Feeding Ecology of the Killer Whale (*Orcinus orca*)

by

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FEEDING ECOLOGY OF THE KILLER WHALE (<u>ORCINUS</u> <u>ORCA</u>)

by

Frederic L. Felleman

1.0) INTRODUCTION

Numerous isolated accounts in the scientific and popular literature describe predation by the killer whale, or orca (<u>Orcinus</u> <u>orca</u>). The common name, orca, will be used in lieu of killer whale because it does not imply a simplified or anthropocentric characterization of its feeding strategies, the diversity of which is the subject of this thesis. Anecdotes have traditionally provided the only basis for considering orcas the "top" predator of the sea. However, long-term field studies have started to provide insights into the diversity of orca feeding behavior both within and between populations.

The most intensive field studies of this species have been conducted in the inland waters of the Pacific Northwest of North America (Spong et al. 1970; Bigg et al. 1976; Bigg 1982; Balcomb et al. 1980; Ford and Fisher 1982; Osborne et al. 1984, 1985; Felleman and Osborne 1986) and in Patagonia, Argentina (Lopez and Lopez 1984). These long-term studies have utilized the technique of photo-identifying uniquely marked individuals, developed by Bigg and his colleagues, to evaluate the impact of cropping individuals from the Pacific Northwest population for aquariums (Bigg and Wolman 1975; Bigg et al. 1976; 1983). Recently, photo-identification has also been used to assess the size of orca populations in Alaska (Leatherwood et al. 1984) and Norway

(Lyrholm 1984).

Martinez and Klinghammer (1970) were the first to attempt to formulate a general understanding of orca feeding behavior from a comparison of the literature. Their review provides several examples of cooperative foraging techniques directed towards a variety of prey species. However, numerous other accounts of orca predation and results from longterm field studies have been published since that paper had been written. Since longterm field studies had not begun when they wrote their paper, they were unable to address the diversity of foraging behavior exhibited by an intensively studied population.

In this thesis, the literature on orca feeding behavior worldwide is reviewed and compared with findings from orca research in the Pacific Northwest. Bigg (1982) has defined three socially isolated populations of orcas (northern resident, southern resident, transient) which temporarily inhabit the inland waters of Washington and British Columbia, Canada. I compare the feeding ecology of the three orca populations in the Pacific Northwest which provides a model example of the diversity in prey choice which can be exhibited among sympatric orca populations. Although a few stomach contents have been analyzed, most of the evidence I present on the type of prey orcas select is inferential. However, I use of an independent set of variables to distinguish between populations which have been the subjects of extensive observation thus providing comparative support for my characterization of each population.

Prey choice by orcas in the Pacific Northwest are indicated from observations of their surface behavior, orientation to the tidal current, core area of disribution, group size, and seasonal occurence in the study area. In addition, the spatial and temporal characterization of prey availability is reviewed which provides an indication of how orca feeding behavior may be responsive to their prey distributions. My field work has emphasized the analysis of the influence changes in the tidal current have on the orcas' direction of travel and prey availability. I chose to conduct tidal analysis because of the assumed importance of tides to a marine predator as it affects the distribution of prey. In addition, tides are a readily observable, independent variable, which I have found can be used as a means of distinguishing the predatory behavior of sympatric orca populations.

I conducted retrospective tidal and behavioral analysis on seven years of field data collected by the Whale Museum, Moclips Cetological Society (MCS), from 1976 to 1982 on southern resident and transient orca pods to generate the hypotheses tested by three years of my field research on the same orca populations in the Pacific Northwest. In addition, I conducted a pilot study in July 1985 which extended my tidal and behavioral analyses to observations of the northern resident population.

Another preliminary, but supportive indication of variations in prey choice among sympatric orca populations is suggested by differences in the accumulations of PCB and DDT found in the blubber of two orcas which were collected after they had died and analyzed by the Cascadia Research Collective (Calambokidis et al. 1984, 1985).

In addition, extensive hydroacoustic (fish-finder) recordings were made in the presence of feeding orcas from 1983 to 1985 (Felleman and Thomas 1985; Felleman 1985a, 1985b) as a non-invasive indication of prey choice. However, only preliminary findings are presented because the complete analysis of these data are still underway.

Previously published work on the Pacific Northwest orca population are used to develop a comprehensive understanding of orca feeding ecology. The baseline photo-identification and stomach content data provided by Dr. Bigg and his collegues at the Pacific Biological Station in Nanaimo, British Columbia as well as by Ken Balcomb and his associates at the Whale Museum (MCS), with whom I have worked since 1980 in Friday Harbor, Washington, have made this detailed study possible. The behavioral categories used in this study were derived from Osborne (1986) of the Whale Museum (MCS).

A comparison with terrestrial social predators is presented, suggesting similar selective pressures have favored variations in group sizes observed in these species. The possibile influences of competition among the orca communities is addressed. Finally, some considerations of the impacts on the Washington State fishery are presented.

1.1) REVIEW OF THE LITERATURE ON ORCA PREDATION

Orcas prey on many different species and exhibit varying degrees of cooperative foraging (for reviews: Martinez and Klinghammer 1970; Hoyt 1984). Cooperative foraging in orcas has been described by observations of group movements from synchronous respirations while chasing prey (Ljungblad and Moore 1983) and encirclment of prey (Steltner et al. 1984) to divisions of labor in the attack of prey (Tarpy 1979) and the sharing of prey (Lopez and Lopez 1985). Since Eschricht's (1862) often misquoted account of the remnants of 13 porpoises and 5 seals in the stomach of an orca, as if it had eaten them on one occassion, the name "killer whale" has been firmly established. It seems that one cannot avoid the term "voracious," used to describe the eclectic appetite of orcas, especially when fellow marine mammals are subject to their predation.

Hoyt (1984) has compiled the most current list of known orca prey, which include 24 species of cetaceans, 14 species of pinnipeds, 31 species of fish, 9 species of birds, 2 species of cephalopods, 1 species of turtle and 1 species of otter. The diversity of species on lists like this one has been the primary reason why orcas are currently considered the highest order predator of the sea. In addition, the nature of the wear observed on their 10-13 (mean=11) uniquely interlocking oval teeth on each side of both jaws (Watson 1981) has been suggested to be indicative of "...their ferocious and highly predatory feeding behavior, or the functional modifications of their cranial anatomy which support this behavior (p. 139)" (Caldwell and

Brown 1964).

Another indication of orcas' predatory status is demonstrated by the avoidance responses elicited from the following cetacean species when subjected to underwater recordings of orca vocalizations: beluga whales, Delphinapterus leucas (Fish and Vania 1971); gray whales, Eschrichtius robustus (Cummings and Thompson 1971) and southern right whales (Eubalaena glacialis) (Cummings et al. 1972, in Herman and Tavolga 1980). The most common response in these studies entailed an immediate change in direction of travel away from the sound source. The deceived prey species often stopped vocalizing and made a stealthy departure without splashing. Gray whales were also observed to hide in the kelp and occassionally spy hop similar to observations of gray whales in the presence of orcas (Cummings and Thompson 1971; Baldridge 1972).

It is interesting to note that only mammalian prey have been shown to exhibit avoidance responses to orca vocalizations. Less acoustically acute fish prey such as the Pacific herring (Clupea harengus pallasi), did not exhibit an avoidance response to underwater recordings of orca vocalizations (Schwarz and Greer 1984). Similarly, during preliminary playback experiments with salmonid prey species, including adult coho salmon (Oncorhynchus kisutch), chinook salmon (O. tshawytscha) (Abbott 1970; Felleman and Ferraro unpubl data) and steelhead trout (Salmo gairdneri) (Abbott 1970) the fishes did not exhibit avoidance responses.

Summaries of orca prey from around the world can be misleading when addressing the feeding strategies of any one population. Rather than label orca foraging strategies as "opportunistic" (Martinez and Klinghammer 1970; Defran and Pryor 1980; Dahlheim 1981) because of the diversity of its prey species, I suggest orcas are more accurately characterized as facultative specialists or switching generalists, for reasons I will discuss in section 4.1. Although cooperative foraging techniques has made a wide range of prey available to them, it appears that orcas exhibit specializations in prey choice which may vary with seasonal fluctuations in prey availability. Consequently, it is suggested that the diversity of species in Hoyt's (1984) list of prey species is more a reflection of the global distribution of discrete orca populations, rather than the feeding ecology of a given population.

Seasonal movements of orcas, if not all cetaceans, seem to be responsive to prey distributions (Norris and Dohl, 1980). Orca occurrence has been found to be postively correlated with the presence of herring in the North Atlantic (Jonsgaard and Lyshoel 1970), elephant seal pupping in the southwest Indian Ocean (Condy et al. 1978), sea lion and elephant seal pupping along the Patagonian coast (Lopez and Lopez 1985), adult sea lions and pups along the west coast of North America (Norris and Prescott 1961; Norris and Dohl 1980; B. Mate, personal communication), gray whales with calves along the west coast of North America (Morejohn 1968; Baldridge 1972), minke whales in the Southern Ocean (Mikhalev et al. 1981; Budylenko 1981), and returning adult salmon in Pacific Northwest inland waters (Spong et al. 1970;

Balcomb et al. 1980; Felleman and Heimlich-Boran 1984; Heimlich-Boran 1986b). Although co-occurrence is not proof of predator/prey relationships, it appears that some orca populations do respond to the seasonally predictable movements of preferred prey.

The clearest example of specializations in prey choice among sympatric orca populations is provided by the stomach content analysis from the Soviet catch of 906 orcas during the 1979-80 whaling season in the Antarctic Ocean (Berzin and Vladimirov 1983). The Soviet investigators made several distinctions between populations from their analysis of the contents from 785 orca stomachs. The offshore orca population consisted of groups of 10 to 15 individuals whose stomach contents contained 89.7% marine mammals, 3.2% fishes, and 7.1% squid (Berzin and Vladimirov 1983). In contrast, the inshore population consisted of groups of 150 to 200 individuals whose stomach contents contained 98.5% fishes, 0.4% marine mammals, and 1.1% squid (Berzin and Vladimirov 1983). The individuals in the inshore population were approximately 1 meter smaller than individuals in the offshore population. The Soviet investigators assert that the differences observed in the body and pod size of these groups were caused by specializations in prey choice among populations which led the investigators to propose a new species, <u>Orcinus glacialis</u>, for the inshore group (Berzin and Vladimirov 1983). Similarly, previous Soviet investigators have tentatively proposed another Antarctic orca species, <u>Orcinus nanus</u>, based primarily on apparently discrete population ranges, smaller body sizes, and more corpora in females of the "dwarf" variety (Mikhalev et al. 1981). Berzin and Vladimirov (1983) also found the smaller variety to have a higher incidence of pregnancy than that of the larger variety. Perrin (1982) suggests that these variations are more likely to reflect, at most, a subspecific level of differentiation. Whether or not these groups are different species is unclear, but the distinctions in their prey choice is striking. Clearly, groups of orcas can occur sympatrically and still retain discrete predation strategies.

Prey choice also appears to vary between individuals within an orca population. Orca stomach content data from populations in the eastern north Pacific (Rice 1968), western north Pacific (Nishiwaki and Handa 1958) and northeast Atlantic (Jonsgaard and Lyshoel 1970) indicate that prey choice varies between age and sex classes, with larger individuals eating a greater percentage of marine mammals. Consequently, stomach content data must be sorted by age and sex classes if differences in prey choice within and between populations are to be discerned.

Yablokov et al. (1974) state that, "The size of the food base <u>determines</u> the animal population size, while the distribution of the food <u>determines</u> the animal distribution and migration (p. 319)."(my emphasis). While it is important to recognize the basic influence that prey abundance and distribution has on the movements and distribution of the predator, it is also important to recognize the predator has preferences for specific prey and that social factors govern group cohesion as well. However, the primary focus of this thesis addresses the importance of prey selection, which has been shown to influence patterns of dispersion (Slatkin 1985) and intraspecific variations in the sociality of terrestrial social carnivores (Beckoff et al. 1984).

1.2)NATURAL HISTORY OF *Orcinus orca*

Orcas are odontocete cetaceans commonly placed in the family *Delphinidae*, but appear to be more closely associated with the family *Globicephalidae* (Nishiwaki 1963; Watson 1981) sharing morphological and genetic similarities with *Pseudorca*, *Globicephala*, and *Feresa* (Duffield 1986). The similarities observed in the banded karotypes and morphological features with the previously mentioned species suggest orcas are a relatively modern cetacean form, having evolved in the mid to late Miocene (Slijper 1962; Gaskin 1976; Duffield 1986). However, orcas show a significantly different rate of karotype evolution which is possibly indicative of a unique breeding system (Duffield 1986).

They occur throughout the world's oceans, most commonly within 800 km of the continental coast (Mitchell 1975). The greatest densities of orcas are found in high latitudes, (Leatherwood and Dalheim 1979; Perrin 1982), but group sizes vary within regions of abundance (Berzin and Vladimirov 1983). Group sizes range from lone animals, to groups of about 50 which are thought to be closely related, and temporary aggregations of 100 to 300 (Bigg 1982; Perrin 1982; Matkin and Leatherwood 1986). However, there has not been a systematic survey to estimate their global abundance (Braham and Dahlheim 1981). They appear to be migratory in some areas and resident in other areas (Dahlheim 1981; Bigg 1982) which is most likely in response to the temporal and spatial distribution of prey resources. Repeated observations of resident populations is often a cause for overestimations of their local abundance (Balcomb 1984), but like other predators, their population abundances are well below those of their prey (Gittleman and Harvey 1982).

Orcas are easily recognized by their large size and distinctive black and white markings. The dorsal fin grows to almost 1 meter in females and to almost 2 meters in males (Matkin and Leatherwood 1986)(Plate I). Adult male orcas have been recorded to grow to lengths of 9 meters, and females have been recorded up to 8 meters in length (Matkin and Leatherwood 1986). There appears to be large variations in mean size recorded for individuals in different populations around the world. In the Antarctic, significant size variations were found between populations (Mikhalev et al. 1981; Berzin and Vladimirov 1983). However, results from the Soviet investigators have to be considered preliminary until a more formal presentation of their complete data set is made.

The white markings consist of an eye patch, most of the ventral surface, and a whitish-gray "saddle patch" located behind the dorsal fin. The saddle patch is unique to each individual and, along with the shape of the dorsal fin, has been used extensively for photo-identification (Bigg et al. 1976, 1983). The white markings have also been shown to vary between geographically and socially isolated populations (Yablakov 1966; Evans et al. 1982; Berzin and Vladimirov 1983).

Plate I. **Photograph of L-Pod taken in 1985 by the author.**

Gestation in captivity has varied between 15 and 18 months (Steve Leatherwood personal communication). Newborn orcas average 1.7 meters in length (Bigg and Wolman 1976; Bigg 1982). Sexual maturity has not been precisely documented, but photogrammetric studies of male dorsal fin growth suggests this sexual dimorphism occurs at 12 to 13 years of age (Heimlich-Boran 1986a). Sexual maturity in females is believed to occur at 9-10 years (Bigg 1982). However, social maturity, the age at which sexually mature individuals enter the breeding system, may not occur in either sex until a much later age. This is suggested because similar delays in attaining mates have been shown to occur in other social mammals (Wasser and Barash 1983) and there is an apparent disparity in the number of females which produce most of the calves in a pod.

The life span of the orca is unknown, but estimates based upon death rates in the British Columbia population suggest that longevity is 55 years in males and 75 years in females (Bigg 1984). A minimum calving interval of 3 years has been found in the Washington and British Columbia populations (Balcomb et al. 1982; Bigg 1982), but since only a few females produce the majority of the calves in these populations, the average calving interval is closer to 8 years (Bigg, 1982).

From the measurement of 13 cranial volumes, the average weight of an orca brain is estimated to be 7,064 grams (Osborne and Sundsten 1981). The calculation of the encephalization quotient (EQ) (Jerrison 1981) indicates that for its body size, the orca brain is about 2.3 times larger than the average mammal's and is the largest of the cetaceans (Osborne and Sundsten 1981). Similar comparisons between varyingly social canids and felids suggests that brain size, behavioral flexibilty, and vocal diversity increases with the degree of sociality (Kleiman and Eisenberg 1973).

Like other odontocetes, orcas are highly vocal and are known to echolocate which may serve an important role in their feeding ecology (Norris and Mohl 1983). Ford and Fisher (1982) provide a concise review of the characteristics of orca vocalizations, which they state can be divided into three categories: 1)Clicks - are believed to function as echolocation signals. They are very short (0.8 to 25.0 ms) pulsed sounds containing energy over a wide bandwidth. Click trains have been recorded with repetition rates from 1 to 300 clicks per second with frequencies up to 35 Khz (Ford and Fisher 1982). However, Schevill and Watkins (1966) state that the fundemental frequencies of a click train are between 350 and 500 Hz. 2)Whistles - are characterized by continuous, non-pulsed, narrow band waveforms. Whistles are commonly emitted between 6 Khz and 12 Khz, but range from 1.5 Khz to 18 Khz. Their durations vary from 50 ms to 12 seconds (Ford and Fisher 1982). 3)Screams - are considered the most characteristic orca vocalization. They are characterized by rapid pulsed signals of up to 25 Khz in frequency and repetition rates of up to 5000 per second. Durations of most screams occur between 0.5 and 1.5 seconds, but vary from 50 msec to over 10 seconds in length (Ford and Fisher 1982).

1.3) PACIFIC NORTHWEST ORCA POPULATION

The orcas of Washington and British Columbia live in stable family units called "pods" (Bigg et al. 1976; Bigg 1982). From extensive photographic documentation of pod associations during the spring to fall over the last decade, it appears that a pod is an extended matrifocal family unit composed of mothers and their offspring. The adult bulls of the pod are thought to be sons of the matriarchs (Heimlich 1981; Bigg 1984; Heimlich-Boran 1986). It is generally believed that in most cases both sexes spend their entire life spans in their maternal subgroups, remaining within their natal pods (Bigg 1982, 1984; Heimlich-Boran 1986). This proposed social organization is similar to the "familial route" to eusociality which Vehrencamp (1980) states is common in carnivores, but most pronounced in canids which retain their offspring in the group past sexual maturity. The term eusociality is used to describe a system in which the reproductive effort of the offspring is directed into helping their parents produce siblings rather than into the production of their own offspring. However, this is just speculative until genetic evidence is provided to define the breeding system. In addition, it is not known if this proposed social structure is exhibited by resident pods through the winter, by the sporadically occurring transient pods in Washington and British Columbia, or by orca pods in other parts of the world.

The population in Washington and British Columbia waters has been subdivided into three distinct pod communities: northern resident (N = 155, 16 pods), southern resident (N = 77, 3-4 pods), and transient (N =

48, 17 pods); total: 280 orcas in 36 pods (Bigg 1984; Bigg, personal communication). Each pod community has distinct call dialects (Ford and Fisher 1982, 1983), different degrees of social interactions between pods (Osborn et al. 1985; Jacobson 1986), varying feeding strategies, Felleman and Thomas 1985; Felleman 1985b; Bigg et al. 1985; Felleman and Osborne 1986) and varying pod sizes (Bigg 1982). The transient community travels throughout the range of both resident communities (Bigg 1982) and at least one pod has been observed in southeast Alaska (Leatherwood et al. 1984). The two resident communities have non-overlapping ranges (Bigg et al. 1976) corresponding to the tidal boundary in the northern Strait of Georgia (Tully and Dodimead 1957; Felleman and Heimlich-Boran 1984; Felleman 1985b) (Figure 1).

On only one occasion, in ten years of observation, were orcas from the southern resident community observed to leave their pod. This occurred when a subgroup of five whales from L pod immigrated to K pod (Osborne et al. 1984). However, there appears to be more mixing between pods in the northern resident community than in the southern resident community. The degree of interchange between pods is likely to be influenced by the proximty of pods to each other which is much greater in the northern resident population than in the southern resident population.

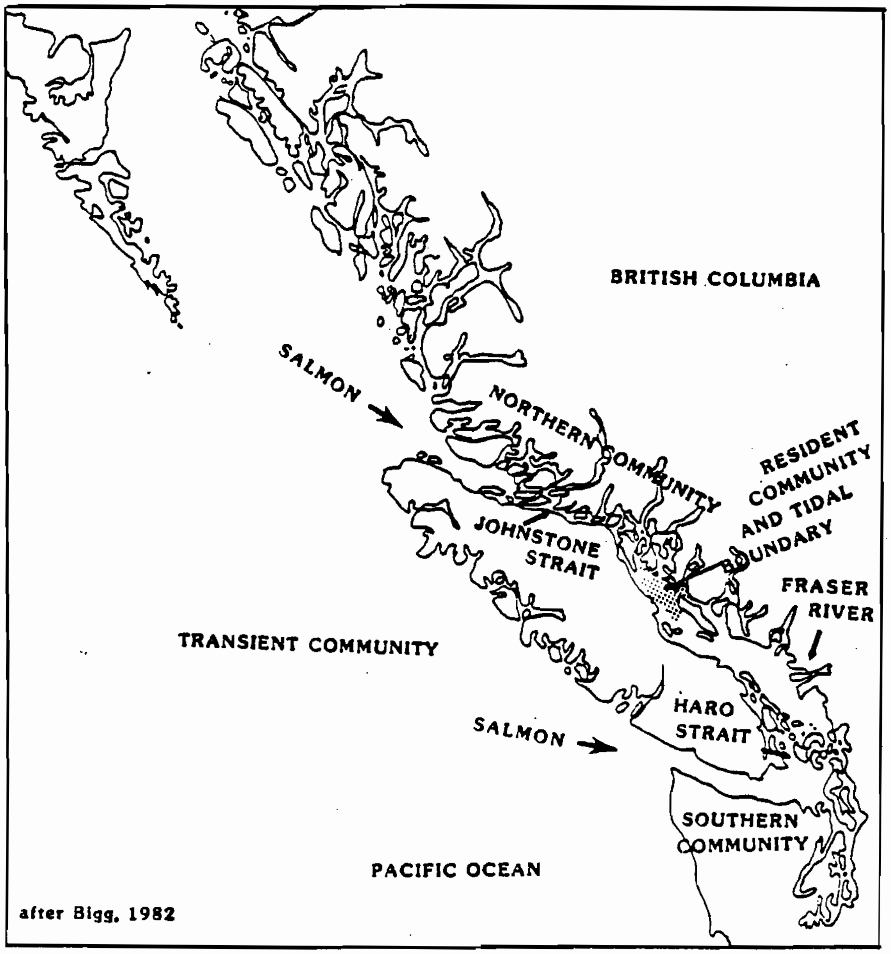


Figure 1. Home Range of Pacific Northwest Orca Communities

Pods from one community have never been seen to interact with pods from the other communities (Bigg 1982, 1984). Preliminary genetic analyses of chromosomal differences between communities (Duffield 1986) suggest that each community is reproductively isolated. Phenotypic distinctions are also apparent between pod communities. Transient orca dorsal fins are less curved and are more sharply pointed than resident orca dorsal fins (Bigg 1984). In addition, transient orca saddle patches are characteristically wider and completely white, as compared to resident orca saddles which often have black openings in their saddles (Bigg 1984). However, "open" saddles are more prevalent in the southern than in the northern resident community. From the few observations of copulation in these pods that have been documented, it appears that breeding may occur between individuals from different pods, but only within the same pod community (Bigg 1984; Osborne et al. 1985). Since observations of copulation do not necessarily imply reproductive success, the nature of the breeding system cannot be adequately addressed without genetic analysis. All the pods in the southern resident community exhibit female-biased sex ratios, whereas the northern resident and transient pods exhibit both male-biased and female-biased sex ratios (Bigg 1982).

Although orcas do not commonly strand themselves, there are several early accounts of whole pods stranding in the study area (Carl 1945; Pike and MacAskie 1969). Klinowska (1985) states that live strandings are exclusively mistakes caused by magnetic anomolies which confuse cetaceans using geomagnetic topography for navigation. However, the cooperative social organization of a pod may facilitate group strandings when only one or a few individuals are disoriented or in distress.

In 1968 Rice observed, "In Puget Sound, where the killer whale population is probably denser than anywhere else in the world, the marine mammal population... does not appear large enough to provide a major proportion of the killer whale diet. It is widely believed that runs of spawning salmon (Oncorhynchus sp.) are a major food there during the summer, but no data are available to support this assumption" (p. 38). Since Rice (1968) there have been numerous photographic (Jewell 1965; Balcomb et al. 1980) and written accounts (Spong et al. 1970, 1971, 1972; Balcomb et al. 1980; Felleman and Heimlich-Boran 1984; Heimlich-Boran 1986) of orca predation on salmon in this region. However, after more than a decade of field research, the question of what prey resources orcas are exploiting has become more complex because of the recognition of differences in the feeding strategies, both within and between pod communities (Osborne et al. 1985; Felleman 1985b; Bigg et al. 1985; Felleman and Osborne 1986).

I suggest that the resident communities are more similar to each other in their behavior and ecology than they are to the transient community due to similarities in their prey choice. During the spring to fall, large resident pods scan vast amounts of water in response to temporal cues of season and tide, which are indicative of salmon predation and limit their range to areas where these and other fishes can be found consistently. In contrast, small transient pods travel great distances, sporadically occurring through the ranges of both resident communities. Transient pod movements within the inshore waters appear to reflect the movements and distribution of harbor seals and bottom fish rather than salmon. These prey are mostly resident to the inshore waters and site tenacious, enabling small transient pods to use the spatial predictability of their prey to direct their search. In this thesis a series of comparisons are made to distinguish the variations in prey choice exhibited between transient and resident pods which occur sympatrically but do not interact with each other.

2.0) METHODS

A fisheries-oceanographic approach is employed to determine how orcas temporally and spatially utilize their habitat. Owen (1981) has shown that fronts and eddies in the open ocean can cause patterned patches of organisms that predators are able to exploit. Japanese whaling fleets have shown how this kind of information can be successfully used to exploit cetaceans commercially (Uda and Nasu 1956; Uda and Suzuki 1958; Nasu 1966). However, more recently, this type of oceanographic information has been incorporated into field studies of cetacean ecology (Evans 1971; Gaskin 1976; Saayman and Tayler 1979; Norris and Dohl 1980; Wursig and Wursig 1980; Shane 1980; Felleman and Heimlich-Boran 1984; Felleman 1985b; Felleman and Thomas 1985). These studies have shown that in order to understand why cetaceans occur in some areas more than others, one must first account for the response of the prey to localized oceanographic conditions and habitat features.

In addition, a comparative approach to the study of the ecological determinants of group sizes in terrestrial social predators is applied to the analysis of the various orca group sizes observed worldwide.

2.1) ANALYTICAL METHODS

The primary focus of my field work addressed the feeding behavior of Greater Puget Sound orcas by observing their behavior concurrent with their orientation to the tidal current. Every fifteen minutes I would note if they were moving with, against or non-oriented to the current and if their direction changes were independent of tidal changes. A half hour on either side of the slack current prediction listed in the tidal current tables was used as the time of minimal current, during which time all behavior would be termed non-oriented. Consequently, a direction change would have to occur just prior to, during, or just after the hour slack interval for it to be considered associated with the change in the tidal current.

The direction of the tidal current was extracted from the tidal current tables of the Pacific Coast of North America and Asia for the study on the southern resident and transient communities. The Canadian tide and current tables were used for the study on the northern resident community rather than the U.S. tables because of the greater accuracy associated with the primary stations maintained in Canadian waters. In addition, several publications were particularly useful for extrapolating the phase differences between the tide stations and the locations of the whales: Mofjeld and Larsen (1984), Crean (1983), and Thomson (1981).

A summary of observational data used in this analysis is presented in Table 1. Data collected primarily during the spring to fall by the staff of the Whale Museum (MCS) comprising 688 hours of observation on southern resident pods from 1976 to 1979 were analyzed retrospectively in relation to tidal data and used to generate the hypothesis tested in this study. The MCS data were collected with a continuous sampling technique which precludes the use of discrete statistics (Altmann 1974) unless the data is transformed into equal sized units.

During the spring to fall from 1983 to 1985 I collected 242 hours of observation on the southern resident community by means of a scan sampling technique (Altmann 1974) in which the movements and behaviors of the whole pod or pod subgroup relative to their orientation to the tidal current were recorded every fifteen minutes. These data can be analyzed with discrete statistics because scan sampling provides equal-sized samples and autocorrelation analysis reveals that each scan can be treated as an independent sample (Box and Jenkins 1976)(Appendix A1-A3). A Pearson's Chi square with Cochran's correction for continuity (Zar 1984) has been applied to the 2 by 2 contingency tables in order to test the null hypothesis on the independence of changes in the orcas' direction of travel from changes in the tidal current.

The transient pod data set was composed of both continuous and scan samples due to the collaboration between the Whale Museum and the author. In order to make the transient data set comparable with the resident data set, the transient data set from 1976 to 1982 was divided into fifteen-minute units, enabling me to combine my observations with those made by the staff of the Whale Museum (MCS). These combined observations of transient pods in the Greater Puget Sound total 44.5 hours. Although the limited amount of observations with transient pods suggets that these data be treated as preliminary, additional support is drawn from other observations (Erickson 1976; Bigg 1982) which reveal similar consistencies in the movement and behavior of transient pods that clearly distinguishes them from resident pods.

In addition, I collected 38.5 hours of fifteen minute scan-sample observations in July of 1985 during a pilot study on the northern resident community. This study was conducted to test if the northern resident community utilized the tidal current similar to the southern resident community. The way in which pods orient to the tidal current are are used to compare their foraging strategies. Although I only collected a limited amount of observations on the northern resident pods, the findings from this study were in agreement with previous authors, which implies that these data may be treated with more confidence than the sample size suggests. The combined data collected by the staff of the Whale Museum (MCS) and myself totals 1013 hours of observation, of which 45.6% involved feeding related behaviors, making this one of the largest analysis of data collected on known individuals from a free-ranging cetacean population (Table 1).

Table 1. Observational Data Base

Pod Community	Years Observed	Minimum Obs. Hrs.	Maximum Obs. Hrs.	Mean Obs. Hrs.	Ttal Obs. Hrs.
Southern Resident	1976-79	0.1	37.5	3.7	688
Southern Resident	1983-85	0.25	13.5	2.5	242
Northern Resident	1985	2.5	10.0	5.5	38.5
Transient	1976-85	0.5	6.3	2.5	44.5
				Total Obs. Hrs. =	1013

2.2) SURVEILLANCE METHODS

The Whale Museum (MCS) has maintained a toll-free 24-hour telephone reporting system which has been advertised and used year-round since April 1976 to receive sighting reports of whales from the public. These reports were very useful for determining the range of the whales especially in regions peripheral to the study area. The sightings were also used to locate whales for vessel encounters, and served to compensate partially for the seasonal bias in field observations.

Behavioral and photographic data were collected either from shore observation points or from research vessels in proximity of the whales. Shore based observations were conducted from houses which I rented on the west side of San Juan Island and from the Whale Museum's research lab at Limekiln lighthouse. Both these locations afforded me a view of Haro Strait, the primary route of the southern resident pods through the study area. Vessel observations made during the 1983 summer season were conducted from a 17-foot Boston Whaler on loan from the National Marine Mammal Laboratory in Seattle, Washington. The Cooperative Fishery Research Unit at the University of Washington provided me with a 17-foot Boston whaler during the 1984 and 1985 field seasons. Both boats were equipped with hydroacoustic gear (fish-finder) enabling the density and depth distributions of fish to be determined. Details of the hydroacoustic sampling design and analysis techniques will be presented after further data analysis has been conducted. On occasion, sailing vessels of various types, associated with the Whale Museum (MCS), were employed for extended evening observations. Vessel encounters in U.S. waters were conducted in accordance with Permit No. 454 under the Marine Mammal Protection Act and Endangered Species Act, issued to the Whale Museum, Moclips Cetological Society.

I recorded behavioral observations in code directly on data sheets while in the field. The behavioral coding system included surface activity descriptions of group speed, direction, and orientation to the tidal current, individual space, age, and sex composition, and noted overt behaviors such as breech, spyhop, prey in mouth, etc. Behavior categories were taken from operational definitions derived from Osborne (1986). The description of these categories are reviewed in section 3.2.1.

In addition to the ecological focus of this study, significant contributions to the photo-identification of these orcas were submitted to the Whale Museum (MCS) and Dr. Bigg at the Pacific Biological Station in Nanaimo, B.C., in collaboration with all orca researchers in the Pacific Northwest. With this cooperation, Dr. Bigg has been able to assess the status of this population over many years and has generously shared his results and insights with the investigators. Close-up identification photographs of individuals were taken using 35mm cameras with 200-300mm lens and high-speed black and white film. Readily identifiable individuals were noted directly on data sheets.

Various configurations of fixed hydrophone arrays were installed and sometimes monitored on a 24-hour basis at either the Orca Survey Research Facility or the Whale Research Lab on San Juan Island. Portable hydrophones were also deployed from research vessels.

Acoustic monitoring served as an audible surveillance to within approximately 8 km of the source. These data provided an indication of the orcas' presence and direction of travel, which were used to direct my search effort. Although I have made only a limited number of recordings, a review of the acoustical research of Ford and Fisher (1982, 1983), Osborne (1986), and Hoezel and Osborne (1986) is summarized to provide a broader understanding of the variety of influences prey choice may have on the life history characteristics of this species.

2.3) DESCRIPTION OF THE PACIFIC NORTHWEST HABITAT

The primary study area of the southern resident community referred to as "Greater Puget Sound" lies between 47° and 49° north latitude and 122° and 124° west longitude. This region includes the glacially carved estuarine waters of Puget Sound proper, waters east of Whidbey Island, Hood Canal, the Strait of Juan de Fuca, the San Juan Archipelago and southern Strait of Georgia (Figure 1). Since no observations were made in Puget Sound proper during 1983 to 1985, only the description of the northern straits will be presented. The core area of the northern resident community is centered in Johnstone Strait, which lies approximately at 50° 30' north latitude and between 126° 55' and 126° 20' west longitude.

The Strait of Georgia is the widest of the inland seas. It is 140 nm long and 10-30 nm wide. Average depth is 100-200 meters, with a maximum of 400 meters (Tully and Dodimead 1957). The southern strait has moderate to fast currents (average 50 cm/sec) driven primarily from the Fraser River, which contributes 75% of the fresh water. Maximum freshwater output from the Fraser River occurs from June to July (11,000 m^3/sec) (Tully and Dodimead 1957). Salinity and temperature vary predictably with proximity to the Fraser River, but also show significant variations over tidal cycle between stations located away from the direct influence of the Fraser River plume (Tully and Dodimead 1957).

The most frequent path of the southern resident pods extends from Haro Strait to Boundary Pass which is 30 nm long, 2.5 to 5.0 nm wide, with an average depth of 200-300 meters. The narrow straits characterizing the study area transform the rise and fall of the tide into current vectors. The velocity is limited by the channel morphology but is also influenced by wind and river water input. The tides are mostly the mixed semidiurnal type with two high and low tides of unequal magnitude. Maximum flood and ebb precede high and low water by approximately 3 hours. (Thomson 1981). The NOAA current predictions were quite accurate for describing the mid-strait flow of this relatively wide and regularly contoured strait. However, coastal back-eddies and climatic influences occassionally required insitu corrections of slack predictions. Currents reach up to 250 cm/sec. The ebb is stronger on the east side of the strait, while the flood is stronger on the west side (Figure 2 from Crean 1983).

Reverse!
- SV

Rosario Strait is 3-6 nm wide, with an average depth of 60 meters. Rosario Strait carries only one-third the volume of water that leaves the Strait of Georgia via Haro Strait (Thomson 1981).

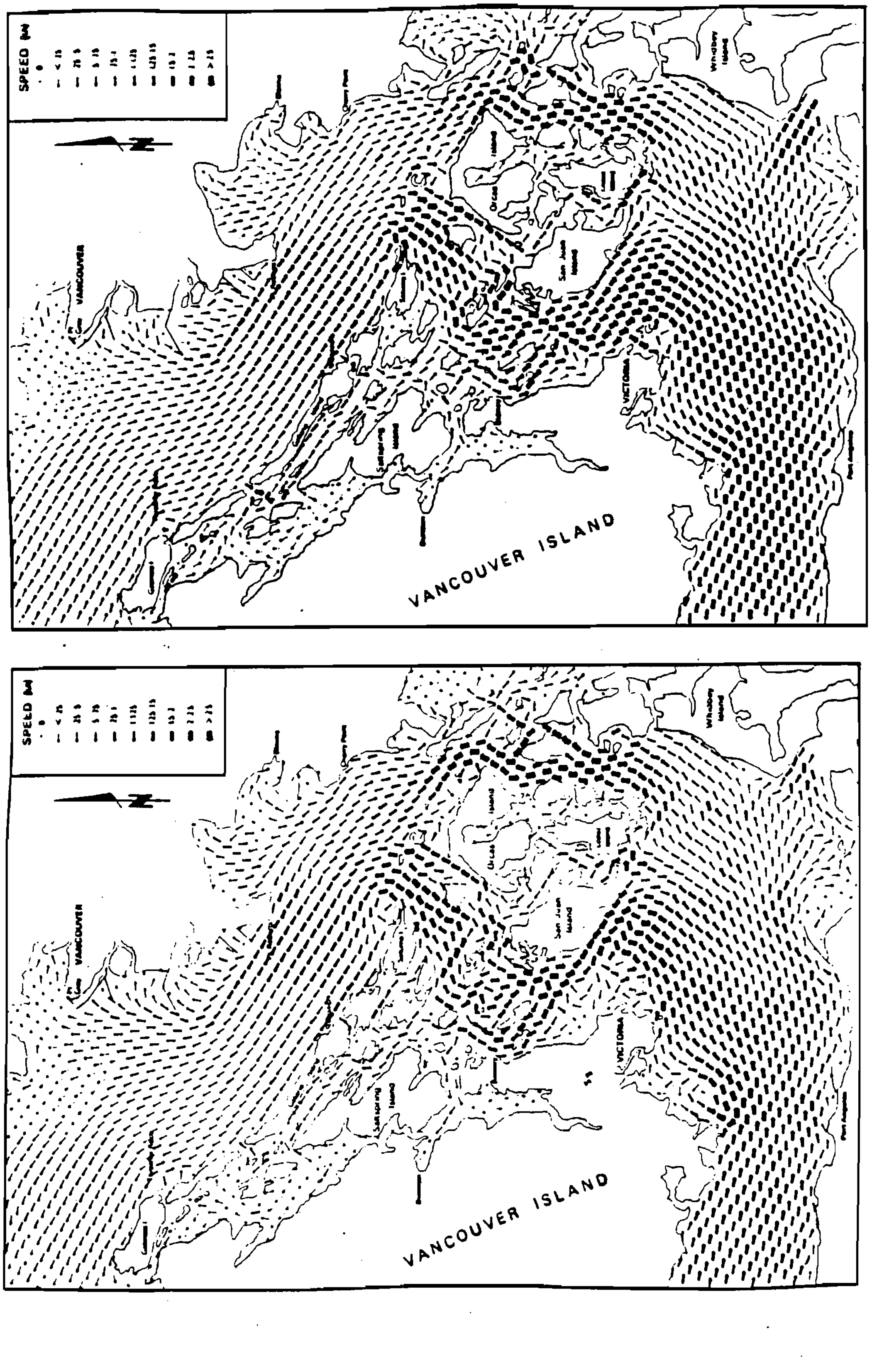


Figure 2. Ebb and Flood Tidal Current Velocities.

San Juan Channel is 30 nm long, 2-3 nm wide, and an average of 60 meters deep. A major constriction in San Juan Channel occurs at Cattle Pass and results in high-velocity currents, but little volume passes through this strait due to frictional forces (Thomson 1981).

The Strait of Juan de Fuca is 75 nm long, 11 nm wide, and 200 meters deep at the Pacific boundary, shoaling to less than 60 meters at the eastern inland end. Of all the salt water entering the inland waters through the Strait of Juan de Fuca, it is estimated that 50% goes through Haro Strait, 20% goes through Rosario Strait, 5% goes through San Juan Channel, and 25% goes into Puget Sound (Thomson 1981).

Johnstone Strait is one of the narrowest major channels that make up the inside passage of British Columbia, varying in width from 1.9 to 2.4 nm (Thomson 1981). It is one of the deepest basins, increasing from 70 m to the east to 300 m at its western extent (Thomson 1981). As with the other straits described, Johnstone Strait exhibits estuarine circulation in which the primary surface flow is towards the sea, while the current at depth moves inland, but reverses with the tide (Thomson 1981). At the surface, the ebb current is stronger than the flood current and the maximum currents vary predictably over the 15-day tidal cycle (Thomson 1981). Maximum dominant ebb currents reach 75 cm/s, whereas maximum flood currents are less than 50 cm/sec (Thomson 1981).

2.4) CHARACTERIZATION OF ORCA PREY

My analysis of the potential prey species orcas may select in Greater Puget Sound and British Columbia are reviewed based on the those qualities of the prey which are considered most important to a predator. The spatial predictability (eg. preferred habitats) and temporal predictability (eg. migrations, tidally dependent movements) of the prey are expected to affect the types of search techniques needed to detect the prey. The overall size of the prey assemblage (eg. fish school, lone baleen whale) is also suggested to affect the orcas' likelihood of encountering these prey in a patchy environment. The relative size of the prey and their defensive responses to predation are also likely to affect the degree of cooperatation needed to capture them. The characterization of orca prey in the Pacific Northwest is described in section 3.1.

Based on my observations of orca predation in the Pacific Northwest (reviewed in sections 3.2-3.5), I suggest that the ecological characteristics of the prey orcas select influence the group sizes and foraging strategies orcas exhibit worldwide. In section 3.7 I review some of the similarities between reports in the literature of orca predation on various prey species and suggest that there are characteristics of prey which exert similar selective pressures on orca foraging strategies. There are also some obvious distinctions between observations of foraging strategies which appear to reflect specializations to a particular habitat or prey type. By attempting to characterize the salient ecological qualities of orca prey, I hope to provide some insight into of the ecological determinants of orca group sizes. Similar analyses have been conducted with terrestrial social predators, for they are known to exhibit a high degree of specificity in prey choice (Beckoff et al. 1984). The type of prey selected has been shown to influence group sizes in wild dogs (Estes and Goddard 1967), wolves (Mech 1970) and lions (Schaller 1972; Caraco and Wolf 1975). Comparisons with these species are made because it is suggested that orca group sizes are subject to similar selective pressures. The ability of a group of predators to capture prey larger than can be caught by a single predator is the most commonly cited benefit of group living in social carnivores (for a review of the literature see: Kleiman and Eisenberg 1973; Gittleman and Harvey 1982; Beckoff et al. 1984). For example, wolves which hunt rabbits travel in smaller groups than wolves which hunt moose (Mech 1970).

In order to see if a similar relationship is apparent from observations of orca and their prey, I have made a simplified analysis of the relationship between pod size and prey size based on comparisons of my observations of orca predation in the Pacific Northwest with descriptions of orca predation from the literature.

3.0) RESULTS

3.1) ORCA PREY IN THE PACIFIC NORTHWEST

Orcas in the Pacific Northwest can be expected to have a high degree of familiarity with the distribution of their preferred prey since they have been historic residents of the region (Scammons 1874; Scheffer and Slipp 1948) and known individuals have been observed utilizing the same parts of the habitat for at least 14 years (Spong et al. 1970; Bigg 1984). The degree to which prey are spatially and temporally predictable are probably the two most important variables affecting their availability to orcas. The following description of the distribution of potential orca prey is not to be considered absolute, but rather a means of making some generalizations about the influence different prey taxa may have on orca feeding ecology.

3.1.1) Fishes as Prey

Fish species that are both solitary and sedentary are also often site tenacious, making them easily localized and non-migratory. However, they can be quickly depleted if consumed in large quantities at a specific site. Potential orca prey species exhibiting these qualities include some members of the rockfish (Sebastodes sp.), lingcod (Ophiodon sp.), cabezon (Scorpaenichthys sp.), and to a lesser extent various other bottom fish such as flatfish, ratfish and rays (Hart 1973). In addition, the confined rocky habitat associated with some sedentary bottom fish may enable even solitary orcas to herd them against the substrate.

In contrast to solitary and sedentary fishes there are schooling and migratory species. Schooling fishes are less predictably localized and may require a greater search effort, but may occur in large, quickly replenished patches. The seasonal occurrence, tidal movements, and preferred habitats of migratory species provide a resource which is predictably available in time and temporally aggregated at specific locations. Potential prey exhibiting these characteristics include five species of salmon and potentially: herring, anchovy, candlefish, smelt, pollack, hake, halibut, dogfish and some rockfish species (Hart 1973).

The distribution of a loosely schooling, migratory fish, such as salmon, is influenced strongly by the seasonal run timing and tidally-dependent homing behavior of returning adults. There are distinct peaks in the run timing of salmon through the study area, providing a temporally predictable, but fluctuating prey resource from June through September (Figure 3). During the winter months steelhead and cutthrout trout are available along with resident coho and chinook salmon (Hart 1973; Mathews and Bergman 1970). The precision of their migratory behavior is demonstrated by the distinct genetic differences that can be observed among stocks in neighboring streams (Hasler 1960).

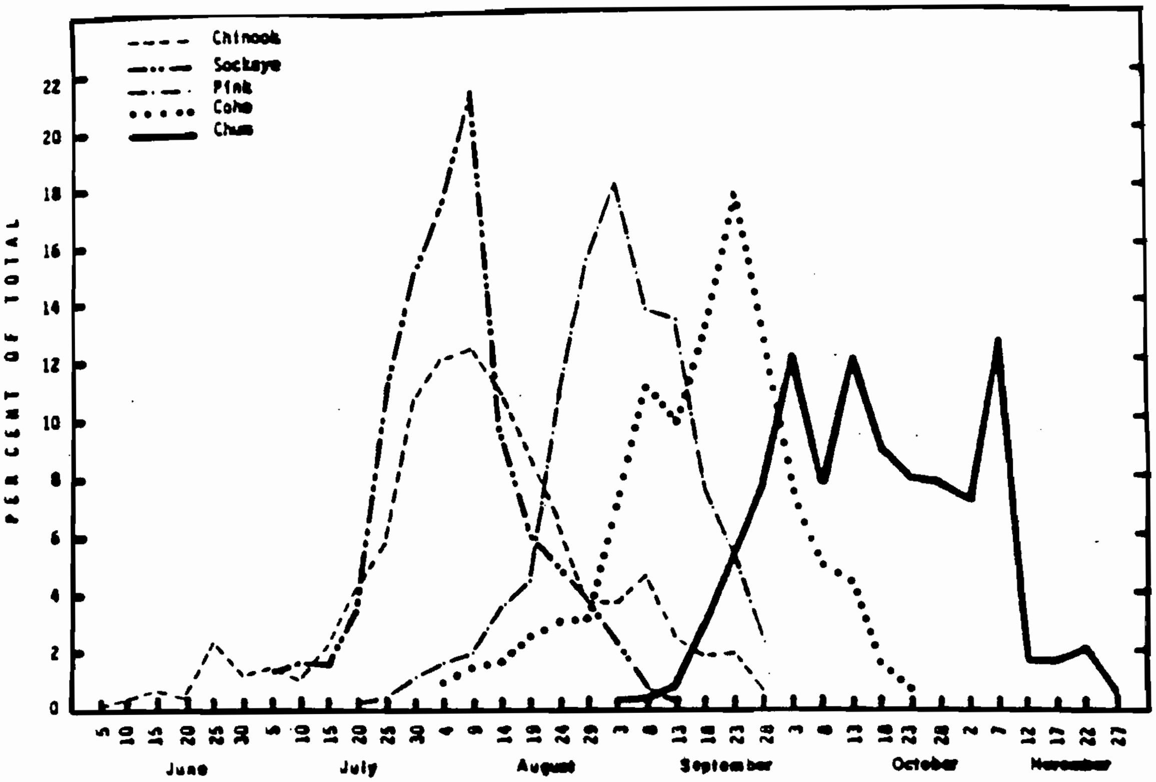


Figure 3. Salmon Run Timing - San Juan Islands (Jewell et al. 1971)

The progression of salmon through an estuarine system is influenced by the velocity of the tidal current, as demonstrated by commercial fishing techniques and results from sonic tagging studies (Stasko et al. 1973, 1976). Sonically tagged Fraser river pink salmon (<u>O. gorbuscha</u>) and sockeye salmon (<u>O. nerka</u>) progress through the southern community's range by traveling away from the shore and following the axes of the tidal currents (Stasko et al. 1973, 1976). A salmon's ability to progress north to the Fraser River is limited by the current since the ebb currents in Haro Strait can exceed 2.5 knots (Figure 2) and the average swimming speed of sonically tagged salmon was approximately 1.2 knots (2.2 km/hr)(Stasko et al. 1973,1976). Sonically tagged salmon progressed north during the flood currents, but only those fish that were able to withstand the ebb current were termed "active" (Stasko et al. 1973, 1976). In addition, sonically tagged salmon were observed to mill at slack currents or where two currents met, which suggests that they rely on currents to impart directional information (Stasko et al. 1973, 1976). Preliminary results from tracking salmon equipped with a depth sensor through Johnstone Strait, suggest that they travel in the upper 3-15 m of the water column at a speed of 1.1 knots (2 km/hr)(Quinn pers comm.)

Observations of commercial salmon seiners appear to support the results of the tagging studies. I have made extensive observations of salmon seiners while monitoring the currents in Haro Strait and have spoken with numerous fishermen to confirm my observations. The most profitable sets are made at slack low, with the opening of the seine pointing to the south. The seines are pursed after the flood current has begun to flow. The flood current brings salmon from the Strait of Juan de Fuca in high densities to the shoreline of San Juan Island (Figure 2) which is where most of the fishing effort is directed. The seiners move back and forth along the west side of San Juan Island following the leading edge of the currents. The convergence of the flood and ebb currents appear as distinct fronts (tide lines) on the surface.

A proximate cue suggested to be of primary importance for salmon homing in the estuarine waters is the olfactory detection of fresh water emanating from their natal stream. The migratory movements of fishes depending on olfactory cues have been modeled by Dodson and Dohse (1984) based on findings by Hasler and Wisby (1951). This freshwater signal oscillates predictably with the tidal current in this region (Thompson and Miller 1928; Tully and Dodimead 1957) (Figure 4). Creutzberg (1959) has shown that migratory elvers (*Anguilla vulgaris*) can distinguish between the flood and ebb based on the olfactory detection of fresh water. The potential of salmon utilizing a similar strategy is feasible because of the presence of a sufficient olfactory signal (Figure 4.). A salmon's ultimate goal is to arrive at its natal stream and to spawn at such a time as to maximize the likelihood of its reproductive success (Miller and Brannon 1981). Consequently, salmon are a temporally predictable prey for orcas.

The Fraser River contributes 75 per cent of the fresh water in the Strait of Georgia (Thomson 1981). The majority of salmon on both sides of Vancouver Island are destined for the Fraser River (Aro and Shepard 1967), and are therefore available to both resident communities (Fig. 1). All five species of Pacific salmon return to the Fraser River, but most of the runs are composed of sockeye salmon (*Oncorhynchus nerka*) and pink salmon (*O. gorbuscha*). The latter are the most abundant, but return only on odd-numbered years (Neave 1966).

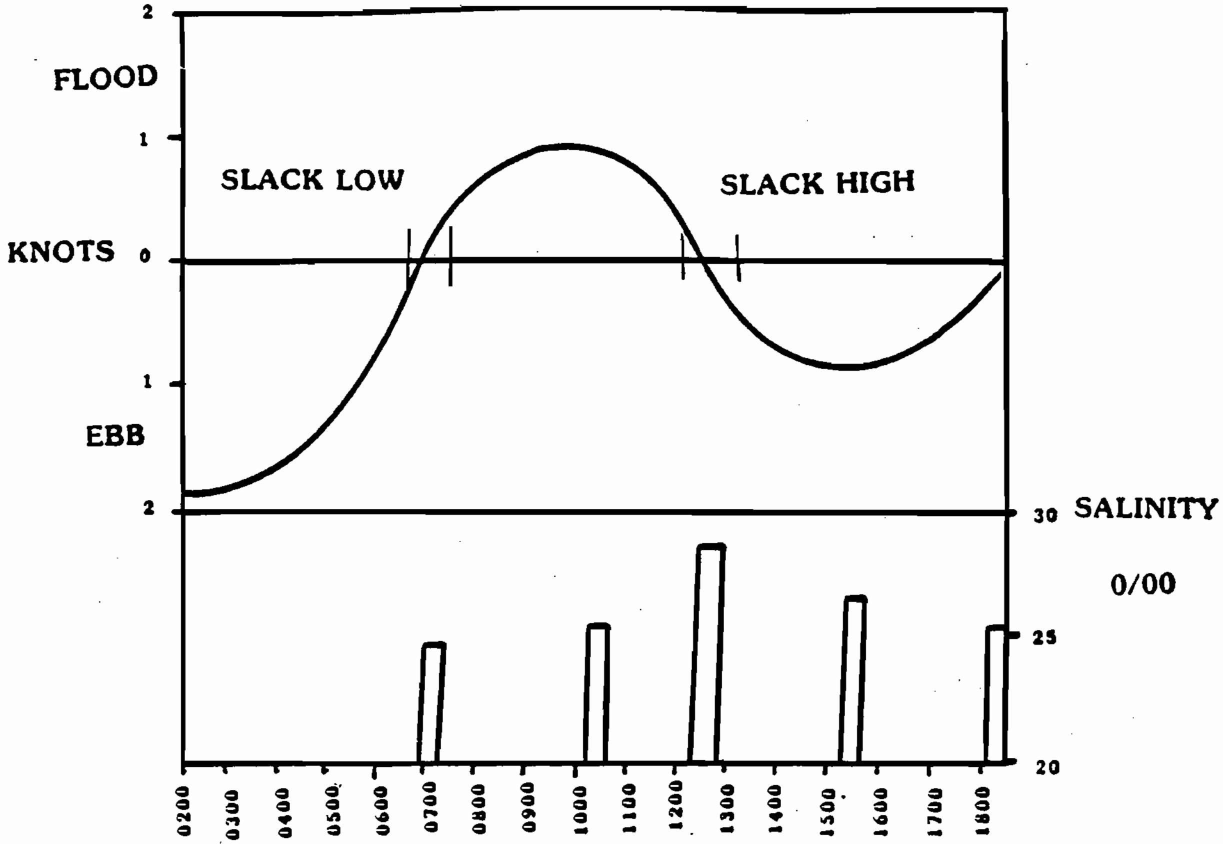


Figure 4. **Salinity Variations with Tidal Currents in Haro Strait** There is 3 ppt more fresh surface water at slack low than at slack high. Salinity data from Crean and Ages (1971).

Groot and Quinn's (1986) review of International Pacific Salmon Fishery Commission (IPSFC) data reveals that since 1978, 22% to 85% (average 53%) of Fraser River sockeye have returned along Johnstone Strait. In previous years 80% have on average migrated along the Strait of Juan de Fuca. Groot and Quinn (1986) have shown that the specific route of travel around Vancouver Island used by migrating salmon is responsive to the direction of Fraser River discharge. These findings are in agreement with previous research by Favorite (1961) and Wickett (1977), who have shown that the direction in which freshwater plumes extend into the Pacific Ocean affects the route by which Fraser River sockeye salmon return along Vancouver Island. Many environmental factors are associated with river runoff, leaving the precise mechanisms of homing unresolved. However, the hypothesis that salmon use olfactory cues originating from their natal stream for homing as stated by Hasler and Wisby (1951) still remains to be disproven.

3.1.2) **Marine Mammals as Prey**

Marine mammal prey can also be characterized in terms of the predictability of their spatial and temporal distribution. Harbor seals (*Phoca vitulina*), like some species of bottomfish, are both resident to the inshore waters and site tenacious to their haul out rocks. Their site tenacity makes them a spatially predictable resource, but also causes them to be vulnerable to localized extinctions if subject to extensive predation pressure.

All other potential pinniped prey species in the Pacific Northwest occur seasonally (Everitt et al. 1979). Seasonally occurring pinnipeds include elephant seals (*Mirounga angustirostris*), California sea lions (*Zalophus californianus*), and Steller's sea lions (*Eumetopias jubatus*). Elephant seals are a encountered opportunistically because they only occur singly in open water and never haul out on rocks when they temporarily inhabit local waters during the spring and fall (Angell and Balcomb 1982). The two seasonal sea lion species are encountered considerably less opportunistically. They occur singly and in small foraging groups in open water, but are also known to haul out in late fall to spring at Race Rocks, located along the southeast corner of Vancouver Island as well as various other places throughout the study area (Spalding 1964; Everitt et al. 1979). They have also been observed with increasing frequency in Puget Sound (Calambokidis et al. 1984, 1985). Sea lion haul-out areas in this region are not used for breeding or mating and often contain both species together (Everitt et al. 1979). However, most of the sea lions observed in the study area are *Z. californianus*. During the summer months it has been estimated that 70% of the Steller's sea lion population is concentrated on two rookeries at Cape St. James and the Scott Islands off the northwest end of Vancouver Island (Spalding 1964). Steller's sea lions come inshore in late fall till spring and are known to haul out on Race Rocks, Sombrio Point, and Sucia Island (Angell and Balcomb 1982) and have been observed in Puget Sound.

Most cetaceans show some consistency in using tidal fronts and seamounts as feeding areas (Gaskin 1976; Evans 1971). Norris (1967), first suggested that most marine mammals could detect accumulations of prey by passive listening techniques. Evans (1971) demonstrated with radio telemetry that the movements of the common dolphin (*Delphinus delphus*) were nonrandomly directed towards deep water escarpments and seamounts, where prey are known to aggregate.

The most common potential cetacean prey include the two porpoise species which are primarlly resident to the inshore waters. The Dall's porpoise (*Phocoenoides dalli*), occurs in small groups of 3 to 10 individuals along the more open water areas which include Juan de Fuca Strait, Haro Strait, Rosario Strait and Johnstone Strait (Angell and Balcomb 1982; Pike and MacAskie 1969). The harbor porpoise (*Phocoena phocoena*), once the most abundant cetacean in Puget Sound (Scheffer and Slipp 1948), appears to have diminshed in numbers due in part to increased human interaction. They are found in small groups, nearshore, and are quite skittish near boats as compared to the robust bow-riding behavior of the Dall's porpoise which appears to be flourishing throughout the region. The two baleen whales, minke whales (*Balaenoptera acutorostrata*) and gray whales (*Eschrichtius robustus*) both exhibit predictable migratory movements into the study area (Dorsey 1983; Everitt et al. 1979). Like all marine mammals, they are acoustically sensitive and are likely to show avoidance responses to orca vocalizations which has been documented with gray whales (Cummings and Thompson 1971).

As potential orca prey, the migratory gray whales and minke whales are temporally predictable and exhibit some site tenacity on their summer feeding grounds (Dorsey 1983; Oliver and Kviteck 1984) making them spatially predictable as well. The banks and inshore amphipod beds form patches where orcas can predictably find small aggregations of minke whales and gray whales respectively (Dorsey 1983; Oliver and Kvitek 1984). When a gray whale calf was subject to predation, the mother did not appear to have defensive techniques against orcas other than hiding for her own life (Baldridge 1972).

Gray whales have also been observed to form close subgroups when orcas approach as if attempting to benefit from schooling (Ljungblad and Moore 1983). However, aggressively defensive reactions to orcas have been observed in humpback whales (Whitehead and Glass 1985) and right whales (Cummings et al. 1972 in Ljungblad and Moore 1983) in which the intended prey did not flee, but began to violently slash its tail as if to ward off orcas. This alternate strategy of fleeing or holding ground is analogous to observations of the responses ungulate prey exhibit to the approach of wild dogs (Estes and Goddard 1967) and Wolves (Mech 1970). Another similarity between terrestrial predators and orcas of interest to note, is the tendency for both canids and orcas to encircle their prey and attempting to imobilize it with individuals grasping the forward and rear extremes of the prey. Orcas appear to feed preferentially on the lips and tongue of baleen whales (Baldridge 1972; Hancock 1965), but sometimes appear to just take bites out of baleen whales possibly "testing" for vulnerable individuals (Whitehead and Glass 1985). Further comparisons with terrestrial predators are reviewed in section 4.2.

The porpoises are usually found in small groups of three to ten individuals which exhibit some habitat preferences, but are not easily localized unless they are vocalizing. Predation on porpoises, like other schooled prey is expected to occur by the whales corralling their prey which has been observed in British Columbia (Pike and MacAskie 1969). However, on two separate occassions orcas were observed to attack solitary porpoise (Osborne et al 1984). Although it would appear to benefit the prey to disperse when they detect an orca, living in the school reduces the likelihood of an individual being singled out by a predator (Williams 1964). It has also been suggested that the school serves to confuse the predator by appearing as a single large prey (Springer 1957). Neither of these adaptations appear to be effective in providing defense from orca predation. To the contrary, orcas appear to be aware of the skittish grouping tendancies of their prey and use it to their adavantage. Since orcas are known to attack large baleen whales (Tarpy 1979) as well as schools of fish (Christensen 1981) and schools of porpoise (Steltner et al. 1984), it would not appear to benefit a prey species to appear as just another prey species for orcas. In addition porpoise may also attempt to use the school as a defense for their young, thereby benefitting from the selfish herd (Hamilton 1971). However, if a pod of orcas attempts to encircle a school of porpoises or other small marine mammal, it is likely to result in the predation of the whole school (Steltner et al. 1984; Pike and MacAskie 1969). Consequently, it would appear that the best strategy for small schools of marine mammal prey would be to disperse in hopes of confusing the orcas or by making the chase less profitable for them. However, orcas appear to have learned how to keep their prey concentrated which will be reviewed in section 3.7.

Although there are various species in the Pacific Northwest which orcas are known to prey upon in other parts of the world, there appears to be a high degree of specificity in the prey choice exhibited among orca communities. Large baleen whales and schools of small marine mammals do not appear to be targeted orca prey in Pacific Northwest inland waters. Instead, cooperative foraging techniques by resident pods during the spring to fall, appear to be directed towards salmon as well as other fishes. Cooperative foraging techniques are facilitated by large pod sizes for the detection and capture of loosely schooled salmonid prey in the wide straits of the southern resident community (mean=20 Bigg 1982) and smaller groups in the narrow straits of the northern resident community (mean=11 Bigg 1982)(Figure 1). In contrast, transient pods appear to specialize on lone marine mammals and bottom fish which can be successfully detected and captured by small groups (mean=3) or even by individuals (Bigg 1982). In this scheme, orca feeding strategies in the inland waters can be broadly defined as either "resident" or "transient" after Bigg's (1982) original population distinctions based on pod size, compositon and individual morphologies. These populations have been suspected of exploiting different prey (Balcomb et al. 1980), but a systematic means of analyzing their differences has yet to be published.

I will provide evidence to suggest that from the spring to the fall, large resident pods collectively scan vast amounts of water for the detection and capture of their seasonally and tidally predictable salmonid prey. During these seasons, they confine their core area to where these and other prey fishes can be found consistently. In contrast transient whales occur sporadically in the study area, foraging in small groups on relatively small marine mammals and easily localized bottomfish, relying upon the site tenacity and year round residence of their prey for its detection, and individual techniques for its capture. In addition, tide height is likely to temporally influence the availability of seal prey, for they are found more frequently in open water during high tide (Everitt et al. 1979). In support of this assumption, Hoyt (1984) recalls an account of orcas waiting for the tide to rise in order to prey on northern sea lions (E. jubatus) which were forced off their haul-out with the advancing tide. Since known individuals of all the pods have been observed in the study area for many years, one can be assured they have a high degree of familiarity with the habitat. Consequently, distinctions between the way resident and transient communities utilize the habitat within the same region are good indications of differences in their prey choice. In the descriptions that follow, the major ecological features that distinguish their feeding strategies are outlined and illustrated with plots of their typical daily patterns.

3.2) FEEDING ECOLOGY OF SOUTHERN RESIDENT PODS

Data on the southern resident community used in the present description include 930 hours of observation, 448 hours (48.2%) of which involved observations of feeding behaviors (Tables 1, 2). These data were collected between 1976 and 1985 by the Whale Museum (MCS) and the author (Table 1). The southern resident community consists of pods J, K and L, which currently total 77 whales (Bigg, personal communication 1985). J pod is resident to the inland waters between Olympia, Washington to the south, Powell River, B.C. to the north, and Race Rocks in the Strait of Juan de Fuca to the west. J pod is believed to reside permanently within this region, whereas K and L pods also forage along the outer coasts of the Olympic Peninsula and Vancouver Island (Balcomb et al. 1980; Bigg 1982)(Figure 1). K and L pods seem to spend most of their time along the outer coast in the winter and spring. During this same season some subgroups of J pod have been documented to separate from the rest of the pod for up to a few days (Osborne 1986), which is possibly a reflection of alternate foraging strategies when salmonid prey is scarce (Figure 3). Although the occurrence of resident pods appears to decrease during the winter months, it must be noted that there is a distinct reduction in sighting effort this time. However, J pod has been observed throughout the year by researchers living on the west side of San Juan Island, indicating that J pod does not travel far from the study area (Figure 5). However, the extent of all the pods' movements during the winter is virtually unknown.

L pod contains 48 individuals (Bigg, pers comm. 1985) and is the largest of the three pods. However, independent subgroups of L pod are encountered more often than is L pod as a whole, and there is growing evidence to consider them as two to three closely associated pods with assorted subgroups, rather than one large pod. J and K pods contain 18 and 11 individuals respectively (Bigg, pers comm. 1985), but rarely divide into smaller subgroups for more than a few hours.

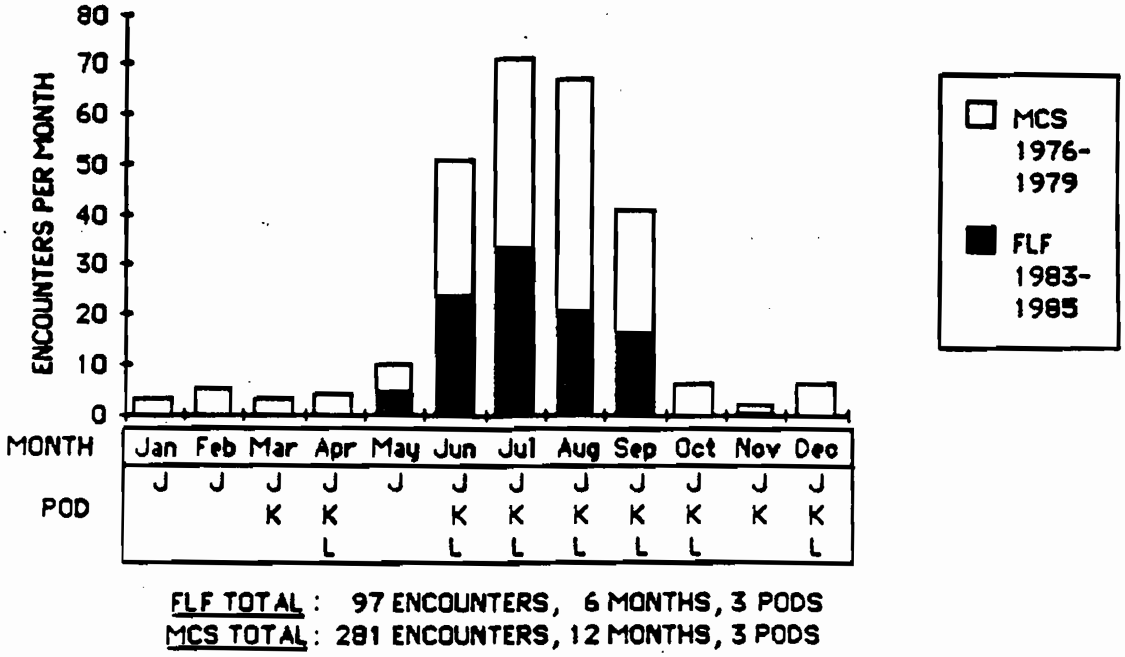


Figure 5. Seasonal Occurrence of Southern Resident Pods
(FLF = my data, MCS = Whale Museum data)

The core range of the southern resident community is along the path that the majority of salmon follow to the Fraser River (Foerster 1936; Wickett 1977; Groot and Quinn 1986)(Figure 1). The occurrence of whales in this area corresponds significantly to times when salmon are caught by the Washington State sport fishery (Balcomb et al. 1980; Heimlich-Boran 1986). The whales and fishing boats are most commonly observed along the west side of San Juan Island, which provides a natural barrier for salmon actively transported there from the Strait of Juan de Fuca by the flood current (Figure 2). This is also a particularly good fishing area because fifty per cent of the flood current entering from the Pacific Ocean moves north through this strait (Thomson 1981) and is carried over several banks, thereby advecting the salmon into a shallow region which creates localized areas of high salmon density. In addition, tidal fronts frequently occur along Haro Strait, especially during ebb tides, (Mofjeld and Larsen 1984) which may serve to aggregate prey (Owen 1981).

3.2.1) Feeding Behavior

Osborne (1986) has described the surface behavior of Greater Puget Sound orcas from 967 hours of data collected between 1976 and 1981. In his analysis nine categories of behavior were recognized (travel, percussive travel, rest, play, intermingling, forage, percussive forage, mill, marine mammal predation) and described as percentages of the total time of observation. In the present discussion, this behavioral system has been applied in my observations from 1983 to 1985, but only those behaviors associated with feeding (forage, percussive forage, mill, marine mammal predation) are presented at this time. Although these data were collected primarily during the spring to the fall, the consistency with which these distinctions in behavior were observed during the extensive duration of observation, suggests that these distinctions are justified. Since orcas do not commonly dive for longer than five minutes and much of their predatory behavior is directed to prey occupying the upper water column (eg. salmon and harbor seals), the observations of feeding behavior described herein are adequate to begin the characterization of feeding strategies. In addition, by using the same criterion to characterize the feeding strategies of socially isolated communites, further insights into the distinctions in prey choice among communities are afforded by such comparisons.

Foraging is characterized by loose forward oriented travel interspersed with brief instances of non-directional milling by subgroups or peripheral individuals (Osborne 1986). This sporadic milling is presumed to indicate the detection and pursuit of prey. Prey capture during this activity was suggested by the occasional observation of fish being herded in the immediate presence of milling whales (Boran et al. 1981; Felleman and Heimlich-Boran 1984; Osborne 1986). The presence of salmonid prey during this activity is further supported by direct observations of prey capture which have also been photographically documented (Jewell 1965; Balcomb et al. 1980). In addition, hydroacoustic recordings made in the presence of milling whales reveal a predominance of single large targets in the upper water column which are indicative of salmon (Felleman and Thomas 1985, Felleman 1985b). The only stomach content collected from a resident pod came from adult bull L-8. Its stomach contained only fish remains, including salmon and bottomfish (Balcomb et al. 1980).

The basic foraging pattern which extends over a 3-10 km range typically consists of a flank formation of the pod oriented perpendicular to the shoreline. It appears that orcas will commonly swim in flank formation when searching for prey and either encircle it as a group or break into smaller subgroups for its capture. Norris and Dohl (1980) suggest that a group of odontocetes swimming in flank formation can effectively scan more water than lone individuals in search of prey because of the collective sensory integration of the group. In addition, the ability of the orcas to encircle their prey appears to be facilitated by the flank formation which has been observed in the herding of small schooled prey (eg. common dolphins: Brown and Norris 1956; sea lions: Norris and Prescott 1961; narwhals: Steltner et al. 1984; salmon: Hoyt 1984; this study) as well as in the immobilization of single large prey (eg. blue whale: Tarpy 1979; minke whale: Hancock 1965; Budylenko 1981). I suggest in section 3.7 that the similarities in orca foraging strategies has resulted from convergent selection for large group sizes when orcas prey upon species which occur in large groups or as single large individuals even though the prey taxa vary considerably. In the southern resident community, small clusters of females and calves often travel in either loose or tight subgroups, and adult males and females travel individually or in pairs. During foraging behavior, adult female and calf groups commonly engage in percussive splashing just prior to milling. Percussive behaviors include tail lobs, pectoral fin slaps, dorsal fin slaps and breeches. This percussive activity is suggestive of a form of herding (Wursig and Wursig 1980; Felleman and J. Heimlich-Boran 1984) and may also serve to coordinate group changes in direction (Felleman 1985b); this will be discussed further in section 3.2.2.

Hoyt (1984) provides a description of group coordination for the capture of schooled salmon by a northern resident pod of 16 orcas. The pod was initially observed resting in a tight cluster. They increased their speed and spread out into a flank formation which extended a mile into Johnstone Strait from the Vancouver Island shore. They began to tail lob as they formed a circle which Hoyt (1984) likened to a purse seine. The pod closed the circle while individuals took turns swimming through the middle presumably to eat the entrapped prey. The presence of salmon was confirmed by observations of the fishes jumping in the presence of the whales and from the catch of two seiners who had just caught salmon 50 yards from the orcas. Although there are many similarities between Hoyt's (1984) account and my observation of salmon predation by pods in the southern resident community, I have never observed an entire pod maintian a circle while inidividuals swam through the middle of it. However, observations of flank formation travel and percussive activites prior to milling, which often occurs with individuals oriented towards each other, suggests a basic similarity in foraging strategies between northern and southern resident communities.

In the southern resident community, there are often individuals or subgroups which exhibit foraging behavior peripheral to the pod. In peripheral foraging, cooperative facilitation in the capture of prey is less apparent. In this peripheral strategy, adult males typically forage individually as much as 3 kilometers from the nearest individual, though still traveling in pace with the pod. When adult females exhibit this behavior they are usually in pairs. These peripheral subgroups, often exhibit rapid sharp turns at the surface. This behavior is probably indicative of the rapid turning avoidance tactics of salmon which I have observed in the presence of foraging whales. On one occassion in 1984, my chairman and I observed a lone male swimming in tight circles with his dorsal fin at a 45 degree angle to the surface of the water. I positioned the boat to within 10m of the whale and turned the engine off. The whale continued to swim rapidly while trying to make turns at the apparent limits of its turning radius. After observing this behavior for approximately fifteen minutes, we saw an adult salmon swimming at the surface around the boat as if to hide from the whale. Although actual consumption was not observed, the intent of this highly demonstrative behavior was apparently an individual staregey for salmon predation.

Its is common to see individuals in peripheral subgroups to orient towards each other as they dive which possibly enables them to herd fish. In contrast, females with calves close inshore rarely exhibit high speed chases for fish at the surface. They may be more commonly exploiting the less mobile bottomfish associated with the kelp beds and rocky substrate which would not be found in the deep waters of the mid-strait (Simenstad et al. 1979; Long 1983).

Differences in the dispersion patterns observed between age and sex classes of orcas in the southern resident community, suggestive of distinctions in prey choice, may help to account for variations in the composition of stomach contents collected within discrete orca populations in other parts of the world. Consequently, the higher incidence of marine mammal remains found in males than females and calves suggets that prey choice varies within populations (Nishiwaki and Handa 1958; Rice 1968; Jonsgaard and Lyshoel 1970). Wilson (1975) suggests that it is advantageous for species which have to "browse" over large areas, for males and nursery groups of variable sizes be able to travel independently.

During foraging behavior, all whales present will sometimes engage in continuous milling behavior for extended periods of time. Continuous milling occurred for a minimum duration of 0.2 hours, a maximum of 4.0 hours and a mean of 1.5 hours (Osborne 1986). Milling often occurred at slack current in areas known for salmon abundance (Felleman 1985b). The occurrence of milling at slack current is discussed in section 3.2.2. These areas are characterized by high relief bottom topography that are oriented perpendicular to the tidal currents, implying an area of increased upwelling which may attract prey, as well as providing potential barriers against which to herd prey (Felleman and Heimlich-Boran 1984).

Predation on marine mammals by southern resident pods was observed on only two occasions, which amounts to less than 1% of the total observations (Osborne et al. 1984) (Table 2). Both instances involved a female and calf subgroup in L pod preying on porpoise. The first instance took place during August 1976 in Haro Strait and involved 20 minutes of coordinated chase and/or play with a neonate harbor porpoise (Phocoena phocoena) followed presumably by consumption (Chandler et al. 1977; Balcomb et al. 1980). The other instance occurred in July 1982 involving a Dall's porpoise, (Phocoenoides dalli)(Osborne et al. 1984). Again an L pod subgroup of females and calves was involved and again they engaged in about 20 minutes of coordinated chase/play before the porpoise disappeared. It is likely that the observations of porpoise predation were more indicative of play behavior rather than foraging, for porpoise do not appear to be a common prey item for southern rsident pods and the whales did not appear to be determined to kill the porpoises quickly. Similar extensive handling of sea lion prey has been suggested as a form of "malicious joy" (Norris and Prescott 1961). Although the dietary importance of these observations cannot be ignored, there appears to be ample indication that different orca pods exhibit specializations in their prey choice. Whereas, an opportunistic strategy would entail eating prey in the proportion of their abundance in the environment.

On many other occasions, resident pods, including L pod, have been observed in the proximity of porpoise (P. dalli and P. phocoena) minke whales (Balaenoptera acutorostrata) and harbor seals (Phoca vitulina) without any noticeable reaction by the orcas, or their potential prey. Similarly, Mikhalev et al. (1981) have noted the "peaceful coexistence" between orca and potential ceatcean prey in the Antarctic which may be likened to the coexistence of prdators and prey on the Serengeti plains of East Africa (Sinclair 1985).

In the southern resident community, feeding behaviors occurred in 49.6% of the 242 hours of my observations and 43.1% of the 688 hours of observations by the Whale Museum (MCS) (Tables 1, 2). Foraging represents 15.5%, percussive foraging 15.3%, and milling 18.8% of all my observations (Table 2). These data are in close agreement with those previously collected by the Whale Museum (MCS) (Table 2) and provide some indication of the amount of time southern resident orcas spend feeding during the day light hours in the spring to fall.

Table 2. Occurrence of Feeding Behavior

Pod Community	Forage	Percussive Forage	Milling	Marine Mammal	Total
S. Resident, 1976-79	19.1	19.0	4.7	0.3	43.1
S. Resident, 1983-85	15.5	15.3	18.8	0	49.6
N. Resident, 1985	13.1	8.5	9.8	0	31.4
Transient, 1976-79	50.6	0.6	19.1	3.9	74.2

3.2.2) Tidal Orientation

Observations on the southern resident orcas' orientation to the tidal current suggest that the whales are influenced by the tidally dependent movements of salmon. Orcas often confine the area of their daily range by changing their direction of travel after milling at slack current (Table 4) in areas of salmon abundance. Orcas change their direction of travel within an hour of slack current 7 times more frequently than would be expected by chance ($P < .0001$)(Table 3). I suggest that this association is a reflection of the orcas' knowledge of the limitations that currents impose on salmon movements. Sonically tagged salmon have also been shown to mill at slack currents (Stasko et al. 1973, 1976). The whales appear to coordinate their direction changes at slack current with percussive behaviors. Although I have not enumerated my observations, it is common for a single individual to tail lob or breech after the pod has milled at slack current. Martinez and Klinghammer (1978) have noted the same behavior with limited observations of the southern resident community. Whitehead (1985) has reviewed several accounts of percussive behaviors which support the likelihood of their role in communication.

Although the orcas direction changes are non-random with respect to the current (Table 3), orcas spend equivalent amounts of time moving with and against the current (Table 4). Although the orcas do not maintain a constant rheotaxis (orientation to the current)(Lyon 1904), their orientation cannot be called random. I suggest orcas can detect the direction of the current visually by drifting in the flow and observing the coast or bottom topography moving. Lyon (1904) originally proposed that fishes could maintain positive rheotaxis (orientation against the current) by visual cues and more recently Creutzberg (1959) has shown that some fish can discriminate between the ebb and flood with olfactory cues.

Similarly, Shane (1980) observed that bottlenose dolphins (Tursiops truncatus) also move against ebb currents a high proportion of the time. This implies that the whales' orientation to the current may be random or due to factors given higher priority than hydrodynamic efficiency. It is conceivable that the whales could swim with the current continuously by maintaining the appropriate orientation to the current when they change directions at slack. Since swimming against the current may either slow down the rate the whales travel or increase the energetic cost of travel, enhanced feeding success may account for the persistence of this behavior.

Results from studies which tracked sonically tagged salmon through the study area suggest that Fraser River sockeye (O. nerka) and pink (O. gorbuscha) progress north through the estuarine waters by moving north with the flood current, holding ground during the ebb current, and milling at slack current (Stasko et al. 1973, 1976). There appears to be a trade-off between the encounter rate and ease of prey capture. The whales can effectively scan more water for salmon when oriented against the flood current, because they will be approaching the prey in the opposite direction (Stasko et al. 1973, 1976).

Table 3. Effect of Tidal Current Changes on Pod Movements

	Southern Resident Community TIDE CHANGE			Northern Resident Community TIDE CHANGE			Transient Community TIDE CHANGE		
DIRECTION CHANGE	Yes	No		Yes	No		Yes	No	
Yes	29 (4.2)	15 (39.8)	44	14 (2.0)	4 (16.0)	18	0 (0.86)	11 (10.1)	11
No	64 (88.8)	860 (835.2)	924	3 (15.0)	132 (120.0)	135	14 (13.1)	153 (153.9)	167
	93	875	968 (242 hrs)	17	136	153 (38.25 hrs)	14	164	178 (44.5 hrs)
	$X^2_C = 122.3$ $(p < 0.0001)$			$X^2_C = 82.67$ $(p < 0.0001)$			$X^2_C = 0.334$ $(0.75 < p < 0.50)$		

X^2_C = Chi Square with Cochran Correction for Continuity

Note: Frequency from fifteen-minute scan-sample. Key: $\frac{\text{OBS}}{(\text{EXP})}$.

Table 4. Tidal Orientation of All Behavior Combined

S. Resident, 1976-79	Flood	Ebb	Slack	Total
With	27.5	17.0	--	44.5
Against	12.7	23.3	--	36.0
Non-oriented	2.2	0.9	16.4	19.5
Total (688 hours)	42.4	41.2	16.4	100
S. Resident, 1983-85				
With	20.0	15.0	--	35.0
Against	15.6	23.6	--	39.2
Non-oriented	4.0	3.3	18.5	25.8
Total (242 hours)	39.6	41.9	18.5	100
N. Resident, 1985				
With	14.4	20.3	--	34.7
Against	13.7	24.2	--	37.9
Non-oriented	3.3	5.2	19.0	27.5
Total (38.5 hours)	31.4	49.7	19.0	100
Transient, 1976-1985				
With	11.2	10.1	--	21.3
Against	3.9	15.2	--	19.1
Non-oriented	2.8	16.9	39.9	59.6
Total (44.5 hours)	17.9	42.2	39.9	100

Note: All behaviors are non-oriented during slack tides by definition.

In order for a predator to be efficient, optimal foraging theory predicts that a predator should try to maximize its net rate of food intake while foraging (Krebs 1978). I suggest there are two reasons that the salmon are more difficult to catch when the whales swim against, rather than with the flood current. Initially, the whales would be approaching the salmon head-on, which may enable the salmon to visually detect and avoid the orcas. In addition, the whales would be approaching the salmon at a higher velocity than if they were traveling in the same orientation as salmon relative to the current. Consequently, they would be reducing the time they have to respond to the presence of prey which is assumed to reduce their hunting efficiency.

However, there is a tendency for the whales to move with flood currents and against ebb currents (Table 4), thereby maintaining the same relative orientation to the current as returning adult salmon. Since orcas can move than the currents, they will be able to approach their salmonid prey from behind as stable targets. This tidal orientation is suggested to be more efficient because it may enable the orcas to approach their prey closely without being detected. It is also suggested that salmon would be easier to catch when the orcas are in their same direction of motion because they will have more time to respond to the fishes movements than when they are traveling in opposite directions.

The stable target hypothesis is also supported by observations of the behavior of orcas and salmon at slack current. Observations of the times milling behavior ocurred as a percentage of the tidal observations are summarized in Table 5. The data collected from 1976 to 1979 reveal that milling occurred during 11.5 per cent of all observations of slack current, which is a considerably larger percentage than what has been observed during flood and ebb currents. However, retrospective tidal analysis of data collected by the Whale Museum (MCS) does not provide as accurate an indication of the time of true slack as tidal data collected in the field because climatic conditions can cause discrepancies between the predicted values and observed conditions.

During 1983 to 1985 observations of slack current were confirmed by using my boat as a drogue buoy. In addition, there is a higher occurrence of milling behavior in my data set as compared to the MCS data set (Table 2). This disparity is due to the fact that foraging is defined as travel with interspersed milling (Osborne 1986) and I tended to record short bouts of milling as milling, rather than foraging. However, the implication that the whales are feeding is the same and the propensity for the orcas to mill during slack tide is pronounced in both data sets (Table 5). This non-directional milling by the orcas is assumed to reflect the lack of oriented movements by the salmon, which have also been shown to mill at slack currents (Stasko 1975; Stasko et al. 1973, 1976), presumably because they rely on currents to impart directional cues for homing (Hasler and Scholz 1983, Dodson and Dohse 1984, Felleman and Heimlich-Boran 1984).

Table 5. Occurrence of Milling Behavior as % of Tidal Observation

Pod Community	Flood	Ebb	Slack
S. Resident, 1976-79	4.8	2.1	11.5
S. Resident, 1983-1985	7.8	7.2	68.7
N. Resident, 1985	7.5	8.8	13.9
Transient, 1976-85	13.9	33.3	6.9

A similar strategy of stable target orientation can be inferred from Fish and Vania's (1971) observations of beluga whale (Delphinapterus leucas) tidal orientation during predation in Kvichak River which is the origin of the world's largest run of Sockeye salmon. Fish and Vania (1971) state "...belugas (Delphinapterous leucas) commonly travel 20 to 30 km up Alaska's Kichak River on the flood tide and back down on the ebb, foraging on available food organisms along the way." The beluga whales inhabit the estuary from May to June, which coincides with the downstream migration of smolts from Lake Iliama (Fish and Vania 1971).

I suggest that beluga whales exhibit similar foraging strategies to southern resident orcas because of the similarities in the temporal predictability of their prey. The upstream and downstream migration of salmon occur in mass synchrony during a narrow time interval which causes smolts and adults to be temporally predictable. The tidal current also appears to have similar temporal effects on both prey and predator. The beluga whales would travel up the river with the flood when smolts are prevented from moving downstream as they are oriented against the current. The belugas changed their direction with the tide change and traveled downstream in the same orientation as the smolts migration to the sea (Fish and Vania 1971). Similar to orcas, the belugas did not orient against the flow of prey and changed their direction in accordance with tide changes. When prey are so abundant that extensive search is not required, it appears that the whales use the tides to benefit their (stable target) capture technique rather than to maximize their encounter rate with prey.

Norris et al. (1983) studied the tidal orientation of of gray whales (Eschrichtius robustus) in the lagoons of Baja California. They found that the whales would often pace against a strong current, at the lagoon entrance and would often change their direction of travel corresponding with a change in tide height once inside the lagoon (Norris et al. 1977 in Norris et al. 1983). Similarly Shane's (1980) observations with Tursiops truncatus suggest they also spend significant portions of time oriented against the current and change direction in apparent response to a change in the current.

Although these observations appear to be similar to my observations with orca, it is important to recognize that the social conditions and feeding behavior of these species and the tidally dependent movements of their prey are likely to differ. Apparently, gray whales are not actively feeding in the lagoons, but respond to changes in the tide height to prevent their calves from stranding (Norris and Dohl 1980). In addition, Saayman and Tayler (1979) have shown that humpback dolphins (Sousa sp.) feed on the incoming tide, but suggest they use the low tide as a defense against predators since sharks and orcas would not be able cross over the nearshore reef at low tide. It has also been observed that cetceans often rest oriented against the current (Shane 1980, Felleman and Heimlich-Boran 1984). Rest behavior in the southern resident community is defined as slow, tight, synchronous travel which is rarely associated with any vocalizations (Osborne 1986). Therefore, resting against the current may as a means of "jogging in place," so as not to bump into things while resting the sensory system. In addition, diurnal rhythms may override the influences of tides on the direction which cetaceans travel (Saayman and Tayler 1979; Wursig and Wursig; 1980; Shane 1980). Osborne (1981) suggests that the behavior of the southern resident community is not influenced by diurnal rhythyms. However, the behavioral sample is biased by primarily daylight observations which limits our ability to recognize diurnal influences on orca behavior. More evening observations are needed before we can adequately address this question.

Consequently, it is difficult to extrapolate further than recognizing that tides are an important variable in several components of the life history of cetaceans. However, it is informative to distinguish between behaviors associated with specific tidal current orientation and those associated with changes in the tide height in order to evaluate the type of tidal influence and to isolate the effects diurnal rhythms may have on the incidence of behavior. In addition, the dependence of the prey's movements to the tide must be addressed in order to ascertain the relative orientation and availability of the prey to the predator.

3.2.3) **Acoustic Behavior**

Underwater acoustic recording of southern resident pods revealed the occurrence of general vocal activity during 83% of the observations of foraging behavior and 91% of the observations of milling behavior (Osborne 1986). Milling behavior had the highest percentage of phonatory activity recorded for any behavior category (Osborne 1986). This suggests that vocalizations may be most important in coordinating this behavior (Hoelzel and Osborne 1986). Since orca vocalizations are mostly well above 1.5 Khz (Ford and Fisher 1981), and salmonids are generally insensitive to frequencies above 1 Khz (Abbott 1970), it is not surprising that these fishes do not exhibit avoidance responses to recordings of orca vocalizations (Abbott 1973; Felleman and Ferraro unpub data). Shaw (1978) has demonstrated the importance of vision in maintaining the cohesion of fish schools. If vision is also used by fishes to avoid orcas, then it would benefit orcas to approach fishes from behind which I have suggested is a consequence of stable target orientation.

It has been suggested that odontocetes, including orcas, can use their vocalizations to debilitate prey (Norris and Mohl 1983). Therefore, it might be expected that salmon can detect the lower frequencies of echolocation clicks which have been recorded at 300 to 500 Hz (Schevill and Watkins 1966). Though I have yet to observe any direct evidence of this effect, on three occasions during 1985, southern resident whales were observed to swim with a whole dead salmon across their rostrums for up to 30 minutes. How the fish was initially immobilized is unknown.

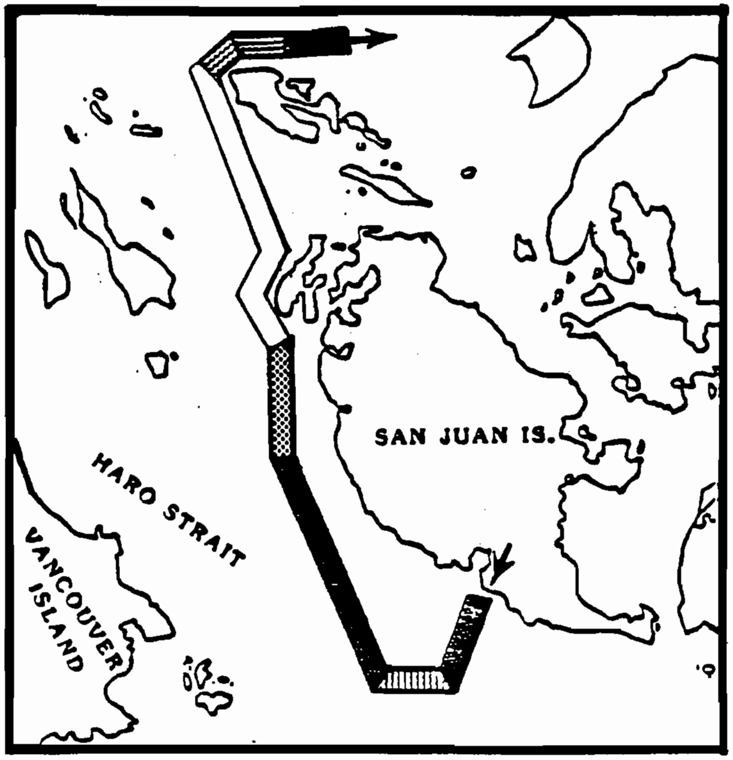
3.2.4) Characteristic Encounter

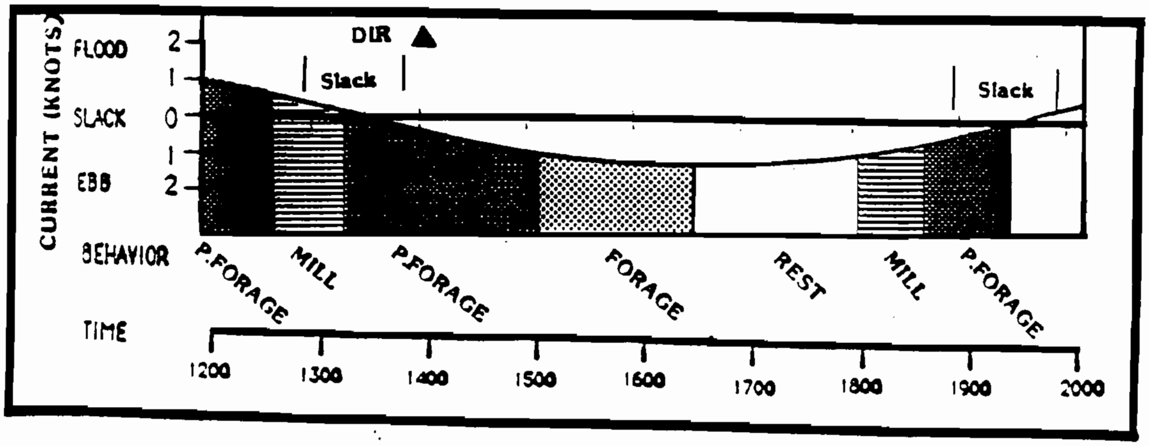
Figure 6. Example of Southern Resident Pod Daily Activity

Southern resident J pod and K pod were observed traveling together for 7.5 hours on 7/17/83. They were first observed exhibiting percussive foraging behaviors against the flood current for 0.5 hours. They then began to mill off Middle Bank, known for its salmon abundance at slack high. They changed directions during slack and proceeded to percussive forage against the ebb current for 2.0 hours. They continued to forage against the ebb current for another 1.25 hours and then proceeded to rest for 1.75 hours. They began to mill just prior to slack low at Turn Point which is characterized by kelp beds and turbulent currents. They milled around Turn Point and proceeded to percussive forage with the flood current.

During this time, the whales were observed to travel approximately 10 nautical miles in 7.5 hours. Their average ground speed was only 1.3 knots because they were traveling against the current throughout most of the observation. They mill close to both slack currents and changed their direction of travel corresponding to the first change in current. Because of their change in direction, they traveled only approximately 8.7 linear nautical miles, though they swam for 10 nautical miles. The occurrence of foraging behaviors at known areas of salmon abundance and the correspondance of their direction change with a change in the tidal current are assumed indications of salmon predation.

ENCOUNTER #18 **SOUTHERN RESIDENT** **J. K. PODS**
07-17-83





3.3) Feeding Ecology of Northern Resident Pods

Northern resident pods were observed for 38.5 hours during a pilot study I conducted during July 1985 (Table 1). This study was conducted to determine if northern resident pod movement and behavior in relation to tidal currents is similar to that of the southern resident pods. Previous observations by Spong et al. (1970, 1971, 1972) and Morton (1985) are used to compare with the findings from this study. The total northern resident community consists of 16 pods numbering approximately 155 individuals (Bigg 1984). However, only 3 subgroups of A pod, one subgroup of I pod and all of B pod and C pod were observed during the pilot study.

The northern resident community travels predominantly along a 25-km stretch of Johnstone Strait during the summer months (Ford and Fisher 1982), but ranges as far as Bella Bella to Campbell River, Vancouver Island (Figure 1). Similar to the southern resident community core area, the northern resident community core area is located at an initial point of aggregation for returning adult Fraser River salmon (Figure 1). Johnstone Strait creates a dramatic constriction in the salmon migratory route to the Fraser River, making this region also a prime site for the commercial salmon fishery (Hilborn and Ledbetter 1979). Although on average 80% of Fraser River salmon have annually migrated through the Strait of Juan de Fuca since 1978, more recently, 53% on average have migrated through Johnstone Strait (Quinn and Groot 1986). However, there are twice as many resident whales (Bigg 1982) and twice as much Canadian purse seine fishing effort in the northern straits than in the southern straits (Hilborn and Ledbetter 1979). Perhaps the narrow contours of Johnstone Strait create higher prey densities in the northern straits with equivalent amounts of salmon as in the southern straits, thereby facilitating prey capture by orcas and fishermen alike.

3.3.1) Feeding Behavior

The occurrence and tidal orientation of feeding behavior observed in the northern resident community are summarized in Tables 2 and 4. These orcas exhibited feeding behaviors in 31.4% of the total 38.5 hours of observations (Table 2). Milling behavior occurred during 9.8% of the observations (Table 2) and in 13.9% of the observations of slack current they were milling (Table 5). From these preliminary data it appears that the feeding behavior and the orientation to the tidal current exhibited by the northern resident community is similar to that observed in the southern resident community. Addtional support for these preliminary observations in relation to the analysis of tidal influences is drawn from previous studies which will be reviewed in section 3.3.2.

However, there was less high-speed traveling or "porpoising" observed in the northern resident community than in the southern resident community which agrees with observations by Ford and Ford (1981). Although porpoising has been suggested to be less energetically expensive than traveling at high speed underwater, it is still considered energetically costly (Blake 1983). Porpoising is commonly observed in the southern resident community just prior to milling at slack tide (Felleman and Heimlich-Boran 1984). This suggests that orcas can benefit from fast travel if they can use it to feed at specific locations during slack current. Ford and Ford (1983) speculate that the lack of porpoising observed in the northern resident community may be due to a higher concentration of prey in the Johnstone Strait region than in Haro Strait. I am in agreement with their suggestion because equal amounts of salmon traveling through Johnstone Strait and Haro Strait (Groot and Quinn 1986) will cause salmon densities to be greater in the narrow contours of Johnstone strait. Consequently, southern resident pods may benefit from porpoising because they have to travel greater distances between prey concentrations than northern resident pods. Another possible indication that there is a greater prey encounter rate in Johnstone Strait than Haro Strait is that although there are twice as many orcas in the northern community than in the southern community, southern resident pods are larger (mean = 20) (Bigg 1982) than the northern resident pods (mean = 11) (Bigg 1982) and would therefore benefit more from the sensory integration of a larger group which has been suggested to aid in the detection of diffuse prey (Norris and Dohl 1980). There are other reasons to suggest, which will be discussed again in section 4.2, that prey abundance is not limiting the minimum group size.

Predation on marine mammals by northern resident pods has never been documented. However, some chasing interactions have been noted between northern resident pods and Dall's porpoise (Jacobson 1986). In general, as with the southern resident community, the northern resident orcas do not appear to select available marine mammal prey (Spong et al. 1971; Hoyt 1984; Jacobson 1986). Consequently, marine mammals do not appear to be a limiting food resource for either resident community.

3.3.2) Tidal **Orientation**

Spong et al. (1971, 1972, 1973) were the first to recognize the association between the temporal effects of tide and season on orca and salmon occurrence in the northern resident community. Like the southern resident community their occurrence coincides with peaks of salmon abundance. Spong et al. (1970) noted that the whales spent equal amounts of time moving with and against the current, but often changed direction and behavior at slack tides. Morton (1985) also noted that northern resident orcas travel with and against the current with equal freuency in Johnstone Strait, but observed them traveling against the current with greater frequency in the more narrow straits.

Their findings are in agreement with results from this pilot study. My observations suggest that directions changes in the northern resident community, like those of the southern resident community, are 7 times more likely to occur within an hour of slack current, than would be expected by chance (P< .0001)(Table 3). However, the northern resident community appears to change directions more consistently at specific geographic locations than the southern resident community. In addition, I observed the northern resident pods to travel with and against the current with equal frequency, but stable target orientation cannot be inferred from these data because the extended ebb current which occurred during this study caused a sample bias resulting in a disproportionate amount of ebb observations (Table 4). Although the data sets are not of sufficient size to make an absolute comparison of the two resident communities, the similarity between my findings and those of previous investigators supports my contention that the resident communites exhibit similar foraging strategies.

Another possible association of tides, salmon, and whales was observed during the 1985 pilot study. In Johnstone Strait there is a predictable five-day ebb current which corresponds with monthly neap tides (Thomson 1981). During these times, the flood current is not strong enough to counteract the estuarine flow of river water at the surface moving towards the ocean. Consequently, the amount of fresh water at the surface is at a maximum during these times which is analogous to an extended slack low current as depicted in Figure 4. All Fraser River salmon runs were late in 1985 (IPFSC 1985) and so was the arrival of most of the northern resident community pods. Only three pods were observed in Johnstone Strait just prior to and during the five-day ebb period, July 23 through 28 July, 1985. Sockeye salmon catches for that week were estimated to reach their maximum at 8,100 on the 28th (IPFSC 1985). The following day when the tides began their normal reversing process the estimated sockeye catch increased to 262,000 (IPFSC 1985). This coincided with the arrival of three additional northern resident pods into the region for the first time that season. I suggest that the adult salmon were waiting offshore for olfactory cues to lead them back to their natal stream. These cues are presumably associated with the freshwater which was abundant during the prolonged ebb current. However, I suggest the salmon could not progress far inshore until the flood currents resumed. Apparently, some of the pods waited for the majority of salmon before they entered the inshore waters.

A similar association between the timing of returning adult Atlantic salmon and freshwater influences was observed by Huntsman (1936). The predictive value of the association between orcas, salmon, and tides can greatly help to direct research on orcas and salmon alike. Although the seasonal association between run timing and tides is preliminary, previously collected data are currently being compiled to test this hypothesis more rigorously.

3.3.3) Acoustic Behavior

The northern resident community pods are acoustically unique in that they display two separate call repertoires (Ford 1983). This means that some of the northern resident pods that travel together produce completely different calls, yet engage in social interactions and are thought to interbreed. Among the southern resident and transient communities, it appears that all socially interacting pods share the same, or similar, call repertoires, though individual pods can be acoustically recognized by their pod dialects (Ford and Fisher 1982, 1983; Ford 1983; Hoelzel and Osborne 1986; Healy et al. 1983). I am not familiar with any studies addressing the incidence of northern resident vocalizations with feeding behaviors and therefore cannot make comparisons between communities based on this variable.

3.3.4) Characteristic Encounter

Figure 7. Example of Northern Resident Pod Daily Activity

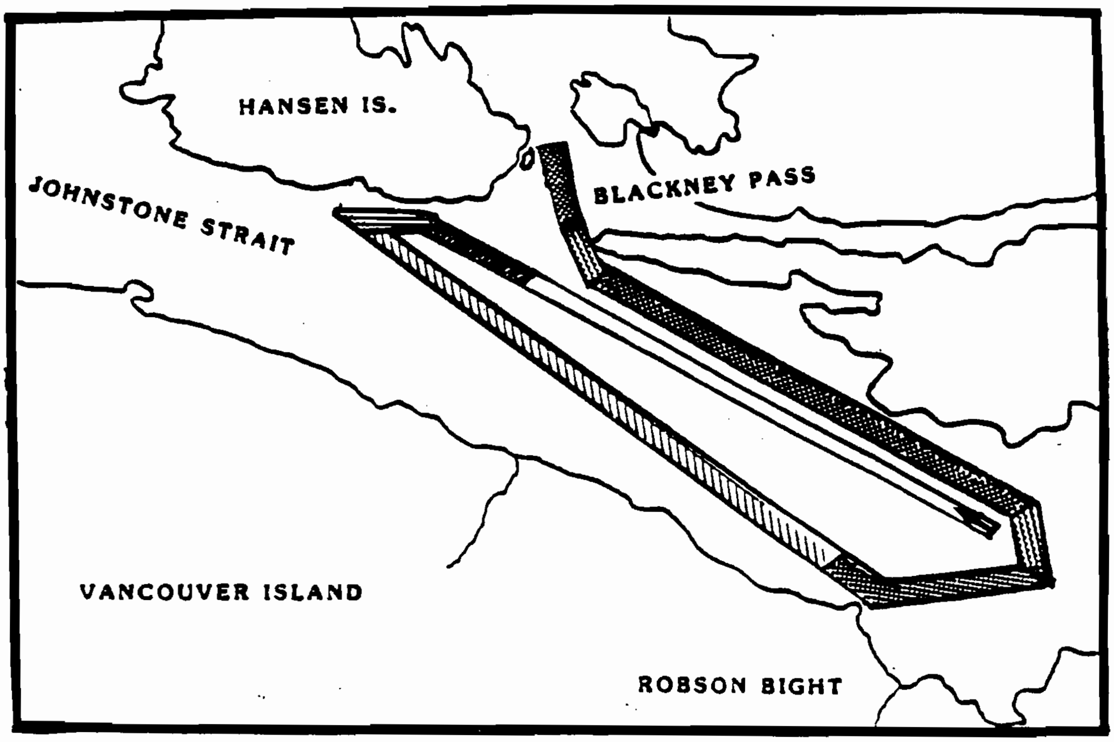
Northern resident subgroup of A pod was observed for 5.5 hours on 7/20/85. They were initially observed resting with the ebb current for 0.75 hours. They began to forage at slack current and then changed their direction of travel after milling for 0.25 hours. They then proceeded to travel with the flood current for 1.5 hours to Robson Bight where they foraged for 1.0 hour. They changed direction again after milling at slack current and proceeded to forage and mill for the remaining 0.5 hours of observation. They were last observed foraging with the ebb current through Blackney Pass which has strong currents due to its narrow constriction in the flow of water from Queen Charolette Sound and Johnstone Strait.

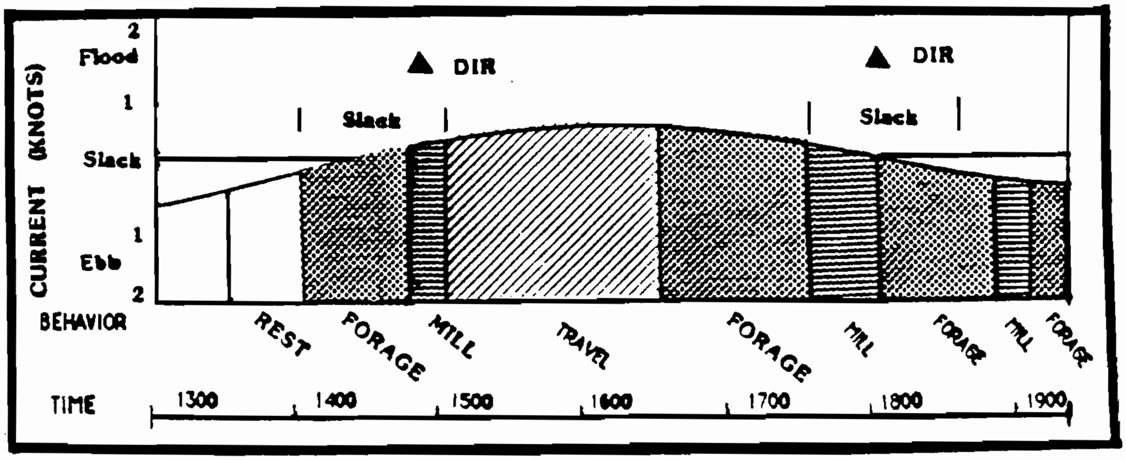
During this time, the whales were observed to travel approximately 50 nautical miles in 5.5 hours. Their average ground speed was 4.5 knots traveling with the current for most of the observation time. They changed their direction of travel at both slack currents after milling for 0.5 hours. They traveled only 18 linear nautical miles because they confined their range by changing directions along Johnstone Strait. However, they actually swam for approximately 50 nautical miles. Similar to the southern resident pod movements, the propensity for northern resident pods to change their direction of travel after milling at slack current (Table 5) in areas known for salmon abundance is indicative of salmon predation (Figures 6,7).

ENCOUNTER #01
07-20-85

NORTHERN RESIDENT

A. POD



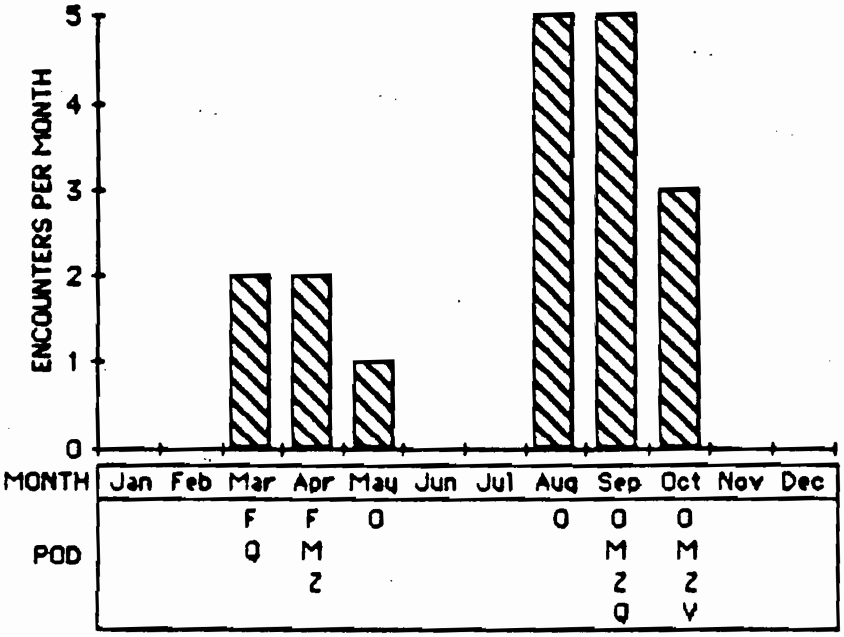


3.4) Feeding Ecology of Transient Pods

The transient community is not as well understood as the two resident communities because their occurrence is sporadic (Figure 8) throughout all regions of Washington and British Columbia (Figures 1). Their ranges may extend throughout the North Pacific including S.E. Alaska (Leatherwood et al. 1984) and possibly Oregon and Northern California.

Although there is also a seasonal bias in the sighting effort for transient pods, it is apparent they never occur as frequently at any given locality as the southern resident pods (Figures 6,8). However, there may also be a regional bias in the sighting effort. Since transient pods often occur in different parts of the habitat than resident pods, their occurrence may go unnoticed. It can be asserted that they occur less frequently than resident pods in Haro Strait throughout the year.

Observations of transient pods presented here include 44.5 hours of data collected between 1976 and 1985 on six pods totaling 13 individuals (Table 1). These same pods have been documented at the north end of Vancouver Island by Bigg and his colleagues, along with eleven other transient pods (Bigg 1982). Transient pods are small, with fewer than six individuals (mean = 3), and in some instances they are just lone bulls or cows (Bigg 1982). Transient pods are regularly encountered in small channels and bays, rather than along the major straits frequented by resident pods. During the late summer and fall, transient pods are most frequently encountered entering the inland waters from the Strait of Juan de Fuca by Race Rocks, located at the southeast end of Vancouver Island. This area is known to be a sea lion haul-out later in the season (Angell and Balcomb 1982), though I have not observed predation of them.



TOTAL : 18 ENCOUNTERS, 6 MONTHS 6 PODS

Figure 8. Seasonal Occurrence of Transient Pods
(MCS and FLF combined data)

3.4.1) Feeding Behavior

Feeding behavior ocuurred during 74.2% of the observations on transient pods (Table 1). Transient pod fish foraging behavior is very similar to peripheral adult foraging among resident pods. There is a general directional trend in the movement of the pod, interspersed with periods of individual nondirectional milling. However the whales do not mill frequently at slack current (Table 5). In addition, transient pods tend to follow coastlines and spend extended time milling in the same general area before moving on to the next location. This propensity for hugging shorelines would appear to explain why transient pods have been observed in dead-end bays.

Their use of the coastal habitat would suggest a feeding strategy more consistent with the distribution of bottomfish and seals, rather than predation on salmon or schooling fish which occur more commonly mid-strait (Stasko et al. 1973, 1976; Simenstad et al. 1979; Long 1983). In addition, the lack of percussive behavior exhibited during fish predation by transient pods suggests they are exploiting prey species that are unaffected by a surface herding strategy (Table 2). However, the repeated use of tail lobs during seal predation appears to be effective in "disarming" their pinniped prey. Although the stomach content samples taken of transient whales did not contain any fish remains, they could have been overlooked (Bigg pers comm). Additional support of the importance of bottomfish to transient pods is provided by hydroacoustic (fish-finder) recodings made in the presence of Q pod milling. Preliminary analysis reveals the presence of large multiple targets associated with the bottom which are indicative bottomfish (Felleman 1985b).

Harbor seals are the only marine mammal species that can be considered as targeted by transient pods in the inland waters. Since harbor seals are easily localized, small, unschooled prey, their capture by transient pods does not require large cooperative foraging groups. Marine mammal predation by transient pods has been observed on four occasions involving individuals from four of the six transient pods documented in the study area. In every instance the whales were preying on harbor seals (Phoca vitulina). This represented 3.9% of transient observations which is a considerably larger proportion than observations of marine mammal predation by southern resident pods (Table 2). Harbor seal predation occurred with a minimum duration of 0.3 hours., a maximum of 0.4 hours. and a mean of 0.35 hours. (Osborne et al. 1984).

In addition to the data presented here, M.A. Bigg also notes one observation of harbor seal predation by adult bull M-1 (M.A. Bigg, personal communication). Radio tagged members of O pod were also observed to attack a harbor seal (Erikson 1976). The only transient whale stomach content that have been examined were from adult bull O-1. Its stomach contained only marine mammal remains: elephant seal claws and harbor seal bones (Balcomb et al. 1980). There have been at least two other stomach contents analyzed of lone male orcas which were assumed to be transient whales. Their stomach contents contained primarily harbor seal remains, but also included remains of sea lions an elephant seal, and unidentified cetacean skin (Bigg pers comm.). It is perhaps surprising that on at least two occassions, elephant seals were subject to predation, having suggested in section 3.1.2 that they were only encountered opportunistically. However, it is impossible to suggest how common an occurrence this type of predation is, whereas it appears that harbor seals are subject to orca predation with some regularity. In addition, it is important to note that there have been several accounts of small orca pods preying on sea lions and minke whales in this area (Pike and MacAskie 1969; Hancock 1965). Although these pods were not photo-identified, their group size and predatory behavior is more suggestive of transient whales than resident whales. Though I cannot assert this supposition in hindsight, it appears that large cetacean species are occassionally subject to orca predation in the study area. The only observations of marine mammal predation by known transient individuals in the southern range, involved harbor seals as prey.

The harbor seal predation that was observed included both cooperative and individual hunting strategies. In both cases hunting is assumed to be a tactic of silent sneak attack on single seals encountered in the water. In the cooperative strategy the seal is surrounded by circling whales and the whales took turns swimming rapidly at the seal, striking it with their bodies, flukes, dorsal or pectoral fins. Visual cues may serve as the primary form of group coordination, since the whales were in close proximity to one another and transient whale vocalizations have been rarely recorded by researchers (Ford and Fisher 1983; Ford 1983; Osborne 1986). In the solitary strategy, only a single individual within the pod repeatedly tail-lobs on top of the seal. In all instances, after 18 to 24 minutes of attack the seal disappeared and the pod milled in a small area, as though sharing the kill. In one instance, 10 minutes after the seal disappeared a whale surfaced with what appeared to be entrails draped on its dorsal fin (Osborne et al. 1984). Lopez and Lopez (1985) have observed orcas sharing pinniped prey in Patagonia, Argentina. However, Rice (1968) has also reported that small pinniped prey is often swallowed whole.

In all cases of seal predation the extended handling of the prey appeared to reflect an intentional activity. However, additional observations would be needed to discern if these behaviors represent cautious predation, play, or serve some other function such as instructing the young, as has been observed in Patagonia, Argentina (Lopez and Lopez 1985). The rocky shorelines where harbor seals haul out in the southern range necessitate that seals be captured while they are free-swimming. In Patagonia, large concentrations of pinnipeds haul out on gravel beaches, where orcas have been observed to temporarily strand themselves in order to capture pinnipeds located on the beach and to pull them into the water with the pinniped in their mouth (Lopez and Lopez 1985).

3.4.2) Tidal Orientation

Transient pods frequently occur in areas of minimal tidal current, although their distribution is not limited to such areas. Their prolonged nondirectional milling and apparent lack of destination is in contrast to the usually directional movements of resident pods (Table 4). Although transient pods have been documented to travel approximately 550 kilometers in six days (Ford and Ford 1981), once inshore they tend to move quickly across major straits and remain in restricted areas for extended periods. They were observed to mill during only 6.9% of slack observations (Table 5) which suggests that their prey do not exhibit the same tidal dependence as those of resident pods. However, protected bays and channels will often remain essentially slack throughout the tidal cycle, but migratory species rarely enter into such ares. The inconsequence of tide changes on transient pod direction of travel (Table 3) and their avoidance of the major tidal axis of deep channels are further indications of the distinctions in prey choice between resident and transient communities.

Although transient whales do not seem to respond to the change in direction of the tidal current, all observations of seal predation occurred during positive tide heights. Since these whales attack while seals are off their haul-out areas, it appears that transient foraging ecology may be more appropriately analyzed in response to tide heights rather than tidal currents. Seals are known to be off their haul-outs during high tides because these areas are mostly submerged during these tides (Everitt et al. 1979). Hoyt (1984) recalls an account of unidentified orcas waiting for the high tide to force sea lions (_E. jubatus_) off their haul-out. However, more data are needed on transient whale tidal orientation to quantify this relationship. In 1976 there was an 11 day tracking of radio tagged transient whales from O pod, during which time a harbor seal was consumed (Erickson 1976). Unfortunately, a tidal analysis or formal presentation of these data has yet to be conducted, but plans are underway for the author to enter into a joint effort to analyze and publish these data.

3.4.3) Acoustic Behavior

From preliminary findings it appears that transient pods may all share the same acoustic call repertoire (Ford 1983). However, transient pods have been silent in the majority of instances when they were acoustically monitored (Ford and Fisher 1983; Ford 1983; Osborne 1986). On one occasion a few vocalizations were recorded during daylight foraging, but this represents less than 2% of the daylight acoustic sample on transient whales (N = 4.6 hours,. Osborne et al. 1984).

The prevalence of acoustic silence among transient pods could be a means of avoiding detection by their acoustically sensitive mammalian prey. Results from playback experiments (Fish and Vania 1971; Cummings and Thompson 1971; Schwarz and Greer 1984; Abbot 1970; Felleman and Ferraro unpublished data) suggest that the vocalizations of orcas may have varying effects depending on the acoustic sensitivity of their prey. Consequently, the degree to which orcas vocalize while foraging may provide further indication of their prey choice. Herman and Tavolga (1980) have attributed similar adaptive significance to the incidence of silence in orca foraging behavior.

In support of this assumption, Ljundblad and Moore (1983) noted that there were no vocalizations during their observations of orcas chasing gray whales in the northern Bering Sea. Yablokov (1966) suggests that the high degree of contrast in the pigmentation of orcas may facilitate visual coordination. In addition, Norris (1967) recognized the importance of passive listening in the feeding behavior of cetaceans. Therefore, group coordination in the detection and capture of marine mammal prey can be accomplished without vocalizations, which provides the predator the benefits of a sneak attack. Herman and Tavolga (1980) have recognized the adaptive value of silence in this context. In addition it may be suggested that transient pods vocalize infrequently to avoid detection by resident pods (Osborn et al. 1985). This consideration will be addressed again in section 4.3.

It is not known what effect dialect differences have upon feeding ecology, other than serving to identify individuals, pods and communities. However, orca phonation characteristics other than dialects may be important in ecological considerations of how cooperative foraging is coordinated (Hoelzel and Osborne 1986), and in relation to potential prey capture techniques associated with acoustic stunning (Norris and Mohl 1983). A clearer understanding of how these acoustic variables affect feeding ecology awaits further research.

3.4.4) Characteristic Encounter

Figure 9. Example of Transient Pod Daily Activity

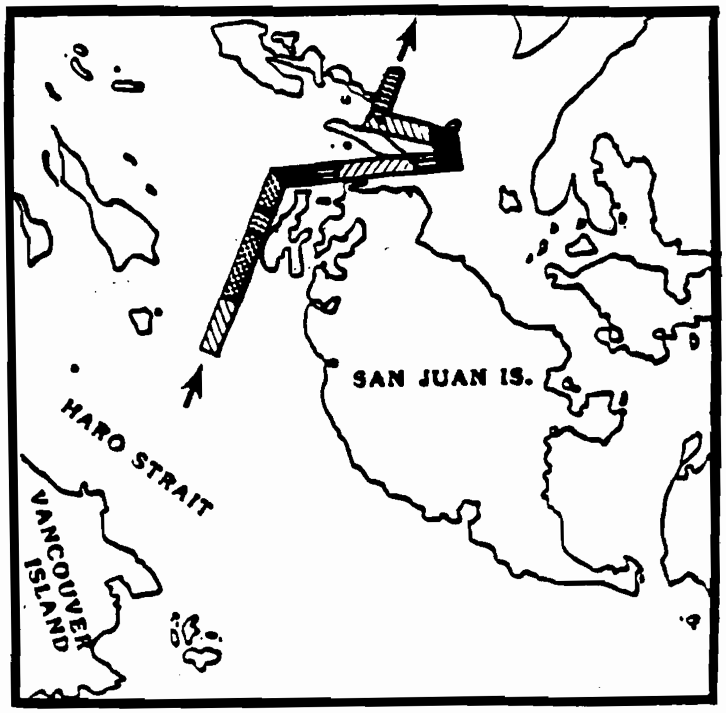
Transient whales from M pod were observed for 6.5 hours on 9/18/84. They were initially observed for 0.5 hours traveling quickly across Haro Strait with the flood current. They proceeded to forage and mill for 1.5 hours along the west side of Henry Island, characterized by upwelling currents and abundance of fishes. A minke whale passed by them before they encountered their first harbor seal in the water, just south of Battleship Island at slack high current. The seal was initially surrounded by the three whales (male, female, juvenile). The male proceeded to tail lob on top of the seal which appeared too frightened or stunned to flee. The female joined in the tail lobbing before the 3 whales converged on the seal for an extended mill. The attack lasted approximately 0.5 hours and the 3 whales appeared to share the kill, though no consumption was observed. The whales then proceeded to travel and intermittently mill against the ebb current along Spieden Channel for 2.0 hours. A second harbor seal was encountered 2.5 hours after the previous one. A similar procedure of approximately 0.5 hours of tail lobbing the seal occurred as if to knock it out before being consumed. The presence of the juvenile and the extended handling time of the seal suggested the possibility of this being an instructional session. The whales then changed direction again and traveled west into the current around small islands in New Channel. They were last observed milling in a notherly direction towards Boundary Pass.

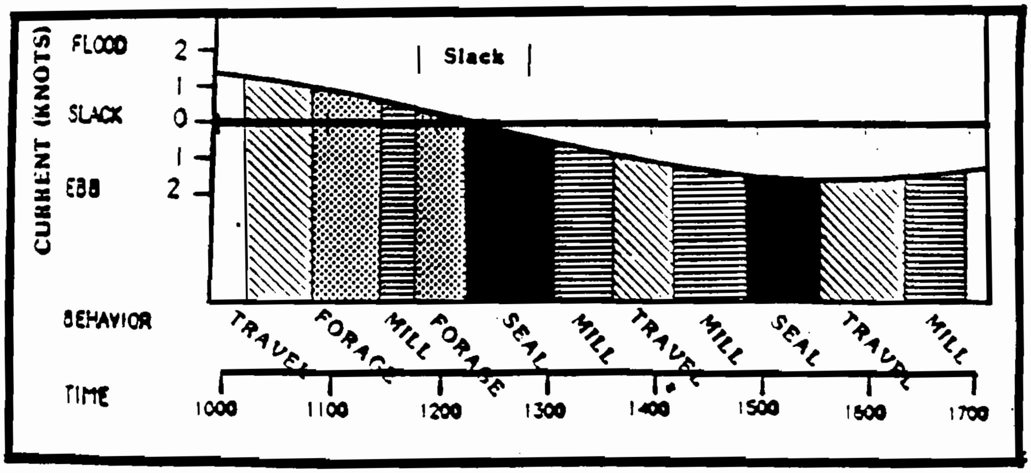
During this time, the whales were observed to travel approximately 7.3 nautical mile in 6.5 hours. Their average ground speed was only 1.12 knots, covering a linear distance of 4.7 nautical miles. They traveled both with and against the current and milled independent of slack current. None of their direction changes actually caused them to turn around and were therefore not scored as true direction changes. However, their interspersed milling behaviors frequently occurred independent of slack current. Both harbor seals were taken during positive tide heights. Other than the direct observations of predation, their occurrence in narrow channels, known for harbor seal abundances and the observed erratic surfacings over small distances, independent of slack current, appears to be indicative of seal predation and is easily distinguished from resident strategies.

ENCOUNTER #61
09-18-84

TRANSIENT

M. POO





3.5) Summary of Results from Pacific Northwest

I suggest that the resident communities are more similar to each other in their behavior and ecology than they are to the transient community because of similarities in their prey choice. Observations during the spring to fall of resident pods assumed to be associated with fish predation include: 1) the presence of salmon and bottomfish remains and the absence of marine mammal remains in the stomach contents of southern resident bull L-8, 2) direct observations of salmon predation 3) increased occurrence into the study area corresponding with peaks in runs of migratory salmon, 4) regular surfacings, from headland to headland, along the major straits used by migratory salmon and salmon fisherman, 5) echo traces of large single targets in the upper water column, suggestive of salmon, collected in the presence of foraging resident orcas, 6) selective use of tidal currents by resident pods, similar to that proposed for migratory salmon, and 7) frequent vocalizations both during the day and night, with the highest density and variety of vocalizations occurring during active feeding.

Observations of transient pods primarily from spring to fall assumed to be associated with seal and bottom fish predation include: 1) the predominance of seal remains in the stomach content of transient bull 0-1, 2) 5 documented observations of transient pods feeding on harbor seals, 3) non-seasonal occurrence into the study area, indicative of the resident prey selected, 4) erratic surfacings with many direction changes independent of the tidal current which is assumed to reflect the non-migratory movements of their prey, 5) prolonged milling in sheltered areas associated with harbor seal haul-outs and bottomfish habitat, 6) preliminary hydroacoustic (fish-finder) recordings made in the presence of foraging transient pods revealing echo traces of large multiple targets associated with the substrate which are suggestive of bottomfish, 7) infrequent vocalizations, which is assumed to be a predatory tactic in response to the acoustic sensivity of their mammalian prey.

Estimates of the average daily distance and rate orcas travel are difficult to summarize due to the effect their orientation to the tidal current has on their rate of progress (Figures 6,7,9). The southern resident example reveals an average ground speed of 1.3 knots with the whales traveling against the current (Figure 6). In contrast, the northern resident pod averaged 4.5 knots traveling with the current (Figure 7). On average the resident pods are estimated to travel between 3.0 and 4.0 knots. Although the transient pods are known to travel great distances, their propensity to mill for extended periods in small regions of the habitat makes it difficult to estimate their average speed of travel without a long sequence of observations. During Erickson's (1976) eleven day tracking of radio tagged individuals from O-pod, their daily average rate of travel ranged from 1.65 knots to 3.56 knots.

3.6) PREY CHOICE AND EXPOSURE TO POLLUTION

A potentially dangerous consequence of the transient feeding strategy and another indication of the distinction in their prey choice from resident pods is reflected in the high accumulation of PCBs (polychlorinated biphenyls) in the blubber of transient bull O-1. Levels of PCB at 250 parts per million wet weight and DDE (2,2-bis-(p-chlorophenyl)-1,1-dichloroethylene) levels of 640 ppm wet weight were found in its blubber (Calambokidis et al. 1984). Its stomach contained remains of elephant and harbor seals (Bigg pers comm). In contrast southern resident bull L-8, whose stomach contained only remains of salmon and bottomfish (Balcomb et al. 1980), had PCB levels of 38 ppm wet weight and DDE levels of only 59 ppm wet weight (Calambokidis et al. 1984).

Because of their wide distribution, transient whales are exposed to a variety of toxic sources. In the study area especially, they eat harbor seals and bottomfish that are highly polluted (Malins et al. 1982; Calambokidis et al. 1984). As the top level carnivores in the food chain, transient whales are at a high risk of deleterious effects resulting from "bioaccumulation" (Aguilar 1984). Any reproductive disorders that may result could have devastating effects on the transient community whose rate of population increase is very slow (Bigg 1982). Five dead neonates were collected from northern resident community waters (Bigg pers comm) and one dead neonate was collected from Puget Sound in 1983. It is not known if these dead whales were from resident or transient pods, but it should be noted that all transient pods frequenting Greater Puget Sound waters also range through the northern waters (Bigg 1982).

Although there are only 2 samples, I would expect that resident pods have lower levels of pollution in their blubber than transient pods because they do not eat harbor seals. However, a larger sample of pollution levels in orcas and their prey is needed before this hypothesis can be rigorously tested.

3.7) PREY CHOICE AND GROUP SIZES WORLDWIDE

It is instructive to review the literature on orca group sizes worldwide and to draw upon comparisons with other marine and terrestrial social predators in order to have a comparative-ecological context from which to address observations from the Pacific Northwest.

Alexander (1974) suggests there are no universal benefits to group living but rather several universal and automatic detriments, which include: 1) increased competition for resources, including mates; 2) increased likelihood of disease and parasite transmission; 3)increased conspicuousness rendering a species less effective as a predator or more vulnerable as prey. Alexander (1974) suggests that an exhaustive list of benefits which could offset the aformentioned detriments may be encompassed by three general categories, which include: 1) reduced susceptibility to predation due to aggressive group defense or by taking refuge within a school or herd; 2) the nature of the food resource may make splintering from the group less profitable. This can occur when cooperative foraging techniques are needed for the capture of large prey or when seaching for a large widely distributed food supply which individuals would not be likely to encounter frequently on their own; 3) extreme localization of some resource (eg. haul-outs) requires individuals to aggregate.

Since orcas have no known predators and since they are known to forage cooperatively, orca group size is more likely to be a reflection of prey type they select as it relates to the preys' detection and catchabilty, rather than a response to predation pressure. Therefore, differences in the size, mobility, and distribution of prey are likely to contribute to variations in group size and foraging strategies observed in orcas globally. This method of interpretation is in agreement with Wells et al. (1980). A similar suggestion was made by Budylenko (1981) from observations of orca predation in the Antarctic. The ability of a group of predators to capture prey larger than a single predator is perhaps the most commonly cited benefit of group living for terrestrial social predators: lions (Caraco and Wolf 1975); wild dogs (Estes and Goddard 1967); wolves (Mech 1970); for a review of the carnivore literature see (Kleiman and Eisenberg 1973; Gittleman and Harvey 1982; Bekoff et al 1984). In order to test if a similar relationship exists between the size of orca pods and the size of their prey I have scaled the size of prey reporterd in the literature and from my observations in the Pacific Northwest. Though I recognize that my characterization of prey size is not absolute, the similarities in the reported observations of orca predation suggest that cooperative foraging bestows advantages to individuals foraging in groups of similar size for various types of prey.

Most reports of predation describe the pod size to within an individual. However, when characterizing the pod size of the Pacific Northwest population, I have chosen to take an average of the northern and southern resident populations, for they are both fish eaters. A separate average for the transient population was taken since they are listed as harbor seal predators. These calculations yield a mean resident pod size of 13 and a mean transient pod size of 3 (Table 6). Averages are used because the typical pod size in which orcas travel is assumed to reflect an adaptation to a particular foraging strategy. Seasonal aggregations of several pods are not included in these estimates because of their ephemeral existence and apparent social importance. This analysis is attempting to characterize the selective forces regulating the minimum pod size required for the successful detection and capture of prey. Selection against temporary large pods would be simply due to the abundance of prey available to support orcas in high density. However, there would be no apparent limitation on the size of the prey they could attack in such a group. Competition over small prey can lead to aggression in large groups of carnivores (Beckoff et al. 1984).

I have treated the Soviet data similar to the Pacific Northwest data. The Soviet whaling data from the Antarctic Ocean presented in section 1.1, demonstrated striking differences in prey choice and group sizes between populations inhabiting similar regions (Berzin and Vladimirov 1983). The population which ate 98.5% fish traveled in much larger groups (150-200) than the population which ate mostly marine mammals (10-15) (Berzin and Vladimirov 1983). Although the species of prey were not presented Budylenko (1981), reviewing work by Doroshenko (1978) among others, states that the minke whale constitutes 85% of the orcas' diet in the Antarctic. From the analysis of 15 years of whaling data, Budylenko (1981) states that in the Antarctic, group sizes of orcas occur in the following frequency: 10 (55%), 10-20 (15%), 20-50 (10%), 50-100 (11%). However, he noted during observations of large aggregations that smaller groups could be distinguished within the larger group (Budylenko 1981). He attributed these variations in group size to be in response to their hunting strategy, though the only explanation given was that orcas will try to encircle their prey (Budylenko 1981). Although Budylenko's (1981) review of of orca group sizes contrasts with Berzin and Vladimirov (1983), his suggestion that these large groups are tempory aggregations of smaller groups seems likely. Therefore, the Antarctic sample will be characterized by group sizes of 15 orcas which accounts for approximately 70% of the the Soviet sightings. The minke whale is considered the principal prey, for it was represented in 85% of the stomach samples (Budylenko 1981).

Prey size is scaled relative to the size of a single prey item multiplied by the number of those items present. However, if only a single prey item is selected from the group, which is common when large baleen whales are prey, only the size of the targeted individual is estimated. Although the space between each prey item in the group will contribute to the size of the group, that space will be ignored in these estimations because it was rarely decribed in the literature. The size of mammalian prey is approximated from an average adult size unless specified otherwise by the account in the literature.

The size of fish schools is assumed to be approximately 15 m as dervived from side scan sonar observations of various fish schools along the California coast (Smith 1970 in Anderson 1981). The sonar data were used to develop a stochastic model for the size of fish schools (Anderson 1981). This estimation is limited by the lack of species identification associated with the sonar observations, but it appears that anchovy may have been the most abundant species present (Anderson 1981). This model suggests that 15 m may be a good general estimate of the size of schools of small fishes, whereas large fishes may tend to have a wider range of large diameters schools (Anderson 1981). Therefore, 15 m may be a good approximation of the size of herring schools, but may under estimate the size of salmon schools, which I assume to be 20m. In addition, the life history stage of the fishes as well as environmental and behavioral variables may affect the size of schools (Springer 1957; Anderson 1981). Consequently, without recordings made concurrent with observations of orca predation and without an indication of the space between schooled mammalian prey, these estimations of prey size are only meant to serve as a first attempt at estimating one of the parameters I consider necessary for developing a model of the ecological factors affecting orca group sizes worldwide.

The references listed in Table 6 were selected because of the reliability of their estimations of pod size and prey abundance. Data in Figure 10 were generated from references summarized in Table 6. Large seasonal aggregations of orcas which only form temporarily are not included in this discussion because of the likelihood that social factors are overriding ecological influences on group size when prey abundance is not limiting. For example, seasonal aggregations of approximately 80 orcas are known to "intermingle" (Osborne 1985) during the peaks of the salmon runs in the Pacific Northwest. Temporary large aggregations of possibly several hundred orcas have been reported in both the Arctic and Antarctic (Braham and Dahlheim 1981; Budylenko 1981). I suggest these seasonal gatherings are a reflection of their breeding system rather than a predation strategy. Similarly, the understanding of fluctuations in the group size of lions and other social terrestrial predators has required the consideration of social as well as ecological factors (Caraco and Wolf 1975; Bertram 1976; Nudds 1978). Insight into the social factors affecting group size is drawn from terrestrial comparisons in section 4.2.

It appears from the references used in this analysis that selection has favored similar group sizes for the detection and capture of single baleen whales and small schooled prey (Figure 10; Table 6). Even though orcas exhibit specializations to their habitat which is refelected in their prey choice, I suggest there are similarities between accounts of orca predation which are more basic to understanding orca foraging strategies than the details of how each prey type is consumed.

Table 6. **Literature Used in the Analysis of Orca Group Sizes**

Orca Group Size	Prey Type	Estimated Cumulative Prey Size	Approximate Latitude	Location	Reference
$\bar{X}$= 3	Harbor seal	2m	48 N.	San Juan Island, Wash.	Osborne et al. 1985
$\bar{X}$= 3	Elephant seal/sea lion pup	3m	42 S.	Punte Norte, Argentina	Lopez and Lopez 1985
5	Male sea lion	3m	37 N.	California coast	Rice 1968
5	Gray whale calf	5m	37 N.	Carmel, Calif.	Baldridge 1972
7	Minke whale	8m	48 N.	Barkley Sound, B.C., Canada	Hancock 1965
$\bar{X}$= 15	Minke whale	8m	50 S.	Antarctic, Ocean	Budylenko 1981
$\bar{X}$= 10	Gray whale	12m	63 N.	N. Bering Sea	Ljunblad and Moore 1983
9	Schooled herring	15m	65 N.	Norway	Christensen 1981
12	8 Dall's porpoise	18m	48 N.	British Columbia, Canada	Pike and MacAskie 1969
$\bar{X}$= 13	Adult salmon	20m	23 N.	B.C., Canada and Washington	Osborne et al. 1985
30	60' blue whale	20m	48 N.	Baja California, Mexico	Tarpy 1979
6	10-15 sea lions	25m	25 N.	Santa Barbra Is., Calif.	Norris and Prescott 1961
$\bar{X}$= 17	3 humpback whales	42m	44 N.	Newfoundland, Canada	Whitehead and Glass 1985
$\bar{X}$= 20	100 dolphins	230m	25 N.	N. Pacific Ocean	Brown and Norris 1956
$\bar{X}$= 35	200 Narwhals	800m	65 N.	N.W. Territory, Canada	Steltner et al. 1984

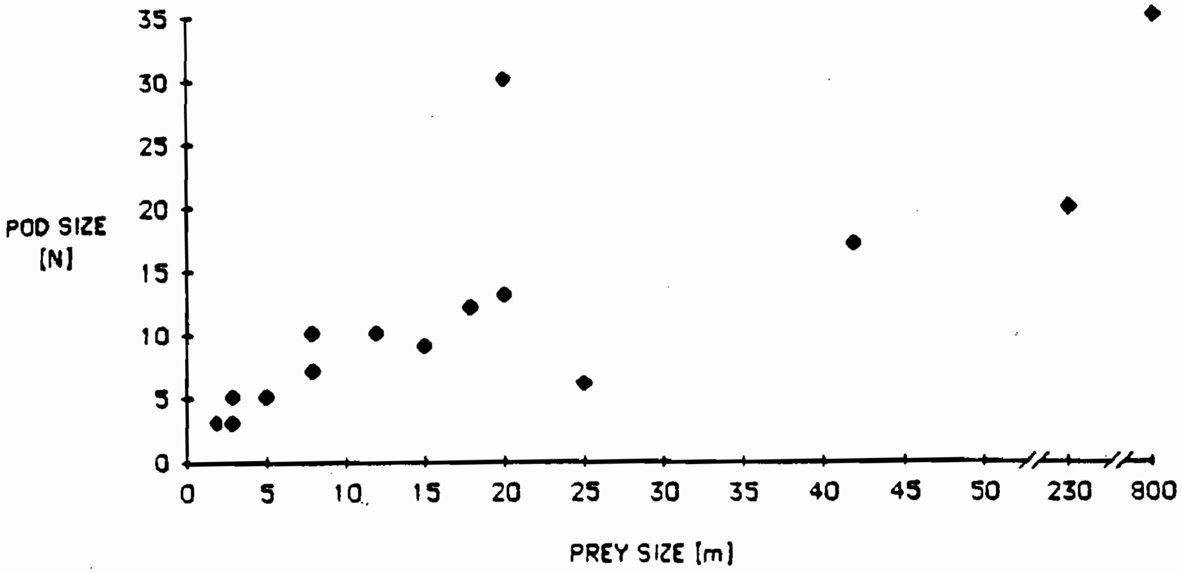


Figure 10. Relationship Between Prey Size and Pod Size

Strategies to attack pinnipeds which are hauled-out, such as the temporary stranding of orcas on the beaches of Patagonia, Argentina (Lopez and Lopez 1985) are similar to reports in the S.E. Indian Ocean (Condy et al. 1978). In both of these instances, as well as with the transient pods of Greater Puget Sound, pod sizes are small and prey are easily localized due to their association with haul-outs. When orcas prey on large widely distributed baleen whales, schools of marine mammals or schools of fishes, they appear to benefit from a large pod to detect and capture their prey. Orcas exhibit specializations in the way they attack large baleen whales which appears to include the preferential removal of the prey's lips and tongue (Baldridge 1972). In addition, distinct divisions of labor have been observed in orcas attempting to slow down the prey by biting the flukes and fins while others remove chunks of flesh (Tarpy 1971) similar to the way in which wild dogs collectivley eviscerate large ungulate prey (Estes and Goddard 1967).

However, despite the obvious distinctions between the strategies orcas employ to consume various types of prey, I suggest there are some basic similarities among the strategies which provides similar selective advantages to individuals living in large pods for the detection and capture of single large prey and small schooled prey. It appears that orcas will often attempt to encircle their prey from behind (sea lions: Norris and Prescott 1961; dolphins: Brown and Norris 1956; blue whale: Tarpy 1979; minke whale: Budylenko 1981; herring: Christensen 1981; gray whales: Ljungblad and Moore 1983; narwhal: Steltner et al 1984; salmon: Felleman and Heimlich-Boran 1984; Hoyt 1984; this study). The technique of encircling the prey appears to concentrate small schooled species and prevent large species from escaping. In addition, orcas are able attack with stealth by approaching their prey from behind. Orcas also appear to increase the stealth of their attack by approaching mammalian prey in silence (right whales: Cummings et al. 1972 in Ljungblad and Moore 1984; gray whales: Ljungblad and Moore 1984; harbor seals: Osborne et al. 1985).

The overall size of the prey is also expected to affect the likelihood of orcas encountering it based on its relative grain size in a patchy environment (MacArthur and Pianka 1966). The tendancies for orcas to swim in flank or crescent formations may also improve their ability to detect prey through their combined sonsory capabilities (Norris and Dohl 1980) and/or passive listening techniques (Norris 1967). Other factors which also appear to contribute to the number of orcas needed for the detection and capture of prey include: the site tenacity, temporal predictability, and acoustic detectability of prey.

From their review of the literature, Martinez and Klinghammer (1970) suggest that orcas use a similar predatory technique for the capture of various types of prey which involve approaching from behind, diving, and then surfacing from underneath the prey. However, they suggest that baleen whale predation requires a completely different strategy. I am in agreement with their interpretation of the literature, but suggest that the techniques required for predation on baleen whales impart selective pressures on pod size similar to that required for predation on schooled prey. Support for this assumption and Figure 10 is drawn from the similarity of direct quotes from the literature describing orca predation on a variety of species.

Quotes from four observations of predation on large baleen whales reveals a striking similarity among the strategies. Doroshenko (1978) states in reference to orca predation on baleen whales in the

Antarctic, "Group hunting reminiscent of wolves, spread into a wide arc (p. 107)." Ljungblad and Moore (1983) state, "At 1350, we sighted four killer whales....swimming nearly abreast in a crescent formation chasing a lone gray whale (p. 362)." Tarpy (1979) states, "The predators exhibited distinct divisions of labor. Some flanked the blue (whale) on either side, as if herding it. Two others went ahead and two others stayed behind (p. 459)." Finally, Budylenko's (1981) description of orca predation on minke whales in the Antarctic, independently summarizes the previous quotes by stating, "The killer whales approach their prey in line with the aim of encircling it (p. 525)."

There are equally similar reports of orca predation on schooled marine mammal prey. Norris and Prescott (1961) describe the predation of 10-15 sea lions, "It was obvious the sea lions were terrified. The killer whales appeared to stay in a crescentic formation at the rear and side of this closely packed group of sea lions (p. 334)." Norris and Brown (1956) recall a report of orcas attacking 100 common dolphins, "...the killers swam in circles around the dolphin school gradually crowding them tighter and tighter (p. 326)." Steltner et al. (1984) describe a highly coordinated attack upon 200 narwhals, "The narwhals were completely encircled by the killers and continued to move around us in all directions (p. 459)." Steltner et al. (1984) summarizes their review of orca predation by suggesting, "...a comon pattern in attacks by killer whales on social odontocetes involving encirclement of the prey school, followed by individual or mass attack

(p. 462)."

A final series of quotes from the literature on fish predation will be used to illustrate the similar influences these divergent prey taxa have on orca foraging strategies. Christensen (1981) states, "Sometimes the pod is seen to form a semi-circle when moving ahead. If a school of herring is found in the open sea, the pod concentrates the herring by swimming in circles around the school. When a compact school has been formed, some of the whales dive under the herring and eat, while the rest of the pod holds the school closely together (p. 635)." Hoyt (1984) describes salmon predation by northern resident orcas. "Ignoring the fishermen, the whales form a wide circle. The bulls at one end of the line speed ahead, gradually turning in and slowing down, leading the pod into a netlike formation.... The whale circle closes, the odd whale still smacking its tail. Several long, silvery salmon, suddenly trapped, begin leaping, boiling in the cauldron. We watch as each whale, in turn, enters the arena (p. 143)." Similar reports of a strategy involving the encirclement of schooled prey fishes by porpoises have been observed (Springer 1957; Fink 1959) which suggests this technique may be common for social odontocetes. The striking similarity that orcas try to encircle the various types of prey they select suggests that the overall size of the prey is likely to have effects on pod size (Figure 10).

Advantages for individuals to cooperatively forage in large pods are most likely at a minimum when hunting for small, site tenacious prey, which can be located and consumed by solitary orcas. Whereas, benefits to individuals foraging cooperatively are probably at a maximum when large, schooled, or potentially dangerous prey are selected.

It is interesting to note that the largest group size of foraging orcas reported was with a school of 200 narwhals (Monodon monoceros) as prey (Steltner et al. 1984)(Table 6). Single narwhals have been observed to be crushed between two orcas or struck by the tail of a single orca (Steltener et al. 1984), similar to the technique observed with harbor seals (Phoca vitulina) (Osborne et al 1985; Felleman 1985b). However, an entire school of narwhals, each with their potentially dangerous swordlike tooth, probably requires the utmost in cautious coordination. This does not imply that the same size pod could not of attacked a smaller school of narwhals, but it is suggested that a large school of narwhals could not have been as effectively corralled by a smaller pod of orcas.

Group selectionist explanations for the evolution of cooperative foraging in orcas need not be invoked because it appears that pod members are closely related and are known to remain associated with each other for many years (Bigg 1982). Consequently, the apparent benefits to an individual's inclusive fitness (Hamilton 1964) and feeding success, suggest that kin selection (Hamilton 1964), individual selection (Williams 1966), and/or reciprocity (Trivers 1971) can parsimoniously account for the persistence of group living in orcas.

Consequently, one must be cautious in interpreting the numerous reports of the occurrence of great densities of orcas in high latitudes as only a result of prey abundance (Leatherwood and Dahlheim 1979; Martinez and Klinghammer; 1970; Balcomb 1984). Although the largest groups of orcas have been observed near the poles, large groups do not commonly occur (Budylenko 1981). The plot of the effect latitude has on pod sizes from the literature listed in Table 6 is depicted in (Figure 11). It appears from this sample that pod size varies more consistently with prey size than with latitude (Figures 10, 11).

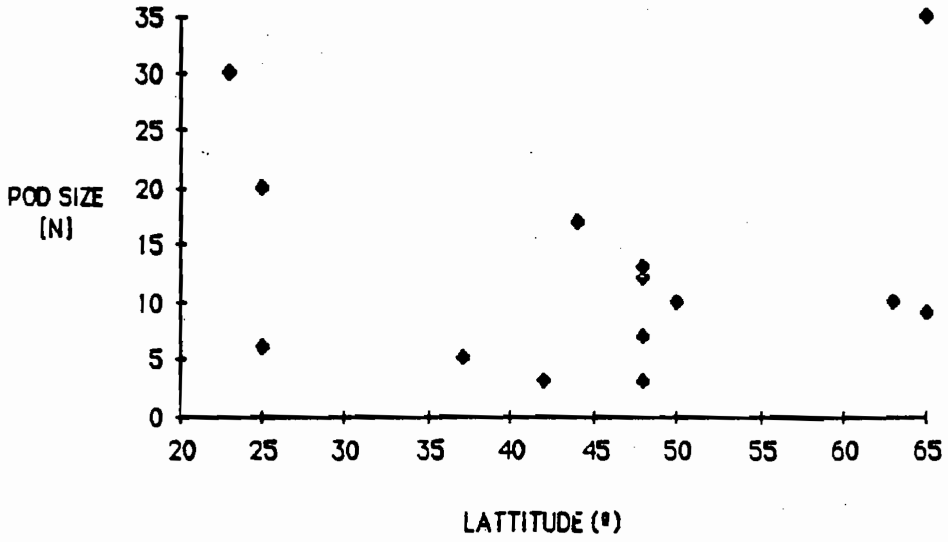


Figure 11. Relationship Between Latitude and Pod size

The wide range of prey available to orcas and the propensity for orca populations to exhibit preferences for specific types of prey is reflected in the range of group sizes exhibited by orcas, even within the same habitat. Therefore, orcas may occur in greater densities in areas rich in food resources, but the group sizes exhibited by a population are more likely to vary according to the type of prey selected, not just the absolute abundance of prey.

4.0) DISCUSSION

The discrete nature of a pod and/or a community of pods provides ample opportunity for preferences or "traditions" to become established. Norris and Dohl (1980) state, in reference to dolphins, that "learning capabilities provide for a high level of behavioral flexibility in nature and that this is translated into local variations in group behavior that we might call cultures (p. 253)." Differences between transient and resident pods' behavior and ecology are evident, yet members of these communities are of the same species, live in overlapping habitats, and feed on partially overlapping prey. Members of resident and transient pods look different, vocalize differently, travel in groups of different sizes and socially interact within separate, closed communities. They follow traditional community-specific geographic routes and employ different feeding strategies.

4.1) PREY CHOICE AND THE THEORY OF FEEDING STRATEGIES

Since orcas are intelligent social predators, differences in foraging strategies may be expected to develop between discrete populations similar to that observed among terrestrial social carnivores (Beckoff et al. 1984). The flexibility to take a wide variety of prey sizes, facilitated by cooperative foraging strategies helps to explain why there are so many species subject to orca predation worldwide. However, each population is bound to become specialized to their habitat. The tendency for terrestrial social carnivores to exhibit preferences for specific prey out of the wide variety available to them has been well documented (Bekoff et al. 1984) and appears to be a primary factor influencing the feeding ecology of orcas as well.

Schoener (1971) states the four key aspects of feeding strategies are: 1) the optimal diet, 2) the optimal foraging space, 3) the optimal foraging period and 4) the optimal foraging group size. It is important to note as Lewontin (1977) has stated, "The dynamics of natural selection does not include foresight, and there is no theoretical principal that assures optimization as a consequence of selection (p. 12)." Consequently, one cannot be sure that adaptive compromises which make certain adaptations appear suboptimal are occurring. However, when certain behaviors have defined energetic costs (eg. porpoising and swimming against the current), optimality theory helps focus attention to those trade-offs which may offset such apparent costs. If used cautiously, optimal foraging theory can direct research questions to be stated as testable hypotheses. I am not asserting that enough is currently known about the energetic and reproductive consequences of orca behaviors to exclude competing hypotheses, but we can learn more about these evasive study subjects as we direct our questions to testable problems. The tidal analysis presented in this thesis has provided a predictive index as to the likelihood of the whales changing direction in relation to a change in the tidal current (Table 3). Each change in the tidal current is another test to study new variables associated with prey encounter rate or individual variations which coordinate group movements.

In the review that follows, I will use Schoener's (1971) four key aspects of foraging strategies in an attempt to classify orca predatory behavior that I believe has been historically misunderstood. My goal is to summarize what is already known, providing a theoretical context which can be used to direct future research.

1) Optimal Diet: all models reviewed suggest that as prey abundance increases, predator selectivity increases (Schoener 1971; Griffiths 1975; Pyke 1984). According to theory, whether or not a prey item is eaten should depend on the absolute abundance of only high ranking food types (eg. having the highest food gain to average handling time ratio). An animal should never specialize on low ranked food types regardless of its abundance (Pyke 1984).

Yablokov et al. (1974) suggests that cetacean feeding adaptations can be expressed as a combination of the eight categories orginally defined by Tomlin. These include ichthyophages, benthoichthyophages, teuthoichthyophages, teuthophages, sarcophages, river benthoichthyophages, river benthophages and phytophages. They suggest that the prey preferred by these groups are those which are most abundant. However, they recognize the somewhat arbitrary classification by feeding adaptation type, noting the importance of behavioral flexibility in overriding morphological specializations, distinctions in prey choice between age and sex classes, and between seasons (Yablokov et al. 1974).

Yablokov et al. (1974) and Gaskin (1976) placed orcas in the sarcophage (flesh eating) category. However, after reviewing the diversity of prey items from orca stomach content analysis, Yablokov et al. (1974) suggest calling them ichthyoteuthosarcophages, for lack of a better name. This classification implies that orcas are opportunists which I consider inappropriate. Until the data sets are sorted by populations, controlling for age, sex and season, the summation of stomach content data will continue to provide only an indication of what orcas "can" eat, not what a discrete population "does" eat.

Grant (1971) provides empirical evidence in support of my concerns about the dangers associated with making generalizations about the feeding ecology of entire populations. From analysis of variation between morphological features of birds living on islands and those living on the mainland, Grant (1971) showed that intraspecific variation within populations were larger than comparisons between regions. He originally thought his bird population was composed of generalist feeders, but found it to be composed of various types of specialists. Grant (1971) suggets that his results may be accounted for by Van Valen's (1965) hypothesis which states, under spatially uniform environments, selection favors little interindividual variation in feeding ecology and associated morphology, whereas under patchy conditions the opposite occurs.

It is surprising to me that after Yablokov et al. (1974) recognizes these points, they perpetuate the use of these categories. I am similarly surprised that a systematic survey of the orca stomach content and morphological data from the Antarctic, presented by Berzin and Vladimirov (1983), has not been analyzed using the coefficient of variation index which Yablokov (1966) rigorously developed to discern the level at which variations occur. However, Defran and Pryor (1980) were able to draw general parallels between cetacean behavior and feeding classification. They also place orcas in the sarcophage category, suggesting they share opportunistic tendencies with _T. truncatus_ and _P. crassidens_. However, their orca sample is based on few observations with the southern resident community, which limits their ability to account for individual or population-specific variations. Although there seems to be some general agreement between most cetaceans' sociality in nature and ease of training in captivity, it is difficult for me to see how one can draw an analogy between the captive behavior of _Feresa_, which are known to be quite aggressive and _Orcinus_, which are known to be quite approachable in captivity (Defran and Pryor 1980), even though both species are known to attack fellow cetaceans (Pryor et al. 1965; Best 1970).

Bekoff et al. (1984) state in their article on the social ecology of carnivores that, "... the way in which food resources are exploited (located, hunted, scavenged, defended) and the nature of the available food (quality, quantity, spatial distribution) strongly influence interspecific relationships and result in marked intraspecific variations in social organization (p. 217)." Rosenzweig (1966) suggests that since carnivores must expend considerable energy to stalk, chase, or ambush and kill their prey, an individual will achieve greater foraging efficiency if it only selects profitable prey, which may relate to its relative size.

In recognition of these variables it would perhaps be more informative to attempt a detailed type of classification which one can apply to observations of specific populations. The flexibility in a species prey choice must be addressed in order to classify its foraging strategy. Species have been defined as generalists rather than specialists if they eat a greater range of food types, a greater variance of food types, a greater breadth of food types, exhibit a wider repertoire of feeding behaviors, or a greater ability to extract energy from food (Schoener 1971). There are ecological conditions which favor a specialist strategy and others that favor a generalist strategy. All theories of optimal diet reviewed predict that when prey are scarce a predator should take items proportional to their abundance. However, low ranked prey items should not be included at any time (Pyke 1984). The degree to which a predator is obligatorily or facultatively limited to its strategy is an important variable to consider when addressing its ability to "switch" between prey types. Cornell (1975) defines predator switching as the ability of a general predator to become conditioned to its most abundant prey, so that its attacks are more frequent than would be predicted by chance. This strategy requires that the predator exhibits a flexible search image, influenced by learning.

Cornell (1975) distinguishes two types of search strategies. Undirected searchers take prey in proportion to their occurrence in the predator's range. This best describes a truly opportunistic strategy, whereas directed searchers spend time seeking specific prey species at the exclusion of others. Obligate specialists and switching generalists are considered directed searchers. The switching generalist retains the efficiency of search image formation as well as the advantage of taking a diversity of prey (Cornell 1975). Although these assumptions are largely untested, certain predictions can be made which favor switching behavior in general predators. 1) patchy prey in space and time, 2) non-sessile searching predator, 3) use of sensory detection systems which work at a distance (Cornell 1975). Orcas meet all the above criterion to be considered switching generalists.

The environmental cues which make prey predictable (season, tide, habitat) are suggested to contribute to orca search images. Braham and Dahlheim (1982) suggest that orcas in Alaska can switch to marine mammals when fish prey are less abundant. However, we do not have enough information on orcas in Alaska to identify what their "preferred" prey are. Ballenberghe et al. (1975) provide strong evidence to suggest that the wolves of Minnesota continued to seek their preferred deer prey even when populations of other prey were seasonally more abundant. However, in order for similar results to be available for orcas a better indication is needed of their winter activities.

Other cetacean species, such as the bottlenose dolphin (Tursiops truncatus), which are also considered generalist predators (Wells et al. 1980; Defran and Pryor 1980) do not exhibit the distinct morphological specializations that have been observed among orca populations (Sergeant 1978; Bigg 1982; Berzin and Vladimirov 1983; Osborne et al. 1985). It is the community-specific traditions in prey choice and morphological variations that distinguish orcas from generalists. Recognizing that specializations in prey choice are common among carnivores (Bekoff et al. 1984) and that cooperative foraging techniques facilitate greater flexibility in the range of prey selected, I suggest orcas can be best described as facultative specialists. However, until we begin to address the individual level of variation in prey choice, we will not be able to make further distinctions in their predatory strategies.

2) Optimal Foraging Space: Schoener (1971) suggests we need to know the temporal and spatial distribution of food resources, resource gradients, locations of patches, rate of resource depletion, and how predictable the abundance of food is in order to predict how an animal can maximize its fitness as a function of its home range size, patch selection or exclusiveness of territory.

In section 3.1 I have made some characterizations of the temporal and spatial distributions of orca prey in the Pacific Northwest. However, two further distinctions between transient and resident orca foraging strategies can be discerned by considering the ecological influences of differing prey distributions. Web (1984) provides evidence to suggest that "sit and wait" predators tend to select prey of large absolute and relative size. He suggets that small or intermediate sized items or patches are too widely distributed to be exploited economically without "cruising" search capabilities. Web

(1984) has shown how selection has favored different propulsion mechanisms in fish based on their predatory behavior. These strategies can be interpreted into the terminology of optimality currency. The cruisers can be thought of as number maximizers, searching for large quantites of small diffuse prey. In contrast, the "sit and wait" predator can be thought of as an energy maximizer, taking fewer large prey. However, the relative efficiency of prey capture among the two groups must also be compared.

The alternate foraging strategies observed in the Pacific Northwest orca population appears to fit into these broad categories even though they exhibit the same morphological adaptations for locomotion. The large resident pods are the cruisers, scanning wide areas for their relatively small, loosely schooled salmonid prey. Although transient pods are known to travel at least 760 nm (Leatherwood et al. 1984), once inshore their prolonged milling in small regions of the habitat appears to reflect a "swim and wait" strategy in response to their locally abundant, relatively large, pinniped prey. Since the salmonid prey of the resident pods are continuously being replaced during the spring to fall, with almost every flood tide, these whales can remain in a core area of their range without severly depleting their patch. In contrast, the site tenacious harbor seal prey of the transient pods can be locally exterminated, thereby requiring the transient pods to travel large distances between patches.

3) <u>Optimal Foraging Period</u>: Schoener (1971) states the basic

components which constitute an optimal foraging period involve the metabolic costs of various activities under different climatic conditions and times of varying prey abundance. Pacific Northwest orcas have been observed to spend between 40% and 70% of their daily activity foraging (Table 2). However, it is not known how much of the observed foraging behavior involves searching behavior versus actual prey consumption. The milling behavior of transient pods is probably more a reflection of them waitng for seal encounters or socializing rather than being indicative of continuous fish predation. It may be predicted that orcas should expand their feeding periods during times when food is sparse, energy demands are high, or when they can best convert their food into descendents (Schoener 1971). Although the time it takes orcas to handle prey fishes is difficult to estimate, harbor seals appear to take 0.5 hours of handling before consumption. However, these observations are biased to fair weather conditions during the spring to fall. Therefore, better seasonal data are needed to address the effects of variable prey densities on the time allocated to foraging.

4) Optimal Foraging Group Size: Schoener (1971) suggests three hypotheses can be used to evaluate the selective value of group foraging, which include: a) the group may hinder feeding, but there are other benefits to being gregarious, b) animals aggregate in proportion to prey concentration, but group size may be of neutral selective value, or c) groups may allow animals to feed more effeciently. A comparative review of the social terrestrial predators, will be used to

summarize the information covered in this section.

4.2) Comparisons with Terrestrial Social Predators

Kleiman and Eisenberg (1973) have reviewed the convergent evolutionary trends in canid and felid social systems. They provide evidence to suggest that similar selective forces have favored cooperative foraging in three canid species, wolf (Canis lupus), dhole (Cuon alpinus), and cape hunting dog (Lycaon pictus) and one felid species, lion (Panthera leo) even though these species have followed distinctly different evolutionary paths since the mid-Pliocene. They suggest that cooperative foraging was the primary adaptation which enabled these species to feed on large herbivores in the open savanna even though the methods employed by canids and felids differ. Although the canids rely on speed and group coordination in their hunts, the lion, which is the only cooperative felid, relys more on stealth than speed and is distinctly less cooperative amongst conspecifics at the kill (Kleiman and Eisenberg 1973). Bekoff et al. (1984) state that carnivores are an excellent group for studying adaptive patterns of life history traits due to the great variation within the order. They note that carnivores are known for dietetic preferences and suggest that the variation observed in life histories is associated with food habits.

The effects of prey type on group sizes exhibited in these diverse species is striking. Caraco and Wolf (1975) state that selection has favored the capacity of social animals to respond to the temporal and spatial patterns of resource availability. They suggest further, that the two primary variables influencing group size are individual prey biomass and capture efficiency. When hunting small prey (eg gazelle), group sizes averaging 2 lions are maintained for maximizing hunting efficiency (Caraco and Wolf 1975). However, when preying on large, abundant herbivores, lion prides are apparently larger than one would predict based on hunting efficiency alone. Although larger groups of lions may be more successful at attacking larger prey and keeping scavangers away, it appears that group sizes are larger than needed for maximum hunting efficiency. Average group sizes of 6 to 8 lions appear to be maintained because of the benefits bestowed on pride members' reproductive success due to cooperation between females raising cubs (Caraco and Wolf 1975).

Wild dogs appear to exhibit varying group sizes depending on the size of the prey, retaining 4 to 6 individuals as a minimum for an effective pack (Estes and Goddard 1967). Wolves also exhibit varying group sizes with prey type, but like lions often occurr in group sizes apparently larger than one would expect for hunting efficiency (Nudds 1978). Benefits to group members' inclusive fitness may account for the acceptance of larger than optimum foraging group sizes if the additional individuals are kin (Bekoff et al. 1984).

There are also seasonal and population-specific variations in group size which can also be attributed, in part, to the ecological characteristics of prey types. Bekoff et al. (1984) suggest that interspecific variation in carnivore social evolution as a response to prey resources is the rule for cooperative foraging groups. Pride lions appear to maintain home ranges which will support them year round. The annual herbivore migrations provide a seasonal fluctuation in the size and abundance of available prey. Prides have been known to fragment during the dry season, whereas, the nomadic lions follow their migratory prey (Schaller 1972). Similarly, Mech (1970) found temporal changes in wolf pack size with decreasing deer density. However, Zimen (1976) points out that the size of a wolf pack is a result of the density of the wolf population, size of the main prey species, as well as the changes in the population density of prey species.

Similar variations in prey choice, group size and home range are apparent in the Pacific Northwest orca populations. Like other social predators, the discrete nature of an orca pod and the propensity for pods to exhibit preferences in prey choice are underlying factors in the evolution of such apparent distinctions between populations. Consequently, it appears that similar selective pressures have favored the evolution of cooperative foraging groups in divergent taxa.

Caraco and Wolf (1975), among others, have suggested that selection has favored the capacity of social animals to adjust their group size in response to ecological variables, primarly the temporal and spatial patterns of resouce availability. The alternate ecological strategies observed between nomadic and pride lions provides the most direct analogy I have found to the transient/resident distinction in orcas. Schaller (1972) noted that prey capture efficiency in lions increased with increased group size and that larger groups had more multiple kills. However, Caraco and Wolf (1975) provide a more detailed analysis of the ecological determinants of group sizes which helps to distinguish the nomadic from the pride strategy.

Pride lions utilize permanent home ranges and defend territories which are large enough to support them throughout the year (Schaller 1972). Pride lions disperse to hunt in groups of 2-8 or more individuals. The annual herbivore migrations on the Seregeti, like the the returning adult salmon to the Fraser River, predictably alter the size and abundance of prey available to pride lions and resident orcas alike (Caraco and Wolf 1975; Felleman and Heimlich-Boran 1984). In contrast, nomadic lions follow the migratory prey across the plains and into the woodlands each dry season (Caraco and Wolf 1975).

Transient pods have been observed to travel 550 km in 6 days (Ford and Ford 1971) and into S.E. Alaska (Leatherwood et al. 1984) however, it is not known if the nature of their occurrence is a reflection of the seasonal and regional biases in the sighting effort. It has been suggested that transient pods may be more or less resident to the inshore waters (Bigg et al. 1985) but occurring in areas less intensively covered by researchers. Since transient pods can exploit harbor seals and bottomfish anytime during the year, their occurrence is not expected to be seasonal. However, I doubt the likelihood that transient pods reside in the inshore waters when they have been observed in Alaska and appear to exhibit a foraging strategy adapted to regions of high pinniped abundance. The increasing poplations of pinnipeds to the inshore waters may provide the transient pods with a stable food supply. However, they may use this region for social reasons. Therefore their occurrence may not be limited by prey, but it may not directed by it either. The seasonal fluctuations in the abundance of salmon and resident pods (Heimlich-Boran 1986b) may imply that the resident orcas follow their prey, similar to the nomadic lion strategy. However, the winter occurrence of all the pods is virtually unknown making this question still a point for speculation.

It should be noted that lions respond to the seasonal fluctuations of their preferred prey, not just the absolute abundance of all potential prey (Bourliere 1963). There is ample evidence of specialization in prey choice between orca communities as well. The ecological influences on lion group sizes and social organization provide intriguing directions for future research. Perhaps, of greatest interest to ecologists and managers is the influence of alternate ecological strategies on reproductive success. Bigg (1982) has evidence to suggest that transient pods exhibit significantly lower reproductive success than resident pods. Nudds (1978) showed that the optimal pack size for wolves is a function of prey size, but packs are often larger than would be expected for hunting efficiency. Caraco and Wolf (1975) have suggested that when prey is not limiting, prides are sometimes larger than would be expected for hunting efficiency.

It appears that the benefits of sociality on a lion's inclusive fitness may outweigh costs associated with increased energetic requirements of larger groups (Rodman 1981). Large prides contain 6-8 closely related females who protect and even communally nurse each others' cubs (Schaller 1972). Apparently, due to this cooperation, half of the cubs born in prides survive past 2 years of age, while less than one third of nomadic lionesses' cubs reach that age (Schaller 1972). However, Bertram (1976) suggests suckling is not indiscriminate, for there is competition within prides for limited resources. However, combinations of kin selection (Hamilton 1964), reciprocal altruism (Trivers 1971) and idividual benefits to breeding synchronously all appear to contribute to communal nursing. Vehrencamp (1980) suggets that in addition to benfits from synchronous parturition, communal nursing can occur in species such as elephants, which have long lactation periods resulting in a high degree of overlap between lactating females. Vehrencamp (1980) also notes that steps towards eusociality in mammals involving divisions of labor and "altruistic" sacrificing of reproductive effort occurs most frequently in older individuals. Evidence in support of the importance of older helpers in cetacea is provided by Kasuya and Marsh (1984) who have shown that post-reproductive short-finned pilot whales (Globicephala macrorhynchus) continue to lactate.

In addition, there are numerous other benefits of group living for orcas and most odontocetes. Herman and Tavolga (1980) review several accounts of allomaternal behavior in delphinids. An excellent example of epimeletic behavior was demonstrated by a pod of orcas in British Columbia which supported a conspecific at the surface for several days after it was hit by a ferry (A Field Report 1974). The pod also serves a social fascilitation function in which calves learn the to live and hunt with the group. Norris and Dohl (1980) state with reference to social learning in dolphins, "The school is the social unit within which such learning must find its meaning (p.244)." Lopez and Lopez (1985) have observed adult orcas tossing sea lions they have caught to juveniles. This behavior is similar to the techniques lionesses use to teach their cubs to hunt. Lionesses are known to bring maimed prey to their cubs so they can learn stalking and killing techniques (Beckoff et al. 1984). These reports support my inclination that the extensive lobtailing that was observed during M pod's predation of a harbor seal was to allow the calf to be involved in the hunt.

A series of hypotheses can be generated from these comparisons, utilizing optimal foraging theory, inclusive fitness and reciprocity theory to direct future research. For example, ascertaining the extent to which resident communities are reproductively isolated and whether the transient community attempts to breed with the resident community as nomadic lions do with pride lions, is critical to our understanding of the breeding system. Although some carnivores are highly inbred (eg wolves), there is little indication of inbreeding depression (Beckoff et al. 1984). However, the fact that dispersal in orcas appears to be minimal, suggests that Pacific Northwest population may consist of a mosaic of highly inbred pods. The application of genetic analysis through biopsy sampling of this population, proposed by my colleague A.R. Hoezel at Cambridge University, may enable these and other questions regarding orca sociality to be addressed in the near future.

4.3) COMPETITION BETWEEN COMMUNITIES?

The importance of competition in determining an organism's coexistence with other organisms as well as many other facets of its life history characteristics has been recently subject to critical review (Connell 1980; Simberloff 1982; Schoener 1983; Sih et al. 1985). Although even our ability to determine the existence of competition has been questioned (Connell 1980), Schoener's (1983) review of 164 field-experimental studies on interspecific competition found that 90% of them demonstrated the existence of competition. No significant differences in the occurrence of competition between freshwater, marine, or terrestrial environments appear to exist (Schoener 1983). However, these studies recognize the need for more empirical hypothesis-oriented field studies before the role of competiton can be adequately addressed. I am not proposing that such information is available from this orca field study, but by reviewing some observations I have made in the context of current competition theory, I hope to provide some hypotheses which can be tested by future research. Although most of theories reviewed involve factors influencing interspecific competition, I suggest they can be applied to address the possibility of intraspecific competition between socially isolated orca communities without altering their premises.

Schoener (1983) suggests there are 6 forms of competition which are subsets of 2 generally recognized classes: exploitative and interference. Since detailed data are not available for more in-depth analysis, only these larger classes will be addressed. Exploitative competition involves some individuals using resources, depriving other individuals from the benefits of those resources. Interference competition is the more classical, direct confrontation between individuals for resources (Schoener 1983).

One of the basic premises underlying competition theory is that two species cannot coexist if they are too similar in their resource requirements. However, more recent investigators have also recognized the need to consider the frequency and distribution of resource utilization (Schoener 1983). Connell (1980) suggests there are two ways to account for the origin of species coexistence in the same habitat: they may have evolved seperately, becoming preadapted to specific aspects of the environment, or they both could have coevolved under competition pressure, causing them to diverge into different parts of the habitat. Co-occurrence increases the likelihood of coevolution by enhancing the ability of two species to affect each others reproductive success. The more interdependent two species are (eg. predator/prey), the more likely they will co-occur. Finally, interacting species which do not seek each other out, but are competing for similar resources will increase their co-occurrence as their prey selection overlaps (Connell 1980). However, the likelihood of coevolution will be reduced due to environmental variability which can reduce the frequency of co-occurrence if habitats exist in small patches. Temporal variability can reduce the timing of co-occurrence. Biological variability, as it relates to species diversity , will also reduce the likelihood of coevolution (Connell 1980).

I will use Schoener's (1974) review of the types of complimentarity which facilitate co-occurrence, tempered by Connell's (1980) and Simberloff's (1982) "competing" hypotheses in this discussion. Schoener (1974) reviews five categories of complimentarity as follows: 1) Food type and habitat - species that overlap may eat different foods, 2) Food type and time - temporal separation of the diurnal or seasonal scale may permit species to eat the same prey without directly competing, 3) Habitat and time - climatic variations can permit different species to be active during different times of day or year, 4) Habitat and habitat - involves the vertical and/or horizontal partitioning of the habitat, 5) Food type and food type - involves specializations in prey choice which is often regulated by the relative size of the prey. The variation in the size of prey selected has been ascribed to account for the coexistence of various sympatric carnivores of similar size (Rosenzweig 1966). His study further suggets the importance of specializations in prey choice among carnivores.

Gittleman and Harvey (1982) found that, after correcting for metabolic requirements, diet was the only ecoloigical factor that correlated with interspecific comparisons of carnivore home range sizes. In addition, they found a wide variation in intraspecific ranging behavior, which they also attributed to food availability. Furthermore, they state that the tendancies for carnivores to adapt to the variety of habitats they range through makes objective classification of their "typical" habitat difficult (Gittleman and

Harvey 1980).

The extreme behavioral and ecological differences between resident pods and transient pods may have enabled them to coexist in overlapping habitats, while the ecological similarities between the two resident communities may have caused them to partition their prey resource by maintaining distinct home ranges. The strong association between resident orca movements in relation to the tidal current appears to be indicative of salmon predation (Table 3). This further suggests that the division of the resident community ranges is not coincidental with the tidal boundary in the Strait of Georgia (Figure 1). This boundary does not limit the orcas' movements, but provides a natural barrier by to partition their salmonid resources because their tidal orientations would have to reverse if they were to cross the boundary.

Bigg (1982) has estimated the home range size of the southern resident, northern resident and transient community to be be 230 nm, 300 nm, and 340 nm respectively. The distance between the core areas of both resdient communities is approximately 210 nm, which is only 2.5 days traveling at an average of 3.5 knots (Bigg 1982). The proximity of the two discrete communities suggests that their division is not coincidental. With further research on the offshore movements of the transient community and the winter movements of all communities, the estimates of these ranges may be increased. For example, the recent observation of M Pod in Southeast Alaska during the summer of 1984 (Leatherwood et al. 1984) doubles the Bigg (1982) estimate of the transient range.

Observations with the Pacific Northwest orca community fit Schoener's (1974) complimentary classification numbers 1,3,4 and 5. The amount of prey overlap between resident communities may have been great enough for them to form discrete home ranges, while the transient community appears to be able to coexist by eating prey not preferred by resident pods. In addition they are able to partition the habitat by occupying regions not frequented by resident pods.. There also appears to be a temporal separation between transient and resident occurrence. Although transient pods are never observed as commonly as resident pods in Haro Strait, they have not been observed at all during June and July, when resident pods are most commonly observed (Figures 5, 8).

Brown and Orians (1970) state that home ranges may be defined by 1) mutual avoidance, 2) preference for an unexploited food supply, 3) physical barriers, or 4) differing habitat preferences. In combination with community-specific traditions in prey choice, all these variables appear to contribute to the structure of these orca communities. Without prior knowledge of how these pod communities originated, and since no aggressive interactions between pod communities have been observed, it is difficult to assess the role of competition in the maintenance of these discrete populations. Consequently, one cannot simply invoke the "ghost of competition past" to account for what is presently observed (Connell 1980). However, these types of explanations have been used by Yablokov et al. (1974) and Sergeant (1978) to account for the ecological distinctions in the niches cetaceans currently occupy. For example, Yablokov et al. (1974)

suggest that the differences in the baleen of the mysticetes has resulted from competitive exclusion for preferred prey sizes which currently enables them to co-occur.

Ecological overlap itself does not indicate competition, but may result from interspecific tolerance, whereas low overlap may result from interspecific exclusion (Schoener 1983). Slatkin (1974) has also shown by modeling the population dynamics of competing species that it is possible for two similar species to coexist in the same region as it is possible for one species to exclude another from the same region. In order to demonstrate the existence of coevolution between species, Connell (1980) states three things need to be proven. 1) divergence in resource utilization has occurred between two species, 2) that it has occurred from competition and not some other variable, 3) that the divergence has a genetic, not just a phenotypic basis. For these reasons it is very dificult to prove the existence of competition in natural environments. In addition, it cannot be asserted that food is limiting in the Pacific Northwest because the occurrence of orcas has not varied despite the fact that the size of salmon runs have fluctuated by orders of magnitude due to 1) the race of the Fraser River sockeye run returning that year, which has varied between 2 and 20 million (Groot and Quinn 1986), 2) the alternating occurrence of pink salmon every odd year, which contributes an additonal 3 to 8 million fish to the annual catch of Washington and British Columbia (IPSFC 1985), 3) the anomolous advection of warm water from the equator, known as the El Nino event of 1983, which significantly reduced salmon stocks (IPSFC 1984), 4) the number of Fraser River sockeye salmon which travel through Johnstone Strait has varied from 22% to 85% (IPSFC 1984) thereby significantly varying the proportion of salmon allocated to each resident community.

It is probably a tribute to the Fraser River salmon runs that resident pods of orcas occur with such high abundance and frequency in this estuarine system. However, the numerous other salmon and steelhead rivers, herring spawning grounds, and bottomfish habitats that characterize this region are also likely to contribute to the orcas' residency (Aro and Shepard 1967; Simenstad et al. 1979; Long 1983; Trumble and Humphreys 1985). In addition, the growing number of harbor seals and sea lions throughout the state (Calambokidis et al. 1984, 1985) continue to provide transient pods with a stable prey resource.

Having addressed these concerns, I suggest that the resident communities are partitioning their resources, while the differences characterizing transient pod feeding ecology are more likely a reflection of their distinct origins, reflected in their alternate feeding adaptations, rather than a result of direct competition. However, transient and resident pods do appear to avoid interacting with each other, although no direct evidence of territorial defense has been observed. The infrequent vocalizations of transient pods may serve to keep interactions between the communities to a minimum, in addition to its purported adaptive value in foraging. Similarly, wild dogs, wolves, and lions are known to avoid encounters with other conspecific groups, but are known to fight if they come into contact with each other (Wilson 1975).

Connell (1980) suggests we may be able to detect the existence of competition by comparing populations in allopatry with those in sympatry. If environmental features can be controlled for, we may be able to attribute the relevant differences between populations to the absence of one species in allopatry (Connell 1980). Comparisons based on these distinctions may be the most fruitful way of addressing the importance of competition between the allopatric resident communities with the sympatric coexistence between resident and transient communities.

The high degree of social isolation observed between populations makes the application of management strategies based on global stock areas inappropriate for orcas (Perrin 1982). It is suggested that the concept of "population stock" as stated in the Marine Mammal Protection Act of 1972, in which each population is managed independently of the status of the whole species, is more appropriate. It is hoped that insights derived from this long-term field study can be applied to management questions such as stock management and to the growing concerns over interactions with fisheries.

4.4) CONSIDERATIONS OF FISHERY IMPACTS

In order to address the impact marine mammals have on a particular fishery, one must be able to specify the nature of the impact, recognize the limits of the data base available to address the magnitude of the impact, and weigh the perceived economic costs of the impact against the estimated value (aesthetic, ecological, commercial) of the presence of marine mammals. The application of competition theory can be useful in formulating questions specifying the type of impact to be addressed. Marine mammals have been implicated as being competitors with humans. In order to evaluate the nature and extent of the interaction it would be useful to distinguish between the types of competition as either exploitative or interference. Beverton (1985) refers to these interactions as either biological or operational, respectively. Interference competition includes the incidental take of marine mammals, damages to fishing gear, and a reduction in the amount of effective fishing time. Exploitative competition includes ecosystem interactions involving marine mammals which may be eating commercially targeted species, serving as hosts to parasites affecting commercial stocks, or eating species which may be prey or predator of commercial species (Beverton 1985). It is obviously easier to evaluate the economic impacts of interference competition by estimating the cost of gear lost and time not spent fishing versus trying to evaluate the role marine mammal predation plays on the prey community. However, when marine mammals benefit a fishery by directing it to the location of commercial stocks, as in the association between tuna and porpoise, the evaluation process is less clear. In addition, the recent concerns over the fate of discarded net on marine mammal mortality is similarly difficult to evaluate.

Since orcas are not known to destroy fishing gear or to be subject to incidental mortalities from fisheries-related activities, I will limit my discussion to a review of some considerations of exploitative competition. It should be noted that there has not been an empirical demonstration of marine mammals depleting the abundance of commercial fish stocks (Beverton 1985). Although the incidental take of porpoise in the tuna and salmon fishery has been extensive, there has not been conclusive evidence that suggets this has caused a dramatic reduction in the cetacean stocks (Beaverton 1985). Consequently, it may be premature to call these interactions truly competitive. This is not to say there is no reason for concern. Marine mammals have been proteced in the United States since 1972 and may be expected to return to their pre-exploitation population levels. In addition, as human populations continue to grow, our demands from the sea will expand and increase the likelihood of interactions with marine mammals.

However, a perceived impact to a fishery may cause special interest groups to demand "solutions" to the "problem". When commercially valued species are subject to any predation pressure other than human, the fishing industry has in the past influenced the implementation of dramatic predator control measures, even when the magnitude of the impact had not been carefully evaluated. As a worst case example, the United States Navy killed hundreds of orcas in Iceland because it was believed they were depleting herring stocks (Hoyt 1984). There have also been numerous concerns over the impacts marine mammals have on the salmon stocks in the North Pacific which are subject to predation pressure during all phases of their life history (Hokoyo 1959; Spalding 1964; Fish and Vania 1971; Fiscus 1982). In addition, marine birds may significantly contribute to the mortality of juvenile salmon (Furness 1982). Fiscus (1982) reviewed the stomach content data from 34 species of marine mammals inhabiting the North Pacific. He found that 15 species (44%) were known to prey on salmon, while several other species were noted to eat salmon infrequently (Fiscus 1982). In his review, Fiscus concluded that humans were still the most significant salmon predators, but recognized the limitations of the methodology available to address the magnitude of an impact a cetacean could have on a particular fishery.

Furness (1982) reviews a series of techniques helpful in conducting such an evaluation. He presents them in their order of increasing precision: 1) population census data combined with consumption estimates from captivity, 2) simulation models combining population data with bioenergetic equations derived from laboratory studies, and 3) direct measurements of metabolic rate in free ranging mammals. Investigators have used these techniques to make estimates of marine mammal predation over very broad areas. Utilizing bioenergetic equations of metabolic rate and population census data, Hain et al. (1985) have estimated the food requirements of cetaceans inhabiting the shelf-edge of the Northeast United States to be 480,000 tons per year. An even more dramatic estimation is provided by Yablokov et al. (1974), who suggest that the total daily consumption of all cetaceans is approximately 2 million tons! However, a number of qualificaitons must be made of such estimates before we are able to extrapolate what impact these metabolic requirements may have on particular fisheries. A detailed review of the relative merits of these techniques is beyond the scope of this thesis, but the first comprehensive review of case studies utilizing various techniques, primarily involving pinnipeds, can be found in Beddington et al. (1985). However, the treatment of impacts by cetaceans is significantly more difficult, because we are unable to analyze scat or make as accurate population assessments.

Instead of comparing the various methodologies employed in these studies, I will review some of the parameters needed to make estimates of impacts by cetaceans on fisheries and point out some of the limitations in the data sets to make such calculations. Initially, an accurate estimation of the size of a cetacean population is prerequisite to calculating the biomass requirements of the population. Unfortunately, these data, when available, are frequently biased because they have historically come from the whaling industry which conducts non-random searches for target species and has been known to falsify their data in order to continue fishing. Consequently, an independent estimation of population size utilizing photo-identification or dedicated research vessels (boat or plane) traveling at randomized transects is recommended. The same is true for estimations of the size of fish stocks assumed to be impacted. Variations in the experience of fisherman effect the applicability of catch per unit effort (CPUE) calculations for making stock assessment. Experimental fishing is recommended to control biases in fisherman's ability and diligence in reporting the locations and durations of their fishing effort.

An evaluation of cetacean feeding habits is difficult, but we need to know to what extent are cetaceans exploiting prey which are either not available to the fishery due to regional limits or not selected by the fishery. Cetaceans may be meeting a significant portion of their metabolic requirements on prey of no commercial value. This was empirically demonstrated by Fitch and Brownell Jr. (1968) who found a high occurrence of myctophids in the stomach contents of pelagic dolphins. In additon, if cetaceans are eating prey which are predators to a commercial stock, then their consumption would aid the fishery. This type of relationship has been demonstrated between sea lions eating lamprey that would otherwise be parasitic to salmon (Beddington 1985).

Since orcas have been historical residents of the Pacific Northwest (Scammons 1874) and have been shown to exhibit very low fecundity (Bigg 1982), whatever predation pressure they exert is expected to be relatively constant. Maynard Smith and Slatkin (1973) and Sih et al. (1985) provide several examples in which predators and prey can coexist at equilibrium. In addition, "unexpected" keystone predator effects, in which predation pressure can actually increase prey abundance have also been observed (Sih et al. 1985).

Perhaps most difficult of all to ascertain is what extent does prey choice vary between individuals and populations throughout the year? This theme of my thesis should be addressed in impact statements as it is likely to cause significant variance in estimates of predation. Estimates of the prey selected by cetaceans have been considered impossible to address without access to stomach content data. However, the application of hydroacoustic technology may provide a non-invasive alternative. The development of a catalogue of recordings made in the presence of different age and sex classes in populations over several seasons may provide a indication of the type and variability of prey selected (Felleman 1985b, Felleman and Thomas 1985). In addition, a characterization of the habitats cetaceans occupy throughout the year, in conjunction with an analysis of the distribution of potential prey, may provide enough information to formulate management related proposals.

Cetaceans can be implicated for observed reductions in fish stocks if one can address the following : 1) effects of over-fishing and habitat reduction 2) the evaluation of the impact other predators may also be contributing to the instantaneous mortality of the stock (eg. birds and seals), 3) the evaluation of what percentage of the stock's instantaneous mortality is considered "allowable" for predation pressure? 4) the extent which the perceived impact may be due to interannual variations in recruitment. Wooster (1983) reviews numerous examples of variations in year class strength of fish stocks which appears to be attributed to oceanographic conditions during the early life history stages of several fish species in the Gulf of Alaska and Berring Sea. Consequently, it is extremely dangerous to try to ascribe the success or failure of predator/prey management based solely on these data.

The limitations in available data to address these questions leads me to agree with Ray (1981) who states, "Indicators of their (marine mammal) ecological relationships are how obligate or facultative they are in their food preferences, what their time/energy requirements are, and what their social organization is during feeding and reproduction. Such considerations may well be more important, even, than quantitative estimates of how much they eat (p.402)." I have provided some comparative-ecological evidence to suggest orcas are best described as facultative specialists. Classifications as such do not provide a complete picture of all species selected by a population, especially considering the limitations in the seasonality of the data base. However, species exhibiting opportunistic strategies are far more difficult to evaluate as to their impact on a particular fishery. The extended observations which have enabled me to suggest this classification does provide a general index of the variability in prey choice between populations and suggests some indications of variability within populations as well. The application of hydroacoustic technology has aided me in comming to these conclusions.

Once we have some indication of the preferred prey species and an accurate assessment of the population size, worst case estimations can be made of the marine mammals' potential impact on a particular fishery. This can be accomplished by calculating the populations' energetic requirements based on one of the techniques reviewed by Furness (1982). These estimates are usually expressed as a percentage of an individual's body weight, which can be extrapolated to the age and sex class distribution of the population.

These calculations are particularly applicable to the Pacific

Northwest orca population, because their population composition has been intensively monitored since 1974 (Bigg et al. 1976) and Seargent (1969) has made calculations of orcas' metabolic requirements from a comparison of captive animals. Seargent (1969) found orcas in aquariums feed at a rate equivalent to approximately 4% of their body weight. Balcomb et al. 1980) used a range of 2.5% to 5.0% of the southern resident community's estimated total body weight. They made a worst case estimation by assuming the orcas eat 100% salmon for 50% of the year. which was used as an average duration of their stay in the inland waters. Their results reveal a consumption rate of 772 metric tons to 1545 metric tons, equivalent to 3% to 7% of the combined 1977 Washington State sport and commercial salmon catch (Balcomb et al. 1980). I have made similar calculations and have found comparable results, depending on the average weight chosen for each age class. However, Balcomb et al. (1980) did not include the population of 13 transient orcas which frequent the southern community's range. Using the same parameters, I found that the transient community consumes another 124 to 248 metric tons of food in half a year. However, it would be inappropriate to add these feeding rates to the impact on the salmon fishery in recognition of their distinctions in prey choice. Assuming the average harbor seal weighs 150 pounds (Angell and Balcomb 1982) and the average salmon weighs 10 pounds, it may be approximated that for every seal eaten, the transient pods "save" 15 salmon. However, even if salmon comprised 25% of their diet, it would only constitute another 31 to 62 metric tons, which would not significantly alter their impact on the Washington State salmon fishery. The impact of harbor seals and sea lions on the British Columbia fishery has been estimated to be 2.5% of the annual commercial salmon catch and 4% of the annual commercial herring catch, neither of which were considered to significantly impact the fishery (Spalding 1964). This calculations are considered "worst" case because they do not account for the benefit to the salmon when orcas eat salmon predators (eg seal and sea lions) or fish which are not even available to the Washington State fishery.

However, managers are often confronted with the problem of having to respond to perceived impacts without the necessary data base to address the real nature of the problem. The perceived threat to a fishery usually involves the direct interference of marine mammals with fishermen, which can draw much attention from the media. "Herschel the hungry sea lion" at the Ballard Locks has been a prime example of one such locally perceived threat. Several sea lions (_Z. californianus_) have been implicated by the Washington State Department of Game of causing the downfall of the native steelhead trout returning to the Lake Washington watershed. This was due, in part, to the direct interaction between sea lions and steelhead sport fisherman at the locks. If an attempt was initially made to observe feeding rates and census the sea lion population frequenting the locks, as I have recommended to the agencies, metabolic calculations could have been used to make a worst case estimate, assuming that steelhead was all they were eating. These calculations would have provided the managers with a preliminary indication of whether the sea lions' feeding rates could be contributing to the declinig steelhead stocks. This would have been one way of preventing this particularly localized and tractible interaction from becoming national news. Instead, it has taken several years of attempts to keep the sea lions away from the locks before it has been decided to try to estimate the impact the sea lions may be having on the trout stocks. A study has been initiated this year by the Washington State Department of Game which should provide the first accurate assessment of the severity of this problem.

However, even during such a visible fishery conflict, there were crowds of people coming to the locks with expectations of seeing the sea lions catch fish. The visitors were not just environmentalists, but included those residents and tourists who valued the opportunity to see a wild marine mammal in action. Such aesthetic values of marine mammals must be recognized when trying to calculate the economic consequence of their impact on an industry. In addition, restaurants and salespeople in the neighborhood enjoyed the increased business as a result of the media coverage.

Similarly, the whale watch cruise industry has grown significantly since my first summer in Friday Harbor. From 1980 to 1985, the whale watch industry has increased from 0 to approximately 5 vessels. In addition, the real estate agents in Friday Harbor are keenly aware of the value of being able to sell their west side property as having a view of the whales. Once we recognize that there will always be special interest groups making their opinions heard regarding real or perceived threats to fish and marine mammals, the best we can do as biologists and managers is to integrate their views into compromises, which as Scheffer (1985) says, "...is essential in the resolution of marine mammal-fishery conflicts (p. 262)."

The accesibility of the Pacific Northwest orca population has scientific as well as aesthetic and commercial value. The intensive and extensive nature of this field study would not have been possible if it were not for the ideal logistical setting of being able to conduct research on a wild cetacean population in a relatively developed region. However, it is apparent that the whales are there for the same reasons the fisherman are. As a biologist I consider this association a basic necessity for research, but the perceptions of those who see these whales as competitors or potentially new aquarium performers, may not recognize the value of this long-term field study. I do not mean to imply that aquariums are not also of value and that fishermen do not have rights too, but the only means of characterizing the social and ecological context in which cetaceans have evolved, requires that field studies maintain a long-term monitor of a population as unobtrusively as possible.

It is only after more than a decade of research that the feeding ecology of the Pacific Northwest orca can be addressed in this detail. As a result of this in-depth study, similarities with terrestrial predators have become increasingly apparent providing a context from which we can begin to synthesize a general understanding of the feeding ecology of O. orca. In addition, insights have been drawn from comparisons with the numerous isolated accounts of orca predation in the literature. These comparisons are intended to provide a broader contribution to our understanding of orca feeding ecology than simply an account of another species subject to orca predation. The diverse backgrounds of the numerous investigators working on the Pacific Northwest orca population have brought this study "beyond bean counting and whales tales" (Le bouf and Wursig 1985). However, more information is still needed on individual variations in prey choice and on the seasonal dispersal patterns of the resident and transient communities before a complete comparison of their feeding ecology can be presented. It is hoped that investigations on this population continue indefinitely, but it must be recognized that such studies can only be conducted through the long term cooperation among the field biologists who maintain the longitudinal data set and the funding institutions which recognize the value of these data.

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6.0)APPENDIX A: Autocorrelation Analysis of Direction Changes

A.1)Southern Resident Community 1983-1985

```
     AUTO.  STAND.
LAG  CORR.   ERR.    -1   -.75 -.5  -.25  0   .25  .5   .75   1
                      :----:----:----:----:----:----:----:----:
  1 -0.024  0.032                        .*.
  2  0.071  0.032                        .:*
  3  0.071  0.032                        .:*
  4  0.000  0.032                        .*.
  5  0.024  0.032                        .*.
  6  0.024  0.032                        .*.
  7 -0.024  0.032                        .*.
  8 -0.024  0.032                        .*.
  9  0.047  0.032                        .:*
 10  0.000  0.032                        .*.
 11  0.023  0.032                        .*.
 12 -0.024  0.032                        .*.
 13  0.023  0.032                        .*.
 14 -0.024  0.032                        .*.
 15  0.095  0.032                        .:.*
 16  0.047  0.032                        .:*
 17  0.023  0.032                        .*.
 18  0.023  0.032                        .*.
 19 -0.001  0.032                        .*.
 20 -0.025  0.032                        .*.
 21  0.070  0.032                        .:*
 22 -0.001  0.032                        .*.
 23 -0.025  0.032                        .*.
 24 -0.001  0.032                        .*.
 25 -0.025  0.032                        *:.
 26 -0.001  0.032                         *.
 27  0.046  0.032                        .:*
 28 -0.025  0.032                        *:.
 29 -0.049  0.032                        *:.
 30  0.094  0.032                        .:.*
```

A.2)Northern Resident Community 1985

```
     AUTO.  STAND.
LAG  CORR.    ERR. -1  -.75 -.5 -.25   0   .25  .5   .75   1
                   :----:----:----:----:----:----:----:----:
  1 -0.071  0.080                   . *:  .
  2  0.054  0.079                   .  :* .
  3  0.116  0.079                   .  : *.
  4 -0.011  0.079                   .  *  .
  5  0.051  0.078                   .  :* .
  6 -0.139  0.078                   *  :  .
  7  0.120  0.078                   .  : *.
  8 -0.070  0.078                   . *:  .
  9 -0.008  0.077                   .  *  .
 10 -0.135  0.077                   *  :  .
 11  0.061  0.077                   .  :* .
 12  0.060  0.077                   .  :* .
 13 -0.059  0.076                   . *:  .
 14 -0.108  0.076                   .* :  .
 15  0.142  0.076                   .  :  *
 16  0.086  0.075                   .  : *.
 17 -0.041  0.075                   . *:  .
 18  0.099  0.075                   .  : *.
 19 -0.028  0.075                   . *:  .
 20  0.034  0.074                   .  :* .
 21 -0.092  0.074                   .* :  .
 22 -0.030  0.074                   . *:  .
 23  0.032  0.073                   .  :* .
 24  0.094  0.073                   .  : *.
 25 -0.025  0.073                   . *:  .
 26 -0.026  0.073                   . *:  .
 27  0.162  0.072                   .  :  *
 28 -0.091  0.072                   .* :  .
 29 -0.022  0.072                   .  *  .
 30 -0.015  0.071                   .  *  .
```

A.3)Transient Community 1976-1985

```
       AUTO.   STAND.
LAG    CORR.     ERR. -1   -.75   -.5 -.25    0   .25  .5   .75    1
                      :----:----:----:----:----:----:----:----:
  1    0.031    0.074                  .  :* .
  2   -0.067    0.074                  . *:  .
  3   -0.067    0.073                  . *:  .
  4    0.030    0.073                  .  :* .
  5    0.223    0.073                  .  : ..*
  6    0.029    0.073                  .  :* .
  7    0.028    0.073                  .  :* .
  8   -0.063    0.072                  . *:  .
  9    0.034    0.072                  .  :* .
 10   -0.064    0.072                  . *:  .
 11   -0.064    0.072                  . *:  .
 12   -0.064    0.072                  . *:  .
 13   -0.059    0.071                  . *:  .
 14    0.038    0.071                  .  :* .
 15   -0.059    0.071                  . *:  .
 16   -0.060    0.071                  . *:  .
 17   -0.054    0.070                  . *:  .
 18    0.042    0.070                  .  :* .
 19   -0.055    0.070                  . *:  .
 20    0.042    0.070                  .  :* .
 21    0.041    0.070                  .  :* .
 22   -0.056    0.069                  . *:  .
 23    0.040    0.069                  .  :* .
 24   -0.057    0.069                  . *:  .
 25    0.234    0.069                  .  :  . *
 26    0.039    0.068                  .  :* .
 27   -0.058    0.068                  . *:  .
 28   -0.058    0.068                  . *:  .
 29   -0.059    0.068                  . *:  .
 30    0.232    0.068                  .  :  . *
```