Ecology of migrant shorebirds in New Zealand, focussing on Farewell Spit, North-West Nelson

A thesis presented in partial fulfilment of the
requirements for the degree of Masterate in Ecology
at Massey University

Philip Frank Battley

1996

Dedicated to the memory of R. B. (Dick) Sibson (1911-1994),
who did so much to encourage so many in the
study of waders in New Zealand

ABSTRACT

Migratory shorebirds are a dynamic component of New Zealand's coastal fauna, alternating between distant breeding and non-breeding grounds. The Red Knot *Calidris canutus*, Bar-tailed Godwit *Limosa lapponica* and Pied Oystercatcher *Haematopus ostralegus finschi* were studied on Farewell Spit, North-West Nelson. The first two species breed in the Arctic and migrate to New Zealand for the non-breeding season. Over the southern summer they experience low thermostatic costs and generally improving prey conditions over the summer. Oystercatchers are resident over autumn and winter, so experience rising costs and declining prey quality in some species. One bivalve species, *Macomona liliana*, shows seasonal depth changes in the sediment, and so is largely inaccessible even to a long-billed bird such as the oystercatcher.

Despite this, oystercatchers feed for less time than is available, and achieve intake rates sufficient to cover estimated needs. The energy needs of the Arctic waders rise as they prepare to migrate, and they achieve at least part of this by increasing the duration of feeding. Knots during spring tides in the premigratory period feed for the entire low-water period. Godwits are apparently less stressed, underutilising nocturnal feeding opportunities over summer. They are thought to increase feeding time by using this night-time feeding.

The high energy demands for migrating birds come from the need to deposit nutrients for migration, and knots around the Auckland region are estimated to increase in mass from 115 to 185 g prior to migration. Fat deposition is not the only physiological preparation, however, and a sample of knots shot from Northland (illegally, recovered by DoC) revealed complex interactions between organs. Large amounts of fat were deposited, mostly in a subcutaneous layer but also in the abdominal cavity. Muscle protein was also deposited in flight and heart muscles, presumably to prepare for the extreme effort involved in trans-oceanic flights. At the same time, digestive organs decreased in mass. This is interpreted as freeing up muscle protein which is then deposited in organs for use during flight.

Knots and godwits migrated from Farewell Spit in March. Most departures occurred in the evening and on rising tides. The former probably allows for the use of multiple navigational cues, while the latter may maximise feeding opportunities immediately before the flight. Most departures occurred after the passage of a low-pressure system or with the approach of a high-pressure system. This enabled favourable winds to be gained, so that the mean wind vector was a small tailwind. Thus, while departure directions were intermediate between the expected directions for flights to either Australia or northern New Zealand, it is probable they were able to fly across the

top of a high-pressure system and gain wind assistance for a direct flight to Australia. However, the variability in flight range estimates depending on assumptions of travel-speed and protein deposition makes predicting migration routes difficult.

Numbers of godwits have increased on Farewell Spit over the past decade, while oystercatchers have remained static Knots have shown a slight decline. Knot numbers are independent of national census counts so are presumably determined largely by factors operating on Farewell Spit itself. A possible mechanism that could give to a slowly declining population could be if a certain sector of the population fails to deposit sufficient nutrients to successfully migrate and return. If site-fidelity is very high (as it generally is in waders) then a long-term decrease could ensue.

TABLE OF CONTENTS

Title page i
Dedication ii
Abstract iii
Table of contents v
Acknowledgements ix
List of figures and tables xii

Chapter 1 **General introduction** 1

Chapter 2 **Study site: physical features, biological features and history**
Geomorphology 8
Fieldwork 9
Climate 12
Vegetation 12
Fauna 13
Status 14
Scientific research 14

Chapter 3 **Prey availability**
Abstract 15
Introduction 16
Methods 18
Results
  Total biomass 20
  Size relationships in bivalves 25
  Sizes of shellfish 29
  Size-mass relationships 31
  Worms 40
Discussion 42
  Approaches to studying benthic food supplies 44

Chapter 4 **Behaviour, diet and energy intake**

Abstract 47
Introduction 48
Methods 49

Results

Roosting areas 52
Feeding areas 52
Distances travelled during feeding 54
Site fidelity to roosting areas 54
Activity 57
Feeding method and prey type 61
Pied Oystercatcher: diet and intake rates 63
Red Knot: diet and intake rate 68
Bar-tailed Godwit: diet and intake rates 76

Discussion

Use of space 77
Feeding time 79
Pied Oystercatcher: energy requirements, diet and energy intake 81
Red Knot: diet, energy requirements and energy intake 84
Bar-tailed Godwit: diet, energy demand and energy intake 90
Dietary overlap between species 92
Seasonal energy demands and intake 92

Chapter 5 **Seasonal mass changes in knots in New Zealand**

Abstract 94
Introduction 95
Methods 95
Results 96
Discussion 99
Is the juvenile mass increase adaptive? 101

Chapter 6 **Body composition of Knots *Calidris canutus rogersi* from northern New Zealand in the premigratory period**

(Co-authored with Dr. Theunis Piersma, submitted to *Notornis*)

Abstract 105
Introduction 106
Methods 108
Results 109
Discussion 117

Chapter 7 **The northward migration of arctic waders in New Zealand: departure behaviour, timing and possible migration routes of Red Knots and Bar-tailed Godwits from Farewell Spit, North-West Nelson**

(Submitted to *Emu*)

Abstract 121
Introduction 122
Methods 124
Results
    Premigratory and migratory behaviour 126
    Patterns of departures 128
    Direction of departures 130
    Influence of weather 132
    How far might New Zealand knots be able to fly? 135
Discussion
    Migratory behaviour 135
    Timing of departure 136
    Effect of weather 139
    Flight ranges 139
    Do knots fly to Australia direct or via Northland? 140

Chapter 8 **Population processes and wader limitation: a theoretical excursion** 143
Carrying capacity: concepts and utility 144
Mortality and selection 151

Chapter 9 **General discussion**
Food supply and usage 154
Migratory preparation 155
Numbers of birds on Farewell Spit: are they limited? 156
  Evidence for limitation? 161
  Interactions with Black Swans 163
  Energetic costs: implications for wader distributions around New Zealand 164
  Future research 167

References 170

Acknowledgements

First, thanks must go to the Department of Conservation, Takaka, for deciding that Farewell Spit warranted formal research, and furthermore, for fronting up with money and logistics to make it possible. Special thanks to Kaye Stark for organising all sorts of things in Golden Bay, without which this work would not have been possible. Geoff Rennison (DoC Takaka) kindly provided facilities for living in and using at the end of the spit, and Kath Walker (DoC Nelson) gave permission to work there.

Paddy Gilooly and crew from Collingwood Safaris generously and regularly transported people, mail and groceries along the spit which made life nutritionally and socially viable. Cheers! Jock Lill did likewise. Many DoC staff also regularly helped out in various ways: Grant King, Nigel Orpwood, Bill Crump, Simon Walls, John Taylor.

On occasions people lent willing (?) hands to aid in benthic sampling, that most exciting of recreational pursuits - thanks to Andrew Crossland, Andrea Booth, but most of all Kaye Stark, Nigel Orpwood and Grant King who ended up spending many winter hours questioning why Phil wanted to know how many shellfish an oystercatcher couldn't reach.

Back in the North Island, I must of course thank the Ecology Department, Massey University both for enabling me to do this work, and also for allowing and putting up with my long absences from this topic while pursuing sideline interests. Thanks especially to my superviser, Ed Minot, for encouraging me in these, and for giving me a free rein which, for better or worse, has resulted in this thesis being as it is.

My first introduction to the world of wader research came about as a result of the 20th International Ornithological Congress in Christchurch in 1990. It was the end of my second year at university, and I was convinced that studying waders was the way to a truly interesting existence. What better way to gain insight into how to go about it than to pick the brains of those who already know? It was for this reason that I pounced upon Theunis Piersma, from the Netherlands Institute for Sea Research, when I saw him appear the top of a flight of stairs. (My ability to do this so convincingly had him bemused for the next four years, as he had no recollection of having his name-tag on at the time.) I introduced myself, explaining my desire to work on waders, but it was three days before we got to meet again properly. In typical Piersma fashion his opening line was "So, why don't you come out to the Netherlands next year to do some work with us?" I hummed and ha-ad for

about three seconds, before replying "Sure, why not." That northern autumn spent on the sandflats on the Dutch Waddensea and the labs of the NIOZ proved the perfect grounds for learning the basic ropes of waderology, especially as it coincided with the annual conference of the Wader Study Group. That this contact has maintained and developed itself since then has been beyond my highest expectations. ("So, Phil, do you want to go to Ghana?". "Ummm, sure, why not?"). Many thanks to Tunafish, Petra de Goeij and Ingrid Tulp for their hospitality during my stays in The Netherlands. Theunis has been a constant source of inspiration, reprints, preprints and manuscripts. I greatly value our regular contact and look forward to much more! I still have the goal of writing a paper on waders without a Piersma reference in it, just for the challenge...

A large number of people have contributed in differing ways to this thesis. Nick Davidson kindly provided a copy of his thesis and reprints and a manuscript, hospitality and whiskey-primed late-night conversations in August 1994, all of which I appreciated (especially the latter). Dov Lank also donated a copy of his very stimulating thesis and gave incisive comments on a chapter. Following my semi-enforced stay in the Netherlands in 1994, Popko Wiersma and Martin Poot's discussions on migration, wader ecology, music and cinema when strolling hot salty lagoons in Ghana were also appreciated.

In addition to Ed Minot from Massey University, I wish to thank the following people: Don Morrisey (NIWA, Hamilton) made preliminary identifications of worms and crustacea which increased my knowledge almost infinitely (Chapter 3). Simon Thrush (NIWA, Hamilton) discussed sampling strategies. Stephen Davies and Theunis Piersma commented on Chapter 5. Ray Pierce, Department of Conservation, Whangarei, made available the corpses analysed in Chapter 6, and organised their transport to the Netherlands. Anne Dekinga, Anita Koolhaas, Sylvia Klos and Ingrid Tulp lent a hand in the labwork processing the birds. Chapter 7 (migration) was greatly improved by the comments of many people: Ingrid Tulp, Kees Hulsman, Mark Barter, Robin Fordham and especially Paul Sagar, Dov Lank and Theunis Piersma. Ed Minot and Ian Henderson gave statistical advice. John MacArthur, department of Geography, Massey University, has been a regular fielder of obscure and not-so-obscure queries about geomorphology and climatology over the past few years. The nicer figures in chapter 6 were drawn by Dick Visser.

Regular hospitality was provided by Gail, Tony, Tessa and Kelly Quayle whenever I passed through Nelson. Their fine taste in music always made it a pleasure.

The knot mass and morphometric data (Chapter 5) were the result of a large amount of effort over many years by members of the New Zealand Wader Study Group (formerly the Miranda Banders), led by Adrian Riegen and Stephen Davies. Thanks to them for generously allowing the data to be used. The Miranda Naturalists Trust helped with finance in the catching operations. Climate data (Chapters 4 & 5) were supplied by NIWA Climate, Wellington (Elaine Fouhy). Bird count data are the hard-won results of Ornithological Society of New Zealand, Nelson branch, surveys, led by the late Jenny Hawkins. Long may they continue!

Finance for this project came from DoC, Takaka, a Massey University Postgraduate Awards Masterate Scholarship, and from the D.H. Battley Trust. The generosity of the latter has enable me to avoid debt most of my university life. For that I am extremely grateful.

I would also like to thank my cohort(s) in the Ecology Department for making life enjoyable in those brief periods when I was around, including Jackie Townsend, Vanessa Munro, Dave Hodgson, Rosemary Miller, Grant Blackwell, Andrea Booth, Hirani Himona, Wayne Linklater, Elissa Cameron and Suzanne Bassett. Also other Ecology-contacts Doug Armstrong, Wendy French and Katerina for such good food and off-beat entertainment (101 games to play with a human baby...), and Alastair Robertson. A truly large round of appreciation goes to Kath Hay and Craig Steed for being such good friends despite me clearing off to odd places so often.

I finish these acknowledgements with a round of thanks to the two people who have always encouraged me and helped me pursue such an oddball direction in life - my parents Eleanor and Don Battley. Since 1983 they've had to put up with me wanting to use their their spare time to visit muddy places populated by grey-brown birds, and have done so willingly. Their faith in me, encouragement, and financial support have made a big difference these past years. Many thanks indeed!

List of Figures and Tables

Figures

Figure 2.1 Location of Farewell Spit
Figure 2.2 Detail of study site at the tip of Farewell Spit
Figure 2.3 Mean windspeed recorded at the Farewell Spit lighthouse.
Figure 2.4 Mean temperature at the Farewell Spit lighthouse.

Figure 3.1 How the harvestability of a prey item depends on its ingestibility, profitability and accessibility.
Figure 3.2 Biomass of main taxonomic groups of organisms at Tip1 sampling site.
Figure 3.3 Biomass of main taxonomic groups of organisms at Tip2 sampling site.
Figure 3.4 Biomass of main taxonomic groups of organisms at Pan and Tip1-Tip2 sampling sites.
Figure 3.5 Biomass of main taxonomic groups of organisms at Flat1 and Chan1 sampling sites.
Figure 3.6 Pied Oystercatcher prey biomass levels at four main sampling sites.
Figure 3.7 Knot prey biomass levels at three main sampling sites.
Figure 3.8 Godwit prey biomass levels at four main sampling sites.
Figure 3.9 Relationship between hinge height and shell length for cockles.
Figure 3.10 Relationship between hinge+top height and shell length in cockles.
Figure 3.11 Ingestibility limitation of cockles for knots.
Figure 3.12 Relationship between hinge+top length and shell length in the pipi.
Figure 3.13 Ingestibility limit for knots feeding in pipi.
Figure 3.14 Mean cockle shell length and mean deviation by month (1994).
Figure 3.15 Size distribution of cockles at Tip3 in January, June and December 1994.
Figure 3.16 Size distributions of mussels present near the tip of Farewell Spit in late summer (February) and early winter (June).
Figure 3.17 Seasonal changes in flesh content of 15, 25 and 35 mm cockles.
Figure 3.18 Seasonal changes in density of cockles at Tip3 in 1994.
Figure 3.19 Seasonal changes in total biomass in cockles at Tip3 in 1994.
Figure 3.20 Seasonal changes in flesh content in *Macomona* of 15, 25 and 35 mm length in 1994.
Figure 3.21 Average depth of 15, 25 and 35 mm *Macomona*.
Figure 3.22 Seasonal variation in harvestable biomass of *Macomona* to knots and oystercatchers.

Figure 3.23 Flesh mass as a function of shell length in pipi over summer (November-April).
Figure 3.24 Ratio of predicted summer mass to winter mass for four sizes of pipi.
Figure 3.25 Flesh content as a function of shell length in mussels in late summer
Figure 4.1. Generalised movements of feeding waders at low tide.
Figure 4.2 Counts of knots roosting near Bush end Point and the shellbanks from 14-1-1994 to 8-3-1994.
Figure 4.3 Counts of godwits roosting near Bush end Point and the shellbanks from 14-1-1994 to 8-3-1994.
Figure 4.4 Percentage of feeding knots over all tides in the basic period, relative to tide.
Figure 4.5 Percentage of feeding godwits over all tides in the basic period, relative to tide.
Figure 4.6 Percentage of feeding knots over all tides in the premigratory period, relative to tide.
Figure 4.7 Percentage of feeding godwits over all tides in the premigratory period, relative to tide.
Figure 4.8 Percentage of feeding oystercatchers over all tides in summer, relative to tide.
Figure 4.9 Percentage of feeding oystercatchers over all tides in winter, relative to tide.
Figure 4.10 Size of mussels eaten by Pied Oystercatchers at the hummocks in February and June 1994.
Figure 4.11 Mussel selection by oystercatchers at the hummocks.
Figure 4.12 Proportion of biomass per mm size class contributing to diet of oystercatchers feeding on mussels.
Figure 4.13 Estimated daily energy intake of Pied Oystercatchers feeding on four prey types in summer and early winter.
Figure 4.14 Localities used in grouping of knot faeces
Figure 4.15 Size distribution of pipi recovered from knot faeces (all localities combined).
Figure 4.16 Size distribution of pipi recovered from knot faeces and present in sediment for 1993/94 over all sites.
Figure 4.17 Size distributions of pipi taken by knots, estimated from faeces and regurgitates.
Figure 4.18 Size distribution of cockles taken by knots with all localities combined,estimated from faeces.
Figure 4.19 Size distribution of cockles from knot faeces and regurgitates in 1993/94.
Figure 4.20 Size distribution of cockles taken by knots (estimated from faeces) and present in sediment for 1993/94 over all sites.
Figure 4.21 Intake rate of knots over all sites and times.
Figure 4.22 Maintenance metabolism of Pied Oystercatchers at Farewell Spit.
Figure 4.23 Maintenance metabolism of Red Knots on Farewell Spit.

Figure 4.24 Maintenance metabolism of Bar-tailed Godwits on Farewell Spit.

Figure 5.1 Localities of knot catching operations in the Auckland region.
Figure 5.2 Mass of knots though the year, separated into 3rd, 2nd and 1st-year birds.

Figure 6.1 Schematic representation of how a sample of birds on a single day can approximate the "fattening" trajectory of a hypothetical individual.
Figure 6.2 Relationship between body mass and total fat mass and total fat-free dry mass for knots.
Figure 6.3 Relationship between the four components of total fat mass, and total fat mass in knots.
Figure 6.4 Total FFDM plotted against fat mass in knots.
Figure 6.5 Organ FFDM plotted against total fat mass in knots.

Figure 7.1 Map of localities in Australasia mentioned in the text.
Figure 7.2 Daily pattern of observed departures of knots and godwits from Farewell Spit, March 1994.
Figure 7.3 Pattern of departures relative to time of day (top), and observer time in field (lower).
Figure 7.4 Pattern of observed departures relative to tidal stage.
Figure 7.5 Directions of departures for knot and godwit.
Figure 7.6 Degree of wind drift experienced by departing flocks.
Figure 7.7 Wind vectors for departing flocks.
Figure 7.8 Plot of departure occurrences relative to prevailing weather systems.
Figure 7.9 Estimated flight range of knots.
Figure 7.10 Tidal Influence Index, plotted against tidal height.

Figure 8.1 Effects of habitat loss on bird populations.

Figure 9.1 Count of knots at Farewell Spit from 1983 to 1995.
Figure 9.2 Counts of godwits at Farewell Spit from 1983 to 1995.
Figure 9.3 Percentage deviation from three-year running mean for counts of knots on Farewell Spit
Figure 9.4 Percentage deviation from three-year running mean for counts of godwits on Farewell Spit.
Figure 9.5 Count of oystercatchers at Farewell Spit from 1984 to 1995.

Figure 9.6 Percentage deviation from three-year running mean for winter counts of oystercatchers on Farewell Spit
Figure 9.7 Maintenance metabolism for knots at the Firth of Thames, Farewell Spit and Southland.
Figure 9.8 Maintenance metabolism for knots at the Firth of Thames , Farewell Spit and Southland.

Tables

Table 3.1 Sampling dates for invertebrates.
Table 3.2 Intercept, exponent and explained variance for power functions relating shell length to biomass (mg AFDM) for cockles in different months.
Table 3.3 Intercept, exponent and explained variance for power functions relating shell length to biomass (mg AFDM) for *Macomona* in different months.

Table 4.1 Feeding method on main prey types for knots, godwits and oystercatchers.
Table 4.2 Intake, pecking/probing and pacing rates of foraging oystercatchers.
Table 4.3 Composition of knot diet assessed from faeces according to locality, for all years combined.
Table 4.4 Mean size (mm) of pipi taken by knots, summarised by locality and summer.
Table 4.5 Mean size (mm) of cockles taken by knots, summarised by locality and summer.
Table 4.6 Energy intake of godwits feeding on worms (*Travisia* and 'slender worms').

Table 6.1 Physical and plumage details of all analysed knots, listed in order of decreasing total body mass.
Table 6.2 Correlations of body mass, fat mass, total FFDM, FFDM of all body parts and three structural measures, with fat mass and total FFDM for adult knots.
Table 6.3 Comparison of body part masses for adult and juvenile knots.

Table 7.1 Flock sizes, vocalisation and presence of visible sun at departures for knot and godwit, at Farewell Spit, March 1994.
Table 7.2 Departing flock formation and changes in knots and godwits at Farewell Spit, March 1994.

Chapter 1

General introduction

The lives of many animals are constrained by the schemes of men, but the determination in these lives, their traditional pattern of movement, is a calming reminder of a more fundamental order. The company of these birds in the field is guileless. It is easy to feel transcendent when camped among them. Birds tug at the heart and mind with a strange intensity.

Barry Lopez: Arctic Dreams. Imagination and
Desire in a Northern Landscape. (1986)

Barry Lopez, in this quote from his experiences in the American and Canadian Arctic captures what is the very essence of the effect of the natural world on the human individual. Anyone with any sensitivity for the aesthetics of nature cannot fail to be impressed and moved by experiences had in the wild. Such experiences serve to reestablish humanity's place in nature by bringing home the vastness of the natural world, the world beyond the urban boundaries we increasingly belong to. Concomitant with these is a realisation of the responsibility our history has bestowed on us, to steward wisely ourselves in nature. It is with this background that I approached biology, firstly with a strangely consuming interest in birds, and secondly with a hope that here would be a way in which to do something beneficial.

Birds are a globally prominent group of animals, and one in which some of the most dramatic biological phenomena take place. Each year, millions of birds migrate from breeding grounds to wintering grounds, which may lie anywhere from a hundred to over ten thousand kilometres distant. Migration of birds is usually a more subtle affair than the massed migrations of wildebeest, and can be easily overlooked. But for those who know to be in the right place at the right time, seeing a small bunch of seemingly frail waders rising steeply, achieving formation, and disappearing against the setting sky can be a very exciting and profoundly moving experience.

This seasonal redistribution of avian biomass may be a relatively recent development. The landscape we know now is a vastly different one to that which was present in the past, and it is probable that many of the biological patterns we observe now were seeded in the Pleistocene glaciations. The huge icesheets of the Northern Hemisphere are thought to have greatly reduced and fragmented Arctic wader populations. Knots *Calidris canutus* may have been restricted to a couple of areas with a population of perhaps only 500 pairs (Baker *et al.* 1994). Glaciations are also likely to have had major effects on New Zealand's habitat and wader fauna. Most of the inland South Island would have been covered by ice and snow at the peak of the Last Glaciation (c. 18,000 years BP) making it unavailable for breeding. With a drop in sea level of perhaps 130-140 m, the edge of the continental shelf would have been reached in some places, leaving little scope for the development of intertidal land. During the Flandrian Transgression, the period of rising sea level up to 6-7,000 years BP, coastal habitat may have been restricted through marine sediments becoming covered by the rising sea, with the slower process of conversion from dry land to tidal flat taking place. At the same time, however, breeding habitat on inland riverbeds would have been increasing as glaciers retreated, leaving extensive moraine deposits. As runoff increased, river channels may have developed from straight to braided, which would further increase habitat. During this period, then, competition for wintering habitat may have been severe, which may have led to the establishment of migration in species such as the Pied Oystercatcher *Haematopus ostralegus finschi* and the Banded Dotterel *Charadrius bicinctus*. It is only since the Flandrian Transgression that intertidal habitat has been at all stable.

It is not clear when Arctic waders may first have migrated to New Zealand. The eastern Siberian and Alaskan tundra zones apparently remained ice-free during the Pleistocene (Piersma 1994), so breeding habitat is likely to have been much less restricted than in Arctic Canada or western Siberia and Europe. Nevertheless, in winter this area would have been inhospitable (as it is today) so migration presumably would have occurred on some scale. The length of migration would be determined by the type and quality of habitat along the western Pacific rim, and the number of competitors. This brings us to a major question when trying to interpret migration patterns: why do birds undertake long-distance migrations?

Theories of long-distance migration

Two main ideas to explain migration patterns of waders have arisen in the past fifteen years. In essence, one proposes that competition causes birds to migrate long-distance, while the other claims that in doing so birds 'track' the carrying capacity across a wide latitudinal range.

The assumption in the first model is that there is a cost to long-distance migration, especially for juveniles. Therefore, individuals will attempt to settle as near to the breeding grounds as possible, but many are prevented from doing so by competition (Pienkowski & Evans 1984; Pienkowski & Evans 1985; Pienkowski *et al.* 1985). Predictions arising from this are (1) competition is greatest near the breeding grounds, (2) sites nearest the breeding grounds are always near carrying capacity, and (3) non-breeding survival of birds wintering near the breeding grounds should exceed that of birds migrating further (Hockey *et al.* 1992).

The second model is based on the assumption that carrying capacity (see Chapter 8) increases from north to south in the non-breeding season. Benthic productivity increases towards the equator, so temperate regions show lower productivity than the tropics. In the Southern Hemisphere, production occurs in the non-breeding season for waders. Therefore, because production and predation peak synchronously, the carrying capacity of southern regions is greater than equivalent northern sites where these are asynchronous. This proposal (Hockey *et al.* 1992) seems to have incorporated the ideas of Schneider (1981) and Schneider & Harrington (1981).

The development of ideas seems fairly regional: the first hypothesis is European in origin and support, while the second has been more prominent in North America and South Africa. Unfortunately, the only analysis which purports to test these hypotheses (and finding the former hypothesis unsupported: Hockey *et al.* 1992) had such unrealistic assumptions that its conclusions cannot be immediately accepted. They did, however, formalise the fact that Southern Hemisphere sites experience high prey levels when bird pressure is high, and thermostatic costs low.

Our thinking is influenced by our experience and knowledge, which are limited, yet we seek to find generalisations on the basis of this. Arguments about wader migration based on the East Atlantic Flyway may not be directly applicable to other flyways. For instance, the majority of birds in the East Asian/Australasian Flyway (which stretches from eastern Siberia and western Alaska down to Australasia) undertake long-distance migration. The population concentrations on this flyway differ greatly from that in the East Atlantic Flyway. The climate in western Europe is ameliorated by the presence of the Gulf Stream current, and as a consequence possesses a large wintering bird population. In contrast, the Chinese coast in the North Pacific is much more extreme in winter: bird concentrations are much further south. The relative importance of competition over production as a driving force in migration may well differ between flyways and populations.

While I obviously cannot attempt to evaluate these forces in the New Zealand context, it is worth bearing in mind the question of why birds migrate to New Zealand, and whether they have open to them any other options. The same question operates on a smaller scale: why birds settle on a certain tidal flat, and whether they have any options available.

The study of shorebird biology in the non-breeding season

Shorebirds are prominent members of the coastal fauna in most parts of the world, and in many places occupy that narrow strip between the terrestrial and marine ecosystems, the intertidal zone. One of the driving forces for the study of shorebird ecology over the past twenty-five years has been the fact that globally, intertidal land is increasingly under pressure from human development (Davidson *et al.* 1994; Davidson *et al.* 1991). Concerns about rising sea levels raise further concerns. From a conservation viewpoint, the demand has been to determine how bird numbers relate to invertebrate densities, and what factors may affect the intake rate (and presumed survival) of wintering waders (eg. Evans 1976; Evans & Dugan 1984; Goss-Custard 1980; Goss-Custard 1984b; Goss-Custard *et al.* 1977; Pienkowski 1982). This then had to be interpreted in the context of habitat loss through land-claim activities (Evans *et al.* 1991; Evans *et al.* 1979; Goss-Custard 1977; Goss-Custard 1979; Goss-Custard 1984a; Meire 1991; Meire & Kuijken 1987; Schekkerman *et al.* 1994). Finally, processes had to be formalised into models that would, qualitatively and hopefully quantitatively, predict the effects of habitat loss on shorebird populations (Goss-Custard *et al.* 1995a; Goss-Custard *et al.* 1995b; Goss-Custard & Durell 1990; Goss-Custard & Yates 1992; Sutherland & Goss-Custard 1991). These are outlined in Chapter 8.

Of course, migrational aspects are an all-pervading consideration in the study of the ecology and population dynamics of waders, and the second main area of shorebird research has focussed on documenting and understanding the migration strategies of shorebirds (eg. Alerstam & Lindström 1990; Davidson & Evans 1988; Dick *et al.* 1987; Evans 1981; Evans & Davidson 1990; Evans & Townshend 1988; Pienkowski and Evans 1984; Pienkowski and Evans 1985; Piersma *et al.* 1987a; Piersma *et al.* 1991). The international nature of these migrations meant that international cooperation would be required to achieve advances, and the Wader Study Group, founded in England in 1971, has been instrumental in fostering healthy cooperation.

Shorebirds have proved excellent animals for the study of migration, and ecological studies are aided by the fact they live in wide open spaces, and feed on a food supply that is often readily quantifiable (eg. Zwarts & Blomert 1992; Zwarts *et al.* 1992; Zwarts & Wanink 1991; Zwarts & Wanink 1994). Certain generalisations have emerged about the ecological situation of waders which warrant mention.

* The harvestable food supply for waders in not a simple function of density (Zwarts and Wanink 1994). Limitations of detectability, accessibility and ingestibility define the available fraction, and this interacts with profitability to define the harvestable fraction. Furthermore, this is not static, with changes in burying depth, density, flesh content and size affecting this.

* Latitudinal generalisations in food supply have been hard to make (Piersma *et al.* 1994a). While the processes above may occur, their relative importance in determining the food supply for waders will not be intuitively obvious at different localities.

* Shorebirds have an unusually high level metabolic rate, which may be a consequence of high energy demands imposed by a migratory lifestyle (Kersten & Piersma 1987). The seasonal energy demands of a wader will varying with both internally (moult, mass deposition) and externally (thermostatic cost: a function of environmental variables) imposed costs. Failure to take into account varying levels of energy demand will result in inaccurate conclusions. Fortunately, Dutch researchers have applied their typically rigorous methodology to this problem, and the tools for estimating maintenance metabolism are now available for waders (Wiersma & Piersma 1994).

This introduction to the recent history of shorebird studies I hope will have set the scene a little for what follows. Two main points emerge to me from surveying the shorebird literature. First, the study of waders around the world is an active and prolific one. Second, it is also uneven in its geography. This is understandable, given the large concentrations of researchers in certain areas (primarily western Europe). This means that researchers in understudied parts of the world (eg. New Zealand) have access to much comparative data and they have an important role to play in filling in gaps in knowledge.

Shorebird studies in New Zealand have seldom focussed on tidal flats, being more involved with endemic breeders (eg. Wrybill *Anarhynchus frontalis*, Banded Dotterel, Black Stilt *Himantopus novaezealandiae*, Shore Plover *Thinornis novaeseelandiae*, Subantarctic Snipe *Coenocorypha* spp.). An exception to this is the Pied Oystercatcher which was studied on the Avon-Heathcote Estuary, Christchurch, in the late 1960s and early 1970s by Allan Baker (eg. Baker 1969).

Numerically, the wader fauna of New Zealand is dominated by three species in the intertidal zone. The commonest New Zealand breeder in the Pied Oystercatcher, with a population in the mid 80,000s (P.M. Sagar pers. comm.) The other two abundant species are Northern Hemisphere breeder, the Red (or Lesser) Knot *C. c. rogersi*, with 40-65,000 reaching New Zealand annually, and the Bar-tailed Godwit *Limosa lapponica baueri*, with 80-100,000 each year. Knots reaching New Zealand probably breed in eastern Siberia, perhaps in the Chukotski Peninsula region (Barter 1992; Tomkovich 1992), while at least some of our godwits come from western Alaska (A.C. Riegen, pers. comm.: Barter 1989).

No formal studies have been undertaken in New Zealand into the diet, food supply and ecology of these Arctic waders, despite the fact that New Zealand holds a very large fraction of the world population of their subspecies. Basic studies into diet and food supply are a necessary first step for being able to intelligently assess the vulnerability of a species at a site. Ens *et al.* (1990), editing the results of two major Dutch expeditions to the Banc d'Arguin, Mauritania, conclude that ". . . our work highlights the need for continuing scientific investigations in unspoiled ecosystems to understand these systems" (p. 6). New Zealand is fortunate then, that one of its most splendid depositional landforms which is one of the premier wader spots, is also a protected Scientific Nature Reserve, with restricted access only. On Farewell Spit, Golden Bay, we have as unaffected an intertidal habitat as any, which holds a large portion of New Zealand's waders, protected by law. Protection on its own is not enough, however: there is a need to understand the factors that lead to a site possessing the qualities it does, and the likely consequences of changes in these. Why, for instance, does Farewell Spit host so many waders? Is it simply because it is vast, or is the food supply especially good? How tightly linked are waders to their food supply, and how variable is this food source? Are there any parts of the year in which birds may be stressed in their quest for energy balance? What exactly do they feed on, and how much?

It is obvious that these questions are far too expansive to be addressed by a single individual on a limited time-frame (". . . delving into the mysteries of bird migration requires many years of hard work.": Ens *et al.* 1990). It is perhaps worth including one more Ens *et al.* quote: "Nonetheless, it is a sobering thought that it took Goss-Custard and his team 15 years of intensive field studies before they felt sufficiently confident to estimate the carrying capacity of the mussel beds in the Exe estuary for oystercatchers." (Ens *et al.* 1994).

In this thesis I attempt to shed some light on what it is that waders do in New Zealand, and why. Firstly, after introducing the physical environment of Farewell Spit (chapter 2) I look at the resource base available to birds near the tip of the spit (chapter 3), although time and labour limitations preclude a full benthic survey. I then examine the diet and energy intake of the three species in this study: godwit, knot and Pied Oystercatcher (chapter 4). This is compared with estimates of energy expenditure at the same time, and through the year. While in New Zealand, Arctic waders face large energy demands through having to deposit mass prior to migration. In chapter 5 I take advantage of a large data set accumulated on knots near Auckland by bird banders of the New Zealand Wader Study Group (Stephen Davies and Adrian Riegen) to document mass changes in knots through the year. Given that mass deposition appears to be largely endogenously controlled (Gwinner 1990; Rankin 1991) and the flights undertaken by these birds are of similar magnitude (chapter 7) these should be comparable with Farewell Spit birds. Mass change is only one apparent result of premigratory condition. Other internal changes can take place (Lindström & Piersma 1993; Piersma 1990; Piersma & Barter 1991; Piersma *et al.* 1993), and in chapter 6, with Theunis Piersma, I analyse the body composition of knots illegally shot in Northland in 1992, recovered by the Department of Conservation. This also allows intraspecific comparisons to be made with other subspecies of knots, adding to the growing pool of physiological data addressing the consequences of migration. Having prepared for migration, a bird then does it, and chapter 7 documents the behaviour of departing flocks of godwits and knots as they leave Farewell Spit in the southern autumn. The penultimate chapter (8) brings us back to ground with a consideration of the factors that might limit bird numbers in a migrant species. The final chapter (9) attempts to evaluate the findings of chapters 3-8 in light of the background of chapter 8. In summarising the knowledge to this point, I suggest important avenues of research that could be followed up in the future.

Chapter 2

Study Site: physical features, biological features and history

Geomorphology

Farewell Spit (40°30.5´S, 172°45´E to 40°33.5´N 173°02´E) is a long consolidated sand spit enclosing inner Golden Bay, NW Nelson (Figure 2.1). The source of sediment deposited on the spit is the eroding slopes of the western Southern Alps mountain range. Quartzite sediment flowing down rivers to the West Coast is swept by the Westland current northwards, around the NW tip of the south island, and eastward towards Cook Strait. Meeting an opposing current flowing northwest from Tasman Bay, sand is deposited on Farewell Spit. Furket (1947, cited in Jane 1989) estimated 3.4 X 10^6 m^3 of sand to be deposited annually on the spit. While the spit is considered to be growing south-eastwards, the high-tide land has shown no obvious trends over the last several decades (Bartlett 1985). However, a narrow intertidal or shallow subtidal tongue extends up to around 7 km further on from the limit of dry land.

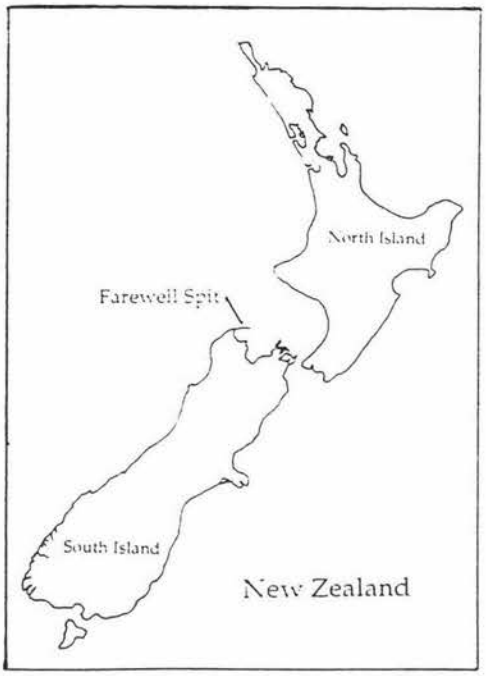


Figure 2.1 Location of Farewell Spit

Physically, Farewell Spit consists of three main topographical types (Figure 2.2). First, on the northern side there is a firm sandy beach and mobile sand dunes, interspersed with flat sandy pans that periodically flood through tides or rain. On the western third of the spit large sandy plateaux occur. Second, there is a series of small parallel vegetated dunes on the inner half of the spit proper. Many ephemeral and a few permanent freshwater lakes occur in the western third of the spit in this zone. Finally, on the southern side there are extensive saltmarshes grading into relatively vast tidal sandflats, which may extend 8 km or more at low tide. The high tide dry land portion of the spit reaches about 1 km in width. The only shellbanks on the spit are present at the tip.

The spit is probably accreting in all three directions. Northward growth of c.100 m is obvious from the remnants of a jetty used in the 1940s by the lighthouse which is now well removed from the sea. Intertidal and subtidal growth south-eastwards means shipping must give the spit a 10 km berth. Numerous ships have been wrecked or beached on the spit over the past 150 years. The extensive tidal flats on the inside of the spit are growing from sand transported across the spit by wind. There is a barely perceptible bend in Farewell Spit, from an ENE direction at the base, to a SW direction at the tip

The extent of the Farewell Spit Nature Reserve has been estimated at

Landmass	1,960 ha
Intertidal zone	9,943 ha
Total	11,903 ha

(Walker 1987)

Fieldwork

Fieldwork was undertaken at the tip of Farewell Spit, and places mentioned in the text, including sampling sites, are shown in Figure 2.2.

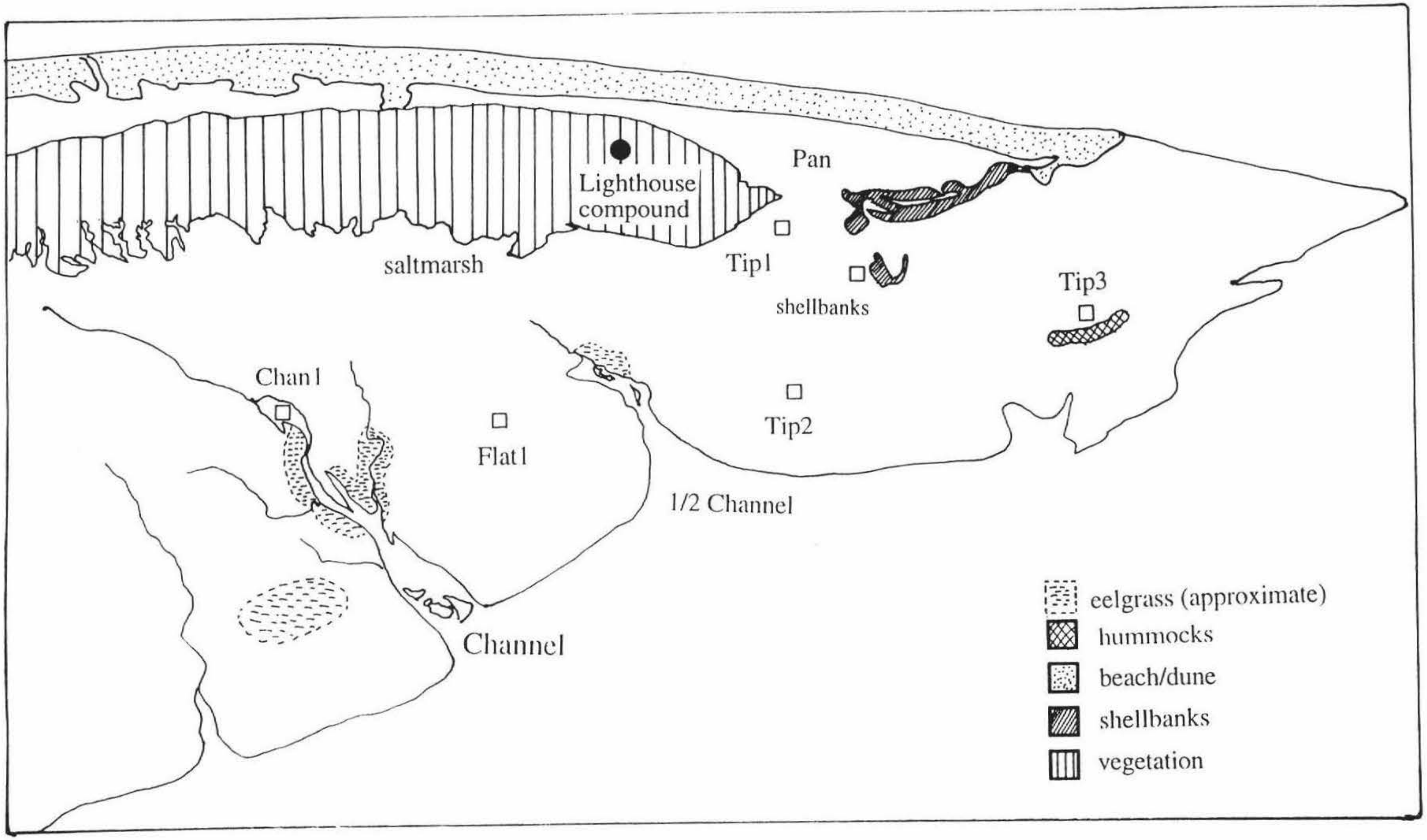


Figure 2.2 Detail of study site at the tip of Farewell Spit

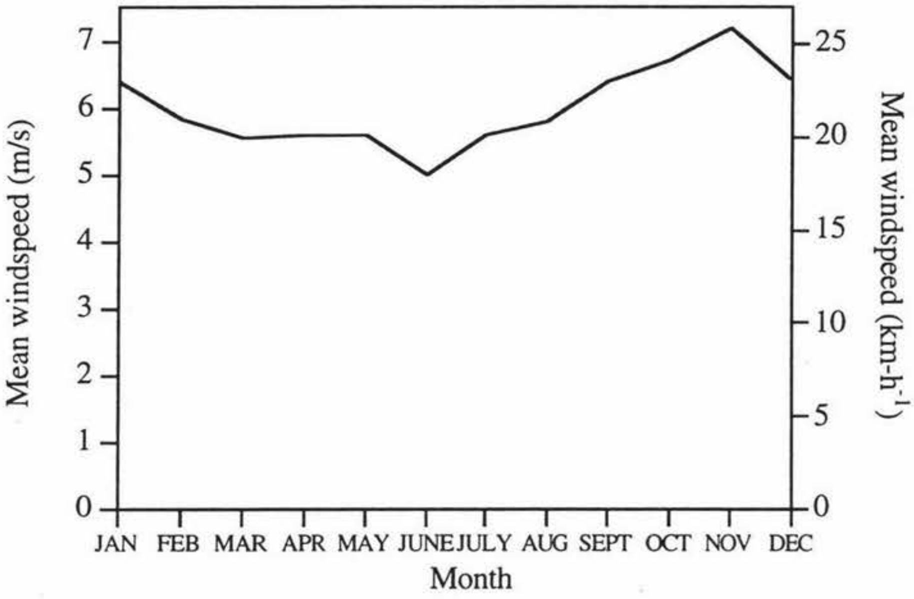


Figure 2.3 Mean windspeed recorded at the Farewell Spit lighthouse. Data from 1961-1980

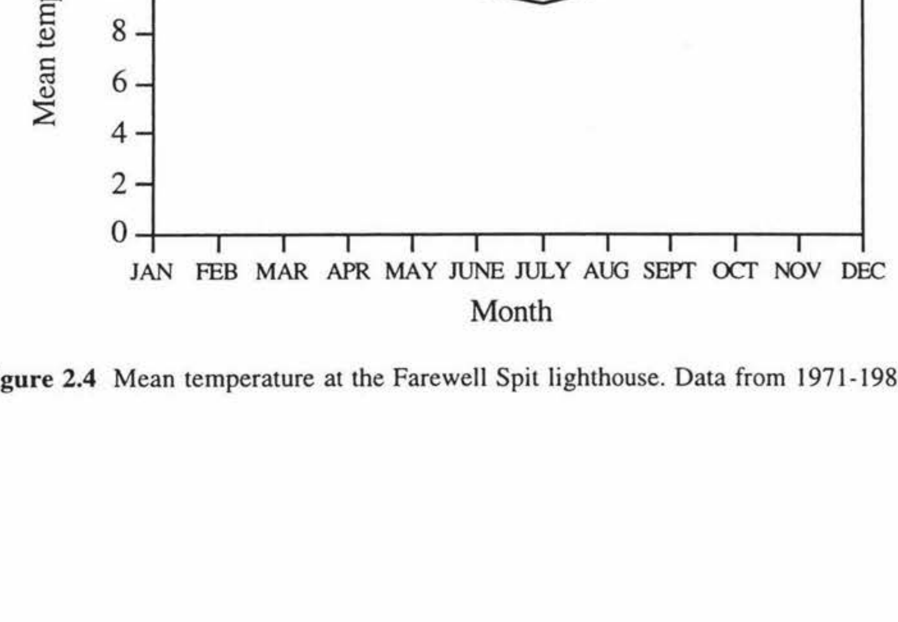


Figure 2.4 Mean temperature at the Farewell Spit lighthouse. Data from 1971-1980.

Climate

Farewell Spit is best known for its wind: monthly mean windspeed is shown in Figure 2.3. There is little variation through the year, with highest winds occurring in early summer, and lowest winds in late autumn/early winter. Over 100 days per year expect gusts of over 63 km-h^{-1}

Temperatures are greatest in summer, with a mean temperature in February of 17.7° C (Figure 2.4). Minimum mean temperature of 9.1° C occurs in July.

Vegetation

The vegetation of Farewell Spit is heavily modified through human influence. Maori used the spit for food gathering, and it is thought that the vegetation was modified in pre-European times. In 1874 Farewell Spit was leased for farming, and since then it has been burnt several times, and grazed periodically until 1973. The last cattle were removed by late 1976.

Young mobile sand dunes are dominated by the introduced marram grass *Ammophila arenaria*.. A few patches of pingao *Desmoschoenus spiralis* occur and spinafex *Spinafex sericeus* is slowly increasing following stock removal. Spinafex seems to be preferentially grazed by hares *Lepus europaeus* and possums *Trichosurus vulpecula*, though (pers. obs.). More stable dunes contain marram, yellow lupin *Lupinus arboreus*, wireweed *Meulenbeckia complexa*, *Coprosoma acerosa* and grasses. Inner dunes, with more established vegetation, have regenerating kanuka *Kunzea ericoides* forest, gorse *Ulex ueropaeus*, and in damp areas, dense flax *Phormium tenax* swamps. Blackberry *Rubus fruticosus* is widespread.

On the inside of the spit, the grass and scrub of dunelets gives way to saltmarsh vegetation, dominated by jointed wirerush *Leptocarpus similis*, then the sea rush *Juncus maritima*. The latter is frequently inundated by the tide on larger tides. These give way to low saltmarsh herbfields of glasswort *Sarcocornia quinqefolia* and sea primrose *Samolus repens*. Halfstar *Selliera radicans* is found in some higher areas and in swamps. These saltmarsh herbfields can extend out onto the flats quite extensively as raised islands. The tidal flats themselves are covered in very sparse to very dense eelgrass *Zostera* spp. Sea lettuce *Ulva* and the bright green algae *Enteromorpha* can also be found on the flats, the latter sometimes very extensively.

The saltmarshes appear to be somewhat dynamic in nature, as evidenced by remnant mud deposits with old crab holes extending onto the sandflats in many areas, indicating the presence of former saltmarsh.

Fauna

Farewell Spit is most famous for its large and varied bird populations, of which wading birds (order Charadrii) dominate. Few species of coastal bird breed on Farewell Spit, the exceptions being Banded Dotterel *Charadrius bicinctus*: (low numbers breeding on the beach and dunelets), Variable Oystercatcher *Haematopus unicolor* (20+ pairs spread evenly along the outer beach), Black-backed Gull *Larus dominicanus*:(colonies at Gull Gap and the shellbanks, odd pairs on both dunes and inner saltmarsh), Caspian Tern *Sterna caspia* (colony at shellbanks) and Australasian Gannet *Morus serrator* (colony at shellbanks). Red-billed Gulls *Larus novaehollandiae* and White-fronted Terns *Sterna striata* formerly bred on the shellbanks but have been displaced since the arrival of gannets.

Migrant birds consist of both internal migrants (Pied Oystercatcher and Banded Dotterel) and international long-distance migrants (Bar-tailed Godwit, Red Knot and Turnstone *Arenaria interpres*). In summer, the godwit and knot dominate numerically, whereas in the southern winter oystercatchers are the commonest. While turnstones are fewer in number than godwit and knot, Farewell Spit often holds more of this species than anywhere else in the country.

The other common species on Farewell Spit is the Black Swan *Cygnus atratus*, which uses the spit as a moulting site. They feed in shallow water in the intertidal zone, and there has of late been interest and concern about any possible effect the large numbers (up to 15-18,000 birds) may be having on the intertidal ecosystem and wading birds.

Mammals present on the spit include Australian Brush-tailed Possums hares, stoats *Mustela ermina*, hedgehogs *Erinaceus europaeus*, rats *Rattus rattus* and mice *Mus musculus* and feral cats *Felix domesticus*. Red Deer *Cervus elaphus* roam the spit. Culls in recent years have reduced numbers somewhat, while revealing that numbers were much higher than suspected.

The invertebrate fauna of the spit has been little studied. A University of Canterbury group visited the spit in the late 1970s, apparently finding nothing unusual, although no formal results have emerged from the visit (K. Stark, pers. comm.). Apart from a single transect sampled across the intertidal zone near Stockyard Point in the late 1970s, nothing has been done on the benthos of the tidal flats.

Status

Farewell Spit is a protected Scientific Nature Reserve. The first official status for the spit came in 1938 when it was set aside as a flora and fauna reserve and the tidal flats set aside for wildlife protection. In 1980 it was designated a nature reserve. It was one of the first New Zealand sites to be made a Wetland of International Importance by the International Council for Conservation of Nature (IUCN).

Access is strictly by permit only, apart from the base of the spit where foot access is allowed on the first couple of kilometres. Two concessions have been given for four-wheel drive tours up the outer beach to the lighthouse at low tide. These run almost daily over the summer. One operator has a concession to take small parties to view the gannet colony once Caspian Terns have finished breeding. Other visitors to the spit are mainly Department of Conservation staff, Ornithological Society members, and staff of the Ministry of Transport or the Meteorological Service servicing the lighthouse or weather-recording station respectively.

Scientific research

Little formal scientific investigation has taken place on Farewell Spit. Regular bird censuses have been made over the past 15 years (Heinekamp & Hawkins in prep.), and Robertson & Dennison (1979) briefly studied the roosting and feeding behaviour of some waders, although this was a largely descriptive study. Hawkins (1988) detailed the establishment of the gannetry at the tip.

The Auckland University Field Club visited the spit in 1977, the results being published in Wright (1978).

The vegetation of the spit was well surveyed in the mid-1980s (Bartlett 1985).

Chapter three

Prey availability

ABSTRACT The benthic invertebrate fauna at the tip of Farewell Spit was investigated to give insight into the food supply for waders and to generate useable relationships for reconstructing diet and energy intake with in Chapter 4. A full survey of the benthos was not attempted. There were large differences between sites in the composition of the biomass, with bivalves (primarily the cockle *Austrovenus stuchtburyi*) dominating offshore sites. Polychaete worms were important at offshore sites, while small crustacea (especially amphipods and isopods) contributed most of the biomass on the upper shore sampling site. Not all components of the fauna are relevant to each bird species, and the relevant biomass at the different sites was apportioned to Pied Oystercatcher, Bar-tailed Godwit and Red Knot. The cockle *Austrovenus* did not show unequivocal density changes through a year of sampling, but there was variation in flesh content and size-structure in the population, causing biomass to be lowest in winter. An overall increase in condition (mass per unit length) occurred through the study, hampering interpretation. Condition changes in shellfish were not equivalent through all sizes, so the variability encountered by a bird may depend on its size-selection. Another bivalve, the wedgeshell *Macomona liliana*, did not show distinct changes in condition though the year. An increase in depth for all size classes over winter, however, caused a decrease in the harvestable biomass for oystercatchers over winter. Virtually no *Macomona* biomass was harvestable by knots. Approaches to investigating latitudinal variation in harvestability of bivalves are discussed. The main contribution to this topic of this study was the finding that Tellinid bivalve (*Macomona*) depth changes are not restricted to cold-temperate areas, where they have been well documented in the past.

INTRODUCTION

Relationships between birds and their prey are seldom simple. Recent studies have shown that density measurements alone are in most cases insufficient to describe the situation encountered by birds (Piersma *et al.* 1994a; Zwarts and Blomert 1992; Zwarts and Wanink 1994). Limitations of detectability, accessibility, ingestibility, digestibility and profitability, all interact to define the ***harvestable*** fraction of the infaunal biomass. *Detectability* refers partly to the fact that for a tactile-searching bird, the chance of encountering a prey item will depend on the surface area of the prey: a small item will be harder to detect than a large item. In addition, the behaviour of the prey may also affect their detectability (eg. worms retreating down burrows). Sandflats are not two-dimensional habitats, however, as is assumed in a simple random-touch model, and invertebrates may vary in their depth in the sediment. This means that prey deeper than the bill-length of a foraging bird will not be *accessible*. Furthermore, some individual prey items will grow too large to be swallowed (especially in shellfish): an *ingestibility* limitation exists for foragers which swallow their prey whole. For invertebrates with a significant amount of inorganic material in their bodies (eg. exoskeleton of crustacea), the *digestibility* of an item may be affected. In extreme cases this may lead to a digestive bottleneck (Zwarts & Dirksen 1990). Finally, not all prey are *profitable* - small prey may provide insufficient a reward for the energy expended in searching for and ingesting them. So the *harvestable fraction* may be only a small proportion of the total biomass for an area. The interaction of limitations of *profitability*, *ingestibility*, and *accessibility* is shown graphically in Figure 3.1 (from Piersma 1994).

Recent studies have focussed on determining the within- and between-year variability in harvestable prey biomass at a site (Beukema *et al.* 1994; Piersma *et al.* 1994d; Zwarts *et al.* 1992; Zwarts and Wanink 1994), and also looked at the relationship between prey biomass and bird numbers (Piersma *et al.* 1994b). Piersma *et al.* (1994a) have furthered this by looking for latitudinal comparisons to be made within the diet of the Red Knot *Calidris canutus*. This approach should in theory prove useful in investigating the migration and evolutionary ecology and shorebirds in a more detailed manner than attempted thus far (c.f. Hockey *et al.* 1992), allowing the confirmation or refinement of assumptions in modelling procedures.

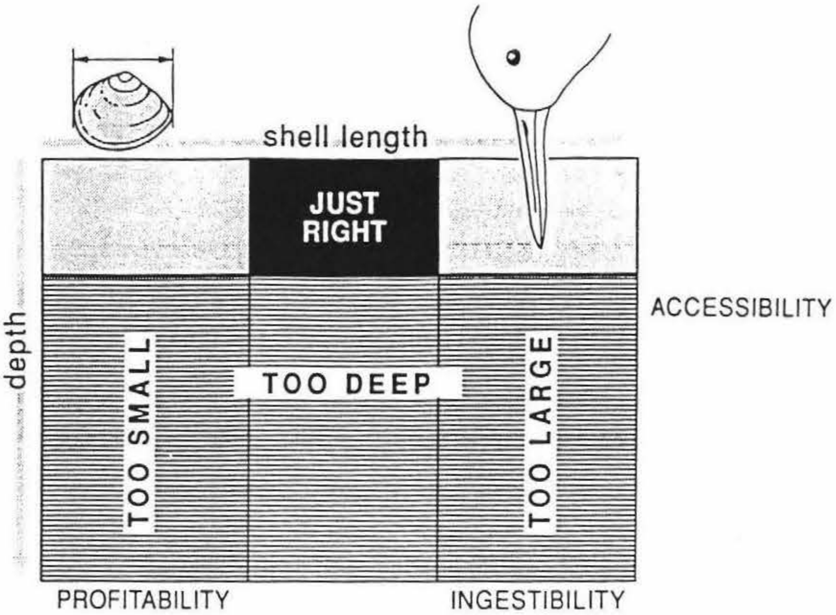


Figure 3.1 How the harvestability of a prey item depends on its ingestibility, profitability and accessibility. Reprinted with permission from the author.

Piersma *et al.* (1994a) were unable to show any latitudinal differences in the harvestable fraction for mollusc-eating knots. However, the importance of depth over size limitations did vary considerably, so in some invertebrate species accessibility was the limiting factor, while in others ingestibility was. This community-based approach has so far not provided any biological generalisations.

Another approach to evaluating latitudinal differences could be a taxon-based one: it may be that any overall patterns (if they exist) are best elucidated by investigation of taxonomically similar species. For example, *Macoma balthica*, the Baltic tellin, is a common prey for mollusc-specialist predators in the North Atlantic. It shows pronounced changes in harvestability which are reflected in the diet of its predators (Piersma *et al.* 1994b; Piersma *et al.* 1993; Zwarts and Blomert 1992). The bivalve *Macomona (Tellina) liliana* could thus be expected to be a useful New Zealand analogue to *Macoma* in the Atlantic. It is thin-shelled, widespread, has been found to occur in the diet of both knots and oystercatchers, and leaves obvious siphon-feeding marks which could used as cues by feeding oystercatchers.

Most studies on benthos as bird-food have been conducted in cold-temperate zones (especially Europe). We do not yet know how similar or different conditions are in warm-temperate zones.

One of the aims of this chapter is to give insight into benthic harvestability in New Zealand and sources of variation in prey 'quality'. This involves any of mass, density and depth changes in different taxa. This should allow assessment of the relevance of generalities derived from cold-temperate studies to the New Zealand intertidal zone. The second aim is somewhat more earthy, to calculate for various invertebrate species, appropriate measurements on size and biomass for use in dietary studies in Chapter 4.

Due to the large size of the intertidal area used by birds and the its physical heterogeneity, I am unable to provide an overall estimate of benthic biomass for the area. However, the individual site values will give examples of prey levels encountered by birds as well as some indications of the variability in time and space that birds must contend with.

METHODS

Four sites were sampled in full benthic surveys (Figure 2.2), giving a range of tidal heights and distance from shore. Characteristics of each site are given below:

TIP1. 150-250 m from shore adjacent to Bush end Point. Innermost row of sample square not covered in small neap high tides. No eelgrass cover. Much organic sub-surface matter.

TIP2. 1850-1950 m from shore. Only 200-300 m in from small neap low tides. Consists of alternating bands of exposed sand and belts of shallow water (c. 5-25 cm deep). Eelgrass cover 30 %, light.

FLAT1. 1750 m from shore 2000 m west of TIP2. . Moderately dry sand during most low tides. Eelgrass cover 80 %, sparse. Much sub-surface eelgrass root matter

CHAN1. 1500 m from shore out from saltmarsh, 3000 m west of Bush End Point. Situated in bottom of tidal channel extending almost to shore. Sampling area covered open sandy area on island in channel. Eelgrass cover 50 %, light. Subject to high water velocities during both ebb and flow tides.

Each site was arranged in a 4 X 4 grid of 25 m X 25 m squares, giving a total area of one hectare, aligned roughly parallel to the shore. One core sample (0.179 m^2) was taken at a randomly-derived point in each square, to a depth of 25 cm if possible. Each core was sieved on site through a 0.565 mm sieve and all invertebrates collected. Unfortunately large sand grain sizes at most sites and organic matter at TIP1 meant that this had to be meticulously sifted through with a teaspoon, mainly to find all small crustacea (amphipods, isopods and cumaceans). When no more were found after about two minutes of searching the core was considered completed. This would often involve 20-25 minutes of searching per core. Invertebrates were then either preserved in formalin (5%, in seawater) or frozen. While preservation can affect biomass of invertebrates, formalin erodes calcium rather than protein, and studies have indicated little change in biomass of samples in formalin (Leuven *et al.* 1985). Ash-free dry mass was thus not adjusted for duration of formalin preservation. Unfortunately a technical problem with the deep-freezer at Massey University mean that most 1992-93 samples deteriorated and could not be analysed. One taxon not sampled adequately in this fashion was *Eatoniella*, a tiny black snail which occurred in the diet of knots (Chapter 4). This was counted independently in core imprints on eelgrass leaves on which the snail lived.

Sampling dates for these sites are given in Table 3.1.

Table 3.1 Sampling dates for all invertebrates (Tip1-Pan), cockles *Austrovenus* (Tip3) and wedgeshells *Macomona*.

	June 93	Dec 93	Jan 94	Feb 94	Mar 94	Apr 94	May 94	June 94	July 94	Aug 94	Sept 94	Oct 94	Nov 94	Dec 94
Tip1	X	X				X								
Tip2	X	X				X		X						
Tip1-2						X								
Flat1		X												
Chan1		X												
Pan						X								
Tip3		X	X	X	X	X		X		X	X	X		X
Shell-banks		X	X	X	X	X		X		X	X	X		X

Shellfish sampling

Two sites were sampled at the beginning of each month for a year to determine changes in density and available biomass. Three months (May/July/November) were not able to be sampled due to logistical difficulties.

The wedgeshell *Macomona liliana* was sampled at a high-density site adjacent to the shellbanks (Figure 2.1). Layout of the plot was similar to all other plots, except that one corner plot was moved to avoid a tidal channel and placed at the opposite end of one side. In addition to the 16 density samples, a collection of shellfish was made to determine the depth distribution. A core of sand was taken adjacent to the sampling site and placed vertically on the surface. This was then sliced through vertically with a knife until a bivalve was found. The distance from the top of the bivalve to the surface of the core was measured to the nearest 0.5 cm from 0 to 5 cm depth and the nearest 1 cm thereafter. Shellfish were placed in labelled containers corresponding to the depth classes, and bagged and frozen upon completion.

Cockles *Austrovenus stuchtburyi* were sampled at a site just inshore from the hummocks around 1000 m south of the shellbanks (Figure 2.1). As this species shows little variation in depth, only density samples were taken.

RESULTS

In total around 70 invertebrate taxa were recorded on the tidal flats. Most of these were worms, with around 41 taxa noted (mostly polychaetes but also 2 nemertines and 1 probable oligochaete). 20 crustacea were found, including 10 amphipods, 2 isopods, 1 cumacean, 3 shrimps and 4 crabs. Only four bivalves were present, but at least five gastropods.

Total biomass

Total biomass at the four sampling sites varied between 2.1 and 10.9 g AFDM/m^2, with the biggest contributors being bivalves and worms (mainly polychaetes, with the occasional nemertine and possible oligochaete). The biomass for major groups of organisms are shown in Figures 3.2 to 3.5. In addition to large differences in biomass and composition between sites, there can be large changes over time, such as a tenfold increase in the biomass of cockles *Austrovenus* at Tip2 over twelve months.

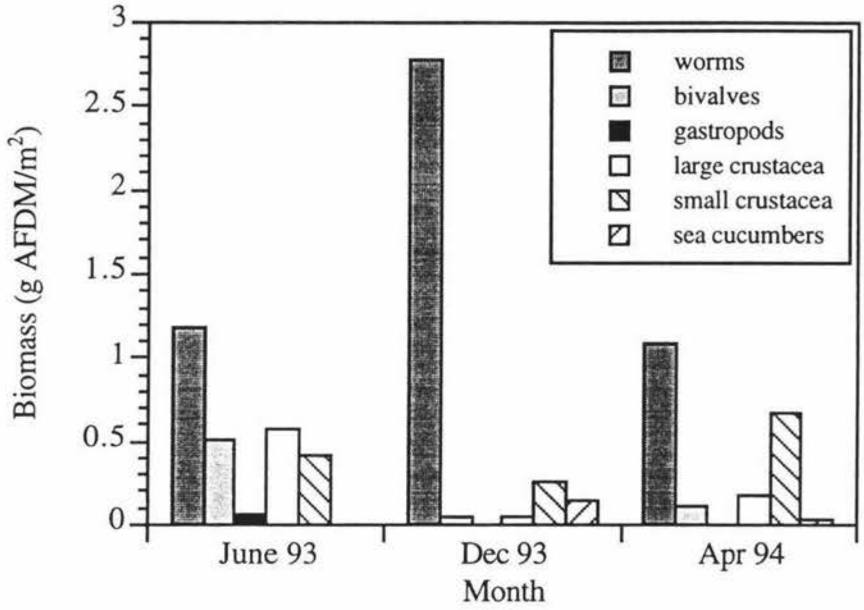


Figure 3.2 Biomass of main taxonomic groups of organisms at Tip1 sampling site.

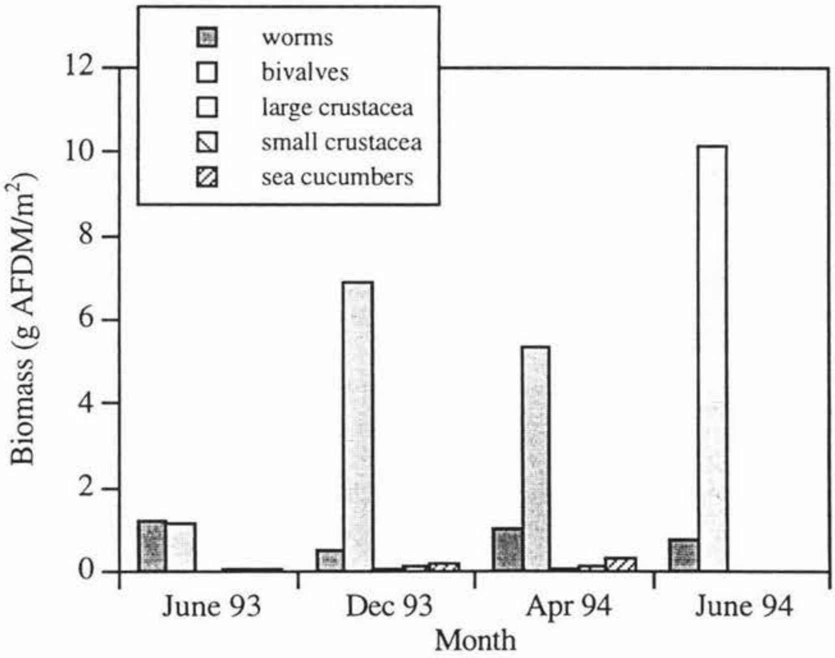


Figure 3.3 Biomass of main taxonomic groups of organisms at Tip2 sampling site.

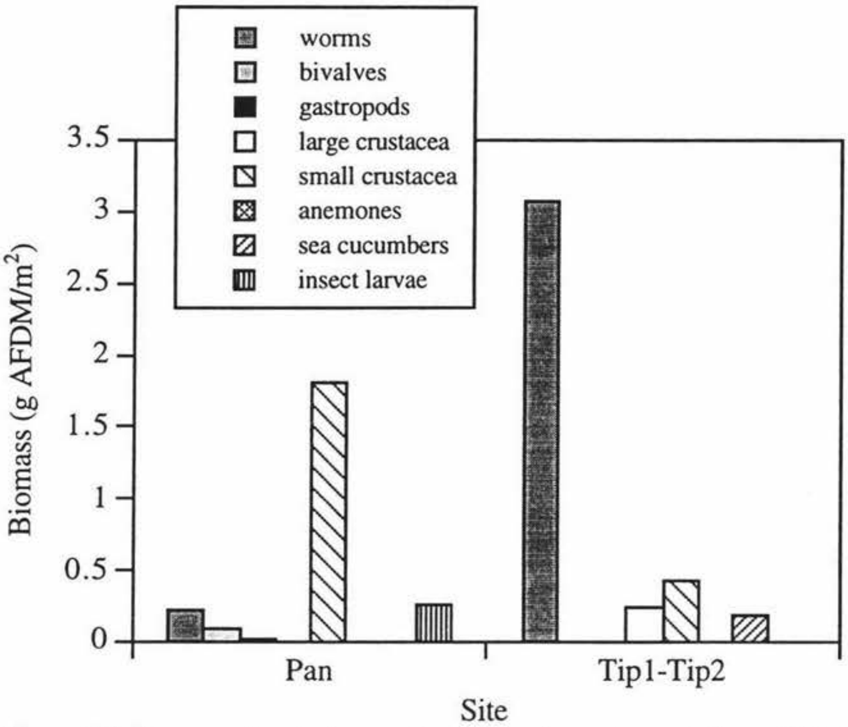


Figure 3.4 Biomass of main taxonomic groups of organisms at Pan and Tip1-Tip2 sampling sites.

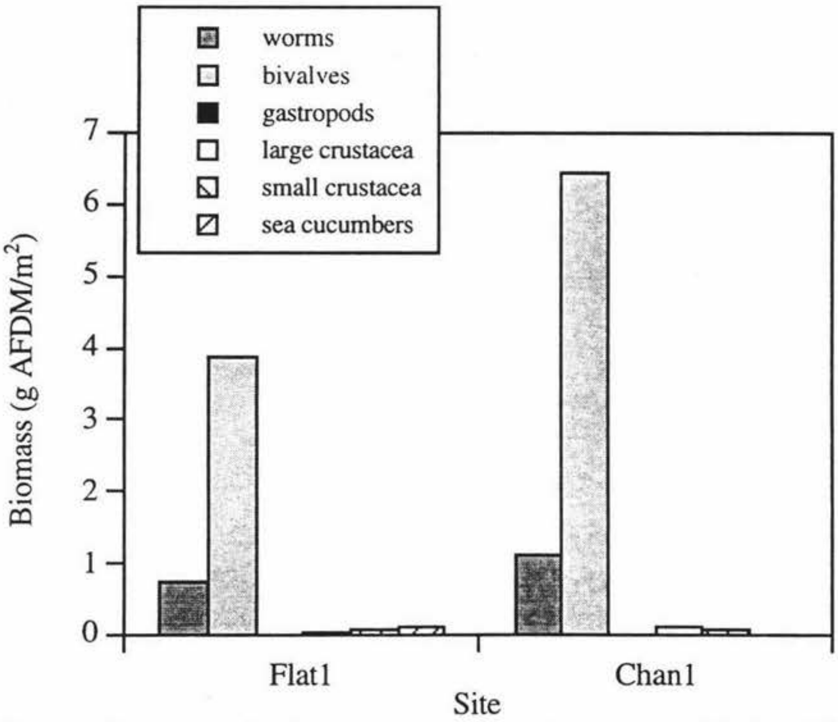


Figure 3.5 Biomass of main taxonomic groups of organisms at Flat1 and Chan1 sampling sites.

Not all of this biomass is relevant to different predators, of course, and Figures 3.6 to 3.8 coarsely summarise conditions for the main three bird predators of Pied Oystercatcher, Red Knot and Bar-tailed Godwit. The relevant portions of biomass were treated as:

Pied Oystercatcher	*Austrovenus* and *Amphidesma* (Pipi) $\geq$ 15 mm, all *Travisia olens*, *Abarenicola affinis* (Lugworm), Maldanid bamboo-worms and Orbiniid worms.
Red Knot	*Austrovenus* $\leq$ 14 mm, *Amphidesma* $\leq$ 22 mm, all small crustacea (Amphipoda, Isopoda, Cumacea)
Bar-tailed Godwit	All worms

This is somewhat oversimplistic, as the diets of these species are broader than indicated by this, but it contains the main contributors to the diet of these species that were present in sampling (Chapter 4; small gastropods in the diet of knot were not sampled formally).

Biomass relevant to oystercatchers varied from around 1 to 11 g AFDM/m^2 (Fig 3.6), even within the same site (Tip2). The offshore sites (Tip2, Flat1, Chan1) all had large bivalve values due mainly to the presence of large numbers of cockles.

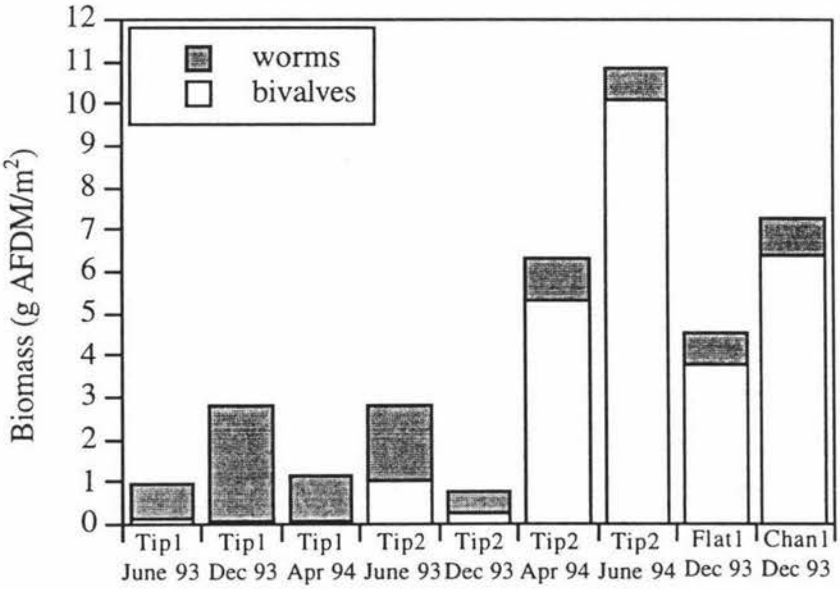


Figure 3.6 Pied Oystercatcher prey biomass levels at four main sampling sites.

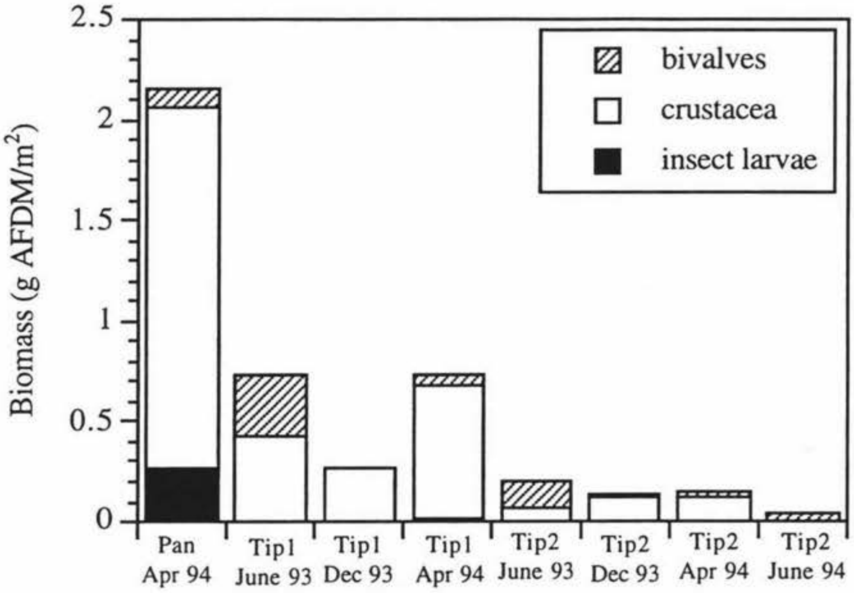


Figure 3.7 Knot prey biomass levels at three main sampling sites. Biomass at Flat1 and Chan1 (not shown) for both bivalves and crustacea lay between 0.075 and 0.087 g AFDM/m^2.

Knot prey biomass levels were generally low, especially for their favoured bivalve prey, in which biomass varied between 0.006 and 3 g AFDM/m^2. In upper-shore samples (Pan and Tip1) small crustacea dominated the biomass, while insect larvae (Diptera) were not insignificant on the Pan.

Biomass of worms available to godwits varied between about 0.5 and 2.75 g AFDM/m2, seldom being below 1 g AFDM/m^2 (Figure 3.8).

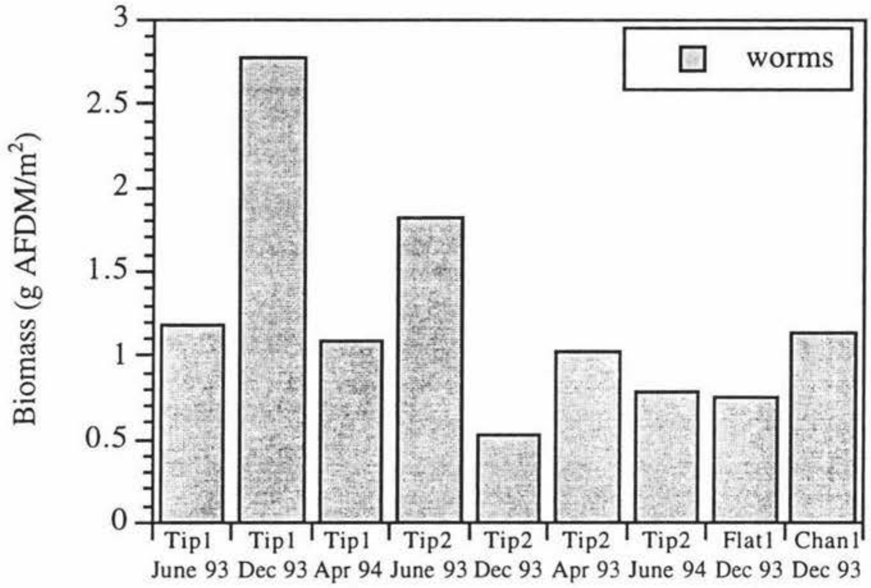


Figure 3.8 Godwit prey biomass levels at four main sampling sites.

The tiny snail *Eatoniella* was absent from Tip1 and Chan1. Tip2 had a mean density of 11.1 indiv/core (n=10), or 62.2 indiv/m^2 where eelgrass was present. With 30% eelgrass cover this equates to 18.7 indiv/m^2. Flat1 had an overall density of 15.3 indiv/m^2. These densities represent very small biomass values: 0.014 g AFDM/m^2 at Tip2 and 0.011 g AFDM/m^2 at Flat1.

Size relationships in bivalves

Useable regressions for relating hinge height and hinge+top height to shell length in cockles are shown in Figures 3.9 and 3.10 (note that workers at distant sites should check the validity of these equations before using them). While there is a levelling off at large hinge and hinge+top lengths, these regressions will be used for reconstructing ingested shellfish in knots, which are able to take only small individuals, so this will not lead to errors. Hinge+top height has a slightly higher explained variance than hinge alone. However, in practice hinge height is easier to measure in most cases in shell fragments.

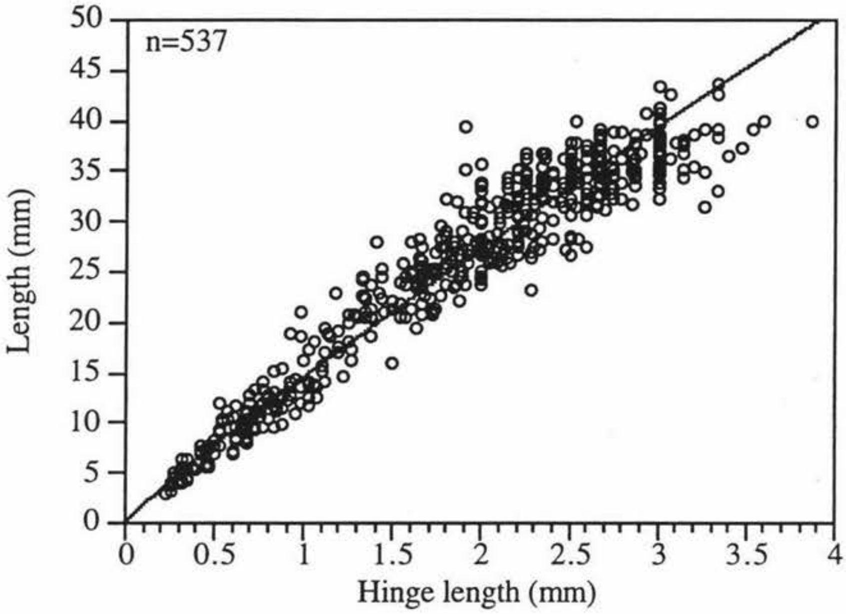


Figure 3.9 Relationship between hinge height and shell length for cockles. Length =14.62*hinge$^{0.903}$ (R^2=92.1%).

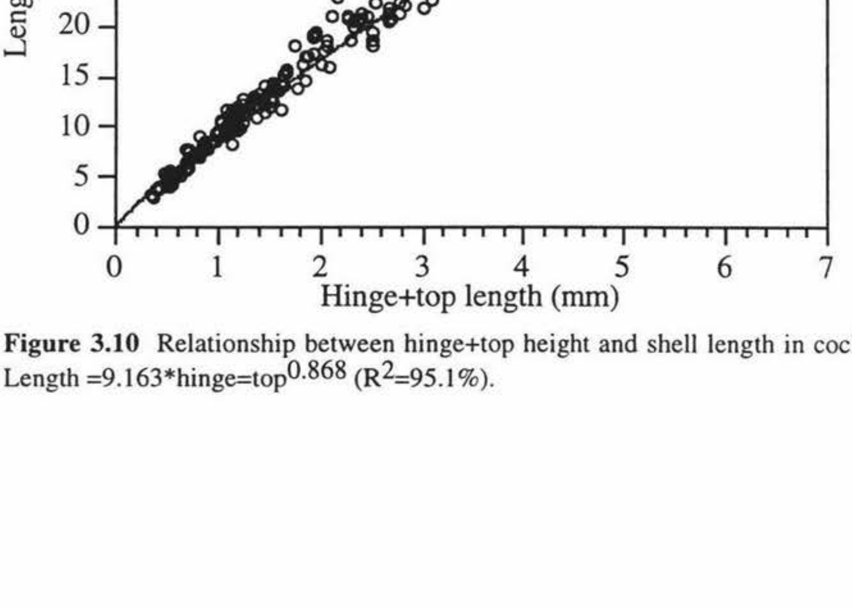


Figure 3.10 Relationship between hinge+top height and shell length in cockles. Length =9.163*hinge=top$^{0.868}$ (R^2=95.1%).

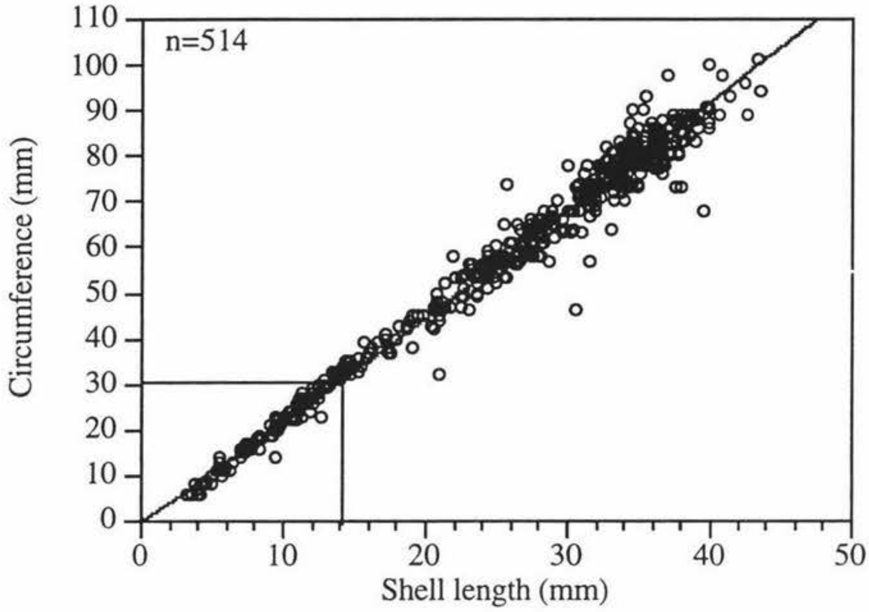


Figure 3.11 Ingestibility limitation of cockles for knots. Circumference =1.92 $*\text{hinge}^{1.049}$ (R^2=97.7%). The box in the lower left corner shows a gape limitation of 30.8 mm corresponds to a shell length of 14.1 mm.

Not all shellfish are ingestible, however, as there is a limit imposed by gape size, which in knots has been estimated at 30.8 mm (Zwarts and Blomert 1992). Figure 3.11 shows that knots can probably not ingest cockles larger than around 14 mm.

The relationship between hinge+top height and shell length for the pipi is shown in Figure 3.12. As pipi are long and elongate, they are theoretically ingestible at a larger shell length than the rounded cockles (Figure 3.13).

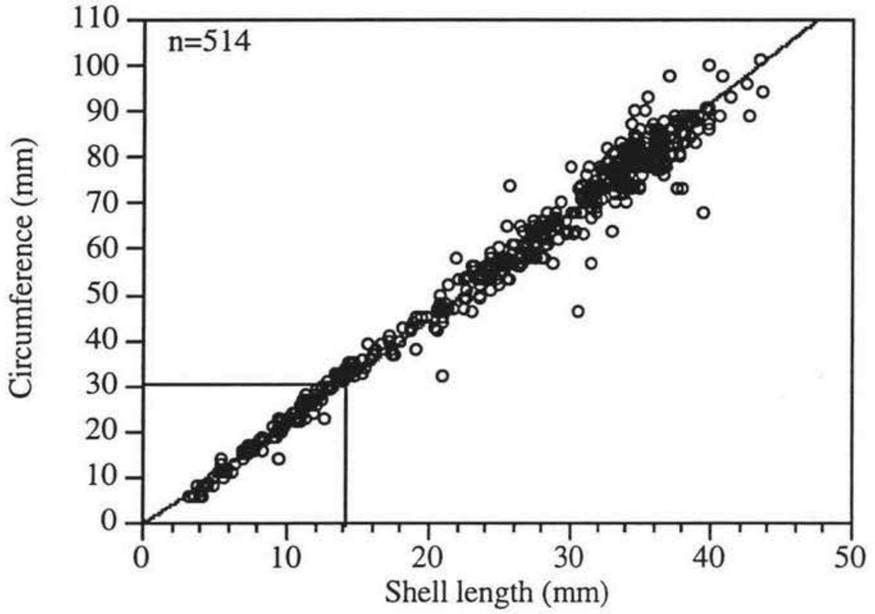


Figure 3.12 Relationship between hinge+top length and shell length in the pipi. Length =10.307*hinge+top$^{0.977}$ (R^2=96.2%).

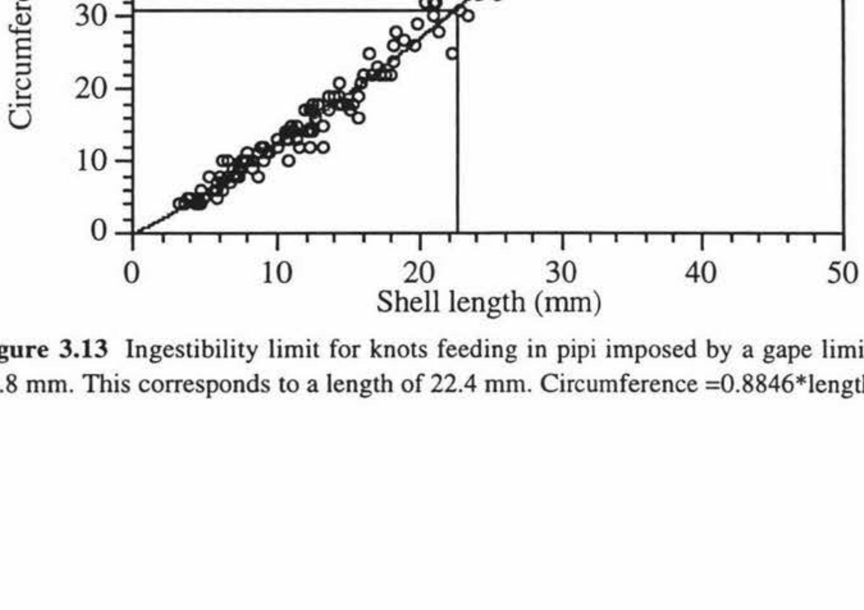


Figure 3.13 Ingestibility limit for knots feeding in pipi imposed by a gape limitation of 30.8 mm. This corresponds to a length of 22.4 mm. Circumference =0.8846*length$^{1.142}$ (R^2=98.7%).

Sizes of shellfish

There were small, but significant, differences in mean shell length of cockles at Tip3 (Oneway ANOVA, F_8=2.31, P=0.031) with mean shell length increasing through winter (Figure 3.14). Smaller cockles.(<20 mm) were absent from March to October. This is probably due to growth of these individuals over summer/autumn, with immigration of small cockles from upshore in spring. The variance of the monthly mean lengths reflects this, decreasing over winter (Levene's Test (Van Valen 1978), Oneway ANOVA, F_7=4.77, P<0.001: Figure 3.14) . Plots illustrating the main differences (June 93, Jan 94, June 94 and Dec 94) are shown in Figure 3.15. Plots for all months are provided in Appendix 1.

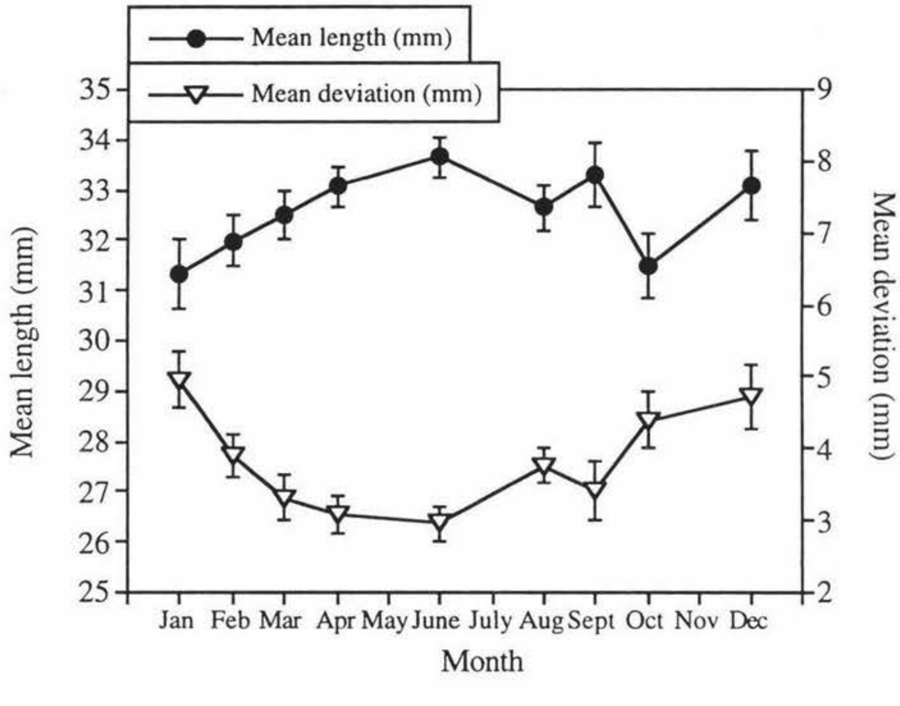


Figure 3.14 Mean cockle shell length (Y_1 axis) and mean deviation (Y_2 axis: absolute value of difference of original datum from mean of sample) by month (1994). Bars are standard errors of the mean. Note the different scales. Mean sample size equals 80.8 for both measures.

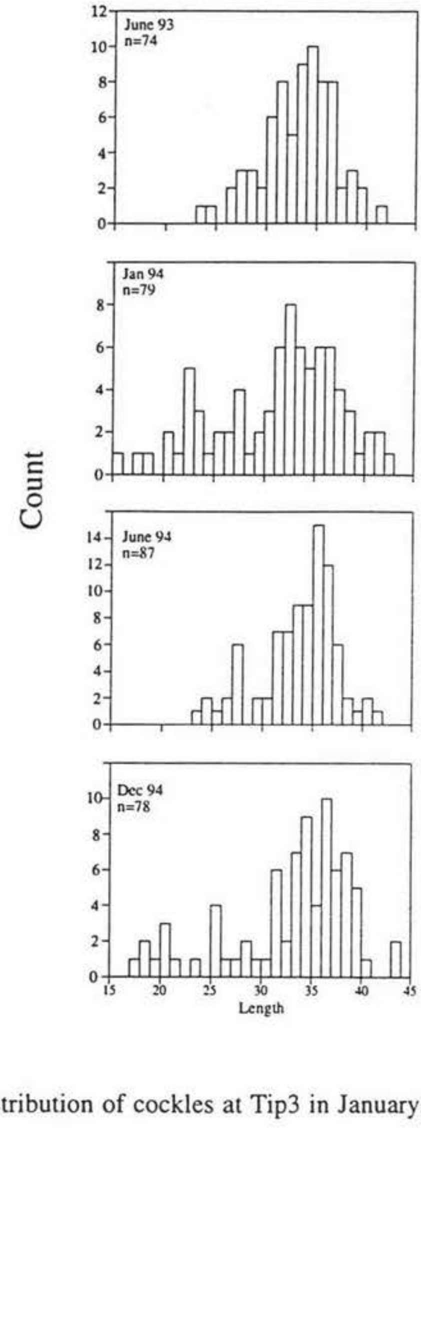


Figure 3.15 Size distribution of cockles at Tip3 in January, June and December 1994.

Mussels

Mussels *Modiolus neozelanicus* were sampled in late summer (February) and in early winter (June) at the hummocks south of the main shellbank. Only mussels larger than 10 mm in length were measured. Figure 3.16 plots the relative size distributions of cockles in samples at each time. While there was only a small increase in the mean size of mussel present (mean February=16.534, sd=2.5066; mean June=17.218, sd=3.7191) the June sample had relatively more small and large mussels present. This may represent growth from both small (<10 mm) and medium (15-18 mm) cohorts over the intervening period.

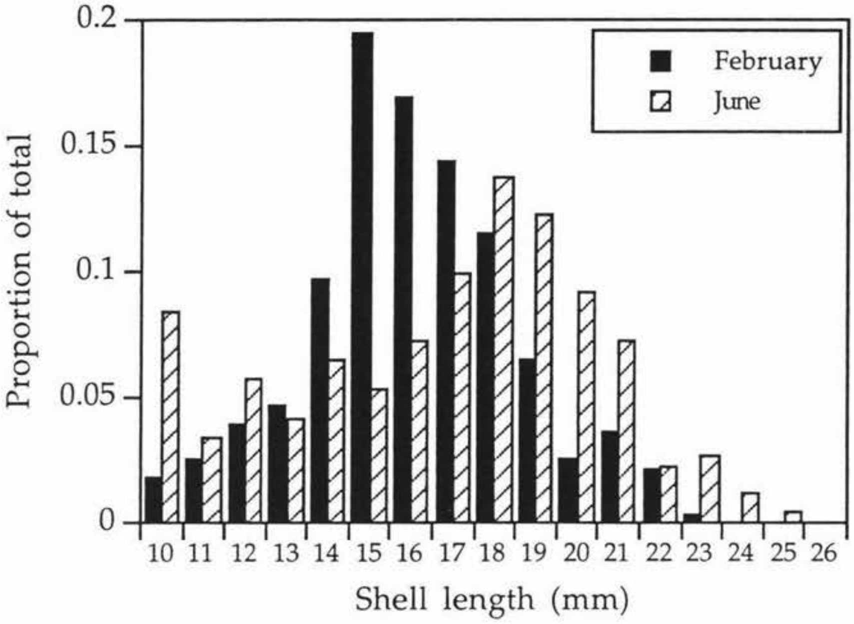


Figure 3.16 Size distributions of mussels present near the tip of Farewell Spit in late summer (February) and early winter (June). N=278 in February and 261 in June.

Size-mass relationships

The flesh content of cockles varied through the year. Table 3.2 gives the intercepts and exponents for the relationship between shell length and AFDM for cockles. This is based on cockle density samples at Tip3, extra cockles collected on occasions with *Tellina* density samples at the Shellbanks site, and during total invertebrate density sampling at Tip1, Tip2, Flat1 and Chan1 sites. Power functions ($y = ax^b$) were used as they gave the best fit and there was no reason to expect other functions to be more biologically appropriate. Large differences were present in the intercept, indicating that flesh content varied seasonally for all sizes. However, the exponent values also differed (between 2.6 and 3.3 for months with small cockles sampled) indicating that the form of the function differed also between months. Exponents rose from Dec 93 to March 94, decreased through early winter, then rose again in late winter before levelling off. This may represent a biological reality rather than a statistical artefact.

Table 3.2 Intercept, exponent and explained variance for power functions relating shell length to biomass (mg AFDM) for cockles in different months. Only months when supplementary collections of small cockles (<20 mm) were made are presented. $N_{determinations}$ refers to the number of samples of pooled individuals weighed, while $N_{individuals}$ gives the total number of individuals involved. Values in italics are months in which no small cockles were collected (minimum Feb=18 mm, Sept=20 mm).

Month	Intercept (e^{-03})	Exponent	R^2 (%)	$N_{determinations}$	$N_{individuals}$
June 93	9.7755	2.6374	97.4	31	102
Dec 93	17.87	2.5353	89.0	40	63
Jan 94	7.5231	2.7889	95.3	51	132
Feb 94	*2.6393*	*3.2331*	*93.1*	*19*	*89*
Mar 94	2.7753	3.1789	95.0	40	118
Apr 94	6.6595	2.9065	92.1	34	114
June 94	10.049	2.7543	84.6	46	132
Aug 94	4.4809	2.9826	94.3	32	109
Sept 94	*3.587*	*2.4775*	*94.8*	*18*	*50*
Oct 94	5.6152	3.0128	97.3	27	82
Dec 94	2.0243	3.3354	97.3	28	88

Seasonal changes in flesh content for a given size of cockle were calculated for sizes 15, 25 and 35 mm, by estimating the mean value from the equations in Table 3.3 for months in which all size classes were collected. The greatest absolute difference was present in the 35 mm size class (Figure 3.17), where estimated mass ranged from 147 mg to 286 mg AFDM. This also showed the greatest variability with a relative standard deviation (RSD; stdev/mean*100) of 23.9 (35 mm), compared with 15.5 (25 mm), 11.0 (15 mm), although this might be expected simply from the use of power functions. Flesh content of large cockles (35 mm) in December 1994 was almost twice that of December 1993. The December 1994 peak may represent the March 1994 peak, but at a higher level and earlier in the summer. As estimated mass for small cockles (<10 mm) is likely to be unreliable based on regressions for all sizes, it is preferable to derive new predictions based on only these small sizes. Too few data were gathered to allow this by month, so estimated mass for 5 mm cockles was compared between summer (November-April) and winter (June-October). Estimated mass was 60% greater in winter than summer (summer mass=0.94 mg AFDM, winter mass=1.50 mg AFDM).

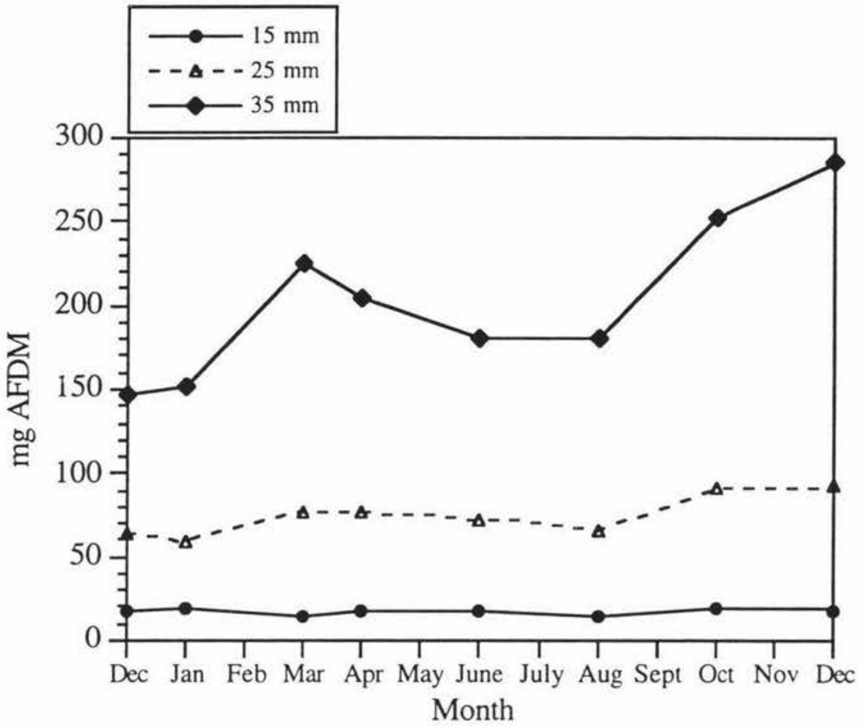


Figure 3.17 Seasonal changes in flesh content of 15, 25 and 35 mm cockles, estimated from monthly equations relating shell length to flesh content (Table 3.2: n=50-132 individuals weighed in each month).

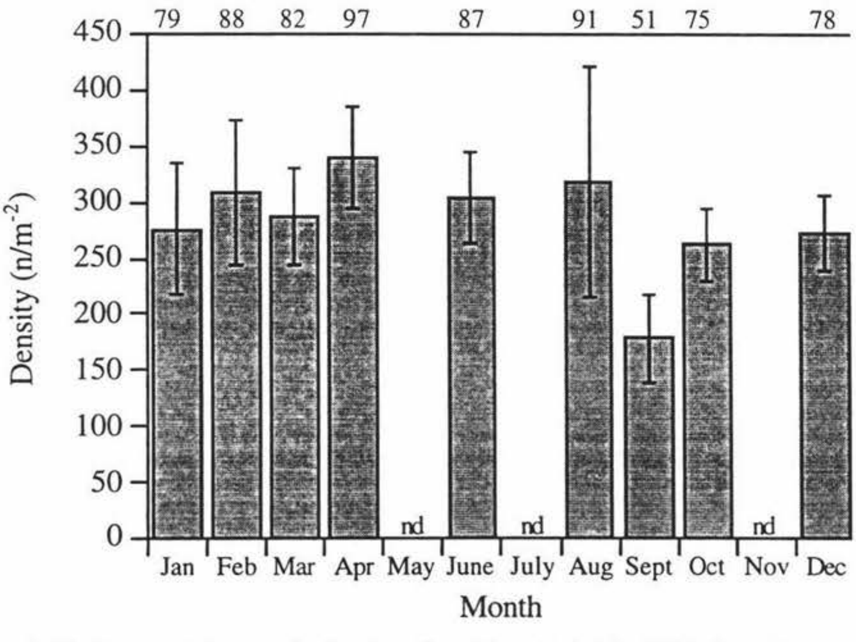


Figure 3.18 Seasonal changes in density of cockles at Tip3 in 1994. Sampling covered 0.3 m2. Actual number of cockles per 16 cores is given above the plot. Bars represent one standard error of the mean.

Cockle density also varied between months, but not significantly (One-way ANOVA, F_8=0.70, P=0.69) and changes at Tip3 site (occupied by individuals generally ≥20 mm in length) are shown in Figure 3.18. It should be noted that 31 of the 91 cockles in August were contained in one core sample: this exceptional count may mask any possible decrease in density in the other 15 cores.

As the flesh content of cockle is not constant, density changes alone are insufficient measures of food supply. The total biomass per site may be a more meaningful measure (Figure 3.19), and a decrease from autumn (Mar/Apr) to winter (June-Sept) is obvious, despite the high density in August. Total biomass in December 1994 was almost twice that of January 1994, due to the great increase in flesh content of large cockles.

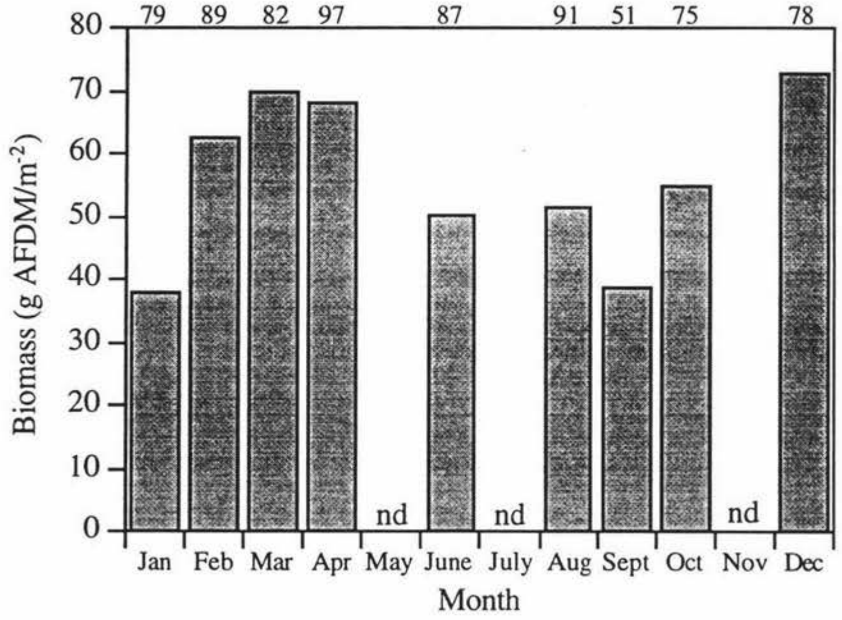


Figure 3.19 Seasonal changes in total biomass in cockles at Tip3 in 1994. Sampling covered 0.3 m^2. Actual number of cockles per 16 cores is given above the plot.

Macomona showed smaller seasonal variation in flesh content over the year than cockles, and most exponents of length-mass relationships lay between 2.6 and 2.9 (Table 3.3). There was a sustained increase in this from late winter, although this was accompanied by a decrease in the intercept. The net effect was thus only a moderately small increase in flesh content in spring 1994 (Figure 3.20). The three size classes showed similar levels of seasonal variation in flesh content [RSD = 12.6 % (15 mm), 10.2 % (25 mm) and 13.2 % (25 mm)].

Table 3.3 Intercept, exponent and explained variance for power functions relating shell length to biomass (mg AFDM) for *Macomona* in different months. $N_{determinations}$ refers to the number of samples of pooled individuals weighed, while $N_{individuals}$ gives the total number of individuals involved.

Month	Intercept (e^{-03})	Exponent	R^2 (%)	$N_{determinations}$	$N_{individuals}$
June 93	5.4323	2.6761	90.1	50	94
Dec 93	9.7476	2.6451	61.3	39	56
Jan 94	10.056	2.6207	94.4	47	91
Feb 94	8.0395	2.7043	94.3	41	99
Mar 94	9.7716	2.6096	97.3	31	62
Apr 94	8.7251	2.6729	87.0	37	73
June 94	10.482	2.6866	94.5	36	78
Aug 94	4.9171	2.864	93.2	28	57
Sept 94	4.818	2.8804	75.2	22	30
Oct 94	4.4918	2.9126	89.7	33	81
Dec 94	1.313	3.272	77.2	35	78

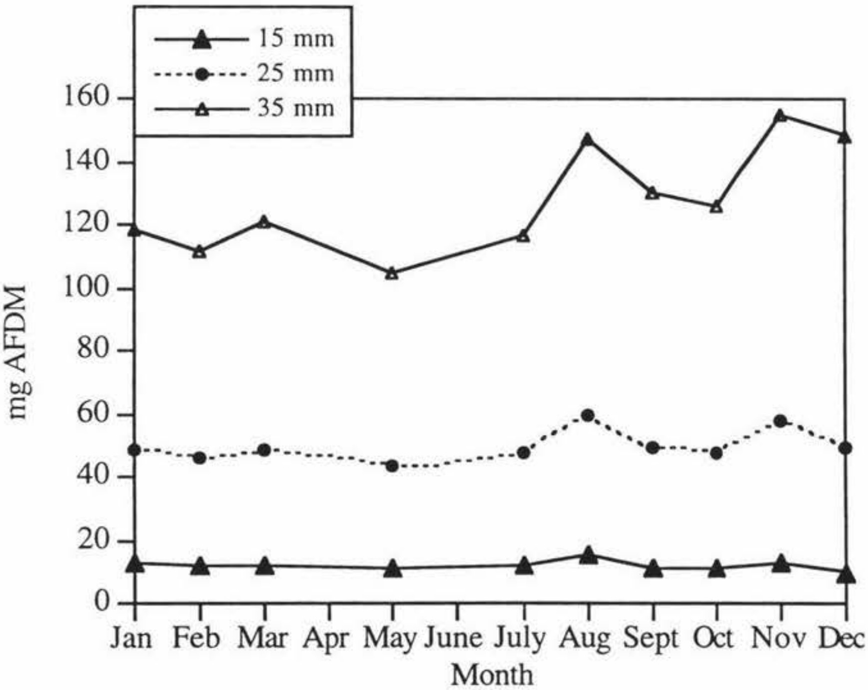


Figure 3.20 Seasonal changes in flesh content in *Macomona* of 15, 25 and 35 mm length in 1994, estimated from monthly regressions relating shell length to flesh content (Table 3.3: n=30-99 total individuals weighed in each month).

Macomona showed pronounced depth differences through the year, with a maximum depth in mid-late winter (Figure 3.21). The deepness of *Macomona* means that most of the biomass is unavailable to predators (Figure 3.22).

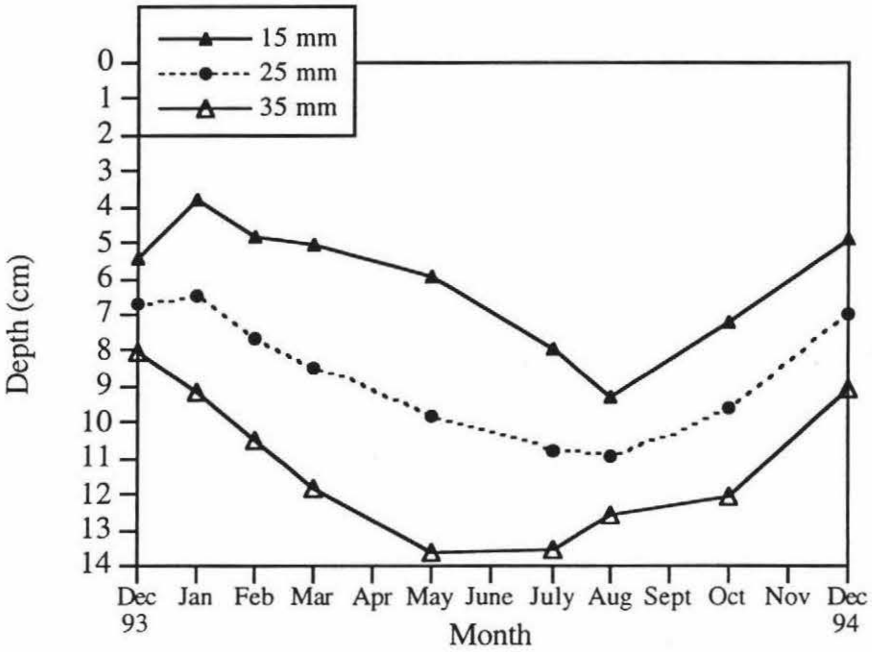
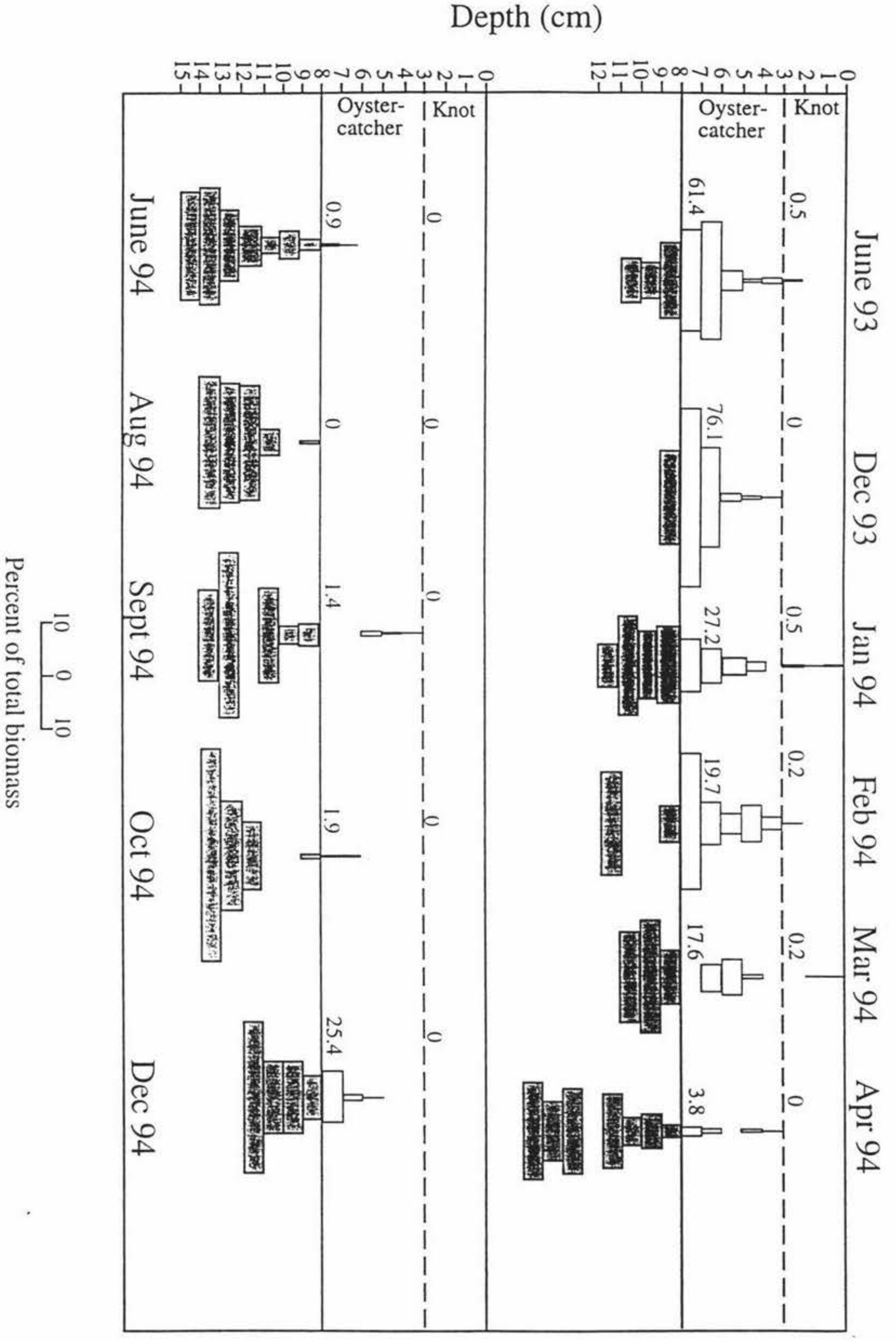


Figure 3.21 Average depth of 15, 25 and 35 mm *Macomona*, estimated from monthly linear regressions relating shell length to depth (n=43-75 individuals measured in each month).

Figure 3.22 Changes in available biomass of *Macomona* to knots and oystercatchers. The biomass relevant to knots is given in black and is demarcated by the 3 cm line. The limit for oystercatchers (8 cm) is given by the second horizontal line. The shaded portions of the biomass are unavailable to either species. the percentage of each month's biomass available to the two species is given in the small figures adjacent to each pyramid.



Fewer pipi were sampled than cockles, and I am unable to provide as detailed a picture of flesh changes. Instead data for summer/autumn and winter seasons have been pooled (there being complete overlap in mass values within these periods). As expected, flesh mass increased with shell length in both summer (Figure 3.23) and winter (not shown). The poor fit at large shell masses may be partially due to the preponderance of small individuals in the data. Using regressions based on sizes 25 mm or under (no pipi larger than this were measured during winter), the mass of 5, 10, 15 and 20 mm pipi were estimated for summer and winter. The ratio of summer mass to winter mass is shown in Figure 3.24. For the smaller sizes (which are taken most by knots) flesh mass is actually greater in winter than summer

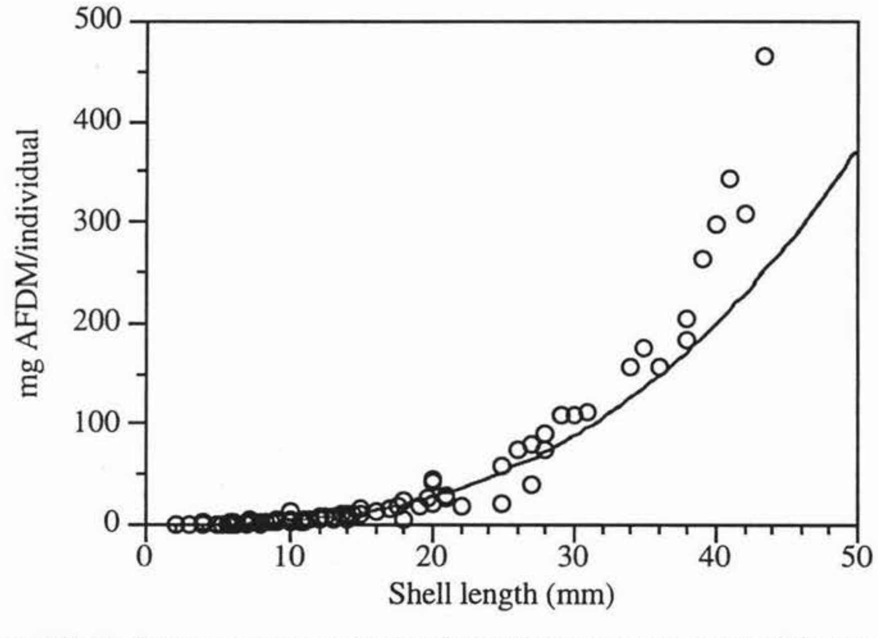


Figure 3.23 Flesh mass as a function of shell length in pipi over summer (November-April). Line fitted is a power function where mass (mg AFDM)= $0.0059161 \cdot \text{length}^{2.826}$, R^2=95.2%. $N_{\text{determinations}}$=114, $n_{\text{individuals}}$=205.

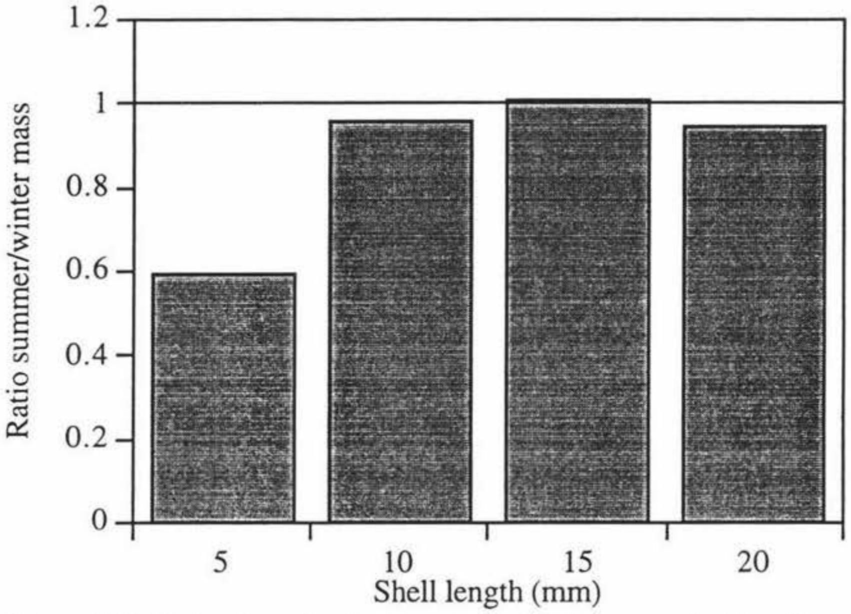


Figure 3.24 Ratio of predicted summer mass to winter mass for four sizes of pipi. Horizontal line denotes equal masses. Equations used for predicting mass were: summer 5+10 mm mass (mg AFDM)=0.0090755*length$^{2.6158}$, R^2=56.8%, n=70 determinations,154 individuals; summer 15+20 mm mass (mg AFDM)= 0.006205*length$^{2.7453}$, R^2=56.7%, n=26,31; winter 5+10 mm mass (mg AFDM) =0.046019*length$^{1.9306}$, R^2=66.7%, n=24,33; winter 15+20 mm mass (mg AFDM) =0.003379*length$^{2.9668}$, R^2=86.9%, n=23,25.

Flesh content of mussels increased to the exponent 2.6 of shell length in February (Figure 3.25). The relationship was even steeper in June, however, with flesh scaling to the exponent 3.24. This greater flesh content in June was probably due to gonadal growth in preparation for reproduction, while the low February condition may represent a post-reproductive condition. The duration of this heightened flesh content is unknown. Nevertheless, mussel feeders encounter the unusual situation of entering winter with a larger food supply than in summer.

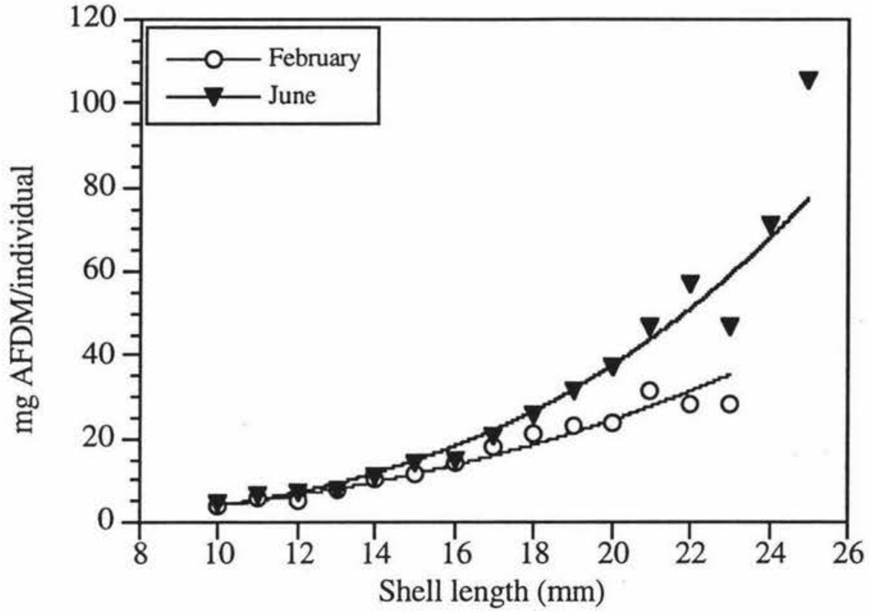


Figure 3.25 Flesh content as a function of shell length in mussels in late summer (February) and early winter (June). Flesh = $0.0096734x^{2.6141}$ in February (r^2=0.93562); $0.0022699x^{3.2412}$ in June (r^2=0.93329). N=278 in February and 261 in June.

Worms

The length-mass relationship for the stout Opheliid polychaete *Travisia olens* differed between early summer (December 1993) and early autumn (April 1994), with a much higher flesh content in April than December (December mass (mg) = $0.021522 \times \text{length}^{2.0714}$ [r^2=70.8%, $n_{\text{determinations}}=5$, $n_{\text{individuals}}=23$]; April mass (mg) = $0.04402 \times \text{length}^{2.0146}$ [r^2=90.6%, $n_{\text{determinations}}=7$, $n_{\text{individuals}}=86$]). In addition to this increase in flesh content, the mean size of individuals increased also, with the result that whereas the mean *Travisia* in December contained only 0.92 mg AFDM, the equivalent individual in April contained 17.98 mg AFDM. The quality of food for predators feeding on this worm increases markedly over the summer.

In winter 1994, however, very few *Travisia* could be located on the tidal flats, indicating a collapse in the population over the intervening two months. For oystercatchers remaining on the spit over the winter, *Travisia* may occur at densities too low to be harvestable. While little weight can be given to a regression based on three points, the suggestion is that flesh content per unit length had dropped also (mass (mg) = $0.013586*\text{length}^{2.3937}$ [r^2=95.0%, $n_{\text{determinations}}$=3, $n_{\text{individuals}}$=5]).

The lugworm *Abarenicola affinis* also showed a different mass-length relationship in December 93 and April 94, with condition (mass per length class) being higher in April. In December the relationship was mass (mg) =$0.0012945*\text{length}^{2.699}$ (r^2=84.4%, $n_{\text{determinations}}$=9, $n_{\text{individuals}}$=13). In April both the intercept and exponent differed: mass (mg) $0.010294*\text{length}^{2.1907}$ (r^2=77.4%, $n_{\text{determinations}}$=9, $n_{\text{individuals}}$=18). The mean biomass per individual based on these samples was 59.25 mg AFDM in December, and 43.82 mg AFDM in April, despite this increase in prey quality. Given the non-proportional scaling of mass to length and a small sample size, the addition of just a single large individual could affect these estimates greatly. It is possible though, that the size-structure of the populations did differ at these times, leading to a smaller mean size in April (and consequent lower biomass). An average value of 51.5 mg AFDM/individual is suggested for use in intake rate measurements.

Maldanid bamboo-worms (*Macroclymenella* and *Clymene*) in April had a mean biomass of 5.353 mg AFDM (n=75 individuals). Small sample sizes may have affected estimates in December and June in which mean biomass values were higher, at 6.614 mg (n=7) and 8.192 mg (n=12) respectively. Part of the cause of this low sample size was the high number of broken worms or individuals missing (usually anterior) segments. The relationship between length and mass for broken worms differed from that of whole worms in the June sample (whole mass (mg) = $0.0006013*\text{length}^{2.393}$ [r^2=93.0%, $n_{\text{determinations}}$=11, $n_{\text{individuals}}$=12]; broken mass (mg) = $0.014768*\text{length}^{1.7038}$ [r^2=88.7%, $n_{\text{determinations}}$=9, $n_{\text{individuals}}$=9]), presumably because the broken worms represent 'artificially shortened' longer worms with a disproportionately higher flesh content. Flesh content in whole worms in April scaled according to mass (mg) = $0.0052554*\text{length}^{1.9412}$ (r^2=88.7%, $n_{\text{determinations}}$=18, $n_{\text{individuals}}$=75).

The final group of worms analysed were Spionid and Orbiniid worms (not *Travisia*), which are pooled for this account. As expected, the flesh content increased from December to April. The exponents were similar (1.4121 for December [$n_{\text{determinations}}$=19, $n_{\text{individuals}}$=25], 1.3742 for April [$n_{\text{determinations}}$=7, $n_{\text{individuals}}$=8]) while the intercept was 49 % higher in April, indicating an increase in prey quality of that magnitude (small sample size notwithstanding).

The mean mass for all worms on the tidal flats (excluding the pan) 10 mm or greater in length was 12.67 mg AFDM in December (n=37) and 14.14 mg in April (n=15), an increase of only 12 %.

DISCUSSION

Without very extensive infaunal surveys (eg. Hicklin & Smith 1984; Piersma *et al.* 1994b) it is inappropriate to attempt to estimate the total mean biomass for an area, as there can be very large physical and biotic variability in soft-bottomed sediments (Thrush 1991). This seems true for Farewell Spit. For instance, mean cockle biomass between months varied between 38 and 70 g AFDM/m^2 at Tip3. These are similar values to those recorded by Zwarts & Wanink (1994) for annual changes in biomass at a site in the Dutch Wadden Sea. However, at three other comparable offshore sites of full benthic sampling in my study, total bivalve biomass ranged from only 1.18 to 10.1 g AFDM/m^2. Large-scale heterogeneity (eg. presence or absence of cockle beds) means that biomass differences between sites can be large. However, certain values do warrant note, such as the low biomass recorded for knots at all sites (Figure 3.7). European knots require a biomass of around 1 g AFDM/m^2 when feeding on *Macoma balthica* (Piersma *et al.* 1994b). The only values reaching that on Farewell Spit were recorded on the pan, in which the bulk was contributed by tiny crustacea. These were almost certainly the dominant prey at that site (though prey were unable to be seen, even at 15 m with a telescope!). The low values recorded at other sites despite the presence of feeding knots suggest either knots are able to subsist at a much lower biomass level than in Europe, or that my sampling regime may have been insufficient to account for local variability.

So while I am unable to compare fully the food supply for waders on Farewell Spit with equivalent sites globally, my results do confirm that certain features of overseas studies are applicable in New Zealand.

Biomass values within a species vary with size, but also season. Furthermore, these seasonal changes are not necessarily equivalent between size classes. In cockles, for instance, the lowest condition of large cockles coincided with the highest condition of small ones. Nor is the variability within a year equivalent - 35 mm cockles had a much greater relative standard deviation than smaller cockles. The variability encountered by a foraging bird will thus vary with any prey size selection.

The relationship between season and biomass is not simple either. Both between and within species there are differences. For mussels, their condition was much greater in winter (June) than in summer (February). For cockles, there was a decrease in condition of large sizes from autumn to winter. This is complicated by the fact that they experienced a large net increase in mass over the entire year, due mainly to spring growth. Whether summer 1993/94 values were low (or perhaps late), or summer 1994/95 values high, is unknown. For both cockles and pipi, winter mass was two-thirds greater than summer mass in 5 mm individuals. There is thus not any robust generality about shellfish condition through the year. It is probable that life-history features at least partially contribute to differing size-mass relationships through the year (eg. gonad growth for reproduction).

Density changes also interact with condition changes, and we have seen that cockles at Tip3, while not showing an unequivocal decrease in density over winter, nevertheless had a much decreased biomass, due to condition changes. This contrasts with *Macomona* which did not decrease in flesh content over the winter.

Macomona did, however, show large seasonal changes in depth for all size classes. Such changes have been demonstrated in studies in cold-temperate areas (eg. Great Britain, The Netherlands: Reading & McGrorty 1978; Zwarts *et al.* 1992), but this finding indicates that this can be an important component of harvestability changes in warm-temperate areas also. *Macomona* is a fairly extreme example of deep-living, with individuals recorded at deeper than 21 cm. Their deep-living means that only a very small percentage of the biomass is available to even long-billed predators such as oystercatchers (0-27 % for the main period of oystercatcher residence: Figure 3.22). Deep-living certainly acts to reduce the predation risk from surface-dwelling predators. An increase in depth in winter could conceivably reflect increased predation pressure by wintering oystercatchers. The fact that *Macomona* reach such extreme depths (far beyond the reach of the bill of any bird predators) suggests that bird predation is not necessarily a strong factor. Predation by feeding rays is likely to be a stronger influence, and ray feeding holes up to about 30 cm deep were found on the tidal flats at low tide in summer. While this could help explain deep living in general, it does not explain an increase in depth in winter. Shellfish growth in summer and a need to increase nutrient intake could possibly require shallower living.

All worm groups showed increases in flesh content over the summer (excepting Maldanids: see problems with breakage above). The net result of this for foraging birds, however, varied hugely between taxa. For lugworms, mean biomass per individual decreased by 26%, while *Travisia* experienced a tenfold magnitude increase. Such differences result from the interaction of condition with size. Growth of individuals can increase the mean mass (as in *Travisia*) while size-specific predation on large individuals could reduce it. (In lugworms, the observed decrease in mean mass could potentially result from larger individuals burying deeper in the sediment and thus eluding sampling.)

The interactive nature of harvestability changes mean that inferring too much from limited data should be avoided. In summary, however, through the course of a southern summer, condition increases in worms and larger shellfish should be expected. These are not necessarily paralleled in smaller shellfish. Combined with these are changes in the size-structure of populations which may affect the mean prey size. If predators are not selecting prey sizes then this will affect their intake rate.

Detailed information on seasonal changes in density, and on timing of reproduction and subsequent growth rates are lacking for most taxa. As very different portions of the prey spectrum may be relevant to different predators (eg. small bivalves for knots, large for oystercatchers), data on the variation in these, including inter-annual differences, become very important. Interpretation of condition changes in large cockles, for instant, is hampered by the fact that it is not known whether December 1993 or December 1994 is showing an abnormal level. Only long-term data-sets will provide this luxury.

Approaches to studying benthic food supplies - community-based or taxon-based approaches?

The approach taken to try to discern general patterns in food supply over a wide latitudinal gradient has generally been community-based, that is, evaluating the overall stock of a certain resource (eg. bivalves in the diet of knots: Piersma *et al.* 1994d) at different sites. This has given many insights into the situations likely to be encountered by a migrant bird, but has not shown any systematic differences in the harvestable fraction across a latitudinal gradient. What it has revealed is that there are certain basic differences in the benthic fauna of these areas, such as the tropics having a greater variety of taxa, including such groups as brachiopods and echinoderms (Piersma *et al.* 1994d). The fact that no systematic differences have been shown in harvestability of bivalves may be largely due to the fact that the component taxa in each community are themselves fundamentally different. Different phylogenetic and life-history constraints have given rise to species with a great diversity of life-styles: shallow deposit-feeders, deep-living suspension-feeders, species whose maximum size is smaller than the gape-size of a knot. Until we find two communities with sufficiently similar components, then direct comparisons will be hard to make. A taxon-based approach provides another option, in which the comparison of taxonomically similar species could provide insights into general principles where community comparisons were unable to.

It was thus expected that *Macomona* could be a useful study organism, being of sufficiently similar taxonomic status to *Macoma* in the North Atlantic. On investigation, however, it proved to be of limited value as it lives far too deep in the sediment for birds to reach most individuals, especially for knot. Its distinctive siphon feeding marks would also be of limited value to visually-feeding oystercatchers, as these often had a horizontal element in their path, so even they would not be reliable as indicators of a detectable shellfish. As prey for knots, it grows to a far larger size than is ingestible, so only a very small percentage of the total biomass is harvestable. As mentioned, though, it does demonstrate that pronounced depth changes can be expected (phylogenetic constraints of individual species notwithstanding) in warm-temperate as well as cold-temperate areas.

A taxon-based approach will probably not help greatly to predict food levels at different sites, given the huge range of (eg.) molluscan fauna that can be found globally. The suite of potential prey items around the world means that the precise "componentry" of the community may not be predictable - this can only be found out by getting out in the field and sampling directly. What it can provide, though, is insight into likely limitations to harvestability that may occur, including beyond the time-frame of an expedition. As an example, two tellinid bivalves on opposite sides of the world, *Macoma balthica* and *Macomona liliana*, are both known to show seasonal depth changes. thus, if a community contains a tellinid bivalve, it is likely to show depth changes in winter, which may affect its harvestability. Likewise, a cockle (eg. *Cerastoderma edule*, *Austrovenus stuchtburyi*) will remain shallow - a small siphon necessitates this. Insight into the biology of similar organisms will help us make general predictions. We will nevertheless still require the basic groundwork of describing accurately the benthos. What is exciting is the prospect of developing the taxon-based approach within a species, thus factoring out phylogenetic problems. This should give the most direct evidence for general biological principles. *Macoma balthica* would be a prime candidate for this, being present from as far north as Norway (Alerstam *et al.* 1992) and as far south as at least New England, USA (Gilbert 1977), giving a wide latitudinal range. Factoring out the effects of local predation characteristics which may affect the behaviour of individuals might prove to be difficult, however.

The biggest problem with generating insights into taxon-specific traits is simply the amount of effort required. The four snapshot studies compared by Piersma *et al.* (1994d) do "not do justice to the enormous seasonal and long-term variability which we know to exist in the size and depth distribution of intertidal bivalves." To adequately describe this is a big ask, and is beyond the scope of short-duration expedition research. But where possible, seasonal changes in depth and flesh content should be combined with density measurements, especially where the community has similar species to communities already described. By focussing on selected species within a community, we may yet discern patterns of importance globally. But all the general principles in the world will be worth little without the raw material of basic data - the first stop in studies of foraging birds will always be assessment of the immediate food supply.

Chapter four

Behaviour, diet and energy intake

ABSTRACT The behaviour, diet and energy intake of Pied Oystercatchers, Red Knots and Bar-tailed Godwits was studied near the tip of Farewell Spit. Feeding time was assessed for knots and godwits in mid-summer (basic period) and prior to migration (premigratory period). Knots increased their feeding duration by 28 %, which is in accord with the predicted amount to enable sufficient body mass increase for migration. Godwits only increased feeding time by 8 %, indicating that nocturnal feeding opportunities were not fully utilised over summer. Oystercatchers increased their feeding time from summer to early winter, but less than the increase in predicted thermostatic requirements over the same period. The diets of the three species was found to be similar to those recorded overseas. Oystercatchers specialised on cockles, mussels, *Travisia olens* (a stout Orbiniid polychaete) or slender polychaetes. *Travisia* gave the highest energy intake, but was apparently depleted over autumn and was absent in winter 1994. Estimates of energy intake in oystercatchers were sufficient to cover predicted requirements on all diets except slender worms. Methodological problems may account for a large part of the apparent shortfall. Godwits also fed on polychaete worms, and achieved an extremely high energy intake due to the prominence of *Travisia* in the diet. The diet of knots centred on molluscs, especially the bivalves *Amphidesma australe* (pipi), *Austrovenus stuchtburyi* (cockle) and *Nucula hartvigiana* (nutshell). However it was broader than diets recorded overseas, incorporating at least three gastropod species, plant seeds and substantial amounts of small crustacea (amphipods and isopods). While intake rates proved too unreliable to give realistic estimates of energy intake, the broad diet and long working day is interpreted to suggest that knots face marginal living conditions on Farewell Spit in the premigratory period. Low bivalve populations may be offset by a wide scope of potential prey items and low thermostatic costs.

INTRODUCTION

In assessing the capacity of a habitat to support bird populations, or to understand why birds utilise an area it is necessary to determine the way in which birds and their prey relate. Are birds restricted in their options for feeding? Is their intake rate sufficient to meet their needs and what affects this? Are their any periods of the year when demands are especially high? Conversely, are there any periods when their energy intake is likely to be limited, e.g. through prey harvestability changes? Prey availability is dealt with in Chapter 3. This chapter examines the behaviour, diet, and energy intake of godwits, knots and oystercatchers near the tip of Farewell Spit.

The energy demands of a migratory bird are far from static. For the period that Arctic-breeding waders are in New Zealand they must complete a body moult, moult their flight feathers, remoult their body plumage and deposit sufficient nutrients for migration. The environment also imposes thermoregulatory costs on birds, and this varies seasonally, being highest in winter when temperatures are low, solar radiation reduced and winds often high. The behaviour of birds must be sensitive to these variable costs if they are to achieve energy balance. Birds are also social creatures, spending much of their time in flocks, both when feeding and roosting, which may entail both benefits and costs. While most studies have focussed on antipredator benefits (Abramson 1979; Caraco *et al.* 1980; Lima 1995; Lindström 1989; Pöysä 1987b; Stinson 1980; Westcott & Cockburn 1988) , starvation risk (Ekman & Hake 1988; Ekman & Rosander 1987), information transfer (Alonso *et al.* 1994; Ward & Zahavi 1973) and prey variability (Lindström 1989; Rands & Barkham 1981) , Wiersma & Piersma (1994) also demonstrate considerable thermostatic advantages can be gained through flocking.

Factors affecting the intake rate of foraging shorebirds, in theory at least, are well documented (Evans 1976). Actual studies on shorebird foraging, however, have been very uneven. The oystercatcher *Ostralegus haematopus* dominates the literature. But even within this species effort is not representative. Because of the benefits to researchers, studies on mussel *Mytilus edulis* beds are over-represented relative to other prey types (Cayford & Goss-Custard 1990; Durell 1984; Durell *et al.* 1993; Ens 1982; Ens & Goss-Custard 1984; Evans 1976; Goss-Custard & Durell 1984; Goss-Custard & Durell 1988; Goss-Custard & Durell 1994; Goss-Custard *et al.* 1982; Goss-Custard *et al.* 1981; Meire & Ernwynck 1986; Norton-Griffiths 1967; Sutherland & Ens 1987; Zwarts & Drent 1981) . Other studies have dealt with oystercatchers feeding on cockles *Cardium edule* (Hulscher 1976; O'Connor & Brown 1977; Sutherland 1982a; Sutherland 1982b) , other bivalves (Hulscher 1982; Swennen 1990; Zwarts & Wanink 1984) and various prey (Baker 1974a). Oystercatchers feeding on polychaete worms have been little studied, except as a component of Boates & Goss-Custard (1992) and Durell *et al.* (1993).

In contrast, godwits have had surprisingly little published research into their ecology and diet (Dann 1979; Evans & Smith 1975; Piersma 1982; Piersma *et al.* 1993; Smith & Evans 1973) despite being one of the most widespread Palaearctic shorebirds. Knots have recently been the focus of much international research, although much of this relates to migration (eg. Dick *et al.* 1976; Gudmundsson *et al.* 1991; Ntiamoa-Baidu 1993; Piersma *et al.* 1987b; Piersma & Davidson 1992a; Piersma *et al.* 1991; Uttley *et al.* 1987; Wiersma and Piersma 1994) . Some of the most notable advances in wader biology have been made with the knot, however, due to the relative ease with which its prey is quantified and the success with which it can be studied in captivity (Dekinga & Piersma 1993; Moreira 1994; Piersma *et al.* 1994a; Piersma *et al.* 1994b; Piersma *et al.* 1993; Piersma *et al.* 1994c; Piersma *et al.* 1994d; Tulp & de Goeij 1994; Zwarts and Blomert 1992; Zwarts *et al.* 1992) .

In New Zealand, no detailed studies have been made on feeding of godwits or knots (but see Piersma 1991) , while Alan Baker studied oystercatchers (including the Pied Oystercatcher) in detail on the Avon-Heathcote estuary and elsewhere (Baker 1969).

The behaviour of waders is expected to vary with energy demands. Paramount in this for migratory species is the need to achieve a positive energy balance to deposit mass for migration. The main way this can be done is by increasing feeding time (Zwarts *et al.* 1990a). In this chapter I firstly examine bird behaviour, and estimate feeding time per tide for all three species. This is done in times of low energy demand (summer, before mass increase was thought to have begun) and high energy demand (during the premigratory mass increase period) for the arctic waders. Feeding time should also reflect changes in thermostatic requirements, and is compared in summer and early winter for oystercatchers. The diet and energy intake of all three species is studied. This is then compared with estimated energy demands over the same period.

METHODS

Bird behaviour

Godwits, knots and pied oystercatchers were observed (with 10 X 40 binoculars, and 20, 25 and 40 X 60 telescopes) over the tidal cycle on the tidal flats and adjacent sand pan at the eastern end of Farewell Spit. Activity was gauged by scanning flocks to determine the percentage of feeding birds over the tidal cycle. As birds, especially oystercatchers, tended to group into subflocks of a certain activity (eg. preening or roosting groups), it was necessary to scan as much of the population as was physically possible. The scans represent as many birds as were visible at that time: flocks were not generally subsampled to a set target figure (c.f. Piersma *et al.* 1994b; Tulp and de Goeij 1994). While more time-consuming than subsampling, it provided more robust estimates of population activity.

When birds were feeding on the tidal flats scanning provided no real problems (apart from heat haze and wind) but as birds ceased feeding and moved in towards to pan to roost this could be more difficult. This was especially pronounced in pied oystercatchers, in which there was a gradual progression of individuals or small flocks flying from the tidal flats. over the shellbanks (and hence out of site from the tidal flats), to the beach to roost. Observations of oystercatchers were then made from the top of a marram-covered island adjacent to the shellbanks, height c. 6 m. As roosting birds on the beach were sometimes out of sight, counts of visible birds at times were corrected for population sized based on total flock counts over the high tide. This problem also affected another roost of birds, on the 'saltmarsh' west of the lighthouse, in which birds flew to the pan on the outer side of the spit from flats on the inside, on larger tide. Observations of birds in these flocks were hence restricted to small tides.

Activity of godwits and knots was assessed in December/January (92/93 and 93/94) to determine activity prior to premigratory preparation, and again in February/March (1994) to see if feeding time was increased in this period (Zwarts *et al.* 1990a). These periods are referred to as 'basic' and 'premigratory'. Pied Oystercatcher activity was assessed in summer (December - February) and early winter (May/June) in both study years. Due to the difficulty of getting accurate counts of oystercatchers, less data were gathered for oystercatchers than for godwits and knots. As disturbed birds usually altered their behaviour (feeding birds usually forming non-feeding flocks) no scans were made within 15-30 minutes of a disturbance (these usually being the passage of a small plane, or Arctic or Pomarine skua (*Stercorarius parasiticus* or *S. pomarinus).*

Feeding behaviour, diet and intake rate

Feeding birds were encountered as closely as possible or necessary to determine diet and intake rate. Intake rates were dictated into a portable tape-recorder and later transcribed in minute-long intervals. A bird was usually observed for as long as possible. As oystercatchers showed two or more main feeding methods (visual feeding on cockles *Austrovenus stuchtburyi*, visual feeding on mussels *Modiolus neozelanicus*, visual feeding on worms, tactile feeding on *Travisia olens*) special attention was paid to each of these. Where possible, all paces, pecks/probes and prey were recorded for visual foraging birds, while for sewing birds (tactile feeders) paces and prey captures (visible by either swallowing actions or visible as the prey passed up the bill) were recorded.

Diet of knots was assessed mainly through faecal analysis, which has been experimentally shown to be very robust (Dekinga and Piersma 1993) where they feed wholly on molluscs (as appears to be the norm for knots). Faeces were collected mainly from the tidal flats after the passage of feeding birds, but also sometimes from roosts or subroosts on the flats. Knot faeces are readily distinguished from all other wader droppings on Farewell Spit, being cylindrical, 10-20 mm in length, and about 3 mm in width. Godwit faeces are larger, largely composed of sand ingested while feeding (or as gut contents of worms) and with a typical messy splash of uric acid. Oystercatcher droppings are usually extremely liquid and smelly, while other smaller waders were low in abundance in the study area, and had very small faeces. On occasion, regurgitates from knots were also collected from roosts. These were superficially like faeces, but had much more obvious and larger shell fragments, and lacked the sandy content and uric acid of faeces.

Where possible, intake rates of knots were determined visually, which was possible only at very close range, with a telescope (25 or 40 X 60 mm). As most prey were too small to be identified, collections of knot faeces were made from feeding grounds on the tidal flats. These were used to describe the diet and reconstruct the size distributions of ingested cockles and pipi *Amphidesma australe*. This has been experimentally shown to be robust (Dekinga and Piersma 1993).

Faeces were dried to constant mass at 60°C, and sieved through a 300 μm mesh sieve to remove most sediment. All intact bivalve hinges were separated and measured under a binocular microscope, and the estimated shell length determined on the basis of species-specific regressions of shell length on hinge height (Chapter 3). Time and reference-collection limitations precluded full analysis of the gastropods (Dekinga and Piersma 1993; Piersma *et al.* 1993) .

It was problematic to estimate prey size in most situations. Polychaete worms can stretch greatly when being pulled from their burrow, but as the benthic fauna was limited the taxon was usually identifiable. Godwits frequently swallowed their prey when probing even before removing the bill from the sediment. When sewing on *Travisia* the passage of the worm up the bill was too rapid to allow an estimation of size. Trying to find empty cockle shells where oystercatchers had been feeding proved unsuccessful due to the heterogeneous nature of the local habitat and presence of other shell matter. Because of these difficulties in accurately estimating the size of prey for godwits and oystercatchers, average prey biomass figures are used for each prey type for which I have intake observations. The exception was empty mussel shells, which were collected from around mussel clumps where oystercatchers were observed feeding. Mussels that had been broken while opening were obviously from oystercatcher feeding, but many that were empty and gaping, sometimes loosened, were also considered to have been preyed upon by oystercatchers. Intake rates of oystercatchers is based on mean prey values for these mussels.

The energy requirements of birds vary according to both external and internal changes. The former includes factors such as windspeed, ambient temperature and solar radiation: these collectively determine the *operative temperature*. The internal requirements of an individual are not static either, with moult requiring extra nutrients for deposition in feather tissue, and migration necessitating maintaining a positive energy budget (intake of nutrients exceeding usage) to enable nutrient deposition as fat or protein. The equations of Wiersma and Piersma (1994) are used to estimate the thermostatic cost imposed by the environment, given data on air temperature, windspeed and radiation. Benefits through flocking reducing airspeed are also be incorporated. The energy cost of activity is estimated on the basis of measured costs in knots (Poot & Piersma 1994) or as a function of maintenance metabolism and a constant metabolic cost for activity.

RESULTS

Roosting areas

Shellbank Pan: Birds roosted on exposed bare sand during high tide. Pied oystercatchers were extremely site-specific in their choice of roosting site, with part of the flock always roosting on the small dunelets adjacent to the beach directly opposite the observation island. On larger tides all oystercatchers roosted there, but on neap tides many birds roosted on the shellbanks, and some around Bush End Point. Godwits and knots, in contrast, usually roosted on the flat sand on the pan or on the dunelets next to this. On extreme neap tides they often roosted on exposed sand on the southern side of Bush End Point. On spring tides they frequently roosted only a few hundred metres east of the lighthouse. On one occasion few birds could be found and it was concluded that they had moved entirely up the pan to join the saltmarsh flock on the next pan (see below).

Saltmarsh: All three species roosted on the saltmarsh situated between the rushes and the tidal flats on smaller tides (≤ 3.8 m). Covered in *Sarcocornia quinqefolia* and *Samolus repens*, these provided some shelter from wind, as did small runnels through the marsh. On larger tides, however, they were forced to fly over the vegetated inner half of the spit to roost on the pan or beach on the outer half. This is the usual situation for most of the spit, and it is only the tip flocks which are able to roost next to the tideline on larger tides.

Feeding areas

There were few totally predictable discrete feeding grounds, which partially reflects the feeding behaviour of the birds. As the tide receded most godwits and knots flew or spread out to the flats immediately off Bush End Point. Godwits feeding on burrowing worms (lugworms and Maldanid bamboo worms) were reliant on worm activity to make themselves available, so followed the tide edge out. On the outgoing tide they were usually locatable, sometimes in a single flock comprising almost the entire local flock, in a broad band next to the waters edge, anywhere from the hummocks to past the half-channel (see map: Figure 4.1). As the tide came in the godwits preceded it in a band 100-150 m wide. Godwits feeding on *Travisia* did not follow the tide edge, and were found sewing in wet sand in the mid-flat region, towards the hummocks. Eelgrass beds were also fed in, probably both for crabs as well as worms.

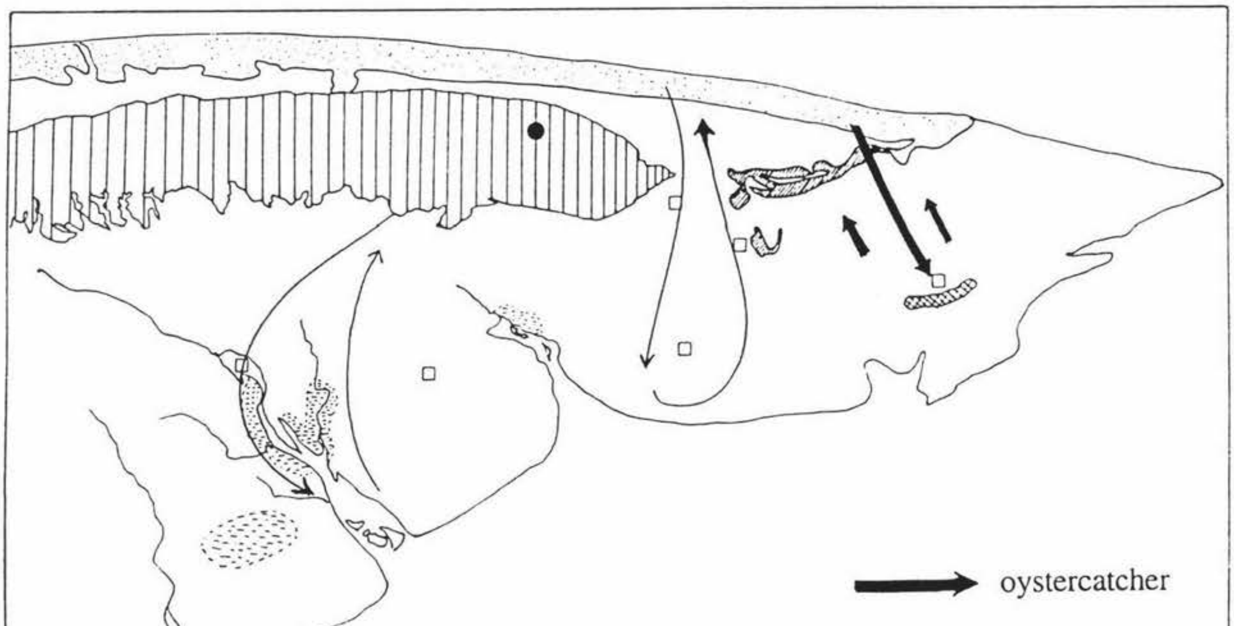


Figure 4.1. Generalised movements of feeding waders at low tide.

Oystercatchers likewise fed in various areas. Cockle-feeders fed mainly in the area around or just inside the hummocks, or along the outer flat region west of Tip2 sampling site. while burrowing-worm feeders followed the tide as with godwits. Oystercatchers sewing for *Travisia* fed in the same areas as godwits, especially between the southern shellbank and the hummocks. On spring tides oystercatchers could be seen distantly on sandbanks approximately 3.5 km out from Bush End Point. Mussel feeders were few and were restricted to the small area of mussels contained within the hummocks.

Knots tended to not feed in large flocks, but were found in smaller foraging flocks of a few tens to a few hundreds of individuals. However, a large proportion of the total population could be present in the immediate area, although feeding in widely spread smaller flocks. There were no apparent fixed feeding localities. Dense eelgrass beds were utilised frequently (especially by the saltmarsh flock, which was near to the beds by the main channel), although not by all birds, nor for the whole tide. They were often found feeding near godwits towards the tide edge. On higher tides the pan behind the shellbank became flooded, sometimes retaining surface water for the entire low tide period. Very often large numbers of knots would feed for much, and sometimes all, of the tide on the pan.

Distances travelled during a feeding session

The tidal flats at the end of Farewell Spit are among the smallest on the spit. On neap low tides the tide edge reaches only about 2.25 km from Bush End Point, while on spring tides this can extend to around 3.5 km. Even for birds following the tideline, the distance travelled over a tide could be as low as 4.5-5 km of travel, usually on foot interspersed with small flights ("leapfrogging" from the back of the flock to the front was regularly seen in godwits) (see Figure 4.1). For oystercatchers feeding at the hummocks, the distance travelled is fixed at only 2-3 km round trip. A reasonable maximum estimate for a disturbed or mobile knot flock roosting behind the shellbanks which moved to the half-channel mouth, across to the hummocks, then back in to the pan is 9-10 km. In contrast, when feeding is possible on the pan itself, many knots might move only a matter of 500-750 m over the entire low water period. Birds roosting at the saltmarsh, especially godwits, did feed probably 4-5 km distant from the roost, so presumably would move up to 10 km or more in a tide. How far birds move in the centre of the spit, where tidal flats may extend perhaps 8-10 km at low tide, is unknown.

How much individual site fidelity is there to roosting areas?

As mentioned, oystercatchers roosted in almost exactly the same place each high tide, give or take a few hundred metres. Flock site fidelity is obviously very high. But how much variation is there in individuals comprising any given flock? Without individually marked birds this is difficult to assess, but regular counts and some, albeit very limited direct evidence, may give an indication.

On a few occasions observations were made which suggest there is some fidelity to both roosting and feeding areas. On one occasion (22.1.94) at the base of the half-channel, godwits and knots were flying to subroosts NW on the flats, in preparation for roosting at the saltmarsh. At the same time, birds were also flying directly to Bush End Point, despite other subroosting flocks being visible nearby in the other direction. On 23.2.94 as birds were pushed off the tidal flats at the saltmarsh, many flew east to Bush End Point and beyond. One small group of godwits was also seen flying across the spit by the lighthouse compound, presumably to roost on the pan behind Bush End Point. These suggests individual preferences may exist. Small groups of knots also sometimes spread along the shore between the saltmarsh and the shellbanks, close to shore, especially in strong westerly winds, so there is potential for interchange on the tidal flats and even near the roosting sites.

On 3.3.94, a large high tide, only 262 godwits were present on the pan behind the shellbanks and Bush End Point, whereas 802 were roosting there the day before, and 1009 birds were counted at the tide edge earlier in the day. I expected to find the missing birds further towards the lighthouse, but did not. However, the saltmarsh flock, roosting on the pan a kilometre or so west of the lighthouse and beyond a medium-sized sand-dune, contained 1680 godwits. Although this flock was not regularly counted, the indications were that this typically numbered around 1000-1200 birds, so was presumably holding the missing tip birds. As the tide receded and the first birds started to feed, a flock estimated at 505 godwits flew eastwards down the pan at about 20 m high and joined the birds on the exposing flats. This seems to provide strong evidence that these birds, having changed their roosting location that day for some reason, chose to return to their regular roosting or feeding ground rather than joining saltmarsh birds which would have been flying across the vegetated dunes to the inside saltmarsh and flats at the same time. These observations, though few, suggest that birds may show a preference for roosting areas and also perhaps for feeding areas. The fact that numbers of birds at these roosts are not stable, however, shows that this is not fixed, and that there is some movement.

The discreteness of the flocks can be assessed by regular accurate counts. The counts of godwits and knot were usually accurate to within a few tens of individuals, if not even a few individuals. Figures 4.2 & 4.3 show counts over a 56 day period prior to the northward migration in 1994, of knots and godwits roosting around Bush End Point and the shellbanks. While there are few series of consecutive counts, there is obviously much variation in the numbers of roosting birds over time at this site. Equally so, there are also periods of relative stability, eg. days 13-18 for godwits.

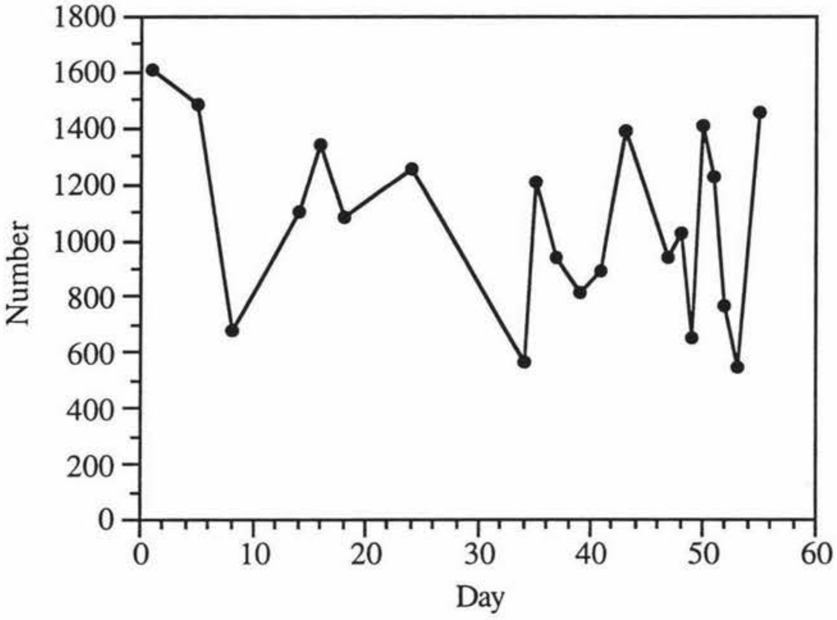


Figure 4.2 Counts of knots roosting near Bush end Point and the shellbanks from 14-1-1994 to 8-3-1994.

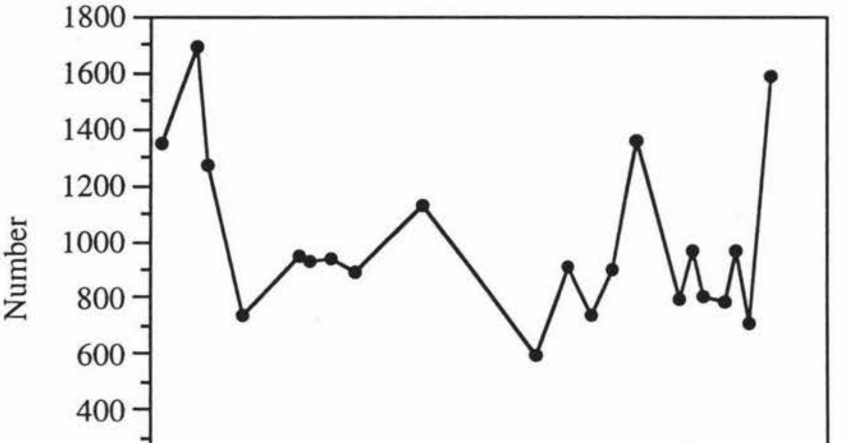


Figure 4.3 Counts of godwits roosting near Bush end Point and the shellbanks from 14-1-1994 to 8-3-1994.

Activity

The feeding activity of godwits and knots during the basic period is given in Figures 4.4 & 4.5. These figures combine both spring and neap tide scans, and an estimate of overall foraging time during each period was made by hand-fitting a line to the data and counting squares on grid paper underneath that line, converted to hours of foraging per tidal cycle. In the basic phase, knots fed for around 7.4 hours per tide, godwits for 6.9 hours. Knots showed more scatter, especially on an incoming tide. To test whether this was due to spring tides forcing curtailment of feeding (on spring tides knots fed right up until all feeding areas in the pan were covered, whereas most godwits had ceased feeding before this), the data were sorted into larger and smaller tides (spring tides being 4.0 m above datum and above, neap tide being 3.9 m and below). These plots showed no difference for either godwit and knot for spring and neap tides. Hence while knots were forced off the tidal flats by spring tides, they still managed to feed for approximately the same period of time.

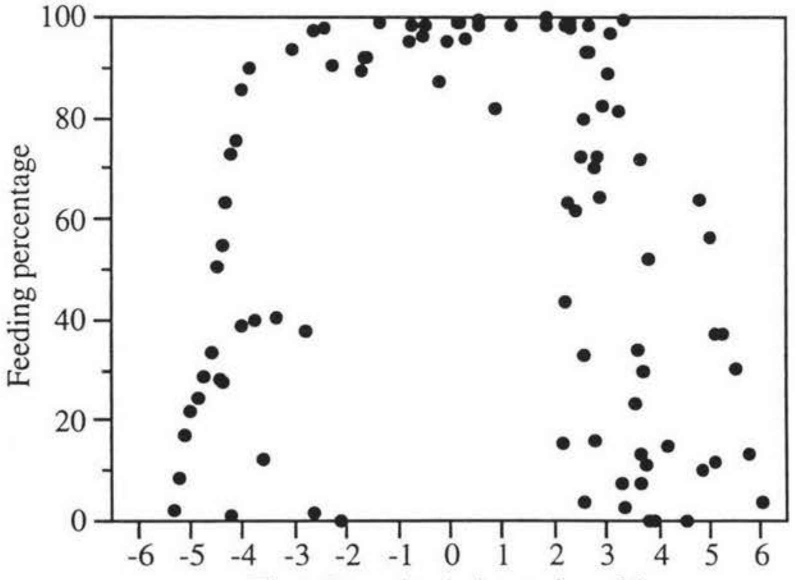


Figure 4.4 Percentage of feeding knots over all tides in the basic period, relative to tide. Each point represents a scan of virtually all visible birds at that time. Mean number of birds per scan = 545 (N=94 scans).

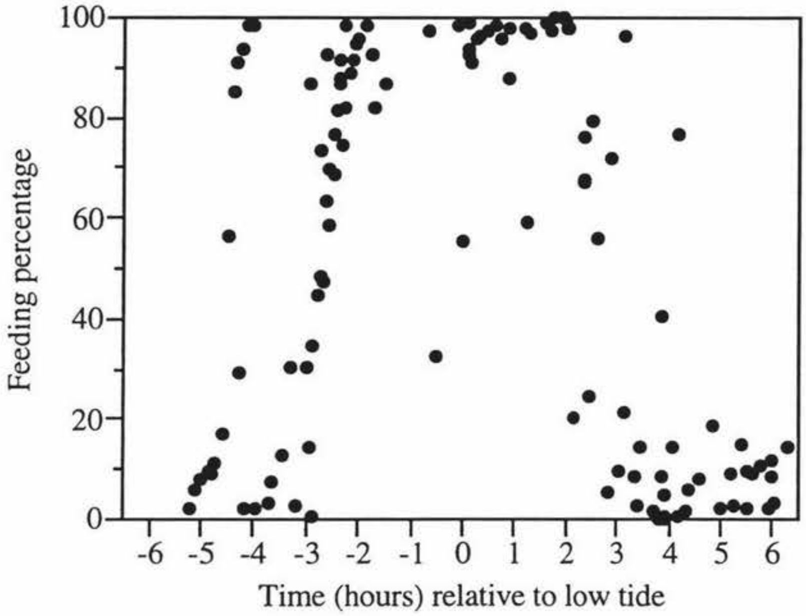


Figure 4.5 Percentage of feeding godwits over all tides in the basic period, relative to tide. Each point represents a scan of virtually all visible birds at that time. Mean number of birds per scan = 531 (N=121 scans).

During the premigratory period waders depositing nutrients need to increase their net energy intake. This can be done by either feeding for longer in the day (Zwarts *et al.* 1990a) or by increasing their intake rate (Swennen *et al.* 1989; Zwarts 1990) . To test for the former, feeding times from the basic and premigratory periods were compared (Figures 4.6 & 4.7 for all tides combined).

There is the suggestion for knots that feeding time is extended both on neap and spring tides during the premigratory period. For neap tides, there were no points of high feeding later than 3-4 hours past low tide for the basic period, while there were few low feeding points before 4 hours past low tide for the premigratory period. For spring tides there was a well-defined drop in feeding activity at around 4 hours past low tide, and also no departure from virtually 100% feeding prior to that.

The godwit data are rather patchy, but do not suggest there is any difference in spring tide activity levels. For neap tides there is somewhat less scatter in activity around low tide in godwits, but there are no scans from 3 hours before to low tide, which hampers interpretation. Overall feeding time is estimated (as above) at 9.4 hours per tide for knots and 7.4 hours for godwits. In summary, knots did increase their feeding time prior to migration, while godwits did not greatly lengthen the duration of feeding. They probably did, however, maintain a higher level of feeding through the middle of the tide, which helped increase overall feeding time. It was noted that during the premigratory period the last thirty birds or so to keep feeding were all apparently juveniles.

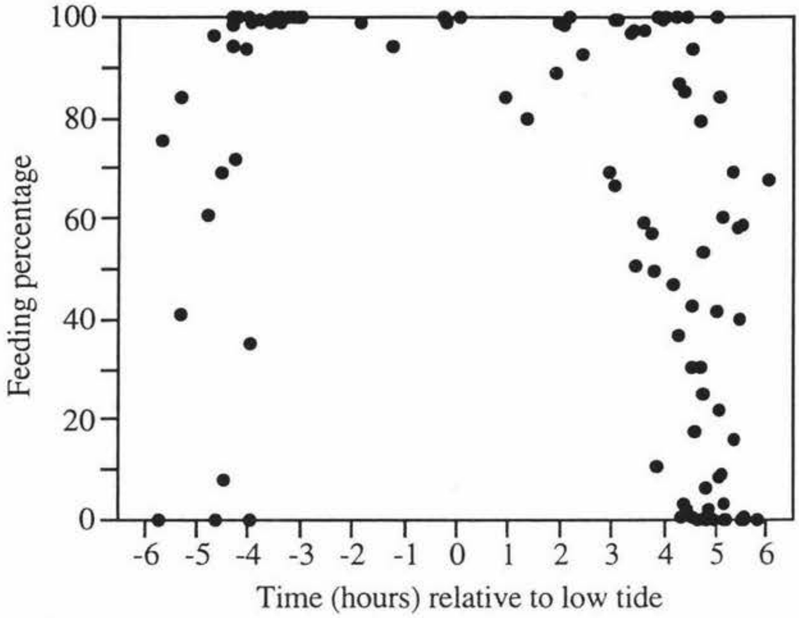


Figure 4.6 Percentage of feeding knots over all tides in the premigratory period, relative to tide. Each point represents a scan of virtually all visible birds at that time. Mean number of birds per scan = 743 (N=101 scans).

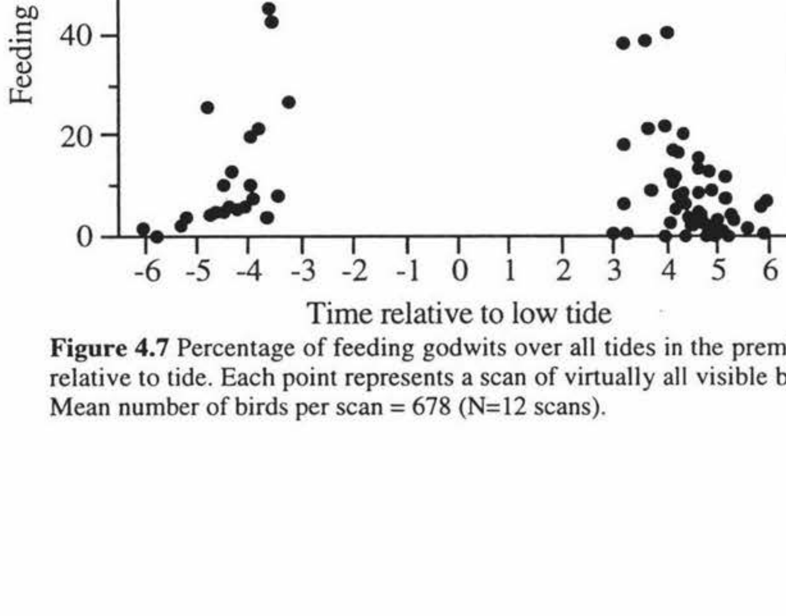


Figure 4.7 Percentage of feeding godwits over all tides in the premigratory period, relative to tide. Each point represents a scan of virtually all visible birds at that time. Mean number of birds per scan = 678 (N=12 scans).

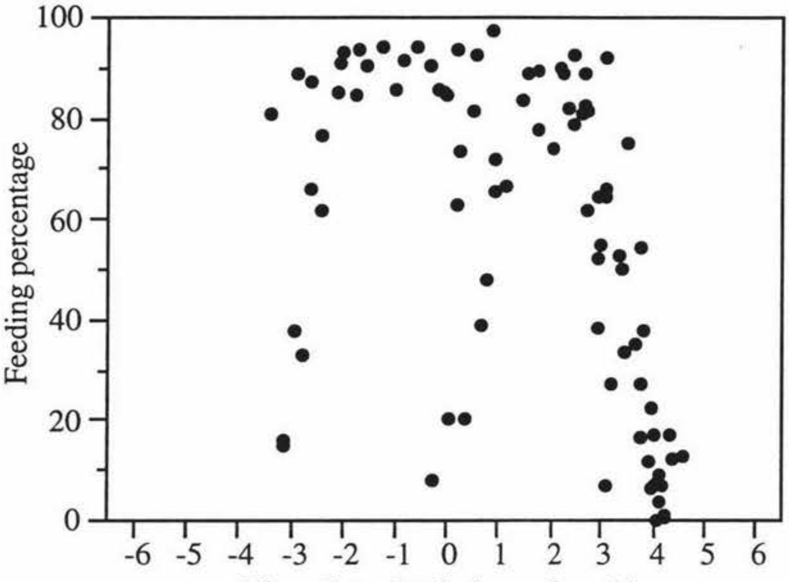


Figure 4.8 Percentage of feeding oystercatchers over all tides in summer, relative to tide. Each point represents a scan of virtually all visible birds at that time. Mean number of birds per scan = 766 (N=87 scans).

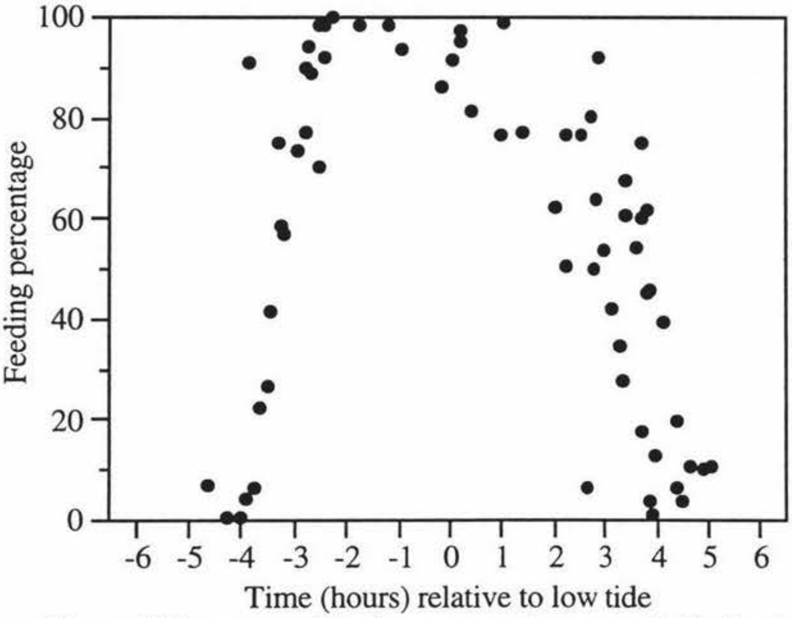


Figure 4.9 Percentage of feeding oystercatchers over all tides in winter, relative to tide. Each point represents a scan of virtually all visible birds at that time. Mean number of birds per scan = 722 (N=65 scans).

Oystercatcher data were too few to allow for separation by tide. They fed for the smallest period of the three species, estimated at 5.90 hours per tide in summer (Fig. 4.8) and 6.76 hours in early winter (Fig. 4.9). The only real difference between activity in these two periods is the curious number of low feeding activity points around low tide during summer, which are lacking in early winter. It may be that oystercatchers extend their feeding activity in this way.

Feeding method and prey type

All species showed different prey-specific (or prey-type-specific) feeding methods, both visual and tactile. Prey type and feeding method are summarised in Table 4.1. Visual feeders rely on cues given by the prey to locate them, if they are not obvious. For oystercatchers, cockles are only available when a bird can insert its bill between the valves of the shellfish to sever the adductor muscle (Baker 1974b; Hulscher 1976), unless they can hammer through the shell (e.g. where weakened through the burrowing activity of the worm *Polydora ciliata* (Baker 1974b), but this behaviour was not seen on Farewell Spit). Oystercatchers therefore walk slowly through shallow water or wet sand, peering down to try to see the extended siphons of feeding bivalves, then inserting their bill between the valves. Cockles were often removed from the sand before extraction of the flesh. Mussels were all visible, forming small clumps around which a bird could walk. These were attacked from the end opposite to the hinge, and the flesh was removed both without breaking the shell, and with breaking the shell, the latter presumably being more time-consuming and energetically costly than the former. Birds attempting this would often turn as much as 180° in their body angle to the shellfish during an attack.

Table 4.1 Feeding method on main prey types for knots, godwits and oystercatchers. Brackets denote prey types which are taken infrequently.

	Mollusca		Annelida: Polychaete worms			Crustacea
	Bivalvia	Gastropoda	Lugworm *Abarenicola*	Maldanidae	Opheliidae *Travisia*	Amphipoda/ Isopoda
Knot	tactile	visual	-	-	-	tactile/visual
Godwit	(tactile?)	-	visual	visual	tactile	-
Oystercatcher	visual	-	visual	visual	tactile	(tactile)

Both oystercatchers and godwits fed on polychaete worms, but these were restricted in their availability through having burrows longer than the bill length of the birds. The birds therefore have to wait until a worm backs up its burrow to defaecate before they can grasp it and pull it out. Oystercatchers approached this problem while feeding on lugworms in two ways. One was to walk extremely quickly over a wide area trying to encounter an available worm (the defaecation process only takes a few seconds), while the other was to stand almost motionless, scanning the immediate area for the inevitable defaecation to take place. Lugworms were only taken on upper-shore flats where densities were high. Godwits generally fed by walking at a moderate pace, in reasonably diffuse flocks (making accurate estimates of mean body-length distances difficult), probing now and then, and plunging their bill deep into the sediment when after a worm. The worm was sometimes swallowed before the bill was extracted from the sediment. The sandy tube of a tubeworm was sometimes partially or wholly stripped before the worm was swallowed, presumably to reduce the sediment load in the digestive system.

Tactile feeding was shown by all three species, and consisted of 'sewing' while walking slowly forward. At times forward movement was hardly perceptible. Sewing was not usually continuous, but instead interspersed with short runs. It is probable that birds were sampling the substrate for some signal about prey levels, and that almost stationary birds were feeding in areas of high prey density.

While knots usually do feed in a tactile fashion (Piersma *et al.* 1994c), their breadth of diet on Farewell Spit required visual feeding also. Specifically this was on small gastropods found in or on eelgrass. Birds were seen picking a tiny snail (*Eatoniella*) from eelgrass leaves, and it is probable that the other snails in the diet were also taken visually. The amphipod *Paracorophium* could be seen swimming in puddles on the sandy flats, and other amphipods could also be seen swimming in the pan as the flowing tide covered it. Knots were observed pecking in areas of high amphipod density on or near the pan on prey too tiny to be seen, which were almost certainly *Paracorophium*. Small swarms of flies were also sometimes found on the pan and knots fed on these, and a few individuals were once seen picking immobilised larger flies from the froth at the tide edge as it flowed up the pan on a spring tide.

Other prey were also noted infrequently only, or on habitat away from the tidal flats. Godwits feeding around saltmarshes fed both on worms and the crab *Helice crassa*. Crabs were dug from their sandy burrows, the godwit sometimes having to follow the down a burrow while digging away the 'roof'. The crab was then dismembered before being swallowed. Crabs were also taken in dense eelgrass and from in a pile of dead cockle shells in the bottom of a tidal channel. Some oystercatchers were seen visually feeding on a very small prey on the tidal flats, but which involved a small hammering motion. It turned out that the prey was an anemone *Anthopleura* which attaches to the shell of cockles. While situated below the sand surface, it keeps the area above it clear of sand, so birds are able to use this to locate the anemone, although the energetic reward must be extremely low. Baker (1969) also records oystercatchers feeding on anemones from the shells of pipi at Collingwood, Golden Bay. Knots were once observed feeding on tiny (c. 5 mm) sand flounder *Rhombosolea plebeia* at the edge of a small drainage channel across the flats, and also occasionally pulling out fine worms from the Pan. A knot seen with a small lugworm probably discovered the worm on the surface of the sand (lugworms could regularly be discovered exposed on the surface).

Pied Oystercatcher: diet and intake rates

The only food type for which actual prey sizes could be measured were mussels (*Modiolus neozelanicus*), which were fed on by a small number of individuals (up to 30) at the hummocks. The size of mussels eaten in February and June are shown in Figure 4.10. Birds in June took a smaller range of mussels, despite the range of available size classes being greater (Chapter 3). Mean size taken was 17.5 mm in February and 18.2 mm in June (T_{404}=2.79, P=0.0055).

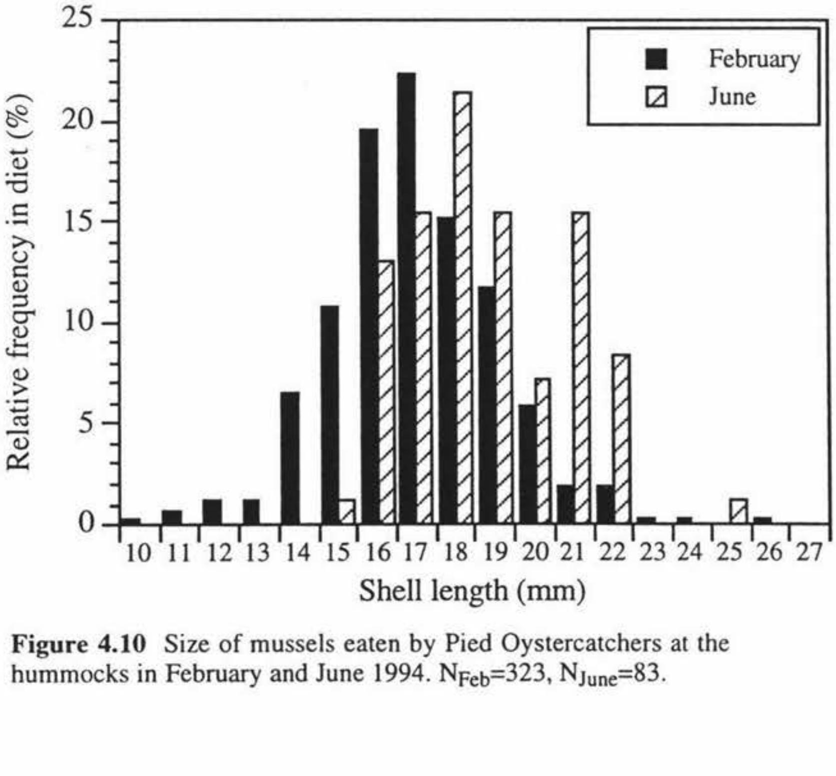


Figure 4.10 Size of mussels eaten by Pied Oystercatchers at the hummocks in February and June 1994. N_{Feb}=323, N_{June}=83.

Whether the difference in sizes taken results from active selection, or represents a different size-structure in the available mussels can be evaluated by calculating the selection index, the proportion taken divided by the proportion present, for each size class. A value of greater than one indicates selection for this size class, as it is being taken disproportionately often.

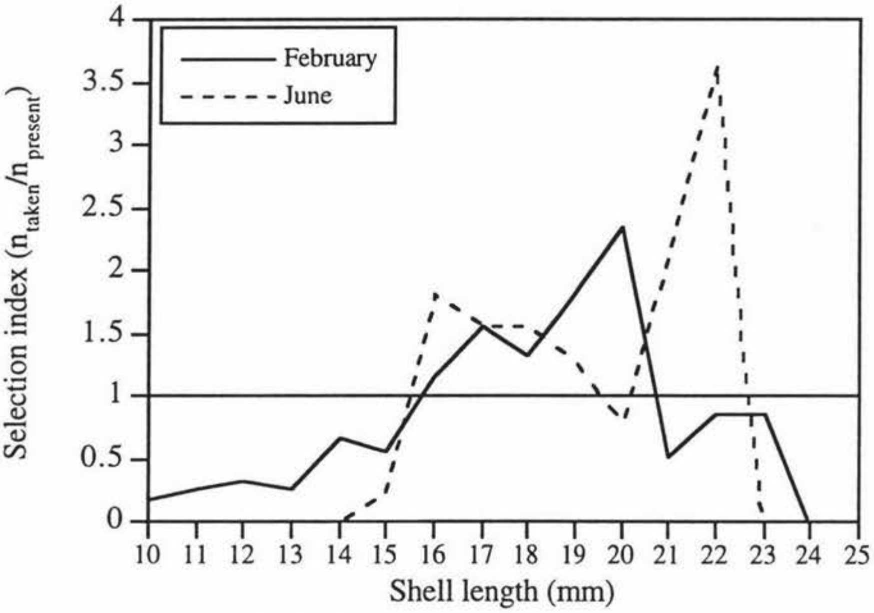


Figure 4.11 Mussel selection by oystercatchers at the hummocks. Single mussels of 26 mm (February) and 25 mm (June) are omitted, as only none and one were found respectively in availability samples, leading to impossible or misleading selection indices. $N_{Feb}=322$, $N_{June}=82$.

In February birds selected for mussels 16-20 mm in length, while in June there appears selection for 16-19 mm and 21-22 mm size classes (Figure 4.11). This bimodality may be partially due to sampling error (N is only 82 for June), but birds were clearly totally ignoring small size classes while selecting the largest ones.

The fact that larger sizes contain proportionately more flesh than smaller ones (Figure 3.25) means that the contribution to the energy intake of large sizes will be proportionately greater than that of small ones. The size distribution of the eaten mussels can be adjusted by the flesh content (Figure 3.25 to give the contribution to the energy intake of the different sizes (Figure 4.12). The high contribution of the large sizes in June becomes obvious. Biomass of the mean mussel in February was 11 mg AFDM and 35 mg AFDM in June.

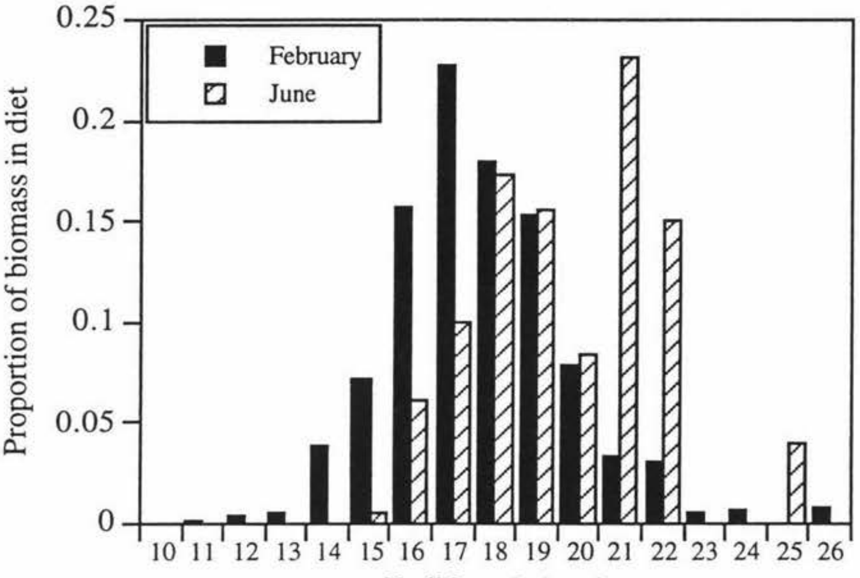


Figure 4.12 Proportion of biomass per mm size class contributing to diet of oystercatchers feeding on mussels. Calculated from the size of mussels taken, adjusted by the flesh content of that size at each time period.

In total 430 minutes of intake data were gathered for Pied Oystercatchers feeding on four prey types. As each minute was not an independent sample, observation blocks on an individual were pooled, and the mean for each variable calculated. These then became the data points, and were not weighted by the length of observation. Non-parametric statistical tests were used to test for differences between prey types. Intake, pacing and pecking rates are summarised in Table 4.2.

In summer (February), sufficient data were gathered for analysis only on *Travisia* and cockles. *Travisia* provided the highest recorded intake rate, although this was not significantly higher than cockles in February (Mann-Whitney [Wilcoxin] test, W=167, N=6,14 P=0.1078). *Travisia* was not present in winter 1994 so did not allow for seasonal comparisons. Oystercatchers feeding on cockles in winter had a virtually identical prey capture rate in February and June (mean = 0.2901 and 0.2811 cockles/min respectively), but because of the lower flesh content of cockles, a slightly lower intake rate in June (Mann-Whitney [Wilcoxin] test, W=124.5 N=6,13 P=0.661). There were significant differences between the three prey types recorded in winter for all of intake rates, pacing rates and pecking rates (Kruskall-Wallis test, $H_{21,10,13}$=21.95 [intake], $H_{21,11,13}$=25.47 [paces], $H_{21,10,13}$=13.688 [pecks], P<0.001 for all), although for intake rate and pecks the largest two values did not differ (Mann-Whitney [Wilcoxin] test: mussel intake vs cockle intake W=140, N=13,10 P= 0.3364; cockle pecks vs worm pecks W=246, N=21,13 P=0.5235).

Table 4.2 Intake, pecking/probing and pacing rates of foraging oystercatchers. The two sample size figures refer to the number of independent observation periods, and the total number of observation minutes respectively. "Worms" refers to birds feeding on long worms (ie. not *Travisia*).

Month	Prey type	Intake rate (mg AFDM/min)			Pecks/probes			Paces		
		mean	se	n	mean	se	n	mean	se	n
February	*Travisia*	**91.6**	5.9	14,107	**sewing**	-	-	**32.8**	13.7	14,106
February	Cockles	**58.3**	19.6	6,91	**9.7**	1.9	5,65	**82.6**	9.7	6,77
June	Mussels	**62.4**	7.5	10,80	**9.5**	0.9	10,80	**47.5**	6.8	10,80
June	Cockles	**46.3**	7.5	13,182	**16.1**	1.2	13,179	**104.2**	4.1	13,180
June	Worms	**15.8**	1.4	21,170	**15.3**	0.8	21,170	**77.5**	3.7	21,170

Taking the energy content of prey to be 21.8 kJ/g^{-1} AFDM (Zwarts and Wanink 1994), the intake rates in Table 4.2 translate to between 0.34 and 2.00 kJ/min. Mean feeding time was 5.9 hours per tide in summer and 6.8 hours per tide in winter. Assuming day- and night-time feeding to be equal in duration and profitability, the energy intake of oystercatchers feeding on different prey types for 1.9 tides per day is estimated in Figure 4.13. Rather than using a standard multiple of Basal Metabolic Rate (BMR) to estimate Daily Energy Expenditure (DEE) (Kersten and Piersma 1987), I have assumed thermostatic and activity costs to be additive, with Maintenance Metabolism (MM) of 3.16 W in February and 4.34 W in June (see discussion), and activity costs of 1.5 X Basal Metabolic Rate (T. Piersma, pers. comm.). With BMR equalling 3.16 Watts (W, =joules/sec; see discussion), estimated costs are 682.6 kJ (7.9W) in February and 784.5 kJ (9.08 W) in June. These are shown as double horizontal lines in Figure 4.13. All the recorded intake rates are sufficient, or nearly so, to cover energy needs except for worms, in which estimated assimilated energy is 3.4 times too low.

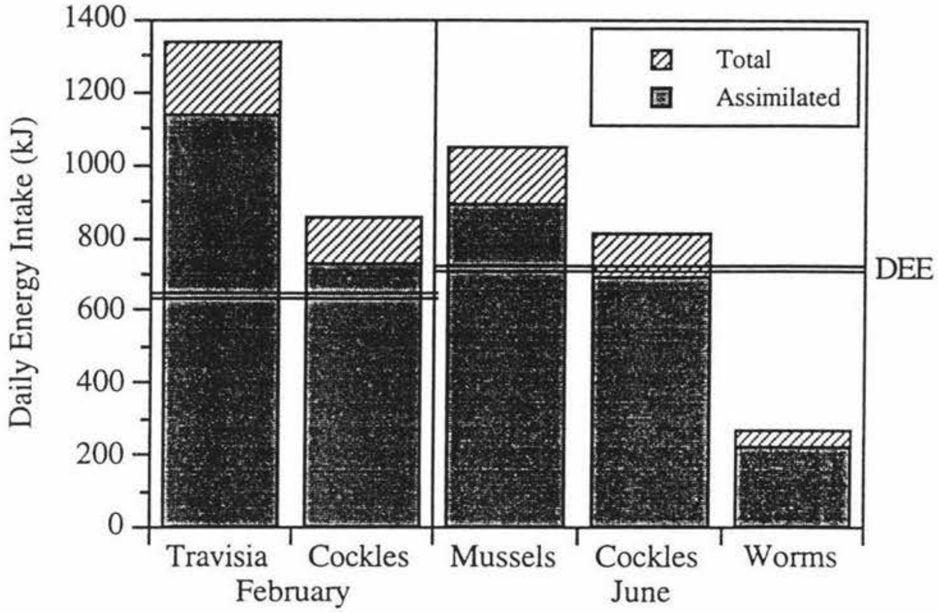


Figure 4.13 Estimated daily energy intake of Pied Oystercatchers feeding on four prey types in summer and early winter. Daily energy expenditure (DEE) is shown (see text) by the double horizontal line.

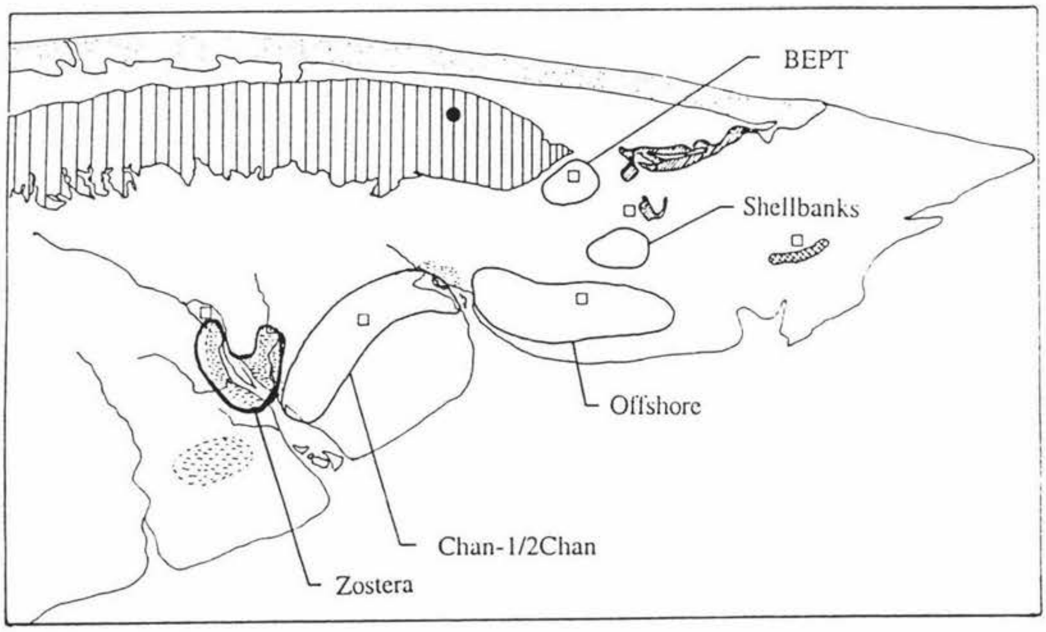


Figure 4.14 Localities used in grouping of knot faeces

Red Knot: diet and intake rate

Knot faecal data were separated into summer and broad localities, shown in Figure 4.14. Most bivalves on sandy flats were pipi *Amphidesma* and cockles *Austrovenus*, but on eelgrass beds the nutshell *Nucula hartvigiana* dominated (Table 4.3). Gastropods were present in most samples. Small crustacea consistently occurred in the diet on the upper flats around Bush End Point. Other prey in faeces included polychaete mandibles (23), *Macomona liliana* (4), limpets (2), insect larvae (3) and one adult beetle. Observations of feeding birds also recorded shrimps (1), small sand flounder (2), amphipods (7) and unidentified fish (8, possibly Gobiomorph bullies).

Table 4.3 Composition of knot diet assessed from faeces according to locality, for all years combined. Numbers of measurable hinges or individual gastropods are given with means (bold values) and standard errors (in brackets). Values for crustacea and seeds are subjective measures based on a scale where 0 equals absent and 4 = abundant in faeces.

	N_{samples}	$N_{\text{droppings}}$	Pipi	Cockle	Nutshell *Nucula*	Gastropoda	Crustacea*	Seeds
Zostera	5	359	**0.24**	**0.58**	**1.48**	**0.17**	**0**	**0**
			(0.44)	(0.21)	(0.79)	(0.05)		
Chan-	3	35	**0.36**	**0.92**	**0.18**	**1.66**	**0**	**0**
1/2Chan			(0.22)	(0.34)	(0.14)	(0.32)		
Offshore	5	338	**2.36**	**0.13**	**0.0002**	**1.78**	**1.10**	**0.90**
			(1.19)	(0.03)	(0.0002)	(0.69)	(0.40)	(0.29
BEPt	7	650	**0.73**	**0.18**	**0.10**	**0.46**	**1.71**	**0.22**
			(0.42)	(0.10)	(0.09)	(0.32)	(0.51)	(0.15)
Shellbanks	2	142	**6.04**	**0.32**	**0**	**2.72**	**1.75**	**2.5**
			(5.12)	(0.27)		(2.68)	(1.25)	(0.5)
Total	22	1594	**1.42**	**0.38**	**0.39**	**1.06**		
			(0.57)	(0.10)	(0.21)	(0.31)		

---

* Gastropods were represented by at least four taxa, primarily the tiny (0.75 - 2.75 mm) black *Eatoniella* (*limbata*?). *Micrelenchus* (*huttoni*?) was common in eelgrass samples, with low numbers only of very small whelks, probably *Cominella glandiformis*. Occasional *Zeacumantus* (*lutulensis* or *subcarinatus*, not determined) were also present.

The mean size of pipi recovered from faeces differed between localities and summers (Table 4.4).Mean size was larger in 1993/94 than 1992/93 (T_{2112}=8.15, $P<0.0001$). While this difference was only 1.1 mm, it still represents an 18% increase in size.

The size of pipi taken ranged from 1.9 to 15.3 mm. The range of sizes taken was similar in both 1992/93 and 1993/94 summers (Figure 4.15), though proportionally more large individuals were taken in 1993/94.

Table 4.4 Mean size (mm) of pipi taken by knots, summarised by locality and summer. Bold values are means, with standard error and number of reconstructed lengths (from hinge measurements) in brackets.

	1992/1993	1993/1994	1994/1995
Channel: *Zostera*	**5.72** (1.70, 65)		
Channel-1/2 Channel		**8.21** (2.38, 35)	
Offshore	**6.87** (1.61, 666)	**6.27** (1.53, 20)	**5.45** (2.16 307)
Bush End Point	**7.06** (2.26, 68)	**7.56** (2.69, 105)	
Shellbanks	**6.17** (1.42, 1155)		
All sites	**6.43** (1.57, 1953)	**7.54** (2.55, 160)	

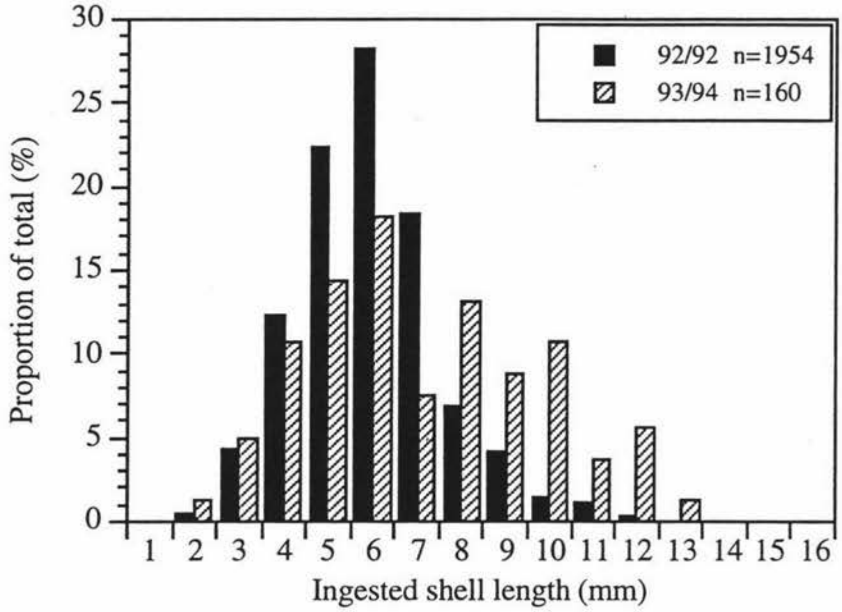


Figure 4.15 Size distribution of pipi recovered from knot faeces (all localities combined).

The size distribution of pipi taken in 1993/94 roughly matched the available sizes, except that individuals larger than 13 mm were not taken in proportion to their presence in the sediment (Figure 4.16). This could result both from selection for against larger sizes, but also from reconstructions from faeces being biased towards smaller individuals. Three samples of regurgitates of knots were collected from roosts in 1993/94 (totalling 31 regurgitates). The mean size of pipi present in these was significantly larger than in faeces (Figure 4.17: mean in regurgitates=11.43 mm, sd=2.34, n=97; T_{2524}=26.7, P<0.0001). Dekinga & Piersma (1993) showed that regurgitates of *Macoma balthica* from knots in the Netherlands also contained remains of significantly larger individuals than faeces. Given the much lower rate of production of regurgitates compared to faeces (one roost containing 15 regurgitates had over 400 faeces present), faeces are probably the most appropriate source of shell fragments from which to reconstruct diets. However, regurgitates may extend the size classes taken. The maximum size recorded (16.6 mm) fell far short of the theoretical maximum (22.4 mm: Chapter 3).

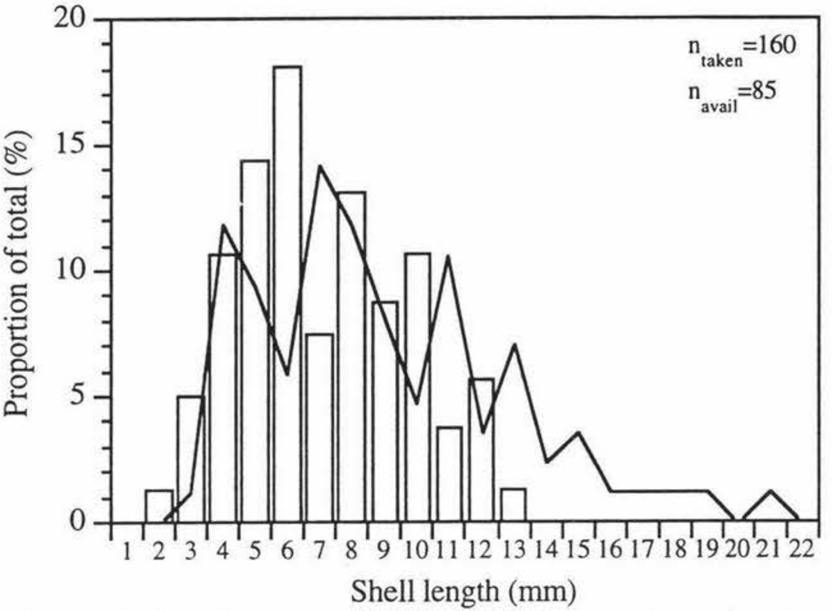


Figure 4.16 Size distribution of pipi recovered from knot faeces (bars) and present in sediment (line) for 1993/94 over all sites.

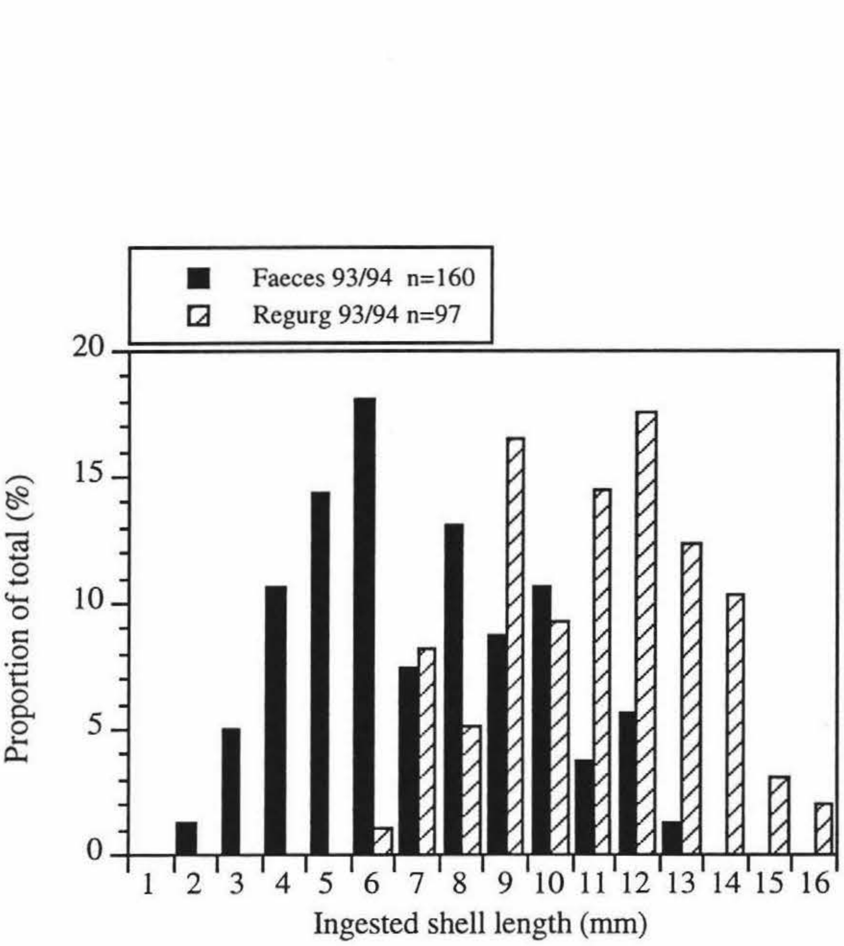


Figure 4.17 Size distributions of pipi taken by knots, estimated from faeces and regurgitates.

Mean cockle size was also larger in 1993/94 than 1992/93 by 0.86 mm (14%: Table 4.5). The range of sizes taken was from 1.1-14.3 mm, with a larger range in 1993/94 than 1992/93 (Figure 4.18). Regurgitates yielded a larger mean size (9.9 mm) in 1993/94 (T_{684}=11.37, $P<0.0001$: Figure 4.19) and a larger maximum size (15.3 mm). While the maximum size of cockle from faeces therefore almost exactly matched the size predicted by gape limitation (14.1 mm, Chapter 3) the largest individual from regurgitates exceeded this. This probably reflects variation in shell circumference and bird gape size. Larger cockles were taken less frequently than expected, while medium-sized ones (8-9 mm) were apparently selected for (1993/94: Figure 4.20).

Table 4.5 Mean size (mm) of cockles taken by knots, summarised by locality and summer. Bold values are means, with standard error and number of reconstructed lengths (from hinge or hinge+top measurements) in brackets.

	1992/1993	1993/1994	1994/1995
Channel: *Zostera*	**5.4032** (2.0318, 87)	**7.9858** (2.0075, 87)	
Channel-1/2 Channel	**6.6953** (1.1099, 17)	**7.5217** (2.2012, 67)	3.3538 (1.4583, 16)
Offshore	**5.1123** (2.1975, 25)	**5.0874** (1.8268, 9)	
Bush End Point	**7.8841** (2.1464, 90)	**6.2559** (2.7942, 114)	
Shellbanks	**5.1290** (1.9905, 60)		
All sites	**6.1972** (2.5314, 279)	**7.0589** (2.5314, 277)	

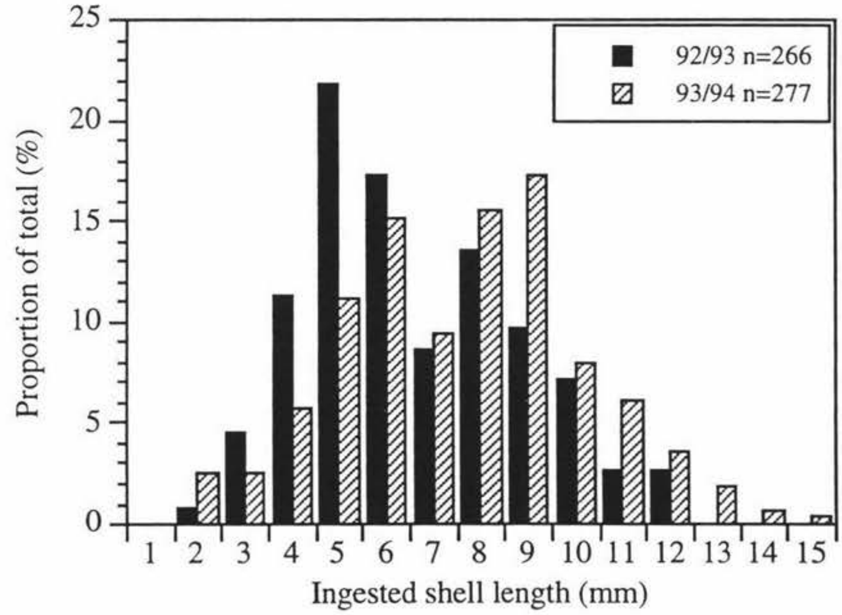


Figure 4.18 Size distribution of cockles taken by knots with all localities combined, estimated from faeces.

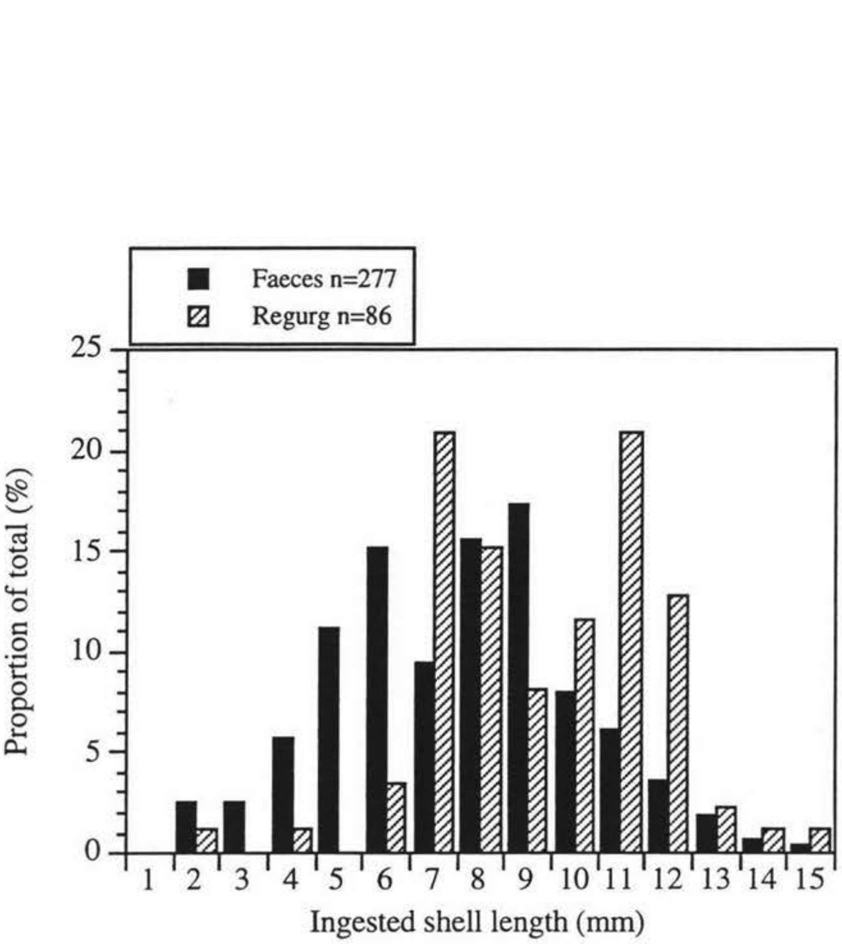


Figure 4.19 Size distribution of cockles from knot faeces and regurgitates in 1993/94.

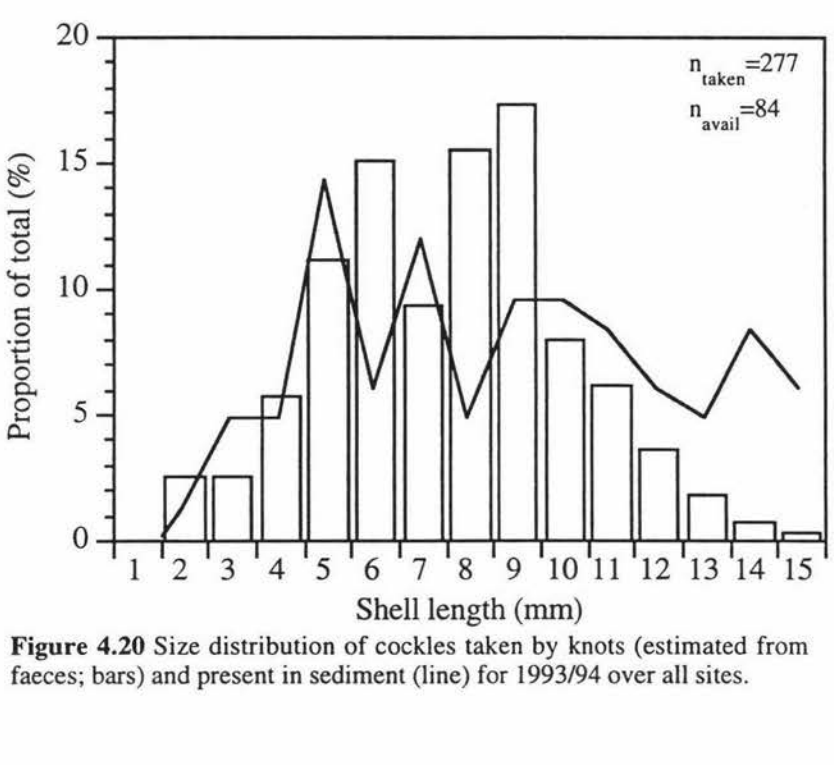


Figure 4.20 Size distribution of cockles taken by knots (estimated from faeces; bars) and present in sediment (line) for 1993/94 over all sites.

While knots at times were fairly approachable, the small size of their prey meant that very few items could actually be identified directly. Prey were classed as small prey (when a swallowing movement was seen but usually not the prey item), 1/5 bill length or 2/5 bill length for larger items. As this is fairly uninformative, the contribution of different prey items to the intake was assessed from faecal analysis, and weighted according to the ratio of individual pipi, cockles and snails in faeces from that locality or nearby. Biomass values were calculated for the mean size of bivalve from Tables 4.4 and 4.5 for the appropriate locality and year. The contribution of the larger gastropod *Micrelenchus* to the snail category could not be accurately assessed, as most were crushed too much to allow estimation of size. This was taken from eelgrass beds, however, for which no intake rates are analysed so this should not affect estimates much, although it was recorded in some faeces with a sandy/eelgrass mix.

The resulting intake rates are shown in Figure 4.21. Due to the skewed distribution, the mean intake rate (45.34 mg AFDM/min, sd=6.33, n=37,168) is rather larger than the median (2.63 mg AFDM/min). The median may be the more appropriate measure. These should be regarded as minimum estimates, as they do not incorporate the contribution of crustacea, plant matter or the occasional fish which may be taken.

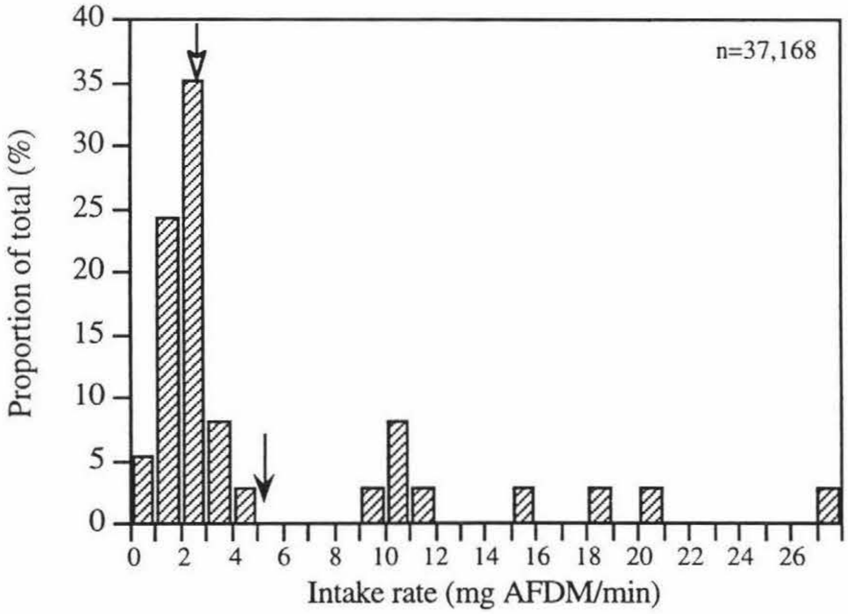


Figure 4.21 Intake rate of knots over all sites and times. N gives number of observations and total number of minutes. Dark arrow shows the mean, pale arrow shows the median.

With an energy content of 21.8 kJ/g AFDM and a feeding time of 7.4 hours per tide in the basic period, and 9.4 hours in the premigratory period, the intake rates translate to assimilated DEI (with 1.9 tides per day and 0.85 assimilation efficiency) of 41.3-83.4 kJ (median and mean intake rates respectively) in the basic period, and 52.4-106.0 kJ in the premigratory period.

Bar-tailed Godwit: diet and intake rates

Godwits fed on a receding tide in a broad band 1-200 m wide in shallow water, leapfrogging from the upper shore to the lower shore side. The speed at which they moved and their readiness to fly further out made it impossible to gain any intake rate observations on the outgoing tide. On the incoming tide they regularly fed in a band preceding the incoming tidal front by about 100 m, also leapfrogging to the inside. Preceding this probably acted to avoid interference by the flowing water with feeding. By my sitting quietly on the tidal flat the flock was usually not disturbed and merely parted on either side of me while carrying on feeding.

Most prey items were swallowed without being seen, but the swallowing action could be readily noted, allowing prey capture rates to be calculated. Birds fed mainly by sewing, interspersed by probing. Close observations and investigation of the benthos revealed the main prey to be the Orbiniid worm *Travisia*, which was captured by tactile sewing. Birds would also regularly catch slender worms, some of which were identified as Maldanids, while others (pale worms) were probably Spionids and Orbiniids. It is possible that amphipods comprised some of the small prey items, although this was never confirmed. Small fish or shrimps (noted as "zippy" prey) were also regularly caught. The intake data for offshore observations are summarised in Table 4.6.

Table 4.6 Energy intake of godwits feeding on worms (*Travisia* and 'slender worms'). Bold values are means, with standard errors in brackets. Energy content of AFDM is 21.8 kJ/g. Feeding per tide in the premigratory period equals 7.4 hours. Assimilation efficiency equals 85%. Small prey were treated as shrimps for 3.6 % and *Travisia* for 96.4% (ratio of 'zippy' to other small prey [44/1236 total]) giving a mean value of 17.46 mg AFDM per individual. Worms were taken as 5.353 mg AFDM..

Worms /min	Small prey/ min	Intake (mg AFDM/min)	Intake (J/min)	Intake per tide (kJ)	Assimilated per tide (kJ)	Number of observations
0.166	**5.44**	**95.8**	**2088.7**	**927.4**	**788.3**	59,232
(0.0489)	(0.340)	(5.89)	(128.4)			

DISCUSSION

Use of space

Use of space in non-breeding shorebirds has received little attention beyond studies relating bird abundance to prey abundance or biomass (e.g. Bryant 1979; Evans and Dugan 1984; Goss-Custard *et al.* 1977; Rands and Barkham 1981; Wilson 1990) , microhabitat (Mouritsen & Jensen 1992) or some combination of these (Goss-Custard *et al.* 1992). Other studies have addressed territoriality (Townshend 1985; Townshend *et al.* 1984; Wood 1986) and movements within an estuarine complex (Symonds *et al.* 1984). Myers (1984) defined four main distinct levels of organisation in spacing behaviour in terms of their spatial and temporal scales: individual, local, regional and global. The second of these, the local scale, has been the least addressed. This scale addresses "processes occurring within the daily home range of a foraging shorebird: its movements from roosts to foraging sites and between different foraging areas, and the pattern of roost dispersion" (Myers 1984).

Roosting behaviour has garnered little research (Myers 1984) with most discussion focussing on whether roosts might facilitate information transfer about feeding sites (Ward and Zahavi 1973) and of antipredator advantages of roosts (although most research on this actually relates to feeding flocks). Piersma *et al.* (1994b) suggested that roost site choice around the island of Griend, in the Dutch Waddensea, was influenced by predators to the degree that certain waders were prepared to fly an extra 29.6 km per day to roost on a large sandbank free from raptors. Actual predator avoidance might not be expected to be a major selective force in roosting flocking on Farewell Spit or New Zealand in general, given the virtual absence of avian predators in most coastal areas. The Australasian harrier *Circus approximans* is the only coastal raptor in New Zealand, and this is no real threat to waders in most places (although red-necked avocet Recurvirostra novaehollandiae and sandpipers (Scolopacidae) have been recorded in harrier diet in Australia: Marchant & Higgins 1993) . It may be, however, that flocking is maintained even in the absence of selective forces, through habit.

One striking observation which shows that a bird's behaviour is affected by its history is provided by the difference in response to passage of a skua (Arctic or Pomarine). Whenever a skua flew by, every godwit and knot in the vicinity took instant flight, despite the fact that skuas never showed any interest in waders. In contrast, most oystercatchers remained undisturbed on the tidal flats. Skuas are a very real threat to arctic waders on the breeding grounds, so we would expect evasive behaviour to be shown by these species: oystercatchers never experience skuas except on the nonbreeding grounds where they are not a threat, and they seldom show a response to skuas. All species, however, flew when harriers were present, which relates to the fact that any raptor will be a possible predator on the breeding grounds be they in Siberia or New Zealand, including for oystercatchers. This shows that there is an historical aspect to bird behaviour, and roosting behaviour could reflect this. As long as there is no cost to group roosting then it will be maintained. Stinson (1980) shows theoretically that predation attempts on flocks need not be frequent for flocking to be selectively advantageous.

Oystercatchers roosted directly in from their main feeding areas around the hummocks. On neap tides they roosted on shellbanks, on higher tides on the beach. Their extreme site-specificity to the beach site may reflect the fact that much of the population doesn't change feeding location between tides and this is as useful a place as any to roost. They generally never fed inside the shellbanks on the pan, and moved to the roost well before water flooded the pan. Godwits and knots, however, did feed on the pan, did move around considerably on the tidal flats, and were variable in their roost site choice. The latter may be effected by the flooding of the pan by the tide. Just what determines this is unknown though.

Few studies have attempted to quantify intertidal movements on the local scale. Piersma et al. (1994b) showed that knots in the Dutch Waddensea used an area with a diameter of 45-50 km, covering as much as 800 km^{-2} of tidal habitat. They contrasted this with the case for knots in the Banc d'Arguin, Mauritania, where they used only 10-15 km^{-2}.

The Farewell Spit situation provides another interesting contrast to the Dutch one. Knots at the tip of Farewell Spit are estimated to cover only 5-6 km^2 during a tidal cycle, and the almost sedentary birds when feeding on the pan are possibly the least active of any knots in the world. Piersma *et al.* (1994b) suggest that tropical knots in Mauritania may not have to move around as much as in Europe to keep track of an ever changing food supply due to vertical movements of prey in the sediment and other perturbations (e.g. human shellfishing). This is because in the Banc d'Arguin the food supply is all relatively shallow, diverse, and whose non-synchronous biomass fluctuations give rise to a generally constant food supply. The food supply on Farewell Spit is hardly spatially or temporally constant, however (see Chapter 3). The flocking behaviour on the flats also differed, with Dutch flocks typically being very large, dense groups (pers. obs, Piersma *et al.* 1994b) while Farewell Spit birds fed in highly spread-out subgroups, themselves often well spaced.

It is considered that predation is a major influence on flocking and spacing behaviour of birds (Stinson 1980; Whitfield 1988), but other factors such as the spatial dispersion of the food supply (Lindström 1989; Pöysä 1987a) can play a primary role in some cases. Benefits of flocking, such as decreased individual vigilance (Abramson 1979; Alonso *et al.* 1994; Burger & Howe 1975; Fleischer 1983; Lima 1995; Smith and Evans 1973) must be balanced against costs such as interference, prey depletion and reduced prey activity (Goss-Custard 1980; Goss-Custard 1984b).

It is my conviction that when we can come to grips with issues of ecological scale and spatial variation in prey for waders, then such differences may be explained. The influence of prey variability, dispersion and grain should be studied in several contrasting localities. An intimate knowledge of the benthos, combined with detailed studies of the movements of birds (individually marked, preferably involving radio-tracking) and energy intake rates (augmented with captive studies) would be required to achieve this. New Zealand has a bonus as a study site as predation risk is essentially factored out of the equation, with the only coastal raptor being the Australasian harrier, which is not a real threat to foraging waders (falcons being the main aerial predators of shorebirds: Bijlsma 1990; Dekker 1988; Page & Whitacre 1975; Whitfield 1988) Until that time, it remains that the behaviour of knots at least at the end of Farewell Spit is in striking contrast with that in the Dutch Waddensea. Studies from elsewhere in New Zealand would complement this.

Feeding time

That waders differ in their feeding times has been well demonstrated, and between species there has been shown a negative relationship between body mass and feeding time, scaling to the exponent of -0.22. This approximates the -0.25 exponent expected if intake rate (and hence feeding time) is proportional to mass (Zwarts *et al.* 1990a) . This relationship, studied in a range of waders wintering in West Africa, only appeared when nocturnal feeding was taken into account, as not all species utilised nocturnal feeding opportunities equally. Other studies, however, have shown this negative relationship when only daylight feeding is considered (Dann 1987; Engelmoer *et al.* 1984; Pienkowski 1978/1979) . While I was unable to investigate nocturnal activity on Farewell Spit, waders did feed at night.

There was a negative relationship between body mass and feeding time in the three species studied here in the basic period over all tides, described by the equation

$$\text{feeding time (hours)} = 14.8 * \text{mass (g)}^{-0.14} \quad (R=0.94)$$

This differs from the -0.22 exponent above, and probably relates to the fact not all species were utilising nocturnal feeding opportunities equally (below).

Knots were limited in their ability to increase feeding time by the tides, especially on spring tides. They did, however, effect some increase through extending this where possible, and through maintaining a higher level of activity within this feeding time. There is still a fair degree of scatter in the data during the premigratory period (Figure 4.5). This may relate to daily variation in tidal covering of the flats. On spring tides knots face an absolute coverage of feeding areas right up the pan, and the timing of this will depend on tidal height, wind and barometric pressure. Cessation of feeding on neap tides may relate to the size of the previous high tide, as major prey for knots at the top of the tidal flats and on the pan are small crustacea (amphipods and isopods). When tides are on the increase, it may be up to a week since an area was flooded, which make it dry and in effect unavailable. When tides are getting smaller, there is be a greater area of damp sand above the moving tidal front which may allow feeding near high tide. Alternatively, birds may be sensitive to increases in maintenance metabolism through changes in wind, temperature and radiation and adjust their intake accordingly. However, whether any changes would be of any great magnitude, and whether birds assess this instantaneously, or cumulatively over a period of days, is debatable.

Godwits, in contrast, showed no signs of greatly extending their feeding time, despite their stopping feeding when tidal flats were still exposed (Figure 4.6). They may have increased their activity slightly around low tide, but in general they maintained a low activity level even in the premigratory period. Two possibilities could explain this. The first is that feeding is profitable on an incoming tide only on the lower flats, due to prey levels/activity. The second possibility is that godwits were not stressed in their feeding and were not fully utilising nocturnal feeding opportunities.

If feeding high on the flats were unprofitable, then birds would then be forced to cease feeding even when flats were exposed. Certainly, it was only juveniles that remained feeding during the premigratory period once the tide reached the pan. This would indicate either that it was only juveniles that had not yet learnt that feeding there was in fact unprofitable, or due to lower feeding efficiency it was this sector of the population that required this feeding to maintain their energy balance. Juvenile waders have often been shown to be less effective foragers than adults (Burger 1980; Burger & Gochfeld 1985; Espin *et al.* 1983; Groves 1978; Heppleston 1971; Puttick 1979). Detailed data on intake rates of juveniles on the pan, and juveniles and adults on the flats would answer this.

Alternatively, godwits were not stressed in their feeding and were not fully utilising nocturnal feeding opportunities. They could thus achieve a higher overall intake rate by extending feeding at night. The profitability of nocturnal feeding has been much debated. During the 1970s it was assumed that waders would feed at night only when unable to meet their energy requirements by day, and it was presumed that nocturnal feeding was much less efficient than in the daytime. Research since then has shown nocturnal foraging to be widespread, but difficult to make predictions about due to factors such as changes in prey availability at night (Dugan 1981; Evans 1987). Nevertheless, waders in the Banc d'Arguin, Mauritania, used the nocturnal foraging period to extend their feeding time, where necessary (Zwarts *et al.* 1990a). Given the need to increase energy intake by some 25-30% to experience a body mass increase of 1% per day (Zwarts *et al.* 1990a), unless an increase in feeding time of that magnitude is realised during the daytime period, then it must occur at night, or through an increase in intake rate.

For knots, feeding time in the premigratory period was 1.28 times the basic period while for godwits it was only 1.08 times. This indicates two things. First, the increase shown by knots in feeding time is sufficient to allow a mass deposition rate similar to that shown by waders overseas, conforming with predictions. Second, the increase in daytime feeding in godwits is clearly insufficient to allow this. The conclusion, therefore, is that godwits were not fully utilising nocturnal foraging opportunities during the basic period, but do so in order to increase energy intake for mass deposition, unless they can drastically increase their intake rate in the daytime. That godwits should preferentially feed in daylight is not unexpected, given that much of their feeding is visual, while knots ought to be able to feed equally well in darkness as in light, although this has not been tested. That knots increased their daytime feeding by 28% suggests that they were already utilising nocturnal foraging to a large degree. If they were not, then they might likewise show a smaller increase in feeding activity in daylight. Alternatively, if they had not been, then they could experience an increase of in excess of 28% by extending this nocturnal time also.

Pied Oystercatcher: energy requirements, diet and energy intake

Estimated maintenance metabolism for oystercatchers is shown in Figure 4.22. For the period January to March, there is no thermostatic cost imposed on oystercatchers. Because of their low lower critical temperature (14.7° C) and fairly high operative temperatures over summer, no extra energy is required to maintain body temperature. Peak costs in winter reach 4.95 W, or 1.6 X BMR. By roosting in flocks for almost half of the day, oystercatchers reduce costs by 0.27-0.37 W. This increases the "thermoneutral period" in effect from December to almost April.

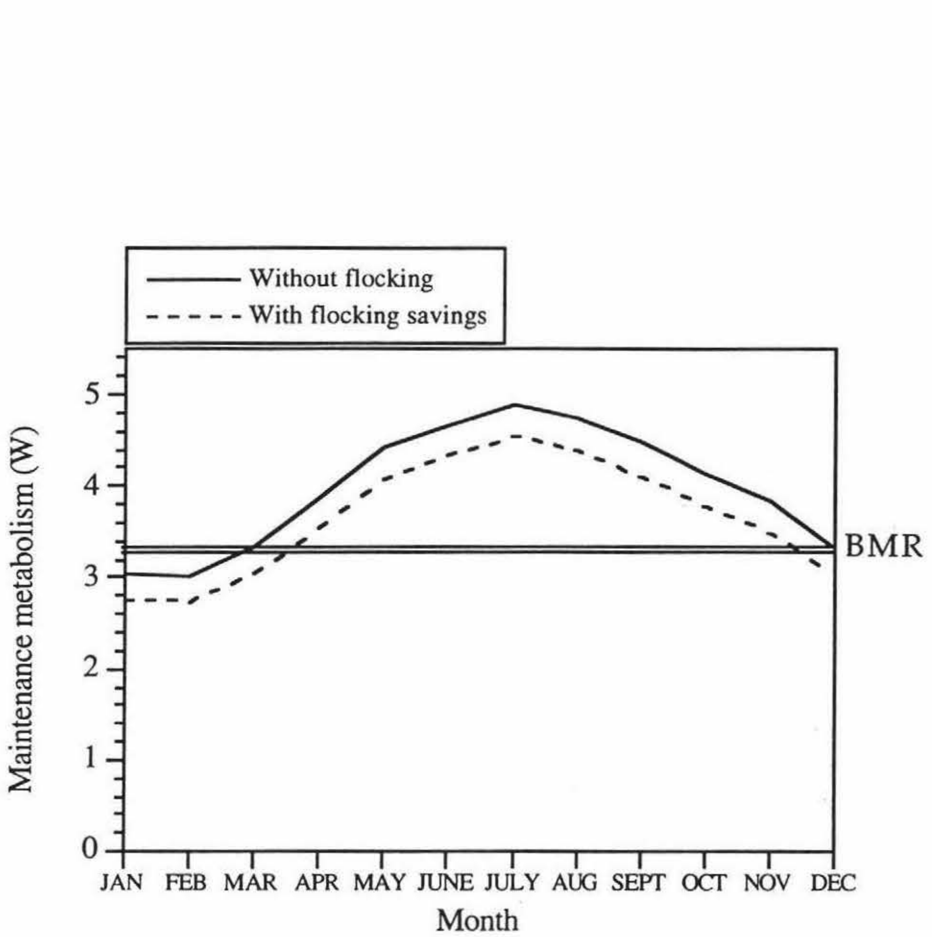


Figure 4.22 Maintenance metabolism of Pied Oystercatchers at Farewell Spit. Parameters used in the calculation were body mass 525 g, BMR 3.16 W (predicted from Kersten & Piersma 1987), lower critical temperature 14.7° C (derived from above two values, assuming conductance of 0.12 W/°C), breast height 0.14 m (see Wiersma & Piersma 1994, Appendix 2). BMR is shown by the double horizontal line.

Deposition costs associated with migration cannot be formally incorporated, as no data on mass changes exist. These will affect birds at two times: when birds are staging on the spit en route to the northern North Island (December/January) and prior to migration south (July). However, any nutrient deposition occurring will not be very large, as the distances likely to be flown (eg. Farewell Spit to the Auckland isthmus or Canterbury breeding grounds; 450 km) would not require large amounts of fat. Nevertheless, peak costs are thus expected to occur in July, when maintenance metabolism is highest and nutrient deposition is occurring.

Dietary specialisation has been recorded in the Pied Oystercatcher in both short- and long-terms (Boates and Goss-Custard 1992; Durell *et al.* 1993) . Without individual recognition of birds, demonstrating fixed feeding preferences is impossible. However, given that birds were observed feeding on different prey types in almost exactly the same locality at the same time, and that only once twice was a bird seen to take another category of prey during an observation period, it is probable that the feeding types described are discrete behaviours. Birds were almost instantly categorisable into feeding type by their foraging behaviour.

The highest rate of energy intake was provided by *Travisia*, which appeared to be the preferred feeding method in summer (72% of 625 birds scanned on 12.2.1994 around the hummocks were feeding tactilely = *Travisia*). This had both the overall highest energy intake, plus the lower pacing rate of the two methods for which data are available in summer. If birds did feed equally during night as in day (as assumed above) then their DEI would exceed requirements by 67%. Unless birds needed to deposit nutrients, then it is probable that they would feed to a much lesser degree at night. Nevertheless, nocturnal feeding is probably required to maintain energy balance on most days. (The shorter duration of feeding for oystercatchers compared with godwits means that areas with *Travisia* will usually be available for foraging, so estimates will not be biased in the same way as for godwits).

As no birds were seen feeding on *Travisia* in June, and none were located by sampling or manual searching of sediment, this high level of predation (combined with that of godwits, see below) was apparently unsustainable in 1994. Depletion of this food source will have required either prey-switching by the oystercatchers specialising on *Travisia* over summer, or movement to other areas where *Travisia* may have still have been present. While there were certainly fewer oystercatchers in June than in February (620-820 in June, typically 1200-1700 over summer), the fact that birds use Farewell Spit as a staging site on their way to northern wintering grounds means that this decrease in numbers could have been due both to migration north as well as food-induced emigration.

For individuals feeding on cockles and mussels, estimated DEI is sufficient to cover needs, but only if nocturnal feeding is sizeable. It should be noted that the estimates of feeding duration used in these calculations were taken from all birds, regardless of feeding type. The observed differences in intake rates could lead to differences in feeding duration also.

The estimate of DEI when feeding on worms, however, is almost three times too low to meet requirements. One possible source of error is that I have assumed that feeding is solely on one prey item, while worm-feeders may take lugworms on a receding tide on upper tidal-flat levels and bamboo-worms once offshore. However, relatively few birds fed on lugworms, and such intake rates as I was able to gather suggested an intake rate lower than that for Maldanids (lugworm intake = 12.8 mg AFDM/min [n=7,92] c.f. 15.8 mg AFDM/min [n=21,170]). This would only lower estimates.

Slender worms were the prey type for which the most uncertainty in estimates occurs. Determining the average biomass for worms proved problematic due to breakage of worms and low samples sizes in June (Chapter 3). If the estimate for average worm biomass in June were correct (8.192 mg AFDM/indiv) rather than the lower value for April which was used (5.353 mg), then the DEI would reach 406 kJ, still 40% short of requirements. Long-term preservation in formalin could account for some of this, but *Travisia*, which provided the highest estimate of DEI, was also preserved in formalin for the same duration. An uncertain aspect of the oystercatcher's intake rate was that it was often difficult or impossible to accurately estimate the size of prey being consumed. Worms were typically recorded as being 1/4 X bill length, 1 X bill length (and these could represent stretched worms), or simply as a worm. If birds were able to select larger individuals, then the non-linear scaling of mass on length would result in a greatly increased DEI. An even greater problem was that many prey could simply not be seen, being swallowed while the bill was still inserted in the sediment. These were recorded as "small prey" and taken to represent 1 cm of Maldanid bamboo-worm. In total 345 small prey were recorded, compared with 335 full worms. Lumping all small prey items together may distort the true picture, but is unavoidable unless detailed information can be gathered on the constitution of these prey items. It is not obvious how this would be easily done.

This analysis has treated energy intake as being the currency likely to be maximised. It is possible that energy *per se* may not be always maximised, with some nutrient requirement necessitating feeding on a prey that would provide insufficient energy to suffice on energetic grounds. This would have to be alternated with an energetically viable prey (eg. shellfish). Only once did I observe a worm-feeder take a cockle, suggesting such prey alternation is unlikely. The most likely cause for the apparent deficit is methodological on my part. Nevertheless, it is gratifying that four of the five estimates do cover proposed energy demand.

Knots: diet, energy requirements and energy intake

Globally, knots are well known to be mollusc specialists on both sandy (Piersma *et al.* 1994b; Piersma *et al.* 1994d; Tulp and de Goeij 1994; Zwarts and Blomert 1992; Zwarts *et al.* 1992) and rocky (Alerstam *et al.* 1992; Summer & Smith 1983) shores. In New Zealand, Piersma (1991) showed knots fed on molluscs at both the Firth of Thames and Puponga, at the base of Farewell Spit. Their diet at Puponga consisted primarily of *Nucula* and gastropods, with lesser amounts of *Tellina* (*Macomona*) and cockles. This reflects the predominance of eelgrass around Puponga, and the possibly higher populations of *Macomona* (pers. obs.).

This mollusc-dominance is supported by this study. Pipi *Amphidesma* are the main bivalve prey on sandy flats, occurring at a higher level in droppings than cockles *Austrovenus*. *Nucula* dominates in eelgrass beds. However, the diet at the tip of Farewell Spit is rather broad in comparison with other studies, incorporating three bivalve species, commonly at least three gastropod species, seeds (presumably from eelgrass) and a variety of tiny crustacea. This could be due in part to a larger suite of potential prey items being present, but classic foraging theory expects foraging selectivity to increase as prey levels rise. Conversely, at low prey levels predators are forced to be less selective in their prey choice. The well-known prey model (Stephens & Krebs 1986) is not directly applicable to predicting diet breadth, as it deals with sequential (not simultaneous) encountering of prey items within a homogenous patch. As knots' foraging environment consists of non-homogenous patches, inference on the basis of combined faecal samples will be inappropriate. Nevertheless, this theory predicts that prey should be either always taken or not taken, prey should be ranked according to their profitability, and inclusion in diet should be independent of encounter rate. Faecal samples were often collected from where birds have been feeding for more than 40-50 minutes (the gut passage-time of a knot) so can be treated as coming from a single patch. Faeces always represented the full scope of potential prey items, suggesting that no prey were being excluded from the diet. In contrast, knots in the Netherlands ignored the tiny mudsnail *Peringia (=Hydrobia) ulvae* until *Macoma balthica* became less harvestable in autumn (Dekinga & Piersma 1993).

Within two bivalve species, *Amphidesma* and *Austrovenus*, knots were not highly selective except at large prey sizes. At large prey sizes the effort required to crack the shell in the gizzard will increase, as may the risk of injury during this process by shell fragments. This may explain the drop-off of large cockles in the diet. Large pipi are unlikely to present such a problem, being thinner-shelled. However, knots were observed rejecting large pipi (estimated size c. 20 mm) after attempting to ingest them, indicating that for an elongate prey item, gape size may not be the only limitation. The absolute length of large pipi may make them too awkward to ingest easily.

Knots in the Netherlands ignore small *Macoma balthica* in favour of large individuals (Dekinga and Piersma 1993; Zwarts and Blomert 1992), because of a profitability threshold in which small prey are unprofitable due to detection, recognition and handling times. Farewell Spit knots clearly do not obey the same laws: extremely small cockles and pipi were present in the diet. This cannot be due simply to flesh content of New Zealand prey lowering this threshold - a 10 mm *Macoma* has an estimated mass of 11.3 mg AFDM (Zwarts and Blomert 1992) while a 10 mm pipi contains only 3.7 mg AFDM in summer. Depth of living can likewise not explain it - smaller individuals live shallower than larger ones, which should reduce handling times and lower the threshold. The most likely reason for a diet of primarily small shellfish on Farewell Spit is an insufficient density of larger ones. Knots theoretically require a harvestable biomass of around 1 g AFDM/m^2 (Piersma *et al.* 1994d), which was not found in any bivalve species in limited sampling on Farewell Spit (Chapter 3). To maintain their energy intake, knots may be forced to expand their diet from a simple bivalve-dominated one, to a wider diet involving more gastropods and crustacea.

The prevalence of crustacea in the diet of knots on upper shores and the Pan is without precedent in the literature. For this to be energetically viable, prey must occur at a very high density, as the mass for amphipods is extremely low (0.07 mg AFDM/indiv for 3177 amphipods from the Pan in April 1994). As the density on the pan is almost excessively high (mean 17,800 m^{-2} on bare sand, N=10), this leads to a mean biomass of almost 2 g AFDM/m^2 (including isopods and cumaceans, Figure 3.4). Immediately offshore, at Tip1, biomass ranged between about 0.3 and 0.7 g AFDM/m^2. In the absence of decent bivalve populations, knots are able to augment their diet with crustacea, due to their high density. Small crustacea can thus be an important component of the diet of an otherwise mollusc-specialist. In most intertidal areas crustacea may occur at too low levels to be harvestable and alternative more preferred prey at high enough levels to not necessitate feeding on them.

The environmental 'cost' (= maintenance metabolism) for knots in summer is around 1.3 Watts (Joules/s: Figure 4.23). By roosting in a tight flock for 50% of the day, this is reduced by about 0.1 W. BMR (approximating 0.95 W) accounts for 73%, with thermoregulatory costs being low. From February to July costs increase due to decreases in mean temperature and radiation: windspeed does not vary greatly between months. Peak requirements for birds remaining on Farewell spit over the southern winter reach 2-2.2 W. This cost is composed largely of thermoregulatory cost (57%) : BMR accounts for less than half (43%).

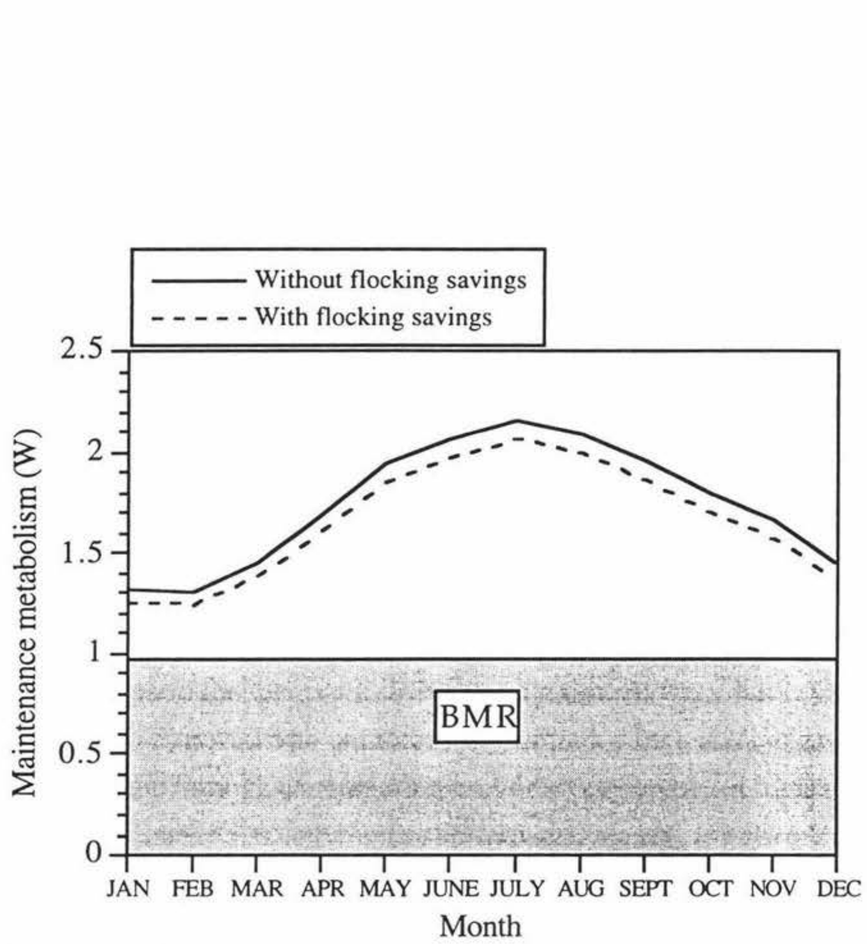


Figure 4.23 Maintenance metabolism of knots on Farewell Spit, based on climatic data (mean windspeed [1971-1980], air temperature [1971-1980] and solar radiation [taken as equalling Nelson Airport, the nearest recording station, 1969-1980) using the method of Wiersma & Piersma (1994). Shaded area represents the basal metabolic rate.

Energy costs of activity of knots feeding on artificial mudflats in the Netherlands was measured by Poot & Piersma (1994) using stable isotope turnover (doubly-labelled water) methods: they estimated costs of activity to be around 1.3 W, in addition to maintenance metabolism of 1.53 W.

Farewell Spit knots fed for 88% longer than Poot & Piersma's experimental knots (18.8 hours per day in the premigratory period, assuming equal nocturnal feeding), so foraging costs could reach 2.82 W. With maintenance metabolism of 1.38 W, costs reach 4.2 W. This does not include costs of tissue synthesis. Taking tissue deposition costs to be 12% of the energetic value of the total deposited tissue (Kersten and Piersma 1987) and mass to increase from 115 to 185 g at a rate of 1.24 g per day (Chapter 5), then the daily cost of tissue synthesis will be 0.65 W (energetic value of fat = 40 kJ/g, so daily energy gain is 1.24/0.88*40=56.4 kJ/day: translating this into Watts (J/s) results in 56.4/24/3.6=0.65 W). This gives a total energy expenditure, including BMR, maintenance metabolism and costs of tissue synthesis of 4.85 W.

This value represents 5 X BMR, which is at the maximum suggested level of sustainable energy expenditure, the *metabolic ceiling* of Drent & Daan (1980) of 4-5 X BMR, and is surprisingly high. Levels of 4 X BMR have been documented in waders in the wild, such as Turnstones *Arenaria interpres* on the breeding grounds in Arctic Canada (4.12 X BMR Piersma & Morrison 1994). The costs on Farewell Spit are large purely because of premigratory activity - an increased working day and tissue deposition cause these costs to rise. The equivalent calculations for mid-summer give a total energy expenditure of only 3.2 W (1.3 W maintenance metabolism plus 1.9 W activity costs, with 14.8 hours feeding per day).

The experimental knots of Poot & Piersma (1994) fed on shellfish stocked at 1,500 bivalves/m^2, or 10 g AFDM/m^2, a level three times higher than natural harvestable prey levels in the Dutch Wadden Sea, the Banc d'Arguin (Mauritania) or Roebuck Bay (NW Australia) (Piersma *et al.* 1994d). This may explain the relatively short foraging time of these birds. Conversely, this also suggests that knots on Farewell Spit are forced to maintain a high level of energy expenditure over the premigratory period through encountering only low prey levels - a higher harvestable biomass would allow a higher intake rate and thus a shorter working day, lowering activity costs. If, however, knots fed less at night than at day, then the activity costs would be reduced and my current estimate too large. Even if knots fed for three hours less than suggested, the total energy estimate is still 4.0 W (1.38 maintenance + 1.95 activity + 0.65 tissue deposition), or 4.1-4.2 X BMR. Knots on Farewell Spit clearly are maintaining a high level of energy expenditure prior to migration.

The measured intake rates, however, fail to reach anything near this level. A DEE of 4.85 W translates to 419 kJ. According to the intake rate calculations for the premigratory period, assimilated DEI using the mean intake rate is only 106 kJ. As the birds do get very noticeably fat and migrate probably directly to Australia (Chapter 7) then there must be some large errors in these estimates.

The route to estimating DEE is admittedly tortuous and requiring many assumptions. The standard way to estimate DEE has generally been to use a multiple of BMR, which does not take into account differences in activity patterns, while I have estimated it on the basis of directly measured costs in captive birds. The difficulty in obtaining measurements of Field Metabolic Rate (energy expenditure of a free-living individual) means that estimation from captive birds is currently the best available method. This requires a direct relationship between the biology of the captive European knots and New Zealand birds. While *rogersi* knots are small (Chapter 6), the knots of Poot & Piersma (1994) were of similar or smaller mass - estimates should not be inflated by mass differences. Any errors in the estimate of activity cost will anyway not solve the shortfall in energy estimates: BMR alone requires 82 kJ, which both of the median intakes would fail to provide. No estimates even cover maintenance metabolism.

A large source of uncertainty in these estimates comes from the presence of non-molluscan prey items. Birds were regularly seen taking small fish, which may provide high energy returns. Crustacea also probably contribute a significant amount of energy to the diet in some areas. These could not be accounted for. Alerstam *et al.* (1992) also found a shortfall in estimates of energy intake of knots in Iceland, which they attributed to polychaete worms in the diet, for which no remains were found in faeces. Alerstam *et al* (1992) estimated energy intake on the basis of the energy-equivalent of faeces, a method recommended by Dekinga & Piersma (Dekinga and Piersma 1993) and used also by Tulp & de Goeij (1994). This requires separating shell fragments from faeces into species, and calculating their energy-equivalent (flesh mass intake they represent) from a known flesh AFDM:shell dry mass relationship. On the basis that what goes in must come out, measured defaecation intervals can then be used to calculate the intake rate. This would be far preferable for the Farewell Spit samples also. Large sand-grain size meant that much was retained with the faeces when sieved, and attempts to separate constituents, even from subsampled masses, proved exceedingly time-consuming. Even this method has its drawbacks. As noted by Dekinga & Piersma (1993), this method "...would be inappropriate in cases where crustaceans contribute significantly to the diet if Knots in intertidal areas...". It is most unlikely that the deficit in estimates is due solely to non-molluscan prey. A more comprehensive data set for intakes might paint a very different picture. Certainly, Figure 4.21 shows that at times knots were achieving a much higher intake rate than the mean. How often they achieve this could greatly affect estimates of total energy intake. At this point, however, I am unable to suggest how readily knots on Farewell Spit achieve their energy requirements.

The indications, though, are that knots are somewhat stressed on Farewell Spit prior to migrating, and the broad diet recorded is, I suggest, a necessity rather than a luxury. Densities of shellfish are apparently low, and their flesh content low also (the mean pipi size taken in 1993/94 [7.5 mm] had a mass of 1.8 mg AFDM; the equivalent sized *Macoma* in Zwarts & Blomert (1992) would have a mass of 4.5 mg). This will make subsisting on a simple bivalve-dominated diet difficult. The two saving graces of Farewell Spit may be its benthic diversity, allowing alternative gastropod and crustacean prey in the diet, and the much lower thermostatic costs than in equivalent European areas. However, the long working day (presumed necessitated by low prey levels) causes energy costs to rise, with the surprising prediction resulting that knots are working near their metabolic limit in the premigratory period. Long-term data on the variability in small bivalve populations would be extremely valuable for assessing the role of prey levels in this.

Bar-tailed Godwit: diet, energy demand and energy intake

There are relatively few data with which to compare the diet of godwits. In general they have been recorded feeding for a large part on polychaete worms (Dann 1979; Piersma 1982; Smith and Evans 1973), although bivalves have also been recorded forming a minor part of the diet (Piersma 1982). During intake observations, no bivalves were noted being taken, but one bird did attempt to swallow a medium-sized *Macomona*. It is probable that small bivalves are taken regularly. The diet away from sandy flats differs quite a bit from that on it, with crabs being a prominent prey in eelgrass beds and saltmarsh channels. No attempt was made to assess the relative importance of these habitats to the overall population energy intake.

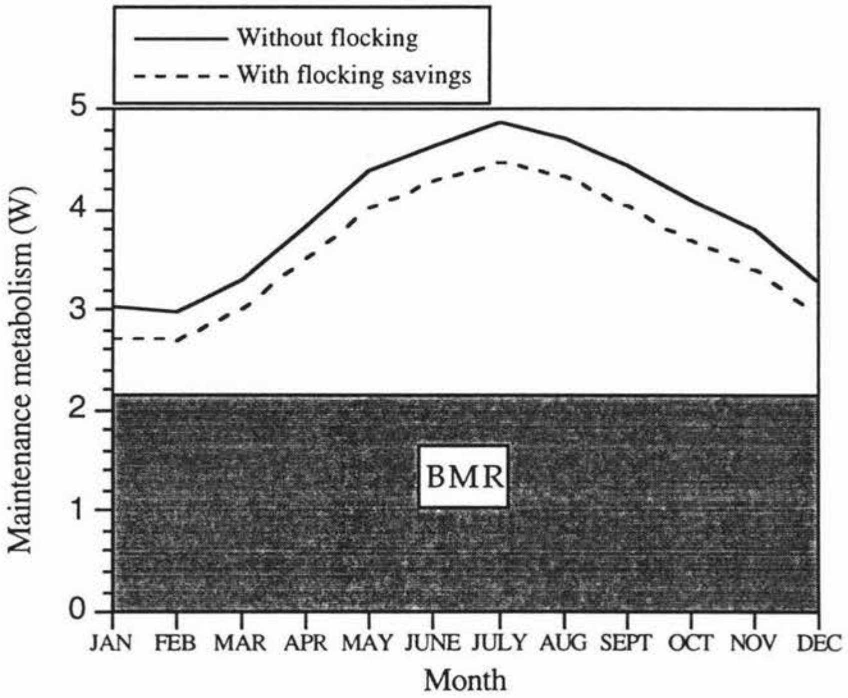


Figure 4.24 Maintenance metabolism of Bar-tailed Godwits on Farewell Spit. Parameters used in the calculation were body mass 310 g, BMR 2.16 W (predicted from Kersten & Piersma 1987), lower critical temperature 20.2° C (derived from above two values, assuming conductance of 0.104 W/°C), breast height 0.13 m (see Wiersma & Piersma 1994, Appendix 2). BMR is shown by the shaded area.

Godwits over summer face thermostatic costs of around 3 to 4.3 W, for which BMR (2.16 W) comprises 50-72% (Figure 4.24). Costs in midsummer are only 1.4 X BMR, while they reach 2.3 X BMR in midwinter.

As activity costs and fat deposition have not been directly measured in godwits, we can only coarsely estimated them. Calculating DEE in the same way as for Pied Oystercatchers (results) we arrive at a basic cost of 5.95 W (MM of 2.7 W + 1.5*BMR [=2.16 W for a 310 g bird]) in the premigratory period. This is around 514 kJ, which by the recorded intake rate calculations could be gained by one tide's feeding alone, with 274 kJ to spare. At this time birds are depositing nutrients prior to migration which raise costs. A probable level of mass deposition would be 200 g, equating to a fat load of 40%. Spread over six weeks this would require 4.8 g of fat to be deposited per day. With a fat deposition efficiency of 88% (Kersten and Piersma 1987), this would require 5.5 g fat intake per day, resulting in a daily cost of tissue synthesis of 5.5 g*40 kJ/g = 220 kJ, or 2.56 W. This raises the estimated DEE to 8.5 W, or 735 mJ. Even with this value, estimated assimilated energy for one tide still exceeds this requirement.

This leaves us with a paradox of sorts - the estimated energy intake from one tide alone would cover costs for the entire day, yet birds did apparently feed at night. Admittedly, all the intake rates came from an incoming tide, as it proved impossible to gain any on the outgoing tide. Intake rates may not necessarily be equal through the feeding period. To affect this problem, intake rates would have to be lower on an outgoing tide. For worms which are available only when defaecating, they are probably more available on an outgoing tide, which may explain why most godwits follow the tideline when feeding. As the main prey taken was fed on tactilely (*Travisia*), it is unlikely that behavioural changes affect its detectability, unless birds detect movements by the worms.

However, the distribution of *Travisia* was far from uniform across the tidal flats. Most godwit intake rates were gained from the region between and beyond Tip2 to the hummocks. The density of *Travisia* in December 1993 was 42 individuals/m^2 and in April 1994 was 38.5 individuals/m^2. In contrast, none were recorded at Tip1, or in a transect from Tip1 to Tip2 in April 1994. *Travisia* is apparently a strongly downshore species. *Travisia* may thus not be available at a high density for an hour or more at either end of a feeding period.

Reducing the duration of feeding at the high intake rate when feeding on *Travisia* (Table 4.6) to 5.5 from 7.4 hours, and assuming the same level of slender worm intake as recorded in Table 4.6 drops the assimilated energy intake to 588 kJ per tide. This is less than the estimated DEI, and would require nocturnal feeding to achieve energy requirements. The uncertainty about the extent of nocturnal feeding (as well as intake rates themselves) means estimating actual DEI is impossible.

Dietary overlap between species

None of the three wader species studied had an exclusive diet, excepting oystercatchers feeding on mussels. There was direct competition between oystercatchers and godwits for both *Travisia* and other slender worms. Combined predation by these two predators may have caused a collapse in *Travisia* populations in 1994. *Travisia* populations were still high in April, just after most godwits migrated, suggesting oystercatcher predation was most important in this. In winter 1993 the situation was very different, with *Travisia* densities in June being similar to those recorded in the following summer. Inter-annual differences in invertebrate populations can thus be pronounced, which will have repercussions both on bird numbers and also predation pressure on alternative prey (Beukema 1994).

Knots and oystercatchers do not directly compete for food, but do so indirectly through sequential harvesting of different size-classes of bivalves, especially the cockle. Predation by knots may affect cohort survival as they grow to a harvestable size for oystercatchers, while oystercatcher predation will presumably affect cockle reproduction and spat (juvenile) settlement. The strength of any density-dependent links in this is open to conjecture.

There is probably some small overlap in diet between knots and godwits with prey such as small bivalves and crustaceans.

Seasonal energy demands and intake

For Arctic-breeding waders migrating to the southern hemisphere, they encounter low thermostatic costs and high prey productivity (Hockey *et al.* 1992), although this may be affected by prey size selection. Peak costs come in late summer with premigratory preparation. The suggestion is that godwits are able to easily achieve their energy demands, with a measured energy intake above that which is required (although in reality this may be an overestimate) and an apparent under-utilisation of nocturnal feeding opportunities.

Knots, in contrast, appear to be time-stressed at this time, evidenced by a long working day. However, their increase in feeding time is in accord with the predicted magnitude, indicating that they can manage to increase feeding sufficiently. Unfortunately the estimates of energy intake are so far short so as to be unrealistic.

Oystercatchers increased their overall feeding time by 15 % from February to June, while their predicted thermostatic costs rose by 45 %. While this would appear to be a deficit, it is complicated by birds in February possibly migrating north and possibly maintaining a higher level of activity than would otherwise be expected. For the most part, however, intake rates suggest that oystercatchers are able to obtain sufficient energy even with the fairly short feeding duration they use.

This study is of course a snapshot, and there is one consideration not addressed here which is worth mentioning. There can be changes in benthic biomass both within and between years (Chapter 3). The susceptibility of a predatory species to changes in prey populations can vary with its diet and size selection. For instance, if reproductive failure occurred in a bivalve (this is well documented in cold-temperate areas and can be prolonged: Zwarts and Wanink 1994), then the absence of small sizes would impact immediately on knots. Oystercatchers, being buffered by the presence of other year-classes, would not suffer reduced prey levels in that year. If reproductive failure continued, then an absence of suitable year-classes would in time be felt by oystercatchers. Knowledge of the biology of birds' prey is required if we are to accurately assess the long-term risks to birds residing at a site such as a tidal flat.

Chapter 5

Seasonal mass changes in knots in New Zealand

ABSTRACT Knots *Calidris canutus* are high-Arctic breeding waders that migrate to temperate and tropical regions for the non-breeding season. I examine seasonal mass changes in knots at the southern end of a migration, in New Zealand. Adults show a large increase in mass in February before their northward migration in March. They are estimated to depart with a fat load of around 45%. Juveniles, which do not migrate north but remain in New Zealand over the breeding season, also show a small mass increase. Mass increases in winter are well-documented for European waders, but I suggest that, contrary to the European situation, this increase in juvenile birds in New Zealand is not necessarily an adaptive strategy to insure against periods of negative energy balance. Instead, it may be a (non-adaptive) byproduct of hormone changes in the premigratory period. Such increases may be more widespread in Arctic waders in the southern hemisphere than is realised.

INTRODUCTION

Waders are renowned for their long-distance migrations, which may span over 100° latitude in some populations of arctic-breeding waders. To fuel the series of flights made to achieve this migration, individuals must undergo several cycles of mass deposition and usage for each journey. For some species this typically involves large flights that may last for 36-48 hours in which stored nutrients are the only source of energy. Failure to deposit enough nutrients can thus have severe consequences, and it is expected that natural selection has given rise to mass cycles which are closely linked with migratory flight requirements.

Knots *Calidris canutus* provide one of the classic examples of a long-distance migrant, breeding in the extreme high Arctic and migrating as far south as South Africa, Australia, New Zealand, and southern South America (Piersma and Davidson 1992a). Five subspecies are recognised, with *rogersi* migrating to Australasia (Barter 1992). Given the geographical range of wintering areas, individuals of different subspecies encounter very different environmental demands during the non-breeding season, and birds migrating to the southern hemisphere or the tropics experience much lower thermostatic costs than birds remaining in north-temperate zones, but face considerably larger flight costs (Piersma *et al.* 1991; Wiersma and Piersma 1994). Body mass levels may be expected to reflect both migratory demands and the risk of food shortage (eg. Davidson 1981b).

Body mass cycles for knots in New Zealand are examined, based on birds captured around the Auckland region, North Island. In adults I show mass changes over the non-breeding season ('winter' as a term will be restricted to the southern winter season) and estimate lean and departure masses for adults. Mass of juveniles is assessed through the year. Possible explanations for body mass cycles in juveniles are compared. Total body mass provides only a crude indicator of seasonal body composition changes, and the body composition of premigratory knots from Northland is examined elsewhere (Chapter 6)

METHODS

Knots were cannon-netted at Jordan's Farm, Kaipara Harbour (36°30'S, 174°20'E) and the Firth of Thames (37°10'S, 75°10'E) (Figure 5.1) by members of the Miranda Banders (New Zealand Wader Study Group) under the direction of S. Davies and A. Riegen, from 1987-1993. In total 3026 knots were caught, of which 1759 were both weighed and aged (some catches were too large to enable full processing of all birds). The large majority were weighed within two hours but, where the catch was very large, for a small number of birds it could be up to four hours between the time of capture and weighing. Masses have not been corrected for mass loss after capture, and this should be kept in mind when interpreting results. Birds were weighed to the nearest gram using Pesola spring balances. Ageing was by primary moult, wear, and presence of breeding plumage (Davies & Riegen, unpublished). Only birds where age was determined are analysed. Individuals were classified as 1st-year, 2nd-year or 3rd-year (this last category including all adults). The 'birthdate' was 1 August.

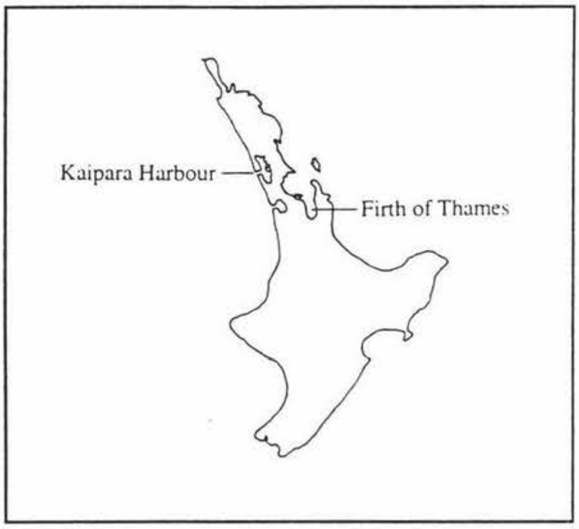


Figure 5.1 Localities of knot catching operations in the Auckland region

RESULTS

Most birds (1289) were 3rd year birds, only 157 were juveniles (1st-years) but 313 2nd-years were weighed. Seasonal mass changes for all three age-groups are given in Figure 5.2.

While the data are limited, they indicate a premigratory mass of around 110-115 g. A mass of 115 g is hereafter used as a basic mass level. To estimate departure mass, a regression equation was derived for the premigratory mass increase period, using 30 January as the beginning of this increase. This gives around 6 weeks to increase mass, similar to periods given in the literature (Zwarts *et al.* 1990b). Furthermore, Zwarts *et al.* (1990b) show that mass increase is synchronous with moult into breeding plumage. The first knots on Farewell Spit, north-west Nelson, show breeding plumage by mid January, and by the end of January almost 40% are entering breeding plumage (pers. obs.). 30 January is apparently not too early to use as a starting date; a catch of knots around this time would determine what proportion of birds had started increasing mass by that date.

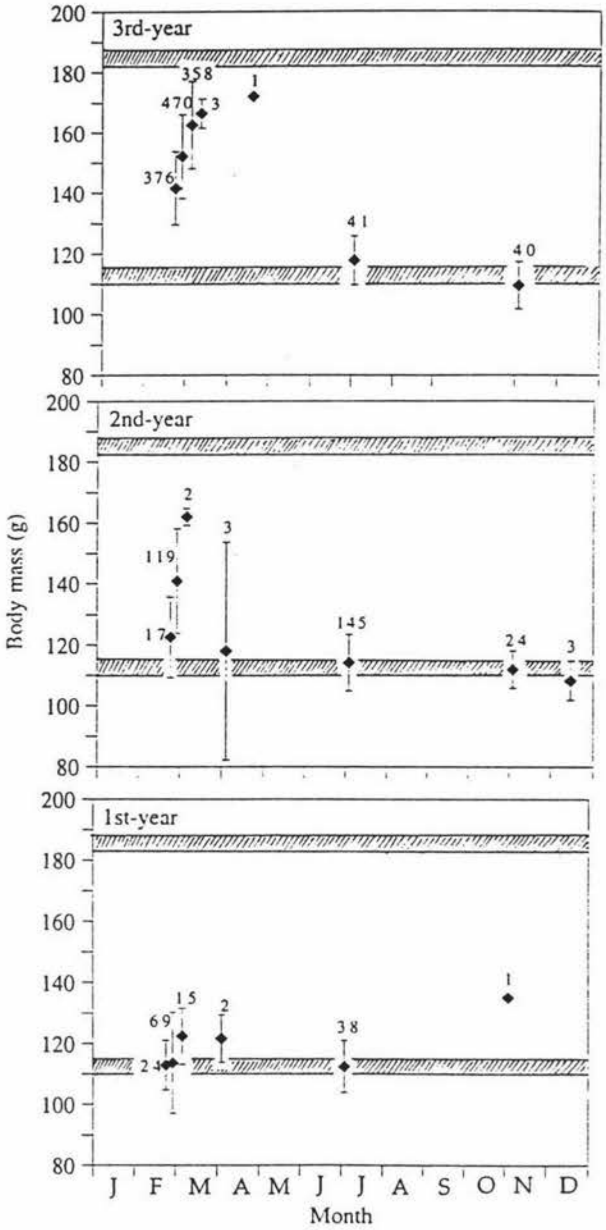


Figure 5.2 Mass of knots though the year, separated into 3rd, 2nd and 1st-year birds. Sample size is indicated by the figure adjacent to or above the bar. The two shaded regions represent the estimate basic and departure masses.

Extrapolating through to 19 March (mid-departure period, from observations of departing knots on Farewell Spit (Chapter 7) and from counts of knots at Manawatu Estuary [P.F.Battley unpublished]) indicates a departure mass of around 175 g. As masses were not corrected for post-capture mass loss (Castro *et al.* 1991; Davidson 1984a), which would affect primarily these large pre-departure catches, actual departure mass is probably higher. If birds lost mass at 1.5%/h (Castro *et al.* 1991; Zwarts *et al.* 1990b), the mean masses could be 8-10 g higher for the large catches. It is probable that 185 g is a more realistic departure mass. By as early as 28 February some birds were in excess of this figure (up to 198 g) indicating that migration was imminent. As the summer (premigratory) catches were not large, mass loss will have been low, and is accounted for by using the basic mass of 115 g.

The rate of mass increase estimated here is 1.24 g per day, equivalent to 1.1% of basic body mass per day. A departure mass of 185 g represents a 'fat' load of 44% if lean mass is 104 g (see discussion: this would be 41% if lean mass is around 109 g, Battley & Piersma MS). Birds at 200 g (recorded on 7 March) must have a 'fat 'load of 45-48%.

Interestingly, both categories of juvenile knots also showed a mass increase during the 'premigratory period', despite the fact that these are assumed to remain in New Zealand over the breeding season (Figure 5.2). Mean mass increased by about ten grams.

Birds staying over the winter in New Zealand are generally assumed to be first-year birds, but a large number of these are apparently 2nd-years. Figures 2-4 also suggest that all three age-classes are present in New Zealand over the winter, with the July catch showing masses of 38 1st-years, 145 2nd-years and 41 3rd-years. For substantial numbers of adults to be staying the winter is surprising. Small numbers of old or sick birds staying might be expected, but the number recorded suggests that the ageing criteria used may be less accurate over the winter than over the summer. They should probably be treated as 2nd-years. However, while there is no difference in mean wing length between the two age-classes in the July catch (t_{216}=1.03, P>0.4), mean mass of supposed 3rd-years is significantly higher (117.73 g cf. 114.13; t_{184}=2.976, P<0.005). This suggests that the ageing criteria do distinguish between different subgroups of birds, but this could possibly be simply heavier birds that have completed a moult that makes them indistinguishable from adults on the basis of plumage. Ageing of birds over winter obviously requires more investigation, and given the uncertainties in this, these data should be regarded with caution.

Some very low masses were recorded; as low as 98 g for 3rd-years (November), 92 and even 80 g for 2nd-years (July and April respectively) and 92 g for 1st-years (February).

DISCUSSION

Determining a lean (ie. fat-free) mass for New Zealand-wintering knots is problematic. A certain amount of fat is retained by waders over the non-breeding period, but the level varies between geographic areas. Furthermore, there is considerable structural variation between the different subspecies of knots (Piersma and Davidson 1992a), and lean (ie. fat-free) mass can vary seasonally within populations (Davidson 1981a).

Waders in South Africa show around 6-7 % fat over the non-breeding season (Summers & Waltner 1978), and if New Zealand knots had similar levels of fat then their lean mass would be around 102 - 107 g. Support for this is provided by Piersma & Barter (1991) who analysed one Australian knot of 117 g which carried 15.4 g of fat, giving a lean mass of 101.6 g.

Barter & Wang (1990) estimated lean mass for north-western Australian knots as 103.2 g, and for south-eastern birds as 108.8 g, using the same method as we did (that is, assuming fat to be 7 % of body mass). It might be surprising for New Zealand knots to have a lower lean mass than Australian birds, given that waders maintain lower lean masses in warmer climates (Barter and Wang 1990; Davidson 1981a; Davidson 1983), especially if lean mass is a function of field metabolic rate (Piersma *et al.* in press). However, Battley & Piersma (MS) performed body composition analysis on 15 knots illegally shot at Great Exhibition Bay, Far North, New Zealand in March 1992 and estimated the lean mass of adults to be 111-113 g. As these birds were depositing protein prior to migration this will overestimate non-breeding lean mass. Lean mass of four juveniles was around 109 g, which is in accord with the Australian estimate, although I have shown here that even juveniles may increase in mass (which could include non-fat tissue). This would indicate that New Zealand birds, while no leaner in the sense of non-fat body mass, may carry relatively low amounts of fat. Body composition analysis of both SE Australian and New Zealand birds would be instructive here. Lean mass of New Zealand knot apparently lies somewhere between 104 and 109 g, though probably nearer the latter.

Barter & Wang (1990) also recorded 12 knots in Shanghai that had recently completed a long-distance flight with a mean body mass of only 87.6 g. How might this discrepancy arise? It is necessary to distinguish between nutrient **stores** and nutrient **reserves** when looking at 'lean' masses. Nutrient stores are strategically deposited in anticipation of a period of shortage, such as before a long-distance flight. In contrast, nutrient reserves are the tissues that a bird can metabolise before it dies of starvation (King & Murphy 1985; Lindström and Piersma 1993; van der Meer & Piersma 1994); these would be used only in emergencies. If a bird ran out of nutrient stores during a flight, it would then have to utilise nutrient reserves, which would lead to a body mass lower than normal 'lean' (ie. fat-free) mass. Hence, the birds with a mass of 87.6 g in Shanghai had probably depleted not only nutrient stores, but also protein reserves. This 88 g estimate should not then be used in the calculation of flight ranges, as it will lead to the overestimation of the level of premigratory deposition (cf. Barter 1992; Tulp *et al.* 1994). While birds obviously have the ability to use their protein reserves, it is only in extreme situations that they will do so. Buxton (1989) caught juvenile knots (*C. c. islandica*) in the Western Isles of Scotland with masses as low as 76 g.

New Zealand birds also were recorded with very low body masses. While some of this could be just structural variation, the extreme low values must surely reflect depleted nutrient reserves, although the reasons for this are not clear. The low 3rd-year value could be the result of recent migration, but the low 2nd and 1st-year birds are probably birds that for some reason have failed to feed successfully over the preceding months. Injury, sickness or parasitism could affect this.

New Zealand knots are apparently quite fat when they depart on migration. However, the rate of mass increase suggested here (1.1% per day) is rather low relative to other studies of waders (Zwarts *et al.* 1990; Table 4) which suggests that our starting date for the estimation of mass increase may be too early. If it were later it would increase departure mass. However, Zwarts *et al.* (1990) listed studies showing rates of mass gain in waders from around the world. The eight cases from the southern hemisphere (two from Australia, six from South Africa) all showed low rates of mass increase, of 1.5 % per day or less. In contrast, only 12 of 34 northern hemisphere cases had rates of increase this low. It is possible, then, that low rates of increase are shown by waders at the southern end of a migration route (note that cases for Mauritania and Kenya also showed low rates) so the estimate for New Zealand knots may be reasonable.

Is the juvenile mass increase adaptive?

1st-year knots showed a small mass increase in the premigratory period. Through using mean mass, the size of some increases is obscured. While the mean mass reached only 122 g, some 1st-years had reached 138-141 g. Six birds aged as 1st-years had masses of between 153 and 170 g. As these were possibly mis-aged they were excluded from the analysis. If these birds are included the mean mass rises to around 127 g in March. Barter et al. (1988) also record 1st-year knots with masses of up to 168 g in Victoria, Australia. Whatever the status of these very heavy birds, it remains that some 1st-years apparently did achieve a considerably higher mass over this period than expected over the summer.

The question arises of whether this increase reflects actual fattening of resident birds at the capture sites, or whether the increase might be migration-related in some fashion. One possibility is that the population could consist of some individuals which were to undergo a northward migration of sorts, and others that would not. This could give rise to an increased mean body mass, with a subsequent decrease as the heavier migrants departed from the local population. Knowledge of movements of Arctic waders within New Zealand is very poor, and we have no evidence for any such movements or lack thereof. We can estimate the potential flight range of juvenile knots based on the mass levels from our catches (but see Zwarts *et al.* 1990b for problems with these) . Using the formula of Davidson (1984b) , which gives moderate estimates, with a lean mass of 104 g, peak mass of 125 g and flight speed of 65 km^{-h}, the estimated flight range is 1440 km. This is inadequate for a trans-Tasman flight, so any movements could only be to Northland, New Zealand (although extremely heavy birds presumably might be able to fly to Australia). Comparison of counts of knots in Northland over eight summer and subsequent winter censuses made by the Ornithological Society of New Zealand shows that Northland has proportionately fewer birds than the rest of New Zealand recorded in the winter census compared with the summer count (Northland mean = 5.6%, s.d. = 6.5, n = 8; rest of New Zealand mean = 9.7%, s.d. = 2.1, n = 8). If birds were moving northward we would expect Northland's proportion to be larger (although this could well be masked by the summer count involving birds still moving southwards within New Zealand). Furthermore, in three of nine winter censuses no birds were recorded and in another two under two hundred were counted. In only two of the eight seasons for which data are available was the proportion of birds present in the winter season compared to the previous summer census higher for Northland than for the rest of New Zealand. There is no suggestion, then, that any juveniles move north in this fashion.

Alternatively, birds with high mass could be birds carrying residual fat having just migrated to the Auckland region. While 1st-years do come to New Zealand from Victoria, Australia, this occurs in October/November (S.J. Davies, pers. comm.). They could possibly have migrated from the South Island. There is no information on movements of arctic waders within New Zealand, but the fact that the increase was synchronous with that of adults argues against this. For juveniles to be migrating northwards within New Zealand prior to the migration of adults is unlikely. The occurrence of apparently similar mass increases elsewhere (below) also argues against this.

The fact that juvenile knots show a mass increase during the premigratory period is surprising, given that these birds remain in New Zealand over the winter (ie. non-breeding season), so do not require nutrients for migratory flight. Mass increase in birds is usually considered to be adaptive (Blem 1990), and mass peaks in early winter followed by a subsequent decrease have been well-documented for European waders (Davidson 1981a; Johnson 1985). This is considered to buffer birds against increased energetic costs and decreased prey availability, when birds are unable to maintain a positive energy balance (although actually *increasing* total energy costs).

The strongest evidence for a temperature- (or climate-) dependent correlate in mass levels comes from dunlin *Calidris alpina* wintering in Britain (Davidson *et al.* 1986; Pienkowski *et al.* 1979). Dunlin wintering in colder areas had a mid-winter peak in body mass, followed by a decrease, while birds in milder areas lacked any increased mass in early winter. There was a significant negative correlation between total body mass and mean December temperature (Pienkowski *et al.* 1979). Much of this difference in fact was due to variation in lean mass (which was also negatively correlated with temperature) rather than fat mass, but the majority of the difference was still due to fat levels (Davidson *et al.* 1986). In New Zealand, conditions are less severe than in Europe. The temperatures experienced in the study areas in Britain were lower than those around the Auckland region in winter (mean January temperatures being generally 3.5° C to 7° C in Britain, mean July temperature in the Firth of Thames being 10.3°C: NZMS undated) . Given that dunlins are much smaller than knots, and their surface to volume ratio consequently larger, we would not necessarily expect the temperatures in New Zealand to cause such mass increases.

Given that depositing nutrient stores actually increases energy demand, their value is probably as insurance against temporary food shortages, such as through tidal flats freezing or remaining covered during storms. The former certainly never happens in northern New Zealand, Knots can feed in fields in winter at the Firth of Thames (pers. obs.), though whether this is forced on them by low prey levels is unknown.

Another possibility is that the mass increase in juvenile birds is not an adaptive response to the environment at all, but is instead an 'involuntary' increase in the premigration period, a 'hormonal byproduct', as it were. That this might be the case is suggested by the fact that the mass increase is totally synchronous with that of adults. Premigratory mass deposition is initiated partly endogenously (Gwinner 1990; Rankin 1991), interacting with daylength (Gwinner 1990). Changes in hormone levels in non-migrant first-year birds have not, to my knowledge, been studied, but the expectation would be that these are much reduced, if present at all. Supporting this is that juvenile *islandica* knots kept in captivity showed a lower mass increase in their first spring than in later ones (Piersma *et al.* 1995). Individual variation in hormone levels could give rise to variation in the degree of fattening experienced. If daylength change is an important factor in premigratory deposition, then perhaps the stimulus is strongest at higher latitudes, where daylength changes are pronounced. The knots in this study were situated at 36-37° south. Only knots further south in New Zealand, in south-eastern Australia and in southern South America occur at higher latitudes in the southern hemisphere.

A subsequent decrease in weights over the winter could then be brought about by decreasing hormonal activity allowing body mass to drop to a seasonally appropriate level. As transport costs increase steeply with mass, any excess mass above requirements will have an energetic cost. That another species at the Firth of Thames which does not migrate at the same time as knots, the Wrybill, shows no such mass increase (S.J.Davies, pers. comm.), supports this explanation.

On balance, it seems likely that the mass increase in juvenile knots does not require an adaptive explanation for increasing winter survival, but may represent a hormonally-induced 'premigratory' increase in non-migrant birds. This could be regarded as non-adaptive, given that it will incur an energetic cost. It is apprently not so maladaptive to be selected against, however, and could even allow for exploratory northward movements along possible future staging sites, although there is no evidence for that within New Zealand (above). Whether heavier birds do fly to Australia remains to be seen.

Comparative data on mass changes from sites in northern and southern New Zealand would be invaluable in assessing the role of nutrient stores during the non-breeding season..

Mass increases in juvenile waders in the premigratory period are not unknown in the literature. Barter et al. (1988) showed that 1st-year knots in Victoria increase in mass in March. Summers & Waltner (1978) showed increases for turnstone *Arenaria interpres,* knot, sanderling *Calidris alba* and terek sandpiper *Tringa terek*, in the southern winter (ie. non-breeding period) and Elliot *et al.* (1976) showed the same for curlew sandpiper *Calidris ferruginea* (all in South Africa). For knots and turnstones this increase happened in April and could have been 'incipient premigratory fattening' (Summers and Waltner 1978), rather than winter fattening as such. Summers et al. (1989) recorded some first-year turnstones in Scotland undergoing premigratory fattening, and assumed that some birds migrated with the adults, but noted that many remain in the wintering area. McNeil et al. (1994) suggested that digenian trematode infestations might play a role in causing delayed moult and fat deposition and be important in causing birds to remain on the non-breeding grounds. However, their hypothesis related to delayed or nonexistent fattening, and the synchronicity of the juvenile mass increase recorded here with that of adults suggests an endogenous cause.

Juvenile mass increases may be more widespread than is realised, but in higher latitudes in the southern hemisphere there will always be the problem of disentangling any environmental effects caused by winter from endogenous effects. Recent developments in the modelling of thermostatic costs of free-living birds (Wiersma and Piersma 1994), combined with detailed ecological studies, mean that accurate assessment of the costs and risks associated with living at different localities is possible. This will allow meaningful conclusions about the adaptive value of behaviours to be made in a quantitative manner.

Chapter 6

Body composition of Knots *Calidris canutus rogersi* from northern New Zealand in the premigratory period

Submitted to *Notornis*

Co-authored with Dr. **Theunis Piersma,** *Netherlands Institute for Sea Research (NIOZ), P.O. Box 59, 1790 AB Den Burg, Texel, The Netherlands*

ABSTRACT The body composition of ten adult and five juvenile Knots *Calidris canutus rogersi* in the premigratory period from Northland, New Zealand, was studied. Basic physical measurements of all individuals are provided. Adults were heavier than juveniles, but showed a large variation in mass - some were at estimated departure mass while others apparently were only in the early stages of mass increase, allowing an investigation of changes during the "fattening" procedure. Changes in fat-free dry tissue (protein) of organs were complicated, with pectoralis and heart muscles increasing with total fat mass, while intestine and stomach mass decreased. This resulted in total fat-free dry tissue firstly increasing with fat mass, then levelling off or decreasing. This reallocation of protein is interpreted as being a method of freeing up muscle protein for redeposition in other organs during premigratory fuelling. Most fat was deposited subcutaneously, apparently in a linear fashion. In contrast, abdominal fat increased in deposition rate while other organs decreased in fat deposition rate over time. Adults were significantly larger than juveniles in ten organ comparisons, but only four of these were clearly migration-related. *Rogersi* subspecies knots are shown to be much smaller than European-wintering *islandica* birds, and slightly smaller than African-wintering *canutus* birds in organ sizes. Curiously, salt gland mass of New Zealand knots is much larger than European birds. Lean mass is estimated at around 109 g.

INTRODUCTION

Long-distance migration, such as that undertaken by Knots *Calidris canutus* is a stressful process. Birds firstly must increase their net energy intake rate prior to departure to deposit enough nutrients for the flight ahead. Once aloft, they may face a flight of possibly 36 to 48 hours, during which no nutrients are ingested. They must manage to maintain protein turnover during this "starvation period" as well as utilise (and not exceed) stored nutrient deposits for fuel.

To evaluate flight ranges it is of crucial importance to know the stores of fat and protein before departure in addition to information on wind speeds and wind patterns.

Shorebirds have long been known to increase mass prior to migration (e.g. Pienkowski *et al.* 1979; Summers and Waltner 1978) . However, not all of this increase is necessarily fat - birds often show substantial protein deposition (Lindström and Piersma 1993; Piersma 1990). There are other possible organ-related changes prior to migration, such as in stomach mass (Piersma *et al.* 1993) , other organs (Piersma *et al.* 1996) and flight muscles (Davidson and Evans 1988; Evans *et al.* 1992).

To study premigratory changes in body composition, one should ideally take regular and random samples over time from a focal population (Lindström and Piersma 1993). Because "one cannot kill a bird twice" (Lindström and Piersma 1993) this would require the deaths of many birds, which we deem to be appropriate only when previous data suggest it would be an informative and fruitful move. Instead, we can be opportunistic with our acquisition and usage of incidental casualties, such as from catching operations (Piersma and Barter 1991). This can give many valuable insights into body composition and premigratory changes.

Lacking independent time-series data, we may be able to approximate this if we assume birds "fatten" along a certain trajectory, from a general starting point (non-breeding "winter" mass) to a certain end point (departure mass). As birds do not all fatten synchronously (there is much variation in the timing of increase), a sample on a single day will encounter birds at different stages of preparation along their individual trajectories (Figure 1). Many migrant wader species moult into breeding plumage before migration, so degree of breeding plumage should also be expected to reflect position along this trajectory (Piersma & Jukema 1993). As long as we assume that different individuals' trajectories follow the same form (inter-individual differences in preparation are small) then a sample on a single day can thus be used to approximate changes over time. This is complicated by the fact that there can be structural variation among individuals

(Piersma & Davidson 1991) which should be accounted for in analyses. If this is done, then the approach outlined above can roughly approximate a "fattening" trajectory for an individual.

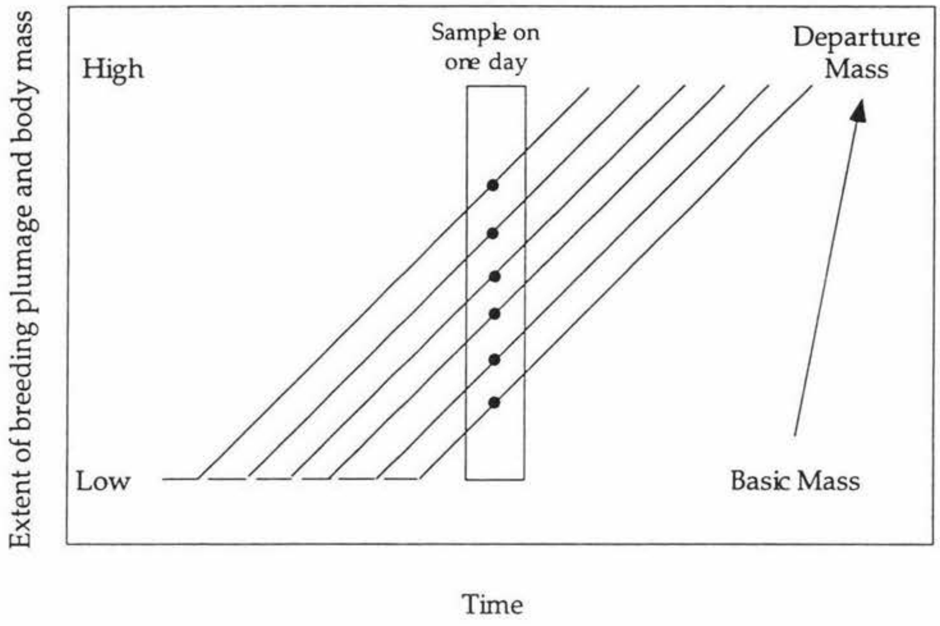


Figure 6.1 Schematic representation of how a sample of birds on a single day can approximate the "fattening" trajectory of a hypothetical individual. Time increases along the x-axis, mass and concomitant degree of breeding plumage along the y-axis. Each individual increases mass and breeding plumage over time. However, they do not initiate this synchronously. As a result, a sample on a single day (vertical box) will encounter birds at different stages along their respective trajectories. A larger fat mass will represent a "later" stage along the time axis. Assuming migratory preparation is similar between individuals, then fat mass and degree of breeding plumage can be used to infer changes over time.

In addition to assessing changes within a population, carcasses also give the opportunity to explore subspecific differences in body composition. Waders often show large differences between populations or subspecies in migration routes and nonbreeding quarters, and there can be large differences in body measurements (Piersma and Davidson 1992a) between these. Also, there is evidence for subtle variations in body composition at the organ level in response to environmental conditions (Piersma *et al.* 1996).

Knots are ideal subjects for studies of body composition and premigratory changes. A classic long-distance migrant, five recognised subspecies winter in fairly discrete regions, and their migration phenologies are reasonably well documented (Piersma and Davidson 1992a). In addition, they have been the focus of much in-depth study into their migration and ecology along the East Atlantic Flyway (eg. Piersma 1994; Piersma *et al.* 1991). Although information on predeparture body composition of knots is available, the *rogersi* subspecies (which occurs in New

Zealand) has smaller dimensions and therefore the published data cannot be used. In New Zealand, knots are the second most abundant Arctic wader, with 40,000 to 65,000 counted annually in Ornithological Society of New Zealand wader surveys since 1983 (P.M. Sagar, pers. comm.). Arriving from September onwards, they depart mainly in March (P.F. Battley, unpubl.).

In this study we take advantage of knot carcasses from northern New Zealand to investigate the body composition of knots in the premigratory period. A small sample size was beyond our control, so our ability to make strong conclusions will be limited. Nevertheless, it is through opportunistic studies such as this that we will begin to fill in the gaps in our knowledge about the physiology of migrant birds.

METHODS

15 dead knots were recovered at Great Exhibition Bay, Northland (173°08' E, 35°45' S), on 7 March 1992, having been illegally shot, probably that day. They had probably been feeding on Houhora Harbour earlier that day (R.J. Pierce, pers. comm.). The birds were confiscated by the Department of Conservation, Whangarei, frozen, and after a successful court case against the poachers were flown to the Netherlands Institute for Sea Research, where the birds were analysed. Birds were weighed, measured (bill, total head length, tarsus + middle toe, wing and wingspan where possible [in some cases this was not possible due to primary moult]), scored for moult, aged (based on wing moult: adult or juvenile), scored for breeding plumage on a scale of 1-7, and then plucked (separating flight [primaries, secondaries, tertials and retrices], back and wing, and underpart and head feathers). The birds were then dissected and sexed. Four measurements on the sternum were made, following Piersma et al. (1984), to determine standard muscle volume, SMV.

The following organs or body parts were separated: pectoralis, supracoracoideus, heart and leg muscles; stomach, intestines kidneys, liver; lungs, saltglands, brain; skin (including half the tibia, the tarsus and the feet) and the "rest". A separate layer of fat (see Summers *et al.* 1992) was also removed from the abdomen. All these were weighed, dried in an oven for three days at 60° C to remove water, then reweighed. They were then packaged in filter paper and fat-extracted in a Soxhlet apparatus using petroleum ether as the solvent. After redrying they were weighed for a final time. From this we could determine the fresh mass, dry mass, fat-free dry mass (FFDM), fat mass and water content of FFDM. Only dry mass was determined for the saltglands.

RESULTS

Structural details of the birds are given in Table 6.1. Birds showed a large variation in body mass, indicating that while some birds were at or near the departure mass of 185 g (Battley, unpublished), others were still in the early stages of fattening. The plumage score of adults was positively correlated with total fat mass (R=0.6585), confirming that our scheme in Figure 1 is valid. Thus, we implicitly treat increases in fat mass of adult birds as approximating changes over time.

Figure 6.2 shows that the large majority of the increase in total body mass was fat, although FFDM appears to increase at a low rate. However, as juveniles were smaller in most organs than adults (see below), this relationship may be misleading. We now treat only adults in our analyses of organ changes.

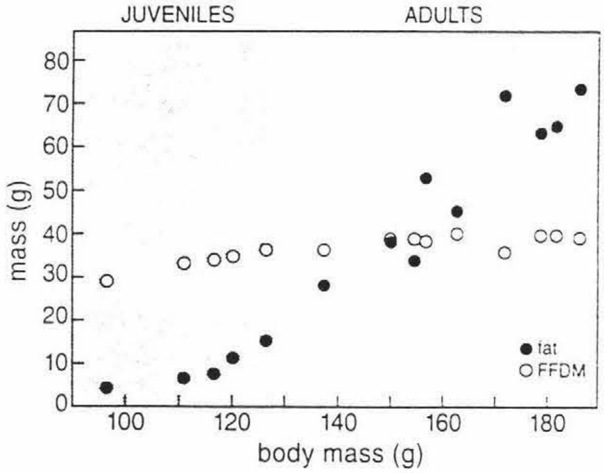


Figure 6.2 Relationship between body mass (x-axis) and total fat mass and total fat-free dry mass (FFDM) on the y-axis. Juveniles (non-migrants) lie to the left of the vertical dotted line. Fat mass symbols are filled dots; FFDM symbols are open diamonds.

Table 6.1 Physical and plumage details of all analysed knots, listed in order of decreasing total body mass. Abbreviations are as follows: ToHe = total head length, Tato = tarsus + mid-toe length, Wing = wing span, SMV = standard muscle volume, plum = plumage, BMlt = body moult, WMlt = wing moult and Mass = total body mass. Units for Bill, ToHe, Tato, Wing is mm; SMV is cm^3; Plum is a scale from no breeding plumage (1) to full breeding plumage (7) (see Zwarts et al. 1990); BMlt score 0 denotes no blood quills in the plumage, 1 denotes light moult with a few blood quills, and 2 medium moult with about 20% of feathers being replaced; WMlt is the sum of moult scores for the ten primaries on one wing where 0 = old, 1 = pin and 5 = new; Mass is grams. As juvenile birds were moulting primary feathers no wing measurements are given.

Mass	Indiv	Sex	Age	Bill	ToHe	Tato	Wing	SMV	Plum	BMlt	WMlt
185.3	1	F	ad	32.9	62.2	58	176	12.19	5	1	0
182.0	2	F	ad	31.4	59.3	59	170	13.95	4	2	0
178.9	3	F	ad	34.1	62.8	59	172	12.45	3	2	0
172.0	4	M	ad	29.8	60.1	57	171	11.98	4	2	0
163.1	5	F	ad	32.0	60.5	56	169	12.40	2	1	0
157.1	6	M	ad	31.6	58.9	58	165	12.28	5	2	0
154.9	7	M	ad	31.2	60.3	56	176	14.69	2	2	0
150.4	8	M	ad	33.1	60.8	58	171	11.96	4	2	0
150.2	9	M	ad	32.0	60.1	59	164	12.48	2	1	0
137.8	10	F	ad	31.8	61.7	57	174	12.81	2	1	0
126.9	11	M	juv	32.8	62.1	57	*	11.91	1	0	29
120.4	12	M	juv	32.4	62.2	58	*	12.65	1	0	12
117.2	13	F	juv	34.8	63.4	60	*	13.16	1	0	49
111.4	14	M	juv	32.9	61.4	60	*	11.45	1	0	49
96.9	15	M	juv	30.5	58.9	57	*	12.65	1	0	41
147.0	Mean			32.2	61.0	57.9	170.8	12.62			
(27.6)	(stdev)			(1.29)	(1.4)	(1.3)	(4.1)	(8.73)			

To assess whether body part and organ masses in adults related to the structural "size" of the birds or reflected migration-related changes, total fat mass and total FFDM were correlated against all analysed components, and three structural measures (Table 6.2). Total FFDM largely reflects the birds' "size", with bill length (which is often taken as a measure of size in wild birds) giving the only structural correlation (but as its explained variance was low (39.9%) we have not corrected organ FFDMs for this). In contrast, fat mass was very strongly correlated with total body mass, strengthening our contention that fat mass can be used to assess migrational changes.While many parts showed no significant correlations with either fat mass or FFDM, those that did so are unambiguous: four organs showed significant migration-related changes, with pectoralis and heart muscles increasing in mass, while stomach and intestine decreased (these directional changes are also mirrored in supracoracoideus, liver and kidney); FFDM only significantly correlated with one organ, the kidneys.

The large majority of fat was deposited under the skin (Figure 6.3). Figure 6.3 shows that this fat was apparently deposited at a uniform rate throughout the fattening period. In contrast, abdominal fat (which accounted for a much smaller proportion of total fat) was not deposited linearly, but showed an accelerated rate of increase at higher total fat masses (Fig. 6.3). The leanest juveniles possessed no abdominal fat at all. The plots of intestinal and other organ fat masses indicate that this fat may 'level out' in its deposition rate as the birds get heavier.

It is now recognised that birds may deposit protein (reflected in FFDM levels) in addition to fat. The lack of a significant correlation between FFDM and fat mass in this sample would suggest this is not occurring, yet we have also shown that heart and pectoral muscles do increase in mass. Why this discrepancy? Figure 6.4 plots total FFDM against total fat mass for all individuals; FFDM seems to increase and then decrease in adults. What component organs give rise to this pattern?

Table 6.2 Correlations of body mass, fat mass, total FFDM, FFDM of all body parts and three structural measures, with fat mass and total FFDM for adult knots (n=10). Abbreviations as follows: Pect (pectoralis muscles), Supra (supracoracoideus muscles), Intest (intestines), FlightF (flight feathers), ContourF (contour feathers), ToHead (total head length), Tato (tarsus + mid-toe length). Figures given are correlation coefficient r. Significance is denoted by asterisks, with * ($P < 0.05$), ** ($P < 0.01$), *** ($P < 0.001$). Asterisks in brackets denote significance marginally less than the given level.

	BodyM	Fat	FFDM	Pect	Supra	Leg	Heart	Stomach	Intest	Liver	Kidneys
Fat	0.923^{***}	-	0.482	0.799^{***}	0.509	0.049	0.715^{*}	-0.704^{*}	-0.772^{**}	-0.312	-0.153
FFDM	0.377	0.482	-	0.435	0.321	0.278	0.171	0.323	0.373	0.507	$0.723^{(**)}$

	Lungs	Abdom	Brain	FlightF	ContourF	Skin	Rest	Saltglands	Bill	ToHead	TaTo
Fat	0.039	0.173	0.005	0.228	0.390	0.276	0.312	0.355	-0.054	0.337	0.083
FFDM	0.564	0.167	-0.025	0.162	0.400	0.118	0.482	-0.542	0.632^{*}	0.274	0.084

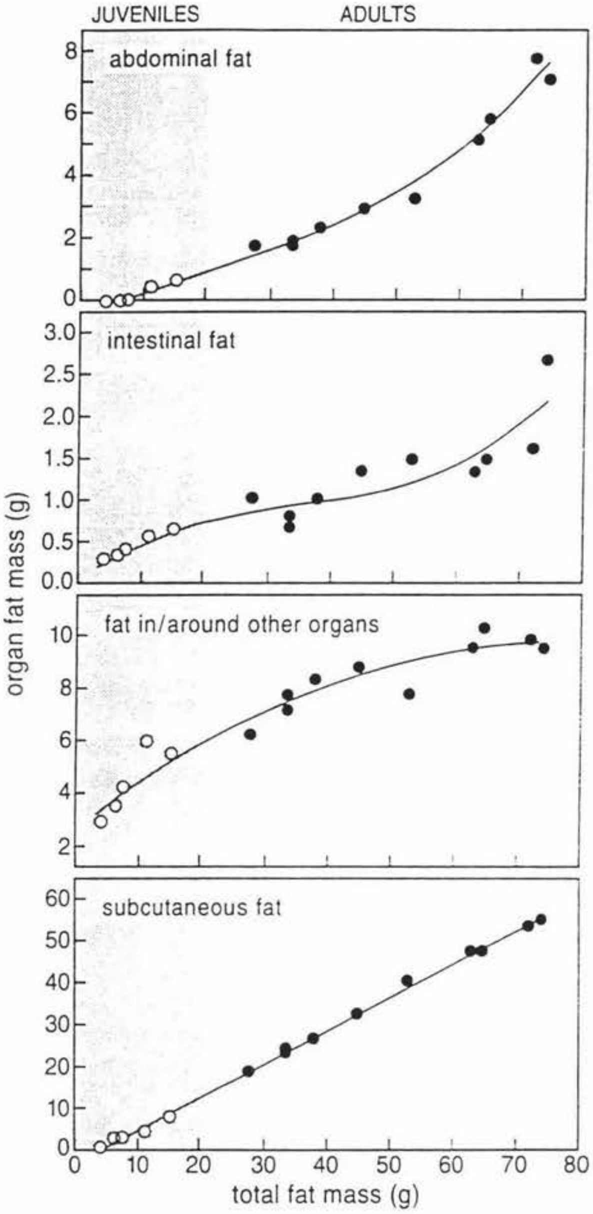


Figure 6.3 Relationship between the four components of total fat mass, and total fat mass. Juveniles have less than 20 g fat. Fitted lines are distance-weighted least squares smoothing curves.

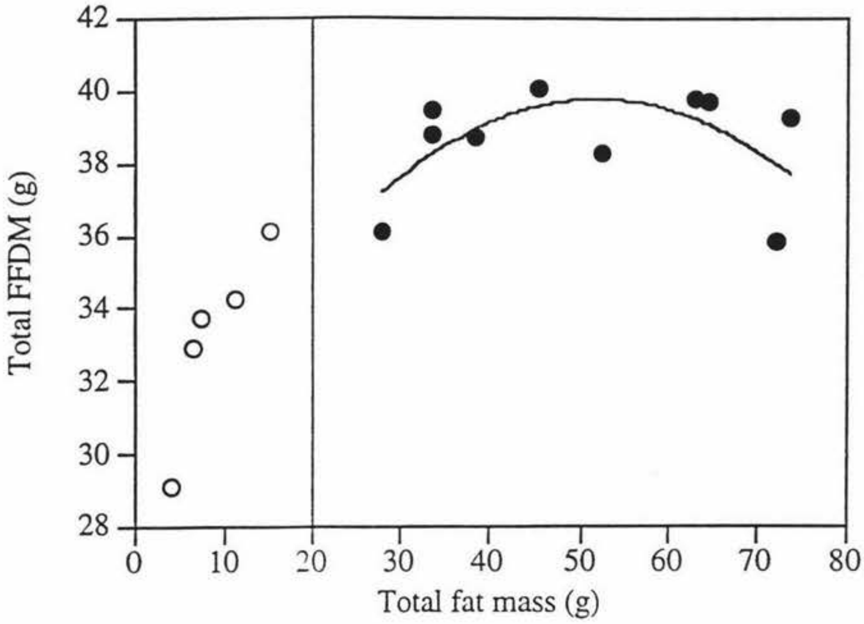


Figure 6.4 Total FFDM plotted against fat mass. Juveniles have less than 20 g fat.A polynomial regression describes the adult relationship ($Y = 27.804 + 0.4612*X - 0.0044404*X^2$, $R = 0.57$).

Figure 6.5 gives the plots of organ FFDM against total fat mass, grouped into three categories - muscles (pectoralis, supracoracoideus, leg and heart), nutritional organs (stomach, intestine, liver and kidneys) and "rest" (lungs, skin, rest). We can see that all muscle groups increase in mass, possibly levelling out at around 50 g fat. In contrast, nutritional organs decrease over the same fat masses, resulting in a levelling off or net loss of protein at higher fat masses (Figure 6.4).

Given the complex inter-relationships between FFDM of organs, and lacking the size and independence of samples to accurately estimate protein deposition (see Lindström and Piersma 1993) we will only coarsely estimate lean mass. We distinguish three groups of birds: juveniles showing no breeding plumage and little total fat (4-15 g; individuals 11-15), adults in the early to mid-stages of migratory preparation with 20-60 g fat (individuals 5-10), and adults in the late stages of preparation, with over 60 g of fat (individuals 1-4). The mean lean masses (total mass minus fat mass) were as follows: juvenile 105.8 g (sd 7.6, n=5), light adult 113.7 g (sd 6.2, n=6) and heavy adult 111.1 g (sd 7.9, n=4). One juvenile was extremely light (total mass 96.9 g; lean mass 92.9 g). If this is removed, mean juvenile mass becomes 109.2 g (sd 2.86, n=4).

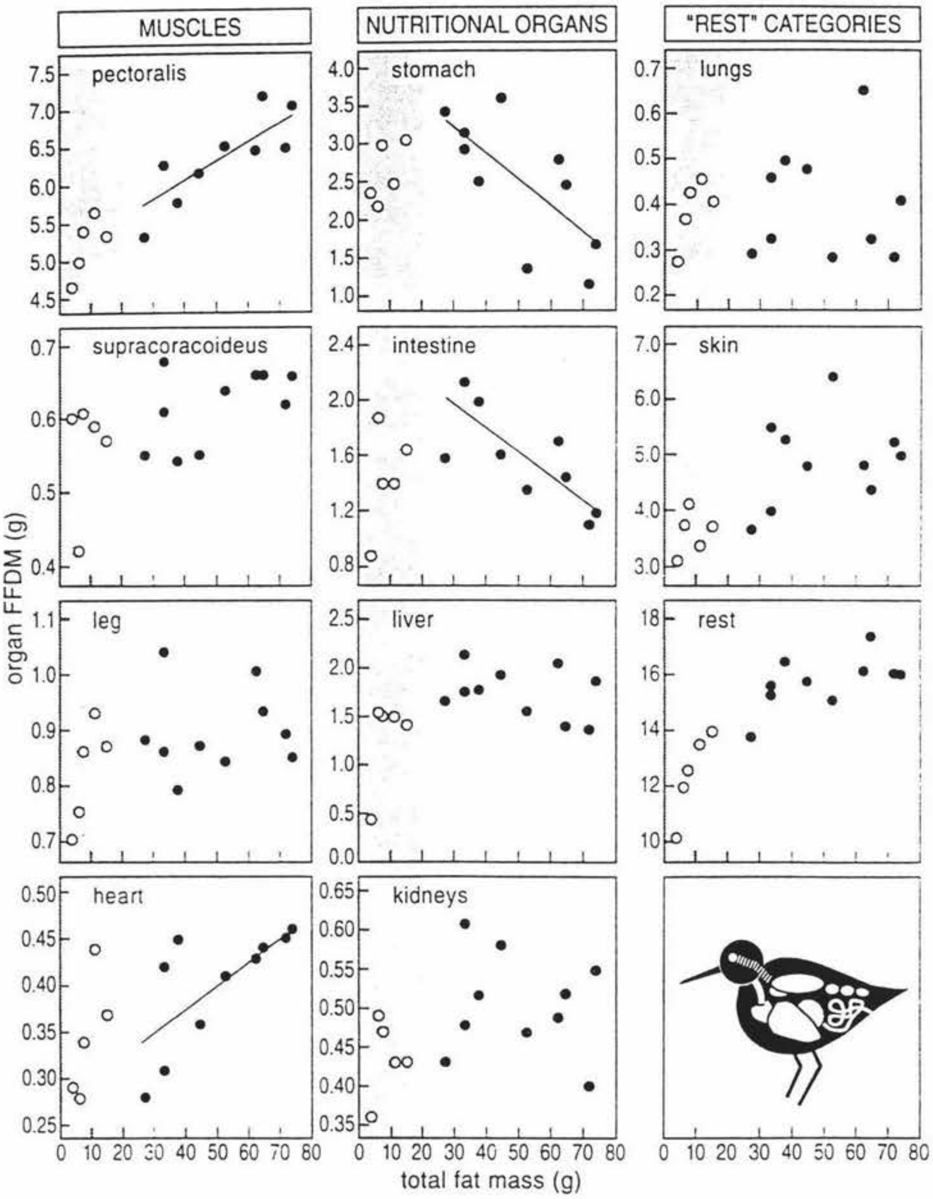


Figure 6.5 Organ FFDM plotted against total fat mass. Juveniles have less than 20 g fat. Significant ($P<0.05$) relationships have fitted regressions.

Table 6.3 Comparison of body part masses for adult and juvenile knots. Unless stated, n = 10 for adults and n = 5 for juveniles. Results of t-tests for difference between means are given in the right two columns. DF = 13 unless stated. Significant values are given in bold. Percentage breakdown of components of total FFDM are given. Water % is the percentage water of fat-free mass, ie. total lean mass = $\text{FFDM}/(1-\frac{\text{Water \%}}{100})$

	Adult			Juvenile				
	Mean Mass	SD	%	Mean Mass	SD	%	T-value	P
Body M	163.7	15.8		114.56	11.35		6.09	**0.0000**
Fat	50.49	17.0		8.74	4.34		5.28	**0.0001**
FFDM	38.60	1.48		33.24	2.58		5.18	**0.0002**
Water %	0.6568	0.0136		0.6858	0.00572		-4.51	**0.0006**
Pect	6.315	0.538	16.36	5.194	0.387	15.62	4.13	**0.0012**
Supra	0.6170	0.0527	1.60	0.5580	0.0785	1.68	1.74	0.11
Leg	0.8960	0.0772	2.32	0.8220	0.0942	2.47	1.63	0.13
Heart	0.4010	0.0630	1.04	0.3440	0.0650	1.04	1.64	0.13
Stomach	2.482	0.861	6.43	2.602	0.396	7.83	-0.29	0.77
Intestine	1.622	0.391	4.20	1.434	0.363	4.31	0.90	0.39
Liver	1.741	0.259	4.51	1.264	0.468	3.80	2.58	**0.023**
Kidneys	0.5050	0.0649	1.31	0.4360	0.0498	1.31	2.08	0.058
Abdom	0.0710	0.0367	0.18	0.0140	0.0195	0.04	3.22	**0.0068**
Lungs	0.439	0.144	1.14	0.4240	0.0847	1.28	0.21	0.84
Brain	0.1033	0.0229	0.27	0.09250	0.00957	0.28	0.89	0.39 (a)
Skin	4.895	0.782	12.39	3.616	0.372	10.88	3.42	**0.0045**
Rest	10.959	0.410	28.39	10.294	0.551	30.97	2.65	**0.020**
FlightF	1.620	0.161	4.20	1.304	0.117	3.92	3.88	**0.0019**
ContourF	5.903	0.441	15.29	5.116	0.559	15.39	2.99	**0.010**
Saltglands	0.0977	0.0146		0.0974	0.0215		0.03	0.98 (b)

a. DF = 11. N = 9 for adults and 4 for juveniles
b. DF = 12. N = 10 for adults and 4 for juveniles

Mass of body parts for adult and juvenile knots is given in Table 6.3. In ten of the eleven comparisons with significant differences, adults had the greater mass. In the final significant result (percentage water) the level for juveniles was higher.

DISCUSSION

Zwarts et al. (1990b) suggested that plumage score of birds might be able to be used to estimate degree of preparation for migration, but noted that it is likely to give underestimates of departure mass. They treated birds as ready to take off when they completed or suspended their body moult. Our data show a positive correlation between adult plumage score and fat mass. However, Table 1 shows that there is much variation present. One bird had reached a plumage score of 5 while having a body mass of only 157.1 g, while another bird had reached 178.9 g with a plumage score of only 3. There was also no clear trend in the body moult scores for adults. So while plumage certainly does on average increase with migratory preparation, its value as a quantitative tool based on small samples seems limited.

The knots shot in Northland were highly varied in their preparation for migration. The heaviest birds were probably very near to migrating (knots were observed departing from Farewell Spit, NW Nelson, from 8-27 March: Battley MS), while the light adults were presumably only in the early stages of premigratory preparation. As such, we are lucky to have an even spread of masses for comparison. It is remarkable, given the small sample size, how strong some of the relationships were between body parts.

Most of the mass deposited by these birds was fat, but protein was also being deposited in muscle tissue, with pectoralis muscles (used for flight) increasing with fat mass (supracoracoideus muscles, also used for flight, increased but non-significantly [P=0.133]). Some organs were also involved, with heart mass increasing with fat mass.

This indicates that the long non-stop flights undertaken by shorebirds such as knots require a certain level of preparation. Flight is an energetically demanding activity, with costs generally estimated at around 12 X basal metabolic rate (BMR: the level of energy expediture for a resting animal in the thermoneutral zone: see Castro & Myers 1988). Increased heart mass may allow for a prolonged raised heart rate and pumping of thicker blood (Piersma *et al.* MS-a), while an increase in flight muscles may be needed for the actual flight itself. However, Davidson & Evans (1988) calculated that the variation in breast muscles, and their usage during long-distance flight, by knots was less than predicted by aerodynamic theory. This meant that substantial protein stores would be retained onto the breeding grounds, for use either as protection against inclement weather or for deposition in eggs.

The predicted mass increase of pectoralis muscles (from the regression of pectoralis mass on fat mass: pectoralis = 5.05 +0.0251 fat mass) with an increase in body mass from 115 g to 185 g (representing an increase from 1.9 g to 71.9 g fat (where fat mass = -113 + 0.999 body mass); premigratory and departures masses, Chapter 5) is 34%. This is similar to the increase shown by Dunlin *Calidris alpina* captured on their wintering grounds in England and prior to departing on the final leg of their migration to the breeding grounds (30%: Davidson and Evans 1988). Knots in New Zealand are probably at least three flights away from their Siberian breeding grounds, yet are apparently storing as much protein in breast muscles as waders about to depart on the final leg of a migration. The first period of nutrient storage for a long-distance migrant will be the least time-stressed of any, so it may be advantageous to store protein then rather than later. Alternatively, flight costs could be greater from New Zealand than from Europe so larger protein stores might be required during the flight. However, the exponent of the relationship between pectoralis mass and body mass (0.59) was similar to that of knots in Norway prior to departure (0.64), which suggests that preparation for these flights is similar (Davidson and Evans 1988).

Nutritional organs, however, may decrease in mass before migrating. As birds will not be feeding during a flight, any protein may best be stored in a usable form, such as in muscle tissue elsewhere in the body. But for a mollusc-eating bird such as the knot (see eg. Piersma *et al.* 1994d; Zwarts and Blomert 1992) a big stomach is probably a prerequisite for processing large amounts of hard food. It is tempting to suggest, then, that stomach mass in knots might increase in size from a low level held by juveniles to a higher level by adults while increasing mass, but then, once a certain mass is reached (one within which departure mass is readily achievable), decrease quickly before migrating (see Figure 6.4). This would free protein to be incorporated into other organs in preparation for migration: Figure 6.5 shows that stomach and intestine FFDM drops at 35-35 g fat mass, parallelled by increases in pectoralis and supracoracoideus muscles, and heart mass. If knots do atrophy their stomachs prior to migrating, we have to assume that the benefits of flying with a reduced stomach mass are greater than the costs of arriving at a new location with a small one.

Wiersma & Piersma (Wiersma & Piersma 1995) show that abdominal fat mass in islandica and canutus knots correlated well with fat mass (r = 0.88) and body mass (r = 0.81). Their data consisted primarily of birds held in captivity, with only 6 freshly-wild birds. Our data show much less scatter, and the plot of abdominal fat mass on total fat mass clearly shows an increase in relative fat content at high masses, which is not apparent from the equivalent plot (Figure 2B) in Wiersma & Piersma (1995). However, their data points for wild birds (which had high fat masses) do show show a steeper slope than the general relationship for captive ones. It is possible, therefore, that this "last-minute" filling of the abdominal cavity might be a feature of wild birds that is not shown in captive birds. As transport costs increase with mass, and captive birds will have a much lower level of activity, then they could well sustain a higher mass earlier on without any adverse effects.

Eleven significant differences were found between adults and juveniles. At least three of the differences (body mass, fat mass, pectoralis mass) were probably due to migratory preparation. FFDM was also lower in juveniles. This may be partially migration-related, with adults initially increasing FFDM tissue levels, but juveniles may also have not yet achieved an adult body size: a sample from mid-summer would determine this. Differences in feather masses may have partially arisen from moult (juveniles were in primary moult so were lacking a few quite major feathers), although Piersma & Barter (1991) showed similar differences in contour feathers of two adult and two juvenile Great Knots *Calidris tenuirostris*.

These data confirm *rogersi* knots to be small in comparison with the European-wintering *islandica* subspecies, both in linear measurements and also most internal organs (c.f. Piersma *et al.* 1996). They are much more similar to the tropical African-wintering *canutus* subspecies (c.f. Piersma *et al.* 1996 but note that these birds were not premigratory individuals). This accords with the explanation that organ size reflects energetic requirements - the milder the conditions experienced, the less a bird requires large organs to allow a high level of energy expenditure for survival (as in a European winter). That *rogersi* tend overall to be even smaller than *canutus*, however, suggests that other factors in addition have been important in shaping the size of New Zealand-wintering knots.

One curious result from this analysis is that *rogersi*'s salt glands are very large. The mean fresh saltgland mass in a sample of ten wild-caught knots from Europe (subspecies *islandica*) was around 180 mg (range 110-230: Fig 30, p.131 in Piersma 1994). Estimating fresh mass of our *rogersi* birds, assuming a 75% water content (so fresh mass = 97.7*4), suggests a fresh mass of around 390 mg, over twice the size of their conspecifics'.

Two possible explanations for this would be that the birds from Northland were either feeding on hypersaline food or were suffering from heat stress and needing to drink frequently to maintain water balance. Neither of these seems particularly likely: remains of the bivalve *Nucula hartvigiana* were found in their stomachs which is not expected to be any more hypersaline than any other bivalves around the world on which knots feed, and temperatures in Northland are cooler than in Africa, where canutus knots winter. However, the negative correlation between salt gland mass and total FFDM (r=0.-0.542, P=0.106) suggests that this is not related to body size as such, and so could be migration-related (indeed, the *rogersi* sample consisted of birds preparing for migration, whereas the measured saltglands of the European birds were sampled in the non-breeding season before premigratory preparation). However, the variation in saltgland mass in our sample is such that no clear pattern or explanation is obvious.Nevertheless, two other organs are larger in rogersi than in *islandica* and *canutus* - kidneys and liver. This suggests that for some reason the salt-processing capability of *rogersi* knots from Northland needs to be large.

Lean mass of knots around Auckland was estimated (Chapter 5) to be around 104 g (based on weights of live birds and assuming a 7% fat content). This is much lower than the lean masses derived for these birds, except for the juveniles. That adults were higher is not unexpected as they were depositing FFDM as well as fat. However, the mean mass of the four larger juveniles was over 5 g more than the estimate above. This suggests that New Zealand knots may carry less fat than assumed over the non-breeding season. Only a sample of knots in the middle of summer (ie. pre-deposition) will clarify this. The 7% figure was based on waders in South Africa (Summers and Waltner 1978); why waders in New Zealand might carry less fat is not intuitively obvious.

Chapter seven

The northward migration of arctic waders in New Zealand: departure behaviour, timing and possible migration routes of Red Knots and Bar-tailed Godwits from Farewell Spit, North-West Nelson

Submitted to *Emu* for publication

Summary The departure behaviour of northward migrating Bar-tailed Godwits and Red Knots was studied on Farewell Spit, New Zealand, from 8 to 27 March 1994. Most flocks left in the evening and on rising tides. An exception occurred when waders responded to weather conditions favourable for migration, having had their departure suppressed by strong winds for the previous five days. On average, flocks left with a slight tailwind, although some left with headwinds of up to 12 km h^{-1}. Most departures occurred after the passage of a low-pressure system or at the approach of a high-pressure system, which produced favourable southerly winds. Despite observed departure directions being intermediate between those expected for flights to either northern Australia or northern New Zealand, most flocks probably encountered easterly winds from high-pressure systems and flew to Australia with some wind assistance. Varied assumptions of flight speed and the level of protein deposition show that flight range estimates can differ so widely that predicting migration routes is difficult.

INTRODUCTION

Migrations of waders (Charadrii) have been the subject of much study over the past thirty years. Most information has come from the East Atlantic and the Western Hemisphere Flyways, but there are few comparative data from other major flyways, such as that of the East Asia/Australasian.

The East Asian/Australasian Flyway extends from western Alaska and eastern Siberia at the northern extreme, down the Asian coast and through South East Asia to Australasia in the south. An estimated 4-6 million waders use this flyway in their annual migrations (Parish *et al.* 1987). New Zealand is situated at the southernmost extent of this flyway, and some 120-140,000 Arctic-breeding waders spend the non-breeding season there (P.M. Sagar, pers. comm.). These are primarily Red Knots *Calidris canutus rogersi* (40,000 to 65,000; P.M. Sagar, pers. comm.) and Bar-tailed Godwits *Limosa lapponica* (80,000 to 100,000). Of the five subspecies of knot currently recognised (Roselaar 1983; Tomkovich 1992) *C. c. rogersi* is one of the most poorly known (Davidson & Piersma 1992).

The Ornithological Society of New Zealand has conducted biannual counts throughout coastal New Zealand from 1983-1994, so that knowledge of the distribution of coastal waders in New Zealand is now very good. Information on movements within the country is, however, lacking. Likewise, information about movements between New Zealand and Australia is limited, although leg-flagging is proving very successful (Riegen 1995). From this we know that many knots pass through Victoria on the southward migration to New Zealand, but not on the return journey north: New Zealand knots are presumed to fly directly to northern Australia (A.C. Riegen, pers. comm.). Irregular counts over the past 25 years from the Far North of New Zealand (published in annual Classified Summarised Notes in *Notornis)* suggest waders may reach large numbers before departing on the northward migration. This raises the question of whether birds from the South Island as well as the North Island use the Far North prior to crossing the Tasman Sea.

Farewell Spit is situated at the north-west corner of the South Island and in summer holds large populations of Arctic waders. Birds there have two options - fly directly to Australia; or fly to northern New Zealand, refuel, and then cross the Tasman Sea. Potential flights would be in the order of 900 km (Northland, New Zealand), 2500 km (east coast, Australia) or up to 3900 km (Gulf of Carpentaria, northern Australia). In general an initial heading should not be extrapolated to indicate probable area of destination (Piersma *et al.* 1990b). Farewell Spit is, however, perhaps the one place in New Zealand where such inference is feasible. Being south-west of the North Island, the direction taken by waders leaving Farewell Spit might allow predictions about the destination. Given data on departure directions and potential flight ranges (based on body mass and nutrient stores at departure) possible migration routes could be constructed (e.g. Tulp *et al.* 1994).

This paper examines the departure behaviour of migrating waders, a field which has been fruitfully studied in the northern hemisphere (e.g. Alerstam *et al.* 1990; Lank 1989; Piersma *et al.* 1990a; Piersma *et al.* 1990b). The aim is to combine observed departure directions with information on contemporary weather systems to detect whether waders on Farewell Spit migrate directly to Australia. Using data on mass change in knots from northern New Zealand (P.F. Battley & T. Piersma, unpubl. data), potential flight ranges of knots are calculated under a variety of constraints (too few data exist to allow this approach for godwits), and the migration strategy of New Zealand-wintering knots is discussed.

METHODS

Observations of migrating arctic waders were made from near the tip of Farewell Spit, Golden Bay, New Zealand (40°33´S, 173°01´E) (Fig. 7.1) during March 1994. Intensive watches were made from small knolls (c.3 m high) overlooking tidal flats for around three hours before dusk each night, the time when most flocks are likely to depart (Lank 1989; Piersma *et al.* 1990b). However, I was in the field over much of the day (Fig. 3b) and the departures of only a few flocks are likely to have been missed. An area of up to 10 km^2 at low tide was scanned with 10X40 binoculars and flocks were followed with a 25X60 telescope. Any migration activity was noted whenever I was on the sandflats during the rest of the day.

When a flock of departing waders was observed the following details were noted: species, number of birds, time, flock flight formation (after Piersma *et al.* 1990b : bunch, cluster, vee and echelon, and transitions between these), whether the sun was visible and whether flocks were vocalising. Whenever possible the flight direction of migrating flocks was determined by compass. If a flock passed more than about 300 m away, no direction was recorded to avoid substantial parallax problems.

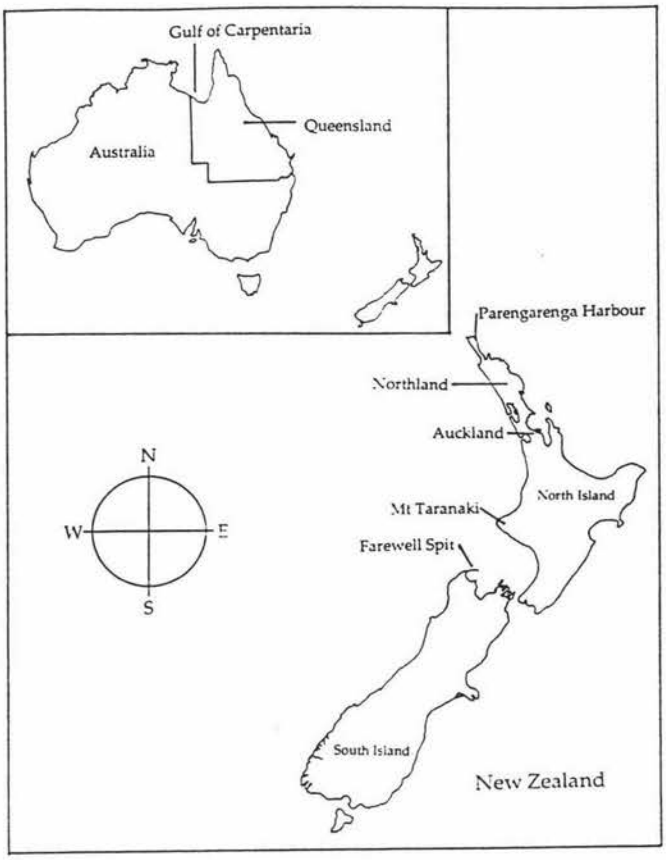


Figure 7.1 Map of localities in Australasia mentioned in the text.

When departing flocks were observed, an estimate of wind speed in 5-knot intervals was made (based upon regular reading of the anemometer at the Farewell Spit lighthouse over the previous four months). Wind speed usually varied little throughout the course of an evening, and the anemometer on the lighthouse was normally checked both before and after an evening watch. In addition, wind direction was noted in one-eighth compass directions (e.g. NW, W, SW etc.). With the wind speed and direction, and bird speed (assumed to be 65 km h^{-1} although when climbing this may be expected to be lower) and direction known, the wind effect can be calculated. The formula for calculating the wind effect (from Piersma & Jukema 1990) is:

$$\Delta W = W \cdot \cos a + \{A^2 - (W \cdot \sin a)^2\}^{0.5} - A$$

where W is the wind speed (km h^{-1}); a is the angular difference between the track (*t*, departure direction of birds) and the wind direction (w), so $a = w \pm 180° - t$.; and A is the bird's air speed (taken as 65 km h^{-1}). A positive wind vector is referred to as a tail-wind, and a negative vector a headwind.

A generalised synoptic weather map was used to plot where departures occurred relative to major weather systems at that time. This approach has been successfully used in the northern hemisphere for migrating waders (e.g. Lank 1983; Richardson 1979). This gives a static frame of three pressure systems and associated fronts, and wind directions. My map is a reversal (for southern hemisphere conditions) of the one used by Richardson (1979) and Lank (1983). In these maps, the land moves relative to fixed weather systems, rather than the other way around. This allows an aggregate picture to be formed of the way in which birds respond to large-scale weather conditions (in contrast to local conditions detailed above). Daily weather maps were taken from the Dominion newspaper, March 1994. The position of the NW South Island relative to the generalised weather systems was estimated from these maps and actual conditions at departure .

In addition to computing the standard arithmetic mean flock size ($\sum x/n$), the mean flock size as experienced by the average bird ($\sum x^2/\sum x$) was also calculated. In effect, this method weights the flocks according to their size, so the number of birds experiencing a given flock size is accounted for in the analysis (Piersma *et al.* 1990b).

Potential flight range estimates for New Zealand knots were calculated using four predictive methods: Summers & Waltner (1978), Davidson (1984b), Castro & Myers (1989) and Pennycuick (1989). Many studies of waders have assumed a flight speed of 75 km h^{-1} (e.g. Barter and Wang 1990; Castro and Myers 1989; Thomas 1987), while others suggest this may be too high (Alerstam *et al.* 1990; Gudmundsson 1993; Zwarts *et al.* 1990b). Therefore, speeds of 75 km h^{-1} and 65 km h^{-1} were used (except for Pennycuick's method, which calculates its own maximum range flight speed). Much of the premigratory mass increase in birds can consist of protein, while equations treat it as being solely fat (Lindström and Piersma 1993; Piersma 1990). Protein provides only one eighth the energy of fat (Piersma and Jukema 1990), so these estimates need to be devalued accordingly. It is probable that both supplies of protein and fat in the bird oscillate in tandem, with protein becoming exhausted as well as fat (T. Piersma, pers. comm.). For the purpose of this analysis I regarded protein as being used constantly through the flight, and not kept in store until fat reserves run out. This does not affect the pattern of weight loss assumed in the above methods. Assuming that only 70% of the increase is due to fat, and 30% to protein, the energetic 'worth' of the reserve becomes 70% of (fat) reserve times 100% energy, plus 30% of (protein) reserve times 12.5% energy, giving a factor of 0.7375, which is then multiplied by the original flight range estimate. Calculations for protein levels of 0.3, 0.2 and 0.1 have been calculated in this fashion for knots. A lean mass was taken as 109 g, and departure mass as 185 g (P.F. Battley & T. Piersma, unpubl. data).

Circular statistics follow Batschelet (1981).

RESULTS

Premigratory and migratory behaviour

Conspicuous 'premigratory' flights were largely lacking. The first evidence of premigratory restlessness was shown by thirteen birds on 5 March. These flew eastward over the tidal flats parallel to the land for about 4 km, slowly gaining height, before turning around, flying westward and returning to ground, having flown at least 8-9 km in five minutes. Most departing flocks were located after they had flown from distant tidal flats: only six actual lift-offs or pre-flight behaviours were noted. Birds involved in one of the first flock of knots to depart, 25 birds on 8 March, were conspicuous on the ground beforehand. In a flock of 990 roosting birds facing into the wind, about 26 birds in very strong breeding plumage walked through the flock, calling. These calls were mainly a characteristic clear 'huit-huit-huit', but also included a low chucking, which can also be heard from feeding birds (pers. obs.). There was also a 'ke-ke-ke', on the same note. Over the next hour several groups (of 43, 44, 6, 8, 5, 4 and 6) flew away from the main flock, calling as they went, but settled again 200 m away and were not seen to migrate before dark. Eventually, a flock of 28 birds flew, 3 birds returned to the ground after two minutes, but the rest migrated. The breakaway groups began feeding, despite the high tide, and eventually all but 160 knots were feeding. This unusual high-tide feeding may have been induced by premigratory restlessness, by disturbance by an Arctic skua *Stercorarius parasiticus* (feeding is often a displacement activity for disturbed roosting waders: pers. obs.), or by a neap tide that left some feeding habitat still exposed. Equally conspicuous behaviour was shown by godwits on 19 March, with small groups of noisy birds taking small flights away from a roosting flock, and then not dispersing out to the tidal flats as they became exposed. Eventually only the separated non-feeding flock was left near the shore, and they departed soon after.

A total of 42 separate flocks of wader (15 knot, 27 godwit) was recorded, totalling 1581 birds (491 knot, 1090 godwit). All but two flocks were monospecific, the exceptions being 3 knots each time flying with flocks of 27 and 48 godwits respetively (for analysis the knots in these flocks have been ignored). Flock characteristics are given in Table 7.1. Godwit flocks ranged from 8 to 110 birds, knots from 13 to 75, but the difference in mean flock size (arithmetic) was not significant (t_{38}=1.16).

Table 7.1 Flock sizes, vocalisation and presence of visible sun at departures for knot and godwit, at Farewell Spit, March 1994. Arithmetic mean flock size is $\sum x/n$, while the average bird flock size is $\sum x^2/x$, where x is flock size.

	Flock size:	Flock size:	Vocals			Sun	
	arithmetic mean	average bird	Yes	No	?	Yes	No
Knot	33.7	40.3	15	0	-	7	8
Godwit	40.4	53.0	16	2	9	10	17

Most flocks of knots and godwits were recorded vocalising (Table 7.1). A visible sun was clearly not required for migration (Table 7.1).

Many flocks appeared to require some time to settle on their departure direction, and would proceed in a series of small zigzags, similar to behaviour noted for knots elsewhere (Swennen 1992). Flock structure also changed during the first few minutes of flight, with flocks tending to 'evolve' to an echelon or vee (Table 7.2). There is also the suggestion from Table 2 that godwits achieved an ordered flock formation sooner than knots. This could have resulted, though, from godwits leaving mainly from the tideline, whereas knots were often spread over the tidal flats.

Table 7.2 Departing flock formation and changes in knots and godwits at Farewell Spit, March 1994. Categorisation of flocks follows Piersma *et al.* (1990a). A cluster was a group of birds with no obvious flock structure; a vee was formed by two lines of birds trailing a single leader; while an echelon was a straight line of birds. (The latter two were not always distinguishable.)

	cluster	cluster-vee/ech	vee	vee-ech	echelon	cl-vee-ech
Knot	4	9	2	-	-	-
Godwit	-	12	9	4	1	2

Patterns of departures

The daily pattern of observed departures is shown in Fig. 7.2. While the last recorded departing flocks were on 27 March, there still remained small numbers of knots in breeding plumage, which suggests that they were going to migrate that season (Zwarts *et al.* 1990b). However, as many of these birds were still present after the first week in April, it is possible that these birds remained on the spit, or at least in New Zealand. Barter *et al.* (1988) showed that many first-year knots enter breeding plumage. However, the knots recorded by Barter *et al.* (1988) reached only weak breeding plumage, in contrast with the knots in this study which were in virtually full breeding plumage. Second-year birds are likely to be more strongly plumaged than first-years, and it appears that many second-year birds do remain in New Zealand over the southern winter (P.F.Battley , unpubl. data). It is possible that these strongly-plumaged birds were second-years, or even adults. The lack of departures from 14 to 18 March was probably owing to constant strong headwinds over that period (see below).

Most flocks departed in the evening (Fig. 7.3a), with the majority of flocks departing on a rising tide (Fig. 7.4). There is the suggestion of a bimodal pattern, with peaks around mid-tide on both rising and falling tides. However, on 19 March (following the period with no departures) 9 out of 10 flocks departed in the evening during the falling tide. Because their departure had been delayed by the weather (see below) the falling tide probably had no influence on their departure. If these flocks are omitted from the analysis, the influence of a rising tide becomes stronger.

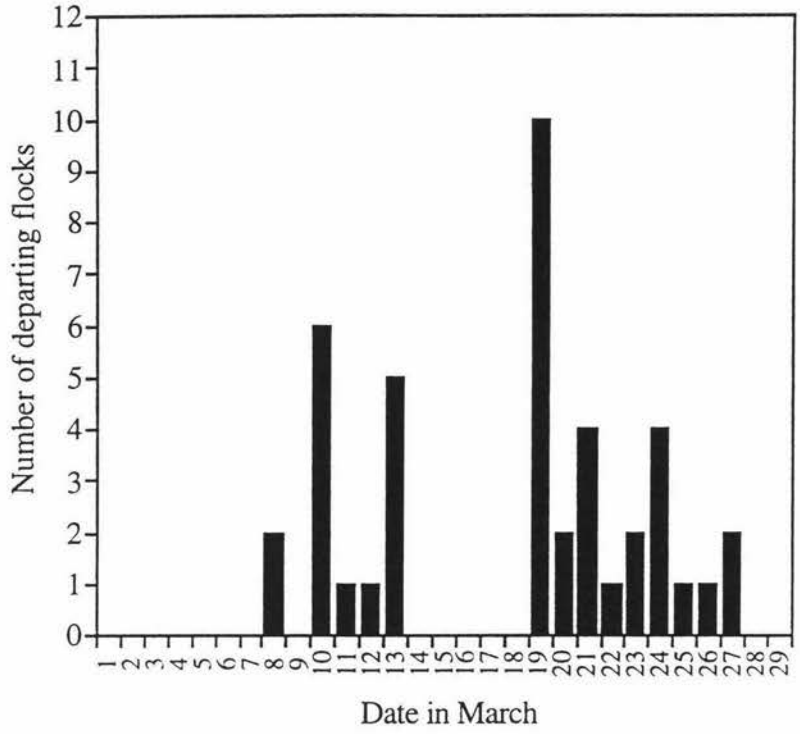


Figure 7.2 Daily pattern of observed departures of knots and godwits from Farewell Spit, March 1994.

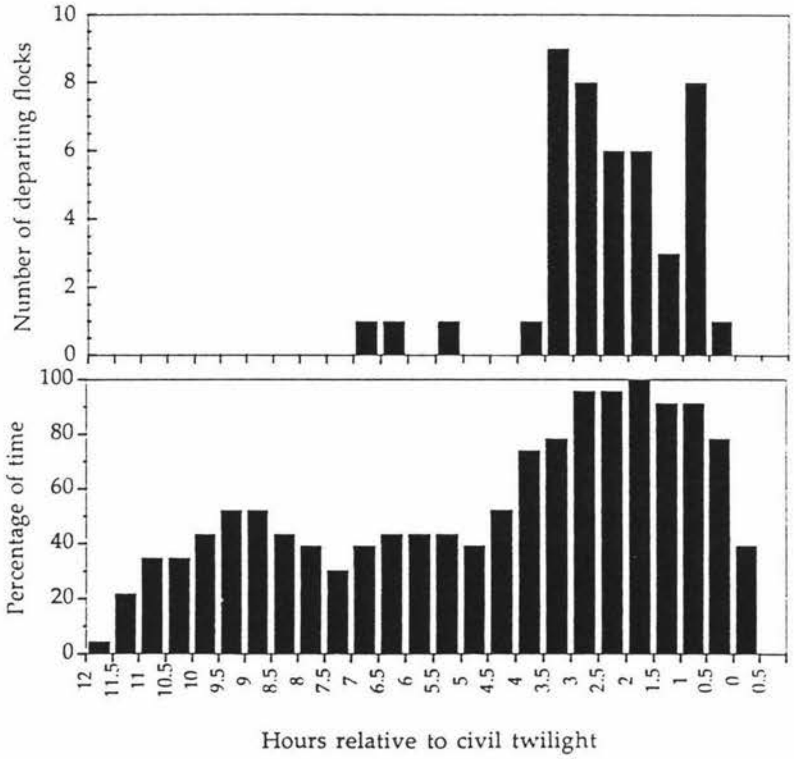


Figure 7.3 Pattern of departures relative to time of day (top), and observer time in field (lower).

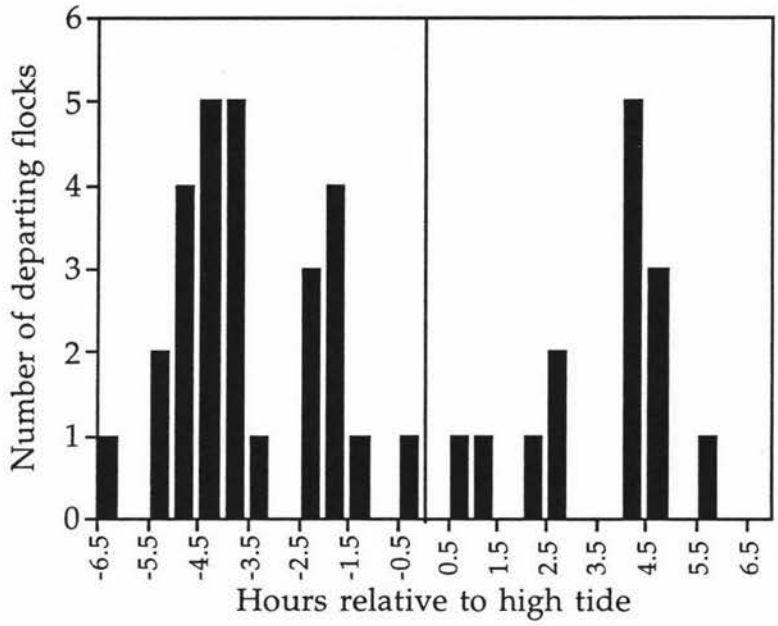


Figure 7.4 Pattern of observed departures relative to tidal stage. Zero denotes high tide (vertical dotted line). X-axis increments are half-hour intervals.

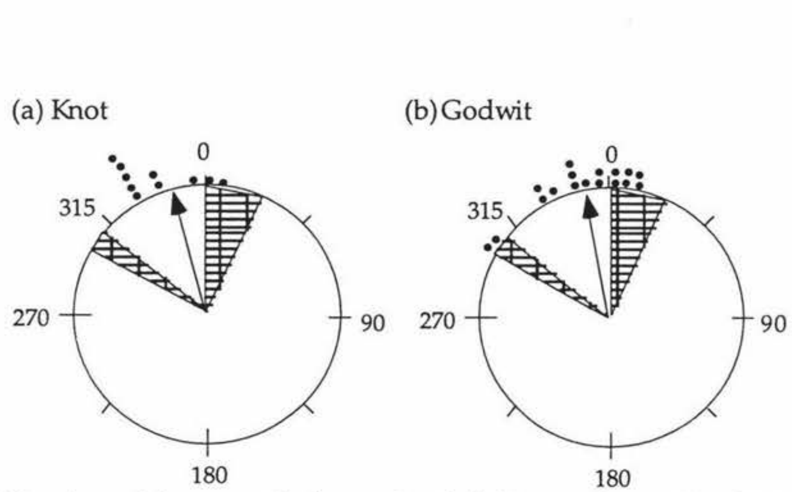


Figure 7.5 Directions of departures for knot and godwit. Dots on the outside of the circle represent flocks for which accurate compass bearing were gained. Flocks are in 5° groups. Mean departure vector and length (r) is given as an arrow from the centre of the circle.Hatched sectors represent directions of northern Australia and northern New Zealand (see text).

Direction of departures

Compass directions were gained for 17 godwit flocks and 10 knot flocks (Figure 7.5). Mean departure vector (track) for godwits was 350.3° (mean vector length $r = 0.944$) and for knots 344.6° ($r = 0.974$), but these differences were not significant (Watson-Williams test, $F_{1,25} =$

0.92; ns). Mean heading direction was also calculated (the heading being the direction a bird actually attempts to fly). This was calculated by adding the track direction vector (the course achieved in the influence of wind; I assumed 65 km h^{-1} ground speed) and the wind vector (which also has a direction and speed). Mean heading for knots was 343.6° (r = 0.954: n = 9 in this case - for one flock no wind details were recorded) and for godwits was 350.3° (r = 0.924).

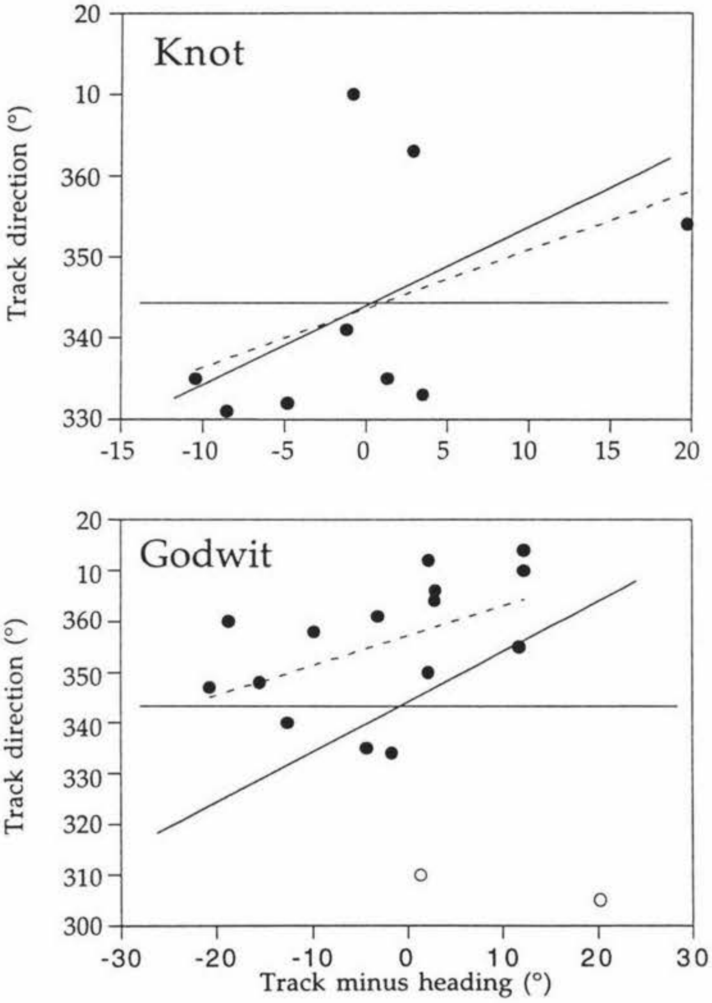


Figure 7.6 Degree of wind drift experienced by departing flocks. The track direction is the observed departure direction. The heading is the direction birds attempted to fly. The difference between the two is the wind effect. The heading was determined by adding the bird and wind vectors, assuming a ground speed of 65 km h^{-1}. The relationship between track minus heading, and track, shows a slope of zero if there is complete compensation for winds, and a slope of one if there is complete wind drift (solid lines). The dotted line shows the regression for the data. The two hollow points in the godwit plot were removed from the analysis (see text).

Whether birds compensate for winds can be determined by regressing the birds' track direction on the track minus heading direction (Alerstam 1976, cited in Piersma *et al.* 1990b). A slope of one for the relationship indicates complete wind drift, while a slope of zero indicates total compensation (solid lines in Fig. 6). Great variability was shown within both species (Fig. 7.6), and knots showed a positive relationship (slope = 0.726, r = 0.43, P = 0.246), godwits a flat one (for all data points, slope = -0.099, r = 0.06, P = 0.827). However, when the two outliers in the godwit plot were removed from the analysis (hollow circles in Figure 7.6) then an almost significant positive relationship emerged (slope = 0.582, r = 0.49, P = 0.063).

Influence of weather

For 26 flocks for which full details were gathered, wind vectors at departure ranged from a tailwind of up to 22 km h^{-1} to a head wind of up to 12.8 km h^{-1} (Figure 7.7). The modal range was -5 to 0 km h^{-1} (Figure 7.7), but the mean wind effect for all 26 flocks was a 3.9 km h^{-1} tailwind.

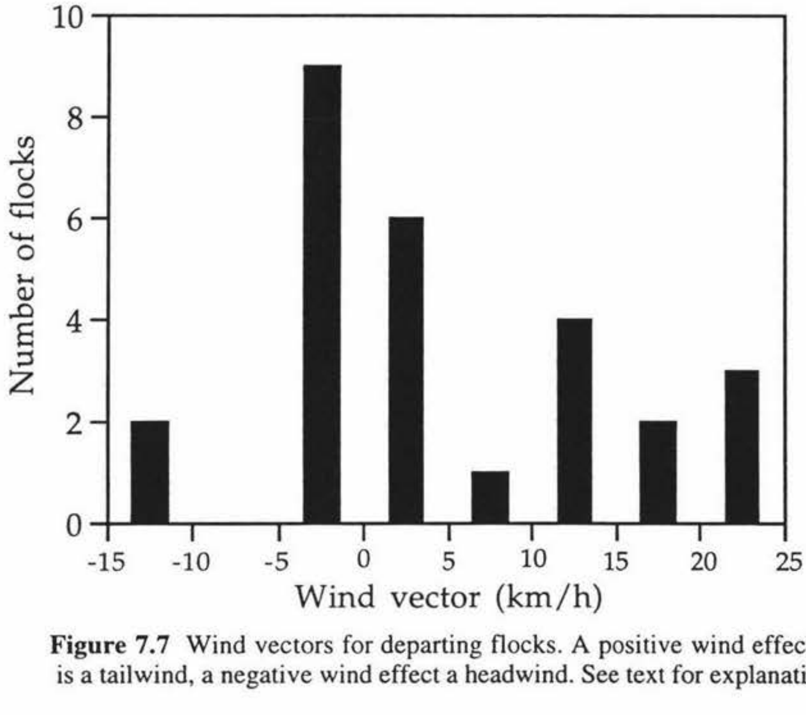


Figure 7.7 Wind vectors for departing flocks. A positive wind effect is a tailwind, a negative wind effect a headwind. See text for explanation.

Winds on Farewell Spit are variable, and frequently strong. From 14 to 18 March, birds faced north-westerly winds of generally 15-20 knots (28-37 km h^{-1}). During this time no flocks were seen to depart, and no obvious premigratory restlessness was observed, so probably no birds departed over this time. taking a mean departure track of 347° and a flight speed of 65 km-h, the calculated wind vector for birds attempting to migrate into a NW wind of 32 km h^{-1} is -29.4 km h^{-1}. Hence if the winds at sea level were at all similar to higher altitude winds, then birds' airspeed would be virtually halved in such conditions. The lack of of migratory behaviour from 14 to 18 March, combined with the large numbers of departures on 19 March (Figure 7.2) indicates that migration was suppressed over the former period. When conditions became favourable again (winds on the evening of 19 March were southeasterly, 15-20 knots) a larger than normal cohort was physiologically ready to migrate.

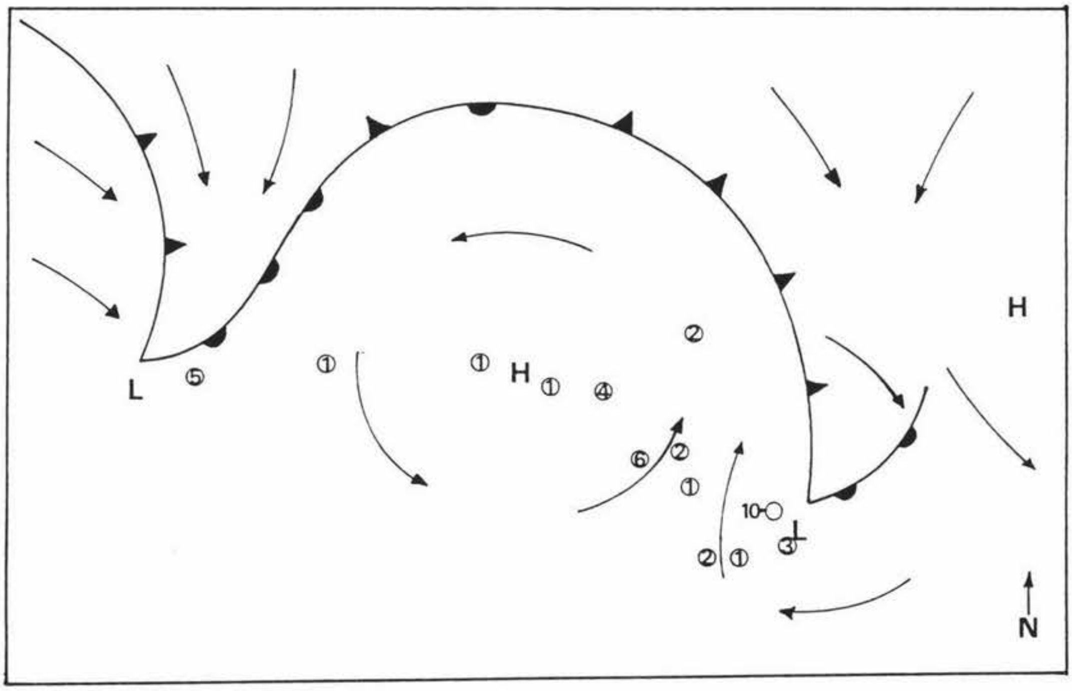


Figure 7.8 Plot of departure occurrences relative to prevailing weather systems. H= high pressure, L = low pressure. Arrows show wind directions. Each circle represents a day on which flocks departed. The number inside the circle shows how many flocks were seen.

The weather systems prevailing over the period 14-18 March showed clearly why migration was suppressed: a large slow-moving low-pressure system centred over the mid-Tasman Sea caused prolonged north and northwesterly winds to occur. This moved southeast below New Zealand on 17 March, and a new low developed just west of the northern South Island, and moved east over the country on 19 March, bringing with it southeasterly winds suitable for migration. The position of days on which flocks departed relative to major weather systems is plotted in Figure 7.8. The majority of flocks departed after the passage of a low-pressure system, or with the approach of a high-pressure system.

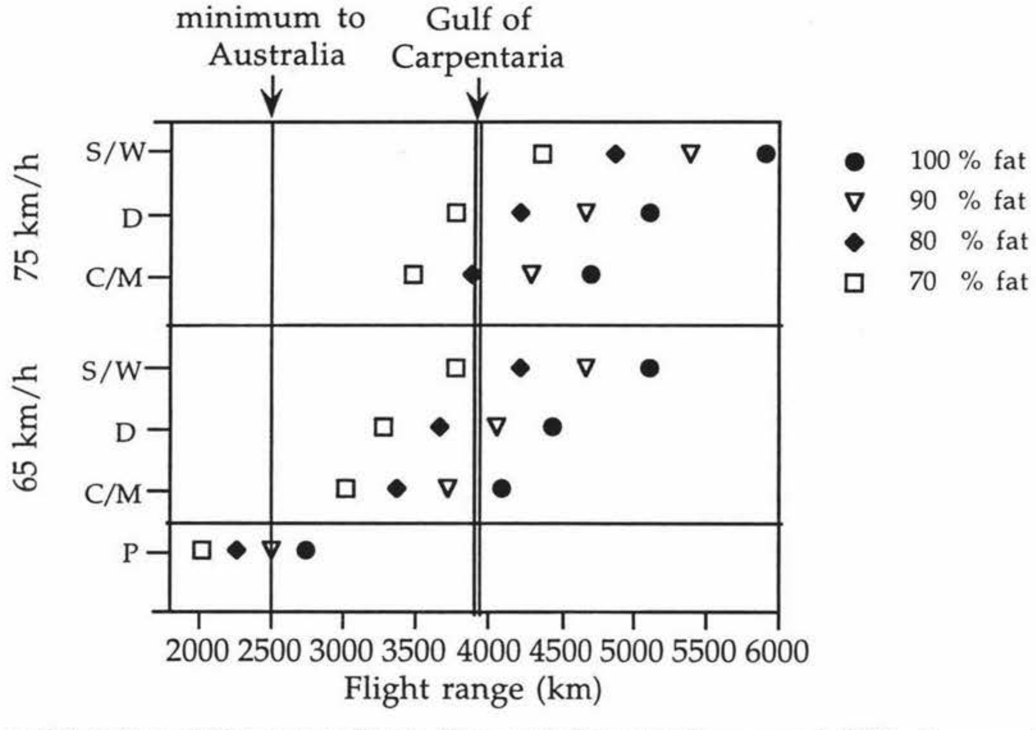


Figure 7.9 Estimated flight range of knots. Four predictive methods were used: S/W = Summers & Waltner (1978), D = Davidson (1984), C/M = Castro & Myers (1989), P = Pennycuick (1989). Flight speeds of 75 km h^{-1} and 65 km h^{-1} were used for the first three methods: Pennycuick (1989) calculates its own maximum range flight speed (49 km h^{-1}). The four estimates for each method show different levels of fat deposition (see text): filled circles = 100% fat, hollow triangles = 90% fat, filled diamonds = 80% fat, hollow squares = 70% fat. Vertical line gives the minimum distance from New Zealand to Australia, the double vertical line from New Zealand to the Gulf of Carpentaria, northern Australia. Variables used were lean mass 109 g, departure mass 185 g (Chapter 5), wingspan 47.5 cm (Tulp *et al.* 1994), wing length 16.75 cm (NZWSG unpubl. data, n = 1871).

How far might New Zealand knots be able to fly

Predicted flight ranges for knots are shown in Figure 7.9, and show that there is great variability in the estimates depending on both assumed level of protein deposition and flight speed. Under Pennycuick's model, knots would not be able to fly to Australia unless their mass increase consisted of 90% fat. Under all other models at 65 km-h^{-1} knots could fly at least 3000 km and reach Australia, but not reach the Gulf of Carpentaria unless 80% to 100% of their mass increase was fat. At 75 km-h^{-1}, all but Davidson's and Castro & Myers's models at 70% fat could reach the Gulf of Carpentaria.

DISCUSSION

Migratory behaviour

Flock sizes of migrating waders show large differences between localities. The average flock size of godwits on Farewell Spit was considerably lower than that of north-western Australia (Tulp *et al.* 1994) and the Banc d'Arguin, Mauritania (Piersma *et al.* 1990b), but was only slightly less than that of The Netherlands during the northward migration (Piersma *et al.* 1990b). Knot flocks were similar in size to those departing from Roebuck Bay, north-western Australia (Tulp *et al.* 1994) and the Banc d'Arguin, Mauritania, but much smaller than those from the Dutch and German Wadden Sea (Piersma *et al.* 1990b; Swennen 1992). Given a limited pool of individuals, of which only some may be physiologically ready to migrate, differences in migrating flock size could relate to the local population size. Piersma *et al.* (1990b) showed that mean flock size for godwits and knots departing from Mauritania was larger during peak departure times (the decade(s) during which most flocks left).

There are, unfortunately, few data with which to test this assertion. On Farewell Spit, the local flocks of knot and godwit were each around a thousand birds. Tulp *et al.* (1994) recorded only up to 2000 knots in their study area in north-western Australia during the migratory period, and had flock sizes only slightly larger than those at Farewell Spit, which is consistent with this hypothesis. While numbers of knots wintering on the Banc d'Arguin are vast (c. 362,000: Piersma *et al.* 1992), the relevant factor is the size of the local population immediately prior to migration, particularly those on tidal flats. Lank (1983) found differences in flock sizes of migrating Semipalmated Sandpipers *Calidris pusilla* migrating from Kent Island, Bay of Fundy, and from Sibley Lake, North Dakota (with oceanic flocks at the Bay of Fundy being larger than overland flocks in North Dakota), but found no significant correlation between local population size and flock size. Instead, he concluded the differences may have arisen from differential selection pressures on flock size in coastal and inland sites, owing to prevailing weather conditions (e.g. navigational and/or aerodynamic factors). While all the sites mentioned above for godwits and knots are coastal, they presumably experience different weather conditions, given that some are temperate and some are tropical. However, as differences in flock size have been recorded for sites along the same flyway (Piersma *et al.* 1990b) used by the same populations (Banc d'Arguin and the Netherlands; (Dick *et al.* 1987; Piersma and Jukema 1990), differences in flock sizes here may reflect some local departure-specific factor (or factors) rather than a basic underlying difference, as in Semipalmated Sandpipers.

The tendency of birds to vocalise strongly, evolve flock structure towards a vee or echelon, and to have apparent difficulty in settling on a final course, have been well documented (Piersma *et al.* 1990b; Swennen 1992). The zig-zagging of flocks setting off could be owing to them both attempting to settle on a course, and to trying to maintain that course in crosswinds.

Timing of departure

Since Lank (1989) published his thought-provoking results on the timing of shorebird migration, much interest has focused on clarifying the effects of time and tide on migration of waders (Alerstam *et al.* 1990; Marks & Redmond 1994; Piersma *et al.* 1990b; Tulp *et al.* 1994). The pattern emerging is that with an increase in tidal amplitude, there is an increase in the influence of a rising tide on departures. Departures from Farewell Spit (tidal range 2-4 m) seem also to conform to this pattern, with most departures on a rising tide. Tulp *et al.* (1994) calculated a 'tidal influence index', which confirmed the influence of tidal range on departures, with sites with a larger tidal range in general having a larger tidal influence index.

However, the way in which the data were treated means that their index does not actually relate at all to tide. Because they summed the *absolute* differences between observed and expected frequencies of departures, any information on whether a part of the tidal cycle was above or below this expected level is lost. Therefore what is measured is the magnitude of the deviation from the expected distribution. Hence even an oscillating distribution of departures with no relation to tide at all could show a high tidal influence index. The level of this index would then be determined by the amplitude of the oscillations.

I have calculated a new 'tidal influence index', in which the difference between the observed frequency distribution of departures and the expected frequency distribution (departures spread equally among time periods: $\sum$departures/13) is calculated for each part of the tide. This is then summed (retaining positive or negative sign) for the incoming and outgoing tide periods (the hour around high tide being combined with outgoing tides). A positive sign then indicates more departures than expected for that part of the tidal cycle; a negative sign fewer. (As all the deviations combined will equal zero, the outgoing tide index will equal the incoming tide index, but with an opposite sign.) The absolute magnitude of the number then becomes the indicator of how strong this effect is - the larger the index, the greater the deviation from expected.

Figure 7.10 plots this tidal influence index for incoming tides. Two points are given for Farewell Spit. The smaller is based on the complete data set and the larger on the set minus all departures on 19 March, when birds were migrating apparently in response to favourable weather conditions. The influence of incoming tides appears to increase with tidal amplitude.

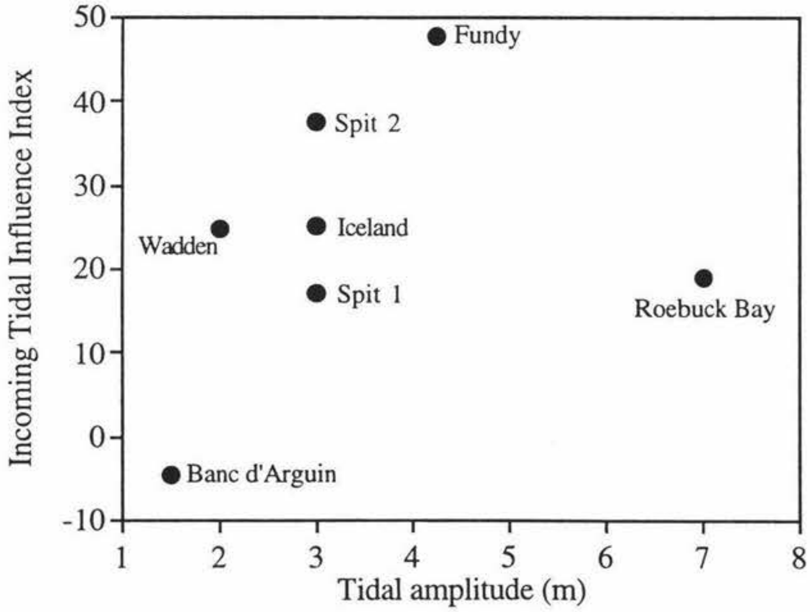


Figure 7.10 Tidal Influence Index, plotted against tidal height. The y-axis represents the deviation from a uniform pattern of migratory departures over the whole tidal cycle. A positive value shows more departures occurred on an incoming tide than outgoing. The magnitude of the index indicates how strong the tidal effect is, in either direction. Abbreviations and source of data: Banc d'Arguin (Piersma et al. 1990b); Fundy = Bay of Fundy (Kent Island: Lank (1989)); Roebuck Bay = NW Australia (Tulp et al. 1995); Iceland (Alerstam et al. 1990); Farewell Spit 1 and Farewell Spit 2, this study (see text).

However, the relationship is not simple. At Roebuck Bay, which has a high tidal range (Figure 7.10), many waders departed on the outgoing tide. This was due to an aberrant tidal cycle in which high tides usually fell in the middle of the day. Departures on the outgoing tide were therefore in response to time of day effects (i.e. in the pre-dusk period). The majority of departures on the outgoing tide on Farewell Spit also appeared to be in response to time of day, combined with suitable winds (see below). The few departures on outgoing tides recorded by Lank (1983) did so in response to favourable weather conditions.

Disturbance by moving water might trigger birds to migrate (Gudmundsson & Lindström 1992; Piersma *et al.* 1990b; Tulp *et al.* 1994). In this study many flocks formed away from the tidal edge, so this explanation could not relate to them. Thus I cannot accept an incoming moving water front as being any more than a partial explanation.

Tidal range is only one factor affecting the speed of water movement, though. The gradient of the tidal flats also determines how far out water goes. An area with a small tidal range could experience fast incoming tides if the gradient of its flat was low, while a large tide on a steeper shore could have a slow incoming tide. Thus analyses of tidal movement should ideally allow for the effect of coastal beach gradient.

The feeding priority hypothesis (Lank 1989), proposes that waders migrate on the incoming tide in order to maximise potential feeding time prior to this. Staying over high tide, when feeding is impossible, has no energy benefit, so departures are concentrated on the incoming tide. Lank (1989) suggested this was important for coastal Semi-palmated Sandpipers in the Bay of Fundy. Departures of Farewell Spit knots and godwits appear to fit this model, probably interacting with time of day effects.

The diurnal effect on timing of departure of birds from Farewell Spit was pronounced, as for other migrating waders (Alerstam *et al.* 1990; Gudmundsson 1993; Lank 1989; Piersma *et al.* 1990b; Tulp *et al.* 1994). The tendency for evening departures may be due to a complex array of potential flight and navigational benefits (Piersma *et al.* 1990b), including skylight polarisation, stars and sun. While waders at both the Banc d'Arguin and the Netherlands departed in sight of a setting sun, the majority of flocks from Farewell Spit were unable to do so (although sky was sometimes visible). Where sky was visible, skylight polarisation patterns could have been utilised.

Effect of weather

Most flocks departing from Farewell Spit gained from wind assistance. Birds were obviously sensitive to weather conditions and did not migrate in strong headwinds. Figure 7.8 shows that birds were departed when large-scale weather systems were favourable for migration. This suggests a strong relationship between local and large-scale weather conditions, in contrast with the study of Piersma *et al.* (1990a) in tropical Mauritania, in which the intensity of migration was not correlated with ambient wind circumstances (as ambient wind circumstances themselves were uncorrelated with higher-altitude winds). The results from Farewell Spit are, however, in accord with temperate northern hemisphere studies (Blokpoel & Richardson 1978; Lank 1983; Richardson 1978; Richardson 1979) in which favourable winds behind a cold front were utilised for migration.

Despite this purported sensitivity to wind conditions, birds were not seen making extensive "pre-migration flights" during which birds would have the opportunity to assess windspeeds. That birds were not doing so implies that they either had already 'decided' whether to migrate on the basis of winds experienced earlier in the day (e.g. when feeding on the tidal flats) or that they could fairly accurately assess windspeed independent of their own flight.

Flight ranges

The utility of flight range estimates is open to dispute, as they are subject to many sources of error (Zwarts *et al.* 1990b). Until recently, all of the premigratory increase in mass in birds has been assumed to consist solely of fat, with protein levels maintaining a constant 'structural' level. A sizeable portion of this mass increase can, however, consist of protein (Lindström and Piersma 1993; Piersma 1990), but flight range equations are based on flight metabolism using only fat. Increasing protein deposition would decrease predicted flight ranges. Waders are assumed to adjust their flying altitude to maximise tailwind assistance (or minimise headwind hindrance), while flight range equations assume no wind effects. This would, in most cases, tend to increase predicted ranges. Other factors affecting flight range estimates are energetic savings by flock flying, which would increase distance, and determination of flight speed. Most studies have used a flight speed of 75 km h^{-1} for waders, but 65 km h^{-1} may be a more realistic estimate (see Piersma *et al.* MS-b). Nevertheless, flight range estimates have been widely used, and allow first estimates of magnitude of potential flights and comparison between populations and areas.

This study formally accounted for protein deposition and different flightspeeds in estimating flight ranges. Varying protein levels resulted in differences of up to 1549 km (Summers & Waltner method, 75 km h^{-1}), and varying flightspeed from 75 km h^{-1} to 65 km h^{-1} gave a maximum difference of 787 km (Summers and Waltner method). Obviously, both of these variables can greatly affect flight range estimates, so without either detailed information on levels of protein deposition (Lindström and Piersma 1993) or details of winds en route (Piersma and Jukema 1990; Piersma & van de Sant 1992; Tulp *et al.* 1994) any predictions will be subject to potentially large errors.

Do knots fly to Australia direct or via Northland?

Through banding records and, recently, leg-flagging, some information about movements of knots within Australasia is known. Many knots travelling to New Zealand use south-eastern Australia on the southward migration, but do not use this area in the northward migration (Barter 1992). There are, however, records of New Zealand knots from south-eastern Queensland and Irian Jaya, and it is probable that the Gulf of Carpentaria is extensively used on both migrations (Barter 1992). Alcorn *et al.* (1994) suggest, however, that birds arriving on south-eastern mudflats in January to February could have been from New Zealand, although it is more likely that this involves birds still moving south within Australia. The destination for knots leaving New Zealand on the northward migration is presumably northern rather than south-eastern Australia, and the Gulf of Carpentaria is probably the only regular stop for knots flying north through Australia (A.C. Riegen, pers. comm.).

It was anticipated that migrating godwits and knots would show a clear distinction in departure flight path which would indicate whether they were flying direct to Australia from Farewell Spit, or were staging in northern New Zealand. Bird leaving from the spit have a clear and visible landmark in the form of Mt Taranaki (39°18´S, 174°04´E), 190 km away at 50° from the spit. Birds flying to the Auckland isthmus area would require a course holding 25°06´, while a course of 359°01´ would place birds at Parengarenga Harbour in Northland. A constant compass bearing course (Rhumbline) to the Gulf of Carpentaria, northern Australia, would be 309°, while the great circle course would depart at 299°.

The recorded compass bearings for godwit and knot flocks from Farewell Spit seem too far east for a direct flight to Australia, unless they encounter a predictable easterly wind stream en route. On 10 of the 13 departure days migrating birds would have been able to fly into or across the top of a high pressure zone, thus getting assistance from easterly winds. Parallel isobars frequently indicated a windstream that would extend from the southern North Island to the Queensland coast. The fact that flocks were not compensating for wind drift accords with a relationship with large-scale weather patterns - predictably changing wind patterns (eg. around a high-pressure system) could mean that fine-tuning migration directions might not be necessary until further on in the trans-Tasman flight. For the remaining three days (eight flocks totalling 178 godwit [16% of the total individuals] and 56 knot [11% of the total individuals]), to encounter southerly wind flows would have required flying across a low front. For the majority of birds, however, the large-scale weather systems present at the time of departure could have given assistance in a trans-Tasman flight. The rest could perhaps have staged in Northland before attempting to cross. The issue then becomes how much flexibility birds have in their migration systems - would birds encountering less favourable winds still attempt to migrate across the Tasman or do they have the latitude to change their direction and pause en route? Unfortunately, the Far North of New Zealand is poorly studied during the migration period, so the magnitude of any possible influxes there is unknown.

It is probable that birds from Farewell Spit attempt to fly directly to Australia. The uncertainty in the use of flight range estimates, however, makes predictions about migration routes difficult to make. New Zealand knots certainly do deposit a large amount of fat before migration (Battley and Piersma MS), so that most of the estimates of flight range (Figure 7.9) suggest ranges well in excess of the minimum trans-Tasman flight, the majority allowing a successful flight to northern Australia or beyond. It may be that such apparent "overloading" is a mechanism to allow for extended flight ranges when weather conditions are favourable, and to increase the chance of successful migration when they are not.

Recoveries of banded birds or sightings of leg-flagged individuals in Queensland and Irian Jaya (Pook 1992; Riegen & Davies 1993) might provide support for this interpretation. If the Gulf of Carpentaria is the primary destination for New Zealand knots, birds may put down in Queensland because they are unable to make the distance (e.g. through encountering poor flying conditions). Since knots routinely fly long-distances (Piersma & Davidson 1992b), it is difficult to envisage knots staging in northern Australia and then making only the short flight to Irian Jaya, and birds stopping there could be those that encountered good flying conditions across the Tasman and were able to overfly northern Australian sites. Overloading (putting on more fat than is necessary for a given flight) and bypassing of potential staging sites is predicted for some situations by time minimisation theory, and it has been suggested that knots may show such behaviour (Gudmundsson *et al.* 1991). If feeding conditions in New Zealand were better than those in northern Australia for knots, then arriving with some fat could be beneficial.

Unfortunately, the variability in flight range estimates precludes making strong conclusions (Figure 7.9). This contrasts with claims that knots are depositing sufficient reserves for extreme long-distance flights (Barter 1992; Barter and Wang 1990). This arises mainly because of the way in which flight range estimates have been utilised. Here, I account for the influence of protein and different flight speeds. Tulp *et al.* (1994) use the even lower species-specific maximum flight range speeds calculated by Pennycuick's (1989) program, although Figure 8 suggests that Pennycuick's method gives unrealistically low estimates. Both Barter (1992) and Tulp *et al.* (1994) used a lean mass of 87-88 g for knots in their calculations. This is inappropriate because it represents a large depletion of nutrient reserves during a migratory flight, which differ from nutrient stores involved in flight range formulae (see Lindström and Piersma 1993; van der Meer and Piersma 1994). The fact that these knots had depleted their reserves to this level shows that knots, despite their seeming mastery of long-distance flights, can and do have trouble in migrating successfully on occasion.

Both travel speed (= flight + wind speed) and protein level need to be accounted for if we are to have robust flight range estimates (Figure 7.9). Knots from northern New Zealand deposit some protein prior to migration (Chapter 6), but our single small sample is unable to assess this accurately. The indication, however, is that protein deposition is probably small relative to fat deposition. Determining the probability of birds being able to achieve a given flightspeed across the Tasman Sea would seem to be the course likely to aid our interpretation more. If they were able to gain some wind assistance and achieve high airspeeds, then it is possible that quite large flight ranges might occur. The most direct insights would come from intense coordinated trans-Tasman ringing efforts in an attempt to get departure and arrival condition data (see Piersma & Jukema 1990 for an example of this approach with godwits on the East Atlantic Flyway). Leg-flag sightings could indicate sites that would be suitable for such efforts in the future.

In New Zealand there is no evidence for Arctic wader mortality being prominent over the non-breeding season, and it is probable that migration may be a major cause of mortality for these birds. Given that waders are long-lived birds with high adult survival, periodic selection may be sufficient to drive migration patterns. A corollary of this is, of course, that when looking at the evolution and maintenance of migratory strategies, obvious strong selection pressures may be realised only intermittently.

Chapter 8

Population processes and wader limitation: a theoretical excursion

A common question intertidal ornithologists face is whether more birds could ‘fit in’ to an area, such as a certain estuary or harbour. Paraphrased, the question becomes “What factors, if any, are affecting (or limiting) the numbers or distribution of birds at a locality?” If feeding habitat is a limiting resource, then reducing their size should result in fewer birds. This has been a concern for European biologists working on waders over the past 25 years due to high pressure on intertidal areas from developers. In this case the question posed has been what the consequences of land-claim of estuaries are for the birds inhabiting the area. This equates to an increase in bird density, as does the question of whether more birds can fit in to an area.

A question such as “What factors determine the numbers of birds at this site” contains several separate proposals. The first is that numbers are restricted in some way or another: this is a logical conclusion based on the fact that neither habitat nor bird populations are infinite. The numbers of birds settling at a site is a balance between the pool of migrant individuals arriving, and the capacity of the habitat to support them over a given time-frame. 1000 birds living at a given site could result from only 1000 birds arriving at that site despite the fact that more could be supported, or it could result from more birds arriving but limited resources forcing a certain number to move elsewhere or die.

Bird populations at a site can hence be limited by resources present at that site (eg. low prey levels). Alternatively, the population might be limited elsewhere, such as on the breeding grounds or through mortality during migration. This could result in the population of an area being below the capacity of the area. For migratory birds, studying population dynamics is excessively difficult, if not impossible, as you cannot yet track individuals through their lifetime. Nevertheless, some theoretical work has been done, and considerations of limitation must necessarily address off-site considerations. Most effort, however, has naturally addressed questions of on-site limitation, through studying the relationships between bird predators and their benthic prey. There is a burgeoning literature on this, but there still remains much work to be done. Below, I attempt to outline the relevant considerations for studies on intertidal waders, regarding how birds may be limited by their food resources.

Firstly, biological research is often limited by problems of ecological scale and our ability to come adequately account for it in studies. Ideally, to maximise our understanding of ecological processes we should be studying at the finest scale possible, in order to truly come to grips with the complexity of nature. Do we study at the community, population, or individual level? Can we avoid having to study at them all?

Given that a community is composed of populations which are composed of individuals, a progressive program should ideally investigate all these levels. While the questions they ask will differ, they are all by necessity linked. As natural selection operates at the level of the individual, Ens *et al.* (1994) claim that it is necessary to understand the behaviour of individuals if you are to understand the dynamics of a population, and it is these two aspects that I shall concentrate on. To attempt a full review of processes and examples from the literature is not what I shall attempt, but instead to allude to those aspects which may relate directly to this study.

Carrying capacity: concepts and utility

Carrying capacity has been a contentious concept. It refers to the idea that there is some maximum population level which a habitat can support, so that further increases cannot be accommodated. The result must then be either emigration or mortality. The questions become then: (1) Are all the feeding areas that are used at the moment fully exploited? and (2) Are there other feeding areas, not at present used, which could take birds? (Goss-Custard & Charman 1976). Before addressing these questions it is necessary to have an operational definition of carrying capacity that contains a functional aspect which is investigable. Piersma (1987) suggests that the relevant measurements to make on benthic productivity and shorebird foraging is the *production of acceptable biomass*. This is the renewal rate of organisms acceptable as food for a certain species of shorebird. The idea is that cumulative predation may be a limiting factor for birds, and if benthic productivity (production/somatic growth and immigration) is compared with shorebird usage (cumulative amount of benthic biomass removed at a site over the same time-frame) then potential limitation can evaluated.

That shorebirds can and do deplete standing stocks of invertebrates is well known (see e.g. Baird *et al.* 1985; Goss-Custard 1980; Goss-Custard 1984b; Schneider 1978; Zwarts and Drent 1981). Goss-Custard (1984b), reviewing studies to that time, concluded that in general prey are reduced by 25-45%, although Evans *et al.* (1979) calculated that birds removed 90% of the standing stock of large *Hydrobia* and *Nereis* during a single winter following land-claim on the Tees Estuary. Schneider (1978) also recorded monthly consumption of up to 84% by shorebirds. Baird *et al.* (1985) calculated the amount of benthic productivity consumed by shorebirds at five sites in Britain to range from 6-44%. However, they felt that the high levels of consumption recorded need not indicate that benthic production might be limiting for bird numbers. This was in part because the relationship between annual production and utilisation is not simple - given high selectivity by birds, production in any one invertebrate is not equally available to all predators. A larger bird may rely on invertebrate cohorts from a year or more previous, so whether production is in the form of reproduction or growth can have large effects on availability of prey.

Sutherland & Goss-Custard (1991) discussed the term carrying capacity, given that Dhondt (1988) suggested it should be abandoned due to the confusion of differing definitions used over the years. In view of its strong intuitive appeal, that resources must at some stage become limiting if populations continue to increase, they maintained it as a concept. Their definition "rests on the assumption that various forms of feedback from bird density to the rate at which individuals can feed will cause an increasing proportion to fail to achieve adequate intake rates as the local bird density increases. Eventually, density will reach a level at which the addition of one further bird would result in another either starving or leaving that locality to seek a better feeding area. When this point is reached, no net increase in bird density can take place, and the carrying capacity would have been reached".

While this is of good heuristic value, translating this into empirical predictions has proved difficult, but recent advances in behavioural ecology and modelling have proved very profitable (Goss-Custard *et al.* 1995a; Goss-Custard *et al.* 1995b; Goss-Custard *et al.* 1995c; Goss-Custard *et al.* 1995d; Goss-Custard and Durell 1990). Figure 8.1 (from Figure 2, Sutherland & Goss-Custard 1991) provides a framework for considering the effect of habitat loss (= increased bird density) on bird populations.

It can be seen that there are two aspects to this scheme. One is the direct influence of increased local density on survival, the other being an indirect feedback through density-dependent birthrates. The steps in the diagram below are detailed by Sutherland & Goss-Custard (1991) from which this summary is drawn.

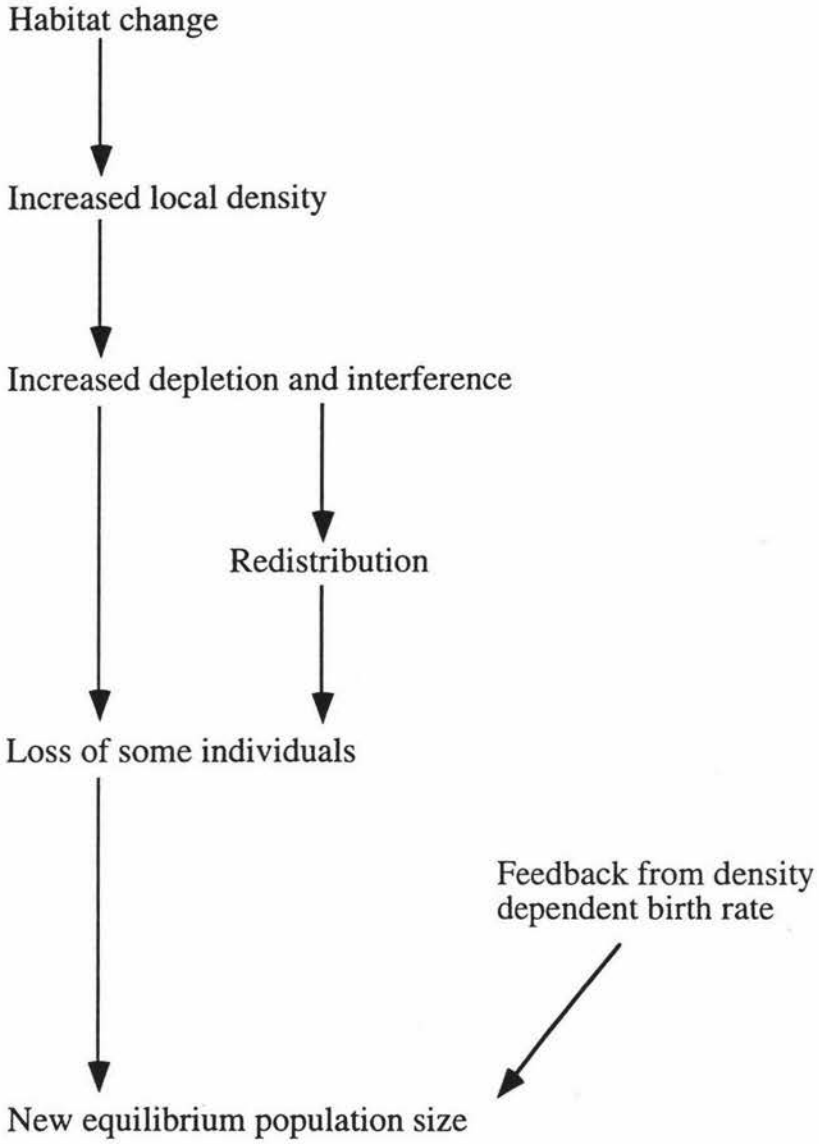


Figure 8.1 Effects of habitat loss on bird populations. Redrawn from Sutherland & Goss-Custard (1991)

Increased local density > increased depletion and interference

Greater pressure on food resources means that prey may be depleted to a greater extent (e.g. Evans *et al.* 1979), and species susceptible to interference (Goss-Custard 1980) may suffer a decreased intake rate. This will be especially pronounced in species which either fight regularly for food, or whose prey is sensitive to disturbance. For flock-feeders depletion is likely to be more important.

Increased depletion and interference > redistribution

As feeding grounds can be viewed as consisting of a series of interlocking gradients of quality and birds will attempt to settle in areas with initial high prey densities, if depletion is important, then prey levels over a wider area will be depleted earlier in the season, so individuals will have to move down the gradient to lower quality sites. If interference predominates, then birds will spread right out over the food gradient to avoid this, as high prey areas will suffer high interference. As the density increases, a greater proportion of the birds will start the season by settling in lower quality areas. Hence either mechanism can give rise to an increasing proportion of birds occurring in less preferred areas.

Redistribution > death of poor competitors

Individuals differ in competitive ability, and birds of the highest competitive ability should occur on the richest parts of the gradient. Poor competitors would have reduced intake rates by both depletion and interference and by having to settle in low quality habitats. Death could occur through starvation and increased predation risk.

Loss of poor competitors > new equilibrium population size

If birds compete for the best breeding grounds, there can be strong density-dependence in birth rate. Modelling suggests that this could easily regulate population sizes (Goss-Custard and Durell 1990). Additional (to breeding ground regulation) density-dependent mortality of young birds in the non-breeding season can also reduce the equilibrium population size (Goss-Custard and Durell 1990).

This brief resumé has shown that there is a good theoretical basis for expecting regulation of populations with increasing density. Is this supported by any empirical studies of habitat loss?

Evans *et al.* (1979) studied the Tees Estuary, north-east England. This estuary had been progressively land-claimed since the 1800s, reducing from 2,400 ha to 400 ha by 1969. Further land-claim in 1973 reduced it to 140 ha. It was calculated from benthic invertebrate populations and bird numbers that most wader species would have been unable to maintain the same number of bird-days on the reduced 140 ha area in the winter in 1973/74 as they had in the winter of 1972/73, prior to the reclamation.

The Oosterschelde/Krammer-Volkerak estuary in the south-west Netherlands lost 33% of its intertidal area through the construction of a storm surge barrier and dams between 1982 and 1987 (Schekkerman *et al.* 1994). Numbers of waders decreased over the whole area, while ducks increased. There was a seasonal shift from a midwinter number peak to autumn. Within the Oosterschelde area, where 17% of the flats disappeared, numbers of intertidal foragers decreased.

The conclusion was that intertidal foragers forced to move were generally not able to settle into the remaining areas. Both dispersal and mortality were thought to be important for different species. In contrast with this was the situation when a nearby estuary, the Grevelingen, was closed to the sea in 1971. Oystercatcher and Bar-tailed Godwit numbers increased in the western Oosterschelde region (Lambeck *et al.* 1989; van Latesteijn & Lambeck 1986), and numbers in the adjacent Krammer-Volkerak also increased (Leewis *et al.* 1984). Numbers in the whole Delta area, however, showed no obvious decrease (Leewis *et al.* 1984). In this case, the displaced birds were apparently able to be accommodated elsewhere within the Delta complex.

On a broader spatial scale, Moser (1988) showed that numbers of Grey Plover *Pluvialis squatarola* increased in Great Britain over the period 1970-86. However, rates of increase were not uniform between estuaries, and some estuaries showed no increase. He suggested there was sequential filling of areas (most preferred areas followed by less preferred areas) and a density-dependent limit to numbers able to winter on individual estuaries. This was taken to show that at some estuaries Grey Plovers had reached a carrying capacity beyond which further increases were not possible.

These examples show that in some cases birds were not apparently able to be accommodated at a higher density (in the remaining habitat after land-claim or through increases in absolute population), while in others they were. There is no reason to expect all estuaries to be at or near a carrying capacity, given differences in benthic biomass and bird populations at different sites. Furthermore, carrying capacity is not static - large inter-annual variations in abundance of benthos (Beukema *et al.* 1994) must necessarily cause variations in the capacity of an estuary to support birds. However, the increased precision and elegance of research over the past 15-20 years means that theoretically at least, it should be possible to determine whether sites have any leeway for population increases. Many of the aspects mentioned here have been touched on earlier in different sections of this thesis. I shall now outline the information necessary for an accurate assessment of this.

It is generally taken that energy is the relevant currency for studying the ecology of shorebirds, the assumption being that shorebirds attempt to maintain a positive daily energy balance (Pienkowski *et al.* 1984). For this we need accurate estimates of both energy requirements and intake. We also need to know what factors affect energy intake.

The energy requirement of an individual can be viewed as being comprised of three components. The Basal Metabolic Rate (BMR) represents the basic working level of the body at rest, and is directly measured (e.g. by oxygen respirometry or with doubly-labelled water) in an inactive, post-absorptive state in the thermoneutral zone. If mass, or preferably lean mass, is known, BMR can be estimated from allometric equations (Kersten and Piersma 1987). Superimposed upon this are two variable costs. One is the thermoregulatory cost imposed by the environment, the net effect of temperature, windspeed and radiation. Through the use of heated taxidermic mounts, predictive equations for estimating the maintenance metabolism (BMR plus thermoregulation costs) are available, for waders at least (Wiersma and Piersma 1994). These can take into account behavioural responses (e.g. flocking) which may affect energy requirements. The third component is activity costs, such as of foraging and flying. These are usually roughly estimated as a multiple of BMR, although it is probable that work with captive birds will sooner rather than later allow more accurate assessment of these costs if detailed behavioural information is gathered. Currently, total daily energy expenditure (DEE: maintenance metabolism plus activity costs) has often been estimated simply as a single multiple of BMR which doesn't account for varying costs through time (e.g. Meire *et al.* 1994), but allows a first rough estimate. Costs of maintenance and tissue synthesis will vary as birds moult (Lindström *et al.* 1994) and deposit mass for migration or winter storage (this is estimable from knowledge of mass levels and tissue deposition efficiency).

From these, an accurate picture of the energy costs per individual could be calculated for a given time frame, and with information on bird numbers, be converted into a population or community energy demand. This would then have to be compared with the energy available in the benthos for the birds. Here, it is not sufficient to simply measure the standing crop of invertebrate biomass. (It would be, however, if you knew that there was no immigration or production of biomass occurring in the invertebrates over the time-frame under investigation.) The energy demand is likely to be expressed in 'bird-days' or 'biomass-bird-days', a cumulative figure. Hence the energy available would also need to be cumulative in nature. This comes back to Piersma's (1987) definition, the renewal rate of organisms acceptable as food for a certain species of shorebird. It also brings in the next important point, that different species of birds have greatly different portions of the benthos that are relevant to them. Recent work by Zwarts & Wanink (1994), Zwarts *et al.* (1992), Piersma *et al.* (1994b), and others has shown how the harvestable fraction of prey is a function of detectability, accessibility, ingestibility and profitability. This harvestable fraction can be at times only a very small fraction of the total biomass present. There is furthermore great seasonal and annual variation in levels of prey biomass at an individual site (Beukema *et al.* 1994; Piersma *et al.* 1994b; Zwarts *et al.* 1992; Zwarts and Wanink 1994) , as well as large differences between sites (Piersma *et al.* 1994a). Failure to account for such differences can lead to potentially grossly erroneous conclusions (e.g. Hockey *et al.* 1992). Determining benthic productivity accurately is difficult (for methods see Crisp 1984) and most workers instead rely on a general relationship between biomass and production, the P/B ratio, to estimate this. A direct estimate is far preferable, of course. Benthic production varies seasonally, and it is therefore important to determine the relationship between production and predation pressure by birds (which also varies) to see whether there are any times of the year when bird numbers may be limited by food (Kalejta 1992).

So far, energy requirements have only been indirectly estimated - a more direct method is to determine the actual intake rates birds achieve in the field. These can then be compared with the allometric equations' predictions. Dietary studies are also necessary to determine which portions of the benthic biomass are relevant to the species in question. As birds may show intake rates dependent on prey density (Holling's functional response: Piersma *et al.* 1994c; Wanink & Zwarts 1985) , knowing how intake rates vary, and how the prey density varies around the habitat in question would be informative. Factors affecting intake rates of birds could also be evaluated, and their likely importance through the year assessed (Evans 1976; Evans 1979; Goss-Custard 1984b; Pienkowski 1981; Pienkowski 1983a; Pienkowski 1983b). A major problem with studying feeding directly is the fact that most shorebirds do feed nocturnally, although with presumably differing efficiencies depending on prey type and behaviour, and feeding style of the birds (Dugan 1981; Evans 1987; Kalejta 1992; Robert & McNeil 1989; Turpie & Hockey 1993; Wood 1986).

So the tools are there for estimating the birds' energy requirements, intake rates and food supply. This should allow identification of periods of potential 'stress' for the birds. Knowledge of energy requirements and intake rates should allow assessment of whether birds are maintaining their energy balance. Studies of mass changes and body composition of birds through the year would be instructive. These would show if birds were attempting to deposit mass to cover periods of negative energy balance (e.g. winter cold spells: Davidson 1981a; Davidson 1981b; Davidson & Clark 1985) and allow investigation of the migrational requirements of the birds (Piersma and Jukema 1990).

Overall, there are two main parameters to be estimated (Goss-Custard *et al.* 1995d). The first is the point at which density-dependence has an effect on survival, that is, the population at which competition between individuals causes mortality. If this point has been reached, then habitat loss will reduce populations. The second is the form of the density-dependent function, that is, how increases in population affect the mortality rate. This is difficult to determine, but has been attempted with a game-theory model for oystercatchers feeding on mussel *Mytilus edulis* beds (Goss-Custard *et al.* 1995a; Goss-Custard *et al.* 1995b). Both of these measurements are perhaps easier made with a species such as the oystercatcher, in which interference can be easily quantified in a detailed study, and their feeding resource also (in this case mussels) than in widely-moving flock-feeding birds feeding on a more dispersed prey.

It is easy to see how incredibly hard and time-consuming such an enterprise would be (my failure to accurately estimate intake rates of knots, and oystercatchers feeding on worms proving this...), and to do it well would require a large research team working concurrently on all aspects mentioned. Anything we do manage will likely be a compromise between information and time/effort. However, given the outline of the problem and approaches above, we should be able to infer from bird behaviour and some knowledge on the intertidal habitat something about the likelihood of limitation.

Mortality and selection

So far, I have discussed the processes that might give rise to population limitation and how these could be studied. I have not discussed the ramifications of failing to meet energy requirements, beyond outlining the steps in Sutherland & Goss-Custard's (1991) framework.

There are two ways in which limitation can be expressed: mortality, and emigration. Mortality, however, can happen directly (on site) or further down the track due to the consequences of decreased feeding opportunities. While mortality on the feeding grounds is obvious evidence for limitation, lack of it need not mean it does not occur as a consequence of density-related factors on the feeding grounds. Take, for example, a long-distance migrant bird which requires a certain amount of fat and protein to be deposited to successfully complete a migratory flight. Failure to deposit mass at a sufficient rate could cause it to fail to successfully migrate (ie. it dies en route). Any factors which depressed its intake rate (e.g. through the mechanisms outlined before) could effect this. So limitation could be expressed both immediately through starvation, or subsequently through failure to deposit reserves.

This brings us to the problem of translating migratory decisions into fitness consequences for an individual. We need to know about the consequences of variation in a given trait on survival and fitness, e.g. level of nutrient deposition prior to migration. We have seen (Chapter 5) that waders are capable of depleting nutrient reserves in the course of a migratory flight. The indications are also that birds depart with varying fat loads. Do birds have a "fattening trajectory" that has as its goal some optimal departure mass, which is presumably a tradeoff between migratory distance, transport costs, predation risk and intake rate capacity? This could be expected if birds are energy-minimising in migrations, ie. attempting to migrate using the least possible energy. By keeping mass at the lowest level possible transport costs are decreased, so the migration can be done cheaply. But is this an over-riding concern? Alternatively, it could be expected that birds will deposit mass as quickly as they can, to reach the highest mass they can before migrating. Any increases beyond a minimum departure mass (which could be the optimum departure mass above) will not be viewed as being disadvantageous, given that they will allow potential bypassing of staging sites en route, and be a buffering against unpredictable feeding conditions en route. This is predicted if birds are time-minimising rather than energy-minimising (Alerstam and Lindström 1990; Gudmundsson *et al.* 1991; Lindström & Alerstam 1992).

The most likely consequence of competition is failure to achieve energy requirements. This need not express itself as mortality, as during the premigratory period birds are seeking to deposit mass rather than just achieve an energy balance. This could then lead to either mortality during a flight, or depletion of bodily protein reserves. The question for the latter case becomes what are the consequences of this? Davidson & Wilson (in press) show that knots with above average nutritional status migrating through Iceland and Norway to breeding grounds in northern Canada and Greenland were more likely to be encountered again than those of low status. Hence for this last leg of a migration, mass can affect both survival and also, presumably, productivity. But how does a depleted mass two to three migratory flights away affect this? Wilson & Morrison (1992) show that the fattening rate of knots with low body masses upon arrival in Iceland was higher than that for birds of greater mass, so that arrival condition probably has little relevance to departure condition. This would suggest that direct mortality is the main cost. However, if birds are time-minimising, then the extra day or two required to redress nutrient imbalances could be a sizeable cost. If there is a premium on earlier arrival time on the breeding grounds then this could affect territory acquisition and breeding success.

Any post-wintering mortality will obviously not be visible on-site, but will affect the equilibrium population size (see Goss-Custard and Durell 1990), which would then feed back to the site in subsequent seasons, given high site-fidelity in waders.

It may be, of course, that migratory populations experience most mortality due to factors away from the wintering ground. For instance, while waders are long-lived birds, periodic harsh Arctic summers can cause significant mortality (Boyd 1992). Variation in breeding success also arises in Arctic-breeding waders through the interaction of predators and lemmings, whereby when lemming abundance is high, predators feed on them, so birds suffer only low depredation themselves. Lemming abundance generally cycles with a three-year period, and in years of low lemming abundance birds suffer high depredation of eggs and chicks (Dhondt 1987; Owen 1987; Summer 1986; Summers & Underhill 1987; Underhill *et al.* 1993). This is reflected in bird numbers reaching wintering grounds, especially in the southern end of the range, where fluctuations in juveniles are especially prominent (Martin & Baird 1988; Underhill *et al.* 1989). Variations in mortality through migratory flights away from the wintering ground can also give rise to large population changes.

Changes in populations on the wintering grounds can thus arise through variations in numbers arriving, as well as through habitat restrictions limiting the number that can successfully stay.

Chapter 9

General discussion

Food supply and usage

The shorebird fauna of Farewell Spit is dominated by two Arctic-breeding species and one New Zealand-breeding species. There is a three month overlap in the bulk of their populations being present, with Arctic waders arriving from late September and leaving in March and early April, while the equivalent period for oystercatchers runs from late March to July/August. In all species non-breeding individuals are present year-round in low numbers.

The feeding conditions experienced will thus vary, especially as prey- and size-selection differs between the species. For most invertebrate taxa, condition increased through the summer, leading to improving conditions for Arctic waders prior to migration (Chapter 3). This was both a consequence of growth (eg. *Travisia*) and increase in condition (eg. cockles *Austrovenus*). These relationships were not equivalent between, and even within, species, though. The increase in condition of large *Austrovenus* was proportionally greater than in smaller ones, and the condition of the smallest ones was actually greater in winter than summer. So while an oystercatcher will encounter peak cockle condition in summer, most knots will be faced with bivalves of relatively low condition. For mussels *Modiolus* condition in June was twice that of in February. This almost certainly relates to the spawning cycle in this species (which is unknown). Life-history characteristics will not be equivalent between taxa.

It is thus not simple to characterise feeding conditions for all waders through the year. Certain other considerations are more fixed. The thermostatic cost of residing at Farewell Spit is lowest over summer, and increases over winter, due to lowered temperatures and solar radiation. Farewell Spit is somewhat unusual in that windspeed declines from November to June. Arctic waders experience low maintenance metabolism requirements over the summer, contrasting with populations which "winter" in the northern hemisphere. Oystercatchers face rising costs over the winter. Energetic considerations in choice of wintering locality are discussed elsewhere (see below).

Attempts at estimating energy intake were variable in their success (Chapter 4). Oystercatchers certainly managed a high level of energy intake in summer, whether feeding on *Travisia* or cockles, though in winter the latter prey provided only just enough energy. The short feeding duration of these birds suggests that this may reflect accurate budgeting on the birds' part rather than marginal feeding, as feeding time could be increased. Godwits feeding largely on *Travisia* had an extremely high energy intake rate. How predictable *Travisia* is between years, is important in assessing the long-term suitability of Farewell Spit to these waders.

The diet of the three waders was similar to those shown globally. There is considerable segregation in diet between knots and the other two species, which is not at all unexpected. There are few small mollusc-specialists other than knots. Indirect interactions between knots and oystercatchers are probable, with harvesting of small size-classes of bivalves by knots presumably affecting numbers reaching maturity. Conversely, harvesting of reproductive-age individuals could affect spat (juvenile) densities eaten by knots. How density-dependent these processes are is open to conjecture.

Direct competition between godwits and oystercatchers is evident in their diets, with both *Travisia* and other worms constituting most of the godwit diet and all of one sector of the oystercatcher population's diet. The combined predation on *Travisia* apparently led to depletion over autumn in 1994.

I have not formally addressed individual variations in diet apart from in oystercatchers. Godwits also showed greater variation in diet than indicated here, with birds feeding in saltmarsh channels taking the crab *Helice crassa*, and birds on eelgrass beds feeding on both polychaete worms and crabs. Dietary specialisation does reduces predation pressure on any one food source, but whether this a cause of specialisation or a consequence of uneven competitive ability remains to be determined.

Migratory preparation

Preparation for migration is both behavioural and physiological. On the coarsest level birds must increase their net energy intake rate. This is achieved at least in part by expanding feeding time in knots probably during both night and day (Chapter 4). Godwits probably achieve most of their increase at night.

Physiological preparation was investigated only in knots, due to lack of data on other species. A sample of 33 Bar-tailed Godwits, shot at the same time as the knots analysed in Chapter 6, have recently been analysed in Dr Theunis Piersma's lab in the Netherlands (February 1996). This will allow us to greatly expand our knowledge and predictions about godwit migration.

Knots in New Zealand become very fat prior to migration, which is clearly visible in birds in March. In fact, the visible abdominal profile of knots has recently been suggested to be a viable tool for assessing cohort preparation for migration (Wiersma and Piersma 1995). Our analysis shows that indeed the abdominal cavity of knots is used for fat deposition, and that it accelerates this at high fat levels. This "last-minute filling" will thus lead to differences in profiles.

Fat is not the only substance deposited, and our data add to the growing pool indicating complex interactions between organ protein deposits (Davidson and Evans 1988; Evans *et al.* 1992; Piersma *et al.* 1996; Piersma *et al.* 1993). That birds can shift nutrients freely within their bodies came as a revelation to me, and raises the questions of why, and why also the variation between species or populations there appears to be (Lindström and Piersma 1993). It is likely that protein turnover during a long-distance flight is high, and is required to maintain proper organ functioning during this high energy expenditure starvation phase. Protein levels should reflect imminent demand. The degree of protein deposition in premigratory mass increase is important when making estimates of potential flight range (Chapter 7), as its energetic return is much less than that of fat. Lack of knowledge of this in New Zealand waders hampers predictions about migratory capabilities. Even more important may the wind conditions en route. Knots departing from Farewell Spit did so at times when both local and large-scale weather conditions were favourable (Chapter 7). They probably obtained wind assistance by utilising high-pressure systems to gain following winds, with northern Australia as their destination. While the destination for birds departing from Farewell Spit and Auckland are thus the same, the assumption that fat levels are also equivalent depends on birds having equal feeding opportunities. If knots are pressured in the premigratory period (Chapter 4) then this may not necessarily be valid. New Zealand is a prime location for studying migratory preparation, being the end of a migratory flyway. Optimisation criteria may differ between wintering grounds and short-duration staging sites, and studies in New Zealand have much to offer as an accessible study region for some of the longest shorebird migrations in the world.

Numbers of birds on Farewell Spit: are they limited?

If numbers are limited on Farewell Spit, then we expect to see fairly constant numbers, independent of national trends. Twice-yearly full censuses of birds on Farewell Spit have been made by the Ornithological Society of New Zealand since 1983. These counts show knot numbers in summer have been decreasing slowly over the past decade or so (Figure 9.1). In contrast, godwits show a clear increase (Figure 9.2).

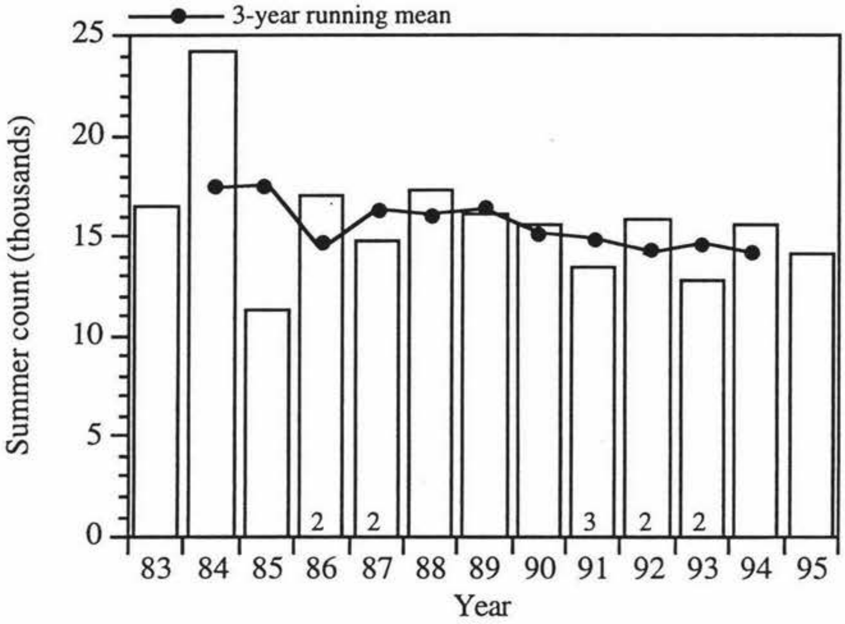


Figure 9.1 Count of knots at Farewell Spit from 1983 to 1995. Bars represent the summer count in that year, while the line is the three-year running mean (mean of the year in question and the year before and after this). Where the summer count represents the mean of more than one count, this is indicated by a number above the year.

The difference between the actual count in any year and the three-year running mean can be a useful measure to assess any cyclicity in populations that may be obscured by an increasing or decreasing overall population. The plots for these (Figures 9.3 & 9.4) reveal that both species tend to alternate between high-count years and low-count years. However, they are not synchronous, with a high count in one species tending to occur with a low count in the other (r = -0.77). Clearly, different factors are affecting the summer populations of these two arctic waders on Farewell Spit.

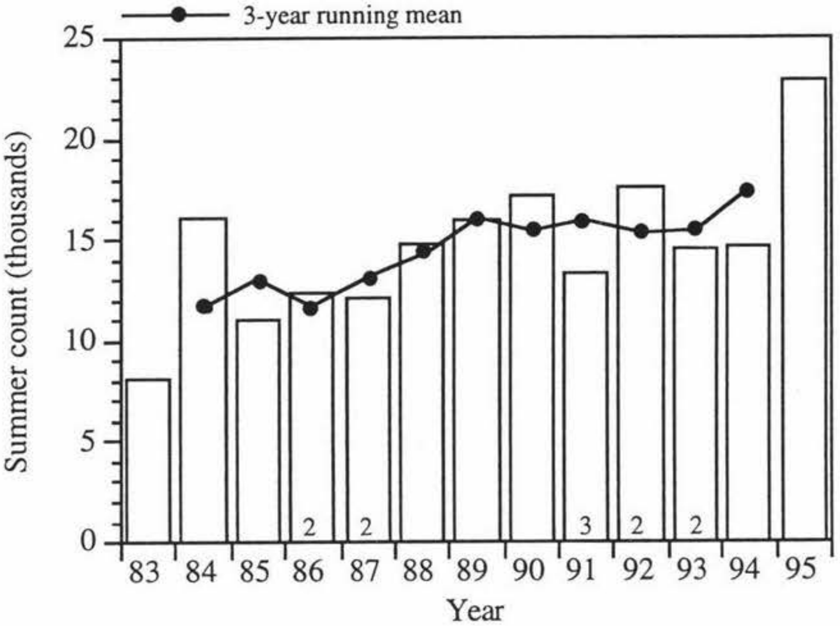


Figure 9.2 Counts of godwits at Farewell Spit from 1983 to 1995. Bars represent the summer count in that year, while the line is the three-year running mean (mean of the year in question and the year before and after this). Where the summer count represents the mean of more than one count, this is indicated by a number above the year.

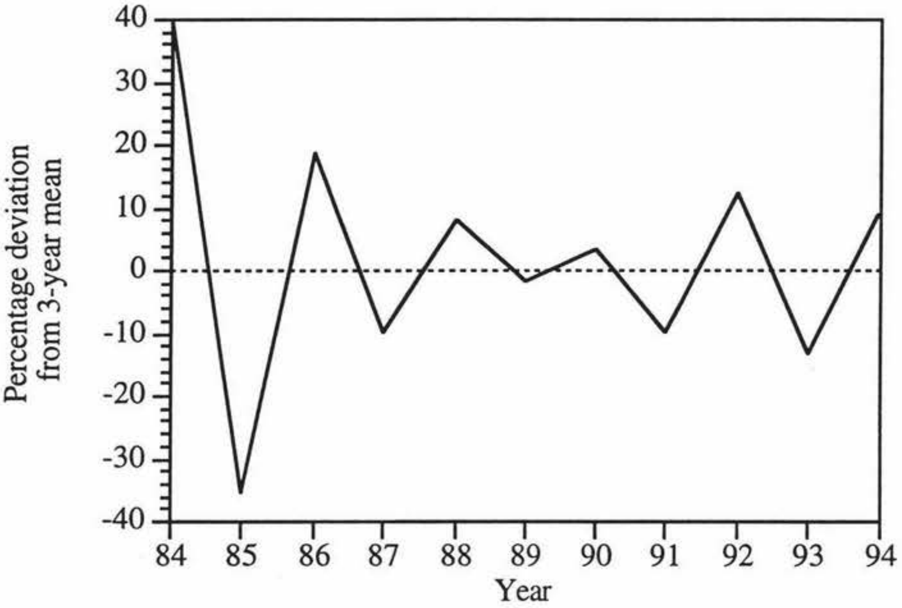


Figure 9.3 Percentage deviation from three-year running mean for counts of knots on Farewell Spit

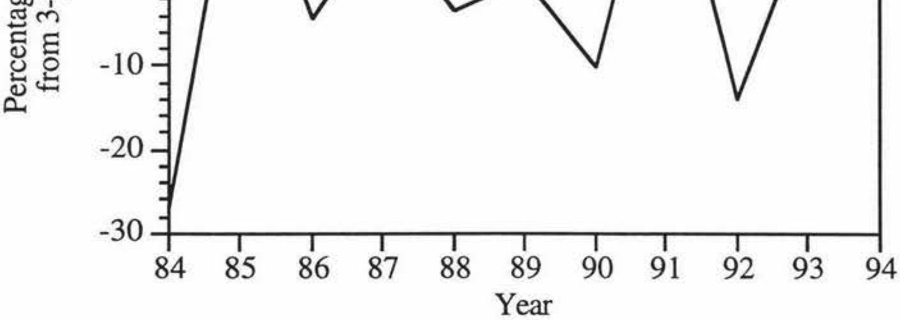


Figure 9.4 Percentage deviation from three-year running mean count for counts of godwits on Farewell Spit.

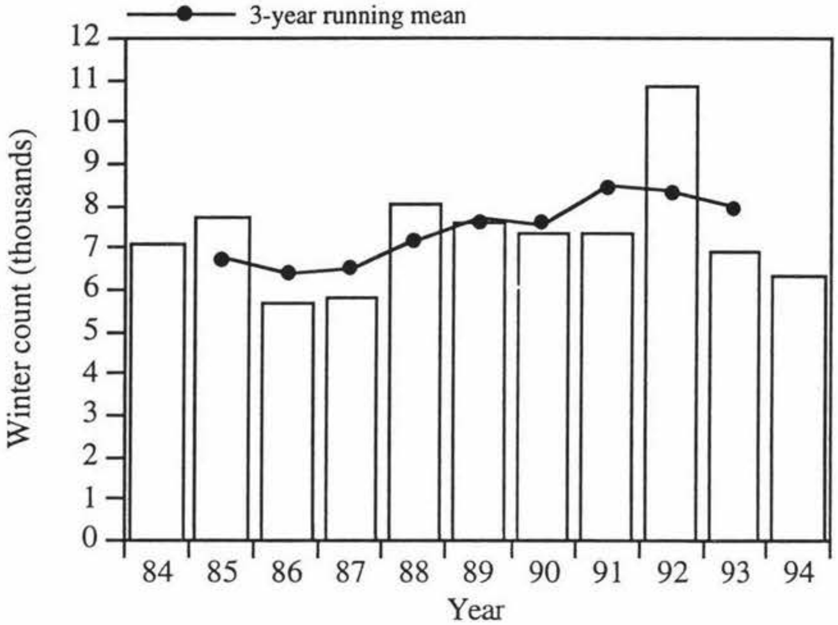


Figure 9.5 Count of oystercatchers at Farewell Spit from 1984 to 1995. Bars represent the winter count in that year, while the line is the three-year running mean (mean of the year in question and the year before and after this).

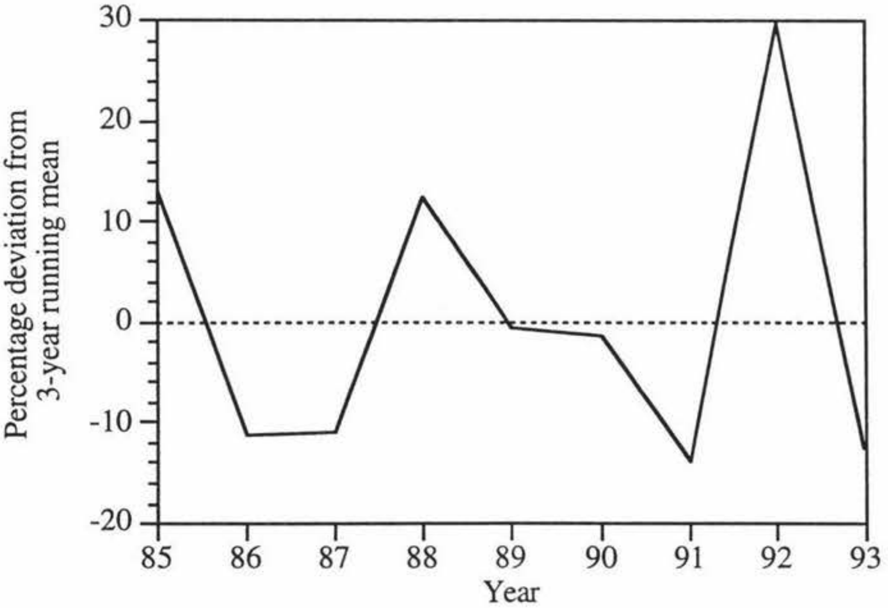


Figure 9.6 Percentage deviation from three-year running mean count for winter counts of oystercatchers on Farewell Spit

Pied Oystercatcher maximum numbers in winter have shown generally only small variations over the past decade (Fig 9.5), with the exception of a large count in 1992. Without the influence of that count, the net result would be a static population over the ten-year period. There is no evidence for any cyclicity in the population (Fig 9.6).

Knot and oystercatcher numbers are not increasing on Farewell Spit - is this due to factors on the spit or does it relate to a static national population size? For knots, a negative correlation for both actual summer counts and 3-year running means between Farewell Spit and national censuses shows that numbers on the spit are essentially independent of national numbers (counts, $r = -0.17$; 3-year mean, $r = -0.55$). This suggests knot numbers may be limited at the spit by on-site factors. In contrast, there are stronger positive relationships between these measures for godwits, indicating that their numbers on the spit are determined to a large degree by numbers arriving in New Zealand (counts, $r = 0.52$; 3-year mean, $r = 0.59$).

Pied Oystercatchers show virtually no relationship between winter counts on Farewell Spit and national censuses ($r = 0.21$), and a shallow negative relationship in 3-year running means ($r = -0.38$). Oystercatcher numbers are apparently also largely independent of the national population.

Evidence for limitation?

If numbers are limited, then we should expect evidence of any of competition/interference, depletion of food, and regulation of numbers (Chapter 8). The indications are that godwit numbers are currently increasing, while oystercatchers are fairly static. Knot numbers are slowly decreasing. Knots and oystercatchers may thus be expected to show some of the other characteristics associated with a population at carrying capacity.

In knots, four pieces of evidence point towards a difficult existence.

1. A long working day (Chapter 4). On spring tides during the premigratory period knots can only just maintain the same feeding time as on neap tides, due to tidal covering of feeding grounds. In absolute terms, feeding time in the premigratory period is very long.
2. Due to this long working day and probable extensive fat deposition (Chapter 5: both Farewell Spit and Firth of Thames birds face similar flight lengths), it appears that knots may approach their metabolic ceiling, which sets a physiological limit to working capacity.

3. Low prey levels (Chapter 3). While benthic sampling was insufficient to definitively prove that prey levels are low, the harvestable biomass of bivalve shellfish at all sampling occasions was much lower than comparative sites globally. That this is not fiction is implied by the next point.
4. A broad diet, representing the full suite of possible prey species, including crustacea. Classical foraging theory predicts that as prey levels rise, so does specialisation. The unspecialised of knots is consistent with low prey abundance. The presence of small crustacea in the diet tidal flats indicates that these were being taken to supplement an insufficient bivalve presence.

These points, combined with the fact that numbers show no relation to national censuses provide strong inferential evidence for knots being limited on Farewell Spit. Detailed studies on the biology (focussing on reproduction and growth) of bivalves might suggest whether there are systematic factors causing knot numbers to decline. Hampering this is the fact that we know nothing of mass changes in these birds. The estimate of basic and departure masses (Chapter 5) comes from Auckland. It would be preferable to have direct data on fattening rates from Farewell Spit. However, a knot leg-flagged in Auckland was seen on Farewell Spit (per. obs.) indicating that there is some interchange between these areas, and the fact that Farewell Spit knots probably do fly to Australia (Chapter 7) supports the use of these data (but see above). The assumption here is that departure equates with success, but I have discussed in Chapter 8 how mortality may be expressed off-site. A long-term decrease in knot populations on Farewell Spit could arise through a small percentage of the population failing to deposit enough nutrients to migrate and return successfully. Waders can show very high site-fidelity, so it is important to discover how discrete wader populations are around New Zealand. While Auckland-banded godwits and knots have been seen on Farewell Spit, these are only three and one individuals respectively out of totals flagged of 248 and 382 respectively (A.C.Riegen, pers. comm.). If knots are highly site-faithful then a declining population could arise through birds failing to return from migration.

Oystercatcher numbers are fairly static, and show no relation to national counts. They feed for the smallest time of any of the three waders studied, and estimates of food intake suggest they can meet their requirements on most prey types. There is not then any obvious explanation for the lack of correlation between national and Spit numbers. For a bird such as the oystercatcher, interference is the likely density-dependent mechanism that can lower intake rates (Chapter 8). Individual variations in feeding and fighting success then become important in determining intake rates. The degree of individual dietary specialisation in oystercatchers leads to lower competition than if all birds fed on the same prey. The degree of flexibility in feeding then becomes important - if a prey is exhausted (eg. *Travisia*) then those specialists must either emigrate or change their diet. If attempting the latter they will probably be at a competitive (or morphological, given differences in bill shape with diet) disadvantage. Dietary specialisation, while enabling coexistence of many birds when prey diversity is adequate, may restrict their options at times when it is not.

A brief (single-year) study is unlikely to reveal the causes of a long-term restriction in population. Carrying capacity is dynamic (Chapter 8), with changes in benthic biomass between years being likely, even within a species. Condition of invertebrates can vary within and between years (Chapter 3), all of which affect the carrying capacity. Shorebirds can and do deplete stocks of benthic invertebrates (Chapter 8). This is most likely to happen with high densities of birds and high energy demands. If there is a minimum biomass or density threshold below which birds cannot successfully feed, then they could suffer limitation without total depletion. I do not have the data to assess this on Farewell Spit. Important taxa to focus on will be small bivalves (pipi and cockles) for knots, and *Travisia* for oystercatchers.

Interactions with Black Swans?

One area of concern to managers is possible interactions between Black Swans *Cygnus atratus* and waders. Black Swans occur in very large numbers on Farewell Spit when moulting, but their behaviour minimises interaction with waders. When feeding, most swans precede the tide out, feeding in water of less than about one metre depth so do not interact directly with waders. Swans regularly are seen on the tidal flats, especially during strong winds, but waders (which are present at generally low densities on the tidal flats) took no notice of any swans present.

Sagar *et al.* (1995) reviewed the ecological role of the Black Swan in New Zealand. Most studies concerned freshwater systems and relations to macrophytes and eutrophication. One gap in knowledge was the impact of swans on eelgrass beds, which requires quantitative data on *Zostera* biomass and growth rates. Byrom and Davidson (1992) noted swans cropped only the leaves of eelgrass, and were not seen grubbing for roots. I did see areas of disturbed eelgrass in sandy areas, but was never able to discern whether this was due to swans or rays. it is probable that rays are a greater source of disturbance of eelgrass in sandy areas than are swans.

If swans are neither directly interacting with waders, nor disturbing the sediment and invertebrates, then any interactions will be indirect. Aquatic herbivores typically have a low assimilation efficiency (Buchsbaum *et al.* 1986), and Mitchell & Wass (1995) estimated this to be 50 % for Black Swans. They will thus return much of their nutrient intake to the local ecosystem almost immediately, which can lead to increased growth and productivity of the beds, provided that eelgrass growth is sufficient to avoid depletion. There is no evidence for depletion around

Farewell Spit presently. It is possible that grazing by swans increases the throughput of nutrients in the estuarine system, "speeding up" the cycling. This could lead to enhanced invertebrate populations. Mapping of eelgrass beds of the Farewell Spit tidal flats (perhaps using infra-red aerial photography) would provide invaluable reference data for long-term comparisons.

Energetic costs: implications for wader distributions around New Zealand

The distribution of shorebirds within New Zealand should be viewed as a cost-benefit tradeoff, involving both energetic and competitive aspects. From a strictly energetic point of view, Arctic waders should settle in the Far North, where they incur lower travel and thermostatic costs than further south. If they did so, of course, then density-dependent interactions would become huge, and the fact that Arctic waders spread along the entire length of New Zealand (and even to the Chatham Islands) shows that this does not happen. Migration through the Far North would be very well suited to optimal migration modelling (Alerstam and Lindström 1990). Pied Oystercatchers can reduce travel costs by wintering close to the breeding grounds, but incur greater thermostatic costs.

I have modelled the energetic costs of living at three major sites for waders in New Zealand: the Firth of Thames (latitude 37° 08' S), Farewell Spit (latitude 40°33' S) and Southland (Invercargill: latitude 46°25' S). Southland is the coldest of the three sites, while Farewell Spit the windiest (twice as windy as the Firth of Thames). Solar radiation varies the least between the three sites of any of the climatic variables.

The costs for knots are shown in Figure 9.7. The greatest costs over summer are experienced in Southland, where the mean cost from October to March is 1.7 W (1.8 X BMR). The equivalent cost for Farewell Spit is 1.5 W (1.6 X BMR) and for the Firth of Thames is 1.15 W (1.2 X BMR). Spending the southern summer in the south of New Zealand is thus around 1.5 times as expensive as in the north, based on thermostatic costs alone.

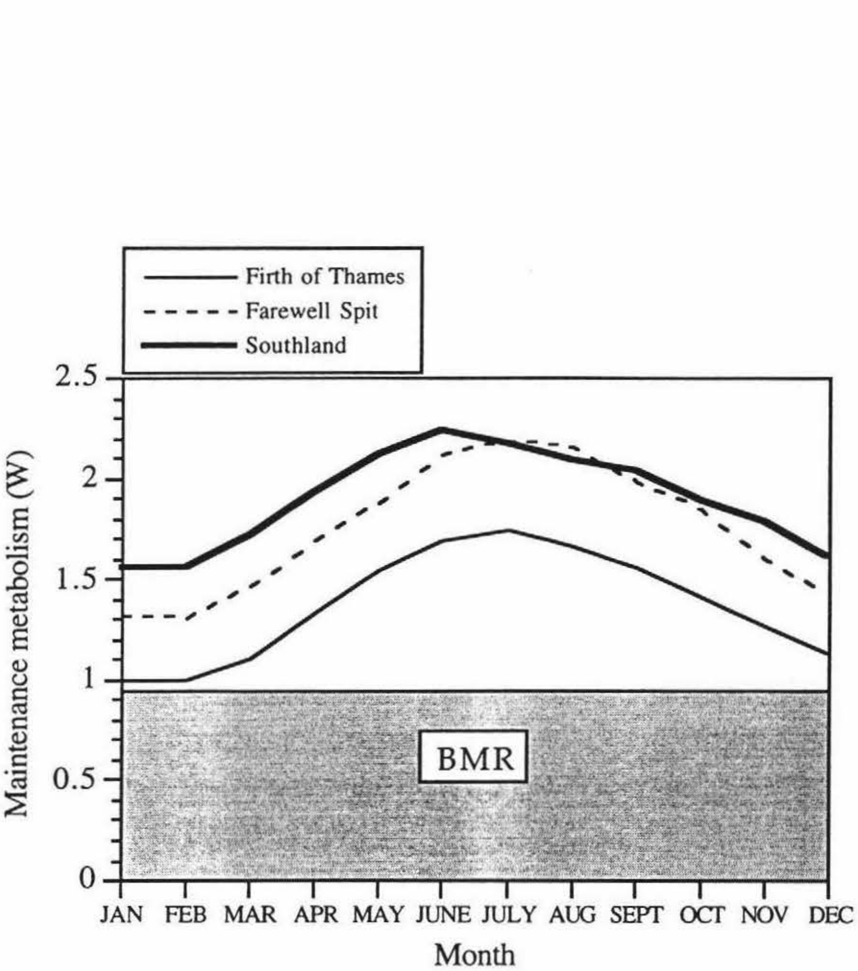


Figure 9.7 Maintenance metabolism for knots at the Firth of Thames (FoT), Farewell Spit and Southland. Predicted from climatic records using equations from Wiersma & Piersma (1994). Hatched area represents the Basal Metabolic Rate (BMR). Data for temperature are: Firth of Thames, 1946-1980; Farewell Spit, 1971-1980; and Southland (Invercargill airport), 1948-1980). Mean windspeed: Firth of Thames, 1959-1980; Farewell Spit, 1971-1980; Southland (Invercargill airport), 1942-1980. Global solar radiation: Firth of Thames, estimated from Auckland International Airport values, 1969-1980, adjusted for the difference in monthly mean sunshine hours at Auckland and the Firth); Farewell Spit, taken as equalling those at Nelson airport, 1969-1980, which is the nearest recording station; Southland (Invercargill airport), 1954-1980.

In addition to this is the travel cost. In the absence of direct information, this can be estimated by substituting into the equation of Davidson (1984b) the distance travelled and lean mass to calculate the required fat mass. The Southland estuaries are some 1350 km south of the Firth of Thames. For a 115 g knot flying at 65 km-h^{-1}, this would require 21 g of fat. For simplicity's sake, I assume an equivalent opposite movement in the northward migration, so that a total extra fat mass of 42 g is used in this return journey. This represents 1,680 kJ (1 g fat = 40 kJ energy). Translating this into W (J/s) over the six months results in 1,680,000 J/213 days/24 hours/60 mins/60 secs = 0.09 W. Compared with the 0.55 W thermostatic cost incurred by living in Southland rather than northern New Zealand, this travel cost is fairly insignificant. This is of course an oversimplification, as these birds may not stage in northern New Zealand at all, but it illustrates the point: travelling to southern New Zealand is likely to cost around 1.5-1.6 times the energy of stopping in northern New Zealand for the summer (1.79 W/1.15 W).

For Pied Oystercatchers breeding on South Island riverbeds and fields, migrating north incurs travel costs but encounters milder conditions over winter. Figure 9.8 shows the maintenance metabolism for oystercatchers at the three sites. At the Firth of Thames, thermostatic costs are actually lower than BMR up until May. BMR thus becomes the minimum cost over this period. From January to July (the period of main residence for oystercatchers away from the breeding grounds), costs at the Firth of Thames average 3.36 W. Over the same period, costs at Farewell Spit equal 3.9 W, and in Southland 4.1 W. Remaining in Southland is about 22% more expensive than wintering in the Firth of Thames. Counterbalancing this is the cost of flying to the Firth and back. Travel costs (as above, assuming a mass of 525 g and flight speed of 65 km-h^{-1}) result in 59 g of fat used on each journey. Over the seven month wintering period this represents a cost of 0.23 W, raising the cost of wintering in the Firth of Thames to around 3.6 W. This makes remaining in the far south only 14% more expensive. While this nevertheless is still a cost, in absolute terms, 4.1 W is low, being only 1.27 X BMR. Knots, for example, face higher relative costs even in summer on Farewell Spit.

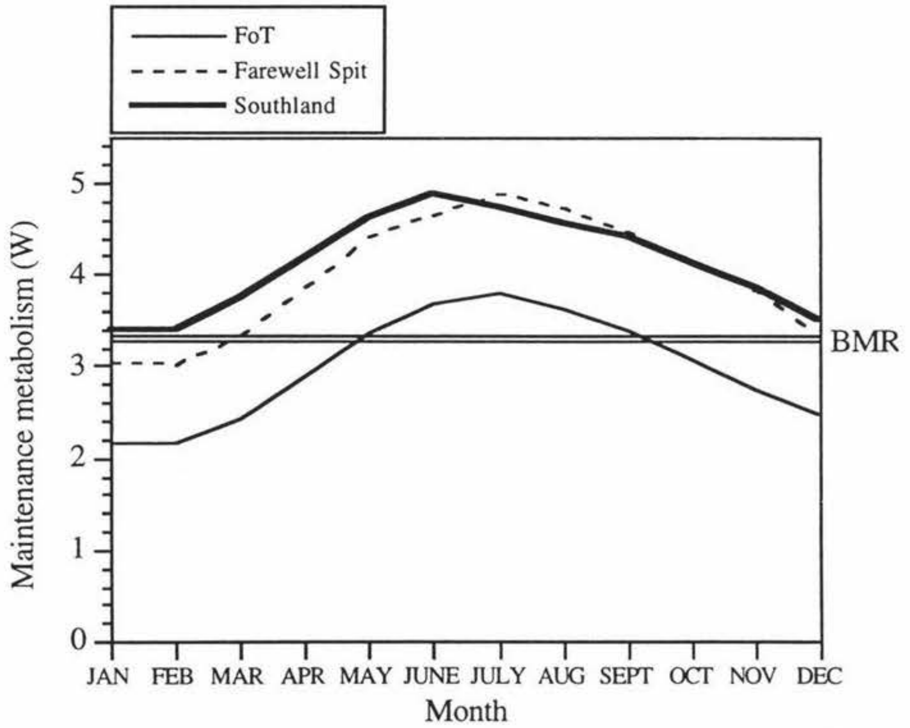


Figure 9.8 Maintenance metabolism for knots at the Firth of Thames (FoT), Farewell Spit and Southland. Predicted from climatic records using equations from Wiersma & Piersma (1994). BMR is shown by the double horizontal line.

Thermostatic costs obviously can be major components of the overall energy budget of migrating birds in New Zealand. The fact that arctic waders do travel to the south of New Zealand, and endemic breeders remain there over winter despite an apparent energetic cost shows that this need not be an over-riding concern. For arctic waders, such distributions could be explicable if competition was a strong force in northern New Zealand, forcing birds to migrate to southerly areas. This has been suggested to be important in wader distributions in the East Atlantic Flyway (Pienkowski and Evans 1984). Another proposed mechanism for long-distance migration is that waders track the carrying capacity of coastal habitat along a flyway, with southern hemisphere sites having high food levels and production over the non-breeding season, while northern hemisphere sites experience decreasing food supplies and high energy demands (Hockey *et al.* 1992). The suggestion that knots on Farewell Spit face low food supplies and a consequent long working day and marginal energy leeway would seems counter to this latter suggestion. This may be a site-specific characteristic, of course. Given that benthic productivity decreases with latitude (Hockey *et al.* 1992), complementary studies in northern and southern New Zealand on the food supply for migrating waders would be invaluable in assessing the likely role or interaction of the competition/production hypotheses.

The New Zealand population of Pied Oystercatchers has increased vastly over the past 50 years. In the Firth of Thames, counts in the 1940s recorded only few hundreds at the most: now censuses can tally almost 25,000 birds (A.C.Riegen, pers. comm.). The large majority of birds migrates to northern New Zealand for the winter, which would be expected on energetic grounds. However, it is probable that the overall energy cost associated with remaining near the breeding grounds is low enough that doing so is equally viable. This may possibly have even been the norm at lower population levels. At the Avon-Heathcote estuary, Christchurch, the current population peak occurs in autumn, with substantial use of the estuary as a staging site of birds en route to northern sites (Crossland 1992). In the past, maximum populations occurred in winter (A.C. Crossland, pers. comm.). Passage to northern sites was apparently small in the past, relative to the wintering population, whereas now it is much larger. This suggests that competition at southern sites is driving the northward migration of oystercatchers. Any (small) energetic benefit may be merely a useful byproduct of competition-necessitated dispersal.

FUTURE RESEARCH

This study has only scraped the surface of a number of topics relating to wader ecology on Farewell Spit and in New Zealand in general. The following topics are suggested as important routes to gaining a better understanding of shorebirds on Farewell Spit and in New Zealand.

Bird numbers On Farewell Spit knot numbers appear to have declined over the past decade. It is imperative that regular monitoring of numbers be continued. It is unfortunate that the national censuses conducted by the Ornithological Society of New Zealand have reached the end of their planned duration, as Farewell Spit counts will now have to be interpreted in isolation. Where possible, a series of counts should be made within a summer - this will allow peak counts to be identified, and variation in timing of numbers (and hence perceived maximum numbers in past counts) assessed.

Benthic food resources I was able to undertake only limited benthic sampling. Widespread benthic surveys would indicate just how representative my sites are. The long-term sustainability of benthic food resources is dependent on reproductive stocks and harvesting rates, and feedback links between the two. Inter-annual variations in food levels may be important. Given likely variation in demographic and condition factors due to environmental conditions, sustained sampling efforts may be required to gain robust interpretable data. Special effort should be directed as small bivalve populations, given their prevalence in the diet of knots.

Nutrient cycling in eelgrass beds and the effects of Black Swans should be investigated. While there does not appear to be any immediate impact on waders, it is important to discover the nature of swan impacts on eelgrass beds in the context of the whole intertidal ecosystem.

Knots The knot is the shorebird on which concern should be focussed, given that its population appears to be static or declining. Concerted effort in determining intake rates in the premigratory period could be successful. Focussing on the knot allows restriction of benthic sampling to small molluscs, although there will always be the problem of accounting for crustacea in their diet.

If the suggested mechanism for a slow long-term decline in knot numbers (the lowest section of the population failing to achieve the required mass for migration) is to be evaluated, we need data on variation in departure condition between individuals. This requires either capturing large amounts of birds, or killing some. As selection on waders may be periodic (see discussion, Chapter 7) inter-annual differences in departure condition would ideally be assessed. Such an enterprise is currently beyond the resources of wader-workers in New Zealand. However, attempts should be made to try catching waders using various methods. Expedition efforts could then be considered in the future (see eg. Ens *et al.* 1990).

Movements within New Zealand Lacking in New Zealand are data on site-fidelity of waders away from the Auckland region (where banding occurs). A few leg-flagged individuals from Auckland have been seen on Farewell Spit. Data on how much mixing occurs between populations is required to assess the importance of site-specific limitation of numbers. For instance, does Farewell Spit regularly receive an "overflow" from northern harbours, or do most birds return directly there, and is there a difference between godwits and knots? If knots are declining on Farewell Spit we need to know whether this is due to mortality affecting the return of birds, or whether birds change their locality in a subsequent year but are not replaced by immigration. These data are required also if we are to assess the relative roles of energetic and competitive factors in explaining the decision to settle at a given site.

References

Abramson, M. (1979). Vigilance as a factor influencing flock formation among curlews *Numenius arquata*. The Ibis 121, 213-216.

Alcorn, M., R. Alcorn & M. Fleming (1994). Wader movements in Australia. Australasian Wader Studies Group, Royal Australasian Ornithologists Union. R.A.O.U Report No. 94.

Alerstam, T., G.A. Gudmundsson & K. Johannesson (1992). Resources for long-distance migration: intertidal exploitation of *Littorina* and *Mytilus* by knots *Calidris canutus* in Iceland. Oikos 65, 179-189.

Alerstam, T., G.A. Gudmundsson, P.E. Jonsson, J. Karlsson & Å. Lindström (1990). Orientation, migration routes and flight behaviour of knots, turnstones and brant geese departing from Iceland in spring. Arctic 43, 201-214.

Alerstam, T. & Å. Lindström (1990). Optimal Bird Migration: The Relative Importance of Time, Energy, and Safety. Bird Migration. Ed. E. Gwinner. Berlin Heidelberg, Springer-Verlag, 331-359.

Alonso, J.A., J.C. Alonso, L.M. Varrascal & R. Muñoz-Pulido (1994). Flock size and foraging decisions in central place foraging White Storks, *Ciconia ciconia*. Behaviour 129, 279-292.

Baird, D., P.R. Evans, H. Milne & M.W. Pienkowski (1985). Utilization by shorebirds of benthic invertebrate production in intertidal areas. Oceanography and Marine Biology AnnualReview 23, 573-597.

Baker, A.J. (1969). The comparative biology of New Zealand Oystercatchers. MSc., University of Canterbury.

Baker, A.J. (1974a). Criteria for aging and sexing New Zealand oystercatchers. N.Z. Journal of Marine and Freshwater Research 8, 211-21.

Baker, A.J. (1974b). Prey-specific feeding methods of New Zealand oystercatchers. Notornis 21, 219-233.

Baker, A.J., T. Piersma & L. Rosenmeier (1994). Unraveling the intraspecific phylogeny of knots *Calidris canutus* : a progress report on the search for genetic markers. Journal für Ornithologie 135, 599-608.

Barter, M. (1989). Bar-tailed Godwit *Limosa lapponica* in Australia. Part 1: Races, breeding areas and migration routes. The Stilt 14, 43-48.

Barter, M. (1992). Distribution, abundance, migration and moult of the Red Knot *Calidris canutus rogersi*. Wader Study Group Bulletin 64, Supplement, 64-70.

Barter, M., A. Jessop & C. Minton (1988). Red Knot *Calidris canutus rogersi* in Australia, Part 2: biometrics and moult in Victoria and North-Western Australia. The Stilt 13, 20-27.

Barter, M. & Tian Hou Wang (1990). Can waders fly non-stop from Australia to China? The Stilt 17, 36-39.

Bartlett, R.M. (1985). Farewell Spit Vegetation. Department of Lands and Survey, Nelson. .

Batschelet, E. (1981). Circular Statistics in Biology. London, Academic Press.

Battley, P.F. (MS). The northward migration of Arctic waders in New Zealand: departure behaviour, timing and possible migration routes of Red Knots and Bar-tailed Godwits from Farewell Spit, North-West Nelson. Emu.

Battley, P.F. & T. Piersma (MS). Body composition of Red Knots *Calidris canutus rogersi* in northern New Zealand during the premigratory period. Submitted to Notornis.

Beukema, J.J. (1994). Increased mortality in alternative bivalve prey during a period when the tidal flats of the Dutch Wadden Sea were devoid of mussels. Netherlands Journal of Sea Research 31, 395-406.

Beukema, J.J., K. Essink, H. Michaelis & L. Zwarts (1994). Year-to-year variability in the biomass of macrobenthic animals on tidal flats of the Wadden Sea: how predictable is this food source for birds? Netherlands Journal of Sea Research 31, 319-330.

Bijlsma, R. B. (1990). Predation by large falcons on wintering waders on the Banc d'Arguin. Ardea 78, 75-82.

Blem , C.R. (1990). Avian energy storage. Current Ornithology. Ed. D. M. Power. New York, Plenum Press. 7.

Blokpoel, H. & W.J. Richardson (1978). Weather and spring migration of snow geese across southern Manitoba. Oikos 30, 350-363.

Boates, J.S. & J.D. Goss-Custard (1992). Foraging behaviour of oystercatchers *Haematopus ostralegus* specializing on different species of prey. Canadian Journal of Zoology 70, 2398-2404.

Boyd, H. (1992). Arctic summer conditions and British numbers: an explanatory analysis. Wader Study Group Bulletin 64, Supplement, 144-152.

Bryant, D.M. (1979). Effects of prey density and site character on estuary usage by overwintering waders (Charadrii). Estuarine and Coastal Marine Science 9, 369-384.

Buchsbaum, R., J. Wilson & I. Valeila (1986). Digestibility of plant constituents by Canada Geese and Atlantic Brant. Ecology 67, 386-393.

Burger, J. (1980). Age differences in foraging Black-necked Stilts in Texas. The Auk 97, 633-636.

Burger, J. & M. Gochfeld (1985). Age-related differences in foraging in the Masked Lapwing *Vanellus miles* in Australia. Emu 85, 49-50.

Burger, J. & M. Howe (1975). Notes on winter feeding behaviour and molt in Wilson's Phalaropes. The Auk 92, 442-451.

Buxton, N.E. (1989). Observations on the low weights of Knot in the Western Isles of Scotland. Ringing and Migration 10, 9-12.

Byrom, A.E. & R.J. Davidson (1992). Investigation of behavioural patterns of Black Swan at Farewell Spit and Whanganui Inlet. . Department of Conservation Nelson/Marlborough Conservancy Occasional Publication No. 3.

Caraco, T., S. Martindale & H.R. Pulliam (1980). Avian flocking in the presence of a predator. Nature 285, 400-401.

Castro, G. & J.P. Myers (1988). A statistical method to estimate the cost of flight in birds. Journal of Field Ornithology 59, 369-380.

Castro, G. & J.P. Myers (1989). Flight range estimates for shorebirds. The Auk 106, 474-476.

Castro, G., B.A. Wunder & F.L. Knopf (1991). Temperature-dependent loss of mass by shorebirds following capture. Journal of Field Ornithology 62, 314-318.

Cayford, J.T. & J.D. Goss-Custard (1990). Seasonal changes in the size selection of mussels, *Mytilus edulis*, by oystercatchers, *Haematopus ostralegus*: an optimality approach. Animal Behaviour 40, 609-624.

Crisp, D.J. (1984). Energy flow measurements. Methods for the Study of Marine Benthos. Ed. N. A. Holme & A. D. McIntyre. London, Blackwell Scientific Publications, 284-372.

Crossland, A.C. (1992). Monthly populations of birds on the Avon-Heathcote Estuary. Appendix 6. The Estuary: where our rivers meet the sea: Christchurch's Avon-Heathcote Estuary and Brooklands

Lagoon. Ed. S.-J. Owen. Christchurch, Parks Unit, Christchurch City Council.

Dann, P. (1979). Food robbing of Bar-tailed Godwits by Silver Gulls in Westernport Bay, Victoria. Corella 3, 84-85.

Dann, P. (1987). The feeding behaviour and ecology of shorebirds. Shorebirds in Australia. Ed. B. Lane. Melbourne, Nelson, 10-20.

Davidson, N.C (1981a). Seasonal changes in nutritional condition of shorebirds (Charadrii) during the non-breeding season. PhD. thesis, University of Durham, England.

Davidson, N.C. (1981b). Survival of shorebirds (Charadrii) during severe weather: the role of nutritional reserves. Feeding and Survival Strategies of Estuarine Organisms. Ed. N. V. Jones & W. J. Wolff. New York and London, Plenum Press, 231-249.

Davidson, N.C. (1983). Formulae for estimating the lean weight and fat reserves of live shorebirds. Ringing and Migration 4, 159-166.

Davidson, N.C. (1984a). Changes in the condition of dunlins and knots during short-term captivity. Canadian Journal of Zoology 62, 1724-1731.

Davidson, N.C. (1984b). How valid are flight range estimates for waders? Ringing and Migration 5, 49-64.

Davidson, N.C. & N.A. Clark (1985). The effects of severe weather in January and February 1985 on waders in Britain. Wader Study Group Bulletin 44, 10-16.

Davidson, N.C. & P.R. Evans (1988). Prebreeding accumulation of fat and muscle protein by arctic-breeding shorebirds. Acta XIX Congr. Internat. Ornithol., Ottawa.

Davidson, N.C., D.d'A. Laffoley & J.P. Doody (1994). Land-claim on British estuaries: changing patterns and conservation imnplications. Coastal Zone Topics: Processes, Ecology and Management 1.

Davidson, N.C., D. d'A. Laffoley, J.P. Doody, L.S. Way, J. Gordon, R. Key, C.M. Drake, M.W. Pienkowski, R. Mitchell & K.L. Duff (1991). Nature conservation and estuaries in Great Britain. Peterborough, Nature Conservancy Council.

Davidson, N.C. & T. Piersma (1992). The migration of Knots: conservation needs and implications. Wader Study Group Bulletin 64, Supplement, 198-209.

Davidson, N.C., J.D. Uttley & P.R. Evans (1986). Geographic variation in lean mass of dunlins wintering in Britain. Ardea 74, 191-198.

Davidson, N.C. & J.R. Wilson (in press). Does nutritional condition in spring influence the breeding-ground survival of adult shorebirds? Journal of Avian Biology.

Dekinga, A. & T. Piersma (1993). Reconstructing diet composition on the basis of faeces in a mollusc-eating wader, the Knot Calidris canutus. Bird Study 40, 144-156.

Dekker, D. (1988). Peregrine falcon and merlin predation on small shorebirds and passerines in Alberta. Canadian Journal of Zoology 66, 925-928.

Dhondt, A.A. (1987). Cycles of lemmings and Brent Geese *Branta b. bernicla*: a comment on the hypothesis of Roselaar and Summers. Bird Study 34, 151-154.

Dhondt, A.A. (1988). Carrying capacity: a confusing concept. Acta Oecologia 9, 337-346.

Dick, W.J.A., M.W. Pienkowski, M. Waltner & C.D.T. Minton (1976). Distribution and geographical origins of Knot *Calidris canutus* wintering in Europe and Africa. Ardea 64.

Dick, W.J.A., T. Piersma & P. Prokosch (1987). Spring migration of the Siberian Knots *Calidris canutus canutus*: results of a co-operative Wader Study Group project. Ornis Scandinavica 18, 5-16.

Drent, R.H. & S. Daan (1980). The prudent parent: energetic adjustments in avian breeding. Ardea 68, 225-252.

Dugan, P.J. (1981). The importance of nocturnal foraging in shorebirds: a consequence of increased invertebrate prey activity. Feeding and survival strategies of estuarine organisms. Ed. N. V. Jones & W. J. Wolff. New York and London, Plenum Press, 251-260.

Durell, S.E.A. le V. dit. (1984). Prey selection within a size-class of mussels, *Mytilus edulis* , by oystercatchers. Animal Behaviour 32, 1197-1203.

Durell, S.E.A.le V. dit., J.D. Goss-Custard & R.W.G. Caldow (1993). Sex-relayed differences in diet and feeding method in the oystercatcher *Hamatopus ostralegus*. Journal of Animal Ecology 62, 205-215.

Ekman, J. & M. Hake (1988). Avian flocking reduces starvation risk: an experimental demonstration. Behavioural Ecology and Sociobiology 22, 91-94.

Ekman, J. & B. Rosander (1987). Starvation risk and flock size of the social forager: when there is a foraging cost. Theoretical Population Biology 31, 167-177.

Elliot, C.C.H., M. Waltner, L.G. Underhill, J.S. Pringle & W.J.A. Dick (1976). The migration system of the Curlew Sandpiper *Calidris ferruginea* in Africa. Ostrich 47, 191-213.

Engelmoer, M., T. Piersma, W. Altenburg & R. Mes (1984). The Banc d'Arguin (Mauritania). Coastal waders and wildfowl in winter. Ed. P. R. Evans*et al.* Cambridge, Cambridge University Press, 293-310.

Ens, B. (1982). Size selection in mussel-feeding oystercatchers. The Wader Study Group Bulletin 34, 16-20.

Ens, B.J. & J.D. Goss-Custard (1984). Interference among oystercatchers *Haematopus ostralegus*, feeding on mussels *Mytilus edulis*, on the Exe Estuary. Journal of Animal Ecology 53, 217-231.

Ens, B.J., T. Piersma & R.H. Drent (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., T. Piersma, W. J. Wolff & L. Zwarts (1990). Homeward bound: problems waders face when migrating from the Banc d'Arguin, Mauritania, to their northern breeding grounds in spring. Ardea 78, 1-16.

Espin, P.M.J., R.M. Mather & J. Adams (1983). Age and foraging success in Black-winged Stilts *Himantopus himantopus*. Ardea 71, 225-228.

Evans, A. (1987). Relative availability of the prey of wading birds by day and night. Marine Ecology Progress Series 37, 103-107.

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

Evans, P.R. (1979). Adaptations shown by foraging shorebirds to cyclical variations in the activity and availability of their intertidal prey. Cyclic phenomena in marine plants and animals. Ed. E. Naylor & R. G. Hartnoll. Oxford, Pergamon Press, 357-366.

Evans, P.R. (1981). Migration and dispersal of shorebirds as a survival strategy. Feeding and survival strategies of estuarine organisms. Ed. N. V. Jones & W. J. Wolff. New York and London, Plenum Press, 275-290.

Evans, P.R. & N.C. Davidson (1990). Migration Strategies and Tactics of Waders Breeding in Arctic and North Temperate Latitudes. Bird Migration. Ed. E. Gwinner. Berlin Heidelberg, Springer-Verlag, 387-398.

Evans, P.R., N.C. Davidson, T. Piersma & M.W. Pienkowski (1991). Implications of habitat loss at migration staging posts for shorebird populations. Acta XX Int. Orn. Congr.

Evans, P.R., N.C. Davidson, J.D. Uttley & R.D. Evans (1992). Premigratory hypertrophy of flight muscles: an ultrastructural study. Ornis Scandinavica 23, 238-243.

Evans, P.R. & P.J. Dugan (1984). Coastal birds: numbers in relation to food resources. Coastal waders and wildfowl in winter. Ed. P. R. Evans*et al.* Cambridge, Cambridge University Press, 8-28.

Evans, P.R. , D.M. Herdson, P.J. Knights & M.W. Pienkowski (1979). Short-term effects of reclamation of part of Seal Sands, Teesmouth, on wintering waders and Shelduck. 1. Shorebird diets, Invertebrate densities, and the impact of predation on the invertebrates. Oecologia (Berl.) 41, 183-206.

Evans, P.R. & P.C. Smith (1975). Studies on shorebirds at Lindisfarne, Northumberland. 2. Fat and pectoral muscle as indicators of body condition in the bar-tailed godwit. Wildfowl 26, 64-76.

Evans, P.R. & D.J. Townshend (1988). Site faithfulness of waders away from the breeding grounds: how individual migration patterns are established. IX Int. Orn. Congr., Ottawa.

Fleischer, R.C. (1983). Relationships between tidal oscillations and Ruddy Turnstone flocking, foraging, and vigilance behaviour. The Condor 85, 22-29.

Gilbert, M.A. (1977). The behaviour and functional morphology of deposit feeding in *Macoma balthica* (Linne, 1758), in New England. Journal of mollusc studies 43, 18-27.

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

Goss-Custard, J.D. (1979). Effect of habitat loss on the numbers of overwintering shorebirds. Studies in Avian Biology 2, 167-177.

Goss-Custard, J.D. (1980). Competition for food and interference among waders. Ardea 68, 31-52.

Goss-Custard, J.D. (1984a). Foraging behaviour of wading birds and the carrying capacity of estuaries. Behavioural Ecology - Ecological Consequences of Adaptive Behaviour. Ed. R. M. Sibley & R. H. Smith. Oxford, Blackwell Scientific Publications, 169-188.

Goss-Custard, J.D. (1984b). Intake rates and food supply in migrating and wintering shorebirds. Shorebirds: migration and foraging behaviour. Ed. J. Burger & B. L. Olla. New York, Plenum Press, 233-270.

Goss-Custard, J.D., R.W.G. Caldow & R.T. Clarke (1992). Correlates of the density of foraging oystercatchers *Haematopus ostralegus* at different population sizes. Journal of Animal Ecology 61, 159-173.

Goss-Custard, J.D., R.W.G. Caldow, R.T. Clarke, S.E.A. le V. dit. Durell & W.J. Sutherland (1995a). Deriving population parameters from individual variations in foraging behaviour. I. Empirical game theory distribution model of oystercatchers Haematopus ostralegus feeding on mussels Mytilus edulis. Journal of Animal Ecology 64, 265-276.

Goss-Custard, J.D., R.W.G. Caldow, R.T. Clarke & A.D. West (1995b). Deriving population parameters from individual variations in foraging behaviour. II. Model tests and population parameters. Journal of Animal Ecology 64, 277-289.

Goss-Custard, J.D. & K. Charman (1976). Predicting how many wintering waterfowl an area can support. Wildfowl 27, 157-158.

Goss-Custard, J.D., R.T. Clarke, K.B. Briggs, B.J. Ens, K.-M. Exo, C. Smit, A.J. Beintema, R.W.G. Caldow, D.C. Catt, N.A. Clark, S.E.A. le V. dit Durell, M.P. Harris, J.B. Hulscher, P.L. Meininger, N. Picozzi, R. Prys-Jones, U.N. Safriel & A.D. West (1995c). Population consequences of winter habitat loss in a migratory shorebird. I. Estimating model parameters. Journal of Applied Ecology 32, 320-336.

Goss-Custard, J.D., R.T. Clarke, S.E.A. le V. dit Durell, R.W.G. Cladow & B.J. Ens (1995d). Population consequences of winter habitat loss in a migratory shorebird. II. Model predictions. Journal of Applied Ecology 32, 337-351.

Goss-Custard, J.D. & S.E.A. le V. dit. Durell (1984). Feeding ecology, winter mortality and the population dynamics of Oystercatchers on the Exe estuary. Coastal Waders and Wildfowl in Winter. Ed. P. R. Evans*et al.* Cambridge, Cambridge University Press, 190-208.

Goss-Custard, J.D. & S.E.A. le V. dit. Durell (1988). The effect of dominance and feeding method on the intake rates of oystercatchers, *Haematopus ostralegus*, feeding on mussels. Journal of Animal Ecology 57, 827-844.

Goss-Custard, J.D. & S.E.A.le V.dit Durell (1990). Bird behaviour and environmental planning: approaches in the study of wader populations. The Ibis 132, 273-289.

Goss-Custard, J.D. & S.E.A. le V. dit Durell (1994). The availability and quality of the mussel prey (*Mytilus edulis*) of oystercatchers (*Haematopus ostralegus*). Netherlands Journal of Sea Research 31, 419-439.

Goss-Custard, J.D., S.E.A. le Vit dit Durell, S. McGrorty & C. Reading (1982). Use of mussel *Mytilus edulis* beds by oystercatcher *Haematopus ostralegus* according to age and population size. Journal of Animal Ecology 51, 543-554.

Goss-Custard, J.D., S.E.A. Le V dit Durell, S. McGrorty, C.J. Reading & R.T. Clarke (1981). Factors affecting the occupation of mussel (*Mytilus edulis*) beds by oystercatchers (*Haematopus ostralegus*) on the Exe estuary, Devon. Feeding and survival strategies of estuarine organisms. Ed. N. V. Jones & W. J. Wolff. New York and London, Plenum Press, 217-229.

Goss-Custard, J.D., D.G. Kay & R.M. Blindell (1977). The density of migratory and overwintering Redshank, *Tringa totanus* (L.) and Curlew, *Numenius arquata* (L.), in relation to the density of their prey in South-East England. Estuarine and Coastal Marine Science 5, 497-510.

Goss-Custard, J. D. & M.G. Yates (1992). Towards predicting the effect of salt-marsh reclamation on feeding bird numbers on the Wash. Journal of Applied Ecology 29, 330-340.

Groves, S. (1978). Age-related differences in Ruddy Turnstone foraging and aggessive behaviour. The Auk 95, 95-103.

Gudmundsson, G.A. (1993). The spring migration of arctic birds in southwest Iceland, as recorded by radar. The Ibis 135, 166-176.

Gudmundsson, G.A. & Å. Lindström (1992). Spring migration of Sanderlings *Calidris alba* through SW Iceland: wherefrom and whereto? Ardea 80, 315-326.

Gudmundsson, G.A., Å. Lindström & T. Alerstam (1991). Optimal fat loads and long-distance flights by migrating Knots *Calidris canutus*, Sanderlings *C. alba* and Turnstones *Arenaria interpres*. The Ibis 133, 140-152.

Gwinner, E. (1990). Circannual Rhythms in Bird Migration: Control of Temporal Patterns and Interactions with Photoperiod. Bird Migration. Ed. E. Gwinner. Berlin Heidelberg, Springer-Verlag, 257-268.

Hawkins, J.M. (1988). The Farewell Spit gannetry: a new sea level colony. Notornis 35, 249-260.

Heppleston, P.B. (1971). The comparative breeding ecology of oystercatchers (*Haematopus ostralegus* L.) in inland and coastal habitats. Journal of Animal Ecology 41, 23-51.

Hicklin, P.W. & P.C. Smith (1984). Selection of foraging site and invertebrate prey by migramt Semipalmated Sandpipers, *Calidris pusilla* (Pallas), in Minas Basin, Bay of Fundy. Canadian Journal of Zoology 62, 2201-2210.

Hockey, P.A.R., R.A. Navarro, B. Kalejta & C.R. Velasquez (1992). The riddle of the sands: why are shorebird densities so high in southern estuaries? The American Naturalist 140, 961-979.

Hulscher, J.B. (1976). Localisation of cockles (*Cardium edule* L.) by the Oystercatcher (*Haematopus ostralegus* L.) in darkness and daylight. Ardea 64, 292-310.

Hulscher, J.B. (1982). The Oystercatcher *Haematopus ostralegus* as a predator of the bivalve *Macoma balthica* in the Dutch Wadden Sea. Ardea 70, 89-152.

Jane, G.T. (1989). Farewell Spit Nature Reserve and Puponga Farm Park. A Resource Summary. Deprtment of Conservation, Nelson Regional Office. Management Plan Series 2.

Johnson, C. (1985). Patterns of seasonal weight variation in waders on the Wash. Ringing & Migration 6, 19-32.

Kalejta, B. (1992). Time budgets and predatory impact of waders at the Berg River Estuary, South Africa. Ardea 80, 327-342.

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

King, J.R. & M.E. Murphy (1985). Periods of nutritional stress in the annual cycles of endotherms: fact or fiction? American Zoologist 25, 955-964.

Lambeck, R.H.D., A.J.J. Sandee & L. de Wolf (1989). Long-term patterns in the wader usage of an intertidal flat in the Oosterschelde (SW Netherlands) and the impact of the closure of an adjacent estuary. Journal of Applied Ecology 26, 419-431.

Lank, D.B. (1983). Migratory behaviour of semipalmated sandpipers at inland and coastal staging areas. Unpublished PhD thesis, Cornell University.

Lank, D.B. (1989). Why fly by night? Inferences from tidally induced migratory departures of sandpipers. Journal of Field Ornithology 60, 154-161.

Leewis, R.J., H.J.M. Baptist & P.L. Meininger (1984). The Dutch Delta. Coastal Waders and Wildfowl in Winter. Ed. P. R. Evans*et al.* Cambridge, Cambridge University Press, 253-260.

Leuven, R.S.E.W., T.L.M. Brock & H.A. van Druten (1985). Effects of preservation on dry- and ash-free dry weight biomass of some common aquatic macroinvertebrates. Hydrobiologia 127, 151-159.

Lima, S.L. (1995). Back to the basics of anti-predatory vigilance: the group-size effect. Animal Behaviour 49.

Lindström, Å. (1989). Flock finch size and risk of hawk predation at a migratory stopover site. The Auk 106, 225-232.

Lindström, A. & T. Alerstam (1992). Optimal fat loads in migrating birds: a test of the time-minimization hypothesis. American Naturalist 140(3), 477-491.

Lindström, Å., S. Daan & G.H. Visser (1994). The conflict between moult and migratory fat deposition: a photoperiodic experiment with bluethroats. Animal Behaviour 48, 1173-1181.

Lindström, Å. & T. Piersma (1993). Mass change in migrating birds: the evidence for fat and protein storage re-examined. The Ibis 135, 70-78.

Lopez, B. (1986). Arctic Dreams. Imagination and Desire in a Northern Landscape. London, Picador.

Marchant, S. & P.J. Higgins, Ed. (1993). Handbook of Australian, Antarctic and New Zealand Birds. Volume 2. Raptors to Lapwings. Melbourne, Oxford University Press.

Marks, J.S. & R.L. Redmond (1994). Migration of Bristle-thighed Curlews on Laysan Island: timing, behaviour and estimated flight range. The Condor 96, 316-330.

Martin, A.P. & D. Baird (1988). Lemming cycles - which Palearctic migrants are affected? Bird Study 35, 143-145.

McNeil, R., M.T. Diaz & A. Villeneuve (1994). The mystery of shorebird oversummering. Ardea 82, 143-152.

Meire, P. (1991). Effects of a substantial reduction in intertidal area on numbers and densities of waders. Acta XX Int. Orn. Congr., Christchurch.

Meire, P. & A. Ernwynck (1986). Are oystercatchers (*Haematopus ostralegus*) selecting the most profitable mussels (*Mytilus edulis*)? Animal Behaviour 1427-1435.

Meire, P. & E. Kuijken (1987). A description of the habitat and wader populations of the Slikken van Vianen (Oosterschelde, Netherlands) before major environmental changes and some predictions on expected changes. Le Gerfaut 77, 283-311.

Meire, P.M., H. Schekkerman & P.L. Meininger (1994). Consumption of benthic invertebrates by waterbirds in the Osterschelde estuary, SW Netherlands. Hydrobiologia 282/283, 525-546.

Mitchell, S.F. & R.T. Wass (1995). Food consumption and faecela deposition of plant nutrients by black swans (*Cygnus atratus* Latham)in a shallow New Zealand lake . Hydrobiologia.

Moreira, F. (1994). Diet and feeding rates of Knots *Calidris canutus* in the Tagus Estuary (Portugal). Ardea 82, 133-136.

Moser, M.E. (1988). Limits to the numbers of Grey Plovers Pluvialis squatarola wintering on British estuaries: an analysis of long-term population trends. Journal of Applied Ecology 25, 473-485.

Mouritsen, K.N. & K.T. Jensen (1992). Choice of microhabitat in tactile foraging dunlins *Calidris alpina* : the importance of sediment penetrability. Marine Ecology Progress Series 85, 1-8.

Myers, J.P. (1984). Spacing behaviour of nonbreeding shorebirds. Shorebirds: Migration and Foraging Behaviour. Ed. J. Burger & B. L. Olla. New York, Plenum Press, 271-321.

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

Ntiamoa-Baidu, Y. (1993). Trends in the use of Ghanaian coastal wetlands by migrating knots *Calidris canutus*. Ardea 81, 71-79.

NZMS (undated). Summaries of climatological observations to 1980. New Zealand Meteorological Service. Miscellaneous Publication 177.

O'Connor, R.J. & R.A. Brown (1977). Prey depletion and foraging strategy in the oystercatcher *Haematopus ostralegus*. Oecologia 27, 75-92.

Owen, M. (1987). Brent Goose *Branta b. bernicla* breeding and lemmings - a re-examination. Bird Study 34, 147-149.

Page, G. & D.F. Whitacre (1975). Raptor predation on wintering shorebirds. The Condor 77, 77-83.

Parish, D., B. Lane, P. Sagar & P. Tomkovitch (1987). Wader migration systems in East Asia and Australasia. Wader Study Group Bulletin 49, supplement, 4-14.

Pennycuick, C.J. (1989). Bird flight performance. A calculation manual. Oxford, Oxford University Press.

Pienkowski, M.W. (1978/1979). Differences in habitat requirements and distribution patterns of plovers and sandpipers as investigated by studies of feeding behaviour. Verh. orn. Ges. Bayern 23, 105-124.

Pienkowski, M.W. (1981). How foraging plovers cope with environmental effects on invertebrate behaviour and availability. Feeding and survival strategies of estuarine organisms. Ed. N. V. Jones & W. J. Wolff. New York and London, Plenum Press, 179-192.

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

Pienkowski, M.W. (1983a). Changes in the foraging pattern of plovers in relation to environmental factors. Animal Behaviour 31, 244-264.

Pienkowski, M.W. (1983b). Surface activity of some intertidal invertebrates in relation to temperature and the foraging behaviour of their shorebird predators. Marine Ecology Progress Series 11, 141-150.

Pienkowski, M.W. & P.R. Evans (1984). Migratory behaviour of shorebirds in the western Palearctic. Behaviour of marine animals. Ed. J. Burger & B. L. Olla. Plenum Press, New York. 6, 73-123.

Pienkowski, M.W. & P.R. Evans (1985). The role of migration in the population dynamics of birds. Behavioural ecology: ecological consequences of adaptive behaviour. Ed. R. M. Sibly & R. H. Smith. Oxford, Blackwell Scientific Publications, 331-352.

Pienkowski, M.W., P.R. Evans & D.J. Townshend (1985). Leap-frog and other migration patterns of waders: a critique of the Alerstam and Hogstedt hypothesis, and some alternatives. Ornis Scandinavica 16, 61-70.

Pienkowski, M.W., P.N. Ferns, N.C. Davidson & D.H. Worrall (1984). Balancing the budget- measuring the energy intake and requirements of shorebirds in the field. Coastal waders and wildfowl in winter. Ed. P. R. Evans*et al.* Cambridge, Cambridge University Press, 29-55.

Pienkowski, M.W., C.S. Lloyd & C.D.T. Minton (1979). Seasonal and migrational weight changes in Dunlins. Bird Study 26, 134-148.

Piersma, T. (1982). Foraging of Bar-tailed Godwits. Wintering waders on the Banc d'Arguin. Ed. W. Altenburg*et al.* Leiden, Stichting Veth tot steun aan Waddenonderzok, 135-148.

Piersma, T. (1987). Production by intertidal benthic animals and limits to their predation by shorebirds: a heuristic model. Marine Ecology Progress Series 38, 187-196.

Piersma, T. (1990). Pre-migratory 'fattening' usually involves more than the deposition of fat alone. Ringing and Migration 11, 113-115.

Piersma, T. (1991). Red Knots in New Zealand eat molluscs too: preliminary diet observations at Miranda, Firth of Thames and Farewell Spit in November 1990. The Stilt 19, 30-35.

Piersma, T. (1994). Close to the edge: energetic bottlenecks and the evolution of migratory pathways in Knots. Den Burg, Texel, The Netherlands, Uitgeverij Het Open Boek.

Piersma, T. & M. Barter (1991). Wader catching casualties for body condition analyses: rationale and first results for great knots. The Stilt 19, 36-38.

Piersma, T., A.J. Beintema, N.C. Davidosn, OAG. Munster & M.W.

Pienkowski (1987a). Wader migration systems in the East Atlantic. Wader Study Group Bulletin 49, supplement, 35-56.

Piersma, T., D. Bredin & P. Prokosch (1987b). Continuing mysteries of the spring migration of Siberian knots: a progress note. Wader Study Group Bulletin 49, 9-10.

Piersma, T., L. Bruinzeel, R. Drent, M. Kersten, J. Van der Meer & P. Wiersma (1996). Variability in basal metabolic rate of a long-distance migrant shorebird (Red Knot, *Calidris canutus*) reflects shifts in organ sizes. Physiological Zoology 69.

Piersma, T., N. Cadee & S. Daan (1995). Seasonality in basal metabolic rate and thermal conductance in a long-distance migrant shorebird, the knot (*Calidris canutus*). Journal of Comparative Physiology B 165, 37-45.

Piersma, T., N. Davidson & P. Evans (1984). Estimation of the protein reserves of waders: the use and mis-use of standard muscle volume. Wader Study Group Bulletin 42, 19-22.

Piersma, T. & N.C. Davidson (1991). Confusions of mass and size. The Auk 108, 441-444.

Piersma, T. & N.C. Davidson (1992a). The migration of Knots. Wader Study Group Bulletin 64, Supplement (210 pages).

Piersma, T. & N.C. Davidson (1992b). The migrations and annual cycles of five subspecies of Knots in perspective. Wader Study Group Bulletin 64, Supplement, 187-197.

Piersma, T., P. de Goiej & I. Tulp (1994a). An evaluation of intertidal feeding habitats from a shorebird perspective: towards relevant comparisons between temperate and tropical mudflats. Netherlands Journal of Sea Research 31, 503-512.

Piersma, T., R. Drent & P. Wiersma (1991). Temperate versus tropical wintering in the world's most northerly breeder, the Knot: metabolic scope and resource levels restrict subspecific options. Acta XX Congressus Internationalis Ornithologici, Christchurch, New Zealand.

Piersma, T., J.M. Everaarts & J. Jukema (MS-a). Build-up of red blood cells in refuelling Bar-tailed Godwits in relation to individual migratory quality. The Condor.

Piersma, T., A. Hedenström & J.H. Bruggemann (MS-b). Climb and flight speeds of shorebirds embarking on an intercontinental flight: do they achieve predicted optimal behaviour? Submitted to Ibis.

Piersma, T., R. Hoekstra, A. Dekinga, A. Koolhas, P. Wolf, P.F. Battley & P. Wiersma (1994b). Scale and intensity of intertidal habitat use by knots *Calidris canutus* in the western Wadden Sea in relation to food, friends and foes. Netherlands Journal of Sea Research 31, 331-357.

Piersma, T. & J. Jukema (1990). Budgeting the flight of a long-distance migrant: changes in nutrient reserves levels of Bar-tailed Godwits at successive staging sites. Ardea 78, 215-337.

Piersma, T. & J. Jukema (1993). Red breasts as honest signals of migratory quality in a long-distance migrant, the Bar-tailed Godwit. The Condor 95, 163-177.

Piersma, T., M. Klaassen, J. H. Bruggeman, A-M. Blomert, A. Gueye, Y. Ntiamoa-Baidu & N. E. Van Brederode (1990a). Seasonal timing of the spring departure of waders from the Banc d'Arguin, Mauritania. Ardea 78, 123-134.

Piersma, T. , A. Koolhaas & A. Dekinga (1993). Interactions between stomach structure and diet choice in shorebirds. The Auk 110, 552-564.

Piersma, T. & R.I.G. Morrison (1994). Energy expenditure and water turnover of incubating turnstones: high costs under arctic climatic conditions. The Auk 111.

Piersma, T., P. Prokosch & D. Bredin (1992). The migration system of Afro-Siberian Knots *Calidris canutus canutus*. Wader Study Group Bulletin 64, Supplement, 52-63.

Piersma, T., I. Tulp & H. Schekkerman (in press). Final countdown of waders during starvation: terminal use of nutrients in relation to structural size and concurrent energy expenditure. Physiological Zoology.

Piersma, T. & S. van de Sant (1992). Pattern and predictibility of potential wind assistance for waders and geese migrating from West Africa and the Wadden Sea to Siberia. Ornis Svecica 2, 55-66.

Piersma, T., J. van Gils, P. de Goeij & J. van der Meer (1994c). Signals from the sediment: does Holling's functional response model accurately describe the intake rate of probe-feeding knots? T. Piersma. Close to the edge: energetic bottlenecks and the evolution of migratory pathways in Knots. PhD thesis, University of Groningen. Ed. . Den Burg, Uitgeverij Het Open Boek.

Piersma, T., Y. Verkuil & I. Tulp (1994d). Resources for long-distance migration of knots *Calidris canutus islandica* and *C. c. canutus* : how broad is the temporal exploitation window of benthic prey in the western and eastern Wadden Sea? Oikos 71, 393-407.

Piersma, T., L. Zwarts & J.H. Bruggemann (1990b). Behavioural aspects of the departure of waders before long-distance flights: flocking, vocalizations, flight paths and diurnal timing. Ardea 78, 157-184.

Pook, J. (1992). Banding Round-up Complete List. The Stilt 20, 51-76.

Poot, M. & T. Piersma (1994). Energy expenditure of a widely ranging shorebird, the knot *Calidris canutus*, measured by stable isotope turnover under simulated field conditions. .

Pöysä, H. (1987a). Costs and benefits of group foraging in the teal (Anas crecca). Behaviour 103, 123-140.

Pöysä, H. (1987b). Feeding-vigilance trade-off in the teal (Anas crecca): effects of feeding method and predation risk. Behaviour 103, 108-122.

Puttick, G.M. (1979). Foraging behaviour and activity budgets of curlew sandpipers. Ardea 67, 111-122.

Rands, M.W. & J.P. Barkham (1981). Factors controlling within-flock feeding densities in three species of wading bird. Ornis Scandinavica 12, 28-36.

Rankin, M.A. (1991). Endocrine effects on migration. American Zoologist 31, 217-230.

Reading, C.J. & S. McGrorty (1978). Seasonal variations in the burying depth of *Macoma balthica* (L.) and its accessibility to wading birds. Estuarine and coastal marine science 6, 135-144.

Richardson, W.J. (1978). Timing and amount of bird migration in relation to weather: a review. Oikos 30, 224-272.

Richardson, W.J. (1979). Southeastward migration over Nova Scotia and New Brunswick in autumn: a radar study. Canadian Journal of Zoology 57, 107-124.

Riegen, A. (1995). Report on flagged bird sightings from around New Zealand. New Zealand Wader Study Group Newsletter 5.

Riegen, A. & S. Davies (1993). The Miranda Banders, New Zealand. 1979-1992. The Stilt 22, 53-56.

Robert, M. & R. McNeil (1989). Comparative day and night feeding strategies of shorebird species in a tropical environment. The Ibis 131, 69-79.

Robertson, H.A. & M.D. Dennison (1979). Feeding and roosting behaviour of some waders at Farewell Spit. Notornis 26, 73-88.

Roselaar, C.S. (1983). Subspecies recognition in knot *Calidris canutus* and occurrence of races in western Europe. Beaufortia 33, 97-109.

Sagar, P.M., A-M. Schwartz & C. Howard-Williams (1995). Review of the ecological role of the Black Swan (*Cygnus atratus*). NIWA. NIWA Science and Techonology Series No. 25.

Schekkerman, H., P.L. Meininger & P.M. Meire (1994). Changes in the waterbird populations of the Oosterschelde (SW Netherlands) as a result of large-scale coastal engineering works. Hydrobiologia 282/283, 509-524.

Schneider, D. (1978). Equilization of prey numbers by migratory shorebirds. Nature 271, 353-354.

Schneider, D.C. (1981). Food supplies and the phenology of migratory shorebirds: a hypothesis. Wader Study Group Bulletin 33, 43-45.

Schneider, D.C. & B.A. Harrington (1981). Timing of shorebird migration in relation to prey depletion. The Auk 98, 801-811.

Smith, P.C. & P.R. Evans (1973). Studies of shorebirds at Lindisfarne, Northumberland. 1. Feeding ecology and behaviour of the Bar-tailed Godwit. Wildfowl 24, 135-139.

Stephens, D.W. & J.R. Krebs (1986). Foraging theory. Princeton, Princeton University Press.

Stinson, C.H. (1980). Flocking and predator avoidance: models of flocking and observations on the spatial dispersion of foraging winter shorebirds (Charadrii). Oikos 34, 35-43.

Summer, R.W. (1986). Breeding production of Dark-bellied Brent Geese *Branta bernicla bernicla* in relation to lemming cycles. Bird Study 33, 105-108.

Summer, R.W. & S.M. Smith (1983). the diet of the knot (*Calidris canutus*) on rocky shores of eastern Scotland in winter. Ardea 71, 151-153.

Summers, R.W. & L.G. Underhill (1987). Factors related to breeding production of Brent Geese *Branta b. bernicla* and waders (Charadrii) on the Taimyr peninsula. Bird Study 34, 161-171.

Summers, R.W., L.G. Underhill, C.F. Clinning & M. Nicoll (1989). Populations, migrations, biometrics and moult of the Turnstone *Arenaria e. interpres* on the east Atlantic coastline, with special reference to the Siberian population. Ardea 77, 145-167.

Summers, R.W., L.G. Underhill, M. Nicoll, R. Rae & T. Piersma (1992). Seasonal, size- and age-related patterns in body-mass and composition of Purple Sandpipers *Calidris maritima* in Britain. The Ibis 134, 346-354.

Summers, R.W. & M. Waltner (1978). Seasonal variations in the mass of waders in southern Africa, with special reference to migration. Ostrich 50, 21-37.

Sutherland, W.J. (1982a). Do oystercatchers select the most profitable cockles? Animal Behaviour 30, 857-861.

Sutherland, W.J. (1982b). Spatial variation in the predation of cockles by Oystercatchers at Traeth Melynog, Anglesey. II. The pattern of mortality. Journal of Animal Ecology 51, 491-500.

Sutherland, W.J. & B.J. Ens (1987). The criteria determining the selection of mussels *Mytilus edulis* by oystercatchers *Haematopus ostralegus*. Behaviour 103, 187-202.

Sutherland, W.J. & J.D. Goss-Custard (1991). Predicting the consequence of habitat loss on shorebird populations. Acta XX Int. Orn. Congr., Christchurch.

Swennen, C. (1990). Oystercatchers feeding on Giant Bloody Cockles on the Banc d'Arguin, Mauritania. Ardea 78, 53-62.

Swennen, C. (1992). Observations on the departure of Knots from the Dutch Wadden Sea in spring. Wader Study Group Bulletin 64, Supplement, 87-90.

Swennen, C., M.F. Leopold & L.L.M. de Bruijn (1989). Time-stressed Oystercatchers, *Haematopus ostralegus* , can increase their intake rate. Animal Behaviour 38, 8-22.

Symonds, F.L., D.R. Langslow & M.W. Pienkowski (1984). Movements of wintering shorebirds within the Firth of Forth: species differences in usage of an intertidal complex. Biological Conservation 28, 187-215.

Thomas, D. (1987). How far can waders fly? The Stilt 10, 28-30.

Thrush, S.F. (1991). Spatial patterns in soft-bottom communities. Trends in Ecology and Evolution 6, 75-79.

Tomkovich, P.S. (1992). An analysis of the geographical variability in Knots Calidris canutus based on museum skins. Wader Study Group Bulletin 64, 17-23.

Townshend, D.J. (1985). Decisions for a lifetime: establishment of spatial defence and movement patterns by juvenile Grey Plovers (*Pluvialis squatarola*). Journal of Animal Ecology 54, 267-274.

Townshend, D.J., P.J. Dugan & M.W. Pienkowski (1984). The unsociable plover - use of intertidal areas by Grey Plovers. Coastal waders and wildfowl in winter. Ed. P. R. Evans*et al.* Cambridge, Cambridge University Press, 140-159.

Tulp, I. & P. de Goeij (1994). Evaluating wader habitats in Roebuck Bay (Northwestern Australia) as a springboard for northbound migration in waders, with a focus on great knots. Emu 94, 78-95.

Tulp, I., S. McChesney & P. de Goeij (1994). Migratory departures of waders from north-western Australia: behaviour, timing and possible migration routes. Ardea 82, 201-221.

Turpie, J.K. & P.A.R. Hockey (1993). Comparative diurnal and nocturnal foraging behaviour and energy intake of premigratory Grey Plovers *Pluvialis squatarola* and Whimbrels *Numenius phaeophus* in South Africa. The Ibis 135, 156-165.

Underhill, L.G., R.P. Prys-Jones, E.E. Syroechkovski, N.M. Groen, V. Karpov, H.G. Lappo, M.W.J. Van Roomen, A. Rybkin, H. Shekkerman, H. Spiekman & R.W. Summers (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. The Ibis 135, 277-292.

Underhill, L.G., M. Waltner & R.W. Summers (1989). Three-year cycles in breeding productivity of Knots *Calidris canutus* wintering in southern Africa suggest Taimyr Peninsula provenance. Bird Study 36, 83-87.

Uttley, J.D., C.J. Thomas, N.C. Davidson, K.-B. Strann & P.R. Evans (1987). The spring migration of nearctic knots *Calidris canutus islandica*: a re-appraisal. Wader Study Group Bulletin 49, Suppl./IWRB Special Publ. 7, 80-84.

van der Meer, J. & T. Piersma (1994). Physiologically inspired regression models for estimating and predicting nutrient stores and their composition in birds. Physiological Zoology 67, 305-329.

van Latesteijn, H.C. & R.H.D. Lambeck (1986). The analysis of monitoring data with the aid of time-series analysis. Environmental Monitoring and Assessment 7, 287-297.

Van Valen, L. (1978). The statistics of variation. Evolutionary Theory 4, 33-43.

Walker, K. (1987). Wildlife in the Nelson region. Department of Internal Affairs, Wellington. Fauna Survey Unit report 42.

Wanink, J. & L. Zwarts (1985). Does an optimally foraging oystercatcher obey the functional response? Oecologia 67, 98-106.

Ward, P. & A. Zahavi (1973). The importance of certain assemblages of birds as "information centres" for food-finding. The Ibis 115, 517-534.

Westcott, D.A. & A. Cockburn (1988). Flock size and vigilance in parrots. Australian Journal of Zoology 36, 335-349.

Whitfield, D.P. (1988). Sparrowhawks *Accipiter nisus* affect the spacing behaviour of wintering Turnstone *Arenaria interpres* and Redshank *Tringa totanus*. The Ibis 130, 284-287.

Wiersma, P. & T. Piersma (1994). Effects of microhabitat, flocking, climate and migratory goal on energy expenditure in the annual cycle of knots. The Condor 96, 257-279.

Wiersma, P. & T. Piersma (1995). Scoring abdominal profiles to characterize migratory cohorts of shorebirds: an example with Red Knots. Journal of Field Ornithology 66, 88-98.

Wilson, J.R. & R.I.G. Morrison (1992). Staging studies of Knots *Calidris canutus islandica* in Iceland in the early 1970s: body mass patterns. Wader Study Group Bulletin 64, Supplement, 129-136.

Wilson, W.H. (1990). Relationship between prey abundance and foraging site selection by Semipalmated Sandpipers on a Bay of Fundy mudflat. Journal of Field Ornithology 61, 9-19.

Wood, A.G. (1986). Diurnal and nocturnal territoriality in the Grey Plover as revealed by radio telemetry. Journal of Field Ornithology 57, 213-221.

Wright, A.E. (1978). Auckland University field club scientific trip to Farewell Spit, May 1977. Tane 24, 25-27.

Zwarts, L. (1990). Increased prey availability drives premigration hyperphagia in Whimbrels and allows them to leave the Banc d'Arguin, Mauritania, in time. Ardea 78, 279-300.

Zwarts, L. & A.-M. Blomert (1992). Why knot *Calidris canutus* take medium-sized *Macoma balthica* when six prey species are available. Marine Ecology Progress Series 83, 113-128.

Zwarts, L., A-M. Blomert & R. Hupkes (1990a). Increase in feeding time in waders preparing for spring migration from the Banc d'Arguin, Mauritania. Ardea 78, 237-256.

Zwarts, L., A-M. Blomert & J.H. Wanink (1992). Annual and seasonal variation in the food supply harvestable by knot *Calidris canutus* staging in the Wadden sea in late summer. Martine Ecology Progress Series 83, 129-139.

Zwarts, L. & S. Dirksen (1990). Digestive bottleneck limits the increase in food intake of whimbrels preparing for spring migration from the Banc d'Arguin, Mauritania. Ardea 78, 157-178.

Zwarts, L. & R.H. Drent (1981). Prey depletion and the regulation of predator density: oystercatchers (*Haematopus ostralegus*) feeding on mussels (*Mytilus edulis*). Feeding and survival strategies of estuarine organisms. Ed. N. V. Jones & W. J. Wolff. New York and London, Plenum Press, 193-216.

Zwarts, L., B.J. Ens, M. Kersten & T. Piersma (1990b). Moult, mass and flight range of waders ready to take off for long-distance migrations. Ardea 78, 339-364.

Zwarts, L. & J. Wanink (1984). How Oystercatchers and Curlews successively deplete clams. Coastal Waders and Wildfowl in Winter. Ed. P. R. Evans*et al.* Cambridge, Cambridge University Press, 69-83.

Zwarts, L. & J.H. Wanink (1991). The macrobenthos fraction available to waders may represent marginal prey. Oecologia 87, 581-587.

Zwarts, L. & J.H. Wanink (1994). How the food supply harvestable by waders in the Wadden Sea depends on the variation in energy density, body weight, biomass, burying depth and behaviour of tidal flat invertebrates. Netherlands Journal of Sea Research 31, 441-476.

Appendix 1 Size distributions of cockles *Austrovenus stuchtburyi* for all sampling occasions at Tip3 sampling site. Samples represent 16 cores totalling 0.286 m^2. No samples were taken between June 93 and December 93, or in May, July and November 1994.