Dietary specialization in two sympatric populations of killer whales (*Orcinus orca*) in coastal British Columbia and adjacent waters

John K.B. Ford, Graeme M. Ellis, Lance G. Barrett-Lennard, Alexandra B. Morton, Rod S. Palm, and Kenneth C. Balcomb III

Abstract: Two forms of killer whale (*Orcinus orca*), resident and transient, occur sympatrically in coastal waters of British Columbia, Washington State, and southeastern Alaska. The two forms do not mix, and differ in seasonal distribution, social structure, and behaviour. These distinctions have been attributed to apparent differences in diet, although no comprehensive comparative analysis of the diets of the two forms had been undertaken. Here we present such an analysis, based on field observations of predation and on the stomach contents of stranded killer whales collected over a 20-year period. In total, 22 species of fish and 1 species of squid were documented in the diet of resident-type killer whales; 12 of these are previously unrecorded as prey of *O. orca*. Despite the diversity of fish species taken, resident whales have a clear preference for salmon prey. In field observations of feeding, 96% of fish taken were salmonids. Six species of salmonids were identified from prey fragments, with chinook salmon (*Oncorhynchus tshawytscha*) being the most common. The stomach contents of stranded residents also indicated a preference for chinook salmon. On rare occasions, resident whales were seen to harass marine mammals, but no kills were confirmed and no mammalian remains were found in the stomachs of stranded residents. Transient killer whales were observed to prey only on pinnipeds, cetaceans, and seabirds. Six mammal species were taken, with over half of observed attacks involving harbour seals (*Phoca vitulina*). Seabirds do not appear to represent a significant prey resource. This study thus reveals the existence of strikingly divergent prey preferences of resident and transient killer whales, which are reflected in distinctive foraging strategies and related sociobiological traits of these sympatric populations.

Résumé : Deux formes de l'Épaulard (*Orcinus orca*), une forme résidante et une forme errante, vivent en sympatrie dans les eaux côtières de la Colombie-Britannique, du Washington et du sud-est de l'Alaska. Les deux formes vivent indépendamment l'une de l'autre et ont une répartition saisonnière, une structure sociale et un comportement distincts. Ces distinctions sont généralement attribuées à des différences apparentes dans leur régime alimentaire, mais aucune analyse comparative exhaustive de ces régimes alimentaires n'a jamais été faite. Nous avons entrepris une telle analyse par étude de la prédation en nature et par examen des contenus stomacaux d'épaulards échoués sur une période de 20 ans. Au total, 22 espèces de poissons et 1 espèce de calmar ont été inventoriées dans le régime des épaulards résidants. Douze d'entre elles n'avaient jamais été trouvées chez *O. orca*. Malgré la diversité des poissons dans leur régime, les épaulards ont une préférence marquée pour les saumons. Au cours d'observations de l'alimentation en nature, 96% des poissons consommés étaient des salmonidés. Six espèces de salmonidés ont été identifiées à partir de fragments de proies et c'est le Saumon quinnat (*Oncorhynchus tshawytscha*) qui est la proie la plus commune. Les contenus stomacaux d'épaulards échoués démontrent également une préférence pour le Saumon quinnat. En de rares occasions, des épaulards résidants ont été aperçus harcelant des mammifères marins, mais aucune attaque mortelle n'a été observée et les contenus stomacaux des résidants ne contenaient pas de restes de mammifères. Les épaulards errants observés n'ont consommé que des pinnipèdes, des cétacés et des oiseaux marins. Les épaulards ont attaqué six espèces de mammifères, mais plus de la moitié des animaux attaqués étaient des Phoques communs (*Phoca vitulina*). Les oiseaux marins ne semblent pas être des proies recherchées. Cette étude met en relief les différences importantes de préférence de proies entre les épaulards résidants et les épaulards errants, ce qui se reflète dans les stratégies

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distinctives de quête de nourriture et les caractéristiques sociobiologiques associées chez ces populations sympatriques.

[Traduit par la Rédaction]

Introduction

Killer whales (*Orcinus orca*) are common year-round inhabitants of the coastal waters of British Columbia and Washington State. Over the years, anecdotal observations and circumstantial evidence have accumulated indicating that killer whales in the region feed upon a variety of marine mammals and fish. Early reports of killer whale predation mentioned the harbour seal (*Phoca vitulina*), Steller sea lion (*Eumetopias jubatus*), Dall's porpoise (*Phocoenoides dalli*), gray whale (*Eschrichtius robustus*), and minke whale (*Balaenoptera acutorostrata*) (Scheffer and Slipp 1948; Hancock 1965; Pike and MacAskie 1969). Killer whales have also long been suspected of being important predators of Pacific salmon (*Oncorhynchus* spp.) because of their tendency to congregate at times and locations coinciding with the occurrence of migrating salmon and from reports by commercial fishermen of depressed salmon catches following the passage of groups of killer whales (Scheffer and Slipp 1948; Newman and McGeer 1966; Pike and MacAskie 1969). Until the 1970s, however, little more could be said of the feeding habits of killer whales, nor of the biology of the predator itself.

In 1973, M.A. Bigg and co-workers began a long-term field study of the abundance, distribution, and life history of killer whales in the coastal waters of British Columbia using photographs of natural markings to identify individual whales (Bigg et al. 1990*b*). Early in this study it became apparent that two sympatric populations of killer whales inhabited the region (Bigg et al. 1976).[2] Comparatively large groups of whales that had a stable composition and could be found predictably in certain areas during the summer months were termed *residents*. Smaller groups that were encountered sporadically and did not associate with the larger groups were thought to be in transit from one area to another and were termed *transients*. Over the past two decades, additional studies have indicated that residents and transients represent two distinct, socially isolated forms of the species, which differ in morphology, genetics, social organization, diving and movement patterns, vocal behaviour, and apparent dietary preferences (Ford 1984; Bigg et al. 1985, 1987, 1990*a*, 1990*b*; Baird and Stacey 1988; Heimlich-Boran 1988; Bain 1989; Stevens et al. 1989; Hoelzel and Dover 1990; Morton 1990; Felleman et al. 1991; Baird 1994; Barrett-Lennard et al. 1996). Residents appear to feed primarily on fish, especially salmon, whereas transients appear to feed on marine mammals.

Our understanding of the differences in diet between the two populations of killer whales has been limited by a paucity of direct data, particularly concerning the resident form. Several studies of resident killer whales have shown correlations between the distribution of whales and various species of Pacific salmon, but have provided little or no direct evidence of salmon predation (Balcomb et al. 1982; Heimlich-Boran 1986, 1988; Jacobsen 1986; Guinet 1990; Felleman et al. 1991; Hoelzel 1993; Nichol and Shackleton 1996). Although whales have been observed in apparent pursuit of salmon, actual consumption levels and prey species identity have rarely been documented. Non-salmonid fishes have not been reported in the diet of resident killer whales. More direct evidence of prey species composition has been obtained for transient killer whales, probably because attacks on mammals are more conspicuous than attacks on fish. Documented predation has predominantly involved harbour seals (Baird and Stacey 1988; Heimlich-Boran 1988; Felleman et al. 1991), although Baird and Dill (1995) reported transients off southern Vancouver Island also preying on harbour porpoises (*Phocoena phocoena*), sea lions (species unknown), and a northern elephant seal (*Mirounga angustirostris*). Despite suggestions that transients feed on bottom-dwelling fish (Heimlich-Boran 1988; Felleman et al. 1991), no evidence to support this is available.

In this paper we examine the nature and extent of diet specialization in resident and transient killer whale populations in coastal British Columbia and contiguous waters of Washington State and southeastern Alaska. Our data are derived from two sources: (1) observations of predatory events and documentation of prey species by visual means or by systematic retrieval of prey fragments, especially fish scales, and (2) remains of prey found in beached carcasses of killer whales. These data represent the first comprehensive description of the feeding habits of resident and transient killer whales over a wide portion of their range, and provide a foundation for interpreting the evolution and maintenance of divergent foraging strategies and related sociobiological traits of these sympatric yet distinct populations.

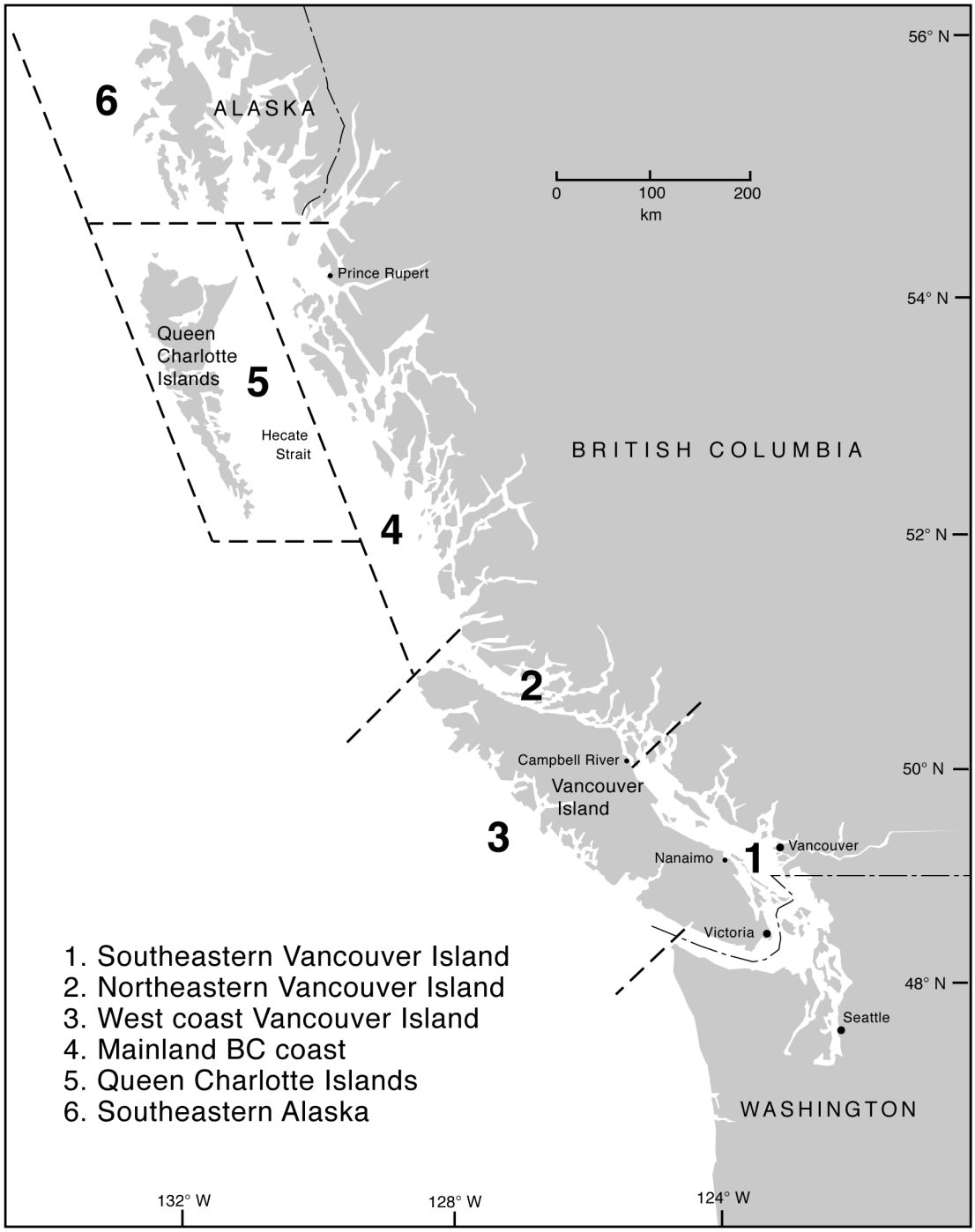
Materials and methods

Study area and populations

Studies were undertaken during 1973–1996, primarily in the nearshore waters of Vancouver Island, mainland British Columbia, and the Queen Charlotte Islands, and secondarily in adjacent coastal waters of Washington State and southeastern Alaska (Fig. 1). Both resident and transient killer whales occur throughout most of the region, but the two forms differ in seasonal abundance and distribution. The resident population is comprised of separate *northern* and *southern* communities with approximately 300 whales in total (1993 census; Ford et al. 1994). These communities are comprised of stable, matrilineal kinship groups (*pods*) typically containing 10–25 whales. The southern resident community contained three pods with a total of 96 whales in 1993. During May to October this community is found mainly in the protected waters off southeastern and southern Vancouver Island, and occasionally off the southwest coast of the island. The northern resident community consisted of 16 pods with 200 whales in 1993. This community ranges from central Vancouver Island north along the mainland coast to a latitude of at least 56°N, in southeastern Alaska. Sum-

[2] M.A. Bigg, I.B. MacAskie, and G. Ellis. 1976. Abundance and movements of killer whales off eastern and southern Vancouver Island with comments on management. Unpublished report by the Arctic Biological Station, Department of Fisheries and Environment, Ste.-Anne-de-Bellevue, Quebec.

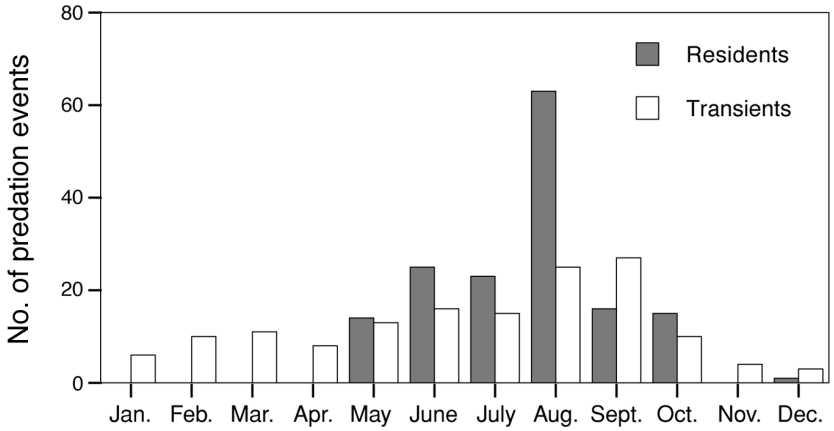
Fig. 1. Study region and subareas 1–6. Sample sizes by subarea for predation events and stomach contents are shown in Tables 1 and 5, respectively.



mer concentrations of northern resident pods occur off northeastern Vancouver Island and in channels along the northern mainland coast of British Columbia. Northern community pods have seldom been observed near the Queen Charlotte Islands. Despite some overlap in range off central Vancouver Island, pods from northern and southern communities have not been seen to mix. The range of most resident pods in winter is unknown, as is the extent of offshore movements at any time of year. Resident pods have been documented in coastal waters during all months of the year, but large aggregations are only seen in summer (Bigg et al. 1976 (see footnote 2), 1990*b*).

A total of 179 whales had been identified in the transient population by 1995, but the sporadic occurrence of many individuals precludes a precise population census (G.M. Ellis, unpublished data). The transient population's range includes coastal waters from central California to approximately 59°N in southeastern Alaska, including the Queen Charlotte Islands (Bigg et al. 1987; Ford and Morton 1991; Ford et al. 1994; Goley and Straley 1994). The extent of their range in offshore areas is unknown. Transients typically travel in groups of 6 or less, although groups occasionally join to form temporary associations of 10 or more whales. The social structure of transients is less stable than that of residents, and

Fig. 2. Numbers of observed predation events by month for resident and transient killer whales.



dispersal of individuals from natal groups has been documented (Bigg et al. 1990*b*; Ford et al. 1994). Like residents, transients can be found in the study area year-round, but they show less pronounced seasonal variation in abundance than do residents (Fig. 2; see also Bigg et al. 1987; Baird and Dill 1995). The occurrence of particular transient groups is less predictable than that of resident pods.

Field procedures

Whales were encountered throughout the year, although most field effort and observations of feeding behaviour took place from June to September, especially for resident whales (Fig. 2). Killer whales were encountered mostly by patrolling waters that they were known to frequent. In some areas, they were located with the help of volunteer observers, who reported whale sightings by telephone or marine VHF radio. Observations were made from a variety of vessels ranging in length from 5 to 20 m. Individual whales present during each encounter were identified visually or from photographs of the dorsal fin and back. Photographic identification procedures are described in Bigg et al. (1987, 1990*b*) and Ford et al. (1994). The majority of observations of predation were recorded during the course of studies that focused on other aspects of the animals' biology, especially during the 1970s and 1980s. Higher priority was given to diet studies during 1990–1996, and about 50% of observations were made during these years. Approximately 15% of predation records were contributed by colleagues (see Acknowledgements).

Incidents of predation or attempted predation were determined from surface observation of interactions between whales and potential prey species. Observations were often made with the aid of binoculars, and some incidents were also recorded photographically with still or video cameras. To collect prey remains, particularly of fish, for species identification, we used the following procedure. Surface behaviours of whales, such as rapid acceleration, sudden direction changes, or circling, often indicated that hunting was taking place. When such behaviours were observed we waited until the whales moved on, then approached the site while it was still marked by changes in the texture of the sea surface. We then swept the water in the vicinity with a fine-mesh dip net with a 4-m handle, taking particular care to retrieve any visible remains. Fish scales recovered in this way were examined for the purpose of species identification and ageing by the Fish Aging Laboratory, Pacific Biological Station (Department of Fisheries and Oceans, Nanaimo, B.C.).

Definitions of observed predation events

Incidents that yielded visual or physical evidence that a prey species was killed and consumed are referred to as *kills*. Visual evidence of kills included sighting portions of a prey species in the mouth of a whale or finding the remains of a kill, such as flesh, blood, or oil, floating in the water following an attack. Incidents where a whale was observed in active pursuit of another species or interacting with a species in an apparently predatory manner, but where no kill could be confirmed, are referred to as *harassments*. We generally use this term in preference to "attacks" because it cannot be assumed that all such events involved intent to kill and consume the prey species. However, many harassments probably represented a true predation attempt, but either the prey escaped or the kill took place underwater and could not be confirmed.

Table 1. Geographical distribution of observed events of predation by resident and transient killer whales.

Subarea	No. of residents	No. of transients
1. Southeastern Vancouver Island	36	37
2. Northeastern Vancouver Island	89	90
3. West coast of Vancouver Island	0	29
4. Mainland B.C. coast	36	6
5. Queen Charlotte Islands	0	24
6. Southeastern Alaska	0	7
Total	161	193

Note: Subarea boundaries are shown in Fig. 1.

Collection and analysis of stomach contents

A total of 14 beached carcasses of killer whales, stranded at different times and locations, were examined for evidence of diet. Stomachs were either excised and retained for later sorting and identification of contents, or prey remains were removed at the scene of stranding. When possible, the whale's mouth, esophagus, and intestine were also examined for prey remains. Remains of mammalian prey, mostly teeth, claws, and vibrissae, were identified from a reference collection at the Pacific Biological Station. Skeletal remains of fish were identified from a reference collection by Pacific Identifications Limited, Victoria, B.C.

Results

Observations of predation

Resident whales

A total of 161 events of predation or apparent predation were documented among individuals belonging to 17 of the 19 resident pods in the study area. Of these events, 126

Table 2. Prey involved in observed predation events (kills and harassments) by resident killer whales.

Prey species	Kill	Harassment	Total
Fishes			
Chinook salmon (*Oncorhynchus tshawytscha*)	60	2	62
Chum salmon (*O. keta*)	6	0	6
Coho salmon (*O. kisutch*)	6	0	6
Pink salmon (*O. gorbuscha*)	14	2	16
Sockeye salmon (*O. nerka*)	3	1	4
Steelhead salmon (*O. mykiss*)	2	0	2
Unidentified salmon (*Oncorhynchus* spp.)	41	9	50
Pacific herring (*Clupea pallasi*)	1	1	2
Yelloweye rockfish (*Sebastes ruberrimus*)	1	0	1
Pacific halibut (*Hippocampus stenolepis*)	1	0	1
Unidentified flatfish	0	2	2
Mammals			
Harbour seal (*Phoca vitulina*)	0	1	1
Harbour porpoise (*Phocoena phocoena*)	0	4	4
Dall's porpoise (*Phocoenoides dalli*)	0	4	4
Total	135	26	161

(78%) involved whales of the northern resident community and 35 (22%) involved southern resident animals. Slightly more than half of the predation events were observed off northeastern Vancouver Island, the remainder being divided evenly between the waters off southeastern Vancouver Island and the northern mainland coast of British Columbia (Table 1). Observations were strongly biased seasonally toward the summer, 80% of predatory events being documented during the months of June–September (Fig. 2).

The overwhelming majority of predation events by resident whales involved fish. All of the 135 confirmed kills were of fish, and of the 26 harassments observed, 17 involved fish and the remaining 9 involved three species of marine mammals. Of the 152 fish kills and harassments documented, 146 (96%) involved salmonids. The remaining 4% of events involved Pacific herring (*Clupea pallasi)*, yelloweye rockfish *(Sebastes ruberrimus*), Pacific halibut (*Hippocampus stenolepis*), and unidentified species of flatfish (Table 2).

Species identity was determined for salmonids involved in 91 kills and 5 harassments. Identifications were made from scale samples recovered from 86 kills, and from the visual appearance of the fish in the remaining 10 cases. Of the six salmonid species identified, by far the most common was chinook salmon, representing 65% of the total sample. The second most common was pink salmon at 17%, followed by chum (6%), coho (6%), sockeye (4%), and steelhead salmon (2%). Scales were collected and aged from 50 kills of chinook salmon. The majority of samples were 3–4 years old, representing estimated mean masses of 3.7–8.1 kg (Table 3). Twelve percent were aged 5–7 years, or weighed >10.5 kg, on average.

The 9 harassments of marine mammals by resident whales involved 8 Dall's or harbour porpoises, all but one of which was a juvenile or calf, and a single harbour seal pup. Pod L01, a member of the southern resident community, was responsible for 8 of the events, and the northern resident pod A04 was involved in 1 event. Most harassments involved the whales chasing, pushing, or ramming the porpoises or seal.

Table 3. Ages and estimated mean masses of 50 chinook salmon killed by resident whales.

Age (yr)	No.	Mean mass (kg)
2	2	1.2
3	17	3.7
4	25	8.1
5	4	10.5
6	1	14.7
7	1	na

Note: Mean masses are based on data for chinook salmon taken in commercial fisheries off eastern Vancouver Island and the central mainland coast of British Columbia (Argue et al. 1983; J. Candy, Department of Fisheries and Oceans, unpublished data).

In each case, the potential prey either escaped or disappeared without confirmation that it was killed or consumed.

Transient whales

A total of 193 predatory events by transient killer whales were observed. Two-thirds of these took place off northeastern or southeastern Vancouver Island, with the remainder along the west coast of Vancouver Island (15%) or in the nearshore waters of the Queen Charlotte Islands (12%) and southeastern Alaska (4%) (Table 1). Predation events were fairly evenly distributed throughout the year, although slightly more than average were documented during August–September and fewer during November–December (Fig. 2), likely because of increased survey effort during summer. A total of 106 of the 179 (60%) transient whales individually identified during the study period were observed during predation events.

All predation events caused by transients involved either mammals or seabirds. No fish were observed to be killed or harassed. Of the 130 documented kills, 94% were mammals and 6% were seabirds (Table 4). Similarly, 70% of harass-

Table 4. Species of prey involved in observed events of predation (kills and harassments) by transient killer whales.

Prey species	Kill	Harassment	Total
Mammals			
Harbour seal (*Phoca vitulina*)	72	8	80
California sea lion (*Zalophus californianus*)	4	4	8
Steller sea lion (*Eumetopias jubatus*)	8	12	20
Dall's porpoise (*Phocoenoides dalli*)	7	11	18
Harbour porpoise (*Phocoena phocoena*)	16	0	16
Pacific white-sided dolphin (*Lagenorhynchus obliquidens*)	1	3	4
Gray whale (*Eschrichtius robustus*)	0	2	2
Minke whale (*Balaenoptera acutorostrata*)	0	1	1
River otter (*Lutra canadensis*)	0	3	3
Unidentified mammal	14	0	14
Birds			
Common Loon (*Gavia immer*)	0	2	2
Western Grebe (*Aechmophorus clarkii*)	0	6	6
Common Murre (*Uria aalge*)	4	7	11
Marbled Murrelet (*Brachyramphus marmoratus*)	1	1	2
Rhinoceros Auklet (*Cerorhinca monocerata*)	2	2	4
Red-breasted Merganser (*Mergus serrator*)	0	1	1
Surf Scoter (*Melanitta perspicillata*)	1	0	1
Total	130	63	193

ments involved mammals and 30% involved birds. Identification of prey species was possible for 108 kills and 44 harassments of mammals. Of the nine species observed, the harbour seals was by far the most common, representing 53% of all kills and harassments. Other important species included the Steller sea lion (13%), Dall's porpoise (12%), and harbour porpoise (11%). California sea lions (*Zalophus californianus*), Pacific white-sided dolphins (*Lagenorhynchus obliquidens*), gray and minke whales, and river otters (*Lutra canadensis*) were uncommonly or rarely involved.

In 90% of cases involving harbour seals, the event ended with the animal being killed and consumed. In the 8 harassments of this species, the seal was not seen to escape but there was no evidence of a kill, as the animal simply disappeared underwater. Of 28 predatory incidents involving Steller or California sea lions, only 12 resulted in a confirmed kill. In the remaining 16 incidents, the sea lion was seen to escape in all but 4 cases. All 16 incidents involving harbour porpoises ended with a successful kill. This was not the case for Dall's porpoises, where only 7 of 18 predation events resulted in a confirmed kill. Nine of the 11 harassments were high-speed chases in which the porpoise appeared to escape. In all remaining incidents with mammalian prey species, harassments equalled or outnumbered confirmed kills. In most cases the potential prey was observed to escape.

No evidence that individual transients specialized on particular mammalian prey species or types was obtained. There was a strong correlation between the number of times an individual was observed in predation events and the cumulative number of different prey species killed or harassed by that animal or the group it was with ($r = 0.876$, $p < 0.001$; Fig. 3). Of the 106 transients involved in predation, 42 (40%) were observed to kill or harass both pinniped and cetacean prey. These individuals tended to be the most commonly observed in the study, with a mean of 11.4 predation events recorded per whale. Twenty-eight transients were involved only in events of predation on pinnipeds and 36 individuals were involved only in events of predation on cetaceans. However, these whales were seldom encountered, with a mean of less than 2 predation events observed per individual. All whales that were observed during 5 or more events were involved in predation on both pinnipeds and cetaceans.

The size of transient groups that made successful kills varied significantly with prey type (ANOVA, $F_{[2,82]} = 5.34$, $p = 0.007$; Fig. 4). Transients involved in kills of harbour seals tended to be in smaller groups ($\bar{x} = 3.75$ whales, $n = 51$) than those involved in Steller and California sea lion kills ($\bar{x} = 5.4$ whales, $n = 10$; Scheffé's test, $p < 0.05$) or small cetacean (porpoises and dolphins) kills ($\bar{x} = 5.0$ whales, $n = 24$, Scheffé's test, $p < 0.05$). There was no significant difference between group sizes for sea lion and small cetacean kills. The only prey seen to be taken by lone transients were harbour seals, and this took place on 3 occasions. Sea lion attacks were only observed with groups of 3 or more transients.

A total of seven species of seabirds were involved in 8 kills and 19 harassments by transient whales (Table 4). The species most commonly involved was the Common Murre (*Uria aalge*). Most events took place as birds swam at the surface, although in one case a bird was grasped as it flew 1 m above the surface. Birds were typically seized by the whale from below, or were struck with the whale's body following a jump. In 3 of the 8 kills the bird's carcass was abandoned.

Analysis of the stomach contents of beached carcasses

Twelve of the 14 beached carcasses of killer whales examined in the study area yielded evidence of diet. Of these,

Fig. 3. Numbers of predation events (mean ± 1 SE) and cumulative numbers of mammalian prey species for individual transient killer whales. Numbers in parentheses are numbers of individuals from a total of 106 whales.

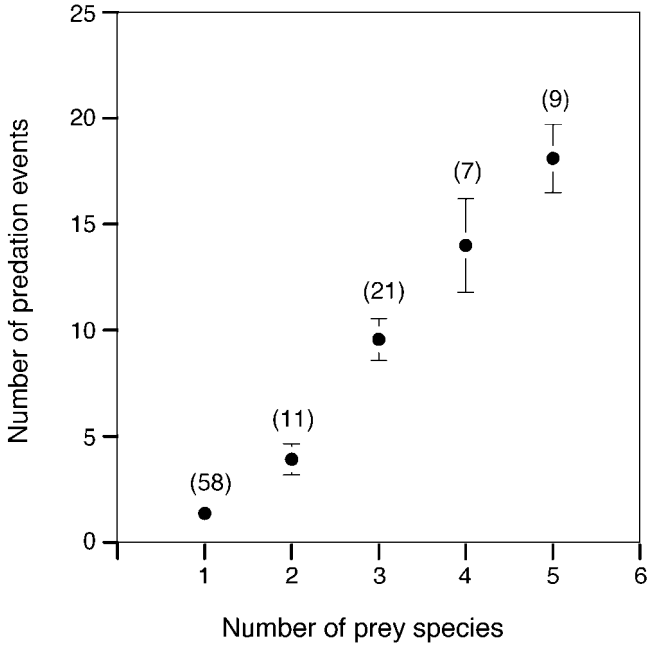
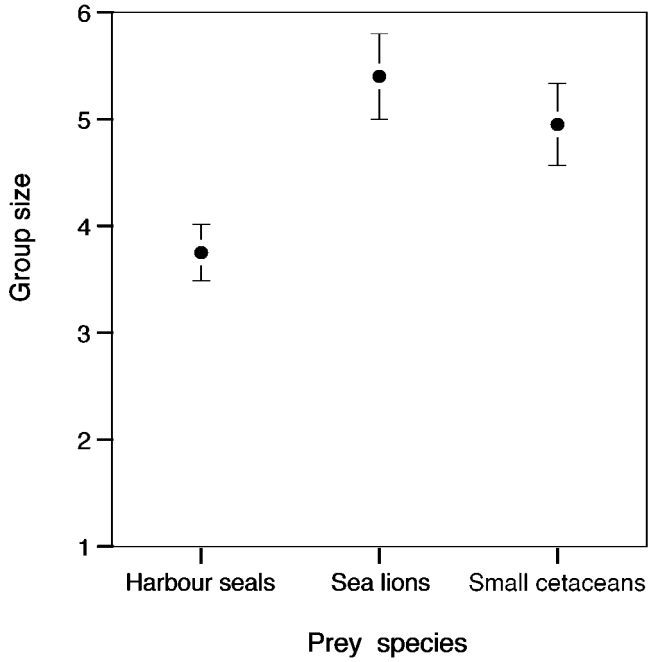


Fig. 4. Group sizes (mean ± 1 SE) of transient killer whales involved in kills consisting of harbour seals (n = 51), sea lions (n = 10), and small cetaceans (n = 24).



8 were resident whales, 1 was a transient, and the remaining 3 were unidentified (Table 5). Nine carcasses were recovered from the shores of Vancouver Island or adjacent islands and the mainland, 2 were found on the northern mainland coast, and 1 was recovered from the Queen Charlotte Islands.

Resident whales

All 8 carcasses of resident whales contained direct or indirect evidence of feeding on fish. No mammal or bird remains were observed. Two carcasses contained hooks or lures designed for salmon fishing, and 2 other carcasses contained hooks used to fish for Pacific halibut. Fish remains were found in 7 stomachs, all of which included salmon flesh or bones. The only salmonid species identified in these stomachs was chinook, which was present in 4 stomachs. Three stomachs contained unidentifiable salmonid remains.

In only 2 stomachs were non-salmonid species of fish identified. In 1 stomach the teeth of a single Pacific lamprey (*Lampetra tridentatus*) were found. The second stomach, that of the female resident A09, was exceptional because of the number of individual fish and the variety of species identified from bony remains. The most numerous of the 13 species identified was chinook salmon, with a minimum of 18 individual fish. These fish were estimated to have been 2–4 kg in size, which is not large for this species. The next most abundant species was lingcod (*Ophiodon elongatus*), with at least 15 individuals. Of these, one was probably >10 kg in mass, another was 2–10 kg, and the remaining 13 were <2 kg. Another 11 species of fish were identified, including at least 1 species of greenling (*Hexagrammos* sp.), 7 species of soles and flounders, 2 sculpin species, and the sablefish (*Anoplopoma fimbria*). It is probable that some of the smaller species may have been secondary prey remains, originating in the stomach of the larger species such as lingcod when the latter were consumed by the whale. Two resident whale stomachs contained beaks of the eight-armed squid (*Gonatopsis borealis*) in addition to remains of chinook salmon.

Transient whales

Only a single identifiable transient whale was recovered as a beached carcass. The stomach of this animal included remains of an unidentified cetacean species, two pinniped species (northern elephant seal and harbour seal), one bird species (White-winged Scoter), and a single squid beak. No fish remains were found. Two of the 3 unidentified whale carcasses were most likely transients, based on their dorsal fin morphology (Ford et al. 1994) and stomach contents. One contained remains of at least 20 individual harbour seals and 2 harbour porpoises. The other also contained harbour seal remains, as well as baleen from a gray whale and cormorant feathers.

Discussion

Observations of predation and analysis of prey remains from kills and stomach-content samples from resident and transient killer whales indicate striking differences in the diets of the two forms. Resident whales fed, or attempted to feed, almost entirely on fish, the overwhelming majority of which were salmonids. Harassments of marine mammals by residents were rare and mostly confined to one particular pod. It is questionable whether these incidents involved an intent to kill and eat the marine mammals. In none of these incidents was the animal seen to be killed or consumed, and no marine mammal remains have been found in stomach contents of resident whales. Of the 22 species of fish we

Table 5. Diet information from beached carcasses of 12 killer whales.

Date	Area	ID No.	Sex	Prey species	Evidence	No.
Residents						
7 Aug. 1973	2	B04	M	Pacific halibut (*Hippocampus stenolepis*) (?)	1 fishing hook	
14 Aug. 1977	1	L08	M	Salmon sp.	1 fishing lure and bones	1
				Unidentified non-salmonid fish	Bones	
14 Aug. 1986	3	L66	F	Salmon sp.	4 fishing hooks	
				Chinook salmon (*Oncorhynchus tshawytscha*)	Flesh and bones	2
22 Apr. 1989	3	L14	M	Salmon sp.	Bones and 2 fishing hooks	
7 Dec. 1990	2	A09	F	Chinook salmon	Bones	18
				Salmon sp.	Bones	1
				Lingcod (*Ophiodon elongatus*)	Bones	15
				Greenling (*Hexagrammos* sp.)	Bones	5
				English sole (*Parophrys vetulus*)	Bones	8
				Sanddab (*Citharichthys* sp.)	Bones	2
				Dover sole (*Microstomus pacificus*)	Bones	2
				Starry flounder (*Platichthys stellatus*)	Bones	2
				Rex sole (*Glyptocephalus zachirus*)	Bones	1
				Rock sole (*Lepidopsetta bilineata*)	Bones	1
				Curlfin sole (*Pleuronichthys decurrens*)	Bones	1
				Staghorn sculpin (*Leptocottus armatus*)	Bones	1
				Great sculpin (*Myoxocephalus polyacanthocephalus*)	Bones	1
				Sablefish (*Anoplopoma fimbria*)	Bones	1
18 June 1994	4	A58	M	Salmon sp.	Flesh	1
				Pacific halibut (?)	1 fishing hook	
4 July 1995	5	?*	F	Chinook salmon	Bones	1
				Pacific lamprey (*Lampetra tridentatus*)	Teeth	1
				Eight-armed squid (*Gonatopsis borealis*)	Beaks	14
21 May 1996	2	?*	F	Chinook salmon	Bones	1
				Eight-armed squid	Beak	1
Transients						
20 Jan. 1979	1	T15	M	Cetacean sp.	Skin	1
				Northern elephant seal (*Mirounga angustirostris*)	Claws and vibrissae	1
				Harbour seal (*Phoca vitulina*)	Claws, vibrissae, and hair	1
				White-winged Scoter (*Melanitta fusca*)	Feathers	2
				Squid sp.	Beak	1
Unidentified						
9 Apr. 1976	3		M	Harbour porpoise (*Phocoena phocoena*)	Flesh and bones	2
				Harbour seal	Flesh and 394 claws	20
				Sea lion sp.	Vibrissae	1
23 June 1981	3		M	Harbour seal	Skin and hair	1
				Cetacean sp.	Skin	1
				Gray whale (*Eschrichtius robustus*)	Baleen	1
				Cormorant (*Phalacrocorax* sp.)	Feathers	1
13 June 1989	3		M	Fish sp.	2 eye lenses	1
				Pacific halibut (?)	Hook and gangion	

Note: Data given are the date of collection, area of stranding (from Fig. 1), identification (ID) number of the individual if known and its sex, prey species and evidence used for identification, and the minimum number of individuals of each prey species represented in the carcass.

*Identified as resident whales belonging to the southern community from mtDNA analysis of tissue samples (L.G. Barrett-Lennard, unpublished data).

documented in the diet of residents whales, only 11 have been reported previously in studies of killer whales in the North Pacific (Scheffer and Slipp 1948; Tomilin 1957; Nishiwaki and Handa 1958; Rice 1968; Pike and MacAskie 1969; Matkin and Saulitis 1994).

In contrast to residents, transient whales fed almost exclusively on a variety of marine mammals and seabirds. No fish was observed to be killed or harassed, and no fish remains were found in the stomachs of one confirmed and two probable transients. The only prey item that was not from a mammal or seabird was a single squid beak, which may well have originated in the stomach of a northern elephant seal, the remains of which were found in the same whale. Squid are known to be an important prey of this pinniped (Antonelis et al. 1987). Earlier suggestions that transients eat bottom fishes (Heimlich-Boran 1988; Felleman et al. 1991)

were made without direct evidence, and no data to support them were obtained in our study.

Although the data we collected suggest strongly that resident whales are restricted to a diet of fish and transients to a diet of mammals and birds, this cannot be concluded with certainty. There are a number of limitations of our study that must be taken into account. First, our observations of predatory behaviour were restricted to events visible at the water's surface. Although these may be effective for detecting predation of marine mammals, birds, and some fish species, particularly salmonids, they provide no information on species that may be killed and consumed at depth. Second, we documented only 1 predation event for residents from November to April, and thus can say little about their diet during this time of year. However, we doubt that these whales, which show such a strong preference for fish during the other months of the year, would switch to a diet of marine mammals in winter and spring. We often observed various marine mammals, including Dall's porpoises, Steller sea lions, and minke whales, swimming in close proximity to resident pods without exhibiting any alarm or avoidance. Similar observations have been made by others (Jefferson 1987; Felleman et al. 1991; Jefferson et al. 1991). This suggests that resident whales do not represent a predation risk to these species.

Although information on stomach contents of residents suggests that these whales feed solely on fish and squid, the sample size of transients' stomachs from the study area is too small to confidently conclude that fish are excluded from the diet of these whales. However, the stomach contents of killer whales from other regions in the northeast Pacific reveal a similar fish versus mammal dichotomy. Of the stomachs of 8 whales collected off Alaska and California and reported by Rice (1968), 2 contained only fish remains and 6 contained only mammal remains (except for one that contained fragments of 1 squid). Similarly, the stomachs of 4 whales stranded in Alaska contained only mammal remains (Barrett-Lennard et al. 1995).[3]

We believe that our results provide sufficient evidence to conclude that if resident killer whales prey on mammals or seabirds, or transient killer whales prey on fish, such events are uncommon or rare.

Dietary specialization of resident whales

Salmon appear to be the predominant prey of resident killer whales, at least during May through October. Over 95% of all predation events documented involved salmonids. All salmonid species found naturally in the study area were observed to be taken, except for the rare sea-run cutthroat trout (*Salmo clarkii*). Analyses of stomach contents also revealed a preference for salmon. Salmon remains or salmon fishing gear were found in seven of the eight resident killer whale carcasses examined.

Although non-salmonids represented only 4% of all fish prey, it seems likely that they are more important in the diet of residents than this would suggest. Hooks used to fish for Pacific halibut were found in the carcasses of 2 residents and 1 unidentified whale. This may have resulted from depredation of long-line halibut-fishing operations, which has been reported in British Columbia (G.M. Ellis, unpublished data) and Alaska (Matkin and Saulitis 1994; Yano and Dahlheim 1995). This species was also seen to be consumed on one occasion by residents, and has been reported in the stomach contents of a killer whale taken off the west coast of Vancouver Island (Pike and MacAskie 1969).

Like the Pacific halibut, the majority of other non-salmonids noted in the diet of resident whales are epibenthic or demersal species. This may account for the scarcity of observations of whales feeding on these species, as they are likely caught and eaten at depth. Other fish species observed in predation events included herring, yelloweye rockfish, and at least one unidentified small flatfish. Of these, only the herring is commonly found near the water surface. The stomach contents of one resident whale (A09; Table 5) included 11 demersal non-salmonid species. Of these, the lingcod was the most numerous and predominant species by mass, followed by the greenling and seven species of flatfish. The stomach contents of a killer whale taken at San Juan Island off southeastern Vancouver Island included the remains of greenling, lingcod, salmon, and squid (Scheffer and Slipp 1948).

Remains of eight-armed squid were found in the stomachs of two southern-community resident whale carcasses recovered on the west coast of the Queen Charlotte Islands and at the northern tip of Vancouver Island. These squid reach a maximum length of 30 cm and are common in oceanic regions of the North Pacific (Roper et al. 1984). The distribution of this prey species, combined with the proximity of the stranding locations to the continental shelf edge (<20 km), suggests that these whales had been feeding in deep-water areas. Squid have not been previously reported as prey of resident killer whales, although the whale taken near San Juan Island and examined by Scheffer and Slipp (1948) was likely a resident. Squid have been noted in stomach contents of killer whales from the northeastern (Rice 1968) and northwestern (Nishiwaki and Handa 1958) Pacific Ocean, although species identity was not determined.

It is interesting that the Pacific herring seems to be unimportant in the diet of resident killer whales. Only 2 predation events were observed on herring, and in one of these cases the wounded fish escaped or was abandoned at the surface. Herring aggregate to spawn in coastal waters of British Columbia in spring, forming very large schools that would be a substantial food resource for killer whales. Although sea lions congregate to feed on spawning herring (Olesiuk and Bigg 1988) in this region, this has not been noted for killer whales. The Atlantic herring represents an important prey species of killer whales off coastal Norway and Iceland, and has a major influence on the seasonal movements of these whales (Similä et al. 1996).

Chinook as preferred salmonid prey of residents

Of the six species of salmonids killed or harassed by resident killer whales, chinook was by far the predominant spe-

[3] L.G. Barrett-Lennard, K. Heise, E. Saulitis, G. Ellis, and C. Matkin. 1995. The impact of killer whale predation on Steller sea lion populations in British Columbia and Alaska. Unpublished report, North Pacific Universities Marine Mammal Research Consortium, Fisheries Centre, University of British Columbia, Vancouver.

cies, representing two-thirds of the identified salmonid samples. Chinook was also the only salmonid species identified in stomach contents of resident killer whale carcasses. However, chinook is one of the least abundant salmonids in the locations and season when most samples were collected. Of 47 identified salmonid samples collected during July–September off northeastern Vancouver Island, 25 (53%) were chinook. During this period, the abundance of chinook in this area is typically less than 2–3% of that of sockeye and pink salmon (P. Ryall, Department of Fisheries and Oceans, Nanaimo, B.C., personal communication; Candy et al. 1995).

Given the relative scarcity of chinook salmon off northeastern Vancouver Island and the significant positive correlation of the occurrence of resident whales with the abundance of sockeye and pink salmon in this area (Guinet 1990; Nichol and Shackleton 1996), the possibility that chinook were overrepresented in our samples should be considered. Our identification of salmon species involved in predation events was based mostly on scales retrieved from the water following a kill at or near the water surface. For this technique to provide an accurate measure of the importance of the various salmon species in the whales' diet, the probability that kills will be detected and scales retrieved must be relatively constant across species. Three main factors may affect the probability of scale collection: (1) the proximity of the kill site to the surface, (2) the likelihood that scales will be shed during a kill, and (3) scale size.

Although salmonids prefer to swim in near-surface waters, chinook are generally found at greater depths than other species. In the Bering Sea, average swimming depths were 10 m or less for sockeye, chum, and pink salmon, but approximately 30 m for chinook (Ogura 1994). Within our study area, ultrasonic telemetry studies indicate that sockeye generally confine their activity to the top 30–40 m of the water column, and prefer depths of less than 20 m (Quinn et al. 1989). Steelhead are highly surface-oriented, typically travelling in the top 1 m (Ruggerone et al. 1990). Chinook, however, spend considerable time at depths of 50 m or more, and often dive to depths exceeding 300 m (Candy et al. 1995). It appears from these data that if any bias exists in scale samples due to fish depth, it would tend to underestimate the abundance of chinook relative to other salmonids, unless prey items are routinely brought to the surface for consumption.

It is possible that prey size may affect the chance of scales being shed during a kill. Observations of captive killer whales indicate that fish larger than about 5 kg are usually bitten in half before consumption, whereas smaller fish tend to be swallowed whole (J. Ford, unpublished data). Chinook, being generally larger than other salmonids and reaching masses of >10 kg, may often be torn apart before being swallowed, thereby shedding scales. Large chinook may also be divided and shared by whales, although this was only observed once. Finally, the size of scales may have affected the probability of their detection and recovery. Scales of mature pink salmon are 2–3 mm in diameter compared with 5–10 mm in other salmonid species. This small size may have reduced the chances of sighting scales in the water column following a pink salmon kill, although the mesh size of the dip nets used for retrieving scales was sufficiently fine to collect them. The minor differences in scale size among other salmonids are unlikely to have affected their relative detectability.

Although these potential biases may have influenced the frequency of occurrence of the various salmonids in our scale samples, we believe that the disproportionate occurrence of chinook in our salmonid samples relative to their availability reflects a real preference for this species in the diet of resident whales. Even when other salmonids are abundant, residents will, at least at certain times, selectively hunt the larger chinook. On several occasions we observed whales taking chinook while evidently ignoring large schools of sockeye and pink salmon visible nearby.

Residents may selectively hunt chinook because of their large size, high fat content, and seasonal distribution patterns. Chinook can be up to 10 times the mass of other salmonids in the study area. In the waters around Vancouver Island, migrating pink salmon have mean masses of 1.71–2.41 kg (Heard 1991), sockeye average 2.73 kg (Burgner 1991), chum salmon are typically 4.0–5.5 kg (Salo 1991), and coho are 2.5–4 kg (Sandercock 1991). Most chinook in our samples were 3 years of age or older, and individuals of this age have mean body masses of 3.7–14.7 kg (Table 3). Chinook in the region commonly reach masses in excess of 25 kg (Healey 1991). In addition to their larger size, chinook typically have a higher fat content than other salmonids (Kizevetter 1971; Bykov 1984). Finally, chinook can be found in coastal waters throughout the year. Although most salmon species spend the marine portion of their life cycle in pelagic waters, the "ocean type" of chinook, which is the predominant form in British Columbia, usually remains in nearshore waters rather than migrating offshore (Healey 1991).

Other resident populations

At least one other killer whale population along the northwest coast of North America appears to specialize on salmon prey. A community of 13 resident-type pods with over 200 whales occurs in Prince William Sound, Alaska, and adjacent coastal waters (Matkin and Saulitis 1994; Matkin et al. 1994). At least two of these pods are seen regularly in southeastern Alaska, where their range overlaps with that of the British Columbian northern residents, and some mixing of the two populations takes place (Dahlheim et al. 1997). In a recent study of the diet of Prince William Sound residents, Saulitis et al.[4] found the predominant prey to be salmonids, 95% of which were coho salmon. These whales appear to hunt coho salmon selectively, despite this species being less common than the smaller but abundant pink salmon. As mentioned previously, chinook salmon are very rare in Prince William Sound, but some predation on this species was observed.

Whether other killer whale populations specializing on salmon exist in the northeastern Pacific Ocean is not known. The southern resident community of British Columbia and

[4] E. Saulitis, C. Matkin, K. Heise, L. Barrett-Lennard, and G. Ellis. Foraging strategies of sympatric killer whale (*Orcinus orca*) populations in Prince William Sound, Alaska. In preparation.

Washington State does not appear to range farther south than 47°N. Most killer whales identified farther south off Oregon and California are of the transient form, and only predation on mammals has been noted (Goley and Straley 1994; N.A. Black, personal communication). Perhaps resident populations extended to this region historically, prior to the decline of local salmon populations (Groot and Margolis 1991).

Dietary specialization of transient whales

A total of seven marine mammal and five seabird species were observed to be consumed by transient killer whales or were identified in the stomach contents of a stranded transient individual. An additional three species of mammals and three species of seabirds were harassed in an apparent predatory manner. Harbour seals represented two-thirds of observed marine mammal kills by transients, and thus clearly represented the preferred prey species. The beached carcass of a probable transient male contained claws from at least 20 different harbour seals. In a study of predation by transient killer whales off southern Vancouver Island, harbour seals were also the predominant prey (Baird and Dill 1995).

The importance of harbour seals in the diet of transient killer whales reflects the abundance of this prey species in the study area and most probably its relative ease of capture. The harbour seal is by far the most common marine mammal in the region, with a population of approximately 75 000 – 88 000 in coastal British Columbia (1988 estimate, increasing by 12.5% per year; Olesiuk et al. 1990*a*). The species is widely distributed throughout inshore waters, from coastal inlets to open straits and sounds. At a mean adult mass of 60–80 kg it is, next to the sea otter (*Enhydra lutris*), the smallest marine mammal in the area. Transient whales had a high success rate in attacks on harbour seals, with over 90% of observed attacks ending in a kill. Steller and California sea lions are less abundant in the region (Olesiuk and Bigg 1988) and were less frequently attacked and killed than harbour seals. Fewer than 50% of observed attacks ended in a successful kill. Compared with harbour seal attacks, sea lion attacks usually involved greater expenditure of time and energy, as well as larger whale groups. This is no doubt due to the greater size and strength of sea lions, which are capable of dangerous defensive actions. Most harbour seals were killed within 5 min, whereas sea lion attacks often continued for 1–2.5 h before the prey was killed. When attacking a sea lion, individual whales took turns rushing toward the animal and striking it with their flukes or, less commonly, their head. Once the animal was sufficiently debilitated, it was carried underwater and drowned. As with other mammalian prey, the carcass was typically torn apart and shared among whales in the group.

The only other pinniped species taken by a transient killer whale in this study was a northern elephant seal, identified from the stomach remains of the stranded transient male T015. This species has become increasingly common over the past few decades as a result of population expansion, but appears to be a rare prey item for transients in the region. Baird and Dill (1995) noted only 1 attack on an adult male elephant seal among 138 prey attacks by transients off southern Vancouver Island.

Dall's porpoises, harbour porpoises, and Pacific white-sided dolphins are found throughout most of the study area, but abundance estimates are not available (Gaskin 1992; Calambokidis and Baird 1994; Heise 1996). The number of observed predation incidents involving porpoises and dolphins was about half that involving harbour seals. Attacks on Dall's porpoises and harbour porpoises were observed with roughly equal frequency, but success rates varied considerably. All 16 attacks on harbour porpoises resulted in the animal being killed, but in 11 of 18 (61%) pursuits of Dall's porpoises the potential prey escaped. Harbour porpoise attacks were generally of short duration and entailed little activity that was visible from the surface. Attacks on Dall's porpoises were characterized by prolonged high-speed swimming with high aerial leaps by the whales, and chases often continued over distances of several kilometres. Attacks were successful when the whales caught up to the porpoise and rammed it from beneath or landed on it following a high leap. Dall's porpoise, considered one of the fastest swimming odontocetes (Law and Blake 1994), may escape transient killer whales more frequently than the harbour porpoise. Because Dall's porpoise attacks entailed highly visible, energetic surface behaviours, it is likely that they were more readily sighted than attacks on harbour porpoises. Harbour porpoise attacks may thus be underrepresented in our observations. Groups of transients attacking porpoises or dolphins were larger than when they attacked harbour seals. Larger groups of whales may be needed to chase and corral porpoises and dolphins in open water than are required to take harbour seals.

Transient killer whales were only seen attacking Pacific white-sided dolphins on 4 occasions, all in 1995, and only one animal was successfully killed and consumed. These dolphins were uncommon in protected inshore waters during the 1970s and early 1980s, but have become abundant within the past decade (Heise 1996). The scarcity of Pacific white-sided dolphins throughout much of the study's duration may be responsible for the few attacks observed. Transient killer whales appear to hunt Pacific white-sided dolphins by herding a group, which may comprise 50 or more animals, into the shallows or an enclosed bay. Individuals are then separated from the group and pursued. Predation on Pacific white-sided dolphins by transient killer whales has also been noted in southeastern Alaska (Dahlheim and Towell 1994).

Two other cetacean species, the minke whale and gray whale, were observed in apparent unsuccessful attacks by transients on 1 and 2 occasions, respectively. The two gray whale incidents involved cows with young calves, as is typical of gray whale attacks observed in other areas (Jefferson et al. 1991; Goley and Straley 1994). The stomach of a probable transient found stranded contained gray whale baleen (Table 5). Large cetaceans seem not to represent important prey of transients in this region, at least in inshore waters. Hancock (1965) observed a group of seven killer whales kill and eat a minke whale on the west coast of Vancouver Island in 1964. The remains of a young minke whale bearing killer whale tooth marks were found floating near northern Vancouver Island in 1980 (Ford and Ford 1981). Humpback whales (*Megaptera novaeangliae*), the only other common inshore cetacean in the study area, were not seen to be ha-

rassed or attacked, but this has been reported in the region (Jefferson et al. 1991).

Attacks on seabirds documented in this study usually resulted in the bird escaping. It seems doubtful that seabirds are significant in the diet of transient whales. Most attacks were made by subadult whales, and involved techniques similar to those seen during predation on pinnipeds or small cetaceans. Seabird attacks may involve play by young whales that helps individuals develop prey-hunting and -handling skills.

Individuals or groups of transient killer whales do not appear to specialize on particular types of marine mammal prey. Although many individual transients were observed to attack only pinnipeds or only cetaceans, this was probably a function of small sample sizes for those whales. As the number of observations of predation by individual transients increased, so did the variety of prey species they attacked. Both pinnipeds and cetaceans were represented in the case of all transient whales present in more than 5 predation events. As mentioned previously, group sizes of transients varied with prey type. Small transient groups seen taking harbour seals when alone were often observed attacking porpoises or sea lions while foraging with other groups. Whether transient groups combine in order to take larger or more difficult prey, or for social purposes and are able to take such prey secondarily, is not known, but we suspect the latter to be the case.

In a study of transient whales off southern Vancouver Island, Baird and Dill (1995) found that certain groups appeared to use a nearshore foraging tactic and were seen primarily during the harbour seal pupping and weaning period, and others were present year-round and usually foraged farther offshore. Most of the predation in their study involved harbour seals. We did not observe such seasonality or specialized hunting techniques for particular individuals or groups, including the groups observed by Baird and Dill (1995). This is likely due to the larger study area, longer duration, and greater diversity of habitats and prey species availability that we consider. However, transient groups almost certainly have preferred hunting tactics and sites within their overall range.

Foraging behaviour and strategies of eastern North Pacific killer whales

Resident whales

Resident killer whales are primarily inshore salmon feeders for at least half the year. From April through October they tend to congregate in areas and at times that correlate with the seasonal migrations of salmon (Heimlich-Boran 1986, 1988; Guinet 1990; Nichol and Shackleton 1996). Our data confirm that salmon are the predominant prey of resident whales during this period, and chinook is the favoured salmonid species. Little is known of the distribution or diet of resident whales between November and March. The stomach of one stranded whale recovered during December contained the remains of chinook salmon and a variety of non-salmonid species.

While foraging for salmon, resident pods typically disperse over several square kilometres. Whales usually travel in small subgroups comprising a female and her young offspring, and adult males often travel alone at the periphery of the group (Osborne 1986; Ford 1989; Bigg et al. 1990*b*; Hoelzel 1993). Subgroups tend to travel in the same direction and at a similar pace, but dive and surface independently. Resident whales are highly vocal while foraging, emitting both social signals and echolocation click trains, presumably to maintain intrapod contact and for orientation and prey detection (Ford 1989). Salmon do not appear to be sensitive to the frequencies of killer whale vocalization, so are unlikely to be affected by the whale's signals (Barrett-Lennard et al. 1996).

When foraging in narrow channels and straits, females and young usually swim within 50–100 m of the shoreline and mature males often forage farther from shore. The pursuit and capture of salmon are generally undertaken by individuals or, at the most, subgroups containing a female and one or two of her offspring. There may be two explanations for the tendency of residents to forage close to shore. First, steep and rocky shorelines typical of the region may provide a barrier against which the whales can corral and capture salmon (Heimlich-Boran 1988). Second, chinook salmon tend to be found very close to shorelines, more so than other salmonids (Stasko et al. 1976; Quinn et al. 1989; Candy et al. 1995; T. Quinn, University of Washington, personal communication, 1996). Along the central coast of British Columbia, resident whales foraged even more consistently along shorelines than in other parts of the region, and 100% of identified salmon kills in this area were chinook. Chinook may occur at such low densities that schooling as a means of reducing predation is neither possible nor advantageous. When few conspecifics are available, fish can avoid predation more effectively by seeking refuge than by schooling in open water (Pitcher and Parrish 1993). It is interesting to note that in Prince William Sound, resident-type killer whales feed primarily on coho salmon and tend not to forage close to shore (Saulitis et al., see footnote 4). Chinook are rare in Prince William Sound and comprised less than 5% of salmon kills observed by Saulitis et al. (see footnote 4).

The relatively large pods of resident killer whales do not seem to be required for prey herding and capture in nearshore, protected waters. Cooperative circling and capture of fish by groups, as seen in Norwegian killer whales feeding on herring (Similä and Ugarte 1993), have not been observed among resident whales by ourselves or others (Osborne 1986; Heimlich-Boran 1988; Felleman et al. 1991; Hoelzel 1993). It is possible that such tactics are used in open, offshore waters, but few observations of resident whales have been made in such areas. Large resident groups, when dispersed during foraging, may increase the efficiency of locating patchily distributed salmon prey, which are then pursued by individuals and subgroups (Heimlich-Boran 1988; Bigg et al. 1990*b*; Hoelzel 1993). Salmon schools are clearly a food resource that is plentiful enough to sustain large groups, especially during the summer and fall salmon migration period. It is during this season that pods congregate at locations where migrating salmon are concentrated as a result of geographic features. Resident killer whales have an unusually stable social system that may play a role in their foraging strategy. Resident pods are multigeneration kinship groups from which no dispersal of individuals has been observed in more than 20 years of observation (Bigg et

al. 1987, 1990*b*; Ford et al. 1994). This long-term persistence of pods and long life-span of individuals (Olesiuk et al. 1990*b*) allow the development of behavioural traditions that are maintained by cultural transmission across generations. Pod-specific vocal dialects within the resident population are an example of such behavioural traditions (Ford 1991). It is reasonable to expect that specialized foraging strategies develop within pods and become established as traditions that are passed on from generation to generation. There is evidence that certain resident pods have particular travel patterns and areas which they preferentially frequent within the overall range of the community (Bigg et al. 1976; Ford et al. 1994; Nichol and Shackleton 1996). A foraging strategy focused on salmonids may require considerable experience and learning in order to successfully intercept the many runs of salmon, with their various migratory routes, timing, and destinations (Groot and Margolis 1991). Pods may specialize on certain runs, particularly of chinook, that migrate predictably through coastal waterways at different times of year. Individuals may benefit from natal-group philopatry through continued access to the successful foraging traditions of the pod.

Transient whales

Transient killer whales appear to be specialized hunters of small marine mammals and seabirds in coastal waters yearround, and depend on a foraging tactic involving stealth. The relatively long dive times of transients and their erratic underwater swimming patterns (Morton 1990) minimize visual detection by pinnipeds at the surface or on haulouts. Their restricted underwater sound production while foraging (Ford 1984; Morton 1990; Barrett-Lennard et al. 1996) reduces detection by acoustically sensitive pinniped and cetacean prey.

The small group sizes of transients in the study area allow the efficient capture and sharing of individual seals, sea lions, and porpoises. The most common prey, harbour seals, are relatively small, likely the easiest to capture, and are taken, on average, by the smallest groups. Baird and Dill (1996) suggested that the modal group size of 3 whales ($\bar{x}$ = 4.21 whales) which they observed off southern Vancouver Island maximizes the energy intake of individuals when hunting harbour seals. We found similar group sizes of transients preying on harbour seals (mode = 3, $\bar{x}$ = 3.74 whales). The significantly larger group sizes we observed in attacks on sea lions ($\bar{x}$ = 5.4 whales) and porpoises ($\bar{x}$ = 4.96 whales) may result from greater difficulty of capture or larger prey sizes that allow sharing by more whales. Transient whales attacking gray whales in Monterey Bay, California, were observed in groups of 15–20 (Goley and Straley 1994; N.A. Black, personal communication). Such large groups are rarely seen in our study area.

As with resident killer whales, the foraging specializations of transients are likely learned traditions that have developed over many generations. The mammal-hunting life-style of transients, with associated behavioural and social adaptations, appears to have become firmly established to such an extent that fish have been effectively excluded as a significant food source. For example, suppressed echolocation during foraging may enhance the success of hunting for mammals, but echolocation may be required for locating fish (Barrett-Lennard et al. 1996). The requirement for stealthy hunting in small groups is met by greater fluidity of social structure among transients than among residents. Dispersal of individuals from the natal group is common among transients, and groups with more than 5 whales are seldom observed (Bigg et al. 1990*b*; Ford et al. 1994). The behavioural specializations of resident and transient populations seem to have resulted in social insularity of each form, so that whales only mix and, presumably, reproduce with other members of their population. When resident and transient groups are in close proximity, they either pass with no evident change in behaviour, or the transients change course, apparently to avoid contact with the residents (Morton 1990; Baird and Dill 1995). In one instance near Nanaimo, B.C., a resident pod of 17 whales actively pursued and aggressively attacked a group of 3 transients (G.M. Ellis, unpublished data).

Other regions

Socially isolated populations with specialized foraging strategies may be common in *O. orca*. For example, a situation similar to that in British Columbian killer whales appears to exist among those in the Antarctic Ocean. Berzin and Vladimirov (1983) described two forms with overlapping ranges that differ in morphology, group size, and diet, with one form preying predominantly on mammalian prey and the other on fish. The two forms were not seen to mix, despite their occurrence in the same vicinity. In northern Norway, killer whales congregate to feed on overwintering herring, often using highly coordinated "carrousel" feeding techniques (Similä and Ugarte 1993; Similä et al. 1996). Killer whale groups in the subantarctic Crozet Islands (Guinet 1992) and in Patagonia, Argentina (Lopez and Lopez 1985; Iñíguez 1993), use specialized tactics involving intentional temporary stranding in shallow water to hunt elephant seals (*Mirounga leonina*) and southern sea lions (*Otaria flavescens*). As with British Columbian killer whales, these hunting strategies appear to be traditions that are passed across generations by imitation (Guinet 1991; Iñíguez 1993; Guinet and Bouvier 1995). It may well be that a geographic mosaic of killer whale populations, some sympatric and others allopatric, exists in the world's oceans. Each may have distinctive foraging and behavioural traditions that have evolved over long periods, which in turn has led to some degree of social insularity, reproductive isolation, and genetic discreteness.

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