Seasonal movements and foraging behaviour of resident killer whales (Orcinus orca) in relation to the inshore distribution of salmon (Oncorhynchus spp.) in British Columbia /

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Seasonal movements and foraging behaviour of northern resident killer whales (*Orcinus orca*) in relation to the inshore distribution of salmon (*Oncorhynchus* spp.) in British Columbia

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Abstract: The hypothesis that northern resident killer whales (*Orcinus orca*) move in response to the seasonal availability of salmon (*Oncorhynchus* spp.) was tested using sightings and acoustic recordings of whales and data on the timing and abundance of salmon in Johnstone Strait, off Vancouver Island, between 1984 and 1988, and from King Island, on the central British Columbia coast, for a 2-month period in 1989. Whales were most abundant in Johnstone Strait between July and October when salmon migrate through the strait. Individual whales seen in the strait during summer were observed around King Island in spring 1989, coinciding with local sockeye and chinook salmon runs. In Johnstone Strait during summer 1988, whales foraged along the shore and in areas of strong current, where salmon occur in high densities. However, less than half of the 16 pods in the northern resident community were present on more than 15% of summer days (1984–1988). The occurrence of 6 pods (A1, A4, A5, C1, D1, and H1) in Johnstone Strait during summer was positively and significantly associated with sockeye and pink salmon abundance, whereas pod G1 was positively and significantly associated with chum salmon. Although we demonstrate an association between certain pods and certain salmon species, we cannot determine whether this reflects the true preference of pods or represents differences in the whales' arrival times in Johnstone Strait that are related to other factors. Our data suggest that within the northern resident community, pods may have seasonal ranges.

Résumé : Nous avons éprouvé l'hypothèse selon laquelle les Épaulards (*Orcinus orca*) résidants de la zone nordique se déplacent en fonction de la disponibilité saisonnière des saumons (*Oncorhynchus* spp.); des observations visuelles, des enregistrements sonores et des données sur la présence et l'abondance des saumons ont été recueillis dans le détroit de Johnstone, au large de l'île de Vancouver, entre 1984 et 1988, et près de l'île King, le long du centre de la côte de Colombie-Britannique, au cours d'une période de 2 mois en 1989. Les épaulards sont présents en abondance dans le détroit de Johnstone entre juillet et octobre, période de migration des saumons dans le détroit. Les individus observés dans le détroit au cours de l'été ont été vus au voisinage de l'île King au printemps de 1989, période d'abondance des Saumons rouges et quinnats dans la région. Dans le détroit de Johnstone au cours de l'été de 1988, les épaulards se nourrissaient le long des rives et dans les zones de courant fort où la densité des saumons est importante. Cependant, moins de la moitié des 16 bancs d'épaulards de la communauté résidante du nord ont été présents pendant plus de 15% des jours d'été (1984–1988). La présence de six bancs (A1, A4, A5, C1, D1 et H1) dans le détroit de Johnstone au cours de l'été était en relation positive significative avec l'abondance des Saumons rouges et roses, alors que la présence de G1 était en relation positive significative avec l'abondance des Saumons kétas. Bien que nous puissions démontrer qu'il existe des relations entre certains bancs d'épaulards et certaines espèces de saumons, nous ne pouvons pas déterminer si ces relations reflètent des préférences réelles ou si les moments différents d'arrivée des divers bancs dans le détroit sont attribuables à d'autres facteurs. Nos données semblent indiquer qu'au sein de la communauté nordique résidante, les différents bancs occupent des territoires saisonniers.
[Traduit par la Rédaction]

Introduction

Worldwide, killer whales (*Orcinus orca*) eat a variety of fish, cephalopods, pinnipeds, and other cetaceans (Hoyt 1984; Lowry et al. 1987; Rice 1968), but within populations they may feed preferentially on specific prey types (Condy et al. 1978; Evans 1988; Heimlich-Boran 1986; Jonsgard and Lyshoel 1970; Voisin 1972). Despite their global occurrence in pelagic and coastal waters (Dahlheim 1981; Leatherwood and Reeves 1983), the most detailed studies of killer whales have been made along coastal British Columbia and northern Washington State (Balcomb et al. 1982; Bigg 1982; Ford and Fisher 1982). Here they are highly social, living in cohesive groups or "pods" (Bigg et al. 1987, 1990), comprising three distinct communities (northern and southern residents and transients (Bigg 1982; Ford et al. 1994). Transient killer whales along the Pacific Northwest coast feed extensively on marine mammals and their movements are less predictable,

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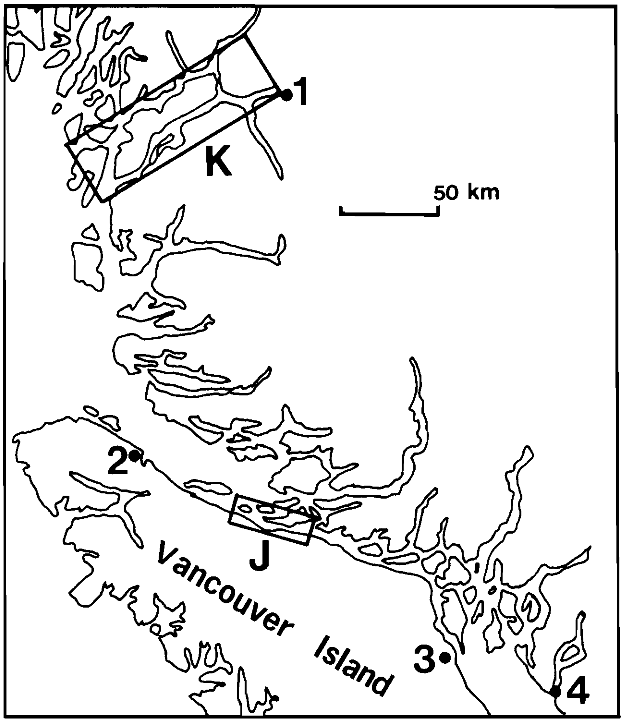
Fig. 1. Map of the southwest coastline of British Columbia, Canada, showing the approximate boundaries of the Johnstone Strait (J) and King Island (K) study areas. 1, Bella Coola; 2, Port Hardy; 3, Campbell River; 4, Powell River.



although there is a trend towards increased sightings near harbour seal haulouts during the pupping season (Heimlich-Boran 1988; Baird 1994). By contrast, residents feed primarily on salmon (*Oncorhynchus* spp.) and other fish (Ford et al. 1994; Rice 1968; Spong et al. 1970), and their movements are temporally and geographically fairly predictable.

Some seasonal movements of resident killer whales appear to be related to salmon abundance. Using sport-fishing data, Heimlich-Boran (1986) analysed the seasonal occurrence of southern residents in Haro Strait and adjacent waterways for a 3-year period and showed that it was correlated positively with salmon abundance. Guinet's (1990) data for a single summer also suggested a general positive correlation between the occurrence of northern resident killer whales and salmon abundance in Johnstone Strait. Here we examine the seasonal movements of each northern resident pod in two areas of their range in relation to salmon abundance estimates from the Canadian Department of Fisheries and Oceans (DFO). We used data for Johnstone Strait from a 5-year period and from King Island for a single season. We test three predictions of the hypothesis that killer whales feed on salmon and move seasonally throughout their ranges to areas where salmon are abundant: (1) If killer whales follow migrating salmon, they should be seen more frequently in Johnstone Strait during summer, when salmon are most abundant, than during any other period. In addition, their occurrence in the strait will be positively related to salmon numbers. (2) Killer whale occurrences will be positively related to salmon abundance in other parts of the northern community range (e.g., around King Island) when salmon are relatively scarce in Johnstone Strait. (3) The behaviour and foraging activities of killer whales in Johnstone Strait will indicate that they are feeding on salmon.

Table 1. Weeks of consecutive daily observer effort on killer whales (*Orcinus orca*) in Johnstone Strait.

Year	Observation period	No. of weeks
1984	1st week in July – 2nd week in September	11
1985	4th week in June – 4th week in September	14
1986	4th week in June – 4th week in September	14
1987	3rd week in July – 4th week in August	7
1988	4th week in June – 1st week in October	15
Total		61

Methods

Study animals

Between 1984 and 1989, the northern resident community comprised approximately 190 killer whales in 16 pods (Ford et al. 1994), which ranged in size from 3 to 23 individuals. Each pod is a social grouping of related individuals. There is no permanent exchange of individuals among pods and, in this sense, pod membership is stable over time; however, pods often split into subpods. Typically each pod consists of 1–3 subpods, and as with pods, there is no exchange of individuals among subpods (Bigg et al. 1990).

Study areas

Northern resident killer whales were studied in two areas (Fig. 1). Johnstone Strait is off northeastern Vancouver Island and is approximately 50 km from east to west and 3.5–4.5 km wide. King Island, about 180 km north of Johnstone Strait, encompasses Burke, Dean, and Labouchere channels, as well as North Bentick Arm to the mouth of the Bella Coola River. This is a circuit of about 200 km, and each channel is about 3.5–4.5 km wide.

Sighting records

Daily sighting records of killer whales in Johnstone Strait in summer were compiled from several sources. The majority of sighting records are stored at the Pacific Biological Station in Nanaimo. Additional sighting records were received from other researchers and the remainder were collected by the senior author. Each sighting record includes an identification of the subpod observed. Individual whales and hence subpods are identified from unique characteristics of their dorsal fins and saddle patches (Bigg 1982).

In all, 61 weeks of sighting records from the period 1984–1988 were selected from these sources for analysis because of their completeness (Table 1). During July, August, and September of these years, there was daily observer effort over consecutive weeks, and not only were subpods reported when present, but days without whale sightings were also reported.

In addition to daily summer sighting records from Johnstone Strait, we analysed sighting records from the nonsummer months between January 1985 and February 1989. We combined these records with the summer sightings and with acoustic data to describe the annual pattern of killer whale occurrence in Johnstone Strait. Nonsummer sighting records were collected incidentally and provide no indication of observer effort.

Sightings of killer whales near King Island were collected by the senior author and two colleagues (D. Bain and B. Kriete) between April 28 and June 12, 1989. We recorded the identity of subpods as well as days without whales and days without observer effort.

Table 2. Months from which acoustic data for killer whales (*Orcinus orca*) were used.

Year	Months	Monitoring location
1985[a]	Jan., Apr.	Telegraph Cove
1985[b]	Oct., Nov., Dec.	Orca Lab
1986[b]	Jan., Feb., Mar., Apr., May, June	Orca Lab
1986	Mar., June, Oct.	Orca Lab; Telegraph Cove
1987	Sept., Oct., Nov., Dec.	Orca Lab
1988	Oct., Nov., Dec.	Orca Lab
1989	Jan., Feb.	Orca Lab

[a]Acoustic data previously analysed (J. Ford, unpublished data) (used with permission, J. Ford, personal communication).

[b]Acoustic data previously analysed (C. Guinet, see footnote 2) (used with permission, C. Guinet, personal communication).

Acoustic records

Each resident killer whale pod has a unique dialect that can be identified aurally and by spectrographic analysis of audio recordings (Ford and Fisher 1982). We used acoustic recordings of the vocalisations produced by the whales to provide data on their presence and movements in Johnstone Strait during nonsummer months. Acoustic recordings were obtained from Orca Lab (a permanent acoustic monitoring station on Hanson Island) and from J. Ford. Recordings were analysed using a model 5500 Kay DSP spectrum analyser. Pod-specific calls were identified by comparing the screen display of a call structure with the call parameters documented by Ford (1987) and by aural comparison with previously recorded and identified examples. Although the monitoring effort was not always known, the recordings analysed represented 52 days during nonsummer months from 1986 to 1989 (Table 2). In addition, we included in our analysis pods identified acoustically by C. Guinet[2] and J. Ford (unpublished data) from 1985 and 1986.

Salmon abundance estimates

The South Coast Division of DFO in Nanaimo provided weekly estimates of the abundance of the three commercially important salmon species in Johnstone Strait, sockeye (*Oncorhynchus nerka*), pink (*Oncorhynchus gorbuscha*), and chum (*Oncorhynchus keta*), for July, August, September, and October from 1984 to 1988.

The total number of each salmon species is estimated from catch, escapement, and diversion rate. The diversion rate is the proportion of salmon that migrate via Johnstone Strait as opposed to the Strait of Juan de Fuca. The migration curves for each species are smooth, normal curves and are DFO's estimation of the pattern and timing through Johnstone Strait. Historical information on catch, escapement, stock identification, and test fishing catch per unit effort have been used to produce the migration curves (L. Hop Wo, DFO, personal communication; W. Luedke, DFO, personal communication; Gould et al. 1988, 1991).

We were unable to include chinook (*Oncorhynchus tschawytscha*) and coho (*Oncorhynchus kisutch*) salmon in our analysis because similar estimates of their numbers and timing through Johnstone Strait were not available. Both chinook and coho salmon are less abundant than sockeye, pink, and chum salmon in the area (P. Starr, DFO, personal communication).

DFO in Bella Coola (S. Hutchings, personal communication) provided catch and escapement data on sockeye, pink, chinook, and chum salmon, as well as estimates of the periods of peak abundance for each species in the King Island area during May and June 1989. From the catch and escapement data we estimated the total number of each salmon species in the study area during spring. Unlike Johnstone Strait, there are no estimates of weekly salmon abundance for King Island.

Estimating killer whale abundance in Johnstone Strait throughout the year

Daily summer sighting records combined with acoustic data and incidental sightings provided data for 36 months between January 1985 and February 1989. We used these data to calculate the average number of whales present during each month of the annual cycle.

Acoustic versus visual estimates of whale abundance

Estimates of whale abundance during nonsummer months were derived mainly from acoustic recordings, whereas summer estimates were derived from sightings. To determine if the two data sets could be used interchangeably to estimate whale abundance throughout the year, we compared estimates of whale abundance derived by the two methods when collected simultaneously on 27 days in July and August 1980, 1981, 1982, and 1983 (J. Ford, unpublished data). Assuming that all members of a pod were present, the numbers of whales estimated by the two methods were then compared in a simple regression, using analysis of variance to test the significance of the relationship (Wilkinson 1988, p. 475; Zar 1984, p. 268). Student's t test was used to test whether the slope of the regression differed from zero (Zar 1984, p. 271).

Estimating numbers of whales

Killer whale vocalisations allow identification of pods but not which of their subpods are actually present. Furthermore, pods G1 and G12 are not yet distinguishable acoustically. For analyses we assumed that when a pod other than G1 or G12 was identified acoustically all members of the pod were present. When "G" calls were identified we assumed that pods G1 and G12 were both present.

For comparison with acoustic data in this analysis only, summer sightings of subpods were converted to pods when at least one subpod of a pod was present. When multiple subpods of a pod were seen on a day, they were counted as only one pod sighting.

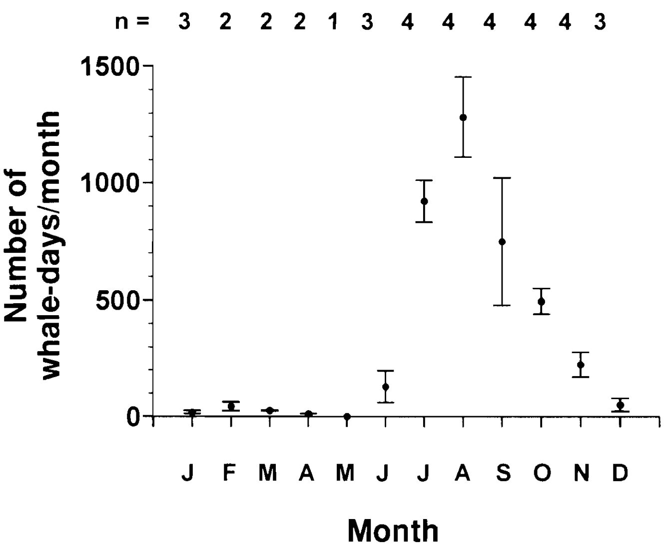
Each whale in a pod present on 1 day was counted as "1 whale-day," and the whale-days were summed for each month. Each month of the year, except May, was represented by at least 2 years of data. The mean number of whale-days per month in the annual cycle was calculated by averaging replicate months between January 1985 and February 1989.

Regression analyses

Using only the 61 weeks (1984–1988) of daily summer sighting records in Johnstone Strait (Table 1), the number of whales present

[2] C. Guinet. 1986. Étude deux populations sympatriques d'orques le long côtes de Columbie Britannique. Unpublished manuscript.

Fig. 2. Numbers (mean ± SEM) of whale-days per month estimated from sightings and acoustic data from killer whales (*Orcinus orca*) in Johnstone Strait, B.C., between January and December of 1985–1989 (*n* is the number of replicate months).



was regressed against the number of salmon present for each of the 16 northern resident pods separately. The whale-days for each northern resident pod were summed each week, and the number of whale-days per week was regressed against weekly numbers of each of the three salmon species in a multiple regression analysis. Analysis of variance was used to test the significance of each multiple regression (Wilkinson 1988, p. 480; Zar 1984, p. 335).

The co-occurrence of killer whales and salmon in the King Island study area was examined qualitatively because weekly estimates of salmon numbers were not available.

Behavioural sampling

Killer whales were observed in Johnstone Strait between July 7 and September 1, 1988, from a 5-m outboard-powered boat at a minimum distance of ≥300 m inside the Michael Bigg Robson Bight Ecological Reserve, and ≥100 m elsewhere in the strait. Observation sessions ranged from 3 to 8 h. At 15-min intervals, the behaviour of each individual in the group was scanned and recorded as 1 of 5 activities (foraging, travelling, socialising, resting, and rubbing), defined by recognisable surface behaviours, surfacing intervals, and the degree of group synchrony in respiration (Ford 1988; Jacobsen 1986; Osborne 1986). For each 15-min scan, the behaviour of a group was taken as the behaviour exhibited by >50% of the individuals (Ford 1988). This criterion was acceptable because killer whales in a subpod are typically synchronous in their behaviour. The percentage of time whales engaged in each behaviour was calculated by summing the time spent in each behaviour over all sessions and dividing this by the total minutes of observation in all sessions.

Results

Occurrence of killer whales in Johnstone Strait throughout the year

A comparison of acoustic and visual estimates of whale abundance showed that acoustic estimates may slightly underestimate the number of whales when levels of effort are similar and assuming that all members of a pod are present ($Y = 3.95 + 0.78X$, $r^2 = 0.78$, $P < 0.001$, $n = 27$; *t* test

Table 3. Killer whale (*Orcinus orca*) pods identified in Johnstone Strait in 1985–1989.

July–Oct.	Nov.–June
A1	A1
A4	A4
A5	A5
B1	
C1	C1
D1	
G1, G12[a]	G1, G12[a]
H1	
I1	
I2	
I11	I11
I18	
I31	I31
R1	
W1	

Note: Data are from both sighting and acoustic records.

[a]Includes G1 and (or) G12 because these pods cannot, as yet, be distinguished acoustically.

for slope, $P < 0.05$). This underestimation occurred either because not all pods that were identified visually vocalised during recording sessions or because they were out of range of the recording equipment. Combined sightings and acoustic data from January 1985 to February 1989 show that killer whales were far more abundant in Johnstone Strait from July to October than during December through June (Fig. 2). Furthermore, killer whales were not only less frequent in Johnstone Strait outside of summer, but only 7 pods were identified acoustically between November and June of 1985–1989 (Table 3).

Salmon abundance and killer whale occurrence in Johnstone Strait

The timing of salmon, especially pink and sockeye, migrations through Johnstone Strait during July, August, and September coincides well with the occurrence of killer whales (Fig. 3). During these months sockeye and pink salmon peak in abundance between late July and mid-August and chum salmon in early October, while killer whale sightings peak between late July and early September. During peak weeks between 1984 and 1988, numbers of sockeye salmon ranged from 150 000 to 1.4 million, pink salmon from 250 000 to 2 million, and chum salmon from 280 000 to 900 000.

Salmon abundance and killer whale occurrence near King Island

Between late April and mid-June, neither killer whales nor salmon were abundant in Johnstone Strait. Near King Island, however, subpods from nine northern resident pods, A1, A4, A5, C1, D1, G12, I1, I2, and R1, were observed over 36 days between April 28 and June 12 1989 (Fig. 4). DFO catch and escapement data indicated that chinook and sockeye salmon predominated in the area at this time. According to DFO

Fig. 3. Mean numbers of salmon (*Oncorhynchus* spp.) (×1000) and whale-days per week on Johnstone Strait, B.C., between July and October (n = 5 summers, 1984–1988).

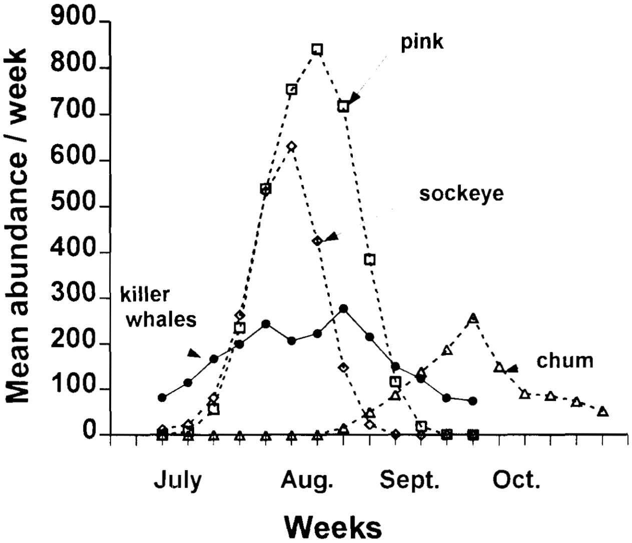
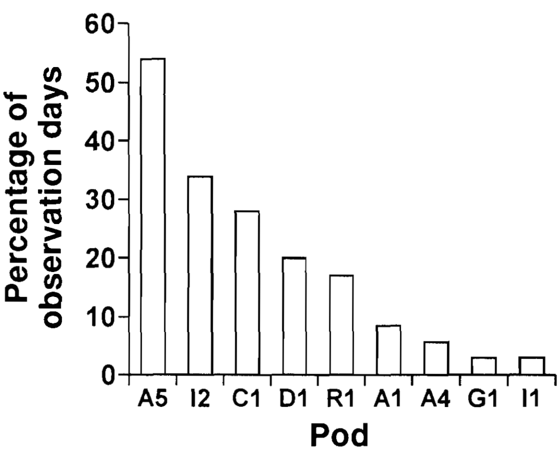


Fig. 4. Frequency of occurrence of all, or parts, of each northern resident killer whale (*Orcinus orca*) pod seen in the King Island, B.C., study area during May and June 1989 (36 days of observation). Pods are arranged from the most to the least frequently observed.



(S. Hutchings, personal communication), chinook salmon appeared in the channels during early April, with peak numbers occurring in mid-June. The number of returning chinook is estimated to have been about 30 000. Sockeye salmon appeared in Burke and Dean channels in mid-May and peaked in abundance by early July. The total number of returning sockeye salmon was about 38 000 (Fig. 5).

Pod usage of Johnstone Strait during summer

Generally, killer whales were most abundant in Johnstone Strait during July, August, and September (Fig. 2), but only whales from pods A1 and A5 were present in Johnstone Strait on more than 50% of the days during these months (1984–1988). Most other pods spent considerably less time in the strait (Fig. 6). Consequently, peak weekly numbers of whale-days during summer averaged 277 per week, as

Fig. 5. Mean numbers of whale-days each week in the King Island, B.C., study area during May and June 1989 (n is the number of observation days each week). Broken lines indicate weeks when chinook and sockeye salmon were present. The vertical arrow indicates peak chinook salmon abundance.

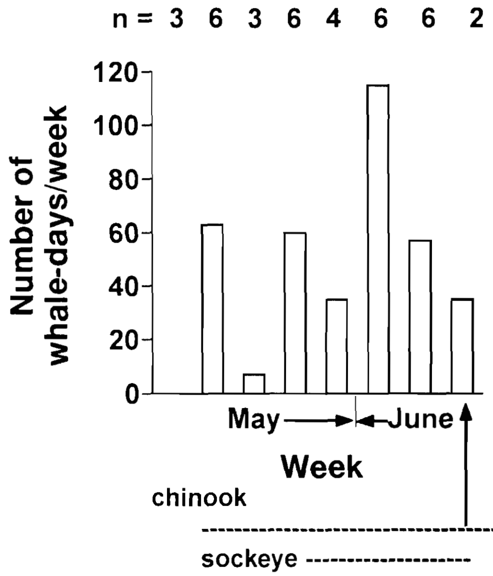
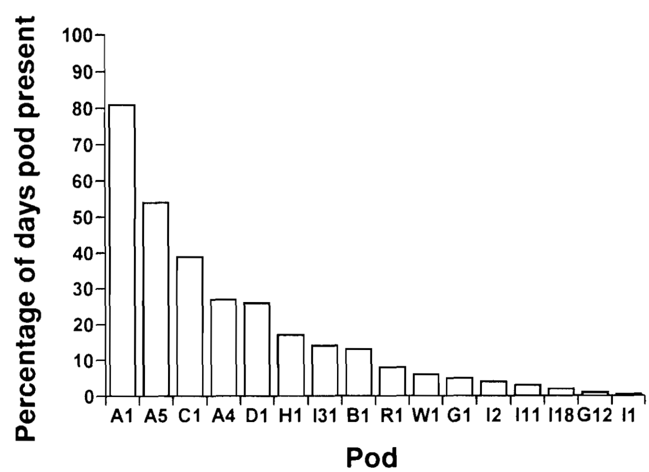


Fig. 6. Frequency of occurrence of all, or parts, of each northern resident killer whale (*Orcinus orca*) pod seen in Johnstone Strait between July and September of 1984–1988. Values represent the percentage of all observation days from 1984 to 1988 (n = 430 days).



opposed to about 1300 per week which would be expected if the entire northern resident community were present (Fig. 7).

Results regression between occurrence of killer whales and salmon abundance in Johnstone Strait

Sightings of 7 of the 16 pods of the northern resident community were positively and significantly associated with estimates of one or more species of salmon (Table 4). Pods A1, A5, and C1 associated positively with sockeye and pink salmon, while A4, D1, and H1 associated positively with sockeye salmon only, and G1 associated positively with chum salmon only (Table 4).

Fig. 7. Numbers (mean ± SEM) of whale-days per week estimated from sightings of killer whales (*Orcinus orca*) in Johnstone Strait, B.C., between July and September of 1984–1988 (*n* is the number of replicate weeks).

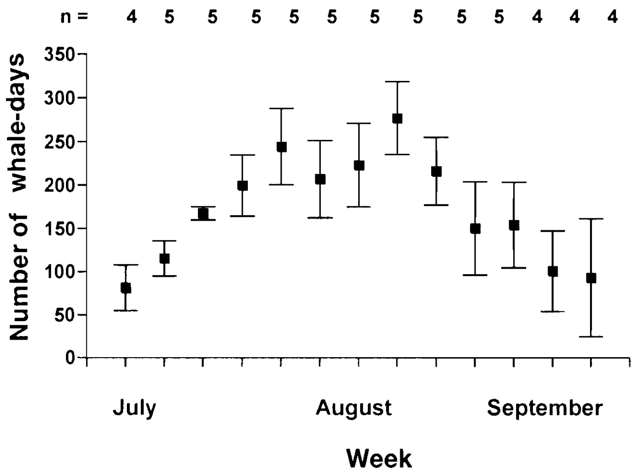


Table 4. Results of multiple regression between 16 northern resident killer whale (*Orcinus orca*) pods and three species of salmon in Johnstone Strait during July, August, and September of 1984–1988 (n = 61 weeks).

Pod	R^2	R	n	Salmon[a]
A1	0.28**	0.53**	61	s, p
A4	0.10*	0.32*	61	s
A5	0.37**	0.61**	61	s, p
B1	0.04	0.19	61	
C1	0.35**	0.59**	61	s, p
D1	0.10*	0.31*	61	s
G1	0.10*	0.32*	61	c
G12	0.05	0.22	61	
H1	0.17*	0.41*	61	s
I1	0.01	0.12	61	
I2	0.03	0.18	61	
I11	0.06	0.24	61	
I18	0.07	0.27	61	
I31	0.04	0.20	61	
R1	0.06	0.25	61	
W1	0.04	0.20	61	

Note: R^2 is the coefficient of multiple determination, R^2 is the multiple correlation coefficient, and n is the number of weeks of data used.

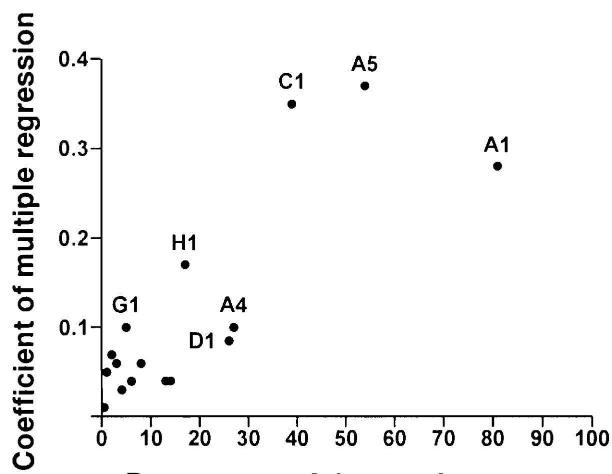
[a]Only species for which a significant relationship was found are indicated; s, sockeye salmon (*Oncorhynchus nerka*); p, pink salmon (*O. gorbuscha*); c, chum salmon (*O. keta*).

**$P < 0.001$.

*$P < 0.01$.

The amount of time pods spent in Johnstone Strait during July, August, and September (data from Fig. 6) was positively correlated with the regression between whales and salmon (Fig. 8; $r = 0.83$, $P < 0.001$, $n = 16$) (data from Table 4). Even though the 7 pods (A1, A4, A5, C1, D1, H1, G1) represent only 49% of the northern resident community, they constituted most of the weekly whale-days between 1984 and 1988 ($\bar{x} = 87.6\%$, SEM = 1.52, $n = 59$).

Fig. 8. Correlation between the percent time spent in Johnstone Strait by killer whale (*Orcinus orca*) pods during July, August, and September and the strength of the regression with salmon (*Oncorhynchus* spp.) ($r = 0.83$, $p < 0.001$, $n = 16$). Points representing pods with significant, positive relationships with salmon abundance are labelled with the pod's name.



Behaviour of killer whales

Pod A1 spent the most time in Johnstone Strait during the summer (see Fig. 6). Almost all observations were of pod A1. Two of its subpods (A2 and A12) were observed for a total of 133 h during 22 daily sessions between July 7 and September 1, 1988. We found that the proportions of time these whales spent in the various activities were as follows: 38% foraging, 32% travelling, 15% resting, 12% socialising, and 3% rubbing.

Killer whales foraged along the Vancouver Island shore from the Michael Bigg Robson Bight Ecological Reserve to Blinkhorn Point (a distance of about 13 km), along West Cracroft and Hanson islands, and in the strong current at the junction of Blackney Pass and Johnstone Strait. Pursuit of prey by killer whales was evident by their brief bouts of erratic swimming, and on five occasions salmon were directly observed being pursued or captured by killer whales in these shoreline areas by the senior author and J. Jacobsen (personal communication).

Detailed behavioural observations were not made in the King Island area, but killer whales were observed swimming mainly along shorelines and travelling long distances. On eight occasions killer whales were tracked for 6–10 h travelling distances of 40–85 km. This is in contrast to their more localized movements in Johnstone Strait during summer.

Discussion

Killer whales and salmon in Johnstone Strait and near King Island

We have shown quantitatively, using sighting and acoustic data, that there is an annual increase in the frequency of killer whale occurrences in Johnstone Strait during July through October. This finding is consistent with the impressions of researchers and tour operators who have worked in

Johnstone Strait for many years (e.g., M. Bigg, personal communication; B. MacKay, personal communication). Of the pods we observed around King Island in May and June of 1989, most were seen in Johnstone Strait between July and October, further illustrating the seasonal movements of these whales. Moreover, since 1989, many of the same northern resident killer whale pods have been observed annually during spring surveys in the King Island area (G. Ellis, personal communication). In both our study areas, the occurrence and increases in killer whale numbers coincided with local runs of salmon, supporting the hypothesis that northern resident whales move seasonally in response to the temporal availability of salmon. Southern resident killer whales appear to behave similarly, using their habitat seasonally in response to salmon abundance (Heimlich-Boran 1986).

Although the regression analyses of whale and salmon numbers were statistically significant, variation unaccounted for was high. It could be due to the predatory efficiency of killer whales, the accuracy of weekly salmon abundance estimates, or both. Killer whales are probably highly efficient predators that use both sight and sonar to locate prey before capturing them. Consequently, beyond a certain density of fish, it is possible that even large increases or decreases in salmon numbers may be unimportant to the whales (see Fig. 3). At the same time, the salmon data from DFO are estimates and, as such, can be expected to contain errors in terms of weekly numbers of salmon. For example, although salmon migration curves are presented as smooth, normal curves, it is known that salmon migrate in schools that pass through the strait in pulses. Consequently, even when salmon densities are, on average, high, there may be days when in fact the numbers of salmon in the strait are low (W. Luedke, DFO, personal communication).

The sport-fishing catch data Heimlich-Boran (1986) used to correlate occurrence of southern resident whales with salmon abundance also probably provided inaccurate estimates of weekly salmon numbers because no measure of fishing effort was used. Similarly, Guinet (1990) used commercial catch data without any measure of fishing effort in his single-season correlation of northern resident whales. Nonetheless, despite inaccuracies in all three salmon data sets, results are consistent among them and together support the existence of a seasonal relationship between resident killer whales and salmon in coastal regions of the Pacific Northwest.

Foraging behaviour of killer whales

Observations of killer whales pursuing and eating salmon while in Johnstone Strait provided additional evidence that the temporal co-occurrence of whales and salmon reflects a predator–prey relationship. Erratic surface swimming associated with pursuit of prey is also documented among southern resident killer whales (Hoezel 1993). In addition to our observations, fresh fish-scale samples collected on the water near foraging resident killer whales indicate that 95% of detected kills are of salmon (J. Ford, personal communication).

In Johnstone Strait, A1, a pod with a significant positive association with sockeye and pink salmon, was found to forage primarily along shorelines and in areas of strong current. Around King Island, killer whales were also observed to swim very close to the shore. Commercial fishing activity, catch data, and ultrasonic tagging studies of salmon in Johnstone Strait suggest that shorelines and areas with strong currents are also regions of high salmon densities (C. Groot, DFO, personal communication, 1990; Gould and Hop Wo 1986; Quinn and teHart 1987). In Johnstone Strait, "hot spots" reported by fishermen and chum salmon test fishing locations used by DFO occur along the shores of Vancouver and Hanson islands and off Cracroft Point and in Blackney Pass (C. Groot, personal communication, 1990; Gould and Hop Wo 1986). These are all areas where killer whales were observed to forage. Ultrasonic tagging of sockeye salmon revealed why these areas are hot spots. Migrating salmon become temporarily disoriented when they encounter headlands, entrances to bays, or intersections of channels, possibly because of confusing current flows resulting from tides and wind deflection. As a result, salmon tend to aggregate temporarily until they reorient themselves (Quinn and teHart 1987).

Around King Island, killer whales travelled over much greater distances than when in Johnstone Strait during the summer. Lower salmon densities may account for the greater daily distances covered around King Island because salmon runs are considerably smaller than in Johnstone Strait.

Previous studies illustrating a significant relationship between the occurrence of killer whales and of salmon did not distinguish pods or salmon species in statistical analyses (Heimlich-Boran 1986; Guinet 1990). By analysing pods and salmon species separately in a multiple regression we showed differences among pods in their usage of Johnstone Strait. Although we demonstrate an association of certain pods with certain salmon species, we cannot determine whether this reflects true preferences by pods for specific salmon species or represents differences in the whales' arrival times in Johnstone Strait that are related to other factors.

Seasonal ranges

Our analysis of the occurrence of each pod separately suggests that pods may have seasonal ranges. We demonstrated that (*i*) the occurrence of northern resident whales in Johnstone Strait is seasonal, (*ii*) there is a seasonal movement between King Island and Johnstone Strait, (*iii*) weekly numbers of whales and salmon in Johnstone Strait during summer are positively related, and (*iv*) observations of resident killer whales indicate that they do prey on salmon in Johnstone Strait. Together these findings support the hypothesis that killer whales use their habitat seasonally to take advantage of the varying availability of salmon. Furthermore, based on the differences we found in the frequency of occurrence of each northern resident pod in Johnstone Strait, we hypothesize that within the northern resident community, each pod has its own pattern of seasonal range use.

It was clear that only part of the northern resident community visited Johnstone Strait frequently during summer and that the occurrence of <50% of the community was positively associated with salmon abundance in this area. These results raise the question of why the majority of northern resident whales spend so little time in the strait when there would seem to be numerically sufficient salmon between July and October to feed the entire community. Perhaps the relatively low numbers of whales in Johnstone Strait during summer is partly because their presence decreases actual prey availability (resource depression). Though salmon are abundant in the strait, they may be wary of foraging whales and become harder to catch once they are aware of the presence of whales. The importance of resource depression caused by predators in determining a predator's movements and foraging decisions can be equal to or greater than that of actual prey abundance (Charnov et al. 1976). Consequently, killer whale pods may need to distribute themselves to avoid excessive overlap if they are to forage efficiently.

We include here several corollaries to our seasonal range hypothesis that are based upon the observations and results of this study. (*i*) A pod's seasonal range consists of several feeding locations where salmon are abundant during the same season, and the pod travels among them. Even among pods whose occurrence was positively associated with salmon abundance in Johnstone Strait, most still spent most of the summer elsewhere, presumably in other areas along the coast where salmon are concentrated. (*ii*) Pod seasonal ranges overlap and many feeding locations are used simultaneously by more than one pod. This is suggested by the observation that different pods used Johnstone Strait and the area around King Island simultaneously. Although seasonal ranges overlap spatially, there may be some temporal separation. For example, pod G1 spent very little time in Johnstone Strait during the summer and yet its occurrence was positively associated with that of chum salmon, which peak in abundance in fall. This suggests temporal partitioning (Schoener 1974) of the salmon resource. (*iii*) Seasonal feeding locations are visited annually by the same pods, which have developed preferences for feeding in these areas. Each summer, it is the same pods that are frequent visitors to Johnstone Strait. Traditional use of certain areas could develop because it is advantageous to feed in areas where pod members have accumulated knowledge over many years about the local distribution of salmon. (*iv*) The summer ranges of over half the northern resident community include feeding areas distant from Johnstone Strait. This is supported by the observation that pods whose occurrence in the strait was not significantly associated with salmon abundance were infrequent visitors to the strait.

We emphasise here that few or no data are available to confidently describe the full extent of the northern resident community range or of their range-use patterns. Further study of killer whale usage of areas beyond Johnstone Strait would greatly assist our understanding of northern resident range-use patterns and the importance of salmon to these whales.

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