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EXECUTIVE SUMMARY

1. This report describes the changes observed in the number of wintering Knot and Oystercatcher on the Wash, England between 1968 and 1998 and investigates the causes behind the declines observed in both populations between 1990-1998. During this period there was also a decline in mussel and cockle stocks which led to the closure of the mussel fishery. We determine whether bird survival was linked to winter severity and shellfish stocks and whether changes in survival and recruitment were sufficient to explain observed changes in the wintering bird populations.

2. The Wash is the most important British estuary in terms of the number of wintering waterfowl it supports (1993-1998 average: 310,000 birds) and it is the most important British estuary for Knot and the fourth most important for Oystercatcher. During the period 1970-1985, the number of wintering Oystercatcher remained steady at approximately 20,000 and then increased to a peak of 40,000 in 1998/89 before declining to 10,000 birds in 1998/99. Knot numbers showed a different pattern and declined from 80,000 to 20,000 during the period 1970/71-1976/77 and then increased in numbers to a peak of 110,000 birds in 1990/91 before declining to a low of 25,000 birds in the winter of 1995/96. After this, numbers recovered and increased to 30-40,000 between 1997-1999. In total, this was a loss of 100,000 Oystercatcher and Knot.

3. Ringing recoveries have established the breeding areas of Oystercatchers and Knot wintering on the Wash. The Oystercatchers predominately breed in Norway and Knot in Greenland and Arctic Canada. Smaller numbers of Siberian-breeding Knot pass through the Wash on passage.

4. Stocks of cockle and mussel declined at a similar time to the wintering bird populations. Censuses of cockle stocks are carried out in May and the quotas for that year are set at approximately 30% of the current stock. The fishery opens in June and remains open until that quota is fulfilled; in recent years this has been up to 6 weeks long. Cockle stocks were moderate, high or abundant in 9 of the 15 years between 1970 and 1985 (1972 is excluded due to missing data) but were low in 10 of the 13 years between 1986 and 1998. In the remaining three years the stocks were classed as moderate. The mussel fishery underwent a catastrophic collapse from 1982, the date from which detailed census information is available. The ‘natural’ commercial beds have been closed from 1993-2000 at least and only limited fishing has been permitted on mussels which are on re-laid mussel beds. The relaying and farming of sub-tidal mussels into the intertidal areas has successfully increased the available stocks and in the late 1990s the mussel harvest has been from this re-laid stock. The reasons for the collapse are unknown but fishing mortality on the commercial beds was high in the years preceding the crash. By early 2000, mussel farming covered an area of approximately 140 ha.

5. A winter severity index (Ijnsen index) was calculated using data gathered at the meteorological station at Terrington St Clement at the south of The Wash. Between 1967/68 and 1998/99, all winters were classed as mild apart from 1978/79, 1984/85 and 1985/86 which were classed as moderate. None were classed as severe.

6. A demographic approach was taken to investigate the link between changes in wader numbers and shellfish stocks. For Knot and Oystercatcher, sufficient birds had been ringed by the Wash Wader Ringing Group and subsequently recovered to permit an analysis of survival using ringed birds which had been found dead and reported to the British and Irish bird ringing scheme. Survival models were constructed in the package MARK (White & Burnham 1999) and annual survival estimates were calculated for both species between 1 June and 31 May. Tests were performed to determine whether age-dependence (first-year or adult) or time dependence in survival and reporting rates was required. The number of recoveries of Oystercatchers originally ringed as juveniles was low and could not therefore be used in survival models that incorporated time periods of less than one year. The number of recoveries of adult Oystercatchers was sufficient to allow additional modelling of survival over 6-month periods rather than annual periods. The periods were from 1 October to 31 March (the winter period) and 1 April to 30 September (the summer period).

7. The parsimonious fit for the annual Oystercatcher survival model included annual survival rates and a constant reporting rate. The inclusions of age-dependent survival in the annual models was not required. For the 6-monthly models, the parsimonious fit was one which had constant survival rate in summer, time-dependent winter mortality, a constant winter reporting rate and a linear reporting rate in summer. Age-dependent survival could not be modelled due to lack of data from juvenile birds but the results of the annual model showed that it was not necessary. Adult Oystercatcher survival stayed approximately constant during the study period except for three winters: 1992/93 (survival = 73.8% ± 7.6 SE), 1995/96 (85.5% ± 5.5 SE) and 1996/97 (90.4% ± 4.2 SE). These 'kills' occurred in January and February. Average winter survival, excluding these 'kill' years was 97.98% ± 0.15 SE and 96.61% ± 0.87 SE including all winters. Summer survival was on average lower than in winter at 92.02% ± 0.9% presumably because predation pressure is low in winter and the summer period includes migration to and from Norway and a higher risk of mortality from predation and anthropogenic sources (*e.g.* cars) in the breeding grounds.

8. As too few Knot were ringed in their first year it was possible only to estimate annual survival parameters for adult birds. The best-fit model was one with annual survival rates and a constant reporting rate. Knot survival rates varied between 70.2% to 97.3% per annum with a mean of 87.98% +/- 1.18. Survival tended to be more variable in Knot than Oystercatchers in average years, but major 'kill' years were not observed in Knot. Survival was lowest in the two years when there was severe spring weather in the springs of 1972 and 1974 in Greenland.

9. The mussel stock index, cockle stock index and the severity of the winter were significant factors in determining the winter (October-March) survival of adult Oystercatchers. Major kills of Oystercatchers occurred when both cockle and mussel stocks were low. If either one or other of the shellfish stocks was classed as being higher than 'low' then survival was greater than 95% for the winter. The addition of re-laid mussel stock in the late 1990s, when both the cockle and mussel stocks were low, is likely to have made a significant contribution to increasing Oystercatcher survival in those winters as they effectively doubled the mussel stock at a time when cockle stocks were low. The severity of winter weather contributed relatively little to the estimation of survival rates and this is probably because winters in the Wash tend to be mild compared with areas such as the Wadden Sea where winters tend to be more severe and Oystercatcher mortality is higher as a result. Survival of Knot was not found to be dependent on winter weather or the cockle or mussel spat index.

10. Population models, based on recruitment and survival provide a reasonable description of the observed changes in the Knot and Oystercatcher populations. Based on average survival and recruitment rates, the Oystercatcher population was predicted to have increased by 1.9% per annum from 1969 to 1999 while the Knot population was predicted to be stable over the same time period. For both species, recruitment rates contribute relatively more than survival rates to inter-annual variation in the population index. For Oystercatcher, changes in recruitment of juveniles to the Wash winter population determined the changes in the population index until 1992/93 when changes (declines) in annual survival coupled with poor recruitment to the Wash drove the population down. For Knot, where no large-scale changes in survival have taken place, recruitment rates explained most of the variation in the population index. Based on a model with average survival rates and variable recruitment, it seems likely that the major declines observed in the Knot population can be explained by poor recruitment since 1990, although emigration may well also be a factor. Sensitivity analyses show that for these long-lived species even small changes in adult survival rate (1-2%) have very large effects on overall population size. Changes in juvenile survival rates have a relatively smaller effect.

11. Confidence in survival estimates increases with time, due to the fact that rings may not be returned until some time after they were found and also because additional years of data reduce the confidence limits associated with a particular survival estimate. Ring returns can not be used to provide quick assessments of Oystercatcher survival unless major mortality is taking place. A measure of body condition based around the proportion of birds in catches showing abnormal wing moult was found to be a good predictor of winter survival in Oystercatchers. Two measures were used: the first was the proportion of birds which showed suspended moult of flight feathers in the period from January to September (0-15%) and the second was the proportion of birds in active moult but with a very small moult gap (i.e. about to suspend) caught between August and December (0-5%). Both measures were highly significant indicators of winter mortality.

12. A link has been shown to exist between the state of shellfish stocks on the Wash and Oystercatcher survival. Even a small change in survival can have a very large effect on population size and can cause an increasing or stable population to undergo a major crash. The Wash has been designated as an Special Protection Area (SPA), due in part to its internationally important populations of Knot and Oystercatcher. The Wash also contains economically important fisheries and there is a need for both a healthy shellfishery and stable populations of birds.

13. The exact role of the fishery and its effect on birds is not yet understood as different fractions of the available stock may be exploited by fishermen and birds. There is evidence from the Burry Inlet that, although birds and fishermen overlap in the size of cockles taken, most bird predation of cockles is of size classes smaller than the fishermen can take. Competition may be mostly sequential rather than direct and the effects of fishing on birds may be through the effects of fishing mortality on the cockle spawning stock and its consequences for future spatfall. The implication is that sustainable management of fisheries will lead to healthy bird populations. The Oystercatcher condition indicator may be able to be used as an indicator of shellfish stocks and fed into the fishery management process. Moult can be used as an indicator of survival from September onwards and could therefore be fed to the fishery management decision making process the following year.

14. Further research would be required to determine the exact relationship between cockles, fishing and Oystercatchers in the Wash, as Oystercatcher prey choice differs between estuaries. The effects of re-laid mussel stocks on over-winter survival of Oystercatchers and whether this could be used as an effective management tool for both bird populations and the shellfish industry should also be investigated. These studies could vary in scale from taking a modelling approach, based on parameters collected either in the field or using published estimates of the many Oystercatcher studies, to a large field project based around following individual birds. Further analysis of the Wash Wader Group database would permit a more detailed examination of Oystercatcher survival in the Wash, based on retraps of live birds, *i.e.* are kills restricted to certain parts of the Wash or affect all areas. Estimates of emigration could also be obtained. This would provide a more robust analysis and also allow estimates of interchange of birds between different areas in the Wash to be made.

1. INTRODUCTION

1.1 Background and context

At several points over the past 50 years, there has been an uneasy relationship between shellfishery managers and shellfish-eating birds and, at times, this relationship has become a major political and conservation issue. Lack of understanding of the relationship between shellfish-eating birds and shellfish stocks led to the culling of approximately 10,000 Oystercatchers in the Burry Inlet during the winters of 1973/73 and 1973/74 (Andrews 1974, Prater 1974) causing major public outcry. Since this incident the treatment of this problem has been less drastic and a more considered approach has been taken to managing shellfisheries and a great deal of resources have been expended to investigate this problem.

The relationship between shellfish-eating birds (Oystercatchers and Knot) and their food has been explored in great detail through studies which have quantified foraging parameters (Stillman *et al.* 1996, Goss-Custard *et al.* 1996b, Moody *et al.* 1997, Ens *et al.* 1996 a,b, Triplet *et al.*1999), determined the effects of predation on shellfish populations (Goss-Custard *et al.* 1996a, Zwarts *et al.* 1996a, McGrorty 1997, Hilgerloh & Siemoneit 1999), determined the effects of changes in shellfish abundance on shorebird populations (Beukema 1993, Neve & van Noordwijk 1997, Norris *et al.* 1998, Smit *et al.* 1998, Durell *et al.* 2000), built models to predict the distribution of organisms in the environment (Meire 1996, van der Meer & Ens 1997) and estimated the effects of factors such as habitat change on populations (Meire 1996, Ens & Alting 1996, Sutherland 1996). Through this work, the relationship between shellfish-eating birds and their prey has become much better understood and these studies have fed into management of both fisheries and protected areas.

Since the mid-1980s, large changes in the Wash, England, have taken place. Shellfish populations crashed and the populations of commercially-fishable intertidal mussel declined to such an extent that the mussel fishery closed in 1994. The cockle stocks also underwent a decline and the fishery has been at a low ebb since the 1980s.

These changes in shellfish were also mirrored in the wintering Knot and Oystercatcher populations. In north-west Europe, Oystercatchers, in particular, are heavily reliant on cockles and mussels in winter and studies have shown that they tend to select shellfish of intermediate or large size, trading off the energy content gained with the energy needed to find and open the shellfish and also risk from infection with parasites (Zwarts *et al.* 1996b, Norris *et al*. 1998). Knot tend to take smaller molluscs notably *Macoma* and *Hydrobia* but, at times, also feed extensively on cockle and mussel spat.

Since 1990, approximately 100,000 birds of these two species combined have disappeared from the Wash (Cranswick *et al.* 1999) and, in three winters, several hundred dead Oystercatchers were reported. During these winters, Oystercatchers also started to feed in fields well inland of sea-walls, which is atypical behaviour for Wash Oystercatchers (Clark 1993, 1996) and in one year, birds even fed on grassy roundabouts in Kings Lynn surrounded by busy roads.

In other studies of Oystercatcher mortality, both winter weather and shellfish stocks are important in determining over-winter survival. Severe weather seems to have a larger effect in the Wadden Sea (Camphuysen *et al.* 1996) where winters tend to be harsher than in other north-west European study areas, *e.g.* the Exe estuary in south-west Britain (Durell *et al.* 2000). Both cockle and mussel stock levels are important in determining over-winter survival in the Wadden Sea (Camphuysen *et al*. 1996).

In this study, we investigate the relationship between the large-scale changes in both Knot and Oystercatcher populations on the Wash, England since 1985 and declines in the Wash's cockle and mussel stocks which took place over a similar time period. We analyse the change in numbers of Knot and Oystercatcher on the Wash and draw comparisons between trends from the Burry Inlet and the Thames estuary, which are two other major cockle fishing areas. We then look for evidence of whether Knot and Oystercatcher have moved away from the Wash, through analysis of ringing recoveries, and to which regions birds have moved to. The major part of the analysis appears in

Chapter 4 where we determine recruitment and survival rates for both Knot and Oystercatcher and ask whether the observed changes in survival are (a) linked to shellfish abundance and (b) sufficient to account for the declines seen in the Wash wintering populations.

1.2 Objectives

This study of Wash shorebird/shellfish interactions was broken down into four separate modules, three of which are reported on here.

Module 1 (BTO): Shorebird population trends of Oystercatcher and Knot since 1970 and comparison with other main cockle/mussel fishery areas in UK (Thames and Burry Inlet) and in Holland.

(i) Description of the annual and seasonal patterns of abundance and any trends using WeBS data.
(ii) Comparison of trends in Oystercatcher and Knot with other shorebird species.
(iii) Description of the biological and conservation importance of the Wash for Oystercatcher and Knot.

Module 2 (BTO/CEFAS): Examination of the effects of shellfish stock declines upon:

(i) Movement patterns of birds, including an analysis of recent recoveries of Wash-ringed Knot and Oystercatchers for signs of changes in wintering areas or of increased mortality.
(ii) The age-structure of the wintering populations and physical condition of birds, using data from the Wash Wader Ringing Group.

Module 3 (CEFAS): Shorebird predation on shellfish: collation of evidence and evaluation of published and unpublished information on Oystercatcher and Knot.

TO BE PRODUCED IN A SEPARATE REPORT

Module 4 (BTO/CEFAS): Synthesis

(i) Comparison of Wash shorebird trends with fluctuations in shellfish stocks.
(ii) Discussion and Conclusions.

2. SHOREBIRD POPULATION TRENDS IN THE WASH, BURRY INLET AND THE THAMES.

2.1 Methods

The Wetland Bird Survey (formerly the Birds of Estuaries Enquiry) has provided counts of waders at most British estuaries since 1969 and represents the most complete set of counts for assessing changes in wader numbers in the United Kingdom. In this chapter, we look at changes in numbers of all regularly indexed wader species in the Wash. We also show changes in numbers of Oystercatcher and Knot at a national scale as well as at two other sites where shell-fishing takes place, the Thames estuary and the Burry Inlet.

The WeBS counts take the form of monthly counts over the course of a year. For producing national indices of abundance, the months December through to February are traditionally used to calculate indices and we have followed this approach. Counts are assessed as to their quality through comments on observers forms (*e.g.* when high levels of disturbance or extreme weather cause poor quality counts) and by the proportion of sub-sites counted in a site. For poor quality counts and missing counts, the values are imputed using the Underhill method (Underhill & Prys-Jones 1994), which models counts as a function of site, year and month.

A second technique has recently been developed to smooth some of the annual variation found by the Underhill method and reveal the underlying trend. The assessment of population change for waders and wildfowl needs to be carried out using smoothed indices calculated from the original count data. There are various methods to calculate smoothed indices but the use of General Additive Models (Fewster *et al.* in press) are recommended for this purpose. These explicitly incorporate the smoothing factor as part of the modelling process, which is preferable to applying a smoothing process on the index itself. GAMs allow smoothed population indices to be calculated at national, regional or site level in a similar manner to other indexing techniques.

GAMs treat counts as a smooth function of year, month and site. The degrees of freedom (d.f.) for the year parameter in the GAM model controls the degree of smoothing which is applied to the WeBS counts data. Maximum degrees of freedom allows an unconstrained model to be run which is equivalent to a log-Poisson Generalised Linear Model with site, year and month factors (*i.e*. similar to the process used as a base for the Underhill method). Minimum degrees of freedom constrain the fit to a linear trend.

The aim of the smoothing is to remove major year-to-year fluctuations in the Underhill index but reliably reveal the underlying trend in the index data. No exact rule can be applied to the amount of smoothing needed and the choice is necessarily somewhat arbitrary. Fewster *et al.* (in press) recommend that, for the year parameter in the GAM model, degrees of freedom equivalent to 0.3 times the number of years is suitable for CBC data and we use this, following recommendations by Atkinson *et al.* (1999).

2.2 Results and Discussion

2.2.1 Changes in shorebird numbers in the Wash

Figure 2.1 shows the changes in numbers of eleven species of wader on the Wash. The two shellfish-eating species, Knot and Oystercatcher, have shown large declines since the late 1980s. Oystercatcher numbers remained steady at approximately 20,000 birds from 1970/71 to the early 1980s before climbing to a peak of *c.* 40,000 in 1988/89. Numbers then crashed and by 1998/99 numbers were *c.* 10,000, approximately 25% of the peak population which had been reached 10 years previously. Knot numbers underwent a decline from 70,000 birds to 20,000 birds between 1970/71 and 1976/77 before recovering to *c.* 80,000 by the mid-1980s. The numbers remained high, peaking at 110,000 in 1990/92 before declining to 40,000 by 1998/99. Approximately 100,000 Knot and Oystercatcher have disappeared from the Wash over a ten-year period. The threshold population for a site to be designated of international importance is 9,000 Oystercatcher and 3,500 Knot.

Other shorebird species have also shown major changes in numbers but these species do not specialise on shellfish. Of the larger species, Bar-tailed Godwit has shown a steady increase over a similar time period, Curlew have remained stable and Black-tailed Godwit have shown a very large recent increase following a similar pattern to that shown by Black-tailed Godwits in other estuaries (Cranswick *et al.* 1999). This indicates a healthy benthos of other invertebrates. Redshank showed an increase from 1970 to 1987/88 from *c.* 2,000 birds to 5,000 before declining to previous levels by 1990/91. The reasons for the large increase are unknown but the general decrease was, in part, due to the very high mortality suffered by Redshank during a period of severe weather in February 1991 (Clark *et al*. 1993). There was no subsequent effect of this period of cold weather on Oystercatcher, Grey Plover, Knot, Dunlin or Curlew populations (Clark *et al.* 1993)

Of the smaller species, more similar in body size to Knot, there is a mixed story. Ringed Plover, Turnstone and Sanderling, species which are not usually associated with fine-sediment mud, have shown no major trends over the period 1970/71-1998/99. There are two exceptionally high counts of Ringed Plover in 1994/95 and 1997/98 and it is not yet possible to tell if these changes are indicative of a general increase of the wintering population. Dunlin numbers have fluctuated and, since 1990, have also undergone a decrease in population, from a peak of 40,000 to current levels of 20-25,000. Grey Plover are increasing in line with the national picture.

2.2.2 Comparison with national trends

Neither Knot nor Oystercatcher have shown the same large fluctuations in numbers nationally as has been observed on the Wash (Figure 2.2). Numbers of Oystercatcher increased nationally since 1970/71, peaking in 1990/91. Since then, there has been a slight decline of *c.*10% in the national wintering population but numbers are currently stable. Knot numbers underwent a catastrophic decline in the early 1970s, due probably to increased adult mortality in the summer breeding area due to poor weather conditions (Boyd 1992), but have remained at a similar level of numbers since the mid- to late-1970s.

During the mid-1980s the Wash supported approximately 35% of the British Knot population in mid-winter and up to 60-80% during spring passage. The national number of Knot has remained stable and the Wash now only supports 15-20% of the national wintering population. At its peak, the Wash supported 10-15% of the national Oystercatcher population (but a higher proportion of Norwegian-breeding birds) and since the decline now only supports at most 5% of the national population.

2.2.3 Comparison of Wash trends with other shell-fishing areas

The Thames Estuary and the Burry Inlet support economically important cockle fisheries and internationally important populations of wintering Knot and Oystercatcher. The trends in the two areas are contrasting (Figure 2.3 & 2.4). On the Burry Inlet, numbers of Oystercatcher remained stable or increased slightly from 1970 to 1986 before declining to 1993 and then recovering slightly. On the Thames there has been a consistent increase in numbers, despite an increase in cockle dredging, from 5,000 birds in at the start of the 1970s to 16,000 in 1997/98.

The Burry Inlet is not an important wintering site for Knot and only in some years did it pass the threshold for international importance. As a peripheral area, it might be expected that small changes in the national population would have proportionally larger changes in the outlying areas. The decline in the early 1970s may have been related to breeding conditions in the breeding grounds (Boyd 1992) but the reasons for the large decrease in the early 1990s is unknown, although not unprecedented as in the winter of 1978/79 a very low number of birds wintered in the Burry. As with Oystercatcher, Knot have undergone a very large increase on the Thames. Increase was steady from 1972 to 1990/91. From 1991/92 to 1995/96 a very large increase took place with an additional 25,000 birds wintering on the Thames. This period coincided with the very large decline on the Wash and may have been a result of birds moving from the Wash to winter on the Thames. No ringing data is available to back this up but it is certainly a possibility, as Knot tend to be mobile between estuaries.

3. ARE THE DECLINES IN KNOT AND OYSTERCATCHER CAUSED BY BIRDS MOVING AWAY FROM THE WASH? EVIDENCE FROM RINGING RECOVERIES

3.1 Introduction

In terms of numbers of wintering waterfowl, the Wash is the most important estuary in Britain supporting on average 310,000 birds in the winters 1993/94 to 1997/98 (Cranswick *et al.* 1999). Only the Ribble Estuary (300,000 birds) and Morecambe Bay (250,000 birds) support similar numbers of birds and no other individual estuary in Britain supports more than 200,000 birds in winter. As such, the Wash is designated under the Ramsar Convention, a Specially Protected Area (SPA) and is designated along with the North Norfolk Coast as a Special Area for Conservation (SAC).

The Wash is also important as a staging post for many species. Several distinct populations of breeding birds can pass through the Wash at different times of year. For example, the northern European population of Bar-tailed Godwit *Limosa lapponica* migrates to the Wash in early autumn where they stay to moult. Birds which breed further east in Siberia pass through later in the autumn, using the Wash as a stop-over point before migrating to West Africa to winter (Atkinson 1996).

The breeding origin of Oystercatcher and Knot wintering on the Wash are well-known. The vast majority of Oystercatchers which winter on the Wash are from breeding areas on the Atlantic coast of Norway with smaller numbers from the Iceland, Orkney, Shetland and the Wadden Sea (Figure 3.1). Oystercatchers tend to move to the breeding grounds from mid-March onwards, breed and then the earliest birds arrive back on the Wash in late July (presumably non-breeders) or August. The majority of Knot that winter on the Wash breed in Greenland and north-east Canada (Figure 3.2). Occasional birds from the Siberian populations occur in autumn but these pass through to winter in West Africa. The numbers of birds from the Siberian populations passing through the Wash in autumn is unknown but is unlikely to make up a large proportion of that population. In spring, the majority of the Siberian birds pass through the Wadden Sea in May after the Greenland birds have left in April (Poot *et al.* 1996). The birds recovered in the Vendee region of France and in the Wadden Sea in May are presumably birds from this population, as most Greenland birds would be back on the breeding grounds by this date.

3.2 Methods and Results

No formal analysis of recoveries has been carried out due to the nature of the data. For Knot, too few birds had been recovered to make any sensible conclusions as to whether birds had moved away from the Wash. For Oystercatcher, sufficient recoveries are available to look at changes in recovery patterns between years, prior to and after the first major kill. The analysis could include both ringed birds found dead or alive but the number of birds caught alive depends heavily on catching effort outside the Wash and without a measure of this effort interpretation is very difficult. We have therefore restricted this analysis to birds found dead.

We took recoveries of Wash-ringed Oystercatchers and split them into two groups, based on whether they were from before the first major kill of Oystercatchers in the winter of 1992/93 (pre-kill) or during or after (post-kill). To look at whether there is evidence for a change in moulting or wintering area we have taken a subset of these recoveries using birds recovered during the period September through to February. This is not a strict definition of 'winter' as in the early part of the period birds will be moulting but once adults arrive on the Wash they tend to remain and this set of birds was considered to be a representative sample of the Wash wintering population. The 'post-kill' group of birds included 7 year-long periods and so only recoveries up to 7 years prior to 1992/93 were included in the 'pre-kill' group.

When plotted, there is a clear pattern of more birds switching wintering areas since the start of the problems in 1992/93 (Table 3.1; Figure 3.3). Prior to this date, very few birds were recovered outside the Wash in autumn or winters. In the 'pre-kill' group, eight birds were recovered in the Netherlands, 15 in France, and three others to north west Europe. There were also small numbers found on other UK estuaries. The birds in Norway were presumably birds on breeding areas. The 'post-kill' group included many more recoveries (17 recoveries post-kill, zero pre-kill) to the north of the Wash, in particular to the north Lincolnshire coast, the Humber Estuary, Cleveland and Durham (Table 3.1). There were also more recoveries than expected in the Netherlands (eight in the pre-kill period and 22 in the post kill period). There is therefore evidence that some Oystercatchers moved out of the Wash up the east coast of Britain and to the Delta area & Wadden Sea areas of the Netherlands. Inspection of Table 3.1 shows that the higher than expected number of recoveries occurs only in kill years and the number of recoveries returns to normal pre-kill levels in years when survival is high. Several more local movements occurred during January and February 1993 when many birds were dying around the Wash. Birds were found dead on farmland between 20-40 miles inland in Cambridgeshire and one inland in Norfolk, indicating that some birds moved many mile inland in search of food on agricultural fields.

An estimate of the number of birds which moved away from the Wash can be made. From survival rates and the number of birds ringed in each six-month period it can be calculated that 6,000 Wash-ringed Oystercatchers were alive at the beginning of the 1992/93 winter declining to 4,500 in 1998/99 (Figure 3.4). We have taken annual mortality rates estimated from the models and the average reporting rate of 8%. During the post-kill period 57 recoveries were reported away from the Wash (Table 3.1). If 57 birds were recovered during that period then the total number of birds dying outside the Wash would be calculated by the formula 57 * (1 / reporting rate) which is 57 * (1 / 0.08) = 713 dead birds. If a hundred birds were alive in 1992/93, based on the annual summer and winter mortality estimates we would expect 44.5 birds to die over the 7 years since. The 713 dead birds would therefore represent 1,600 Wash-ringed birds (100/44.5 * 713) that have moved away from the Wash. The number of birds with rings on varied between 4,500 and 6,000 during the same period and therefore we would expect the proportion of birds moving to be in the range of 36% (1,600/4,500) to 27% (1,600/6,000).

With an initial population of 46,000 birds, this represents a range of between 12,000 to 16,000 birds moving. This suggests that a substantial proportion of birds moved out of the Wash during the kill years. As there is no evidence of birds permanently moving away, these birds either returned to the Wash in future winters or died away from the Wash.

4. THE EFFECTS OF CHANGES IN SHELLFISH STOCKS AND WINTER WEATHER ON SHOREBIRD POPULATIONS: RESULTS OF A 30-YEAR STUDY ON THE WASH, ENGLAND.

4.1 INTRODUCTION

This chapter quantifies the changes that have taken place in the survival of and recruitment to Knot and Oystercatcher populations on the Wash, asks whether these are related to winter weather and shellfish stocks and assesses whether the changes are sufficient to explain the observed changes in the wintering population. Simple matrix population models are used to look at the relative contribution of the observed changes in annual survival and recruitment to those seen at a population level. These models help determine whether changes in survival, recruitment or both have driven the declines seen in the Wash Knot and Oystercatcher populations.

4.2 METHODS

4.2.1 Changes in abundance of birds and shellfish on the Wash

4.2.1.1 Birds

Population indices for Knot and Oystercatcher were calculated by applying the Underhill method (Underhill & Prys-Jones 1994) to December to February counts from the Wetland Bird Survey (WeBS). WeBS is the UK national waterbird monitoring scheme and counts have taken place on the Wash since 1970 (Cranswick *et al.* 1999). These counts have been carried out at monthly intervals on 24 different sectors on the Wash running in an unbroken line from Gibraltar Point (53°-05'N 0°-20'E) to Holme (52°-51'N 0°-34'E). The Underhill method calculates indices by modelling counts as a function of site, year and month; missing counts are imputed where necessary. Counts were only used from each site if they had been made on more than half of possible occasions. The total number of observed and imputed bird months are summed and used as the index. Prior to 1982, approximately a third of counts were from imputed measures but coverage has improved since 1982 and less than 5% of the counts were imputed annually between 1983 and 1998.

4.2.1.2 Shellfish stock and spat indices

Shellfish stock and spat assessments were obtained from the CEFAS/ESFJC surveys (Dare & Walker 1992, Dare in litt.) (Figure 4.1 a-c). Although survey estimates of cockle and mussel stock abundance are intermittently available going back to *c*1920, quantitative estimates of the mussel stock (Figure 4.1 d) are only available from 1982 onwards and for cockles from 1990 (Dare & Walker 1992). The estimates of mussel stock are from the major economic beds and excludes a number of non-economic beds. The commercial beds make up the majority of the intertidal mussels available to the birds. The remaining beds support lower densities of Mussels and tend to have a lower meat content.

For analysis of Oystercatcher survival, the level of both cockle and mussel stock may be important and survival analyses including shellfish covariates have only been carried out for data after 1982 when assessments of both species are available. Spat indices for the whole of the study period 1970-1998 were included as covariates in the Knot models.

Both stock and spat abundance were expressed as an index. Cockle stock and spat indices were taken from Dare & Bannister (in prep) and a five point scale was used: 0 = nil or scarcely abundant, 1 = low stock level, 2= moderate stock level, 3= high stock level, 4=abundant stock level (Figure 4.1 a,b). For mussels, a similar index was used for mussel spat but actual estimates of stock abundance on the commercial beds were available and an index similar to that used by Neve & van Noordwijk (1997) was calculated. A five point scale was used: 1 = less than half the mean stock level, 2 = less than 1 SE from the mean but greater than half the mean, 3 = mean ± SE, 4 = greater than the mean + SE but less than double the mean and 5 = greater than double the mean (Figure 3.1 d).

Estimates of stock abundance for mussel for 1982-1999 refer to the wild stock. During the autumn of 1997, 1,680 tonnes of sub-littoral mussels were re-laid into the intertidal zone in the western and southern parts the Wash. These would have become available to the birds from that time, although only during spring low tides, as re-laid Mussels are laid at the bottom of the intertidal zone. These Mussels became established and a further 1,200 tonnes were re-laid in September 1998. The wild stock assessment was 1,679 tons for 1997 and 1,554 tons for 1998, so the stock potentially available to the birds approximately doubled with the first addition of re-laid stock and increased by another third with the second. The stock re-laid in 1997 became marketable in January 1999 and the 1998 stock in January 2000.

4.2.2 Estimating bird survival using time- and age-dependence in survival and reporting rates

Survival estimates and reporting rates were estimated using the computer package MARK (White & Burnham 1999) based on birds which were trapped and ringed on the Wash by the Wash Wader Ringing Group (WWRG), subsequently found dead and reported to the British and Irish ringing scheme. Between 1959 and 1998, WWRG caught approximately 36,000 Oystercatchers and 51,500 Knot on the Wash. Most birds (more than 90% in each case) were caught using cannon nets and the remainder using mist-nets; birds caught using both methods were included in these analyses. Prior to 1967, catching effort and success was patchy and data from these years were excluded. Since 1967, both species have been caught annually. On capture, birds were ringed, aged using criteria in Prater *et al*. (1977) and released. For the purposes of this analysis, birds were divided into two age classes - juveniles if they were in their first year of life (taken from June to May) and 'adults' of greater than one-year-old. This group will include a small fraction of two and three-year old immatures.

Only very small numbers of Oystercatchers and no Knot breed on the Wash. For both species, annual survival estimates were calculated around a ringing year running from 1 June, which is the time when fewest birds occur on the Wash. Too few data were available to model juvenile survival in periods of less than one year but sufficient data were available to model adult Oystercatcher survival for six-monthly periods running from 1 October to 31 March (hereafter termed the winter period) and 1 April to 30 September (the summer period). These periods were chosen to make best estimates of the relative importance of winter mortality, when the state of shellfish stocks may be important, and summer mortality, where factors in the breeding grounds are more likely to affect true adult survival.

The survival models for Knot and Oystercatcher (annual and 6-monthly) tested the need for inclusion of: age-dependent survival of one to three age classes (first, second and adult birds, but for the annual Oystercatcher dataset only); time-dependent or fixed survival estimates; and time-dependent (fully time-dependent, where possible linear or quadratic function) or fixed reporting rates. Immigration/emigration to the sites was assumed not to vary over the study period. The need for age-dependence was tested only for the annual Oystercatcher data set, as the juvenile data were too sparse for inclusion in the 6-monthly models.

Birds which had been shot may have had a different reporting rate to those found dead from natural causes. This was not an issue for Oystercatcher, as a very small percentage of the birds reported had been shot. For Knot there were two periods in which large numbers of shot birds were reported. In 1972 and 1974, 20 and 24 Wash-ringed birds were shot in Greenland during spring migration and reported. This coincided with a period of cold spring weather when birds became less wary and easy to hunt. The need for inclusion of separate reporting rates for these 2 years in the survival models was tested.

The effects of environmental variables, such as winter weather and shellfish abundance, were tested by setting survival as a logistic function of the environmental variable. This link function was used to ensure that all survival estimates lie between 0 and 1, as estimates outside this range are not valid (White & Burnham 1999). Other possible indicators of survival, such as body condition, were treated in a similar manner. The effects of shellfish stock abundance were tested for both Oystercatcher and Knot. For Knot, which only eat shellfish less than one year of age (recently settled spat), the effects of spat abundance indices on survival were tested. For Oystercatcher, data on mussel stocks were only available from 1982 onwards. Hence shellfish and winter weather covariates were only included in the models from this date onwards and previous winters' survivals were time-dependent.

Throughout the analysis, nested models were tested using a likelihood-ratio test (LRT) and the Akaike Information Criterion. The significance of covariates were tested using an analysis of deviance (ANODEV) which compares the amount of deviance explained by the covariate against the amount of deviance not explained by the covariate (White & Burnham 1999).

4.2.3 Estimating recruitment

The term recruitment is here defined as the recruitment to the local Wash wintering population, rather than the flyway population as a whole.

No data on the productivity of either bird species in their breeding grounds were available and recruitment to the Wash was estimated as the juvenile:adult ratio in the samples of birds caught by the Wash Wader Ringing Group in catches during October to March. Birds of unknown age were excluded. On the Wash, juveniles tend to arrive later than adults, and as the population indices were calculated for the winter period, only catches in October through to March were considered for both species. For Oystercatcher, too few birds were caught in 1992/1993 to estimate recruitment and a mean recruitment figure has been used.

4.2.4 Population models

Simple matrix models were constructed to estimate the population trend from annual estimates of survival and recruitment and the sensitivity of these to small changes in recruitment and survival explored.

4.2.5 Estimating measures of body condition as an indicator of survival

Both the state of moult and weight were initially used as an estimate of body condition or physiological stress. Body weight was not found to be a useful predictor and was therefore excluded from further analysis. Body condition was therefore assessed using the proportion of birds caught showing abnormal moult patterns using two different sets of criteria.

Adult Oystercatchers usually arrive back on the Wash from late July onwards and immediately start to moult. The period over which the population as a whole moults lasts five months and generally finishes in December. However, when waders are in poor body condition during the moulting season, birds can arrest, suspend or fail to moult. In most years on the Wash, a small number of adult Oystercatchers are caught in suspended moult from December onwards with a mix of new moulted primaries and older unmoulted primaries. These older feathers are characterised by being very worn and a sandy-brown colour, rather than the more usual black, and these two generations of feathers are easily picked out by a trained eye. The first measure of abnormal moult was therefore the proportion of birds caught which had suspended moult. This measure was only available from December onwards and the bulk of records of suspended moult in the Wash samples are recorded from January onwards.

Most of the ringed birds which were reported dead to the BTO were found dead in January and February. For an indicator of survival to be effective as a management tool it is necessary to have an indication that major mortality will take place before it actually does. This first measure does not satisfy this purpose.

The second measure of abnormal moult therefore involved the collection of information while birds were actively moulting. It is possible to assess when birds are likely to suspend moult by examining the moult gap (number of actively moulting feathers). During normal moult, Oystercatchers actively moult 2 to 5 feathers but when a bird is about to suspend this gap is generally reduced to one feather only. We looked at those birds which had a moult gap of one, i.e. one moulting feather in between a fully grown new feather inside of it and one old feather to the outside of it. Birds in this group, whose remaining moulting feather was more that one-third grown and had more than one remaining old primary, were included in the measure. Within this group, birds which had only just started to grow this one actively moulting feather (up to one-third grown) were excluded as it was possible that these birds had yet to lose another old primary. The dropping of the outermost primary is also variable and so only birds which were more than one remaining old-type feather were included. These strict conditions make this estimate of the number of birds about to suspend moult a conservative one.

4.2.6 Winter weather

Weather data from the Meteorological Office station at Terrington St Clement (52º-45[1]N 0º-17[1]E) was obtained and a measure of winter severity was calculated as the number of ‘cold’ days between January 1st and March 31st each year (Camphuysen *et al.*1996). The ‘cold’ days score is calculated as follows. Each day with an average air temperature (maximum + minimum divided by two) of 0 to -5ºC scores one, a day with a mean between -5 and -10 ^{o}C scores two and a mean less than -10 ^{o}C scores three.

4.3 RESULTS

4.3.1 Oystercatcher

4.3.1.1 Estimation of survival rates and recruitment

As too few recovery data were available to sensibly model juvenile survival rates in six-month blocks, the need for age-dependent survival was tested using annual models (Table 4.1a). Using AIC as a basis for model selection the inclusion of age dependence was not found to be necessary.

The parsimonious fit for the six-monthly models (adult Oystercatchers only) was one which included time-dependent winter and constant summer survival rates, and a constant winter and linear summer reporting rate (Table 4.1b). The need for time dependence in reporting rates was tested but the survival models did not converge and many of the 130 parameters were not estimated. The reason for this is that probably due to the large number of parameters being estimated. This final model shows that annual survival remained constant and maybe even showed a slight upward trend from 1970 to 1991 but that major mortality occurred during the winters of 1992/93 and then in 1995/96 and 1996/97 (Figure 4.2 a). Outside these three ‘kill-years’, mortality returned to pre-1992 levels.

Oystercatcher survival stayed approximately constant during the study period except for three winters: 1992/93 (survival = 73.8% ± 7.6 SE), 1995/96 (85.5% ± 5.5 SE) and 1996/97 (90.4% ± 4.2 SE). Average winter survival, excluding these ‘kill’ years was 97.98% ± 0.15 SE and 96.61% ± 0.87 SE including all winters. Summer survival was on average lower than in winter with an average of 92.02% ± 0.9%, presumably as this period included migration to and from Norway and a higher risk of mortality from predation and anthropogenic sources. Average annual survival was 89.0%.

Recruitment to the winter population varied between 0 and 0.58 juveniles per adult (Figure 4.4). In 1992, less than 100 birds were caught in the winter period and the mean recruitment rate value of 0.15 was used in calculating the population trajectory.

During each kill-year, mortality occurred in the first half of the calendar year (Table 4.2) and the total number of recoveries in the three months from January to March during the three kill years outnumbered those collected during the whole period 1969-1998 excluding the kill-years. In ‘average’ winters, mortality was low at the beginning of the winter period and increased but, even during January to March, an average of only 2 to 3 recoveries were reported per month (Figure 4.3). In the kill-years the total recoveries for this 3 month period were 139 in the 1992/93 winter, 37 in 1995/6 and 53 in 1997/98. When broken down by week in the 1992/93 winter, the frequency distribution of the number of dead birds reported to the BTO was effectively bi-modal, with a peak in the first two weeks of January 1993 and again in mid-February. In 1995/96 only one peak was seen, occurring in mid-February, and in 1996/97 the number of reported birds peaked in early January.

4.3.1.2 Changes in population – observed and predicted

From the monthly WeBS counts, Oystercatchers showed a slow increase from 1970 to 1987, a large increase in 1988 almost doubled the number of birds and then the population declined to approximately a quarter of the peak population but back to near 1972-74 levels (Figure 4.5). The population model for Oystercatcher provides a reasonable fit to the smoothed indices (Figure 4.5) and explains 49% of the variation in the smoothed observed data. The model successfully predicts the slow increase in the Oystercatcher population during the period 1973 to 1987 and then the decline from 1990 to 1997. As expected in a long-lived species, sensitivity analyses (not shown) indicate that the model index is relatively insensitive to small changes in juvenile survival and recruitment but very sensitive to small changes in adult mortality. By studying the population index for the period 1970-1996 (Figure 3.6a) and looking at the trends associated with firstly time-dependent survival rates alone and then time dependent recruitment rates alone, there is clear evidence that annual recruitment contributes most to the population trajectory of the population trend, with survival only having a major impact in the kill-years.

The model indicates that, with mean survival and recruitment rates the population would be increasing at a rate of 1.9% per annum over all years (Figure 4.6), or at 3.9% excluding the kill years. During the relatively stable period between 1973 and 1987, the Oystercatcher Underhill index increased at 1.88% per annum, which is in line with the predicted increase.

4.3.1.3 Effects of environmental factors

For 6-month survival estimates, the inclusion of shellfish and winter weather data significantly improved the fit from the null model (Table 4.1c, Figure 4.7) which incorporated time dependent survival rates to 1981/82 and the a constant survival rate afterwards. Table 4.1 (c) shows that changes in deviance between the null model and successive models which include all the main effects and the cockle*mussel interaction term. The addition of cockle and mussel abundance as covariates of winter survival significantly improved the fit from the null model (cockles: LRT Models 7 & 5, χ^2 = 83.6, df=1, $P < 0.001$; mussels LRT Models 7 & 4, χ^2 = 158.4, df=1, $P < 0.001$; cockles & mussels: LRT Models 7 & 3, χ^2 = 225.5, df=2, $P < 0.001$). Winter weather made a relatively relatively small contribution (LRT Models 7 & 6, χ^2 = 6.6, df=1, $P = 0.01$).

The largest jump in deviance occurred with the inclusion of an interaction term between cockles & mussels (Model 2). The inclusion of winter weather accounted for a slightly improved fit (LRT models 1 & 2, χ^2 = 5.3, df=1, P =0.02) and significantly improved the fit from the null model (ANODEV: F= 9.93, $P < 0.001$). The un-transformed logit parameters shown in Table 4.2 show a positive relationship between survival and shellfish but the interaction term indicates that the relationship is non-linear and that survival remains high when either cockle or mussel stocks are high but is low when both mussel and cockle indices are low.

The fit between the survival estimated from shellfish parameters and that which was calculated by the time dependent model shows that the fit is reasonable for the period when Oystercatcher survival was stable from 1982 to 1991, during the large drop in survival in 1992/93, the subsequent recovery in the following two winters and the fall in survival during the 1995/96 winter (Figure 4.7). However, during the last 3 years of the time series (1996/97 to 1998/99), the shellfish model predicts that survival should be lower than was estimated from the time-dependent model, although the shellfish-weather model does show a lower survival in 1996/97 and then an increase in the last two years which is similar to the time-dependent model.

4.3.1.4 State of moult as an indicator of survival

The proportion of birds showing abnormal moult was a better predictor of survival over the winter period than shellfish stocks and winter weather (Table 4.1d, Figure 4.8). Both moult parameters, suspension and small moult-gap, successfully predicted that survival was lower in the three kill years and were a better overall predictors than the shellfish-weather model. In years when mortality was high, the proportion of birds in the catches showing abnormal active moult during the period August-

December was generally lower (3-5%) compared with birds which had suspended moult (7-15%). This is presumably because birds were caught pre-suspension in August to December.

4.3.2 Knot

4.3.2.1 Estimation of survival and recruitment rates

For adult Knot, the best-fit model is one which included time dependent survival and a fixed reporting rate; the models which included a fixed reporting rate for all years but 1972 and 1974 which were allocated separate reporting rates did not converge. The survival trend shows that adult survival shows more year-to-year variation than in Oystercatcher but shows no trend across the time series, apart from a reduced survival during the early 1970s (Figure 4.2). None of the large dips in survival observed in Oystercatcher were observed with Knot.

Annual survival varied between 69.9 and 97.6% and the lowest two estimates occurred in the years when large numbers of birds were shot in Greenland (1972: 78.0 +/- 0.03; 1974: 69.9 +/- 0.4%). On average, annual survival was 88% +/- 0.12 SE.

Recruitment rates varied widely between years and were typical of a high-latitude breeding wader, in that recruitment tended to be either very good or very poor and rarely moderate (Figure 4.4 b). Recruitment to the Wash population was high in the three winters from 1978/79 to 1980/81.

4.3.2.2 Changes in the Knot population – observed and predicted

As juvenile survival could not be estimated, a figure of 0.6 was used based on figures in Boyd (1992). The observed population trend, calculated from the Underhill index, shows a decline in the number of birds wintering on the Wash during the 1970s, followed by a large increase throughout the period 1977 through to 1980, a period of relative stability until 1990 and then a rapid decline in numbers. The predicted model, although showing much less variation than the observed figures, provides a good match to the underlying population trend. Sensitivity analyses showed that, although the models are very sensitive to small changes in adult survival, it has been the changes in recruitment that have largely driven the changes in the predicted population size (Figure 4.6 b).

4.3.2.3 Effects of shellfish spat abundance and winter weather on adult Knot survival

No effects of weather or spat abundance could be found on adult Knot survival (Table 4.4).

4.4 DISCUSSION

4.4.1 Variation in survival rates

The overall annual mortality of > 1 year-old Oystercatchers in the Wash is, at 11%, broadly in line with an estimate of 12.1% from two marked populations of Oystercatcher studied on the Wadden Sea (mean values of total estimated mortality in Tables 5 & 6 in Camphuysen *et al.* 1996). However, summer mortality (8%) in Wash Oystercatchers tends to be higher and winter mortality lower (2%) than in the Wadden Sea (3.6± 0.4% in summer and 8.4 ±3.0% in winter averaged across years for the two populations reported on by Camphuysen *et al.* 1996). The reasons for this are at present unknown but winters are less severe on the Wash. The summer period includes two migrations, and spring weather conditions on the breeding areas in Norway may be crucial to survival. However the number of dead Wash-ringed birds reported normally peaks in mid-summer (Figure 4.3) although values for April to August are very similar. Predation and other anthropogenic sources of mortality (*e.g.* cars) would be expected to operate throughout the whole of the breeding season. The figures for summer and mortality on the Wash are similar to the figures obtained on the Exe estuary where winter mortality was estimated to be 3.2% and summer survival at approximately 8% (Durell *et al.* 2000). These birds are from different breeding areas to Wash Oystercatchers, tending to breed in northern Britain.

Oystercatchers and, to a certain extent Knot, have been shown in this study to experience little variation in survival rates between years under normal circumstances. This is similar to the results of other studies on Oystercatcher mortality in British estuaries (*e.g.* on the Exe Estuary, Durell *et al*., 2000). However, Oystercatcher mortality is often much higher in periods of severe weather in the Wadden Sea (Camphuysen *et al*. 1996, Neve & van Noordwijk 1997). It might be expected that the Wash on the east coast of Britain would show a more significant effect of severe weather on survival. O'Connor *et al.* (1982) showed a strong relationship between the number of recoveries received of Oystercatchers in Britain and the number of freezing days, suggesting that Oystercatchers were susceptible to the effects of cold weather. In surveys of the numbers of birds dying during periods of severe weather (Davidson & Evans 1982) the number of Oystercatcher corpses recovered has always been substantial but only a small proportion of the wintering population (Clark 1983, Clark *et al*. 1993). Many of these birds found dead are either juveniles or birds with deformities or injuries and it could be that severe winter weather hastens mortality in susceptible individuals rather than increasing substantially the annual mortality.

The substantial increase of mortality in the 1992/93 winter was associated with dramatic behavioural changes in Oystercatchers around the Wash, with large numbers of birds vacating the normal intertidal feeding grounds and moving inland to feed on earthworms on grass fields, in gardens and even areas of grass in the centre of busy roundabouts (Clark 1983). A similar situation was seen at Morecambe Bay after the severe winter of 1963/63 removed all cockles in the bay for the following 10 years (Dare 1970). The observation in The Wash also corroborates the evidence that there was a substantial reduction in food supplies and that Oystercatchers were unable to switch from feeding on cockles and mussels, their main food supplies on the Wash, to other food sources such as the bivalves *Scrobicularia*, *Macoma* or worms, *Arenicola* and *Nereis*. In winter, these food sources tend to be less available, as the organisms bury deeper in the mud. As average temperature decreases there may come a point when these organisms are too low in the mud for Oystercatchers to feed on and hence cause the large kills. Normally these organisms are of low value to the birds and do not tend to normally figure highly in the winter Oystercatcher diet (Zwarts *et al.* 1996b). When faced with a shortage of cockles and mussels in 1990/91, Oystercatchers in the Wadden Sea took what were thought to be small Cockles, *Macoma, Mya* and *Arenicola* (Zwarts *et al.* 1996b, Beukema 1993) although mortality in that winter was high (Camphuysen *et al.* 1996). Oystercatchers tend to be less mobile that Knot in winter due to an apparent higher degree of site fidelity and with these differing strategies, Oystercatchers tend to be more susceptible than Knot to severe weather or food shortages.

The inland feeding of Oystercatchers during winter time is common on some south and west coast estuaries but is relatively rare on the east coast of Britain. In these areas it is seen to be a strategy to 'top up' on food if birds were unable to find sufficient food during the tidal cycle (Goss-Custard *et al.* 1994). The lack of inland feeding around the Wash prior to 1992/93 is probably in part related to sufficient food resources being available inter-tidally, the lack of substantial areas of permanent pasture around the Wash and also possibly to the colder winter temperatures on the east coast making inland feeding less dependable, due to an increased risk of frozen ground.

In contrast with Oystercatchers, the only periods of substantial decline in Knot survival were in the early 1970s in years that coincided with extremely late Arctic thaw across Greenland and northern Canada when large numbers of Knot are known to have died soon after arrival on the breeding grounds (Boyd 1992). Knot are known to be highly mobile both within estuaries and between estuaries (Rehfisch *et al*. 1996). It has been suggested that this is in part related to their ability to exploit highly variable food supplies. In years when there is good spatfall of cockles on the Wash, Knot are often seen to concentrate on this food resource especially in autumn and early winter (Yates, pers. comm.). Low recruitment to the Wash population coupled with this ability to move between estuaries to exploit peaks in food resources probably explains why there were no substantial declines in Knot survival during periods of low cockle and mussel recruitment on the Wash.

4.4.2 Factors affecting recruitment

Catches of waders using either cannon-nets or mist-nets are known to be biased (Pienkowski & Dick 1977). This is not surprising as Oystercatcher roosts, in particular, are known to show considerable variation in the quality of birds using them and the proportion of juveniles (Swennen 1984). However, the Wash Wader Ringing Group has been operating on a regular basis, making over 30 catches of waders each year and any bias is unlikely to have changed during this period. It is important to emphasise, however, that the values for the recruitment parameter used in this model do not necessarily refer to the adult production of juveniles, as recruitment to the Wash will be related to breeding success and the attractiveness of the Wash as a site for juvenile birds to settle. This is likely to vary between years with food supplies and other factors. Although, in the case of Oystercatchers, juveniles have been shown to feed mainly on *Arenicola* in their first winter and only switching to cockles and mussels as they become sub-adults (Goss-Custard *et al.* 1994). Although juvenile birds are more mobile than adults (Rehfisch *et al*. 1996), the vast majority settling on an estuary as a juvenile will return to that estuary for the rest of their life (Dare 1970, Anderson & Minton 1978).

The situation for Knot is similar. The decision for a juvenile bird about whether to stay or move on to a different estuary will be determined, in part, by the quality of the site. This study has shown that poor recruitment of juvenile Knot to the Wash wintering population is likely to have been a major cause in the decline in the number of Knot using the Wash. This poor recruitment may be local or global but at present we are not in a situation to determine which. Knot populations are stable in Britain as a whole and poor spatfalls may well be responsible for the poor recruitment of juvenile to the Wash. Further work is recommended to explore this further.

4.4.3 Comparison of model predictions with population counts

Both the Oystercatcher and Knot results generated from the population models agree reasonably well with data from the long-term WeBS counts on the Wash. However, the models for both species suggest less annual variation in the birds than do the counts. This is not surprising, as extremely large flocks of waders on the Wash, sometimes flocks of over 100,000 in the case of Knot, are notoriously difficult for observers to count accurately (*e.g.* Prater 1981). This is the main reason why, for comparing the importance of sites within Britain, average maximum counts over five years are taken to represent the relative importance of an estuary. Variations in the national indices for the two species, excluding the Wash and taking into account a very large number of sites, show very much less variation between years and probably more accurately reflect the scale of annual variations at the individual estuary level. There appears to be a difference between the models and the counts for Oystercatchers in the four-winter period period 1988-1991, The counts showed dramatic declines occurring but the model shows a stable or slightly increasing population. Evidence from ringing recoveries suggest that there was a highly significant increase in the number of Oystercatchers that had been ringed on the Wash and were subsequently recovered on other east coast and north-west European estuaries, suggesting that a significant proportion of the Oystercatcher population moved out of the Wash to winter on other sites during this period. Such movements have been recorded before (Sutherland, 1982) and appear to be a response to extreme events.

4.4.4 Predicting periods when food supplies are likely to affect survival

We have shown that low food supplies have led to significant increases in the mortality of Oystercatchers. However, the major problem with these models is that at any given time the accuracy of our estimates of mortality is poor for the preceding year and it is only after two or three further years of subsequent data that we can rely on the estimates of mortality produced by analyses of ringing recovery information.

The occurrence of aberrant moult in Oystercatchers is strongly correlated with periods of increased mortality for the population as a whole and aberrant moult in early and late autumn has been shown to be an indicator of poor survival in the coming winter. Once a bird has suspended moult, it is unlikely to restart and so can be used as indicator from the time when it suspends to when it next moults, a period of up to 10 or 11 months. Weight was probably not a good predictor as it can vary greatly over time and for it to be a useful indicator it may be that birds have to be caught at exactly the time that they are in poor condition.

Cockle stock assessments are carried out by Eastern Sea Fisheries Joint Committee in May of each year, and quotas set in the light of these stock assessments to allow the taking of 30% of the fishable stock. We have demonstrated a link between shellfish stocks and Oystercatcher survival but at present we do not have sufficient information to determine the exact effects of shell-fishing on Oystercatcher populations. Fishermen and birds may be exploiting different size classes of cockle or mussel and further studies would be needed to determine the role of fishing and fishery management (*e.g.* quota) on the food supply for birds. The study has highlighted the potential role of re-laid mussel beds and fishermen report that many Oystercatchers use these beds. Mussel farming is increasing in the Wash and since 1997 the distribution of mussel lays has changed from being almost exclusively on the west coast of the Wash near Boston to being more evenly spread (ESFJC pers. comm.). A 3-year farming rotation is normally practised thus making a wide range of size classes available to birds. While both cockle and 'natural' mussels stocks were still low in the Wash during the late 1990s, it may be that these farmed mussels provided sufficient food to prevent a major mortality of Oystercatchers which the shellfish-weather survival model suggested otherwise would have occurred. In the winter of 1999/2000 there were licences for approximately 140 ha of mussel lays within the Wash (ESFJC) and these would potentially be a substantial resource for birds although further work would be needed to determine the scale of its effects.

5. RECOMMENDATIONS

5.1 Further monitoring and research work

- Regular monitoring is needed to determine the health of the Wash Oystercatcher population. This would entail the catching of, at least, 200 and preferably 400 actively moulting birds during the period August to December. Catches during January to March are also recommended as birds' condition may deteriorate during the course of a winter.

- The number of birds showing abnormal moult is a good indicator of forthcoming over-winter survival. The ways that this information can be fed into the fishery management process should be investigated.

- Further work is recommended to investigate the relationships between shellfish, Oystercatchers and fishermen to determine whether (a) competition is direct or (b) exploitation patterns differ and (c) what these consequences are. This exercise could also determine whether relaying Mussels in the intertidal zone is likely to increase Oystercatcher survival in winters when 'natural' shellfish stocks are low. This could take the form of a combined field/modelling study.

- This study does not fully explain the low recruitment to the Wash Knot population. By bringing together productivity data from breeding studies and measurements of the adult:juvenile ratios from other wintering areas we should be able to analyse whether there are Wash-specific factors determining recruitment or whether it is more of a general phenomenon.

- Further analysis of the WWRG dataset is recommended using re-trapped birds rather than dead birds. Movements within the Wash, area-specific mortality and the extent of emigration could be examined in much greater detail. This would be especially profitable for Knot due to the small sample size of dead birds recovered.

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Table 3.1. Numbers of recoveries of dead Wash-ringed Oystercatchers in the seven years prior to and post the first major kill of Oystercatchers in 1992/93. Shaded cells indicate the three 'kill' years. A summary table below groups these recoveries by region.

Winter (85 = winter 85/86)	Belgium	Denmark	Netherlands	Norway (October)	Norway March)	France	Sussex	Cambridgeshire	Cleveland	Durham	Essex	Grampian	Hampshire	Humberside	Lancs	Merseyside	North Yorkshire	Northumberland	Tyne & Wear	Lincs	Norfolk	Grand Total
85			2		1	3														2	5	13
86		2	2			4														2	1	11
87			1			1														1	1	4
88					1	1														6	3	11
89			2		1	3						1								6	5	18
90		1				1					2									4	17	25
91			1			2														1	6	10
92	1		11		1		1	2	1	2	1			3			1			77	54	155
93					1	1														2	1	5
94			1						1											1	6	9
95		1	6			4	1		1	1			1	2				1		27	19	64
96			4	1										2					1	20	14	42
97																1				2	3	6
98														1	1							2
Grand Total	1	3	30	1	5	20	2	2	3	3	3	1	1	8	1	1	1	1	1	151	135	375

	Belgium	Denmark	Netherlands	Norway (October)	Norway March)	France	Sussex	Cambridgeshire	Cleveland	Durham	Essex	Grampian	Hampshire	Humberside	Lancs	Merseyside	North Yorkshire	Northumberland	Tyne & Wear	Lincs	Norfolk
No before kills	0	3	8	0	3	15	0	0	0	0	2	1	0	0	0	0	0	0	0	22	38
No after Kills	1	1	22	1	2	5	2	2	3	3	1	0	1	8	1	1	1	1	1	129	97

Region	Before	After
France	15	5
Inland	0	2
North-east UK	0	17
North-west Europe	11	24
North-west UK	0	2
Norway (breeding)	3	3
Scotland	1	0
South coast	0	1
South-east UK	2	3

Table 4.1 Results of Oystercatcher survival models estimating (a) annual survival rates using both adult and juvenile Oystercatchers and (b) six-month survival rates for adult Oystercatchers only and testing (c) whether winter survival rates are related to shellfish stock abundance and (d) whether the proportion of birds showing abnormal moult is an indicator of survival.

S = annual survival, *R* = annual reporting rate. *AD* = adult birds, *JUV* = first-year birds. *SS* = summer survival (April-September), *SW* =winter survival (October-March), *RS* = summer reporting rate, *RW* = winter reporting rate. Parameters: *c* = constant parameter, *t* = time dependent, *lin* = linear function of time, *muss* = function of the mussel index, *cock* = function of the cockle index, *cock*muss* = cockle*mussel interaction term, *weath* = function of winter severity index, $_{int}$ = Intercept.

(a) Annual survival rates testing age-dependence

Model	AIC	Delta AIC	Number of parameters	Deviance
S_t , R_c	19498.98		32	1193.62
S_t , R_{ADc} R_{JUVc}	19499.52		33	1192.15
S_t , R_{lin}	19500.97		33	1193.61
S_{ADt} S_{JUVc} , R_{ADc} R_{JUVc}	19561.47		34	1252.10
S_{ADt} S_{JUVlin} , R_{ADc} R_{JUVc}	19561.73		35	1250.35
S_{ADt} S_{JUVc} , R	19573.78		33	1266.41
S_c R_c	19821.37		2	1576.09

(b) Six monthly survival rates.

Model	AIC	Delta AIC	Number of parameters	Deviance
SS_c SW_t , RS_{lin} RW_c	17686.6		36	1709.4
SS_c SW_t , R_c	17688.8		34	1715.7
SS_c SW_t , RS_c RW_{lin}	17690.0		35	1714.8
SS_c SW_t , RS_c RW_c	17690.4		35	1715.3
SS_t SW_t , RS_c RW_c	17715.7		65	1680.3
SS_t SW_c R_c	18197.7		34	2224.5
SS_c SW_c R_c	18205.8		3	2294.7

Table 4.1 (contd.)

(c) Testing the effects of shellfish stock abundance on adult Oystercatcher survival.

	Model	AIC	Delta AIC	Number of parameters	Deviance
1	SS_c $SW_{cock, muss, cock*muss, weath}$, RS_{lin} RW_c	17778.7	0.0	24	1825.6
2	SS_c $SW_{cock, muss, cock*muss}$, RS_{lin} RW_c	17782.0	3.3	23	1830.9
3	SS_c $SW_{cock, muss}$, RS_{lin} RW_c	17933.4	154.7	22	1984.3
4	SS_c SW_{muss} , RS_{lin} RW_c	17998.5	219.8	21	2051.4
5	SS_c SW_{cock} , RS_{lin} RW_c	18071.3	292.6	21	2126.2
6	SS_c SW_{weath} , RS_{lin} RW_c	18148.3	369.6	21	2203.2
7	SS_c SW_{NULL} RS_{lin} RW_c	18152.9	374.2	19	2209.8

(d) Testing whether abnormal moult is an indicator of adult Oystercatcher survival

Model	AIC	Delta AIC	Number of parameters	Deviance
SS_c $SW_{moult(AUG-DEC)}$, RS_{lin} RW_c	17711.9		16	1774.8
SS_c $SW_{moult(DEC-OCT)}$, RS_{lin} RW_c	17757.3		14	1824.2
SSc $SW_{NULL(DEC-OCT)}$, RS_{lin} RW_c	18155.7		13	2238.6
SSc $SW_{NULL(AUG-DEC)}$, RS_{lin} RW_c	18168.2		15	2233.1

Table 4.2 Parameter estimates and 95% confidence intervals for the survival model SS_c $SW_{cock, muss, cock*muss, weath}$ RS_{lin} RW_c (see Table 3.1 for details).

Parameter	**Estimate (logit scale)**	**Lower 95% CI**	**Upper 95% CI**
Intercept	-3.61878	-4.39558	-2.84199
Mussel	1.692337	1.486258	1.898415
Cockles	3.22268	2.738932	3.706428
Cockles*Mussels Interaction	-0.75507	-0.87344	-0.63669
Weather	-0.02126	-0.03933	-0.00319

Table 4.3 Number of dead Wash-ringed Oystercatchers birds reported to the British Ringing Scheme by members of the public between 1990 and 1999.

Year	**Jan**	**Feb**	**Mar**	**Apr**	**May**	**Jun**	**Jul**	**Aug**	**Sep**	**Oct**	**Nov**	**Dec**
90	4	3	9	8	6	6	3	7	2	3		1
91	3	17	7	6	4	3	9	6			1	2
92	2	4	2	7	6	5	9	3	8	6	5	15
93	93	40	23	12	5	2	5	3	1		1	1
94	1	1	2	4	5	3	1	5	2	1	1	2
95	5	3	2	4	5	5	1	4	2	2	5	10
96	36	28	11	7	6	3	1		1	2	5	2
97	36	6	1	8	4	3	2	2	3	1	1	1
98		2	1	1	2	5	3	4		1		
99		1		-	-	-	-	-	-	-	-	-

Table 4.4 Results of Knot survival analysis. Notation as for Table 4.1.

		AIC	No Parms	Deviance
(a)	*Testing variable reporting rate*			
1	S_t , R_c	3742.1	31	298.9
	S_t , $R_{c\ +\ 72\&74\ seperate}$	3743.3	33	298.1
2	S_t , R_{linear}	3752.0	32	308.8
3	S_t , $R_{linear+\ 72\&74\ separate}$	3890.3	34	447.1
(b)	*Testing effects of shellfish covariates*			
1	S_{cock} , R_c	3733.4	3	346.2
2	$S_{muss,\ cock,\ muss*cock,\ weath}$, R_c	3733.4	6	340.2
3	$S_{muss,\ cock}$, R_c	3733.5	4	344.4
5	S_{muss} , R_c	3733.4	3	346.2
6	S_{weath} , R_c	3735.3	3	348.2
7	$S_{NULL\ ,}$ R_c	3733.6	2	348.5

Figure 2.1 Changes in numbers of the regularly indexed wader species on the Wash between 1970/71 and 1998/99. Counts are mean monthly counts for the period December to February and missing counts are imputed using the Underhill method (see text for details). Solid line = count based on Underhill method, dashed line = counts which have been smoothed using General Additive Models to reveal the underlying trend.

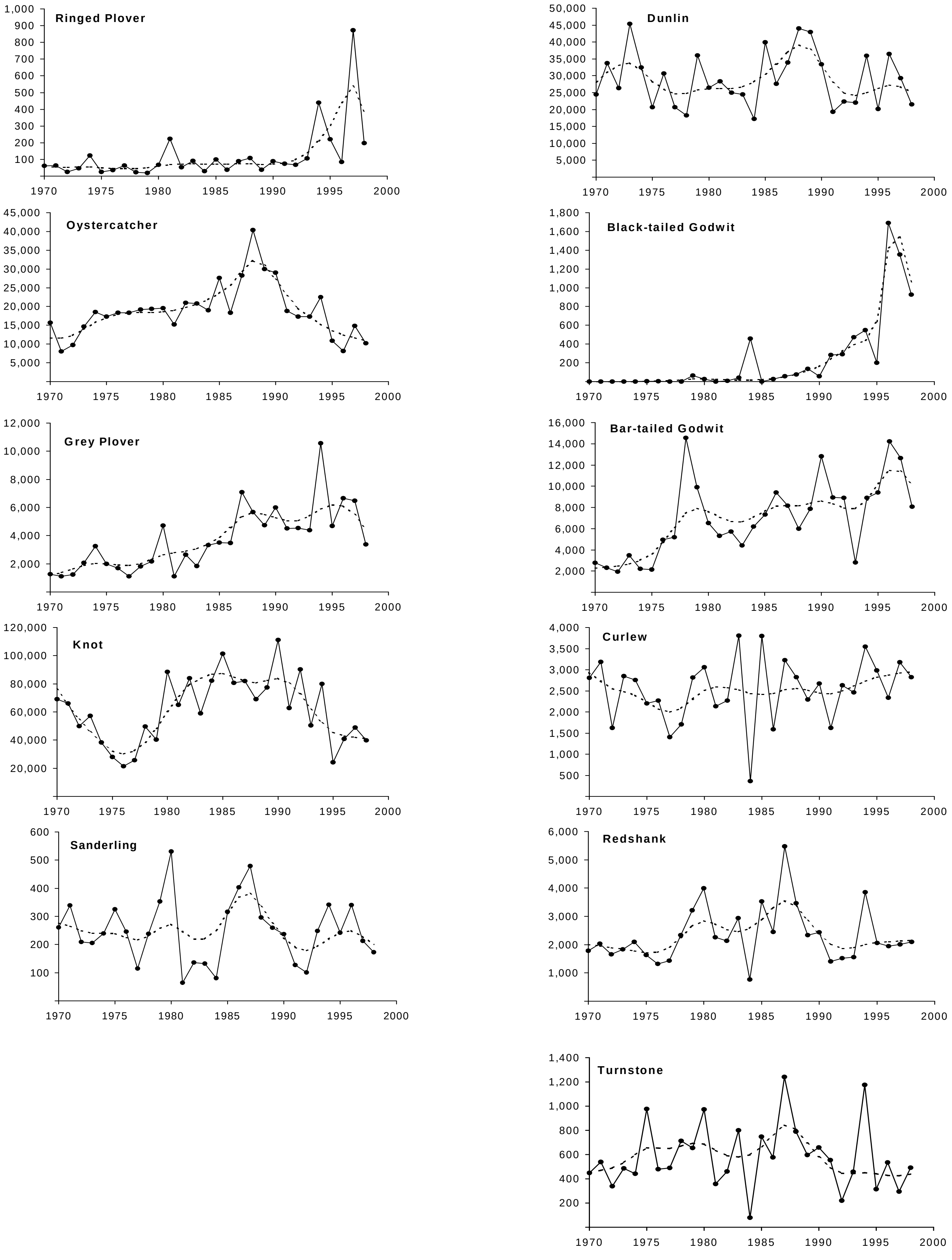
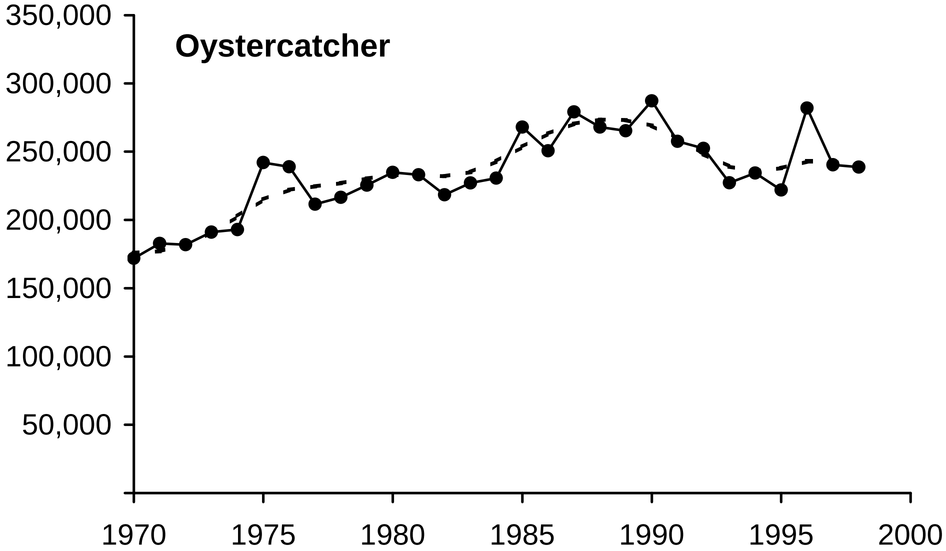


Figure 2.2 Changes in the national Knot and Oystercatcher populations. Numbers are the average number of birds counted per month during December to February each year. Missing or poor quality counts are imputed using the Underhill method. Solid line = numbers calculated using the Underhill method, dashed line = the smoothed trend line. Years: 1970 = the winter of 1970/71.



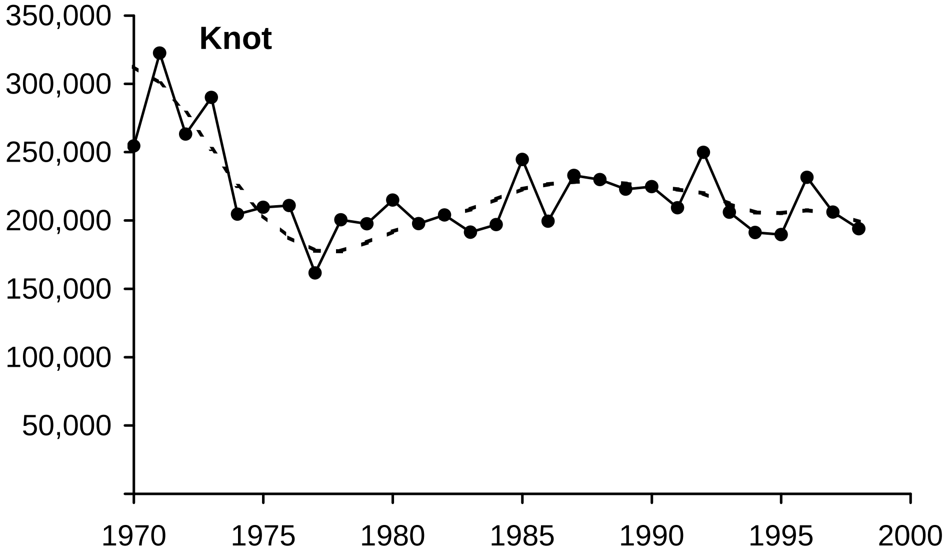
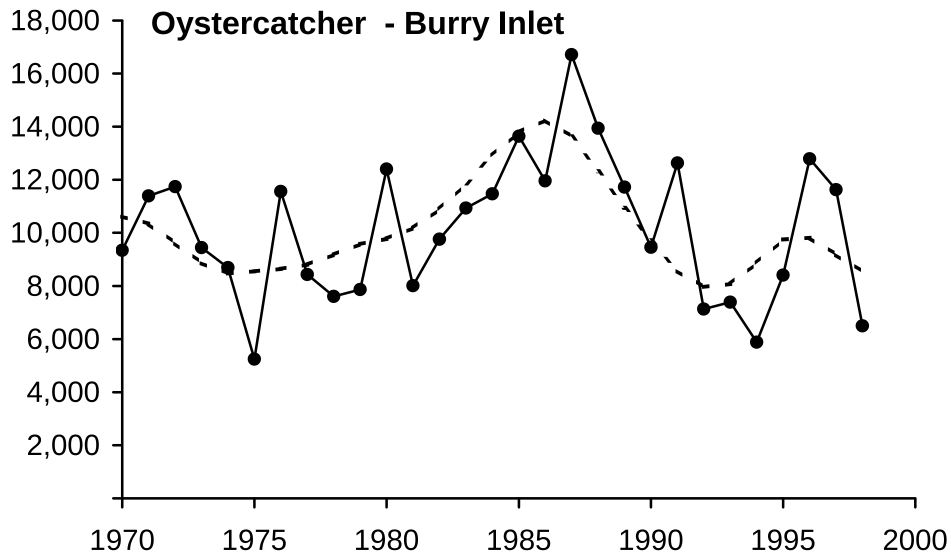


Figure 2.3 Changes in the Knot and Oystercatcher populations in the Burry Inlet. Numbers are the average number of birds counted per month during December to February each year. Missing or poor quality counts are imputed using the Underhill method. Solid line = numbers calculated using the Underhill method, dashed line = the smoothed trend line. Years: 1970 = the winter of 1970/71.



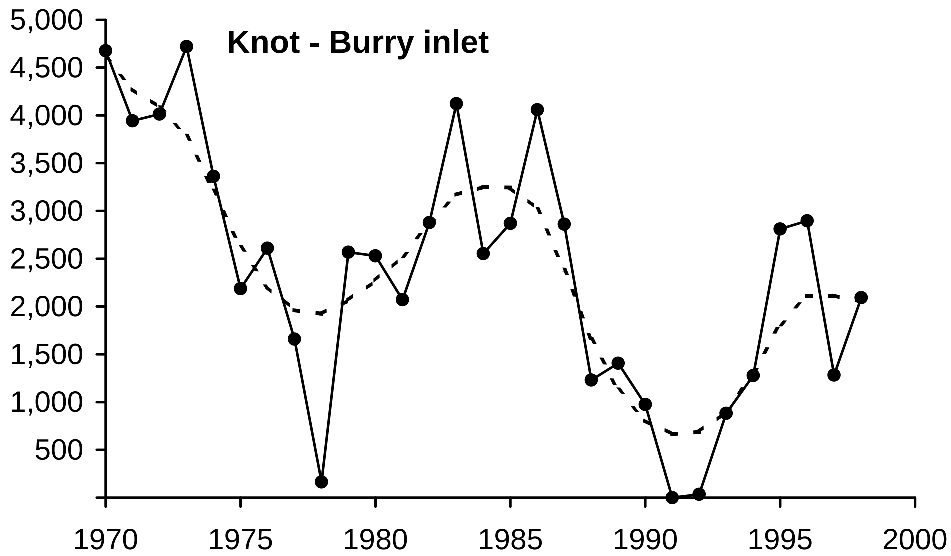
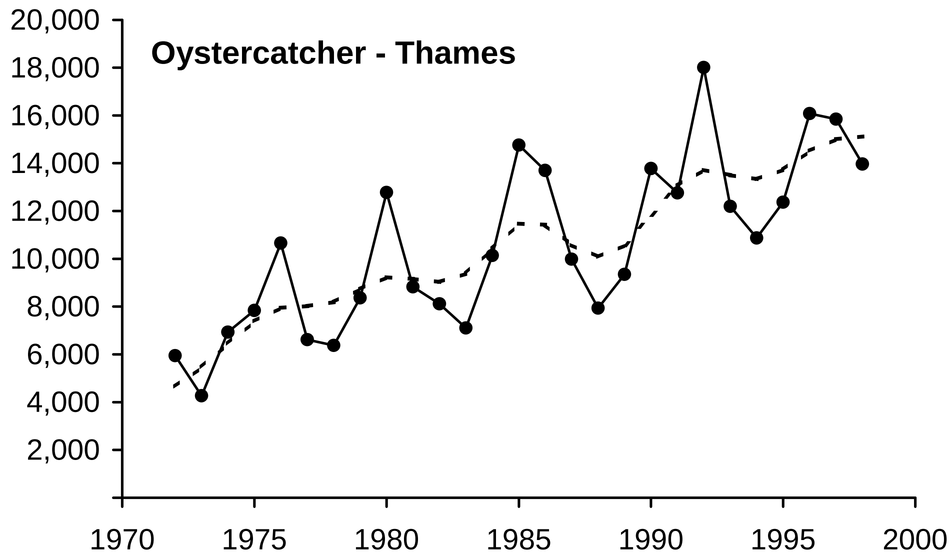


Figure 2.4 Changes in the Knot and Oystercatcher populations in the Thames estuary. Numbers are the average number of birds counted per month during December to February each year. Missing or poor quality counts are imputed using the Underhill method. Solid line = numbers calculated using the Underhill method, dashed line = the smoothed trend line. Years: 1970 = the winter of 1970/71.



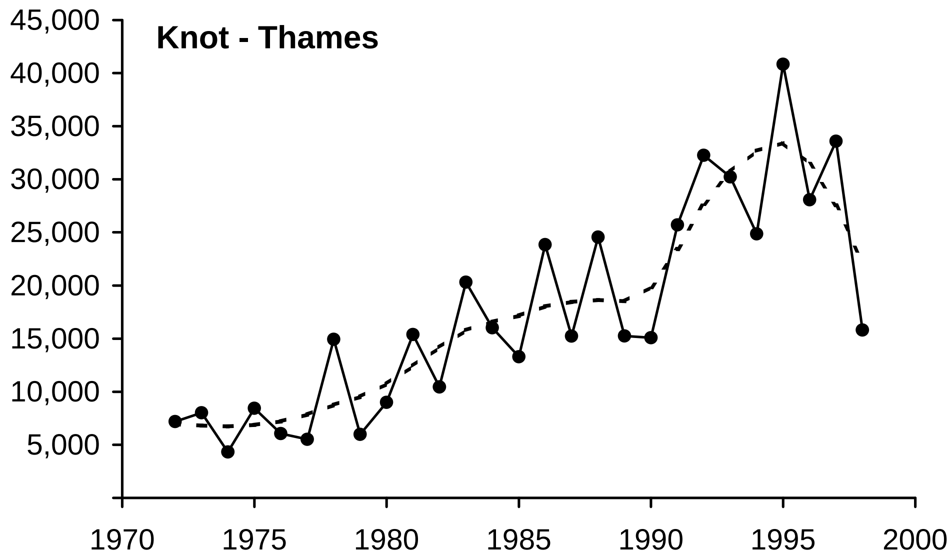


Figure 3.1 Recoveries of Oystercatchers originally ringed on the Wash at any time and found dead during the breeding season (May to July inclusive). Each line represents the movement of a single bird.

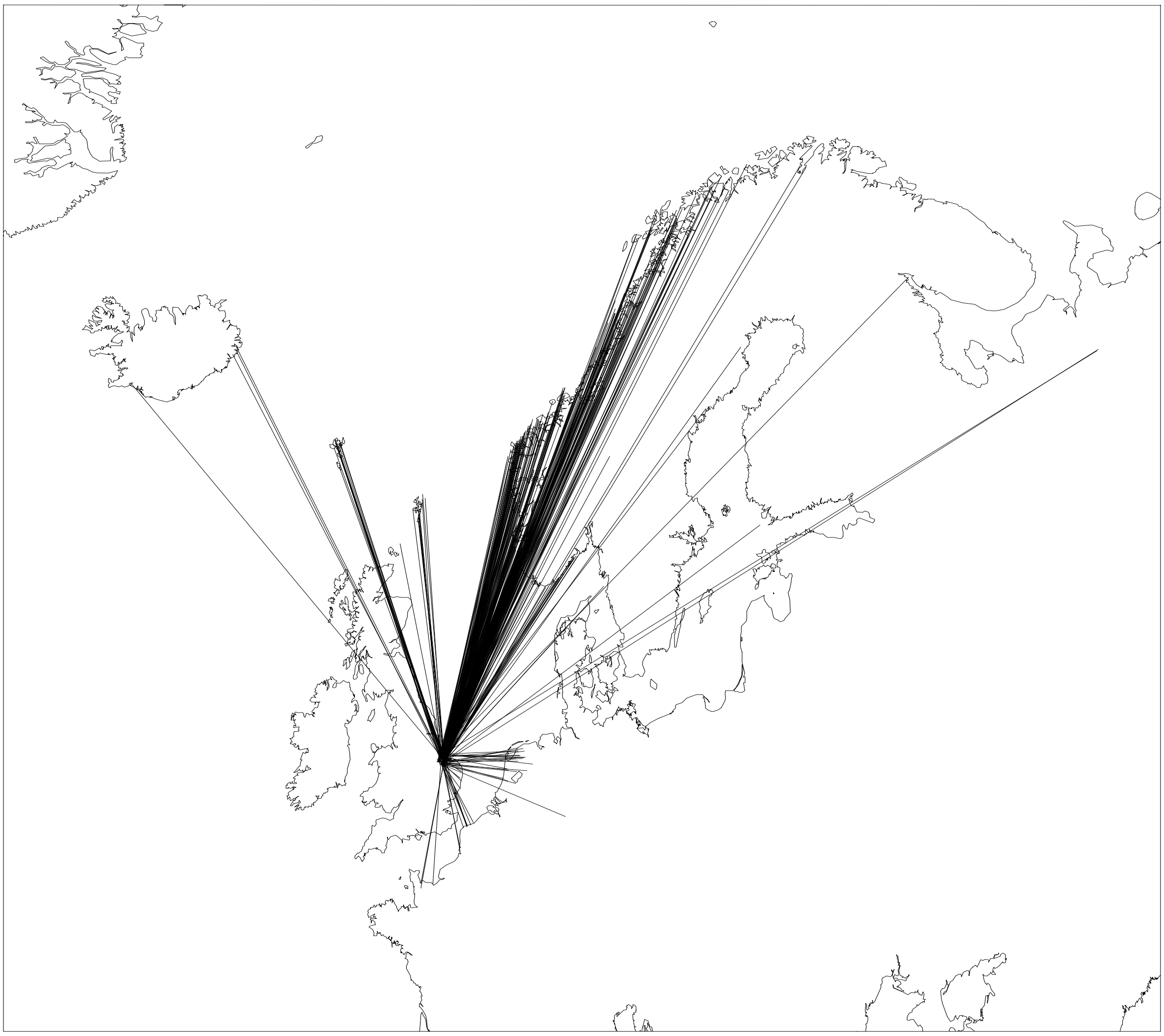


Figure 3.2 Recoveries of Wash-ringed Knot (dead birds and controls of living birds) during the months May to July. Wash Knot predominately breed in Greenland and north-east Canada but the birds in the Vendee region and in the Wadden Sea in May are likely to be from the Siberian-breeding population which winter in west Africa.

Figure 3.3 Recovery locations of Oystercatchers ringed on the Wash between September to February and recovered in a subsequent year during September to March, indicating a change in moulting or wintering area.

● Birds ringed from the winter of 1991/2 onwards

▲ Birds ringed prior to or during the winter of 1991/92

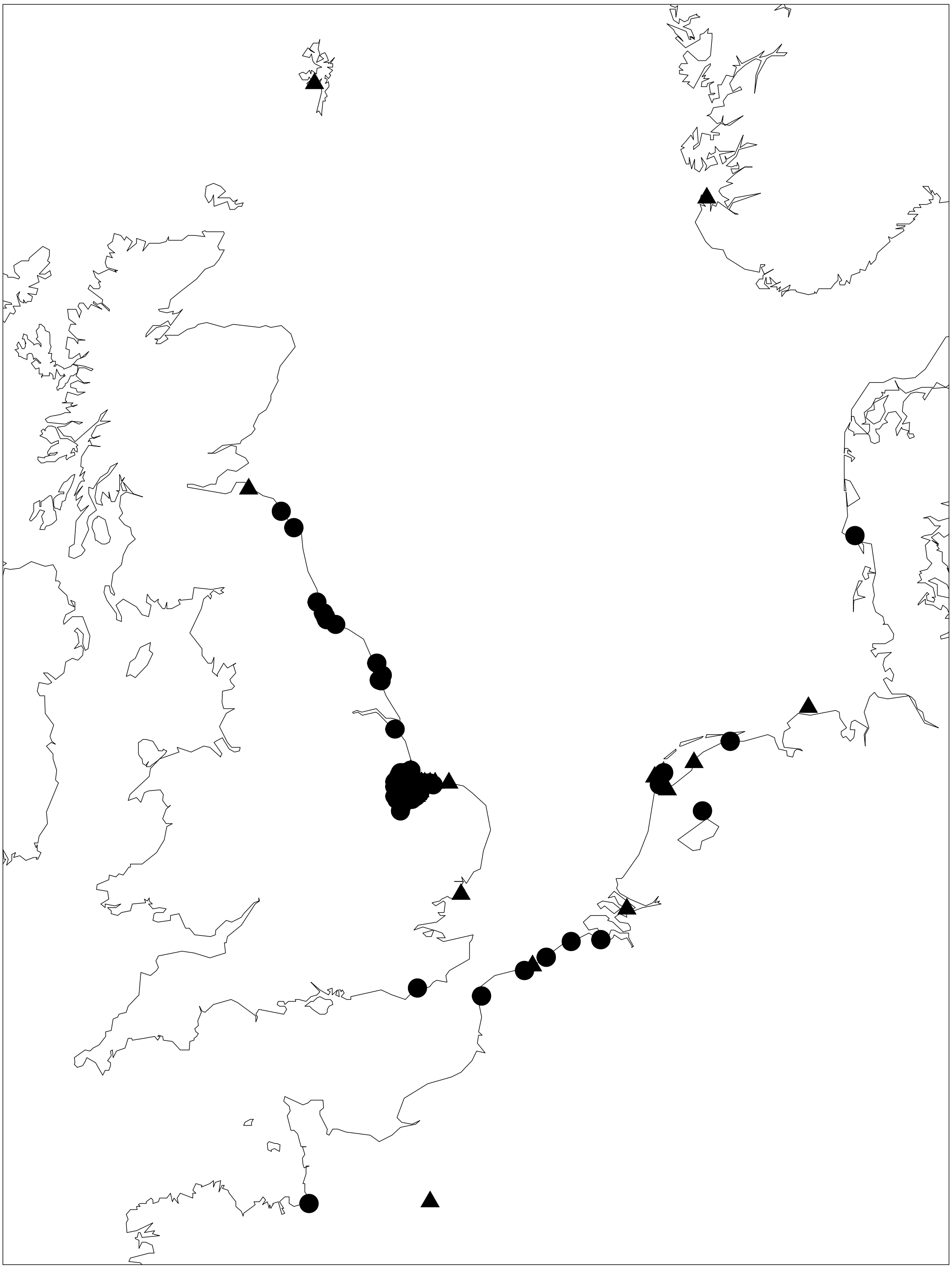


Figure 3.4 The number of Wash-ringed Oystercatchers alive during the period 1967/68 to 1998/99 based on ringing totals and survival over 6 month periods. W = Winter (October to March), S = Summer (April to September).

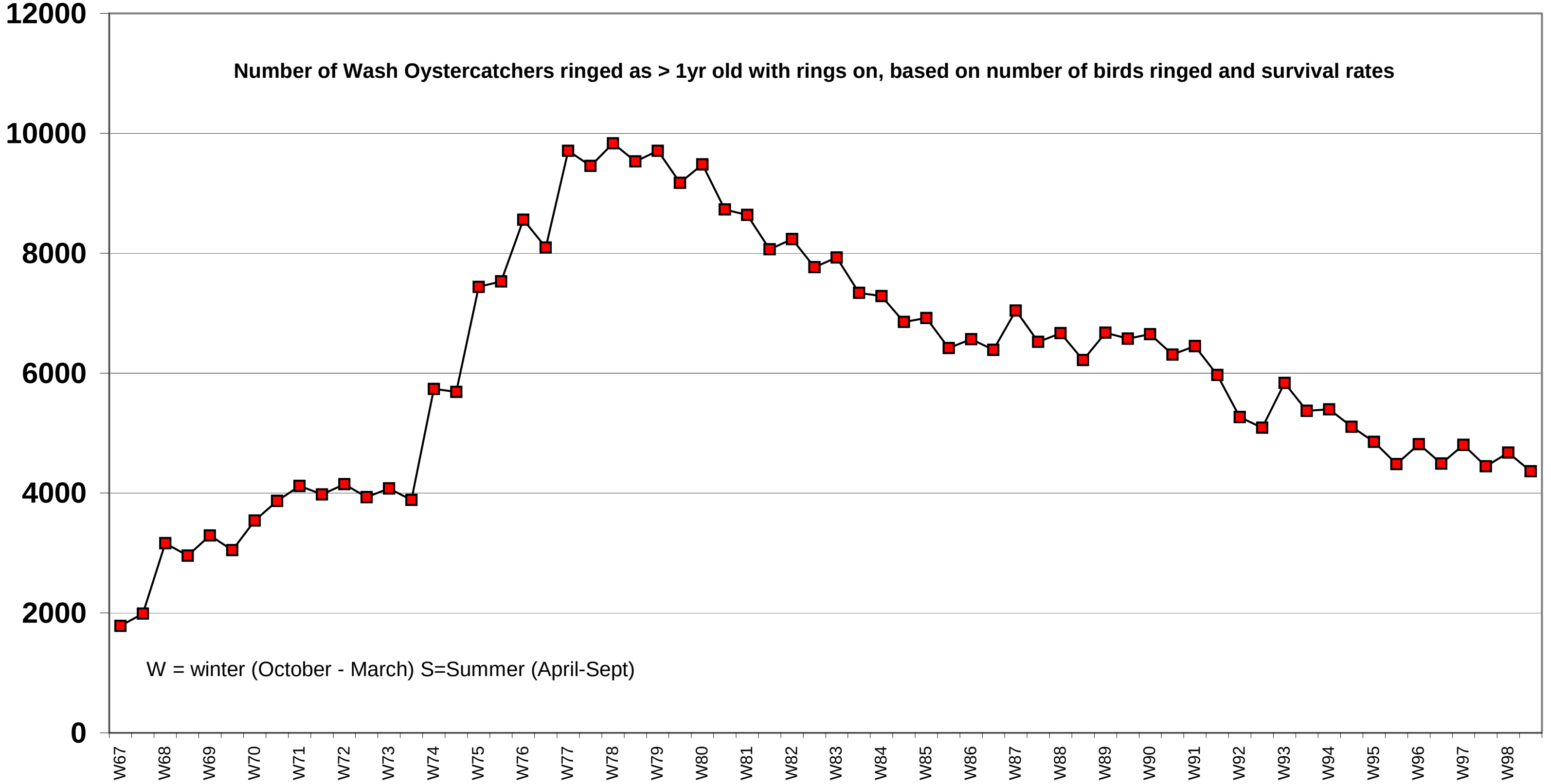
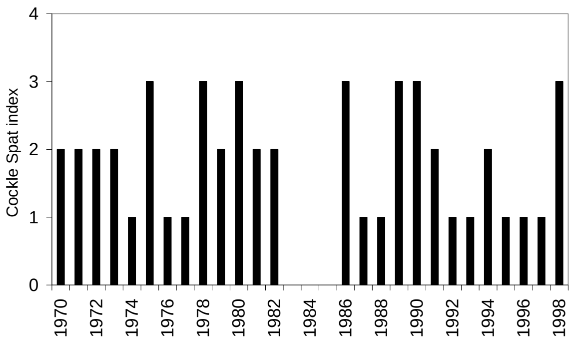
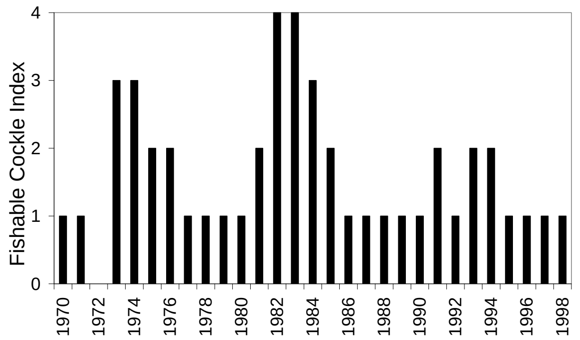


Figure 4.1 Changes in the Wash Mussel and Cockle fishery 1970-1998. (a) changes in cockle spat index; (b) changes in fishable cockle stock index, (c) changes in the mussel spat index, (d) changes in the mussel stocks (tonnes). Indices are explained in the text.

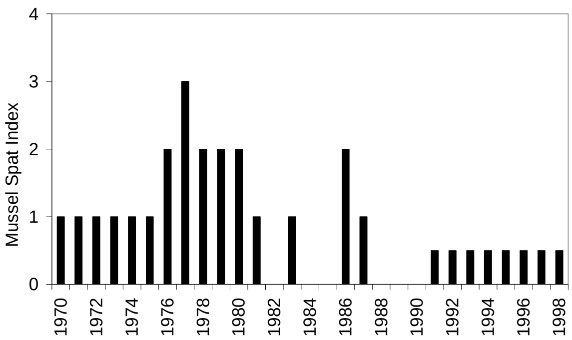
(a)



(b)



(c)



(d)

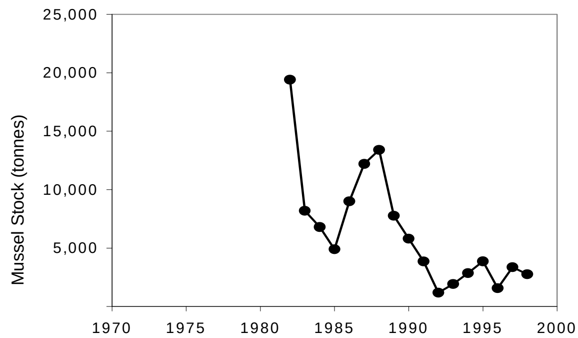
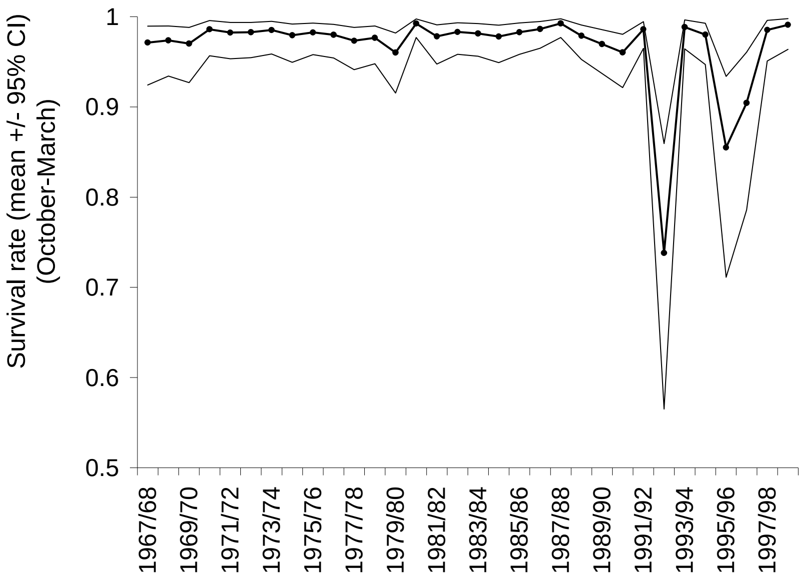


Figure 4.2 Survival rates for Oystercatcher and Knot on the Wash. (a) Winter survival rate of Oystercatcher on the Wash (mean ± 95% CI) and (b) annual survival rates of Knot (mean ± 95% CI).

(a) Oystercatcher



(b) Knot

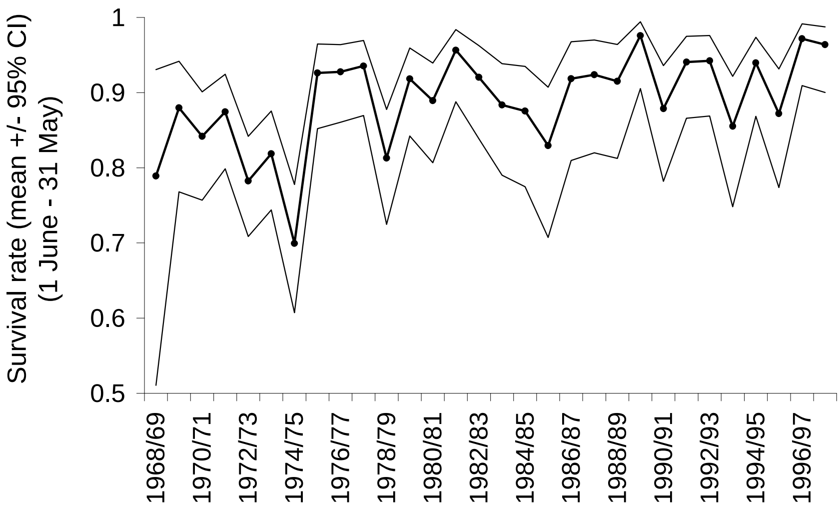


Figure 4.3 Mean number (+/- SE) of dead Oystercatcher recoveries reported to the British Ringing Scheme excluding the three 'kill' years 1992/93, 1995/96 and 1996/97.

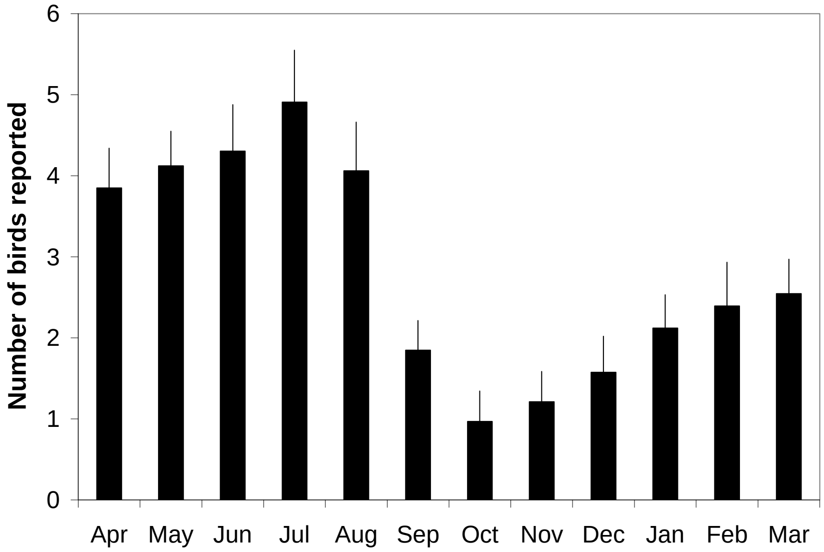
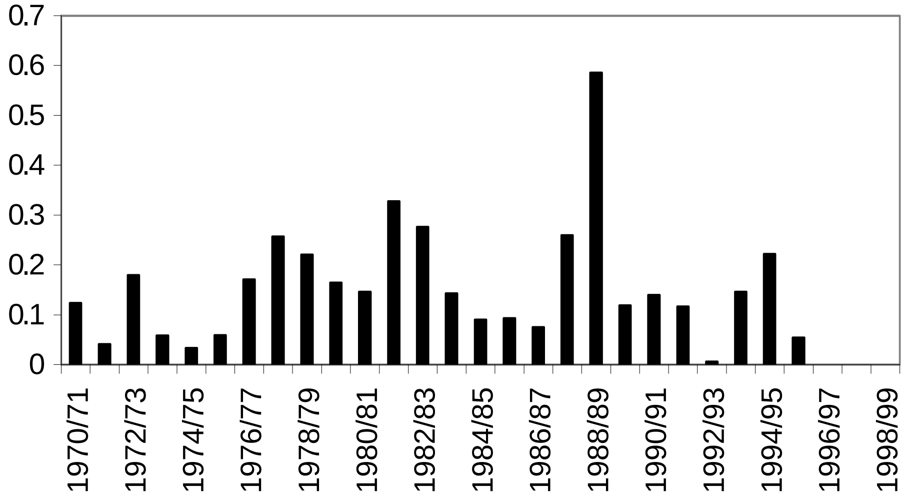


Figure 4.4 Number of juvenile birds per adult in catches by the Wash Wader Ringing Group from October through to March. (a) Oystercatcher, (b) Knot

(a) Oystercatcher



(b) Knot

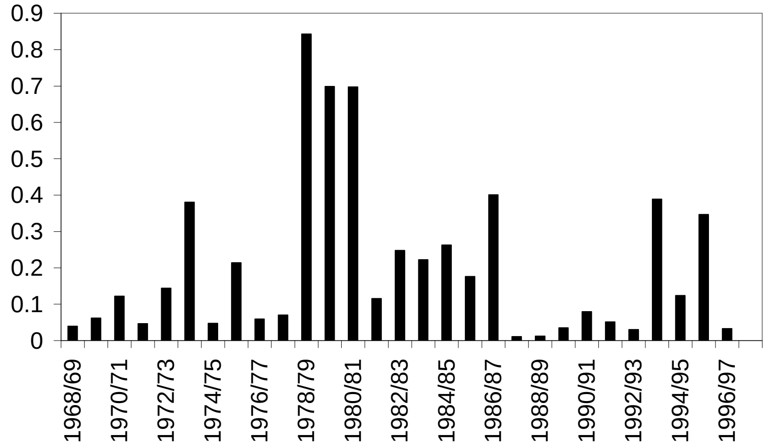
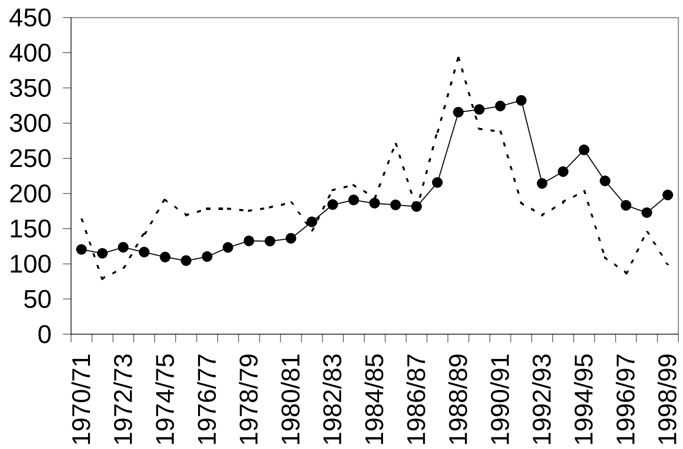


Figure 4.5 Underhill Index (last year set to a value of 100) and population trajectory from a model based on survival and recruitment estimates for (a) Oystercatcher (1970/71 to 1998/99) and (b) Knot (1970/71 to 1997/98). Dashed lines indicate the Underhill index and solid lines the model prediction.

(a) Oystercatcher



(b) Knot

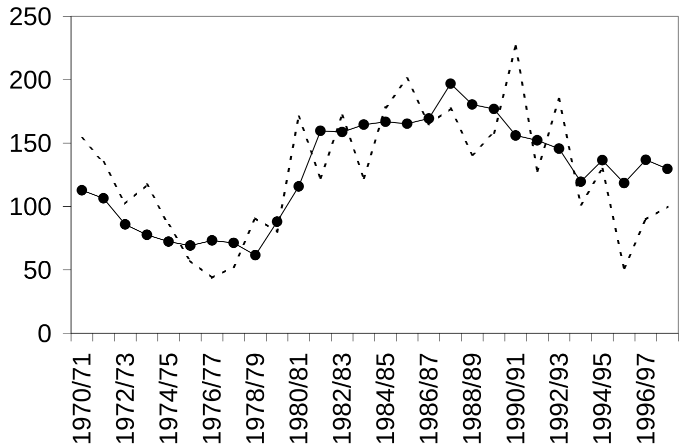
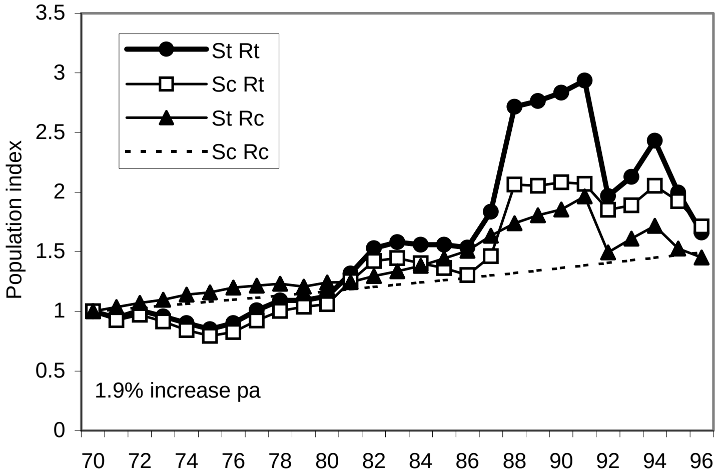


Figure 4.6 Relative contributions of survival and recruitment to the population model for (a) Oystercatcher and (b) Knot. The graphs presents population trajectories based on time dependent survival and recruitment rates (St Rt), time dependent survival rates and mean recruitment rates (St Rc), mean survival rates and time-dependent recruitment rates (Sc Rt) and mean survival and recruitment rates (Sc Rc).

(a) Oystercatcher



(b) Knot

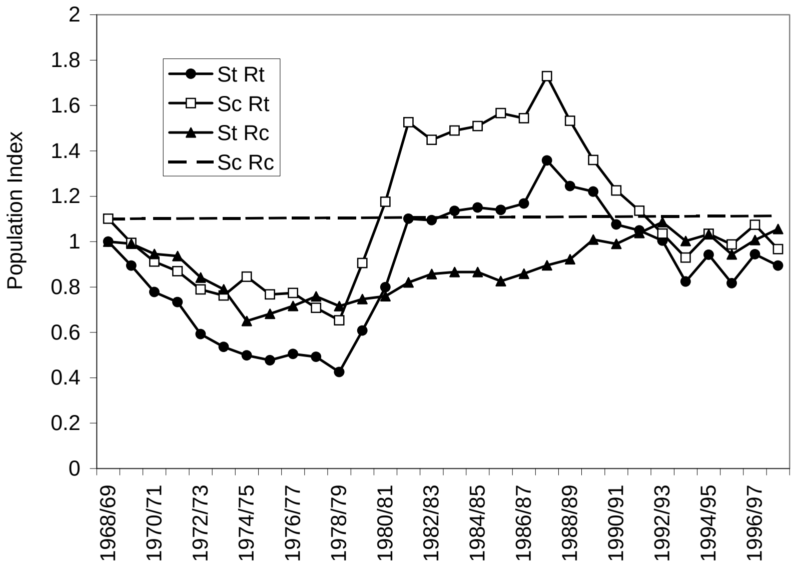


Figure 4.7 Results of the shellfish-winter weather models compared with the fully time-dependent Oystercatcher model. Survival estimates +/- 95% CI are shown.

(filled circles) – Shellfish-weather model. Survival estimates are time dependent from 1967/68 until 1981 (not shown) and from 1982/83 are a function of shellfish and weather.

(open circles) Time dependent winter survival estimates (from Model 1 in Table 3.1 b).

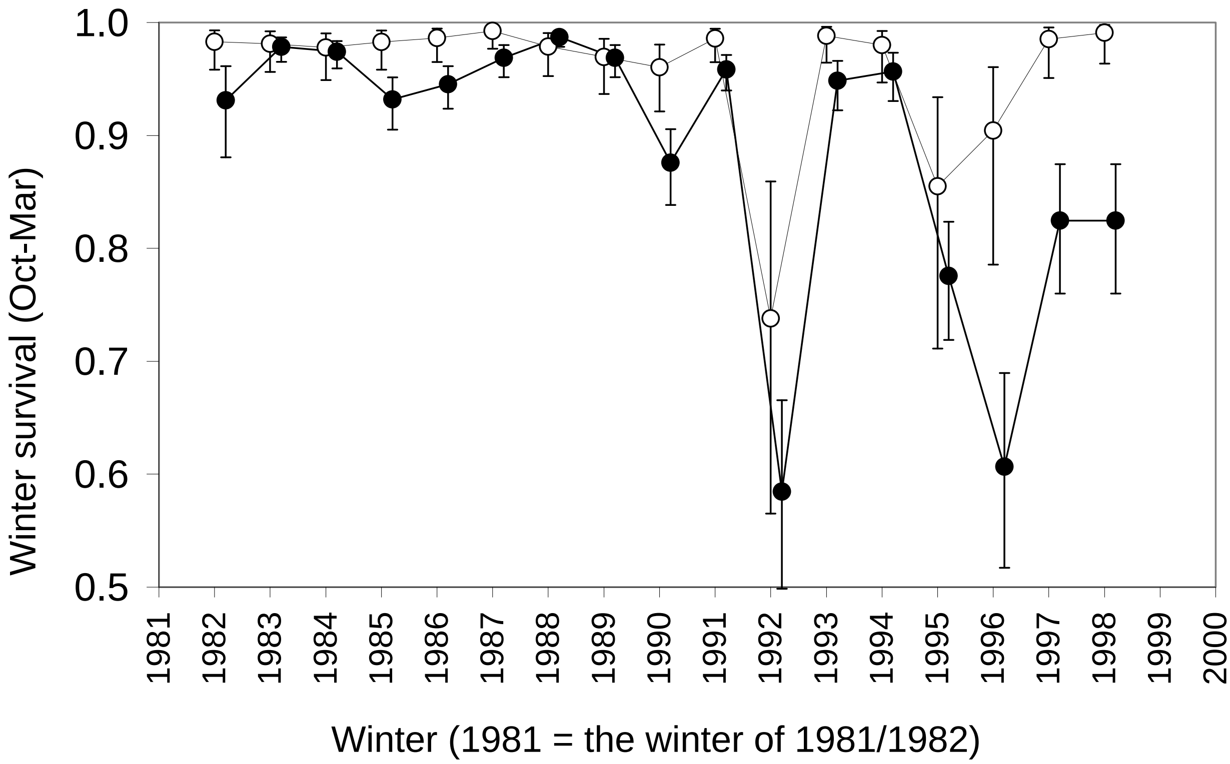
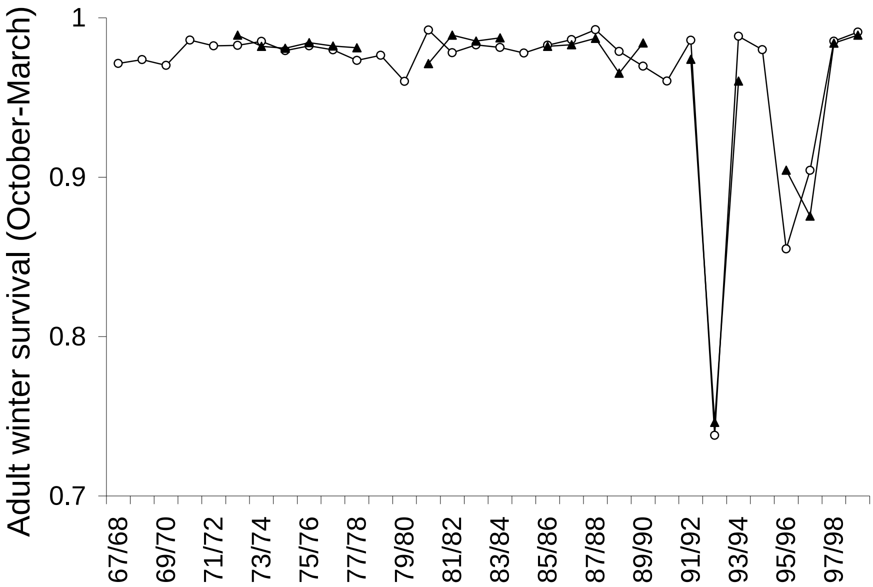


Figure 4.8 Modelling adult Oystercatcher winter survival as a function of the proportion of birds showing abnormal moult patterns. (a) proportion of birds showing a small moult gap in the period August-December; (b) proportion of birds caught showing suspended moult during the period December-September. Missing data indicates that sufficient birds were not caught during that period.

Open circles = actual survival; closed triangles = survival predicted from the moult survival model.

(a) birds showing an abnormally small moult gap in the period August to December.



(b) birds showing suspended moult in the period December to September.