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Prey selection and food sharing by fish-eating ‘resident’ killer whales (*Orcinus orca*) in British Columbia

Sélection des proies et partage de la nourriture par les épaulards (*Orcinus orca*) « résidants » piscivores, en Colombie-Britannique

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ABSTRACT

Three distinct, socially-isolated populations, or ecotypes, of killer whales (*Orcinus orca*), inhabit coastal waters of British Columbia, Washington State, and southeastern Alaska. The so-called *transient* population feeds primarily on marine mammal prey, the *resident* population feeds primarily on fish, and the diet of the *offshore* population is not known. A previous study of the diet of the resident and transient populations using opportunistic collection of prey remains from kill sites as a primary measure of prey selection found that resident killer whales feed predominantly on salmonids, particularly on chinook salmon (*Oncorhynchus tshawytscha)*. To address uncertainties concerning potential biases in the prey fragment sampling technique and questions regarding seasonal and geographic variability in diet, we conducted field studies of foraging behaviour during 1997-2004. Foraging by resident killer whales often involves cooperation among kin-related group members, and prey items are frequently shared by two or more whales. Adult males share prey less often than do females and subadults. Prey sharing does not appear to be related to prey size. Prey fragments left at kill sites result mostly from prey handling and sharing, and are reliable indicators of selection for different salmonid species by resident killer whales. Chinook is the predominant prey species taken by both northern and southern resident communities during May-August, but chum salmon (*O. keta*) is more prevalent in September-October, at least in northern residents. Coho salmon (*O. kisutch*) are taken in low numbers in June-October, but sockeye (*O. nerka*) and pink (*O. gorbuscha*) salmon are not significant prey species despite their high seasonal abundance. Non-salmonid fishes do not appear to represent an important component of resident whale diet during May-October. Their strong preference for chinook salmon may influence the year-round distribution patterns of resident killer whales in coastal British Columbia and adjacent waters.

RÉSUMÉ

Trois populations distinctes (ou écotypes) d'épaulards (*Orcinus orca*), isolées les unes des autres, vivent dans les eaux côtières de la Colombie-Britannique, de l'État de Washington et du sud-est de l'Alaska. Ce qu'on est convenu d'appeler la population *migratrice* se nourrit principalement de mammifères marins, alors que la population *résidante* se nourrit surtout de poisson. Toutefois, on ne connaît pas le régime alimentaire de la population *océanique*. Une étude antérieure sur l'alimentation des populations résidante et migratrice, basée sur la collecte opportuniste des restes de proies dans les lieux de prédation comme principale méthode de mesure de la sélection des proies, a permis de conclure que les épaulards résidants se nourrissent surtout de salmonidés, et particulièrement de saumon quinnat (*Oncorhynchus tshawytscha)*. Afin de résoudre les incertitudes concernant les erreurs possibles de la technique d'échantillonnage des fragments de proies, de même que les questions de variabilité saisonnière et géographique du régime alimentaire, nous avons mené des études de terrain portant sur le comportement de recherche de nourriture, au cours de la période de 1997 à 2004. Les épaulards en quête de nourriture font souvent appel à la collaboration entre les membres d'une même famille et les proies sont fréquemment partagées entre deux épaulards ou plus. Les mâles adultes partagent moins souvent leurs proies que les femelles et les subadultes. Le partage des proies ne semble pas lié à la grosseur de celles-ci. Les fragments de proies, laissés sur les lieux de prédation, résultent surtout du déchiquetage et du partage des proies, et constituent des indicateurs fiables de la sélection de diverses espèces de salmonidés par les épaulards résidants. Le saumon quinnat est l'espèce-proie de prédilection des deux communautés résidantes du Nord et du Sud au cours de la période de mai à août; toutefois, le saumon kéta (*O. keta*) constitue la proie la plus courante au cours des mois de septembre et d'octobre, du moins au sein de la population résidante du Nord. De petites quantités de saumon coho (*O. kisutch*) sont consommées de juin à octobre, mais le saumon rouge (*O. nerka*) et le saumon rose (*O. gorbuscha*) ne représentent pas des espèces-proies importantes malgré leur abondance saisonnière. Les poissons autres que les saumons ne semblent pas constituer une partie importante du régime alimentaire des épaulards résidants au cours de la période de mai à octobre. La préférence marquée des épaulards résidants pour le saumon quinnat peut influencer leur répartition géographique, tout au long de l'année, dans les eaux côtières de la Colombie-Britannique et dans les eaux adjacentes.

Introduction

Three genetically-distinct sympatric populations of killer whales (*Orcinus orca*), known as *residents*, *transients*, and *offshores*, inhabit coastal waters of British Columbia, Washington State, and southeastern Alaska (Bigg et al. 1985, 1990; Barrett-Lennard 2000; Ford et al. 2000). These socially-isolated populations differ in many aspects of their life history and behaviour, but most striking are differences in their diets. Transient killer whales specialize on marine-mammal prey, while residents feed primarily on fish and are not known to consume marine mammals (Bigg et al. 1985, 1990; Baird and Dill 1985; Ford et al. 1998, 2000; Ford and Ellis 1999). Although the diet of the offshore killer whales is not known, their seasonal distribution and behaviour patterns suggest that they do not share the same foraging ecology as either residents or transients.

Resident killer whales congregate at particular coastal locations during summer and fall in association with high densities of migrating salmon. Heimlich-Boran (1986) documented positive correlations between the occurrence of killer whales and the size of sports fishery catches of salmon in Haro Strait and adjacent inshore waters of Washington State over a three-year period. Guinet (1990) noted a positive relationship between killer whale occurrence in Johnstone Strait, off northeastern Vancouver Island, and the size of commercial salmon catches in a single year. Nichol and Shackleton (1996) investigated in greater detail the association between resident killer whales and salmon abundance in Johnstone Strait over a five-year period, and found positive correlations between the occurrence of resident killer whales and pink (*Onchorhynchus gorbuscha*), sockeye (*O. nerka*) and chum salmon (*O. keta*). Potential associations between killer whale occurrence and abundance of chinook (*O. tshawytscha*) and coho salmon (*O. kisutch*) were not examined, as these salmonid species are far less abundant in the area than pink, sockeye and chum salmon during summer and fall (Groot and Margolis 1991; Nichol and Shackleton 1996).

Ford et al. (1998) investigated the diet of resident killer whales in coastal waters of British Columbia and Washington State by observing predation, collecting fish scales and other prey fragments from kill sites, and examining stomach contents of stranded whales during 1973-96. All 135 kills by resident whales documented during June-September were of fish, the great majority (98%) of which were salmonids. The only non-salmonid prey observed were single Pacific herring (*Clupea pallasi*), yelloweye rockfish (*Sebastes ruberrimus*) and Pacific halibut (*Hippocampus stenolepis*). Identification of salmonid species revealed a high proportion of chinook salmon (65%), followed by pink salmon (17%), chum (6%), coho (6%), sockeye (4%) and steelhead salmon (*O. mykiss*) (2%). Salmonids were identified in the stomachs of all 7 stranded resident whales examined that contained food remains. Chinook was the only identifiable salmonid species, and was found in 4 of the 7 stomachs. One of these stomachs contained remains of 18 chinook salmon, plus remains of 15 lingcod (*Ophiodon elongatus*), 5 greenling (*Hexagrammos* sp.), 1 sablefish (*Anoplopoma fimbria*), and 9 species of small sculpins and flatfish, which likely originated from the stomachs of the larger fish. Two other stomachs contained beaks of eight-armed squid (*Gonatopsis borealis*) in addition to chinook salmon remains.

Although stomach content analysis provided support for the conclusion that resident killer whales feed preferentially on chinook salmon, the predominance of this species in scale samples was unexpected. Given the species' very low abundance compared to that of sockeye and pink salmon in locations and at times that sampling was conducted, far fewer chinook samples were expected (Ford et al. 1998). As a result, potential biases were identified in the sampling method that may have led to over-representation of chinook and under-representation of other species in feeding samples. Chief among these was the possibility that chinook, being larger than other salmonids, were more prone to being broken up prior to being eaten, thus shedding more scales than other salmonids in the process (Ford et al. 1998). However, without knowledge of the details of prey handling and consumption of salmonid 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).

Ford et al. (1998) provided the first direct evidence that salmonids, particularly chinook, are important in the diet of resident killer whales. However, the sample size of feeding events in that study was quite limited, both seasonally and geographically. Essentially no data were available for November-April in any part of the range. Also, small sample sizes precluded examination of potential differences in prey selection at the level of the community, clan or pod (as suggested by Nichol and Shackleton 1996), or by different sex or age classes (e.g. Bain 1989).

In order to address these and other gaps in knowledge of resident killer whale diet, we undertook field studies of foraging behaviour and feeding by residents in 1997-2004 to build upon the data presented in Ford et al. (1998). In particular, field efforts in 2003-04 were focused on documenting the detailed aspects of prey capture and handling to assess the validity of using prey fragment sampling to interpret dietary preferences. In this report, we present new information on the frequent occurrence of cooperative foraging and prey sharing in resident killer whales, and the implications of this behaviour with respect to the use of prey fragments as indicators of diet. Extensive sampling of feeding events also allowed us to quantitatively evaluate prey selection in regard to prey species availability, as well as by age and sex class and group membership of feeding whales.

Study Population and Methods

Study area and population

Studies were undertaken in coastal waters of British Columbia during 1973-2004, primarily in nearshore waters off eastern Vancouver Island, the central and northern mainland coast, and near Langara Island off the northwest coast of Graham Island. Two communities 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 and southern resident communities contained 219 and 84 individuals, respectively, in 2004 (Ford and Ellis, unpubl. data; Center for Whale Research, unpubl. data). The northern resident community is found mostly from mid Vancouver Island to southeastern Alaska, and the southern resident community off the southern half of Vancouver Island and in the inland waters of Washington state. Whales from the two communities 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 (Ford et al. 2000; Wiles 2004).

The basic social unit of resident killer whales is the *matriline*, which consists of individuals that are closely related by matrilineal descent. Matrilines generally contain an old female, or matriarch, and 1-3 generations of her descendents of both sexes. Dispersal of individuals from the matriline is extremely rare (Ford et al. 2000). Matrilines are comprised of an average of 6 members (range 1-26, SE = 0.59, n = 50) individuals. Resident killer whales typically travel in *pods*, which consist of related matrilines that spend the majority of their time together (Bigg et al. 1990). Although some pods originally described in the 1970s and 1980s have maintained their stability, others have split in recent years (Ford et al. 2000; Ford and Ellis 2002). Pods and matrilines have distinct vocal dialects that reflect their matrilineal genealogy (Ford 1991). *Clans* are comprised of pods and matrilines that have descended from a common matrilineal ancestor and have a unique set of shared dialects. The northern resident community consists of 3 clans, A, G, and R, while the southern resident community is made up of a single clan, J. Northern resident clans frequently associate with one another.

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. 1987, 1990; Olesiuk et al. 1990; Ford 1989, 1991; Ford et al. 1998, 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 after 1990 (Ford et al. 1998, 2000). In 2003-04, 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). A total of 123 field days were devoted to encountering and studying resident killer whales in 2003-04.

Field studies in 1974-2002 were conducted using a variety of vessels from 5-20 m in length. In 2003-04, dedicated studies on 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 whales 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 immediately (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 50-150 m to document subsequent feeding events. Focal individuals and subgroup were followed (Altmann 1974; Mann 1999) for as long as the whale(s) continued active foraging or until focal animals joined other groups and could no longer be followed individually.

The behaviour of focal individuals and subgroups was monitored closely and constantly during feeding sessions. Particular attention was given to direction of travel, regularity of dive durations, and extent 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 25 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 situated approximately 4 m above the water surface on the command bridge of the study vessel. This position 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 100% 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 the current analyses we included only positive salmonid identifications based on scales or tissue samples to eliminate this potential source of error. Fish scales were analyzed by the Fish Ageing 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 (see Table 3) 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 examined for species identification using DNA analysis by the Molecular Genetics Laboratory at the Pacific Biological Station. Methodology of these analyses is described in Beacham et al. (2003).

General analyses

Statistical analyses were performed using SPSS Version 11.0. The standard error (SE) of the mean is given as a measure of variability.

Results

A total of 487 feeding events were observed during 197 encounters with resident killer whales between 1974 and 2004. Of these, 291 (60%) were recorded during dedicated feeding studies in 2003-04. Feeding events were documented from May to December (Fig. 1). Prey samples (tissue or fish scales) were recovered from 426 feeding events (87.5%), while the remaining 12.5% were documented by observation only (Table 1). A mean of 4.8 scales per feeding event (range 1-28, SE = 0.24) were collected from 394 of the 487 feeding events (80.9%). Tissue fragments were only systematically collected during dedicated foraging studies.

A total of 419 (86%) feeding events involved northern residents, and 68 (14%) events involved southern residents. All 4 resident clans and all but 2 of the 19 resident pods in the northern and southern communities are represented in this dataset (exceptions are I17 and W1 pods; Ford et al. 2000). Samples were collected from most regions of the coast, but two-thirds came from waters off northeastern Vancouver Island, an important core area for northern residents (Table 2; Ford et al. 2000).

All feeding events involved fish, at least 96.7% of which were salmonids (Table 2). Ten samples (2%) could not be identified to species, and some of these may also have included salmonids. The only non-salmonids identified were 3 Pacific herring, 1 yelloweye rockfish, 1 quillback rockfish (*Sebastes maliger*), and 1 Pacific halibut.

Overall salmonid species and age composition

Six of the seven species of Pacific salmon (*Oncorhynchus* spp.) found in the study area were represented in feeding samples (the exception was the cutthroat trout, *Oncorhynchus clarki*). Species identity was determined for 396 salmonids, 20 by DNA analysis and the remainder from scale analysis. The frequency distribution of these species is shown by region in Table 2. Chinook salmon was by far the predominant salmonid observed, representing 72.2% of 396 salmonid kills identified to species. The second most important salmonid was chum at 21.5% of samples. Coho, pink, sockeye, and steelhead together represented less than 7% of the salmonids identified. Ages were determined for 317 salmonids (Table 3).

Chinook was the principal species taken by resident killer whales in all regions of the coast (Table 2). It was the most common species in feeding samples from both northern and southern communities, as well as from each of the 3 northern resident clans. (Fig. 2). Only chinook was found in the relatively few samples collected from R clan of the northern community. Chinook represented over 80% of all salmonid samples collected from residents during May through August (Table 4, Fig. 3). In September and October samples, however, chum salmon was the predominant species identified from feeding events. Pink salmon occurred in small numbers in July-September samples, as did coho salmon during July-October. Southern residents were responsible for the only sockeye salmon sample, collected in July, and the two steelhead samples, collected in November and December.

Foraging behaviour

Systematic studies of foraging behaviour of resident killer whales were undertaken in 2003-04 to improve understanding of feeding tactics and prey selection. A total of 291 feeding events were observed on 51 days during this period. Focal subgroups or individuals were followed and observed for a total of 61.7 h during 34 feeding sessions, which we defined as the period between the first and last feeding events in a series by that individual or subgroup. Feeding sessions lasted an average of 1.9 h (range, 0.4-9.25 h, SE = 0.29). A total of 170 feeding events were documented during these 34 sessions, for an average of 5 feeding events per session (range 2-15, SE = 0.47). Intervals between feeding events ranged from 2-120 min, with an average of 25.8 min (SE = 1.84, *n* = 136 intervals). Almost one-third of feeding events in a session were 10 min or less apart (Fig. 4).

An average of 4.5 matrilines were present during encounters in which feeding was documented (range 1-12 matrilines, SE = 0.37, *n* = 51 encounters). Whales generally foraged in a widely-dispersed manner, with individuals or small subgroups (2-6 whales) separated by 200 m or more. Subgroups usually consisted of complete matrilines or partial matrilines comprised of mothers and their young offspring. Subgroups were formed occasionally by members of two or more matrilines. Adult males usually foraged independently or in association with their mother, especially in cases where the mother had no subadult offspring. Whales often foraged close to shorelines, especially in the deep, narrow channels and straits frequented by residents during summer and fall. Adult males usually foraged further offshore than subgroups. Individuals and subgroups foraging nearshore followed the coastline closely, often within 50 m of shore. Whales foraging offshore often swam in a zig-zag pattern rather than in a straight line along a channel.

Signs of prey pursuit and capture were at times very conspicuous. When an appropriate prey item was detected, an individual would break suddenly into a high-speed chase that continued for 10-30 sec, or rarely up to 3 min. Chases were both directional and non-directional, the latter accompanied by fast turns and rolls at the surface. Chases often took place along steep shorelines, with whales swimming at high speed within a few metres of the rocks. Although vigorous chases were obvious indicators of predation, more often signs of feeding were quite subtle, and close attention to several behavioural cues was necessary in order to detect them. For example, a change in the otherwise consistent swimming speed and direction of foraging whales often indicated that a pursuit was underway. An unusually long 5-7 min dive following an extended series of regular, 2-3 min dives was also a good indication of prey pursuit and possible capture.

Whale interactions during feeding events suggested that the majority of prey items were shared by 2 or more animals. Typically, a whale that made a kill was joined by others, and the group would swim together for 2-3 surfacings before splitting up once again. Individuals converged on the successful whale from as far as 400 m, though more often joining animals were within 100-200 m when the kill took place. On other occasions, several whales were involved in the pursuit, and would work cooperatively to take prey that sought refuge in crevices along rocky shorelines or in kelp beds. After making the kill, members of the group joined at the surface and swam together for several surfacings. Inspection of the site at which whales joined in such situations invariably revealed fish scales or bits of tissue in the water. Often, as the whales swam together after joining, a trail of prey fragments was left in the water, indicating that the prey item was being torn up along the way.

Close observations of prey handling and consumption during a number of feeding events provided strong evidence that sharing was taking place in such circumstances, and that intentional provisioning of other whales was also frequently involved. On several occasions, members of a subgroup milled at the surface while one of the group was underwater on a long dive. Upon surfacing with prey, the whale was seen to carry the fish in the direction of the milling animals. Scales or tissue were found where the animals joined. On other occasions, a whale was observed to surface with prey and carry it for 3-5 shallow dives and surfacings while another individual swam quickly in its direction. Although small numbers of scales were often seen in the water in the trail of the whale carrying the fish, much larger numbers of scales and bits of tissue were observed at the site of joining, indicating that prey consumption was delayed until the whales were together.

Observations during 235 feeding events provided sufficient evidence to judge with reasonable confidence whether or not sharing had taken place. In 57 of these feeding events (24%), only single individuals were involved in the kill and there was no indication of any sharing. In the other 178 cases (76%), sharing was either clearly evident or strongly suspected. Between 2 and 6 whales, including the animal making the kill, were involved in shared feeding events, though it was generally not possible to determine how many individuals actually took part in prey consumption. Most often, two whales (60%) or three (35%) were involved in shared feeding events. The frequency of sharing by members of different age and sex classes of whales differed significantly ($\chi^2 = 30.8$, $df = 2$, $P<0.001$; Table 5). There was evidence of sharing in 96% of kills by adult females but only in 17% of kills by adult males (Table 5). Kills by subadult whales, which were not distinguished by sex, also tended to be shared (80% of cases, Table 5).

The relationship of individuals sharing in kills was determined for 128 shared kills (Table 6). Whales that captured a prey item shared it mainly among close kin in the same matriline. In only 7 of 128 cases (5.5%) were prey items shared solely with individuals belonging to another matriline. Adult females shared 60% of their kills only with their offspring, and 21% with their offspring plus others in the matriline. Adult males shared their prey with their mothers (3 of 8 cases) or siblings (5 of 8 cases). Subadults also shared their prey mostly with their mother and siblings.

Prey selection versus whale age/sex class and sharing

Chinook salmon was the predominant prey species taken by adult males, adult females, and subadults (Fig. 5). Chum and coho salmon were also taken by each sex and age category, though the proportion of chum in salmonid kills by adult males was significantly greater than in adult females and subadults ($\chi^2 = 10.4$, $df = 1$, $P<0.01$). All 11 pink salmon kills by identified whales were by subadults. In fact, 6 of the 11 pink salmon kills were made during a single 1.5 h long feeding session by a one-year old calf. Because pink salmon are the smallest of the Pacific salmonids (Quinn 2005), the age distribution of chinook salmon kills was examined to determine whether smaller fish tended to be taken more frequently by subadult than adult whales (Fig. 6). Although subadults took 2 and 3 year old chinook more often than did adult whales, the overall trend was marginally insignificant ($t = 1.96$, $df = 157$, $P = 0.052$). The mean age of chinook taken by adult males (4.50 years, SE = 0.13, *n* = 38) and adult females (4.26 years, SE = 0.08, *n* = 86) did not differ significantly (*t* = 1.70, *df* = 122, *P* = 0.09)

Four of the six salmonid species taken by resident killer whales were identified from both shared and non-shared feeding events (Table 7). The great majority (84%) of chinook salmon tended to be shared, while a significantly lower proportion of chum salmon were shared (55%; $\chi^2 = 4.47$, *df* = 1, *P*<0.05). Although chinook are often larger than chum salmon (Healey 1986), larger size may not be the reason for the higher proportion of sharing of chinook. Chum salmon formed a higher proportion of the prey samples from adult males than females, and because males shared prey less frequently than females, the proportion of chum that were not shared may as a result be higher than other species. Both coho and pink salmon, which tend to be smaller than chum (Healey 1986), were noted in both shared and non-shared feeding events. Also, a comparison of the age distribution of chinook salmon taken in shared versus non-shared feeding events, shown in Figure 7, showed no significant difference (*t* = 0.05, *df* = 137, *P* = 0.96), suggesting that fish size had no effect on likelihood of sharing.

Prey selection versus availability

To assess the extent to which foraging resident killer whales select for particular species or size of salmonids, the species and age composition of kills sampled off northeastern Vancouver Island was compared to salmonid availability. Relative availability of salmonid species was determined from catch statistics resulting from Fisheries and Oceans Canada test seine fisheries[1], which were undertaken concurrently with and in close proximity to our sampling of killer whale kills (Fig. 8). Figure 9 illustrates the species composition of salmonids caught in test fisheries during July-August, 2004. From mid July to mid August, the test catches were dominated by migrating sockeye and pink salmon, which together comprised over 90% of salmon sampled. During this period, 59 salmonid kills by resident killer whales in the area were documented, all of which were chinook (95%) or coho (5%).

Over the second half of August, 2004, chinook, chum and coho became more significant in the test catch as the sockeye migration diminished (Fig. 9). A comparison of test fishery catches and killer whale kills during 22-31 August 2004 is shown in Figure 10A. Chinook still represented > 96% of kills during this period, despite the species forming < 6% of the test catch. However, during the period of 12-18 October 2004, fall-migrating chum salmon comprised 97% of the test fishery catch (Fig. 10B). During this period, chum was the predominant salmonid taken by feeding killer whales, though chinook still represented 5% of kills despite being extremely scarce in test catches (1 of 57,435 salmon sampled).

To evaluate whether resident killer whales foraged selectively for larger-sized salmonids, the age distribution of chinook salmon taken by whales was compared to the age distribution of chinook available to them for waters off northeastern Vancouver Island in 2000-2004. Relative abundance of chinook age classes was determined from estimates developed by the Pacific Salmon Commission Joint Chinook Technical

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[1] Data available from http://www-ops2.pac.dfo-mpo.gc.ca/xnet/content/salmon/testfish/default.htm

Committee[2] (R. McNicol, Pacific Biological Station, Nanaimo, BC, pers. comm.). Although killer whales took all 5 year classes available to them (Fig. 11), the frequency distributions were significantly different, with killer whales taking a greater proportion of older chinook than the proportions of ages available. The mean age of chinook taken by whales was 4.20 years (SE = 0.06, n = 124), significantly older than the mean of 3.52 years (SE = 0.03, n = 976,212) for available chinook (t = -10.3, df = 167, P<0.001). Older year classes of chinook are significantly larger and have greater masses than younger ages (Table 8).

Discussion

Cooperative foraging and food sharing

An important finding of our recent dedicated field observations of predation by resident killer whales is the extensive occurrence of sharing of salmonid prey. Sharing was involved in the majority of feeding events, and both adult and subadult whales, as well as both sexes, shared their prey. Sharing of consecutive kills, many spaced 10 min or less apart, was documented during focal observations of whale subgroups. Intentional provisioning of other whales by individuals making a kill was also regularly observed. Although sharing of salmonid prey was noted earlier in our studies of resident killer whale predation (Ford et al. 1998), the extent of this behaviour was not recognized until close focal animal and subgroup observations were undertaken during feeding sessions. Signs of prey capture, handling and consumption are subtle and easily overlooked, and consistent detection of these cues requires considerable experience and acquired skill. Given this difficulty, it is not surprising that previous descriptions of resident killer whale foraging behaviour, which were generally based on less field effort and/or on opportunistically-collected samples, have not reported food sharing (Jacobsen 1986; Heimlich-Boran 1988; Felleman et al. 1991; Hoelzel 1993; Nichol and Shackleton 1996; Saulitis et al. 2000). Hoelzel (1993), who rarely observed prey capture during his studies of foraging behaviour of southern resident killer whales, suggested that cooperative prey searching was likely involved in group foraging, but that cooperative prey capture was not. In contrast to Hoelzel's (1993) conclusion, we did observe cooperative prey capture, but more importantly we found food sharing to be an important feature of resident killer whale foraging. Our observations are consistent with reports of such behaviours in other killer whale populations. Cooperative hunting and sharing appears to be characteristic of killer whale predation on a wide variety of prey types, including cetaceans (Silber et al. 1990; Jefferson et al. 1991; Ford et al. 1998, in press; Pitman et al. 2001), pinnipeds (Lopez and Lopez 1985; Hoelzel 1991; Baird and Dill 1995; Ford et al. 1998), sea turtles (Caldwell and Caldwell 1969; Pitman and Dutton 2004), sharks (Fertl et al. 1996; Visser et al. 2000), rays (Visser 1999), and herring (Similä and Ugarte 1993). Herring is a comparatively small prey species for killer whales, which feed on them by encircling schools then striking at them with tail flukes to stun the fish. Herring debilitated in this manner are consumed by multiple individuals in the group, though sharing of individual fish has not been observed (Similä and Ugarte 1993; Similä 1997; T. Similä, pers. comm.).

The matrilineal social structure that appears typical of killer whale populations (Baird 2000; Ford et al. 2000) is highly conducive to the evolution of a foraging strategy dependent on cooperative food capture, sharing and provisioning (Hoelzel 1991; Connor

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[2] Pacific Salmon Commission Joint Chinook Technical Committee Report TCCHINOOK (0-4)-4: Annual Exploitation Rate Analysis and Model Calibration. Available from http://www.psc.org.

et al. 1998; Heithaus and Dill 2002). This is especially true of the resident population in British Columbia, in which dispersal of individuals from the natal group is extremely rare (Bigg et al. 1990; Ford et al. 2000). Resident killer whales pursued, captured and shared prey primarily with close kin belonging to the same matriline, which would enhance the inclusive fitness of participants due to their high degree of relatedness. Although most sharing events involved mothers and their subadult offspring, killer whales of all ages shared prey. Adult males shared the minority of their prey, but when they did so, it was with their mother or younger siblings. Adult males tended to forage alone and often at a distance from other individuals and subgroups, a tendency that has been noted previously (Jefferson 1986; Bain 1989; Hoelzel 1993; Ford 1989).

Prey fragments as indicators of diet

The validity of our data on prey selection by resident killer whales is dependent on all prey species having a reasonable – ideally equal – probability of being sampled. Concerns about potential biases of the prey fragment sampling technique that have been raised include 1) the possibility that large fish, such as chinook, are more subject to being torn up prior to consumption and thus more likely to shed scales or tissue than smaller fish, and 2) the possibility that whales foraging at depth are less likely to bring prey to the surface prior to consumption than prey captured in the upper portion of the water column (Ford et al. 1998; Baird 2000; Baird et al. 2005). Our observations suggest that neither of these potential biases is important enough to alter the patterns of prey preference we report here, at least with respect to salmonid prey. First, most feeding events, especially those with females and subadults, involved the transport of the prey item to the surface, where it was broken up for sharing or provisioning. Chinook, chum, coho, and pink salmon, which differ widely in average size (Healey 1986; Groot and Margolis 1991), were all shared, suggesting that sharing of salmonids takes place regardless of prey size. Also, the age distribution of chinook salmon taken in shared versus non-shared feeding events did not differ significantly, adding further evidence that sharing is generally independent of prey size. Thus, we conclude that salmonid prey is typically brought to the surface and torn apart for sharing and provisioning, rather than to facilitate the consumption of large prey items. It is not clear why salmonid prey is brought to the surface in non-shared feeding events, but there is no evidence that prey size is a significant factor. Second, there is no evidence that proximity to the surface affects the likelihood of salmonid prey species being represented in feeding samples. For example, fish tracking studies in the western Johnstone Strait area, where the majority of our salmonid prey samples were collected, found that chinook travelled at a mean depth of 69.9 m, compared to 14.9 m in sockeye salmon (Candy and Quinn 1999). Despite being deeper and much less abundant than sockeye in this area during July-August (Fig. 9), chinook was by far the predominant species observed in feeding events and no sockeye salmon were found in prey samples.

For the same reasons outlined above, prey fragment collection from feeding events should reveal kills of demersal, non-salmonid fish species as well as salmonids. For example, lingcod, which are known from stomach remains of a stranded resident whale (Ford et al 1998), reach similar sizes to chinook salmon and are most abundant at depths of 10-100 m, which overlap the preferred depths of chinook salmon (Cass et al. 1990; Candy and Quinn 1999). Lingcod have extremely small scales that are unlikely to be shed or recovered, but fish species identification is not reliant on scales alone. Tissue samples, from which species identity can be readily determined using molecular techniques, were collected from 60% of kills during focal animal and group sampling in 2003-04.

Prey selection

Although our data on feeding by resident killer whales are far more extensive than those reported in Ford et al. (1998), they are still mostly confined to only half the year, May-October. During this period, salmonids are clearly the preferred prey type of resident killer whales, representing over 98% of identified prey. The only non-salmonids found were a Pacific halibut, a quillback rockfish, a yelloweye rockfish, and 3 herring. Although the halibut was eaten, both rockfish were abandoned by the whales after being partially consumed. We suspect that rockfish may be an undesirable prey type due to their prominent dorsal spines, as this part of the fishes' body was discarded. It seems unlikely that the herring were targeted prey items, since herring scales were collected only during feeding sessions involving chinook prey. As chinook feed extensively on herring (Healey 1991), it is likely that herring scales may have been released when whales killed and broke chinook apart or were left in the water after chinook kills of herring.

Chinook is the predominant salmonid species taken by resident whales during May-August. This is not surprising for May and June, since chinook is the primary salmonid found in nearshore waters during these months (Groot and Margolis 1991; Quinn 2005). However, chinook remains the predominant prey species in July and August, when migrating sockeye and pink salmon form the overwhelming majority of salmonids available to the whales (Figure 9; Nichol and Shackelton 1990; Groot and Margolis 1991; Wydoski and Whitney 2003; Quinn 2005). With only a single sockeye kill sample collected, it seems that this species is rare in the diet of resident killer whales. Pink salmon were also very uncommon in our samples, and it is noteworthy that kills were made mostly by subadult whales. Like sockeye, pink salmon does not appear to be a significant component of the diet of resident killer whales. Coho salmon are relatively uncommon throughout these months (Groot and Margolis; Wydoski and Whitney 2003; Quinn 2005), but were also consistently represented in small numbers in killer whale feeding events.

During the months of September and October, the diet of northern resident killer whales in waters off northeastern Vancouver Island shifts to predominantly chum salmon, though chinook are also taken frequently. This period coincides with the migration of chum salmon through the area, which starts in mid September, peaks in mid October, and is over by late October (Ryall et al. 1999). It appears likely that southern resident whales also target chum salmon in addition to chinook in the fall, as their movement into waters of Puget Sound in late October and November coincides with migratory aggregations of these species (Osborne 1999).

Comparisons of prey selection by different resident communities and clans revealed few significant differences, though these comparisons were constrained by small sample sizes for some groups. Northern and southern resident communities both fed predominantly on chinook. The greater proportion of chum in the samples of northern resident clans A and G likely resulted from their presence in western Johnstone Strait during September-October, 2003-04, when extensive field sampling was undertaken. Little sampling of southern resident feeding events during fall has yet been undertaken. The rare steelhead and sockeye salmon kills were observed only in southern residents, but this might be due to chance as a result of such small sample sizes. Different age and sex classes of residents did show some differences in salmonid prey selection. Chinook, chum and coho were taken by both adults and subadults and by both sexes, but adult males took a significantly higher proportion of chum salmon than did adult females. This may be a result of their tendency to forage further offshore and over deeper water than females. Baird et al. (2005) observed male southern residents to dive deeper more frequently than adult females. Bain (1989) suggested that adult males may forage apart from females to reduce competition, and that their larger body size may allow them to dive more deeply than females, and take larger prey than females. However, we noted no difference in the mean ages of chinook taken by the two sexes. As already noted, juveniles were responsible for all pink salmon kills where the age class of whale was determined.

Prey selection by predators is influenced by several factors, including rates of encounters with a prey species and its profitability, which is determined by the prey item's net energy value and the amount of time needed to catch and handle it (Stephens and Krebs 1986; Scheel 1993; Bowen et al. 2002). Important determinants of prey preference of resident killer whales are likely a prey species' body size and energy density as well as its seasonal availability. Chinook salmon are the largest of the salmonids, commonly reaching masses of 10-20 kg (Healey 1991; Brett 1995; Quinn 2005), and also have the highest average lipid content (Stansby 1976; Healey 1986; Brett 1995; Osborne 1999; Winship and Trites 2003), and thus would have the greatest net energy value per fish. It seems reasonable that this species would be chosen over other available salmonids, provided search and prey handling time does not reduce its relative profitability. Prey size and energy value appears to be important factors in prey selection by fish-eating killer whales in other regions. In Prince William Sound, Alaska, Saulitis et al. (2000) found that resident killer whales preyed selectively on coho salmon, which are larger and have higher lipid content than the far more abundant pink that were available to the whales during their study. Chinook are rare in Prince William Sound during July-August, when prey sampling was conducted (Saulitis et al. 2000).

Killer whales in Prince William Sound and in the Bering Sea are also known to take fish from longline fisheries, but they do so selectively according to energy value and size. Pacific halibut, sablefish and Greenland turbot (*Reinhardtius hippoglossoides*) are among the favoured species, and the whales take the largest individuals of these species from the fishing lines while ignoring other species such as Pacific cod (*Gadus macrocephalus*), walleye pollock (*Theragra chalcogramma*), and rockfish (*Sebastes* spp.) (Matkin and Saulitis 1994; Yano and Dahlheim 1995). Favoured species have higher average lipid content and energy densities than species that are shunned (Stansby 1976; Winship and Trites 2003).

Chum salmon, which are the predominant prey taken by northern residents in the fall, are relatively large at a mean mass of 5.0 kg (Salo 1991), almost twice the size of sockeye (mean mass = 2.73 kg; Burgner 1991) and more than double the size of pinks (mean masses = 1.7-2.4 kg; Heard 1991). They are also larger than coho (mean mass = 2.95 kg; Sandercock 1991), but tend to have lower lipid content than these other salmonids (Stansby 1976; Brett 1995). Chinook still seems to be taken preferentially in late September-October, but the species' abundance is lower than during July-August and it represents a smaller proportion of the diet of resident whales. Sockeye and pink salmon are not available in significant numbers at this time of year.

Although reasons for the shift to chum as the principal prey of residents in fall are apparent, it is less clear why sockeye and pink salmon are not preyed upon to any significant degree during their migration through coastal waters in July-August. Although the net energy value per fish is lower than chinook, the vastly greater abundance of these two species should make them a potentially profitable choice of prey. Sockeye, which range in length from 537-602 mm (Healey 1986), are small relative to chinook, but their size does overlap with that of 2 year old chinook, which were taken by resident whales. It seems likely that the strong preference for chinook salmon is related to their consistent year-round availability as a prey resource for resident killer whales. Chinook tend to mature at a greater age than other salmonids and, unlike most other salmonids, can be found throughout the year in nearshore waters of the region (Healey 1991). The timing of adult migration is highly variable, and different populations of chinook can may enter freshwater from mid-spring and through into the fall (Healey 1991). Migrating chinook also tend to travel at a slow rate of speed compared to other salmonids (Candy and Quinn 1999). Sockeye, chum, and pink salmon, on the other hand, have oceanic distributions most of their lives and only pass through coastal regions en route to spawning rivers (Groot and Margolis 1991). The timing of their migration through coastal waters is relatively narrow, and they move quickly to spawning rivers (Candy and Quinn 1999). The oceanic range of these salmonids is vast (Groot and Margolis 1991), with fish distributed widely at densities that are likely too low for whales to effectively utilize. Although resident killer whales range extensively up and down the coast, there is no evidence that they undertake long distance movements to offshore areas (Ford et al. 2000). Sockeye, chum, and pink salmon, the three most abundant salmonids in the North Pacific, are thus only available for predation by residents for a small portion of the year compared to chinook salmon.

During May-June, northern residents are generally found along the coasts of the northern mainland of British Columbia and the Queen Charlotte Islands, where they congregate in areas of high chinook density and feed primarily on this species (Ford et al. 2000; Ford and Ellis, unpubl. data). This period coincides with the earliest of chinook runs in the region, which are destined for the Skeena and Nass Rivers (Riddell 2004). During early July, they begin to occur regularly off northeastern Vancouver Island, concurrently with an increase in chinook abundance in the area and the arrival of migrating sockeye and pink salmon. From mid July to late August, when sockeye and pink are transiting these waters, chinook salmon are also available at relatively high densities. Although their absolute abundance is far lower than these smaller species, there are likely sufficient numbers of chinook available to meet the needs of resident whales without their switching to pink and sockeye.

Killer whale populations throughout the world exploit a variety of different prey types and typically employ specialized foraging tactics in order to do so (Hoelzel 1991; Guinet 1991; Baird 2000; Saulitis et al. 2000; Pitman and Ensor 2003). These tactics appear to be learned traditions that are passed across generations by imitation or, in one documented case, by apparent teaching (Hoelzel 1991; Guinet and Bouvier 1995; Ford et al. 1998). As chinook salmon are the preferred prey of residents for at least half the year, and possibly year-round, these whales likely have foraging tactics that are highly adapted for the exploitation of this species. This specialization may determine the distribution patterns of resident whales which, as described above, appear to coincide with the movements of chinook salmon. Residents may also be particularly skilled at finding and capturing chinook, which tend to travel more individually, at greater depths and closer to shore than smaller, schooling salmonids (Groot and Margolis 1991; Candy and Quinn 1999). The echolocation signals of resident killer whales are well suited for the detection of echoes from individual chinook at ranges of 100 m or more (Au et al. 2004).

Killer whales are generally predators of large-bodied animals, and salmonids are at the small end of the size range of their preferred prey types. Resident killer whales that have foraging tactics specialized for capturing solitary prey such as chinook may not be adept at exploiting smaller, schooling salmonids such as pink and sockeye salmon. Efficient predation of these species would probably require elaborate tactics such as the unusual 'carousel' technique utilized by killer whales to feed on herring in northern Norway (Similä and Ugarte 1993). It is noteworthy that resident killer whales do not target the large seasonal concentrations of spawning herring that occur in coastal waters throughout their range.

A major gap in our knowledge of resident killer whale feeding ecology is their diet during November-April. Chinook remain available during these months in the summer and fall concentration areas of resident killer whales, but mostly at low densities (B. Riddell, Pacific Biological Station, Nanaimo, B.C., pers. comm.). Whales disperse from these areas during winter and spring, but their whereabouts are for the most part unknown (Ford et al. 2000; Wiles 2004). Their prey may shift in winter and early spring to include more non-salmonid fish, but there is little evidence to determine the extent to which their diet may change. The stomach of a northern resident whale that died in mid- to late-November off northeastern Vancouver Island contained remains of chinook salmon and a variety of demersal fish species, including lingcod, sablefish, and greenling (Ford et al. 1998). It is probable that the resident killer whales' preference for chinook continues throughout the winter, and that they travel more widely over remote parts of the coast in pursuit of this species. The winter range of chinook salmon is not well known, but likely includes waters off the northern British Columbia coast and southeastern Alaska (B. Riddell, pers. comm.). Future studies will be needed to find resident whales during these months, and to determine whether chinook salmon is indeed their prey of choice throughout the year.

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Table 1. Evidence for 487 kills by resident killer whales documented during 1974-2004.

Evidence of predation	Number of kills	%
Observation only	61	12.5
Both tissue and scale samples	84	17.2
Tissue samples only	32	6.6
Scale samples only	310	63.7
Total	487	100

Table 2. Species composition of fish killed in 487 feeding events during 1974-2004 in different B.C. coastal regions. Species identity was determined by scale analysis or from DNA evidence. *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, 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
North coast and QCI	1-6	33	21	4	0	0	0	0	1[a]	6	1
Central coast	7-11	65	47	3	1	1	0	0	0	11	2
NE Vancouver Island	12-13	325	177	76	6	12	0	0	2[b]	45	7
SE Vancouver Island	14-19, 28-29	46	27	2	2	0	1	2	1[c]	10	1
W Vancouver Island	20-27	18	14	0	0	0	0	0	2[d]	2	0
Total		487	286	85	9	13	1	2	6	74	11
% of identified salmonids			72.2	21.5	2.3	3.3	0.3	0.5			

[a] – 1 Pacific halibut
[b] – 1 yelloweye rockfish, 1 herring
[c] - 1 quillback rockfish
[d] – 2 herring

Table 3. Ages of 317 salmonids killed by resident killer whales. Ages given are in the European system, in which years in fresh water after hatching and years in salt water are identified and separated by a period (see Groot and Margolis 1991).

Species	*n*	Age											
		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	219	1	26	87	46	1	3	16	28	9	1		1
Coho	9						8					1	
Chum	77			49	26	2							
Pink	12	12											

Table 4. Salmonid species sampled from resident killer whale feeding events by month, 1974-2004. *n* = 396 kills.

Month	Species					
	Chinook	Chum	Coho	Pink	Sockeye	Steelhead
May	19	0	0	0	0	0
Jun	21	4	0	0	0	0
Jul	87	8	1	0	1	0
Aug	139	3	4	11	0	0
Sep	11	22	1	2	0	0
Oct	8	48	3	0	0	0
Nov	1	0	0	0	0	1
Dec	0	0	0	0	0	1
Total	286	85	9	13	1	2

Table 5. Incidence of sharing in feeding events by resident killer whales where age and/or sex class of individuals making kills could be determined.

Sharing	Age/sex class			Total
	Adult Male	Adult Female	Subadult	
Yes	9	97	36	142
No	44	4	9	57
Total	53	101	45	199

Table 6. Sex and/or age class of whales observed to make kills, and the sex and/or age class and relationship of individuals sharing the prey, in 128 feeding events where it was possible to record such data. The 'subadult' category includes whales from 1-12 years old.

Whale making kill	Individual(s) sharing	*n*	%
Adult female	Subadult offspring	47	52.2
	Adult son	7	7.8
	Offspring & other matriline member(s)	19	21.2
	Other matriline member(s) (not offspring)	10	11.1
	Outside matriline	7	7.7
	Total	90	100
Adult male	Mother	3	37.5
	Subadult siblings	5	62.5
	Total	8	100
Subadult	Mother	2	6.7
	Grandmother	1	3.3
	Mother & sibling(s)	9	30.0
	Sibling(s)	15	50.0
	Sibling(s)s & other subadult in matriline	3	16.7
	Total	30	100

Table 7. Incidence of sharing of different salmonid species killed in feeding events.

Sharing	Prey species				Total
	Chinook	Chum	Coho	Pink	
Yes	141	29	3	1	174
No	27	24	3	1	55
Total	168	53	6	2	229

Table 8. Mean fork lengths and mass (± SE) of chinook salmon at different ages. Data are from seine caught fish in the Mark Recovery Program of Fisheries and Oceans Canada (Kuhn 1988).

Age (years)	Length (mm)	Mean mass (kg)	*n*
2	425 ± 1.19	1.1 ± 0.01	3072
3	581 ± 2.14	3.1 ± 0.04	3206
4	808 ± 3.43	8.5 ± 0.11	917
5	939 ± 4.21	13.3 ± 0.20	426
6	961 ± 15.0	13.7 ± 0.72	37

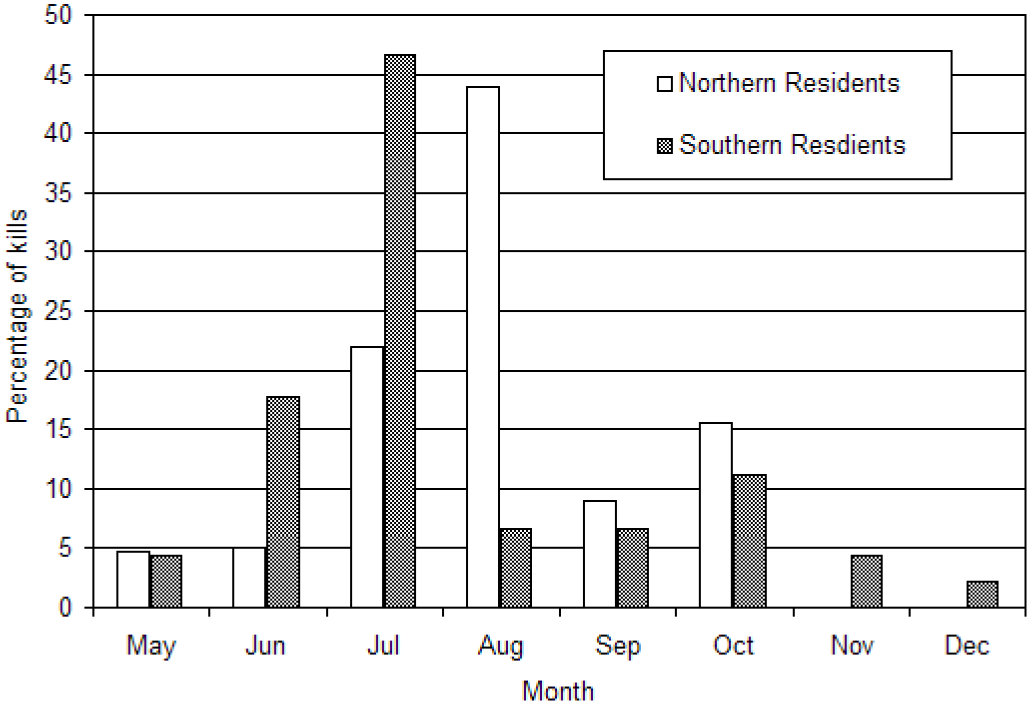


Figure 1. Frequency distribution of feeding events by northern (open bars) and southern (closed bars) resident killer whales. Residents were encountered rarely during January through April, and no feeding events were documented during this period.

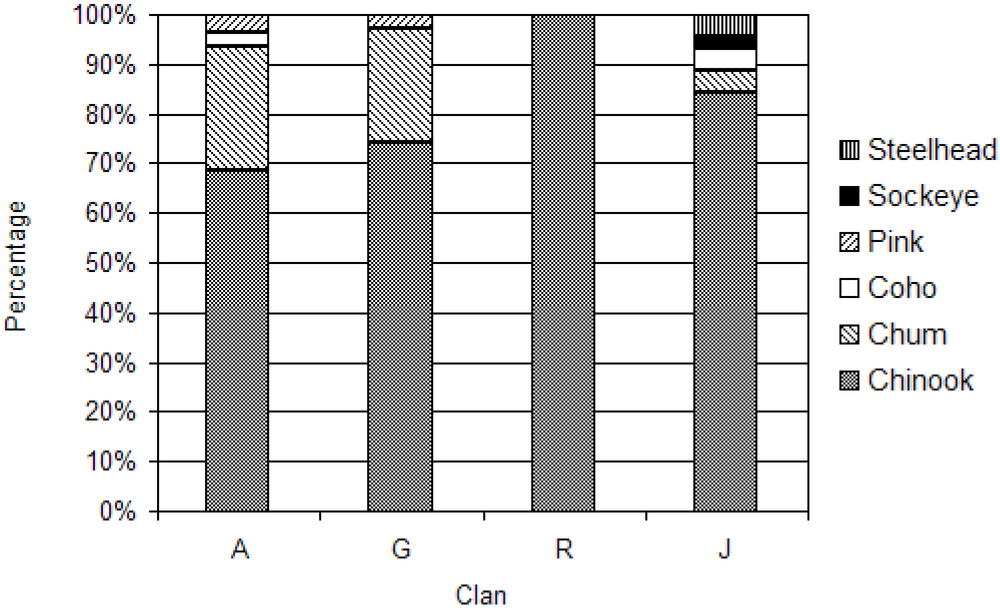


Figure 2. Frequency distribution of salmonid species taken by the three northern resident clans, A (*n* = 254), G (*n* = 70), and R (*n* = 16), and the southern resident J clan (*n* = 46).

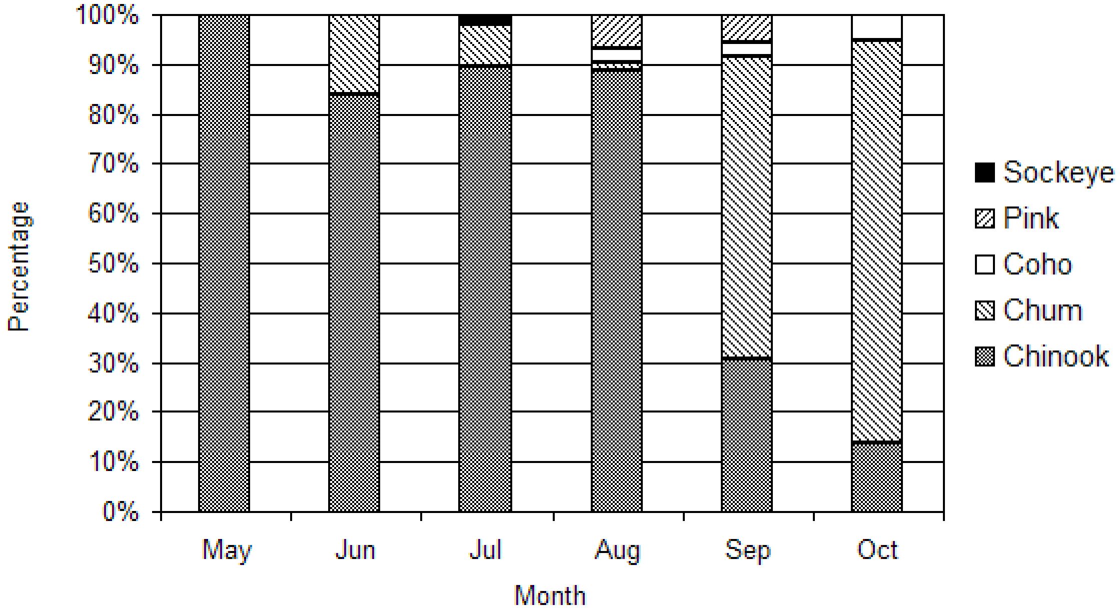


Figure 3. Frequency distribution of salmonid species in resident killer whale feeding events during May-October, based on data provided in Table 4 (*n* = 396 kills).

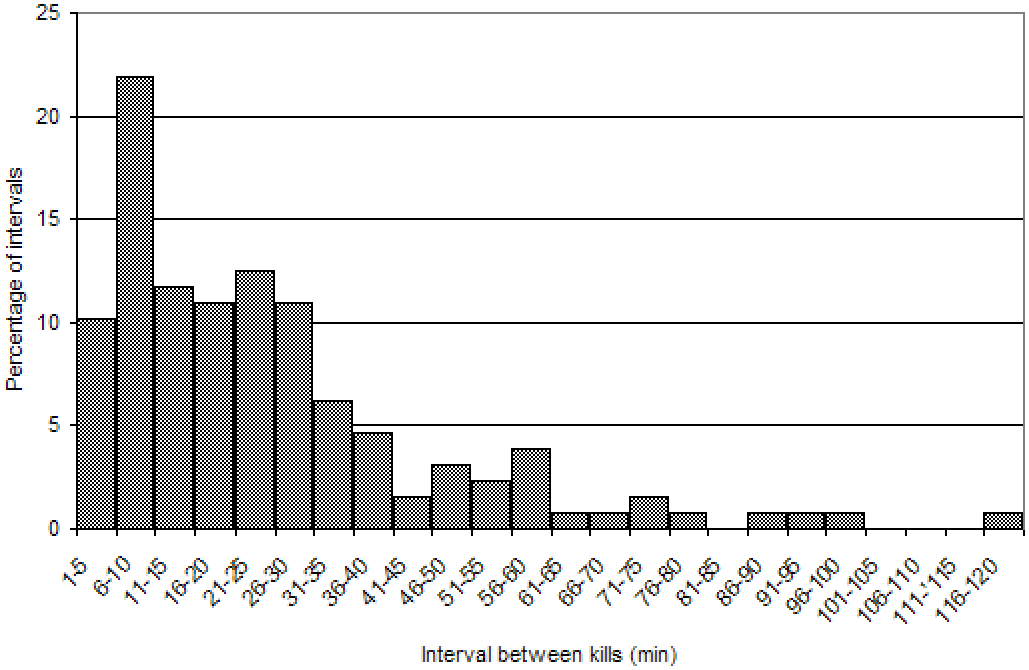


Figure 4. Intervals between consecutive kills during feeding sessions by focal subgroups and individuals. *n* = 170 kills during 34 sessions.

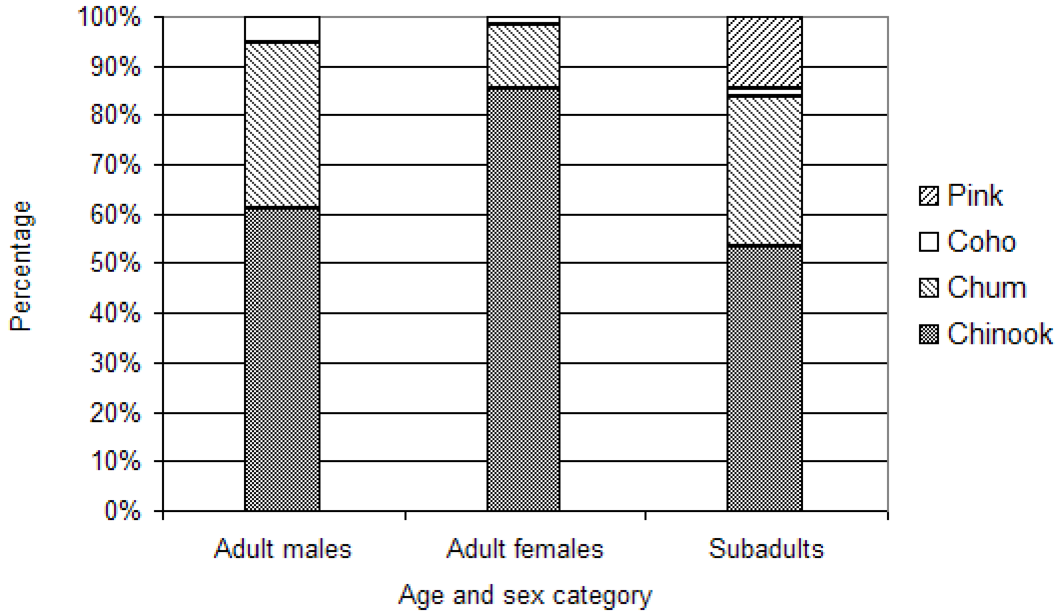


Figure 5. Salmonid species killed by different age and sex category of resident killer whales. *n* = 77 kills by adult males, 122 by adult females, and 75 by subadults.

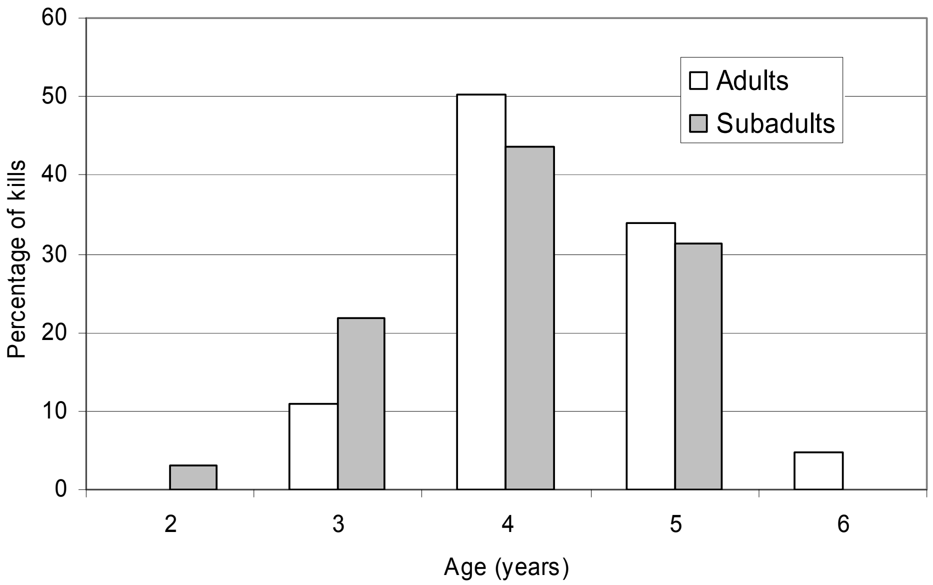


Figure 6. Age distribution of chinook salmon taken by adult (*n* = 127 kills) and subadult (*n* = 32 kills) resident killer whales.

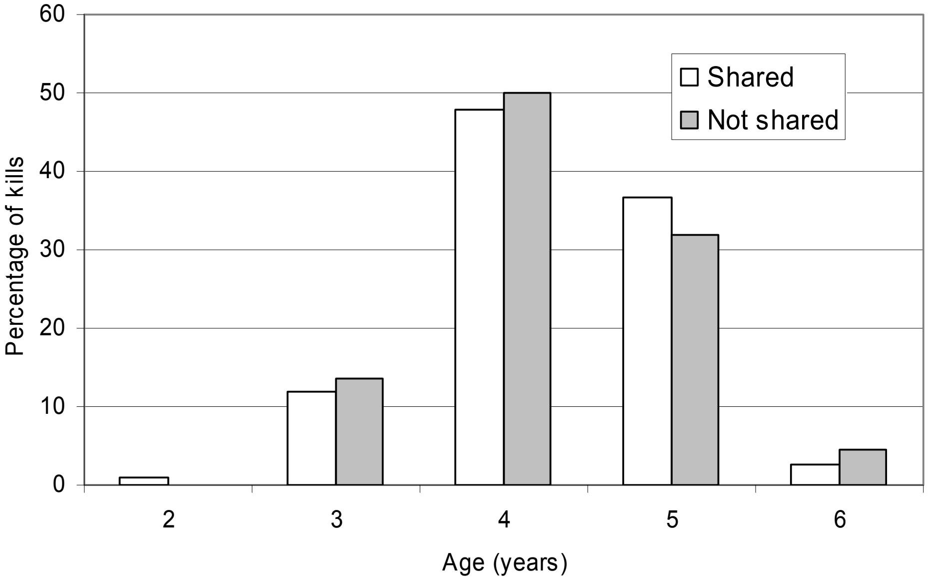
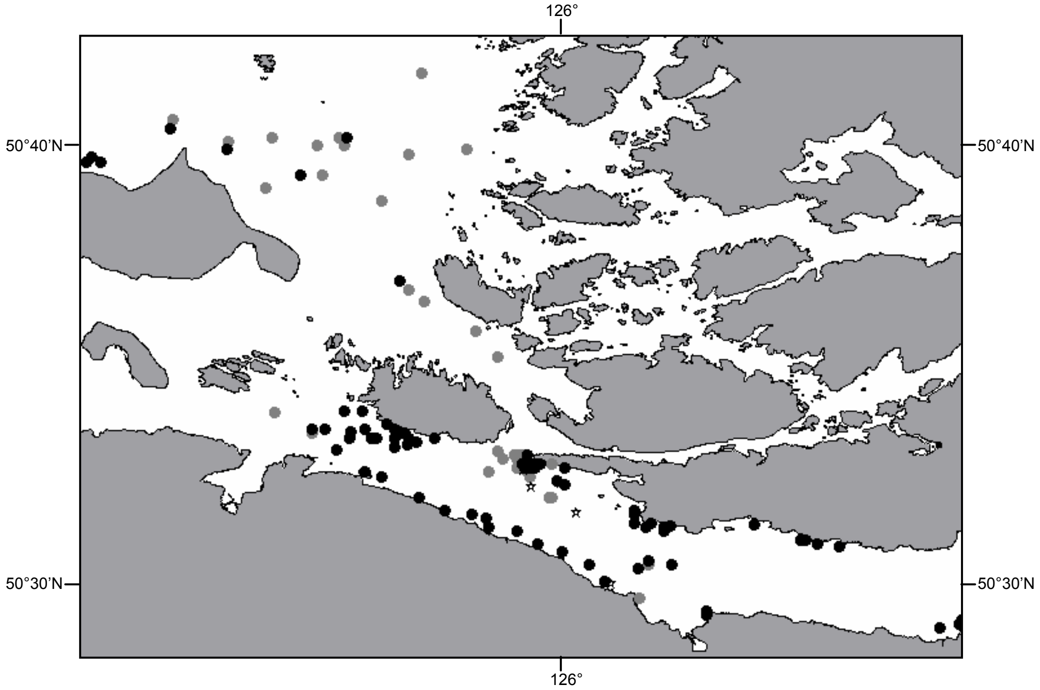


Figure 7. Age distribution of chinook salmon taken in shared (*n* = 144 kills) and non-shared (*n* = 46 kills) feeding events.

A. Locations of salmonid feeding events



B. Locations of test seine fishery sets

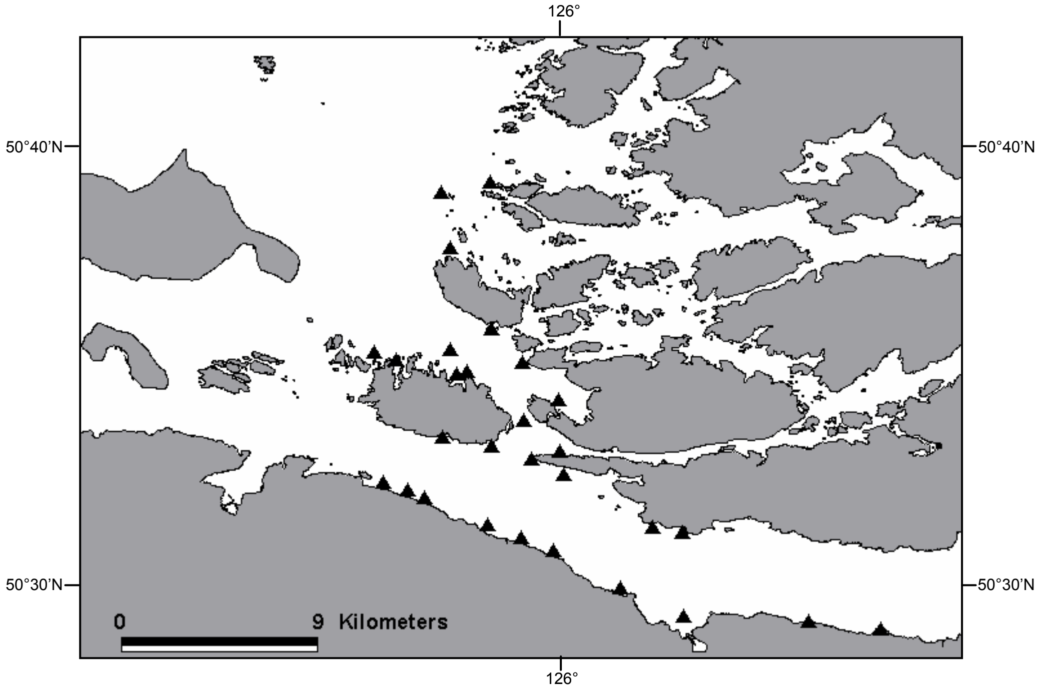


Figure 8. Locations of feeding events by killer whales and test seine fishery set locations, western Johnstone Strait, B.C., July-October 2004. A) Locations of kills of chinook (black circles), chum (grey circles) and coho (stars) salmon; B) Locations of seine test fishery sets (black triangles).

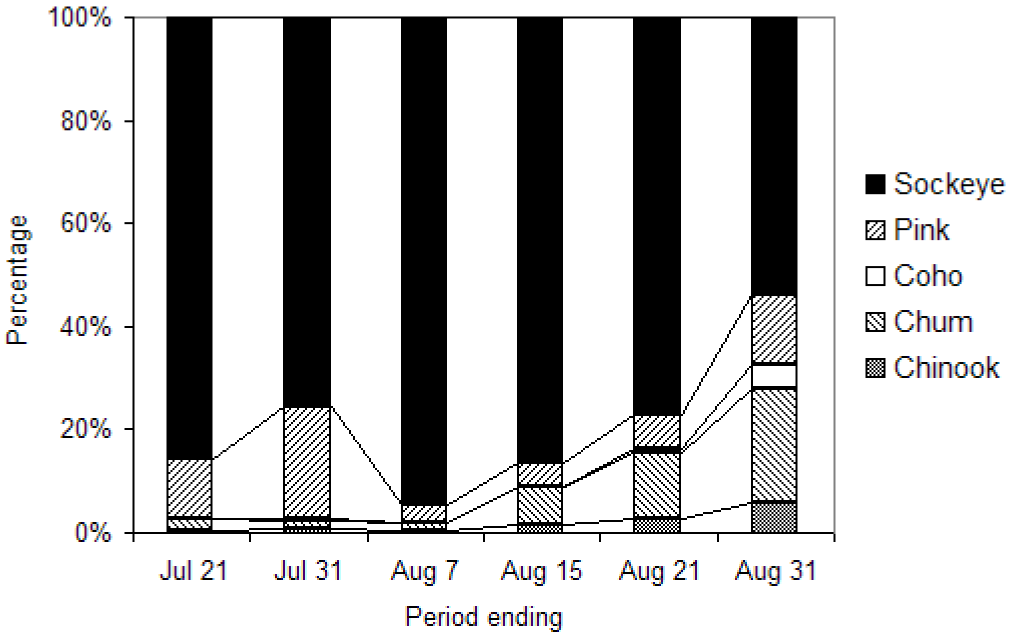
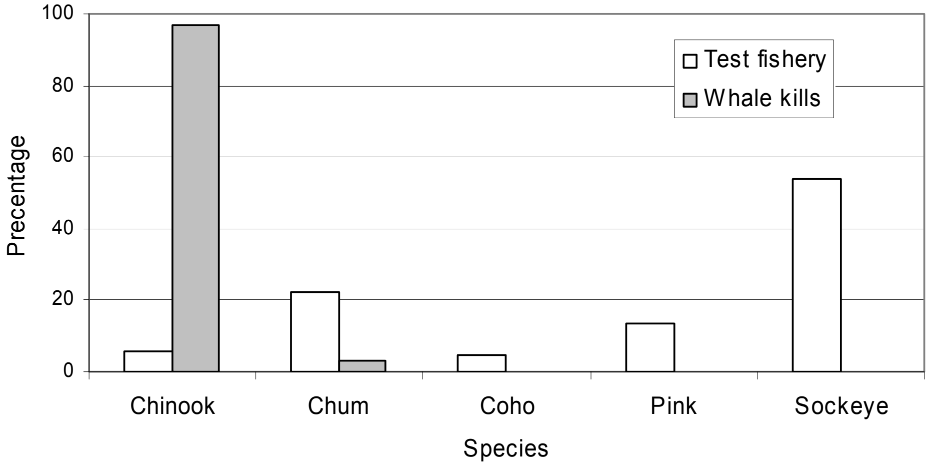


Figure 9. Species composition of salmonids caught during test seine fisheries in western Johnstone Strait, July-August 2004. *n* = 69,847 fish caught in 245 sets.

A. 22-31 August 2004



B. 12-18 October 2004

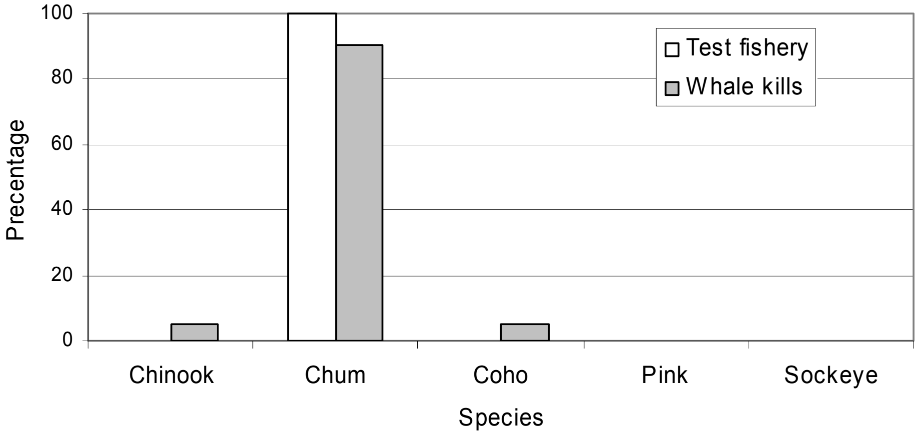


Figure 10. Species composition of salmonids caught in test seine fisheries and by resident killer whales in the western Johnstone Strait area, 22-31 August (A) and 12-18 October (B), 2004. Samples sizes were: August - 1548 (test fishery) and 30 (whale kills), October - 57435 (test fishery) and 41 (whale kills).

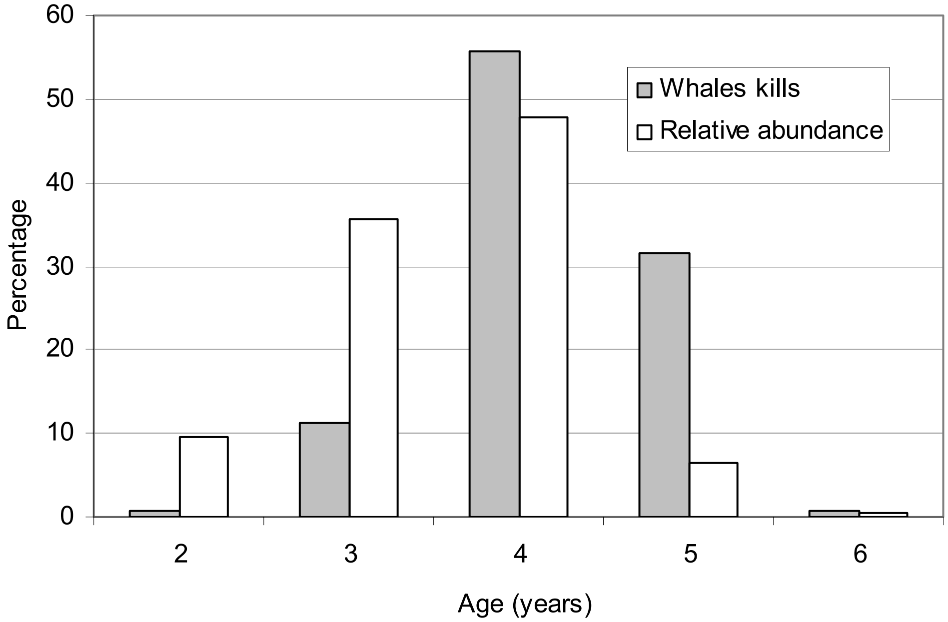


Figure 11. Age distribution of 124 chinook salmon fed upon by resident killer whales in Pacific Fisheries Management Area 12 (northeastern Vancouver Island) during 2000-2004, compared to the relative abundance of chinook age classes estimated to have been available to them in the area during the same period. Age distribution of available chinook was derived from cumulative abundance estimates of 976,212 fish over the 5-year period.