NOAA Technical Memorandum NMFS-NWFSC-54

Status Review of Southern Resident Killer Whales (*Orcinus orca*) under the Endangered Species Act

December 2002

U.S. DEPARTMENT OF COMMERCE
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December 2002

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EXECUTIVE SUMMARY

Background

On 2 May 2001, the National Marine Fisheries Service (NMFS) received a petition from the Center for Biological Diversity and 10 co-petitioners requesting that Southern Resident killer whales (*Orcinus orca*) be listed as threatened or endangered under the Endangered Species Act (ESA) and that NMFS designate critical habitat for these whales. NMFS reviewed the petition, decided that the petition presented substantial scientific information indicating that an ESA listing may be warranted in light of the recent population decline, and committed to conducting an ESA status review of Southern Resident killer whales. Because the ESA stipulates that listing determinations should be made on the basis of the best available scientific and commercial information, NMFS formed a Biological Review Team (BRT), comprised of scientists with diverse backgrounds, to conduct the status review. The BRT considered a variety of scientific and technical information. This document reports the results of its comprehensive ESA status review of the Southern Resident killer whale population.

There are three types of killer whales in the North Pacific: residents, transients, and offshores. Resident killer whales forage primarily for fish in relatively large groups in coastal areas. Transient killer whales, whose range extends over a broader area, primarily hunt marine mammals. In addition, transient pods are usually smaller than residents pods. Little is known about offshore killer whales, but their prey does include fish. All three of these types are currently classified as the same species (*O. orca*). The petitioned Southern Resident killer whale population consists of three pods that reside primarily in Puget Sound (Washington State), the Strait of Juan de Fuca (between the United States and Canada), and the Strait of Georgia (British Columbia) during the spring, summer, and fall. Northern Residents and the closely related Alaska Residents occupy adjacent ranges in British Columbia and Alaska. The ranges of transients are known to overlap those of residents.

A number of differences have been documented between Southern Residents and the neighboring Northern Residents. The most apparent difference is that the spring, summer, and fall ranges of these populations have little known overlap. Although both populations may feed primarily on salmon, Southern Residents feed on salmon returning to rivers in Washington and southern British Columbia, whereas Northern Residents feed mainly on salmon returning to rivers in central and northern British Columbia and perhaps southeast Alaska. In addition to these seasonal geographic and dietary differences, the shape of the white “saddle patch” behind the dorsal fin of killer whales is different in each population. Finally, there are genetic differences between these two groups of resident whales.

Status of the Southern Resident Killer Whale Population

Since 1974 the Center for Whale Research, Friday Harbor, Washington, has conducted an annual census of Southern Resident killer whales using photo-identification methods. The 1974 census counted 71 Southern Resident individuals, whereas the most recent count in 2001 was 78

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whales, an overall annual increase of 0.3% per year. However, during these 27 years the population has fluctuated considerably (Figure ES-1). More significantly, in the past 5 years, the population has declined 20%.

These population fluctuations were accompanied by large differences in survival rates between age and sex categories and by large changes in survival rates through time. Reproductive-age females had the highest survival rate, followed by juveniles, post-reproductive-age females, and young males. Calves and old males had the lowest survival rates.

Large changes in survival rates suggest an external cause (e.g., changes in prey availability) rather than demographic variation. However, no obvious factors have been found that have the same temporal patterns as those for survival. Changes in survival could be caused by fluctuations in environmental conditions (e.g., El Niño events), during which prey availability is altered. In addition, several other potential risk factors have been suggested: 1) high levels of organochlorines or other contaminants in these whales could cause a decline in survival through mechanisms such as immune suppression; 2) noise generated by whale-watching vessels could mask the acoustical signals that the whales need for foraging and reproductive success; 3) disease and parasites, in combination with other stressors, could affect health; 4) declines in stocks of salmon, a primary prey species, could affect nutrition; and 5) catastrophes such as oil spills and blooms of harmful algae could cause direct mortalities. Although potential risk factors have been identified, few quantitative data are available to precisely determine which, if any, of these potential risk factors (or combinations of factors) are likely to place this population in imminent danger of extinction.

Genetic Data

Two types of genetic data have been collected for killer whales that have proven useful for identifying distinct population segment (DPS) boundaries in other species: microsatellite (nuclear) DNA and mitochondrial DNA (mtDNA). Each type of genetic data offers a unique and valuable perspective on the ecology and evolutionary history of killer whales. Microsatellite data are available for killer whales from seven populations: Southern Residents (SR), Northern Residents (NR), Southern Alaska Residents (SAR), offshores (OFF), Gulf of Alaska Transients (GAT), West Coast Transients (WCT), and AT1 Transients from Prince William Sound in Alaska. The magnitude of the genetic differences between Southern and Northern Residents was about half that found between residents and transients and about twice that found between Northern Residents and Southern Alaska Residents (Figure ES-2). These differences indicate that the Southern, Northern, and Alaska Resident populations are reproductively isolated populations, and that the isolation of Southern and Northern Residents from each other is greater than the isolation between Northern and Southern Alaska Residents.

Two mtDNA sequences have been found in North Pacific resident killer whales. The Southern Residents have one mitochondrial sequence and the Northern Residents have another that differs by one DNA nucleotide. Southern Alaska Residents have both sequences. Both males and females inherit the mtDNA of their mothers, so these data indicate that females from the Southern Resident and Northern Resident populations have not been migrating between populations within at least the recent evolutionary history of these populations.

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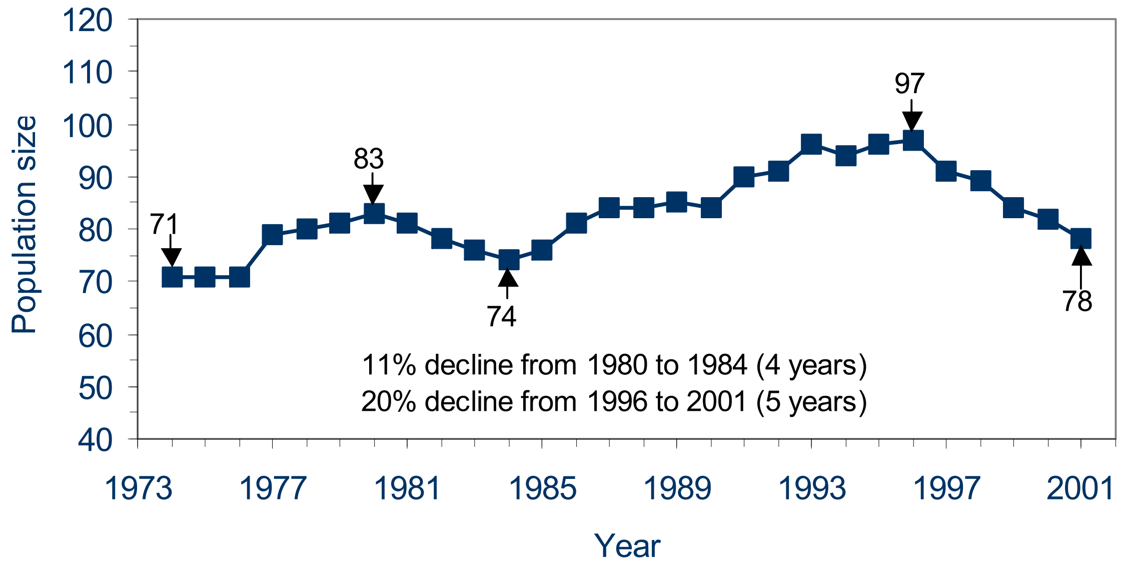

Figure ES-1. Southern Resident killer whale population size through time.

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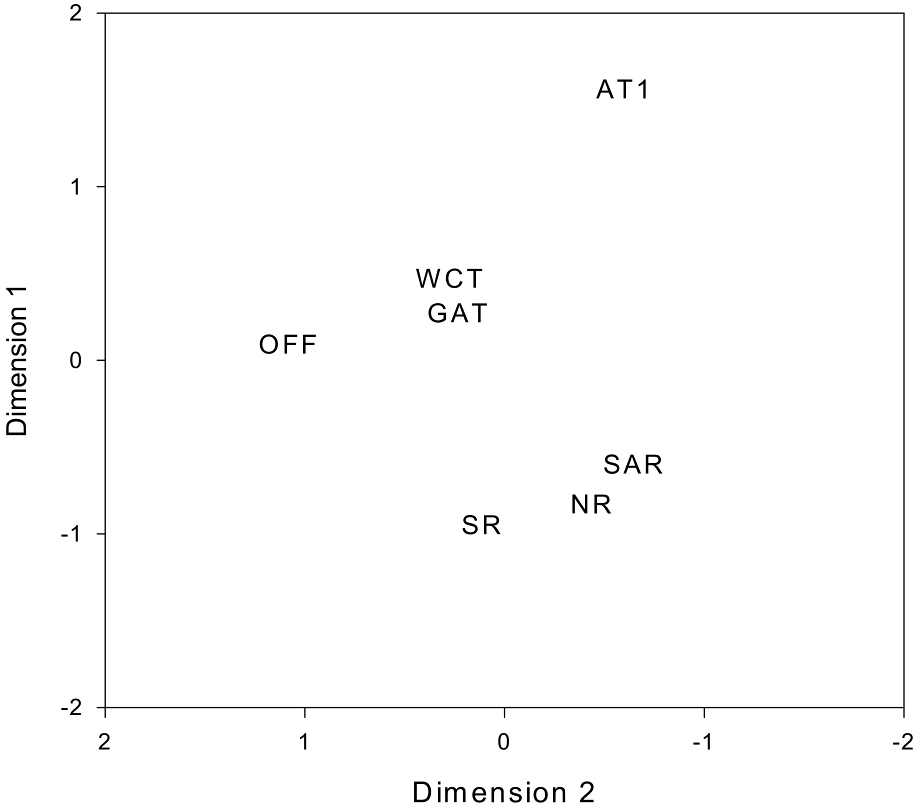

Figure ES-2. Genetic similarity of nuclear genes (microsatellites) for seven killer whale populations in the North Pacific. (Abbreviations are: SR = Southern Residents, NR = Northern Residents, SAR = Southern Alaska Residents, OFF = Offshore, WCT = West Coast Transients, GAT = Gulf of Alaska Transients, AT1 = AT1 Transients from Prince William Sound, Alaska.)

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Determination of DPS

Based on genetics and other information, the BRT determined that Southern Residents meet the criterion for "discreteness" under the joint NMFS and U.S. Fish and Wildlife Service (USFWS) ESA policy. However, the determination of "significance" was far more difficult (Figure ES-3), largely because of issues surrounding killer whale taxonomy. Correctly identifying the killer whale taxon is critical, because the criteria used to evaluate "significance" of a DPS are defined relative to other populations within that taxon. The BRT concluded that the current designation of one global species for killer whales is likely inaccurate, because available data suggest that additional species and subspecies of killer whales probably exist. However, formal taxonomic changes are often slow to occur and lag behind current knowledge.

In the determination of "significance," Southern Residents were judged with respect to the taxon represented by the currently recognized global species (*O. orca*). Each of the NMFS/USFWS ESA criteria for establishing "significance" will be discussed below, first presenting the arguments that received most of the BRT support and then those that received less support.

Arguments Against Southern Residents as a DPS of the Global Species

The following arguments regarding "significance" criteria received most (more than 90%) of the BRT support, and therefore, the BRT concluded that Southern Residents are not a DPS of the global species.

1. *Persistence in an ecological setting that is unusual or unique for the taxon*. The habitat used by Southern Resident killer whales is very similar to that of the neighboring Northern Resident population segment (coastal fjord system, significant freshwater input, seasonal availability of concentrations of salmon) and quite different from habitats that killer whales occupy globally. In addition, Southern and Northern/Alaska Residents consume salmon from different oceanographic systems, but this difference is quite minor when comparing Southern Resident killer whales to coastal fish-eating killer whales that target herring in the North Atlantic Ocean.

2. *Loss would represent a significant gap in the range of the taxon*. Because transient killer whales occupy the same range as Southern Resident killer whales, extinction of Southern Resident killer whales might not result in a gap in the range of the taxon. In addition, other resident or offshore animals could potentially recolonize the current range of Southern Residents, should that population be extirpated.

3. *Evidence that the Southern Residents differ markedly from other populations in genetic characteristics*. Southern Residents are genetically differentiated from other residents, but there is a lack of consensus about whether the magnitude of these differences should be considered "marked."

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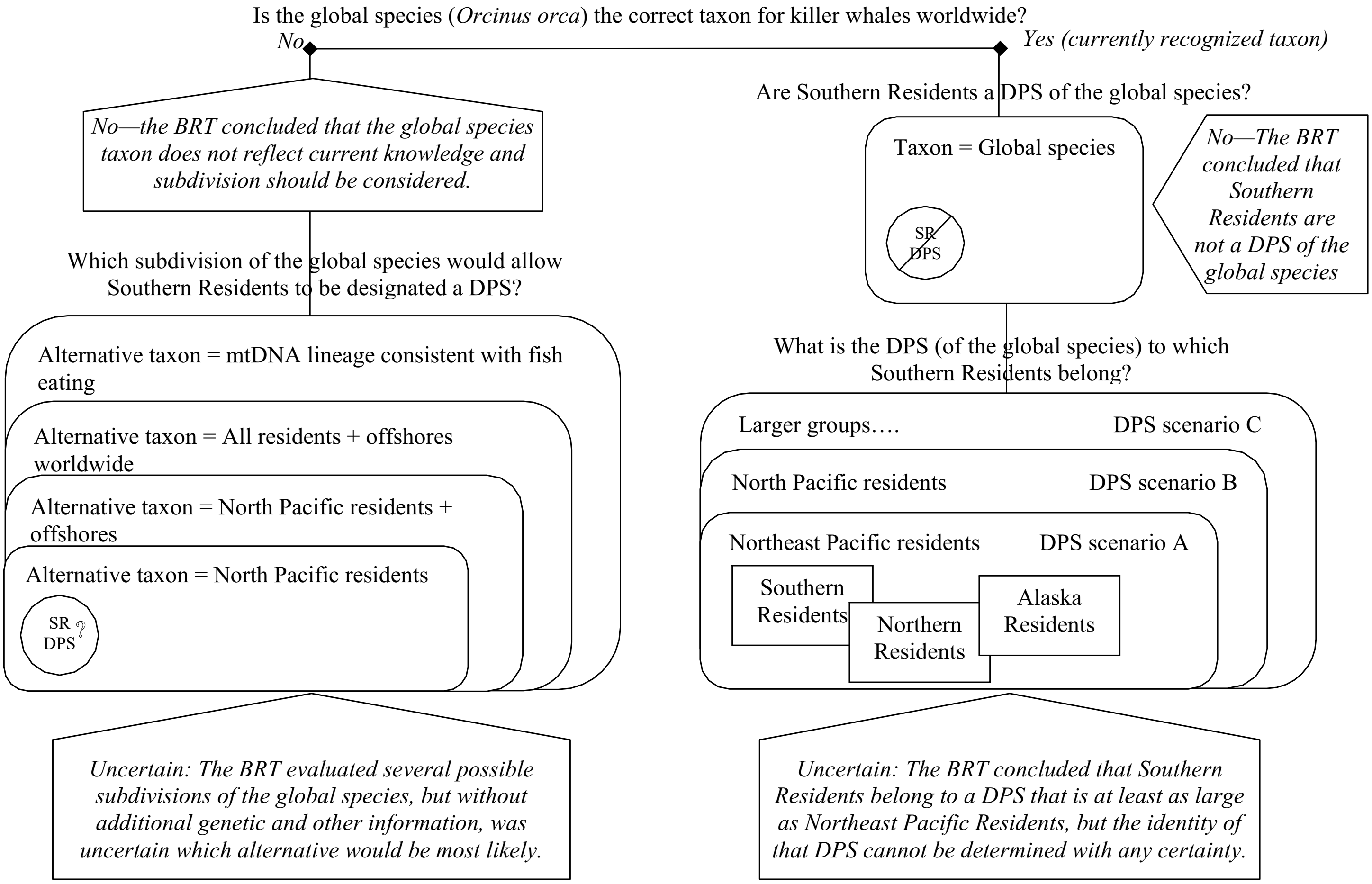

Figure ES-3. Decision tree for determining taxa and DPS used in evaluating "significance" criteria under the ESA.

Arguments in Favor of Southern Residents as a DPS of the Global Species

There are some indications that Southern Resident killer whales might be remnants of a more extensive population that extended to the south, and if this hypothesis is accurate, the following arguments regarding "significance" criteria would have merit. However, this hypothesis received only a little BRT support.

1. *Persistence in an ecological setting that is unusual or unique for the taxon*. Southern Residents may feed primarily on salmon with different population dynamics than that of salmon utilized by other resident populations and may also occupy habitat, particularly in the late fall and winter, that has different oceanographic characteristics from habitat of other residents.

2. *Loss would represent a significant gap in the range of the taxon*. In the past, a larger Southern Resident population may have utilized the coastal habitat from southern British Columbia to California (i.e., range contraction has occurred). Although killer whales are known to eat fish in other locations around the world, there is no evidence that resident whales specializing on coastal salmon exist outside the North Pacific. Therefore, the extended range of Southern Residents would represent a significant portion of the range of resident killer whales. If Southern Residents were extirpated, it is not known whether resident killer whales would recolonize the current range of Southern Residents.

3. *Evidence that the Southern Residents differ markedly from other populations in genetic characteristics*. Southern Residents have genetic diversity consistent with a larger population and almost certainly not consistent with a population that has a long-term abundance equal to the current abundance. In addition, Southern Residents may have lost social complexity (e.g., number of acoustic clans and pods) when compared to other residents and they also have frequency differences in saddle patch pigmentation when compared to other resident populations.

Other Considerations—Southern Residents as a DPS of the Global Species

The BRT considered other factors in determining whether Southern Residents are a DPS of the global species. If Southern Residents are a DPS, it would imply that the killer whale taxon comprises many DPSs. This scenario seemed unlikely to the BRT. In addition, BRT members recognized the importance of the Southern Residents to the culture in the Pacific Northwest, but concluded that this has no bearing on whether the population is genetically distinct, evolutionarily or ecologically significant, or at risk of extinction. BRT members also discussed the importance of pod-specific traits, such as acoustic repertoire, and agreed that these could not be used in support of a DPS decision because there was insufficient evidence to indicate whether these traits were inherited or learned.

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Determining the DPS of the Global Species to which Southern Residents Belong

After concluding that Southern Residents are not a DPS of the global species, the BRT attempted to define the DPS to which Southern Residents belong under a global species taxon (Figure ES-3). Little effort was spent in defining this DPS, because the BRT had concluded that the global species is an outdated concept that needs to be updated. The strongest support (one-third of the vote) was for a DPS that includes all North Pacific residents (i.e., Southern, Northern, Alaska, and Western North Pacific Residents). The rationale for this vote included similar habitat use (primarily coastal), pod size/structure (large pod size), and feeding ecology (all animals feed primarily on salmon) among all the North Pacific resident whales. Another quarter of the votes supported the next larger DPS—North Pacific resident and offshore killer whales. In addition, other larger DPSs to which Southern Residents might belong received varying amounts of BRT support (see subsection 3.4.3 in the report).

Southern Residents as a DPS of Alternative Taxa

The BRT discussed which of several population units of killer whales might be designated the taxon that would include Southern Resident killer whales if the global species were to be subdivided into two or more taxa (Figure ES-3). About equal support was given to each of four alternative taxa: 1) North Pacific resident killer whales, 2) North Pacific resident and offshore killer whales, 3) fish-eating killer whales worldwide, and 4) the mtDNA lineage that includes resident and offshore killer whales. Then the BRT decided on whether the Southern Resident population would qualify as a DPS with respect to each of these alternative taxonomic scenarios.

1. *North Pacific Resident killer whales as the taxon*. The strongest support for considering Southern Residents as a DPS was found under the most restricted (smallest) taxon considered by the BRT—North Pacific resident killer whales. When this taxonomy was assumed to be correct, about half of the support went to Southern Residents qualifying as a DPS. The summer range of Southern Residents would represent a significant portion of the North Pacific resident taxon's range. In addition, the level of genetic differentiation, coupled with frequency differences in morphological traits that are consistent with reproductive isolation and potential local adaptation, could be considered "marked" genetic differences.

2. *North Pacific resident and offshore killer whales as the taxon*. About one quarter of the BRT vote supported Southern Residents as a DPS of this alternative taxon. Southern (and other) Residents have marked differences in microsatellite DNA from offshore whales (Figure ES-2). In addition, Southern Residents occupy a more coastal habitat than do offshores. Furthermore, arguments based on dietary specialization on salmon can be made, as offshore whales are not known to similarly specialize in salmon.

3. *BRT consideration of other alternative taxa and DPS*. The BRT gave little support to the remaining alternative taxa—"Fish-eating killer whales worldwide" and "the mtDNA lineage that includes resident and offshore-type killer whales," so those will not be summarized here but can be found in the body of the report.

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Risk Assessment

A Population Viability Analysis was conducted to synthesize the potential biological consequences of a small population size, a slowly increasing or declining population trend, and the potential risk factors identified by the petitioners and this status review. The probability of the Southern Resident population going extinct, as well as the probability of the Northeast Pacific residents (i.e., Southern, Northern, and Alaska Residents) going extinct, was estimated using demographic information for Southern and Northeast Pacific Residents. Under the assumption that growth rates in the future will more accurately be predicted by the full (1974–2001) time series of available data, the model predicts that Southern Resident extinction probability is less than 1-5% in 100 years (and 5-50% in 300 years), with the higher values associated with higher probability and magnitude of catastrophic mortality events (e.g., oil spills), as well as with a smaller carrying capacity (i.e., where K is carrying capacity and K = 100) (Figure ES-4). Alternatively, under the assumption that population declines seen from 1992–2001 will continue into the future (Figure ES-4), the Southern Residents have a 12-30% probability of extinction in 100 years (and 86-98% probability of extinction in 300 years).

According to the model, extinction risk for the larger Northeast Pacific resident killer whale population is zero over 100 years and is less than 5% over 300 years, regardless of carrying capacity. Larger groups of populations were not considered because sufficient data were not available. However, the probability of such groups of populations going extinct would be less than that of Northeast Pacific residents going extinct.

Conclusions of the Status Review

1. The BRT concluded that Southern Resident killer whales are not a DPS of the global species taxon.

2. The BRT decided that the current designation of one global species for killer whales is inaccurate, because available data suggest that the present taxonomy does not reflect current knowledge and that additional species or subspecies should be officially recognized.

3. If the global species is the taxon considered, most of the BRT support was in favor of a DPS that was larger than the Southern Resident population (and likely would include the Southern, Northern, Alaska, and Western North Pacific Resident populations). However, little effort was spent defining this DPS, because the BRT had concluded that the global species is an outdated concept that needs to be updated.

4. The BRT gave roughly equal support to four different scenarios for the taxon to which Southern Residents might belong if the global species were to be subdivided—the taxon could be as small as North Pacific resident killer whales, but no larger than the mtDNA lineage consistent with fish-eating whales.

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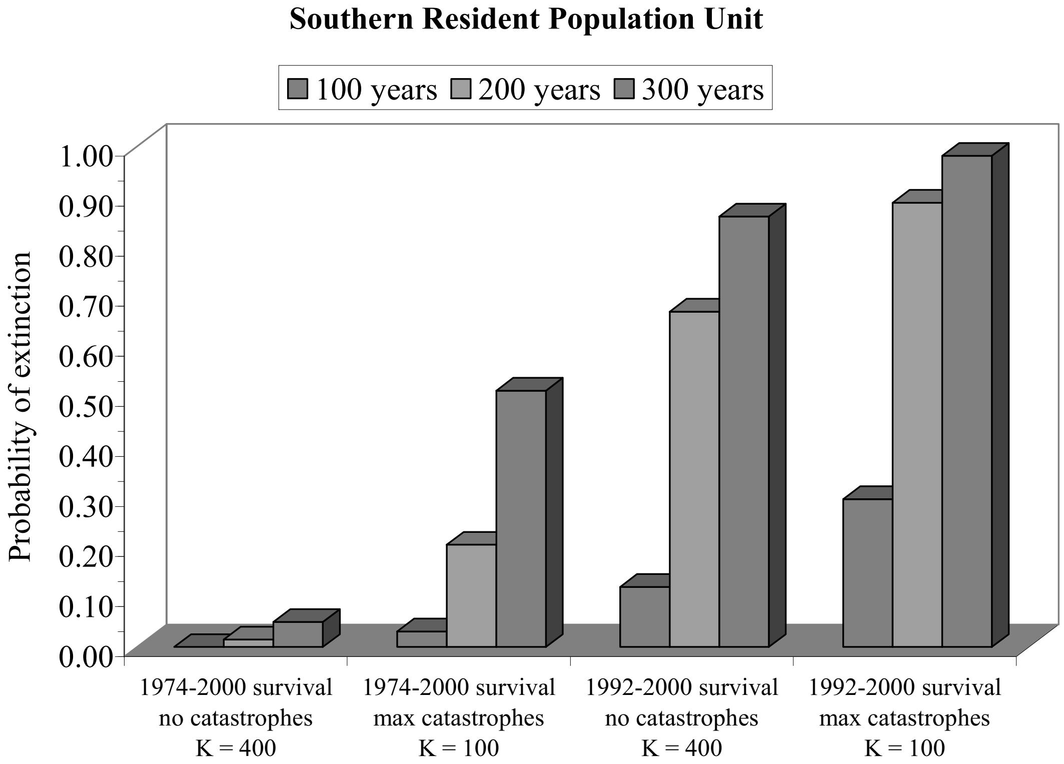

Figure ES-4. Estimated risk of extinction at 100, 200, and 300 years for the Southern Resident population, assuming 1974–2000 survival rates continue, with no catastrophes and with the maximum probability of catastrophe (2% probability of a catastrophe with an average of a 20% decline in survival for 1 year), or assuming 1992–2000 survival rates continue, with no catastrophes and with the maximum probability of catastrophe (2% probability of a catastrophe with an average of a 20% decline in survival for 1 year).

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5. The BRT gave the strongest support (half the vote) to considering the Southern Resident population its own DPS when the taxon was assumed to be North Pacific resident whales (a group that includes Southern, Northern, Alaska, and Western North Pacific Residents), but consensus was not reached. Support for Southern Residents as their own DPS diminished as the hypothesized taxon grew larger.

6. The Southern Residents have greater than 10% estimated probability of extinction in 100 years (>85% in 300 years) under the assumption that the population declines observed from 1992–2001 continue. If the full time series of data available (1974–2001) is used to predict population growth, the rate the extinction probability is 1-5% in 100 years and 5-50% in 300 years. Higher values are associated with increased risk of catastrophes.

7. Extinction risk for the larger Northeast Pacific resident killer whale population unit is negligible over 100 years and less than 5% over 300 years.

8. The BRT considered whether factors that currently pose a risk for Southern Residents might continue in the future. Because exposure to contaminants is not likely to decrease in the foreseeable future, Southern Residents may be at risk for chronic, serious sublethal effects. Other risk factors that may continue to impact Southern Residents are reductions in prey quality or quantity, oil spills, and possibly whale watching.

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ACKNOWLEDGMENTS

A great many individuals have contributed to the status review of Southern Resident killer whales by providing information to the National Marine Fisheries Service (NMFS). The quality and quantity of information gathered by the Biological Review Team (BRT) was improved because of the assistance from these individuals. Several individuals presented material for the BRT's consideration at a meeting of the Biological/Technical Committee on 26 September 2001. Others brought documents to the meeting, forwarded them later, or attended the Comanagers Meeting in March 2002.

The BRT appreciates the efforts of Harriet Allen, Carlos Alvarez, David Bain, Ken Balcomb, Kelley Balcomb-Bartok, Elsa Carlisle, Jeff Dickison, Dave Ellifrit, Candice Emmons, Christine Erbe, Fred Felleman, Joe Gaydos, Steve Jeffries, Jennifer Johnson, Birgit Kriete, Liana Lara, Laura Leschner, Steve Lindley, Matthew Mattson, Ruth Milner, Kate Myers, Peter Olesiuk, Joe Olson, Sandie O'Neill, Rich Osborne, Elizabeth Petras, Brent Plater, Donna Sandstrom, Mark Sears, Jodi Smith, Andrew Trites, Glenn Van Blaricom, Val Viers, Bill Waknitz, Laurie Weitkamp, Rob Williams, and Terry Wright.

A number of scientists provided essential information about killer whales, their habitat, and their food sources in direct response to questions from the BRT. We appreciate information written for the BRT on current and historical salmon abundance by Laurie Weitkamp, Northwest Fisheries Science Center (NWFSC). Also, Andy Dizon and Rick LeDuc from Southwest Fisheries Science Center (SWFSC) shared some preliminary mtDNA results from killer whales that was helpful in BRT deliberations. In addition, we thank Rus Hoelzel for his numerous contributions on killer whale genetics and valuable insights into killer whale stock structure. Dr. Hoelzel shared unpublished data and was extremely cooperative in all communications with the BRT. We also appreciate the contributions of John Ford and Graeme Ellis, who provided their data for winter sightings of Southern Residents.

We also wish to thank those who reviewed and commented on the drafts of this document, either in writing or at the Comanagers Meeting in March 2002, including John Ford, Department of Fisheries and Oceans Canada; Harriet Allen and Steve Jeffries, Washington Department of Fish and Wildlife; Kit Rawson and Craig Bowhay, Northwest Indian Fisheries Commission; Robert Mattlin, Marine Mammal Commission; Tom Eagle, National Marine Fisheries Service (NMFS); and Herman Williams, Tulalip Tribes.

The BRT members were: from NWFSC, Dr. Peggy Krahn, Dr. John Stein, Gina Ylitalo, Dr. Steven Kalinowski, Dr. Robin Waples; from Alaska Fisheries Science Center, Dr. Paul Wade, Robyn Angliss, Dr. Marilyn Dahlheim, Dr. Brad Hanson; and from SWFSC, Dr. Barbara Taylor. In addition, Dr. Douglas DeMaster served as a technical adviser to the group. Other advisers were Steve Stone, Brent Norberg, and Garth Griffin from the NMFS Northwest Regional Office, and Lisa Van Atta from NOAA's Office of General Counsel.

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1. INTRODUCTION

1.1. Scope and Intent of the Status Review

On 2 May 2001, the National Marine Fisheries Service (NMFS) received a petition from the Center for Biological Diversity and 10 co-petitioners requesting that, in light of the recent population decline, Southern Resident killer whales (*Orcinus orca*) be listed as threatened or endangered under the Endangered Species Act (ESA). In addition, the petitioners requested that NMFS designate critical habitat for the Southern Resident killer whale. The petitioned population consists of three pods (J, K, and L) that reside primarily in Puget Sound (Washington State), the Strait of Juan de Fuca (between the United States and Canada), and the Strait of Georgia (British Columbia) during the spring, summer, and fall (Figure 1). Little is known about their winter distribution. These whales overlap in range to some extent with Northern Resident killer whales that reside in British Columbia (Figure 1), as well as with two nonresident forms—offshores and transients. The petitioners state that the Southern Resident whales have undergone a recent decline that is expected to continue.

The NMFS Northwest Region Protected Resources Division, Northwest Fisheries Science Center (NWFSC), Alaska Fisheries Science Center (AFSC), and NOAA's General Counsel Northwest reviewed the petition and concluded that the petition presented substantial scientific information indicating that an ESA listing may be warranted, as recorded in the Federal Register (NMFS 2001). By accepting this petition, NMFS committed to completing an ESA status review of Southern Resident killer whales. Because the ESA stipulates that listing determinations should be made on the basis of the best available scientific and commercial information, NMFS formed a team of scientists with diverse scientific backgrounds—the Biological Review Team (BRT) for Southern Resident killer whales—to conduct this review. The BRT included the following members: 1) from NWFSC, Dr. Peggy Krahn (Team Leader, contaminants), Dr. John Stein (toxicology), Gina Ylitalo (contaminants), Dr. Steven Kalinowski (Lead, distinct population segments), Dr. Robin Waples (genetics); 2) from AFSC, Dr. Paul Wade (Lead, risk assessment), Robyn Angliss (conservation biology), Dr. Marilyn Dahlheim (conservation biology/photo-identification), Dr. Brad Hanson (habitat/foraging ecology/whale watching), Dr. Douglas DeMaster (marine mammal biology/technical adviser); and 3) from the Southwest Fisheries Science Center (SWFSC), Dr. Barbara Taylor (genetics/risk modeling). The BRT considered a variety of scientific information during its status review, including published and unpublished literature and technical information submitted to the ESA administrative record. In addition, a public meeting was held at NWFSC on 27 September 2001 to solicit new biological and technical data from comanagers, species experts, and the interested public. This document reports the results of the BRT's comprehensive ESA status review of the Southern Resident killer whale population.

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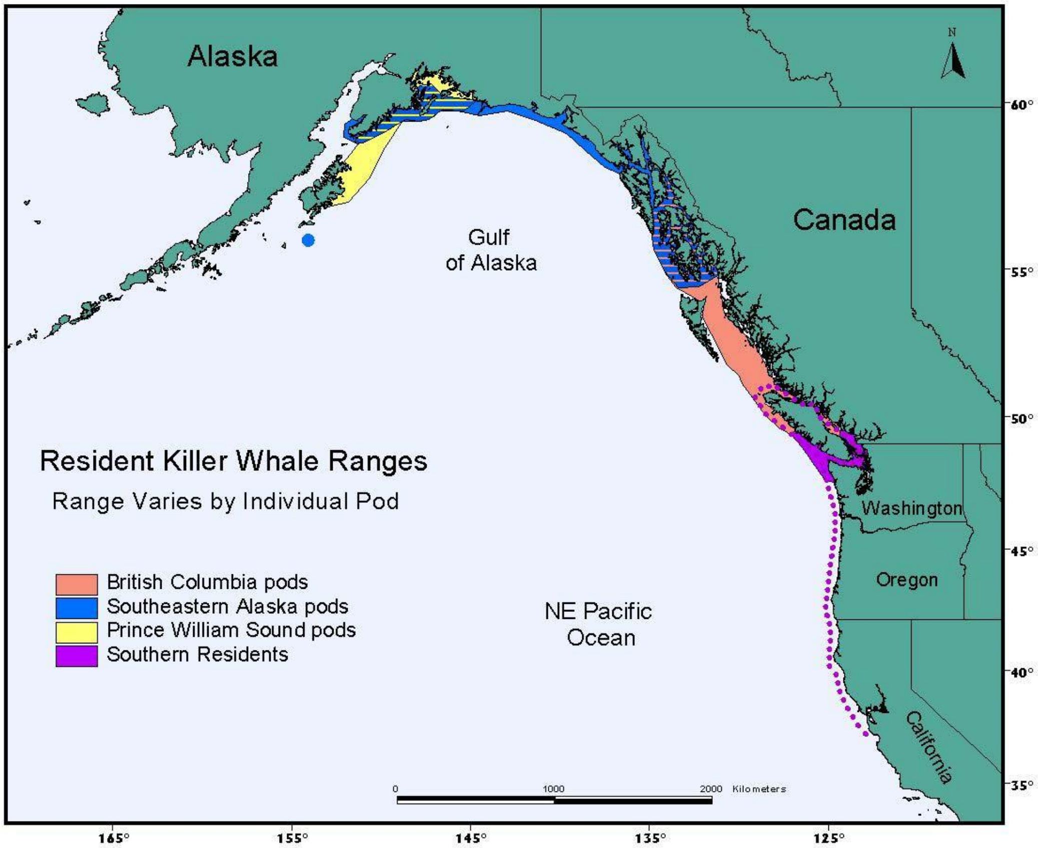

Figure 1. Ranges of resident killer whales in the Northeast Pacific Ocean. Since the legend does not use the same terms for these resident whales as used in the Status Review, the following should be noted: 1) Southern Residents = Southern Residents in the legend, 2) Northern Residents = "British Columbia pods," 3) Southern Alaska Residents are represented by both "Southeastern Alaska pods" and "Prince William Sound pods," and 4) Western Alaska Residents have not yet been mapped.

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1.2. Key Questions in ESA Evaluations

1.2.1. The "Species" Question

For the purpose of the ESA, Congress has defined a species as: "any subspecies of fish or wildlife or plants, and any distinct population segment of any species of vertebrate fish or wildlife which interbreeds when mature." As amended in 1978, the ESA allows listing of distinct population segments (DPSs) of vertebrates, as well as named species and subspecies. Guidance on what constitutes a DPS is provided by the U.S. Fish and Wildlife Service (USFWS) and NMFS interagency policy on vertebrate populations, as indicated in the Federal Register (USFWS and NMFS 1996). To be considered "distinct," a population or group of populations must be "discrete" from other populations and "significant" to the taxon (species or subspecies) to which it belongs. A population segment of a vertebrate species may be considered discrete if:

1) it is markedly separated from other populations of the same taxon as a consequence of physical, physiological, ecological, or behavioral factors (quantitative measures of genetic or morphological discontinuity may also provide evidence of this separation); or
2) it is delimited by international governmental boundaries within which differences in control of exploitation, management of habitat, conservation status, or regulatory mechanisms exist that are significant in light of Section 4(a)(1)(D) of the ESA.

If a population segment is considered discrete, NMFS must then consider whether the discrete segment is "significant" to the taxon to which it belongs. Criteria that can be used to determine whether the discrete population segment is significant include:

1) persistence of the discrete segment in an ecological setting unusual or unique for the taxon;
2) evidence that loss of the discrete segment would result in a significant gap in the range of the taxon;
3) evidence that the discrete segment represents the only surviving natural occurrence of a taxon that may be more abundant elsewhere as an introduced population outside its historic range; and
4) evidence that the discrete segment differs markedly from other populations of the species in its genetic characteristics.

A discrete population segment needs to satisfy only one of these criteria to be considered significant. Furthermore, the list of criteria is not exhaustive; other criteria may be used, as appropriate.

Finally, Congress has instructed NMFS to use the authority to define DPS "sparingly and only when the biological evidence indicates such action is warranted" (Senate Report 151, 96th Congress, 1st Session, 1979).

1.2.2. The "Extinction Risk" Question

The ESA (Section 3) defines the term "endangered species" as "any species which is in danger of extinction throughout all or a significant portion of its range." The term "threatened species" is defined as "any species which is likely to become an endangered species within the foreseeable future throughout all or a significant portion of its range." The ESA states that a

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variety of information should be used in evaluating the level of risk faced by a species or a DPS. Important considerations include:

1) the present or threatened destruction, modification, or curtailment of its habitat or range,
2) overutilization for commercial, recreational, scientific, or educational purposes,
3) disease or predation,
4) the inadequacy of existing regulatory mechanisms, or
5) other natural or manmade factors affecting its continued existence.

According to the ESA, the determination of whether a species is threatened or endangered should be made on the basis of the best scientific information available on its current status, after taking into consideration conservation measures that are proposed or in place. The BRT develops scientific conclusions about the risk of extinction faced by the identified DPS, but the NMFS Northwest Regional Office decides which conservation measures will be considered in making ESA-listing recommendations.

1.2.3. Factors Not Considered in ESA Evaluations

The petitioners and comanagers suggested many factors that NMFS could use to support listing Southern Resident killer whales under the ESA. The following factors were not considered by the BRT:

1. *Southern Residents comprise a "stock" under the Marine Mammal Protection Act (MMPA)*. The definition of "stock" under the MMPA is "a group of marine mammals of the same species or smaller taxa in a common spatial arrangement that interbreed when mature." Further guidance on stocks clearly indicates that stocks should be management units. In contrast, one goal of the ESA is to conserve species that are important from an evolutionary standpoint. Thus, although a population unit defined under the ESA could be the same as a stock defined under the MMPA, this would only be the case if the population unit also fit the definition of a DPS. Thus, the fact that the Southern Residents have been designated a "stock" under the MMPA has no direct bearing on whether the population should qualify as a DPS.

2. *Southern Residents are delimited from other populations by significant jurisdictional boundaries*. NMFS policy on the definition of a species, indicated in the Federal Register (NMFS 1991), states that it may be appropriate to list U.S. populations of species under the ESA, but only if the population fits the definition of an evolutionarily significant unit (ESU), analogous to a DPS. Thus, the presence of a jurisdictional boundary does not provide support, by itself, for identification of a DPS.

3. *Southern Residents are culturally significant in the Pacific Northwest*. Neither the policy for determining what constitutes a DPS nor the policy for the definition of species includes any indication that the significance of a species to human culture should be considered in evaluating the status of a species under the ESA.

4. *Southern Residents, because of their role as a top predator, are important to their ecosystem*. NMFS policy on the preliminary definition of an ESU, indicated in the Federal Register (NMFS 1991), states that, although one of the purposes of the ESA is to "provide a means whereby the ecosystems upon which endangered and threatened species depend may be conserved," unless the population of concern can be shown to be distinct (and presumably

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significant) under the guidelines for determining a DPS, efforts to conserve ecosystems must be accomplished outside the purview of the ESA. Further, an argument could be made that every population is important to its environment; given that argument, it is not possible to see how this factor by itself could provide support to designating a particular population as a DPS.

5. *Southern Residents could be listed consistent with the congressional findings at the beginning of the ESA, which states that various species are of aesthetic, educational, historical, recreational, and scientific value to the nation*. Although the concept of preserving species because of these values may be a good justification for why the ESA is necessary, it does not provide good justification for why a population may or may not meet the criteria for a DPS. NMFS policy on the preliminary definition of an ESU (NMFS 1991) indicates that attempting to preserve a population based on the esthetic, educational, historical, recreational, and scientific value is not related to whether or not a species (or ESU/DPS) is genetically distinct (or significant according to the DPS guidelines), or whether the population is likely to become extinct.

1.3. Summary of Information Presented by the Petitioners

The petition from the Center for Biological Diversity and co-petitioners (Plater 2001) highlights key issues for NMFS to consider, including: 1) genetic, behavioral, and ecological evidence indicating that Southern Resident killer whales may be a DPS; 2) population data documenting a recent decline in Southern Resident killer whales and analyses indicating that these whales may be at some risk of extinction; and 3) an array of threats that may account for the decline in Southern Resident killer whales.

1.3.1. The DPS Question: “Discreteness”

The petitioners present the following arguments that Southern Resident killer whales are “discrete” from other population segments.

Southern Residents are different from other Pacific Northwest killer whale types

The Southern Residents have physical, physiological, ecological, and behavioral factors that are markedly different from transient, Northern Resident, and offshore whales. Although the transient form overlaps extensively in range with the resident form, genetic evidence suggests they do not interbreed. Behavioral evidence suggests that offshore and transient pods rarely interact with the resident pods. Distinct feeding habits exist, with transient killer whales primarily preying on other marine mammals and Southern Residents primarily subsisting on fishes. Other documented differences between transients and residents include measurable differences in morphology and behavioral differences in group size, social organization, and acoustic repertoire.

The petitioners state that Southern Residents have association patterns, saddle patch pigmentation patterns, and genetic compositions that are distinct from the Northern Residents. Behavioral interactions have not been observed between individuals from the different resident populations. Furthermore, differences in physical appearance and mitochondrial DNA (mtDNA)

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suggest that these communities are reproductively isolated. The Northern and Southern Residents have different haplotypes, with a fixed one base pair difference between the two populations. Although this difference is not as great as the difference noted between transients and residents, it is significant because it is manifested in notable differences in the morphology of the Southern Residents. The petitioners state that Southern Residents have a statistically significant difference in saddle patterns and pigmentation compared to the Northern Residents. These differences are indicative of genetic differentiation between the two populations.

The petitioners indicate that Southern Residents are markedly distinct from the offshore form. For example, offshores and residents have been noted to have distinct dorsal fin shapes. In addition, the offshores were not found to be closely related genetically (using microsatellite [nuclear] DNA) to either the residents or the transients.

Southern Residents are delimited by significant jurisdictional boundaries

The petitioners state that, because killer whales regularly move between Canada and the United States, protection measures in Canada are directly relevant to the conservation of killer whales in the United States. At the time the petition was filed, the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) had listed the Southern Resident killer whale population as "threatened."[1] The petitioners further state that, "Although this is a positive first step in the preservation of the population, without additional protections in the U.S. the protective status in Canada will not provide meaningful conservation for the population. Thus, listing under Section 4 of the ESA is necessary and appropriate."

Southern Resident killer whales comprise a "stock" under the MMPA

The petitioners point out that, although the analysis under the MMPA of whether a given marine mammal population is a separate "stock" differs somewhat from that of the NMFS/USFWS ESA listing policy, Southern Residents satisfy all of the criteria necessary to delineate a separate stock under the MMPA. First, the information available on distribution shows that Southern Residents utilize summer and winter areas that are distinct from those of other populations. Second, the documented decline of the Southern Residents is occurring independently from the dynamics of any other killer whale population for which information is available. Third, there are observed differences in morphology. And fourth, there are observed genetic differences between Southern Residents and other killer whale populations.

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[1] In 1999, North Pacific "resident" populations, which include the Southern Resident, Alaska Resident, and Northern Resident groups, were designated as "threatened" under COSEWIC. In 2001, the North Pacific "resident" population was formally recognized as two populations under COSEWIC: the Northeast Pacific Southern Resident population (the unit petitioned under the ESA) and the Northeast Pacific Northern Resident population. When the two resident populations were separated in 2001, the Northeast Pacific Southern Resident population was designated as endangered under COSEWIC based on the small size of the population, a 20% population decline from 1995-2001, and a restricted distribution. However, there are important differences between COSEWIC and the ESA; for example, COSEWIC allows the use of international boundaries in listing decisions and a variation of the International Union for Conservation of Nature and Natural Resources (IUCN) criteria is used to determine the status of a population. A designation of "endangered" under COSEWIC does not imply that listing a population as "endangered" under the ESA would also be appropriate.

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1.3.2. The DPS Question: "Significance"

The petitioners present the following arguments to demonstrate that Southern Resident killer whales are "significant" to the taxon to which they belong.

The Southern Resident killer whale occupies a unique ecological setting

The Southern Resident population has the most urbanized habitat of any killer whale population in the world, centered on Puget Sound and the Strait of Juan de Fuca. The J pod of the Southern Resident killer whale population is the only group of killer whales to spend the winter within the waters of Puget Sound on a semiregular basis. All other killer whale populations are generally known to migrate out to sea during the winter, although the exact locations of their winter habitats is currently not known. The year-round site fidelity of J pod is a unique ecological characteristic, maintaining a seasonal range distinct from other populations of killer whales. In addition, the Southern Residents are the only resident killer whales to occupy the majority of the habitat in Puget Sound. Although transients are sympatric (overlapping range of distribution), they play a separate role in the ecosystem in this area because they forage on marine mammals, not on fish.

Loss of the Southern Residents would result in a gap in the species' range

The petitioners state that a loss of the Southern Residents would create a significant gap in the range of the taxon, as it would eliminate the only resident killer whales known to persist in the Puget Sound environment. This is particularly true because of J pod's tendency to winter in Puget Sound. If the Southern Residents were to go extinct, the loss of J pod would create a distinct gap in the winter range of the killer whale. There is no evidence to show that migration from other killer whale populations into the Southern Residents' range would be successful.

Southern Residents differ markedly from other killer whales

As noted above (subsection 1.3.1), the Southern Residents differ markedly from other populations of killer whales in behavior, morphology, ecology, and range.

Southern Residents are culturally significant in the Pacific Northwest

The petitioners indicate that a loss of the Southern Residents would eliminate a significant portion of killer whales in the most accessible viewing location in the United States. This would impact the culture and identity of people in the Pacific Northwest. The area has been an important area for human interaction with killer whales for thousands of years. It is believed that the Southern Residents in the area are the direct descendants of the first killer whales noted in the human record, and human interactions continue to this day with an active whale-watching industry.

Southern Residents comprise a "stock" under the MMPA

As noted above (subsection 1.3.1), the Southern Resident killer whales are currently considered a stock under the MMPA.

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1.3.3. Abundance and Population Trends

The petition presents detailed narrative information, based on available data from the annual killer whale censuses, that show the stock (as defined under the MMPA) has gone through periods of growth and decline from a low of less than 70 animals in 1973, to a high of 97 individuals in 1996, followed by a period of decline to 82 individuals at the beginning of 2000.

The petition presents the results of a photographic census of Southern Resident whales that the Center for Whale Research (Friday Harbor, Washington) has conducted annually since 1974. Records from capture operations extend the record back to 1960, supplementing the census information. The petitioners state that population levels before 1960 are not known with any accuracy, but are presumed to be greater than even the highest levels seen in the past 40 years. The Southern Residents numbered over 100 individuals in the mid-1960s. Since that time, three major declines have occurred in the population. The first decline, caused by live-capture operations for public display, occurred between 1967 and 1973. Approximately 34 whales were taken during this period, leading to a decline of at least 30% in the Southern Residents. The second decline of 12% occurred between 1980 and 1984. Both of these declines were followed by periods of population growth. The third recorded decline began in 1996 and continues today. From 97 adults and juveniles at the beginning of 1996, the Southern Residents have declined 12.8% to 82 at the beginning of 2000.

1.3.4. Risk Factors

The petitioners assert that variability in recruitment and survival, reduced food resources, residual effects from live captures in the 1960s and 1970s on the current age and sex structure of the population, behavioral changes associated with increased whale-watching disturbance, and increased levels of toxic contaminants are possible threats faced by the species.

According to the petition, the Southern Residents' extinction trajectory has been caused by several anthropogenic factors. During the late 1960s and early 1970s, approximately 34 Southern Residents were captured and removed for display in aquaria; perhaps a dozen more Southern Residents were killed in the process of capture. These captures altered the sex and age ratio of the Southern Residents, creating a reproductive gap that led to population declines in the 1980s. Concentrations of organochlorines (OCs) in Southern Residents have recently been determined to be greater than levels at which harmful effects have been documented in other marine species. The contamination may be affecting the survivability of the population. Chinook salmon (*Oncorhynchus tshawytscha*) stocks—the Southern Residents' supposed main food source—have been declining throughout the Pacific Northwest due to overharvesting and destruction of salmon habitat. The reduction of this food source may be reducing the carrying capacity of the Southern Residents' historical range, and may be enhancing the effects of bioaccumulated toxic chemicals, according to the petitioners. Disturbances caused by whale-watching and shipping vessels are also a likely factor in the Southern Resident killer whale's decline. Vessel traffic can affect individual whale behavior and lead to fatal collisions with ships.

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1.3.5. Risk of Extinction

To estimate the probability that the Southern Resident killer whale group may go extinct, the petitioners conducted two population viability analyses (PVAs), based on the known life history parameters of the Southern Resident killer whale and the population data collected over the past quarter century by the Center for Whale Research.

The set of PVAs provided in the original petition (Plater 2001) used data from 1974–2000 to estimate mortality and fecundity rates. Depending on what assumptions were made about carrying capacity, sex ratio at birth, and potential effects of risk factors on vital rates, the median time to extinction ranged from an estimated 113 to greater than 300 years. Again, depending on model assumptions, the petitioners concluded that Southern Residents have an estimated 36-100% chance of extinction within the next 300 years.

The petitioners conducted a second series of PVAs that incorporated a wider range of assumptions and risk levels (Taylor and Plater 2001), using data from the 1996–2000 decline to estimate mortality and fecundity rates. These models—which included the multiple impacts of higher inbreeding, oil spills, epizootics, and reduced food supply—resulted in greatly increased risk of extinction: a 33-100% chance of extinction in 100 years. Regardless of the assumptions made in these PVAs, the population was always calculated to go extinct within 200 years and the median predicted time to extinction ranged from 54 to 112 years, depending on the assumptions made in the model.

1.4. New Information—Not Included in the Petition and Not Considered by the BRT

The BRT recognized that new information on many aspects of killer whale biology, particularly Southern Resident biology or population dynamics, might become available at any time. However, in order for the BRT to meet its deadline and be able to efficiently review and evaluate the information, the BRT generally did not use information that became available after 1 October 2001. For example, the two new calves born to the Southern Resident group in late 2001 were not included in BRT analyses or deliberations.

Very recently, two juvenile killer whales, one from a Southern Resident pod and one from a Northern Resident pod, left their natal pods. The Southern Resident animal was recently identified on the outer coast of northwest Vancouver Island as L98, which was previously assumed to have died at approximately 1 year of age. Thus the absence of this whale was counted in the decline in the Southern Resident population. Although neither situation provides evidence of “dispersal,” because the animals must survive to adulthood and reproduce in order to successfully disperse, both animals provide a suggestion that animals that leave their natal pods may not be dead and that dispersal is possible.

As a comanager of the Southern and Northern Resident killer whale populations, the Department of Fisheries and Oceans Canada (DFO) submitted comments on a draft of the status review. As part of the written comments submitted on 26 March 2002, DFO provided new information that indicated the Northern Resident killer whale population has declined 8.7%

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between 1997 and 2001. The best information available to the BRT prior to this date was that the Northern Resident population was increasing (Olesiuk et al.1990). Fortuitously, changes in the risk assessment model presented in this status review were not necessary, as the model used to address the larger potential DPS used the same pattern for survival rates demonstrated for the Southern Resident group. The results of the risk assessment model for this larger potential DPS have, however, been reinterpreted in light of the new information provided by DFO (see subsection 4.5.2).

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2. BACKGROUND INFORMATION ON BIOLOGY AND HABITAT OF KILLER WHALES

2.1. General Killer Whale Biology

2.1.1. Identifying Characteristics

Color patterns

Killer whales are one of the most strikingly pigmented of all cetaceans, making field identification easy. Killer whales are black dorsally and white ventrally. The white region extends from the tip of the lower jaw posteriorly, constricts medially between the flippers, widens slightly posteriorly, and ends just caudal of the urogenital region. A lateral white flank patch that expands dorsoposteriorly above the urogenital region is continuous with the ventral white area. The ventral aspect of the flukes is white or light gray, and may be bordered in black. A conspicuous white oval patch is located slightly above and behind the eye. A highly variable gray or white saddle is usually present posterior to the dorsal fin. Saddle shape varies among individuals, pods, and from one side to the other on a single animal (Baird and Stacey 1988a). The saddle patch of young individuals may be indistinct (Bigg et al. 1976).

In young animals, white areas are yellowish in color (Scheffer 1971). Animals born at SeaWorld and Marineland (USA) had white areas that were described as light orange to ocher in coloration (B. Andrews[2]). The yellowish hue has also been reported on adult whales from the Antarctic (Berzin and Vladimirov 1982, 1983, Evans et al. 1982) and on some animals in the North Pacific (Scammon 1874, Scheffer and Slipp 1948). In the case of adults, yellowish coloration may be due to diatom deposits on the skin (Hart 1935). Melanistic individuals (Scammon 1874, Scheffer and Slipp 1948), and partially albinistic animals (Scheffer and Slipp 1948, Carl 1960), have been seen in the North Pacific. Haley (1973) reported one killer whale that was white in coloration as a result of Chediak-Higashi Syndrome. The scientific documentation of the syndrome was provided by Taylor and Farrell (1973).

Individual and geographical variations in the pigmentation pattern are well established (Carl 1946, Evans et al. 1982). Many individuals in the Antarctic have lighter pigmented skin, revealing the primitive delphinid “cape” pattern defined by Perrin (1972). This cape is present on at least some fetuses from the North Atlantic (Guldberg and Nansen 1894). Many of the Southern Hemisphere animals are also characteristically lighter in color posterior to the dorsal fin.

Size and shape

Sexual dimorphism occurs in body size, flipper size, and height of the dorsal fin. Females attain a body length of up to 7.7 m and males to 9.0 m. Although few animals have been weighed, maximum accurate weights of 3,810 kg for a 6.70 m female and 5,568 kg for a

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[2] B. Andrews, SeaWorld, 7007 SeaWorld Dr., Orlando, FL 32821. Pers. commun., 1991.

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6.75 m male have been obtained (Andrews footnote 2). A length/weight equation of W (kg) = 0.000208 L $(cm)^{2.577}$ has been calculated (Bigg and Wolman 1975). In adult males, the dorsal fin is erect and may be from 1.0 to 1.8 m tall, whereas the dorsal fins of females are less than 0.7 m and distinctly falcate. Height of the dorsal fin is a useful characteristic for identifying adult male composition within pods.

The head of the killer whale is somewhat rounded, with a slight demarcation of a beak. The relatively large ovate flippers are positioned about one-fourth the distance from the snout to the flukes. The flipper shape contrasts sharply with the sickle-shaped flippers of most delphinids. Flipper length may attain 20% of the body length in males and 11-13% of the body length in females (Eschricht 1866). Total spread of the flukes may be one-fifth of the body length for both sexes (Nishiwaki 1972).

Internal anatomy—skeleton

Skulls of adult *O. orca* are typically distinguished from those of other species by their large size (condy-basal length to 100 cm), dental formula, and large teeth. Skulls from subadult killer whales may be confused with those from false killer whales (*Pseudorca crassidens*). In killer whales, the width across the premaxillae is usually less than 50% of the rostral width (measured just anterior to the antorbital notches) and the lateral border of the premaxillae is slightly more sigmoid and wider distally. The pterygoids are widely separated in killer whales and their teeth are compressed anteroposteriorly at the roots (Glass 1974). The tympanic and periotic bone complex of *O. orca* is characterized by the lack of a ventral keel, closure of the elliptical foramen, and massive anterior and posterior periotic processes (Kasuya 1973). The temporal fossa is noticeably large, indicating a large and powerful temporalis muscle for jaw closure. Ness (1967) reported that the degree of skull symmetry in *Orcinus* is high compared with other odontocetes; however, Heyning (1989) noted scaling problems with Ness's analysis due to rostral lengths and reported that killer whales exhibit skull asymmetry similar to other delphinids. The lower jaw is relatively short.

The dental formula is usually listed as 10-12/10-12; however, up to 14 teeth per row have been counted (Eschricht 1866, Scammon 1874). The adult tooth may be as long as 13 cm (Nishiwaki 1972). Both the mandibular and maxillary aveoli are deep, with approximately two-thirds of the tooth embedded. The tips are pointed and curved inward and backward. When the jaws close, the upper and lower teeth interlock. Older animals may exhibit extensive wear on the teeth (Caldwell and Brown 1964).

The vertebral count is 7 C, 11 to 13 T, 10 to 12 L, and 20 to 24 CA, for a total of 50 to 54 vertebrae (Eschricht 1866, Nishiwaki 1972). Rib counts range from 11 to 13 per side (Eschricht 1866), with the anterior 6 or 7 ribs attached to the vertebrae by both the capitulum and tuberculum and the remainder attached only by the tuberculum. Ribs 1 through 6 attach to the sternum.

The phalanges are wider than they are long. The phalangeal formula is listed as I 1, II 4 to 6, III 3 to 4, IV 2 to 3, and V 2 (Heyning and Dahlheim 1988). The ends of the phalanges and most carpal elements were composed of cartilage for an adult male examined by Eschricht

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(1866). Harmer (1927) hypothesized that the accelerated secondary growth of the flippers in maturing males was related to the continued growth of these cartilages.

Internal anatomy—organs

Little information is available on the internal anatomy of killer whales. The tongue of *O. orca* is more protrusible than that of *Tursiops* (Donaldson 1977). The general plan of the digestive system is similar to that of other delphinoids. The forestomach is large and extremely distensible to accommodate large prey items (Eschricht 1866). The intestines of one individual measured 54.2 m (Eschricht 1866). The reniculi of the kidneys are arranged in units of four that are contiguous therein (Cave 1977). The renicular venous drainage is intrarenicular, with no peripheral venous plexus (Cave 1977). The nasal diverticulae and associated facial musculature are similar to these features in other delphinids except some structures seemed proportionately smaller (Mead 1975). The melon is also relatively small in *O. orca* (Mead 1975).

The brain of *Orcinus*, like those of other odontocete whales, has highly convoluted cerebral hemispheres and lacks olfactory bulbs or olfactory nerves. The width of the brain exceeds its length and the corpus callosum is small relative to the huge size of the brain (Ridgway 1986). Of the cranial nerves, the eighth is the largest, with a particularly well developed auditory component. Ridgway and Brownson (1984) estimated the average brain mass of 5,617 ± 968 g from killer whales averaging 5.5 m in length.

2.1.2. Taxonomy—Genus and Species: *Orcinus Orca* (Linnaeus, 1758)

The killer whale is the largest species within the family Delphinidae. The genus *Orcinus* has been placed in the subfamily Orcininae or Globicephalinae by several taxonomists. This taxon is inconsistent in its membership and may include *Orcinus*, *Pseudorca*, *Globicephala*, *Orcaella*, and *Feresa* (Slijper 1936, Fraser and Purves 1960, Mead 1975) or only *Pseudorca* and *Orcinus* (Kasuya 1973). A cladistic analysis of the myoglobin amino acid sequence indicates that *O. orca* is more similar to *Globicephala melas* than to *Stenella attenuata*, *Delphinus delphis*, or *Tursiops truncatus* (Meuth et al. 1981).

Various scientific names have been assigned to the killer whale (Hershkovitz 1966, Heyning and Dahlheim 1988). These various names can be explained by sexual and age differences in the size of the dorsal fin, individual variations in color patterns, and the cosmopolitan distribution of the animals. The genus *Orcinus* is currently considered monotypic with geographical variation noted in size and pigmentation patterns (Heyning and Dahlheim 1988). Two recently proposed Antarctic species, *O. nanus* (Mikhalev et al. 1981) and *O. glacialis* (Berzin and Vladimirov 1982, 1983), both appear to refer to the same type of smaller individuals. The data presented to support a new species indicate modal differences in several aspects of morphology and ecology. Of the smaller type (referred to as "yellows" because of their diatomaceous algae covering), 98.5% of 629 stomachs contained fish. In contrast, of 156 stomachs examined of the normal type killer whales, 89.7% contained marine mammals. Unfortunately, sample sizes were not given for the length frequency distributions that revealed large modal differences and also suggested different ages at maturity. Detailed measurements were made of only 3 males and 3 females. Hence at this time these new taxa have not yet been widely accepted by the scientific community. Recent genetic investigations note marked

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differences between the resident and transient form of killer whale (Hoelzel and Dover 1991, Hoelzel et al. 1998, Barrett-Lennard 2000, Barrett-Lennard and Ellis 2001). In addition, smaller genetic differences were shown between Southern Resident killer whales and Northern Resident whales (Hoelzel et al. 1998, Barrett-Lennard 2000, Barrett-Lennard and Ellis 2001). A worldwide review of specimens is needed to document geographical variation in morphology.

Numerous large delphinoid teeth, primarily from the Pliocene, have been attributed to species within the genus *Orcinus*. Such teeth have been reported from the Pliocene of Italy (Sarra 1933) and Japan (Matsumoto 1937). One of the few fossils represented by a good skull is *O. citoniensis* (Capellini 1883) from the Pliocene of Italy. It appears to be a smaller species than *O. orca* with an estimated total length of less than 4 m. *Orcinus citoniensis* has a slightly higher tooth count (14/14) and proportionately smaller teeth than the extant species. In these characteristics, *O. citoniensis* seems to be intermediate between the more typical delphinids and *O. orca* (Pilleri and Pilleri 1982).

2.1.3. Global Distribution

Killer whales are the world's most widely distributed marine mammal (Leatherwood and Dahlheim 1978, Heyning and Dahlheim 1988). Although observed in tropical waters and the open sea, they are most abundant in coastal habitats and high latitudes. Whales inhabiting coastal areas often enter shallow bays, estuaries, and river mouths (Leatherwood et al. 1976). Killer whales occur throughout the Pacific Ocean and have been documented as far north as the Chukchi and Beaufort Seas in the Arctic Ocean (Lowry et al. 1987). In the northeastern Pacific Ocean, killer whales occur in the eastern Bering Sea (Braham and Dahlheim 1982) and are frequently observed near the Aleutian Islands (Scammon 1874, Murie 1959, Waite et al. 2001). They reportedly occur year-round in the waters of southeastern Alaska (Scheffer 1967) and the intracoastal waterways of British Columbia and Washington State (Balcomb and Goebel 1976, Bigg et al. 1987, Osborne et al. 1988). There are occasional reports of killer whales along the coasts of Washington, Oregon, and California (see Table 1) (Norris and Prescott 1961, Fiscus and Niggol 1965, Rice 1968, Gilmore 1976, Black et al. 1997), both coasts of Baja California (Dahlheim et al. 1982), the offshore tropical Pacific (Dahlheim et al. 1982), the Gulf of Panama, and the Galapagos Islands. In the western North Pacific, killer whales occur frequently along the Soviet coast in the Bering Sea, the Sea of Okhotsk, the Sea of Japan, and along the eastern side of Sakhalin and the Kuril Islands (Tomlin 1957). There are numerous accounts of their occurrence off China (Wang 1985) and Japan (Nishiwaki and Handa 1958, Kasuya 1971, Ohsumi 1975). Data from the central Pacific are scarce. They have been reported off Hawaii, but do not appear to be abundant in these waters (Tomich 1986). The current stock assessment report for killer whales in Hawaii indicated that no killer whales were observed during surveys conducted from 1993 to 1998.

Killer whales are also widely distributed in the North Atlantic Ocean (Hammond and Lockyer 1988, Reeves and Mitchell 1988a). Killer whales are noted off Greenland (Heide-Jörgensen 1988), Iceland (Sigurjónsson et al. 1988), and in the Barents and White Seas (Tomlin 1957). Many records document their presence off Norway (Christensen 1988, Lien et al. 1988a, Lyrholm 1988, Oien 1988), the Faroe Islands (Bloch and Lockyer 1988), Great Britain and Ireland (Evans 1988), Denmark, Holland, Belgium, and France. Reports from the Mediterranean are sparse (McBrearty et al. 1986). Records are available from Western Africa (Cadenat 1959).

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Table 1. Summary of known sightings of Southern Resident killer whales along the outer Pacific Ocean coast. Also listed are known sightings of Southern Resident killer whales in "winter" (December-April) in the inside waters of British Columbia and Washington (the Strait of Juan de Fuca and east).*

Date	Location	Identification	Source	Comments
British Columbia outer coast				
Summer and fall	Tofino/Barkley Sound area	L pod	J. Ford, PBS/DFO	Multiple sightings made in summer and fall
Sept. 4, 1997	Off Carmanah Point	L pod	Observed by P. Gearin, NMML	Identified by D. Ellifret
Oct. 21, 1987	Coal Harbor, north Vancouver Island	Part of L pod	J. Ford, PBS/DFO	Were way up inlet a long distance from open ocean
Jan. 31, 1982	Barkley Sound, west coast of Vancouver Island	L pod	Ford et al. 2000 and J. Ford, PBS/DFO	Off shore of Sound
May 3, 1989	Tofino, west coast of Vancouver Island	K pod	WMSA	
June 1995	Queen Charlotte Islands	Southern Resident haplotype	J. Ford, PBS/DFO	Carcass found on beach, ID only by genetics
Washington outer coast				
Sept. 20, 1996	Off Sand Point	L pod	Observed by P. Gearin, NMML	Identified by D. Ellifret
Sept. 13, 1989	Off Cape Flattery	L pod	Calambokidis	Photos were sent to Balcomb
Mar. 17, 1996	Grays Harbor	L pod	R. Osborne, WMSA	2 mi. off outer coast
Apr. 4, 1986	Westport/Grays Harbor	L pod	Bigg et al. 1990 and J. Ford, PBS/DFO	
Oregon				
Mar. 2000 (week of 20th)	Yaquina Bay	L pod	J. Ford, PBS/DFO	
Apr. 1999	Depoe Bay	L pod	J. Ford, PBS/DFO	

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Table 1. Continued. Summary of known sightings of Southern Resident killer whales along the outer Pacific Ocean coast. Also listed are known sightings of Southern Resident killer whales in "winter" (December-April) in the inside waters of British Columbia and Washington (the Strait of Juan de Fuca and east).*

Date	Location	Identification	Source	Comments
California				
Jan. 2000	Monterey	K and L pods	Nancy Black	Seen and photographed feeding on fish (chinook?)
Inside waters of Washington and British Columbia				
Feb. 1, 1976	Beecher Bay, BC, Strait of Juan de Fuca, 10 mi. west of Victoria, BC	K and L pods	J. Ford, PBS/DFO	
Feb. 3, 1982	Victoria, BC	K and L pods	J. Ford, PBS/DFO	Off Victoria
Feb. 26, 1975	Chatham Point, BC, central east coast Vancouver Island	L pod	J. Ford, PBS/DFO	
Apr. 17, 1976	Victoria, BC	K and L pods	J. Ford, PBS/DFO	Off Victoria
Possible Southern Resident sightings on outer coast				
July 20, 2000	14 mi. west of Ucluelet, west coast Vancouver Island	50+ whales	R. Osborne, WMSA	No Southern Residents were known to be in inland waters at the time
July 26, 2001	Off La Push, WA	10-20 whales	R. Osborne, WMSA	Possible Southern Resident
July 29, 2001	Off Cape Flattery, WA	20-30 whales	R. Osborne, WMSA	
Aug. 15, 1994	10-20 mi. off Westport, WA	3-5 whales	R. Osborne, WMSA	Photos taken
Apr. 11, 1997	Mouth of the Columbia River	Large pod	R. Osborne, WMSA	
Apr. 18, 1997	Off La Push, WA	18 Whales	R. Osborne, WMSA	

*Observations are from a variety of sources. PBS/DFO is the Pacific Biological Station, Dept. Fisheries and Oceans Canada, Nanaimo, BC. NMML is the AFSC's National Marine Mammal Laboratory, Seattle, WA. WMSA is the Whale Museum (Friday Harbor, WA) Sighting Archives, 1978–2001.

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In the western North Atlantic, their occurrence has been recorded off Baffin Island and in Lancaster Sound (Sergeant and Fisher 1957, Reeves and Mitchell 1988b), and south along the eastern coasts of Canada and the United States (Katona et al. 1988, Lien et al. 1988b, Mitchell and Reeves 1988). They occur in the Gulf of Mexico, but are considered uncommon (Caldwell et al. 1956). Reports from Florida (Moore 1953), the West Indies, the Bahamas (Backus 1961), and St. Vincent are noted.

2.1.4. Regional and Global Nomenclature of Killer Whales

Killer whales in the Northeast Pacific have been classified into resident, transient, and offshore whales. The three forms vary in morphology, ecology, behavior, and genetic characteristics (see also subsections 2.1.1, 2.1.5, and 2.2). The BRT discussed many groupings of killer whale communities and forms that might constitute either a DPS or a taxon (species or subspecies; see subsection 3.2.2). The descriptions of each population unit (i.e., resident, transient, and offshore) are provided in the following subsections.

Resident killer whales

Resident killer whales in the eastern North Pacific are noticeably different from both the transient and offshore forms. The dorsal fin of resident whales is rounded at the tip and falcate. Resident whales have a variety of saddle patch pigmentations with five different patterns recognized (Baird and Stacey 1988a). Resident whales occur in large, stable pods with membership ranging from 10 to approximately 60 whales. Their presence has been noted in the waters from California to Alaska. The primary prey of resident whales is fish. A recent summary of the differences between resident and transient forms is found in Baird (2000).

Resident killer whales in the North Pacific consist of the following groups: Southern, Northern, Southern Alaska, Western Alaska, and Western North Pacific Residents (see Figure 1). Under the MMPA, residents are separated into two stocks, the eastern North Pacific southern resident stock, which is the petitioned unit, and the eastern North Pacific northern resident stock, which includes the Northern (British Columbia) Residents, the Southern Alaska Residents and the Western Alaska Residents. However, because the BRT generally did not use the MMPA stock names during their deliberations, the descriptions of the groups used are provided here.

Southern Residents—The Southern Resident killer whale assemblage, considered a “stock” under the MMPA, contains three pods: J pod, K pod, and L pod. Their home range during the spring, summer, and fall includes the inland waterways of Puget Sound, the Strait of Juan de Fuca, and the Strait of Georgia (Figure 1). Their occurrence in the coastal waters off Washington, Vancouver Island, and more recently off the coast of central California has been documented. Little is known about the winter movements and range of the Southern Resident community. Southern Residents have not been seen to associate with other resident whales. Genetic studies suggest reproductive isolation between Southern and Northern Resident killer whale stocks (Hoelzel et al. 1998, Barrett-Lennard 2000, Barrett-Lennard and Ellis 2001).

Northern Residents—The Northern Resident killer whales assemblage contains approximately 16 pods. They range from the Strait of Georgia to southeast Alaska (Figure 1) (Ford et al. 1994, Dahlheim 1997). On occasion they have been known to occur in Haro Strait, British Columbia.

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Although some overlap in range occurs between the Northern and Southern Residents, no intermixing of pods has been noted. However, off southeast Alaska, Northern Resident whales are known to associate with Southern Alaska Residents (Dahlheim et al. 1997) and there may be some gene flow between the two populations (Hoelzel et al. 1998, Barrett-Lennard 2000, Barrett-Lennard and Ellis 2001).

Alaska Residents—There are two groups of Alaska Resident animals: Southern Alaska Residents and Western Alaska Residents. These are described as follows.

Southern Alaska Residents—The resident whales of southeast Alaska and Prince William Sound comprise the Southern Alaska Resident killer whale assemblage. At least 15 pods have been identified in these two regions (Figure 1). Resident killer whales photographed in southeast Alaska travel frequently to Prince William Sound and intermix with all the resident groups from this area (Dahlheim et al. 1997, Matkin and Saulitis 1997). Prince William Sound Resident whales have not been seen in southeast Alaska, but have been noted off Kodiak Island intermixing with other, yet unnamed resident pods (Dahlheim 1997, NMML unpubl. data).

Western Alaska Residents—There are 241 killer whales photographed in western Alaska that have been provisionally identified as residents, but the number of pods represented is unknown (NMML unpubl. data). Recent vessel surveys in the southeastern Bering Sea have provided preliminary estimates of approximately 400 killer whales (Waite et al. 2001). Although it is not yet known how many of these animals are residents, the survey does document that killer whales occur both nearshore and offshore in the Bering Sea.

Western North Pacific Residents—Resident killer whales co-occur with salmon along the coasts of Washington, British Columbia, and Alaska. If this pattern is assumed to continue (or used to continue) further to the west, then resident killer whales might be expected to occur also along the coastline of Russia and Japan. Although there is documentation of killer whales in these areas, little is known about whether they are more similar to resident, transient, or offshore types.

Transient killer whales

Several important differences between transient and resident killer whales have most recently been summarized in Baird (2000). The dorsal fin of transient whales tends to be more erect (i.e., straighter at the tip) than that of resident and offshore whales. Saddle patch pigmentation of transient killer whales is restricted to three patterns (Baird and Stacey 1988a). Pod structure is small (i.e., <10 whales) and dynamic in nature. Transient whales occur throughout the Northeast Pacific, with a preference toward coastal waters. Their geographical range overlaps that of the resident and offshore whales. Individual transient killer whales have been documented to move great distances while in pursuit of prey, reflecting a large home range (Goley and Straley 1994, NMML unpubl. data). The primary prey of transient killer whales is other marine mammals. Transient whales do not intermingle with resident or offshore whales. Significant genetic differences occur among resident, transient, and offshore killer whales (Stevens et al. 1989, Hoelzel and Dover 1991, Hoelzel et al. 1998, Barrett-Lennard 2000, Barrett-Lennard and Ellis 2001). At this time, only one stock of transient killer whales is recognized in Northeast Pacific waters, although recent genetic investigations indicate that up to

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three genetically different groups of transient killer whales exist in the Northeast Pacific: the West Coast Transients, the Gulf of Alaska Transients, and AT1 pod (Barrett-Lennard 2000, Barrett-Lennard and Ellis 2001).

Offshore killer whales

Offshore killer whales are poorly understood. Morphologically they are similar to resident whales (i.e., their dorsal fins appear to be more rounded at the tip). Most saddle patches appear to be closed (NMML unpubl. data). Offshore whales have been seen in groups ranging from 10 to 70 whales. They are known to range from central coastal Mexico to Alaska and occur in both coastal and offshore waters (e.g., 500 km off Washington State). Their main target while foraging is assumed to be fish, but observational data on feeding events are extremely limited. Offshore whales are not known to intermingle with resident or transient whales. Genetic analysis suggests that offshores may be reproductively isolated, but they do appear to be more closely related to the Southern Residents than to Northern Residents (Hoelzel et al. 1998).

2.1.5. Feeding Ecology and Food Requirements

Killer whales are classified as top predators in the food chain and, from a global perspective, their diets vary regionally and seasonally (Heyning and Dahlheim 1988). The type of prey consumed depends considerably on the form of killer whale. Resident whales feed primarily on fish (Ford et al. 1998), transient whales forage primarily on marine mammals (Baird 2000), and offshore whales are thought to consume fish. A complete list of prey consumed by killer whales is provided in Jefferson et al. (1991).

Dietary habits of North Pacific killer whales are based primarily on observational data (e.g., killer whale occurrence during fish runs, collection of fish scales at the surface when whales are present). Killer whales from the North Pacific are reported to consume a wide variety of prey items including squid, fish, birds, turtles, and marine mammals (Dahlheim and Heyning 1999). A comparison of foraging strategies of Northeast Pacific resident and transient whales is presented by Felleman et al. (1991). Resident killer whales in Northeast Pacific waters frequent regions of high relief topography along salmon migration routes, whereas transient whales forage for pinnipeds in shallow, protected waters (Heimlich-Boran 1988, Saulitis et al. 2000). When foraging for cetaceans, transients employ a more offshore foraging strategy (Baird and Stacey 1988b).

Sergeant (1969) reported that killer whales maintained in captivity consumed an equivalent of 4% of their body weight daily. Food consumption of a female killer whale held in captivity for 11 years is summarized in Kastelein and Vaughan (1989). Kriete (1995) stated that, in general, immature killer whales require 85,000 kcal per day, juveniles 100,000 kcal per day, adult females 160,000 kcal per day, and adult males 200,000 kcal per day. Based on these values, Osborne estimated that each whale would thus need to consume approximately 25 adult salmon per day to maintain energetic requirements, so the Southern Resident whale population would require 800,000 adult salmon annually to maintain current numbers and metabolic rates (unpubl. data).

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2.1.6. Diving Behavior

The oxygen capacity of the blood is reported to be moderate for cetaceans (Lenfant 1969), suggesting that killer whales may not be deep divers. For example, killer whales trained by Bowers and Henderson (1972) did not prove to be deep divers compared to pilot whales (*Globicephala macrorhynchus*). However, the oxygen carrying capacity of the blood may vary among killer whale pods (D. A. Duffield[3]) and this oxygen capacity may affect diving ability (Ridgway and Johnston 1966).

Norris and Prescott (1961) stated that, in general, killer whales took three to five short dives of 10 to 35 seconds duration followed by a longer dive lasting l to 4 minutes. Erickson (1978), summarizing data collected from two radio-tagged transient killer whales, reported a mean dive cycle of 5.77 minutes. The cycle consisted of a long dive followed by three or four surface blows of 3 to 4 seconds spaced a mean of 21 seconds apart. The longest recorded dive was 17 minutes. Respiration rates have been shown to vary depending on whale activity level (Ford 1989). The maximum recorded dive depth of a trained killer whale was 260 m (Bowers and Henderson 1972). Swimming speeds usually are 6 to 10 km per hour with a maximum of 40 km per hour (Lang 1966).

Southern Resident whales remain underwater 95% of their time, with 90% spent between the surface and a depth of 20 m, although they dive regularly to depths of 200 m (Baird et al. 1998, Baird unpubl. data). Although Southern Residents make about two dives per hour at depths greater than 50 m, they spend less than 2.5% of their time at these greater depths.

2.1.7. Social Behavior

Resident killer whales are members of the only mammalian population in which no dispersal of either sex has been recorded (Baird 2000). Recent events indicate that dispersal may occur (see subsection 1.4); however, the significance of these events to our understanding of dispersal of killer whales is not yet understood.

Pod structure

Studies addressing killer whale social structure were initiated by Michael Bigg in 1973. Based on field observations and photographs collected from 1973 to 1987, Bigg et al. (1990) examined the social organization and genealogy of resident killer whales in the coastal waters of British Columbia and Washington State (Northern and Southern Resident whales). The authors classified the social organization of resident whales into communities, pods, subpods, and matrilineal groups. They defined these terms as follows: a community is composed of individuals that share a common range and are associated with one another; a pod is a group of individuals within a community that travel together the majority of time; a subpod is a group of individuals that temporarily fragment from its pod to travel separately; and a matrilineal group consists of individuals within a subpod that travel in very close proximity. Matrilineal groups are the basic unit of social organization and consist of whales from two or three generations.

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[3] D. A. Duffield, Dept. Biology, Portland State Univ., PO Box 751, Portland, OR 97207. Pers. Commun., 1986.

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Membership at each group level is typically stable for resident whales except for births and deaths.

Breeding

Mating and calving seasons often span several months. Breeding cycles do not seem to be synchronized worldwide, but synchronization may occur within restricted areas. In the Northeast Atlantic, mating reportedly occurs from late autumn to midwinter (Jonsgård and Lyshoel 1970). In the western North Pacific, most mating is suspected to occur between May and July (Nishiwaki 1972). In Washington State and British Columbia waters (Northern and Southern Resident stocks), most births occur between October and March (Olesiuk et al. 1990), indicating a mating season from May to September. Killer whales are polygamous, with most males mating with females outside their home pod.

Reproductive physiology—At sexual maturity, the length of males ranges from 5.2 to 6.2 m (Perrin and Reilly 1984) and their age generally ranges between 10 and 15 years. One male in captivity became sexually mature at an estimated age of 16 (Duffield and Miller 1988). Harrison et al. (1972) determined that an individual 6.56 m in length, with testis masses of 3,632 g (L) and 2,270 g (R), was not mature, whereas a different animal 7.24 m in length with 11,400 g (L) and 12,200 g (R) testes was sexually mature. An investigation of 57 mature males from the Antarctic indicated an average testis mass of 10,000 g and a maximum mass of 23,100 g (Mikhalev et al. 1981).

Females attain sexual maturity between 4.6 and 5.4 m (Perrin and Reilly 1984). Some of this variation in size at maturity is geographic, with animals from the northeastern Atlantic maturing at the low end of the size range and Antarctic animals at the high end (Perrin and Reilly 1984). Ovaries from mature Antarctic killer whales were reported to average about 10 to 12 cm in length by 5 to 7 cm in width (Mikhalev et al. 1981). A female with a 91 cm fetus had a corpus luteum measuring 7.6 by 5.1 cm (Turner 1872). A study conducted by Walker et al. (1988) provides the first description of reproductive hormone profiles in captive whales during ovarian cycles and pregnancy. Off British Columbia and Washington State, female resident killer whales gave birth to their first viable calves at approximately 15 years old (Olesiuk et al. 1990).

Of the mature females taken by Norwegian whalers, 37.3% were pregnant (Christensen 1984), which calculates to an annual pregnancy rate of 26.3% based on a 517 day (17 month) gestation. Data from Soviet whaling in the Southern Hemisphere indicates that 27.5% of mature females were pregnant, yielding an annual pregnancy rate of 19.2%. Based on an average calving interval of 5.32 years for reproductive females in British Columbia and Washington State (Olesiuk et al. 1990), an annual pregnancy rate of 18.8% can be calculated, although this figure does not include all mature females. It is not known whether this lower annual pregnancy rate actually represents a lower rate than for other populations or if the calculation is compromised by not including all mature female animals in the population.

Observational data from British Columbia and Washington State (Northern and Southern Resident whales) show a sex composition of 19 to 24% adult males and 29 to 33% adult females (Olesiuk et al. 1990). Of the mature females in this region, only one-half to two-thirds were observed to give birth during the 15-year study period (Olesiuk et al. 1990). The

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nonreproductive females have been termed either "post-reproductive females" (Olesiuk et al. 1990) or "barren females" (Heimlich-Boran 1986). These barren females seem to exhibit relatively high levels of allomaternal behavior, which may be related to either a social hierarchy or kinship (Haenel 1986, Heimlich-Boran 1986).

Birth, growth, and development of calves—Based on progesterone levels, gestation is estimated at 517 days (Asper et al. 1988). Detailed embryological and placental morphology of *O. orca* has been described for several fetuses (Turner 1872, Guldberg and Nansen 1894, Benirschke and Cornell 1987). The maximum size of fetuses differs regionally and has been documented as 255 cm for the North Atlantic (Perrin and Reilly 1984), 274 cm for the North Pacific (Nishiwaki and Handa 1958), and 250 cm for the Antarctic (Mikhalev et al. 1981). The smallest neonates recorded are 183 cm for the North Atlantic, 228 cm for the North Pacific, and 220 cm for the Antarctic (Perrin and Reilly 1984). Average size of Northeast Pacific calves is 2,360 cm (Heyning and Dahlheim 1988). Duffield and Miller (1988) provide a listing of killer whales born in captivity. Sex ratios at birth are probably 1:1.

Asper et al. (1988) carried out a study on the development of a captive killer whale calf. They reported that tooth eruption of the upper teeth began at approximately 10 weeks, and that the animal began to eat fish at 11 weeks. At 5 months, the calf was eating 6.6 kg per day of smelt; at 15 months, the calf was eating 22 kg per day of herring and squid. Nursing ceased at 18 months. Heyning (1988) indicates that killer whales may begin eating solid food at a younger age than most delphinids.

Parental and pod care of young—The nurturing and development of the calf takes place primarily within its mother's pod. Calf dependency in the wild has been reported by Balcomb et al. (1979) to last at least 2 years. Caregiving is well documented (Caldwell and Caldwell 1966). Waite (unpubl. data) describes alloparental care (an animal showing parental behavior toward young that are not its own) in killer whales, mostly performed by adolescent females. Nonreproductive females and males were also observed to alloparent and adult bulls have been observed to "baby-sit" groups of calves and juveniles (Osborne et al. 1988).

2.2. Genetics of Killer Whales

Two types of genetic data have been collected for killer whales that have proven useful for identifying DPS boundaries: microsatellite (nuclear) DNA and mitochondrial DNA (mtDNA). Each type of genetic data offers a unique and valuable perspective on the ecology and evolutionary history of killer whales. Understanding the strengths, limitations, and unique characteristics of each data type is necessary to interpret these data. A brief introduction to these types follows.

2.2.1. Introduction to the Interpretation of Genetic Data

Because obtaining direct data on population discreteness for marine species is often impossible, genetic data are often used to quantify differences between populations and to infer the evolutionary processes that gave rise to those differences. Reproductive isolation gives rise to genetic differences at both microsatellite DNA and mtDNA loci. In general, the longer

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populations are reproductively isolated, the more their gene frequencies change. This process, called genetic drift, occurs more rapidly in small populations than in large populations. (See the last paragraph in this subsection for a discussion of effective population size.) Genetic drift and migration act in opposition. Genetic drift within isolated populations makes populations genetically different, whereas migration between populations makes populations genetically similar. Additionally, if populations are isolated, mutations will eventually produce unique DNA sequences in each population.

Both mtDNA and microsatellite DNA data are usually assumed to be selectively neutral. This means that the specific genetic sequence found in each individual should not affect the fitness of the individual and that natural selection should not influence the gene frequencies within populations. Therefore, genetic differences between populations at microsatellite DNA and mtDNA loci only indicate that those populations have been isolated from each other. Despite this isolation, the populations may be very similar for genes that affect fitness. This makes evaluating the biological significance of genetic differences between populations difficult.

The most important difference between mtDNA and microsatellite DNA relevant to inferring the evolutionary history of killer whales is that mtDNA is inherited maternally. Mothers give their mtDNA haplotype to all their offspring (males and females). In many cetaceans, migratory routes and feeding habits are learned from the mother (Clapham 1996). Thus, animals using different feeding grounds can have different mtDNA frequencies or even fixed differences, even though animals from those feeding grounds use a single breeding ground. Further, any male that disperses into a matrilineal group would be immediately apparent because he carries a different mtDNA haplotype. However, he will not pass that haplotype on to his offspring. Thus, mtDNA can be used to detect male-mediated dispersal if the male remains in his new population. In contrast, the genetic composition of populations at microsatellite DNA loci reflects the ecology and evolutionary history of both male and female individuals. For evolutionary differences to develop, gene flow would be expected to be low for both mtDNA and nuclear DNA.

Another genetic phenomenon that may be important to interpreting killer whale genetics is called "lineage sorting." Imagine that there is a large population that has lived in an ocean basin for many thousands of generations. This population would contain many haplotypes, which can be thought of as family names. Some names will be old and some new and these names may differ by many letters. If new populations are created from the large old population, there is the possibility that the new populations will contain different frequencies of the names. In contrast, if these new populations are small and drift such that they end up with only a single name (lineage), then interpretation of the relationship of these new populations to one another can be incorrect without understanding the history. For example, if one population ended up with an "old" name and its neighbor ended up with a "new" name, then one could incorrectly infer that they had been separated for a time long enough to develop all the letter changes (mutations) between the names. The correct relationship (that they have been recently founded from a large population) can only be reached by considering lineage sorting.

Many different statistical approaches are used to describe the population structure using genetic data. The most commonly used statistic for quantifying genetic differences between populations at microsatellite loci is F_{ST}. This statistic ranges between zero (when there is no

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population structure) and one (when the populations are so isolated that there is no genetic overlap). Evaluating the evolutionary or biological significance of F_{ST} values is notoriously difficult. There are genetic differences between virtually all populations, and these genetic differences will be detected if sufficient genetic data are collected. The statistical power to detect genetic differences between populations is proportional to the number of alleles at the loci examined, and microsatellite loci usually have enough alleles for a high probability of detecting even modest genetic differences between populations (Hedrick 1999). Therefore, the point estimate of F_{ST} is usually more informative than the statistical test of whether that estimate is significantly greater than zero. However, interpreting these estimates is not easy, because many different evolutionary histories can give rise to the value of F_{ST}. For example, two populations that were separated by glaciers in the last ice age might be no more different than a small population recently founded from a large population by a small number of individuals. In either case, the relevant time scale to describe the accumulation of these genetic differences is measured in generations. This is especially important to keep in mind when considering such a long-lived species as the killer whale. For example, population geneticists may regard 10 generations as an insignificant length of time (for it is not likely to be long enough for natural selection to change a population appreciably), but this is over 200 years for killer whales.

As mentioned above in this subsection, genetic differentiation depends on both the level of gene flow between populations and also on population size. The reason that population size influences genetic differentiation is because small populations tend to drift apart more rapidly (genetic drift), due to chance events in the inheritance of genes. Further, geneticists use a special term, "effective population size," that incorporates differences in mating system and life history. The effective size of populations is less than the census size of populations. Fluctuating population size, skewed sex ratio, and a high variance in reproductive success all decrease effective population size. There has been no formal estimation of effective population size in killer whales. The relationship between census size and effective population size varies widely across species. Although an average effective population size is about 40% of the census size (Frankham 1995), killer whales have an unusual life history that is likely to make their effective population size smaller. For example, both the traits of having many post-reproductive females and having a skewed adult sex ratio will reduce the effective population size relative to the census size.

2.2.2. Microsatellite Genetic Data

Barrett-Lennard (2000) and Barrett-Lennard and Ellis (2001) have presented the most comprehensive microsatellite data on killer whales to date. These data include samples from seven populations: Southern Residents (abundance $N = 78$, sample size $n = 8$), Northern Residents ($N = 214$, $n = 126$), Southern Alaskan Residents ($N > 360$, $n = 82$), Gulf of Alaska Transients ($N > 60$, $n = 8$), West Coast Transients ($N = 219$, $n = 30$), and AT1 Transients from Prince William Sound in Alaska ($N = 11$, $n = 8$). Identities of the Southern Residents sampled for genetics are in Table 2. The data include 11 loci that have an average of 7.8 alleles per locus. This number of loci and amount of genetic diversity is comparable to similar studies in the scientific literature. Over all populations, F_{ST} was estimated to be 0.21, which indicates a substantial amount of genetic differentiation (Table 3). A matrix of pair-wise values of F_{ST}, visualized with multidimensional scaling (Figure 2), shows that resident and transient killer whales in the Northeast Pacific have substantial genetic differences between each form and that

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Table 2. Identities of Southern Resident killer whales sampled for chemical and genetic analyses.[a]

Whale ID	**Sex**	**Age[b]**	**Alive/ dead**	**Sampling method (number = year)**			**Types of analyses[c]**
				Biopsy	***Necropsy***	***Suction cup[d]***	
J1	Male	51	Alive	X			Chemistry (IOS); genetics (LBL?)
J2	Female	90	Alive	X			Chemistry (NWFSC); genetics (RH)
J3	Male	42	Dead	X			Chemistry (IOS); genetics (LBL?)
J4	Female	38	Dead		X (95GE)		?
J6	Male	42	Dead	X			Chemistry (IOS); genetics (LBL?)
J8	Female	69	Alive	X?			Genetics (RH); cytochrome (MM)
J11	Female	30	Alive	X			Chemistry (IOS); genetics (LBL?)
J17	Female	25	Alive			X? (RB)	Genetics (RH)
J18	Male	22	Dead	X	X		Chemistry (IOS; biopsy/necropsy?); genetics (LBL?)
J20	Female	17	Dead	X			Chemistry (IOS); genetics (LBL?)
J26	Male	11	Alive	X?			Genetics (RH)
K1	Male	42	Dead	X			Chemistry (NWFSC); genetics (RH)
K12	Female	30	Alive			X (97RB)	None
K13	Female	30	Alive			X (97RB)	None
K14	Female	25	Alive			X	Genetics (RH)
K21	Male	16	Alive			X	Genetics (RH)
K22	Female	15	Alive			X (97RB)	None
K28	Female	8	Alive			X	Genetics (RH)
K40	Female	39	Alive	X?			Genetics (RH); cytochrome (MM)
L3	Female	52	Alive			X (97RB)	None
L8	Male	23	Dead		X(78MB)		Genetics (RH and LBL?)
L10	Male	43	Dead	X			Chemistry (NWFSC); genetics (RH)
L11	Female	42	Dead	X			Chemistry (NWFSC); genetics (RH)
L14	Male	17	Dead		X(89MB)		Genetics (RH)
L26	Female	46	Alive			X	Genetics (RH)
L27	Female	37	Alive			X? (RB)	Genetics (RH)
L39	Male	25	Dead			X? (RB)	Genetics (RH)

Table 2. Continued. Identities of Southern Resident killer whales sampled for chemical and genetic analyses.[a]

Whale ID	**Sex**	**Age[b]**	**Alive/ dead**	**Sampling Method (number = year)**			**Types of analyses[c]**
				Biopsy	***Necropsy***	***Suction cup[d]***	
L41	Male	25	Alive	X			Chemistry (NWFSC); genetics (RH)
L44	Male	24	Dead			X (97RB)	None
L51	Female	26	Dead		X (99GE)		?
L57	Male	25	Alive	X			Chemistry (NWFSC): genetics (RH)
L58	Male	22	Alive	X? (GE)			?
L60	Female	30	Alive/ dead	X	X		Chemistry (NWFSC; necropsy); genetics (RH & LBL?)
L61	Male	23	Dead	X			Chemistry (NWFSC); genetics (RH)
L66	Female	62	Dead		X (86MB)		Genetics (RH and LBL?)
L67	Female	17	Alive			X? (RB)	Genetics (RH)
L77	Female	15	Alive	X			Chemistry (NWFSC); genetics (RH)
L78	Male	13	Alive			X? (RB)	Genetics (RH)
L79	Male	13	Alive			X	Genetics (RH)
L91	?	7	Alive			X? (RB)	Genetics (RH)
L92	Male	7	Alive	X?			Genetics (RH)
L98	Male	3	Alive	X (GE)			?

[a] Abbreviations: IOS = Institute of Ocean Sciences, Dept. Fisheries and Oceans Canada, Sidney, BC; NWFSC = Northwest Fisheries Science Center, NMFS, NOAA, Seattle, WA; RH = Rus Hoelzel (University of Durham, England); LBL = Lance Barrett-Lennard (Vancouver Public Aquarium); MB = Michael Bigg (deceased – Dept. Fisheries and Oceans Canada); GE = Graeme Ellis (Dept. Fisheries and Oceans Canada); RB = Robin Baird (NOAA); MM = Michael Moore (WHOI); ? = pending confirmation.

[b] Age of whale in 2002.

[c] Samples are being held by individual/agency listed. In some cases, the analyses of the samples have not as yet been completed.

[d] R. Hoelzel suggests that certain whales should be resampled if still alive because DNA was extracted from skin attached to a suction cup and insufficient DNA was obtained. In a few cases, samples are available from both biopsy (whale alive) and then necropsy sampling when the whale was found dead.

Other samples analyzed for genetics not listed in above table: 1) Lolita, female 32-35 years of age, alive in captivity, 2) 11/13/87 calf, 3) 3/26/78 calf, 4) 11/5/76 calf, 5) 10/7/86 neonate.

residents differ most strongly from offshores. The large offshore to resident differences are an interesting result because offshore whales are thought to be fish eaters.

The amount of genetic differentiation between Southern Residents and the nearest resident population (i.e., the Northern Residents) is approximately half the value of the genetic differentiation between residents and transients and approximately twice the amount of genetic differentiation between Northern Residents and their nearest resident neighbors to the north, Southern Alaska Residents. Evaluating the biological significance of the genetic differences between Southern and Northern Residents is difficult. For example, if the Southern Resident population has occupied the Georgia Basin for hundreds (or thousands) of generations at a relatively constant size (perhaps larger than the current size), then these genetic differences indicate low levels of gene flow between Southern and Northern Residents. This scenario would favor evolution of local adaptation. Alternatively, these genetic differences may have arisen from founding of the Southern Resident population from pod fission of the Northern Resident or Southern Alaska Resident population in the more recent past. Under this evolutionary scenario, there would be less of an opportunity for local adaptation. If Southern Residents were founded by pod fission from the Northern Residents, lineage sorting would have had to subsequently remove the Southern Resident haplotype from the Northern Resident population.

An initial inspection of genetic diversity seen in microsatellite data (Barrett-Lennard 2000, Barrett-Lennard and Ellis 2001) indicates Southern Residents have nearly the same number of alleles as Northern Residents (28 vs. 35), despite a much smaller sample size (8 vs. 126). This is consistent with a hypothesis that Southern Residents may have recently been a much larger population. In other words, if Northern Residents can be viewed as representing the expected genetic diversity of populations of their size (214), then Southern Residents may have been a similar size in the recent past. The question of whether the current abundance of Southern Resident whales is “normal” is relevant to considerations of:

- Risk—can a separate population of this small effective size remain extant?
- Ecological role—has the range of Southern Resident whales been recently reduced and did they function as top predators throughout the distribution of their apparent favored prey, chinook and other salmon species?
- Evolutionary legacy—are Southern Resident whales a remnant of residents that specialized in salmon governed by the California Current oceanic system?

2.2.3. Mitochondrial Genetic Data

The first studies using mtDNA sequences revealed strong differences between residents and transients and small but fixed differences between two neighboring resident populations (Hoelzel et al. 1998). Barrett-Lennard (2000) and Barrett-Lennard and Ellis (2001) confirmed and extended these results using a longer mtDNA sequence. Residents and transients had six fixed base pair differences, compared with a single fixed difference found between Southern Residents and Northern Residents. Barrett-Lennard (2000) and Barrett-Lennard and Ellis (2001) never observed more than one haplotype within a pod. To date only two haplotypes have been discovered for residents. The Southern Residents are fixed for one haplotype and the Northern Residents fixed for the other. Southern Alaska Residents are split—the AB-acoustic clan has the Northern Resident haplotype and the AD-acoustic clan has the Southern Resident haplotype.

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Table 3. Estimates of F_{ST} (Weir and Cockerham 1984) for killer whales obtained from 11 microsatellite loci.[a] (Reproduced from Barrett-Lennard 2000.)

	SR	NR	SAR	OFF	WCT	GAT	AT1
SR[b]	-	0.144	0.187	0.321	0.229	0.226	0.429
NR[c]		-	0.076	0.278	0.278	0.251	0.430
SAR[d]			-	0.305	0.259	0.234	0.399
OFF[e]				-	0.153	0.182	0.422
WCT[f]					-	0.065	0.224
GAT[g]						-	0.290
AT1[h]							-

[a] F_{ST} is the most commonly used statistic for quantifying genetic differences between populations at microsatellite loci. Each estimate is statistically different from zero ($p < 0.001$).

[b] Southern Residents

[c] Northern Residents

[d] Southern Alaska Residents

[e] Offshore

[f] West Coast Transients

[g] Gulf of Alaska Transients

[h] AT1 Transients from Prince William Sound, Alaska

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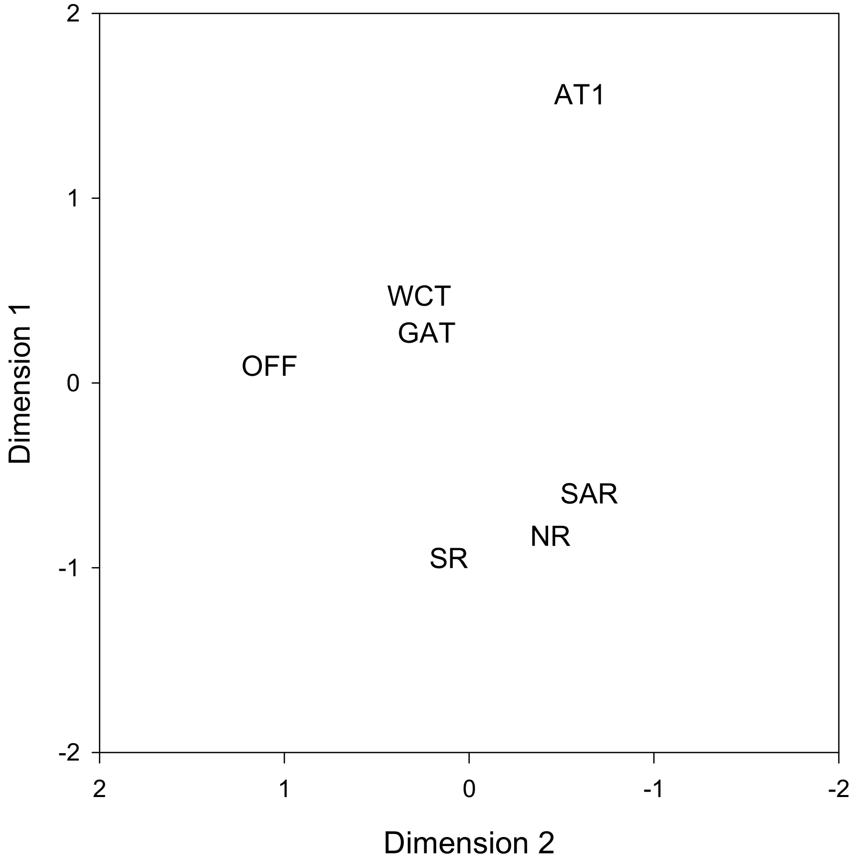

Figure 2. Multidimensional scaling plot of pair-wise F_{ST} estimated from 11 microsatellite loci. (F_{ST} is the most commonly used statistic for quantifying genetic differences between populations at microsatellite loci.) Data was obtained from Table 3. Abbreviations are: SR = Southern Residents, NR = Northern Residents, SAR = Southern Alaska Residents, OFF = Offshore, WCT = West Coast Transients, GAT = Gulf of Alaska Transients, AT1 = AT1 Transients from Prince William Sound, Alaska.

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A maximum likelihood phylogram of killer whale genetics worldwide revealed two strongly differentiated groups: transients and all other populations (residents, offshores, and two samples from the Atlantic). Further unpublished analysis (SWFSC unpubl. data) of killer whales from a wider geographic range (from Alaska through the eastern tropical Pacific and also Antarctica) did not contradict the general idea of residents and transients belonging to separate lineages. However, the dietary preferences of most of the sampled individuals in this latter analysis are unknown. Thus it remains uncertain whether mammal-eating killer whales and fish-eating killer whales have arisen only once or multiple times. The lineage that contains residents and offshores (but no known transients) will subsequently be referred to as the "mtDNA lineage consistent with fish eating."

2.2.4. Morphological Data

It is not possible to know whether Southern Resident killer whales have undergone local genetic adaptation to their range that differentiates them from Northern Residents. If such an adaptation had taken place, one would expect to see strong evidence of discreteness, and depending on the time scale, possibly other evidence of differences in behavior and morphology. The strongest evidence along these lines is a documented difference in morphology: Southern Residents have statistically significant differences in their saddle patch patterns from Northern and Alaska Residents (Baird and Stacey 1988a). Differences in color patterns have often been associated with a strong degree of separation in delphinids, often recognized to be at the species or subspecies level (e.g., species of *Delphinus*, subspecies of *Stenella*). However, these differences in saddle patch pigmentation between Southern Residents and the other resident groups are frequency differences, not fixed differences. Though these differences provide no direct evidence of adaptation, they are at least consistent with the occurrence of local adaptation.

2.2.5. Nuclear DNA, mtDNA, and Morphological Genetic Data

Considered together, the mtDNA, nuclear DNA, and morphological data seem to present different pictures of the genetic discreteness of the various killer whale groups (residents, transients, and offshores). The mtDNA data indicate that offshores and residents are quite closely related and more closely related to each other than either are related to transients. In contrast, the nuclear data show the greatest differences between residents and offshores and much smaller differences between offshores and transients. Some of these results may stem from the very poor sample size for offshores (n = 7); however, these are the only data available to assess relationships between these groups. The genetic data are consistent with a hypothesis that the "parent" of residents is offshores (and hence the close mtDNA signal), but there has been complete or nearly complete reproductive isolation since the "birth" of residents (hence the strong nuclear differentiation).

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2.3. Features and Environmental History of the Northeast Pacific Ocean and Inland Waters of Washington and British Columbia

2.3.1. General Features

The scope of the following summary is restricted to the marine waters of the Pacific Ocean from central California to southeast Alaska, a region spanning approximately 2,000 km. From central California to Washington State, the coastline is generally typified by an abrupt edge with few embayments or islands. Three primary features punctuate this region: the entrance of San Francisco Bay, the mouth of the Columbia River, and the Strait of Juan de Fuca. Although there are numerous small rivers and associated estuaries that drain the coastal mountains of this region, these three main coastline features are notable because they drain large inland watersheds, and as a result, provide significant fresh water inputs to the Pacific Ocean. The Sacramento and San Joaquin Rivers drain the Sierra Nevada Mountains through the Central Valley into San Francisco Bay. The Columbia River drains a large part of Washington, Oregon, Idaho, and British Columbia and contributes the primary source of freshwater input between San Francisco and the Strait of Juan de Fuca (Landry et al. 1989). The Fraser River drains a large portion of British Columbia and empties into the Strait of Georgia.

From Puget Sound north to southeast Alaska, the coastline includes many areas where offshore islands protect inshore waters. Vancouver Island and the Queen Charlotte Islands are located offshore along the continental coast of British Columbia and small islands are located inshore from the larger islands. In southeast Alaska, Prince of Wales Island, Chichigof Island and Baranof Island are the largest islands in the Alexander Archipelago. These islands are located on the outer coast and additional islands exist between these large islands and the continent. The large islands form a barrier between the open ocean and the continent, creating numerous waterways, including Queen Charlotte Strait, Hecate Strait, Dixon Entrance, Sumner Strait, Chatham Strait, and Icy Strait.

2.3.2. Environmental History

Native peoples have inhabited the west coast of North America for several thousand years. Their relatively small populations were widespread throughout this region and consisted of numerous tribes or clans that either lived a subsistence lifestyle or had trade-based economies utilizing local resources on a relatively small scale. Settlement of the U.S. West Coast by Europeans began in the mid-1850s. Early use of this region was characterized by extensive resource extraction, which included mining, timber harvest, agriculture, and fisheries (particularly salmon). Over the ensuing decades, these human activities, as well as damming of major rivers for irrigation and hydropower, have contributed to declines in the availability or quality of habitat, which has affected many regional salmon stocks. For example, the extensive mining activities that occurred in central California and the harvesting of old growth forests on a large scale throughout California, Oregon, Washington, and some regions of British Columbia has led to increased silt formation, which is harmful to young salmon. Extensive damming of the major rivers of California, Oregon, and Washington has provided hydropower that attracted industry throughout the region. In addition, the irrigation provided by dams allowed for extensive development of agriculture in the Central Valley of California and eastern Washington

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and Oregon. Damming of rivers for hydropower and irrigation that began in the 1930s and continued through the 1970s significantly altered the hydrography of many rivers. In addition, significant modifications were made in certain river channels for these agricultural and industrial uses. The impacts of impoundment of water by dams on the Columbia River possibly extends beyond river systems, because the seasonal surface salinities of the Pacific Ocean from California to Alaska have likely been altered (Ebbesmyer and Tangborn 1992). Recent increases in human populations are concentrated in certain areas, including the ports of San Francisco, Portland, Seattle, and Tacoma in the United States and Vancouver in Canada. The major urban centers that have developed around these ports have resulted in severe reductions in wetland areas, which in turn have had an adverse impact on many wildlife and fish species due to reduction of habitat. In addition, the pollution generated by industrial development near these cities has unfavorably impacted the environment. For example, juvenile chinook salmon from an urban estuary in Puget Sound contained elevated concentrations of pollutants (McCain et al. 1990). Finally, large-scale salmon harvesting has occurred throughout these areas and in some cases has had major direct impacts on the stocks.

2.3.3. Geological and Climatic History

The current form of the west coast of North America is due to the downward movement (subduction) of the Juan de Fuca and the more northerly Pacific plates under the North American plate, resulting in the creation of the coastal, Sierra Nevada, and Cascade mountain ranges (Orr and Orr 1996). The Cascades and the surrounding terrain have also been modified by volcanism (Orr and Orr 1996). The terrain north from the southern extent of Puget Sound was extensively modified by the massive glaciation that covered this region 15,000 years ago (Burns 1985).

Climatic history has shaped the environment and habitat of Northeast Pacific Resident killer whales and their prey since the last ice age. The current climate ranges from bordering on Mediterranean-like in central California, through a temperate marine climate from northern California through Vancouver Island, before becoming subarctic near southeast Alaska (Greenland 1998). The region from northern California to southeast Alaska is subjected to heavy precipitation due to the Aleutian low-pressure system during the winter. In contrast, during the summer, subtropical high-pressure systems dominate from northern California to central Vancouver Island.

The climate in this region has likely varied historically on several temporal scales—ranging from long-term climate modifications (e.g., the ice ages) to short-term oscillations (e.g., El Niño). Although no records are available prior to 150 years ago, it is likely the climate was modified during the period of medieval warming that occurred from 1000 to 1300 and the Little Ice Age that occurred between 1300 and 1900, but the degree of variability was likely tempered by the ocean (Greenland 1998). The only certainty about the climate in this region prior to 1000, is that it was considerably cooler during the last major ice age 15,000 years ago. Medium-scale warming and cooling temporal cycles have been reported to occur every 50-70 years (Minobe 1997, Enfield and Mestas-Nuñez 1999, Minobe 1999, 2000) and also every 15-25 years—the latter cycle known as the Pacific Decadal Oscillation (PDO) (Mantua et al. 1997). During this century, cold regimes existed from 1900 to 1924 and from 1947 to 1976, whereas warm regimes occurred from 1925 to 1946 and 1977 to 1997 (Mantua et al. 1997). An additional regime shift may have occurred in 1989 and possibly again in 1998 (Hare and Mantua 2000). A similar type

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of climactic signature is associated with El Niño (Mantua et al. 1997), except this short-term oscillation usually occurs on a 3-7 year timeframe (Barber 1988).

Several salmon species have been known to exist on the Pacific west coast since prehistoric times. The large expanse of the ice sheets 10,000 years ago in this area likely reduced available habitat, and thus the range, of many species of Pacific salmon. Consequently, killer whales that eat salmon were probably not present in this region at that time and their present distribution may have co-evolved with the development of salmon runs since that time.

2.3.4. Geomorphological and Oceanographic Features

Biological productivity varies greatly with particular geomorphological and oceanographic features, such as continental shelf width and ocean currents. The continental shelf along the U.S. West Coast is relatively narrow compared to those in other regions of the world. For example, the shelf (200 m isobath) is only 10-40 km wide off California and gradually widens to 25-60 km off Washington and Oregon (Byrne 1963, McManus 1972). Similar variations in shelf width are found off British Columbia and southeast Alaska. In the nearshore waters, Hecate Strait and Dixon Entrance have relatively deep basins, as do parts of the southern Strait of Georgia and Puget Sound.

Three oceanic domains occur in the Northeast Pacific: 1) the Coastal Upwelling Domain along the west coast of the continental United States and southern British Columbia (Ware and McFarlane 1989); 2) a Coastal Downwelling Domain, extending from Queen Charlotte Sound in British Columbia northward to the Aleutian Islands; and 3) the Central Subarctic Domain that is bounded by the Subarctic Current, the South Alaska Current to the east, and Alaska Current to the north. The primary ocean currents that affect the west coast of North America are the east flowing North Pacific Current and the Subarctic Current (Dodimead et al. 1963). These wind-driven currents originate in the central North Pacific and split near the coast of Vancouver Island to form the Alaska Current flowing north and the California Current flowing south. In summer, upwelling of cold, nutrient-rich water from the subarctic Pacific Ocean occurs along the west coast of the continental United States and southern British Columbia (Parrish et al. 1981). In the winter, the upwelling dissipates and warm, equatorial water from the south flows inshore (Favorite et al. 1976).

Four factors create a latitudinal gradient within the California Current and regulate biological production (Bottom et al. 1998). These factors include: 1) a north-south pattern in the variability of winds, currents, and upwelling (Huyer 1983); 2) a latitudinal cline relative to the proportions of subarctic, transitional, and equatorial species (Chelton et al. 1982); 3) the north-south gradient of freshwater from the Columbia River found along the Oregon coast in the summer (Landry et al. 1989); and 4) the southward decrease in the relative proportion of protected inland bays and estuarine habitat from British Columbia to California (Nickelson and Lichatowich 1984, Bottom et al. 1986).

The oceanographic conditions of inland waters are not influenced by the coastal currents. The oceanographic features of Johnstone Strait and the Strait of Georgia/Haro Strait regions are both classified as homogenous zones (Herlinveaux and Giovando 1969).

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Variability in the ocean conditions also occurs temporally on timeframes that are on the order of decades and centuries and are related to those that occur with climate (see subsection 2.3.3) (NOAA 1994), although the connection may not be a simple one-to-one correspondence (Bottom et al. 1998). For example, during the "warm" regime of the PDO, the coastal sea surface temperatures are anomalously high as far north as Vancouver Island (Mantua et al. 1997). These conditions appear to be unfavorable to west coast Pacific salmon, and although the mechanisms are unclear, it is likely related to a decrease in preferred prey availability (Hare et al. 1999), or an increase in predators, or both.

2.3.5. Marine Species in the Northeast Pacific

The oceanographic domains noted in subsection 2.3.4 also appear to have unique species associated with them, as summarized by Ware and McFarlane (1989). The oceanic (Central Subarctic Domain), continental shelf (Coastal Downwelling Domain), and upwelling (Coastal Upwelling Domain) regions typically have different levels of primary productivity. The oceanic domain typically has the lowest primary productivity and the smallest size of phytoplankton species, whereas the upwelling region typically has the highest production, as well as macrophytoplankton. These domains also appear to have differences in fish species and total biomasses that reflect differences in primary productivity. A notable difference in coastal fish species occurs near the north end of Vancouver Island (Allen and Smith 1988), where the approximate boundary of the coastal upwelling and coastal downwelling zones occurs. The Coastal Upwelling Domain's major fish species include four pelagic (northern anchovy [*Engraulis mordax*], Pacific sardine [*Sardinops sagax*], Pacific hake [*Merluccius productus*], Pacific mackerel [*Scomber japonicus*]) and three non-pelagic (jack mackerel [*Trachurus symmetricus*], Pacific herring [*Clupea pallasii*], and sablefish [*Anoplopoma fimbria*]) species. Both pelagic and demersal fishes dominate the Coastal Downwelling Domain—pelagic species include walleye Pollock (*Theragra chalcogramma*), Pacific herring, chinook salmon, and coho salmon (*Oncorhynchus kisutch*) and demersal species include Pacific halibut (*Hippoclossus stenolepis*), Pacific cod (*Gadus macrocephalus*), and sablefish. The primary species of the Central Subarctic Domain are pink (*O. gorbuscha*), chum (*O. keta*), and sockeye salmon (*O. nerka*) and pomfret (*Brama japonica*), Pacific saury (*Cololabis saira*), albacore tuna (*Thunnus alalunga*), and jack mackerel during summer.

Temporal variability of ocean conditions can influence the distribution and abundance of these species. Primary and secondary production and pelagic species in the California Current have been observed to fluctuate on 40-60 year cycles (Ware and Thomson 1991). The abundance of salmon in the North Pacific Ocean has been shown to follow the long-term fluctuation in the Aleutian low pressure system (Beamish and Bouillon 1993). In particular, salmon appear to be sensitive to decadal regimes (e.g., PDO) (Mantua et al. 1997). Alaska salmon appear to have benefited from the warm regime that existed since 1977, whereas west coast salmon have generally declined during this period (Hare et al. 1999).

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2.4. Ecology of Southern Resident Killer Whales

2.4.1. Current Range and Distribution

The range occupied by Southern Resident killer whales has been determined from opportunistic resightings of photo-identified individuals or from strandings. Southern Resident killer whales use different summer and winter habitats, and the amount of information available to determine the precise extent of their seasonal ranges is very different.

Summer

The summer range of Southern Residents has been fairly well defined based on numerous sightings over the past 27 years (Heimlich-Boran 1988, Osborne unpubl. data). All three Southern Resident pods regularly occur in the waters of the Georgia Basin (the Strait of Georgia, Haro Strait, and the Strait of Juan de Fuca) during late spring, summer, and early fall (Heimlich-Boran 1988, Osborne unpubl. data). Although J pod occurs intermittently throughout the year in this area, K and L pods typically arrive in May or June and, with the exception of forays of a few days, typically remain in the Georgia Basin through October or November (Osborne unpubl. data). During this period, their movements are concentrated primarily in Haro Strait and the Strait of Georgia (Heimlich-Boran 1988, Felleman et al. 1991). There are occasional sightings along the southern outer coast of Vancouver Island in the vicinity of Tofino and Barkley Sound (Table 1). Southern Resident killer whales clearly have a core summer range area that is spatially separate from Northern Resident whales, which predominantly frequent the waters of central and northern British Columbia, and offshore killer whales, which occur along the coast.

Fall, winter, and spring

The range of Southern Residents throughout the rest of the year is not well known. As noted previously, J pod is intermittently observed throughout the Georgia Basin during the rest of the year, but its location during apparent periodic absences is unknown. Even less is known of the movements of K and L pods after they leave the inland waters. Over the 27 years since 1974 that the identities of the individuals of these pods have been known, there have been relatively few verified sightings of these pods in seasons other than summer.

Using information from 1976 to 1997, Osborne (unpubl. data) summarized Southern Resident sighting information from the inland waters of Washington and British Columbia (from the Strait of Juan de Fuca to the east). During the early fall, movements of Southern Residents, particularly J pod, expand to include Puget Sound (Osborne unpubl. data). As the fall progresses, L and K pods are seen less and less frequently in inland waters. These pods are typically observed to exit and enter through the Strait of Juan de Fuca, rather than the Strait of Georgia, suggesting movements in the region of Vancouver Island and Washington State rather than Alaska. There have been a few sightings of L and K pod in September-October along the southern outer coast of Vancouver Island (Table 1). In addition, there was one sighting in late October of L pod near the northwest corner of Vancouver Island, far up an inlet near Coal Harbour. These few sightings verify that Southern Residents, particularly K and L pods, may at least occasionally spend some time along the west coast of Vancouver Island, but due to the very

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limited and opportunistic nature of the sighting effort, it is unclear if the whales spend a substantial portion of their time in these areas or are simply transiting through the area. There has also been one sighting (possibly two) of L pod along the outer Washington coast in fall.

The late fall and winter range of Southern Resident killer whales is poorly understood. From 1976 to 1997, for the 6 months from November to April, K pod was seen in inland waters in 21 of the 132 months and L pod was seen in only 10 of the 132 months (Osborne unpubl. data) (see also Table 1). L pod was seen only four times in inland waters from January through April, and K pod was seen only three times in inland waters during January or February; all these sightings occurred prior to 1983. From January through April, there have been six sightings of L or K pod along the outer coast of North America: one in Canada (along the southern outer coast of Vancouver Island) and five in the continental United States. Four of those six sightings have been during the last 5 years, but it is impossible to know whether this represents a change in distribution pattern or an increased rate of observations along the outer coast.

Bigg et al. (1990) indicated Southern Residents range south to Grays Harbor, Washington, and Ford et al. (2000) found these whales range south to the mouth of the Columbia River, but no details are given regarding dates or pods seen in either case. These assertions are supported by two confirmed sightings of L pod along the southern Washington outer coast, one near Westport and one near Grays Harbor that occurred in 1986 and 1996, respectively (Table 1). Recent sightings have extended the southern limit of their range past Washington. There were two sightings of L pod along the Oregon coast (one in 1999 and one in 2000). In addition, K and L pods were observed together off Monterey Bay, California (Black et al. 2001), in January 2000. The California sighting is noteworthy, not only for the extension of the known maximum range of Southern Residents, but also because K and L pods were thought to be feeding on salmon. These few sightings suggest the potential of an extended range for Southern Residents in coastal waters of the U.S. West Coast.

In the spring, there has been at least one sighting of K pod near Tofino, British Columbia, in May (Table 1). On a few occasions Southern Residents have entered the Strait of Georgia in spring through Johnstone Strait (Ford et al. 2000), implying that they transited the northern end of Vancouver Island. Also, Ford et al. (2000) reported that a carcass of one Southern Resident (identified using genetics) was found in June 1995 on the west coast of the Queen Charlotte Islands and another in May (year unknown) off Cape Scott (J. K. B. Ford[4]), locations well north of any other known sighting of Southern Resident killer whales. However, given that these animals may have been sick prior to death, it may not be valid to assume that the stranding locations reflect normal distribution. As mentioned above, all three pods have generally returned to inland waters by May or June.

The general paucity of sighting data, lack of effort in coastal and offshore areas, and potentially high mobility of this species confounds drawing definitive conclusions about their overall winter range, much less defining areas of core use. Despite this limited information, particularly on the distribution of the animals from October through April, the range of Southern Resident killer whales appears to have limited overlap with the range of the Northern Resident

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[4] J. K. B. Ford, Marine Mammal Research, Pacific Biological Station, Dept. Fisheries and Oceans Canada, 3225 Stephenson Point Rd., Nanaimo, BC V9T 1K3. Pers. commun., 2002.

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killer whale community; the extent of range overlap with the offshore community is unknown (Bigg et al. 1987, Ford et al. 1994, Osborne unpubl. data).

2.4.2. Population Dynamics

Beginning in 1973–74, the Southern and Northern Resident killer whales have been studied by the Center for Whale Research using photo-identification methods (e.g., Hammond et al. 1990). Photographs are taken of a lateral view of a whale's dorsal fin and saddle patch (a light-colored area just posterior and lateral to the dorsal fin). The shape of the dorsal and the coloration pattern of the saddle patch, as well as distinctive scratches, nicks, or other marks, allows individual whales to be identified. In May and June of each year, sufficient photographs are taken to identify essentially every Southern Resident individual, so that the annual survey amounts to a census of the entire population. This census allows a detailed examination of the population dynamics of the Southern Resident community.

Previous studies

Balcomb and Bigg (1986) first estimated the rate of increase of the Southern Residents as 2.6% from 1974 to 1980. Olesiuk et al. (1990) summarized the basic life history of Southern and Northern Residents as follows. Females have a life expectancy of about 50 years and may have a maximum age of 80-90 years. The youngest female to give birth was age 11 and the mean age of first birth was 15. Females produce on average about 5.35 viable calves (calves that survive to their first summer) over a 25-year reproductive lifespan. Males have a life expectancy of about 29 years. Males reach sexual maturity at a mean age of 15 years and reach physical maturity at about 21 years. The populations were composed of 50% juveniles, 19% mature males, 21% reproductive females, and 10% post-reproductive females.

Olesiuk et al. (1990) formed an age-specific life table for the combined Northern and Southern Resident populations, which resulted in an estimated intrinsic rate of growth equal to 1.0292 (2.92% per year). The observed rates of increase were 2.9% (1979–1986) for the northern community, virtually identical to the predicted rate, and 1.3% for the southern community (1974–1987), which was less than half the expected intrinsic rate. This discrepancy was explained by Olesiuk et al. (1990) as being mainly due to: 1) a disproportionate number of females that became post-reproductive just prior to or early in the study (for unclear reasons), and 2) fewer females than expected that became mature during the study because of live-capture removals of juvenile females in the years prior to the study.

Using a stage-structured model, Brault and Caswell (1993) estimated the intrinsic rate of growth of the Southern Residents as 1.025 (2.5%) and the observed rate of increase of females as 0.7%. Looking at only the female component of the population, they did not find a significant departure from stable stage distribution, but provided no explanation for the discrepancy between the observed rate of increase and the estimated intrinsic rate of growth.

Results from new analyses

The Center for Whale Research has continued its annual census of the Southern Resident population. For several reasons, it is appropriate to update the analyses of population dynamics

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of Southern Resident killer whales carried out by Olesiuk et al. (1990). First, annual counts of the total population size now show the population has declined by 20% from 1996 to 2001 (Figure 3). These recent declines raise the possibility that the overall dynamics of the population have changed over the 27-year study. Second, there are now 14 additional years of data since the previous studies (based on data from 1974 to 1987; Olesiuk et al. 1990) that allow a more detailed examination of the population's demography. With a time series of 28 years, it is possible to look for changes in survival and fecundity rates (conditional on the survival of the adult female) over time and between age and sex classes, thus allowing an investigation into demographic factors that may have contributed to the recent decline. The following summary of new results is from Wade (unpubl. data).

Population abundance and trends—In the original 1974 census, the Southern Resident population comprised 71 whales, whereas the most recent census in the summer of 2001 counted 78 whales, which represents an overall annual increase of 0.3% per year. However, the population has fluctuated over the 27 years of the study: increasing from 1974 to 1980 at 2.6% per year, then declining at 2.8% per year until 1984, then increasing again at 2.3% per year until 1996, and finally declining at 4.3% per year through 2001 (Figure 3). On average, there have been 3.0 births and 2.7 mortalities per year.

Estimates of survival—All mammals tend to have differences in survival with age, with relatively low early survival, high adult survival, and declining survival in older individuals (Caughley 1966). Killer whales have been shown to follow this pattern, as well as to exhibit differences in survival between sexes (Olesiuk et al. 1990).

Olesiuk et al. (1990) reported that most births take place from October to March. Newly born whales are not counted until they are seen during the summer field season (typically May and June). The "calf" survival rate estimated here is survival from the first summer to the second summer. For example, calf survival for a 6-month-old calf first seen in June will be survival from 6 to 18 months. Some individual killer whales do not have their sex identified until they are approximately 10 years old, although other individuals are identified at a much earlier age. Therefore, all males, females, and unknown sex whales aged 1-10 were assigned to the "juvenile" age class. Age 10 also provides a useful break point for females, because the youngest female to give birth in this population was age 12, meaning she was sexually mature at age 11. Whales older than age 10 were considered "adult" for this study, even though it is recognized that males do not reach sexual maturity until age 15 on average and may not reach physical maturity until age 20 or greater (Olesiuk et al. 1990). The oldest female to give birth was estimated to be 41 years old. Therefore, females aged 11-41 were placed into a single category "reproductive-age females" and those 42 and older were designated "post-reproductive-age females." However, a few females in this category have not been observed with a calf, so membership in this category does not imply that the animal is reproductively successful. Males aged 11-21 were placed into another category, called "young adult males." The age 21 was chosen as the upper bound because this is the average age at which physical maturity is attained. Males aged 22 and older were designated "old males." Although not stated explicitly, Olesiuk et al. (1990) assumed that there is no social control of reproductive rates.

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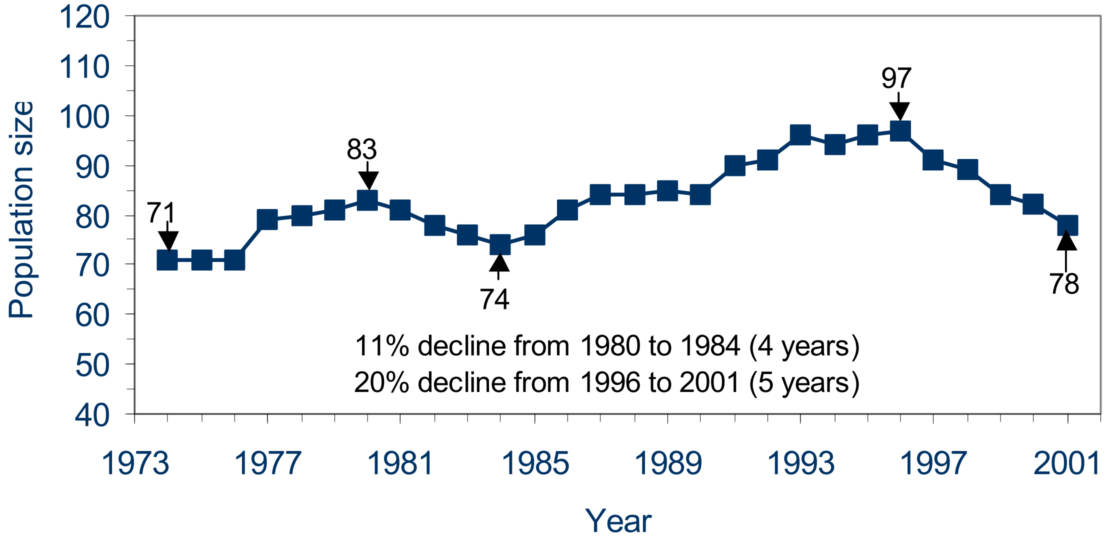

Figure 3. Southern Resident killer whale population size through time.

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Therefore, the six different age and sex classes examined for survival were:

1) calves (age 0, whales seen in their first summer),
2) juveniles (ages 1-10),
3) females (ages 11-41, reproductive-age females),
4) females (ages 42+, post-reproductive-age females),
5) males (ages 11-21, young males), and
6) males (ages 22+, old males).

Survival estimates for each of the six age and sex classes, pooled across the entire period from 1974 to 2001, were calculated. Reproductive-age females had the highest survival rate, followed by juveniles, post-reproductive-age females, and young males (Table 4). Calves and old males had the lowest survival rates.

Annual survival averaged over all age and sex classes (referred to as the "crude" survival rate) has varied between 1.00 (1977, 1990, and 1992) and 0.921 (1998), with an overall mean of 0.969 (Figure 4). Survival was above average from 1974 to 1979, mostly below average from 1980 to 1984, above average from 1985 to 1992, and was below average again from 1993 to 2000 (Figure 4). A simple linear regression of crude survival on year results in a significant decline in survival through time ($p<0.01$), but a linear decline clearly does not provide a good description of the data, as there is a distinct pattern to the residuals.

To better investigate temporal patterns in survival, a variety of crude survival models were proposed and fit to the data: 1) a constant survival rate over time, 2) a trend in survival over the 28 years, 3) periodic fluctuations in survival, 4) a different survival rate for each year, and 5) a different survival rate that remained constant for a specified number of years, using periods from 2 to 12 years in length. The models were compared using Akaike's Information Criterion (AIC), which is based on the maximum likelihood estimates for the parameters. AIC provides a measure of which model fits that data best. The best fitting model for crude survival had constant survival for 6-year periods, starting with a full 6-year period in 1974 (and thus ending with a truncated period of only 3 years) (Figure 5).

Additionally, survival models that were stratified across age and sex categories were also fit to the data. The same temporal survival models (described above) were used with independent survival rates for each age and sex category (a so-called multiplicative model). Where appropriate, some survival models were also compared using so-called additive models, where each age and sex category had identical patterns in survival, but scaled differently for each category. The best model, as selected by AIC, was an additive model with the same temporal pattern selected for crude survival—6-year periods, starting with a full period in 1974 (Table 5, Figure 6). In other words, this model has an identical pattern in survival through time across all age and sex categories, but scaled differently to account for the large differences in mean survival of each category (Table 4). This model had a smaller AIC than the crude survival model and was therefore judged to be the best model overall.

Thus, there are large differences in survival rates of Southern Resident killer whales between different age and sex categories, but there have also been large changes in survival rates through time. These changes have been characterized by periods of relatively constant survival for approximately 6 years, followed by a shift to a different level of survival for the next 6 years, and so on. Survival has shifted from relatively high levels in the 1970s, to low levels in the early

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Table 4. Estimates of annual survival (1974–2000) of Southern Resident killer whales.

Age and sex class	**Estimate**	**Standard error**	**Lower CI***	**Upper CI***
Calves (0)	0.914	0.031	0.830	0.958
Juveniles (1-10)	0.973	0.006	0.957	0.983
Females (11-41)	0.995	0.003	0.986	0.999
Females (42+)	0.956	0.010	0.932	0.972
Males (11-21)	0.962	0.013	0.925	0.981
Males (22+)	0.919	0.019	0.874	0.949

*Confidence interval

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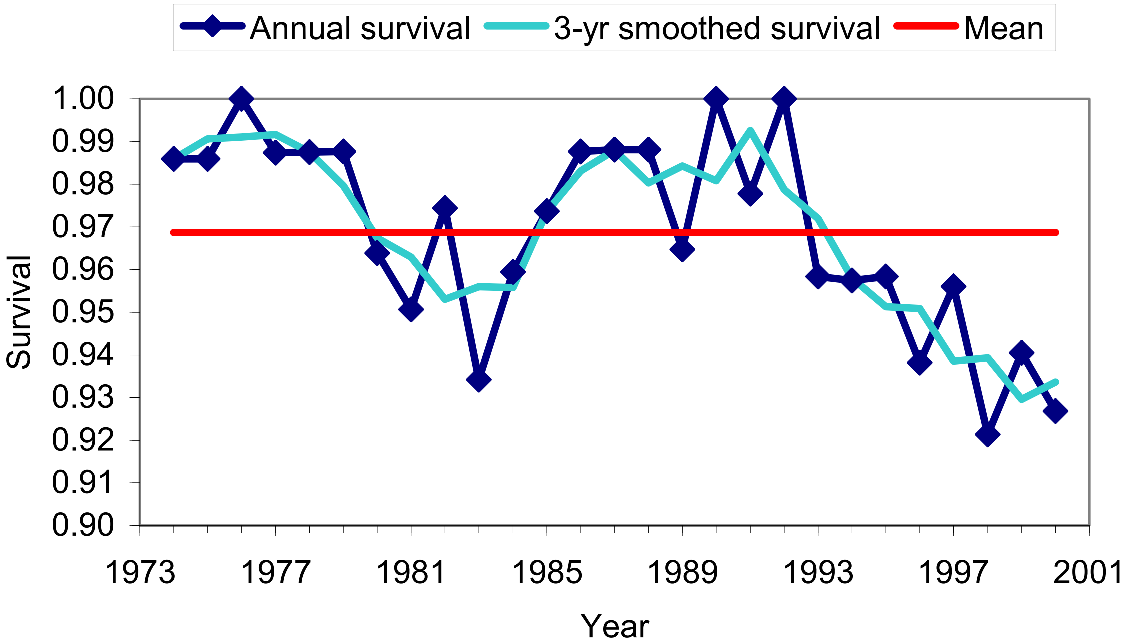

Figure 4. Southern Resident killer whale annual crude survival estimates (diamonds). Also shown are a 3-year running average of annual survival and the mean survival from 1974 to 2000.

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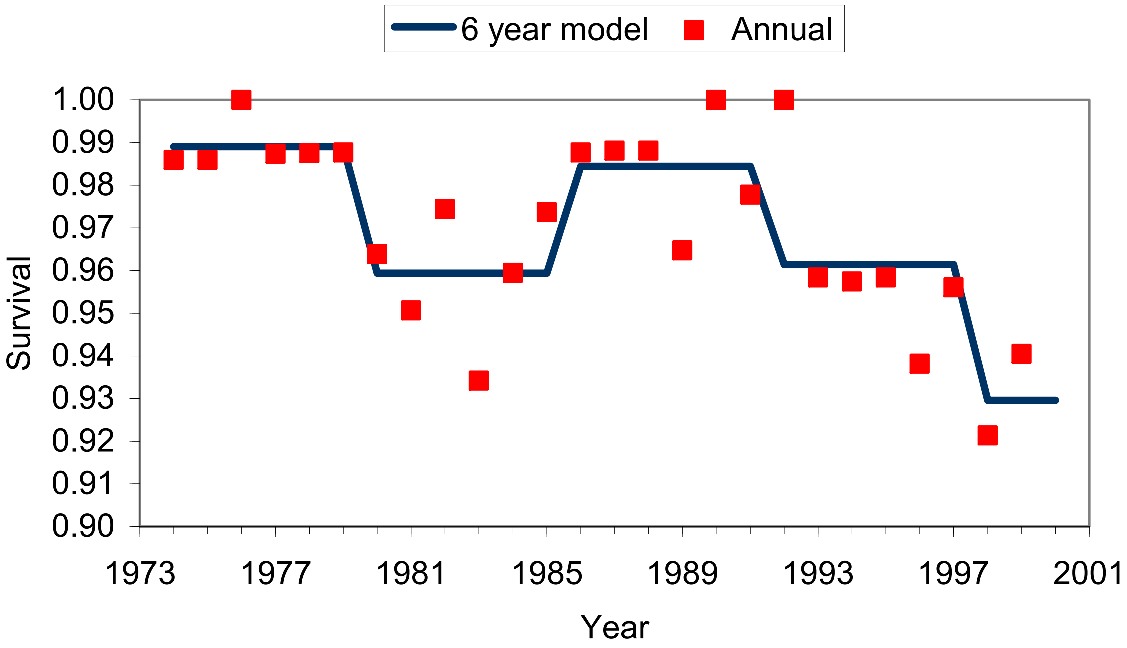

Figure 5. Best fitting model of crude survival (line), 6-year periods of constant survival, starting with a full 6-year period in 1974. Also shown are annual estimates of survival.

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Table 5. Estimates of annual survival from the model that provided the best fit to the data: 6-year periods of constant survival, scaled differently for each age and sex category, starting with a full period in 1974.

Age and sex class	**Years**	**Estimate**	**Standard error**
Calves (0)	1974–79	0.967	0.019
	1980–85	0.886	0.047
	1986–91	0.954	0.023
	1992–97	0.886	0.045
	1998–00	0.785	0.079
Juveniles (1-10)	1974–79	0.992	0.004
	1980–85	0.969	0.010
	1986–91	0.988	0.005
	1992–97	0.969	0.009
	1998–00	0.936	0.019
Females (11-41)	1974–79	0.999	0.001
	1980–85	0.995	0.003
	1986–91	0.998	0.001
	1992–97	0.995	0.003
	1998–00	0.989	0.007
Females (42+)	1974–79	0.985	0.007
	1980–85	0.946	0.016
	1986–91	0.979	0.009
	1992–97	0.946	0.016
	1998–00	0.892	0.031
Males (11-21)	1974–79	0.987	0.007
	1980–85	0.953	0.019
	1986–91	0.982	0.009
	1992–97	0.953	0.018
	1998–00	0.905	0.036
Males (22+)	1974–79	0.971	0.015
	1980–85	0.896	0.030
	1986–91	0.958	0.017
	1992–97	0.896	0.029
	1998–00	0.802	0.056

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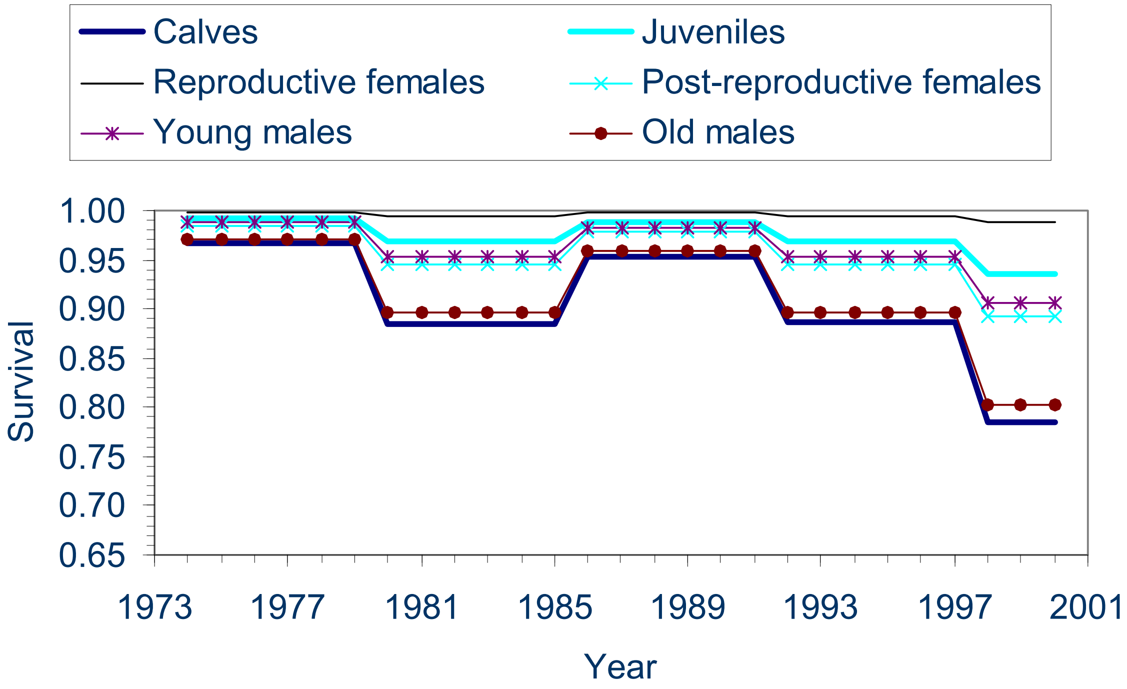

Figure 6. Best fitting model overall, an additive model with 6-year periods of constant survival, starting with a full 6-year period in 1974, scaled differently for each age and sex category.

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1980s, to high levels in the late 1980s and early 1990s, then back to low levels again for the last 9 years, with particularly low survival the last 3 years.

Such temporal changes in survival suggest an external cause, such as changes in prey availability. The survival analysis showed that these changes were not due to just demographic stochastic variation in small populations (due to the random nature of births and deaths), nor were they just fluctuations in survival from year to year. Unfortunately, there is no obvious factor that has the same temporal pattern as that for survival, so it is not clear what is causing these changes in survival. Fluctuations in survival could be caused by fluctuations in environmental conditions, similar to those seen in other marine mammals, such as in pinnipeds when prey becomes unavailable during El Niño events (Trillmich and Ono 1991). As discussed in subsections 2.1.5 and 2.4.3, there is much uncertainty in the food habits of Southern Resident killer whales, particularly in winter. However, it has been suggested that chinook salmon are a primary prey, at least in summer. An analysis was undertaken to examine whether temporal changes in Fraser River chinook, Puget Sound chinook (using estimates of total run strength for both) and PDO index could serve as a significant covariate to explain the temporal patterns in survival, but this hypothesis was not supported in preliminary results (Wade unpubl. data). This certainly does not rule out prey availability as an important factor. It could be a combination of different prey or prey at another time of year such as winter that is most important. Further analyses should be undertaken to explore this issue.

Whale-watching activity steadily increased through the years until recently, when there was a moderate decline in the last few years. Although one cannot rule out the possibility that whale watching might be detrimental to the whales, the trend in whale watching shows no relationship to the trends in survival.

It is plausible that the high levels of OCs or other contaminants in these whales could be causing a decline in survival (see subsection 2.4.3) through mechanisms such as immune suppression (Ross et al. 2000). However, at first glance the timing does not appear to be correct. The concentrations of OCs in Puget Sound likely peaked in the 1970s, but have declined since the ban on the manufacture of OCs in the United States. Therefore, it seems unlikely that OCs alone could account for fluctuations in survival that have occurred on an approximately 6-year period. Additionally, levels of OCs in harbor seals (*Phoca vitulina*) in Puget Sound have been declining through time, but appear to have stabilized (Calambokidis et al. 2001), which contrasts with recent years having the lowest killer whale survival rates seen yet. However, killer whales are much longer lived than harbor seals, so many whales that were alive during the time of peak concentrations of OCs in Puget Sound are still alive today. Moreover, concentrations of OCs have been shown to accumulate with age in male killer whales and with age in females until they become reproductively active (Ross et al. 2000, Ylitalo et al. 2001). OC concentrations in juveniles and adults are also heavily influenced by the initial burden of OCs that a calf receives from its mother, primarily through lactation (Ylitalo et al. 2001). These findings make it plausible that peak concentrations of OCs in killer whales could substantially lag peak concentrations in the environment, particularly if concentrations in the environment did not decline rapidly.

It has been suggested that during times of nutritional stress OCs could be mobilized into the blood stream along with stored lipids from the blubber (Ylitalo et al. 2001). Once in the

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bloodstream, OCs could then cause immune suppression or have other physiological effects detrimental to the health of killer whales. Therefore, it is possible that a combination of high levels of OCs and nutritional stress could lead to fluctuations in survival rate through time. If this is the case, it can be hypothesized that old males might be more adversely affected than other age and sex categories because they would be carrying the highest loads of OCs. Although the best survival model had the same pattern through time for each category, the largest decline in survival over the last 9 years was seen in old males. Additionally, the fraction of the population represented by males 15 years old or older has declined through time, indicating that older males have experienced a greater decline in survival than females (Figure 7). Olesiuk et al. (1990) estimated that males 15 years old or older represented about 19% of the Southern and Northern Residents and that this was close to the expected percentage for a population experiencing stable age and sex distribution. For Southern Residents, this fraction started at about 19%, but declined to about 11% in 2001. Given this recent decline, it can be concluded that some factor changed in the population recently, presumably the survival rate of older males. Although this is not proof that OCs are the cause, it does suggest a hypothesis that OCs may have contributed to the recent decline in Southern Resident killer whales.

One further analysis was done investigating whether there were temporal differences in survival rates between the three different Southern Resident pods (J, K, and L). No differences in temporal patterns were found. Indeed, the decline in survival in the early 1980s as well as in the 1990s can be seen in each pod.

Estimates of fecundity—All calculations of fecundity were made for “recruited” calves (Olesiuk et al. 1990), which are defined as calves that survive until their first summer. Note that it has been estimated that there is substantial neonate mortality in Southern and Northern Residents, perhaps as high as 43% (Olesiuk et al. 1990). This reflects calves that are born but do not survive until their first summer. Therefore, the fecundity rates reported here are likely to be much less than the true birth rate, as the fecundity rate is a product of the birth rate and the neonate survival rate.

The number of recruited calves as a percent of total population size (the gross annual reproductive rate) was on average 3.5%, with a high of 11.3% (8 calves in 1976) and a low of 0%. From 1974 to 2000, the average observed calving interval (years between recruited calves) was 5.65. The reciprocal of the calving interval can be used to estimate the fecundity rate (Olesiuk et al. 1990). However, in this case it would overestimate the fecundity rate of reproductive-age females (11-41), because it is based on the observed calving intervals that eliminate the years before and after the first and last observed calves. Fecundity was directly estimated from the number of recruited calves per reproductive-age female as 12%, with a high of 38% and a low of 0%. The reciprocal of 12% (0.12) is 7.7 years, which represents the average interval between recruited calves for every female from age 11 to 41.

There was no significant trend in fecundity over time, using a simple linear regression of annual fecundity rate and year. To further investigate temporal trends in fecundity, various models were fit to the fecundity data and compared using AIC, in a fashion similar to the survival analysis. The model that fit the data best was a periodic function that ranged between 0.052 and 0.187, with approximately 8 years between peaks (Figure 8). This corresponds well to

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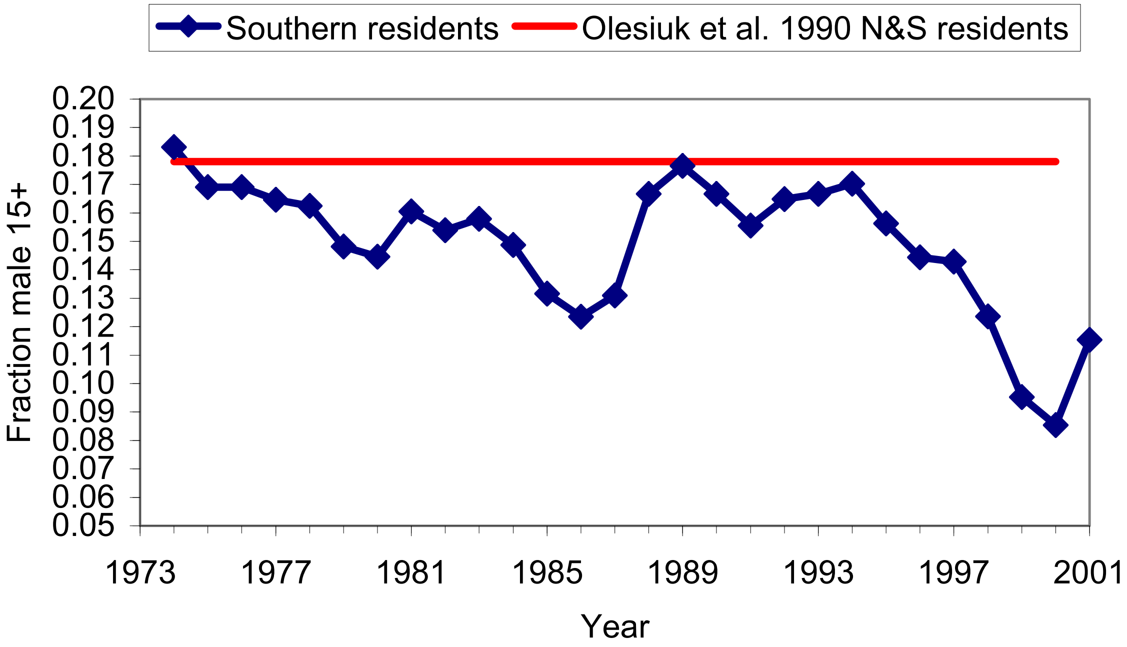

Figure 7. Fraction of adult males (15 or older) in the population per year (diamonds). Also shown is the expected fraction of adult males (Olesiuk et al. 1990), calculated from the life history estimates for Southern and Northern Residents combined.

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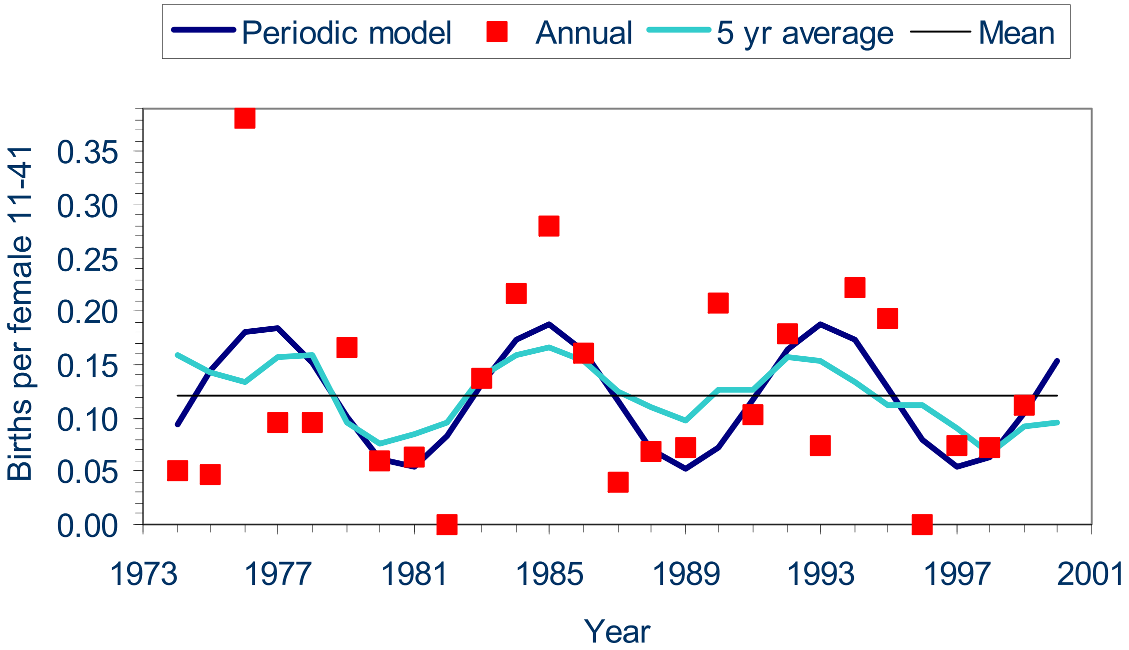

Figure 8. Best fitting model of fecundity (recruited calves per reproductive age female), a periodic function with about 8 years between peaks. Also shown are annual fecundity, a 5-year running average of annual fecundity, and the mean fecundity from 1974 to 2000.

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the estimated calving interval of 7.7 years calculated above. Low points in the periodic model occurred in 1981, 1989, and 1997, and high points occurred in 1977, 1985, and 1993.

For such a small population with relatively few reproductive age females, it is not surprising that there is a lot of variability in the fecundity rate from year to year. This would be expected from demographic variability, which is just the random chance of whether an individual becomes pregnant or not. However, the fact that a periodic function fits the data best implies that something other than just demographic variance is occurring. A certain amount of synchronicity in fecundity is occurring between females, which could be due to changes in the environment. Two of the low points in fecundity (1981 and 1997) coincide with periods of low survival, indicating there could be a common causal mechanism, such as low prey availability. However, that the third low point in fecundity (1989) occurred at a time of high survival contradicts this idea. One possible explanation is that if reproductive females became somewhat synchronized in the timing of their births by environmental conditions at one point in time, this would lead to some periodicity in calving even if the environment stayed constant in subsequent years. In other words, if the low fecundity in 1981 did occur at least partially from reproductive-age females delaying reproduction because of poor environmental conditions (as suggested by the coincidental low survival rate), then the population would have been building a surplus of females ready to calve. This could then result in many females giving birth once conditions were good again, creating a “baby boom,” which would then be echoed by another low in fecundity because of few females being available to calve, even if conditions were good. In summary, it is possible that the observed periodicity in calving could be a result of occasional poor environmental years causing a synchronization of calving between females that is echoed for a certain period of time thereafter.

2.4.3. Potential Risk Factors

There are several potential threats that may pose risks to the Southern Resident killer whales. The following provides a description of each potential risk, and when possible, some assessment of the degree of risk.

Prey availability

Although direct information on the diet of Southern Resident killer whales is limited, it is generally agreed that these animals feed primarily on fish and that salmon comprise the majority of fish in their diet (Balcomb et al. 1979, Heimlich-Boran 1986, Bigg et al. 1987, Bigg et al. 1990, Felleman et al. 1991, Ford et al. 1998). Furthermore, there is some evidence that the Southern Resident community, like Northern Residents (Ford et al. 1998), may target chinook salmon (J. K. B. Ford[5])—at least from late spring to early fall.

The petitioners (Plater 2001) state that the Southern Resident population of killer whales historically relied on Pacific salmon as primary prey. The preferred salmon species appears to be chinook, which are thought to make up about 65% of the identified salmonids, followed by pink salmon (15%), with coho, chum, and sockeye salmon and steelhead (*Oncorhynchus mykiss*)

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[5] J. K. B. Ford, Marine Mammal Research, Pacific Biological Station, Dept. Fisheries and Oceans Canada, 3225 Stephenson Point Rd., Nanaimo, BC V9T 1K3. Pers. commun., 2001.

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contributing 7% or less (Ford et al. 1998). In addition, salmon of unknown species comprise 31% of the total salmonids (identified and unidentified) (Ford et al. 1998). The petitioners state that “although some summertime runs of salmon may be relatively abundant in some years, the fall, winter, and spring runs of salmon are at historically low levels…leading to salmon deprivation during some months” (Plater 2001). They argue that the severely depressed state of Northeast Pacific salmon populations indicates the Southern Residents’ main food source is threatened with extinction. However, a thorough assessment of the status of prey availability for Southern Resident killer whales is complicated by the large number of other salmon runs that could be potential prey, as well as gaps in prey data and the influence of other variables, such as hatchery releases of salmon.

Because killer whales rarely strand, only a few stomach content samples have been examined (Rice 1968). Chinook salmon were found in four of eight stomachs of stranded whales from the coastal British Columbia (Ford et al. 1998). Other salmon species, which may include pink, coho, chum, and sockeye salmon and steelhead, were also found in the stomachs (Ford et al. 1998). Non-salmonid species were also reported (Ford et al. 1998). Although Southern Resident whales mainly eat fish and rarely consume marine mammals, the “L” pod has been known to prey on marine mammals on at least three occasions (Felleman et al. 1991). Similarly, transient whales are frequently seen pursuing marine mammal prey, but there are instances of transient whales eating both fish and marine mammals in southeast Alaska (Matkin 1990) and Prince William Sound, Alaska (G. M. Ellis[6]).

Observational data on prey preferences—Although Southern Resident killer whales prey on five species of salmon, as well as on steelhead and herring (Ford footnote 5), it is uncertain which species are most important. Chinook salmon are suggested to be the preferred prey of Southern Residents; however, the sample size for determining the frequency of prey selection is extremely small (Ford footnote 5). This trend in prey preferences appears to be similar to that of Northern Residents, but the total number of observed predation events for both whale communities combined is still very limited (Ford et al. 1998). Furthermore, potential biases associated with the technique of monitoring predation events through surface observations have been acknowledged (Ford et al. 1998). Only five stomachs have been recovered from Southern Residents. Although three stomachs had chinook remains, the other two had the remains of other salmon species (Ford et al. 1998). It is also important to note that most of these observational data were collected during the summer, when the whales were in inland waters. No information other than contents of one stomach is available on prey preferences in winter.

Killer whale and salmon co-occurrence regarding prey preferences—One additional dimension of uncertainty in determining the relative importance of salmon to Southern Resident killer whales is introduced by the lack of information about which specific salmon runs these whales are targeting. As a result, it is difficult to directly relate change in abundance of any particular salmon run to the potential risk imposed on Southern Resident killer whales. Researchers have attempted to assess which runs the whales are targeting by examining the co-occurrence of killer whales and salmon, based on temporal distribution of the whales relative to catch or escapement records. The high frequency of occurrence of the Southern Residents

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[6] G. M. Ellis, Marine Mammal Research, Pacific Biological Station, Dept. Fisheries and Oceans Canada, 3225 Stephenson Point Rd., Nanaimo, BC V9T 1K3. Pers. commun., 1989.

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between the south end of San Juan Island and the mouth of the Fraser River from spring through fall (Heimlich-Boran 1988) suggests salmon returning to this system might be their preferred prey (Osborne unpubl. data). This hypothesis seems reasonable in that the Fraser River is the largest salmon producer in the world (Northcote and Atagi 1997) and the movement patterns of some runs (sockeye and pink) are known to occur along the route the whales frequent (Groot and Quinn 1987). In the late 1970s, Heimlich-Boran (1986) found a correlation between salmon catch and killer whale occurrence in the San Juan Islands and central Puget Sound. However, no association was found between certain salmon “indicators” (i.e., relative frequency of Fraser River salmon or salmon sport catch) and killer whale presence in this region in a later and longer term dataset. This information led Osborne (unpubl. data) to suggest that the indicators may have been unsuitable or relative salmon abundance does not influence the number of whales present.

Consequently, the potential exists that some of the numerous other runs that occur in the lower Strait of Georgia or adjacent Puget Sound may be important. For example, a correspondence was found between whale presence and relative frequency of estimated chum salmon runs in Puget Sound in the fall (Osborne unpubl. data). However, the association of killer whales and salmon becomes less clear during the winter when both the locations of the whales and the distribution of salmon stocks are largely unknown. The limited sighting information on K and L pod during this season suggests that they range from central California (Black et al. 2001) to central Vancouver Island (WMSA unpubl. data). This region is within migratory paths of numerous salmon species from the U.S. West Coast as they emerge and return to their natal rivers (Weitkamp et al. 1995, Johnson et al. 1997, Myers et al. 1998). Although species emerging from rivers north of Cape Blanco tend to move north and those to the south apparently remain in that general region, their winter distributions are unclear.

Trends in salmon abundance—The assessment of the potential impact of changes in the abundance of salmon runs that Southern Residents utilize is compounded by the lack of comprehensive, uniform, and accurate estimates of salmon abundance within the known range of these whales. The trends in abundance of the primary salmon species occurring in this region are listed in Table 6. Estimates of the magnitudes of numerous runs are not readily available or have been pooled over large-scale areas that are inconsistent with the regions that Southern Resident killer whales may occupy. Furthermore, the comparability of these numbers is limited because the type of data used varies between sources. Some estimates are based on catch data, others on escapement, and in some cases, both data types have been combined to estimate total run size. Certain studies included both wild and hatchery fish, whereas others included only one of these groups. In addition, the methods that were used to develop these estimates varied between studies. Despite these limitations, some general trends do appear. Most notably, major reductions of most species in most regions occurred decades ago, so that by the mid-1900s most runs were very low in abundance (e.g., Puget Sound chinook), as indicated in Table 6. Although some species in certain regions continued to decline (e.g., Columbia River chinook), others partially rebounded by the 1980s (e.g., Fraser River sockeye). Many species suffered significant declines beginning in the early to mid-1990s (e.g., Fraser River pink), yet others have recently rebounded (e.g., Fraser River coho). A key feature of these data appears to be the substantial amount of interannual variability that occurs.

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Table 6. Summary of historical and recent estimates of numbers of salmon produced by west coast North American river systems between the Strait of Georgia and Central California (numbers in thousands, ND for no data).

Region	Period of time	Species				
		Chinook	**Coho**	**Sockeye**	**Pink**	**Chum**
Fraser River	Mid- to late 1800s	750[a]	1,200[a]	34,230[a]	23,850[a]	800[a]
	Mid-1900s	150[a]	160[a]	6,750[a]	4,320[a]	390[a]
	Mid-1980s to early 90s	170-250[b]	40-100[a]	4,000-24,000[c]	6,000-22,000[c]	~1,300[d]
	Early 90s to current	150-350[b,d]	Increasing[e]	3,000-10,000[c,e]	700-3,500[c,e]	13 X increase since 1997[e]
Puget Sound	Mid- to late 1800s	250-700[f]	700-2,200[f]	ND	ND	ND
	Mid-1900s	40-70[f]	250-600[f]	150-550[g]	300-1,000[g]	300-600[g]
	Mid-1980s to early 90s	80-140[g]	450-800[g]	100-500[g]	1,250-1,700[g]	600-1,300[g]
	Early 90s to current	120-170[g,h]	250-500[g]	100[g]	1,000-1,700[g]	750-1,000[g]
					Steelhead	
Coastal Washington	Mid- to late 1800s	190[i]	ND	ND	ND	ND
	Mid-1900s	ND	ND	20-130[g]	ND	80-100[g]
	Mid-1980s to early 90s	60-120[g]	40-130[g]	20-80[g]	35-50[g]	20-325[g]
	Early 90s to current	50-60[g]	30-80[g]	20-80[g]	30-40[g]	60-175[g]
Columbia River	Mid- to late 1800s	5,000-9,000[j]	2,600-2,800[j]	900-1,700[j]	570-1,350[j]	500-1,400[j]
	Mid-1900s	ND	ND	ND	ND	ND
	Mid-1980s to early 90s	1,500[j]	714[j]	58[j]	200[j]	2[j]
	Early 90s to current	250-950[k]	450-250[k]	13-115[k]	250-800[k]	0[k]
Mid-north coastal Oregon	Mid- to late 1800s	300-600[l]	1,700[m]			
	Mid-1900s	ND	ND			
	Mid-1980s to early 90s	30-50% decline[l]	100[m]			
	Early 90s to current	ND	ND			

Table 6. Continued. Summary of historical and recent estimates of numbers of salmon produced by west coast North American river systems between the Strait of Georgia and Central California (numbers in thousands, ND for no data).

Region	Period of time	Species	
		Chinook	**Coho**
North coast California	Mid- to late 1800s	300[i]	1,200[n]
	Mid-1900s	250[n]	200-500[p]
	Mid-1980s to early 90s	ND	13[p]
	Early 90s to current	~ 10-50[o]	ND
Central Valley California	Mid- to late 1800s	1,000-2,000[q]	
	Mid-1900s	400-500[q]	
	Mid-1980s to early 90s	200-1,300[q]	
	Early 90s to current	300-600[q]	

[a] Northcote and Atagi (1997); catch and escapement
[b] Dept. Fisheries and Oceans Canada (1999); catch and escapement
[c] Pacific Salmon Commission (2001); catch and escapement
[d] Dept. Fisheries and Oceans Canada (2001)
[e] Dept. Fisheries and Oceans Canada (2001)
[f] Bledsoe et al. (1989); catch only
[g] Johnson et al. (1997); wild run sizes only
[h] B. Sanford (unpubl. data)
[i] Myers et al. (1998)
[j] Northwest Power Planning Council (1986)
[k] USACE (2002)
[l] Nicholas and Hankin (1989)
[m] Nickelson et al. (1992)
[n] California Dept. Fish and Game (1965)
[o] Mills et al. (1997)
[p] Brown et al. (1994)
[q] Yoshiyama et al. (1998)

Herring have also been identified as a prey item of Southern Resident killer whales (Ford footnote 5). However, the frequency with which Southern Resident killer whales feed on herring is unknown. Populations of herring are located within the Georgia Basin as well as along the west coast of North America (Stout et al. 2001). One large stock of herring, found at Cherry Point near Bellingham, Washington, has undergone a significant decline (Stout et al. 2001). This stock likely migrates to areas off the coasts of Washington and southern British Columbia during the summer (Lemberg et al. 1988) and it is caught in commercial fisheries; thus its importance to Southern Resident killer whales is unknown.

Because the distribution range and diet composition of Southern Resident killer whales are imperfectly understood—as well as species- and region-specific differences in salmon population trends, distribution, and abundance—the effects of salmon declines on the health of killer whale populations are difficult to evaluate. Several additional factors further complicate such evaluations (see the six paragraphs that immediately follow).

Artificial propagation—One issue not discussed by the petitioners that may have an effect on foraging habits of killer whales is the extensive hatchery production of Pacific salmon (see Mahnken et al. 1998 for an historical perspective). The production was implemented to mitigate losses associated with dams and enhance commercial fisheries. For example, between 1953 and 1993, an average of 43 million hatchery-reared chinook salmon were released into Puget Sound annually (Myers et al. 1998) and approximately 45-60 million chinook were released annually from British Columbia facilities during 1990–1996 (Salmon Enhancement Program 1998). This hatchery production supports sport and recreational fisheries (Pacific Fishery Management Council 1999) and, in certain cases, has offset declines in wild salmon populations. Hatchery and wild fish should have similar nutritional composition, because they both gain the vast majority of their mass in the marine environment.

Salmon size—Sizes as well as numbers affect the value of salmon resources for killer whales, because fish size might influence foraging effectiveness or could simply reduce caloric intake for a given level of effectiveness. Bigler and Helle (1994) documented recent declines in adult size of many populations of several species of Pacific salmon. Weitkamp et al. (1995) found evidence for a sharp decline in adult size of coho salmon from Puget Sound (but not coastal Washington or Oregon) from the mid-1970s to the mid-1990s. These data suggest that an analysis that only considers population abundance might overestimate the biomass of salmon resources available to killer whales.

Salmon distribution—As a result of natural events, habitat alteration, and hatchery and harvest management practices, the geographic distribution of salmon production has changed over the last century, and particularly so over the last 30-50 years (Bledsoe et al. 1989). Some populations that were historically productive are no longer so, whereas others have increased in abundance or have been replaced elsewhere with hatchery production. Preliminary evidence suggests that hatchery production may not strongly affect ocean distribution patterns of coho salmon (Weitkamp unpubl. data), but hatchery locations and release sites can strongly affect nearshore behavior and thus availability of salmon to predators.

Seasonal availability—The same combination of natural and human-mediated events that have affected salmon distribution also affect the seasonal availability of salmon resources. For

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example, hatchery management of Puget Sound chinook salmon includes delayed releases that promote permanent residence within Puget Sound, which should provide a more continuous supply of prey for resident killer whales. On the other hand, a variety of human-mediated factors have reduced spring-run chinook salmon populations within Puget Sound more than later spawning runs, and this reduction in diversity can be expected to reduce the availability of salmon prey for killer whales in at least some locations during at least part of the year. On longer time scales, the availability of plentiful pink salmon only in odd years and the ecological correlates of the dominant 4-year cycle for Fraser River sockeye salmon may have profound implications for the availability of salmon resources for killer whales. In addition, estimating the availability of salmon is complicated because ocean harvest removes fish that are potential prey. Because several different runs of the same species commingle on the fishing grounds, it is sometimes impossible to know the origin of the fish that are caught. Consequently, these fish cannot be added back to a particular river system's escapement to more accurately estimate total run size.

Decadal variability—The association between long-term variations in climatic/oceanic conditions on salmon production was only recently described as the PDO (Mantua et al. 1997) (see subsections 2.3.3 and 2.3.5). There appears to be an inverse relationship between Pacific salmon production in Alaska and the west coast during these two different regime types (Hare et al. 1999). The adverse impact of the warm phase of this regime on the west coast salmon during its presence from about 1920 to 1940 is difficult to assess due to concomitant habitat loss and overexploitation. More recently, it appears that the warm regime that began in 1977 again adversely impacted west coast Pacific salmon production while benefiting Alaska salmon production (Hare et al. 1999). However, more recently it is thought that following the 1997–1998 El Niño, a cold regime may have developed (Hare and Mantua 2000) that may account for the recent increases in returns of several west coast Pacific salmon runs (DFO 2001).

Impacts of other marine mammals on prey availability—Populations of other marine mammals, in particular harbor seals and California sea lions (*Zalophus californianus*), increased substantially in the summer range of Southern Resident killer whales since the early 1970s before reaching a plateau (Jeffries et al. in press). However, the extent to which these increasing populations may have impacted the prey resources of killer whales is likely limited. The California sea lions present in waters of the Georgia Basin are males that return to Southern California during the spring and early summer for the breeding season. Consequently, these animals are absent during the period that Southern Residents frequent the Georgia Basin. Although harbor seals are year-round residents in this region, salmon is a relatively small component (about 3%) of their diet (Olesiuk 1993).

Prey availability summary—Most west coast Pacific salmon runs have declined significantly over the past 150 years. In many cases the major portion of the declines occurred decades ago, primarily due to anthropogenic causes, and most significantly during recent times, due to unfavorable ocean conditions. However, a number of complicating factors, including major increases in hatchery production and changes in salmon size and distribution, make it difficult to fully evaluate overall effects on prey availability for Southern Resident killer whales.

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Whale watching

Cetaceans—in particular the odontocetes, which include killer whales—have a highly developed acoustic sensory system. Killer whales likely rely heavily on their acoustic sensory system while navigating and foraging. There is a hypothesis that noise generated by boats watching whales could mask the signals that the whales need, and thus adversely affect their foraging and reproductive success (Bain and Dahlheim 1994). In addition, it has been suggested that shifts in hearing threshold could occur in response to the noise, even after the exposure ended, that could result in impairment of echolocation or communication (Erbe 2002). Currently available data are insufficient to determine the thresholds for the variety of potential acoustic factors associated with vessel noise production that may adversely impact Southern Resident whales.

Vessel-based whale watching by the general public of Southern Resident killer whales in their summer habitat range has increased significantly since the late 1980s (Baird 1999, Koski et al. 2001, Otis and Osborne 2001). Two groups of vessels—commercial whale-watching vessels and private vessels—engage in whale watching. In particular, a substantial commercial whale-watching industry has developed, consisting of a fleet of about 80 vessels of various sizes and configurations (Koski et al. 2001, Otis and Osborne 2001). In addition, because the San Juan Islands are a popular cruising destination, private boaters contribute substantially to the number of boats engaged in whale watching. In 2001 the total average number of boats observed watching whales at any one time was 19, of which approximately two-thirds were commercial whale-watching vessels and the remainder was private boaters. However, it is important to note that substantial numbers of vessels can aggregate near the whales, and occurrences of 100 boats near whales have been recorded (Koski et al. 2001, Otis and Osborne 2001).

All boats engaged in whale watching are prohibited by federal law from harassing whales and they generally follow the guideline of maintaining a minimum distance of 100 yards from the whales. A long-term study of killer whale/whale-watch boat interactions has not documented any large-scale (e.g., whales avoiding the area) or small-scale (e.g., short-term avoidance) impacts (Baird et al. 1998). However, small-scale whale-watching impacts on Northern Resident killer whales in the Johnstone Strait region were indicated in one study (Kruse 1991), although subsequent research suggests habituation may have occurred since then (Williams et al. 2001).

Disease and predation

There is very little known about the existence of disease in killer whale populations, and no information on the extent to which disease could threaten the existence of killer whale groups or populations. Killer whale teeth often show extensive wear and are worn flush with the gumline, resulting in exposure of the pulp cavity. Infection may penetrate through the pulp cavity, causing jaw abscesses. Simpson and Gardner (1972) reported frequent abscessed follicles of the vestigal hair on the rostrum of captive animals, a condition that eventually spread over the entire skin surface. Greenwood and Taylor (1985) reported the causes of death for captive killer whales (n = 32) to be pneumonia (25%), systemic mycosis (22%), other bacterial infections (15.6%), and mediastinal abscesses (9.4%), with 28% remaining undiagnosed. Whether this would also be representative of the causes of death experienced by killer whales in the wild is unknown. Severe atherosclerosis was found in the coronary arteries of one old stranded female

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(Roberts et al. 1965). Hodgkin's disease has been reported in killer whales (Yonezawa et al. 1989). Mass strandings of killer whales are not common, with only about one dozen records worldwide (Mitchell and Reeves 1988). It is not known whether these mass strandings are directly or indirectly caused by disease. Currently, it is not possible to estimate the probability that disease poses a major risk to the Southern Resident killer whale group.

Killer whales have no known predators except humans.

Parasitism

Killer whales are known to have the following endoparasites: Trematoda, *Fasciola skriabini*; Cestoda, *Trigonocotyle spasskyi*, *Phyllobothrium* sp.; and Nematoda, *Anasakis simplex* (Dailey and Brownell 1972). Killer whales are relatively free of external parasites, but barnacles *Xenobalanus globicipitis* (Heyning and Dahlheim 1988) and *Cryptolepas rhachianecti* (Samaras 1989) have been observed on the rostrum and trailing edge of the flukes of a calf. However, the attachment of these barnacles, one of which is considered to be host-specific to gray whales (*Eschrichtius robustus*), is considered a rare phenomenon. Lockyer (1979) photographed a remora (*Echeneididae*) attached to a killer whale. Diatoms on the skin of killer whales found in high latitudes have been noted (Hart 1935, Nemoto et al. 1980). The ectoparasite *Cyamus orcini* has been found on killer whales (Leung 1970). At this time, it is generally believed to be unlikely that parasites pose a major risk to the Southern Resident killer whale group.

Current impacts of past events

Until recently, both Southern and Northern Resident killer whale populations were thought to be generally increasing. This increase was usually assumed to be due to recovery from a variety of known human removals of killer whales in recent decades and implied that Southern Residents were at a somewhat higher population level in the recent past.

Live-capture operations for oceanaria removed killer whales from British Columbia and Washington from 1962 to 1973 (Bigg and Wolman 1975, Asper and Cornell 1977, Hoyt 1990, Olesiuk et al. 1990). Olesiuk et al. (1990) reported that 68 whales were either removed or killed in the live-capture operations—34 of these were known to be Southern Residents and 14 additional whales were presumed to be Southern Residents because they were captured in southern Vancouver Island or inland Washington waters. Of the 48 Southern Residents removed, 10 were immature females, 17 immature males, 8 mature females, 9 mature males and 4 young whales of unknown sex. Therefore, 60% of the whales removed whose sex was known were male.

There have been many reports of killer whales being shot in the Northeast Pacific (Carl 1946, Scheffer and Slipp 1948, Pike and MacAskie 1969, Hoyt 1990). This has been confirmed in several incidents. A necropsy of Namu, a Northern Resident male taken into captivity in 1965, found a .30-06 caliber slug in his body (B. Hanson[7]). In another account, a lone 10-foot-long whale, first seen near Nanaimo, British Columbia, was taken into captivity in 1977, where ballistic experts and veterinarians confirmed it had been injured by a bullet from a .22 caliber

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[7] B. Hanson, NMFS, 7600 Sand Point Way NE, Seattle, WA 98115. Pers. commun., 2002.

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rifle (Hoyt 1990). A killer whale shot in a salmon trap in False Bay on San Juan Island in the summer of 1929 (Scheffer and Slipp 1948) was likely to be a Southern Resident, given its location and its stomach contents (salmon, greenling [*Hexagrammos decagrammus*], lingcod [*Ophiodon elongates*], and squid). During live captures of Southern Residents in Puget Sound, there were reports that 25% of the whales captured had what appeared to be bullet hole wounds (Hoyt 1990).

Olesiuk et al. (1990) and others cite Carl (1946) for evidence of bombing or strafing of killer whales in British Columbia by the Royal Canadian Air Force. Although Carl (1946) mentions this as a possible explanation for a stranding of 18 killer whales on the west coast of Vancouver Island, he actually concludes there was no evidence to support that theory. It is documented that the U.S. Air Force on at least one occasion, at the request of Icelandic authorities, dropped depth charges on killer whales in Icelandic waters (Vangstein 1956), but no evidence can be found of military bombing or strafing of killer whales in British Columbia and Washington.

Although reasonably accurate numbers of animals removed by live capture exist, it is impossible to quantify mortality from shooting. However, it is known that at least since 1929, killer whales in the Northeast Pacific have been shot. Shooting of marine mammals became illegal after the passage of the Marine Mammal Protection Act in 1972 and presumably the shooting of killer whales declined or ceased at that time, if not earlier.

Environmental contaminants

Exposure to high levels of toxic chemical contaminants, including OCs, is thought to be one of the factors contributing to the decline of Southern Resident killer whales (Plater 2001). OCs include several classes of pesticides and industrial chemicals (e.g., polychlorinated biphenyls [PCBs], chlordanes, DDTs) that are frequently found in abiotic and biotic compartments of the marine environment. These persistent compounds are highly lipophilic and can bioaccumulate to relatively high concentrations in top-level predators of the marine food web through trophic transfer. Because several of these contaminants are toxic to wildlife and humans, manufacture of PCBs in the United States was stopped in 1977 (Beeton et al. 1979) and the use of DDT was banned in the United States in 1972 (Ahmed 1991). However, these compounds continue to be used as agricultural and industrial chemicals in other parts of the world, including countries of South America and Asia (Schmidt 1998). The OCs enter the marine environment via several sources (e.g., atmospheric transport, ocean current transport, terrestrial runoff) and are found in environmental samples from all over the world, including remote, nonindustrial areas such as Alaska, the Canadian Arctic, and Greenland (AMAP 1998, Barrie et al. 1992, Muir et al. 1992, Iwata et al. 1993).

Only a few studies have provided contaminant data for Northeast Pacific killer whales (Jarman et al. 1996, Calambokidis et al. 1984, Hayteas and Duffield 2000, Ross et al. 2000) See Table 2 for identities of Southern Residents that have been sampled for chemical analysis. In most of these studies, OCs were the primary contaminants measured in the whale tissues. Moreover, killer whale stranding events occur infrequently along the U.S. West Coast (Geraci and Lounsbury 1993), so few samples from internal tissues have been available for determinations of chemical contaminants. High levels of OCs such as PCBs have been measured

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in biopsy blubber samples of free-ranging Southern Residents (Jarman et al. 1996, Ross et al. 2000) and blubber of stranded Southern Residents (Jarman et al. 1996). The mean ∑PCB level reported by Ross et al. (2000) in blubber of Southern Resident males (146 ± 33 µg/g, lipid) was much higher than the mean concentration (18 ± 13 µg/g, lipid) measured in biopsy blubber of free-ranging resident male killer whales from the Prince William Sound and Kenai Fjords region (Ylitalo et al. 2001). The ∑PCB concentrations of Southern Resident killer whales were also much higher than the mean levels measured in blubber of free-ranging harbor seal pups and blubber of stranded harbor seals that reside in waters of Washington State and coastal British Columbia (Hong et al. 1996, Ross et al. 2000). However, caution should be used when comparing contaminant levels in stranded marine mammals to the concentrations in free-ranging animals. It appears that the concentrations of OCs are influenced by the body condition of the animal (Aguilar et al. 1999). Marine mammals lose weight during various stages of their life cycles due to different stresses such as disease, migration, or reduced prey abundance. The mobilization of lipid associated with weight loss could lead to either redistribution of OCs to other tissues or retention of OCs in blubber that would result in an increase in OC concentrations. The fluctuations of blubber OC concentrations during changes in physiological condition are complex and poorly understood, and need further investigation (Aguilar et al. 1999).

High levels of OCs including PCBs are expected to accumulate in tissues of North Pacific killer whales due to their life history and feeding ecology. These whales are relatively long-lived, with mean life expectancies of approximately 50 years for females and 30 years for males, and maximum life expectancies of 80-90 years for females and 50-60 years for males (Bigg et al. 1990). They are top-level predators: resident whales feed primarily on salmon, as well as on benthic and demersal fish species, and transients consume primarily marine mammals (Ford et al. 1998, Saulitis et al. 2000). In addition, killer whales have a large lipid storage compartment (blubber) where many lipophilic contaminants such as OCs can accumulate to high levels.

Southern Resident killer whales are exposed to OCs primarily through diet. As previously noted (see "Observational data on prey preferences" above), Southern Residents prey on various species of adult salmon as well as steelhead and herring during the summer months. Although salmon appear to be the preferred prey, the data on food habitats is too limited to know what proportion salmon comprise of the diet of Southern Residents. Several studies have measured OCs in tissues of potential prey species in the Puget Sound region, including salmon (Landolt et al. 1987, Brown et al. 1998, West et al. 2001). The ∑PCB concentrations (based on wet weight) measured in muscle samples of coho salmon, various species of rockfish (*Sebastes* spp.), and English sole (*Pleuronectes vetulus*) ranged from 0.5 to 140 ng/g (West et al. 2001) (Table 7). The levels of ∑PCBs (based on wet weight) in whole bodies of Pacific herring and chinook salmon ranged from 18 to 344 ng/g (West et al. 2001, Ylitalo unpubl. data). Although all these fish were captured in Puget Sound, the sources of contaminants, especially for adult salmon, may not be from Puget Sound, but are most likely non-point sources from the North Pacific.

These studies provide important baseline OC data for potential prey species from the Puget Sound region, but they do not help identify the preferred prey of Southern Residents. To help determine the probable prey of Southern Resident killer whales, ratios of ∑DDTs / ∑PCBs of muscle or whole body samples of potential prey were calculated and compared to the ratios of

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Table 7. Concentrations (mean ± SD) of total PCBs and summed DDTs in tissues of various fish species collected from Puget Sound, Washington, from 1997 to 2001.

Species	**Age (year)**	**Tissue analyzed**	**∑PCBs (ng/g, ww)**	**∑DDTs (ng/g, ww)**	**Percent lipid**
Chinook Salmon[a]	4	whole body	42 ± 20	23 ± 7.0	4.0 ± 0.98
Coho Salmon[b]	3	muscle	19 ± 15	12 ± 4.3	3.3 ± 2.1
Pacific Herring[b]	3	whole body	100 ± 85	29 ± 29	5.4 ± 3.0
English sole[b]	6	muscle	22 ± 25	1.2 ± 0.8	0.3 ± 0.2
Quillback rockfish[b]	28	muscle	28 ± 26	1.1 ± 1.4	0.5 ± 1.2

[a] Ylitalo (unpubl. data)
[b] West et al. (2001)

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those contaminants in blubber of Southern Resident whales (Figure 9). These data indicated that Southern Residents likely feed primarily on salmon. For example, the ratio of ∑DDTs / ∑PCBs (mean ± SD) in Southern Resident killer whales was 1.3 ± 0.60. The ratios determined for chinook and coho salmon (0.61 ± 0.18 and 0.71 ± 0.26, respectively) were much higher than the mean ratios (0.05 to 0.47) of other potential prey species (e.g., quillback rockfish [*Sebastes maliger*], English sole, Pacific herring). A selective transfer of DDTs compared to PCBs occurs from fish to marine mammal, resulting in an approximately twofold increase in ∑DDTs / ∑PCBs ratio due to trophic transfer (Muir et al. 1988). Thus, killer whales with a ∑DDTs / ∑PCBs ratio of 1.3 would likely be consuming prey with a ratio of about 0.65. These contaminant ratio results indicate that the Southern Resident killer whales were more likely feeding predominantly on salmon than other prey fish species from the Puget Sound region. If the Southern Resident diet consisted of higher proportions of non-salmon fish than salmon, then the mean ratio of ∑DDTs / ∑PCBs in the whales should have been much lower than 1.3.

Life history parameters such as age, sex, and reproductive status influence the concentrations of OCs in killer whales. For example, previous marine mammal studies have shown that reproductively active females contained much lower OC concentrations than sexually mature males in the same age group (Aguilar and Borrell 1988, Krahn et al. 1999, Tilbury et al. 1999, Ross et al. 2000, Ylitalo et al. 2001). These studies have also shown that the OC concentrations in juvenile animals of both sexes increase until sexual maturity. Males continue to accumulate these lipophilic contaminants throughout their lives. In contrast, a reproductive female's OC levels decrease due to maternal transfer of lipophilic OCs to her offspring during gestation and lactation (Wagemann and Muir 1984, Aguilar and Borrell 1994, Beckmen et al. 1999, Krahn et al. 1999). Furthermore, in some odontocetes (e.g., killer whales, pilot whales, short-finned pilot whales) after a female reaches senescence, her OC levels again increase with age (Tanabe et al. 1987, Tilbury et al. 1999, Ross et al. 2000).

Recruitment (birth) order also appears to affect the OC levels in marine mammals. For example, Ylitalo et al. (2001) found that first-recruited adult male resident whales contained significantly higher levels of OCs than were found in non-first-recruited males in the same age range (see Figure 10). Lee et al. (1996) estimated that a female Steller sea lion (*Eumetopias jubatus*) transfers approximately 80% of her OC burden to her first-recruited offspring during lactation. In another study, it was calculated that a first-recruited offspring of a female fin whale (*Balaenoptera physalus*) received approximately 1g ∑PCBs and 1.5 g ∑DDTs, but that the levels of these lipophilic contaminants transferred to subsequent offspring gradually decreased to a minimum of 0.2 g ∑PCBs and 0.3 g ∑DDTs in old females (Aguilar and Borrell 1994). It appears that the OC burden transferred from mother to offspring decreases as reproductive females mature, because older females that have gone through several lactation cycles have successively lower OC burdens (Ridgway and Reddy 1995). These data suggest that first-recruited killer whales are likely to be exposed to higher OC burdens than subsequent offspring and, because of these higher OC burdens, may be at higher risk of toxicological effects of these contaminants than later offspring.

A large body of evidence links OC exposure to a wide range of deleterious biological effects (e.g., immunosuppression, endocrine disruption) in several species of marine mammals (O'Hara and O'Shea 2001). For example, immunosuppressive effects were observed in captive

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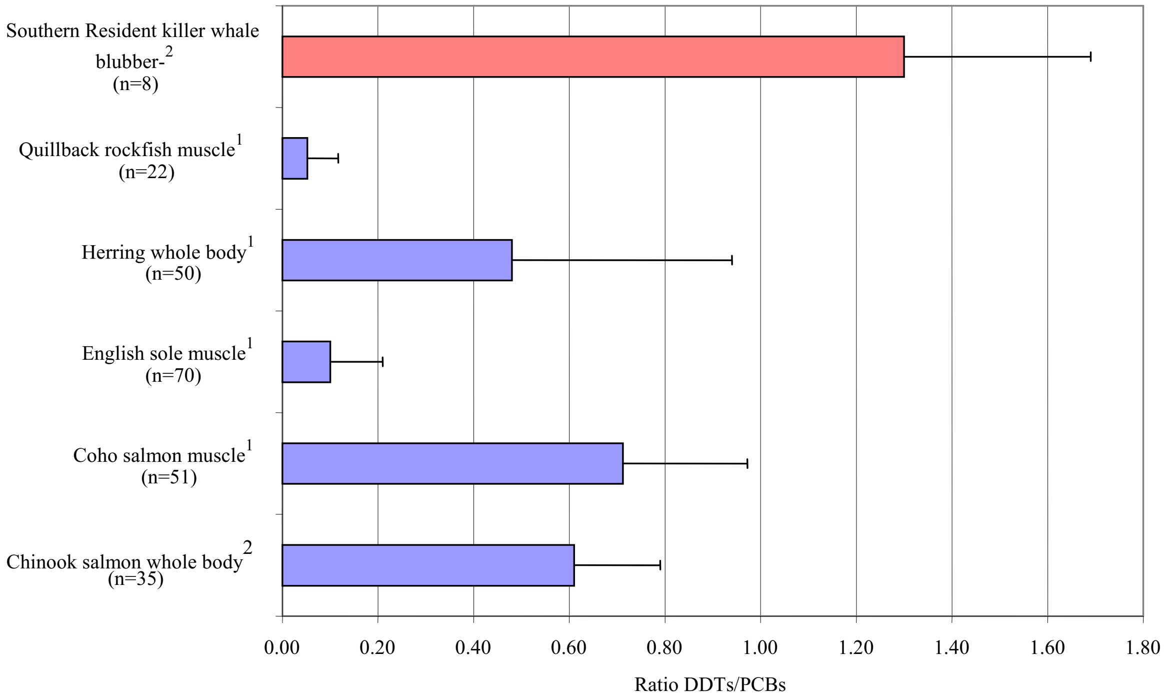

[1] West et al. (2001)
[2] Ylitalo (unpubl. data)

Figure 9. Ratio ∑DDTs / ∑PCBs in killer whales and potential prey (n is sample size).

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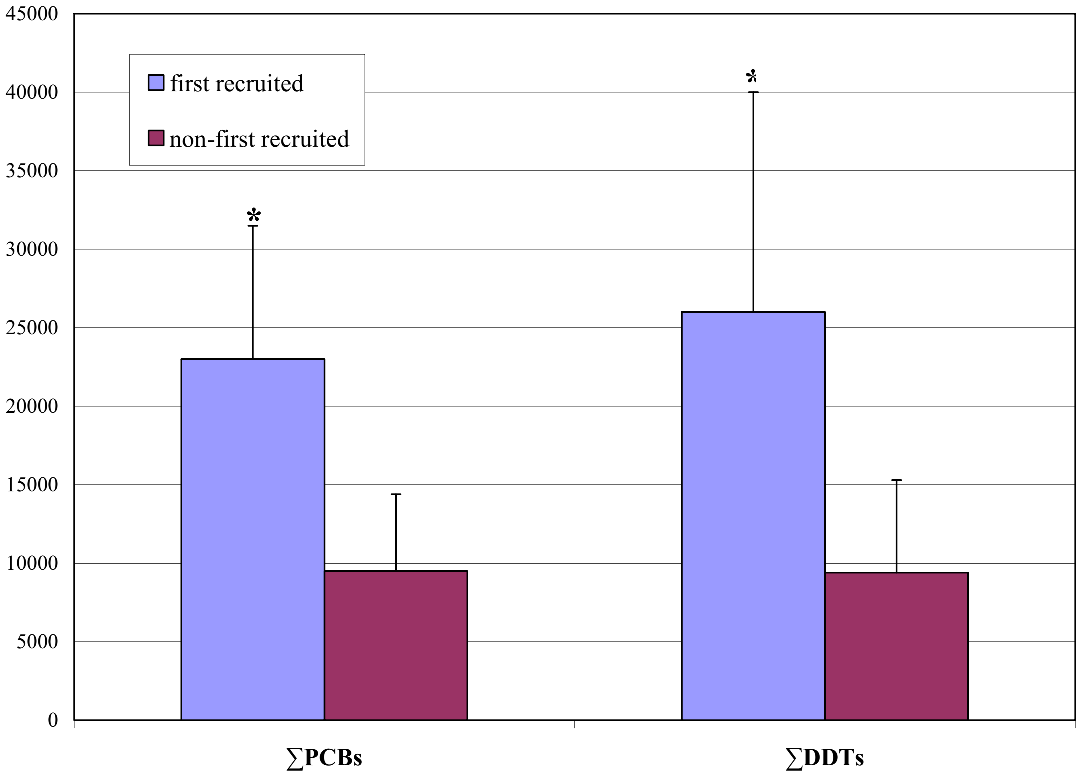

Figure 10. Mean concentrations of ∑PCBs and ∑DDTs (ng/g lipid) measured in blubber biopsy samples of sexually mature male resident killer whales from Prince William Sound and Kenai Fjords, Alaska, grouped by birth order. Bars with asterisks indicate significantly higher concentrations using Tukey-Kramer HSD test, $p < 0.05$.

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harbor seals that were fed herring from the contaminated Baltic Sea (DeSwart et al. 1994, Ross et al. 1995), and decreased *in vitro* lymphocyte response in free-ranging bottlenose dolphins (*Tursiops truncatus*) is associated with increased whole-blood concentrations of PCBs and DDTs (Lahvis et al. 1995). The international Arctic Monitoring and Assessment Program (AMAP) evaluated the recent literature and reports concentrations of OCs above which there is cause for concern for toxic effects in marine mammals (AMAP 1998). This assessment found, for example, that concentrations of ∑PCBs above 77,000 ng/g, lipid weight are linked to reproductive dysfunction in ringed seals (*Phoca hispida*), harbor seals, and otters, and immune suppression in Rhesus monkeys (*Macaca mullata*) (AMAP 1998). The mean concentrations of ∑PCBs measured in Southern Residents by Ross et al. (2000) were comparable to or above this threshold effect concentration. The area of greatest uncertainty is extrapolating chronic sublethal effects to alterations in age-specific survival and reproduction. As noted in subsection 2.4.2, exposure to OCs coupled with nutritional stress could lead to fluctuations in survival rate through time. Therefore, older first-recruited male Southern Residents killer whales could be most at risk for chronic toxicity from OC exposure.

One issue that was not addressed in detail by the petitioners was how body condition of a whale can influence OC burdens in the blubber of these animals (Aguilar et al. 1999). As previously discussed, marine mammals can lose weight during certain stages of their life cycles due to various stresses such as reduced quantity or quality of prey. As the animal loses weight and mobilizes lipid stores, the OCs are ultimately redistributed to other tissues from blubber. But initially there is an increase in OC concentrations in blubber during weight loss. For example, Kleivane et al. (1995) found that harp seals (*Phoca groenlandica*) from the Barents Sea showed seasonal changes in OC levels related to changes in blubber thickness, with the highest OC levels found in the leanest seals. If OCs are redistributed to other tissues in a killer whale due to stress, then the increased levels of OCs may cause immune suppression. Therefore, if a killer whale has lost weight due to reduced prey abundance or quality, the animal may be more susceptible to various diseases compared to a whale that is in better nutritive condition.

The transport of OCs through atmospheric processes is resulting in redistribution of these substances from equatorial regions of the world to temperate and arctic environments, particularly marine environments. Furthermore, global atmospheric transport is a continuing major non-point source of OCs to these environments. The ban on the manufacture and use of several OCs by several countries including Canada and the United States in the 1970s led to a marked decline in the levels of many classes of OCs in marine species through the mid-1980s. Since then, however, the concentrations of OCs in tissues of marine mammals have declined little, if at all. As an example of the temporal dynamics of OCs in marine mammals, the concentrations of PCBs in harbor seal pups in Puget Sound decreased from a mean level of more than 100,000 ng/g, wet weight in 1972 to a mean concentration of 20,000 ng/g, wet weight in 1990 (Calambokidis et al. 2001), but have not declined further during the last decade. Their current tissue levels are similar to concentrations known to cause immune dysfunction in these animals (Calambokidis et al. 2001). No comparable time series for contaminant concentrations exists for any population of killer whales. These findings suggest that for the foreseeable future, exposure of Southern Residents to OCs will not change appreciably, and the redistribution of OCs globally by oceanic and atmospheric transport is a source of OCs to North Pacific ecosystems.

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Oil spills

Large oil spills probably present the greatest short-term threat to coastal organisms, whereas non-point sources of petroleum contamination create chronic problems. Coastal cetaceans may contact petroleum during migration, feeding, or breeding. Usually cetaceans contact oil at the water's surface where they may inhale volatile hydrocarbons, the oil may adhere to their skin or eyes, or their prey may become contaminated.

To assess the impact of the *Exxon Valdez* oil spill in 1989 on the abundance and distribution of Prince William Sound killer whales, photographic studies were conducted. Several pods of killer whales were seen to transit through oiled waters (Dahlheim and Matkin 1994) and high mortality was exhibited by the AB pod (a resident pod). Photographic analysis revealed 14 animals missing from AB pod over a 3-year period (1989–1991). Because killer whales have not been known to disperse, animals that are missing are presumed to be dead. The mortality rates for AB pod ranged from 3.1% in 1988 to 19.4% in 1989, 20.7% in 1990, and 4.3% in 1991 (Matkin et al. 1994). Annual pod mortality rates on the order of 20% are unprecedented for North Pacific killer whales. There is a spatial and temporal correlation between the loss of the 14 whales and the *Exxon Valdez* oil spill, but there is no clear cause-and-effect relationship (Dahlheim and Matkin 1994).

Another group of Prince William Sound killer whales may have been impacted by the *Exxon Valdez* oil spill. Eleven members of the AT1 Transients have been missing and presumed dead since the oil spill. Four of these whales were seen directly behind the *Exxon Valdez* tanker immediately following the spill. Most of these whales disappeared during the 1989–1990 period (Matkin and Saulitis 1997). As is the case with the resident AB pod, there is no clear cause-and-effect relationship between the loss of these whales and the oil spill.

Given their close proximity to tanker traffic that delivers crude oil to refineries in the Strait of Georgia and Puget Sound, Southern Resident killer whales certainly could be at risk if an oil spill occurred. For example, several major spills (more than 100,000 gallons) have occurred from oil tankers or barges in Washington State waters over the last 15 years (WDOE 1997). Furthermore, the risk of an oil spill in Puget Sound may have increased when a Washington State law, enacted after the *Exxon Valdez* accident to increase the safety of oil tanker traffic in Puget Sound, was overturned by the U.S. Supreme Court in favor of more lenient federal maritime law (Anderson 2000).

Harmful algal blooms

Harmful algal blooms (HABs) occur in coastal marine environments throughout the United States, including waters of Puget Sound and off the coasts of Washington, Oregon, and California. There is evidence that HABs have increased in frequency, magnitude, and seasonal duration over the past 10 years, possibly due to global climate change, toxic algal species extending to new areas, and human-related eutrophication of coastal regions (Trainer 2001). Because certain single-celled algae that make up the base of the marine food chain produce the toxins found in harmful blooms, these toxins can accumulate in fish, shellfish, and other marine biota, including marine mammals. Along the U.S. West Coast, some of the most deleterious

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algal toxins include paralytic shellfish poison, domoic acid, and *Heterosigma akashiwo* (Horner et al. 1997).

Although the petition does not address the potential effects of HABs on Southern Resident killer whales, recent studies indicate that certain marine mammal strandings and mass mortality events are linked to biotoxin exposure. For example, several humpback whales (*Megaptera novaeangliae*) died off the coast of Cape Cod, Massachusetts, in 1987 and these deaths were thought to be related to saxitoxin produced by a dinoflagellate (Geraci et al. 1989). In 1998 more than 70 California sea lions from the Monterey Bay region died during an algal bloom of *Pseudonitzschia australis* (Scholin et al. 2000). Using data gathered from multidisciplinary studies (e.g., histopathology, epidemiology, oceanography), it was determined that these animals died from causes related to domoic acid exposure (Scholin et al. 2000, Trainer 2001). Domoic acid was found in samples of sea water, algae, and stomachs of anchovies (planktivorous species), as well as serum, urine, and feces of stranded sea lions, thus demonstrating the transfer of this biotoxin through a marine food web (Scholin et al. 2000).

A measure of the sensitivity of a species to the neurotoxic effects of biotoxins is the ability of a toxin to bind to target receptors in neural tissue. Trainer and Baden (1999) report that brevetoxin, a neurotoxin produced by the dinoflagellate *Gymnodinium breve,* had a high affinity for binding to nerve preparations of manatee (*Trichechus manatus*) brain. Similarly, these researchers showed that saxitoxin, another neurotoxin that is responsible for paralytic shellfish poisoning, had high affinity and specific binding to nerve preparations of brains of gray whale, humpback whale, California sea lion, and manatee. These recent affinity-binding studies and the studies showing exposure to toxin from contaminated prey indicate that marine mammals are at risk of exposure to marine toxins from HAB events and are susceptible to the physiological effects of toxin exposure that can lead to mortality.

The only marine mammal stranding on the U.S. West Coast that has been unequivocally linked to a HAB is the 1998 stranding of more than 70 California sea lions off Monterey Bay. With respect to risk of exposure of Southern Resident killer whales to marine biotoxins, a recent retrospective study suggests that paralytic shellfish poison events have increased in frequency and geographic range within Puget Sound (Eberhart and Wekell unpubl. data). However, there are no data to indicate that Southern Resident killer whale prey (e.g., adult Pacific salmon) accumulate high levels of toxic phytoplankton during a HAB event. It appears as though planktivorous fish species accumulate the highest levels of biotoxins during a HAB event (Scholin et al. 2000), and were the primary vector of domoic acid exposure of California sea lions during the mass mortality event off the California coast in 1998. The apparent increased frequency of HAB events and high affinity binding of biotoxins at target receptors of marine mammals suggest that Southern Residents are at risk of toxic effects from a HAB event if exposed to a biotoxin. However, since their known primary prey species (i.e., salmon) are not planktivorous fish species, the risk of exposure appears to be minimal.

Incidental mortality of killer whales in commercial fisheries

Mortality of killer whales incidental to commercial fishing operations appears to be quite rare. No recent records of fishery-caused mortality or serious injuries of animals from the Southern Resident population are reported in the stock assessment report for this stock (Forney et

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al. 2000). Over the past 10 years, an estimated 1.4 killer whales per year are killed incidental to all commercial fisheries in Alaska (Ferrero et al. 2000) and one animal was killed incidental to fishing operations in the California/Oregon thresher shark *(Alopias vulpinus*)/swordfish (*Xiphias gladius*) drift gillnet fishery between 1994 and 1998 (Forney et al. 2000). However, both of these fisheries are conducted outside the likely range of the Southern Resident population (the California/Oregon fishery occurs well offshore), and thus would not be expected to cause mortalities. One killer whale encountered a commercial fishing net in Canada in 1994, but the animal did not become entangled in the net (Guenther et al. 1995). Although a groundfish trawl fishery occurs off the coast of Washington and Oregon, to date no mortalities of killer whales have been reported. However, the observer effort has historically been very low, so mortalities may not have been observed.

Killer whales have been occasionally seen in close proximity to commercial fishing gear in Washington State waters, but no entanglements have been recorded (Forney et al. 2000). Further, although killer whales have been observed preying on fish caught on longline gear in Alaska (Yano and Dahlheim 1995), there have been no reports of similar interactions between killer whales and longline operations in Washington and Oregon. Historical accounts exist of interactions between killer whales and fishing gear in inland waters of Washington, including one confirmed mortality of a juvenile female (presumably a Southern Resident) that was killed in a salmon set gillnet off Hat Island, Snohomish County, in July 1943 (Scheffer and Slipp 1948). However, based on the lack of recent accounts, it seems likely that the risk of incidental mortality of Southern Resident killer whales in commercial fisheries is small.

2.4.4. Historical Population Size, Carrying Capacity, and Range

Genetic data can be useful in estimating the census size of the population in the past. The genetic data of Barrett-Lennard (2000) and Barrett-Lennard and Ellis (2001) show that Southern Residents have approximately the same amount of genetic diversity as Northern Residents, even though the Southern Resident population is approximately one-third the size of the Northern Resident population (see subsection 2.2.2). This indicates that the Southern Resident population has most likely been larger in the past, because if the Southern Resident population has been small for many generations (or even a few generations), it would have less genetic diversity than the Northern Resident population. Given that the Northern Resident population is greater than 200 whales, the Southern Resident population could have been this size in the past.

Another way of inferring the historic size of the Southern Resident population is to estimate what the carrying capacity of the region may have been by examining the historical abundance of prey. Southern Resident killer whales are known to prey on salmon (subsection 2.4.3). Historical and recent numbers of salmon along the west coast of North America are summarized in Table 6. Although there are many caveats to the historical numbers presented in the table (see subsection 2.4.3), the overall picture is that there has been a decline in regional salmon abundance since the mid-to-late 1800s, with most of the major reductions occurring decades ago. Southern and Northern Resident killer whales are suspected of preferring chinook salmon (Ford et al. 1998). If this is so, the chinook salmon that are targeted in the summer and fall would be those returning to the Fraser River and Puget Sound. In both of these areas, chinook salmon abundance may be less than a half or a quarter of the mid-1800s levels (Table 6). Similar or even greater declines in chinook salmon may have occurred on the Washington coast,

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in the Columbia River, along the Oregon and California coasts, and in the Central Valley of California. Particularly large declines have occurred in the Columbia River Basin and the Central Valley of California. Declines of similar magnitude have occurred in other salmon species in most of these regions (Pess et al. in press). The importance of other potential prey of Southern Residents is difficult to determine due to the limited information available about their prey preferences. Herring, for example, have recently been in decline in U.S. waters of the Georgia Basin, but have recovered somewhat in Canadian waters (DFO 2002).

Due to the nature of the information, it is difficult to make a quantitative estimate of the decline of potential prey of Southern Resident killer whales. However, it seems likely that there has been a substantial decline in prey available to Southern Residents since the mid- to late 1800s. Although uncertain, this decline could have been as much as 50% or greater. It is therefore possible that the carrying capacity of Southern Residents, in terms of prey, was twice or more as large as it is currently. If Southern Residents are close to their current carrying capacity, this implies that the population could have been twice as large 150 years ago if they were at their carrying capacity at that time. If Southern Residents are below their current carrying capacity, it is conceivable that the carrying capacity 150 years ago was even greater than twice the current population levels. If the Southern Resident killer whale population declined in concert with salmon in the region, the decline would have occurred decades ago before the population was monitored.

Given that Southern Residents eat chinook and other species of salmon, it would not be surprising if their historical range extended to the limits of the chinook range, which extends as far south as central California. In particular, the two largest historical sources of chinook south of Alaska were the Columbia River and the Central Valley of California, so it is possible that Southern Residents foraged extensively in areas where adult fish could be found. Although the distribution of Southern Resident killer whales is centered in Washington and British Columbia waters in summer, their distribution in winter is poorly understood (subsection 2.4.1). Of the small number of sightings of K and L pods in winter, five sightings are from the southern coast of Washington, Oregon, and central California. As noted previously, K and L pods were observed off Monterey, California, in January 2000. Given the quantity of salmon that historically entered the Columbia River, it is interesting to note accounts of killer whales in that area in 1932 (Shepard 1932), 1940, and 1942 (Scheffer and Slipp 1948). However, no historical accounts have been found of killer whales being seen in San Francisco Bay, which presumably might have occurred if killer whales were preying on Central Valley chinook. If the normal historical range of Southern Residents did extend to central California, this implies that their historical carrying capacity could have been larger than that suggested by the historical abundance of salmon in only the Georgia Basin.

One other suggestion that the population size of Southern Residents has declined comes from their social structure. The Northern Resident population contains 3 acoustic clans and 16 pods, the Southern Alaska Resident population contains 2 acoustic clans and 11 pods, whereas Southern Residents contain 1 acoustic clan and 3 pods (from Fig. 4.1, p. 52, in Barrett-Lennard 2000). Because the Southern Resident population has fewer acoustic clans and pods when compared with other resident populations, one could infer that the Southern Resident population had more acoustic clans and pods at some previous time and they have been lost.

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Given the speculative nature of some of this information, it is difficult to make conclusive statements about the past abundance of Southern Residents and what the current or past carrying capacity may have been. However, several lines of evidence indicate that population sizes in the past may have been larger.

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3. DETERMINATION OF DPS

3.1. Taxonomic Uncertainty

Understanding the taxonomy of killer whales is necessary in evaluating whether Southern Residents qualify for protection under the ESA. Currently, only one species of killer whales (*O. orca*) is globally recognized. However, for the reasons described below in section 3, the taxonomy of killer whales needs to be reviewed by taxonomic experts to determine whether more than one species or subspecies should be officially designated, because a "taxon" as described under ESA policy must be an officially recognized species or subspecies. Correctly identifying the taxon may be critical, because at least two of the criteria used to evaluate ESA significance are defined relative to other populations within that taxon. For example, a population segment will qualify as a DPS if it occupies an "ecological setting unusual or unique for the taxon" or if "loss of the discrete population segment would result in a significant gap in the range of the taxon."

Accumulating evidence suggests that the currently recognized global species of killer whales may need to be divided into multiple species. Berzin and Vladimirov (1982, 1983) proposed that the small fish-eating killer whales within the Antarctic pack ice are a new species. This species proposal is based on differences in body size, coloration, skull morphology (including numbers of teeth), reproductive differences, and dietary differences (fish vs. marine mammals). Interpretation of these data is controversial, however. Rice (1998), an authority in killer whale taxonomy, did not accept the Antarctic species proposed by Berzin and Vladimirov (1982, 1983), citing the need for more analyses of skull morphology. Unfortunately, no genetic evidence was available for the putative Antarctic species. Because collecting skulls of killer whales is difficult, accumulating the evidence needed to formally describe the putative new species in Antarctica may take years.

Furthermore, additional revision of killer whale taxonomy may be warranted because resident and transient killer whales may be two separate species or subspecies. Resident and transient killer whales are sympatric, but these ecotypes have striking genetic differences (see subsections 2.2.2 and 2.2.3). These differences indicate reproductive isolation of these two ecotypes of killer whales on an evolutionary scale, which is the fundamental criterion for defining species under the Biological Species Concept (Mayr 1963). At mtDNA loci, residents and transients are differentiated by six fixed base pair differences. This difference is similar in magnitude to differences observed in several other pairs of marine mammal species and greater than some. For example, there is only one fixed base pair difference between short-beaked common dolphins (*Delphinus delphis)* and long-beaked common dolphins (*D. capensis),* albeit within a shorter segment of the control region (Heyning and Perrin 1994). At nuclear loci, genetic differences between residents and transients are greater than differences between the most geographically distant pair of resident populations that have been compared for microsatellite diversity (Southern Residents vs. Southern Alaska Residents; see subsection 2.2.2). These differences are evidence of reproductive isolation on an evolutionary scale between both male and female residents and transients. In addition—and perhaps more importantly—residents and transients have different diets and different external morphology.

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This suggests that if residents were extirpated, transients might not fill the vacant ecological niche left open in an ecological timeframe.

Deciding whether the differences between residents and transients are substantial enough to identify each ecotype as different species is likely to be at least as controversial as the question of how many species of killer whales are found in the Antarctic. Knowing how often dietary specialization (marine mammal vs. fish) has evolved among killer whales would be useful. If dietary specialization evolved only once, then this single evolutionary event is of high significance. In contrast, if such dietary specialization has evolved many times, then it becomes more plausible that dietary specialization will evolve again if one dietary group becomes locally extinct. However, even if dietary specialization has evolved independently in multiple oceans, differences between residents and transients may still be substantial enough to define several subspecies or species. In any case, residents and transients in the Northern Pacific, although sympatric, are almost certainly reproductively isolated. Further clarification by taxonomists is needed.

The uncertainty surrounding killer whale taxonomy is characteristic of marine mammals. Nomenclature has not caught up with knowledge (particularly genetic information), due to the difficult and time-consuming traditional process of obtaining and classifying skulls needed to formally describe what many scientists recognize as discrete taxonomic entities. Subspecies have been named for only a small number of marine mammal species. For example, the dwarf minke whale (*Balaenoptera acutorostrata*) is referenced by Rice (1998) as an “unnamed subspecies.” Forms, ecotypes, and races are three terms that can be used to describe populations or groups of populations that will likely be designated formal species or subspecies sometime in the future. Implications of this taxonomic uncertainty are discussed in subsection 3.4.

3.2. Data Relevant to Determining ESA Discreteness and Significance

The requirements related to “discreteness” and “significance” for a population segment to qualify as a DPS are covered in subsection 1.2.1. The discreteness criteria include consideration of data that would help determine if Southern Residents are “markedly” separated from other populations of the same taxon as a consequence of physical, physiological, ecological, or behavioral factors. Quantitative measures of genetic or morphological discontinuity may also provide evidence of this separation. Physical data that were considered are found in subsections 2.1.1 and 2.1.2. Physiological, ecological, and behavioral data that were considered are included in subsections 2.1.5, 2.1.6, 2.1.7, and 2.4.1. Genetics data considered are found in subsection 2.2. Data relevant to the second criterion for discreteness, that is, “delimited by international governmental boundaries within which differences in control of exploitation, management of habitat, conservation status, or regulatory mechanisms exist that are significant in light of Section 4(a)(1)(D) of the ESA,” are covered in subsection 2.4.1.

If a population segment is considered discrete, NMFS must then consider whether the segment meets any one of the four criteria for “significance” (see subsection 1.2.1 and the following descriptions). Data considered relevant to the first criterion, that is, “persistence of the discrete population segment in an ecological setting unusual or unique for the taxon,” are

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included in subsections 2.1.3, 2.1.4, 2.2, and 2.4.1. Information related to the second criterion, that is, "evidence that loss of the discrete population segment would result in a significant gap in the range of the taxon," can be found in subsections 2.1.3 and 2.4.1. Because Southern Resident killer whales are clearly not a "discrete population segment representing the only surviving natural occurrence of a taxon that may be more abundant elsewhere as an introduced population outside its historic range," this criterion was not considered applicable. Data relevant to the fourth criterion, that is, "evidence that the discrete population segment differs markedly from other populations of the species in its genetic characteristics," are presented in subsections 2.2.2 to 2.2.5. The joint NMFS/USFWS ESA policy states that the list of criteria is not exhaustive and other criteria may be used as appropriate (see subsection 3.2.1).

3.2.1. Other Information

One question in establishing "significance" under ESA is deciding whether loss of a DPS would result in a significant gap in the range of the taxon. In other words, if the Southern Resident population were extirpated, would a gap result in the range currently occupied by Southern Residents because other resident killer whales would not recolonize the area. It is unclear how recolonization of this region by resident whales would take place. There are no known resident whales to the south of the range of Southern Residents. Therefore, recolonization would have to take place from Northern Residents, Alaska Residents, or offshores. Alaska Residents have never been seen as far south as Washington and Northern Residents have been seen there only once. Moreover, Northern Residents have been increasing as a population for the last 26 years without expanding to the south, so presumably this population has not reached a point where it has an incentive to explore new habitat. Similarly, resident whales in southeast Alaska appear to have been increasing over the last 12 years (M. E. Dahlheim[8]) and seldom have been observed to explore new habitat to the south. However, the presence of Southern Residents in their current range may pose a deterrent to colonization by other populations, so it is not known what would actually occur if the Southern Resident territory were to become unoccupied.

Resident killer whales have long life spans and stay in their natal pod. One of the unusual features of killer whale biology is the large proportion of post-reproductive females. The few other species that have evolved this strategy include humans and elephants. It was recently shown (McComb et al. 2001) that old female elephants serve the herd through their memory of interactions with neighboring herds (e.g., whether they were friend or foe). Similarly, the older whales in a pod may be a valuable resource because they carry social knowledge and perhaps also pass the legacy of foraging distribution from generation to generation. It is not possible to predict whether or when Northern or Alaska Residents might expand into the area currently occupied by Southern Residents if Southern Residents were lost together with the memories of the older females.

There have been numerous examples among cetaceans where regions of local extirpations by overharvest have not yet experienced recolonization despite healthy neighboring populations (Clapham 1999). Perhaps the most relevant example comes from belugas (*Delphinapterus leucas*) in Hudson Bay. During part of each year, these whales forage by

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[8] M. E. Dahlheim, NMFS, 7600 Sand Point Way NE, Seattle, WA 98115. Pers. commun., 2001.

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following salmon runs up rivers. Whales were extirpated from the Great Whale River Estuary in Eastern Hudson Bay by overhunting in the 1850s and 1860s (Reeves and Mitchell 1989). Although other belugas that follow salmon runs are present within Hudson Bay, this river system has never been recolonized. Thus the prospect of recolonization of the full range of Southern Residents by other residents is unknown but may be remote based on comparisons with other cetaceans.

3.2.2. Population Units of Killer Whales Considered as either a Taxon or a DPS

The BRT had to identify both the taxon and the DPS for Southern Residents to evaluate the "significance" of a Southern Resident DPS with respect to "the taxon to which it belongs." To facilitate its deliberations, the BRT identified seven hierarchical population units that might qualify as a taxon or DPS. The summary of each killer whale population unit considered as a possible taxon or DPS, organized from smallest to largest grouping, is as follows:

Group		Potential taxon?	Potential DPS?
I.	Southern Residents	No	Yes
II.	Northeast Pacific resident killer whales	No	Yes
III.	North Pacific resident killer whales	Yes	Yes
IV.	North Pacific resident and offshore killer whales	Yes	Yes
V.	All resident and offshore killer whales worldwide	Yes	Yes
VI.	The mtDNA lineage consistent with fish eating	Yes	Yes
VII.	The currently recognized global killer whale taxon	Yes	No

Nomenclature of the killer whale population units is described in subsection 2.1.4; the actual groupings and the rationale for considering each as a taxon, a DPS, or both are as follows.

Group I, Southern Residents (DPS only)

The Southern Residents were not considered as a taxon.

The BRT considered the possibility that the Southern Residents as defined in subsection 2.1.4 constitute a DPS of the possible taxons identified as III-VII below based on general similarity in:

- Habitat use (relying on salmon in the California Current is unique)
- Significant gap in the range (represent the southern portion of the range of residents)
- Genetics (represent the group that differs most in nuclear DNA from all other groups)
- Morphology (differ in frequency of saddle patch types from other residents)

Group II, Northeast Pacific resident killer whales (DPS only)

This grouping (subsection 2.1.4) includes the Southern Residents, the Northern (British Columbia) Residents, as well as both Southern and Western Alaska Residents, and is consistent with combining the eastern North Pacific southern resident and eastern North Pacific northern resident stocks as defined under the MMPA.

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The BRT did not believe that available information supported the possibility that the Northeast Pacific resident killer whale group could be a taxon.

Consideration of this grouping as a possible DPS is reasonable because of general similarity in:

- Habitat use (frequent inland waterways, primarily coastal)
- Pod size and structure (large pod size, matrilinear structure)
- Feeding ecology (all animals feed on fish and the preferred prey may be salmon)
- Morphology (all animals have more rounded dorsal fins and exhibit a wider variety of saddle patch morphologies than transients or offshores)

Although there are only small mtDNA differences, nuclear DNA of Southern Residents differs from that of their neighbors to the north to about the same degree that transients differ from offshores (see subsection 2.2.2). In addition, genetic exchange between some assemblages is known to occur (e.g., Northern Residents and Southeast Alaska Residents) or between-assemblage mating seems likely based on co-occurrence (e.g., Prince William Sound Residents have been observed to mix with large resident pods off Kodiak). It is notable that experts in Southern Resident and Northern Resident killer whales feel confident that they can identify “new” animals in western Alaska as either residents or transients based on the characteristics of residents listed above (i.e., habitat use, pod size, feeding ecology, and morphology).

Group III, North Pacific resident killer whales

This grouping (subsection 2.1.4) includes the Southern Residents, the Northern (British Columbia) Residents, both Southern and Western Alaska Residents and possible residents in the unsurveyed area in the western North Pacific. Although residents have been confirmed in the Bering Sea through association with previously identified residents from the Gulf of Alaska and southeast Alaska (Dahlheim footnote 8), very little is known about killer whales in the western North Pacific. BRT members assumed that residents may extend to this area based on the fact that salmon runs extend to this area. The BRT thought that the full distribution of residents, including potential populations in the western North Pacific, was a potential killer whale unit to consider as a potential DPS under the ESA. The BRT also believed that this was the smallest possible taxon of killer whales that might exist, because of the relatively large genetic differences between all known North Pacific resident animals and transient and offshore animals.

The rationale for considering this grouping a potential taxon of killer whales is:

- Genetic evidence (mtDNA) indicates resident killer whales differ markedly from transient killer whales.
- Resident killer whales forage on fish. Although little is known about killer whales in the western North Pacific, residents may be found in this area based on the fact that salmon runs extend to this area.

Grouping the western North Pacific resident killer whales with the known resident killer whale assemblages for consideration as a possible DPS can be justified because of assumed similarity in:

- Habitat use (primarily coastal)

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- Pod size and structure (large pod size)
- Feeding ecology (all animals feed primarily on fish)

Group IV, North Pacific resident and offshore killer whales

This grouping includes all residents in the North Pacific (subsection 2.1.4) and all offshore killer whales in the North Pacific.

The rationale for considering this grouping a potential taxon of killer whales is:

- Mitochondrial DNA evidence indicates that offshore killer whales are more closely related to resident killer whales than to transient killer whales.
- Resident killer whales forage on fish; based on what little is known about offshore killer whales, it appears that they also forage on fish.

The rationale for considering residents and offshores as a DPS is:

- Nuclear DNA differences are insufficient to be considered “marked.”
- Habitat differences between offshores and residents are not different enough to be considered as unusual habitats separately.
- A loss of residents alone from the North Pacific would not represent a significant gap in the range of this taxon.

Group V, all resident and offshore killer whales worldwide

Although there are currently no direct data that residents and offshores exist beyond the North Pacific, sampling in other ocean basins is poor. Therefore, for completeness, the BRT also considered potential worldwide distribution.

The rationale for considering this group a taxon is as in IV above, only extended to a larger geographical range.

The rationale for considering this group a DPS is as in IV above, but extended to the larger unit.

Group VI, the mtDNA lineage consistent with fish eating

Recent mtDNA analysis at the NMFS Southwest Fisheries Science Center (SWFSC unpubl. data) of killer whale samples from Alaska to the Antarctic suggests that most killer whales fall into two lineages. The first lineage includes all residents in the North Pacific, at least one group identified as the offshore form, other killer whales sampled both from near coastal waters and truly pelagic waters, an animal sampled from Iceland, and most killer whales sampled in waters of the Antarctic. The second includes all transient animals and two killer whales sampled in the waters of Antarctica. Because the samples identified to dietary preference fell into one lineage or the other, the data are at least consistent with a large fish-eating taxon (the first lineage). However, until the dietary preferences of more samples within the phylogram are known, it remains plausible that the hypothetical taxon may include both killer whales that forage primarily (or exclusively) on fish and killer whales that forage on marine mammals.

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The rationale for considering this a taxon would use the mtDNA phylogram as a classification scheme.

The rationale for considering this lineage as a DPS is:

- Genetic differences at less than this phylogenetic level are not considered marked.
- Loss of all residents and offshores worldwide would not constitute a significant loss in the range of the taxon.
- There are no unusual or unique habitat usages within the residents and offshores worldwide.

Group VII, the currently recognized global killer whale taxon

At this time, killer whales are recognized as one taxon worldwide (Heyning and Dahlheim 1988).

The BRT deliberations and conclusions about DPS and taxa are detailed in subsection 3.4.

3.3. BRT Determinations of ESA Discreteness

The BRT unanimously concluded that Southern Resident killer whales are discrete from other killer whale population segments, such as the transient killer whales in Puget Sound, Northern Resident killer whales in British Columbia, and offshore killer whales. For example, both microsatellite DNA and mtDNA genetic data (see subsections 2.2.2 and 2.2.3) clearly show that Southern Resident killer whales belong to an independent population. These genetic differences are accompanied by differences in summer range described in subsection 2.4.1.

3.4. BRT Determinations of ESA Significance

The BRT spent the majority of its time debating the DPS designation for Southern Residents and was unable to come to consensus. Taxonomic uncertainty, lack of key scientific information (e.g., genetics of worldwide killer whales) and differences in opinion within the BRT were the primary reasons for this result. A summary of BRT deliberations follows. The decision tree the BRT used for determining the taxa and DPS used in evaluating “significance” under the ESA is shown in Figure 11.

3.4.1. BRT Deliberations Process

The BRT used a series of ballots to survey the diversity of opinion within the team. In these votes, each of the members was given 10 points to distribute among alternatives on the ballot in proportion to the member’s confidence in the particular alternative. In other words, the distribution of points among multiple alternatives was a means of expressing an individual’s overall uncertainty; that is, a vote in which several of the alternatives were given a few points each would be more uncertain than a vote in which one or two of the alternatives were given a higher number of points. The BRT began its DPS deliberations by addressing the petition

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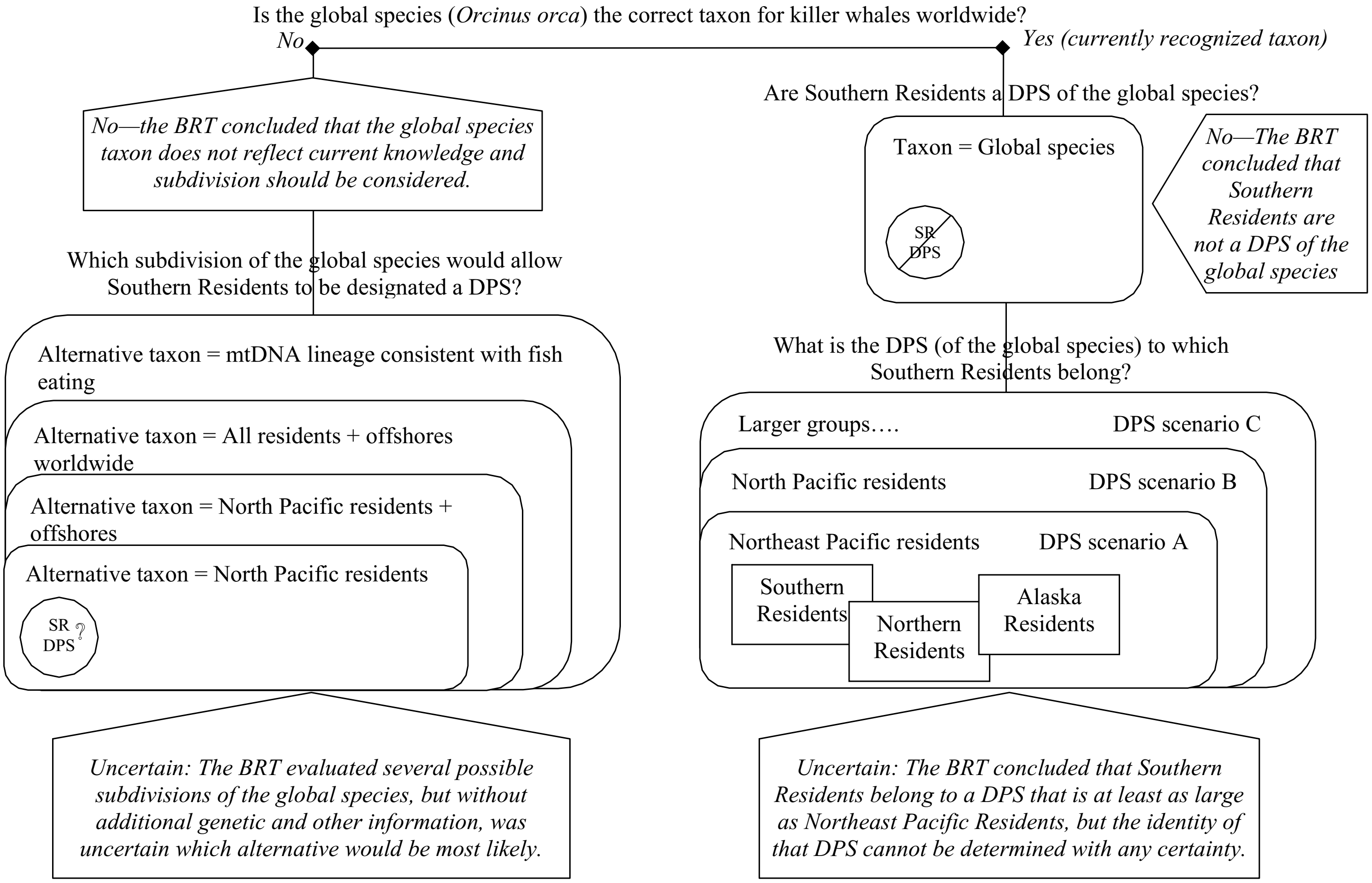

Figure 11. Decision tree for determining taxa and DPS used in evaluating "significance" criteria under the ESA.

(subsection 1.1) that requested NMFS to list the Southern Residents as a DPS of the currently recognized global species. See subsection 3.2 for a more complete presentation of the data the BRT evaluated and subsection 1.2.1 for a summary of the NMFS criteria the BRT used to identify DPS boundaries.

3.4.2. Are Southern Residents a DPS of the Global Species?

In this determination, "significance" of Southern Residents was judged with respect to the taxon represented by the currently recognized global species (*O. orca*) (Figure 11). Although the BRT found little support (see Table 8) for Southern Residents being a DPS of the currently recognized species, they also found little support for considering killer whales to be a global species (see subsections 3.1 and 3.4.4). Each of the NMFS/USFWS ESA criteria for delineating DPS boundaries will be discussed, presenting first the arguments that received most of the BRT support and then those that received much less support.

Arguments against Southern Residents as a DPS of the global species

The following arguments received most of the BRT support, and therefore, the BRT concluded that Southern Residents are not a DPS of the global species.

Persistence in an ecological setting that is unusual or unique for the taxon—The habitat used by Southern Resident killer whales—at least during the spring, summer, and fall—is very similar to that of the neighboring Northern Resident population segment (coastal fjord system, significant freshwater input, seasonal availability of concentrations of salmon) and quite different from habitats that killer whales occupy globally. For example, throughout their worldwide range, killer whales use coastal or oceanic habitats, spanning tropical to polar environments. The primary difference between Southern and Northern/Alaska Residents is that each group may primarily consume salmon from different oceanographic domains (California Current vs. Alaska Gyre). Nevertheless, this difference is quite minor when comparing Southern Resident killer whales to coastal fish-eating killer whales in the North Atlantic Ocean that target herring. Another difference between Southern and Northern/Alaska Residents—and one that is cited in the petition—is that Southern Residents live in a highly urbanized environment. However, this habitat difference is not relevant to the ESA discussion, because there is no evidence that Southern Residents have adapted (in the evolutionary sense) to urbanization in Puget Sound.

Loss would represent a significant gap in the range of the taxon—Extinction of the Southern Resident killer whales would not result in a significant gap in the global range of the currently recognized species of killer whales. Because transient killer whales occupy the same range as Southern Resident killer whales, extinction of Southern Resident killer whales might result in no gap in the range of the taxon. In addition, the inland waterway habitat has been recolonized by residents after ice age coverage in the past. Although there are no data to evaluate whether other resident or offshore animals might recolonize the current range of Southern Residents should that population be extirpated, it is possible that this could occur.

Evidence that Southern Residents differ markedly from other populations in genetic characteristics—Southern Residents are genetically distinct from other residents, but there is a lack of consensus whether this is a "marked" difference. However, the difference (Figure 2)

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Table 8. The BRT's distribution of points in votes to select the most appropriate DPS (I to VII) for Southern Resident killer whales.[a]

DPS / Taxon	I[b]	II[c]	III[d]	IV[e]	V[f]	VI[g]	VII[h]
III	48	27	25	-	-	-	-
IV	22	34	42	2	-	-	-
V	11	20	43	26	0	-	-
VI	9	12	39	28	12	0	-
VII	7	10	33	28	14	8	0

[a] Results for several plausible taxonomic scenarios (III–VII) are presented. During each vote, each member of the BRT was given 10 points to cast for the most appropriate DPS into which to place Southern Residents, given a presumed taxonomy. The table is read across; each row shows results for a different taxonomic scenario. For example, the first row in the body of the table indicates that when the BRT assumed Southern Residents belonged to a taxon consisting of Northern Pacific residents (III), designating Southern Residents (I) a DPS received 48 points (48% of vote), designating Northeast Pacific resident killer whales (II) a DPS received 27 points, etc. A previous vote (not shown) indicated that each of the taxa (III to VI) received nearly equal support from the team; the taxon II received little support, so it is not included in the table. Results are presented for taxon VII (global species) because this is the currently accepted taxonomy that is used in the petition requesting that Southern Resident killer whales be listed as a threatened or endangered species.

[b] I. Southern Resident killer whales only

[c] II. Northeast Pacific resident killer whales

[d] III. North Pacific residents killer whales

[e] IV. North Pacific resident and offshore killer whales

[f] V. All resident and offshore killer whales

[g] VI. The mtDNA lineage containing Southern Residents (SWFSC unpubl. data)

[h] VII. The currently recognized global species of killer whales

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between residents and transients that BRT members agree is significant is much greater than the difference between resident groups.

Arguments in favor of Southern Residents as a DPS of the global species

There are some indications that Southern Resident killer whales might be a remnant of a more extensive population that extended to the south, and if this hypothesis is accurate, the following arguments would have merit. However, this hypothesis received only a little BRT support (Table 8).

Persistence in an ecological setting that is unusual or unique for the taxon—There are large oceanographic differences between the California Current system and the Alaska Gyre system, but the relevance of these differences depends upon how Southern and Northern Residents use habitat in late fall and winter (currently unknown). In addition, Southern Residents may feed primarily on salmon with different population dynamics than that of salmon utilized by other resident populations, as there is an inverse production regime between salmon in the California Current system versus salmon in the Alaska Gyre system. However, lack of detailed studies prior to the loss of major salmon runs in the Columbia River and Central Valley of California make it difficult to reach any conclusions concerning historical distribution of residents.

Loss would represent a significant gap in the range of the taxon—The Southern Resident population was perhaps significantly larger in the past. One hypothesis is that this larger population may have utilized the coastal habitat from southern British Columbia to California more frequently than current observations would suggest (i.e., range contraction has occurred). Additionally, given the general lack of sighting data in the winter, Southern Residents may use outer coast waters in Washington, Oregon, and California more frequently than is currently recognized. Although killer whales are known to eat fish in other locations around the world, there is no concrete evidence that resident whales (defined genetically and as an ecotype specializing in coastal salmon) exist outside the North Pacific. Therefore, the extended range (California to southern British Columbia) of the Southern Residents represents a significant portion of the range of resident killer whales, which extends at least from California to the central Aleutian Islands (and may extend further westward to Russia and Japan). If Southern Residents were extirpated, it is not known whether resident killer whales would recolonize the Northeast Pacific, so the continued existence of residents in this area may be dependent upon the persistence of the current Southern Resident population.

Evidence that Southern Residents differ markedly from other populations in genetic characteristics—Southern Residents have genetic diversity in nuclear markers consistent with a larger population size and likely not consistent with a population that has a long-term abundance equal to the current abundance. Differences in mtDNA between Southern and Northern Residents most likely stem from a colonization event (from Alaska Residents) following the last ice age. However, the isolation-by-distance indicated by the nuclear genetic data signifies that Southern Residents are now only distantly related to Alaska Residents (Figure 2; i.e., as different as offshores are from transients). Also, it was not possible to do genetic studies to estimate historical abundance, because the Southern Residents are either insufficiently sampled or relevant samples are unavailable for analysis. In addition, Southern Residents may have lost social complexity (e.g., number of acoustic clans and pods) when compared with other residents.

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Furthermore, a frequency difference exists in saddle patch pigmentation types between Southern Residents and other resident populations. This is not sufficient evidence to conclude they are markedly different, but such differences in morphology are consistent with possible local adaptation.

Other considerations—Southern Residents as a DPS of the global species

Other factors were discussed by the BRT in determining whether Southern Residents should be considered a DPS of the global species. If Southern Residents were considered as such and the geographic area known to be occupied by the Southern Residents were replicated globally, it would imply that the killer whale taxon consists of many, many DPS units. This scenario seemed unlikely to nearly all BRT members. In addition, BRT members discussed the importance of the Southern Residents to the culture in the Pacific Northwest and concluded that, although Southern Residents are certainly a very important cultural icon, this has no bearing on whether the population is genetically distinct, evolutionarily or ecologically significant, or at risk of extinction. BRT members discussed the importance of pod-specific traits, such as acoustic repertoire, that have been described by some biologists as "cultural" traits of Southern Resident killer whales. BRT members generally agreed that there was insufficient evidence to indicate whether these "cultural" traits were inherited or learned, and thus whether they truly signify an evolutionarily important trait.

3.4.3. What is the DPS (Global Species Taxon) to which Southern Residents Belong?

After concluding that Southern Residents are not a DPS of the global species, the BRT attempted to define what is the DPS to which Southern Residents belong within the global species taxon (see Figure 11). However, little effort was spent defining this DPS, because the BRT had concluded that the global species is an outdated concept that needs to be updated.

The strongest support (about a third of the votes) was for a DPS that includes all North Pacific Residents (i.e., Southern, Northern, Alaska, and Western North Pacific Residents) (Table 8). The rationale for this vote would include similar habitat use (primarily coastal), pod size and structure (large pod size), and feeding ecology (all animals feed primarily on fish) among all the North Pacific resident whales. Another quarter of the votes supported the next larger DPS—North Pacific resident and offshore killer whales. Arguments for this DPS include that nuclear DNA differences are insufficient to be considered "marked," habitat differences between offshores and residents are not different enough to be considered as unusual habitats separately, and a loss of residents alone from the North Pacific would not represent a significant gap in the range of this taxon. In addition, the BRT considered other larger DPSs to which Southern Residents might belong, but there was little support for these other DPS possibilities (Table 8).

3.4.4. Would Southern Residents Be a DPS of an Alternative Taxon?

There is sufficient new information on the genetics and ecology of killer whales to warrant reexamination of their taxonomic classification. Therefore, the BRT's conclusion that Southern Residents do not qualify as a DPS within the current taxonomy (subsection 3.4.1) did not resolve the question of whether Southern Residents qualify as a DPS within an undefined

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smaller taxon (see Figure 11). As described in subsection 3.2.2, the BRT compiled a list of all taxa to which Southern Residents might belong, and five alternatives were proposed: (III) North Pacific resident killer whales, (IV) Northern Pacific killer whales, (V) all resident and offshore killer whales, (VI) all populations of killer whales within the mitochondrial lineage consistent with fish eating, and (VII) the global species of killer whales.

The BRT believed that Southern Residents belong to a taxon as small as North Pacific resident killer whales, but no larger than the mtDNA lineage consistent with fish eating (see subsection 3.2.2 and footnote a of Table 8). In order to evaluate the effect of this taxonomic uncertainty upon the DPS designation for the Southern Residents, the BRT members voted their points to designate the DPS to which Southern Residents belong under each of the alternative taxa III to VI (Table 8). The BRT votes expressed a large degree of uncertainty: team members cast their points for at least two and no more that four of the alternatives, with the exception of one team member giving all points to the taxon III alternative. The reasoning for Southern Residents being a DPS of each of the following alternative taxa is given below.

Taxon—North Pacific resident killer whales

The strongest support for considering Southern Residents as a DPS was found under the most restricted (smallest) taxon considered by the BRT—North Pacific resident killer whales (III). When this taxonomy was assumed to be correct, about half of the support went to Southern Residents qualifying as a DPS (Table 8). The summer range of Southern Residents would represent a significant portion of the (North Pacific resident) taxon's range (known to be from Washington State to the central Aleutians, and assumed likely to include the California Current, as well as coastal Russia and Japan). However, if the extended range of Southern Residents is considered (California to southern British Columbia), this would represent an even larger portion of the taxon's range. In addition, if only North Pacific resident killer whales are considered, differences in prey preferences (e.g., consumption of salmon from the California Current by Southern Residents) become more important. Moreover, the genetic differentiation of Southern Residents, as well as differences in saddle patch types, should be considered, even if the differences are small when compared to other residents.

The remainder of the BRT vote was split equally between two other possible DPSs—Northeast Pacific residents or the entire unit of North Pacific residents—within the North Pacific resident taxon. Arguments in favor of these DPSs would include different interpretations about whether the primary range of Southern Residents constitutes "a significant portion" of the range of the taxon. If their range is considered to be confined mainly to Washington and southern British Columbia (i.e., sightings off Oregon and California represent only occasional forays outside a limited foraging area), then their primary range represents a much smaller portion of the range of the taxon North Pacific resident killer whales. Southern Residents may eat salmon from a different current system from other residents, but there is no reason to consider this an unusual ecological setting for resident killer whales in the North Pacific. Furthermore, genetic difference between Southern Residents and other North Pacific residents can be considered inconsequential, as differences between Southern Residents and other residents are considerably smaller than those between residents and other populations (e.g., transients and offshores) in the North Pacific. In addition, the biological significance of variation in saddle patch morphology in killer whales is uncertain.

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Taxon—North Pacific resident and offshore killer whales

The next largest taxon considered North Pacific residents and offshores together (IV). Although there are few observations, offshores are considered to be fish eaters. Offshores differ little in their mtDNA, but differ strongly in nuclear DNA, indicating extremely low gene flow between these groups. About a quarter of team points supported defining Southern Residents as a DPS assuming this taxon. The arguments for Southern Residents as a DPS relative to this taxon would be similar to those in the previous subsection showing that Southern Residents differ significantly from other resident populations, but adding arguments for differences between Southern Residents and offshores. For example, Southern Residents (and other residents) have marked differences in microsatellite DNA from offshore-type whales (Figure 2). In addition, Southern Residents occupy a more coastal habitat than do offshores. Furthermore, arguments based on apparent specialization in salmon can be made, as offshore-type whales are not known to similarly specialize in salmon.

Another third of the points supported Northeast Pacific residents as a DPS. The rationale for this vote would include that, although Southern Residents are too similar to other Northeast Pacific residents for Southern Residents alone to constitute a DPS, residents on either side of the North Pacific basin would likely be isolated by distance combined with a significant habitat difference through the Aleutian region. The scenario most strongly supported by the BRT vote (about 40%) was the DPS comprising all North Pacific residents (as opposed to offshores). During this deliberation, some team members emphasized the ecology of offshore killer whales is not well known. Those supporting this DPS designation thought that there were no unusual habitats within the range of residents in the North Pacific and that only loss of all residents would constitute a significant gap in the range with respect to offshores taken together with residents in the North Pacific. Only the genetic differences between offshores and residents would be considered "marked."

Taxon—resident and offshore (fish-eating) killer whales

The next taxon considered global distributions of residents and offshores (or perhaps fish eaters if the group is monophyletic, i.e., has arisen only once). The actual distribution of this "taxon" is unknown, as global sampling remains poor. Although residents and offshores are clearly more similar to several Atlantic samples than they are to transients, it is not clear that the Atlantic samples would be considered either residents or offshores. The sampling of offshores is very poor (n = 7; Barrett-Lennard 2000, Barrett-Lennard and Ellis 2001), making it impossible at this stage to assess their relation to killer whales in other ocean basins. Nevertheless, this "taxon" generally considers a distribution that is larger than the North Pacific. About 10% of the points were cast for Southern Residents as a DPS within this taxon, believing that the unknown increase in range did not change their view of qualifying under the criteria. However, there was a clear shift toward support for larger and larger DPS units as the taxon became larger. For example, a quarter of the vote supported all North Pacific residents and offshores as a DPS. The rationale for this decision would consider that the genetic differences between offshores and residents are not "marked," that only loss of all residents and offshores in the North Pacific would result in a significant gap in the range, and that there were no unusual habitats within the North Pacific.

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Taxon—the mtDNA lineage

The final taxon considered plausible was the mtDNA lineage that includes fish eaters. A maximum likelihood phylogram revealed two strongly differentiated groups (see subsection 2.2.3): 1) the mtDNA lineage including residents, offshores, and two samples from the Atlantic, and 2) transients. Preliminary work at the NMFS Southwest Fisheries Science Center suggested that the mtDNA lineage also includes individuals from the Pacific, Atlantic, and Antarctic and the transient group includes two killer whales from Antarctica. As previously mentioned, the actual dietary preferences of at least the Antarctic individuals is unknown. In addition, the exact range of the mtDNA lineage globally is unknown. There was correspondingly less support within the BRT for calling Southern Residents a DPS of this alternative taxon. Although about 10% of the vote indicated that Southern Residents still met at least one of the DPS criteria, an equal proportion of the vote indicated that, given this taxon, the DPS should be the global distribution of residents and offshores. Thus at least some members believed that habitat found in different ocean basins would not qualify as "unusual," that it would take the loss of all residents and offshores globally to constitute a "significant gap in the range," and that there were no marked differences genetically in the global resident and offshore killer whales.

3.4.5. DPS Summary

In the discussion above, the team considered only the scientific plausibility of the various taxa and DPS scenarios. No attempt was made to consider the DPS decision in light of extinction risks. Taxonomic uncertainty, lack of key scientific information (e.g., genetics of worldwide killer whales), and differences in opinion within the BRT prevented the team from reaching a consensus regarding the DPS to which Southern Resident killer whales belong. The BRT agreed on two points: 1) Southern Resident killer whales are not a DPS of the currently recognized global species of killer whales, and 2) there are unrecognized species or subspecies of killer whales within the currently recognized taxon (the global species). The strongest support for recognizing Southern Residents as a DPS occurred when the North Pacific resident killer whales were considered as the taxon. About half the BRT vote supported Southern Residents as a DPS of this taxon.

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4. ASSESSMENT OF EXTINCTION RISK

4.1. Previous Assessments of Extinction Risk

The only previous assessments of extinction risk for Southern Resident killer whales were the PVAs conducted by the petitioners (Plater 2001, Taylor and Plater 2001). These are briefly summarized in subsection 1.3.5.

4.2. Population Viability Analysis: Approach

PVA models are used to integrate various risks a population faces into an estimate of the probability the population will go extinct. PVAs generally involve fairly complex models, with many parameters that need to be specified. Generally, population models are used that include demographic and environmental variability, as well as Allee effects (reduction in the population's growth rate that occurs when a population is at a very small size). Often an age-structured model is used and a variety of other factors are included, such as density dependence and catastrophes (large mortality events). Several recent papers have summarized current practices in the use of PVAs (Beissinger and Westphal 1998, White 2000). Current PVA methods, particularly those using general software programs such as VORTEX (Bob Lacy, Dept. Conservation Biology, Chicago Zoological Society, Brookfield, IL) and RAMAS (Applied Biomathematics, Setauket, NY), rarely incorporate parameter uncertainty despite a concern that such uncertainties in ecological data are often very large. PVAs that ignore uncertainty in classifying populations according to risk (such as under International Union for Conservation of Nature and Natural Resources [IUCN] criteria) or in estimating the probability of extinction can be misleading and inaccurate (Taylor 1995, Ludwig 1996, Ralls and Taylor 1997, Ludwig 1999, White 2000, Taylor et al. in press, Wade in press).

A population model was developed to assess the extinction risk for Southern Resident killer whales. It was age-structured, sex-structured (to account for differences in survival between males and females), and pod-structured (to track the dynamics of different killer whale pods separately). Factors incorporated into the model included demographic and environmental variance, an Allee effect based on killer whale breeding biology, density dependence, and large mortality events (to simulate the possibility of a "catastrophe," such as an oil spill, that could have a relatively large impact on the population). Finally, uncertainty from sampling error in the survival estimates was incorporated into the analysis.

As discussed in section 3, there is uncertainty regarding whether Southern Resident killer whales represent a DPS by themselves or whether they are part of some larger DPS. Therefore, two scenarios were examined—one for each of two possible population units. The first scenario was one for Southern Resident killer whales alone and the second assumed that Southern Residents were part of a larger population unit that included Northern and Alaska Residents (Northeast Pacific Residents; also this is the "eastern North Pacific northern resident" stock defined for management under the MMPA and is the smallest likely DPS of the global species).

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4.3. Surrogates for Extinction Risk

An alternative to a PVA is to use a surrogate measure, for example, a declining population or a small population size that is thought to be a strong indicator of extinction risk. The IUCN Red List uses this approach to categorize species as vulnerable, endangered, or critically endangered. This system is designed to provide a relatively objective method for classifying a wide variety of species with varying amounts and kinds of data available.

A species with less than 50 mature (breeding) individuals qualifies as critically endangered on the IUCN Red List. The IUCN set this threshold because experience and modeling have shown that populations this small are at high risk of extinction from demographic and environmental stochastic variation, as well as from Allee effects (see subsection 4.4). As of June 2001, there were a total of 34 Southern Resident killer whales that were either females age 11-41 or males older than age 15. Two more individuals would be included if males down to age 11 are considered and there are an additional three females age 42-49. Therefore, if the Southern Resident killer whales were a recognized species, they would qualify as critically endangered under the IUCN classification system.

Southern Resident killer whales are not currently listed under IUCN, where the focus has been on listing species-level units. However, there have been an increasing number of subspecies level populations listed in recent years (e.g., North Island Hector's dolphins [*Cephalorhynci hectori*], one of at least three populations of that species).

4.4. Population Viability Analysis: Models and Inputs

As noted above, an age-, sex-, and pod-structured stochastic population model was used. The numbers of whales alive in each age class of each sex and of each pod membership were tracked from one year to the next. Pods were assumed to have the same survival and fecundity rates (Wade unpubl. data). The initial pod size, age structure, and sex structure was that from the year 2001.

Because the PVA was initiated at the current estimated age and sex distribution of the population, it should implicitly include any demographic effects caused by the disruption to the age and sex structure of the population that took place from the live-capture removals that occurred from 1964 to 1975. It is possible to imagine other consequences of the removals, such as disruption of the social structure of individual pods, which could have unknown consequences on reproduction and survival. Although it has been suggested that the removals led to reduced reproduction after the mid-1970s, the population generally increased into the 1990s. Further, the recent decline in the population has been more a consequence of an unprecedented 9-year period of relatively poor survival, rather than a period of poor reproduction.

Simulations to project the population for 300 years were repeated 10,000 times, each time keeping track of the fate of the projected population. The number of times a simulated population went extinct was tabulated after 50, 100, 200, and 300 years. Extinction occurred when either no females or no males remained in the population.

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Demographic variance was incorporated by sampling births and deaths from a binomial distribution, using the specified fecundity or survival rate. For example, if a survival rate for a particular age and sex class was 0.98 and five whales were in that category, a random number was drawn from a binomial distribution with probability 0.98 with five trials. The number of "successes" represents the number of whales that survive, which can range from 0 to 5. This is one of the standard ways in which demographic variance is incorporated into a PVA, as this should correctly mimic the random nature of births and deaths in nature.

Environmental variance was incorporated using the temporal survival model that best fit the data based on the AIC criterion. This model held survival constant for 6-year periods, starting with a full 6-year period, with survival scaled differently for each age and sex category (Table 5). There are five periods with different survival rates (4 of 6 years, and 1 of 3 years), which represent five sets of survival rates for each age and sex category. In the model, survival rates were specified by randomly sampling one of these five sets of survival rates, then keeping these survival rates constant for the appropriate number of years (either 6 or 3). Having a long timeline of highly detailed information available on the population dynamics of Southern Resident killer whales is a significant advantage in this analysis, because the parameter estimates directly model the specific fluctuations in survival observed in this population. Usually, PVA models have to make assumptions about how much environmental variance there is in life history parameters.

The usual practice of using only point estimates of parameters in specifying PVA models ignores parameter uncertainty (White 2000, Taylor et al. in press, Wade in press). Parameter uncertainty was incorporated by sampling survival rates from beta distributions, with mean and standard deviation equal to the estimates of survival and their associated standard error respectively. For example, if the estimated survival rate were 0.953 with a standard error of 0.019, a survival rate would be randomly sampled from a beta distribution with those parameter values. Of those randomly selected values, 90% would be between 0.919 and 0.979, and 99.99% would be between 0.847 and 0.995. These values would be held constant over the entire duration of a projection.

Although Allee effects are difficult to study and little is generally known about these effects in marine mammals (Fowler and Baker 1991, Wade in press), it is necessary to make assumptions in many PVAs about what kind of Allee effect would occur in a small population. In the absence of direct evidence of the level at which an Allee effect would take place, or what the mechanism of the effect would be, PVAs often include a pseudo-extinction level (a threshold set at a low population size, where it is assumed that extinction is inevitable if that threshold is reached). However, the killer whale paternity study (Barrett-Lennard 2000, Barrett-Lennard and Ellis 2001) provides direct evidence for a biological mating system that would cause an Allee effect, allowing this effect to be directly incorporated into the model. Barrett-Lennard (2000) and Barrett-Lennard and Ellis (2001) found that resident killer whales typically mated outside their pod. If this mating behavior is strictly followed by Southern Residents, then the birth rate of females in one pod would drop to zero if there were no sexually mature males in any of the other pods, even if there were mature males in the female's own pod. Thus an Allee effect was incorporated into the model by tabulating the number of sexually mature males in each pod and then reducing the fecundity for a pod to zero if there were no adult males left in any other pod.

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Whether and how density dependence is included in the PVA has been shown to have a strong influence on the model results (Mills et al. 1996). In particular, the level assumed for carrying capacity can have a strong influence on the PVA. Density dependence was included in the PVA for Southern Resident killer whales through a decrease in both fecundity and survival at carrying capacity. Fecundity and survival declined by 10% and 1%, respectively, for each year the population was at or above carrying capacity. Once the population returned to a level below carrying capacity, fecundity and survival increased by 10% and 1% for each year the population remained below carrying capacity, until fecundity and survival had returned to their expected level in the absence of density dependence. This resulted in a gradual increase in the density dependent response, rather than the usual abrupt form of density dependence that would result from a typical parametric model, such as a logistic function. It was also designed to roughly mimic a situation where continued lack of resources at carrying capacity for multiple years leads to increasingly poor condition in individuals, resulting in lower fecundity or survival.

Implementing density dependence in this way is also a relatively mild restriction on the population, because there is no effect of density dependence other than to create an upper bound which the population will not exceed by any substantial amount. A logistic function, as used in VORTEX or RAMAS, would cause declines in fecundity or survival at levels well below carrying capacity and would lead to a higher risk of extinction. Implementing density dependence as described above, therefore, results in a lower risk of extinction than a logistic function for a given carrying capacity. The rationale for using this form of density dependence is that if the population is currently near carrying capacity, then any density dependent effects that occur at population levels below carrying capacity will have already affected the population. This would make sense, because the population has only increased at a small overall rate during 27 years. These density-dependent effects will already be encapsulated in the estimated survival and fecundity rates of the population.

Because this is a density-dependent model, the survival and fecundity rates become lower when the population reaches the carrying capacity level specified in the model. Because the population approached 100 in the mid-1990s (97 in 1996), if carrying capacity truly was around 100, the population would have experienced some density dependent decline in vital rates. When using the full time-series of data, the maximum vital rates (survival and fecundity rates when the population is well below carrying capacity) would be underestimated to an unknown degree and would lead to the model overestimating the risk of extinction. Given that the population spent little time near a level of 100, it is unlikely this was a strong bias if carrying capacity truly was approximately 100 animals. However, there is little conclusive evidence of what the carrying capacity might be for Southern Resident killer whales (subsection 2.4.4). Therefore, a range of values from 100 to 400 for carrying capacity was considered.

Large mortality events, or catastrophes, were implemented as a binomial probability. The probabilities of occurrence of catastrophes of 0% (no mortality events), 1%, or 2% per year were selected because they bracket the likely range of possible catastrophes. A uniform random number between 0 and 1 was generated, and if it was below 0.01 (for example), a catastrophe would occur in that year. The magnitude of the event was randomly drawn from a normal distribution with mean of 10% and standard deviation of 2%. This represents the fractional decline in survival that occurs, which is a mean of 10%, staying mostly within the range 6-14%. A fourth case was specified with a 2% probability of occurrence of a catastrophe and a

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magnitude of mean 20%. Potential sources of such mortality events are oil spills and disease (see subsection 2.4.3). To put these magnitudes in context, over the four years following the *Exxon Valdez* oil spill, the AB pod from Prince William Sound lost 40% of its members. The PVA model did not use a magnitude this high (40%), because all the models consider not just pods but rather populations composed of many pods distributed over a larger area than that affected by the Prince William Sound oil spill.

Two different survival scenarios were simulated in order to bracket the possible ranges of future population dynamics. In the first scenario, the survival rates were taken from the entire study period, 1974–2001. This scenario assumes that the fluctuations in survival seen over the last 28 years are representative of the expected variability in survival in the future. In the second scenario, the survival rates were taken from the last 9 years of the study, 1992–2000, which represented the period with the lowest survival rates. This scenario is the most pessimistic. It assumes that whatever has caused the decline in survival will not reverse itself and that survival rates will stay at this low level for the foreseeable future. This is not necessarily a worst-case scenario, as survival has apparently declined over the last 9 years (see Figure 5), and could conceivably continue to decline.

PVA scenarios were examined for two different population units. In the first, Southern Resident killer whales alone were considered to be a unit. The initial population was set to the known age and sex distribution in May/June 2001, at a population size of 78. In the second scenario, Southern, Northern, and Alaska Residents were considered a population unit. The stock assessment report for Northern and Alaska (i.e., Northeast Pacific) Residents revealed a total minimum population size of approximately 717 (Hill and DeMaster 1999). Therefore, a minimum population size would be approximately 795 (~717 + 78) whales. As a result, the initial population was set to 800 in 21 pods with an age and sex distribution similar to that of Southern Residents. This roughly mimics the current pod, age, and sex distribution of this combination of populations.

4.5. Population Viability Analysis: Results

4.5.1. Southern Residents as the Population Unit

Using 1974–2000 survival rates

As expected, carrying capacity had a strong influence on the estimated risk of extinction (Figure 12), with all simulations using a level of 200 or more having nearly identical results (i.e., the risk of extinction was 0% at 50 years and 100 years, 2% after 200 years, and 5% after 300 years). When carrying capacity was reduced to 100, the risk of extinction was the same out to 100 years, but rose to 3% in 200 years and 18% after 300 years.

When a 1% probability of a large mortality event was included, the estimated risk of extinction rose a small amount (Figure 13). There was still little chance of extinction after 50 or 100 years, but with carrying capacity at 200 or more, the chance of extinction was 2-3% after 200 years and 7-8% after 300 years. At a carrying capacity of 100, the chance of extinction rose to 5% after 200 years and 23% after 300 years. At higher catastrophe rates and magnitudes, the

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risk of extinction rose as high as 21% after 200 years and 51% after 300 years (Figure 14 and Figure 15).

Using 1992–2000 survival rates

Under this pessimistic scenario, survival rates of Southern Residents would continue at the low levels seen over the last 9 years. The risk of extinction was mostly independent of any assumption about carrying capacity, because the simulated populations were on average declining, and as a result, spent little time near carrying capacity (Figure 16 to Figure 19). Similarly, the rate and magnitude of catastrophes made little difference to the overall results. With a declining population, extinction is inevitable, so catastrophes just hasten the demise of the population. At 50 years with no catastrophes, the risk of extinction was less than 1% (Figure 16), but was more than 2% for the severest level of catastrophes (Figure 19). Risk of extinction was 12-30% at 100 years, 67-89% at 200 years, and 86-98% at 300 years.

4.5.2. Southern, Northern, and Alaska Residents as the Population Unit

Using 1974–2000 survival rates

This scenario assumes this entire population unit would experience the same survival and fecundity rates that the Southern Residents have experienced the last 27 years. Before new information on population declines of Northern Residents was received (see subsection 1.4), this was considered a somewhat pessimistic scenario, because Northern Residents had been thought to have experienced a greater increase in population size than Southern Residents (Olesiuk et al. 1990, Brault and Caswell 1993). The new information makes this scenario more likely; however, even under this scenario, there was zero risk of extinction according to the model, even at 300 years with the severest level of catastrophes (Figure 20 and Figure 21).

Using 1992–2000 survival rates

This scenario assumes that Northern and Alaska Residents would experience the same low survival rates as Southern Residents have over the last 9 years. Before the information on the population declines of Northern Residents was received, there was little reason to consider this scenario plausible for this total unit, as it represents a period of low survival for Southern Residents that occurred during a period of substantial population decline. However, this scenario is still somewhat pessimistic, because residents in southeast Alaska have increased steadily (Dahlheim footnote 8) over the last 28 years, even if Northern Residents have experienced a recent decline. For completeness, this scenario was examined for the larger population size of 800.

When carrying capacity was 800 whales, the risk of extinction was near zero at 50 and 100 years, 5% at 200 years, and was as high as 20% for a population experiencing the most severe rate of catastrophes (Figure 22). The risk of extinction was nearly zero under the assumption that carrying capacity was 1,600 whales (Figure 23).

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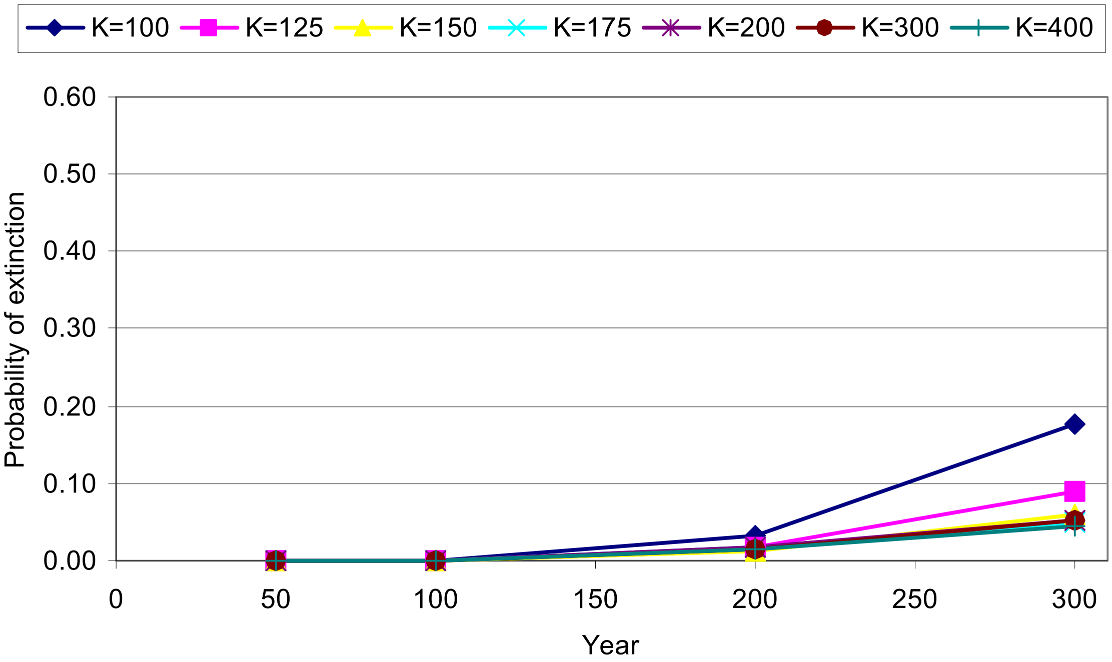

Figure 12. Estimated risk of extinction at 50, 100, 200, and 300 years for the Southern Resident population, assuming 1974–2000 survival rates continue, with no catastrophes (K is carrying capacity).

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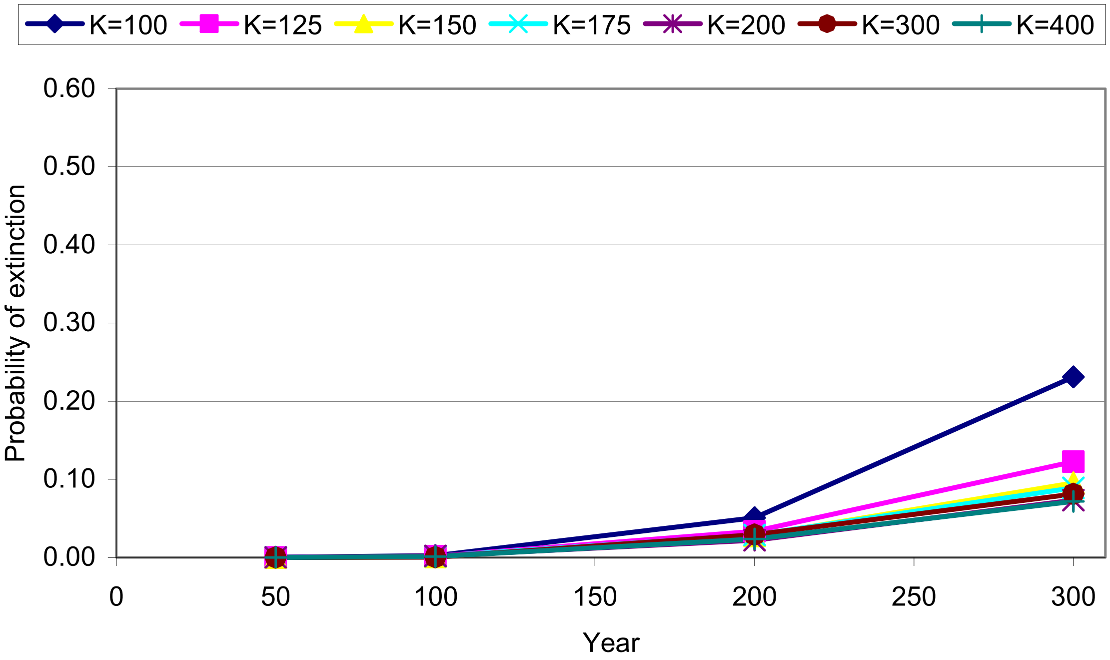

Figure 13. Estimated risk of extinction at 50, 100, 200, and 300 years for the Southern Resident population, assuming 1974–2000 survival rates continue, with a 1% probability of a catastrophe with an average of a 10% decline in survival for 1 year (K is carrying capacity).

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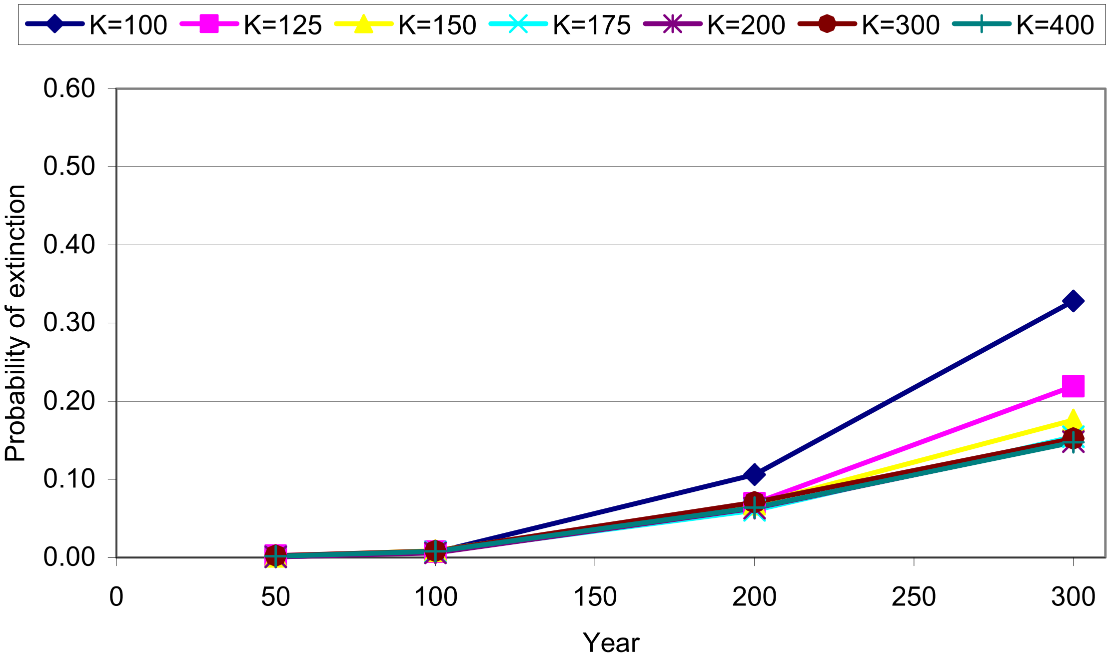

Figure 14. Estimated risk of extinction at 50, 100, 200, and 300 years for the Southern Resident population, assuming 1974–2000 survival rates continue, with a 1% probability of a catastrophe with an average of a 20% decline in survival for 1 year (K is carrying capacity).

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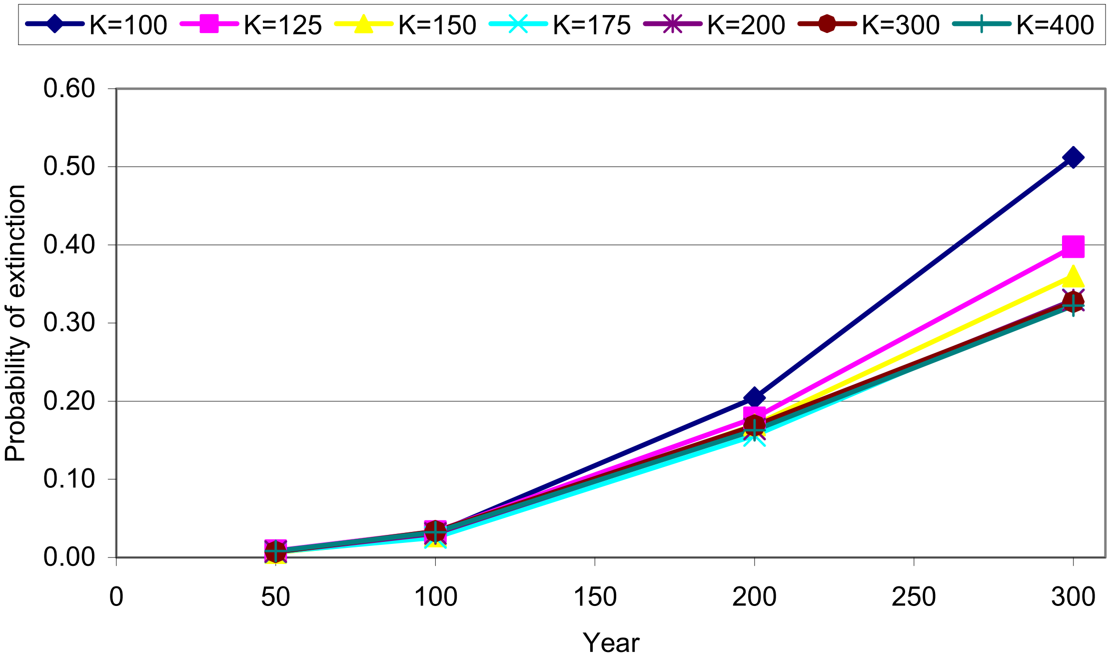

Figure 15. Estimated risk of extinction at 50, 100, 200, and 300 years for the Southern Resident population, assuming 1974–2000 survival rates continue, with a 2% probability of a catastrophe with an average of a 20% decline in survival for 1 year (K is carrying capacity).

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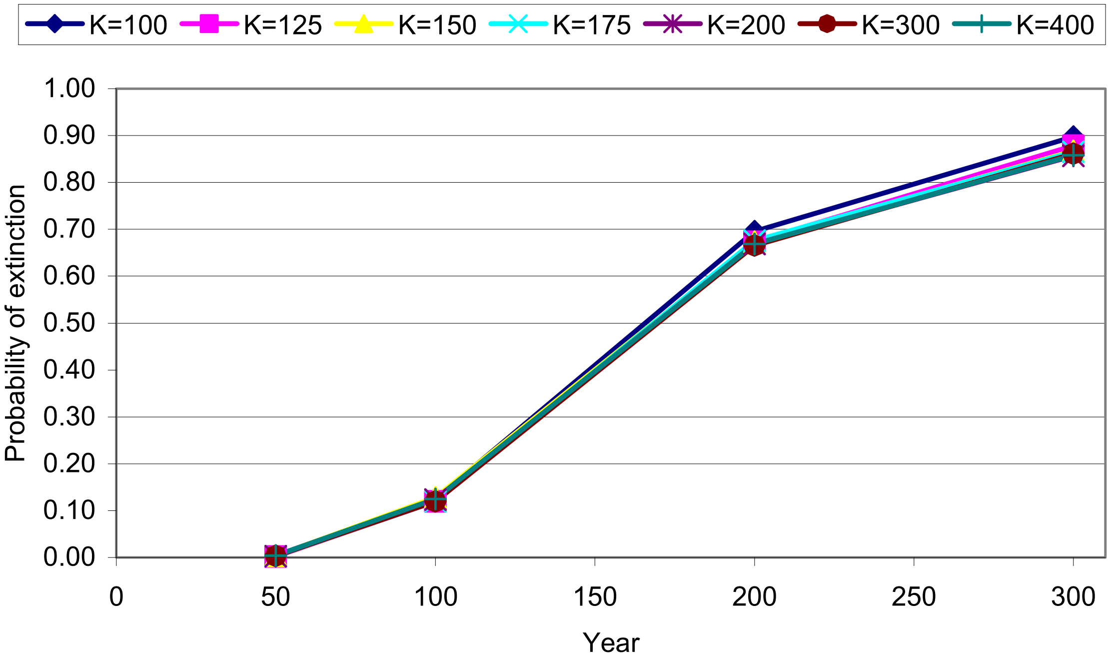

Figure 16. Estimated risk of extinction at 50, 100, 200, and 300 years for the Southern Resident population, assuming 1992–2000 survival rates continue, with no catastrophes (K is carrying capacity).

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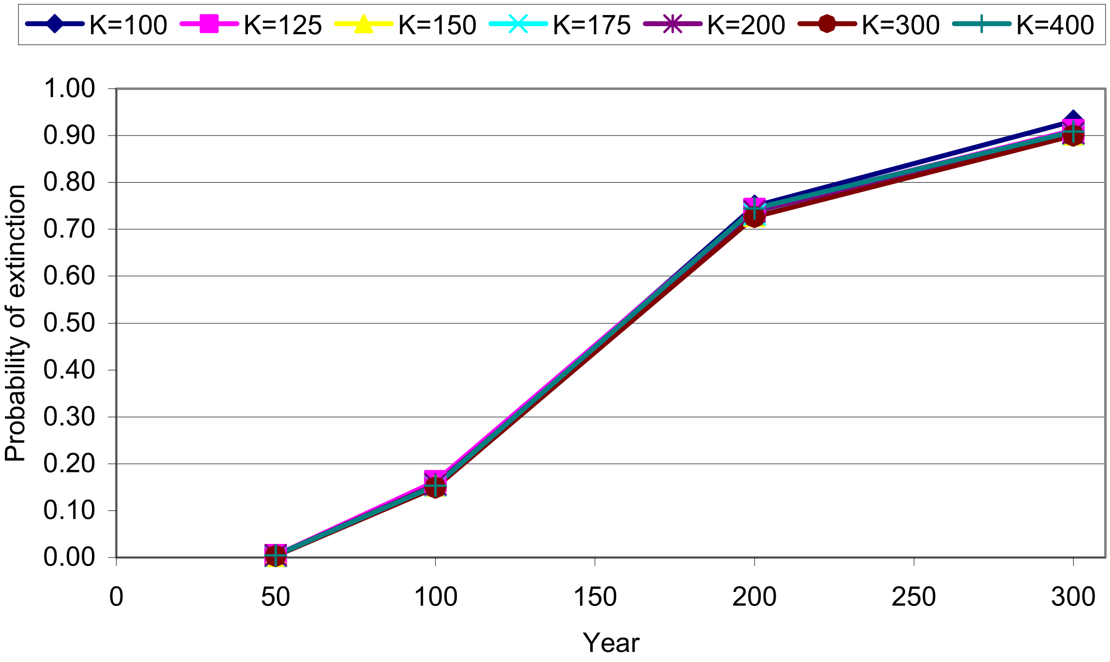

Figure 17. Estimated risk of extinction at 50, 100, 200, and 300 years for the Southern Resident population, assuming 1992–2000 survival rates continue, with a 1% probability of a catastrophe with an average of a 10% decline in survival for 1 year (K is carrying capacity).

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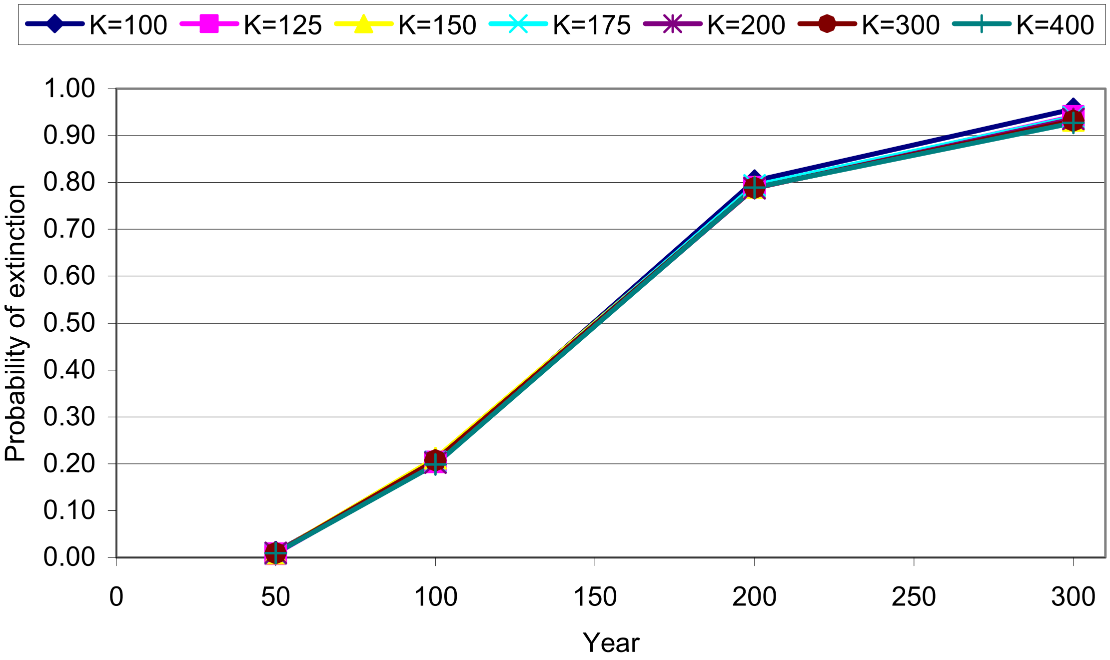

Figure 18. Estimated risk of extinction at 50, 100, 200, and 300 years for the Southern Resident population, assuming 1992–2000 survival rates continue, with a 1% probability of a catastrophe with an average of a 20% decline in survival for 1 year (K is carrying capacity).

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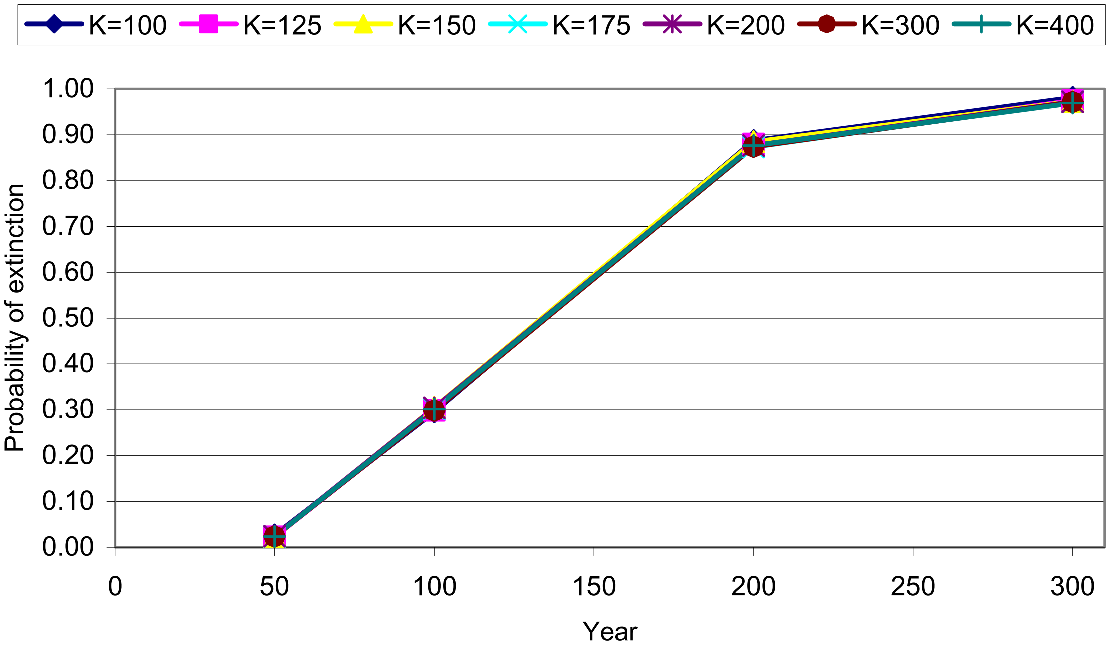

Figure 19. Estimated risk of extinction at 50, 100, 200, and 300 years for the Southern Resident population, assuming 1992–2000 survival rates continue, with a 2% probability of a catastrophe with an average of a 20% decline in survival for 1 year (K is carrying capacity).

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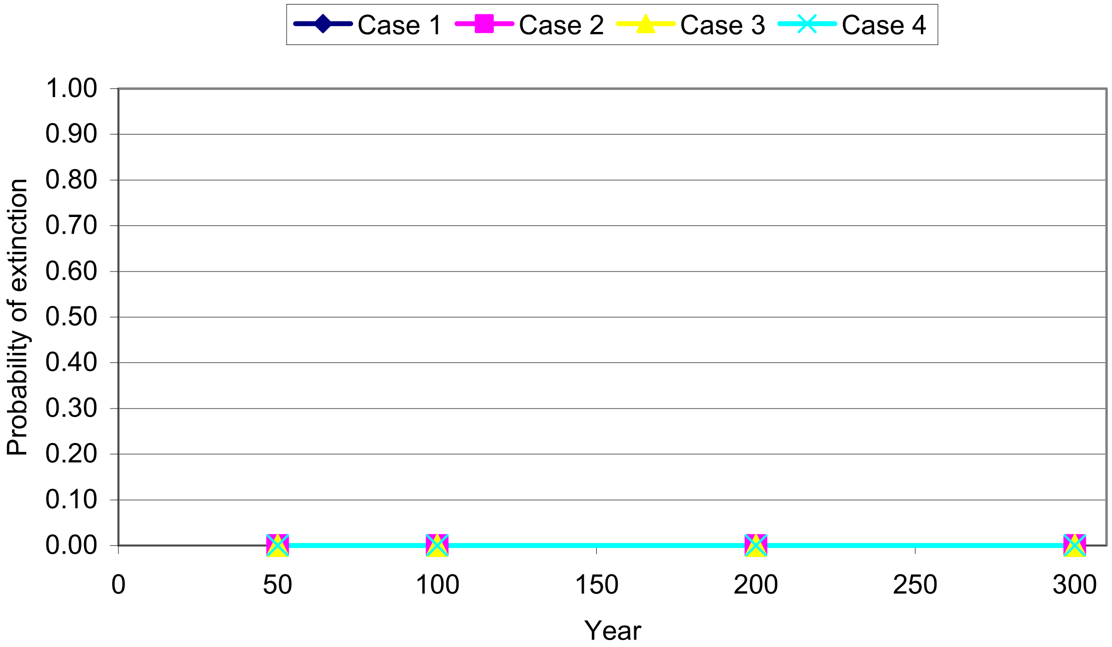

Figure 20. Estimated risk of extinction at 50, 100, 200, and 300 years for the combined populations of Southern, Northern, and Alaska Residents, assuming 1974–2000 survival rates of Southern Residents are experienced by both Southern and Northern Residents. Carrying capacity was set at 800 whales. Case 1 is no catastrophes, Case 2 is a 1% probability of a catastrophe with an average of a 10% decline in survival for one year, Case 3 is a 1% probability of a catastrophe with an average of a 20% decline in survival for 1 year, and Case 4 is a 2% probability of a catastrophe with an average of a 20% decline in survival for 1 year.

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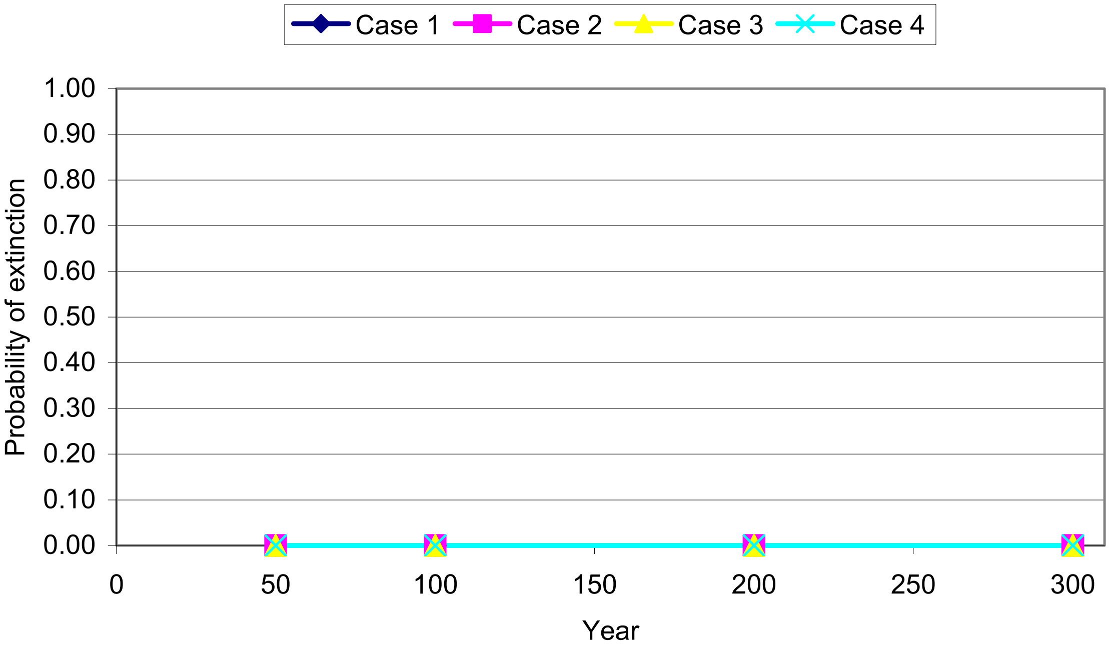

Figure 21. Estimated risk of extinction at 50, 100, 200, and 300 years for the combined populations of Southern, Northern, and Alaska Residents, assuming 1974–2000 survival rates of Southern Residents are experienced by both Southern and Northern Residents. Carrying capacity was set at 1,600 whales. Case 1 is no catastrophes, Case 2 is a 1% probability of a catastrophe with an average of a 10% decline in survival for 1 year, Case 3 is a 1% probability of a catastrophe with an average of a 20% decline in survival for 1 year, and Case 4 is a 2% probability of a catastrophe with an average of a 20% decline in survival for 1 year.

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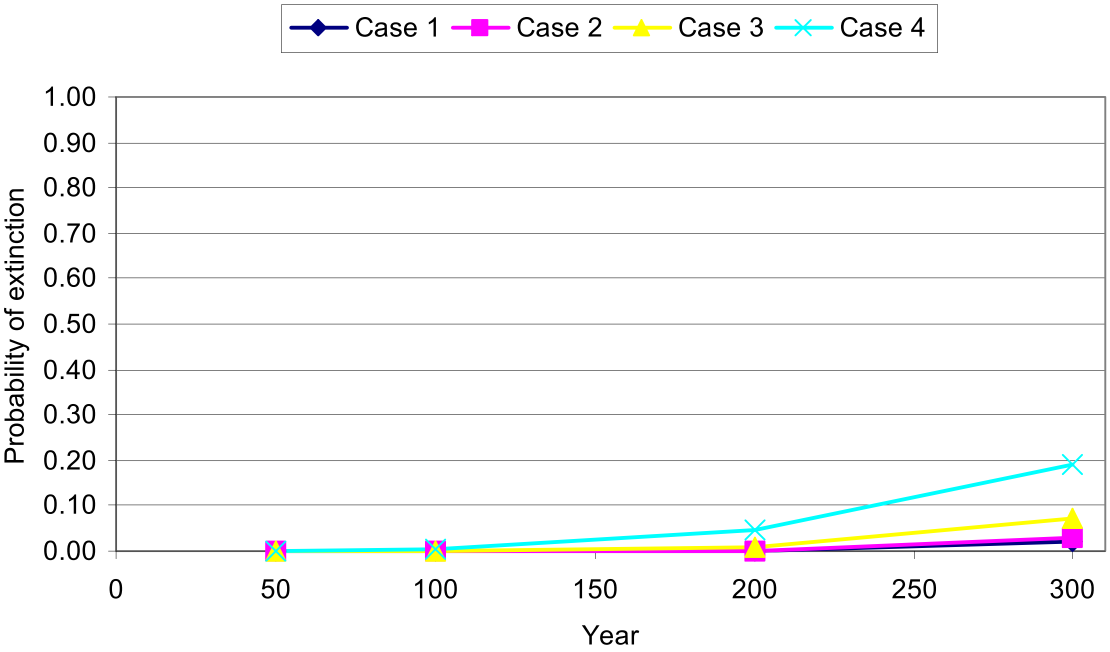

Figure 22. Estimated risk of extinction at 50, 100, 200, and 300 years for the combined populations of Southern, Northern, and Alaska Residents, assuming 1992–2000 survival rates of Southern Residents are experienced by both Southern and Northern Residents. Carrying capacity was set at 800 whales. Case 1 is no catastrophes, Case 2 is a 1% probability of a catastrophe with an average of a 10% decline in survival for 1 year, Case 3 is a 1% probability of a catastrophe with an average of a 20% decline in survival for 1 year, and Case 4 is a 2% probability of a catastrophe with an average of a 20% decline in survival for 1 year.

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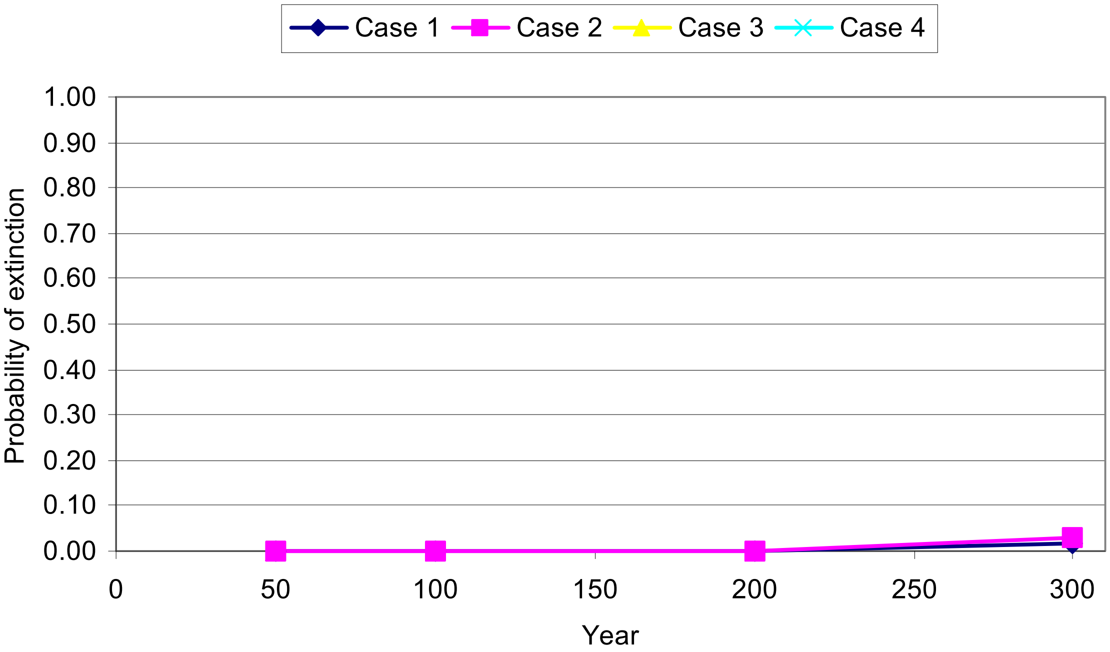

Figure 23. Estimated risk of extinction at 50, 100, 200, and 300 years for the combined populations of Southern, Northern, and Alaska Residents, assuming 1992–2000 survival rates of Southern Residents are experienced by both Southern and Northern Residents. Carrying capacity was set at 1,600 whales. Case 1 is no catastrophes, Case 2 is a 1% probability of a catastrophe with an average of a 10% decline in survival for 1 year, Case 3 is a 1% probability of a catastrophe with an average of a 20% decline in survival for 1 year, and Case 4 is a 2% probability of a catastrophe with an average of a 20% decline in survival for 1 year.

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4.5.3. Differences between NMFS PVA and Petitioners' PVA

The PVA conducted by the petitioners shared many similarities with the NMFS PVA. Although there were many similarities, the BRT made some different choices regarding the specific implementation of their analyses. The following represents a brief summary of the main differences between the NMFS PVA conducted for this status review and the petitioners' PVA.

1. In the NMFS PVA, environmental variance was incorporated using the best-fitting models of variability of survival and fecundity through time, which included correlated periods of survival and fecundity through time. The petitioners incorporated environmental variation in survival and fecundity that were not correlated. Additionally, uncertainty in the estimation of survival rates was incorporated into the petitioners' PVA analysis.

2. The NMFS PVA had the model population start with the known age and sex distribution of Southern Residents. The petitioners initiated their PVA at the stable age distribution associated with the given life history parameters.

3. The NMFS PVA incorporated an Allee effect using known pod structure and the assumption that males only breed outside their natal pod. The petitioners incorporated an Allee effect based on a low population size.

4. The NMFS PVA considered various levels for carrying capacity, from 100 to 400 whales. The petitioners fixed the carrying capacity of the population at 100 whales for most analyses, and also considered a lower value of 50.

5. The NMFS PVA did not include any effect of inbreeding, whereas the petitioners included the effects of inbreeding as lethal equivalents.[9]

6. Although both PVAs considered scenarios using all of the available data (1974–2000 or 1974-2001), the NMFS PVA considered a different second time period (1992–2001) compared to the second period (1996–2000) that was used by the petitioners.

7. Slightly different scenarios regarding the frequency and magnitude of large mortality events (e.g., oil spills, epizootic events) were considered in each analysis.

8. The NMFS PVA incorporated at least 10,000 iterations per scenario; the petitioners used 200 iterations for all scenarios.

9. The NMFS PVA modeled scenarios for two population units; the petitioners included only scenarios for the Southern Resident population.

In general, the NMFS PVA model had many similarities to the petitioners' PVA model. Most of the changes made in the NMFS model were either to explore a greater range of parameter values (e.g., a greater range for carrying capacity) or to create a model closer to the

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[9] A lethal equivalent is a genetic defect that can cause mortality when the recessive gene is received from both parents. The probability that mortality from lethal genes will occur increases substantially when a population becomes very small.

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true biology of Southern Resident killer whales (e.g., incorporate current age, sex, and pod structure of the population). Many of these changes were possible because the NMFS PVA was developed as custom software for this purpose. In contrast, the petitioners were limited to the options in the VORTEX software package. For example, environmental variance was incorporated using the observed patterns of temporal correlation, whereas VORTEX only allows environmental variance in vital rates that are independent in each year. Correlated periods of relatively poor survival will increase the risk of extinction relative to independent environmental variance. However, VORTEX was able to incorporate inbreeding depression in the form of "lethal equivalents per zygote (fertilized egg)" because it is an individual-based model, whereas the NMFS PVA could not directly incorporate that effect because it is an age- and sex-based model.

One substantial difference in the specifications was that the petitioners used the 1996–2000 survival data in their "B" scenarios, a period that had lower average survival than the 1992–2000 period used in half of the NMFS PVA scenarios. Using just the last few years of survival will lead to a greater risk of extinction in 100 years because the population, on average, is declining at a greater rate. However, the NMFS PVA used the 1992 and later time periods because these were the time periods identified as being statistically different from previous time periods in the survival analysis and the last partial time period of only 3 years did not provide sufficient data to incorporate environmental variability in survival.

4.5.4. Discussion and Conclusions for Risk Analysis

The NMFS PVA was conducted using available demographic information for Southern and Northeast Pacific Residents. According to the model results, the Southern Residents have a greater than 10% probability of extinction in 100 years and greater than 85% probability of extinction in 300 years, under the assumption that population declines seen over the last 9 years continue into the future (Table 9). Under the assumption that population growth rates in the future will more accurately be predicted by the full 27-year time series of data available, the model predicted that extinction probability is 1-5% in 100 years and 5-50% in 300 years, with the higher values associated with higher probability and magnitude of catastrophic mortality events.

The estimated risk of extinction was therefore very sensitive to the assumption regarding survival rates in the future. If one assumes that the last 27 years are a good indicator of what will happen in the future, then the risk is much lower than if one makes the more pessimistic assumption that the last 9 years are a good indicator of what will happen in the future. Under the pessimistic assumption, uncertainties with respect to the level of carrying capacity and the rate and magnitude of catastrophes are less important. In contrast, under the more optimistic prediction using 1974–2000 survival rates, the risk of extinction is strongly influenced by the assumption made about carrying capacity and is also somewhat influenced by the level and magnitude of catastrophes.

The effects of carrying capacity can also be considered in light of the previous discussion on historical carrying capacity (subsection 2.4.4). Even though the population trend is slightly positive over the 1974–2000 period, when carrying capacity is less than 200 the population will go extinct, though this may take hundreds of years. The precarious nature of such a small long-

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Table 9. Estimated risk of extinction in 100 years for different risk models.[a]

	——Risk model——		**——Population units——**		
Baseline for survival	Probability of catastrophe	Magnitude of catastrophe	Southern Residents K[b] = 100	Southern Residents K = 200	Northeast Pacific residents[c]
1974–2000	0%	0%	*1-2%*	*1%*	0%
	1%	10%	*1-2%*	*1%*	0%
	1%	20%	*2%*	*1%*	0%
	2%	20%	**4%**	**3%**	0%
1992–2000	0%	0%	**12%**	**12%**	0%
	1%	10%	**15%**	**15%**	0%
	1%	20%	**20%**	**20%**	0%
	2%	20%	**30%**	**30%**	0%

[a] Risks above the endangered criterion threshold for North Atlantic right whales are in bold. Risks that are near the right whale criterion are in italics.
[b] K is carrying capacity.
[c] This includes Southern, Northern, and Alaska Residents.

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term population size is consistent with conservation biology theory that indicates demographic stochastic variations—random fluctuations in abundance resulting from chance birth and death events that become exaggerated in very small populations—play a large role for populations. The abundance when demographic stochastic variations begin asserting a negative effect on the probability of population survival depends on the life history of the organism. The NMFS PVA indicates that for killer whales, demographic stochastic variation is important when carrying capacity is less than 200. These results provide another line of evidence that the current population may be at less than its historical numbers, because a carrying capacity of 100 seems not to be an evolutionarily stable strategy. An alternative interpretation is that, when conditions were marginal for residents, Southern Residents were formed from a larger population through fission, and that populations are expected to come and go from this area as ecological conditions vary through time.

According to the NMFS PVA model, extinction risk over 100 years for the larger Northeast Pacific resident killer whale DPS as a whole was negligible (Table 9). The larger population size (at least 800 whales) sufficiently buffers this population segment from extinction risk, even under the most pessimistic scenarios of population decline combined with relatively frequent catastrophic events.

In comparing the results of the NMFS PVA to the petitioners' PVA, it can be seen that for a similarly specified scenario the estimated risk of extinction was nearly the same. For example, the petitioners' "A2" scenario had similar specifications to the NMFS PVA scenario in Figure 12 (using K=100) and the estimated risk of extinction in both cases was nearly identical—0% in 100 years, 3% in 200 years and 18.5% in 300 years. These results are not too surprising, because the population dynamics model in each PVA can give essentially the same behavior with a few exceptions. Therefore, most of the differences in the results were due to different specifications of parameter values, such as the lower average survival rates from 1996–2000.

As mentioned previously, one major difference between the two PVAs was the lack of inbreeding depression in the NMFS PVA model. Experience has shown that the effect of inbreeding depression on small populations is highly unpredictable. Some small populations show strong deleterious effects, whereas other populations exhibit little effect. These differences in response may be explained by the past history of a population. A population that has persisted at a relatively low level may have already experienced the effects of inbreeding depression in the past and such populations no longer carry a "genetic load" (deleterious alleles in a population). Inbreeding depression might not be a factor that affects Southern Resident killer whales, but it cannot be ruled out as a possibility, given that the historical size of the population is unknown. The petitioners' PVA suggested that, if inbreeding depression occurs, it could substantially increase the risk of extinction to the population, even at a time horizon of 100 years. Therefore, if inbreeding depression occurs, the NMFS PVA underestimates the risk of extinction.

Another apparent source of underestimating risk in the NMFS PVA analyses arises through the effect of time lags. Because killer whales can live for up to 80 years, it is possible that a population remains extant many years beyond the time when extinction is inevitable. The effect of time lags can be seen in the extinction curves that show very low probabilities of extinction in 100 years but much greater levels shortly thereafter. Certainly some of the populations that were still extant in year 100 were not viable and would have no prospect of

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recovery. The BRT recognized that this time lag effect would make the risk at year 100 appear less than the actual extinction risk and suggested ways to correct for this apparent bias, but time prevented further improvements to the PVA. Therefore, by not accounting for time lags, the extinction rates shown are optimistic.

Population viability analyses are intended to project the future fate of populations, but they are usually based on assumptions that conditions observed in the past will continue into the future. Thus predictions of future risk are dependent upon this assumption. Many factors that potentially affect Southern Resident killer whales could change in the future. Where a clear scenario can be identified, these future changes can be incorporated into a PVA. For example, it has been predicted that global warming may have a major influence on the abundance and distribution of salmon in the North Pacific (Welch et al. 1998). If these changes occur, they may affect the estimated risk of extinction and PVAs can be revised as new information becomes available.

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5. CONCLUSIONS OF THE STATUS REVIEW

Correctly identifying the killer whale taxon is critical, because at least two of the criteria used to evaluate "significance" of a DPS are defined relative to other populations within that taxon. For example, a population segment will qualify as a DPS if it occupies an "ecological setting unusual or unique for the taxon" or if "loss of the discrete population segment would result in a significant gap in the range of the taxon." The BRT concluded that the current designation of one global species for killer whales is likely inaccurate, because available data suggest that present taxonomy does not reflect current knowledge and additional species or subspecies of killer whales should be "officially" recognized. Thus, how killer whale taxonomy is resolved in the future will determine the DPS to which Southern Resident killer whales belong with respect to the ESA.

The BRT concluded that Southern Resident killer whales are not a DPS of the currently recognized global species taxon. After reaching this conclusion, the BRT attempted to define what is the DPS to which Southern Residents belong within the global species taxon. Most of the BRT support was in favor of a DPS that was larger than the Southern Resident population (and would likely include at least the Northern, Alaska, and Western North Pacific Resident populations). Little effort was spent defining this DPS, because the BRT had already concluded that the global species is incorrect and needs to be updated.

The BRT gave roughly equal support to four different scenarios for the taxon to which Southern Residents might belong if the global species were subdivided. Next the BRT had to decide under which of these taxonomic scenarios the Southern Resident population would be a DPS. The strongest support for a Southern Resident DPS occurred when the taxon was assumed to be North Pacific resident whales (a group that includes Southern, Northern, Alaska, and Western North Pacific Residents), but there was no consensus. Support for Southern Residents as their own DPS diminished as the hypothesized taxon grew larger.

The BRT considered whether certain factors that currently pose a risk for Southern Residents might continue in the future. Reduced quantity and quality of prey are expected to continue to affect the Southern Resident population. In addition, levels of OC contaminants are not declining appreciably or may even be increasing in the habitat used by Southern Residents and their prey. Therefore, Southern Residents may be at risk for chronic, serious, sublethal effects, because OC concentrations in these animals currently exceed those shown to have serious, sublethal effects in other marine mammal species (e.g., immunotoxicity in harbor seals). Other risk factors that may continue to impact Southern Residents are oil spills and whale watching.

A PVA was conducted using Southern Resident demographic data and another PVA was conducted using demographic data for Northeast Pacific residents, which includes Southern, Northern, and Alaska Residents. According to the model results (Table 9), the Southern Residents have a greater than 10% probability of extinction in 100 years and greater than 85% probability of extinction in 300 years under the assumption that population declines seen from 1992–2001 continue into the future. Under the assumption that growth rates in the future will more accurately be predicted by the full 27-year time series of data available, the model predicts

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that extinction probability is 1-5% in 100 years and 5-50% in 300 years, with the higher values associated with higher probability and magnitude of catastrophic mortality events (e.g., oil spills). According to the model, extinction risk for the larger Northeast Pacific resident killer whale DPS is negligible over 100 years and less than 5% over 300 years.

Neither NMFS nor USFWS has defined quantitative thresholds for extinction risk. A report of a recent workshop that was convened to develop recovery criteria for large whales (Angliss et al. 2002) provides some guidance. Workshop participants recommended that, if the probability of a species going extinct was less than 1% in 100 years, that species might be a candidate for recovery from "endangered." This approach has been included in a draft recovery plan for North Atlantic right whales (*Eugalaena glacialis*) that was recently made available for public comment. If the same logic is appropriate for assessing the degree of extinction risk for other species, then a species or a DPS that exceeded an extinction risk threshold (e.g., 1% in 100 years) could be considered at risk of extinction. The results of the NMFS PVA (Table 9) indicated that, if Southern Residents are considered a DPS (a configuration deemed likely in only 1 of 4 taxonomic scenarios; see subsection 3.4.4) and the "1% in 100 years" criterion were used, Southern Residents would exceed the threshold for extinction, particularly if the population decline of the last few years (1992–2001) continues into the future. In contrast, the PVA results also indicated that, if the DPS is larger than Southern Residents (several larger DPSs were considered likely under all four taxonomic scenarios; see subsection 3.4.4), then the "1% in 100 years" criterion would not be met.

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