

**FORAGING BEHAVIOUR AND ECOLOGY OF TRANSIENT KILLER WHALES  
(ORCINUS ORCA)**

by

**Robin William Baird**

B.Sc., University of Victoria, 1987

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**FORAGING BEHAVIOUR AND ECOLOGY OF TRANSIENT KILLER  
WHALES (ORCINUS ORCA)**

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Foraging behaviour and ecology of transient killer whales (Orcinus orca)

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(date)

**ABSTRACT**

The foraging behaviour and ecology of transient killer whales (Orcinus orca) around southern Vancouver Island was studied from 1986 through 1993. Predation on marine mammals (mostly harbour seals) was observed on 136 occasions, and no predation on fish was observed. Transient killer whale occurrence and behaviour varied seasonally and between pods; some pods foraged almost entirely in open water and were seen throughout the year, while others spent much of their time foraging around pinniped haul-outs and other near-shore areas, and used the area primarily during the harbour seal weaning and post-weaning period. Overall use of the area was highest during that period, and energy intake at that time was significantly greater than during the rest of the year. Energy intake varied with group size, with groups of three having the highest energy intake rate per individual, and the lowest risk of an energy-shortfall. The typical size of groups comprised of adult and sub-adult whales, engaged primarily in foraging and feeding, was 3.29, implying that these individuals are found in groups consistent with the maximization of energy intake hypothesis. However, larger groups were also regularly seen.

Near the end of this study, a time-depth recorder/VHF radio tag was deployed on six residents and one transient, to look for differences in diving behaviour between the two forms. While detailed information was only obtained for 23 hours, the data suggest that foraging-related differences in diving behaviour may exist. The proportion of time spent at depth differed between the two forms, with the residents spending the majority of their time at shallower depths than the single transient individual.

Utilizing information collected during this study and from previous research, a model of indirect interactions between transient and resident killer whales was formulated. The model suggests that the evolution of foraging specializations in these populations may have occurred through frequency-dependent indirect interactions acting in concert with density-dependence within populations and disruptive selection on prey-type specific foraging characteristics. I suggest the two forms of killer whales may be in the process of speciating, i.e, they may be incipient species.

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## PROLOGUE

This thesis is about the behavioural ecology of foraging killer whales (Orcinus orca), and is unique in several respects. First, cetaceans have played little role in the development or testing of behavioural ecological theory for the function and evolution of animal behaviour. Second, behavioural studies of predation by mammalian carnivores have largely been limited to a few species that hunt in open areas, a situation conducive to the observation and recording of predation events, including information on prey species, and the size and composition of the hunting group. While research on the behaviour of cetaceans has increased dramatically in recent years with respect to the diversity of species studied, the geographic scope of research efforts, and the range of research foci, relatively little research has been done on the foraging ecology or foraging behaviour of cetaceans. Of that which has been done, most has been descriptive and inferential, utilizing information on stomach contents, estimated energetic expenditures, surfacing patterns, and a largely incomplete knowledge of the populations and behaviour of potential prey species.

The most intensive studies on the killer whale have focused on populations that feed primarily on fish well beneath the water's surface, thus limiting the researcher's ability to study the interactions among the predators or between them and their prey. In several areas of the world, however, the predictable occurrence of killer whales hunting near-shore marine mammals has allowed more detailed investigation of these types of interactions. These sites include the Crozet Archipelago in the Indian Ocean (Guinet 1992), and the Punta Norte region of Argentina (Hoelzel 1991). Shore-based observations

of killer whales hunting elephant seals or sea lions in the surf zones of these areas have provided extensive information on the dynamics of group hunting, hunting tactics, and various factors affecting prey capture. Unfortunately, such studies have been limited by the relative inaccessibility of these sites, as well as by the lack of opportunity to study the whales when they were not in nearshore areas. One geographic area has been identified where killer whales regularly feed on marine mammals, where weather and logistical considerations allow for year-round vessel-based observations, and where it is possible to make frequent observations of prey capture, including information on prey species, size, duration of handling time, and the sex, size and identity (and often presumed relatedness) of individuals in the hunting group. That location is southern Vancouver Island, British Columbia, the site of my dissertation research - a study of the foraging behaviour and ecology of the so-called transient killer whales.

Some background on the history and development of killer whale research is relevant. Prior to 1970, research on this species world-wide was largely based on the examination of beach-cast animals or those taken in whaling operations, as well as a few studies with captive animals. Field studies in British Columbia were first initiated by Spong et al. (1970), and have been continued by a variety of investigators. Notable has been the work of Bigg and his colleagues (Bigg et al. 1976, 1987, 1990; Bigg 1982), using photo-identification of individual animals based on distinctive acquired and congenital characteristics of the dorsal fin and saddle patch. They first described the occurrence of the two forms of killer whales recognized today. These two forms were originally termed residential or transient to particular areas based on movement patterns; throughout this dissertation they are referred to as resident and transient, as the names have subsequently been shown not to be descriptive. Occurrence of transient killer whales is

much less predictable than that of residents, both temporally and geographically. Combined, the smaller group sizes and erratic surfacing patterns have made transients more difficult to find and follow, and the vast majority of research to date has focused on the resident populations around northern and southern Vancouver Island. An extensive network of spotters around the southern tip of Vancouver Island and the discovery of the somewhat predictable occurrence of transients in that area led to the initiation of my study of transients in 1986.

My dissertation is divided into four chapters, each representing a stand-alone investigation of a specific aspect of transient foraging behaviour or ecology. Chapter I sets the context, describing the occurrence and behaviour of transient killer whales in the study area, and how both vary seasonally and between transient pods (maternal groups); this variation is also shown to be related to differences in foraging tactics between pods. Chapter II provides a preliminary examination of killer whale diving behaviour; this is a previously uninvestigated topic that intrigues me both for its ability to provide insight into what the animals do the 95% of the time they are invisible below the water's surface, as well as for the opportunity to investigate differences in diving behaviour between transient killer whales and the sympatric fish-eating residents. Because of the dichotomy in prey choice between these two forms of killer whale (residents eat fish, while transients eat marine mammals), interpretation of diving behaviour can be undertaken in the comparative context of prey searching strategies. Chapter III investigates the meat and potatoes of transient hunting - the energetic benefits of foraging in different sized groups and how that relates to transient killer whale dispersal patterns and social structure. In Chapter IV a simple model is presented outlining potential indirect ecological interactions between transient and resident killer whales through the food web. The model

itself is not unusual, simply applying Lotka-Volterra equations to a killer whale food web, but it provides a basis for the development of a verbal model which might explain the evolution of the foraging specializations seen in killer whales today. Together these papers represent an investigation into the foraging behaviour and ecology of a large social carnivore, providing a new understanding of the complexity of killer whale foraging tactics, differences between the sympatric residents and transients which may be relevant to processes of speciation between the two forms, and how factors such as the relationship between food intake and group size may have influenced transient killer whale social structure and dispersal patterns.

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CHAPTER I

OCCURRENCE AND BEHAVIOUR OF TRANSIENT KILLER WHALES: SEASONAL AND  
POD-SPECIFIC VARIABILITY, COOPERATIVE HUNTING AND PREY HANDLING

## Summary

Extensive research has been undertaken on so-called resident killer whales (Orcinus orca) in British Columbia and Washington State, while comparatively little is known about the so-called transients, that occur sympatrically. I studied the occurrence and behaviour of transient killer whales around southern Vancouver Island from 1986 - 1993, focusing on foraging behaviours, cooperative hunting techniques and prey handling. Occurrence and behaviour varied seasonally and among pods; some pods foraged almost entirely in open water and were recorded in the study area throughout the year, while others spent much of their time foraging around pinniped haul-outs and other near-shore sites, and used the study area primarily during the harbour seal (Phoca vitulina) weaning/post-weaning period. Overall use of the area was greatest during that period, and energy intake at that time was significantly greater than at other times of the year, likely due to the high encounter rates and ease of capture of harbour seal pups. Multi-pod groups of transients were frequently observed, as has been reported for residents, but associations were biased towards those between pods which exhibited similar foraging tactics. Despite the occurrence of transients and residents within several kilometres of each other on nine occasions, mixed groups were never observed and transients appeared to avoid residents. Combined with previous studies on behavioural, ecological and morphological differences, such avoidance behaviour supports the supposition that these populations are reproductively isolated.

## Introduction

Numerous studies have been undertaken on killer whales (Orcinus orca) in British Columbia and in Washington State. Based on photo-documentation of individual association patterns and movements, research in the early 1970s identified the existence of three discrete associations of killer whale pods (i.e., long-term maternal groups) around Vancouver Island, each with different home ranges (Bigg 1979). Pods in two of these associations had largely non-overlapping ranges which centred on northern and southern Vancouver Island respectively, and were seen predictably in these areas over several years. Pods in the third association were seen throughout the home ranges of pods from the other two associations on a periodic basis, yet did not appear to interact with them. These differences in movement patterns led to the descriptive classification of pods in these associations as residential or transient within a particular area (Bigg et al. 1976). As noted by Guinet (1990), more recent research has demonstrated that these names are not particularly descriptive, but they have been retained (referred to hereafter as resident and transient), due both to their historical usage and the lack of adequate alternative designations.

Research over the past 20 years has focused in areas where encounters with killer whales is highest, in Johnstone Strait off northeastern Vancouver Island and in Haro Strait, a transboundary area between southeastern Vancouver Island and the U.S. San Juan Islands. Concentrations of resident killer whales were found in both areas, and virtually all studies have focused on these populations, covering a diverse range of subjects, including foraging and feeding (Nichol 1990; Felleman et al. 1991), habitat use

(Heimlich-Boran 1988), vocal traditions and acoustic behaviour (Hoelzel and Osborne 1986; Ford 1989, 1991), alloparental care (Waite 1988), life history characteristics and population dynamics (Olesiuk *et al.* 1990), and social behaviour and social structure (Bigg *et al.* 1990; Jacobsen 1990; Rose 1992). Opportunistic encounters with transients in these areas added little to the understanding of their behaviour, yet cumulative information collected continued to imply that the transient individuals did not associate with the sympatric populations of residents. By the late 1980s, a combination of genetic and morphological data emerged to suggest that these populations might be reproductively isolated (Bigg *et al.* 1987; Baird and Stacey 1988a; Bain 1989; Hoelzel 1989; Stevens *et al.* 1989), which appears to have spurred more detailed investigation of the transient population (e.g., Baird and Stacey 1988b; Guinet 1990; Morton 1990; Baird *et al.* 1992, Chapter IV; Barrett-Lennard 1992; Chapter III).

Regardless, considerably less is known about the behaviour or ecology of transient killer whales. In this chapter I report on a study of transients around southern Vancouver Island from 1986 through 1993. Behavioural data were collected during 434 hours of observation, and predation on other marine mammals was observed on 136 occasions (Chapter III). Here, I present information on the occurrence and behaviour of transient killer whales, focusing on foraging and feeding behaviours, including cooperative hunting and prey handling. While previous investigators have discussed age and sex differences in killer whale behaviour (e.g., Guinet 1991a; Jefferson *et al.* 1991), seasonal, individual or pod-specific differences in occurrence and behaviour have received less attention. In this study I examine how occurrence and behaviour vary seasonally and among transient pods (i.e., long-term maternal groups).



## Methods

### Study area and other marine mammal populations

Data were collected over an area of approximately 3,000 km<sup>2</sup> centred around the southern tip of Vancouver Island, British Columbia, Canada, and including the western San Juan Islands, Washington State, USA (Fig. 1.1). The study area is considered a "core area" for southern resident killer whales. Individuals from this population, which contains approximately 96 individuals (D. Ellifrit, personal communication), use the region on about 80% of the days during the summer months (R.W. Osborne, personal communication). Populations of several other species of marine mammals inhabit the study area (Osborne et al. 1988; Calambokidis and Baird 1994). Five species of pinnipeds have been recorded; four of these are fairly common. Harbour seals (Phoca vitulina) are the most abundant marine mammal, with an estimated total year-round population of approximately 3,000 (P. Olesiuk, personal communication). While harbour seals are found throughout the study area, concentrations occur primarily at haul-out sites. Over 60 haul-out sites are known within the study area, although most seals are found at a small number of major sites (12 have over 100 individuals; Baird, unpublished; P. Olesiuk, personal communication). All but two of the major harbour seal haul-outs and most of the minor haul-outs within the study area have a rock substrate; the remainder have a sand or pebble substrate. Harbour seals use these haul-outs year-round, and pupping occurs from late June through early September (Bigg 1969). Unlike most other phocids, mothers and pups of this species regularly enter the water during the three to six week nursing period (Oftedal et al. 1987).

California sea lions (Zalophus californianus) and Steller sea lions (Eumetopias

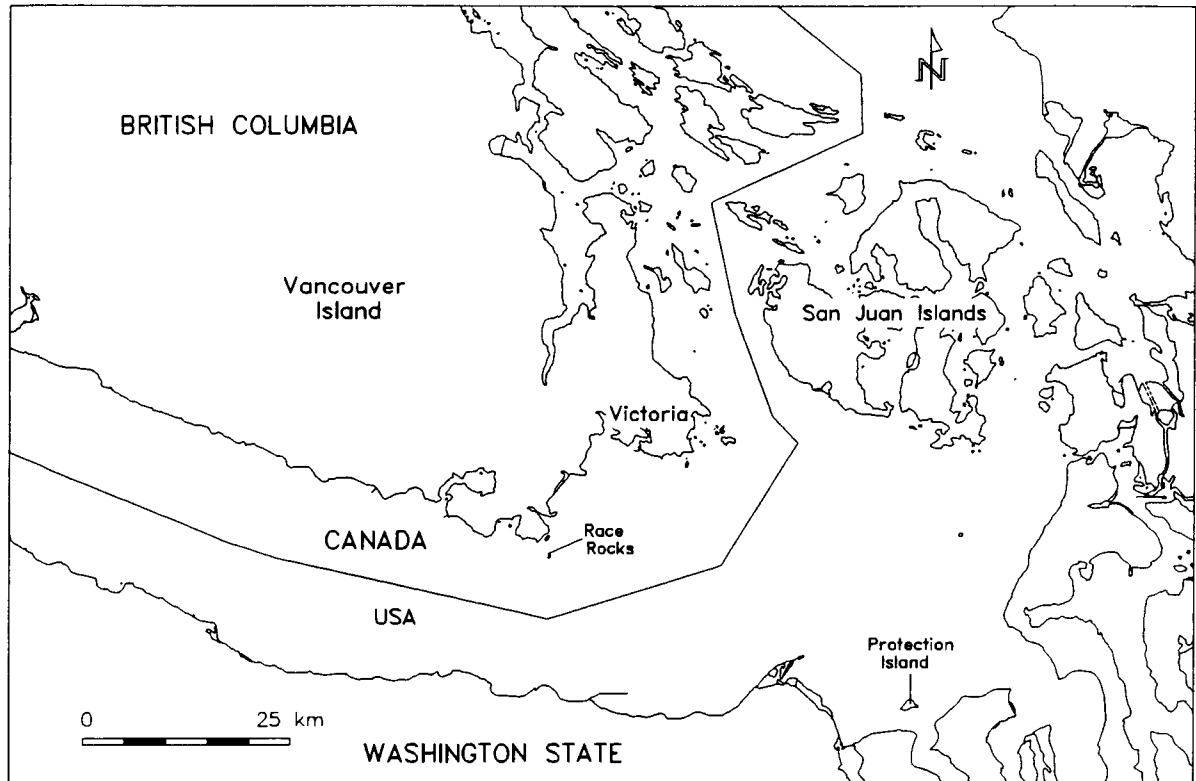


Fig. 1.1. Map of the study area showing place names mentioned in the text.

jubatus) are seen occasionally during summer, but are common within the study area from September through May, with a peak of approximately 1,000 individuals in October and November. Only one major sea lion haul-out is found within the region, at Race Rocks (Fig. 1.1). Northern elephant seals (Mirounga angustirostris) are seen regularly in the study area, both in open water and hauled out on shore, but no concentrations exist. Four species of cetaceans, other than killer whales, are also found regularly in the study area. Dall's porpoise (Phocoenoides dalli) are the species most frequently encountered, and are regularly seen in deeper (> 50 m) areas, while harbour porpoise (Phocoena phocoena) are occasionally found in waters less than 100 m in depth. Minke whales (Balaenoptera acutorostrata) and gray whales (Eschrichtius robustus) are also seen within the region, but no interactions with killer whales have been observed locally (but see Jefferson et al. 1991).

### Observational methods and analyses

Sightings of transient killer whales were reported by whale-watching vessels, lighthouse keepers, sports fishing charter operators, other research vessels, and members of the public. These records were used both to locate whales for encounters and to monitor seasonal occurrence.

Encounters were defined as periods of 15 min or greater in duration where all whales present in a group were identified and distance between the whales and the observer was short enough to record specific behavioural events and classify behavioural state (see below). Observations were made by one to four observers from one or two of several small vessels (to 8 m). Onset and termination of encounters was ad lib. (after

Altmann 1974); encounters usually terminated when whales were lost, or due to darkness, sea conditions or fuel considerations. Data were voice-recorded continuously throughout encounters, using a microcassette recorder. Whales were visible at the water's surface during surfacing periods that generally lasted 1-2 minutes; intervals between surfacing periods typically ranged from 2-8 minutes. During surfacing periods individual whales usually surfaced 3-6 times. Because group size was typically small, all visible behaviours of all individuals could be recorded simultaneously (focal-group sampling, all occurrences of all behaviours; after Altmann 1974). Data recorded included date, time, location, direction of travel, identity of whales present, distance between and orientation of individuals, relative speed of travel, dive durations, synchronization of respirations between individuals in the group, and the occurrence of discrete behaviours (e.g., breach, spyhop, tail lob, prey capture; see Jacobsen 1986). This information was used to define general behavioural state (Table 1.1). The occurrence of all other marine mammals visible at the surface or hauled out nearby was noted, including species, number, behaviour, and relative location. Sea state, other environmental conditions, and the number and type of other nearby vessels were also recorded.

Periods during which group size and composition remained constant were considered single observation periods, and the time spent in each behavioural state was divided by the duration of the observation period to give the proportion of time spent in each behaviour. All proportion data were arcsine-square root transformed before statistical analyses to normalize the data (Martin and Bateson 1988). To determine an overall behavioural budget, the time spent in different behaviours was summed over all observation periods, and divided by the total time spent observing transients.

Table 1.1. Behavioural categories used in this study.

Category	Description
Haul-out Foraging	Within 200 m of a harbour seal or sea lion haul-out, not including short duration (less than 30 second) passes by haul-outs; synchronization of respirations variable; direction of travel variable.
Nearshore Foraging	Following contours of shoreline in and out of bays, around headlands.
Offshore Foraging	Respirations asynchronous; direction of travel not consistent (zig-zagging); whales generally greater than five body lengths apart, in open water.
Foraging/Travel	Respirations synchronous; direction of travel consistent; whales generally less than five body lengths apart, in open water; occasionally catch prey during periods of this behaviour; otherwise indistinguishable from "Travel".
Feeding	Prey or prey parts seen. Feeding was defined as the period from when prey were first attacked to when the last remains of prey were consumed (cf. prey handling time).
Resting	Respirations synchronous; direction of travel consistent; whales generally less than one body length apart, in open water or nearshore; usually no net motion relative to land or movement backwards in a current; occasional hanging motionless at surface, in open water.
Fast Travel	Respirations usually synchronous; direction of travel consistent, whales generally less than two body lengths apart; high speed, often porpoising part way out of the water.
Travel	Respirations synchronous; direction of travel consistent; whales generally less than five body lengths apart; in open water; no prey captured during periods of this behaviour, otherwise indistinguishable from "Foraging/Travel".
Social/Play - all	Interactive movements between individuals, not associated with prey capture; all individuals in a group involved; includes percussive behaviour (e.g., tail lob) by lone individuals.
Social/Play - some	Interactive movements between individuals, not associated with prey capture; only some individuals in a group involved.

Individual whales present in each encounter were identified visually and/or from photographs, using the catalogues of Bigg *et al.* (1987) and Ellis (1987), and unpublished catalogues maintained at the Center for Whale Research (Friday Harbor, WA), the Marine Mammal Research Group (Victoria, B.C.), and the Pacific Biological Station (Nanaimo, B.C.). Pod designations use the alphanumeric (e.g., M1, Q3, Y1) system of Bigg *et al.* (1987), and pod membership and age of whales were determined using sightings from this study as well as sighting information provided by the above-mentioned organizations. For groups with extended sighting histories (e.g., greater than several years) the first sighting of a very small individual could be used to estimate approximate year of birth, and size relative to known-aged or adult individuals could be used to estimate age for subadults.

Prey handling time was defined as the period from when the whales first appeared to encounter a prey item until the last signs of prey were observed. This period could be broken down into the time from encounter to prey death ( $T_K$ ), and the time from death to complete consumption or abandonment of the prey carcass ( $T_E$ ). In many cases it was not possible to determine accurately when the prey was killed, resulting in a period during which prey status (dead or alive) was unknown. For each prey capture a variety of factors were recorded: time, whale group size, identity and age of individual whales involved, prey species, size and caloric value (cf. Chapter III), tidal height and direction (flood vs. ebb), time since/to sunrise/sunset, and foraging type (Table 1.1) prior to the kill. Tidal height and direction were determined using Canadian Tide and Current Tables published yearly by the Department of Fisheries and Oceans, and time since/to sunrise/sunset were calculated from values presented in the Canadian Almanac and Directory.

In just over half the prey captures (57%), prey species could be determined by direct visual observations of prey, either in whales' mouths or at the surface amongst a group of whales, combined with observations of blood, blubber or meat in the water. The remaining prey captures (43%) were detected without direct observations of intact prey, and were based on observations of prey parts in whales' mouths or in the water. In these cases prey species identification was based on a combination of location, observations of potential prey in the area prior to capture, prey handling time, behaviour, and quantity of blubber observed in the water. Per capita energy intake values, taking into account the size of prey and the size of killer whales in the hunting group, were calculated as described in Chapter III. All seasonal comparisons were made between the harbour seal pupping/weaning/post-weaning period (July through September) and the non-pupping/weaning period (October through June). Comparisons between pods were made using only those pods encountered on greater than 10 occasions each.

## Results

Transient killer whales were reported within the study area on 384 occasions from 1987 through 1993. Transients were encountered 99 times during this period, and an additional encounter from 1986 was also used in the analyses. Approximately 434 hours of behavioural observations were recorded during these encounters. Changes in group size or composition during an encounter resulted in a total of 217 observation periods of constant group size and composition, ranging in duration from 15 min to 9 h and 11 min. Group size ranged from 1 to 15 individuals, but the most frequently recorded group size was three individuals (see Chapter III). During the 100 encounters, a total of 62 different individuals from 26 separate pods were recorded. Not all pods were seen with equal

frequency (Fig. 1.2). Several pods were regularly resighted throughout the study, both within and between years. Others were seen only occasionally, and new pods were recorded within the study area each year (Fig. 1.3), suggesting that the total number of transients that use the region is much greater than 62 individuals. Most of the pods (23 of 26) had been previously sighted elsewhere, but three were documented for the first time in this study.

### Seasonal occurrence

The seasonal distribution of sighting records and of encounters is shown in Fig. 1.4. Transient killer whales were recorded in the study area in all months of the year, with a peak in both sighting records and encounters in August and September. There were no encounters with transients during December or January due to weather constraints. Sighting effort is high from May through September; thus the large number of records in August and September compared to May through July implies an increase in transient use of the area during that period. The average individual energy intake rate was also significantly higher during the July-September period than during the remainder of the year (Table 1.2, Mann-Whitney U-test,  $p = 0.005$ ).

Pod-specific differences in seasonal occurrence were found. Considering the 6 pods seen on more than 10 occasions each, three (Q3, T3, Y1) were seen almost entirely (63 of 70 encounters) during the harbour seal pupping/weaning/post-weaning period (hereafter referred to as the seal pupping period), while three others (M1, O4, O20) were encountered both during the pupping period (21 of 50 encounters) and at other times throughout the year (29 encounters). Taking all pods into account (including those seen



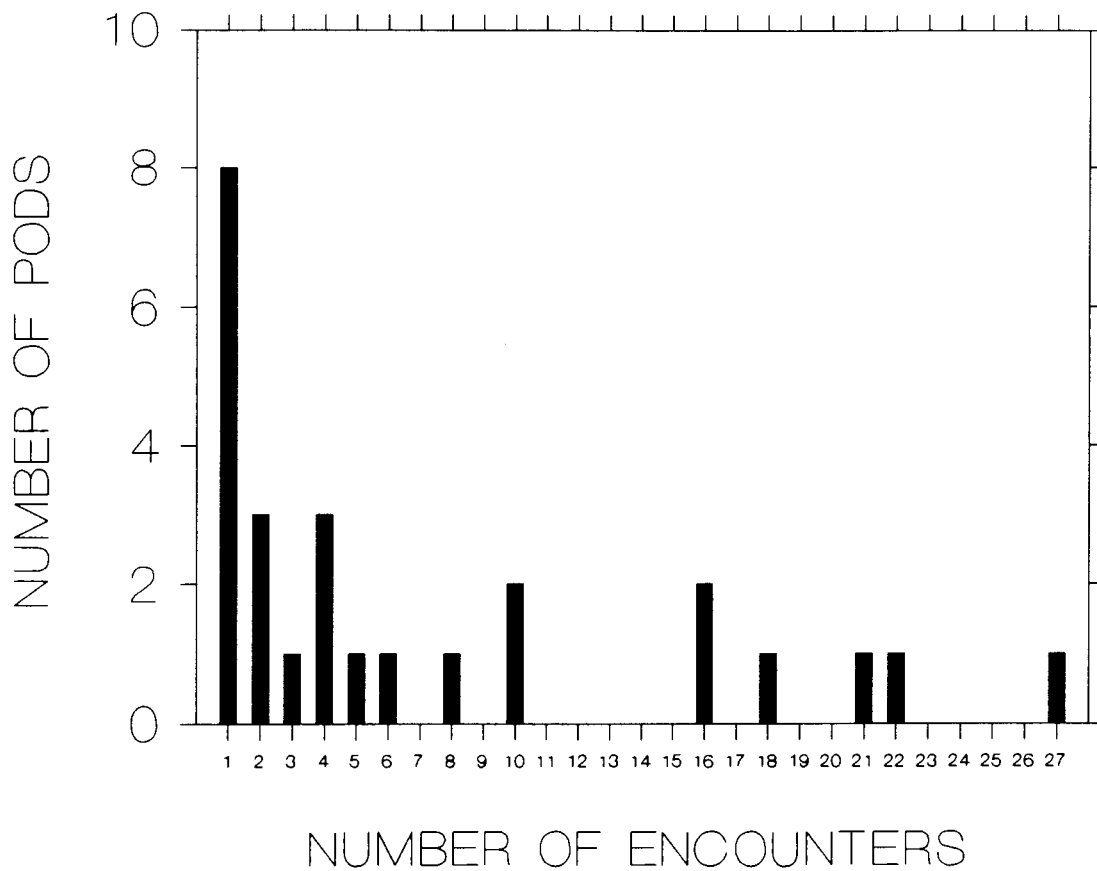


Fig. 1.2. Frequency of encounters recorded for different pods.

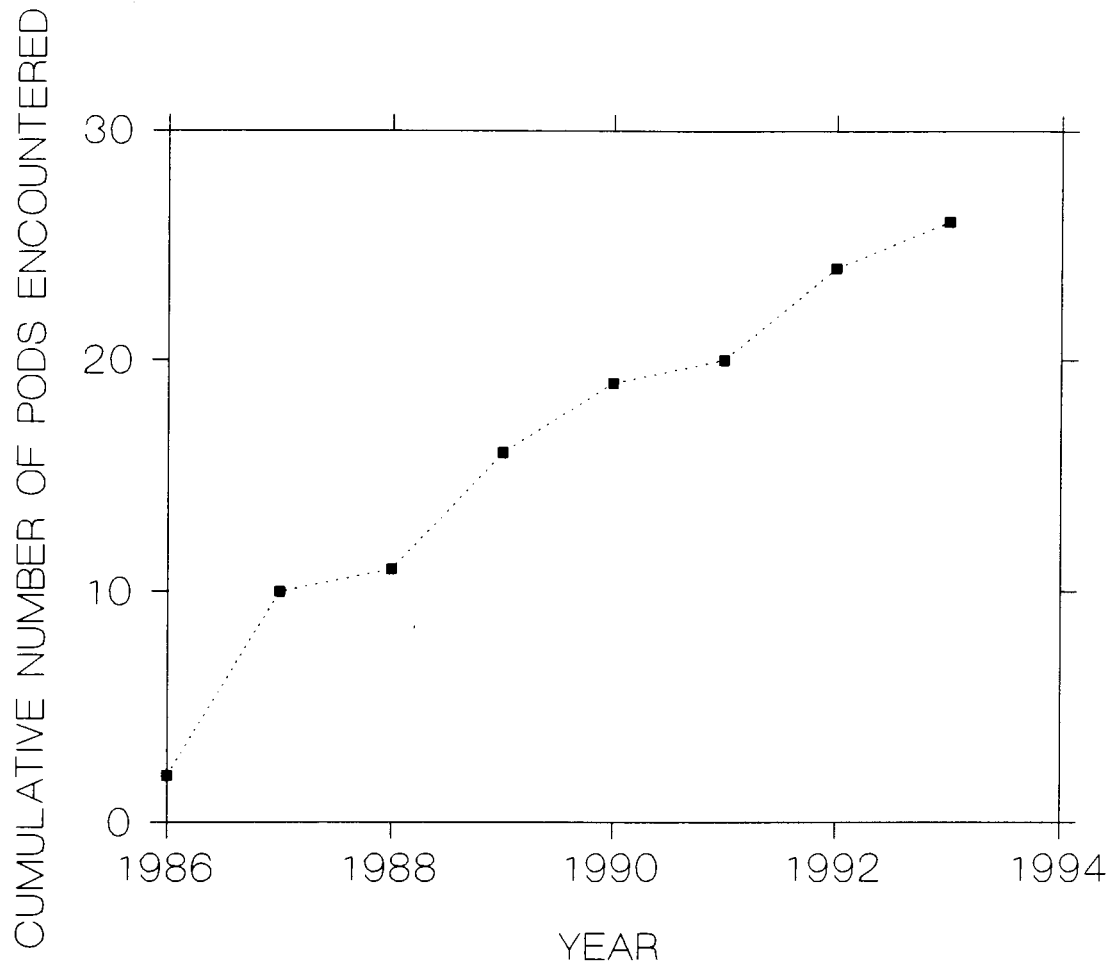


Fig. 1.3. Cumulative number of pods encountered during the study. While many pods were resighted both within and between years, new pods were regularly encountered throughout the course of the study.

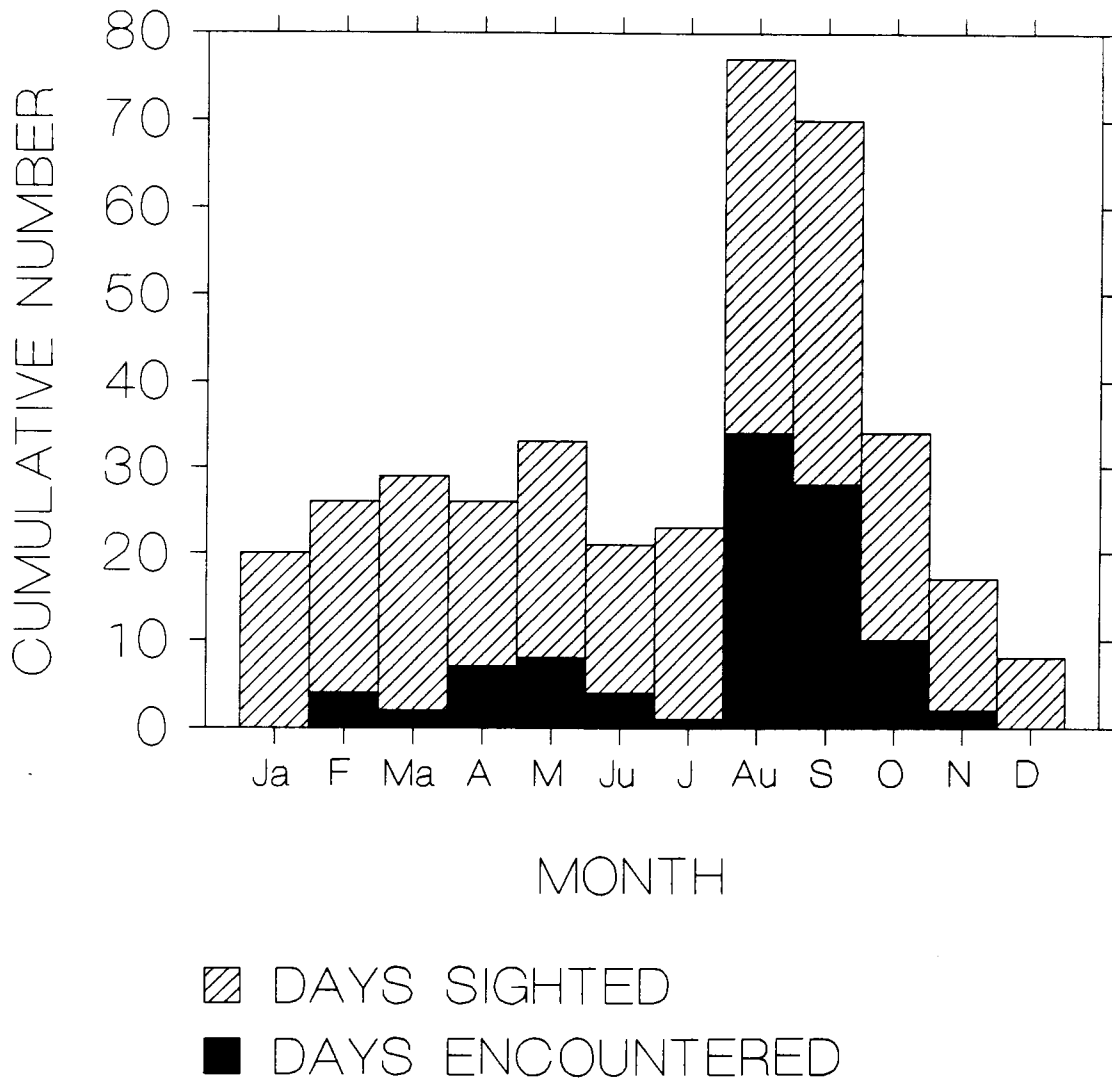


Fig. 1.4. Seasonal distribution of transient killer whale sightings and encounters. Sighting effort between October and April was low, thus the decrease in records during this period does not necessarily reflect a decrease in transient killer whale presence in the study area.

Table 1.2. Summary of seasonal differences in transient occurrence and behaviour.

	Harbour seal pupping, weaning/post-weaning period (July-September)	Non-weaning/post- weaning period (October-June)	Statistical significance
Occurrence	relatively high	relatively low	-
Average food intake <sup>1</sup> (kcal/kg/day)	76.8	33.4	p = 0.005
Percentage time foraging	49.61	47.93	NS
Percentage time haul-out foraging	7.16	1.68	p < 0.001
Percentage time near-shore foraging	12.91	3.08	p = 0.002
Percentage time social/play behaviour	4.73	2.15	NS
Mean group size	3.96	4.39	NS
Pods present	most	primarily non-haulout foragers	-
Average prey handling time (min)	42.0	20.8	p = 0.003

<sup>1</sup>Average energy intake is calculated as presented in Chapter III.

on 10 or fewer occasions) also indicates that some pods appear to use the area preferentially during the seal pupping period, while others are seen primarily in the non-pupping period (Fig. 1.5).

### Foraging patterns

Foraging behaviours (including feeding) occupied 63.13% of the total observation time (Table 1.3). Behaviour during foraging is extremely variable: as noted in Table 1.1, foraging can be divided into several sub-categories based on location (seal haul-outs, other near-shore areas, open water), spacing between individuals, synchronization of respirations, and directionality of travel. Foraging around seal haul-outs and other near-shore areas typically involves close following of the contours of the shoreline or circling of rocks or small islets. Distance between individuals is variable during foraging, ranging from less than one body length (~ 3-8 m) to over a kilometre. The pattern of alignment of individuals in a foraging group, in terms of travelling abreast, staggered or clumped, is also variable.

Percentage of time spent foraging decreased with an increase in group size (Fig. 1.6; weighted regression on transformed percentages,  $r^2 = 0.68$ ,  $df = 227$ ,  $p < 0.001$ ). Foraging type varied seasonally; significantly more time was spent foraging in haul-out and near-shore areas during the harbour seal pupping period than during the rest of the year (Table 1.2, Mann-Whitney U-test,  $p < 0.001$  and  $p = 0.002$  for haul-out and near-shore, respectively). While the proportion of time spent foraging did not differ significantly among pods (Kruskal-Wallis one-way ANOVA,  $n = 6$  pods,  $p = 0.82$ ), the occurrence of different foraging types did differ among pods (Kruskal-Wallis one-way ANOVA,  $p =$

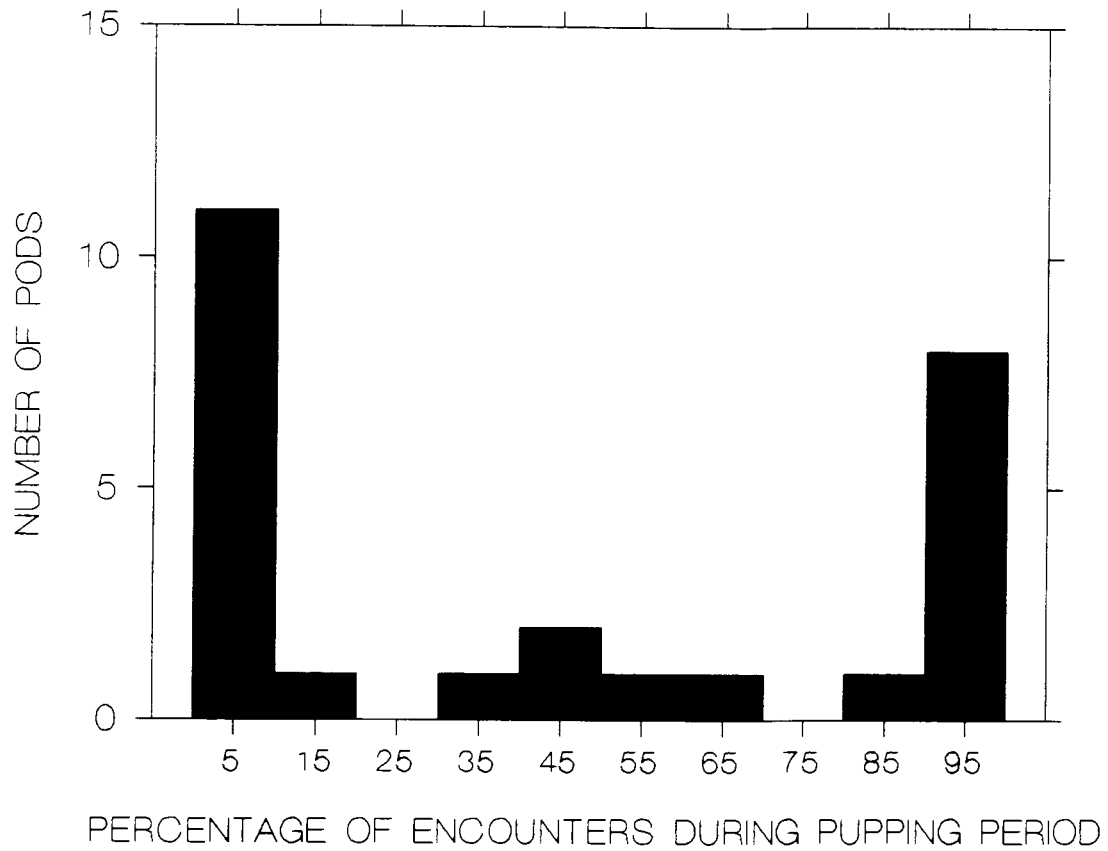


Fig. 1.5. The proportion of time that pods were seen during the pupping vs. non-pupping periods differed between pods. Some were seen primarily during the pupping period (right side), while others were seen primarily during the non-pupping period (left side). Each value shown on the abscissa represents the mid-point of the percentage category (e.g., a value of 5 represents values between 0 and 9.9 percent).

Table 1.3. Behavioural budget of transient killer whales based on 434 hours of behavioural observations (see Table 1.1 for description of behavioural categories).

Behaviour	Percentage Time for each category	Percentage Time for each sub-category
Foraging	63.13	
- Haul-Out Foraging		5.15
- Nearshore Foraging		9.31
- Offshore Foraging		24.92
- Foraging/Travel		9.60
- Feeding		14.15
Fast Travel	0.30	
Travel	31.07	
Rest	1.72	
Social/Play	3.78	
- Social/play, all		1.79
- Social/play, some		1.99
TOTAL	100	

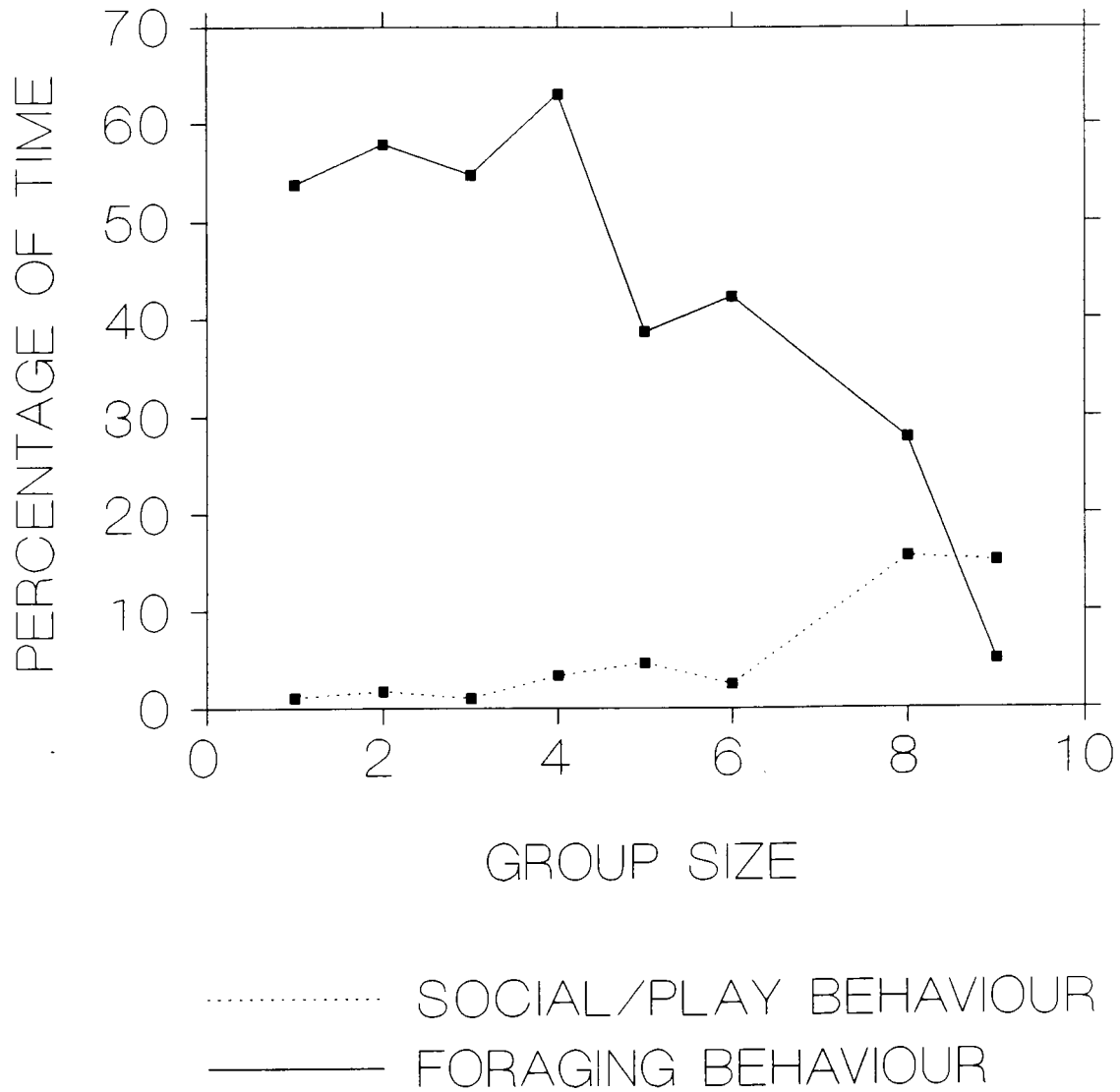


Fig. 1.6. Variation in foraging and social/play behaviour with group size. Only group sizes with more than three observation periods (group sizes 1-9, not including 7) are shown.



0.02). Some pods (M1, O4, O20) spent virtually no time (i.e., < 2%) haul-out or near-shore foraging, while others (Q3, T3, Y1) spent between 25-50% of their time engaged in these types of foraging. Those pods which generally did not forage in near-shore areas spent more time engaged in offshore foraging (Table 1.4).

### Feeding behaviour

As a behavioural state, feeding was defined as the period from when a prey item was first encountered until consumption was completed. Just less than 15% of the whales' time was engaged in feeding behaviour (Table 1.3). In many cases, feeding behaviours overlapped with other behaviours, i.e., time spent feeding did not prevent the whales from engaging in other behaviours. For example, portions of a prey item could be carried for extended periods while foraging continued or the whales engaged in travel or social/play behaviour.

I observed 138 prey attacks, 136 of which were successful (Chapter III); thus all but two of the prey attacks were included in the feeding category. The vast majority of prey killed (130/136) were or were suspected to be harbour seals (see Chapter III); the remaining prey included three harbour porpoises, two sea lions (exact species identification not possible) and an adult male elephant seal. When a prey item was first captured by a member of a foraging group, all whales in the group typically converged, sometimes from distances of up to a kilometre. Prey were seen in whales' mouths during 93 of the 136 observed kills (68%). Multiple whales in a group carrying all or part of a prey item during a particular kill, suggesting prey sharing, were observed for 51% of these kills. Active prey division or transfer was also observed on 15 occasions, involving two

Table 1.4. Behavioural budgets for transient pods which regularly forage in nearshore areas (Q3, T3, Y1) and for those which do not (M1, O4, O20), when only a single pod was present.

Behaviour	Percentage Time for each category and sub-category	
	Nearshore foragers	Non-nearshore foragers
Foraging	87.54	67.35
(Haul-Out Foraging)	(10.23)	(0)
(Nearshore Foraging)	(25.41)	(1.56)
(Offshore Foraging)	(18.80)	(46.84)
(Foraging/Travel)	(12.87)	(7.34)
(Feeding)	(20.23)	(11.61)
Fast Travel	0	0
Travel	10.03	31.38
Rest	2.21	0
Social/Play	0.22	1.27
(Social/play, all)	(0.15)	(0.06)
(Social/play, some)	(0.07)	(1.21)
TOTAL	100	100
Hours	68.6	90.9

whales ripping a seal apart, or one whale dropping a prey item and a second whale recovering it. On several occasions two whales were seen approaching each other slowly head on, one carrying the seal. Both whales then grasped the seal, and backed away from each other, pulling it apart. On several other occasions, two whales were seen swimming side by side, one carrying a seal. The second individual grasped one end of the seal and both individuals then moved their heads apart, pulling the seal in two.

Cooperation and/or division of labour between individuals was apparent in many prey attacks. During one attack on a Dall's porpoise by a group of three killer whales, two whales alternated engaging the porpoise in a high speed chase. In several cases when harbour seals appeared to hide in underwater rock crevices or caves, whales appeared to co-ordinate time below water so that at least one whale was always underwater, preventing the seals from escaping. During several harbour seal attacks in which  $T_k$  (the time from prey encounter to death) was prolonged, an adult male in a group appeared not to be directly involved in attacking the prey. In these cases, while a group of females or subadults made passes by the seal, striking it with their tails or pectoral flippers, adult males occasionally appeared to prolong their dive times, possibly to stay beneath the seal and prevent its escape.

Prey handling time was extremely variable, ranging from less than 2 min to over 3 h (Fig. 1.7). Taking into account prey ranging in size from harbour seal pups (ca. 10 kg) to an adult male elephant seal (ca. 1700 kg), handling time increased significantly with prey size (regression,  $r^2 = 0.47$ ,  $df = 44$ ,  $p < 0.001$ ). However, this effect was largely due to the influence of the single elephant seal kill observed; without this observation, no effect of prey size on handling time was apparent (regression,  $r^2 = 0.05$ ,  $df = 43$ ,  $p = 0.13$ ).

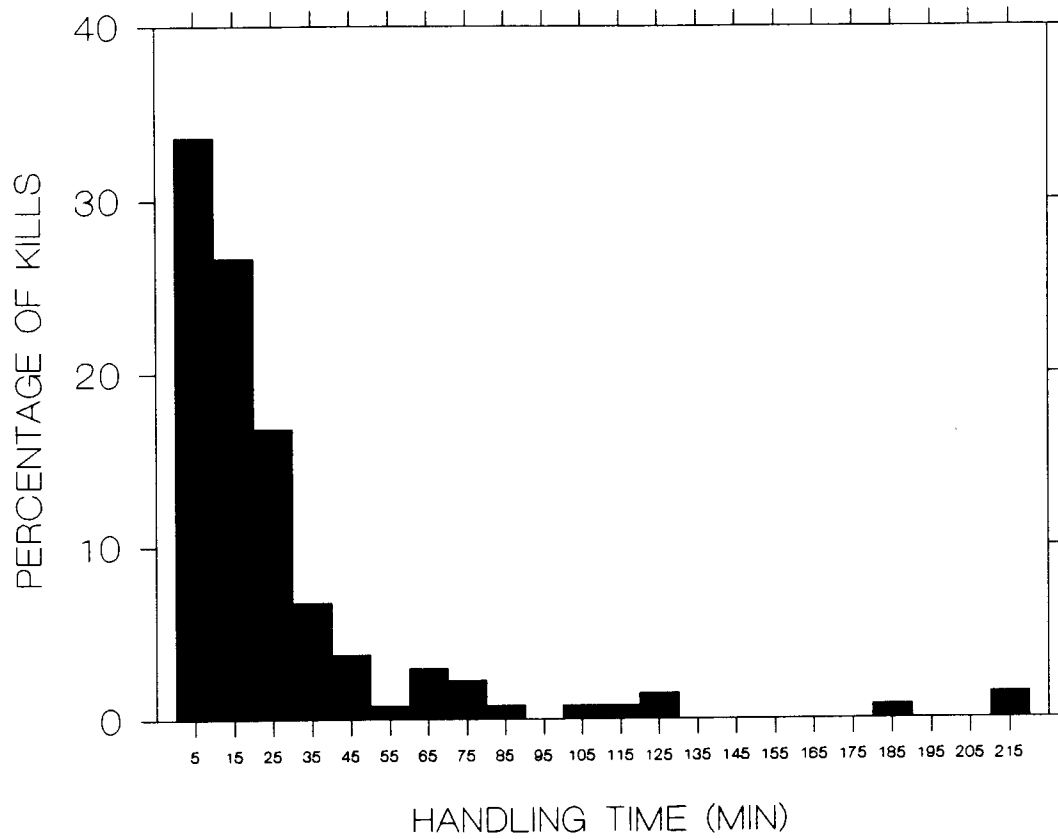


Fig. 1.7. Frequency distribution of prey handling times. Values on the abscissa represent the mid-point for each time period (i.e., a value of 5 represents handling times ranging from 1-10 minutes).

For harbour seals, both  $T_k$  and  $T_e$  (the time from prey death to consumption) were variable, ranging from less than 1 min to 38 and 178 min for  $T_k$  and  $T_e$ , respectively (Fig. 1.8). Regressions of total handling time,  $T_k$ , and  $T_e$  against killer whale group size, the age of the youngest and second youngest whales in the group, tide height, tide direction (ebb vs. flood), sea state, and time since sunrise or to sunset were not significant.

Unfortunately, observation periods were not long enough to be able to estimate the whales' hunger state. No significant differences in handling time existed between pods, but a seasonal difference did exist (Mann-Whitney U-test,  $p = 0.003$ ), with a longer average handling time during the non-pupping/weaning period (Table 1.2).

### Social/play behaviour

Social/play behaviours included body contact and/or interactive movements between individuals (e.g., chasing, one whale rolling over top of another), as well as percussive and other behaviours (e.g., breaching, spyhopping, taillobbing, pectoral flipper slapping, penile extrusion). While frequently occurring in conjunction with feeding, social/play behaviour of this type also occurred independently of other behaviours for 3.78% of the observation time. When it occurred independently, I termed this "pure" social/play behaviour. The percentage of time engaged in pure social/play behaviour increased with group size (Fig. 1.6; weighted regression on transformed percentages,  $r^2 = 0.49$ ,  $df = 227$ ,  $p < 0.001$ ), and was twice as high during the seal pupping period (4.73% versus 2.15% during the non-pupping period; Table 1.2), although this difference was not significant (Mann-Whitney U-test).

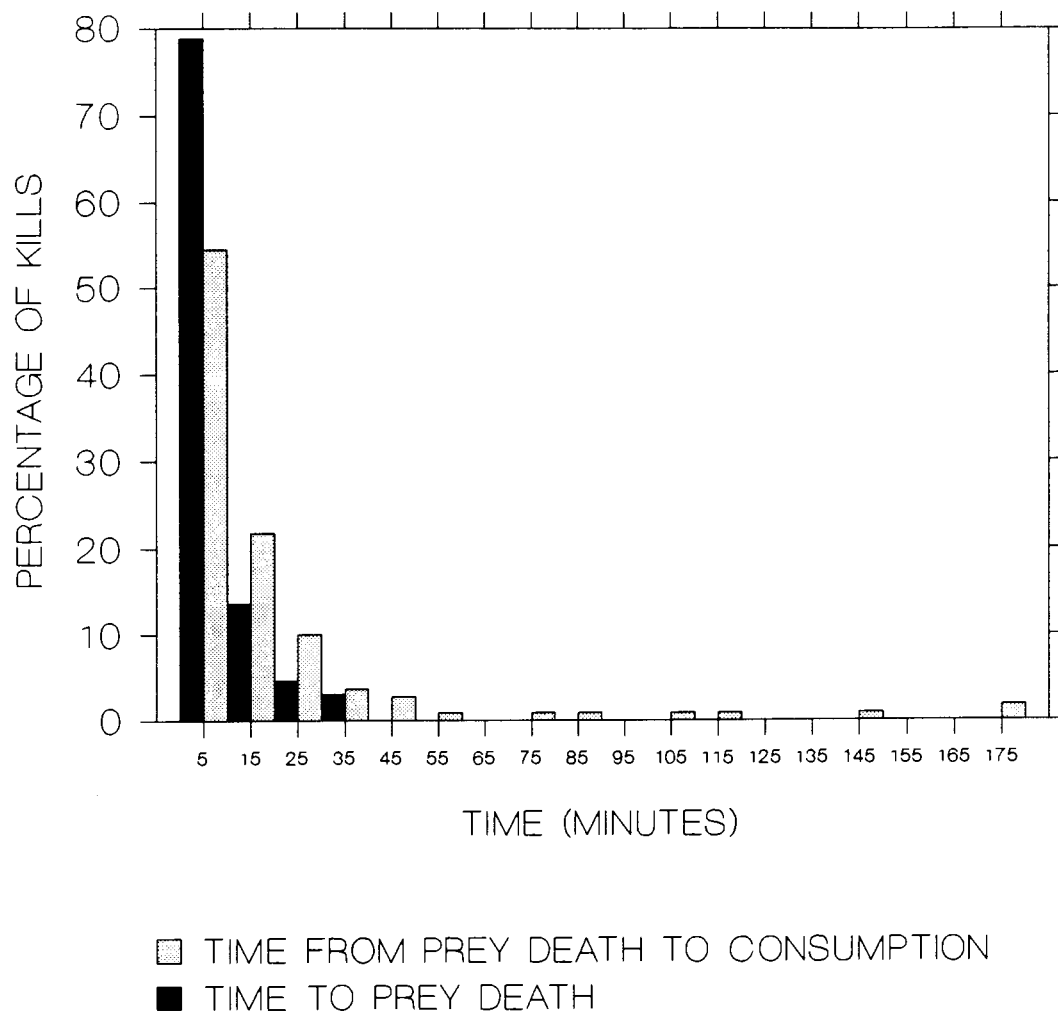


Fig. 1.8. Frequency distribution of prey handling time, divided into its two components:  $T_K$ , the time from when the prey is encountered until it is killed; and  $T_E$ , the time from prey death until it is completely consumed.

### Multi-pod associations and interactions with resident killer whales

Resident killer whales were reported and observed much more frequently within the study area than were transients (Baird, unpublished). While multi-pod associations of transients were regularly observed in this study (Chapter III), residents and transients were never observed travelling together, even though the two types of whale were recorded within several kilometres of each other on nine occasions. On four occasions, when the two types were not on intersecting courses, no obvious changes in the transient killer whale travel patterns were observed. On five occasions where residents and transients were on intersecting courses, the transients changed their direction of travel, effectively avoiding contact with the residents. No change in the direction of travel of resident groups was observed when they were in proximity to transients.

Virtually all transient pods observed in the study have been seen associating with one or more other transient pods, either in this study or elsewhere. However, associations between transient pods were non-random. Pods which foraged primarily in open water (M1, O4, O20) were more likely to be found associating with each other than with pods which regularly foraged at seal haul-outs and other nearshore areas (Q3, T3, Y1), and vice versa (21 of 26 multi-pod associations involving at least two of these pods were between pods with similar foraging habitat preferences). Such patterns were not due to a lack of opportunity for associations between pods which foraged in different ways. Those that foraged in nearshore areas also spent up to or over 40% of their time (Table 1.4) in offshore areas. Thus, there was the potential for interactions between pods that foraged in these different areas.

## Discussion

Sighting and encounter records showed a clear peak in transient killer whale presence in the study area during the latter two thirds of the harbour seal pupping/weaning/post-weaning period (Fig. 1.4). The average per capita energy intake rate during the seal pupping/weaning period is significantly greater than during the remainder of the year (Table 1.2), implying that transients may preferentially use the study area during this period due to the increase in prey availability, as suggested for other areas (Condy et al. 1978; Lopez and Lopez 1985; Guinet 1991b). The relatively small number of sightings and encounters in the first of this three month period (July) implies that it may be the harbour seal weaning and post-weaning periods that result in the greatest increase in prey availability, rather than pupping per se. Because the timing of pupping varies along the British Columbia coast (Bigg 1969), it is possible that during July transients may be spending the majority of their time in other areas where pupping has occurred earlier.

If this research had been land-based (as in the other studies mentioned in the Introduction), a seasonal peak in occurrence would be even more pronounced than is apparent in this study, due to the seasonal differences in use of near-shore areas. However, because these differences in habitat use were largely pod-specific, a conclusion that transients utilize the area more during the pupping period is not strictly accurate. Rather, some groups of transients appear to use the area regularly year-round, while others (those who appear to specialize in foraging around pinniped haul-outs and other near-shore areas) seem to use the area preferentially during the weaning/post-weaning period (Fig. 1.5).



Such conclusions, and others I draw below, hinge upon my assumption that the presence of my research vessel and other recreational or commercial vessels around the whales had little or no effect on their occurrence or behaviour within the study area. Recreational and commercial vessel traffic in the study area is greatest during the seal pupping/weaning period. Increased use of the area by transient killer whales during August and September suggests that their broad-scale use of the study area may not be greatly affected by the presence of vessel traffic. Similarly, Osborne (1991) noted that southern resident killer whales appear to have increased their use of Haro Strait in recent years despite an increase in the amount of commercial whale watching traffic, suggesting that the increase in vessel traffic has not resulted in broad-scale shifts in their habitat use. Little information is available on the potential short-term impacts of vessels on killer whale behaviour or spatial patterns. Kruse (1991) claimed that northern resident killer whales increased their speed in the presence of boats, but her conclusions were not supported by the data presented (Duffus and Dearden 1992). Evidence collected during a study in progress in Haro Strait on boat/killer whale interactions suggests that resident killer whales do not change their behaviour in the presence of boats (R. Otis, personal communication; see Phillips and Baird 1993). For transients, I (Chapter III) noted that observed food intake was approximately twice the animals' predicted energetic needs, suggesting that at least in terms of prey capture, transients were not greatly affected by the presence of the research boat. For all these reasons, I believe that the occurrence and behaviour of transients in this study were not greatly affected by my presence.

### Behavioural budgets

Comparisons with previous studies which present behavioural budgets for transient

killer whales are problematic for several reasons. Other researchers have focused on acoustical recordings (e.g., Morton 1990; Barrett-Lennard 1992; Saulitis 1993), or have used observational methods developed for behavioural observations of resident killer whales (e.g., Felleman et al. 1991). In both cases the distances between the observer and the whales are so great that they preclude recording the majority of prey captures (cf. Chapter III). Thus, observations of feeding appear to have been under-represented in their samples, and behaviours often associated with feeding, such as social/play behaviours, might have been interpreted in a purely social context. As well, previous behavioural budgets have generally not included feeding as a discrete behaviour, lumping it with other foraging behaviours. Sample sizes have also been small, resulting in biased representations of actual behaviour (e.g., no social behaviour - Felleman et al. 1991, Barrett-Lennard 1992; no resting behaviour - Morton 1990). Seasonal and pod-specific differences in occurrence and behaviour (summarized in Tables 1.2 and 1.4), corresponding to differences in prey availability and foraging tactics, also affect comparisons between studies. Taking into account differences in study design and behavioural categories, no obvious differences in the amount of time spent foraging were apparent between this study and previous work; to be noticed, however, such differences would have to be extreme, all things considered.

### Foraging patterns

Harbour seal haul-outs make up less than 1% of the study area, yet 12.4% of the total time transients were observed foraging was spent in these areas, and 35% of the seal kills occurred there. Prolonged foraging at a haul-out often resulted in multiple kills, particularly during the harbour seal pupping period. Adult and sub-adult harbour seals

were frequently observed to move into shallow water or to haul out on shore after becoming aware of the presence of foraging transients, so prey capture probably becomes more difficult during prolonged foraging at haul-outs. However, haul-out foraging occurred more often during the harbour seal pupping and weaning period (Table 1.2), and inexperienced individuals (i.e., pups) seemed less likely to haul-out in the presence of foraging transients (personal observations).

Transients were not seen intentionally stranding to capture hauled-out seals, as is regularly observed elsewhere (e.g., Lopez and Lopez 1985; Guinet 1991a; Hoelzel 1991). One such event has been noted locally, however, on a pebble beach at Protection Island (P. Gearin, personal communication; see Fig. 1.1 for location). Such behaviour is likely infrequent for this population of transients for several reasons. Sites where intentional killer whale stranding occurs elsewhere appear to be comprised of steeply sloping pebble substrates, and such sites are only rarely used by harbour seals in my study area.

Intentional stranding to obtain prey also carries a risk of mortality (Guinet 1991a) and such behaviour should only occur when the benefits outweigh the costs. In the area around southern Vancouver Island prey abundance and food intake rates are so high (Chapter III) that such behaviour may not be worth engaging in. Intentional stranding as a prey capture technique also appears to be a learned behaviour, requiring extensive practice and training (Guinet 1991a); as such its value as a hunting technique likely increases with use, and it may not be profitable to use on only an occasional basis.

Sixty-five percent of the observed kills occurred away from seal haul-outs. There are several possible explanations for the occurrence of such a large proportion of kills occurring in non-haul-out areas. One possibility is that the whales "trapline" - foraging

extensively at a haul-out before moving to another, occasionally capturing prey in between, as suggested by Barrett-Lennard (1992). Data on travel routes collected in this study (Baird, unpublished) do not support such a conclusion, however, because routes of whales leaving haul-outs vary considerably, with whales switching to any one of the other foraging types. Fast travel was rarely observed (Table 1.3), and never between haul-outs. Another possibility is that foraging offshore may allow for capture of prey other than harbour seals. Saulitis (1993), for example, noted that all the kills she observed while watching whales foraging in open water were Dall's porpoise, while all marine mammals killed near shore were harbour seals. While both Dall's porpoise attacks and two of the three harbour porpoise kills in this study were in open water, the large number of harbour seal kills offshore (55) implies that foraging offshore in the area around southern Vancouver Island does not function solely to allow predation on other species of marine mammals. Rather, such observations seem to be best explained by the pod-specific differences in foraging patterns noted above.

### Feeding behaviour

Division of prey was difficult to observe, requiring positioning of the research vessel in front of or beside whales carrying prey, at distances less than 5 m. Handling time during many prey captures was very short, and much of the prey handling occurred far beneath the surface with only blood or bits of blubber seen; thus, in many cases it would not have been possible to observe division of prey even if it occurred. Guinet (1992) observed a killer whale in the Indian Ocean consuming prey away from its group, but no such observations were made in this study. Although multiple whales in a group were documented carrying prey on only 35% of the kills, I believe division of prey

between individuals in a hunting group occurred more frequently.

Almost 15% of the whales' time was spent feeding, but other behaviours often occurred after a prey had been killed but before it had been completely consumed. Whales often engaged in social/play behaviours after a kill. Because transient killer whales appear to hunt by stealth (Morton 1990; Chapter IV, Baird *et al.* 1992; Barrett-Lennard 1992; Saulitis 1993), and social/play behaviours are characterized by frequent body contact between individuals and extensive percussive behaviour (such as breaches, spyhops, taillobes, and cartwheels), engaging in social/play behaviour during foraging periods may reduce foraging success. Once a prey item has already been captured, social/play behaviour can be exhibited without the consequent negative impact on future short-term foraging success.

The time feeding on a prey item varied from less than 2 min to over 3 h (Fig. 1.7). Such variability in prey handling time is typically ignored in studies of foraging theory (Stephens and Krebs 1986), prompting me to investigate possible factors responsible for it. That handling time should increase with prey size or in response to prey defenses seems intuitively obvious (see Werner 1974; Forbes 1989). However, excluding the single elephant seal caught (which weighed much more than the whales could possibly have consumed), there was no relationship between handling time and prey weight (for prey ranging from 10-300 kg). Similarly, no significant relationship exists between handling time and the defensive abilities of the prey. I divided handling time into  $T_K$ , the time from when the prey was captured until it was killed, and  $T_E$ , the time from when the prey was killed until it was consumed. For harbour seals, both  $T_K$  and  $T_E$  could be very short (i.e., less than one minute each). The required minimum  $T_K$  appears to be prolonged (i.e.,  $> 1$

minute) only for more difficult to capture or dangerous prey, such as Dall's porpoises or sea lions, respectively, while the minimum value for  $T_E$  is likely only prolonged when the prey is very large (i.e., close to or exceeding the maximum stomach capacity for killer whales), as are adult sea lions and elephant seals.

Another factor which might affect handling time is whale group size (although it is difficult to predict whether handling would be prolonged in larger groups due to conflicts over prey allocation, or reduced due to a greater number of whales consuming prey of a particular size). However, there was no relationship between whale group size and handling time. Similarly, handling time was not related to environmental factors such as tide height, tide direction (ebb vs. flood) or time since sunrise or to sunset. Thus, for harbour seals, prey handling longer than about two min appears to be an unnecessary allocation of time, assuming that prey handling has no function other than the direct outcome of killing and consuming prey. Prolonged prey handling was often characterized by behaviours typical of social/play behaviour. Play behaviour frequently decreases with increasing age, associated with a presumed function of learning in young animals (Fagen 1981; Harcourt 1991a). I suspected that prolonged prey handling by killer whales might thus serve the function of allowing young to learn prey handling techniques, and tested this hypothesis, but found no significant relationship between the age of the youngest or second youngest whale in a group and the duration of prey handling, or the duration of  $T_K$ . The function of extended prey handling for transients thus remains unclear.

#### Social/play behaviour

Based on a sample of approximately 43 hours of behavioural observations,

Felleman *et al.* (1991) reported that percussive behaviour in transient killer whales is only regularly exhibited during predation. However, transients in this study engaged in social/play behaviours, not associated with prey captures, for 3.78% of their time, and this typically involved percussive behaviour. The frequency of such social/play behaviour varied both with group size (Fig. 1.6) and seasonally (Table 1.2). As the small groups seen most frequently are usually comprised of related individuals (Bigg *et al.* 1987; Chapter III), the increase in social/play behaviour with group size may reflect increased mating opportunities, or opportunities to learn courtship or mating skills in larger, multi-pod groups (Chapter III), as has been suggested for residents (Rose 1991).

While the average group size was similar between the seal pupping period and the rest of the year (mean of 3.96 and 4.39 individuals, respectively), social/play behaviour was more than twice as frequent during the seal pupping period. The decrease in social/play behaviour during the non-pupping period may be related to the lower food intake during those months (Table 1.2). Potential prey may be alerted by the percussive activity characteristic of killer whale social/play behaviour, and harbour seals may be more difficult to catch during the winter months; as the pups age they likely gain experience in detecting killer whales and assessing the associated danger. Thus, the costs associated with social/play behaviour (i.e., alerting prey) may be greater during the non-pupping period (cf. Harcourt 1991b). Alternatively, play behaviour may decrease due to increased hunger levels during the non-pupping period, a trend seen in a variety of organisms (Fagen 1981).

### Multi-pod associations and interactions with residents

Associations between pods of killer whales which inhabit a particular area are not random. Variability in association patterns has been noted within a resident community (Bigg *et al.* 1990), and has also been used to delineate sympatric populations (Bigg 1979). In this research resident killer whales were observed more frequently than transients, and while multi-pod associations were observed for both transients and residents, the two forms were never seen associating with one another. Morton (1990) described three interactions between transients and residents; in all cases the transients appeared to avoid the residents, and in one instance the residents also changed their direction of travel, apparently to avoid the transients. In this study transients appeared to avoid residents whenever the two forms were on intersecting courses. Because transient killer whales are usually silent, while residents vocalize frequently (Morton 1990), it is more likely that transients will detect resident killer whales while remaining undetected themselves. A recent observation by G. Ellis (personal communication) provides some functional basis for transient avoidance of residents: a group of southern resident killer whales appeared to attack and chase a group of transients off Nanaimo, British Columbia. Combined with the morphological, genetic, ecological, and behavioural differences noted in previous studies (summarized in Chapter IV and the Epilogue), such observations of avoidance and possible aggression between the two forms supports the supposition that transient and resident populations are reproductively isolated.

Variability in association patterns within the transient population was also apparent. As noted in Chapter III, pods containing young whales were found disproportionately often in association with other pods, and pod-specific differences in



association patterns were also observed in this study. The ability to discriminate between pods in terms of foraging tactics and seasonal patterns of habitat use has provided a possible functional explanation for these pod-specific association patterns for transients; pods preferentially associate with others that share similar foraging specializations. As with my (Chapter IV) argument as to why transients should not associate with residents, preferentially travelling with hunters who share similar foraging abilities may be advantageous to an organism which benefits from cooperatively hunting in small groups (Chapter III; see also Ritchie 1991; Trowbridge 1991). Intraspecific variability in foraging techniques, possibly corresponding with differential association patterns, have also been observed in other cetaceans (e.g., humpback whales, Megaptera novaeangliae; Weinrich 1991).

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**CHAPTER II**

**DIVING BEHAVIOUR OF KILLER WHALES**

## Summary

The diving behaviour of killer whales (Orcinus orca) around southern Vancouver Island was investigated using a recoverable, suction-cup attached time-depth recorder (TDR)/VHF radio-tag. TDR tags were deployed on six residents and one transient, resulting in a total of 23 hours of diving data, with depth recorded once per second. The shape of dive profiles was extremely variable, with parabolic, flat-bottomed u-shaped, irregular u-shaped (frequent changes in bottom depths), and v-shaped dives recorded. Dive depth was strongly correlated with dive duration for both the transient and all residents, although residents were more variable, with some long dives near the surface, some to mid-water, and others to the bottom (to 173 m). Long dives for the transient were less variable, with the majority to between 20 and 60 m depth, even when bottom depth was greater. The proportion of time spent at different depths also differed between the residents and the transient. While residents typically dove much deeper than the transient, the majority of their time (> 66%) was spent at depths less than 20 m; the transient spent the majority of its time deeper than 20 m. I suspect these differences in use of the water column result from differences in prey species, since residents feed primarily on fish and transients feed primarily on harbour seals (Phoca vitulina). In open water, transients may spend the majority of their time at depth and detect prey visually, using silhouettes of prey against the surface.

## Introduction

Cetaceans spend the majority of their time beneath the water's surface, yet little is known of their activities there. Research on the diving capabilities of trained captive dolphins in the open ocean began in the mid-1960s (Ridgway et al. 1969; Hall 1970), and several species have been studied in this way (e.g., Williams et al. 1993). In 1970, Evans (1971) first collected information on the diving behaviour of a wild, free-ranging small cetacean, the common dolphin (Delphinus delphis). Several common dolphins, and later a short-finned pilot whale (Globicephala macrorhynchus), were captured and instrumented with radio-tags which transmitted information on the maximum depth of dives (Evans 1974). The large size of transmitters and the difficulty of capturing animals limited studies with wild small cetaceans, however, and little information has been collected on the subsurface activities of free-ranging small cetaceans since then. Such logistical constraints are less prevalent with studies of the diving behaviour of large cetaceans, since their thick blubber layer and large size allows for the remote attachment of relatively small penetrating tags (e.g. Goodyear 1993; Watkins et al. 1993). However, technological advances, and increasing concerns regarding anthropogenic impacts on populations and biases in estimating population size, have spurred recent work on the diving behaviour of small cetaceans. Such work has used satellite-linked transmitters on beluga whales, Delphinapterus leucas (Martin and Smith 1992), and narwhals, Monodon monoceros (Martin et al. 1994), as well as time-depth recorders on harbour porpoise, Phocoena phocoena (Westgate et al. 1993), and spotted dolphins, Stenella attenuata (Scott et al. 1993). These efforts have provided the first detailed information on the subsurface activities of free-ranging small cetaceans.



In this study, as part of an on-going effort to document and understand differences in the behaviour and ecology of transient and resident killer whales, Orcinus orca (Baird and Stacey 1988; Baird et al. 1992; Chapters I, III, IV), a recoverable, suction-cup attached time-depth recorder (TDR) was used to obtain the first detailed information on the diving behaviour and sub-surface activities of free-ranging wild killer whales.

### **Background of diving and tagging studies of killer whales**

Heezen and Johnson (1969) suggested that killer whales dove deeply, based on an animal reportedly entangled in a submarine cable brought up from 1030 m off the west coast of Vancouver Island. Additional information on the diving behaviour of killer whales was obtained during a U.S. Navy study using two resident killer whales (captured in Washington State in 1968) in a deep object recovery program in the open ocean off Hawaii (Bowers and Henderson 1972). While the study was not completed (and thus the maximum diving depth was not determined) due to unexpected circumstances (one whale escaped and the other became sick), one dove to 260 m, the other to 152 m.

Several additional projects have incorporated radio-tagging to study killer whales. In 1973 a single resident whale which had been captured off southern Vancouver Island was VHF radio-tagged and tracked for about 8 hours after release (M.A. Bigg, personal communication). In 1976, two transient whales were captured in Puget Sound, then tagged and tracked for 10 days after release (Erickson 1978). Numerous studies have been undertaken on the behaviour and activities of killer whales in the inshore waters of British Columbia and Washington State since these early radio-tracking projects. However, these studies have not addressed long-range movements or broad-scale habitat use. The

narrow spatial focus of these studies, combined with the frequent presence of identifiable individuals in calm, inshore waters has generally limited the need for radio-tracking to monitor behaviour or movement patterns in these populations.

Thus, despite evidence of the diving capabilities of killer whales and extensive behavioural research on this species, virtually all studies have focused on activities visible at the water's surface. Observations of underwater behaviours visible from the surface (within the top 5 m of the water column) have been used to document cooperative foraging behaviour and prey captures of transient killer whales off southern Vancouver Island (Chapters I and III). Elsewhere in their range (off Norway) another study has documented some underwater behaviours using 5 hours of underwater video footage collected with a remotely operated camera (Simila and Ugarte 1993).

## Methods

### Tag design

Suction-cup attached TDRs were used to record information on diving behaviour. The tags used, designed and constructed by J. Goodyear, were modified versions of "remora" tags used in earlier studies on humpback (Megaptera novaeangliae), right (Eubalaena glacialis), fin (Balaenoptera physalus), and minke (B. acutorostrata) whales (Goodyear 1981, 1989, personal communication). Components included a Telonics Dart 4 VHF radio transmitter (Mesa, AZ) with a battery and flexible wire antenna, and a Wildlife Computers Mk5 TDR (Woodinville, WA). These components were mounted in a tag body made of an epoxy/glass microsphere mixture ("Eccofloat", Grace Syntactics, Canton, MA), giving the tag positive buoyancy in water. A 7.8 cm diameter rubber suction cup

was attached to the tag body using flexible plastic tubing. A galvanic/magnesium release system was incorporated to release suction of the suction cup so the tag would detach from a whale after a pre-set period, and float for recovery. The system included a threaded stainless steel tube mounted through the stock of the suction cup, and a magnesium cap which was machined to 0.01 inch for attachment. A spring between the suction cup and the magnesium cap was used to hold a stainless steel ring against the cap, to maintain a continuous contact for galvanic activity. Timing of tag release was tested by attaching several suction cups with magnesium release mechanisms to the bottom of the research vessel, and moving through waters of the study area at speeds similar to killer whale travel speeds.

The prototype tag, deployed in 1991, weighed 246 grams and was cylindrical in shape. This tag lacked a TDR, as it was designed to test the recoverability of the tag and suction attachment method. In 1993 two Mk5 TDRs were used, and the exact dimensions of each tag varied slightly, although both were rectangular in shape. Complete tags weighed between 226 and 246 grams. Maximum dimensions of the tag body (not including antenna or suction cup) have been to 25 cm in length, 6.5 cm in width, and 4 cm in depth. The VHF radio antenna is placed away from the TDR unit, so that tags float with the antenna clear of the water.

Two sensors were activated in each TDR, a pressure (depth) sensor and a salt water (wet/dry) switch. The precision of the depth sensor was +/- 1 m. Sensors were set to record data once per second; these data were stored in memory for later retrieval. Calibration factors for the depth sensors in each TDR were tested by lowering the tags to known depths (25, 50 and 100 m). The depth sensor for one TDR (No. 92-079) read 11%

high, while the other (No. 92-078) read 32% high prior to calibration. The inclusion of the salt water switch in the TDR is intended primarily for studies of pinnipeds, which occasionally haul out on land, but it did allow for the occasional recording of periods when the tag was exposed at the surface (the switch was activated when the water connection between two electrodes was broken). However, due to the low placement of tags on a whale's body, dry readings were only recorded occasionally.

### Tag deployment and behavioural observations

Killer whales were encountered opportunistically in Juan de Fuca Strait (Fig. 2.1). Whale identifications and ages were determined using the catalogue of Bigg et al. (1987) and an unpublished catalogue maintained at the Marine Mammal Research Group (Victoria, B.C.). Tags were deployed from a small (4.7 m) vessel using a 3-4 m pole (1 case in 1991) or a 45 kg pull crossbow (all other taggings). For crossbow deployments, tags were loosely attached to a modified arrow, with the tip of the arrow inserted into a hole on the upper surface of the suction cup. Recovery of arrows after tagging attempts was facilitated using either a float or a deploying line (Game Tracker, Flashing, MI) attached to the arrow. On most tagging attempts an attempt was made to apply the tag to the dorsal surface of a whale, immediately in front of or below the dorsal fin.

Whale reactions to tagging attempts were categorized in the same way as humpback whale reactions to biopsy darting (Weinrich et al. 1991). When a tag was attached successfully, whales were tracked visually or by VHF signals received with a hand-held 3-element Yagi antenna. Concurrent with tracking, LORAN-based positions, whale behaviour (see Chapter I), and associations with other whales were recorded. Bottom depths were later determined from Canadian Hydrographic Service nautical charts

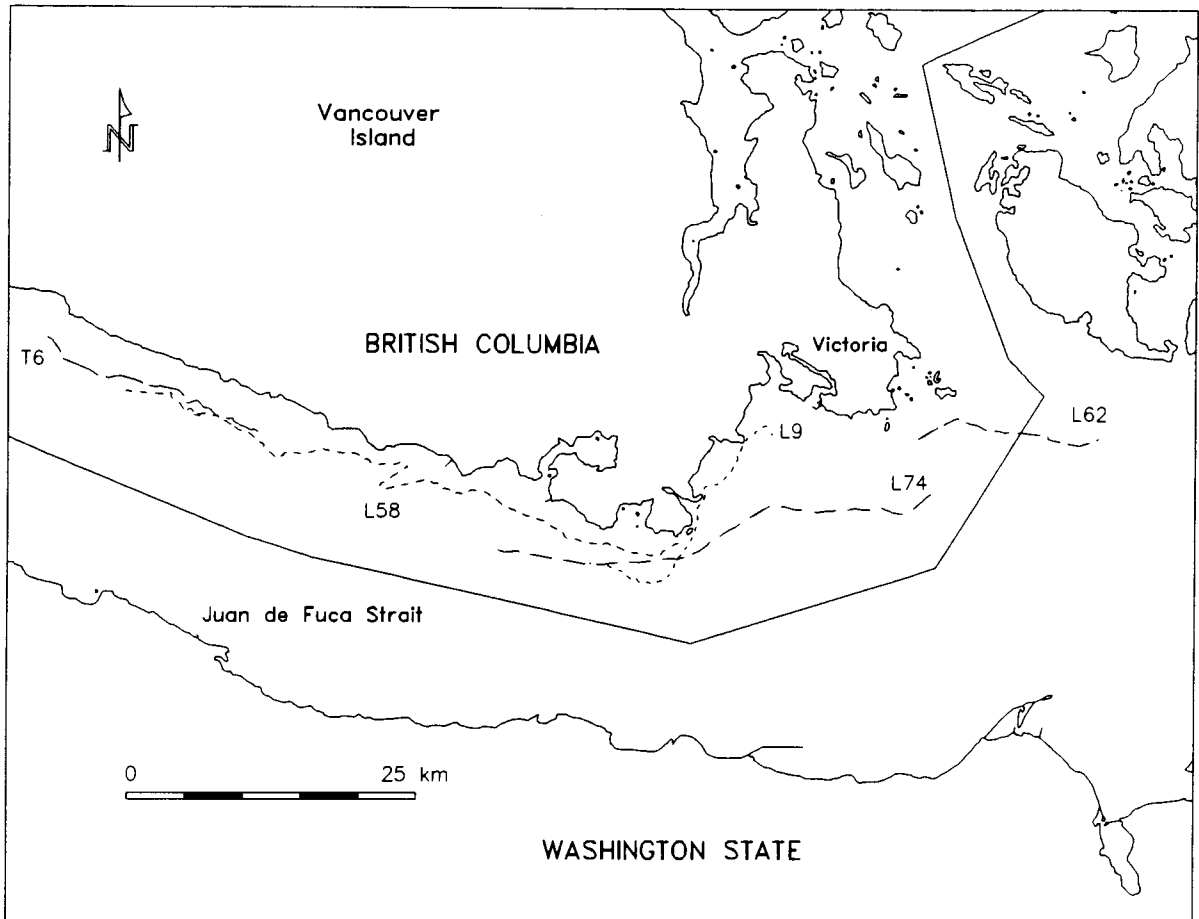


Fig. 2.1. Map of study area showing routes of all whales tagged for longer than 1 hour in 1993. Routes are shown for four resident killer whales from L pod (L9, L58, L62, L74) and one transient killer whale (T6), with whale identifications shown associated with each route.

using the LORAN positions.

### Data analysis

Tags were recovered after each deployment. Data were downloaded from the TDR in two forms. In both cases data were manipulated to correct for shifts in the zero reading caused by changes in temperature, and to calibrate the depth sensor. Decimal formatted data were imported directly into a statistical program (SYSTAT) and manipulated to produce information on percentage of time spent at depth. In this format, all depth readings were used. Data were also downloaded in a hexadecimal format for use with Dive Analysis software (Wildlife Computers). Each dive, defined as a period in which a whale travelled below 2 m and back above 2 m, was represented visually on a computer monitor, and a variety of statistics were automatically calculated and saved in a format appropriate for import into a statistical program. The statistics calculated were average rates of descent and ascent, maximum rates of descent and ascent (calculated over a time interval representing 10% of the duration of each dive), dive duration, maximum depth, and duration of time spent at the bottom of the dive (defined as below 85% of the maximum depth of that dive). The shapes of dive profiles were characterized visually using the Dive Analysis software, taking into account the constancy of the rates of ascent and descent, the proportion of time spent at the bottom of the dive, and whether the time spent at the bottom was at a relatively constant depth or at variable depths. Dive shape categories were defined with reference to previous studies of diving mammals (Hindell et al. 1991; Le Boeuf et al. 1993; Martin et al. 1994).

## Results

### Pole deployment

Three tagging attempts were made using the pole deployment method, two in 1991 and one in 1993. One attempt on a transient in 1991 using this method was successful, but the tag did not contain a TDR. Reactions observed during the three pole deployments included two low-level reactions and one strong reaction (after Weinrich et al. 1991). One low-level reaction involved a skin flinch, while in the other case the whale slowly rolled laterally a full 360 degrees, just beneath the surface. In the strong reaction the whale immediately swam at high speed away from the boat, and stayed away from its pod for approximately 60 min.

### Crossbow deployment

Sixty attempts using the crossbow method were made on 24 separate days in 1993, resulting in seven successful deployments (Table 2.1). Reactions of whales to crossbow tagging attempts are summarized in Table 2.2. No reaction was observed in almost half the attempts (48%), and moderate or strong reactions were never observed. Whales reacted less to near-misses of the tag than on occasions when the tag hit the whale's body, but reactions when tag attachment was successful appeared slightly less frequent than reactions for all tag hits (Table 2.2). Whales did not appear more difficult to approach after tagging attempts than before. As well, surface behaviours of tagged whales were similar to the typically observed behaviours of these whales (cf. Osborne 1986; Chapter I).

Tags remained attached for periods ranging from 15 min to 8 h 24 min (mean =

Table 2.1. Details on tagged killer whales

Identification	Age	Sex	Date	Tagging Duration	Location	TDR Number
M9	3	F	8 October 1991	3 h, 30 min	S Becher Bay to Constance Bank	none
L58	13	M	24 June 1993	8 h, 24 min	Race Rocks to E of Sombrio Pt	92-079
L57	16	M	13 July 1993	15 min	Pedder Bay to Bentinck I	92-078
L21	>40	F	13 July 1993	1 h	Becher Bay to Secretary I	92-078 <sup>1</sup>
L9	>40	F	19 July 1993	3 h, 55 min	Albert Head to Beechey Head	92-078
T6	6	?	13 September 1993	3 h, 10 min	Jordan River to Sombrio Point	92-078
L74	7	M	2 October 1993	5 h, 30 min	S of Discovery to S of Sooke	92-078
L62	13	M	11 October 1993	2 h, 30 min	SE of Trial to SW of Cattle Pt	92-079

<sup>1</sup>A technical problem with downloading data in the hexadecimal format resulted in these data not being usable for the analyses of dive types or average and maximum rates of ascent and descent.



Table 2.2. Reactions of whales to crossbow tagging attempts (percentages in parentheses)

	No Reaction	Low Reaction	Total
All attempts	29 (48)	31 (52)	60
Misses	14 (74)	5 (26)	19
Hits, total	15 (37)	26 (63)	41
Hits, no attachment	12 (35)	22 (65)	34
Hits, attachment	3 (43)	4 (57)	7
Repeated attempts within a day			
- first attempt	3 (37)	5 (63)	8
- all subsequent attempts	5 (45)	6 (55)	11
- last attempt	3 (37)	5 (63)	8
Repeated attempts across days			
- first attempt, first day	6 (55)	5 (45)	11
- last attempt, last day	8 (73)	3 (27)	11

3 h 32 min). Six individual resident killer whales from L pod (cf. Bigg et al. 1987) and one transient killer whale from T3 pod (cf. Chapter III) were tagged. Variability in duration of tag attachment appeared to be related to tag location on the body, behaviour of the tagged whale, and the effectiveness of the magnesium release mechanism. The two tags attached for short durations (15 min and 1 h) were attached on the side and the base of the dorsal fin, respectively. All other tags were placed more anteriorly and on the flatter surface of the back. Two tags detached after a prolonged (> 5 min) period of high speed swimming by the whale, during which the tag progressively slid posteriorly along the whale's body. The remaining tags detached due to the release of suction by the magnesium release mechanism.

Travel routes of the five whales tagged in 1993 for longer than one hour are shown in Fig. 2.1. In total, 23 h of depth data, sampled once per second and comprising 1779 dives, were recorded. The typical temporal pattern of diving for both the single transient and all residents was a single long duration dive (> 1 min) followed by a series of 3-6 short duration (< 1 min) dives. Mean and maximum dive durations were 0.74 and 8.47 minutes for the resident whales (SD = 1.08 min), and 1.10 and 7.62 minutes for the transient whale (SD = 2.01 min), respectively.

Maximum dive depths recorded for the transient and residents were 73 m and 173 m respectively, but tagged whales were not tracked in waters deeper than 185 m. One minute was arbitrarily chosen as the dividing point between long- and short-duration dives. Similarly 20 m was chosen for distinguishing shallow and deep dives. For residents 90.5% of the dives were less than 20 m in depth, while 82.6% of the dives for the transient were less than 20 m in depth. Not surprisingly, there was a strong positive

relationship between maximum dive depth and dive duration, for both the single transient (regression,  $r^2 = 0.91$ ,  $df = 160$ ,  $p < 0.001$ ) and for all residents combined ( $r^2 = 0.55$ ,  $df = 1539$ ,  $p < 0.001$ ). Many of the deep dives for both residents and the transient were to the bottom, but for residents the depths of dives greater than one minute in duration were much more variable than those of the transient, with some long dives near the surface, some to mid-water, and others to the bottom (see e.g., Fig. 2.2). Long dives for the single transient whale were less variable than those of residents, with the majority to between 20 and 60 m depth, even when the bottom depth was greater (Fig. 2.3).

Five dive types were recognized from their profiles: 1) parabolic; 2) v-shaped; 3) u-shaped with a flat bottom; 4) u-shaped with changes in depth along the deepest part of the dive; and 5) variable dives. Dive types 2-4 were characterized by a relatively constant rate of ascent and descent, and varied in the amount of time spent at or near the bottom (v-shaped vs. both u-shaped categories), and by whether the time spent in the deepest portion of the dive was at a constant depth (u-shaped, flat bottom) or at variable depths (u-shaped, changing depths). Rates of ascent and/or descent for dives of category 5 (variable dives) were not constant. Examples of several dive types are shown in Fig. 2.4. The proportion of different dive types observed varied with dive duration and depth, and between the residents and the transient (Table 2.3).

Short-term rates of descents and ascents reached 8 m/sec for one resident individual, and 6 m/sec for all other tagged individuals. Average rates of ascent and descent for the residents were 1.198 (SD = 1.167) and 1.088 m/sec (SD = 1.052), respectively. The average rates of ascent and descent for the transient were greater; 1.832 (SD = 1.448) and 1.822 m/sec (SD = 1.510), respectively. The average rate of

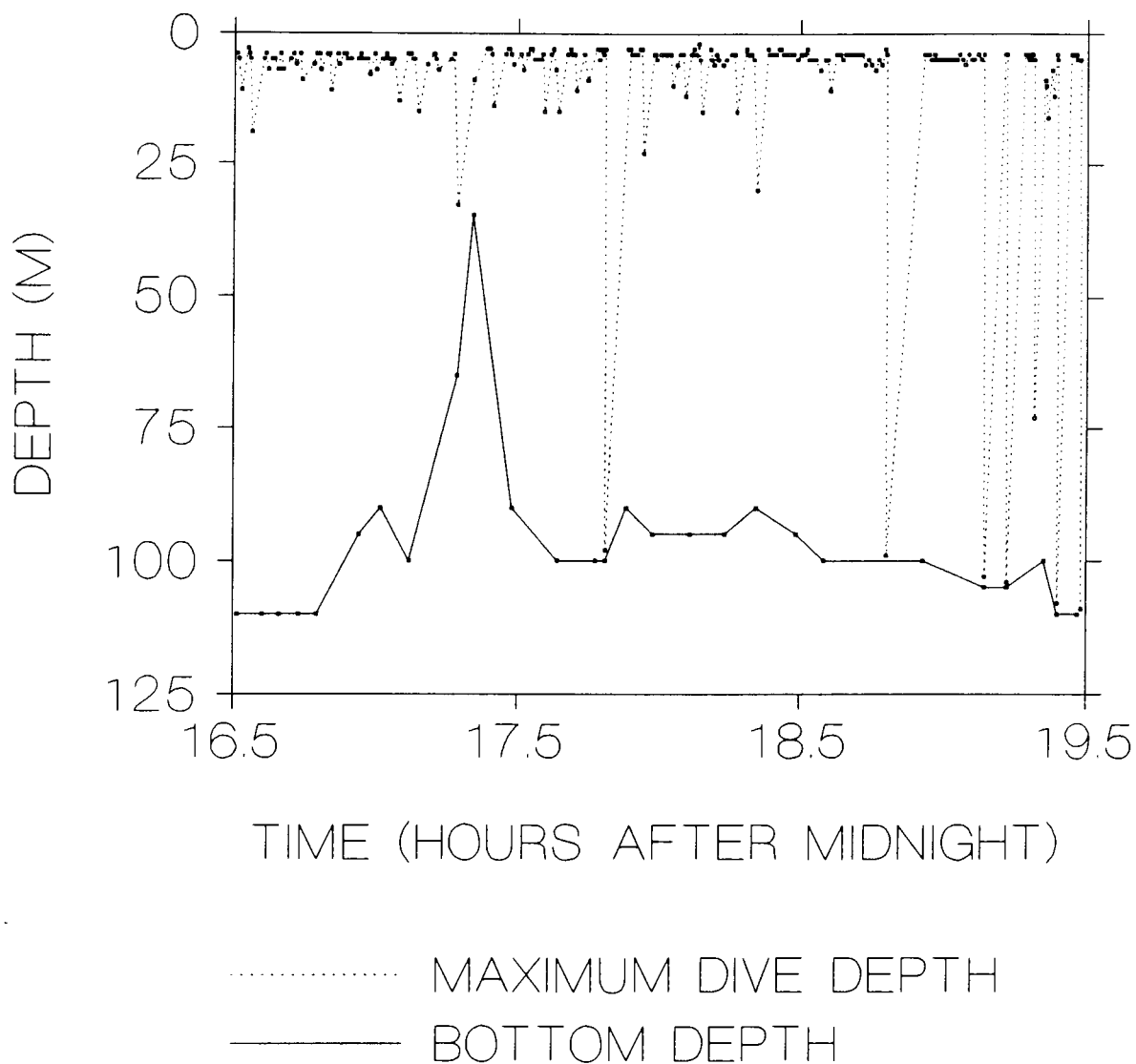


Fig. 2.2. Three hours of dive data (totalling 244 dives) for a resident killer whale (L58). LORAN coordinates from whale locations were recorded periodically during tracking to determine the bottom depths shown. Distance travelled over this period is approximately 20 km, thus the steepness of bottom contours is exaggerated. Only one point is shown for each dive, representing the maximum depth.

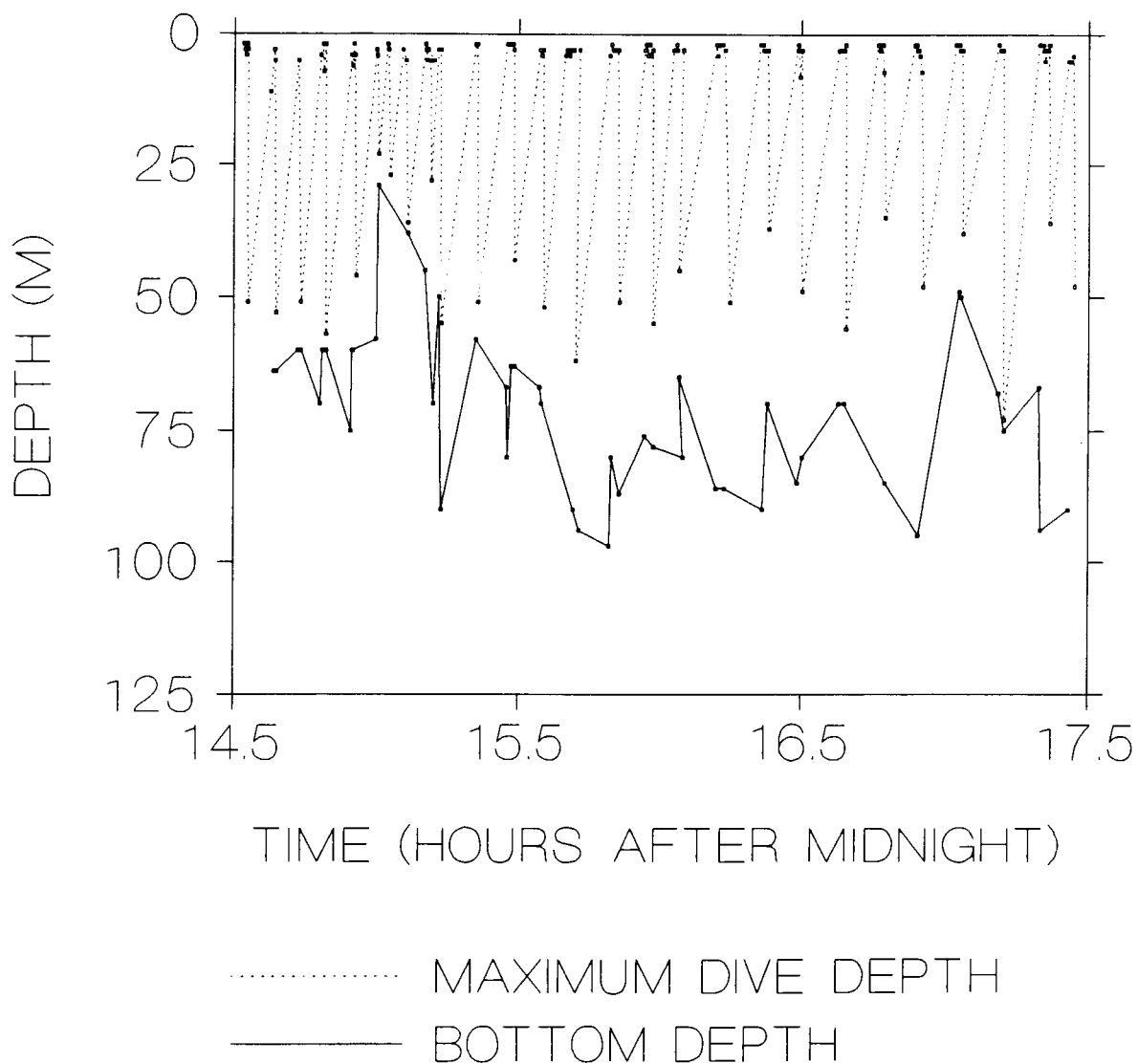


Fig. 2.3. Three hours of dive data (totalling 157 dives) for the transient killer whale (T6). LORAN coordinates from whale locations were recorded periodically during tracking to determine the bottom depths shown. Distance travelled over this period is approximately 20 km, thus the steepness of bottom contours is exaggerated. Only one point is shown for each dive, representing the maximum depth.

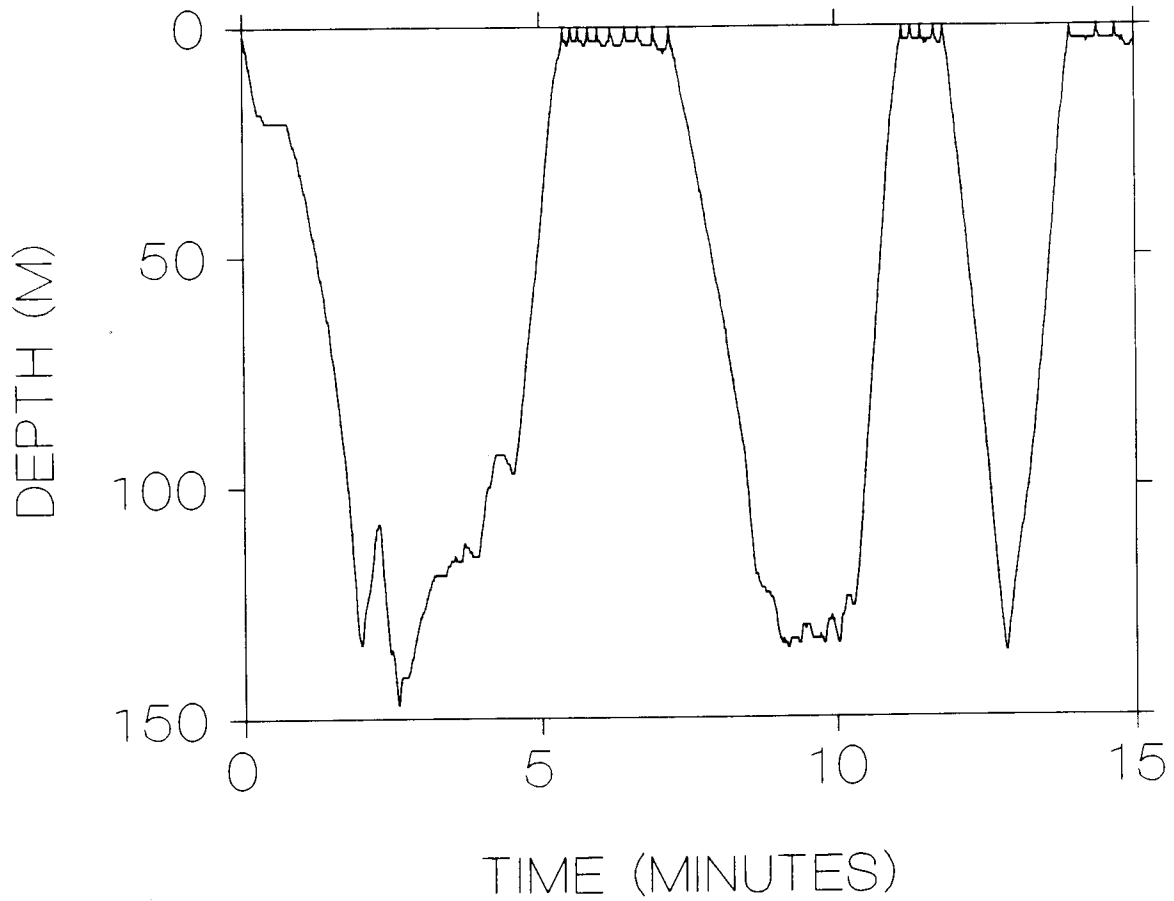


Fig. 2.4. Series of dives for a resident killer whale (L58), showing variability in dive profile. Depth data collected once per second are shown (a total of 900 data points for the 15 min period). Dive profiles of the three deep dives (from left to right) were classified as: type 5 (variable); type 4 (u-shaped with changing depth); and type 2 (v-shaped). All three deep dives shown in this example were to, or near to, the bottom.

Table 2.3. Frequency of dive types with dive duration and depth, and between residents and the transient (numbers shown are percentages)

Dive type	Dive characteristics					
	Long-duration shallow		Short-duration shallow		Long-duration deep	
	<u>Resident</u>	<u>Transient</u>	<u>Resident</u>	<u>Transient</u>	<u>Resident</u>	<u>Transient</u>
1. Parabolic	22.0	0	9.2	9.4	13.2	6.9
2. V-shaped	1.1	0	0.5	2.9	16.7	0
3. U-shaped, flat bottomed	50.5	0	86.5	83.3	22.2	20.7
4. U-shaped, variable	20.9	0	2.2	2.9	28.5	55.2
5. Variable	5.5	0	1.6	1.5	19.4	17.2
Number of dives	91	0	1276	138	144	29

descent by residents was weakly but significantly correlated with the maximum depth of dives, for dives greater than 20 m in depth (regression,  $r^2 = 0.18$ ,  $df = 144$ ,  $p < 0.001$ ); no such relationship existed for the transient ( $p = 0.179$ ). The average rate of ascent from deep dives was strongly correlated with the maximum depth of dive for residents (regression,  $r^2 = 0.60$ ,  $df = 144$ ,  $p < 0.001$ ), but not for the transient ( $p = 0.732$ ).

The proportion of time spent at different depths differed between the residents and the one transient. While residents typically dove much deeper than the transient, all residents spent the majority of their time (> 66%) at depths less than 20 m (see e.g., Fig. 2.5A). The majority of the transient's time (> 66%) was spent below 20 m (Fig. 2.5B).

## Discussion

While extensive research has been undertaken previously on the behaviour of killer whales, this study provides the first detailed information on the diving behaviour of this species. It also demonstrates the value of TDR/VHF radio tags, attached with a suction cup, as a tool for examining dive behaviour and sub-surface activities of killer whales. Due to the large distances that this species can travel in a short period of time, use of the galvanic/magnesium release mechanism is required to allow for consistent recovery of the tag before the animal has moved out of calm, inshore areas. Remote-deployment using a crossbow or pole system provides a low-cost, relatively non-intrusive method of tag attachment.

However, the question remains whether the data produced by these TDRs are biased by the whale's reaction to tagging or tagging attempts, or by other factors



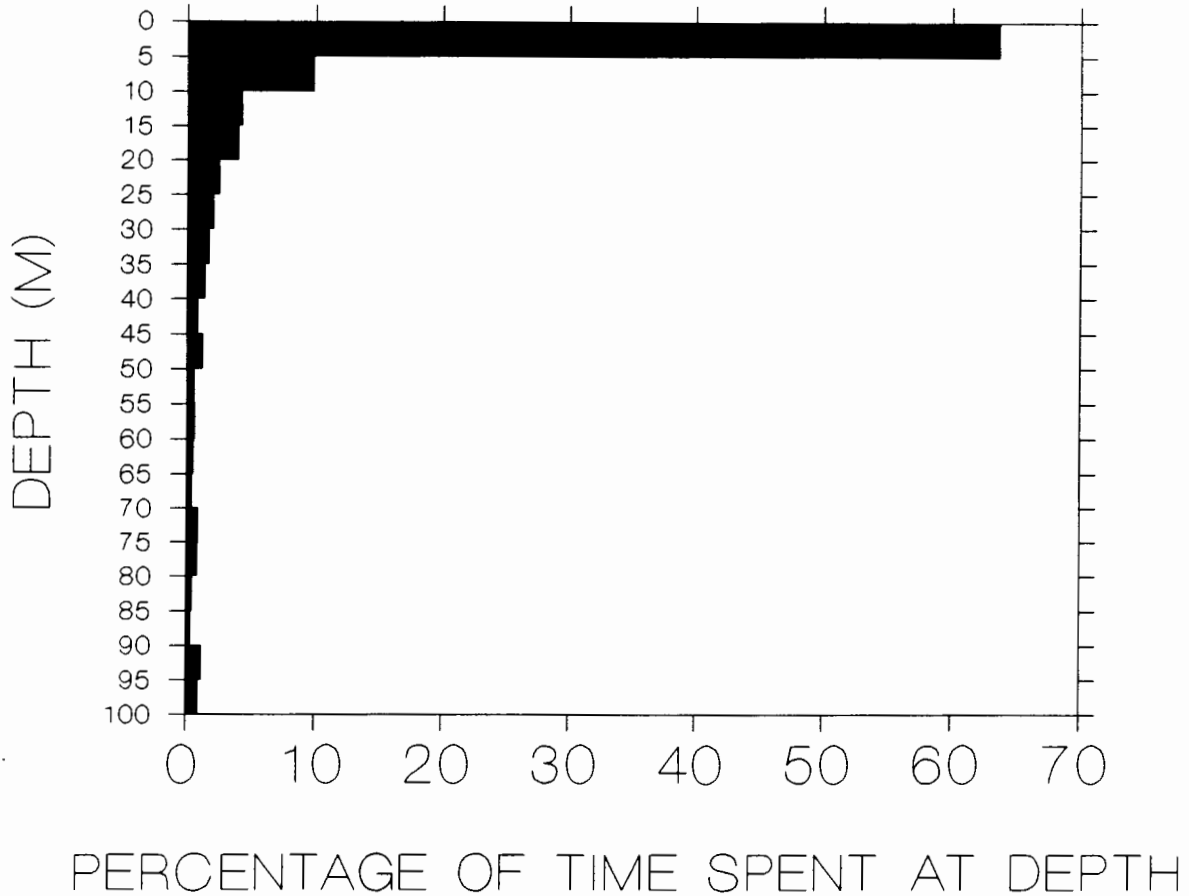


Fig. 2.5. A. Proportion of time spent at depth for a resident killer whale (L58). All residents spent the majority of their time (> 66%) at depths less than 20 m.

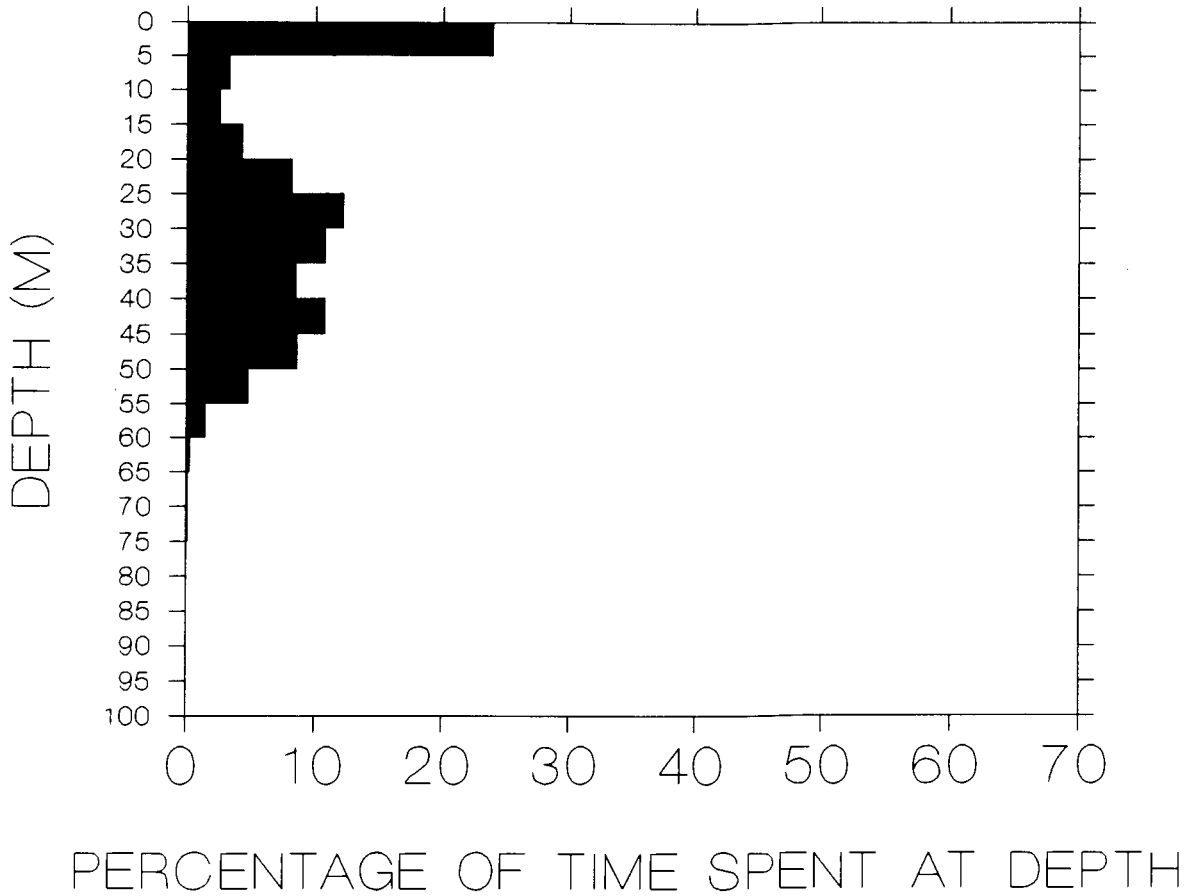


Fig. 2.5. B. Proportion of time spent at depth for the transient killer whale (T6). The majority of its time (>66%) was spent at depths between 20 and 60 m.

associated with the sampling method. All studies of the diving behaviour of pinnipeds and most other studies of the diving behaviour of cetaceans have involved the capture of animals (Martin and Smith 1992; Scott et al. 1993; Westgate et al. 1993; Martin et al. 1994) or the use of penetrating tags (Goodyear 1993; Watkins et al. 1993). Use of a remotely deployed tag which does not penetrate the skin presumably should minimize the potential for adverse reactions. Using the classification system for humpback whale reactions to biopsy darting (Weinrich et al. 1991), killer whales appear to respond less to tagging attempts using a suction-cup attachment (Table 2.2) than do humpback whales to biopsy darting (Weinrich et al. 1991). No moderate or strong level reactions were observed with the crossbow deployment method, yet such reactions comprise 46% and 3%, respectively, of those observed in humpbacks. Individuals did not appear to be more difficult to approach during a particular encounter while tags were attached, suggesting that behaviour was not greatly modified. The types and range of behaviours exhibited by tagged whales also generally matched the behavioural repertoire of both transient and resident killer whales, as did the travel routes of tagged whales. While tagged, the whales remained within their social groups and surface behaviours exhibited by tagged whales were no different from those of other whales in the groups. Data from the TDRs themselves also suggest that reactions to tagging attempts are minimal, with rate of descent on the first dive after tag attachment actually being lower than the average rate of descent for 5 of 7 whales.

Several other potential biases inherent in other studies of marine mammal diving behaviour were minimized in this study. As noted by Testa et al. (1993) studies of pinniped diving behaviour may be biased towards individuals which are easiest to capture. Tagged whales in this study included both sexes and a broad range of ages (Table 2.1).

All resident individuals tagged were from only one of the three southern resident pods (L1 pod), but represented several different maternal groups (Bigg et al. 1987). The lone transient tagged was from one of the most frequently encountered transient pods recorded around southern Vancouver Island (Appendix I). Sampling rate biases can greatly affect the detection of short duration events (such as short duration dives), as well as the resolution and subsequent classification of dive profiles (see below) (Boyd 1993; Oliver et al. 1993; Testa et al. 1993). In this study, due to the relatively short duration of tag attachments, memory constraints in the TDRs were not a problem and sampling interval could be set at one second, eliminating any such sampling bias.

Maximum dive depth recorded was 173 m, far less than the maximum dive depth suggested by the observations of a killer whale entangled in a submarine cable off the west coast of Vancouver Island (Heezen and Johnson 1969). While bottom depths in Juan de Fuca Strait and surrounding waters reach 330 m, depths along the tracks of tagged whales did not surpass 185 m, limiting the maximum dive depth. Information on breath-hold capabilities and average rates of descent can be used to predict a maximum dive depth, as was done for narwhals by Martin et al. (1994). Erickson (1978) reports a maximum dive duration of 17 minutes for a transient. Using the average rates of descent and ascent for the 162 dives of the transient killer whale (approx 1.8 m/sec for both) and a 17 minute dive duration, and assuming a v-shaped dive, the predicted maximum dive depth is 918 m. For residents, using the greatest average rates of ascent and descent recorded for dives lasting more than one minute (2.63 and 3.73 m/sec, respectively), and again assuming a 17 min dive duration, a v-shape dive and constant velocity, the predicted maximum depth of dive would be approximately 1560 m.

Categorization of dives based on visual representations of their profiles is a frequent outcome of marine mammal diving studies. As noted above, the sampling interval of one second allows for the discrimination of small changes in depth over short periods of time, and may allow for greater resolution of dive shapes. Dive profiles were extremely variable (Fig. 2.4), but some generalities were observed. Shallow short-duration dives were similar for all whales and of relatively simple structure (i.e., no sudden changes in depth that might be associated with prey chases or prey capture). This likely reflects the primary function of these short duration shallow dives, i.e., a sequence of surfacings to allow the animal to replenish oxygen stores before a longer, deeper dive.

As is the case for pinnipeds (e.g., Le Boeuf et al. 1993) longer duration deep dives likely constitute a prey searching pattern. The occurrence of long shallow dives by residents (Table 2.3) may reflect their foraging on salmon (Oncorhynchus spp.) near the surface. Based on observations of prey brought to the surface, salmon were the most frequently recorded prey taken by resident killer whales (Bigg et al. 1990). While no studies of salmon depth distribution have been undertaken in the area where whales were tagged, anecdotal information from fishermen implies that the majority of salmon in that area during the summer months are congregated in the top 30 m of the water column. Studies of salmon depth distribution elsewhere in the coastal waters of the eastern North Pacific suggest that several species spend the vast majority of their time in the upper levels of the water column (Quinn and terHart 1987; Quinn et al. 1989; Ruggerone et al. 1990; Olson and Quinn 1993). Observations of prey brought to the water surface are likely biased towards prey captured near the surface, but information from stomach contents of several beach-cast residents implies that they also take bottom fish. Regular dives recorded in this study to the sea bottom (100-180 m) also suggests that residents

may regularly feed on prey other than salmon.

The variability in the maximum diving depth of residents may reflect opportunistic foraging for a broad range of prey species. Maximum diving depth for the lone transient was much less variable, with the majority of the long dives to between 20 and 60 m (Fig. 2.5B). Transients in the area around southern Vancouver Island feed almost entirely on harbour seals, Phoca vitulina (Chapter III). While dive data for harbour seals in British Columbia have not been analyzed to examine the proportion of time animals spend at different depths (P. Olesiuk, personal communication), because harbour seals must regularly return to the surface to breathe it is likely that they spend a large proportion of their time in the upper part of the water column. Why then do transients not spend more time near the surface? Two possibilities are: (1) that deeper diving functions to prevent seals from escaping to the bottom; and/or (2) that vision is important for the detection of prey. Each of these possibilities is discussed below.

Particularly when encountered in open water, harbour seals have virtually no chance of escape (Chapters I, III). If it were first spotted below or lateral to a whale, however, there is some chance that a seal could seek refuge in hiding sites at the bottom. Detecting prey from below reduces the likelihood of this.

The use of vision in prey detection may be more relevant to understanding transient use of the water column. Transients rarely echolocate while foraging, and several authors (Hoelzel 1991; Barrett-Lennard 1992; Guinet 1992) have suggested that passive listening may be important for detection of marine mammal prey in nearshore areas. However, data in Chapter III indicate that prey captures observed in the presence

of outboard-motor powered boats more than account for the animals' energetic needs, implying that boat sounds do not seriously affect transient detection of prey. Fristrup and Harbison (1993) discussed the potential use of vision for prey detection by sperm whales (Physeter macrocephalus), and suggested that sperm whales may detect prey silhouetted against downwelling surface light. If the diving pattern observed for the single transient in this study is supported by additional data for other transient killer whales, this would support the hypothesis that transients in open water detect prey visually, using silhouettes of prey against the surface. White sharks (Carcharodon carcharias) seem to do something similar (W.R. Strong, University of California, Santa Barbara, personal communication).

Clearly more data, particularly for transients, are needed to support and quantify the differences in diving behaviour between transient and resident-type killer whales suggested by this study. However, the resident/transient system, with sympatrically occurring closely related forms of whales, specializing on different prey types, may prove valuable for understanding the functions of different dive patterns, which may aid in the interpretation of data from other studies of diving mammals. TDR tags could also be used to examine nocturnal behaviour of killer whales, something which has received virtually no research attention to date due to the logistical difficulties of following and observing killer whales at night.

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**CHAPTER III**

**ECOLOGICAL AND SOCIAL DETERMINANTS OF GROUP SIZE  
IN TRANSIENT KILLER WHALES (ORCINUS ORCA)**

**ABSTRACT**

Most analyses of the relationship between group size and food intake of social carnivores have shown a discrepancy between the group size that maximizes energy intake and that which is most frequently observed. Around southern Vancouver Island, British Columbia, killer whales of the so-called transient form forage in small groups, and appear to prey exclusively on marine mammals. Between 1986 and 1993, in approximately 434 h of observations on transient killer whales, I observed 138 attacks on 5 species of marine mammals. Harbor seals were most frequently attacked (130 occasions), and the observed average energy intake rate was more than sufficient for the whales' energetic needs. Energy intake varied with group size, with groups of three having the highest energy intake rate per individual, and the lowest risk of an energy-shortfall. While groups of three were most frequently encountered, the group size experienced by an average individual in the population (i.e., typical group size) is larger than three. However, comparisons between observed and expected group sizes should utilize only groups engaged in the behavior of interest. The typical size of groups comprised only of adult and sub-adult whales which were engaged primarily in foraging and feeding activities (3.29 individuals) implies that these individuals are found in groups which are consistent with the maximization of energy intake hypothesis. Larger groups may form for: 1) the occasional hunting of prey other than harbor seals, for which the optimal foraging group size is probably larger than three; and 2) the protection of calves and other social functions.

## INTRODUCTION

Group hunting behavior has been recorded in numerous taxa (e.g., Bednarz, 1988; Estes and Goddard, 1967; Hector, 1986; Kruuk, 1972; Packer and Ruttan, 1988; Pitcher et al., 1982). Schaller's (1972) seminal treatise has received the lion's share of attention, with numerous authors re-examining his data focusing on the energetic benefits of foraging in groups (Caraco and Wolf, 1975; Clark, 1987; Giraldeau and Gillis, 1988; Packer, 1986; Rodman, 1981). Caraco and Wolf (1975) noted that observed group sizes for lions matched the optimum for energy intake for small prey, but were larger than the optimum for large prey, and suggested that the lions may have been balancing energy intake with other determinants of fitness, such as preventing scavenging by other carnivores. Clark (1987) suggested that the group sizes of lions hunting large prey maximized survival, rather than energy intake, by reducing the variance in food intake. A further re-analysis by Giraldeau and Gillis (1988) indicated that the maximization of energy intake hypothesis might account for observed group sizes, but suggested that existing data precluded acceptance of either the energy-maximizing or the survival-maximizing hypotheses. These latter authors noted that the original presentation of Schaller's (1972) data did not take into account the variability associated with sexual dimorphism of body size, hunting efficiency, or genetic relatedness of hunting individuals. Despite the widespread interest in using Schaller's data to examine the question of an optimal foraging group size, numerous other problems exist with the presentation of the data which make them unacceptable for examining such a question (Packer et al., 1990). A subsequent field study by Packer et al. (1990) examined group-size specific foraging efficiency in lions, and concluded that factors such as territorial defence and defence of cubs from infanticidal males are largely responsible for the observed group sizes.

Regardless, group hunting can have energetic benefits. An increase in foraging success could result from the synergistic effect of several individuals hunting together, either by increasing prey encounter and capture rates, or by decreasing the costs involved in the capture of large or difficult-to-handle prey. As with lions, most analyses of the relationship between group size and food intake for social carnivores have shown a discrepancy between the group size which is optimal for maximizing energy intake rate and that which most frequently occurs. Group sizes of social hunters are often larger than the predicted optima, possibly due to the benefits of increased vigilance and protection against predators and scavengers, improved use of information in the presence of scarce, patchily distributed resources, or the cooperative defence of territories or young (Clark and Mangel, 1986; Smith and Warburton, 1992).

In this study I examine the group hunting behaviour of transient killer whales (Orcinus orca) around southern Vancouver Island, British Columbia. Research undertaken since the early 1970s has demonstrated the existence of two discrete forms of killer whales in that area, one which specializes on marine mammal prey (termed transient killer whales), and one which specializes on fish prey (termed resident killer whales) (Bigg et al., 1987). My study has focused on the grouping patterns and group-size-specific individual energy intake rates for transient killer whales, to determine whether the observed frequency of occurrence of different sized groups can be explained by the energy maximizing hypothesis. I examine how the group size experienced by an average individual (i.e., typical group size; Jarman, 1974) varies with the presence of calves and juveniles in the group, and discuss my results in the context of other potential functions of grouping in this population.

## STUDY ANIMAL

Intensive field research by numerous researchers has been undertaken on killer whales in British Columbia and in Washington State since the early 1970s. All individuals can be identified based on distinctive acquired and congenital characteristics of the dorsal fin and post-dorsal fin pigmentation patch (termed saddle patch) (Bigg et al., 1987). Using documentation of individual movements and association patterns, early research identified the existence of the two forms of killer whale mentioned above. These forms were originally termed transients and residents based on their site fidelity, although recent investigation has demonstrated that such names are not particularly descriptive of the movement patterns of the two forms. The resident form appears to be sub-divided into two distinct populations, one found generally from central and northern British Columbia to southeast Alaska (northern residents; Bigg et al., 1987; Dahlheim and Waite, 1992), and the other found in southern British Columbia and in Washington State (southern residents; Bigg et al., 1987). Individuals of the transient form are found throughout the ranges of both communities of resident whales. No form of territoriality, as may exist for resident communities, has been noted for transient individuals or groups. These resident and transient forms should not be confused with the territorial and nomadic or floater individuals seen in other social animals; all the evidence suggests that the two forms are genetically isolated and may in fact be incipient species (Chapter IV). Such evidence includes differences in behavior, ecology, external morphology (Bain, 1989; Baird and Stacey, 1988; Bigg et al., 1987) and mitochondrial DNA (Hoelzel and Dover, 1991; Stevens et al., 1989). Baird et al. (1992, Chapter IV) review the foraging tactics of the two forms, suggesting that observed differences between the two may be due to specialization on different prey types.

In general, research efforts have focused on the resident form. One unusual finding is the lack of dispersal by residents, with offspring of both sexes remaining closely associated with their mother throughout their lives (Bigg et al., 1990). For residents, a matrilineal group comprised of from 1-4 generations of individuals associates with one or more other matrilineal groups for long periods (i.e., greater than 20 years; Bigg et al., 1990). Such a long-term grouping is termed a "pod", and is defined as a group of individuals spending at least 50% of their time together, over a long period (i.e., years; after Bigg et al., 1990). A transient pod appears to be comprised of a single matrilineal group with 1-2 generations (Baird, unpublished). Transient pod size changes only through birth, death or emigration; to date, no cases of long-term immigration of individuals into a pod have been recorded. Short-term associations between individuals from different pods occur for both residents and transients. Social behavior is regularly observed in these larger associations. For transients, periods of social activities involve interactive movements between individuals, not associated with the capture of prey (Chapter I). Percussive (e.g., taillobbing) and aerial (e.g., spyhopping) behaviors are frequently observed in the context of social behavior (Chapter I).

Transients in British Columbia have been recorded feeding on four of the five species of pinnipeds found there, and five species of cetaceans (Jefferson et al., 1991). Foraging for marine mammals occurs over a wide variety of habitats, from harbor seal (Phoca vitulina) haul-out sites and other near-shore areas, to open water. Killer whale behavior during foraging is extremely variable (Chapter I). Foraging behavior around seal haul-outs and near-shore areas is characterized by close following of the contours of the shoreline or circling of rocks which seals typically frequent. Spacing between individual whales and synchronization of surfacings in such situations, as well as during foraging in



open water, is extremely variable, however. Prey can be captured while the individuals in a group are separated by less than one whale body length, or when separated by up to a kilometer or more. In both situations, individuals converge on the prey item once captured. Prey handling time, defined as the period from when prey is first seen in close association with a whale until no further remains of prey are seen, is also variable, ranging from less than one min to several hours (Chapter I). Sometimes the prey is killed quickly (i.e., in less than a min); other times the period before the prey is killed is prolonged, occasionally up to an hour or more. Similarly, once killed, prey consumption can be very quick (i.e., less than a min), or can be prolonged for periods ranging from several min to an hour or more. Further information on transient killer whale foraging behavior can be found in Chapter I.

## **METHODS**

### **Study area and observational methods**

Data were collected over an area of approximately 3,000 km<sup>2</sup> centered around the southern tip of Vancouver Island, British Columbia, Canada, including the western San Juan Islands, Washington State, USA (Figure 3.1). This area is considered a core area for the southern resident community, and transient killer whales are regularly seen there.

I located whales through sightings reported by other researchers, whale watching charter operations, fishermen, lighthouse keepers and the public, and by traversing the study area by boat. Observations were made by one to four observers from one or two of several small vessels (to 8 m). Killer whales were encountered on an occasional basis year-round from 1986 through 1993. Onset and termination of sampling sessions was ad lib. (after Altmann, 1974); termination of sessions was usually when subject animals were

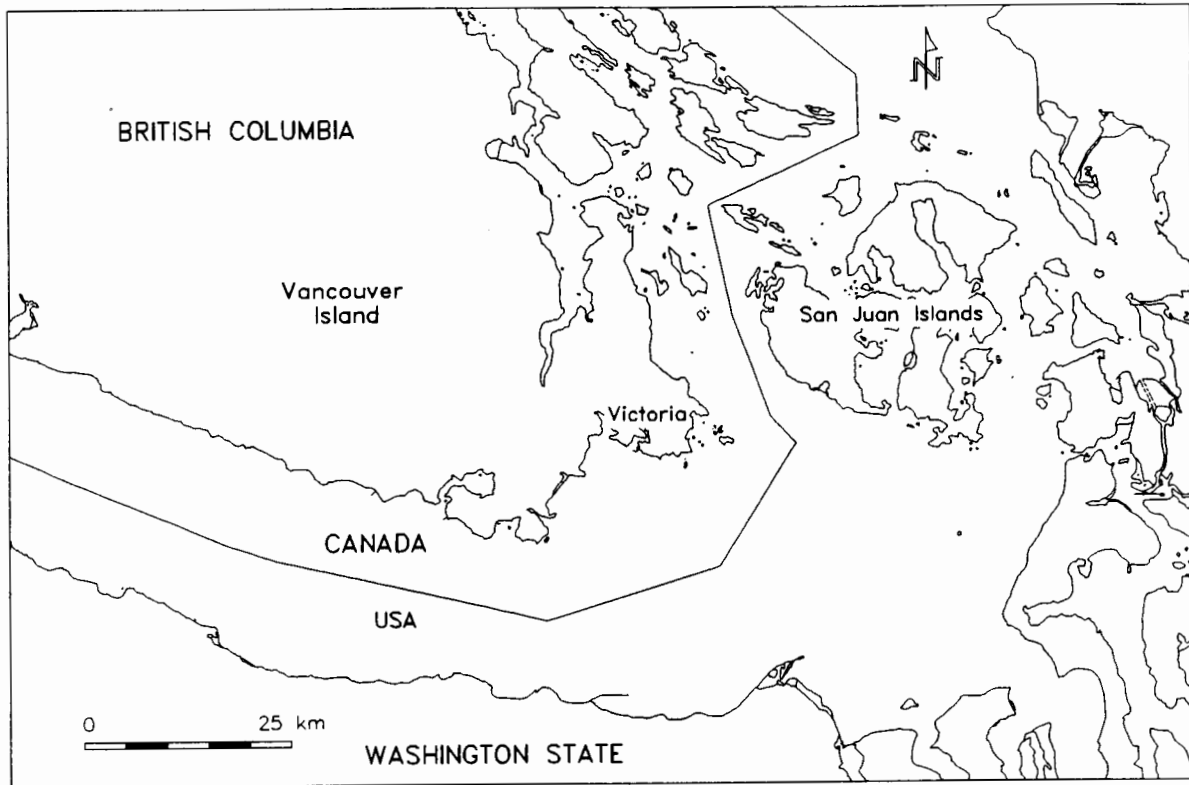


Figure 3.1. Map of study area showing place names mentioned in text.

lost or when lighting, sea conditions or fuel considerations forced the cessation of observation periods. Behavioral data were voice-recorded continuously throughout encounters, using a microcassette recorder.

Subjects were visible at the water's surface during surfacing periods that generally lasted 1-2 min; intervals between surfacing periods typically ranged from 2-8 min. During surfacing periods individual whales usually surfaced 3-6 times. Since group size was typically small and visible behaviors were usually interspersed with periods when whales were not visible, all visible behaviors of all individuals could be recorded simultaneously (focal-group sampling, all occurrences of all behaviors; after Altmann, 1974). A primary assumption of this sampling regime is that the activities visible at the surface are representative of below-water activities not visible to the observer. I discuss the validity of this assumption later. Data recorded included date, time, location (either estimated in relation to known landmarks, triangulated using a hand-held compass, or by LORAN), general behavioral state (foraging, feeding, travelling, resting, social behavior, or a combination of these), identity of whales present, and distance between individuals. The occurrence of all other marine mammals visible at the surface or hauled out on nearby rocks was noted, including species, number, behavior, and relative location. Sea state and other environmental conditions and the number and type of other nearby vessels were also recorded.

#### **Group composition and measures of grouping tendencies**

Individual whales present in each encounter were identified visually and/or using photographs, using the catalogues of Bigg et al. (1987) and Ellis (1987), and unpublished catalogues maintained at the Center for Whale Research (Friday Harbor WA), the Marine

Mammal Research Group (Victoria BC), and the Pacific Biological Station (Nanaimo BC). For the purposes of this study a "group" was defined as all whales acting in a coordinated manner during the observation period, which were within visual range of the observers. All members of a killer whale group, regardless of age, were included in counts of group membership. No information is available to estimate precisely the age at which a calf becomes a fully functional member of a foraging group, but calves estimated to be younger than one year of age were present in only a small proportion of encounters (11%). Group size and composition changed both within and between encounters.

Pod composition was determined both from this study and from unpublished sighting records provided by the aforementioned organizations. Pods remained stable within each encounter, but could change between encounters via births, deaths, or emigration. The shortest interval between encounters when a change in pod size was recorded was seven months. Each group, as defined above, was comprised of members from one or more pods. During an encounter with the whales one or more individuals from a pod occasionally separated and acted independently from other pod members. Such individuals temporarily spent time either alone or with members of a different pod. Thus, within a particular encounter, individuals from one pod could be considered members of separate "groups", as defined above. Accordingly, for any particular observation period, the group size could be smaller than the pod size, unless pod size was one. Such temporary separation of pod members was usually of short duration and individuals remained within a few kilometers of other pod members; the longest such period of separation of pod members recorded in this study was 112 min.

Overall measures of grouping tendencies were calculated both for "groups" and

"pods". Measures used to describe grouping tendencies include the modal (most frequently observed), mean, and "typical" sizes. As noted by Jarman (1974), mean group size may not accurately represent what individuals experience; because larger groups contain more individuals they must be proportionately weighted in any calculation of the group size experienced by the average individual. Jarman (1974) termed this the "typical" group size, and it is calculated as:

$$G = \frac{\sum_{i=1}^n x_i^2}{\sum_{i=1}^n x_i}$$

where  $x_i$  is the number of individuals in the  $i^{\text{th}}$  group. Typical group size was calculated using all observations of all groups ( $n = 217$ ). Each observation period of a group of constant size was weighted by the duration of that observation period, and represented a single  $x$  value in the calculation. Thus, particular individuals and groups may have been counted more than once in determining typical group size. In calculating typical pod size, each pod enters the equation only once, regardless of the number of times that pod may have been seen during the study. For pods whose size changed during the study ( $n = 5$ ), the sizes of the pods when last encountered were used in calculations of mean and typical pod size. For some pods which were seen on only a few occasions and for which insufficient supplementary information was available, it was not possible to determine pod size accurately. These ( $n = 6$ ) were not included in calculations of pod size.

Gender was noted for most individuals, as previously determined by Bigg et al. (1987) or based on external morphology for adult males or pigmentation in the genital

area for subadults. Gender could not be determined for some juveniles and for some adult female-sized animals which had not previously been recorded in this study or elsewhere. Size (and thus approximate age of juveniles) was estimated by comparing the size relative to known adult whales, using photographs and/or visual observations.

### **Prey captures and energy intake calculations**

In just over half the cases (57%), prey species was determined by direct visual observations of prey, either in whales' mouths or at the surface amongst a group of whales, combined with observations of blood, blubber or meat in the water. The remaining prey captures (43%) were detected without direct observations of intact prey, and were based on observations of prey parts in whales' mouths or in the water. For these latter cases prey species was determined using a combination of location (52% were at harbor seal colonies; e.g., Figure 3.2), observations of potential prey in the area prior to capture, prey handling time, behavior, and quantity of blood or blubber observed in the water.

More than one prey was captured during some observation periods. Since prey handling can last up to several hours (Chapter I), distinguishing between consecutive prey captures can be problematic. Determination of the capture of a second or subsequent prey item was only made under certain conditions. Another kill was recorded when an intact prey was observed in a whale's mouth or at the surface after a prey item had been partially eaten or dismembered. In some cases, after a prey capture, it was clear that none of the whales in a group were carrying prey in their mouths. When timing and direction of travel would have prevented retrieval of a carcass which had been dropped earlier, and



Figure 3.2. Transient killer whale hunting at a harbor seal haul-out, Victoria, B.C.

when whales were subsequently seen with prey, this was also considered another prey capture. Behavioral information was also used to aid in discrimination of separate prey captures. Behaviors which were often associated with observed prey captures included sudden changes in speed or direction of travel, or distance between individuals.

When intact prey were observed they could usually (79%) be categorized as adult, juvenile or pup/calf. Average weights and caloric values of different-sized prey were estimated from published values (Deutsch et al., 1990; Leatherwood and Reeves, 1983; Olesiuk, 1993; Olesiuk and Bigg, 1988). Within a species, body composition varies regionally, seasonally, and with age, sex and reproductive condition (Bowen et al., 1992; Pitcher, 1986; St. Aubin et al., 1978). As body composition has not been examined in my study area for any of the prey species, and I was generally unable to assess factors such as sex, reproductive condition, or age accurately, I assumed that all prey were comprised of 30% blubber, 60% proteinaceous tissue, and 10% indigestible matter. These estimates are intermediate for body composition values of harbor seals reported from southeast Alaska and several locales in the North Atlantic (Bowen et al., 1992; Markussen et al., 1992; Pitcher, 1986; St Aubin et al., 1978).

Due to variation in body size, killer whale groups of equal size but composed of individuals of different age/sex categories differ in their total energetic needs. To standardize energetic values for groups of different age/sex composition, I calculated energy intake rates per adult female equivalent in each group. To simplify calculations, individuals were classified into four categories: adult males, adult females/sub-adult males, juveniles, and calves. Energetic needs relative to an adult female-sized animal, based on food consumption of captive killer whales at the Vancouver Public Aquarium and



at Sealand of the Pacific, Victoria (unpublished data), were chosen to be 1.4 for adult males, 1.0 for adult females/sub-adult males, 0.5 for juveniles, and 1.0 for calves less than one year of age. The latter value was due to a doubling of food intake for lactating adult female killer whales in captivity (Vancouver Public Aquarium, unpublished data). Later, I discuss the resiliency of the analyses to changes in these values.

Little information is available on weights of adult killer whales from the British Columbia populations, so to allow comparison with a study on killer whale energetics being undertaken by another worker, I have adopted the weight estimate used for adult female-sized killer whales (4000 kg) in that study (Kriete B, personal communication). Strictly for the purposes of calculating average per capita energy intake rates for different sized groups and for the population as a whole, based on relative food intake (above) I thus assumed adult males weighed 5600 kg, juveniles weighed 2000 kg, and calves less than one year of age weighed the same as an adult female.

Each block of time during which group size and composition remained constant was considered a single observation period. The per capita energy intake rate (kcal/kg/day) for each period was calculated using the caloric content of the prey captured (taking into account their number, species, and estimated size), the combined energy requirements of the whales in the group (expressed by their combined, metabolically-adjusted weights), and the duration of the observation period. Only group sizes for which there were three or more observation periods greater than 59 min in duration were used for statistical tests. For comparisons between group sizes, I pooled all observations of groups of each size.

Minimization of the risk of an energy-shortfall was examined using a graphical solution that takes into account changes in both the mean and variance of energy intake (Stephens and Charnov, 1982).

To determine whether observed prey captures accounted for the animals' energetic needs, an average per capita energy intake rate was also calculated. This took into account all observations of all group sizes (including short-duration encounters; i.e., those less than 59 min in length), and the caloric value for all prey captured during the study. The group size (in adult female energetic equivalents) was multiplied by the duration for each observation period, resulting in a measure of the observation time of a single adult female-sized whale (e.g., 4 adult females observed for 6 hours each equalled 24 observation hours, as did 2 adult males observed for 8.57 h). These values were summed over all observation periods, and divided by 24, producing a measure of the number of days of observations (in adult female equivalents). The summed caloric value of prey was then divided by this value and by 4000 (the weight of an adult female) to produce the average per capita energy intake rate (kcal/kg/day).

## **RESULTS**

### **Group composition and measures of grouping tendencies**

Approximately 434 h of behavioral observations were obtained in 100 encounters from 1986 through 1993. Killer whale group sizes ranged from 1 to 15 individuals. Group size and/or composition changed occasionally during some encounters, or groups were lost for short periods, resulting in a total of 217 periods of constant group composition. These periods ranged in duration from 3 min to 9 h 11 min. During the 100 encounters, 62

different individuals from 26 separate pods were recorded.

Pod size changed for five pods during the study, either through a birth ( $n=3$ ), or death or emigration of an individual. One emigration was positively documented, but no deaths of individuals could be confirmed during the study, as the re-sighting interval for transient killer whales can be 12 years or more (Ellis GM, personal communication) and animals that die are rarely found. In two cases pod size remained constant after a birth, as one individual disappeared from each pod. For the 20 pods where size was available (Table 3.1, Figure 3.3), mean size was 2.05 individuals. Maximum pod size was 4 individuals, and typical pod size was 2.46 individuals.

The amount of time groups of different sizes were observed is shown in Figure 3.4. Groups larger than three individuals were almost always temporary associations of two or more pods. Conversely, groups of three or less individuals virtually never contained members of more than one pod, implying that pods containing one or two individuals do not join to form foraging coalitions of three individuals. Based on hours of observation, the modal group size observed was 3 individuals, the mean group size was 4.21 individuals, and the typical group size was 5.62 individuals. Typical group size was also calculated using only those groups comprised of adult and subadult whales ( $> 5$  years of age), that were engaged in foraging and feeding activities at least 85% of the time. The typical size of these groups was 3.29 individuals (Figure 3.5).

#### **Prey capture and energy intake**

In total, 136 of 138 recorded attacks on marine mammals were successful (Table 3.2).

Prey attacked included 2 California (Zalophus californianus) or Steller (Eumetopias jubatus)

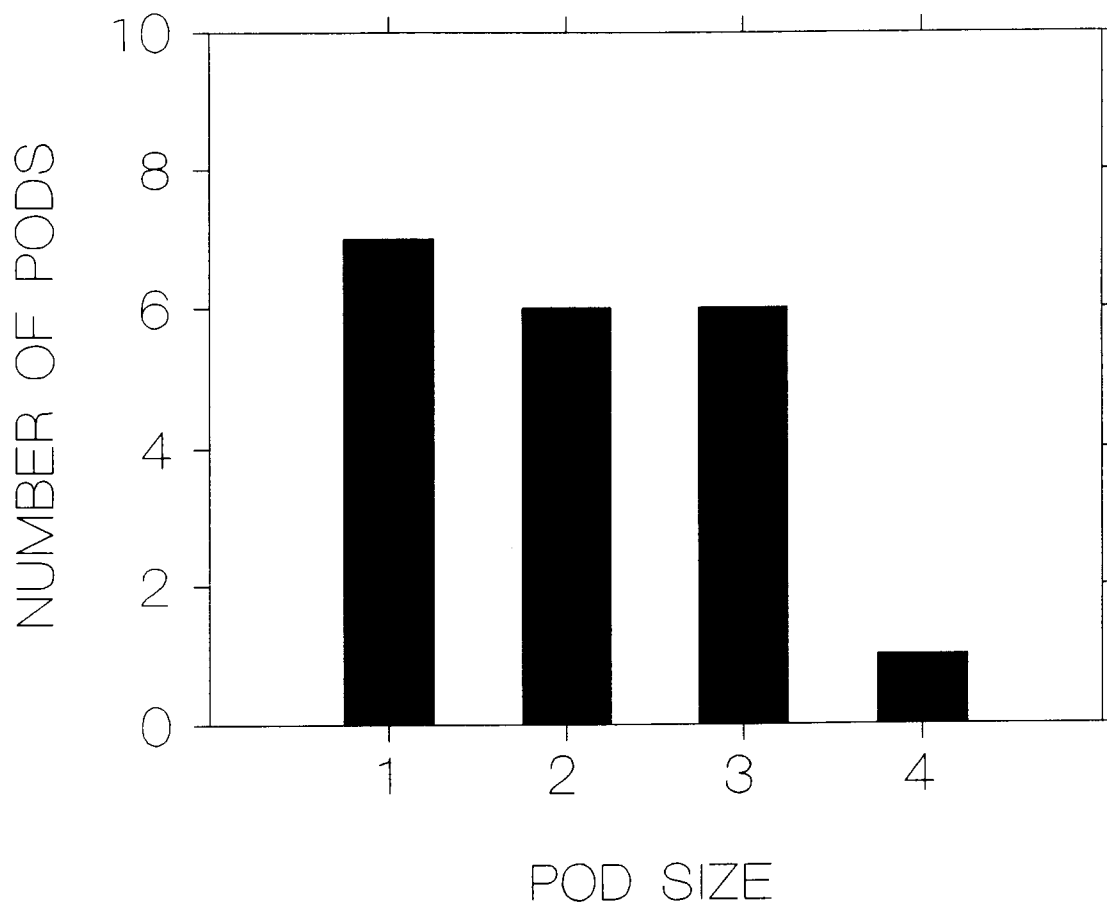
Table 3.1

## Pod identity and size

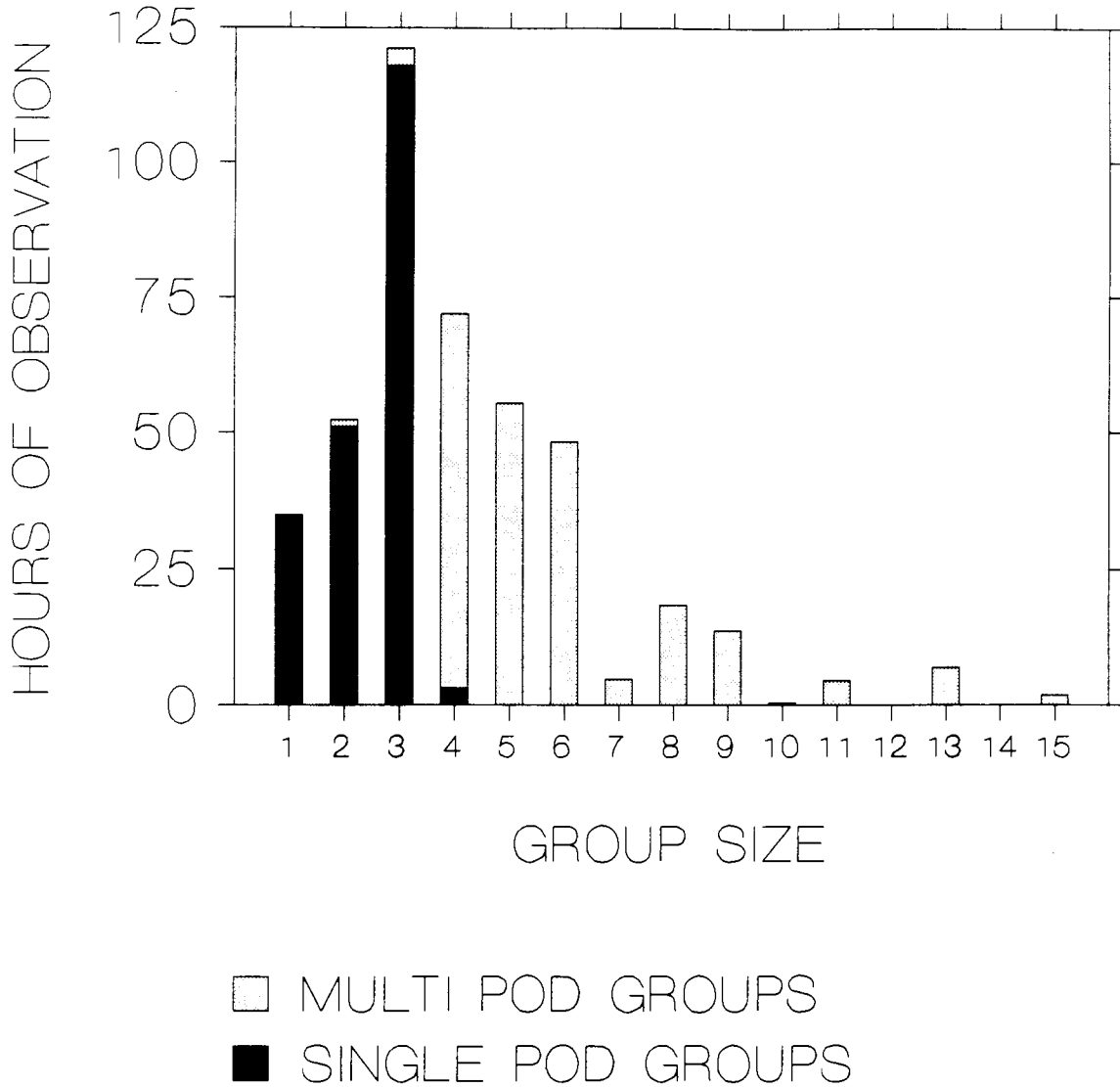
Pod size	Identity
1	AM33 (?), E12, F1, M4, P1, T2, V1, X10
2	AL4 (?), E10 (1-2), M20 (?), O2, O4, Q3 (3-2), Q4, Y1 (3-2)
3	AO1, M1 (3-4-3), O20, P28 (?), Q1, Q9, T3 (2-3)
4	F15, F19 (?), T125 (?)

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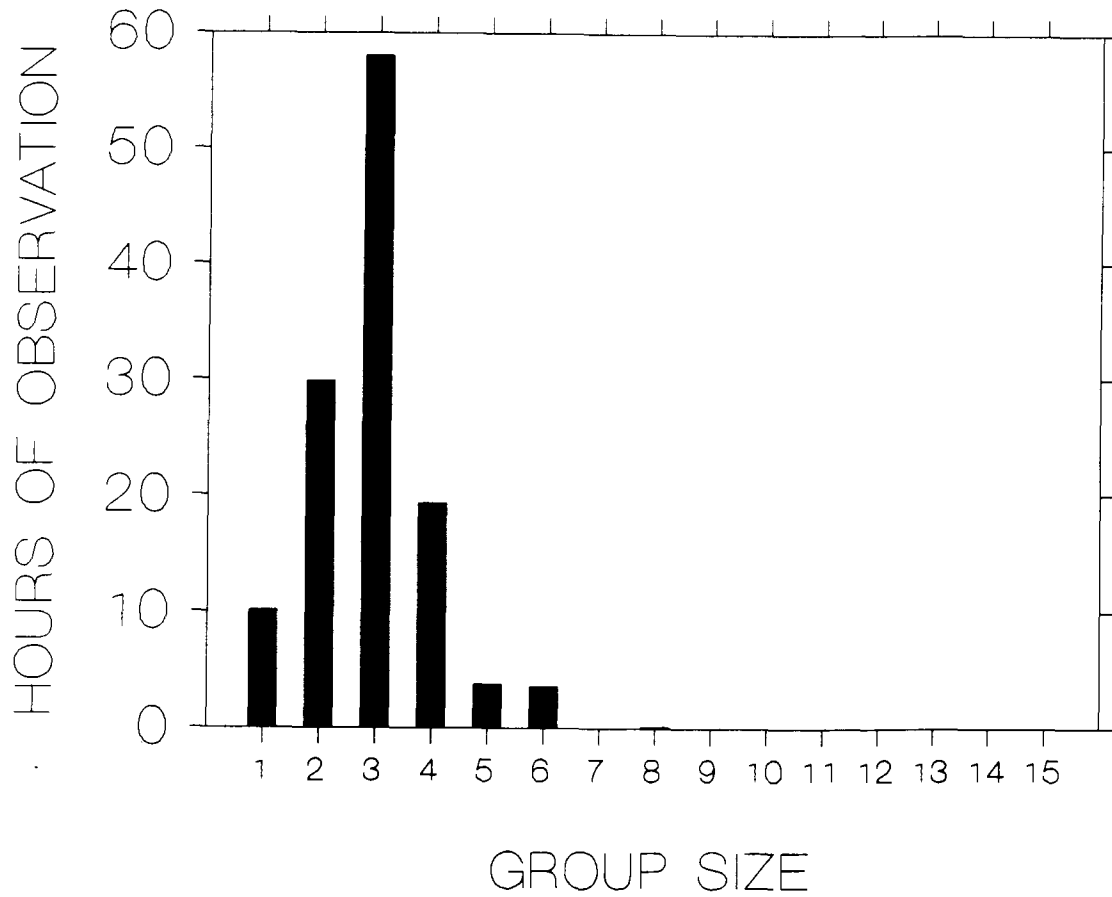
Pod designations and sizes after Bigg et al. (1987), Ellis (1987), Bigg MA and Ellis GM (personal communications), and Baird RW (unpublished). Insufficient information was available for six of the groups seen on only a small number of occasions to assess pod size accurately (indicated with a "?"). Where pod size changed during the duration of the study, the range of pod sizes is shown in parentheses (in the order from pod size when first encountered to pod size when last encountered).



**Figure 3.3.** Number of pods of each size observed during the study. Pods appear to be comprised only of close relatives, and pod size appears to change only through births, deaths or emigration; no long-term immigration into a pod has been recorded. Maximum pod size seen in this study was four individuals. For the five pods whose size changed during the study, the pod size when last encountered is used.



**Figure 3.4.** Total hours of observations for each group size. All encounters, regardless of duration, are included. Times spent observing groups comprised only of members of a single pod are shown in black, while times spent observing groups containing members of more than one pod are shown in gray. In all but one observation period, groups larger than three individuals were temporary associations of two or more pods.



**Figure 3.5.** The total hours of observation for groups comprised only of adult and subadult whales engaged primarily in foraging and feeding activities. The typical size of these groups was 3.29 individuals.

Table 3.2

Attack success and whale group sizes for different prey types

Prey Type	Number of Attacks	Number of Successful Attacks	Average Number of Individuals	Range in Number of Individuals
Harbor seal	130	130	3.84	1-11
Harbor porpoise	3	3	3	-
Dall's porpoise	2	0	3	-
Elephant seal	1	1	3	-
Sea lion	2	2	6	4-8



sea lions (exact species was not identified), 3 harbor porpoise (Phocoena phocoena), 2 Dall's porpoise (Phocoenoides dalli), and 1 northern elephant seal (Mirounga angustirostris). Only 3 of 20 sea birds attacked were eaten, and thus are not considered further in these analyses (see Stacey et al., 1990 for further details). Seventy-two definite observations of harbor seal attacks were recorded, and the remaining 58 marine mammal attacks were categorized as harbor seals, based on a variety of characteristics. During the three known captures of large prey (elephant seal and sea lions), handling times were extended (average of 138 min), and large quantities of blubber were observed at the water surface. Similarly, handling time during the three harbor porpoise kills was prolonged (average of 66 min), and all porpoise attacks involved high speed chases where prey were clearly visible at the surface. During known harbor seal captures handling times were shorter (average of 28 min) and only small quantities of blubber were observed in the water. During unidentified marine mammal kills (which were classified as harbor seals) behavior did not include high speed chases, and only small quantities of blubber were observed. The handling time during these kills averaged 20 min. The beginning of these kills (i.e., when the seal was first captured) was usually not noted by the observer; thus the handling time recorded was truncated. There were no significant differences in handling time for harbor seals of different sizes (Kruskal-Wallis one-way ANOVA,  $p = 0.41$ ). Thus there is no evidence to indicate that the size frequency of unknown kills (classified as harbor seals) differed from the size frequency of known harbor seal kills.

No predation of fish was observed. Many kills recorded were based only on visual observations of prey in the whales' mouths, and were not accompanied by sightings of live prey or portions of prey at the surface. Surface observations during these kills are similar to those categorized as fish-foraging behavior by Felleman et al. (1991). They

(Felleman et al., 1991; Thomas and Felleman, 1988) have stated that transient killer whales in the current study area feed on fish, although the evidence they present does not support such a conclusion. The observational methods used by Felleman et al. (1991) were such that many kills of harbor seals could have been mistakenly interpreted as foraging for fish, because of the generally large distance between the observer and the whales (Osborne RW, personal communication).

Sharing of prey between individuals in a group was difficult to observe since most prey handling occurred beneath the surface. Prey sharing was confirmed on many occasions, however. Guinet (1992) noted observations of killer whales in the Indian Ocean consuming prey away from their group, but no such observations of an individual obviously attempting to consume prey away from the rest of a group were noted in my study. For purposes of calculating per capita energy intake, I assumed that prey captured was shared proportionately (i.e., relative to energetic needs) among all individuals in a feeding group. In lions, feeding groups are often larger than the groups involved in hunting (Packer, 1986), but in my study there was no difference between killer whale hunting and feeding group sizes.

Relative prey age (and thus size) was determined for the sea lion and elephant seal kills (all adults), two of the three harbor porpoise kills (juveniles) and for 57 of the harbor seal kills (34 pups (59.6%), 12 adults (21.1%), and 11 juveniles (19.3%)). The average weights for the age/size class of each species attacked were used in energetic calculations. For those harbor seal prey whose size was not determined, the caloric value was estimated from the above ratio of known sized prey. To be conservative, for the two sea lion kills observed I used weights of California sea lions, the smaller of the two

potential species. It was not possible to note accurately the proportion of each prey eaten, but Rice (1968) provides evidence that entire animals, including the skull and skeleton, are eaten by killer whales at least some of the time. Remains larger than 1% of the estimated body size of the prey were observed on only four occasions, and all occurred during the period when prey abundance and vulnerability was highest (during the harbor seal pupping and weaning period). It is likely that portions of the prey which are not eaten do not always float to the surface, and are thus not visible to the observer, so for the purposes of energetic calculations I assumed that 90% of each harbor seal, harbor porpoise, and sea lion was eaten. I assumed that only 17% of the single adult male elephant seal killed was eaten, based on the size and number of whales present and their potential stomach capacities (cf. Hoyt, 1990). Average per capita energy intake, calculated for all observations of all group sizes, was approximately 62 kcal/kg/day.

Energy intake rates calculated from observation periods shorter than 60 minutes in duration were significantly higher than those calculated from longer observation periods (Mann-Whitney U-test,  $p < 0.001$ ). However, energy intake rates did not vary with the duration of observation period among those periods longer than 59 min (Kruskal-Wallis one-way ANOVA,  $p = 0.781$ , observation periods in one h blocks). Therefore, only group sizes with three or more such observation periods (lasting greater than 59 min in duration) were used for statistical analyses. One hundred and thirty-one observation periods, on group sizes from 1 to 9 (not including groups of 7), fit this criterion. During these periods (totalling 373.5 h) a total of 112 marine mammal kills were observed. Summary statistics for these observations are presented in Table 3.3.

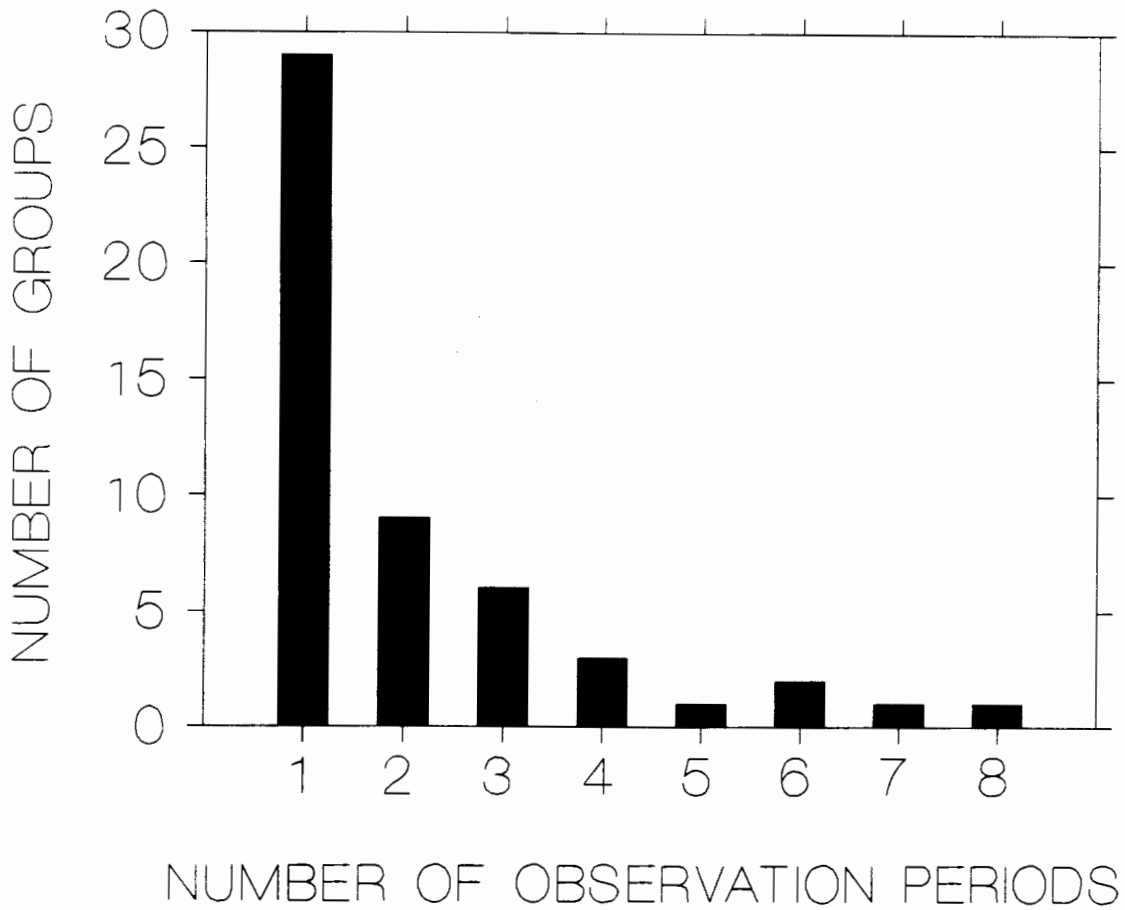
Repeat observations were made on some groups. Figure 3.6 shows the number of

Table 3.3

Group size vs. energetic intake

Group size	Number of observation periods	Average energy intake (kcal/kg/day)	Standard Deviation	Number of kills	Duration (hrs)
1	10	9	29	2	31.9
2	12	88	173	12	41.6
3	33	153	144	53	111.4
4	19	67	75	15	65.8
5	14	22	36	9	51.6
6	12	46	51	18	42.4
8	5	52	60	3	15.6
9	4	0	-	0	13.2

Only group sizes for which there are at least three observation periods, each longer than 59 min in duration, are included.



**Figure 3.6.** Frequency distribution of the number of observation periods for each group of a unique composition, showing only those used in statistical analyses. For example, observations from 29 unique groups were recorded only once, 8 unique groups were recorded twice, and so on.

observation periods used in statistical analyses, for each unique combination of individuals. The majority of observation periods (71%) used in statistical analyses were for groups observed for four or fewer periods each. To test whether these repeat observations on particular groups may have biased my results, I compared energy intake rates between several groups (of constant composition) seen repeatedly during the study. For five different groups seen repeatedly (each of three individuals), no significant differences in the average per capita energy intake rate was found (Kruskal-Wallis one-way ANOVA,  $p = 0.12$ ).

Individual energy intake (kcal/kg/day) for group sizes ranging from 1 to 9 individuals is shown in Figure 3.7. Energy intake rate depends on group size (Kruskal-Wallis one-way ANOVA,  $p < 0.001$ ), due to a higher energy intake rate for individuals in groups of three (Mann-Whitney U-test,  $p < 0.001$ ; group size of three vs. all others combined). The lower energy intake rate for small groups was not due to these groups utilizing different hunting areas (Baird, unpublished). The graphical solution (Figure 3.8) shows that foraging in groups of three individuals also minimizes the risk of energy-shortfall. Thus, both the energy-maximizing and risk-minimizing group size is three individuals, the modal group size observed in this study.

## **DISCUSSION**

### **Energy intake and prey capture**

I had to assume that the prey captures observed represented the vast majority of prey actually caught by the whales. The observed average energy intake rate gives some support to the validity of this assumption. The estimated average energy intake rate of about 62 kcal/kg/day, while based on several assumptions regarding the size and

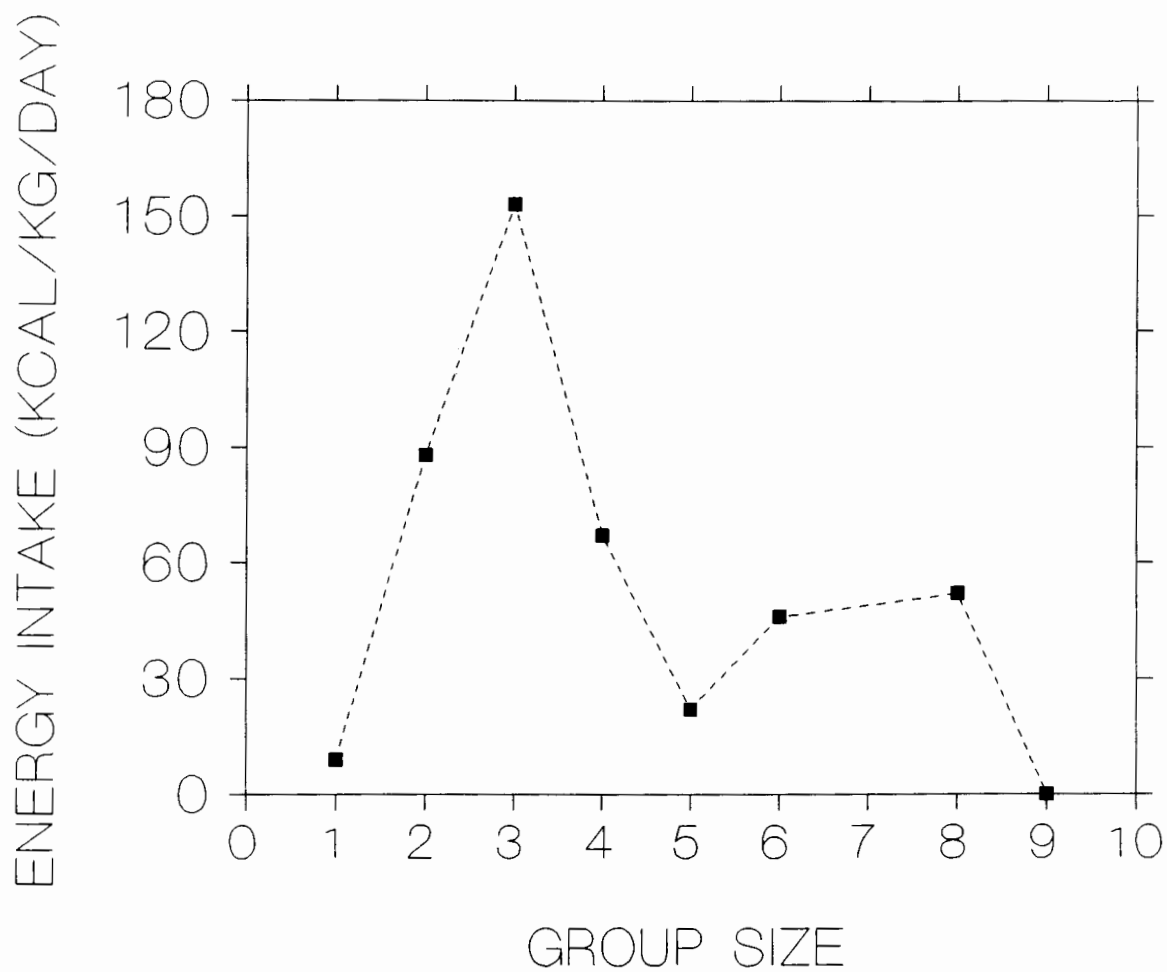


Figure 3.7. Daily per capita energy intake for each group size, expressed as mean consumption rate (kcal/kg/day). The energy-maximizing group size is equal to three individuals.

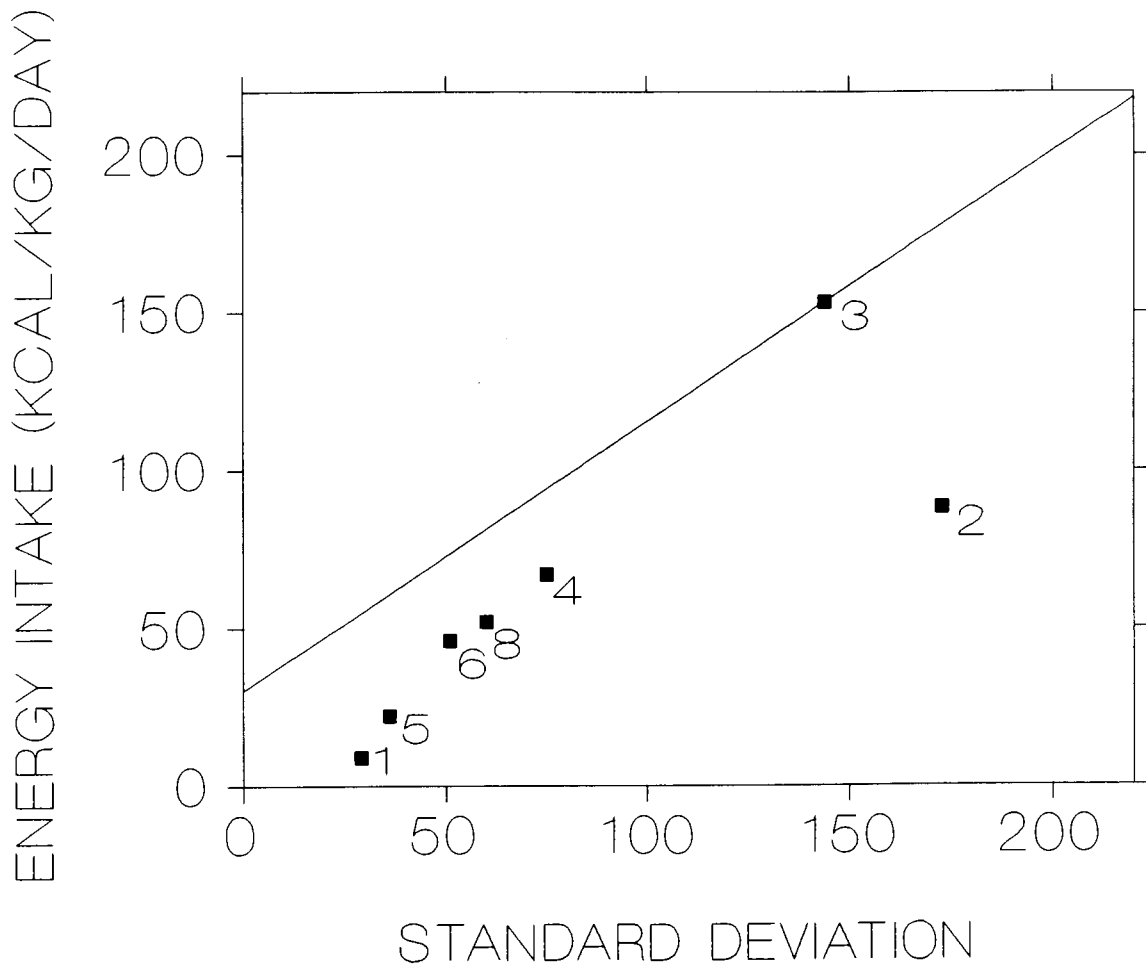


Figure 3.8. Mean energy intake versus standard deviation of energy intake for each group size. The Y-intercept for the line shown is equal to the lower estimate of energetic requirements for killer whales. The slope of the line is greatest when tangent to the value for a group size of three individuals, indicating that the risk of energy-shortfall is minimized in groups of this size (Stephens and Charnov, 1982).



proportion of prey eaten, is still substantially greater than the predicted energetic needs of the animals. Using breathing rates and physiological measurements of captive whales and swimming velocities of free-ranging animals Kriete (1991 and personal communication) calculated energetic requirements of between 30-35 kcal/kg/day for free-ranging adult females. I thus believe that the observed prey intake must account for the vast majority of prey actually captured during the observation periods, i.e., at most only a small proportion of attacks could have been missed by the observers.

This study's estimate of energy intake rate based on observed prey captures is unique for killer whales. Energy intake estimates in other studies of marine mammals have usually been based on captive animals or examination of stomach contents from wild animals. Both methods have numerous biases which limit their value for estimating energy intake of free-ranging animals. One other study has discussed food intake of wild killer whales, but only presented data on weight of prey captured as a proportion of estimated whale body weights (Hoelzel, 1991).

There are several possible reasons why the average per capita energy intake rate estimate from this study is substantially higher than the energetic requirements estimated by Kriete (1991 and personal communication). Harbor seal abundance in the study area is approximately four times higher than for the coast of British Columbia as a whole (Olesiuk PF, personal communication); thus killer whales might increase their energy intake in this area to compensate for decreased prey abundances in other areas of the coast (cf. Katz, 1974). An examination of transient killer whale time-budgets is relevant, to determine whether whales observed in this study spent a disproportionate amount of time foraging compared to transients in other areas. A time budget for transients around southern

Vancouver Island is presented in Chapter I. Observations of prey capture are less frequent in other studies (Barrett-Lennard, 1992; Morton, 1990), but such comparisons are confounded by differences in observational methods. Both of the other studies focused on acoustic recordings, and the distances between the observer and the whales likely precluded the recording of many prey captures (Chapter I). A comparison of the amount of time spent foraging (rather than prey captures per se) may be more relevant; taking into account differences in the definitions of behavioral categories, no obvious difference in the proportion of time spent foraging between the three studies is apparent (Chapter I). Sample sizes in these other studies are small, however, resulting in biased representations of actual activities (i.e., no social behavior - Barrett-Lennard, 1992; no resting behavior - Morton, 1990). Thus, while it appears that whales observed in this study were not biased towards groups that were foraging, a re-comparison of time-budgets when more data become available from other areas would be warranted.

Another possible reason for the high estimate of energy intake is that food intake may be lower at night than during the day. Limited evidence from a radio-tracking study implies that behaviors at night are generally similar to those during the day (Erickson, 1978), but this possibility also warrants further study. Similarly, if a lower proportion of each prey item is consumed, my estimate of an average energy intake rate would be high. Inaccuracies in my estimates of the relative energetic needs of different-sized/aged individuals could also affect my estimate for the average energy intake, although no information is available to suggest whether this would increase or decrease the average estimate.

The energy maximizing group size for transient killer whales hunting harbor seals is

three individuals (Figure 3.7). The biases discussed above would also affect group-size specific energy intake rates. Changes in the proportion of each prey consumed or the amount of prey caught at night should not affect my conclusions, however, as these biases should apply equally for different sized groups. To examine what effect changes in my estimates of the relative energetic needs of different sized/aged individuals would have, I analyzed group size specific energy intake rates using six alternate values (as well as combinations of these values) for different age/size classes. Compared to the energetic requirements of an adult female, these values were 1.5 or 1.6 for adult males, 0.7 or 0.8 for juveniles, and 0.7 or 0.8 for calves less than one year of age. Each analysis produced the same results; individuals in groups of three had significantly higher energy intake rates than individuals in other group sizes. Thus my basic conclusion regarding an energy maximizing group size appears to be resilient to changes in my assumptions regarding the proportion of prey consumed, the body composition of prey, or the relative energetic needs of different sized or aged individuals.

The peak in energy intake for groups of three may occur because of a trade-off in detection abilities between killer whales and their potential prey. As killer whale group size increases there should be an increase in their ability to detect prey (cf. Pitcher et al., 1982), and the prey encounter rate should increase. The proportion of prey captured when encountered probably also increases with group size, because larger groups are able to cooperate in chasing fleeing prey (Chapter I). Conversely, larger groups of killer whales should be easier for prey to detect (cf. Bertram 1978; Goss-Custard, 1976), and marine mammals may have a variety of options to avoid predation once they have detected a potential predator. Pinnipeds may haul out to avoid capture if they are close to a haul out site, or in open water may dive deeply or remain motionless at the surface, to avoid being

detected (cf. Thomas et al., 1987). Similarly, porpoises may either flee, or reduce motion in an attempt to avoid being detected. Even when detected by hunting transients, I suspect that seals may occasionally be able to escape, albeit temporarily, into underwater hiding sites. While individual killer whales in a group may alternate spending time at the bottom waiting for a hiding seal to run out of air (Chapter I), a lone whale would have to leave the seal unguarded in a hiding site to return to the surface to breathe. (Presumably seals in such situations may be more willing to enter into anaerobic respiration than a lone killer whale.) Such factors likely contribute to the initial increase in energy intake with group size.

### **Grouping patterns**

Having demonstrated that there is a group size that maximizes energy intake, the next step is to compare this to observed transient killer whale group sizes, which can be expressed using a variety of measures, including mean, modal, and typical group size. The appropriate measure is sensitive to the frequency distribution of group sizes; when observed group sizes are bimodally distributed, as in the examples given by Jarman (1974) and Clutton-Brock and Harvey (1984), or when they are skewed towards smaller groups (e.g., Barrette, 1991) the mean or modal group size may greatly misrepresent the group size experienced by the average individual in the population, and the typical group size should be used. In this study, the distribution of observed group sizes is unimodal, but is skewed towards smaller groups (Figure 3.4). Three individuals is the group size most frequently observed, both in terms of number of encounters and duration of observation time, but the typical group size is much larger (5.61 individuals). However, several potential biases in my data collection lead me to believe this value is inflated. First, large groups are easier to spot than small groups, thus biasing the typical group size

value upwards. As well, groups were occasionally lost during data collection, and such groups were always of 4 or fewer individuals. I believe the modal group size would not be similarly affected by these biases, however, due to the clear peak in observations of groups of three and to the relatively small impact on sightability of a small increase in group size (i.e., between a group of two and three individuals). Unfortunately, no precise information is available to determine the magnitude of the effect, but unless it was very large, the group size experienced by an average individual in the population would remain larger than the energy maximizing optimum.

Giraldeau and Gillis (1988) noted that comparisons between predicted and observed group sizes should be limited to groups which are engaged in the behavior of interest. Two lines of evidence suggest that larger groups contain a disproportionate number of calf and juvenile whales (less than six years of age), and groups containing young whales may not be appropriate for comparison with the energy maximizing group size. While the proportion of groups which contain calves and juveniles should increase with group size, based on chance alone, the proportion of calves in groups also increased significantly (regression,  $p = 0.001$ ,  $r^2 = 0.896$ ; group sizes 2-9, not including 7). Such an increase was not due to higher productivity in larger groups since these were temporary associations of several pods. Longitudinal information on two pods (T3 and M1) encountered both before and for more than three years after the birth of a new calf in each, also support the supposition that larger groups have a disproportionate number of young whales. In these cases, the typical group sizes when the calves were less than two years of age (12.28 and 8.31 individuals, respectively for the two pods) were substantially greater than the size of groups before the births and after the calves were greater than two years of age (5.34 and 5.08 individuals, respectively for the two pods),

due to increased association with other pods. I suggest below that these larger groups serve a function other than maximization of energy intake. For comparisons of the observed group sizes with the predicted group size, I thus excluded groups containing calves and juveniles less than six years of age. In addition, I included only observation periods during which whales were engaged in foraging or feeding activities for at least 85% of their time. The typical size of groups composed of adults and subadults primarily engaged in foraging and feeding was 3.29 individuals, a value more similar to that predicted by the energy maximizing hypothesis (Figure 3.5).

As noted above, the group size which appears to minimize the risk of an energy-shortfall is also three individuals (Figure 3.8). However, the energetic stores of killer whales should be large enough to buffer short-term variation in energy intake, and a proper analysis of risk-minimization would have to look at variance in food intake over time scales more relevant to the whales, i.e., weeks or months. It is thus unlikely that minimizing the short-term risk of an energy-shortfall is important in determining killer whale group size.

### **Functions of large multi-pod groups**

I explore two possibilities for the occurrence of groups larger than the energy-maximizing optimum: 1) the occasional hunting of prey (other than harbor seals) for which the optimal foraging group size is larger than three; and 2) social functions of large groups, such as the protection of calves and the provision of opportunities for mating or alloparental care.

Other authors have suggested the existence of a group size/prey size relationship for killer whales (Guinet, 1991), as occurs with many other social carnivores (Earle, 1987).

While an increase in prey size may allow additional individuals to feed from a kill without increasing competition for food, it appears that large prey size per se is not a factor which drives the formation of larger foraging groups. The elephant seal kill observed, and that observed by Samaras and Leatherwood (1974), were both of adult males, who are very large but not very manoeuvrable, and the killer whale group sizes involved were only three and two individuals, respectively. Large groups may be more important for increasing the success rates for prey which are difficult to capture, such as Dall's porpoise, and/or whose capture entails risk of injury, such as sea lions. Indeed, the mean group size noted for the two instances where sea lions were captured (6.0) was higher than the mean observed for harbor seal captures (3.84; Table 3.2). Both observed Dall's porpoise attacks were unsuccessful, and both were with small groups (three individuals); two successful Dall's porpoise attacks observed locally were with groups of four and eight individuals (Claridge D, Walters EL, personal communications). Thus, the occurrence of large groups observed in this study may be related in part to the occasional taking of more difficult to capture prey, either in the study area or elsewhere on the coast, where the whales spend part of their time. Indeed, larger average group sizes are found in areas where harbor seals are less abundant and other species are more regularly included in the diet (e.g., Morton, 1990).

Social functions of large groups may also be important. Haenel (1986) and Waite (1988) discussed the benefits of alloparental care, and Rose (1991) discussed the value of learning courtship or mating skills that may occur in larger groups of resident killer whales. In my study, the frequency of social behavior increased with group size; groups of from 1-7 individuals generally spend less than 5% of their time engaged in social activities, whereas groups larger than 7 individuals generally spend greater than 15% of

their time in such activities (Chapter I). The occasional formation of larger groups may thus function to provide opportunities for mating, alloparental care, and/or learning courtship or mating skills. Packer et al. (1990) noted that the benefits of group living in lions include defending of territories, preventing scavengers or conspecifics from stealing prey, and preventing infanticide. As noted above, transient killer whale calves and juveniles are disproportionately common in large groups. GM Ellis (personal communication) recently observed a large group of southern resident killer whales (approximately 14 individuals) attack and chase a small group of transients (3 individuals) off Nanaimo, British Columbia. It is possible that the disproportionate presence of calves and juveniles in larger groups of transients functions to protect these more vulnerable individuals from attacks by residents. Bigg et al. (1990) suggested that the absence of dispersal by resident killer whales might arise from a particularly strong requirement for reliable and familiar associates for hunting or maintaining territorial boundaries, or from a unique breeding structure. Similarly, the formation of large groups of transients might function to allow familiarization of young whales with other individuals in the population. Such familiarization may be important for future associations between individuals, particularly to facilitate the cooperative hunting of dangerous prey such as sea lions or gray whales (Eschrichtius robustus).

### **Pod size and dispersal**

Although most large groups result from multi-pod associations, individual pods larger than the energy-maximizing optimum may also occur due to constraints on dispersal from matrilineal groups. Dispersal has twice been noted from transient matrilineal groups, once in this study and once by other researchers (Bigg et al., 1987). Which individuals are most likely to disperse from transient matrilineal groups cannot be stated with certainty, but



some probable rules of dispersal can be suggested, based both on the two observed cases and on the age/sex composition of pods. Dispersal may be limited by dependence on maternal care. In one instance dispersal of a male occurred at between six and seven years of age (Bigg MA, personal communication); thus, at least in the case of males, individuals may need to be about this age to survive independently. Sexual maturity for males is reached at approximately 15 years of age (Olesiuk et al., 1990), so an individual at six to seven years of age would still be considered a juvenile or adolescent (Haenel, 1986). Both recorded cases of dispersal occurred within a couple of years of the birth of a new offspring into the group. No information is available on the precise timing of dispersal in the first instance, but in the second case dispersal did not occur until the new offspring was over two years of age. It is possible that the young age of the recent calf prevented it from participating in hunting, and thus the older individual was still needed as a member of the hunting group. Both cases of dispersal occurred from the same matrilineal group, which also contained an adult male, likely the first-born maternal sibling of the two dispersing individuals (Bigg et al., 1987). Because no transient pods recorded in B.C. contain two adult males, but many contain a single adult male, it is possible that all males other than the first-born disperse before the onset of sexual maturity. At this stage, suggestions as to the age and sex classes of dispersing individuals remain speculative due to the small sample size of known cases of emigration. Due to the large geographic range of individuals in this population, the low frequency of repeat sightings of known animals, and long calving intervals, further support for such rules must await additional long-term studies. It is reasonable to suggest, however, that selection for efficient foraging has led to the differences in dispersal patterns between transient and resident pods.

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CHAPTER IV

POSSIBLE INDIRECT INTERACTIONS BETWEEN TRANSIENT AND RESIDENT KILLER  
WHALES: IMPLICATIONS FOR THE EVOLUTION OF FORAGING SPECIALIZATIONS IN  
THE GENUS ORCINUS

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## Summary

Two distinct forms of killer whale (Orcinus orca) occur off the coast of British Columbia, Alaska and Washington State. These have different diets, and may be reproductively isolated. Because the primary food of transient whales (pinnipeds) is a potential competitor for the primary food of resident whales (salmon), or for the smaller fishes on which salmon feed, there should be an indirect interaction between the two forms of killer whale. I use simple mathematical models to show that this interaction will be either of a "plus-minus" type, or a "plus-plus" type (indirect mutualism), depending on whether or not pinnipeds and residents are on the same trophic level. In the case of the "plus-minus" interaction, increasing the population density or improving the environmental conditions of transients will increase the population density of residents, while increasing resident populations will reduce the equilibrium population size of transients. In the case of the "plus-plus" interaction, increasing the population density or improving the environmental conditions of transients will increase the population density of residents, and vice versa. Such effects may not be currently manifest due to reduced populations at most levels in the food web. Regardless, considering such indirect interactions may be important for the management of many of the species involved, and can also provide a valuable framework for examining the evolution of the two forms of killer whales. Frequency-dependent indirect interactions, acting in concert with density-dependence within populations and disruptive selection on prey-type specific foraging characteristics, may have favoured reproductive isolation of the two forms of killer whales. I suggest that these two forms of whale are in the process of speciating, i.e., the two forms are incipient species.

## Introduction

It has recently been recognized that there are two forms of killer whale (Orcinus orca) found in the coastal waters of western North America from Washington State through Alaska, with the forms differing in foraging behaviour, habitat use and group dynamics. Differences in association patterns, shape of dorsal fin, pigmentation patterns, and mitochondrial DNA (Bigg et al. 1987; Baird and Stacey 1988a; Hoelzel 1989; Stevens et al. 1989) suggest limited gene flow between the two forms at best. The two were originally termed transient and resident based on their presumed associations with particular areas (Bigg et al. 1976). As noted by Guinet (1990), this distinction based on association with a certain area has since become less clear, but the two names have been retained, mainly because of their widespread use and the lack of appropriate alternative designations. Bigg et al. (1987) have suggested that these two forms could be considered separate "races". For my purposes, it will be assumed that all residents (there are several "communities") form a single population, that the same is true of transients, and that the two killer whale populations are totally distinct. While the possibility of occasional exchange of individuals between social groups of the two forms cannot be entirely ruled out, there have been no documented cases during the past 15 years, during which time all residents and most transients have been recognized individually.

The population of transient whales feeds primarily on pinnipeds (i.e. harbour seals, Phoca vitulina), while the resident whale population feeds primarily on fish (i.e. salmon, Oncorhynchus spp.) (Bigg et al. 1990). The fact that pinnipeds also feed primarily on fish



(Spalding 1964; Perez and Bigg 1986; Olesiuk et al. 1990b) raises the possibility that the two whale groups may influence each other's food supply indirectly. The present study uses simple mathematical models to explore these potential indirect effects. The potential exists for each population to have an impact on the average population size and evolutionary changes that occur in the other. The simple types of models presented are meant to suggest possibilities rather than to make precise predictions about the dynamics of the species/forms under consideration. None of the indirect effects discussed below are likely to be important unless one or both whale populations experience significant density dependence in mortality and/or natality. Largely due to human exploitation, resident killer whales now appear to be significantly below their carrying capacity (Olesiuk et al. 1990a), while the status of transients relative to their carrying capacity is not known. Also due to human exploitation, the populations of many of the other species in the food web are well below aboriginal levels. However, it is important to be aware of the possibility of indirect effects, as such effects are relevant to the management of several of the species included in the models. As well, the theoretical framework presented to examine potential indirect effects is useful in considering the evolution of the two forms of killer whale. This is explored further in the discussion.

## **Biological Background**

Table 4.1 lists some of the behavioural and ecological differences between transient and resident killer whales. For present purposes, the most important differences relate to diet and habitat use. Transient killer whales in British Columbia have been recorded eating four of the five species of pinnipeds found there (summary in Jefferson et al. 1991): harbour

Table 4.1. A summary of differences between resident and transient killer whales (from Bigg et al. 1987, Baird and Stacey 1988b, Bain 1989; Morton 1990; Chapters I and III).

	<u>resident</u>	<u>transient</u>
Group size	large (3-80)	small (1-15)
Dispersal from maternal group	no	yes
Seasonal occurrence	w/salmon runs	unpredictable
General foraging area	deep water	shallow water
Dive duration	short, consistent	long, variable
Echolocation during foraging	yes	no
Prey type	fish	marine mammals
Prey size	small	large
Sharing of prey	generally no	generally yes

seal; northern elephant seal, Mirounga angustirostris; Steller sea lion, Eumetopias jubatus; and California sea lion, Zalophus californianus. The fifth species of pinniped found in B.C., the northern fur seal (Callorhinus ursinus), has not been recorded as prey there, but has been recovered from stomach contents of killer whales off Alaska (Zenkovich 1938). Recent evidence collected around southern Vancouver Island suggests that harbour seals may be the most common prey of transients (Baird et al. 1989, 1990, Chapters I and III). For the purposes of simplifying the models, however, all species of pinnipeds are lumped together, and equations dealing with pinnipeds consider a hypothetical "average" species. The diet of residents is much easier to characterize; in British Columbia and Washington State, the vast majority (approx. 90%) of prey observed to be eaten have been salmon (Bigg et al. 1990). However, the possibility remains that other fish species may be taken but consumed underwater or at times of the year when observer effort is minimal.

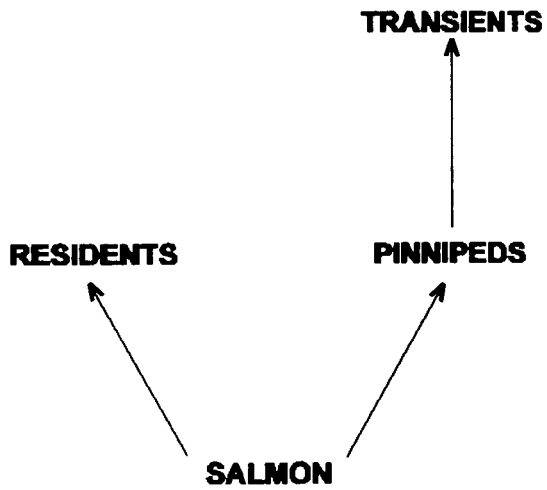
Resident and transient killer whales generally use the various portions of the habitat to different degrees (Heimlich-Boran 1988; Morton 1990). This can be related to their prey choice, since there is some habitat separation between the major prey of residents (salmon), and the major prey of transients (pinnipeds). Because pinnipeds eat fish (including salmon) they obviously do not occupy completely different habitats from salmon, but they spend a significant proportion of their time associated with haul-out sites, and other nearshore areas. Salmon are generally found in major waterways, especially during migration. Because pinnipeds are air-breathing mammals and must return to the surface to breath, it is also likely that the distribution in the water column of the two prey types is different, with pinnipeds spending more time nearer the surface, and salmon spending more time in deeper water. Of course, this may vary among pinniped and salmon

species, with the age and sex of the individual, and with the time of year.

There is some dietary overlap of pinnipeds and resident killer whales (see Fisher 1952; Spalding 1964; Olesiuk and Bigg 1988; Olesiuk et al. 1990b; Bigg et al. 1990). In addition, pinniped diets overlap with those of salmon (Hart 1973). Present information is inadequate to assess the type and degree of overlap accurately (see Discussion). However, the possibility of the indirect effects illustrated in the two food webs shown in Figure 4.1 exists.

In Figure 4.1A, resident whales and pinnipeds are shown as direct competitors for a common food resource; each would have a negative effect on the other's population size. In Figure 4.1B, resident whales and pinnipeds have a more indirect interaction, with pinnipeds primarily consuming the smaller fish species that are the food of salmon (Hart 1973), which, in turn, are the primary food of resident whales. The interaction illustrated in Figure 4.1B implies that larger pinniped populations indirectly reduce salmon populations (by reducing their food supply), and therefore reduce the food available to resident whales. Higher resident whale population density decreases salmon density, which increases the supply of smaller fish consumed by pinnipeds. Available data are not sufficient to determine positively which of these two food webs is a better representation of the whale-pinniped-fish system; therefore models of both types of system will be explored below. They have very different consequences for the interactions between the two types of whales.

Model A



Model B

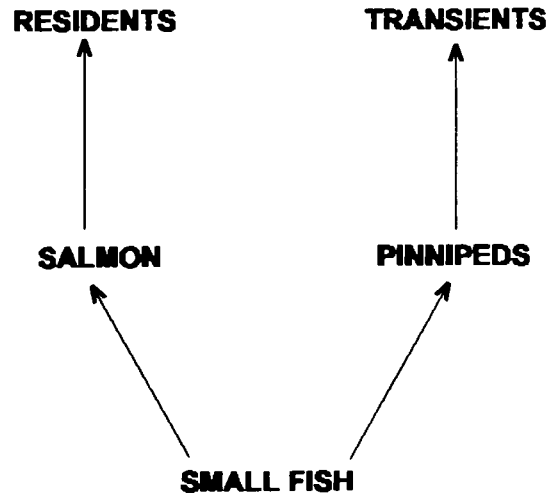


Fig. 4.1. Potential food web types. A. In Model A, pinnipeds and residents compete for salmon and other fish. B. In Model B, pinnipeds compete with salmon for smaller fishes (e.g. herring).

## Lotka-Volterra type models

### A. Resident whales and pinnipeds are competitors

The simplest representation of the system described in Figure 4.1A includes three populations. The transient whales may be modeled as predators that consume only one of two competing species. If the population densities of pinnipeds, residents, and transients are denoted  $P$ ,  $R$ , and  $T$ , respectively, then the basic interactions are represented by:

$$\begin{aligned}
 dR/dt &= r_R R(K_R - R - \alpha P)/K_R && \text{(resident whales)} \\
 dT/dt &= T(BCP - D_T) && \text{(transient whales)} \\
 dP/dt &= r_p P[(K_p - P - \beta R)/K_p] - CPT && \text{(pinnipeds)} \quad (1)
 \end{aligned}$$

where  $r_R$  and  $K_R$  are the intrinsic rate of increase and carrying capacity, respectively, for resident whales;  $r_p$  and  $K_p$  are the equivalent values for pinnipeds;  $\alpha$  and  $\beta$  are competition coefficients between pinnipeds and resident whales, and vice versa;  $C$  is the number of pinnipeds captured per unit time per unit pinniped density by an average transient whale;  $B$  is the efficiency with which transient whales consume and assimilate pinnipeds; and  $D_T$  is the density-independent death rate of transient whales.

This is a special case of the Lotka-Volterra type of one predator-two competing prey model that has been explored by Vance (1978) and Gilpin (1979). Hutson and Vickers (1983) present a more general analysis which does not assume that per capita growth rates are linear functions of population densities. The pinniped-whale system is a

special case of these models because the predator (transient whales) eats only one of the two competitor types (pinnipeds). Present knowledge of the natural history of these species suggests limitations on some of the parameter values. Because there appear to be differences in the relative species composition of the diets of pinnipeds and resident whales (Fisher 1952; Spalding 1964; Perez and Bigg 1986; Olesiuk and Bigg 1988; Olesiuk et al. 1990b; Bigg et al. 1990), the product of the competition coefficients should be less than one (Abrams 1983). Because whales are much larger and consume a much greater amount of prey than do pinnipeds,  $K_R$  should be significantly smaller than  $K_p$ , and  $\beta$  should be much greater than  $\alpha$ .

The model assumes that the instantaneous per capita population growth rate of transient whales is independent of their own population density. Because of the complex social behaviour of this species and the presence of group hunting, this assumption is probably invalid at sufficiently low whale population densities. However, what occurs at higher whale densities is most relevant, when per capita growth rates are probably less influenced by whale density and more influenced by food supply.

Equations (1) have a single equilibrium point with positive population densities of all three types. This is specified by:

$$P = D_T/BC$$

$$R = K_R - (\alpha D_T/BC)$$

$$T = (r_p/CK_p)[K_p - (D_T/BC) - \beta K_R + (\alpha\beta D_T/BC)] \quad (2)$$

Standard methods (see e.g. Sanchez 1968) show that this equilibrium point is always

locally stable (assuming positive equilibrium populations of all species).

The expressions for equilibrium densities can be compared with the equilibrium density that each type of whale would attain in the absence of the other. These are:

$$R = (K_R - \alpha K_p)/(1 - \alpha\beta),$$

$$T = (r_p/CK_p)(K_p - (D_T/BC)) \quad (3)$$

Comparison of the formulas for resident density in (2) and (3) shows that when both types are present at equilibrium the density of resident whales (R) must be larger than when transients are absent. Conversely, it seems probable that the transient whale population will be smaller when both whales are present; the condition for the presence of residents to decrease the transient population equilibrium is:

$$BCK_R > \alpha D_T \quad (4)$$

It is necessary that  $BCK_p$  be greater than  $D_T$  in order for transients to exist in the absence of residents. Although  $K_R$  is much smaller than  $K_p$ ,  $\alpha$  is very much less than one because pinnipeds have a much lower fish consumption rate than whales, and because of likely differences between pinnipeds and whales in the species of fish that they exploit. This makes it very likely that condition (4) is satisfied, and that the presence of residents decreases the equilibrium population size of transients.

The above discussion suggests that there should be a "plus-minus" interaction



between the densities of the two types of whale, i.e., the presence of transients increases the equilibrium density of residents, while the presence of residents decreases the equilibrium density of transients. However, such a simple characterization can obscure the variety of effects that may occur as the result of indirect interactions between two types (Abrams 1987). If the two whale populations are in fact genetically isolated, evolutionary changes may occur independently in the two, and environmental changes may affect the parameters of population growth of one but not the other. The indirect interaction may be better understood by considering the effects of evolutionarily favoured changes in the parameters of the growth equation of one type on the two equilibrium densities. Increases in the carrying capacity of residents ( $K_R$ ) will increase their equilibrium population size, while decreasing the equilibrium population size of transients. If the food intake rate required for zero population growth in the transients ( $D_T/B$ ) is decreased, the equilibrium density of both types of whales will increase. If the consumption rate constant ( $C$ ) of transient whales increases, the population density of residents will increase, while that of transients will increase if  $C < 2D_T(1-\alpha\beta)/B(K_p - \beta K_R)$ .

All of these results are consistent with the generalization that favourable environmental changes (or evolutionarily favoured changes) in the resident whales will decrease the population density of the transients, while environmentally favourable or evolutionarily favoured changes in the transients will increase the population density of residents. Further, it can easily be shown that if the population density of transients is maintained above its normal equilibrium level (e.g. by immigration), this will increase the equilibrium density of residents; if the density of residents is maintained above its normal equilibrium level, this will decrease the equilibrium density of transients.

There are many reasons why a Lotka-Volterra type model is too simple a description of whale and pinniped population dynamics. However, the simple model analyzed above makes several points that are likely to be true for a wide range of models that have the same trophic structure. If there is competition between resident whales and pinnipeds, there is likely to be a positive effect of the transient whales on the population density attained by the residents, and a negative effect of resident density on transient density. Of course, these conclusions depend upon my assumptions about the biology of the system: (i) the existence of competition, and (ii) the absence of other direct or indirect interactions between residents and transients.

#### B. Resident whales and pinnipeds have an indirect interaction

If pinniped diets overlap with salmon diets (as shown in Figure 4.1B), then a Lotka-Volterra type model of the system must contain at least four different populations. The basic interactions may be represented as follows:

$$\begin{aligned}
 dR/dt &= R[B_R C_R S - D_R] && (\text{resident whales}) \\
 dT/dt &= T[B_T C_T P - D_T] && (\text{transient whales}) \\
 dP/dt &= r_p P[1 - (P/K_p) - (\alpha S/K_p)] - C_T P T && (\text{pinnipeds}) \\
 dS/dt &= r_s S[1 - (S/K_s) - (\beta P/K_s)] - C_R S R && (\text{salmon}) \quad (5)
 \end{aligned}$$

The parameters have meanings analogous to the parameters in equations (1), except that  $\alpha$  and  $\beta$  are now competition coefficients between pinnipeds and salmon. The assumption of a linear relationship between food consumption and per capita population growth is common in food web models (Pimm 1982). It is again probable that the product  $\alpha\beta$  is less

than one because of dietary differences between salmon and pinnipeds. The equilibrium population sizes in this system are:

$$\begin{aligned}
 S &= D_R/B_R C_R \\
 P &= D_T/B_T C_T \\
 R &= (r_s/C_R)[1 - (D_R/K_s B_R C_R) - (\beta D_T/K_s B_T C_T)] \\
 T &= (r_p/C_T)[1 - (D_T/K_p B_T C_T) - (\alpha D_R/K_p B_R C_R)]
 \end{aligned}
 \tag{6}$$

This sort of system has been studied by ecologists interested in indirect effects (Vandermeer 1980), and it is known that increases in either of the two top predators (the two whale populations) will cause increases in the equilibrium density of the other; such a "plus-plus" interaction is referred to as indirect mutualism. It also follows directly from equations (6) that evolutionarily favoured changes in any of the parameters of either whale population growth equation (larger B, larger C, lower D) will increase the equilibrium population size of the other. The system described by equations (5) again always has a stable equilibrium when  $\alpha\beta < 1$ . The models considered here are more likely to have a stable equilibrium than are models that incorporate convex functional responses (Murdoch and Oaten 1975). Results on other simple three and four-species models suggest that adding or deleting a species is likely to have an effect on the stability of the remainder of the food web (e.g. Abrams 1987).

## Discussion

The interactions between resident and transient whales may be either "plus-plus" or "plus-minus", depending on the particular food web used in the model. Given what is currently

known about the diets of pinnipeds, Model B (and thus a "plus-plus" interaction) seems more likely. Regardless of which food web is assumed the model predicts a stable equilibrium ratio of resident and transient densities. Model B further suggests that each population's equilibrium density will be higher in the presence of the other than it would be if there were only one form of killer whale. It is also worth noting, based on trophic level efficiency arguments and equations (4) and (5), that resident density should be greater than that of transients. This is supported by the current population estimates for the two forms (Bigg et al. 1987).

#### A. The model vs. the real world

As noted above, the simple types of models explored here are meant to suggest possibilities rather than to make predictions about the precise dynamics of the species/forms under consideration. If an attempt were made to use these or similar models to derive quantitative testable predictions about population dynamics, many additional factors would have to be taken into consideration. First is the question of how to delineate the populations to be considered. At the present time, information on the total geographic range of populations of killer whales is unknown, particularly with regard to offshore movements. In fact, there is evidence of an offshore "community" of killer whales off British Columbia, of which little, beyond their existence, is known (Bigg pers. comm.; Walters et al. 1992). Because the range of individual transient whales may span the range of two or more "communities" of resident whales (Bigg 1982), it would be difficult to draw the lines for which populations to include. Similarly, the entire pinniped population fed upon by transients does not compete with residents (because their ranges

only overlap partially). Seasonal movements of some of the pinniped species also make it difficult to estimate the overall extent of such competition, and it is likely that this would have to be done separately for each pinniped species in any event.

I have had to make assumptions about the diets of each species/form as well, based on the best current information. However, methods of evaluating food habits vary between species and studies, and have numerous biases which make accurate comparisons difficult (e.g. Bigg and Fawcett 1985; Antonelis et al. 1987; Harvey 1989). Current population sizes are not well established for any of the species for the area under consideration, but all are probably lower than historical levels due to culling, hunting, and live-capture. Thus, population sizes may have been reduced by human activities to such an extent that no indirect effects are currently manifested. If an attempt were made to assess whether indirect effects were occurring in the real world, details on the life histories, food habits, seasonal movements and population sizes of five species of pinnipeds (harbour seal, northern elephant seal, Steller sea lion, California sea lion and northern fur seal), both forms of killer whales, and an untold number of species of fish would need to be available. Depending on the food web model used, it might even be necessary to include Dall's porpoise (Phocoenoides dalli) and harbour porpoise (Phocoena phocoena), both of which are found in B.C., eat fish, and are consumed by transient killer whales (Jefferson et al. 1991; Chapter III).

The models assume that all species/types experience indirect density dependence via depletion of their food supply. There has been no evidence of density-dependence in population growth parameters for resident killer whales during the period 1973-1989 (Olesiuk et al. 1990a). Surveys of density-dependence in many species (Fowler 1988)

suggest that large, slowly growing species generally do not experience density-dependence until their population sizes are significantly above one-half of their carrying capacity. If this is true of both whales and pinnipeds, then the predicted indirect effects may not be evident until whales are closer to their carrying capacity.

The true situation may be even more complicated than indicated in Figure 4.1. Firstly, the residents may compete with only some pinniped species; other pinniped species may compete more directly with salmon. Thus, a more realistic scenario may contain elements of both food webs illustrated in Figure 4.1. Secondly, some pinnipeds may feed on fish which feed on salmon (i.e., lamprey and dogfish) (see Beverton 1985). If so, transient predation on pinnipeds would decrease pinnipeds but increase the abundance of other salmon predators, which would tend to dampen any indirect effect of transients on residents.

In theory (and if data were available) it would be possible to construct a model incorporating the above complexities of food web organization and spatial scale. However, the very complexity of such a model would obscure its most important lesson - that transients and residents may have effects on one another's population sizes, regardless of the precise mechanism by which these come about. One value of the models, even in their present simplified state, is that they stress the need to find out more about the indirect interactions between resident whales and pinnipeds, because these may have important implications for the population biology of transient whales. Additionally, over and above implications for potential present-day or future indirect interactions between the populations, the models can provide new insight into the evolution of the two forms. For this I assume that the above described indirect effects may have occurred in the

evolutionary history of the local killer whales.

### B. The evolution of foraging specializations in the genus Orcinus

Consideration of the potential for indirect effects of various sorts to influence the equilibrium densities of residents and transients provides a new theoretical paradigm to understand the evolution of these very different forms of killer whale. Below, I will develop a scenario in an attempt to deduce how these two forms may have come to exist. For this purpose, I will assume the application of Model B.

I assume that at some point in the evolutionary past there was a single form of killer whale in the eastern North Pacific. If this early form specialized on a single type of prey (i.e., fish or marine mammal), as do the current forms, the first step in diversification would be for some individuals to begin to specialize on the alternative food-type. Because such a food-type would be abundant, its utilization would be profitable even if individuals were not initially well adapted to exploit it (Wilson and Turelli 1986). Foragers of the two types would likely differ behaviourally from one another in a number of ways. Differences in habitat and depth of the water column between pinnipeds and fish (Table 4.1) would require some habitat segregation, and different foraging tactics would be needed to encounter and subdue different sizes of prey. These differences are evident between residents and transients today.

Group sizes differ significantly between residents and transients, which can be related to the degree and type of co-operative hunting possible for their major prey types. Factors important in the evolution of cooperative hunting include prey size, and whether

single or multiple prey are captured (Packer and Ruttan 1988). Fish can be considered multiple small prey, whereas pinnipeds can be considered single large prey. Whales feeding on fish could not share individual prey, and the capture of each fish would not significantly affect the capture by other individuals of other fish, or the subsequent capture of other fish by the same individual. This is because fish do not have the same options available for them to escape as seals or sea lions might. Fish may be able to evade killer whales to some degree, but would not be as effective at doing so as pinnipeds, because pinnipeds may escape onto land once they become aware of the presence of hunting whales. Pinnipeds may also require extended handling to be subdued (see Chapter I). Thus capture of one prey likely decreases the probability of the whales capturing subsequent prey. Also, due to their large size and agility, some pinnipeds (such as adult sea lions) may frequently be able to defend themselves successfully from attacking killer whales. Thus, the efficiency of a foraging group of pinniped eaters (transients) may be limited by the size of the prey, the number of individuals needed to subdue it, the division of the prey among members of the hunting group, and perhaps earlier detection (and thus avoidance) by the prey as group size increases. Such effects may lead to a maximum foraging group size for transients, and evidence is available that transients have a higher individual food intake rate when foraging in smaller groups (Baird et al. 1989, 1990, Chapter III). Fish eater (resident) group size is less likely to be constrained, given the large size of the fish schools on which they feed.

Resident killer whales use echolocation to detect fish, and the limited current evidence suggests that fish do not recognize the sound of echolocation as a threat (Schwarz and Greer 1984; Felleman 1986). Transients appear to be largely silent when foraging, presumably to limit detection by their mammalian prey (Ford 1984; Morton



1990; Hubbard-Morton 1990). Transients also appear to modify their respiratory rate (Morton 1990), and perhaps the amplitude of individual exhalations (Appendix II), in such a way as to decrease detection by marine mammal prey. To summarize, in order to maximize successful encounters with marine mammals, and thus presumably energy intake rate, transients hunt through stealth, and have habitat use patterns, respiration rates and group sizes which differ from those of residents.

In accordance with the indirect interactions outlined in Model B, both forms of killer whale would increase in density owing to a "plus-plus" interaction (indirect mutualism), and the relative frequency of individuals adopting the novel, alternative foraging strategy would increase in the population until density-dependent effects became important, i.e., close to overall carrying capacity. The two forms would eventually reach an equilibrium ratio by a combination of density- and frequency-dependence. Density-dependence (operating within the population as a whole) and frequency-dependence (in terms of indirect interactions operating between sub-populations) ensure that the fitness of each type of whale is equal at this equilibrium density ratio. (One of the early ideas about these two forms was that because of their smaller group sizes, and population size, transients were "relegated" to the less "desirable" niche [see e.g. Bigg 1979]. These models suggest that this is not the case.)

At this stage in their evolution individuals of the two forms might still have interbred freely, and the two strategies could be said to have co-existed in an evolutionary stable state (ESS) (Maynard Smith 1982; Gross 1984). An ESS involves two different pure strategies at the population level, with each strategy having equal fitness owing to negative frequency-dependence. The genetic structure is polymorphic, that is, individuals

adopting each strategy are genetically distinct (this contrasts with a mixed ESS, which is monomorphic, with all individuals capable of exhibiting both behaviours). The very behavioural adaptations which increase the ability of transients to feed on pinnipeds, are likely to decrease their ability to encounter scattered fish schools. Resident tactics to maximize encounters with fish would similarly decrease the likelihood of their encountering marine mammal prey. These mutually exclusive co-adapted suites of characteristic foraging tactics, corresponding to transient and resident strategies, suggest that the fitness of either prey specialist would be greater than that of a generalist who searched for both prey types simultaneously. This is another important feature of an ESS (Gross 1984).

There is another way to be a generalist, and that is to switch back and forth between tactics. But, if hunting tactics are learned, and require a long period of practice or guidance from other individuals, learning all tactics for both strategies might prohibit such switching. That learning is important for the development of killer whale hunting techniques was suggested by Lopez and Lopez (1985), and may be reflected in the long juvenile (2 to 6 years of age) and adolescent (6 to approx. 13 years of age) periods (Haenel 1986). The locations of pinniped or fish concentrations might also have to be learned.

Morphological adaptations specific to each foraging strategy could also have evolved. Morphological differences have been found between populations of killer whales in the Antarctic (Berzin and Vladimirov 1983), which might be due to differences in diet (Bain 1989). Bain (pers. comm.) has speculated that foraging related differences in the thickness of the proximal end of the mandible may exist, reflecting a trade-off of an

increase in strength needed to withstand forceful movements of large prey, and a decrease in thickness for improved reception of sound. Improved sound reception through the mandible may be important for echolocating resident killer whales foraging for fish (see e.g. Brill et al. 1988). Unfortunately, testing for differences in morphology at this time is difficult, due to the paucity of available skeletal specimens.

It might seem beneficial for individuals specializing on different prey types to associate with one another, owing to what has been called the "skill pool effect" (Giraldeau 1984). According to this hypothesis, associations between individuals that have specialized on different prey types results in an overall increase in prey available to the group. However, if transients are constrained to a small group size by the size and availability of prey, and all individuals hunt cooperatively, then having an individual hunter who is unfamiliar with the foraging tactics needed, and thus unable to contribute to the hunt, would not be advantageous to the transient group, who presumably would therefore prohibit such joining. Resident groups might be more willing to include transients.

Extensive field observations (Bigg et al. 1987; Morton 1990; Chapter I) suggest that resident and transient groups remain spatially isolated, with no social interaction between the two forms; this sets the stage for reproductive isolation. Such isolation would be favoured by the sorts of disruptive selection on intermediates discussed above. Morphological and molecular divergence between the two forms, for which there is clear evidence (see Introduction), would be the result. I therefore suggest that disruptive selection for prey type (= size) may have resulted in the two forms of killer whales found in the eastern North Pacific today.

Although I have not ruled out the possibility of allopatric speciation, my scenario is one of sympatric speciation, which is theoretically possible when frequency- and density-dependence are combined with disruptive selection (e.g. Wilson and Turelli 1986). Indeed, foraging specializations resulting in various degrees of sympatric isolation have been suggested for a variety of organisms, including Galapagos finches (Grant and Grant 1979, 1989), bluegill sunfish (Ehlinger and Wilson 1988), insects (Tauber and Tauber 1989), and possibly threespine sticklebacks (McPhail 1992). I therefore suggest that killer whales in the eastern North Pacific are in the process of speciating, i.e., the two forms are actually incipient species. Only further work will show if this scenario seems plausible. This will require detailed examination of external and skeletal morphometrics (with emphasis on functional differences), genetic comparisons, and long-term behavioural, social and ecological research. Such ecological research should further explore the potential for competition and indirect effects with other organisms in the food web.

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## EPILOGUE

Case studies of incipient speciation provide an important window into understanding the general causes and consequences of reproductive isolation between populations (Otte and Endler 1989). My research into the foraging behaviour and ecology of transient killer whales provides an increased understanding of the differences between transients and residents, as well as of their possible causes and consequences. This study provides heretofore unavailable detail on many aspects of transient killer whale biology, that can be combined with information collected in the few other studies undertaken on transients. This information can be compared with the extensive base of knowledge of the biology of resident killer whales gained through the far more numerous studies on these animals. The purpose of this epilogue is to briefly review the current state of knowledge regarding differences between these two forms and the taxonomic implications of these differences.

An early idea regarding the two forms was that transients were likely individuals who were rejected from resident pods (M.A. Bigg, pers. comm.), accompanied with the stigma of low productivity and relegation to a less desirable lifestyle (Bigg 1979). By 1987, Bigg et al. had termed these forms "races", and this term has been adopted, I suggest uncritically, by many investigators. The term "race" is usually defined in a geographic sense, implying geographically isolated populations which are typically given subspecific designation (Mayr and Ashlock 1991). In Chapter IV, I suggested that transients and residents should be considered incipient species, that is, in the process of speciation. The two forms might even be considered separate species, according to the

biological species concept (Mayr 1969; Stuessy 1990).

An updated list of differences, and potential differences, between transients and residents is shown in Table E.1. Genetic differences reported by Stevens et al. (1989) and Hoelzel (1989) were based primarily on mitochondrial DNA. While these differences suggest reproductive isolation between the two forms, the maternal inheritance of mitochondrial DNA precludes absolute determination of such isolation. Although several morphological differences between the two forms have been noted (Table E.1), also implying reproductive isolation, no information is available to determine how complete such isolation might be. I argued in Chapter IV that disruptive selection on prey-type specific foraging specializations may have favoured reproductive isolation of these populations. Such a scenario has been postulated with other species-pairs in sympatric situations (Benkman 1993; Grant and Grant 1989; McPhail 1992; Schluter 1993; Schluter and McPhail 1992, 1993; Tauber and Tauber 1989).

If residents and transients were allopatric, no conclusions regarding their status as biological species could be reached. However, as noted by Mayr (1969), sympatry can be viewed as a test for the validity of biological species; if reproductive isolation is maintained in sympatry, divergent forms should be considered good biological species. I believe the available information, much of which is summarized in this thesis, is conclusive enough to suggest that residents and transients currently behave as different biological species. However, the tradition of applying a morphological species concept (rather than a biological one) to cetacean taxonomy makes such a suggestion unlikely to be accepted by the majority of cetacean taxonomists. Regardless, I do not mean to imply that the capacity to exchange genetic information does not exist between the two forms,

Table E.1. Evidence to suggest reproductive isolation between residents and transients.

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Differences in mitochondrial DNA - Hoelzel 1989; Stevens et al. 1989

Differences in the shape of the dorsal fin - Bain 1989

Differences in saddle patch pigmentation - Baird and Stacey 1988

Possible differences in eye patch pigmentation - D. Ellifrit, pers. comm.

Differences in behaviour and ecology

- diet - Chapter III; Bigg et al. 1990
- travel patterns - Morton 1990
- respiration patterns - Morton 1990
- vocalizations - Morton 1990; Ford and Hubbard-Morton 1990
- echolocation - Barrett-Lennard 1992
- amplitude of exhalations - Chapter IV; Appendix II
- diving patterns - Chapter II
- group size - Chapter III; Morton 1990
- dispersal from maternal group - Chapter III; Bigg et al. 1987
- seasonal occurrence - Chapter I; Morton 1990
- geographic range - Bigg et al. 1987

Avoidance of residents by transients - Chapter I; Morton 1990;

Possible aggression by residents towards transients - G. Ellis, pers. comm.

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especially considering the frequency with which interspecific and even intergeneric hybrids have been recorded in cetaceans (both in the wild and captivity; e.g., Nishiwaki and Tobayama 1982; Herzing 1990; Arnason and Gullberg 1993), only that such exchange does not appear to be occurring today, consistent with the biological species concept.

Several pieces of evidence are needed about the resident/transient system to flesh-out the causes and consequences of reproductive isolation. One of these is the determination of a behavioural isolating mechanism. The clear differences in underwater sounds produced by these two forms (Ford and Hubbard-Morton 1990) is the obvious candidate; monitoring the reactions of resident whales to playbacks of transient sounds, and vice versa, as well as of residents and transients to their own sounds, would demonstrate experimentally whether the differences in sound are used as a behavioural isolating mechanism, and would supplement the few observations of reactions of transients when near residents in the wild. More information on ecological separation of the two forms, through expanded studies of diving behaviour using TDR tags like those used in Chapter II, as well as studies of the behaviour and ecology of both forms at night, is also necessary. Lastly, the consequences of reproductive isolation, in terms of skeletal and other morphological differences between the two forms, needs to be investigated, particularly looking for the kinds of foraging-related differences suggested in Chapter IV. As noted in Chapter III, due to the large geographic range of individuals, the low frequency of resightings of known animals and the long calving intervals, continuing long-term studies will be necessary to provide detailed information on dispersal, as well as to provide the sort of life-history information available for residents (Olesiuk et al. 1990). The information in Chapter I on pod-specific differences in behaviour, habitat use and seasonal

occurrence also suggests that studies must be expanded geographically and seasonally to take into account the intra-form variability evident for killer whales. When studies of transients expand and resident research matures, information from this system may become of more general interest to investigators working on the mechanisms, causes and consequences of reproductive isolation between populations, that is, the processes of speciation.

Another consequence of this work, often overlooked in biological studies, is its implications for the conservation and management of killer whales. Information on transient diet presented throughout the thesis and the food web connections described in Chapter IV imply that human perturbations of any of the components of the transient/resident food web may affect residents, transients or both. Clearly, an ecosystem approach to management must be taken if these populations are to be maintained in spite of increasing human presence and disturbance of their environment. Information on the importance of group hunting for killer whales (Chapter III), the presence of pod-specific foraging tactics (Chapter I), and the probable role that learning and familiar hunting associates may play in prey capture (Chapter IV), also imply that live-capture programs for this species world-wide must be reconsidered in light of the potential for disruption of the social groupings of the animals which remain in the wild. Increased understanding of the biology of killer whales, and in particular their habitat use, is needed to properly manage these populations.

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## APPENDIX I

**OBSERVATION PERIODS GREATER THAN 59 MINUTES IN DURATION FOR EACH GROUP  
OF UNIQUE COMPOSITION.**

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Observation	Group Composition
Periods Per Group	
1	(Q7); (X10); (Y1); (Y3); (O2, O3); (M1, M2, M9); (P26, P28, P32); (Q9, Q11, Q13); (Y2, Y3, E10); (AO1, AO2, AL4, AL14); (O20, O21, O22, E12); (Q3, Q12, Q4, Q8); (Q4, Q8, E10, E12); (T125, T126, T127, T128); (Y1, Y2, Q3, Q12); (M1, F15, F16, F17, F18); (O4, O5, Q3, Q7, Q12); (O20, O21, O22, O4, O5); (Q4, Q8, Q9, Q11, TO12C); (T3, T6, T11, E10, E13); (F19, F20, F21, F22, F23, AM33); (O20, O21, O22, Q3, Q7, Q12); (O20, O21, O22, Q9, Q11, Q13); (Y1, Y2, Y3, T3, T11, E10); (AO1, AO2, AO4, AL4, AL14, M2, M9, M4); (O4, O5, T3, T6, T11, M20, M21, E12); (O20, O21, O22, E12, F15, T75A, F17, F18); (O4, O5, Q1, Q2, Q10, Q9, Q11, Q13, P1); (O20, O21, O22, Q9, Q1, TO12C, M2, M9, M4)
2	(F1); (M1, M2, M4); (M2, M4, M9); (O4, O5, M2, M9); (Y1, Y2, Y3, E10); (M1, M2, M9, O4, O5); (T3, T6, T11, Q9, Q11, Q13); (M1,



M2, M4, M9, F15, F16, F17, F18); (M1, M2, M4, M9, F15, F16,  
F17, F18, T2)

3 (AO1, AO2, AO4, M4); (M1, M2, M4, M9); (Q3, Q7, Q12, P1); (Q3,  
Q7, Q12, T3, T11); (O20, O21, O22, Q9, Q11, T012C); (Y1, Y2,  
Y3, Q3, Q7, Q12)

4 (V1); (Q3, Q7, Q12); (Y1, Y2, Q3, Q7, Q12)

5 (Y1, Y2)

6 (O4, O5); (O20, O21, O22)

7 (Y1, Y2, Y3)

8 (T3, T6, T11)

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Each observation period represents a single datum (a continuous period of time during which group size and composition remained constant). Only those periods lasting longer than 59 minutes, for group sizes with three or more observation periods, are shown.

## APPENDIX II

AN EXAMINATION OF DIFFERENCES IN THE "BLOWS" OF TRANSIENT AND RESIDENT  
KILLER WHALES

In Chapter IV, I suggested that transients might modify the amplitude of their exhalations to minimize detection by potential prey. During field research in 1989 I noted that transient exhalations (blows) sounded quieter than resident blows. Such differences were apparent over a range of killer whale behavioural states, whether foraging, feeding or travelling. In an attempt to quantify this difference, I made recordings of killer whale blows in the field in 1990, 1992 and 1993. Recordings were made using a Sony Professional WM-D6C cassette recorder, and a Audio-Technica AT815a Condenser ("shot-gun") microphone. Due to masking by other noises, recordings could only be made on days when wind speed was less than 5 kph, sea state was Beaufort 0, the whales were travelling slowly, and no other power vessels were in the area. Due to the difficulty of measuring and maintaining a precise distance and orientation from the whales, the sound pressure level (SPL) of an exhalation could not be measured directly. Consequently, the duration of the exhalation was chosen as a potential indicator of SPL, since SPL should be greater for exhalations of shorter duration (assuming a constant exhalation volume). Exhalation duration was measured from sonograms using a Kay DSP Sona-Graph model 5500.

Two hundred and sixty three exhalations were recorded from residents, and 391 exhalations were recorded from transients. Because the whales were usually in groups,

information on individual identity was not available for all recorded blows; thus classification of individuals as to age and sex was not always possible. In many cases exhalations of two or more individuals overlapped, which prevented the measurement of blow duration. Distance from the subjects and the presence of other vessels in the area also affected the quality of recordings; measurement of duration for many blows recorded at large distances or with vessels nearby was not possible. Considering only those individuals with five or more blows of sufficient quality to measure exhalation duration, and utilizing only adult individuals (since relatively few measurements were available for sub-adult animals), resulted in a total of 56 usable blows for residents and 145 for transients. These included exhalations recorded from 13 individuals: 3 transient males, 2 resident males, 5 transient females, and 3 resident females. Number of exhalations analyzed for each individual ranged between 7 and 49 (mean = 15.5, SD = 11.0).

The mean exhalation duration for each of these whale types is shown in Table A.II.1. Exhalations of transient males are significantly longer than those of transient females (Mann-Whitney U-test,  $p < 0.001$ ), but no difference between the blows of male and female residents was found (Mann-Whitney U-test,  $p = 0.814$ ). A comparison of transients versus residents for each sex separately indicates that transient male exhalations are of longer average duration than those of residents (Mann-Whitney U-test,  $p = 0.005$ ), while no difference exists between the exhalation durations for females of the two types (Mann-Whitney U-test,  $p = 0.478$ ).

The increased duration of the exhalations of transient males should result in a decrease in loudness, and such a decrease could function to decrease detection by harbour seals. Alternatively, such differences in the characteristics of the exhalation may

Table A.II.1

Descriptive statistics for killer whale exhalation durations (sec).

Killer whale type	Mean	SD	N	
			Individuals	Blows
<u>Resident</u> males	0.636	0.121	2	22
" females	0.614	0.144	3	34
<u>Transient</u> males	0.723	0.116	3	83
" females	0.613	0.121	5	62

simply reflect differences in the lung capacity of the two forms, since transients typically take much longer dives than residents (Morton 1990). Why no differences were found between females of the two forms is unclear. Differences in amplitude noted in the field appear consistent for both male and female transients, suggesting that some mechanism other than an increase in the duration of the exhalation must be partly responsible for the apparent decrease in amplitude. Measurements of amplitude from audio recordings made using a directional microphone and a cassette recording system, in combination with determination of distance to the whales using a video system might allow for more direct quantification of differences between transient and resident blows.

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