Population Viability Analysis

for the

Southern Resident Population

of the

Killer Whale

(Orcinus orca)

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ABSTRACT

Analysis of a 26 year record of Southern Resident killer whale demography revealed a statistically increasing trend in adult mortality. In the past 5 years, the population has fallen by 4.9% per year. Fecundity has also been lower than long term average in recent years.

These declines in survival and fecundity are unlikely to be merely the temporary result of natural cyclic variation in habitat quality and food supply. Southern Resident killer whales have extreme levels of tissue contamination by persistent organochlorine pollutants, which is expected to result in reduced fecundity and a higher risk of epizootic disease.

During the 1990's there have been declines in abundance of salmon, which are the main food source for killer whales. These declines are also unlikely to be solely explained by natural climatic cycles. There has also been an increase in boat traffic and industrial activity in the killer whales habitat that may disrupt normal behavior and increase risk of death from oil spills. Global warming, increased shipping traffic, coastal development, wild salmon loss, increased salmon farming and pollution suggest that the recent declines are part of a downward trend.

Population viability analysis by stochastic population modeling suggested that the Southern Resident population is likely to go extinct in the foreseeable future unless ongoing habitat degradation is halted. Only the most optimistic of models free of adverse impacts to habitat resulted in predictions of population stability. Incorporation of plausible impacts such as oil spills, epizootics, and reduced salmon food stocks greatly increased predicted extinction risk to as high as 54.5% in the next 100 years, even under the optimistic assumption that the long-term average fecundity and mortality would otherwise continue unchanged.

If the reduced fecundity and adult survival seen since 1996 were assumed to continue indefinitely rather than returning to the lower levels seen over the previous 22 years, the risk of extinction of the Southern Resident population extinction within 100 years is highly likely, even in the absence of additional risks of oil spills, epizootics or reduced food supply. The most plausible such scenario incorporating risks of inbreeding depression and mate limitation at small population size, oil spills, epizootics and reduced food supply predicted a median time to extinction of 74 years with a 95% confidence interval of 33-121 years.

However, adult mortality may increase further if recent trends continue. If adult mortality continues to increase at the same rate, then extinction risk would be even higher.

INTRODUCTION

Once abundant throughout the waters of the Pacific Northwest, the Southern Resident killer whale, *Orcinus orca,* is now one of the most imperiled killer whale stocks in the world, and since 1996 has been declining. The decline has been attributed to several anthropogenic sources, primarily from depletion of preferred food stocks, toxic pollution, and disturbance from whale watching boats and other shipping traffic.

Killer whale stocks

Killer whales in the Pacific Northwest of North America are divided into four component stocks that are distinct genetically, behaviorally, and morphologically, but which occupy adjacent or overlapping ranges (Baird 1999). Although the term "form," "subspecies," or even "species" should perhaps be applied to distinguish these distinct types of killer whales, all are currently classified as one

species. We will continue to use the term "stock" to describe these different types.

Transient killer whales primarily prey on other marine mammals such as seals, while Residents primarily subsist on fish (Morton 1990). Transients and Residents differ in morphology, group size, social organization, and acoustic repertoire (Ford and Ellis 1999, Bain 1989, Baird 1994). Transient and Resident populations have overlapping ranges. However, genetic evidence suggests that they have been isolated for thousands of years (Bigg et al. 1987, Hoelzel et al. 1998). Transients actively avoid Resident pods and interactions have been rarely reported (Jacobsen 1990, Morton 1990, Barrett-Lennard 1992, Baird and Dill 1995).

Residents in the Pacific Northwest are divided into three stocks: Northern, Southern, and Offshore. Each stock has distinct patterns of association, pigmentation and genetics (Bigg et al. 1987, Baird and Stacey 1988, Bain 1989, Ford et al. 1998, Hoelzel et al. 1998, Matkin et al. 1998, Barrett-Lennard 2000).

Although the three Resident stocks have partly overlapping ranges, behavioral interactions are rare. Genetic and morphological differences suggest that they are reproductively isolated (Baird and Stacey 1988, Stevens et al. 1989, Hoelzel and Dover 1991, Hoelzel et al. 1998, Barrett-Lennard 2000). Southern residents have low genetic diversity for several nuclear and mitochondrial DNA markers implying that inbreeding depression may be likely for this stock (Hoelzel and Dover 1991, Hoelzel et al. 1998, Barrett-Lennard 2000).

Southern Resident demography

The home range of the Southern Residents includes the international inland waters of Puget Sound, Juan de Fuca and Georgia Straits. Although not well documented, it is believed that their home range also includes regions outside the entrance to Juan de Fuca Strait, extending as far as south to Monterey Bay, and north to Cape Scott on Vancouver Island. (Figure 1, Ford et al. 1994).

The Southern Residents are divided into three "pods" that tend to travel and feed together in particular "territories." Within pods, Southern Residents are matrifocal, that is, siblings tend to stay in close proximity to each other and their mothers. There is evidence however, that pods are not necessarily composed of close relatives (Dahlheim and Heyning 1999 p. 296). Mating is found to occur primarily outside of a pod (Barrett-Lennard 2000), although paternity analysis has revealed at least one case of within-pod mating (Hoelzel et al. 1998).

Figure 1. Range map for Resident Killer whales. The Transients overlap ranges of both Northern and Southern Residents. Offshore Residents occupy waters further into the ocean (after Ford et al. 1994)

METHODS

The published record of births and deaths for the period 1974-2001 from the Center for Whale Research (van Ginneken et al. 2000) with corrections by University of Washington whale biologist, Dr. David Bain and updates for the July 1, 2001 census of returning whales were used to calculate age and sex distributions, and annual mortality and fecundity statistics. These data are shown in the Appendix.

Annual age and sex distributions, fecundities and mortalities were calculated from the individual life histories and analyzed by probit regressions and time series analysis in the program SYSTAT to quantify possible trends, cycles, and cross correlations. Probit regressions of mortality and fecundity on time were used with the caveat that the assumption of year-to-year independence is clearly violated. Before doing such regressions, autocorrelations within series were examined before probit regression to confirm that autocorrelations were not substantial or significant.

Averages for life history parameters were then calculated and environmental components of variances estimated by removing pure demographic variance using the method of Lacey et al. (2000). Best estimates of life history variables were then used for successive simulations of the Vortex modeling algorithm (Lacey et al., 2000). Estimates were varied systematically to model the effects of plausible changes in parameters on population extinction probabilities.

RESULTS AND DISCUSSION

Population trends

A census of the Southern Residents has been taken annually since 1974 by the Center for Whale Research. Records from capture operations extend the record back to 1960, supplementing that census information.

The Southern Resident population numbered at least 100 individuals in the mid-1960's, but may well have been much higher (Richard Osborne, Whale Museum, pers. comm.). Since that time, three major declines have occurred in the population (Fig. 2).

The first decline occurred between 1967 and 1972, and was caused presumably by live-capture operations for public display. Approximately 34 Southern Residents were taken during this period, leading to a population decline of at least 30%. The Southern Residents were down to 71 in 1974 (Fig. 2).

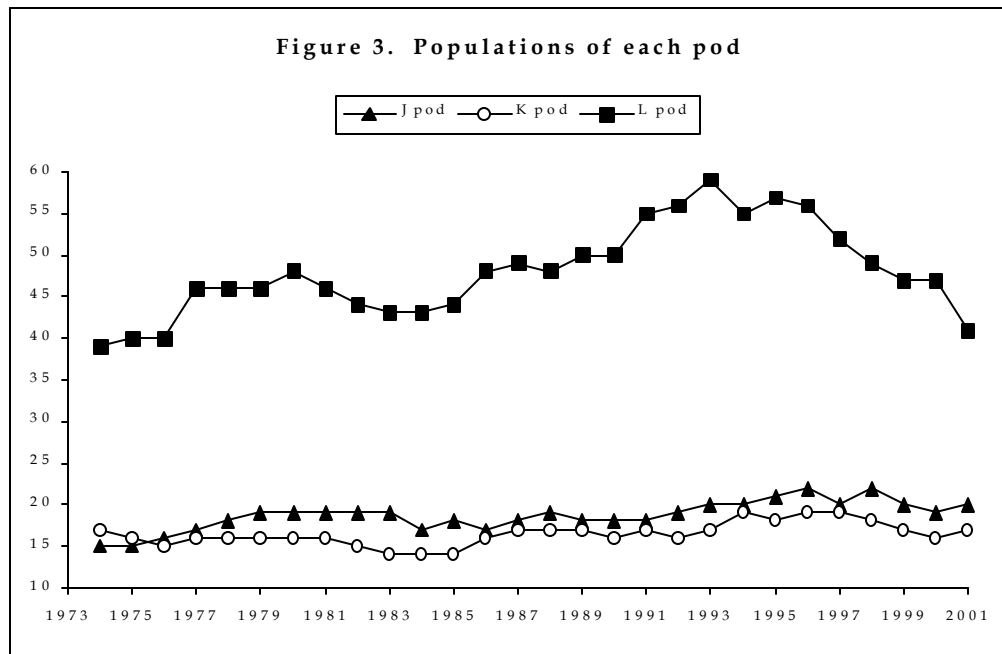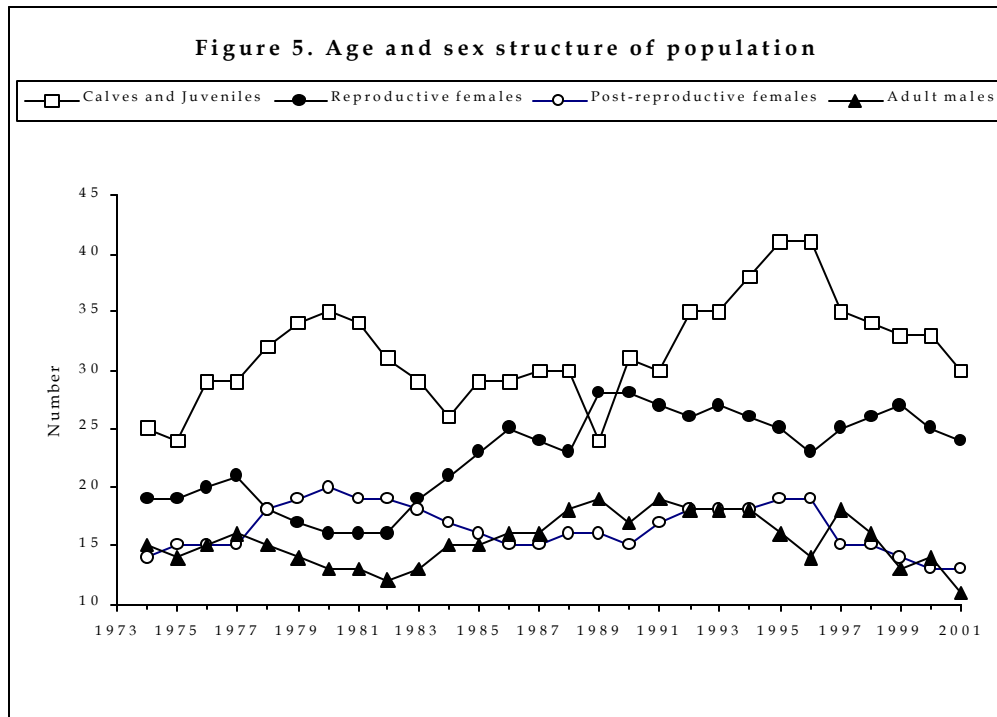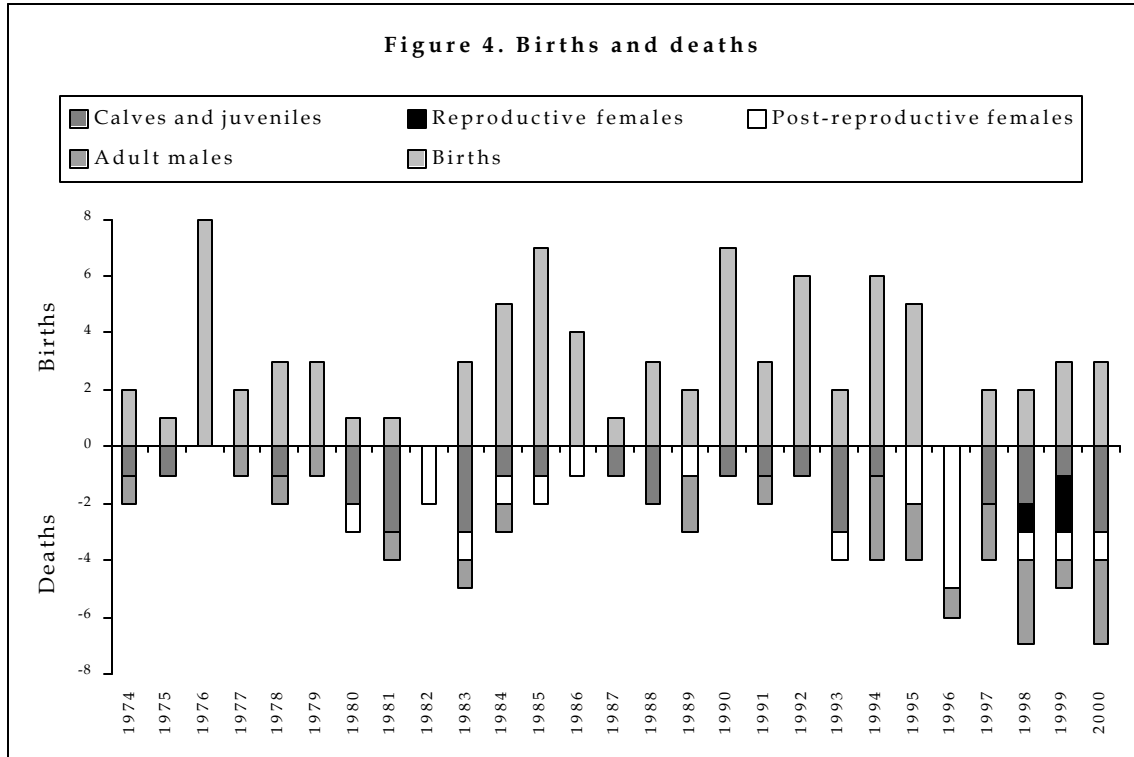**Figure 2. Southern Resident killer whale population**
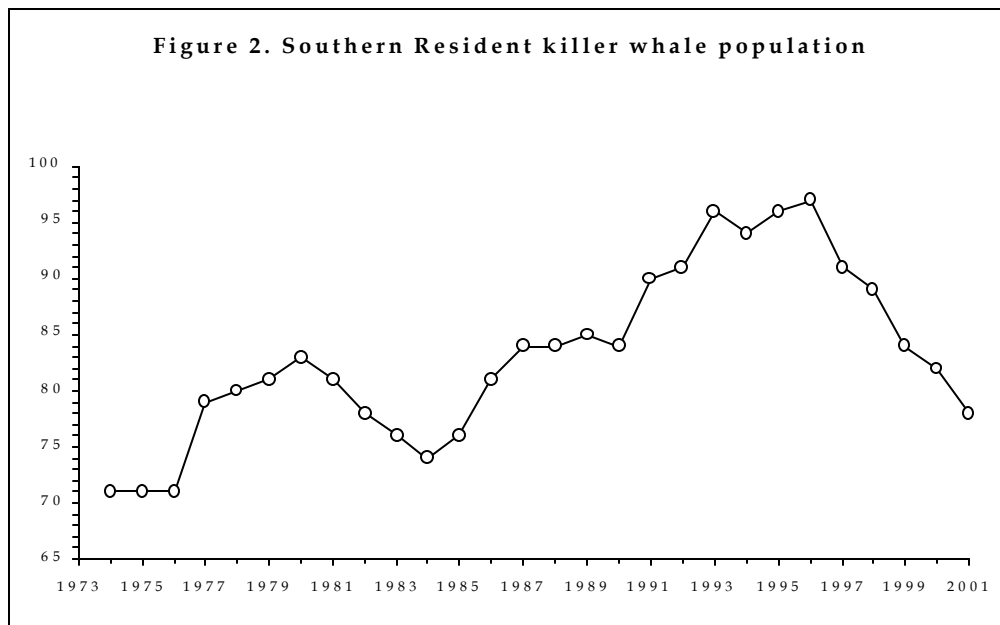
After several years of steady recruitment — including a good calf crop in 1976—and low mortality, the population grew to a peak in 1980 (Fig. 2). The second decline occurred from 1980 to 1984, when the population declined from 83 to 74 in four years, a 3% annual rate of decline. L pod suffered the greatest reduction, while J pod appeared to be unaffected during this period (Fig. 3). This period of decline seems to have resulted from elevated mortality of older females and juveniles in concert with lower fecundities (Figs 2-4). The age structure of the population shows a relatively aging population of adult females during this period, with more post-reproductive than reproductive-aged females (Fig. 5). As the influx of new calves from the burst of reproduction in the mid 1970's began to mature, adult female and male numbers began to climb from the mid 1980's (Fig. 5), showing that the mid 1980's decline may have resulted primarily from demographic effects.

A period of recovery continued until 1993 and held steady until 1996 concordant with a rising

population of adult males and reproductive aged females. After the peak of population in 1996, higher mortalities and lower fecundity resulted in a sustained decline that continues to the present (Figs. 2,4). The rise in mortality preceded the decline in fecundity, showing a noticeable increase from 1993. As shown below, there is a significant rising trend in reproductive adult mortality through the 26 year record. In contrast to the earlier decline, all age and sex classes have been affected. All three pods suffered concurrent declines, but by the July 2001 census, six individuals of L pod were reported missing, resulting in a sharper decline in the L pod numbers (Fig. 3). As in the 1980-1984 decline, juvenile and post-reproductive female mortalities were elevated and L pod was the most affected of the three.

Unlike the earlier decline, the recent decline also involved elevated mortality of younger juveniles, reproductive females and adult males. Juveniles and calves have been dying at younger ages (average 2.9 years) than in the 1980-84 decline (average 5.4 years). Reproductive female deaths were unrecorded until the two years 1998 and 1999. The three females that died in those years were aged 37, 28 and 18. So the increased mortality was not age related. A sharp rise in adult male mortality has led to a corresponding decline in male numbers (Fig. 5). Whatever was causing the increased deaths may also have eliminated fecundity in 1996. Fecundity thereafter has been lower than the long-term average although this difference is not statistically significant (Figs 2, 4). Unlike the 1980-84 decline the recent population decline is not associated with a relative excess of older adults, indeed numbers of reproductive females are still almost double what they were in that earlier period (Fig. 5).

Figure 3. Populations of each pod

Figure 4. Births and deaths

Legend: Calves and juveniles, Reproductive females, Post-reproductive females, Adult males, Births

Figure 5. Age and sex structure of population

Legend: Calves and Juveniles, Reproductive females, Post-reproductive females, Adult males

From 1996-2001, the Southern Resident stock declined from 97 to 78, approximately 4.9 % per year. Several factors make this recent decline unique and alarming:-

1. The decline is the most precipitous on record without an obvious cause such as captures or age structure. A parallel decline has not been seen for the neighboring population of Northern Resident killer whales (Center for Biological Diversity 2001).

2. The decline results from lower fecundity and increased mortality in all age and sex classes but particularly of reproductive females. The L pod which seems to range further afield than other pods, also suffers higher mortality and fluctations in numbers possibly as a consequence of greater exposure to risk factors.

3. Disturbances caused by whale watching and water traffic have increased dramatically, potentially disrupting normal activities.

4. Bio-accumulative organochlorine pollutants are very high and have been increasing in these waters (McCain et al. 2000). On the coastline of Puget Sound alone there are 13 "superfund" toxic waste sites with polychlorinated biphenyls or PCBs. Five of these are known to be contaminating freshwater or marine food chains in the Sound (Center for Biological Diversity 2001, App. D).
Ross et al. (2000) found that adult Southern Resident killer whales had PCB body burdens which exceeded immunological effects thresholds established for seals. Although no outbreak has yet been recorded, viral epidemics for other cetaceans have been linked to organochlorine toxicants in the Atlantic and Mediterranean (Simmonds and Mayer 1997).

5. The Southern Resident's main food sources, salmon of various species, are declining. The Southern Residents are salmon specialists with an apparent preference for chinook salmon (Center for Biological Diversity 2001). The commercial catch of chinook in Washington and British Colombia has like all other salmon declined dramatically from the mid 1980's to the present (Figure 6).   These data must be viewed with some caution however. Catch data likely to not well represent actual salmon abundance in Southern Resident habitat, because catch is regulated to stabilize "escapement," the numbers of salmon escaping capture and arriving at their spawning grounds.   Thus although the decline in catch represents a response to declining abundance, it also represents a decline in effort forced by regulation. At least for sockeye salmon, this means that escapement to the Straits of Georgia has been more stable than declining catch would suggest.
Fraser River sockeye salmon were less abundant in the years 1995-2000 compared to the high levels that were observed in the late 1980's and early 1990's (Jim Woodey, International Pacific Salmon Commission pers. comm.). Salmon populations declined in the Straits of Georgia coincident with a climatic "regime shift" starting in 1989 (Beamish et al. 1999), a shift that has alleviated somewhat in 1999 and 2000 (Richard Beamish, CDFO, pers. comm.)
A 50-60 year cycle in the northern hemisphere climate is thought to cause cycles in fish stocks (Klyashtorin 1998) and there is some concordance between observed catch and the expected peak at 1990 and subsequent decline expected from this cycle. There is good reason to believe however, that recent declines are not merely the low points of a climatic cycles but reflect a declining trend in habitat quality due to human caused impacts of riverine and coastal development, overfishing and global warming.

Figure 6. Salmon catch Washington & British Colombia

Legend: Salmon, WA — Chinook, WA — Salmon, BC
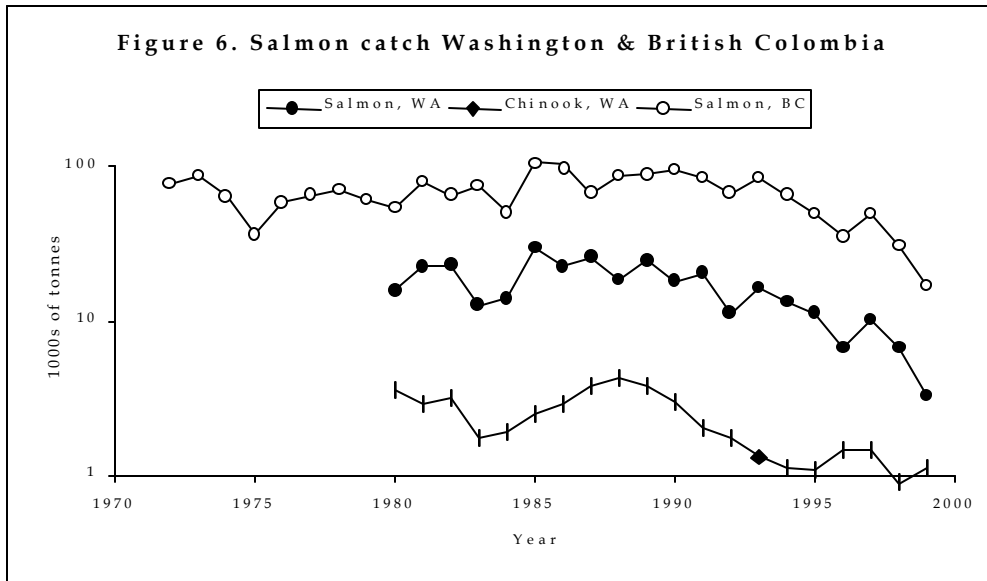
NOTE. Catch data are shown on a log scale. Chinook catch in 1998 fell below 1000 tonnes. Data from U.S. National Marine Fisheries Service or NMFS and Canadian Department of Fisheries and Oceans or CDFO.

Several studies suggest loss or substantial reduction of salmon stocks from global warming impacts on rivers in Europe and North America. In Europe shifts towards cyprinid and percid dominance and drastic decrease and collapse of salmonid and other coldwater fish populations is expected (Lehtonen 1996). In the US, comparison with paleo-climate suggests possible declines of 30-60% in salmonids in the Colombia basin, USA with global warming (Chatters-Chatters et al. 1995). Other models predict probable salmonid disappearance from the Rocky Mountains (Keleher and Rahel 1996). Warmer streams result in earlier migration and better marine survival for Fraser River pinkeye salmon (Henderson et al. 1995) but lower final weight and reproductive success (Hinch et al. 1995).

A directional shift and contraction in marine habitat for salmon is expected from poleward shifts in the zone of thermal suitability, below which other pelagic fish from the subtropics are expected to move in and displace salmon (Welch et al. 1998).

Global warming may explain the recent northward diversion of returns by salmon to their spawning grounds. The number of Fraser River sockeye salmon returning through Johnstone Strait has been relatively high in recent years (1991-2000 average = 60%) relative to the portion moving through the more southerly Juan de Fuca, with some years as high as 82% in 1998. This northward shift is higher than in any preceding decade and has been associated with a recent spate of El Niño's in 1992, 93, 94 and 1997, 98 which in turn may be a result of global warming. In 2000, however, the northward shift dropped back to 36% (Jim Woodey, International Pacific Salmon Commission pers. comm.). A northward shift in migration patterns could result in pre-emption of the returning salmon food source by Northern Residents at the expense of Southern Residents.

National Marine Fisheries Service (1997) in a status review of salmonids in the Pacific region, found that 41 stocks in the Puget Sound/Washington coast area were facing a high to moderate extinction risk in 1997. Global warming may not be the only or even the main culprit, but the decline in salmon stocks is clearly a real phenomenon.

There is added concern that loss of salmon will force Southern Residents (a) to move further

afield for a larger part of the year thus exposing them to more conflicts with competitors and to risks of open ocean travel that they are not normally exposed to, especially entanglement and bycatch in fishing nets or lines, and/or (b) to compensate by preying upon bottom fish and rockfish that may be more contaminated with organochlorines.

Sex ratio, mating system and mate limitation

The total of 65 births with known sex of offspring observed since 1974 show a male-biased primary sex ratio of 57% males (Binomial SD 6%). This may represent an adaptation to compensate for female-biased sex ratios in adult life that result from higher male mortalities, or may be a temporary adaptive compensation for the loss of males during the 1960's. However, it was not significantly different from 50% sex ratio expected with Mendelian segregation of sex chromosomes (Binomial test P=0.11).
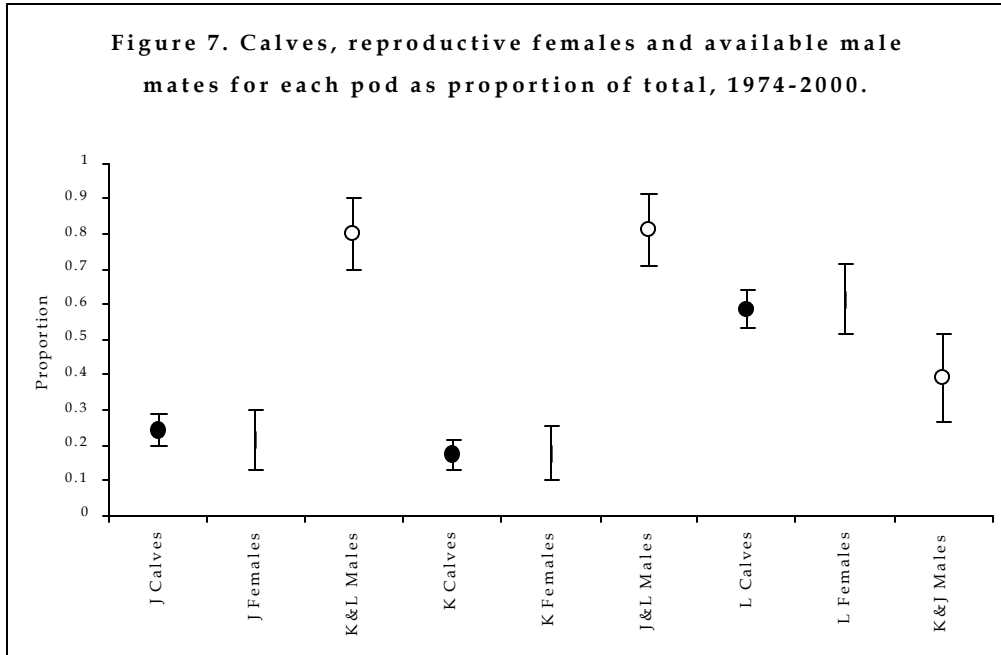
Reproductive adult sex ratio is consistently female-biased with a surplus of reproductive females (Fig. 5). The adult sex ratio ranged from 36% in 1980 to 49% in 1988, with an overall mean of 42% males (SD 3.5%).

Although Hoelzel et al. (1998) found evidence of within pod paternity for Southern Residents, the general pattern of pod exogamy is well supported by more detailed studies for other resident stocks (Barrett-Lennard 2000). Assuming that pods are primarily exogamous, that is, they mate preferentially with members of other pods, then radically different operational sex ratios are found for different pods (Fig. 7). Since L is the largest pod, available J and K adult males as a proportion of all males is less than the proportion of L females in the population, showing that there would be a scarcity of available mates for L-pod females (Fig. 7). Conversely the proportion of available mates for J and K pod females is greater than the proportions of females in those pods, showing that mates are in excess for females in these smaller pods (Fig. 7). However, the proportions of all calves produced by each pod are concordant with the relative proportions of reproductive females in the pod (Binomial tests of significance). Thus fecundity did not differ significantly between pods (Contingency table χ^2 test Fig. 7).

To test a mate limitation hypothesis for L pod, namely that fecundity within L is limited by adult male numbers in K and J pods, we examined cross correlations between time series for L pod fecundity and sex ratio. Operational sex ratio for L pod was calculated as the number of adult males in the K and J pods per reproductive female in the L pod. No significant correlation was found, indicating that mates were not limiting for L females during the period of study.

However the high mortality of males has resulted in declining numbers of males in recent years (Fig. 5). Losses of all J and K pod mature males is likely in the near future, and may yet result in future failures of L pod females to find a mate.

Although Dahlheim and Heyning (1999 p. 292), observe that killer whales are polygamous, insufficient data on paternity exists to support this claim. Absolute numbers of calves produced by all L pod females were compared with number of possible fathers (adult males in J and K pod). Only L pod was examined because it was the only relatively male-scarce pod of the three, and therefore the most likely to show clear polygamy. In all years, numbers of calves produced were less than the numbers of possible fathers. This was true even assuming a late minimum (as distinct from average) age of 15 for male sexual maturity. Although polygamy is likely based on morphological evidence, available data do not provide unambiguous evidence of polygamy among Southern Residents.

Figure 7. Calves, reproductive females and available male mates for each pod as proportion of total, 1974-2000.

Fecundity

Fecundity is calculated as the number of calves per year per female of reproductive age. The minimum and maximum breeding ages are estimated further below as 13 and 40 respectively for females. Fecundity had a skewed age-specific distribution of high early peak with a slow decline to reproductive senescence, but also with a clear late peak of reproduction just prior to reproductive senescence (Fig. 8). Fecundity showed a suggestion of cyclic variation through time (Fig. 9). However, there were no significant autocorrelations within the series and Fourier analysis of the de-trended series found no significant periodicities.

Figure 8. Age specific fecundity across all years

Figure 9. Annual fecundity
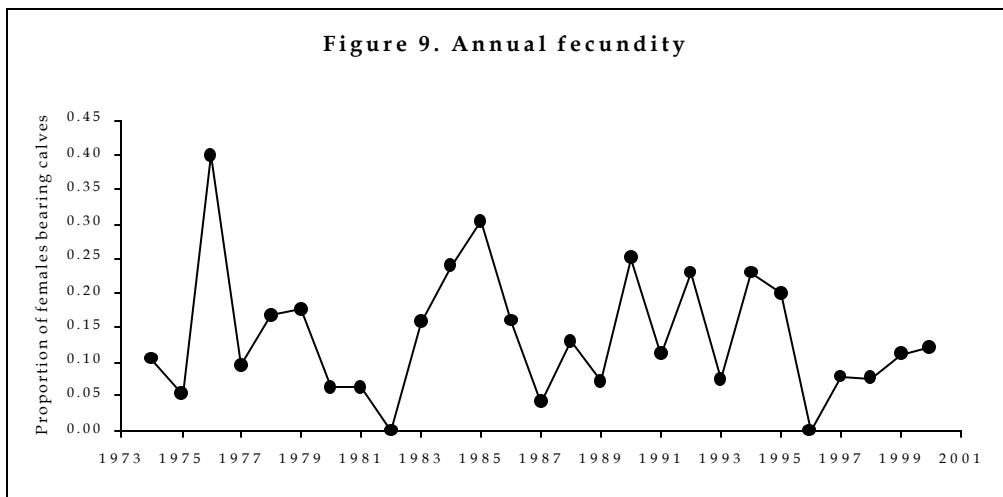
NOTE. Data for 2001 are not yet complete.

The possibility of density dependence was examined by calculating cross-correlations between fecundity and population size series. No significant cross-correlations were found. The cross-correlation between fecundity and the population size three years prior was marginally significant (P=.088), suggesting the possibility of lagged density dependence of fecundity. Probit regression of fecundity on year did not show any significant time-trend. Fecundity during the 1996-2001 period of population decline was lower than the average across previous years, but the difference was not significant in a Kruskal-Wallis test.

Other studies have suggested that fecundity is density dependent for killer whales (reviewed in Dahlheim and Heyning 1999). Brault and Caswell (1993) suggested that variance among pods in population growth rates is largely due to differences in pod-specific fecundity. No such differences were found in this study, however.

Minimum and maximum breeding ages

The earliest recorded female age at breeding was 12 years (Fig. 8). Although this female's age is known exactly, her calf died within the year.

The next recorded age for first breeding was 13. Three females gave birth at age 13. For two

of these female ages were known from observation. Olesiuk et al. (1990) cite 15 as the age at which females first gave birth to "viable calves." The available data do not support this observation. Calves of the three 13-year-old mothers all survived their first year. For the purposes of population modeling however, the median age of first reproduction is used, which was 16 for all recorded first- births of southern resident females.

Olesiuk et al. (1990) found that male sexual maturity, defined as time at which male dorsal fin was distinguishable from female ranged from 10 to 17.5 with mean of 15 for males. Male reproductive success is harder to observe than for females. Gestation averages 517 days or nearly one and a half years (Dahlheim and Heyning 1999). Minimum male age at first reproduction was assumed for purposes of calculating life history parameters to occur at age 11, following Olesiuk et al. (1990). However for purposes of population modeling, an average age at birth of first offspring of males of 16 is used, the same as the median for females.

Olesiuk et al. (1990) estimated that the age of last breeding averaged 40 years for females. The maximum age of a female giving birth was 41 in the available data (Fig. 9). However, the age of this female and indeed the ages of any females older than 27 were all estimated, not known exactly. Hence an estimate of 40 years for maximum breeding age is employed as the best available.

Female longevity is similar to that for modern humans. The two oldest living females are "Granny" (85) and "Lummi" (84). However, the birth years of these females and hence their ages are estimated, not known.

No maximum age for male sexual reproduction is recorded in the literature. However, males have higher mortalities and shorter lifespans than females. The maximum recorded age for males is 51, the present age of "Ruffles." However, no other male ages above 43 have yet been recorded, and as for females, the actual ages for males older than 27 are not known with certainty.

Age 40 was therefore set as the maximum breeding age for both males and females for purposes of population viability modeling.

Calf and juvenile mortality

The "calf" stage is defined from birth to one year of age. Killer whales face their highest mortality rates during this period, up to 50% according to Olesiuk et al. (1990). However great variability in mortality estimates is expected from the small numbers of calves born in any one year and the limitations of observation. Therefore calves and juveniles were considered as a single class for calculation of life history parameters.

Juveniles were defined as males from 1 to 10 years of age, and females 1-12 years of age. Annual mortality of combined juveniles and calves also showed extreme variability, but the variability showed no significant pattern or trend in time series analysis and no significant probit regression on time (Fig. 10). There were no significant cross-correlations between population size and calf and juvenile mortality.

Figure 10. Calf and juvenile annual mortality
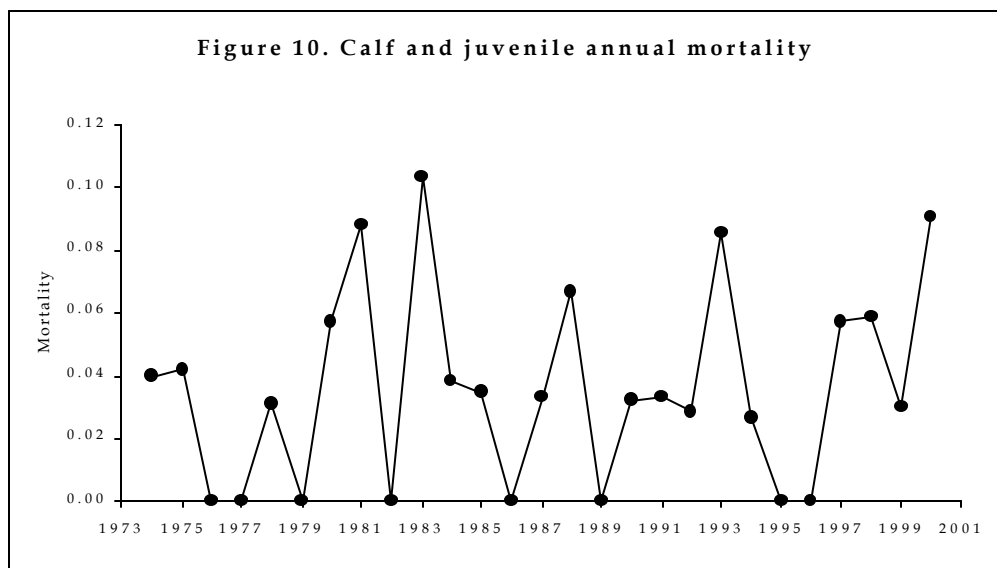
NOTE. Data for 2001 are not yet complete.

Adult mortality

Reproductive-age females were defined as females between the ages of 13 and 40. Reproductive female mortality was zero for every year except 1998 and 1999 (Fig. 11). Probit fitted regression on year was not significant, but sample sizes were small, resulting in a test of little power.

Post-reproductive females are defined as females age 41 and over. The data show an increase in mortality in recent years, with a dramatic peak in mortality in 1996 (Fig. 11). Probit regression of post-reproductive female mortality on year was statistically significant but is not shown here for clarity.

Figure 11. Adult female mortality

Figure 12. Total reproductive adult & adult male mortality
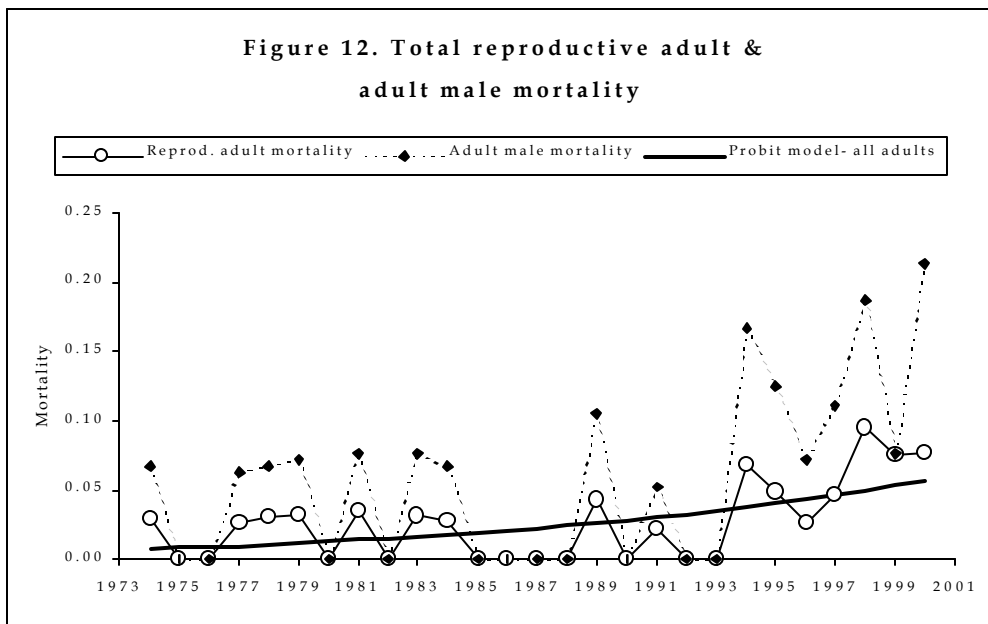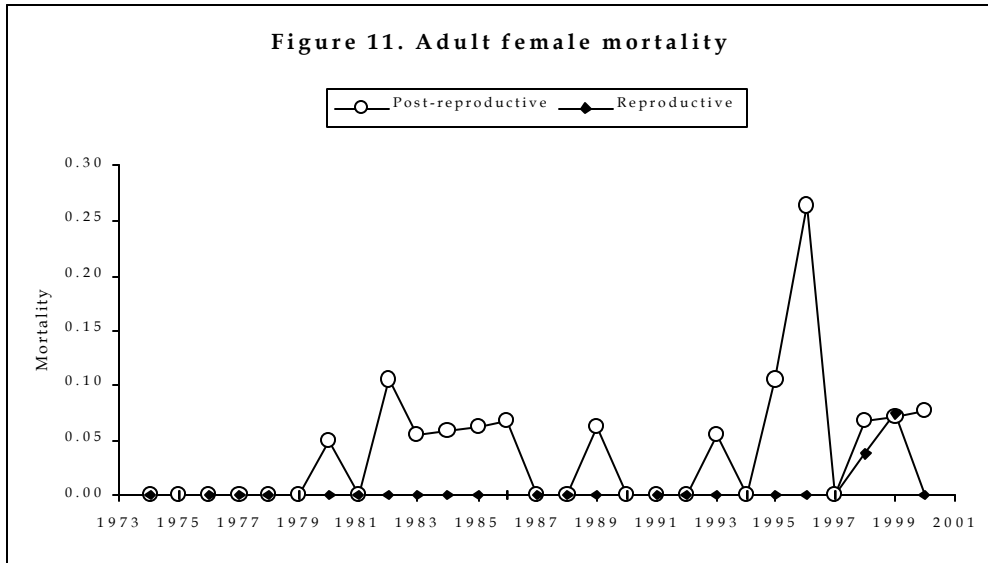
NOTE. Data for 2001 are not yet complete.

Adult male mortality is defined as mortality for males age 11 and over. Male mortality was highly variable as for other classes analyzed. There was a significant probit regression of adult male mortality on year. Combining reproductive female mortality in with male mortality the probit regression of mortality of all adults on year had a higher level of statistical significance[1] (Fig. 12).

There was no significant cross-correlation between fecundity and mortality of any age/sex class. However, post-reproductive female, adult male and reproductive adult mortality were significantly positively cross-correlated with population size in the previous 2-3 years in time series analysis.

This indicates that either mortality for adults is density dependent, with cyclic population upswings above carrying capacity driving upswings in mortality, or that cycles in exogenous environmental factors drive both mortality cycles and population cycles. Brault and Caswell (1993) have argued that intra-pod growth rates are controlled in a density dependent fashion. Without additional independent evidence, however, it is not possible to determine which of the above hypotheses fit the data.

The Vortex algorithm cannot model lagged density- dependence of mortality.

The years from 1996-present have seen significantly higher adult mortality (Fig. 12). This and the lower fecundity since 1996 (Fig. 9) are the proximate causes of the population decline since 1996. Whether this is a trend that will persist or is part of a longer term demographic or environmentally driven cycle is impossible to determine with present data.

However, the known deterioration in food supply and habitat conditions suggests that a trend to mortalities are more likely to stay at higher levels or increase yet further rather than return to earlier, lower levels.

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[1] Non-linear probit regression using maximum likelihood estimation for the model:-
 Mortality = ZCF(-2.436+0.033*Time) where ZCF is the cumulative normal distribution function and the first parameter has 95% CI of [-2.847, -2.025] and the second [0.010,0.056] based on rescaled asymptotic standard error estimates.

Population Viability Modeling

Population viability simulation fell into two classes of scenarios:

A) assume that the average mortality and fecundity over the known record will continue indefinitely into the future.

B) assume that the higher average mortality and lower fecundity observed from 1996-2000 will continue indefinitely into the future.

For both classes, stochastic population simulations using the Vortex algorithm v 8.41 (Lacey et al. 2000) were calculated for different sets of parameters (scenarios), based on the following general criteria and assumptions:

1. 200 iterations were run for a maximum time frame of 300 years.
2. Life table parameters were calculated as described in Methods (see Table 1). Parameters were assumed to vary randomly with the estimated environmental variance. Arithmetic means and standard deviations of annual mortalities and fecundities across years were used as basic parameters in the model. Binomial demographic variance was subtracted from sample variance of mortality or fecundity to estimate the environmental component of variance of the parameters. Binomial demographic variance is the variance attributed solely to sampling rather than environmental causes, and was calculated as the average across years of binomial variance $p*(1-p)/(N-1)$ where p is proportion of class dying and N the number in the class. Modeling of trend or cyclic patterns in life table parameters was not possible in Vortex.
3. No age structure was defined. Simulations began at the calculated stable age structure.
4. Mating was assumed freely polygamous in a single, panmictic population, ignoring social structure, without immigration or emigration. The likely effects of male limitation at low population sizes were accounted for by incorporating an Allee effect, which provided for a sharply declining fecundity for population sizes below about 10 (Fig. 13).
5. Average age of first breeding for both females and males was 16. All adult males were assumed to be in the breeding pool.
6. Maximum breeding age was 40 for both sexes.
7. Twinning was assumed not to occur. Hence fecundity is equivalent to the percentage of reproductive females breeding in any year.
8. Sex ratio at birth was generally set to the observed sex ratio at birth in the data of 57% males (N=65, including only those births that were recorded with certainty).
9. Carrying capacity was set arbitrarily at 100, just above the maximum population size in the record but was reduced in some simulations to 50 to account for depletion of the salmon food supply (Fig. 5).
10. No concordance between environmental variance in mortality and variance in fecundity. Cross-correlations between fecundity and mortality time series were found to be not statistically significant.
11. Models incorporated two levels of inbreeding based on data in Ralls et al. (1988). The number of lethal equivalents per individual for humans and chimpanzees of 2.0 was taken as a conservative minimum. Killer whale longevity and social structure as some similarities to higher primates. However, cetaceans are closer phylogenetically to artiodactyls. The means of lethal equivalents calculated for eight species of captive wild-caught artiodactyls from Table 2 of Ralls et al. (1988) was found to be 2.975. Thus a high limit of 3.0 lethal

equivalents was also used in Vortex simulations, with 50% of genetic load being due to lethal alleles.

Figure 13. Density dependence of fecundity
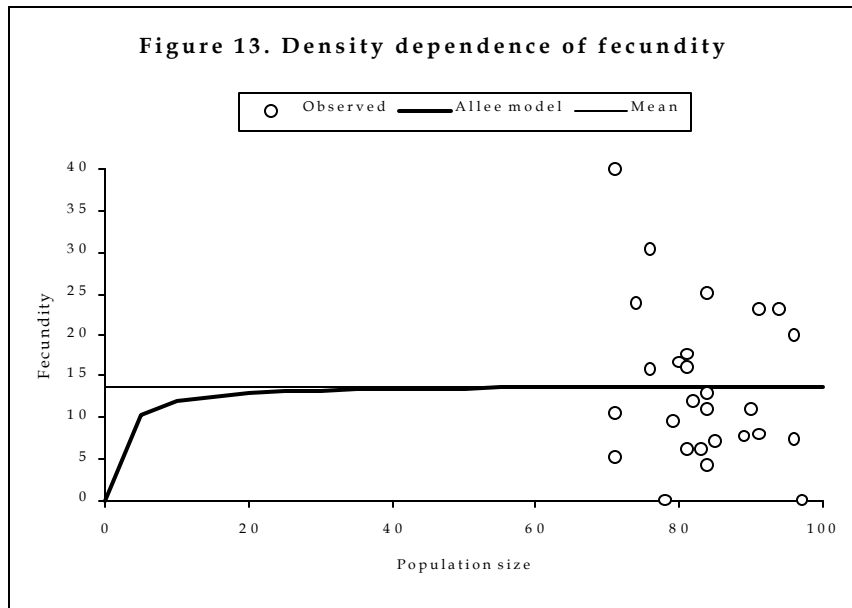
Table 1. Annual mortality and fecundity of Southern Residents.
Means across years and estimates of environmental standard deviation (ESD).

Period		Calf & juvenile annual mortality (%)	Reproductive female annual mortality (%)	Adult male annual mortality (%)	Fecundity (%)
1974-pres.	Mean	3.6	0.4	5.9	13.7
	ESD	0.0	1.0	1.7	6.1
1996-pres.	Mean	4.7	2.3	13.2	7.8
	ESD	0.0	1.7	0	0

Table 2: Results of simulations.

MODEL PARAMETERS	A1 1974-2000 data	A2 50:50 SR	A3 no in-breed. depr.	A4 high in-breed. depr.	A5 oil spill	A6 epi-zootic	A7 Allee effect	A8 reduced food supply	A9 comb-ined models 4-8	A10 comb-ined models 2,3, 5-8
Lethal equivalents per zygote	2	*	0	3	*	*	*	*	3	0
Sex ratio at birth (% males)	57	50	*	*	*	*	*	*	*	50
Fecundity as % reprod. age females giving birth (ESD)	13.7 (6.1)	*	*	*	a	b	c	*	a,b,c	a,b,c
Calf and Juvenile Mortality % (ESD)	3.6 (0.0)	*	*	*	a	b	*	*	a,b	a,b
Reproductive female mortality % (ESD)	0.4 (1.0)	*	*	*	a	b	*	*	a,b	a,b
Adult Male Mortality %, (ESD)	5.9 (1.7)	*	*	*	a	b	*	*	a,b	a,b
Carrying capacity	100	*	*	*	*	*	*	-> 50[d]	-> 50[d]	-> 50[d]
Starting population size	71	*	*	*	*	*	*	*	*	*

MODEL RESULTS	A1	A2	A3	A4	A5	A6	A7	A8	A9	A10
Finite rate of increase λ	0.995	1.000	0.995	0.995	0.993	0.985	0.997	0.995	0.984	0.989
% extinct at 100 yr	0	0	0.5	0	1	29.5	0	1.5	54.5	38
% extinct at 200 yr	19.5	3.0	17	27.5	44	88	29	62	99	95.5
% extinct at 300 yr	69.0	18.5	45.5	78.0	87.5	100	77	95.5	100	99.5
Median years to extinction	262	>300	>300	250	208	129	247	185	97	113

Table 2: (Continued)

MODEL PARAMETERS	B1 1996-2000 data	B2 1996-2000 data, mod. 2&3	B3 mod.1 fecund.	B4 mod.1 juv. mort.	B5 mod.1 fem. mort.	B6 mod.1 male mort.	B7 mods. 5-8	B8 mod A10 w inbr. & incr. adult. mort
Lethal equivalents per zygote	*	0	*	*	*	*	3	*
Sex ratio at birth (% males)	*	50	*	*	*	*	*	50
Fecundity as % reprod. age females giving birth (ESD)	7.8 (0.0)	7.8 (0.0)	*	7.8 (0.0)	7.8 (0.0)	7.8 (0.0)	a,b,e	* a,b,c
Calf and Juvenile Mortality % (ESD)	4.7 (0.0)	4.7 (0.0)	4.7 (0.0)	*	4.7 (0.0)	4.7 (0.0)	4.7 (0.0) [a,b]	* a,b
Reproductive female mortality % (ESD)	2.3 (1.7)	2.3 (1.7)	2.3 (1.7)	2.3 (1.7)	*	2.3 (1.7)	2.3 (1.7) [a,b]	2.3 (1.7) a,b
Adult Male Mortality %, (ESD)	13.2 (0.0)	13.2 (0.0)	13.2 (0.0)	13.2 (0.0)	13.2 (0.0)	*	13.2 (0.0) [a,b]	13.2 (0.0) [a,b]
Carrying capacity	*	*	*	*	*	*	-> 50 [d]	->50 [d]
Starting population size	97	97	97	97	97	97	97	97
MODEL RESULTS								
Finite rate of increase λ	0.960	0.965	0.979	0.965	0.970	0.960	0.950	0.979
% extinct at 100 yr	97.5	90	33	88.5	84.5	87	100 [f]	83
% extinct at 200 yr	100	100	100	100	100	100	100	100
% extinct at 300 yr	100	100	100	100	100	100	100	100
Median years to extinction	70	77	112	78	83	80	54	74

* same as model A1.

a - oil spill catastrophes at 2% probability of occurrence in any one year (one per fifty years), that eliminates all reproduction for a year, and kills 11% of all individuals regardless of age or sex.

b - epizootic catastrophes at 2% probability of occurrence in any one year (one per fifty years), that does not impact reproduction but kills 50% of all individuals regardless of age or sex.

c - fecundity = $[14.5 - (14.5-14)*(N/100)^{0.5}]*N/(N+2)$ see Fig. 13

d - Carrying capacity 100 with ESD of 10, and declines to 50 over 50 years .

e - fecundity = $[8.5 - (8.5-8)*(N/100)^{0.5}]*N/(N+2)$

f - 40% chance of extinction within 50 years.

Models A: Long term average mortality, fecundity continues indefinitely.

Model A1. Basic model. This model used all life table data for 1974-2000 incorporating inbreeding depression at the 2.0 average lethal equivalents reported for higher primates. Simulations of this model predicted relatively high likelihood of population persistence, but nevertheless with a greater than 50:50 chance of extinction within 300 years and a median time to extinction of 262 years. The model is unrealistic in that it assumes no future change in life history parameters, no mate limitation, no catastrophes and no net change in the environment.

Models A2-3. The Vortex algorithm was sensitive to inbreeding and primary sex ratio. Setting primary sex ratio to the theoretical 50% rather than the observed 57% greatly reduced extinction risk. Likewise elimination of any inbreeding depression significantly reduced extinction risk. The effect of reducing proportion of males to the theoretical value is to increase births of females. For polygynous mating systems, males are always in excess in terms of population growth and so any increase in females is bound to increase population growth and stability. Because the observed value was not statistically different from the theoretical value, model 2 represents a more plausible scenario than model 1.

Model A4. Inbreeding depression is highly likely both as a result of small population size and low genetic diversity of Southern Residents (Hoelzel et al. 1998, Barrett-Lennard 2000). Genetic diversity in Southern residents is very low, suggesting that effective population size is low and that populations have undergone sustained bottlenecks (Barrett-Lennard 2000). Unfortunately, no quantitative estimate of inbreeding depression is available for Southern residents. The best available estimate may be the mean lethal equivalents observed for wild artiodactyls of 3.0 per individual. This is higher than that observed for higher primates but lower than the median for all mammals of 3.14 (Ralls et al. 1988). Predicted extinction risk increased but was still a moderate 78% within 300 years, after inclusion of inbreeding depression at 3 lethal equivalents per individual.

Model A5. The Exxon Valdez oil spill in Alaska resulted in the death of about one third of all members of one Northern Resident killer whale pod (Matkin and Saulitis 1997). To model the effect of such a catastrophe on Southern Residents, a one-year failure of all births and death of 11% (A third of one of the three pods) of all Southern Residents evenly across all age classes, was incorporated with a chance of one event per fifty years. A one in fifty year event like the Exxon-Valdez spill is conservative for the Southern Residents' habitat. There have been a total of 17 oil spills offshore in Alaska and Washington states in just the past 30 years. Tanker traffic is expected to increase through Puget Sound with the opening of new loading facilities at Cherry Point (Center for Biological Diversity 2001). Simulation of such oil spill catastrophes increased the predicted extinction risk substantially to 87.5% within 300 years, with a median extinction time of 208 years.

Model A6. No epizootic has yet been observed among killer whales or Pacific ocean marine mammals that is equivalent to the spate of Atlantic and Mediterranean mass mortalities of dolphins, whales and pinnipeds during the last two decades (Simmonds and Mayer 1997). In some of these events, morbillivirus outbreaks were the cause, killing up to 60% of local populations. Organochlorine contamination causes immune suppression, and thus may potentiate such outbreaks.
To model the effect of such a catastrophe on Southern Residents, simulations were run

including death of 50% of the population evenly across all age classes, with a probability of 2% per year (one event per one fifty years). A one in fifty year event may also be conservative for the Southern Residents' habitat, considering their high body loads of PCBs and the alarming increase in such epizootics during the last two decades for other marine mammals. In recent years, at least one Northern resident killer whale is known to have died from a virulent, antibiotic-resistant bacterial infection that probably originated in farmed Atlantic salmon, and spread into the wild Pacific salmon population.[2] Now that a moratorium on new fish farms has been lifted, it seems likely that this source of disease risk will increase, along with the risk to wild salmon food stocks from diseases carried by farmed fish. Other cetacean deaths from infections have been recorded in the Pacific and Gulf of Mexico in recent years, although not on a mass scale.

Incorporation of risk of epizootics increased predicted extinction risk dramatically to 30% within the next century, with a median time to extinction reduced to 129 years relative to the baseline model.

Model A7. Vortex does not allow explicit modeling of the pod-based social structure of the Southern Residents. If most pods are exogamous, then as total population gets smaller, smaller pods such as J and K are likely to have no males, reducing the chance of females in the larger L pod to find a mate. No evidence of such mate limitation was found at present populations sizes. However, binomial probabilities of there being no males in one or more pods become significantly different from zero below population sizes of 20. Fecundity may be reduced for small populations due to stochastic mate scarcity for females, an Allee effect. Vortex models the Allee effect with fecundity a declining function of population size as shown in Fig. 13. Model parameters were selected to best fit the mean observed fecundity, and to result in appreciably lower fecundities only at population sizes below 10. Introduction of an Allee effect did not however, increase predicted extinction risk substantially.

Model 8. Reduced Food Supply.
Research as cited above suggests that drastic declines in salmon food stocks can be expected due to a combination of human caused factors, in particular global warming. A reduction of carrying capacity to 50 over the next 50 years along with introduction of environmental variance with coefficient of 10-20% was simulated to assess the impact of declining salmon stocks on extinction risk. Predicted extinction risk in the 200 and 300 year time frame increased dramatically, and median time to extinction of simulations was reduced to 185 years.

Model 9,10. Combining impacts. Combining the multiple impacts of higher inbreeding, oil spills, epizootics, Allee effect and reduced food supply resulted in greatly increased risk of extinction to 54.5% in the next century with a median extinction time of 97. Allowing for no inbreeding depression and a 50:50 primary sex ratio did not greatly alter this prediction.

Models B1-7: Lower survival, fecundity since 1996 continues indefinitely.
The assumption in models A1-10 that 1974-2000 average levels of mortality and fecundity will continue indefinitely is conservative. At least adult mortality has shown a statistically increasing

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[2] Whale and Dolphin Conservation Society news bulletin
http://www.wdcs.org/dan/publishing.nsf/allweb/562E705E90AE79C5802568F50040C5E5

trend through the period of observation (Fig. 12). The recent declines in survival are statistically significant and are likely to reflect a trend in deterioration in environmental conditions that may continue or at least not improve in the foreseeable future without active intervention.

Only demographic data for the recent years of increased adult mortality and lower fecundity 1996-2000 were used for these simulations. Mortality estimates were all higher and fecundity estimates lower than those calculated on the entire data set (Table 1).

Predicted extinction risk was drastically greater than for A class simulations, at 97.5% within 100 years and a median time to extinction of only 70 years. Note that the assumption is that adult mortality will not increase any more than it has. If adult mortality were to continue increasing extinction risk would be even higher.

Relaxing the assumption of inbreeding depression and using the theoretical rather than observed primary sex ratio did not greatly alter this prediction (Model B2). To determine which of the life history parameters had greatest impact on extinction risk, each in turn were reset to their 1974-2000 averages (models B3-B6). Reduced mortalities whether of juveniles, females or males did not greatly alter the predicted extinction risk indicating that the model was relatively insensitive to these parameters taken alone. However, restoring fecundity to the long term average, significantly reduced extinction risk to only 33% in the next 100 years (model 13), indicating that the model was more sensitive to the recent decline in fecundity than to the concurrent increases in mortalities. This indicates that the recent reduction in average fecundity is a critical area of needed research. Is the decline temporary or is it likely to continue?

Finally, higher inbreeding depression, oil spills, epizootics, Allee effects and reduced food supply were incorporated into simulations along with the higher mortality and lower fecundities of recent years to produce a "worst case" scenario in which extinction risk is 40% within the next 50 years and 100% with the next century (Model B7).
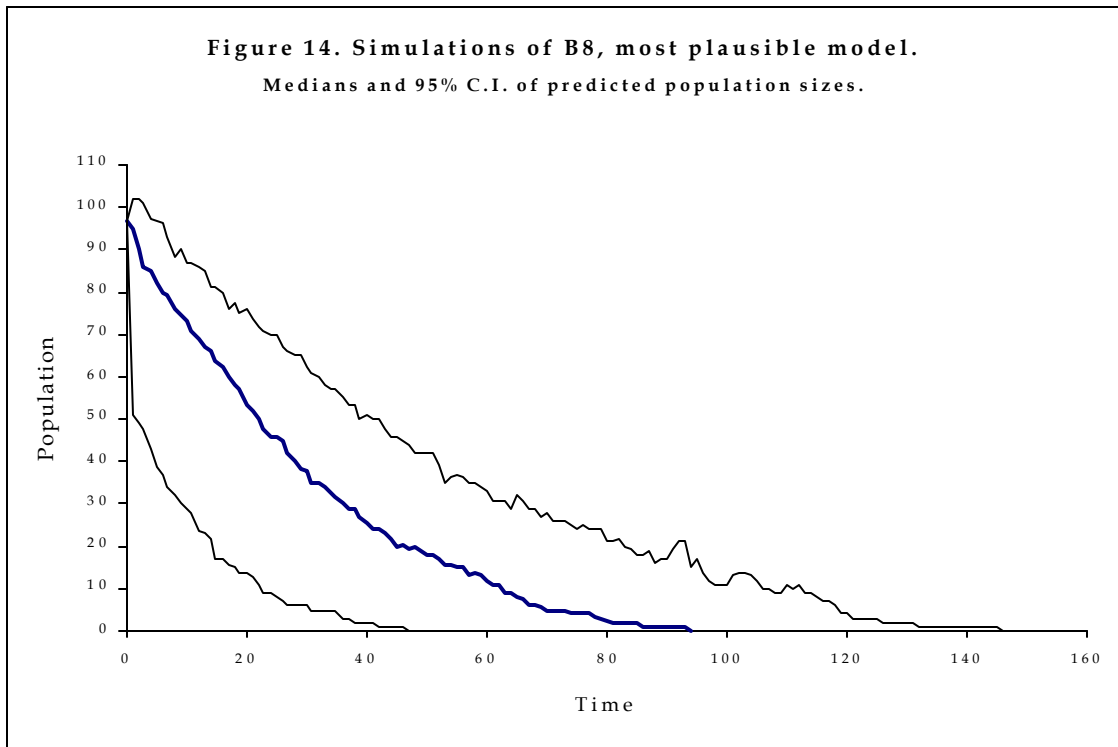
Model B8. Most plausible scenario.

The analysis of life history data indicates that a) primary sex ratio was not significantly different from 50% and b) only adult mortality showed an increasing trend over time, while juvenile mortality and fecundity did not. Therefore a more plausible version of the B class models has inbreeding at the lower level of 2 lethal equivalents, 50% primary sex ratio, fecundity and juvenile mortality maintained at the long term 1974-2000 averages, but adult mortalities continuing at elevated 1996-2000 levels, declining carrying capacity, Allee effect, oils spill and epizootic risks as in previous models. For this scenario, predicted extinction risk was still high within 100 years, with median time to extinction of only 74 years with a 95% confidence interval of 33 - 121 years. The population trajectories of the simulations showed wide variability (Fig. 14). Note that time at which median predicted population size reaches zero is not the same as median time to extinction. Extinction is defined as extinction of one sex, and so is expected to occur earlier than death of all individuals.

Effects of earlier maturity, monogamy.

Other model iterations not presented here showed that earlier male maturity, or later maximum breeding age (45) did not significantly affect model A1 predictions. Earlier female maturity did however significantly reduce extinction risk. However, median age of first breeding is well known

for females and there is no compelling reason to simulate an earlier age.

Model predictions were little affected by mating system. Monogamy only slightly increased predicted extinction risk over that found for polygamy.

Figure 14. Simulations of B8, most plausible model.
Medians and 95% C.I. of predicted population sizes.

Limitations of the Vortex model

The Vortex model adds more sophistication to extinction prediction than provided by the more elementary approach of calculating the intrinsic rate of increase or λ from life table data. However, use of these additional modeling features is only as good as the data available to estimate model parameters.

Many model parameters that have a substantial impact on predictions are not well known or are known for too short a period to permit strong confidence in conclusions. The basic model was sensitive to primary sex ratio, however models incorporating all impacts (model A9) and the more recent life table data alone (model A1) were not as sensitive to primary sex ratio or inbreeding.

All the foregoing Vortex models assume random mating, uniform age-specific fecundity or reproductive capacity and no time trends or cycles in mortality or fecundity. Real life violations of these assumptions are all likely to increase the risk of extinction beyond those predicted here.

In particular there is no provision in Vortex for delayed density dependence or other cyclic dynamics that typically result from multi-species interactions. Incorporation of cyclic dynamics to population models is also likely to increase stochastic extinction risk for small populations beyond those obtained by Vortex. Other limitations are detailed by Lacey et al. (2000).

CONCLUSIONS

The foregoing models suggest that the Southern Resident population is very likely to go extinct in the foreseeable future unless action is taken to arrest declining habitat quality. All combinations of life history parameters derived from various subsets of the available data generated estimates of intrinsic rates of increase (λ) below 1, except for the most optimistic of the models (model 2), indicating that the population is expected to decline in the long term, if present conditions persist or worsen.

None of the foregoing models incorporate density dependence or the cyclic or chaotic dynamics that are expected from delayed density dependence or interactions with prey populations. Cyclic or chaotic dynamics are suggested by the actual population record (Fig. 2) but could not be simulated by Vortex. It is likely, therefore that extinction risk has been underestimated, as cyclic dynamics for small populations are more likely to result in stochastic extinctions. Neither do the models explicitly incorporate the pod based social and mating structure of this stock, except via a presumed Allee effect.

Incorporation of anticipated ecological impacts such as oil spills, epizootics, and reduced salmon food stocks greatly increased predicted extinction risk to as high as 54.5% in the next 100 years, even given the optimistic assumption that the long-term average fecundity and mortality would otherwise continue indefinitely.

Of great concern is the recent rise in reproductive female mortality as part of a significantly rising trend in adult mortality generally (Fig. 12) and the recent concurrent reduction in fecundity, which has the greatest impact on extinction risk (model B3). If the reduced fecundity and adult survival seen in the census years after 1996 continues indefinitely rather than returning to the low levels seen over the previous 25 years, the risk of extinction of the Southern Resident population is almost certain within the next 100 years, and extinction within 70 to 100 years is likely. If adult mortality continues to rise as it has across the 1974-2000 record, extinction risk is even higher.

Although some caution is needed in projecting the possibly temporary circumstance of recent reduced fecundity and survival into the future, the known and anticipated downwards trends in habitat quality due to global warming, salmon depletion, development, pollution and boat traffic suggest that the lower survival and fecundity of recent years is not merely temporary or cyclic but part of downward trend caused by habitat degradation. For this reason class B models may be considered the most likely scenarios. Within class B models, the most plausible scenario (B8) predicted a median extinction time of 74 years with 33-121 years 95% confidence interval.

Protection for this population is urgently needed to achieve recovery to historical levels with an adequate margin of safety that will allow the population to survive likely future catastrophes and perturbations. Effort should therefore be directed at identifying the causes of the recent increases in adult mortality and declining fecundity and at finding ways of halting or mitigating any human impacts that might be implicated. If the higher risks of death and impaired reproduction created by oil spills, salmon reduction, pollution and disease are reversed, then there is a low likelihood of extinction in the foreseeable future. If these risks are not substantially removed, extinction is certain.

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APPENDIX: Life histories of all known southern resident killer whales.

Males and sex unknown

No.	Name	Sex	BORN	DIED
J01	Ruffles	M	1949 *	
J03	Merlin	M	1952 *	1994
J06	Ralph	M	1957 *	1998
J15	N/A	M	1975	1981
J18	Everett	M	1977	1999
J21	E.T.	Unk.	1981	1983
J23	N/A	M	1986	1991
J24	N/A	Unk.	1971	1971
J25	N/A	Unk.	1987	1988
J26	Mike	M	1991	
J27	Blackberry	M	1991	
J29	N/A	M	1992	1992
J30	Riptide	M	1994	
J33	Keet	M	1995	
J34	DoubleStuf	M	1997	
J36	N/A	Unk.	1999	
J37	N/A	M	2000	
K01	Taku	M	1954 *	1997
K02	N/A	M	1949 *	1974
K05	Sealth	M	1952 *	1991
K15	N/A	Unk.	1970 *	1975
K17	Pacheena	M	1965 *	1994
K19	Neptune	M	1952 *	1984
K20	Spock	M	1985	
K21	Cappuccino	M	1985	
K23	N/A	Unk.	1988	1988
K24	N/A	Unk.	1990	1990
K25	Scoter	M	1990	
K26	Lobo	Unk.	1992	
K29	Sigurd	M	1995	1998
K31	Tatoosh	M	1998	
K32	N/A	Unk.	2000	2001
K33	N/A	Unk.	2001	
K46	N/A	Unk.	1973	1981
L01	Oskar	M	1958 *	2001
L06	Podner	M	1961 *	1983
L08	Moclips	M	1957 *	1977
L10	Okum	M	1958 *	1997
L13	Orpheus	M	1949 *	1979
L14	Cordy	M	1971	1989
L16	N/A	M	1948 *	1978
L20	Trident	M	1954 *	1981
L33	Chinook	M	1962 *	1995
L36	N/A	Unk.	1974	1974
L38	Dylan	M	1964 *	1998
L39	Orcan	M	1974	2001
L41	Mega	M	1976	
L42	Mozart	M	1972 *	1994
L44	Leo	M	1973	1998
L48	Flash(1)	Unk.	1976	1983
L49	N/A	Unk.	1978	1980
L50	Shala	M	1972	1989
L52	Salish	Unk.	1979	1983
L56	Disney	Unk.	1977	1981

Females

No.	Name	BORN	DIED	Offspring				
J02	Granny	1915 *		J12?				
J04	Mama	1951 *	1995	J11	J15	J19	J21	
J05	Saratoga	1937 *	1996	J13?	J17			
J07	Sucia	1938 *	1983	J03?	J16			
J08	Spieden	1932 *		J04				
J09	Neah	1922 *	1985	J05?	J10?			
J10	Tahoma	1961 *	1999	J18	J20	J22		
J11	Blossom	1971 *		J25	J27	J31		
J12	Sissy	1934 *	1996	J24	J14			
J13	N/A	1970 *	1980					
J14	Samish	1973		J23	J30	J37		
J16	Slick	1970 *		J26	J33	J36		
J17	Princess Angeline	1976		J28	J35			
J19	Shachi	1978		J29				
J20	Ewok	1980	1998	J32				
J22	Oreo	1984		J34				
J28	Polaris	1992						
J31	Tsuchi	1994						
J32	Rhapsody	1995						
J35	Tahlequah	1997						
K03	Sounder	1956 *	1998	K15?	K14	K16	K29	
K04	N/A	1931 *	1999	K12?				
K07	Lummi	1916 *		K11?	K02?	K01?		
K08	Tumwater	1929 *	1989	K05?	K03?			
K11	Georgia	1932 *		K13				
K12	Sequim	1970		K22	K28	K31		
K13	Skagit	1971		K20	K25	K27		
K14	Lea	1976		K23	K24	K26		
K16	Opus	1984		K32				
K18	Kiska	1947 *		K40?	K17?	K46	K21	
K22	Sekiu	1986		K33				
K27	Deadhead	1993						
K28	Raven	1993						
K30	N/A	1928 *	1982	K19?				
K40	Raggedy	1962 *						
L02	Grace	1953 *		L39	L67	L78	L88	
L03	Oriana	1946 *		L33?	L51	L59	L74	
L04	Sonar	1950 *	1996	L27?	L61?	L55	L86	
L05	Tanya	1963 *		L58	L73			
L07	Canuck	1960 *		L53	L76			
L09	Hopi	1930 *	1996	L03?	L05?			
L11	Squirty	1955 *	2001	L42?	L41	L64	L77	L94
L12	Alexis	1930 *		L11?	L10?			
L15	Gracie	1929 *	1980	L13?	L20?			
L21	Ankh	1937 *		L47	L48			
L22	Spirit	1970 *		L75	L79	L89		
L23	N/A	1939 *	1982	L14?	L49?			
L25	Ocean Sun	1924 *		L23?				
L26	Baba	1955 *		L60	L52	L71	L90	
L27	Ophelia	1964 *		L62	L68	L80	L93	
L28	Misky	1950 *	1993	L38?	L69	L85		
L32	Olympia	1954 *		L22?	L44	L56	L63	L87
L35	Victoria	1942 *	1996	L01?	L50?	L54	L65	
L37	Kimo	1932 *	1984	L07?	L43?			

ID	Name	Sex	Birth	Death
L57	Faith	M	1976	
L58	Sparky	M	1979	
L59	Fred	Unk.	1978	1978
L61	Astral	M	1972 *	1996
L62	Cetus	M	1979	2001
L63	Scotia	M	1983	1995
L64	Radar	Unk.	1984	1985
L68	Elwa	M	1984	1994
L69	Sumner	Unk.	1983	1984
L71	Hugo	M	1985	
L73	Flash	M	1985	
L74	Saanich	M	1985	
L76	Mowgli	Unk.	1986	1987
L78	Gaia	M	1988	
L79	Skana	M	1988	
L80	Odessa	Unk.	1989	1993
L81	Raina	M	1989	1997
L84	Nyssa	M	1990	
L85	Mystery	M	1990	
L87	Onyx	M	1991	
L88	Wavewalker	M	1992	
L89	Solstice	M	1992	
L91	Muncher	Unk.	1994	
L92	Crewser	M	1994	
L94	Calypso	Unk.	1994	
L95	Nigel	M	1995	
L96	Bernardo	M	1995	1997
L97	Tweak	Unk.	1998	1999
L98	Luna	Unk.	1999	2001
L99	N/A	Unk.	1999	2001

ID	Name	Birth	Death	Offspring		
L43	Jelly Roll	1972 *		L72	L95	
L45	Asterix	1937 *	1995	L36	L57	
L47	Marina	1973		L83	L91	L99
L51	otka	1972 *	1999	L84	L97	
L53	Lulu	1976				
L54		1976				
L55	Nugget	1976		L82	L96	
L60	Rascal	1970*		L81	L92	
L65	Aquarius	1983	1993			
L66	Mata Hari	1923*	1986	L45?	L08?	
L67	Splash	1984		L98		
L72	Racer	1985				
L75	Panda	1985	1993			
L77	Matia	1986				
L82	Kasatka	1990				
L83	Moonlight	1990				
L86	Surprise	1990				
L90	Ballena	1992				
L93	Nerka	1994	1998			

NOTES

* birth year was estimated

Individual ID numbers start with pod of whale (J, K or L).