Chinook salmon predation by resident killer whales: seasonal and regional selectivity, stock identity of prey, and consumption rates

John K B Ford
Fisheries and Oceans Canada, Pacific Biological Station

Brianna Wright
Fisheries and Oceans Canada

AR031671

Fisheries and Oceans Canada / Pêches et Océans Canada
Science / Sciences

C S A S / **S C C S**

Canadian Science Advisory Secretariat / **Secrétariat canadien de consultation scientifique**

Research Document 2009/101 / **Document de recherche 2009/101**

Chinook salmon predation by resident killer whales: seasonal and regional selectivity, stock identity of prey, and consumption rates

Prédation du saumon quinnat par les épaulards résidents : sélectivité saisonnière et régionale, identité des stocks de proies et taux de consommation

John K.B. Ford
Brianna M. Wright
Graeme M. Ellis
John R. Candy

Fisheries and Oceans Canada,
Pacific Biological Station
3190 Hammond Bay Road,
Nanaimo, BC V9T 6N7 CANADA

ISSN 1499-3848 (Printed / Imprimé)
ISSN 1919-5044 (Online / En ligne)

Canada

Correct citation for this publication:

Ford, J.K.B, Wright, B.M., Ellis, G.M., and Candy, J.R. 2010. Chinook salmon predation by resident killer whales: seasonal and regional selectivity, stock identity of prey, and consumption rates. DFO Can. Sci. Advis. Sec. Res. Doc. 2009/101. iv + 43 p.

ABSTRACT

Resident killer whales (*Orcinus orca*) found in coastal waters of the cold-temperate northeastern Pacific are fish-feeding predators that specialize on Pacific salmon. Field studies have shown that although most available salmonids are consumed, Chinook salmon (*Oncorhynchus tshawytscha*) is the whales' primary prey species, most likely because of its large size, high lipid content, and year-round occurrence in coastal waters. Chinook salmon availability appears to be important to the survival and recovery of resident killer whale populations. In this report we describe the results of recent field studies and analyses aimed at improving our understanding of the role played by Chinook salmon in the seasonal foraging ecology and energetics of resident killer whales. An additional 410 prey items identified from scale and tissue samples collected at the sites of resident feeding events provide further support for the importance of Chinook salmon in most seasons and coastal areas. Genetic stock identification of prey samples indicate that killer whales feed on Chinook salmon originating from a variety of regions between Southeast Alaska and Oregon, with stocks in the Fraser River system being of particular importance both coast-wide and in Critical Habitats. An updated analysis confirms the long-term correlation between survival of resident killer whales and range-wide Chinook abundance, though recent declines in Chinook abundance have not yet been associated with increased mortality rates. Estimates of Chinook salmon consumption based on daily prey energy requirements and diet composition suggest that resident killer whale populations at their current abundance may require over 1,000,000 Chinook per year, roughly equivalent to recent annual levels of harvests of this species in commercial and recreational marine fisheries. Estimates of Chinook salmon requirements for northern and southern resident killer whale populations in their Critical Habitats are also provided, as is an estimate of the Chinook abundance that would be required to support killer whale recovery over the next decade. Although the information in this report may be useful for future conservation and management of resident killer whales and their primary prey, further studies are needed to resolve existing uncertainties about year-round diet composition and feeding rates.

RÉSUMÉ

Les épaulards résidents (*Orcinus orca*) des eaux côtières de la zone froide tempérée du nord-est du Pacifique sont des prédateurs piscivores qui préfèrent le saumon du Pacifique. Des études sur le terrain ont démontré que même si la plupart des salmonidés disponibles sont consommés, le saumon quinnat (*Oncorhynchus tshawytscha*) est la principale espèce proie des épaulards, fort probablement en raison de sa grande taille, de sa teneur élevée en lipides et de sa présence dans les eaux côtières toute l'année. La disponibilité de saumon quinnat semble importante pour la survie et le rétablissement des populations d'épaulards résidents. Dans ce rapport, nous décrivons les résultats des études sur le terrain et des analyses récentes visant à améliorer notre compréhension du rôle que joue le saumon quinnat pour l'écologie alimentaire saisonnière et l'énergétique des épaulards résidents. Les 410 proies supplémentaires identifiées à partir des restes d'écailles et de tissus recueillis sur les sites d'activités d'alimentation des épaulards résidents soulignent encore plus l'importance du saumon quinnat pour la plupart des régions côtières et des saisons. L'identification du stock génétique des restes de proies indique que les épaulards résidents se nourrissent de saumon quinnat provenant de diverses régions situées entre le sud-est de l'Alaska et l'Oregon, les stocks du système du fleuve Fraser étant particulièrement importants à la fois sur toute la côte et dans les habitats critiques. Une analyse actualisée confirme la corrélation à long terme entre le taux de survie des épaulards résidents et l'abondance de saumon quinnat pour toute l'aire, malgré le fait que la récente diminution d'abondance du saumon quinnat n'a pas encore été associée avec les taux de mortalité accrus. Les estimations de consommation du saumon quinnat en fonction des besoins énergétiques quotidiens en proies et de la composition de la diète portent à croire que les populations d'épaulards résidents, selon leur abondance actuelle, peuvent nécessiter un million de saumons quinnat par année, soit approximativement l'équivalent des récents niveaux annuels de capture des pêches marines commerciales et récréatives pour cette espèce. On donne aussi des estimations des besoins en saumon quinnat pour les populations d'épaulards résidents du nord et du sud dans leurs habitats critiques, de même qu'une estimation de l'abondance de saumon quinnat qui serait nécessaire pour favoriser le rétablissement de l'épaulard au cours de la prochaine décennie. Même si l'information donnée dans ce rapport peut être utile pour la conservation et la gestion futures des épaulards résidents et de leur principale proie, d'autres études sont nécessaires pour trouver une réponse aux incertitudes actuelles sur la composition de la diète et le taux de consommation toute l'année.

INTRODUCTION

So-called 'resident' killer whales are one of three sympatric ecotypes of *Orcinus orca* found in the coastal waters of the cold-temperate northeastern Pacific. Each ecotype is ecologically specialized and has a distinct diet. Residents are fish feeders, and in particular specialize on Pacific salmon (Ford et al. 1998). The so-called 'transient' killer whale ecotype is a mammal-hunting specialist, feeding on pinnipeds and small cetaceans but not fish (Ford et al. 1998). The so-called 'offshore' killer whale ecotype is a poorly-known fish feeder found primarily on the outer coast and may specialize on sharks and other large fish (Ford et al. 2000; Dahlheim et al. 2008; Cetacean Research Program, Pacific Biological Station, unpubl. data).

Resident killer whales in British Columbia and adjacent coastal waters of Washington State have been the focus of annual field studies since the early 1970s (Bigg et al. 1976; Bigg 1982). A key method in these long-term studies has been photographic identification of individual whales using natural markings on the dorsal fin and back. This work has provided a great deal of information on the social organization, life history, population dynamics, and behavioural acoustics of these whales (e.g., Bigg 1982; Bigg et al. 1990; Olesiuk et al. 1990, 2005; Ford 1991; Ford et al. 2000).

Knowledge of the foraging ecology of resident killer whales has taken somewhat longer to acquire, mostly due to the difficulties in studying feeding behaviour in wild cetaceans. The association between seasonal aggregations of resident killer whales in inshore waters near Vancouver Island and the spawning migration of Pacific salmon has long suggested that that these whales feed extensively on this prey type (Heimlich-Boran 1986; Guinet 1990; Nichol and Shackleton 1996), but the first detailed evidence of salmonid consumption was documented by Ford et al. (1998). This study investigated diet by observing predation events, examining stomach contents of stranded whales and, in particular, opportunistically collecting fish scales and other prey fragments from kill sites during 1973-96. An unexpected finding of this research was that despite feeding on most available salmonid species, resident killer whales appeared to exhibit a strong preference for Chinook salmon (*Oncorhynchus tshawytscha*), the largest and most energy-rich salmonid in the region, but also one of the least common. The far more seasonally abundant pink (*O. gorbuscha*) and sockeye salmon (*O. nerka*) appeared not to be significant in the whales' diet.

Although stomach contents analysis supported field observations that resident killer whales may feed preferentially on Chinook salmon, we had concerns that the prey fragment sampling technique used to identify prey species was biased in favour of large fish such as Chinook salmon (Ford et al. 1998). It seemed possible that Chinook, being larger than other salmonids, were more prone to being broken up prior to being eaten, thus shedding more scales in the process (Ford et al. 1998). However, without knowledge of the details of prey handling and consumption of salmonids and other fish species by resident killer whales, it was not possible to evaluate the significance, if any, of this potential bias. It was concluded that resident whales have a preference for Chinook, but the extent of this preference remained uncertain (Ford et al. 1998).

To address these concerns and to generally improve understanding of the diet of resident killer whales, we undertook dedicated field studies of foraging behaviour, including focal animal observations to document the details of prey capture, handling and consumption, during 2002-04. This research revealed that most salmonid feeding events involved sharing of prey among animals within the group, and that scales and tissue fragments were shed when fish were broken apart for this purpose (Ford and Ellis 2005, 2006). All salmonid species and sizes appeared to be shared, which suggested that any bias in prey sampling was likely to be minimal, at least with respect to salmonid prey. This study provided strong support that Chinook salmon is the primary prey species of residents, and that the smaller pink and sockeye salmon were not significant components of the whales' diet. It also revealed that chum salmon (*O. keta*) was an important prey species during late September and October.

Chinook salmon may be of such importance as primary prey of resident killer whales that its availability plays a role in their population dynamics. Ford et al. (2005, 2010) showed that mortality rates of resident killer whales were negatively correlated with Chinook salmon abundance over a 25-year period, from 1979-2003. In particular, a sharp decline in Chinook abundance during the late 1990s was associated with killer whale mortality rates up to 2-3 times greater than expected, which resulted in population declines in both resident killer whale populations, the so-called northern and southern residents. Calving rates showed a weaker, but still significant, positive correlation with Chinook salmon abundance. Ward et al. (2009) also found a significant association between Chinook abundance and reproductive rates in the southern resident population.

Resident killer whales are listed under the Species at Risk Act in Canada, with the northern population designated as threatened and the southern population as endangered (Fisheries and Oceans Canada 2008). The southern resident population is similarly listed as endangered under the U.S. Endangered Species Act (NMFS 2005). A primary objective in the Recovery Strategy for resident killer whales is to *Ensure that resident killer whales have an adequate and accessible food supply to allow recovery* (Fisheries and Oceans Canada 2008). Since Chinook salmon is the primary prey of resident killer whales and its abundance may directly affect survival and recovery, it is important that an improved understanding of the seasonal and geographic importance of this prey resource is obtained. In particular, information is needed on the specific Chinook salmon populations that are exploited by resident killer whales at different times of the year and in different parts of their range, and the overall abundance of Chinook that may be needed to support the existing resident killer whale population and to provide for sustained growth and recovery.

In this report, we describe new information and analyses on a variety of aspects of the dynamics between resident killer whales and their primary prey, Chinook salmon. First, we build on our understanding of diet composition described in Ford and Ellis (2005, 2006) by presenting the results of new prey sampling undertaken in 2005-09. We then describe the population identity of Chinook salmon sampled from resident killer whale feeding events to assess the regional importance of different stocks to foraging whales. Next, we investigate the effects of variations in Chinook salmon availability by updating the Ford et al. (2005) analysis of the relationship between resident killer whale mortality and Chinook abundance, and by examining potential prey shifts during periods of high and low Chinook abundance. Finally, we estimate the numbers of Chinook salmon that may be consumed by resident killer whales based on diet composition and energetic requirements, both annually and within designated Critical Habitat, and predict the abundance of Chinook salmon that may be needed to allow for population recovery over the next decade.

STUDY POPULATIONS AND DATA COLLECTION

Studies were undertaken in coastal waters of British Columbia during 1973-2009, primarily in nearshore waters off eastern and southwestern Vancouver Island, the central and northern mainland coast, and near Langara Island off the northwest coast of Graham Island. Two populations of resident killer whales, northern residents and southern residents, can be found in these waters in all months of the year, but mostly during May-November. The northern resident population is found mostly from mid Vancouver Island to southeastern Alaska, and the southern resident population off the southern half of Vancouver Island and in the inland waters of Washington state (Figure 1). Whales from the two populations have not been seen to associate despite extensive overlap in their ranges (Ford et al. 2000). Large aggregations of residents can be found in certain coastal locations during summer. Residents greatly reduce the use of these locations in winter and spring, and their range during this period is poorly known but is suspected to be more extensive in outer coast waters (Ford et al. 2000; Wiles 2004).

The northern and southern resident populations contained 86 and 252 individuals, respectively, in 2008 (Figure 2). Both populations have grown since first censused in 1974. The northern population has more than doubled in size, from 122 to 252 animals, while the southern population is only 21% larger (71 in 1974, 86 in 2008). Both populations grew at an overall annual rate of 2-3% from the early 1970s to the mid 1990s, and then experienced a decline in abundance in the late 1990s. This decline was driven by a sharp increase in mortality rates and, to a lesser extent, decreased recruitment (Ford et al. 2005; Olesiuk et al. 2005). The southern resident population has yet to recover from this period of decline, but the northern resident population is currently at its greatest abundance since the study began.

FIELD EFFORT AND PROCEDURES

Data on predation by resident killer whales have been collected annually since 1973, as part of long-term studies on the life history, social organization, acoustic behaviour, and population genetics of these animals (Bigg 1982; Bigg et al. 1990; Olesiuk et al. 1990, 2005; Ford 1989, 1991; Ford et al. 1998, 2000; Barrett-Lennard 2000). Data collected during 1973-2002 consisted mostly of surface observations of feeding events and opportunistic collection of prey fragments from the vicinity of kills. Effort varied widely according to changing research objectives, but predation studies were given higher priority during 1990-2002 (Ford et al. 1998, Ford and Ellis 2005). In 2003-09, field studies were dedicated to systematically documenting foraging behaviour and collecting predation data, in addition to conducting the annual census of individuals by photo-identification (Bigg et al. 1987; Ford et al. 2000).

Field studies in 1974-2002 were conducted using a variety of vessels from 5-20 m in length. In 2003-09, dedicated studies of resident killer whale feeding were undertaken mainly from a 10-m long command-bridge power vessel. When whales were encountered, individuals were observed visually or photographed to determine identity from natural markings on the dorsal fin and back. Photographic identification procedures are described in Bigg et al. (1987) and Ford et al. (2000). Once the identity of killer whales present in the encounter was established, effort was directed to documenting foraging behaviour and collecting scales and tissue fragments from prey killed during feeding events. Activity state of the whales was determined from surfacing and dispersion patterns (see Ford 1989 for definitions of activity states). When foraging, whale groups typically spread out over several square kilometres, with individuals and subgroups swimming and diving independently but travelling generally in the same direction. Surfacing individuals and groups were scanned by eye or binoculars for signs of prey pursuit or capture. When apparent feeding was observed, the site of the kill was approached promptly (while taking care to avoid disturbing the animals) in order to determine or confirm identities of the whale(s) involved and to search for prey fragments in the water. Whether or not prey fragments were found, the individual or subgroup was then followed at distances of 25-50 m to document subsequent feeding events. These focal individual and subgroup follows (Altmann 1974; Mann 1999) were maintained for as long as the whale(s) continued active foraging. Focal follows were terminated when animals joined other groups and could no longer be followed individually, when subgroups merged or split, or when other circumstances necessitated ending the session.

Focal individuals and subgroups were monitored closely and constantly during feeding sessions. Particular attention was given to direction of travel, regularity of dive durations, and degree of subgroup cohesion, as changes in these variables often signalled a feeding event. Individuals or subgroups suspected to have captured a prey item were approached to within 10 m to observe prey handling and consumption. To collect evidence of feeding, the surfacing locations of the feeding whale or subgroup were also examined for prey fragments at the surface or in the water column. The boat driver was positioned approximately 4 m above the water surface on the command bridge of the study vessel, which afforded a high-angle view into the water as the boat was manoeuvred. A second observer stood on the vessel's bow, holding a fine-mesh dip net (mesh size approximately 1 mm) with 5-m telescoping handle, and also searched for fragments. When fish scales or bits of tissue were seen, the boat was immediately stopped and the net was deployed to retrieve the fragments. Fragments were collected mostly at depths of 0-2 m, but occasionally as deep as 3-4 m in calm conditions with good water clarity. Rain, winds greater than 10 kts, and high water turbidity reduced the success rate of fragment location and collection.

When prey fragments were collected, they were placed immediately in a 5 ml vial containing 95% ethanol. The date, time, and geographical position (from a differential GPS instrument) of the feeding event was recorded, as well as the identity of the individual making the kill and others involved in the prey capture or consumption.

PREY SPECIES IDENTIFICATION AND AGEING

Many species of fishes are readily identifiable at a distance by an experienced observer, but salmon species can be difficult to distinguish without close examination. Although Ford et al. (1998) included salmonid identifications based on field observations, in Ford and Ellis (2005) and the current analyses we chose to include only positive salmonid identifications based on scales or tissue samples to eliminate this potential source of error. Fish scales were analyzed by the Sclerochronology Laboratory at the Pacific Biological Station (Department of Fisheries and Oceans, Nanaimo, B.C.) to determine species identity and age according to procedures outlined in MacLellan (2004). Age was designated using the European method and age class was assigned according to the internationally-accepted January 1st birthdate. Species identification was based on diagnostic scale characteristics (MacLellan 2004).

Scales that could not be positively identified to species and tissue samples collected from feeding events were submitted to the Molecular Genetics Laboratory at the Pacific Biological Station for species identification using allelic size range of genomic DNA. Variation at twelve microsatellite loci were used to identify species as well as assign individual Chinook salmon to region of origin using a mixture analysis program cbayes (Neaves et al. 2005). The baseline consisted of 268 populations ranging from south-east Alaska to California using methodology reported in Beacham et al. (2003, 2006).

RESULTS

DIET OF RESIDENT KILLER WHALES BY SEASON AND REGION

Ford and Ellis (2005) described results of observations of predation and prey species identification from field studies of resident killer whales conducted during 1974-2004. They provided results of analyses of 487 feeding events documented during 197 encounters with resident killer whales over the 30 year study period. Sixty percent of these feeding events were documented in the last two years of this time series, reflecting a shift in research focus to foraging behaviour and diet. Feeding events were recorded during May to December, but none in January to April.

Continued field studies of resident killer whale diet since 2004 have almost doubled the dataset used in the Ford and Ellis (2005) analysis, and have broadened sampling both geographically and seasonally. The total dataset now available, and which forms the basis of the current analysis, includes 937 feeding events documented during 341 encounters with northern (n = 715 events) and southern (n = 222 events) resident killer whales. Feeding events were observed in all years between 1973 and 2009, although 81% of events were documented during dedicated studies of foraging since 2000 (Figure 3). Evidence used to identify prey for the 937 feeding events is provided in Table 1. Over 90% of feeding events were documented by collection and analysis of fish scales, tissue, or both.

The monthly distribution of feeding events for northern and southern resident killer whales is shown in Figure 4. Feeding was documented in all months except April, with 80% of events sampled during the summer months of June through September. The overall locations of feeding events involving northern and southern residents are depicted in Figure 5. To facilitate regional comparisons of diet composition, the coastal waters of British Columbia were divided into 6 regions, shown with the Pacific Fisheries Management Areas (PFMA) they encompass in Figure 6. Sample sizes of feeding events and prey species composition for each of these regions are tabulated in Table 2.

Prey species identification from this more extensive dataset provides further support for the conclusions reached by Ford and Ellis (2005, 2006). All feeding events involved fish, at least 97.4% of which were salmonids (Table 2). Twenty-four samples (2.5%) could not be identified to species, and some of these may also have included salmonids. The only non-salmonids identified were 2 Pacific herring (*Clupea pallasi*), 4 Pacific sardine (*Sardinops sagax*), 1 yelloweye rockfish (*Sebastes ruberrimus*), 1 quillback rockfish (*Sebastes maliger*), 1 sablefish (*Anoplopoma fimbria*), and 1 Pacific halibut (*Hippoglossus stenolepis*).

Chinook salmon was by far the predominant salmonid species consumed, representing 71% of the 806 salmonid kills identified to species. Chum salmon was second in importance at 24%, and coho, pink, sockeye and steelhead salmon were minor components of the whales' diet at less than 3% each. The monthly distribution of salmonid species consumed is tabulated in Table 3 and shown graphically in Figure 7. Chinook salmon was the predominant prey species in all months except October and November, when chum salmon were consumed more frequently. Sample sizes for winter months are small, but Chinook salmon was the only prey species documented in January-March. Chinook salmon was also the predominant prey species in all coastal regions (Figure 8, Table 2).

Table 4 presents the ages of salmon consumed by resident killer whales as determined from scale samples recovered from feeding events. Of the 431 Chinook salmon samples aged, 325 (75%) were 'ocean' type fish as indicated by 0 years in fresh water, and 106 (25%) were 'stream' type fish that spent 1-2 years in fresh water prior to entering the sea. Stream type Chinook tend to migrate to the open ocean and only return to coastal waters during their spawning migration (Healey 1991). Ocean type Chinook, on the other hand, spend their entire life cycle within continental shelf waters and may thus be more available to the whales throughout the year.

POPULATION IDENTITY OF CHINOOK SALMON CONSUMED BY RESIDENT KILLER WHALES

In order to assess the seasonal and regional importance of different Chinook salmon populations in the diet of resident killer whales, we undertook genetic stock identification analyses of scale and tissue samples collected from feeding events. A total of 474 prey samples of Chinook salmon resulted in DNA suitable for stock region identification (Beacham et al. 2006). Chinook salmon prey of killer whales originated in 19 of the 38 regional stocks described in Beacham et al. (2006). Chinook from stock regions within the Fraser River system comprised 58% of samples. Also important were stocks in the east coast (10%) and west coast (8%) of Vancouver Island regions. In the following subsections, we present stock identities for Chinook sampled in the different coastal regions indicated in Figure 6.

Queen Charlotte Islands – PFMA 1-2

Locations and months of Chinook salmon sampled from feeding events and stock region identifications are shown in Figure 9. Thirty-three samples were collected from the north coast of the Queen Charlotte Islands, mostly in the vicinity of Langara Island, during May-July. Eleven stock regions are represented in these samples, from the Skeena River in the north to Coastal Oregon in the south. The South Thompson region was the most common with 38% of samples, but the regions within the Columbia River system were also important, totalling 24% of samples. A significant portion of Chinook were from regions in closer proximity, such as the North Mainland (18%) and three regions in the Skeena River system (total of 9%).

North mainland coast – PFMA 3-6

A total of 52 Chinook salmon kills sampled during May-July in the north mainland coast area (Figure 10) were assigned to stock regions. Sixteen stock regions were represented, with the West Coast Vancouver Island and South Thompson regions being most important. Although distant regions such as the Upper Columbia River and Coastal Oregon were also represented, a greater proportion (38%) of Chinook originated in local regions in the Skeena River system, Nass, and North Mainland.

Central coast area – PFMA 7-11

Only 24 Chinook samples were available for this area, as shown in Figure 11. Of these, almost half (n = 11) were Chinook from local stocks in the North Mainland region. Seven fish were from the Columbia River system; these were all collected in outer coast waters off the western entrance to Queen Charlotte Strait.

Northeastern Vancouver Island – PFMA 12-13

The greatest number of Chinook salmon samples (n = 205) were collected from this area, which includes the waters of eastern Queen Charlotte Strait and Johnstone Strait, which have been designated as Critical Habitat for northern resident killer whales (Fisheries and Oceans Canada 2008). Most samples were collected during July-September. Well over half (62%) of Chinook salmon sampled in this area were from stocks within the Fraser River system (Figure 12). Of these, the South Thompson region was the particularly important with 42% of overall samples. Other significant Chinook regions were East Coast Vancouver Island (16%) and West Coast Vancouver Island (8%).

Southeastern Vancouver Island – PFMA 14-19, 28-29

Despite the small sample size for this region (n = 24), they were collected over 8 months of the year, May-November and January (Figure 13). Some of these samples were collected in U.S. waters near San Juan Island and in Puget Sound. As would be expected, all Chinook sampled in this inshore area were from local regions, mostly the Fraser River system (n = 16) but also the East Coast Vancouver Island, South Mainland and Puget Sound regions. Stock regions identified in this area are consistent with those identified from more extensive Chinook samples collected from southern residents by Hanson et al. (in press).

West coast Vancouver Island – PFMA 20-27

A total of 136 Chinook samples were collected in this area, mostly in or near the entrance to Juan de Fuca Strait (Figure 14). Most samples were collected within waters designated as Critical Habitat for southern resident killer whales in Canadian waters. More than three-quarters of these Chinook were from stocks within the Fraser River system, with the South Thompson being clearly the most important region (39% of the total samples). Other regions represented include Puget Sound (13%) and West Coast Vancouver Island (7%).

EFFECTS OF VARIATIONS IN CHINOOK SALMON AVAILABILITY

Chinook salmon plays such an important role in the diet of resident killer whales that this prey species' availability appears to affect the whales' survival and, to a lesser extent, reproductive rates. Ford et al. (2005, 2010) showed that over the period of 1979-2003, there was a strong negative correlation between the mortality rates of both northern and southern resident killer whales and the coast-wide abundance of Chinook salmon, and a lesser though still significant positive correlation with calving rates. Particularly striking was the period of very low Chinook abundance in the mid to late 1990s, which was correlated with mortality rates 2-3 times higher than expected in resident killer whales. Unusually high mortalities were observed broadly among different killer whale groups and different age/sex categories.

The longer time series of data now available on resident killer whale population dynamics and foraging behaviour has allowed us to further investigate the effects of fluctuations in Chinook salmon abundance.

Mortality rates versus Chinook salmon abundance

Comparisons between the population dynamics of resident killer whales and Chinook salmon abundance described in Ford et al. (2005, 2010) extended from 1979, the first year of the annual Pacific Salmon Commission (PSC) Chinook abundance, to 2003, the last year for which whale population data were available. With an additional five years of data now available, we have repeated the correlation analysis between mortality and Chinook abundance to determine whether the same relationship has been maintained in recent years. The procedure used for this analysis is essentially the same as that described in Ford et al. (2005). An index of mortality was derived by calculating the ratio of the number of deaths observed in the populations to the number expected for each year. The number of expected mortalities was calculated from sex- and age-specific mortality schedules provided in Olesiuk et al. (2005), for a period of unrestrained growth during 1973-96. Because there was sometimes uncertainty associated with exact year of death of some individuals, and deaths might be influenced by effects that were cumulative over several years (e.g. nutritional stress), we expressed the observed to expected ratios as 3-year running averages. These annual mortality indices were compared to an annual index based on the total estimated Chinook salmon abundance across six coastal regions, developed by the PSC Chinook Technical Committee (PSC 2008). In our earlier analyses (Ford et al. 2005, 2010), we modified the PSC Chinook abundance index by referencing each year's abundance to the average annual abundance over the 1979-2003 time series, rather than the 4-year base period (1979-82) used by the PSC. In the current analysis, we have used the PSC index without modification.

The mortality indices for northern and southern resident killer whales and annual PSC Chinook abundance indices for the 1979-2008 period are depicted in Figure 15. An updated regression analysis for this time series (Figure 16), with killer whale mortalities lagged by one year following salmon abundance, confirms the strong relationship between killer whale survival and coast-wide Chinook abundance. Although the correlation is not as strong as for the earlier period ($r^2 = 0.777$ (1979-2003) vs $r^2 = 0.487$ (1979-2008)), it is still highly significant ($F_{1,27} = 25.6$, $p < 0.001$). In the years since the earlier analysis, the Chinook salmon abundance index has fluctuated considerably, from values above the base period in 2003-04, to below the base period in 2005-08. On average over the 1979-2008 period, a killer whale mortility index above 1 was associated with a coast-wide Chinook abundance index of 1.1 or less (calculated from regression in Figure 16). Despite lower Chinook abundance in the most recent years, killer whale mortality rates have yet to exhibit an increase.

Prey selection versus Chinook salmon abundance

During the period of unusually low Chinook salmon abundance and high resident killer whale mortality rates in the mid to late 1990s, there was very little field effort to document foraging behaviour and diet (Figure 3). As a result, there is no information available on the effect this reduced abundance of the whales' preferred prey may have had on prey selection or foraging behaviour. Since 2002, however, substantial effort has been dedicated to such studies and during this period the abundance of Chinook has fluctuated considerably. Table 5 presents salmonid prey species taken during foraging in each of these years, together with the total PSC index for that year. Despite a Chinook salmon abundance as high as 1.3 in 2003, and as low as 0.62 in 2007, no shift in prey species composition is evident. No significant difference was found when comparing the proportions of Chinook salmon to chum salmon taken in years of high Chinook abundance (2003-06) versus low Chinook abundance (2007-08) (Fisher's exact test, p = 0.16). Coho salmon comprised 10.5% of total kills in 2008, but 7 of the 10 samples were from a single day and there was no broad shift to this species.

ESTIMATED CONSUMPTION RATES OF CHINOOK SALMON

To assess the quantity of Chinook salmon consumed by resident killer whales, our analysis involved the following four general steps:

1) Estimate the metabolic needs of resident killer whales
2) Estimate the caloric value of Chinook salmon consumed by killer whales based on prey size and energy density
3) Estimate the proportion of the whales' diet that is composed of Chinook salmon
4) Estimate the total numbers of Chinook salmon consumed by the current northern and southern resident killer whale populations

Metabolic needs of resident killer whales

Estimation of the energetic requirements of killer whales requires accurate estimates of the body mass of individuals based on age and sex. Our methods generally follow those of Noren (in press), who has recently undertaken a similar assessment of the energetic requirements of southern resident killer whales. Whales less than 1 year old were discounted from these analyses as they were assumed to be completely dependent on their mother for nourishment. For whales 1-12 years old, sexual dimorphism is minimal so males and females were combined in the same categories based on age in years. For whales 13 years or older, separate categories were made for each sex by age in years to account for sexual dimorphism and thus the greater energetic requirements of adolescent and adult males as compared to females of the same age. Changes in energetic requirements for adult females during pregnancy and lactation were not accounted for in the calculations.

Estimated body mass values were then determined for each age and sex class. For whales aged ≤12 years, body mass was calculated (as in Noren, in press) using a formula that estimates body weight based on age in days for female killer whales in aquaria (Clark et al. 2000):

$$y = 2763.0\exp(\text{-}2.3\exp(\text{-}0.0007x)) \qquad (1)$$

where y = body mass in kg, x = age in days, and exp = e raised to the power of a given number. In Noren (in press), body masses for southern resident whales ≥13 years were estimated using maximum lengths of whales measured during the live-capture fishery in British Columbia and Washington state from 1962-1973 (Bigg and Wolman 1975). In order to estimate terminal adult body masses (≥20 years) for resident killer whales in this analysis, we used the average lengths for southern resident males (677 cm) and females (600 cm) 20 years of age or older, measured by Durban et al. (2009) using aerial photogrammetric techniques. Although measurements of killer whales are available from other sources, we chose these measurements as being the least biased and most applicable since they were taken from the same (in the case of southern residents) or a closely related (in the case of northern residents) population to the whales in this study. Body lengths were next converted to mass as in Noren (in press), using an equation developed by Bigg & Wolman (1975) from measurements of live-captured killer whales:

$$M = 0.000208L^{2.577} \qquad (2)$$

where M = body mass in kg, and L = length in cm. Once terminal body masses for adult whales ≥20 years had been determined (Table 6), the estimated body mass for each of the intervening age and sex-classes was calculated, assuming a constant yearly growth rate between the estimated mass at 12 years (calculated from equation of Clark et al. 2000) until terminal body mass was reached at 20 years (Table 6).

The daily prey energetic requirements (DPERs) of individual resident killer whales were calculated using formulae developed by Noren (in press):

$$DPER_{\min} = 413.2 M_b^{0.75} \quad (3)$$

$$DPER_{\max} = 495.9 M_b^{0.75} \quad (4)$$

where *DPER* = daily prey energy requirements in kcal/d and M_b = body mass in kg. Minimum and maximum values of DPER reflect the range of field metabolic rates estimated by Noren (in press) to be 5 to 6 times the basal metabolic rates predicted for mammals by Kleiber (1975). DPER values also take into account digestive efficiency for killer whales, which is estimated to be about 84.7% (Williams et al. 2004). Killer whales must therefore consume an additional 15.3% of their estimated field metabolic rate value each day in order to meet their energy requirements.

Results of DPER calculations for individuals by age- and sex-class are presented in Table 6 and Figure 17. The DPER values for individual whales were multiplied by the number of whales in each age/sex-class to obtain DPER values for the entire population. These calculations were done separately for northern (Table 7, Figure 18) and southern (Table 8, Figure 19) residents to account for differences in population size and demography. The resulting range of DPER values for the entire northern resident population (n = 241 animals ≥ 1 year old, 2008 census) is 34,025,721 - 40,835,806 kcal/day. DPER for the southern resident population (n = 85 animals ≥ 1 year old, 2008 census) is 12,753,120 - 15,305,596 kcal/day.

Energetic value of Chinook salmon consumed by resident killer whales

In order to convert DPER of resident killer whales into the number of Chinook salmon required to sustain each of the two populations, we first needed to determine the energetic value of Chinook salmon consumed by the whales. Because a range of age classes (and therefore sizes) of Chinook salmon is taken by resident killer whales, the caloric content of each prey item may vary widely. A profile of ages determined for Chinook killed by northern and southern residents is presented in Table 9. Energy content of different age classes of Chinook salmon was determined using average fork lengths by age from Ford and Ellis (2006) and a regression of fork length to energy content developed by O'Neill et al. (in prep.; Figure 20). By dividing DPER values by the estimated energy content per fish for each age class of Chinook salmon, we calculated the number of fish each of age class that each resident population would have to consume in order to meet their daily energy requirements, assuming a diet of 100% Chinook salmon. The results for northern residents are shown in Table 11 and southern residents in Table 12.

Estimated numbers of Chinook salmon consumed by resident killer whales

Assuming a 100% Chinook salmon diet, the estimated daily requirement for northern resident killer whales is 3063 - 3676 Chinook salmon, and for southern residents, 1338 - 1606 Chinook salmon. Our estimates for southern residents are higher than the 775 - 928 Chinook per day calculated by Noren (in press) for this population, likely as a result of our incorporating the age structure of Chinook salmon actually taken by killer whales into our estimates, rather than using an average mass and caloric value for adult fish.

Although prey sampling suggests that Chinook salmon may well represent 100% of the whales' diet at certain locations and times of the year, this is clearly not the case on an annual basis. Chinook is the predominant prey species observed in most regions (Figure 8) and during most months (Figure 7), but chum salmon are more important than Chinook during their spawning migration in October. Diet in winter is also poorly known, although Chinook salmon still appear to be targeted by resident whales from the few feeding events sampled. Although non-salmonids such as Pacific halibut, lingcod, and Dover sole (*Microstomus pacificus*) appear to comprise a relatively small component of the diet of resident killer whales based on prey sampling and stomach contents analysis (Ford et al. 1998; Ford and Ellis 2005; Hanson et al. in press), such demersal prey may be more important during winter. As a result, estimates of the annual consumption rate of Chinook salmon by resident killer whales are fraught with uncertainty.

Despite these uncertainties, it is useful to provide some estimates of the potential range of annual consumption rates of Chinook salmon by resident killer whales to assess its magnitude with respect to coast-wide Chinook abundance and harvest levels in fisheries. Tables 13 and 14 present estimates of the daily and annual Chinook salmon consumption by northern and southern resident killer whales, respectively, at levels between 50 and 100% diet composition. At the 70% level, which corresponds to the overall proportion of Chinook salmon in prey samples identified to species (Table 2), northern residents would require 782,482 to 939,092 Chinook per year and southern residents 341,917 to 410,350 per year. At this predation level, the two populations at their current abundance would consume a total of about 1,124,000 to 1,350,000 Chinook salmon annually.

Key foraging habitats for resident killer whales are the waters of eastern Queen Charlotte Strait and Johnstone Strait (northern residents) and the waters of the Strait of Georgia, Juan de Fuca Strait, and Puget Sound (southern residents) (Ford et al. 2000; Krahn et al. 2004). These areas have been designated as Critical Habitats (CH) under the Species-at-Risk Act in Canada (for waters in Canada's jurisdiction) and the Endangered Species Act in the U.S. (for U.S. waters) (Ford 2006; NMFS 2006; Fisheries and Oceans Canada 2008). The whales use these CH areas predominantly during summer and fall, and their occurrence coincides with that of migrating Chinook salmon (Ford and Ellis 2006; Hanson et al. in press). Both of these areas are also used extensively for commercial and recreational salmon fishing, the latter of which generally targets Chinook salmon. We assessed the probable numbers of Chinook salmon taken by killer whales in CH during July-August, as these are the peak months of resident killer whale occurrence and their diet is predominantly Chinook salmon during this period (87% of prey samples in northern resident CH (this study) and 91% of prey samples in southern resident CH (Hanson et al. in press).

To estimate the quantity of Chinook salmon preyed upon by resident killer whales in their Critical Habitats, we calculated the number of days that whales are typically present in the two CH areas during July-August, and then multiplied this by the DPER values provided in Table 7 according to the numbers and age- and sex-class of killer whales present on those days. Total DPER of whales each day was then converted to number of Chinook salmon as in Tables 11 and 12. It was assumed that 90% of the whales' diet was composed of Chinook salmon, which corresponds closely to the proportion of Chinook in identified prey samples during this period for northern residents (87%, this study) and southern residents (91%, Hanson et al. in press). It should be noted that Chinook may represent more than 90% of the whales' energetic requirements during this period, as Chinook salmon are larger and have higher energy densities per fish than do fish making up the remaining 10% of prey species (coho, pink, sockeye, and chum salmon).

The entire southern resident population tends to spend the July-August period within Canadian and US waters designated as CH in their respective jurisdictions. Hauser et al. (2007) noted that the population can be found in inshore waters of eastern Juan de Fuca Strait, the Strait of Georgia and Puget Sound on 80% of summer days. It is probable that on the majority of the remaining 20% of days, the whales mostly use western Juan de Fuca Strait, which is within the CH boundaries, or areas on Swiftsure Bank, which is near the entrance to Juan de Fuca Strait but outside CH (Ford 2006; Cetacean Research Program, Pacific Biological Station, unpubl. data). We thus assumed that the southern resident population is present in CH waters on a minimum of 90% of days in July-August. The resulting estimated Chinook salmon requirement for southern residents in their CH (in both U.S. and Canadian waters) during July-August is 1204 to 1445 fish per day, or approximately 67,000 to 81,000 fish over the two month period.

Estimating Chinook salmon requirements of northern residents in their CH was not as straightforward as for southern residents because only a portion of the population utilizes these waters, even during the peak months of July-August. As a result, we calculated an average total number of 'whale days' (number of whales present in CH per day) for the July-August period based on whale occurrence during these months in 1998-2008. An average of 32.1 whales (± 2.9 SE) were present in CH per day during July-August, 1998-2008, which represents 14.5% of the average 222 animals in the population across those years. These 'whale days' were then partitioned according to the average demographic composition for resident killer whales (Olesiuk et al. 2005), the mean DPER for these age- and sex-classes was applied, and the number of Chinook salmon required was calculated as described above. This analysis resulted in an estimated Chinook salmon requirement for northern residents in their CH during July-August of 419-503 fish per day, or approximately 26,000 to 31,000 fish over the two month period.

The estimates of total annual Chinook salmon predation provided in Tables 13 and 14 reflect the requirements of northern and southern resident killer whales in 2008. As continued population growth is considered a priority in the Recovery Strategy for Resident Killer Whales, we have estimated the potential future requirements for Chinook salmon by the two populations assuming optimal growth over the next decade. For this analysis, we assumed an annual growth of 2.6%, the rate observed in the populations during the period of unrestrained growth between 1973 and 1995, and an average age- and sex-class composition described by Olesiuk et al. (2005). The annual increase in Chinook salmon requirements, assuming a 70% diet composition, over the period 2008-2018, is shown in Figure 21. By 2018, the total abundance of resident killer whales would be 445 (332 northern and 113 southern residents), and their annual requirement for Chinook salmon would be in the range of 1,480,000 to 1,780,000 fish.

DISCUSSION

Since our last assessment of resident killer whale diet (Ford and Ellis 2005, 2006), we have doubled the dataset on salmonids identified from feeding events, from 396 to 806. Larger sample sizes are now available for most coastal regions, especially for important feeding areas for southern residents off southwestern Vancouver Island. Although few in number, we now have prey samples collected from resident feeding events during the winter months. This much larger dataset provides further support for our past conclusions: that Chinook salmon is clearly the preferred and most important prey of resident killer whales and that the smaller pink and sockeye salmon are not significant prey despite their greater seasonal abundance. Chum salmon is also an important species, particularly during the fall as these fish migrate through inshore waters. Coho salmon make up a small portion of the whales' catches in some regions, but only represent 2.5% of prey items overall. Of the 7 feeding events sampled in December-March, 5 were Chinook salmon, 1 was a chum salmon, and 1 was a steelhead salmon.

Chinook salmon are not only numerically the most frequently consumed prey species in most months, they are also generally larger in body than other salmonids. Killer whales appear to select for large Chinook, and so most prey are 4-5 year old fish which have mean body masses of 8-13 kg (Ford and Ellis 2005). This is considerably larger than mature chum salmon (4.0-5.5 kg) and more than double the typical size of coho, pink and sockeye salmon (Ford et al. 1998). As Chinook salmon also tend to have the highest lipid content of salmonids, the energy content per fish is considerably greater than other salmonid species.

The updated assessment of the relationship between mortality rates of resident killer whales and coast-wide Chinook salmon abundance has continued to show that there is a significant long-term negative correlation. The correlation is not as strong in recent years, due primarily to low mortality and continued growth in the northern resident population despite relatively low Chinook abundance since 2006 (Pacific Salmon Commission 2008). On-going annual monitoring will determine whether this trend continues.

Our observations of foraging behaviour of resident killer whales suggest that fluctuations in coast-wide Chinook salmon availability have little effect on prey selection, at least during the summer months. Further studies are needed to quantitatively assess the balance between the energetic costs of foraging in low Chinook density conditions and the caloric value of prey obtained.

Genetic stock identification of Chinook salmon prey samples indicates that resident killer whales consume fish originating from a wide variety of coastal regions, some quite distant from the place of capture. For example, almost one-quarter of Chinook taken by residents off the northern Queen Charlotte Islands originated from the Columbia River, the mouth of which is over 1000 km to the south. This is consistent with northern British Columbia troll catches where the predominant stock groupings were South Thompson, followed by North and Central Oregon and Upper Columbia Summer and Fall (Winther and Beacham in press). Stocks from the Fraser River system were represented most frequently in feeding events in most parts of the coast, and comprised 58% of samples overall. This is not unexpected, given that the Fraser River system is the largest producer of Chinook salmon in Canada (Parken et al. 2008). The predominance of Fraser River Chinook was particularly notable in samples collected from feeding events in Critical Habitat areas off northeastern and southwestern Vancouver Island. Fraser River stock regions comprised 64% of Chinook consumed by northern residents in their Critical Habitat, and 75% of Chinook taken by southern residents in their Critical Habitat. South Thompson was the most prevalent of the Fraser River stock regions.

Although the Fraser River system may be the most important source of Chinook salmon for resident killer whales generally, other stock regions may also be important at certain times of year. Chinook originating from smaller, local river systems were significant prey of resident killer whales along the north and central mainland coasts. Many of the northern resident groups feed in these areas early in the summer, before moving south to the Critical Habitat area off northeastern Vancouver Island later in the summer (Ford 2006). Thus, whales may rely on a range of Chinook stocks at different times of year and in different parts of the coast. The results presented here are preliminary; further effort is needed to determine the seasonal importance of particular Chinook salmon stocks to whales in different geographic areas, and the conservation status of these stocks should be evaluated in this context.

Our assessment of the quantity of Chinook salmon needed to sustain current resident killer whale populations indicates that a substantial number of fish may be consumed each year. Although there is considerable uncertainty in the actual proportion of the whales' year-round diet that is composed of Chinook, a reasonable conservative estimate is that about 70% of their nutritional needs may be supplied by this species. If this is the case, consumption by the current resident populations may be over 1,000,000 fish per annum (range of estimate 1,124,400 to 1,349,443). This is roughly equivalent to the total combined commercial and recreational harvest of Chinook salmon in marine waters between Southeast Alaska and Oregon during 2006 (Pacific Salmon Commission 2007; R. McNicol, Pacific Biological Station, pers. comm.).

If resident killer whales are near the carrying capacity of their habitat and if that capacity is determined by the availability of Chinook salmon, as the correlation between mortality and Chinook abundance implies (Ford et al. 2005), then greater numbers of Chinook salmon will be required to provide for recovery. Assuming that resident killer whale populations grow at their maximum rate of 2.6% over the next 10 years, an estimated 1.5-1.8 million Chinook may be needed to support these populations each year by 2018.

Critical Habitats that have been designated for northern and southern resident whales under Canada's Species at Risk Act and the U.S. Endangered Species Act are prime feeding areas during the peak of the summer salmon migration period. It is thus imperative that sufficient prey resources be available to the whales in these areas at this important time of year. Extensive prey sampling in Critical Habitats suggests that Chinook salmon represents about 90% of resident killer whale diet during July-August. Southern residents foraging in Critical Habitat (in Canadian and U.S. waters combined) would thus require approximately 1200 - 1400 Chinook salmon per day, or roughly 67,000 - 81,000 over the two month period. On average, only 14.5% of the northern resident population uses their designated Critical Habitat on a daily basis during July-August. As a result, Chinook salmon requirements in this area are less than for southern resident Critical Habitat: about 420 - 500 fish per day, or 26,000 - 31,000 total over the two months. As the great majority of Chinook taken in both Critical Habitat areas are from Fraser River stocks, it can be concluded that adequate Chinook production in this river system is essential to the continued function of resident killer whale Critical Habitats.

It should also be noted that estimates of Chinook salmon consumption rates are based on the whales' predicted daily prey energy requirements. However, it may well be that during certain times of year, especially during the summer Chinook salmon migration, the whales feed at rates that surpass their daily requirements and, in so doing, create blubber reserves that are needed during periods of reduced prey availability. Further research on foraging behaviour and prey selection, particularly in winter and spring, is necessary to better understand the year-round prey composition, feeding rates, and energetics of resident killer whales.

ACKNOWLEDGEMENTS

We thank the many research colleagues and volunteers who helped in the collection of data reported here, including R. Abernethy, E. Ashe, K. Balcomb, L. Barrett-Lennard, J. Borrowman, L. Dalla Rosa, V. Deecke, M., B., & R. De Roos, J. Durban, B. Falconer, B. Gisborne, J. Hildering, M. Malleson, C. McMillan, L. Nichol, B. Paterson, L. Spaven, J. Towers, J. Watson, R. Williams, and H. Yurk. K. Balcomb, Center for Whale Research, provided updated demographic data for southern resident killer whales. S. MacLellan and staff in the Sclerochronology Lab at the Pacific Biological Station (PBS) undertook species identification and ageing, and the laboratory staff at the Molecular Genetics Lab at PBS conducted the DNA analyses. D. Noren, Northwest Fisheries Science Center, NOAA, kindly allowed us to refer to her manuscript on energetics of southern resident killer whales. R. Abernethy prepared the maps and M. Boogaards helped with data entry. We appreciate the assistance of G. Brown, R. McNicol, and C. Parken in providing data and information on Chinook salmon.

LITERATURE CITED

Altmann, J. 1974. Observational study of behavior: sampling methods. Behaviour 49: 227-265.

Barrett-Lennard, L.G. 2000. Population structure and mating patterns of killer whales (*Orcinus orca*) as revealed by DNA analysis. Ph.D. Thesis, University of British Columbia, Vancouver, BC. xi + 97 p.

Beacham, T.D., Candy, J.R., Supernault, K.J., Wetklo, M., Deagle, B., Labaree, K., Irvine, J.R., Miller, K.M., Nelson, R.J., and Withler, R.E. 2003. Evaluation and application of microsatellites for population identification of Fraser River chinook salmon (*Oncorhynchus tshawytscha*). Fish. Bull. 101: 243-259.

Beacham, T.D., Candy, J.R., Jonsen, K.L., Supernault, J., Wetklo, M., Deng, L., Miller, K.M., Withler, R.E., and Varnavskaya, N. 2006. Estimation of stock composition and individual identification of Chinook salmon across the Pacific Rim using microsatellite variation. Trans. Amer. Fish. Soc. 135: 861-888.

Bigg, M.A. 1982. An assessment of killer whale (*Orcinus orca*) stocks off Vancouver Island, British Columbia. Rep. Int. Whal. Commn. 32: 655-666.

Bigg, M.A., Ellis, G.M., Ford, J.K.B., and Balcomb, K.C. 1987. Killer Whales: A study of their identification, genealogy and natural history in British Columbia and Washington State. Phantom Press and Publishers, Nanaimo, BC. 79 p.

Bigg, M.A., MacAskie, I.B., and Ellis, G. 1976. Abundance and movements of killer whales off eastern and southern Vancouver Island with comments on management. Unpubl. Rep., Arctic Biological Station, Dept. of Fisheries and Environment, Ste Anne-de-Bellevue, QC.

Bigg, M.A., Olesiuk, P.F., Ellis, G.M., Ford, J.K.B., and Balcomb, K.C. III. 1990. Social organization and genealogy of resident killer whales (*Orcinus orca*) in the coastal waters of British Columbia and Washington State. Rep. Int. Whal. Commn. Special Issue 12: 383-405.

Bigg, M.A., and Wolman, A.A. 1975. Live-capture killer whale (*Orcinus orca*) fishery, British Columbia and Washington, 1962-73. J. Fish. Res. Bd Can. 32: 1213-1221.

Clark, S.T., Odell, D.K., and Lacinak, C.T. 2000. Aspects of growth in captive killer whales (*Orcinus orca*). Mar. Mamm. Sci. 16: 110-123.

Dahlheim, M.E., Schulman-Janiger, A., Black, N., Ternullo, R., Ellifrit, D., and Balcomb, K.C. III. 2008. Eastern temperate North Pacific offshore killer whales (*Orcinus orca*): occurrence, movements, and insights into feeding ecology. Mar. Mamm. Sci. 24: 719-729.

Durban, J., Fearnbach, H., Ellifrit, D. and Balcomb, K. 2009. Size and body condition of southern resident killer whales. Contract report to the Northwest Regional Office, National Marine Fisheries Service. Order number AB133F08SE4742, Requisition number NFFP5000-8-43300. 21 p.

Fisheries and Oceans Canada. 2008. Recovery Strategy for the Northern and Southern Resident Killer Whales (*Orcinus orca*) in Canada. *Species at Risk Act* Recovery Strategy Series, Fisheries & Oceans Canada, Ottawa, ON. ix + 80 p.

Ford, J.K.B. 1989. Acoustic behaviour of resident killer whales (*Orcinus orca*) off Vancouver Island, British Columbia. Can. J. Zool. 67: 727-745.

Ford, J.K.B. 1991. Vocal traditions among resident killer whales (*Orcinus orca*) in coastal waters of British Columbia. Can. J. Zool. 69: 1454-1483.

Ford, J.K.B. 2006. An assessment of critical habitats of resident killer whales in waters off the Pacific coast of Canada. DFO Can. Sci. Advis. Sec. Res. Doc. 2006/072. iv + 34 p.

Ford, J.K.B., and Ellis, G.M. 2005. Prey selection and food sharing by fish-eating 'resident' killer whales (*Orcinus orca*) in British Columbia. DFO Can. Sci. Advis. Sec. Res. Doc. 2005/041. ii + 30 p.

Ford, J.K.B., and Ellis, G.M. 2006. Selective foraging by fish-eating killer whales *Orcinus orca* in British Columbia. Mar. Ecol. Prog. Ser. 316: 185-199.

Ford, J.K.B., Ellis, G.M. and Balcomb, K.C. 2000. Killer Whales: The natural history and genealogy of *Orcinus orca* in British Columbia and Washington, Second edition. UBC Press and University of Washington Press, Vancouver, BC and Seattle, WA. 104 p.

Ford, J.K.B., Ellis, G.M., Barrett-Lennard, L.G., Morton, A.B., Palm, R.S., and Balcomb, K.C. III. 1998. Dietary specialization in two sympatric populations of killer whales (*Orcinus orca*) in coastal British Columbia and adjacent waters. Can. J. Zool. 76: 1456-1471.

Ford, J.K.B., Ellis, G.M., and Olesiuk, P.F. 2005. Linking prey and population dynamics: Did food limitation cause recent declined of 'resident' killer whales (*Orcinus orca*) in British Columbia? DFO Can. Sci. Advis. Sec. Res. Doc. 2005/042. ii + 27 p.

Ford, J.K.B, Ellis, G.M., Olesiuk, P.F., and Balcomb, K.C. 2010. Linking killer whale survival and prey abundance: food limitation in the oceans' apex predator? Biol. Lett. 6:139-142. Published on-line before print September 15, 2009.

Guinet, C. 1990. Sympatrie des deux catégories d'orques dans le détroit de Johnstone, Colombie Britannique. Rev. Ecol. (Terre Vie) 45(1): 25-34.

Hanson, M.B., Baird, R.W., Ford, J.K.B., Hempelmann-Halos, J., Van Doornik, D., Candy, J.R., Emmons, C.K., Schorr, G.S., Gisborne, B., Ayres, K.L., Wasser, S.K., Balcomb, K.C., Balcomb-Bartok, K., Sneva, J.G., and Ford, M.J. In press. Species and stock identification of prey selected by endangered “southern resident” killer whales in their summer range. End. Species Res.

Hauser, D.D.W., Logsdon, M.G., Holmes, E.E., VanBlaricom, G.R., and Osborne, R.W. 2007. Summer distribution patterns of southern resident killer whales *Orcinus orca*: core areas and spatial segregation of social groups. Mar. Ecol. Prog. Ser. 351: 301-310.

Healey, M.C. 1991. Life history of chinook salmon (*Oncorhynchus tshawytscha*). *In* Pacific Salmon Life Histories. Edited by C. Groot and L. Margolis. UBC Press, Vancouver, BC. pp. 313-393.

Heimlich-Boran, J. 1986. Fishery correlations with the occurrence of killer whales in greater Puget Sound. *In* Behavioral Biology of Killer Whales. Edited by B.C. Kirkevold and J.S. Lockard. Alan R. Liss, Inc., New York, NY. pp. 113-131.

Kleiber, M. 1975. The Fire of Life: An Introduction to Animal Energetics, Second edition. Robert E. Kreiger Publishing, Huntington, NY. 478 p.

Krahn, M.M., Ford, M.J., Perrin, W.F., Wade, P.R, Angliss, R.P., Hanson, M.B., Taylor, B.L., Ylitalo, G.M., Dahlheim, M.E., Stein, J.E., and Waples, R.S. 2004. 2004 status review of southern resident killer whales (*Orcinus orca*) under the Endangered Species Act. U.S. Dept. of Commerce, NOAA Tech. Memo. NMFSNWFSC-62. xviii + 73 p.

MacLellan, S.E. 2004. Guide for sampling structures used in age determination of Pacific salmon. Pacific Biological Station, Fisheries and Oceans Canada, Nanaimo, British Columbia V9T 6N7.

Mann, J. 1999. Behavioral sampling methods for cetaceans: a review and critique. Mar. Mamm. Sci. 15(1): 102-122.

Neaves, P.I., Wallace, C.G., Candy, J.R., and Beacham. T.D. 2005. CBayes: Computer program for mixed stock analysis of allelic data. Version v5.01. Free program distributed by the authors over the internet from http://www.pac.dfo-mpo.gc.ca/sci/mgl/Cbayes_e.htm

Nichol, L.M. and Shackleton, D.M. 1996. Seasonal movements and foraging behaviour of northern resident killer whales (*Orcinus orca*) in relation to the inshore distribution of salmon (*Oncorhynchus* spp.) in British Columbia. Can. J. Zool. 74: 983-991.

NMFS. 2005. Endangered and Threatened Wildlife and Plants: Endangered Status for Southern Resident Killer Whales, Federal Register, 70 FR 69903.

NMFS. 2006. Designation of critical habitat for southern resident killer whales: Biological Report, October 2006. 44 p. Available at http://www.nwr.noaa.gov/Marine-Mammals/Whales-Dolphins-Porpoise/Killer-Whales/ESA-Status/upload/SRKW-CH-Bio-Rpt.pdf

Noren, D.P. In press. Estimated field metabolic rates and prey requirements of resident killer whales. Mar. Mamm. Sci.

Olesiuk, P.F., Bigg, M.A., and Ellis, G.M. 1990. Life history and population dynamics of resident killer whales (*Orcinus orca*) in the coastal waters of British Columbia and Washington State. Rep. Int. Whal. Commn. Special Issue 12: 209-242.

Olesiuk, P.F., Ellis, G.M. and Ford, J.K.B. 2005. Life history and population dynamics of northern resident killer whales (*Orcinus orca*) in British Columbia. DFO Can. Sci. Advis. Sec. Res. Doc. 2005/045. iv + 75 p.

O'Neill, S.M., Ylitalo, G.M., West, J.E., Bolton, J., Sloan, C.A. and Krahn, M.M. In prep. Regional patterns of persistent organic pollutants in five Pacific salmon species (*Oncorhynchus* spp.) and their contributions to contaminant levels in northern and southern resident killer whales (*Orcinus orca*). NOAA, National Marine Fisheries Service, Northwest Fisheries Science Center.

Pacific Salmon Commission. 2007. 2007 annual report of catches and escapements, exploitation rate analysis and model calibration. Joint Chinook Technical Committee Report TCCHINOOK (07)-2.

Pacific Salmon Commission. 2008. 2008 annual report of catches and escapements, exploitation rate analysis and model calibration. Joint Chinook Technical Committee Report TCCHINOOK (08)-2.

Parken, C.K., Candy, J.R., Irvine, J.R., and Beacham, T.D. 2008. Genetic and coded wire tag results combine to allow more-precise management of a complex Chinook salmon aggregate. N. Am. J. Fish. Manage. 28(1): 328-340.

Ward, E.J., Holmes, E.E., and Balcomb, K.C. 2009. Quantifying the effects of prey abundance on killer whale reproduction. J. Appl. Ecol. 46(3): 632-640.

Wiles, G. J. 2004. Washington State status report for the killer whales. Washington Department of Fish and Wildlife, Olympia, WA. 106 p.

Williams, T.M., Estes, J.A., Doak, D.F., and Springer, A.M. 2004. Killer appetites: assessing the role of predators in ecological communities. Ecology 85(12): 3373-3384.

Winther, I., and Beacham, T.D. In press. The application of Chinook salmon stock composition data to management of the Queen Charlotte Islands troll fishery, 2006. In C. C. Krueger, and C. E. Zimmerman, editors. Sustainability of the Arctic-Yukon-Kuskokwim salmon fisheries: what do we know about salmon ecology, management, and fisheries? American Fisheries Society, Symposium XX, Bethesda, Maryland.

TABLES

Table 1. Evidence for 937 feeding events by resident killer whales documented during 1974-2009.

Evidence of predation	Number of events	%
Observation only	78	8.3
Both tissue and scale samples	263	28.1
Tissue samples only	54	5.8
Scale samples only	542	57.9
Total	937	100

Table 2. Species composition of fish killed by resident killer whales in 937 feeding events during 1974-2009 in different B.C. coastal regions. Species identity was determined by scale analysis or from DNA evidence. Also shown is the frequency distribution (%) of different salmonid species among the 806 salmonid prey items identified to species. PFMA refers to the Pacific Fisheries Management Areas of Fisheries & Oceans Canada. UnSa are salmonids that were observed as prey in the field but not sampled for species identification, or salmonids that could not be identified to species. UnFi are fish that could not be positively identified to species and could include either salmonids or non-salmonids.

Region	PFMA	*n*	Species								
			Chinook	Chum	Coho	Pink	Sockeye	Steelhead	Other	UnSa	UnFi
QC Island	1-2	40	36	0	0	0	0	0	2[a]	5	3
North coast	3-6	80	54	20	0	0	0	0	0	5	1
Central coast	7-11	72	50	6	1	1	0	0	0	11	3
NE Vancouver Island	12-13	507	247	159	7	13	2	0	6[b]	62	10
SE Vancouver Island	14-19, 28-29	61	36	5	2	0	1	3	1[c]	12	3
W Vancouver Island	20-27	171	146	5	10	0	1	1	1[d]	2	4
Total		937	569	195	20	14	4	4	10	97	24
% of identified salmonids			71.0	23.8	2.5	1.7	0.5	0.5			

[a] – 1 Pacific halibut, 1 herring
[b] – 1 yelloweye rockfish, 4 sardine, 1 herring
[c] – 1 quillback rockfish
[d] – 1 sablefish

AR031694

Table 3. Salmonid species sampled from resident killer whale feeding events by month, 1974-2009. n = 806 feeding events.

Month	Species						Total
	Chinook	Chum	Coho	Pink	Sockeye	Steelhead	
Jan	4	0	0	0	0	0	4
Feb	1	0	0	0	0	0	1
Mar	1	0	0	0	0	0	1
Apr	0	0	0	0	0	0	0
May	21	0	0	0	0	0	21
Jun	96	15	0	0	0	0	111
Jul	159	16	1	1	3	1	181
Aug	212	4	5	11	1	0	233
Sep	60	59	10	2	0	1	133
Oct	12	96	4	0	0	1	112
Nov	3	4	0	0	0	0	7
Dec	0	1	0	0	0	1	2
Total	569	195	20	14	4	4	806

Table 4. Ages of 634 salmonids (identified to species level) determined from scales collected from feeding events by resident killer whales during 1974-2009. Age classes are given according to the European system: the years spent in freshwater after hatching preceed the years in salt water, separated by a decimal point.

Species	n	European Age Class											
		0.1	0.2	0.3	0.4	0.5	1.1	1.2	1.3	1.4	1.5	2.1	2.2
Chinook	431	1	41	179	101	3	2	26	55	20	2	0	1
Chum	180	0	2	122	52	4	0	0	0	0	0	0	0
Coho	19	7	0	0	0	0	11	0	0	0	0	1	0
Sockeye	4	0	0	0	0	0	0	2	2	0	0	0	0

Table 5. Salmonid species sampled from resident killer whale feeding events during May-September, 2003-08. PSC Index is the total (all regions) Chinook abundance index from the Pacific Salmon Commission. Samples for October-November are not included due to the preponderance of chum salmon in the whales' diet at that time of year, and the unequal sampling effort during these months in different years.

Year	PSC Index	Species						Total
		Chinook	Chum	Coho	Pink	Sockeye	Steelhead	
2003	1.3	59	13	1	0	0	0	73
2004	1.16	137	17	3	0	0	0	157
2005	0.94	38	22	0	0	0	0	60
2006	0.76	66	15	0	0	2	0	83
2007	0.62	102	8	1	0	0	0	111
2008	0.68	69	13	10	1	1	1	95
Total		471	88	15	1	3	1	579

Table 6. Estimated body masses and minimum and maximum Daily Prey Energy Requirements (DPER) for individual resident killer whales, based on age- and sex-class membership.

Age- and Sex-Class	Age (days)	Body Mass (kg)	Min DPER (kcal/day)	Max DPER (kcal/day)
age 1	365	465	41396	49681
age 2	730	695	55949	67146
age 3	1095	949	70650	84790
age 4	1460	1208	84645	101587
age 5	1825	1455	97359	116845
age 6	2190	1682	108510	130228
age 7	2555	1881	118014	141634
age 8	2920	2051	125941	151147
age 9	3285	2194	132447	158956
age 10	3650	2311	137720	165284
age 11	4015	2406	141944	170354
age 12	4380	2482	145303	174385
age 13, male	4745	2684	154076	184914
age 13, female	4745	2547	148143	177793
age 14, male	5110	2886	162688	195249
age 14, female	5110	2612	150970	181186
age 15, male	5475	3088	171151	205406
age 15, female	5475	2677	153779	184557
age 16, male	5840	3290	179477	215398
age 16, female	5840	2742	156571	187908
age 17, male	6205	3491	187676	225238
age 17, female	6205	2807	159346	191239
age 18, male	6570	3693	195757	234937
age 18, female	6570	2872	162106	194551
age 19, male	6935	3895	203728	244504
age 19, female	6935	2937	164850	197844
age ≥20, male	≥7300	4097	211597	253947
age ≥20, female	≥7300	3002	167562	201098

Table 7. Population DPERs (kcal/day) calculated from demographic information (2008 census) for northern resident killer whales (n = 241, aged ≥1 yr).

Age- and Sex-Class	# whales/ class	Min DPER (kcal/day)	Max DPER (kcal/day)	Population Min DPER	Population Max DPER
age 1	11	41396	49681	455358	546495
age 2	15	55949	67146	839230	1007197
age 3	14	70650	84790	989095	1187058
age 4	13	84645	101587	1100388	1320626
age 5	8	97359	116845	778869	934756
age 6	9	108510	130228	976594	1172055
age 7	4	118014	141634	472057	566537
age 8	4	125941	151147	503763	604589
age 9	9	132447	158956	1192026	1430604
age 10	5	137720	165284	688599	826418
age 11	8	141944	170354	1135556	1362832
age 12	5	145303	174385	726515	871924
age 13, male	3	154076	184914	462228	554741
age 13, female	1	148143	177793	148143	177793
age 14, male	2	162688	195249	325375	390497
age 14, female	5	150970	181186	754849	905929
age 15, male	0	171151	205406	0	0
age 15, female	2	153779	184557	307558	369114
age 16, male	3	179477	215398	538430	646194
age 16, female	1	156571	187908	156571	187908
age 17, male	2	187676	225238	375351	450476
age 17, female	6	159346	191239	956078	1147433
age 18, male	2	195757	234937	391514	469873
age 18, female	6	162106	194551	972635	1167303
age 19, male	2	203728	244504	407457	489008
age 19, female	2	164850	197844	329699	395687
age ≥20, male	33	211597	253947	6982705	8380261
age ≥20, female	66	167562	201098	11059076	13272498
Total Population	*241*	*n/a*	*n/a*	*34025721*	*40835806*

Table 8. Population DPERs (kcal/day) calculated from demographic information (2008 census) for southern resident killer whales (n = 85, aged ≥1 yr).

Age- and Sex-Class	# whales/ class	Min DPER (kcal/day)	Max DPER (kcal/day)	Population Min DPER	Population Max DPER
age 1	3	41396	49681	124188	149044
age 2	1	55949	67146	55949	67146
age 3	4	70650	84790	282599	339159
age 4	3	84645	101587	253936	304760
age 5	4	97359	116845	389435	467378
age 6	2	108510	130228	217021	260457
age 7	2	118014	141634	236029	283269
age 8	1	125941	151147	125941	151147
age 9	0	132447	158956	0	0
age 10	2	137720	165284	275439	330567
age 11	0	141944	170354	0	0
age 12	3	145303	174385	435909	523154
age 13, male	2	154076	184914	308152	369827
age 13, female	3	148143	177793	444430	533380
age 14, male	0	162688	195249	0	0
age 14, female	1	150970	181186	150970	181186
age 15, male	3	171151	205406	513453	616218
age 15, female	2	153779	184557	307558	369114
age 16, male	3	179477	215398	538430	646194
age 16, female	0	156571	187908	0	0
age 17, male	2	187676	225238	375351	450476
age 17, female	1	159346	191239	159346	191239
age 18, male	1	195757	234937	195757	234937
age 18, female	2	162106	194551	324212	389101
age 19, male	2	203728	244504	407457	489008
age 19, female	0	164850	197844	0	0
age ≥20, male	6	211597	253947	1269583	1523684
age ≥20, female	32	167562	201098	5361976	6435150
Total Population	*85*	*n/a*	*n/a*	*12753120*	*15305596*

Table 9. Age profile of Chinook salmon killed by northern (n = 318; predation samples collected from 1975-2008) and southern (n = 159; collected from 1974-2008) resident killer whales.

Chinook Age (years)	Northern Residents		Southern Residents	
	n	%	n	%
2	1	0.3	6	3.8
3	36	11.3	15	9.4
4	153	48.1	69	43.4
5	111	34.9	60	37.7
6	16	5.0	7	4.4
7	1	0.3	2	1.3
Total	*318*	*100*	*159*	*100*

Table 10. Average fork lengths (mm) and energy content (kcal/fish) for Chinook salmon by age-class membership (from Ford and Ellis 2006 and O'Neill et al. in prep.).

Age (year)	Length (mm)	Energy content (kcal/fish)
2	425 ± 1.19	1601.5
3	581 ± 2.14	4249.9
4	808 ± 3.43	11898.3
5	939 ± 4.21	19018.5
6	961 ± 15.0	20444.2

Table 11. Proportion of DPER (kcal/day) for northern resident killer whales obtained from each age class of Chinook salmon, based on an assumed diet composition of 100% Chinook. Minimum (min) and maximum (max) number of Chinook consumed was calculated based on values of kcal/fish obtained from a regression of fork length and energy content (O'Neill et al. in prep.; Table 10).

Chinook Age (years)	% of kills	Min DPER	Max DPER	Min fish per day	Max fish per day
2	0.31	106,999	128,414	66.8	80.2
3	11.32	3,851,968	4,622,921	906.4	1087.8
4	48.11	16,370,866	19,647,416	1375.9	1651.3
5	34.91	11,876,903	14,254,008	624.5	749.5
6	5.03	1,711,986	2,054,632	83.7	100.5
7*	0.31	106,999	128,414	5.2	6.3
Total	*100*	*34,025,721*	*40,835,806*	*3063*	*3676*

*As no length data were available for 7 yr old Chinook, the 6 yr old fork length measurement was used.

Table 12. Proportion of DPER (kcal/day) for southern resident killer whales obtained from each age class of Chinook salmon, based on an assumed diet composition of 100% Chinook. Minimum (min) and maximum (max) number of Chinook consumed was calculated based on values of kcal/fish obtained from a regression of fork length and energy content (O'Neill et al. in prep.; Table 10).

Chinook Age (years)	% of kills	Min DPER	Max DPER	Min fish per day	Max fish per day
2	3.8	484,619	581,613	302.6	363.2
3	9.4	1,198,793	1,438,726	282.1	338.5
4	43.4	5,534,854	6,642,628	465.2	558.3
5	37.7	4,807,926	5,770,210	252.8	303.4
6	4.4	561,137	673,446	27.4	32.9
7*	1.3	165,791	198,973	8.1	9.7
Total	*100*	*12,753,120*	*15,305,596*	*1338*	*1606*

*As no length data were available for 7 yr old Chinook, the 6 yr old fork length measurement was used.

Table 13. Minimum and maximum DPERs (kcal/day) supplied by Chinook salmon depending on diet composition, and the resulting numbers of Chinook per day and per year required by the northern resident killer whale population (n = 241 whales).

% Chinook in diet	Min DPER	Max DPER	Min fish/d	Max fish/d	Min fish/yr	Max fish/yr
100	34,025,721	40,835,806	3063	3676	1,117,832	1,341,561
90	30,623,149	36,752,226	2756	3308	1,006,049	1,207,404
70	23,818,005	28,585,064	2144	2573	782,482	939,092
50	17,012,861	20,417,903	1531	1838	558,916	670,780

Table 14. Minimum and Maximum DPERs (kcal/day) supplied by Chinook salmon (depending on diet composition), and the resulting numbers of Chinook per day and per year required by the southern resident killer whale population (n = 85 whales).

% Chinook in diet	Min DPER	Max DPER	Min fish/d	Max fish/d	Min fish/yr	Max fish/yr
100	12,753,120	15,305,596	1338	1606	488,453	586,215
90	11,477,808	13,775,036	1204	1445	439,608	527,593
70	8,927,184	10,713,917	937	1124	341,917	410,350
50	6,376,560	7,652,798	669	803	244,227	293,107

FIGURES

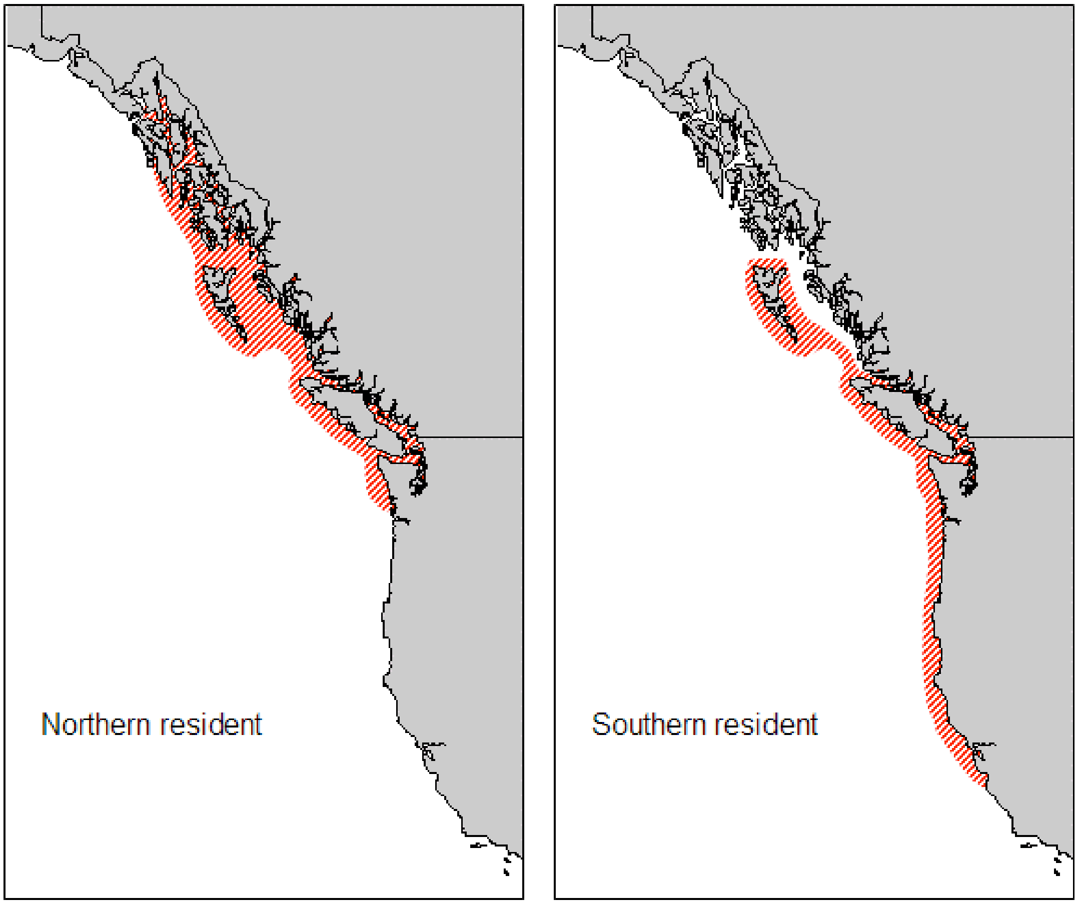

Figure 1. Ranges of northern (left panel) and southern (right panel) populations of resident killer whales. The two populations are not known to associate despite overlapping ranges.

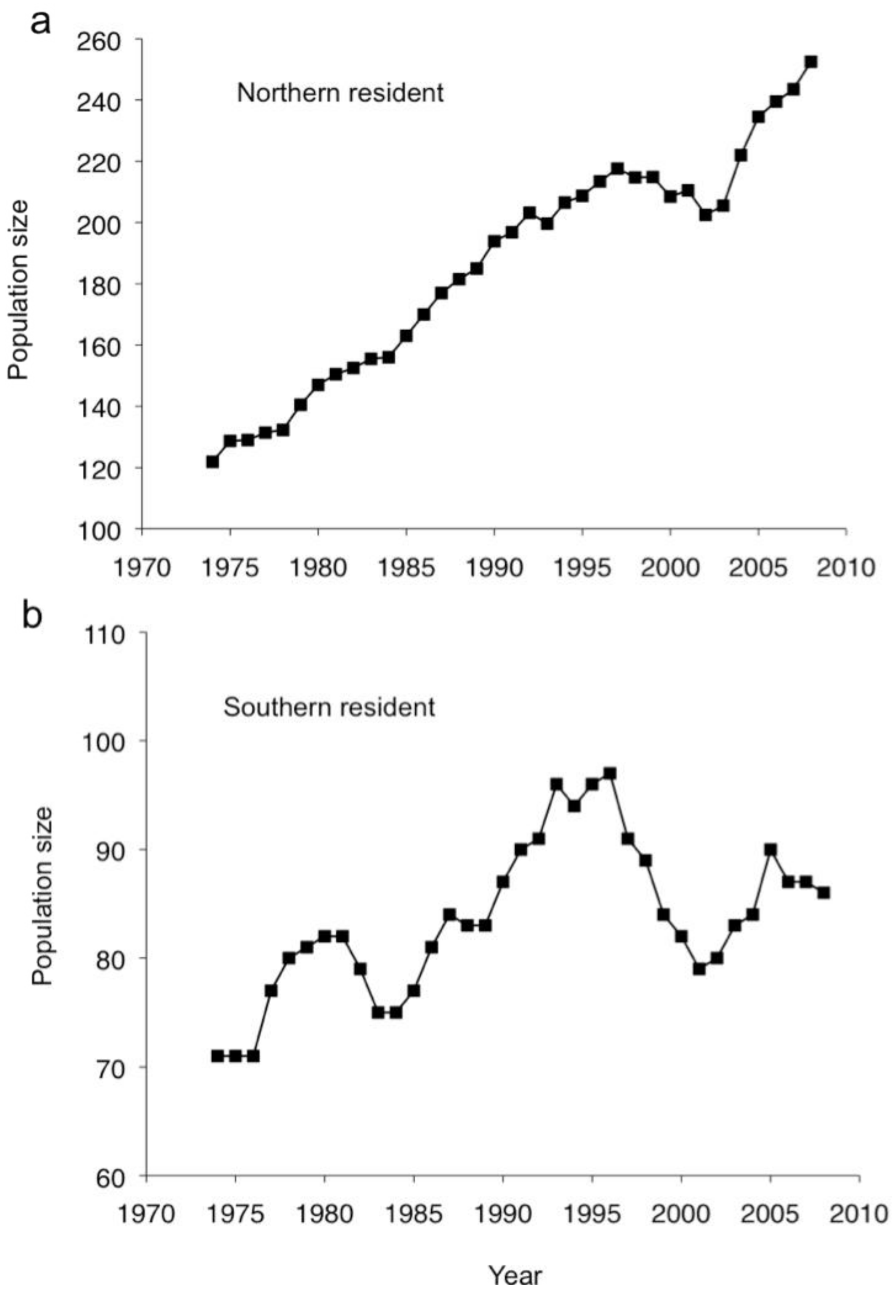

Figure 2. Population sizes of northern (a, top panel) and southern (b, bottom panel) resident killer whales, 1974-2008.

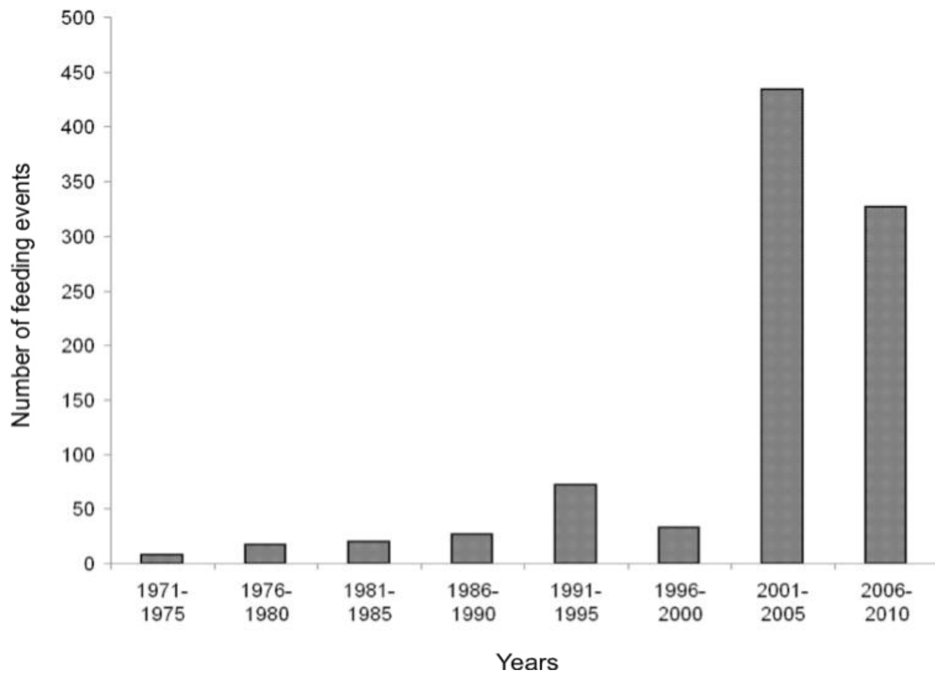

Figure 3. Number of feeding events observed during field studies of resident killer whales, 1973-2009.

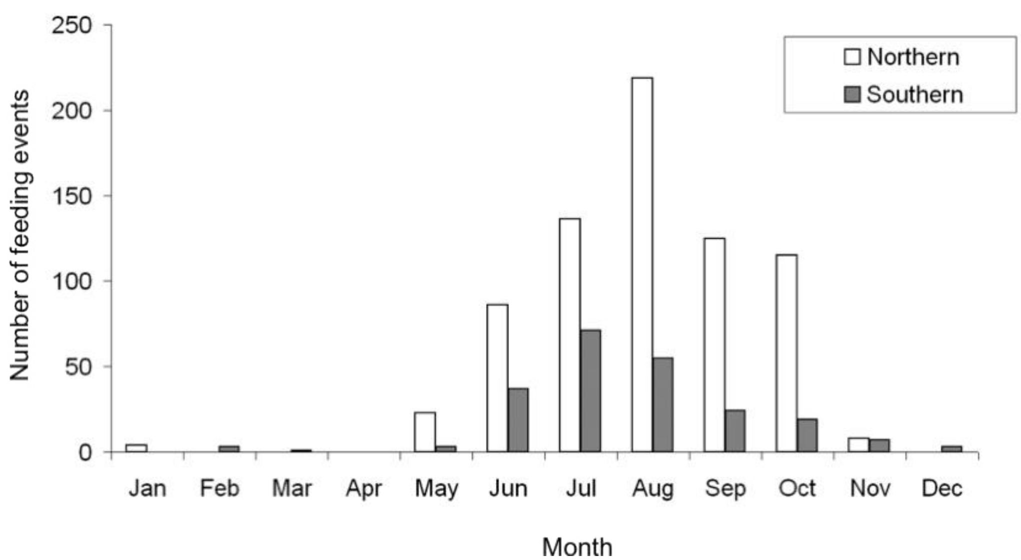

Figure 4. Monthly distribution of feeding events by northern (open bars, n = 715) and southern (closed bars, n = 222) resident killer whales.

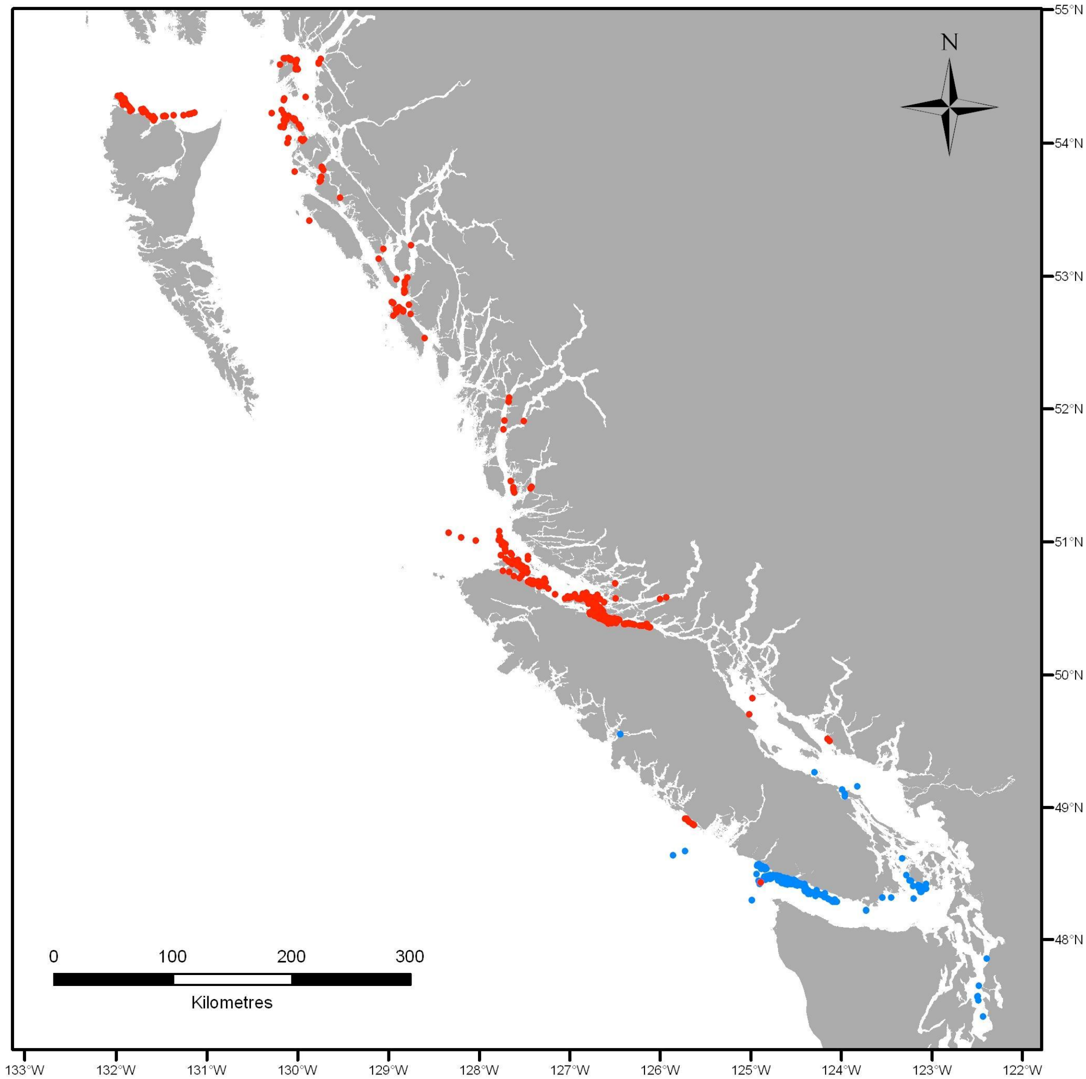

Figure 5. Locations of 937 feeding events by resident killer whales documented during 1974-2009. Red dots indicate feeding events by northern residents, blue dots by southern residents.

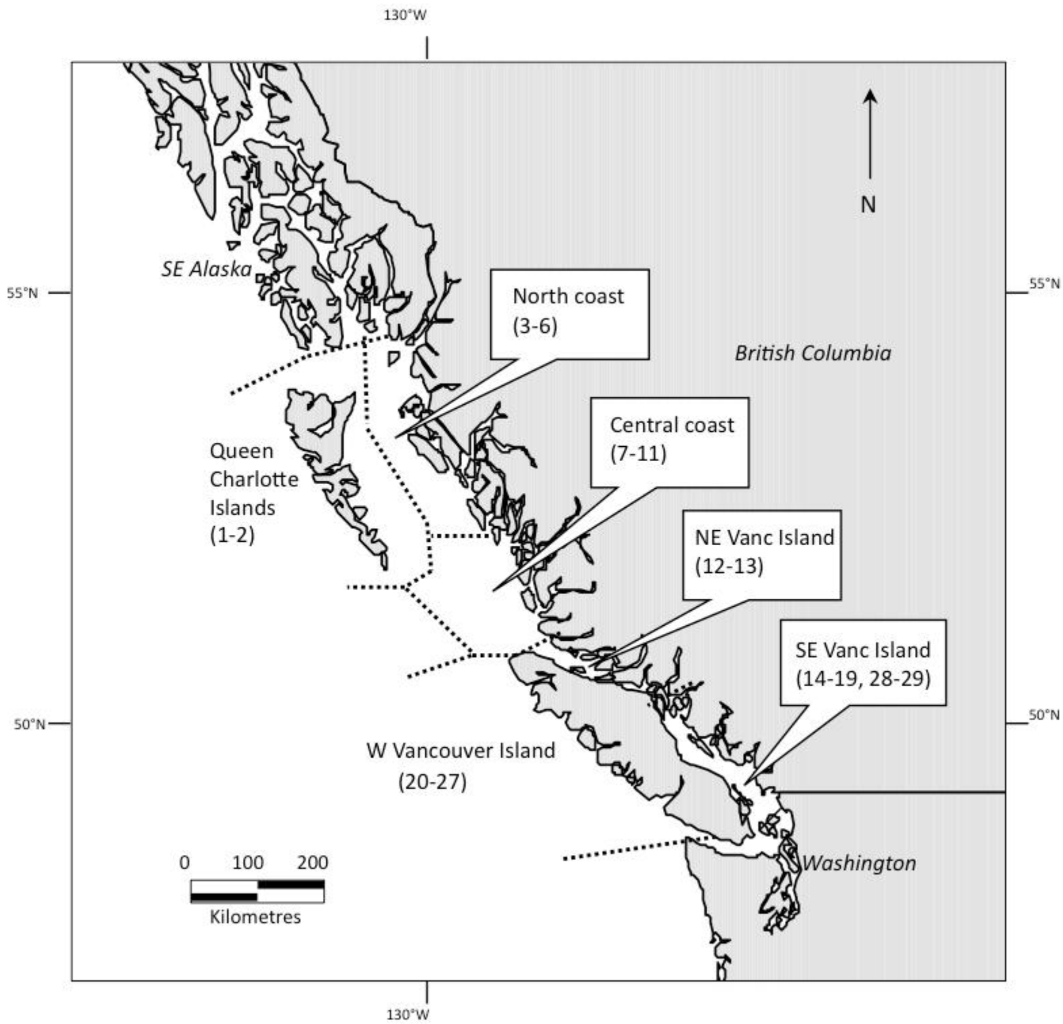

Figure 6. Coastal regions in British Columbia where killer whale predation samples were collected. Numbers in parentheses indicate Pacific Fisheries Management Areas (PFMA) encompassed within each region. Sample sizes for each region are provided in Table 2.

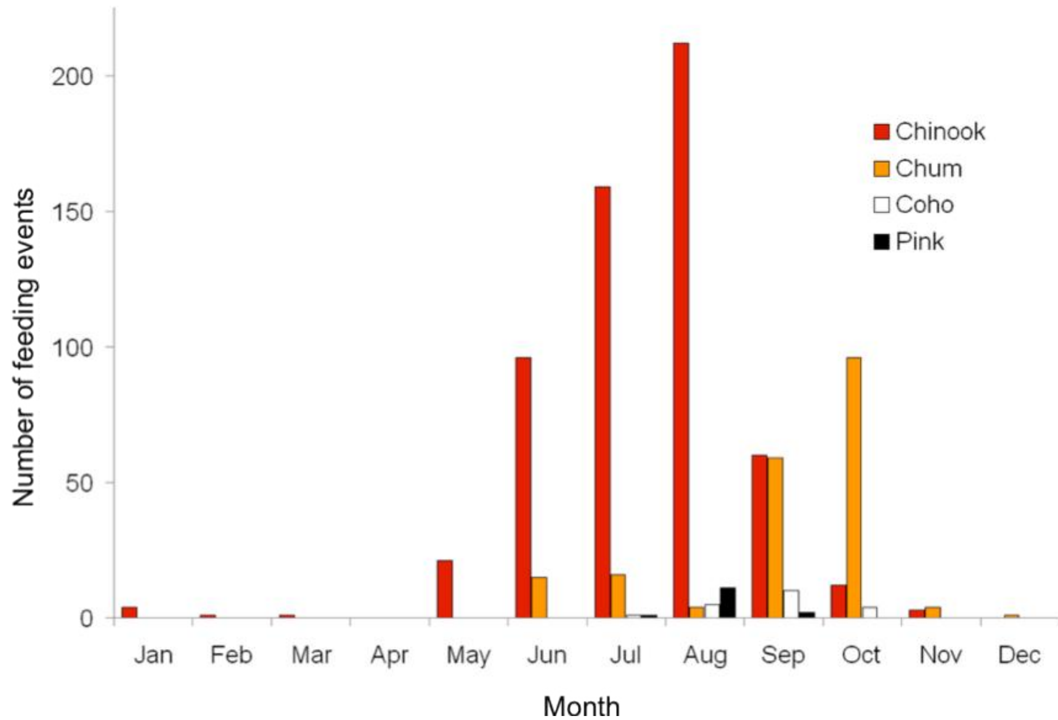

Figure 7. Monthly distribution of salmonid species in resident killer whale feeding events, based on data provided in Table 3 (n = 806 feeding events). Sockeye and steelhead salmon are not illustrated due to their rarity in prey samples.

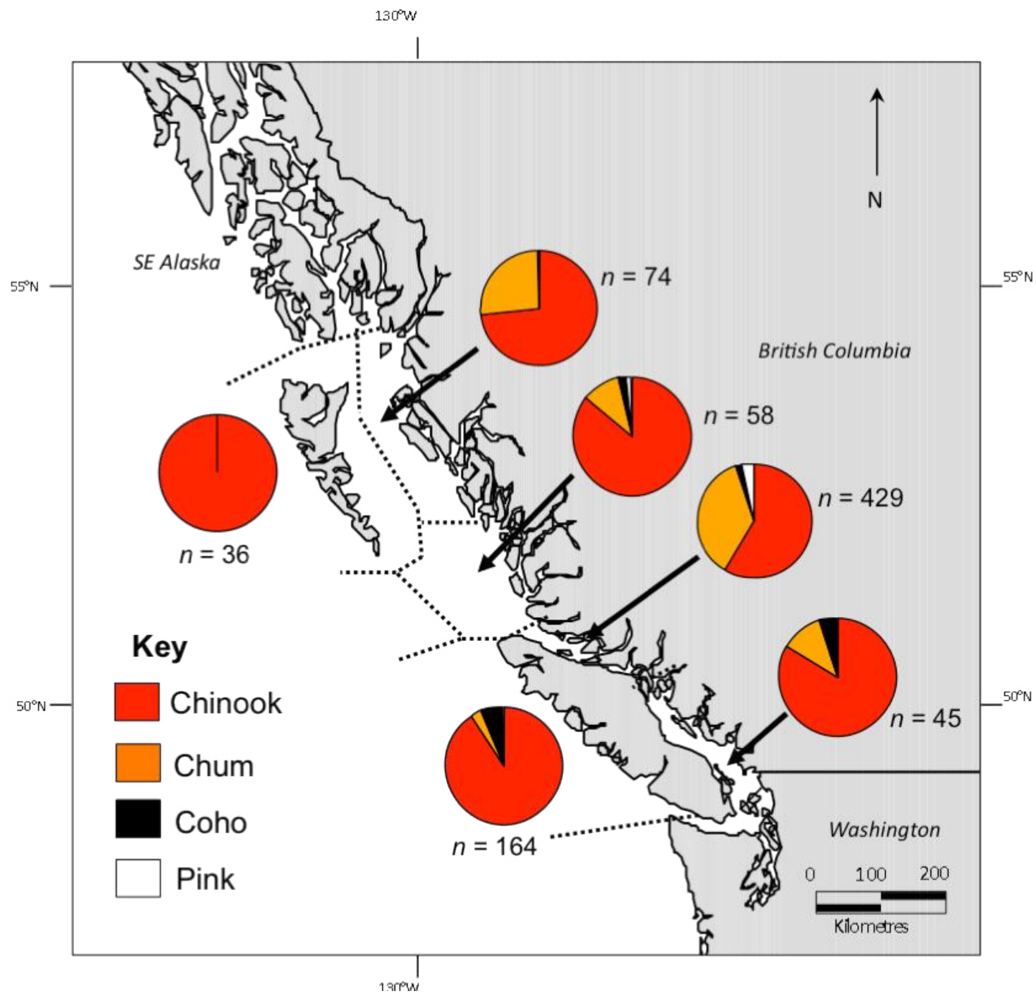

Figure 8. Frequency distribution of salmonid species consumed by resident killer whale in different coastal regions. Regions correspond to those shown in Figure 5, and predation data are provided in Table 2 (n = 806 feeding events). Sockeye and steelhead salmon are not illustrated due to their rarity in prey samples.

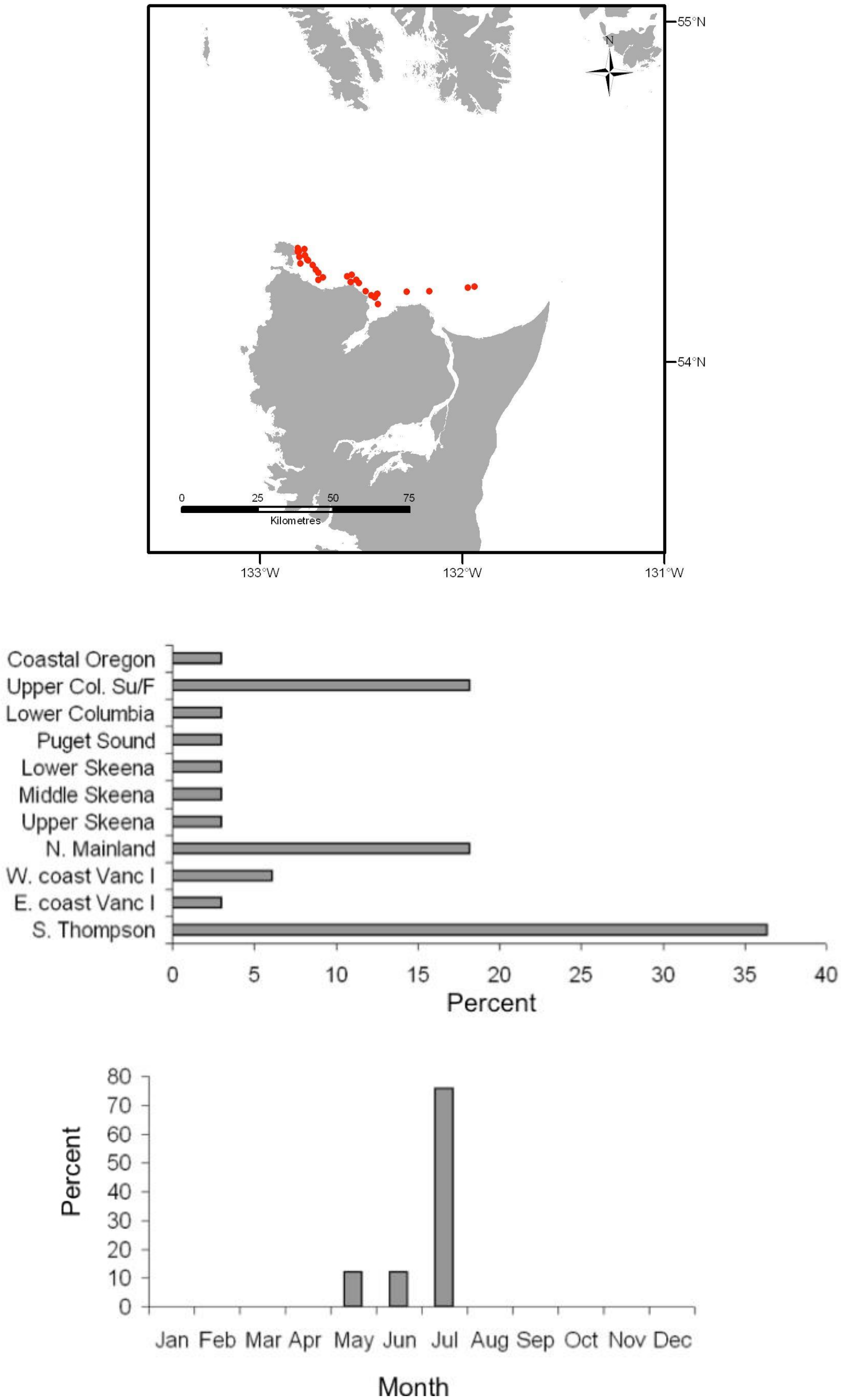

Figure 9. Locations of sampling (top), stock regions (middle), and monthly distribution (bottom) of Chinook salmon sampled from feeding events by northern resident killer whales in the northern Queen Charlotte Islands (PFMA 1). n = 33.

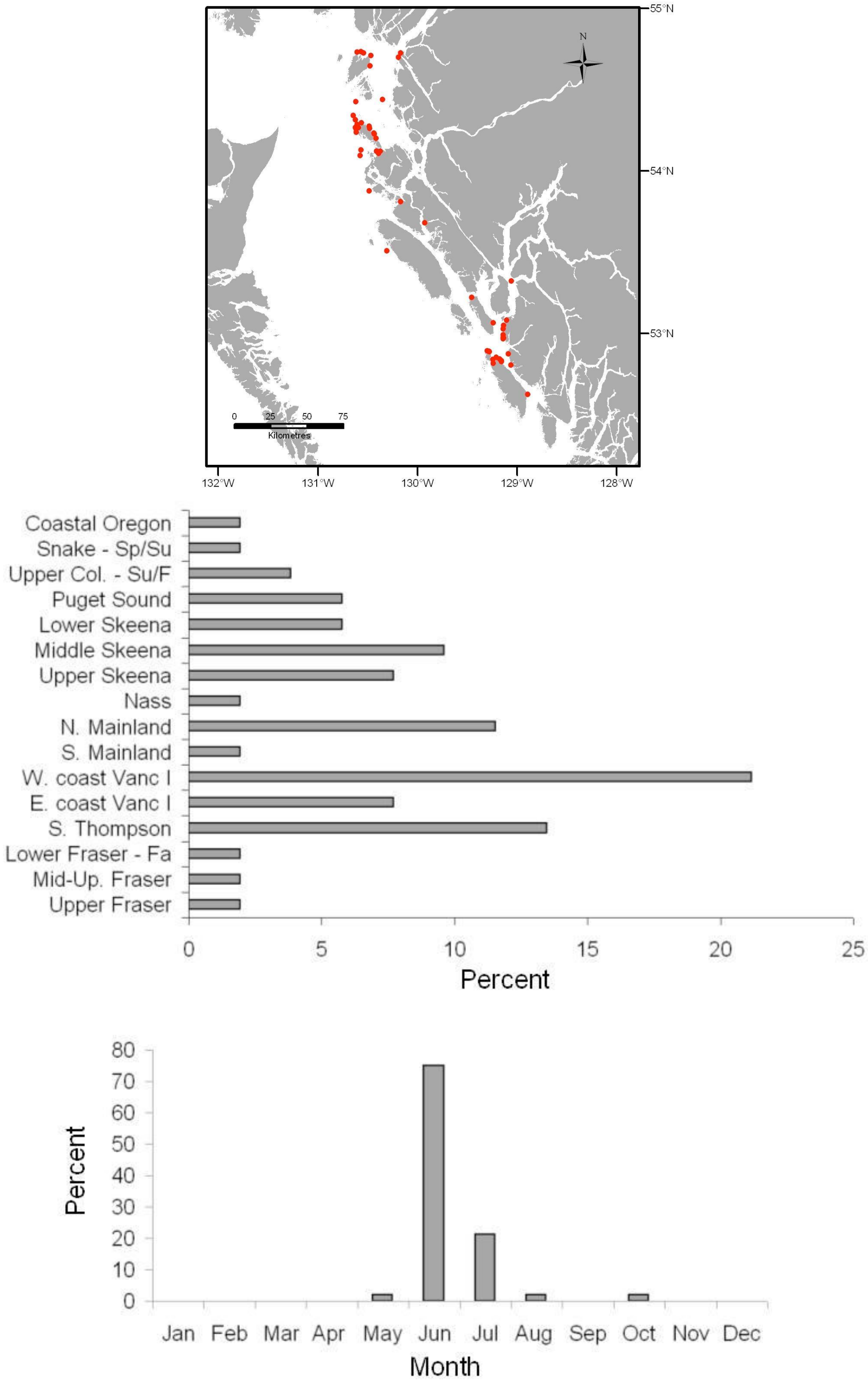

Figure 10. Locations of sampling (top), stock regions (middle), and monthly distribution (bottom) of Chinook salmon sampled from feeding events by northern resident killer whales in the northern mainland coast region (PFMAs 3-6). n = 52.

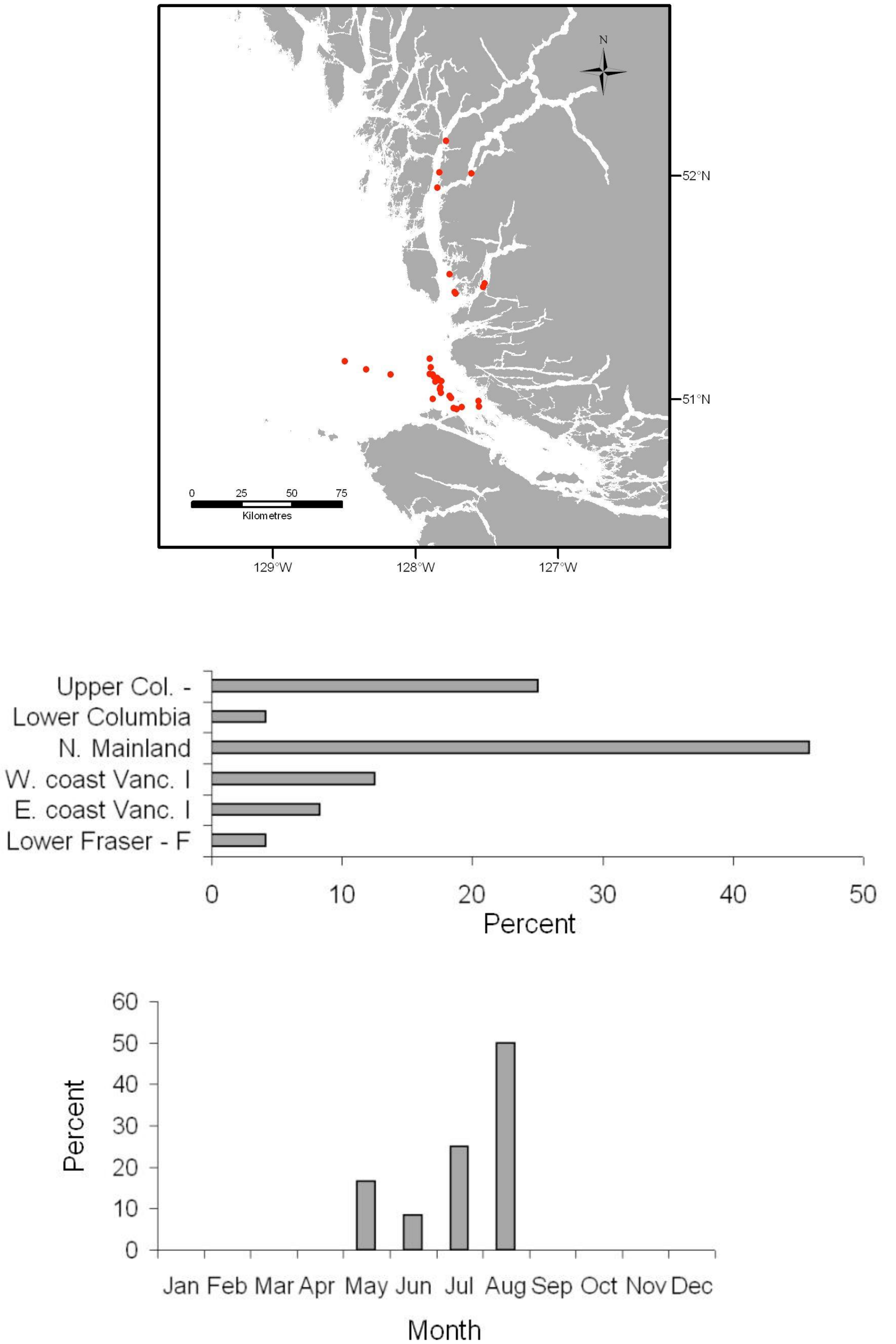

Figure 11. Locations of sampling (top), stock regions (middle), and monthly distribution (bottom) of Chinook salmon sampled from feeding events by northern resident killer whales in the central mainland coast region (PFMAs 7-11). n = 24.

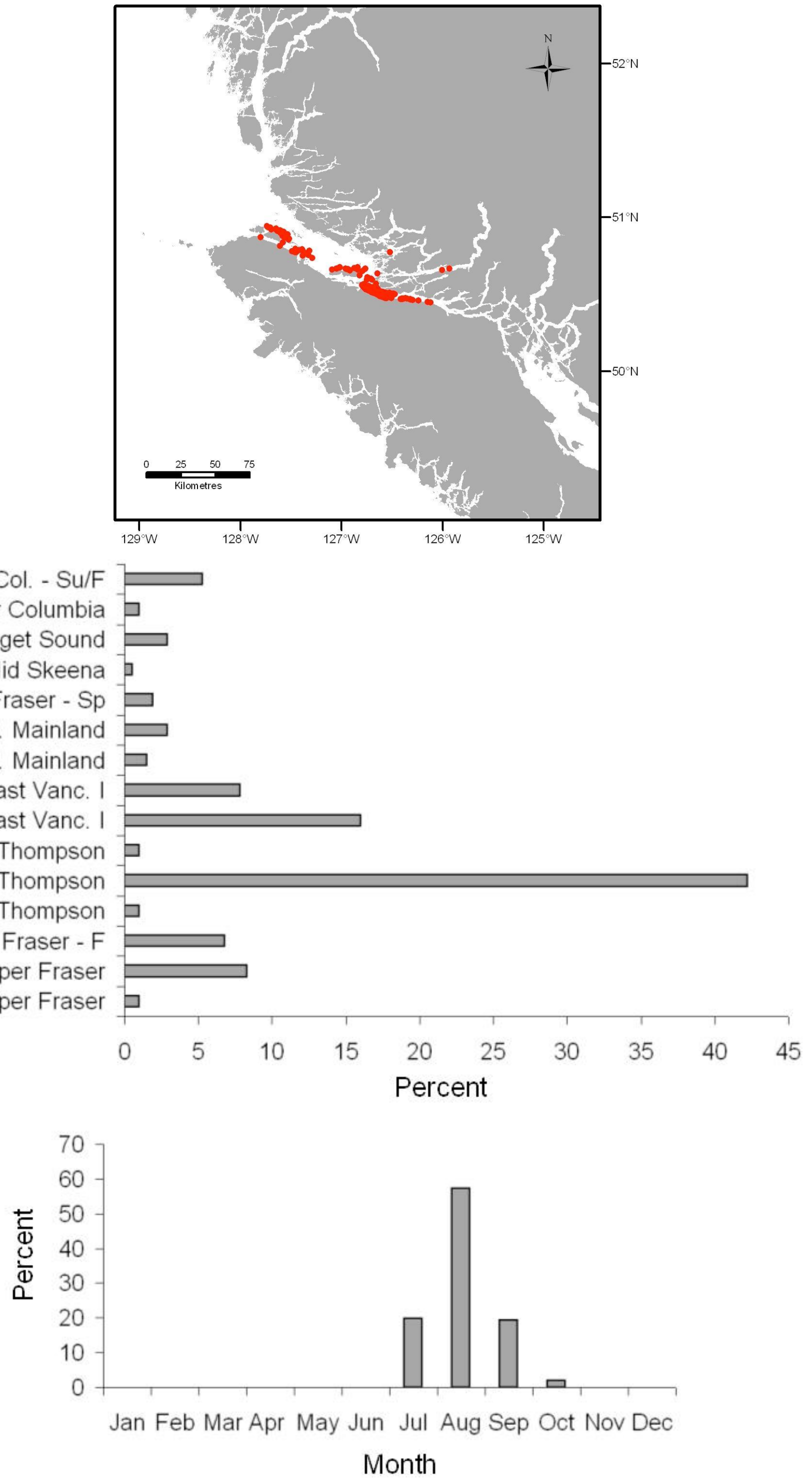

Figure 12. Locations of sampling (top), stock regions (middle), and monthly distribution (bottom) of Chinook salmon sampled from feeding events by northern resident killer whales in the northeastern Vancouver Island region (PFMAs 12-13). n = 205.

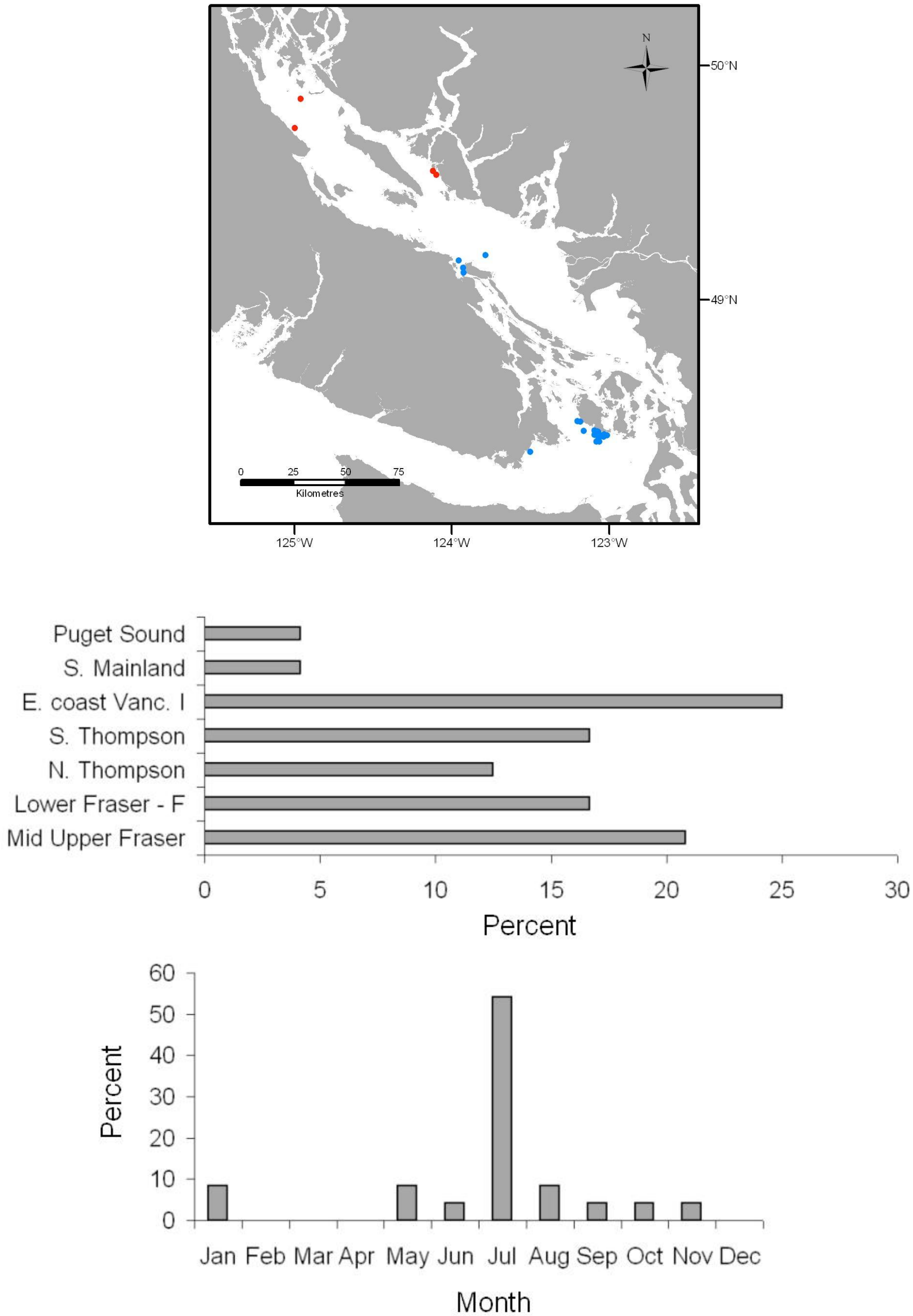

Figure 13. Locations of sampling (top), stock regions (middle), and monthly distribution (bottom) of Chinook salmon sampled from feeding events by resident killer whales in the southeastern Vancouver Island region (PFMAs 14-19 and 28-29). Red dots indicate feeding events by northern residents, blue dots by southern residents. n = 24.

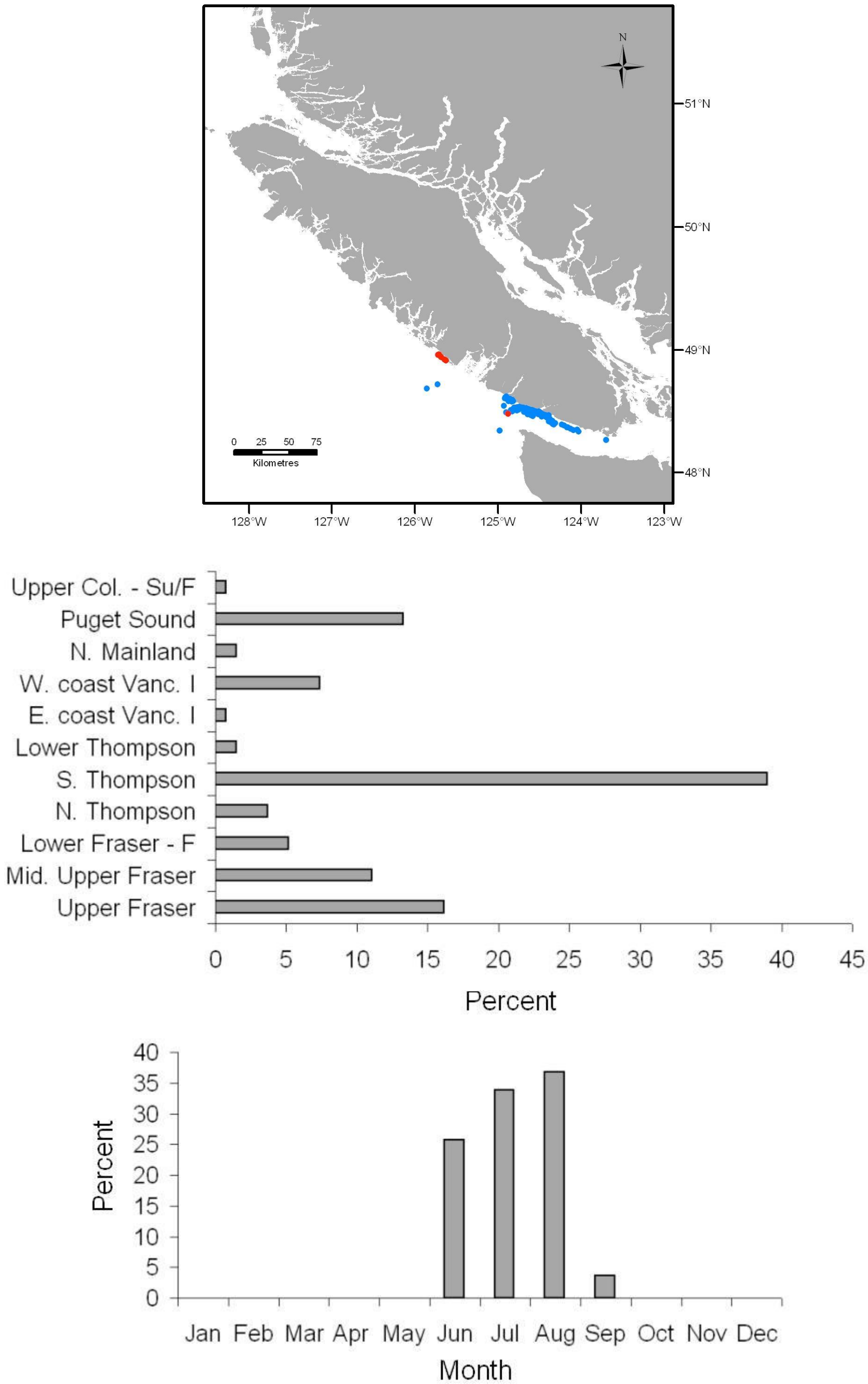

Figure 14. Locations of sampling (top), stock regions (middle), and monthly distribution (bottom) of Chinook salmon sampled from feeding events by resident killer whales in the western Vancouver Island region (PFMAs 20-24). Red dots indicate feeding events by northern residents, blue dots by southern residents. n = 136.

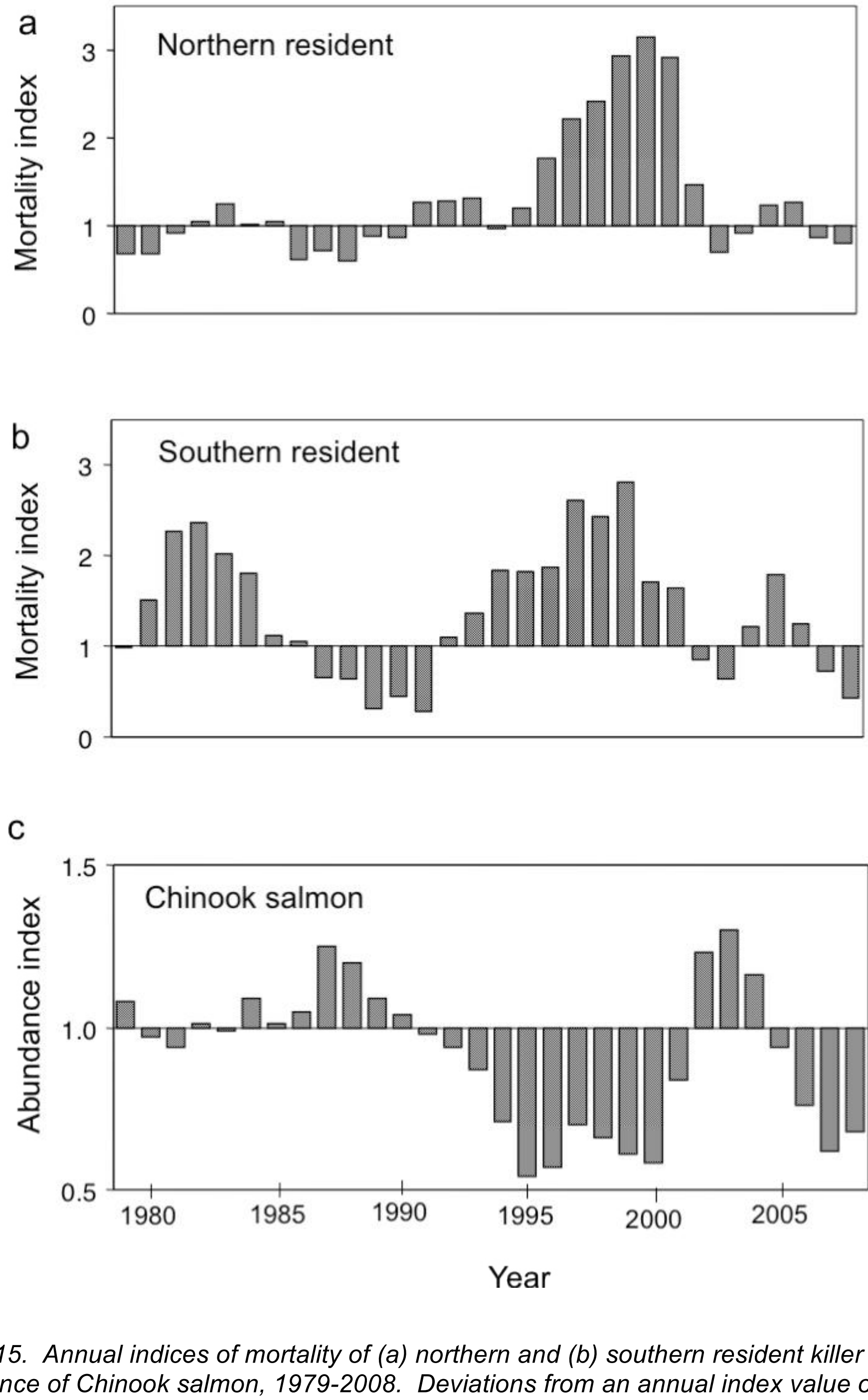

Figure 15. Annual indices of mortality of (a) northern and (b) southern resident killer whales and (c) abundance of Chinook salmon, 1979-2008. Deviations from an annual index value of 1 (a,b) indicate higher or lower than expected mortality rates. Annual abundance indices for Chinook salmon are from the Pacific Salmon Commission Chinook technical committee (PSC 2008).

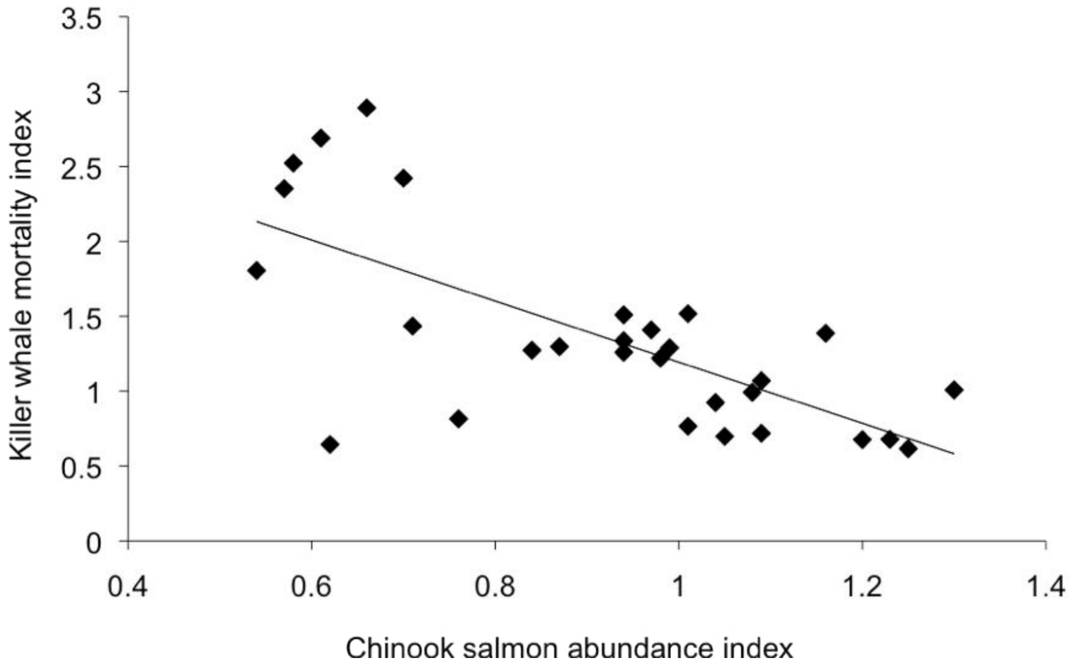

Figure 16. Relationship between annual indices of Chinook salmon abundance and resident killer whale mortalities, 1979-2008. Killer whale mortality index values are the ratio of observed to expected deaths in the population for each year. Mortality indices are lagged one year following Chinook salmon abundance ($y = -2.0412x + 3.2334$, $r^2 = 0.48673$).

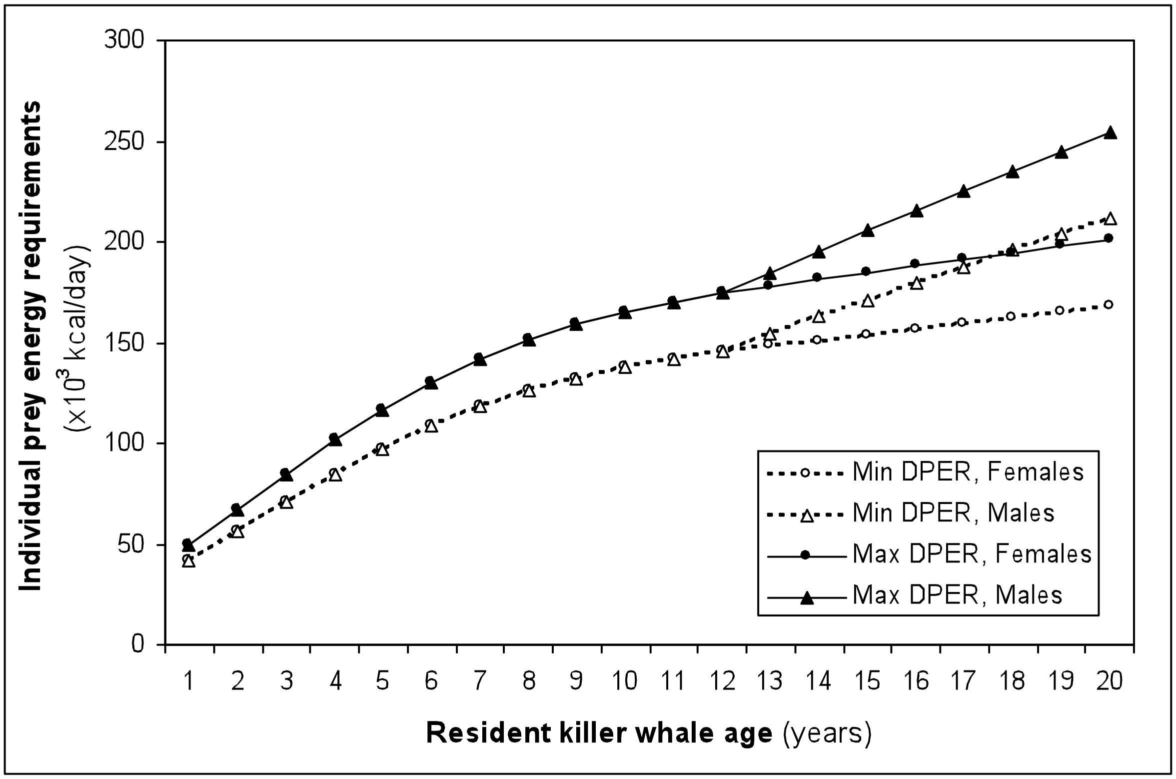

Figure 17. Upper and lower bound Daily Prey Energy Requirements (DPER) for male and female resident killer whales by age-class (years). Note that DPER values for whales aged 12 and under are equivalent for males and females (not differentiated by sex).

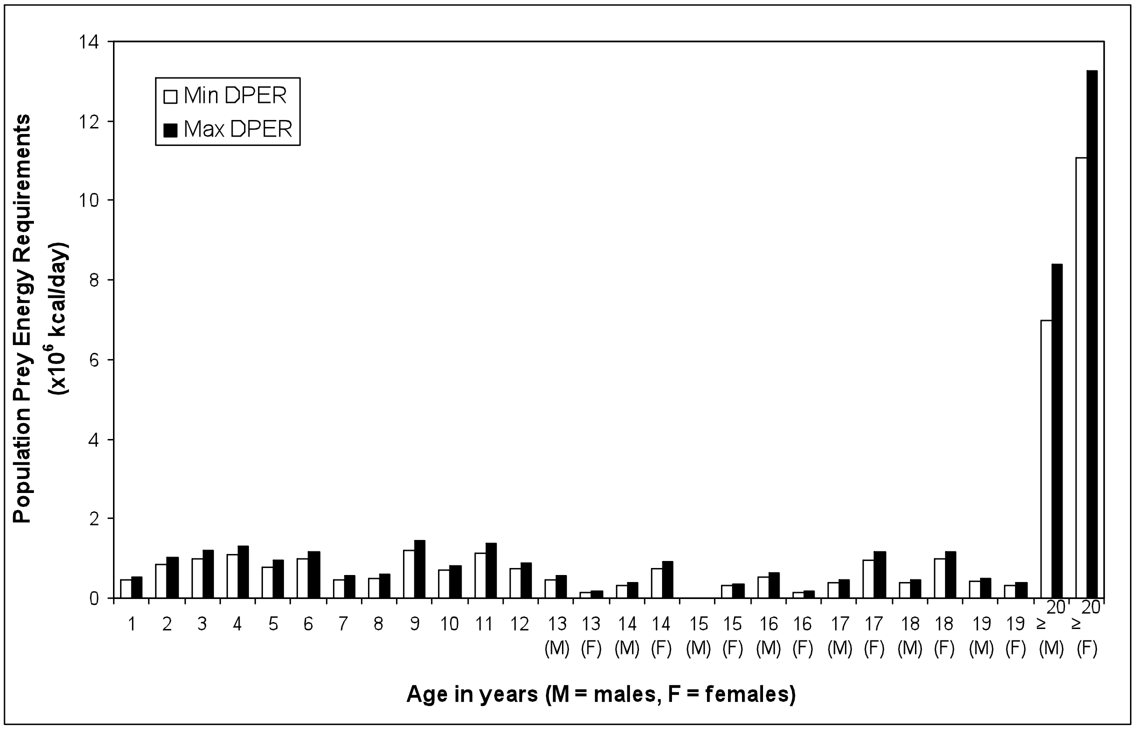

Figure 18. Lower and upper bound population daily prey energy requirements (DPERs) for northern resident killer whales (n = 241) by age- and sex-class.

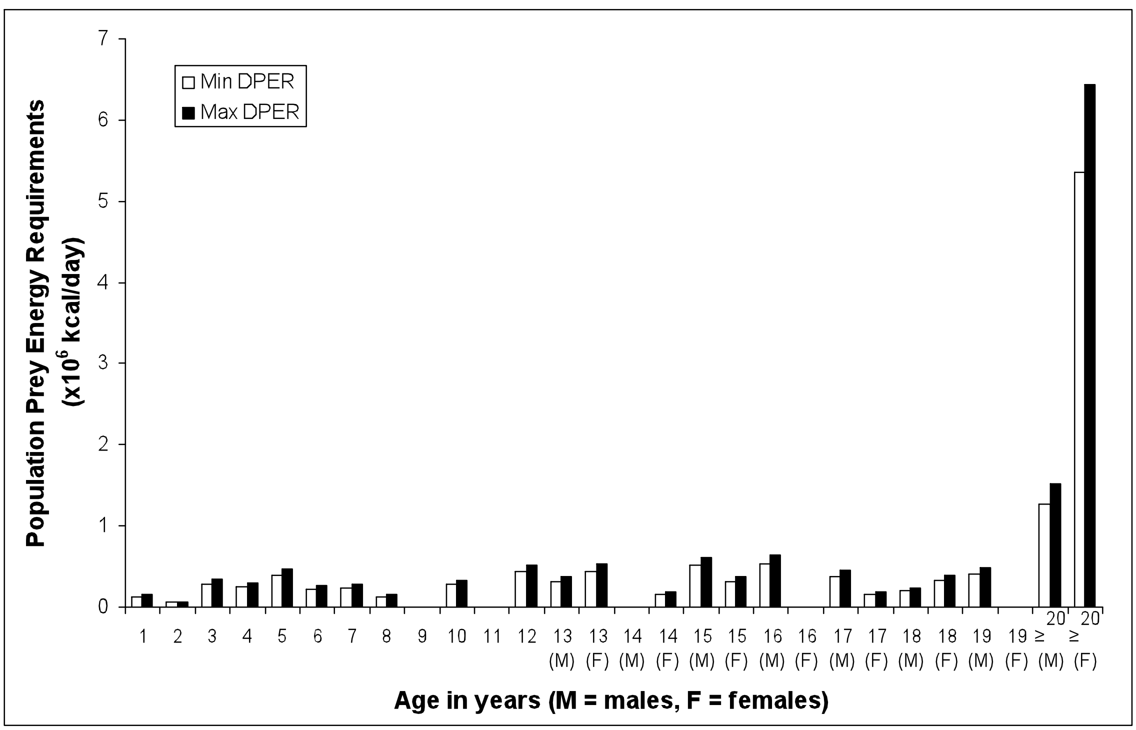

Figure 19. Lower and upper bound population daily prey energy requirements (DPERs) for southern resident killer whales (n = 85) by age- and sex-class.

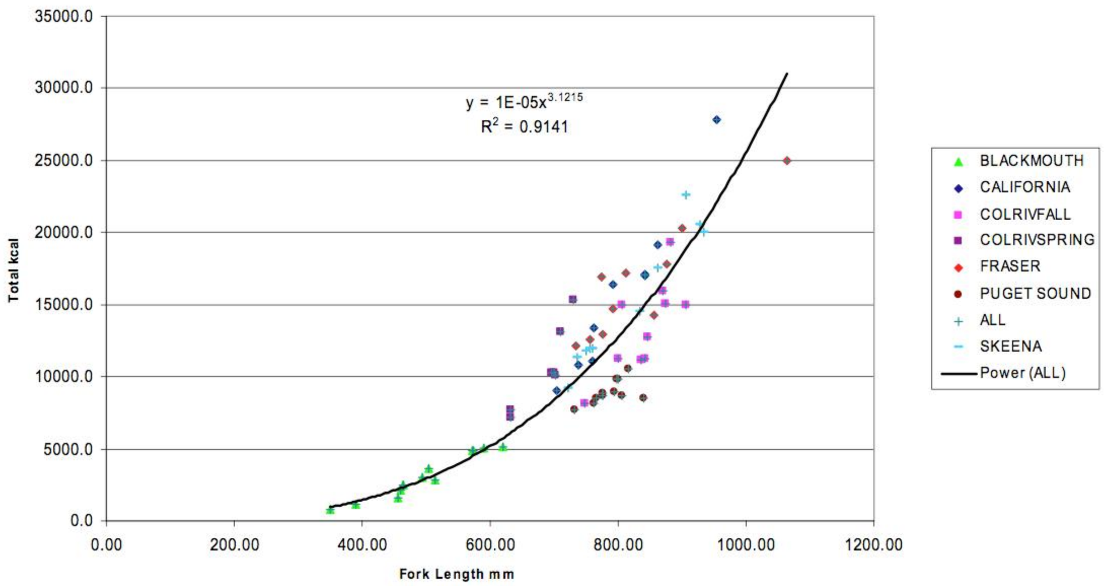

Figure 20. Regression of fork-length of Chinook salmon to energy density in kilocalories (from O'Neill et al., in prep.).

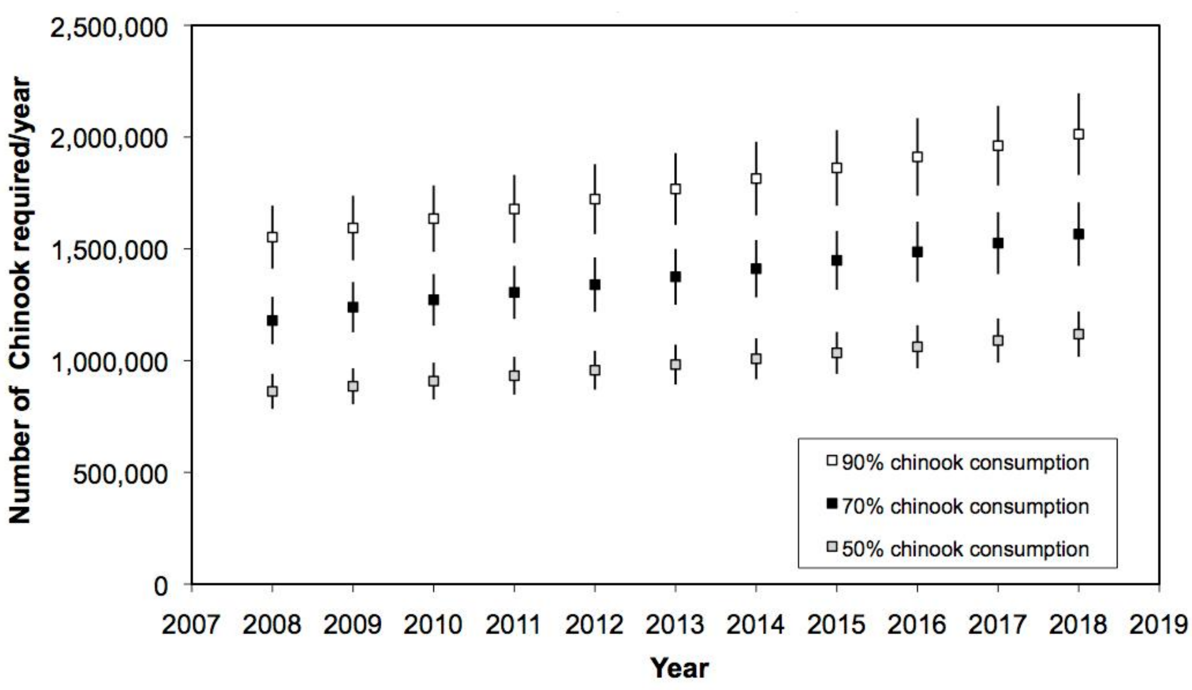

Figure 21. Projected increase in requirements of Chinook salmon by resident killer whales assuming a 2.6% annual population growth rate between 2008 and 2018 and diet compositions of 90%, 70% and 50% Chinook salmon.

AR031718