



## Life history and population dynamics of southern Alaska resident killer whales (*Orcinus orca*)

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### ABSTRACT

Resident (fish eating) killer whales (*Orcinus orca*) in the North Pacific have been the subject of long-term studies in several geographical regions. The current study examines population parameters in the southern Alaska resident population from 1984 to 2010 and develops a population model. The southern Alaska resident population ranges from southeastern Alaska through the Kodiak archipelago and contains over 700 individuals. We follow the life histories of 343 identifiable whales in 10 pods from two clans born before and during the study. Population parameters were comparable to those of the British Columbia northern resident population during the 1970s and 1980s, except that age of maturity was approximately one year earlier. The average annual rate of increase was slightly higher in Alaska (3.5%) than for the British Columbia northern residents (2.9%) and probably represents a population at r-max (maximum rate of growth). Reasons for the high growth rate in Alaska could be a recovery following past anthropogenic mortalities, or more likely, a response to increasing salmon returns in recent decades, resulting in an increase in carrying capacity. The slow maturation and low rate of reproductive response makes these whales slow to recover from natural or anthropogenic catastrophes.

Key words: killer whales, *Orcinus orca*, population dynamics, southern Alaska, life history, residents.

Killer whales have a cosmopolitan distribution and are top-level predators. Studies in the eastern North Pacific indicate that at least three ecotypes exist in this region: residents, transients, and offshores (Matkin *et al.* 1999a, Ford *et al.* 2000). Despite their sympatric distribution, these ecotypes do not associate or interbreed and are acoustically and genetically distinct (Hoelzel and Dover 1991; Hoelzel *et al.* 1998, 2007; Barrett-Lennard 2000; Yurk *et al.* 2002).

The resident ecotype preys almost exclusively on fishes (Ford *et al.* 1998, Saulitis *et al.* 2000) and has been studied along the length of the eastern North Pacific coast from California to the Aleutian Islands and the southern Bering Sea (Matkin *et al.* 1999a, Ford *et al.* 2000, Matkin *et al.* 2007). It has been separated by genetic analysis,

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acoustics, and association into three populations (Matkin *et al.* 1999a, Barrett-Lennard 2000, Ford *et al.* 2000, Yurk *et al.* 2002, Allen and Angliss 2010). The southern resident population has been the subject of studies centered in Puget Sound and Washington State waters since the late 1970s (Balcomb *et al.* 1982, Bigg *et al.* 1990, Olesiuk *et al.* 1990, Ford *et al.* 2000) and has been listed as endangered under the U.S. Endangered Species Act and the Canadian Species at Risk Act. The British Columbia northern resident population is listed as threatened in Canada and is encountered primarily in the waters of British Columbia although they range into southeastern Alaskan waters where there is overlap with at least two pods in this study (Bigg 1982, Bigg *et al.* 1990, Ford *et al.* 2000). A third population, the southern Alaska residents, ranges from southeastern Alaska at least as far west as the Kodiak archipelago (Matkin *et al.* 1999a, Allen and Angliss 2010). It is the subject of this analysis.

Our analysis is possible because of unusual attributes of resident killer whales that are not shared by the other ecotypes. They are relatively accessible with a high probability of encountering individuals on an annual basis, and they travel in maternal groupings that change composition only as a result of births or deaths. These permanent associations facilitate the repeated identification of individuals and allow accurate annual tracking of individuals within maternal groups and for a substantial segment of the population.

The field and analytical techniques we use were first developed in long-term studies in British Columbia and Washington State. Using direct observation, annual photographic census, and statistical inference, Bigg *et al.* (1990) established genealogies and estimated ages of individuals for the northern and southern resident populations of killer whales. These techniques were later applied to the southern Alaska resident population by Matkin *et al.* (1999a, b). Olesiuk *et al.* (1990) estimated life history parameters and described population dynamics of northern and southern resident killer whales based on the demographic changes observed from 1973 to 1987. More recently, Olesiuk *et al.* (2005) used updated information to examine changes in population trajectory and to develop a new population model for northern residents from 1973 to 2004.

An understanding of the dynamics of killer whale populations provides insight into how they function and respond to various impacts. For example, Olesiuk *et al.* (1990) used their model to assess long-term impacts of a killer whale live-capture fishery that had altered the sex- and age-structure of the populations in British Columbia and Washington State. Later, Olesiuk *et al.* (2005) demonstrated possible impacts of prey abundance on the population trajectory of the northern residents. We used some earlier results from our work to examine the effects of the *Exxon Valdez* oil spill (Matkin *et al.* 2008).

In the current study, we modify methodologies originally developed by Olesiuk *et al.* (2005) to describe life histories, develop population parameters, and construct a population model for southern Alaskan resident killer whales. The study was based on systematic long-term photo-identification surveys conducted annually from 1984 to 2010. Here, we detail the parameters of the model to describe a population increasing at a rate approaching r-max but vulnerable to changes in environment or prey populations.

## METHODS

### *Study Area and Population*

The range of the southern Alaska resident pods described in this study includes the northern Gulf of Alaska and inshore waters from southern southeastern Alaska

through the Kodiak archipelago (Matkin *et al.* 1999b, Fig. 1). Most pods appear to have a more limited range within this region (Matkin *et al.* 1997, Matkin *et al.* 1999a, Scheel *et al.* 2001) and the extent that these whales use waters south and west of Kodiak Island is unclear. Past and current studies in Alaska west of the Shumagin Islands have not identified individuals from the resident pods described here (Dahlheim and Waite 1992, Dahlheim 1997, Matkin *et al.* 2007, Durban *et al.* 2010). Parsons *et al.* (in press) has determined genetic strata from nDNA analysis that suggest a population separation of resident type killer whales that occurs south of Kodiak Island.

At the southeast end of their range, in southeastern Alaska, the southern Alaska residents have been observed in close proximity to members of the British Columbia northern resident population, but mixing between these groups has not been reported (Dahlheim *et al.* 1997, Barrett-Lennard 2000, Ford *et al.* 2000). A genetic separation of southern Alaska residents from the parapatric British Columbia northern residents was indicated by the examination of 11 microsatellite loci (Barrett-Lennard 2000), although there may be occasional matings between the groups. In contrast, observation and analysis indicates that pods and individuals within the southern Alaska resident population examined here regularly intermingle and interbreed (Matkin *et al.* 1997, Matkin *et al.* 1999b, Barrett-Lennard 2000).

In our analyses the southern Alaska residents were considered as a single and separate population consisting of two sympatric, freely interbreeding acoustic clans that are separable by mtDNA haplotypes and by acoustic repertoire (Yurk *et al.* 2002). Within our study population, genetic evidence indicates successful breeding occurs primarily between individuals from the more distantly related pods within the clan

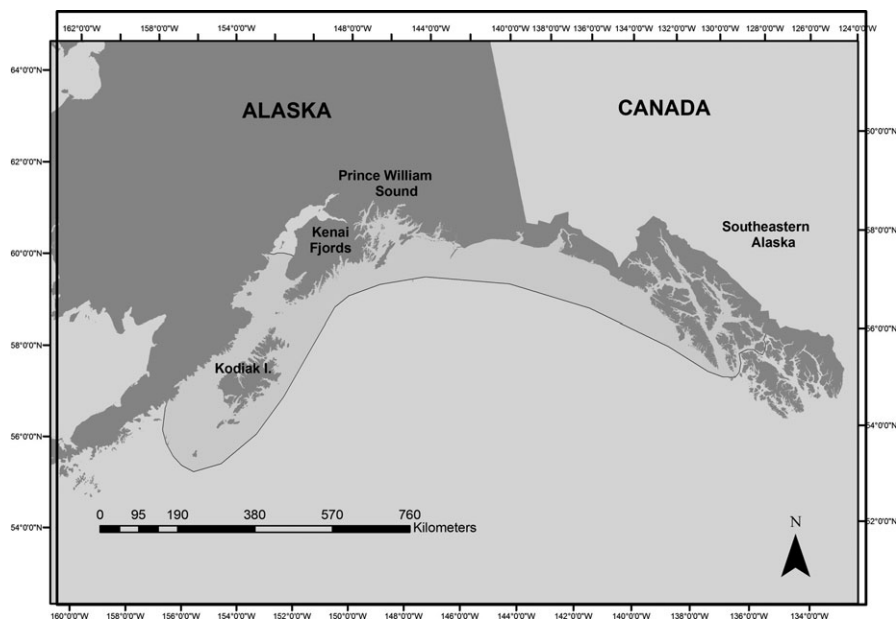


Figure 1. Range of the southern Alaska resident killer whale population in the eastern North Pacific.

(Barrett-Lennard 2000). Our analysis focuses on a subset of pods from both acoustic clans that are most likely to be repeatedly encountered on an annual basis and whose size ranges from 6 to 42 individuals. Our results describe only the dynamics of this large subset of the population although it may reflect overall population characteristics as suggested by Olesiuk *et al.* (1990).

### *Data Collection*

Our study required an annual census that was initiated in 1984 and continued through 2010, though effort declined following 2005 and some pods were not seen in all of the last five years. We annually attempted to photographically identify each individual whale in the 10 pods that comprised our sample. We did not include the well-described AB pod in our analysis due to the anomalous mortalities following the *Exxon Valdez* oil spill reported elsewhere (Matkin *et al.* 2008). Data collection procedures followed those described by Bigg *et al.* (1990) and Matkin *et al.* (1999b). Although some fieldwork occurred in all months of the year, in all years the vast majority of effort and encounters with killer whales occurred from early May through October. Our data are considered annual surveys of the population that occurred during the spring, summer, and fall period.

The techniques used to approach and photograph the whales were consistent over the duration of the study. Whales were approached from the left side or from behind to a lateral distance of 15–30 m. Photographs were always taken of the left side of each whale showing details of the dorsal fin and gray saddle patch. In the most useful photographs the whale filled at least 50% of the frame. We attempted to obtain photographs of all whales in each encounter; however, this was not always possible due to conditions of weather or light, and for larger groups it often required multiple encounters to completely photograph all whales.

Initially a 35 mm SLR Nikon FM2 camera with a manual focus 300 mm lens and shoulder brace mount was used, but in the 1990s autofocus cameras were introduced and for many years a Nikon F-100 camera with an autofocus 300 mm f:4.5 lens was the preferred tool. In the early years Illford HP5 400 ASA black and white negative film was used and push-processed to 1600 ASA; later Fuji Neopan 1600 proved to be the most useful film. In recent years photographs have been acquired with Nikon D-200 or D-700 digital cameras with a 300 mm autofocus lenses.

### *Individual Identification*

All film negatives collected during the fieldwork were examined under a Wild M5 or M8 stereomicroscope with 10× eyepieces. Digital images were examined using PhotoMechanic software (Camera Bits Inc., Hillsboro, OR) on an Apple computer with a 24 in. high resolution LCD screen. Identifiable individuals in each frame were recorded. When identifications were not certain, they were not included in the analysis. Reference files of 5 × 7 prints of each individual were replaced on an annual basis if new marks, fin maturation or other changes necessitated an update. Each individual was labeled based on an alphanumeric code developed at the beginning of the study (Leatherwood *et al.* 1990) and used in sequential catalogs (Matkin *et al.* 1999a, b). The first character in the code is “A” to designate Alaska, followed by a letter (A–Z) indicating the individual’s pod. Individuals within the pod received sequential numbers. For example, AB03 is the third whale designated in the AB pod. New calves were identified and labeled with the next available number. If a pod split, each new

pod was designated after the alphanumeric code of a primary matriarch, but the alphanumeric designation of individuals remained the same and new animals were designated using the original alphabetic pod designation.

Olesiuk *et al.* (1990) showed that the male fin of northern resident killer whales could be statistically distinguished from that of females when it reached a height-to-width ratio (HWR) of 1.4, which appears to occur during adolescence and concurrently with development of other secondary sexual characteristics such as enlargement of pectoral fins and the downturn of fluke tips. For males, we calculated maturation statistics for the age at which HWR reached this threshold, and for the age at which the dorsal fin reached its full height and males were judged to be completely mature.

#### *Age Estimation*

Following the approach developed by Bigg *et al.* (1990) and modified by Olesiuk *et al.* (2005) for British Columbia and Washington State resident killer whales, we used genealogies developed for southern Alaska resident killer whales (Matkin *et al.* 1999a, b) to establish ages. Killer whales used in this analysis were aged using the following criteria:

- (1) Animals born during or just prior to the study were aged on the basis of year first observed, which in most cases corresponded with year they were born ( $n = 187$ ). Growth is rapid the first few years, facilitating age estimation up to about 3 yr from size (Olesiuk *et al.* 1990, 2005). Animals estimated from their size to be  $\leq 3$  yr old when first seen were assumed to be known-age ( $n = 42$ ).
- (2) Most older juvenile animals born prior to the study were aged based on the year they matured. However, for a few animals that died prior to maturation, birth year was estimated from size. Nine animals were aged in this group with a possible aging error of  $\pm 3$  yr.
- (3) Females that were juvenile-sized when first seen but larger than average 3 yr old whales were aged by subtracting mean age of first recruitment (13 yr), as estimated from known-age animals from the year they were seen with their first calf. Twenty-one females were aged using this calculation with a possible aging error of  $\pm 2$  yr.
- (4) Forty females that were adult-sized when first seen were aged by subtracting mean age of first reproduction (AFR, 13 yr) from year of birth of their oldest known calf. We did not use a correction factor as in Olesiuk *et al.* (2005) to compensate for older calves that may have died before the beginning of the study (see Discussion).
- (5) Males that were juveniles when first seen but too large to estimate based on size were aged by subtracting mean age of onset of sexual maturity (13) determined in this study (below). There were 22 whales aged in this manner with a potential error of  $-3$  to  $+2$  yr.
- (6) Males that were sexually but not physically mature when first seen were aged by subtracting mean age of onset of physical maturity (18) determined in this study (below). Six whales were aged in this manner with a potential error of  $\pm 3$  yr.
- (7) Males that were physically mature when first seen were aged on the basis of the year they were first seen by subtracting the average age of onset of physical maturity (18 yr). These were considered minimum ages. A total of 16 whales were aged in this manner.

*Age of First Reproduction (AFR) and Reproductive Rates*

We estimated the mean age at first reproduction using the method by DeMaster (1978) based on the proportion of females and males mature at each age. For females, we defined maturation as the age at which they began contributing to recruitment in the population, which was the age at which we observed their first calf. Calving season apparently occurred during the November to April period, since most calves were born prior to the annual census which was not initiated until early May, and few calves were born during the May–October field season. We were essentially censusing the recruitment of calves from 1 to 6 mo of age, not birth rate. No female less than 11 yr old was observed with a calf, so only females seen each year from age 11 until the recruitment of their first calf were included in the analysis. Known-age females excluded from calculations of mean age at first reproduction due to a missing observation were reincluded in the analysis of other population parameters.

In calculating variance, DeMaster's (1978) method assumes that observations at each age are independent, which cannot be justified in longitudinal samples such as those obtained here (or by Olesiuk *et al.* 1990, 2005). We therefore used bootstrap sampling (Efron 1982) of individual whale sighting histories to estimate variances and confidence intervals around mean age of sexual maturity. A bias exists in this estimator as applied by Olesiuk *et al.* (1990, 2005) in that the sex of most juveniles is not determined until sexual maturity is reached, and some whales disappeared before their sex was known. This introduces a negative bias due to exclusion of some immature animals and overestimation of the proportion mature at a given age. We present estimates without correction for this bias in order to compare to results of Olesiuk *et al.* (2005), as well as estimates in which we include juveniles of unknown sex in our bootstrap sampling with an additional bootstrap assignment of sex from an even sex distribution to exclude approximately half of the unknown sample. This method still retains some bias due to the small difference in age at maturity of the two sexes, which creates a slight underestimate of age at maturity in females and an overestimate for males. This correction was not needed for male age at full maturity because of the long physical maturation period for males as evidenced by the gradual growth of the dorsal fin. The sex was known for all males used in that calculation well before the youngest age for full maturity had been reached. In all cases, the bootstrap median was closer to the direct calculation of mean age of maturity (DeMaster 1978) than the bootstrap mean, and we report only the median estimate.

We established one measure of female fecundity by estimating the intervals between successive calves and determining the probability of calving in a given year:

$$FEC = 1/CI,$$

where *FEC* is the proportion of females giving birth each year and *CI* is the interval between successive calves. For instance, if females gave birth once every five years, the probability of giving birth in any given year is 0.2. We used bootstrap sampling (Efron 1982) of individual calving records to determine the median and confidence interval.

Age-specific fecundity rates of females  $FECf(x)$  was defined as the proportion of females aged  $x$  giving birth to viable calves each year:

$$FECf(x) = NCf(x)/Nf(x),$$

where  $NCf(x)$  denotes the number of calves of either sex born to females aged  $x$ , and  $Nf(x)$  the total number of females aged  $x$ . We used all females, but inclusion of

females aged by the birth of their first calf would have caused a spurious spike of births at age 13. We therefore distributed those births normally around the most unbiased estimated age of first successful reproduction (AFR) as calculated above for purposes of smoothing the age-specific rates around the AFR. There are gaps in the resighting records in which calving events are reconstructed from mother-offspring associations discovered when the pods were resighted and these have a potential to create a small but off-setting bias to adult reproductive rates and calf survival. With the very high survival rates observed here, the potential bias is small. We used a second order polynomial logit model in the R statistical package *glm* (R Development Core Team 2010) to smooth the age-specific reproductive curve beginning at age 11, the earliest observed age for a first surviving calf.

### *Mortality and Survival Rates*

Mortality and survival rates were estimated by monitoring individuals over time. In 36 yr of monitoring resident whales in British Columbia and Washington, and 26 yr in Alaska, there is no evidence of dispersal from matriline (Bigg *et al.* 1990, Matkin *et al.* 1999a, Olesiuk *et al.* 2005, Matkin *et al.* 2008). Animals that disappeared were thus assumed to have died. Rates were estimated as:

$$MR(x) = 1 - SR(x) = D(x)/N(x),$$

where  $MR(x)$  represents the annual mortality rate or probability of dying in the next year at age  $x$ ,  $SR(x)$  the annual survival rate or probability of surviving the next year at age  $x$ ,  $D(x)$  the number of animals aged  $x$  that died before reaching age  $x + 1$ , and  $N(x)$  the number of animals in the study population aged  $x$  that were monitored to age  $x + 1$ . Where year of death was uncertain, we amortized the death over the 2–3 yr of uncertainty in the manner of Olesiuk *et al.* (2005).

Because mortality and survival often changes most rapidly early in life, and to take advantage of larger samples sizes for younger age groups, we pooled data into progressively wider age categories: 0.5–1.5 yr, 1.5–2.5 yr, 3.5–5.5 yr, 6.5–9.5 yr, and 10.5–14.5 yr, which are the same categories used by Olesiuk *et al.* (1990, 2005). New calves were assumed to be approximately 0.5 yr of age since most births occur in winter and recruited calves are not observed until months later. Animals that were not seen as calves, but later aged by their size or apparent maturity, were excluded from analyses in the first year of sighting because of the positive bias created in survival to that age. The effect of uncertainty in the ages of larger juveniles was negligible due to the pooling of the older categories. Standard errors and confidence intervals of the estimates were calculated by bootstrap sampling of individuals (Efron 1982). To account for decreasing sample sizes and increasing imprecision in age estimates with age, we pooled observations in 5 or 10 yr increments for the oldest age classes. Since we do not know the maximum ages with certainty, the older classes may encompass a larger range than indicated.

### *Population Model*

As a heuristic tool a population model was constructed for comparison with the observed population dynamics and those of the northern resident population. Estimated age-specific survival and birth rates were applied to the starting population age/sex structure in 1984 and projected forward until a constant growth rate and

stable structure was reached. This was verified by life table analysis using Lotka's fundamental equation (Lotka 1907, Olesiuk *et al.* 2005). The survival and birth schedules for the northern resident killer whale population studied by Olesiuk *et al.* (2005) was also modeled, duplicating the model described by those authors but allowing direct comparison of our results without ambiguity that might arise from rounding-off and other discrepancies in demographic estimates. Since we were uncertain of maximum ages in our study, we allowed the same maximum ages (age 90 for females and age 70 for males) in our model as did Olesiuk *et al.* (2005). In practice, truncation at age 60 for females and age 40 for males had negligible effect on age structure. Population growth ( $\lambda$ ) is defined as the quotient of total population size in successive years ( $N_t/N_{t-1}$ ), either from observations or as modeled. Applying the population model to the starting age/sex structure in the population allowed a comparison of population growth and structure which should have occurred if vital rates were constant as estimated over the study to those actually observed.

Our modeling efforts were, in part, intended to confirm the validity of our vital rate estimates, but also to explore the implications of subtle differences that might be seen in between our observed and modeled growth and age structure, and between our results and those of Olesiuk *et al.* (2005) for the northern resident killer whales of British Columbia. We used the survival data in Table 2 and the polynomial regression of calving rates in Figure 4 to estimate population growth and age/sex structure from the observed population size and age/sex composition in 1984. We used the most precise estimates of survival and calving rates available from Olesiuk *et al.* (2005: table 7, 8 for survival and table 10 for fecundity) for the northern resident killer whale population during its period of exponential growth (1973–1996) to recreate their life table model and standardize comparisons between the two populations. The “postreproductive” class in both studies is somewhat problematic because the reproductive criterion (no calves in last 10 yr) used by Olesiuk *et al.* (1990, 2005) is of limited utility at the end of a study lasting only 20 or 30 yr, and because the gradual decline in reproduction with age (Fig. 4 and Olesiuk *et al.* 2005: fig. 15) makes such determination ambiguous. We have used the “average age of senescence” of 40.5 yr (Olesiuk *et al.* 2005) as a general cut-off between reproductive and postreproductive classes in our analysis.

## RESULTS

We have identified over 700 whales in the southern Alaska resident population during this study. However, we were able to regularly locate and reidentify only 343 of these whales, which composed 10 pods. There were four pods from the AD clan (AD05, AD16, AE, and AK) and six from the AB clan (AF05, AF22, AG, AI, AJ, and AN10). We excluded two other pods (AB and AB25) that experienced atypical mortalities following the *Exxon Valdez* oil spill (Matkin *et al.* 2008). These 10 study pods and the number of whales in each are presented in Table 1.

All individuals from all of our monitored pods were not photographed in every year with one year intervals between documentation occurring 8% of the time, two year intervals 2% of the time and three year intervals 1% of the time (Table 2).

The number of whales in 10 pods that were seen from 1984 to 2005 increased from 121 whales to 240 at a mean annual growth rate of 3.4%. The seven pods seen from 1984 to 2010 increased from 82 to 152 at a mean annual rate of 2.6% (Fig. 2). Because 3 of the pods (AF05, AF22, AG) in southeastern Alaska (Matkin *et al.* 1997,



Table 1. Recruitment, mortalities, and total number of whales by pod, 1984–2010, with exceptions of AF05 and AF22 (last counted in 2005), and AG, (last counted in 2008).

| Pod   | Total<br>1984 | Total<br>recruited | Total<br>died | Total |
|-------|---------------|--------------------|---------------|-------|
| AD05  | 13            | 16                 | 10            | 19    |
| AD16  | 6             | 8                  | 6             | 8     |
| AE    | 13            | 13                 | 9             | 17    |
| AF05  | 12            | 32                 | 6             | 38    |
| AF22  | 12            | 25                 | 9             | 28    |
| AG    | 15            | 30                 | 6             | 39    |
| AI    | 6             | 4                  | 3             | 7     |
| AJ    | 25            | 42                 | 12            | 55    |
| AK    | 7             | 15                 | 7             | 15    |
| AN10  | 12            | 29                 | 10            | 31    |
| Total | 121           | 182                | 78            | 264   |

1999a) were usually out of our study area, they could not be tracked consistently between 2005 and 2010 and our examination of population characteristics is based on the 1984–2005 data from all pods. The difference in growth rates (Fig. 2) is at least partly explained by a female-skewed adult sex ratio in these three large pods that were not observed consistently in the final years. It is likely that the inter-pod variance in growth rate also is due to variance in adult reproductive output based on individual life histories (Brault and Caswell 1993).

#### Life History Parameters

Thirty-eight known-age females >10 yr of age were initially considered for analysis of AFR, but seven were excluded because of gaps in their sighting history in the period when they were 11–15 yr of age, the age range at which first calves were observed among females without resighting gaps. Excluding the nine juveniles of unknown sex led to a calculated mean (after DeMaster 1978) AFR of 12.8 (SE = 0.15), and a bootstrap median AFR of 13.1 (bootstrap 95% CI = 12.6–13.7, SE = 1.40). Median AFR including nine unsexed juveniles was 13.3 (bootstrap 95% CI = 12.7–13.8, SE = 1.18; Fig. 3). Among known-age females observed with a first calf, the modal AFR was 12 yr, indicating a positive skew in the distribution of AFR.

At an age range of 10–16 yr, the fins of a total of 44 known-aged males were estimated to have attained a height to width ratio (HWR) of 1.4, which is the ratio that marked the onset of sexual maturation developed by Olesiuk *et al.* (1990) in British Columbia. The estimated mean age at onset of sexual maturation (after DeMaster 1978), excluding juveniles of unknown sex, was 12.4 (SE = 0.14). The bootstrap median age at onset of sexual maturation of that sample was 12.4 yr (bootstrap 95% CI = 12.0–12.9, SE = 1.12); for the sample including unsexed juveniles ( $n = 53$ ) the median was 12.5 yr (bootstrap 95% CI 12.1–13.0, SE = 1.01; Fig. 3).

At the age range of 15–21 yr, 22 known-age males reached physical maturity during the study as indicated by a fully developed dorsal fin. Direct calculation of the average age of full maturity (after DeMaster 1978) from 36 known-age males  $\geq 15$  yr of age produced an estimate of 18.3 yr (SE = 0.19). Bootstrap median age of full maturity was 18.3 (bootstrap 95% CI = 17.6–19.0, SE = 1.45; Fig. 3).

Table 2. Intervals between annual photodocumentation of individuals within each pod from 1984 to 2005 with proportion of total in parentheses ( $n = 3,610$ ).

| Pod   | 0 yr         | 1 yr       | 2 yr      | 3 yr      | 4 yr | 5 yr |
|-------|--------------|------------|-----------|-----------|------|------|
| AD05  | 281          | 15         | 4         | 6         | 2    | 1    |
| AD16  | 118          | 9          | 5         | 2         | 0    | 0    |
| AE    | 227          | 26         | 2         | 1         | 0    | 0    |
| AF05  | 353          | 29         | 22        | 5         | 1    | 0    |
| AF22  | 353          | 61         | 25        | 3         | 0    | 0    |
| AG    | 469          | 46         | 14        | 2         | 0    | 0    |
| AI    | 141          | 0          | 0         | 0         | 0    | 0    |
| AJ    | 668          | 53         | 10        | 0         | 0    | 0    |
| AK    | 228          | 8          | 0         | 0         | 0    | 0    |
| AN10  | 388          | 32         | 0         | 0         | 0    | 0    |
| Total | 3,227 (0.89) | 279 (0.08) | 82 (0.02) | 19 (0.01) | 3    | 1    |

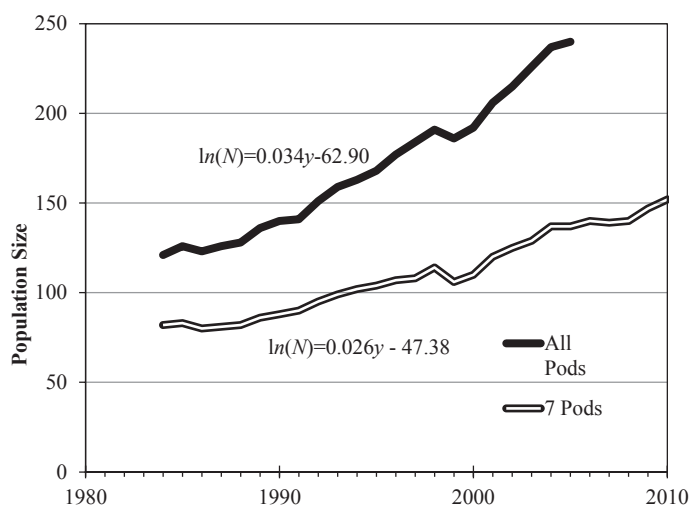


Figure 2. Population trend for 10 pods of southern Alaska resident killer whales from 1984 to 2005 (top) and for seven of those pods that were monitored through 2010.

We documented the intervals between births of 198 viable calves of 59 females for which at least two births were recorded (139 intervals). Calves were produced at intervals of 2–14 yr (Fig. 4), but most were separated by 3–7 yr (mean 4.9, bootstrap median = 4.8, SE 0.63, 95% CI = 4.4–5.2). The bootstrap median annual calving rate (FEC) among these reproductive females was 0.21 (SE = 0.01, 95% CI = 0.19–0.23).

There was little evidence that calving intervals changed over the period of the study (regression slope = 0.05,  $P = 0.15$ ). Mean calving intervals increased significantly (regression slope = 0.22,  $P < 0.01$ ) with age of the mother, from 4.3 yr at age 20 to about 6.5 yr by age 40. The number of calves produced by each individual per year declined with age (Fig. 5) due to the longer calving intervals and apparent onset of senescence. This pattern was also observed in the northern resident killer whale

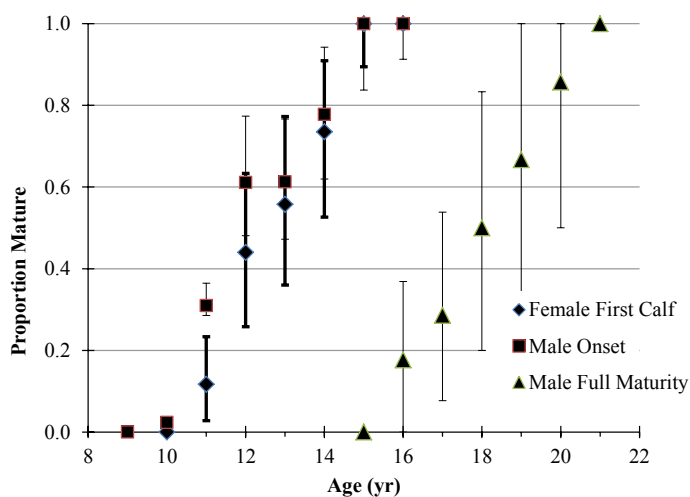


Figure 3. Age of sexual maturity (first calf) in known-age females and males (onset of dorsal fin growth) and male full maturity as judged by dorsal fin development for southern Alaska resident killer whales.

population in British Columbia (Olesiuk *et al.* 2005) and in the short-finned pilot whale (*Globicephala macrorhynchus*) (Marsh and Kasuya 1986).

Survivorship for both males and females conformed to the classic mammalian U-shaped curve (Table 3), indicating that the youngest and oldest animals experienced the highest mortality; however, the curve was narrower for males than females with a significant increase in mortality for males in the 30–41 yr range and for females in the 50–54 yr range, indicating a longer lifespan for females. Mortality rates for juveniles could not be estimated separately for each sex because deaths of immature animals (as old as 15 yr) could not be accurately assigned to sex. For this reason, and to facilitate comparison to northern resident killer whales, survival rates were estimated for both sexes pooled up to the age of 15.5 yr, as per Olesiuk *et al.* (2005).

#### Population Dynamics

While the average annual population growth rate ( $\lambda$ ) of all pods from 1984 to 2005 was 1.035 ( $e^{0.0341}$ ; Fig. 2), the initial modeled growth declined during the course of the study, and converged to 1.024 at stable age distribution. However, the sex ratio of whales observed as juveniles and reaching the age of 15.5 yr was skewed toward females (55:45). While not a statistically significant deviation from an even sex ratio ( $P = 0.18$ ), in this study, where all individuals are tracked, it creates observed effects on population growth. It is not known whether the skewed sex ratio was present at birth or the result of differences in neonatal and juvenile mortality up to maturity. To compensate we modified our model by creating a 55:45 female to male ratio which elevated the modeled growth rate from 1999 to 2005 slightly (1.026 *vs.* 1.024 in 2005), and gave a growth rate of 1.029 when stable age structure is achieved (Fig. 6). Mean annual growth rate and number of deaths in the modeled population were identical to

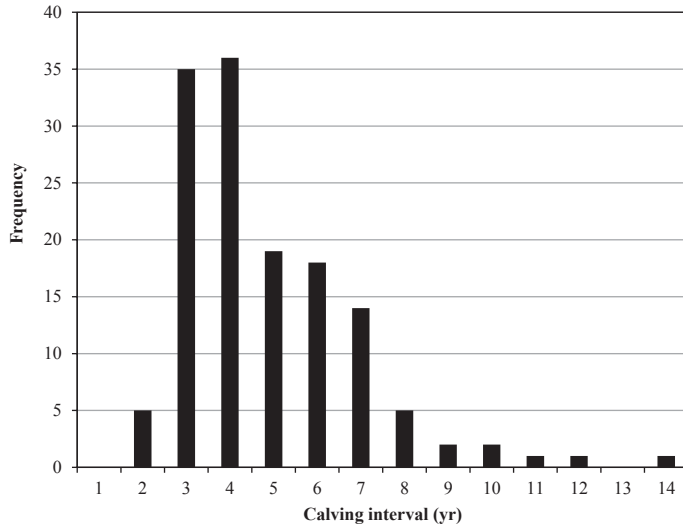


Figure 4. Frequency distribution of calving intervals for southern Alaska resident killer whales.

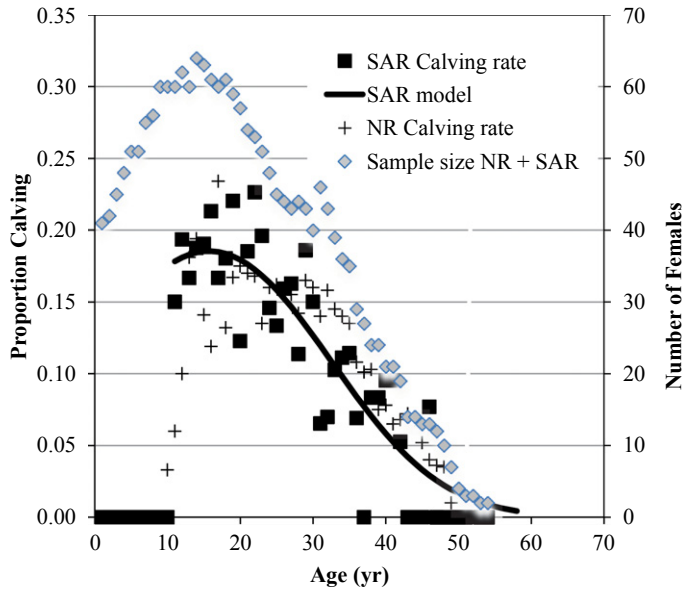


Figure 5. Age-specific fecundity (calves/female) for both southern Alaska resident (SAR) and northern resident (NR) and sample sizes for all females (both populations). Sample shown includes 21 SAR females that were first observed as juveniles and aged by the year in which they were first seen with a calf; these were distributed normally around the estimated age of first reproduction (13.3 yr) from ages 11 to 16. Model for SAR was a 3rd order logit polynomial fit to ages 11–52.

Table 3. Age and sex-specific annual survival rates from bootstrap analysis of southern Alaska resident killer whales.

|            | Age class | <i>n</i> | Upper 95% | Median survival | Lower 95% | Mean  | SE    |
|------------|-----------|----------|-----------|-----------------|-----------|-------|-------|
| Both sexes |           |          |           |                 |           |       |       |
|            | 0–1.5     | 165      | 0.976     | 0.945           | 0.903     | 0.946 | 0.019 |
|            | 1.5–2.5   | 181      | 1.000     | 0.997           | 0.991     | 0.997 | 0.003 |
|            | 3.5–5.5   | 179      | 0.998     | 0.991           | 0.981     | 0.990 | 0.004 |
|            | 6.5–9.5   | 163      | 0.996     | 0.989           | 0.979     | 0.988 | 0.005 |
|            | 10.5–14.5 | 141      | 0.998     | 0.992           | 0.983     | 0.992 | 0.004 |
| Females    |           |          |           |                 |           |       |       |
|            | 15–19     | 63       | 1.000     | 0.996           | 0.988     | 0.996 | 0.004 |
|            | 20–24     | 56       | 1.000     | 0.987           | 0.970     | 0.987 | 0.008 |
|            | 25–29     | 44       | 1.000     | 0.990           | 0.973     | 0.989 | 0.007 |
|            | 30–34     | 43       | 0.984     | 0.960           | 0.924     | 0.959 | 0.016 |
|            | 35–39     | 27       | 0.992     | 0.968           | 0.932     | 0.968 | 0.016 |
|            | 40–50     | 19       | 0.989     | 0.958           | 0.922     | 0.958 | 0.016 |
|            | 50–54     | 4        | 1.000     | 0.800           | 0.500     | 0.783 | 0.146 |
| Males      |           |          |           |                 |           |       |       |
|            | 15–19     | 66       | 0.998     | 0.986           | 0.967     | 0.985 | 0.008 |
|            | 20–24     | 47       | 0.985     | 0.964           | 0.933     | 0.962 | 0.014 |
|            | 25–29     | 32       | 0.993     | 0.965           | 0.932     | 0.964 | 0.015 |
|            | 30–34     | 20       | 1.000     | 0.970           | 0.921     | 0.966 | 0.020 |
|            | 35–41     | 11       | 0.945     | 0.857           | 0.731     | 0.854 | 0.054 |

those observed (1.033 and 69, respectively), while calf production differed by 1 (190 *vs.* 191).

The observed rate of population growth lagged the model growth early in the study (Fig. 6) with somewhat higher than average rates of calving and juvenile recruitment in the final six years (Fig. 7). The decline in modeled growth rate (Fig. 6) is the result of a higher proportion of adult, particularly reproductive, females at the start of the study in comparison to a stable distribution, but the increased calf and juvenile recruitment after 1999 appears to have increased the juvenile proportion relative to earlier in the study, and brought it up to a higher proportion than predicted by the model at stability (Fig. 7).

There are some minor artifacts in the model that largely stem from the averaging of estimated demographic parameters. The shift in reproductive and postreproductive females beginning in 1993 (Fig. 7) is likely an artifact of underestimating the age of females that should have been in the postreproductive class at the beginning of the study, and this may be responsible for the model overestimating population growth in the early years of the model, and underestimating growth later due to having underestimated fecundity. There were eight females that were classified as postreproductive in 1984 by the criterion that they produced no offspring in the next 10 yr, but their ages were likely underestimated by a conservative age determination referenced to the likely age of their oldest known offspring. If those animals (estimated ages 18–36 yr, mode = 31) were distributed across the 40–55-yr-old ages, the modeled population growth would have declined to  $\sim 1.034$  at the beginning of the study instead of 1.043 (Fig. 6).

The rates and stable age/sex structure of the model developed for southern Alaska resident killer whales is very similar to that of northern resident killer whales in their period of unrestrained population growth (Olesiuk *et al.* 2005) (Table 4).

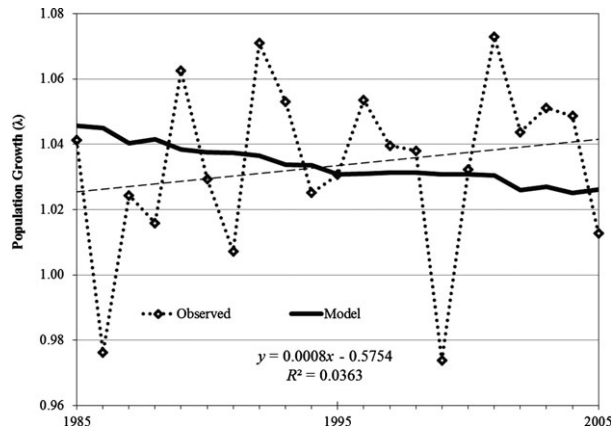


Figure 6. Observed and modeled rates of annual population growth of resident killer whales, demonstrating a weak positive trend from the observations. Model estimates were based on estimated average rates of survival and calving applied to the starting age/sex structure of killer whales in 1984, and an observed skew toward females (55:45) in newly matured whales.

Vital rates in our study produced slightly more reproductive females and juveniles, and slightly fewer males and fewer postreproductive females. Expected lifetime production of calves was slightly higher in the northern residents, but stable population growth was essentially equal. The evidence for a difference is strongest in age of maturity, where southern Alaska residents of both sexes were estimated to mature roughly a year earlier than those of Olesiuk *et al.* (2005). However, the bootstrap variation was substantially higher, and our inclusion of unsexed juveniles lead to higher estimates such that there was virtually complete overlap in the estimates of all age-specific parameters from the two populations (see Fig. 5 and Table 3). In both studies it is likely that some bias occurs in prime-age survival and reproductive rates as a result of underestimating the ages of mature females at the beginning of the study, but the exercise of distributing some of these to later ages indicated that the numbers and bias are probably small.

## DISCUSSION

Although the two populations are genetically distinct (Barrett-Lennard 2000, Matkin *et al.* 1999a), the population biology of the southern Alaska residents was remarkably similar to that of the northern residents of British Columbia during the 1970s through early 1990s when that population was increasing at 2.9% annually (Olesiuk *et al.* 1990, 2005). The 3.5% rate of growth reported for the southern Alaska residents we suspect reflects a population at r-max. The expansion of the Alaska population continued through 2005 while the northern resident population declined after 1996 (Olesiuk *et al.* 2005), then resumed rapid growth after 2001 (Ellis *et al.* 2011). There was such extensive overlap in the estimates of vital rates in these populations, and our use of bootstrap methods points to substantial underestimation of parameter variance for the northern resident study, that it is difficult to

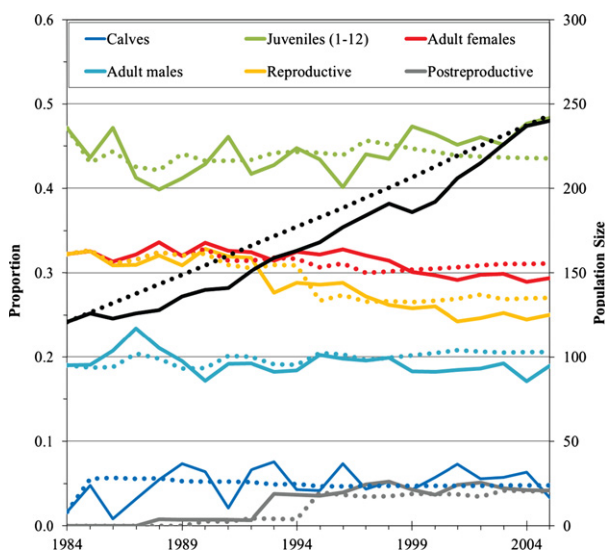


Figure 7. Observed (solid lines) and modeled (dotted lines) population size and age/sex structure in 10 pods of southern Alaska resident killer whales. Black lines are total population.

Table 4. Comparison of age/sex structure of southern Alaska resident killer whales as observed from 1984 to 2005, as modeled to a stable age structure, and as modeled for northern resident killer whales from parameters given by Olesiuk *et al.* (2005) for that population's period of unrestrained growth (1973–1996). Age categories were standardized, though Olesiuk *et al.* (2005) estimated a longer juvenile stage (1–15) due to later estimated ages of maturity.

|  | S.A.R population average | S.A.R stable model | B.C. northern residents |
|--|--------------------------|--------------------|-------------------------|
| Calves (<1)                              | 0.050                    | 0.049              | 0.046                   |
| Juveniles (<13)                          | 0.443                    | 0.444              | 0.412                   |
| Adult females ( $\geq 13$ )              | 0.314                    | 0.309              | 0.331                   |
| Adult males ( $\geq 13$ )                | 0.192                    | 0.199              | 0.211                   |
| Reproductive females ( $\geq 13, < 40$ ) | 0.286                    | 0.275              | 0.254                   |
| Postreproductive females ( $\geq 40$ )   | 0.027                    | 0.033              | 0.077                   |
| Population growth ( $\lambda$ )          | 1.034                    | 1.029              | 1.027                   |
| Lifetime reproduction                    |                          | 3.41               | 3.92                    |

conclude that there was anything but stochastic differences in the life history traits of these two populations during comparable periods of unrestrained growth.

Olesiuk *et al.* (1995, 2005) noted that the estimated ages of females that were fully adult at the start of the study would be biased downward by the potential deaths of their oldest offspring prior to the study. Based on calving rates and survival rates of calves, a probabilistic correction factor was calculated by Olesiuk *et al.* (2005) to compensate for older calves that may have died before the beginning of the study. The corrections increased as a function of the age of the oldest known offspring when first seen, and ranged from 0.7 when the oldest known offspring was first seen at age 0, to 1.4 when first seen at age 10, to 2.8 when first seen at age 20, to 5.4 when first

seen at age 30. We found this method flawed because (1) it takes no account of the number of known offspring for these females (usually several), (2) the correction factor is largely irrelevant because the oldest known offspring could rarely be established at >20 yr old when first seen, and (3) demographic calculations for older females required pooling of samples across age ranges much larger than the correction factor. Their correction factor also had extremely wide confidence limits, typically ranging from <0 to >20 yr, and failed to impart the actual effect of not observing the oldest offspring, pushing a small number of females into a much older age category rather than incrementing the ages of most older females by 1–3 yr. Eliminating the correction factor slightly decreases the age-specific reproductive and survival estimates in the older female age categories but has negligible effect on classification of females into postreproductive age classes.

The overall mortality pattern for killer whales in this study as well as studies in British Columbia (Olesiuk *et al.* 2005) followed the typical mammalian U-shaped curve (Caughley 1966), with mortality rates highest for the youngest and oldest animals of both sexes. The curve was broader and shallower for females than males; male mortality increased at the time they reached physical maturity and started breeding. Barrett-Lennard and Ellis (2001) found that all genetically identified fathers were older, physically mature males, indicating the importance of survival of the older males for their genetic contribution.

Pregnancy rate may be substantially higher than the recruitment rate (Olesiuk *et al.* 1990), with calves not surviving in years in which the mother cannot support the newborn nutritionally. Pregnancy has a relatively small energetic cost compared to the energetic cost of rearing a calf that may nurse for several years. The upward skew in reproductive intervals of up to 10 yr between successful calves in some cases reflects decreased fecundity due to age. However, it also may reflect the inability of females to support new calves energetically in some years during the first few months after birth due to nutritional stress.

Because there have not been marked changes in the rate of growth of our population during the period of this study, it is difficult to assess the role of various population parameters in response to changing conditions. The decline in AB pod was due to the *Exxon Valdez* oil spill (Matkin *et al.* 2008) and not reflective of changes in natural conditions. In our actual and modeled population structure over the course of the study (Fig. 6) the greatest fluctuation from the model is in the proportion of calves and juveniles, and although there may be some stochasticity involved, this indicates the potential importance of these groups in population response. Olesiuk *et al.* (2005) suggested that slow steady growth of resident killer whale populations with periods of higher mortality due to unfavorable conditions or catastrophes may be the typical pattern. However, responses to negative long-term changes in carrying capacity may be more complex. In this regard, the killer whale cannot be compared to terrestrial predators such as the grey wolf (*Canis lupus*) which has an early age of first reproduction (2–4 yr), the ability under favorable conditions to produce multiple offspring (4–8 per litter), and a relatively short lifespan (8–16 yr) (Mech 1970, Peterson *et al.* 1984, Fuller 1989). These characteristics allow wolf populations to respond relatively quickly to changes in prey density or other environmental factors and create the potential for relatively rapid shifts in abundance of predator and prey. Southern Alaska resident killer whale life history parameters indicate more modulated changes in numbers and less dramatic shifts in predation pressure since life history parameters constrict population response (Cole 1954, Testa *et al.* 2012).



This implies a slower ability to recover following a catastrophic event such as an oil spill (Matkin *et al.* 2008) or other perturbations.

Both in our study population and in the British Columbia northern resident population from 1973 to 1996 there was a steady increase in numbers. This may reflect a recovery from some past perturbation that reduced the population size. Although Olesiuk *et al.* (2005) suggest the possibility of mass strandings, there is little evidence that resident type killer whales are prone to these events. In the past, shooting of killer whales may have been a regular occurrence as evidenced by bullet wounds observed in 25% of the whales taken into captivity in the 1960s and early 1970s in British Columbia (Hoyt 1981). Bullet wounding and unexpected mortalities in AB pod during interactions with commercial long-line fisheries in the mid-1980s suggests that historic interactions also may have had a negative impact on southern Alaska resident killer whale numbers. No direct evidence for this exists, however. The *Exxon Valdez* oil spill resulted in long-term impact on both a large resident pod and transient group in Prince William Sound (Matkin *et al.* 2008). This was followed by a protracted recovery period for AB pod and is a contributing factor to what appears to be the eventual extinction of the AT1 transient population. However, this is a modern anthropogenic effect and does not have historical implications.

Alternately, there may have been an increase in carrying capacity for southern Alaska resident killer whales in recent decades. Salmon populations in the region have rebounded from low population levels recorded during the period from 1945 to 1975 that appear linked to the Pacific Decadal Oscillation (Kaeriyama *et al.* 2009). Coho salmon (*Oncorhynchus kisutch*) and Chinook salmon (*Oncorhynchus tshawytscha*) appear to be primary prey for this population (Saulitis *et al.* 2000; COM, unpublished data). In Prince William Sound and the Copper River the average permitted catch (based on run strength) for Chinook salmon from 1950 to 1975 was 17,576 (SD = 7,228) fish, and for coho salmon 231,500 (SD = 131,000) fish which essentially doubled during the 1976 to 2010 period to 36,342 (SD = 15,695) Chinook, and 476,228 (SD = 242,000) coho. The substantial increase in southern Alaska resident killer whales observed during the period of our study may be a result of the increased abundance of salmon species important in killer whale diet. Eventually we would expect to see increased mortality and a leveling of the southern Alaska resident population. The post-1996 decline in the northern resident population due to increased mortality was linked to a decline in prey availability, specifically Chinook salmon (Ford *et al.* 2010). From feeding habits studies in our area, it is likely that the trajectory of the resident killer whale population is tied to the strength of Chinook and coho salmon returns.

The parameters we developed indicate a population that exhibits a lengthy period of maturation, a low recruitment rate, extensive birth intervals, and the production of a single offspring. As exemplified by the AB pod following the *Exxon Valdez* oil spill (Matkin *et al.* 2008), rapid recovery from natural or anthropogenic catastrophes cannot be expected, nor can they respond rapidly to improved conditions in their environment and changes in carrying capacity.

During the 1984–2005 period, the southern Alaska resident killer whale population increased at an average annual rate of 3.5% which is probably representative of the population at r-max. This suggests a recovery from earlier perturbation or more likely, changes in carrying capacity, specifically increases in annual returns of Chinook and coho salmon over recent decades. Healthy stocks of these salmon species are essential for the continued success of the southern Alaska resident killer whale population.

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## LITERATURE CITED

- Allen, B. M., and R. P. Angliss. 2010. Alaska marine mammal stock assessments, 2009. U.S. Department of Commerce, NOAA Technical Memorandum NMFS-AFSC-206. 276 pp.
- Balcomb, K. C., J. R. Boran and S. J. Heimlich. 1982. Killer whales in greater Puget Sound. Report of the International Whaling Commission 32:681–685.
- Barrett-Lennard, L. G. 2000. Population structure and mating systems of northeastern Pacific killer whales. Ph.D. thesis, University of British Columbia, Vancouver, Canada. 97 pp.
- Barrett-Lennard, L. G., and G. M. Ellis. 2001. Population structure and genetic variability in northeastern Pacific killer whales: Toward an assessment of population viability. DFO Canadian Science Advisory Secretariat Research Document 2001/065. 35 pp.
- Bigg, M. A. 1982. An assessment of killer whale *Orcinus orca* stocks off Vancouver Island, British Columbia. Report of the International Whaling Commission 32:655–666.
- Bigg, M. A., P. F. Olesiuk, G. M. Ellis, J. K. B. Ford and K. C. Balcomb, III. 1990. Social organization and genealogy of resident killer whales *Orcinus orca* in the coastal waters of British Columbia and Washington State. Report of the International Whaling Commission (Special Issue 12):383–405.
- Brault, S., and H. Caswell. 1993. Pod-specific demography of killer whales *Orcinus orca*. Ecology 74:1444–1454.
- Caughley, G. 1966. Mortality patterns in mammals. Ecology 47:906–918.
- Cole, L. C. 1954. The population consequences of life history phenomena. Quarterly Review of Biology 29:103–137.
- Dahlheim, M. E. 1997. A photographic catalog of killer whales, *Orcinus orca*, from the Central Gulf of Alaska to the Southeastern Bering Sea. U.S. Department of Commerce, NOAA Technical Report NMFS 131.
- Dahlheim, M. E., and J. M. Waite. 1992. Abundance and distribution of killer whales *Orcinus orca* in Alaska in 1992. Annual report to the MMPA Assessment Program, Office of Protected Resources, NMFS, NOAA, 1335 East-West Highway, Silver Spring, MD 20910.
- Dahlheim, M. E., D. K. Ellifrit and J. D. Swenson. 1997. Killer whales of Southeast Alaska: A catalogue of photo-identified individuals. Day Moon Press, Seattle, WA.
- DeMaster, D. P. 1978. Calculation of the average age of sexual maturity in marine mammals. Journal of the Fisheries Research Board of Canada 35:912–915.
- Durban, J., D. Ellifrit, M. Dahlheim, et al. 2010. Photographic mark-recapture analysis of clustered mammal-eating killer whales around the Aleutian Islands and Gulf of Alaska. Marine Biology 157:1591–1604.
- Efron, B. 1982. The jackknife, the bootstrap, and other resampling plans. Society of Industrial and Applied Mathematics CBMS-NSF Monographs 38.
- Ellis, G. M., J. R. Towers and J. K. B. Ford. 2011. Northern resident killer whales of British Columbia: Photo-identification catalogue and population status to 2010. Canadian Technical Reports of Fisheries and Aquatic Sciences 2942. v + 71 pp. Available at <http://www.dfo-mpo.gc.ca/Library/343923.pdf>.

- Ford, J. K. B., G. M. Ellis, L. G. Barrett-Lennard, A. B. Morton, R. S. Palm and K. C. Balcomb, III. 1998. Dietary specialization in two sympatric populations of killer whales *Orcinus orca* in coastal British Columbia and adjacent waters. *Canadian Journal of Zoology* 76:1456–1471.
- Ford, J. K. B., G. M. Ellis and K. C. Balcomb. 2000. Killer whales: The natural history and genealogy of *Orcinus orca* in the waters of British Columbia and Washington. UBC Press and University of Washington Press, Vancouver, BC and Seattle, WA.
- Ford, J. K. B., G. M. Ellis, P. F. Olesiuk and K. C. Balcomb. 2010. Linking killer whale survival and prey abundance: Food limitation in the oceans' apex predator? *Biology Letters* 6:139–142.
- Fuller, T. K. 1989. Population dynamics of wolves in north-central Minnesota. *Wildlife Monographs* 105.
- Hoelzel, A. R., and G. A. Dover. 1991. Genetic differentiation between sympatric killer whale populations. *Heredity* 66:191–195.
- Hoelzel, A. R., M. Dahlheim and S. J. Stern. 1998. Low genetic variation among killer whales *Orcinus orca* in the eastern North Pacific and genetic differentiation between foraging specialists. *Journal of Heredity* 89:121–128.
- Hoelzel, A. R., J. Hey, M. E. Dahlheim, C. Nicholson, V. N. Burkanov and N. A. Black. 2007. Evolution of population structure in a highly social top predator, the killer whale. *Molecular Biological Evolution* 24:1407–1415.
- Hoyt, E. 1981. *Orca, the whale called killer*. E. P. Dutton, New York, NY.
- Kaeriyama, M., H. Seo and H. Kudo. 2009. Trends in run size and carrying capacity of Pacific salmon in the North Pacific ocean. *North Pacific Anadromous Fisheries Commission Bulletin No. 5*:293–302.
- Leatherwood, S., C. O. Matkin, J. D. Hall and G. M. Ellis. 1990. Killer whales, *Orcinus orca*, photo-identified in Prince William Sound, Alaska, 1976 through 1987. *Canadian Field-Naturalist* 104:362–371.
- Lotka, A. J. 1907. Relation between birth rates and death rates. *Science* 26:21–22.
- Marsh, H., and T. Kasuya. 1986. Evidence for reproductive senescence in female cetaceans. *Report of the International Whaling Commission (Special Issue 8)*:57–74.
- Matkin, C. O., D. R. Matkin, G. M. Ellis, E. L. Saulitis and D. McSweeney. 1997. Movements of resident killer whales in southeastern Alaska and Prince William Sound, Alaska. *Marine Mammal Science* 13:469–475.
- Matkin, C. O., G. M. Ellis, E. L. Saulitis, L. Barrett-Lennard and D. R. Matkin. 1999a. Killer whales of southern Alaska. *North Gulf Oceanic Society, Homer, AK*.
- Matkin, C. O., G. M. Ellis, P. Olesiuk and E. Saulitis. 1999b. Association patterns and inferred genealogies of resident killer whales, *Orcinus orca*, in Prince William Sound, Alaska. *Fisheries Bulletin, U.S.* 97:900–919.
- Matkin, C. O., L. Barrett-Lennard, H. Yurk, D. Ellifrit and A. Trites. 2007. Ecotypic variation and predatory behavior of killer whales *Orcinus orca* in the eastern Aleutian Islands, Alaska. *Fisheries Bulletin, U.S.* 105:74–87.
- Matkin, C. O., G. M. Ellis, E. L. Saulitis, P. Olesiuk and S. D. Rice. 2008. Ongoing population-level impacts on killer whales *Orcinus orca* following the *Exxon Valdez* oil spill in Prince William Sound, Alaska. *Marine Ecological Progress Series* 356: 269–281.
- Mech, L. D. 1970. *The wolf, the ecology and behavior of an endangered species*. Doubleday, New York, NY.
- Olesiuk, P. F., M. A. Bigg and G. M. Ellis. 1990. Life history and population dynamics of resident killer whales *Orcinus orca* in the coastal waters of British Columbia and Washington. *Report of the International Whaling Commission (Special Issue 12)*: 209–242.
- Olesiuk, P. F., G. M. Ellis and J. K. B. Ford. 2005. Life history and population dynamics of resident killer whales *Orcinus orca* in the coastal waters of British Columbia Research Document 2005/045. Fisheries and Oceans Canada, Nanaimo, B.C., Canada.

- Parsons, K., J. Durban and A. Burdin, *et al.* In press. Ecological specialization and the genetic structuring of killer whale populations in the northern North Pacific. *Journal of Heredity*.
- Peterson, R. O., J. D. Woolington and T. N. Bailey. 1984. Wolves of the Kenai Peninsula, Alaska. *Wildlife Monographs* 88:1–52.
- R Development Core Team. 2010. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Saulitis, E. L., C. O. Matkin, K. Heise, L. G. Barrett-Lennard and G. M. Ellis. 2000. Foraging strategies of sympatric killer whale, *Orcinus orca*, populations in Prince William Sound, Alaska. *Marine Mammal Science* 16:94–109.
- Scheel, D., C. O. Matkin and E. L. Saulitis. 2001. Distribution of killer whale pods in Prince William Sound, Alaska over a thirteen-year period, 1984–1996. *Marine Mammal Science* 17:555–569.
- Testa, J. W., K. J. Mock, C. Taylor, H. Koyuk, J. Coyle and R. Waggoner. 2012. Agent-based modeling of the dynamics of mammal-eating killer whales and their prey. *Marine Ecological Progress Series* 466:275–291.
- Yurk, H., L. G. Barrett-Lennard, J. K. B. Ford and C. O. Matkin. 2002. Cultural transmission within maternal lineages: Vocal clans in resident killer whales in southern Alaska. *Animal Behaviour* 63:1103–1119.

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