**BTO Research Report No 469**

# Monitoring survival of waders in Britain

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**CONTENTS**

**Page No.**

LIST OF TABLES

LIST OF FIGURES

Page No.

# 1. INTRODUCTION

Worldwide there is much concern over the high proportion of wader (shorebird) species that are declining, particularly amongst Arctic-breeding species (e.g. IWSG 2003, CHASM 2004). To fully understand why these changes are occurring, it is necessary to understand how and why the underlying demographic parameters (recruitment and survival) of a population are changing, both temporally and spatially. Such an understanding requires long-term demographic monitoring programmes. For some species (mostly temperate breeders) these programmes are readily established on the breeding grounds, but for Arctic species monitoring breeding birds poses immense logistical difficulties, so monitoring on the non-breeding grounds may be required. For such monitoring to be effective, however, clear methodologies, comparable between species and regions, need to be established.

## 1.1 Why do we need demographic monitoring?

Essentially, populations change as a result of variation in productivity or survival of individuals (e.g. Boyd & Piersma 2001). Immigration and emigration are often irrelevant at a population level, but might need to be accounted for if distribution patterns are changing, for example, as a result of climate change or human disturbance (Austin & Rehfisch 2005; Sutherland 1996). It is necessary to monitor changes in the two key demographic parameters (recruitment and survival) as well as changes in population numbers to fully understand the causes of population change, and for planning effective management (e.g. Goss-Custard 1996; Green 1999; Fox 2003). Long-term population monitoring is also required to diagnose population declines and ascertain whether the magnitude of the declines is sufficient to warrant conservation concern; studies lasting only a few years may confuse short-term variation with population trend. Long-term monitoring can also help in identifying sites of conservation importance and may form part of international commitments (e.g. Stroud *et al.* 1990; Pienkowski 1991).

Longer-term changes in survival or recruitment may be evident before changes in population numbers and signal a potential change in conservation (Baillie 2001). Changes in environmental conditions may have an impact on demographic parameters directly, for example reduced food availability may lower survival and hence result in a fall in population numbers. Demographic monitoring can therefore be an early barometer of future population change (e.g. Monaghan *et al.* 1989), as there may be significant breeding population buffering in long-lived species due to the presence of non-breeding individuals (e.g. Bruinzeel 2004; Piersma & Baker 2000), which may delay impacts on breeding population size. Demographic monitoring can identify the critical life-cycle stage(s) on which environmental factors are operating to cause population change, and exclude others which are less relevant, by identifying the primary cause for population change (e.g. Green 1999; Piersma & Lindstrom 2004). Monitoring also provides useful information on average demographic rates both to identify normal levels for the demographic rate, though these may be population specific (e.g. Stroud *et al.* 1990), and to provide information for broader ecological models and adaptive management programmes (e.g. Perrins *et al.* 1991; Nichols 1991; Stillman *et al.* 2001).

## 1.2 Monitoring survival

Long-term monitoring programmes have a venerable history in the field of ornithology (e.g. Dunnet 1991; Perrins *et al.* 1991). Developing such a programme to provide useful information can be fraught with difficulties, not least because projects are usually not envisaged to be long-term in the beginning (e.g. Krebs 1991; Bearhop *et al.* 2003). Although waders are popular study organisms, long-term studies of population dynamics are few (Thompson & Thompson 1991). Consequently, there still remain significant gaps in our knowledge and understanding of wader population trends (Piersma *et al.* 1987; Wetlands International 2002).

Waders are generally long-lived birds, with longevity records for most exceeding ten years and some larger species living more than thirty years. This is a consequence of high annual survival (often 70-

90% in adults), but populations can be quite sensitive to changes in survival even if it occurs over only a short period (e.g. Goss-Custard *et al.* 1996; Hitchcock & Gratto-Trevor 1997; Boyd & Piersma 2001; Atkinson *et al.* 2003). Information on mortality causes may be gathered from, for example, surveys of beached birds (e.g. Camphuysen *et al.* 1996, though this may be less effective for waders), but monitoring survival requires the fate of individual birds to be known. This requires applying individually identifiable marks to a representative sample of individuals in the population. Usually waders are marked with either individually numbered metal leg rings that can be read when the bird is re-caught or found dead, or colour marks that can be read from a distance. For monitoring survival (and recruitment from recapture histories) individually identifiable combinations are required; there are few situations where cohort or group marking is preferable to individual marking.

Survival, however, can differ between breeding, non-breeding and migratory periods, requiring the synthesis of information collected across the annual cycle (Nebel & Lank 2003). Examples among waterbirds are provided by studies of individually marked geese. For some populations, rates of daily survival were lower during migration than during breeding or non-breeding periods (Owen & Black 1991; Clausen *et al.* 2001), possibly as a consequence of hunting (Ward *et al.* 1997). Other studies documented lower survival rates during the breeding seasons, or concluded that breeding, wintering, and even migration seasons had similar rates of natural mortality (Gauthier *et al.* 2001; Madsen *et al.* 2002).

Demographic monitoring is of most use when used in combination with counts in an integrated framework (e.g. Baillie 2001). Such integrated monitoring can help to understand the causes of population change and to inform management decisions (Peach *et al.* 1994; Goss-Custard 1996; Atkinson *et al.* 2003). New methods are being developed which allow consideration of demographic and census data in one analysis, which should provide for improved understanding of population processes (e.g. Brooks *et al.* 2004); the application of these to wader monitoring is briefly discussed in 5.4.

## 1.3 Monitoring wader survival in Britain

Scientific ringing of birds in Britain & Ireland began in 1909, with the BTO operating the scheme since 1937 (Wernham *et al.* 2002). About 25,000 waders are ringed each year, and a number of individuals and groups of ringers across the country particularly focus on catching them. Several hundred are also re-found each year, either re-caught as live controls or found as dead recoveries.

Wader catching poses a number of challenges, particularly in terms of obtaining sufficient numbers useful for monitoring purposes. Many waders that are common in Britain during the non-breeding period, and which are present in internationally important numbers (Collier *et al.* 2005), breed in the sub- to high-Arctic, where logistic constraints for wide-scale field programs are great. Additionally, most species breed at very low densities, making study of large numbers difficult. During the non-breeding season, waders congregate in large flocks, particularly in high-tide roosts, which makes catching large numbers easier. However, such roosts may be in difficult to access areas, and catching a sample from them usually involves assembling a (preferably large) team of people to make a catch, and such catches are sensitive to adverse weather conditions, so development of standardised catching in randomly selected locations on particular dates is unlikely to be possible. In this report we investigate the feasibility of using these efforts to develop annual monitoring of wader survival.

Firstly, we present an overview of wader ringing in Britain, assessing the number of birds caught and recovered for each species. Next, we explore the feasibility of monitoring survival in two species, Dunlin *Calidris alpina* and Redshank *Tringa totanus*. These two species are amongst the more commonly caught waders and both are ‘Amber’ listed because of recent population declines (Gregory *et al.* 2002). Finally, we draw together these results with those from other studies undertaken on waders in Britain to provide some recommendations for future ringing efforts.

## 1.4 Estimating Survival Rates

Survival rates may be estimated from either ring-recapture histories or from recoveries of dead birds that have been ringed. In either case, two sets of parameters are required, the survival rates ($\phi$) and probability of recapture or recovery (p) (Lebreton *et al.* 1992). Note, $\phi$ may underestimate true survival if there is permanent emigration away from the study areas, thus estimates of survival rates from studies of birds recovered dead (which may be found anywhere) tend to yield less-biased estimates of survival than mark-recapture studies (which are conditional on a particular ringing site, Sandercock 2003).

In most cases, and particularly for monitoring purposes, annually varying survival rates are of most interest, since these can be related to environmental variables, and can be interpreted directly in terms of demography and population change. However, it is also possible to estimate survivals for blocks of two, three, or more years – in extremis, one could estimate a time invariant (i.e. constant) survival rate for a particular site, though of course this may be of less use for monitoring purposes. Estimating survival for blocks of years requires much less data, but may be more difficult to interpret, especially if you combine years when the 'true' survival rates are very different. Additionally, mark-recapture models assume an 'instantaneous' ringing period (see below), an assumption that is increasingly untenable when longer periods are considered. An alternative might be to relate survival to some known environmental factor (such as temperature or lemming density), however, this depends on data on the environmental factor being available, and a close relationship between the factor and survival rates (in terms of a high proportion of the variability in survival explained), which often is not the case. Thus, although annual survival rates are the most difficult to measure (in terms of achieving a useful sample size), they are probably the only real option for monitoring purposes.

In this study, models aimed to establish whether these parameters were constant or age- or time-dependent, i.e. whether annual survival estimates could be produced, either separately for adults and first-year birds or for all birds combined. Data were modelled using Program MARK Version 5.0 (White & Burnham 1999). To determine whether assumptions were valid, goodness-of-fit tests provided by the U-CARE Version 2.2 software (Choquet *et al.* 2005) were used to inform initial data selection (see below). A combination of likelihood ratio tests (LRTs) and Akaike's Information Criterion (AIC), adjusted for overdispersion and sample size ($QAIC_c$: Burnham & Anderson 1998; White & Burnham 1999), was used to select the model that best described the data (typically that with the lowest $QAIC_c$ value). The various forms of AIC measure model parsimony, *i.e.* they balance the model fit with the number of parameters used. Of two models which 'explain' the data similarly (as measured by the amount of residual deviance, the model with the smaller number of parameters should be preferred, as the 'simpler' explanation.

## 1.5 Assessing Goodness of Fit

The standard Cormack-Jolly-Seber (CJS) model makes a number of assumptions about the survival and capture probabilities of birds, notably that all individuals behave in a similar fashion, that they are equally likely to be caught and that their chances of capture do not depend on their capture history (i.e. whether or not they have been caught previously). In most cases, these assumptions will not be met to a greater or lesser degree. In some cases, identifying and correcting for this will be relatively straightforward, for example by stratifying the sample, perhaps by age or sex; in other cases, however, reasons for lack of fit may be more subtle. Thus, checking the goodness-of-fit (GoF) to the model and understanding the reasons for lack of fit is critical to assessing the performance of the survival rate estimates, and may also lead to biological insight into the population.

Standard GoF tests involve simple chi-square comparisons of the number of birds caught in different time intervals. The overall comparison can be broken down into four component tests, each assessing a different facet of fit, with the convenient property that the sum of the components equals the total.

These tests are:

- Test 3.SR – of individuals caught at time *i*, how many were seen again or not seen again, this effectively tests for the presence of transient individuals in the marked population (*i.e.* birds only available to be caught on one occasion).
- Test 3.Sm - of individuals caught at time *i*, does when they were seen again depend on whether or not they were marked before time *i*? This effectively tests whether survival is different between marked/unmarked birds
- Test2.CT - are individuals equally likely to be recaptured if they were caught or not (but known to be alive) on the previous occasion, *i.e.* whether there is any evidence of trap-dependence
- Test2.CL – is there a difference in the time of next recapture between individuals captured and not captured at time *i*? There is no simple biological interpretation of this test.

Thus, the two Test 3 statistics (the names of the tests are completely uninformative!) effectively test the assumptions of equal survival, while the two Test 2 statistics test for equal catchability. In the context of wader populations, Tests 3.SR and 2.CT are of most relevance, since population structuring and habitat use are likely to influence the probability of (re-)catching an individual, particularly when effort is (necessarily) variable.

There are two additional assumptions of the CJS model, which should be noted briefly for the sake of completeness: that there is no ring loss (likely to be minimal with incoloy rings, which are made of a particularly hard-wearing alloy) and that the release period is instantaneous relative to the subsequent recapture period, though the model seems relatively robust to failures in this assumption, i.e. having an extended ringing period does not affect the survival rate estimation too much (O'Brien *et al.* 2005), providing the ringing pattern does not change markedly over time. A corollary of this assumption is that it is assumed there is no mortality during the marking period (as it is effectively instantaneous). Clearly, this is unlikely to hold for real data, in most cases wader marking occurs over the winter period, typically November to February, but in some cases longer, during which mortality may be significant, particularly if there is cold weather (Clark 2002a). Because of this one should keep the marking period as short as possible (though clearly there will be a trade-off with the number of birds marked during the chosen period). An investigation of how important this assumption is would also be useful, probably using data simulations.

## 2. NUMBERS OF WADERS RINGED IN BRITAIN

### 2.1 Introduction

Waders are present in Britain throughout the year; some as breeders, others as migrant visitors. However, relatively few birds (particularly adults) of most species are caught on the breeding grounds, mostly because birds breed in remote locations and, usually, at low densities, thus a high degree of effort is required to locate and catch individuals. Consequently, most birds are caught in non-breeding areas, either on passage or wintering, when they are relatively aggregated.

### 2.2 Methods

In Britain, most waders are usually caught in coastal, primarily estuarine, situations. Birds are caught primarily either in high tide roosts with cannon nets and/or coming into roost using mist-nets; in these analyses we do not distinguish between the two methods, although there will be different biases associated with each capture method (see discussion). Throughout Britain there are a number of individuals and ringing groups that focus on catching waders. Most of these are based around a particular estuary or stretch of shoreline, such as The Wash, Moray Firth or the North Wales coast.

As most waders are caught during the non-breeding season, for the purposes of this initial summary we classified the year into three periods, based on the date of ringing. The main wintering period covers the months November to February. During this period, the degree of movement for most species is much lower than at other times of year, with birds generally remaining on the same estuary throughout the period. It should be noted, however, that some movement can occur, *e.g.* in response to periods of extreme cold weather. Either side of the main wintering period, we summarised observations for the autumn migration period, from July through October and the period of spring passage (March through June). During these two periods there will be greater heterogeneity in the populations present with birds moving between wintering and breeding grounds. This may be further complicated by the presence of different populations or races, each moving between different areas, possibly at different times in different years.

For each of the species that are caught sufficiently frequently to make analysis sensible, we tabulated the number of birds (average per year) found dead or caught alive (controlled) at a site other than that of original ringing (unless it is on the same estuary, or has moved less than 30 km) and the number re-trapped at the same 'site' as the original ringing (*i.e.* caught on the same estuary, or within 30 km of the original ringing site), for the groups which catch the largest number of waders in each of the three periods. Note these tables refer only to information held in the central BTO databases. It is possible that there could be additional information available, increasingly so in years prior to 1995.

### 2.3 Results & Discussion

There are around 20 different groups who catch large numbers of waders, although most groups catch a relatively limited range of species. A number of these groups have been operating for several decades, notably the Wash Wader Ringing Group, which has been ringing for nearly fifty years. Other groups which catch large numbers of waders include Highland Ringing Group (on the Moray Firth and surrounding area), Morecambe Bay Ringing Group, Hilbre Bird Observatory (Dee) and SCAN (North Wales coast). Between them these groups provide a good geographical sample of Britain's estuaries (Table 2.3.1). Most information is gained from the recovery of birds (either dead or alive), as these have survived a defined period (Robinson *et al.* 2005), though this should be related to ringing effort.

#### Recovered Dead

Relatively few ringed birds are recovered dead. Numbers found dead are highest for species like the Oystercatcher *Haematopus ostralegus*, which is large, black and white, and readily found, and for estuaries like The Wash on the east coast of Britain, which experiences occasional spells of very severe weather, where a relatively high proportion of birds carry rings and which are closer to human populations centres. On other estuaries there are fewer ringed birds, so mortality is not recorded in same way. Unsurprisingly, numbers of dead recoveries are generally highest for winter ringed birds and, because of concentrated ringing effort, birds that pass through the Wash on migration. For most sites and species there are unlikely to be sufficient recoveries of dead birds each year to estimate annual survival rates, however, for Oystercatcher and Knot *Calidris canutus* (some sites) there may be.

**Recovered Alive**

As for recoveries of dead birds, recoveries of live birds away from the site of ringing (controls) are relatively sparse, but highest for birds ringed in winter. For most species there are unlikely to be sufficient recoveries to estimate site-based annual survival rates. Dunlin, Knot and Oystercatcher are the species with the greatest number of recoveries, and so most likely to provide a means of estimating survival rates. Note, however, there may be significant population structuring within a catching site which may mean relatively more recoveries are required, see below.

**Re-traps**

Numbers of birds re-trapped on the same site tend to be higher than birds recovered alive or dead. In general re-traps of birds are highest for those ringed in winter, which are likely to spend the longest time on the site. Some sites also yield good numbers of re-traps for birds of particular species on either spring or autumn passage. Note for many sites there will be a greater number of years of recapture data potentially available than is indicated in the table, as these tables refer solely to data held in the BTO Oracle database. Ringing data have been routinely submitted to BTO in computerised format since 1995; in many cases individual ringers and groups also began submitting records of re-trapped birds at this time, since they had entered them for their personal use anyway. Processing of re-trapped birds prior to these data (or subsequently for those ringers continuing to submit on paper schedules) was not possible due to the administrative burden. From 2005 submission of information on re-trapped birds was made mandatory, so the size of the dataset of these birds should increase.

**Colour-ringing**

As an alternative to re-trapping metal-ringed birds, colour-marking can provide a large amount of information for survival analyses (*e.g.* Gill *et al.* 2001); colour-marking could be either in the form of colour rings, or coloured leg flags with engraved characters. Colour-marking is likely to be particularly successful, for larger waders, or those which spend time at sites close inshore (e.g. Turnstone *Arenaria interpres*), so that the colour marks may be easily read. While they have the potential to provide large amounts of information, they are not without problems (Bearhop *et al.* 2003; Robinson *et al.* 2005). Currently, relatively little colour mark information (particularly of subsequent sightings) is collected nationally, so it is unlikely that they could usefully contribute to a national monitoring program.

**Summary**

There are a number of species that are apparently caught in sufficient numbers to suggest that monitoring of survival rates may be possible; these are listed in Table 2.3.2. In most cases, greatest numbers of birds come from re-trapped birds, particularly from North Wales (SCAN RG), the Moray Basin (Highland RG) and The Wash (Wash Wader RG).

## 3. ANNUAL SURVIVAL RATES OF DUNLIN *CALIDRIS ALPINA*

### 3.1 Introduction

Dunlin are one of the most numerous waders occurring in Britain and are caught in the greatest numbers. They breed in north temperate, boreal and Arctic areas and winter from northern Europe to the southern tropics (Clark 2002c). There is a complex array of subpopulations with as many as 11 races recognised, three of which occur in Britain. Populations of the nominate *C. a. alpina* breed in Fennoscandia east to Siberia and winter in Britain, whereas birds of *C. a. schinzii* breed in northwest Europe (including Britain) and winter primarily in west Africa. The third race, *C. a. arctica*, comprises a relatively small population (*c.* 15,000 individuals) that breeds in north-east Greenland, and passes through Britain in small numbers, also on its way to wintering grounds in West Africa.

Dunlin occur in large numbers on many of Britain's estuaries, and are ringed in good numbers on several (Chapter 2). In this chapter, we look at Dunlin ringed at two estuaries, Poole Harbour on the south coast of England, and The Wash in eastern England. For birds in Poole Harbour we estimate survival rates from live recaptures, while for Wash birds we set out to examine both recapture and dead recovery data. Birds were aged as either being in their first year or older (adult) largely on the basis of plumage characteristics (e.g. presence of terminal, or sub-terminal, fringes; Prater *et al.* 1977).

### 3.2 Poole Harbour

#### 3.2.1 Introduction

Poole Harbour is a small estuary (*c.* 3,700 ha) on the south coast of England (SZ0189), formed from the confluence of two rivers. In addition to Dunlin, the site is important for a number of other waterbirds during passage periods and the winter, as well as breeding seabirds in summer and as such is designated a Special Protection Area (SPA; Stroud *et al.* 2001). The mouth of the harbour is restricted by two sand spits and most of the intertidal sediment is soft mud. The town of Poole is on the northern side of the estuary, and it is here that most of the birds are caught.

#### 3.2.2 Methods

Birds were caught using mist-nets during the winter months (October to March) and a high level of catch effort was maintained, with birds being caught regularly throughout each winter period. The survival period is thus from one winter to the next. All birds caught in the period 1978 to 2002 were included in the analyses. Annual survival rates were estimated separately for first-year and adult birds, based on the number ringed and re-trapped each year (Table 3.2.1). Previous work has shown that wader survival may be related to winter severity, in particular to periods of prolonged cold when survival can decrease markedly (Clark 2002a). To test this hypothesis, we calculated the greatest number of consecutive days in which the daily minimum temperature at Poole weather station (SZ005938) was less than 0˚C. Daily data were extracted from the Met Office dataset (hosted by BADC) for the period 1978-1999 (subsequent data were not available).

The number of individuals recaught was modelled as a function of survival rate ($\phi$) and recapture probability (p). The basic CJS model has separate terms for each age class (a: first-year, adult) and each year (t: 1978, 79, …, 2002), and is thus denoted 'at' and has 2*24 survival + 2*24 recapture = 96 parameters, though the recapture and survival rate parameters for the last year cannot be estimated individually (i.e. in reality 95 parameters are potentially estimable). A major problem in survival estimation is the presence of 'transient' birds; these birds typically have a much lower recapture rate, either because they are moving through the capture site (*i.e.* only available to be caught for a short period), or, perhaps, normally frequent an adjacent area, and only occasionally stray into the main capture area. To account for the presence of transient individuals, the basic CJS model was expanded to include separate parameters (t') for survival and recapture in the first year following capture for each of the 24 intervals. These were either independent of (at,t') or additive with (at+t') the corresponding rate for birds caught more than one year previously. This also allows accommodation of a trap-dependence effect (*i.e.* birds modifying their behaviour following the initial capture event). Note this can only be applied to adult birds, as first-year birds were only caught in one year, thus emigration from the site cannot be separated from mortality, as in neither case will a bird be recaptured. This will also have the effect of underestimating the 'true' survival rate of first-years by an unknown, though possibly small, amount.

To assess the effects of sample size on how well annual survival rates were estimated we took two approaches, both based on the data collected, rather than simulating data afresh. This means the structure of the data will be accurately reflected, but the results may not be quite so generally applicable as from a more simulation based approach.

Firstly, we simply looked at the annual estimates of the best-fit survival model, and related the standard errors of these to the number of birds ringed or re-trapped in each year. From this, we would expect the precision of the estimates to increase with sample size, *i.e.* the standard error should decrease. This is quite a simple approach; to improve on this we investigated the precision that would have been achieved had the datasets available been smaller. To do this, we listed all capture occasions of all birds and deleted (randomly) a certain percentage to achieve a lower sample size. We then re-created the apparent survival for each bird, re-fitted the survival estimation models and assessed the average standard error across the across the survival parameters that were estimable. A third approach would be to fully simulate the data and perform formal bootstrap analyses of these simulated data, however, the time requirements for this were beyond the resources available for this project.

### 3.2.3 Results

#### Goodness of Fit

Overall, the goodness-of-fit to the standard CJS model was poor (Table 3.2.2), with the primary reason for lack of fit being the presence of transient individuals amongst both adults and first-years (Test 3.SR). For first-year birds, none of the other tests were significant, but for adults Test 2.CL was significant (and test 3.Sm less so), which suggests there may be some long-term memory of capture as ringed adults are less likely to be caught within a given period subsequently.

#### Model Selection

As might be predicted from the results of the goodness-of-fit testing, the basic CJS model [$\phi$(at)p(at)] provides a relatively poor fit to the data (Table 3.2.3). Including a transient effect in the recapture probability, or better, the recapture and survival probabilities greatly reduces the residual deviance, *i.e.* results in a much better fitting model, as might be expected (because there are more parameters), but also a lower AIC indicating a more parsimonious fit. For both the survival and recapture parts of the model, there is no evidence that the rates in the first year after capture (for adults) vary in parallel with those caught previously (the models with independent parameters for the first year after capture [at,t'] have lower AICs than those where these vary in parallel with other years [at+t']).

#### Survival and Recapture Rates

Perhaps unsurprisingly given the nature of the site, recapture probabilities were relatively high for a wader ringing study, reflecting the high level of catch effort maintained. Recapture probabilities averaged 0.29 ± 0.01 for adult and 0.40 ± 0.02 for first-year birds; recapture probabilities for adults in the first year after capture were marginally (but significantly, LRT: $\chi^2$=10.95, $p$ < 0.001) lower than subsequently (0.25 ± 0.01), indicating some avoidance of the nets within a winter following a capture event.

Predictably, survival probabilities of adult birds (0.795 ± 0.006) averaged much higher than that of first-year birds (0.457 ± 0.021). It must be borne in mind, though, that the survival rates for first-years will be biased low, because of the presence of transient birds. Apparent survival rates of adult birds in the first year following capture were also much lower (0.495 ± 0.017), suggesting that temporary emigration (62%) from the 'site' (actually the catchable part of the population) was significant, and that survival of first-year birds may not actually be much lower than that of adult birds.

Survival rates varied markedly from year to year (Fig. 3.2.1). Annual adult survival generally varied between 0.6 and 0.9, but the wide confidence limits preclude identifying significant differences between years (which there undoubtedly are, as all models with annual survival have much lower AICs than a model based only on $\phi(a)$, Table 3.2.2). First-year survival was much more variable, and the confidence limits were generally wider. Indeed in three years it proved impossible to estimate a survival rate for these birds (1989, 1995, 2000), due to the low sample sizes.

Much of the annual variation in first-year survival, and somewhat less for the adults, is related to the severity of winter weather (Fig. 3.2.2). In particularly cold years, when there was a long period of air frost, survival appears relatively high. This is particularly applicable to the first-year birds, which would otherwise have a predicted mortality of 100%, but also seems to be true to a certain extent of the adults.

**Sample Size and Estimation Accuracy**

As would be predicted, in years when greater numbers of birds were ringed or re-trapped the precision of the estimate tends to be greater (lower standard error, Fig. 3.2.3). However, this is not a linear decline, with initially a large increase in precision, but lower gains when sample sizes are increased from higher levels; there are thus diminishing returns from increasing sampling efforts. Examination of Fig. 3.2.3 indicates that in the region of 120-200 birds need to be ringed each year (and 80-100 birds re-trapped) for reasonable precision to be obtained (se of 0.1 or less). Sample sizes much smaller than this cause the precision of the estimates to deteriorate markedly.

A perhaps more satisfactory way of estimating sample size considerations is to consider estimation accuracy over a number of years, which we accomplished by selectively thinning the dataset of capture occasions (Fig. 3.2.4). Again this shows that precision decreases rapidly as sample sizes are reduced, though there is an indication that beyond 150-200 adults (or 80-100 first-years) changes in precision of the survival estimates may be smaller. Interestingly, and perhaps counter-intuitively, the precision of estimation of the first-year survival rates is greater (for a given sample size), than those of the adults. This may be an artefact of the common error structure imposed by the model. The accuracy of first-year survival estimates for individual years is similar to or greater than the estimates of adult survival (*cf* Fig. 3.2.3a), but because *on average* relatively few first-year birds are ringed, the points in Fig. 3.2.4 appear left-shifted. An additional factor may be that the estimates of first-year survival are only for one cohort per year, whereas adult estimates average across a number of cohorts, which introduces extra heterogeneity. This effect can be seen by comparing the variability of adult survival rates in the first year following capture with that of the annual estimates for birds in subsequent years after capture (Fig. 3.2.4). However, it should also be noted that first-year survival rates tended to be inestimable (*i.e.* they settled on an unrealistic 'boundary' estimate of 0 or 1) more frequently than adult estimates, particularly as the sample sizes were reduced.

### 3.2.4 Discussion

Even in a small estuary, such as Poole Harbour it is difficult to sample (catch) all birds equally, this results in many birds appearing to be transient (to the catching sample), i.e. only being caught once. This may have been exacerbated by a relatively wide winter window (October through to March), meaning that some passage birds were included in the sample; these birds will obviously have lower re-capture rate than birds spending an entire winter on the site. Care is needed in defining a winter period, and this may vary between sites, though experience suggests that the period November to February may be suitable in many cases (Clark 2002a), at least in north-west Europe.

Despite problems with the presence of transient birds in the Harbour, the survival models appeared to give reasonably reliable estimates of both first-year and adult survival, although the ‘true’ survival rates remain unknown, of course. What represents a ‘reasonable’ accuracy for survival rate estimation will clearly depend somewhat on the use to which the estimates will be put. For the purposes of large-scale national monitoring where one wishes to detect broad trends, a lower level of accuracy may suffice than that required for constructing detailed demographic models, which may be sensitive to small changes in parameter values. Examination of Fig. 3.2.3 suggests that the precision obtainable initially increases quite quickly with increasing sample size, but that beyond 100-150 birds caught per year increasing the sample size has a much less marked effect on the precision of the estimated survival rates. Similarly, inspection of Fig 3.2.4 suggests that catching fewer than 150 birds per year markedly decreases the precision of the estimates, at least for adult birds. It appears that a greater number of adult than first-year birds need to be caught for a given level of precision; this may reflect the greater degree of heterogeneity present because of multiple cohorts of adult birds, but requires further exploration.

On the basis of this, it seems that, ideally, one would aim to catch in excess of 150 birds each year, in order to achieve ‘good’ precision about annual survival rates.  If survival rates were being estimated over a longer interval, smaller numbers might be required, though these would be less useful for monitoring purposes (see 1.4). It should be noted, though, that these results are likely to be typical of situations where relatively high recapture rates can be achieved. Partly as a consequence of its small size and isolated nature, and even though catching occurs on only a small part of the estuary, recapture probabilities averaged 29% for adult and 40% for first-year birds. Sites with lower recapture rates are likely to require greater numbers of birds caught initially.

A further point to note is that, even a survival estimate with a standard error (se) of 0.1 implies quite a wide degree of statistical uncertainty in the estimate. For example, a survival estimate of 70% with a se = 0.1, will typically have confidence limits in the range of 50% to 85% or 90%. If the survival estimate were towards the bottom or top of this range, drawing conclusions for monitoring or population modelling purposes would be very different. This may reflect the ecological variation inherent in a population that is drawn from a very wide (and largely undefined) area, where a range of factors may have very different impacts in different parts of the range and on different subpopulations. More work is required to characterise this variation.

The error estimate about the estimated survival rates actually comprises two separate components, a biological component, known as process variance, which incorporates such factors as individual variation in survival probabilities (due to factors such as age, sex or condition) and sampling or measurement variance. There are statistical procedures to separate these two quantities, though they are probably not realistically applicable in this context. It is however, possible to look at environmental correlates of survival, such as weather variables.

The relationship between survival and cold weather is not unexpected, since Dunlin are known to suffer heavy mortality during periods of low temperatures (e.g. Clark 2002a). Most waders are sufficiently robust enough to survive a short period of even quite low temperatures, when mortality really occurs is when low temperatures occur for extended periods of time. This applies to both minimum and maximum temperatures since low values of either, or in combination, can influence resource availability or thermoregulatory activity. There was evidence that in winters with particularly prolonged periods of cold weather, birds had higher survival than expected, perhaps because they wintered elsewhere. However, Poole Harbour, being in the southwest, is likely to be one of the more clement estuaries in Britain, so may actually also receive birds from elsewhere (further east where average temperatures tend to be lower in winter) during cold weather periods; this may account for some of the transient birds present in the population.

## 3.3 The Wash

### 3.3.1 Introduction

The Wash is Britain's largest estuary (c. 108,000 ha) on the east coast of England. It consists largely of intertidal mudflats and saltmarsh. It is Britain's most important site for waders, with peak populations of around 200,000 birds using the area (Collier *et al.* 2005). It holds internationally important numbers of 12 wader species and consequently has a number of conservation designations, notably as a Ramsar site, Special Protection Area (SPA) and National Nature Reserve (Stroud *et al.* 2001).

Dunlin are amongst the most numerous species present, with 30,000 to 40,000 birds recorded at peak each year (Collier *et al.* 2005). (Note this is almost certainly a large underestimate of the number of birds actually using the site, due to significant turnover of individuals, and the difficulty of counting all birds present). All three races of Dunlin present in Britain use The Wash, though only a few birds of the *arctica* race are present in most years (Clark 2002c). Birds of the race *schinzii* are present mostly in early autumn (July through early September) on their way to their wintering grounds in Africa, where they undergo their post-breeding moult. Birds of the nominate race (*alpina*) arrive later (from August) and commence their post-breeding moult shortly after arrival. Most of these birds winter in Britain, but do not necessarily remain on The Wash, a significant number move to estuaries further south and west.

There is a long tradition of wader catching on The Wash, beginning in the late 1950s, when many of the techniques for large-scale catching of waders using cannon (then rocket) nets were pioneered (Kew 1999). Birds are caught using both mist and cannon nets, particularly in the autumn months, during the period of peak wader moulting flocks and passage at a variety of sites on the south, east and west shores.

### 3.3.2 Methods

Dunlin are caught in all months on The Wash, and at most of the regular catching sites (Table 3.3.1). Most birds are of race *alpina* caught in autumn, on passage (Table 3.3.2); relatively few are caught in the winter months as their high tide roosts are less accessible for catching.

Very few recoveries of dead Wash-ringed Dunlin have been found over the years, consequently, fitting annual survival models proved a frustrating task, so here we concentrate on using recaptures to estimate survival. Almost half of all birds are caught on Terrington Marsh (TE), on the eastern half of the southern shore, and it is only here that catches have been consistently made in all years. Catching at other sites and other times of year has been more infrequent, reflecting a lack of catching opportunities, or issues of team logistics. For this reason, we concentrate on estimating annual survival from autumn to autumn, rather than winter to winter, as might be more usual.

Such inconsistent catching creates problems for the survival modelling procedure, as it introduces heterogeneities in capture/re-capture probabilities, particularly when birds do not move freely between sites, i.e. there is some population structuring. Such problems are particularly marked on The Wash, which is a large estuary, and, although some birds do move between different parts of The Wash, particularly between winters, there is a high degree of site fidelity (Rehfisch *et al.* 1996). Thus, rather than being treated as a single site, the estuary needs to be treated as a complex of linked sites, estimating both survival and transition probabilities between sites. Some degree of site amalgamation may be possible, but this will require a reasonable knowledge of intra-estuary movements to delineate particular population units. A further problem is the presence of multiple races of birds with different breeding and wintering areas, which means that it is not sensible to estimate an overall survival rate, as each race is likely to face different survival pressures and have different recapture probabilities.

It is much more sensible to look at survival of particular biological populations, in this case particular races. For this project we considered survival in the nominate race, which spends the winter in Britain. For these analyses, we used all birds explicitly identified as *alpina* (on the basis of plumage characteristics) and all birds that were in active wing moult, together with any birds caught in September or October (by which time most *schinzii* will have left The Wash, NA Clark pers. comm.). The capture period was thus July to October, and annual survival estimates calculated between subsequent catching periods. Birds were aged as first-year or adult on the basis of plumage characteristics (Table 3.3.3). Only birds ringed in the years 1981 to 1999 were used for this analysis as there appeared to be extremely few re-traps of individuals ringed in later years. This may be a result of reduced catching success in traditionally used sites induced by topographical changes (the saltmarsh is generally accreting providing alternative roosting areas). Even amongst those years used the number of individuals subsequently re-trapped was relatively small, particularly of first-year birds, reflecting the large area of The Wash and the size of the population using it.

The number of individuals recaught was modelled as a function of survival rate (ϕ) and recapture probability (p). The basic CJS model has separate terms for each age class (a) and each year (t), denoted 'at' and has 2*20 + 2*20 = 80 parameters, though the recapture and survival rate parameters for the last year cannot be estimated individually (i.e. in reality 78 parameters are estimable). As with the Poole analysis (3.2), to account for the presence of transient birds this model was expanded to include (40) separate parameters for ϕ and p for the first year following capture of adult birds which were either independent of (at,t') or additive with (at+t') the corresponding rate for birds caught more than one year previously. Note, again, this can only be applied to adult birds, as first-years were only caught in one year as first-years, thus emigration from the site cannot be separated from mortality.

Previous work has shown that wader survival on The Wash is related to winter severity, in particular to periods of prolonged cold when survival can decrease markedly (Clark 2002a). To test this hypothesis we calculated the greatest number of consecutive days over which the daily minimum temperature at Terrington St Clement weather station (TF545187), close to where most birds were caught, was less than 0˚C. Daily data were extracted from the Met Office Land Surface Station dataset (hosted by BADC, http://badc.nerc.ac.uk/).

We investigated the relationship between sample size and precision in a similar manner to that described for the Poole Harbour analysis (see 3.2.2).

### 3.3.3 Results

**Goodness of fit**

Probably as a consequence of the number of different sites and races present, initial GoF testing for all the autumn data revealed a large amount of apparent transience in the population, with Test 3.SR being highly significant; the other GoF tests were also significant to varying degrees. Restricting the data to particular sites, or groups of sites, reduced sample sizes but did not much reduce the significance of the GoF tests, indicating these problems were probably due to the presence of mixed races. Despite including a number of catching sites in the input matrix, GoF testing indicated a relatively good fit of the standard CJS model to the *alpina* (only) dataset (Table 3.3.4), though the sparseness of the data probably means power to detect a lack of fit is low.

**Model Selection**

As might be predicted from the results of the goodness-of-fit testing, the basic CJS model [ϕ(at)p(at)] provided a relatively poor fit to the data (Table 3.3.5). Including a transient effect in the recapture probability, or better, the recapture and survival probabilities greatly reduced the residual deviance, i.e. resulted in a much better fitting model. For both the survival and recapture parts of the model, there was no evidence that the rates in the first year after capture (for adults) varied in parallel with those caught previously (the models with independent parameters for the first year after capture [at,t'] have much lower AICs than those where these vary in parallel with other years [at+t']). This reflects very closely the results from Poole Harbour, (See 3.2), however, most of the parameters of this model appeared to be inestimable, probably due to the relatively low recapture rate, consequently we use the model $\phi$(at+t')p(at+t'), for which most parameters could be estimated.

**Survival and Recapture Rates**

Recapture rates of Dunlin on The Wash were very low (adults: mean = 0.016 ± 0.002; first-years: mean = 0.008 ± 0.002), reflecting the relatively limited sampling of a large population.

Perhaps surprisingly, average apparent survival rates were similar for adults (mean = 0.620 ± 0.026) and first-years (mean = 0.604 ± 0.057), but varied markedly between years (Fig. 3.3.1). There was insufficient data to give sensible annual estimates of first-year survival (*cf* the number of re-traps in Table 3.3.3), or for adult survival in the years 1996-1999. Although annual survival rates varied markedly between years, this did not appear to be related to winter severity ($r$ = 0.30, ns, Fig. 3.3.2).

**Sample Size and Estimation Accuracy**

There was little indication that the number of birds ringed or re-trapped each year influenced the precision of the survival rate estimates, at least for adults (Fig. 3.3.3).

### 3.3.4 Discussion

This analysis of Dunlin survival rates on the Wash yielded an interesting result, in that problems with transient birds revealed by the goodness of fit tests were not solved by restricting the sites which contributed as expected, but rather by restricting the birds that contributed to a particular race. The issue of site delimitation is a big one (see 5.2). Most Dunlin are caught on the south and east shores of the Wash, and although they do exhibit some degree of site fidelity (Rehfisch *et al.* 1996), there may be some interchange between the birds on the different catching sites. Alternatively the survival estimates may actually be based largely on data from the Terrington catches, as this is where the majority of birds are caught. Different populations of Dunlin, however, come from (and may go to) very different breeding (or wintering) areas, where environmental factors on survival rates may differ greatly. This appeared to be the case here, with restriction of birds to the *alpina* race, irrespective of the catching site apparently resolving the transience issues. In Dunlin, different races are (in theory at least) distinguishable on the basis of biometrics, in other species this may not be the case, where it is practicable to do so, such races or populations should be distinguished each time the bird is captured.

At first sight the apparent lack of a relationship between the number of birds ringed or re-trapped and the precision of the survival rate estimates seems surprising. The re-trap rate was very low in most years (c. 1%), because a relatively large population is being sampled; average peak mid-winter counts of Dunlin on The Wash are around 35,000 birds. Consequently, the number of re-traps is also very low (*cf*, for example, the number attained in Poole Harbour), thus there is perhaps not enough variation to examine this relationship properly.

The annual pattern of variation in survival appears almost cyclical, which may suggest a link to lemming population cycles; such links are found in many high Arctic breeders (e.g. Summers & Underhill 1987). However, no data supporting such a link were found here, and, given, the large breeding range over western Siberia and Fennoscandia, from which the wintering *alpina* population is drawn it is uncertain whether a clear relationship would be expected. There also does not seem to be a clear relationship between survival and winter temperatures, even though Dunlin are known to suffer heavy mortality during cold winters (Clark 2002a), and adult survival from autumn 1991 to autumn 1992 (36 ± 16%), spanning the coldest winter of the study period, was the lowest recorded. This perhaps suggests (unlike in Poole Harbour) that the intensity of the cold weather, such as the minimum temperature reached (the measure used by Clark [2002a]), more than the length is important in determining survival.

Analysis of The Wash data highlights a very important point in the use of ringing data for survival monitoring: it is not enough simply to collect data for many years. For survival monitoring (and there are other reasons why ringing data is collected), some degree of structure is required for an effective sampling program to be maintained. In particular, the relatively small number of birds ringed and, especially, re-trapped after 1995 seriously compromised the ability to produce annual survival rate estimates. A regular data review process highlighted this, but it resulted from a fall in numbers on sites with catchable flocks due to changes in saltmarsh topology; the marsh is generally accreting, providing birds with alternative roosting areas. Such environmental changes require a flexible catching policy, with regular reviews, and highlight the difficulty of maintaining long-term standardised catching protocols using particular sites. The main assumption of survival models, that birds in the population are equally likely to be caught, needs to be borne in mind when determining catching strategies, though it is likely to be an ideal to be aimed at, rather than a goal to be achieved, given the practical difficulties of catching waders.

# 4. ANNUAL SURVIVAL RATES OF REDSHANK *TRINGA TOTANUS*

## 4.1 Introduction

The Redshank is one of the most familiar birds on British estuaries. The race breeding in Britain (*T. t. brittanica*) is widespread in lowland marsh areas, both coastal and inland, and many of these breeders remain in Britain for the winter. They are supplemented in winter by a significant number of birds from Iceland (*T. t. robusta*, Clark 2002b). These Icelandic birds tend to winter further north and west within Britain (Burton *et al.* 2002). Birds of the nominate race *T. t. totanus*, which breed in continental Europe, are also present on passage.

Three previous studies have analysed ring-recapture data collected by UK ringing groups to estimate Redshank survival rates. Burton (2000) and Burton *et al.* (2006) used colour-ring resighting data to estimate the survival of adult Redshank before and after a loss of habitat at Cardiff Bay in south Wales. Annual survival of Cardiff Bay Redshank declined from 85% in the two years prior to habitat loss to 78% in the three years following because of a decline in winter survival (Burton *et al.* 2006). In comparison, there was no change in the annual survival rate of 86% calculated using ring-recapture data for Redshank at neighbouring Rhymney over this time. Ring-recapture data from the SCAN Ringing Group also indicated that adult survival at a north Wales control site increased from 73% in the years before habitat loss to 93% afterwards.

Insley *et al.* (1997) investigated variation in the survival of Redshank on the Moray Firth using data from the Highland Ringing Group. Their study found that first-year survival varied with time – averaging just 43% – and that adult survival could be split into two otherwise constant rates of 67% for birds between their second and third winters and to 74% for older birds; survival was also found to be affected by the severity of winter weather.

Freeman *et al.* (pers. comm.) also used ring-recapture data to model survival rates of Redshank (and Dunlin) caught on the Orwell Estuary in the period 1991-2004. Recapture rates were less than 1% for Redshank and thus it was only possible to estimate an overall survival rate – of 88% – with tolerable precision and not annual survival rates. Here, we investigate whether ringing group data can be used to produce annual (winter to winter) estimates of Redshank survival and how the precision of the estimates derived might be improved. Data are analysed for two study sites – the Lavan Sands / Traeth Lafan area of north Wales and The Wash. In each case, we attempt to estimate survival rates from live recaptures as there were too few recoveries of dead birds. Birds were aged as either being in their first year or older (adult) largely on the basis of plumage characteristics (following Prater *et al.* 1977).

## 4.2 North Wales

### 4.2.1 Introduction

The Lavan Sands / Traeth Lafan area of north Wales is designated as an SPA for its internationally important population of Oystercatcher (Stroud *et al.* 2001). In addition to this species, the area also supports nationally important numbers of Redshank, with an average of almost 1,300 in winter (Collier *et al.* 2005). Birds of both the *brittanica* and *robusta* races winter, though the latter predominate (Burton *et al.* 2002).

### 4.2.2 Methods

The SCAN Ringing Group have been catching and ringing Redshank in north Wales since 1971 by cannon- or mist-netting at high tide roosts, with catching sites spread between Caernarfon and Rhos-on-Sea (Fig. 4.2.1). Numbers of Redshank caught in relation to catching site and year are summarised in Table 4.2.1.

Within this region, catching effort was greatest in the Conwy Estuary (catching sites CON, LLJ and TYC) during the 1970s, but since 1979/80 has been concentrated in one main area along the southern shore of Traeth Lafan (catching sites BAN, OGW, SPF, WIG, ABE and LLA) (SH5972 to SH6674).

For the previous comparison with Cardiff Bay Redshank (Burton *et al.* 2006), SCAN data were collated from the catching sites along the southern shore of Lavan Sands to estimate adult survival over the period 1988/89 to 2002/03. The final model indicated that recapture rates (p) varied fully with time, but that survival ($\phi$) was greater in the period following the closure of the Cardiff Bay barrage (2000-2002) than beforehand (see above).

Here, data were initially considered from all 15 catching sites where Redshank had been caught over the period 1979/80 to 2003/04. Mark-recapture models assume zero mortality during the period of recapture, and though this assumption is often violated, it does not necessarily bias estimates; conversely by retaining data, the precision of survival estimates may in fact be increased (O'Brien *et al.* 2005). The initial option, therefore considered data from all months when Redshank were caught, i.e. July to April.

### 4.2.3 Results

**Goodness of Fit**

Goodness-of-fit test 3.SR indicated considerable heterogeneity in the capture histories in the initial dataset of birds caught between July and April and specifically that previous capture history may have affected an individual's subsequent probability of recapture or survival (Table 4.2.2). Consequently, we tried restricting the data to the main catching area by Lavan Sands, but tests on this also indicated poor goodness-of-fit. Restricting the study area further to exclude Bangor (where catches of first-year birds tended to be higher) lessened the significance of the non-directional ($\chi^2$) version of test 3.SR (option 3). However, it was necessary to further restrict the recapture period to the months of October to February – to exclude passage birds – to provide a dataset that did not violate model assumptions (option 5). These months matched those used by Burton *et al*. (2006); Insley *et al.* (1997) used a similar period of September to February. The consequences for sample size of this restriction are also shown in Tables 4.2.1 and 4.2.3.

**Survival and Recapture Rates**

Models describing the survival rates and recapture probabilities for Redshank caught by the SCAN Ringing Group in north Wales are compared in Table 4.2.4. The recapture probability for these birds was relatively low, with a mean of 0.085 (±0.005) in the base model in which both $\phi$ and p were assumed to be constant.

Where survival rates were allowed to vary with time, neither survival rates nor recapture probabilities were estimable for all years. The reduction in estimable parameters affected the $QAIC_c$ value and thus the apparent relative fit of the models. The best fit model suggested that recapture probabilities varied fully with time, but not between age classes and that adult and first-year survival rates varied separately with time. However, a model with time-varying survival equal between the two age-classes did not have a much higher AIC ($\Delta$AIC=0.50), suggesting weak statistical support for a difference in the survival rates of the two age-classes. In three of the 24 years considered (when numbers of birds caught were 1, 6 and 0), no birds were recaptured and thus recapture probabilities were not estimable. Adult survival rates were estimable for 16 years and first-year survival for 17 years, though confidence limits were extremely wide (Fig. 4.2.2). Survival of the two age classes was positively correlated ($r$ = 0.660).

Although it was not possible to estimate survival for every year, it was possible to look for trends through time. Both adult and first-year survival showed significant positive increases over the study period (LRT: $\chi^2_1$ = 7.21, $P$ = 0.0073), the increase for first-year birds being significantly greater (Fig. 4.2.2; LRT: $\chi^2_1$ = 6.74, $P$ = 0.0095).

**Sample Size and Estimation Accuracy**

Standard errors of the annual survival estimates from the best fit model in relation to numbers caught are shown in Fig. 4.2.3. The graph for first-year survival suggests that standard errors may be reduced to less than 0.2 once samples of birds caught reach ca. 80 birds and to 0.15 with ca. 150 birds. The relationship for adults was less convincing – perhaps as adult survival is not solely calculated from birds caught in the previous winter, but also birds caught in earlier winters.

Standard errors of survival estimates also decreased in relation to numbers recaptured per year, though the relationship for first-year survival was weak (Fig. 4.2.4). The relationship for adult survival rates suggested that 25 re-traps per year would be needed to attain a standard error of 0.2 and 75 to achieve a standard error of 0.1.

Due to the low numbers of birds recaptured and difficulties in estimating survival parameters, it was not possible to test the effect of decreasing sample size on the precision of survival estimates.

### 4.2.4 Discussion

There are a number of reasons why it was difficult to derive annual estimates of Redshank survival from the north Wales dataset and why the precision of those estimates that could be calculated was limited.

Firstly, recapture probabilities were low. The value of 0.085 found for north Wales was a little lower than that reported for the Redshank caught on the Moray Firth by Insley *et al.* (1997) where sample sizes were similar. In that study, it was also not possible to determine annual estimates for adult survival in three of 16 years and the best fit model only provided constant survival rates for second year birds and those in their third year or older.

The analysis of SCAN Ringing Group data indicated that increases in the numbers of Redshank caught and re-trapped could reduce the standard errors of annual survival estimates. Data for first-year birds suggested that ca. 80 birds would need to be caught per year to attain a standard error of 0.2, while data from adults suggested that the same error could be achieved with 25 birds re-trapped per year. The relationship between the accuracy of survival estimates and the numbers of birds caught or re-trapped is likely to be dependent on the overall recapture rate at the study site. However, much larger samples than were caught in north Wales would be needed to provide the precision found in some of the studies reported by Robinson *et al.* (2005).

Secondly, there was considerable variation in the total numbers of birds caught between years and also changes in the catching sites used within the study area over time. For the north Wales study site, poor goodness-of-fit meant that data had to be restricted to catches from a group of just five catching sites.

Thirdly, restricting the datasets to the winter period – necessary due to the presence of passage birds in autumn and spring – will have reduced sample size and so potentially lowered the number of estimable survival parameters and precision of those that could be estimated.

Although earlier analysis of SCAN data showed no difference in the estimated survival of British and Icelandic Redshank in north Wales (Burton *et al.* 2006), it is also important to consider whether there are differences between races, if both are present in high numbers. To be able to do this, though, it is imperative that data are collected on bill, wing and tarsus-toe length. As moult may prevent the measurement of wing-length in the autumn, it would again be preferable to increase the numbers of birds caught in winter.

## 4.3 The Wash

### 4.3.1 Introduction

The Wash holds internationally important numbers of Redshank with a population of 3,500 present each winter (Collier *et al.* 2005). Although the site supports birds of both the British and Icelandic races, the majority that winter there originate from Iceland (Clark 2002a). Some nominate *totanus* birds from central Europe and Scandinavia may also pass through in autumn or even winter (Clark 2002b).

### 4.3.2 Methods

The Wash Wader Ringing Group (and earlier ringers) have been catching and ringing Redshank since 1959 at catching sites spread throughout The Wash. Numbers of Redshank caught in relation to catching site and year are summarised in Table 4.3.1a for the period 1967/68 to 2003/04. This summary is repeated in Table 4.3.1b for a more restricted winter period of October to February (as above).

Within the area, catching effort of Redshank has been concentrated at Terrington, where 54% of all captures have been made. As numbers of birds caught at the other 15 catching sites were much fewer and catching effort at these sites varied greatly over time, and to help minimise biases in capture histories between different cohorts of birds, only data from Terrington were used in the following analyses. Data were considered for the period 1974/75 – when catching of Redshank became more regular – to 2003/04.

### 4.3.3 Results

**Goodness of Fit**

With data separated for first-year and adult birds, goodness-of-fit tests indicated considerable heterogeneity in the capture histories – specifically that there were transients in the population (Table 4.3.2, test 3.SR). To minimise the problems caused by the lack of recaptures, data from age classes were therefore combined in order to create a single group with the largest possible sample size. Goodness-of-fit tests suggested that the general CJS model did provide a reasonable fit to these data – i.e. for Redshank of all ages caught at Terrington from 1974/75 within a recapture period running from July to April (Table 4.3.2). Numbers of birds marked and recaptured each year are shown in Table 4.3.3.

The earlier analysis of SCAN Ringing Group data suggested that adult survival rates did not differ between birds of the British and Icelandic races (Burton *et al.* 2006). For The Wash, biometric data were not collected prior to 1988 and this meant that it was not possible to determine the race of many individuals (information on bill, wing and tarsus-toe length from each bird is needed to assess probable race: see Summers *et al.* (1988) for methods). Approximately 70% of Redshank found dead on The Wash during severe weather in February 1991 were found to be of Icelandic origin (Clark 2002a).

**Survival and Recapture Rates**

Models describing the survival rates and recapture probabilities for Redshank caught by the Wash Wader Ringing Group are compared in Table 4.3.4.

The majority of captures of Redshank made on The Wash were from the autumn (July to September). Even including data from these months, though, recapture probabilities of Redshank on The Wash were extremely low mean = 0.028 (± 0.002) for the dataset that comprised all captures regardless of age class. In 10 of the 29 years considered, no first-year birds were recaptured at all; indeed, only 45 birds first caught as first-year birds were ever recaptured in subsequent years.

As with the SCAN Ringing Group analysis, neither survival rates nor recapture probabilities were estimable for all years. The best fit model suggested that both recapture probabilities and survival rates varied annually. In two of the 29 years considered, where the numbers of birds caught were 8 and 31, no birds were recaptured and thus recapture probabilities were not estimable. Due to this and low recapture probabilities in other years, survival rates were estimable for just 12 of 29 years and confidence limits were again wide (Fig. 4.3.1). Note in this figure the particularly low survival estimate for 1991 ($\phi = 0.244 \pm 0.137$), when winter temperatures were particularly low, resulting high mortality (Clark 2002a). In contrast to Redshank in north Wales, there was no trend through time in survival rates (LRT: $\chi^2_1 = 0.01$, $P = 0.9288$).

Standard errors of annual survival estimates from the best fit model in relation to numbers caught and recaptured per year for adult and first-year birds are shown in Fig. 4.3.2. In both cases, relationships were weak. Due to the low numbers of birds recaptured and difficulties in estimating survival parameters, it was not possible to test the effect of decreasing sample size on the precision of survival estimates.

### 4.3.4 Discussion

In comparison to north Wales, recapture rates of Redshank on The Wash were exceedingly low and this severely impeded the ability to derive annual survival estimates. In some years, no birds were recaptured at all on The Wash or, indeed, in north Wales. The extremely low numbers of first-year birds recaught on The Wash prevented analysis of age-specific survival at this study site.

In both study areas, though particularly on The Wash, a large proportion of birds are caught in the autumn (July to September) when both passage birds and winter residents would be present. As a result, the assumption that survival and recapture probabilities do not differ between cohorts of individuals may not be met. Obviously, by including autumn catches, the survival rates estimated may also not refer solely to those birds that use the study site in winter and at this time the proportions of the two races may also differ.

Restricting datasets to the winter period, however, may critically reduce sample sizes (Table 4.3.1) and consequently lower the number of estimable survival parameters and precision of those that can be estimated. In the case of The Wash, analysis would not have been possible using winter data alone and though goodness-of-fit tests suggested that using data from throughout the year did not invalidate model assumptions, this may have simply been because the low recapture rates meant there was too little power to detect a lack of fit.

## 4.4 Uses of current Redshank ring-recapture data

Although analyses have shown that estimation of annual survival rates may be difficult, the ring-recapture data currently available for Redshank are nevertheless of value.

The number of parameters being estimated and thus confidence limits can be reduced by grouping years or simply looking for trends over time. For north Wales, for example, analyses indicated increases in the survival of both adult and first-year Redshank over the study period.

This dataset was also used to provide a control for variation in survival due to regional weather conditions when comparing Redshank survival in periods before and after habitat loss at Cardiff Bay in south Wales (Burton *et al.* 2006).

It may also be possible to investigate which environmental factors influence survival. Insley *et al.* (1997), for instance, reported correlations between adult survival and the number of snow days in winter and between first-year survival and winter rainfall. First-year survival was low in dry (and cold) winters and also in winters with very high rainfall, but higher in winters with average rainfall. In the present study, Redshank survival on The Wash was found to be particularly low in 1991, following a particularly severe winter when temperatures fell below zero for nearly two weeks.

In a similar manner, it would also be possible to investigate whether survival is affected by population size (e.g using Wetland Bird Survey data). Survival rates of waders, particularly of first-year birds, may potentially be depressed when densities are high due to increased density-dependent competition (Durell *et al.* 2000, 2001).

## 5. DISCUSSION

In this report we have investigated the possibilities of using wader capture- mark-recapture studies, in the context of monitoring wader survival with a view to to establishing a national monitoring programme. Other studies have used similar data, but in a more local context, however the experiences of the these analyses are relevant to the broader aim considered here, so we briefly review some of the more recent studies.

Freeman *et al.* (pers. comm.) attempted to model survival rates of Redshank and Dunlin present during the winter on the Orwell Estuary in the period 1991 - 2004 using mark-recapture of birds at three catching locations in the estuary. For each species, a little under 200 birds were caught each year on average, and they defined a ringing season from July to October, based on the pattern of numbers caught. For both species, recapture rates were very low, < 1% for Redshank, and even lower for Dunlin (with negligible numbers of this species re-caught). Consequently, they were unable to calculate any estimates of Dunlin survival. For Redshank, they were able to estimate an overall survival rate with tolerable precision (± 10%, 95% confidence interval), but were unable to estimate annual survival rates. This was, almost certainly, in large part to the low number of recaptures and to the heterogeneity in catching effort between years, which was significant.

Atkinson *et al.* (2003) studied survival of Oystercatcher and Knot based on birds which were trapped and ringed on the Wash by the Wash Wader Ringing Group and subsequently found dead. Annual estimates of survival were calculated for both species, and additionally there was suffcient data to estimate six-monthly survivals (summer and winter) for Oystercatcher. For oystercatchers, annual survivals were estimable with reasonable precision, and juvenile and adult survival rates did not differ (echoing results found here). Six-monthly estimates were only estimable in relation to covariates (shellfish abundance and weather). For Knot, although annual survival rates were estimable, the most parsimonious model (in terms of AIC) was for constant survival rates, reflecting the sparse dataset; the annual survival rates were estimated with relatively poor precision. They were, however, looking for relatively large differences in survival, so even models with poor precision were acceptable.

These results are in accord with those presented here, in that in a few cases, where numbers of re-encountered birds are sufficient, it is possible to generate robust estimates of (annual) survival rates, but that these cases are probably the exception rather than the rule. They also highlight the need of being clear what is required of the analysis, greater precision (and hence sample sizes) will be required for detailed annual monitoring than for identifying odd years of very low survival (as Atkinson *et al.* 2003) did. A further key point is that, often, it will be necessary to estimate survival rates for particular races or populations, rather than for all individuals within a species, as environmental pressures on each population may differ. These issues are discussed below.

### 5.1 Sample Sizes and Estimation Accuracy

A key priority for any sampling programme is determining the number of samples required for a given level of precision (Greenwood & Robinson 2006). For estimating survival rates, the number of re-encounter occasions each year is a better predictor of the precision of annual estimates than the number of birds ringed, at least for analyses of mark-recapture data (Fig. 5.1.1; Robinson *et al.* 2005). This is because re-trap (or recovery) occasions give definite information on a period of survival, so each such occasion is clearly many times more useful (in terms of survival estimation) than a single ringing event. However, the two numbers will clearly be closely related, the greater the ringing effort, the more likely individuals are to be re-trapped. With an idea of the likely mean re-trap rate, the appropriate ringing effort could be determined.

The question of what level of precision is appropriate very much depends on the study in question. If all one wants to do is to identify occasional years or groups of years of severe mortality (as found by Atkinson *et al.* (2003) in Oystercatchers, for example), then relatively large errors may be acceptable. In contrast, even small differences in survival rates can have a large influence on conclusions in population models (particularly for long-lived birds like waders). Pragmatically, for most studies a standard error for annual estimates of (adult) survival of in the region of 0.05 to 0.10 is likely to be the best that is achievable (Robinson *et al.* 2005). This is equivalent to a confidence limit of somewhere between 10% and 20%, leading to considerable uncertainty in interpretation, as a change in survival rate of only 5% can have large impacts on the population dynamics of long-lived birds, such as waders (Clobert & Lebreton 1991). Ideally, a monitoring programme at a site would aim for 80 to 100 re-encounter occasions (more than this may not reduce the standard error in proportion with the effort put in), but a minimum of 50 in some years may be acceptable. (Note that the minimum in any guidelines should be set nearer to 100 rather than 50, as there is always a tendency to accept 'just below' any minimum bar.) Colour-marking individuals may make achieving these targets more achievable, but this is only likely to work for a relatively limited range of (large) species in situations where birds can be easily observed at relatively close range. It also requires co-ordination of the re-sighting effort, which may be a significant resource commitment, particularly if a large number of sightings is expected (see Bearhop *et al.* (2003) and Robinson *et al.* (2005) for a discussion of some of these issues).

Without further encouragement, this sort of level of effort is unlikely to be achievable for many species. Currently, only three wader ringing groups achieve this sort of re-trap level for at least some species (based on the tables in the Oracle database – see Table 2.3.1); these are SCAN (North Wales), the WWRG (Wash) and the Highland Ringing Group (Moray). Even when a dedicated team is available, there needs to be a sufficient number of birds to catch for reliable parameter estimation (as shown by a decline in the number of Dunlin catchable on the wash in the mid-1990s, see 3.3). In this context it would be useful to investigate population numbers at estuaries throughout Britain, to assess, in principle, whether there are is a sufficient population to potentially make catching for survival rate estimation a viable proposition. Further consideration would then need to be given in terms of the practicality of regular catches.

### 5.2 Definition of a site

A major consideration when dealing with wader mark-recapture data is what constitutes a study site? Estuaries range in size from relatively small river outlets (e.g. Poole Harbour) to major inter-tidal ecosystems (such as The Wash). Although waders often exhibit a high degree of site fidelity, even within small estuaries there may be movement of birds within the estuary between catching sites. There may also be exchange of birds between estuaries, depending on their proximity. Such movements create problems for mark-recapture analyses, since they introduce heterogeneity between birds in their capture and (re-capture) probabilities. Clearly, goodness of fit tests can be used to identify such problems, though resolving them may require a bit more thought. There has been very little work done defining 'sites' (i.e. areas with relatively little interchange of birds between them), which are likely to be at the within estuary scale (Rehfisch *et al.* 1996).

Recent advances in statistical techniques and software (notably M-SURGE) allow multi-site systems to be modelled explicitly, with additional parameters to account for the movements between sites; but these require large amounts of data in order to estimate all the parameters needed satisfactorily, so will almost certainly not be applicable to estimating survival rates for many of the wader species considered here, although the technique has been used successfully in the case of Oystercatchers caught in North Wales (PW Atkinson pers. comm.).

An analysis is needed to identify the species and catching locations, which represent more or less discrete population units. The aim should be to identify probably a small number of study sites at which catching efforts can be targeted each year, in a manner similar to the BTO's Ringing Adults for Survival (RAS) scheme.

## 5.3 Feasibility of national annual monitoring programmes

A number of factors need to be taken into account when considering the feasibility of an annual monitoring program, at a national scale, bearing in mind that fully stratified random sampling program (as might be planned for some census schemes, for example) is unlikely to be realistically achievable.

- Are there sufficient (and representative) sites where enough birds can be caught reliably in the long-term?
- Does the UK host several distinct breeding populations of the species? For some species this may be relatively easy to determine, for species with a wider breeding range, although the breeding range is continuous, there may be little interchange between different areas, and very different factors operating in each. Trying to identify the breeding source areas of each wintering site would be extremely helpful, but difficult as they may mot be separable on biometric or plumage characteristics.
- Is the demography of the population homogenous, i.e. are changes in survival between years (expected to be) similar at each site. Any differences will need to be carefully assessed.

### 5.3.1 Dunlin

Typically, annual survival is monitored from breeding season to breeding season, or (more usually amongst waders) from winter to winter. As the results for Dunlin show (Section 3.3), providing a suitable population can be defined, monitoring of birds during the passage period also appears to be feasible (in that credible estimates of survival can be generated).

There seemed to be little correspondence between the annual adult survival rates of birds in Poole Harbour and The Wash, nor in the changes between years (Fig. 5.3.1). Although the survival rates are measured over slightly different periods (Wash: autumn to autumn; Poole: winter to winter), this perhaps implies that birds using these sites do not breed in the same area and that processes outside Britain account for a larger part of the variation in survival. However, if there was similar variation between other sites where Dunlin might be monitored (e.g. Moray Basin), there might be some difficulty in interpreting the overall survival rate.

Dunlin is the wader species caught in the greatest numbers in Britain, and on the greatest number of sites. However, the situation is complicated by the number of populations present. Even though during the winter months these are mostly likely to be *alpina* birds. This race, however, does have a wide breeding distribution (Clark 2002c) and it is not known how much differentiation of breeding populations on different wintering sites there is. Such issues could be potentially addressed by the use of stable isotopes (at least in pre-moulting birds), though extensive ground-truthing of the isotope ratios would probably be necessary, and which may show annual variation.

### 5.3.2 Redshank

The Redshank, like Dunlin, is a common wintering species in the UK and considerable numbers are caught each year by some ringing groups, again notably SCAN (North Wales), the WWRG (Wash) and the Highland Ringing Group (Moray). However, as with Dunlin, there may be considerable variations in catching effort (and success!) and retrap rates between years, meaning that currently it may be difficult to measure annual survival rates (rather than an average across) years at any one site, l*et al.* one a representative national measure.

As with Dunlin, more than one race of Redshank occurs in this country in the non-breeding seasons. The British race *brittanica* predominates in the south, while the Icelandic race *robusta* predominates in the north, particularly in Scotland (Burton *et al.* 2002). Earlier analysis of SCAN data showed no difference in the estimated survival of British and Icelandic Redshank in north Wales (Burton *et al.*

2006). Any attempt to monitor survival nationally would need to take race into account, though if winter was the major time of mortality, multi-site indices of survival may be more useful. There are also likely to be large differences in survival between sites due to climatic differences – survival on The Wash and the Moray Firth may be extremely low in some years due to severe cold weather (Insley *et al.* 1997, Clark 2002a) whereas on the west coast, survival in winter may be higher due to more clement weather (Norman & Coffey 1994). Burton (2000) and Burton *et al.* (2006) found that the monthly survival of Redshank wintering at Cardiff Bay was greater in winter than during the passage periods and summer. Given these factors, it is unlikely that it would be possible to calculate truly representative national survival estimates from the limited number of datasets presently available.

### 5.3.3 General Considerations

Estimation of survival rates is only one reason for catching waders, catches also provide much valuable information on many other facets of wader biology, such as recruitment (Clark *et al.* 2004), movements (Wernham *et al*. 2002) and moult strategies (Serra *et al.* 2006); the recommendations presented here need to be considered in this wider context. However, while ringing of waders is useful for many purposes (and should fulfil as many aims as possible), data requirements for survival monitoring are relatively exacting, and perhaps incompatible with more general wader ringing. In some cases it has proven possible to use data from general ringing to estimate how survival rates have changed in response to particular environmental changes (e.g. Atkinson *et al.* 2003); thus for focussed studies with particular aims where there is the ability to fully explore the data analyses may be possible. This level of analytical detail may not be appropriate for more routine analyses typical of monitoring programmes.

Presently, data sufficient for estimating annual survival rates appear only to be available for relatively few wader species. Even for these, there are difficulties in obtaining precise estimates at the site level every year, due to variable catching rates and low recapture rates. There seemed to be little correspondence between the patterns of annual survival rates at each site (within a species). There is considerable geographic variation in site quality for waders between British estuaries (e.g. Austin & Rehfisch 2005), and each species may consist of several populations which breed in different areas (Wernham *et al.* 2002). At present, therefore, it would seem most prudent to provide recommendations that aim to improve the reliability of survival estimates for individual sites (that might be used to help explain local population changes) rather than aiming to produce a national monitoring programme.

## 5.4 Recommendations for future monitoring

This work has highlighted the importance of a consistent sampling program at particular sites in order to estimate annual survival rates, both to ensure good numbers of birds for accurate estimation of survival rates, and help achieve similar capture probabilities for birds in the sample. Estimation techniques for survival rates are quite sensitive to heterogeneity in capture effort and missing catches in any time period can seriously hamper estimation of survival rates. Clearly, if a catching attempt is not made at a site, then birds cannot be caught there, meaning they will appear to be transient in the population, i.e. not catchable.

- Encourage ringers to focus on a core set of sites and species where a regular catching effort is maintained between (and, where appropriate, within) years. While such ringing may be possible within current general ringing activities for some species and sites, it is likely that additional focussed effort will be required.

In these analyses we have looked at how precision of the annual survival estimates varies with sample sizes. The number of re-encounter occasions seemed to be more important in determining the precision of estimates than the simple number of birds marked. Marking as many birds as possible would be the ideal, though in these cases there seemed to be little to be gained by marking more than a sufficient number of birds to ensure a re-encounter rate of of 80-100 birds year. Marking many fewer than 50 birds generally led to much poorer standard error estimates, at least where estimates of first-year and adult birds were attempted. These are very general guidelines, and it is likely the optimal sampling strategy will vary between different sites, depending on factors such as the size and structure of the population, whether there is exchange of birds between other (nearby) sites/populations and site-specific catching factors, as well as how survival rates are modelled (e.g. do several sites contribute to the estimate). Similar results have been obtained for a small range of passerine species from the RAS scheme, though in general the number of re-encounter occasions needed was lower, perhaps because capture probabilities of breeding adult passerines are less heterogeneous.

The issues surrounding required sample sizes for survival estimation need to be explored further, probably through some simulation studies. However, on the basis of the analyses presented here

- We suggest a catching effort, for survival estimation purposes, of a sufficient number of birds for there to be 80-100 re-encountered birds per year in most years. Sites where there are many fewer than 50 re-cencounters per year are likely to yield poor estimates of survival, though ringing effort there may provide useful information for other purposes, e.g. monitoring recruitment.

Careful thought should also be given to the timing of the capture effort. Many wader species have a high degree of population structuring, both at the sub-species and population levels. Therefore capture needs to be targeted at particular populations (which also need to be identifiable, see below). Thus, in situations where different populations move through a site at different times, ringing should focus on a particular population (or at least be able to differentiate between populations). Care should also be taken not to extend the capture period over too a long a time (within a year). Strictly, capture-mark-recapture models assume zero mortality during the capture period. Although it is thought that violating this assumption should not lead to too much bias in survival rate estimation, because the winter period (typically when most waders are caught) can be a time of high mortality, care should be taken not to extend the capture period unnecessarily.

As alluded to earlier, survival rate estimates need to be based on biological populations rather than species as a whole. Thus, it is critical, where possible, that birds are identified to these populations. For some species, this can be done on the basis of biometrics, plumage, or moult strategy, at least at certain times of year. In some cases, as with Redshank (Section 4), it may be possible to show that survival rates do not differ between races, though it should be noted that this may be a statistical, rather than a biological, lack of difference. Where populations come from widely dispersed areas that cannot be identified, estimating useful annual survival rates may prove difficult.

- Encourage identification of races/populations of birds of all birds handled where possible, using a combination of plumage, moult or biometric characteristics. This should be regarded as minimum information (subject to welfare considerations) to be taken on every bird (even those that are not otherwise fully processed).

Estimation of survival rates from birds re-sighted, re-trapped or recovered dead present very different biases and problems (Robinson *et al.* 2005). For highly mobile species, recoveries or colour-marking may prove the most successful way to estimate survival rates, though this method works best on large species using sites where they can be approached relatively closely. This area needs further consideration.

At least on the basis of these limited analyses, production of national annual survival rate estimates on an annual basis is likely to prove impossible, for both biological and statistical reasons, even for many species that are regularly caught. Consequently, at least initially, the focus should be on obtaining useful estimates of survival at suitable sites for a limited range of species. The issue of multiple races and populations is a thorny one, as they will constitute differing proportions of the populations in different areas, and may be subject to different demographic influences outside of the wintering ground. This creates extra heterogeneity and wider error limits in survival rate estimates, even if the sampling protocol is good. Of course these proportions may well change over time, creating further challenges for the estimation of survival rates.

It is possible that using dead recoveries from a range of sites across Britain may provide a useful method for estimating annual survival rates, though fluctuations in catching success between sites (and hence heterogeneity of capture) as well as, for some species, relatively low recovery rates may hamper these efforts. An alternative may be to consider estimating survival as averages over intervals of longer than a year, either a constant interval, e.g. 2 or 5 years, or a variable interval, perhaps related to periods of similar rates of population change, either on the breeding or wintering grounds, as appropriate for the species, or to look for trends. The possibility of combining live retraps and dead recoveries to estimate survival rates should also be considered, though the assumptions required may be too restrictive.

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| **Dead Birds** | BATGO | | | | CURLEW | | | | DUNLIN | | | | GREPL | | | | KNOT | | | | OYSTE | | | | REDSHANK | | | | SANDERLING | | | | TURNSTONE | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | **N** | A | *W* | S | **N** | A | *W* | S | **N** | A | *W* | S | **N** | A | *W* | S | **N** | A | *W* | S | **N** | A | *W* | S | **N** | A | *W* | S | **N** | A | *W* | S | **N** | A | *W* | S |
| Clyde | | | | | 1 | 0 | 4 | 0 | 1 | 0 | 1 | 0 | | | | | | | | | 4 | 0 | 3 | 2 | 11 | 2 | 3 | 1 | | | | | | | | |
| Dee | 5 | 1 | 1 | 1 | 14 | 0 | 1 | 1 | 28 | 2 | 2 | 1 | 2 | 0 | 1 | 1 | 19 | 1 | 3 | 1 | 31 | 6 | 10 | 2 | 35 | 2 | 2 | 2 | 16 | 1 | 0 | 1 | 13 | 0 | 1 | 1 |
| Durham | 3 | 3 | 0 | 0 | 11 | 2 | 0 | 1 | 18 | 1 | 1 | 0 | 8 | 1 | 1 | 0 | 17 | 0 | 3 | 0 | 14 | 2 | 1 | 0 | 23 | 2 | 1 | 0 | 11 | 0 | 1 | 1 | 8 | 1 | 2 | 0 |
| Exe | 2 | 1 | 1 | 0 | 8 | 2 | 1 | 0 | 7 | 0 | 1 | 0 | | | | | 1 | 1 | 0 | 0 | 21 | 4 | 4 | 1 | 9 | 1 | 1 | 0 | | | | | | | | |
| Forth | 3 | 0 | 1 | 0 | 8 | 1 | 1 | 1 | 9 | 0 | 2 | 0 | 1 | 0 | 3 | 0 | 7 | 0 | 3 | 0 | 19 | 1 | 3 | 1 | 24 | 1 | 2 | 0 | | | | | 11 | 1 | 2 | 1 |
| Humber | 2 | 1 | 0 | 1 | 9 | 1 | 0 | 0 | 26 | 2 | 1 | 0 | 1 | 1 | 0 | 0 | 2 | 1 | 0 | 0 | 2 | 1 | 1 | 0 | 8 | 1 | 1 | 0 | | | | | 3 | 0 | 0 | 1 |
| Montrose | | | | | 2 | 2 | 0 | 0 | 3 | 1 | 1 | 0 | | | | | 1 | 1 | 0 | 0 | 14 | 2 | 1 | 0 | 14 | 4 | 1 | 1 | | | | | | | | |
| Moray | 16 | 1 | 1 | 0 | 16 | 1 | 1 | 0 | 11 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 12 | 0 | 2 | 0 | 30 | 7 | 6 | 3 | 25 | 3 | 1 | 1 | | | | | 6 | 1 | 0 | 0 |
| Morecambe | 1 | 1 | 0 | 0 | 8 | 3 | 1 | 0 | 20 | 1 | 2 | 2 | | | | | 13 | 1 | 6 | 2 | 25 | 9 | 16 | 2 | 18 | 2 | 2 | 1 | 10 | 0 | 0 | 1 | 14 | 2 | 0 | 1 |
| North Wales | 1 | 0 | 1 | 0 | 12 | 5 | 1 | 0 | 23 | 0 | 2 | 0 | | | | | | | | | 37 | 6 | 6 | 3 | 25 | 2 | 1 | 0 | | | | | 5 | 0 | 2 | 1 |
| Plymouth | | | | | 1 | 0 | 3 | 0 | 6 | 0 | 1 | 0 | | | | | | | | | 1 | 7 | 0 | 0 | | | | | | | | | 6 | 0 | 0 | 1 |
| Poole | 4 | 0 | 1 | 0 | 9 | 1 | 1 | 0 | 16 | 0 | 1 | 0 | 2 | 0 | 1 | 0 | 2 | 1 | 1 | 0 | 22 | 2 | 1 | 0 | 5 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | | | | |
| Severn | | | | | 12 | 1 | 1 | 1 | 17 | 0 | 2 | 1 | | | | | | | | | 9 | 0 | 2 | 0 | 10 | 0 | 1 | 0 | | | | | 1 | 0 | 0 | 1 |
| Solent | | | | | 6 | 1 | 0 | 0 | 18 | 1 | 1 | 1 | 5 | 0 | 1 | 0 | | | | | 12 | 1 | 1 | 1 | 23 | 2 | 1 | 0 | | | | | 2 | 1 | 0 | 1 |
| Solway | 1 | 0 | 3 | 0 | 2 | 1 | 1 | 1 | 12 | 1 | 0 | 1 | | | | | 2 | 0 | 5 | 0 | 18 | 1 | 5 | 1 | 3 | 1 | 0 | 0 | 5 | 0 | 0 | 3 | 5 | 0 | 0 | 1 |
| Suffolk | | | | | 16 | 1 | 0 | 0 | 35 | 1 | 1 | 0 | 5 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 8 | 0 | 2 | 1 | 40 | 2 | 1 | 1 | | | | | 3 | 1 | 0 | 0 |
| Tay | 3 | 0 | 1 | 0 | 6 | 1 | 0 | 1 | 10 | 1 | 1 | 0 | | | | | 4 | 1 | 2 | 0 | 24 | 2 | 1 | 1 | 24 | 3 | 1 | 0 | 1 | 0 | 1 | 0 | 3 | 1 | 0 | 0 |
| Thames | 4 | 1 | 0 | 0 | 16 | 3 | 2 | 1 | 31 | 2 | 3 | 1 | 11 | 1 | 0 | 0 | 2 | 0 | 5 | 0 | 6 | 1 | 2 | 0 | 27 | 3 | 1 | 1 | | | | | 1 | 1 | 0 | 0 |
| Wash | 28 | 2 | 0 | 0 | 39 | 5 | 1 | 0 | 41 | 10 | 2 | 0 | 35 | 5 | 3 | 1 | 39 | 7 | 4 | 2 | 41 | 30 | 8 | 6 | 42 | 14 | 2 | 1 | 24 | 3 | 0 | 1 | 30 | 3 | 1 | 1 |
| Western Is | 3 | 1 | 0 | 0 | 2 | 0 | 1 | 0 | 5 | 0 | 0 | 1 | | | | | 1 | 2 | 0 | 0 | 10 | 1 | 0 | 0 | 10 | 0 | 0 | 1 | 3 | 1 | 0 | 0 | | | | |
| Ythan | | | | | 6 | 2 | 0 | 0 | 4 | 1 | 0 | 0 | | | | | 2 | 0 | 0 | 1 | 10 | 0 | 1 | 2 | 15 | 3 | 1 | 0 | | | | | 1 | 2 | 0 | 0 |

**Table 2.3.1** Sample sizes of birds found either dead, controlled (caught alive by ringers other than the original ringer) or re-trapped (caught alive by the original ringer). For each species the number of consecutive years for which data are available (N) is given, along with the average number of birds per year for the autumn (A, Jul-Oct), winter (W, Nov-Feb) and Spring (S, Mar-June) for the most commonly caught species.

| **Controls** | BATGO | | | | CURLEW | | | | DUNLIN | | | | GREPL | | | | KNOT | | | | OYSTE | | | | REDSHANK | | | | SANDERLING | | | | TURNSTONE | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | **N** | A | *W* | S | **N** | A | *W* | S | **N** | A | *W* | S | **N** | A | *W* | S | **N** | A | *W* | S | **N** | A | *W* | S | **N** | A | *W* | S | **N** | A | *W* | S | **N** | A | *W* | S |
| Clyde | | | | | **2** | 1 | *2* | 0 | **4** | 1 | *2* | 0 | | | | | | | | | **10** | 0 | *2* | 1 | **13** | 2 | *2* | 2 | | | | | | | | |
| Dee | **7** | 1 | *1* | 1 | **16** | 0 | *1* | 1 | **34** | 3 | *6* | 4 | **3** | 0 | *1* | 0 | **24** | 3 | *6* | 1 | **37** | 7 | *10* | 3 | **37** | 2 | *2* | 4 | **21** | 2 | *0* | 3 | **18** | 1 | *2* | 3 |
| Durham | **5** | 4 | *0* | 0 | **17** | 1 | *0* | 1 | **32** | 4 | *2* | 1 | **9** | 1 | *1* | 0 | **22** | 1 | *4* | 0 | **16** | 4 | *1* | 0 | **26** | 2 | *1* | 1 | **12** | 1 | *1* | 1 | **9** | 1 | *2* | 1 |
| Exe | **2** | 1 | *1* | 0 | **9** | 2 | *1* | 0 | **10** | 1 | *1* | 0 | **1** | 0 | *1* | 0 | **4** | 1 | *1* | 0 | **22** | 5 | *5* | 1 | **10** | 1 | *1* | 0 | | | | | | | | |
| Forth | **4** | 1 | *2* | 0 | **10** | 1 | *1* | 1 | **17** | 0 | *3* | 0 | **1** | 0 | *3* | 0 | **11** | 0 | *5* | 0 | **29** | 1 | *3* | 2 | **36** | 1 | *2* | 1 | | | | | **18** | 1 | *2* | 1 |
| Humber | **2** | 1 | *0* | 1 | **9** | 1 | *0* | 0 | **35** | 4 | *2* | 1 | **2** | 1 | *0* | 0 | **3** | 4 | *0* | 0 | **8** | 2 | *1* | 0 | **9** | 1 | *1* | 0 | | | | | **4** | 1 | *0* | 1 |
| Montrose | | | | | **3** | 1 | *0* | 0 | **7** | 1 | *1* | 0 | **1** | 1 | *0* | 0 | **2** | 1 | *0* | 0 | **16** | 1 | *1* | 1 | **17** | 4 | *1* | 1 | | | | | | | | |
| Moray | **16** | 2 | *1* | 0 | **21** | 1 | *1* | 0 | **21** | 1 | *3* | 0 | **1** | 1 | *0* | 0 | **16** | 1 | *4* | 1 | **35** | 6 | *6* | 4 | **29** | 3 | *2* | 1 | | | | | **10** | 1 | *0* | 1 |
| Morecambe | **1** | 1 | *0* | 0 | **21** | 1 | *0* | 1 | **31** | 2 | *4* | 6 | | | | | **17** | 2 | *17* | 5 | **42** | 7 | *11* | 2 | **32** | 1 | *1* | 1 | **16** | 1 | *0* | 1 | **23** | 3 | *0* | 2 |
| North Wales | **2** | 0 | *2* | 0 | **16** | 4 | *1* | 0 | **32** | 1 | *9* | 1 | | | | | **3** | 0 | *1* | 1 | **41** | 8 | *7* | 3 | **28** | 2 | *2* | 1 | | | | | **16** | 0 | *3* | 1 |
| Plymouth | | | | | **2** | 4 | *1* | 1 | **9** | 0 | *4* | 1 | | | *0* | | | | *1* | | **3** | 3 | *4* | 1 | **2** | 1 | *2* | 0 | | | *1* | | **6** | 0 | *1* | 1 |
| Poole | **7** | 0 | *1* | 0 | **13** | 1 | *2* | 0 | **29** | 1 | *4* | 0 | **3** | 0 | | 0 | **5** | 1 | | 0 | **25** | 2 | *0* | 1 | **10** | 0 | *1* | 0 | **1** | 0 | | 0 | | | *0* | |
| Severn | | | | | **13** | 1 | *1* | 1 | **30** | 1 | *3* | 4 | | | *1* | | **4** | 0 | *0* | 0 | **11** | 0 | *2* | 0 | **16** | 0 | *1* | 1 | | | *1* | | **4** | 0 | | 1 |
| Solent | | | | | **8** | 1 | *1* | 0 | **31** | 2 | *6* | 1 | **7** | 0 | | 0 | **1** | 0 | *1* | 0 | **15** | 2 | *2* | 1 | **32** | 2 | *2* | 0 | | | | | **2** | 1 | *0* | 1 |
| Solway | **2** | 0 | *3* | 0 | **20** | 1 | *0* | 1 | **16** | 1 | *3* | 4 | | | *1* | | **3** | 0 | *1* | 0 | **41** | 1 | *2* | 1 | **26** | 0 | *1* | 1 | **11** | 0 | | 9 | **10** | 0 | *0* | 2 |
| Suffolk | | | | | **16** | 0 | *0* | 0 | **44** | 3 | *0* | 0 | **6** | 1 | | 0 | **3** | 0 | *12* | 0 | **23** | 1 | *3* | 1 | **42** | 2 | *0* | 1 | | | *0* | | **7** | 1 | *1* | 2 |
| Tay | **4** | 1 | *1* | 0 | **10** | 1 | *0* | 1 | **17** | 1 | *3* | 0 | | | *1* | | **12** | 1 | *1* | 0 | **26** | 2 | *1* | 1 | **26** | 4 | *1* | 0 | **5** | 1 | | 0 | **5** | 1 | *1* | 0 |
| Thames | **5** | 1 | *0* | 0 | **16** | 1 | *0* | 1 | **43** | 6 | *2* | 2 | **15** | 1 | | 0 | **5** | 1 | *2* | 0 | **8** | 0 | *1* | 0 | **34** | 3 | *1* | 1 | **1** | 1 | *9* | 0 | **3** | 1 | *1* | 0 |
| Wash | **30** | 4 | *1* | 0 | **39** | 3 | *2* | 0 | **46** | 31 | *6* | 2 | **35** | 5 | *0* | 1 | **42** | 16 | *3* | 3 | **43** | 37 | *1* | 7 | **44** | 15 | *1* | 1 | **27** | 6 | *0* | 2 | **35** | 4 | *0* | 1 |
| Western Is | **2** | 2 | *0* | 0 | **3** | 5 | *1* | 0 | **13** | 1 | *4* | 2 | | | *3* | | **2** | 2 | *7* | 0 | **26** | 1 | *10* | 2 | **16** | 0 | *2* | 3 | **3** | 1 | *1* | 2 | **2** | 0 | *2* | 1 |
| Ythan | | | | | **5** | 0 | *1* | 0 | **9** | 2 | *0* | 0 | | | | | **1** | 0 | *0* | 2 | **18** | 1 | *0* | 2 | **18** | 5 | *0* | 0 | | | *0* | | **1** | 2 | *1* | 0 |

**Table 2.3.1** (continued)

| **Re-traps** | BATGO | | | | CURLEW | | | | DUNLIN | | | | GREPL | | | | KNOT | | | | OYSTE | | | | REDSHANK | | | | SANDERLING | | | | TURNSTONE | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | **N** | A | *W* | S | **N** | A | *W* | S | **N** | A | *W* | S | **N** | A | *W* | S | **N** | A | *W* | S | **N** | A | *W* | S | **N** | A | *W* | S | **N** | A | *W* | S | **N** | A | *W* | S |
| Dee | | | | | | | | | **1** | 1 | *0* | 0 | **1** | 0 | *1* | 0 | | | | | | | | | **2** | 1 | *0* | 0 | | | | | **3** | 1 | *0* | 0 |
| Durham | | | | | **1** | 0 | *0* | 1 | **2** | 2 | *0* | 0 | **2** | 1 | *1* | 0 | **3** | 1 | *1* | 0 | **1** | 1 | *0* | 0 | **3** | 3 | *0* | 0 | **3** | 0 | *2* | 3 | **2** | 0 | *5* | 1 |
| Exe | | | | | | | | | | | | | | | | | | | | | **3** | 0 | *11* | 0 | | | | | | | | | | | | |
| Forth | | | | | | | | | **2** | 0 | *1* | 0 | | | | | | | | | **1** | 1 | *0* | 0 | | | | | | | | | **2** | 1 | *0* | 0 |
| Humber | | | | | | | | | **3** | 1 | *0* | 1 | | | | | **1** | 0 | *0* | 1 | | | | | **1** | 1 | *0* | 0 | | | | | | | | |
| Moray | 23 | 10 | 18 | 4 | **22** | 16 | *12* | 3 | **23** | 2 | *46* | 3 | | | | | **20** | 1 | *33* | 5 | **26** | 70 | *105* | 26 | **28** | 100 | *92* | 35 | | | | | **24** | 10 | *9* | 14 |
| Morecambe | | | | | **1** | 0 | *1* | 0 | **35** | 8 | *10* | 21 | | | | | **15** | 1 | *19* | 12 | **13** | 8 | *12* | 4 | **13** | 11 | *5* | 2 | **25** | 3 | *1* | 4 | **31** | 24 | *4* | 12 |
| North Wales | | | | | **9** | 14 | *4* | 0 | **9** | 0 | *86* | 0 | | | | | | | | | **9** | 97 | *71* | 6 | **9** | 18 | *46* | 1 | | | | | **8** | 1 | *14* | 0 |
| Poole | 2 | 0 | 1 | 0 | **1** | 1 | *0* | 0 | **4** | 0 | *33* | 0 | | | | | | | | | | | | | **1** | 0 | *1* | 0 | **1** | 0 | *1* | 0 | | | | |
| Severn | | | | | **1** | 0 | *1* | 0 | **2** | 0 | *1* | 0 | | | | | | | | | | | | | **2** | 0 | *0* | 2 | | | | | | | | |
| Solent | | | | | | | | | **3** | 1 | *7* | 0 | **2** | 0 | *1* | 1 | **2** | 0 | *15* | 0 | **2** | 0 | *2* | 1 | **4** | 4 | *3* | 0 | | | | | **2** | 0 | *1* | 4 |
| Solway | 1 | 2 | 0 | 0 | | | | | **2** | 1 | *0* | 1 | | | | | | | | | **3** | 1 | *2* | 0 | | | | | **5** | 0 | *0* | 19 | **2** | 8 | *1* | 4 |
| Suffolk | | | | | **2** | 1 | *1* | 0 | **6** | 1 | *1* | 0 | | | | | | | | | **2** | 2 | *0* | 1 | **6** | 8 | *1* | 0 | | | | | **1** | 0 | *1* | 0 |
| Tay | | | | | | | | | **1** | 0 | *2* | 0 | | | | | | | | | | | | | **4** | 0 | *1* | 0 | **1** | 0 | *1* | 0 | **1** | 0 | *10* | 0 |
| Thames | 9 | 2 | 2 | 0 | **8** | 1 | *1* | 0 | **8** | 1 | *5* | 0 | **16** | 3 | *0* | 0 | | | | | **2** | 1 | *0* | 0 | **14** | 4 | *2* | 0 | | | | | | | | |
| Wash | 6 | 11 | 1 | 0 | **7** | 13 | *0* | 0 | **8** | 52 | *9* | 2 | **7** | 4 | *2* | 0 | **11** | 5 | *6* | 0 | **9** | 34 | *31* | 9 | **7** | 12 | *1* | 1 | **7** | 4 | *28* | 24 | **8** | 5 | *10* | 2 |
| Western Is | | | | | **4** | 1 | *0* | 1 | **2** | 1 | *0* | 1 | | | | | | | | | **4** | 0 | *0* | 2 | **1** | 0 | *0* | 1 | **2** | 0 | *0* | 7 | **1** | 0 | *0* | 1 |
| Ythan | | | | | **1** | 2 | *0* | 0 | | | | | | | | | | | | | | | | | | | | | | | | | | | | |

**Table 2.3.1** (continued)

| Species | Recoveries (Dead) | Recoveries (Controls) | Re-traps |
|---|---|---|---|
| Bar-tailed Godwit | - | - | *Moray (A,W)*<br>*Wash (A)* |
| Curlew | - | - | *Moray (A,W)*<br>*Wash (A)* |
| Dunlin | *Wash (A)* | *Wash (A)* | Moray (W)<br>Morecambe (W,S)<br>**North Wales (W)**<br>Poole (W)<br>**Wash (A)** |
| Grey Plover | - | - | - |
| Knot | - | *Morecambe (W)*<br>*Suffolk (W)*<br>*Wash (A)* | Moray (W)<br>*Morecambe (W)*<br>*Solent (W)* |
| Oystercatcher | *Dee (W)*<br>*Morecambe (W)*<br>Wash (A) | *Dee (W)*<br>*Morecambe (W)*<br>Wash (A)<br>*Western Isles (W)* | *Exe (W)*<br>**Moray (A, W)**<br>*Morecambe (W)*<br>**North Wales (A,W)**<br>Wash (A,W) |
| Redshank | *Wash (A)* | *Wash (A)* | **Moray (A,W)**<br>*Morecambe (A)*<br>**North Wales (A,W)**<br>*Wash (A)* |
| Sanderling | - | - | *Solway (S)*<br>Wash (W,S) |
| Turnstone | - | - | *Moray (A)*<br>*Morecambe (A,S)*<br>*North Wales (W)*<br>*Tay (W)*<br>Wash (W) |

**Table 2.3.2** Species for which more than 10 (*italic*), 25 (normal) and 50 (**bold**) birds are recovered dead, controlled or re-trapped each year on average from birds ringed at individual study sites in a particular season (A Autumn; W Winter; S Spring).

a) Adults

| Year | Ri | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | Total |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1978 | 350 | 36 | 27 | 19 | 16 | 6 | 5 | 0 | 2 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 113 |
| 1979 | 141 | | 17 | 24 | 11 | 2 | 3 | 5 | 2 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 65 |
| 1980 | 125 | | | 23 | 18 | 10 | 4 | 4 | 4 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 65 |
| 1981 | 251 | | | | 49 | 16 | 16 | 4 | 2 | 0 | 1 | 1 | 2 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 92 |
| 1982 | 324 | | | | | 45 | 17 | 17 | 6 | 1 | 8 | 3 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 99 |
| 1983 | 151 | | | | | | 26 | 24 | 14 | 2 | 1 | 2 | 1 | 1 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 73 |
| 1984 | 196 | | | | | | | 25 | 26 | 6 | 1 | 3 | 2 | 2 | 1 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 68 |
| 1985 | 246 | | | | | | | | 53 | 5 | 8 | 7 | 1 | 3 | 2 | 3 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 84 |
| 1986 | 319 | | | | | | | | | 20 | 25 | 13 | 16 | 2 | 4 | 1 | 1 | 0 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 85 |
| 1987 | 74 | | | | | | | | | | 15 | 13 | 5 | 3 | 4 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 41 |
| 1988 | 132 | | | | | | | | | | | 26 | 12 | 4 | 5 | 2 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 53 |
| 1989 | 144 | | | | | | | | | | | | 34 | 11 | 12 | 7 | 1 | 2 | 2 | 1 | 1 | 0 | 0 | 0 | 0 | 71 |
| 1990 | 200 | | | | | | | | | | | | | 29 | 37 | 0 | 1 | 1 | 3 | 1 | 1 | 0 | 0 | 0 | 0 | 73 |
| 1991 | 166 | | | | | | | | | | | | | | 41 | 13 | 6 | 3 | 3 | 2 | 3 | 1 | 0 | 0 | 1 | 73 |
| 1992 | 263 | | | | | | | | | | | | | | | 59 | 46 | 19 | 9 | 6 | 0 | 1 | 1 | 0 | 0 | 141 |
| 1993 | 138 | | | | | | | | | | | | | | | | 43 | 7 | 7 | 8 | 2 | 4 | 1 | 0 | 1 | 73 |
| 1994 | 174 | | | | | | | | | | | | | | | | | 33 | 22 | 16 | 6 | 2 | 2 | 1 | 1 | 83 |
| 1995 | 146 | | | | | | | | | | | | | | | | | | 15 | 11 | 4 | 1 | 0 | 0 | 0 | 31 |
| 1996 | 168 | | | | | | | | | | | | | | | | | | | 20 | 12 | 5 | 7 | 0 | 0 | 44 |
| 1997 | 145 | | | | | | | | | | | | | | | | | | | | 35 | 9 | 7 | 0 | 3 | 54 |
| 1998 | 144 | | | | | | | | | | | | | | | | | | | | | 16 | 19 | 1 | 5 | 41 |
| 1999 | 94 | | | | | | | | | | | | | | | | | | | | | | 16 | 6 | 3 | 25 |
| 2000 | 94 | | | | | | | | | | | | | | | | | | | | | | | 7 | 7 | 14 |
| 2001 | 57 | | | | | | | | | | | | | | | | | | | | | | | | 4 | 4 |

**Table 3.2.1** Numbers of (a) adult and (b) first-year Dunlin ringed (Ri) and re-trapped each year in Poole Harbour.

b) First-years

| Year | Ri | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | Total |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1978 | 20 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 |
| 1979 | 27 | | 6 | 3 | 5 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 15 |
| 1980 | 30 | | | 6 | 4 | 2 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 14 |
| 1981 | 85 | | | | 8 | 3 | 5 | 0 | 2 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 21 |
| 1982 | 53 | | | | | 6 | 4 | 1 | 3 | 3 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 19 |
| 1983 | 57 | | | | | | 12 | 5 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 20 |
| 1984 | 104 | | | | | | | 16 | 13 | 2 | 3 | 4 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 40 |
| 1985 | 193 | | | | | | | | 40 | 6 | 5 | 8 | 2 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 65 |
| 1986 | 78 | | | | | | | | | 8 | 10 | 8 | 7 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 35 |
| 1987 | 38 | | | | | | | | | | 5 | 5 | 2 | 1 | 3 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 17 |
| 1988 | 143 | | | | | | | | | | | 27 | 11 | 6 | 7 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 54 |
| 1989 | 68 | | | | | | | | | | | | 18 | 4 | 7 | 1 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 33 |
| 1990 | 129 | | | | | | | | | | | | | 24 | 21 | 2 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 49 |
| 1991 | 157 | | | | | | | | | | | | | | 58 | 7 | 4 | 3 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 74 |
| 1992 | 126 | | | | | | | | | | | | | | | 35 | 16 | 10 | 6 | 1 | 1 | 0 | 2 | 0 | 1 | 72 |
| 1993 | 168 | | | | | | | | | | | | | | | | 63 | 13 | 10 | 5 | 1 | 1 | 1 | 1 | 2 | 97 |
| 1994 | 109 | | | | | | | | | | | | | | | | | 31 | 17 | 7 | 5 | 3 | 1 | 0 | 0 | 64 |
| 1995 | 78 | | | | | | | | | | | | | | | | | | 16 | 7 | 6 | 2 | 1 | 1 | 0 | 33 |
| 1996 | 118 | | | | | | | | | | | | | | | | | | | 22 | 12 | 7 | 5 | 2 | 1 | 49 |
| 1997 | 80 | | | | | | | | | | | | | | | | | | | | 25 | 8 | 5 | 0 | 0 | 38 |
| 1998 | 114 | | | | | | | | | | | | | | | | | | | | | 26 | 13 | 2 | 2 | 43 |
| 1999 | 70 | | | | | | | | | | | | | | | | | | | | | | 21 | 4 | 4 | 29 |
| 2000 | 56 | | | | | | | | | | | | | | | | | | | | | | | 5 | 4 | 9 |
| 2001 | 72 | | | | | | | | | | | | | | | | | | | | | | | | | |

**Table 3.2.1** (continued)

| Test | Adults | | | First-years | | |
|---|---|---|---|---|---|---|
| | d.f. | $\chi^2$ | P | d.f. | $\chi^2$ | P |
| 3.SR | 23 | 169.8 | <0.0001 | 23 | 169.0 | <0.0001 |
| 3.SM | 58 | 82.6 | 0.02 | 29 | 40.0 | 0.08 |
| 2.CT | 22 | 25.6 | 0.27 | 22 | 30.1 | 0.11 |
| 2.CL | 80 | 114.3 | 0.007 | 48 | 44.9 | 0.60 |
| Total | 183 | 392.3 | <0.0001 | 122 | 284.0 | <0.0001 |
| All Groups | | | | 305 | 676.3 | <0.0001 |

**Table 3.2.2** Goodness of fit statistics for Poole Harbour Dunlin data 1978-2002. For the meaning of the tests see text.

| Model | N Parameters | Deviance | ΔAIC |
|---|---|---|---|
| φ(at,t') p(at,t') | 131 | 3580 | 0.00 |
| φ(at,t') p(at+t') | 108 | 3652 | 24.2 |
| φ(at+t') p(at+t') | 88 | 3751 | 81.9 |
| φ(at) p(at,t') | 113 | 3795 | 177 |
| φ(at) p(at+t') | 95 | 3842 | 187 |
| φ(at) p(at) | 91 | 3897 | 233 |
| φ(a) p(a) | 6 | 4166 | 329 |

**Table 3.2.3** Fitted models for Poole Harbour Dunlin data 1978-2002. For each model the number of fitted parameters (as estimated by MARK) is given, model fit (deviance) and relative parsimony (AIC). Models are specified in terms of survival (φ) and recapture rates (p) with both depending on age (a) and time(years, t); additionally, a separate parameter (t') is used for transient birds (which may vary independently, or in parallel with (+) the main adult time parameter.

a) Autumn

| Year | BE | BU | FR | FS | HL | HO | LV | NW | SN | TE | WA | WL | WR | Total |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1981/82 | | 344 | | | | | 695 | | 1 | 1,802 | | 17 | | 2,859 |
| 1982/83 | | | | | | | 162 | | 43 | 1,256 | 69 | 74 | | 1,604 |
| 1983/84 | 285 | | 122 | | | | 228 | 226 | | 128 | | 56 | | 1,045 |
| 1984/85 | 259 | 121 | | | | | | | | 270 | | 57 | | 707 |
| 1985/86 | | | 361 | | | | 11 | | | 624 | | 29 | | 1,025 |
| 1986/87 | 154 | | 182 | | | | 394 | | | 705 | | 7 | | 1,442 |
| 1987/88 | 42 | | 190 | | | | 217 | | | 280 | 42 | | | 771 |
| 1988/89 | 265 | 72 | | | 44 | | 43 | | | 4,895 | 109 | | | 5,428 |
| 1989/90 | 577 | | | 4 | 214 | | | | | 2,151 | 1 | | 108 | 3,055 |
| 1990/91 | 995 | 3,054 | 37 | | 108 | | | | | 1,802 | | | 372 | 6,368 |
| 1991/92 | 43 | 510 | 119 | 1,338 | 311 | | 157 | | 68 | 1,687 | 6 | | 878 | 5,117 |
| 1992/93 | | 792 | 232 | 607 | | | 1,364 | | | 295 | 108 | | 175 | 3,573 |
| 1993/94 | 166 | 408 | | 28 | 663 | 6 | | | | 309 | 34 | | 1,355 | 2,969 |
| 1994/95 | | 540 | | 8 | 656 | | 332 | | 5 | 410 | 1 | | 251 | 2,203 |
| 1995/96 | | 133 | | 5 | 9 | | 120 | | | 1,190 | | | 136 | 1,593 |
| 1996/97 | | 44 | | | 767 | | 1,070 | | | 860 | | | 24 | 2,765 |
| 1997/98 | | 267 | | 228 | | | 3 | | | 621 | | 16 | | 1,135 |
| 1998/99 | | 153 | | | | | 6 | | | 407 | | | | 566 |
| 1999/00 | | 376 | | | | | | | 4 | 551 | | 40 | 4 | 975 |
| 2000/01 | 65 | | | 6 | | | | | | 365 | | | | 436 |
| 2001/02 | | | | | 22 | | 9 | | | 1,093 | | | | 1,124 |
| 2002/03 | | | | | | | | | | 680 | | | | 680 |
| 2003/04 | | | | | | | | | | 840 | 2 | | | 842 |
| Total | 2,851 | 6,814 | 1,243 | 2,224 | 2,794 | 6 | 4,811 | 226 | 121 | 23,221 | 372 | 296 | 3,303 | 48,282 |

**Table 3.3.1** Numbers of Dunlin (of all races) caught on The Wash in (a) autumn (July to October) and (b) winter (November to February). Site codes (with side of Wash in parenthesis): BE - Benington (W), BU - Butterwick (W), FR - Friskney (W), FS - Freiston (W), HL - Holbeach (S), HO - Holme (E), LV - Leverton (W), NW - North Wootton (E), SN - Snettisham/Heacham (E), TE - Terrington (S), WA - Wainfleet (W), WL - Wolferton (E) and WR - Wrangle (W).

b) Winter

| Year | BE | HE | TE | WL | Total |
|---|---|---|---|---|---|
| 1981/82 | | | 5 | 34 | 39 |
| 1982/83 | | | | 1 | 1 |
| 1983/84 | | | | 120 | 120 |
| 1984/85 | | 17 | | | 17 |
| 1985/86 | 6 | | 31 | 50 | 87 |
| 1986/87 | | | | 36 | 36 |
| 1987/88 | | 1361 | | 20 | 1,381 |
| 1988/89 | | | 52 | | 52 |
| 1989/90 | | 2 | | | 2 |
| 1990/91 | | | 168 | | 168 |
| 1991/92 | | 19 | 219 | | 238 |
| 1992/93 | | | 41 | 7 | 48 |
| 1993/94 | 3 | | | | 3 |
| 1994/95 | | 5 | 101 | | 106 |
| 1995/96 | | | 22 | 82 | 104 |
| 1996/97 | 70 | 1 | 10 | | 81 |
| 1997/98 | 121 | 22 | 136 | 91 | 370 |
| 1998/99 | | | 1 | | 1 |
| Total | 200 | 1,427 | 786 | 441 | 2,854 |

**Table 3.3.1** (continued)

| Year | BE | FR | FS | HE | HL | LV | TE | WA | WL | WR | Total |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 1981 | | | | | | 182 | 451 | | 3 | | 636 |
| 1982 | | | | | | | 242 | | 74 | | 316 |
| 1983 | | 119 | | | | 6 | 15 | | | | 140 |
| 1984 | | | | | | | | | 57 | | 57 |
| 1985 | | 361 | | | | 11 | 253 | | 29 | | 654 |
| 1986 | | 182 | | | | | 140 | | 7 | | 329 |
| 1987 | 42 | 2 | | | | 217 | 124 | 41 | | | 426 |
| 1988 | 1 | | | | 28 | | 712 | | | | 741 |
| 1989 | 84 | | | | 56 | | 376 | | | 108 | 624 |
| 1990 | 139 | | | | 28 | | 293 | | | | 460 |
| 1991 | 129 | 9 | 54 | 54 | 131 | 7 | 1286 | | | 13 | 1683 |
| 1992 | 35 | 231 | 13 | | | 59 | 144 | 7 | | 13 | 502 |
| 1993 | 220 | | 8 | | 619 | | 52 | 1 | | 222 | 1122 |
| 1994 | 191 | | | 5 | 656 | 332 | 254 | | | 37 | 1475 |
| 1995 | 61 | | 1 | | | 17 | 227 | | | 21 | 327 |
| 1996 | 2 | | | | 32 | 57 | 132 | | | | 223 |
| 1997 | 35 | | 16 | | | | 234 | | 16 | | 301 |
| 1998 | 80 | | | | | | 313 | | | | 393 |
| 1999 | 17 | | | 4 | | | 298 | | 40 | | 359 |
| 2000 | 5 | | | | | | 199 | | | | 204 |
| 2001 | | | | | | | 381 | | | | 381 |
| 2002 | | | | | | | 444 | | | | 444 |
| 2003 | | | | | | | 220 | | | | 220 |
| Total | 1041 | 904 | 92 | 63 | 1550 | 888 | 6790 | 49 | 226 | 414 | 12017 |

**Table 3.3.2** Numbers of *alpina* Dunlin caught on the Wash in the autumn (July to October). Site codes (with side of Wash in parenthesis): BE - Benington (W), FR - Friskney (W), FS - Freiston (W), HE – Heacham (E), HL - Holbeach (S), LV - Leverton (W), TE - Terrington (S), WA - Wainfleet (W), WL - Wolferton (E) and WR - Wrangle (W).

a) Adults

| Year | Ri | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | Total |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1981 | 518 | 11 | 0 | 0 | 3 | 3 | 0 | 1 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 20 |
| 1982 | 268 | | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 |
| 1983 | 108 | | | 0 | 6 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 7 |
| 1984 | 28 | | | | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 1985 | 439 | | | | | 3 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 4 |
| 1986 | 242 | | | | | | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 4 |
| 1987 | 320 | | | | | | | 1 | 4 | 3 | 4 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 14 |
| 1988 | 370 | | | | | | | | 6 | 3 | 8 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 18 |
| 1989 | 251 | | | | | | | | | 0 | 4 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 5 |
| 1990 | 320 | | | | | | | | | | 8 | 4 | 0 | 3 | 0 | 1 | 1 | 0 | 0 | 0 | 17 |
| 1991 | 979 | | | | | | | | | | | 1 | 6 | 3 | 1 | 3 | 1 | 0 | 0 | 0 | 15 |
| 1992 | 356 | | | | | | | | | | | | 1 | 2 | 1 | 1 | 0 | 0 | 0 | 0 | 5 |
| 1993 | 732 | | | | | | | | | | | | | 21 | 0 | 5 | 1 | 0 | 0 | 0 | 27 |
| 1994 | 1120 | | | | | | | | | | | | | | 4 | 9 | 2 | 0 | 0 | 0 | 15 |
| 1995 | 232 | | | | | | | | | | | | | | | 8 | 2 | 0 | 0 | 0 | 10 |
| 1996 | 176 | | | | | | | | | | | | | | | | 0 | 1 | 0 | 0 | 1 |
| 1997 | 201 | | | | | | | | | | | | | | | | | 1 | 0 | 0 | 1 |
| 1998 | 96 | | | | | | | | | | | | | | | | | | 1 | 0 | 1 |
| 1999 | 119 | | | | | | | | | | | | | | | | | | | 1 | 1 |

**Table 3.3.3** Numbers of adult and juvenile ringed (Ri) and re-trapped each year on the Wash

b) Juvenile

| Year | R(i) | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | Total |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | 113 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| 2 | 47 | | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 3 | 32 | | | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 4 | 29 | | | | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 5 | 205 | | | | | 2 | 0 | 2 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 5 |
| 6 | 87 | | | | | | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 2 |
| 7 | 104 | | | | | | | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 8 | 364 | | | | | | | | 3 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 5 |
| 9 | 337 | | | | | | | | | 0 | 1 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 4 |
| 10 | 139 | | | | | | | | | | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| 11 | 654 | | | | | | | | | | | 3 | 0 | 2 | 1 | 1 | 1 | 0 | 0 | 0 | 8 |
| 12 | 139 | | | | | | | | | | | | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| 13 | 386 | | | | | | | | | | | | | 2 | 1 | 2 | 0 | 0 | 0 | 0 | 5 |
| 14 | 341 | | | | | | | | | | | | | | 0 | 5 | 0 | 0 | 0 | 0 | 5 |
| 15 | 90 | | | | | | | | | | | | | | | 2 | 0 | 0 | 0 | 0 | 2 |
| 16 | 47 | | | | | | | | | | | | | | | | 0 | 0 | 0 | 0 | 0 |
| 17 | 98 | | | | | | | | | | | | | | | | | 0 | 0 | 0 | 0 |
| 18 | 291 | | | | | | | | | | | | | | | | | | 1 | 0 | 1 |
| 19 | 236 | | | | | | | | | | | | | | | | | | | 0 | 0 |

**Table 3.3.3** (continued)

| Test | Adults | | | Juveniles | | |
|---|---|---|---|---|---|---|
| | df | $\chi^2$ | P | Df | $\chi^2$ | P |
| 3.SR | 16 | 5.84 | 0.99 | 9 | 5.28 | 0.81 |
| 3.SM | 4 | 1.47 | 0.83 | - | - | - |
| 2.CT | 12 | 17.7 | 0.13 | 9 | 6.41 | 0.70 |
| 2.CL | 14 | 9.74 | 0.78 | 6 | 1.92 | 0.93 |
| Total | 46 | 34.8 | 0.89 | 24 | 13.6 | 0.96 |
| All Groups | | | | 70 | 48.3 | 0.98 |

**Table 3.3.4** Goodness of fit statistics for Wash *alpina* Dunlin data 1981-1999. For the meaning of the tests see text.

| Model | N Parameters | Deviance | ΔAIC |
|---|---|---|---|
| S(at,t')L(at,t') | 69 | 99.66 | 0 |
| S(at,t')L(at+t') | 56 | 141.79 | 15.8 |
| S(at+t')L(at+t') | 57 | 175.43 | 51.5 |
| S(at)L(at) | 65 | 162.13 | 54.4 |
| S(a)L(a) | 4 | 360.66 | 130 |

**Table 3.3.5** Fitted models for Wash *alpina* Dunlin data 1981-1999. For each model is given the number of fitted parameters (as estimated by MARK), model fit (deviance) and relative parsimony (AIC). For model specification see text.

| Year | ABE | BAN | BEA | CAE | CON | LLA | LLJ | OGW | PEB | PEN | PEP | POR | RHO | SPF | TYC | WIG | Total | * |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1971/72 | | | | | | | | | | | | | | | 40 | | 40 | 0 |
| 1972/73 | | | | | 23 | | | | | | | | | | 9 | | 32 | 0 |
| 1973/74 | | | | | | | | 53 | | | | | | | | 21 | 74 | 74 |
| 1974/75 | | | | | | | | | | | | | | | 91 | | 91 | 0 |
| 1975/76 | | | | | | | | | | | | | | | 468 | | 468 | 0 |
| 1976/77 | | | 5 | | | | | 133 | | | | | | | | | 138 | 133 |
| 1977/78 | | | | | | | | 2 | | | 40 | | | | | | 42 | 2 |
| 1978/79 | | | | | | 1 | | | | | | | 1 | | | | 2 | 1 |
| 1979/80 | | | 1 | | | | | | | | | | 42 | | | 661 | 704 | 661 |
| 1980/81 | | 25 | | 5 | | | | 7 | | | | | | | | 16 | 53 | 23 |
| 1981/82 | | | 9 | 3 | | 53 | | 695 | 11 | | | 2 | | | | 6 | 779 | 754 |
| 1982/83 | 2 | 176 | 14 | 14 | | 66 | | 117 | | | | 7 | 29 | | 2 | 204 | 631 | 389 |
| 1983/84 | | 141 | | | | | 4 | 316 | | | | 7 | | | 237 | 36 | 741 | 352 |
| 1984/85 | | 135 | | | | | | 166 | 4 | 10 | | | | | | 7 | 322 | 173 |
| 1985/86 | | 73 | | 2 | | 24 | | 144 | | | 47 | | 4 | | | | 294 | 168 |
| 1986/87 | | 82 | | | | 50 | | 27 | | | | | 20 | | | 8 | 187 | 85 |
| 1987/88 | | 36 | | | | | | | | | 7 | | 15 | | | 118 | 176 | 118 |
| 1988/89 | | 140 | 1 | | | | | 246 | | | | | | | | 32 | 419 | 278 |
| 1989/90 | | 1 | | | | | | 373 | | | | | | | | | 374 | 373 |
| 1990/91 | | 95 | | | | | | 20 | | | | | | | | | 115 | 20 |
| 1991/92 | | 55 | | | | 68 | | 314 | | | | | 61 | | | | 498 | 382 |
| 1992/93 | | 47 | | | | | | 136 | | | | | | | | | 183 | 136 |
| 1993/94 | | 60 | | | | 20 | | 58 | | | | | | | | | 138 | 78 |
| 1994/95 | | 143 | 2 | | | | | | | | | | | | | | 145 | 0 |
| 1995/96 | | 50 | | | | | | 210 | | | | | | | | | 260 | 210 |
| 1996/97 | | 13 | | | | 5 | | 89 | | | | | 24 | | | | 131 | 94 |
| 1997/98 | | 67 | | | | 9 | | | | | | | | 114 | | | 190 | 123 |
| 1998/99 | | 59 | | | | 26 | | 259 | | | | | | | | 9 | 353 | 294 |
| 1999/00 | | 37 | | | | 98 | | 121 | | | | | | | | | 256 | 219 |
| 2000/01 | | 46 | | 7 | | 15 | | 103 | | | | | | | | | 171 | 118 |
| 2001/02 | | 90 | | | | 54 | | 414 | | | | | | | | 18 | 576 | 486 |
| 2002/03 | | 34 | | 1 | | 10 | | 267 | | | | | 20 | | | | 332 | 277 |
| 2003/04 | 4 | 72 | 1 | | | 24 | | 15 | | | | | | | | 6 | 122 | 49 |
| Total | 6 | 1677 | 33 | 32 | 23 | 523 | 4 | 4285 | 15 | 10 | 94 | 16 | 216 | 114 | 847 | 1142 | 9037 | 6070 |

**Table 4.2.1** Numbers of Redshank caught by the SCAN Ringing Group in relation to site and year (July to April). ABE = Aber; BAN = Bangor; BEA = Beaumaris; CAE = Caernarfon; CON = Conwy; LLA = Llanfairfechan; LLJ = Llandudno Junction; OGW = Ogwen; PEB = Penmon Beach; PEN = Penrhyn Bay; PEP = Penmon Pool; POR = Porthamel Hall; RHO = Rhos-on-Sea; SPF = Ogwen Estuary field; TYC = Tal-y-cafn; WIG = Wig; * = captures at ABE, LLA, OGW, SPF and WIG (the main area used in final analyses).

| Option | Sites | Recapture period (months) | Number of Redshank ringed (n) and re-trapped (r) in later winters | | | | Test 3.SR | Test 2CT |
|---|---|---|---|---|---|---|---|---|
| | | | Adult (n) | Adult (r) | 1st-year (n) | 1st-year (r) | | |
| 1 | All | Jul-Apr | 3,382 | 931 | 2,011 | 364 | z = 5.89, *P* < 0.0001, $\chi^2_{22}$ = 82.59, *P* < 0.0001 | z = 1.01, *P* = 0.3123, $\chi^2_{22}$ = 27.70, *P* = 0.1859 |
| 2 | Main | Jul-Apr | 2,949 | 905 | 1,879 | 358 | z = 5.73, *P* < 0.0001, $\chi^2_{22}$ = 74.46, *P* < 0.0001 | z = 0.79, *P* = 0.4299, $\chi^2_{22}$ = 24.90, *P* = 0.3018 |
| 3 | Main - Bangor | Jul-Apr | 2,634 | 675 | 1,434 | 208 | z = 3.48, *P* = 0.0005, $\chi^2_{20}$ = 36.39, *P* = 0.0138 | z = -0.40, *P* = 0.6912, $\chi^2_{19}$ = 15.32, *P* = 0.7023 |
| 4 | Main - Bangor | Sep-Mar | 2,404 | 562 | 1,246 | 185 | z = 2.35, *P* = 0.0187, $\chi^2_{19}$ = 20.11, *P* = 0.3882 | z = -0.29, *P* = 0.7698, $\chi^2_{19}$ = 12.65, *P* = 0.8560 |
| 5 | Main - Bangor | Oct - Feb | 2,019 | 342 | 988 | 135 | z = 1.30, *P* = 0.1926, $\chi^2_{13}$ = 7.50, *P* = 0.8747 | z = -0.83, *P* = 0.4042, $\chi^2_{12}$ = 8.12, *P* = 0.7761 |

**Table 4.2.2** Results of goodness-of-fit tests performed on Redshank mark-recapture data for north Wales.

| Year | BAN | BEA | CAE | CON | LLA | OGW | PEB | PEN | PEP | POR | RHO | SPF | TYC | WIG | Total | * |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1971/72 | | | | | | | | | | | | | 40 | | 40 | 0 |
| 1972/73 | | | | 23 | | | | | | | | | | | 23 | 0 |
| 1973/74 | | | | | | | | | | | | | | 16 | 16 | 16 |
| 1974/75 | | | | | | | | | | | | | 7 | | 7 | 0 |
| 1975/76 | | | | | | | | | | | | | 456 | | 456 | 0 |
| 1976/77 | | 5 | | | | 133 | | | | | | | | | 138 | 133 |
| 1977/78 | | | | | | 2 | | | 40 | | | | | | 42 | 2 |
| 1978/79 | | | | | 1 | | | | | | | | | | 1 | 1 |
| 1979/80 | | 1 | | | | | | | | | 42 | | | 495 | 538 | 495 |
| 1980/81 | 25 | | 5 | | | 7 | | | | | | | | | 37 | 7 |
| 1981/82 | | 9 | 3 | | 52 | 682 | 11 | | | 2 | | | | 6 | 765 | 740 |
| 1982/83 | 170 | 14 | 14 | | 30 | 2 | | | | 7 | | | 1 | 12 | 250 | 44 |
| 1983/84 | 141 | | | | | 1 | | | | 7 | | | 237 | | 386 | 1 |
| 1984/85 | 135 | | | | | | 4 | 10 | | | | | | 7 | 156 | 7 |
| 1985/86 | 73 | | 2 | | 24 | 11 | | | 47 | | 4 | | | | 161 | 35 |
| 1986/87 | 82 | | | | 50 | | | | | | 20 | | | | 152 | 50 |
| 1987/88 | 36 | | | | | | | | | | 4 | | | 118 | 158 | 118 |
| 1988/89 | 140 | 1 | | | | 117 | | | | | | | | 32 | 290 | 149 |
| 1989/90 | 1 | | | | | 187 | | | | | | | | | 188 | 187 |
| 1990/91 | 95 | | | | | 20 | | | | | | | | | 115 | 20 |
| 1991/92 | 55 | | | | 68 | 226 | | | | | 61 | | | | 410 | 294 |
| 1992/93 | 47 | | | | | 44 | | | | | | | | | 91 | 44 |
| 1993/94 | 60 | | | | 20 | 58 | | | | | | | | | 138 | 78 |
| 1994/95 | 62 | 2 | | | | | | | | | | | | | 64 | 0 |
| 1995/96 | 50 | | | | | 135 | | | | | | | | | 185 | 135 |
| 1996/97 | 13 | | | | 5 | 89 | | | | | 24 | | | | 131 | 94 |
| 1997/98 | 67 | | | | 9 | | | | | | | 114 | | | 190 | 123 |
| 1998/99 | | | | | 26 | 259 | | | | | | | | 9 | 294 | 294 |
| 1999/00 | 37 | | | | 59 | 121 | | | | | | | | | 217 | 180 |
| 2000/01 | 46 | | 7 | | 15 | 103 | | | | | | | | | 171 | 118 |
| 2001/02 | 90 | | | | 50 | 414 | | | | | | | | | 554 | 464 |
| 2002/03 | 17 | | 1 | | 10 | 267 | | | | | 20 | | | | 315 | 277 |
| 2003/04 | 72 | 1 | | | 20 | 15 | | | | | | | | | 108 | 35 |
| Total | 1514 | 33 | 32 | 23 | 439 | 2893 | 15 | 10 | 87 | 16 | 175 | 114 | 741 | 695 | 6787 | 4141 |

**Table 4.2.3** Numbers of Redshank caught between October and February by the SCAN Ringing Group in relation to site and year (See Table 4.2.1. for details of site codes).

| Model | $QAIC_c$ | Parameters | Model deviance |
| --- | --- | --- | --- |
| $\phi$c(ad = fy) pc(ad = fy) | 4920.77 | 2 | 1295.54 |
| $\phi$t(ad = fy) pc(ad = fy) | 4608.99 | 15 | 957.62 |
| $\phi$c(ad = fy) pt(ad = fy) | 4231.45 | 22 | 565.93 |
| $\phi$c(ad, fy) pt(ad = fy) | 4214.67 | 23 | 547.12 |
| $\phi$t(ad = fy) p(adt, fyt) | 4212.24 | 50 | 489.55 |
| $\phi$1(ad, fy) pt(ad = fy) | 4209.49 | 24 | 539.91 |
| $\phi$(adt, fyt) p(adt, fyt) | 4208.94 | 64 | 457.31 |
| $\phi$(ad1, fy1) pt(ad = fy) | 4204.78 | 25 | 533.18 |
| $\phi$t(ad = fy) pt(ad = fy) | 4204.59 | 38 | 506.52 |
| **$\phi$(adt, fyt) pt(ad = fy)** | **4204.09** | **55** | **471.10** |

**Table 4.2.4** Evaluation of mark-resighting models for Redshank for the Lavan Sands area of north Wales using data from the SCAN Ringing Group. Models evaluated whether annual survival rates ($\phi$) and resighting rates (p) were constant (c), showed a linear trend (l) or varied fully with time (t) or between age classes (ad = adult; fy = first-year). Bold type indicates the best-fit model (i.e. that with the lowest $QAIC_c$ value).

a) All year

| Year | BE | BU | FR | FS | GI | HB | HE | HO | LE | NW | SN | TE | TH | WA | WL | WR | Total |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1967/68 | | | | | | 286 | 7 | | | | 466 | 61 | | | | | 820 |
| 1968/69 | | | | | | | 7 | | | 63 | 229 | 141 | | | | | 440 |
| 1969/70 | | | | | | | 20 | | | 64 | 8 | 129 | | | 238 | | 459 |
| 1970/71 | | | | | | | 1 | | | | 25 | | | | 2 | | 28 |
| 1971/72 | | | | | | | 7 | | | | 32 | 14 | | | | | 53 |
| 1972/73 | | | | | | | | 14 | | 125 | 1 | 147 | | | 139 | | 426 |
| 1973/74 | 68 | | 7 | | | | 50 | | | 155 | 4 | | | | 29 | | 313 |
| 1974/75 | 165 | | 79 | | 8 | | 7 | 10 | | | 53 | 495 | | | 203 | | 1,020 |
| 1975/76 | | | 87 | | | | 111 | 3 | | | 286 | 858 | | 34 | 13 | | 1,392 |
| 1976/77 | 187 | | 162 | | | | | 26 | | | 76 | 115 | | 2 | 21 | | 589 |
| 1977/78 | 2 | | 97 | | | | 2 | 11 | | 37 | 70 | 62 | | | 8 | | 289 |
| 1978/79 | 68 | | | | 17 | | 19 | | | 154 | 4 | 150 | | 7 | 36 | | 455 |
| 1979/80 | | | 120 | | | | 2 | 7 | | | 3 | 50 | | | 106 | 18 | 306 |
| 1980/81 | 8 | | | | | | 7 | 3 | 67 | | | 204 | | | 45 | | 334 |
| 1981/82 | | 12 | | | | | | | 78 | | | 991 | 2 | | | | 1,083 |
| 1982/83 | | | | | | | 1 | | 37 | | 2 | 282 | | 2 | 8 | | 332 |
| 1983/84 | 73 | | 108 | | | | 1 | | 1 | | 3 | 20 | | | 9 | | 215 |
| 1984/85 | | | | | | | 3 | | | | 28 | 81 | | | | | 112 |
| 1985/86 | | 5 | 33 | | | | 3 | | | | 3 | 171 | | 32 | 13 | | 260 |
| 1986/87 | 13 | | | | | | | | 24 | | 7 | 69 | | | | | 113 |
| 1987/88 | | | 318 | | | | | | 30 | | | 449 | | | 4 | | 801 |
| 1988/89 | 35 | 75 | | | | | 33 | | | | 1 | 783 | | 1 | | | 928 |
| 1989/90 | 40 | | | 3 | | | 44 | | | | 2 | 8 | | | | 1 | 98 |
| 1990/91 | 17 | 2 | 10 | | | | | 2 | | | 2 | 323 | | | | | 356 |
| 1991/92 | | | | 11 | | | | | | | 9 | 54 | | 9 | | | 83 |
| 1992/93 | | 32 | | 1 | | | | | 1 | | | 12 | | | | | 46 |
| 1993/94 | | 1 | 14 | | | | 95 | 1 | | | 1 | 104 | | | | 25 | 241 |
| 1994/95 | | 9 | | | | | | | | | 2 | 11 | | | | | 22 |
| 1995/96 | | 2 | | | | | 51 | | 1 | | | 55 | | | 3 | 8 | 120 |
| 1996/97 | | 1 | 1 | | | | | | 1 | | | 47 | | | | 75 | 125 |
| 1997/98 | | 57 | | 5 | | | 12 | | 2 | | | 46 | | | 22 | | 144 |
| 1998/99 | | 22 | | | | | | | | | | 31 | | | | | 53 |
| 1999/00 | | | | | | | | | | | | 198 | | | 1 | | 199 |
| 2000/01 | | | | | | | | | 15 | | | 259 | | | | | 274 |
| 2001/02 | | | | | | | | | 4 | | 18 | 267 | | 3 | | | 292 |
| 2002/03 | | | | | | | | | | | | 313 | | | | | 313 |
| 2003/04 | | | | | | | 3 | | | | | 150 | | | | | 153 |
| Total | 676 | 218 | 1,036 | 20 | 25 | 286 | 486 | 77 | 261 | 598 | 1,335 | 7,150 | 2 | 90 | 900 | 127 | 13,287 |

**Table 4.3.1** Numbers of Redshank caught by the Wash Wader Ringing Group in relation to site: (a) all year (July to April) (b) in winter (October and February). BE = Benington; BU = Butterwick; FR = Friskney; FS = Freiston; GI = Gibraltar Point; HE = Heacham; HB = Holbeach; HO = Holme; LE = Leverton; NW = North Wootton; SN = Snettisham; TE = Terrington; TH = Thornham; WA = Wainfleet; WL = Wolferton; WR = Wrangle.

b) In winter

| Year | Benington | Butterwick | Friskney | Gibraltar | Heacham | Holme | Snettisham | Terrington | Thornham | Wolferton | Total |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 1967/68 | | | | | 6 | | | | | | 6 |
| 1968/69 | | | | | 6 | | | | | | 6 |
| 1969/70 | | | | | 6 | | 8 | | | | 14 |
| 1970/71 | | | | | 1 | | 25 | | | | 26 |
| 1971/72 | | | | | 7 | | 24 | | | | 31 |
| 1972/73 | | | | | | 12 | | 144 | | 3 | 159 |
| 1973/74 | 13 | | 7 | | 3 | | 4 | | | 1 | 28 |
| 1974/75 | | | 33 | 8 | | 10 | 48 | | | | 99 |
| 1975/76 | | | 29 | | 3 | 2 | 190 | 73 | | 1 | 298 |
| 1976/77 | | | | | | 26 | 67 | | | 4 | 97 |
| 1977/78 | | | | | 2 | 11 | 70 | | | 4 | 87 |
| 1978/79 | | | | 17 | 18 | | | | | 4 | 39 |
| 1979/80 | | | | | 1 | 7 | 1 | 3 | | 8 | 20 |
| 1980/81 | | | | | 7 | | | | | 3 | 10 |
| 1981/82 | | | | | | | | 145 | 2 | | 147 |
| 1982/83 | | | | | 1 | | 1 | | | 6 | 8 |
| 1983/84 | | | | | 1 | | 3 | | | 5 | 9 |
| 1984/85 | | | | | 2 | | 28 | | | | 30 |
| 1985/86 | | 5 | | | 3 | | 2 | | | 1 | 11 |
| 1986/87 | | | | | | | 7 | | | | 7 |
| 1987/88 | | | | | | | | | | 4 | 4 |
| 1988/89 | | | | | 1 | | 1 | 2 | | | 4 |
| 1989/90 | | | | | 5 | | 2 | 1 | | | 8 |
| 1990/91 | | | | | | 2 | 2 | 285 | | | 289 |
| 1991/92 | | | | | | | 9 | 19 | | | 28 |
| 1992/93 | | | | | | | | 4 | | | 4 |
| 1993/94 | | | | | 1 | 1 | 1 | 48 | | | 51 |
| 1994/95 | | | | | | | 2 | 11 | | | 13 |
| 1995/96 | | | | | | | | 9 | | 3 | 12 |
| 1996/97 | | 1 | | | | | | | | | 1 |
| 1997/98 | | 49 | | | 3 | | | 8 | | | 60 |
| 1998/99 | | | | | | | | 9 | | | 9 |
| 1999/00 | | | | | | | | 7 | | | 7 |
| 2000/01 | | | | | | | | 1 | | | 1 |
| 2001/02 | | | | | | | 18 | 63 | | | 81 |
| 2002/03 | | | | | | | | 40 | | | 40 |
| 2003/04 | | | | | 3 | | | 14 | | | 17 |
| Total | 13 | 55 | 69 | 25 | 80 | 71 | 513 | 886 | 2 | 47 | 1,761 |

**Table 4.3.1** (continued)

| Option | Ages considered | Recapture period (months) | Number of Redshank ringed (n) and re-trapped (r) in later winters | | Test | Age | |
|---|---|---|---|---|---|---|---|
| | | | n | r | | | |
| 1 | Adults & first-year birds | Jul-Apr | Adult = 4,652, First-year = 1,169 | Adult = 399, First-year = 42 | 3.SR | Adult | z = 0.83, *P* = 0.4064, $\chi^2_{20}$ = 15.35, *P* = 0.7560 |
| | | | | | 3.SM | Adult | $\chi^2_{10}$ = 5.33, *P* = 0.8683 |
| | | | | | 2.CT | Adult | z = 1.04, *P* = 0.3000, $\chi^2_{20}$ = 31.57, *P* = 0.0481 |
| | | | | | 2.CL | Adult | $\chi^2_{22}$ = 31.81, *P* = 0.0807 |
| | | | | | 3.SR | First-year | z = 3.68, *P* = 0.0002, $\chi^2_{14}$ = 6.42, *P* = 0.9548 |
| | | | | | 3.SM | First-year | $\chi^2_{2}$ = 0.00, *P* = 1.0000 |
| | | | | | 2.CT | First-year | z = 0.69, *P* = 0.4908, $\chi^2_{13}$ = 8.49, *P* = 0.8105 |
| | | | | | 2.CL | First-year | $\chi^2_{15}$ = 2.78, *P* = 0.9998 |
| 2 | No age classes | Jul-Apr | 5,852 | 452 | 3.SR | | z = 1.25, *P* = 0.2098, $\chi^2_{23}$ = 13.81, *P* = 0.9322 |
| | | | | | 3.SM | | $\chi^2_{11}$ = 9.79, *P* = 0.5491 |
| | | | | | 2.CT | | z = 1.43, *P* = 0.1541, $\chi^2_{22}$ = 33.41, *P* = 0.0563 |
| | | | | | 2.CL | | $\chi^2_{28}$ = 29.22, *P* = 0.4016 |

**Table 4.3.2** Results of goodness-of-fit tests performed on Redshank mark-recapture data for Terrington on The Wash.

| Year | Ri | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 | 29 | 30 | Total |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1974 | 483 | 31 | 12 | 4 | 10 | 0 | 2 | 10 | 2 | 1 | 0 | 1 | 0 | 3 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 79 |
| 1975 | 838 | | 14 | 3 | 11 | 2 | 7 | 22 | 3 | 0 | 0 | 2 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 66 |
| 1976 | 115 | | | 1 | 3 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 11 |
| 1977 | 61 | | | | 4 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 5 |
| 1978 | 150 | | | | | 1 | 1 | 14 | 3 | 0 | 0 | 0 | 0 | 5 | 3 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 28 |
| 1979 | 49 | | | | | | 0 | 3 | 4 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 8 |
| 1980 | 203 | | | | | | | 18 | 3 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 23 |
| 1981 | 904 | | | | | | | | 31 | 2 | 2 | 8 | 3 | 11 | 4 | 0 | 9 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 70 |
| 1982 | 280 | | | | | | | | | 3 | 0 | 6 | 0 | 3 | 9 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 23 |
| 1983 | 20 | | | | | | | | | | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 1984 | 81 | | | | | | | | | | | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 1985 | 171 | | | | | | | | | | | | 0 | 1 | 7 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 10 |
| 1986 | 69 | | | | | | | | | | | | | 3 | 2 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 8 |
| 1987 | 445 | | | | | | | | | | | | | | 58 | 0 | 4 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 66 |
| 1988 | 778 | | | | | | | | | | | | | | | 0 | 13 | 4 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 3 | 1 | 1 | 1 | 25 |
| 1989 | 8 | | | | | | | | | | | | | | | | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 |
| 1990 | 307 | | | | | | | | | | | | | | | | | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 2 | 0 | 0 | 0 | 4 |
| 1991 | 54 | | | | | | | | | | | | | | | | | | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 3 |
| 1992 | 12 | | | | | | | | | | | | | | | | | | | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 2 |
| 1993 | 103 | | | | | | | | | | | | | | | | | | | | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 3 |
| 1994 | 11 | | | | | | | | | | | | | | | | | | | | | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| 1995 | 55 | | | | | | | | | | | | | | | | | | | | | | 0 | 0 | 0 | 0 | 2 | 1 | 0 | 0 | 3 |
| 1996 | 47 | | | | | | | | | | | | | | | | | | | | | | | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 1997 | 43 | | | | | | | | | | | | | | | | | | | | | | | | 0 | 1 | 1 | 1 | 1 | 0 | 4 |
| 1998 | 31 | | | | | | | | | | | | | | | | | | | | | | | | | 0 | 2 | 2 | 0 | 0 | 4 |
| 1999 | 195 | | | | | | | | | | | | | | | | | | | | | | | | | | 7 | 5 | 1 | 0 | 13 |
| 2000 | 254 | | | | | | | | | | | | | | | | | | | | | | | | | | | 4 | 6 | 0 | 10 |
| 2001 | 259 | | | | | | | | | | | | | | | | | | | | | | | | | | | | 6 | 4 | 10 |
| 2002 | 301 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |

**Table 4.3.3** Numbers of Redshank ringed (Ri) and re-trapped each year at Terrington on The Wash. 1974 = 1974/75 etc.

| Model | $QAIC_c$ | Parameters | Model deviance |
|---|---|---|---|
| ϕc pc | 4887.11 | 2 | 926.29 |
| ϕt pc | 4642.65 | 15 | 655.75 |
| ϕl pt | 4372.30 | 29 | 357.20 |
| ϕc pt | 4370.28 | 28 | 357.21 |
| **ϕt pt** | **4353.09** | **39** | **317.78** |

**Table 4.3.4** Evaluation of mark-resighting models for Redshank caught at Terrington on The Wash by the Wash Wader Ringing Group. Models evaluated whether annual survival rates ϕ and resighting rates p were constant (c), showed a linear trend (l) or varied fully with time (t). Bold type indicates the best-fit model (i.e. that with the lowest $QAIC_c$ value).

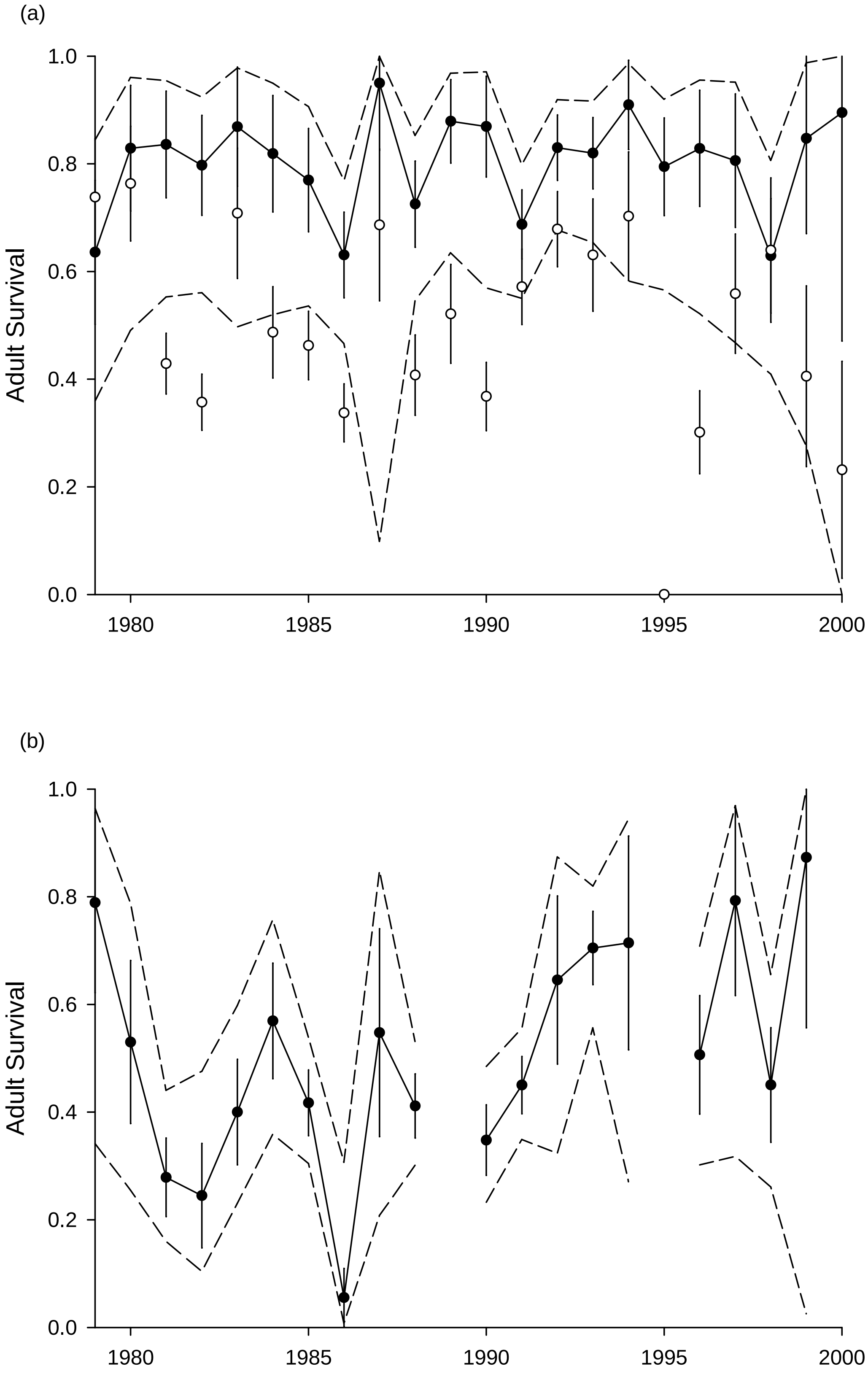



**Fig 3.2.1** Annual survival of (a) adult and (b) first-year Dunlin ringed in Poole Harbour 1978 to 2000. Dotted lines indicate 95% confidence limits, and bars 1 standard error. For adults the apparent survival rate in the first year is shown by the open symbols.

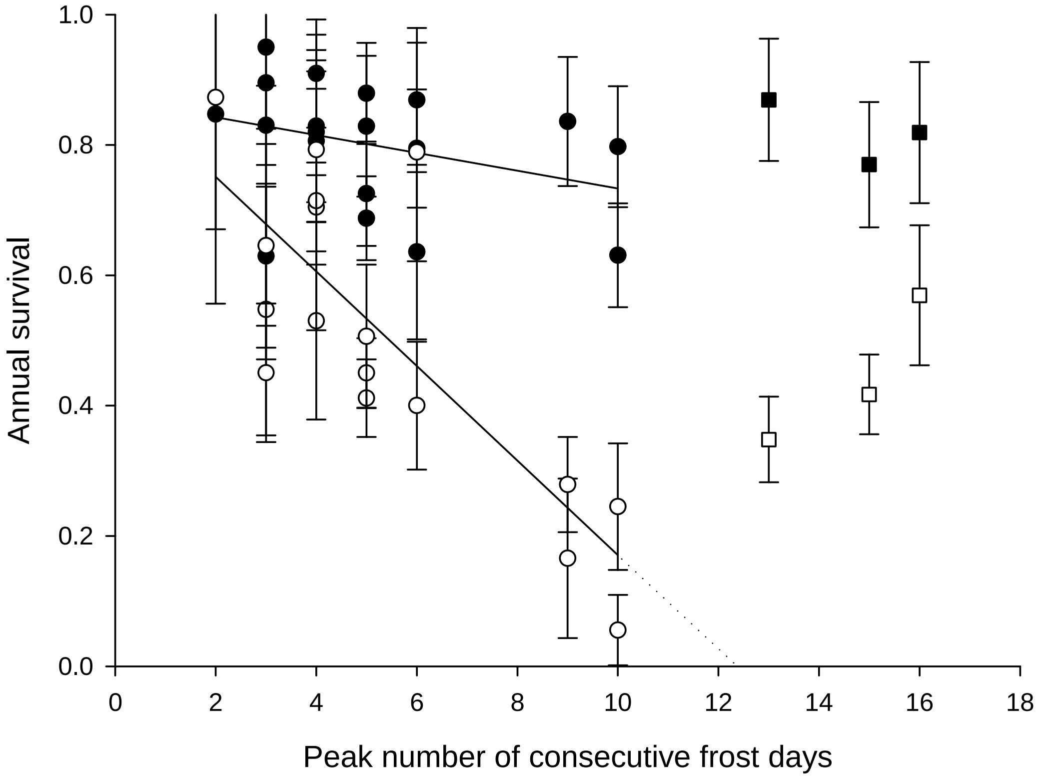



**Fig. 3.2.2** The effect of winter severity (as measured by the greatest number of consecutive days on which the minimum temperature was below 0˚C) on survival of adult (closed symbols) and first-year (open symbols) Dunlin in Poole Harbour. Regression lines are through the circles only (see text): adults $\phi = 0.869 - 0.013x$, $R^2 = 0.11$; first-years $\phi = 0.896 – 0.073x$, $R^2 = 0.65$. For all data: adults $\phi = 0.820 – 0.003x$, $R^2 = 0.02$; first-years $\phi = 0.676 – 0.027x$, $R^2 = 0.26$.

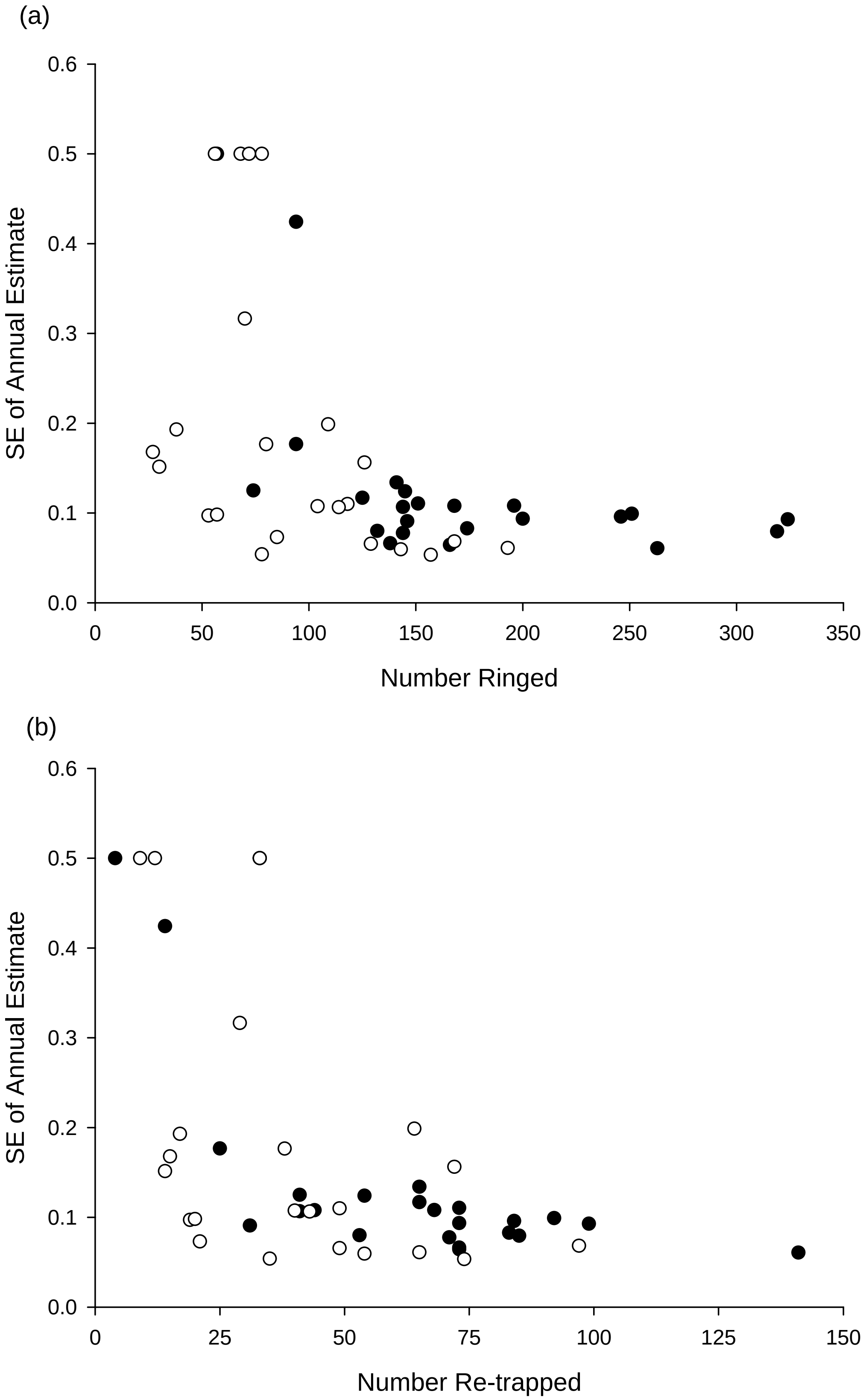



**Figure 3.2.3** Effect of (a) numbers of birds ringed each year and (b) number of birds re-trapped each year on the precision of annual survival rate estimates for adult (closed symbols) and first-year (open symbols) Dunlin caught in Poole Harbour. Note SE = 0.5 indicates a boundary estimate was obtained as data were too sparse to estimate a survival for that year.

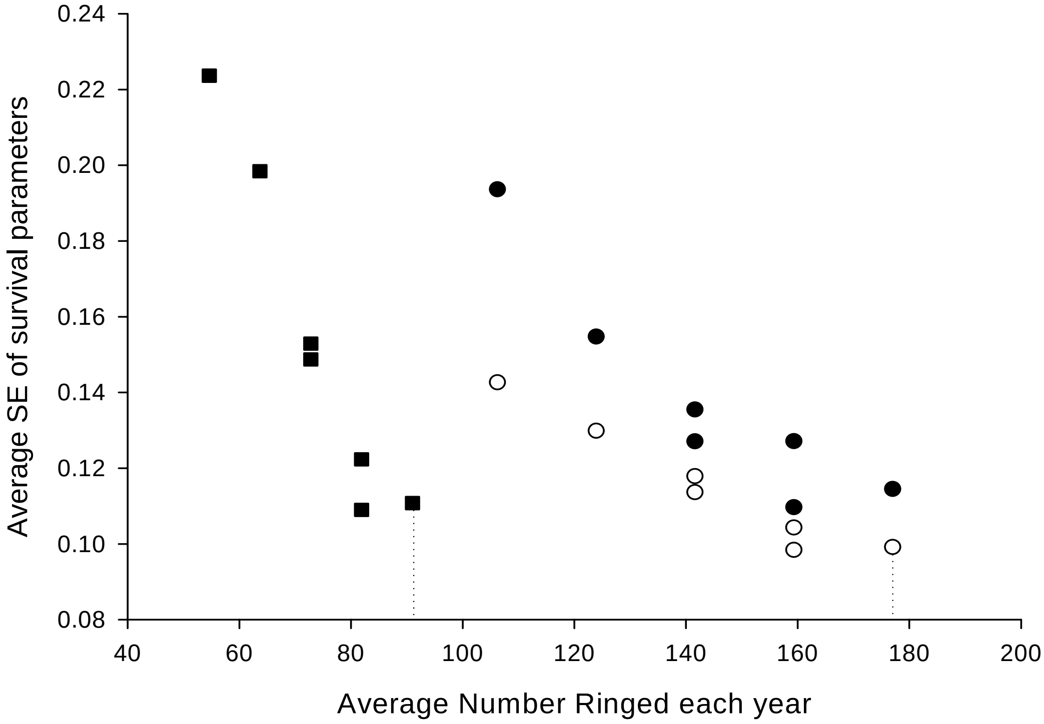



**Figure 3.2.4** Variation about survival rate estimates in relation to number of adult (circles) and first-year (squares) Dunlin ringed each year in Poole Harbour. For adults variability in survivals during the first year following capture (open circles) is differentiated from that in all subsequent years (closed symbols). Each point represents an analysis of the dataset with a proportion of the data removed (i.e. simulating fewer ringing/re-capture events to give the number ringed each year on the x axis); dotted lines indicate the full dataset (i.e. where no data have been removed).

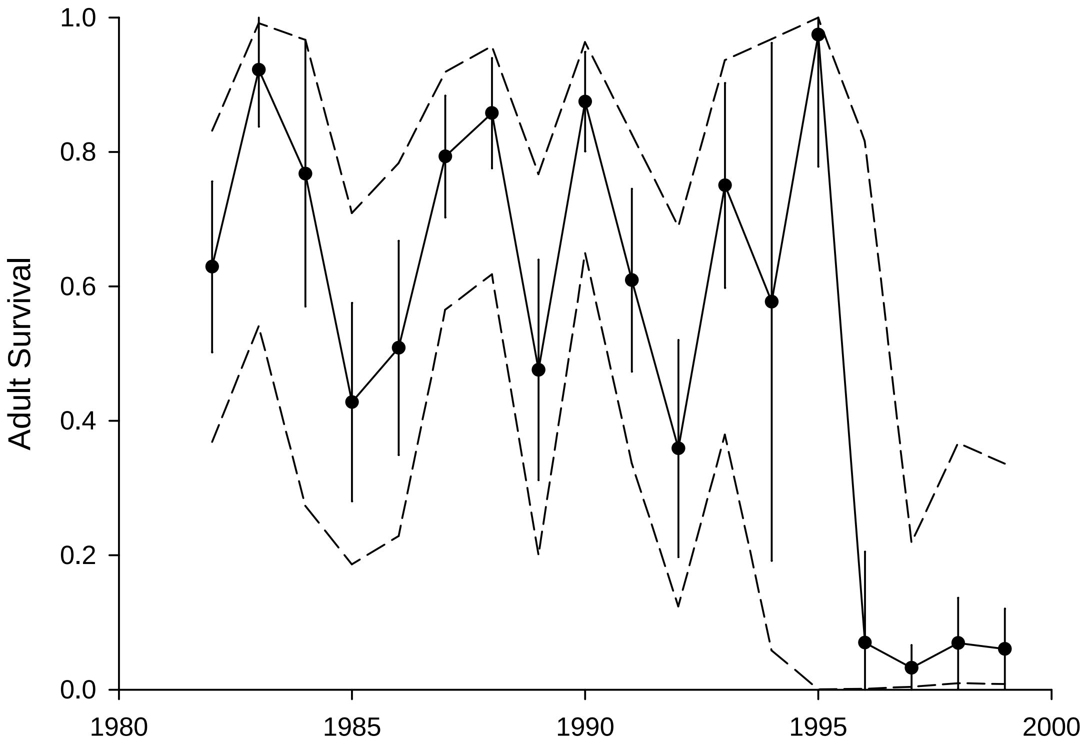



**Figure 3.3.1** Annual survival of adult Dunlin ringed on The Wash 1982-1999. Dotted lines indicate 95% confidence limits, and bars 1 standard error.

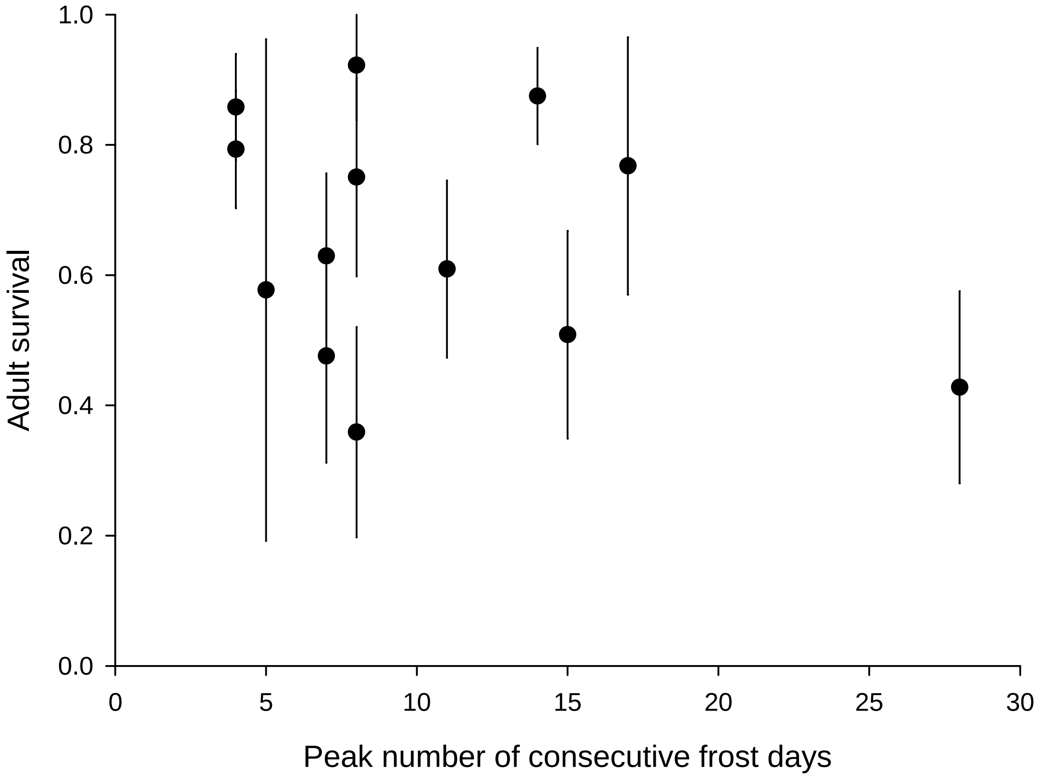



**Figure 3.3.2** The effect of winter severity (as measured by the greatest number of consecutive days on which the minimum temperature was below 0˚C) on the survival of adult Dunlin on The Wash 1982-1994.

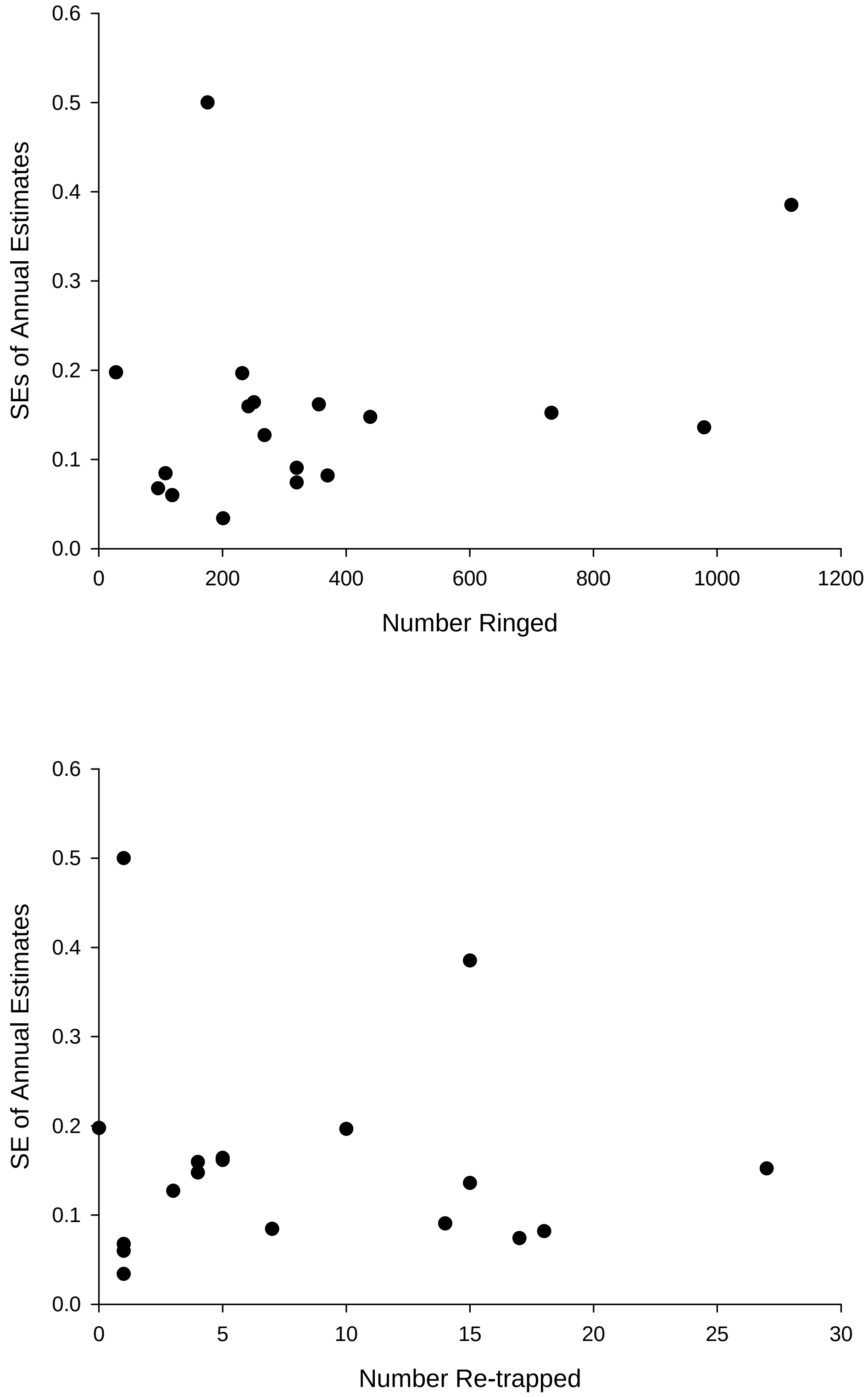



**Figure 3.3.3** Effect of (a) numbers of birds ringed each year and (b) number of birds re-trapped each year on the precision of annual survival rate estimates for adult Dunlin caught on The Wash. Note SE = 0.5 indicates a boundary estimate was obtained in that year.

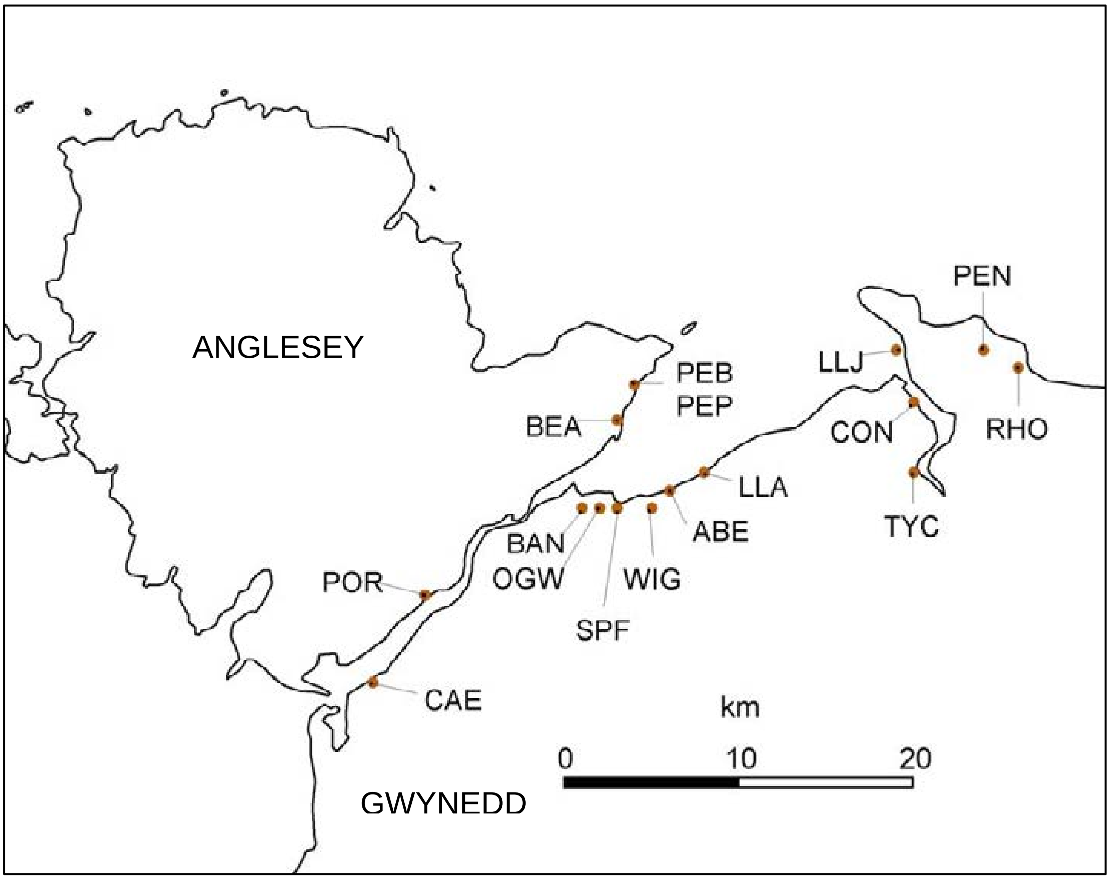
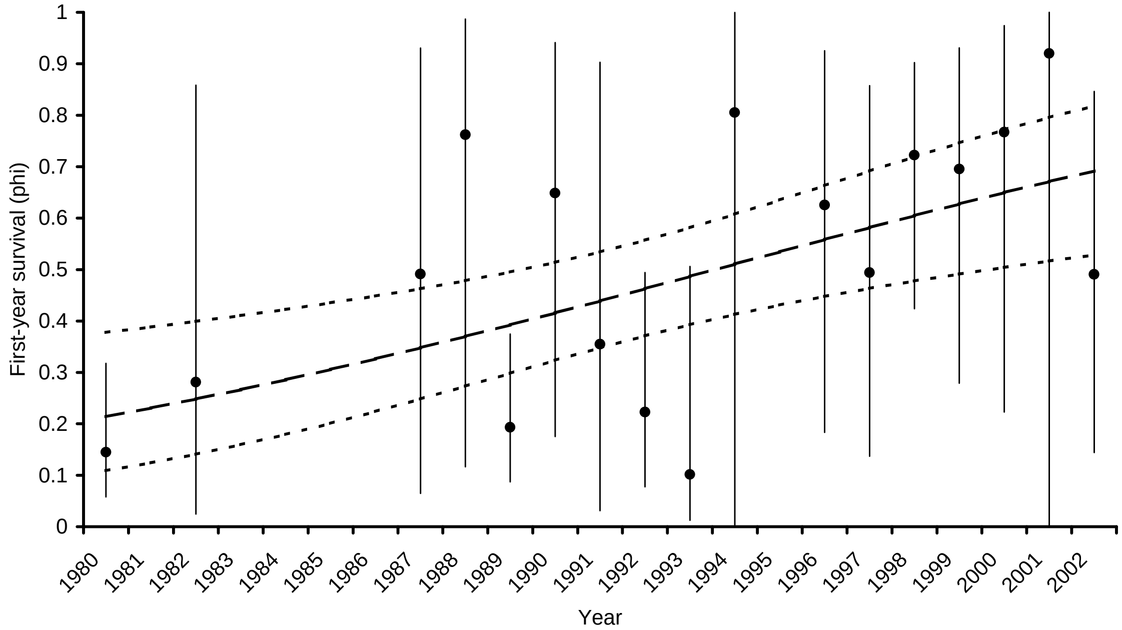



**Figure 4.2.1** Sites in north Wales where Redshank have been caught by the SCAN Ringing Group. ABE = Aber; BAN = Bangor; BEA = Beaumaris; CAE = Caernarfon; CON = Conwy; LLA = Llanfairfechan; LLJ = Llandudno Junction; OGW = Ogwen; PEB = Penmon Beach; PEN = Penrhyn Bay; PEP = Penmon Pool; POR = Porthamel Hall; RHO = Rhos-on-Sea; SPF = Ogwen Estuary field; TYC = Tal-y-cafn; WIG = Wig.

(a)




(b)

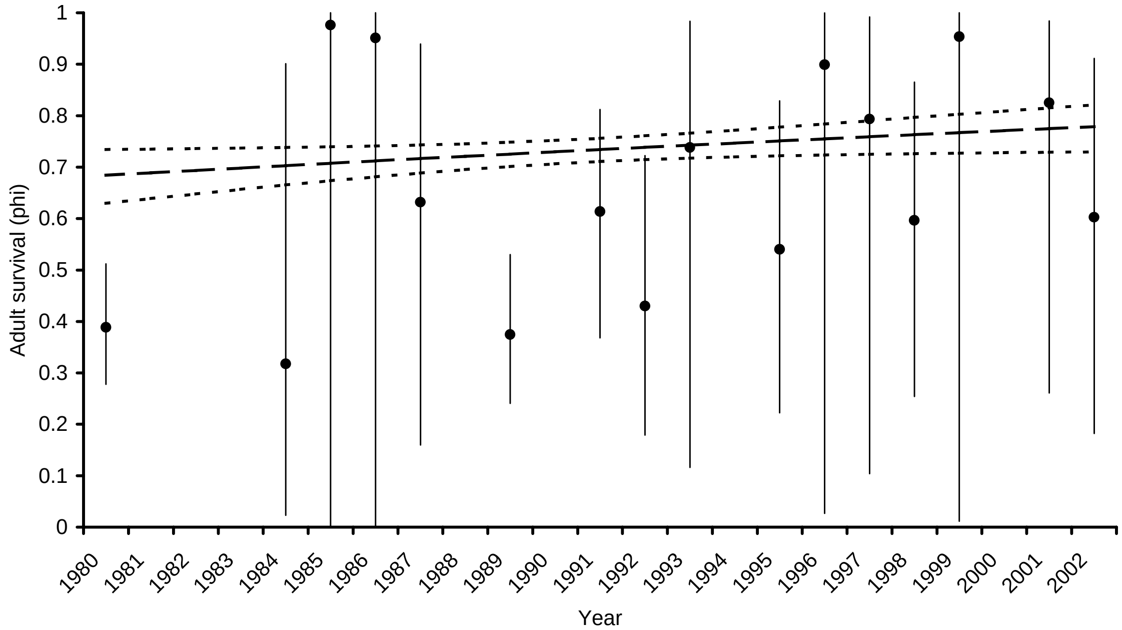



**Figure 4.2.2** Annual variation in (a) first-year and (b) adult survival of Redshank in the Lavan Sands area of north Wales, using SCAN Ringing Group data. Estimates are taken from the final model in Table 4.2.4 and shown with 95% confidence limits. Dashed lines (also with 95% confidence limits) indicate (significant) trends through time.

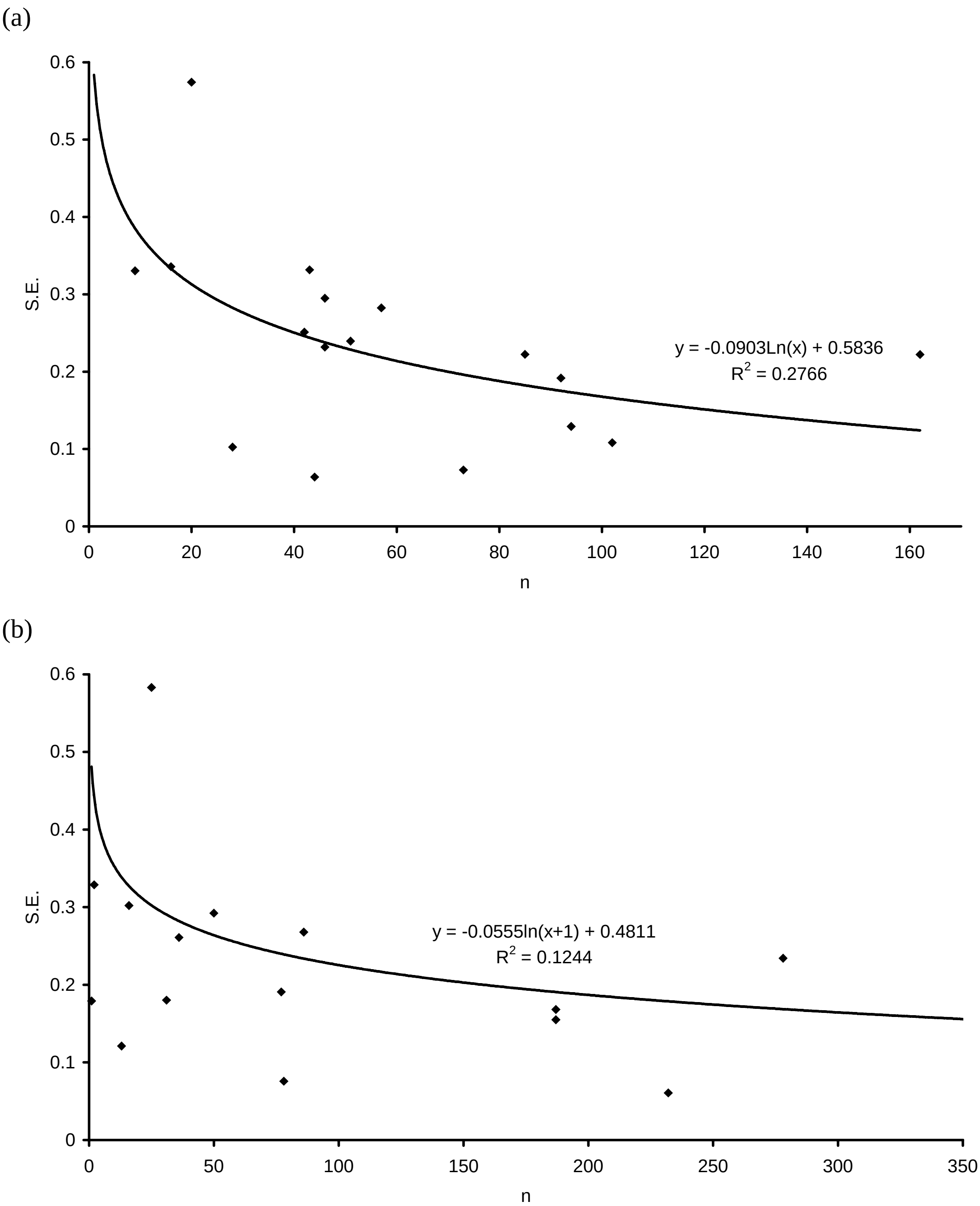
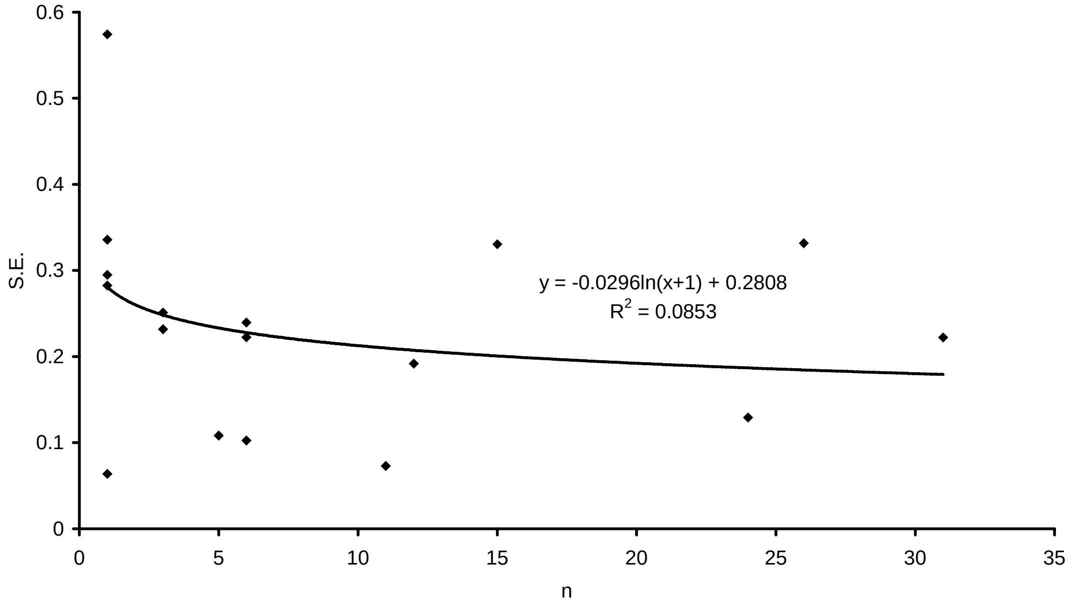



**Figure 4.2.3** Relationship between the standard error of (a) first-year and (b) adult Redshank survival rates and the numbers of birds caught at the start of the period; birds caught at Lavan Sands by the SCAN Ringing Group.

(a)




(b)

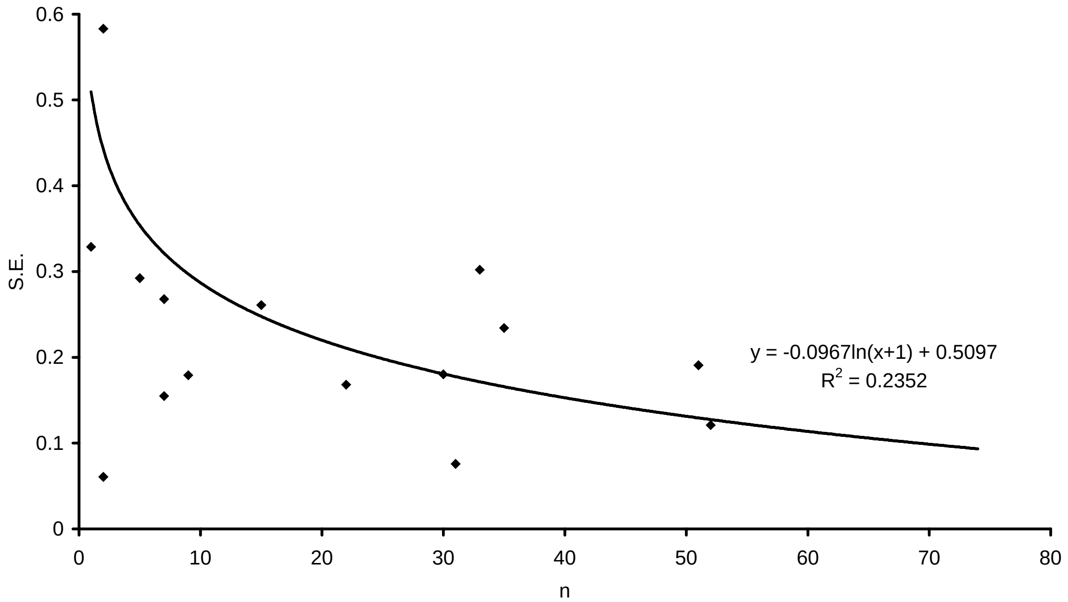



**Figure 4.2.4** Relationship between the standard error of Redshank survival rates and the numbers of birds re-trapped each year for (a) first-year and (b) adult Redshanks; birds caught at Lavan Sands by the SCAN Ringing Group.

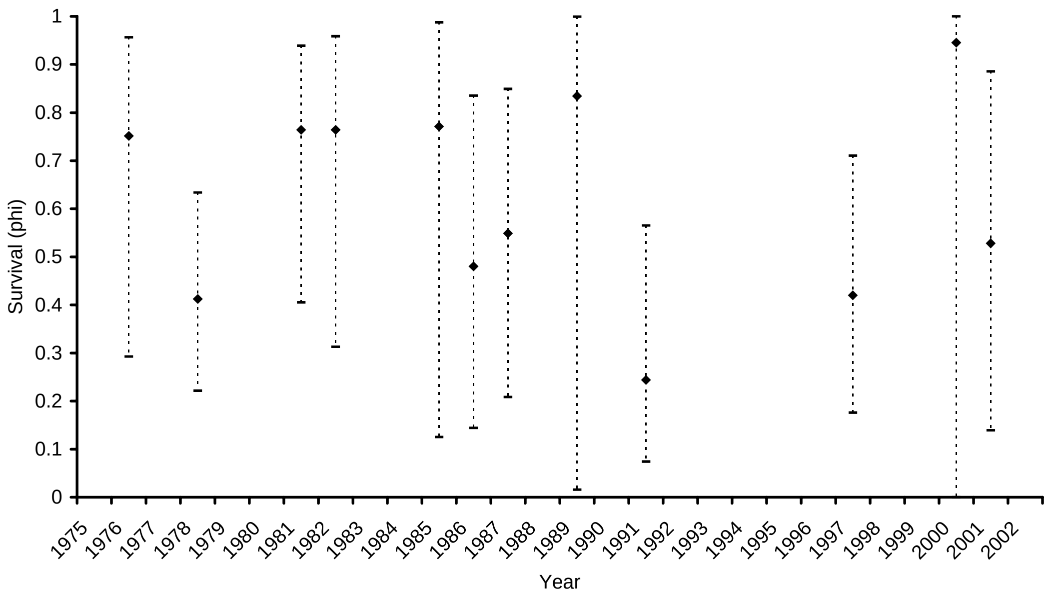



**Figure 4.3.1** Annual variation in the survival of Redshank caught at Terrington on The Wash by the Wash Wader Ringing Group. Estimates are taken from the final model in Table 4.3.4 and shown with 95% confidence limits.

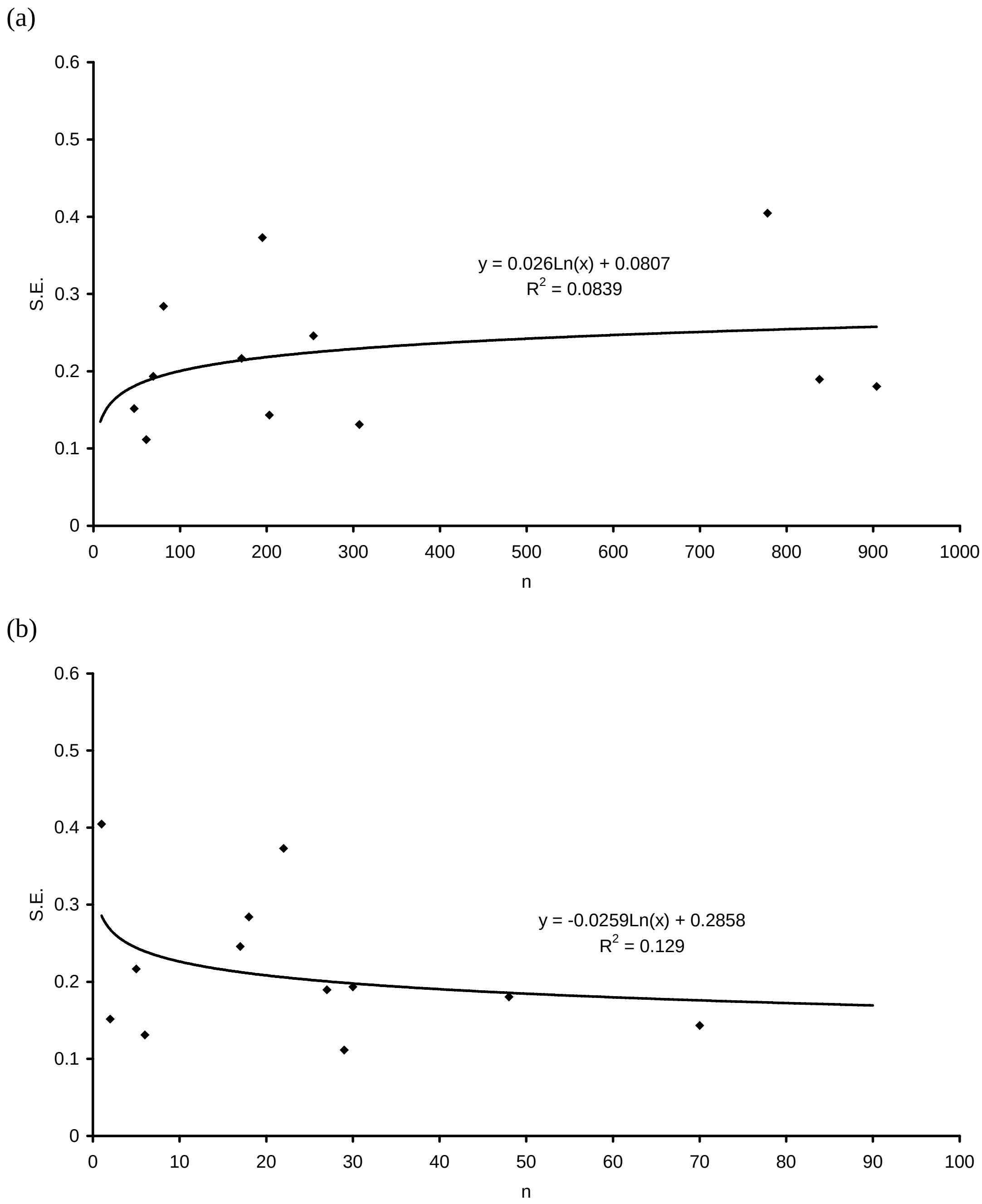



**Figure 4.3.2** Relationship between the standard error of Redshank survival rates and the numbers of birds (a) ringed and (b) re-trapped at the start of the period; birds caught at Terrington by the Wash Wader Ringing Group.

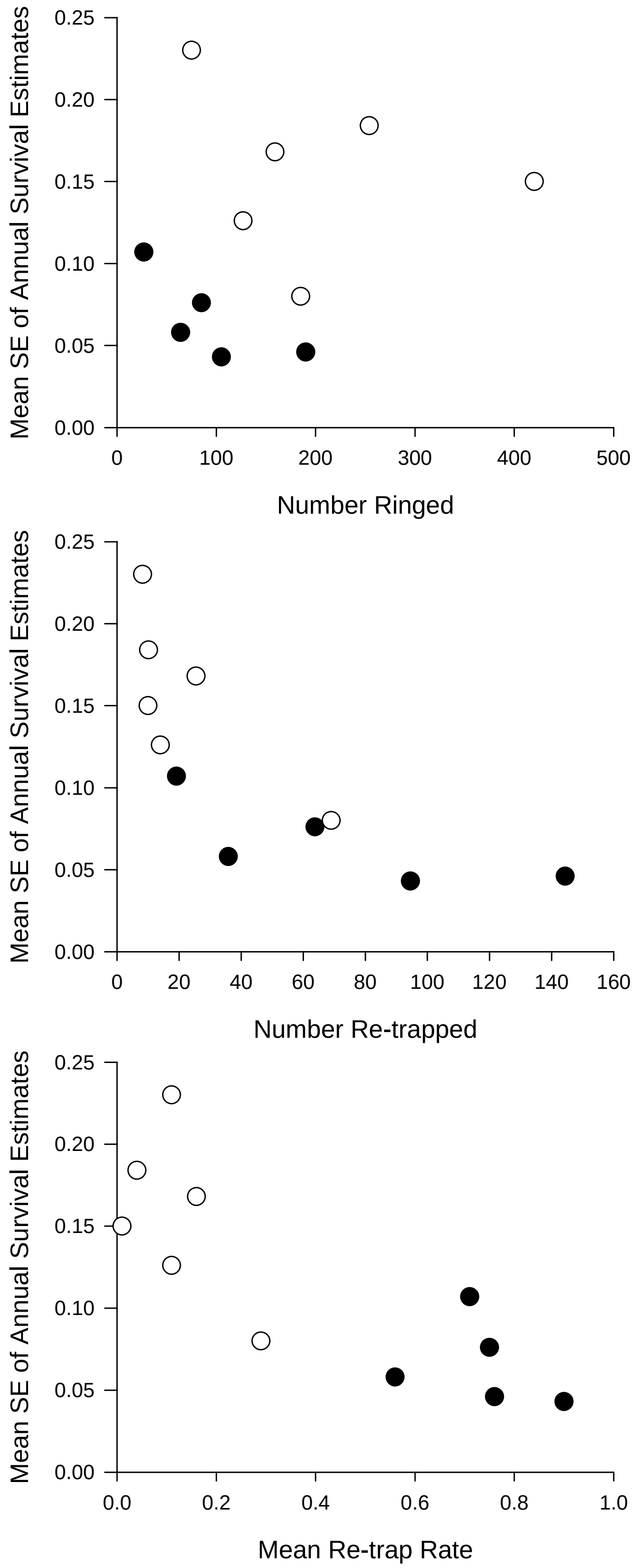



**Figure 5.1.1** Precision of survival estimation for Dunlin (expressed as mean standard error of the annual estimates) in relation to (a) the average number of birds ringed each year, (b) the average number re-trapped or re-sighted each year, and (c) the mean re-capture/re-sight rate. Mark-recapture studies are denoted by open symbols, those involving re-sightings of colour-ringed individuals by closed symbols.

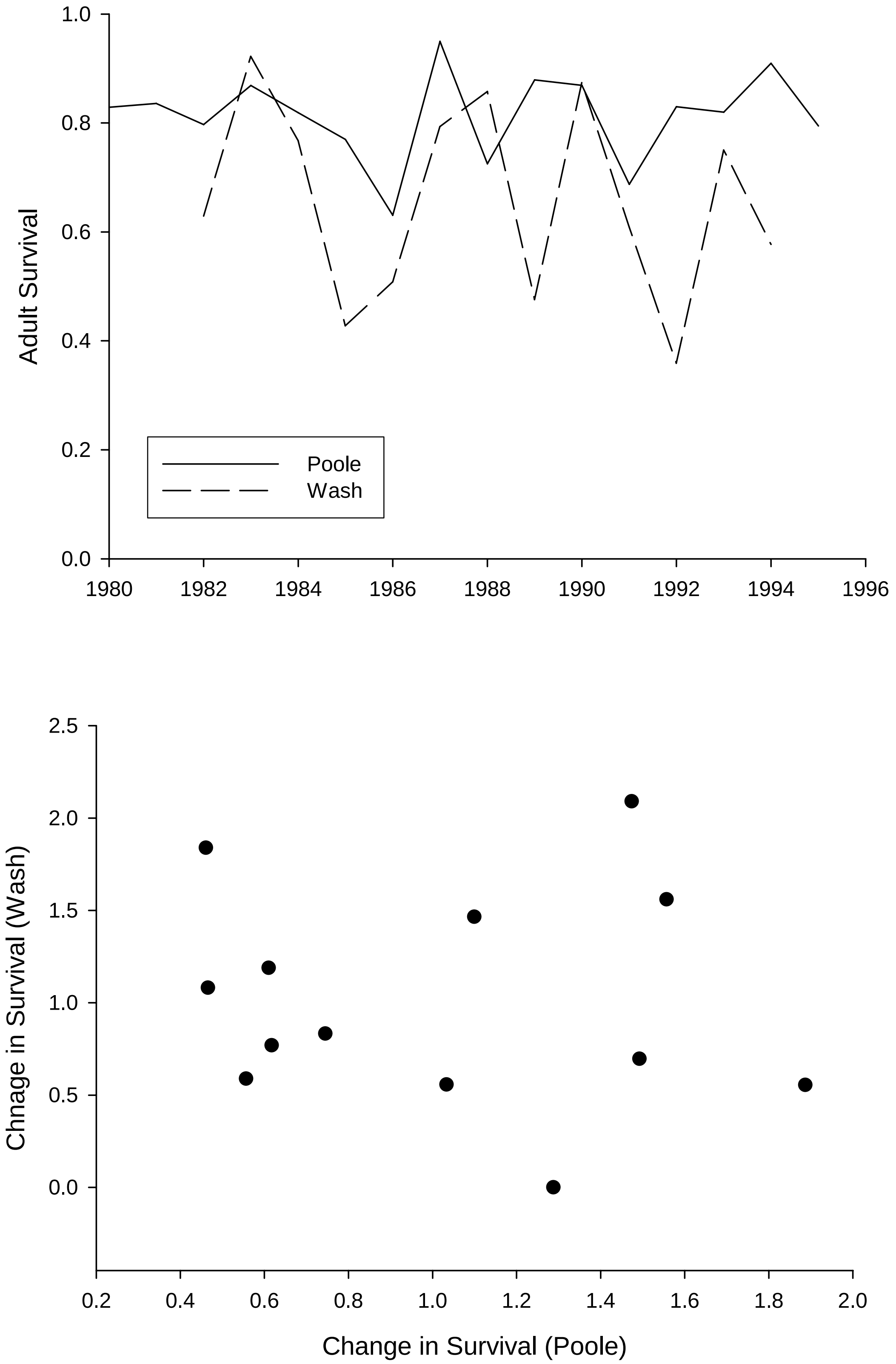



**Figure 5.3.1** Similarity in adult survival estimates in Dunlin caught in Poole Harbour and The Wash. (a) Annual estimates of adult survival (b) Change in survival between consecutive years.