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Life History and Population Dynamics of Northern Resident Killer Whales (*Orcinus orca*) in British Columbia

Cycle biologique et dynamique de la population des épaulards (*Orcinus orca*) résidents du nord de la Colombie-Britannique

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This paper is dedicated to the memory of late Dr. Michael A. Bigg, who pioneered this long-term photo-identification study and shared his insight into the population biology of killer whales. Despite our diverse backgrounds, skills and interests, it's quite remarkable that we each regard him to have been a mentor.

PO, GE and JF.

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ABSTRACT

Annual photo-identification surveys conducted between 1973-75 and 2004 were used to estimate life history parameters and develop a population model for the northern resident population of killer whales that inhabits coastal waters of British Columbia. During the 1970's, 80's and early 90's, the population grew exponentially (r^2=0.986; $F_{1,22}$=1,568.5; P<0.001) at an annual rate of 2.6% (95% *CI* 2.48-2.76%). Although the population almost doubled in size from about 125 to 217 animals, there was no evidence of a slowing of the growth rate ($F_{1,21}$=0.25; P=0.622), suggesting the population was unrestrained and increasing at its maximum intrinsic rate. The population peaked abruptly in the mid-1990s, declined by 7-9%, and then exhibited a small increase, resulting in no discernible trend over the last decade ($F_{1,10}$=1.36; P=0.271), indicating that something was restraining its growth. Life history and population parameters were thus estimated separately for 1973-96, a period of unrestrained growth; and 1996-2004, a period of no net change. During the period of unrestrained growth, females had a mean life expectancy of 46 years and maximum longevity was on the order of 80 years. Females typically gave birth to their first viable calf at 14.1 years of age (*SE*=0.050; range 10-21 years) and those that survived produced a total of 4.7 calves at mean intervals of 4.9 years (*SE*=0.18; range 2-11 years) over a reproductive lifespan typically lasting about 24 years. Older females exhibited reproductive senescence, with about 50% being post-reproductive by 38 years of age, and none reproducing after 46 years of age. Based on development of the dorsal fin – a secondary sexual characteristic – males typically attained sexual maturity at 13.0 years of age (*SE*=0.046; range 9-18 years) and the fin continued to develop for an average of 5.5 years (*SE*=0.113; range 3-7 years), such that males had typically attained physical maturity by 18.5 years of age. Males had a mean life expectancy of 31 years and maximum longevity was probably on the order of 60-70 years. Mortality curves were U-shaped for both sexes, indicating most mortality occurred early and late in life, but the right limb was steeper for males, resulting in a sex ratio that was progressively skewed toward females with increasing age (1:1 at age 15, 2:1 by age 34, and 3:1 by age 41 years). A sex- and age-structured model incorporating these parameters predicted that a population would increase at a rate of 2.4% per annum and be comprised of 46% juveniles, 22% reproductive females, 10% post-reproductive females, and 22% adult males. During 1973-96, the study population actually increased at 2.6% and was comprised, on average, of 46% juveniles, 21% reproductive females, 11% post-reproductive females and 22% adult males, indicating a good fit with the model predictions. Surprisingly, there were no major changes in reproductive parameters as the population stabilized during 1996-2004. Mean age at first birth increased slightly but significantly from 14.1 to 15.4 years (t_{49}=3.23; P=0.002), mean age of onset of post-reproductive senescence increased from 38.4 to 40.6 years (t_{61}=2.84; P=0.006), and calving intervals were marginally longer (5.5 versus 4.9 years; t_{97}=2.92; P=0.091). The overall effect was a slight drop in the estimated reproductive potential of females from 4.7 to 4.5 calves. The recent decline in productivity was due almost entirely to increases in mortality, which were evident and statistically significant ($7.63<\chi^2<8.14$; P<0.01) across all sex- and age-categories. Survival of viable calves to age 15 (about the age they are recruited to the adult population) dropped from 80% to 61%, and mean life expectancy declined from 46 to 30 years for females and from 31 to 19 years for males. Because the increase in mortality was broadly distributed across all sex- and age-classes, the predicted sex and age structure of the stable population remained almost unchanged at 47% juveniles, 24% reproductive females, 11% post-reproductive females, and 18% adult males. The life history parameters for neighbouring resident killer whale populations in Alaska and Washington appear to fall within the range of our unrestrained and stable models for northern BC residents, suggesting the models represent the general population biology of the resident ecotype of killer whale. We believe such models provide a useful construct for exploring and developing a better understanding of the factors that may regulate or impact killer whale populations.

RÉSUMÉ

Des relevés annuels par identification photographique menés entre 1973 et 1975 et en 2004 ont servi à estimer les paramètres du cycle biologique et à élaborer un modèle de la population d'épaulards résidents du nord qui vit dans les eaux côtières de la Colombie-Britannique. Pendant les années 1970, les années 1980 et le début des années 1990, la population a augmenté de façon exponentielle (r^2 = 0,986; $F_{1,22}$ = 1 568,5; P < 0,001) à un taux annuel de 2,6 % (IC à 95 % = 2,48 – 2,76 %). Bien que l'effectif ait presque doublé, passant d'environ 125 à 217 individus, on n'a pas constaté de ralentissement du taux de croissance ($F_{1,21}$ = 0,25; P = 0,622), ce qui laisse présager une croissance soutenue de la population à son taux intrinsèque maximal. La population a grimpé abruptement au milieu des années 1990, a diminué de 7 à 9 %, puis a augmenté légèrement, de sorte qu'on n'a pas observé de tendance perceptible pendant la dernière décennie ($F_{1,10}$ = 1,36; P = 0,271), ce qui indique que quelque chose empêchait cette population de prendre de l'expansion. Les paramètres du cycle biologique et de la dynamique de la population ont donc été estimés séparément pour 1973 à 1996, période de croissance soutenue, et pour 1996-2004, période sans changement net. Pendant la période de croissance soutenue, les femelles avaient une espérance de vie de moyenne de 46 ans et une longévité maximale de l'ordre de 80 ans. Dans l'ensemble, les femelles ont donné naissance à leur premier baleineau viable à 14,1 ans (erreur-type = 0,050; plage de 10 à 21 ans) et les survivants ont produit au total 4,7 petits à des intervalles moyens de 4,9 ans (erreur-type = 0,18; plage de 2 à 11 ans) sur une durée de vie féconde d'habituellement 24 ans environ. Les femelles âgées affichaient une sénescence sexuelle, 50 % d'entre elles environ étant post-reproductrices à l'âge de 38 ans et aucune ne se reproduisant après l'âge de 46 ans. Selon le développement de l'aileron dorsal – caractéristique sexuelle secondaire – les mâles atteignent la maturité sexuelle à 13,0 ans (*erreur-type* = 0,046; plage de 9 à 18 ans). Leur aileron continue de se développer pendant 5,5 ans en moyenne (*erreur-type* = 0,113; plage de 3 à 7 ans). Ils atteignent d'ordinaire la maturité physique à l'âge de 18,5 ans. Les mâles ont une espérance de vie de 31 ans en moyenne et leur longévité maximale est probablement de l'ordre de 60 à 70 ans. Les courbes de mortalité sont en forme de U pour les deux sexes, ce qui indique que la plupart des décès surviennent tôt ou tard dans la vie, mais le côté droit de la courbe est plus abrupt pour les mâles, ce qui entraîne un rapport entre les sexes penchant progressivement vers les femelles avec l'âge (1:1 à l'âge 15, 2:1 l'âge 34 et 3:1 à l'âge 41). Un modèle structuré selon le sexe et l'âge, incorporant ces paramètres, a prévu que la population augmentera à un taux de 2,4 % par an et sera composée à 46 % de juvéniles, à 22 % de femelles fécondes, à 10 % de femelles post-reproductrices et à 22 % de mâles adultes. Pendant la période de 1973 à 1996, la population à l'étude a en fait augmenté à un taux de 2,6 % et était composée, en moyenne, à 46 % de juvéniles, à 21 % de femelles fécondes, à 11 % de femelles post-reproductrices et à 22 % de mâles adultes, ce qui concorde bien avec les prévisions du modèle. Étonnamment, il n'y a pas eu de variation importante dans les paramètres de reproduction, et la population s'est stabilisée durant la période de 1996 à 2004. L'âge moyen à la première naissance a augmenté légèrement, mais de manière significative, de 14,1 à 15,4 ans (t_{49} = 3,23; P = 0,002), l'âge moyen du début de la sénescence sexuelle est passé de 38,4 à 40,6 ans (t_{61} = 2,84; P = 0,006), et les intervalles entre les mises bas ont été légèrement plus longs (5,5 versus 4,9 ans; t_{97} = 2,92; P = 0,091). L'effet global a été une légère baisse du potentiel reproducteur estimé des femelles, qui est passé de 4,7 à 4,5 baleineaux. Le déclin récent de la productivité a été presque entièrement attribuable aux hausses de la mortalité, qui ont été évidentes et statistiquement significatives ($7{,}63 < \chi^2 < 8{,}14$; P < 0,01) pour toutes les catégories de sexe et d'âge. Le taux de survie des baleineaux viables jusqu'à l'âge de 15 ans (âge approximatif de leur recrutement au sein de la population adulte) a chuté de 80 % à 61 %, et l'espérance de vie moyenne a diminué de 46 à 30 ans pour les femelles et de 31 à 19 ans pour les mâles. Puisque l'augmentation de la mortalité a été largement répartie dans toutes les catégories de sexe et d'âge, la structure prévue par sexe et par âge de la population stable est restée pratiquement inchangée : 47 % de juvéniles, 24 % de femelles fécondes, 11 % de femelles post-reproductrices et 18 % de mâles adultes. Les paramètres du cycle biologique des populations d'épaulards résidentes voisines de l'Alaska et de l'État de Washington semblent correspondre à nos modèles de croissance stable et soutenue pour les épaulards résidents du nord de la C.-B., ce qui laisse entrevoir que les modèles représentent la biologie de la population générale de l'écotype des épaulards résidents. Nous croyons que de tels modèles sont des outils utiles pour explorer les facteurs qui peuvent régir les populations d'épaulards ou avoir une incidence sur elles et pour acquérir une meilleure compréhension de ceux-ci.

1. INTRODUCTION

The killer whale (*Orcinus orca*) is the largest member of the family Delphinidae. The species has a cosmopolitan distribution, but appears to be most abundant in coastal waters and at higher latitudes, and relatively uncommon at tropical latitudes (Leatherwood and Dahlheim 1978; Dahlheim and Heyning 1999; Forney and Wade, in press). Although only one species is currently recognized (Hoelzel et al. 1998, Rice 1998, Barrett-Lennard 2000; Reeves et al. 2004), sympatric but distinct forms or ecotypes have been reported in both the Antarctic (Mikhalev et al. 1981; Berzin and Vladimorov 1983; Pitman and Ensor 2003) and NE Pacific Oceans (Ford et al. 1998, 2000; Baird 2000; Barrett-Lennard and Ellis 2001). Due to its inshore distribution, distinct black and white markings and prominent dorsal fin, and having been popularized by display in aquaria and appearances in movies, the killer whale is arguably the easiest recognized and most familiar species of cetacean in coastal waters, and many consider it an icon of the marine ecosystem.

Despite its widespread distribution and high profile, until recently relatively little was known about the life history and population biology of the species. Killer whales were never intensively harvested, and only a single animal was known to have been taken among the nearly 25,000 whales processed by coastal whaling stations in British Columbia between 1908 and 1967 (Pike and MacAskie 1969; Gregr et al. 2000; Nichol et al. 2002). None were reported among the 2,698 whales processed at the Bay City whaling plant in Grays Harbor, Washington, during its 14 years of operation from 1911-1925 (Scheffer and Slipp 1948, Crowell 1983), but apparently five were taken off California during 1962-1967 (Carretta et al. 2002). Some information has been gleaned from stranded animals, but these too are surprisingly rare, with only 7-8 carcasses having been recovered around the world each year (Raverty and Gaydos 2004).

The only significant sample of killer whales to be examined in detail were 316 animals taken off Norway during 1978-80 (Christensen 1982, 1984). While those studies provide useful information on morphometrics and body growth, interpretation of life history and population parameters was confounded by uncertainty about length of the gestation period and problems inherent in ageing killer whales from dentinal layers in teeth. The authors assumed gestation was 12 or 15 months, whereas data from captive animals has since shown it to be 17 months (Walker et al. 1988). Moreover, it's now recognized that killer whales cannot be accurately aged beyond about 20-30 years of age from annual growth layers teeth (IWC 1980; Yochem et al. 1987; Myrick et al. 1988).

In recent years, our understanding of the life history and population biology of killer whales has been advanced by longitudinal studies of recognizable individuals over time. The first photo-identification studies were initiated in the Pacific Northwest in the early 1970s (Bigg et al. 1976; Balcomb et al. 1982; Bigg 1982), and have been continued annually to the present, providing a record that now spans over 3 decades. All individuals in two populations that congregate in local waters off British Columbia and Washington, known as 'northern resident' and 'southern resident' killer whale communities, have been catalogued and monitored (Bigg et al. 1987; Ford et al. 1994, 2000, 2002), providing a nearly complete record of births, deaths and other demographic events in these populations.

The photo-identification studies have led to a number of population assessments as the work progressed and our understanding of population biology evolved. The first major population assessment was by Bigg (1982), who showed that all individuals in these small, closed population could be recognized and monitored over long periods, and provided the first

description of the basic social structure of pods[1]. He also noted a surprisingly high number of barren females and was the first to suggest that older females exhibited reproductive senescence. Bigg (1982) made preliminary calculations indicating that killer whales were much longer-lived than previously believed, although the time-series available at the time was too short to reliably estimate longevity. In the next major assessment, Olesiuk, Bigg and Ellis (1990) developed methods for ageing individuals that had been born prior to the start of the study based on the development of the dorsal fin of males, and the age of the oldest offspring of females. The authors derived the first estimates of sex- and age-specific life history parameters, and developed a population model for an increasing population. Their analysis was based on a 15-year time-series from 1973 to 1987, at which point known-aged animals recruited at the beginning of the study were just beginning to mature. However, sample sizes were limited and comparisons lacked statistical power, so data were pooled for the northern and southern resident populations, the latter of which had been heavily impacted by a live-capture fishery during 1965-75 (Bigg and Wolman 1975).

In this paper, we update and refine our assessment of the life history and population biology of resident killer whales based on more recent photo-identification surveys, which now span a 32-year time-series from 1973 and 2004. This longer time frame dramatically increases sample sizes, allowing us the benefit of focusing on the northern resident population, which was relatively unaffected by the live-capture fishery. The longer time series, combined with recent declines in population growth (COSEWIC 2003), also provides some initial insight into how life history parameters vary with and influence population status. The resulting population model serves as a framework for understanding demographic changes, and in a companion paper (Ford et al. 2005) we use it to examine temporal and geographic patterns in changes in mortality and survival rates, and the factors that may have be driving them.

2. STUDY POPULATION AND DATA COLLECTION

2.1 Killer Whale Ecotypes

Long-term photo-identification studies have shown that three distinct ecotypes of killer whales inhabit coastal waters of NE Pacific Ocean, referred to as the *resident*, *transient*, and *offshore* forms (Bigg et al. 1987; Ford et al. 1999, 2000, 2002; Baird 2000, 2002). The three ecotypes are genetically distinct (Hoelzel and Dover 1991; Hoelzel et al. 1998; Barrett-Lennard 2000; Barrett-Lennard and Ellis 2001) and readily distinguishable on the basis of a number of morphological and behavioural traits such as fin shape and saddle patch patterns, diet and foraging ecology, vocalizations and dialect, and group size and social structure (Table 1). Bigg et al. (1987) and Ford et al. (1994) described the basic differences between the two forms. Ford et al. (2000, 2002) provide updated descriptions of the resident form, and Ford and Ellis (1999) the first detailed description of the transient form. Much less is known about the offshore form, which is rarely seen in inside waters, and presumably ranges in outer coastal or offshore waters (Ford et al. 1994; Ford and Ellis 1999).

[1]The term *pod* has traditionally and widely been used to describe assemblages of animals belonging to related matrilines that tend to travel together (Bigg et al. 1990). However, over the course of the study, as the sex- and age-structure of matrilines has evolved, its become apparent the social associations between matrilines is more dynamic than previously believed (Ford et al. 2000; Ford and Ellis 2002). Nowadays, groups are recorded in terms of matrilines, which change only through births and deaths, but which often associate with one another to form larger, more dynamic assemblages.

A detailed description of the biology of the *resident* form of killer whale is beyond the scope of this paper, but several key biological characteristics are important for understanding our general approach to this population assessment. First, *resident* killer whales live in small populations known as 'communities' that exhibit genetic differences (Barrett-Lennard and Ellis 2001) and are closed to immigration and emigration (Bigg et al. 1990)[2]. Second, the whales belonging to these communities have specific but overlapping geographic ranges and traditionally congregate in predictable core areas during summer months (Bigg et al. 1987; Ford et al. 1994, 2000). These two features make it practical to identify and monitor most, if not all, individuals within the population on an annual basis. Third, resident killer whales exhibit a unique social system in which neither sex disperses from their natal matrilines – both females and males maintain close associations and continue to travel with their mothers throughout life. This is important for two reasons: 1) its possible to establish the genealogical relationships among individuals within matrilineal groups (Bigg et al. 1990; Matkin et al. 1999), which provides additional information on reproductive histories of females prior to the start of the study; and 2) the lack of dispersal from matrilines – which always travel together as a cohesive group – means that the disappearance of an animal from the matrilineal group indicates it has died. Combined, these features have made it possible to maintain a complete registry for all individuals in the population as to which gave birth or died each year. Given the completeness of the record, our assessment essentially represents an actuarial analysis of how the probabilities of giving birth or dying vary with sex and age, and over time, in contrast with more conventional approaches in which mark-recapture model are used to estimate these probabilities from incomplete sighting records.

2.2 Resident Killer Whale Populations

At least 4 resident killer whale communities occupy the coastal waters of the Northeast Pacific Ocean. The two best known populations are the *southern residents*, which congregate in the inside waters off southern Vancouver Island and Washington State during summer months, but have been seen as far north as the Queen Charlotte Islands and far south as California, and the *northern residents*, which congregate in the inside waters off northern Vancouver Island but have been seen as far north as Glacier Bay in Alaska, and as far south as Washington State (Figure 1). Both populations have been monitored since the early 1970s (Bigg et al. 1987; Ford et al. 1994, 2000). Although their ranges overlap, and matrilineal groups within each community often associate with one another, matrilineal groups from the two populations have never been observed traveling together (Bigg et al. 1990).

A third resident population known as the *southern Alaskan residents* occurs to the north from SE Alaska to Kodiak Island in the Gulf of Alaska. This population has been the subject of annual photo-identification studies since about 1984 (Matkin and Leatherwood 1986; Dahlheim et al. 1997), and their life history and population biology appears similar to the southern and northern residents (Olesiuk et al. 2001; Matkin et al. in prep.). In recent years what appears to be a fourth resident killer whale population, referred to as the *western Alaskan residents*, was discovered when photo-identification surveys were expanded into the Aleutian Islands and Bering

[2]Although there is no evidence of dispersal of animals among resident populations, and individuals from each population have not been seen traveling with members outside their populations, we know little about the distribution and biology of any of the resident populations during winter months, and genetic analysis has not ruled out the possibility that males many mate with females from outside their community (Barrett-Lennard 2000; Barrett-Lennard and Ellis 2001).

Sea. Resident-type whales may also inhabit coastal waters off Asia (Krahn et al. 2002), but detailed surveys have not been conducted.

2.3 Social Organization and Genealogy

Studies of association patterns among resident killer whales have indicated that both males and females maintain a bond and continue to travel with their mothers throughout life (Bigg et al. 1990; Matkin et al. 1999). Given this lack of dispersal, mothers and their descendents form matrilineal groups typically spanning 2-3 (occasionally 4) generations. These matrilineal groups always travel together as a cohesive unit, and are now recognized as the fundamental social unit of resident killer whale populations (Bigg et al. 1990; Ford and Ellis 2002).

Matrilineal groups within populations often associate and travel with one another, and in some cases these association patterns can persist over many years or several decades. Closely related matrilines tend to associate more often than distantly related matrilines. Early in the study, these groups were referred to as *pods* (Bigg 1982), and individual whales were named on the basis of pod membership. As the fluidity of pods became apparent, they were subsequently defined as assemblages of matrilines that spent at least 50% of their time together, as indicated by them occurring together during at least 50% of encounters (Bigg et al. 1990). However, it is now recognized that the associations among matrilines can wax and wane (Ford and Ellis 2002; Parsons et al. 2005) and as a result pod structure may evolve over longer time frames. We have thus moved toward a more generic use of the term pod to define assemblages of whales, and now prefer to describe social organization in terms of matrilines.

2.4 History of Exploitation

Killer whales in the Pacific Northwest have never been hunted to any degree for subsistence or commercially. Although various cetaceans have been commonly found in middens during anthropological excavations, only two specimens of killer whales have ever been documented (R. Wigen, University of Victoria, Victoria, B.C., pers. comm.). Their scarcity may be due to the special mythological significance of killer whales in the culture of local First Nations (Cavanagh-Ford 1984; Tanami 1984). The journals of early explorers of the west coast of North America made no reference to the exploitation of killer whales. Killer whales were never the target during commercial whaling, but were occasionally taken incidental to other species. The only documented commercial kill in British Columbia was a photograph of an adult male being processed at a local whaling station in 1955 (Pike and MacAskie 1969).

Prior to about 1970, killer whales were widely regarded as a nuisance species, as it was believed they preyed on commercial fish stocks and posed a hazard to small fishing vessels. During the 1940s, the Royal Canadian Air Force reportedly used killer whales for targets in practice bombings (Carl 1946), but no records were maintained on the magnitude or location of potential kills. In 1960, the Canadian Department of Fisheries installed a machine gun post in Seymour Narrows off Vancouver Island in an attempt to deter animals, which were perceived as a threat to the burgeoning sport tyee fishery, but the machine gun was never fired (Ford et al. 2000). Nevertheless, these attempts reflect the general public attitude toward killer whales, and it is possible substantial numbers may have been injured or killed opportunistically by fishermen, fisheries personnel, and sportsmen during an era of widespread predator control. Bullet wounds were evident in up to 25% of the animals taken during the live-capture fishery in the 1960s and

early 1970s (Keyes cited in Hoyt 1981). Shooting by fishermen has been cited as one of the contributing factors to the unusually high mortality experienced by AB-pod in Prince William Sound, which had developed a habit of taking black cod off long-lines (Matkin et al. 1986).

Since the 1970s, local attitudes toward killer whales have changed dramatically. The display of killer whales in captivity led to an appreciation they were gentle and intelligent animals. Surveys with commercial fishermen conducted in the mid-1980s indicated that relatively few (11%) still considered killer whales more than a minor problem (Olesiuk, unpublished data). The species has been protected since 1970 in Canadian waters under the Fisheries Act, and since 1972 in the United States by the Marine Mammal Protection Act.

Despite their protection, killer whales in the Pacific Northwest were exploited during the 1960s and 70s in a live-capture fishery to supply animals for display in aquaria. A total of 68 whales, primarily (63%) juveniles, were known to have been taken or accidentally killed during capture operations (Table 2) (Bigg and Wolman 1975). The pods could be established for 53 of these animals based on photographs or pod-specific dialects (Bigg 1982; Ford and Fisher 1982), indicating that 48 (91%) were the resident ecotype. Given their greater prevalence in coastal waters, it was assumed most of the remaining 15 whales were also residents (Olesiuk et al. 1990). Based on pod identities, or location where pod identity could be established, it was estimated that 48 animals were cropped from the southern resident community, compared with 15 from the northern resident community. All three southern resident pods appear to have been heavily cropped, which undoubtedly reduced its size and altered its sex- and age-composition (Olesiuk et al. 1990). In contrast, only one northern resident pod (A05), from which 12 animals were removed during 1968-69, was known the have been heavily cropped, and single animals taken from C01 and I11 pods. The live-capture fishery thus probably had little effect on the northern residents at the population level, but undoubtedly impacted A05 pod.

2.5 Photo-identification Surveys

The fundamental sampling unit during field work was a whale *encounter*. Animals were located by searching or waiting in areas known to be frequented by whales, by listening for and then moving toward underwater vocalizations, or by following-up reports of sightings from local mariners, coastal residents or other researchers. When located, the group of whales was approached and in most cases an effort was made to photograph all individuals using a hand-held 35mm cameras equipped with a 300mm telephoto lens using high speed black and white film (Bigg et al. 1983; Mizroch and Bigg 1990). Virtually all animals could be visually identified by an experienced observer, and additional notes were made on the appearance of newborn calves or apparent disappearance of known individuals, associations among animals, particularly young calves and their mothers, and other information indicating the age and status of animals, such as relative size, distinct colouration of or presence of fetal folds on neonates, and development of the dorsal fins of males. In addition to our own encounters, we compiled similar data from other researchers, naturalists and whale-watchers, or photographs submitted by the general public and maritime community. One of us (*GME*) examined all photographs, being very conservative to not tabulate the presence of a known individual or appearance of a new calf unless it could be positively identified. We were careful not to designate an animal as dead until we were confident there were a sufficient number of good-quality encounters with an animal's matriline to be sure it had in fact disappeared.

Although a few individuals were seen or identified in photographs dating back as early as 1958, the first systematic photo-identification surveys were initiated in 1973. The early 1970s represented a period of discovering new pods and cataloguing their members. The first 6 pods totaling 54 animals – nearly half the northern resident population – were documented during the initial field season in 1973. Two additional pods comprised of 19 animals were first seen in 1974, and 7 pods comprised of 49 individuals were first documented in 1975. Only one other small pod comprised of 4 individuals (W01 Pod), which was first encountered in 1979, has been discovered since the early 1970s. In addition to the 127 animals that were present when their pods were first encountered, 234 animals were subsequently born over the course of the study (not including the 6 calves born in the same year their pods were first seen), bringing the total number of individuals catalogued to 361. Of these, 142 had died by the most recent field season in 2004, leaving the current population at 219 animals.

Despite a considerable annual resighting effort (Figure 2a) and a cumulative total of nearly 3,300 encounters, no new pods have been seen since 1979 (Figure 3). The only new animals added to the registry have thus been those born to females in the population. Colleagues monitoring resident killer whale populations in adjacent waters in Alaska and Washington have also amassed thousands of encounters, and not observed any new northern resident pods, or seen any evidence of dispersal of individuals[3] from the northern resident population (K. Balcomb, Centre for Whale Research, Friday Harbor, WA and C. Matkin, North Gulf Oceanic Society, Homer, AK, pers. comm.). We are thus confident all northern resident community members have been catalogued, and that it represents a closed population with respect to immigration or emigration.

Photo-identification surveys were conducted annually from 1973-2004, but the number of encounters has varied (Figure 2a). The number of encounters generally increased during the 1970s to early 1980s, was highest between the mid-1980s and mid-1990s, averaging about 175 encounters per year, and has been relatively stable at about 120 encounters per year since the mid-1990s. The number of encounters in the first few years underestimates actual effort, as much time was spent observing whales, but not recorded systematically as encounters. Despite the effort, not all individuals in the registry have been seen every year (Figure 2b). Since 1975, an average of 87% (range 64 - 100%) of individuals have been encountered and positively identified during the annual surveys. In most cases (90.2%) animals were seen in consecutive years, but there were occasionally gaps of 1 or 2 years (7.3 and 1.4% of all cases respectively), and in a few instances longer gaps between sightings ranging from 3-10 years, although the latter collectively comprised only 1.1% of the total sample (Table 3). In most cases animals were missed because its entire matriline was not encountered, or less often because photographic surveys of its matriline were incomplete.

There was a distinct seasonal pattern to resightings (Figure 4), with the majority of encounters taking place during July-August (60% of encounters) when animals typically congregated in core areas. Most of the remaining encounters occurred during the shoulder seasons in May-June (10% of encounters) and September-November (28% of encounters), when animals still frequented core areas and inshore waters. Very few encounters took place during

[3]There have been two exceptions where young animals have become separated from their natal pods. In one case, A73 (Springer) apparently became separated from its matriline when we suspect its mother wandered off and died in 1998. A73 was found a short time later by itself in southern Puget Sound, but was subsequently captured and reunited with a closely related matriline, with which it was still traveling when last seen in 2005. In another case, a southern resident, L98 (Luna), became separated from its pod in 2002, and lived by itself in Nootka Sound off the west coast of Vancouver Island until its death in 2006.

December-April (2% of all encounters), because of shorter days and inclement weather, and because animals appear to be much less prevalent in inshore waters. Little is known about their winter distribution, but it is suspected animals spend more time in outer coast waters or further north.

In essence, the photo-identification surveys represent a July-August census of the population. In tallying which individuals were present each year, we did so on the basis of the annual summer survey period, as opposed to calendar year, depending on whether an animal was present (and whether it had given birth or matured) by the July-August census. In a few cases where encounters made outside the main field season indicated that calves had been born or disappeared subsequent to the July-August field season, the birth or death was not tallied until the next July-August census.

2.6 Calving Season

Despite intensive field work, there have only been a handful of cases in which females have been observed giving birth, suggesting that the main calving season is outside the July-August survey period. Jacobsen (1980) observed the birth of a northern resident on 20-Sept-1980, and Emery (1960) gave an account of a set of twins being born off eastern Vancouver Island in March, 1949. In addition, a newborn calf was captured during the live-capture fishery in February, 1967 (A. Wolman, US National Marine Fisheries Service, pers. comm.), and another calf was born in February to a female being held during the live-capture fishery (T. Newby, University of Washington, pers. comm.). There have also been a number of standings of fresh neonate carcasses in the study area (see Table 5 in Olesiuk et al. 1990), and on 04-December-1998 a female was observed carrying a dead neonate carcass. From encounter records, particularly encounters made toward the end or just after the main field season, Olesiuk et al. (1990) were able to establish the exact month of birth for 4 calves born in the southern and northern resident communities up to 1987, and delineated the birth of 8 others to one of several months. Since their analysis, the sample-size has increased appreciably, and we could now establish the exact month of birth for an additional 13 calves, and delineate 17 others to one of several months. As in Olesiuk et al. (1990), we amortized the latter births equally over the period they could have occurred. For example, if a calf was born sometime (anytime) between 1st December and 15th January, it was tallied as two-thirds a birth in December and one-third a birth in January.

Summarizing data from all three sources, it appears that calving is diffusely seasonal, with a peak in autumn (Figure 5). As noted by Olesiuk et al. (1990), the autumn peak is likely, to some extent, an artifact as it represents the tail-end of our field season. The lack of mid-winter births is almost certainly attributable to the absence of sightings during that period. Nevertheless, its seems clear our summer survey period represented the non-calving season. If we take September as the beginning of the calving season, and July as the beginning of our field season, its estimated that we typically census the population when calves are an average of 6.7 months of age. Given the aforementioned bias in underestimating mid-winter births, which would tend to reduce the average survey age, we assumed that populations were surveyed mid-way between births when calves are on average about 6 months of age, recognizing that some calves may actually be as young as a month or two, and some may be approaching their first birthday.

2.7 Population Trends

The annual total population size was estimated by tallying the number of animals present during each July-August census. In a few cases (n=18; 7.5% of all births) where, judging from the size of the calf when first seen, it could have been born in either of two years, we amortized the birth uniformly over the two-year period in question. For example, an animal that was born in either 1975 or 1976 would have been tallied as half a birth in each year, and counted as half an animal in 1975 and one animal in 1976. Similarly, in cases the exact year of death was unknown and the animal may have died in either of two years (n=24; 16.9% of all deaths) or in a few cases over wider periods ranging from 3-11 years (n=13; 9.2% of all deaths), the death was amortized over the period in question. For example, an animal that died sometime over a 3-year period between 1980 and 1982 was tallied as one-third death in each year, and was counted as 2/3's an animal in 1980 (1/3 chance it had died), and 1/3 an animal in 1981 (2/3's cumulative chance it had died). In years in which the amortizations resulted in uncertainty in population size, we calculated the minimum and maximum population size. The minimum was obtained by assuming that all animals that could have been born had not yet been born, and that all animals that could have been dead had died. Conversely, the maximum population size was calculated by assuming that all animals that could have been born had been born, and that all animals that could have died were still alive. These resulting uncertainties introduced little error in the estimated population size, with minimums and maximums averaging ±0.7% of the mean, and never exceeding ±2.9% of the estimated population size.

For early years before all pods had been discovered (1973-78), we estimated the total population size based on the trends observed in the subset of pods that had been catalogued:

[2.6.1] $$N_{t-1} = N_t \cdot C_{t-1} / C_t$$

where t represents the year, C_t the number of animals in catalogued pods in year t, and N_t the estimated size of the population. This equation merely re-scales the trends observed in censused pods in terms of the entire population size, the underlying assumption being that population trends in the subset of pods that had been catalogued were representative of the entire population.

The most recent survey in 2004 was 95% complete, with the status of only 10 of 219 animals not known because we did not have good encounters with their matrilines. We projected what proportion of these 10 animals would have survived (and the number of calves they would have produced) based on average survival and fecundity rates for animals in their sex- and age-category (see Section 4.2.4).

During the 1970s, 1980s and early 1990s, the northern resident population increased exponentially:

[2.6.2] $$N_t = N_o\, e^{rt}$$

such that:

[2.6.3] $$\ln N_t = \ln N_o + r \cdot t \qquad (r^2=0.986;\ F_{1,22}=1{,}568.5;\ P<0.001)$$

with an annual rate of increase, r, of 2.6% (95% CI 2.48-2.76%) (Figure 6). Although the population almost doubled in size from about 125 in 1973 to 213 animals by 1996, adding a second-order polynomial term did not improve the fit ($F_{1,21}$=0.25; P=0.622), indicating there was

no evidence of a slowing of the growth rate. This suggests that growth was unrestrained and the population was increasing at its maximum intrinsic rate, commonly referred to as R_{max}.

The population peaked abruptly in the mid-1990s, declined by 7-9% over the next few years, then showed a small increase (Figure 6). By 2004 the population was just over 50 animals shy of the number expected had the population continued to increase exponentially. Instead, the population exhibited no discernible trend over the last decade ($F_{1,10}$=1.36; P=0.271), indicating that something was restraining its growth. The trajectory of the population as through the transition was modeled using a generalized logistic equation:

$$[2.6.4] \qquad N_{t+1} = N_t + N_t \cdot r\,[1-(N_t/K)^Z]$$

where K indicates the level at which the population stabilized (or fluctuated around), and Z a shape parameter indicating how abruptly the stabilization occurred (Birch 1999). The parameters were estimated iteratively using *Maximum Likelihood Estimation (MLE)*, and confidence limits derived by bootstrapping with 1,000 replicates.

The intrinsic rate of increase, R_{max}, that would occur at low densities was estimated at 2.8% (SE=0.0004). The level at which the population stabilized, K, was estimated at 210.3 animals (SE=0.054) with the shape parameter Z, estimated at 40.0 (SE=0.90), indicating the leveling off occurred very abruptly. The approximate relationship between Z and maximum net productivity level, *MNPL*:

$$[2.6.5] \qquad MNPL \approx 1 / (Z+1)^{1/Z}$$

suggests that maximum productivity occurred at about 91% of K, which equates to a population level of about 192 animals. The fit of the generalized logistic could be improved slightly by incorporating a time lag of one or two years, in which case the growth rate in year t was proportional to the size of the population in year t+1 or t+2 (i.e. $[1-(N_{t-1}/K)^Z]$ or $[1-(N_{t-2}/K)^Z]$ respectively), which results in the population oscillating around K. However, because the leveling-off occurred so recently, the time-series is considered too short to establish the long-term population trends.

Given the rather abrupt change in population status that occurred in about 1996, for subsequent analyses we partitioned the time series into two components: 1973-96, representing a period of unrestrained population growth, and 1996-2004, representing a period in which the population fluctuated but showed no net change in size.

3. LIFEHISTORY

3.1 Age Estimation

Various methods were used to estimate the ages of animals in each sex- and age-category (Table 4). Animals were aged sequentially from youngest to oldest, as in some cases life history parameters derived from younger animals (e.g. age at first birth) were used to estimate the ages of older age-classes (e.g. adult females that were aged in reference to the year they gave birth to their first calf). The following sections outline the techniques used, their likely precision, and potential biases.

3.1.1 Juveniles

The 240 calves recruited during the study were aged in reference to the year they were born. As noted in Section 2.5, births generally occurred between field seasons, so we assumed animals were censused at their pivotal ages (i.e. midpoint between birthdays). In actual fact, because calving was seasonally diffuse through the fall, winter and spring (Figure 5), calves could have been born anywhere from just after the preceding July-August survey in which they were not yet present, to just before the first July-August survey they were encountered. These age estimates are thus considered precise to within ± 0.5 years.

In some cases (n=36; 15% of all births) where calves were born during an interval in which their mother had not been seen every year, the year of birth was estimated based on the size of the calf relative to known-aged calves. Because growth was rapid during the first few years, this technique was deemed to be reliable for ageing calves up to about 3 years of age. This method was also used to age the 18 animals that were very small juveniles when first seen at the beginning of the study, and judged to have been born 1-3 years prior to the first encounter with their pod. In cases (n=17) where there was uncertainty as to exact year of birth, it was amortized over the two years it could have been born, so the precision of these ages was ± 1.0 years.

We refer to the 258 animals aged in this manner *known-age* animals, which includes virtually all animals born just prior to or since the beginning of the study, and thus includes some animals that are now aged in their late-20s or early-30s. The known-aged animals were particularly useful for estimating juvenile mortality, age at maturation, and survival and fecundity of young adults.

In most cases, animals that were older than about 3 years of age when first encountered at the beginning of the study were aged in reference to the year they matured (see Sections 3.1.2 and 3.1.3). However, this was not possible for 7 animals that were first seen as large juveniles (including 2 that died before the systematic surveys began), but died before maturing. Their approximate ages were subjectively estimated based on their size when first seen, and probably range in precision from ± 1-2 years for those judged to have been about 3 years old when first seen, to ± 3-5 years for those judged to be about 10 years old when first seen.

3.1.2 Adult Females

The year of birth of 9 females that were juvenile-sized when first seen and matured during the study were aged in reference to the year they gave birth to their first viable calf. The probability of a female being born x years prior to the birth to her first viable calf was estimated as:

$$[3.1.1] \quad \Pr(YB_{Mother} = [YB_{First\ Calf} - x]) = \Pr\,(MAT_{f(x)})$$

where $\Pr(MAT_{f(x)})$ represents the estimated proportion of females giving birth to their first viable calf at age x (see Section 3.2.1). The corresponding point estimate was obtained by integrating the probability distribution:

$$[3.1.2] \qquad YB_{Mother} = YB_{First\ Calf} - \sum x \cdot \Pr(MAT_f(x)) \quad \text{for } x = 9,..,21$$

(the summation represents the range in age over which females give birth to their first viable calf), which simplifies to the year of birth of first calf minus the mean age of females at first birth, MAT_f:

$$[3.1.3] \qquad YB_{Mother} = YB_{First\ Calf} - MAT_f$$

Since most females (77%) produce their first viable calf between 11 and 17 years of age, but a few as early as 9 or as late as 21 years of age (Section 3.2.1), the precision of these estimates was typically ± 3 years, but in a few cases could have been ± 6 years.

An extension of this technique was used to estimate the year of birth for all but 3 (see last paragraph of this Section) of the 43 northern resident females that were adult-size when first seen, and had given birth to their first calf prior to or early in the study (or because they were adult-size when first seen could have given birth and lost their oldest calf prior to the start of the study). They were aged in reference to the year of birth of their oldest known offspring, which we assumed was their first calf, in which case it represented the year in which the female matured. For example, if a female's oldest calf was born in 1968 (5 years old when the study began in 1973), she was assumed to have been born 14 years earlier (the mean age at first birth) in 1954.

The above estimates tend to be negatively biased due to the assumption the oldest *known* offspring was in fact the female's first, since she may actually have given birth earlier but lost the first calf or calves before the study began. Following Olesiuk et al. (1990), we thus applied a correction factor to account for calf loss, *CFCL*, prior to the start of the study:

$$[3.1.4] \qquad YB_{Mother} = YB_{Oldest\ Known\ Calf} - MAT_f - CFCL$$

The *CFCL* used in this assessment represents a refined version of the simplified procedure originally employed by Olesiuk et al. (1990). The simplified *CFCL* assumed females gave birth to calves at fixed 5-year intervals. If a female had lost her first calf prior to the start of the study, she was considered to have been 5 years older than estimated by equation [3.1.3]; if she had lost her first two calves prior to the start of the study, she was considered 10 years older than estimated by equation [3.1.3], and so forth. The procedure allowed for the loss of up to 5 calves, which represents the average number born to a female over her reproductive lifespan (see Section 4.1.2). The overall *CFCL* was calculated by weighting the size of the correction factor corresponding with the loss of *N* calves (5 years for one calf, 10 years for two calves, and up to 25 years for 5 calves) by the probability that the first *N* calves had all died prior to the start of the study:

$$[3.1.5] \qquad CFCL_{SIMPLE} = \sum [\Pr(Lose{=}N) \cdot (N \cdot 5)] \quad \text{for } N = 1,..,5$$

where the probabilities of losing calves was estimated from the survivorship schedule. Olesiuk et al. (1990) provide further details.

In this paper, we derived a somewhat more realistic *CFCL* based on the same underlying principle, but allowing calving intervals to vary over the range observed during the study, rather than assuming calves were born at fixed 5-year calving intervals. Derivation of the refined *CFCL* involved three steps (Note: readers may prefer skipping down several paragraphs to the graphical illustration before delving into the math). First, we began by tallying the probabilities that the

*N*th additional calf, C_N, would have been born x years prior to the year of birth of the oldest known calf:

$$[3.1.6] \qquad \Pr(C_N = [l_1 + \ldots + l_N]) = \sum[\Pr(CI_n = l_x) \cdot \ldots \cdot \Pr(CI_N = l_x)]$$

summed over l_x = 2,..,11 (the observed range in calving intervals) for each of the N = 1,..,5 calving intervals. The $\Pr(CI=l_x)$ represents the observed proportion of calving intervals that were x years (see Section 3.3.1). Equation [3.1.6] merely calculates the $(11\text{-}2+1)^N$ possible combinations for N calving intervals, and tallies up the probabilities of the *N*th calf being born $x=l_1+l_N$ years prior to the birth of the oldest surviving calf. The underlying assumptions were that calving intervals did not vary with age, and were independent of one another, both of which seemed reasonable (see Section 3.3.1).

The second step was to calculate, for each possible combination of calving intervals, the corresponding probabilities that *all* the first N calves would have died prior to the start of the study for each. For estimating survival probabilities, it was assumed that the sex ratio of calves was equal at birth (see Section 3.4.1), such that cumulative probability of surviving to age x was given by:

$$[3.1.7] \qquad SURV_{(x)} = [\prod SV_{f(x)} + \prod SV_{m(x)}] / 2 \qquad \text{for } i=1,..,x$$

where $SV_{f(x)}$ and $SV_{m(x)}$ represent the age-specific survival rates of females and males aged x years respectively (see Section 3.4[4]). The probability of losing all the first N calves, $\Pr(L=N)$, was thus estimated as:

$$[3.1.8] \qquad \Pr(Lose=[C_1 + \ldots + C_N]) = \prod[1\text{-}SURV(C_i)] \qquad \text{for } i=1,\ldots,N$$

where $SURV(C_i)$ represents the probability the ith calf survived, such that $1\text{-}SURV(C_i)$ is the probability it died. As was the case for calving intervals, it was assumed that deaths of calves were independent events. Finally, the probability of losing no calves was estimated by:

$$[3.1.9] \qquad \Pr(Lose=0) = 1 - \sum \Pr(Lose=x) \qquad \text{for } i=1,\ldots,N$$

Given the probability distribution of the potential size of the correction for calf loss (i.e. number of years between the first and oldest surviving calf) and the associated probability of it occurring (i.e. the oldest calves all having died prior to the start of the study), the overall *CFCL* was obtained – as per equation [3.1.5] – by integrating the two probability density distributions:

$$[3.1.10] \quad CFCL_{REFINED} = \sum [\Pr(Lose = C_1 + \ldots + C_N) \cdot (C_1 + \ldots + C_N)]$$

Following Olesiuk et al. (1990), the integration was truncated at N=5 calves, the average number born by a female over her reproductive lifespan. However, since the probabilities of losing that many consecutive calves diminished to negligible levels, the truncation point chosen had little tangible effect on the age estimates. For example, if we extend the integration to 7

[4]Age-specific survival rates for older females could not be derived before their ages were estimated, so we instead used the crude survival rate for all reproductively active females combined (0.9967), which in retrospect was very close to the average age-specific estimate subsequently derived for females aged 15-39 years (0.9974; Table 8).

calves – the maximum number of viable calves ever observed to be born by a female – the *CFCL* increases only marginally, from 0.01 years for the youngest females aged by this method, to 1.2 years for the oldest female aged by this method.

The notation for calculating *CFCL* is awkward and the math tedious, but the underlying principle is straightforward and perhaps best conveyed graphically (Figure 7). The top panel shows the potential frequency distribution of 1, 2, …, 5 calves that may have been born but died prior to the start of the study. The frequency distribution for the 1st calf is the same as the frequency distribution of calving intervals observed during the study (see Figure 11). The possible range over which the 2nd calf and subsequent calves could have been born becomes increasingly larger due to the cumulative variability of successive calving intervals. For example, since the intervals between calves may vary from as little as 2 to as many as 11 years, its possible, albeit highly unlikely, that a 2nd calf could have been produced in as few as 4 years or as many as 22 years.

The next step is to calculate the probability that the first *N* consecutive calves had all died prior to the start of the study, which is a function of the age of the oldest surviving offspring. The lower panels shows examples where the oldest surviving offspring was aged 10, 20 and 30 years at the beginning of the study. For a female with a calf aged 10 years when first seen (Figure 7 - bottom panel), the age of the next oldest calf would have been about 5, and since most calves survive to that age, there was only about a 20% chance she had lost a calf her first calf. If she had lost her first two calves, her oldest would have been about 10 years older than her oldest surviving calf, but the chances of losing two young calves in a row was only about 5%, so it was quite unlikely (2%) she would have lost more than two consecutive calves. There was thus a reasonably high probability (73%) she had not lost any offspring prior to the start of the study.

In comparison, for a female with a calf aged 30 years when first seen (Figure 7 - second panel from top), her next oldest calf would have been about age 35 years, and there was a 45% chance it would have died prior to the study. It was also quite possible the had lost 2 (23%) or 3 (13%) or even more (11%) calves, in which case she would be 10, 15 or even 20-25 years older than expected. Indeed, the chances were only about 8% her oldest known calf was in fact her first born. As a result of the increasing probabilities of calf loss with age of the oldest known offspring, the size of the correction factor increased from 0.8 years for females for which the oldest known calf was born at the beginning of the study, to 1.9 for females whose oldest known calf was aged 10 at the beginning of the study, to 4.5 when the oldest known calf was aged 20 years, and to 8.9 years when the oldest known calf was aged 30 years at the beginning of the study (Figure 8). As indicated by the histograms in Figure 8, the precision of the age estimates for older females was skewed, with long right hand tails indicating there were small probabilities that they could have been born appreciably earlier than estimated. Table 4 and Figure 7 shows the typical level of precision (80% probability) and likely upper and lower limits (95% probability) for the estimates as a function of the age of the oldest known offspring.

The correction for calf loss, *CFCL*, can only account for natural mortality. Females in cropped pods may have had additional progeny removed during the live-capture fishery that occurred just prior to the start of the study, especially since it was selective toward juveniles (Table 2). Loss of these calves would result in negative bias in the correction factor, resulting in the females being older than estimated. Following Olesiuk et al. (1990), we therefore only applied this ageing technique to females in cropped pods (A05 pod) if they had produced at least 4 calves, or where the estimated birth dates of their calves spanned at least 20 years. Since females typically produce about 5 calves over a 24 year reproductive lifespan (see Section 4.1.2),

females meeting these criteria were unlikely to have had progeny removed. The 3 females (A07, A08 and A09) that failed to meet these criteria were crudely aged in reference to the mean year of birth of their known offspring. We assumed the mean birth date coincided with the midpoint of their reproductive lifespan. Depending on the span between the birth dates of their known calves, these age estimates likely varied in precision from ± 6 years to as much as ± 12 years. The problems associated with ageing older females were much more prevalent in the southern resident community, as all 3 pods had been heavily cropped prior to the start of the study.

3.1.3 Adult Males

The 16 males that were juvenile-sized when first seen were aged in reference to the development of their dorsal fins (see Section 3.2.2). Being a secondary sexual characteristic, the point at which the dorsal fin begins to "sprout" (i.e., a period of rapid pubescent growth in height) probably coincides with the onset of sexual maturity. Males can be statistically distinguished from females when the height to width ratio (*HWR*) of their dorsal fin exceeds 1.4 (Olesiuk et al. 1990), at which point we considered them to be sexually mature. The year of birth of males that attained sexual maturity during the study were thus aged in reference to the year the dorsal fin *HWR* exceeded 1.4:

$$[3.1.10] \qquad \Pr(YB_{Male} = x) = YB_{HWR>1.4} - MAT_{m(x)}$$

where $MAT_{m(x)}$ represents the proportion of known-aged males for which the dorsal fin *HWR* attained a ratio of 1.4 at age *x* (see Section 3.2.2). A point estimate was obtained by integrating the probability distribution:

$$[3.1.11] \qquad YB_{Male} = YB_{HWR>1.4} - \sum x \cdot \Pr(YB_{Male} = x) \qquad \text{for } i = 9,..,18$$

which equates to the year the *HWR* exceeded 1.4 minus the mean age of sexual maturity of males:

$$[3.1.12] \qquad YB_{Male} = YB_{HWR>1.4} - MAT_{m(x)}$$

Since males typically (81%) attain sexual maturity between 11 and 15 years of age, but a few as early as 9 years or as late as 18 years of age (Section 3.2.2), the precision of these estimates was typically ± 2 years, but in a few cases could have been ± 4 years.

Once attaining a *HWR* ratio of 1.4, the male dorsal fin continues to grow in height for an average of 5.5 years (*SE*=0.11; range 3-7 years). Males are referred to as physically mature once the dorsal fin has attained its asymptotic height. Five males that were sexually but not physically mature when first seen were aged in reference to the year the dorsal fin attained its asymptotic height:

$$[3.1.13] \qquad \Pr(YB_{Male} = x) = YB_{HWR=Max} - PMAT_{m(x)}$$

where $PMAT_{m(x)}$ represents the proportion of known-aged males for which development of the dorsal fin was completed at age *x* (see Section 3.2.2). Once again, a point estimate was obtained by integrating the probability distribution:

$$[3.1.14] \quad YB_{Male} = YB_{HWR=Max} - \sum x \cdot \Pr(YB_{Male} = x) \qquad \text{for } i = 9,..,18$$

which equates to the year the dorsal fin reached its asymptotic height minus the mean age of physical maturity of males:

$$[3.1.15] \qquad YB_{Male} = YB_{HWR=Max} - PMAT_{m(x)}$$

An additional 25 males were physically mature when first seen at the beginning of the study, and there was no way of knowing when they might have matured. We could therefore only use the above procedure to determine their minimum age assuming they had attained physical maturity in the same year they were first seen. However, it's possible they were considerably older, as some males live for extended periods after attaining physical maturity. Indeed, two of the males that were physically mature when first seen in 1974-79 (and a third in the southern community) were still alive when last seen in 2004, indicating they had been physically mature for at least 3 decades.

3.2 Maturation

3.2.1 Females

We determined maturity in females on the basis of the age at which they gave birth to their first viable calf. A calf was considered *viable* when it was born between surveys and survived to the first July-August census, at which point it was generally about 6 months of age (Section 2.5). This avoided the problem of missing non-viable calves that may have been stillborn or did not survive long enough to be censused. From a population perspective, the production of viable calves is perhaps the most meaningful measure of maturation, as it represents the age at which females began contributing towards recruitment.

A total of 47 known-aged females gave birth to their first calf over the course of the study, 26 during the initial period of unrestrained growth, and 21 during the more recent period of no net change. In both periods, the youngest females to give birth to viable calves were aged 10 years, and several females did not produce their first viable calf until their early 20s (age 20 years in the first period of unrestrained growth, and 22 years in the second period of no net change). However, most females (77%) gave birth to their first viable calves at 12-17 years of age.

Sample sizes for known-aged females tended to decline with age (Table 5) over the indeterminate period (which would bias a simple average), so we estimated the mean age at first birth, MAT_f, using the method developed by DeMaster (1978) based on the proportion of females mature at each age:

$$[3.2.1] \qquad MAT_f = x \cdot [f(x) - f(x\text{-}1)]$$

with variance:

$$[3.2.2] \qquad \mathrm{Var}(MAT_f) = \sum f(x) \cdot [1\text{-}f(x)] \,/\, n_f(x)\text{-}1$$

where $f(x)$ denotes the proportion of females mature by age x, such that $f(x) - f(x\text{-}1)$ represents the proportion maturing at each age, and $n_f(x)$ the number of known-aged females in the sample at age x.

Mean age at first birth was estimated to be 14.1 years (*SE*=0.23) during the initial period of unrestrained growth, and increased slightly to 15.4 years (*SE*=0.27) during the later period of stability (Table 5). The increase was statistically significant (t_{49} = 3.23; *P*=0.002). The maturation curves (Figure 9) indicate the difference between the two periods occurred at an early age and was maintained over the entire indeterminate period. This suggests that a few more females matured atypically young, and slightly more matured atypically late, during the latter period of no net change.

The gestation period for captive killer whales averages 17 months (range 15-18 months) (Duffield et al. 1995), so females must have ovulated at least 1.4 years before giving birth to their first viable calf. Moreover, we are aware of three instances (A24, A43 and A52) in which females gave birth to non-viable calves that did not survive to the next July-August survey period, prior to giving birth to a viable calf. By our definition, these females were still classified as immature. Interestingly, however, all 3 females gave birth to their first viable calves by the following field season, indicating they must have become pregnant almost immediately after losing their non-viable calves. Because our main field season occurs outside the primary calving period, we do not typically see very young calves until they are about 6 months of age, so there were probably many other instances where non-viable calves were lost before females produced their first viable calf. While this has no effect on our population model (production of non-viable calves doesn't affect the age at which females begin to contribute to recruitment), it's an important consideration when comparing our estimates of age at maturation to those in the literature based on ovulation or pregnancy data (e.g. Christensen 1984).

3.2.2 Males

Adult male killer whales can be distinguished from juveniles and adult females by their prominent dorsal fins, a secondary sexual characteristic. In adult males, the dorsal fin attains a height of about 1.5 meters, compared with a maximum of about 0.9 meters in adult females (Bigg 1982). Olesiuk et al. (1990) showed that the male fin could be statistically distinguished from females when it reached a height-to-width ratio (*HWR*) of 1.4, which appears to occur during adolescence. We therefore defined sexual maturity in reference to the year the *HWR* attained or exceeded 1.4.

The fins of a total of 52 known-aged males attained a *HWR* of 1.4 over the course of the study, 27 during the period of unrestrained growth, and 25 during the more recent period of no net change. The indeterminate period was the same for both periods; the youngest males showing evidence of 'sprouting' fins were aged 9 years, but a few did not begin to sprout until 18 years of age. In most cases (81%) the fin attained a *HWR* of 1.4 between 11-15 years of age.

Sample sizes for known aged males also diminished with age over the indeterminate period (Table 6), so we again estimated the mean age at male maturation, MAT_m, using the method developed by DeMaster (1978) based on the proportion of males mature at each age:

$$[3.2.3] \qquad MAT_m = x \cdot [m(x) - m(x\text{-}1)]$$

with variance:

$$[3.2.4] \qquad \mathrm{Var}(MAT_m) = \sum m(x) \cdot [1\text{-}m(x)] \,/\, nm(x)\text{-}1$$

where *m(x)* denotes the proportion of males mature by age *x*, such that *m(x) – m(x-1)* represents the proportion maturing at each age, and *nm(x)* the number of known-aged males in the sample at age *x*.

Mean age at onset of sexual maturity was estimated to be 13.0 years (*SE*=0.22) during the initial period of unrestrained growth, and 12.8 years (*SE*=0.21) during the later period of stability (Table 6). The difference was not statistically significant ($t_{0.05,40}$=0.49; *P*=0.63) and the maturation curves essentially overlapped (Figure 10), so data for both periods were pooled. The mean age at onset of sexual maturation of males over the entire study period was estimated to be 12.9 years (*SE*=0.26).

After the fin begins to sprout, it continues to develop for a number of years before attaining an asymptotic *HWR* (Olesiuk et al. 1990). Once the fin is completely developed, males are referred to as *physically mature*. During the study, a total of 47 males were observed from the beginning to end of the fin development period. Growth was occasionally completed in as few as 3 years, and sometimes required as long as 7 years, but in the majority of cases (87%) was completed in 5-6 years. The overall mean was 5.5 years (*SE*=0.11), implying that the mean at onset of physical maturity was 18.4 years. Males typically attained physical maturity at 16-21 years of age.

Mating activity was rarely observed, so it could not be established when males actually begin to mate. Judging from other animals, it likely involves a combination of physiological maturity (spermatogenesis) as well as social maturity (social dominance). Using DNA analysis, Barrett-Lennard (2000) and Barrett-Lennard and Ellis (2001) established the paternity for 17 northern resident calves, and narrowed it to either of two males in two additional cases. In all cases, the identified fathers were what we would have regarded as physically mature males.

3.3 Reproductive Rates

3.3.1 Calving Intervals

One measure of the performance of reproductively active females is the interval at which they give birth to successive calves. Generally, the reciprocal of the calving interval measured in years, *CI*, provides an estimate of the annual fecundity rate, FEC_{REP}:

$$[3.3.1] \qquad FEC_{REP} = 1 / CI$$

During 1973-95, the period of unrestrained growth, we documented the intervals between the birth of 90 viable calves (Figure 11). In most cases (90%), calves were born at 3-7 year intervals, although in a few cases intervals were as brief as 2 years (3%) and occasionally as long as 8-11 years (7%). Overall, the mean calving interval was 4.88 years (*SE*=0.793), representing an annual fecundity rate of 0.205 calves per year.

During 1996-2004, the period of population no net change, we documented the intervals between the birth of an additional 61 calves (Figure 11). The mean calving intervals was slightly longer at 5.53 years, representing an average fecundity rate of 0.180 calves per year. Calving intervals also tended to be considerably more variable (*SE*=1.103). Although the difference in calving interval was small, it was marginally significant (*ANOVA* for unequal variances; $F_{1,97}$=1.71; *P*=0.091). The main reason for the slight increase and higher variability calving

intervals was the small number (n=4) of unusually long intervals of 12-14 that occurred in the latter part of the study (Figure 12).

The fecundity estimates for both periods were slightly biased, because there were probably a small number of viable calves (0.2-0.6% of all viable births during 1973-96, and 1.1-2.9% during 1996-2004) that were born during gaps in annual encounters and died before being catalogued (see Section 4.0.0). Examination of the sightings for the females (A23, D11, H05, I12, R18) exhibiting the abnormally long calving intervals indicate there were gaps in all but one (A23's 11-year calving interval) of their encounter records. Some of the gaps spanned 2-6 years, in which these females could have given birth and lost calves. If the 5 abnormal calving intervals greater than 10 years are excluded, there was no indication at all that calving intervals changed over the course of the study (Figure 11) ($F_{1,149}$=3.05; P=0.083 for all intervals; $F_{1,149}$=3.05; P=0.438 excluding 5 intervals greater than 10 years). Thus, we suspect the small apparent difference in calving intervals was largely an artifact due to increased calf loss between surveys, rather than a real change in the rate at which reproductive females produced calves during the two periods.

There was no evidence that calving intervals varied with the age of the mother (Figure 12b) ($F_{1,149}$=1.34; P=0.248). Moreover, consecutive calving intervals for a particular female didn't seem to follow any specific pattern ($F_{1,87}$=0.57; P=0.45), and as often as short intervals were followed by long intervals, long intervals were followed by short intervals (Figure 13).

3.3.2 Age-Specific fecundity

Another measure of reproductive performance is the age-specific fecundity rate of females, $FEC_{f(x)}$, defined here as the proportion of mature females aged x giving birth to viable calves each year:

$$[3.3.3] \qquad FEC_{f(x)} = NC_{f(x)} / N_{f(x)}$$

where $NC_{f(x)}$ denotes the number of calves of either sex born to females aged x, and $N_{f(x)}$ the total number of females aged x.

For young adult females, we examined fecundity patterns for 108 known-aged females that attained ages 10 or greater during the study (63 during the first phase of unrestrained growth, and 45 during the second period of no net change). These adolescent females exhibited a distinct pattern in fecundity that was similar during both periods (Figure 14). Fecundity rates increased sharply and peaked at 12-14 years of age, as this represented the period most females were maturing and giving birth to their first viable calf. There was a subsequent drop in fecundity at about 16 years of age, by which age most animals had already given birth to their first calf, but few were yet producing a second calf. The second peak at 17-18 mainly represents females giving birth to their second calves, with a few still producing their first calf, particularly in the latter period. Beyond age 20, sample sizes of known-aged females had diminished (to 32 and 17 females in the two periods), and oscillations for subsequent calves tended to be obscured by the cumulative variability of calving intervals.

For older adult females, fecundity was examined for all mature females, including both known-aged animals and those that had been aged in reference to the year of birth of their first

offspring[5]. The analysis was based on 64 females aged 20+ years representing a total of 845 animal-years during the initial period of unrestrained growth, and on 70 females aged 20+ years representing a total of 434 animal-years during the second period of no net change. These females produced 86 calves during first period, and 47 during second period, representing average fecundity rates of 0.101 and 0.108 respectively. Because many of these females had been aged on the basis of the year they matured, which typically varied within ± 3 years, age-specific fecundities were calculated using a ± 3 year running averages for each age.

For both periods, there was a pronounced and highly significant decline in fecundity with age (Figure 15) ($F_{1,29}$=239.0 and $F_{1,26}$=42.9 respectively; P<0.001). However, the rate of decline tended to accelerate with increasing age ($F_{1,28}$=45.2 and $F_{1,25}$=80.6 respectively; P<0.001), and in both cases the trend could better be described by a second order polynomial:

[3.3.4] $$FEC_{MATf(x)} = 0.085 + 0.0765 \cdot x - 0.000187 \cdot x^2$$

($F_{2,28}$=324.2; r^2=0.957; P<0.001) for the initial period of unrestrained growth, and:

[3.3.5] $$FEC_{MATf(x)} = -0.213 + 0.0035 \cdot x - 0.000052 \cdot x^2$$

($F_{2,25}$=127.6; r^2=0.911; P<0.001) for the second period of no net change. During the initial period of unrestrained growth, average fecundity dropped from 0.16 calves per year for females in their twenties, to 0.12 for females in their thirties, and to 0.05 for females in their forties. Similarly, during the more recent period of no net change, average fecundity dropped from 0.15 calves per year for females in their twenties, to 0.13 for females in their thirties, and to 0.05 for females in their forties. In both cases, fecundities had declined to zero by about 45-50 years of age. This was not attributable to small samples (sample sizes were 108 and 67 animal-years for females aged 50+ in the first and second periods respectively), but rather it was because the older females simply stopped producing calves.

The steady decline in fecundity with age (Figure 15) at first seems to be at odds with the absence of any discernible change in calving intervals with the age (Figure 12). The difference is due to reproductive senescence – females that were reproductively active continued to produce calves at the same rate, but older females stopped calving altogether, resulting in a decline in fecundity but no change in calving interval with age. Almost all young females (35 of 37 females[6]) had produced calves by the time they reached their twenties. While some continued to produce calves at regular intervals, others stopped producing as they aged. Some of the oldest females in the population did not give birth throughout the study, but had surviving progeny born prior to the start of the study. Since only a small proportion (4 of 151) of calving intervals were longer than 10 years, it was unlikely that a female that had not calved for a decade would calve again. We therefore defined mature females as being either reproductive if they had produced a calf within the last decade, or post-reproductive if they had not. Since we could not tell whether a female would give birth again or not, there was a 10-year lag before a female could be classified as being post-reproductive.

[5]The 3 females (A07, A08 and A09) in cropped pods that were crudely aged in reference to the average age of their offspring were excluded from the analysis of age-specific fecundity rates.

[6]The exceptions were A28, a female born in 1974 that had not given birth when last seen at age 30 in 2004, and R13, a female born in 1979 that had not given birth when last seen at age 25 in 2004. We refer to females that attained age 20 without giving birth as *barren females*. [Addendum: R13 subsequently gave birth to her first viable calf in 2005]

We re-calculated age-specific fecundity rates for only females that were reproductively active, $FEC_{REP(x)}$, by excluding post-reproductive animals we knew had not calved for at least a decade. For the initial period of unrestrained growth, fecundity increased slightly but significantly ($F_{2,17}$=16.0; r^2=0.654; P<0.001) with age (Figure 16a):

[3.3.6] $$FEC_{REPf(x)} = 0.197 - 0.0044 \cdot x + 0.000129 \cdot x^2$$

Part of the increase in the apparent fecundity rate for older females is probably due to the fact that females were designated post-reproductive right after the birth of their last offspring, such that by definition, every female gave birth in the last year she was considered reproductively active. Normally, when calculating fecundity by equation [3.3.3], females get tallied in the numerator both before, within, and after the year they give birth, providing an unbiased estimate of fecundity. However, when restricting the analysis to reproductively active females, animals get tallied in the numerator only in the years leading up to and in which they give birth, but not in the years following the birth of their last calf, thus inflating the estimate for older animals. We don't see any way around this problem. It should also be noted that relatively few females were still reproductively active in their late 30s, so the right-hand portion of the regression was also subject to small sample biases, such as a few females happening to have had short calving intervals at the end of their reproductive lifespan.

During the second period of no net change, there was no discernible change in fecundity with age (Figure 16b) ($F_{1,18}$=0.009; r^2=0.001; P=0.927). However, the analysis for this period was confounded by the fact there were many females included in the analysis for which the reproductive status was not known. It will be another decade before the females who just recently gave birth to their last calf can be designated as post-reproductive.

3.3.3 Reproductive Lifespan

Since the difference in fecundity rates between reproductively active females and all mature females appeared to be due to reproductive senescence, the ratio of these fecundities provides an estimate of the proportion of females that were post reproductive, $PR_{f(x)}$, at age x:

[3.3.7] $$PR_{f(x)} = 1 - (FEC_{MATf(x)} / \mathrm{FEC}_{REPf(x)})$$

The same technique used to estimate mean age at maturation (Section 3.2) can then be applied to estimate mean age an onset of reproductive senescence:

[3.3.8] $$PR_f = x \cdot [pr(x) - pr(x\text{-}1)]$$

with variance:

[3.3.9] $$\mathrm{Var}(PR_f) = \sum pr(x) \cdot [1\text{-}pr(x)] / nf(x)\text{-}1$$

where $pr(x)$ denotes the proportion of females that were post-reproductive by age x, such that $pr(x) - pr(x\text{-}1)$ represents the proportion becoming senescent at each age, and $n_f(x)$ denotes the number of females in the sample at age x.

During the initial period of unrestrained growth, the first females showed signs of reproductive senescence in their mid-20s, but most females (88%) were still reproductively active

at age 30 years (Figure 17a). The onset of reproductive senescence was rather abrupt thereafter, with half of all females being post-reproductive by age 36 years, and relatively few giving birth after their 40s. The oldest female to calve during this period was estimated to be 46 years old, but sample sizes of females that old but still considered reproductive were extremely small. Moreover, the precision of age estimates for females that old was probably on the order of -7 to +9 years (Section 3.1.2). Mean age at onset of reproductive senescence was estimated at 37.8 years (*SE*=0.40 years).

During the more recent period of no net change, the first females showed signs of reproductive senescence in their late 20s, half of all females were post-reproductive by age 41, and relatively few (25%) gave birth in their 40s (Figure 17b). The oldest female to calve during this period was again estimated to be 44 years old, but sample sizes for reproductive females that old were even sparser for this period, and once again the precision of age estimate for females that age was probably on the order of -6 to +8 years (Section 3.1.2). Mean age at onset of reproductive senescence was estimated at 41.5 years (*SE*=0.40 years), which was significantly greater than during the initial period of unrestrained growth ($t_{2,37}$=6.78; P<0.001). The primary reason for the difference was higher prevalence of young reproductively senescent females estimated to be less than 30 years of age during the period of unrestrained growth. To some extent this may have been biased by the lower precision of the age estimates for these older females early in the study (because they were based on older offspring with higher chances of calf loss prior to the study) than equivalent age estimates later in the study (because they were based on age of maturation or very young offspring).

3.4 Survival and Mortality

Resident killer whales exhibit a unique social system in which neither males nor females disperse from natal matrilines. Thus, the only way of joining a matriline is by being born into it, and the only way of leaving is by dying (Bigg et al. 1990). Since animals in a matriline travel as a cohesive group, they are virtually always encountered together, and any members missing from the group can be presumed to have died. Nevertheless, we have been very conservative in not designating an animal as dead until we were confident we had sufficient high-quality encounters to be sure it was missing. There has never been an instance when an animal presumed to have died had to be resurrected.

Annual survival and mortality rates, $SV_{s(x)}$ and $MR_{s(x)}$, were estimated based on the proportion of animals of sex s that died between age x and age x+1:

$$[3.4.1] \qquad SV_{s(x)} = L_{x+1,t+1} / L_{x,t} = 1\text{-}MR_{s(x)} = 1 - D_{x+1,t+1} / L_{x,t}$$

with, being reciprocal binomial variates, variance:

$$[3.4.2] \qquad \mathrm{Var}(SV_{s(x)}) = \mathrm{Var}(MR_{s(x)}) = SV_{s(x)} \cdot MR_{s(x)} / L_{(x),t}$$

where $L_{x,t}$ is the number of animals alive at age x in year t, L_{x+1} the number of those that survived to age x+1 in year t+1, and D_{x+1} the number that died before reaching age x+1 in year t+1. Only animals for which the status was known in the proceeding year were included in the calculation, such that $L_{x+1,t+1} + D_{x+1,t+1} = L_{x,t}$ (i.e. all animals in the sample either survived or died). As a result, there was always a one-year lag in determining annual survival, such that we won't be able to calculate how many animals present in 2004 survive or die until the 2005 survey is completed.

3.4.1 Juveniles

The survival and mortality rate of juveniles to age 15.5 (the approximate age at which they are recruited into the adult population – see Section 3.2) was estimated based on the proportion of known-aged animals that died or lived. In many cases the sex of young animals could not be determined until they matured such that many juveniles died before being sexed, so both sexes were pooled for the analysis of juvenile survival and mortality rates. Since we expected any changes in survival and mortality to be more pronounced early in life (Olesiuk et al. 1990), and to take advantage of larger sample sizes for younger age-classes, we grouped animals into progressively wider age categories: age 0.5 years, age 1.5-2.5 years, age 3.5-5.5 years, and age 6.5-9.5, and age 10.5-14.5. The differences in mortality and survival rates between these age-categories was highly significant (χ^2=12.83; *P*=0.012)

During the initial period of unrestrained growth in 1973-96, juvenile survival and mortality was calculated from 171 known-aged animals that were juveniles for at least part of the period, 24 of which died (Table 7). The animals provided a total sample of 1,534 animal years, representing a mean annual mortality rate of 1.6%. However, mortality rates decreased systematically with age, from a high of 2.9% at age 0.5 years, to a low of 0.6% for animals aged 10.5-14.5 years. Overall, the cumulative survival to age 15.5 years, approximately the age by which animals are recruited into the adult population, was estimated to be 81.9%, indicating that only 18.1% of juveniles died before reaching adulthood.

During the more recent period of no net change in 1996-2004, juvenile survival and mortality was calculated from 144 known-aged animals that were juveniles for at least part of the period, 28 of which died (Table 7). The animals provided a total sample of 832 animal years, representing a mean annual mortality rate of 3.4%. This was just over double the rate observed during the period of unrestrained growth, and the difference was highly significant (χ^2=8.14; *P*=0.008). Once again, mortality rates tended to decrease with age, but interestingly, the decline was not as systematic, with animals aged 4.5-6.5 experiencing especially high mortality. The mortality for that age group was significantly higher than that the preceding or proceeding age groups during the same period, and significantly higher than the same age-group during the period of unrestrained growth (χ^2=4.54 and P=0.049; χ^2=7.39 and P=0.008; and χ^2=10.06 and *P*=0.003 respectively). A more detailed inspection of the records for these animals indicated that in most cases (9 of 12) these young juveniles died in the year of birth or year following the birth of a younger sibling. Because of the elevated mortality rates, cumulative survival to age 15.5 years was estimated to be 60.8%, indicating that 39.2% of juveniles (twice as many as when the population was growing) died before reaching adulthood.

As noted in Section 2.4, not all animals were seen every year. Its was therefore possible that viable calves were born but died during gaps in encounters before being catalogued. We estimated the number that may have been missed using two techniques. The first method was based on the observed mortality rates of juveniles (Table 7) and the number and size of gaps in encounters (Table 3). For example, cumulative survival of juveniles to age 1.5 years is 0.9715, so we would expect to have missed 2.85% of all calves born during one-year gaps; cumulative survival to age 2.5 years was 0.9469, so we would expect to have missed 5.3% of all calves born within two-year gaps, and so forth. The second method was based on observed fecundity rates (Section 3.3), which we used to calculate the expected number of calves that should have been born during the gaps, with the shortfall from the number actually observed representing the

number of calves lost before being seen. During 1973-96, we estimated 0.3 calves would have been missed based on mortality rates, whereas the shortfall in fecundity was 1.0 calves. During 1997-2004, we estimated 1.0 calves would have been missed based on survival rates, but the shortfall in fecundity was 2.5 calves. Its unclear why the method based on survival gave consistently lower estimates, unless there was some reason we were less likely to have encountered a female in years she lost a calf. In any event, regardless of how it's calculated, the number of viable calves likely to have been missed was small, ranging between 0.2-0.6% of all viable births (1.2-4.0% of all juvenile deaths) during 1973-96, and 1.1-2.9% of all viable births (3.4-8.1% of all juvenile deaths) during 1997-2004. We did not make any adjustments for these calves to the juvenile survival estimates, since they would have been exactly cancelled by opposite adjustments to fecundity rates.

As noted above, in many cases the sex of animals was not established until they matured, so the sex of most juveniles that died, particularly those that died at an early age, was not known. Although it was impossible to directly compare mortality rates for males and females, an essentially equal number of males and females (70 females and 67 males) attained age 15.5 years during the study. Assuming the sex ratio was equal at birth, this suggests that mortality was equal for males and female juveniles (or that any disparity in sex ratio at birth was cancelled by disparity in survival of juveniles). In either case, recruitment of adults was about equal for both sexes.

We made no attempt to estimate mortality within the first 6 months of life. Since most births occurred outside our field season, calves were generally first encountered when they were about 6 months of age. Although this makes it impossible to estimate neonate mortality from the summer survey data, we suspect mortality at birth and in the first few months of life is high. Olesiuk et al. (1990) inferred it could be as high as 37-50%, although in retrospect that is probably on the high side. One indication of high neonate mortality has been the surprising number of neonate carcass strandings in the study area. Olesiuk et al. (1990) reported data for 8 such strandings during 1975-87 (and one from 1944), compared with only 3 carcasses of older killer whales having been recovered over the same time period. For unknown reasons, however, we have not documented any additional neonate stranding since 1987, although one of us (*GME*) observed a southern resident female (J11) carrying a dead neonate carcass on 04-December-1998. Another indication of high neonate mortality has been the surprising number of calves encountered when are very young, usually just after the main field season, that have disappeared before the next summer census. We know of at least 12 newborn calves (9 in the southern community and 3 in the northern community) seen outside the summer field season that had disappeared by the next field season. Since none of the deaths of these non-viable calves correspond with the neonate strandings (which by itself indicates we are missing a high proportion of both), the two sources of information combined indicate a minimum of 19 southern and northern resident neonates died, representing at least 5.4% all known births. This is undoubtedly a gross underestimate, since many if not most neonate deaths likely go unnoticed.

3.4.2 Adult Females

The survival and mortality rate of adult females aged 15.5 years or older was estimated based on the proportion of animals that lived or died respectively. Because of the increasing imprecision of the age estimates with increasing age (Table 4), females were grouped into a 5-year category of 15.5-19.5 years, which was comprised mainly of known-aged females and those aged on the basis of the birth of known first viable calf, which were typically precise to within ±3

years, and subsequently into a series of 10-year age-groups of 20.5-29.5, 30.5-39.5, and 40.5-49.5 years that were comprised mainly of females aged on basis of oldest progeny with corrections for calf loss, for which precision ranged from ±3 to ±5 years. Due to small sample sizes and imprecision in age estimates, all females older than 50.5 years were pooled.

During the initial period of unrestrained growth in 1973-96, adult females exhibited extremely low mortality throughout their reproductive lifespan. Despite a sample size of 208 animal years – the equivalent to monitoring 20.8 animals for a decade each – we didn't observe any deaths of females aged 15.5-19.5 years. Mortality rates continued to be very low, varying from 0.34 to 0.37%, for females aged 20.5-29.5 and 30.5-39.5 years respectively. As a result, an estimated 93% of females that matured would have survived to the age 40.5 years, roughly the end of their reproductive lifespan. Mortality of females subsequently increased abruptly, which coincided with the onset of reproductive senescence. Annual mortality increased by an order of magnitude to 4.7% for females aged 40.5-49.5 years, and to 6.2% for females aged greater than 50.5 years.

During the more recent period of no net change during 1997-2004, adult females still exhibited low mortality throughout their reproductive lifespan, but not as low as during the period of unrestrained growth. Although our sample size of young adult females aged 15.5-19.5 years was about half the size of the initial period of unrestrained growth (208 versus 115 animal-years respectively), we saw the first 2 instances of such young females dying, although it still only represented an annual mortality rate of 1.5%. Mortality of females aged 20.5-29.5 and 30.5-39.5 subsequently averaged about 1.9% (range 0.5-2.5%). As a result, an estimated 68% of females that matured would have survived to the age 40.5 years, roughly the end of their reproductive lifespan. Mortality subsequently increased abruptly, coinciding with the onset of reproductive senescence, to 5.8% for females aged 40.5-49.5 years, and to 6.8% for females aged greater than 50.5 years.

3.4.3 Adult Males

The mortality of adult males was estimated based on the proportion of animals aged 15.5 years or older that died. Because of the increasing imprecision of the age estimates with increasing age (Table 4), males were grouped into a 5-year category of 15.5-19.5 years, which was comprised mainly of known-aged males and those aged on the basis of the year they attained sexual maturity, which provided age estimates that were typically precise to within ±3 years. Depending on available sample sizes, the next category was either animals aged 20.5-24.5 years (1973-96) or 20.5-29.5 years (1996-2004) years, which mainly included males aged in reference to the year they attained sexual or physical maturity, which were typically precise to within ±2 or ±5 years respectively. Our ability to examine age-related patterns in mortality for older animals was limited, especially in the first period, because only the minimum ages could be established for the oldest males. Consequently, all males aged 25.5+ years were pooled for the initial period of unrestrained growth during 1973-96, and all males aged 30.5+ years were pooled for the more recent period of no net change during 1996-2004.

During the initial period of unrestrained growth, adult males exhibited low mortality in early adulthood, with mortality estimated at 1.1% for males aged 15.5-19.5 years. Mortality rates began to increase coinciding with the onset of physical maturity, rising to 4.2% for males aged 20.5-25.5 years and to 5.8% for males aged 25.5+ years. During the more recent period of no net change, young adult males also exhibited fairly low mortality, estimated at 2.5% for males aged

15.5-19.5 years. However, mortality rates increased dramatically at the onset of physical maturity, to 8.1% for males aged 20.5-29.5 years (4.8% for those aged 20.5-24.5 years), and to 18.3% for males aged 30.5+ years.

3.4.4 Survival and Mortality Patterns

The overall survival pattern for killer whales follows the typical mammalian U-shaped curve (Caughley 1966) (Figure 18), indicating that the very youngest and very oldest animals experience the highest losses. During the period of unrestrained growth, the survival curve was remarkably shallow and broad for females, indicating they experienced negligible mortality throughout their reproductive lifespan. Indeed, the death of a reproductively active female was an extremely rare event, having only been observed twice in a sample representing over 750 animal-years (the equivalent of 2 deaths after following 75 animals for a decade). We cannot imagine any biases that would have caused us to underestimate mortality in this or any other age-class (except of course neonate mortality prior to their first encounter). The curve was somewhat shallower and narrower for males, with mortality increasing abruptly at about the time they attained physical maturity and presumably started breeding.

For the more recent period of no net change, the mortality followed the same general pattern, but the mortality curve was shifted upwards, indicating all sex- and age- classes experienced greater losses. The curve was also noticeably narrower for males, indicating that the youngest and oldest (and presumably most vulnerable) age-classes exhibited the greatest increase in mortality. We can get a sense of the magnitude of the increase in mortality during the recent period of no net change, by comparing the observed number of animals dying with the expected number had mortality rates been the same as those observed during the initial period of unrestrained growth. During 1996-2004, there were 229% more juvenile deaths than expected, 173% more adult female deaths than expected, and 246% more adult male deaths than expected. Obviously, reduced survival played a major role in the recent decline in productivity of the northern resident killer whale population. We examine this in greater detail in the next section using our population model.

4. POPULATION DYNAMICS

4.1 Life Tables and Projection Matrix

In this section, the life history parameters derived in Section 3 for the various components of the population are integrated into survival and reproductive schedules over the entire lifespan. The schedules are examined for a theoretical cohort of animals using life tables. We also employ the finite approximations of Lotka's (1907a,b) classic population equations (Cole 1954) to examine population dynamics. The sex- and age-specific survival and fecundity rates also incorporated into a Leslie-type matrix projection model (Lewis 1942, Leslie 1945, Usher 1972, Caswell 2000), but extended to include both sexes and post-reproductive animals, and used to project populations through time.

Given the abrupt change in status of population around 1996 (Section 2.6), coinciding with an increase in mortality (Section 3.4.4), we developed separate population models for 1973-

96, representing a period of unrestrained population growth, and 1996-2004, representing a period of no net change.

4.1.1 Survival Schedules

Survivorship schedules are most often inferred from latitudinal (cross-sectional) data on the sex- and age-composition of a sample of animals taken over a relatively brief period (relative to the lifespan). Interpretation of such data requires knowledge, or necessitates assumptions, about population trends. For example, if it's known or assumed the population has not changed in size over time, such that all cohorts (age-classes) represented in the population were initially the same size when recruited, the decline in prevalence of animals with age reflects mortality. If, on the other hand, the population has not been stable, the age-structure will reflect both changes in recruitment over time and survival with age, which seriously confounds population analyses based on latitudinal samples.

Survivorship schedules inferred form longitudinal (time-series) data on the fate of animals over time are not subject to the same biases. In practice, however, it is difficult to monitor a cohort of animals over their entire lifespan, especially long-lived or highly mobile species such as cetaceans, and sample sizes often diminish due to increasing mortality with age.

The killer whale photo-identification study provides a relatively long time-series, one of the longest we know of for a cetacean, for estimating survival from longitudinal data. However, the study period still hasn't covered an entire lifespan, and it may be another 50 years or so before animals recruited early in the study have all died. We thus modeled survivorship for an imaginary cohort of 1000 whales. Because survival changed with age, and censuses were conducted annually, the survivorship schedule was developed over finite increments of one year, from age x to x+1 years. Given the differences in survival patterns between females and males, we examined cohorts for each sex, s, separately. Since calving was diffusely seasonal, and we generally surveyed the population during the non-calving season, we assumed animals were first seen at age 0.5 years and censused at their pivotal ages. We assumed the sex ratio was unity at birth, which appeared to be the case (Section 3.4.1). Setting $L_{f(0.5)} = Lm_{(0.5)} = 1{,}000$, the survival of our imaginary cohort was constructed as follows:

$$[4.1.1] \quad L_{s(x+1)} = L_{s(x)} \cdot SV_{s(x)}$$

where $SV_{s(x)}$ represents the probability an animal of sex s and age x survived to age x+1, as per Tables 7, 8 and 9. It is worth noting that calculating the survivorship schedule required no knowledge or involved any assumptions about population status or structure, and was based solely on the probabilities of animals surviving or dying, and not on their abundance or composition in the population (for example, in estimating mortality of juveniles, we only included known-aged animals that had been born during the study, and ignored all other juveniles aged in reference to when they matured).

The survivorship schedules are shown in Tables 10 and 11 for females and males during the initial period of unrestrained growth; and Tables 12 and 13 for more recent period of no net change. For females, survival was very high during the period of unrestrained growth, with 81% surviving to the mean age at which they first calve (14 years) and 75% to the mean age of onset of reproductive senescence (38 years), at which point they began experiencing elevated mortality. In contrast, during the more recent period of no net change, only 62% of females survived to the

mean age at which they produce their first viable calve (15 years), and 41% to the end of their reproductive lifespan (41 years), at which point the increase in mortality was even more abrupt. For males, 77% survived to the mean age of physical maturity (19 years) during the initial period of unrestrained growth, but this dropped to 56% during the more recent period of no net change.

The survivorship schedule represents the relative number of animals surviving to age x. Summing from any particular age to the end of the series thus provides an estimate of the animal-years yet to be lived by the cohort subsequent to that age, and therefore dividing by the size of the cohort at that particular age provides an estimate of further life expectancy, $E_{s(x)}$:

$$[4.1.2] \quad E_{s(x)} = \sum L_{s(x)} \; / \; L_{s(x)} \qquad \text{for } i = x,\ldots,\text{maximum age}^{7}$$

The mean life expectancy for females aged 0.5 years was 45.8 years during the initial period of unrestrained growth, but fell to 30.0 years during the more recent period of no net change. Life expectancy subsequently increased slightly with age, to a maximum of 46.4 years at age 3 years during the initial period of unrestrained growth, and to a maximum of 34.5 years at age 6 years during the period of no net change. These small increase indicates that the prospects of animals improved slightly once they survived through the first few vulnerable years of life. Life expectancy then steadily declined, and by the time females reached the mean age of onset of reproductive senescence, further life expectancy had fallen to about 19 years during initial period of unrestrained growth, and to 15 years during the more recent period of no net change.

The mean life expectancy of males aged 0.5 years was 31.0 years during the initial period of unrestrained growth, but fell to 19.3 years during the more recent period of no net change. Life expectancy subsequently declined with age, to 20 years subsequent to the mean age at onset of sexual maturity during initial period of unrestrained growth, compared with only 11 years during the more recent period of no net change.

It should be noted that life expectancy is conventionally expressed from the time of birth. However, since we lacked a reliable estimate of neonate mortality during the first 6 months of life, this was not possible for killer whales. We suspect neonate mortality is very high, in which case life expectancy from birth could be appreciably lower than estimated for viable calves that had attained 0.5 years of age, but the life expectancies for age 0.5 years and beyond would not be affected.

4.1.2 Reproductive Schedules

A schedule of the reproductive performance of females over their entire lifespan was constructed from the age-specific fecundity estimates, $m_{(x)}$. Early in adulthood, fecundity is a complex function of the rate of maturation and length of calving intervals. The fecundity of adolescent and young adult females was thus estimated from annual fecundities of known-aged animals as per Figure 14. For older females, all of which have matured, these complex patterns become obscured by the variability in preceding calving intervals, and imprecision in our age

[7]Maximum longevity is a difficult parameter to define or estimate. We truncated the survivorship and reproductive schedules at the point where, rounded to the nearest decade, a cohort in a stable population had diminished to less than 1% its initial size. This truncation point was generally of little consequence, since older animals comprised only a very small proportion of the total population, and all old females were post-reproductive. The only exception is the estimation of mean life expectancy for older animals, which becomes more sensitive to the truncation point with increasing age.

estimates. Nevertheless, the general pattern is a decline in fecundities with age, which begins with females in their early 30s, and accelerates through the early 40s, such that most had produced their last viable calf by their mid 40s. The fecundities for these females were estimated from equations [3.3.4] and [3.3.5], as illustrated in Figure 15. It is sometimes convenient to express fecundity in terms of just female or male offspring, so assuming the birth ratio was equal at birth, we set $m_{f(x)} = m_{m(x)} = 0.5 \cdot m_{(x)}$.

We debated whether to calculate reproductive schedules separately for the initial period of unrestrained growth during 1973-96, and the more recent period of no net change during 1996-2004. Although there were statistically significant differences between the two periods for mean age at first birth, calving intervals, and mean age at last birth, the differences were small and appeared to be of little biological importance. Moreover, we suspect some if not most of the difference may have been attributable to a slight increase in the biases associated with missing viable calves during gaps in annual sightings. This bias increased in the latter part of the study because young juveniles exhibited elevated mortality rates. Missing several calves would have resulted in a few atypically long calving intervals that accounted for the statistical difference. Similarly, if young females lost their first viable calf before it was seen, they would not have been recorded as maturing until the birth of their second viable calf, explaining the increase in maturity. Nevertheless, we calculated separate schedules so that the biological significance of changes in survival could be compared with the biological significance of changes in apparent reproductive rates, even though the latter may have been slightly exaggerated.

Not surprisingly, the reproductive schedules, $m_{(x)}$, were very similar for the two periods (Tables 10 and 12). In the initial period of unrestrained growth, females that survived to the end of their reproductive lifespan would be expected to produce 4.7 calves, compared with 4.5 during the more recent period of unrestrained calves. In both cases, the most fertile period was 12 to 40 years, which accounted for 89-91% of total calf production. These values indicate the *reproductive potential* of females, although the realized reproductive rate would be somewhat lower due to mortality prior to and during their reproductive lifespan.

4.1.3 Reproductive Value

Combining the survival and fecundity schedules provides an estimate of the *realized reproductive rate* of calf production for females. The expected number of calves born subsequent to age x, $RV_{(x)}$, can be estimated as:

$$[4.1.3] \qquad RV(x) = \sum l_{f(x)} \cdot m_{(x)} \qquad \text{summed over } i=x,\ldots,\text{maximum age}$$

which was estimated at 3.6 calves, representing 77% of the reproductive potential, during the initial period of unrestrained growth. The rate was high because 81% of females survived to reproduce, and only 7% of those died before the onset of reproductive senescence. In contrast, the realized reproductive rate fell to 2.2 calves, representing only 50% of the reproductive potential, for the more recent period of no net change. The rate decreased because only 61% of females survived to reproduce, and 36% of those died before the onset of reproductive senescence.

The mean generation time, G, which represents the span between the birth date of a female, and the mean birth date of her viable offspring, can be calculated as:

[4.1.4] $G \approx 0.5 \ln RV_{(0.5)} / r$

where r is the intrinsic rate of population growth (see Section 4.2.1). Although the realized reproductive rates and population growth rates differed markedly between the two periods, these differences essentially cancelled in equation [4.1.4], and generation time was estimated to be 25.4 years during initial period of unrestrained growth, and virtually unchanged at 24.7 years for more recent period of no net change. The lack of discernible difference in generation time resulted because most of the difference in the realized reproductive rate was attributable to loss of females due to elevated mortality, whereas the females that survived continued to produce calves at the same rate.

4.2 Population Parameters

4.2.1 Population Growth

The $l_{(x)m(x)}$ schedule incorporates the probabilities of both dying and reproducing, and if we limit the series to just female offspring, $l_{f(x)}m_{f(x)}$, it provides a measure of the rate at which females replace themselves. This is the basis for Lotka's (1907a) first fundamental equation, from which an estimate of the population growth rate, r, can be obtained:

[4.2.1] $\sum e^{-rx} \cdot l_{f(x)}m_{f(x)} = 1$ summed for x=0.5,…,maximum age

which, solved by iteration, and converted to an annual finite growth rate, λ:

[4.2.2] $\lambda = e^{r}$

gives a predicted rate of population growth of 2.4% for the initial period of unrestrained growth, which is close to the maximum intrinsic rate of increase, R_{max}, of 2.8% estimated when the generalized logistic equation was fit to population counts. We would expect the observed r to be slightly lower than R_{max}, as the generalized logistic equation indicated some restraint of growth was actually occurring in the early and mid-1990s, which was included in our estimates of survival and mortality for the initial period of unrestrained growth.

The predicted rate of population growth for the more recent period of no net change was 0.5%, which fell within the 95% confidence interval for the slope of the non-significant trend observed during this period (Section 2.6).

The population growth rate represents the net difference between births and deaths. The finite birth rate for each sex, β_s, can be obtained using Lotka's (1907) second fundamental equation:

[4.2.3] $\beta_s = 1/\sum l_{s(x)} \cdot e^{-r(x+1)}$ summed for x=0.5,…,maximum age

which can be combined into an overall weighted crude birth rate, β:

[4.2.4] $\beta = \beta_f \sum l_{s(x)} + \beta_m \sum l_{s(x} / \sum l_{s(x)} + l_{s(x)}$ for x=0.5,…,max age

representing the number of calves born of either sex per animal of either sex in a population with a stable sex-and age-structure. The corresponding *crude death rate*, δ, indicating the proportion

of animals of either sex dying in a population with a stable sex- and age-structure, can be calculated from:

[4.2.5] $\delta = \beta \cdot (1-\lambda)$

During the initial period of unrestrained growth, the crude birth rate was calculated to be 0.044 and the crude death rate to be 0.020. In comparison, during the more recent period of no net change, the crude birth rate remained essentially unchanged at 0.045, but the crude death rate increased by a factor of two to 0.040

While most comparisons of productivity among populations are based on annual growth rates, this confounds comparisons between species with differing lifespans. Although a population growth rate of 2.5% may at first seem modest, it actually represents an impressive rate for such a long-lived species as the killer whale. More meaningful comparisons inter-specific comparisons can be made by expressing growth in terms of generation time, *GOG*:

[4.2.6] $GOG = \lambda^G / G$

which, interestingly, provides an estimate of the replacement ratio for females. A value of less than one indicates females are reproducing too slowly or dying too soon to replace themselves, and the population will decline. A value of more than one indicates they are producing more than sufficient offspring to replace themselves, and the population will increase.

We calculated growth within one generation to be 1.8 during the initial period of unrestrained growth, and 1.1 for the more recent period of no net change. In other words, females were producing almost twice as many offspring as required to replace themselves and the population almost doubled in size within the span of one generation during the initial period of unrestrained growth, but barely enough offspring to replace themselves resulting in little net change in population size during the more recent period of no net change.

4.2.3 Sex- and Age-Structure

Populations are actually comprised of a series of cohorts that start life at different times. For non-stationary populations that are increasing or decreasing over time, the initial size of cohorts will vary in size over time, and the relative size of age-classes will be due to combination of some animals having died, and not as many being present when the cohort was initially recruited. The stable sex and age-structure is thus a function of both the population growth rate and survivorship, and can be obtained from Lotka's (1907a) third fundamental equation:

[4.2.7] $P_{s(x)} = \beta \cdot l_{s(x)} \cdot e^{-r(x+1)}$

which represents the number of animals in each sex, *s*, and age, *x*, class in population with a *stable* sex- and age-structure. By stable, we mean that life history parameters had remained constant for a sufficiently long period of time, in which case the population would have attained an equilibrium in which the *relative* proportion of animals in each sex- and age-class remains stable over time. If the sex- and age-structure has attained stability *and* the population is also not increasing or declining in size over time, it is said to be *stationary, in which case the absolute numbers of animals in each sex- and age-class remains constant over time*.

The predicted stable sex- and age-composition for our theoretical population is shown in Figure 19. Despite the pronounced difference in the status of the population (growing at its maximum intrinsic rate versus no net change), the predicted sex- and age-structures are surprisingly similar. During unrestrained growth, a stable population would be comprised of 46% juveniles, 22% reproductive females, 10% post-reproductive females, and 22% adult males. During the period of no net change, a stable population would be comprised of 45% juveniles, 23% reproductive females, 10% post-reproductive females, and 22% adult males. The only noticeable difference is the lack of older males during the latter period.

The observed sex- and age-structure over the course of the study was very similar to sex- and age-structure predicted by the models (Figure 20). During 1973-96, the observed population was comprised, on average, of 46% juveniles, 21% reproductive females, 11% post-reproductive females and 22% adult males. During 1997-2004, the observed population was comprised, on average, of 47% juveniles, 24% reproductive females, 9% post-reproductive females and 20% adult males. The structure conforms with that predicted for both periods, but the two periods are nearly indistinguishable from one another (Figure 20).

In their original assessment, Olesiuk et al. (1990) considered the close correspondence between the observed and predicted stable sex- and age-structure as powerful evidence that their population model had accurately captured the dynamics of killer whale populations. Since the survival and reproductive schedules were derived from longitudinal data on the fate of animals over time, which is unaffected by the prevalence of various sex- and age-classes in the population or sample, the stable sex- and age-structure subsequently predicted from these rates represents an independent test of the fit of the model. However, in retrospect it appears there is one special case in which such a comparison is not very informative, and that occurs when the status of population is dictated by changes in mortality that show little or no consistent pattern with sex or age. In such a case, changes in the mortality would affect all sex- and age-classes equally, and the population structure will remain unchanged regardless of how fast the population is increasing or decreasing. This, unfortunately, appears to be the situation for the northern resident killer whale population.

4.2.4 Population Projections

In order to facilitate predictions of population size and its sex- and age-structure over time, the survival and reproductive rates can be organized into a projection matrix, ***M***:

$$[4.2.8] \quad \mathbf{M} = \begin{bmatrix} F_{(0.5)} & 0 & F_{(1.5)} & 0 & F_{(2.5)} \ldots & 0 & F_{(\max)} \\ F_{(0.5)} & 0 & F_{(1.5)} & 0 & F_{(2.5)} \ldots & 0 & F_{(\max)} \\ SV_{f(0.5)} & 0 & 0 & 0 & 0 \ldots & 0 & 0 \\ 0 & SV_{m(0.5)} & 0 & 0 & 0 \ldots & 0 & 0 \\ \vdots & \vdots & \vdots & & & \vdots & \vdots \\ 0 & 0 & 0 & 0 & SV_{m(\max)} \ldots & 0 & 0 \\ \vdots & \vdots & \vdots & \vdots & \vdots & \vdots & \vdots \\ 0 & 0 & 0 & 0 & 0 \ldots & 0 & SV_{f(\max)} \end{bmatrix}$$

such that if the number of animals in each sex- and age-class in year t is arranged in a vector:

$$[4.2.9] \quad \boldsymbol{N_t} = \begin{bmatrix} N_{f(0.5)} \\ N_{m(0.5)} \\ N_{f(1.5)} \\ N_{m(1.5)} \\ \vdots \\ N_{m(\max)} \\ \vdots \\ N_{f(\max)} \end{bmatrix}$$

the size and structure of the population in time t+1 can be estimated from:

$$[4.2.10] \qquad \boldsymbol{N}_{t+1} = \boldsymbol{M} \cdot \boldsymbol{N}_t$$

or, more generally, the size and structure at any future time, t+z, from:

$$[4.2.11] \qquad \boldsymbol{N}_{t+1} = \boldsymbol{M}^Z \cdot \boldsymbol{N}_t$$

In order to evaluate how well the models predicted births and deaths, we calculated the number of births and deaths expected each year by projecting the observed sex- and age-structure in the population in one year increments, and tallying the number of animals that were born or died. The model for the growing population predicted a total of 156 births and 78 deaths during 1973-96, whereas we actually observed 162 births and 77 deaths during the same period. However, if we apply the same model to the more recent period, there should have been 79 births and 29 deaths. whereas we observed 77 births and 64 deaths. The second model predicts about the same number of births (76), but 62 deaths, and thus seems to have accurately captured the change in survival that occurred around 1996. The close correspondence between the predicated and observed number of births and deaths is not surprising, since the fecundity and survival rates that went into the model were based on the numbers of animals born and dying during the study. Unlike the comparison with the predicted sex- and age-structure, the birth and death comparison does not represent an independent test of the model, but rather merely indicates we have not introduced serious biases by the selection of subsets of animals for estimating life history parameters.

4.3 Comparison of Population Parameters

Our updated population parameters for the initial period in which the northern resident population was growing are similar to the parameters derived in our previous population assessment for the northern and southern resident population combined (Table 14). In this latest assessment, we avoided the issues of pooling the two communities, which circumvented the problems associated with ageing older females in cropped pods, and we refined our age estimation procedure and now have a longer time-series and increased sample sizes. Nevertheless, our general impression of the life history and population dynamics of resident killer whales in British Columbia has not changed markedly. In their assessment of pod-specific demography, Brault and Caswell (1993) found no evidence of significant variation among the pods that make up the southern and northern resident communities. Moreover, recent analyses for neighbouring resident killer whale populations in southern Alaska, which have been increasing exponentially since photo-identification studies were initiated in 1984, indicate that the

life history and population dynamics is similar to that in British Columbia and Washington State (Table 14). This suggest these models may be generally representative of killer whale populations, or at least the resident ecotype.

DISCUSSION

Long-term photo-identification studies have re-shaped our fundamental understanding of the life history and population dynamics of killer whales. It has become clear that killer whales can live much longer than the 25-30 years suggested by annuli in teeth (Mitchell and Baker 1980; Christensen 1982, 1984) or survival rates of captive animals (Small and DeMaster 1995). Most of the females that were in their teens when our study began 3 decades ago, are still alive today. Indeed, several of the females that were post-reproductive, suggesting they were at least in their 30s or 40s when the study began, are still alive. Similarly, although we can't estimate their exact ages, several males that were physically mature at the beginning of the study, suggesting they were in their late teens, and possibly much older, are still alive. Furthermore, it has since been shown that dentinal annuli in killer whale teeth are completely occluded by about 30 years of age, and there is some indication survival rates of killer whales in captivity may have increased as husbandry techniques improved (Woodley et al. 1997).

Although there is still considerable uncertainty associated with the age estimates of the oldest females in the population, the consequences of this uncertainty is waning as the study progresses. In our previous assessment, age at first birth was estimated from known-aged animals that had just begun to mature, but age-specific reproductive rates for older females had been inferred largely from genealogies (Bigg et al. 1990), which were subsequently validated by genetic analysis (Barrett-Lennard 2000), and which provided information on calving intervals prior to the start of the study. That is no longer the case. There is little doubt about the genealogies of females that were in their teens and early twenties when the study began, whose calves would have been very young and tightly associated with their mothers (Bigg et al. 1990), and in these circumstances our corrections in ages to account for calf loss are trivial. These females are now in their forties or early fifties, having completed their reproductive lifespan over the course of the study period, providing us with much greater confidence in our overall reproductive schedules. Thus, the uncertainties associated with our age estimates remaining for the oldest animals in the population would mainly affect only our estimates of survival patterns late in life and maximum longevity.

In addition to being long-lived, we now also appreciate that killer whales have a remarkably limited reproductive potential. Bigg (1982) was surprised by the prevalence of non-reproductive females in the population, and Olesiuk et al. (1990) attributed it to reproductive senescence. Reproductive senescence has now been found in several other odontocetes, including both short-finned (Kasuya and Marsh 1984; Marsh and Kasuya 1986) and long-finned pilot whales (Martin and Rothery 1993), and probably occurs in sperm whales (McAuliffe and Whitehead 2005). In killer whales, females do not produce their first calf until they are in their mid-teens, and single calves are subsequently born at 5-year intervals over a reproductive lifespan lasting about 25 years, so reproductive potential is only about 5 calves per female. The result is a population comprised of a high proportion of juvenile and post-reproductive animals, with a crude birth rate of about 4.5%. Interestingly, females appear to have maintained this maximum reproduction rate throughout the study period, regardless of whether the population was growing or stable. Given their low reproductive potential, the general strategy of females may be to

maintain calf production at the maximum rate, with changes in survival the main determinant of population status.

It is not known why the northern resident population was increasing exponentially during the 1970s, 1980s and to the mid-1990s. The growth implies the population had been depleted, but the species was never exploited to any extent for subsistence or commercial whaling. Moreover, the impact of the live capture fishery on the northern resident population was likely small compared with the magnitude of population growth that has occurred since the 1970s (Olesiuk et al. 1990). Its not clear whether or to what extent incidental shooting and harassment could have depleted the population. Interestingly, the southern Alaskan resident population has also been increasing exponentially since photo-identification studies were initiated a decade ago. The southern resident population has exhibited periods of growth, but these have been interspersed with periods of high mortality and population declines (Ford et al. 2005). In contrast to the birth rate, which seems to be biologically constrained at about 4.5%, the death rate could potentially vary over a much wider range. During the study period, it doubled from 2% when the population was growing, to 4% as growth subsided. One could imagine bouts of much higher mortality during unfavorable conditions or caused by catastrophes, such as mass strandings (Cameron 1941; Carl 1946). Given the low potential for populations to recover from such events, the normal pattern may be for populations to exhibit long periods of slow, steady growth interspersed with brief periods of high mortality, which seems to be consistent with the observed pattern (Ford et al. 2005).

In their previous assessment, Olesiuk et al. (1990) speculated about the demographic changes that might occur as the population growth subsided. Based on general mammalian patterns, it was expected changes in population productivity would initially be mediated through changes in reproductive rather than survival rates (Eberhardt 1977; Eberhardt and Siniff 1977). One would expect that during less favourable conditions, individuals would exhibit chronic effects, such as delayed onset of reproduction or prolonged calving intervals, before the situation became acute and they succumbed. We anticipated major changes in sex- and age-structure would accompany the changes in reproductive rates, and had hoped these might assist in interpreting the status of other killer whale populations that can't be monitored in as closely, such as the west coast *transients*. Obviously, that has not been the case, and to date virtually all changes in population productivity have been attributable to changes in mortality. Since all sex- and age-classes experienced higher mortality during less favourable conditions, the result has been a lack of any measurable change in sex- or age-composition with population status.

Until now, our main goal has been to develop a killer whale population model that fits observations as closely as possible, which would describe the fundamental dynamics of populations under average conditions. We are increasingly confident that goal has been achieved. Our refined analysis for the period of population growth isn't much different than the original assessment published 15 years ago, and neighbouring resident killer whale populations in Washington State and southern Alaska appear to conform to the same general model. We think it's time to shift the focus, from how well the model fits, to patterns in and reasons for departures from it, such as the recent increase in mortality rates. Our population model provides a useful framework for exploring these deviations from the norm, and we hope will ultimately lead to a better understanding of the factors regulating productivity of resident killer whale populations (Ford et al. 2005).

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TABLES

Table 1. Overview of main distinguishing characteristics of the 3 ecotypes of killer whales that occur in the NE Pacific Ocean.

Characteristic	*Resident*	*Transient*	*Offshore*	Source
Populations	-4 populations identified: southern residents, northern residents, southern Alaskan residents, and western Alaskan residents. -possibly additional population(s) of western North Pacific residents off eastern Russia or Japan	-3 populations recognized: west coast transients, from southern California to northern SE Alaska; Gulf of Alaska transients; and a small group known as the AT1's that frequent Prince William Sound and Kenai Fjords.	-poorly known, but only one population known.	Bigg 1987; Ford et al (1994, 2000, 2002); Matkin and Leatherwood 1986; Krahn et al. (2004);
Movements	-Small geographic range; -Congregate in predictable core areas during summer months; -Winter distribution largely unknown.	-Range over much larger areas than residents; -Movements unpredictable and do not congregate; -Sightings show less seasonal variability than residents.	-Large range extending from southern California to eastern Aleutian Islands; -Presumably resides mainly offshore (seen up to 500 km offshore).	Krahn et al. (2002, 2004); Ford et al. 2000; Walters et al. 1992; Wiles 2004
Group Size	-Animals in matrilineal groups always travel as a cohesive group; -Related matrilines tend to associate and travel together;	-Smaller groups of usually less than 10 individuals; -Group-size varies with prey type.	-Large groups of 20-75	Ford and Ellis (1999); Baird (2000); Bigg et al. 1990; Ford et al. 1998; Baird and Dill (1996); Morton 1990
Social Structure	-No dispersal of either sex from natal matrilines, comprised of up to 4 generations of both sexes.	-More fluid social system.	-Unknown, but apparently some long-term associations??	Bigg et al. 1990; Baird and Whitehead 2000; Matkin et al. 1999
Diet	-Fish eaters, mainly salmon, with distinct preference for chinook. -Occasionally harass, but have never been seen consuming warm-blooded prey.	-Prey on warm blood prey including seals, sea lions, other cetaceans, and occasionally sea birds.	Unknown – perhaps fish or squid or sharks??	Ford et al. 2000. 1998; Heise et al. 2003; Ford et al. (in prep.); Saulitis et al.
Vocalizations	-Commonly vocalize while foraging; -Discrete calls with pod-specific variations of dialects, which are distinct among communities.	-Quiet while foraging, but vocalize after making a kill; -Pacific transients all share same dialect, although may be some local variations.	Undetermined – some evidence of group-specific dialects??	Ford (1989, 1991); Deeke et al. 2000; Ford et al. 2000, Barrett-Lennard et al. 1996; Ford and Ellis 1999; Morton 1990.
Genetics	-genetically distinct from transients and offshores; -tend to breed with unrelated males within the population, but mating outside population has not been ruled out.	-generically distinct from residents and offshores; -the 3 populations do not interbreed;	Genetically distinct, but more closely related to residents.	Hoelzel et al. (1998); Barrett-Lennard and Ellis (2001)
Morphology	-Dorsal fin more curved and rounded at the tip; -Saddle patch pigmentation more variable i(5 types) ncluding open saddles.	-Dorsal fin straighter at the tip than in residents or offshore types. -Saddle patches pigmentation less variable (2 types) and not open.	-Smaller body size; -Dorsal fins and saddle patches resemble those of residents.	Ford and Ellis (1999); Ford et al. (2000); Baird and Stacey (1988); Walters et al. (1992)

Table 2. Summary of the number of killer whales captured or killed by pod, date, length (meters) and sex (M, F, or ?) during the live-capture fishery in British Columbia and Washington State (modified from Bigg 1982 and Olesiuk et al. 1990).

Pod / Location	Date of Capture	Total	Physically Immature						Mature		
			< 3.5 meters			3.5-4.5m			≥ 4.5 meters		
			M	F	?	M	F	?	M	F	?
Southern Residents											
J01, K01 or L01	Jul 1964	1	-	-	-	-	-	-	1	-	-
J01, K01 or L01	Oct 1965	2	-	-	-	-	1	-	-	1	-
K01	Feb 1967	8	1	2	-	2	1	-	1	1	-
J01, L01	Oct 1968	5	-	-	-	3	-	-	2	-	-
J01, K01 or L01	Aug 1970	11	2	-	2	3	2	-	1	1	-
L01	Aug1971	3	-	1	-	1	1	-	-	-	-
J01	Mar 1972	1	1	-	-	-	-	-	-	-	-
K01	Aug 1973	1	-	-	-	-	-	-	-	1	-
L01	Aug 1973	2	-	-	-	-	-	-	1	1	-
Subtotal		**34**	**4**	**3**	**2**	**9**	**5**	**-**	**6**	**5**	**-**
Northern Residents											
C01	Jun 1965	1	-	-	-	-	-	-	1	-	-
I11	Jul 1967	1	-	-	-	1	-	-	-	-	-
A05+	Apr 1968	6	1	-	-	-	1	-	1	3	-
A05	Dec 1969	6	-	2	2	1	-	-	1	-	-
Subtotal		**14**	**1**	**2**	**-**	**3**	**2**	**-**	**3**	**3**	**-**
Transients											
M01	Mar 1970	3	-	-	-	-	2	-	-	1	-
Q01	Aug 1975	2	-	-	-	1	1	-	-	-	-
Subtotal		**5**	**-**	**-**	**-**	**1**	**3**	**-**	**-**	**1**	**-**
Unknown											
S. Vancouver Island[1]	Sep 1962	2	-	-	-	-	-	-	2	-	-
S. Vancouver Island[1]	Jul 1966	1	1	-	-	-	-	-	-	-	-
S. Vancouver Island[1]	Feb 1968	2	-	-	-	1	-	-	-	1	-
S. Vancouver Island[1]	Apr 1969	2	-	-	-	-	-	-	1	1	-
S. Vancouver Island[1]	Oct 1969	1	-	-	-	-	-	-	-	-	1
S. Vancouver Island[1]	Feb 1970	1	-	-	-	-	-	1	-	-	-
S. Vancouver Island[1]	Aug 1970	1	-	1	-	-	-	-	-	-	-
S. Vancouver Island[1]	Aug 1977	1	-	1	-	-	-	-	-	-	-
Washington State[1]	Nov 1971	2	-	-	-	2	-	-	-	-	-
Washington State[1]	Mar 1973	1	-	-	-	-	-	-	-	1	-
NE Vancouver Isl.[2]	Jul 1968	1	-	-	-	1	-	-	-	-	-
Subtotal		**15**	**1**	**2**	**-**	**4**	**-**	**1**	**3**	**3**	**1**
Total		**68**	**6**	**7**	**2**	**17**	**10**	**1**	**12**	**1 2**	**1**

[1] Assumed to have been taken from southern resident population.
[2] Assumed to have been taken from northern resident population.

Table 3. Prevalence and duration of gaps in annual sightings of individuals over the course of the study.

Duration of Gap (years)	Number of Instances	Proportion of Total
Seen Next Year	4,777	0.9018
1	389	0.0734
2	73	0.0138
3	35	0.0066
4	3	0.0006
5	10	0.0019
6	5	0.0009
7	1	0.0002
8	3	0.0006
9	0	0.0000
10	1	0.0002
Total	5,297	1.0000

Table 4. Summary of ageing methods used for various sex- and age-classes, and the likely precision (~80% probability) and upper and lower limits (~95% probability) of the age estimates.

Sex- and Age-Category (when first seen)	Reference Point for Age Estimate	Number of Animals	Estimated Precision	
			Likely (80%)	Limits (95%)
Born during study	Year of birth	240	±0.5 to ±1.0 yrs	±0.5 to ±1.0 yrs
Small Juveniles	Size when first seen	18	±0.5 to ±1.0 yrs	±0.5 to ±1.0 yrs
Larger Juveniles	Approximate size when first seen	7[1]	±1-2 to ±3-5 yrs	±1-3 to ±2-8 yrs
Adolescent Females	Year of birth of first viable calf	9	±3 yrs	±6 yrs
Adult Females	Year of birth of oldest known offspring	(40 total)		
	-First calf born ~start of study	13	±3 yrs	±6 yrs
	-First known calf ~10 yrs old	15	± 5 yrs	-6 to +11 yrs
	-First known calf ~20 yrs old	8	-6 to +8 yrs	-8 to +16 yrs
	-First known calf ~30 yrs old	4	-7 to +9 yrs	-11 to +16 yrs
Adult Females (A05 Pod)	Average year of birth of known offspring	3	±10 yrs	±15 yrs
Adolescent Males	Year dorsal fin attained *HWR* > 1.4	16	±2 yrs	±5 yrs
Young Adult Males	Year fin attained its asymptotic *HWR*	5	±5 yrs	±7 yrs
Older Adult Males	Year first seen as a physically mature male	25	Minimum Ages	
	TOTAL	363[1]		

[1] Includes 2 individuals that died before the study officially began, but were included as they provided useful information on the calving histories of animals present when the study began.

Table 5. Rate of Maturation of known-age females based on year they gave birth to their first viable calf. See text for details.

Age x	Total Number $N_{f(x)}$	Number Immature $1\text{-}NC_{f(x)}$	Proportion Mature $Mat_{f(x)}$	Proportion Maturing $f_{f(x)}$	Age Weighted by Proportion Maturing	Standard Error
			1973-95 (Unrestrained Growth Period)			
8	50.0	50.0	0.000	0.0000	0.00	0.0000
9	49.0	49.0	0.000	0.0000	0.00	0.0000
10	46.0	40.5	0.120	0.1196	1.20	0.0023
11	43.0	35.0	0.186	0.0665	0.73	0.0036
12	41.0	29.0	0.293	0.1066	1.28	0.0052
13	37.0	19.5	0.473	0.1803	2.34	0.0069
14	33.5	13.5	0.597	0.1240	1.74	0.0074
15	32.0	9.5	0.703	0.1061	1.59	0.0067
16	29.5	7.0	0.763	0.0596	0.95	0.0064
17	23.5	2.5	0.894	0.1309	2.23	0.0042
18	19.0	1.0	0.947	0.0538	0.97	0.0028
19	18.0	1.0	0.944	-0.0029	-0.06	0.0031
20	17.0	1.0	0.941	-0.0033	-0.07	0.0035
21	17.0	0.0	1.000	0.0588	1.23	0.0000
22	12.0	0.0	1.000	0.0000	0.00	0.0000
Overall Mean (Standard Error):					**14.14**	**0.0521**
			1996-2004 (Period of No Net Change)			
8	14.0	14.0	0.000	0.0000	0	0.0000
9	15.0	15.0	0.000	0.0000	0	0.0000
10	17.0	16.0	0.059	0.0588	0.59	0.0035
11	18.0	17.0	0.056	-0.0033	-0.04	0.0031
12	20.0	18.0	0.100	0.0444	0.53	0.0047
13	22.0	17.0	0.227	0.1273	1.65	0.0084
14	22.5	13.0	0.422	0.1949	2.73	0.0113
15	19.0	7.0	0.632	0.2094	3.14	0.0129
16	19.5	6.0	0.692	0.0607	0.97	0.0115
17	24.5	5.0	0.796	0.1036	1.76	0.0069
18	25.0	3.0	0.880	0.0841	1.51	0.0044
19	22.8	1.0	0.956	0.0760	1.44	0.0019
20	21.3	1.0	0.953	-0.0031	-0.06	0.0022
21	16.0	1.0	0.938	-0.0154	-0.32	0.0039
22	18.5	0.0	1.000	0.0625	1.38	0.0000
23	18.5	0.0	1.000	0.0000	0.00	0.0000
Overall Mean (Standard Error):					**15.29**	**0.0748**

Table 6. Rate of Maturation of known-age males based on year their dorsal fins attained a height to width ratio (HWR) of 1.4. See text for details.

Age x	Total Number $N_{f(x)}$	Number Immature $1\text{-}NC_{f(x)}$	Proportion Mature $Mat_{f(x)}$	Proportion Maturing $f_{f(x)}$	Age Weighted by Proportion Maturing	Standard Error
			1973-95 (Unrestrained Growth Period)			
8	45.0	45.0	0.000	0.0000	0.00	0.0000
9	41.0	40.5	0.012	0.0122	0.11	0.0003
10	38.0	34.0	0.105	0.0931	0.93	0.0025
11	34.0	24.0	0.294	0.1889	2.08	0.0063
12	28.0	14.5	0.482	0.1880	2.26	0.0092
13	27.0	10.5	0.611	0.1290	1.68	0.0091
14	24.0	5.5	0.771	0.1597	2.24	0.0077
15	21.0	2.0	0.905	0.1339	2.01	0.0043
16	19.0	1.5	0.921	0.0163	0.26	0.0040
17	16.0	1.0	0.938	0.0164	0.28	0.0039
18	13.5	0.0	1.000	0.0625	1.13	0.0000
19	12.0	0.0	1.000	0.0625	1.13	0.0000
1973-2004 Mean (Standard Error):					**12.96**	**0.0475**
			1996-2004 (Period of No Net Change)			
8	12.0	12.0	0.000	0.0000	0.00	
9	15.0	15.0	0.000	0.0000	0.00	0.0000
10	17.0	16.0	0.059	0.0588	0.59	0.0035
11	20.0	15.0	0.250	0.1912	2.10	0.0099
12	24.0	14.0	0.417	0.1667	2.00	0.0106
13	22.0	6.0	0.727	0.3106	4.04	0.0094
14	23.0	2.0	0.913	0.1858	2.60	0.0036
15	24.0	2.0	0.917	0.0036	0.05	0.0033
16	23.0	1.0	0.957	0.0399	0.64	0.0019
17	20.0	1.0	0.950	-0.0065	-0.11	0.0025
18	20.5	0.0	1.000	0.0500	0.90	0.0000
19	12.0	0.0	1.000	0.0000	0.00	0.0000
1996-2004 Mean (Standard Error):					**12.81**	**0.0447**
			1973-2004 (Entire Study Period)			
8	57.0	57.0	0.000	0.0000	0.00	0.0000
9	56.0	55.5	0.009	0.0089	0.08	0.0002
10	55.0	50.0	0.091	0.0820	0.82	0.0015
11	54.0	39.0	0.278	0.1869	2.06	0.0039
12	52.0	28.5	0.452	0.1741	2.09	0.0050
13	49.0	16.5	0.663	0.2113	2.75	0.0101
14	47.0	7.5	0.840	0.1772	2.48	0.0194
15	45.0	4.0	0.911	0.0707	1.06	0.0164
16	42.0	2.5	0.940	0.0294	0.47	0.0114
17	36.0	2.0	0.944	0.0040	0.07	0.0020
18	34.0	0.0	1.000	0.0556	1.00	0.0000
19	30.0	0.0	1.000	0.0000	0.00	0.0000
Overall Mean (Standard Error):					**12.87**	**0.0699**

Table 7. Data used in the calculation of juvenile survival and mortality rates.

1973-96 (Period of Unrestrained Growth)						
Age Group	$L_{(x)}$	$L_{(x+1)}$	$D_{(x)}$	$SV_{(x)}$	$MR_{(x)}$	*SE*
0.5	155.0	150.6	4.4	0.9715	0.0285	0.0132
1.5-2.5	299.8	292.2	7.6	0.9747	0.0253	0.0090
3.5-5.5	368.8	362.9	5.9	0.9849	0.0151	0.0062
6.5-9.5	386.9	382.8	4.1	0.9894	0.0106	0.0052
10.5-14.5	323.5	321.5	2.0	0.9938	0.0062	0.0044
Mean	1534.0	1510.0	24.0	0.9844	0.0156	0.0032
1996-2004 (Period of No Net Change)						
0.5	69.5	63.5	6.0	0.9137	0.0863	0.0325
1.5-2.5	126.0	124.0	2.0	0.9841	0.0159	0.0111
3.5-5.5	175.9	164.0	11.9	0.9323	0.0677	0.0184
6.5-9.5	208.8	206.3	2.5	0.9880	0.0120	0.0075
10.5-14.5	251.5	245.7	5.8	0.9771	0.0229	0.0094
Mean	831.7	803.5	28.2	0.9661	0.0339	0.0063

Table 8. Data used in the calculation of adult female survival and mortality rates.

1973-96 (Period of Unrestrained Growth)						
Age Group	$L_{(x)}$	$L_{(x+1)}$	$D_{(x)}$	$SV_{(x)}$	$MR_{(x)}$	*SE*
15.5-19.5	208.0	208.0	0.0	1.0000	0.0000	0.0000
20.5-29.5	297.0	296.0	1.0	0.9966	0.0034	0.0034
30.5-39.5	272.5	271.5	1.0	0.9963	0.0037	0.0037
40.5-49.5	202.4	193.0	9.4	0.9534	0.0465	0.0145
50.5+	101.4	95.1	6.3	0.9382	0.0618	0.0233
Total	1081.3	1063.6	17.7	0.9836	0.0164	0.0039
1996-2004 (Period of No Net Change)						
15.5-19.5	114.8	113.0	1.8	0.9847	0.0153	0.0114
20.5-29.5	209.8	204.5	5.3	0.9750	0.0250	0.0107
30.5-39.5	95.0	94.5	0.5	0.9947	0.0053	0.0074
40.5-49.5	64.8	61.0	3.8	0.9420	0.0579	0.0284
50.5+	67.9	62.8	5.1	0.9322	0.0678	0.0298
Total	552.2	535.9	16.3	0.9705	0.0295	0.0072

Table 9. Data used in the calculation of adult male survival and mortality rates. Note that two slightly different age-groupings were used because of the better age estimates and larger sample sizes of older males by the second period of the study. For comparison, the estimates for the same age-groupings used during 1973-96 are shown in parentheses.

1973-96 (Period of Unrestrained Growth)						
Age Group	$L_{(x)}$	$L_{(x+1)}$	$D_{(x)}$	$SV_{(x)}$	$MR_{(x)}$	*SE*
15.5-19.5	175.5	173.5	2.0	0.9886	0.0114	0.0080
20.5-24.5	120.5	115.5	5.0	0.9585	0.0415	0.0179
25.5+	304.6	287.0	17.6	0.9422	0.0578	0.0132
Mean	600.6	576.0	24.6	0.9590	0.0410	0.0081
1996-2004 (Period of No Net Change)						
15.5-19.5	99.5	97.0	2.5	0.9749	0.0251	0.0156
(20.5-24.5)	(62.0)	(59.0)	(3.0)	(0.9516)	(0.0484)	(0.0268)
20.5-29.5	104.5	96.0	8.5	0.9187	0.0813	0.0258
30.5+	82.4	67.3	15.1	0.8172	0.1828	0.0462
Mean	286.4	260.3	26.1	0.9089	0.0911	0.0170

Table 10. Life table for females during the initial period of unrestrained growth during 1973-1996. The table is condensed beyond 20 years of age by providing estimates at 5-year intervals.

Age	$SV_{f(x)}$	$L_{f(x)}$	$Mat_{f(x)}$	$PR_{f(x)}$	$FEC_{f(x)}$	$m_{f(x)}$	$E_{f(x)}$	$P_{f(x)}$
0.5	0.972	1000.0	0.000	0.000	0.000	0.000	45.8	1000.0
1.5	0.975	971.5	0.000	0.000	0.000	0.000	46.1	949.0
2.5	0.975	946.9	0.000	0.000	0.000	0.000	46.3	903.6
3.5	0.985	922.9	0.000	0.000	0.000	0.000	46.4	860.4
4.5	0.985	909.0	0.000	0.000	0.000	0.000	46.1	827.8
5.5	0.985	895.4	0.000	0.000	0.000	0.000	45.8	796.5
6.5	0.987	881.9	0.000	0.000	0.000	0.000	45.5	766.4
7.5	0.987	870.6	0.000	0.000	0.000	0.000	45.1	739.0
8.5	0.987	859.4	0.000	0.000	0.000	0.000	44.7	712.7
9.5	0.987	848.4	0.000	0.000	0.000	0.000	44.2	687.3
10.5	0.991	837.5	0.100	0.000	0.033	0.017	43.8	662.8
11.5	0.991	830.1	0.167	0.000	0.060	0.030	43.2	641.7
12.5	0.991	822.8	0.275	0.000	0.100	0.050	42.5	621.4
13.5	0.991	815.5	0.458	0.000	0.181	0.090	41.9	601.6
14.5	0.991	808.4	0.597	0.000	0.194	0.097	41.3	582.5
15.5	1.000	801.2	0.703	0.000	0.141	0.070	40.6	564.1
16.5	1.000	801.2	0.763	0.000	0.119	0.059	39.6	551.0
17.5	1.000	801.2	0.894	0.000	0.234	0.117	38.6	538.3
18.5	1.000	801.2	0.947	0.000	0.132	0.066	37.6	525.8
19.5	1.000	801.2	0.944	0.000	0.167	0.083	36.6	513.7
20.5	0.997	801.2	0.941	0.000	0.159	0.080	35.6	501.8
25.5	0.997	787.8	1.000	0.046	0.159	0.079	31.2	438.9
30.5	0.996	774.7	1.000	0.117	0.147	0.074	26.7	383.9
35.5	0.996	760.6	1.000	0.387	0.125	0.063	22.1	335.3
40.5	0.953	746.7	1.000	0.597	0.092	0.046	17.5	292.9
45.5	0.953	588.4	1.000	0.751	0.048	0.024	16.4	205.3
50.5	0.932	463.7	1.000	1.000	0.000	0.000	15.0	143.9
55.5	0.932	337.2	1.000	1.000	0.000	0.000	14.6	93.1
60.5	0.938	245.2	1.000	1.000	0.000	0.000	13.9	60.2
65.5	0.938	178.2	1.000	1.000	0.000	0.000	13.1	38.9
70.5	0.938	129.6	1.000	1.000	0.000	0.000	11.9	25.2
75.5	0.938	94.2	1.000	1.000	0.000	0.000	10.4	16.3
80.5	0.938	68.5	1.000	1.000	0.000	0.000	8.2	10.5

Table 11. Life table for males during the initial period of unrestrained growth during 1973-1996. The table is condensed beyond 20 years of age by providing estimates at 5-year intervals.

Age	$SV_{m(x)}$	$L_{m(x)}$	$Mat_{m(x)}$	$PMat_{m(x)}$	$E_{m(x)}$	$P_{m(x)}$
0.5	0.972	1000.0	0.000	0.000	31.0	1000.0
1.5	0.975	971.5	0.000	0.000	30.9	949.0
2.5	0.975	946.9	0.000	0.000	30.7	903.6
3.5	0.985	922.9	0.000	0.000	30.4	860.4
4.5	0.985	909.0	0.000	0.000	29.9	827.8
5.5	0.985	895.4	0.000	0.000	29.3	796.5
6.5	0.987	881.9	0.000	0.000	28.8	766.4
7.5	0.987	870.6	0.000	0.000	28.1	739.0
8.5	0.987	859.4	0.000	0.000	27.5	712.7
9.5	0.987	848.4	0.000	0.000	26.8	687.3
10.5	0.991	837.5	0.132	0.000	26.1	662.8
11.5	0.991	830.1	0.257	0.000	25.4	641.7
12.5	0.991	822.8	0.446	0.003	24.6	621.4
13.5	0.991	815.5	0.537	0.014	23.8	601.6
14.5	0.991	808.4	0.625	0.073	23.0	582.5
15.5	0.989	801.2	0.833	0.200	22.2	564.1
16.5	0.989	792.1	0.875	0.346	21.4	544.7
17.5	0.989	783.0	0.912	0.491	20.7	526.0
18.5	0.989	774.0	1.000	0.591	19.9	508.0
19.5	0.989	765.2	1.000	0.719	19.1	490.5
20.5	0.959	756.4	1.000	0.848	18.3	473.7
25.5	0.942	612.0	1.000	1.000	17.0	340.9
30.5	0.942	454.5	1.000	1.000	16.9	225.2
35.5	0.942	337.5	1.000	1.000	16.7	148.8
40.5	0.942	250.7	1.000	1.000	16.5	98.3
45.5	0.942	186.2	1.000	1.000	16.2	64.9
50.5	0.942	138.2	1.000	1.000	15.8	42.9
55.5	0.942	102.7	1.000	1.000	15.3	28.3
60.5	0.942	76.2	1.000	1.000	14.6	18.7
65.5	0.942	56.6	1.000	1.000	13.6	12.4
70.5	0.942	42.1	1.000	1.000	12.3	8.2

Table 12. Life table for females during the more recent period of no net change during 1996-2004. The table is condensed beyond 20 years of age by providing estimates at 5-year intervals.

Age	$SV_{f(x)}$	$L_{f(x)}$	$Mat_{f(x)}$	$PR_{f(x)}$	$FEC_{f(x)}$	$m_{f(x)}$	$E_{f(x)}$	$P_{f(x)}$
0.5	0.914	1000.0	0.000	0.000	0.000	0.000	30.0	1000.0
1.5	0.984	913.7	0.000	0.000	0.000	0.000	31.7	909.5
2.5	0.984	899.2	0.000	0.000	0.000	0.000	31.2	890.9
3.5	0.932	884.9	0.000	0.000	0.000	0.000	30.7	872.8
4.5	0.932	825.0	0.000	0.000	0.000	0.000	31.9	809.9
5.5	0.932	769.1	0.000	0.000	0.000	0.000	33.1	751.6
6.5	0.988	717.0	0.000	0.000	0.000	0.000	34.5	697.5
7.5	0.988	708.3	0.000	0.000	0.000	0.000	33.9	685.9
8.5	0.988	699.7	0.000	0.000	0.000	0.000	33.3	674.4
9.5	0.988	691.2	0.000	0.000	0.000	0.000	32.7	663.2
10.5	0.977	682.8	0.059	0.000	0.056	0.028	32.1	652.2
11.5	0.977	667.1	0.056	0.000	0.000	0.000	31.8	634.2
12.5	0.977	651.7	0.100	0.000	0.050	0.025	31.5	616.8
13.5	0.977	636.7	0.227	0.000	0.136	0.068	31.2	599.8
14.5	0.977	622.0	0.395	0.000	0.279	0.140	31.0	583.3
15.5	0.985	607.7	0.611	0.000	0.222	0.111	30.7	567.2
16.5	0.985	598.4	0.676	0.000	0.054	0.027	30.1	556.0
17.5	0.985	589.3	0.787	0.000	0.340	0.170	29.6	545.0
18.5	0.985	580.3	0.875	0.000	0.125	0.063	29.0	534.3
19.5	0.985	571.5	0.954	0.000	0.046	0.023	28.5	523.7
20.5	0.975	562.8	0.951	0.000	0.128	0.064	27.9	513.3
25.5	0.975	495.8	1.000	0.000	0.149	0.074	26.2	442.0
30.5	0.995	436.7	1.000	0.018	0.150	0.075	24.4	380.5
35.5	0.995	425.4	1.000	0.118	0.132	0.066	20.0	362.2
40.5	0.942	414.3	1.000	0.387	0.095	0.048	15.4	344.7
45.5	0.942	307.4	1.000	1.000	0.038	0.019	14.8	250.0
50.5	0.932	228.1	1.000	1.000	0.000	0.000	13.9	181.3
55.5	0.932	160.6	1.000	1.000	0.000	0.000	13.6	124.7
60.5	0.932	113.1	1.000	1.000	0.000	0.000	13.1	85.8
65.5	0.932	79.6	1.000	1.000	0.000	0.000	12.4	59.0
70.5	0.932	56.0	1.000	1.000	0.000	0.000	11.4	40.6
75.5	0.932	39.4	1.000	1.000	0.000	0.000	10.0	27.9
80.5	0.932	27.8	1.000	1.000	0.000	0.000	7.9	19.2

Table 13. Life table for males during the recent period of no net change during 1996-2004. The table is condensed beyond 20 years of age by providing estimates at 5-year intervals.

Age	$SV_{m(x)}$	$L_{m(x)}$	$Mat_{m(x)}$	$PMat_{m(x)}$	$E_{m(x)}$	$P_{m(x)}$
0.5	0.914	1000.0	0.000	0.000	19.3	1000.0
1.5	0.984	913.7	0.000	0.000	20.0	909.5
2.5	0.984	899.2	0.000	0.000	19.3	890.9
3.5	0.932	884.9	0.000	0.000	18.6	872.8
4.5	0.932	825.0	0.000	0.000	18.9	809.9
5.5	0.932	769.1	0.000	0.000	19.2	751.6
6.5	0.988	717.0	0.000	0.000	19.5	697.5
7.5	0.988	708.3	0.000	0.000	18.7	685.9
8.5	0.988	699.7	0.000	0.000	17.9	674.4
9.5	0.988	691.2	0.000	0.000	17.2	663.2
10.5	0.977	682.8	0.132	0.000	16.4	652.2
11.5	0.977	667.1	0.257	0.000	15.7	634.2
12.5	0.977	651.7	0.446	0.003	15.1	616.8
13.5	0.977	636.7	0.537	0.014	14.4	599.8
14.5	0.977	622.0	0.625	0.073	13.7	583.3
15.5	0.975	607.7	0.833	0.200	13.0	567.2
16.5	0.975	592.4	0.875	0.346	12.3	550.4
17.5	0.975	577.5	0.912	0.491	11.6	534.1
18.5	0.975	563.0	1.000	0.591	10.9	518.3
19.5	0.975	548.9	1.000	0.719	10.1	503.0
20.5	0.919	535.1	1.000	0.848	9.4	488.1
25.5	0.919	350.1	1.000	1.000	7.8	312.1
30.5	0.817	229.1	1.000	1.000	5.5	199.6
35.5	0.817	83.5	1.000	1.000	5.5	71.1
40.5	0.817	30.4	1.000	1.000	5.5	25.3
45.5	0.817	11.1	1.000	1.000	5.5	9.0
50.5	0.817	4.0	1.000	1.000	5.5	3.2
55.5	0.817	1.5	1.000	1.000	5.5	1.1
60.5	0.817	0.5	1.000	1.000	5.5	0.4
65.5	0.817	0.2	1.000	1.000	5.4	0.1
70.5	0.817	0.1	1.000	1.000	5.4	0.1

Table 14. Comparison of key life history and population parameters among resident killer whale assessments and populations.

Population	Northern Residents		Southern and Northern Residents Combined	Southern Residents	Southern Alaskan Residents
Study Period	1973-96	1996-2004	1973-87	1973-2004	1984-2001
Initial and Final Population Size	127 to 213	213 to 219	71 to 84 for SR 126 to 178 for NR	71 to 84	121 to 204
Population Trend	Steady increase	Stable but fluctuations	Overall slow increase but fluctuations for SR Steady growth for NR	Overall slow increase but fluctuations	Steady increase
Observed rate of Increase	2.5%	No net change	1.3% and 2.6%	0.6%	3.3%
Predicted rate of increase	2.4%	0.5%	2.9%	--	2.7%
			Females		
Mean age at first birth	14.1 yrs	15.4 yrs	14.9 yrs	--	~15 yrs
Average calving interval	4.9 yrs	5.5 yrs	5.3 yrs	6.1 yrs	4.9 yrs
Mean reproductive senescence	38 yrs	41 yrs	40 yrs	--	45 yrs
Average reproductive lifespan	24 yrs	27 yrs	25 yrs	--	30 yrs
Reproductive potential	4.7 calves	4.5 calves	5.4 calves	--	5.7 calves
Mean life expectancy	46 yrs	30 yrs	50 yrs	--	39 yrs
Maximum Longevity	~ 80 yrs	~ 80 yrs	~ 80-90 yrs	--	~ 60-70 yrs
Realized calf production	3.6 calves	2.2 calves	4.1 calves	--	4.0 calves
(% of potential)	(77%)	(50%)	(76%)		(80%)
			Males		
Mean age sexual maturity	13.0 yrs	13.0 yrs	15.0 yrs	--	--
Mean age physical maturity	18.5 yrs	18.5 yrs	21.0 yrs	--	--
Life Expectancy	31 yrs	19 yrs	29 yrs	--	31 yrs
Maximum Longevity	~ 60-70 yrs	~ 40-50 yrs	~ 50-60 yrs	--	~ 50-60 yrs
			Population Composition		
Juveniles	46%	47%	50%	--	51%
Reproductive Females	21%	24%	21%	--	22%
Post-Reproductive Females	10%	11%	10%	--	5%
Adult Males	22%	18%	19%	--	23%

FIGURES

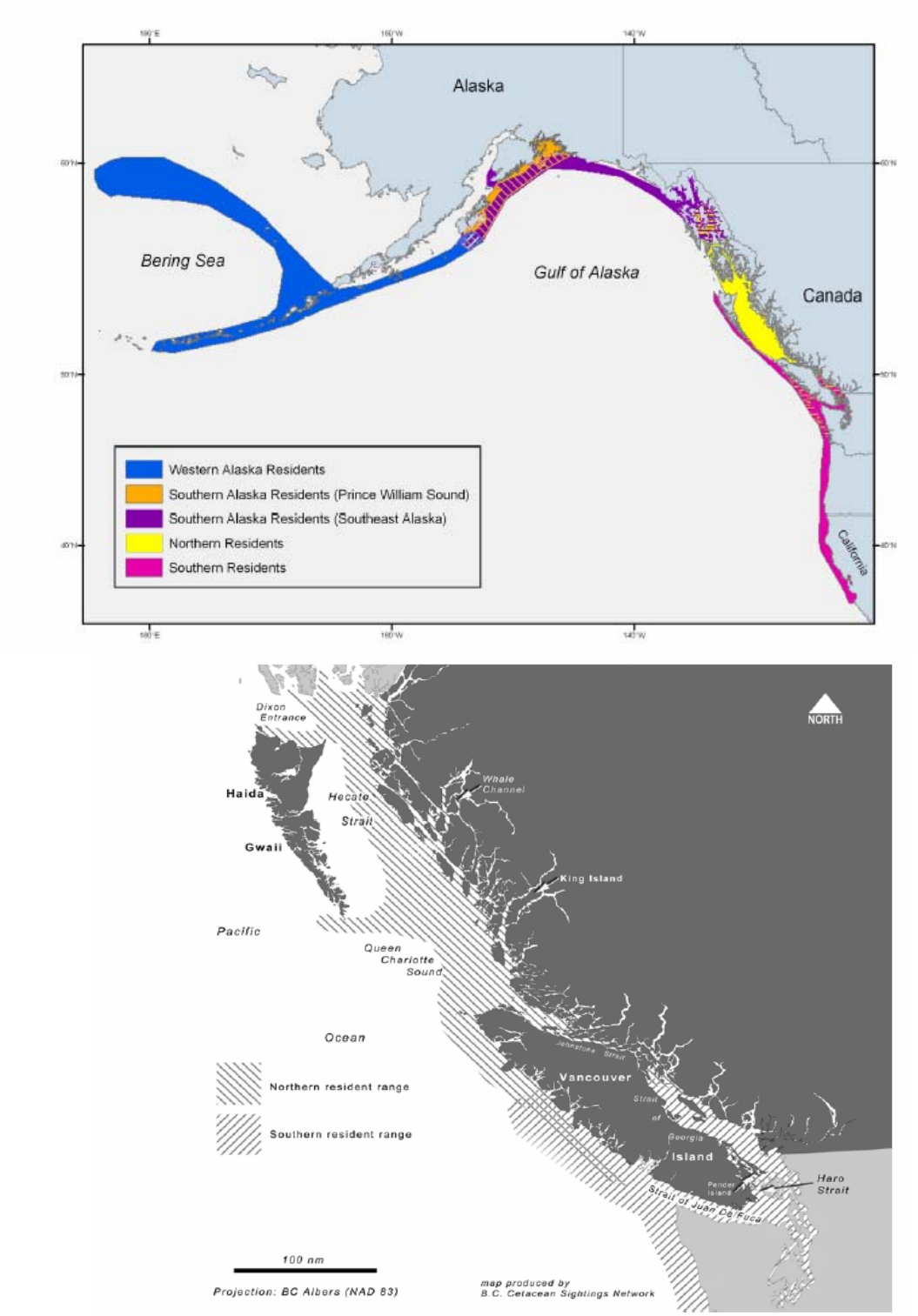


Figure 1. Maps showing geographic ranges of the resident communities in the NE Pacific Ocean (reproduced from Krahn 2004) and main distribution of the northern and southern resident communities (from KWRT 2005).

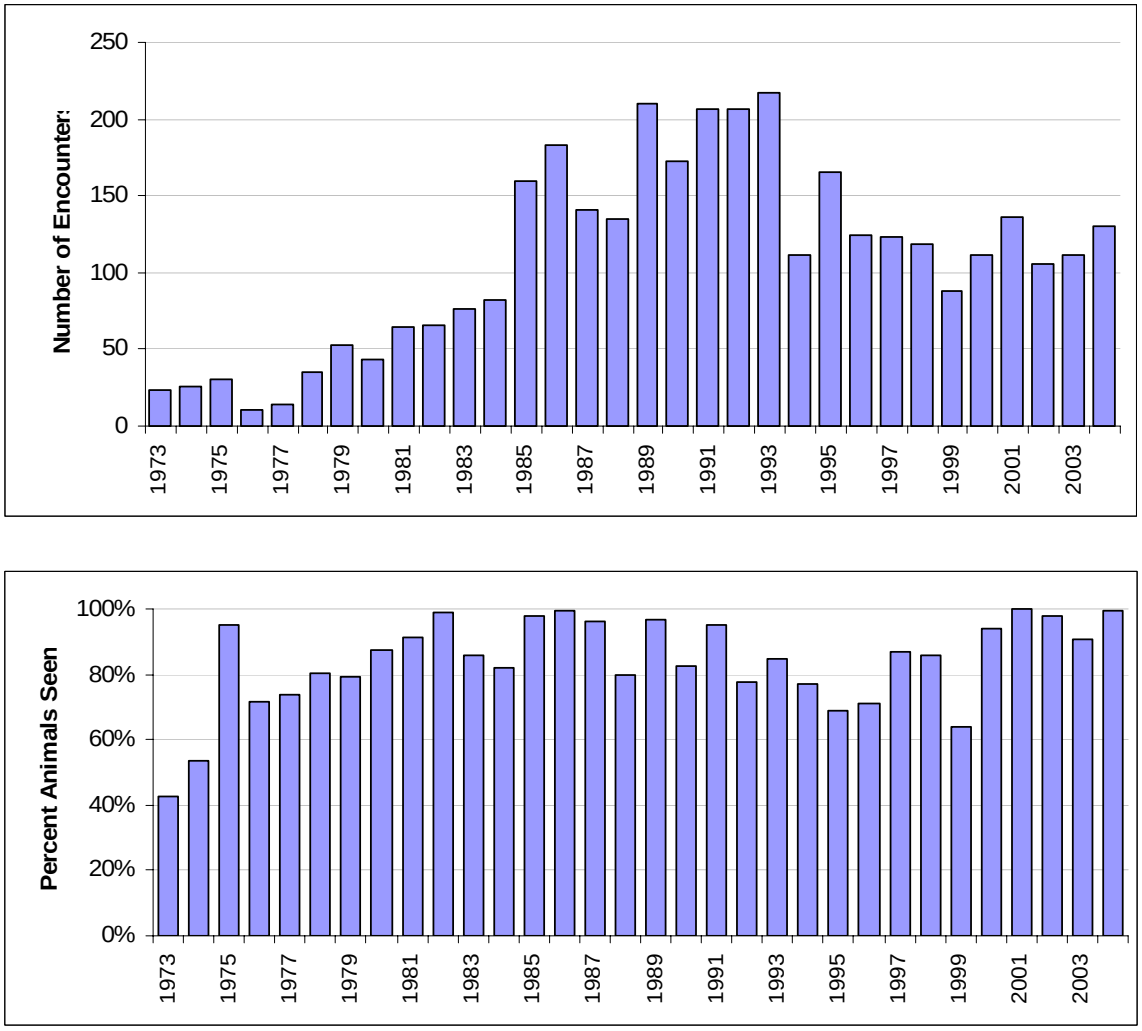


Figure 2. Annual number of encounters (top panel) and percent of all animals positively identified each year (lower panel).

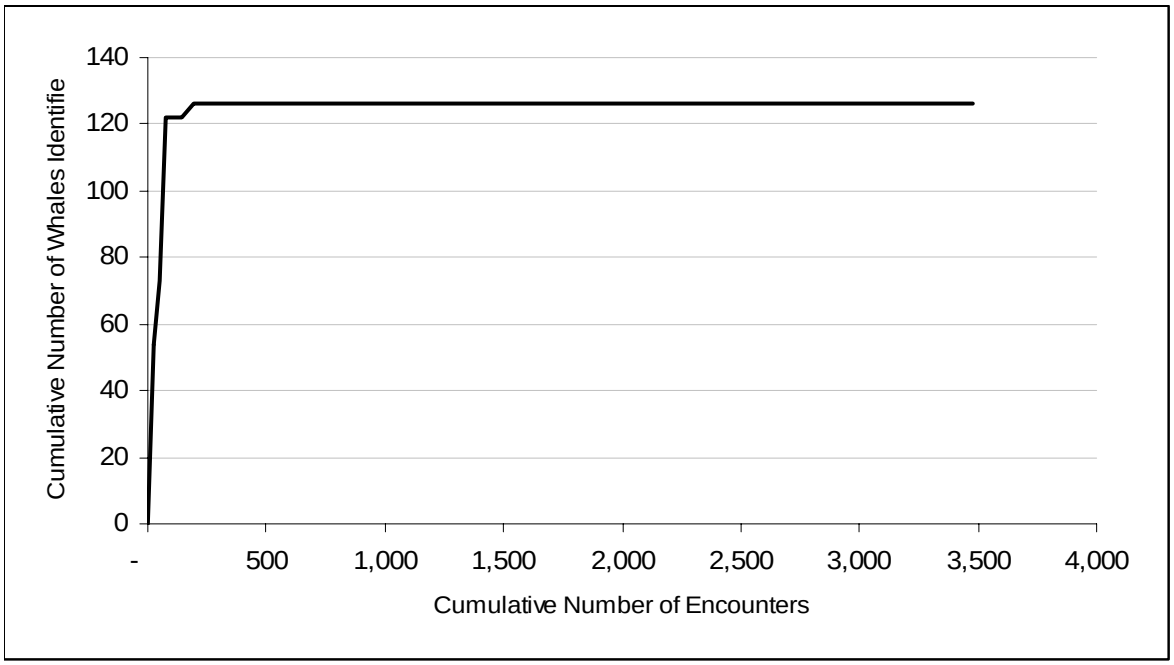


Figure 3. Rate of discovery of new northern resident whales (not including animals born during the study) as a function of cumulative number of encounters.

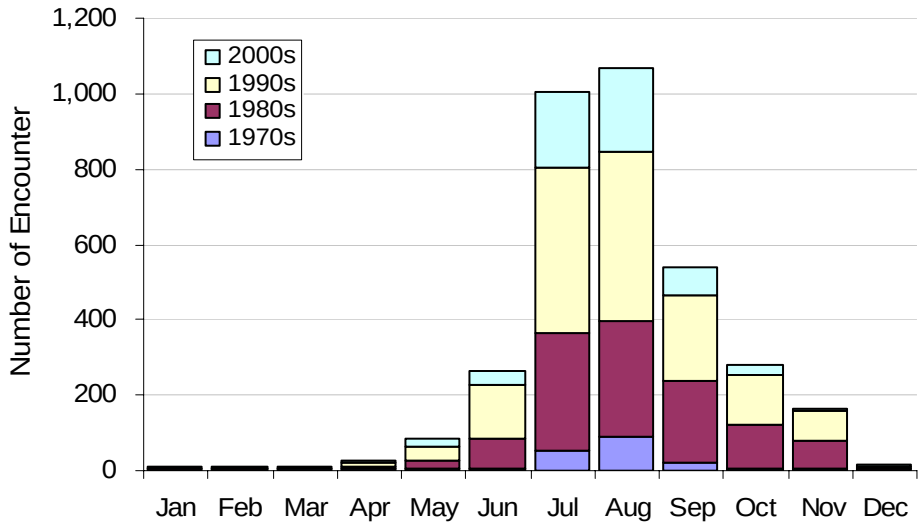


Figure 4. Number of encounters by month showing seasonality of sightings.

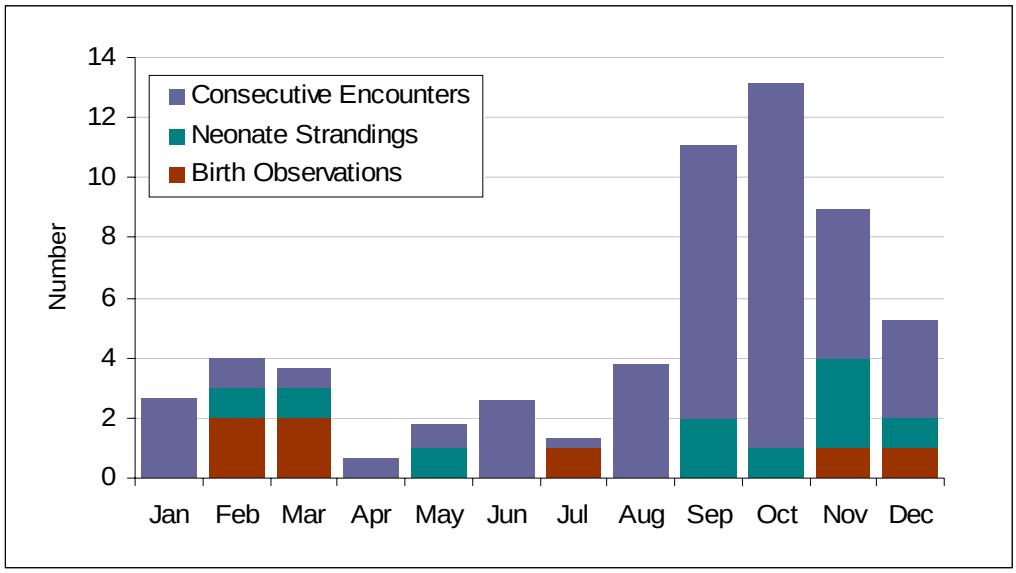


Figure 5. Seasonality of calving based on: 1) observations of births events or newborn calves; 2) strandings of fresh neonate carcasses in the study area; and 3) birth dates delineated from encounters for animals in which the birth date could be established to within one or several months.

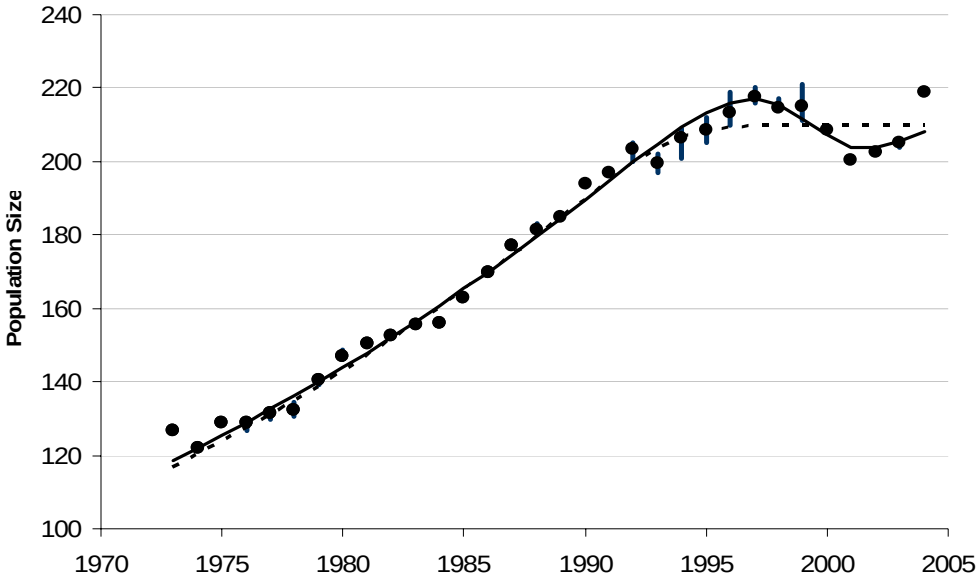


Figure 6. Trends in size of the northern resident killer whale population during the study period. The symbols represent the annual abundance estimates, and vertical bars the potential range in population size due to uncertainty in the exact year of births and deaths. The solid line represents a generalized logistic with a two-year lag, and the dashed line a generalized logistic with no lag.

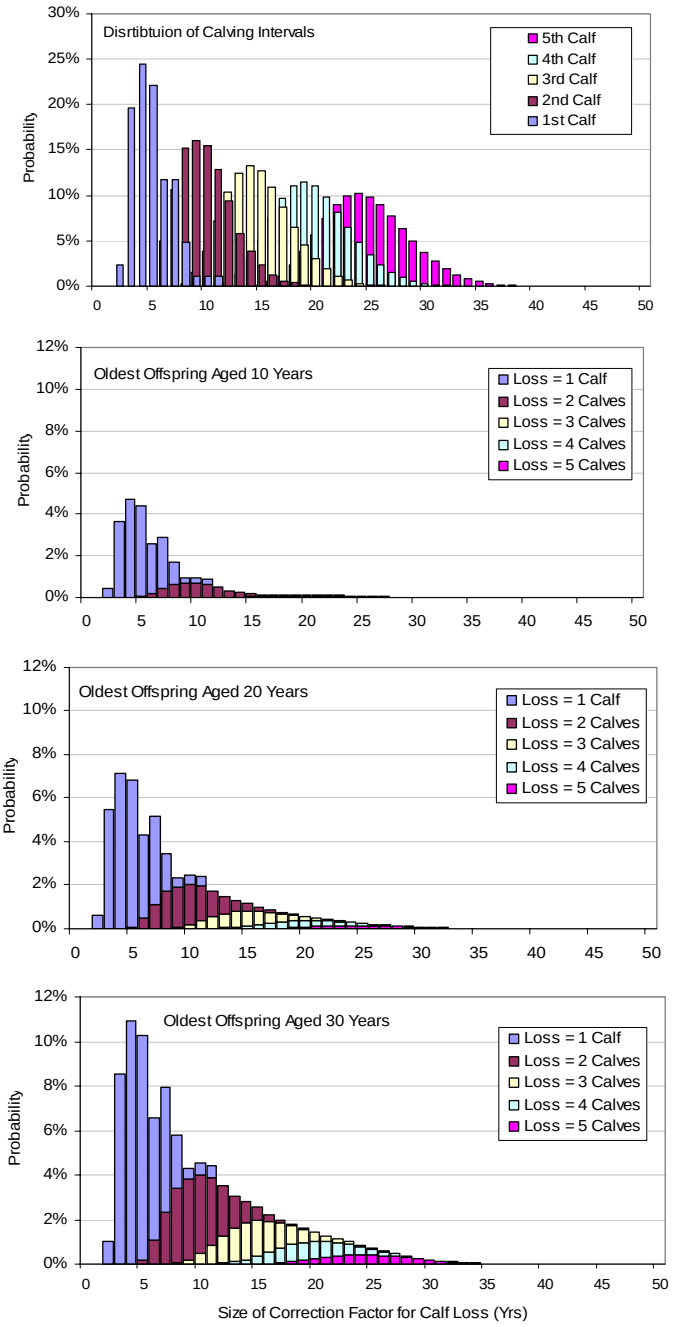


Figure 7. Illustration of method used to derive correction factor for calf loss (*CFCL*) prior to the start of the study. The top panel shows the expected distribution of birth of 1st, 2nd, 3rd, 4th and 5th potential additional calves based on the frequency distribution of calving intervals observed during the study (see Figure 11). The lower three panels show the probability of the first calves all dying prior to the start of the study, for females with oldest known offspring aged 10 years, 20 years and 30 years when first encountered.

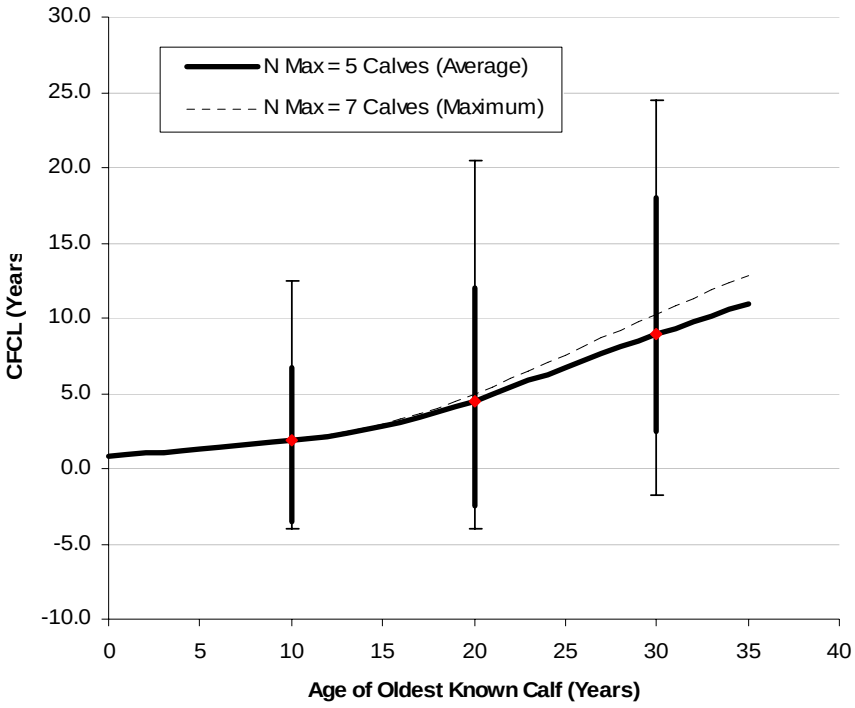


Figure 8. Size of correction factor for calf loss (*CFCL*) as a function of the age of the oldest known offspring at the start of the study. The solid trend line shows the correction used to age females based on a maximum calf loss set at 5 calves (the average number expected to be produced be females), and the thin line the effect of extending calf loss to 7 calves (the maximum observed in the wild). The vertical bars show the likely range in the *CFCL* that encompasses 80% of the probability density distribution (thick bars), and the upper and lower limits based on 95% of the probability density distribution (thin bars).

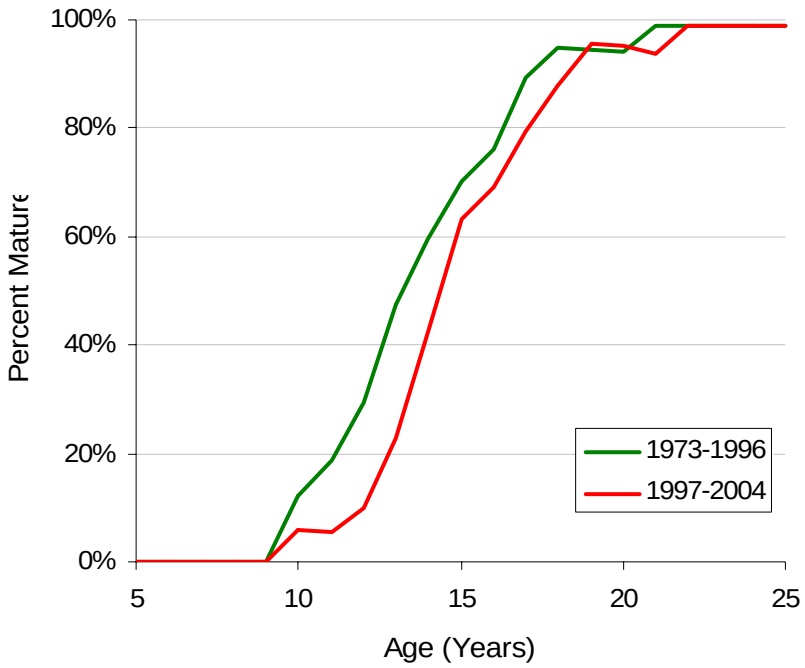


Figure 9. Proportion of females mature as a function of age. Females were considered mature when they gave birth to their first viable calf.

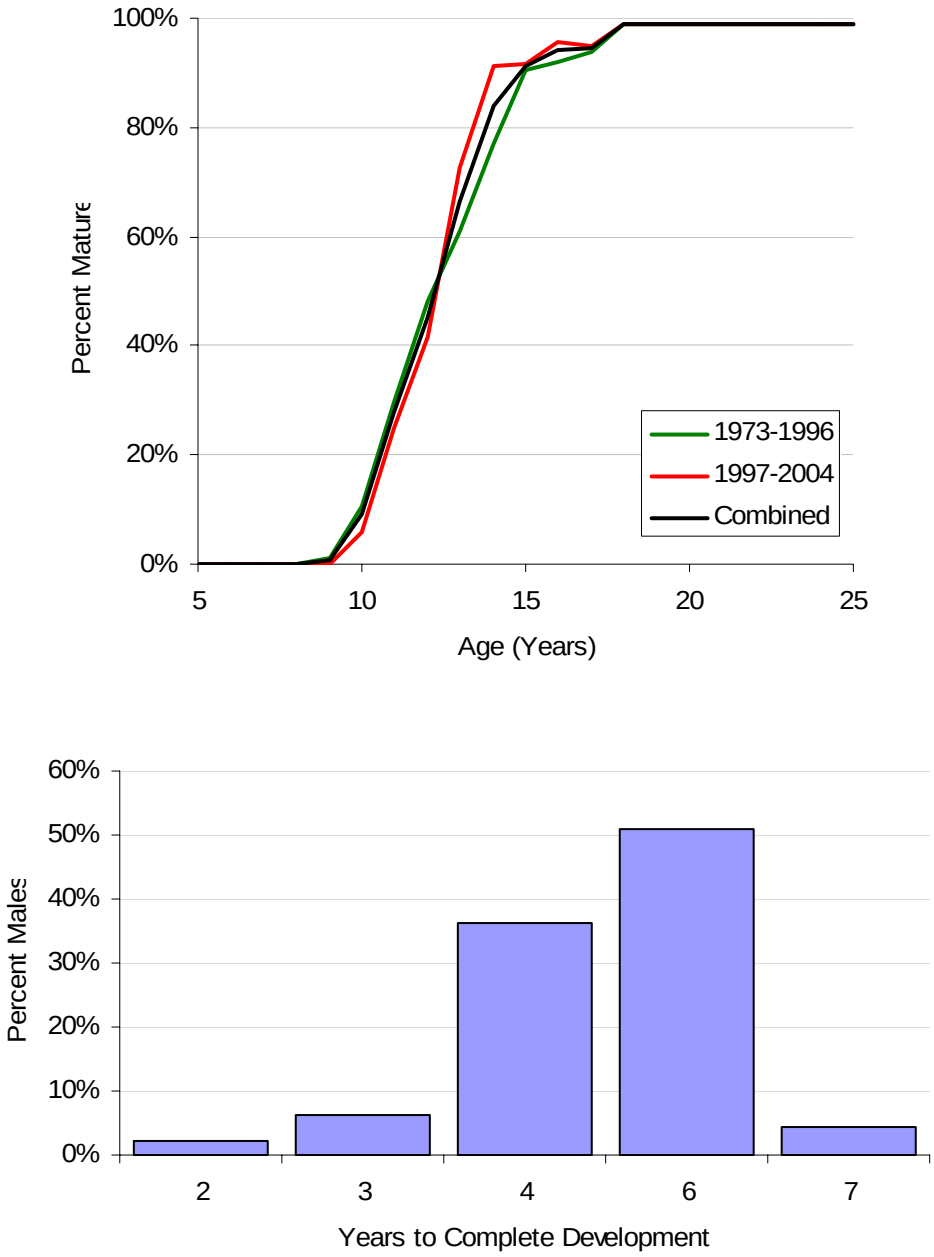


Figure 10. Proportion of males sexually mature as a function of age (top panel). Males were considered sexually mature when their dorsal fin began to "sprout" during a period of rapid pubescent growth, as indicated by a fin height to width ratio (*HWR*) exceeding 1.4. The bottom panel indicates additional years of development until the fin attains its asymptotic height, at which point males are considered to be physically mature.

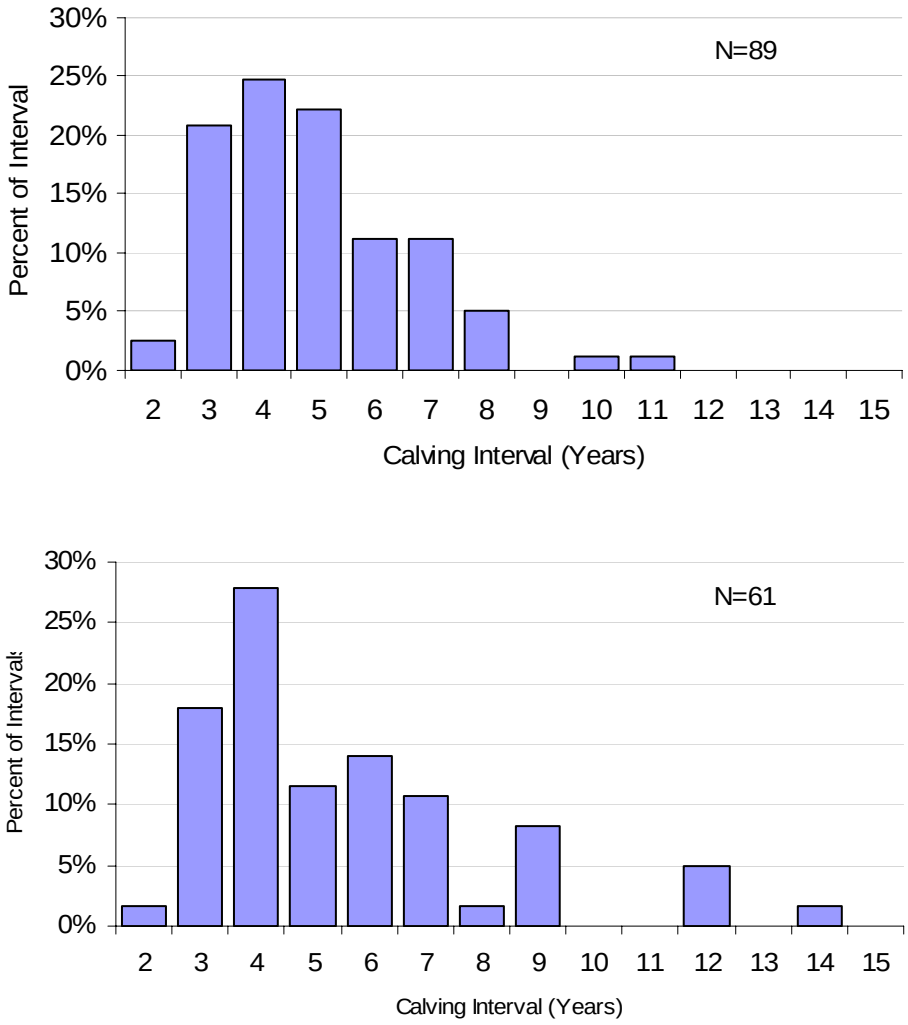


Figure 11. Observed calving intervals completed during 1983-95 (top panel) and 1996-2004.

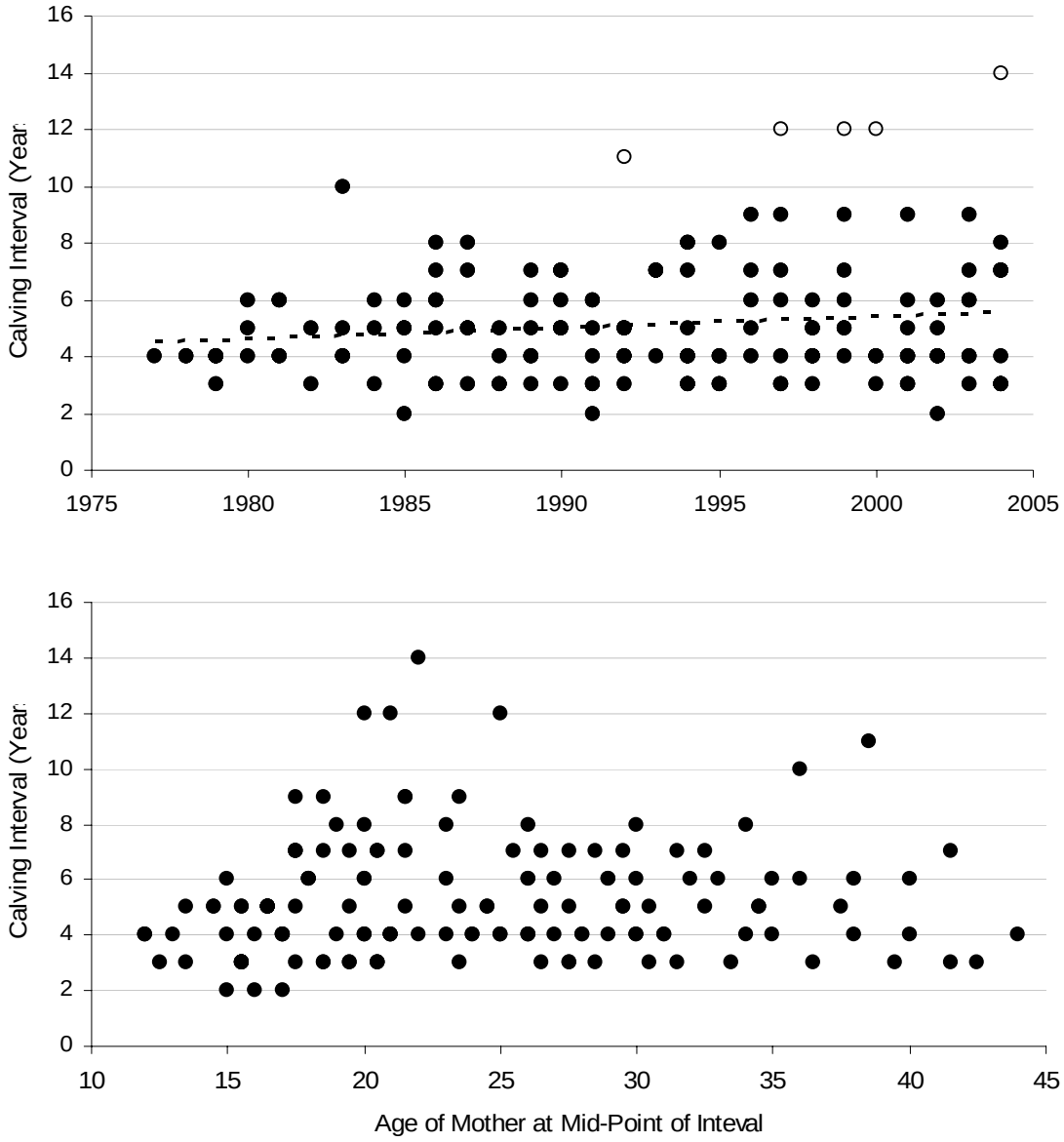


Figure 12. Calving period as a function of the year they were completed (top panel) and an the estimated age of the mother at the mid-point of the interval. The dashed line in the top panel represents a least squares regression, which was marginally significant but driven due to several unusually long intervals late in the study (open circles).

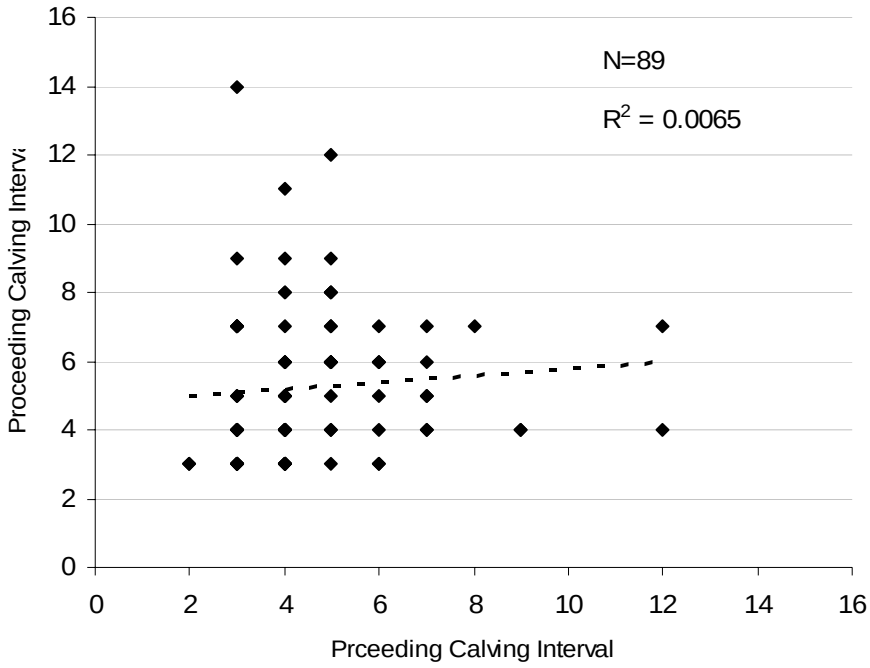


Figure 13. Correlation between successive calving intervals, indicating that long intervals and followed by short intervals about as frequently as short intervals are followed by long intervals.

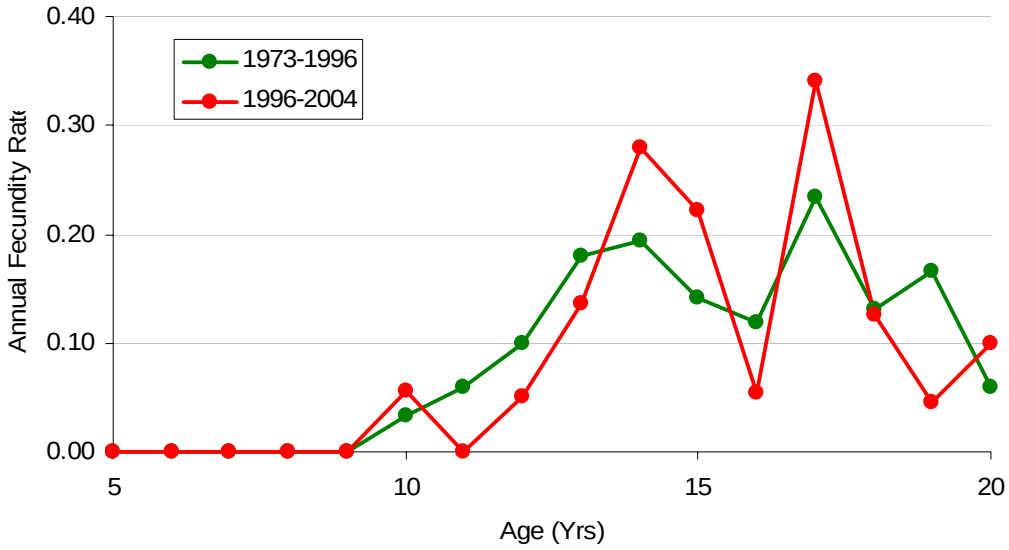


Figure 14. Annual fecundity rate (proportion giving birth to viable calves of either sex) of adolescent and young adult females as a function of the their known ages.

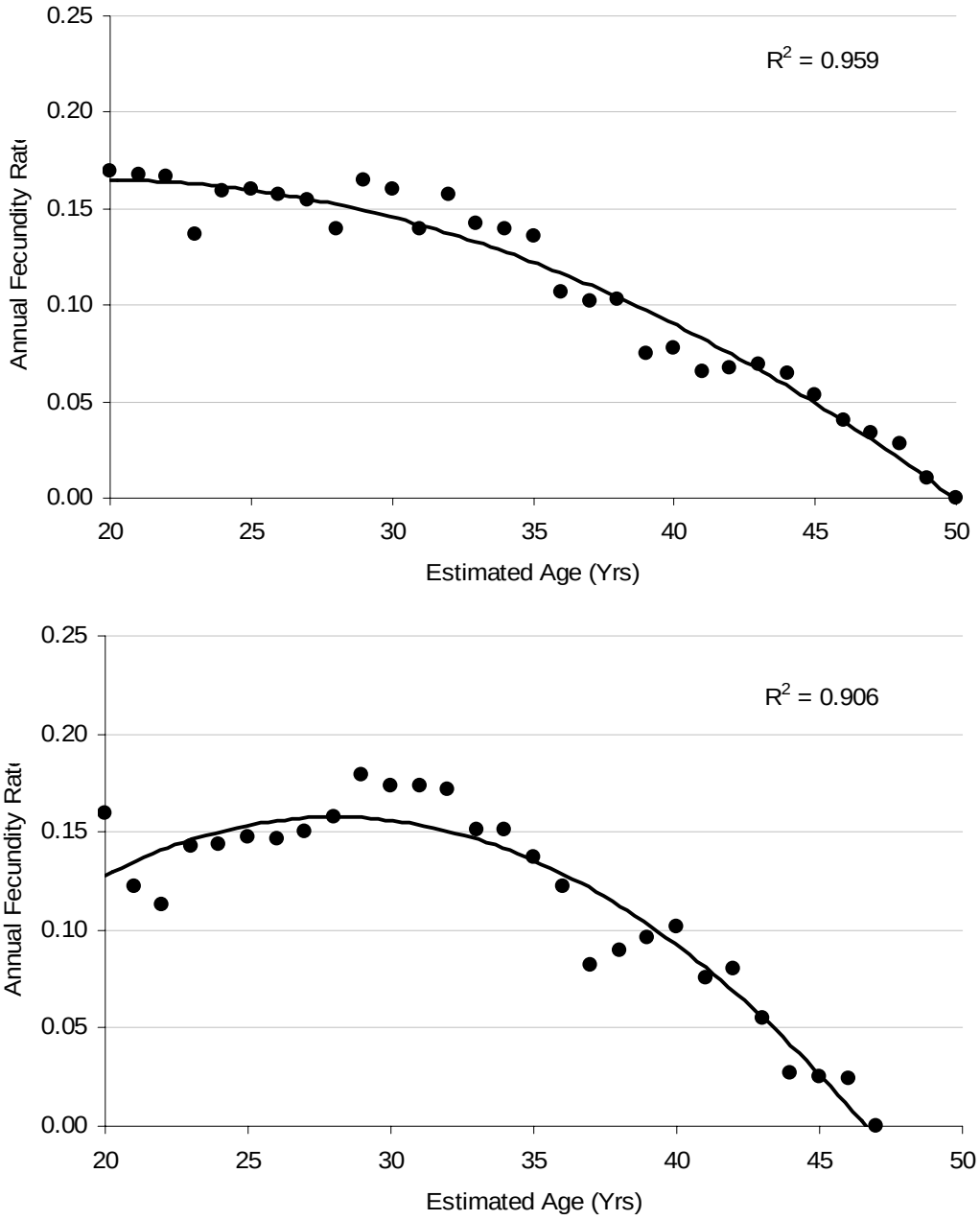


Figure 15. Annual fecundity rate (proportion giving birth to viable calves of either sex) of all mature females as a function of their estimated age during 1973-96 (top panel) and 1997-2004 (bottom panel). Solid lines represent second-order polynomial regressions.

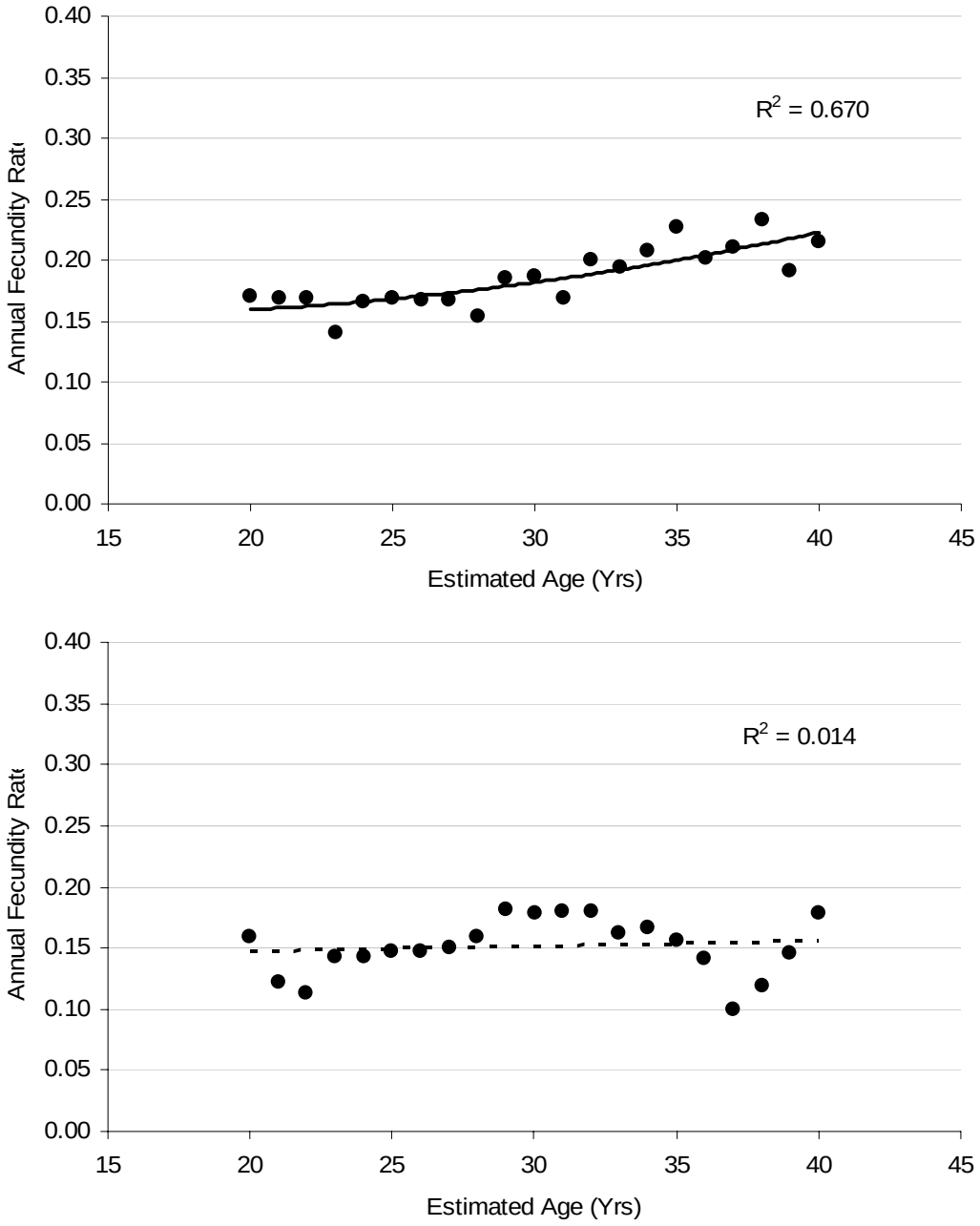


Figure 16. Annual fecundity rate (proportion giving birth to viable calves of either sex) of reproductively active females (defined as those having given birth within the last decade) as a function of their estimated age during 1973-96 (top panel) and 1997-2004 (bottom panel). The numbers of reproductively active females aged greater than 40 years were too small to calculate their fecundities. The solid line in the top panel represents a second-order polynomial regression, and the dashed line in the lower panel indicates a non-significant regression line.

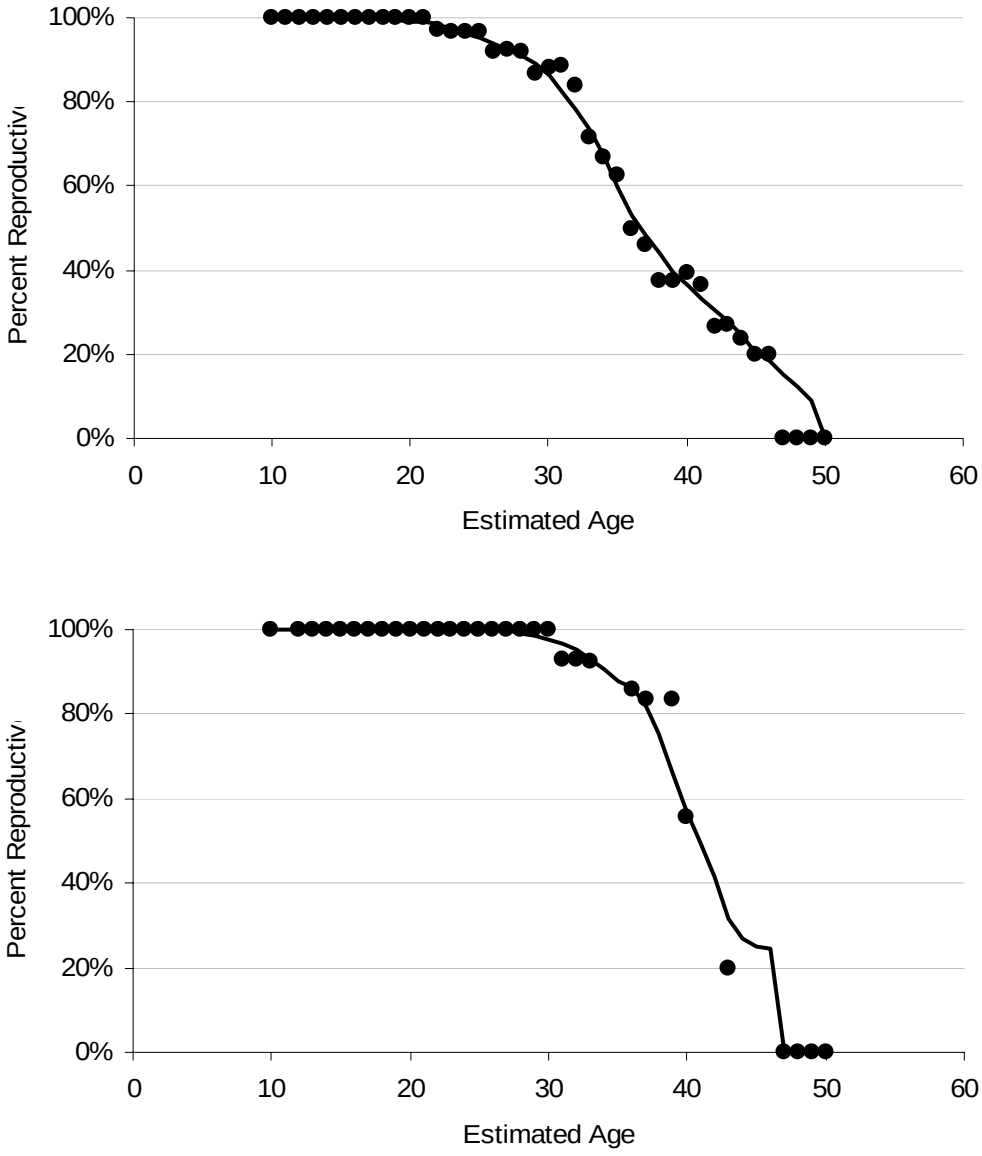


Figure 17. Estimated proportion of females that were still reproductively active as a function of their estimated age, for the period 1973-1996 (top panel) and 1996-2004 (bottom panel). The symbols represent the ratio of the estimated fecundity rates of reproductive females to the fecundity rates of all mature females in each age-class. The trend lines represent the same ratio for the ± 3-year running averages.

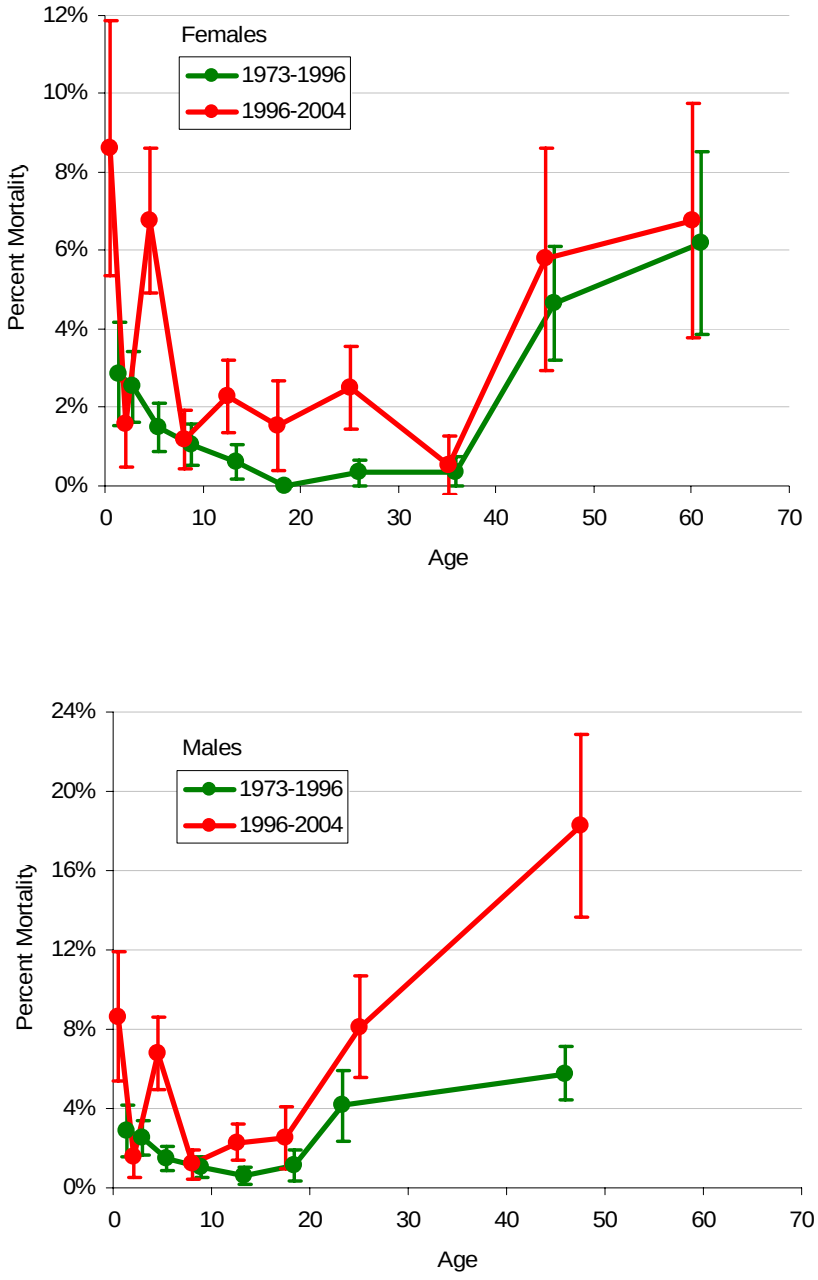


Figure 18. Age-specific annual mortality rates by age-category for females (top panel) and males (lower panel). The vertical bars represent standard errors for each estimate. Note that male mortality rates are plotted on a scale twice that of females.

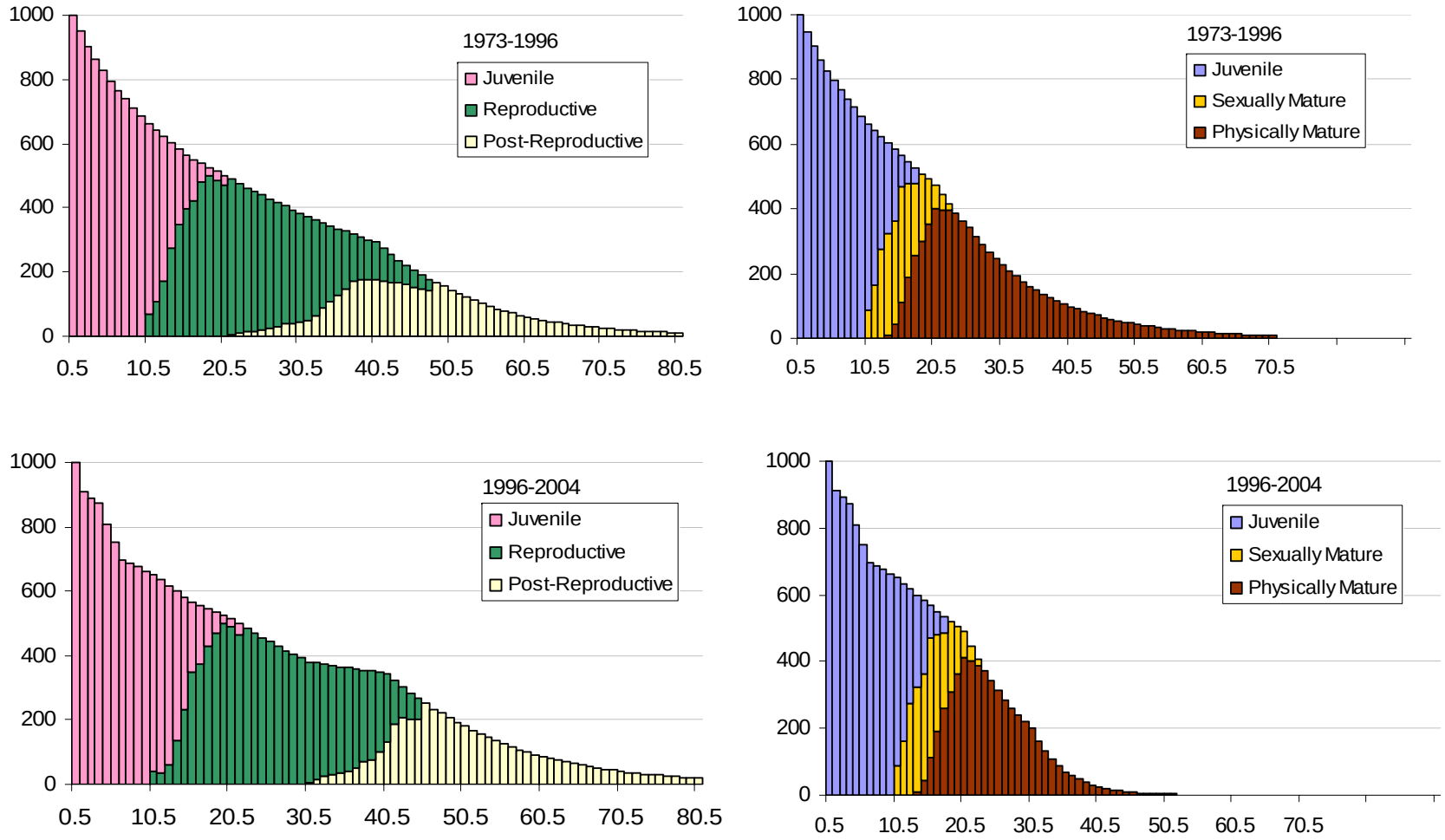


Figure 19. Predicted stable sex- and age-distribution for females (left) and males (right) in a population exhibiting unrestrained growth (top panels) and exhibiting relative stability (bottom panels).

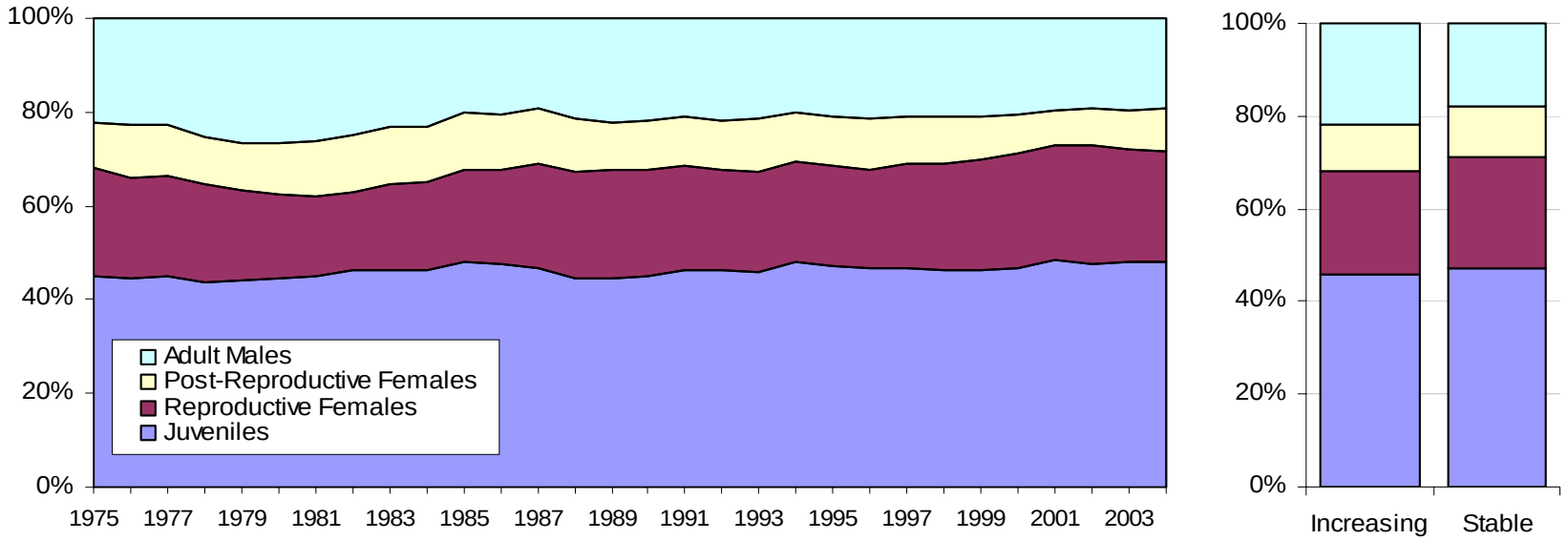


Figure 20. Observed sex- and age-structure in the northern resident population over the course of the study (left) compared with stable sex- and age-structure predicted for populations exhibiting unrestrained growth and stability (right).