BTO Research Report No.307

Arrival and weight gain of Red Knot *Calidris canutus*, Ruddy Turnstone *Arenaria interpres* and Sanderling *Calidris alba* staging in Delaware Bay in spring

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This report was funded by the Delaware Coastal Programs pursuant to
United States National Oceanic and Atmospheric Administration
Award No.NA170Z1117

February 2003

British Trust for Ornithology, The Nunnery, Thetford, Norfolk, IP24 2PU
Registered Charity No. 216652

British Trust for Ornithology

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Published in February 2003 by the British Trust for Ornithology
The Nunnery, Thetford, Norfolk, IP24 2PU, UK

ISBN 1-902576-52-7

CONTENTS

EXECUTIVE SUMMARY

1. Delaware Bay is an important spring staging area for shorebirds migrating north along the eastern American coast, with birds relying heavily on Horseshoe Crab *Limulus polyphemus* eggs during their stay. While many species use the Bay, three species are of particular interest: Red Knot *Calidris canutus*, Ruddy Turnstone *Arenaria interpres* and Sanderling *Calidris alba*.

2. This report analyses patterns of weight gain in these three species of shorebirds over a six year period between 1997 and 2002. Birds were caught in May of each year on both the Delaware and New Jersey sides of the Bay using cannon nets.

3. A total of 10,118 Red Knot, 10,203 Ruddy Turnstone and 7,768 Sanderling were caught, of which 9,692, 10,106 and 7,755, respectively, were weighed.

4. Virtually all birds caught, of each species, were adult (*i.e.* at least two years old); in each case <2% were in their first calendar year.

5. The average weight of birds increased through the month. The mean (± 1 standard error) arrival weights of birds were: Red Knot 112 ± 4g, Ruddy Turnstone 99 ± 1g and Sanderling 53 ± 1g. During their stay, Red Knot gained in weight by an average of 61 ± 7g, Turnstone 58 ± 4g and Sanderling 38 ± 7g. This rate of increase, however, was not linear, but rather followed a logistic growth pattern, with the period of greatest weight gain being in the middle of May, with the exact dates varying between species.

6. There was much variation in the rate of weight gain and many birds, particularly those arriving later were able to put on weight at a faster rate than indicated by the average. In some cases, the rate gain exceeded $12g.day^{-1}$.

7. Analysis of the frequency distributions of the weights of Red Knot caught showed that, in most years, there was a first arrival around May 10 followed by a second main arrival around May 20.

8. In 1998, when most birds arrived in a single cohort, virtually all (95%) birds had achieved the 'target' weight of 180g by May 25 leaving a few days buffer, before the 'normal' departure date of May 28.

9. In most other years, most birds that arrive in these two cohorts are likely to make the 'target' weight. However, there was evidence of an increased frequency of lighter than expected Red Knot in 2001 and 2002.

10. In 2002, although most (84%) of those arriving in the early cohort were predicted to have achieved their target weight by May 28, only a minority (42%) of the birds arriving in the second cohort had, despite a faster rate of weight gain.

11. A total of 125 Red Knot were re-trapped in the same year as their original capture. Analyses of these data came to similar conclusions to the cohort analysis. It predicted that Red Knot arriving before the May 16 would be likely to reach 180g by the May 28 but those arriving after this date would not, even though they gained weight at a faster rate.

12. Ruddy Turnstone and Sanderling followed a similar weight gain schedule to the Red Knot. Turnstone put on about 55%, on average, of their initial body weight during their stay in Delaware Bay (a similar relative weight gain to that in Red Knot), whereas Sanderling put on 70% of their arrival weight. Sanderling put on weight relatively slowly (peak weight gain, 4.5 ± 1.3 $g.day^{-1}$), whereas Ruddy Turnstone are able to put weight much faster (7.2 ± 1.1 $g.day^{-1}$).

13. Analyses of the weight gain in individual years revealed significant variation between years for Turnstone but not for Sanderling. Analysis of the Red Knot data was complicated by the presence

of multiple cohorts in each year, however, there was little evidence that the amount of weight gained by each cohort had declined substantially during the years of the study period.

14. Between 1999 and 2002, 30%-50% of the birds caught on May 23/24 in each year could be assigned to the second cohort (1999 43%, 2000 50%, 2001 30%, 2002 44%). In 1998, most birds seem to have arrived as a single cohort in early May, with only 17% of birds assignable to the second cohort. In 2002, though, a large number of birds arrived late; the continued presence of low weight birds suggests birds may even have been arriving as late as May 26/27.

15. It is also notable that birds in the later arriving cohorts gained a similar amount of weight as the early arriving birds. To do this, the late arriving birds must have put on weight at a faster rate. This was clearly so in 2002, when the early birds put on weight at a peak rate of around 4.5g day^{-1} whereas birds in the second cohort appeared to put on weight at nearly three times this rate.

16. The implications of a substantial portion of the Red Knot population not reaching target weight in some years and the cost to the individual of putting on weight at very high levels is discussed. Such costs may be indirect and the effects may be manifested at other points in the life cycle, for example, in reduced survival breeding success.

17. Possible reasons for the increasing portion of the population that is arriving later in Delaware bay in recent years are discussed however no firm conclusions could drawn from the trends in the data over the last six years.

18. Possible biases in the data are discussed and it is concluded that none of these could account for the observed trends in the data over the last six years.

1. INTRODUCTION

Delaware Bay is one of the most important sites for migratory shorebirds in the world, having been identified as a primary staging area on the Eastern American flyway. During the spring it hosts up to one million birds who use the littoral resources in the Bay on their northward migration from wintering grounds in South America to the breeding grounds in the arctic (Botton *et al.* 1994). Following the identification of conflicts between the use of Horseshoe Crabs *Limulus polyphemus* by the birds and a currently declining fishery, the Delaware Coastal Program of the Delaware Department of Natural Resources and Environmental Control have instigated a programme of population monitoring of the key shorebird species using the Bay. This has five main goals, of which two are addressed in this report: (1) to monitor arrival and departure times of Red Knot *Calidris canutus*, Ruddy Turnstone *Arenaria interpres* and Sanderling *Calidris alba*, and (2) to monitor whether these species can accumulate sufficient reserves to migrate to the breeding grounds and breed successfully (Carter *et al.* 2002).

Red Knot are highly migratory breeding in the high arctic and spending the winter, either in low temperate northern latitudes or in the southern hemisphere. On their spring journey north, a major proportion of the American flyway population stages in Delaware Bay, before making the final journey to their breeding grounds in arctic Canada. During their stay in Delaware Bay, which typically spans three to four weeks in May, birds feed on the eggs of Horseshoe Crabs, almost doubling their lean body mass with fat deposits for the 3 000 km journey north. To achieve this, the rate at which they lay down fat deposits is amongst the highest recorded in the avian world.

There is concern that the flyway population of Red Knot has declined markedly in the last few years (Brown *et al.* 2001) and one hypothesis advanced to explain this is that birds are leaving Delaware Bay in lower weight or poorer condition resulting in depressed survival or productivity on the breeding grounds. This could be because Red Knot are arriving in the Bay later, thus giving them a shorter time-window to put on weight, or that the rate at which they are able to put on weight during their brief stay has declined. In recent years, the harvest of Horseshoe Crabs has decreased from a peak of around three million in 1997 to one million in 2001. The scale of the harvest was such that this has lead to for calls for the closure of the fishery to ensure that the population of Horseshoe Crab does not decline to a level where it cannot support the migratory bird populations that depend on them.

Substantial populations of Ruddy Turnstone and Sanderling also stage in Delaware Bay at the same time. These are also arctic breeders, with birds wintering from the southern United States through to southern South America. Although these birds also rely heavily on the eggs of Horseshoe Crabs for food, there is not currently the same concern over population levels. Thus, although we consider all three species in this report, we focus on the Red Knot.

In this report, we analyse patterns of weight gain over a period of six years (1997-2002) to determine whether the ability of birds to put on sufficient weight for their final flight north has deteriorated. We also aim to distinguish between the hypotheses that any changes are caused by birds arriving later or because overall rates of weight increase have declined. These two hypotheses are not mutually exclusive.

2. METHODS

Birds, of all species, were cannon-netted on beaches on both the Delaware and New Jersey sides of Delaware Bay. After capture, all birds were extracted from the net into keeping cages where they awaited processing. All birds were banded with individually numbered rings and most also had colour bands indicating site and year of capture applied. Virtually all birds were weighed (using either an electronic balance or a Pesola spring balance); for a proportion of bird's wing length (maximum chord), culmen length, total head + bill length were also recorded. A number of birds were also scored for the extent of summer plumage present, based on a seven-point scale (Table 1). All birds were processed and released within four hours of capture.

Patterns of weight gain were analysed by two complementary methods: an analysis of mean weights of birds captured by cannon-netting and an analysis of birds which were caught more than once in a season. Since the number of birds re-trapped was small for each species (<2% of all birds caught) the two analyses can be considered independent. Although an individual's weight varies with body size (here approximated by wing length) and initial analysis (presented below) for Red Knot suggested that such variation did not introduce systematic biases in the data. As wing lengths were not available for all birds, weights are presented uncorrected for body size, unless stated otherwise.

Individual Red Knot cohorts were identified with techniques for decomposing multiple Gaussian curves using the FAO-ICLARM Fish Stock Assessment Tools package (FiSAT, Gayanilo & Pauly 1997). Individual cohorts were initially identified using the graphical method of Bhattacharya (1967) and separated using a maximum likelihood method (Pauly & Caddy 1985).

3. RESULTS

A total of 95 catches of Red Knot were made during May between 1997 and 2002, of which 52 yielded more than 50 birds, with multiple catches on the same day were treated as one (Appendix 1). Note that, for convenience, the very few catches made in the first few days of June in some years are referred to as having been caught in May, for example a catch on the June 1 is referred to as May 32. Individually numbered bands were put on 10,118 birds and 9,692 were, at least, weighed. Additionally, a total of 10,203 Ruddy Turnstone and 7,768 Sanderling were caught, of which 10,106 and 7,755, respectively, were weighed.

Most of the Red Knot caught were adults (*i.e.* in their second year after hatching, coded ASY) and the few juvenile birds (*i.e.* known to be in their second calendar year from hatching, coded SY) identified tended to retain much of their winter plumage. The weight of individual birds was dependent on their body size (Fig. 1). There were statistically significant differences in wing length between sides of the Bay (GLM with log link: $\chi^2_1 = 90.94$, $p < 0.0001$), between years ($\chi^2_5 = 111.1$, $p < 0.0001$) and through the month ($\chi^2_1 = 26.02$, $p < 0.0001$), however, differences in mean wing length were slight, generally being less than 2mm. Although juvenile birds (mean ± 1 standard deviation 132g ± 17, n = 30) tended to be lighter than adult birds (153g ± 28, n = 2143), once variation in day and wing length was accounted for (Fig. 1), the difference was not significant ($\chi^2_1 = 2.11$, $p > 0.1$). Similarly, virtually all (> 98%) of the Ruddy Turnstone and Sanderling caught that were aged were adult birds, as might be expected for birds that do not breed in their first year. Most Ruddy Turnstone, even the few 2nd year birds were in close to full summer plumage (Table 2), whereas most sanderling (>80%) were still moulting into their summer plumage (plumage scores mostly in the range of a quarter to three-quarters summer plumage).

3.1 Weight gain of Red Knot cohorts

The weight distribution of Red Knot caught varied between days and years, with birds tending to weigh less earlier in the month (Appendix 3). Inspection of the frequency distributions by catch showed that the distribution of individual weights was largely static for catches before the May 11 and similar between years. This weight frequency distribution (without correction for body size) was essentially log-normal and is likely to accurately reflect the weights of Red Knot as they arrive in Delaware Bay from staging grounds further South (Fig. 2a). The average weight of birds increased through the month. The mean (± 1 standard error) arrival weight of birds (corrected for body size) was 114.9g ± 1.6 and during their stay, average weight increased by 70.3g ± 3.6 (Fig. 2b). This rate of increase, however, was not linear, but rather followed a logistic growth pattern, with the period of greatest weight gain being between May 12 and May 26.

From the initial distribution of weights (Fig. 2a), and the average rate of weight change (Fig. 2b), the expected distribution of weights of this initial cohort can be calculated for any given day. This method accounts for individual variation in weight, but assumes growth is deterministic, and also constant across years. Although the assumption of deterministic growth should not bias the interpretation of the data, it does mean that small deviations of the observed weight distributions from those expected by this method are probably not biologically relevant. There is no evidence that growth rates varied significantly between years (Table 4, and see below). Comparison of these predicted distributions, with those actually caught (Appendix 4) clearly shows that more than one cohort is present in the cannon net samples. These cohorts are characterised by different arrival dates. In particular, in most years the first substantial arrival occurs around May 10 (when the first catches are made), with a subsequent arrival around May 20. The relative number of Red Knot weighing less than would be expected assuming an arrival date of May 11 has increased through time (Fig. 3). This suggests that more birds are arriving after this date. The increase has been similar in the first and second half of May, suggesting that individuals in both the first (arriving *c.* May 10) and second (arriving *c.* May 20) cohorts are arriving later than has been the case, certainly in the early years of the study.

In general, Red Knot cohorts gain weight according to a logistic curve, although in some years (and cohorts) only a linear change in weight is detected (Fig. 4), which might reflect a relative lack of early and late catches. Despite the presence of a number of cohorts, the overall pattern of weight gain is remarkably consistent between cohorts. In general, Red Knot arrive from their wintering grounds or staging sites further South weighing around 120g and put on 70g to 80g during their stay, and in many cases will put on in excess of 10g day^{-1} (Table 3). Although arrival date varies, the system appears to have an inbuilt buffer allowing later arriving birds to put on weight faster (Table 3); the consequences of this will be discussed below.

In order to reach the breeding grounds successfully, Baker et al. (in press) suggested that individual Red Knot needed to leave Delaware Bay weighing approximately 180g. The number of birds that reach this target weight varies between years (Fig. 5). In 1998, when most birds arrived in a single cohort (Fig. 4) virtually all (95%) birds had achieved the 'target' weight of 180g by May 25 leaving a few days buffer to re-ingest their gut and associated material, before the 'normal' departure date of May 28 (pers. obs.). In 2002, in contrast, although most (84%) of those arriving in the early cohort were predicted to have achieved their target weight by May 28, only a minority (42%) of the birds arriving in the second cohort had, despite a faster rate of weight gain (Fig. 4).

3.2 Weight gain of individual Red Knot

A total of 125 Red Knot were re-trapped in the same year as their original capture (Appendix 2). The change in weight between capture occasions varied by both initial weight and day of initial capture, but not between years (Table 4). Although the total weight gained by birds did not differ between years, the rate at which they gained it did (Table 4). The primary reason for this difference was a greater rate of weight gain in 2002 (Fig. 6). Thus, a bird caught at 120g in 1998, 1999 or 2001 would be expected to put on weight at about 5g day^{-1}, in 2002 its rate of weight gain would be nearer 8g day^{-1}. Given an average arrival weight of around 120g, those birds that arrive before May 16 are predicted to increase in weight sufficiently, that they reach 180g by May 28 (Fig. 7); birds arriving after this date do not appear to do so.

3.3 Weight gain of Ruddy Turnstone and Sanderling

Ruddy Turnstone and Sanderling followed a similar weight gain schedule to the Red Knot (Fig. 8). Both Red Knot and Ruddy Turnstone put on about 55%, on average, of their initial body weight during their stay in Delaware Bay, whereas Sanderling put on 70% of their arrival weight. Sanderling put on weight relatively slowly (peak weight gain, 4.5 ± 1.3 $g.day^{-1}$), whereas Ruddy Turnstone are able to put weight much faster (7.2 ± 1.1 $g.day^{-1}$); Red Knot are intermediate (5.5 ± 1.7 $g.day^{-1}$).

The average rate of weight gain for Ruddy Turnstone varied between years (Table 5; Appendix 5). Weight gain rates were particularly high in 1998 and 2000, and seemed to be related to a later initiation of the main period of growth as total weight gain was similar to the average across all years. Although the fitted logistic curve indicated a much lower amount of weight gain in 1999, this was heavily influenced by a catch of two low weight birds caught in early June; excluding these two birds indicates an average weight gain of 55g, which is similar to the average across years.

Analysis of the individually re-trapped Ruddy Turnstone (Appendix 2) also indicated a (weakly) significant difference in weight gain between years (GLM: year term $\chi^2_4 = 10.82$, $p = 0.029$). There was no consistent trend across years: weight gain was particularly low in 1998 and 2001 and relatively high in 2000; 1999 and 2002 were intermediate. However, the magnitude of the differences between years was small (<10%).

Analysing weight gain by Sanderling on an annual basis revealed little evidence for a logistic growth curve, with the data for most years being statistically indistinguishable from a linear rate of gain (Appendix 5). With the exception of 1998, when relatively few catches were made, the rate of growth was similar between years (average rate of growth: 1998 0.63 ± 0.18 $g.day^{-1}$, 1999 1.14 ± 0.15 $g.day^{-1}$, 2000 1.40 ± 0.28 $g.day^{-1}$, 2001 1.22 ± 0.16 $g.day^{-1}$, 2002 0.95 ± 0.31 $g.day^{-1}$). These rates of growth will be lower than the peak rates of growth from the logistic function, since weight gain is averaged over a longer period. There is also no evidence of a consistent temporal change in growth rates. Similarly, analysis of the individually re-trapped birds (Appendix 3) suggested there was no significant difference in weight gain between years (GLM: year term $\chi^2_4 = 2.00$, N.S.).

4. DISCUSSION

During their stay in Delaware Bay, Red Knot are time-stressed with regard to foraging following the initial period of gut construction (although there is some evidence that late arriving birds may shorten this initial period, Battley *et al.* 2000). However, equally, there are costs to carrying fat, particularly when birds are migrating long distances (Kvist *et al.* 2001), and the fat load an individual bird departs from Delaware Bay, represents the outcome of a series of optimising decisions (*e.g.* McNamara & Houston 1990; Clark & Butler 1999). Calculations by Baker *et al.* (in press) suggest that, on average, a typical bird might require to weigh 180g to migrate successfully to the arctic breeding grounds. Clearly, once individuals reach this weight, their fattening urge is likely to abate. Indeed, many Red Knot are seen loafing on the upper reaches of beaches towards the end of May, which may be doing just this. This is likely to bias the sample of cannon netted birds, relative to the population as a whole, towards lower weight birds (discussed further below), thus mean weights of the cannon net sample cannot be taken at face value and further analysis is required.

This paper presents two complementary analyses of the rate of weight gain of Red Knot (and Ruddy Turnstone and Sanderling) during their stay in Delaware Bay: one based on the average trajectories of a particular 'cohort' which arrive on the same, or adjacent, days and one based on the weight gain of individual birds caught more than once in the same season. Given that the number of Red Knot (125) caught more than once in the same season amounts to less than 1.5% of the total number of birds caught, the two analyses can, for all practical purposes, be regarded as independent. These yield very comparable results, though slight differences are apparent, due to differing biases inherent in each method (discussed further below).

4.1 Arrival dates of Red Knot

In most years, the Red Knot staging in Delaware Bay appear to arrive in two distinct periods, a main arrival in early May, generally between May 6 and May 10, and a separate, later, arrival generally between May 20 and May 24. The exact arrival dates of each cohort are likely to vary slightly from year to year with prevailing wind direction and weather conditions experienced on the flight north to Delaware Bay (Butler *et al.* 1997). This is supported by an examination of Appendix 3. All birds (with only the odd exception) caught in the early half of May had gained substantially in weight, none were re-trapped at a similar weight, *i.e.* 'changed' cohorts.

Between 1999 and 2002, 30%-50% of the Red Knot caught on May 23/24 in each year could be assigned to the late arriving cohort (1999 43%, 2000 50%, 2001 30%, 2002 44%). In 1998, most birds seem to have arrived as a single cohort in early May, with only 17% of birds assignable to the second cohort. In 2002, though, a large number of birds arrived late; the continued presence of low weight birds suggests birds may even have been arriving as late as May 26/27 (Appendix 4). The number of low weight individuals (compared to that expected given the predicted rate of growth of an initial, early arriving, cohort) has increased over time (Fig. 3). This increase is similar in the both early and late May, so does not just reflect an increasing proportion of birds in the second cohort. It could be that the first cohort is also arriving a few days later, or that they have delayed the main period of weight increase compared to earlier years. Although the statistical significance of the linear trend is weak (as might be expected with only five years of data), it is notable that arrival dates for 2001 and 2002 were later than the preceding three years; close monitoring is required to determine if this is a continuing trend, or two aberrant years.

The impact of weather on the Red Knot's migratory schedule was seen in 1999, during which a La Niña event occurred, and the Red Knot migrating to Delaware were subject to extended, strong headwinds. In mid-May flocks in excess of 1,000 Red Knot were recorded at coastal sites along the south-eastern seaboard of the USA in sites where they did not normally occur (*in litt.*). The graphs in Appendix 4 suggest the main cohort arrived around May 14, almost a week later than in other years. Although most Red Knot had left Delaware Bay by the end of May there was a record of several thousand Red Knot in central Canada in mid June suggesting that many birds did not reach the breeding grounds or quickly returned south without breeding in that year. It is possible that the birds that did not put on weight or even lost weight in that year had already assessed that they were not in a good enough condition to breed and hence had changed their fattening strategy.

The population of Red Knot staging in Delaware Bay is thought to winter in three areas: a population of around 10 000 birds wintering in Florida and S Carolina (*C. canutus roselaari*) and populations of *C. c. rufa* wintering in Northern Brazil and Tierra del Fuego, these last presumably also stage in Brazil or the Caribbean on their way north. It is tempting to conclude that the different cohorts reflect the various wintering areas with the later birds presumably coming primarily from the population wintering in Tierra del Fuego, However, stable isotope analysis of feathers from birds in the various wintering areas (currently underway) would be needed to confirm this.

4.2 Rates of weight gain

The amount of weight gain by Red Knot during their stay in Delaware Bay did not differ significantly between years. This is borne out by both the individual re-trap analysis, where year was not included as a significant term in the minimum adequate model (Table 4), and the cohort analysis, where the total weight gain (W_D) where the total weight gain was around 70g to 80g in most cases. The notable exception to this was 1999. However, as has already been remarked, this year was atypical.

It is also notable that Red Knot in the later arriving cohorts increased in weight to a similar degree as the early arriving birds. To do this, the late arriving birds must have put on weight at a faster rate. This was clearly so in 2002, when the early birds put on weight at a peak rate of around 4.5g day^{-1}, birds in the second cohort appeared to put on weight at around three times this rate (Table 3). This conclusion is also drawn from the analysis of individually re-trapped birds, with day of capture included as a significant term in the minimum adequate model (Table 4). This pattern of higher weight gain in later arriving birds is likely to account for the apparently faster rates of weight gain observed amongst the re-trapped individuals in 2002 (Fig. 6), as there were more late arriving birds present in 2002 than other years. Although these birds may have had sufficient to migrate successfully to the breeding grounds, they may suffer reduced breeding success, or other, indirect, physiological costs as a result of this accelerated weight gain, as discussed below.

The rate of weight gain of individual birds clearly depends on the rate at which birds can find and ingest their food, in this case Horseshoe Crab eggs. This is influenced by two factors the density of eggs and the number of competitors, and the interference they cause. Intake rate is generally related to the density of eggs (a relationship known as the functional response, Sutherland 1996), usually in a non-linear fashion. Preliminary work has shown that the three key species have similar functional responses, *i.e.* their intake rate is equal at any given level of food abundance (Stillman *et al.* 2003). Red Knot are the biggest species considered and consequently put on the greatest amount of fat (in absolute terms, Fig. 8). As their intake rate is the same as that of the other species, it might be expected that Red Knot would be the first species to suffer adverse consequences from a reduced food supply, and hence intake rate.

4.3 Proportion of Red Knot reaching departure weight

The proportion of Red Knot at high weights in late May has varied between years. Baker *et al.* (in press) calculated that in order to have enough energy to complete their northward journey and to have sufficient reserves to survive a few days in the arctic under poor foraging conditions if snowmelt has not occurred by the time they arrived, birds need to put on 50g – 70g of fat in Delaware Bay. Analysis of the cohort data (Table 3) suggests that, if anything, birds actually put on fat at the upper end of this range. In all years except 1999, birds in both the first and second cohorts achieved this level of weight gain, on average, though not all would have done so by May 28, when many birds are expected to depart. Late departure may force birds into sub-optimal habitat if the best breeding sites are already occupied.

The analysis of individually re-trapped Red Knot, suggests that birds which arrive after May 16 are unlikely to put on sufficient weight to migrate North successfully, *i.e.* they fail to reach the 'target' weight of 180g by May 28. However, there are few individuals from the late cohort who are re-trapped (Appendix 2), and the cohort analysis suggests that the situation may not be so stark. Virtually all birds in the early arriving cohorts are likely to reach a weight of 180g, in good years, such as 1998, most birds may do this well before the average leaving date of May 28, allowing them sufficient time to re-ingest their gut before leaving, and hence a more fuel efficient journey. However, in poor years, such as 2002, a small, but significant, minority of even this early cohort may fail to reach the 'target' weight. Birds in the later arriving cohort clearly struggle to do so. In 2002, less than half of birds reached 180g by May 28. Although such birds can stay a few days longer in Delaware Bay and still leave at an appropriate weight, they are likely to be disadvantaged in finding high quality breeding sites.

Note that although, for the purposes of convenience, we have assumed that Red Knot have a 'target' of reaching 180g by May 28, this is largely arbitrary, however, between year differences and the pattern of relative numbers leaving successfully each year are likely to be similar, whatever the exact figures chosen are. It should also be noted that a single target weight and date for departure is likely to be an oversimplification, whilst it is likely to hold true for the population average, the strategy followed by individual birds is likely to be the result of a series a trade-offs influenced by their size, condition (both their own and relative to others), arrival date and probably other factors (Clark & Butler 1999; Sutherland 1996). Consequently, there is likely to be some variation in the time at which individuals depart, and the weight at which they do so, for example, although a weight of 180g may be sufficient, many birds achieve weights of over 200g, and one bird was trapped weighing in excess 240g.

4.4 Implications for the Red Knot population

The *C. c. rufa* population of Red Knot exhibits one of the longest distance migratory journeys of any bird. Their specialised feeding habit restricts the locations that it can stop to refuel on route to the arctic. In the past, there were substantial populations of Horseshoe Crabs in the Chesapeake Bay area and other food resources on the eastern seaboard of the USA. The crab eggs are the only food source that is available to them to refuel in spring making the survival of the *rufa* Red Knot population dependant on there being an abundant supply of accessible eggs throughout the last three weeks of May. This analysis clearly shows that if birds arrive around the 10th of May they are able to reach suitable take off weights to reach the arctic and breed. However, the later a bird arrives the lower the chance of it achieving a suitable departure weight, and reducing its chance of survival (Atkinson *et al.*2003).

There are a number of individual costs to arriving late in Delaware Bay. At one extreme, birds may have insufficient weight for the journey north to the breeding grounds to be successful. These birds may opt to forego the trip to the breeding grounds and spend some time in lower boreal or temperate latitudes before making the return journey. There is some evidence that this happened in the La Niña year of 1999. In terms of overall fitness, this may not have long-term consequences as the individual has 'saved' itself the costs of breeding and possibly some migration costs, which may be not insignificant. In population terms, for a bird that is likely to be breed for five or more years, the consequences of one failed breeding season may be relatively small. It seems likely that some inexperienced birds (those in their 2nd or 3rd year) may do this routinely, as in other waders.

Alternatively, birds may attempt to put on weight, as normal, but leave for the breeding grounds at a later date. This is likely to put them at severe disadvantage, both in terms of finding a high quality breeding site, but possibly also in having insufficient time during the short arctic summer to raise a brood successfully. At worst an individual may incur the full costs of breeding for little or no reproductive success. Even if an individual does manage to put on sufficient weight by some given date through accelerating it's rate of fat deposition, there are likely to be associated costs. For example, individuals may have insufficient time to re-ingest their gut, resulting in decreased flight efficiency, and by deploying physiological resources to the process of fat deposition, may compromise other aspects of their condition, such as their immuno-competence.

Both delayed / reduced take-off weight, and increased rates of weight gain are likely to result in increased mortality and Atkinson *et al*. (2003) have shown that birds with a predicted take off weight of less than 195g have a substantially reduced chance of survival. As outlined above sub-optimal fattening prior to arrival on the breeding grounds is likely to profound consequences for an individual's chances of breeding success, as has been shown for other arctic breeding waders (Gill *et al.* 2001). Thus if the trend towards later arrival continues it is likely that the population will continue to decline rapidly.

4.5 Why are Red Knot arriving later in Delaware Bay?

There is no clear reason to explain why birds are arriving later now. It is possible that there has been a change in weather patterns that has held up northward migration. This was known to have happened in 1999, but there is no evidence that this is the case in more recent years. Further it would be expected to have affected a range of species not just Red Knot. It is possible that there has been a reduction in quality at their staging point between Tierra del Fuego and Delaware thought to be somewhere in Brazil however we do not have any information on changes in the habitat quality of these sites or, for that matter, information on exactly where they all are. A third option is that the population is suffering from the progressive effects of increased stress during migration as a result of a reduction in the number of beaches which have a high enough density of eggs for fattening. This could lead to an increased density of birds on the remaining good beaches resulting in a progressive increase in the stress levels in the population leading to immuno-suppression. This could have a compound effect year on year.

To date there is not sufficient information to either confirm or reject any of these hypotheses but until such information is available, all avenues need to be explored. The original hypothesis, that birds in Delaware are failing to put on sufficient weight to reach their arctic breeding grounds and breed, receives only limited support from these analyses. Clearly, a small, though in some years significant, proportion of birds do fail to put on sufficient weight and it is likely that this number has increased in recent years, however, the majority of birds do still put on sufficient weight during the period. There is no evidence that the rate of weight gain of individuals has declined, there being relatively little between year variation in the pattern of weight gain by birds re-trapped in the same year. The primary reason for an decrease in the number of birds putting on sufficient weight for their migratory flight is due to an increased proportion of late arrivals. It should also be noted that the second cohorts in both 2001 and 2002 weighed some 10g less on arrival than the early arriving cohorts (Table 3), suggesting they may need greater total levels of weight gain. This may also indicate a failure to achieve sufficiently good condition in the wintering or staging grounds further south. Population levels of migratory birds, such as the Red Knot will be affected by conditions on both breeding and wintering grounds, as well as any intermediate staging grounds, and a deterioration in the quality of any may well have consequences for the pattern of use of the others (Sutherland & Dolman 1994). It is therefore vital to identify demographic parameters at both ends of the migratory system (Gill *et al*. 2001)

Over the last decade, the area of Delaware Bay that is used by Red Knot has reduced as they have used that area south of Reeds Beach on the New Jersey shore less and less. This area has a different aspect to other parts of the bay and if it is no longer used buy spawning crabs then it is possible that there will be no areas where there is fresh spawning in periods of westerly winds, which may have consequences for overall weight gain in years when such winds prevail. In the meantime, it is vital that everything is done to maximise the egg availability to Red Knot so that the maximum number of individuals can reach take off weights on time. A reduction in the crab population to a level to a point where eggs are no longer super abundant to the birds will almost certainly lead to the extinction of the *rufa* population.

4.6 Biases in the data

Catching samples of birds by any method is likely to catch non-random selections of the population. For instance, the first birds to land from a flock are likely to be juveniles (Clark 1983) or poor condition birds. All the samples caught since 1997 have used cannon nets. Most of the catching sites in Delaware Bay are on relatively narrow beaches where shorebirds are feeding. As a result this method is likely to have few capture biases especially in the first half of the season when all birds are likely to be keen to fed. Later in the season, flocks of birds of are often seen roosting on wider beaches. Many of these flocks make very characteristic pre-migratory calls and it is likely that they are assimilating their gut contents and reducing their internal organs prior to departure (Piersma *et al.* 1999). These flocks are much more difficult to catch and this is likely to introduce a bias towards different weight birds, particularly towards the end of May. However, these flocks have only been seen after the 25th May (pers. obs.) and it is likely that birds in the flocks are within a day or two of departure. The net result is for estimates of the mean weight of the population to refer to feeding birds and to assume that those birds that are roosting have already left the system. Given that the birds have stopped feeding, they will not be putting on any more weight so it will not be affecting the peak weights achieved.

There are two other sources of variation that could be taken into account in the analysis: body size and weight loss after capture. This paper has shown that body size is strongly correlated with wing length (Fig. 1). A Red Knot with a wing length of 160mm weighed about 20g less than one with a wing length of 180mm. There was very little variation in the mean wing length between catches (2mm or less) so this should not introduce biases in the analyses of weight change in the population as a whole. Red Knot lose some 5% of their capture weight in the first three hours after capture approximately equivalent to the amount of weight that they gain each day. The majority of this weight loss is in the first hour after capture (Clark *et al.* 2002); most birds are weighed between one and three hours after capture. Consequently, the weights recorded are likely to underestimate the weight immediately before capture by around 9g. This is well within the range of variation attributable to body size, so for practical purposes the effect is likely to be small. Additionally, most of this weight loss arises from a voiding of gut contents, so the sample could be considered merely to represent the state of affairs prior to the current feeding bout at some point earlier in the day.

The most likely effect of taking weight loss after capture and body size into account is to decrease the variation within cohorts, making it easier to distinguish between cohorts. However there are about 25% of the catches for which this data has not been collected (more in the early years of the study). If all the data with missing values were excluded, then there would be some years for which the data could not be analysed. As a result, we opted to analyse that maximum amount of data all be it at with a reduced level of precision. A clear recommendation is that wing length and time after capture that weighing has taken place should be routinely recorded in future even is it results in reduced sample sizes on the larger catches.

A further potential source of error is an effect of handling, whereby catching and handling birds depresses weight gain for a period after capture. Although this may affect all birds, it is an analytical consideration for those birds that were re-trapped only. It is likely to mean that the extent of weight gain by individuals is under-estimated to a certain extent. However, an examination of Appendix 2 suggests that this effect, if present, is likely to be small as, with the exception of 1999, very few birds, even amongst those with short re-trapping intervals, lost weights and many birds with short re-trap intervals gained appreciably in weight.

Acknowledgements

The monitoring of shorebirds in Delaware Bay has been a collaboration of many individuals, all of whose efforts have contributed indirectly to the results this report and we are extremely grateful for their time and enthusiasm. In particular, the monitoring programme was begun by Alan Baker and efforts have been co-ordinated by Dave Carter (DNREC) and Larry Niles (New Jersey FWS), we thank them for their continued support.

Many professionals and volunteers, from all parts of the globe, have willingly and freely given up their time to help catch the birds, in particular Clive Minton, who helped start the international catching efforts, and Phil Ireland of the Wash Wader Ringing Group. A number of other people deserve thanks for their contributions to the monitoring, in particular Kathy Clark, Kimberley Cole, Jim Hewes, Humphrey Sitters and Mark Peck. We would also like to thank Jacquie Clark, Simon Gillings and Kimberley Cole (on behalf of DNREC) for their comments on the report and the analyses presented.

The monitoring programme has been funded by grants from Delaware Department of Natural Resources, New Jersey Fish & Wildlife Service and the National Oceanic & Atmospheric Administration. We are grateful to them for their continued support.

References

Atkinson, P.W., Robinson, R.A. & Clark, N.A. (2003) Survival rates and body condition of Red Knots in Delaware Bay – influence of body condition at departure on survival. In Atkinson, P.W., Appleton, G.F., Clark, J.A., Clark, N.A., Gillings, S.G., Henderson, I.G., Robinson, R.A., & Stillman, R.A. (eds) *Red Knots* Calidris canutus *in Delaware Bay 2003. Survival, foraging and marking strategy.* BTO Research Report 308. British Trust for Ornithology, Thetford.

Baker, A.J., Gonzalez, P.M., Niles, L.J., Piersma, T., Nascimento, I.L.S., Atkinson, P.W., Clark, N.A., Minton, C.D.T., Peck, M., Sitters, H. & Aarts, G. (2003) Rapid population decline in Red Knots *Calidris canutus rufa* since 2000: fitness consequences of late arrival and decreased refuelling rates in Delaware Bay. *Science* 299: *In press.*

Battley, P.F., Piersma, T., Dietz, M.W., Tang, S., Dekinga, A. & Hulsman, K. (2000) Empirical evidencefor differential organ reductions during trans-oceanic bird flight. *Proceedings of the Royal Society of London, Series B* **267**, 191-195.

Bhattacharya, C.G. (1967) A simple method of resolution of distribution into Gaussian components *Biometrics* **23**, 115-135.

Botton, M.L., Loeveland, R.E. & Jacobsen, T.R. (1994) Site selection by migratory shorebirds in Delaware Bay, and its relationship to beach characteristics and abundance of horseshoe crab (*Limulus polyphemus*) eggs. *Auk* **111**:605-616.

Brown, S., Hickey, C., Harrington, B. & Gill, R. (2001) *The United States Shorebird Conservation Plan, 2nd edition.* Manomet Center for Conservation Sciences, Manomet, MA.

Butler, R.W., Williams, T.D., Warnock, N. & Bishop, M.A. (1997) Wind assistance: a requirement for migration of shorebirds. *Auk* **114**, 456-466.

Carter, D.B., Clark, N.A. & Hewes, J.D. (2002) Delaware Bay – 2000/2001: the Delaware Shorebird Monitoring Team bi-annual report, DENREC, Dover, DE.

Clark, C.W. & Butler, R.W. (1999) Fitness components of avian migration: a dynamic model of western sandpiper migration. *Evolutionary Ecology Research* **1**, 443-457.

Clark, N.A. (1983) *The ecology of dunlin* Calidris alpina *wintering on the Severn estuary.* Ph. D. Thesis, University of Edinburgh.

Clark, J.A. (2002) *Effect of severe weather on wintering waders*. M. Sc. Thesis, University of East Anglia, Norwich.

Gayanilo, F.C. Jr. & D. Pauly (eds.) (1997) *The FAO-ICLARM Stock Assessment Tools (FiSAT) Reference Manual*. FAO Computerized Information Series (Fisheries). No. 8. FAO, Rome.

Gill, J.A., Norris, K., Potts, P.M., Gunnarsson, T.G., Atkinson, P.W. & Sutherland, W.J. (2001) The buffer effect and large-scale population regulation in migratory birds. *Nature* **412**, 436-439.

Kvist, A., Lindstrom, A., Green, M., Piersma, T. & Visser, G.H. (2001) Carrying large fuel loads during sustained bird flight is cheaper than expected. *Nature* **413**, 730-731.

McNamara, J.M. & Houston, A.I. (1990) The value of fat reserves and the trade-off between starvation and predation. *Evolutionary Ecology* **4**:298-311.

Pauly, D. & J.F. Caddy (1985) A modification of Bhattacharya's method for the analysis of mixtures of normal distributions. *FAO Fisheries Circular* **781**,1-16.

Piersma, T., Gudmundsson, G.A. & Lilliendahl, K. (1999) Rapid changes in the size of different functional organ and muscle groups during refuelling in a long-distance migrating shorebird. *Physiological and Biochemical Zoology* **72**, 405-415.

Redfern, C.P.F. & Clark, J.A. (2002) *The Ringers' Manual*. British Trust for Ornithology, Thetford.

Stillman, R.A., Atkinson, P.W., Clark, N.A., Gillings, S.G., Henderson, I.G., Love, S.E., Robinson, R.A., Weber, R.G., & Bardsley, S.L. (2003) Functional responses of shorebirds feeding on horseshoe crab eggs. *In* Atkinson, P.W. et al. (eds) *Red Knots* Calidris canutus *in Delaware Bay 2003. Survival, foraging and marking strategy.* BTO Research Report 308. British Trust for Ornithology, Thetford.

Sutherland, W.J. (1996) *From individual behaviour to population ecology*. Oxford University Press, Oxford.

Sutherland, W.J. & Dolman, P.M. (1994) Combining behaviour and population dynamics with applications for predicting the consequences of habitat loss. *Proceedings of the Royal Society of London, Series B* **255**, 133-138.

Table 1. Plumage scoring system, following Redfern & Clark (2002).

Score	Extent of Summer Plumage
1	None (Full winter)
2	Trace summer
3	25% summer
4	50% summer
5	75% summer
6	Trace winter only
7	Full summer

Table 2. Plumage scores for each age class.

Red Knot	Plumage Score							
	1	2	3	4	5	6	7	Total
Juvenile (SY)	27%	24%	24%	10%	3%	8%	5%	63
Adult (ASY)	0%	0%	5%	13%	23%	32%	27%	3155
Not aged (AHY)	0%	1%	9%	16%	26%	22%	25%	3845

Ruddy Turnstone	Plumage Score							
	1	2	3	4	5	6	7	Total
Juvenile (SY)	3%	3%	6%	4%	8%	37%	38%	70
Adult (ASY)	0%	0%	5%	9%	18%	18%	49%	7132
Not aged (AHY)	0%	0%	1%	4%	14%	15%	65%	3000

Table 3. Pattern of growth of individual Red Knot cohorts in Delaware Bay 1998 – 2002. Arrival weight (W_A, g) and total weight gain (W_D, g) are represented by the bounds of the logistic curve, and approximated from the predicted weights on the first catch and weight on May 28 where growth is linear. The day of maximum growth rate (G_{Max}, the point of inflection in the logistic curve) is given together with the instantaneous growth rate (G_{Max}, g day^{-1}) on this day. For linear curves, G_{Max} is simply the slope of the curve. Standard errors are given where appropriate.

Year	Cohort	W_A	W_D	D_{Max}	G_{Max}	F	*p*
1998	May 9	117.8 ± 4.1	78.3 ± 7.6	18.4 ± 0.7	9.24 ± 2.65	90.5	<0.001
1999	May 11	123.9 ± 7.8	54.0 ± 9.0	17.1 ± 0.4	16.7	19.1	0.004
2000	May 13	128.6	(63.2)	-	4.20 ± 0.29	204	<0.001
2001	May 10	123.1 ± 1.6	71.0 ± 2.9	20.6 ± 0.2	8.14 ± 0.74	621	<0.001
	May 20	111.6	(61.2)	-	5.47 ± 1.14	22.7	0.009
2002	May 12	117.2 ± 9.4	84.7 ± 27.6	20.4 ± 2.6	4.65 ± 2.35	172	<0.001
	May 16	108.2 ± 3.5	90.2 ± 21.3	25.7 ± 1.0	14.2 ± 5.5	99.6	<0.001
	May 26	120.8	(26.8)	-	13.4 ± 5.3	6.32	N.S.

Table 4. Minimum Adequate Models of total weight gain and daily rate of weight gain by individual Red Knot caught twice in the same year.

Parameter	d.f.	Estimate	Log Likelihood	χ^2	*p*
Overall Weight Gain					
Intercept	1	-43.8 ±24.5	-1164.6		
Day Diff.	1	4.45 ± 0.34	-1056.4	108.2	< 0.0001
Weight	1	0.24 ± 0.19	-1014.1	42.35	< 0.0001
Day	1	5.28 ± 1.18	-1003.8	10.32	0.0013
Weight * Day	1	-0.034 ± 0.009	-989.1	14.65	0.0001
Year	4		-986.3	2.86	N.S.
Rate of Weight Gain					
Intercept	1	-16.79 ± 4.92	-688.3		
Day	1	1.77 ± 0.24	-685.0	3.28	0.07
Weight	1	0.11 ± 0.04	-626.3	58.7	<0.0001
Year	4		-620.1	6.20	N.S.
1998		4.66 ± 2.27			
1999		7.34 ± 1.91			
2000		11.44 ±3.58			
2001		3.89 ± 2.38			
2002		-			
Day * Weight	1	-0.010 ± 0.002	-585.4	34.8	<0.0001
Day*Year	4		-561.1	24.3	<0.0001
1998		-0.30 ± 0.13			
1999		-0.48 ± 0.11			
2000		-0.83 ± 0.22			
2001		-0.24 ± 0.13			
2002		-			

Table 5. Pattern of growth of Sanderling and Ruddy Turnstone foraging in Delaware Bay 1998 – 2002. Arrival weight (W_A, g) and total weight gain (W_D, g) are represented by the bounds of the logistic curve. The day of maximum growth rate (G_{Max}, the point of inflection in the logistic curve) is given together with the instantaneous growth rate (G, g day^{-1}) on this day. All parameters are given ±1 standard error and a test of significance of the overall regression is given. Form of the logistic growth curve: $y = W_A + W_D / (1 + (x/D_{Max})^{-G})$, where y is weight and x day in May.

Year	W_A	W_D	D_{Max}	G	F	*p*
Sanderling						
All	53.1 ± 1.4	37.7 ± 6.6	22.2 ± 2.0	4.48 ± 1.29	104.9	<0.0001
Ruddy Turnstone						
All	99.3 ± 1.2	57.8 ± 3.8	23.1 ± 0.6	7.23 ± 1.10	341.9	<0.0001
1998	97.9 ± 2.3	59.0 ± 12.1	22.0 ± 1.3	8.45 ± 4.40	67.1	<0.0001
1999	101.0 ± 3.7	44.1 ± 7.2	20.1 ± 1.4	7.55 ± 4.17	26.9	<0.0001
2000	107.1 ± 3.5	58.0 ± 10.6	23.6 ± 1.3	8.77 ± 3.52	42.8	<0.0001
2001	98.7 ± 1.7	65.7 ± 7.3	25.2 ± 0.9	7.96 ± 1.73	176.7	<0.0001
2002	98.0 ± 2.7	76.0 ± 17.3	25.2 ± 2.3	5.24 ± 1.53	98.4	<0.0001

Figure 1. Relationship between weight and body size. Mean weight (±1 standard deviation) for each 2mm wing length category. Fitted model (to original data) includes a categorical term for day (d.f. = 22) with a log link function; weight = exp(0.0060 ± 0.0004*wing), χ^2_1 = 211.8, *p* , 0.0001.

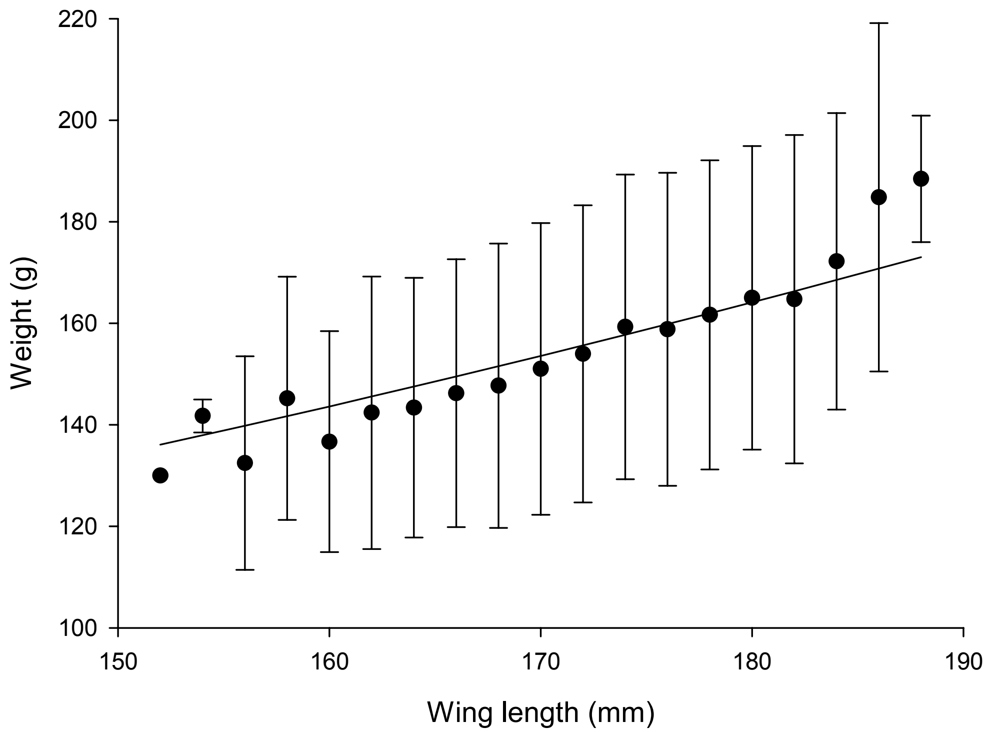


Figure 2. Average weights of Red Knot caught in Delaware Bay. (a) Frequency distribution of 852 birds caught on or before May 11. Fitted log-normal curve *f*(x) = 0.033*exp(-0.5(ln(x/123.1)/0.098)^2), $F_{2,15} = 157.0$, $p < 0.0001$, $R^2 = 0.948$. (b) Average weight by day (± 1 standard deviation) corrected for body size. Fitted logistic curve: y=114.8 + 70.29/(1+(x/19.22)^(-4.94)), $F_{3,7216} = 1480$, *p* , 0.0001, $R^2 = 0.381$.

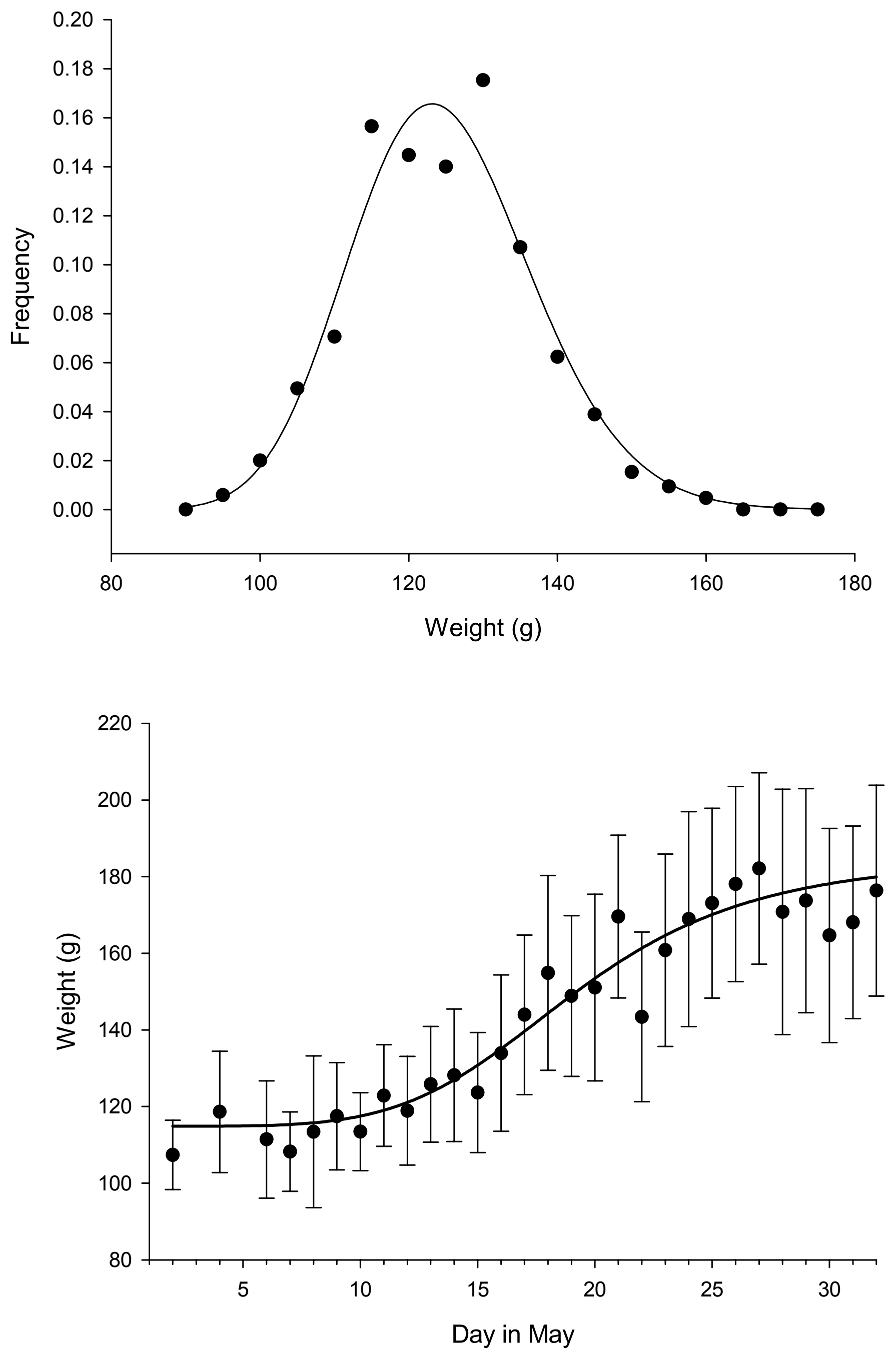


Figure 3. Frequency of birds weighing less than predicted for a cohort arriving on May 9 (calculated from Figure 2). Each point represents one catch: filled circles catches before May 22, open circles catches on or after May 22. Regression line parameters: intercept = -90.6 ± 26.5 (standard error), slope = 0.045 ± 0.013, F = 11.75, $p = 0.001$, $R^2 = 0.19$; dashed lines represent 95% confidence limits.

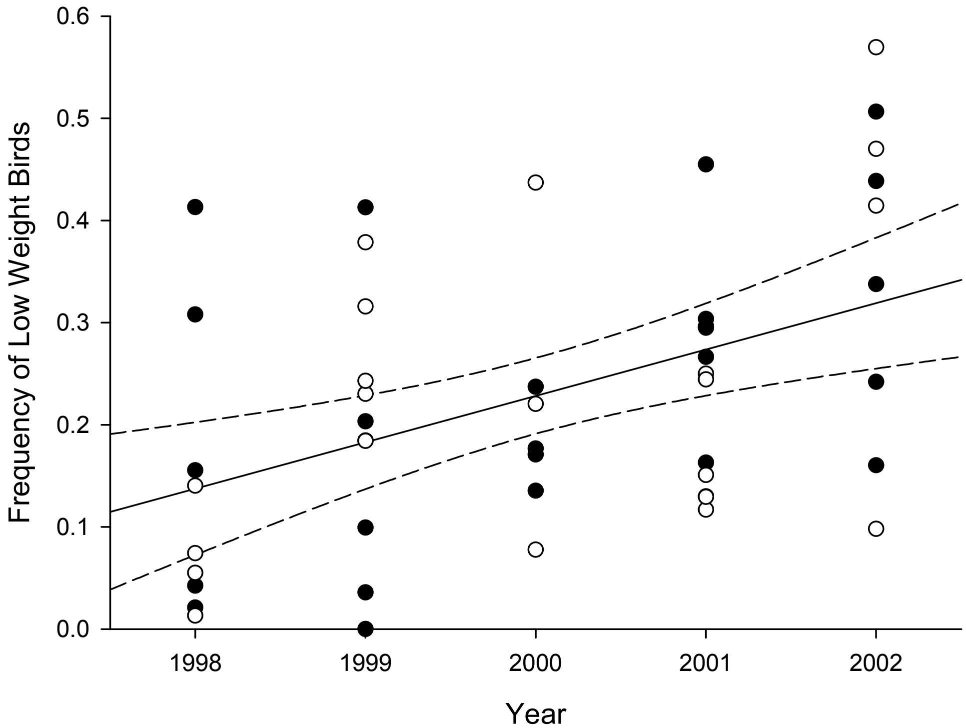


Figure 4. Pattern of weight change in individual cohorts of Red Knot present in Delaware Bay 1998 – 2002. Means ± 1 standard deviation of decomposed distributions are shown, together with best fit (least squares) logistic or linear curves are fitted to these means of assumed repeat samplings of the same cohorts.

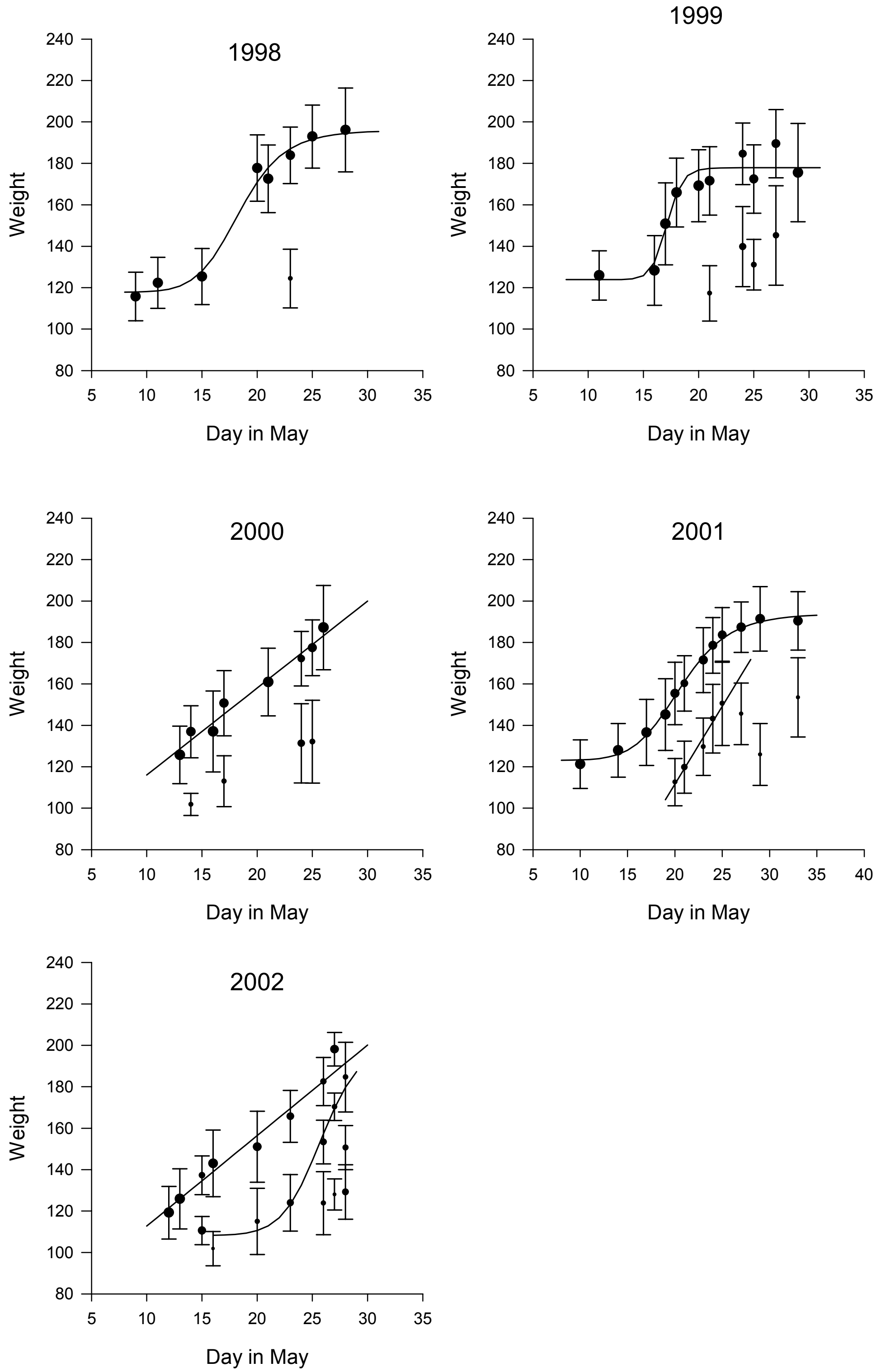


Figure 5. Cumulative proportion of birds in each cohort reaching a 'target' weight of 180g by a particular date. Solid line 1998 (only one cohort present), dashed lines 2002 (two cohorts present, one arriving by May 10 the other by May 20.

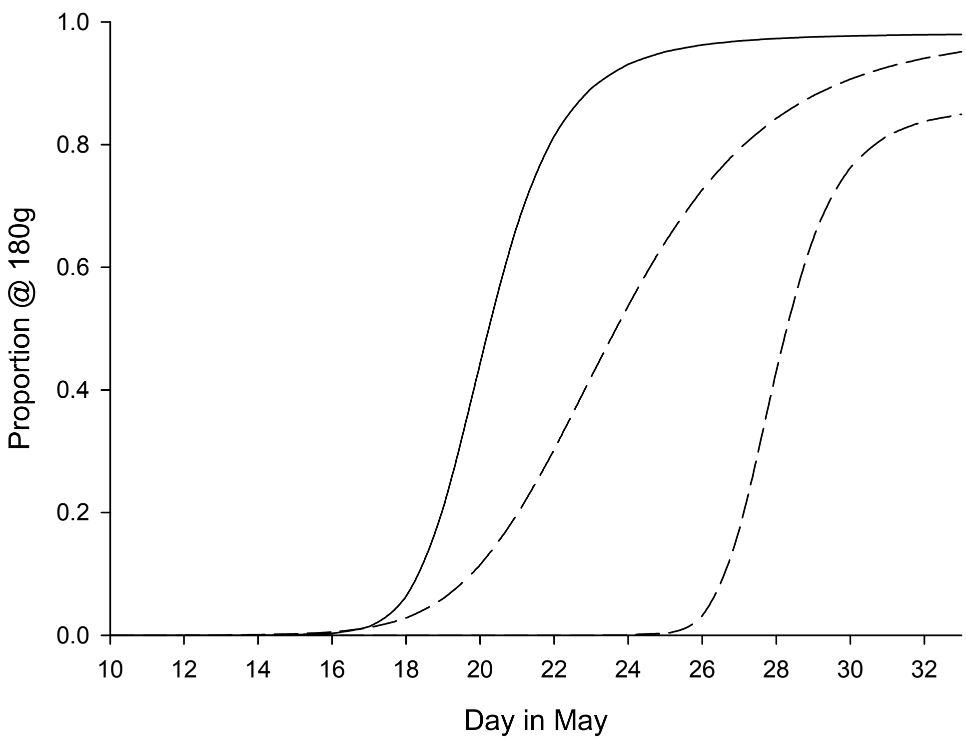


Figure 6. Rate of weight gain in individually recaptured Red Knot with date of first capture and weight on first capture. Note data were too sparse to produce a reliable plot for 2000 (See Appendix 2).

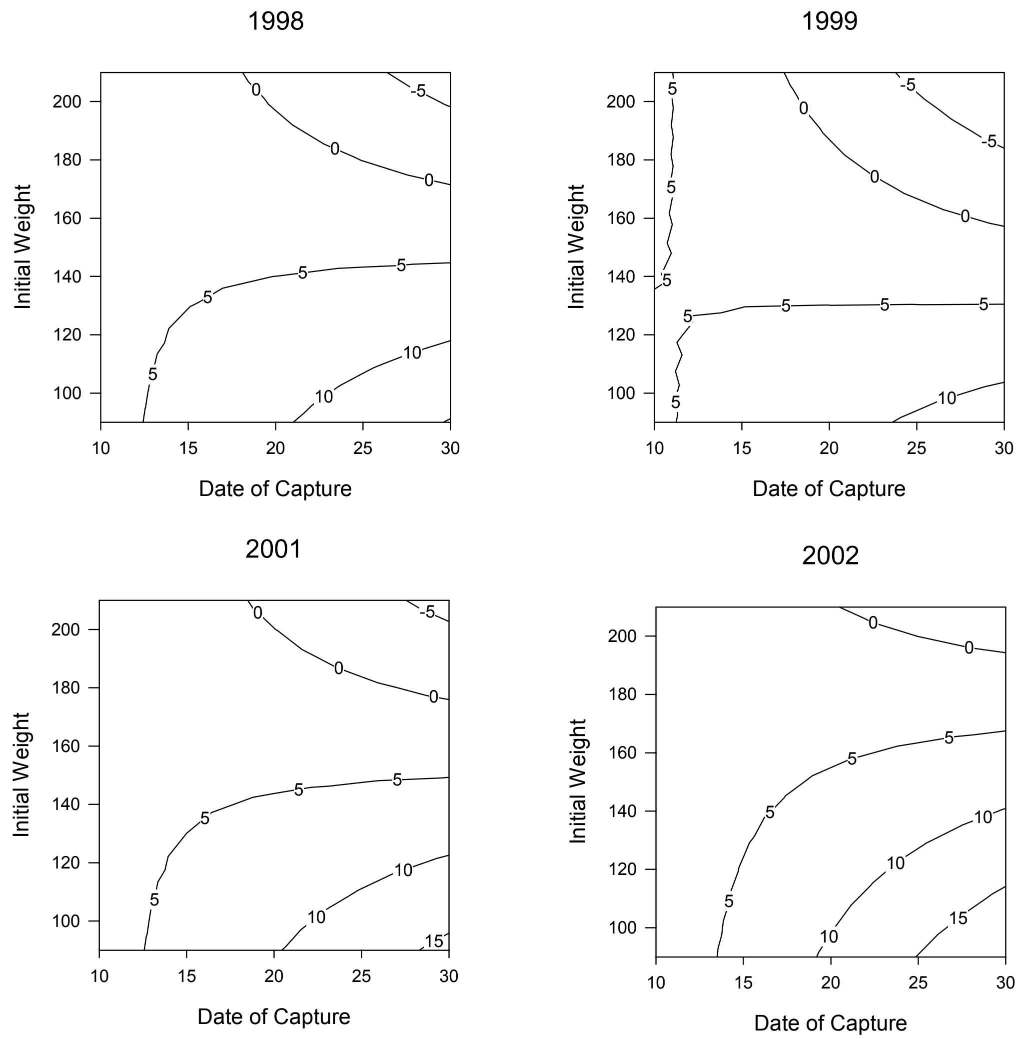


Figure 7. Predicted weight gain of Red Knot by May 28 in relation to 'current' date and weight. The hatched area indicates implausible day weight combinations.

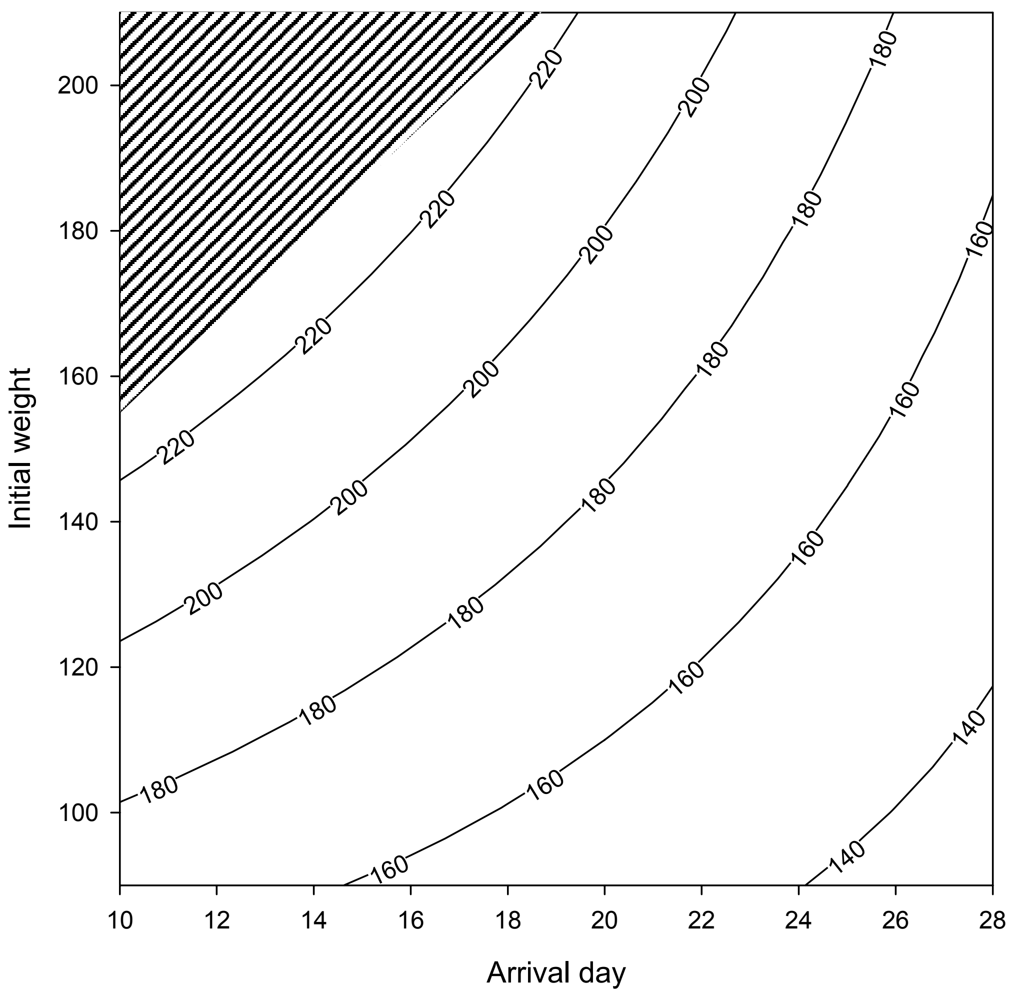
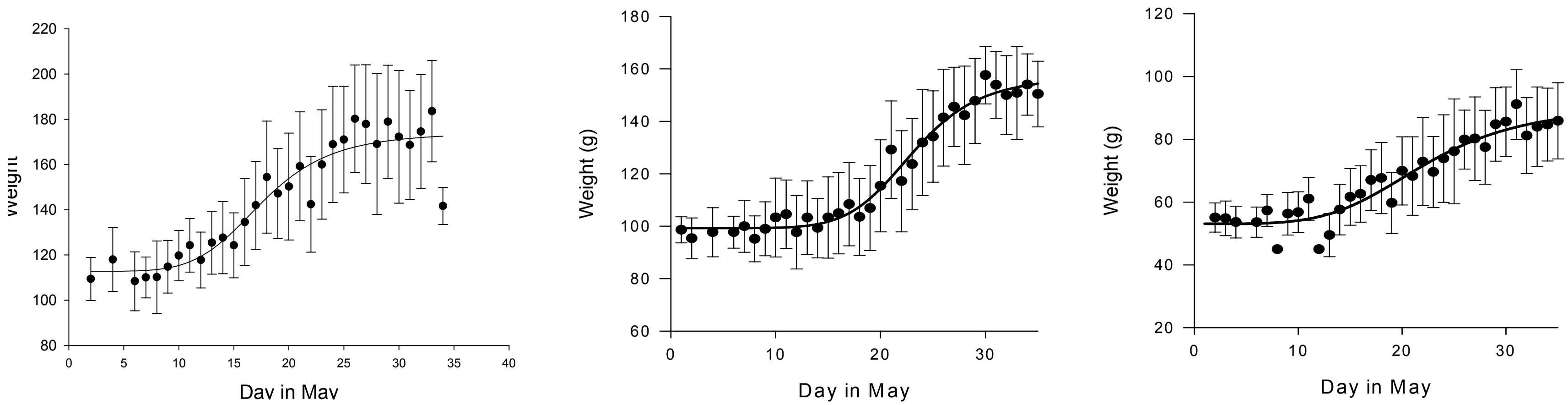


Figure 8. Weight gain by (a) Red Knot (b) Ruddy Turnstone and (c) Sanderling during May in Delaware Bay. Circles indicate average weight by day (across all years) ± 1 standard deviation. Fitted logistic curve is $y = W_A + W_D / (1 + (x/D_{Max})^{-G})$. Arrival weight ($W_A$, g) and total weight gain (W_D, g) are represented by the bounds of the logistic curve. The day of maximum growth rate (D_{Max}, the point of inflection in the logistic curve) is given together with the instantaneous growth rate (G, g day^{-1}) on this day.

	W_A	W_D	G	D
Red Knot	112.8	61.3	5.54	17.6
Ruddy Turnstone	99.3	57.8	7.23	23.1
Sanderling	53.1	37.7	4.48	22.2



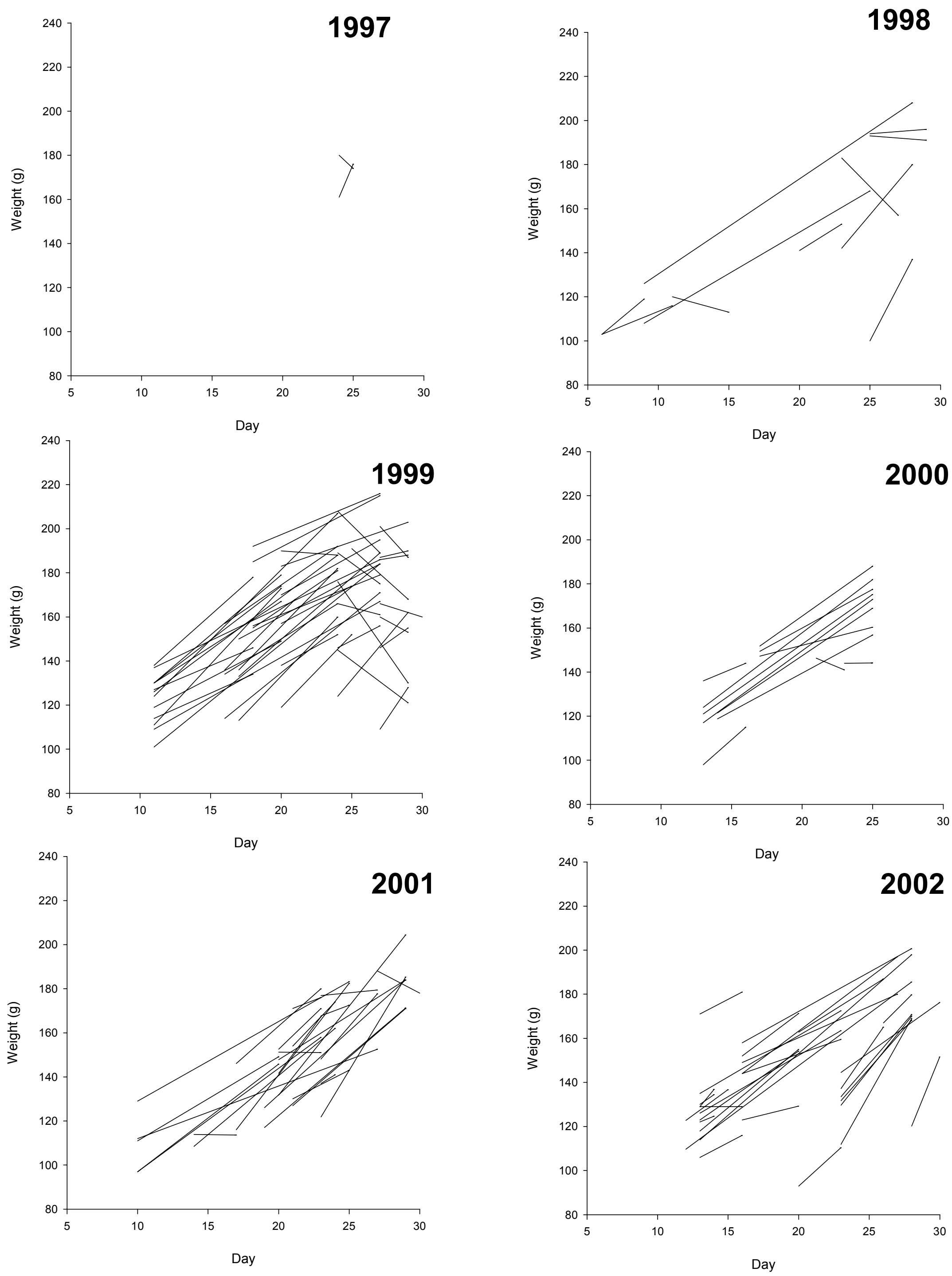
Appendix 1. Catches of more than 50 birds made in Delaware each year. Note catches made on the same day on either side of the Bay are treated as one catch. For each catch, the number of birds weighed is given

Day		Place	State	No Birds
1997				
	22	Slaughter Beach	DE	172
	23	Slaughter Beach	DE	196
	24	Mispillion Harbour	DE	249
		Slaughter Beach	DE	92
	25	Mispillion Harbour	DE	53
	26	Mispillion Harbour	DE	131
1998				
	9	Mispillion Harbour	DE	92
		Slaughter Beach	DE	32
	11	Reed's Beach	NJ	172
	15	Reed's Beach	NJ	229
	21	Reed's Beach	NJ	88
	23	North Bowers	DE	193
	25	Slaughter Beach	DE	102
	27	Reed's Beach	NJ	75
	28	North Bowers	DE	103
1999				
	11	Cook's Beach	NJ	441
	16	Mispillion Harbour	DE	100
	17	Villas	NJ	60
	18	Villas	NJ	98
	19	Slaughter Beach	DE	49
	20	Villas	NJ	188
	21	Slaughter Beach	DE	60
	24	Cook's Beach	NJ	209
		Slaughter Beach	DE	134
	25	North Bowers	DE	102
		Kimble's Beach	NJ	22
	27	Cook's Beach	NJ	206
		Mispillion Harbour	DE	278
		Reed's Beach	NJ	167
	29	North Bower's	DE	317
2000				
	13	Villas	NJ	172
	14	Mispillion Harbour	DE	86
		Villas	NJ	20
	16	Sunray Beach	NJ	111
	17	Slaughter Beach	DE	176
	21	North Bowers	DE	87
	24	Mispillion Harbour	DE	54
	25	North Bowers	DE	267
		Sunray Beach	NJ	79
	26	Reed's Beach	NJ	93
2001				
	10	Reed's Beach	NJ	116
	14	Slaughter Beach	DE	77
	17	Mispillion Harbour	DE	105
		Reed's Beach	NJ	51
	19	Egg Island, Fortescue	NJ	36
		Ted Harvey WR	DE	95
	20	Mispillion Harbour	DE	372
	21	Fortescue Beach	NJ	125
	23	Fortescue Beach	NJ	189
		Slaughter Beach	DE	276
	24	Reed's Beach	NJ	98
	25	Cook's Beach	NJ	92

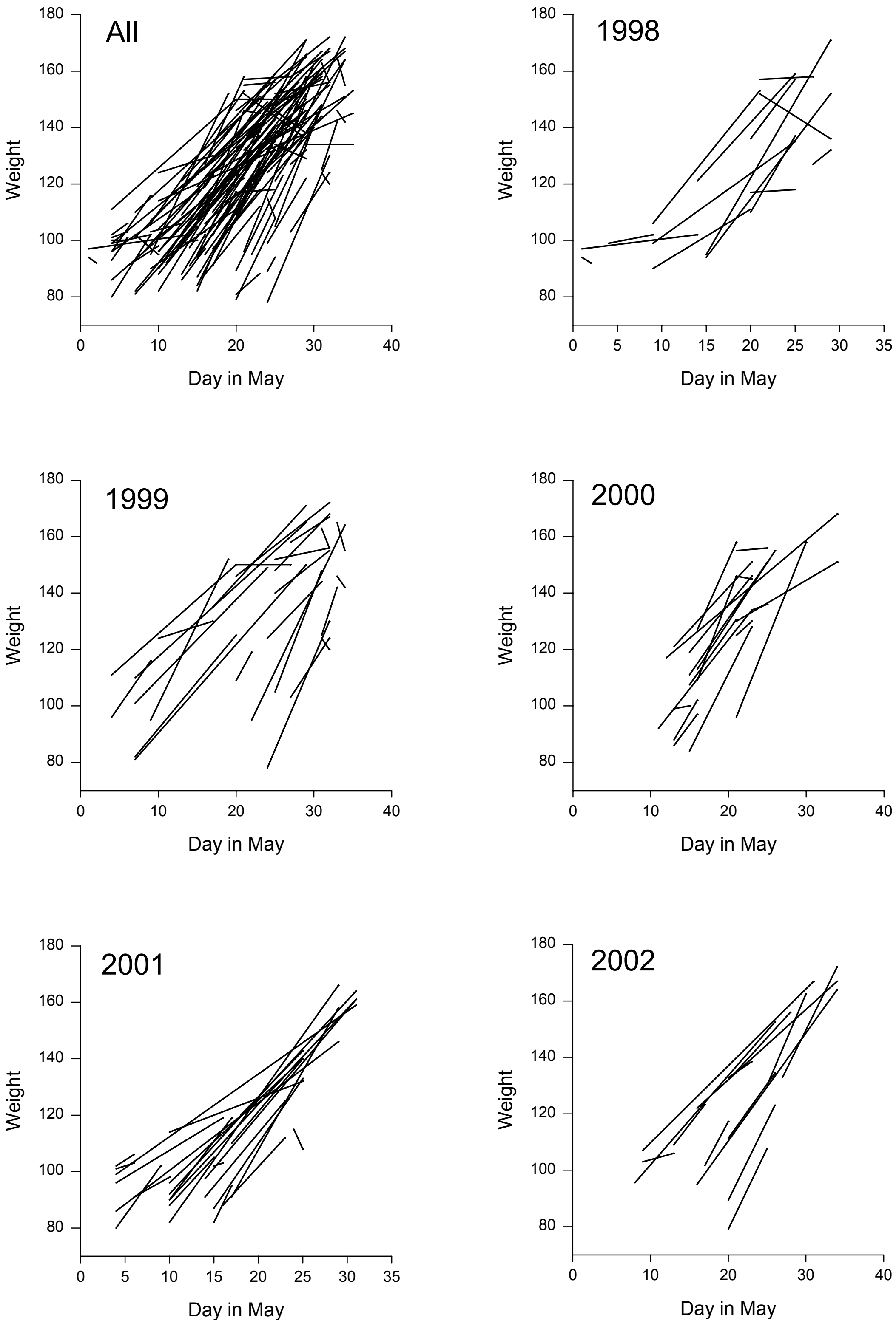
		Reed's Beach	NJ	23
		Slaughter Beach	DE	220
	27	Mispillion Harbour	DE	90
	29	Mispillion Harbour	DE	76
		Reed's Beach	NJ	58
		Kimble's Beach	NJ	77
	2 June	Fortescue Beach	NJ	58
2002				
	12	Mispillion Harbour	DE	65
	13	Cook's Beach	NJ	362
	15	Mispillion Harbour	DE	78
	16	Sunray Beach	NJ	71
	20	Slaughter Beach	DE	177
	23	Mispillion Harbour	DE	273
	26	Slaughter Beach	DE	48
	27	Cook's Beach	NJ	51
	28	Mispillion Harbour	DE	224

Appendix 2. Weight change of individual birds re-trapped in the same season.

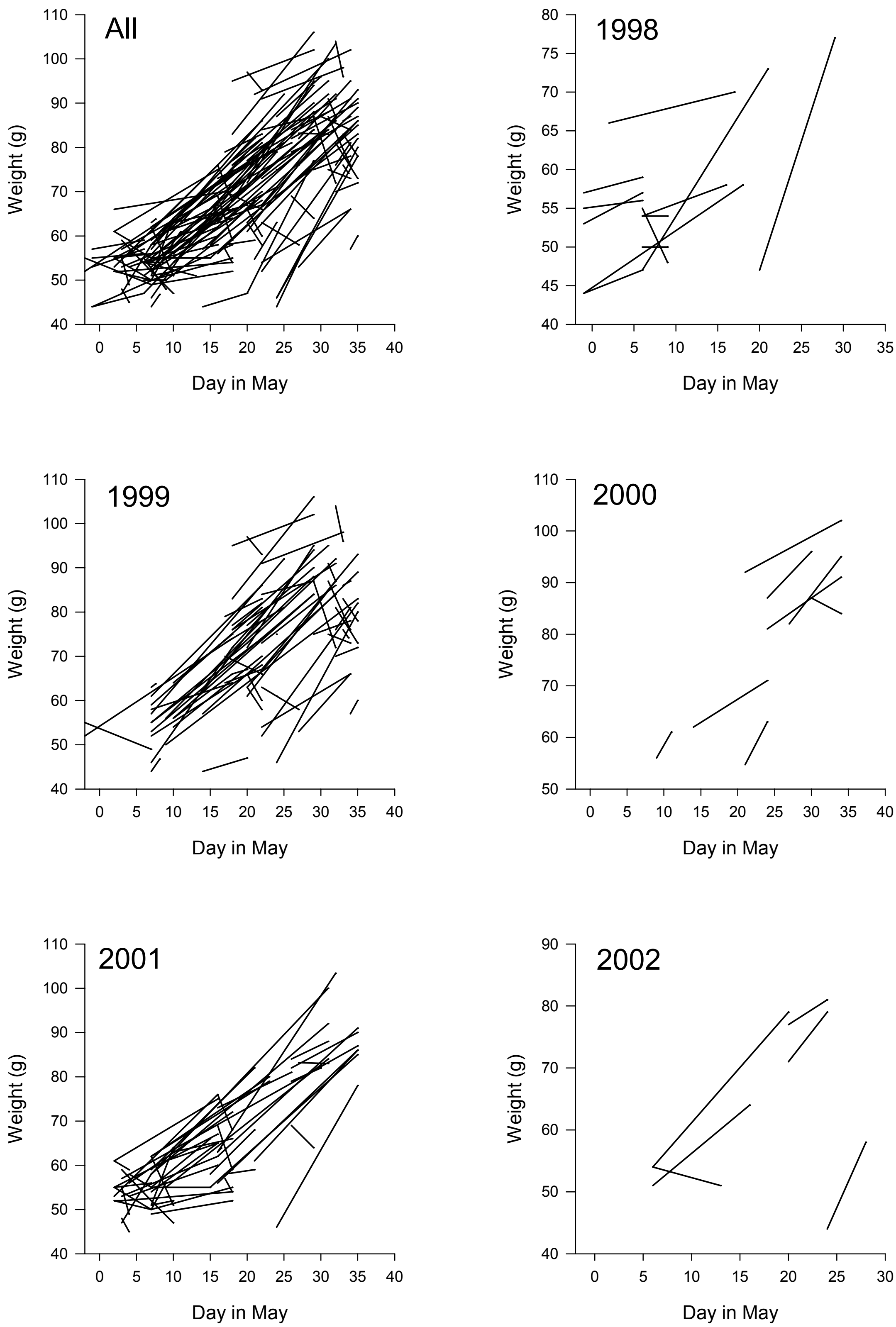
(a) Red Knot



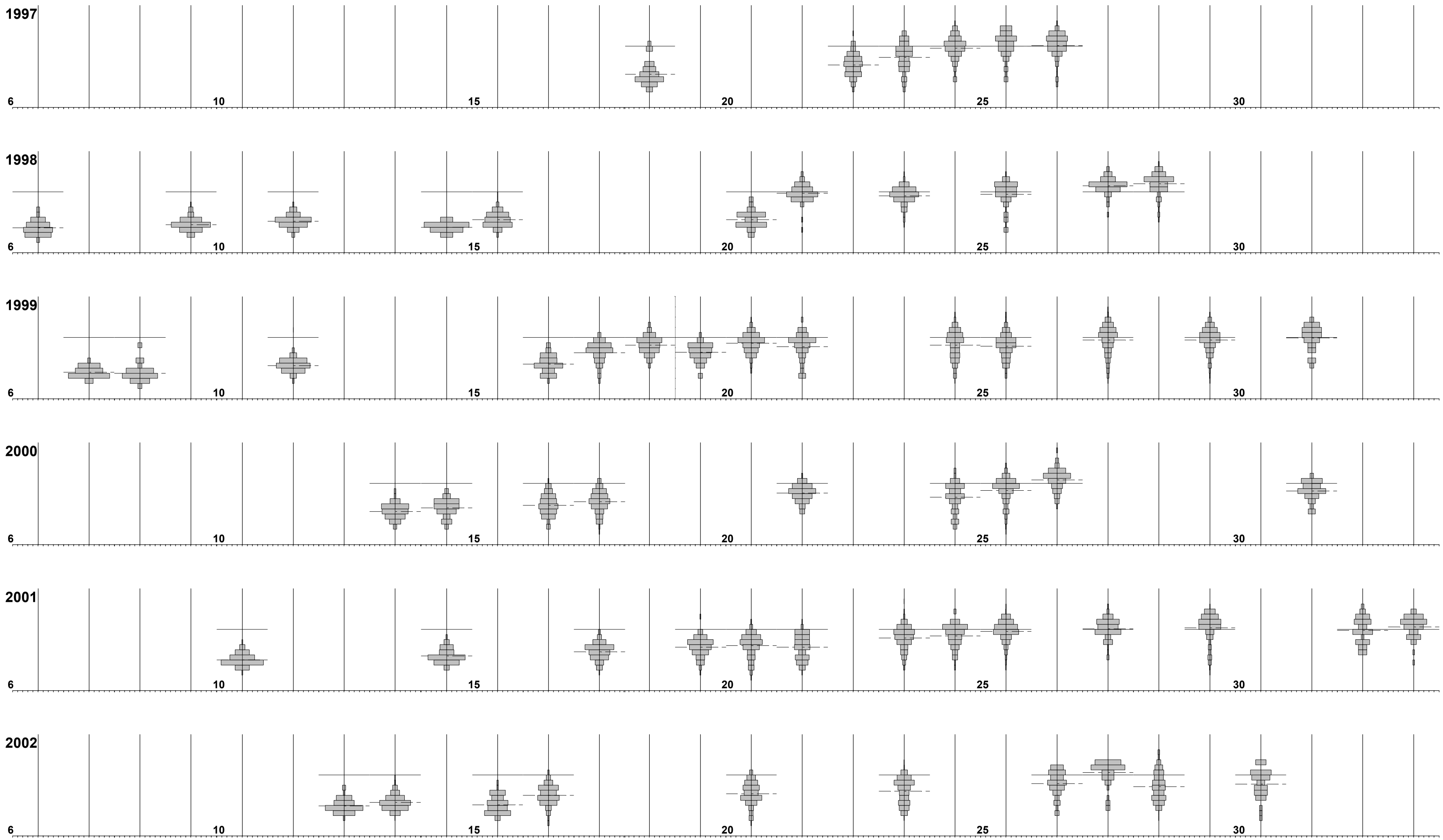
(b) Ruddy Turnstone



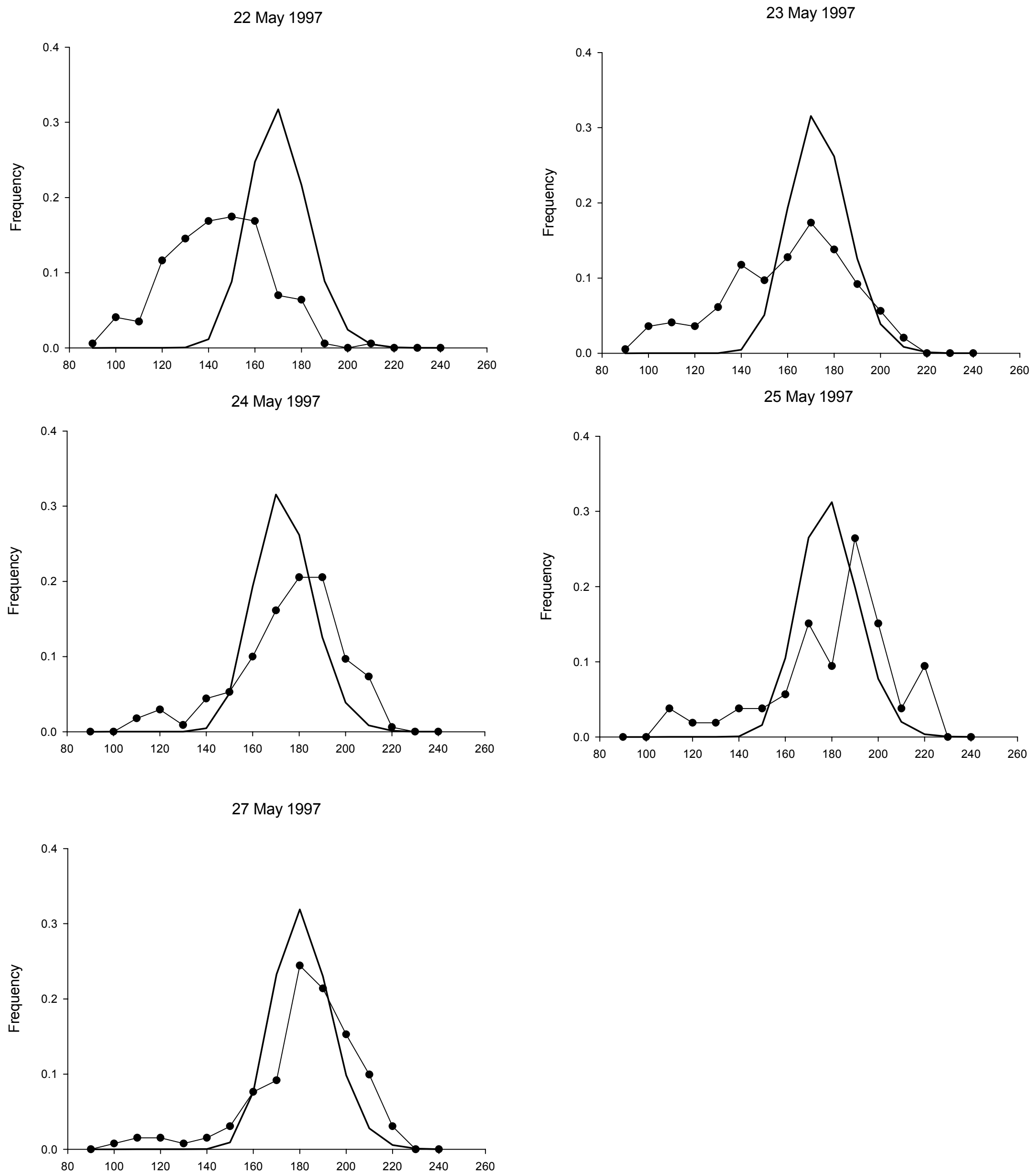
(c) Sanderling

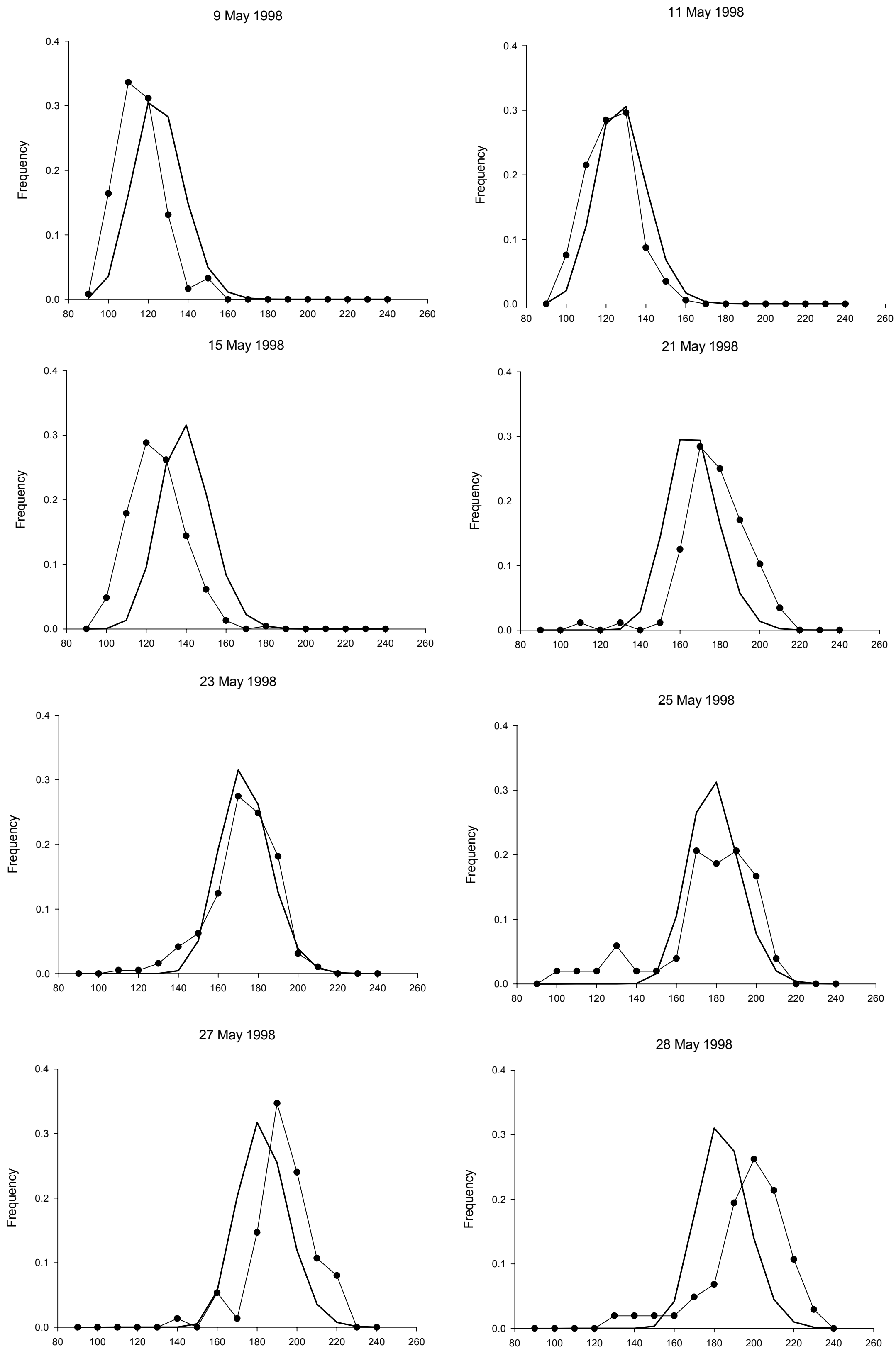


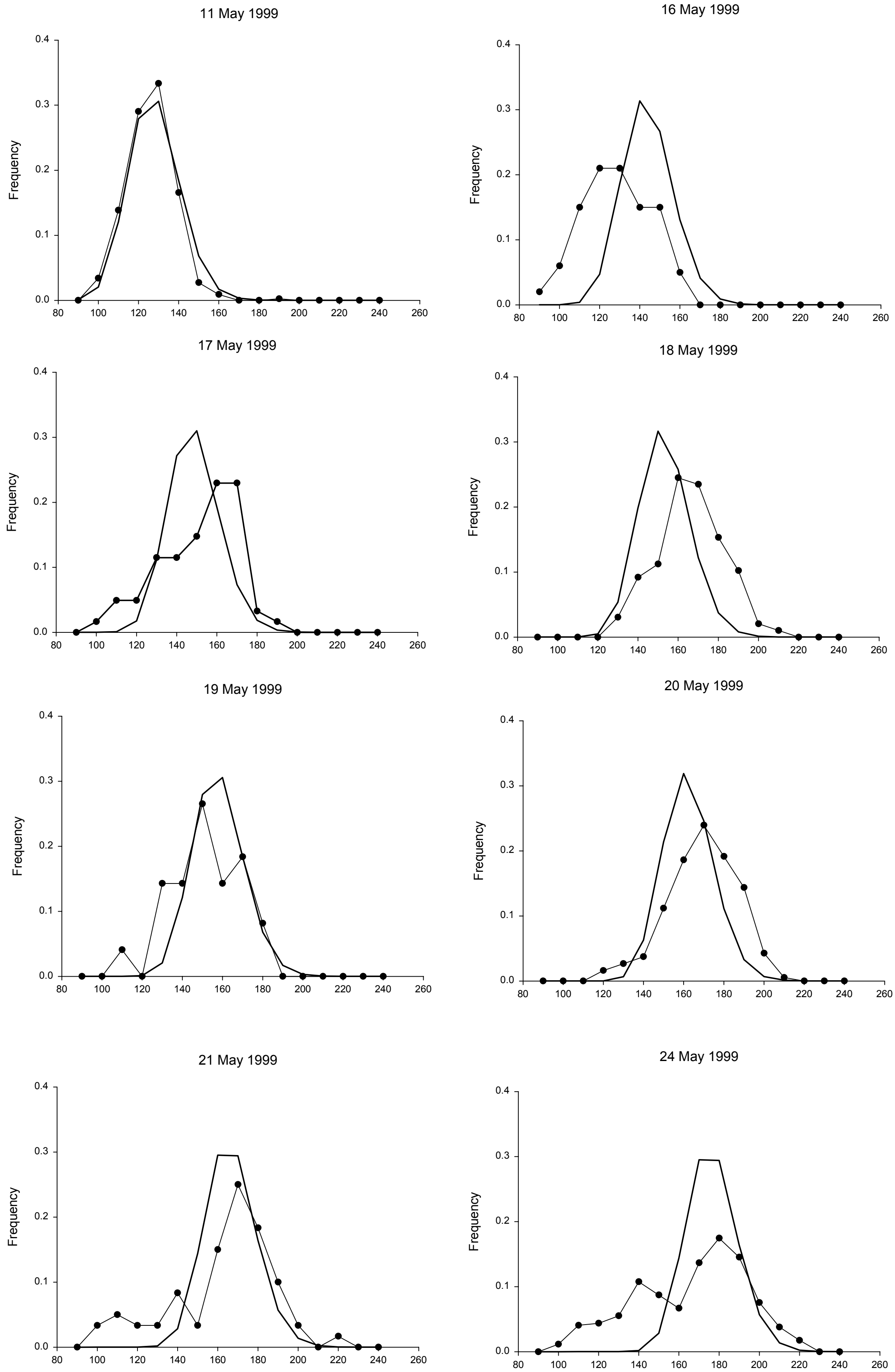
Appendix 3. Weight frequency distributions for catches of Red Knot of more than 30 birds 1997-2002. Each tick mark on the horizontal axis represents 5% and numbers at the bottom left indicate date of catch (every 5 days). A solid horizontal line is included on each graph to indicate 180g (putative departure weight). The mean of each catch is also indicated, by the dashed line.



Appendix 4. Weight gain in Red Knot. Weight frequency distribution observed, in catches of more than 50 Red Knot (line with points) for the years 1998 - 2002. The solid line indicates the frequency distribution of birds that would be predicted had all birds arrived on May 9, with an initial frequency distribution and growth curve depicted in Fig. 2. Catch date is indicated above each graph.




9 May 1998
11 May 1998
15 May 1998
21 May 1998
23 May 1998
25 May 1998
27 May 1998
28 May 1998
Frequency


11 May 1999
16 May 1999
17 May 1999
18 May 1999
19 May 1999
20 May 1999
21 May 1999
24 May 1999
Frequency
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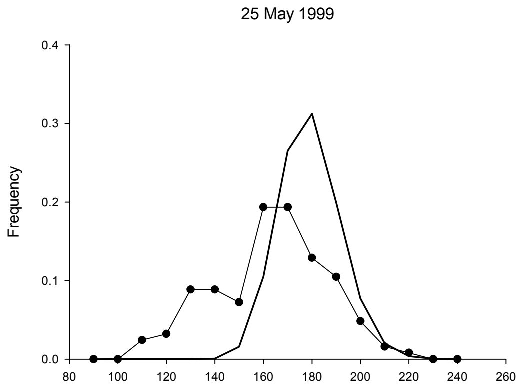
0.1
0.2
0.3
0.4
80
100
120
140
160
180
200
220
240
260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Frequency
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0.4
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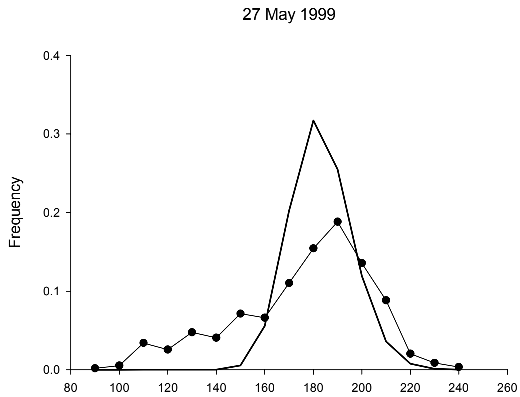
100
120
140
160
180
200
220
240
260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Frequency
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0.3
0.4
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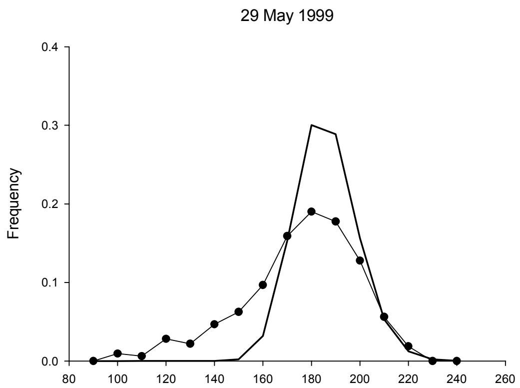
100
120
140
160
180
200
220
240
260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Frequency
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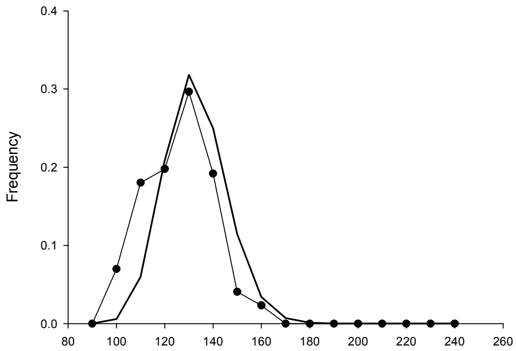
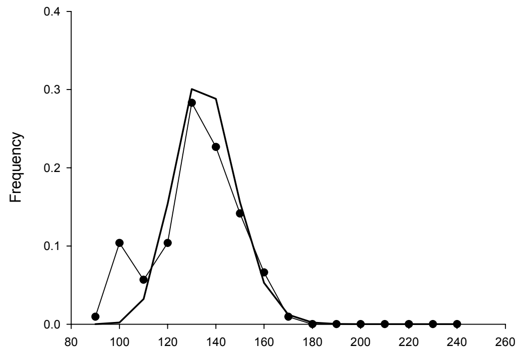
0.4
80
100
120
140
160
180
200
220
240
260

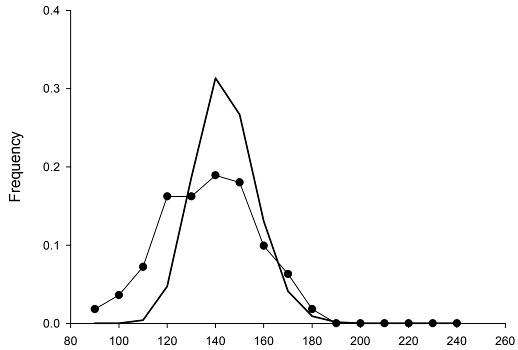
13 May 2000



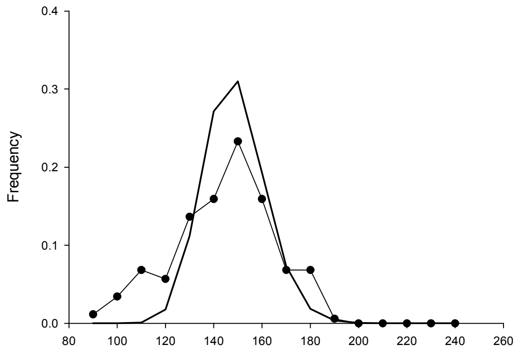
14 May 2000



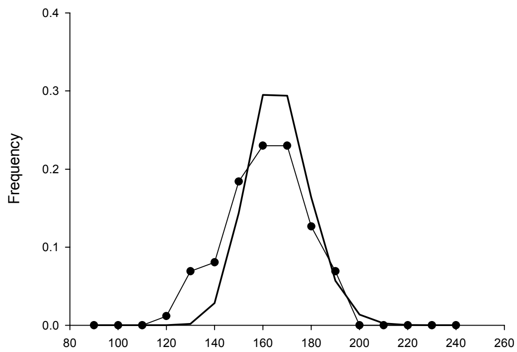
16 May 2000



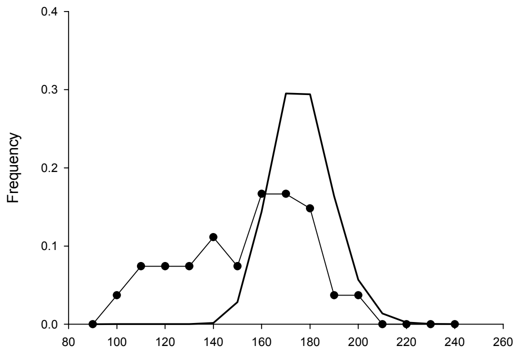
17 May 2000



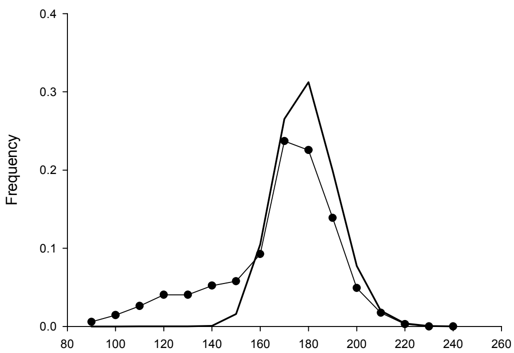
21 May 2000



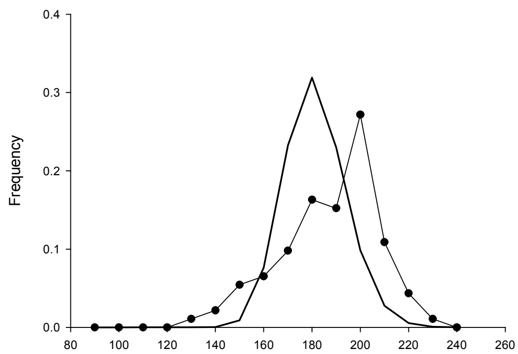
24 May 2000

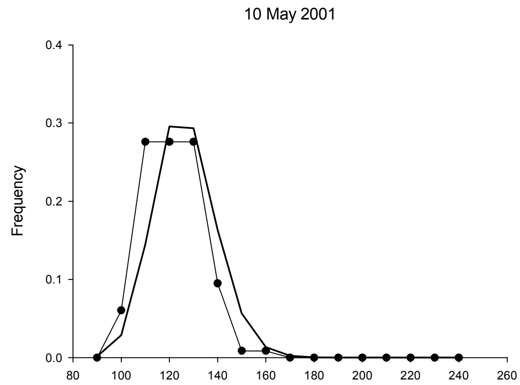


25 May 2000



26 May 2000




10 May 2001
Frequency
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0.3
0.4
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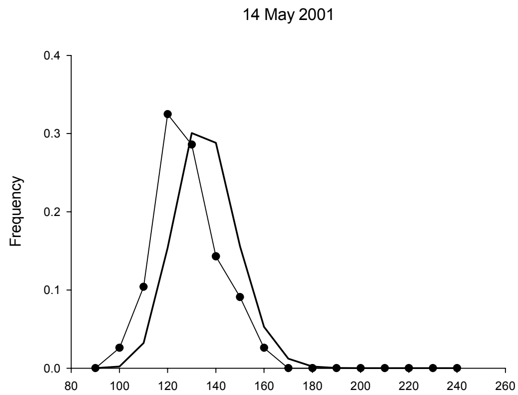
14 May 2001
Frequency
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0.2
0.3
0.4
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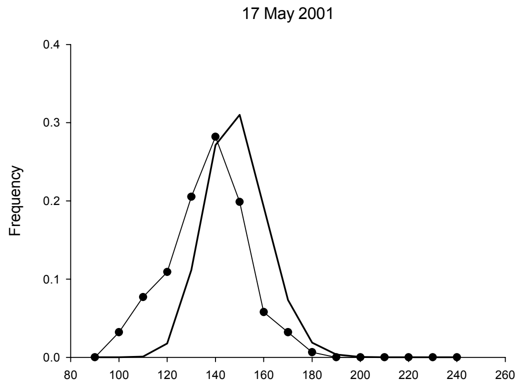
17 May 2001
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0.3
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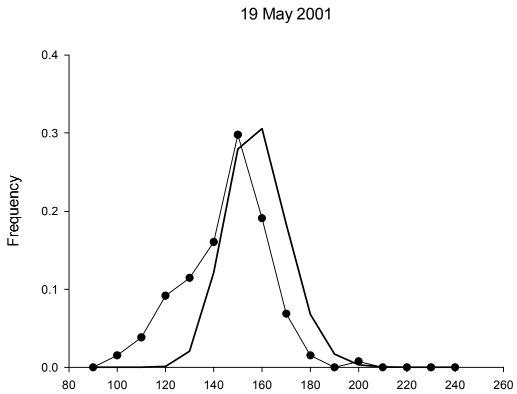
19 May 2001
Frequency
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0.3
0.4
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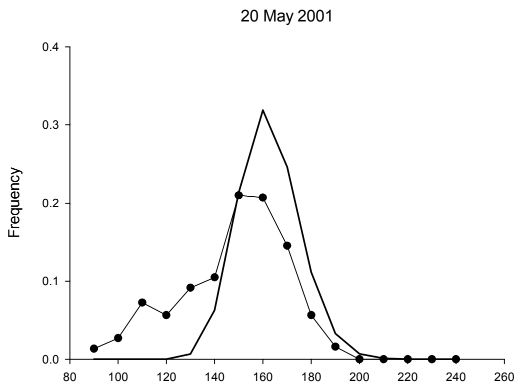
20 May 2001
Frequency
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0.2
0.3
0.4
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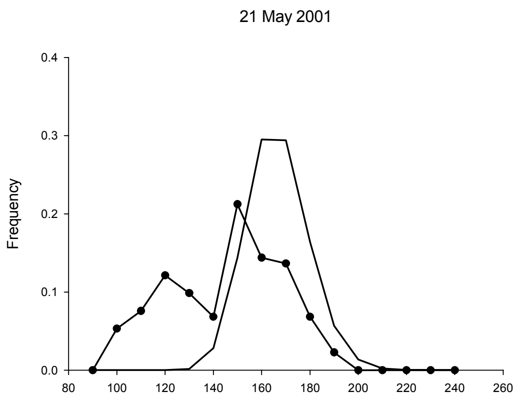
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Frequency
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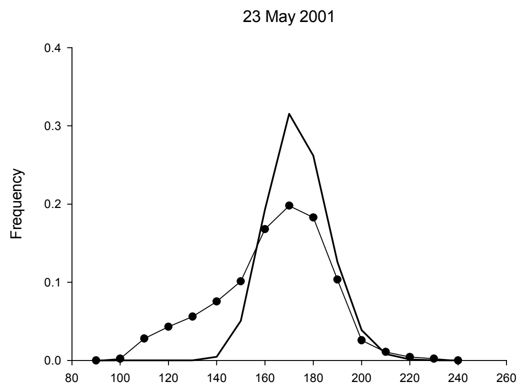
23 May 2001
Frequency
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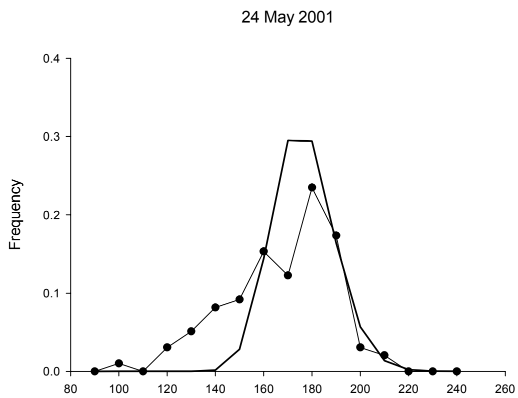
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Frequency
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0.3
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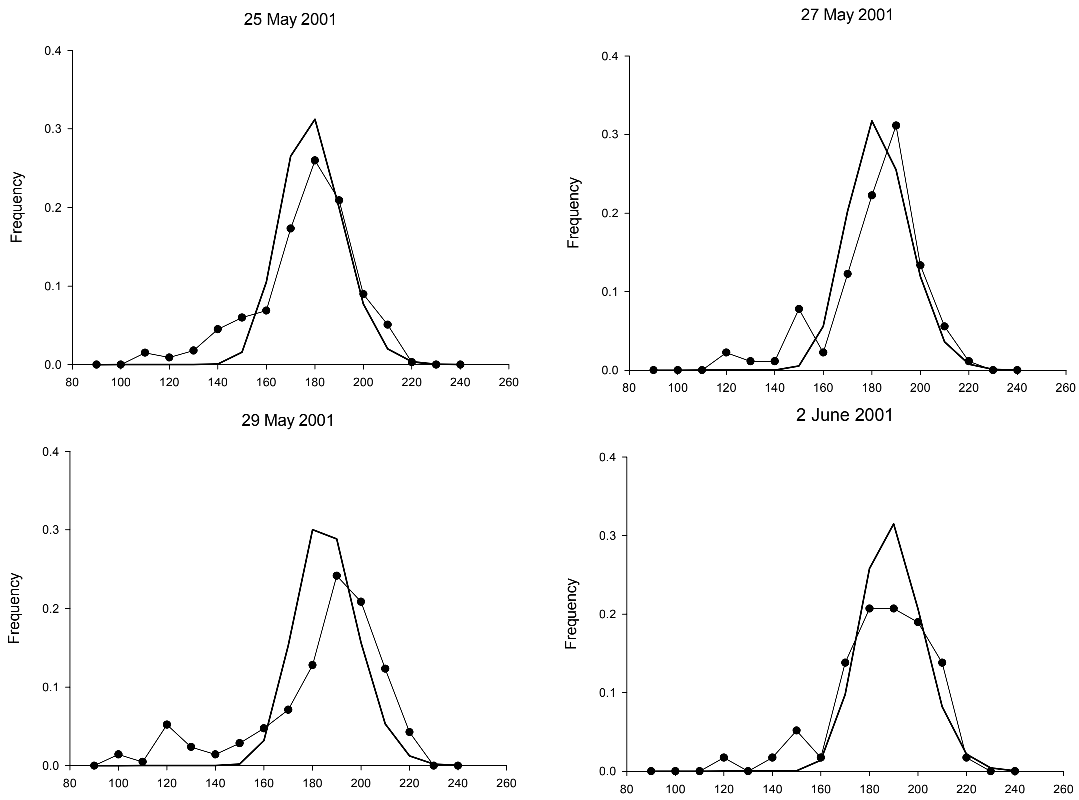
25 May 2001
27 May 2001
29 May 2001
2 June 2001
Frequency
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0.2
0.3
0.4
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100
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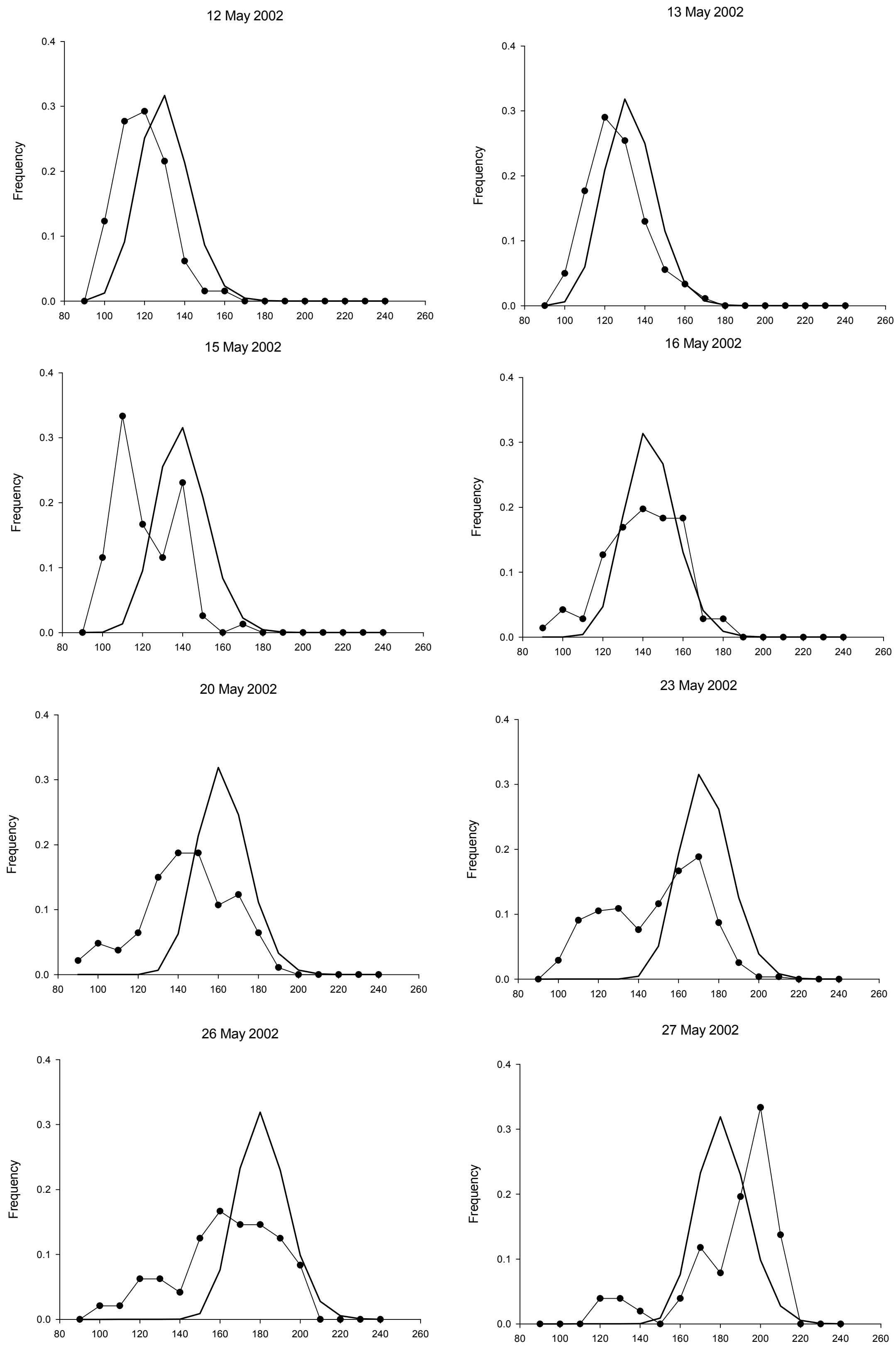
180
200
220
240
260


12 May 2002
13 May 2002
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20 May 2002
23 May 2002
26 May 2002
27 May 2002
Frequency
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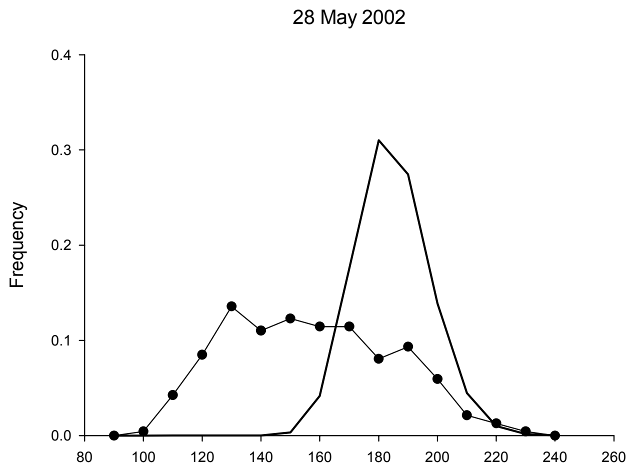
100
120
140
160
180
200
220
240
260


28 May 2002
Frequency
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0.2
0.1
0.0
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100
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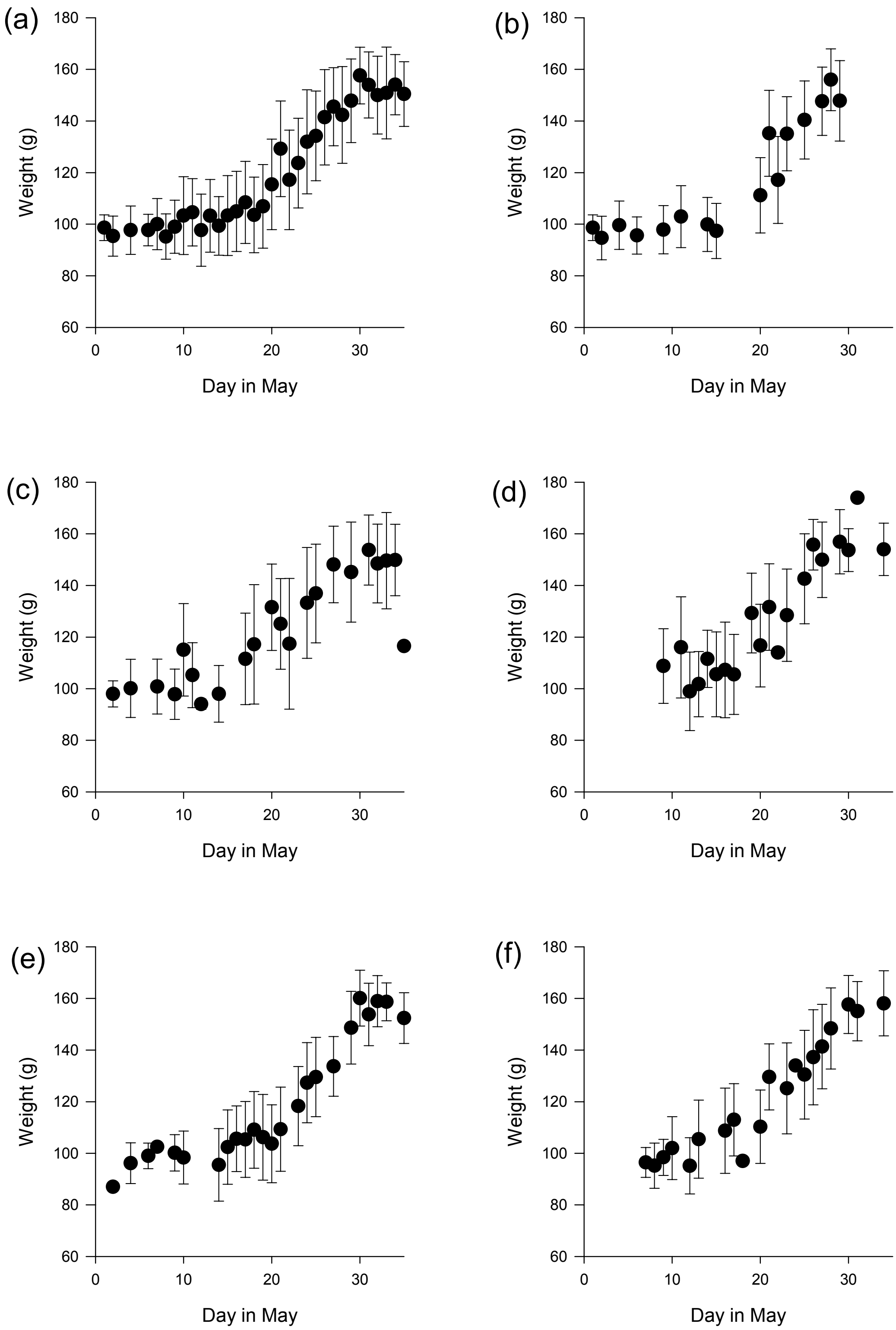
140
160
180
200
220
240
260

Appendix 5. Weight gain in Ruddy Turnstone and Sanderling in (a) all years, (b) 1998, (c) 1999, (d) 2000, (e) 2001 and (f) 2002. Bars represent 1 standard deviation around the mean.

Ruddy Turnstone



Sanderling