, 1996-99

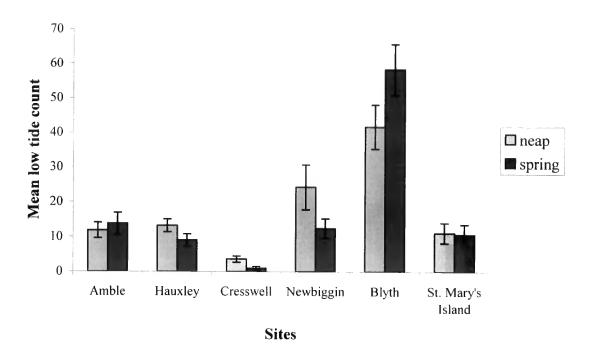


Error bars show one standard error either side of the mean.

Two sites showed significant differences in the number of Purple Sandpipers present on spring and neap high tides over the three study winters (Figure 4.6). Hauxley held significantly more Purple Sandpipers on neap high tides (Mann-Whitney U test z=2.79, P<0.01) than spring high tides when all suitable roosting sites were covered by the tide. Conversely, Blyth had a higher mean count during spring high tides (Mann-Whitney z=2.546, P<0.05). This marked increase may have been due, at least in part, to the larger number of sites available for roosting in Blyth Harbour on neap tides, which meant roosting birds were more likely to escape being counted. On spring tides these sites, such as the ledges along the concrete pier base, were covered by the tide and birds were forced to roost in more visible positions. There may have been a small influx of birds into Blyth from St. Mary's Island, where a number of roost sites are

covered by spring high tides. On very high tides, the island itself is the only remaining roost site for Purple Sandpipers; if disturbed by fishermen, birds moved to Blyth to roost.

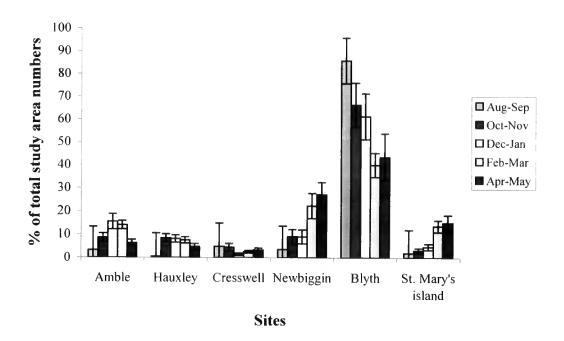
Figure 4.7: Comparison between counts of Purple Sandpipers made at spring and neap low waters, 1996-99



Error bars show one standard error either side of the mean.

There was closer agreement in numbers (Figure 4.7) of Purple Sandpipers at each rocky shore site between spring and neap low tide counts than at high tide which suggests that birds that may have left a site at high tide due to the lack of suitable roosting space returned to feed at low tide e.g. at Hauxley. No site showed a significant difference in mean number of birds between neap and spring low tides, although Blyth had greater numbers on spring tides. Conversely numbers at Newbiggin were lower on spring low tides, suggesting that some birds flew to North Blyth to feed.

Figure 4.8: Seasonal changes in Purple Sandpiper distribution between rocky shore sites, 1996-99



Error bars show one standard error either side of the mean.

As stated previously, the principal site used by Purple Sandpipers within the study area was Blyth. However, the proportion of the birds in the study area found at Blyth declined through the wintering period in each of the three study years, with corresponding increases at St. Mary's Island and Newbiggin. Figure 4.8 shows that significant changes in the proportion of the total study area numbers they supported through the overwintering period occurred at four sites: Amble (Kruskall-Wallis, $\chi^2 = 19.6$, d.f. = 4, P < 0.01), Hauxley ($\chi^2 = 22.4$, d.f. = 4, P < 0.01), Newbiggin ($\chi^2 = 18.9$, d.f. = 4, P < 0.01) and St. Mary's Island ($\chi^2 = 18.4$, d.f. = 4, P < 0.01).

The two sites nearest Blyth (Newbiggin and St. Mary's Island) showed an increase in the proportion of the study area numbers throughout the wintering period. Both sites had a very low proportion of the total numbers in August-September (3.57% and 1.96% respectively), but the numbers recorded rose gradually through the winter, reaching 22.3% and 13.6% respectively by late winter (February-March) and an even higher proportion in the spring (27.2% at

Newbiggin, 15.0% at St. Mary's Island). The increases at these two sites closely mirrored the decline in the proportion of the population at Blyth. Sightings of colour-ringed birds (see Chapter 6) confirmed that this change was due to birds dispersing from Blyth to Newbiggin and St. Mary's Island in the late winter and spring.

Figure 4.9: The distribution of Purple Sandpiper roosts within the study area, 1985 to 1999, from WeBS data and from fieldwork reported in this thesis

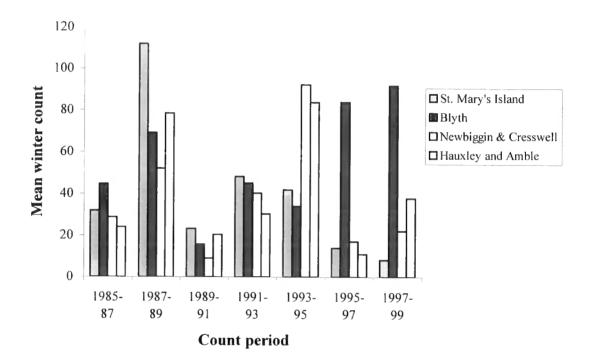


Figure 4.9 shows how the numbers of wintering Purple Sandpipers roosting at the different rocky shore sites changed between 1985 and 1999. A relatively low proportion of the total population - approximately 30% - used the four rocky shore sites from Newbiggin north to Amble. The exception to this trend was in the 1989-91 period, when 60% of the (rather low) wintering Purple Sandpiper numbers were at Amble and Hauxley. This brief increase may have been related to a change in the distribution of birds in the south of the study area. In the two periods 1985-87 and 1987-89, St. Mary's Island held the majority of the south Northumberland wintering population. After the 1989-91 period, the proportion at St. Mary's Island was greatly reduced, with between 57% and 94% of the total population being present at Blyth.

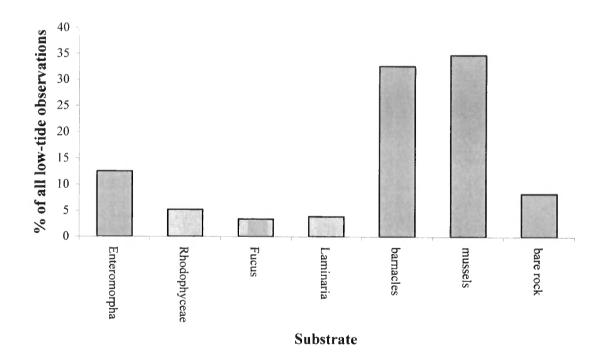
Significant variation in the mean number of birds counted in the seven two-year periods were recorded at two of the four locations: St. Mary's Island (Kruskall-Wallis $\chi^2 = 15.1$, d.f. = 4, P < 0.01) and North Blyth ($\chi^2 = 14.8$, d.f. = 4, P < 0.01).

4.3.2 Foraging behaviour of Purple Sandpipers

4.3.2.1 Foraging substrate choice

Foraging Purple Sandpipers showed clear preferences in substrate selection, as reported in Figure 4.10, which shows selection over the low tide at Blyth during the winter (Nov-Mar) in all three years (n = 3177)

Figure 4.10: The choice of foraging substrate at low water (tide heights < 3.7m O.D.) by Purple Sandpipers at Blyth



Purple Sandpipers at North Blyth foraged mainly upon rocks covered with barnacles and mussels. When compared with actual % cover of the intertidal area as derived from 1:10,000 aerial photographs birds significantly favoured mussel-covered rock and foraged less than would be expected by chance upon *Fucus* and

Enteromorpha (Chi-square, $\chi^2 = 8.24$, d.f. = 3, P < 0.05), Table 4.3. Data were available for mussels, *Fucus*, *Enteromorpha* and bare and barnacle-covered rocks combined but not other categories (see Chapter 2).

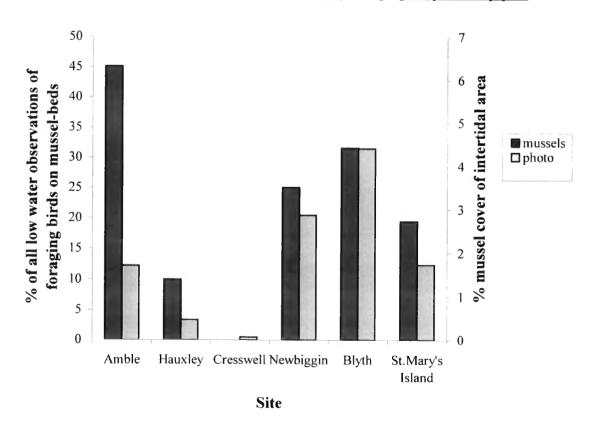
<u>Table 4.3: Observed and expected frequencies of feeding on different types of substrate by Purple Sandpipers over low water at Blyth</u>

n = 3177	Mussel-bed	Fucus	Enteromorpha	Bare/barnacle
Expected	162	241	1317	1457
frequency				
Observed	1114	472	442	1149
frequency				

Derived from % cover of intertidal area as derived from aerial photographs.

However the availability of substrate types did influence the selection of foraging substrates. Figure 4.11 shows the use of mussel-covered substrates by Purple Sandpipers at all of the six rocky shore sites.

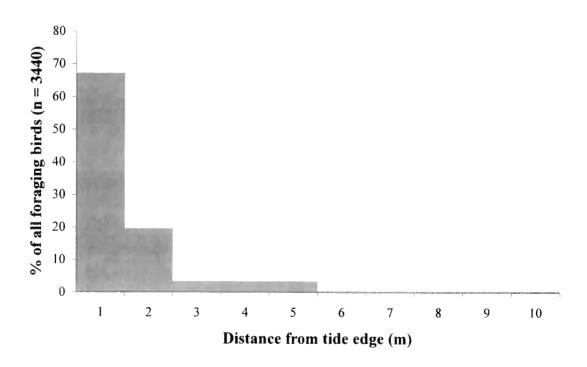
Figure 4.11: The use of mussel-covered substrate by foraging Purple Sandpipers



At all sites except Cresswell, mussel-covered rock was utilised by foraging birds far more than would be expected by chance. For example, birds at Amble spent 45% of low-tide foraging time on mussels despite this substrate being only 1.7% of the total available. The exception was Cresswell, where the very small area of mussel-bed cover was on steeply sloping rocks unsuitable for Purple Sandpiper foraging. There was a significant relationship between the abundance of mussel-covered rock and the proportion of foraging time Purple Sandpipers spent on this microhabitat (Spearman's rank correlation, r = 0.733, n = 6, P < 0.05).

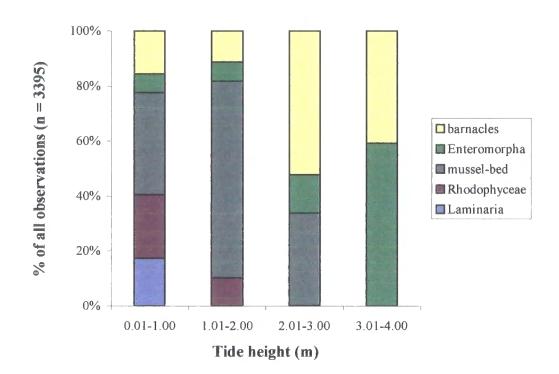
Figure 4.12 illustrates the marked preference of Purple Sandpipers for feeding at the tide edge at Blyth (this behaviour was similar at other sites within the study area). Nearly 90% of all foraging was done within approximately 2 m of the tide's edge. Birds followed it across the intertidal area on the ebbing tide, and then retreated in front of the rising tide. Birds feeding further away from the edge almost invariably foraged in shallow rock pools.

Figure 4.12: Observations of the location relative to tide's edge of foraging Purple Sandpipers at Blyth, 1996-99



The availability of the various substrate types used by Purple Sandpipers (Figure 4.10) changed with tidal height, as all rocky shores have some degree of invertebrate zonation (e.g. Moore & Seed 1985). This effect is illustrated by Figure 4.13, which shows how choice of foraging substrate changed over the tidal cycle at North Blyth.

Figure 4.13: The choice of foraging substrate by Purple Sandpipers at North Blyth at different tidal states

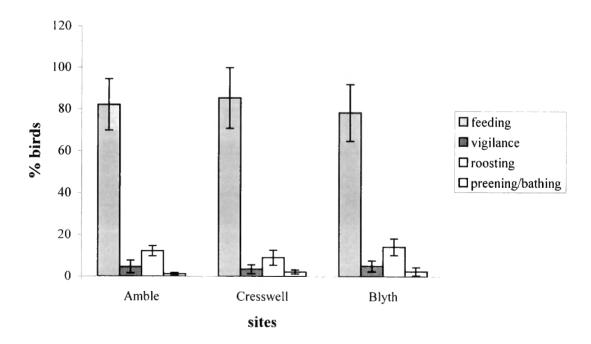


The use of the different foraging substrates over the tidal cycle reflects the availability of these microhabitats on the tide's edge. *Laminaria* and Rhodophyceae are only found near the low water mark (*Laminaria* is only exposed by spring low tides) while the main expanses of mussel bed at Blyth and other Northumberland sites are also on the lower shore. At higher tidal levels, the proportion of birds feeding on mussel-beds declines due to the decline in availability of this microhabitat.

4.3.2.2 Behaviour over the tidal cycle

Data on behaviour at low water were collected from Purple Sandpipers at each rocky shore site. There was no significant difference in the percentage of all low water observations of the four main behaviour categories amongst the six sites: feeding (Kruskall-Wallis, $\chi^2 = 6.89$, d.f. = 5, not significant), preening/bathing (Kruskall-Wallis, $\chi^2 = 2.05$, d.f. = 5, not significant), roosting (Kruskall-Wallis, $\chi^2 = 3.34$, d.f. = 5, not significant) and vigilance (Kruskall-Wallis, $\chi^2 = 0.98$, d.f. = 5, not significant). Figure 4.14 shows the proportion of time during low water that birds devoted to each of these activities at three of the six sites. Purple Sandpipers at the other three sites exhibited similar behaviour, although fewer data were collected at the other sites. It must be noted that vigilance may have been over-recorded as my presence on the foreshore may have alarmed birds on occasions, although behavioural observations were not made when disturbance was obvious.

Figure 4.14: The behaviour of Purple Sandpipers during low water at three rocky shore sites



Error bars show on standard error either side of the mean.

At all sites within the study region Purple Sandpipers spent approximately 80% of the low water period (tide <3.7 m O.D.) foraging.

The time that Purple Sandpipers began to roost was studied in detail at three sites; Amble, Cresswell and Blyth. Table 4.4 gives the mean tidal height at which 50% of the birds present at a site had started roosting.

<u>Table 4.4: The tidal heights at which 50% of Purple Sandpipers arrived at the</u> roost at three sites

Site	Amble	Cresswell	Blyth
Mean	3.9	3.9	3.4
Range	3.6-4.2	3.5-4.4	3.1-3.8

There was a significant difference between sites in the mean tidal height at which birds began roosting (Kruskall-Wallis, $\chi^2 = 12.38$, d.f. = 2, P < 0.01), with birds at Blyth leaving the feeding area to roost at a tidal height 0.5 m lower than birds at Amble and Cresswell. This difference equates to approximately 30 minutes of foraging time on an average tide (and up to 65 minutes on extreme neap tides).

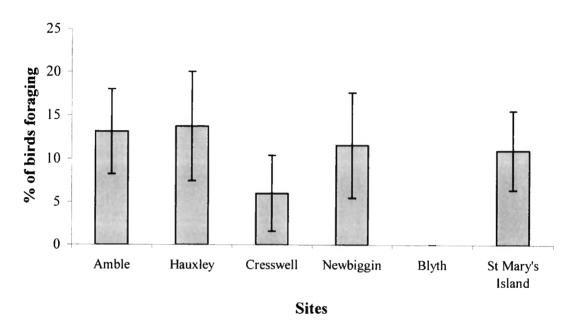
Although the return to foraging by birds on the falling tide was not studied in the same detail, qualitative observations strongly suggest that a similar pattern exists, with birds at Cresswell and Amble resuming foraging earlier than those at Blyth. If this interpretation is correct then birds at Amble and Cresswell would have spent an extra 60 minutes foraging per tidal cycle (7.9% additional foraging time).

Small numbers of Purple Sandpipers were observed foraging over the high tide period regularly at all rocky shore sites except Blyth. No rocky intertidal area is left exposed on high tides at North Blyth. Very occasionally, birds would be observed foraging on the concrete base of the harbour piers where they roosted, usually single birds foraging for a minute or so before returning to roosting.

Figure 4.15 shows the mean proportion of the birds present that foraged at some time during high water at each rocky shore site. For this analysis, the high tide

period was defined as one hour either side of high water, as the definition of over 3.7 m O.D. used elsewhere in this thesis would sometimes encompass birds still feeding on the rising tide (see Table 4.3, above) rather than those feeding throughout the high water period.

Figure 4.15: % of Purple Sandpipers foraging over high water at each rocky shore site, 1996-99



Error bars show on standard error either side of the mean.

No significant differences between the proportions of birds foraging over neap or spring high waters were found at the five sites with appreciable levels of high tide foraging (Mann-Whitney U test, Amble z = 0.14, Hauxley z = 0.74, Cresswell z = 0.12, Newbiggin z = 0.84, St. Mary's Island z = 1.04, all not significant).

4.3.3 Faecal samples as an indicator of Purple Sandpiper diet

The bulk of faecal samples were collected from the North Blyth foreshore, 257 samples from 24 occasions between August and April in 1997-98 and 1998-99. A minimum of five samples was collected on each sampling occasion. Samples were collected over the low tide period from tide heights of 0.6 m OD to 3.5 m

O.D. Although the foreshore at North Blyth is exposed at tide heights up to approximately 3.9 m O.D., access from the sea wall is impossible at that stage.

Faeces were collected from three other rocky shore sites within the study area; Amble (21 faeces on five dates), Hauxley (31 faeces on six dates) and St. Mary's Island (39 faeces on five dates). These samples were collected from birds feeding at low tide during mid-winter (December to February).

Samples generally included little organic matter, but rather fine ground shell remnants, grit and sometimes arthropod limbs and mouthparts. In addition, 3.1% (eight of 257) of all faecal samples contained algae that appeared to be filamentous chlorophyceae such as *Enteromorpha* spp. which Purple Sandpipers were observed eating on a number of occasions at North Blyth, and once at Hauxley.

The commonest components of faeces were mussels, littorinids, dogwhelks (Nucellus lapillus) and another intertidal gastropod, Rissoa parva (var. interrupta). In addition fragments were found of other molluscs; Barnacles (probably Semibalanus balanoides) and the gastropods Gibbula cineraria and Lacuna vincta. Crustacean remains were highly fragmented and hard to specifically identify but included small shore crabs Carcinus maenus, Idotea spp. and Gammarus spp.

Identification of littorinid fragments was often impossible, so in most cases the presence of littorinid spp. was recorded. However larger fragments and intact shells allowed the identification of *Littorina littorea*, *L. mariae*, *L. saxatilis* and *L. neritoides*. Highly fragmented shell remains were often classified simply as gastropods.

Due to the highly fragmented nature of prey items in faeces it was not possible to measure prey size distributions except for *R. parva*. However the size of intact items in faeces may be an extremely biased subset of those ingested. Intact *R. parva* were used to establish a relationship between shell length and width of the terminal whorl. Frequently shells were damaged on the upper spire but intact on

the final whorl. 50 randomly chosen intact shells were measured lengthwise and across the final whorl, and the lengths were linearly regressed against width to calculate the relationship between the two. This approximation enabled the length of broken shells to be estimated. The relationship between length and width was highly significant ($r^2 = 0.375$, P < 0.01) and defined by the equation L = W × 0.662 + 1.504, where L = length and W = width in millimetres.

The mean lengths of intact and damaged R. parva shells were significantly different (Mann-Whitney U test, two-tailed, z = 6.55, P < 0.01), with intact shells being smaller (mean length of intact shells = 2.12 mm, damaged shells = 2.62 mm). This finding suggests that small shells were more likely to escape destruction during the digestive process, and that measurements of intact shells can therefore not be used as an indication of the size of R. parva preyed upon. The damaged shells used in this analysis were still intact across the final whorl and operculum; even larger individuals may have a greater likelihood of complete destruction.

This selective destruction of shells meant that faecal samples were not suitable for investigating Purple Sandpiper's selection of prey size with any confidence. Maximum sizes of intact individuals of other prey species included 7.2 mm for mussels, 6.4 mm for *L. littorea* and 7.7 mm for *N. lapillus*. In addition fragments of gastropods, particularly *N. lapillus*, suggested that individuals of up to approximately 10 mm were taken. Crab claws were compared with those on intact specimens and estimated to be individuals between approximately 6 and 10 mm (carapace width).

Although an attempt was made to quantify the amount of each prey type in each dropping, I felt that this measure was unreliable with poor accuracy. Similarly it was impossible to get accurate counts of the number of individuals in a single dropping as shells were frequently so fragmented to make the identification (and therefore counting) of one particular shell feature (i.e. gastropod columella) impossible. Therefore analysis is based upon the % occurrence of prey species; the proportion of faeces from each individual sampling occasion that contained the species in question. It was possible to see that droppings often contained

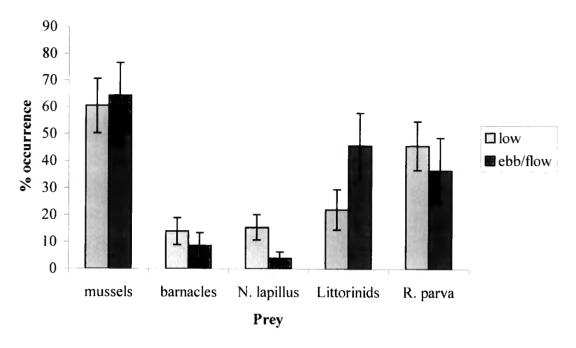
many individual prey items; up to 27 *R. parva* and 18 mussels were counted in individual samples.

There was considerable variation between faecal samples collected on the same occasion from birds feeding within a few metres of each other on the same substrate at the same time. Of 24 Blyth sampling occasions, seven (29.1%) included droppings that contained nothing but mussels as well as droppings that contained no mussel fragments at all. Of eight faecal samples collected from a group of ten Purple Sandpipers feeding amongst mussels and Rhodophyceae on 30th April 1998, only one contained shore crab fragments, but this sample contained nothing but crab fragments from a minimum of eight individuals. Such variation in faecal content strongly suggests significant differences in prey intake by individual birds feeding in the same locations.

In addition to differences between samples taken on the same occasion, variation between different sampling occasions was very large, even when tidal and seasonal differences were controlled for. Data from sampling occasions at low water at North Blyth during mid-winter (January-February) varied significantly in the % occurrence of mussels (Kruskall-Wallis $\chi^2 = 19.6$, d.f. = 10, P < 0.01), *R. parva* ($\chi^2 = 38.08$, d.f. = 10, P < 0.01) and littorinids ($\chi^2 = 30.62$, d.f. = 10, P < 0.01).

So a large degree of intrinsic variation was found in faecal composition, both between samples collected on the same occasion and between superficially similar sampling occasions. The following analysis attempts to find differences in faecal contents (and by inference, Purple Sandpiper diet) between different foraging situations (microhabitats, tidal stages, season), but any differences may well have been masked by this inherent variation between samples.

Figure 4.16: Variation in the composition of samples of Purple Sandpiper faeces at different tidal states at North Blyth (n = 257)



Error bars show on standard error either side of the mean.

Variation in faecal composition over the tidal cycle at North Blyth is shown in Figure 4.16. Although this graph does show some change, there was no significant difference in the % occurrence of any major faeces component between the two different tide heights, both when four tidal categories were considered or when data were collated into simply low and ebbing/flowing (0.5 – 2.0 m and 2.1 - 3.5 m O.D. respectively) categories (Table 4.5). Material takes approximately 40 minutes to pass through the gut of Purple Sandpiper (Dierschke 1994), which meant that the material in most faeces was excreted in the same period of the tidal cycle as it was ingested. Purple Sandpipers were not observed coughing up pellets, so the material in faeces was probably representative of the diet and not just a certain proportion of it.

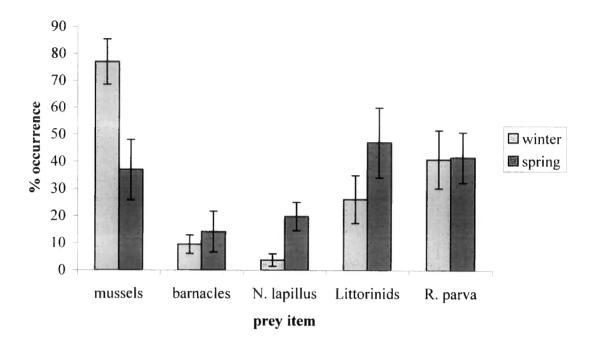
Table 4.5: The variation in % occurrence of faecal contents at aggregated tide heights

	Tide height (m)			
Prey	0.1-2.0	2.1-4.0	\overline{Z}^{1}	Sig.
	(n = 140)	(n = 117)		
Mussels	60.4%	64.3%	0.50	N.S.
Littorinids	22.0%	45.6%	1.37	N.S.
N. lapillus	15.4%	3.9%	1.66	N.S.
R. parva	45.7%	36.5%	0.69	N.S.

Mann-Whitney U test, two-tailed.

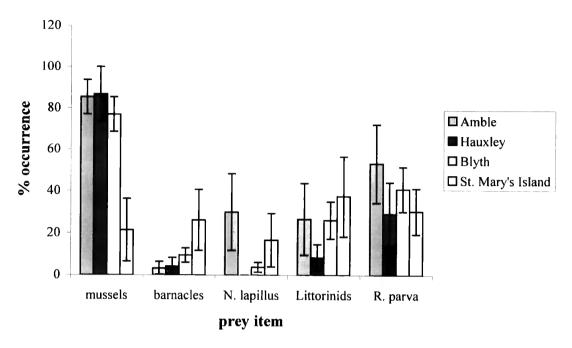
Mid-winter variation between individual droppings, and between different sampling occasions, is significant enough to mask any variation that may occur due to differences in diet at different tidal stages or from birds feeding on different substrates (Table 4.5). However, significant differences were found between faecal samples collected in winter and in spring. Samples from North Blyth were grouped as "winter" (December – March inclusive) and "spring" (April – May). Figure 4.17 illustrates the changes in % occurrence between these two periods for the principal prey items. Significant seasonal variation in content was found for two prey items; the occurrence of mussels decreased significantly in spring (Mann-Whitney z = 2.6, P < 0.01) and *N. lapillus* increased in spring (z = 2.53, z = 0.01). The increase in the occurrence of littorinids in faeces in spring was considerable but not significant.

<u>Figure 4.17: Seasonal variation in the prey composition of samples of Purple</u> Sandpiper faeces at North Blyth



This change in faecal sample content in spring suggests a change in diet, possibly due to a change in the relative abundances of the relevant prey species (or their accessibility). However invertebrate sampling conducted at North Blyth to look for prey depletion over the 1997-98 winter (Eaton 1998) failed to detect a change in invertebrate abundance between sampling dates in November and April.

Figure 4.18: Variation in the composition of Purple Sandpiper faeces between sites (low tide and mid-winter only)



N values: Amble = 21, Hauxley = 31, Blyth = 257, St. Mary's Island = 39. Error bars show on standard error either side of the mean.

As can be seen from Figure 4.18, there was considerable variation between faecal samples from different sites, with in particular a low occurrence of mussels in samples from St. Mary's Island. However the small sample sizes from sites other than North Blyth meant that this variation was not statistically significant for any of the five main prey items (Kruskall-Wallis, d.f. = 3; mussels $\chi^2 = 7.24$; barnacles $\chi^2 = 3.13$; *N. lapillus* $\chi^2 = 2.5$; littorinids $\chi^2 = 1.07$; *R. parva* $\chi^2 = 19.6$).

4.4 Discussion

4.4.1 Purple Sandpiper distribution and overall numbers

The number of Purple Sandpipers using the south Northumberland coast varied widely both between the three study winters and within these winters. Some species of waterfowl and shorebirds wintering in Britain show fluctuations in numbers due to cold weather movements e.g. Wigeon Anas penelope and Teal A. crecca (Ridgill & Fox 1990), Ringed Plover Charadrius hiaticula (Pienkowski 1982), Dunlin Calidris alpina (Pienkowski 1984) and Redshank Tringa totanus (Davidson & Clark 1985). However, Purple Sandpipers in Britain show a number of significant ecological differences from the species that exhibit these coldweather movements. Northumberland is towards the southern edge of the distribution of Purple Sandpiper during winter. Although birds do winter as far south as Iberia, numbers there are very low and those in France, the Low Countries and southern Britain are also insignificant relative to the total numbers wintering in Europe (Atkinson et al. 1978, Cramp & Simmons 1983, Boere 1984). Many more Purple Sandpipers winter further north, along the coasts of Norwegian and north-western Russia where winter conditions are very harsh (Summers et al. 1990b). Alerstam (1982) estimated that several hundred thousand Purple Sandpipers winter along the Norwegian coast.

Wintering Purple Sandpipers have two physical characteristics that may be adaptations to allow wintering at high latitudes. Kersten & Piersma (1987) found the plumage mass to be 11% heavier than would be expected for the birds' body mass, and the breast and belly feathers are of a similar length to those of much larger species such as Eurasian Golden Plovers (Summers *et al.* 1992). This adaptation may provide greater thermal insulation than in other wader species. Secondly, Purple Sandpipers have large breast muscles in comparison with other small waders wintering in Britain (Davidson 1990). Summers *et al.* (1992) considered three possible explanations for these large muscles in wintering birds: (1) for use in long distance flight, (2) as a nutrient store to facilitate survival in periods of low food intake, and (3) as a heat-producing organ. The first two

hypotheses were rejected on the grounds that in early and mid-winter Purple Sandpipers are not preparing for migration and because fat is a better reserve for periods when energy intake does not meet requirements. Therefore it is possible that Purple Sandpipers have enlarged breast muscles to generate heat during cold winter periods. Thomas *et al.* (1975) made a similar suggestion to explain the large pectoral muscles on wintering Ruffed Grouse *Bonasa umbellus* and it may also be true for other tetraonid grouse at high latitudes (Thomas & Popko 1981, Thomas 1982).

In addition to these features, Purple Sandpipers are unusual in that they undergo less mid-winter fattening than other waders; Atkinson (1981) failed to find any variation in Purple Sandpiper body mass during the winter while Summers *et al.* (1992) found a difference of between 1% and 4.1% between Purple Sandpiper mass at the winter peak (November-December) and trough (March). This range is much less than for other *Calidris* species: 12.6% for Knot *C. canutus* (Johnson 1985), 6.1% for Sanderling *C. alba* (Johnson 1985) and 12.4-15.2% and 14.2% for Dunlin *C. alpina* (McEwan & Whitehead 1984, Pienkowski *et al.* 1979). Even Purple Sandpipers wintering in northern Norway carry average fat levels of only 6.5% of fresh body mass (Summers *et al.* 1998).

Body reserves (mainly fat) are thought to be carried by wintering birds as insurance against food shortages and severe weather (Dugan *et al.* 1981) with fat levels being at their highest at times of highest risk. The low levels of fat in Purple Sandpipers would suggest that they are less likely to suffer from such an energy shortfall than other waders. Low fat stores may also be carried by birds that experience a high risk of predation which may be a consideration for Purple Sandpipers in Northumberland (Chapter 2) and elsewhere. High body mass may impair agility and speed in flight (Gosler *et al.* 1995, Metcalfe & Ure 1995, Bednekoff 1996, Kulberg *et al.* 1996). However, recent studies have contradicted this conclusion as the fat reserves carried by many birds may be insufficient to affect take-off speed (Kulberg 1998). Birds may be able to compensate for effects of body mass on velocity when they are alarmed (Veasey *et al.* 1998) or may even increase their body mass due to the loss of foraging time caused by predation risk (Lilliendahl 1998). The physiological adaptations mentioned

previously may ameliorate the impact of cold temperatures but the other major factor may be the reliability of their food resources. Waders that feed in soft sediments may be at risk from starvation in cold conditions as their prey species retreat farther into the sediment, or produce less visible signs of their presence that aid hunting birds (e.g. Goss-Custard 1969, Pienkowski 1982, Zwarts & Wanink 1989). Purple Sandpipers are rarely found away from rocky shores where their epibenthic mollusc prey is unable to retreat in this manner. Inclement weather conditions may hamper their feeding ability (Feare 1966), but food availability remains the same and starvation is less likely. However measurements of variability in fat reserves in relation to invertebrate densities have not been made and it is not known whether Purple Sandpipers significantly deplete their food supplies through the winter; Dierschke (1994) suggested reduced prey densities might have been the cause of dietary changes in Purple Sandpipers wintering at Helgoland.

Summers *et al.* (1990b) found that Purple Sandpipers wintering in northern Norway had a higher mass than Scottish birds of a similar size. These reserves may be accumulated as a safeguard against adverse conditions that may be more likely at this higher latitude (or could be an indication of a lower predation risk). In addition these birds have larger intestine and liver size, suggesting that they have the ability to process more food, in order to cope with the higher thermoregulatory demands of wintering within the Arctic Circle (Summers *et al.* 1998).

The nature of Purple sandpiper diet, the physiological adaptations to cold weather and the comparatively element climate of the Northumberland coast, compared with wintering grounds used by birds at a latitude over 13° further north, all suggest that movements away from the study area due to harsh winter weather are highly unlikely. This conclusion was supported by the comparison of bird numbers with local weather data. However such a comparison does not reveal whether numbers could be influenced by influxes of birds *into* the region from other wintering areas. The data from my fieldwork, and those collected between 1985-95, show considerable variation in mean numbers between years. It is possible that these fluctuations are due to severe weather conditions in other



wintering grounds further north, with between-year variation in weather causing less or more birds to move south to Northumberland. Despite the general ability of Purple Sandpipers to survive at high latitudes, hard-weather movements out of Scandinavia do occur (Burton & Evans 1997, Hake *et al.* 1997). However years that had high mid-winter numbers also had high numbers in early winter (October-November) which is before hard-weather conditions could be expected to have had an impact on the birds wintering further north. This comparison suggests that fluctuations in the number of birds wintering in Northumberland may be due to fluctuations in the size of the population as a whole, possibly as a result of variation in breeding success.

A number of Arctic-breeding shorebirds and waterfowl show periodic fluctuations in their breeding success in the Arctic. This variation seems to be related to the dynamics of populations of microtine rodents such as the collared lemming Dicrostonyx groenlandicus and tundra vole Microtus oeconomus which affect the numbers and prey choice of shorebird predators, in particular arctic foxes Alopex lagopus (Underhill et al. 1993, Summers et al. 1998). In the absence of high numbers of rodents arctic foxes "prey-switch" and forage on bird nests, having a negative impact on the breeding success of species such as Curlew Sandpipers Calidris ferruginea (Summers et al. 1998), Brent Geese Branta bernicla (Summers 1986) and Bewick's Swans Cygnus columbianus (Syroechkovskiy et al. 1991). If such an impact occurred on breeding Purple Sandpipers, it could be the cause of fluctuations in wintering numbers in Northumberland. Between year fluctuations in food resources on the breeding grounds (for both adults and chicks) may also influence breeding success. Corse & Summers (1999) suggested that variation in the proportion of first-year birds in the Orkney population of Purple Sandpipers reflected betweenyear variation in breeding success. However, as a long-lived shorebird with correspondingly low mortality, recruitment to the population would be expected to be low, and proportions of first-year birds insufficient to cause between-year variation on the scale recorded in Northumberland.

Whether breeding success, winter weather conditions or other factors, it seems unlikely that the variations in the population wintering in Northumberland are

due to factors intrinsic to the coast itself. This variation does however complicate attempts to look for long-term trends in the wintering population at each study site. No significant change in numbers was detected over the 1985 to 1999 period for which data were available. This finding is at odds with that of the non-estuarine wader survey (NEWS) organised by the BTO over the 1997-98 winter (Rehfisch *et al.* 1999). Counts from this survey were compared with the previous comparable attempt, the 1984-85 Winter Shorebird Count (Moser & Summers 1987). Preliminary analysis of results has shown a marked decline in Purple Sandpiper numbers on most British coasts, with a 38% decline in Northumberland, and 16.6% and 46.5% in neighbouring Durham and the Scottish Borders respectively. 15 of the 18 coastal English counties showed a decline between the two surveys (S. Holloway, pers. comm.).

The reliance of such nationwide surveys on single counts is unavoidable, due to the large organisational and manpower requirements of such surveying. So the results, and the conclusions drawn from them, are at the mercy of short-term fluctuations in numbers and counting inaccuracy. Many counts would have been made along coasts not normally covered by regular surveying, so observers may be prone to missing birds due to unfamiliarity with the area and, especially in the case of an inconspicuous shorebird such as Purple Sandpiper, the birds themselves. The counts made by volunteer recorders along the Northumberland coast were far lower than those made by myself over the same period (a mere six birds were counted at North Blyth, the principal site for Purple Sandpipers within my study area). In view of the problems faced by such nationwide surveying it would be valuable if the accuracy of counts in some sections could be validated against longer time-series of counts.

Although the WeBS counts from Northumberland do not show a decline in the order of that found by the 1997-98 NEWS survey, it is possible that a less severe decline has occurred and been masked by the between-year variation in numbers. It seems unlikely that the Northumberland population would have remained constant if a nationwide decline has occurred. A study at Hartlepool, Durham, 40 km south of the Northumberland study area over the 1999-2000 winter found that Purple Sandpiper numbers had declined by 31% since 1994 (Eaton 2000).

As well as between-year fluctuations in the total number of Purple Sandpipers within the study area, there were shifts in the distribution of birds between sites, both within my three-year study period and previously, as recorded in the available WEBS counts. The most noticeable change in distribution between 1985 and 1995 was the decrease in birds roosting and feeding in the St. Mary's Island/Seaton Sluice area and the corresponding increase in birds at Blyth. This change occurred in the early 1990s, which corresponds with an increase in the public usage of the St. Mary's island area; the development of a visitor centre and increased car parking provision encouraged people of the nearby Newcastle conurbation to use the area for recreation. The disturbance to both feeding and roosting birds from dog-walkers and fishermen appears to have been sufficient to cause the large majority of birds to move up the coast and does not appear to reflect any change in food resources.

Between-year variations in Purple Sandpiper distribution during the 1996-99 study period could be attributed to variation in settlement of mussel spat and/or changes in raptor activity. The settlement of mussel larvae onto substrates can change greatly between years, with some years showing massive recruitment (e.g. Suchanek 1978, Griffiths 1981) and others little or even no recruitment (Brown & Seed 1977, Comely 1978). Subsequent to settlement, large amounts of settled spat, and older mature mussels, can be scoured off intertidal rocks by mid-winter storms (Paine & Levin 1981). Although the invertebrate surveying conducted as part of the coastal monitoring was not sufficiently detailed to pick up changes in abundance of suitable sized mussels (up to 7 mm, Summers *et al.* 1990, Dierschke 1994) casual observations at Amble suggested that there was a considerable increase in the area of intertidal rock covered by fresh mussel settlement in the autumn of 1997 that remained over the course of the following winter.

The three raptor species likely to prey upon Purple Sandpipers along the Northumberland coast are Peregrine, Merlin and Sparrowhawk; all three were either seen catching or attempting to catch Purple Sandpipers during the course of my fieldwork. The results of the modelling of habitat variables and bird

densities in Chapter 2 suggested that raptor predation could have an important role in determining Purple Sandpiper distribution. The contribution of avian predators was clearly demonstrated in the significant change in Purple Sandpiper distribution in the southern half of the study area in the 1998-99 winter. The presence of two Peregrines and one Merlin was sufficient to cause a major shift in Purple Sandpipers' feeding areas. Sparrowhawks are fairly evenly distributed along the Northumberland coast, whereas the scarcer Merlin was generally only seen at the sites with the highest warder densities, in particular high Dunlin densities. Peregrines appeared to be dependant on having suitably undisturbed roosting locations i.e. the chimneys of the power station at Blyth and on Coquet island.

4.4.2 Purple Sandpiper foraging behaviour

Purple Sandpipers showed a clear preference for a few microhabitats within the rocky shore area. In particular birds preferred barnacle and mussel covered rocks. The considerable proportion of foraging time on *Enteromorpha*-covered substrate was probably due to birds foraging on the mussel bed underneath these algal mats. The preference for mussel beds, and the important role of mussels in the diet (see below), concurs with the importance of mussel bed area in determining Purple Sandpiper density found by the modelling analysis in Chapter 2.

By feeding within one or two metres of the tide edge, Purple Sandpipers ensure that they are always feeding on wetted substrate which confers an advantage, as invertebrate prey are more active and easier to detach from the substrate (Feare & Summers 1985). Gastropods are likely to emerge from rock crevices used as sheltering sites during the exposed portion of the tidal cycle and are less firmly attached to the substrate if mobile. This combination of possibly greater prey availability and lower energetic costs of catching prey is obviously sufficient to outweigh the increased energetic costs of avoiding incoming waves, and the foraging time lost in doing so; Feare (1966) estimated Purple Sandpipers at Robin Hood's Bay, North Yorkshire, lost between 2.8% and 13.3% of foraging time to avoiding waves, depending on weather conditions.

Almost invariably, birds feeding away from the tide's edge did so in shallow rock pools, where the advantages of wetting were still present. That more birds did not do so may have been due to prey depletion; whereas the area wetted from the tide's edge is constantly moving and covers the whole intertidal area over the course of the tidal cycle, rock pools are fixed. None of the Northumberland study sites has a large proportion of rock pools (the greatest proportion at any site is 5.6%, at Hauxley) so if these pools were used intensively by foraging birds, prey would be rapidly depleted.

The behaviour of birds wintering at Blyth, the principal site for Purple Sandpipers within the study area, differs from that at the five other rocky shore sites in two ways. Due to the sea defences, there are no upper tidal rocks for Purple Sandpipers to forage on, and no sandy shores to collect the wrack deposits that occur at other sites. Therefore Purple Sandpipers roost for longer over the tidal period; approximately 60 minutes longer than birds at Amble and Cresswell and probably similarly longer than birds at Hauxley, Newbiggin and St. Mary's Island although data were not collected from these three sites. In addition there is no feeding over high tide at Blyth, whereas between 6% and 13.7% of bird-time during high water is spent foraging at the five other sites. Therefore, birds at Blyth forage for a shorter period over the tidal cycle that those at other sites. This comparison suggests that individuals at Blyth are able to achieve a higher biomass intake rate over low tide than those elsewhere and subsequently need to forage for a shorter time period. By reducing their foraging time and spending more time roosting, birds at Blyth may be minimising their predation risk, as they can choose secure roosting sites and/or devote more time to vigilance. It is also possible that there was a difference between sites in the benefits of foraging during the night; Purple Sandpipers at Blyth may have been able to achieve a greater energy intake over the night than birds at other sites (see Chapter 6).

The high numbers of birds present at Blyth over the winter period declined in the spring as birds dispersed to Newbiggin and St. Mary's Island which suggests that the high density of birds in the winter caused a significant depletion of the available food resources, to the point where it became more profitable for some birds to forage elsewhere. Although invertebrate sampling failed to find a decline

in prey densities, it is likely the crude methodology used was insufficient to detect such changes, particularly considering the small size of Purple Sandpiper prey. Alternatively, prey resources at other sites might have increased, attracting birds away from Blyth, but there is no evidence to support that hypothesis. A third possibility is that although sufficient prey density remained at Blyth for birds to maintain their intake, it did not allow for the increase needed to support pre-migratory fat deposition (Davidson 1981, Davidson & Evans 1989). A number of shorebird species have been recorded foraging for longer in the spring in order to increase their energy intake (Zwarts *et al.* 1990). However, the lack of upper tidal areas at Blyth means that Purple Sandpipers there were not able to increase their intake by foraging for longer through the tidal cycle and so may have needed to forage elsewhere to achieve the required levels of food intake.

4.4.3 Purple Sandpiper diet

It has to be recognised that the use of faecal analysis can be deeply flawed due to differences that may exist in the digestion of different food types and the difficulty of identifying remains. However Purple Sandpipers take very small prey items, usually swallowing them without raising the head and often with the bill under water, making direct observation of diet nearly impossible.

My observations of feeding birds and the evidence from faecal samples suggest that molluscs and small gastropods are by far the most important component of Purple Sandpipers' diet throughout the non-breeding season in Northumberland.

Strann & Summers (1990) studied the diet of Purple Sandpipers wintering in Troms County, northern Norway by the more accurate method of examining undigested prey in the oesophagi and gizzards of shot birds. Of ten birds collected from a rocky shore habitat, six contained *M. edulis*: 50.7% of all intact items were of this species. *Littorina littorea* and *L. saxatilis* comprised a further 20.7% of all items. However, these authors found a much higher incidence of arthropods, particularly *Gammarus locusta*, than my study. This difference could be due to the deficiencies of faecal analysis; arthropod parts still detectable in the gizzard may be absent by the time gut contents are expelled. However a further

study by Summers *et al.* (1990a) on the gizzard contents of 37 Purple Sandpipers (either cannon-netting casualties or deliberately collected birds) from sites in eastern and northern Scotland found a much lower incidence of arthropods. Their study found large differences in birds collected from different sites; nearly 50% of identified food items from birds collected in Arbroath were *M. edulis*, whereas this bivalve was not found at all at four of the other seven sites. Such variation in gizzard content may be due to regional variations in diet, conversely it may be due the small sample size and the fact that sampling by collecting birds is very susceptible to bias due to time of collection, tidal states, weather conditions etc. Feare (1966) relied on faecal samples as an indication of the diet of a small wintering flock of Purple Sandpipers at St. Robin Hood's Bay, North Yorkshire. As with my study he found that the diet was almost completely molluscs, with littorinids and *N. lapillus* predominating, up to approximately 5% *M. edulis* and occasional crab fragments.

Green algae were observed in some faeces from Robin Hood's Bay by Feare (1966) and in gizzard contents from Peterhead by Summers *et al.* (1990a). In addition Dierschke (1994) found that Purple Sandpipers at Helgoland, German Bight ate a variety of algae including *Ulva* sp., *Blidingia* sp. and *Ulothrix* sp., the latter almost exclusively during one spring period. He suggested that birds might feed on algae to acquire essential nutrients, particularly prior to migration.

Despite the importance of mussels in Purple Sandpiper diets, birds were recorded feeding on mussel beds for only 35% of the low tide period, and spent 33% of foraging time on barnacle-covered rock despite only occasionally eating barnacles. These results illustrate the error inherent in my substrate classifications; areas classified as barnacle-covered still had high populations of *M. edulis*. Indeed in some cases these areas may have been more suitable for foraging Purple Sandpipers as they had high numbers of small immature mussels whereas some areas of mussel beds contained mainly more mature mussels that were too large for Purple Sandpipers to handle.

There was a very large degree of variation in the composition of faecal samples, which strongly suggests that individual birds may have had different diets. This

variation masked any patterns that may have occurred in diet over the tidal cycle and between sites, although with a more intensive sampling program it seems likely that significant differences would have been found between sites. However, the inherent variation did not mask a seasonal change in diet; birds at Blyth foraged less on *M. edulis* in the spring and more on *N. lapillus* and other gastropods. Mussels were a very important component of Purple Sandpiper diet at Blyth; as mentioned previously intense foraging by a relatively high density of birds may have resulted in a significant decline in food resources, causing some individuals to leave Blyth. It is also possible that winter storms may have removed large amounts of mussels from the intertidal area at Blyth (although there is no evidence this process occurred). The significant decline in mussels in the diet supports this hypothesis.

It is possible also that changes in the behaviour of prey were responsible for changes in Purple Sandpiper diet e.g. *N. lapillus* and Littorinids migrate down the shore in autumn and back up in spring. Therefore the increased incidence in Purple Sandpiper faeces in spring could be due to increased availability.

4.4.4 Summary

The results given in this chapter form a detailed data set that accurately describes the use of the study area by wintering Purple Sandpipers. This information will act as a baseline to look for any future impacts due to the "knock-on" effects of the reduction in sewage inputs along the Northumberland coast. However, analysis has revealed a large amount of variation that may mask any future changes in the number and distribution of birds using the study area. Overall population levels fluctuate between years, possibly due to changes in breeding success or weather conditions on wintering grounds further north. Distribution between sites can be influenced by naturally occurring fluctuations in food resources, and by factors unrelated to food such as raptor activity and human disturbance. Data were collected on diet, but the limitations of analysing faecal samples meant that fine variations in diet could not be detected. These data did indicate, however, that there might be a large degree of intrinsic variation in the diets of individual Purple Sandpipers.

In addition, the monitoring results suggest that although Purple Sandpipers in Northumberland may experience relatively easy wintering conditions compared to birds remaining within the Arctic Circle, there was a difference in conditions between the six rocky shore sites. Birds at the site with the highest density, Blyth, foraged for a shorter period over the tidal cycle and so may have reduced their risk of predation by raptors. However these habits may have resulted in a significant depletion of food resources that lead to an exodus of birds to neighbouring sites in the late winter and spring, and a change in diet of those birds that remained (although evidence of depletion was not proved by invertebrate sampling). If depletion (of mussels, a major part of Purple Sandpiper diet in Northumberland) occurred it would suggest that food resources, and in particular mussels, may be a limiting on Purple Sandpipers. The rise in bird density at Amble that accompanied a possible increase in mussel spat supports this possibility. Therefore a change in this food resource caused by improved handling of human sewage has the potential to affect the Purple Sandpiper population.

Chapter 5

Use of the south Northumberland coast by Turnstones

5.1 Introduction

The work described in this chapter was conducted with the same aims as the research on Purple Sandpipers described in Chapter 4. To reiterate briefly, these aims were:

- To establish a baseline of bird numbers and spatial distribution, to allow comparison with numbers and distribution after the installation of new sewage treatment and disposal facilities.
- To discover what ecosystem components are important to Turnstones in south Northumberland, in order to allow predictions or interpretations of the impact of the improvements in sewage treatment and dispersal.
- To describe the behaviour of the study population as a whole in order that the significance of variation in the behaviour of individual birds can be assessed (Chapter 7).

5.2 Methods

To a large extent the methods of study were the same as for the studies on Purple Sandpipers, described in Chapter 4.

5.2.1 Counts and analyses

The nine coastal stretches and three estuaries (Figure 2.2) were counted at least once a fortnight from September to May inclusive, and once a month over the summer. Counts were made over both high and low water on alternate fortnights at each site, meaning that at least one low water and one high water count were made in every month. Whereas for Purple Sandpipers it was often possible to use high-tide counts as an indication of the numbers of birds feeding at a site at low tide, this extrapolation was not feasible for Turnstones, due to birds moving between sites on rising and falling tides. However, counts made on the rising tide tended to provide more accurate counts of Turnstone numbers than those made over low water itself and could be made before any movement between sites occurred. Therefore, in the 1997-98 and 1998-99 winters, rising tide counts were frequently used to monitor numbers of birds present at a site over low water. Additional counts were made during the course of other fieldwork over all tidal states.

As in Chapter 4, the classification of low and high water was based on tidal height and not time, with high water being defined as above or equal to 3.7 m O.D. For the analysis of Turnstone data, winter was defined as October to March (inclusive), rather than November to March as used for Purple Sandpipers, as wintering Turnstone numbers were relatively stable over this period (Figure 5.1).

As for Purple Sandpipers, WeBS counts for winters from 1984-85 to 1994-95 were obtained from the BTO to provide information on trends in Turnstone numbers before the start of this study. Mean winter counts were derived as described in Chapter 4.

To determine whether Turnstone numbers at Amble and Hauxley over high water varied according to the amount of wrack deposited along the high water mark (see Chapter 2), regressions were performed of Turnstone numbers against length of wrack deposits (at each site separately).

5.2.2 Habitat use and behaviour

Habitat use and behavioural data were collected in the same manner as for Purple Sandpipers (Chapter 4.2.2). In addition, field notes on the feeding behaviour of Turnstones were taken on occasions throughout all three winters of study.

5.2.3 Faecal samples

Faecal samples were thought to be not as good as an indication of diet for Turnstones as for Purple Sandpipers, due to (i) the larger variation of Turnstone diets and hence the much larger sampling regime required, and (ii) the greater prevalence in their diets of soft-bodied invertebrates less likely to be detected in faeces (and harder to identify). However, between five and seven samples were collected on eight occasions in order to gain an approximate picture of Turnstone diet. As with Purple Sandpiper samples, they were stored in alcohol and later examined under low power using a binocular microscope. The species present in each sample were identified, but size measurements were not made.

5.3 Results

5.3.1 Counts of Turnstones

5.3.1.1 Seasonal and annual variation in total numbers

Figure 5.1: Turnstone numbers in the study area, 1996-99

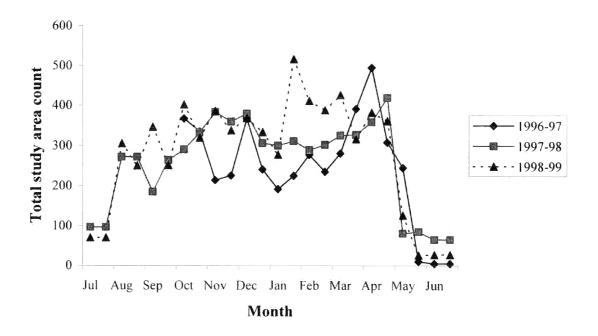


Figure 5.1 shows that most Turnstones were present in the study area from August to April inclusive but that a small number spent the summer in the study area each year (June counts varied between 5 and 65). Most wintering birds arrived by October, although higher numbers occurred later in all three winters. The timing of winter peaks varied between the three study seasons; numbers peaked during October and December in 1996-97, November and December in 1997-98 and in January in 1998-99. Peaks in counts during spring were detected in 1997 and 1998 but not 1999.

The fluctuations in numbers may have been due in some part to occasional incomplete counts, particularly at the north end of the study area where birds flew to and from Coquet Island. During visits to Coquet Island in the three study winters (in January 1997, December 1997 and January 1999, at mid to high water

on neap tides) 65, 77 and 73 Turnstones respectively were seen, suggesting that about 70 birds winter on Coquet Island. However, on higher spring tides, Turnstones from the mainland at Amble and Hauxley flew to Coquet Island to join the roost, resulting in lower counts being made on the mainland. On other occasions, attractive high water feeding conditions on the mainland resulted in birds usually resident on Coquet Island moving to the mainland to feed (see Chapter 7), increasing the numbers counted within the study area.

The lower numbers of Turnstones counted in the 1996-97 winter (my first winter of study) may have resulted from undercounting during low water, when Turnstones can be hard to detect, especially when feeding amongst *Fucus* algae. In addition, some roosting birds may have been missed during high water surveys; in particular, the roost site at Lynemouth, used by Turnstones from Cresswell on extreme spring tides, was not discovered until autumn 1997. Similarly, several inland feeding locations used occasionally by Turnstones in stormy conditions (e.g. the ploughed fields at Amble and pasture south of Cresswell Pond) were not discovered until the 1997-98 winter, although it is not known for sure whether these sites were used by Turnstones in 1996-97.

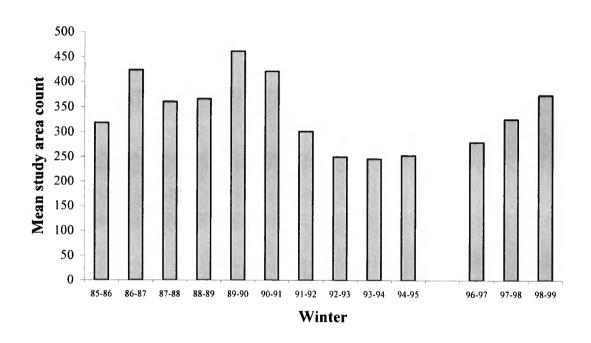
Despite the probable undercounting over the 1996-97 winter, it seems very likely that real differences in the number of Turnstones within the study area occurred between years. Table 5.1 gives the mean and peak counts for each of the three study winters. Mean wintering Turnstone numbers increased steadily over the three winters, but the peak count in 1998-99 was much higher than that of 1997-98 or 1996-97.

Table 5.1: Mean and peak Turnstone counts for each winter

Winter	Mean	S.E.	Peak winter count
1996-97	279	19.9	391
1997-98	325	9.4	383
1998-99	373	18.3	516

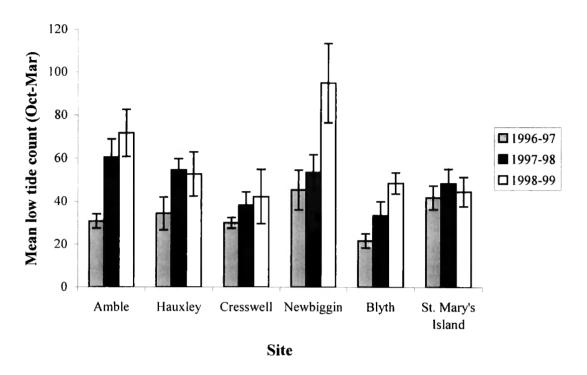
Figure 5.2 shows the winter mean from WeBS roost counts of Turnstones in the study area from 1985-86 to 1994-95, together with means from the three winters of my study. Mean winter counts varied from 246 to 461, and annual peak counts from 285 to 581. Turnstone numbers rose in the mid and late 1980s before declining to a lower level in the early 1990s and then rising again in the late 1990s.

Figure 5.2: Mean Turnstone winter (Oct-Mar) counts from WeBS (1985-95) and my fieldwork (1996-99)



5.3.1.2 Distribution between sites

Figure 5.3: Mean winter counts of Turnstones at low water at rocky shore sites, 1996-99



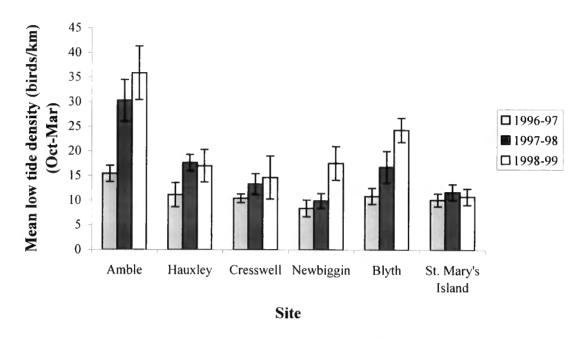
Error bars show one standard error either side of mean.

Figure 5.3 illustrates the differences in mean Turnstone numbers between years at each rocky shore site. At four of the sites (Amble, Cresswell, Newbiggin and Blyth) the mean number increased between each winter, as would be expected from the overall increase in Turnstones shown in Table 5.1 and Figure 5.2. At four sites the difference in Turnstones between years was statistically significant; Amble (Kruskall-Wallis, $\chi^2 = 15.85$, d.f. = 2, P < 0.01), Hauxley ($\chi^2 = 7.85$, d.f. = 2, P < 0.05), Newbiggin ($\chi^2 = 6.03$, d.f. = 2, P < 0.05) and Blyth ($\chi^2 = 11.24$, d.f. = 2, P < 0.01).

Figure 5.4 presents the same data, but as densities (birds per km coastline). It can be seen that in the 1996-97 winter, when overall numbers were relatively low, Turnstone densities were broadly similar at all six rocky shore sites. The increase in numbers in the two subsequent winters served to emphasize the differences in

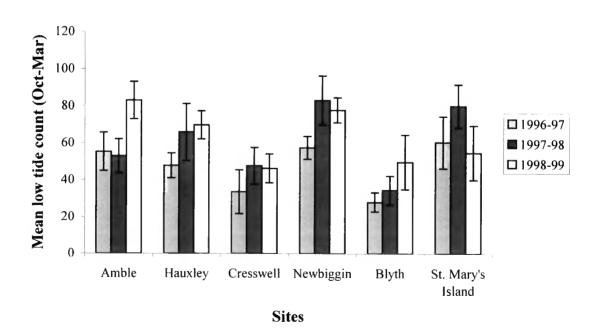
density, with Amble in particular holding a higher density of Turnstones than other sites.

Figure 5.4: Mean winter densities of Turnstones at low water at rocky shore sites, 1996-99



Error bars show one standard error either side of the mean in both Figure 5.4 & 5.5.

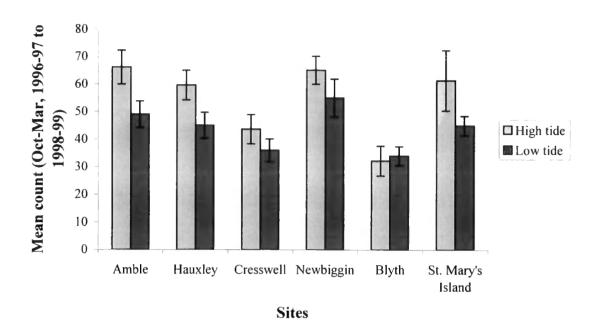
Figure 5.5: Mean Turnstone high water counts at rocky shore sites, 1996-99



The marked increase in the numbers of Turnstones counted at low water over the three winters (Figure 5.3) was not matched by a similar increase in mean high water counts (Figure 5.5), which showed no significant difference between winter means at any site.

As stated before, the increase in Turnstone numbers over the three years of this study may have been exaggerated by undercounting in the 1996-97 winter. Turnstones are much easier to count at high water, when they congregate either at regular roost sites or in flocks feeding on the tideline, than at low water when they may be distributed over a large intertidal area. Low water counts during my first winter of study may have missed some of these birds, whereas high water counts were more accurate (hence the greater increase in low water counts in following years). As would be expected if this source of error applied, the two sites with the greatest increase in mean count between the first two winters were Amble and Hauxley, sites with large areas of intertidal *Fucus* beds that made counting difficult. Conversely, St. Mary's Island, a site almost entirely overlooked by low cliffs that made counting easy and Turnstones less likely to be overlooked, showed the smallest increase between 1996-97 and 1997-98.

Figure 5.6: Comparison between recorded numbers of Turnstones at low and high water, 1996-99



At all sites except Blyth, the mean of high water counts for all three winters was higher than the low water mean. The difference in Turnstone means was significant at Hauxley (Scheirer-Ray-Hare test, $\chi^2 = 3.87$, d.f. = 1, P < 0.05) and St. Mary's Island ($\chi^2 = 4.914$, d.f. = 1, P < 0.05) but not Amble ($\chi^2 = 1.09$, d.f = 1), Cresswell ($\chi^2 = 0.77$, d.f. = 1), Newbiggin ($\chi^2 = 0.66$, d.f. = 1) or Blyth ($\chi^2 = 0.54$, d.f. = 1). The difference in counts at Hauxley may have been due to aforementioned difficulty in making complete and accurate counts at low water. However, at St. Mary's Island counts over low water were believed to be accurate but were still significantly lower than those made at high water. The higher mean number of Turnstones at high water may have been due to birds moving to the site from other (uncounted) areas to the south, such as Whitley Bay and Cullercoats.

As well as there being changes in Turnstone distribution between high and low water, the height of these tides – whether spring or neap – also had an effect on Turnstone numbers at the different rocky shore sites (Figures 5.7 & 5.8).

Figure 5.7: Comparison between numbers of Turnstones at spring and neap high waters

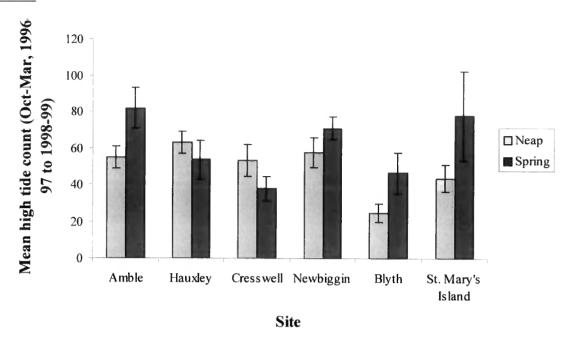
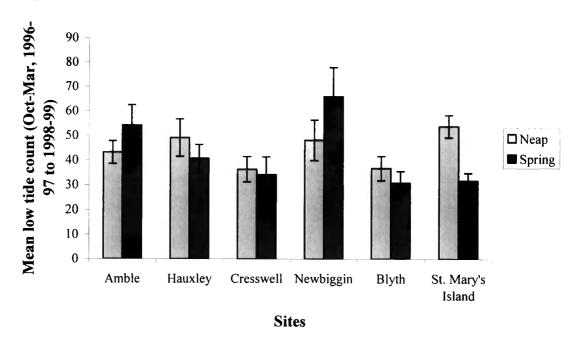


Figure 5.7 shows that there was a significant difference between mean Turnstone counts at high tide during spring and neap tides at Amble (Scheirer-Ray-Hare test, $\chi^2 = 3.94$, d.f. = 1, P < 0.05) and Blyth ($\chi^2 = 6.328$, d.f. = 1, P < 0.01) but not at Hauxley ($\chi^2 = 2.89$, d.f. = 1), Cresswell ($\chi^2 = 2.24$, d.f. = 1), Newbiggin ($\chi^2 = 0.61$, d.f. = 1) or St. Mary's Island ($\chi^2 = 0.03$, d.f. = 1). In both sites where the difference was significant, a higher mean count was made on spring high tides. At Amble, the increase in numbers on spring high tides was matched by a (lesser) decrease in numbers at Hauxley, which suggests that some birds moved north to Amble on spring tides.

<u>Figure 5.8: Comparison between numbers of Turnstones at spring and neap low</u> waters

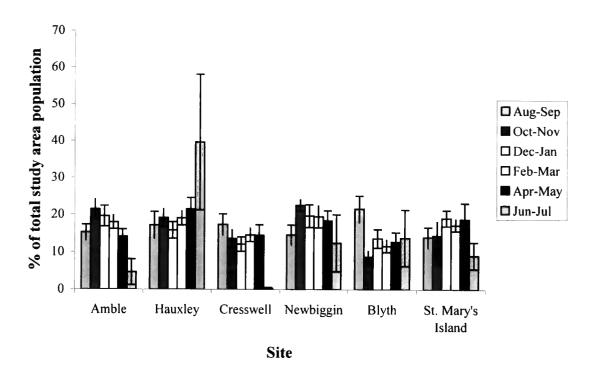


Error bars show one standard error either side of the mean.

A significant difference between numbers on spring and neap low tides was found at St. Mary's Island only (Scheirer-Ray-Hare test, $\chi^2 = 3.94$, d.f. = 1, P < 0.05). There was no significant difference at Amble ($\chi^2 = 0.33$, d.f. = 1), Hauxley ($\chi^2 = 0.19$, d.f. = 1), Cresswell ($\chi^2 = 0.16$, d.f. = 1), Newbiggin ($\chi^2 = 1.17$, d.f. = 1) or Blyth ($\chi^2 = 0.47$, d.f. = 1). Rather surprisingly, the difference in numbers at St. Mary's Island was in an opposite direction to that shown at high water; the mean number was *greater* on neap tides than on spring tides. It is possible that the greater intertidal area exposed on spring low water meant that some Turnstones were missed during counts at St. Mary's Island.

The effect of the spring-neap tidal cycle on Turnstone numbers was more pronounced over high water than low. Only one site showed a significant difference in mean winter number over low water, whereas two did at high water and a comparison of Figures 5.6 and 5.7 shows that the differences between spring and neap tides at all sites were more pronounced at high water (Figure 5.7).

Figure 5.9: Seasonal changes in Turnstone distribution between rocky shore sites, 1996-99



Error bars show one standard error either side of the mean.

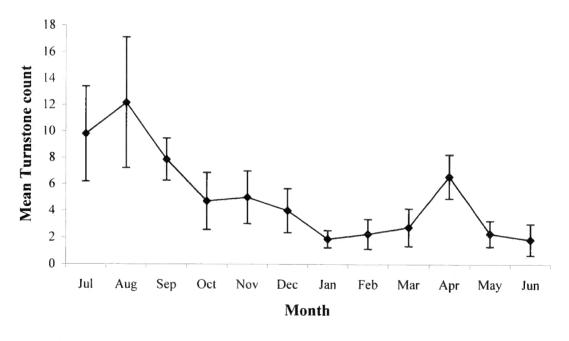
Figure 5.9 shows the proportion of the mean count from the total study area at each study site in six two-month periods (data from all three years combined). Two sites showed a significant seasonal variation in the proportion of the study area total present; Amble (Kruskall-Wallis, $\chi^2 = 14.3$, d.f. = 5, P < 0.05) and Cresswell ($\chi^2 = 15.8$, d.f. = 5, P < 0.01). There was no significant difference at the other sites; Hauxley ($\chi^2 = 5.1$, d.f. = 5), Newbiggin ($\chi^2 = 7.4$, d.f. = 5), Blyth ($\chi^2 = 9.2$, d.f. = 5) and St. Mary's Island ($\chi^2 = 8.3$, d.f. = 5). At both Amble and Cresswell there was a significant decrease in the proportion present in June and July which was mirrored by a large (but not statistically significant) increase in the proportion of the population present at Hauxley. These changes suggest that either there was a movement of birds to Hauxley from these two neighbouring sites in the summer or more Turnstones that had wintered at Hauxley subsequently remained over the summer.

The other noticeable seasonal change in importance of a site was at Blyth, which held a mean of 21.6% of all Turnstones in the study area in August-September,

compared with between 8.8% and 13.8% in other periods. This high proportion was caused by high numbers of Turnstones roosting on North Side Staithes over high water during this period. These counts were not matched by similarly high numbers of birds feeding at North Blyth over low water. For example on 9th September 1998, 114 birds roosting on the Staithes, but only 40 were counted at North Blyth over low water. The "extra" Turnstones were feeding in the Blyth Estuary over low water.

Turnstones showed a similar seasonal use of the Coquet Estuary (Figure 5.10), where numbers were low throughout the winter, showed a small peak in spring but a larger peak in numbers in August. The lack of colour-ringed individuals amongst the Turnstones using the estuary during this period (Chapter 7) suggests that these birds were in transit. The only time Turnstones were observed in the Wansbeck Estuary was also during August and September, although only in small numbers.

Figure 5.10: Mean monthly counts of Turnstones in Coquet Estuary, 1996-99



Error bars show one standard error either side of the mean

Figure 5.11: Turnstone distribution at high water within the study area, 1985 to 1999, from WeBS data and fieldwork

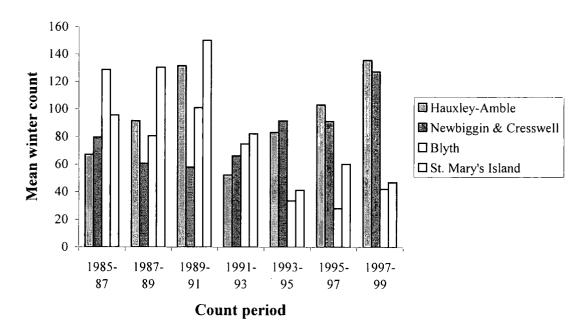


Figure 5.11 shows the mean number of Turnstones present at high water in four stretches of the south Northumberland coast, amalgamated into two-year periods for simplification, from 1985-86 to 1998-99. These data indicate whether there has been any change in the distribution of Turnstones along the south Northumberland coast in recent years. As WeBS count sections, which were used for 1985-86 to 1994-95, do not match those used by this study, counts for Amble and Hauxley and Cresswell and Newbiggin had to be combined.

Each of the four sites showed a significant variation in mean number between the two-year count periods (Kruskall-Wallis, St. Mary's Island $\chi^2 = 20.5$, d.f. = 6, P < 0.01, Blyth $\chi^2 = 24.4$, d.f. = 6, P < 0.01, Newbiggin-Cresswell $\chi^2 = 32.4$, d.f. = 6, P < 0.01, Hauxley-Amble $\chi^2 = 32.3$, d.f. = 6, P < 0.01). Both St. Mary's Island and Blyth showed a decline in numbers over the periods for which data were obtained, whereas mean numbers increased at Newbiggin-Cresswell and Hauxley-Amble. Interestingly, as well as rising towards the end of the period, numbers at Hauxley-Amble peaked during the period when numbers of Turnstones within the study area were at their highest (1989-90 and 1990-91, Figure 5.2). These changes in distribution concur with Figure 5.3 and 5.4 which showed how numbers at Amble rose disproportionately to those at other sites

while the total in the study area as a whole increased through the three-year study period.

5.3.1.3 Turnstone numbers at Amble and Hauxley in relation to wrack deposits

In order to determine whether the availability of wrack deposits (used for feeding over the high water period) affected the numbers of Turnstones at a site, the data obtained at high water at Amble and Hauxley were regressed against the amount of wrack deposited along the high water mark (m/km). High water counts and estimates of wrack deposits were collected over the 1997-98 and 1998-99 winters (October-March) on 22 dates at Amble and 26 dates at Hauxley. There was no significant relationship between wrack deposits and Turnstone numbers at either Amble (r = 0.09, d.f. = 21, F = 0.16) or Hauxley (r = 0.225, d.f. = 25, F = 1.27). However, data was not collected on the age of wrack deposits, which is probably of greater importance in determining their attractiveness to Turnstones.

5.3.2 Turnstone behaviour and foraging substrate use over the tidal cycle

5.3.2.1 Substrate choice

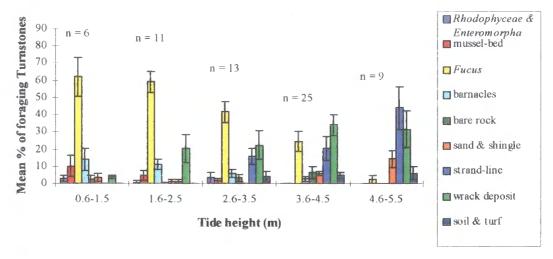
Figure 5.12 shows the change in substrate use over the tidal cycle by Turnstones at each of the six rocky shore sites. At five of the six rocky shore sites, Turnstones showed an approximately similar use of substrates. Towards low water, a large proportion of foraging was amongst live *Fucus* beds, with fewer birds feeding on *Enteromorpha* and Rhodophyta beds (especially at Cresswell) and on mussels. At higher tidal heights areas of algal growth become covered by the tide and so Turnstones moved to feed upon other resources. At some sites, most notably Hauxley and St. Mary's Island, feeding over high water was mainly upon the large aggregations of detached wrack classified as "wrack deposits". At others, Turnstones foraged among smaller amounts of *Fucus*, *Laminaria* and other detritus thrown up on the tideline in small patches and clumps ("strandline").

Turnstones at Blyth favoured markedly different substrates from those at the other five sites. The scarcity of *Fucus* beds on the North Blyth intertidal area (Chapter 2) meant that foraging on *Fucus*-covered rocks was correspondingly low. At low water, Turnstone foraged heavily upon mussel-beds, with barnacle-covered and bare rock being utilised at mid-tidal levels. At higher tidal levels the proportion of Turnstones foraging upon *Fucus* was higher, and at high water almost all foraging was upon *Fucus*. This foraging was not observed at North Blyth, where all the intertidal area was covered at tidal heights below approximately 4.2 m O.D, but on the shore of the Blyth Estuary near North Side Staithes, the principal Turnstone roost site. Although the vast majority of Turnstones foraging at Blyth over high tide were on *Fucus*, the actual number and proportion of total birds present was very small, as most birds roosted over this period (see Figure 5.14).

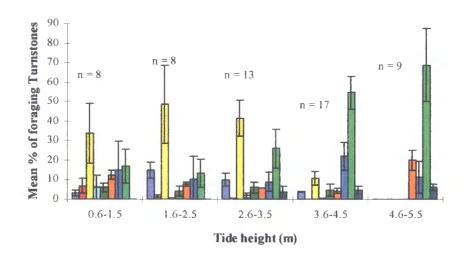
Figure 5.13 shows the position of Turnstones relative to the tide's edge while foraging on three different substrates (data from all sites combined). Turnstones feeding on mussels-beds kept close to the tide's edge, with 66% of birds within 5 m. Similarly, of Turnstones recorded feeding upon wrack deposits 47% were

Figure 5.12: Choice of foraging substrate by Turnstones at different tidal states

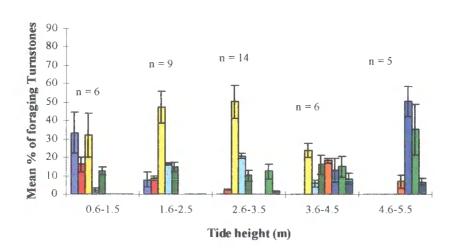
a) Amble, n = days of observation



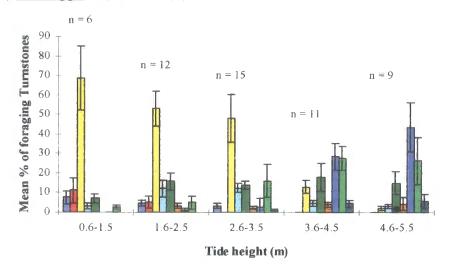
b) Hauxley (legend as for (a))



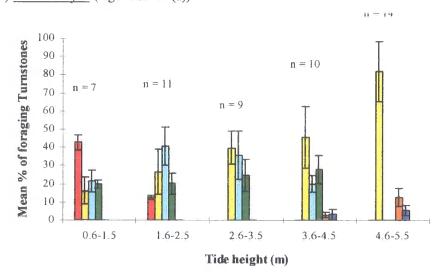
c) Cresswell (legend as for (a))



d) Newbiggin (legend as for (a))



e) North Blyth (legend as for (a))



f) St. Mary's Island (legend as for (a))

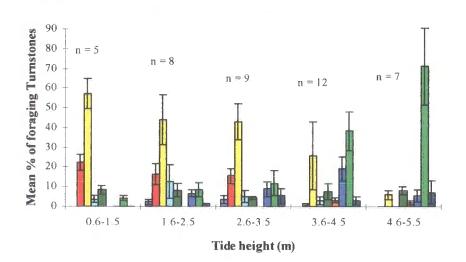
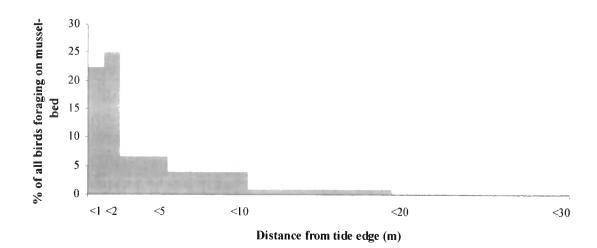
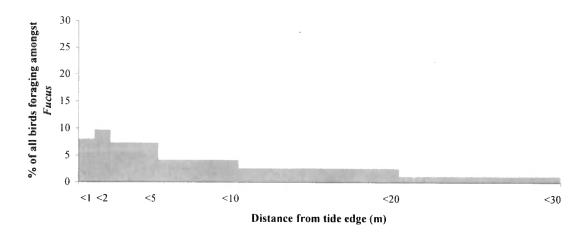


Figure 5.13: Location relative to the tide's edge of Turnstones foraging on the three main substrates; all rocky shore sites, Oct-Mar

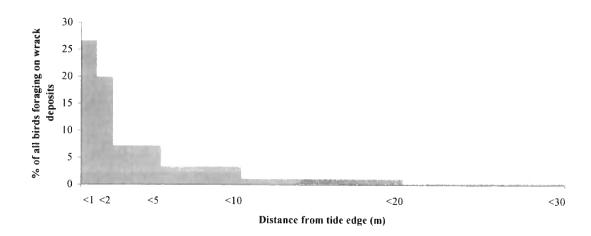
a) mussel-bed



b) Fucus



c) wrack deposits



within 2 m and 69% within 5 m of the tide's edge. However, birds foraging upon *Fucus* beds were much more evenly distributed across the intertidal area, with only 38% within 5 m of the tide's edge.

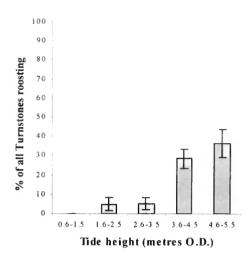
The proportion of birds feeding over the tidal cycle was compared to determine whether birds at some sites had to feed for longer than birds at others. Figure 5.14 shows the percentage of birds roosting in five tidal height categories at each rocky shore site. There was no significant difference between the six rocky shore sites in the pattern of roosting over all five categories of tidal height (Scheirer-Ray-Hare test, $\chi^2 = 7.45$, d.f. = 5, not significant). When the mean proportions of Turnstones roosting at each of the six sites were compared for each tidal category separately, there was no significant difference in four categories (Kruskall-Wallis: 0.6-1.5 m O.D., $\chi^2 = 5.5$, d.f. = 4, 1.6-2.5 m O.D., $\chi^2 = 5.72$, d.f. = 4, 2.6-3.5 m O.D. $\chi^2 = 6.21$, d.f. = 4, 3.6-4.5 m O.D. $\chi^2 = 6.21$, d.f. = 4). However, at the highest tidal category (4.6-5.5 m O.D.) there was a significant difference in the proportion of Turnstones roosting between sites (Kruskall-Wallis, $\chi^2 = 6.21$, d.f. = 4, P < 0.05). At this tidal height category, a mean of 97% of Turnstones at Blyth were roosting; a far greater proportion than at the five other sites (between 40 and 55%).

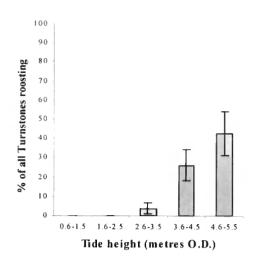
Blyth is different from the other five rocky shore sites, in that there are few opportunities for feeding over high water due to the removal of upper shore levels with sea defences. The low proportion of birds feeding over high water at that site is due to the lack of feeding opportunities, and may be compensated for by more feeding at other stages of the tide. The pattern of roosting over the tidal cycle is shown in Figure 5.15 using time, rather than tide height categories. Data from Newbiggin and St. Mary's Island have not been included as fewer observations were made at these two sites. The difference in behaviour at Blyth compared to the other three sites is obvious, with a far higher percentage of roosting Turnstones at high tide. However fewer birds roosted on the rising tide, suggesting that Turnstones at Blyth compensated for the lack of foraging opportunities at high water by feeding for longer beforehand.

Figure 5.14: % of Turnstones roosting at different tide heights at six study sites

a) Amble

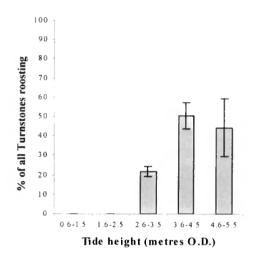
b) Hauxley

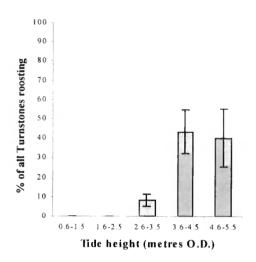




c) Cresswell

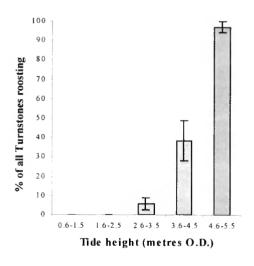
d) Newbiggin





e) Blyth

f) St. Mary's Island



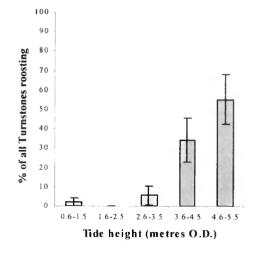
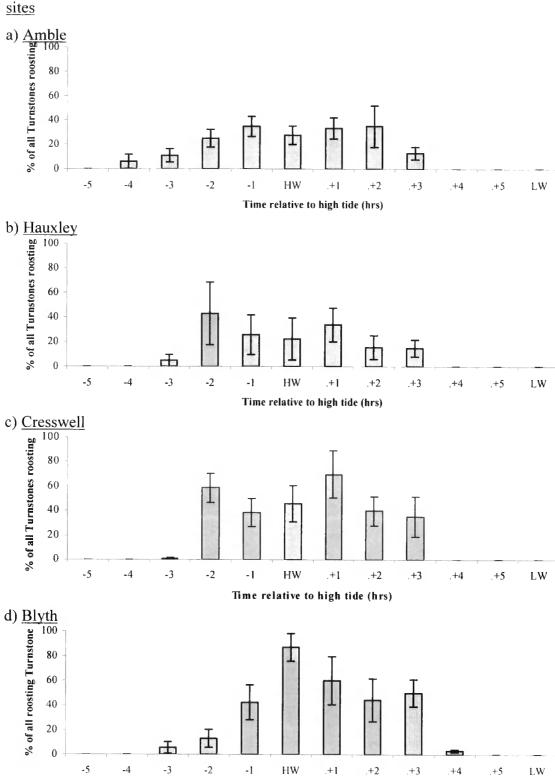
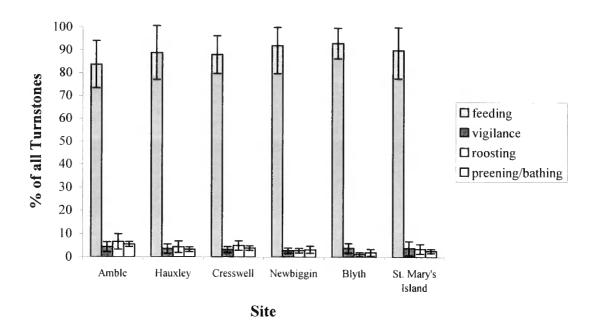


Figure 5.15: Changes in the % of Turnstones roosting over the tidal cycle at four sites



Time relative to high tide (hrs)

Figure 5.16: Low water (below 3.7 m O.D.) behaviour of Turnstones at the six rocky shore sites



The behaviour of birds over low water was examined to see if Turnstones at Blyth compensated for the lack of high water feeding by reducing the time engaged in non-foraging behaviours over low water. Figure 5.16 compares the behaviour of Turnstones over low water at the six rocky shore sites. There was no significant difference in the proportions of the Turnstones at each site engaged in the four behavioural categories recorded (Scheirer-Ray-Hare test, $\chi^2 = 4.11$, d.f. = 5, not significant), with the vast majority of Turnstone time being spent foraging. However, it is noticeable that the highest proportion of feeding Turnstones was at Blyth, the site with the highest proportion at roosting birds at high water (Figure 5.14d), while the lowest proportion was at Amble, the site with the lowest proportion of roosting birds at high water (Figure 5.14a).

5.3.3 Turnstone faecal samples

A total of 45 Turnstone faeces were collected and examined; the contents are summarised in Table 5.2

Table 5.2: Contents of Turnstone faeces

Site	Date	Tide	Main contents	Also present
North Blyth	15/12/97	Low	Mussel	Nucella
n = 6			Barnacle	lapillus
			Littorinid	Hyale nilssoni
Newbiggin	13/1/98	High (roost)	Crab	Barnacle
n = 5				
Hauxley	13/1/98	High (roost)	Littorinid	
n = 5			Crab	
Hauxley	22/2/98	High	Few hard	Beetle
n = 6	1 1	(feeding)	parts	
	!		Talitrus	
			saltator	
Amble	2/12/97	Low	Gammarus	Crab
n = 11			Barnacle	
	,	1	Littorinid	
			Mussel	
Amble	24/2/98	High (roost)	Barnacle	Littorinid
n = 7			Mussel	1
			Talitrus	,
		i	saltator	
Amble	24/2/98	High	Few hard	Crab
n=5		(feeding)	parts	
			Talitrus	
			saltator	

5.3.4 Observations of feeding Turnstones

Coquet Estuary

During the winter, the few Turnstones in the Coquet Estuary fed predominantly amongst *Fucus* for unidentified prey. The larger numbers present in late summer and early autumn foraged by vigorously overturning the *Enteromorpha* which

covered a large proportion of the mudflats and appeared to feed on invertebrates within or just below this algal mat.

Rocky shore sites - low water

Turnstones fed on all available substrates in the intertidal zone (Figure 5.12). Away from areas of algal growth, Turnstones were observed feeding on mussels, taking small individuals whole but occasionally probing apart the valves of larger specimens to extract the flesh. Birds on barnacle-covered rock fed on either the barnacle themselves, forcefully chipping them off the rock, or small prey items in rock crevices, probably including littorinids and *N. lapillus*. Turnstones pecked at small prey items on bare rock and amongst areas of Rhodophyta growth. Unlike Purple Sandpipers, feeding in rock pools was rarely observed. Foraging on wrack beds was vigorous, with birds using the bill, head and chest to overturn fronds. Searching for prey amongst *Fucus* appeared to be visual. Most prey items were swallowed whole, but birds were sometimes observed extracting the flesh from large littorinids, and larger shore crabs (up to approximately 4 cm carapace width) were often carried to an area of open rock where they were given a few heavy blows with the bill before being placed upside down and eaten.

Rocky shore sites - high water

As Figure 5.12 shows, the majority of birds feeding at high water did so either on large concentrations of wrack deposited on the high water mark, or on smaller amounts of debris along the tide's edge. Feeding on the former was energetic, with birds "ploughing" through decomposing wrack, overturning it in order to feed upon *Coleopa frigida* larvae. Some individuals would also peck (often in mid-air) at adult *Coleopa*. Decomposing carcasses of fish, crabs and birds were often found amongst these wrack deposits, and often attracted several Turnstones at a time to feed upon the flesh. Birds feeding amongst the debris on the tide's edge would peck at small prey items amongst the surf, often running in and out of the waves in a manner reminiscent of Sanderling (*Calidris alba*).

Turnstones would frequently be seen on the quaysides at Amble and Blyth during high water. These birds were observed feeding upon gull-droppings, fish scraps discarded by fishermen and even chips and bread fed to the gulls and Eiders (*Somateria mollissima*) by tourists.

Birds were observed foraging inland at all sites except Blyth. The favoured habitat was short grass, which was found in pasture at Cresswell and Hauxley, on the golf courses at St. Mary's Island and Newbiggin and the playing fields at Amble. Birds here probed in the turf, presumably for larvae (e.g. Tipulid larvae) and also for earthworms. At Amble up to 110 birds were observed feeding in ploughed fields sown with Winter Wheat in both the 1997-98 and 1998-99 winters up until the crop was several centimetres high. Unlike feeding on turf, birds fed in these arable fields in dry weather conditions.

Although Turnstones roosted inland, on the water's edge at Cresswell Pond and Hauxley Nature reserve, feeding was very rarely seen at these sites; occasionally birds would snap at flying insects along the waterline.

5.4 Discussion

5.4.1 The distribution and overall numbers of Turnstones

The number of Turnstones present within the south Northumberland study area varied between the three winters of study. In addition, WeBS counts for the winters 1985-86 to 1994-95 also showed considerable variation in the mean count between years. However, although the mean numbers of Turnstones in the study area varied nearly two-fold between different winters within the 1985-99 period, the differences between successive years were much smaller. The greatest increase in mean winter count between successive years was 31%, between 1985-86 and 1986-87, while the greatest decrease was one of 29% between 1990-91 and 1991-92. The mean variation between successive winters was 15% for the period covered by WeBS data and 13% between the three winters of this study.

Large between-year variations in numbers should not be expected in a species, such as Turnstone, that shows high site fidelity between years, low mortality, and is not prone to relocating during hard weather. There are four possible causes of the changes in the number of wintering birds:

- 1. A change in the fidelity of wintering birds, with birds that had wintered in south Northumberland in previous years moving out of the study area, or contrarily, birds from other sites moving to winter within the study area.
- 2. A change in the mortality of adults, with unusually low or high annual mortality at any point during the life history resulting in higher or lower numbers (respectively) returning to the study area in the following autumn.
- 3. A change in breeding success, with fluctuations in wintering numbers being caused by variation in the number of first-year birds arriving in south Northumberland in the autumn.
- 4. A change in settlement in the study area by first-year birds, with a varying level of recruitment into the wintering population from year to year.

Previous studies have found both high fidelity and low mortality in British Turnstones (Whitfield 1985a, Burton 1995) which would suggest that 1) and 2) above are unlikely to be the cause of between year variations, unless Turnstones within the study area differ from those in previous studies. The colour-ringing research described in Chapter 7 provides information on the fidelity and mortality of Turnstones within the south Northumberland study area and so further discussion of the between year variation in mean winter number can be found in that chapter.

There was no obvious trend in numbers over the period counts are available for (1985-86 to 1998-99), although the considerable between-year variations could mask all but the most significant changes in abundance. Recent national surveys

have suggested a sizeable decline in Turnstone numbers around most of the British coast (Rehfisch et al. 1999). Preliminary analysis of results from the nonestuarine wader survey (NEWS) conducted over the 1997-98 winter has revealed Turnstone declines in many British counties, compared with the counts made for the 1984-85 Winter Shorebird Count (Moser & Summers 1987). Declines of over 50% were recorded in Cornwall, Devon, Cumbria, Dyfed, Gwynedd, Dumfries & Galloway, Highland Region, Grampian, Fife and Lothian, with for example the last two counties showing declines of 79% and 82% respectively. A decline in the number of Turnstones in Northumberland of 46% was found between the two surveys. The WeBS counts illustrated in Figure 5.2 do not show a decline of this magnitude. As was mentioned in Chapter 4, there was no significant decline in Purple Sandpiper numbers in south Northumberland between 1985-86 and 1998-99, but the comparison of the 1984-85 and 1997-98 BTO surveys found a decline of 38% in the region. For both species the declines in Northumberland found by the 1997-98 survey appear to be the result of short-term fluctuations in numbers, and possibly of counting inaccuracy. Although it seems extremely likely that the results of the non-estuarine wader survey do in fact represent an actual national decline in numbers, the numbers of Turnstones in Northumberland appear to be unaffected. This discrepancy must also cast doubt of the validity of the magnitude of declines in other counties.

As well as variation in numbers between years, there were fluctuations in Turnstone numbers within winters, such as the peak of 516 in January 1999. As stated previously, Turnstones are not prone to making hard weather movements. This is probably because Turnstones feed primarily upon invertebrates on rocky shores that are unable to retreat into the substrate during periods of cold weather. However, the ability of Turnstones to forage may be affected by winter storms. Figure 5.13 shows how Turnstones foraging on both mussel-beds over low water and wrack deposits over high water fed close to the tide's edge. On mussel-beds this habit gives the advantage of feeding on wetted substrate with higher invertebrate activity, while wrack deposits near the tide's edge are disturbed by wave action that exposes invertebrates within the deposit. In stormy weather, Turnstones feeding close to the tide's edge have to spend a considerable amount of time avoiding incoming waves. While this may not be prohibitively expensive

in terms of energy expenditure (Bruinzeel *et al.* 1999), the foraging time lost could be considerable. In stormy conditions, Turnstones frequently moved to feed on inland sites. It is not known whether this was because of a decline in the profitability of foraging in the intertidal area, or opportunistic exploitation of improved feeding conditions inland, as heavy rain caused earthworms to move nearer the ground surface.

The availability of rocky shore invertebrates remains relatively constant in periods of cold weather (compared to those utilised by shorebirds of soft substrates (Goss-Custard 1970)), which means that shorebirds that forage upon rocky shores have a reliable food resource and a much lower risk of starvation during winter than other waders. However, Turnstones at five of the six rocky shore sites in the study area spent a considerable amount of time foraging on wrack deposits on the high water mark. For example, at Amble 38% of all foraging was spent either on wrack deposits or strand-line debris. These foraging habitats are very ephemeral; large and prey-rich concentrations of wrack can be deposited or removed over the course of one high tide; in the 1998-99 winter there was a period of over five weeks in which there were no substantial deposits of wrack on the foreshore at Amble or Hauxley, whereas before and after this period, both sites had very large areas of rotting seaweed rich in invertebrates. No significant relationship was found between the numbers of birds at Amble and Hauxley and the amount of wrack deposited on the upper foreshore. It is likely that such a relationship did exist; at all sites except Blyth the largest high water Turnstone counts coincided with periods when large and food-rich wrack deposits were present. The method of measuring wrack deposits (m of wrack deposits over 50 cm per km) may not have been a suitable measure of the attractiveness of these deposits to Turnstones as it does not reflect the invertebrate prey they contained which was primarily determined by the age of the deposit.

The results of the colour-ringing study (Chapter 7) indicate that Turnstones do travel between sites to exploit wrack deposits. Fluctuations in numbers within the study area were probably due to birds moving in and out of the area in order to feed at sites immediately to the north and south. In particular it is known that

birds moved to and from Boulmer, a rocky shore site 7 km north of Amble which sometimes held over 200 Turnstones. In late January 1999, when numbers in the study area peaked at 516, Amble had 140 Turnstones feeding on wrack at high water. These numbers included birds usually resident at Boulmer that had moved to Amble to feed and also birds usually resident on Coquet Island (see Chapter 7). Similar fluctuations in numbers also occurred at St. Mary's Island and probably involved birds that normally fed and roosted to the south of the study area.

5.4.2. Turnstone distribution within the study area

Turnstones in the south Northumberland study area showed a number of changes in distribution over both the daily tidal cycle and the longer spring-neap cycle. A number of these differences were probably (at least in part) due to counting inaccuracy, particularly in counting birds at low water at sites such as Hauxley with large areas of *Fucus*-covered intertidal rocks. However, other changes in Turnstone numbers were clearly due to birds moving between sites. For example, the number of Turnstones at Hauxley during high water was lower on spring tides than neap tides as some individuals moved north to Amble (this supposition was confirmed by observations of colour-marked individuals, Chapter 7). This may have been because Amble had a greater area at upper tidal levels that was suitable for feeding and roosting upon during spring high tides. Although Turnstones at Hauxley would use the islands in the freshwater pools on the Nature Reserve to roost, for an unknown reason they rarely did so during midwinter.

Two major seasonal changes were found in the distribution of Turnstone within the study area. Few birds summered at Amble and Cresswell, while a large proportion of the study area total (nearly 40%) were found at Hauxley. This disparity suggests that either that Turnstones that wintered at Hauxley were more likely to remain at Hauxley over the following summer, or that birds that had wintered elsewhere moved to Hauxley during the summer. This question was answered by the colour-ringing studies in Chapter 7 and is discussed in detail in that chapter.

The other notable change in the distribution of Turnstones within the study area was the peak in the proportion at Blyth in early autumn (August-September) comprising of birds that were feeding within the Blyth Estuary and roosting on the North Side Staithes. This peak in estuary-feeding birds was also shown by counts on the Coquet (Figure 5.10) and Wansbeck Estuaries. No colour-ringed birds were seen in the Coquet Estuary during August, despite the fact that in both 1998 and 1999 birds ringed in the previous winter(s) had returned to Amble by this time (see Chapter 7). This finding strongly suggests that the birds in Coquet Estuary, and probably those in the Wansbeck and Blyth, were not locallyresident birds but passage migrants. Whitfield (1985a) noticed influxes of migrant Turnstones through his Lothian (non-estuarine) study site in early August and Burton (1995) believed high numbers of Turnstones at Hartlepool in September to include passage birds. Migrants during this period may be either birds from the Fenno-Scandinavian and West Russian breeding population which pass through Britain en route to wintering grounds in West Africa, or birds from the Nearctic breeding population that winters in Britain (Cramp & Simmons 1983). The European breeding population passes through Britain on autumn migration, but in spring, most birds take a route through continental Europe (Branson et al. 1978). It could be that this population was the source of birds using estuaries in the study area in the autumn, as return passage through the Coquet or Blyth Estuaries in the spring was much lighter.

Figure 5.11 illustrates the significant change in the distribution of Turnstone within the study area during the period spanned by available WeBS counts. There was a significant reduction in the numbers of Turnstones wintering at the two WeBS count sections in the southern part of the study area, and an increase in the two northern sections. Purple Sandpipers also declined at St. Mary's Island over this period. The explanation proffered for their decline may also be true for Turnstones; increased public recreational use of this area has increased disturbance to birds and may have caused birds to leave to winter elsewhere, or deterred first-year birds from settling in the autumn. Birds moving away from St. Mary's Island may have been the cause of the increase in Turnstone numbers wintering in the two sections in the northern part of the study area. The decline in numbers at Blyth is less readily explainable. It is possible that there is a

connection with the construction of nine large wind turbines along the East Pier at Blyth in late 1992, but the decline in Turnstone numbers at Blyth was already ongoing by this time. Little (1996) detected no significant adverse effects from the turbines on the Purple Sandpipers that roost on the pier immediately next to them, so it is unlikely Turnstones were affected.

5.4.3 Turnstone foraging behaviour

As would be expected for a shorebird that feeds on rocky shores, a highly stratified habitat, the substrate that Turnstones foraged upon varied over the tidal cycle. Turnstones at five of the six rocky shore sites within the study area exhibited broadly similar habitat preferences, but birds at Blyth displayed considerable differences in foraging behaviour (see below). At low tidal states (those below neap low tide, and so not available for foraging on all low tides) a small proportion of birds foraged amongst Rhodophyta. Other substrates used by foraging Turnstones over low water included *Enteromorpha*, bare and barnacle covered rock, and between 6% (Hauxley) and 22% (St. Mary's Island) of birds foraged on mussel-beds. However, the majority of foraging observations at low tidal heights were of Turnstones feeding amongst *Fucus* beds; at all five sites, this substrate was the most heavily used type in the lowest three tide height categories.

At low water very few Turnstones were observed feeding on wrack deposits, although on a few occasions a small number of birds (<30) were observed foraging on such deposits throughout the tidal cycle. More birds would move on to wrack deposits on the rising tide as other feeding substrates were covered, and the deposits themselves may have become better feeding sites as they became disturbed by incoming waves, which would have exposed more invertebrates buried within the deposits. Even without this tidal disturbance, wrack deposits were extremely rich in suitable prey. Although no attempt was made to measure intake rates of foraging on different substrates it may well have been that foraging on wrack deposits offered the highest rates of energy intake for these birds. Dierschke (1994) found that rates of energy intake for Purple Sandpipers

feeding on deposited wrack were higher, at 16.8W, than for birds foraging in any other habitat; mussel-beds, for example, only provided 5.5W.

That Turnstones did not forage on wrack deposits throughout the tidal cycle may be due to disturbance from humans; lower shore areas received much less disturbance from walkers and dogs than the upper levels of sandy beaches where wrack was deposited. In addition, the risk of predation from raptors was probably greater for birds feeding higher on the shore. This may be a significant cause of mortality for Turnstones wintering in Britain (Whitfield 1985a & b). At all six rocky shore sites within the study area higher shore areas gave reduced visibility due to the proximity of seawalls, dunes and low cliffs. Birds foraging on the upper shore were probably more likely to be caught by raptors, particularly Sparrowhawks *Accipiter nisus* and Merlins *Falco columbarius*, which frequently hunted by flying low behind the dunes at the top of beaches before "flipping" over to catch by surprise the birds feeding below. In addition to experiencing a higher risk of mortality, birds feeding on the upper beach probably lost more foraging time to vigilance. Metcalfe (1984) found that Turnstones feeding in areas with reduced visibility increased the duration of vigilance scans.

Wrack deposits are a rich source of invertebrate prey utilised by Turnstones, other shorebirds and a wide range of other birds. In south Northumberland birds regularly found feeding upon wrack deposits included Purple Sandpipers, Dunlin Calidris alpina, Sanderling C. alba, Redshank, Oystercatcher Haematopus ostralegus, Gulls Larus spp., Meadow and Rock Pipits Anthus pratensis and A. petrosus, Pied Wagtails Motacilla alba and Starlings Sturnus vulgaris. Wrack deposits are formed when strong wave action during storms detach macroalgae, principally Fucus and Laminaria, from intertidal and near sub-tidal rocks. If tide and wind conditions are suitable wrack is deposited along the high tide mark, sometimes in large amounts. In Northumberland wrack deposits would attract large number of adult wrack flies, Coelopa frigida, followed within days by an abundance of larvae. In addition, sand-hoppers Talitrus saltator would be abundant amongst the wrack and in the sand around and underneath deposits. Concentrations of T. saltator, and to a lesser extent C. frigida, would sometimes

persist in the sand for several days after a wrack deposit had been removed by tidal action and continue to attract Turnstones to feed over high water.

Feeding on turf was very dependant on weather conditions, and was either observed during very stormy conditions when beach feeding became too difficult for birds (particularly on spring high tides), or after periods of heavy rain. After such rain, large numbers of Turnstones could be observed upon areas such as St. Mary's and Newbiggin Golf Courses and the pasture around Cresswell Pond feeding on earthworms along with large numbers of Oystercatchers, Redshanks, Dunlin and other shorebirds. This example shows the frequently opportunistic nature of Turnstones; other observations included birds feeding on dead fish (both on beaches and in Amble and Blyth Harbours), dead birds, on gull droppings and even on chips thrown to the birds by tourists in Amble Harbour.

The analysis of faecal samples, while not intended to be comprehensive or quantitative, gave a rough picture of Turnstone diet within the study region. Further information was gained by observing foraging birds and noting both prey items and foraging methods. At low water, Turnstone foraged upon small mussels *M. edulis*, taken whole, and larger individuals which were prised open and the flesh extracted. Barnacles *Balanus* sp. were hammered off rocks. However the largest proportion of time was spent foraging amongst *Fucus*, taking littorinids, crabs and other crustaceans such as *Gammarus* sp.

5.4.4 Variation in Turnstone behaviour between the six rocky shore sites

At five of the six rocky shore study sites the mean proportion of Turnstones roosting over high water peaked between 38% (Amble) and 53% (St. Mary's Island). However, at Blyth nearly all Turnstones roosted at high water. At high tide, none of the North Blyth foreshore is left exposed due to the sea wall, which has removed the upper tidal levels.

The sea wall at North Blyth also means there is nowhere for detached wrack to be deposited. The nearest sandy shore with intact upper tidal levels is immediately to the north of North Blyth. However, due to the prevailing north-

to-south current along the Northumberland coast, and the wind direction during winter storms (usually northerly), wrack deposits in the south Northumberland study area are invariably deposited to the south of the intertidal rock and offshore scars that the *Fucus* and *Laminaria* originate from. In the case of North Blyth, this detached wrack is dispersed into the bay south of the harbour mouth and probably cast up, thinly dispersed, along South Blyth Beach. Therefore there are no wrack deposits – the major substrate for high water foraging at the other south Northumberland sites – at North Blyth.

Although Turnstones at Blyth did very little feeding around the time of high tide, (see Figure 5.12) a relatively small proportion of the Turnstones at Blyth roosted during the period of rising tide. It appears that birds compensated for the lack of feeding opportunities at Blyth at high tidal heights by feeding for longer before going to roost. Although pre-roosts were seen on the North Blyth foreshore, most birds would continue feeding until pushed off by the rising tide, and then move to feed on the shore inside the estuary opposite the roost site. This strategy did not, however, entirely compensate for the loss of feeding time over high water; Turnstones at Blyth spent 25% of the tidal cycle roosting, compared with between 15 and 21% at the other rocky shore sites.

There was no significant difference between the behaviour of Turnstones at the six rocky shore sites in behaviour at low water. Although not significant, it was noticeable that the greatest mean proportion of feeding birds was at Blyth, the site with the lowest proportion of feeding birds at high water. This observation suggests that the lack of feeding opportunities at high water caused Turnstones at Blyth to compensate by spending less time engaged in other activities over low water. In addition, there was a difference in the foraging substrates utilised by Turnstones at Blyth over low water. These birds spent less time foraging on Fucus beds than Turnstones at other sites (less then half the % of some sites) and more time foraging on mussel-beds and, most noticeably, more time on bare and barnacle-covered rocks than at other sites. This change in foraging habitat may have been due to the relative scarcity of Fucus growth at Blyth (only 6% of intertidal area). The relative profitability of foraging on the substrate types is not known.

Turnstones feeding on substrates such as mussel-beds and bare and barnacle-covered rock appeared to do so in a more tactile manner than those individuals foraging amongst *Fucus*, which obviously relied upon visually detecting prey items. Feeding by touch may mean that, although Turnstones at Blyth may not be able to feed as long through the tidal cycle as birds elsewhere, and a smaller area of the preferred substrate to feed upon, they may be able to compensate by having more substrate that is suitable for night-time foraging using touch.

To summarise, there seems to be a significant difference in the foraging behaviour of Turnstones at Blyth compared to the other rocky shore sites within the south Northumberland study area. Due to the sea defences at North Blyth, there are few opportunities for Turnstones to forage at high water and in particular, nowhere for detached wrack to be deposited; at other sites this resource provides valuable foraging for Turnstones over high water. Therefore nearly all Turnstones at Blyth roost over high water. This loss of foraging time is compensated for to a certain extent by more foraging on the rising tide, with fewer Turnstones pre-roosting than at the other sites.

5.4.5 Summary

The monitoring of Turnstones revealed several fluctuations in numbers and distribution, both over the high-low and spring-neap tidal cycles, seasonally and annually.

The aim of the colour-ringing and radio-tagging conducted during this study, and described in Chapter 7, was to find evidence for variation in the behaviour between individual Turnstones within the south Northumberland population. However, even without studying individual birds, such differences have been detected, as birds wintering at Blyth showed a distinctly different pattern over the tidal cycle than Turnstones at other sites. Over low water, birds at Blyth spent a higher proportion of time foraging on bare and barnacle-covered rock and on mussel-beds than at other sites. At high water very few birds foraged at Blyth – on neap high tides a few would forage on *Fucus* inside the Blyth Estuary – as all intertidal areas on the foreshore were submerged. Due to the topography of the

foreshore detached wrack was not deposited along the high water mark at Blyth; this substrate was very important for foraging Turnstones at the other five rocky shore sites.

Monitoring programs should aim to either encompass all variation in counts due to tidal and seasonal variation, or to control for this variation by only counting under fixed conditions i.e. spring high waters during mid-winter. However, this second approach may not detect some changes in the use of an area by a population of birds that, for example, may still use the same roost sites at high water but move to different feeding areas at low water, or show a change in the use of a site only in certain seasons. The monitoring program describe in this chapter has encompassed all scales of temporal variation, and hence should be sufficient to reveal any changes in the use of the study area by Turnstones that may occur.

Chapter 6

Individual variation in the behaviour and site and habitat use of Purple Sandpipers

6.1 Introduction

6.1.1 Individual variation in behaviour

The approach of investigating ecology and behaviour at a population or sub-population level (in effect, to measure the *average* ecology and behaviour for a number of individuals) can be misleading. Variation within populations can be significant, with individual birds utilizing different strategies in both the breeding and non-breeding seasons. In recent years it has become apparent to many researchers that knowledge of how the behaviour of individual organisms within a population varies is vital to the understanding of population processes and to the ability to make predictions of the impact of environmental changes on populations (see Goss-Custard 1996, Sutherland 1996).

Variation in foraging strategy between individual birds has been detected in a number of shorebird species. Most notably, Oystercatchers have been shown to exhibit considerable specialisation in diet, both in prey selection (Goss-Custard & Sutherland 1984, Hulscher & Ens 1991) and in the foraging methods used to take these prey (Hulscher 1997). This high degree of specialisation may be unusual, possibly due to the technical difficulty of handling their prey species (Sutherland *et al.* 1997). Alternatively, this degree of individual specialisation may not be rare amongst birds and other taxa, but in most cases has simply not been researched. Amongst shorebirds, variations in foraging strategy have also been found between individual Grey Plovers (*Pluvialis squatarola*) (Turpie 1995), Turnstones (Whitfield 1985, 1990) and Curlews (*Numenius arquata*) (Ens & Zwarts 1980).

Two studies have previously looked for individual variation in the behaviour of wintering Purple Sandpipers. Summers *et al.* (1990a) found differences in diet between male and female Purple Sandpipers at several Scottish sites, with larger females selecting larger prey than the smaller males, although both took the same species. Burton (1995) studied colour-ringed Purple Sandpipers at Hartlepool, Cleveland and found that the social status of individual birds influenced their behaviour both on the low water feeding areas and at the roost site.

This chapter presents the results of colour-ringing and radio-tagging studies on individual Purple Sandpipers. The aim was to discover what (if any) variation occurred between individual birds in their choice of foraging habitat, time budgets and site use (in particular, the movements between rocky shore sites and fidelity to favoured feeding sites) within the south Northumberland study area.

An attempt was made to relate the behaviour of individual birds to phenotype – sex, race, age and size – in order to look for the mechanism(s) controlling behaviour. Purple Sandpipers show a high degree of sexual size dimorphism, as well as size variation between the different breeding populations, and hence exhibit a larger size range than most shorebirds. Whether competitive displacement on the wintering grounds was the cause for the evolution of this sexual dimorphism is not known (Summers *et al.* 1990a). Regardless of how and where this size difference arose, it gives the opportunity for considerable variation in the prey taken by individual Purple Sandpipers during the winter and therefore in the time budgets, habitat selection and site use by these individuals.

Variation in the behaviour of wintering Purple Sandpipers may be due to niche differentiation based on bird size. Alternatively, it may be caused by the competitive exclusion by dominant birds of subordinate birds to suboptimal feeding areas or strategies. Burton (1995) and Burton & Evans (2001) found that larger Purple Sandpipers were dominant over smaller birds, and to a lesser extent adults were dominant over first-years. Social status influenced behaviour, with, for example, dominant birds occupying the best (most sheltered) positions at the roost site.

The use of some rocky shore sites may provide greater fitness benefits to Purple Sandpipers than others. Therefore, as discussed in Chapter 2, Purple Sandpipers arriving in the autumn seek to settle at the site that offers the highest probability of surviving the winter and departing in good condition in the spring, and seek to utilise the best food resources at that site. However, not all individuals can feed at the most optimal sites, and thus some individuals may choose to feed at other sites with lower food density but less competition, or to switch to a different feeding strategy such as taking different prey species (e.g. Goss-Custard 1977a, 1977b).

If there is a differing pay-off between different behavioural strategies then we might expect to find dominant birds utilising the best wintering strategies and subordinate birds forced to use suboptimal strategies. Alternatively, if all strategies have an equal pay-off, birds distribute themselves regardless of social status. The benefits of differing strategies are not simply determined by food intake, as factors such as the availability of roost sites and, in particular, the risk of predation (Dierschke 1998), may also be important.

6.1.2 Site fidelity and mortality

By observing colour-ringed Purple Sandpipers over three winters, it was possible to calculate the minimum annual survival rate and the site fidelity between winters of Purple Sandpipers in the study area. A change in mortality on migration or during breeding might affect the numbers of Purple Sandpipers returning to Northumberland in the autumn, leading to a decrease in wintering numbers unrelated to conditions within the study area. Care must be taken, however, to distinguish (if possible) between birds not returning to the study area and those that do, but do not settle over the winter. The movement away from the study area by birds that had previously wintered may be an indication of an unfavourable change in conditions. Observations of such birds might be made in the autumn, but not later in the winter.

6.1.3 Nocturnal behaviour

The vast majority of research upon shorebirds has concentrated on diurnal behaviour, as there are obvious difficulties with conducting night-time research. However, night-time feeding may be an important part of the ecology of many shorebird species, and recently more researchers have concentrated on documenting nocturnal behaviour. In particular in mid-winter, when daylight hours restrict daylight feeding time (when high tide falls around noon intertidal areas can be exposed for as little as two or three daylight hours) nocturnal feeding can greatly increase the opportunity for food intake.

McNeil *et al.* (1992) hypothesised that night-feeding by shorebirds was either "supplementary" (being done to supplement more important day-feeding) or "preferred" (night-feeding was preferred to day-feeding). This approach was expanded by Sitters (2000) to encompass five hypotheses: a preference for day-feeding, a preference for night-feeding (both with the alternative minimised), indifference with both being utilised equally, feeding whenever possible, or feeding spread between day and night in order to avoid peaks of body weight.

It was originally thought that Purple Sandpipers did not feed at night (Feare 1966), and more recent research into foraging behaviour (McKee 1982, Dierschke 1994) and diet (Summers *et al.* 1990a) did not investigate night-feeding. However Strann & Summers (1990) recognised that feeding at night must be more important than day-time feeding for Purple Sandpipers in Northern Norway, particularly in mid-winter. Summers (1994) radio-tagged a single individual on the Isle of May, Fife and confirmed that this bird was feeding over low water during the night.

Accurate comparisons of the relative profitability of night-time foraging are difficult to make, but in some cases shorebirds have been found to forage as much at night as during the day. McCurdy *et al.* (1997) found the density of droppings deposited by Semipalmated Sandpipers *Calidris pusilla* was not significantly different during day and night, suggesting that nocturnal foraging

may have provided a prey intake comparable to diurnal foraging. However, Piping Plovers *Charadrius melodus* breeding in New Jersey had a lower peck rate when foraging at night (Staine & Burger 1994), as did Grey Plover and Whimbrel *Numenius phaeopus* wintering in South Africa (Turpie & Hockey 1993). This latter study found that both species were sighting prey from a shorter distance than during the day, but still managed to maintain a similar energy intake rate at night. Species that forage visually may alter their strategy to cope with lower light levels at night; Black-winged Stilts *Himantopus himantopus* feed by visual pecking during the day but may switch to tactile feeding at night (Rojas *et al.* 1999). The level of moonlight may be important for visual feeders; McNeil & Rompre (1995) found that both Willets *Catoptrophorus semipalmatus* and Whimbrels foraged more on moonlit nights, as did Thibault & McNeil (1994) for Wilson's Plover *Charadrius wilsonia*. Therefore tactile foragers may be better adapted to feeding at night, as they are not reliant upon (variable) light conditions.

Calidrid sandpipers are adapted for tactile foraging, having mechano- and chemosensitive bill tips (Heezik *et al.* 1983, Gerritsen *et al.* 1983, Gerritsen & Sevenster 1985). Gerritsen & Heezik (1985) studied foraging in captive Purple Sandpipers, and described them as extremely successful touch-hunters. The standard foraging technique used by Purple Sandpipers – probing in rock crevices and amongst large mussels for small prey – would not seem to be sight dependent. Indeed, nocturnal foraging may confer an advantage to Purple Sandpipers due to the absence of raptors, which are possibly the greatest cause of winter mortality (Dierschke 1998).

6.2 Methods

6.2.1 Catching birds

Purple Sandpipers were caught at three of the six rocky shore sites within the study area; Amble (six), Cresswell (five) and Blyth (32). Birds were caught at night-time by dazzling with a powerful hand-held spotlight, powered by a 12V car battery carried in a rucksack frame. After becoming transfixed with the light beam, birds were caught in a 75 cm diameter fisherman's landing net on a 4 m extendable pole. This technique only proved successful in extremely inclement weather conditions; strong (preferably gale-force) onshore winds, total cloud cover and rain or snow. In better (calmer) weather conditions birds were either able to see or hear me before or during dazzling, and were more inclined to take flight than in windy conditions. Birds were also caught at Amble and Cresswell by cannon-netting while feeding on wrack deposits at high water.

After capture, Purple Sandpipers were aged by the presence or absence of pale fringing on the coverts (Prater *et al.* 1977). Mass was weighed to the nearest 1 g with a Pesola balance, wing-length (maximum chord, Evans 1976) to the nearest 1 mm with a stopped rule and bill-length to the nearest 0.1 mm using Vernier callipers. All birds were colour-ringed with a unique combination of four Darvic rings in addition to the standard BTO metal ring.

To control for variation in mass due to bird size the method of Summers (1988) was used, using the following equation:

Adjusted mass = observed mass $\times (30^{0.835}/\text{bill-length}^{0.835})$

Where 0.835 was the value to which bill-length needs to be raised in order to make it directly proportional to mass. This index adjusts the mass of each bird to that equivalent to a bird with a 30 mm bill.

6.2.2 Molecular sexing of Purple Sandpipers

Birds were sexed on bill-length (Prater *et al.* 1977). However, a number of individuals had bill-lengths that lay within the overlap of males from the "long-billed" population and females from the "short-billed" population. These birds were sexed using DNA analysis (Griffiths *et al.* 1999) along with a number of birds that were able to be sexed using biometrics in order to validate the accuracy of the molecular method.

DNA was extracted from feathers collected from the mantle and back of 24 individuals during ringing (2-3 feathers per bird). The feathers were stored in the dark at room temperature until DNA was extracted. The terminal 3mm of feather roots was chopped finely with a surgical blade and then heated in 200μl 5% Chelex and 2.5μl proteinase K at 60°C for 2 hours. For some individuals this procedure proved insufficient to produce results after PCR, so incubation was repeated with an additional 2.5μl proteinase K. PCR was conducted using the method of Griffiths *et al.* (1999), using the P8 (5' –CTCCCAAGGATGAGRAA TTG- 3') and P2 (5; -TCTGCATCGCTAAATCCTTT- 3') primers to isolate the CHD-Z gene carried by both sexes and the CHD-W gene carried by female birds only.

The results of PCR were run on 0.45 mm thick gels of 5% polyacrylamide and 1.6 M urea. After electrophoresis, gels were stained using a silver stain (Bassam *et al.* 1991). All samples showed a band indicating the presence of the CHD-Z gene whereas only samples from females showed a band for the CHD-W gene.

6.2.3 Radio-telemetry

Seven Purple Sandpipers were radio-tagged in the 1997-98 winter and 13 in 1998-99. In all cases birds were tagged with 2.5 g back-attached radios supplied by Biotrack Ltd (Dorset, England). Feathers were clipped to approximately half-length in a small (approximately 2×3 cm) area on the lower back, above the preen gland, and the tags affixed using either epoxy resin or superglue.

Table 6.1: Capture of radio-tagged Purple Sandpipers

Date	Site	Number
17 Nov '97	Blyth	2
12 Jan '98	Blyth	1
19 Jan '98	Blyth	4
20 Oct '98	Amble	1*
14 Jan '99	Blyth	4
1 Jan '99	Blyth	1
18 Jan '99	Cresswell	1
29 Jan '99	Amble	1
3 Feb '99	Amble	3

^{*} Caught by cannon-netting. All other individuals caught by dazzling.

Birds were tracked using a Wildlife Materials Inc. receiver and hand-held Yagi antenna, which allowed signals to be received from approximately 1 km distance. Battery life was about six months, although a number of birds lost their tags before the battery had expired.

Birds were located by scanning for signals from high vantage points – usually dune- and cliff-tops – at approximately 1 km intervals along the Northumberland coast. When signals were located birds were approached for visual confirmation of location. As Purple Sandpipers were almost invariably feeding near the tide's edge a single telemetry bearing was usually sufficient to locate birds. Nocturnal tracking, when a visual confirmation of tracking was not possible, was done by triangulating from two tracking locations a minimum of 100 m apart.

6.2.4 In-field observations

6.2.4.1 Age, sex and breeding population of Purple Sandpipers

Purple Sandpipers were aged in the field by the presence of pale fringing on the coverts on the closed wing (Prater *et al.* 1977, Cramp & Simmons 1983). This was only done before January in each winter, as feather wear after this date made aging unreliable.

The bill lengths of birds in the field were estimated, with birds being classified as short-, medium- or long-billed by comparison between bill length and the distance between the base of the bill and the back of the head level with the bill. This distance was measured on three captured birds and two corpses, and averaged 30 mm. Birds observed in the field with bills clearly shorter than their head-width were classified as "short-billed", those with bills approximately equal to this distance as "medium-billed" and those with longer bills as "long-billed". The accuracy of this method of estimation was assessed by comparing estimated classifications of 18 colour-ringed birds with the actual bill lengths measured from those birds.

6.2.4.2 Observations of colour-ringed Purple Sandpipers

Colour-ringed Purple Sandpipers were looked for at all sites within the study area at least once a month in June and July, once a fortnight in August and September, and once a week from October to May. Blyth was visited at least twice weekly (a minimum of one low and one high water visit) over the 1996-97 and 1998-99 winters. Coquet Island was visited once in each winter. In 1998-99 additional effort was put into locating Purple Sandpipers at Blyth, Amble and Cresswell, the three sites where Purple Sandpipers were colour-ringed. Sites known to hold Purple Sandpipers along the coast as far south as Hartlepool (approximately 45km) and as far north as Stag Rocks, Bamburgh (40 km) were checked twice in each winter to look for birds that may have left the study area.

On site visits, all Purple Sandpipers present were checked for colour-rings. The locations, behaviour and substrate of all colour-ringed birds were recorded. Repeated observations were made by scan-sampling (Altmann 1974) at five-minute intervals. All observations were made with Optolyth 10×40 binoculars and/or a Kowa TSN-2 25×80 telescope.

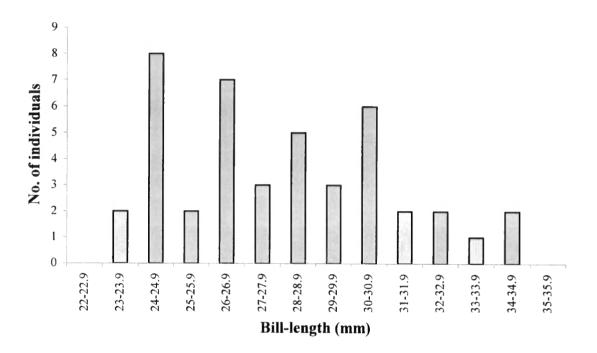
Peck rates of 13 foraging colour-ringed Purple Sandpipers were recorded in the 1998-99 winter. All records were made of birds foraging on mussel-bed at or near low water to control for variation caused by substrate or tidal state. The number of pecks made in five one-minute periods was recorded for each colour-ringed bird - no attempt was made to assess whether pecks were successful or not.

6.3 Results

6.3.1 The sex ratio and origins of Purple Sandpipers in the study area

6.3.1.1 Biometric measurements

Figure 6.1: Distribution of bill-lengths of all 43 Purple Sandpipers caught in study area



Of the 43 Purple Sandpipers that were captured, 26 had bill-lengths that allowed them to be sexed under the guidelines given by Summers *et al.* (1992). Five (11.6%) of these had bills of over 32.2 mm long and so were classified as females of the "long-billed" breeding population. A further 21 (48.8%) individuals had bills shorter than 27.6 mm and hence were classified as males of the "short-billed" breeding population. The remaining 17 birds had bill-lengths in the intermediate size range and so it was not possible to sex them using biometrics alone. Figure 6.1 shows the distribution of bill-lengths for all captured birds.

DNA was successfully extracted from the feather samples from 24 birds, including all of those that were radio-tagged. Of these birds, 16 (66.6%) were males and eight (33.3%) were females. 13 of these were birds that had previously been sexed using biometrics (above). In 11 cases the results of the molecular analysis concurred with the original biometrics-based sexing. However, in two cases the sex of an individual as revealed by DNA analysis was not that as determined by the measurement of bill length. One individual with a bill length of 26.1 mm was sexed by DNA analysis as a female, despite this size being 1.5 mm below the lower limit for female bill length (27.6 mm), and another with a bill of 33.4 mm was sexed as a male but was 1.2 mm over the length thought to be the upper limit (32.2 mm) for a male of the "long-billed" breeding population.

There was not thought to have been any contamination during the processing of feather samples and the extraction of DNA from them. Furthermore, the analysis of 13 samples was repeated with no change in results; both individuals mentioned above were tested twice with the same result. It is extremely unlikely that error in bill measurement caused the bill lengths of these two individuals being recorded as outside previously recorded limits. Five Purple Sandpipers were recaptured and had their bill measurements repeated; in only two cases did the two measurements differ, and then only by 0.1 mm.

The discovery of two individuals with bill lengths outside the range previously recorded for their sexes increases the range of the intermediate bill length group, which comprises both males from the "long-billed" population and females from the "short-billed" population. Therefore the proportion of individuals that can be sexed by biometrics alone is reduced. If the range of the intermediate bill length group is increased from 27.6 - 32.2 mm to 26.1 - 33.4 mm, in order to encompass the two new extreme bill lengths for "long-billed" males and "short-billed" females, the number of birds able to be sexed by bill length is reduced from 26 to 16. With the addition of the birds sexed by DNA analysis, a total of 33 birds were sexed and assigned to breeding populations as shown in Table 6.2. There were 25 (75.8%) males and eight (24.2%) females, of which 24 (72.7%) were from the

"short-billed" breeding population and nine (27.3%) from the "long-billed" population.

Table 6.2: Sex and breeding origins of Purple Sandpipers caught at each rocky shore site

	Short	-billed	Long		
Site	Males	Females	Males	Females	Unknown*
Amble	1	3	2		
Cresswell	4	1			
Blyth	13	2	4	3	10
Total	18	6	6	3	10

^{*} Either "long-billed" male or "short-billed" female.

6.3.1.2 In-field assessment of bill lengths

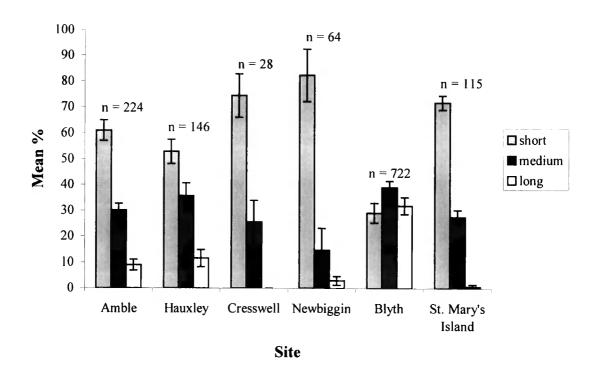
Estimations of bill-length category were checked for accuracy by making assessments of colour-ringed birds (of known bill-length). A total of 65 separate assessments were made on 18 individuals (Table 6.3).

Table 6.3: Accuracy of in-field assessments of bill length

	Assessed as; no. occasions (no. individuals)					
Actual bill length	"short"	"medium"	"long"			
"short"	23 (8)	4 (2)				
"medium"	2 (2)	17 (6)	5 (2)			
"long"			14 (4)			

83.1% of estimates of the bill length category of individuals of known bill length were correct; 85.2% of estimates of "short-billed" birds, 70.8% of "medium-billed" birds and 100% of "long-billed" birds.

<u>Figure 6.2: Proportions of Purple Sandpipers in the three bill-length categories at</u> each site



Error bars show one standard error either side of the mean. N values refer to the total number of birds assigned to a bill-length category on all visits.

The bias towards short-billed birds found by bill measurements was supported by field observations at five of the six sites, but at Blyth there were fewer birds with short bills and more with long bills. The distribution of birds of the three bill-length categories differed significantly from that expected if birds were uniformly distributed between sites ($\chi^2 = 34.2$, d.f = 10, p < 0.001). The differences arose mainly from the composition of the birds at Blyth.

The in-field observations from Blyth show a considerable discrepancy from the data from captured birds. The estimates of the proportions of birds from the two breeding populations shown in Figure 6.3 were generated using the equations:

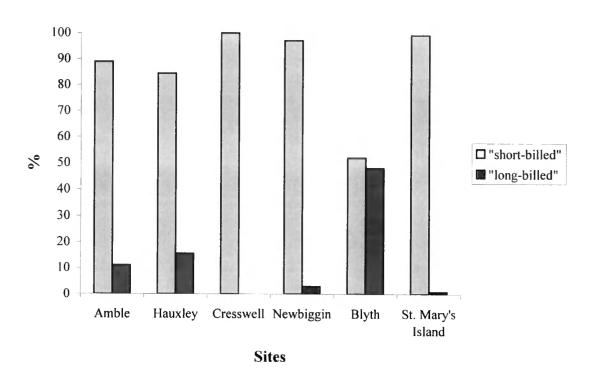
proportion of "short-billed" birds = k(a + qa)proportion of "long-billed" birds = k(c + rc)

Where a = proportion of birds in short bill class, c = proportion of birds in the long bill class, q = the number of short-billed females for each short-billed male,

r = the number of long-billed males for every long-billed female and k = 100/(a + qa + c + rc) (see Nicoll *et al.* 1988).

These proportions were combined with the mean winter count for each site to produce an overall estimate for the study area of 75.8% "short-billed" birds and 24.2% "long-billed" birds. The distribution of birds from the two populations was obviously not even between the six rocky shore sites, with far higher proportion of "long-billed" birds at Blyth than at other sites; the observed number of "long-billed" birds at Blyth was 84.6% of the total in the whole study area.

Figure 6.3: Calculated proportions of the two Purple Sandpiper breeding populations at each rocky shore site



The calculated proportion of long-billed birds at Blyth (48.1%) is higher than that derived from the bill measurements and DNA analysis of caught birds, which found that 31.8% of identifiable birds were "long-billed". This result suggests that there may have been some bias in the catching method (dazzling and netting) used at Blyth.

6.3.1.3 Ages

5 of the 43 (11.6%) Purple Sandpipers caught were aged as first-years. The proportion of first-year birds at each site, as assessed in the field, is shown in Figure 6.4.

25 20 % of 1st year birds 15 1996-97 10 1998-99 5 0 Amble Hauxley Cresswell Newbiggin Blyth St Mary's Site

Figure 6.4: Percentage of first-year Purple Sandpipers at each rocky shore site

Error bars show one standard error either side of the mean.

There was no significant variation between winters in the percentage of first-year Purple Sandpipers (Scheirer-Ray-Hare test, $\chi^2 = 0.21$, d.f = 2, non-significant) or between the proportions of first years at each site (Scheirer-Ray-Hare test, $\chi^2 = 6.1$, d.f = 2, non-significant). However, it was noticeable that Cresswell had the highest proportion and Blyth the lowest proportion of first-year Purple Sandpipers in two of the three study winters. The mean proportion of first-year birds in the whole study area was 12.7% in 1996-97, 11.7% in 1997-98 and 11% in 1998-99.

6.3.2 Mortality

A number of individuals were not seen again after capture and so are presumed to have either died or left the study area. Of the 18 ringed at Blyth in the 1996-97 winter, four (22%) were not seen subsequently during that winter. One individual, however, returned the following winter. Another individual was not seen or detected after radio-tagging at Amble in early 1999. In addition, a first-year individual radio-tagged at Blyth on 17th November 1997 was not seen subsequently within the study area, but was found later in the same winter on 22nd January 1998 at Seaham, County Durham, 28 km south of the capture site. This case is the only known instance of a bird being caught in the study area but settling in another area to winter.

Of the 15 colour-ringed birds seen regularly over the 1996-97 winter, 13 returned in the 1997-98 winter, while of 23 present in 1997-98, 19 returned in 1998-99. These records give minimum annual survival rates of 86.7% for 1996-97 to 1997-98 and 82.6% for 1997-98 to 1998-99.

<u>Table 6.4: Dates of last sightings of Purple Sandpipers that failed to return in the following winter</u>

No. sightings	Date of last sighting	Notes
5	9 th May 1997	
10	30 th April 1997	
61	7 th May 1998	
1	22 nd January 1998	At Seaham
15 ¹	17 th March 1998 ²	
4	14 th May 1998	-
8	26 th April 1998	
	5 10 6 ¹ 1 ¹ 15 ¹	5 9 th May 1997 10 30 th April 1997 6 ¹ 7 th May 1998 1 ¹ 22 nd January 1998 15 ¹ 17 th March 1998 ² 4 14 th May 1998

¹ Radio-tagged.

Table 6.4 shows that the individuals that were present in one winter but not the next were all observed until normal departure dates, except one that may not have

² Before expected date of normal departure

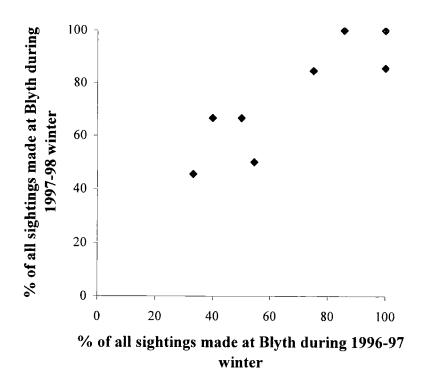
survived beyond 17th March. Hence there was little mortality over the 1996-97 and 1997-98 winters. In the 1998-99 winter, the mortality of two individuals was detected. A bird radio-tagged at Amble on 20th October 1998 was recovered, having been killed by a raptor on the 28th or 29th of the same month. A colour-ringed Purple Sandpiper was observed being taken by a female Sparrowhawk at St. Mary's Island. In addition a further four birds were last sighted in January 1999, suggesting they either died or left the area. All four birds were radio-tagged, but had been seen on at least three dates after tagging and had appeared to be unaffected by the tag. It is felt that the removal of feathers for the attachment of the tag was minimal and not likely to affect the thermal insulation of the birds.

6.3.3 Site fidelity

The majority of birds were marked during the study at Blyth (no individuals were caught elsewhere until March 1998) and, subsequent to colour-ringing and in some cases radio-tagging, these individuals were observed at Blyth on numerous occasions. In addition, sightings were made of several at St. Mary's Island, Newbiggin and Cresswell. There was an obvious disparity between individuals in their tendency to visit sites other than Blyth as some were never observed elsewhere while others were frequently recorded at neighbouring rocky shore sites.

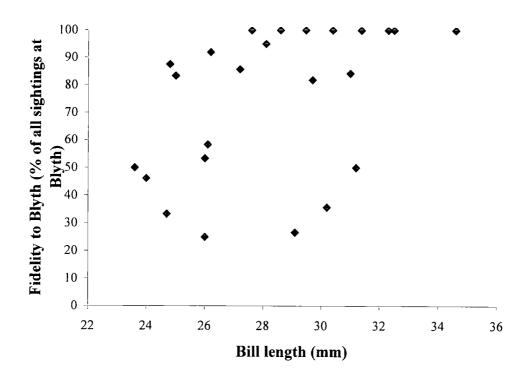
There was a significant relationship between winters in the degree of site fidelity shown by individual Purple Sandpipers colour-ringed at Blyth: those that were highly faithful in one winter were likely to be so in the following winter (Figure 6.5). There was a significant relationship between the fidelity of individuals to Blyth between different winters, with fidelity being measured as the percentage of all sightings of a bird that were at Blyth (with only one sighting being recorded for a site on one day). This relationship was found between both pairs of successive winters; between 1996-97 and 1997-98 (Spearman's rank correlation, n = 8, r = 0.867, one-tailed P < 0.001) and 1997-98 and 1998-99 (n = 6, r = 0.88, one-tailed P < 0.05).

Figure 6.5: Site fidelity in two successive winters of individual Purple Sandpipers colour-ringed at Blyth



There was a significant relationship between the bill length of an individual Purple Sandpiper and its site fidelity at Blyth: longer billed birds were more site faithful (Figure 6.6). ($r_s = 0.35$, n = 25, P < 0.05).

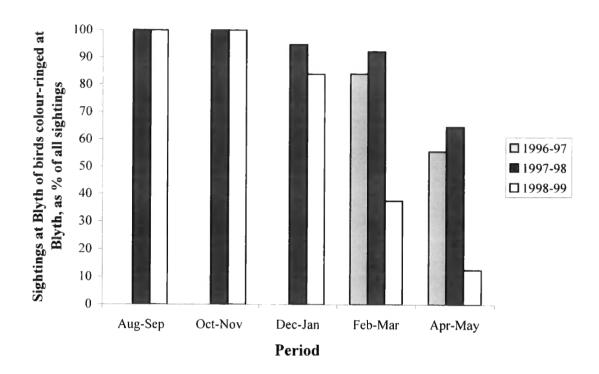
Figure 6.6: Relationship between bill length and site fidelity at Blyth



There was a significant difference in the fidelity to Blyth between birds of known sex. Females (n = 4) were more site-faithful than males (n = 13) (Mann-Whitney, z = 2.35, P < 0.05).

Movements away from Blyth by colour-ringed individuals (as measured by sightings at other sites, not by absence from Blyth) did not occur at the same rate throughout the wintering period. Figure 6.7 illustrates how the incidence of movements away from Blyth increased through the wintering period and into spring in the three years.

Figure 6.7: Seasonal changes in the site-fidelity of Purple Sandpipers at Blyth over the wintering period, 1996-99



The increase in sightings of Purple Sandpipers from Blyth at other rocky shore sites in the late winter and spring was due both to more individuals moving away from Blyth and to those individuals doing so with a greater frequency.

Figure 6.7 shows that the fidelity of colour-ringed individuals to Blyth was far lower in the late winter and spring of 1999 than in the two previous years. This decline in fidelity corresponded with the drop in overall numbers of Purple Sandpipers at Blyth caused by a Merlin using the Blyth Harbour roost site. Of 13 Blyth colour-ringed birds seen during February-March 1999, eight were recorded at sites up to 10 km away from Blyth.

Table 6.5 gives the mean bill lengths of the birds that were never seen away from Blyth and those that were, in each of the two-month periods in which birds moved from Blyth (all three years combined). Both groups showed a slight increase in mean bill-length over the winter, as slightly larger birds began to move away from Blyth later in the winter, but this change was not significant.

Table 6.5: Mean bill length of resident and itinerant Purple Sandpipers at Blyth in different winter periods

	Dec-Jan		Feb	-Mar	Apr-May		
	Resident	Itinerant	Resident	Itinerant	Resident	Itinerant	
Mean bill	29.1	26.8	29.0	27.4	29.9	27.4	
length (mm)							
S.E.	0.85	1.05	0.97	0.85	1.37	0.77	

The birds that left Blyth to feed at other sites (St. Mary's Island, Newbiggin and Cresswell) showed a clear preference for which other site they visited. The nature of these visits varied; in some cases birds would feed at a neighbouring site such as Newbiggin but return to Blyth to roost over high water (although this was not the case in 1999 when disturbance at the roost was the chief cause of birds leaving Blyth). Other birds would move to and from neighbouring sites, often staying there for a number of days before returning to Blyth, while other birds moved to neighbouring sites in the late winter or spring and were not seen back at Blyth until the following autumn. On no occasion was any individual observed moving from Blyth in order to roost elsewhere and returning to Blyth to feed at low water; it appeared that movement away from Blyth was in order to feed at other sites.

Of the 19 individuals that moved from Blyth on at least one occasion, 13 were seen at only one other site; the other six individuals were seen at two. Of the 11 birds that were seen away from Blyth in more than one winter, none varied between years in the site to which they moved.

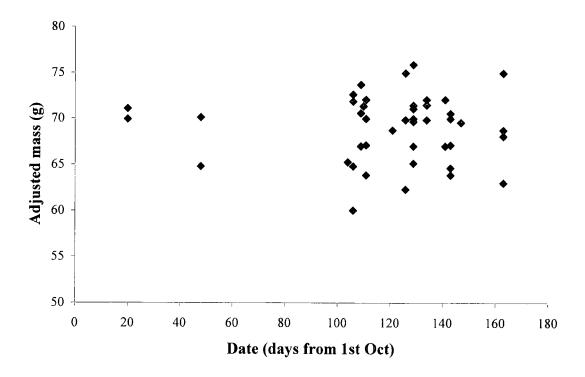
There was no difference in the size of birds that moved to the three sites other than Blyth; Cresswell (mean bill length 28.7 mm, n = 3), Newbiggin (27.3 mm, n = 11) and St. Mary's Island (26.6 mm, n = 9) (Kruskall-Wallis, χ^2 = 1.52, d.f. = 2, not significant).

The pattern of increasing itinerancy in the late winter and spring shown by Purple Sandpipers colour-ringed at Blyth was in marked contrast to that shown by the (few) birds colour-ringed elsewhere. Instead of showing an increase in itinerancy the four individuals colour-ringed in March 1998 at Cresswell showed increasing site faithfulness over the following winter. Sightings of the two birds that returned in August 1998 were either at Blyth or Newbiggin until October, and the other two individuals also visited Blyth as well as Amble and Hauxley when they returned later in the autumn. Only 46% of all sightings of individuals ringed at Cresswell in October-November were at Cresswell, significantly different for the 100% of Blyth-ringed individuals at Blyth for the same period (Mann-Whitney U test, z = 3.86, n = 15, P < 0.01). Conversely, later in the winter (after January) none of these birds were observed away from Cresswell, except on two occasions on spring high tides when the Lynemouth roost was disturbed and they moved to Newbiggin, as no other roost sites were available at Cresswell. The birds colour-ringed and radio-tagged at Amble were not recorded further away than Hauxley.

6.3.4 Bird mass in relation to site fidelity

The body masses of captured birds were standardised to control for variation in size following Summers *et al.* (1992), adjusting the mass of each bird to the equivalent mass for a bird with a bill length of 30 mm. Figure 6.8 shows that there was no significant variation in the mean adjusted mass of birds caught in each month from October to March (one-way ANOVA, d.f. = 4, F = 1.56, not significant). It is not known whether catching methods used resulted in any bias in the birds caught.

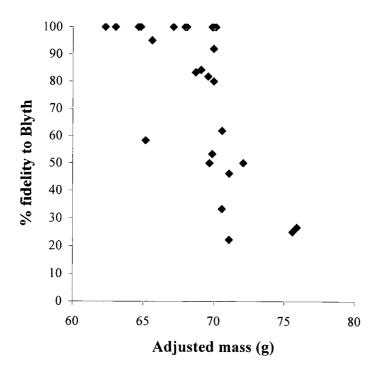
Figure 6.8: Variation in adjusted mass of Purple Sandpipers over the wintering period (birds caught at all sites in all three winters)



As there was no significant variation in adjusted mass (and presumably therefore in the fat stores being carried by individual birds) through the winter, data from all capture dates were included in the analysis of adjusted masses. In several passerine species, subordinate birds tend to be heavier than dominants during winter. I tested whether itinerant Purple Sandpipers might differ from residents in this way.

There was a highly significant negative relationship (Spearman's rank correlation, $r_s = -0.54$, N = 27, P < 0.01) between the adjusted mass of Purple Sandpipers caught at Blyth and their fidelity to that site; birds that remained at Blyth all or most of the time were comparatively lighter (probably because they had smaller fat stores) than more itinerant individuals (Figure 6.9).

Fig 6.9: Relationship between adjusted mass and fidelity to Blyth of birds colourringed at Blyth



This relationship was not simply due to an underlying relationship between adjusted mass and bill length (individuals with high fidelity at Blyth tending to be larger than itinerant birds, Figure 6.6); such a relationship did not exist ($r_s = 0.03$, n = 43, not significant).

Birds with less stored fat (e.g. lighter individuals) may have access to more reliable food resources. The adjusted masses of birds at different sites were compared to see if there was a difference in body condition at these sites. Birds caught at Blyth had a lower mean adjusted mass (68.4 g) than those from Amble (70 g) and Cresswell (70.4 g), although not significantly so (one-way ANOVA, d.f. = 2, F = 0.95, not significant). There was no significant difference in adjusted mass between sexes ('t'-test, d.f. = 33, t = 1.128, not significant) or birds from the two breeding populations (d.f. = 33, t = 0.48, not significant).

6.3.5 Arrival and departure dates

Colour-ringed Purple Sandpipers were recorded returning to the study area from 24^{th} August onwards. There was a significant difference in the mean arrival dates of birds from the two breeding populations (Mann-Whitney U test, n = 13, z = 1.95, P < 0.05), 23 September for short-billed individuals and 8 November for long-billed individuals. There was no difference between breeding populations in mean date of departure in the spring, (short-billed birds 17 April, long-billed birds 7 April, n = 14, z = 0.7, n.s.).

6.3.6 Difference in the behaviour and use of sites by individuals

6.3.6.1 Roosting and other behaviour over high water

Purple Sandpipers were not often observed foraging over high water; for example only 13% of all birds at Amble and 6% of birds at Cresswell fed over high water (tide heights over 3.7 m O.D.), and none did so at Blyth (Chapter 4). All but one of the (n = 43) colour-ringed individuals behaved in this way, an individual marked at Amble in January 1999. This bird was observed feeding on deposits of detached wrack along the strand-line, in the company of larger numbers of Turnstones and up to six other Purple Sandpipers during high water on nine occasions during January, February and March 1999; on four of these dates it was the only Purple Sandpiper present. In addition this bird, with up to three others, fed on a wrack deposit throughout the whole tidal cycle on three days in February 1999. It was a first-year female of the "short-billed" race and was caught whilst feeding on a wrack deposit at high water. Five further birds caught in similar circumstances were all adult (4) or first year (1) males of the "short-billed" population. Thus it may be that small, short-billed birds are more likely to feed on wrack deposits over high water.

The behaviour of individual birds at Blyth was compared to see if some fed for longer over the tidal cycle, possibly to compensate for a lower rate of food intake. Colour-ringed Purple Sandpipers were observed moving to roost at Blyth on 11

dates in the 1997-98 winter and 13 in the 1998-99 winter. There was no significant difference between individuals in the mean tidal height at which they departed to roost (using individuals that were observed on a minimum of five dates in any one winter) (one-way ANOVA, d.f. = 10, F = 0.94, not significant).

6.3.6.2 Foraging behaviour over low water

Purple Sandpipers were studied in detail at Blyth to see if individual birds varied in their choice of foraging substrate, which could have been an indication of a difference in diet between birds, and possibly a difference in the profitability of foraging. There was no difference between individuals in the selection of foraging substrate over low water (defined as tides below 2.0 m O.D.); detailed data were gathered on nine individuals, none of which showed any marked deviation from the substrate use shown in Figure 4.12 (Scheirer-Ray-Hare, $\chi^2 = 4.23$, d.f = 8, non-significant).

It is extremely difficult to make estimates of prey intake rates by small shorebirds such as Purple Sandpipers. Peck rates, although not indicative of the success of pecks or the energetic value of prey items consumed, were measured to see if birds fed at differing rates. Observations were made on 13 colour-ringed and/or radio-tagged birds at four sites within the study area (Amble, Cresswell, Blyth and St. Mary's Island). All observations were made of birds feeding over low water on areas of mussel-bed between November and March to control for effects of tidal state, foraging habitat and season. There was no relationship between peck rate and Purple Sandpiper bill length (Spearman's rank correlation, $r_s = 0.08$, n = 13, not significant); birds of different size did not feed with different peck rates. There was also no significant difference in the peck rate at the four different sites from which data were collected (one-way ANOVA, F = 0.41, d.f. = 3, not significant) (Table 6.6).

There was a large degree of variation in peck rates both between individual birds feeding immediately next to each other and between peck rates recorded for the same individual on the different occasions. It seems that variation in peck rate

due to small-scale changes in habitat type and/or quality may provide too much "noise" for an investigation on this limited scale to determine differences in food intake rate between individuals.

Table 6.6: Mean peck rates of Purple Sandpipers at three rocky shore sites

		Peck rate (min ⁻¹)			
Site	No. individuals	Mean	S.E.		
	observed	ved			
Amble	3	36.7	6.7		
Cresswell	3	28.4	8.2		
Blyth	9	34.0	3.9		
St. Mary's	2	40.0	6.6		
Island					

6.3.6 Nocturnal behaviour

Of the seven Purple Sandpipers radio-tagged at Blyth in the 1997-98 winter, four were tracked at night at Blyth (four) and Cresswell (one). In the following winter nine individuals were radio-tracked at night at Amble (three), Cresswell (one), Newbiggin (one) and Blyth (five).

Amble

Purple Sandpipers were radio-tracked at Amble over the course of five separate nights in January-March 1999. Two individuals moved to Coquet Island at or before dusk on each occasion and remained there throughout the night, regardless of tidal movements. They either moved directly to Coquet Island from the Amble foreshore, or from the roost in the Amble Harbour breakwater on mid-afternoon rising tides with up to 40 other Purple Sandpipers. These birds remained in the usual roosting location until after dusk when they moved to Coquet Island. No birds were found at this roost site on four night time inspections and so it is presumed all birds moved to Coquet Island to roost. Radio-tag signals were either weak or entirely absent during high water, with little variation in signal strength

which suggests that birds may have been using the roost site on the east side of the island that was used during the day. Signals from both individuals indicated that they left the roost on the falling tide and were active, presumably foraging, over the entire low water period. However, due to the impossibility of accurately interpreting what these birds were doing, their diurnal and nocturnal activity cannot be compared.

The third individual roosted on Coquet Island over night time high waters, but returned to the Amble foreshore to forage over low water. It left the Amble foreshore to roost at a mean tide height of 3.3 m O.D., significantly lower than its diurnal departure tide height of 3.8 m O.D. ('t'-test, t = 2.98, d.f. = 11, P < 0.01). If this individual returned to feed at a similarly lower tidal state on the falling tide, it would have spent 80 minutes less foraging on nocturnal tidal cycles than during the day – approximately 24% less time.

The individual that foraged on the Amble foreshore at night showed a similar use of the area nocturnally as diurnally. It spent most of the low water period on the rocks immediately south of the Harbour mouth before moving southwards to Welhaugh Point on the rising tide.

Cresswell

Only one radio-tagged Purple Sandpiper was present at Cresswell in both the 1997-98 and 1998-99 winters. Therefore only limited quantitative data was collected on nocturnal Purple Sandpiper behaviour from this site. There were no discernible variations from diurnal behaviour, with the radio-tagged individuals roosting at Cresswell or Lynemouth and moving to the intertidal area over low water, presumably to feed.

Blyth

Purple Sandpipers were radio-tracked at Blyth in both the 1997-98 (four birds) and 1998-99 (five birds) winters. On no occasion did any individual exhibit any behaviour radically different from that recorded during the day. Birds roosted in the Harbour at night, either on the East or West Pier, as during the day. All

individuals were present on the North Blyth foreshore over low water.

Observations made with the image intensifier and during the course of dazzling birds suggested that Purple Sandpipers foraged on mussel-beds in a similar fashion as during the day.

Tables 6.7 and 6.8 list the mean tide heights at which individual radio-tagged birds left and returned to the North Blyth foreshore at night and during the day. Every individual left the roost at a significantly lower tide height during the night than during the day, and similarly returned to the roost at a lower tidal height. There was no difference between individuals in the tidal height at which they left (one-way ANOVA, F = 0.46, d.f. = 6, not significant) or returned (one-way ANOVA, F = 1.03, d.f. = 5, not significant) to the roost site; on average Purple Sandpipers spent 3 hours 20 minutes at North Blyth over the nocturnal tidal cycle, 37.4% less than during the day. Although sufficient data were not available from birds radio-tracked at Amble to allow a statistical comparison, they suggest that Purple Sandpipers at Blyth may have spent less time foraging at night than those at Amble.

Table 6.7: Tide heights at which radio-tagged Purple Sandpipers moved to the roost at Blyth on the rising tide; a comparison of diurnal and nocturnal behaviour

		Departure to Blyth Harbour (metres O.D.)					_	
		Day Night			t'-test			
Individual	Winter	Mean	S.E.	Mean	S.E.	d.f.	t	Signif.
W/Gm GY	1997-98	3.43	0.07	2.72	0.14	9	4.63	P < 0.01
W/Gm LY	1997-98	3.31	0.10	2.54	0.08	11	4.84	P < 0.01
W/Gm LO	1997-98	3.31	0.1	2.5	0.12	10	5.63	P < 0.01
W/Gm LW	1997-98	3.48	0.07	2.53	0.18	12	5.82	P < 0.01
W/Rm WR	1999-99	3.28	0.11	2.5	0.14	8	4.33	P < 0.01
W/Rm WO	1999-99	3.4	0.05	2.62	0.08	8	7.64	P < 0.01
W/Rm RW	1999-99	3.2	0.08	2.68	0.12	10	3.79	P < 0.01

Table 6.8: Tide heights at which radio-tagged Purple Sandpipers left the roost at Blyth on the falling tide; a comparison of diurnal and nocturnal behaviour

		Departure from Blyth Harbour (metres O.D.)						
		Day Night			't'-test			
Individual	Winter	Mean	S.E.	Mean	S.E.	d.f.	t	Signif.
W/Gm GY	1997-98	3.24	0.11	2.18	0.12	8	6.45	P < 0.01
W/Gm LO	1997-98	3.07	0.08	2.2	0.09	6	7	P < 0.01
W/Gm LW	1997-98	2.94	0.10	2.28	0.14	8	3.81	P < 0.01
W/Rm WR	1999-99	3.07	0.11	2.02	0.22	6	4.13	P < 0.01
W/Rm WO	1999-99	3.02	0.09	2.45	0.13	7	3.01	P < 0.01
W/Rm RW	1999-99	3.25	0.07	2.4	0.11	7	5.68	P < 0.01

Two Purple Sandpipers were radio-tracked at Blyth at night in April-May; W/Gm GY on four dates in 1998 and W/Rm WR on three dates in 1999 (the other radio-tagged individuals had either moved to other sites, left the study area or suffered radio-tag failure/loss by this time). Both individuals spent less time at North

Blyth at night during the spring than in the winter. In the spring W/Gm GY left the roost site at a significantly lower tide height (winter mean = 2.18 m O.D., spring mean = 1.77 m O.D., two-tailed 't'-test, t = 2.1, d.f. = 6, P < 0.05) and returned at a significantly lower height on the rising tide (winter mean = 2.72 m O.D., spring mean = 2.17 m O.D., two-tailed 't'-test, t = 2.36, d.f. = 6, P < 0.05). W/Rm WR also left the Blyth Harbour at a lower tidal height in the spring (winter mean = 2.02 m O.D., spring mean = 1.62 m O.D., two-tailed 't'-test, t = 1.83, d.f. = 6, P < 0.05) and returned on a lower tide height, although not significantly so (winter mean = 2.5 m O.D., spring mean = 2.16 m O.D., two-tailed 't'-test, t = 1.75, d.f. = 6, not significant). In addition, on one date in May 1999 W/Rm WR did not leave the Blyth Harbour at all overnight. These changes in behaviour resulted in a mean reduction in the time spent on the North Blyth intertidal area at night of 21.1% for W/Gm GY and 34% for W/Rm WR.

6.3.7 Nocturnal diet

12 faecal samples were gathered at Blyth from Purple Sandpipers feeding at night on two dates in January 1999. In addition, samples were obtained from several individuals during the course of colour-ringing and/or radio-tagging. Mussel fragments were present in 85% of these samples; 43% of the samples consisted of nothing but mussel-shell. Other prey present in samples included *R. parva* (43%), Littorinids (33.3%), *N. lapillus* (19%) and *C. maenus* (9%).

6.4 Discussion

6.4.1 Composition of the wintering population of Purple Sandpipers in south Northumberland

Of the 43 Purple Sandpipers caught during this study, 73% were from the "short-billed" Scandinavian breeding population. This figure concurs with the findings of previous studies, which found a predominance of "short-billed" birds in southeast Scotland and north-east England (Nicoll *et al.* 1988). The distribution of birds from the two breeding races around the coasts of Britain is not surprising, given the direction of their arrival in the autumn; "long-billed" birds from Canada predominate in the far north and west while "short-billed" birds from Scandinavia are more abundant on the east coast.

As with previous studies in Britain, a sex bias was found amongst Purple Sandpipers in the study area. The ratios calculated in this study were one female to 1.38 males amongst 24 "short-billed" birds and one female to four males in the small number (nine) of "long-billed" birds. The ratio for "short-billed" birds is very close to that found by Nicoll *et al.* (1988) for this population in Britain as a whole (one female to 1.34 males). However, the overwhelming predominance of males in the "long-billed" population is nearly double that calculated by Nicoll *et al.* (one female to 2.11 males).

Males outnumber females in the southern part of the Purple Sandpiper wintering range in Europe (Atkinson *et al.* 1981, Buxton *et al.* 1985, Nicol *et al.* 1988), which strongly suggests that more females remain to winter further north. But Summers *et al.* (1990b) found a ratio of one female to 1.5 males even at Troms in northern Norway. Higher female mortality can be ruled out as the cause of that sex bias because first-year birds showed a similar female to male ratio, as they do in Britain (Nicoll *et al.* 1988, Corse & Summers 1999). It has yet to be discovered where females are in the majority during the winter. The monogamous breeding system of Purple Sandpipers suggests that a 1:1 sex ratio should exist.

As there is evidence (see below) that larger female birds are able to displace smaller males from the best wintering sites in Northumberland, it is possible that the same mechanism is occurring on a much larger scale; if high sub-arctic latitudes are the best wintering sites, females could remain there but competitively exclude males, which have to move further south to winter. However, there is another possible explanation which does not have to invoke competition: larger individuals have a relatively lower thermal conductance than small (Aschoff 1981), and so should find it easier to winter in the harsh climate of northern latitudes. For the smaller males any advantage accrued by reducing the distance migrated would be outweighed by the disadvantage of remaining in harsh arctic winter conditions and reducing their chances of survival.

The exaggeration in the sex bias in birds from the "long-billed" population in Northumberland may be due the small sample size. However, it is also possible that the low proportion of female birds arises because Northumberland is near the south-eastern limit of the wintering range of Nearctic "long-billed" birds in Britain; few winter further south on the east side of the country than Yorkshire. The relatively small numbers of large, long-billed birds found in the south of England are believed to originate from a Russian breeding population (Nicoll *et al.* 1988). If females may displace males from wintering grounds closer to their breeding areas (competitive displacement on an "international" scale), leading to the sex bias in the British population as a whole, it may be that in the "long-billed" population most females winter in north and west Scotland and mainly males migrate as far as north-east England.

The discovery of two individuals with bill lengths outside the "accepted" limits for Purple Sandpipers of their sex (i.e. those used by Nicoll *et al.* 1988, Summers *et al.* 1992, Burton 1995, Burton & Evans 2001) does not have serious implications for the results of this study. It does, however, suggest that there may have been some inaccuracies in the sex ratios reported by earlier studies.

6.4.2 Mortality and recruitment

The minimum annual survival rates calculated in this study, 86.7% and 82.6%, are comparable with those reported by Burton & Evans (1997) and Dierschke (1998), who found that Purple Sandpipers exhibit low annual mortality and high between-year site fidelity. The actual survival rates may have been even higher, as one bird was recorded over 20 km from the study area after ringing and thus other birds may have left the wintering region.

No mortality was recorded amongst marked birds in the first two study winters, which suggests that mortality is greatest away from the wintering grounds in agreement with the findings of Burton & Evans (1997). The known deaths in the 1998-99 winter were due to predation by raptors, which were the chief cause of winter mortality in Purple Sandpipers in Helgoland (Dierschke 1998).

The proportion of first-year birds in the study area as a whole was remarkably constant, with between 11% and 12.7% in the three winters of study. These proportions are lower than those recorded by Atkinson *et al.* (1981), Burton (1995) and Corse & Summers (1999), and would be insufficient to maintain the population at present levels if the observed year-to-year resighting rates were identical to the actual annual survival rate.

A small decline has occurred in Purple Sandpiper numbers wintering in south Northumberland since the mid 1980s. A decline has also been recorded on a national scale (Rehfisch *et al.* 1999). A study at Hartlepool over the 1999-2000 winter (Eaton 2000) found that a drop in the recruitment of wintering birds had probably caused the decline there, as there had been no change since the early 1990s in the annual mortality of birds colour-ringed during the course of Burton's earlier study (1991-92 to 1993-94). Therefore it seems possible that the low proportion of first-year Purple Sandpipers recorded in south Northumberland in the three years of this study was symptomatic of a reduction in the recruitment of young birds into the British wintering population. It is possible that climate change is responsible for a decline in wintering numbers. Birds already recruited

into the British wintering population are likely to continue returning, but juvenile birds may be more likely to remain further north if winters are milder, leading to a decline in recruitment.

6.4.3 Variation in the behaviour of individual Purple Sandpipers, and possible determinants

Section 6.4.1 above described the overall composition of Purple Sandpipers wintering in south Northumberland. However, within this area significant variation was found in the origins of the Purple Sandpipers present at each of the well-separated rocky shore sites. In particular, Blyth held a significantly higher proportion of individuals from the "long-billed" breeding population than the other five sites.

A clear relationship was found between the size (bill-length) of colour-marked and radio-tagged individuals at Blyth and their site fidelity. The larger an individual, the more likely it was to be seen only at Blyth; smaller birds often spent days or weeks away from Blyth feeding at other rocky shore sites. The degree of faithfulness of individuals to Blyth was maintained between winters.

In south Northumberland, Blyth was the site most favoured by Purple Sandpipers; this site held by far the highest density of birds in winter, and was the first site to be "filled up" when birds arrived in the area in autumn. This preference may have been due to the large area of intertidal mussel-bed at Blyth, as mussels were a major component of diet and mussel-bed a preferred feeding substrate (Chapter 4). All Purple Sandpipers at Blyth fed for a shorter period over the tidal cycle than birds at the other five sites (Table 4.4), suggesting that they were able to achieve their required daily food intake in a shorter period. As stated previously, obtaining sufficient food does not appear to present a problem for wintering Purple Sandpipers, even in Northern Norway (Strann & Summers 1990, Summers *et al.* 1998). However, feeding at a site where a higher intake rate is obtainable confers the advantages of allowing birds to spend less time foraging, and more time in vigilance or on the roost site, allowing birds to reduce

the risk of predation, a major cause of mortality in Purple Sandpipers (Dierschke 1998). Two colour-marked birds are known to have been taken by birds of prey in Northumberland, neither of them at Blyth.

There was a significant negative relationship between site fidelity of Purple Sandpipers at Blyth and adjusted mass: birds that were resident at Blyth (and therefore larger and possibly with a higher social status) carried less stored fat than those that moved to other sites more frequently. This fidelity would be expected if birds at Blyth experience a better, more reliable food source, which would reduce the requirement to store fat to anticipate periods of food shortage. By minimising the fat carried, these individuals could reduce the risk of predation; lighter birds of several species are able to take off more quickly, are manoeuvrable in flight and more likely to escape predation than heavier individuals (e.g. Gosler *et al.* 1995, Metcalfe & Ure 1995, Bednekoff 1996 and Kulberg *et al.* 1996, 1999, 2000). The data in Figure 6.9 support the hypothesis that the advantage of wintering at Blyth was the reduction in the risk of predation.

In the final year of this study, an attempt was made to quantify the relative benefits of feeding at the different rocky shore sites. Peck rates of birds were measured at four sites, but no significant differences were detected. Any variation that may have existed was probably masked because the individuals watched were foraging on different prey and different microhabitats; although peck rates were recorded from birds on mussel-beds only, within this habitat there is great variation in mussel cover and size.

If Blyth was indeed the most favourable wintering site, it might be expected that socially dominant birds would choose to winter there, but subordinate individuals might be excluded, or choose to feed at other sites rather than being confined to poorer quality areas at Blyth. Burton (1995) found that large Purple Sandpipers were dominant over smaller individuals at the roost; size appeared to be more important than race and sex in determining social ranking. Thus the pattern I observed amongst feeding birds - larger individuals showing greater fidelity to

Blyth - may have been a result of the higher social status of these birds allowing them to occupy the best wintering site within the study area.

Direct evidence that small Purple Sandpipers were excluded from Blyth by socially dominant larger individuals, rather than by choosing to utilise other sites for some other reason(s) was not available. However there is some support for the hypothesis. Birds from the "short-billed" population returned to the study area on average six weeks before individuals from the "long-billed" population. In this six week period, short-billed individuals were wholly resident at Blyth and "short-billed" birds ringed at other sites were also seen at Blyth. However, when the "long-billed" individuals returned to the study area in November the "short-billed" birds that had previously been resident at Blyth immediately moved to other rocky shore sites. There was no obvious change in environmental conditions, such as invertebrate prey densities, during this period that would suggest an explanation other than competitive exclusion of the small and presumably subordinate "short-billed" birds.

The same pattern was observed much later in the winter, when the number of birds feeding at Blyth declined. Observations of colour-ringed birds showed that the smaller individuals among the birds previously resident at Blyth were moving to utilise other feeding and roosting areas. Presumably worsening in feeding conditions prompted them to leave, although invertebrate sampling at Blyth failed to detect a significant decline in the densities of the major prey species of Purple Sandpipers between November and March (Appendix 2). When this decrease in fidelity to Blyth occurred it was again the smaller individuals that moved to (or at least spent more time at) neighbouring sites. It is conceivable that these smaller birds moved to other sites in order to capitalise on a change in behaviour in invertebrate prey in the spring.

The bias towards larger Purple Sandpipers at Blyth compared with those at other sites was not matched by a similar bias in the age structure. In a number of shorebirds species, adult birds have been shown to be socially dominant over immatures, for example, in two studies of Turnstones (Groves 1978, Whitfield

1985a), and in Oystercatchers (Goss-Custard 1984, Cayford 1988). If this principle holds for Purple Sandpipers, and immature birds are subordinate to adults, then exclusion of first-year birds from Blyth could be expected to occur in the same manner as for small individuals. However, although there was a slightly lower proportion of young Purple Sandpipers at Blyth than at other sites in two of the three study winters, the difference between sites was not significant.

The absence of bias in the distribution of first-year birds suggests that on their arrival in the study area in their first autumn, immature Purple Sandpipers obtain a position in the social hierarchy based on their size (or sex and race if they are the determining factors). Age may not be a significant factor in determining social structure because the large degree of size dimorphism in Purple Sandpipers (both between sexes and breeding populations) results in size effects swamping those of age. Although first-year birds may be lighter than equivalently-sized adults (mean difference 3%, Summers *et al.* 1992) this difference is small compared to that between "long-billed" and "short-billed" birds.

If age is an important factor in the determination of dominance rank, and by extension the use of wintering sites within the study area, we would expect to observe a change in the status and behaviour of individual Purple Sandpipers as they mature. Although the sample size of first-year birds caught (at Blyth) was small, none showed an increase in site faithfulness in later winters that would be expected as a result of a climb in a social hierarchy.

6.4.3 Individual variation in behaviour

Little evidence was found to suggest that different individual Purple Sandpipers employed different foraging behaviours during the wintering period. Although faecal analysis was a useful tool for identifying the prey taken by the population as a whole, it was not possible to use this to study the diet of individual birds in Northumberland. Summers *et al.* (1990a) were able to detect differences in diet by examining the gut contents of collected Purple Sandpipers. Larger (female) birds took larger prey items than smaller (male) birds, but there was no difference

in the prey species taken. As I did not collect birds, I could not confirm whether these habits also occurred in Northumberland.

Although almost all Purple Sandpipers fed only on rocky shores, one individual, colour-ringed at Amble, often foraged on strand-line wrack deposits over the high water period, sometimes accompanied by a few unmarked birds. It is possible, although not proven, that the same birds could have been involved on each occasion. This strategy would have provided the marked bird with extra energy intake, which most other individuals did not appear to require.

Unfortunately this bird was not radio-tagged, so it is not known whether it fed at night. It is not surprising that all radio-tagged birds fed at night (see below) as they were all originally caught while feeding at night. Possibly not all unmarked birds did so, but compensated if necessary by feeding over daytime high waters. This strategy would, however, appear to increase the risk of predation; the majority of attempts by raptors to catch shorebirds were observed over high water when shorebirds were forced to congregate on the upper shore areas which gave poorer all-round visibility than the low water intertidal feeding areas.

It is hypothesised above that Purple Sandpiper distribution may be governed by social status on continental, national and local scales. If so, we may also surmise that within a single site the socially dominant individuals would occupy the best areas for feeding, in the same way that Burton (1995) found them to occupy the prime spots within the roosting flocks. Subordinate birds would therefore be forced to forage on areas that gave lower food intake rates. The bird that foraged over high water at Amble was a first-year female of the "short-billed" race, so may have had a lowly social status.

6.4.4. Nocturnal behaviour

The radio-tagging of Purple Sandpipers in the study area has shown that they appear to feed in much the same manner, and on the same prey, at night as during the day. Although the number of faecal samples examined was small, their analysis suggests that there was no great difference between diurnal and

nocturnal diets, as expected of a species that feeds mainly on stationary or slow-moving prey.

Purple Sandpipers at both Amble and Blyth foraged for a considerably smaller proportion of the tidal cycle at night than during the day, which strongly suggests that Purple Sandpipers favour diurnal foraging, conforming to Sitter's "choice for day" hypothesis (Sitters 2000). This conclusion is further supported by the decline in night feeding in the spring, when milder conditions mean a lower dietary intake in required. However, this latter decrease could also be explained by a decline in the presence of raptors along the Northumberland coast in spring. Two of the three avian threats to Purple Sandpipers, Merlins and Peregrines, are present on the Northumberland coast only in the winter. Foraging at night confers the benefit of avoiding predation by raptors and if this risk were a significant factor, nocturnal foraging would be expected to decrease in the absence of raptors. The fact that (despite the risk of raptor predation during the day) nocturnal foraging was not maximised suggests that the intake rate achievable while feeding at night was low.

Unfortunately the method used for catching the Purple Sandpipers that were colour-ringed – dazzling on intertidal areas at night – meant that all the radio-tagged birds were night-feeders. As nocturnal data could be collected only from radio-tagged individuals it is not known whether all Purple Sandpipers fed at night.

Chapter 7

Individual variation in the behaviour and site and habitat use of Turnstones

7.1 Introduction

The aims of the research described in this chapter are the same as those on Purple Sandpipers in Chapter 6: to describe the variation in behaviour between individual birds and to determine what factor(s) control this variation.

Observations on colour-ringed Turnstones and radio-telemetry were used to determine the movements of individual birds within and between sites in the study area and their use of feeding habitats.

Of particular interest was the importance of deposits of strand-line wrack to feeding Turnstones. Although these wrack deposits provide a rich source of invertebrate food, such as the sandhopper *Talitrus saltator* and larvae of the wrack fly *Coelopa frigida*, they are ephemeral resources. Wrack is deposited on the upper shore in large amounts only after stormy weather (necessary to detach seaweeds from intertidal rocks) with onshore winds (which push floating wrack towards the shore). Wrack deposits are frequently washed away by the tide within a few days, before high densities of invertebrates have developed. However, if deposited sufficiently high on the foreshore by spring tides, wrack deposits may remain for several weeks and allow an abundance of invertebrates to develop. The analysis of Turnstone density in relation to environmental variables (Chapter 3) showed that the abundance of deposited wrack was an important predictor of Turnstone distribution, and previous research has shown that the presence or absence of wrack deposits can have a major impact on abundance of Turnstones (Bradley & Bradley 1993)

Although it was obvious that wrack deposits are an extremely attractive resource for Turnstones in south Northumberland, it was not known whether they hold the same importance for all individuals. Do all Turnstones depend on wrack deposits as a food resource to the same degree, just utilising deposits at high water as and when they occur, upshore of or near their low water feeding sites? Or are wrack deposits important to some birds and not others and, if so, do these birds travel between sites to utilise wrack deposits as and when they occur?

My study aimed to establish whether Turnstones in south Northumberland show individual variation in site fidelity and degree of itinerancy, whether itinerant birds were more dependant on wrack deposits and, if so, what determined which birds exhibit which degrees of itinerancy.

The high density of prey in mature wrack deposits may mean they are a highly favoured feeding resource. Socially dominant birds might be expected to exclude subordinates from wrack deposits, or at least to the poorer areas of them, and to be more vagile, moving between sites with wrack deposits. However, the ephemeral – and erratic – nature of wrack deposits might mean that this strategy is risky, as there could be long periods without any suitable deposits.

The principal prey species that Turnstones forage upon over low water provide stable and dependable food resources, as prey on rocky shores cannot retreat into the substrate during hard weather as easily as invertebrates in soft substrates. Dominant birds may exclude subordinate birds from the most profitable low water feeding areas, and hence subordinates may gain a lower energetic intake over the low water feeding period. Additional feeding on wrack deposits over high water (and travelling between sites to find them if necessary) may be required by subordinate birds to "top up" the food taken over low water and may be a more important food resource for these subordinate individuals.

The above hypotheses depend on maximisation of food intake rate as the factor determining what strategy an individual Turnstones utilises. However, death by starvation is probably comparatively rare for Turnstones wintering in Britain and predation, not starvation, is probably the main cause of death (Whitfield 1985b). It may be that socially dominant Turnstones choose a foraging strategy which minimises their risk of predation. Alternatively, if there is an equal pay-off from all points on the fidelity-itinerancy continuum, one would expect to find no

pattern in the social status of Turnstones along the scale from extreme site fidelity to itinerancy.

The radio-tagging of Turnstones allowed their movement and, to a limited extent, behaviour, to be recorded during the night. As with Purple Sandpipers, nocturnal foraging could be an extremely important component of Turnstone wintering ecology, though the evidence for it in this wader species is fragmentary.

7.2 Methods

7.2.1 Catching and Biometrics

Turnstones were caught by cannon-netting at Amble, Hauxley and Cresswell. Mass was weighed to the nearest 1 g with a Pesola balance, wing length (maximum chord, Evans 1976) to the nearest 1 mm with a stopped rule and bill length to the nearest 0.1 mm using Vernier callipers. All birds were ringed with a unique combination of three or four Darvic rings in addition to a standard BTO metal ring. Birds were aged by the presence of pale buff fringes on the median coverts of juveniles (Prater *et al.* 1977).

In order to control for variation in mass due to variation in bird size "adjusted mass" was calculated for each individual using the formula below which produce a calculated mass equivalent to that of a bird with a wing-length of 155.4mm, the mean for all birds caught during the present study.

Adjusted mass = observed mass \times (155.4 3 /observed wing-length 3)

This method assumes that the cubing of a linear relationship is proportional to mass. Summers (1988) found the exponent that the wing-lengths of Purple Sandpipers had to be raised to in order to be proportional to mass was not significantly different from 3.

7.2.2 Sexing

It is not possible to sex Turnstones using biometrics, as there is a large overlap in measurements between sexes. Therefore 25 individuals were sexed using DNA analysis as described in Chapter 6.2.2. In addition, birds were sexed using summer plumage characteristics before they departed in the spring, and in some cases when they returned in late July and early August. The main plumage features used to sex Turnstones were the extent of the ginger scapular patches and amount of white on the nape (Cramp & Simmons 1983); these features were found to show the most pronounced difference between sexes by Whitfield (1985a).

7.2.3 In-field observations

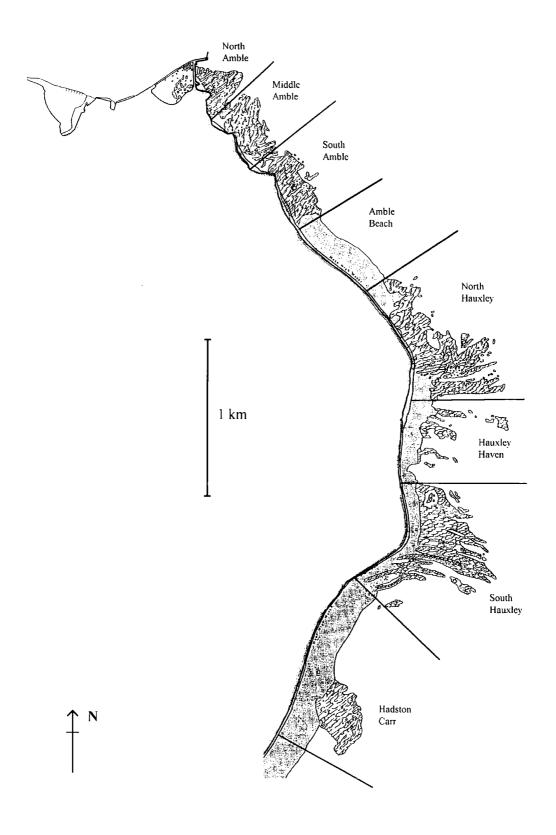
Colour-ringed Turnstones were looked for at all sites within the study area at least once a month in June and July, once a fortnight in August and September, and once a week from October to May. Additional visits were made to Amble and Hauxley so that these sites were visited at least twice weekly (a minimum of one low and one high water visit) over the 1996-97 and 1997-98 winters.

Boulmer (outside the region but visited by colour-ringed Turnstones) was visited at high water twice in the 1996-97 winter and once a month in the 1997-98 and 1998-99 winters. Coquet Island was visited once in each winter.

In 1998-99 additional effort was put into locating Turnstones at Amble, Hauxley and Cresswell where the majority of birds were present. With the occasional exception, Amble and Hauxley were visited at high and low water twice a week over the winter (October to May inclusive) and frequently more often. Cresswell was visited on at least one low and high water every week.

The location of colour-ringed birds was recorded, along with behaviour and feeding substrate (see Chapter 4.2 for classifications of substrate types). Locations were recorded using the site sub-divisions given in Chapter 2; Figure 7.1 shows the divisions used in the Amble-Hauxley area.

Figure 7.1: Map of Amble and Hauxley showing sub-divisions of sites on this shoreline at low water



Four variables were calculated in order to quantify the tendencies of individual Turnstones towards site fidelity and itinerancy. Only data from October to March was used to calculate these variables:

Range -the distance between the northernmost and southernmost sightings within the wintering period.

Mean movement - the mean distance between successive sightings. The distance between locations was calculated from the approximate mid-point of each division i.e. an individual that moved from North Amble to Middle Amble was adjudged to have moved 400 m, regardless of where within these locations it was recorded. Successive sightings at the same location on the same date were removed from the analysis.

Fidelity to low and high water locations. These two variables were calculated as the % of all sightings at the location (site sub-division) that an individual was recorded at the most frequently. As with mean movement, successive sightings at a location on the same date were discarded from the analysis.

7.2.4 Radio-telemetry

Radio-tags were affixed to Turnstones in the same manner as Purple Sandpipers (Chapter 6.2.2) (the method considered standard for small shorebirds). 12 Turnstones were radio-tagged in the 1998-99 winter: 10 at Amble and two at Cresswell. Some problems were experienced with the attachment of radio-tags, as two birds shed their tags within ten days. A further four birds lost their tags between one and four months after attachment. The remaining six birds carried transmitting tags until their departure from the study area (between three and seven months after tagging, depending on dates of tagging and departure).

Observations were made on radio-tagged birds in the same manner as for colourringed birds (above). Individual radio-tagged birds were followed for periods of three hours at a time, with observations of location, behaviour and substrate being made (when possible) every five minutes. Turnstones were radio-tracked at night on 12 occasions between November 1998 and March 1999. Fixes were made on each individual every 15 minutes, or every 5 minutes if an individual was feeding on the mainland. Birds were located by triangulation from two locations a minimum of 100m apart (or if possible three for greater accuracy).

7.3 Results

7.3.1 Catch Details

184 Turnstones were caught over the three years of this study, all but one by cannon-netting at Amble (128), Hauxley (36) and Cresswell (19). 22 birds were re-caught on one later date and one twice.

7.3.1.1 Age

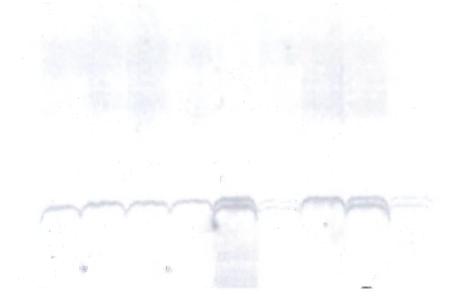
The catching method may have determined the low numbers of juveniles caught, although there is no obvious explanation for cannon-netting producing a bias towards adult birds. Of 63 birds in four separate catches in 1996-97, none were aged as first-years, and of 69 birds in three catches in 1997-98 only four (5.8%) were identified as first-years. However, 18 (30%) of 60 Turnstones caught at Amble on 20th October 1998 were juveniles. First-year birds caught in February and March may have been overlooked due to wear and loss of the diagnostic buff fringes on the median coverts; no bird caught after January was aged as a first-year. Of Turnstones caught before January, 9.7% were first-year birds in 1997-98 and 30% in 1998-99.

7.3.1.2 Sex

25 individuals were sexed by DNA analysis, 12 of which were males and 13 females. Figure 7.2 is a polyacrylamide gel showing the results for several of these birds. Samples with two dark bands are from females, which have the

CHD-W gene as well as the CHD-NW gene carried by both sexes (Griffiths *et al.* 1998). A further 50 birds were sexed in the field by plumage characteristics in spring 1999. For those individuals sexed by both methods (five males, four females) the results agreed. However, the ease of sexing by plumage was biased towards males which were very distinctive in their spring plumage. Some individuals that appeared to be females might have been males that had not yet begun to moult into breeding plumage, particularly those that left the study area in April or early May. Therefore, of the 41 Turnstones sexed by plumage characteristics alone, the ratio of 28 males to 13 females was probably not representative of the population itself.

Figure 7.2: Polyacrylamide gel showing differences between the sexes of Turnstone revealed by DNA analysis



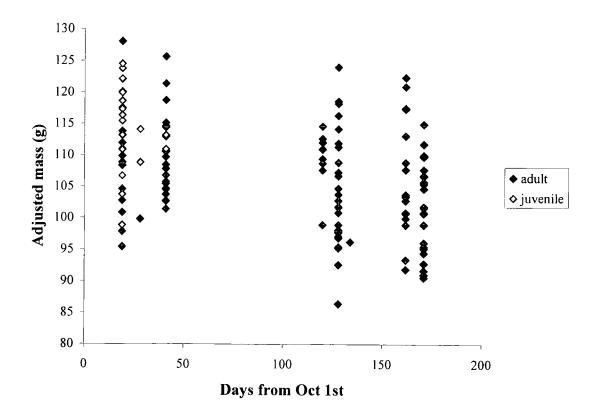
This samples shows five males and four females.

7.3.1.3 Biometrics

Female Turnstones tended to have slightly larger wings than males, but not significantly so, with a mean maximum chord of 157.8 ± 1.2 mm (n = 18) and 156.4 ± 0.6 mm (n = 36) respectively (two-tailed 't'-test, t = 1.12, d.f. = 52, P = n.s.). Adult Turnstones had significantly longer wings than juveniles: adults = 157.8 ± 0.3 mm (n = 143), juveniles = 153.7 ± 0.9 mm (n = 18), (t = 4.4, d.f. = 159, P = 0.01).

Figure 7.3 shows the change in bird mass relative to size (adjusted weight; see section 7.2) over the winter (all three study years combined).

Figure 7.3: Variation in adjusted mass of Turnstones captured during the winter



There was a gradual decline in adjusted mass from the date of the first catch in October to the last in March. However, if juvenile birds are disregarded as they were significantly heavier than adults (see below) and were caught disproportionately more in October (or were overlooked in later catches, see

below) then adjusted mass of adults rose between October and November and declined between February and March.

There was no sign of a premigratory increase in adjusted mass by the date that the latest catch was made, 12th March. It is possible that the actual decline in mass in the late winter was greater than indicated by Figure 7.3 since the method of calculating adjusted mass was dependant on using maximum wing chord as the indicator of bird size and abrasion may have caused this to decrease through the winter. The maximum chord of the only four birds that were caught twice in the same winter averaged 1.5 mm shorter on the second catching occasion (which averaged 3 months later).

Before comparing the masses of different sex and age classes, variation in adjusted mass related to date of catching was allowed for by using the residuals from the mean adjusted mass of all the birds caught on the same date.

Males (mean residual = $+0.19 \pm 0.63$ g, n = 18) averaged slightly but not significantly lighter than females (mean residual = -1.43 ± 0.77 g, n = 36) (two-tailed 't'-test, t = 0.64, d.f. = 50, n.s.). However, juveniles weighed significantly more than adults, by an average of 3.2 g (juvenile mean residual = $+2.81 \pm 0.43$ g, n = 18, adult mean residual = -0.41 ± 0.95 g, n = 142, two-tailed 't'-test, t = 1.99, d.f. = 158, P = 0.05).

7.3.2 Mortality and survival

Of the 63 birds colour-ringed at Amble and Hauxley over the 1996-97 winter, 56 were seen again in the same winter in the study area. 53 (94.6%) of these birds returned the following autumn. 66 marked individuals left the study area in spring 1998 and 55 (83.3%) returned for the 1998-99 winter, including birds colour-ringed at neighbouring sites during the 1997-98 winter and seen again in that winter. This latter value is a minimum over-summer survival rate, which probably underestimates the true rate, since four of the 11 birds that apparently did not return in autumn 1998 were resident on Coquet Island (see below) during

the 1997-98 winter. The island was visited only once during the 1998-99 winter so some of these birds may have returned but were not recorded.

Of the 18 Turnstones colour-ringed at Cresswell in the 1997-98 winter, 16 were seen in the 1998-99 winter, a minimum annual survival rate of 88.9%, comparable with the survival rates calculated for Amble and Hauxley birds.

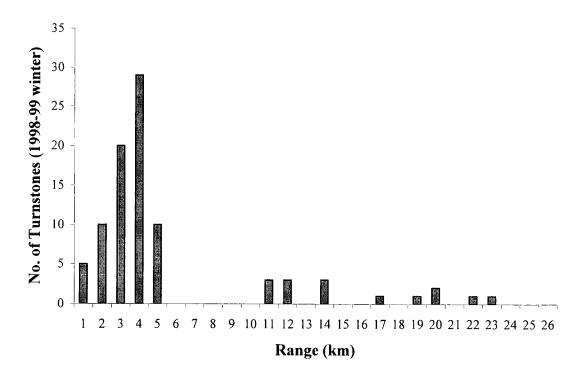
7.3.3 Site fidelity and itinerancy – variation in behaviour amongst Turnstones at Amble and Hauxley

Over the 1998-99 winter, 139 colour-ringed individuals were observed in the Amble-Hauxley area, although no more than 60 were recorded on any given day. Mixing between birds caught at these two adjoining rocky shore sites was high (a number of birds colour-ringed at Amble were chiefly resident at Hauxley and vice versa), and so these birds have been lumped for analysis. (Birds colour-ringed at Cresswell are compared with these Turnstones in section 7.3.6. below).

The fidelity variables described in section 7.2 were calculated for 29 individuals in the 1996-97 winter, 49 individuals in the 1997-98 winter and 98 individuals in the 1998-99. 22 birds provided sufficient data for analysis in two of the three study winters, and 20 in all three winters.

Turnstones colour-ringed at Amble and Hauxley showed wide variation in the their mobility. Figure 7.4 shows the range of movements of individual Turnstones over the 1998-99 winter; while five (5.7%) were not seen outside a 1 km length of coast, most ranged between 2 and 5 km (movement between various localities within the Amble-Hauxley area) while others moved further afield. 15 individuals (16.8%) were seen at other rocky shore sites, 11 at Cresswell, nine at Newbiggin, one at Blyth and one at St. Mary's Island, (34 km from the ringing site). 13 individuals were seen at Boulmer, 8 km to the north of the study area, and presumably some travelled occasionally to other sites further north which were not visited regularly during fieldwork.

Figure 7.4: Ranging behaviour over the 1998-99 winter of 98 Turnstones colourringed at Amble and Hauxley



The "gap" in the distribution of movements shown in Figure 7.4 is due to the geography of the Northumberland coast. The rocky shore sites at Amble and Hauxley are bordered to both north and south by the sandy beaches of Warkworth and Druridge Bay respectively. These beaches were little used by Turnstones (see Chapters 3 and 5) and so individuals either had a maximum range of less than 5 km, meaning that they did not leave Amble-Hauxley, or of over 10 km as they had travelled past these "barriers" north to Boulmer or south to Cresswell, or beyond.

Figure 7.5: Mean distances moved during the 1998-99 winter of 98 Turnstones colour-ringed at Amble and Hauxley

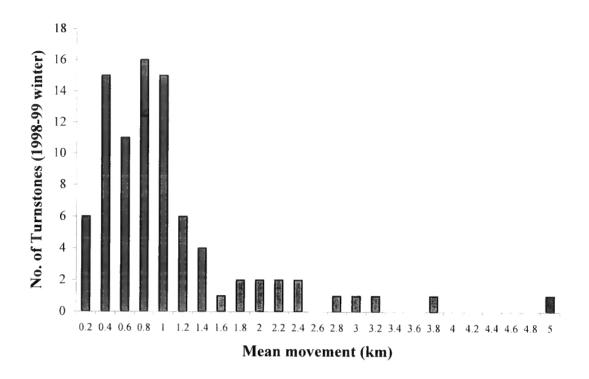
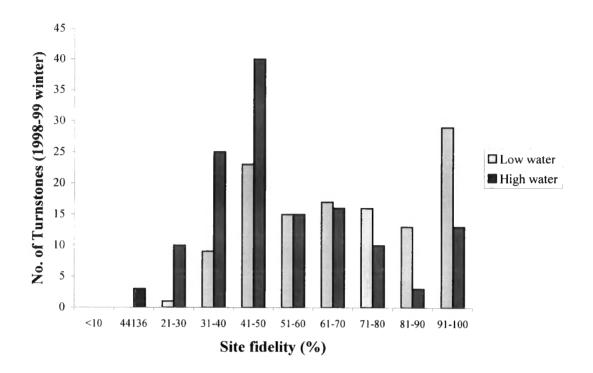


Figure 7.5 shows the mean movements of individual birds between consecutive sightings. Although the actual values themselves revealed little, they allow separation of the behaviour of individuals that may make frequent movements between well-separated sites from those that are mainly sedentary but make an occasional extensive movement.

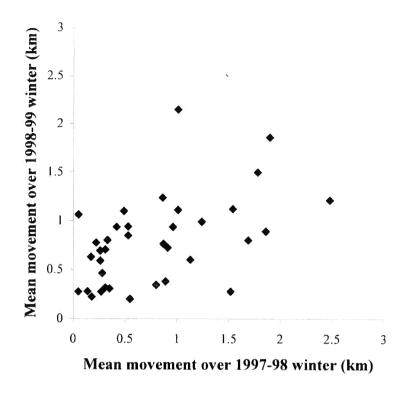
Figure 7.6: Site fidelity over the 1998-99 winter of 98 Turnstones colour-ringed at Amble and Hauxley



Turnstones were more faithful to a low water feeding area than to a high water feeding or roosting site, as shown by Figure 7.6. 29% of all Turnstones were recorded in only one location at low water during the 1998-99 winter, but 13% at only one high water location.

Birds from which data were obtained in more than one winter showed a significant correlation in behaviour between years. For example, the mean distances moved by individuals in 1997-98 were significantly correlated with their mean movements in the 1998-99 winter ($r_s = 0.501$, n = 38, P = 0.01) (Figure 7.7).

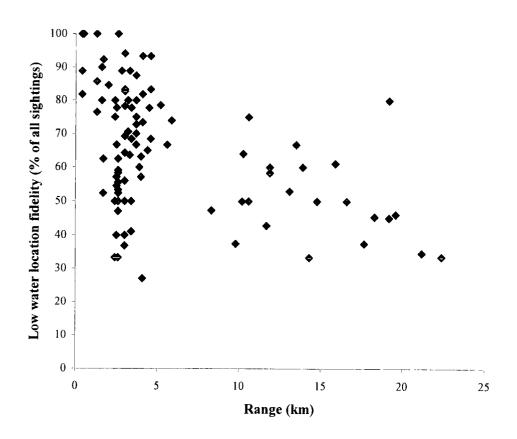
Figure 7.7: Correlation between mean movement of individual Turnstones in the 1997-98 and 1998-99 winters



Birds that showed less movement amongst low water feeding locations were also more faithful at high water ($r_s = 0.26$, n = 132, P = 0.01).

There were significant negative correlations between all fidelity variables and both mean movement distance and range. Figure 7.8 illustrates the relationship between range of movement by an individual and its fidelity to low water feeding location ($r_s = -0.32$, n = 132, P = 0.01).

Figure 7.8: Relationship between fidelity to low water feeding location and range of movement by Turnstones ringed at Amble and Hauxley, 1998-99



To quantify the tendency of each individual Turnstone towards site fidelity/itinerancy by a single measure, an "itinerancy index" was calculated by ranking Turnstones for each of four variables; mean distance moved, range of movement, fidelity to low tide location and fidelity to high tide location. In each case the most site faithful, least itinerant birds (those with low mean distances moved, low range of movement and high fidelity to location) were given the lowest ranking (i.e. rank 1). The four ranks for each bird were summed to produce the itinerancy index. Since 132 Turnstones provided sufficient data for ranking, scores could have lain between 4 and 528. In practice the scores ranged from 18 (extremely site faithful) to 446 (extremely itinerant), with a mean of 244.

7.3.4 Turnstone social status

7.3.4.1 Turnstone dominance data

Almost all aggressive interactions between Turnstones were recorded at high water, either between birds at roost or, more commonly, birds feeding on wrack deposits. 430 such interactions involving colour-ringed individuals were recorded; in 179 cases, both individuals were colour-ringed. In all observations it was easy to identify the aggressor, aggressee and outcome, although the nature and intensity of the interaction varied. Most encounters involved the aggressor approaching the aggressee in the tail-down hunch display, in order to gain access to the food resource that the aggressee was feeding upon or, at roost sites, the particular roosting location the aggressee occupied. An "aggressive rattle vocalisation" (Whitfield 1985) was frequently used. In about 60% of cases the aggressee would move away from the site in contention without confronting the aggressor; on some occasions the aggressor would "press home the advantage", chasing the subordinate individual.

Rarely, the aggressor would peck the fleeing bird. However, on a smaller proportion of instances the bird being attacked would face the aggressor, adopting a similar tail-down hunch display. Usually this posture would result in the aggressee retreating after several seconds of non-violent confrontation, but in less than 5% of cases a fight would occur. When fighting, both birds would stretch upright and run or fly at each other, attempting to land pecks on the head and back of the other bird. Such encounters rarely lasted more than a few seconds before one bird retreated. In such cases the original aggressor was normally the victor. However, they were instances when the original aggressor would back away form the aggressee after it performed a hunch display. In all cases it was clear which bird had won the encounter.

Unfortunately, despite more than 200 hours spent making observations of birds feeding at high water, the number of interactions between colour-ringed birds was insufficient to allow a large number of birds to be accurately ranked in a linear dominance hierarchy. A particular problem was identifying colour-ring

combinations, as most interactions occurred whilst birds were feeding amongst strandline wrack deposits that tended to obscure views of the legs. Nevertheless 14 individuals were placed in such a hierarchy, based on the observation of 63 interactions between 27 pairs of colour-ringed birds. There was a significant relationship between the rank of these 14 individuals and the proportion of the aggressive interactions that they won (Spearman's rank correlation, $r_s = 0.62$, n = 14, P = 0.05); the individual at the top of the hierarchy won all of its 13 interactions while the Turnstone at the bottom won only one out of 12. Therefore it seems that the proportion of encounters that an individual wins can be used as a reliable (though not infallible) indication of a social status. To increase the number of Turnstones for which dominance data were available, the percentage of all aggressive interactions won by each individual (against any other Turnstone whether colour-ringed or not) was used. 33 birds that had been recorded in a minimum of five interactions were included in this analysis.

7.3.4.2 Determinants of social status

Most males had a higher social status than females, although the difference was not significant for either dominance ranking (females (n = 6) median = 10, males (n = 3) median = 2, Mann-Whitney 'U'-test, z = 1.29, n = 9, n.s.) or percentage of aggressive encounters won (females (n = 8) median = 42.5%, males (n = 9) mean = 52.1%, z = 0.48, n = 17, n.s.). Sufficient data were collected only for three first-year birds, but adults (n = 30) won a higher proportion of aggressive encounters (mean = 47.9%) than juveniles (mean = 32.9%), but this difference was not significant (z = 0.35, n = 32, n.s.).

There was no significant relationship between Turnstone dominance ranking and any biometric variable (Table 7.1).

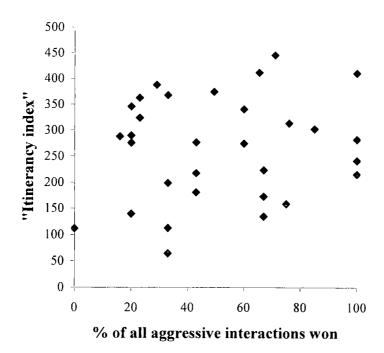
<u>Table 7.1: Results of correlations (Spearman's rank) of measures of Turnstone</u> dominance with biometric variables

Biometric measure	Dominance variable	r_{s}	n	Significance
Wing	Rank	-0.25	14	n.s.
Wing	% encounters won	-0.07	30	n.s.
Residual adjusted mass	Rank	-0.03	14	n.s.
Residual adjusted mass	% encounters won	0.17	30	n.s.

7.3.5 Determinants of Turnstone site fidelity and itinerancy

Both measures of dominance were compared with the measures of site fidelity described in section 7.3.3. More dominant birds were less itinerant, and more site-faithful, than subordinate individuals. Individuals that won a higher percentage of aggressive interactions had significantly lower itinerancy indices $(r_s = -0.36, n = 33, P = 0.05)$ (Figure 7.9) and were more faithful to low water feeding locations $(r_s = 0.34, n = 33, P = 0.05)$. However there were no significant relationships between the percentage of encounters won by an individual and its ranging behaviour $(r_s = -0.15, n = 33, n.s.)$, mean movement distance $(r_s = -0.18, n = 33, n.s.)$ or fidelity to high water location $(r_s = 0.13, n = 33, n.s.)$, although more dominant individuals in the sample studied tended to be more site faithful and therefore less itinerant.

Figure 7.9: Relationship between dominance (as measured by % of aggressive encounters won) and itinerancy in Turnstones at Amble-Hauxley in the 1998-99 winter



Despite the smaller sample size, there were significant relationships between the rankings of the 14 individuals in the linear dominance hierarchy and the itinerancy index ($r_s = 0.58$, n = 14, P = 0.05) (Figure 7.10) and fidelity to low water feeding location ($r_s = -0.61$, n = 14, P = 0.05) (Figure 7.11).

Figure 7.10: Relationship between dominance (rank) and itinerancy in Turnstones at Amble-Hauxley in the 1998-99 winter

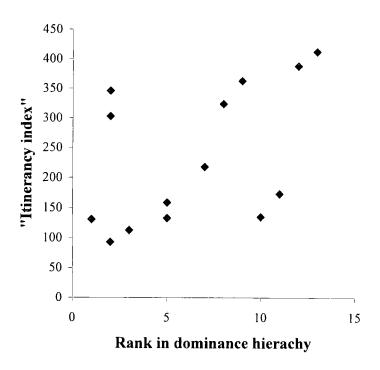
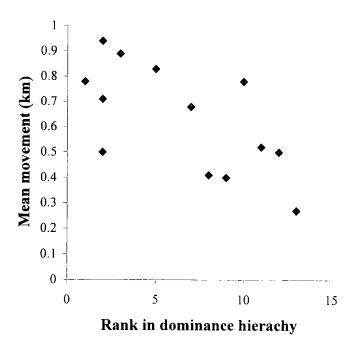


Figure 7.11: Relationship between dominance (rank) and fidelity to low water feeding location in Turnstones at Amble-Hauxley in the 1998-99 winter

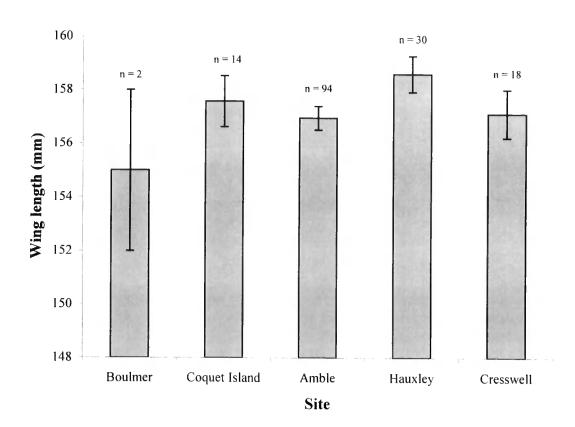


Thus all these results agree that dominant Turnstones were more site faithful and less itinerant than subordinate birds. Although no significant links were found between dominance and age and/or sex (section 7.3.4), the lack of significance may have been due to insufficient data for analysis.

7.3.6 Variation in characteristics of Turnstones at different rocky shore sites

The analysis above concentrated on Turnstones ringed, and in most cases resident, at Amble and Hauxley. In addition to these birds, 19 individuals were colour-ringed at Cresswell. Other colour-ringed individuals were known to be normally resident on Coquet Island, and to the north of the study area at Boulmer. Resident birds were defined as those with at least 50% of low water sightings at one site.

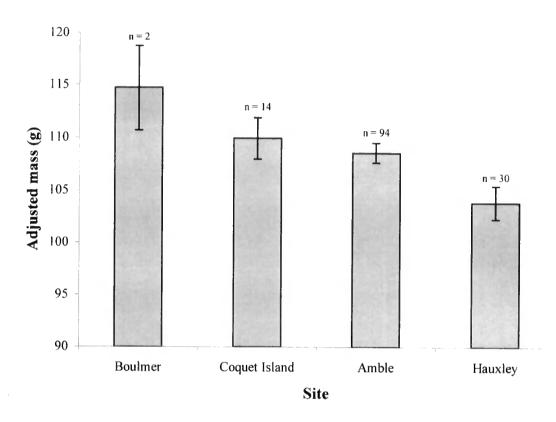
Figure 7.12: Wing-lengths of Turnstones resident at different rocky shore sites, 1998-99 winter



Error bars show one standard error either side of the mean.

There was no significant variation in the wing-lengths of resident Turnstones between all five sites (one-way ANOVA, F = 1.13, d.f. = 4, n.s.).

Figure 7.13: Adjusted masses of Turnstones resident at different rocky shore sites during the 1998-99 winter



Error bars show one standard error either side of the mean.

Turnstones resident at Hauxley had a lower mean adjusted mass than did those at other sites - they presumably carried less fat stores (F = 2.98, d.f. = 3, P = 0.05). Turnstones caught at Cresswell were excluded from this analysis, as they were not caught at the same time of year as birds resident at the other four sites.

The frequency of fieldwork visits was lower at Cresswell than at Amble-Hauxley; that, and the different distances to other rocky shore sites from Cresswell make it inappropriate to compare behavioural variables in detail between the sites. Nevertheless Turnstones colour-ringed at Cresswell showed the same general patterns of behaviour as those at Amble-Hauxley, with some highly resident and others more itinerant, moving to feed at Newbiggin, Hauxley and Amble.

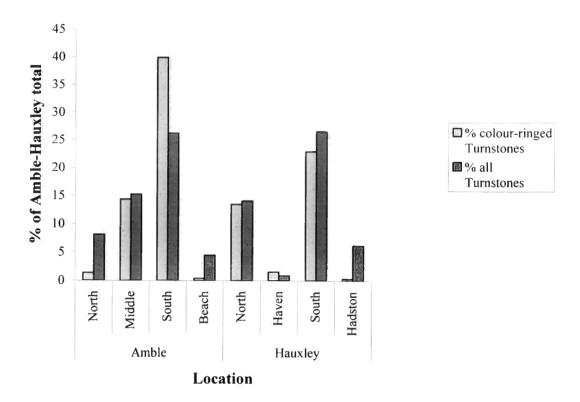
7.3.7 Variation in Turnstone behaviour at locations within the Amble-Hauxley area

Turnstones present within the Amble-Hauxley area tended to have a favoured feeding location within one of the two sites; as demonstrated earlier, their fidelity to this feeding location could be very strong, with some individuals never detected feeding away from it during low water.

Figure 7.14 shows the distribution of colour-ringed Turnstones between feeding locations (see Figure 7.1 for map of divisions). Some feeding locations had few or no resident colour-ringed Turnstones, despite the presence of good numbers of feeding birds. In particular no colour-ringed birds favoured North Amble as a low water feeding location, and sightings of any colour-ringed individuals there were uncommon – just 2.5% of all Amble colour-ring sightings (n = 63), despite a mean of 15% of the total population feeding there. This disparity suggests that the Turnstones that fed at North Amble did not move to wrack deposits at high water to feed along with other Amble Turnstones and hence avoided capture and colour-ringing.

There were also very few sightings (n = 36) of colour-ringed Turnstones at Hadston Carrs, possibly because of the difficulty of obtaining sightings of colour-ringed birds there, since it is not overlooked by low cliffs or dunes. It was necessary to walk out over the intertidal area to look for colour-ringed individuals and the increased disturbance made it considerably harder to record which were present.

Figure 7.14: Detailed distributions of Turnstones at Amble and Hauxley



The behaviour of resident Turnstones at each of four main low water feeding locations (Middle and South Amble and North and South Hauxley) are compared in figures 7.15-17. There was no significant variation in their mean distances of movement (Kruskall-Wallis, $\chi^2 = 7.6$, d.f. = 3, not significant) or range ($\chi^2 = 7.1$, d.f. = 3, n.s.). However there was significant variation in their fidelity to low water location ($\chi^2 = 7.6$, d.f. = 3, P = 0.01), with individuals at North Hauxley less site faithful than birds at the other three locations. This effect was probably simply due to the fact that wrack deposits were rarer at North Hauxley than the other three locations, so some individuals normally resident at North Hauxley may have spent time at other neighbouring locations when wrack deposits were available.

Figures 7.15-17: Variation in Turnstone behaviours between locations

Figure 7.15: Mean distance of movement

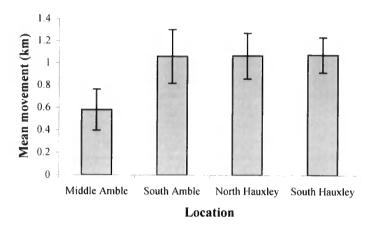


Figure 7.16: Range

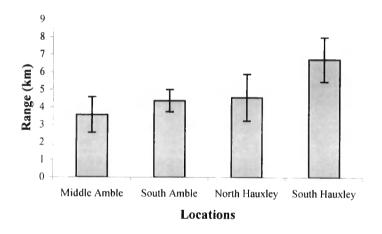
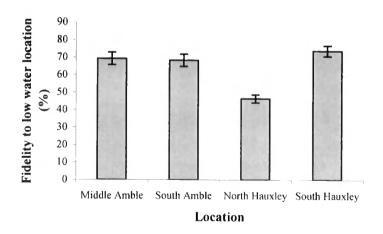


Figure 7.17: Fidelity to low water location



7.3.8 Variation in Turnstone foraging behaviour over the tidal cycle

The results above demonstrate that Turnstones wintering in south Northumberland exhibit a range of degrees of site fidelity. This variation is related to social status (which itself may be related to age and sex) and its magnitude differs amongst sites and between locations within the same site. Further details of individual behaviours were explored by radiotelemetry.

Extensive data were collected on the movements and behaviour of seven radio-tagged individuals in the Amble - Hauxley area. A smaller amount of data was collected from two individuals at Cresswell (see section 7.3.9). As the preliminary analysis of data from colour-ringed birds had shown a difference in the degree of fidelity of birds, radio-telemetry studies were concentrated on determining whether there was any consistent difference between the feeding behaviour of itinerant and resident birds, both at low and at high water. In particular, as I thought the use of strand-line wrack deposits could be a cause of itinerancy in some birds, radio-tracking was concentrated over the high water period to measure any variation between individuals in the amount of time spent foraging on wrack deposits.

For the following analyses, three categories of tidal state were used; low water (<2.0 m O.D.), mid-water (2.1-3.7 m O.D.) and high water (>3.7 m O.D.). Behavioural observations were made as described in section 7.2; only dates upon which a minimum of 10 observations were made on an individual in the appropriate tidal category were entered into the analysis. Table 7.2 gives the number of occasions on which data were collected for each individual. Data collected between November and March (inclusive) only were included in the analyses, in case there were significant changes in Turnstone behaviour in the spring.

<u>Table 7.2: Number of occasions on which adequate behavioural data were</u> <u>collected for each radio-tagged Turnstone</u>

Bird I.D.	LGOR	OmRG	ORLm	OWLm	RGWm	ROWL
Age/sex	Adult	Adult	Adult	Adult	Adult	Adult
	male	female	female	female	male	male
Low water	7	8	10	8	7	7
Mid-tide	5	7	7	8	5	8
High water	9	11	13	12	9	11

7.3.8.1 Individual variation in the amount of time spent foraging

Figures 7.18a-c show the mean percentage of time spent foraging during each of the three tidal stages by the radio-tagged Turnstones resident at Amble-Hauxley. There were no significant differences between individuals in the proportion of time spent foraging at low water (Kruskall-Wallis $\chi^2 = 2.71$, d.f. = 5, not significant) or mid-tide ($\chi^2 = 1.94$, d.f. = 5, n.s.). However some individuals spent considerably more time foraging over high water than others ($\chi^2 = 16.3$, d.f. = 5, P < 0.01). These differences may have been even greater than shown in Figure 7.18c, as this analysis included only those occasions when birds remained on the mainland rather than flying to Coquet Island, presumably to roost. Notably individual LGOR roosted on Coquet Island during diurnal high waters approximately twice as frequently as the other radio-tagged individuals.

Figure 7.18: The mean percentage of time spent foraging by individual radio-tagged Turnstones at different tidal stages (samples sizes in Table 7.2)

Figure 7.18a: Low water

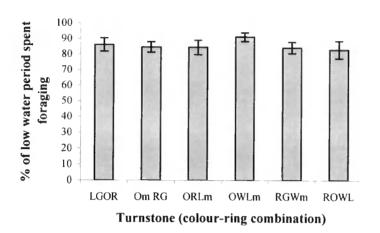


Figure 7.18b: Mid-tide

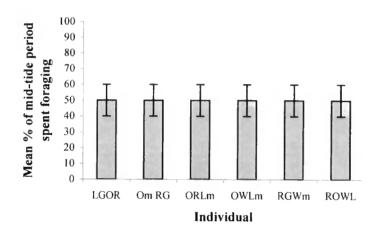
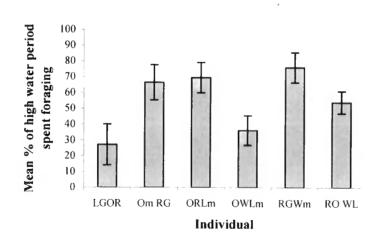


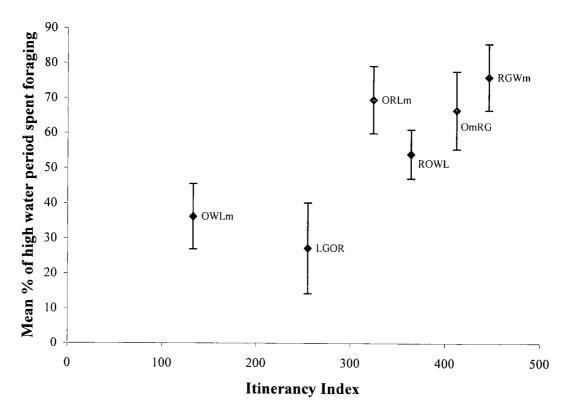
Figure 7.18c: High water



The error bars give one standard error either side of the mean.

There was a significant correlation between the amount of time the six radio-tagged birds spent foraging over high water and the itinerancy index (r_s = 0.398, n = 65, P < 0.01), as demonstrated in Figure 7.19; birds that were less site faithful and more itinerant foraged more over the high water period.

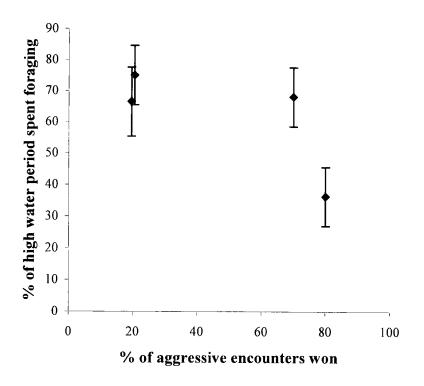
Figure 7.19: Proportion of high water period (>3.7m O.D.) spent foraging by individual radio-tagged Turnstones, plotted against itinerancy index



Error bars show one standard error either side of the mean

There was no significant difference in the amount of time spent feeding over high water by the three male and three female Turnstones (Mann-Whitney, z = 0.59, n = 65, not significant). More high water feeding took place by lower-ranking Turnstones (Figure 7.20), but not significantly so ($r_s = -0.27$, n = 45, not significant). Unfortunately only four of the six birds were recorded in sufficient (i.e. >5) aggressive interactions with other Turnstones to estimate their social status.

<u>Figure 7.20:</u> Relationship between feeding over high water and social status, measured as % of aggressive interactions won, in radio-tagged Turnstones



7.3.8.2 Individual variation in choice of foraging substrate

Figures 7.21a-c show the substrates utilised by foraging radio-tagged Turnstones. At all three tidal stages there were significant differences amongst radio-tagged individuals in their substrate use (Scheirer-Ray-Hare; low water, f = 3.52, d.f. = 20, P < 0.01: mid-tide f = 8.2, d.f. = 20, P < 0.01; high water, f = 4.17, d.f = 20, P < 0.01). A large proportion of this variation lay between LGOR and the other five individuals. Figures 7.21a-c shows how this individual fed amongst live *Fucus* more and on wrack deposits less than the other five Turnstones.

Figure 7.21: Substrate choice by radio-tagged Turnstones foraging at different tidal stages (for sample sizes, see Table 7.2)

Figure 7.21a: Low water

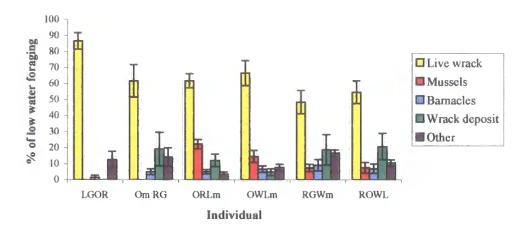


Figure 7.21b: mid-tide

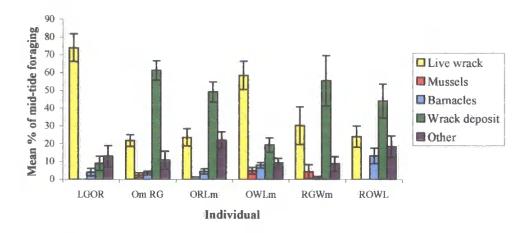
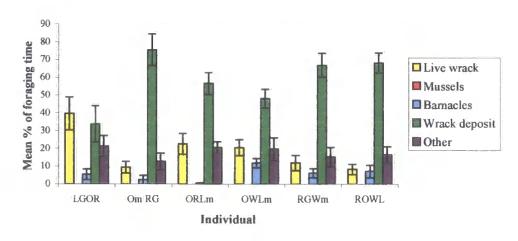


Figure 7.21c: High water



Error bars show one standard error either side of the mean

As mentioned in Section 7.3.8.1 above, this individual also foraged over high water less than the other radio-tagged birds (Figure 7.18c) and frequently flew to Coquet Island at high water, presumably to roost. It was rarely seen on the open coast, rather it fed amongst *Fucus* on the banks of the Coquet Estuary and sometimes roosted in Amble Harbour. Only on c.10% of high waters for which observations were made did it join other Turnstones feeding on wrack deposits at Amble (including, of course, the occasion on which it was originally caught and radio-tagged).

The largest variation in substrate use occurred during the mid-tide stage, Some individuals such as ORLm and OmRG were quicker to move to any available wrack deposits on the rising tide and slower to leave them on the falling tide. There was a significant relationship between the percentage of foraging time that was spent on wrack deposits and both the itinerancy index ($r_s = 0.59 \text{ n} = 40, P < 0.01$) (Figure 7.22) and social status (% of aggressive interactions won) ($r_s = -0.481, n = 27, P < 0.05$) (Figure 7.23) of the six radio-tagged Turnstones.

Figure 7.22: Relationship between foraging on wrack during mid-tide period and itinerancy index

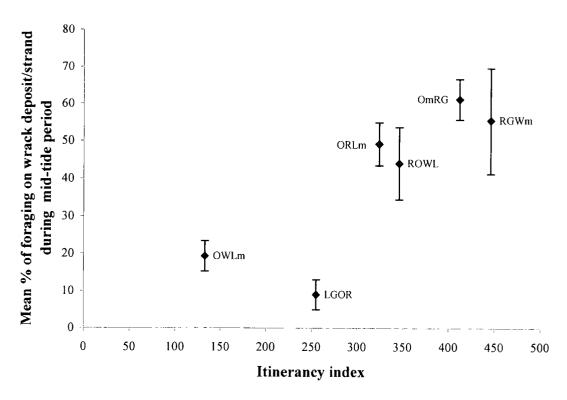
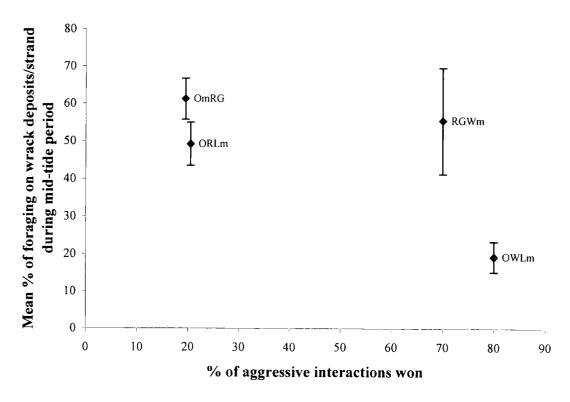


Figure 7.23: Relationship between foraging on wrack during mid-tide period and social status (% of aggressive interactions won)



Error bars show one standard error either side of the mean

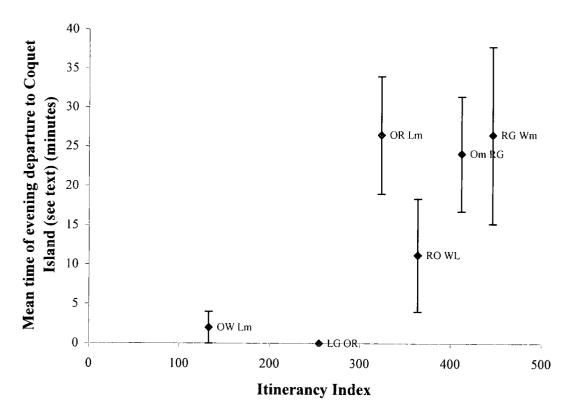
7.3.9 Nocturnal behaviour of radio-tagged Turnstones

7.3.9.1 Turnstones at Amble and Hauxley

Regardless of the tidal state, all radio-tagged Turnstones departed from the mainland to Coquet Island within an hour of dusk. Generally the time of departure was earlier (relative to dusk) on days when high water fell over dusk, but also seemed to vary depending on the availability of wrack deposits and weather conditions. Times of departure, recorded as minutes from the departure of the first radio-tagged individual (set at 0 minutes), were collected on the six radio-tagged individuals at Amble and Hauxley. Some radio-tagged individuals left consistently earlier than others (Kruskall-Wallis, $\chi^2 = 13.2$, d.f. = 5, P < 0.05). Figure 7.24 shows this variation in relation to the itinerancy index of these individuals: there was a highly significant relationship between the itinerancy index and the time of departure, with less itinerant individuals departing earlier ($r_s = 0.48$, n = 30, P < 0.05).

On their arrival at Coquet Island, from the uniformity of signal strength and direction, radio-tagged birds were almost certainly motionless and inactive (roosting), regardless of tidal state.

Figure 7.24: The relationship between itinerancy index and mean relative time of departure to Coquet Island



The error bars show one standard error either side of the mean.

Some birds were active over low water if it fell in the middle part of the night but no activity was detected if low water was shortly after dusk or before dawn. When birds were active four individuals gave signals that frequently varied in strength and direction, indicating they were very probably foraging. In addition these four were recorded feeding on the mainland on at least one night. They were the birds with the highest itinerancy indices and latest departures times from the mainland; the other two individuals, LGOR and OWLm, appeared to be inactive during all nights. Table 7.3 gives an indication of the amount of time spent on the mainland by each bird.

<u>Table 7.3: Nocturnal foraging on Amble-Hauxley mainland by radio-tagged</u>
<u>Turnstones</u>

Bird	Locations visited	No. nights	% active	Mean time
		active	of all	spent on
			nights	mainland
			recorded	
Om RG	North Hauxley	1	12.5	55 mins
RG Wm	North Hauxley	1	14.3	1.05 hrs
RO WL	North Hauxley, South Amble	3	50	2 hrs
OR Lm	North Hauxley, South Amble	3	37.5	2.15hrs ¹

flushed back to Coquet Island on one occasion while radio-tracking.

Although the accuracy of locating Turnstones by triangulation of radio-tag signals (checked during the day) was not great (to the nearest 100 m), birds moving to the mainland at night appeared to be feeding near the tide's edge in areas with a high proportion of wrack cover.

7.3.9.2 Turnstones at Cresswell

The two radio-tagged Turnstones frequently recorded at Cresswell during the day also used the site at night. No difference in behaviour was found between these two birds (RYWL and Gm WR), which continued to feed on the North Scar at dusk until the tide rose to cover the scar (at between 3.3 m and 3.7 m O.D.) when they flew to Coquet Island (a distance of approximately 8 km). These birds were never recorded roosting at Cresswell during the night. On occasions when birds were already roosting at Cresswell at dusk they would depart to Coquet Island soon after. Sight observations suggested that all the Turnstones present at Cresswell flew to Coquet Island to roost.

On five of seven (71%) of the nights over which these individuals were tracked they returned to Cresswell to feed at low water, for about 4 hours. On two occasions they remained on Coquet Island when high water fell in the middle of the night and returned to Cresswell just before dawn as the tide fell. On three of

the five nights when the radio-tagged Turnstones fed at Cresswell they later returned to Coquet Island as the tide rose, but on the other two nights low water was relatively late in the night so the incoming tide did not cover the feeding areas until shortly before dawn. The birds then moved to roost at Snab Point, their normal Cresswell roosting site.

7.4 Discussion

7.4.1 Determinants of social status

Although it proved unexpectedly difficult to rank a large number of Turnstones in a dominance hierarchy, the data gathered in the present study suggest that social status of Turnstones wintering on the south Northumberland coast is determined, at least in part, by age and sex. Previous studies have also found that adults are usually dominant over juveniles (Groves 1978, Whitfield 1985a, Burton 1995) and males are usually dominant over females (Whitfield 1985a, Burton 1995).

Groves (1978) found that adult birds were dominant over juveniles during autumn migration, and were selectively aggressive towards them (resulting in an unquantified loss of foraging time for juvenile birds). She hypothesised that this outcome may have been due to inexperienced juvenile Turnstones responding inappropriately to behavioural cues from adults, and hence triggering adult aggression. However this hypothesis was challenged by Whitfield (1985a) as aggression to juveniles continued throughout the winter, instead of decreasing as would have been expected if juveniles had learnt to interpret these behavioural signals over the winter. Whitfield (1985a) also found that adults (>2 years old) were dominant over immatures (<2 years old). In addition he discovered that amongst adults, males were usually dominant over females, and birds became more dominant as they got older. Past the age of three, birds did not become more dominant by supplanting rivals, but rather just moved up the "ladder" as older birds died.

7.4.2 The effect of social status on site fidelity and itinerancy

The analysis of variables pertaining to the site fidelity and itinerancy of individual Turnstones in the present study clearly showed that individuals utilise different strategies during the winter; some birds are extremely site faithful and never move from a small wintering range of a few hundred metres of coast, while others move large distances up to 20 km, to and fro, along the coast during the course of the winter. These strategies are not discrete, as there appears to be a more or less unbroken continuum between the two extremes of fidelity/itinerancy. However, individual Turnstones did maintain their behaviour between different years.

Previous studies have also found that while some individuals show high site fidelity, other birds move between more distant foraging sites throughout the winter. Burton (1995) found that while some Turnstones were strongly site faithful during the winter within his Hartlepool study area, others were far less so - he classified birds seen on less than 10 of 40 surveys outside of the migration periods as "visitants". The proportion of visitants amongst all colour-ringed birds varied from 37 to 50% in his three study winters. Metcalfe & Furness (1985) classified 13% of adult Turnstones in their Firth of Clyde study area as visitants; this value is not directly comparable with those of Burton as different criteria were used to classify birds. Neither study found a difference (in age, sex or any other descriptive variable) between birds classified as residents or visitants. The present study, however, found a strong correlation between the strategy that individual Turnstones used and their social status. Dominant birds showed higher site fidelity, while subordinates were more itinerant which suggests that there was an advantage to being sedentary during the winter, but that there were not sufficient resources for all Turnstones to use this strategy and so subordinate birds were forced to utilise a different strategy. Sedentary behaviour provides the advantage of familiarity of the wintering area which may offer an advantage when avoiding predators. Sedentary behaviour may also allow birds access to a reliable food resource. Itinerant birds would not have such dependable food intake, but conversely may be able to exploit rich food resources more readily.

7.4.3 Variation in foraging behaviour

Previous studies had shown that social status might affect other aspects of the behaviour of Turnstones. Burton (1995) found that social status determined the location of individual Turnstones within roosting flocks, while Groves (1978) and Whitfield (1985a, 1990) found differences in foraging behaviour.

Whitfield found that amongst Turnstone on the Lothian coast, social status influenced the foraging technique utilized. He classified feeding techniques into six categories: routing (feeding amongst wrack by flicking it aside or "bulldozing" through it), probing, stone-turning, hammer-probing, digging and surface-pecking. High-ranking Turnstones used the routing technique more than subordinate birds, which were excluded from the micro-habitats where routing was the preferred foraging technique. These results suggest that social rank may determine where (and how) an individual Turnstone feeds on a small spatial scale. Both Whitfield (1985a) and Burton (1995) found weak links between size of home range and Turnstone dominance rank, both suggesting that subordinate birds had larger ranges. However both studies concentrated on the low water feeding ranges of basically resident birds and did not consider movements to other sites or the importance of high water feeding.

The results of the present study suggest that social status influences Turnstone behaviour on a larger spatial scale, with subordinates ranging more widely than dominant individuals. It was suggested in the introduction to this chapter that this ranging behaviour may be linked to the use of ephemeral wrack deposits, with individuals moving between sites as and when deposits with high densities of invertebrate prey develop. Strong evidence was found to support this hypothesis. The results of intense radio-telemetry studies on six individuals at Amble-Hauxley revealed that itinerant (subordinate) birds spent more time feeding on wrack deposits than sedentary (dominant) birds, both by moving onto wrack deposits earlier in the tidal cycle (when other intertidal substrates were still accessible) and by feeding for longer (and roosting less) over the high water period.

No significant differences were found between the behaviour of individual Turnstones over low water. However, it seems very likely that dominant Turnstones were able to obtain a higher rate of energy intake over this period and therefore reduce the need to forage over high water. Dominant Turnstones would have been able to forage on the most profitable areas of the intertidal zone and exclude subordinates to areas of lower profitability. It is unlikely that food resources themselves were limiting in the most profitable areas, rather that the despotic aggressive behaviour of Turnstones resulted in there being insufficient space for all birds to feed in these areas.

The number of colour-ringed Turnstones feeding at North Amble was lower than would have been expected if they had had the same probability of capture as birds from other parts of Amble and Hauxley. Not one colour-ringed bird was resident there, despite North Amble being less than 1 km from the site at South Amble where 128 Turnstones were caught and colour-ringed, while feeding on the large wrack deposits there. The North Amble residents probably were the birds seen roosting in the Amble Harbour area, and may have had an even more reliable and better food resource than dominant birds at other locations within the Amble-Hauxley area. North Amble was a unique habitat in this area in that it had a relatively low *Fucus* cover and by far the largest intertidal mussel-bed area (see Chapter 2), which may have provided a better food resource than feeding amongst *Fucus*.

By feeding on the best intertidal areas at low water, thereby minimising their need to feed on wrack deposits at high water, dominant Turnstones may have gained two advantages. Firstly they would have had access to a more reliable food resource over low water, thus minimising any risk of starvation. However, nutrition may not be a major influence on wintering Turnstones. Turnstones exhibit less mid-winter fattening than most other waders in north-west Europe. The lack of any mid-winter catches during the course of this study meant that the degree of mid-winter fattening in Turnstones in south Northumberland is unknown. However, Summers *et al.* (1989) recorded a 5.6% increase in mass at the winter peak and Johnson (1985) a 7.1% increase in mass in Turnstones on the Wash. These values are substantially lower than the 12.6% Johnson (1985)

recorded for the comparably sized Knot, for example. Body reserves (mainly fat) are carried by wintering birds as "insurance" against food shortage and severe weather (Dugan *et al.* 1981). The low levels in Turnstone suggest that they are less likely to suffer from such an energy shortfall than other waders. Mortality rates are low are relatively low; the mean minimum return rate found by this study was 89%, which is comparable to those found in previous studies (Evans & Pienkowski 1984, Metcalfe & Furness 1985, Whitfield 1985, Burton & Evans 1997). Whitfield (1985b) found that the major cause of Turnstone mortality during the winter was predation by raptors, and it may well be that dominant Turnstones are able to utilise a strategy that minimises their risk of predation. Whitfield (1985a) found that itinerant Turnstones suffered higher mortality than resident birds.

By gaining access to a reliable food resource, dominant individuals may be able to minimise the fat reserves needed to act as "insurance" against periods of food shortage. In the present study, juveniles (subordinate) were heavier than adults (more dominant), possibly as juveniles needed greater fat stores to help them survive through periods when there were no wrack deposits available. When the masses of Turnstones resident at different locations were compared, individuals at South Hauxley were significantly lighter than birds elsewhere: the former location had the highest frequency of wrack deposits (Chapter 2). By minimising the fat carried, dominant Turnstones may have increased the likelihood of escaping during aerial attacks by raptors (e.g. Gosler *et al.* 1995, Metcalfe & Ure 1995).

In addition, the choice of foraging site and habitat may influence the likelihood of an individual Turnstone being attacked by an avian predator. The three raptor species that pose a threat to Turnstones in Northumberland – Merlin, Peregrine and Sparrowhawk – all use surprise tactics to catch prey (Ratcliffe 1980, Newton 1986, Cresswell & Whitfield 1994, Cresswell 1995) and hence prefer to take prey close to cover (Whitfield 1985b). During low water, Turnstones are able to feed several hundred metres from the nearest cover in areas with good visibility. However while feeding on wrack deposits over high water Turnstones are close to cover, in particular often close to low cliffs and dunes that provide a covered

approach for hunting raptors. Shanewise & Herman (1979) hypothesised that juvenile Dunlin were taken preferentially by predators because they were excluded to less safe feeding areas by dominant adults, and the same reason was the probable cause of high mortality of juvenile Redshanks found by Cresswell & Whitfield (1994). Therefore it is possible that birds try to minimise their use of wrack deposits over high water to avoid predation and it is for this reason that dominant Turnstones minimise their high water feeding.

7.4.5 Nocturnal behaviour

In chapter 6 it was shown that nocturnal foraging was a very important component of Purple Sandpiper ecology, and that food intake during the night was probably a significant proportion of the total intake. In contrast, Turnstones, move offshore from Amble to Coquet Island and in most cases stay there throughout the night. Even Turnstones that fed at Cresswell during the day, flew to roost on Coquet Island, a 16 km round trip every night. Presumably the island was favoured as it offered protection from predation from foxes *Vulpes vulpes* and other mammalian predators. Observations at Boulmer suggested that birds resident there might also have used Coquet Island to roost at night. Turnstones from further north may fly to the Farne Islands to roost, distances of up to 20 km.

It was presumed that at night, birds on Coquet were not feeding, although it was not possible to visit the island at night to confirm this supposition. Two of six radio-tagged Turnstones that were resident at Amble-Hauxley by day were never recorded feeding at night. The other four birds were recorded leaving Coquet Island to feed on the mainland on an average of less than a third of nights, and for a mean duration of just 1½ hours. There was no difference in the occurrence of nocturnal foraging on moonlit and dark nights. Night foraging was clearly not an important component of Turnstone behaviour. Purple Sandpiper foraging is to a large extent tactile and so is ideal for night foraging, whereas Turnstones tend to forage by sight on prey species hidden amongst *Fucus* and other alga. Unfortunately none of the radio-tagged Turnstones habitually foraged on mussels or barnacles during the day. Had they done so, they might have continued to forage by touch at night. Nocturnal foraging might explain the apparent lack of

high water foraging by Turnstones resident at North Amble where they fed on mussel-beds.

Given that night foraging is so limited for Turnstones at Amble-Hauxley, it is hard to know why birds forage at night at all, especially as the intake rate may be much lower than for diurnal foraging. In this study the individuals that were recorded leaving Coquet Island at night to feed were those that were most itinerant and therefore reliant to some extent on feeding on wrack deposits. Their departure to Coquet Island in the evening tended to be later as they fed for longer in poor light conditions. This observation suggests that night foraging may be used by these birds when they experience a shortfall in prey intake during the day, for example when there are no wrack deposits to provide good high water feeding conditions. Therefore night foraging could be considered to play a "supplementary" role, with Turnstones conforming to the "feed by day" category of Sitters (2000).

The mechanism by which itinerant Turnstones know where the best feeding conditions are remains to be discovered – do, for example, itinerant individuals make frequent exploratory sorties from the current foraging site to neighbouring locations to check on the availability of wrack deposits and other ephemeral food resources? Turnstones are notoriously opportunistic feeders (Beven & England 1977, Cramp & Simmons 1983) and exploit other types of ephemeral food resources e.g. availability of earthworms in coastal pastures due to heavy rain. One possibility is that the nocturnal congregation of birds on Coquet Island from as far apart as Boulmer and Cresswell may provide the opportunity for birds to exchange information about the current availability of food at each site, possibly by assessing the body condition of other birds, or observing whether they leave to forage during nocturnal low waters or not. The hypothesis that roosts act as "information centres" (Ward & Zahavi 1973) remains controversial, and it has been suggested that the observation of other birds feeding by day is a more likely methods for Turnstones to identify the best feeding areas (Summers & Feare 1995).

Chapter 8

General discussion

8.1 Likely changes in the productivity of rocky shores due to reductions in sewage inputs

A number of studies have shown that sewage inputs can have an impact on shorebird and wildfowl numbers by influencing invertebrate densities (e.g. Tubbs 1977, Van Impe 1985, Green *et al.* 1992). These effects have been found in estuaries, where sewage has a longer residence time than on open coastlines where currents cause the rapid dispersal of sewage. One notable example of an impact on birds wintering along an open coast is the decline of Scaup *Aythya marila* and Goldeneye *Bucephela clangula* in the Firth of Forth that followed the introduction of treatment for sewage and distillery waste (Campbell 1978, 1984). However, it was unclear whether these declines were due to the loss of food items taken directly from sewage, or from subsequent decreases in the density of the invertebrates taken by these ducks.

Studies on open coasts and offshore sites have found impacts on a range of other animal species, which suggests that there could also be an effect on bird populations in such ecosystems. Such effects can be very marked, but limited to a relatively small area around outfalls (e.g. Taylor *et al.* 1998, Anderlini & Wear 1992): even very large offshore sewage sludge dump-sites, such as that in the New York Bight, do not show impacts can be detected more than a few kilometres away (Pearce 1995, 2000).

Littler & Stevens (1978) found two distinct food subwebs in a rocky intertidal ecosystem in California affected by sewage inputs, and the same may be true for the south Northumberland coast. One is macrophyte-based, with grazing animals consuming macroalgae: the productivity of this subweb may be increased by the dissolved nutrients discharged in sewage. In particular "opportunistic" species of algae such as *Enteromorpha* and *Ulva* may bloom due to raised nutrient levels

(Littler & Murray 1975, Soulsby *et al.* 1978). In Northumberland, molluscs including limpets, Littorinids and other gastropods such as *R. parva* graze these algae and hence densities of these invertebrates may presently be artificially raised at sites such as Amble and Blyth.

The second subweb consisted of suspension feeders feeding upon plankton and seston. These species can feed directly upon sewage particulates and include barnacles and mussels. A number of studies have found increases in the densities of filter-feeding organisms in the proximity of sewage outfalls, such as mussels and barnacles (López Gappa *et al.* 1993), polychaetes (e.g. *Lumbrineris latreilli*, Crema *et al.* 1991) and the vermatid (sessile tube-dwelling gastropod) *Serpulorbis squamigerus* (Littler & Murray 1975), although often with the consequence of decreased species diversity (Eleftheriou *et al.* 1982, Simboura *et al.* 1995). Increased invertebrate densities can support higher fish populations (Grigg 1994), although some fish species may actively avoid sewage plumes (de Groot 1979).

By 2001 secondary treatment will have been added to every major sewage discharge on the south Northumberland coast. This will reduce the amount of suspended particulate matter in the sewage discharged after treatment by approximately 85% (Welch 1992). Secondary treatment will not strip sewage of all nutrients: dissolved phosphorus is likely to be reduced by 25% only and nitrogen by 50%. However, the lengthening of the outfall pipe at Cambois (to 1 km) will result in a much lower levels of dissolved nutrients from sewage reaching the shore at North Blyth.

The results of analysis of the ratios of stable carbon isotopes in suspended particulate organic matter (Chapter 3) suggested that the sewage discharged at Amble and Cambois contributes a significant proportion of the total POM in inshore waters. Although the limited sampling regime meant that the results could have been subject to considerable error, the contribution of sewage to POM was possibly as high as 60% in the immediate vicinity of outfalls. The proportion of sewage-derived POM decreased with increasing distance to the south (down-current) of discharge points. The productivity of the subweb

involving suspension feeders is likely to have been boosted by sewage inputs, at least in the vicinity (within 1-2 km) of sewage outfalls, and hence will decline with the removal of these inputs. The relative importance of nutrients to the macrophyte-based subweb is not known, but it seems likely that blooms of *Enteromorpha* on the intertidal areas at Amble, Cresswell and Blyth were encouraged by nutrients from sewage.

Given that both subwebs may undergo a decline in productivity, subsequent to the changes in sewage treatment and discharge, there may be a decline in the invertebrate prey species taken by both Purple Sandpipers and Turnstones. This decline could affect these shorebird populations in a number of different ways, which are discussed below.

8.2 Factors affecting the winter distribution of Purple Sandpipers in Europe

The great majority of the European population of Purple Sandpipers winter to the north of Britain, most notably along the coast of Norway, where several hundred thousand may be present during the winter (Alerstam 1982). The British wintering population is very much at the southern edge of the wintering range: although birds do winter as far south as Portugal, numbers to the south of Britain are very small (Cramp & Simmons 1983). Birds wintering in Scandinavia manage to survive despite harsh weather conditions by increasing their intake of food (Summers *et al.* 1999), so obviously do not suffer from a shortage of available prey. By wintering nearer the breeding grounds, birds can minimise the risk of mortality during long migration flights. It is also possible that the risk of predation is lower along the Norwegian coast during winter, as densities of raptors are lower (Cramp & Simmons 1982).

That Britain is near the southern limit of the wintering range of Purple Sandpipers would explain the apparent "empty" habitat in the south and west of England: despite having an abundance of apparently suitable rocky shore habitat, areas such as Devon and Cornwall have very low numbers of Purple Sandpipers (Atkinson *et al.* 1978). Birds arriving in Britain from Arctic and Scandinavian breeding grounds "fill-up" the country from the north southwards with, not

surprisingly, a predominance of birds from Scandinavia in the north-east and from Greenland/Canada in the north-west (Nicoll *et al.* 1988). The birds that winter further south in Europe are probably from the Eastern Siberian population (Hake *et al.* 1997) and hence have a different migration route.

The large number of Purple Sandpipers that winter on the Norwegian coast will not be affected by the Urban Wastewater Directive, as Norway is not a member of the European Community – besides, the low human density on most of the Norwegian coast means that present sewage inputs are not likely to have more than minor localised effects. Although compliance with the Directive in countries further south in Europe may result in a decline in intertidal productivity, numbers of Purple Sandpipers wintering to the south of Britain are so small that it seems highly unlikely that invertebrate densities would decline below the levels necessary to sustain these birds. Therefore, there is a greater likelihood of an impact on Purple Sandpipers in Britain than elsewhere in their European wintering range.

Most Purple Sandpipers in Britain are found in the north and west, on coastlines that are away from centres of human population (indeed, many are on very remote coastlines such as those of the Outer Hebrides and Orkney). Purple Sandpipers in these regions are predominantly from the "long-billed" population (Nicoll *et al.* 1988) and are unlikely to be adversely affected by environmental changes caused by reductions in sewage inputs. Birds from the "short-billed" population are concentrated in eastern Scotland and north-east England, where a larger human population along the coast means that the impact of the Urban Wastewater Directive may be more significant.

Any future changes in the distribution of wintering Purple Sandpipers within Europe are more likely to be associated with climate changes. The numbers of both Purple Sandpipers and Turnstones in southern England declined between the non-estuarine surveys in 1984-85 and 1997-98 (Rehfisch *et al.* 1999), but stayed stable or increased in counties in northern Scotland, suggesting that recent mild winters have caused a northward shift in wintering distribution. The high between-year site fidelity of Purple Sandpipers (Burton 1995, Dierschke 1998,

the present study) suggests that this was not due to birds moving wintering site (northwards) between winters, but rather that the number of young birds settling in southern Britain may have declined.

The present study looked at Purple Sandpiper distribution on a smaller scale, seeking to discover what determined the choice of sites within a region (the south Northumberland coast). The analysis presented in Chapter 2 found a significant relationship between the density of Purple Sandpipers at rocky shore sites within the study area and the area of mussel-bed. Mussels may be the most important prey for Purple Sandpipers in south Northumberland, as mussel fragments were present in a high proportion of faeces (Chapter 4). Birds at the main study site, Blyth, showed a preference for foraging on mussel-beds. Even when not foraging upon areas classified as mussel-beds, Purple Sandpipers take mussels, as they are present at lower densities on most rock substrates except those covered with *Fucus*.

The largest mussel-beds within the study area are at Amble, North Blyth and Seaton Sluice (St. Mary's Island). The first two sites are immediately to the south of major sewage discharges, and the third was until the Seaton Sluice discharge was diverted in the mid 1990s. This proximity to discharges suggests that particulate matter from sewage supports artificially large populations of mussels. The removal of nearly all of this particulate matter may therefore be followed by a decline in the mussel populations at Amble and North Blyth. The mussels in the mussel-bed at Seaton Sluice are, on average, larger than those at the other two aforementioned sites, possibly due to lower recruitment since the cessation of sewage discharge nearby and hence an aging mussel population. This could be a possible explanation for a recent decrease in the number of Purple Sandpipers wintering at St. Mary's island, although other factors, such as human disturbance, may also be involved.

In addition to a decrease in the densities of mussels, a decrease in nutrient loading (if currently significant) will result in fewer Littorinids and *R. parva*, which analysis of faeces also showed to be important prey species.

The models shown in Chapter 2 suggest that Purple Sandpipers settle in the study area proportionately to the food resources (e.g. mussel-beds) available. A change in these resources – such as a decline in mussel-beds at Amble and Blyth – may cause a redistribution of Purple Sandpipers as foraging at these sites becomes less profitable. As the density of food at Blyth (for example) declines, the threshold of Purple Sandpiper density at which it becomes more profitable to settle elsewhere will also become lower, resulting in more individuals choosing to winter elsewhere.

The numbers of Purple Sandpipers at Blyth declined in the spring of each year, with birds moving to the rocky shore sites immediately to the north and south. If this were due to the depletion of food resources by wintering birds then this dispersal will occur earlier if invertebrate populations at the start of future winters are lower due to reduced sewage inputs. However, this dispersal might have been due to birds at Blyth being unable to obtain an increased food intake in the spring to allow for pre-migratory fattening. Unlike the five other rocky shore sites, Blyth has no upper tidal levels, due to man-made sea defences. So whereas at other sites Purple Sandpipers can increase their food intake for feeding for longer over the diurnal tidal cycle, this is not possible at Blyth. This also means that Purple Sandpipers at Blyth cannot compensate for a decline in prey densities in the same manner.

All the Purple Sandpipers radio-tagged during this study were found to forage at night, apparently in much the same manner (and on the same prey) as during the day (Chapter 6). However, birds at both Amble and Blyth spent a shorter period of the tidal cycle foraging at night than during the day, suggesting that diurnal foraging was preferred, despite the higher risk of predation. It also suggests that if a reduction in prey density meant that Purple Sandpipers had to increase the period of time spent foraging they could do so by foraging for longer at night, although the return in prey intake might not be as high as for diurnal foraging.

At sites other than Blyth, Purple Sandpipers would be able to feed for a longer proportion of the tidal cycle in order to compensate for any decrease in intertidal food resources. This would, however, increase the risk of predation (which an

increase in nocturnal foraging would not do, as predation by foxes or owls was not thought to be significant in south Northumberland). Purple Sandpipers are relatively long-lived: the mean minimum annual survival rate found by the present study was 85%, which is similar to that found by other authors (Burton 1995, Dierschke 1998). Few deaths, if any, are due to starvation during the winter, as food availability on rocky shores is not adversely affected by severe weather as it is on soft shores. The major impact of a decline in invertebrate densities would be to cause birds to have to forage for longer, or to spend less time engaged in vigilance while foraging, and hence increase their susceptibility to predation. Foraging during high water may be particularly dangerous for reasons described in Chapters 6 and 7.

The proportion of first-years observed in the whole study area was between 11-13% in all three winters of study. This low level of recruitment into the wintering population may not be sufficient to support the numbers at their present levels, and may be indicative of a decline in the population. Any increase in winter mortality due to increased predation could exacerbate any ongoing decline.

Studies of colour-ringed and radio-tagged birds (Chapter 6) revealed that there is considerable variation in the behaviour of individual birds, which appears to be governed by individuals' social status, which itself is governed by size (Burton 1995, Burton & Evans 2001). Larger (and older) birds had access to the best feeding areas and so were able to minimise the time spent foraging, thus reducing the risk of predation. In addition these individuals were able to carry smaller fat stores, thereby increasing their ability to evade raptors (Gosler 1995, Metcalfe & Ure 1995). If, as seems likely, the prey density at Blyth decreases, then some of the relatively high-ranking individuals that previously wintered there may disperse to other sites, displacing subordinate birds into even poorer habitat. It is these subordinate birds that may either cease to winter within the study area if there is not sufficient "secondary" habitat (Brown 1969) to support them, or if the increased risk of predation faced by birds having to feed for longer (due to a lower rate of prey intake) is prohibitive. As small birds (males and birds of the "short-billed breeding population) are subordinate to larger ones, this means that

it these birds that may be disproportionately affected, as well as juveniles (which are subordinate to adults, Burton 1995).

8.3 Factors affecting the winter distribution of Turnstones in Europe

Turnstones have an extremely widespread non-breeding distribution, with birds being present from Britain down to the end of the Eastern Atlantic flyway in South Africa. The wide range of prey species that Turnstone can take (Cramp & Simmons 1983) means that they can be found in a wide range of habitats. This ubiquity means that the factors that determine the distribution are less clear than those for Purple Sandpiper. Unlike Purple Sandpipers, Turnstones do not winter to the north of Britain, so presumably are less able to survive in the harsh winter conditions and, maybe more importantly, the short daylight period of high latitude winters. Although some radio-tagged individuals were recorded feeding at night, this behaviour was not as prevalent amongst Turnstones as it was for Purple Sandpipers, probably due to the more visual nature of Turnstone foraging.

The multivariate analysis presented in Chapter 3 found that Turnstone density within the study area was best described by the abundance of favoured intertidal foraging substrates, particularly bare/barnacle and *Fucus*-covered rocks. The fit of two of the models was improved with the inclusion of a variable describing the abundance of deposits of wrack and kelp along the high water mark. These deposits were an important food resource for Turnstones at five of the six rocky shore sites within the study area. Unlike Purple Sandpipers, the presence of raptors did not appear to have a modifying effect on Turnstone density, despite the fact that predation by raptors on Turnstones was observed in the study area and has been found to be the major cause of mortality by other studies (Whitfield 1985a).

Turnstones in south Northumberland took a wider variety of prey species than Purple Sandpipers and fed in a wider variety of microhabitats. Amongst the favoured prey species were a number that might be affected by a reduction in dissolved nutrients (Littorinids, shore crabs) and POM (mussels, barnacles). It seems unlikely that growth in *Fucus* and *Laminaria* will be reduced significantly

enough to affect the formation of high water mark wrack deposits, as intertidal macroalgae growth tends to be limited by wave action and exposure rather than nutrient availability. These wrack deposits are of considerable importance to Turnstones at all rocky shore sites within the study area except Blyth, and are exploited by all individuals to a greater or lesser extent.

As with Purple Sandpipers, there was considerable variation in behaviour between individuals. The social status of an individual bird appeared to determine its strategy, both in which site it fed at and on which habitats it foraged within the chosen site (Chapter 7). Dominant birds (males were dominant over females, and adults over first-years) were more resident than subordinates, which travelled between sites to feed on ephemeral strand-line wrack deposits over high water. I have hypothesised that dominant birds did not feed over high water so frequently because they obtained a higher rate of food intake while foraging over low water. This suggests that feeding on wrack deposits was not preferred, despite the superabundance of invertebrates that these deposits often held. There are two obvious explanations for this: (i) that the unreliable nature of wrack deposits as a food resource meant that Turnstones that relied upon wrack suffered a risk of starvation (or having to emigrate to avoid starvation) if deposits were absence for a long period, or (ii) that feeding during high water on the small strip of foreshore left exposed posed a greater risk of predation than feeding on the intertidal area during low water (Whitfield 1985b). As with Purple Sandpipers, dominant Turnstones carried lower fat stores so reducing their probability of being taken by a raptor still further.

So while a decrease in the density of Turnstone prey on the intertidal area is unlikely to cause a direct decrease in Turnstone numbers, it may cause some individuals to change their foraging strategies. A reduction in the density of littoral invertebrates will increase the importance of foraging during high water, on wrack deposits and (to a lesser extent) other ephemeral food resources, particularly for subordinate individuals.

Annual survival of Turnstones is high – the mean value calculated by the present study of 89% is comparable to those found by previous authors (Metcalfe &

Furness 1984, Whitfield 1985a, Burton 1995). Any increase in this mortality, due to Turnstones becoming more susceptible to predation, might have a significant impact on the number of Turnstones wintering within the study area. This could be exacerbated if the density of raptors in the region was to continue to increase as it has done in recent years (Kerr & Johnston 1996, 1997, 1998).

8.4 Implications of the findings of this study for other species

The Urban Wastewater Directive has environmental implications on a far larger spatial scale than merely within the south Northumberland study area, or the coastline of north-east England which is the responsibility of Northumbrian Water plc. All countries along the western seaboard of Europe, with the notable exception of Norway, are required to comply with the directive and implement improvements in the treatment and discharge of sewage that could result in repercussions on populations of wintering birds.

The studies on both species suggest that declines in food resources may not cause a direct decline in bird numbers, as they may not decline below a level at which they become limiting. This is particularly true for Purple Sandpipers, which can survive the winter in far more severe conditions in northern Norway (Summers *et al.* 1999). However, birds may redistribute themselves, as declines in intertidal food resources are likely to be local. In addition, changes in foraging behaviour could increase the risk of predation by raptors, which could be responsible for significant mortality

In addition to Purple Sandpipers and Turnstones, there are a number of other species that might be affected by reductions in invertebrate populations on a larger scale and within the south Northumberland study area. The most obvious of these are the two species for which mussels comprise a large proportion of diet: Oystercatchers and Eiders. Oystercatchers might be affected in much the same manner as Purple Sandpipers, as they feed upon the same intertidal musselbeds. Any effects on Oystercatchers may, however, show a greater time lag after changes in sewage handling due to the selection of mature mussels by Oystercatchers compared with the spat taken by Purple Sandpipers. Similarly,

Eiders take mature mussels, but primarily from subtidal beds. Modelling work by Goss-Custard and co-workers (see Goss-Custard *et al.* 1996b for a review) suggests that the numbers of Oystercatchers in Europe are not limited by prey abundance: even when unrealistic production success was input into models they failed to predict that numbers wintering grounds would reach carrying capacity. However, they did find that local habitat loss (or, as is possible in this case, habitat degradation) might cause local population declines.

This present study has not looked at the effect of reducing sewage inputs in estuaries, where large concentrations of shorebirds and the semi-closed ecosystem means that impacts will be greater. However, the results from this study suggest that the Urban Wastewater Directive could result in significant local effects on invertebrate prey populations of a number of waterfowl species on open coasts. At the very least this could lead to local changes in the distribution of these species, or possibly to local or even widespread declines in wintering numbers. These impacts could affect different components of populations disproportionately.

8.5 Recommendations for further work

The period of the present study extended up until the improvements in the handling of sewage in south Northumberland were about to be introduced. Therefore, this thesis presents a "before" snapshot of the ecology of Purple Sandpipers and Turnstones wintering within the study area. Further study will allow the actual impact of the changes in treatment and discharge of sewage on invertebrate prey densities to be measured.

Several problems were encountered during the collection and analysis of stable isotopes (Chapter 3): the inaccurate determination of nitrogen isotope ratios, the lack of data for inputs from rivers such as the Coquet and the insufficient sampling regime of seawater POM. Further studies would be able to reduce the inaccuracy caused by these problems, resulting in more reliable measurements of both carbon and nitrogen isotope ratios. This would allow the relative importance of sewage inputs to POM to be calculated with more confidence.

Ideally, isotope studies could be advanced up the trophic ladder from particulate matter to, for example, determine what proportion of the diet of intertidal mussels originated from sewage at the separate rocky shore sites in the study area. This approach was used by Achituv *et al.* (1997) to determine the food of Red Sea Barnacles (Cirripedia). It might even be possible to take appropriate samples from birds in order to calculate the proportion of their diets that originally derived from sewage. Previous studies, such as that by Bearhop *et al.* (1999), have used the isotopic composition of feathers to determine the main sources of bird diets.

Much of the research presented in this thesis attempted to examine the various merits of different strategies employed by individual birds, whether this was between birds at different rocky shore sites or those employing different foraging strategies within the same site (Chapters 4 to 7). This was done without much of the empirical data that would have allowed a detailed examination of the benefits of each alternative. To acquire this information would require a great deal of very detailed fieldwork, and even then might be unsuccessful as it is very hard to measure accurately the costs and benefits of different behaviours. Particularly valuable would be the measurement food intake rates of birds employing different foraging strategies. Unfortunately, intake rates are extremely difficult to accurately measure in small shorebirds that forage rapidly and usually on prey items that cannot be seen.

For both study species it was felt that the risk of predation was an important determinant of decisions made about where to winter, and what feeding strategy to adopt. Apart from the observations of raptor presence used as a variable in the multivariate modelling, no attempt was made to quantify this predation risk. Although this may be complicated (and require a great deal of effort) an assessment of the risk to individual birds may be able to confirm the hypothesis that avoiding predation was the major determinant of wintering distribution (on a local scale) of both Turnstones and Purple Sandpipers.

The findings of this and any future studies could help to refine the methods for monitoring Purple Sandpipers and Turnstones, not so much to improve studies such as this (which have the necessary time and effort to produce accurate counts) but to help improve the accuracy of large scale surveys. With ongoing declines and changes in the distribution of both species, and the conservation interest that this arouses, it could be of significant benefit to future studies if more accurate monitoring protocols could be designed.

References

Aboulkassim, T.A. (1992) Impact of sewage disposal on the distribution and flux of detergents in Alexandria coastal waters, Egypt. *Water Sci. Tech.* **25**: 93-100.

Achituv, Y., Brickner, I. & Erez, J. (1997) Stable carbon isotope ratios in Red Sea barnacles (Cirripedia) as an indicator of their food source. *Mar. Biol.* **130**: 243-247.

Alderslade, R. (1981) in *Recent Experience in the United Kingdom:*Characterisation, Treatment, and Use of Sewage Sludge, Eds. P.L. Hermite, & H. Ott, Dordrecht, Reidel Publishing.

Alerstam, T. (1982) Fågelflyttning. Signum, Lund.

Altmann, J. (1974) Observational study of behaviour sampling methods. *Behaviour* **49**: 227-265.

Anderlini, V.C. & Wear, R.G. (1992) The effect of sewage and natural seasonal disturbances on benthic macrofaunal communities in Fitzroy Bay, Wellington, New Zealand. *Mar. Poll. Bull.* **24**: 21-26.

Aschoff, J. (1981) Thermal conductance in mammals and birds: its dependance on body size and circadian phase. *Comp. Biochem. Physiol.* **69**: 611-619.

Atkinson, N.K., Davies, M. & Prater, A.J. (1978) The winter distribution of Purple Sandpipers in Britain. *Bird Study* **25**: 223-228.

Atkinson, N.K., Summers, R.W., Nicoll, M. & Greenwood, J.J.D. (1981) Population, movements and biometrics of the Purple Sandpiper *Calidris maritima* in eastern Scotland. *Ornis Scand.* 12: 18-27.

Bachtiar, T., Coakley, J.P. & Risk, M.J. (1996) Tracing sewage-contaminated sediments in Hamilton Harbour using selected geochemical indicators. *Sci. Tot. Env.* **179**: 3-16.

Baker, J.M. & Wolff, W.J. (1987) *Biological surveys of estuaries and coasts*. Cambridge University Press, Cambridge.

Bassam, B.J., Caetano-Anollés, G. & Gresshoff, P.M. (1991) Fast and sensitive silver staining of DNA in polyacrylamide gels. *Anal. Biochem.* **196**: 80-83.

Bearhop, S., Thompson, D.R., Waldron, S., Russell, I.C., Alexander, G. & Furness, R.W. (1999) Stable isotopes indicate the extent of freshwater feeding by cormorants *Phalacrocorax carbo* shot at inland fisheries in England. *J. Appl. Ecol.* **36**: 75-84.

Bednekoff, P.A. (1996) Translating mass depedent flight performance into predation risk: an extension of Metcalfe & Ure. *Proc. Roy. Soc. Lond. B* **263**: 887-889.

Bernstein, C., Krebs, J.R. & Kacelnik, A. (1991) Distribution of birds amongst habitats: theory and relevance to conservation. In: Perrins, C.M., Lebreton, J.D. & Hirons, J.M.D. (eds), *Bird Population Studies*, Oxford University Press, Oxford.

Boere, G., Roselaar, K. & Engelmoer, M. (1984) The breeding origins of Purple Sandpipers *Calidris maritima* present in the Netherlands. *Ardea* 72: 101-109.

Bradley, R.A. & Bradley, D.W. (1993) Wintering shorebirds increase after kelp (*Macrocystis*) recovery. *Condor* **95**: 372-376.

Branson, N.J.B.A., Ponting, E.D. & Minton, C.D.T. (1978) Turnstone migrations in Britain and Europe. *Bird Study* **25**; 181-187.

Brown, J.L. (1969) Territorial behaviour and population regulation in birds. *Wilson Bull.* **81**: 293-329.

Brown, R.A. & Seed, R. (1977) *Modiulus modiolus* (L.) – an autoecological study. In: *Biology of benthic organisms*, eds. Keegan, B.F., Ócéidigh, P. & Boaden, P.J.S., Pergamon Press, Oxford.

Bruinzeel, L.W., Piersma, T. & Kersten, M. (1999) Low costs of terrestrial locomotion in waders. *Ardea* 87: 199-205.

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

Burger, J. & Olla, B.L. (1984) Behaviour of marine animals, volume 6: Shorebirds, migration and foraging behaviour. Plenum, New York.

Burnett, W.C. & Schaeffer, O.A. (1980) Effects of ocean dumping of ¹³C/¹²C ratios in marine sediments from the New York Bight. *Est. Co. Mar. Sci.* **1**: 605-611.

Burton, N.H.K. (1995) Roosting and associated feeding behaviour of Turnstones Arenaria interpres and Purple Sandpipers Calidris maritima in north-east England. PhD. thesis, University of Durham.

Burton, N.H.K., Evans, P.R. & Robinson, M.A. (1996) Effects on shorebird numbers of disturbance, the loss of a roost site and its replacement by an artificial island at Hartlepool, Cleveland. *Biol. Conserv.* 77: 193-201.

Burton, N.H.K. & Evans, P.R. (1997) Survival and winter site-fidelity of Turnstones *Arenaria interpres* and Purple Sandpipers *Calidris maritima* in northeast England. *Bird Study* **44**: 35-44.

Burton, N.H.K. & Evans, P.R. (2001) Aggressive behaviours and correlates of dominance in Purple Sandpiper *Calidris maritima* at a communal winter roost, *Ibis* **143**: 248-254.

Buxton, N.E., Summers, R.W. & Nicoll, M. (1985) The populations and biometrics of Purple Sandpipers in the Outer Hebrides. *Ring. & Migr.* **6**: 87-92.

Caccamise, D.F. & Morrison, D.W. (1986) Avian communal roosting: implications of diurnal activity centres. *Am. Nat.* **128**: 191-198.

Campbell, L.H. (1978) Patterns of distribution and behaviour of flocks of seaducks wintering at Leith and Musselburgh, Scotland. *Biol. Conserv.* **14**: 111-124.

Campbell, L.H. (1984) The impact of changes in sewage treatment on seaducks wintering in the Firth of Forth, Scotland. *Biol. Cons.* **28**: 173-180.

Cayford, J.T. (1988) The foraging behaviour of Oystercatchers (*Haematopus ostralegus*) feeding on mussels (*Mytilus edulis*). Unpublished PhD. thesis, University of Exeter.

Chan, K.H., Lam, M.H.W., Poon, K.F., Yeung, H.Y. & Chiu, T.K.T. (1998) Application of sedimentary fecal stanols and sterols in tracing sewage pollution in coastal waters. *Water Res.* **32**: 225-235.

Comely, C.A. (1978) Modiolus modiolus (L.) from the Scottish West coast. I. Biology. *Ophelia* 17: 167-193.

Corse, C.J. & Summers, R.W. (1999) The seasonal pattern of numbers, population structure and migration of Purple Sandpipers *Calidris maritima* in Orkney. *Ring. & Migr.* **19**: 275-282.

Craig, H. (1953) The geochemistry of the stable carbon isotopes. *Geochimica et Cosmochimica Acta* **3**: 53-92.

Cramp, S. & Simmons, K.E.L. (1983) *Birds of the Western Palearctic, Vol III*. Oxford University Press, Oxford.

Cranswick, P.A., Pollit, M.S., Musgrove, A.J. & Hughes, R.C. (1999) *The Wetland Bird Survey 1997-98: Wildfowl and Wader counts*. BTO/WWT/RSPB/JNCC, Slimbridge.

Crema, R., Castelli, A. & Prevedelli, D. (1991) Long term eutrophication effects on macrofaunal communities in northern Adriatic Sea. *Mar. Poll. Bull.* **22**: 503-508.

Cresswell, W. (1994) Age-dependent choice of redshank (*Tringa totanus*) feeding location: profitability or risk? *J. Anim. Ecol.* **63**: 589-600.

Cresswell, W. (1995) Selection of avian prey by wintering Sparrowhawks *Accipiter nisus* in southern Scotland. *Ardea* **83**: 381-389.

Cresswell, W. & Whitfield, D.P. (1994) The effects of raptor predation on wintering wader populations at the Tyninghame Estuary, Southeast Scotland. *Ibis* **136**: 223-232.

Dayton, P.K. (1979) Competition, disturbance and community organisation: the provision and subsequent utilization of space in a rocky intertidal community. *Ecol. Monogr.* **41**: 351-389.

Davidson, N.C. (1981) Seasonal changes in the nutritional condition of shorebirds (Charadrii) during the non-breeding season. Unpublished PhD. thesis, University of Durham.

Davidson, N.C. (1990) Body condition of Purple Sandpipers *Calidris maritima* wintering in north-east England. *Wader Study Group Bull.* **58**: 22-24.

Davidson, N.C. & Clark, N.A. (1985) The effects of severe weather in January and February 1985 on waders in Britain. *Wader Study Group Bull.* **44**: 10-16.

Davidson, N.C. & Evans, P.R. (1989) Pre-breeding accumulation of fat and muscle protein by Arctic breeding shorebirds. *Proc.Int. Orni. Con. XIX*, p342-352.

Dayton, P.K. (1971) Competition, disturbance and community organisation: the provision and subsequent utilisation of space in a rocky intertidal community. *Ecol. Monogr.* **41**: 359-389.

De Groot, S.J. (1979) An assessment of the potential environmental impact of large scale sand dredging for the building of artificial islands in the North Sea. *Ocean Manage*. **5**: 211-232.

Dennis, R.H. (1983) Purple Sandpipers breeding in Scotland. *Brit. Birds* **59**: 165-179.

Dierschke, V. (1994) Food and feeding ecology of Purple Sandpipers *Calidris maritima* on rocky intertidal habitats (Helgoland, German Bight). *Neth. J. Sea Res.* **31**: 309-317.

Dierschke, V. (1998) Site fidelity and survival of Purple Sandpipers *Calidris* maritima at Helgoland (SE North Sea). *Ring. & Migr.* **19**: 41-48.

Dugan, P.J., Evans, P.R., Goodyer, L.R. & Davidson, N.C. (1981) Winter fat reserves in shorebirds: disturbance of regulated levels by severe weather conditions. *Ibis* **123**: 359-363.

Eaton, M.A. (1998) Monitoring the effects of changes in sewage treatment and disposal by Northumbrian Water plc. on the Northumberland coast, with ecological studies of Turnstones Arenaria interpres and Purple Sandpipers Calidris maritima. Unpublished report to Northumbrian Water plc, University of Durham.

Eaton, M.A. (2000) Studies on Purple Sandpipers and Turnstones at Hartlepool, 1999-2000: have recent changes in the treatment and discharge of sewage had an impact? Unpublished report to Northumbrian Water plc, University of Durham.

Elefthriou, A., Moore, D.C., Basford, D.J. & Robertson, M.R. (1982) Underwater experiments on the effects of sewage sludge on a marine ecosystem. *Neth. J. Zool.* **16**: 465-473.

Elhmmali, M.M., Roberts, D.J. & Evershed, R.P. (1997) Bile acids as a new class of sewage pollution indicator. *Env. Sci. Tech.* 31: 3663-3668.

English Nature (1992) *Northumberland Shore SSSI notification*. Unpublished report.

Ens, B.J., Piersma, T. & Drent, R.H. (1994) The dependence of waders and waterfowl migrating along the East Atlantic flyway on their coastal food supplies: what is the most profitable research programme. *Ophelia*, Suppl. 6, 127-151.

Ens, B.J. & Zwarts, L. (1980) Wulpen op het wad van Moddergat. *Watervogels* 5: 108-120.

Evans, P.R. (1976) Correct measurement of the wing-length of waders. *Wader Study Group Bull.* **48**: 11.

Evans, P.R. (1981) Migration and dispersal of shorebirds as a survival strategy. In: Burger, J. & Olla, B.L. (eds.) *Behaviour of Marine Animals vol. 5*, *Shorebirds: Breeding Behaviour and Populations*. Plenum Press, New York.

Evans, P.R. & Pienkowski, M.W. (1984) Population dynamics of shorebirds. In: Burger, J. & Olla, B.L. (eds.) *Behaviour of Marine Animals vol. 5, Shorebirds: Breeding Behaviour and Populations*. Plenum Press, New York.

Evans, P.R. & Pienkowski, M.W. (1985) The role of migration in the population dynamics of birds. In: *Behavioural ecology: ecological consequences of adative behaviour*, eds. Sibly, R.M. & Smith, R.H., Blackwell Scientific Publications, Oxford.

Feare, C.J. (1966) The winter feeding of the Purple Sandpiper. *British Birds* **59**: 165-179.

Feare, C.J. & Summers, R.W. (1985) Birds as predators on rocky shores. In: *The ecology of rocky coasts: essays presented to J.R.Lewis*, Eds. Moore, P.G. & Seed. R., Hodder and Stoughton, London.

Fowler, J., Cohen, L. & Jarvis, P. (1998) *Practical Statistics for Field Biology*. John Wiley & Sons, Chichester.

Fretwell, S.D. (1972) *Populations in a seasonal environment*. Princetown University Press, Princetown.

Fretwell, S.D. & Lucas, H.L. (1970) On territorial behaviour and other factors influencing distribution in birds. *Acta Biotheo*. **19**: 16-36.

Furness, R.W. (1973) Roost selection by waders. Scottish Birds 7: 281-287.

Furness, R.W. & Greenwood, J.J.D. & Jarvis, P.J. (1993) Can birds be used to monitor the environment? In: *Birds as monitors of environmental change*, Eds. R.W. Furness & J.J.D. Greenwood, London, Chapman & Hall.

Galloway, B. & Meek, E.R. (1980) *Northumberland's Birds, part 2*. Natural History Society of Northumbria, Newcastle.

Gearing, J.N., Gearing, P.J., Rudnick, P.T., Requejo, A.G. & Hutchins, M.J. (1991) Isotopic variability of organic carbon in a phytoplankton based, temperate estuary. *Geochim. Cosmochim. Acta* **48**: 1089-1098.

Gerritsen, A.F.C. & Sevenster, J.G. (1985) Foraging behaviour and bill anatomy in sandpipers. *Forts. Zool.* **30**: 237-239.

Gerritsen, A.F.C. & Van Heezik, Y.M. (1985) Substrate preference and substrate related foraging behaviour in 3 *Calidris* species. *Neth. J. Zool.* **35**: 671-692.

Gerritsen, A.F.C., Van Heezik, Y.M. & Swennen, C. (1983) Chemoreception in 2 further *Calidris* species (*Calidris maritima* and *Calidris canutus*) - with a comparison of the relative importance of chemoreception during foraging in *Calidris* species. *Neth. J. Zool.* **33**: 485-496.

Ghinsberg, R.C. & Dov, L.B., Sheinberg, Y., Nitzan, Y. & Rogol, M. (1994) Monitoring of selected bacteria and fungi in sand and sea-water along the Tel-Aviv coast. *Microbios* 77: 29-40.

Gibbons, D.W., Reid, J.B. & Chapman, R.A. (1993) *The new atlas of breeding birds in Britain and Ireland: 1988-91*. Poyser, London.

Gosler, A.G., Greenwood, J.J.D. & Perrins, C. (1995) Predation risk and the cost of being fat. *Nature, Lond.* **377**: 621-623.

Goss-Custard, J.D. (1970) The responses of Redshank (*Tringa totanus*) (L.) to spatial variation in the density of their prey. *J. An. Ecol.* **39**: 91-113.

Goss-Custard, J.D. (1996) The Oystercatcher. Oxford University Press, Oxford.

Goss-Custard, J.D., Caldow, R.W.G., Clarke, R.T., Durell, S.E.A. le V. dit & West, A.D. (1995) Deriving population parameters from individual variations in foraging behaviour: I. Emperical game theory distribution model of Oystercatchers *Haematopus ostralegus* feeding on mussels *Mytilus edulis*. *J. Anim. Ecol.* **64**: 265-276.

Goss-Custard, J.D. & Durell, S.E.A. le V. dit (1984) Individual and age differences in the feeding ecology of Oystercatchers *Haematopus ostralegus* wintering in the Exe Estuary, Devon. *Ibis* **125**: 155-171.

Goss-Custard, J.D. & Durell, S.E.A. le V. dit (1987) Age-related effects in Oystercatchers, *Haematopus ostralegus*, feeding on mussels, *Mytilus edulis. J. Anim. Ecol.* **56**: 521-558.

Goss-Custard, J.D., Durell, S.E.A. le V. dit, Goater, C.P., Hulscher, J.B., Lambeck, R.H.D., Meininger, P.L. & Urfi, J. (1996a) How Oystercatchers survive the winter. In: *The Oystercatcher*, (ed.) Goss-Custard, J.D., Oxford University Press, Oxford.

Goss-Custard, J.D., West, A.D., Clarke, R.T., Caldow, R.W.G. & Durell, S.E.A. le V. dit (1996b) The carrying capacity of coastal habitats for Oystercatchers. In: *The Oystercatcher*, (ed.) Goss-Custard, J.D., Oxford University Press, Oxford.

Goss-Custard, J.D., Jenyon, R.A., Jones, R.E., Newbery, P.E. & Williams, R. le B. (1977a) The ecology of the Wash. II. Seasonal variation in the feeding conditions of wading birds (*Charadrii*). *J. App. Ecol.* **14**: 701-719.

Goss-Custard, J.D., Jones, R.E. & Newbery, P.E. (1977b) The ecology of the Wash. I. Distribution and diet of wading birds (*Charadrii*). *J. App. Ecol.* **14**: 681-700.

Goss-Custard, J.D. & Sutherland, W.J. (1984) Feeding specialization in Oystercatchers *Haemotopus ostralegus*. *Anim. Behav.* **57**: 827-844.

Green, P.T., Hill, D.A. & Clark, N.A. (1992) The effects of organic inputs to estuaries on overwintering bird populations and communities. Department of Energy, London.

Griffiths, R., Double, M.C., Orr, K. & Dawson, R.J.G. (1998) A DNA test to sex most birds. *Mol. Ecol.* 7: 1071-1075.

Griffiths, R.J. (1981) Population dynamics and growth of the bivalve *Choromytilus meridionalis* (Kr.) at different tidal levels. *Est. Co. Shelf. Sci.* **12**: 101-118.

Grigg, R.W. (1994) Effects of sewage discharge, fishing pressure and habitat complexity on coral ecosystems and reef fishes in Hawaii. *Mar. Ecol. Prog. Ser.* **103**: 25-34.

Groves, S. (1978) Age-related differences in Ruddy Turnstone foraging and aggressive behaviour. *Auk* **95**: 95-103.

Hake, M., Blomqvist, Pierce, E.P., Järås, T. & Johansson, O.C. (1997) Population size, migration routes and breeding origin of Purple Sandpipers *Calidris maritima* wintering in Sweden. *Ornis Svecica* 7: 121-132.

Hansson, S., Hobbie, J.E., Elmgren, R., Larsson, U., Fry, B. & Johansson, S. (1997) The stable nitrogen isotope ratio as a marker for food web interactions and fish migration. *Ecology* **78**: 2249-2257.

Heezik, Y.M. Van, Gerritsen, A.F.C. & Swennen, C. (1983) The influence of chemoreception on the foraging behaviour of two species of sandpiper, *Calidris maritima* (Pallas) and *Calidris alpina* (L.). *Neth. J. Sea Res.* 17: 47-56.

Hilton, G.M., Ruxton, G.D. and Cresswell, W. (1999) Choice of foraging area with respect to predation risk in redshanks: the effects of weather and predator activity. *Oikos* 87: 295-302.

Holdgate, M. (1979) *A perspective of environmental pollution*. Cambridge University press, Cambridge.

Hulscher, J.B., Alting, D., Bunskoeke, E.J., Ens, B.J. & Heg, D. (1997) Subtle differences between male and female Oystercatchers *Haemotopus ostralegus* in feeding on the bivalve *Macoma balthica*. *Ardea* **84**: 117-130.

Hulscher, J.B. & Ens, B.J. (1991) Somatic modifications of feeding system structures due to feeding on different foods with emphasis on changes in bill shape in Oystercatchers. *Acta XX Con. Int. Orni.* 889-896.

Hunt, C.D., Dragos, P., King, K., Albro, C., West, D., Uhler, A., Ginsberg, L., Pabst, D. & Redford, D. (1993) The fate of sewage dumped at the 106-mile site – sediment trap study results. *J. Mar. Environ. Eng.* **2**: 285-323.

Johnson, C. (1985) Patterns of seasonal weight variation in waders on the Wash. *Ring. & Migr.* **6**: 19-32.

Kalejta, B. & Hockey, P.A.R. (1994) Distribution of shorebirds at the Berg River Estuary, South Africa, in relation to foraging mode, food supply and environmental features. *Ibis* **136**: 233-239.

Kaye, R.B. & Haddad, P.R. (1992) Compliance testing for ocean outfall performance utilizing natural fluorescence of effluent in seawater mixtures. *Water Sci. Tech.* **9**: 41-48.

Kerr, I. & Johnston, A. eds. (1996) *Birds in Northumberland 1995*. Northumberland & Tyneside Bird Club, Northumberland

Kerr, I. & Johnston, A. eds. (1997) *Birds in Northumberland 1996*. Northumberland & Tyneside Bird Club, Northumberland

Kerr, I. & Johnston, A. eds. (1998) *Birds in Northumberland 1997*. Northumberland & Tyneside Bird Club, Northumberland

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

Kullberg, C. (1998) Does diurnal variation in body mass affect take-off ability in wintering Willow Tits? *An. Behav.* **56**: 227-233.

Kullberg, C., Fransson, T. & Jakobsson, S. (1996) Impaired predator evasion in fat Blackcaps (*Sylvia atricapilla*). *Proc. Roy. Soc. Lond. B* **263**: 1671-1675.

Kullberg, C. Jakobsson, S. & Fransson, T. (2000) High migratory fuel loads impairs predator evasion in Sedge Warblers. *Auk* **117**: 1034-1038.

Kwak, T.J. & Zedler, J.B. (1997) Food web analysis of southern California coastal wetlands using multiple stable isotopes. *Oecologia* **110**: 262-277.

Lack, P. (1986) The atlas of wintering birds in Britain and Ireland. T & A D Poyser, Staffordshire.

Lajtha, K. & Michener, R.H. (1994) *Stable isotopes in ecology and environmental science*. Blackwell Scientific Publications, Oxford.

Levin, S.A. & Paine, R.T. (1974) Disturbance, patch formation and community structure, *Proc. Nat. Acad. Sci. U.S.A.* **71**: 2744-2747.

Lilliendah, K. (1998) Yellowhammers get fatter in the presence of a predator. *Anim. Behav.* **55**: 1335-1340.

Little, B. (1996) The effect of wind turbines on bird populations in Blyth Harbour, in: *Birds in Northumberland 1995* (eds. Kerr, I. & A. Johnston). Northumberland & Tyneside Bird Club, Northumberland

López Gappa, J., Tablado, A. & Magaldi, N.N. (1993) Seasonal changes in an intertidal community affected by sewage pollution. *Env. Poll.* **82**: 157-165.

Mariotti, A. (1983) Atmospheric nitrogen is a reliable standard for natural abundance ¹⁵N measurements. *Nature Lond.* **303**: 685-687.

McCurdy, D.G., Boates, J.S. & Forbes, M.R. (1997) Diurnal and nocturnal foraging by Semipalmated Sandpipers *Calidris pusilla*. *J. Avian Biol.* **28**: 353-356.

McEwan, E.H. & Whithead, P.M. (1984) Seasonal changes in body weight and composition of Dunlin (*Calidris alpina*). *Can. J. Zool.* **62**: 154-156.

McKee, J. (1982) The winter feeding of Turnstones and Purple Sandpipers in Strathclyde. *Bird Study* **29**: 213-216.

McNeil, R., Drapeau, P. & Goss-Custard, J.D. (1992) The occurrence and adaptive significance of nocturnal habits in waterfowl. *Biol. Rev.* **67**: 381-419.

McNeil, R. & Rompre, G. (1995) Day and night feeding territoriality in Willets *Cataptrophorus semipalmatus* and Whimbrel *Numenius phaeopus* during the non-breeding season in the tropics. *Ibis* **137**: 169-176.

Metcalfe, N.B. (1984) The effects of habitat on the vigilance of shorebirds: is visibility important? *Anim. Behav.* **32**: 981-985.

Metcalfe, N.B. & Furness, R.W. (1985) Survival, winter population stability and site fidelity in the Turnstone *Arenaria interpres*. *Bird Study* **32**: 207-214.

Metcalfe, N.B. & Ure, S.E (1995) Diurnal variation in flight performance and hence potential predation risk in small birds. *Proc. Roy. Soc. Lond. B.* **261**: 395-400.

Moore, P.G. & Seed, R. (1985) *The ecology of rocky coasts: essays presented to J.R. Lewis*, Hodder and Stoughton, London.

Moore, M.J., Shea, D., Hillman, R. & Stegeman, J.J. (1996) Trends in hepatic tumours and hydropic vacuolation, fin erosion, organic chemicals and stable isotope ratios in winter flounder from Massachusetts, USA. *Mar. Pollut. Bull.* **32**: 458-470.

Moser, M.E. & Summers, R.W. (1987) Wader populations on the non-estuarine coasts of Britain and Northern Ireland: results of the 1984-85 Winter Shorebird Count. *Bird Study* **34**: 71-81.

Myers, E.P. (1974) *The concentration and isotopic composition of carbon in marine in marine sediments affected by sewage discharge*. Unpublished PhD. thesis, California Institute of Technology, Pasadena.

Newton, I. (1986) *The Sparrowhawk*. Poyser, London.

Nicoll, N., Summers, R.W., Underhill, L.G., Brockie, K. & Rae, R. (1988)

Regional, seasonal and annual variations in the structure of Purple Sandpiper

Calidris maritima populations in Britain. Ibis 130: 221-233.

ObiriDanso, K. & Jones, K. (1999) The effect of a new sewage treatment plant on faecal indicator numbers, campylobacters and bathing water compliance in Morecambe Bay. *J. Appl. Microbiol.* **86**: 603-614.

Ogilvie (1996) Rare breeding birds in the United Kingdom in 1993. *Brit. Birds* **89**: 61-91.

Paine, R.T. & Levin, S.A. (1981) Intertidal landscapes: disturbance and the dynamics of pattern. *Ecol. Monogr.* **51**: 145-178.

Pearce, J.B. (1995) The New York Bight – a case study of marine habitat quality, cumulative effects, and management in the 21st century. *Nat. Areas J.* **15**: 37-42.

Pearce, J.B. (2000) The New York Bight. Mar. Poll. Bull. 41: 44-55.

Pehrsson, O. (1976) Food and feeding grounds of the Goldeneye *Bucephala clangula* on the Swedish west coast. *Ornis Scand.* 7: 91-112.

Pienkowski, M.W. (1982) Diet and energy intake of Grey and Ringed Plovers, *Pluvialis squatarola* and *Charadrius hiaticula*, in the non-breeding season. *J. Zool.* **197**: 511-549.

Pienkowski, M.W., Ferns, P.N., Davidson, N.C. & Worral, D.H. (1984) Balancing the budget. In: *Coastal waders and wildfowl in winter*, eds., Evans, P.R., Goss-Custard, J.D. & Hale, W.G. Cambridge University Press, Cambridge. Pienkowski, M.W., Lloyd, C.S. & Minton, C.D.T. (1979) Seasonal and migrational weight changes in Dunlins. *Bird Study* **26**: 136-148.

Prater, A.J., Marchant, J.H. & Vuorinen, J. (1977) Guide to the identification and aging of holarctic waders. BTO Guide 17, Tring, England.

Rands, M.R.W. & Barkham, J.P. (1981) Factors controlling within-flock feeding densities in three species of wading bird. *Ornis Scand.* **12**: 28-36. Ratcliffe, D. (1980) *The Peregrine*. Poyser, London.

Rau, G.H., Sweeney, R.E., Laplan, I.R., Mearns, A.J. & Young, D.R. (1981) Differences in animal ¹³C, ¹⁵N and D abundance between a polluted and an unpolluted coastal site: likely indicators of sewage uptake by a marine food web. *Est. Co. Mar. Sci.* **13**: 701-707.

Rehfisch, M.M., Clark, N.A., Langston, R.H.W. & Greenwood, J.J.D. (1996) A guide to the provision of refuges for waders: an analysis of 30 years of ringing data from the Wash, England. *J. Appl. Ecol.* **33**: 673-687.

Rehfisch, M. Holloway, S. & Austin, G. (1999) Early results of the Non-estuarine Coastal Waterfowl Survey (NEWS). *WeBS Newsletter* **10**: 8.

Ridgill, S.C. & Fox, A.D. (1990) Cold weather movements of waterfowl in Western Europe. IWRB Spec. Publ. 13, Slimbridge, England.

Robinson, J., Hamer, K.C. & Evans, P.R. (1996) Monitoring the effects of new Northumbrian Water Sewage disposal schemes in the marine environment along the Northumbrian, Durham and Cleveland Coast. Unpublished report, University of Durham.

Rojas L.M., McNeil, R., Cabana, T. & Lachapelle, P. (1999) Diurnal and nocturnal visual capabilities in shorebirds as a function of their feeding strategies. *Brain Behav. Evol.* **53**: 29-43.

Shanewise, S. & Herman, S.G. (1979) Flocking behaviour in wintering Dunlin. *Stud. Avian. Biol.* **2**: 191-198.

Simboura, N., Zenetos, A. Panayotidis, P. & Makra, A. (1995) Changes in benthic community structure along an environmental pollution gradient. *Mar. Poll. Bull.* **30**: 470-474.

Sitters, H.P. (2000) The role of night-feeding in shorebirds in an estuarine environment with specific reference to mussel-feeding Oystercatchers. PhD. thesis, University of Oxford.

Soulsby, P.G., Lowthion, D. & Houston, M. (1978) Observations of the effects of sewage discharged into a tidal harbour. *Mar. Pollut. Bull.* **9**: 242-245.

Spies, R.B., Kruger, H., Ireland, R. & Rice, D.W. (1989) Stable isotope ratios and contamination in a sewage-distorted food web. *Mar. Ecol. Prog. Ser.* **54**: 157-170.

Staine, K.J. & Burger, J. (1994) Nocturnal foraging behaviour of breeding Piping Plovers (*Charadrius melodus*) in New Jersey. *Auk* 111: 579-587.

Straan, K-B. & Summers, R.W. (1990) Diet and diurnal activity of Purple Sandpipers *Calidris maritima* wintering in Northern Norway. *Fauna Norv. Ser. C.* **13**: 75-78.

Suchanek, T.H. (1978) The ecology of *Mytilus edulis* L. in exposed rocky intertidal communities. *J. Exp. Mar. Biol. Ecol.* **31**: 105-120.

Suchanek, T.H. (1985) Mussels and their role in structuring rocky shore communities. In: *The ecology of rocky coasts*, Eds. Moore, P.G. & Seed, R., Hodder and Stoughton, London.

Summers, R.W. (1986) Breeding production of Dark-bellied Brent Geese *Branta bernicla bernicla* in relation to lemming cycles. *Bird Study* **33**: 105-108.

Summers, R.W. (1988) The use of linear measurements when comparing masses. *Bird Study* **36**: 77-79.

Summers, R.W. (1994) Diurnal and nocturnal activities of a Purple Sandpiper *Calidris maritima. Wader Study group Bull.* **72**: 33-34.

Summers, R.W. & Feare, C.J. (1995) Roost departure by European Starlings *Sturnus vulgaris*: Effects of competition and choice of feeding site. *J. Avian. Biol.*, **26**, 289-295.

Summers, R.W., Piersma, T., Strann, K-B. & Wiersma, P. (1998) How do Purple Sandpipers *Calidris maritima* survive the winter north of the Arctic circle? *Ardea* **86**: 51-58.

Summers, R.W., Smith, S., Nicoll, M. & Atkinson, N.K. (1990a) Tidal and sexual differences in the diet of Purple Sandpipers *Calidris maritima* in Scotland. *Bird Study* 37: 187-194.

Summers, R.W., Strann, K-B. Rae, R. & Heggås, J. (1990b) Wintering Purple Sandpipers *Calidris maritima* in Troms County, northern Norway. *Ornis Scand*. **21**: 248-254.

Summers, R.W., Underhill, L.G., Clinning, C.F. & Nicoll, M. (1989) Populations, migrations, biometrics and moult of the Turnstone *Arenaria i. interpres* on the East Atlantic coastline, with special reference to the Siberian population. *Ardea* 77: 145-166.

Summers, R.W., Underhill, L.G., Nicoll, M., Rae, R. & Piersma, T. (1992) Seasonal, size- and age-related patterns in body-mass and composition of Purple Sandpipers *Calidris maritima* in Britain. *Ibis* **134**: 346-354. Summers, R.W., Underhill, L.G. & Syroechkovski, E.E. (1998) The breeding productivity of dark-bellied brent geese and curlew sandpipers in relation to changes in numbers of arctic foxes and lemmings on the Taimyr peninsula, Siberia. *Ecography* 21: 573-580.

Sutherland, W.J. (1996) From individual behaviour to population ecology. Oxford University Press, Oxford.

Sutherland, W.J., Ens, B.J., Goss-Custard, J.D. & Hulscher, J.B. (1996) Specialisation. In: *The Oystercatcher*. Ed. Goss-Custard, J.D. Oxford University Press, Oxford.

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Swanberg, P.O. (1945) Om skärsnäppan, *Calidis maritima* (Brünnich), I de svenska fjällen och dess häckningsbiologi. *Fauna och Flora* **40**: 108-133.

Sweeney, R.E. & Kaplan, I.R. (1980) Tracing flocculent industrial and domestic sewage transport on San Pedro shelf, southern California, by nitrogen and sulfur isotope ratios. *Mar. Env. Res.* **3**: 214-224.

Syroechkovskiy, Y.V., Litrin, K.Y. & Ebbinge, B.S. (1991) Breeding success of geese and swans on Vaygach Island (USSR) during 1986-1988 – interplay of weather and arctic fox predation. *Ardea* **79**: 373-382.

Tabachnick, B.G. & Fichell, L.S. (1996) *Using Multivariate Statistics*. 3rd ed. HarperCollins, New York.

Taylor, L.A., Chapman, P.M., Miller, R.A. & Pym, R.V. (1998) The effects of untreated municipal sewage discharge to the marine environment off Victoria, British Columbia, Canada. *Wat. Sci. Tech.* **38**: 285-292.

Thibault, M. & McNeil, R. (1994) Day-night variation in habitat use by Wilson's Plovers in Northeastern Venezuela. *Wilson. Bull.* **106**: 299-310.

Thomas, V.G. (1982) Energetic reserves of Hudson Bay Willow Ptarmigan during winter and spring. *Can. J. Zool.* **60**: 1618-1623.

Thomas, V.G., Lumsden, H.G. & Price, D.H. (1975) Aspects of the winter metabolism of Ruffed Grouse (*Bonasa umbellus*) with special reference to energy reserves. *Can. J. Zool.* **53**: 434-440.

Thomas, V.G. & Popko, R. (1981) Fat and protein reserves of wintering and prebreeding Rock Ptarmigan from south Hudson Bay. *Can. J. Zool.* **59**: 1205-1211.

Tubbs, C.R. (1977) Wildfowl and waders in Langstone Harbour. *Br. Birds*, **70**: 177-199.

Tucker, J., Sheats, N., Giblin, A.E., Hopkinson, C.S. & Montoya, J.P. (1999) Using stable isotopes to trace sewage-derived material through Boston Harbor and Massachusetts Bay. *Mar. Env. Res.* **48**: 353-375.

Turpie, J.K. (1995) Non-breeding territoriality – causes and consequences of seasonal and individual variation in Grey Plover *Pluvialis squatarola* behaviour. *J. Anim. Ecol.* **64**: 429-438.

Turpie, J.K. & Hockey, P.A.R. (1993) Comparative diurnal and nocturnal foraging behaviour and energy-intake of premigratory Grey Plovers *Pluvialis* squatarola and Whimbrels *Numenius phaeopus* in South Africa. *Ibis* **135**: 156-165.

Underhill, L.G., Prys-Jones, R.P., Syroechkovski, E.E., Groen, N.M., Karpov, V., Lappo, H.G., Vanroomen, M.W.J., Rybkin, A., Schekkerman, H., Spiekman, H. & Summers, R.W. (1993) Breeding of waders (Charadrii) and Brent Geese *Branta bernicla bernicla* at Pronchishcheva Lake, Northeastern Taimyr, Russia, in a peak and a decreasing lemming year. *Ibis* 135: 277-292.

Van Dover, C.L., Grassle, J.R, Fry, B., Garritt, R.H. & Starczak, V.R. (1992) Stable isotope evidence for entry of sewage-derived organic material into a deep-sea food web. *Nature Lond.* **360**: 153-155.

Van Impe, J. (1985) Estuarine pollution as a probable cause of increase of estuarine birds. *Mar. Poll. Bull.* **16**: 271-276.

Veasey, J.S., Metcalfe, N.B. & Houston, D.C. (1998) A reassessment of the effect of body mass upon flight speed and predation risk in birds. *Anim. Behav.* **56**: 883-889.

Ward, P. & Zahavi, A. (1973) The importance of certain assemblages of birds as information centres for food finding. *Ibis* 115: 517-534.

Welch, E.B. (1992) *Ecological effects of wastewater*, 2nd ed. E & FN Spon, London.

Whitfield, D.P. (1985a) Social organisation and feeding behaviour of wintering Turnstone (Arenaria interpres). Unpublished PhD. thesis, University of Edinburgh.

Whitfield, D.P. (1985b) Raptor predation on wintering waders in southeast Scotland, *Ibis* **127**: 544-548.

Whitfield, D.P. (1988) Sparrowhawks *Accipiter nisus* affect the spacing behaviour of wintering Turnstone *Arenaria interpres* and Redshank *Tringa totanus*. *Ibis* **130**: 284-287.

Whitfield, D.P. (1990) Individual feeding specializations of wintering Turnstone *Arenaria interpres. J. Anim. Ecol.* **59**: 193-211.

Zeng, E.Y., Khan, A.R. & Tran, K. (1997) Organic pollutants in the coastal marine environment off San Diego, California. 3. Using linear alkylbenzenes to trace sewage derived organic materials. *Env. Tox. Chem.* **16**: 196-201.

Zwarts, L., Blomert, A-M. & Huphes, R. (1990) Increase in feeding time in waders preparing for spring migration from the Banc d'Arguin, Mauretania. *Ardea* **78**: 237-256.

Zwarts, L., Cayford, J.T., Hulscher, J.B. Kersten, M., Meire, P.M. & Triplet, P. (1996) Prey size selection and intake rate. In: Goss-Custard, J.D. (ed) *The Oystercatcher: from individuals to populations*. Oxford University Press, Oxford.

Zwarts, L. & Wanink, J. (1989) Siphon size and burying depth in deposition- and suspension-feeding benthic bivalves. *Mar. Biol.* **100**: 227-240.

Appendix 1

Additional information used in the analysis of relationships between bird density and environmental variables (Chapter 2)

Testing the accuracy of measuring intertidal cover types from aerial photographs

As described in Chapter 2 (page 22), 1:10,000 colour aerial photographs were used to measure the area covered by different substrate types at each site. In order to check the accuracy of this method the assessment of substrate cover at Cresswell was repeated and the results compared with each other (Table 1).

<u>Table 1: Comparison of separate assessments of area covered by different substrate types at Cresswell</u>

<u> </u>	1 st estimate 2 ^{no}		2 nd es	timate	
Substrate type	No. 250m ²	Area	No. 250m ²	Area	%
	squares	covered	squares	covered	difference
Mussel-bed	1	250	1	250	0
Bare/barnacle-	462	115,500	454	113,500	1.73
covered rock					
Fucus	617	154,250	640	160,000	3.72
Rock pool	50	12,500	48	12,000	4
Green algae	287	71,750	279	69,750	2.78
Sand	354	88,500	346	86,500	2.26
Total	1771	442,750	1768	44,200	0.17
intertidal area					

Exact locations of sites used in analysis

Tables 2-5 give the exact positions of the divisions between the sites used in the analysis of bird density and environmental variables in south Northumberland and those in north Northumberland used to test the models.

Table 2: Large-scale South Northumberland sites

Site	Start map ref.	Finish map ref.	Length (m)	
Amble	NU272050	NU284035	2000	
Hauxley	NU284035	NU278008	3100	
Druridge Bay	NU278008	NZ292939	7600	
Cresswell	NZ292939	NZ302937	2890	
Newbiggin	NZ313895	NZ304857	5410	
Cambois	NZ304850	NZ318822	3350	
North Blyth	NZ318822	NZ328807	2000	
South Blyth Beach	NZ323806	NZ336768	4400	
St. Mary's Island	NZ336768	NZ349747	4150	

Table 3: Small-scale South Northumberland sites

Site	Start map ref.	Finish map ref.	Length (m)
North Amble	NU272050	NU274046	530
Middle Amble	NU274046	NU276044	290
South Amble	NU276044	NU279040	550
Amble beach	NU279040	NU284035	630
North Hauxley	NU284035	NU286028	720
Hauxley Haven	NU286028	NU286023	540
South Hauxley	NU286023	NU283017	1040
Hadston Carr	NU283017	NU278008	800
North Druridge	NU278008	NZ273982	2900
South Druridge	NZ273982	NZ292939	4700
North Cresswell	NZ292939	NZ297933	970
Cresswell Beach	NZ297933	NZ302927	470
South Cresswell	NZ302927	NZ313895	1450
Beacon Pt. Newbiggin	NZ313895	NZ317890	950
Middle Beach Newbiggin	NZ317890	NZ317884	600
Church Pt Newbiggin	NZ317884	NZ316879	910
Town Beach Newbiggin	NZ316879	NZ310873	1340
Spital Carr Newbiggin	NZ310873	NZ309866	640
Sandy Bay	NZ309866	NZ304850	970
Cambois Beach	NZ304850	NZ318822	3350
North Blyth	NZ318822	NZ323806	2000
South Blyth Beach	NZ323806	NZ336768	4400
Seaton Sluice	NZ336768	NZ339768	400
Collywell Bay	NZ339768	NZ343763	850
Hartley Bay	NZ343763	NZ347756	840
North St. Mary's	NZ347756	NZ353754	810
St. Mary's Island	NZ353754	NZ352753	570
South St. Mary's Island	NZ352753	NZ349747	680

Table 4: Large-scale North Northumberland sites

Site	Start map ref.	Finish map ref.	Length (m)
Bamburgh	NU163362	NU195347	3160
Seahouses	NU195347	NU225315	5180
Beadnell	NU225315	NU236286	4350
Beadnell Bay	NU236286	NU242259	3800
Newton	NU242259	NU244238	2830
Embleton Bay	NU244238	NU259222	2870
Craster	NU259222	NU262187	3690
Howick	NU262187	NU258164	3050
Boulmer	NU258164	NU284125	4900
Alnmouth	NU284125	NU255073	5640

Table 5: Small-scale North Northumberland sites

Site	Start map ref.	Finish map ref.	Length (m)	
Stag Rocks	NU163362	NU177356	1260	
Bamburgh	NU177356	NU195347	1900	
Monks House	NU195347	NU207333	2000	
The Tumblers	NU207333	NU222323	1800	
Seahouses	NU222323	NU225315	1380	
Annstead	NU225315	NU228303	1320	
North Beadnell	NU228303	NU236294	1330	
Beadnell	NU236294	NU236286	1700	
Beadnell Bay	NU236286	NU242259	3800	
Newton Pt	NU242259	NU242245	2150	
Newton Haven	NU242245	NU244238	680	
Embleton Bay	NU244238	NU248224	1630	
Dunstanburgh	NU248224	NU259222	1240	
Craster	NU259222	NU262187	3690	
Howick	NU262187	NU262173	1850	
Howick Haven	NU262173	NU258164	1200	
Longhoughton	NU258164	NU268153	1880	
Boulmer Steel	NU268153	NU266142	1150	
Boulmer	NU266142	NU265136	600	
Seaton Pt	NU265136	NU264125	1270	
Foxton Hall	NU264125	NU258119	930	
Marden Rocks	NU258119	NU250105	1740	
Alnmouth	NU250105	NU253081	2150	
Birling Carrs	NU253081	NU255073	820	

Appendix 2

Measurement of stable isotope ratios of POM from the Coquet River

Particulate samples were taken from upstream of the weir in Coquet River in autumn 1999. Six replicated pairs were analysed. The mean $\delta^{13}C$ value was – 23.712 (s.e. = 0.025) and mean $\delta^{15}N$ value 9.612 (s.e. = 0.256). The $\delta^{13}C$ value is slightly higher (less negative) than sewage, but would seem to reflect a terrestrial origin of much of the particulate matter with some marine influence. The $\delta^{15}N$ value however is very unusual in that it is considerably higher than the values for marine algae, which itself has higher values than terrestrial sewage. An explanation for this is not obvious, and this rather unexpected result makes it difficult to calculate the impact of riverine inputs as only having reliable measurements for one element makes the use of a three-source mixing model impossible.

Appendix 3

Over-summering by Turnstones

Visits over the summer months were sufficiently frequent to identify a number of colour-ringed individuals that stayed through the second half of June or the first half of July and thus were considered to be over-summering birds. In 1997 only two colour-ringed Turnstones were seen during this period, in 1998 five and in 1999 nine. (The variation in the intensity of summer fieldwork between years means that these figures are not directly comparable).

Table 1: Composition of Turnstones summering within the study area

		Age		Sex (if known)	
Year	No.	Adult	1 st summer	Male	Female
1997	2	2	0	1	0
1998	5	3	2	2	0
1999	9	7	2	0	7

Three of the females summering in 1999 were identified as such by DNA analysis, and the males present in 1998 were easily identifiable by plumage.

The data collected over the 1998-99 winter (and on the occasion of their ringing) for each Turnstone that subsequently summered were compared with those for birds that departed in the spring. Although for most variables there were no significant differences between the two classes of birds, those that summered tended to be less site-faithful, more itinerant and less dominant than those birds that did not summer.

Table 2: Comparison of behavioural variables for Turnstones that summered in Northumberland against those that did not

	Summering		Non-		Mann-Whitney U test		ey U test
	birds		summer	summering			
			birds				
Variable	Mean	s.e	Mean	s.e.	Z	n	Sig.
Dominance rank	11	2	5.9	1.22	1.56	14	n.s.
% of aggressive	19	3.2	51	6	1.51	29	n.s.
encounters won							
Range (km)	6.07	1.67	5.06	0.55	1.61	98	n.s.
Mean movement	1.73	0.81	1.02	0.09	1.28	98	n.s.
(km)							
Low water fidelity	52.1	7.7	70.3	1.8	2.49	138	P = 0.05
High water fidelity	51.9	7.5	54.3	1.7	0.26	138	n.s.
Itinerancy index	305.7	104	237	98.4	1.99	93	P = 0.05

The inclusion of both adults and first-year Turnstones in this analysis may have accentuated these relationships between over-summering and behaviour, if first-years (more likely to be of low dominance status and hence higher itinerancy/lower fidelity) are physiologically more predisposed to over-summering, regardless of social status or wintering behaviour. However, if juveniles were excluded, there were still significant differences between summering and non-summering adult Turnstones in fidelity to low water feeding location (z = 228, n = 107, P = 0.05) and itinerancy index (z = 2.05, n = 72, P = 0.05).

As mentioned in chapter 5, during the June and July Turnstones concentrated at Hauxley. Colour-ringed birds that had been resident in winter at other sites within the study area moved to Hauxley from Amble and Cresswell.

The phenomenon of summering – remaining on "wintering" grounds (non-breeding areas) instead of migrating north to breeding grounds – has been recorded in a number of Arctic-breeding shorebirds, including Turnstones

(Cramp & Simmons 1983). The majority of over-summering birds are first-years (Summers *et al.* 1995) Surprisingly, there were more adult than first-year Turnstones amongst the small numbers summering in south Northumberland, including one bird two years in succession. Adults that remained to summer were of a significantly lower social status than those that departed to breeding grounds. Migration to breeding grounds and then breeding are probably major stressors, so it seems likely that both the low status and over-summering have the same cause. McNeil *et al.* (1994) suggested that over-summering shorebirds might be those that have heavy trematode infestations, which might also affect social status. However, over-summering in consecutive years would not be expected as infected birds would be expected to acquire at least partial immunity to reinfection (McNeil *et al.* 1994).

