Final Report:

Project: Evaluation of factors influencing the population dynamics of the southern resident population of killer whales (*Orcinus orca* [L.])

Submitted to the Orca Relief Citizens' Alliance

August 2001

Carlos M. Alvarez-Flores

Glenn R. VanBlaricom

Washington Cooperative Fish and Wildlife Research Unit

School of Aquatic and Fishery Sciences

University of Washington, Seattle

INTRODUCTION

Five stocks of orcas are recognized in the Eastern North Pacific (Forney *et al.* 1999). One of them, the southern resident community (SRC) is distinguished from other stocks or communities by its particular foraging behavior specialized towards fish consumption, by its localized summer distribution, by a distinct vocal repertoire and by strong maternal association patterns that have led to a small but fixed mtDNA haplotype difference compared to the adjacent northern resident community (Hoelzel *et al.* 1998).

The National Marine Fisheries Service has classified this population as non-strategic in its most recent assessment of U.S. Pacific marine mammal stocks. However, recent information on the abundance of the SRC shows a declining trend starting in 1997 (Bain and Balcomb 1999). Although there was a similar decline in the early 1980s, it has been proposed that the earlier decline could be explained by changes in the age structure as consequence of removals in the 1959-70 period, or by impacts of the major El Niño event of 1982-1983. It was also suggested that such changes in the age structure could account in part for the current reduction in the abundance and that other factors could be mentioned. Such factors include a change in prey availability, reduced survivorship due to toxic chemicals and disturbance caused by boat traffic (Bain and Balcomb 1999).

To address the concerns raised by these observations, a workshop was held in April 2000 at the National Marine Mammal Laboratory, Seattle, and the merits of the different explanatory hypotheses were discussed. In terms of the population's demographic characteristics, it was shown that the population has previously gone through at least one other period of decline (Fig. 1) (Dahlheim *et al.* 2000).

A comparative investigation on contaminant levels of the SRC, the northern residents and the transient population, all stocks using the waters off British Columbia, found that toxic levels in the SRC are very high relative to other marine mammal populations and concluded that it may represent a health risk for the animals (Ross *et al*. 2000). The results also indicate that contaminant levels are "highly reduced" in reproductively active females, presumably because accumulated burdens of lipophilic contaminants are partly transferred to calves during lactation.

With regard to effects of whale watching boats, participants in the workshop concluded that although immediate behavioral responses have been observed (Williams 1999) preliminary results indicate no detectable effect on the survivorship and few detectable effects on the behavior of the animals. Concerns were also raised about the potential disruption of social cohesiveness, but no conclusive evidence on this problem was available at the time of the workshop (Dahlheim *et al*. 2000).

The problem of prey availability was discussed in the workshop without a printed document to summarize the current knowledge on prey distribution, movements and abundance. It was pointed out that there is some information indicating that the SRC preys preferably on Chinook salmon and that pink salmon and sockeye salmon are not as important prey items. This idea needs verification since there may be sampling biases. Also, it was mentioned during the workshop that data on salmon abundance are available, but no analyses have established a cause-effect relationship with orca abundance (Dahlheim *et al*. 2000).

Following from the discussions that took place at the April Workshop, we proposed an investigation on the effect of different factors that might affect orca abundance. Our research evaluated direct quantitative relationships of factors that were suspected to be responsible for changes in orca abundance.

In the following we include the results of evaluations and a discussion about different hypotheses, as well as an evaluation of population stochastic behavior based on the development of an individual based population model. It should be emphasized that, although suggestive, neither the available data and information nor the results of our analysis clearly point to a single factor or a simple model for explanation of decline in the abundance of the SRC. While we may have narrowed the range of possibilities, our analyses leave us with a range of alternative explanations, complicated by the likelihood of higher-order interactions among factors.

METHODS

Data were collected from a variety of sources. Some of the data was obtained from the scientific literature, but printed informal reports, theses and dissertations were also used. Other data were obtained directly from database maintained by the local research community.

Killer whale data

Killer whales are individually identified using the shape of their dorsal fins, the scars on them and by means of the unique pigmentation pattern that is found in the back of the animals immediately behind the dorsal fin (Balcomb *et al*. 1982). The SRC of orcas in the Pacific North West has been studied since 1973 and the individuals in the population have been photographically identified and followed every year since (Balcomb *et al*. 1982; Bigg 1982; Bigg *et al*. 1990; Olesiuk *et al*. 1990). Data about the southern resident community of orcas has been collected by a number of local researchers but has been compiled by D. Bain who kindly made it available to us.

The data provided include the initial year of sighting, the estimated or observed age of the animal and if dead, the year when it was presumed dead. These data were then organized as a capture history where 1 represents an animal observed alive and 0 represents an animal that was not been born or that is already dead. This allows counting the number of animals alive each year at each particular age and sex class.

Because the population is small, age data were pooled mostly according to basic factors the orca biology, including age at sexual reproduction, senescence and longevity and the possibility to differentiate the individual's gender. In this way, the calf age class included animals that were born at one particular year and are considered of age zero. Juveniles included animals between 1 and 9 years of age. The upper boundary for the juvenile class was determined because at that age most individuals can be assigned to a sex class. Mature fertile females were included in the age/sex class if they were between 10 and 40 years. For simplicity, we refer to this group simply as "females". Females 41 and older that are considered reproductively inactive were included in a separate age/sex class and we refer to this group as "old females". Female longevity was set at 84 years.

Males from 10 to 21 were included in the group that we denominated simply as "males" and those 22 and older were placed in the "old male" category. Longevity for males was set to 49 years.

Covariate data

Three covariates were considered for formal analysis to identify potential causes for the observed population behavior: sea surface temperature (SST), Chinook salmon abundance and whale watching boat density.

These covariates were the focus of analyses because of the reasonable possibility that they might contribute to variation in orca numbers, and because data for each exist as a time series similar in duration to the SRC population record. Covariate analyses cannot be done with variates that do not exist in the form of time series data. For example, there is concern that burdens of persistent lipophilic pollutants, or recent scientific sampling of tissues with biopsy darting, may be contributing to recent observed declines in SRC. Although we discuss these factors below, we are unable to incorporate them in covariate analyses because of the absence of a useful time series of data.

Data on SST were used in the form of the Pacific Decadal Oscillation (PDO) index (database kept by N. Mantua at the Joint Institute for the Study of the Atmosphere and Oceans, University of Washington, and available via ftp in ftp://ftp.atmos.washington.edu/mantua/pnw_impacts/INDICES/PDO.latest). This index is obtained as the main principal component of monthly SST anomalies in the North Pacific north of 20° of latitude N. The PDO shows a cyclic behavior similar to the El Niño Southern Oscillation and has shown correlation with major environmental patterns within this ocean basin (Francis *et al*. 1998). The extent of the correlations include a variety of taxa from plankton to marine mammals and includes different fish species such as salmon. The time series extends from the beginning of the century to the present and therefore includes the period of interest for the analysis in the present work.

A recent review of the dietary specialization of orcas in the waters around British Columbia, included both field observations and examination of stranded animals over a period of 20 years (Ford *et al*. 1998). The main results of that work indicate that the preferred prey species of resident killer whales is the Chinook salmon (*Oncorhynchus tshawytscha*). Unlike transient orcas, the residents have been observed harassing marine mammals but no kills have been confirmed and no remains of them were found during stomach content examinations. A time series of Chinook salmon abundance was obtained from the Washington Department of Fish and Wildlife. The data include information on salmon returns (which would include the catch and the escapement) to a series of rivers around the Strait of Juan de Fuca, Rosario Strait, the Hood Canal and the Puget Sound. The data may not include information about the stock called "Spring Chinook", but otherwise is a reliable database (J. Packer pers. comm.), and therefore considered a good proxy for killer whale prey availability.

In regards of information on whale-watching boat density, it was noted during the Seattle workshop that the commercial fleet was originally dominated by the US, but that it is presently dominated by Canada (Dahlheim *et al*. 2000). In addition, there is an unidentified number of private vessels that can also be found around the animals. A reconstruction of the trend in the mean number of commercial whale-watching boats in operation every year was provided by the San Juan Island Whale Museum (R. Osborne pers. comm.) and includes the average for each year. The initial year of this time series is 1976 in which the number of boats was zero. It was therefore assumed that in the same way as in 1976, during 1974 and 1975 there were no commercial whale-watching boats in San Juan.

All data were standardized so that the maximum value for each time series was one. Then the data were then presented as deviations from the mean.

Visual correspondence between different covariates including the orca abundance were made by simultaneous plots of the variates of interest. This is an informal way to explore potential significant effects from the covariates.

Survivorship estimation

The killer whale population has been monitored since 1974 and no dispersal has been observed between resident communities or with the transient orcas around Vancouver Island and the Greater Puget Sound (Bigg *et al.* 1990). For this reason, the population can be considered, in the mark-recapture terminology, as geographically closed (i.e. changes in population size are only caused by the internal demography of the population).

The analysis of survivorship has improved considerably since the work of Olesiuk *et al.* (1990), not only because there are more data, but because novel ideas have been incorporated into the theory for data analysis and they could only have been implemented with the current computer power. For this reason, survivorship estimates can not only be calculated as the proportion of animals alive in one year to the animals alive the previous year N_{t+1}/N_t, but in as many ways as a researcher can modify the assumptions about the processes that are believed to control the population dynamics.

Estimation of parameters of age and sex specific survivorship was conducted using program MARK (White and Burnham 1999). Program MARK calculates survival estimates by fitting a linear model to the data (Cooch 2000). The parameters of such linear models are basically the survivorship parameters represented in a different scale. The simplicity of the process of fitting a linear model makes possible the exploration of alternative assumptions regarding the data. Some of these assumptions include the incorporation of constraints or factors that may explain the data in a better way. The basic model can also include covariates that may have correlation with specific trends. In other words, the use of linear models in MARK allows the exploration of different possibilities that help to understand what may have happened to a given population (Franklin 2000).

In the terminology of MARK phi{ } represents the survivorship parameters and p{ } the capture probabilities. The parentheses include denominations for constraints or covariates. For example, model phi{t}p{t} estimates survivorship and capture probabilities as a function of time, that is one parameter of survivorship and one for capture probability for each year.

Where more than one factor is included in the model, they may act independently or interact with each other. Models with interactions are represented with asterisks and models with no interactions, called additive, are represented with a plus sign. For example, in the case of the orca data, model phi{g*t} describes the situation where survivorship varies as a function of the age/sex group and time and the interaction between both factors. In other words, survivorship estimates are allowed to vary in time independently of their age/sex group. On the other hand, the additive model phi{g+t} produces estimates of survivorship in a way that the resulting trend in survivorship is the same for all age classes, but the intensity of the effect is different for each one of them.

Models that calculate only one parameter for the whole time series of survivorship or capture probabilities are represented with a dot. For example phi{.}p{.} only calculates one survivorship parameter and one for capture probability independently of how many years the data span.

The data for the orcas in the Puget Sound are unique in the sense that the population size and its age composition has been observed (as opposed to estimated) every year. Additionally every animal in the population is observed continuously until dead, a situation called, in the terminology of program MARK, “known fates”. When using the known fates method, it is assumed that capture probabilities in all marking occasions are the same and equal to one, therefore those parameters don’t have to be estimated. The estimates of survivorship (and their standard errors) using known fates proved (phi{t}) to be equivalent to that of the basic Cormarck-Jolly-Seber (CJS) model, either with all capture probabilities estimated for each year (phi{t}p{t}), one capture probability estimated for the whole series (phi{t}p{.}) or fixed to one (phi{t}p{1}; since all live animals are observed every year, capture probability must be one). If the CJS model is used, the difference with estimates using known fates would be the estimation of one parameter and therefore when formally comparing models they are not very different. Still, comparison of alternative hypotheses using the Akaike Information Criteria (Burnham and Anderson 1998) is equivalent if all the tested models are fit with the same method (CJS and variations vs. known fates). Because there were early difficulties using the known fates method, setting up the data was done originally for the CJS and tests conducted that way. Results here were obtained by fitting the CJS and its variants under different hypotheses. When the same database is analyzed with one particular method and its variant models, the resulting estimates describe the same population situation with different levels of resolution.

Population dynamics model.

An individual based population model (IBM) model was coded in C++ using AD Model Builder (© Otter Research). The model controls the trajectory of every individual in the population using the estimated values for survivorship and fecundity. As described before, estimates of survivorship were obtained using program MARK. Survivorship rates (S_g where g is the age/sex group) are assigned to individuals by sex and age group using the estimates obtained with model phi{g+4t}p{.} which provides four survivorship values along the time history for each age/sex class (Table 1). An animal survives to the next year if a number drawn at random from a uniform distribution (0 to 1) is greater than $1 - S_{ga}$.

Fecundity is applied only to the group of females between the ages of 10 and 40. A female produces a calf if a number drawn at random from a uniform distribution is smaller than $1/CI * S_{f10\text{-}40}$, where CI is the calving interval set to six years in the simulations. Calves that survive the first year enter the group of juveniles. Because calves and juveniles are of undetermined gender, if they survive to year 10, half of them are assigned to the males and half to the females. This decision is based on the observation that sex ratios for the SR orcas of ages between 1 and 9 yrs fluctuated around 0.5 (Fig. 2).

The behavior of the population was explored for two periods of time, from 1990 to 2000 and 1994 to 1999. In the first case the decision is based on the time when changes occurred in the environment and in the second when the decline in the orca population occurred. The output of the model is the population size in year 2000. Five hundred stochastic trajectories were simulated and the resulting distribution was generated. The dispersion of this distribution should be interpreted to represent the range of natural variability and its effect on potential population trajectories.

RESULTS AND DISCUSSION

Exploratory data analysis

The southern resident population of orcas in the Pacific Northwest showed a steady decline that started in 1997 (Figs. 1 and 3). The starting point of the decline is defined as the first year when the rate of change is smaller than one. These graphs also show that before 1997 for the most part, the population showed a increasing trend and therefore the decline after 1997 is noteworthy. Since the main forces that drive the dynamics of a population are age-specific fecundity and mortality, different aspects of the two factors were analyzed.

Fig. 4 presents the observed annual fecundity. Because no apparent trend is visible with the data in this form, the standardized changes in fecundity were plotted together with the observed rate of population change (lambda; Fig. 5). It can be seen that the change in population size matches the observed fecundity along most of the series. In particular, both indices are below the average since 1997. It is also noteworthy that in 1999 and 2000 lambda (i.e. the annual rate of population change) appears to be lower than expected for the observed fecundity. That difference can only be attributed to reduced survivorship and apparently there is no other year when lambda is as low for the corresponding level of fecundity.

On the other hand, a plot of the level of calf productivity as a function of total population size produces a cluster of points that shows no apparent trend (Fig. 6). If a model for stock-recruitment with density dependence (Ricker 1954) is fit to the data, the resulting estimates vary depending on the initial values. However, the model parameters that provide the best fit correspond to a curve that grows beyond the range of what seems plausible for the biology of the animals. This result is likely due to the lack of contrast in the data with basically no information at lower or higher population sizes. For this reason it is not recommended to attempt any kind of fit regardless of the model. Also, the cluster of plotted points does not present subsets of outlayer points related to unusual levels of recruitment.

Deaths in the population are rarely observed directly. Every living animal in the SRC is observed at least once every year during the whole period of study. When an animal is missing in any particular year it is assumed dead because no animal has disappeared in one year to reappear at a subsequent time (Olesiuk *et al*. 1990). The plot of the number of animals assumed dead every year (or the fraction they represent in the total population) shows some cyclic behavior, but starting in 1990 an increasing trend is apparent (Fig. 7). The starting point of this trend may be shifted approximately to 1995 if the increase from 1990 to 1995 is considered as part of the regular cyclic change. Nevertheless it is clear that unusual levels of mortality are observed in the most recent part of the time series.

A general conclusion of the exploration of the available data is that although there may be an unusually low level of calf productivity in 1999 and 2000, an increase in the mortality seems to be the most important driving force in the general decline of the population. For this reason, the analysis of the effect of covariates focused on estimated survivorship for the different age/sex groups defined in the methodology. These covariates were sea surface temperature (SST), Chinook salmon abundance and whale-watching boat density.

A first approach to find an informal correlation between the abundance of orcas and the trend in salmon abundance seems to show some degree of correspondence (Fig 8a). However, there are some inconsistencies that require a more careful look at the data. These inconsistencies relate to an apparent immediate response of the cetaceans to changes in fish abundance from 1974 to 1990 and a delayed response in the following years. Salmon abundance shows a sharp decline in 1991 and 1992 with a trend for recovery through 1998. Killer whale abundance continued the increasing trend that started in 1984 until 1996, declining only after 1996. It should be questioned whether the initial correspondence in the abundance trends was due to an immediate whale response to changes in salmon abundance. Alternatively, because salmon and killer whales have different life histories it may be appropriate to consider that the observed correspondence may be better explained by a simultaneous response due to some other unknown factor. It is also possible that the probable correlation of trends is purely serendipitous, and that the recent apparent decoupling of trends may be a more accurate depiction of the actual salmon-orca relationship.

Although the comparison of salmon abundance with killer whale abundance and other parameter trends looks promising, it is important to stress the caveat that the analysis is based on the assumption that Chinook salmon is the most important prey item in the diet of the SRC. Although it seems likely that Chinook salmon is the main prey item in the Puget Sound area and surrounding waters during the summer months, it is quite possible that the diet during the rest of the year, and in areas outside of Puget Sound, may diverge from the perceived Chinook preference. This complicates the interpretation of results because any potential correspondence in trends may be masked by the effect of switching to a different prey item. We also note that data on salmon abundance may not be a direct and accurate index of the availability of salmon as prey to orcas. Salmon abundance indices cannot possibly reflect complex behavioral aspects of salmon stocks, such as depth of travel or pattern of microhabitat use, that may influence prey choice by orcas. Thus, there is a need for caution in interpretation of salmon abundance data in the context of orca foraging ecology.

If we assume that effectively Chinook salmon is the main prey for the SRC, then the time series of fish abundance presents three stages that include years of similar abundance, from 1968 to 1975, from 1976 to 1990 and from 1991 to 1998 (Fig. 8a). Such periods of time could be used in an analysis that considers changes in carrying capacity associated with the corresponding fish abundance.

The analysis by Kriete (1995) allows calculation of the daily food intake by individual animals. Since the photoidentification database follows the individual story of each southern resident, it is possible to make an approximate estimate of the fish that would be consumed by the whole community and compare that intake with the abundance estimates for Chinook salmon. The comparison would allow improved assessment of the adequacy of food supply for the SRC. This analysis has yet to be initiated.

Absolute SST values often are difficult to interpret in an ecological context. However, abrupt changes in long-term SST trends often correlate closely with alterations in marine food web productivity, and consequently with the availability of prey to upper trophic level species. Fig. 8b compares the trends in Chinook salmon abundance with SST. It shows corresponding tendencies until approximately 1988. It is relevant to note that from 1976 to 1988, SST was above the long-term (1968-2000) average. SST was below the average from 1989 to 1991 and back above the average from 1992 to 2000. Salmon abundance was above the average from 1976 to 1990, but shows a sharp decline from 1991 with only a slow recovery trend that does not place the abundance above the average. This situation occurred despite the increase in temperature, making it contradictory with the trend during the previous warm period. If SST plays a relevant role in the trend of salmon abundance, then the decline in salmon abundance must be correlated to a factor other than or in addition to temperature.

Comparison of killer whale abundance directly with the trend in SST (Fig. 8c) indicates that although the magnitude in the variation of orca abundance is much smaller to that of the SST (compare with the magnitude of fluctuation in salmon abundance), and therefore most of the orca residual abundance is closer to zero, it could be speculated that warmer temperatures seem to favor increases in SRC abundance and that the last three years of colder temperatures correspond somehow to the decline in the whale population. We note, however, that the most recent decline in orca numbers began during a year of higher temperature.

The number of whale watching boats shows a steadily increasing trend in time and the overlap of with the series of orca abundance seems to show a strong correspondence (Fig. 8d). It is noteworthy in this preview that orca abundance started to decline when the number of boats reached its maximum.

It is important to emphasize that the visual comparisons presented to this point, had the exclusive intention of exploring potential correlations and by no means should be considered to represent cause-effect relationships.

Survivorship estimation and the effect of covariates

Table 2 shows the output from program MARK that compares the different models that were fitted to the mark-recapture data. Models range from the most complex with the greatest number of parameters estimated (phi{g*t}p{g*t}, with 312 parameters) to the simplest (phi{.}p{.}, with only two parameters).

The plot of the survivorship estimates using the model with the interaction of group and time (Fig. 9) shows that calves are the age-group that presents a higher variability in annual survival, but no apparent trend. Old males appear to have a marked declining trend starting in 1994. Old females also seem to have a declining trend in annual survival in the same period of time, but of lower intensity. The rest of the groups seem to have survival rates that are less variable over time and no declining trend in the annual survival is apparent, particularly in the females. These tendencies are better observed if represented as standardized deviations from the average for each category (Fig. 10). It is clear in this figure that old animals of both sexes have had reduced survivorships starting around 1995, but by 1999 survivorship is back above the average. The calves are also at a lower level in these years, but this age class fluctuates widely along the time series.

Standard errors for each estimate make difficult a simple interpretation of the significance of the survivorship changes in time (Fig. 9). For that reason, the model where the effect of time (and its interaction with the group effect) is eliminated was fitted to the data. This represents a formal statistical test of the hypothesis that there is a general temporal trend in the estimates of survivorship. Because models phi{g*t}p{.} and phi{g}p{.} are nested a likelihood ratio test is possible. The result is that the model with no time effect explains the data in a more satisfactory way ($\chi^2_{157} = 172.057$; $p = 0.104$). This is consistent with the marked difference in the corresponding AIC values (748.15 and 595.66). This result means that although there is a visible change in the survivorship (at least in some groups), there is not a statistically significance to the apparent trend, at least at a Type I error level of $p=0.05$. Despite the apparent trends, this result was expected given the broad confidence intervals (see Fig. 9). It is important to stress that this result does not mean that there has been no change in annual survivorship, only that a trend in annual survivorship was not statistically significant at the predetermined level.

In general, the additive models that consider the effect of groups and temporal effects but no interaction between them yield a better model fit. These results indicate that changes in survivorship affect all age/sexes in the same pattern through time, but with different magnitude. For example, model phi{g+t}p{.} shows that although the general pattern of survivorship is the same for all groups, the variability is more evident in calves and old males (Fig. 11).

When the survivorship is analyzed by intervals of time, all the additive versions of the models yield better fits than any other form with the exception of the model with whale watching boat density as a covariate (discussed later). As noted above, fitting of the additive models will force estimates to vary in the same way across all groups. This problem is particularly evident when the boat density and salmon abundance covariates are incorporated to the analysis (see below). The model in this category that ranks higher is the one with four intervals of 6 years (Fig. 12). This indicates that although there is no general temporal trend in the survivorship, there have been some changes that can be detected by specific periods of time. Again, since these are additive models, the pattern of change through time is the same for all groups but the magnitude of change varies among groups. The analysis does not allow formal discrimination of groups most significantly affected, but observation of the confidence intervals indicate that the effect was greater on old animals and perhaps juveniles. This model fit to the data allows one to visualize in an easier way the general changes in survivorship for each specific group and in conjunction for the whole population. It is evident that the population presents some cyclic behavior but that survivorship is currently at a low level relative to previous periods.

The next set of models that provide good fits to the data are those where the abundance of Chinook salmon and whale-watching boats are added. In particular, boat density appears as the covariate that provides the higher correlation with orca survivorship. However, the model that fits the data best is the one where the interaction between groups and boat density is allowed (Fig. 13). Results show that old males present the highest correlation. Both females and old females show a slight correlation. These analyses do not represent any direct cause-effect explanatory depiction of the problem. However, a recent discussion of the potential effect of sound in the whales (Erbe 2001) may be applied to the results of the survivorship/covariate analysis. Erbe (2001) does not present conclusive evidence of hearing damage in the orcas. Instead, the author presents a reasonable potential scenario where the whale's hearing capabilities may be affected on the long term. If sound produces a cumulative effect, it would be expected that older animals would become less efficient in their use of their hearing capabilities, making them more vulnerable and, over time prone to higher levels of mortality. A potential problem in the interpretation of this data set is that the confidence intervals are large enough to overlap more than would be expected for a significant change in survivorship. Very close to this model is the additive version after adding the boat density covariate (Fig. 14). However, the model with interactions is preferred over the additive because of the aforementioned caveat that the variability in calf survivorship will force the additive fit to show a decline that is not present when estimates are obtained separately for each group.

For every approach that is taken to investigate the effect of whale watching, there are at least two levels of possible interference. One begins in the short term and can be inferred directly from behavior. The second only occurs over the long term, includes demographic effects and may be difficult to detect. Trites and Bain (2000) acknowledged that most studies of the effect of whale watching activities on killer whales have only been able to show short-term effects. None have shown any long term effect. The review by Trites and Bain (2000) includes information indicating that whales change behavior when approached by a single boat, but that the addition of more boats in the same vicinity does not add to the perceived change in behavior. These observations suggest a model in which number of boats present may be less important than the amount of time one or more boats is present in the vicinity of whales.

Williams (1999) reported that both male and female orcas showed significant changes in their behavior, although different in nature, when approached by boats. A difficulty in the interpretation of the data is that the analysis considered changes in direction and speed (other variables were measured but showed no significant change). In both cases, the measurements were taken from a starting point that was defined when a first pair of synchronous positions was recorded. This method of recording data includes the period of time when the whale adjusts to the presence of the boat. During this time, the focal individual may react with intense changes of behavior that may diminish in intensity as the animal gets accustomed to the presence of the boat. If this perception is real, then the observed response of the focal animal would be positively biased and the effect of the boats will be overestimated.

An alternative perception is that orcas don't respond directly to the presence of boats but rather respond to unseen (by the human observers) changes in behavior of prey (fish) that are being followed by the whales. Thus, modifications of behavior as a result of approaching boats are indirect. This latter hypothesis is thought to have some merit since Williams (1999) standardized his observations by recording whale behavior that was accepted to be related to foraging (no recordings were made during traveling, socializing, etc.). Foraging does not necessarily mean that the animals are in direct pursuit of fish. For example, they may be searching for fish. However, the intensity of the response may be linked with the actual level of association of the whales with the fish. If this assumption is correct, then the effect of the boat is difficult to assess. For example, it might be unknown whether the fish scattered enough so that the whales can't consume enough prey, thereby increasing the overall foraging time, or if the fish re-aggregated and the whales followed without difficulty.

The results of Williams (1999) indicate that in the presence of one boat, males increase the distance traveled per unit time by approximately 13% compared to what they covered before the arrival of the boat. The females swam 25% faster. The situation was reversed for both males and females as the number of boats increased. This peculiarity of the whale response complicates interpretations of boat effects over a long period of time when the number of whale watching boats increased. The consequences of these results are relevant to assumptions made by Trites and Bain (2000) in the sense that boat avoidance may be energetically expensive. A derivation of this problem is that prey consumption would increase with boat disturbance, creating the effect of a virtual population that is larger than the real population. Should this occur when the population is at carrying capacity, density dependence would cause a decline in abundance possibly similar to the one that has been reported during the last 4 years. It is important to reiterate that such hypotheses are completely dependent to the assumption that boat density has a negative effect altering orca behavior and increasing energetic needs, and that, to date, this assumption has not been validated satisfactorily.

Similar to the trend in boat abundance, the change in salmon abundance appears to have had a greater effect exclusively in old males. This would be a reasonable conclusion given the high energetic demands of the large old males. However, the model with interactions that produced this result was not ranked in a high position compared to the additive model. The additive model indicates that calves were affected the most followed by the old males (Fig. 15).

In all cases, the group of animals that appears to be most resilient to the effect of the covariates in consideration is the reproductive females. Although the overall decline of SRC is disconcerting, the apparent stability of reproductive females is encouraging. In populations of long-lived mammals, demographic properties often are highly resilient to reduced fecundity, an increased age of first reproduction, or an increase in mortality rate of juveniles. However, demographic characteristics can be affected strongly by an increase in mortality rate of breeding females. Stability of SRC breeding females indicates good prospects for eventual recovery if currently active risk factors can be understood and controlled.

Sea surface temperature did not appear to have a visible effect in survivorship of any age/sex group (Fig. 16). Although variance in sea surface temperature can correlate with profound change in food web dynamics at sea, the linkage of temperature with any one component of a food web may be difficult. If temperature change is contributing to SRC declines, connectivity is sufficiently complex and nonlinear that it cannot be detected with our analyses and available data.

Monte Carlo simulations

Fig 17. shows the results of the simulations conducted using a stochastic model that follows the trajectory of every individual in the population. In most cases, the population size in year 2000 (83 individuals) falls out or near the lower end of the resulting frequency distributions (Fig. 17a, b, d and e). Only the simulations with the most recent survivorship include the actual population size well inside the distributions. The main problem in the interpretation of the simulations is that there is no density dependent response included in the model. For this reason, the simulations with high survivorship values previous to the decline result in final population sizes that may appear higher than any previous expectation. An alternative explanation is that the reduction in survivorship actually represents a form of density dependent response and therefore the current population size is well within the expectation based on pure random effects. From the graphs it is easy to infer that the greater density dependent effect on survivorship the more likely the current population size as a result of pure random processes. Another hypothesis is that survivorship declined for reasons other than a density dependent response.

Preliminary explorations of density dependent responses in a population (applied to fecundity) with life history parameters that resemble the orcas in the SRC have been conducted. The results indicate that, if a carrying capacity level of 100 (not unreasonable in the light of the available data) is exceeded by one or two animals, a decline of approximately six animals can be expected in just one year if the shape parameter is 12 (density dependent effect near carrying capacity). However, tracking and modeling density dependent effects is difficult if the effects apply to multiple factors such as fecundity and survivorship combined. The preliminary model shows that the actual age structure at the moment taken as an initial age structure for the projections is also crucial in the fate of the population in the immediate subsequent years. The exercise is useful because a change in the environmental quality, such as the decline in the major prey item, may represent a shift down in the value of the carrying capacity and a decline of a few individuals may be reasonably expected.

Considerations about contaminants.

Individuals in the Southern Resident Community have been found to have high levels of contaminants (Ross *et al*. 2000). However, historical information obtained from stranded animals indicates that from 1976 to 1989, contaminant levels in the animals did not increase and may have been declining (J. Calambokidis, pers. comm.). Although from 1980 to 1984 there was a decline in the number of orcas, the overall trend from 1976 to 1989 was to increase from approximately 71 individuals to about 86. If, as suggested by Olesiuk *et al*. (1990), the 1980-84 decline is explained by the disruption in the age structure after the live-capture removals in the 60s and early 70s by the aquarium trade, then there would be no evidence that contaminants alone could be responsible for the observed decline in the orca population. This situation is in agreement with the observed response of two populations of harbor seals in the Puget Sound (J. Calambokidis, pers. comm.). The southern Puget Sound population showed its highest level of PCBs in 1972. PCB concentrations declined considerably by 1980 and have since remained stable or declining at a very slow rate. PCB concentrations showed a significant decline from 1972 to 1990 in the seals of Smith Island in Northern Puget Sound..

It is interesting to note that the actual observed trend of contaminant levels in harbor seals shows better agreement with the theoretical expectation of the contaminant dynamics if observed from a spatial perspective than with the biological perspective as suggested by Loganathan and Kannan (1991) for contaminant dynamics for the period 1940 to 1990. Data from harbor seals in the Southern Puget Sound suggest that contaminant levels near a particular source increase sharply over time, with the rate of increase depending on the dumping rate, until the dumping is terminated. From the time of termination contaminant levels decline rapidly for a time, after which the decline becomes very slow. On the other hand, Loganathan and Kannan (1991) suggest that long lived animals that have low capacity to degrade pollutants will accumulate contaminants at a moderate rate (compared to short lived animals such as fish) until 1990 without showing any sign of decline.

Following the assumption that the trend in the accumulation of contaminants in marine mammals resembles more the dynamics from the spatial perspective, the SRC would show a moderate increase in contaminant levels that may have reached its maximum around the mid 70s and is actually declining at a slow rate. It is possible, however, that the contaminant accumulation follows the trend suggested by the curve from a remote source. This may be the case if most of the prey consumed by the orcas of the SRC have spent most of their lives feeding in the open ocean away from the Puget Sound. In this case the contaminants must have accumulated at a slow rate that is currently stable or beginning to decline at a slow rate. In the future will be useful to overlap trends in contaminants with different aspects of killer whale life demography.

Considerations about biopsy sampling.

Recently there has been an increase in concern about the possibility that biopsy sampling of tissues from individual SRC orcas may have contributed to the observed population decline. Eighteen individuals were sampled between 1995 and 1997 and eight out of the 18 (44 %) are reported as dead (R. Osborne pers. comm.).

Biopsy sampling is now a widely used technique in marine mammal science. Biopsy darts are fired from a crossbow or air rifle toward a subject animal during surfacing. For killer whales, darts are tipped with a sharp-edged cylinder that penetrates a maximum of 23 mm (less than an inch) into the skin and blubber, collecting a smaller sample (Barrett-Lennard *et al*. 1996). Darts are buoyant allowing recovery. Samples of skin are used primarily for genetic studies. Samples of blubber can be used for studies of contaminant levels, nutritional ecology, and physiology.

Biopsy dart sampling has been used with most taxa of cetaceans, but there is relatively little information about possible detrimental effects to subject animals. Concern increased recently with the reported death of a common dolphin in the Mediterranean Sea following biopsy darting (Bearzi 2000). The death of this animal occurred almost immediately after the darting and was associated to a dart penetration deeper than expected. The dart hurt muscle and probably caused indirect vertebral trauma or severe stress in the animal.

In general however, available information suggests only minimal short-term effects on the behavior of subject animals (e.g., Hooker *et al*. 2001), although some species of smaller cetacean may be exceptional in this regard. Information on long-term effects of biopsy darting has not been collected to our knowledge.

In the particular case of the SRC orcas, 6 of the deceased individuals were males and 2 females. Of the 6 males, 4 were around 40 years old (39, 41, 42 and 43), the other two were 22 and 24. The male aged 22 was examined and the scar from the biopsy was located far from the region of the body that was associated with the cause of the death (R. Osborne pers. comm.). The two females were 18 and 62. Although longevity for the male orcas in the region has been established between 50 and 60 years, in the history of the SRC, 2240 observations of male age were made in total (many of them correspond to readings of the age of a single individual in consecutive years). Of the total observations of age, only 27 exceeded 40 years and only one individual was older than 43. From these numbers it is clear that most of the dead males were approaching the age of life expectancy at the time of darting. Of the two dead females, one was well beyond the age of reproductive senescence.

The age distribution of the animals from the biopsed group was known since the moment when the darting took place. Researchers in the early biopsy sampling efforts used to target old animals because they were expected to die soon and therefore the data that could be obtained from them would not be available for long (M. Dahlheim pers. comm.). This sampling strategy was modified in time with the purpose of having a more homogenous representation of the population.

The high proportion of dead darted animals tend to be less relevant in terms of its potential negative effect to the population because age effects, and possibly other factors, may confound the understanding of darting effects. We cannot conclusively eliminate possible darting effects in the observed SRC decline with information available to us. However, given lack of significant short-term responses typically observed in medium- and large-sized cetacean species, we suggest that significant effects of biopsy darting on SRC orca mortality rates may be unlikely.

CONCLUSIONS

There is a positive correlation between changes in the survivorship of the orcas and the abundance of Chinook salmon and whale watching boats from San Juan Islands. As strong as the signal may be, cause and effect can not be confirmed with the available data. However, the observed correlations occurred in age/sex classes that would be expected to be sensitive to the particular change in question.

Of all changes, the fluctuations in calf survivorship are the most confusing because of high variability along the time series. This leads us to ask if the average decline in calf survivorship that occurred from 1997 (see Fig. 12) could have had a significant effect on the current population trend. Interpretation of the data is more complicated because some models indicate that although a decline in survivorship occurred, and that the decline is correlated to some diagnosable factors, there is also a sign of recovery (Figs. 9, 13 and 14). Fecundity also appears to be rebounding (Fig. 5) and yet the population is still declining (Figs 1 and 3).

Correlations with salmon and boat numbers show a trend in which the most affected animals are post-reproductive individuals that are not primary contributors in demographic terms to the population (although the social importance of these animals was not considered in the population simulations). The question then is why the population is declining if the animals that matter to the dynamics of the population (i.e. females of reproductive age) are doing well? An interesting hypothesis that could be explored is that reproductive males may have a higher demographic value than is currently assumed. More specifically, it would be useful to explore if there is threshold in the number of available mature males below which, the population would decline. This should be tested at the pod level because overall fecundity is recovering and that would be inconsistent with the hypothesis. Out of this trend is the apparently minor and temporal decline in survivorship of reproductive females (see Figs. 9 and 13). As minor as this change could appear, it is imperative to conduct a sensitivity analysis to explore the consequences of minimal changes as observed in this analysis. Sensitivity analysis should be conducted to explore the particular response of this orca population to all the changes and fluctuations detected in this work.

If further analyses are conducted involving a specific model, we recommend that the individual based model utilized here is modified to include density dependent effects, but we believe that the model remains a promising alternative to explore the population's responses.

While it may not be possible to conclusively prove that observed significant correlations with covariates and age/group specific annual survivorship represent actual cause-effect relationships, the signals are nevertheless strong and it may be difficult to ignore them. With regard to salmon abundance, the lack of correlation between SST and orca survivorship and the departure of the strong apparent correlation between SST and salmon may indicate a potential antropogenic effect. Because of the magnitude of the decline and the lack of recent correspondence with SST, it is possible to infer that over-fishing or some other anthropogenic effect may have been the cause of the decline in salmon availability. However it is important to notice that salmon abundance shows a recovering trend. Therefore, recommended management actions primary involve monitoring to ensure that trends continue and that policies promoting recovery are maintained. Without such monitoring, policies and management actions needed to recover this population of orcas will either be ineffective or highly inefficient.

There is probably no question a this point that the behavior of whale-watching boats should be modified. Although the available evidence concerning effects of boats on the whales is still inconclusive and more research is needed, there is no need to wait to improve on regulations of factor such as the number of boats allowed at any particular moment around a pod of orcas, the proportion of time that orca pods are accompanied by boats, and the number of port departures that should be allowed from areas particularly important to orca feeding and socializing.

One of the major limitations of the present work was data availability. This problem implies that there may be other factors that were not analyzed simply because the data are contradictory, unavailable, insufficient or non-existent.

Finally, we evaluated the alternative of random fluctuation, and found evidence that the idea should be considered as a viable alternative. To our knowledge, the hypothesis of simple random variation has not been given serious consideration to date. The option that the current trend of the SRC may be the result of purely random effect is intriguing and possible based on our results, in particular if there has been a natural decline in environmental quality that has reduced carrying capacity. This suggest that it is possible to consider the likely hypothesis of combined effects of stochastic population behavior, increased harassment due to whale watching, and less available forage. If this "joint" hypothesis is proven acceptable, it will be very difficult to implicate specific anthropogenic sources.

ACKNOWLEDGMENTS

We are thankful to the Orca Relief Citizen's Alliance for funding this project and in particular to M. Anderson for his support. We also want to thank D. Willows for sponsoring the project through the University of Washington Friday Harbor Laboratories. We want to acknowledge the relevant role of D. DeMaster of the NOAA National Marine Mammal Laboratory, not only for supporting the project in its different stages, but for the valuable discussions to help us shape vague ideas and for reviewing manuscripts. We thank the crucial contribution of the following people that not only provided the data that we needed for the analysis, but also spent considerable amounts of time providing guidance and ideas: D. Bain, R. Osborne, J. Packer and C. Sims. Thanks to J. Laake, who solved in three minutes a three month MARK dilemma. Finally we acknowledge the valuable contribution of the following people that provided advice, guidance, ideas and a flow of literature without which we would have been lost: M. Dahlheim, G. Morimoto, J. Smith, J. Calambokidis, and P. Ross.

REFERENCES

Bain, D. and K.C. Balcomb. 1999. Population trends of Southern Resident killers whales (*Orcinus orca*) from 1960-1999. Unpublished report submitted to 1999 SRG meeting in Maui, Hawaii.

Balcomb, K.C. III, J.R. Boran and S.L. Heimlich. 1982. Killer whales in the Greater Puget Sound. Rep. Int. Whal. Commn. 32:681-685.

Barrett-Lennard, L.G., T.G. Smith and G.M. Ellis. 1996. A cetacean biopsy system using lightweight pneumatic darts, and its effect on the behavior of killer whales. Mar. Mamm. Sci. 12(1):14-27.

Bearzi, G. 2000. First report of a common dolphin (*Delphinus delphis*) death following penetration of a biopsy dart. J. of Cetacean Res. and Management 2: 217-221.

Bigg, M. 1982. An assessment of Killer whale (*Orcinus orca*) stocks off Vancouver Island, British Columbia. Rep. Int. Whal. Commn. 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. *In*: P.S. Hammond, S.A. Mizroch and G.P. Donovan. Individual Recognition of Cetaceans: Use of Photo-Identification and Other Techniques to Estimate Population Parameters. Rep. Int. Whal. Commn. Special Issue 12. Cambridge, England. Pp 383-405.

Burnham, K.P. and D.R. Anderson. 1998. Model selection and inference. A practical information-theoretical approach. Springer-Verlag, New York, NY. 353 pp.

Cooch, E. 2000. First steps using program MARK: linear models. Unpublished documentation on the theory and use of program MARK available to the general public in the web site: http://www.cnr.colostate.edu/class_info/fw663/Mark.html.

Dahlheim, M., D. Bain, C. Sims and D. DeMaster (Compilers). 2000. Southern resident killer whale workshop. AFSC Processed report 2000-06. Alaska Fisheries Science Center. National Marine Mammal Laboratory.

Erbe, C.E. 2001. Underwater noise of whale-watching boats and potential effects on killer whales (*Orcinus orca*), based on an acoustic impact model. Unpublished report to Fisheries and Oceans, Canada. 27 pp.

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. Can. J. Zool. 76:1456-1471.

Forney, K., M. Muto, and J. Baker. 1999. U.S. Pacific Marine Mammal Stock Assessments. NOAA Technical Memorandum, NOAA-TM-NMFS-SWFSC-282

Francis, R.C., S.R. Hare, A.B. Hollowed and W.S. Wooster. 1998. Effects of interdecadal climate variability on the oceanic ecosystems of the NE Pacific. Fish. Oceanogr. 7:1-21.

Franklin, A.B. 2000. Exploring ecological relationships in survival and estimating rates of population change using program MARK. Unpublished documentation on the theory and use of program MARK available to the general public in the web site: http://www.cnr.colostate.edu/class_info/fw663/Mark.html.

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.

Hooker, S.K., R.W. Baird, S. Al-Omari, S. Gowans, and H. Whitehead. 2001. Behavioral reactions of northern bottlenose whales (*Hyperoodon ampullatus*) to biopsy darting and tag attachment procedures. Fish. Bull. 99: 303-308.

Kriete, B. 1995. Bioenergetics in the killer whale, *Orcinus orca*. Ph. D. Thesis. Department of Animal Science. University of British Columbia. 138 pp.

Loganathan, B.G. and K. Kannan. 1991. Time perspectives of organochlorine contamination in the global environment. Mar. Poll. Bull. 22(12):582-584.

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 State. *In*: P.S. Hammond, S.A. Mizroch and G.P. Donovan. Individual Recognition of Cetaceans: Use of Photo-Identification and Other Techniques to Estimate Population Parameters. Rep. Int. Whal. Commn. Special Issue 12. Cambridge, England. pp 209-243.

Ross, P.S., G.M. Ellis, M.G. Ikonomou, L.G. Barrett-Lennard and R.F. Addison. 2000. High PCB concentrations in free-ranging Pacific killer whales, Orcinus orca: Effects of age, sex and dietary preference. Mar. Poll. Bull. 40(6):504-515.

Ricker, W.E. 1954. Stock and recruitment. J. Fish. Res. Board Can. 11(5):559-623.

Trites, A. and D. Bain. 2000. Short- and long-term effects of whale watching on killer whales (*Orcinus orca*) in British Columbia. SC/52/WW18. International Whaling Commission. Workshop on assessing the long term effects of whale watching on cetaceans. 12-14 of June, 2000. Adelaide, Australia.

White. G.C. and K.P. Burnham. 1999. Program MARK: Survival estimation from populations of marked animals. Bird Study 46 Supplement, 120-138.

Williams, R.M. 1999. Behavioral responses of killer whales to whale-watching: opportunistic observation and experimental approaches. M.Sc. Thesis. Department of Zoology, University of British Columbia. 61 pp.