The Generally Weak Influence of Density-Dependent Regulation on Natural Animal Populations

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Abstract

Animal population densities are thought to be "regulated" by density-dependent processes (Haldane, 1953; Royama, 1977; Berryman, 1991). The perceived importance of these processes to biologists is evident from the vast amount of research dedicated to this idea (Inchausti, 1994). Most of this research addresses the problem(s) of detecting the effect of density-dependent regulatory processes using time series data. However, the question of the relative importance of density-dependent factors upon rates of change of population abundances is rarely addressed. In this thesis, I quantify the importance of density-dependent factors in 303 natural animal populations. I found that, on average, only ≈19% of the temporal variability in per capita growth rate could be statistically related to population density. Yet research effort concentrates overwhelmingly on density-dependent processes. I conclude that the effects of density-dependent processes within natural animal populations are generally weak and disproportionately studied.

Because many, if not all, ecological processes act on some characteristic temporal or spatial scale (O'Neill et al., 1986; Wiens, 1989; Pimm, 1991; Maurer, 1994; Fleishman, 1995) I also address the question of how the characteristic time of density-dependent regulatory processes might affect the estimates of the influence of regulatory processes on a population's per capita growth rate. I hypothesized that if density-dependent regulatory processes operate on a characteristic temporal scale that sampling with a sampling period commensurate with the characteristic time of these processes would yield the maximal amounts of variability in the per capita growth rate statistically related to the variability in N. Simulated population time series were generated using a logistic growth model with a stochastic term added. Based on the analysis of the simulated time series, the characteristic time of density-dependent regulatory processes is predicted to be independent of life-history traits correlated with body size. The characteristic times are predicted to be integral multiples of 1 year (1, 2, 3 and 4 years) for all modelled body sizes. These predictions, regarding characteristic times, were found to be suspect after further testing supported the contention that these results may be methodological artifacts. I suggest that these results are due to the pragmatic criteria imposed to constrain the number of possible subsamples to be analyzed. I further suggest that to better address the characteristic time hypothesis, time-slices with different time periods between successive population densities are required.

Résumé

Les populations animales semblent être réglées par des processus qui dépendent de la densité (Haldane, 1953; Royama, 1977; Berryman, 1991). L'importance que donnent les scientifiques à ces processus se manifeste dans l'immense quantité de travaux dédiés à ce sujet (Inchausti, 1994). La majeure partie ces de recherches se concentrent sur le(s) problème(s) de détection de l'effet des processus régulateurs dépendants de la densité en se servant de données de séries temporelles. Cependant, la question de l'importance relative des facteurs dépendants de la densité sur les taux de changement de l'abondance des populations est rarement étudiée. Dans cette thèse, je quantifie l'importance des facteurs dépendants de la densité chez 303 populations naturelles d'animaux. J'ai trouvé qu'en moyenne seulement ≈19% de la variabilité temporelle du taux de croissance per capita peut être statistiquement reliée à la densité de la population. Toutefois, les efforts de recherche sont concentrés majoritairement sur les processus dépendants de la densité. Je conclue donc que les effets des processus dépendants de la densité au sein des populations naturelles d'animaux sont généralement faibles et étudiés d'une façon disproportionnée.

La plupart des processus écologiques, sinon tous, agissent sur une échelle temporelle ou spatiale caractéristique (O'Neill et al., 1986; Wiens, 1989; Pimm, 1991; Maurer, 1994: Fleishman, 1995). J'adresse donc la question à savoir comment l'échelle temporelle caractéristique des processus régulateurs dépendants de la densité peut affecter les estimés de l'influence des processus régulateurs sur le taux de croissance par individu d'une population. J'émet l'hypothèse que si les processus régulateurs dépendants de la densité opèrent sur une échelle temporelle caractéristique, un échantillonnage avec une période d'échantillonnage coétendue avec le temps caractéristique de ces processus produirait les quantités maximales de variabilité du taux d'accroissement par individu qui sont reliées statistiquement à la variabilité dans la densité de la population. Des séries temporelles de populations simulées ont été générées à l'aide d'un modèle logistique avec l'ajout d'un terme stochastique. En se basant sur l'analyse des séries temporelles simulées, nous pouvons prédire que le temps caractéristique des processus régulateurs dépendants de la densité est indépendant des caractéristiques de vie qui sont corrélées avec la taille. Nous pouvons prédire que les échelles temporelles caractéristiques sont des multiples entiers d'un an (1, 2, 3, et 4 ans) pour toutes les tailles de corps modélisées. Ces prédictions, concernant les temps caractéristiques, ont été trouvé suspectes à la suite de tests additionnels qui supportent la suggestion que ces résultats pourraient être des artefacts méthodologiques. Je suggère que ces résultats sont attribuables aux critères pragmatiques imposés pour restreindre le nombre possible de sous-échantillons à analyser. De plus, je propose que des sections de temps avec des périodes différentes entre des estimés de la densité de populations soient requises pour mieux étudier l'hypothèse du temps caractéristique.

"The traditional questions and topics of our science can be fruitful sources of inspiration for new research. They can also be intellectual traps. We risk entrapment when we allow the science to become so well defined that the only interesting questions are those which we have always asked, but failed to resolve. This is the final retreat to scholasticism, ..."

Frank H. Rigler & Robert H. Peters (1995)

"It is inappropriate to be concerned about mice when there are tigers abroad"

G. E. P. Box (1976)

"The wrong view of science betrays itself in the craving to be right; for it is not his possession of truth that makes the scientist, but his persistent and recklessly critical quest for truth."

Karl Popper (1968)

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Preface

Chapter 2 is presented here as it was submitted for publication. The style in chapter 2 differs from the rest of this manuscript due to the unique style required by the journal to which it was submitted. Bracketed annotations such as: (see "Monotonicity" on page A.1) have been added to this chapter that were not in the submitted manuscript. These annotations refer to explanatory notes or figures in Appendix A which elaborate on the annotated points to assist in understanding what was done. Similarly, *Abstract*, *Introduction*, *Methods* and *Discussion* titles have been added to help delineate these areas in chapter 2. All references in this chapter are also included, in a more conventional format, in chapter 5.

Chapter 3 is written in a thesis style.

Chapter 5 contains all references cited in this thesis.

Appendix A contains methodological information and background regarding chapter 2.

Appendix B presents additional results and figures parallelling those found in chapter 2. This section focuses on the subset of the populations used in chapter 2 that contain only one population for each unique species.

Appendix C consists of Table C.1 listing the species names, sources and the r_P^2 and r_S^2 values obtained for each population used in chapter 2.

Appendix D presents the data used in chapter 2 along with cross references to Table C.1.

Appendix E contains all the figures for chapter 3 that if presented in chapter 3 would have made chapter 3 unreadable.

CHAPTER 1: General Introduction

What determines the size of a population?

Some populations fluctuate dramatically whereas others tend to vary relatively little. Why this might be so has interested ecologists for years (Begon, 1990). Raising the question "What determines the size of a population" usually leads to the question "What affects the growth rate of a population?" To address the question "What affects the growth rate of a population?" the processes and factors that influence a population's growth rate can be classified into two general categories: density dependent and density independent. Density-dependent processes influence a population's per capita growth rate as some function of the population's current or past density whereas density-independent factors affect a population's per capita growth rate independently of the density of the population.

A regulated population is...

A population is often imprecisely considered to be regulated if density-dependent processes act to increase a population's size when it is small and decrease the population's size when it is large. Though direct density-dependent processes (i.e., density-dependent processes that negatively affect per capita growth rate with increasing density) are a necessary condition for regulation to occur, they are not a sufficient condition. In a strict sense, for a population to be regulated three conditions need to be satisfied: direct density dependent processes must be present; the return tendency must be of sufficient strength to counteract the effects of density-independent factors; and the lag time in which the return tendency manifests its effects must be sufficiently small to prevent divergent oscillations (Turchin, 1995). Furthermore, a population is not considered to be regulated if it fluctuates around a trend (Turchin, 1995).

Populations, regulated or not?

The question as to whether animal populations are regulated or not has been one of the central issues in ecology for 60 years (Cappuccino, 1995). Historically the issue was quite polarized with one side arguing that density-independent environmental factors determine the size of natural populations (Davidson & Andrewartha, 1948) and the other side arguing that all populations must be self-regulating— density-dependent — so that they may persist (Nicholson, 1933). On the environmental side, arguments were supported by statistically relating the variance in population size to the variation in some environmental variable. For instance, temperature and rainfall statistically account for 78% of the variation in *Thrips imaginis* abundance (Davidson & Andrewartha, 1948). In contrast, Nicholson (1933) argued deductively that population regulation was the principal determinant of population abundance and that it was ubiquitous and necessary for the persistence of species. Currently both self-regulatory processes and environmental factors are believed to influence a population's density (Horn, 1968; Strong, 1986; Begon, 1990; Cappuccino, 1995).

Detection of density dependence

Though it is believed that both density-dependent and density-independent factors influence a population's abundance, the predominant focus of population regulation research has been the statistical detection of density-dependent patterns in abundance time series data (Turchin, 1995). An enormous array of statistical tests has been developed to analyze time-series abundance data to determine if a population is regulated or not (Morris, 1959; Varley & Gradwell, 1960; Bulmer, 1975; Slade, 1977; Vickery & Nudds, 1984; Pollard et al., 1987; Reddingius & Den Boer, 1989; Crowley, 1992; and Dennis & Taper, 1994; to name a few).

Each detection test is usually developed in an attempt to overcome the shortcomings of earlier tests (Fox & Ridsdill-Smith, 1995). These shortcomings are often identified by comparative studies involving simulated population models (e.g., Holyoak, 1993) or the application of a test to different populations (e.g., Hassell et al., 1989). Though the cycle of developing or refining existing tests is necessarily an endless task, a pertinent question remains to be asked— with each step in the cycle are we learning more about whether or not populations are regulated? I agree with the opinion, expressed by Wolda (1995), that every attempt "... to test the regulation hypothesis has failed."

What was the question?

Wolda (1995) has suggested that the failure to resolve the population regulation issue is a result of asking the wrong question. The original question stated at the outset of this introduction was "what determines the size of a population?" If we assume that both density-dependent regulatory processes and density-independent factors affect population densities then a more appropriate question would be: how strong are the relative influences of density-dependent regulatory processes versus density-independent factors? It is this question that is the subject of the research in this thesis.

The focus of this thesis

The relative effects of regulatory versus non-regulatory influences

To determine the relative influence of regulatory processes and non-regulatory factors on a population's per capita growth rate requires some measure(s) that relate the variability in a population time-series to density-dependent regulation and density-independent factors. It is relatively easy to evaluate the influence of the regulatory processes because the regulation hypothesis predicts a negative monotonic relationship between a population's per capita growth rate γ and its density N.

Chapter 2 is an empirical study, of 303 natural animal populations, that determines how much of the variability in γ can be statistically related to the variability in N— the relative influence of density-dependent regulation.

The influence of density-independent factors is more difficult to assess because one must identify the environmental factors that affect growth which is beyond the scope of this thesis.

The characteristic temporal scale of density-dependent regulatory processes

Because the vast majority of the time-series used in chapter 2 consist of yearly census data, I was prompted to address the question of how the characteristic time of density-dependent regulatory processes might affect the estimates of the influence of regulatory processes on a population's per capita growth rate. I hypothesized that since density-dependent regulatory processes operate on some characteristic temporal scale, sampling population densities with a sampling period commensurate with the characteristic time of these processes would yield the maximal amounts of variability in γ statistically related to the variability in N.

Chapter 3 is a modelling exercise in which simulated density-dependent population time series are produced and resampled with different sampling periods. Each resampled data set is analyzed using the analysis methods of chapter 2 and the characteristic time of the density-dependent regulatory process is inferred from the sampling period with the maximal amounts of variability in γ explained by N.

A variety of parameter values are used to generate the simulated time series. The parameter values are derived from empirical body-size scaling relationships because it is postulated that characteristic temporal scales may be species specific (Wiens, 1989). Since numerous life-history traits correlate with body size it is hoped that any patterns in the characteristic times could be easily related to actual populations according to body size.

Given the body size of a natural population of interest, I would be able to predict the optimal sampling period for the study of density-dependent regulatory processes within that population. Similarly, I would also be able to evaluate how each estimate of the relative importance of density-dependent regulatory processes within each population, in chapter 2, may have been affected by a yearly sampling strategy.

CHAPTER 2: Factors affecting animal population density changes

Abstract

Animal population growth rates are affected by density-dependent processes, density-independent factors and stochasticity. Density-dependent processes are believed fundamental for a population to avoid extinction. However, the relative strength of these influences upon rates of population change is unclear. Among 303 natural animal populations, only ≈19% of the temporal variability in per capita growth rate could be statistically related to population density. Density-independent or stochastic factors must explain a much greater portion of variability. Thus, natural populations' self-regulatory mechanisms have a limited tendency to affect growth rates so that population extremes are avoided.

Introduction

The densities of natural animal populations often fluctuate dramatically over time. This temporal variability has prompted ecologists to consider which factors or processes determine species' abundances (*1-6*). Fundamentally there are two classes of processes. Density-dependent processes (whose intensity depends upon population abundance) act mainly through biotic interactions such as intraspecific competition. Density-independent factors usually reflect variations in environmental factors. Both types of factors influence population dynamics (*4*, *7-9*), yet their relative importance remains unclear.

The population regulation hypothesis postulates that a population's density must be regulated by density-dependent processes for the population to persist in the long term (*10*, *11*). Population regulation research has centered on the statistical detection of density dependence from time series data (*12*). It has been suggested (*13*) that this focus should shift to the question of "how strong are the regulatory versus disruptive forces" within a population. It is straight forward to evaluate the influence of the regulatory processes because the regulation hypothesis predicts a simple relationship between a population's per capita growth rate and its density. The influence of disruptive forces (density-independent factors) is more difficult to assess because one must identify the environmental factors that affect growth. In this study, we assess the proportion of the variation in the per-capita growth rate attributable to regulatory forces.

In a regulated population, the per capita growth rate $\gamma \equiv \frac{1}{N} \cdot \frac{dN}{dt}$ is a function of N, the population's density (*12*). Although $f(N)$ may have different forms, only a decreasing, monotonic function will stabilize population density around some equilibrium level (*12*). (see "Monotonicity" on page A.1)

One could quantify the effect of density-dependent processes on the rate of population change by observing the Pearson correlation (r_P) between observed γ's and those predicted by $f(N)$. Alternatively, one could observe the Spearman rank correlation (r_S) between γ and N, since a regulated stable population would show a negative monotonic relationship between γ and N. The coefficients of determination (r_P^2 and r_S^2) inferred from these correlations would be estimates of the portion of the temporal variability of γ that could be statistically explained by N, that is, estimates of the importance of density-dependent factors upon population growth.

Methods

We gathered published data describing population densities over time for 303 populations (*14-17*). We included any study of a naturally-occurring animal population that included yearly observations of population density for 9 or more consecutive years.

To estimate γ at a given time t_i, a second degree polynomial was fitted to the point (t_i, N_i) and the two adjacent points (t_{i-1}, N_{i-1}) and (t_{i+1}, N_{i+1}). The slope of the tangent to the polynomial at time t_i, divided by N_i, is the estimate of γ_i. Thus, for each species, we generated a set of (N_i, γ_i) points (see "Calculation of per capita growth rate" on page A.2). Because current growth rate at any given time may depend upon previous population densities (*18*) we also generated lagged sets in which each γ_i value was paired with the density of an earlier year,

$$N_{i-1}, N_{i-2}, N_{i-3}, \ldots, N_{i-L},$$

where L represents the maximum number of years the data are lagged. The maximum lag L is either 10 years or half the number of years $(n/2)$ in each population's data set, whichever is less. (see "Lags" on page A.5)

Since $f(N)$ is unknown, curves were fitted to each of the data sets generated using robust locally-weighted regression (LOWESS) (*19*) (see "Density-vagueness" on page A.1). LOWESS is intended to reveal the shape of a relationship without first specifying a mathematical form. The LOWESS tension parameter was manipulated to yield the negative monotonic curve with the strongest Pearson correlation (r_P) between predicted and observed γ. The smoothed LOWESS curve represents the strongest possible relationship between $f(N)$ and N that satisfies the conditions necessary for density-dependent regulation (see "Estimating $f(N)$" on page A.8). The Spearman rank correlation is also an estimate of the strength of the relationship between γ and N for an unknown $f(N)$. Both statistics were calculated for each lagged- and unlagged-data set, and the strongest r_S and r_P were retained. (see "Pearson correlation" and "Spearman correlation" on page A.10)

Because γ is calculated using N, there may be a spurious correlation between γ and N. We therefore used a randomization procedure to adjust r_S and r_P to remove the effects of any spurious correlation (*20*)(see "Randomization procedure" on page A.11). When abundance data consisted of many estimates of N per year, subsets of the data were created containing a single N per year (*21*). Each subset was analyzed separately, and the largest r_S^2 and r_P^2 among all subset analyses were retained as the estimates of density-dependent regulation for that population (*21*). Similarly, when a data set consisted of abundance data at different life stages of a species (for example, ref. *17*), each life stage's abundance data were analyzed separately and the largest r_S^2 and r_P^2 of these stages was retained for that population.

Results and discussion

On average, relatively little of the temporal variability in per capita growth rate proved to be statistically related to population density: 20.5% (r_S^2) and 17.5% (r_P^2) (Fig. 1). These figures are overestimates because every assumption used during our analysis was chosen to maximize the variance attributable to density-dependent regulation.

The median effect of density-dependent regulation did not differ significantly among the taxonomic classes represented in our data for the r_P^2 estimate ($p = 0.29$) but did differ for the r_S^2 estimate ($p = 0.045$) (Fig. 2). Pairwise median tests (not corrected for multiple comparisons) show that the branchiopods' median r_S^2 is less than those of insects, mammals and birds ($p = 0.0057$). However, after correcting for experimentwise error, these differences become non-significant.

The majority of the populations showed evidence of "direct density dependence" with their maximum values for r_S^2 and r_P^2 occurring most often when per capita growth rates were associated with the previous year's densities (in 61% and 58% of cases, respectively) (Fig. 3). Almost all of the remaining populations (38% and 41%) had maximum r_S^2 or r_P^2 when growth rates were lagged with densities two or more years earlier— "delayed density dependence." Though 38% or 41% of the populations, exhibiting delayed density dependence, is not the majority, it does tend to support Turchin's (*18*) contention that many populations exhibit delayed density-dependent regulation rather than direct density dependence.

Because population regulation is thought to promote long-term species persistence (*1*), one might expect stronger (versus more easily detected (*22*)) density-dependent regulation in longer time-series. Yet we find no consistent relationship between either estimate of density dependence and the number of years in a data set (Fig. 4).

Few studies have explicitly addressed the impact of density-independent factors on per capita growth rate. However, previous studies show that much (21% to 88%) of the variance in population size (N) can be related to density-independent factors (*15, 23*). This suggests that, in contrast to the effect of density-dependent processes, density-independent factors may strongly influence population growth.

The density-dependent processes that prevent population densities from approaching inordinately high or low levels are generally quite weak. In contrast, the literature suggests that stochastic or environmentally-driven effects on density may be quite strong. It is likely that the majority of natural populations do not avoid extinction through intrinsic mechanisms that regulate their densities.

A search of BIOSIS® Biological Abstracts (January 1989 to March 1994) for five journals (*American Naturalist*, *Ecology*, *Journal of Animal Ecology*, *Oecologia*, and *Oikos*) identified 727 papers that dealt with density-dependent factors, and 106 that dealt with density-independent factors. Combining this observed emphasis on density-dependent research with our results, we suggest that to better understand the population dynamics of natural populations, more research is required on non-density-dependent influences.

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20. The randomization procedure consisted of creating 499 randomized sets of the unlagged (N,γ) points. A randomized set was generated by randomly sampling the γ values without replacement and associating each selected γ to a value of N. A set of (N,γ) ordered pairs generated by this approach should be free of any spurious correlations between γ and N. Likewise, the correlation of a randomized set would represent the value expected in the absence of any density-dependent regulation. Each of the randomized sets was analyzed in the same manner as the original data. The mean value of the strongest 499 randomly produced correlations is the correlation expected in the absence of density-dependent regulation. The adjusted correlation is calculated by subtracting the mean random correlation from the correlation for the original data. When the original correlation was weaker than the mean random correlation, the adjusted correlation was considered to be zero. The portion of the temporal variability of γ that could be statistically explained by N was estimated by squaring the adjusted correlation.

21. A number of the data sets used in this study had more than one recorded density within each year. For example, Garsd et al. (*16*) recorded the density of *Microtus californicus* at 6 different times during each year for 21 years. These data sets were analyzed using one of the 6 yearly densities and the corresponding density of

each year (i.e., if the first of the 6 densities of the first year was used, the first of the 6 densities in each subsequent year was also used). This was done for each of the densities within a year and the yearly subset(s) yielding the largest coefficients of determination were selected and their r_S^2 and r_P^2 were used as the estimates of density-dependent regulation for that population.

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Figures

FIGURE 2.1 Histogram of two estimates (r_S^2 and r_P^2) of the percentage of the temporal variability in the per capita growth rate (γ) attributable to density-dependent processes for 303 animal populations. The height of each bar indicates the proportion of the 303 populations with r_S^2 or r_P^2 estimates within the % categories on the x-axis. The numbers above each bar denote the number of populations in each % class. We calculated r_S^2 and r_P^2 for both unlagged and lagged data. For each population, the highest r_S^2 and r_P^2 observed among all lags were used to develop this figure. These estimates of the proportion of variance attributable to density-dependence are probably over-estimates, since all our assumptions maximized the variance attributable to density-dependent factors. Note that, nonetheless, relatively small amounts of the variance in γ can be related to N.

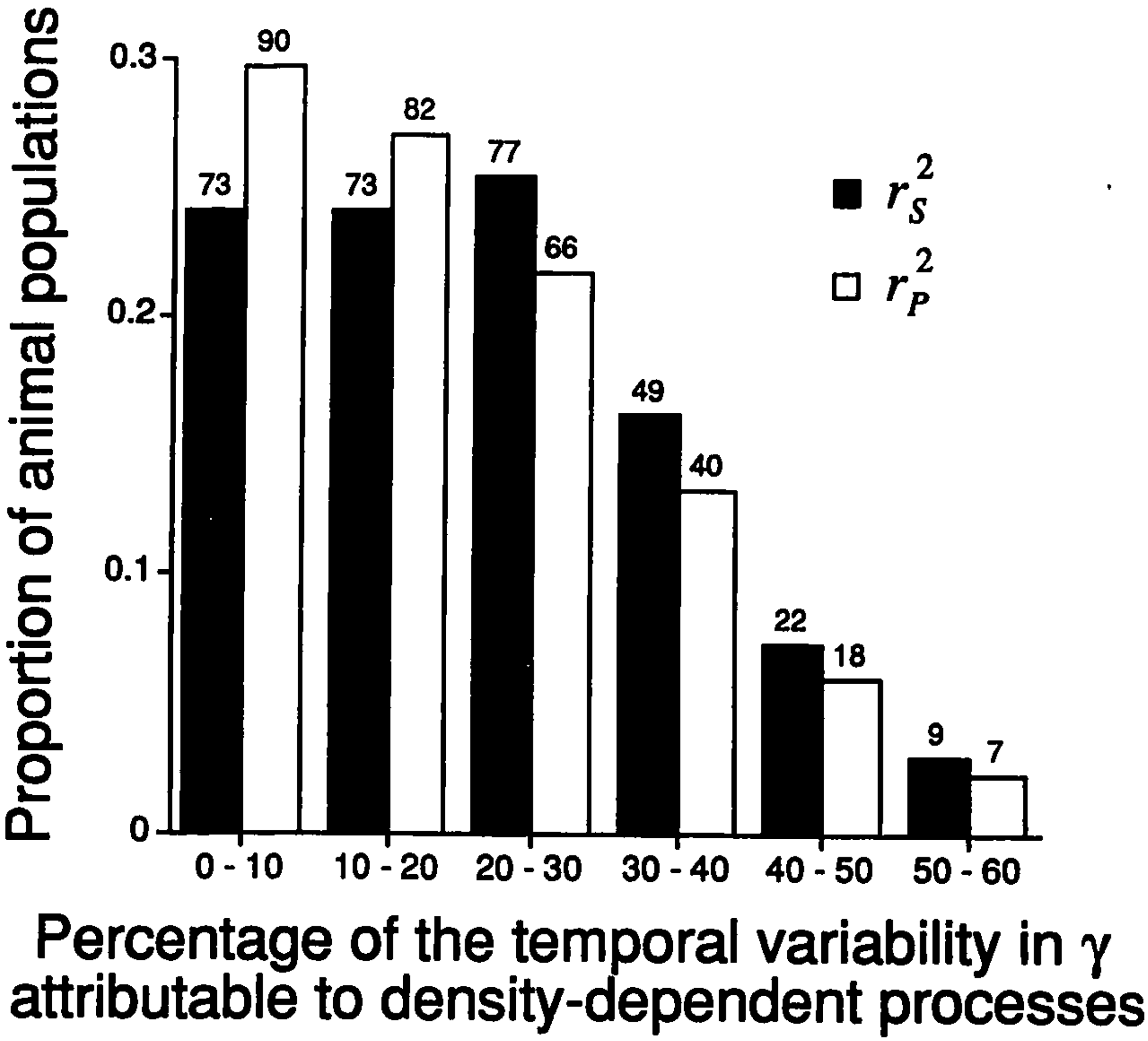

Proportion of animal populations
0.3
0.2
0.1
0
90
82
77
73
73
66
49
40
22
18
9
7
■ r_S^2
□ r_P^2
0 - 10
10 - 20
20 - 30
30 - 40
40 - 50
50 - 60
Percentage of the temporal variability in γ attributable to density-dependent processes

FIGURE 2.2 Notched box plots (24) of the distributions of r_S^2 (panel *a*) and r_P^2 (panel *b*) within animal classes. The median (r_S^2 or r_P^2) for each group is marked by the central horizontal line contained within the notched box. The first and third quartiles are represented by the lower and upper hinges (the horizontal edges of the central notched box). The space between the two hinges represents the interquartile range. The vertical lines ("whiskers") extending from the notched boxes delineate the range of r_S^2 or r_P^2 values that lie outside the hinges and within a distance 1.5 times the span of the interquartile range (25). The notches are the diagonal lines extending from the median to the vertical sides of a box. If the notches of two medians do not overlap, then the medians can be considered to be significantly different ($p \leq 0.05$). There were only two values for the reptile category, so a notched box plot was not drawn. Instead, both points were plotted (•) and their median shown with a horizontal line. Density dependence (r_S^2, panel *a*) is less pronounced for the branchipods than for insects ($p = 0.0058$), mammals ($p = 0.0057$) and birds ($p = 0.0057$) (pairwise median tests using Fisher's exact test for each of the three comparisons). However, if one corrects for multiple comparisons, then the amount of variance attributable to density-dependent factors does not vary among animal classes.

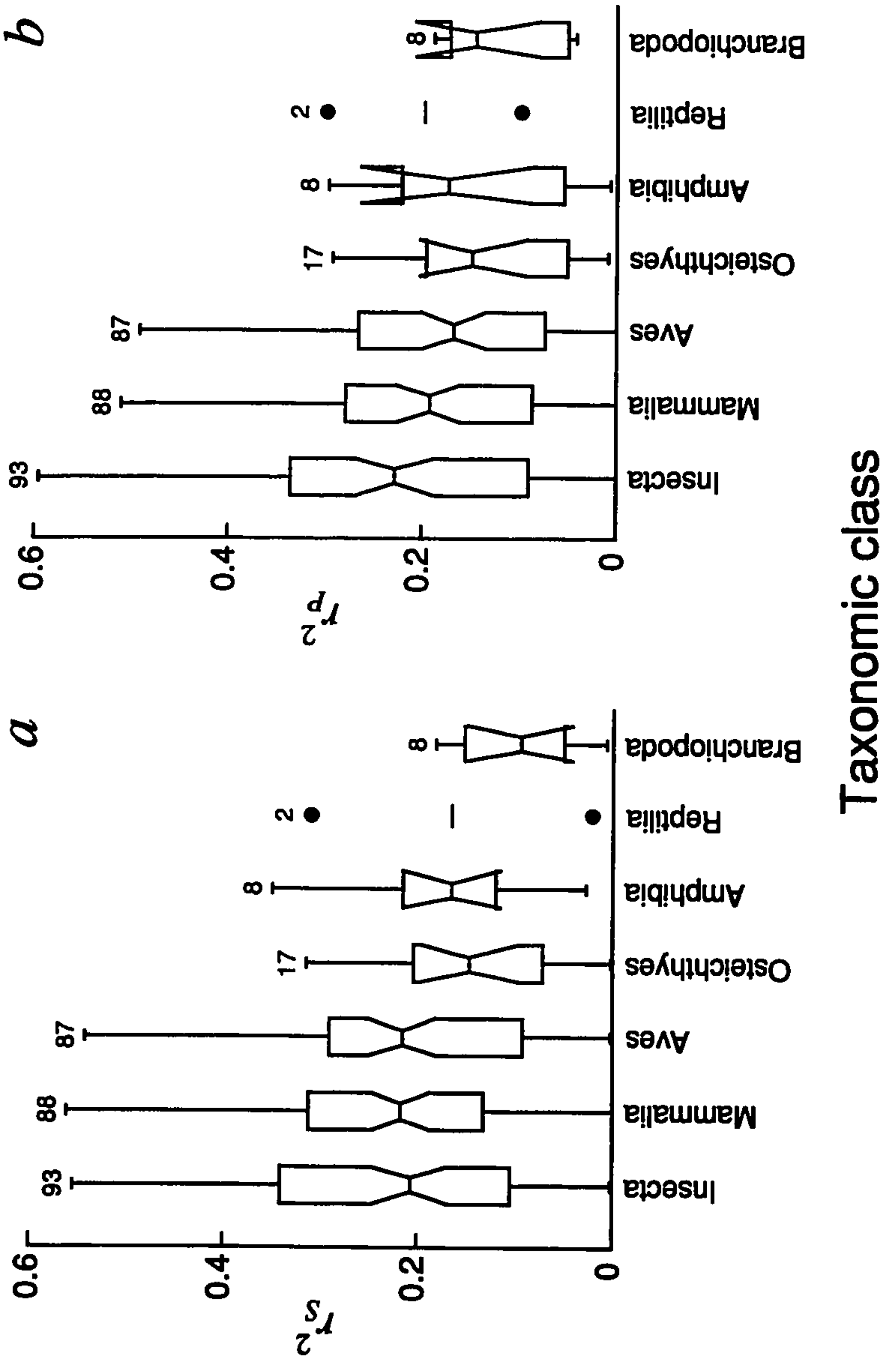

a
r_s^2
0.6
0.4
0.2
0
Insecta
Mammalia
Aves
Osteichthyes
Amphibia
Reptilia
Branchiopoda
93
88
87
17
8
2
8
b
r_p^2
0.6
0.4
0.2
0
Insecta
Mammalia
Aves
Osteichthyes
Amphibia
Reptilia
Branchiopoda
93
88
87
17
8
2
8
Taxonomic class

FIGURE 2.3 A histogram showing the proportion of 303 animal populations for which the highest r_S^2 & r_P^2 were obtained after lagging the data for the number of years represented on the abscissa. Note that the vast majority of populations (185 or 175 of 303) showed maximal density dependence with a lag of one year.

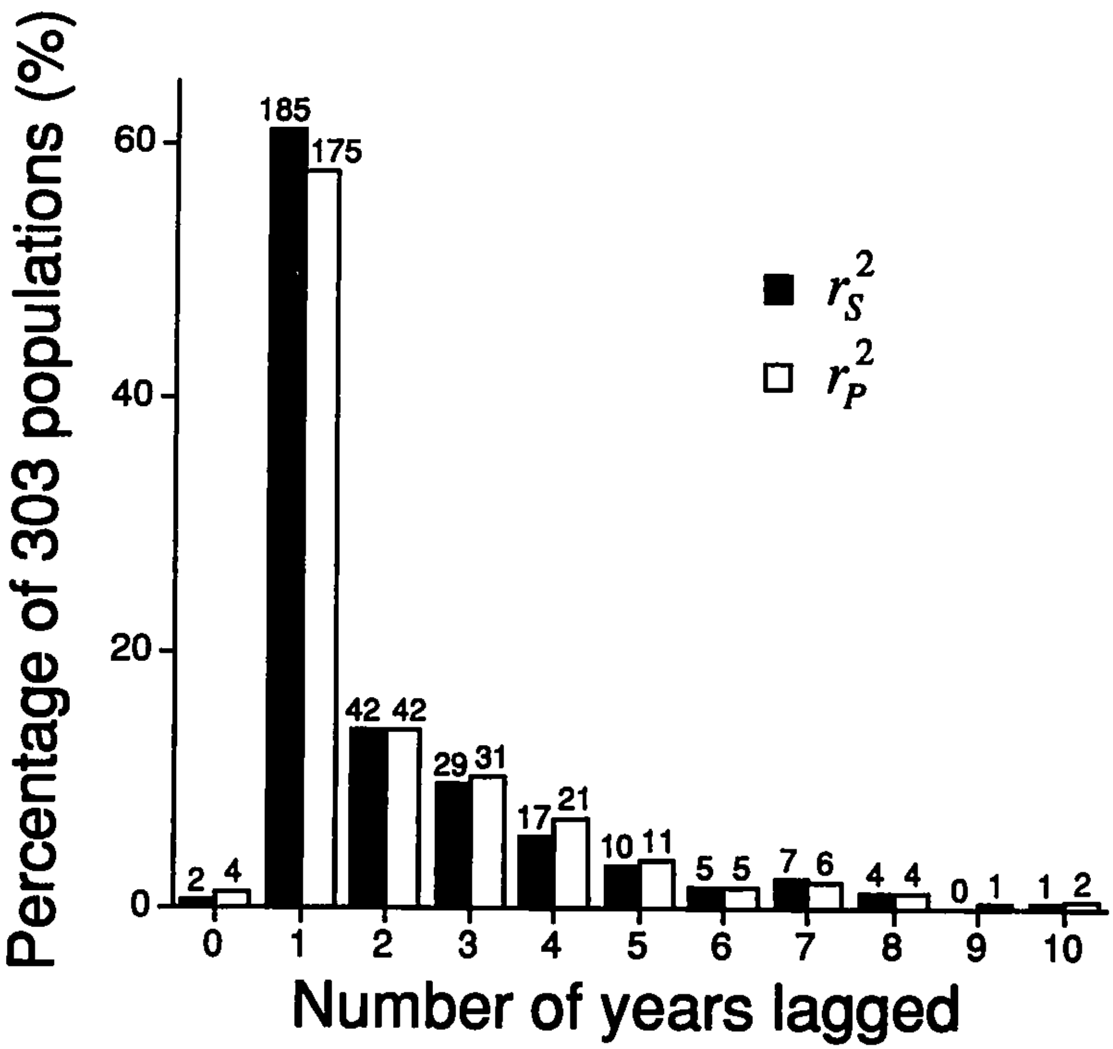
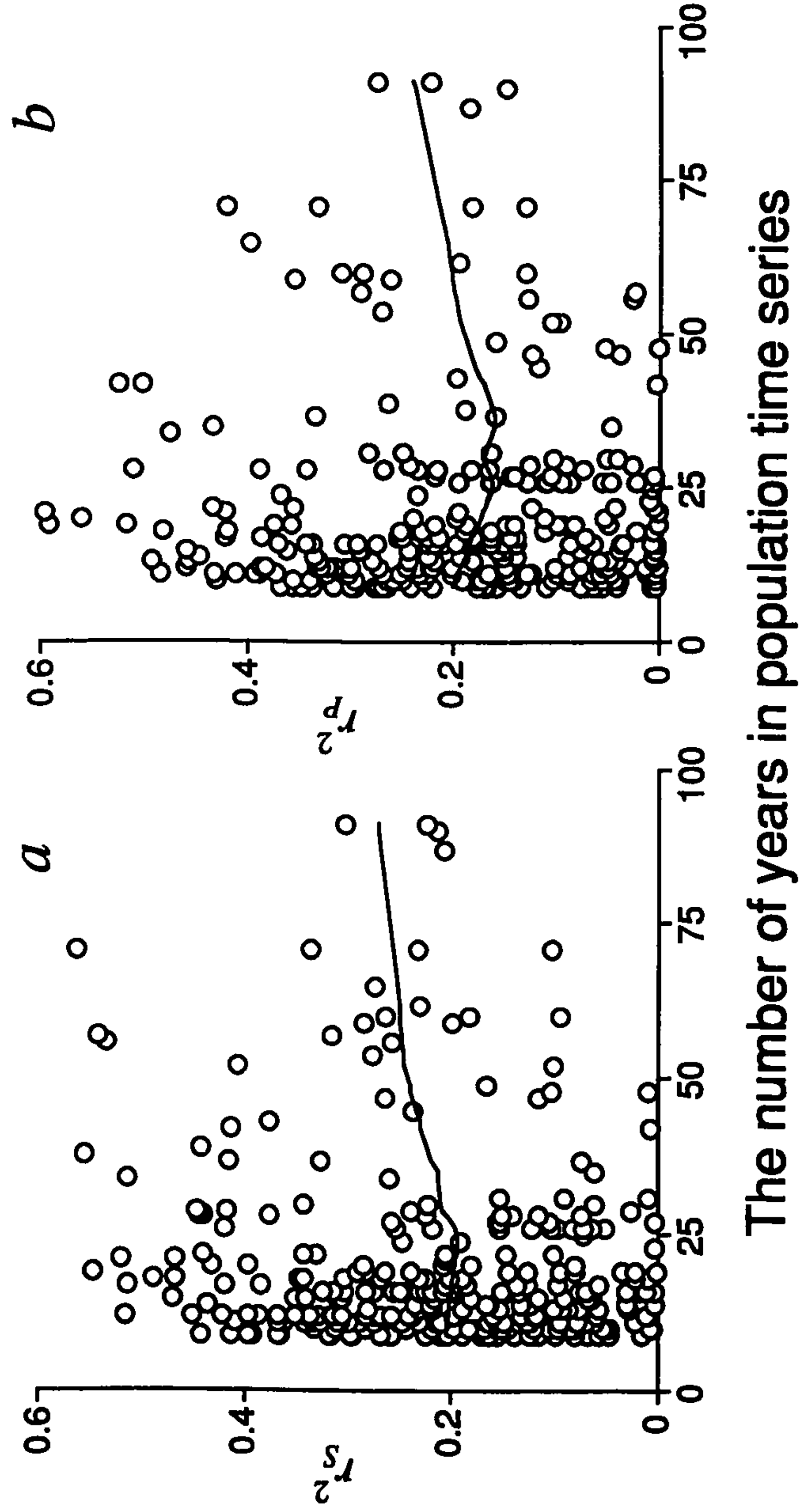

Percentage of 303 populations (%)
0
20
40
60
185
175
42 42
29 31
17 21
10 11
5 5
7 6
4 4
0 1
1 2
2 4
■ r_S^2
□ r_P^2
0
1
2
3
4
5
6
7
8
9
10
Number of years lagged

FIGURE 2.4 LOWESS-smoothed plots of the percentage of the temporal variability in the per capita growth rate attributable to density-dependent processes, according to a non-parametric index (r_S^2, panel *a*) and a parametric index (r_P^2, panel *b*), versus the number of years of data within each population abundance time series. Both LOWESS curves (*19*) were fit with a tension of 0.9. The shape of the LOWESS curves prompted us to test whether a quadratic or a simple linear regression might describe these data. No significant second order regression was found for either r_S^2 ($p = 0.11$) panel *a* or for r_P^2 ($p = 0.59$) panel *b*. The simple regression for r_P^2 was non-significant ($p = 0.75$), while that for r_S^2 was significant but weak ($r_S^2 = 0.001 years + 0.19$, $p = 0.038$, $r^2 = 0.011$, $\mathrm{n} = 303$).


a
b
r_S^2
r_P^2
0.6
0.4
0.2
0
0
25
50
75
100
The number of years in population time series

CHAPTER 3: Temporal Scale Experiment

> "The scale of investigation thus determines the range of patterns and processes that can be detected. If we study a system at an inappropriate scale, we may not detect its actual dynamics and patterns but may instead identify patterns that are artifacts of scale."
>
> Wiens (1989)

Introduction

Many, if not all, ecological processes act on some characteristic temporal or spatial scale (O'Neill et al., 1986; Wiens, 1989; Pimm, 1991; Maurer, 1994; Fleishman, 1995). In this study I define a characteristic temporal scale as the *behavioural characteristic time,* t_C, of a process. t_C is the time required by a process to produce a detectable change in the state of a system— the time in which the effects of a process manifest themselves within a system (Fleishman, 1995). This contrasts the common notion in ecology that scale is considered to be the extent of the study, e.g., a temporal scale of an experiment would be the total time over which measurements were obtained (Wiens, 1989). The major difference between these definitions is that I view a characteristic temporal scale as a function of a system process rather than the arbitrary extent of an investigation.

Density-dependent population regulation is a dynamic ecological process fundamentally concerned with equilibrium conditions. It thus begs the question: how might the characteristic time of density-dependent regulatory processes affect the estimates of the proportion of variance in per capita growth rate statistically related to the variance in density?

For a population regulated by a density-dependent process, with a characteristic time t_C, the maximal effects of the regulating process should be observed with a sampling interval equal to t_C. If observations were made on other temporal scales (e.g., observations made yearly and t_C is a day) the effects would either be attenuated or not observed. Therefore, if the sampling frequency differs from the characteristic temporal scale, we would under-estimate the variance in γ attributable to density-dependent regulatory processes. Knowing which sampling strategies are appropriate or inappropriate to particular populations might affect the inferences and conclusions regarding the proportions of variance in the per capita growth rate γ statistically attributable to population density N made in chapter 2.

The majority of long-term population census data consist of yearly estimates of population numbers. This yearly sampling frequency may correspond to the t_C of some populations but not to others. It would be desirable to select an appropriate sampling scale based on some nonarbitrary operational definition of a temporal scale appropriate to the study population. Weins (1989) suggests that allometric relationships may provide less arbitrary approximations of organism-dependent scales.

Intuitively, generation time t_g, the time till reproductive maturity, is a plausible candidate as an estimate of the characteristic temporal scale for a species. I suggest t_g as an estimate of t_C for a population regulatory process because it is the minimal period of time that a synchronously-breeding, semelparous population can produce offspring. In this simple, albeit not necessarily representative population, t_g would be the minimum time that a change in population size could occur. Therefore it must also be the minimum time period in which per capita growth rate γ can be affected by density-dependent regulatory processes. Since t_g scales with body size (Calder, 1984), generation time is easily approximated by measuring body size W.

Hypotheses

I propose the general hypothesis that the characteristic time t_C of density-dependent regulatory processes is determined by life-history traits. Specifically, I hypothesize that t_C is the generation time of that population.

For any density-dependent regulatory processes operating with a characteristic time t_C, the optimal sampling period which will yield the maximal amount of variance in γ attributable to the variance in N (following the analysis in chapter 2) will be the sampling period equal to t_C. I predict that the maximal amounts of variance will occur at the sampling periods equal to the generation time for that population.

To test this prediction would require a population time series with a high sampling frequency so that the sampling period (time between successive population points) would be significantly less than the generation time. Similarly, the time series would have to be sufficiently long to encompass many successive generations of the population. Given this kind of data, one could sample the data at various sampling frequencies and estimate the amounts of variance in γ statistically attributable to the variance in N using the measures r_S^2 and r_P^2 according to the analysis in chapter 2.

The availability of such data is limited, so I chose to model density-dependent populations for a variety of generation times, as a function of body size, to produce the necessary time series that can be sampled and then analyzed. I use body size W as the primary variable because empirical scaling relationships exist for generation time t_g as well as other life history traits.

Methods

In this section I will first describe the model used to generate the population time series. Next I discuss the values of the parameters used in the model. I then address how the time series are generated and analyzed to produce the r_P^2 and r_S^2 measures of variation in γ statistically related to the variation in N. After a brief discussion regarding the statistical analyses used to determine which sampling periods exhibit the maximal amounts of r_P^2 and r_S^2, I list the expected generation times calculated for each of the body size categories. Finally I present specific predictions regarding sampling periods, characteristic temporal scales t_C, and t_g in a figure.

The model

I generated population time series using the Verhulst logistic growth model (Murray, 1989) with a stochastic term added. Logistic growth is defined by the differential equation

$$\frac{d}{dt}N(t) = \rho N(t)\left(1 - \frac{N(t)}{K}\right) \qquad (3.1)$$

where ρ is the maximum rate of increase per individual, K is the equilibrium population size (or carrying capacity) and $N(t)$ is the population size at time t. I chose the logistic growth model because it is the simplest model of density-dependent population growth and because it possesses two desirable characteristics.

First, the model is based on a simple negative linear relationship between the per capita growth rate and population size

$$\gamma = \left(\frac{-\rho}{K}\right)N + \rho \tag{3.2}$$

where the per capita growth rate $\gamma \equiv \frac{dN}{dt} \cdot \frac{1}{N}$. In (3.2) both ρ and K are constants so $\frac{-\rho}{K}$ is the slope of the linear relationship between γ and N with ρ being the y-intercept.

Second, the differential equation (3.1) can be solved analytically. The solution to (3.1) is

$$N(t) = \frac{K}{1 + \left(\frac{K}{N(0)} - 1\right)e^{-\rho t}} \tag{3.3}$$

where $N(0)$ is the initial population size and e is the base of the natural logarithms (Beltrami, 1987).

Since population size stabilizes exactly at the carrying capacity K following the initial transient behaviour of the logistic model (Renshaw, 1991), I include a stochastic factor in the model to perturb the system away from equilibrium. If the system is perturbed at fixed intervals, (3.3) can be rewritten to include the stochastic term in an iterative form

$$N_n = \frac{K}{1 + \left(\frac{K}{N_{n-1}} - 1\right)e^{-\rho t_n}} + X_n\,, \quad (n = 1, 2, 3, \ldots) \tag{3.4}$$

where n denotes integral time steps, N_n and N_{n-1} are the population sizes at the current and previous time steps respectively, X_n is a normally distributed random variable with a mean $\mu = 0$ and a standard deviation σ, and t_h is 1 hour of time in units appropriate to the units of ρ.

Qualitatively, increasing the σ of X_n should cause the variation in N around K to increase as well. Because X_n acts stochasticly, σ effectively determines the proportion of the variation in N that results from density-independent factors. Not knowing the quantitative relationship between σ and the σ-induced variation in N makes it impossible to predict the proportion of the temporal variation in N attributable to density-dependent regulation. Therefore, it is important to note that in this study, I am not interested in the magnitudes of the variance attributable to density dependence (r_P^2 or r_S^2) but rather the relative magnitudes between different sampling periods.

Parameter selection

Because body size W scales with numerous life-history traits, it was used to select values of ρ in (3.4). Values of ρ were calculated with the empirical scaling relationship of Blueweiss et al. (1978) which is derived from data from a variety of taxa and spans body sizes from viruses to whales

$$\rho = 0.25W^{-0.26} \tag{3.5}$$

where ρ is measured in days^{-1} (d^{-1}) and W in grams. I chose 7 body sizes — 10^{-4} kg, 10^{-3} kg, 10^{-2} kg, 10^{-1} kg, 10^{0} kg, 10^{1} kg and 10^{2} kg — to generate the ρ values 16.6 year^{-1}, 9.0 year^{-1}, 5.0 year^{-1}, 2.7 year^{-1}, 1.5 year^{-1}, 0.83 year^{-1} and 0.45 year^{-1} respectively.

I used 3 values (1000, 10,000 and 100,000 individuals) for the carrying capacity K and three different standard deviations σ $(1, 2, \text{and } 3)$ for the random variable X_n.

Generation of model time series data

For each of the 63 combinations of the parameters ρ, K and σ, I produced a 34 year-long population time series using (3.4). The first year of a time series was used to allow for the initial transient behaviour of the model and was ignored in the analysis portion of the experiment. The next four years and the final four years were used to calculate the per capita growth rate γ for the initial and final population densities of the central 25 year period. The need for these 4 year periods will become clear when I discuss sampling periods below.

Given a specific sampling frequency of interest, ideally, one would exhaustively subsample the model time series at this sampling frequency producing a collection of sampled data sets that differ in their starting points with respect to the first point of the model time series (hereafter referred to as the offset). As the sample frequency increases, the number of data points in a subsample increases and the number of possible offset data sets decreases. Due to the computation-intensive methods required for the calculation of r_P^2 and r_S^2 (outlined in chapter 2) this ideal is impractical. Furthermore, the computation time to calculate r_P^2 and r_S^2 increases nonlinearly with the number of data points in the data set being analyzed. To illustrate, a data set consisting of 25 data points requires 11 to 17 minutes of computer time, whereas a 100 point data set requires about 20 hours. Given the vast number of possible subsamples for a particular sampling frequency and the nonlinear computational time requirements, I constrained the number of subsamples to be analyzed to a fraction of those possible that contain 25 data points.

To select a time series subsample from a model time series, a pseudo-random integer was generated between 1 and 8760 inclusive, where 8760 is the number of hours within one year. This pseudo-random integer was used to select a "time-slice" through the simulated population time series consisting of 25 population data points, 1 point per year with each point at the same hour in each year. Six of these time-slices were used for each combination of ρ, K and σ.

Following the methods in chapter 2, γ was estimated at each of the 25 yearly values of N in a time-slice, by fitting a second degree polynomial to the point N_n and two adjacent points $N_{n-\delta}$ and $N_{n+\delta}$, where N_n is a population data point in the time-slice and the n subscript denotes the specific hour in the model population time series. The δ represents the sampling period and is the number of hours between the population point of interest and the preceding and subsequent points used to estimate

γ. The slope of the tangent to the polynomial at N_n was then divided by the value of N_n to determine γ.

I chose 13 different δ's in hours (h): 24h, 91h, 182h, 365h, 730h, 1460h, 2190h, 2920h, 4380h, 8760h, 17520h, 26280h and 35040h corresponding to 1 day, 0.5 week, 1 week, 2 weeks, 1 month, 2 months, 3 months, 4 months, 6 months, 1 year, 2 years, 3 years and 4 years respectively. Thus, for each of 6 time-slices for all 63 combinations of ρ, K and σ, 13 sets of 25 (N_n,γ_{n_δ}) points were produced differing only in the sample period δ used to determine γ.

I analyzed each data set of (N_n,γ_{n_δ}) points according to the procedures outlined in chapter 2, pages 2-4, 2-14 and appendix A. The measures r_P^2 and r_S^2, which measure the amount of variance in γ accounted for by the variance in N, were tested to determine which sampling period yielded the maximal amount of variation explained.

Statistical analyses of results

To determine which sampling periods (δ) yielded significantly different amounts of r_P^2 or r_S^2, pairwise comparisons of the r_P^2 or r_S^2 values between the 13 δ's were performed. Since percentages from 0 to 100% are rarely normally distributed and because the values of r_P^2 or r_S^2 may not be independent of each other, I performed the sequential Dunn-Šidák method (Sokal & Rohlf, 1995) as an approximate randomization test (Noreen 1989) to determine the significance levels of each pairwise test statistic. This involved randomly allocating the r_P^2 or r_S^2 values to either of the two sampling periods of interest and recalculating Student's *t* statistic— 4999 times. In this way the *p* value of the observed statistic is determined by the empirical distribution of the test statistic.

To determine which sampling period yielded the maximal amounts of r_P^2 or r_S^2, notched-box plots (McGill et al., 1978) of r_P^2 and r_S^2 for the 13 δ's were examined. The δ with the largest median amounts of r_P^2 and r_S^2, and differing significantly from the rest, was identified as the optimal sampling period for that combination of ρ, K and σ parameters.

Examination of the plots of the time-slices (see Figures E.1 to E.7 in appendix E, pages E-2 through E-26) gives the impression that the variation in N is independent of K and possibly σ. Two-way approximate randomization ANOVA's (4999 randomizations) were performed using Manly's (1994) *Randomization Testing* program to determine if r_S^2 or r_P^2 values could be pooled across K's and σ's prior to performing pairwise comparisons between sampling periods. If pooling is appropriate it has the advantage of increasing the power of the statistical tests and has the benefit of reducing the time required to perform the computationally intensive pairwise randomization tests.

Determination of generation time

Generation time t_g scales with body size according to the relation

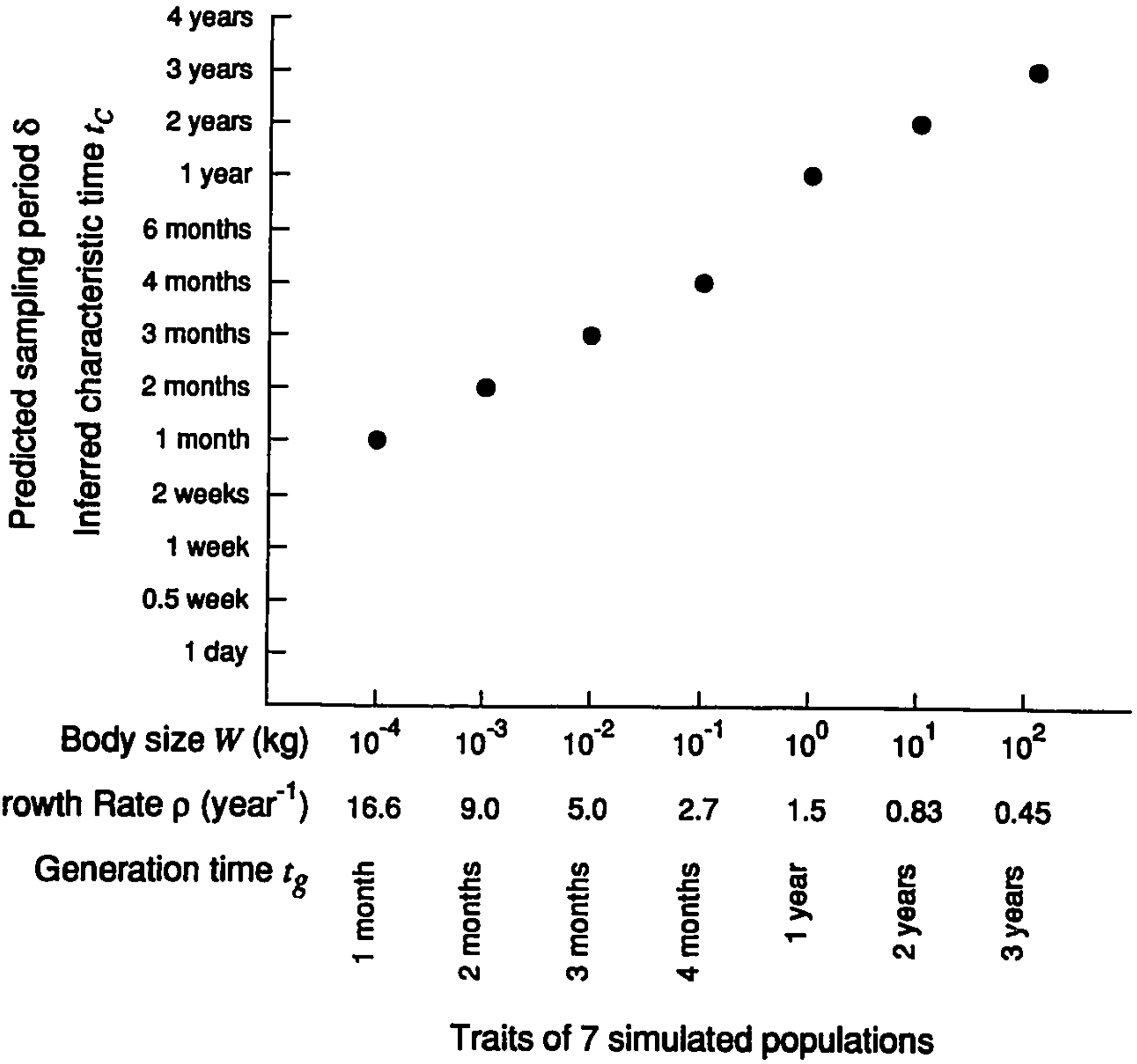
$$t_g = 53W^{0.27} \tag{3.6}$$

where t_g is measured in days (d) and W in grams (Blueweiss et al., 1978). I used **(3.6)** to calculate the generation times: 28d, 53d, 97d, 184d, 342d, 637d and 1187d, corresponding respectively to the body sizes 10^{-4} kg, 10^{-3} kg, 10^{-2} kg, 10^{-1} kg, 10^{0} kg, 10^{1} kg and 10^{2} kg. These generation times, expressed in terms of the units of the previously mentioned sampling periods, correspond approximately to 1 month, 2 months, 3 months, 4 months, 1 year, 2 years and 3 years respectively.

Detailed predictions

Given the generation times for the modelled body sizes, it is possible to make detailed predictions about which sampling periods will yield the maximal amounts of r_S^2 and r_P^2 as a function of W. Figure 3.1 encapsulates these predictions for each of the body size categories explicitly.

FIGURE 3.1 Detailed predictions of the hypotheses. A graphical representation of the predicted characteristic times t_C of density-dependent processes for 7 different simulated populations. The abscissa displays 3 related life-history traits specific to each of the 7 simulated populations: body size W, the maximum rate of growth per individual ρ, and the generation time t_g. Both ρ and t_g were calculated from empirical body-size scaling relationships discussed in the methods. ρ is the biological parameter in the population model (3.4) and t_g is the basis for the predicted characteristic time on the ordinate. The solid circles identify the predicted sampling periods δ on the ordinate expected to yield the maximum amounts of variance in the per capita growth rate γ statistically related to the variance in N. The identified sampling periods are inferred to be the characteristic times t_C of the density-dependent processes operating within each simulated population.


Predicted sampling period δ
Inferred characteristic time t_C
4 years
3 years
2 years
1 year
6 months
4 months
3 months
2 months
1 month
2 weeks
1 week
0.5 week
1 day
Body size W (kg)
10^{-4}
10^{-3}
10^{-2}
10^{-1}
10^{0}
10^{1}
10^{2}
Growth Rate ρ ($year^{-1}$)
16.6
9.0
5.0
2.7
1.5
0.83
0.45
Generation time t_g
1 month
2 months
3 months
4 months
1 year
2 years
3 years
Traits of 7 simulated populations

Results

The time-slices produced for the 10^{-1} kg modelled populations, for all combinations of the parameters, are shown in Figure 3.2. Figure 3.2 is qualitatively representative of the general patterns exhibited by all the time-slice plots for each body size (these plots are presented in Figures E.1 to E.7 in appendix E, pages E-2 through E-26).

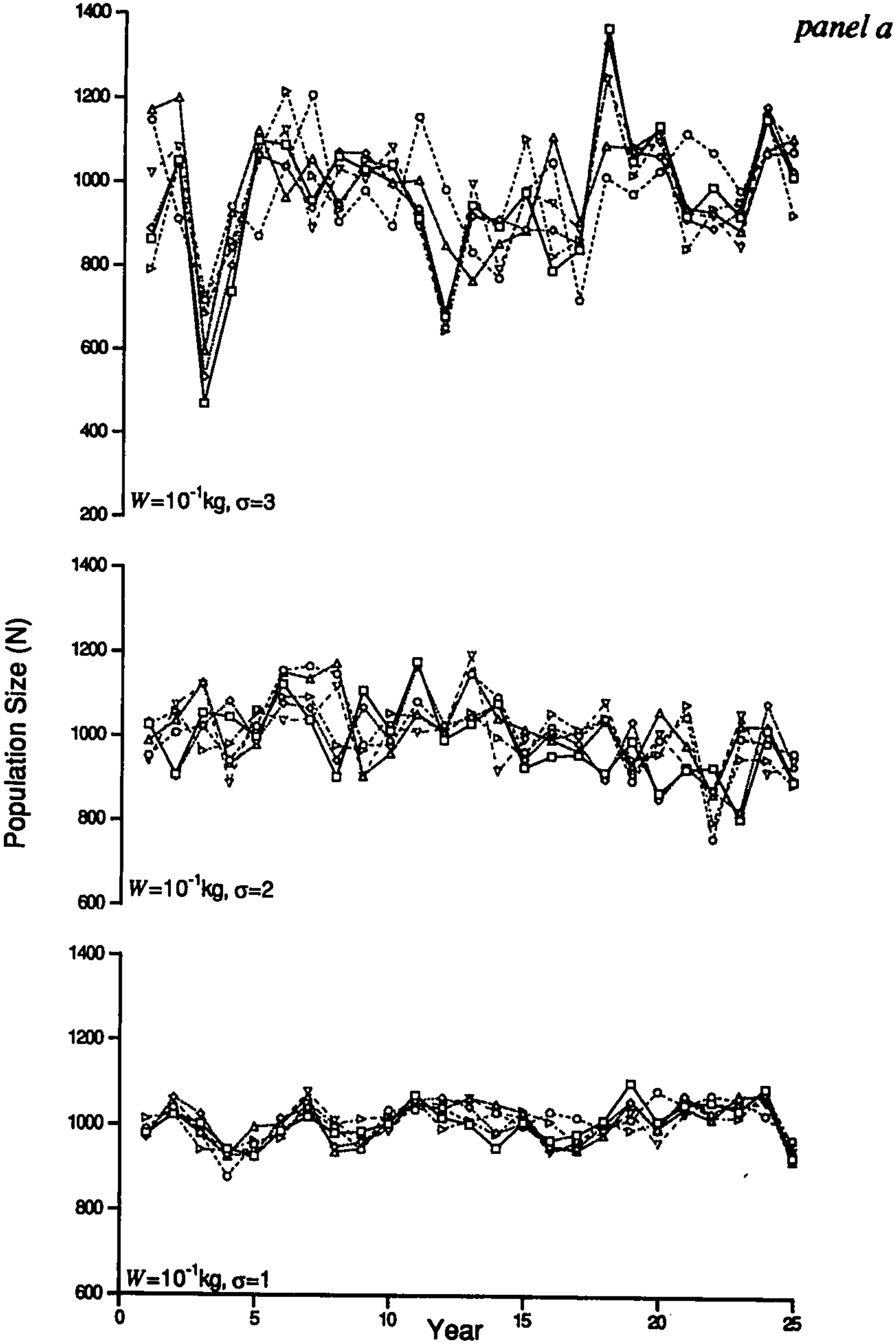
Figure 3.3 shows the distributions of the r_P^2 and r_S^2 estimates determined for the 10^{-1} kg time-slices for all the sampling periods. Again, the patterns observed in Figure 3.3 are qualitatively similar to those observed for the other body sizes (Figures E.8 to E.14, pages E-30 through E-54).

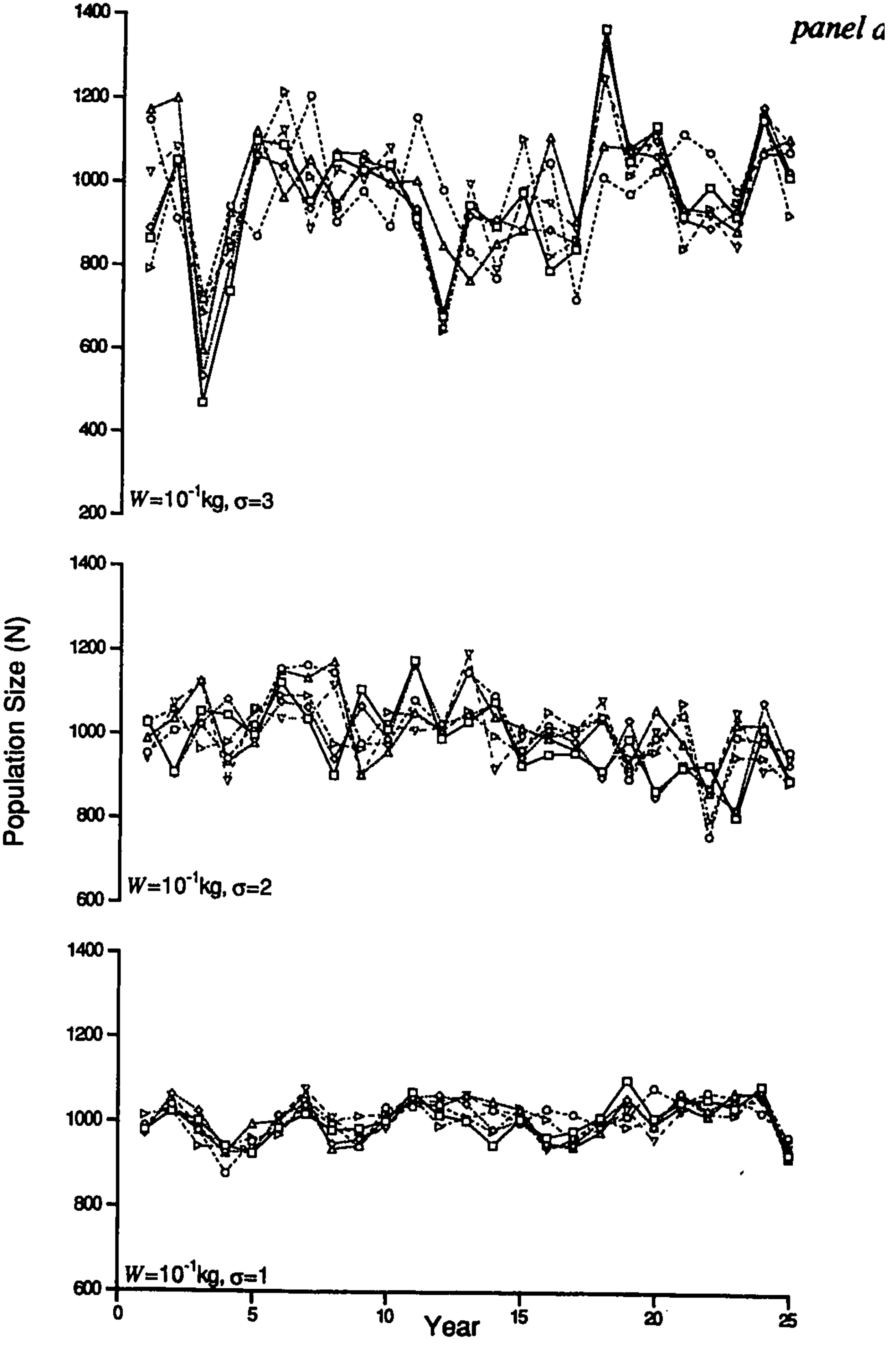
Based on the similarities observed in both the time-slice plots and the results of the 3-way ANOVA's (Table 3.1) the r_P^2 and r_S^2 estimates were pooled across K's and σ's within each body size category. Figure 3.4 presents the pooled r_P^2 and r_S^2 distributions for each body size category.

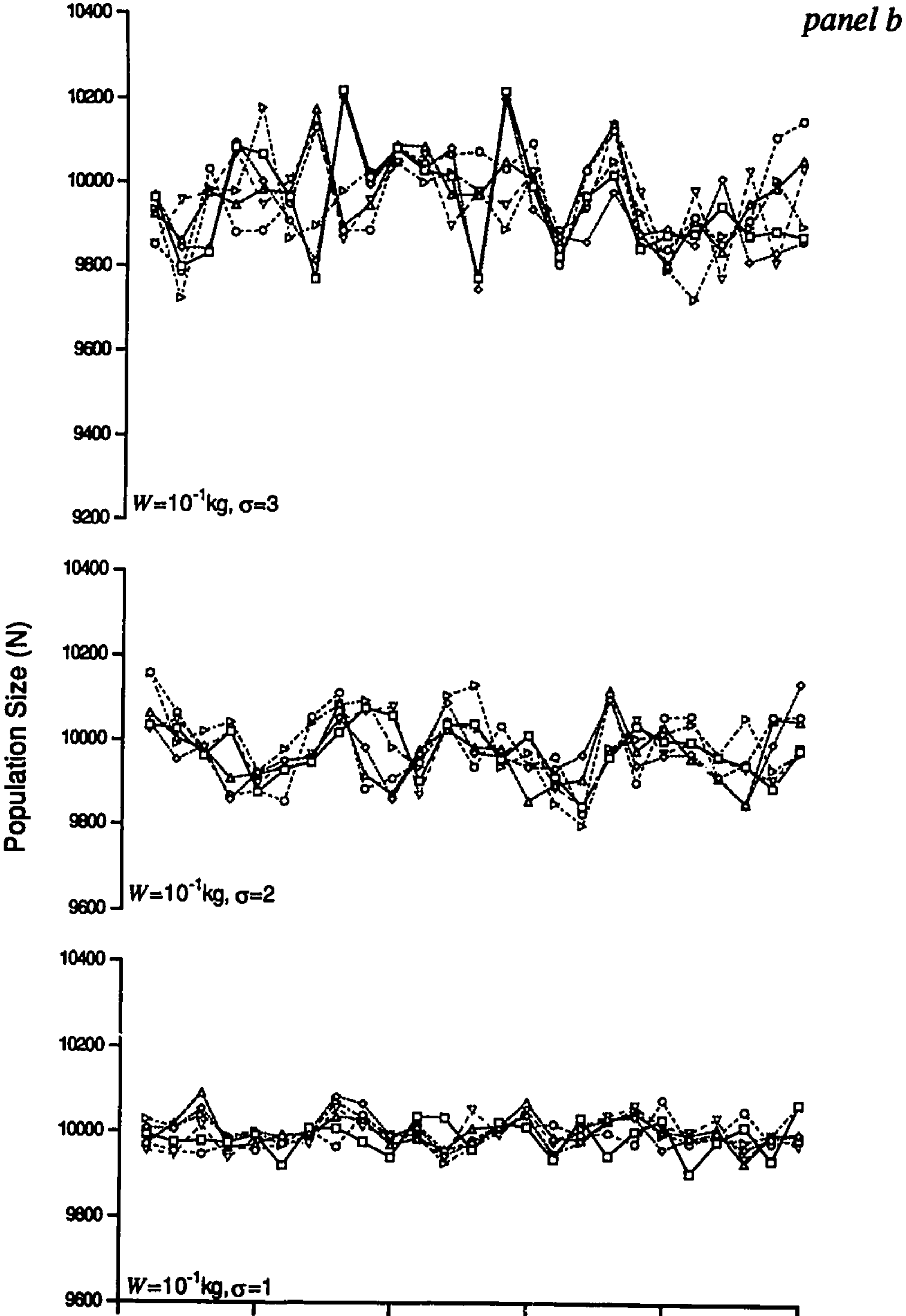
Table 3.2 presents the statistical results of the randomized sequential Dunn-Šidák pairwise comparisons performed on the pooled 10^{-1} kg r_P^2 and r_S^2 distributions with an experimentwise error rate $\alpha = 0.05$.

Figure 3.4 along with the results of the pairwise comparisons (Table 3.2 & Figures E.8 to E.14) were used to determine the sampling periods having the maximum quantities of r_P^2 and r_S^2. These determinations are presented graphically in Figure 3.5.

FIGURE 3.2 Population time-slices for the simulated 10^{-1} kg body size populations. This figure consists of three panels *a*, *b* and *c* on the next three pages, respectively. Every panel presents 3 graphs, one above the other. Each of the 9 graphs of all three panels show the 6 randomly selected time-slices for each combination of the carrying capacity K and the standard deviation σ of the random variable X in model (3.4). Panels *a*, *b* and *c* show the combinations with $K = 1000$, 10,000 and 100,000 respectively. The top graph on each panel have the time-slices with $\sigma = 3$, while the middle and bottom graphs show the time-slices with $\sigma = 2$ and $\sigma = 1$ respectively.


panel a
1400
1200
1000
800
600
400
200
W=10^{-1}kg, σ=3
1400
1200
1000
800
600
W=10^{-1}kg, σ=2
Population Size (N)
1400
1200
1000
800
600
W=10^{-1}kg, σ=1
0
5
10
15
20
25
Year


panel a
1400
1200
1000
800
600
400
200
W=10^{-1}kg, σ=3
1400
1200
1000
800
600
W=10^{-1}kg, σ=2
Population Size (N)
1400
1200
1000
800
600
W=10^{-1}kg, σ=1
0
5
10
15
20
25
Year


panel b
Population Size (N)
10400
10200
10000
9800
9600
9400
9200
W=10⁻¹kg, σ=3
W=10⁻¹kg, σ=2
W=10⁻¹kg, σ=1
0
5
10
15
20
25
Year

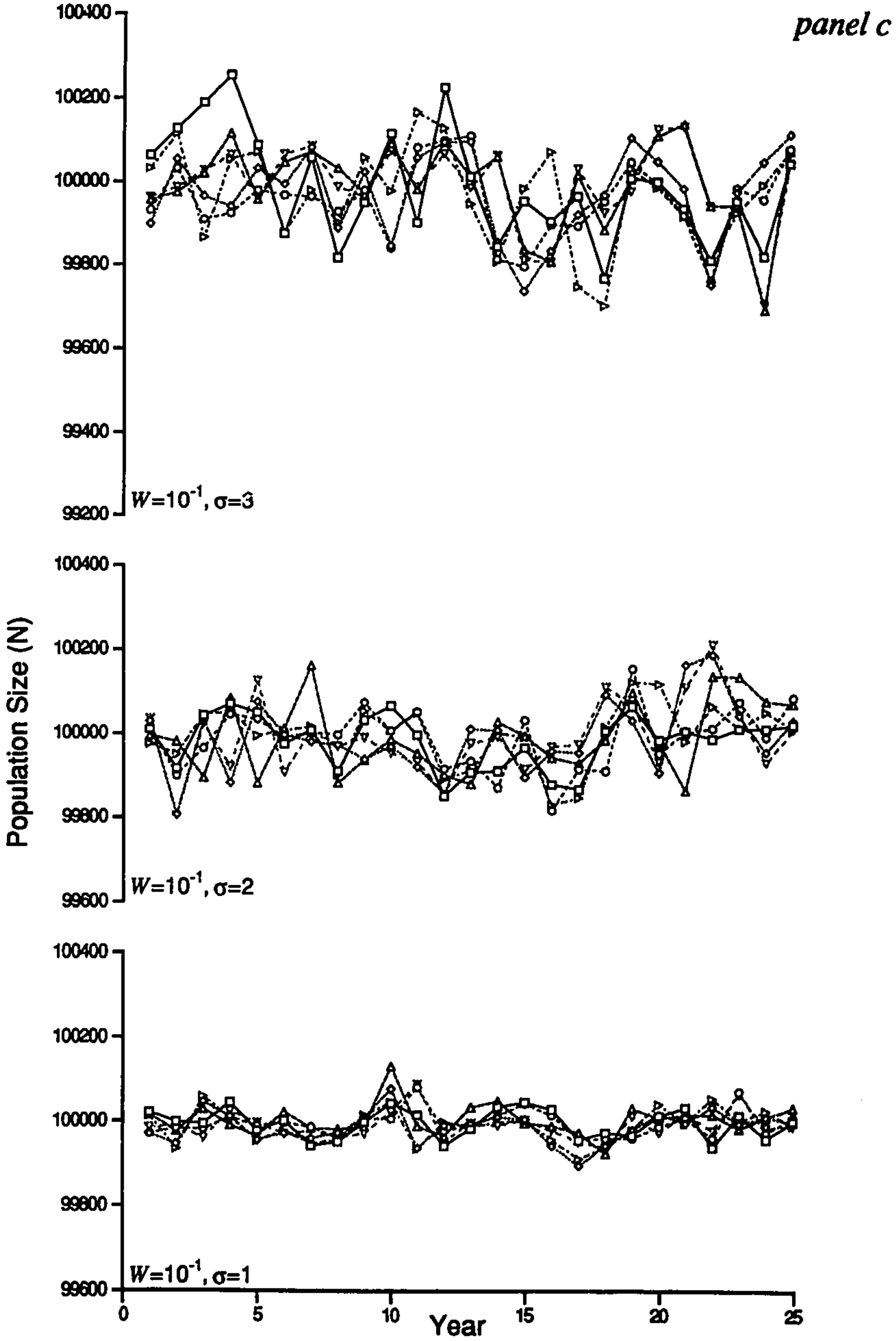
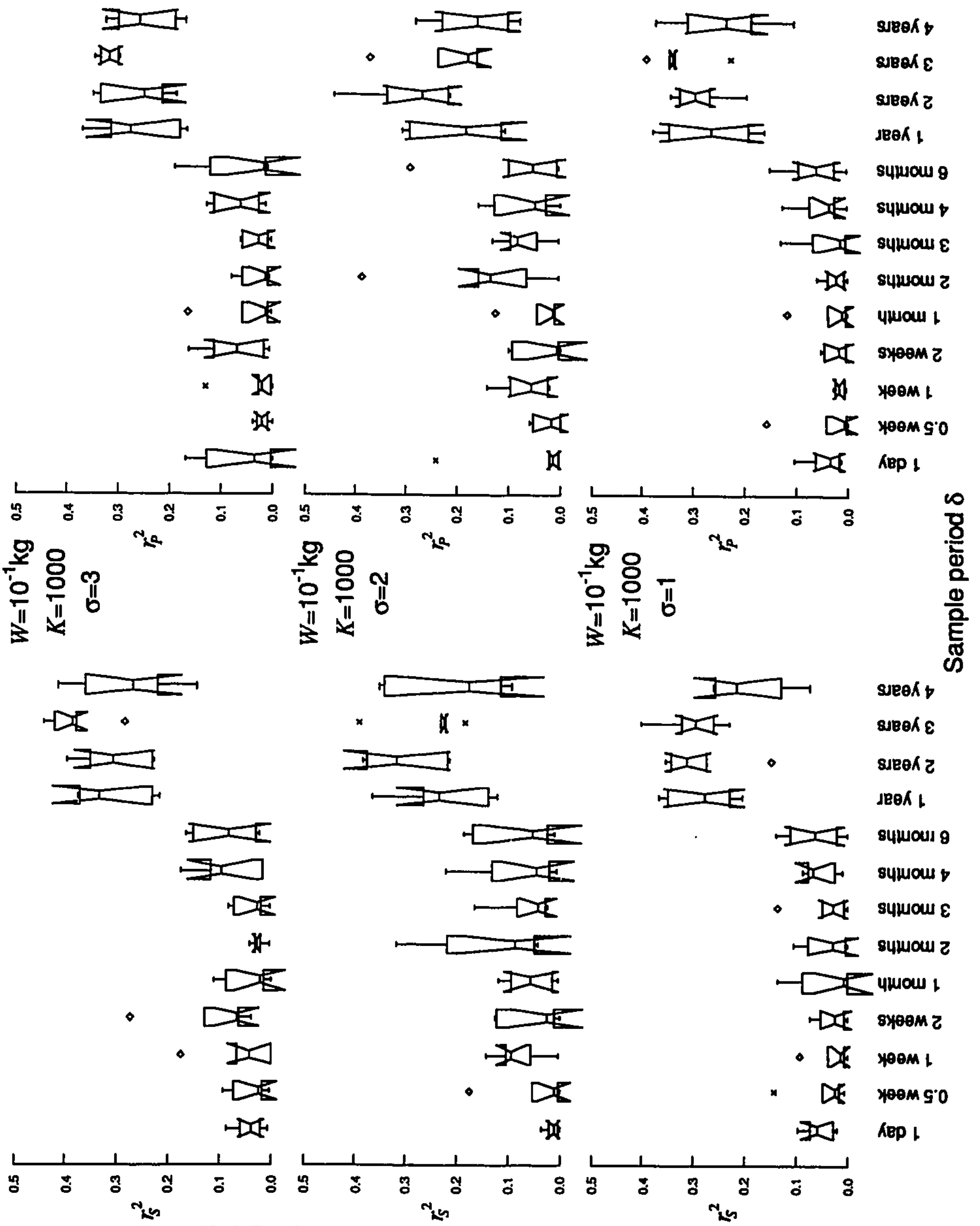
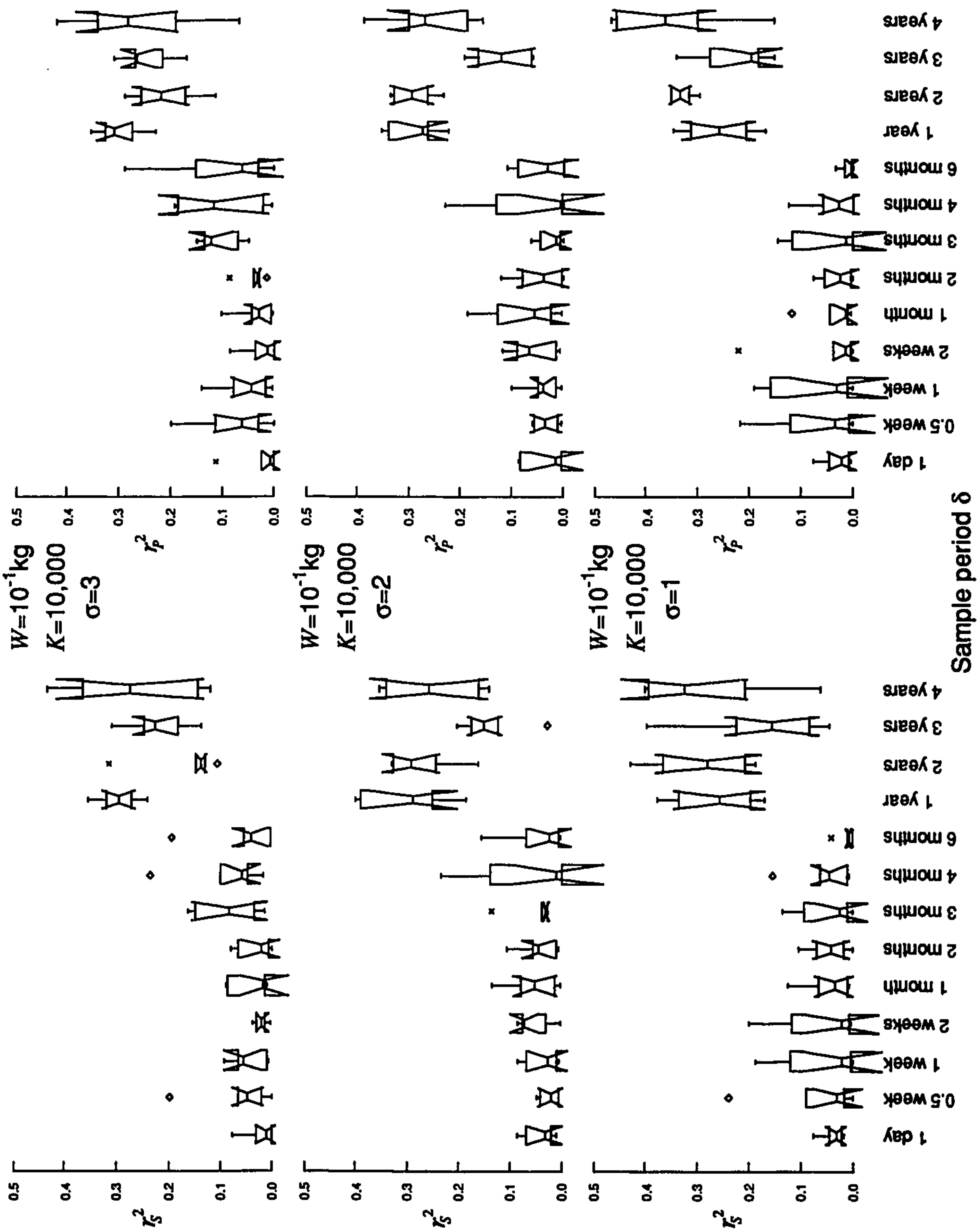

panel c
100400
100200
100000
99800
99600
99400
99200
W=10⁻¹, σ=3
100400
100200
100000
99800
99600
W=10⁻¹, σ=2
100400
100200
100000
99800
99600
W=10⁻¹, σ=1
Population Size (N)
0
5
10
15
20
25
Year

FIGURE 3.3 The distributions of the r_S^2 or r_P^2 statistics for the 10^{-1} kg populations corresponding to the time-slices presented in Figure 3.2. This figure consists of three panels *a*, *b* and *c* on the next three pages, respectively. Every panel presents 3 pairs of graphs, one above the other. Each of the 9 pairs of graphs, of all three panels, show notched-box plots of the r_S^2 or r_P^2 statistics calculated for each randomly selected time-slice in Figure 3.2. Each pair of graphs corresponds to the different combinations of the carrying capacity K and the standard deviation σ of the random variable X in model (3.4) used to produce the time-slices of Figure 3.2. Panels *a*, *b* and *c* show the combinations with $K = 1000$, 10,000 and 100,000 respectively. The top pair of graphs on each panel correspond to the time-slices with $\sigma = 3$, while the middle and bottom pairs of graphs correspond to the time-slices with $\sigma = 2$ and $\sigma = 1$ respectively. Every graph is composed of 13 notched-box plots one for each of the 13 sampling periods δ discussed in the methods. If the notches (the diagonal lines extending from the median to the vertical sides of a box) of two medians do not overlap, then the medians can be considered to be significantly different ($p \leq 0.05$). The hollow diamonds and ×'s identify outliers within each distribution. The diamonds are points that lie between 1.5 times and 3.0 times the interquartile distance outward from the hinges of the notched box and the ×'s are outliers beyond this range (Wilkinson et al. 1992).

panel a


$W=10^{-1}$kg
$K=1000$
$\sigma=3$
$W=10^{-1}$kg
$K=1000$
$\sigma=2$
$W=10^{-1}$kg
$K=1000$
$\sigma=1$
r_S^2
r_P^2
0.0
0.1
0.2
0.3
0.4
0.5
Sample period δ
1 day
0.5 week
1 week
2 weeks
1 month
2 months
3 months
4 months
6 months
1 year
2 years
3 years
4 years

panel b



W=10^-1 kg
K=10,000
σ=3
W=10^-1 kg
K=10,000
σ=2
W=10^-1 kg
K=10,000
σ=1
r_P^2
r_S^2
0.0
0.1
0.2
0.3
0.4
0.5
1 day
0.5 week
1 week
2 weeks
1 month
2 months
3 months
4 months
6 months
1 year
2 years
3 years
4 years
Sample period δ

panel c

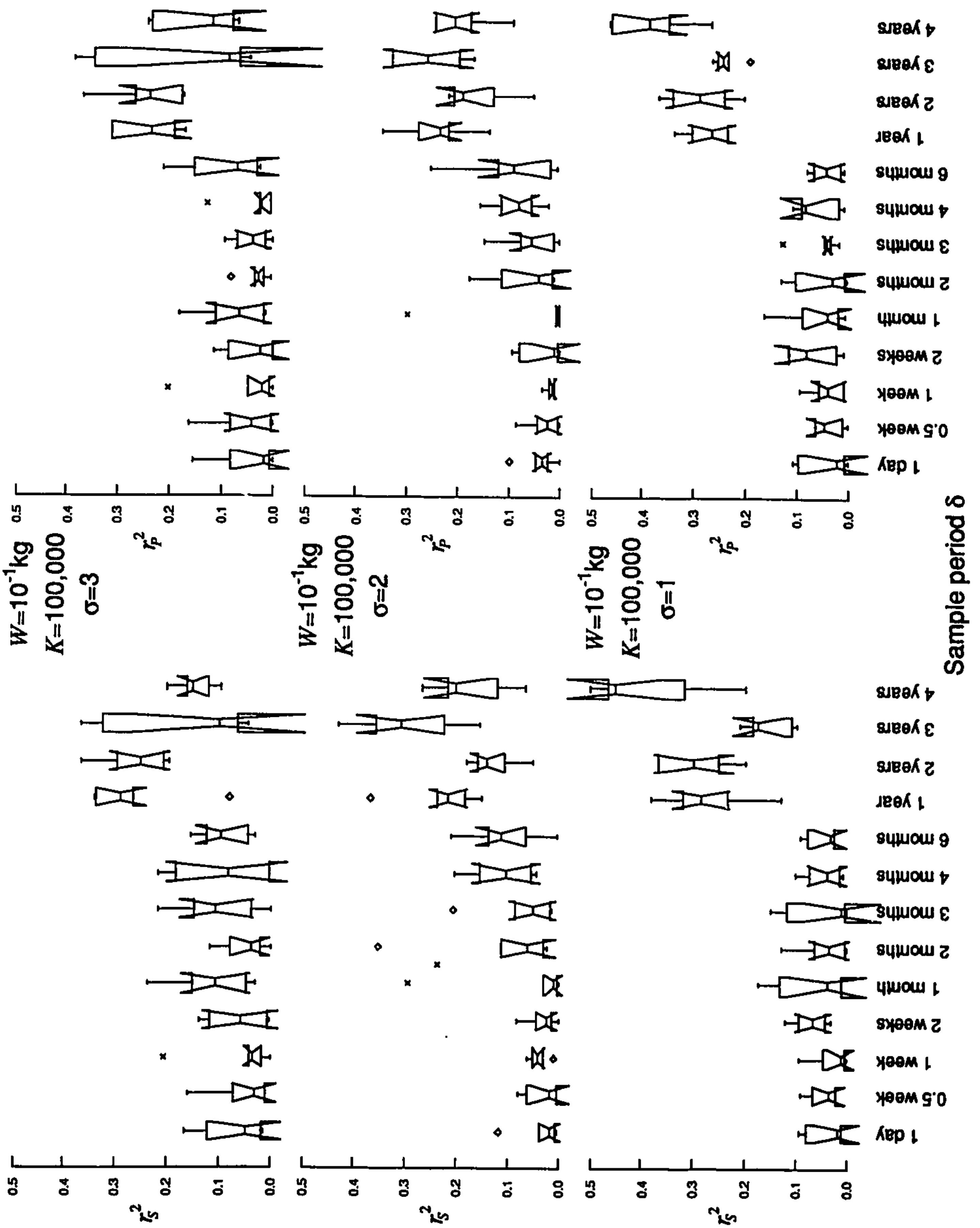
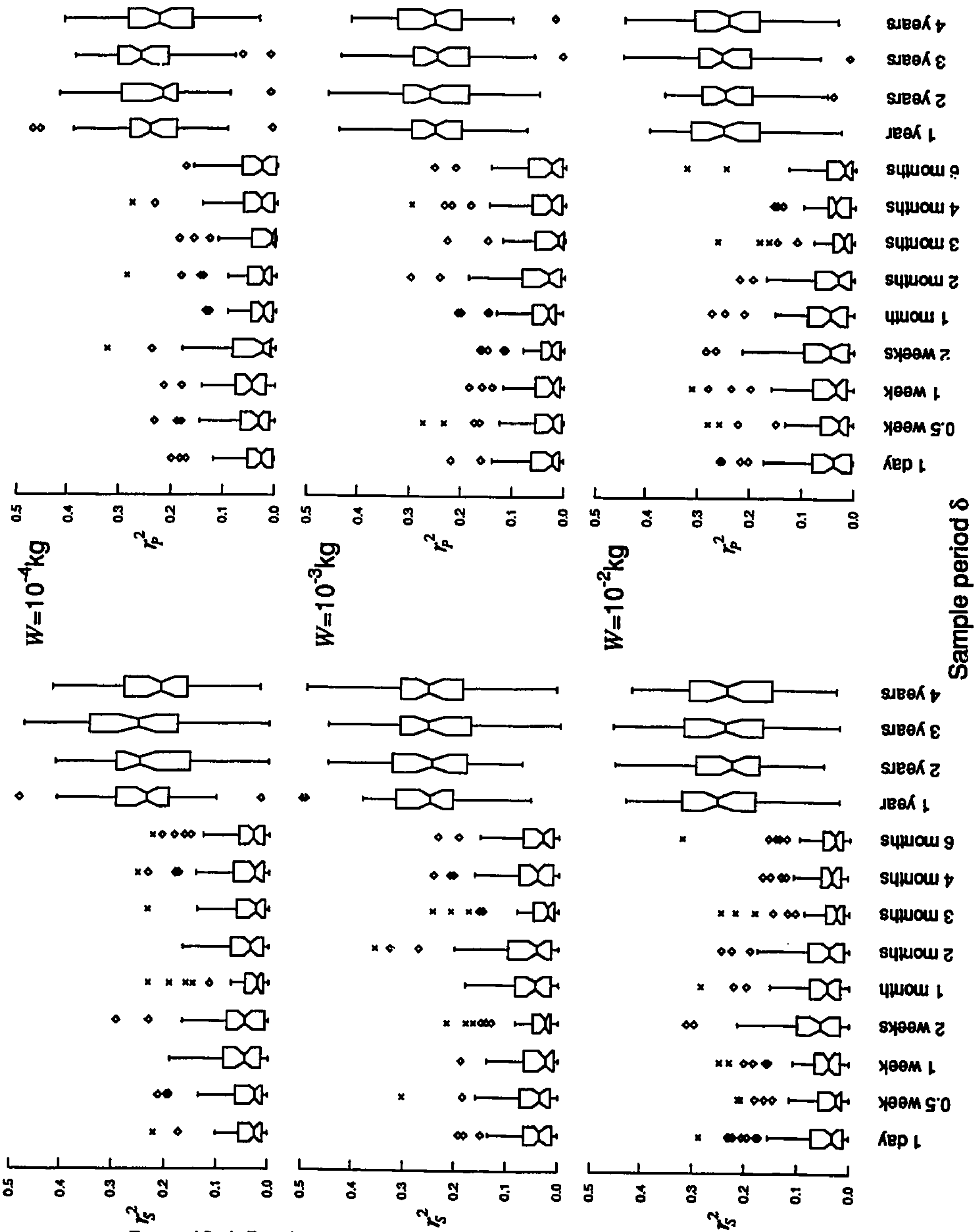

W=10^-1kg
K=100,000
σ=3
W=10^-1kg
K=100,000
σ=2
W=10^-1kg
K=100,000
σ=1
Sample period δ
1 day
0.5 week
1 week
2 weeks
1 month
2 months
3 months
4 months
6 months
1 year
2 years
3 years
4 years
r_P^2
r_S^2
0.5
0.4
0.3
0.2
0.1
0.0

TABLE 3.1 p-values of 3-way ANOVA randomization tests of the effects of σ, K and δ on r_S^2 or r_P^2 for each body size category. All $p \leq 0.05$ are in bold. A dot $\cdot$ between factors, in the factors column, denotes an interaction.

Body size	**10^{-4}kg**		**10^{-3}kg**		**10^{-2}kg**		**10^{-1}kg**		**10^{0}kg**		**10^{1}kg**		**10^{2}kg**	
Factors	r_S^2	r_P^2	r_S^2	r_P^2	r_S^2	r_P^2	r_S^2	r_P^2	r_S^2	r_P^2	r_S^2	r_P^2	r_S^2	r_P^2
σ	0.7059	0.5763	0.4533	0.9192	0.7584	0.4675	0.6877	0.5857	0.3395	0.7355	**0.0134**	**0.0018**	0.1912	0.1386
K	0.5417	0.7017	0.8622	0.6681	0.7139	0.9908	0.3507	0.7215	0.0614	0.4521	0.3475	0.0742	0.0726	**0.0398**
δ	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	1.0000	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**
$\sigma \cdot K$	0.4559	0.8304	0.7924	0.8370	0.2749	0.3789	0.7982	0.6327	0.5469	0.9836	**0.0438**	0.0586	**0.0002**	**0.0020**
$\sigma \cdot \delta$	0.9870	0.9976	0.9922	0.9924	0.9058	0.4951	0.9112	0.6061	0.9058	0.9702	0.0732	0.6995	**0.0002**	**0.0002**
$K \cdot \delta$	0.9976	0.9738	0.9416	0.9920	0.9908	0.2847	0.6647	0.9032	0.8258	0.6655	0.2042	0.7097	0.9506	0.7910
$\sigma \cdot K \cdot \delta$	1.0000	1.0000	1.0000	1.0000	0.9968	0.3045	0.8198	0.9956	0.9994	0.9998	0.6669	0.8648	**0.0370**	**0.0020**

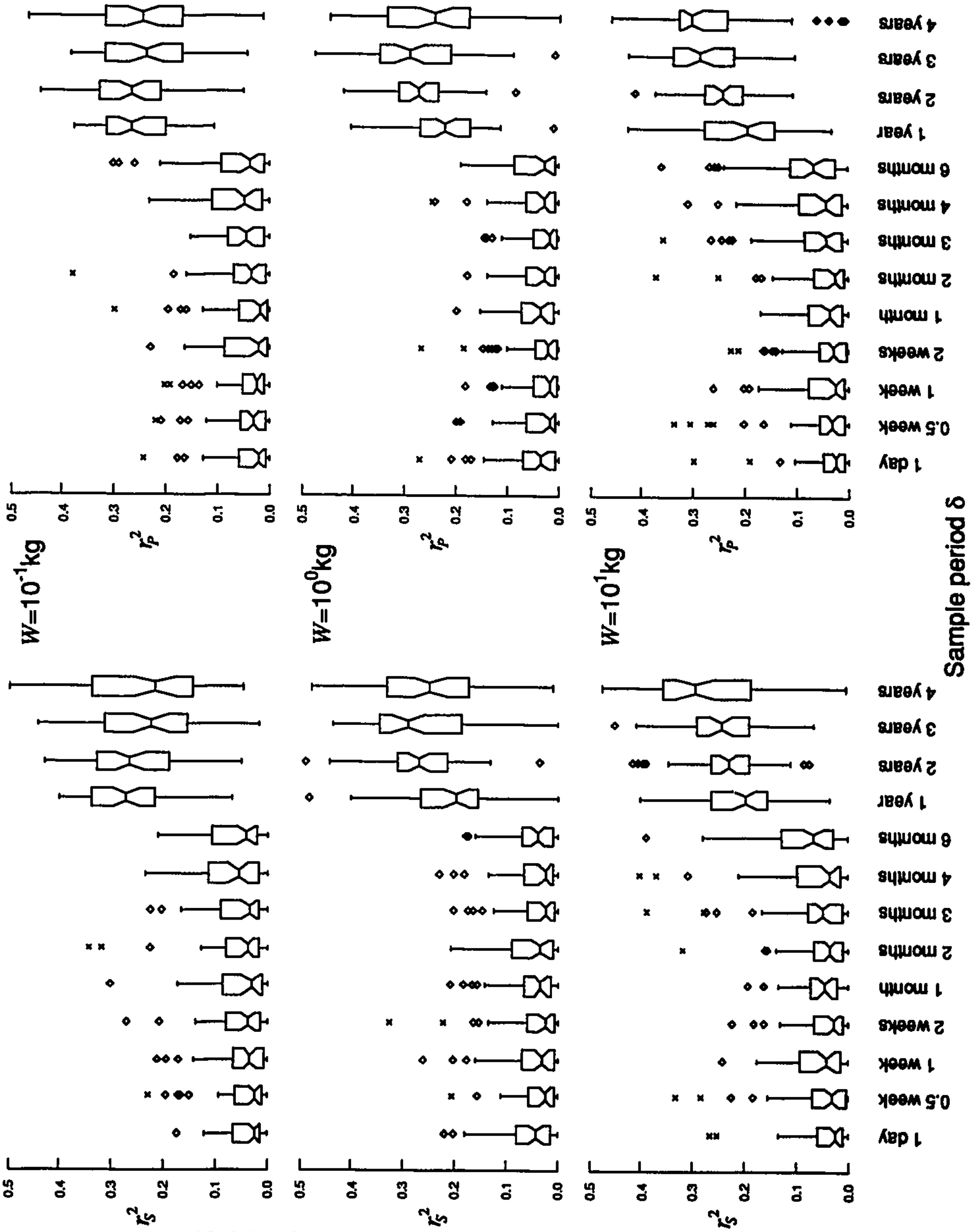
FIGURE 3.4 Pooled results for all body sizes. The distributions of the r_S^2 and r_P^2 statistics for each modelled body-size category— pooled across carrying capacities K and the standard deviations σ in model (3.4). This figure consists of three panels *a*, *b* and *c* on the next three pages, respectively. Panels *a* and *b* each present 3 pairs of graphs while panel *c* shows only 1 pair. Each of the 7 pairs of graphs, show notched-box plots of the r_S^2 or r_P^2 statistics calculated for each of the body-size categories simulated in this experiment. Every graph is composed of 13 notched-box plots one for each of the 13 sampling periods δ discussed in the methods. If the notches (the diagonal lines extending from the median to the vertical sides of a box) of two medians do not overlap, then the medians can be considered to be significantly different ($p \leq 0.05$). The hollow diamonds and ×'s identify outliers within each distribution. The diamonds are points that lie between 1.5 times and 3.0 times the interquartile distance outward from the hinges of the notched box and the ×'s are outliers beyond this range (Wilkinson et al. 1992).

panel a



W=10^{-4}kg
W=10^{-3}kg
W=10^{-2}kg
r_P^2
r_S^2
0.0
0.1
0.2
0.3
0.4
0.5
1 day
0.5 week
1 week
2 weeks
1 month
2 months
3 months
4 months
6 months
1 year
2 years
3 years
4 years
Sample period δ

panel b



W=10^{-1}kg
W=10^{0}kg
W=10^{1}kg
Sample period δ
r_S^2
r_P^2
0.0
0.1
0.2
0.3
0.4
0.5
1 day
0.5 week
1 week
2 weeks
1 month
2 months
3 months
4 months
6 months
1 year
2 years
3 years
4 years

panel c

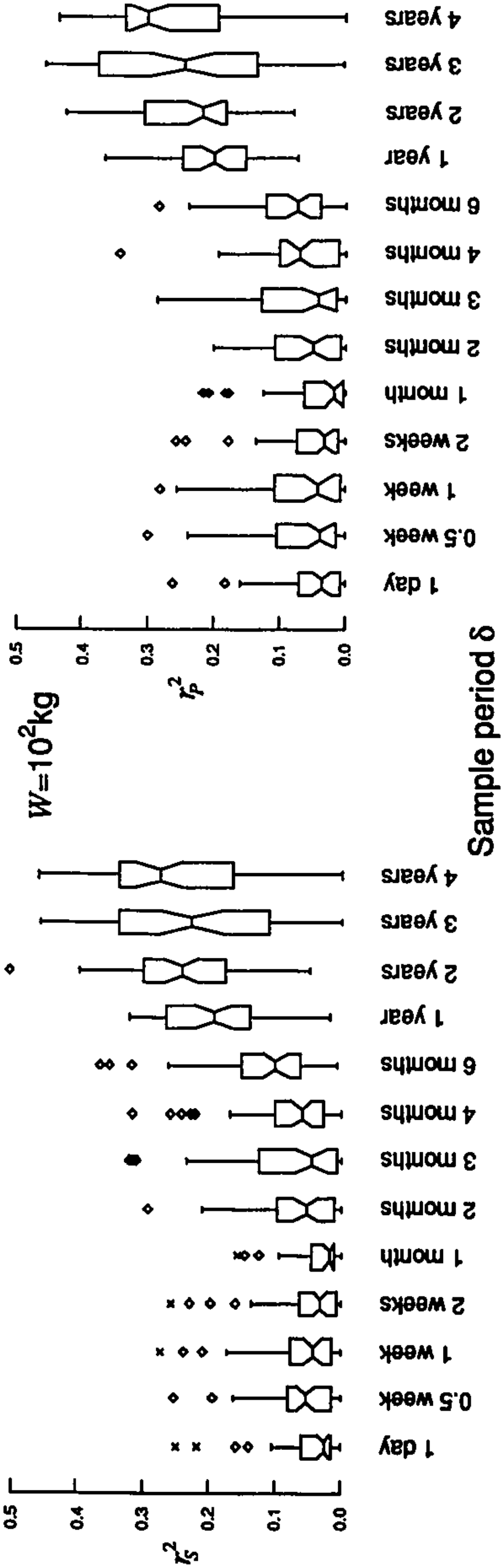
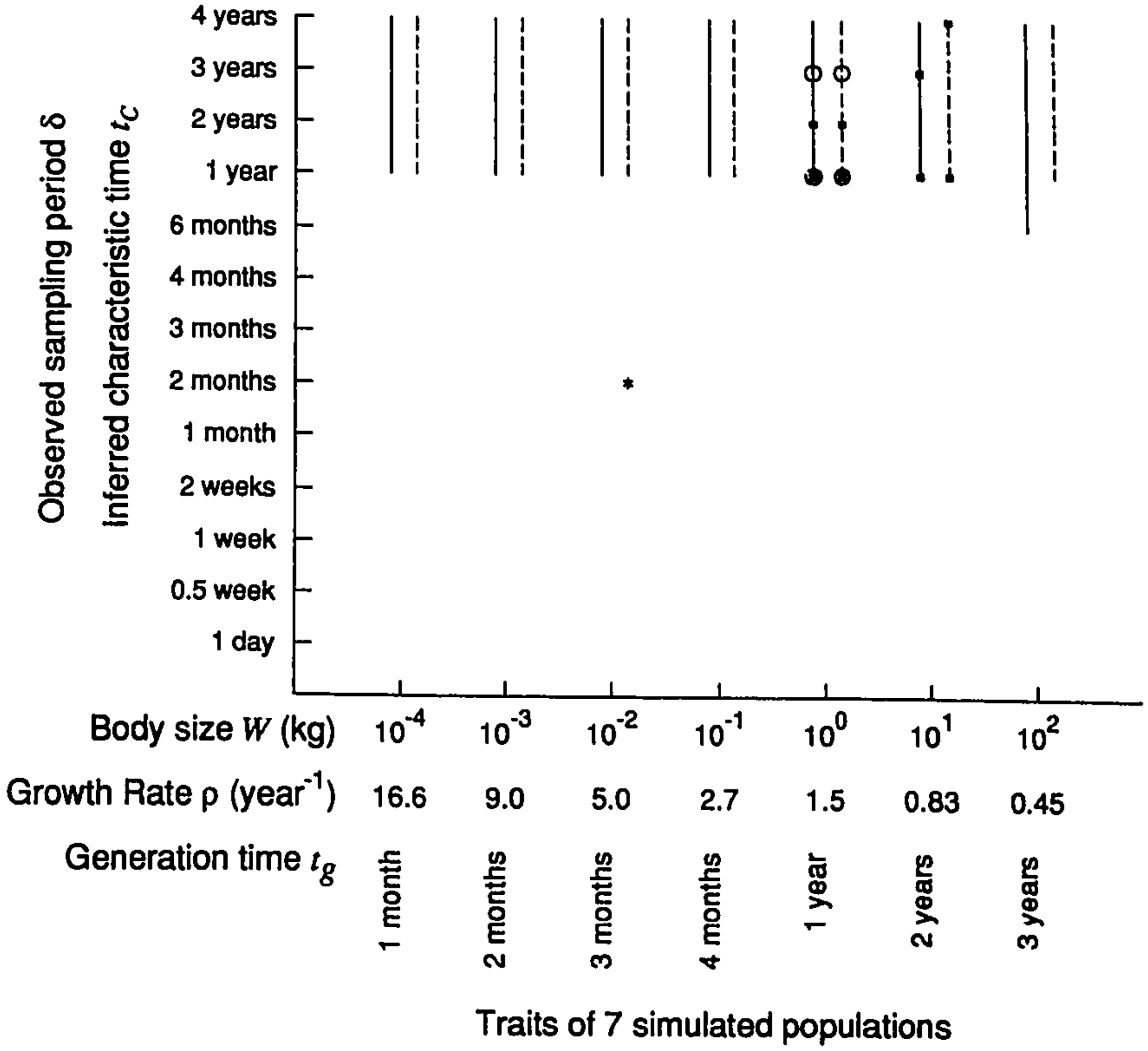

W=10^{2}kg
Sample period δ
r_P^2
r_S^2
0.0
0.1
0.2
0.3
0.4
0.5
1 day
0.5 week
1 week
2 weeks
1 month
2 months
3 months
4 months
6 months
1 year
2 years
3 years
4 years

TABLE 3.2 Pairwise comparisons of r_S^2 and r_P^2 between sampling periods for $W = 10^{-1}$ kg model populations.

r_S^2			r_P^2		
Pairwise Comparison	p	α_C	**Pairwise Comparison**	p	α_C
1 day & 1 year	0.0002	0.00066	1 day & 1 year	0.0002	0.00066
1 day & 2 years	0.0002	0.00067	1 day & 2 years	0.0002	0.00067
1 day & 3 years	0.0002	0.00067	1 day & 3 years	0.0002	0.00067
1 day & 4 years	0.0002	0.00068	1 day & 4 years	0.0002	0.00068
0.5 week & 1 year	0.0002	0.00069	0.5 week & 1 year	0.0002	0.00069
0.5 week & 2 years	0.0002	0.00070	0.5 week & 2 years	0.0002	0.00070
0.5 week & 3 years	0.0002	0.00071	0.5 week & 3 years	0.0002	0.00071
0.5 week & 4 years	0.0002	0.00072	0.5 week & 4 years	0.0002	0.00072
1 week & 1 year	0.0002	0.00073	1 week & 1 year	0.0002	0.00073
1 week & 2 years	0.0002	0.00074	1 week & 2 years	0.0002	0.00074
1 week & 3 years	0.0002	0.00075	1 week & 3 years	0.0002	0.00075
1 week & 4 years	0.0002	0.00077	1 week & 4 years	0.0002	0.00077
2 weeks & 1 year	0.0002	0.00078	2 weeks & 1 year	0.0002	0.00078
2 weeks & 2 years	0.0002	0.00079	2 weeks & 2 years	0.0002	0.00079
2 weeks & 3 years	0.0002	0.00080	2 weeks & 3 years	0.0002	0.00080
2 weeks & 4 years	0.0002	0.00081	2 weeks & 4 years	0.0002	0.00081
1 month & 1 year	0.0002	0.00083	1 month & 1 year	0.0002	0.00083
1 month & 2 years	0.0002	0.00084	1 month & 2 years	0.0002	0.00084
1 month & 3 years	0.0002	0.00085	1 month & 3 years	0.0002	0.00085
1 month & 4 years	0.0002	0.00087	1 month & 4 years	0.0002	0.00087
2 months & 1 year	0.0002	0.00088	2 months & 1 year	0.0002	0.00088
2 months & 2 years	0.0002	0.00090	2 months & 2 years	0.0002	0.00090
2 months & 3 years	0.0002	0.00092	2 months & 3 years	0.0002	0.00092
2 months & 4 years	0.0002	0.00093	2 months & 4 years	0.0002	0.00093
3 months & 1 year	0.0002	0.00095	3 months & 1 year	0.0002	0.00095
3 months & 2 years	0.0002	0.00097	3 months & 2 years	0.0002	0.00097
3 months & 3 years	0.0002	0.00099	3 months & 3 years	0.0002	0.00099
3 months & 4 years	0.0002	0.00101	3 months & 4 years	0.0002	0.00101
4 months & 1 year	0.0002	0.00103	4 months & 1 year	0.0002	0.00103
4 months & 2 years	0.0002	0.00105	4 months & 2 years	0.0002	0.00105
4 months & 3 years	0.0002	0.00107	4 months & 3 years	0.0002	0.00107
4 months & 4 years	0.0002	0.00109	4 months & 4 years	0.0002	0.00109
6 months & 1 year	0.0002	0.00111	6 months & 1 year	0.0002	0.00111
6 months & 2 years	0.0002	0.00114	6 months & 2 years	0.0002	0.00114
6 months & 3 years	0.0002	0.00117	6 months & 3 years	0.0002	0.00117
6 months & 4 years	0.0002	0.00119	6 months & 4 years	0.0002	0.00119
1 day & 4 months	0.0012	0.00122	1 day & 4 months	0.0350	0.00122
1 day & 6 months	0.0058	0.00125	1 day & 6 months	0.0466	0.00125

Note: α_C is the sequential Dunn-Šidák comparisonwise significance level (Sokal & Rohlf, 1995) and p is the p-value of the pairwise randomization test.

FIGURE 3.5 The observed characteristic times inferred from the sampling periods with the greatest amount of variance in the per capita growth rate statistically related to the variance in population density. The vertical solid lines and the vertical dashed lines indicate which sampling periods exhibit the largest values of r_S^2 and r_P^2 respectively. All the observed sampling periods δ that a vertical line intersects do not differ significantly from each other with only a couple of exceptions. Pairs of open circles or solid squares on a vertical line indicate a significant pairwise difference. For instance, the r_S^2 solid line for the 10^0 kg populations has 2 solid squares indicating that the means of the maximum r_S^2's of the 1 year and the 2 years sampling periods differ significantly from each other. Similarly, the two open circles indicate significant differences between the 1 year and the 3 years sampling periods. The asterisk in the 10^{-2} kg category indicates that the 2 months sampling period did not differ from all other sampling categories for the r_P^2 statistic.


Observed sampling period δ
Inferred characteristic time t_C
4 years
3 years
2 years
1 year
6 months
4 months
3 months
2 months
1 month
2 weeks
1 week
0.5 week
1 day
Body size W (kg)
10^{-4}
10^{-3}
10^{-2}
10^{-1}
10^{0}
10^{1}
10^{2}
Growth Rate ρ ($year^{-1}$)
16.6
9.0
5.0
2.7
1.5
0.83
0.45
Generation time t_g
1 month
2 months
3 months
4 months
1 year
2 years
3 years
Traits of 7 simulated populations

Discussion

Examination of Figure 3.5 reveals that the maximal quantities of r_S^2 and r_P^2 do not occur in the sampling periods that I predicted (Figure 3.1). The pattern of the results differ from the predictions in two aspects. First, there is no single δ exhibiting maximum r_P^2 and r_S^2 values. Instead, there are typically 4 adjacent δ's (i.e., 1, 2, 3 and 4 years) that do not significantly differ from each other. Second, the δ's exhibiting maximum r_P^2 and r_S^2 values do not correspond to generation times t_g as predicted (Figure 3.1). Essentially, Figure 3.5 shows that the δ's with maximum r_P^2 and r_S^2 are independent of the body sizes W or the generation times t_g of the model populations.

I predict from these results that independent of W and other correlated life history traits, the characteristic temporal scale on which density-dependent regulatory processes operate is yearly or multiples thereof.

It has been argued that the use of yearly average population densities (i.e., long-term census data) are the appropriate basis for studying density dependence (Dempster & Pollard, 1986; Mountford, 1988). Inherent in these arguments is the assumption of seasonality— univoltine organisms. From a biological perspective these arguments are plausible. Organisms whose reproductive episodes are limited or determined by seasons would, in effect, produce discrete changes in their population size on a yearly basis.

The difficulty with these arguments is their application to the results in this study. There is no seasonality in the model (3.5) used to generate the time series. This makes it difficult to relate the yearly characteristic temporal scales found with the yearly, biologically tantalizing explanations based on seasonality.

I suggest another possible explanation that I will refer to as the "numerical" hypothesis. The numerical hypothesis suggests that the results are an artifact of the experimental design and focuses on the possible effects of the different sampling strategies used to derive γ and obtain N on the coefficients of determination r_S^2 and r_P^2.

The numerical hypothesis is merely based on the observation that the δ's with the most variance in γ statistically attributable to the variance in N are all multiples of 1 year. After re-examining the experimental design I see no apparent reason why this should be logically so. But, in the absence of a deductive explanation, I suggest an hypothesis based on a coincidental observation— that the time between successive N's in a time-slice is *1 year* and that the characteristic temporal scales are multiples of *1 year*. Given this 1 year congruence, it is possible that the characteristic temporal scales obtained by this methodology are some function of the time between successive N's in a time-slice. (Hereafter, I will denote the time period between successive N's in a time-slice with a Δ).

Consider the time-slice obtained from a simulated time series,

$$N_1, N_2, N_3, \ldots, N_{25} \tag{3.7}$$

where N is the population size at the time denoted by the subscript. The subscript denotes successive yearly N's. So N_1 represents the initial population size in the time-slice, N_2 the second point 1 year after N_1, N_3 the third point 2 years after N_1, and so on. As described in the methods, for each N in the time-slice, a corresponding value for γ is calculated using an earlier and a later population size that precede and follow the N by the time period δ.

If the sampling period δ, used to determine γ, is an integral multiple of Δ then there will be more values of N common to both the set of N's used to calculate γ and the set of N's in a time-slice. If δ is not an multiple of Δ then the only N's common to these two sets will be the N's of the time-slice. This point will be made clearer with the following example.

If we examine a specific point N_{12} of the time-slice (3.7) and assume that Δ and δ both equal 1 year, we would use N_{11}, N_{12} and N_{13} to calculate the per capita growth rate γ_{12} associated with N_{12}. If δ was twice the value of Δ (i.e., an integral multiple of Δ) then N_{10}, N_{12} and N_{14} would be used to calculate γ_{12}.

Thus in the case where both Δ and δ equal 1 year, ignoring the end points of the time-slice for simplicity, we produce the set of points:

(N_2,γ_2) with γ_2 derived from N_1, N_2 and N_3;

(N_3,γ_3) with γ_3 derived from N_2, N_3 and N_4;

(N_4,γ_4) with γ_4 derived from N_3, N_4 and N_5;

and so on untill

(N_{24},γ_{24}) with γ_{24} derived from N_{23}, N_{24} and N_{25}.

Similarly for the case where Δ is 1 year and δ equals 2 years we obtain the set:

(N_3,γ_3) with γ_3 derived from N_1, N_3 and N_5;

(N_4,γ_4) with γ_4 derived from N_2, N_4 and N_6;

(N_5,γ_5) with γ_5 derived from N_3, N_5 and N_7;

and so on untill

(N_{23},γ_{24}) with γ_{23} derived from N_{21}, N_{23} and N_{25}.

Note that the N values used to calculate γ are all common to the N's in the set of (N,γ) ordered pairs that are used to determine r_S^2 and r_P^2.

In contrast, if Δ equalled 2 years and δ was 3 years, in the following set of points,

(N_4,γ_4) with γ_4 derived from N_1, N_4 and N_7;

(N_6,γ_6) with γ_6 derived from N_3, N_6 and N_9;

(N_8,γ_8) with γ_8 derived from N_5, N_8 and N_{11};

and so on untill

(N_{22},γ_{22}) with γ_{22} derived from N_{19}, N_{22} and N_{25},

only the mid-points used to calculate the γ's are common to the N's in the set of (N,γ) ordered pairs used to determine r_S^2 and r_P^2. The postulated basis of the numerical hypothesis is that the combinations of Δ and δ that select the two sets of N values (one set consisting of N's and the other consisting of N's to calculate the γ's corresponding to the first set of N's) that have more occurrences of points common to both, will yield larger values of r_S^2 and r_P^2.

If the numerical hypothesis is assumed to be true, it would account for patterns in the results obtained in this study. Furthermore, I predict that if the procedure was repeated with a different value for Δ, the sampling periods with the most r_S^2 and r_P^2 values would be those δ's that are multiples of Δ.

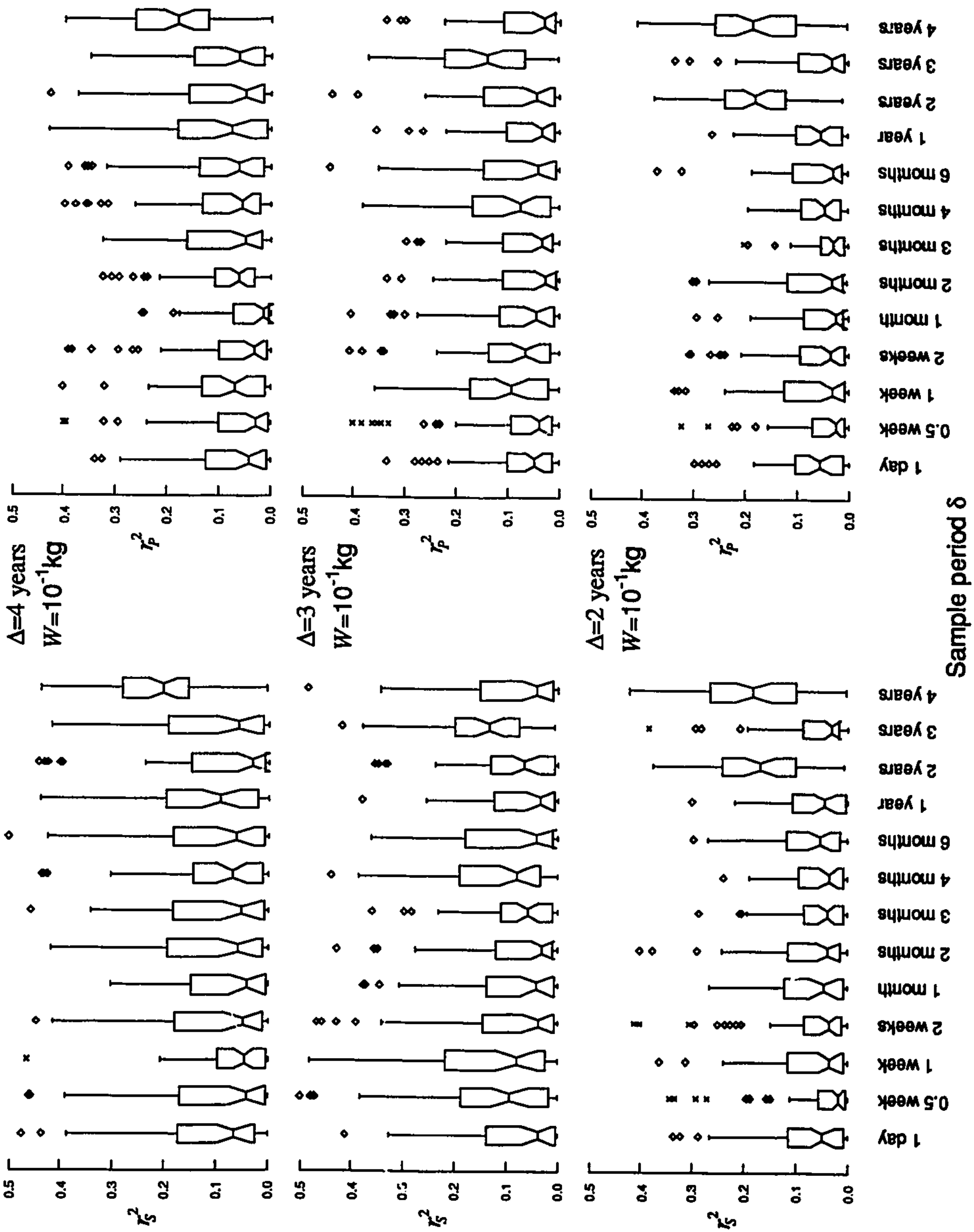
In a limited attempt to falsify the numerical hypothesis I created subsets of the data generated for the 10^{-1} kg modelled populations. Subsets were created by removing alternate points from the 25 year time-slices. So for each 25 point set (i.e, for all combinations of ρ, K and σ) a set of 13 data points was produced by taking the first point, the third point, the fifth point up to and including the twenty-fifth point. These 13-point data sets are data sets with Δ's equal to 2 years. In a similar manner, 9-point data sets and 7-point data sets, with Δ's of 3 years and 4 years respectively, were also produced.

Based on the numerical hypothesis I predict that the 2 year and 4 year sampling periods (δ) for the data sets with Δ's equal to 2 years will have the maximal amounts of r_S^2 and r_P^2. Furthermore, the maximum amounts of r_S^2 and r_P^2 will occur when $\Delta = 3$ years and when $\Delta = 4$ years for the $\Delta = 3$ and $\Delta = 4$ years respectively.

Figure 3.6 shows the results of the analysis of the 2, 3 and 4 year Δ data sets (pooled across K and σ). These results are consistent with the numerical hypothesis suggesting that the yearly characteristic temporal scales obtained in this experiment may be an artifact of the experimental design.

Though I have not fully explored the mathematics inherent in the numerical hypothesis I suspect that there may be a direct mathematical relationship leading to the results obtained from testing the numerical hypothesis. Assuming that my suspicion is correct, I suggest that these results are correct and peculiar to the time-series subsamples that were selected to be analyzed as outlined on page 3-8 of the methods.

FIGURE 3.6 Results from the test of the numerical hypothesis. The three distributions of the r_S^2 and r_P^2 statistics (pooled across K and σ) for the 10^{-1} kg model populations with $\Delta = 2$, 3 or 4 years. These 3 pairs of graphs show notched-box plots of the r_S^2 or r_P^2 statistics calculated from modified time-slices to test the numerical hypothesis as mentioned in the discussion. The top graph was created from the analysis of time-slices with a 4 year period between successive N's, $\Delta = 4$, and the midlle and bottom pairs of graphs correspond to Δ's =3 and 2 respectively. Every graph is composed of 13 notched-box plots one for each of the 13 sampling periods δ discussed in the methods. If the notches (the diagonal lines extending from the median to the vertical sides of a box) of two medians do not overlap, then the medians can be considered to be significantly different ($p \leq 0.05$). The hollow diamonds and $\times$'s identify outliers within each distribution. The diamonds are points that lie between 1.5 times and 3.0 times the interquartile distance outward from the hinges of the notched box and the $\times$'s are outliers beyond this range (Wilkinson et al. 1992).


Δ=4 years
W=10^-1kg
Δ=3 years
W=10^-1kg
Δ=2 years
W=10^-1kg
Sample period δ
r_P^2
r_S^2
0.0
0.1
0.2
0.3
0.4
0.5
1 day
0.5 week
1 week
2 weeks
1 month
2 months
3 months
4 months
6 months
1 year
2 years
3 years
4 years

It is possible that the variation in a sequence ($N_1, N_2, N_3, \ldots$) of population densities is a better predictor of the variation in the growth rate calculated from N_1 to N_2 to N_3 than of the variation in growth rate over other time intervals. Thus if one is interested in yearly variation then a yearly sampling interval is appropriate. Finer sampling may only add noise degrading the estimates of r_S^2 and r_P^2. An implication of this would be that in order to really address the characteristic time hypothesis of this chapter, then for each of the 13 sampling periods δ, time-slices with Δ's equal to each δ need to be generated. Then the amounts of r_S^2 and r_P^2 will be maximized within a sampling category and the predicted patterns for characteristic times might emerge.

Since the numerical hypothesis was loosely based on properties of the analysis method used to determine r_S^2 and r_P^2, it is appropriate to question how these results may affect the findings of chapter 2. If the quantities of variance explained (r_S^2 and r_P^2) in chapter 2 were maximized or inflated due to the analysis method this would suggest that the actual values of r_S^2 and r_P^2 would be less than those reported. This would tend to strengthen the major result of chapter 2 that, on average, relatively little of the temporal variability in per capita growth rate can be statistically related to population density and the main conclusion that the effects of density-dependent regulatory processes are generally quite weak.

Conclusions

Based on the analysis of model abundance time series the characteristic time of density-dependent regulatory processes is predicted to be independent of the life-history traits correlated with body size. The characteristic times are predicted to be integral multiples of 1 year (1, 2, 3 and 4 years) for all modelled body sizes.

These model predictions were found to be suspect after further testing supported the contention that these results may be methodological artifacts. I suggest that these results are due to the pragmatic criteria imposed to constrain the number of possible subsamples to be analyzed. I further suggest that to better address the characteristic time hypothesis of this chapter, time-slices with different time periods between successive population densities are required.

CHAPTER 4: General Discussion and Conclusions

General discussion

I concur with Krebs'(1995) notion that "... the search for density dependence has become a holy grail." Even though population regulation research has been one of the single largest research areas in community ecology (Inchausti, 1994) there has been a failure to resolve the question of whether or not populations are regulated (Wolda, 1995). Royama (1977) has argued that the regulation hypothesis need not be tested because it is *a priori* knowledge derived from the premise of persistence of populations— "Since no population increases without limit, and species only occasionally become extinct, there must be some regulating factors..." (Haldane, 1953). Leaving such anti-verification arguments aside it is this *a priori* belief that has driven population regulation research.

Royama (1977) credits Reddingius (1971) with the view that "it would be unwise to postulate what types of factors regulate populations before a certain statistical relationship between population density and the factors determining it is actually established." It is this "burden of proof" argument (Dennis & Taper, 1994) that forms the philosophical underpinnings of this thesis' research.

By assuming that density-dependent regulatory processes do operate within natural animal populations, the major goal of this thesis was to statistically relate the amount of variance in the per capita growth rate of natural populations to the temporal variance in their densities. In other words, given existing available data, what can be inferred about the influence of density-dependent regulatory processes upon natural animal populations? That only 19% of the variance could be statistically accounted for, suggests that only a small portion of the temporal variability in natural animal populations is influenced by the density-dependent regulatory processes. Couple this with the fact that the majority of population dynamics research has focused on density-dependent regulation, I suggest that this research emphasis switch to non-density-dependent influences.

It could be argued that even if the influence of density-dependent regulatory processes is relatively small it may still be the process fundamentally promoting the persistence of populations. This argument is inescapable if we believe *a priori* that a population must be regulated in order to persist. But if populations can remain between relatively narrow positive bounds for long periods of time (i.e., "stabilization" Den Boer, 1989) without density-dependent regulatory processes (Royama, 1971) there may be no need to postulate that populations must be regulated. The "burden of proof" rests on those presenting the argument. It needs to be demonstrated that density-dependent regulatory processes operating at intermittent intervals are the key to persistence (i.e, that if they were absent the population would become extinct). For instance, merely finding evidence of density-dependent processes operating at one life stage is insufficient to infer population regulation because the effects of these processes are often counteracted at another life stage (Turchin, 1995). With all the problems that have been encountered in attempting to demonstrate that populations are regulated, I think that the argument made at the beginning of this paragraph is without substance and, as well, pointless.

Population regulation research has often been justified by the potential benefits of understanding population processes and the application of this knowledge to conservation issues (e.g., Den Boer, 1990). Though I agree that the intent of this justification has merit, I suggest, given the results of this study, that research into density-independent factors and their effect on populations would be more fruitful. Notwithstanding the preceding admonition, I suggest that an exploratory statistical study relating the proportions of variance found in chapter 2 to a variety of life-history traits as well as geographical and environmental variables may yield some useful patterns. These patterns may provide useful predictions to identify populations that are strongly or weakly influenced by density-dependent processes.

In chapter 3 I attempted to determine, via simulation, how the characteristic time of density-dependent processes might affect the estimates of r_S^2 and r_P^2. Based on the model's behaviour I also hoped to predict how the characteristic time of density-dependent processes would vary with life-history traits. The results were not as expected. Though characteristic times were generated by the model, they did not vary with life-history traits (modelled by the value of ρ, the maximum rate of increase per individual). The characteristic times were all multiples of 1 year independent of the value of ρ.

Taken at face value, these yearly characteristic times may relate to biological arguments regarding a distinct seasonality in population processes (Royama, 1977). On the other hand, further testing revealed an unexpected result indicating that the identified characteristic times are the result of the period of time between successive population densities used to calculate the proportion of variance in the per capita growth rate attributable to the variance in population density. I suggest that the estimates of the proportion of variance explained are maximized when the densities used to calculate the per capita growth rate are from the sequence of densities used to calculate the proportion of variance explained. In other words, if one is interested in the yearly variation in densities, yearly sampling would be appropriate.

That the maximal proportions of variance explained may be a function of the time between successive population densities, tends to vitiate the predictions that the characteristic times are multiples of 1 year and independent of life-history traits. I suggest that characteristic times identified in this study are merely the maximal estimates of the proportion of variance explained for yearly sampling strategies. I suggest that a variety of time-slices, with different periods of time between successive densities, need to be analyzed. Then the maximal proportions of variance explained (occurring at the equivalent sampling periods used to calculate γ) for each of these time-slices can be compared to see which yields the largest explained proportion of variance and would identify the appropriate characteristic times.

Conclusions

I found that relatively little (≈19%) of the variance in the per capita growth rate could be statistically related to the temporal variance in population densities for 303 natural animal populations. Given this result I infer that the effect of density-dependent regulatory processes is relatively small and suggest that to better understand the population dynamics of natural animal populations that research on density-independent factors is required.

Though the analysis of model abundance time series led to the predictions that the characteristic time of density-dependent regulatory processes is independent of the life-history traits correlated with body size, and is an integral multiple of 1 year (1, 2, 3 and 4 years), these predictions may be artifacts of the experimental design.

These model predictions were found to be suspect after further testing supported the contention that these results may be methodological artifacts. These artifacts are likely due to the pragmatic criteria I imposed to constrain the number of possible subsamples to be analyzed. I suggest that to better address the characteristic time hypothesis of this chapter, time-slices with different time periods between successive population densities are required.

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Lack (1954)[4] N (occupied nests)

1928-1944 17 years

121.42,128.57,153.57,132.14,175.00,192.85,250.00,260.71,250.00,239.28,235.71,267.85,285.71,207.14,228.57,171.42,178.57

Larkin & McDonald (1968) N ($\times 10^6$ individuals)

1908-1964 57 years

2.65,1.64,3.53,2.48,1.79,1.04,2.29,2.00,0.91,1.35,2.33,2.72,1.40,0.71,1.77,2.54,2.65,1.60,1.46,1.50,0.62,2.18,1.50,1.34,0.86,0.50,0.90,0.83,1.41,0.76,0.81,1.33,2.36,1.46,0.62,0.53,1.60,1.96,1.00,0.67,2.32,1.17,0.87,1.16,2.33,1.28,0.97,0.21,0.51,0.80,1.44,0.90,0.43,1.79,1.01,0.71,1.53

Le Cren et al. (1977) N ($\times 10^6$)

1941-1966 26 years

3.59,2.44,1.87,1.46,1.38,1.38,1.38,1.14,0.89,0.65,1.46,0.97,1.30,1.22,0.89,0.57,3.75,2.77,2.36,2.12,3.10,2.85,1.46,1.06,0.81,0.65

Loery and Nichols (1985) N

1959-1982 24 years

273.8,126.8,178.1,201.9,151.4,159,183.5,126.5,145.2,85,164.3,328.1,155.7,127.4,194.2,161.2,129,112.8,137.9,147,113.2,157.5,135.7,134.2

MacLellan (1978)[1] N per tree

eggs

1965-1976   12 years

587.1,824.8,2938.9,4731.4,6170,19761.3,17002.9,7132.6,9009.7,13321.4,11910.2,5329.5

neonate larvae

1965-1976   12 years

568.9,770.2,2803.4,4518.5,5877.5,17696.3,15284,6882.2,8734,12807.2,11457.6,4913.2

larvae preparing webs

1965-1976   12 years

497.1,398.3,1194.7,3370.5,4959.2,13117.5,8432.7,4639.4,5537,8724.8,8594.9,3230.1

MacLellan (1978)[2] $\overline{N}$ per tree

eggs

1965-1976   12 years

595.8,844.3,2874.2,4719.5,6128.1,20459.7,17772.3,8738.3,8057.2,10921,11612.9,6207.5

neonate larvae

1965-1976   12 years

568.8,777.1,2730.2,4427.8,5914.9,18501.7,15723.1,8534.7,7709.1,10117.2,10895.2,5680.4

larvae preparing webs

1965-1976   12 years

472.9,380.8,1129.7,3208,4639.4,9369.1,10508.7,4402.9,4893.6,7478.8,7828.1,2139.9

MacLellan (1977)[1] per tree

eggs

1965-1976 12 years

1.8,12.3,36.4,100.4,245.2,345.3,511.2,133.9,98.2,22.2,59.2,56.2

neonate larvae

1965-1976 12 years

1.8,12.3,26.8,86.5,202.5,260.9,420,119.3,77.9,18.2,46.8,48.2

MacLellan (1977)[2] $\bar{N}$ per tree

eggs

1965-1976 12 years

0.001,0.001,35.3,126.5,171.5,113.8,673,52.8,29.3,11,4.3,11.5

neonate larvae

1965-1976 12 years

0.001,0.001,20.3,99.8,110.8,73.8,560.3,40.3,12.8,8.5,4.3,11.5

Marcström et al. (1990) $\bar{N}/100$ trap-nights

1961-1971 11 years 2 points per year 21 points

(0.42,2.57) (0.75,4.17) (1.42,11.37) (1.75,6.39) (2.42,4.76) (2.75,3.32) (3.42,3.02)
(3.75,3.6) (4.42,9.06) (4.75,10.35) (5.42,15.06) (5.75,13.18) (6.42,2.90) (6.75,0.84)
(7.42,0.28) (7.75,2.16) (8.42,4.22) (8.75,14.09) (9.42,4.70) (9.75,7.61) (10.42,0.27)

and continuing...

1976-1985 10 years 2 points per year 20 points

(0.42,0.42) (0.75,1.30) (1.42,2.90) (1.75,10.35) (2.42,2.08) (2.75,1.47) (3.42,1.61)
(3.75,1.02) (4.42,4.96) (4.75,13.90) (5.42,2.98) (5.75,3.32) (6.42,0.42) (6.75,3.27)
(7.42,1.59) (7.75,7.51) (8.42,3.45) (8.75,5.45) (9.42,0.29) (9.75,0.87)

McLain and Shure (1990) $N/0.25\mathrm{m}^{-}$ or N

$N/0.25\mathrm{m}^2$

1979-1989 11 years

4.06,0.9,9.13,5.5,5.35,1.43,33.61,3.15,3.01,5.12,3.58

N

1979-1989 11 years

50700,11300,114200,68800,66900,17900,420100,39400,37600,64000,44700

Messier (1991)[1] N/km^2

1968-1985 18 years

2.11,1.76,1.23,1.53,1.47,1.5,1.42,1.16,0.92,0.98,1.22,1.05,1.04,1.08,1.48,1.43,1.95,1.88

Messier (1991)[2] $N/100\mathrm{km}^2$

1975-1984 10 years

2.72,2.18,2.33,1.89,2.28,1.99,1.75,1.84,1.12,1.46

Messier (1991)[3] $N/100\mathrm{km}^2$

1958-1985 27 years

3.68,4.04,4.041,4.23,3.68,4.78,5.15,4.6,4.041,4.04,3.13,3.31,3.68,4.23,4.41,5.7,7.54,8.09,6.25,7.35,7.9,9.19,5.51,2.57,4.23,4.41,4.04

Messier (1991)[4] N/km^2

1975-1985 11 years

0.75,0.63,0.47,0.65,0.51,0.49,0.43,0.5,0.97,0.54,0.99

Middleton (1934)[1] N

1848-1904 57 years

346,401,471,505,902,1146,644,592,638,782,588,865,954,605,160,185,922,1644,3402,1,4,15,530,1621,3548,89,91,464,1200,1144,314,472,953,820,464,606,292,832,1571,1

324,1534,1670,1966,171,213,1496,2638,1517,1432,2022,1409,930,764,1947,2523,12,351

Middleton (1934)[2] *N*

1849-1904 56 years

2254,2402,2534,2539,4470,5286,2145,742,2060,2880,4448,3910,0.001,637,1914,2548,4743,5700,0.001,0.001,1600,2200,6000,10600,506,583,990,1877,2233,1189,1827,2084,2804,3672,2199,2612,1542,2200,3600,1710,1941,2464,3614,4191,4163,4182,857,2298,2147,3773,5823,7442,4573,3591,1894,1943

Middleton (1934)[3] *N*

1858-1909 52 years

920,1405,1377,1286,772,812,1998,3618,5948,208,336,1019,2107,4379,4073,170,549,1482,3382,3060,1749,2162,1500,2136,3316,1055,1664,3285,5588,4439,4547,1974,4057,3174,3904,5648,5638,4908,6745,1368,2983,3701,5285,4740,360,3043,3140,3550,4060,4627,3969,4604

Middleton (1934)[4] *N*

1897-1924 28 years

1025,786,303,250,1171,1511,1583,2418,1711,2071,1826,1269,1827,2894,3577,4676,4860,2352,2073,2296,1021,483,961,759,1023,1414,2163,1836

Middleton (1934)[5] *N*

1793-1841 49 years

1349,1433,2594,2814,3800,3965,2895,3865,2908,4036,1721,2831,1320,1296,1686,2024,2050,2516,1748,1811,1707,2588,1967,1804,625,1711,1420,1651,1893,2838,3410,2656,2799,1837,2163,1114,1234,676,1074,954,1773,2343,1923,1492,2138,2056,1649,1195,1485

Middleton (1934)[6] *N*

1843-1933 91 years

2676,793,1814,990,4185,2635,4880,3372,3554,2867,3325,1031,1692,1809,2266,3460
,3493,210,3130,1437,2562,2505,1567,1997,2555,3308,3385,2996,2772,3108,2426,17
42,1167,2317,3828,2341,332,2486,3689,3665,3754,5589,8100,3630,7512,1390,5254,
2321,2757,2734,4585,3733,4976,6426,5961,3566,5893,4599,3435,5333,1700,5286,85
12,3165,896,2626,1141,694,2388,3800,2243,4166,4138,882,1962,4177,695,1208,179
4,3995,4460,8527,2874,4279,447,3306,4434,4462,2125,1247,3469

Middleton (1934)[7] *N*

1843-1933 91 years

264,184,177,190,265,288,185,259,202,273,405,226,242,208,435,611,996,172,388,222
,366,150,299,249,112,137,242,272,172,93,141,114,134,162,125,85,8,43,76,41,77,157,
46,32,55,9,73,76,55,133,233,86,63,214,321,146,330,315,403,106,184,155,475,814,13
3,36,117,19,104,29,16,50,229,12,242,261,32,30,96,77,92,215,304,368,48,203,255,133
,70,133,83

Middleton (1934)[8] *N*

1862-1932 71 years

541,727,594,735,919,994,853,921,669,810,1116,894,352,423,1017,1212,1167,191,39
4,922,778,957,201,771,881,1121,692,1112,945,897,1151,651,848,1138,1262,972,636,
559,480,462,751,556,1004,1031,549,1193,564,611,453,728,1082,393,726,911,409,38
5,544,136,351,295,353,507,828,159,191,91,111,304,330,417,223

Middleton (1934)[9] *N*

1879-1932 54 years

327,23,220,1013,838,1003,389,518,556,750,451,371,631,759,929,1023,747,1035,120
7,1632,630,250,250,428,843,166,646,532,947,228,334,500,350,615,942,1062,1082,90
2,332,345,220,253,271,404,507,352,829,393,53,398,409,589,202,63

Middleton (1934)[10] *N*

1889-1933 45 years

2890,1906,4198,3705,5719,3423,4356,5185,6670,3113,3148,3414,3501,2224,515,2117,3601,3095,964,1726,1241,550,3766,7906,1619,5212,5007,648,1544,1410,1701,5207,3238,3454,2638,1413,973,822,135,807,1732,3305,255,867,1789

Middleton (1934)[11] *N*

1897-1924 28 years

45,7,181,203,294,227,148,215,513,669,78,742,178,877,338,179,437,522,519,231,395,284,619,129,578,150,161,188

Middleton (1934)[12] *N*

1836-1844 9 years

6,24,38,21,55,54,34,38,65

and continuing…

1846-1932 87 years

49,65,51,36,17,32,14,53,44,49,60,33,41,39,70,29,55,67,71,86,159,103,64,109,42,45,64,88,115,71,80,77,26,42,24,25,34,45,35,75,62,48,39,51,11,16,50,41,52,46,52,27,36,28,62,39,48,40,37,35,46,71,77,72,45,94,19,94,31,43,30,40,50,68,60,41,39,23,34,34,44,26,50,21,25,34,40

Middleton (1934)[13] *N*

1897-1924 28 years

59,56,31,44,66,75,38,44,30,31,28,66,78,150,92,114,128,45,35,36,23,17,37,59,47,95,27,18

Middleton (1934)[14] *N*

1843-1932 90 years

112,155,159,161,184,173,187,118,92,58,124,179,181,212,269,195,209,88,180,123,297,137,161,142,72,131,276,297,165,116,134,52,100,100,41,52,53,85,18,45,60,74,15,22

,25,6,26,54,45,63,125,48,33,74,113,49,130,109,182,111,63,80,200,309,161,74,95,46,87,132,194,283,240,132,80,64,60,62,71,63,80,156,195,183,90,95,102,78,78,91

Middleton (1934)[15] *N*

1862-1932 71 years

113,206,156,205,334,214,216,302,309,326,353,377,272,296,205,333,371,181,259,489,364,217,108,118,237,415,244,199,200,199,253,268,472,396,376,296,486,326,446,443,365,263,393,353,198,430,222,345,532,525,387,518,464,143,224,244,176,389,485,351,217,320,156,118,220,295,329,330,321,131,141

Middleton (1934)[16] *N*

1902-1932 31 years

331,294,245,370,349,376,247,290,258,224,325,410,375,276,216,147,102,86,71,102,126,184,127,181,120,81,160,114,151

Middleton (1934)[17] *N*

1884-1930 47 years

268,182,116,259,208,726,678,1216,503,521,444,50,215,351,397,552,569,501,309,176,95,230,748,975,1200,1985,2701,2400,1237,832,672,537,437,280,310,317,370,250,649,853,840,812,846,600,110,150,150

Middleton (1934)[18] *N*

1879-1930 52 years

431,258,287,322,309,299,263,221,198,211,242,207,201,178,190,154,179,200,393,360,431,341,305,335,319,336,410,487,394,397,419,339,363,488,459,398,358,298,310,287,297,286,386,397,354,249,258,343,362,356,336,467

Middleton (1934)[19] *N*

1882-1929 48 years

69,56,65,43,53,34,70,131,90,104,132,18,24,79,21,53,98,103,132,198,146,70,48,117,86,125,121,101,121,145,131,106,74,128,131,100,42,45,32,30,33,78,11,31,9,17,19,21

Middleton (1934)[20] *N*

1867-1928 62 years

11615,7201,17270,19197,10210,10665,16072,10424,11388,11185,14910,14308,13851,9161,4989,3925,6918,7373,8263,3131,3161,4236,4106,6095,9353,7024,7250,8132,4118,5615,8486,9717,16456,13846,16222,16407,17187,13359,12038,12342,10867,7761,5122,11667,10265,11274,8082,5191,7683,4993,3029,6524,8234,10858,10616,17878,16445,9709,9027,13137,7648,8054

Middleton (1934)[21] *N*

1869-1933 65 years

723,426,166,189,268,167,435,646,332,336,284,397,275,398,193,364,710,463,330,331,519,474,452,720,396,383,287,505,408,370,542,941,309,305,513,404,464,566,386,351,520,529,518,516,418,417,391,167,246,497,410,484,666,631,580,648,287,351,372,279,375,293,318,220,406

Middleton (1934)[22] *N*

1862-1932 71 years

194,124,111,193,287,210,314,273,106,218,182,196,94,122,45,60,41,24,20,44,64,40,42,66,48,204,235,289,205,65,96,85,122,296,305,280,306,304,260,148,88,293,707,324,208,218,46,137,466,466,264,221,179,175,283,288,431,648,1218,709,420,881,289,315,317,376,418,370,322,221,163

Middleton (1934)[23] *N*

1902-1932 31 years

3607,1428,3986,4916,1667,1822,1760,2190,793,1653,2332,3869,2548,2426,2259,1296,1088,587,2130,2515,663,2437,2599,3139,2368,2740,2147,2812,1998,888,743

Mindell and White (1988)[1] *N* (sites occupied)

1971-1985 15 years

34,34,35,35,33,35,34,32,30,31,30,30,28,31,32

Mindell and White (1988)[2] *N* (sites occupied)

1975-1983 9 years

19,19,21,18,19,20,17,18,22

Møller (1989) *N*

1971-1988 18 years

441,323,410,428,220,310,514,320,224,183,212,206,209,160,133,136,88,133

Morris (1964)[1] *N*

1940-1959 20 years

3.12,5.5,4.64,2.09,2.22,1.12,8.2,19.23,33.95,112.04,132.88,28.63,10.89,9.18,16.21,53.51,84.32,105.85,112.04,22.8

Morris (1964)[2] *N*

1944-1959 16 years

27.99,56.62,176.63,150.13,303.64,494.44,398.11,108.47,176.63,219.37,357.22,258.09,551.03,398.11,398.11,186.46

Morris (1964)[3] *N*

1939-1956 18 years

36.58,89.95,105.44,18.38,10.83,9.24,1.24,7.09,12.04,36.58,94.84,36.58,16.53,7.47,6.72,9.74,20.43,15.68

Morris (1964)[4] *N*

1937-1958 22 years

1.241,1.24,6.72,19.38,3.04,1.99,1.17,1.05,3.04,8.31,6.38,10.27,10.27,2.73,1.111,1.11,2.88,11.41,1.24,7.09,4.4,3.76

Morris (1964)^{5} N

1937-1958 22 years

1.24,2.96,14.22,5.98,1.81,1.06,1.001,1,3.67,2.65,16.73,20.78,12.09,3.48,1.81,12.09,20.78,61.41,16.73,64.83,42.03,35.72

Murdoch et al. (1984)^{1} % parasitism

1956-1965 11 years

78.26,41.84,36.95,98.91,74.45,40.21,39.13,54.34,59.78,84.78,85.86

Murdoch et al. (1984)^{2} $\bar{N}$ per twig

1956-1965 10 years 2 points per year 20 points

(0.42,0.54) (0.75,0.31) (1.42,1.06) (1.75,0.86) (2.42,3.32) (2.75,1.93) (3.42,3.73) (3.75,0.50) (4.42,0.20) (4.75,0.42) (5.42,0.76) (5.75,1.61) (6.42,0.86) (6.75,0.97) (7.42,0.29) (7.75,0.22) (8.42,0.39) (8.75,0.20) (9.42,0.29) (9.75,0.20)

Myers (1988)^{1} N/area

1949-1977 29 years

0.0128,0.0948,0.5259,2.1932,89.8447,89.8447,58.539,12.1695,2.5299,0.2575,0.0302, 0.6067,1.2389,24.8515,77.8891,33.0661,1.2389,0.0009,0.0009,0.1678,0.1678,1.2389, 9.1462,183.4725,67.5245,28.666,0.1678,0.001,0.0006

Myers (1988)^{2} N/area

1949-1977 29 years

0.0073,0.0618,0.2575,5.1663,33.0661,575.0378,119.543,24.8515,1.9014,0.0009,0.0171,0.1455,0.8072,21.5445,324.8132,183.4725,4.4788,0.0005,0.0006,0.0618,0.0822,0.6067,6.874,50.7493,119.543,137.8922,12.1695,0.0007,0.0073

Nedelman et al. (1987) N (adults and young)

1939-1986 48 years

17,21,26,15,18,20,18,21,25,31,30,34,30,25,20,23,20,28,25,27,32,34,36,39,33,30,43,45,43,46,48,54,56,59,50,48,49,56,69,72,74,77,77,74,73,74,87,94

Nelemans et al. (1989) N, or $N/1000\text{m}^{-}$

$N/1000\text{m}^2$

1968-1978 11 years

268,341,238,784,396,604,626,1641,1281,1006,645

N (estimated by Craig I method)

1968-1978 11 years

545,672,398,1296,737,1130,1213,2932,353,263,1394

N (estimated by Craig II method)

1968-1978 11 years

696,878,534,1729,936,1444,1532,3808,467,374,1610

N (estimated by Jolly-Seber method)

1968-1978 11 years

193,220,167,585,431,436,541,1264,232,148,592

Newton & Marquiss (1986)[1] N

nests

1972-1984 13 years

33,36,39,33,34,29,36,32,38,39,32,34,34

clutches

1972-1984 13 years

32,34,32,28,28,24,34,26,24,26,31,29,29

Newton & Marquiss (1986)[2] *N*

nests

1971-1980 10 years

110,105,94,98,87,76,70,64,61,61

clutches

1971-1980 10 years

98,82,75,86,74,68,59,54,51,48

Owen-Smith (1990)[1] N/km^2

1974-1984 11 years

3.04,3.53,3.72,3.8,4.04,3.93,3.35,3.04,2.45,1.79,1.95

Owen-Smith (1990)[2] N/km^2

1974-1984 11 years

1.48,2.38,2.29,2.5,2.94,2.42,2.39,1.94,1.62,1.28,2.27

Parsons et al. (1977) N ($\times 10^6$ elvers)

1933-1947 15 years

10,15.6,20.3,22.7,27.9,24.6,19.9,26.5,30.2,21.5,19.7,15.9,16.5,20.8,17.1

Pechmann et al. (1991)[1] *N*

female breeders

1979-1990 12 years

0,0,2,9,19,112,28,433,400,312,451,595

metamorphosing juveniles

1979-1990 12 years

0,0,12,512,186,2279,0,2418,8418,0,0,186

female breeders and metamorphosing juveniles

1979-1990 12 years

0,0,14,521,205,2391,28,2851,8818,312,451,781

Pechmann et al. (1991)[2] *N*

female breeders

1979-1990 12 years

219,1055,82,507,836,1069,233,2562,808,123,233,685

metamorphosing juveniles

1979-1990 12 years

4000,2904,3,8110,4603,11945,0,0,4767,0,0,0

female breeders and metamorphosing juveniles

1979-1990 12 years

4219,3959,85,8617,5439,13014,233,2562,5575,123,233,685

Pechmann et al. (1991)[3] *N*

female breeders

1979-1990 12 years

45,26,8,43,92,54,15,41,12,0,0,11

metamorphosing juveniles

1979-1990 12 years

1051,2,1,415,514,149,0,0,199,0,0,0

female breeders and metamorphosing juveniles

1979-1990 12 years

1096,28,9,458,606,203,15,41,211,0,0,11

Pechmann et al. (1991)[4] *N*

female breeders

1979-1990 12 years

100,10,105,268,378,261,61,95,46,15,12,102

metamorphosing juveniles

1979-1990 12 years

930,0,3200,7367,1116,3312,0,22,2567,0,0,13

female breeders and metamorphosing juveniles

1979-1990 12 years

1030,10,3305,7635,1494,3573,61,117,2613,15,12,115

Perrins (1965)[1] *N* (breeding pairs)

1947-1963 17 years

42.51,43.93,74.17,43.93,42.04,63.30,44.40,43.46,37.79,33.54,104.88,63.77,105.82,77.95,147.87,58.58,62.83

Perrins (1965)[2] *N* (breeding pairs)

1947-1963 17 years

6.36,20.22,29.77,30.45,31.36,19.31,20.68,30.68,26.36,23.40,48.18,26.81,40.68,50.22,85.00,42.72,38.63

Perrins (1965)[3] *N* (breeding pairs)

1947-1963 17 years

16.13,29.09,43.40,36.36,30.00,21.36,16.59,26.36,16.36,24.31,74.09,27.27,34.77,20.00,43.86,20.90,16.59

Pietiäinen (1989) *N* (pairs)

1977-1988 12 years

29,48,54,70,67,85,82,75,80,85,82,72

Pollard (1991)[1] *N* index

1976-1989 14 years

85.77,8.15,10.35,17.56,31.35,35.33,153.17,273.55,514.18,433.55,569.58,814.91,456.31,456.32

Pollard (1991)[2] *N* index

1976-1989 14 years

321.55,367.47,332.46,1142.8,753.03,904.74,1087.01,670.02,530.44,300.79,513.03,818.55,471.97,1016.83

Pollard (1991)[3] *N* index

1976-1989 14 years

5.84,1.07,7.74,9.74,6.16,1.89,19.73,12.92,58.9,39.25,67.33,35.31,23.53,21.54

Pollard (1991)[4] *N* index

1976-1989 14 years

292.86,264.38,219.15,353.3,303.03,324.42,559.95,426.22,735.64,259.91,215.44,100,62.03,103.47

Roininen et al. (1993) *N*

1983-1991 9 years

0.77,3.1,31.74,56.52,44.13,117.68,44.13,5.42,0.32

Rose et al. (1986) *N* index

1929-1975 47 years

30.66,66.66,30.66,12.00,16.00,18.66,20,22.66,25.33,20.00,22.67,26.66,48.00,78.66,29.33,16.00,56.00,54.66,50.66,28,17.33,77.30,38.66,16,20,42.66,25.33,68.00,66.66,38.66,53.33,140.00,126.66,141.33,152.00,109.33,230.66,273.33,214.66,265.33,106.66,109.33,98.66,72.00,61.33,65.33,52.00

Royama (1981) N/m^2 (larvae)

1945-1972 28 years

0.065,0.075,0.432,3.45,4.177,57.667,56.112,50.298,28.325,66.116,13.538,6.834,24.039,2.109,0.398,0.271,1.008,0.294,0.224,0.064,0.075,0.064,0.054,0.444,2.849,1.694,3.745,12.471

Scheffer (1951)[1] *N*

1911-1941 31 years

15,25,38,58,62,87,96,132,145,156,179,222,179,168,77,60,50,66,45,51,52,57,63,72,74,44,40,38,42,54,56

Scheffer (1951)[2] *N*

1911-1941 31 years

25,40,52,75,92,111,144,155,164,192,250,190,150,200,225,250,250,315,329,404,453,485,673,820,1162,1388,1673,1943,1800,962,850

Semb-Johansson (1992) $\bar{N}$ per km

1966-1978 13 years

3.4,1.6,2,2.1,0.5,0.8,1.2,0.5,0.5,0.1,0.2,0.2,0.3

Sillén-Tullberg (1990)[1] N density

adults

1977-1987 11 years

4.07,1.66,2.44,1.06,0.45,0.05,1.77,6.38,0.68,0.75,0.39

offspring

1977-1987 11 years

7.6,14.02,5.77,6.69,0.59,6.98,16.6,4.88,2.14,1.43,1.21

Sillén-Tullberg (1990)[2] N density

adults

1977-1987 11 years

5.15,0.28,0.1,0.05,0.53,0.49,2.44,3.43,0.22,0.02,0.03

offspring

1977-1987 11 years

2.18,0.49,0.28,1.29,1.85,7.13,10,1.77,0.6,0.35,0.06

Sinclair (1977) N ($\times 10^3$ individuals)

1965-1973 9 years

41.85,45.35,48.41,52.34,55.62,57.59,56.72,55.19,59.56

Siniff et al. (1977)[1] *N* (pups)

1963-1974 12 years

19,32,50,50,70,15,79,57,28,57,60,47

Siniff et al. (1977)[2] *N* (pups)

1963-1974 12 years

62,57,68,83,88,63,72,42,48,95,124,63

Siniff et al. (1977)[3] *N* (pups)

1963-1974 12 years

80,83,72,75,122,41,64,46,40,34,11,43

Siniff et al. (1977)[4] *N* (pups)

1963-1974 12 years

60,67,80,94,160,87,9,39,116,19,112,63

Siniff et al. (1977)[5] *N* (pups)

1963-1974 12 years

101,86,96,151,151,83,142,262,110,221,160,126

Siniff et al. (1977)[6] *N* (pups)

1963-1974 12 years

12,20,28,47,48,32,44,66,47,39,50,52

Siniff et al. (1977)[7] *N* (pups)

1963-1974 12 years

12,8,12,5,0,0.003,5,3,2,2,3,3

Siniff et al. (1977)[8] *N* (pups)

1963-1974 12 years

20,23,40,38,51,14,46,58,18,14,31,45

Siniff et al. (1977)[9] *N* (pups)

1964-1974 11 years

10,13,21,17,2,8,6,9,1,4,4

Siniff et al. (1977)[10] *N* (pups)

1963-1972 10 years

9,15,12,0,18,36,4,0,8,5

Siniff et al. (1977)[11]

Combined *N*'s of Siniff et al. (1977)[1-10]

1963-1974 12 years

380,401,480,578,767,421,488,585,434,501,558,464

Skogland (1985)[1] *N*

1970-1981 12 years

140.34,98.48,47.28,52.31,57.89,396.03,357.91,376.49,315.38,396.03,784.22,1175.6

Skogland (1985)[2] *N*

1970-1982 13 years

71.71,77.43,100,135.94,184.78,238.66,285.47,452.43,501.19,599.48,717.06,857.7,1165.91

Skogland (1990) *N* (number of offspring per 100 females)

1970-1973 4 years

1237,699,1303,4523

and continuing...

1979-1989 11 years

3638,5080,5049,2822,6890,6573,4029,7007,8223,2951,2388

Snorrason et al. (1992) N (total catch— tonnes)

1958-1987 30 years

29.38,40.73,25.31,55.27,38.98,73.31,71.85,60.51,40.73,4.07,4.65,15.13,20.65,41.31,35.78,28.51,13.09,38.69,46.25,67.49,59.35,66.91,64,66.91,53.24,62.25,48.58,40.15,5.82,1

Southwood (1967) N (nests)

1921-1946 25 years

39.64,5.71,25,3.57,26.43,5.71,0.71,83.57,6.07,23.93,0.71,13.57,6.43,22.86,12.86,8.21,-0.36,16.07,13.21,7.5,51.79,7.5,35.71,1.43,39.64

Southwood & Reader (1976)[1] N (original data $\log_{10}N$)

1962-1973 12 years 4 points per year 48 points

(0.5,88.52) (0.67,78.36) (0.83,72.25) (1,44.37) (1.5,46.21) (1.67,42.60) (1.83,37.71) (2,23.16) (2.5,42.6) (2.67,39.28) (2.83,33.38) (3,9.47) (3.5,12.09) (3.67,12.59) (3.83,10.27) (4,7.73) (4.5,20.50) (4.67,19.68) (4.83,16.07) (5,10.27) (5.5,18.15) (5.67,16.73) (5.83,18.90) (6,9.87) (6.5,19.68) (6.67,17.43) (6.83,19.68) (7,9.47) (7.5,36.21) (7.67,34.77) (7.83,37.71) (8,18.15) (8.5,69.37) (8.67,61.41) (8.83,69.37) (9,12.59) (9.5,46.21) (9.67,42.60) (9.83,42.60) (10,13.11) (10.5,28.38) (10.67,26.16) (10.83,27.25) (11,14.81) (11.5,34.77) (11.67,33.38) (11.83,29.55) (12,12.59)

Southwood & Reader (1976)[2] N (original data $\log_{10}N$)

1962-1973 12 years 6 points per year 72 points

(0.17,244.41) (0.33,225.50) (0.5,170.13) (0.67,123.28) (0.83,85.82) (1,48.84) (1.17,82.43) (1.33,79.18) (1.5,46.92) (1.67,46.92) (1.83,43.29) (2,24.64) (2.17,67.40) (2.33,70.17) (2.5,46.92) (2.67,50.85) (2.83,45.07) (3,35.40) (3.17,64.74) (3.33,59.73) (3.5,45.07) (3.67,45.07) (3.83,36.85) (4,19.35) (4.17,46.92) (4.33,50.85) (4.5,35.40) (4.67,36.85) (4.83,38.36) (5,27.80) (5.17,89.34) (5.33,76.05) (5.5,76.05) (5.67,79.18) (5.83,82.43) (6,55.11) (6.17,199.85) (6.33,208.06) (6.5,100.81) (6.67,109.26) (6.83,104.95) (7,79.18) (7.17,208.06) (7.33,216.60) (7.5,177.11) (7.67,163.41) (7.83,199.85) (8,128.35) (8.17,337.27) (8.33,351.12) (8.5,287.11) (8.67,254.45) (8.83,264.90) (9,208.06) (9.17,412.46) (9.33,429.41) (9.5,380.56) (9.67,396.19)

(9.83,380.56) (10,216.60) (10.17,504.43) (10.33,465.41) (10.5,380.56) (10.67,337.27) (10.83,287.11) (11,144.82) (11.17,668.61) (11.33,616.89) (11.5,311.18) (11.67,275.78) (11.83,254.45) (12,177.11)

Southwood & Reader (1976)[3] N (original data $\log_{10}N$)

1962-1973 12 years 6 points per year 72 points

(0.17,70605.28) (0.33,60127.04) (0.5,26929.77) (0.67,22933.22) (0.83,14163.25) (1,1754.63) (1.17,3917.63) (1.33,4600.35) (1.5,2621.83) (1.67,2232.74) (1.83,1901.38) (2,1083.64) (2.17,7448.91) (2.33,6874.00) (2.5,3917.63) (2.67,3615.26) (2.83,3336.23) (3,2232.74) (3.17,60127.04) (3.33,70605.28) (3.5,14163.25) (3.67,14163.25) (3.83,12061.33) (4,6874.00) (4.17,55486.33) (4.33,70605.28) (4.5,24851.28) (4.67,24851.28) (4.83,22933.22) (5,7448.91) (5.17,82909.58) (5.33,89843.86) (5.5,29182.08) (5.67,26929.77) (5.83,29182.08) (6,15347.81) (6.17,60127.04) (6.33,60127.04) (6.5,26929.77) (6.67,29182.08) (6.83,22933.22) (7,13070.11) (7.17,76510.48) (7.33,89843.86) (7.5,55486.33) (7.67,43604.86) (7.83,40239.37) (8,24851.28) (8.17,134247.75) (8.33,105500.81) (8.5,76510.48) (8.67,70605.28) (8.83,60127.04) (9,37133.63) (9.17,235555.36) (9.33,255256.44) (9.5,157642.89) (9.67,134247.75) (9.83,145475.78) (10,70605.28) (10.17,525932.73) (10.33,569920.13) (10.5,299739.65) (10.67,351974.82) (10.83,299739.65) (11,134247.75) (11.17,785866.54) (11.33,669239.24) (11.5,381412.83) (11.67,299739.65) (11.83,299739.65) (12,200597.54)

Southwood et al. (1989)[1]

N eggs per bush ($\times 10^5$)

1963-1978 16 years

0.05,0.19,0.83,0.73,1.02,0.73,1.02,1.46,3.06,6.55,8.98,7.18,8.2,9.08,12.57,7.43

N eggs per leaf ($\times 10^5$)

1963-1978 16 years

1.31,0.81,6.2,6.03,8.05,5.19,6.37,9.57,16.98,31.13,43.09,35.34,35.17,47.47,49.49,47.9
8

Southwood et al. (1989)[2]

N eggs per bush ($\times 10^5$)

1963-1978 16 years

0.01,0.051,0.049,0.05,0.01,0.05,0.01,0.1,0.15,0.19,0.44,0.15,0.151,0.34,0.87,1.06

N eggs per leaf ($\times 10^5$)

1963-1978 16 years

0.17,0.01,0.34,0.17,0.34,0.68,0.51,1.011,1.01,1.35,1.86,0.84,1.01,1.86,2.53,4.56

Stafford (1971) *N* ($\times 10^3$)

1928-1970 43 years

4.059,3.486,3.853,4.105,4.013,4.105,4.151,4.541,4.403,4.541,4.77,4.701,3.669,3.509,3.371,3.807,4.311,4.105,4.128,2.683,2.775,3.555,4.082,4.564,4.724,4.564,4.793,4.426,4.174,4.495,4.059,4.541,4.334,4.655,3.646,2.247,2.385,2.798,2.866,3.188,3.692,3.899,4.128

Stewart (1995) *N*

1979-1993 15 years

230,171,171,244,125,82,57,54,60,90,156,36,21,28,40

Tinkle et al. (1993) *N* per hectare

1969-1979 11 years

237.1,287.1,257.1,137.1,131.4,201.4,162.9,167.1,250,151.4,205.7

corrected for relative catchability

1969-1979 11 years

263.4,319,285.7,152.3,146,223.8,181,185.7,277.8,168.2,228.5

Turchin (1993)[1] *N*

1948-1970 23 years

1.04,9.82,13.28,4.92,8.99,5.29,16.13,9.32,8.68,11.12,4.92,18.26,7.94,9.32,10.93,13.04,2.34,11.94,8.23,12.15,10.73,10.73

Turchin (1993)[2] t

1970-1985 16 years

1.21,1.05,1.18,3.28,8.67,1.21,1.53,18.98,17.26,1.1,1.18,19.91,56.57,42.55,4.79,2.19

Turchin (1993)[3] *N*

1955-1972 18 years

86.79,119.38,24.24,1.19,24.24,701.7,10,17.63,20.31,58.78,609,19.6,49.24,25.12,5.1,1.
07,609,128.14

Turchin and Taylor (1992)[1] *N*

1881-1940 59 years

42.51,9.21,2,2.07,3.09,22.07,406.16,841.2,15.34,2.23,7.41,3.21,5.34,84.89,56.88,2.31,
3.32,10.66,88.04,364.14,146.56,38.11,1.2,1.86,9.91,8.57,3.45,2.4,1.24,1.16,1.12,1.16,
3.32,4.45,35.43,52.88,391.64,189.09,20.52,2.48,1.29,3.45,2.48,31.77,42.51,146.56,32
35.05,1210.61,22.89,27.46,15.91,12.33,76.11,56.88,727.21,131.39,20.52,36.75,47.41

Turchin and Taylor (1992)[2] *N*

1945-1972 28 years

1.34,1.45,7.87,66.68,83.18,1318.26,1180.32,981.75,630.96,1318.26,291.07,139.32,45
2.9,41.3,7.59,5.65,18.37,5.86,4.37,1.29,1.45,1.25,1.08,8.79,55.46,35.65,80.17,280.54

Turchin and Taylor (1992)[3] *N*

1958-1987 30 years

0.062,0.047,0.217,0.434,1.256,1.085,0.419,0.93,1.504,1.504,2.93,0.775,0.341,0.651,2.
093,1.426,1.659,1.752,3.442,1.225,0.0001,0.016,0.031,0.031,0.047,0.155,1.039,3.643,
1.612,0.062

Turchin and Taylor (1992)[4] *N*

1881-1940 60 years

599.48,302.11,32.21,46.42,92.11,2470.91,10184.42,19306.98,3727.59,84.06,66.9,22.3
5,70.02,16.23,8.18,12.92,35.29,30.77,20.4,40.47,5.68,1.101,1.1,10.761,10.76,6.81,5.1

8,10.28,16.23,2.86,1.15,1.151,2.86,2.28,11.26,6.81,20.4,10.28,1.26,1.1,2.17,2.99,1.2,2.28,2.17,61.05,138.95,50.86,26.83,17.78,20.4,182.77,25.63,145.44,219.42,2586.42,3901.84,115.74,18.61,13.52

Turchin and Taylor (1992)[5] *N*

1881-1940 60 years

9.21,6.17,1.08,1.86,5.74,182.33,1167.33,3235.05,651.97,21.28,23.74,11.05,36.75,12.33,7.41,15.91,52.88,54.84,40.99,105.61,13.75,3.21,3.58,42.51,44.08,32.94,24.62,45.72,98.2,17.74,6.64,6.64,17.74,12.79,73.39,36.75,117.8,61.17,5.53,4.96,9.21,11.89,4.14,6.89,5.74,169.53,326.46,70.76,34.17,20.52,17.11,131.39,13.26,70.76,88.04,701.21,938.28,13.75,2.23,1.34

Turchin and Taylor (1992)[6] *N*

1969-1987 19 years

1.06,11.89,1.96,24.62,1.41,12.11,4.87,17.42,5.95,47.41,4.87,26,3.71,17.42,3.15,19.08,13.02,15.62,3.92

Turchin and Taylor (1992)[7] *N*

1937-1958 22 years

1.06,1.04,6.74,18.15,2.79,1.58,1,0.98,2.6,8.88,6.26,10.47,11.48,2.5,1,0.98,2.69,11.27,1.2,5.82,3.89,3.18

Turchin and Taylor (1992)[8] *N*

1954-1979 26 years

7.74,111.59,7742.64,5179.47,173.02,1.61,1.67,4.31,13.89,17.3,288.61,1441.22,322.06,1.73,1.08,1.67,3.34,7.2,25.86,28.86,62.18,49.94,23.18,41.6,12.45,21.54

Turchin and Taylor (1992)[9] *N*

1900-1941 42 years

113.59,141.32,3.58,9.56,226.85,272.13,122.17,210.92,243.98,7.14,3.71,282.22,20.52,1,2.77,13.75,7.14,40.99,91.3,20.52,22.89,157.63,14.79,11.05,10.66,29.54,3.58,16.5,505.31,1085.36,7.41,11.05,22.07,52.88,20.52,29.54,3.99,7.14,98.2,7.97,3.45,1.12

Turchin and Taylor (1992)[10]

1881-1940 59 years

54.32,32.06,77.91,1.09,1.84,36.84,18.93,151.61,92.01,2.36,11.81,48.61,200.08,64.15,
3.39,5.14,11.81,3.89,2.24,2.79,5.58,4.6,5.58,2.17,7.37,6.6,5.14,4.23,5,16.48,27.15,486
.12,264.05,2.11,2.95,2.06,4.12,5.28,44.73,14.34,8.7,6.42,2.17,4.6,3.12,4.73,5,18.93,12
.84,34.85,54.32,5.28,5.74,4.12,43.51,286.97,151.61,358.28,311.87

Turchin and Taylor (1992)[11] *N*

1969-1987 19 years

1.98,1.39,5.9,88.04,406.16,3.06,65.2,7.54,2.75,9.64,4.14,52.4,2.27,4.14,1.03,7.14,7.97
,50.99,147.9

Turchin and Taylor (1992)[12] *N*

1947-1975 29 years

40.03,25.68,13.2,40.03,48.61,94.6,77.91,45.99,6.78,2.06,1.03,12.84,6.42,10,6.24,6.97,
3.21,5.14,3.12,3.12,4.12,3.12,13.95,7.37,13.95,15.16,21.74,89.5,135.68

Turchin and Taylor (1992)[13] *N*

1921-1946 26 years

40.99,6.52,25.53,4.37,26.97,5.85,1.06,83.36,6.29,24.62,1.04,15.34,12.33,8.72,24.18,1
5.34,9.38,1,17.74,15.06,8.57,54.84,8.72,36.08,2.03,40.99

Turchin and Taylor (1992)[14] *N*

1932-1954 22 years

4.46,2.03,1.11,2.52,4.46,29.15,45.03,161.68,236.6,263.79,157.34,157.34,20.47,2.03,1.
11,1.11,2.08,2.03,119.88,286.22,396.67,256.71

Turchin and Taylor (1992)[15]

not given 39 years

9999,4.75,5.23,14.33,9.76,2.67,2.8,31.62,4.02,1.5,5.36,14.68,9.76,2.87,11.55,18.66,11.83,5.11,1.96,11.83,30.14,4.53,8.87,14.68,4.02,2.49,5.11,4.75,1.3,18.66,5.49,1.65,4.64,6.49,10,7.15,7.32,1.07,2

Townsend et al. (1990) N index (0+ abundance)

1978-1986 9 years

38.31,401.95,63.4,287.3,19.11,97.63,31.62,139.91,60.43

Varley (1949)[1] N/m^2 (pupae)

1881-1910 30 years

0.4242,0.0977,0.0149,0.0099,0.0178,0.25,3.9531,8.9967,0.1657,0.0141,0.0819,0.0239,0.0455,0.9103,0.5059,0.0074,0.0212,0.0869,0.9654,3.7276,1.737,0.3772,0.0058,0.0149,0.0869,0.0728,0.0212,0.0125,0.0031,0.0011

and continues…

1913-1940 28 years

0.0111,0.0339,0.2812,0.569,4.4459,1.6379,0.25,0.0062,0.002,0.0302,0.0093,0.2223,0.3772,1.2949,6.707,43.9397,14.3934,0.2357,0.2982,0.1235,0.0611,0.7632,0.4,7.9995,1.9535,0.1474,0.2812,0.4771

Varley (1949)[2] N/m^2 (pupae)

1881-1922 42 years

0.6347,0.2792,0.0211,0.0283,0.0916,2.0516,10,17.9795,3.0935,0.0644,0.0573,0.0188,0.054,0.0132,0.0065,0.0118,0.0338,0.0267,0.0167,0.038,0.0043,0.0008,0.0009,0.0093,0.0093,0.0062,0.0041,0.0078,0.0158,0.0026,0.0009,0.0009,0.0026,0.0017,0.0111,0.0052,0.0177,0.0083,0.0008,0.0009,0.0018,0.0026 and continues…

1924-1940 17 years

0.0018,0.0017,0.048,0.1381,0.0211,0.0188,0.0149,0.0644,0.1464,0.0078,0.1158,0.1963,2.0516,4.148,0.0683,0.0049,0.0019

Varley (1949)[3] N/m^2 (pupae)

1881-1911 31 years

0.0961,0.0289,0.0054,0.0227,0.0961,0.2365,0.4313,0.3825,0.0631,0.0272,0.019,0.0104,0.0227,0.0149,0.0467,0.0289,0.0527,0.044,0.0852,0.0326,0.0256,0.0054,0.0077,0.0061,0.0098,0.0082,0.0068,0.0048,0.0068,0.0042,0.0018

and continues…

1913-1930 18 years

0.019,0.0241,0.1083,0.0326,0.0111,0.0009,0.001,0.0009,0.0022,0.0051,0.0125,0.0346,0.0241,0.056,0.0852,0.0241,0.0111,0.0214

Varley (1949)[4] N/m^2 (pupae)

1881-1940 60 years

0.0609,0.0316,0.082,0.0011,0.0023,0.0401,0.0174,0.1401,0.0924,0.0023,0.0108,0.0452,0.2126,0.0609,0.0037,0.0063,0.0146,0.0047,0.0026,0.0033,0.0067,0.0056,0.0067,0.0022,0.0085,0.008,0.0063,0.0044,0.0056,0.0185,0.0356,0.621,0.2542,0.0026,0.0044,0.0023,0.0053,0.0063,0.0609,0.0185,0.0129,0.008,0.0024,0.006,0.0035,0.006,0.0053,0.0281,0.0137,0.0401,0.0773,0.0063,0.0071,0.0044,0.054,0.1579,0.3857,0.1579,0.4344,0.3634

Varley & Gradwell (1968) N/m^2

eggs

1950-1966   17 years

3859.57,394.6,701.7,377.51,264.9,978.1,614.41,819.33,1247.83,837.68,337.95,61.44,159.19,295.91,574.93,915.25,1363.38

larvae

1950-1966   17 years

98.9,101.11,51.07,18.13,147.05,75.92,92.58,260.78,187.38,57.01,20.69,7.19,12.47,39.2,131.71,266.59,52.2

Varley and Gradwell (1970) N density

1949-1965   17 years

156.88,736.48,3669.24,37321.21,688079.15,4348869.74,1323644.01,235881.4,24611.83,934.29,736.48,4132.72,18280.69,265677.15,3230167.92,2260702.94,39608.28

Varley et al. (1973)[1] N/m^2 (pupae)

not shown   13 years

7.53,41.19,31.03,26.68,92.73,6.01,2.09,1.40,5.90,14.31,21.27,11.20,2.82

Varley et al. (1973)[2] N/m^2 (pupae)

not shown   13 years

5.36,3.35,0.66,2.72,2.38,2.13,1.35,0.12,0.84,0.94,1.86,3.05,4.28

Varley et al. (1973)[3] N/m^2

1950-1966   17 years

8.98,7.24,3.64,0.65,2.17,3.48,3.34,13.23,13.81,6.64,2.58,2.08,0.60,0.77,3.34,7.89,2.93

Varley et al. (1973)[4] N/m^2

1950-1968 19 years

104.36,118.60,55.05,18.96,153.17,77.43,104.36,266.64,197.83,59.95,21.54,7.42,12.92,35.94,123.76,244.84,46.42,9.18,9.18

Varley et al. (1973)[5] N/m^2

1951-1965 15 years

1.03,0.50,0.50,0.30,0.66,0.64,1.32,0.54,0.64,0.66,0.11,0.29,0.56,0.60,1.27

Varley et al. (1973)[6] N/m^2

1957-1965 9 years

76.69,100.86,42.85,15.34,34.89,27.46,20.18,38.67,58.32

Vickery and Nudds (1984)[1] N (breeding pairs)

1952-1977 26 years

17,34,42,21,22,22,27,7,11,12,7,6,18,10,7,5,1,3,9,4,6,9,9,10,55,0.001

Vickery and Nudds (1984)[2] N (breeding pairs)

1968-1976 9 years

14,7,17,15,19,18,11,15,15

Vickery and Nudds (1984)[3] N (breeding pairs)

1952-1977 26 years

57,61,53,32,46,51,43,26,23,19,20,16,11,5,4,8,3,9,8,11,9,11,7,6,10,13

Vickery and Nudds (1984)[4] N (breeding pairs)

1968-1976 9 years

43,19,41,34,44,54,30,35,28

Vickery and Nudds (1984)[5] (breeding pairs)
1952-1977 26 years

16,18,20,12,25,19,15,5,7,8,4,10,21,9,6,5,7,3,14,6,6,11,23,15,31,7

Vickery and Nudds (1984)[6] *N* (breeding pairs)
1968-1976 9 years

6,5,6,17,14,27,10,13,18

Vickery and Nudds (1984)[7] *N* (breeding pairs)
1952-1977 26 years

47,32,44,19,22,20,17,14,4,7,7,3,8,2,3,10,9,15,25,17,19,28,11,19,57,6

Vickery and Nudds (1984)[8] *N* (breeding pairs)
1968-1976 9 years

24,14,9,21,25,27,16,26,25

Vickery and Nudds (1984)[9] *N* (breeding pairs)
1952-1977 26 years

191,166,120,126,115,116,125,53,26,24,13,48,142,44,41,27,17,34,92,57,70,81,150,151,241,113

Vickery and Nudds (1984)[10] *N* (breeding pairs)
1968-1976 9 years

21,23,30,49,63,72,73,73,64

Vickery and Nudds (1984)[11] *N* (breeding pairs)
1952-1977 26 years

140,172,242,137,224,158,186,97,79,55,42,34,58,39,32,37,20,23,41,45,30,41,30,42,87,57

Vickery and Nudds (1984)[12]   (breeding pairs)

1968-1976   9 years

99,30,66,55,86,79,44,60,79

Vickery and Nudds (1984)[13]   *N* (breeding pairs)

1952-1977   26 years

17,9,19,4,10,12,9,4,7,2,7,9,19,5,3,3,1,3,5,5,3,10,3,2,13,16

Vickery and Nudds (1984)[14]   *N* (breeding pairs)

1968-1976   9 years

29,23,17,29,78,44,37,25,38

Vickery and Nudds (1984)[15]   *N* (breeding pairs)

1952-1977   26 years

26,21,6,31,31,19,13,1,5,6,1,2,8,1,2,5,0.001,1,7,5,2,8,14,14,21,4

Vickery and Nudds (1984)[16]   *N* (breeding pairs)

1968-1976   9 years

50,67,82,80,91,105,105,91,103

Vickery and Nudds (1984)[17]   *N* (breeding pairs)

1968-1976   9 years

3,12,13,24,26,26,25,22,13

Vickery and Nudds (1984)[18]   *N* (breeding pairs)

1952-1977   26 years

13,15,27,4,26,10,9,1,5,0.001,2,5,10,6,8,9,1,0.001,12,10,13,14,12,17,12,18

Vickery and Nudds (1984)[19]   *N* (breeding pairs)

1968-1976   9 years

7,7,10,6,10,10,7,19,13

Vøllestad & Jonsson (1988)

ascending

1975-1987 13 years

42945,48615,28518,12180,2457,34776,15477,45750,14500,6640,3412,5145,3434

descending commercial

1978-1987 10 years

695,2067,2547,1594,4725,2209,3319,1278,1251,1741

descending trapped

1975-1987 13 years

5201,3824,5435,4986,2914,3382,2354,3818,3712,3377,4427,3733,1833

Walters et al. (1990)[1] $N \times 10^3$

1974-1983 10 years

15.99,38.95,29.73,43.04,23.15,37.80,17.68,4.67,16.81,38.95

Walters et al. (1990)[2] $N \times 10^3$

1974-1983 10 years

19.93,24.10,17.15,31.89,18.96,142.91,12.71,9.70,31.89,46.16

Walters et al. (1990)[3] $N \times 10^3$

1974-1983 10 years

18.58,21.59,19.93,22.70,12.58,9.32,8.87,14.91,20.54,19.15

Walters et al. (1990)[4] $N \times 10^3$

1974-1983 10 years

22.70,26.37,17.68,30.33,36.31,13.90,28.28,14.62,13.90,11.97

Walters et al. (1990)[5] $N \times 10^3$

1974-1983 10 years

19.15,17.33,9.32,7.48,23.86,19.53,11.61,28.39,43.91,26.37

Walters et al. (1990)[6] $N \times 10^3$

1974-1983 10 years

7.19,9.04,7.40,4.63,8.18,3.26,16.32,2.25,14.76,9.90

Walters et al. (1990)[7] $N \times 10^3$

1974-1983 10 years

13.23,48.53,34.54,15.68,19.53,0.64,6.97,20.95,14.62,25.59

Walters et al. (1990)[8] $N \times 10^3$

1974-1983 10 years

11.61,15.68,16.48,19.93,15.68,14.18,11.38,19.15,26.90,15.21

Woiwod and Hanski (1992) N

1966-1990 16 years

150.31,67.9,7.07,1,1.79,1.03,2.74,22.59,97.98,76.73,6.26,3.84,3.83,3.85,27.14,204.05

Wood and Odum (1964)[1] N

1954-1962 9 years

4,1,2,1,3,1,3,0,3

Wood and Odum (1964)[2] N

1954-1962 9 years

14,5,12,2,2,3,8,7,6

Wood and Odum (1964)[3] N

1954-1962 9 years

2,5,0,2,1,2,3,0,2

Wood and Odum (1964)[4]

1954-1962 9 years

20,13,15,7,9,10,16,12,9

Wood and Odum (1964)[5] N

1954-1962 9 years

73,24,35,32,20,21,22,19,35

Wood and Odum (1964)[6] N

1954-1962 9 years

10,0,7,3,1,1,4,7,3

Wool (1990)[1] $\bar{N}$ per tree

1979-1988 10 years

64.29,22.62,50.6,35.12,126.19,5.36,23.21,25,41.07,21.43

Wool (1990)[2] $\bar{N}$ per tree

1979-1988 10 years

46.8,25.8,21.6,33,21.6,20.4,73.2,12.6,85.8,17.4

Wrigley and Hatch (1976) N

1919-1974 56 years

1457,88,2673,3202,1083,8400,865,4572,659,930,792,2512,1623,1181,3340,884,238,2
33,578,396,251,584,1139,484,372,315,303,1472,91,55,99,287,431,1324,669,324,632,
115,732,1126,190,517,2843,109,422,1766,148,378,739,137,32,24,38,160,65,630

Wyllie & Newton (1991)[1] N (nests)

1971-1980 10 years

110.44,106.14,94.66,99.44,90.36,77.45,70.28,64.54,62.15,62.63

Wyllie & Newton (1991)[2] (nests)

1972-1989 18 years

32.86,36.19,39.52,34.76,34.76,29.05,36.67,32.38,38.1,41.43,32.86,36.19,35.24,32.86, 33.33,36.19,35.71,30.48

Wyllie & Newton (1991)[3] *N* (nests)

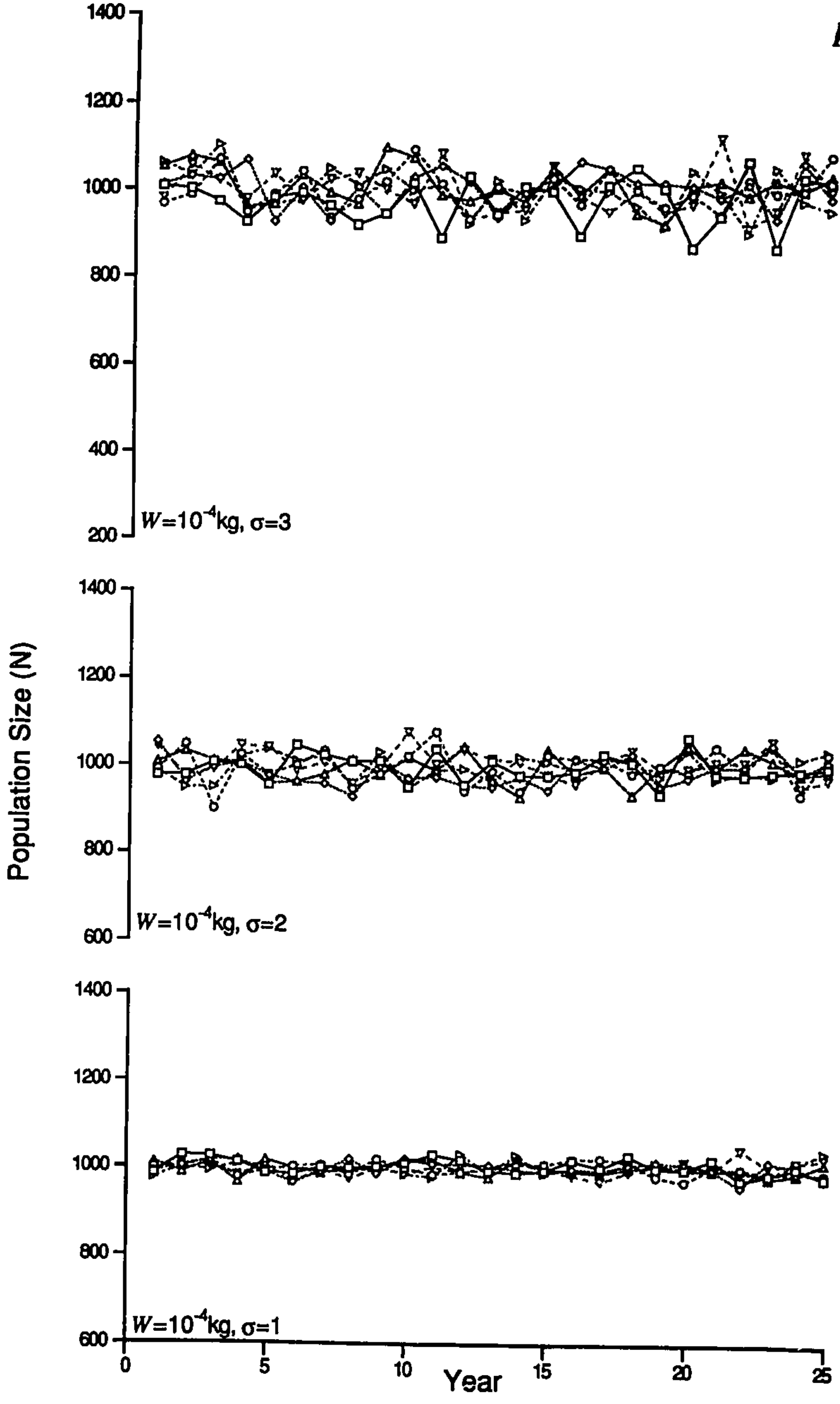
1979-1989 11 years

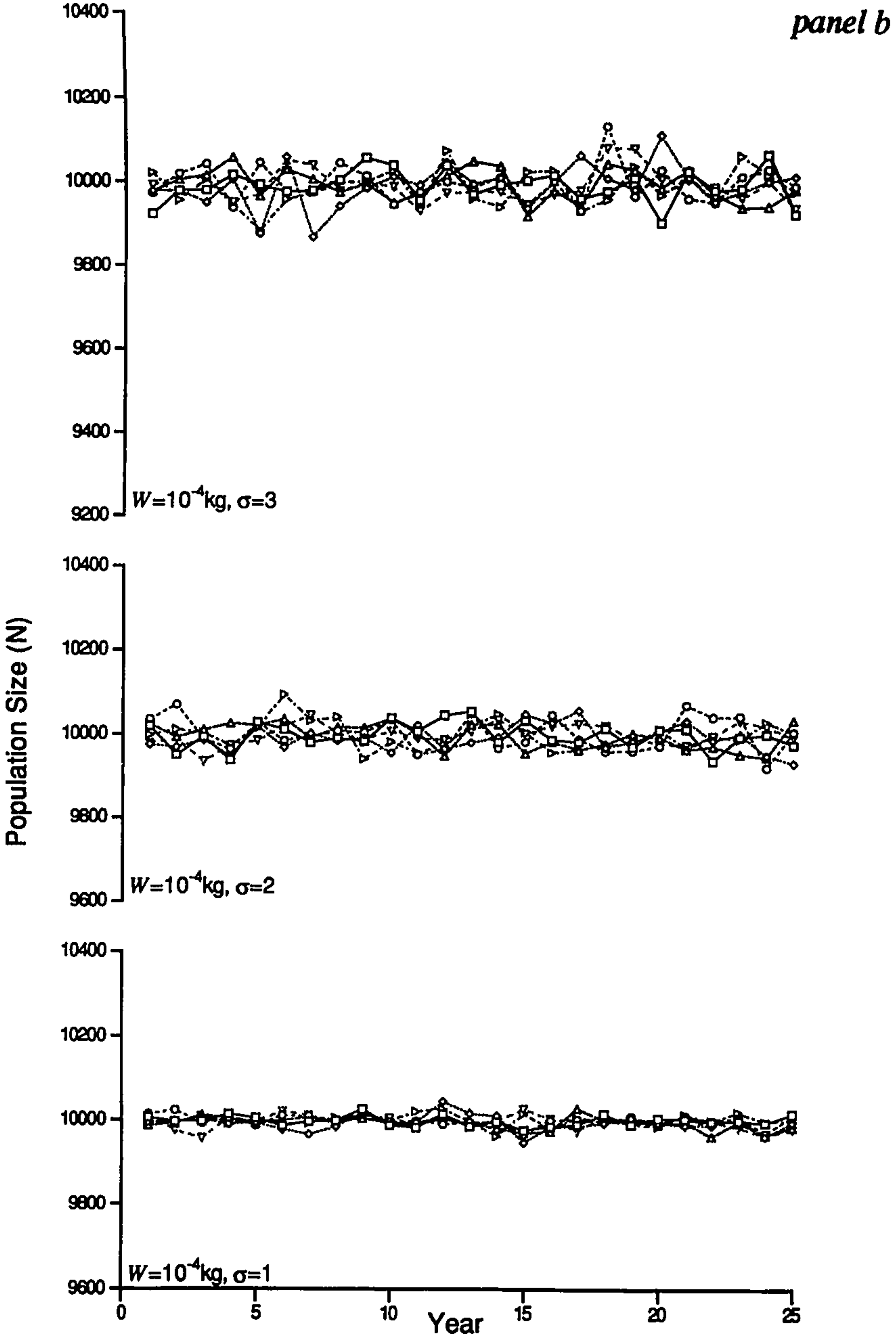
2.86,15.24,24.29,41.9,54.76,50.48,59.05,65.71,66.67,76.67,87.62

APPENDIX E: Extra Figures for Chapter 3

This appendix contains the figures of the population time slices and the distributions of r_S^2 and r_P^2 for each body size class and every combination of ρ, K and σ of the model (3.4) as discussed in the methods of chapter 3.

FIGURE E.1 Population time-slices for the simulated 10^{-4} kg body size populations. This figure consists of three panels *a, b* and *c* on the next three pages, respectively. Every panel presents 3 graphs, one above the other. Each of the 9 graphs of all three panels show the 6 randomly selected time-slices for each combination of the carrying capacity K and the standard deviation σ of the random variable X in model (3.4). Panels *a, b* and *c* show the combinations with $K = 1000$, 10,000 and 100,000 respectively. The top graph on each panel have the time-slices with $\sigma = 3$, while the middle and bottom graphs show the time-slices with $\sigma = 2$ and $\sigma = 1$ respectively.


1400
1200
1000
800
600
400
200
W=10^-4kg, σ=3
1400
1200
1000
800
600
W=10^-4kg, σ=2
Population Size (N)
1400
1200
1000
800
600
W=10^-4kg, σ=1
0
5
10
15
20
25
Year


panel b
Population Size (N)
10400
10200
10000
9800
9600
9400
9200
W=10⁻⁴kg, σ=3
10400
10200
10000
9800
9600
W=10⁻⁴kg, σ=2
10400
10200
10000
9800
9600
W=10⁻⁴kg, σ=1
0
5
10
15
20
25
Year

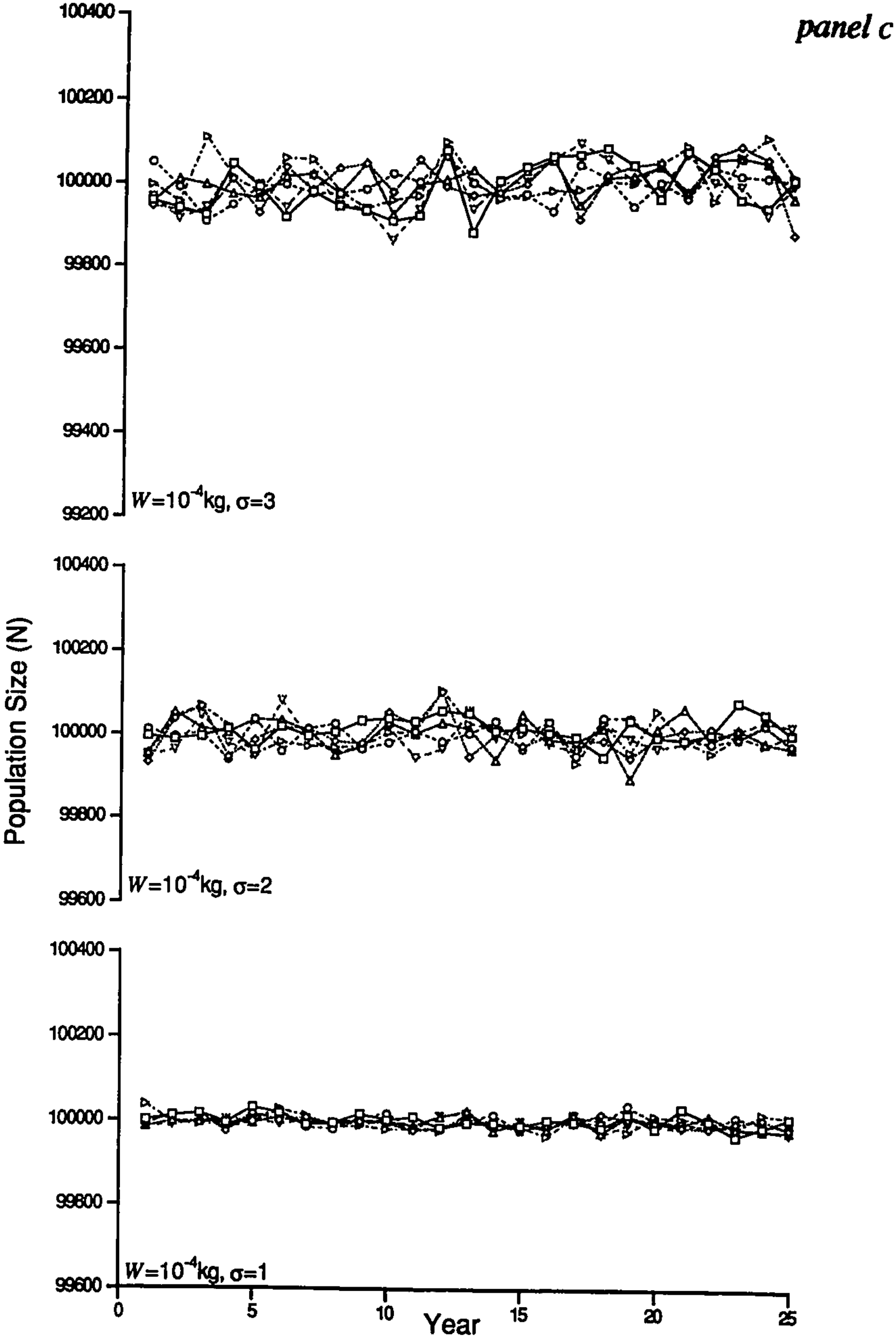
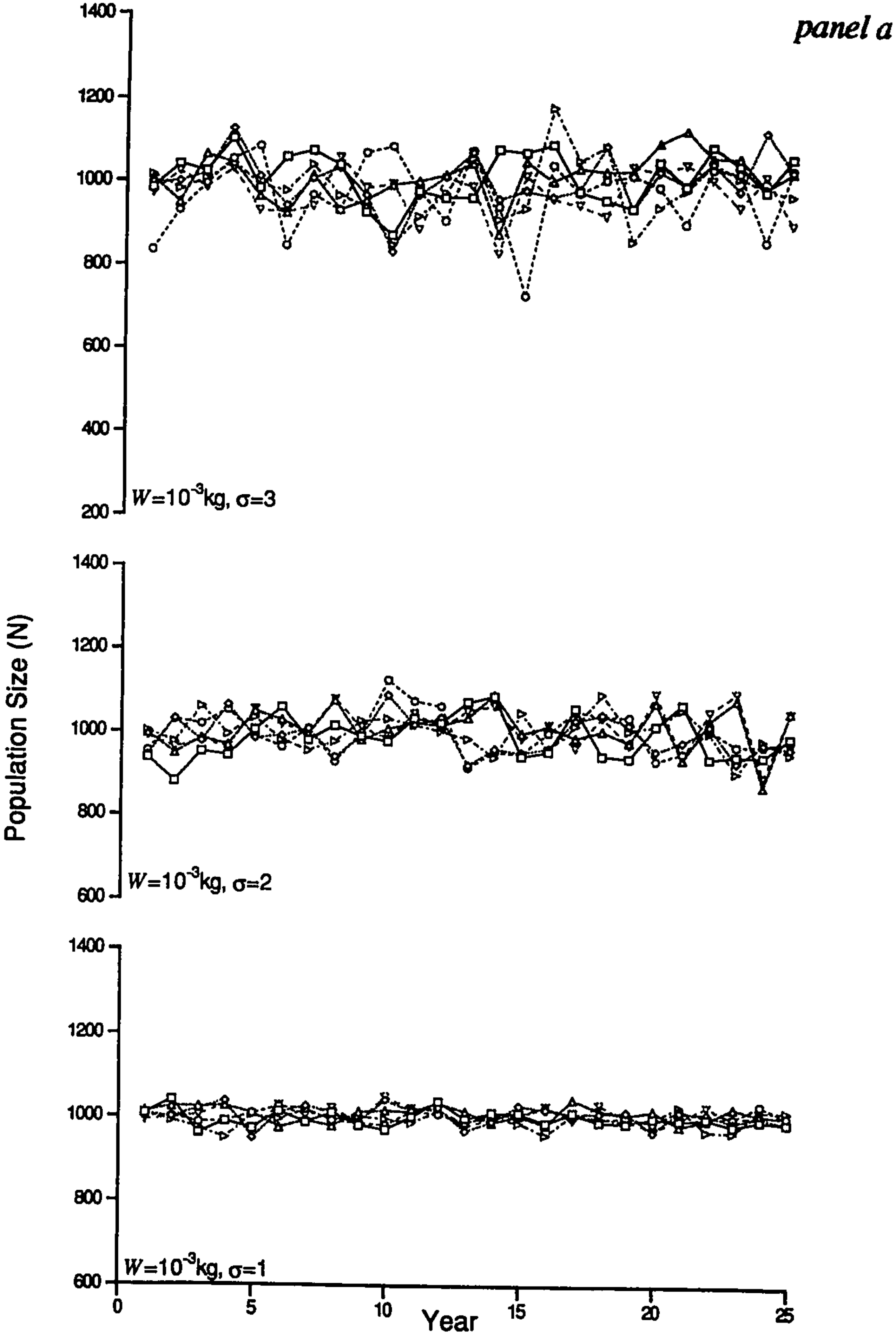
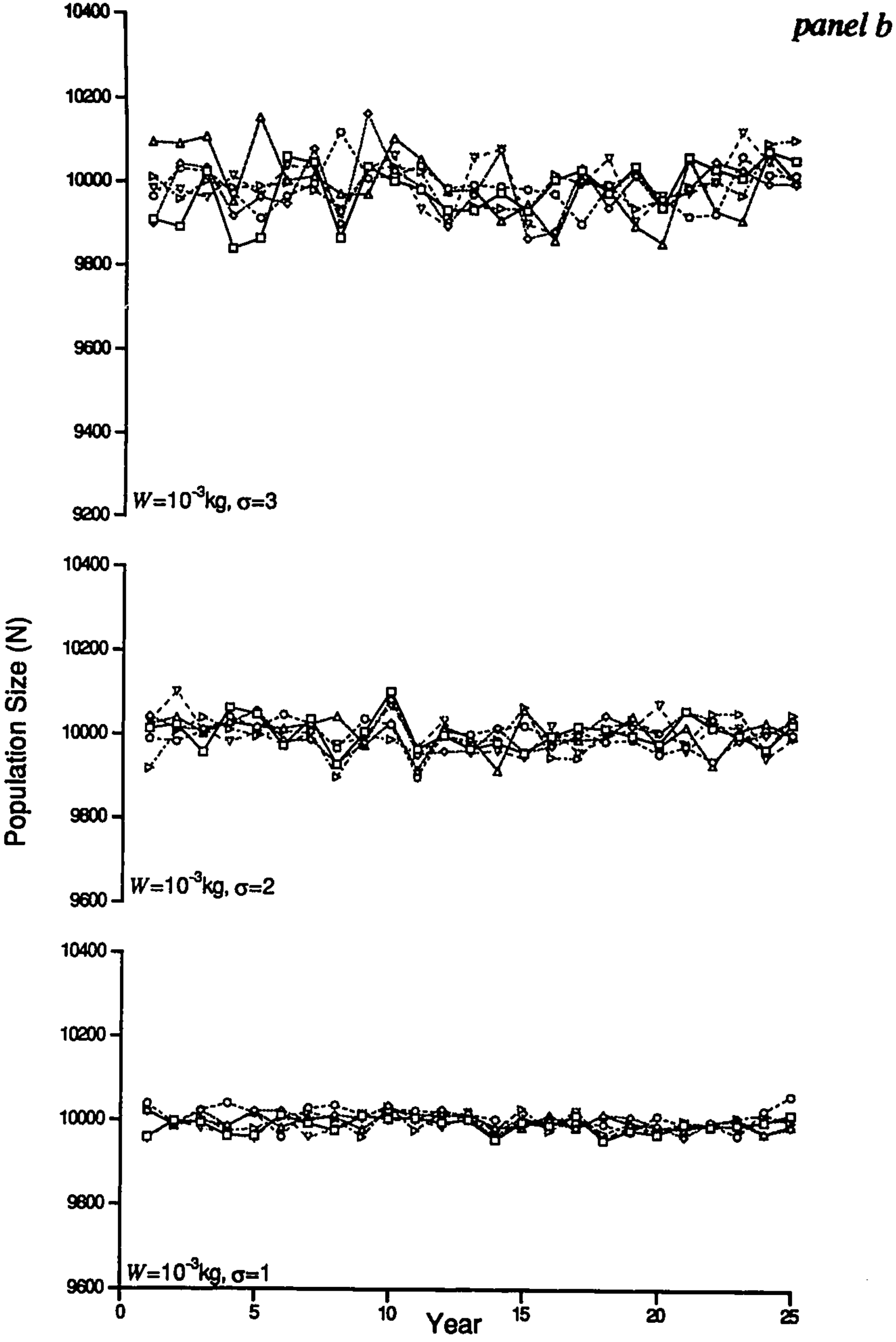

panel c
100400
100200
100000
99800
99600
99400
99200
W=10⁻⁴kg, σ=3
100400
100200
100000
99800
99600
W=10⁻⁴kg, σ=2
Population Size (N)
100400
100200
100000
99800
99600
W=10⁻⁴kg, σ=1
0
5
10
15
20
25
Year

FIGURE E.2 Population time-slices for the simulated 10^{-3} kg body size populations. This figure consists of three panels *a*, *b* and *c* on the next three pages, respectively. Every panel presents 3 graphs, one above the other. Each of the 9 graphs of all three panels show the 6 randomly selected time-slices for each combination of the carrying capacity K and the standard deviation σ of the random variable X in model (3.4). Panels *a*, *b* and *c* show the combinations with $K = 1000$, 10,000 and 100,000 respectively. The top graph on each panel have the time-slices with $\sigma = 3$, while the middle and bottom graphs show the time-slices with $\sigma = 2$ and $\sigma = 1$ respectively.


panel a
1400
1200
1000
800
600
400
200
W=10^-3kg, σ=3
1400
1200
1000
800
600
W=10^-3kg, σ=2
Population Size (N)
1400
1200
1000
800
600
W=10^-3kg, σ=1
0
5
10
15
20
25
Year


panel b
Population Size (N)
10400
10200
10000
9800
9600
9400
9200
W=10^{-3}kg, σ=3
10400
10200
10000
9800
9600
W=10^{-3}kg, σ=2
10400
10200
10000
9800
9600
W=10^{-3}kg, σ=1
0
5
10
15
20
25
Year

panel c

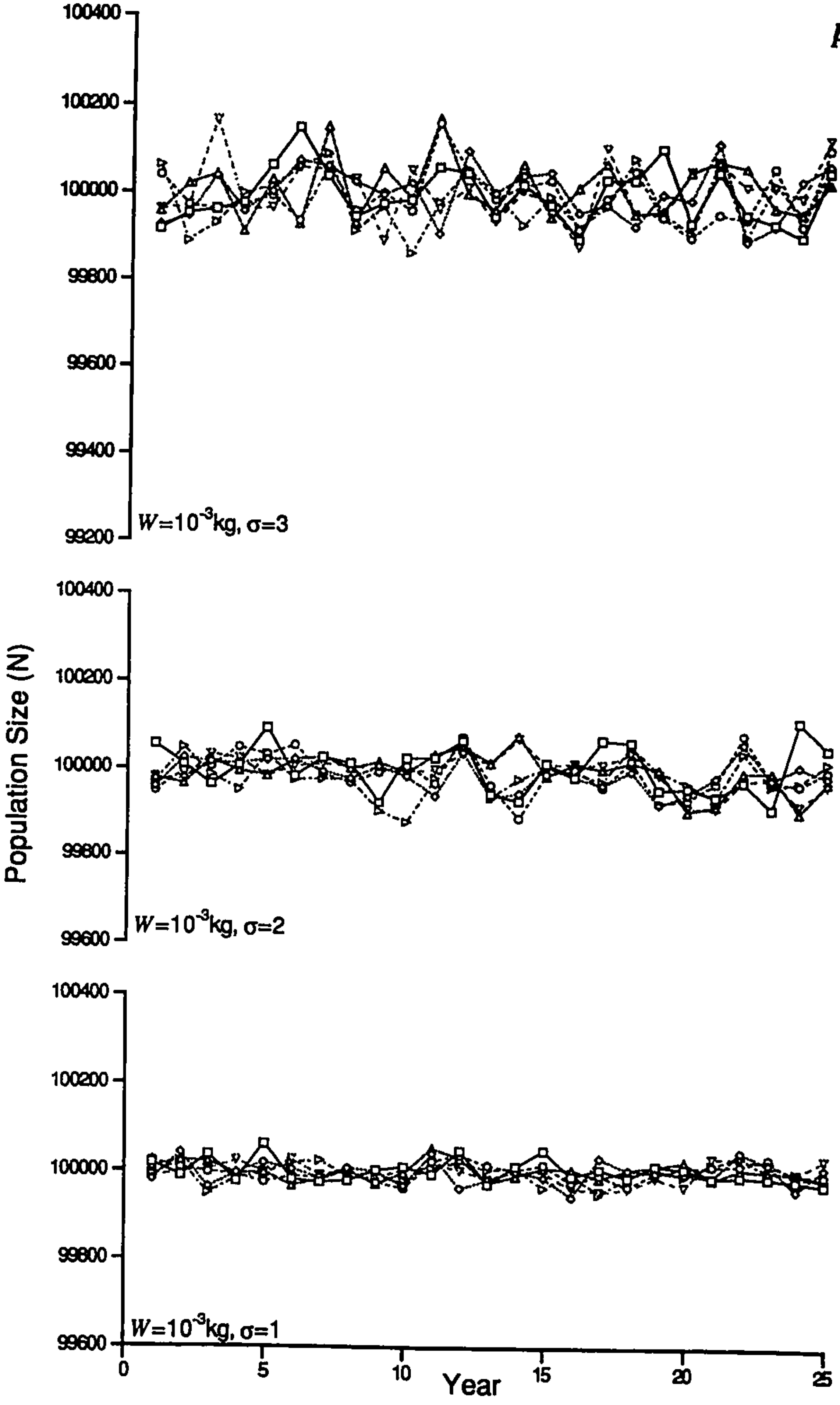
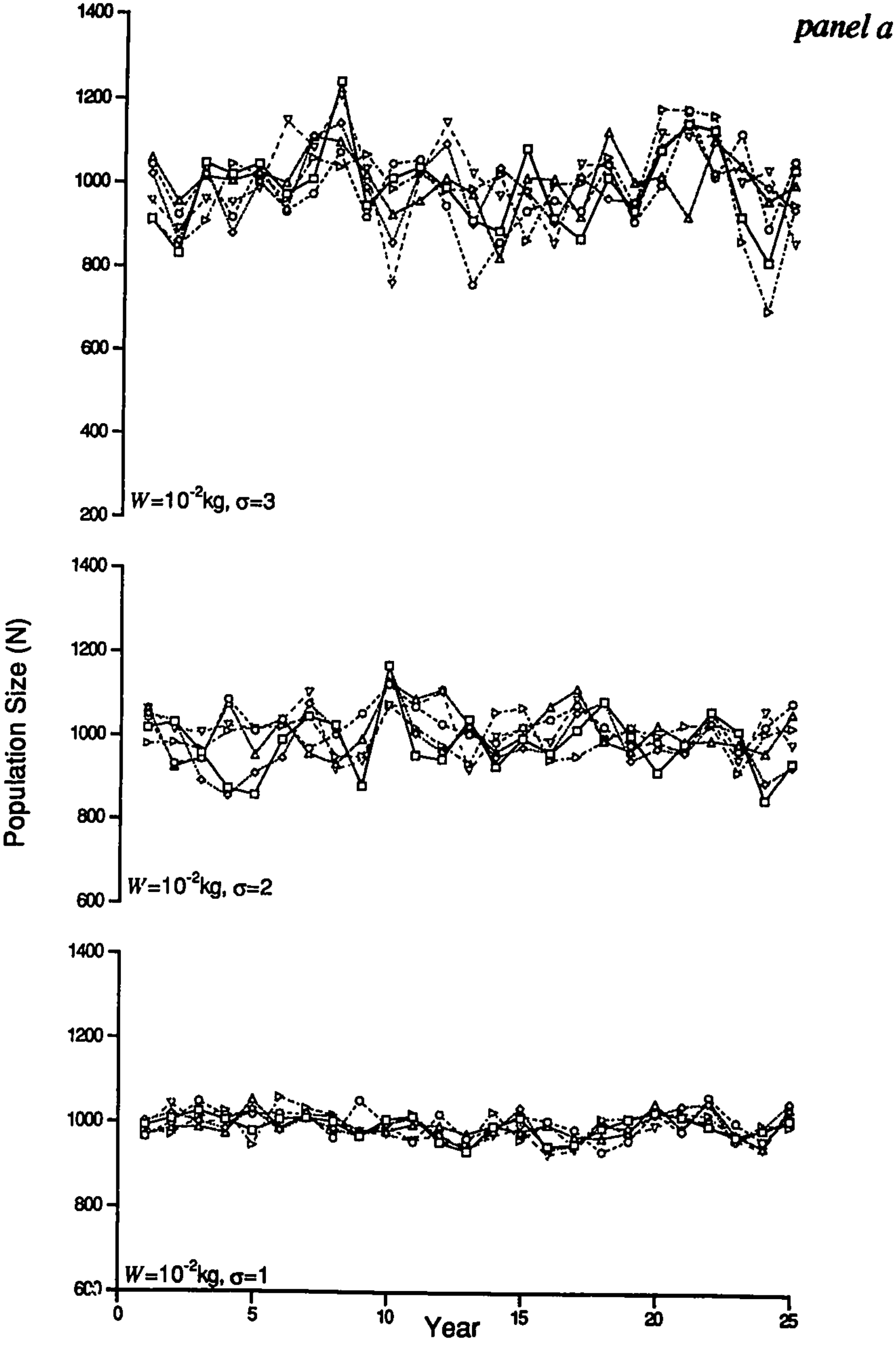
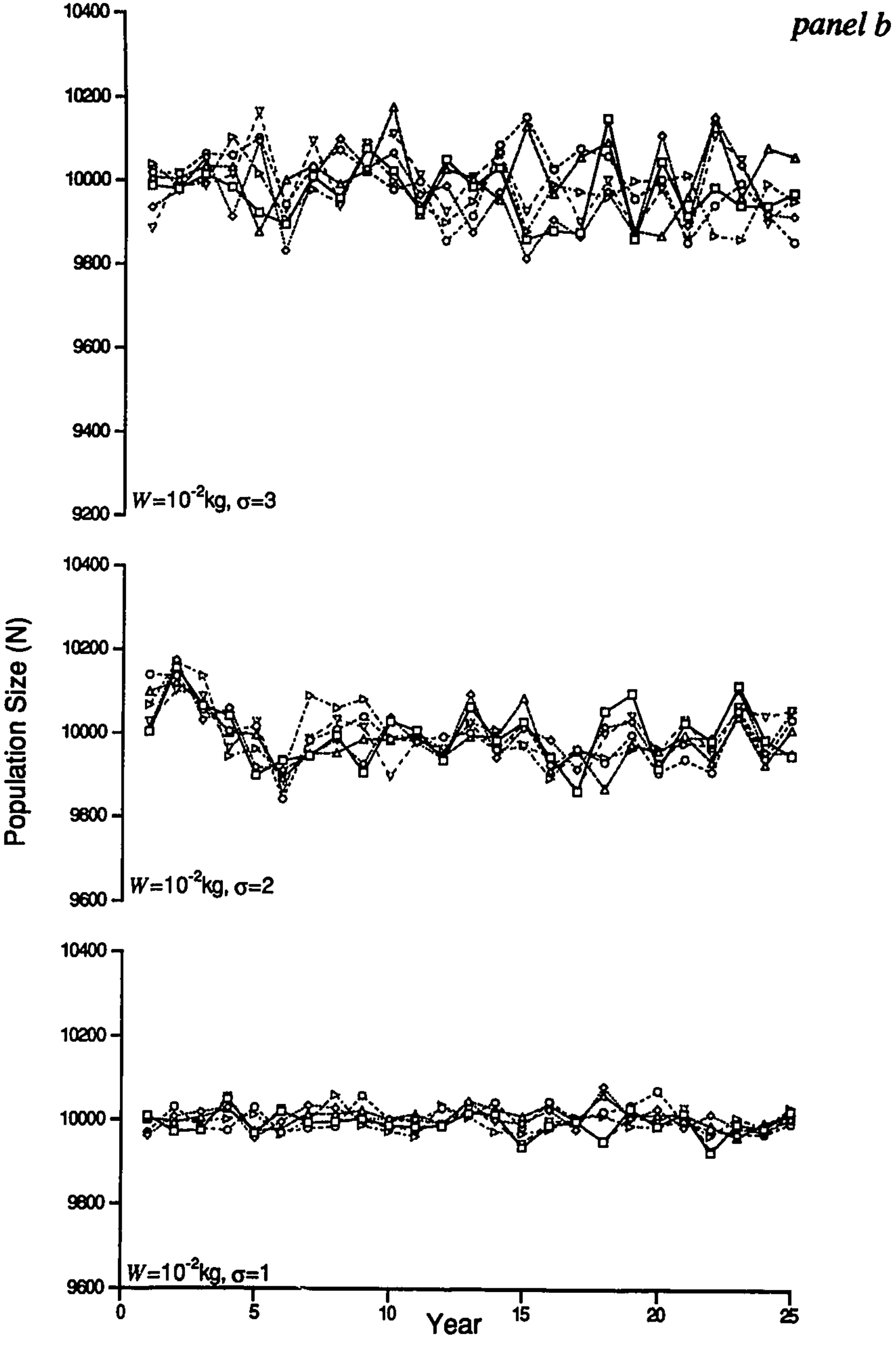

100400
100200
100000
99800
99600
99400
99200
W=10^{-3}kg, σ=3
Population Size (N)
100400
100200
100000
99800
99600
W=10^{-3}kg, σ=2
100400
100200
100000
99800
99600
W=10^{-3}kg, σ=1
0
5
10
15
20
25
Year

FIGURE E.3 Population time-slices for the simulated 10^{-2} kg body size populations. This figure consists of three panels *a*, *b* and *c* on the next three pages, respectively. Every panel presents 3 graphs, one above the other. Each of the 9 graphs of all three panels show the 6 randomly selected time-slices for each combination of the carrying capacity K and the standard deviation σ of the random variable X in model (3.4). Panels *a*, *b* and *c* show the combinations with $K = 1000$, 10,000 and 100,000 respectively. The top graph on each panel have the time-slices with $\sigma = 3$, while the middle and bottom graphs show the time-slices with $\sigma = 2$ and $\sigma = 1$ respectively.


panel a
Population Size (N)
1400
1200
1000
800
600
400
200
W=10^{-2}kg, σ=3
1400
1200
1000
800
600
W=10^{-2}kg, σ=2
1400
1200
1000
800
600
W=10^{-2}kg, σ=1
0
5
10
15
20
25
Year


panel b
10400
10200
10000
9800
9600
9400
9200
W=10^{-2}kg, σ=3
10400
10200
10000
9800
9600
W=10^{-2}kg, σ=2
Population Size (N)
10400
10200
10000
9800
9600
W=10^{-2}kg, σ=1
0
5
10
15
20
25
Year

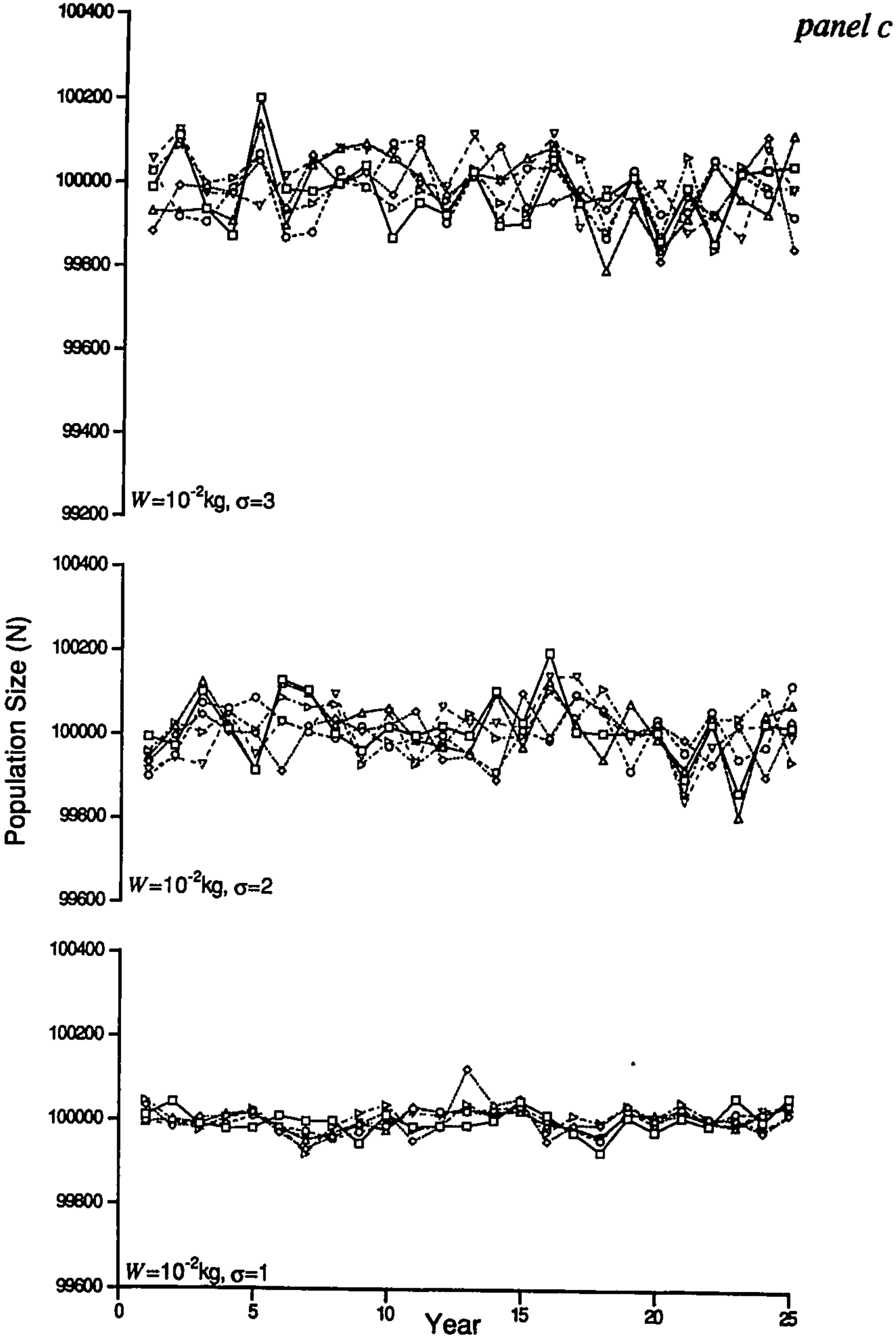
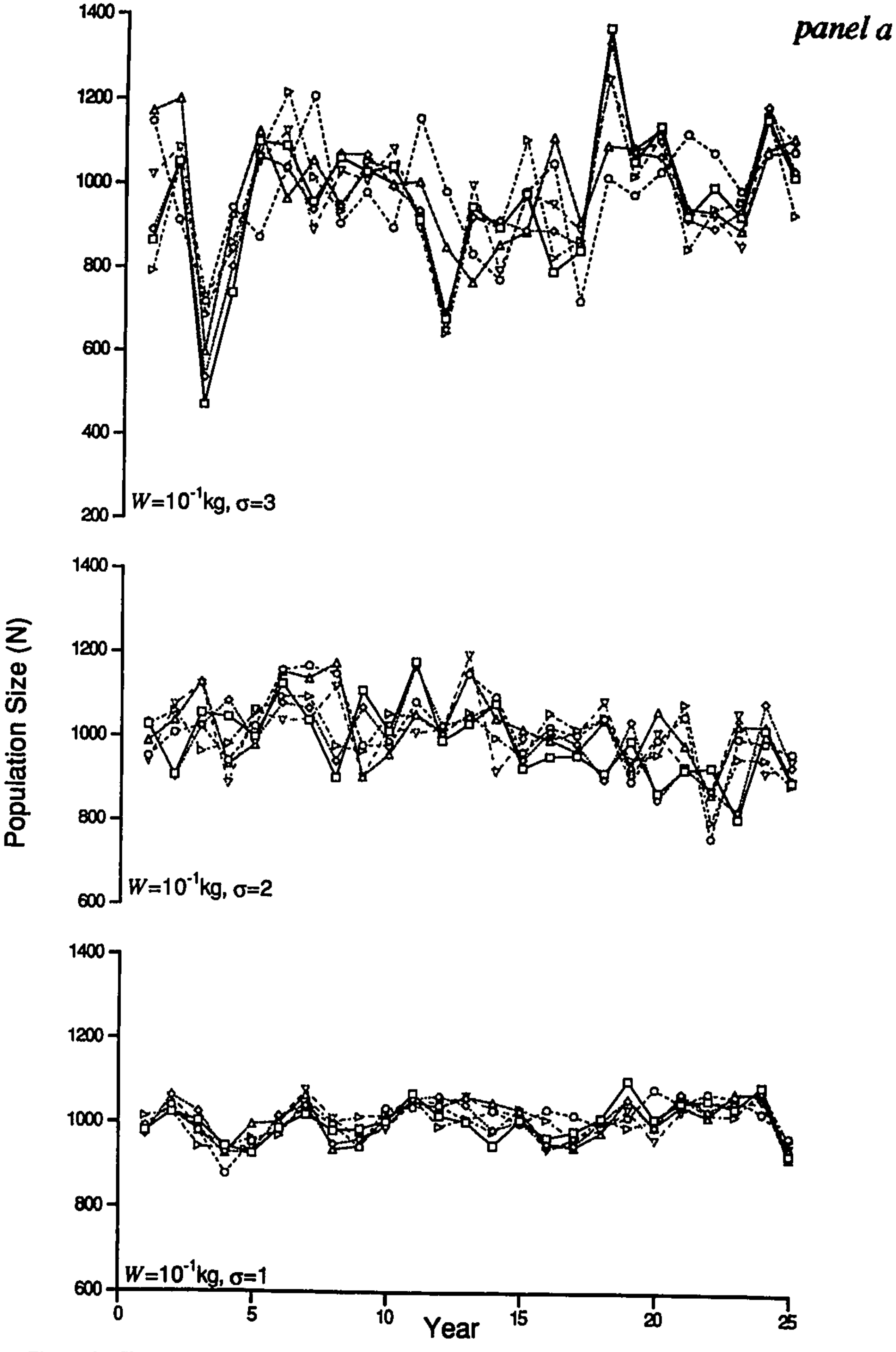
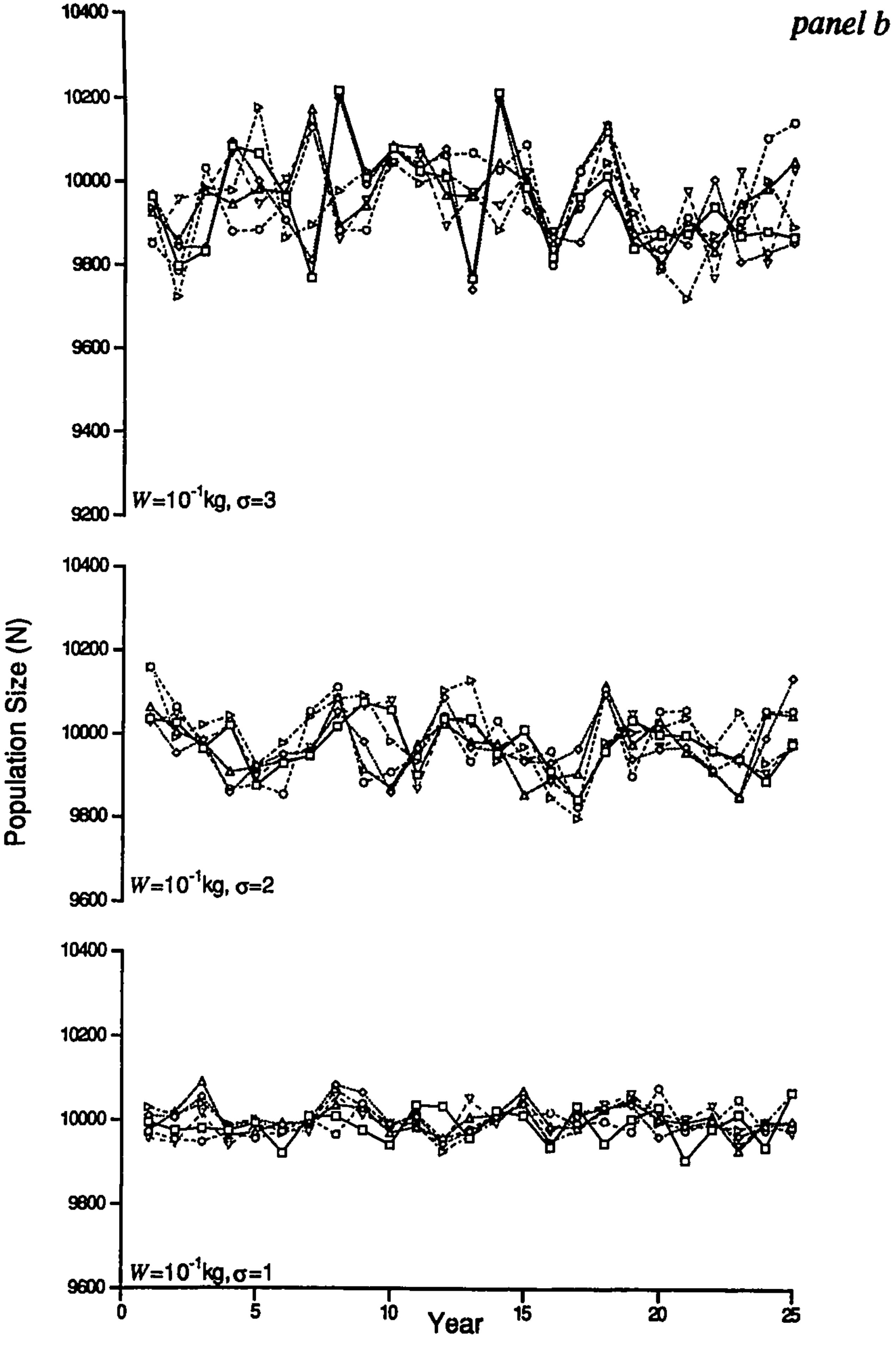

panel c
100400
100200
100000
99800
99600
99400
99200
W=10^{-2}kg, σ=3
100400
100200
100000
99800
99600
W=10^{-2}kg, σ=2
Population Size (N)
100400
100200
100000
99800
99600
W=10^{-2}kg, σ=1
0
5
10
15
20
25
Year

FIGURE E.4 Population time-slices for the simulated 10^{-1} kg body size populations. This figure consists of three panels *a, b* and *c* on the next three pages, respectively. Every panel presents 3 graphs, one above the other. Each of the 9 graphs of all three panels show the 6 randomly selected time-slices for each combination of the carrying capacity K and the standard deviation σ of the random variable X in model (3.4). Panels *a, b* and *c* show the combinations with $K = 1000$, 10,000 and 100,000 respectively. The top graph on each panel have the time-slices with $\sigma = 3$, while the middle and bottom graphs show the time-slices with $\sigma = 2$ and $\sigma = 1$ respectively.


panel a
1400
1200
1000
800
600
400
200
W=10^-1kg, σ=3
Population Size (N)
1400
1200
1000
800
600
W=10^-1kg, σ=2
1400
1200
1000
800
600
W=10^-1kg, σ=1
0
5
10
15
20
25
Year


panel b
Population Size (N)
W=10⁻¹kg, σ=3
W=10⁻¹kg, σ=2
W=10⁻¹kg, σ=1
10400
10200
10000
9800
9600
9400
9200
Year
0
5
10
15
20
25

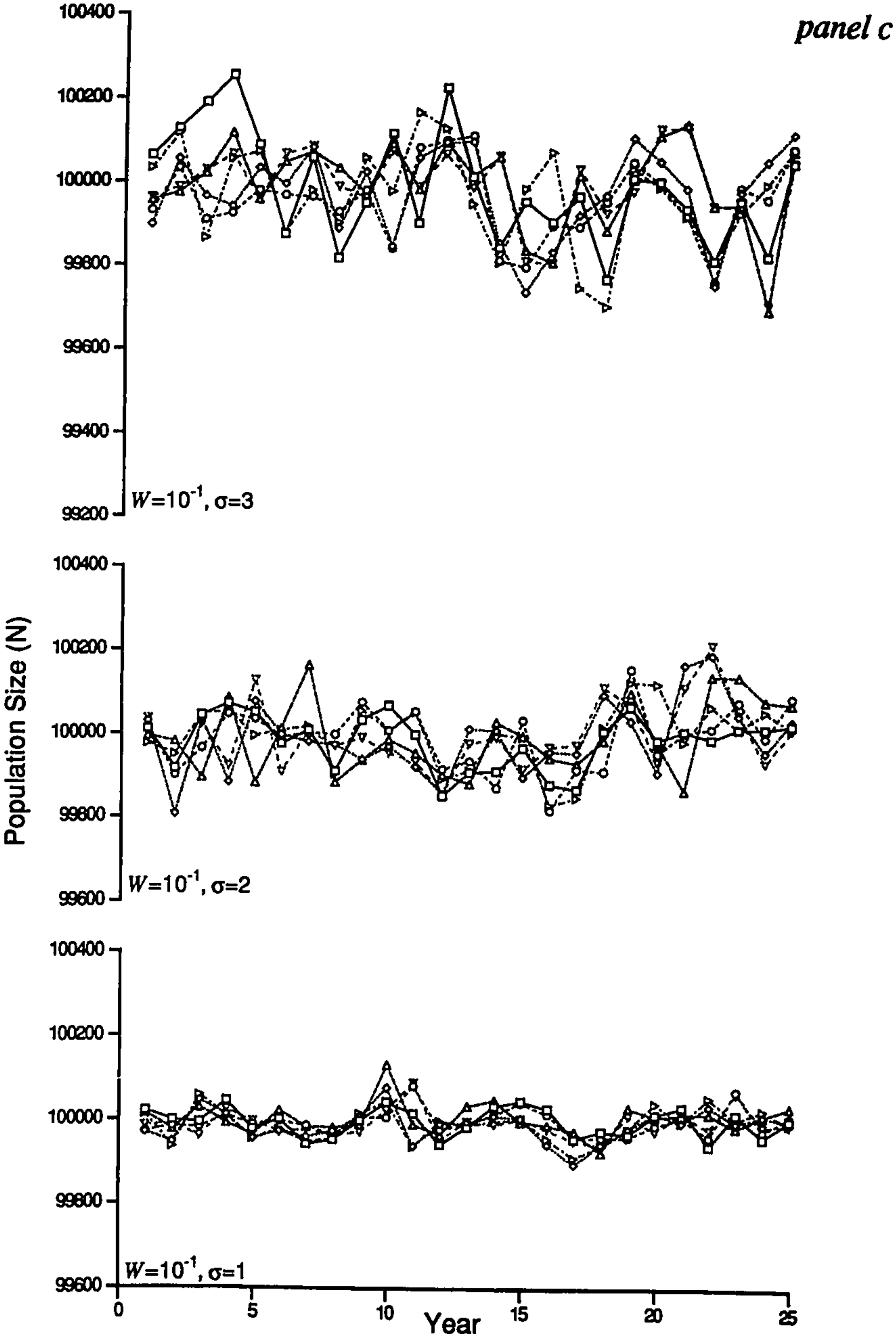
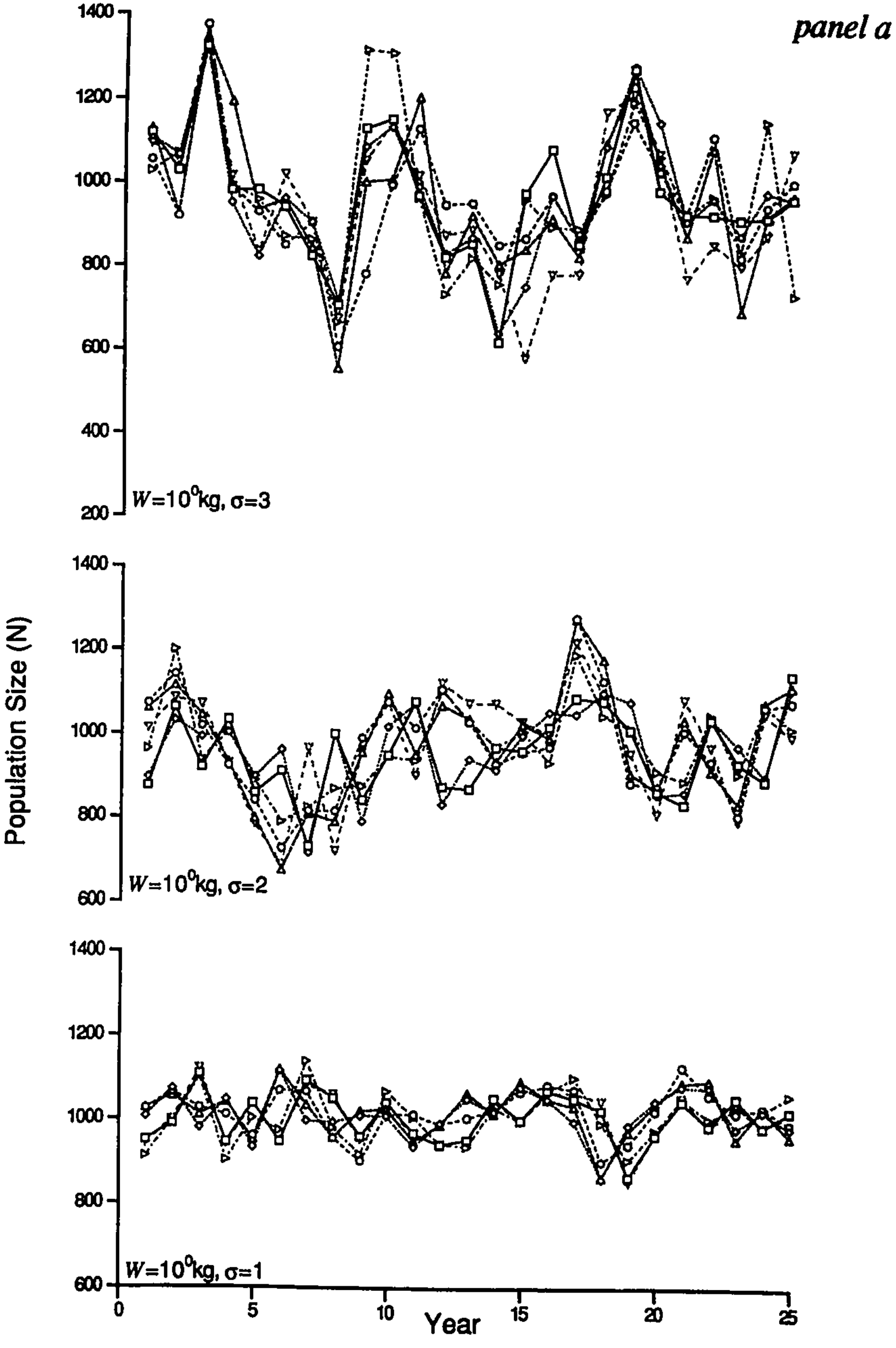
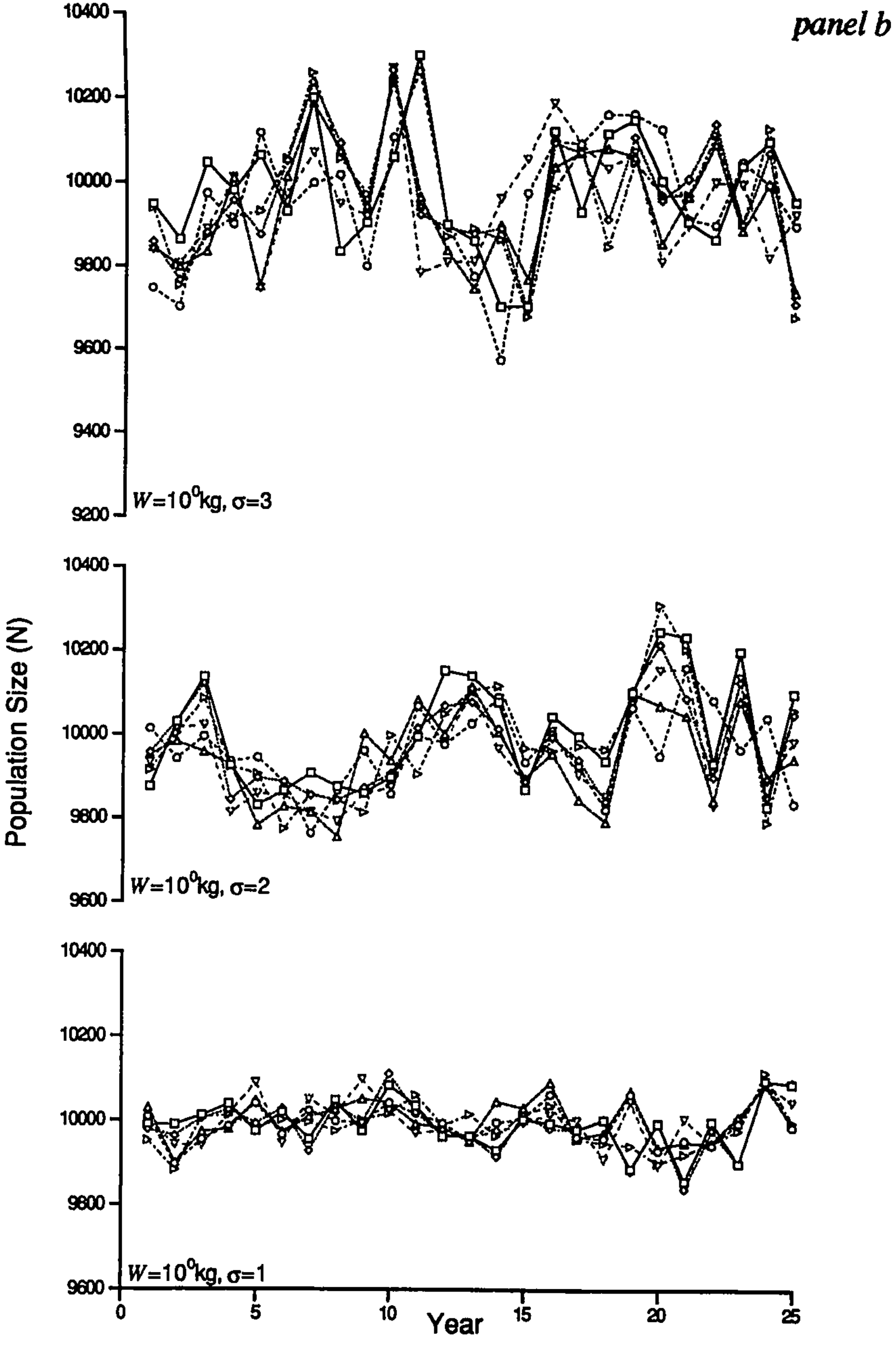
panel c
Population Size (N)
100400
100200
100000
99800
99600
99400
99200
$W=10^{-1}$, $\sigma=3$
100400
100200
100000
99800
99600
$W=10^{-1}$, $\sigma=2$
100400
100200
100000
99800
99600
$W=10^{-1}$, $\sigma=1$
0
5
10
15
20
25
Year

FIGURE E.5 Population time-slices for the simulated 10^0 kg body size populations. This figure consists of three panels *a, b* and *c* on the next three pages, respectively. Every panel presents 3 graphs, one above the other. Each of the 9 graphs of all three panels show the 6 randomly selected time-slices for each combination of the carrying capacity K and the standard deviation σ of the random variable X in model (3.4). Panels *a, b* and *c* show the combinations with $K = 1000$, 10,000 and 100,000 respectively. The top graph on each panel have the time-slices with $\sigma = 3$, while the middle and bottom graphs show the time-slices with $\sigma = 2$ and $\sigma = 1$ respectively.


panel a
1400
1200
1000
800
600
400
200
W=10⁰kg, σ=3
1400
1200
1000
800
600
W=10⁰kg, σ=2
1400
1200
1000
800
600
W=10⁰kg, σ=1
Population Size (N)
0
5
10
15
20
25
Year


panel b
Population Size (N)
10400
10200
10000
9800
9600
9400
9200
W=10⁰kg, σ=3
9600
W=10⁰kg, σ=2
W=10⁰kg, σ=1
Year
0
5
10
15
20
25

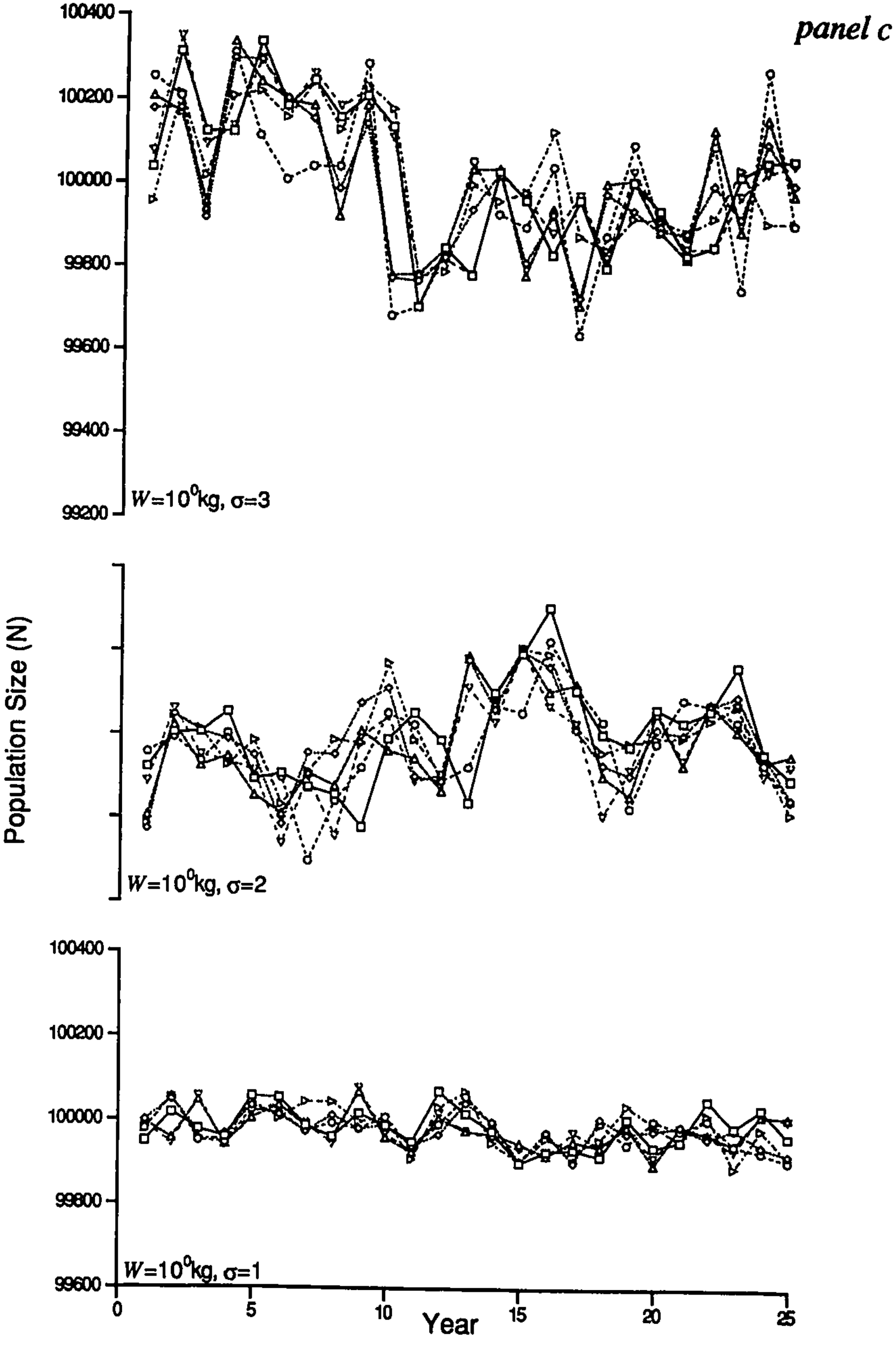
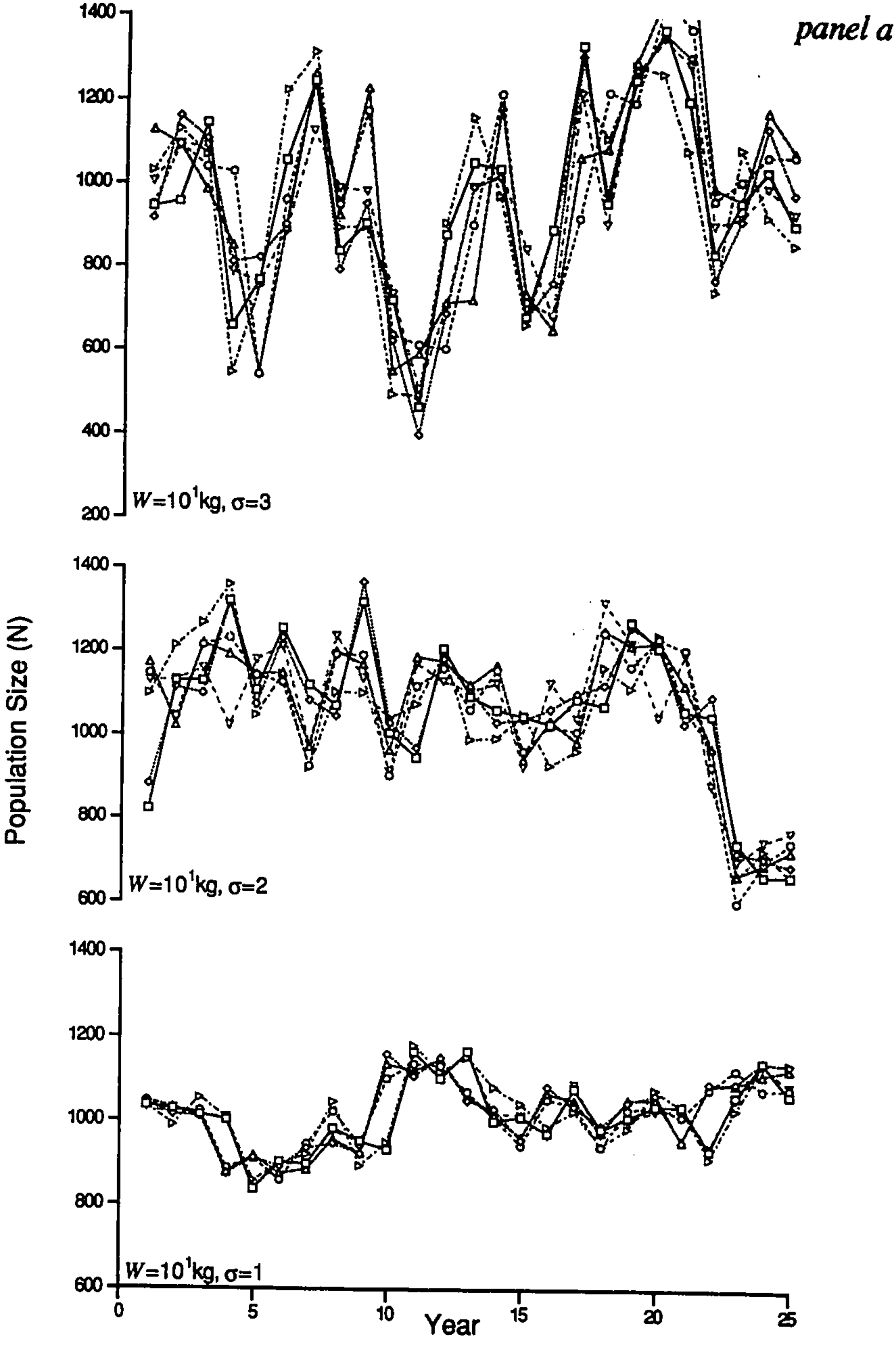
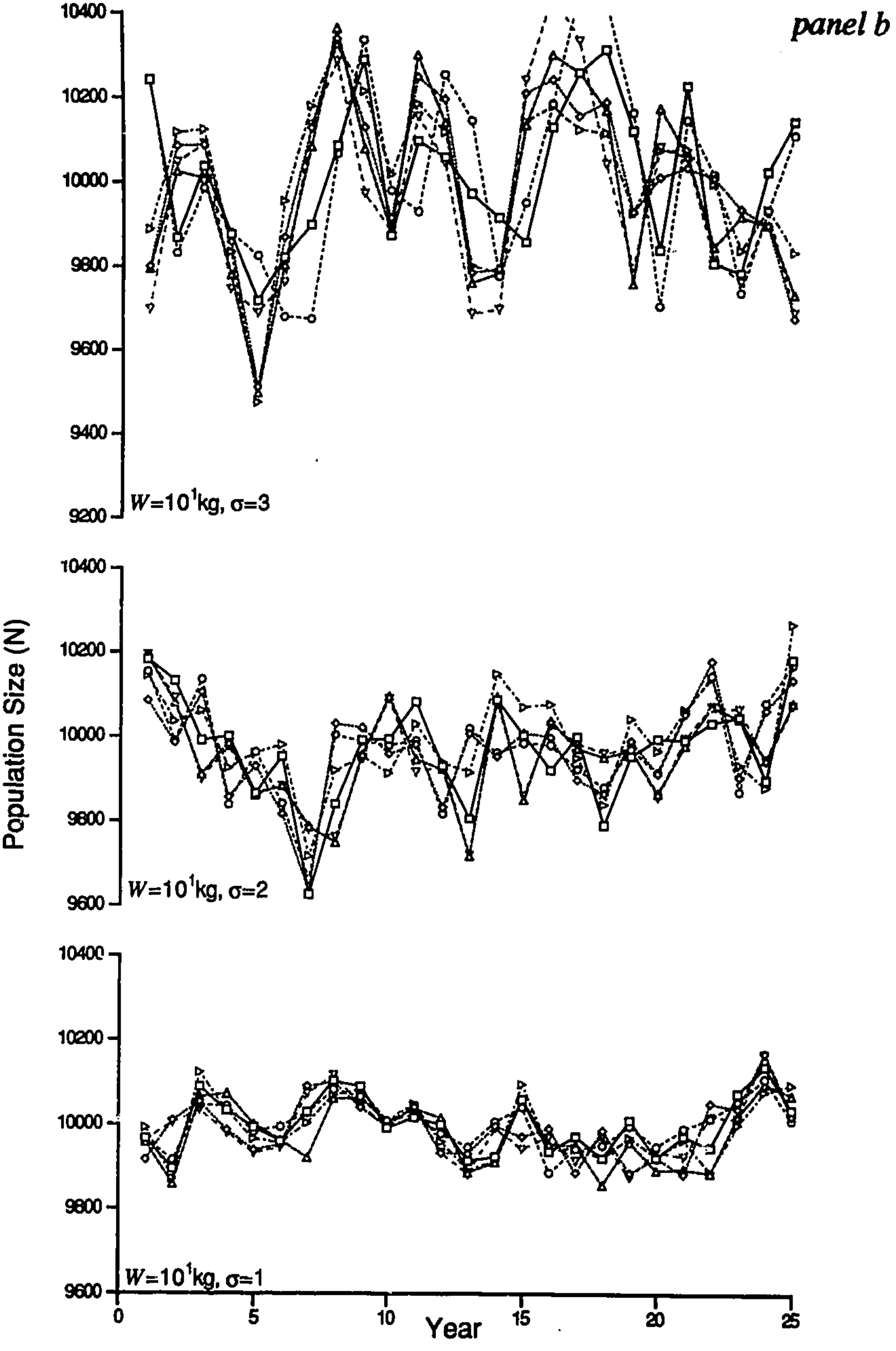
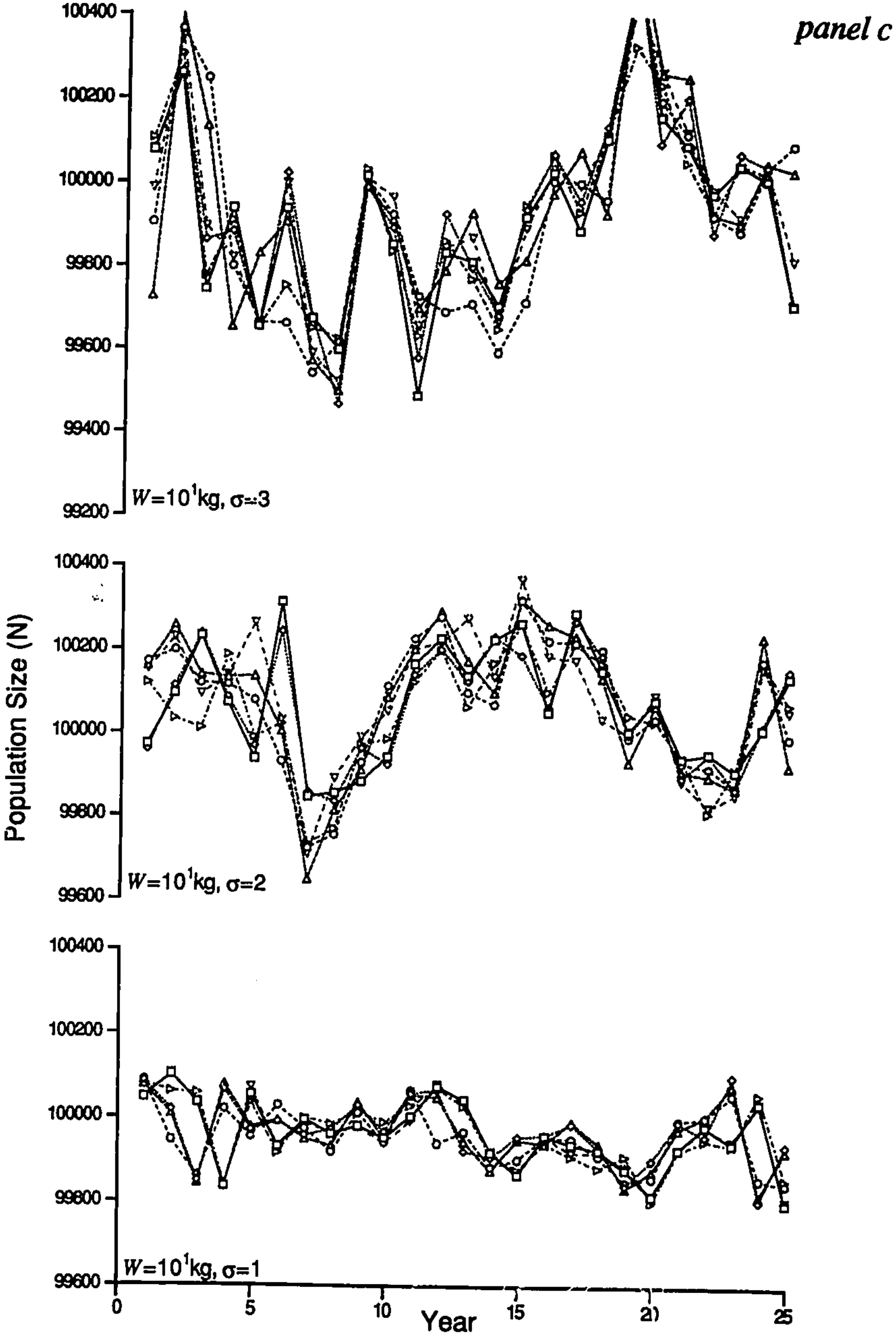

panel c
100400
100200
100000
99800
99600
99400
99200
W=10⁰kg, σ=3
Population Size (N)
W=10⁰kg, σ=2
100400
100200
100000
99800
99600
W=10⁰kg, σ=1
0
5
10
Year
15
20
25

FIGURE E.6 Population time-slices for the simulated 10^1 kg body size populations. This figure consists of three panels *a*, *b* and *c* on the next three pages, respectively. Every panel presents 3 graphs, one above the other. Each of the 9 graphs of all three panels show the 6 randomly selected time-slices for each combination of the carrying capacity K and the standard deviation σ of the random variable X in model (3.4). Panels *a*, *b* and *c* show the combinations with $K = 1000$, 10,000 and 100,000 respectively. The top graph on each panel have the time-slices with $\sigma = 3$, while the middle and bottom graphs show the time-slices with $\sigma = 2$ and $\sigma = 1$ respectively.

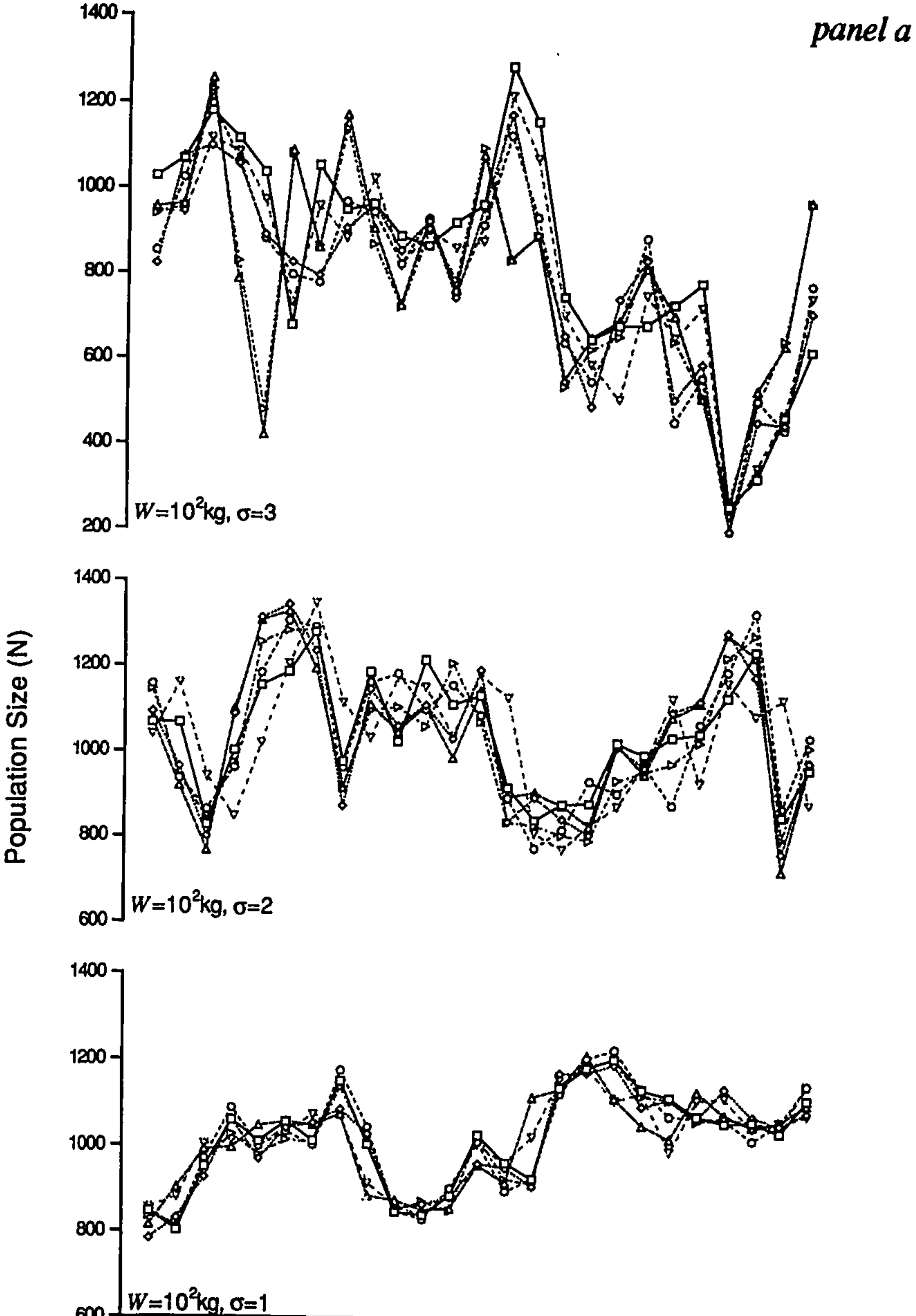

panel a
1400
1200
1000
800
600
400
200
W=10¹kg, σ=3
1400
1200
1000
800
600
W=10¹kg, σ=2
1400
1200
1000
800
600
W=10¹kg, σ=1
Population Size (N)
0
5
10
15
20
25
Year

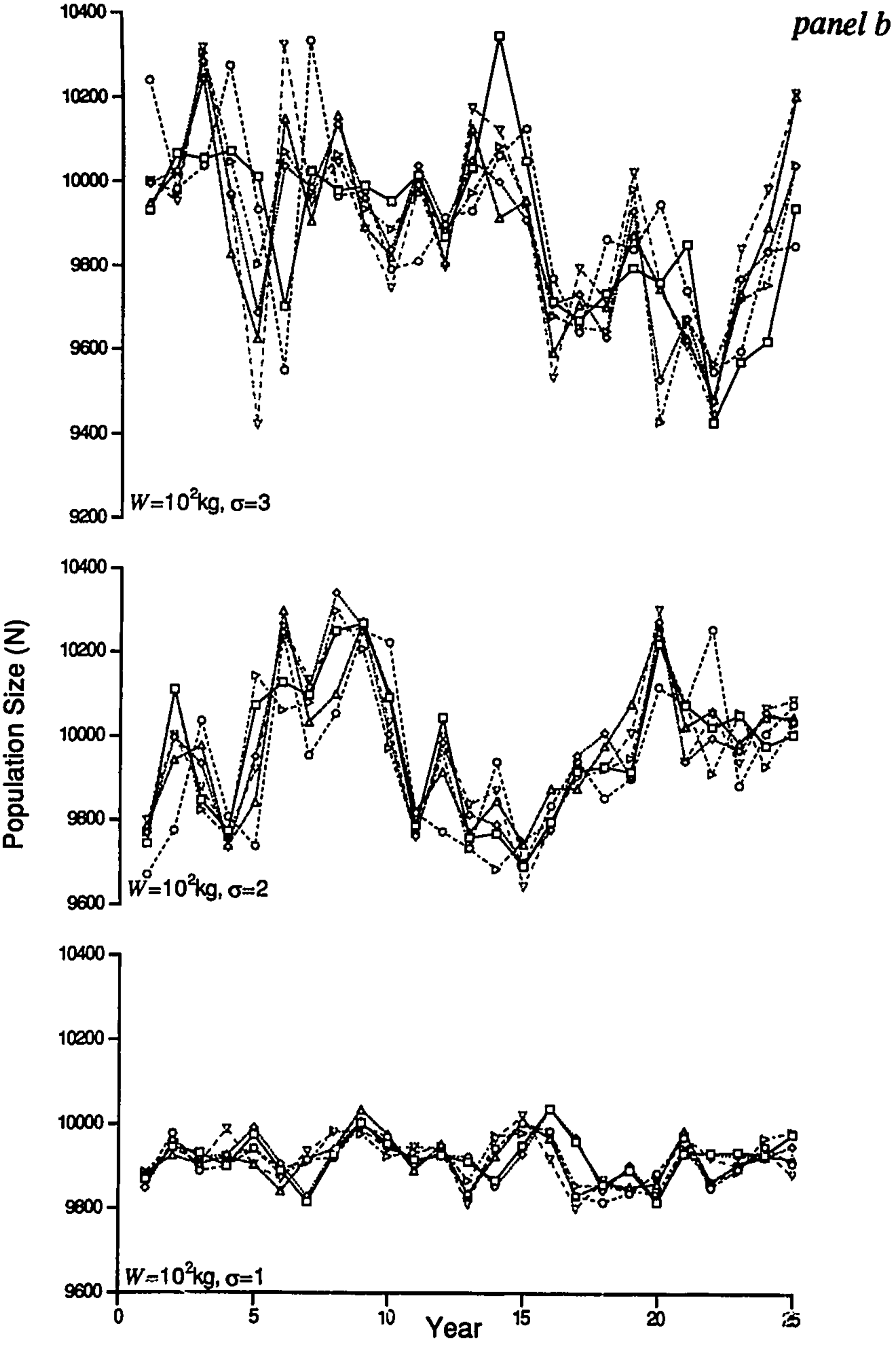

panel b
10400
10200
10000
9800
9600
9400
9200
W=10¹kg, σ=3
10400
10200
10000
9800
9600
W=10¹kg, σ=2
10400
10200
10000
9800
9600
W=10¹kg, σ=1
Population Size (N)
0
5
10
15
20
25
Year



panel c
100400
100200
100000
99800
99600
99400
99200
W=10¹kg, σ=3
100400
100200
100000
99800
99600
W=10¹kg, σ=2
100400
100200
100000
99800
99600
W=10¹kg, σ=1
Population Size (N)
0
5
10
15
20
25
Year

FIGURE E.7 Population time-slices for the simulated 10^2 kg body size populations. This figure consists of three panels *a*, *b* and *c* on the next three pages, respectively. Every panel presents 3 graphs, one above the other. Each of the 9 graphs of all three panels show the 6 randomly selected time-slices for each combination of the carrying capacity K and the standard deviation σ of the random variable X in model (3.4). Panels *a*, *b* and *c* show the combinations with $K = 1000$, 10,000 and 100,000 respectively. The top graph on each panel have the time-slices with $\sigma = 3$, while the middle and bottom graphs show the time-slices with $\sigma = 2$ and $\sigma = 1$ respectively.


panel a
Population Size (N)
Year
1400
1200
1000
800
600
400
200
W=10²kg, σ=3
W=10²kg, σ=2
W=10²kg, σ=1
0
5
10
15
20
25


panel b
10400
10200
10000
9800
9600
9400
9200
W=10²kg, σ=3
10400
10200
10000
9800
9600
W=10²kg, σ=2
10400
10200
10000
9800
9600
W=10²kg, σ=1
Population Size (N)
0
5
10
15
20
25
Year

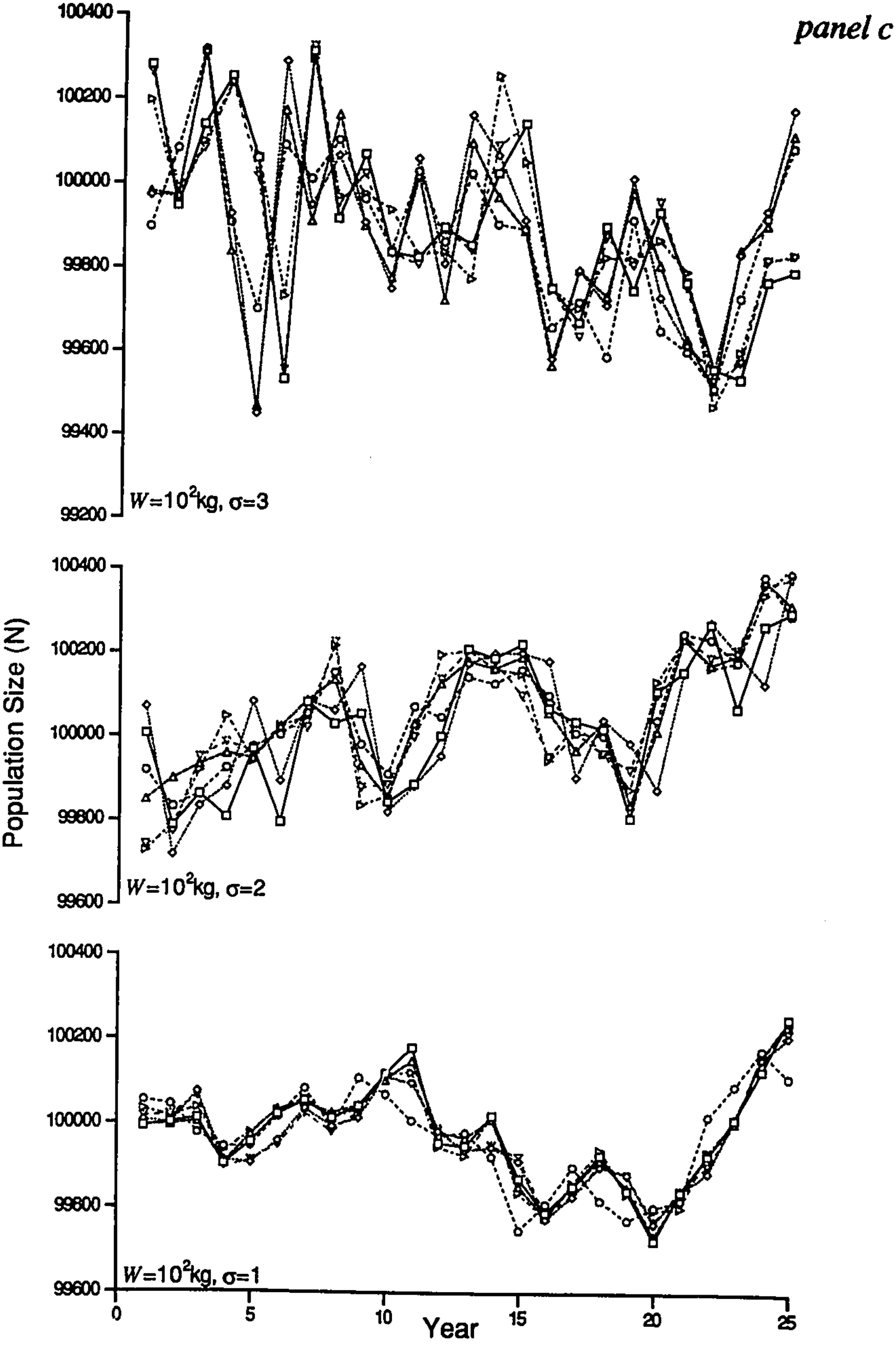
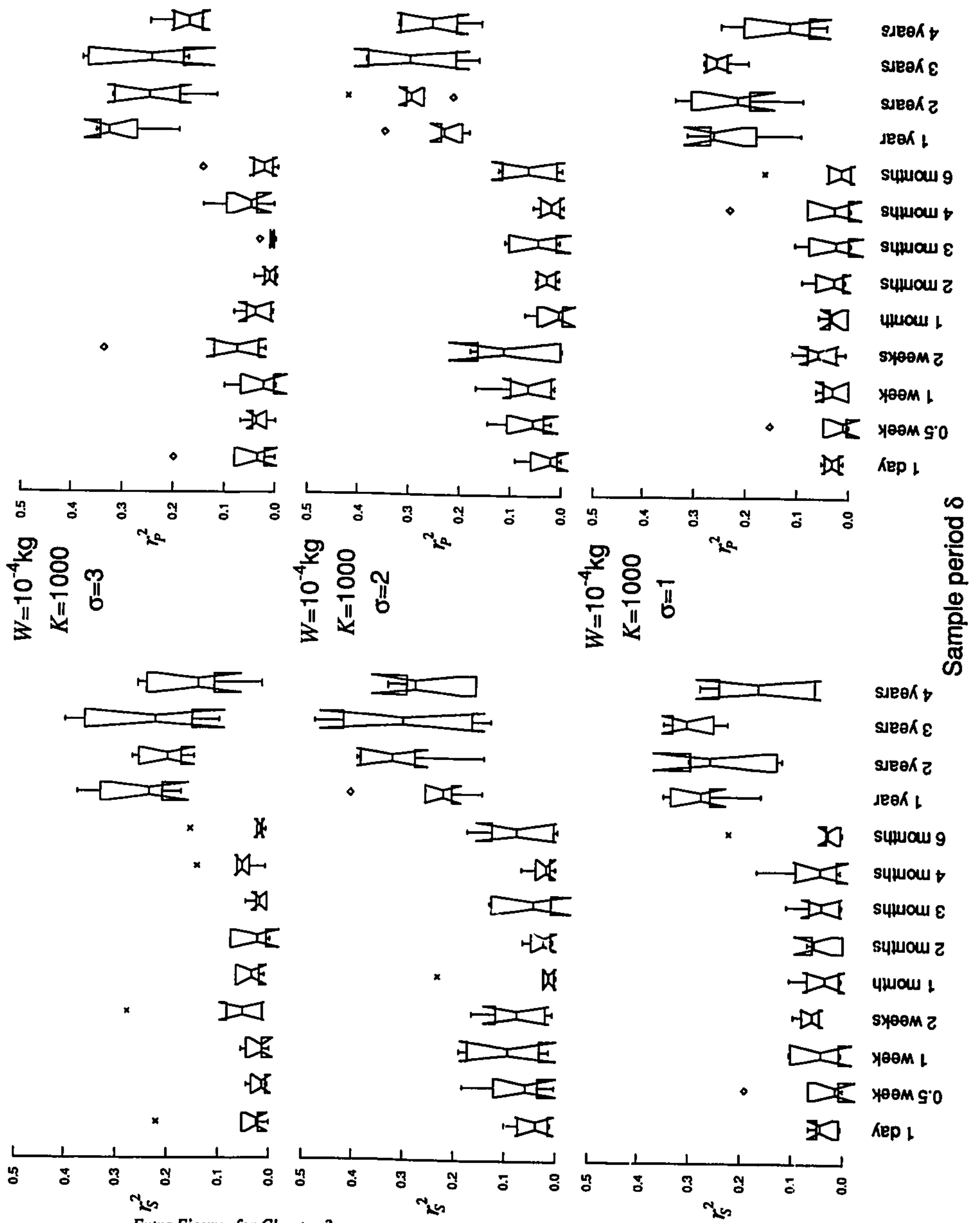
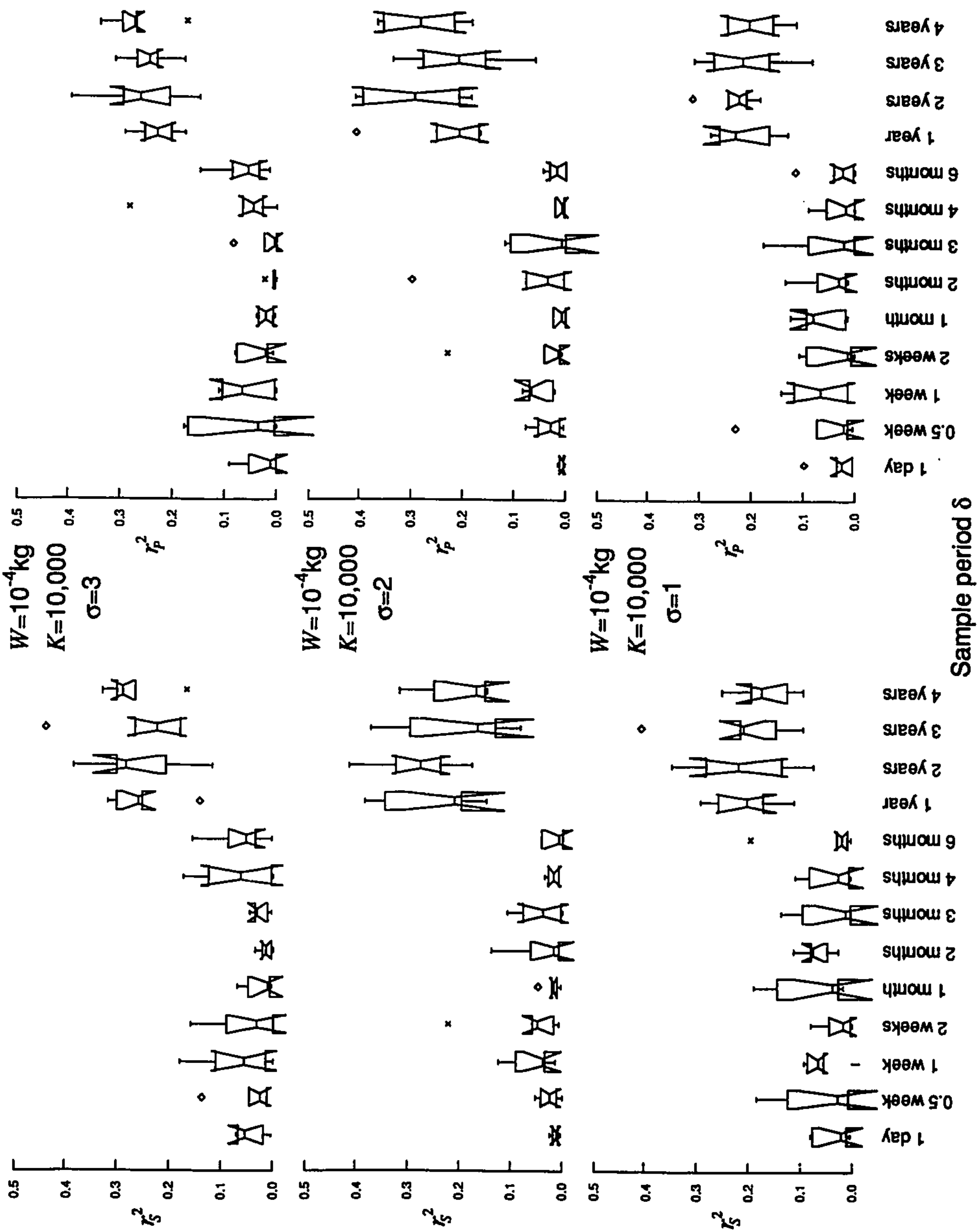

panel c
Population Size (N)
100400
100200
100000
99800
99600
99400
99200
W=10²kg, σ=3
100400
100200
100000
99800
99600
W=10²kg, σ=2
100400
100200
100000
99800
99600
W=10²kg, σ=1
0
5
10
15
20
25
Year

FIGURE E.8 The distributions of the r_S^2 or r_P^2 statistics for the 10^{-4} kg populations corresponding to the time-slices presented in Figure E.1. This figure consists of three panels *a*, *b* and *c* on the next three pages, respectively. Every panel presents 3 pairs of graphs, one above the other. Each of the 9 pairs of graphs, of all three panels, show notched-box plots of the r_S^2 or r_P^2 statistics calculated for each randomly selected time-slice in Figure E.1. Each pair of graphs corresponds to the different combinations of the carrying capacity K and the standard deviation σ of the random variable X in model (3.4) used to produce the time-slices of Figure E.1. Panels *a*, *b* and *c* show the combinations with $K = 1000$, 10,000 and 100,000 respectively. The top pair of graphs on each panel correspond to the time-slices with $\sigma = 3$, while the middle and bottom pairs of graphs correspond to the time-slices with $\sigma = 2$ and $\sigma = 1$ respectively. Every graph is composed of 13 notched-box plots one for each of the 13 sampling periods δ discussed in the methods. If the notches (the diagonal lines extending from the median to the vertical sides of a box) of two medians do not overlap, then the medians can be considered to be significantly different ($p \leq 0.05$). The hollow diamonds and ×'s identify outliers within each distribution. The diamonds are points that lie between 1.5 times and 3.0 times the interquartile distance outward from the hinges of the notched box and the ×'s are outliers beyond this range (Wilkinson et al. 1992).

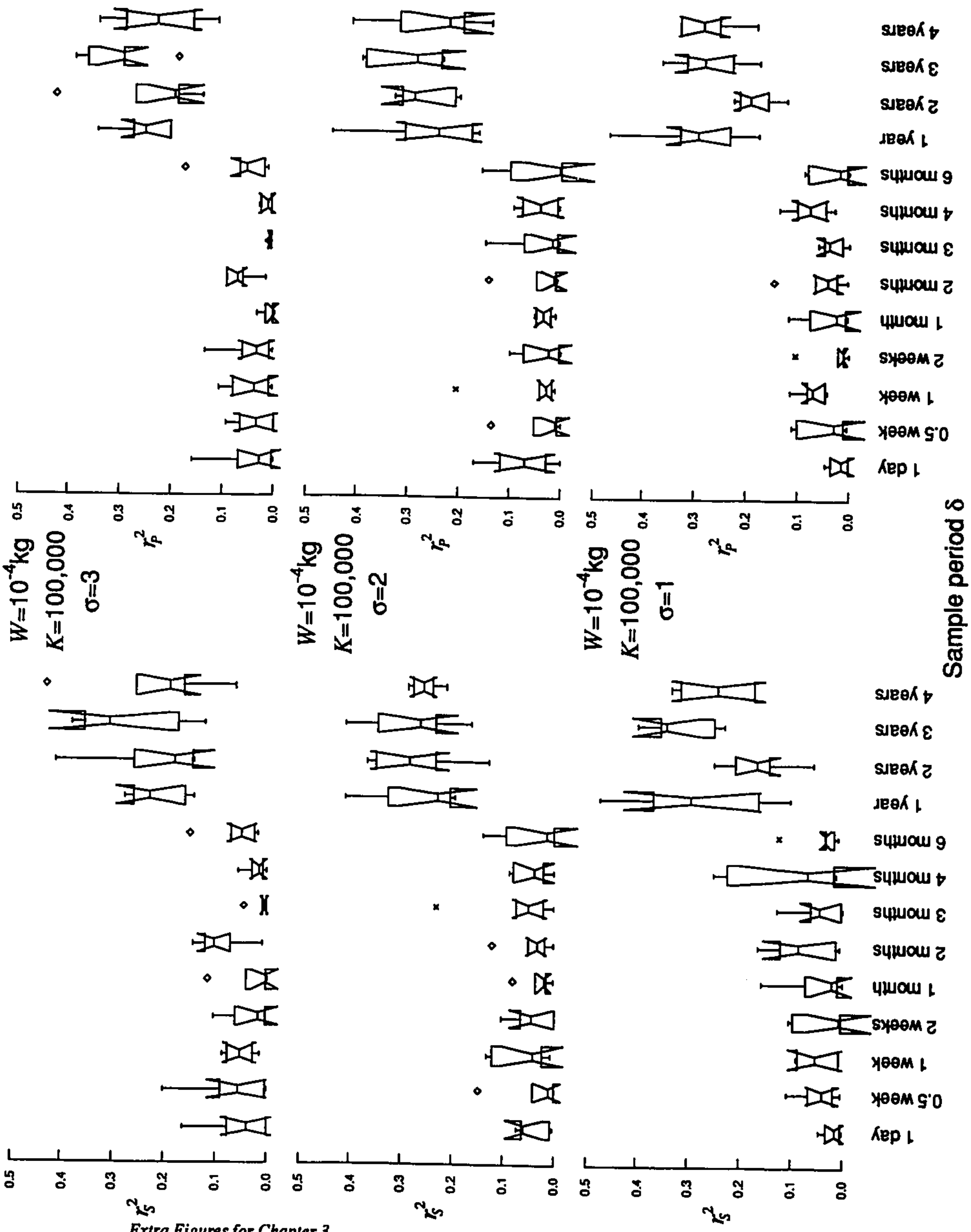
panel a


W=10^-4kg
K=1000
σ=3
W=10^-4kg
K=1000
σ=2
W=10^-4kg
K=1000
σ=1
r_P^2
r_S^2
0.0
0.1
0.2
0.3
0.4
0.5
1 day
0.5 week
1 week
2 weeks
1 month
2 months
3 months
4 months
6 months
1 year
2 years
3 years
4 years
Sample period δ

panel b

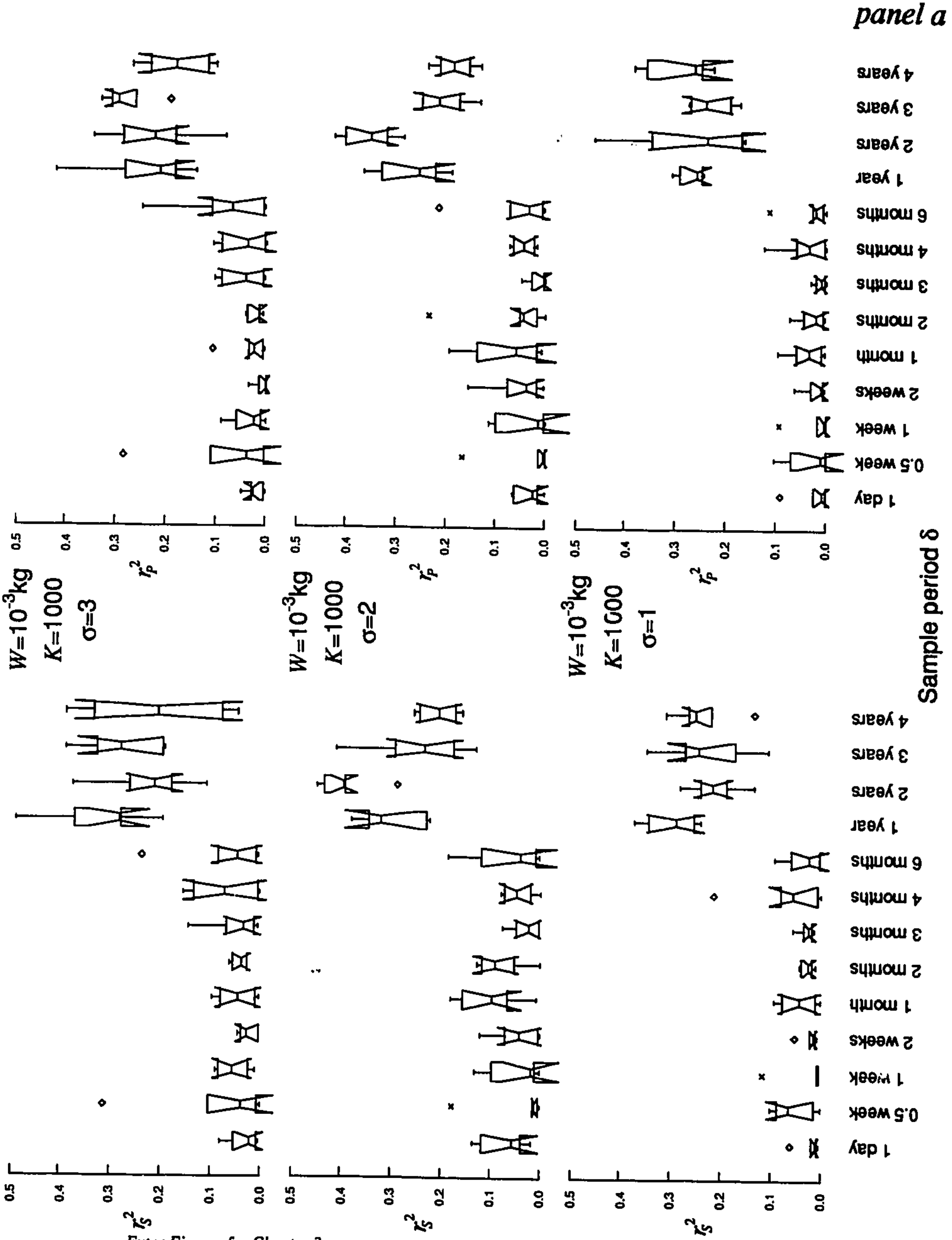

W=10^-4kg
K=10,000
σ=3
W=10^-4kg
K=10,000
σ=2
W=10^-4kg
K=10,000
σ=1
Sample period δ
r_P^2
r_S^2
0.5
0.4
0.3
0.2
0.1
0.0
1 day
0.5 week
1 week
2 weeks
1 month
2 months
3 months
4 months
6 months
1 year
2 years
3 years
4 years

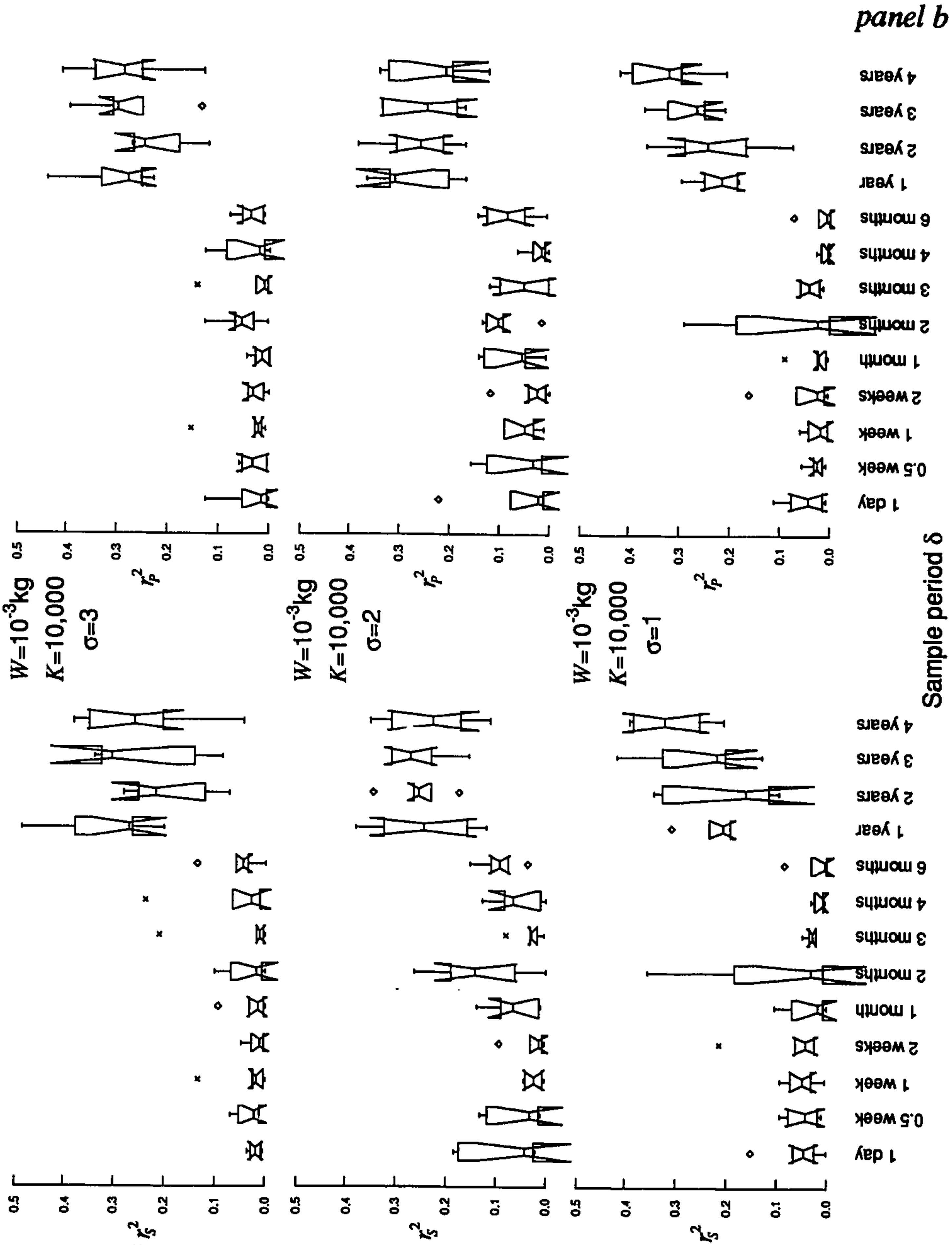
panel c



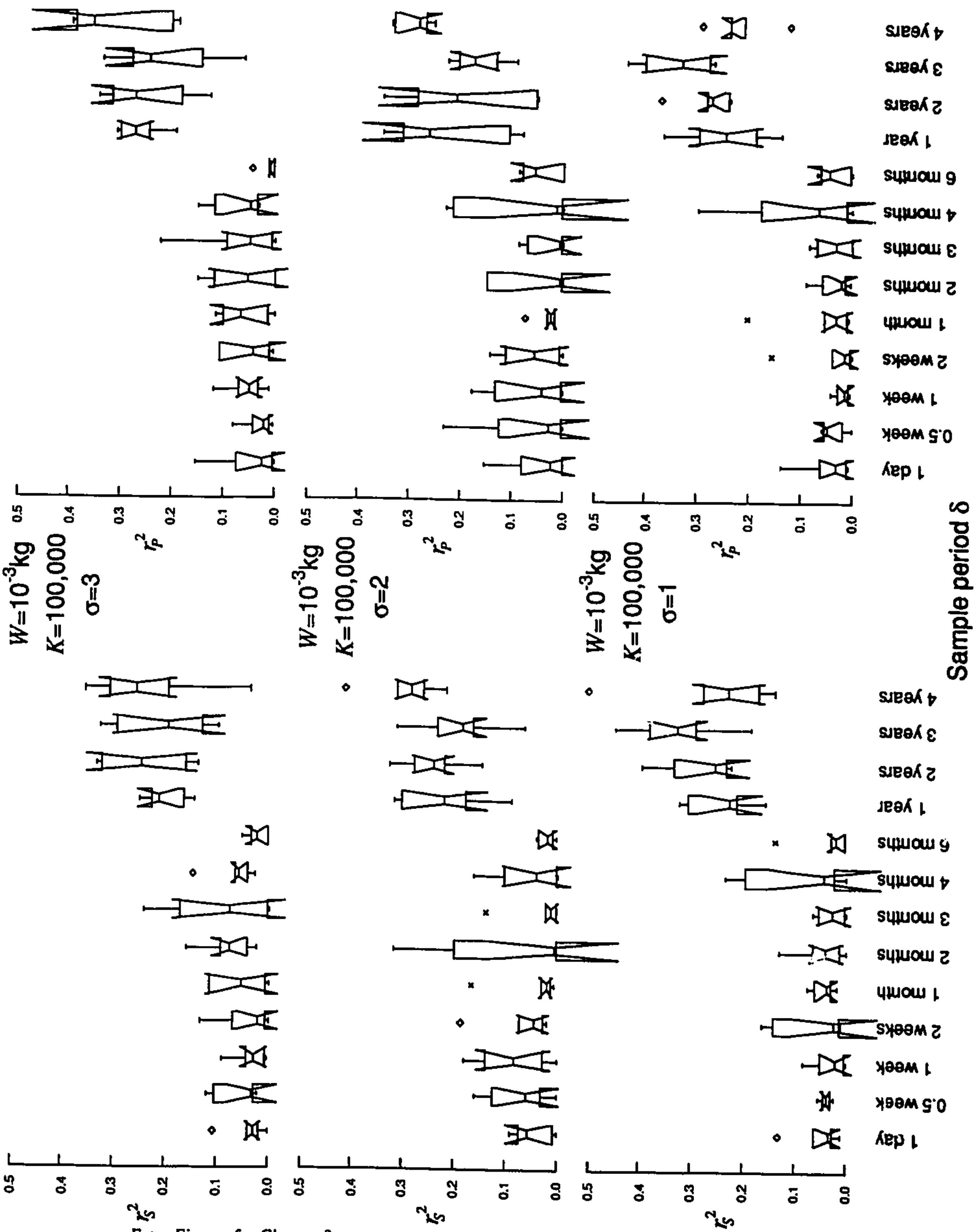
W=10^-4 kg
K=100,000
σ=3
σ=2
σ=1
r_P^2
r_S^2
0.0
0.1
0.2
0.3
0.4
0.5
1 day
0.5 week
1 week
2 weeks
1 month
2 months
3 months
4 months
6 months
1 year
2 years
3 years
4 years
Sample period δ

FIGURE E.9 The distributions of the r_S^2 or r_P^2 statistics for the 10^{-3} kg populations corresponding to the time-slices presented in Figure E.2. This figure consists of three panels *a*, *b* and *c* on the next three pages, respectively. Every panel presents 3 pairs of graphs, one above the other. Each of the 9 pairs of graphs, of all three panels, show notched-box plots of the r_S^2 or r_P^2 statistics calculated for each randomly selected time-slice in Figure E.2. Each pair of graphs corresponds to the different combinations of the carrying capacity K and the standard deviation σ of the random variable X in model (3.4) used to produce the time-slices of Figure E.2. Panels *a*, *b* and *c* show the combinations with $K = 1000, 10{,}000$ and 100,000 respectively. The top pair of graphs on each panel correspond to the time-slices with $\sigma = 3$, while the middle and bottom pairs of graphs correspond to the time-slices with $\sigma = 2$ and $\sigma = 1$ respectively. Every graph is composed of 13 notched-box plots one for each of the 13 sampling periods δ discussed in the methods. If the notches (the diagonal lines extending from the median to the vertical sides of a box) of two medians do not overlap, then the medians can be considered to be significantly different ($p \leq 0.05$). The hollow diamonds and ×'s identify outliers within each distribution. The diamonds are points that lie between 1.5 times and 3.0 times the interquartile distance outward from the hinges of the notched box and the ×'s are outliers beyond this range (Wilkinson et al. 1992).

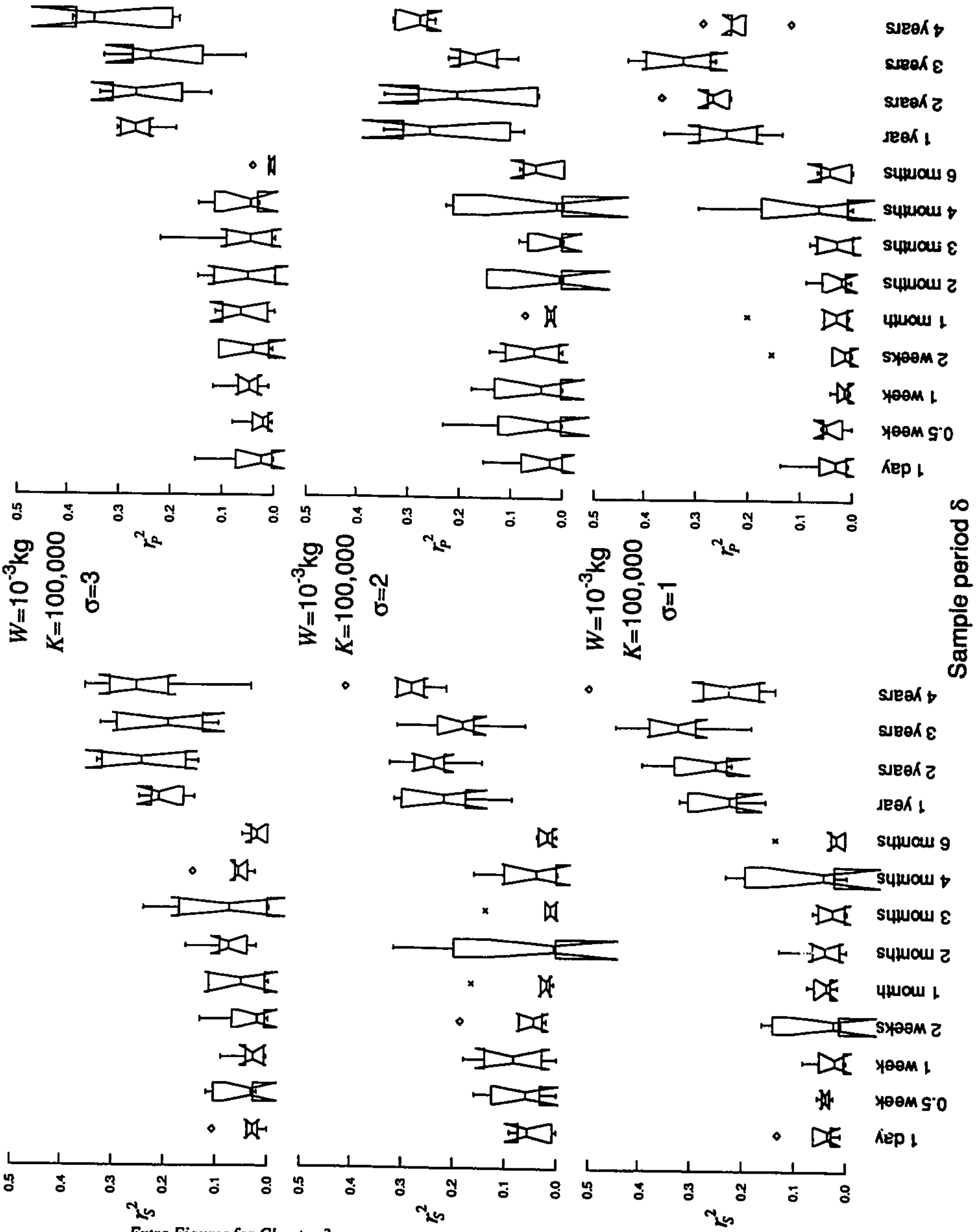

panel a
$W=10^{-3}$kg
$K=1000$
$\sigma=3$
$W=10^{-3}$kg
$K=1000$
$\sigma=2$
$W=10^{-3}$kg
$K=1000$
$\sigma=1$
r_P^2
r_S^2
0.0
0.1
0.2
0.3
0.4
0.5
1 day
0.5 week
1 week
2 weeks
1 month
2 months
3 months
4 months
6 months
1 year
2 years
3 years
4 years
Sample period δ


panel b
W=10^-3kg
K=10,000
σ=3
W=10^-3kg
K=10,000
σ=2
W=10^-3kg
K=10,000
σ=1
r_P^2
r_S^2
0.0
0.1
0.2
0.3
0.4
0.5
1 day
0.5 week
1 week
2 weeks
1 month
2 months
3 months
4 months
6 months
1 year
2 years
3 years
4 years
Sample period δ

panel c

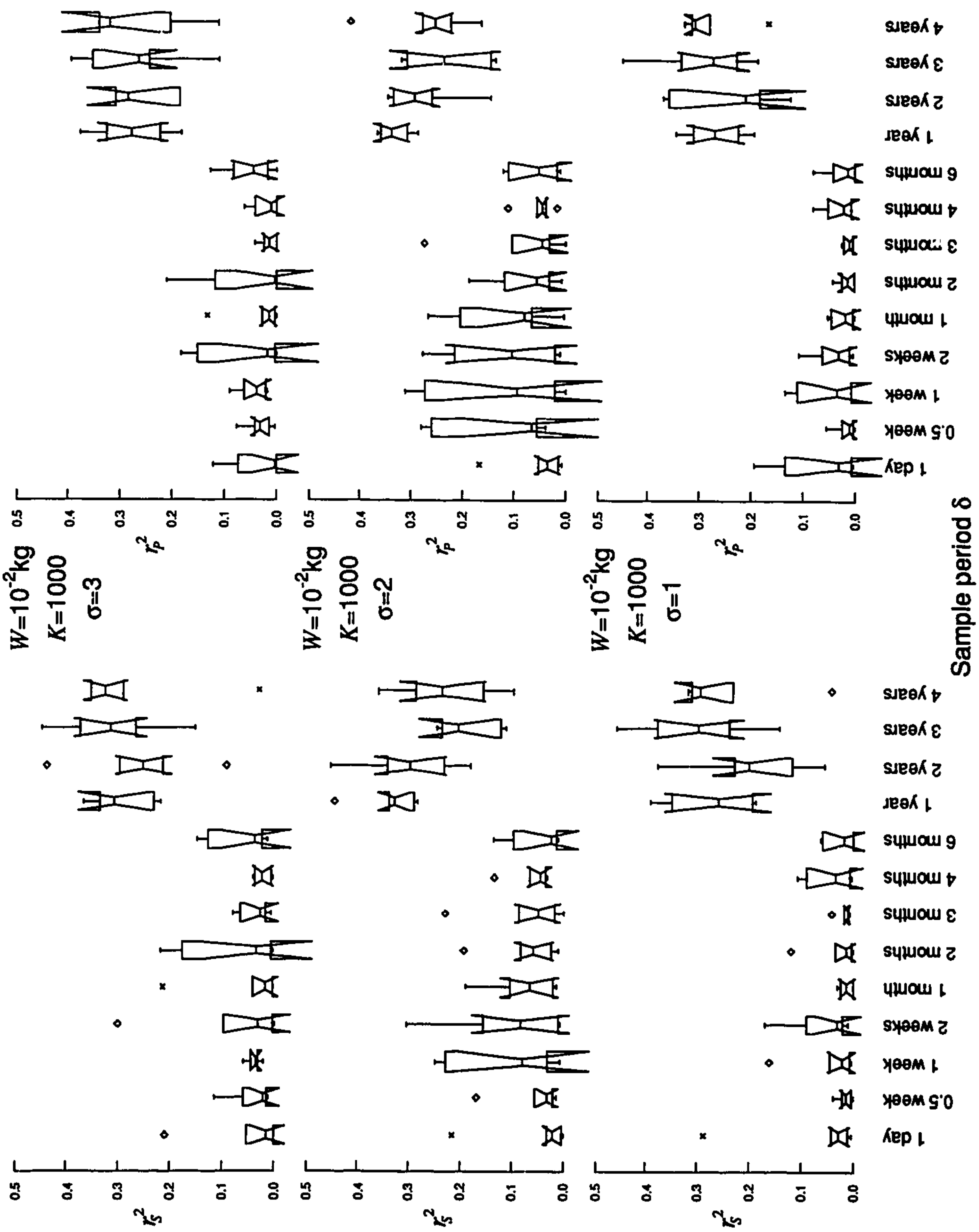

W=10^{-3}kg
K=100,000
σ=3
W=10^{-3}kg
K=100,000
σ=2
W=10^{-3}kg
K=100,000
σ=1
r_P^2
r_S^2
0.0
0.1
0.2
0.3
0.4
0.5
1 day
0.5 week
1 week
2 weeks
1 month
2 months
3 months
4 months
6 months
1 year
2 years
3 years
4 years
Sample period δ

panel c



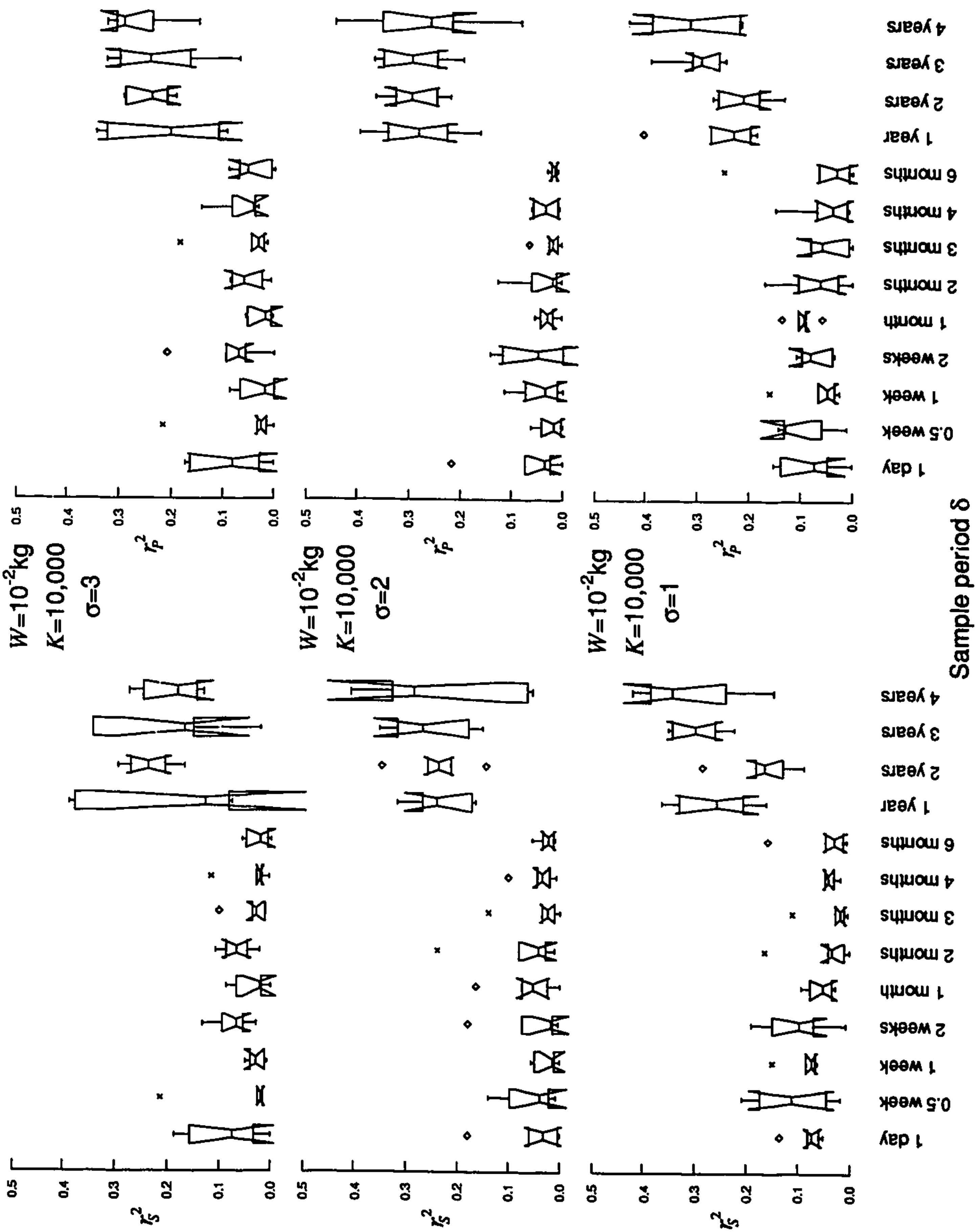
$W=10^{-3}$kg
K=100,000
σ=3
$W=10^{-3}$kg
K=100,000
σ=2
$W=10^{-3}$kg
K=100,000
σ=1
r_P^2
r_S^2
0.0
0.1
0.2
0.3
0.4
0.5
1 day
0.5 week
1 week
2 weeks
1 month
2 months
3 months
4 months
6 months
1 year
2 years
3 years
4 years
Sample period δ

panel a



W=10^-2 kg
K=1000
σ=1
σ=2
σ=3
Sample period δ
r_p^2
r_s^2
0.0
0.1
0.2
0.3
0.4
0.5
1 day
0.5 week
1 week
2 weeks
1 month
2 months
3 months
4 months
6 months
1 year
2 years
3 years
4 years

panel b



W=10^{-2}kg
K=10,000
σ=3
W=10^{-2}kg
K=10,000
σ=2
W=10^{-2}kg
K=10,000
σ=1
r_P^2
r_S^2
0.0
0.1
0.2
0.3
0.4
0.5
1 day
0.5 week
1 week
2 weeks
1 month
2 months
3 months
4 months
6 months
1 year
2 years
3 years
4 years
Sample period δ

panel c

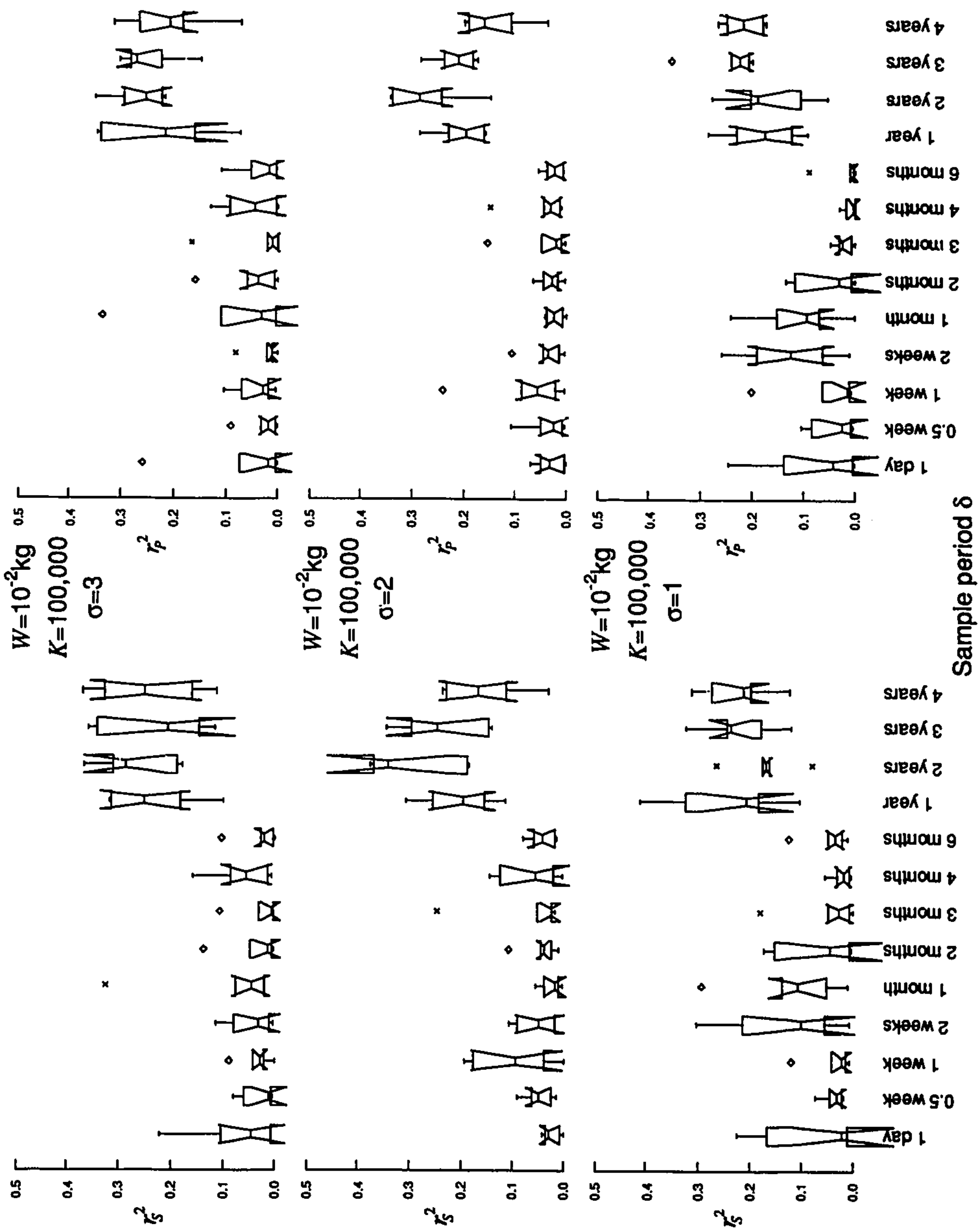
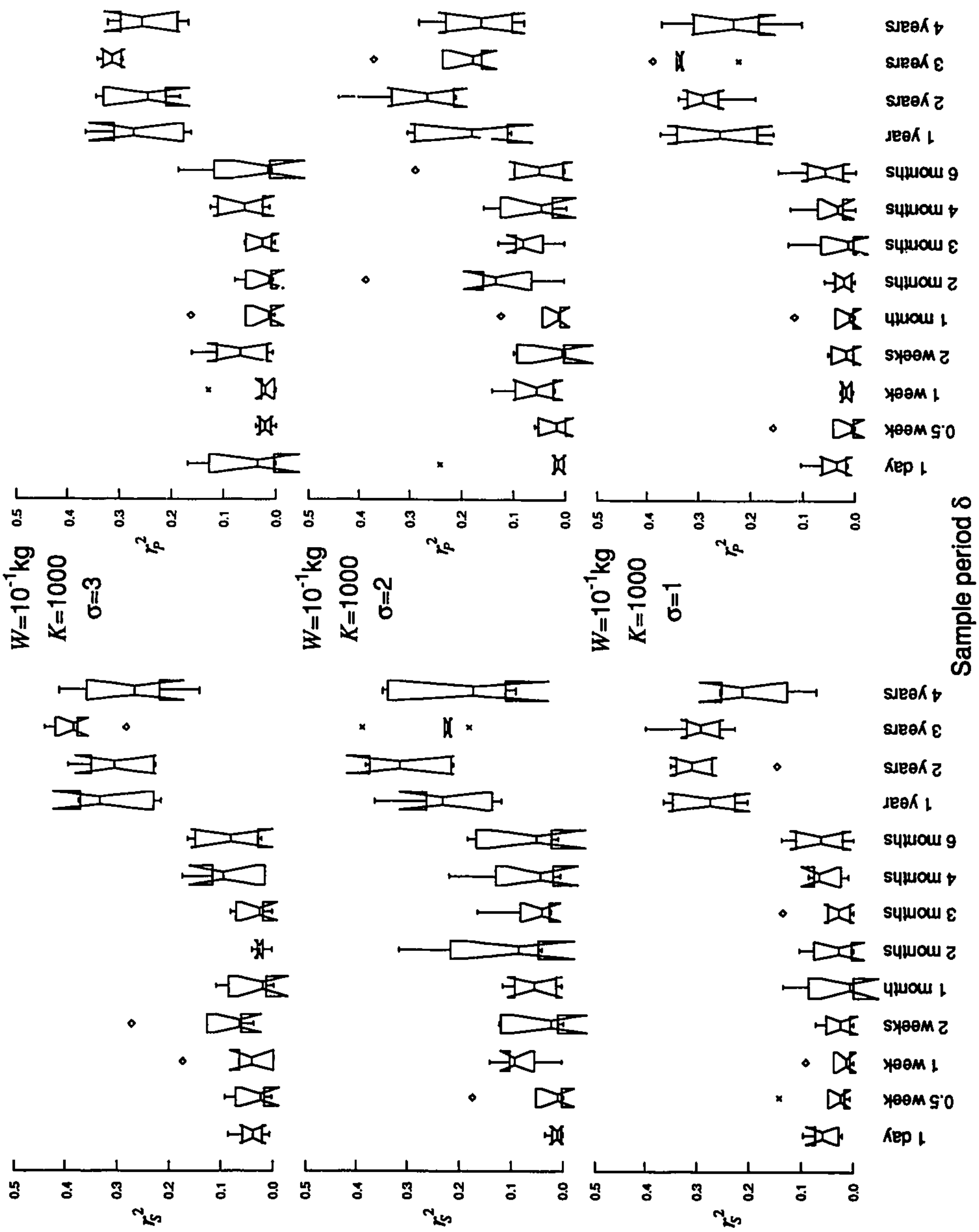
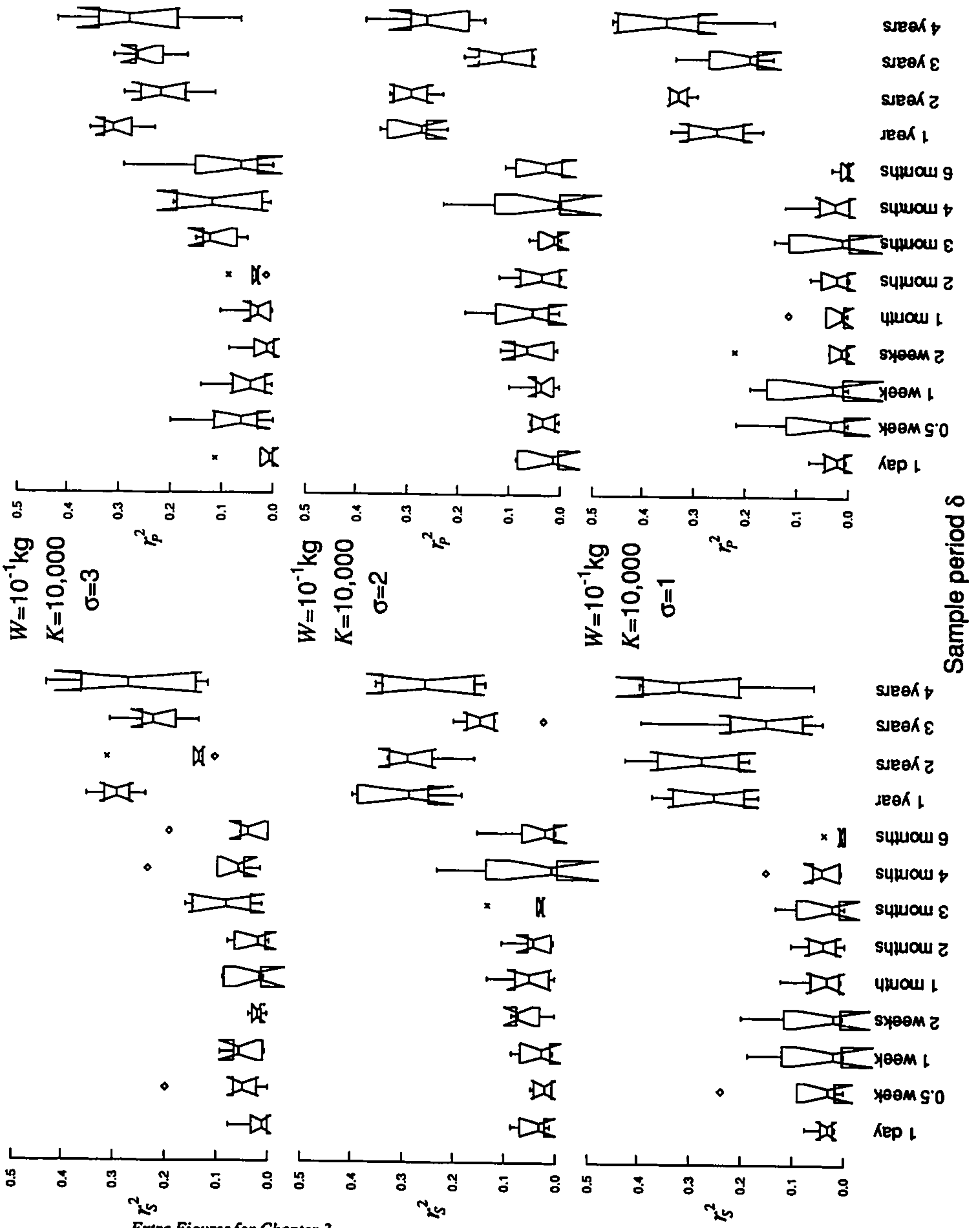

W=10^-2kg
K=100,000
σ=3
W=10^-2kg
K=100,000
σ=2
W=10^-2kg
K=100,000
σ=1
r_P^2
r_S^2
0.0
0.1
0.2
0.3
0.4
0.5
1 day
0.5 week
1 week
2 weeks
1 month
2 months
3 months
4 months
6 months
1 year
2 years
3 years
4 years
Sample period δ

FIGURE E.11 The distributions of the r_S^2 or r_P^2 statistics for the 10^{-1} kg populations corresponding to the time-slices presented in Figure E.4. This figure consists of three panels *a*, *b* and *c* on the next three pages, respectively. Every panel presents 3 pairs of graphs, one above the other. Each of the 9 pairs of graphs, of all three panels, show notched-box plots of the r_S^2 or r_P^2 statistics calculated for each randomly selected time-slice in Figure E.4. Each pair of graphs corresponds to the different combinations of the carrying capacity K and the standard deviation σ of the random variable X in model (3.4) used to produce the time-slices of Figure E.4. Panels *a*, *b* and *c* show the combinations with $K = 1000$, 10,000 and 100,000 respectively. The top pair of graphs on each panel correspond to the time-slices with $\sigma = 3$, while the middle and bottom pairs of graphs correspond to the time-slices with $\sigma = 2$ and $\sigma = 1$ respectively. Every graph is composed of 13 notched-box plots one for each of the 13 sampling periods δ discussed in the methods. If the notches (the diagonal lines extending from the median to the vertical sides of a box) of two medians do not overlap, then the medians can be considered to be significantly different ($p \leq 0.05$). The hollow diamonds and ×'s identify outliers within each distribution. The diamonds are points that lie between 1.5 times and 3.0 times the interquartile distance outward from the hinges of the notched box and the ×'s are outliers beyond this range (Wilkinson et al. 1992).

panel a


W=10^-1 kg
K=1000
σ=3
W=10^-1 kg
K=1000
σ=2
W=10^-1 kg
K=1000
σ=1
r_P^2
r_S^2
0.5
0.4
0.3
0.2
0.1
0.0
1 day
0.5 week
1 week
2 weeks
1 month
2 months
3 months
4 months
6 months
1 year
2 years
3 years
4 years
Sample period δ

panel b



W=10^-1kg
K=10,000
σ=3
σ=2
σ=1
r_P^2
r_S^2
0.0
0.1
0.2
0.3
0.4
0.5
1 day
0.5 week
1 week
2 weeks
1 month
2 months
3 months
4 months
6 months
1 year
2 years
3 years
4 years
Sample period δ

panel c

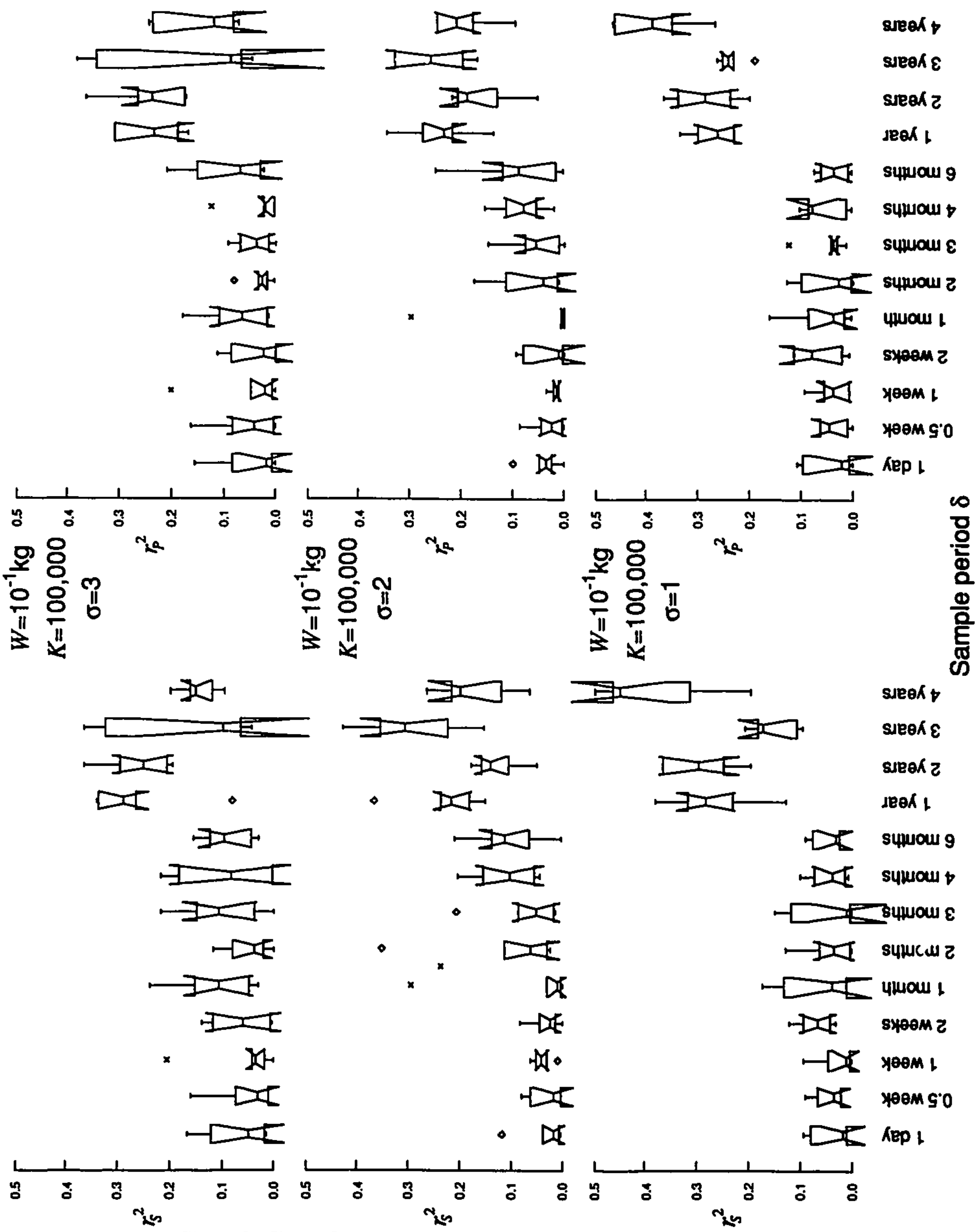
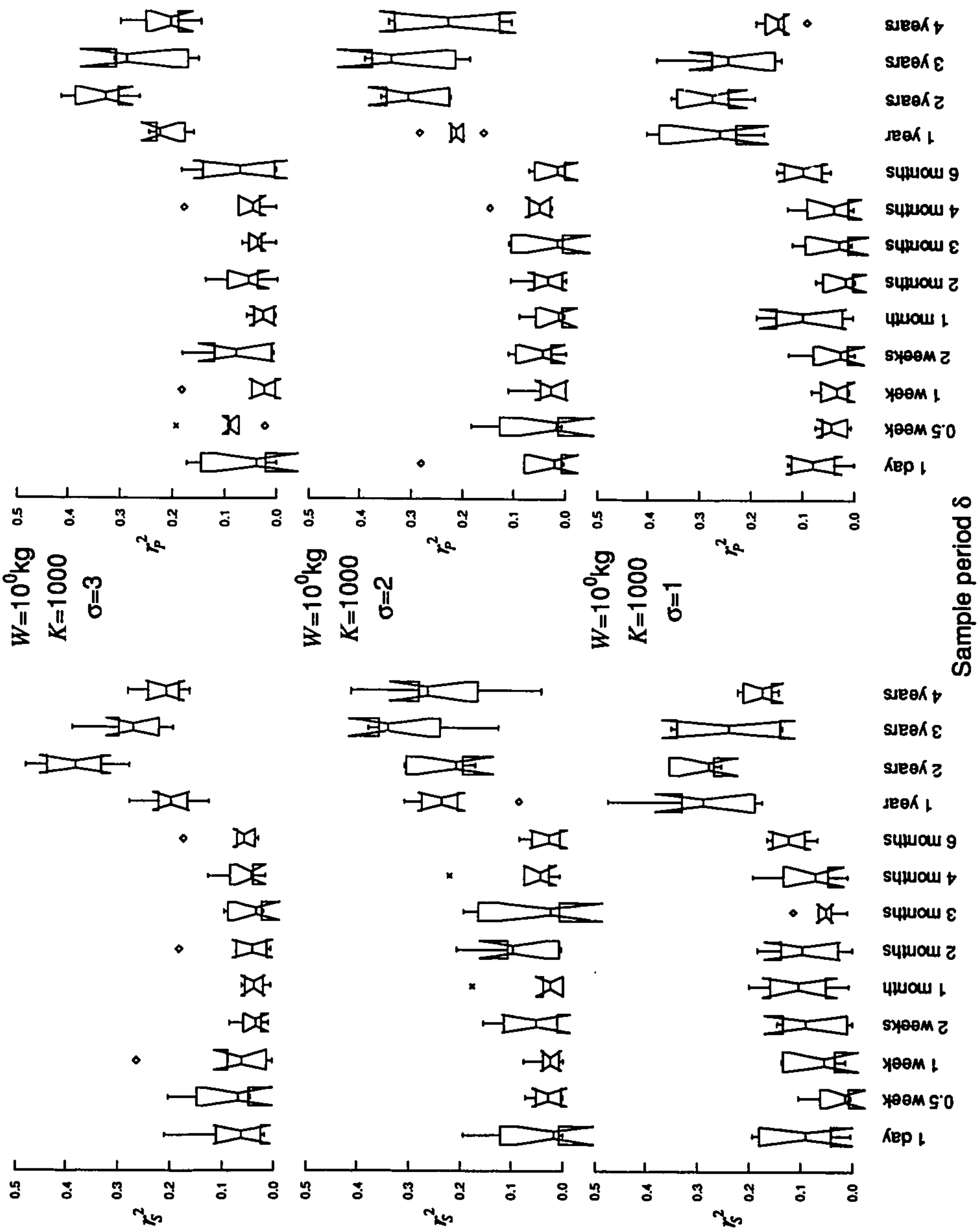

W=10^{-1}kg
K=100,000
σ=3
σ=2
σ=1
r_P^2
r_S^2
Sample period δ
0.0
0.1
0.2
0.3
0.4
0.5
1 day
0.5 week
1 week
2 weeks
1 month
2 months
3 months
4 months
6 months
1 year
2 years
3 years
4 years

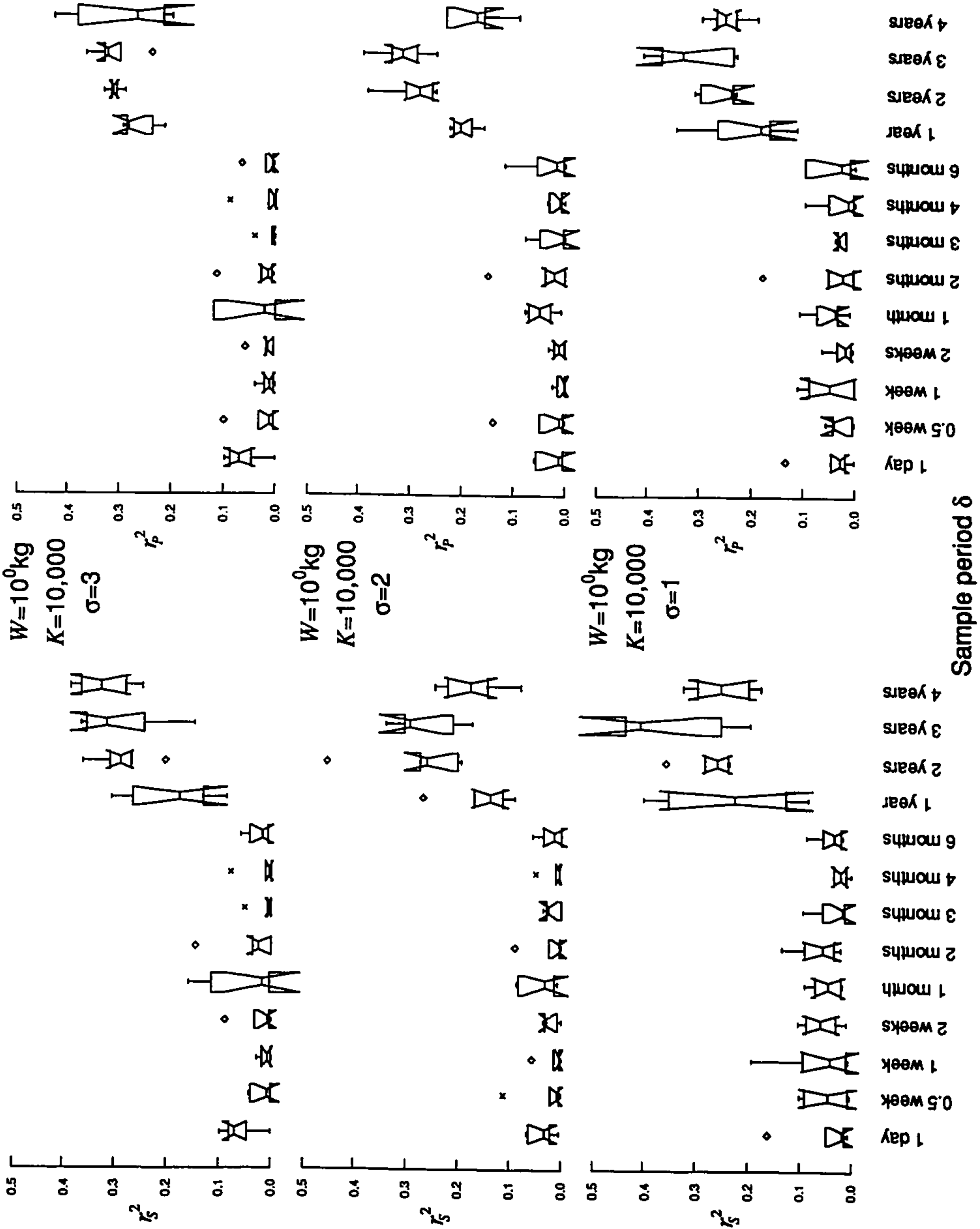
FIGURE E.12 The distributions of the r_S^2 or r_P^2 statistics for the 10^0 kg populations corresponding to the time-slices presented in Figure E.5. This figure consists of three panels *a*, *b* and *c* on the next three pages, respectively. Every panel presents 3 pairs of graphs, one above the other. Each of the 9 pairs of graphs, of all three panels, show notched-box plots of the r_S^2 or r_P^2 statistics calculated for each randomly selected time-slice in Figure E.5. Each pair of graphs corresponds to the different combinations of the carrying capacity K and the standard deviation σ of the random variable X in model (3.4) used to produce the time-slices of Figure E.5. Panels *a*, *b* and *c* show the combinations with $K = 1000$, 10,000 and 100,000 respectively. The top pair of graphs on each panel correspond to the time-slices with $\sigma = 3$, while the middle and bottom pairs of graphs correspond to the time-slices with $\sigma = 2$ and $\sigma = 1$ respectively. Every graph is composed of 13 notched-box plots one for each of the 13 sampling periods δ discussed in the methods. If the notches (the diagonal lines extending from the median to the vertical sides of a box) of two medians do not overlap, then the medians can be considered to be significantly different ($p \leq 0.05$). The hollow diamonds and ×'s identify outliers within each distribution. The diamonds are points that lie between 1.5 times and 3.0 times the interquartile distance outward from the hinges of the notched box and the ×'s are outliers beyond this range (Wilkinson et al. 1992).

panel a



$W=10^0$kg
$K=1000$
$\sigma=3$
$W=10^0$kg
$K=1000$
$\sigma=2$
$W=10^0$kg
$K=1000$
$\sigma=1$
r_P^2
r_S^2
0.0
0.1
0.2
0.3
0.4
0.5
1 day
0.5 week
1 week
2 weeks
1 month
2 months
3 months
4 months
6 months
1 year
2 years
3 years
4 years
Sample period δ

panel b


W=10^0kg
K=10,000
σ=1
W=10^0kg
K=10,000
σ=2
W=10^0kg
K=10,000
σ=3
Sample period δ
1 day
0.5 week
1 week
2 weeks
1 month
2 months
3 months
4 months
6 months
1 year
2 years
3 years
4 years
r_p^2
r_S^2
0.0
0.1
0.2
0.3
0.4
0.5

panel c

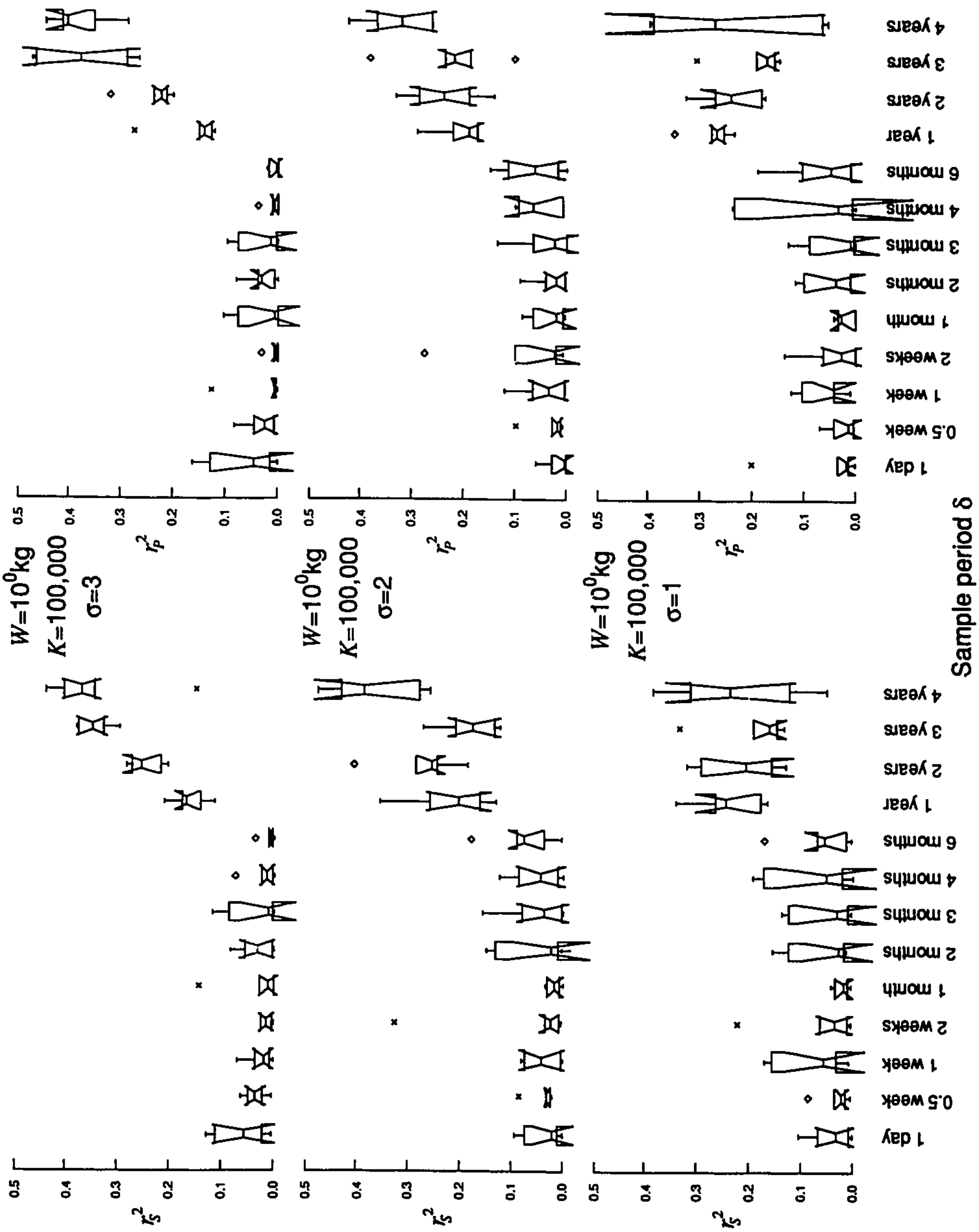
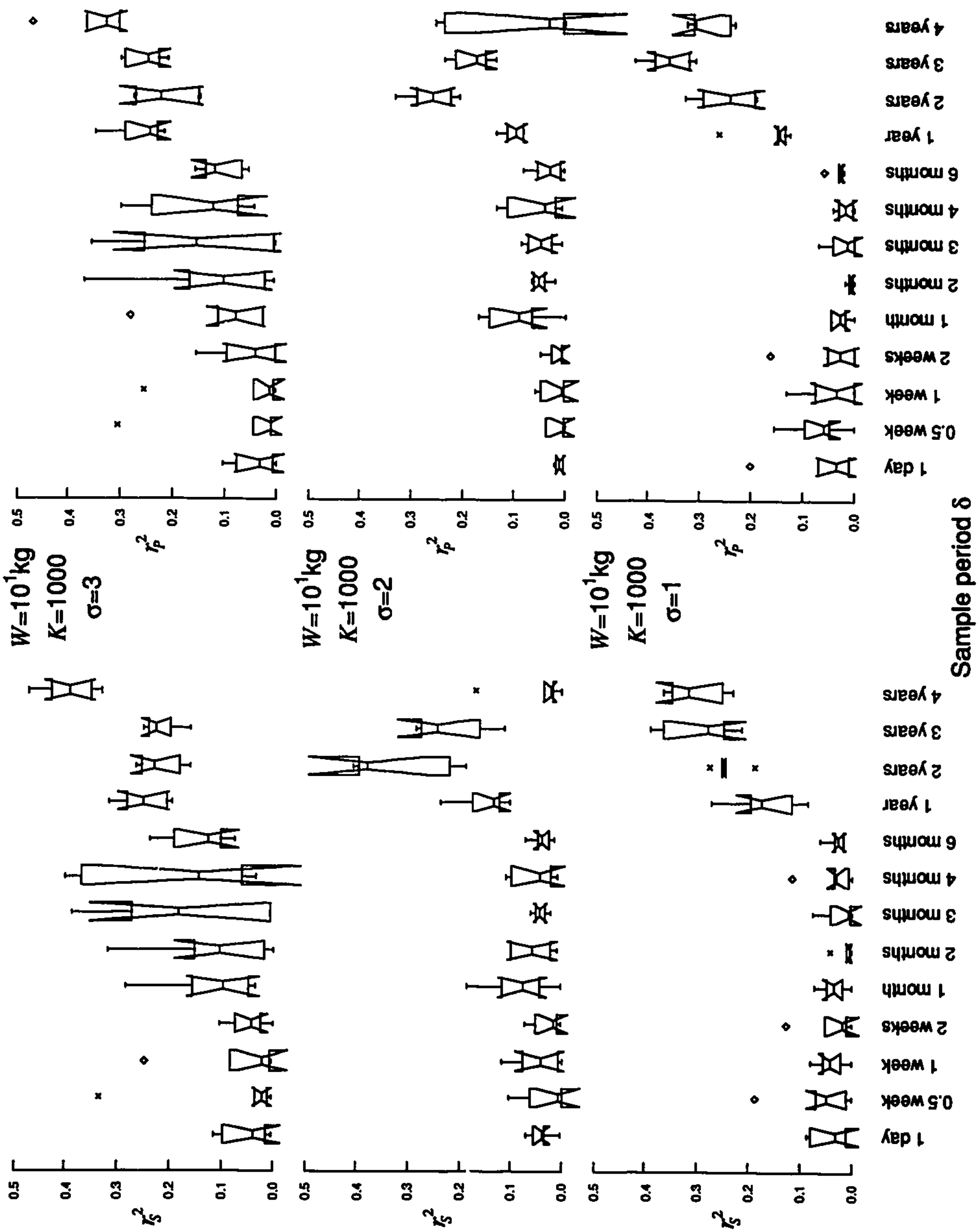

W=10^0kg
K=100,000
σ=3
W=10^0kg
K=100,000
σ=2
W=10^0kg
K=100,000
σ=1
r_p^2
r_s^2
0.0
0.1
0.2
0.3
0.4
0.5
1 day
0.5 week
1 week
2 weeks
1 month
2 months
3 months
4 months
6 months
1 year
2 years
3 years
4 years
Sample period δ

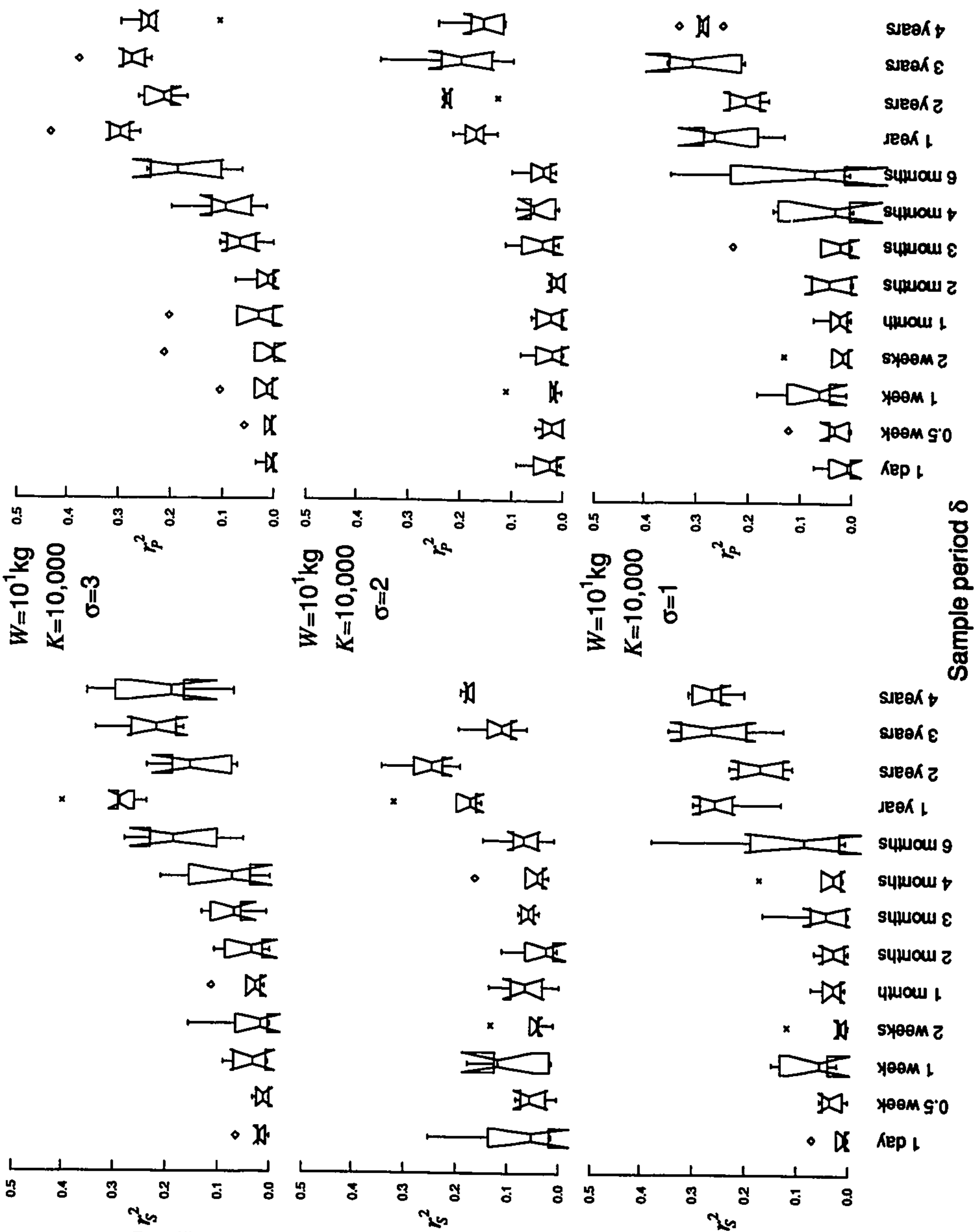
FIGURE E.13 The distributions of the r_S^2 or r_P^2 statistics for the 10^1 kg populations corresponding to the time-slices presented in Figure E.6. This figure consists of three panels *a*, *b* and *c* on the next three pages, respectively. Every panel presents 3 pairs of graphs, one above the other. Each of the 9 pairs of graphs, of all three panels, show notched-box plots of the r_S^2 or r_P^2 statistics calculated for each randomly selected time-slice in Figure E.6. Each pair of graphs corresponds to the different combinations of the carrying capacity K and the standard deviation σ of the random variable X in model (3.4) used to produce the time-slices of Figure E.6. Panels *a*, *b* and *c* show the combinations with $K = 1000, 10{,}000$ and $100{,}000$ respectively. The top pair of graphs on each panel correspond to the time-slices with $\sigma = 3$, while the middle and bottom pairs of graphs correspond to the time-slices with $\sigma = 2$ and $\sigma = 1$ respectively. Every graph is composed of 13 notched-box plots one for each of the 13 sampling periods δ discussed in the methods. If the notches (the diagonal lines extending from the median to the vertical sides of a box) of two medians do not overlap, then the medians can be considered to be significantly different ($p \leq 0.05$). The hollow diamonds and ×'s identify outliers within each distribution. The diamonds are points that lie between 1.5 times and 3.0 times the interquartile distance outward from the hinges of the notched box and the ×'s are outliers beyond this range (Wilkinson et al. 1992).

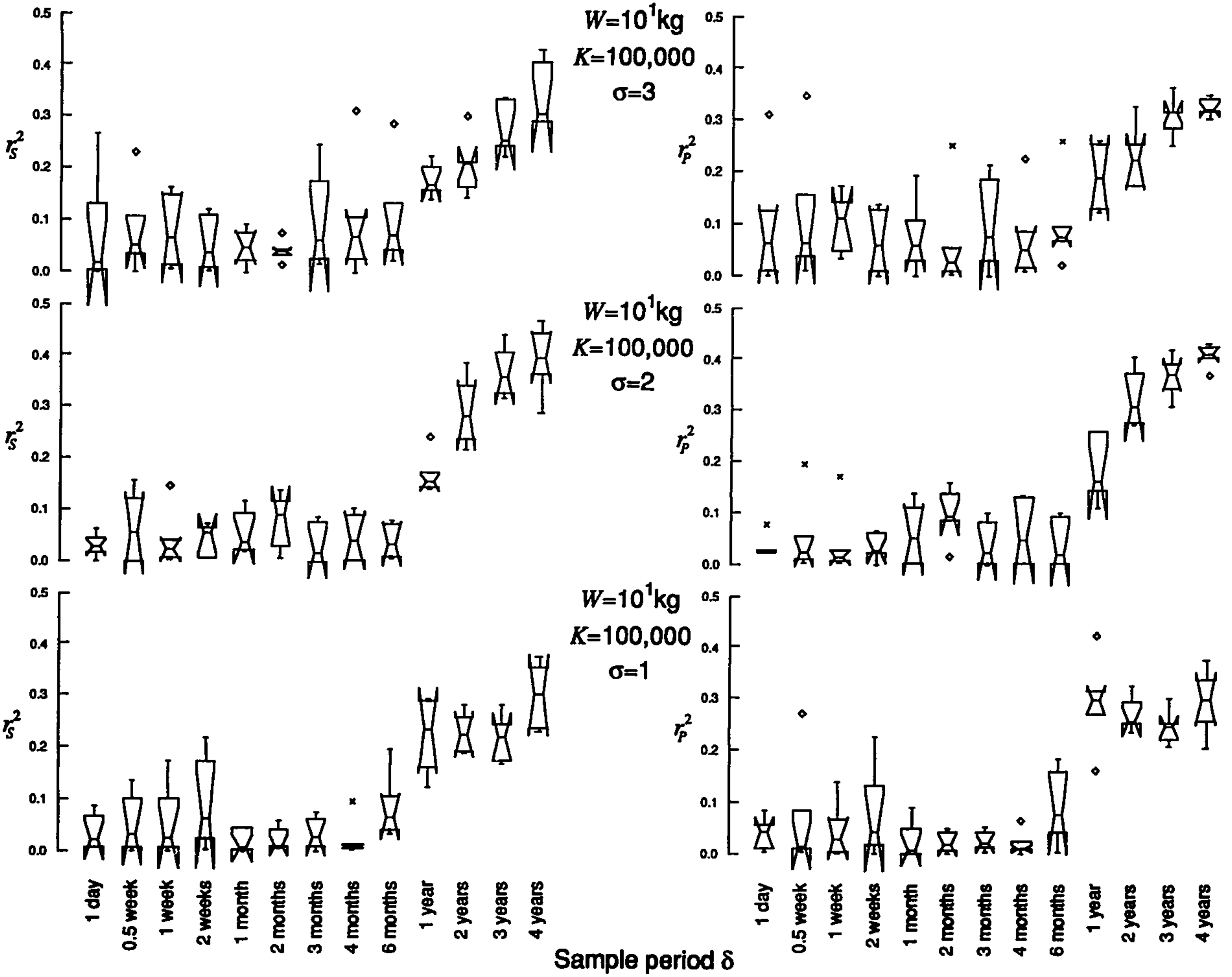
panel a



W=10^1kg
K=1000
σ=3
W=10^1kg
K=1000
σ=2
W=10^1kg
K=1000
σ=1
r_P^2
r_S^2
0.0
0.1
0.2
0.3
0.4
0.5
1 day
0.5 week
1 week
2 weeks
1 month
2 months
3 months
4 months
6 months
1 year
2 years
3 years
4 years
Sample period δ

panel b

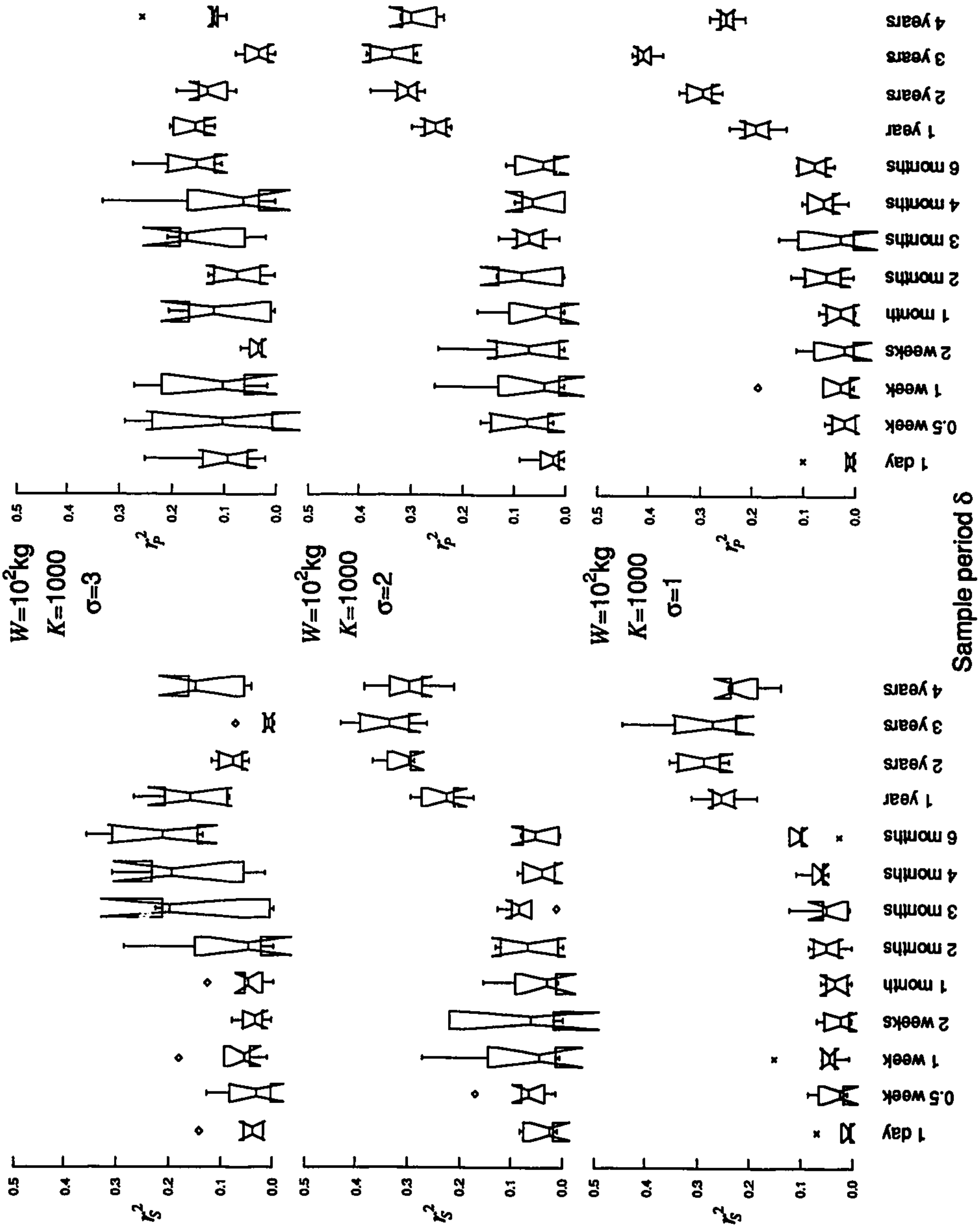

W=10^1kg
K=10,000
σ=3
W=10^1kg
K=10,000
σ=2
W=10^1kg
K=10,000
σ=1
r_p^2
r_S^2
0.5
0.4
0.3
0.2
0.1
0.0
1 day
0.5 week
1 week
2 weeks
1 month
2 months
3 months
4 months
6 months
1 year
2 years
3 years
4 years
Sample period δ

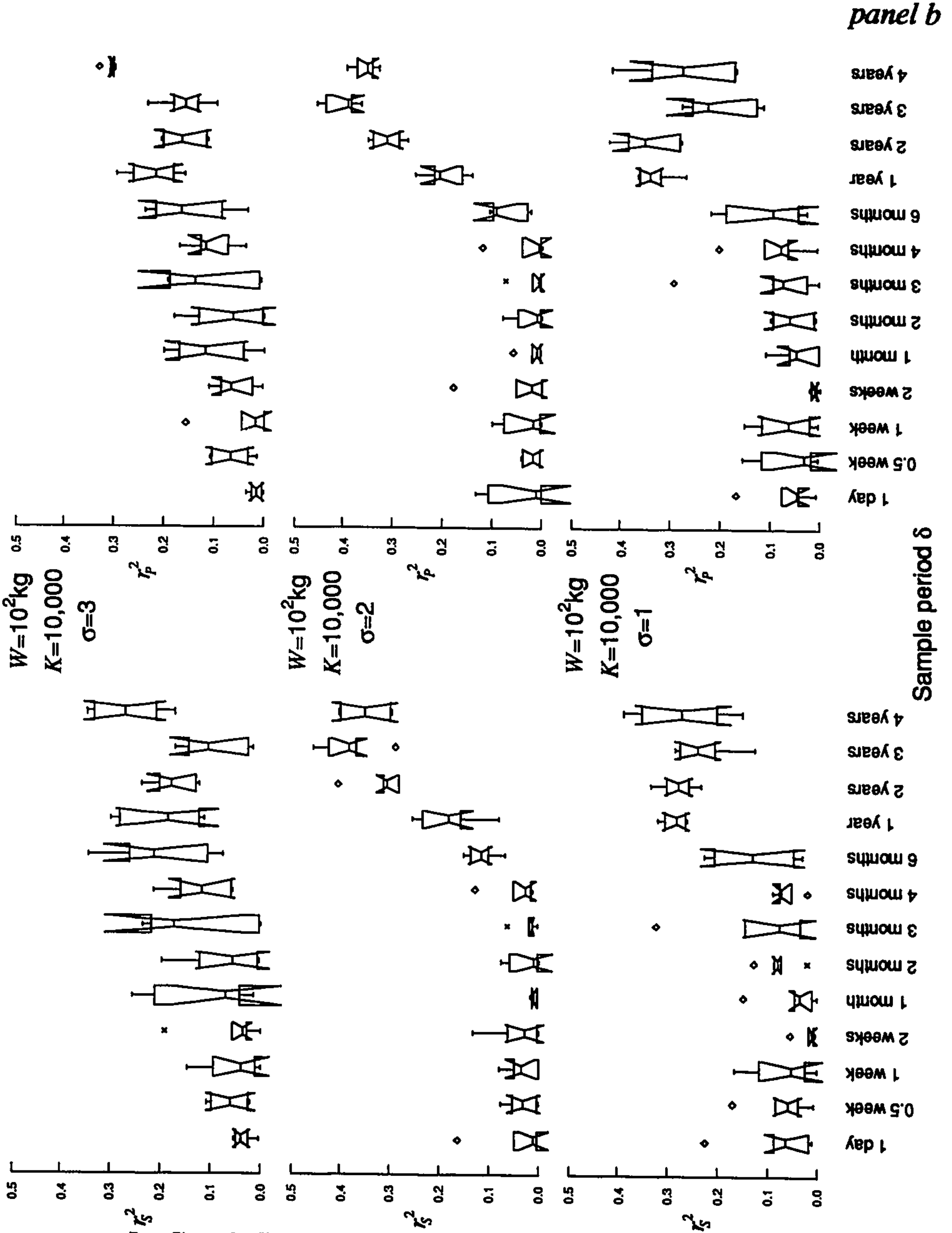

W=10^{1}kg
K=100,000
σ=3
W=10^{1}kg
K=100,000
σ=2
W=10^{1}kg
K=100,000
σ=1
r_S^2
r_P^2
0.0
0.1
0.2
0.3
0.4
0.5
1 day
0.5 week
1 week
2 weeks
1 month
2 months
3 months
4 months
6 months
1 year
2 years
3 years
4 years
Sample period δ

panel c

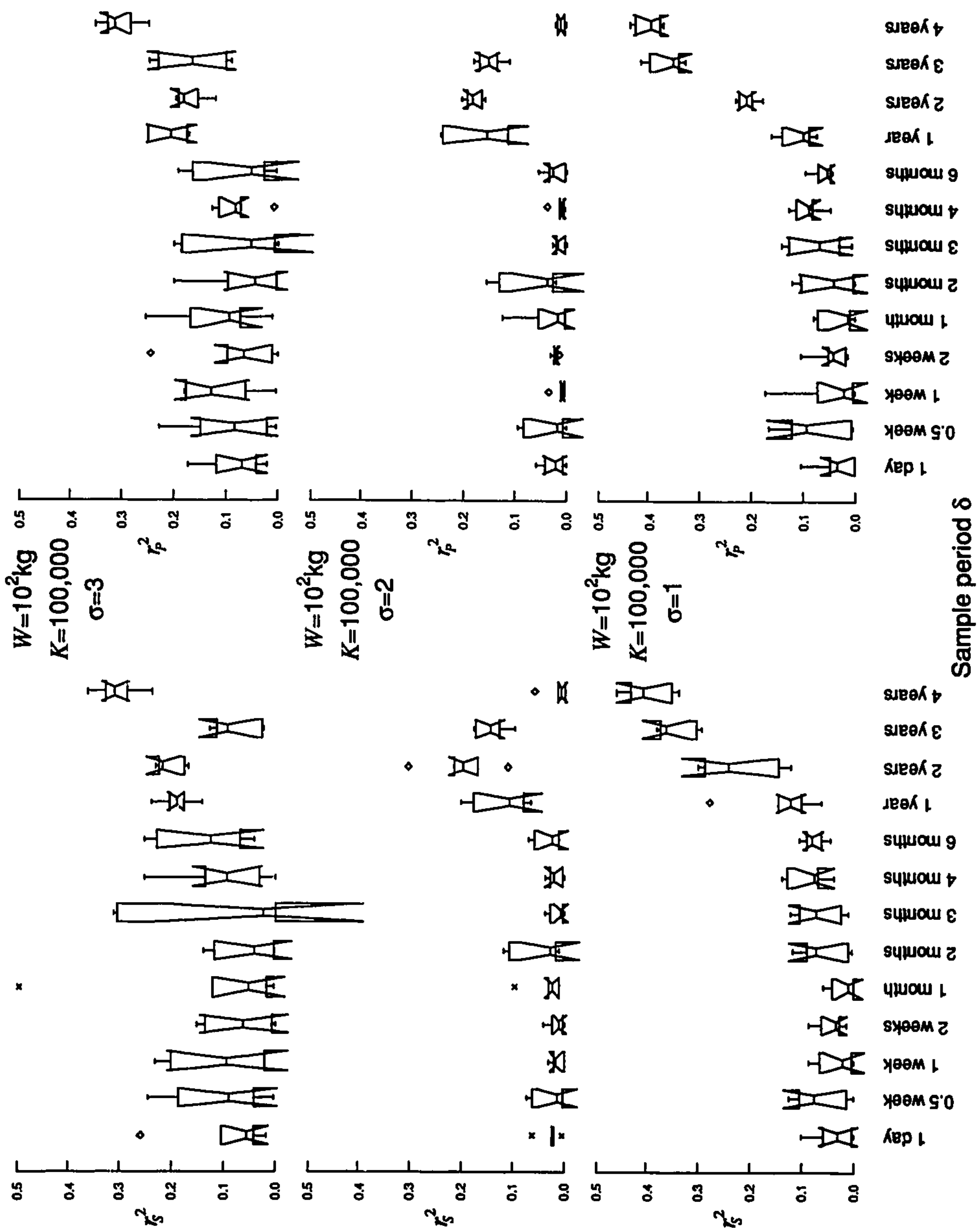
FIGURE E.14 The distributions of the r_S^2 or r_P^2 statistics for the 10^2 kg populations corresponding to the time-slices presented in Figure E.7. This figure consists of three panels *a*, *b* and *c* on the next three pages, respectively. Every panel presents 3 pairs of graphs, one above the other. Each of the 9 pairs of graphs, of all three panels, show notched-box plots of the r_S^2 or r_P^2 statistics calculated for each randomly selected time-slice in Figure E.7. Each pair of graphs corresponds to the different combinations of the carrying capacity K and the standard deviation σ of the random variable X in model (3.4) used to produce the time-slices of Figure E.7. Panels *a*, *b* and *c* show the combinations with $K = 1000$, 10,000 and 100,000 respectively. The top pair of graphs on each panel correspond to the time-slices with $\sigma = 3$, while the middle and bottom pairs of graphs correspond to the time-slices with $\sigma = 2$ and $\sigma = 1$ respectively. Every graph is composed of 13 notched-box plots one for each of the 13 sampling periods δ discussed in the methods. If the notches (the diagonal lines extending from the median to the vertical sides of a box) of two medians do not overlap, then the medians can be considered to be significantly different ($p \leq 0.05$). The hollow diamonds and ×'s identify outliers within each distribution. The diamonds are points that lie between 1.5 times and 3.0 times the interquartile distance outward from the hinges of the notched box and the ×'s are outliers beyond this range (Wilkinson et al. 1992).

panel a


W=10^2kg
K=1000
σ=3
W=10^2kg
K=1000
σ=2
W=10^2kg
K=1000
σ=1
r_P^2
r_S^2
0.5
0.4
0.3
0.2
0.1
0.0
1 day
0.5 week
1 week
2 weeks
1 month
2 months
3 months
4 months
6 months
1 year
2 years
3 years
4 years
Sample period δ


panel b
Sample period δ
W=10^2kg
K=10,000
σ=1
σ=2
σ=3
r_S^2
r_P^2
0.0
0.1
0.2
0.3
0.4
0.5
1 day
0.5 week
1 week
2 weeks
1 month
2 months
3 months
4 months
6 months
1 year
2 years
3 years
4 years

panel c



r_S^2
r_P^2
0.0
0.1
0.2
0.3
0.4
0.5
1 day
0.5 week
1 week
2 weeks
1 month
2 months
3 months
4 months
6 months
1 year
2 years
3 years
4 years
$W=10^2$kg
K=100,000
σ=3
σ=2
σ=1
Sample period δ

APPENDIX A: Methodological Elaborations

The format of this appendix consists of a number of loosely related sections whose headings are referred to in chapter 2. Each section elaborates on some methodological point or consideration in chapter 2.

Monotonicity

A function is a *strict decreasing monotonic* function, if for any 2 values x_1 and x_2, $f(x_2) < f(x_1)$ when $x_2 > x_1$. To be mathematically precise, a function that satisfies the condition $f(x_2) \leq f(x_1)$ when $x_2 > x_1$ is called a *non-increasing* function. In this thesis I am referring to the, less strict, non-increasing definition when I refer to a negative monotonic, or a decreasing monotonic function or relationship.

Density-vagueness

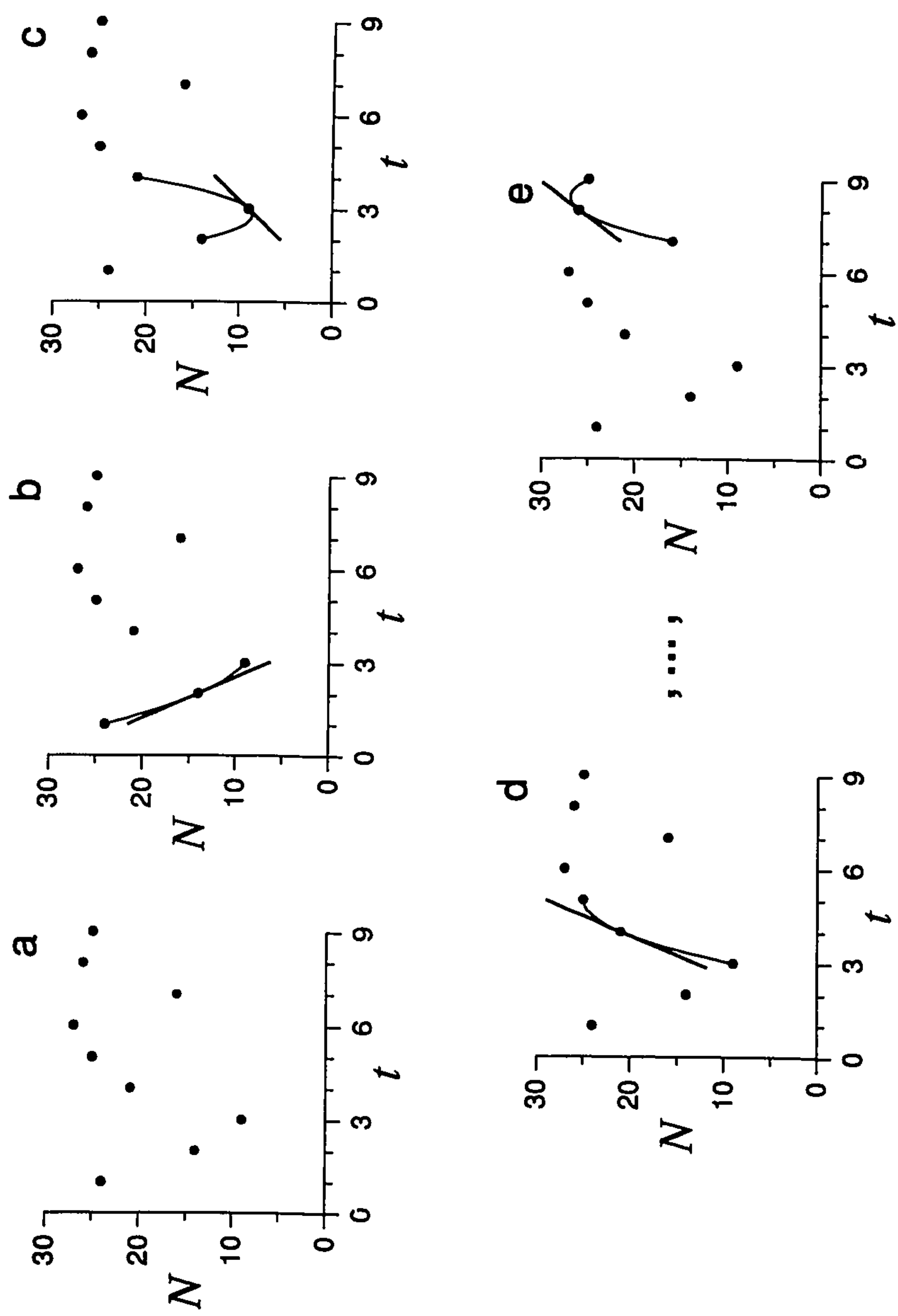
Donald Strong suggested that LOWESS techniques be used to study density-dependent relationships between γ and N in his paper discussing the concept of density-vagueness (Strong, 1986). In chapter 2, LOWESS curves were fit to the data until a negative monotonic relationship between γ and N was achieved. As discussed in the preceding section, successive equal values in the sequence of LOWESS predicted γ's would satisfy the non-increasing criteria imposed in chapter 2. Using the non-increasing function criteria, rather than the strict decreasing monotonic constraints, allows for possible plateaus in the γ versus N relationship. In this way, the r_P^2 analysis of chapter 2 incorporates the medial-plateau aspect of Strong's density-vagueness concept (see the lower panel of figure 1; Strong, 1986). I chose this approach because it permits a more liberal estimate of r_P^2 than would be obtained if strict decreasing monotonicity was required.

Calculation of per capita growth rate

Figure A.1 illustrates the procedure outlined in chapter 2 used to calculate the per capita growth rate γ. Panel a of Figure A.1 shows an example time series of population densities spanning 9 years. In panel b, the curved line represents the 2nd degree polynomial (i.e., a quadratic) fit to the first 3 points (i.e., the 1st, 2nd & the 3rd) in the time series. The straight line in Figure A.1(b) is the tangent to the quadratic at the middle point of the first 3 points— the 2nd point in the time series. The slope of this tangent is the rate of change in population density for the 2nd population point in the time series. In this case $\left.\frac{dN}{dt}\right|_{t=2} = -7.5$. To determine the per capita rate of population change or growth, the slope of the tangent is divided by the value of the middle N, the 2nd point in the series. So for this case, $\gamma = \left.\frac{dN}{dt}\cdot\frac{1}{N}\right|_{t=2} = -0.54$. Thus for the 2nd point in the time series a corresponding γ is calculated.

FIGURE A.1 Estimation of the per capita growth rate. This figure is a pictorial representation of the method (outlined in chapter 2) used to calculate the per capita growth rates for the population densities of a population time series. N is the population size at time t in years. Refer to the "Calculation of per capita growth rate" section on page A.2.

Calculation of per capita growth rate



Similarly, in Figure A.1(c) a quadratic is fit to the 2nd, 3rd and the 4th population points in the time series and a γ is calculated for the 3rd density in the time series. This process is repeated for the next 3 points (the 3rd, 4th and 5th points, Figure A.1(d)) and so on until the last 3 points (the 7th, 8th & 9th, Figure A.1(e)) in the series.

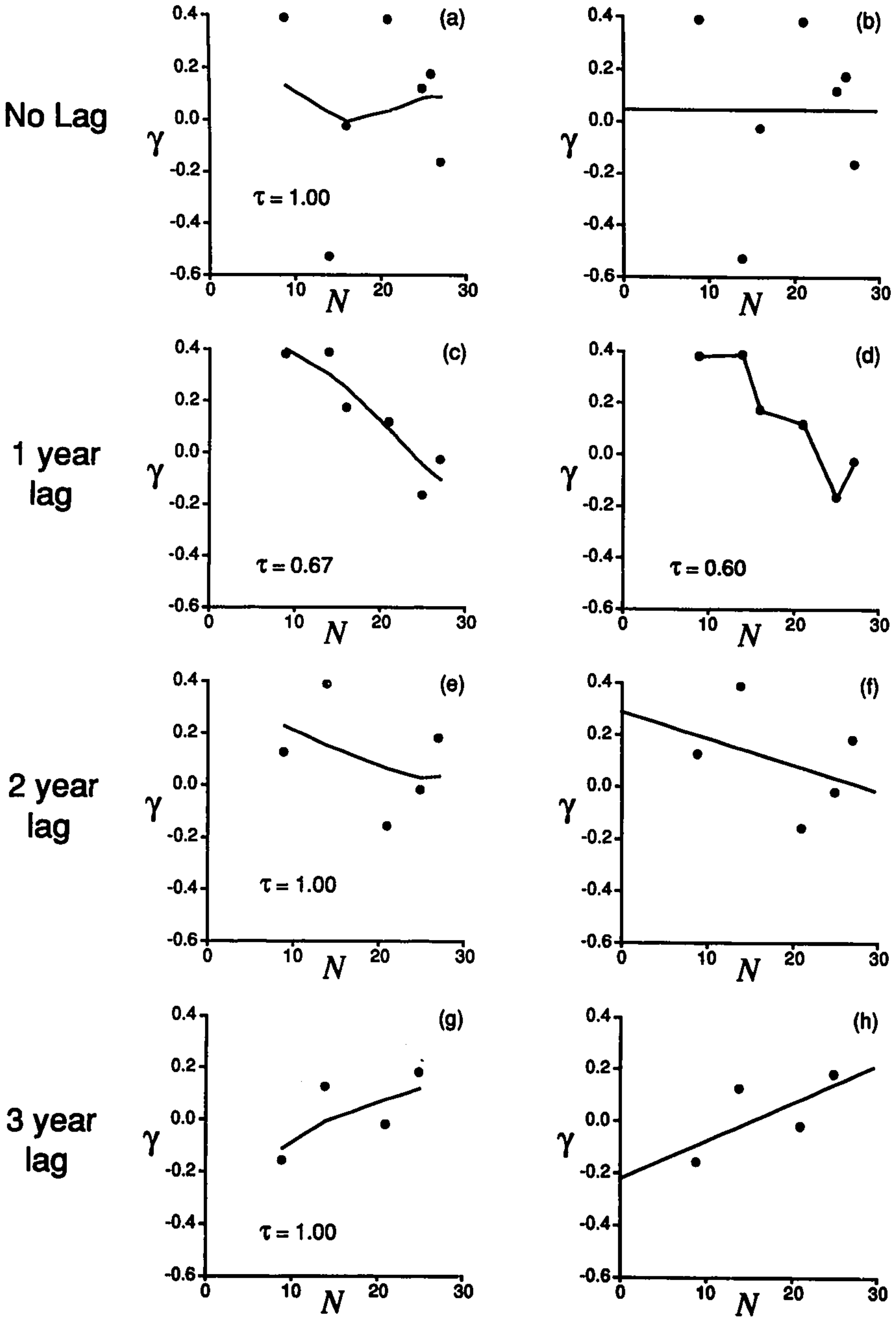
In this way γ's are calculated for the 2nd through 8th population densities in the example time series. Note that no γ is calculated for the initial and final points in the time series because there isn't a preceding or following point permitting the fitting of a quadratic to 3 points.

Lags

The 7 (N,γ) points generated from the example data set of Figure A.1 are shown in the top graphs labelled No lag in Figure A.2. Ignore, for the purposes of this section, the curves and lines shown on each graph in Figure A.2. As well, ignore the right column of graphs (panels b, d, f and h) and focus only on the left column (panels a, c, e and g). Proceeding from the topmost graph (panel a) down to the bottom graph (panel g) the set of (N,γ) points is progressively lagged by one year.

The set of 6 (N,γ) points in the 1 year lag graph (Figure A.2(c)) was produced by associating each γ with the previous years N. For example, the γ calculated for the 3rd point in the example time series (Figure A.1(c) is paired with the 2nd N-point in

FIGURE A.2 Estimation of $f(N)$. This figure depicts the steps (outlined in chapter 2) to create lagged sets of (N,γ) using the example time series of Figure A.1. The fitting of LOWESS curves and regressions to estimate $f(N)$ is also shown. For detailed explanations of this figure, see the sections titled: "Lags" on page A.5; "Estimating $f(N)$" on page A.8; "Pearson correlation" on page A.10; and "Spearman correlation" on page A.10. (N is the population density, γ is the per capita growth rate and τ is the LOWESS smoothing or tension parameter.)


No Lag
1 year lag
2 year lag
3 year lag
(a)
(b)
(c)
(d)
(e)
(f)
(g)
(h)
γ
N
0.4
0.2
0.0
-0.2
-0.4
-0.6
0
10
20
30
τ = 1.00
τ = 0.67
τ = 0.60
τ = 1.00
τ = 1.00

the time series. Doing this for each point produces a set of 6 (N,γ) points lagged by 1 year (Figure A.2(c)). The 2 lower left graphs, Figure A.2(e) and Figure A.2(g), were created by associating each γ with an N 2 and 3 years previous, respectively.

The 4 leftmost graphs in Figure A.2 represent the "lagged data sets" or "lagged sets" (as they are referred to in chapter 2) for the example data time series (Figure A.1).

Estimating *f*(*N*)

This section addresses how the function $f(N)$ describing the relationship between γ and N is estimated by continuing the example described in the previous 2 sections.

The collection of 4 lagged sets of (N,γ) that were produced from the example time series (Figure A.1) are shown in Figure A.2. Horizontal pairs of panels in Figure A.2 (i.e., panels a and b; or c and d; or e and f; or g and h) each show the same set of (N,γ) data. The leftmost graphs (Figure A.2, panels a, c, e, and f) show the LOWESS curve fit to each of the lagged sets. Figure A.2(b), (f) and (h) show the linear regressions that were also fit to these lagged sets. Figure A.2(d) is the exception with another LOWESS curve that I will use to illustrate a point below.

As described in chapter 2, $f(N)$ is estimated by fitting a LOWESS curve to each of the lagged sets of (N,γ) with the minimum LOWESS smoothing tension parameter τ that produces a LOWESS curve satisfying the decreasing monotonic requirement of the population regulation hypothesis. The values of τ that were used were multiples of

0.01. In the example discussed in this appendix only one of the lagged sets produced a negative monotonic curve (Figure A.2(c)). The other 3 sets of (N,γ) points, after being maximally smoothed with $\tau = 1.00$, either show a decreasing and increasing relationship between γ and N (Figure A.2(a)); a predominantly decreasing relationship but with a slight increase at the end (Figure A.2(e)); or an increasing relationship shown in Figure A.2(g). For each of the 3 non-negative monotonic relationships a linear regression was then fit to see if a negative linear relationship could be achieved. For the non-lagged set of (N,γ) points (Figure A.2(b)) a zero-slope regression was found whereas a negative linear relationship was obtained for the 2 year lagged data (Figure A.2(f)). In contrast to these 2 regressions, a positive linear regression was obtained for the data lagged 3 years (Figure A.2(h)). The LOWESS curve of Figure A.2(c) and the regression shown in Figure A.2(f) represent the 2 lagged sets of the (N,γ) points that have the form of the relationship required by the regulation hypothesis.

Panel d of Figure A.2 was included to illustrate how the value of τ affects the LOWESS curve fit to the data. τ varies from 0 to 1 and produces a progressively smother curve through the data. Figure A.2(d) was smoothed with a $\tau = 0.60$ producing a curve that, essentially, joins the dots. Though this fit would produce a correlation of 1 between the observed γ's (plotted points, solid circles in Figure A.2) and the LOWESS predicted γ's (points on the LOWESS curve), it is not the negative monotonic relationship required by the regulation hypothesis. The minimal value of τ

that achieved decreasing monotonicity for the same data was 0.67 (Figure A.2(c)). The minimum value of τ was used because the resulting curve maximized the correlation between the observed and predicted values of γ.

Pearson correlation

A Pearson correlation r_P is calculated between the observed γ's and the predicted γ's for Figure A.2(c) and Figure A.2(f). The larger of the these two correlations (in this case the r_P calculated from Figure A.2(c)) is retained to be adjusted by the randomization procedure for the effect of any spurious correlation (described by Note 20 in chapter 2 on page 2.14).

Spearman correlation

The Spearman rank correlation r_S is calculated between the observed γ's and the population densities N for each lagged set (Figures A.2(a), A.2(c), A.2(e) and A.2(g)). The smallest of the these correlations (in this case the r_S calculated from Figure A.2(c)) is retained to be adjusted by the randomization procedure for the effect of any spurious correlation (described by Note 20 in chapter 2 on page 2.14).

Randomization procedure

The randomization procedure to determine the correlation coefficients that you would expect in the absence of density dependence (discussed in Note 20 of chapter 2 on page 2.14) consists of a randomizing the data and then repeating the procedures outlined in the previous 4 sections.

Continuing the example above, a single randomization step consists of randomizing the set of 7 (N,γ) points in Figure A.2(a) by randomly sampling the γ values without replacement and associating each selected γ to a N value that was also selected randomly without replacement. As discussed above, lagged sets are produced; $f(N)$'s are estimated; Pearson and Spearman correlations are calculated; and the largest and smallest correlation coefficients, respectively, are retained. This randomization step is repeated 499 times. The average of the 499 random Pearson correlations and the average of the 499 random Spearman correlations are subtracted, respectively, from the unrandomized r_P and r_S, of the preceding section. If the unrandomized r_P was less than the mean random Pearson correlation, the adjusted r_P was considered to be zero. Similarly, if the unrandomized r_S was larger than the mean random Spearman correlation, the adjusted r_S was considered to be zero.

The adjusted correlations were then squared to calculate the two coefficients of determination, r_P^2 and r_S^2, referred to throughout this thesis.

APPENDIX B: Unique Species Analysis

Introduction

Many of the 303 populations in chapter 2 are populations with identical species (see Table C.1 on page C-2 for examples). If there was an over-representation of any particular species it is possible that the results of chapter 2 could be skewed. For example, consider the hypothetical scenario in which the 93 insect populations in chapter 2 consist of 72 populations of *Bupalus piniarius*, 17 of *Choristoneura fumiferana* and 4 *Dendrolinus pini*. Any inferences made concerning the class Insecta in this scenario are more likely to reflect characteristics of *Bupalus piniarius* than *Choristoneura fumiferana* or *Dendrolinus pini* or even insects in general. Similarly there could be a disproportionate number of duplicate species in one taxa versus another which may also affect the conclusions drawn in chapter 2.

Continuing the extreme scenario above, assume that 82 of the 88 bird populations are different species with 2 species having 3 and 5 "replicate" populations. The dispersion of the distribution of r_S^2 and r_P^2 values for the insects may be small due to the large number of replicate populations of *Bupalus piniarius*. Whereas the dispersion of r_S^2 and r_P^2 of the bird populations may be much broader than the insects because of the greater number of species present in the Aves populations. This could affect the conclusions made regarding differences in the distributions of r_S^2 and r_P^2 between taxonomic classes in chapter 2.

This appendix presents the results of chapter 2 from a "unique species" perspective to see how chapter 2's conclusions may have been affected by multiple populations of any particular species.

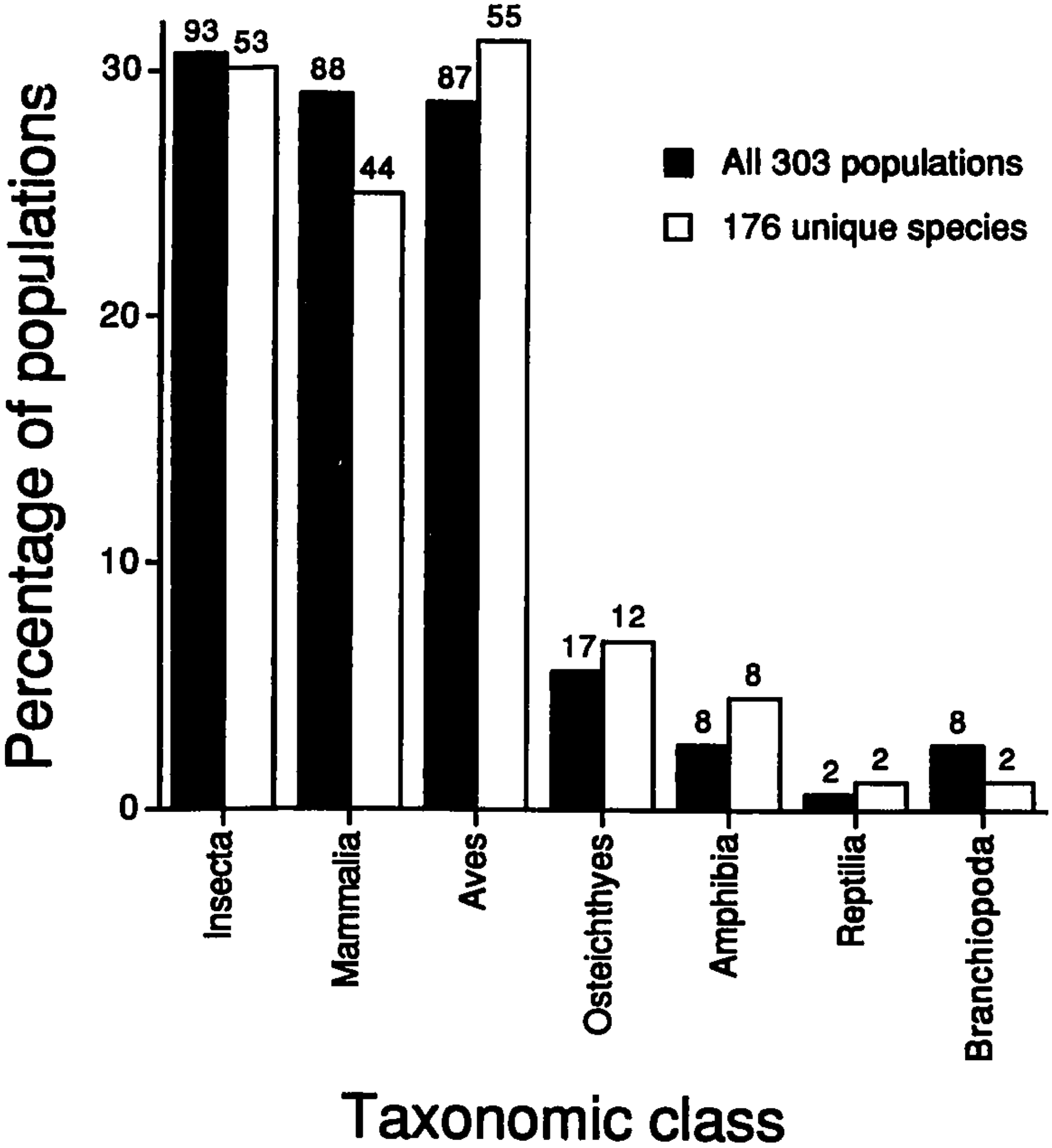
Methods

Using the results of chapter 2 (Table C.1 on page C-2) all populations consisting of identical species were grouped together. From each group of identical species the population with the largest values of r_S^2 and r_P^2 was selected. Thus the set of all such selected populations is a subset of the 303 populations consisting solely of unique species. This "unique species" subset was used to recreate the figures of chapter 2 as well as one additional figure.

Results and discussion

Figure B.1 displays the frequency distributions (as well as the absolute counts) of the number of populations and number of species within each taxonomic class. Note that the relative proportion of populations within taxa is similar to the proportion of species within taxa. This suggests that there is no relative over-representation of any species within any specific class.

FIGURE B.1 The percentage frequency distributions of 303 animal populations and 176 species within broad taxonomic groups. The height of each black bar indicates the proportion of the 303 populations within each taxonomic group. The height of each white bar indicates the proportion of the 176 unique species within each taxonomic group. The numbers above each bar denote the absolute number of populations (black bars) or species (white bars) in each taxonomic group.


Percentage of populations
0
10
20
30
93
53
88
44
87
55
17
12
8
8
2
2
8
2
■ All 303 populations
□ 176 unique species
Insecta
Mammalia
Aves
Osteichthyes
Amphibia
Reptilia
Branchiopoda
Taxonomic class

Results and discussion

Figures B.2, B.3, B.4 and B.5 correspond to Figures 2.1, 2.2, 2.3 and 2.4 respectively. Both sets of figures display similar patterns (with one minor exception) suggesting that the conclusions and inferences made in chapter 2 were not affected by any over-representation of any particular species.

The one difference occurs in Figure B.5, in which the LOWESS curves show a more prominent increase in r_S^2 and r_P^2 as the number of years in a data set increases, when compared visually with Figure 2.4.

FIGURE B.2 Histogram of two estimates (r_S^2 and r_P^2) of the percentage of the temporal variability in the per capita growth rate (γ) attributable to density-dependent processes for 176 unique species animal populations. The height of each bar indicates the proportion of the 176 populations with r_S^2 or r_P^2 estimates within the % categories on the x-axis. The numbers above each bar denote the number of species in each % class. The highest r_S^2 and r_P^2 observed among all populations for each species were used to develop this figure.

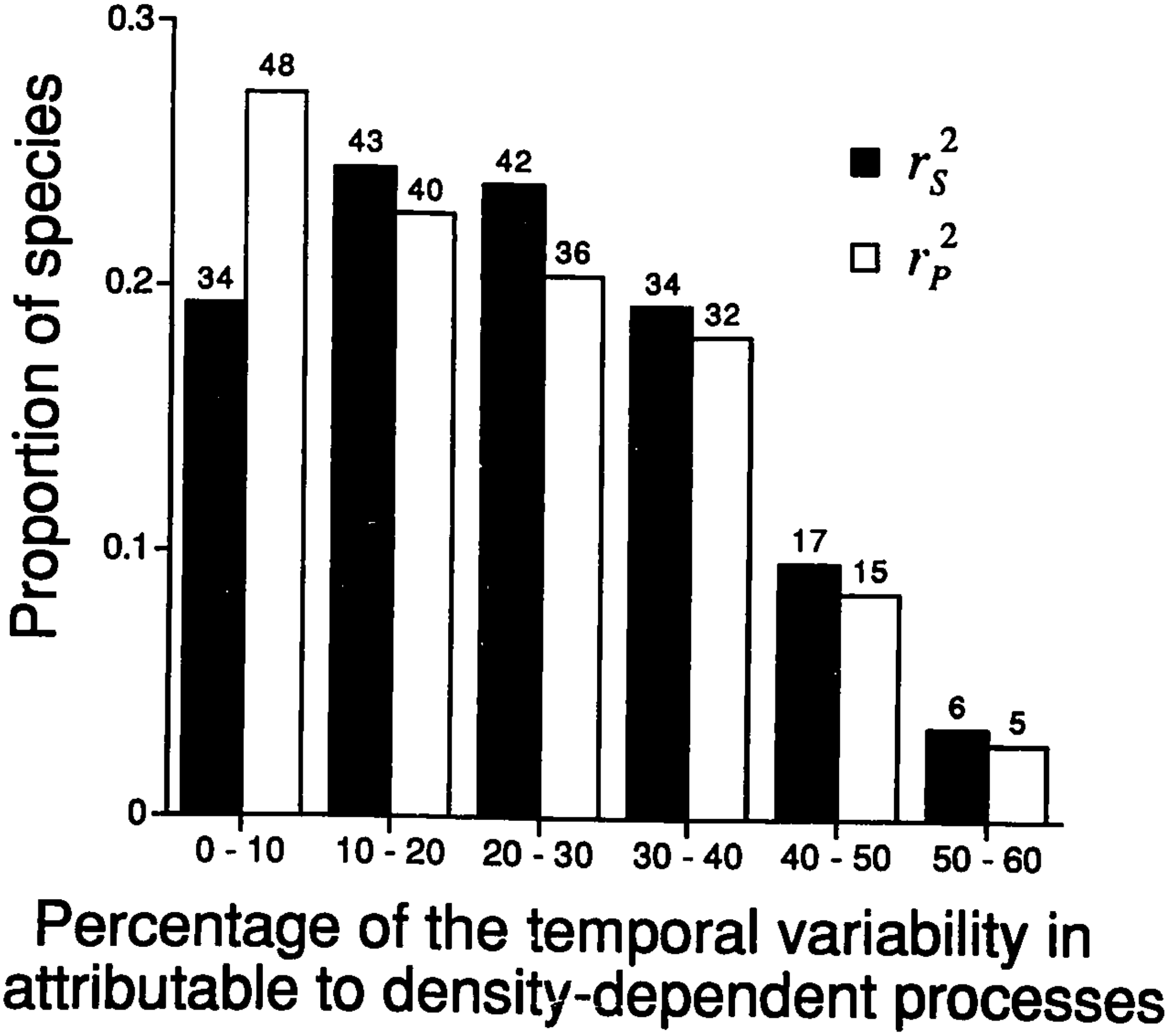

Proportion of species
0.3
0.2
0.1
0
48
43
40
42
36
34
34
32
17
15
6
5
■ r_S^2
□ r_P^2
0 - 10
10 - 20
20 - 30
30 - 40
40 - 50
50 - 60
Percentage of the temporal variability in attributable to density-dependent processes

FIGURE B.3 Notched box plots of the distributions of r_S^2 (panel *a*) and r_P^2 (panel *b*) within animal classes. (Refer to Figure 2.2 on page 2-18 for an explanation of this type of graph.) There were only two values for the reptilia and branchiopoda categories, so notched box plots were not possible. Instead, both points were plotted (•) and their median shown with a horizontal line. Excluding the impossible reptilia and branchiopoda comparisons, the amount of variance attributable to density-dependent factors does not vary among animal classes.

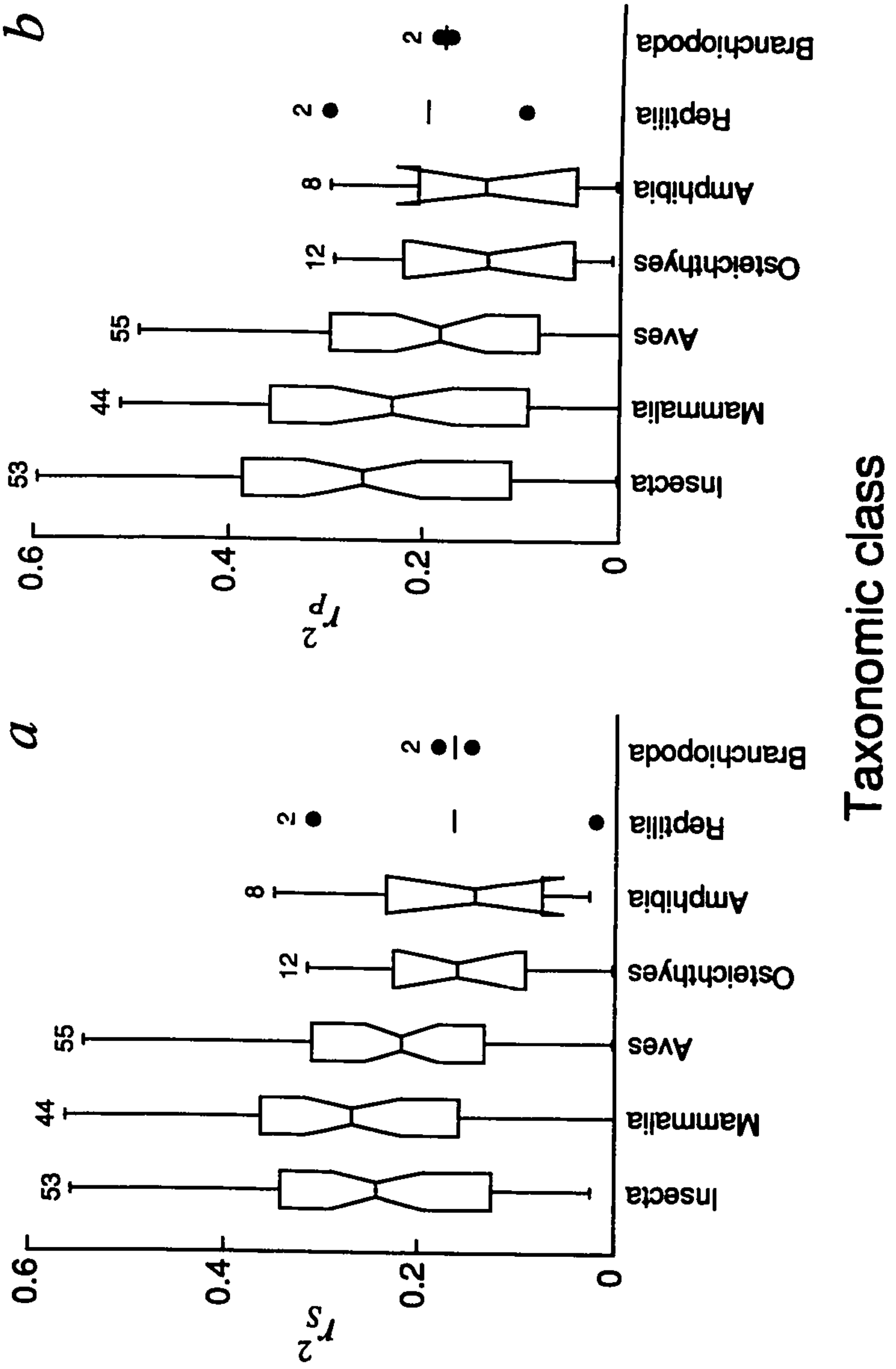

a
r_S^2
0.6
0.4
0.2
0
53
44
55
12
8
2
2
Insecta
Mammalia
Aves
Osteichthyes
Amphibia
Reptilia
Branchiopoda
b
r_P^2
0.6
0.4
0.2
0
53
44
55
12
8
2
2
Insecta
Mammalia
Aves
Osteichthyes
Amphibia
Reptilia
Branchiopoda
Taxonomic class

FIGURE B.4 A histogram showing the proportion of 176 species for which the highest r_S^2 & r_P^2 obtained after lagging the data for the number of years represented on the abscissa. Note that the majority of populations (109 (62%) or 97 (55%) of 176) showed direct density dependence while 67 (38%) or 75 (43%) displayed evidence of delayed density dependent regulation.

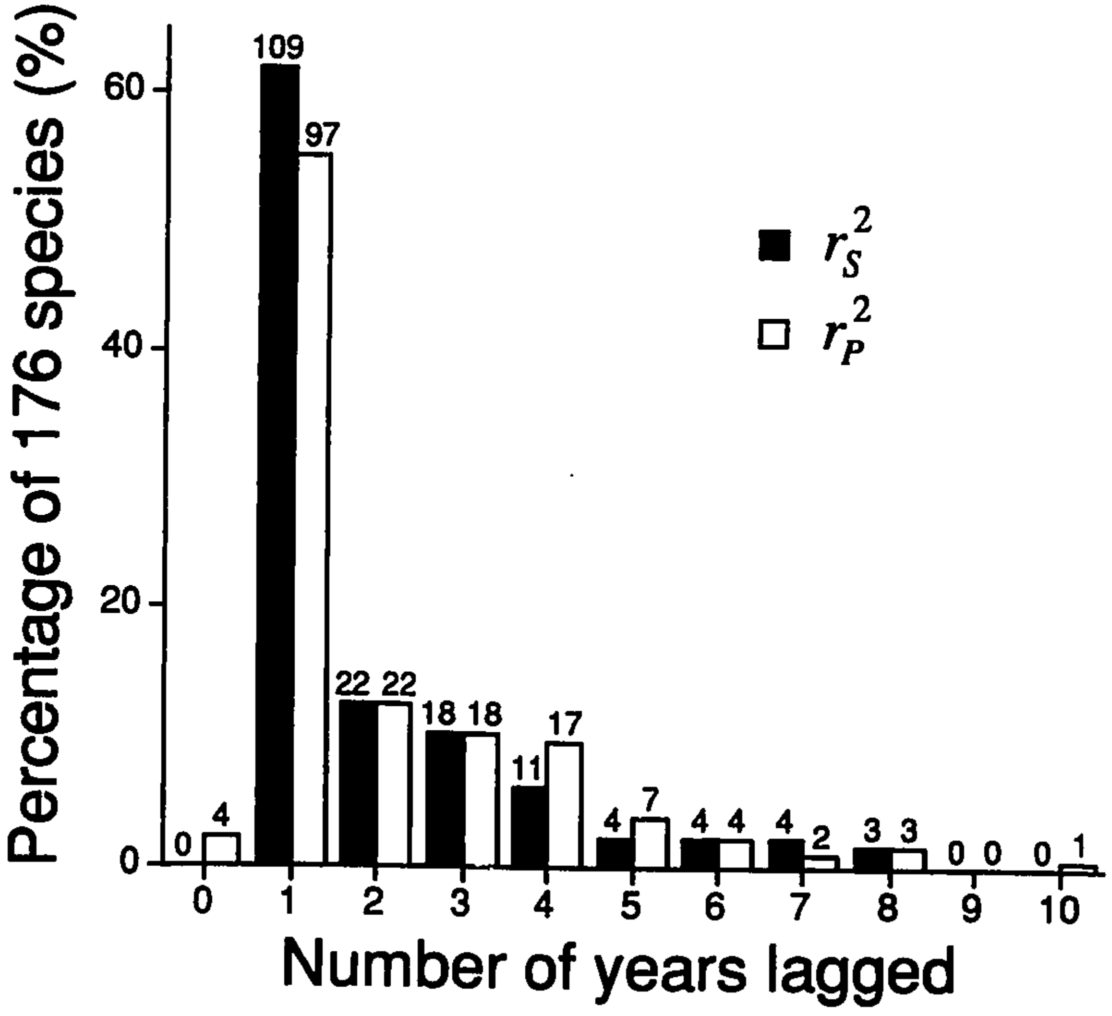
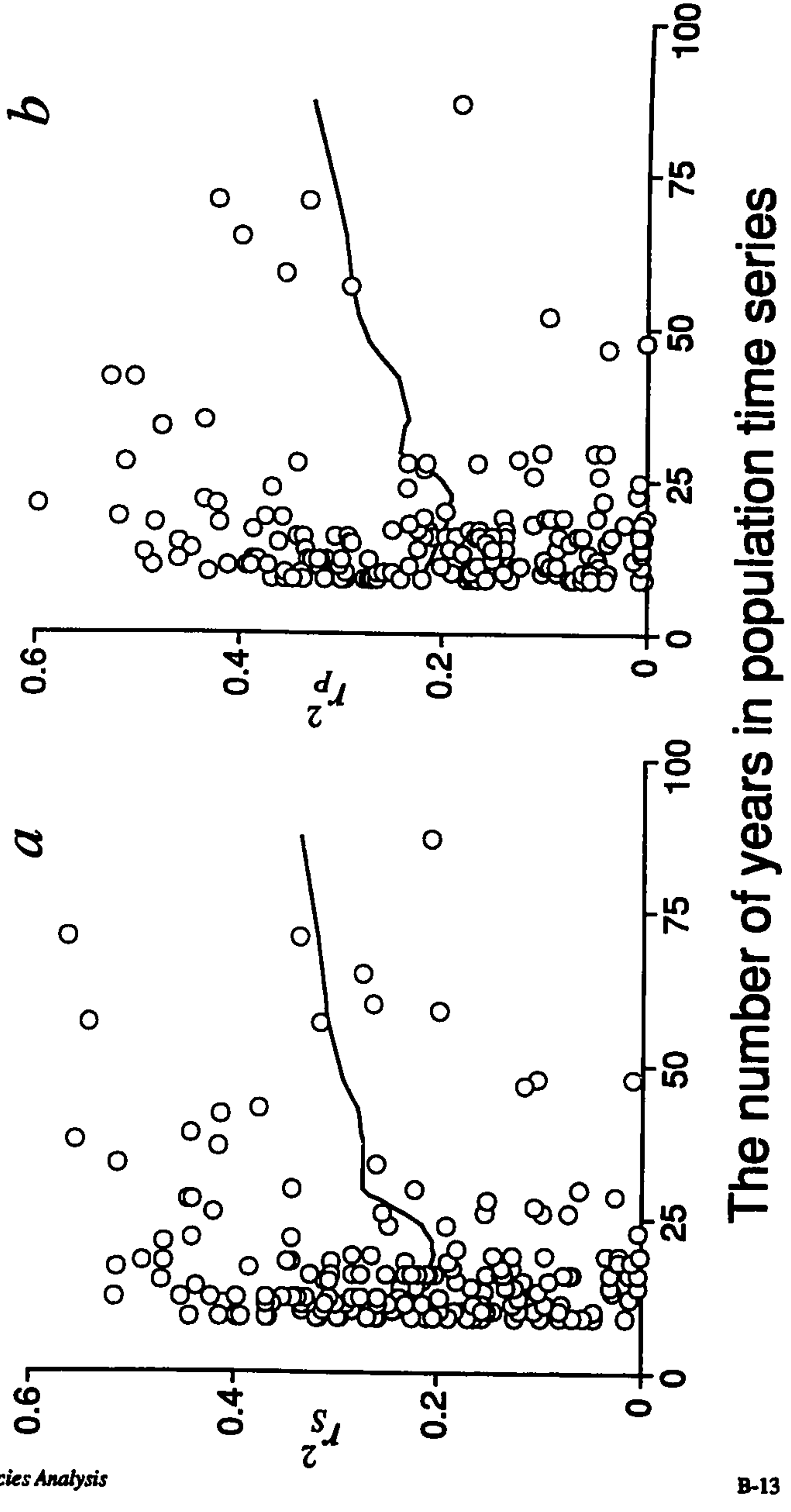

Percentage of 176 species (%)
60
40
20
0
Number of years lagged
0
1
2
3
4
5
6
7
8
9
10
■ r_S^2
□ r_P^2
0
4
109
97
22
22
18
18
11
17
4
7
4
4
4
2
3
3
0
0
0
1

FIGURE B.5 LOWESS-smoothed plots of the percentage of the temporal variability in the per capita growth rate γ attributable to density-dependent processes, r_S^2 (panel *a*) and r_P^2 (panel *b*), versus the number of years of data within each population abundance time series. Both LOWESS curves (McGill et al. 1978) were fit with a tension of 0.9.


a
b
r_s^2
r_p^2
0.6
0.4
0.2
0
0
25
50
75
100
The number of years in population time series

APPENDIX C: Population Data Sources and Analysis Results

Table C.1: The analysis results from chapter 2. For detailed explanations of the terminology and symbols used refer to the methods in chapter 2 pages 2-4, 2-14 and appendix A.

Sources for each data set are shown in the Reference column. A superscript number after a reference identifies a particular population from a reference that provided data for a number of different populations. The reference (and number) can be used to locate the corresponding population data in appendix E. A Species name and Common name is also shown for each population. The taxonomic class of the species is listed under the heading Class. The table is arranged in alphabetical order first by Class and then by Species. Years is the number of years in the data. In the Years column, two numbers separated by a comma (e.g., 10,11) are the number of years in the data subset used to calculate r_S^2 and r_P^2 respectively. Asterisks *** in the Years column identify populations where no density-dependent relationship was found. The r_S^2 lag and r_P^2 lag columns show the number of years the data was lagged to obtain the maximum r_S^2 and r_P^2 values shown.

Table C.1: Data sources, species names and the proportions of variance in γ statistically related to the variance in N: r_S^2 and r_P^2.

Reference	Species name	Common name	Class	Years	r_S^2 lag	r_P^2 lag	r_S^2	r_P^2
Pechmann et al. (1991)[1]	*Ambystoma opacum*	marbled salmander	Amphibia	10	3	0	0.119	0.053
Pechmann et al. (1991)[2]	*Ambystoma talpoideum*	mole salmander	Amphibia	12	4	4	0.350	0.298
Pechmann et al. (1991)[3]	*Ambystoma tigrinum*	eastern tiger salmander	Amphibia	9	1	1	0.123	0.174
Semb-Johansson (1992)	*Bufo bufo* (L.)	common toad	Amphibia	13	1	1	0.026	0.004
Stewart (1995)	*Eleutherodactylus coqui*	Puerto Rican coqui	Amphibia	15	2	1	0.214	0.036
Jaeger (1980)[1]	*Plethodon cinereus*	red-backed salmander	Amphibia	14	1	1	0.029	0.222
Jaeger (1980)[2]	*Plethodon shenandoah*	Shenandoah salmander	Amphibia	14	1	2	0.165	0.192
Pechmann et al. (1991)[4]	*Pseudacris ornata*	ornate chorus frog	Amphibia	12	1	1	0.255	0.099
Wyllie & Newton (1991)[1]	*Accipiter nisus* (L.)	sparrowhawk	Aves	10	4	4	0.166	0.226
Wyllie & Newton (1991)[2]	*Accipiter nisus* (L.)	sparrowhawk	Aves	18	1	1	0.222	0.163
Wyllie & Newton (1991)[3]	*Accipiter nisus* (L.)	sparrowhawk	Aves	11	0	1	0.020	0.267
Newton & Marquiss (1986)[1]	*Acipiter nisus* (L.).	sparrowhawk	Aves	13	1	1	0.279	0.240
Newton & Marquiss (1986)[2]	*Acipiter nisus* (L.).	sparrowhawk	Aves	10	3	4	0.281	0.354
Hörnfeldt (1978)[1]	*Aegolius funereus* (L.)	Tengmalm's owl	Aves	13	4	1	0.217	0.492
Korpimäki & Norrdahl (1989)[1]	*Aegolius funereus*	Tengmalm's owl	Aves	11	1	1	0.366	0.432
Vickery & Nudds (1984)[1]	*Anas acuta*	Northern pintail duck	Aves	26	1	1	0.069	0.020

Table C.1: Data sources, species names and the proportions of variance in γ statistically related to the variance in N: r_S^2 and r_P^2.

Reference	Species name	Common name	Class	Years	r_S^2 lag	r_P^2 lag	r_S^2	r_P^2
Vickery & Nudds (1984)[2]	*Anas acuta*	Northern pintail duck	Aves	9	1	1	0.367	0.296
Vickery & Nudds (1984)[3]	*Anas americana*	American wigeon	Aves	26	1	7	0.152	0.107
Vickery & Nudds (1984)[4]	*Anas americana*	American wigeon	Aves	9	1	1	0.115	0.166
Vickery & Nudds (1984)[5]	*Anas clypeata*	Northern shoveler duck	Aves	26	1	1	0.081	0.126
Vickery & Nudds (1984)[6]	*Anas clypeata*	Northern shoveler duck	Aves	9	3	1	0.201	0.219
Vickery & Nudds (1984)[7]	*Anas crecca*	green-winged teal	Aves	26	6	6	0.102	0.085
Vickery & Nudds (1984)[8]	*Anas crecca*	green-winged teal	Aves	9	1	1	0.267	0.271
Vickery & Nudds (1984)[9]	*Anas discors*	blue-winged teal	Aves	26	7	1	0.049	0.163
Vickery & Nudds (1984)[10]	*Anas discors*	blue-winged teal	Aves	9	1	3	0.396	0.345
Vickery & Nudds (1984)[11]	*Anas platyrhynchos*	mallard	Aves	26	7	7	0.120	0.093
Vickery & Nudds (1984)[12]	*Anas platyrhynchos*	mallard	Aves	9	1	1	0.294	0.297
Vickery & Nudds (1984)[13]	*Anas strepera*	gadwall	Aves	26	1	1	0.216	0.194
Vickery & Nudds (1984)[14]	*Anas strepera*	gadwall	Aves	9	1	1	0.392	0.336
Mindell & White (1988)[1]	*Aquila chrysaetos*	golden eagle	Aves	15	5	5	0.178	0.289
Lack (1954)[1]	*Ardea cinerea*	heron	Aves	19	8	8	0.290	0.372
Lack (1954)[2]	*Ardea cinerea*	heron	Aves	16	1	1	0.312	0.178
Stafford (1971)	*Ardea cinerea*	heron	Aves	43	1	2	0.375	0.195

Table C.1: Data sources, species names and the proportions of variance in γ statistically related to the variance in N: r_S^2 and r_P^2.

Reference	Species name	Common name	Class	Years	r_S^2 lag	r_P^2 lag	r_S^2	r_P^2
Hörnfeldt (1978)[2]	*Asio otus* (L.)	long eared owl	Aves	13	1	1	0.152	0.180
Vickery & Nudds (1984)[15]	*Aytha affinis*	lesser scaup	Aves	26	4	4	0.252	0.011
Vickery & Nudds (1984)[16]	*Aytha affinis*	lesser scaup	Aves	9	1	1	0.208	0.169
Vickery & Nudds (1984)[17]	*Aytha americana*	redhead duck	Aves	9	3	3	0.413	0.297
Vickery & Nudds (1984)[18]	*Aytha valisineria*	canvasback duck	Aves	26	1	8	0.061	0.020
Vickery & Nudds (1984)[19]	*Aytha valisineria*	canvasback duck	Aves	9	3	3	0.317	0.240
Mindell & White (1988)[2]	*Buteo jamaicensis*	red-tailed hawk	Aves	9	1	1	0.296	0.267
Holmes et al. (1986)[1]	*Catharus fuscescens*	veery	Aves	16	1	1	0.200	0.216
Holmes et al. (1986)[2]	*Catharus guttatus*	Hermit thrush	Aves	16	6	6	0.150	0.162
Holmes et al. (1986)[3]	*Catharus ustulatus*	Swainson's thrush	Aves	16	5	1	0.002	0.001
Cooch et al. (1989)	*Chen caerulescens caerulescens* (L.)	lesser snow goose	Aves	18	3	1	0.020	0.019
Lack (1954)[3]	*Ciconia ciconia*	white stork	Aves	11	1	1	0.068	0.001
Lack (1954)[4]	*Ciconia ciconia*	white stork	Aves	17	7	3	0.134	0.212
Holmes et al. (1986)[4]	*Dendroica caerulescens*	black-throated blue warbler	Aves	16	1	1	0.075	0.166
Holmes et al. (1986)[5]	*Dendroica fusca*	Blackburnian warbler	Aves	16	1	1	0.067	0.066
Holmes et al. (1986)[6]	*Dendroica virens*	black-throated green warbler	Aves	16	1	1	0.273	0.335
Croxall et al. (1990)	*Diomedea exulans* (L.)	wandering albatross	Aves	14	1	1	0.218	0.150

Table C.1: Data sources, species names and the proportions of variance in γ statistically related to the variance in N: r_S^2 and r_P^2.

Reference	Species name	Common name	Class	Years	r_S^2 lag	r_P^2 lag	r_S^2	r_P^2
Holmes et al. (1986)[7]	*Empidonax minimus*	Least flycatcher	Aves	13	1	1	0.099	0.055
Grant & Grant (1992)[1]	*Geospiza fortis*	medium ground finch	Aves	16	1	4	0.282	0.062
Grant & Grant (1992)[2]	*Geospiza scandens*	cactus finch	Aves	16	4	2	0.324	0.137
Nedelman et al. (1987)	*Grus americana*	whooping crane	Aves	48	3	3	0.008	0.000
Møller (1989)	*Hirundo rustica* (L.)	swallow	Aves	18,19	6	1	0.006	0.080
Holmes et al. (1986)[8]	*Hylocichla mustelina*	wood thrush	Aves	16	1	2	0.010	0.002
Holmes et al. (1986)[9]	*Junco hyemalis*	dark-eyed junco	Aves	16	6	6	0.215	0.292
Hörnfeldt (1978)[5]	*Lagopus lagopus* (L.)	Norwegian willow grouse	Aves	13	1	1	0.091	0.055
Dobson & Hudson (1992)	*Lagopus lagopus scoticus*	red grouse	Aves	14	1	1	0.163	0.153
Hudson et al. (1992)	*Lagopus lagopus scoticus*	red grouse	Aves	15	1	1	0.304	0.150
Middleton (1934)[1]	*Lagopus scoticus*	grouse	Aves	57	1	1	0.542	0.022
Middleton (1934)[2]	*Lagopus scoticus*	grouse	Aves	56	1	7	0.534	0.023
Middleton (1934)[3]	*Lagopus scoticus*	grouse	Aves	52	1	1	0.406	0.104
Middleton (1934)[4]	*Lagopus scoticus*	grouse	Aves	28	2	4	0.222	0.233
Arcese et al. (1991)	*Melospiza melodia*	song sparrow	Aves	16	1	4	0.248	0.005
Davis & Newton (1981)	*Milvus milvus*	red kite	Aves	30	8	8	0.060	0.040
Curry & Grant (1989)	*Nesomimus parvulus* (Gould)	Galápagos mockingbird	Aves	11	4	4	0.325	0.123

Table C.1: Data sources, species names and the proportions of variance in γ statistically related to the variance in N: r_S^2 and r_P^2.

Reference	Species name	Common name	Class	Years	r_S^2 lag	r_P^2 lag	r_S^2	r_P^2
Chastel et al. (1993)	*Padagroma nivea*	snow petrel	Aves	28	1	1	0.443	0.342
Loery & Nichols (1985)	*Parus atricapillus*	black-capped chickadee	Aves	24	1	1	0.245	0.367
Dhondt & Eyckerman (1980)[1]	*Parus caeruleus*	blue tit	Aves	19	1	1	0.280	0.184
Dhondt & Eyckerman (1980)[2]	*Parus caeruleus*	blue tit	Aves	19	1	1	0.236	0.215
Perrins (1965)[1]	*Parus major*	great tit	Aves	17	5	5	0.056	0.070
Perrins (1965)[2]	*Parus major*	great tit	Aves	17	1	1	0.096	0.143
Perrins (1965)[3]	*Parus major*	great tit	Aves	17	1	1	0.184	0.162
Blank et al. (1967)	*Perdix perdix* (L.)	grey or hungarian partridge	Aves	11	1	1	0.367	0.392
Middleton (1934)[5]	*Perdix perdix*	grey or hungarian partridge	Aves	49	1	1	0.164	0.158
Middleton (1934)[6]	*Perdix perdix*	grey or hungarian partridge	Aves	91	1	1	0.302	0.272
Middleton (1934)[7]	*Perdix perdix*	grey or hungarian partridge	Aves	91	1	1	0.222	0.221
Middleton (1934)[8]	*Perdix perdix*	grey or hungarian partridge	Aves	71	1	1	0.231	0.180
Middleton (1934)[9]	*Perdix perdix*	grey or hungarian partridge	Aves	54	1	1	0.275	0.269
Middleton (1934)[10]	*Perdix perdix*	grey or hungarian partridge	Aves	45	1	1	0.236	0.116
Middleton (1934)[11]	*Perdix perdix*	grey or hungarian partridge	Aves	28	1	1	0.071	0.073
Holmes et al. (1986)[10]	*Pheucticus ludovicianus*	rose-breasted grosbeak	Aves	16	1	1	0.228	0.342
Holmes et al. (1986)[11]	*Picoides pubescens*	Downy woodpecker	Aves	12	1	1	0.010	0.011

Table C.1: Data sources, species names and the proportions of variance in γ statistically related to the variance in N: r_S^2 and r_P^2.

Reference	Species name	Common name	Class	Years	r_S^2 lag	r_P^2 lag	r_S^2	r_P^2
Holmes et al. (1986)[12]	*Picoides villosus*	hairy woodpecker	Aves	16	1	6	0.222	0.085
Holmes et al. (1986)[13]	*Piranga olivacea*	scarlet tanager	Aves	16	1	1	0.134	0.184
Coulson & Thomas (1985)	*Rissa tridactyla* (L.)	kittiwake	Aves	34	3	3	0.512	0.474
Middleton (1934)[12]	*Scolopax rusticola*	woodcock	Aves	87	1	1	0.205	0.184
Holmes et al. (1986)[14]	*Seiurus aurocapillus*	ovenbird	Aves	16	1	1	0.134	0.196
Holmes et al. (1986)[15]	*Setophaga ruticilla*	American redstart	Aves	16	1	1	0.067	0.149
Pietiäinen (1989)	*Strix uralensis* (Pall.)	Ural owl	Aves	12	1	1	0.366	0.326
Middleton (1934)[13]	*Tetrao tetrix*	black grouse	Aves	28	1	1	0.150	0.163
Holmes et al. (1986)[16]	*Troglodytes troglodytes*	winter wren	Aves	9	1	1	0.162	0.039
Holmes et al. (1986)[17]	*Vireo olivaceus*	red-eyed vireo	Aves	16	1	1	0.029	0.032
Holmes et al. (1986)[18]	*Vireo philadelphicus*	Philadelphia vireo	Aves	14	3	1	0.002	0.003
Walters et al. (1990)[1]	*Daphnia rosea*	a zooplankter	Branchiopoda	10	3	1	0.049	0.041
Walters et al. (1990)[2]	*Daphnia rosea*	a zooplankter	Branchiopoda	10	1	1	0.006	0.175
Walters et al. (1990)[3]	*Daphnia rosea*	a zooplankter	Branchiopoda	10	1	2	0.149	0.171
Walters et al. (1990)[4]	*Daphnia rosea*	a zooplankter	Branchiopoda	10	1	1	0.047	0.040
Walters et al. (1990)[5]	*Holopedium gibberum*	a zooplankter	Branchiopoda	10	4	4	0.181	0.188
Walters et al. (1990)[6]	*Holopedium gibberum*	a zooplankter	Branchiopoda	10	3	1	0.050	0.050

Table C.1: Data sources, species names and the proportions of variance in γ statistically related to the variance in N: r_S^2 and r_P^2.

Reference	Species name	Common name	Class	Years	r_S^2 lag	r_P^2 lag	r_S^2	r_P^2
Walters et al. (1990)[7]	*Holopedium gibberum*	a zooplankter	Branchiopoda	10	1	4	0.094	0.143
Walters et al. (1990)[8]	*Holopedium gibberum*	a zooplankter	Branchiopoda	10	1	1	0.182	0.147
Southwood & Reader (1976)[1]	*Aleurotrachelus jelinekii* (Frauenf.)	viburnum whitefly	Insecta	12	1	1	0.236	0.303
Southwood & Reader (1976)[2]	*Aleurotrachelus jelinekii* (Frauenf.)	viburnum whitefly	Insecta	12	3	3	0.422	0.458
Southwood & Reader (1976)[3]	*Aleurotrachelus jelinekii* (Frauenf.)	viburnum whitefly	Insecta	12	1	1	0.131	0.052
Southwood et al. (1989)[1]	*Aleurotrachelus jelinekii* (Frauenf.)	viburnum whitefly	Insecta	16	7	7	0.243	0.272
Southwood et al. (1989)[2]	*Aleurotrachelus jelinekii* (Frauenf.)	viburnum whitefly	Insecta	16	1	1	0.015	0.002
Dempster (1982)[1]	*Apanteles popularis* (Hal.)	a parasitoid wasp	Insecta	9	1	1	0.066	0.005
Pollard (1991)[1]	*Aphantopus hyperantus* (L.)	a butterfly	Insecta	14	4	5	0.435	0.446
Murdoch et al. (1984)[1]	*Aphytis paramaculicornis*	olive scale parasitoid	Insecta	11	1	1	0.076	0.200
Crowley & Johnson (1992)[1]	*Argia fumipennis violacea*	a dragonfly	Insecta	12	1	1	0.195	0.150
Wool (1990)[1]	*Baizongia pistaciae* (L.)	an aphid	Insecta	10	1	1	0.003	0.248
Wool (1990)[2]	*Baizongia pistaciae* (L.)	an aphid	Insecta	10	3	3	0.045	0.001
Varley (1949)[1]	*Baupalus piniarius* (L.)	pine looper	Insecta	28	2	2	0.374	0.388
Broekhuizen et al. (1993)[1]	*Bupalus piniaria* (L.)	pine looper	Insecta	37	2	1	0.414	0.157
Broekhuizen et al. (1993)[2]	*Bupalus piniaria* (L.)	pine looper	Insecta	37	1	1	0.326	0.334
Broekhuizen et al. (1993)[3]	*Bupalus piniaria* (L.)	pine looper	Insecta	37,26	1	6	0.071	0.053

Table C.1: Data sources, species names and the proportions of variance in γ statistically related to the variance in N: r_S^2 and r_P^2.

Reference	Species name	Common name	Class	Years	r_S^2 lag	r_P^2 lag	r_S^2	r_P^2
Broekhuizen et al. (1994)	*Bupalus piniaria* (L.)	pine looper	Insecta	21	3	9	0.203	0.000
Klomp (1966)	*Bupalus piniarius* (L.)	pine looper	Insecta	15	1	1	0.349	0.460
Turchin & Taylor (1992)[1]	*Bupalus piniarius*	pine looper caterpillar	Insecta	59	2	2	0.284	0.260
Varley et al. (1973)[1]	*Bupalus piniarius*	pine looper caterpillar	Insecta	13	1	1	0.069	0.457
Varley et al. (1973)[2]	*Bupalus piniarius*	pine looper caterpillar	Insecta	13	1	2	0.074	0.038
Klomp (1968)[1]	*Buplas piniarius* (L.)	pine looper	Insecta	17,16	1	1	0.189	0.368
Connor & Beck (1993)	*Cameraria hamadryadella*	a leaf miner	Insecta	10	3	2	0.104	0.429
Crowley & Johnson (1992)[2]	*Celithemis elisa*	a dragonfly	Insecta	12	1	1	0.451	0.386
Crowley & Johnson (1992)[3]	*Celithemis fasciata*	a dragonfly	Insecta	12	1	1	0.272	0.048
Woiwod & Hanski (1992)	*Cerapteryx graminis* (L.)	antler moth	Insecta	16	2	2	0.301	0.303
Itô (1972)	*Chilo supressalis*	rice stem borer moth	Insecta	34,35	1	1	0.258	0.433
Royama (1981)	*Choristoneura fumiferana* (Clem.)	spruce budworm	Insecta	28	5	4	0.140	0.181
Turchin & Taylor (1992)[2]	*Choristoneura fumiferana*	spruce budworm	Insecta	28	8	8	0.150	0.213
Kato (1994)	*Chromatomyia suikazurae*	a leafminer	Insecta	10	3	1	0.310	0.087
Varley et al. (1973)[3]	*Cratichneumon culex*	an ichneumonid	Insecta	17	2	2	0.125	0.136
Kowalski & Benson (1978)	*Delia coarctata* (Fall.)	wheat bulb fly	Insecta	9	1	1	0.098	0.052
Jones et al. (1993)	*Delia radicum* (L.)	cabbage root fly	Insecta	9	1	1	0.079	0.071

Table C.1: Data sources, species names and the proportions of variance in γ statistically related to the variance in N: r_S^2 and r_P^2.

Reference	Species name	Common name	Class	Years	r_S^2 lag	r_P^2 lag	r_S^2	r_P^2
Turchin & Taylor (1992)[3]	*Dendroctonus frontalis*	southern pine beetle	Insecta	30	1	10	0.343	0.101
Varley (1949)[2]	*Dendrolimus pini* (L.)	a Lasiocampid moth	Insecta	17,42	2	1	0.125	0.503
Turchin & Taylor (1992)[4]	*Dendrolinus pini*	a Lasiocampid moth	Insecta	60	1	2	0.094	0.308
Turchin & Taylor (1992)[5]	*Dendrolinus pini*	a Lasiocampid moth	Insecta	60	2	2	0.263	0.128
Turchin & Taylor (1992)[6]	*Drepanosiphum platanoides*	sycamore aphid	Insecta	19	1	1	0.033	0.046
Crowley & Johnson (1992)[4]	*Enallagma basidens*	a dragonfly	Insecta	12	5	5	0.304	0.147
Crowley & Johnson (1992)[5]	*Enallagma divagans*	a dragonfly	Insecta	12	1	1	0.236	0.319
Crowley & Johnson (1992)[6]	*Enallagma signatum*	a dragonfly	Insecta	12	5	5	0.515	0.330
Crowley & Johnson (1992)[7]	*Enallagma traviatum*	a dragonfly	Insecta	12	1	1	0.326	0.312
Varley et al. (1973)[4]	*Erannis tilaria*	winter moth	Insecta	19	2	2	0.094	0.094
Ehrlich et al. (1975)[1]	*Euphydryas editha* (Boisduval)	checkerspot butterfly	Insecta	15	1	1	0.061	0.001
Ehrlich et al. (1975)[2]	*Euphydryas editha* (Boisduval)	checkerspot butterfly	Insecta	15	2	1	0.066	0.001
Ehrlich et al. (1975)[3]	*Euphydryas editha* (Boisduval)	checkerspot butterfly	Insecta	9	1	1	0.167	0.354
Harrison et al. (1991)[1]	*Euphydryas editha bayensis*	bay checkerspot butterfly	Insecta	27	2	1	0.153	0.143
Harrison et al. (1991)[2]	*Euphydryas editha bayensis*	bay checkerspot butterfly	Insecta	27	1	1	0.001	0.004
Roininen et al. (1993)	*Euura amerinae*	shoot-galling sawfly	Insecta	9	2	2	0.186	0.262
Varley (1949)[3]	*Hyloicus pinastri* (L.)	pine hawk	Insecta	18	3	3	0.345	0.419

Table C.1: Data sources, species names and the proportions of variance in γ statistically related to the variance in N: r_S^2 and r_P^2.

Reference	Species name	Common name	Class	Years	r_S^2 lag	r_P^2 lag	r_S^2	r_P^2
Morris (1964)[1]	*Hyphantria cunea* (Drury)	fall webworm	Insecta	20	3	2	0.207	0.238
Morris (1964)[2]	*Hyphantria cunea* (Drury)	fall webworm	Insecta	16	1	1	0.195	0.153
Morris (1964)[3]	*Hyphantria cunea* (Drury)	fall webworm	Insecta	18	2	2	0.266	0.250
Morris (1964)[4]	*Hyphantria cunea* (Drury)	fall webworm	Insecta	22	1	1	0.341	0.433
Morris (1964)[5]	*Hyphantria cunea* (Drury)	fall webworm	Insecta	22	2	1	0.100	0.002
Turchin & Taylor (1992)[7]	*Hyphantria cunea*	fall webworm	Insecta	22	1	1	0.330	0.354
MacLellan (1977)[1]	*Laspeyresia pomonella* (L.)	codling moth	Insecta	12	2	2	0.281	0.234
MacLellan (1977)[2]	*Laspeyresia pomonella* (L.)	codling moth	Insecta	12	3	1	0.267	0.271
Crowley & Johnson (1992)[6]	*Lestes vigilax*	a dragonfly	Insecta	12	3	3	0.118	0.381
Sillén-Tullberg et al. (1990)[1]	*Lygaeus equestris*	a seed feeding bug	Insecta	11	2	1	0.060	0.151
Sillén-Tullberg et al. (1990)[2]	*Lygaeus equestris*	a seed feeding bug	Insecta	11	2	2	0.408	0.410
Turchin & Taylor (1992)[8]	*Lymantria dispar*	gypsy moth	Insecta	26	2	2	0.420	0.111
Bejer (1988)	*Lymantria monacha* (L.)	nun moth	Insecta	42	5	5	0.005	0.002
Turchin & Taylor (1992)[9]	*Lymantria monacha*	nun moth	Insecta	42	1	1	0.412	0.525
Varley et al. (1973)[5]	*Lypha dubia*	a tachinid fly	Insecta	15	1	4	0.089	0.074
Pollard (1991)[2]	*Maniola jurtina* (L.)	a butterfly	Insecta	14	1	1	0.122	0.136
McLain & Shure (1990)	*Neacoryphus bicrucis*	ragwort seed bug	Insecta	11	4	4	0.247	0.320

Table C.1: Data sources, species names and the proportions of variance in γ statistically related to the variance in N: r_S^2 and r_P^2.

Reference	Species name	Common name	Class	Years	r_S^2 lag	r_P^2 lag	r_S^2	r_P^2
Nelemans et al. (1989)	*Nebria brevicollis* (F.)	a carabid beetle	Insecta	11	1	1	0.288	0.387
Pollard (1991)[3]	*Ochlodes venata* (B. and G.)	a butterfly	Insecta	14	4	4	0.131	0.087
Varley & Gradwell (1968)	*Operophtera brumata* (L.)	winter moth	Insecta	17	1	3	0.125	0.173
Klomp (1968)[2]	*Panolis flammea* (Hübner)	pine beauty moth	Insecta	16	1	1	0.143	0.223
Turchin & Taylor (1992)[10]	*Panolis flammea*	pine beauty moth	Insecta	59	1	2	0.197	0.353
Varley (1949)[4]	*Panolis flammea* (Schiff.)	pine beauty moth	Insecta	60	1	2	0.181	0.287
Murdoch et al. (1984)[2]	*Parlatoria olaea*	olive scale	Insecta	10	4	4	0.242	0.170
Varley et al. (1973)[6]	*Philonthus decorus*	a staphylinid	Insecta	9	1	1	0.154	0.296
Turchin & Taylor (1992)[11]	*Phyllaphis fagi*	beech aphid	Insecta	19	2	1	0.125	0.517
Turchin & Taylor (1992)[12]	*Phyllopertha horticola*	garden chafer	Insecta	29	7	2	0.024	0.124
Pollard (1991)[4]	*Pyronia tithonus* (L.)	a butterfly	Insecta	14	3	3	0.232	0.332
MacLellan (1978)[1]	*Spilonota ocellana* (D. & S.)	eye-spotted bud moth	Insecta	12	1	1	0.386	0.244
MacLellan (1978)[2]	*Spilonota ocellana* (D. & S.)	eye-spotted bud moth	Insecta	12	1	1	0.397	0.326
Klomp (1968)[3]	*Thera firmata* (Hübner)	-	Insecta	16	1	1	0.208	0.209
Dempster (1982)[2]	*Tyria jacobaeae*	cinnabar moth	Insecta	9	1	2	0.257	0.001
Southwood (1967)	*Vespula*	wasps	Insecta	25	1	3	0.070	0.005
Turchin & Taylor (1992)[13]	*Vespula* app.	wasps	Insecta	26	1	1	0.096	0.002

Table C.1: Data sources, species names and the proportions of variance in γ statistically related to the variance in N: r_S^2 and r_P^2.

Reference	Species name	Common name	Class	Years	r_S^2 lag	r_P^2 lag	r_S^2	r_P^2
Barlow et al. (1986)	*Wiseana cervinata* (Walker)	a moth	Insecta	10	1	1	0.330	0.262
Baltensweiler (1968)	*Zeiaphera griseana* (Hübner)	grey larch bud moth	Insecta	18	2	2	0.487	0.109
Baltensweiler & Fischlin (1988)[1]	*Zeiraphera diniana* (Guen)	larch bud moth	Insecta	38	2	3	0.555	0.188
Baltensweiler & Fischlin (1988)[2]	*Zeiraphera diniana* (Guen)	larch bud moth	Insecta	20	2	1	0.396	0.109
Baltensweiler & Fischlin (1988)[3]	*Zeiraphera diniana* (Guen)	larch bud moth	Insecta	19	2	2	0.546	0.592
Baltensweiler & Fischlin (1988)[4]	*Zeiraphera diniana* (Guen)	larch bud moth	Insecta	21	2	2	0.520	0.596
Baltensweiler & Fischlin (1988)[5]	*Zeiraphera diniana* (Guen)	larch bud moth	Insecta	20	2	2	0.432	0.560
Myers (1988)	*Zeiraphera diniana*	larch budmoth	Insecta	29	2	3	0.446	0.088
Myers (1988)	*Zeiraphera diniana*	larch budmoth	Insecta	29	2	3	0.417	0.025
Varley et al. (1970)	*Zeiraphera diniana*	larch budmoth	Insecta	17	2	4	0.420	0.252
Turchin & Taylor (1992)[14]	-	belyak hare	Mammalia	22	4	4	0.440	0.040
Messier (1991)[1]	*Alces alces*	moose	Mammalia	18	7	7	0.188	0.232
Angerbjörn et al. (1991)[1]	*Alopex lagopus* (L.)	arctic fox	Mammalia	11	1	2	0.342	0.056
Angerbjörn et al. (1991)[2]	*Alopex lagopus* (L.)	arctic fox	Mammalia	22,9	5	9	0.144	0.294
Turchin & Taylor (1992)[15]	*Alopex lagopus*	arctic fox	Mammalia	39	1	1	0.441	0.262
Wrigley & Hatch (1976)	*Alopex lagopus*	arctic fox	Mammalia	56	1	1	0.257	0.127
Gulland (1971)[1]	*Balaenoptera musculus*	blue whale	Mammalia	19	***	***	0.000	0.000

Table C.1: Data sources, species names and the proportions of variance in γ statistically related to the variance in N: r_S^2 and r_P^2.

Reference	Species name	Common name	Class	Years	r_S^2 lag	r_P^2 lag	r_S^2	r_P^2
Gulland (1971)[2]	*Balaenoptera physalus*	fin whale	Mammalia	24	8	7	0.188	0.234
Messier (1991)[2]	*Canis lupus*	wolf	Mammalia	10	3	3	0.004	0.063
Messier (1991)[3]	*Canis lupus*	wolf	Mammalia	27	4	1	0.103	0.217
Gaillard et al. (1993)[1]	*Capreolus capreolus* (L.)	roe deer	Mammalia	12	2	2	0.335	0.244
Gaillard et al. (1993)[2]	*Capreolus capreolus* (L.)	roe deer	Mammalia	12	5	5	0.304	0.322
Brown & Heske (1990)[1]	*Chaetodipus penicillatus*	-	Mammalia	11	1	1	0.153	0.096
Hörnfeldt (1994)[1]	*Clethrionomys glareolus* (Schreb.)	bank vole	Mammalia	18,17	1	8	0.343	0.421
Korpimäki & Norrdahl (1989)[2]	*Clethrionomys glareolus*	bank vole	Mammalia	11	4	4	0.338	0.484
Korpimäki & Norrdahl (1991)[1]	*Clethrionomys glareolus*	bank vole	Mammalia	11	1	3	0.306	0.133
Korpimäki & Norrdahl (1991)[2]	*Clethrionomys glareolus*	bank vole	Mammalia	11	1	1	0.273	0.249
Marcström et al. (1990)	*Clethrionomys glareolus*	bank vole	Mammalia	10,11	1	1	0.217	0.222
Turchin (1993)[1]	*Clethrionomys glareolus*	bank vole	Mammalia	22	1	1	0.204	0.122
Hörnfeldt (1994)[2]	*Clethrionomys rufocanus* (Sund.)	grey-sided vole	Mammalia	17,18	1	1	0.512	0.481
Turchin (1993)[2]	*Clethrionomys rufocanus*	a vole	Mammalia	16	1	1	0.255	0.034
Wood & Odum (1964)[1]	*Didelphis marsupialis*	opossum	Mammalia	9	2	0	0.222	0.062
Brown & Heske (1990)[2]	*Dipodomys merriami*	-	Mammalia	11,10	1	1	0.361	0.256
Brown & Heske (1990)[3]	*Dipodomys ordii*	-	Mammalia	11,10	1	0	0.298	0.102

Table C.1: Data sources, species names and the proportions of variance in γ statistically related to the variance in N: r_S^2 and r_P^2.

Reference	Species name	Common name	Class	Years	r_S^2 lag	r_P^2 lag	r_S^2	r_P^2
Brown & Heske (1990)[4]	*Dipodomys spectabilis*	-	Mammalia	10,11	1	2	0.143	0.370
Turchin (1993)[3]	*Lemmus trimucronatus*	a vole	Mammalia	18	1	1	0.466	0.002
Siniff et al. (1977)[1]	*Leptonychotes weddelli*	Weddell seal	Mammalia	12	4	1	0.117	0.029
Siniff et al. (1977)[2]	*Leptonychotes weddelli*	Weddell seal	Mammalia	12	1	1	0.112	0.220
Siniff et al. (1977)[3]	*Leptonychotes weddelli*	Weddell seal	Mammalia	12	5	5	0.058	0.199
Siniff et al. (1977)[4]	*Leptonychotes weddelli*	Weddell seal	Mammalia	12	1	2	0.159	0.029
Siniff et al. (1977)[5]	*Leptonychotes weddelli*	Weddell seal	Mammalia	12	1	1	0.313	0.331
Siniff et al. (1977)[6]	*Leptonychotes weddelli*	Weddell seal	Mammalia	12	1	1	0.314	0.221
Siniff et al. (1977)[7]	*Leptonychotes weddelli*	Weddell seal	Mammalia	12	1	2	0.239	0.074
Siniff et al. (1977)[8]	*Leptonychotes weddelli*	Weddell seal	Mammalia	12	1	1	0.339	0.219
Siniff et al. (1977)[9]	*Leptonychotes weddelli*	Weddell seal	Mammalia	11	1	1	0.132	0.010
Siniff et al. (1977)[10]	*Leptonychotes weddelli*	Weddell seal	Mammalia	10	1	4	0.084	0.337
Keith (1983)[1]	*Lepus americanus*	snowshoe hare	Mammalia	17	3	3	0.383	0.386
Keith (1983)[2]	*Lepus californicus*	black-tailed jackrabbit	Mammalia	19	3	2	0.262	0.357
Middleton (1934)[14]	*Lepus europaeus*	hare	Mammalia	90	1	1	0.212	0.148
Middleton (1934)[15]	*Lepus europaeus*	hare	Mammalia	71	1	1	0.334	0.330
Middleton (1934)[16]	*Lepus europaeus*	hare	Mammalia	31	3	3	0.089	0.161

Table C.1: Data sources, species names and the proportions of variance in γ statistically related to the variance in N: r_S^2 and r_P^2.

Reference	Species name	Common name	Class	Years	r_S^2 lag	r_P^2 lag	r_S^2	r_P^2
Dannell & Hörnfeldt (1987)[1]	*Lepus timidus*	mountain hare	Mammalia	15	1	1	0.469	0.361
Hörnfeldt (1978)[4]	*Lepus timidus* (L.)	mountain hare	Mammalia	13	1	1	0.217	0.277
Keith (1983)[3]	*Lepus timidus*	arctic hare	Mammalia	19	1	1	0.078	0.147
Keith (1983)[4]	*Lepus timidus*	arctic hare	Mammalia	13	1	1	0.229	0.330
Middleton (1934)[17]	*Lepus timidus*	hare	Mammalia	47	3	3	0.261	0.121
Elton & Nicholson (1942)	*Lynx canadensis*	lynx	Mammalia	71	2	3	0.562	0.421
Wood & Odum (1964)[2]	*Lynx rufus*	bobcat	Mammalia	9	1	1	0.442	0.367
Wood & Odum (1964)[3]	*Mephitis mephitis*	striped skunk	Mammalia	9	1	1	0.315	0.315
Hörnfeldt (1994)[3]	*Microtus agrestis*	field vole	Mammalia	18,17	1	2	0.301	0.223
Garsd & Howard (1982)[1]	*Microtus californicus*	vole	Mammalia	20,21	1	1	0.284	0.193
Garsd & Howard (1982)[2]	*Microtus californicus*	vole	Mammalia	21	1	1	0.466	0.421
Hindell (1991)	*Mirounga leonina* (L.)	southern elephant seal	Mammalia	9	1	1	0.208	0.075
Middleton (1934)[18]	*Mustela vulgaris*	weasel	Mammalia	52	10	1	0.100	0.094
Middleton (1934)[19]	*Mustela vulgaris*	weasel	Mammalia	48	1	1	0.101	0.050
Brown & Heske (1990)[5]	*Neotoma albigula*	-	Mammalia	11,10	2	1	0.161	0.139
Messier (1991)[4]	*Odocoileus virginianus*	white-tailed deer	Mammalia	11	1	1	0.094	0.004
Brown & Heske (1990)[6]	*Onychomys leucogaster*	-	Mammalia	11	1	3	0.124	0.086

Table C.1: Data sources, species names and the proportions of variance in γ statistically related to the variance in N: r_S^2 and r_P^2.

Reference	Species name	Common name	Class	Years	r_S^2 lag	r_P^2 lag	r_S^2	r_P^2
Brown & Heske (1990)[7]	*Onychomys torridus*	-	Mammalia	10	1	1	0.079	0.036
Middleton (1934)[20]	*Oryctolagus cuniculus*	rabbit	Mammalia	62	1	1	0.229	0.193
Middleton (1934)[21]	*Oryctolagus cuniculus*	rabbit	Mammalia	65	1	1	0.272	0.399
Middleton (1934)[22]	*Oryctolagus cuniculus*	rabbit	Mammalia	71	1	1	0.102	0.129
Middleton (1934)[23]	*Oryctolagus cuniculus*	rabbit	Mammalia	31	1	1	0.151	0.281
Brown & Heske (1990)[8]	*Perognathus flavus*	-	Mammalia	11	2	2	0.229	0.411
Brown & Heske (1990)[9]	*Peromyscus eremicus*	-	Mammalia	10,11	1	1	0.172	0.046
Brown & Heske (1990)[10]	*Peromyscus maniculatus*	-	Mammalia	10	1	1	0.196	0.062
Wood & Odum (1964)[4]	*Procyon lotor*	racoon	Mammalia	9	1	1	0.256	0.276
Scheffer (1951)[1]	*Rangifer tarandus*	reindeer	Mammalia	31	3	3	0.115	0.267
Scheffer (1951)[2]	*Rangifer tarandus*	reindeer	Mammalia	31	0	5	0.007	0.248
Skogland (1990)	*Rangifer tarandus*	reindeer	Mammalia	15	1	1	0.309	0.286
Skogland (1985)[1]	*Rangifer tarandus* (L.)	reindeer	Mammalia	12	2	2	0.006	0.000
Skogland (1985)[2]	*Rangifer tarandus* (L.)	reindeer	Mammalia	13	1	1	0.084	0.046
Brown & Heske (1990)[11]	*Reithrodontomys megalotis*	-	Mammalia	10,11	1	0	0.154	0.093
Korpimäki & Norrdahl (1989)[3]	*Sorex araneus*	common shrew	Mammalia	11	3	3	0.208	0.084
Korpimäki & Norrdahl (1991)[3]	*Sorex araneus*	common shrew	Mammalia	11	1	4	0.123	0.164

Table C.1: Data sources, species names and the proportions of variance in γ statistically related to the variance in N: r_S^2 and r_P^2.

Reference	Species name	Common name	Class	Years	r_S^2 lag	r_P^2 lag	r_S^2	r_P^2
Korpimäki & Norrdahl (1991)[4]	*Sorex araneus*	common shrew	Mammalia	11	1	4	0.212	0.061
Festa-Bianchet & King (1991)	*Spermophilus columbianus* (Ord.)	Columbian ground squirrel	Mammalia	9	1	1	0.056	0.165
Sinclair (1977)	*Syncerus caffer*	African buffalo	Mammalia	9	1	1	0.364	0.269
Owen-Smith (1990)[1]	*Tragelaphus strepsiceros* (Pallas)	greater kudu	Mammalia	11	4	4	0.331	0.230
Owen-Smith (1990)[2]	*Tragelaphus strepsiceros* (Pallas)	greater kudu	Mammalia	11	4	2	0.147	0.145
Wood & Odum (1964)[5]	*Urocyon cinereoargenteus*	gray fox	Mammalia	9	2	1	0.014	0.156
Calhoun (1950)[1]	*Vulpes*	fox (red, cross & silver)	Mammalia	27	2	3	0.256	0.140
Calhoun (1950)[2]	*Vulpes*	fox (red, cross & silver)	Mammalia	27	2	2	0.152	0.103
Calhoun (1950)[3]	*Vulpes*	fox (red, cross & silver)	Mammalia	29	3	2	0.238	0.242
Calhoun (1950)[4]	*Vulpes*	fox (red, cross & silver)	Mammalia	28	2	2	0.440	0.511
Wood & Odum (1964)[6]	*Vulpes fulva*	red fox	Mammalia	9	1	1	0.138	0.107
Dannell & Hörnfeldt (1987)[2]	*Vulpes vulpes*	red fox	Mammalia	15	1	1	0.339	0.241
Hörnfeldt (1978)[5]	*Vulpes vulpes* (L.)	red fox	Mammalia	13	1	1	0.187	0.217
Crecco et al. (1986)	*Alosa sapidissima*	american shad	Osteichthyes	19	1	1	0.144	0.139
Parsons et al. (1977)	*Anguilla anguilla* (L.)	silver eel	Osteichthyes	18	1	1	0.200	0.186
Parsons et al. (1977)	*Anguilla anguilla* (L.)	yellow eel	Osteichthyes	18	1	1	0.229	0.230
Vøllestad & Jonsson (1988)	*Anguilla anguilla* (L.)	European eel	Osteichthyes	13,10	2	2	0.054	0.293

Table C.1: Data sources, species names and the proportions of variance in γ statistically related to the variance in N: r_S^2 and r_P^2.

Reference	Species name	Common name	Class	Years	r_S^2 lag	r_P^2 lag	r_S^2	r_P^2
Iles (1981)	*Clupea harengus* (L.).	North Sea herring	Osteichthyes	23	7	4	0.001	0.008
Parsons et al. (1977)	*Elvers*	elvers	Osteichthyes	15	6	1	0.114	0.155
Kipling & Frost (1970)	*Esox lucius*	pike	Osteichthyes	20	1	1	0.079	0.051
Kipling & Le Cren (1984)	*Esox lucius* (L.)	pike	Osteichthyes	20	1	1	0.178	0.196
Rose et al. (1986)	*Morone americana*	white perch	Osteichthyes	47	1	6	0.115	0.037
Larkin & McDonald (1968)	*Oncorhynchus nerka*	sockeye salmon	Osteichthyes	57	1	1	0.315	0.290
Le Cren et al. (1977)	*Perca fluviatilis*	perch	Osteichthyes	26	1	1	0.070	0.044
Townsend et al. (1990)	*Rutilus rutilus* (L.)	-	Osteichthyes	9	1	3	0.046	0.132
Buck & Hay (1984)	*Salmo salar* (L.)	Atlantic salmon	Osteichthyes	11	1	1	0.245	0.126
Elliott (1984)	*Salmo trutta*	brown trout	Osteichthyes	17	1	1	0.204	0.248
Elliott (1985)	*Salmo trutta* (L.)	migratory trout	Osteichthyes	16,17	1	1	0.205	0.180
Kipling (1984)	*Salvelinus alpinus* (L.)	charr	Osteichthyes	35	1	1	0.060	0.046
Snorrason et al. (1992)	*Salvelinus alpinus* (L.)	Arctic charr	Osteichthyes	30	2	3	0.221	0.049
Andrews (1991)	*Anolis limifrons*	a tropical iguanid lizard	Reptilia	19	2	5	0.019	0.097
Tinkle et al. (1993)	*Sceloporus graciosus*	sagebrush lizard	Reptilia	11	1	1	0.309	0.300

APPENDIX D: Population Data Sets

The population data sets that were analyzed in chapter 2 to calculate the r_S^2 and r_P^2 values (Table C.1) are given here in alphabetical order of the authors of the data sources. The data is provided in a comma-delimited form facilitating the use of an optical scanner and character recognition software to easily transfer this data into a computer text or spreadsheet program.

Each population data set begins with a single line identifying the citation source from which the data was obtained followed by the general units of the data. A line preceding the data states the years that the data span and the number of years in the data. If there were numerous life-stage data for a single population, these data are listed as well, with a brief description of the life stage.

The citation source for each data set corresponds to the citation listed in the Reference column of Table C.1.

Andrews (1991) $N/890\text{m}^2$

1971-1989 19 years

77.92,54.72,38.07,44.01,24.39,115.99,74.35,152.27,60.67,52.94,34.5,27.36,0.59,0.01,
0.59,22.6,41.64,11.3,28.55

Angerbjörn et al. (1991)[1] N

1979-1989 11 years

1.56,2.34,143.3,163.55,0.78,7.01,8.57,40.5,44.39,10.9,38.94

Angerbjörn et al. (1991)[2] N

1968-1989 22 years

0.78,117.19,54.69,0.00,1.56,8.59,91.41,1.56,0.00,63.28,117.97,0.78,14.84,86.72,212.5
,0.78,0.78,0.78,0.78,1.56,0.78,5.47

Arcese et al. (1992) N (breeding females)

1975-1990 16 years

35.16,30,45.48,49.03,66.13,8.06,18.06,26.13,56.13,54.84,73.87,63.55,60.65,55.16,3.2
3,9.03

Baltensweiler (1968) $\overline{N}$ (larvae)

1949-1966 18 years

0.12,0.57,3.06,32.68,493.01,2511.89,983.69,166.51,16.38,0.6,0.52,2.51,10.51,174.93,
1692.67,1322.6,20.96,0.12

Baltensweiler & Fischlin (1988)[1] N per kg of branches (larvae)

1949-1986 38 years

0.016,0.092,0.444,5.192,73.846,356.124,146.981,22.692,2.251,0.088,0.076,0.403,1.76
,32.014,322.773,240.316,3.175,0.021,0.002,0.059,0.193,0.976,11.401,252.427,374.07
1,252.427,6.017,0.014,0.008,0.076,0.234,13.879,240.316,307.287,154.387,8.081,0.15
8,0.802

Baltensweiler & Fischlin (1988)[2] N per kg of branches (larvae)

1960-1979 20 years

2.818,24.709,432.229,69.64,84.834,0.411,0.007,0.063,0.373,2.683,13.01,119.832,372.
759,1.721,0.501,0.321,0.744,5.908,51.795,321.472

Baltensweiler & Fischlin (1988)[3] *N* per kg of branches (larvae)

1958-1976 19 years

0.042,0.092,0.515,1.942,11.975,187.941,322.773,3.503,0.012,0.024,0.021,0.202,1.676,12.579,104.182,114.947,11.975,0.193,0.062

Baltensweiler & Fischlin (1988)[4] *N* per kg of branches (larvae)

1960-1980 21 years

0.03,0.169,3.111,54.414,251.189,25.959,0.355,0.027,0.049,0.178,0.821,4.182,9.211,5.095,5.623,6.521,0.581,0.139,0.081,0.196,3.268

Baltensweiler & Fischlin (1988)[5] *N* per kg of branches (larvae)

1961-1970 20 years

0.098,0.641,10.68,145.977,337.731,57.167,0.373,0.063,0.196,0.862,6.207,38.522,57.167,196.271,27.272,4.616,1,0.277,0.206,1.559

Barlow et al. (1986) N/m^2

1974-1983 10 years

4.51,0.55,8.13,14.18,4.07,3.19,6.04,2.2,4.4,6.59

Bejer (1988) *N* (in 12,000 hectares)

1900-1941 42 years

10788.64,12776.03,473.19,1041.01,21293.38,27539.43,11072.56,20347,22996.85,567.82,189.27,28012.62,1041.01,94.64,94.74,1041.01,283.91,3690.85,8990.54,1419.56,1987.38,15236.59,1135.65,567.82,851.74,3028.39,0.001,1324.92,49409,107142,10883.28,473.19,757.1,4353.31,1419.56,2460.57,94.64,662.46,9842.27,283.91,189.27,185.94

Blank et al. (1967) *N* (pairs)

1949-1959 11 years

261,370,371,468,559,614,456,440,561,609,335

Broekhuizen et al. (1993)[1] N/m^2 (pupae)

1953-1989 37 years

1.461,2.379,16.731,19.684,0.763,0.338,0.092,2.379,6.31,4.559,3.875,2.022,0.244,0.468,5.363,10.275,2.799,0.338,0.177,0.288,1.056,4.559,10.275,32.054,5.363,0.057,0.001,0.128,1.461,16.731,162.841,2.379,0.244,0.128,0.763,2.799,14.221

Broekhuizen et al. (1993)[2] N/m^2 (pupae)

1953-1989 37 years

38.141,0.308,0.499,0.585,0.499,2.485,10.55,10.55,7.651,27.661,1.535,0.499,0.308,2.116,6.516,12.389,4.725,1.307,6.516,27.661,14.548,4.024,5.549,10.55,14.548,5.549,1.535,1.113,4.024,5.549,8.984,6.516,0.585,1.535,4.024,3.427,1.535

Broekhuizen et al. (1993)[3] N/m^2 (pupae)

1953-1989 37 years

0.848,0.268,0.373,0.848,0.373,1,0.518,0.373,0.3731,0.719,0.72,0.7201,0.518,0.72,0.373,0.228,0.316,0.518,0.1,0.2681,0.267,0.2677,0.228,0.139,0.228,0.118,0.139,0.1391,0.037,0.72,0.611,0.268,0.268,0.164,0.518,0.0001,0.00015

Broekhuizen et al. (1994) N/m^2 (pupae)

1950-1970 21 years

8.14,2.512,0.046,1.697,2.147,1.342,0.613,0.001,0.149,0.239,1.061,2.717,6.959,5.086,0.086,0.002,0.001,0.0001,0.0002,0.018,0.031

Brown & Heske (1990)[1] $\bar{N}$ per 6 month period

1977-1988 10 years 2 points per year 21 points

(0,0.08) (0.5,2.95) (1,0.65) (1.5,2.54) (2,0.49) (2.5,1.97) (3,0.57) (3.5,1.80) (4,0.49) (4.5,4.34) (5,0.00) (5.5,4.59) (6,0.49) (6.5,3.03) (7,0.08) (7.5,4.18) (8,1.22) (8.5,3.44) (9,0.16) (9.5,6.97) (10,0.00)

Brown & Heske (1990)[2] $\bar{N}$ per 6 month period

1977-1988 10 years 2 points per year 21 points

(0,35.11) (0.5,28.95) (1,24.89) (1.5,11.05) (2,24.10) (2.5,17.63) (3,24.89) (3.5,24.74)
(4,43.76) (4.5,43.68) (5,60.26) (5.5,35.79) (6,38.25) (6.5,27.89) (7,49.00) (7.5,39.21)
(8,52.14) (8.5,38.42) (9,40.87) (9.5,41.05) (10,43.49)

Brown & Heske (1990)[3] $\bar{N}$ per 6 month period

1977-1988 10 years 2 points per year 21 points

(0,1.57) (0.5,1.58) (1,1.83) (1.5,1.32) (2,3.93) (2.5,2.37) (3,5.24) (3.5,4.74) (4,6.03)
(4.5,6.32) (5,15.46) (5.5,9.47) (6,11.00) (6.5,4.74) (7,15.46) (7.5,11.84) (8,14.41)
(8.5,7.63) (9,18.60) (9.5,14.74) (10,18.34)

Brown & Heske (1990)[4] $\bar{N}$ per 6 month period

1977-1988 10 years 2 points per year 21 points

(0,16.58) (0.5,31.70) (1,17.89) (1.5,20.96) (2,12.37) (2.5,23.58) (3,20.26) (3.5,19.13)
(4,17.11) (4.5,31.97) (5,17.89) (5.5,23.84) (6,21.32) (6.5,2.36) (7,0.79) (7.5,6.03)
(8,9.21) (8.5,6.55) (9,7.37) (9.5,7.86) (10,3.68)

Brown & Heske (1990)[5] $\bar{N}$ per 6 month period

1977-1988 10 years 2 points per year 21 points

(0,4.69) (0.5,3.8) (1,1.73) (1.5,2.98) (2,3.21) (2.5,4.30) (3,3.87) (3.5,4.30) (4,7.98)
(4.5,11.65) (5,4.28) (5.5,10.58) (6,6.58) (6.5,7.27) (7,0.82) (7.5,4.96) (8,4.36) (8.5,7.27)
(9,5.02) (9.5,13.06) (10,12.43)

Brown & Heske (1990)[6] $\bar{N}$ per 6 month period

1977-1988 10 years 2 points per year 21 points

(0,2.56) (0.5,2.15) (1,6.28) (1.5,2.15) (2,9.26) (2.5,2.73) (3,6.61) (3.5,0.91) (4,5.37)
(4.5,3.39) (5,10.74) (5.5,2.81) (6,5.29) (6.5,5.79) (7,10.41) (7.5,4.21) (8,7.69) (8.5,2.98)
(9,6.45) (9.5,6.86) (10,6.61)

Brown & Heske (1990)[7] $\bar{N}$ per 6 month period

1977-1988 10 years 2 points per year 21 points

(0,6.83) (0.5,2.55) (1,4.03) (1.5,5.19) (2,7.82) (2.5,3.21) (3,7.65) (3.5,1.89) (4,5.51)
(4.5,7.74) (5,6.42) (5.5,6.26) (6,7.33) (6.5,5.02) (7,4.69) (7.5,3.37) (8,6.50) (8.5,2.47)
(9,1.89) (9.5,4.44) (10,3.95)

Brown & Heske (1990)[8] $\bar{N}$ per 6 month period

1977-1988 10 years 2 points per year 21 points

(0,4.15) (0.5,2.60) (1,1.22) (1.5,1.46) (2,5.77) (2.5,6.26) (3,4.96) (3 5,3.25) (4,6.75)
(4.5,12.36) (5,16.02) (5.5,11.54) (6,0.81) (6.5,0.49) (7,0.00) (7.5,0.49) (8,0.24)
(8.5,0.08) (9,0.24) (9.5,0.41) (10,0.81)

Brown & Heske (1990)[9] $\bar{N}$ per 6 month period

1977-1988 10 years 2 points per year 21 points

(0,0.98) (0.5,1.63) (1,0.33) (1.5,1.14) (2,2.12) (2.5,0.98) (3,1.31) (3.5,1.14) (4,11.27)
(4.5,7.97) (5,2.61) (5.5,4.39) (6,0.82) (6.5,2.11) (7,2.45) (7.5,1.95) (8,7.67) (8.5,2.28)
(9,4.24) (9.5,11.87) (10,22.04)

Brown & Heske (1990)[10] $\bar{N}$ per 6 month period

1977-1988 10 years 2 points per year 21 points

(0,0.00) (0.5,0.16) (1,0.16) (1.5,0.00) (2,0.00) (2.5,0.16) (3,0.16) (3.5,0.65) (4,3.59)
(4.5,6.69) (5,3.43) (5.5,2.94) (6,2.78) (6.5,0.65) (7,1.14) (7.5,0.49) (8,0.00) (8.5,2.29)
(9,5.88) (9.5,14.04) (10,13.06)

Brown & Heske (1990)[11] $\bar{N}$ per 6 month period

1977-1988 10 years 2 points per year 21 points

(0,0.81) (0.5,0.16) (1,0.49) (1.5,0.16) (2,5.85) (2.5,0.82) (3,1.30) (3.5,1.15) (4,17.56)
(4.5,7.87) (5,16.42) (5.5,6.89) (6,8.62) (6.5,4.59) (7,5.85) (7.5,3.77) (8,10.73) (8.5,3.61)
(9,11.54) (9.5,13.77) (10,33.66)

Buck and Hay (1984) *N* (males & females)

1966-1976 11 years

269,214,196,49,90,125,137,225,184,121,164

Calhoun (1950)[1] *N*

1915-1940 27 years

0.3253,0.5414,0.7822,1.2654,1.4373,3.657,2.3253,1.9622,0.9809,0.5894,0.5044,0.5649,0.7822,1.0528,1.2476,1.7522,1.2654,1.083,0.7933,0.679,0.7391,1.1141,1.4996,3504.41,3504.41,3173.5,1562.59

Calhoun (1950)[2] *N*

1915-1940 27 years

0.1259,0.1966,0.6625,0.8678,0.9037,2.3567,4.6288,5.5919,1.6591,0.2907,0.3283,0.3966,0.4419,0.2868,0.7685,2.0871,2.3567,1.5932,1.3549,0.6536,0.5338,0.4791,1.6591,1859.08,1613.97,2573.51,997.98

Calhoun (1950)[3] *N*

1915-1942 29 years

347.68,449.72,648.28,1070.07,1542.54,4558.52,3036.36,2837.53,1481.11,1027.46,1013.64,1241.99,2106.34,2995.51,3874.68,6751.68,5011.87,4318.11,3338.33,2837.53,3293.42,4497.19,5510.32,5363.05,1990.40,1332.71,549.90,358.15

Calhoun (1950)[4] *N*

1915-1941 28 years

98.65,205.01,276.17,347.68,773.1,1403,2164.18,1864.61,675.17,861.58,392.75,398.11,566.16,581.71,1055.67,2687.89,1839.53,1422.14,666.08,551.03,551.03,501.19,973.27,1461.19,2204.62,2264.64,575.44,193.87

Chastel et al. (1993)　　*N* breeding pairs

1963-1990　28 years

58.33,46.67,43.85,14.48,40.23,47.47,37.82,37.82,35.8,45.46,48.68,39.83,37.01,8.05,3
9.83,32.18,34.2,41.03,48.28,37.41,16.49,37.82,14.48,36.61,36.21,20.52,37.82,45.06

Connor and Beck (1993)　　*N* density

1982-1991　10 years

23.48,4.51,1.58,0.01,0.01,0.01,0.04,0.17,0.13,1.86

Cooch et al. (1989)　　*N*

1970-1987　18 years

2266,2954,2761,3037,2789,3092,3725,3505,5679,5514,4440,6642,5569,5927,8844,83
49,7936,6284

Coulson and Thomas (1985)　　*N* nests

1949-1982　34 years

3.93,10.73,11.52,12.57,16.75,20.68,30.89,32.98,34.29,37.7,43.98,51.83,60.73,69.9,83.
25,88.22,104.45,97.64,104.19,96.6,90.31,98.69,84.82,86.91,79.58,71.99,71.99,68.85,6
6.75,73.3,75.13,86.91,87.43,70.42

Crecco et al. (1986)　　*N* (stock size)

1966-1984　19 years

115,167,202,384,413,424,167,111,306,247,435,157,210,247,341,293,501,423,661

Crowley & Johnson (1992)[1]　　*N* (larvae)

1978-1989　12 years

2.88,19.83,7.1,21.1,4.06,8.83,6.47,7.56,18.06,20.46,21.77,4.45

Crowley & Johnson (1992)[2]　　*N* (larvae)

1978-1989　12 years

15.88,179.3,2.98,43.77,150.33,126.03,54.56,157.1,150.33,26.95,71.07,213.87

Crowley & Johnson (1992)[3] *N* (larvae)

1978-1989 12 years

100,47.11,0.09,0.1,61.44,1.86,0.09,0.09,0.1,0.1,15.57,0.11

Crowley & Johnson (1992)[4] *N* (larvae)

1978-1989 12 years

28.06,3.94,16.96,39.91,9.75,48.81,19.73,66.02,48.81,29.51,29.51,0.1

Crowley & Johnson (1992)[5] *N* (larvae)

1978-1989 12 years

78.17,219.91,31.04,62.63,121.78,23.97,26.78,52.07,131.11,8.21,121.78,84.17

Crowley & Johnson (1992)[6] *N* (larvae)

1978-1989 12 years

386.33,211.88,156.91,201.53,286.1,258.85,105.13,135.03,173.43,173.43,19.17,67

Crowley & Johnson (1992)[7] *N* (larvae)

1978-1989 12 years

399.08,692.51,297.44,205.98,535.46,863.32,370.81,332.11,256.79,429.52,344.54,429.52

Crowley & Johnson (1992)[8] *N* (larvae)

1978-1989 12 years

0.12,3.75,0.11,7.97,0.11,3.75,18.76,5.33,29.51,0.11,2.77,0.1

Croxall et al. (1990) *N* (breeding pairs)

1976-1989 14 years

1433,1541,1382,1466,1339,1415,1404,1453,1366,1232,1491,1233,1366,1411

Curry and Grant (1989) N (adults)

1978-1988 11 years

19,36,113,172,159,119,169,140,62,94,65

Dannell and Hörnfeldt (1987)[1] $N/1000$ hectares

1970-1984 15 years

6.91,4.51,4.57,11.01,21.51,18.43,19.28,30.52,32.57,18.25,22.99,30.81,33.89,25.51,32.87

Dannell and Hörnfeldt (1987)[2] $N/1000$ hectares

1970-1984 15 years

3.65,5.18,4.03,4.46,5.31,4.79,3.1,2.99,5.68,4.35,4.86,4.06,4.25,4,4.12

Davis & Newton (1981) N

1951-1980 30 years

30.30,30.30,28.15,30.30,27.30,25.58,25.15,31.16,26.87,24.72,32.45,37.60,36.74,39.75,42.33,44.04,47.48,51.77,56.93,59.07,58.22,64.23,74.11,77.54,73.68,78.40,86.99,86.99,87.42,95.15

Dempster (1982)[1] $N/150\text{m}^2$

1966-1974 9 years

848.34,3202.54,580.41,69.29,2550.31,233.42,59.53,90.37,93.87

Dempster (1982)[2] $N/150\text{m}^2$

1966-1974 9 years

1951.29,16819.25,12040.52,57.29,3046.99,22638.03,1561.52,4937.97,6170.53

Dhondt & Eyckerman (1980)[1] $N/(10\text{ha})$ (pairs)

1960-1978 19 years

12.53,14.02,11.19,6.56,9.85,9.55,9.85,13.58,12.38,10.00,13.73,8.20,10.59,13.88,8.95,13.88,8.50,10.29,8.95

Dhondt & Eyckerman (1980)[2] $N/(10\text{ha})$ (pairs)

1960-1978 19 years

12.48,13.98,10.82,6.31,9.32,9.77,9.62,13.53,12.18,9.62,13.38,7.81,10.22,13.23,8.57,13.23,7.81,9.77,8.42

Dobson & Hudson (1992) N/km^2 (hens breeding)

1976-1989 14 years

892.93,1572.97,3891.92,6601.95,2048.69,2382.59,1078.42,10000,2382.59,1972.8,298.82,1302.43,2294.33,4700.36

Ehrlich et al. (1975)[1] N

1960-1974 15 years

127.04,684.11,1461.76,1414.29,2737.01,4000.83,3336.55,1724.09,1811.61,1323.93,2101.75,793.67,2208.44,672.91,285.23

Ehrlich et al. (1975)[2] N

1960-1974 15 years

166.51,326.8,74.38,84.83,326.8,372.76,834.5,820.89,1508.59,641.42,951.86,425.18,2727.18,1140.63,571.67

Ehrlich et al. (1975)[3] N

1966-1974 9 years

9.52,75.46,151.31,159.02,207.27,20.39,20.39,42.26,9.52

Elliott (1984) N/m^2

1967-1983 17 years 2 points per year 33 points

(0.46,6.17) (0.71,2.38) (1.46,7.42) (1.71,2.00) (2.46,7.47) (2.71,1.50) (3.46,8.20) (3.71,2.50) (4.46,6.05) (4.71,2.41) (5.46,8.22) (5.71,2.60) (6.46,8.85) (6.71,2.73) (7.46,3.12) (7.71,1.96) (8.46,3.66) (8.71,1.89) (9.46,6.62) (9.71,1.90) (10.46,4.72) (10.71,2.32) (11.46,7.67) (11.71,2.33) (12.46,6.35) (12.71,1.85) (13.46,5.30) (13.71,1.44) (14.46,3.47) (14.71,1.80) (15.46,3.40) (15.71,1.97) (16.46,7.80)

Elliott (1985) $N/60\mathrm{m}^{-}$

eggs

1967-1983 17 years

4652,2272,1756,2584,4644,2888,3610,7958,7334,4234,6300,2068,1034,722,7646,7958,2478

alevins

1967-1983 17 years

4622,2267,1622,2311,4333,2489,3334,8400,7444,4489,6222,2000,1089,844,7933,7978,2400

0+ parr, May/June

1967-1983 17 years

346,409,403,460,308,439,412,132,182,354,241,429,334,286,178,158,425

0+ parr, Aug./Sept.

1967-1983 17 years

116,92,74,115,110,112,119,74,88,91,99,105,73,61,87,81,43

1+ parr, May/June

1967-1982 16 years

35,41,27,51,46,48,45,30,42,37,29,46,30,27,44,41

1+ parr, Aug./Sept.

1967-1982 16 years

28,14,30,47,44,45,44,25,23,38,31,38,25,21,37,14

2+ parr, May/June

1967-1981 15 years

4,5,4,8,7,10,8,1,5,2,1,2,3,4,2

2+ parr, Aug./Sept.

1967-1981 15 years

2,5,0,0,0,0,0,0,2,4,0.,0,0,0,0

3+ spawners, Nov./Dec.

1967-1980 14 years

6,4,5,7,7,5,5,2,1,1,5,7,3,3

4+ spawners, Nov./Dec.

1967-1979 13 years

0.001,0,0,0,0,1,0,0,0,2,0,0,0

Elton & Nicholoson (1942) *N*

1821-1891 71 years

4160,2530,2900,2350,1810,4160,6700,15950,23200,21930,8510,3980,2350,2900,561
0,17940,33890,53470,41690,14500,3080,1450,1990,4890,12680,20660,35340,27730,
6160,1080,180,370,360,3620,11780,15220,24650,12870,6880,3440,540,180,1630,815
0,25740,57640,49480,24650,7250,2710,360,1080,4350,8700,24650,27550,19930,906
0,8330,3260,1810,3620,14320,39150,63260,62350,30810,13230,4890,1630,1990

and continues...

1897-1913 17 years

13590,5430,720,1450,3080,12140,25740,46040,53110,33350,6340,360,1080,3080,85
10,12500,17940

and continues...

1915-1934 20 years

6160,7790,1450,180,540,1260,2530,2900,6520,6160,8510,6520,3980,2170,1450,2170
,2710,3620,5430,6340

Festa-Bianchet and King (1991) *N*

1979-1987 9 years

26,56,50,45,57,77,46,42,34

Gaillard et al. (1993)[1]
1979-1990 12 years

199.04,167.73,158.79,149.84,181.15,234.82,241.53,216.93,147.6,80.51,67.09,165.5

Gaillard et al. (1993)[2] *N*
1979-1990 12 years

328.75,337.7,281.79,366.77,505.43,500.96,440.58,324.28,342.17,214.7,174.44,129.71

Garsd & Howard (1982)[1] *N*
1959-1979 21 years 6 points per year 125 points

(0.17,3.64) (0.33,5.47) (0.5,3.64) (0.67,1.82) (0.83,5.47) (1,7.29) (1.17,14.59)
(1.33,62.04) (1.5,18.24) (1.67,3.64) (1.83,16.42) (2,5.47) (2.17,38.32) (2.33,67.51)
(2.5,20.07) (2.67,16.42) (2.83,23.72) (3,10.94) (3.17,14.59) (3.33,118.61) (3.5,40.14)
(3.67,12.77) (3.83,5.47) (4,12.77) (4.17,45.62) (4.33,124.08) (4.5,85.76) (4.67,52.91)
(4.83,56.56) (5,49.27) (5.17,240.87) (5.33,116.78) (5.5,120.43) (5.67,7.29) (5.83,9.12)
(6,5.47) (6.17,14.59) (6.33,51.09) (6.5,3.64) (6.67,3.64) (6.83,14.59) (7,10.94)
(7.17,7.29) (7.33,32.84) (7.5,7.29) (7.67,3.64) (7.83,7.29) (8,10.94) (8.17,14.59)
(8.33,21.89) (8.5,10.94) (8.67,10.94) (8.83,18.24) (9,32.84) (9.17,51.09) (9.33,67.51)
(9.5,26.81) (9.67,2.17) (9.83,25.54) (10,30.14) (10.17,47.44) (10.33,85.76) (10.5,32.84)
(10.67,3.00) (10.83,5.82) (11,1.00) (11.17,3.64) (11.33,1.00) (11.5,1.82) (11.67,1.20)
(11.83,1.40) (12,1.82) (12.17,1.82) (12.33,1.82) (12.5,1.00) (12.67,1.82) (12.83,8.82)
(13,14.59) (13.17,5.47) (13.33,16.42) (13.5,1.82) (13.67,1.82) (13.83,3.29) (14,7.29)
(14.17,3.82) (14.33,8.29) (14.5,1.82) (14.67,2.82) (14.83,1.82) (15,10.94) (15.17,7.29)
(15.33,7.94) (15.5,4.82) (15.67,1.00) (15.83,7.29) (16,43.79) (16.17,7.29) (16.33,43.79)
(16.5,5.47) (16.67,3.64) (16.83,14.59) (17,41.97) (17.17,107.66) (17.33,145.98)
(17.5,52.91) (17.67,7.29) (17.83,1.82) (18,1.82) (18.17,1.82) (18.33,3.64) (18.5,1.82)
(18.67,1.82) (18.83,14.5) (19,7.29) (19.17,31.02) (19.33,36.49) (19.5,7.29) (19.67,3.64)
(19.83,12.77) (20,87.59) (20.17,16.42) (20.33,54.74) (20.5,14.59) (20.67,9.12)
(20.83,5.47)

Garsd & Howard (1982)[2] *N*

1959-1979 21 years 6 points per year 125 points

(0.17,1.875) (0.33,1.875) (0.5,5.625) (0.67,1.875) (0.83,0.875) (1,5.625) (1.17,5.625)
(1.33,9.375) (1.5,3.75) (1.67,1.875) (1.83,13.125) (2,5.625) (2.17,9.375) (2.33,20.625)
(2.5,7.5) (2.67,9.375) (2.83,11.25) (3,9.375) (3.17,11.2) (3.33,41.25) (3.5,13.125)
(3.67,9.375) (3.83,18.75) (4,15) (4.17,33.75) (4.33,56.25) (4.5,37.5) (4.67,37.5)
(4.83,39.375) (5,37.5) (5.17,116.25) (5.33,116) (5.5,60) (5.67,15) (5.83,13.125)
(6,13.125) (6.17,7.5) (6.33,41.25) (6.5,11.25) (6.67,11.25) (6.83,13.125) (7,13.125)
(7.17,31.875) (7.33,18.75) (7.5,7.5) (7.67,1.875) (7.83,3.75) (8,5.625) (8.17,22.5)
(8.33,28.125) (8.5,11.25) (8.67,11.25) (8.83,20.625) (9,43.125) (9.17,28.25)
(9.33,43.125) (9.5,43.125) (9.67,3.75) (9.83,16.875) (10,31.875) (10.17,20.625)
(10.33,46.875) (10.5,20.625) (10.67,1.875) (10.83,7.5) (11,13.125) (11.17,3.75)
(11.33,1.875) (11.5,1.875) (11.67,5.625) (11.83,3.75) (12,0.8) (12.17,3.75)
(12.33,1.875) (12.5,1.875) (12.67,1.875) (12.83,3.75) (13,7.5) (13.17,5.35) (13.33,3.75)
(13.5,3.75) (13.67,5.35) (13.83,9.375) (14,5.625) (14.17,20.625) (14.33,5.625)
(14.5,1.875) (14.67,3.75) (14.83,5.625) (15,1.875) (15.17,15) (15.33,1.875) (15.5,1.875)
(15.67,3.75) (15.83,3.75) (16,11.25) (16.17,1.875) (16.33,7.5) (16.5,5.25) (16.67,5.35)
(16.83,7.5) (17,18.75) (17.17,54.375) (17.33,65.625) (17.5,13.125) (17.67,3.75)
(17.83,1.875) (18,5.625) (18.17,1.875) (18.33,3.75) (18.5,3.75) (18.67,5.35)
(18.83,3.75) (19,7.5) (19.17,11.25) (19.33,28.125) (19.5,3.75) (19.67,5.75) (19.83,3.75)
(20,16.875) (20.17,16.875) (20.33,46.875) (20.5,28.125) (20.67,11.25) (20.83,1.875)

Grant & Grant (1992)[1] *N* (breeding birds)

1976-1991 16 years

511.95,0.01,129.01,122.87,135.15,174.06,67.58,411.6,337.88,0.01,30.72,219.11,0.01,
2.05,120.82,247.78

Grant & Grant (1992)[2] *N* (breeding birds)

1976-1991 16 years

145.39,79.86,98.29,63.48,122.87,126.96,94.2,249.83,212.97,0.01,16.38,51.19,2.05,2.0
5,10.24,38.91

Gulland (1971)[1] *N* index

1946-1964 19 years

1.86,1.12,0.94,0.77,0.77,0.59,0.51,0.39,0.28,0.33,0.24,0.22,0.14,0.08,0.14,0.06,0.06,0.02,0.01

Gulland (1971)[2] *N* index

1946-1969 24 years

2.71,3.06,2.26,2.35,2.01,2.55,2.48,3.18,3.01,3.28,3.04,2.69,2.63,1.95,1.74,1.3,1.11,0.9,0.55,0.2,0.29,0.24,0.41,0.44

Hindell (1991) *N*

1957-1965 9 years

1238,405,818,304,312,815,618,1031,465

Harrison et al. (1991)[1] *N*

1960-1986 27 years

90,175,40,45,175,200,425,425,800,256,713,198,1819,575,567,1819,7227,852,216,244,267,1753,999,1788,143,79,94

Harrison et al. (1991)[2] *N*

1960-1986 27 years

70,350,750,750,1400,2000,1750,900,576,871,820,235,1149,370,177,317,1001,190,341,135,125,316,109,122,31,48,18

Holmes et al. (1986)[1] *N*

1969-1984 16 years

2,2,5,2,1,0,2,2,3,4,3,1,2,3,2,2

Holmes et al. (1986)[2] *N*

1969-1984 16 years

6,8,7,7,4,2,8,5,4,2,0,2,1,1,2,4

Holmes et al. (1986)[3] *N*

1969-1984 16 years

9,8,11,11,9,7,8,7,4,5,7,3,2,1,2,2

Holmes et al. (1986)[4] *N*

1969-1984 16 years

4,8,11,10,11,12,12,11,12,10,15,8,12,14,14,10

Holmes et al. (1986)[5] *N*

1969-1984 16 years

2,6,4,7,4,6,6,2,3,1,2,3,4,5,2,1

Holmes et al. (1986)[6] *N*

1969-1984 16 years

8,9,13,7,6,10,8,8,7,7,10,10,10,9,11,8

Holmes et al. (1986)[7] *N*

1969-1981 13 years

26,28,43,50,57,27,30,28,34,22,22,15,1

Holmes et al. (1986)[8] *N*

1969-1984 16 years

7,6,9,7,4,5,6,5,9,7,7,3,0,2,2,1

Holmes et al. (1986)[9] *N*

1969-1977 9 years

8,4,8,8,2,5,5,6,2

Holmes et al. (1986)[10] *N*

1969-1984 16 years

8,4,6,10,5,8,8,8,6,4,5,7,8,8,5,6

Holmes et al. (1986)[11] *N*

1969-1982 12 years

6,3,3,2,2,2,3,3,3,4,2,4

Holmes et al. (1986)[12] *N*

1969-1984 16 years

2,1,1,2,2,1,2,2,3,2,3,2,2,3,1,2

Holmes et al. (1986)[13] *N*

1969-1984 16 years

4,7,5,8,8,4,3,3,5,5,3,5,6,7,8,5

Holmes et al. (1986)[14] *N*

1969-1984 16 years

6,6,9,9,11,10,18,19,9,13,12,10,10,11,14,11

Holmes et al. (1986)[15] *N*

1969-1984 16 years

12,26,30,29,26,22,39,42,44,32,36,34,22,32,30,13

Holmes et al. (1986)[16] *N*

1969-1977 9 years

1,1,2,1,3,6,2,5,1

Holmes et al. (1986)[17] *N*

1969-1984 16 years

20,24,29,22,26,22,31,30,23,20,16,12,25,23,22,20

Holmes et al. (1986)[18] *N*

1969-1982 14 years

5,8,6,8,4,4,4,4,2,3,2,3,2,2

Hörnfeldt (1978)[1]

1963-1975 13 years

370.66,231.66,38.61,324.32,667.95,15.44,169.88,243.24,84.94,69.5,312.74,864.86,185.33

Hörnfeldt (1978)[2] *N*

1963-1975 13 years

251.92,75,113.46,159.62,192.31,53.85,88.46,80.77,28.85,69.23,196.15,265.38,244.23

Hörnfeldt (1978)[3] *N*

1963-1975 13 years

9923.66,9923.66,9541.98,15076.34,2862.6,1717.56,1240.46,17270.99,4007.63,3244.27,2003.82,5534.35,1812.98

Hörnfeldt (1978)[4] *N*

1963-1975 13 years

20038.17,19083.97,14599.24,24045.8,3244.27,3530.53,5057.25,11354.96,5820.61,4961.83,6679.39,13740.46,5438.93

Hörnfeldt (1978)[5] *N*

1963-1975 13 years

5116.28,6046.51,6705.43,6589.15,6124.03,3798.45,4147.29,5930.23,5077.52,4379.84,5193.8,7635.66,4069.77

Hörnfeldt (1994)[1] $N/100$ trap-nights

1971-1988 18 years 2 points per year 35 points

(0.75,0.53) (1.42,0.35) (1.75,6.57) (2.42,3.42) (2.75,13.23) (3.42,5.08) (3.75,9.64) (4.42,0.26) (4.75,0.53) (5.42,0.26) (5.75,1.58) (6.42,1.49) (6.75,7.27) (7.42,2.63) (7.75,4.12) (8.42,0.26) (8.75,0.61) (9.42,0.70) (9.75,5.69) (10.42,1.31) (10.75,6.22) (11.42,0.88) (11.75,1.31) (12.42,0.44) (12.75,2.28) (13.42,1.75) (13.75,8.41)

(14.42,0.61) (14.75,0.88) (15.42,0.18) (15.75,1.93) (16.42,1.23) (16.75,3.77) (17.42,1.14) (17.75,3.42)

Hörnfeldt (1994)[2] $N/100$ trap-nights

1971-1988 18 years 2 points per year 35 points

(0.75,0.11) (1.42,0.06) (1.75,0.37) (2.42,0.34) (2.75,1.95) (3.42,1.81) (3.75,3.42) (4.42,0.37) (4.75,0.08) (5.42,0.06) (5.75,0.25) (6.42,0.31) (6.75,1.64) (7.42,2.01) (7.75,3.00) (8.42,0.03) (8.75,0.06) (9.42,0.08) (9.75,0.40) (10.42,0.54) (10.75,2.35) (11.42,0.96) (11.75,0.51) (12.42,0.06) (12.75,0.28) (13.42,0.11) (13.75,1.22) (14.42,0.76) (14.75,0.48) (15.42,0.06) (15.75,0.20) (16.42,0.08) (16.75,0.34) (17.42,0.14) (17.75,0.42)

Hörnfeldt (1994)[3] $N/100$ trap-nights

1971-1988 18 years 2 points per year 35 points

(0.75,0.02) (1.42,0.02) (1.75,0.27) (2.42,0.56) (2.75,1.84) (3.42,2.76) (3.75,1.13) (4.42,0.02) (4.75,0.00) (5.42,0.00) (5.75,0.09) (6.42,0.42) (6.75,0.87) (7.42,2.16) (7.75,0.82) (8.42,0.00) (8.75,0.04) (9.42,0.04) (9.75,0.02) (10.42,0.20) (10.75,0.84) (11.42,0.22) (11.75,0.02) (12.42,0.02) (12.75,0.04) (13.42,0.24) (13.75,1.29) (14.42,0.18) (14.75,0.02) (15.42,0.04) (15.75,0.04) (16.42,0.40) (16.75,1.22) (17.42,0.31) (17.75,0.42)

Hudson et al. (1992) N/km^2 hens

1977-1991 15 years

54.25,21.64,7.95,22.74,38.08,46.3,7.4,15.62,39.45,45.75,45.21,54.52,31.78,17.81,45.75

Iles (1981) N index

1952-1974 23 years

2,1.85,1.79,1.79,1.63,1.54,1.23,1.97,1.81,1.56,1.15,1.83,1.86,1.29,1.05,0.81,0.33,0.36,0.31,0.22,0.26,0.23,0.24

Itô (1972) N index

1910-1944   35 years   2 points per year   69 points

(0.25,1.64) (0.75,0.6) (1.25,0.53) (1.75,0.62) (2.25,0.74) (2.75,0.39) (3.25,0.65)
(3.75,0.69) (4.25,1.64) (4.75,1.08) (5.25,1.36) (5.75,1.55) (6.25,1.13) (6.75,0.97)
(7.25,1.57) (7.75,1.11) (8.25,0.55) (8.75,0.46) (9.25,0.97) (9.75,1.15) (10.25,1.36)
(10.75,0.55) (11.25,0.83) (11.75,1.25) (12.25,1.59) (12.75,0.85) (13.25,1.15)
(13.75,3.51) (14.25,0.67) (14.75,0.48) (15.25,1.48) (15.75,2.08) (16.25,0.69)
(16.75,2.28) (17.25,1.43) (17.75,1.02) (18.25,0.81) (18.75,0.86) (19.25,1.20)
(19.75,0.59) (20.25,0.99) (20.75,0.97) (21.25,1.6) (21.75,3.45) (22.25,2.28) (22.75,1.33)
(23.25,0.81) (23.75,0.52) (24.25,1.02) (24.75,0.61) (25.25,1.17) (25.75,1.13)
(26.25,1.35) (26.75,0.77) (27.25,0.52) (27.75,0.83) (28.25,1.40) (28.75,0.32)
(29.25,0.11) (29.75,0.59) (30.25,0.41) (30.75,0.77) (31.25,0.16) (31.75,0.25)
(32.25,0.56) (32.75,0.77) (33.25,0.25) (33.75,0.47) (34.25,0.52)

Jaeger (1980)[1] N/m^2

1966-1979   14 years   2 points per year   28 points

(0.42,32) (0.75,32) (1.42,48) (1.75,27) (2.42,23) (2.75,46) (3.42,31) (3.75,28) (4.42,35)
(4.75,35) (5.42,40) (5.75,40) (6.42,35) (6.75,35) (7.42,37) (7.75,37) (8.42,30) (8.75,29)
(9.42,40) (9.75,40) (10.42,23) (10.75,23) (11.42,42) (11.75,42) (12.42,44) (12.75,27)
(13.42,49) (13.75,49)

Jaeger (1980)[2] N/m^2

1966-1979   14 years   2 points per year   28 points

(0.42,14) (0.75,14) (1.42,15) (1.75,13) (2.42,15) (2.75,19) (3.42,16) (3.75,16) (4.42,14)
(4.75,2) (5.42,2) (5.75,2) (6.42,3) (6.75,3) (7.42,4) (7.75,4) (8.42,3) (8.75,7) (9.42,7)
(9.75,7) (10.42,8) (10.75,8) (11.42,9) (11.75,9) (12.42,13) (12.75,18) (13.42,13)
(13.75,13)

Jones et al. (1993) $\widetilde{N}$ per plant

1981-1989   9 years

5.33,7.89,5.53,7.11,8.88,6.91,6.61,3.45,7.5

Kato (1994) N density

larvae, generation 1

1981-1990 10 years

13986.06,4129.47,22098.91,7894.98,7041.77,1420.10,9195.52,10309.68,5190.77,18973.42

pupae, generation 1

1981-1990 10 years

7356.42,2928.64,8576.96,4641.59,4136.82,1308.18,5843.41,8912.51,3548.13,15252.23

adults, generation 1

1981-1990 10 years

1954.2,1436.12,3101.98,1611.97,2872.06,1231.12,2462.09,8772.91,1436.12,11486.84

larvae, generation 2

1981-1990 10 years

8386.64,9406.37,126762.27,5721.04,28520,753.49,46891.73,93346.86,9406.37,8713.63

pupae, generation 2

1981-1990 10 years

2928.64,4466.84,48231.78,1847.85,9623.51,171.13,18478.5,52079.49,3548.13,4823.18

adults, generation 2

1981-1990 10 years

171.13,152.52,261.02,146.78,261.02,17.11,825.4,735.64,103.91,158.49

Keith (1983)[1] N/km^2 (mares)

1961-1977 17 years

228.75,262.50,108.75,52.50,26.25,33.75,37.50,93.75,150.00,326.25,510.00,251.25,82.50,37.50,3.75,22.50,22.50

Keith (1983)[2] N density index

1963-1981 19 years

14.90,27.95,16.77,13.04,9.31,9.31,42.85,65.21,128.57,91.30,22.36,7.45,3.72,5.59,7.45,24.22,93.16,126.70,264.59

Keith (1983)[3] N

1947-1965 19 years

203.82,189.49,23.88,93.94,9.55,121.01,33.43,42.99,65.28,89.17,202.22,256.36,76.43,106.68,146.49,246.81,90.76,111.46,181.52

Keith (1983)[4] N ($\times 10^3$ individuals)

1963-1975 13 years

201.92,185.89,149.03,235.57,33.65,35.25,49.67,115.38,64.10,51.28,68.91,136.21,57.69

Kipling (1984) N

1939-1973 35 years

7.24,2.23,6.13,7.52,6.41,6.69,14.77,10.03,33.99,23.96,12.26,20.62,21.46,19.23,12.82,15.05,30.65,30.65,22.01,14.77,20.62,39.01,20.9,39.57,46.53,43.19,86.1,90.28,53.78,51.27,62.97,84.15,88.05,63.53,88.33

Kipling & Frost (1970) N ($\times 10^3$)

1944-1963 20 years

23,16,17,16,14,29,25,35,30,29,28,23,20,30,27,26,31,46,41,33

Kipling and Le Cren (1984) N

1954-1973 20 years

57,51,19,31,44,77,103,43,128,101,53,16,52,91,97,84,90,177,80,37

Klomp (1966) $\bar{N}$ per shoot, or

$\bar{N}$ eggs per shoot

1950-1964 15 years

0.1206,0.4945,0.1063,0.014,0.1332,0.0732,0.109,0.0509,0.011,0.0532,0.0663,0.1323,0.2138,0.1019,0.0911

$\bar{N}/\mathrm{m}^2$ (eggs)

1950-1964 15 years

38,136,37,6.3,61,33,58,22,5.4,24,28,61,99,47,42

$\bar{N}$ larvae per shoot (August)

1950-1964 15 years

0.0302,0.0887,0.0046,0.01,0.0251,0.0308,0.0284,0.0042,0.0073,0.0129,0.0178,0.057,0.0536,0.0397,0.0141

$\bar{N}/\mathrm{m}^2$ (larvae, Aug.)

1950-1964 15 years

9.5,24.4,1.6,4.5,11.5,13.9,15.1,1.8,3.6,5.8,7.5,26.3,24.8,18.3,6.5

$\bar{N}$ larvae per shoot (Sept.)

1950-1961 12 years

0.0244,0.0814,0.0037,0.0101,0.0252,0.0266,0.0229,0.0019,0.0044,0.0082,0.0154,0.0556

$\bar{N}/\mathrm{m}^2$ (larvae, Sept.)

1950-1961 12 years

7.7,22.4,1.3,4.5,11.5,12,12.2,0.8,2.2,3.7,6.5,25.6

$\bar{N}$ larvae per shoot (Oct.)

1950-1959 10 years

0.0273,0.0713,0.0036,0.0102,0.0197,0.0164,0.0164,0.0019,0.0051,0.0064

$\bar{N}/\mathrm{m}^2$ (larvae, Oct.)

1950-1959 10 years

8.6,19.6,1.3,4.6,9,7.4,8.7,0.8,2.5,2.9

$\bar{N}/\mathrm{m}^2$ (pupae, Apr.)

1951-1964 14 years

5.42,3.57,0.73,3,3,2.58,1.67,0.12,0.87,1.13,2.25,3.38,5.04,4.63

$\bar{N}/\mathrm{m}^2$ (moths, May-June)

1951-1964 14 years

2.71,1.28,0.1,1.05,1.42,1.52,0.9,0.1,0.48,0.58,1.5,2.13,1.08,0.83

$\bar{N}/\mathrm{m}^2$ (larvae)

1961-1957 15 years

26,23.2,19.8,18.3,13.9,12.2,11.5,8.6,7,5,4.5,4.1,2.8,1.4,1.2

Klomp (1968)[1] $\bar{N}$ per 1000 shoots, or $\bar{N}/\mathrm{m}^2$

$\bar{N}$ per 1000 shoots (larvae)

1950-1966 17 years

25.65,73.05,4,10.82,24.34,29.24,22.5,2.92,6.08,9.49,18.74,69.33,48.06,42.17,10.82,3.9,1.11

$\bar{N}/\mathrm{m}^2$ (eggs)

1950-1966 17 years

34.52,110.94,39.3,6.23,61.08,36.35,56.51,22.21,5.76,25.28,31.93,62.69,113.85,55.06,44.74,3.71,0.29

$\bar{N}/\mathrm{m}^2$ (larvae)

1950-1966 17 years

8.8,22.91,1.64,4.61,14.38,15.95,15.95,0.75,2.29,4.27,6.8,28.17,24.12,22.91,3.75,2.35,0.44

$\bar{N}/\mathrm{m}^2$ (pupae)

1950-1966 17 years

6.07,3.71,0.78,3.01,3.09,2.72,1.7,0.13,0.89,1.12,2.45,3.8,5.33,4.8,0.42,0.32,0.07

(moths)

1950-1965 16 years

2.824,1.327,0.103,1.078,1.552,1.593,0.971,0.096,0.481,0.64,1.678,2.545,1.26,1.05,0.057,0.05

Klomp (1968)[2] $\bar{N}$ per 1000 shoots (larvae)

1951-1966 16 years

0.949,1.825,1.778,0.731,2.027,6.244,1.481,0.38,0.877,1.732,1.17,1.082,0.77,1.481,0.833,0.169

Klomp (1968)[3] $\bar{N}$ per 1000 shoots (larvae)

1951-1966 16 years

2.788,0.957,0.083,0.512,0.211,0.104,0.599,0.32,0.499,0.195,0.247,0.176,0.304,0.211,0.097,0.136

Korpimäki and Norrdahl (1989)[1] N

N (breeding pairs)

1977-1987 11 years

23,2,7,6,3,14,6,2,11,26,1

N (non-breeding males)

1977-1987 11 years

8,0,3,3,3,5,10,0,5,8,2

N (fledglings)

1977-1987 11 years

81,7,17,6,10,56,5,3,39,87,3

N (breeding pairs × 2, non-breeding males and fledglings combined)

1977-1987 11 years

135,11,34,21,19,89,27,7,66,147,7

Korpimäki and Norrdahl (1989)[2]

$N/100\text{km}^2$

1977-1987 11 years

81000,19000,33000,12000,21000,43000,46000,7000,54000,40000,18000

N/km^2 (farmland)

1977-1987 11 years

118,143,43,162,465,85,43,0,14,102,338

Korpimäki and Norrdahl (1989)[3] N density

$N/100\text{km}^2$

1977-1987 11 years

46000,24000,57000,47000,25000,108000,16000,89000,34000,44000,33000

N/km^2 (farmland)

1977-1987 11 years

313,406,925,547,227,1959,192,1274,423,456,183

N/km^2 (woodland)

1977-1987 11 years

601,107,283,429,283,359,142,586,283,442,471

Korpimäki & Norrdahl (1991)[1] N/km^2

1977-1987 11 years 2 points per year 22 points

(0.42,162.24) (0.75,29.5) (1.42,147.49) (1.75,486.73) (2.42,309.73) (2.75,412.98)
(3.42,132.74) (3.75,619.47) (4.42,162.24) (4.75,2477.88) (5.42,29.48) (5.75,870.21)
(6.42,29.5) (6.75,88.5) (7.42,29.51) (7.75,457.23) (8.42,14.75) (8.75,309.73)
(9.42,14.75) (9.75,353.98) (10.42,235.99) (10.75,368.73)

Korpimäki & Norrdahl (1991)[2] N/km^2

1977-1987 11 years 2 points per year 22 points

(0.42,443.79) (0.75,1118.34) (1.42,349.11) (1.75,846.15) (2.42,82.84) (2.75,781.07)
(3.42,17.75) (3.75,195.27) (4.42,5.92) (4.75,17.75) (5.42,260.36) (5.75,1650.89)
(6.42,449.70) (6.75,11.83) (7.42,124.26) (7.75,106.51) (8.42,1254.44) (8.75,1491.12)
(9.42,680.47) (9.75,41.42) (10.42,260.36) (10.75,53.25)

Korpimäki & Norrdahl (1991)[3] N/km^2

1977-1987 11 years 2 points per year 22 points

(0.42,294.12) (0.75,397.06) (1.42,558.82) (1.75,838.24) (2.42,441.18) (2.75,1838.24)
(3.42,470.59) (3.75,1176.47) (4.42,176.47) (4.75,529.41) (5.42,1897.06) (5.75,1794.12)
(6.42,44.12) (6.75,1426.47) (7.42,1382.35) (7.75,941.18) (8.42,397.06) (8.75,1735.29)
(9.42,455.88) (9.75,205.88) (10.42,147.06) (10.75,720.59)

Korpimäki & Norrdahl (1991)[4] N/km^2

1977-1987 11 years 2 points per year 22 points

(0.42,568.05) (0.75,159.76) (1.42,29.59) (1.75,1000.00) (2.42,29.61) (2.75,982.25)
(3.42,106.51) (3.75,384.62) (4.42,177.51) (4.75,437.87) (5.42,71.01) (5.75,437.90)
(6.42,41.42) (6.75,207.10) (7.42,704.14) (7.75,656.80) (8.42,550.30) (8.75,360.95)
(9.42,532.54) (9.75,207.10) (10.42,260.36) (10.75,230.77)

Kowalski and Benson (1978) *N* per hectare

eggs

1965-1973 9 years

1617913.13,2341008.55,1422279.99,1472008.78,457559.74,1954541.07,1157264.95,1099119.21,2281439.73

larvae

1965-1973 9 years

1071426.79,1035097.6,433215.61,70216.94,72057.29,863633.74,585855.21,765411.71,1026209.43

adults

1965-1973 9 years

366361.48,399488.06,148912.89,37926.9,42813.32,256906.09,87066.2,313502.21,243903.48

Lack (1954)[1] *N* (occupied nests)

1934-1952 19 years

326.98,309.68,306.22,346.02,344.29,354.67,287.19,297.57,285.46,316.60,365.05,389.27,340.83,276.81,320.06,384.08,437.71,486.15,449.82

Lack (1954)[2] *N* (occupied nests)

1937-1952 16 years

289.93,253.47,267.36,204.86,217.01,182.29,210.06,286.45,239.58,248.26,105.90,131.94,199.65,236.11,272.56,267.36

Lack (1954)[3] *N* (occupied nests)

1933-1943 11 years

545.13,661.94,729.20,775.22,676.10,654.86,711.50,753.98,559.29,587.61,481.41