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POD-SPECIFIC DEMOGRAPHY OF KILLER WHALES (*ORCINUS ORCA*)[1]

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Abstract. Killer whales live in stable social groups, called "pods." It has been suggested that the structure of such groups may influence the vital rates, and hence the fitness, of their members. To test this suggestion we used data from a long-term study of killer whales in the Pacific Northwest (Bigg et al. 1990). We constructed stage-classified matrix population models for the entire population, two sub-populations, and individuals pods. The population growth rate for the entire population is $\lambda = 1.0254$, with 90% bootstrap confidence interval from 1.0178 to 1.0322. The mean female population stage distribution is not significantly different from the predicted stable stage distribution. Population growth rate is most sensitive to changes in adult and juvenile survival, followed by fertility. Factors that cause even small changes in survival will thus have a large impact on population growth. Pod-specific growth rates range from $\lambda = 0.9949$ to $\lambda = 1.0498$. Most of the inter-pod variance in growth rate is due to variance in adult reproductive output. Randomization tests show that this variance is not significantly greater than expected on the basis of variation in individual life histories within the population. We conclude that there is no evidence for an effect of social structure on pod-specific population growth rate. The restriction of population growth rates to such a narrow range suggests, but does not prove, a possible role for density-dependent processes.

Key words: demography; marine mammals; matrix population models; Orcinus orca; *population growth rate; randomization tests; sensitivity analysis; social structure; stage-classified models.*

INTRODUCTION

The social structure of a population can have important demographic consequences. Population structure (e.g., the stable age distribution) appears in classical demography as a consequence of the birth and death rates. In social animals, however, population structure may be a cause, as well as a consequence, of the vital rates. The caste structure of an ant colony, the distribution of harem sizes in a band of baboons, or the presence of helpers in a family of Scrub Jays may be important determinants of the rate of increase of the colony, the band, or the family. One way to document the effects of social structure is to compare the demography of groups with different compositions. This is the approach we have taken to study the demographic consequences of social structure in killer whales.

Killer whales (*Orcinus orca*; Odontoceti, Delphinidae) are marine mammals of cosmopolitan distribution that live in well-defined social groups, or "pods." Their life history has been summarized by Bigg et al. (1990) and Olesiuk et al. (1990). They are long-lived, with estimated maximum ages of 80–90 yr for females and 50–60 yr for males. Both sexes reach sexual maturity between 10 and 18 yr of age; males become physically mature ≈6 yr after sexual maturity. Females produce single calves (twins occur rarely); the interbirth interval is usually 4–6 yr. Calves are closely associated with their mothers for much of their juvenile period.

Female killer whales become reproductively senescent between 35 and 45 yr of age. Many pods thus contain post-reproductive females, as has also been noted in short-finned and long-finned pilot whales (Kasuya and Marsh 1984, Marsh and Kasuya 1986, 1991, G. Desportes, *personal communication*). Post-reproductive females, of course, make no direct contribution to population growth (i.e., have zero reproductive value). However, it has been suggested that post-reproductive female cetaceans may play an important social role by nurturing other females' young and creating a matriarchal bonding system. They may also contribute to the success of their group by remembering habitat uses in a complex environment (Norris and Pryor 1991).

A typical killer whale pod contains mature females and their young (one to three juveniles per female) and variable proportions of males and/or post-reproductive females. The 18 pods in this study contain between 5 and 63 individuals (Appendix), and a similar range is reported in other regions of the world (Hall 1986, Katona et al. 1988, Oien 1988, Sigurjonnson 1988, Hoelzel 1991).

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Pods appear to be stable social units, possessing their own characteristic dialects of whistles (Ford and Fisher 1983, Ford 1991). In the study on which this analysis is based, 20 yr of observation revealed no instances of migration between pods (Bigg et al. 1990, K. C. Balcomb, III, *personal communication*). Pods can share feeding grounds and meet in other habitats. Mating has rarely been observed, but many workers believe it occurs when pods encounter each other. It is not known how new pods form. Patterns of similarities in dialects between pods suggest that some were probably more closely linked in the past, and may have originated from a common pod (Ford 1991). Within pods there are sometimes groups of individuals (typically, sisters with their calves) whose members associate more with each other than with other members of the pod. This suggests that pods might sometimes split, but this has never been documented.

Our analyses are based on data obtained by the late Michael Bigg and his co-workers (Bigg et al. 1990, Olesiuk et al. 1990) on killer whales in the coastal waters of British Columbia and Washington state. These data are the result of a long-term longitudinal study, begun in 1973 and still continuing, although we have used only published data from 1973 through 1987. Bigg et al. (1990) report yearly observations on almost every individual (recognized through photo identification) in every pod, including records of births and disappearances, and observations of relations with other individuals. Although there are several other marine mammal individual identification projects (Lyrholm 1988, Sigurjonnson et al. 1988; see Hammond et al. [1990] for case studies of other species), this study is unique in its duration and in having followed all individuals in the population. It provides an invaluable resource for the demographic analysis of a long-lived marine mammal.

In their study Bigg and his colleagues identified two resident sub-populations (Bigg 1982, Bigg et al. 1990). The northern sub-population (16 pods, 176 individuals in 1987) ranges from southern Alaska through Johnstone Strait, between Vancouver Island and the mainland. The southern sub-population (3 pods, 105 individuals in 1987) is found from Johnstone Strait south to Washington state. Live-capture exploitation between 1964 and 1973 affected the southern sub-population (34 individuals removed) more heavily than the northern sub-population (14 individuals removed). There may also be unknown environmental differences between the northern and southern regions.

Olesiuk et al. (1990) used age-specific life tables and a two-sex, age-classified matrix model to estimate the rate of increase, stable age distribution, and reproductive value of the entire population. They also examined the sensitivity of population growth rate by numerical methods. Our goal is to extend the demographic analysis to the pod level. Because pods are permanent social elements in this species, pod structure might have important effects on the vital rates, and hence on population growth. It is impossible to use age-classified models at the pod level, because pods contain too few individuals to allow estimation of the necessary parameters. Therefore we used a stage-structured model, based on a set of natural stages in the life cycle: yearlings, juveniles, reproductive adults, and post-reproductive adults. This simplification sacrifices some precision compared to a detailed age-specific model, but allows us to examine the demography of individual pods. Comparison of our results for the total population with those of Olesiuk et al. (1990) suggests that the loss of precision is not great.

We begin by describing the model, the data set, and the methods and results for the parameterization and analysis of the model. We then apply the model to the entire population to obtain a demographic characterization of the killer whale (population growth rate, stable stage distribution, reproductive value, sensitivity, and elasticity), and compare our results with those of Olesiuk et al. (1990). Next we use the model to examine demographic differences between sub-populations and among pods, testing for statistical significance using randomization methods. Finally, we discuss the implications of our results for killer whale biology and management.

The Matrix Model

Our model describes the dynamics of the female portion of the population. We divided the population into four biologically defined stages: (1) yearlings (individuals in the first year of life), (2) juveniles (past the first year but not mature), (3) mature females, and (4) post-reproductive females. Age at maturity was defined by the first observation of an accompanying calf. Onset of the post-reproductive stage was defined retrospectively. If a female is not observed with a calf for 10 yr, she is considered to have become post-reproductive at the beginning of that 10-yr interval.

The model is of the form:

$$\mathbf{n}(t+1) = \mathbf{A}\mathbf{n}(t) \tag{1}$$

where $\mathbf{n}(t)$ is a vector giving the numbers in each stage in the population at time t, and $\mathbf{A}$ is a population projection matrix (Caswell 1989*a*). The projection interval (from t to $t+1$) is 1 yr. The matrix $\mathbf{A}$ and the corresponding life-cycle graph are shown in Fig. 1. The P_i give the probabilities of surviving and remaining in the same stage, and the G_i give the probabilities of surviving and moving to the next stage. In this particular model, $P_1 = 0$, because the length of the yearling stage is equal to the projection interval. The fertility F gives the number of female offspring at $t+1$ per adult female at time t.

The matrix elements are calculated from estimated stage-specific survival probabilities σ_i and transition probabilities γ_i, and from the mean reproductive output $\bar{m}$ of adult females. Because births can occur year-

round (although they are more likely between fall and spring), we used the stage-classified birth-flow formulation (Caswell 1989*a*), resulting in the following formulae:

$$
\begin{aligned}
G_1 &= \sigma_1^{1/2} \\
P_1 &= 0 \\
G_2 &= \gamma_2\sigma_2 \\
P_2 &= (1 - \gamma_2)\sigma_2 \\
G_3 &= \gamma_3\sigma_3 \\
P_3 &= (1 - \gamma_3)\sigma_3 \\
P_4 &= \sigma_4 \\
F_2 &= \sigma_1^{1/2}G_2^{\bar{m}/2} \\
F_3 &= \sigma_1^{1/2}(1 + P_3)\bar{m}/2.
\end{aligned}
$$

(The term F_2 for reproductive output of juveniles corresponds to individuals that mature and reproduce during the projection interval.) Similar stage-structured models have been used for long-lived animals and plants (e.g., Caswell 1986, Crouse et al. 1987). Their main assumption, implicit in the structure of the life-cycle graph, is that all individuals within a stage are effectively identical. Thus the probability of moving from the juvenile to the adult stage, for example, is the same regardless of how long the individual has been in the juvenile stage. This is certainly not true in this, or most other cases. The failure of this assumption is most important for transient analyses; it has much less impact in the calculation of long-term growth rates (Caswell 1989*a*). In our case, we have the advantage of being able to compare our results with a full age-classified analysis for the entire killer whale population (Olesiuk et al. 1991), so we will have some idea of how well the stage-structured approximation works.

Estimating the Matrix Parameters

We based our analyses on the data appearing in Appendix Tables A and B of Bigg et al. (1990). (We did not consider their pod W01, which consisted of a single post-reproductive female and her three sons.) These data, the result of a complex process of age estimation (Olesiuk et al. 1990) and genealogy construction (Bigg et al. 1990), are the best estimates of age and parentage available. The reader is referred to the original papers for details.

For our study, we used the following information:

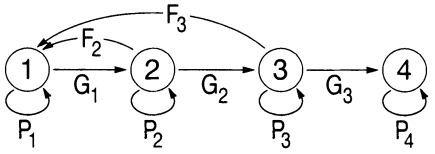
1) The observed year of birth for individuals born during the study, and the estimated year of birth for others;

2) The estimated year at maturity, defined as birth of the first calf;

3) The estimated year at onset of the post-reproductive stage;

4) The observed year at death or disappearance;

5) The sex of each individual, although the sex of juveniles was not always known; and



$$
\begin{pmatrix}
0 & F_2 & F_3 & 0 \\
G_1 & P_2 & 0 & 0 \\
0 & G_2 & P_3 & 0 \\
0 & 0 & G_3 & P_4
\end{pmatrix}
$$

FIG. 1. The life-cycle graph and corresponding stage-classified population projection matrix for killer whale populations. Stage 1: yearlings; stage 2: juveniles; stage 3: reproductive adults; stage 4: post-reproductive adults. Because the duration of the yearling stage is the same as the projection interval, $P_1 = 0$.

6) The total number of female calves observed with a female during the study. All calves of unknown sex were counted as 0.5 female.

Although our model describes the demography of females, we used data on males in two ways. Newborn individuals of unknown sex were assumed to be 50% female, and we used data from males and individuals of unknown sex to estimate juvenile survival. Thus we assumed that juvenile survivorship was equal for males and females, which appears to be borne out by information on sex ratio at maturity (Olesiuk et al. 1990).

Parameterizing the matrix model (Fig. 1), for the population, sub-population, or pod, requires estimates of $\bar{m}$, σ_i, and γ_i from the appropriate group of individuals. We estimated each of these parameters as a ratio of events (births, deaths, maturation) to exposure, where the exposure (in units of individual-years) was obtained from the records of individual whales.

The mean offspring production ($\bar{m}$) was estimated as the ratio of the number of female offspring produced by the group to the number of female-years of exposure during the study. The exposure of an individual was defined as the time period over which that individual was both included in the study and a reproductive adult. For example, an individual who was mature at the beginning of the study and still alive and reproductive at the end of the study was exposed for the entire duration of the study. An individual that became mature during the study and disappeared 3 yr later was exposed for only 3 yr.

The survival probabilities (σ_i) were calculated as one minus the ratio of deaths in stage i to the number of individual-years of exposure in stage i. Exposure was calculated differently for each stage. For yearling survival (σ_1), exposure is just the total number of births. For juvenile survival (σ_2), the exposure was calculated as the number of years of observation of juveniles. Females were treated as juveniles from the year after

birth to either their first calf or last observation. Males were treated as juveniles from birth to last observation or the end of the study, since sexual maturity requires ≈15 yr and physical maturity ≈20 yr (Olesiuk et al. 1990), which is longer than the length of the study. Exposure for adult survival (σ_3) was calculated as the number of years during which that individual was observed as a reproductive adult. It is calculated as the difference between the maximum of the year of first calving and year of first observation and the minimum of the onset of the post-reproductive period and the year of last observation. Exposure for post-reproductive survival (σ_4) was estimated as the number of years of observation of post-reproductive individuals. For individuals entering the study as post-reproductives, this was their duration in the study. For individuals becoming post-reproductive during the study, exposure was the interval between onset of post-reproduction and death or the end of observation.

The growth probabilities (γ_i) were calculated as the reciprocals of the mean stage durations. Because the yearling stage is defined to last exactly 1 yr, $\gamma_1 = 1$. The juvenile growth probability (γ_2) is the reciprocal of the mean length of the juvenile period among those individuals that had a first calf during the study. The duration of the adult stage had to be calculated in an indirect fashion because of the long life-span of the species. It was estimated as the difference between the mean age at onset of the post-reproductive period and the sum of the mean durations of the juvenile and yearling stages. The transition probability (γ_3) from the adult to the post-reproductive stage is the reciprocal of this duration.

These calculations were carried out for the entire population, for the northern and southern sub-populations, and for each pod individually. Because of the small size of some pods, some parameters were not estimable (e.g., it is impossible to estimate the duration of the adult stage if a pod contains no post-reproductive individuals). Our protocol was to use the overall population values for any parameter that could not be estimated for the pod in question. This is a conservative procedure, relative to among-pod demographic differences, since it biases the vital rates toward the population mean.

The estimated parameters for the entire population are

$$\begin{aligned}\sigma_1 &= 0.9554\\ \sigma_2 &= 0.9847\\ \sigma_3 &= 0.9986\\ \sigma_4 &= 0.9804\\ \gamma_2 &= 0.0747\\ \gamma_3 &= 0.0453\\ \bar{m} &= 0.1186,\end{aligned}$$

which leads to a projection matrix

$$\mathbf{A} = \begin{pmatrix} 0 & 0.0043 & 0.1132 & 0 \\ 0.9775 & 0.9111 & 0 & 0 \\ 0 & 0.0736 & 0.9534 & 0 \\ 0 & 0 & 0.0452 & 0.9804 \end{pmatrix}. \quad (2)$$

The values of γ_2 and γ_3 imply a mean juvenile period of 13.4 yr (and thus an age at first reproduction of 14.4 yr) and a reproductive adult stage of 22.1 yr. These are close to the age-specific results of Olesiuk et al. (1990: 219–225), who estimated mean age at first reproduction at 14.9 yr and a reproductive lifespan of 21–27 yr with a mean of 25.2 yr.

Matrix Analyses

The analysis of matrix projection models is detailed in Caswell (1989*a*). The asymptotic rate of population growth is given by the dominant eigenvalue λ of the matrix $\mathbf{A}$; the corresponding continuous-time rate is $r = \log \lambda$. The stable stage structure and reproductive value are given by the corresponding right and left eigenvectors $\mathbf{w}$ and $\mathbf{v}$. The sensitivities of λ to changes in the elements a_{ij} of $\mathbf{A}$ are given by

$$\frac{\partial \lambda}{\partial a_{ij}} = \frac{v_i w_j}{\langle \mathbf{w}, \mathbf{v} \rangle}, \quad (3)$$

where "$\langle\rangle$"denotes the scalar product. The proportional sensitivities, or elasticities, of λ are given by

$$e_{ij} = \frac{a_{ij}}{\lambda} \frac{\partial \lambda}{\partial a_{ij}}. \quad (4)$$

The elasticities sum to 1, and give the proportional contributions of the matrix elements to λ. Simple application of the chain rule permits calculation of the sensitivity and elasticity of λ to lower-level parameters that determine the values of the a_{ij}, such as σ_i, γ_i, and $\bar{m}$.

We used a bootstrap resampling procedure to construct confidence intervals for λ and r (Efron 1982, Meyer et al. 1986, Caswell 1989*a*), using the percentile method (Efron and Tibshirani 1986, Caswell 1989*a*: 192) with a bootstrap sample size of 1000. (Because the bootstrap estimates are very nearly median unbiased, this gives essentially the same results as the bias-adjusted percentile method.) The resampling unit was an individual record from a set describing a population, a sub-population, or a pod, depending on the level of analysis.

The population projection matrix for the entire population yields a growth rate of $\lambda = 1.0254$ ($r = 0.0251$). The bootstrap estimates of λ and r, with their 90% confidence intervals are

Rate	Lower limit	Estimate	Upper limit
λ	1.0178	1.0257	1.0322
r	0.0176	0.0254	0.0317

These values agree well with the observed rate of population increase (the slope of a least-squares fit of log

of female population size vs. time), which is 1.0213. The value obtained by Olesiuk et al. (1990) from a complete age-classified life table ($\lambda = 1.0292$) falls nicely within this confidence interval.

The stable stage distribution and reproductive value are

$$\mathbf{w} = \begin{pmatrix} 0.0369 \\ 0.3159 \\ 0.3227 \\ 0.3244 \end{pmatrix} \qquad \mathbf{v} = \begin{pmatrix} 1.0000 \\ 1.0491 \\ 1.5716 \\ 0 \end{pmatrix}. \tag{5}$$

The stable population structure agrees quite well with the observed female structure, which, averaged over the study period, is

$$\mathbf{w}_{\text{obs}} = \begin{pmatrix} 0.0368 \\ 0.3778 \\ 0.3627 \\ 0.2226 \end{pmatrix}. \tag{6}$$

This is, of course, a somewhat crude estimate, because we have to assume that half of the yearlings and juveniles of unknown sex are female. The observed mean stage distribution (Eq. 6) is not significantly different from the predicted stable stage distribution ($\chi^2 = 6.2544$, df = 3, $P = .0998$).

Our stage-specific reproductive values agree quite well with the age-specific reproductive values for the ages corresponding to the beginning of each stage, as reported by Olesiuk et al. (1990). This is the appropriate point of comparison, because the stages in our model are memoryless.

The sensitivity matrix (with only the sensitivities to the non-zero transitions shown) is

$$\mathbf{S} = \begin{pmatrix} \cdots & 0.3608 & 0.3686 & \cdots \\ 0.0443 & 0.3785 & \cdots & \cdots \\ \cdots & 0.5670 & 0.5793 & \cdots \\ \cdots & \cdots & 0 & 0 \end{pmatrix} \tag{7}$$

and the elasticity matrix is

$$\mathbf{E} = \begin{pmatrix} 0 & 0.0015 & 0.0407 & 0 \\ 0.0422 & 0.3363 & 0 & 0 \\ 0 & 0.0407 & 0.5386 & 0 \\ 0 & 0 & 0 & 0 \end{pmatrix}. \tag{8}$$

These matrices give the sensitivity and elasticity of λ to changes in the entries of the population projection matrix. Because those entries may depend on both growth and survival, we also calculated the sensitivities and elasticities of λ to changes in the lower-level demographic parameters (see Table 1).

TABLE 1. Sensitivity and elasticity of population growth rate to changes in lower level demographic parameters.

Parameter*	Sensitivity	Elasticity
σ_1	.0453	.0422
σ_2	.3941	.3785
σ_3	.5735	.5585
σ_4	.0000	.0000
γ_2	.2062	.0150
γ_3	−.5999	−.0265
τ_2	−.0012	−.0150
τ_3	.0012	.0265
$\bar{m}$	.3649	.0422

* γ_1 and τ_1 do not appear because the duration of the yearling stage is fixed.

Sub-Population and Inter-Pod Differences

We turn now to the analysis of demographic differences between the northern and southern sub-populations, and among the pods. We want to test the statistical significance of these differences; to do so we use nonparametric randomization tests (see Manly [1991] for a lucid review, and Walls et al. [1991] for a demographic application). Although both involve resampling of the data, randomization methods for significance tests should not be confused with bootstrap methods for estimating confidence intervals. The logic of randomization tests is as follows. Consider the two sub-populations. The observed assortment of individuals into these sub-populations produces an observed difference $\Delta\lambda$ in growth rate. This difference might reflect real environmental or structural differences between the sub-populations. Alternatively, the sub-populations might differ only because their members represent sub-samples of the entire population. Under this null hypothesis the life experience of each individual is independent of which sub-population it belongs to. If we examine all possible permutations of individuals into the two sub-populations, and calculate $\Delta\lambda$ for each, we obtain the distribution of $\Delta\lambda$ under the null hypothesis. The fraction of these permutations in which $\Delta\lambda$ exceeds the observed difference gives the probability of obtaining such a large difference, under the null hypothesis. If this probability is small, we reject the null hypothesis. Since the total number of permutations is enormous, we settled instead for a random sample of 1000 permutations (generated using Algorithm P of Knuth [1981]). Note that randomization tests require neither distributional assumptions nor the assumption that the data were obtained by random sampling (Edgington 1980, Manly 1991).

As just described, the randomization procedure yields a one-tailed test; since we have no reason to predict that one sub-population is growing faster than the other, we used a two-tailed test based on the absolute value of $\Delta\lambda$.

Sub-population comparisons

The growth rates from the matrices for the northern and southern sub-populations are $\lambda^{(N)} = 1.0248$ and $\lambda^{(S)} = 1.0249$. The bootstrap estimates and their 90% confidence intervals (calculated as for the entire population above) are

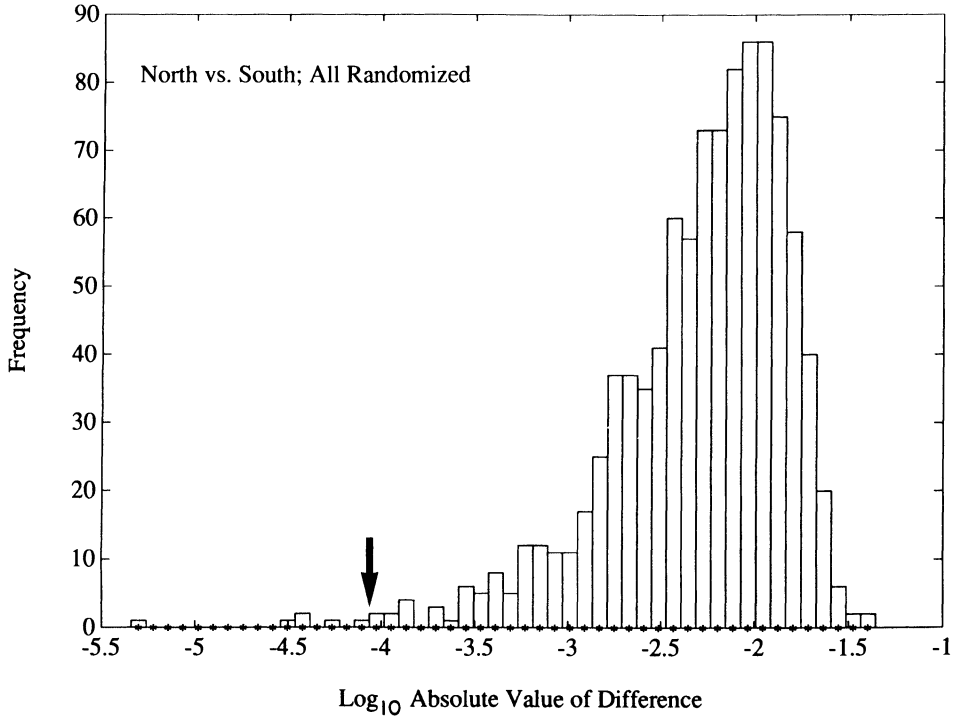


FIG. 2. The randomization distribution of $|\Delta\lambda|$, the absolute value of the difference in population growth rate, λ, between the northern and southern sub-populations of killer whales, under the null hypothesis of no sub-population effect. The arrow indicates the location of the observed difference; it is not significantly large (see *Sub-population and inter-pod differences: Sub-population comparisons*).

Sub-population	Lower limit	λ	Upper limit
North	1.0109	1.0256	1.0349
South	1.0129	1.0250	1.0381

The observed growth rate of the northern sub-population (the slope of a least-squares fit of log of population size vs. time) is 1.0302; the corresponding value for the southern sub-population is 1.0070 (these differ slightly from the values reported by Olesiuk et al. [1990] because we base our calculations only on the female population). The southern population is thus growing less rapidly than its asymptotic rate of increase, although the observed value is only slightly outside the 90% confidence interval.

Fig. 2 shows the distribution, obtained by randomization, for the difference in growth rate, $|\Delta\lambda|$, under the null hypothesis. Not surprisingly, the observed difference, $|\Delta\lambda|_{obs} = 8.01 \times 10^{-5}$, is not significantly large. In fact, it is significantly small; under the null hypothesis such small differences occur $<1\%$ of the time (for possible explanations, see *Discussion: Sub-population and inter-pod comparisons*).

To obtain more detailed information on differences, we repeated our randomization tests, randomizing only females, only males, and only juveniles of unknown sex. Suppose, for example, that group structure affects the vital rates of females, but that males and individuals of unknown sex follow the null hypothesis. Then randomizing females (leaving males and unknowns in their original pods) will destroy the pattern, and the observed difference will appear unusually large relative to the null hypothesis. In contrast, randomizing either males or unknowns will have little effect and the observed variance will not appear significantly large. Thus, by comparing the results of randomizing females, males, and unknowns separately, we can test for demographic differences affecting these groups. However, in this case none of the randomizations yielded a significant result:

Group randomized	Probability
All	.9930
Females	.9970
Males	.9431
Unknown	.9990

We can look more closely at this small difference in λ by decomposing it into contributions from the differences in the matrix elements (Caswell 1989*b*). We write $\Delta\lambda$ as

$$\Delta\lambda \approx \sum_{ij} \frac{\partial\lambda}{\partial a_{ij}} \Delta a_{ij}, \qquad (9)$$

where Δa_{ij} is the difference in a_{ij} between the two sub-populations (southern minus northern). Each term in the summation represents the contribution of a vital rate difference to $\Delta\lambda$. The matrix of these contributions is

$$\begin{pmatrix} 0 & 1.7 \times 10^{-4} & 5.3 \times 10^{-3} & 0 \\ -8.5 \times 10^{-4} & -6.2 \times 10^{-3} & 0 & 0 \\ 0 & -4.2 \times 10^{-4} & 2.1 \times 10^{-3} & 0 \\ 0 & 0 & 0 & 0 \end{pmatrix}. \quad (10)$$

These contributions sum to $|\Delta\lambda|_{\text{pred}} = 8.23 \times 10^{-5}$, which is quite close to $|\Delta\lambda|_{\text{obs}}$, indicating that the approximation (Eq. 9) is good.

We conclude that $\Delta\lambda$ is small not because there are no differences in the vital rates, but because there is an approximate balance between contributions from fertility and adult survival advantages in the southern population and the contribution of a juvenile survival advantage in the northern population.

The predicted and observed stable stage distributions for the two populations are

$$\mathbf{w}^{(N)}_{\text{pred}} = \begin{pmatrix} 0.0338 \\ 0.3099 \\ 0.3075 \\ 0.3487 \end{pmatrix} \quad \mathbf{w}^{(N)}_{\text{obs}} = \begin{pmatrix} 0.0397 \\ 0.4131 \\ 0.4080 \\ 0.1391 \end{pmatrix} \quad (11)$$

$$\mathbf{w}^{(S)}_{\text{pred}} = \begin{pmatrix} 0.0410 \\ 0.3200 \\ 0.3306 \\ 0.3086 \end{pmatrix} \quad \mathbf{w}^{(S)}_{\text{obs}} = \begin{pmatrix} 0.0323 \\ 0.3221 \\ 0.2911 \\ 0.3544 \end{pmatrix}. \quad (12)$$

The difference between the predicted and observed structures is nonsignificant for the southern subpopulation ($\chi^2 = 0.6598$, df = 3, $P = .8826$), but highly significant for the northern subpopulation ($\chi^2 = 15.17$, df = 3, $P = .0017$). This is strange, because the northern population exhibited more consistent exponential growth than the southern population during the course of this study (Olesiuk et al. 1990), so we should expect the stage distribution to be closer to stable. However, most of the deviation of the northern population is due to a deficiency in post-reproductive females in the observed structure. This deficiency contributes to the χ^2 statistic, but because these females have zero reproductive value, the deficiency will not affect the dynamics of the population. A separate test on the first three stages, which do affect population dynamics, was done by recalculating a predicted age structure for these stages only. This test shows that the observed and predicted structures agree almost perfectly ($\chi^2 = 0.0456$, df = 2, $P = .9774$).

Inter-pod comparisons

The elements of the pod-specific projection matrices are given in the Appendix. The resulting r values and confidence intervals are given in Table 2.

We quantified the differences among the pods by the observed variance in the growth rate, λ. This variance should reflect differences among pods in the external environment and in social structure. The null hypothesis is that it reflects only sampling variation. The situation is analogous to deciding, in analysis of variance, whether the variance between treatments is more than to be expected on the basis of the variance within treatments. To test the null hypothesis, we randomly permuted individuals among pods (maintaining observed pod sizes) and calculated the resulting inter-pod variance in λ for each permutation. The probability of the observed variance, given the null hypothesis, was estimated as the fraction of the random permutations that produced a variance greater than or equal to the observed one. Because there is no significant difference between the sub-populations, we do not distinguish sub-populations in this test. We used the same four randomization categories as in the previous section.

TABLE 2. Estimates of λ, the pod-specific population growth rates of Pacific Northwest killer whales, and the 90% bootstrap confidence intervals of those estimates. Pods (social groups) are identified with their labels as assigned by Bigg et al. (1990).

Sub-population	Pod	Lower 90%	λ	Upper 90%
Southern	J01	1.0094	1.0355	1.0835
	K01	1.0104	1.0184	1.2245
	L01	1.0000	1.0153	1.0295
Northern	A01	1.0030	1.0177	1.0811
	A04	0.9810	1.0061	1.0469
	A05	0.9931	1.0059	1.0302
	B01	1.0100	1.0017	1.0348
	C01	1.0253	1.0491	1.0538
	D01	1.0403	1.0498	1.1161
	G01	1.0146	1.0299	1.0552
	G12	1.0293	1.0326	1.0749
	H01	0.9918	1.0018	1.0348
	I01	0.9901	1.0057	1.0585
	I02	1.0293	1.0349	1.0348
	I11	1.0355	1.0403	1.0548
	I18	1.0177	1.0257	1.0314
	I31	1.0348	1.0337	1.0485
	R01	0.9891	0.9949	1.0240

The probability levels resulting from our various randomization tests were

Group randomized	Probability
All	.8530
Females	.8841
Males	.7053
Unknown	.6164

Clearly, the variance in λ among pods is not significantly greater than that expected under the null hypothesis of random assortment of individuals among pods.

A possible explanation is that variation in the vital rates might fail to appear as variance in λ because of patterns of correlation among the rates. To test this possibility, we conducted a multivariate randomization test on the vital rates themselves. The test works as follows. For each pod i we defined a vector-valued observation $\mathbf{x}_i$, composed of the non-zero entries of

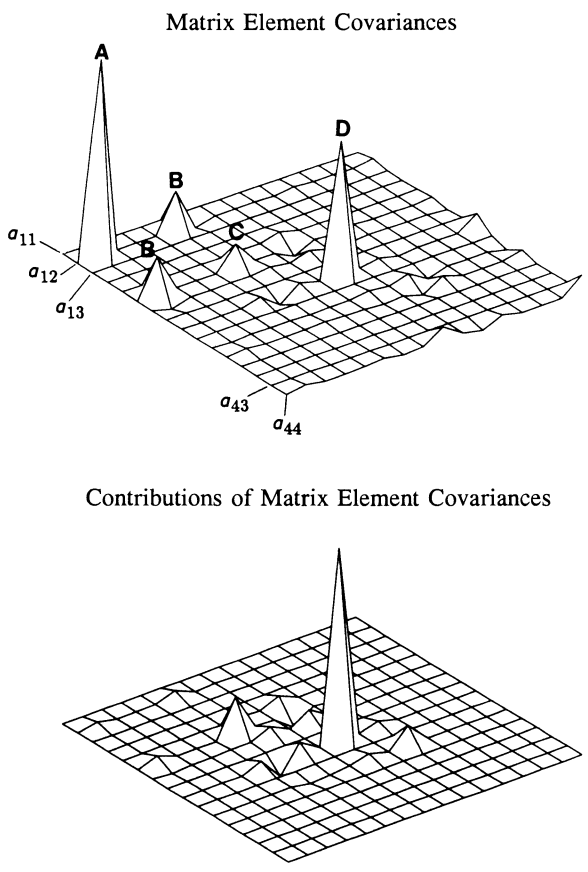


FIG. 3. *Upper:* Surface plot of the covariances of the matrix elements a_{ij} among pods. The a_{ij} are arranged in order from a_{11} to a_{44}. Entries on the diagonal are variances in the matrix elements; off-diagonal entries are covariances. The important peaks are identified by letter. A = the variance in G_1 (yearling survival); B = the covariance between yearling and juvenile survival; C = the variance in P_2 (probability of remaining in the juvenile stage); D = the variance in F_3 (adult fertility). *Lower:* Surface plot of the contributions of the matrix entry covariances to the inter-pod variance in the population growth rate, λ. The variance in yearling survival, which is so prominent in the upper graph, makes almost no contribution to the variance in λ. Most of the variance in λ is due to variance in adult fertility.

the matrix **A** for that pod. The variation in vital rates among pods is summarized by the covariance matrix of the $\mathbf{x}_i$

$$\mathbf{C} = E[(\mathbf{x}_i - \bar{\mathbf{x}})(\mathbf{x}_i - \bar{\mathbf{x}})'], \tag{13}$$

where $\bar{\mathbf{x}}$ is the mean of $\mathbf{x}_i$. The magnitude of this variation is measured by the "generalized variance" (Anderson 1958), given by the square of the determinant of the covariance matrix **C** (we actually used the square root of the generalized variance, a sort of generalized standard deviation). The randomization test proceeded as in the previous cases; we rejected the null hypothesis if the observed generalized variance was significantly large compared to the randomization distribution.

Randomizing individuals among pods and calculating the generalized variance, we found that the observed generalized variance was not unusually large:

Group randomized	Probability
All	.9640
Females	.9231
Males	.6154
Unknown	.7722

Thus, we found no evidence for significant inter-pod differences in demography at either the level of the vital rates or at the level of population growth rate.

The decomposition of inter-pod variance in λ

Although the inter-pod variance in growth rate cannot be distinguished from that resulting from the assortment of individuals among pods, we can nevertheless ask how the variance is produced. The question is the random-effects analogue of the decomposition analysis of fixed treatments in Caswell (1989*b*), which we used above for the comparison of the two subpopulations. Here we want to know how much the variance in each vital rate—and the covariance between each pair of vital rates—contributes to the overall variance in λ. This requires both the variance–covariance structure of the vital rates and the sensitivity analysis of λ, because a particular vital rate may make a small contribution either because it does not vary much or because λ is insensitive to its variation.

Again, we denote by $\mathbf{x}_i$ a vector containing all the elements of the matrix for pod i, and by **C** the covariance matrix of the x. Let **s** denote a vector of sensitivities evaluated at the mean matrix; i.e.,

$$s_i = \left.\frac{\partial \lambda}{\partial x_i}\right|_{\bar{\mathbf{x}}}. \tag{14}$$

The first-order approximation to the variance in λ is

$$V(\lambda) \approx \sum_{i,j}\sum_{k,l} \frac{\partial \lambda}{\partial a_{ij}}\frac{\partial \lambda}{\partial a_{kl}}\mathrm{Cov}(a_{ij}, a_{kl}) \tag{15}$$

$$= \mathbf{s}'\mathbf{C}\mathbf{s}. \tag{16}$$

Fig. 3 is a graphical representation of the covariance matrix of the a_{ij} and the resulting matrix of contributions of those covariances to $V(\lambda)$. The diagonal elements of the graph correspond to variances, the symmetric off-diagonal elements to covariances. The peaks A, C and D correspond to the variances in G_1 (yearling survival), P_2 (probability of remaining in the juvenile stage), and F_3 (adult reproduction), respectively. The pair of peaks labelled B is the covariance between G_1 and P_2: essentially a positive covariance between yearling and juvenile survival. Peaks A and B make almost no contribution to the variance in λ (Fig. 3). Almost all of the variance in λ is due to variance in adult fertility.

Discussion

General demographic results

The picture of killer whale demography revealed by these analyses is of a population with a small but significantly positive rate of increase (≈2.5% per year). The female stable stage distribution contains ≈4% yearlings, and about equal proportions of juveniles, reproductives, and post-reproductives. The observed growth rate and stage distribution are not significantly different from these predictions.

Our elasticity analysis indicates that population growth rate is most sensitive to changes in adult survival (as is typical for long-lived species; e.g., Goodman 1981, Crouse et al. 1987, Trites 1989). Juvenile survival is the next most important, followed (an order of magnitude less) by fertility. Here our conclusions disagree with those of Olesiuk et al. (1990), who present their analysis in terms of adult mortality rather than survival, and conclude that growth rate is very *in*sensitive to changes in mortality. The difference in interpretation is a result of the very low mortality rate—and consequent high survival probability—in this population. Perturbations expressed as proportional changes in a number close to zero (i.e., mortality) produce very small effects on the growth rate, λ. Perturbations expressed as proportions of a number close to one (i.e., survival) produce large effects on λ. Both conclusions are correct analytically, but which is relevant biologically?

It is perhaps an open question whether mortality or survival is more biologically fundamental. Optimists and pessimists may disagree on the matter. However, considering the number of deaths per unit of time may help clarify the issue. The adult survival and mortality rates are $\sigma_3 = 0.9986$ and $\mu_3 = 0.0014$, respectively. In a population of 100 adults, this implies 0.14 deaths/yr. Suppose that some environmental perturbation kills one adult every other year. This corresponds to a reduction in survival probability of 0.36%, but a 358% increase in mortality rate. Clearly, calculations based on small proportional changes in *survival* correspond to enormous changes in mortality. A small proportional change in *mortality* would produce indetectable numbers of additional deaths. If the purpose of the analysis is to shed light on the results of small but detectable perturbations, the survival elasticities are the most relevant results.

In cases like this it is helpful to consider sensitivities as well as elasticities. When perturbations are measured on an incremental rather than a proportional scale, λ is still most sensitive to changes in σ_3, and the effect of changes in μ_3 is identical, but opposite in sign. Thus, we conclude that management plans for killer whales should pay attention to factors that might cause even small changes in survival probabilities, because these changes will have a large impact on population growth. Changes in calf production ($\bar{m}$) are also important, and should certainly not be ignored.

Sub-population and inter-pod comparisons

We found surprisingly little demographic differentiation at either the subpopulation or the pod level. The two subpopulations differ in fertility (southern > northern), adult survival (southern > northern) and juvenile survival (northern > southern), but the contributions of these differences to λ nearly cancel each other. The resulting difference in λ is not significant; in fact it is smaller than expected on the basis of the null hypothesis. At the pod level, λ varies from 0.9949 through 1.0498 (Table 2), but this variation is not significantly greater than would be expected on the basis of the null hypothesis.

Thus, we can find no significant demographic effects of pod size, social structure, or environmental variation. This could reflect a lack of variation in pod size and social structure, but the observed variable proportions of males, females, juveniles, adults, and post-reproductives (Bigg et al. 1990) makes this seem unlikely. A second possibility is the existence of some factor constraining the vital rates within a small range. Density dependence might act in this way; if these populations were at a stable equilibrium, their rates of increase would be restricted to a narrow range around $\lambda = 1$, and it would not be surprising to find an approximate balance between contributions from survival and fertility differences. Although all but one of the estimated rates of increase are >1, and only 5 of the 18 confidence intervals include 1, which might argue against a density-dependent equilibrium, the possible role of density dependence warrants further investigation.

Another possibility is that our tests lack sufficient power to reject the null hypothesis even though it is false. We have no information about the power of our specific tests, but the power of randomization tests in general equals that of the corresponding parametric tests when the assumptions of both are met (Manly 1991). Randomization tests are more powerful when, as in this case, the assumptions of the parametric tests would be violated.

The variance in pod-specific rates of increase is primarily due to variance in fertility (Fig. 3). This results from a combination of the sensitivity of λ to fertility and the amount of variation in fertility. Population growth rate is more sensitive to changes in other parameters, particularly adult survival probability, σ_3, but these parameters vary less among pods. Thus, attempts to explain the variation in λ should focus on factors affecting reproduction.

Methodology

Our stage-classified analysis complements the age-classified analysis of Olesiuk et al. (1990). Ideally, we

would have enough data to construct age-specific life tables for each pod. However, this is impossible, because most age classes were not represented within each pod. Accordingly, we sacrificed precision in the description of population structure (4 stages vs. 90 age classes) in return for the ability to conduct pod-specific analyses.

In spite of the simplicity of our model, our estimates of λ and reproductive value for the whole population agree with those of Olesiuk et al. (1990), and our stable stage distribution agrees with the mean observed stage distribution. Our model thus appears to capture the major events of the killer whale's life history, with fewer parameters to estimate.

Stage-structured models are less dependent on the precision of age estimates, since the model categories are not based on age. This is important in longitudinal studies of long-lived organisms, where the ages of individuals born before the start of the study must be estimated. However, the timing of certain events, such as female maturation and reproductive senescence, is still critical for our model. The age at maturity may be overestimated, even for a known-age female, if a first-born calf dies before being observed. This was hopefully minimized because the observation period coincided with the main calving period.

Detecting reproductive senescence is more difficult. We have followed Bigg and Olesiuk in using an a posteriori definition of senescence, but this can misclassify individuals. Declaring an individual senescent after 10 yr without reproduction, in a 15-yr study, will obviously underestimate senescence and overestimate the length of the reproductive period. The 10-yr criterion was based on the observation that calving intervals rarely exceed 10 yr. A possible improvement to our model would be to include a distribution of calving intervals (cf. Barlow 1990), so that senescence can be defined less arbitrarily.

Final remarks

Long-term longitudinal studies like this one are crucial for understanding the population dynamics of long-lived organisms. They provide information on survival without relying on assumptions about the age distribution. They yield data on individual reproductive histories (cf. Clutton-Brock 1988) that cannot be obtained without identification of individuals. They provide information on social structure and interactions unavailable in cross-sectional studies (e.g., Wells 1991). Because they do not rely on destructive sampling, they are particularly suitable for endangered species. The value of longitudinal studies increases nonlinearly with their length; we hope that this one will continue.

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APPENDIX

Pod-Specific Projection Matrix Elements

This table lists the pod identification number (from Bigg et al. 1990), the pod size (as of 1987), and the values of the matrix elements (see Fig. 1) for each of the 18 pods used in our analyses of Pacific Northwest killer whales.

Sub-population	Pod	No.	G_1	G_2	G_3	P_2	P_3	P_4	F_2	F_3
Southern	J01	22	0.9535	0.0802	0.0414	0.8827	0.9586	0.9752	0.0067	0.1632
	K01	20	1.0000	0.0694	0.0418	0.9020	0.9582	0.9855	0.0062	0.1737
	L01	63	0.9562	0.0722	0.0406	0.9030	0.9530	0.9798	0.0037	0.0988
Northern	A01	15	1.0000	0.0727	0.0485	0.9015	0.9515	0.9667	0.0043	0.1148
	A04	12	0.8165	0.0774	0.0485	0.8903	0.9515	0.9810	0.0042	0.1054
	A05	10	1.0000	0.0730	0.0485	0.9123	0.9515	0.9545	0.0027	0.0732
	B01	8	1.0000	0.0746	0.0485	0.9254	0.9515	0.9810	0.0025	0.0651
	C01	8	1.0000	0.0800	0.0294	0.9200	0.9706	0.9608	0.0047	0.1159
	D01	12	1.0000	0.0759	0.0438	0.9241	0.9562	1.0000	0.0068	0.1761
	G01	24	1.0000	0.0833	0.0714	0.9167	0.9286	1.0000	0.0061	0.1418
	G12	11	1.0000	0.0784	0.0485	0.9216	0.9515	0.9810	0.0050	0.1251
	H01	7	1.0000	0.0746	0.0485	0.9254	0.9515	0.9810	0.0021	0.0542
	I01	7	1.0000	0.0714	0.0485	0.9286	0.9515	0.9810	0.0027	0.0732
	I02	7	1.0000	0.0714	0.0485	0.9286	0.9515	1.0000	0.0045	0.1220
	I11	15	1.0000	0.0714	0.0485	0.9286	0.9515	0.9810	0.0052	0.1428
	I18	13	1.0000	0.0714	0.0485	0.9286	0.9515	0.9810	0.0037	0.0998
	I31	7	1.0000	0.0714	0.0485	0.9286	0.9515	0.9810	0.0047	0.1273
	R01	20	1.0000	0.0595	0.0485	0.8929	0.9515	1.0000	0.0024	0.0797