Foraging behaviour and social group dynamics in Puget Sound killer whales

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Abstract. Social and foraging behaviour was investigated in a population of 82 killer whales, *Orcinus orca*, seasonally resident in the straits of Washington State and British Columbia. Killer whales in this population travel in stable pods and temporarily dissociate into subgroups. Associations in subgroups were determined by photographing individual whales. The relative geographical positions of subgroups were determined by compass triangulation on landmarks. These data were used to determine correlations between individual associations, habitat use and behaviour. Behaviour indicative of pursuing fish prey at the surface (termed fast non-directional) correlated with the whales slowing down, travelling in smaller subgroups, and decreasing the distance between subgroups. This behaviour was not correlated with bottom topography, specific quadrats within the study areas, or the convergence of subgroups (which could be interpreted as group herding of prey). These data suggest that these killer whales may benefit from cooperative food searching, but not necessarily from cooperative food capture. Adult males, which are thought to remain within their natal pods, were most likely to travel alone and to exhibit fast non-directional behaviour when alone.

The killer whales, *Orcinus orca*, inhabiting the straits east and south of Vancouver Island, British Columbia have been investigated extensively since 1973. All individual whales have been photographically identified by idiosyncratic congenital and acquired characteristics (Bigg et al. 1976, 1987; Bigg 1982). Long-term associations within social groups (termed pods) are highly consistent in this population. After more than 15 years there has been no immigration and no direct evidence of dispersal. The whales inhabiting the straits from British Columbia just north of Vancouver Island to Puget Sound (Washington State, U.S.A.) segregate into three 'communities' of pods (Bigg et al. 1976). The community investigated here consists of five resident pods inhabiting the region south of the Campbell River.

A further social division is seen in subgroup associations within pods. When a pod divides into subgroups, general activities and direction of travel are still the same for all individuals within the pod, though the distance between subgroups can be several kilometres. When separated by large distances, it is unlikely that members of one subgroup

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can assist members of another group in prey capture, although they could be searching cooperatively (Norris & Dohl 1980; Hoelzel & Osborne 1986). A number of researchers have interpreted variation in group size as an indicator of the selective advantage of sociality (Caraco & Wolf 1975; Zimen 1976; Lamprecht 1978; Rodman 1981). In this study, I investigated social group dynamics and variation in group size for correlation with surface feeding behaviour to test the hypothesis that cooperative foraging may have played a role in the evolution of sociality in this species. These correlations suggest that whales in this population may search for prey cooperatively, but probably capture prey independently.

METHODS

Whales were observed for 436 h during 82 days in two field seasons (1986 and 1987). Individual whales were identified according to an established photo-identification programme (Bigg et al. 1976, 1987; Balcomb et al. 1979) based on acquired scars and nicks on the dorsal fin, and congenital variation in the pigmentation pattern immediately posterior to the dorsal fin (the 'saddle patch' region).

The study population consisted of five pods from the southern resident subpopulation: J-pod: 18 whales; K-pod: 17 whales; L8-pod: 30 whales; L10-pod: 12 whales; and L35-pod: five whales (after Bigg et al. 1987).

Whales were divided into five age/sex classes: adult males and females (15 years or older), sub-adult males and females (5–14 years) and calves (neonate to 4 years). The age of whales born since 1972 is known precisely, since all births and the photographic identification of individuals have been documented since then (Bigg et al. 1990). Of the 82 whales in the study population, 21 are known to be males more than 4 years old, 41 are females older than 4 years, 14 are calves of unknown sex 4 years or younger, and six are subadults older than 4 years of unknown sex. Two of the calves were born in the second year of the study. The sex ratio for the 62 whales of known sex is 33·9% males to 66·1% females. Females usually bear their first calf by age 15, and males attain physical maturity by this age (Bigg et al. 1990). One female who gave birth in 1986 when she was 14 was classified as an adult.

All individuals in focal subgroups were photo-graphed for later identification. In addition, notes were taken on the identity of individual whales recognized in the field. All photographs were donated to the database at the Pacific Biological Station in Nanaimo, Canada. Their identifications were used to double-check identifications made for the present study.

The position of the subgroup was triangulated on landmarks using a Suunta bearing compass, and data were collected on the behaviour and position of the members of the focal and other subgroups within visual range. The research platform was a 5-m open outboard motor boat with a 60 horsepower motor. The study area was divided into four ranges (Fig. 1), each of which was divided into quadrats of 2×2 km. The total range of the five pods in the study population extends into Canada to the Campbell River, south to lower Puget Sound, and west around the south end of Vancouver Island during the summer (Bigg et al. 1987).

The range divisions for the present study were based on general differences in the local environ-ment. GST is predominantly open strait, NSJ pro-tected inland channels, WSJ a land barrier buffeted by ocean currents, and SSJ shallow banks and open strait (Fig. 1). Triangulation data were used to assign subgroups to quadrats and obtain specific locations for the determination of depth and bottom topography below the subgroup, distance to shore and distance between subgroups.

Bottom topography was classified into eight categories. Depth was distinguished as less or greater than 50 fathoms. Bottom contour below the sighting was classified as open (featureless) when there was no prominent relief or slope within a 500 m radius. Separate classifications were made for sea mounts (submarine relief less than 1 km in radius as indicated on NOAA ocean survey chart 18421), sloping contour, open bays and banks (extended area less than 10 fathoms deep, com-pletely or mostly surrounded by deeper water). Distance to the nearest subgroup was estimated in the field in units of adult whale lengths (one whale length = about 8 m) for distances up to 10 whale lengths, beyond which estimates were made to the nearest 0·5 km. Field estimates were taken to supplement the triangulation data. The time required to reach distant subgroups limited the accuracy and frequency of near-group distance estimations when the distance was greater than 1–2 km.

Behaviour was classified as described in Jacobsen (1986) and Osborne (1986). 'Milling' is slow non-directional swimming behaviour. Speed was esti-mated on a five-point scale based on the boat engine force required to keep pace with the focal group. It is, therefore, a measure of force against the water and not distance per unit time. I attempted to keep the distance between the focal group and the boat constant to control for a possible reaction to the boat, though the whales in Puget Sound are accustomed to power boats, and there was no evi-dence of a response to the research platform at the range maintained.

Whales were located each day based on phoned in sightings, or by sighting from various vantage points along their usual travel routes (most often in areas NSJ or SSJ), and the same method was used during both years. Once encountered they would be followed until out of the study range. Data on focal subgroups were collected in 20-min sampling periods. When additional subgroups were within visual range, the next nearest became the focal group in the next sample period. If not, a new data entry on the position and composition of the cur-rent focal group would be logged each 15–25 min. Notes on behaviour were logged when observed, and recorded to the nearest mintue. After one cycle through all subgroups, the original focal group would be re-sampled. Interval sampling was
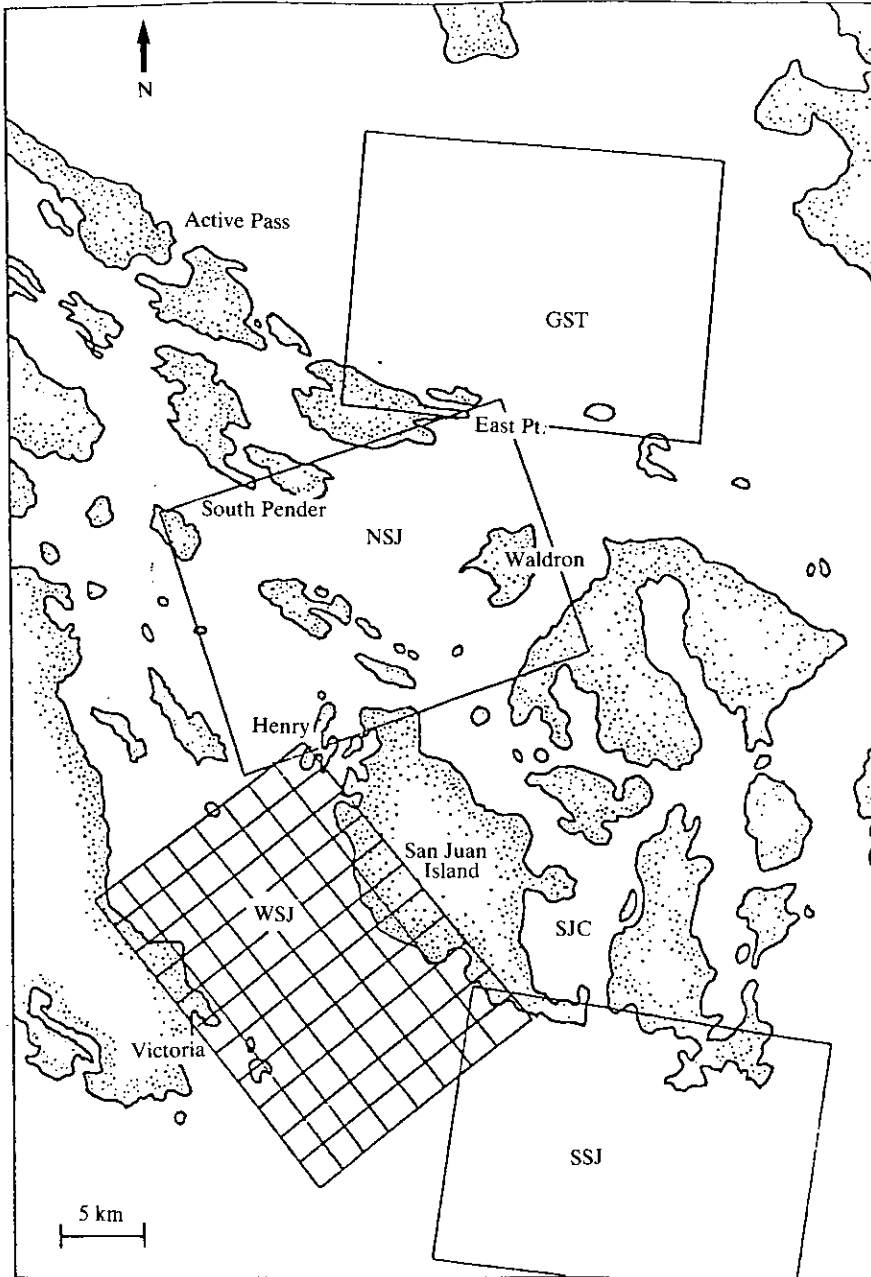
Figure 1. Study area between 48 and 49° N and 122 and 124° W showing the main quadrats within the four major ranges. All quadrats are subdivided into quadrats of 2 × 2 km as illustrated in WSJ. GST = Georgia Strait, NSJ = North San Juan, WSJ = West San Juan, SSJ = South San Juan, SCJ = San Juan Channel

designed to discriminate long associations. By this method, stable subgroups would be sampled more often than temporary associations.

Pair-wise comparisons were made by either the *G*-test for correlation or the Student's *t*-test. Owing to the large number of comparisons and the
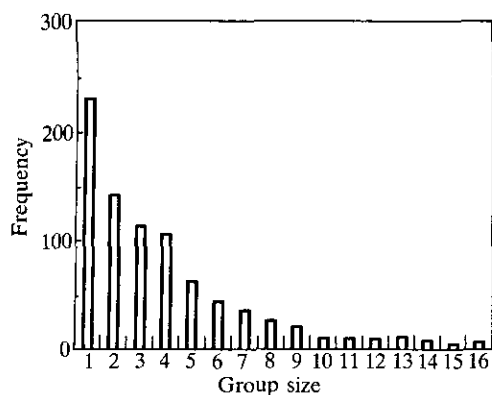
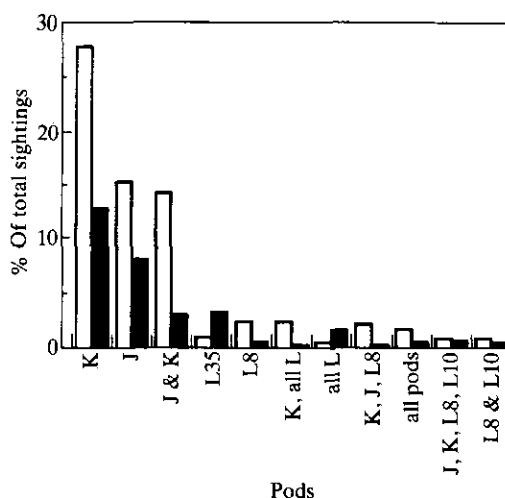**Figure 2.** Sighting frequency of subgroups of different sizes up to 16 whales.

Figure 3. Percentage of total sightings represented by all observed pod combinations. □: Subgroup sightings; ■: whole-pod sightings.

consequent risk of a type I error, a confidence limit of $P = 0.01$ was used. Distance from shore, between subgroups and depth approximated normal distributions; however, the frequency distribution of group size was highly skewed. Therefore, the comparison between group size and foraging rate was made using the non-parametric Spearman's correlation.

RESULTS

Killer whales travelled through the study area in either intact pods (all individuals within 50 m of each other; 30·3% of sightings, $N = 385$), or subgroups (less than 50 m separation within and greater between; 69·7% of sightings, $N = 886$). Data sets were divided into early (May to July) versus late (August and September) seasons.

The size of subgroups varied from 1 to 27 whales (Fig. 2), and the frequency of subgroups diminished with increasing size. There were 581 subgroup sightings when only one pod was present, and 305 with more than one pod. The frequency of sightings for each pod and pod combination is given in Fig. 3. J and K pods travelling alone were seen most frequently, and the study is based primarily on sightings of these two pods. For most pods and pod combinations, subgroup sightings were more common than whole pod sightings.

The frequency of whole pod and subgroup sightings early and late in each year is listed by range in Table I. With the exceptions of late season whole pod sightings in WSJ ($G = 6·5$, $T = 105$, $df = 1$, $P = 0·011$) and SSJ ($G = 12·2$, $T = 52$, $df = 1$, $P < 0·001$),

which were less frequent in 1987 than in 1986, pod versus subgroup frequencies were similar between the two years. Seasonal variation was significant in SSJ in 1986 ($G = 16·8$, $T = 71$, $df = 1$, $P < 0·001$), and in WSJ in 1987 ($G = 15·4$, $T = 366$, $df = 1$, $P < 0·001$). In GST whole pod sightings were seen only in the late season during both years; however, sample sizes were too small for statistical comparison.

Foraging

Prey capture was rarely observed; however, a series of fast turns and rolls at the surface was always seen when an interaction with fish prey was apparent. This behaviour was termed fast non-directional. On several occasions the subject whale was observed in pursuit of a fish underwater following this activity. A similar account is given in Felleman (1986), and interpreted as feeding by Osborne (1986) and Felleman et al. (1991). This behaviour was, therefore, used as an indicator of periods of feeding.

### *Correlations with group size*

The number of fast non-directional events per whale sighting (total sightings × number in group) in subgroups diminished exponentially with increasing group size (Fig. 4; $r_s = 0·83$, $P < 0·001$). The rate of fast non-directional events per whale

Table I. The number of whole pod (Pod) versus subgroup (SG) sightings by year (divided into early and late seasons) and area

Area		1986		1987	
		Early	Late	Early	Late
GST	Pod	0 (0)	9 (60)	0 (0)	4 (33·3)
	SG	14 (100)	6 (40)	17 (100)	8 (66·7)
NSJ	Pod	54 (47)	39 (44·3)	50 (51)	37 (40·7)
	SG	61 (53)	49 (55·7)	48 (49)	54 (59·3)
WSJ	Pod	36 (23·4)	10 (16·4)	77 (23·9)	1 (2·3)
	SG	118 (76·6)	51 (83·6)	245 (76·1)	43 (97·7)
SSJ	Pod	4 (9·8)	16 (53·3)	13 (10·7)	2 (9·1)
	SG	37 (90·2)	14 (46·7)	109 (89·3)	20 (90·9)

Percentage values comparing pod versus subgroup sightings are given in parentheses.
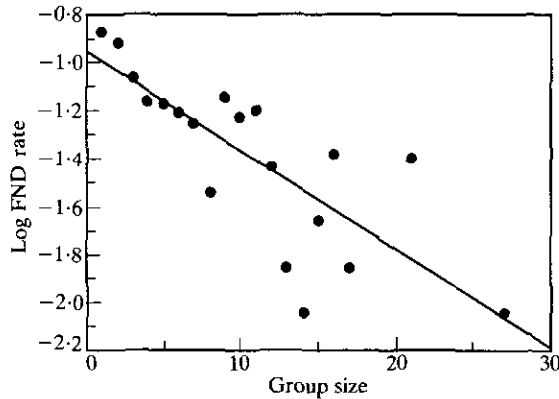
Figure 4. Frequency of fast non-directional (FND) events versus subgroup size. Negative regression is shown on log-transformed data.

averaged over all subgroups was much higher than for whole pod sightings (5·4% in subgroups versus 0·8% in pods, $G=196$, $T=11\,338$, $df=1$, $P<0·001$).

Multi-pod sightings were considerably more common in 1986 than in 1987 ($G=51·5$, $T=1270$, $df=1$, $P<0·001$), and later in the season during both years ($G=96·3$, $T=1270$, $df=1$, $P<0·001$; Table II). In spite of the consequently large number of whales present, fast non-directional rates per whale were the same for single versus multi-pod subgroup sightings (5·4 versus 5·8%, $G=0·09$, $T=3970$, $df=1$, $P=0·76$). There was no seasonal variation in subgroup size for single pod sightings in either year (for both years combined, early: $\bar{X}=3·48$ versus late: $\bar{X}=3·99$, $t=1·24$, $df=580$, $P>0·1$). Subgroup size was lowest in SSJ in 1987 ($\bar{X}\pm\text{SD}=2·36\pm1·96$, $N=124$) where fast non-

Table II. The number of sightings when one to five pods were present during early and late seasons of each year

	Number of pods present				
	1	2	3	4	5
1986					
Early	156	74	0	0	0
Late	36	10	25	26	12
1987					
Early	323	74	0	15	2
Late	56	58	3	0	8

directional rates were highest, largest in NSJ ($\bar{X}\pm\text{SD}=5·51\pm4·47$, $N=102$) where fast non-directional rates were lowest, and higher for

Table III. Distance ($\bar{X} \pm$ SD) between subgroups during sightings that included fast non-directional behaviour within 20 min (FND), compared with those that did not (no FND)

	Season							
	Early				Late			
	FND	N	No FND	N	FND	N	No FND	N
1986	$0 \cdot 22 \pm 0 \cdot 44$	45	$0 \cdot 44 \pm 0 \cdot 53$	116	$0 \cdot 28 \pm 0 \cdot 28$	20	$0 \cdot 36 \pm 0 \cdot 38$	60
1987	$0 \cdot 22 \pm 0 \cdot 15$	28	$0 \cdot 29 \pm 0 \cdot 35$	228	$0 \cdot 38 \pm 0 \cdot 47$	15	$0 \cdot 49 \pm 0 \cdot 58$	57

multipod sightings in 1986 (6·93 versus 3·72, $t =$ 5·75, $df = 349$, $P < 0 \cdot 001$). There was no significant difference between fast non-directional rates early versus late in 1986 (7·0 versus 5·8%, $G = 0 \cdot 8$, $T =$ 1638, $df = 1$, $P = 0 \cdot 4$), but the fast non-directional rate was lower during the late season in 1987 (3·8 versus 7·7%, $G = 10 \cdot 3$, $T = 1813$, $df = 1$, $P = 0 \cdot 001$).

Correlations with distance between subgroups

For both single pod and multiple pod sightings, the distance between subgroups was significantly less during sightings that included fast non-directional events (0·25 km versus 0·36 km for all sightings combined, $t = 2 \cdot 6$, $df = 551$, $P = 0 \cdot 009$; Table III). This pattern was consistent within years and for early versus late seasons, even though average inter-group distance increased during the late season in 1987 from 0·28 to 0·47 km ($t = 2 \cdot 46$, $df =$ 327, $P = 0 \cdot 014$). Decreased inter-group distance during fast non-directional behaviour was also seen for whales travelling alone in 1987, though not in 1986 ($t = 3 \cdot 41$, $df = 125$, $P < 0 \cdot 001$). There was no difference between overall fast non-directional rate (5·8 versus 5·6%) in 1986 and 1987. For all data from WSJ only, the pattern was the same (inter-group distance during fast non-directional = 0·19 km, without fast non-directional = 0·38 km, $t = 5 \cdot 06$, $df = 292$, $P < 0 \cdot 001$). There was no difference in the distance between subgroups for single versus multi-pod sightings (0·37 km versus 0·39 km, $t = 0 \cdot 04$, $df = 240$).

Correlations with area use

Comparing fast non-directional rates per whale by area, there was no difference between areas in 1986 (Table IV). But in 1987, fast non-directional behaviour was significantly more common than expected in SSJ ($G = 26 \cdot 7$, $T = 544$, $df = 1$, $P < 0 \cdot 001$)

Table IV. Percentage of subgroup sightings by area that include fast non-directional behaviour (%FND), and percentage of total subgroup sightings by area (%S), given for each year

	1986		1987	
Area	%FND	%S	%FND	%S
GST	4·8	5·7	5·4	4·6
NSJ	4·2	31·4	2·3	18·8
WSJ	6·8	48·3	5·2	52·9
SSJ	8·2	14·6	13·3	23·7

and less common than expected in NSJ ($G = 17 \cdot 6$, $T = 544$, $df = 1$, $P < 0 \cdot 001$). Fast non-directional and non-fast non-directional sightings were plotted on area maps and compared by quadrat. There were no significant trends within areas. Fast non-directional rates per whale and the proportion of sightings (subgroup only) are shown by year for each area in Table IV. Sightings were significantly less common in NSJ in 1987 ($G = 19 \cdot 13$, $T = 544$, $df = 1$, $P < 0 \cdot 001$) and more common in SSJ in 1987 ($G = 11 \cdot 63$, $T = 544$, $df = 1$, $P < 0 \cdot 001$), consistent with the pattern for fast non-directional behaviour. The same pattern of fast non-directional rates was consistent for early and late season sightings in each year, and when only single pod sightings are considered.

Correlations with speed

A measure of effort against the water (speed) was tested for correlations with fast non-directional behaviour. Speed estimations were divided into two categories: less than medium (referred to as 'slow'), and equal to or greater than medium (referred to as 'fast'). Slow travel was significantly more common in 1986 than in 1987 (49·0 versus 33·5%, $G = 17 \cdot 45$,

$T=770$, $df=1$, $P<0.001$). During both years slow travel was considerably more common during fast non-directional behaviour (in 1986: 74·4 versus 37·9%, $G=29·9$, $T=261$, $df=1$, $P<0.001$; in 1987: 54·6 versus 30·3%, $G=19·5$, $T=519$, $df=1$, $P<0.001$). The same pattern was seen for single pod sightings in WSJ only, and for whole pod sightings. Although fast non-directional behaviour was more common in subgroups, slow travel was more likely during whole pod sightings (76·1% of whole pod sightings versus 38·6% of subgroup sightings; $G=133$, $T=1151$, $df=1$, $P<0.001$), and the pattern was the same for both seasons during both years.

Correlations with milling behaviour

Forty-five sightings (representing approximately 15 h observation time) were made when all individuals in all subgroups were milling. These sightings were more common in the presence of more than one pod ($G=10·0$, $T=1270$, $df=1$, $P>0·002$). Whole pod sightings were as common during milling behaviour as for all sightings, but mean group size was larger during milling (19·0 versus 9·5, including pod and subgroup sightings, $t=2·53$, $df=1268$, $P=0·011$). Fast non-directional behaviour per whale (excluding slow non-directional and milling) was more common during group milling (1·7 versus 0·6%, $G=10·0$, $T=12957$, $df=1$, $P=0·002$). Sightings of this behaviour were as common in all three major areas (NSJ, WSJ and SSJ, not seen GST), but tended to occur further offshore (3·39 versus 1·58 km, $t=3·33$, $df=1268$, $P<0·001$) and in shallower water (48·0 versus 67·0 fathoms, $t=3·06$, $df=1268$, $P=0·002$) than the overall average. Group milling was significantly less likely over shallow slopes (4·8 versus 31·7%, $G=18·4$, $T=45$, $df=1$, $P<0·001$), and tended to be more likely over shallow bathymetric relief and banks (19·0 versus 7·1%, $G=6·0$, $T=45$, $df=1$, $P=0·014$).

Correlations with submarine topography

The submarine topography is highly varied in the study areas, but in general each area has deep open water channels and regions of considerable bathymetric relief. The proportion of each quadrat of 2×2 km that was characterized by these 'sea mounts' and submarine ridges, at a depth of less than 50 fathoms, was estimated for all quadrats within the sighting range for each area. There were no correlations between fast non-directional behaviour and bathymetric relief in any of the areas

during either season in either year. Subgroup sightings were most common over deep open water (40·9%), followed by shallow slopes (31·7%), deep slopes (18·8%), shallow bathymetric relief (3·9%), shallow banks (3·2%), shallow open water (1·0%), and shallow water at the mouth of an open bay (0·5%). Sightings over deep bathymetric relief represented less than 0·1%. None of these bottom topographies correlated with fast non-directional (FND) behaviour (FND versus non-FND for all seven topographies: $G=7·03$, $T=840$, $df=6$, $P=0·29$). A non-significant trend is seen if shallow sea mounts and banks are compared with all other topographies (10·3% FND versus 6·2% non-FND; $G=3·22$, $T=840$, $df=1$, $P=0·07$).

Correlations with group divergences and convergences

A total of 147 group divergences and 136 convergences were observed. There were no differences by area or within areas, with the following exception: there were 15 divergences to one convergence in GST; however, all sightings in this area were heading north into the open strait.

Slow travel was more common during convergences (57·3%), and fast travel was more common during divergences (39·8%, $G=7·2$, $T=238$, $df=1$, $P=0·007$). Percussive behaviour (acrobatic behaviour such as breaching and pectoral fin slapping) was significantly more common during divergences than during either convergences (5·6 versus 2·8% per whale, $G=15·9$, $T=3781$, $df=1$, $P<0·001$) or all sightings (5·6 versus 3·6% per whale, $G=15·4$, $T=14912$, $df=1$, $P<0·001$). The difference between percussive behaviour during convergences and all other sightings was not significant ($G=2·67$, $T=14337$, $df=1$, $P=0·1$), and there was no correlation between fast non-directional and percussive behaviour ($G=0·14$, $T=4125$, $df=1$, $P=0·7$).

There were 36 convergences and 43 divergences associated with fast non-directional behaviour. There was no difference between fast non-directional rates for convergences versus divergences ($G=3·34$, $T=238$, $df=1$, $P=0·07$). Of the sightings associated with fast non-directional behaviour, the majority (60%) involved the convergence of subgroups or individuals, or a temporary divergence followed by a convergence. Twenty-seven per cent involved the division of large groups or whole pods. Ten per cent involved the division of small subgroups. The remainder of the sightings

Table V. Behaviour and sighting frequency by age/sex class

	FND	Percussive	Whales	Sightings
Adult male	31 (27·2)	83 (42·3)	10 (12·2)	739 (20·6)
Subadult male	6 (5·3)	11 (5·6)	15 (18·3)	464 (12·9)
Adult female	63 (55·3)	48 (24·5)	35 (42·7)	1610 (44·9)
Subadult female	4 (3·4)	7 (3·6)	7 (8·5)	394 (11·0)
Calf	10 (8·8)	47 (24·0)	15 (18·3)	379 (10·6)

The number of fast non-directional (FND) and percussive sightings are given, followed by the number of whales in each age/sex class, and the total number of sightings of whales in each age/sex class. Percentage within behaviour or sighting catagory is given in parentheses.

involved the convergence of two or more pods. On several occasions a whole pod was observed diverging and converging repeatedly in quick succession.

Correlations with age/sex class

Individuals exhibiting fast non-directional and percussive behaviour could sometimes be recognized in the field. For other sightings the whale could be classified as, for example, either an adult female or a subadult male. For these sightings the numbers were converted to proportions based on the proportion of whales in each class within the population. The number of fast non-directional and percussive sightings, the total number of whales in each age/sex class, and the number of sightings per class are given in Table V. The six subadult whales of unknown sex were divided between the two classes according to the proportions found for known sex whales. A G-test comparison of sighting frequency and proportion of whales in each age/sex class was non-significant ($G=9\cdot1$, $T=3668$, $df=4$, $P=0\cdot06$). The trend is due to slightly higher adult male and lower calf sightings than expected.

The number of fast non-directional and percussive sightings in each class were compared with the sighting frequency for that class. Adult males were more likely to exhibit percussive behaviour than expected by chance ($G=26\cdot5$, $T=3782$, $df=1$, $P<0\cdot001$). Subadult males were less likely to exhibit either behaviour (FND: $G=7\cdot3$, $T=3700$, $df=1$, $P=0\cdot007$; percussive: $G=11\cdot0$, $T=3782$, $df=1$, $P<0\cdot001$). Adult females tended to exhibit fast non-directional behaviour more often than expected ($G=4\cdot8$, $T=3700$, $df=1$, $P=0\cdot029$) and percussive behaviour significantly less often than expected ($G=33\cdot4$, $T=3782$, $df=1$, $P<0\cdot001$). Subadult females exhibited less than expected for

both types of behaviour (FND: $G=8\cdot4$, $T=3700$, $df=1$, $P=0\cdot004$; percussive: $G=13\cdot9$, $T=3782$, $df=1$, $P<0\cdot001$). Calves were more likely than expected to display percussive behaviour ($G=26\cdot7$, $T=3782$, $df=1$, $P<0\cdot001$).

Most sightings of solitary whales ($N=259$) were of adult males (69·5%) or adult females (25·5%). The remaining 5% were predominantly subadult males. Adult males were significantly more likely to travel alone than either adult females (24·4 versus 4·2%, $G=158$, $T=2349$, $df=1$, $P<0\cdot001$) or subadult males (24·4 versus 1·9%, $G=108$, $T=1203$, $df=1$, $P<0\cdot001$). Adult males had a significantly higher rate of fast non-directional behaviour when alone than when in groups (11·7 versus 1·8%, $G=24\cdot7$, $T=770$, $df=1$, $P<0\cdot001$). The same trend was seen for adult females, but the difference was not significant (8·8 versus 3·7%, $G=3\cdot1$, $T=1673$, $df=1$, $P=0\cdot078$). Although the difference in fast non-directional rates for solo adult males versus females was not significant, adult females tended to have a higher fast non-directional rate than males in groups (3·7 versus 1·8%, $G=5\cdot13$, $T=2168$, $df=1$, $P=0\cdot024$). There was no difference between the rate of percussive behaviour of adult males alone versus in groups; however, females were significantly more likely to exhibit percussive behaviour when alone (19·1 versus 2·3%, $G=27\cdot5$, $T=1658$, $df=1$, $P<0\cdot001$). Adult males were more likely to exhibit percussive behaviour in groups than either adult females (10·6 versus 2·3%, $G=51\cdot1$, $T=2195$, $df=1$, $P<0\cdot001$) or all other classes combined (10·6 versus 3·6%, $G=35\cdot7$, $T=3497$, $df=1$, $P<0\cdot001$).

DISCUSSION

A number of researchers have interpreted tight circling and erratic swimming at the surface (fast

non-directional behaviour) as indicative of killer whales feeding on fish (Felleman 1986; Jacobsen 1986; Osborne 1986; Felleman et al. 1991). During the current study salmon, *Oncorhynchus* sp., were observed in fast avoidance behaviour in front of a whale engaged in fast non-directional behaviour on several occasions.

During the study season (May to September), salmon are abundant in the region. Heimlich-Boran (1986) has found a strong correlation between sighting frequency of killer whales and the success rate of the local sport salmon fishery in Puget Sound and near the San Juan Islands. Hydroacoustic recordings made in the presence of milling killer whales showed a predominance of single large targets indicative of salmon (Felleman 1986). Further, 93% of these fish were within 20 m of the surface. This is consistent with preliminary results on salmon equipped with depth sensors which travelled within 15 m of the surface (Quinn, personal communication, cited in Felleman, 1986). Salmon migrate through the region in large schools, but individual fish are sparsely distributed within the school. Therefore, available data support the interpretation that these killer whales are pursuing individual prey that are distributed near the water surface, and that by chance some proportion of their prey attempt to escape towards the air–water interface, where they are pursued by the whale (seen as fast non-directional behaviour). According to this interpretation, higher fast non-directional rates seen for smaller groups suggest higher feeding rates in smaller groups, and probably not simply behaviour characteristic of a type of feeding strategy that is more common in small groups.

Fast non-directional rate correlated with local variation in sighting frequency in 1987, while in 1986 both sighting frequency and fast non-directional rate were equivalent between areas. This and the decrease in multi-pod sightings in 1987 implies that resources may have been limiting or distributed differently during that year. Catch statistics from the sport fishery in the San Juan vicinity support this possibility showing a stronger run of chinook, *O. tshawytscha*, and coho, *O. kisutch*, in 1986 (chinook: 15 084 versus 13 877 caught in 1987; coho: 12 420 caught in 1986 versus 10 177 in 1987; archive data from the statistics division, Washington State Department of Fisheries, Olympia, Washington, U.S.A.), though these data are only suggestive. There was no difference in the fast non-directional rate between years, but the average number of whales present in the area per day was greater during 1986. In 1986 subgroup size increased during multi-pod sightings. This would be expected if patches of food were restricted in range, but sufficiently abundant to support several individuals within a group. This effect was not seen in 1987.

During both years the number of multi-pod sightings increased in the second season. This effect was more pronounced in 1986. Salmon species move through the area in a series of runs through the summer months, and the strongest peak runs are during the second season as defined above (Jewell et al. 1971). Consistently, Bigg et al. (1990) reported an increase in killer whale sightings during August and September for this population averaged over 15 years (cf. Heimlich-Boran 1986).

Whole pods were usually highly directional and synchronous, and this together with the low rate of fast non-directional behaviour suggests that feeding was less common during whole pod sightings. Group milling behaviour was an exception to this general pattern. During this behaviour multipod associations were most common, and the composition of subgroups changed frequently. The context sometimes implied social interaction, for example, when two or more pods converged after travelling independently (cf. Osborne 1986). However, fast non-directional behaviour was significantly more common during milling than during other sightings, suggesting that some proportion of the time spent in group milling was spent feeding. Group milling was most common at some distance from shore over areas of shallow bathymetric relief. This is consistent with the idea that uneven submarine topography could assist hunting by providing a barrier against which potential prey could be herded (Heimlich-Boran 1988).

However, group milling was seen very infrequently (3·4% of sightings; cf. Osborne 1986). Although about 30% of the study area included regions of shallow relief bathymetry, the whales were most often sighted over deep open water. This was true even during periods of apparent feeding. The fact that fast non-directional sightings were equally likely over all bottom topographies could be due to the distribution of their prey in the water column. If their prey were most common near the surface, as is the case for salmon, then the contour of the ocean floor should affect hunting behaviour only in very shallow areas, or when it affects the pattern of currents at the surface. An effect of topography on currents should be relevant only

when it changes the behaviour of potential prey; for example, areas of upwelling are often rich in nutrients and the planktonic prey of numerous fish species.

Various quadrats within the study ranges were areas of strong riptides, downwellings or upwellings, but there was no statistically significant variation in fast non-directional frequency between quadrats within areas. Unlike behaviour reported for Johnstone Strait (Jacobsen 1986) where killer whales appeared to follow along regions of converging currents (tide lines), whales in this study area most frequently simply passed through areas of strong current, occasionally increasing the frequency of percussive behaviour. Salmon are migratory through the region and form only temporary aggregations in areas of current discontinuity and at slack tide (see Stasko et al. 1973, 1976). Felleman (1986) reported that killer whale milling behaviour was most common during slack tide when salmon also tend to mill. It is possible that group milling behaviour, when not due to social interactions, tends to represent feeding on unusually large shoals of prey over shallow banks or in areas of upwelling.

Various authors have suggested that percussive behaviour could be used to assist herding of prey (Wursig & Wursig 1980; Hoyt 1984; Felleman 1986; Wursig 1986). However, there was no correlation between percussive and fast non-directional behaviour during this study. There was, however, a strong correlation between percussive behaviour and group divisions. Felleman (1986) also suggested a relationship between percussive behaviour and directional changes. In the present study, adult males were more likely to behave percussively in groups than any other age/sex class.

The most consistent correlations with fast non-directional behaviour were with a reduction in the distance between subgroups, and a reduction in speed. In an environment where prey occur in large sparsely distributed patches, as is the case for salmon in the study area, these two types of behaviour would be consistent with the location and exploitation of prey. If sightings when the pod was divided into subgroups but not exhibiting fast non-directional behaviour could be interpreted as foraging, and subgroups engaged in fast non-directional behaviour as feeding, then the following pattern of hunting behaviour would emerge. Foraging generally takes place in moderately sized subgroups travelling quickly through the area and spread out

in flank formation or in the direction of travel with an average distance of about 400 m between groups. Norris & Dohl (1980) have suggested that this type of formation would be highly efficient for foraging in dolphins, which are capable of sonically scanning large areas of the environment.

Feeding generally took place in small subgroups, travelling slowly or milling, with an average distance of about 250 m between subgroups. A reduction in subgroup size would be expected during active feeding if competition within groups limited the feeding rate of individual whales. A reduction in the distance between groups could be interpreted as the convergence of whales on a patch of food of finite size, and/or as a means to facilitate cooperative hunting. If the latter were true it would be expected that subgroups converge and diverge more often during this activity. This was not observed, although some of the convergences and divergences seen concurrently with fast non-directional behaviour were consistent with interpretations related to coordinated feeding behaviour.

In summary, both males and females in this population may benefit from social behaviour through facilitated food finding, but not necessarily cooperative prey capture. However, the adaptive advantage to travelling in groups may be different for males and females. Adult females tended to be more likely to exhibit fast non-directional behaviour when in groups, while adult males travelled alone more than any other age/sex class, and were much more likely to exhibit fast non-directional behaviour when alone than when in groups. Adult male killer whales are nearly twice as massive as adult females. This would imply roughly twice the energetic requirements. If competition within groups is important, then males would be expected to require more time feeding alone, as observed. If cooperation within subgroups is important, this may benefit females more than males.

REFERENCES

Balcomb, K. C., Boran, J. R., Osborne, R. W. & Haenel, N. J. 1979. *Observations of Killer Whales (*Orcinus orca*) in Greater Puget Sound, State of Washington.* Seattle, Washington: Department of Commerce.

Bigg, M. A. 1982. Assessment of killer whale (*Orcinus orca*) stocks Vancouver Island, British Columbia. *Rep. Int. Whal. Comm.*, **32**, 655–666.

Bigg, M. A., Ellis, G. M., Ford, J. K. B. & Balcomb, K. C. 1987. *Killer Whales.* Nanaimo, British Columbia: Phantom Press.

Bigg, M. A., Macaski, I. B. & Ellis, G. 1976. *Abundance and Movements of Killer Whales off Eastern & Southern Vancouver Island with Comments on Management.* Quebec: Arctic Biological Station Ste Anne de Bellevue.

Bigg, M. A., Olesuik, P. F., Ellis, G. M., Ford, J. K. B. & Balcomb, K. C. 1990. Social organization and genealogy of resident killer whales (*Orcinus orca*) in coastal waters off British Columbia and Washington State. *IWC Special Issue Ser.*, **12**, 383–406.

Caraco, T. & Wolf, L. L. 1975. Ecological determinants of group sizes of foraging lions. *Am. Nat.*, **109**, 343–352.

Felleman, F. L. 1986. Feeding ecology of the killer whale (*Orcinus orca*). M.Sc. thesis, University of Washington, Seattle.

Felleman, F. L., Heimlich-Boran, J. R. & Osborne, R. W. 1991. Feeding ecology of the killer whale (*Orcinus orca*). In: *Dolphin Societies* (Ed. by K. Pryor & K. S. Norris), pp. 113–147. Berkeley, California: University of California Press.

Heimlich-Borna, J. R. 1986. Fishery correlations with the occurrence of killer whales in greater Puget Sound. In: *Behavioral Biology of Killer Whales* (Ed. by B. Kirkevald & J. S. Lockard), pp. 113–131. New York: A. R. Liss.

Heimlich-Borna, J. R. 1988. Behavioral ecology of killer whales (*Orcinus orca*) in the Pacific Northwest. *Can. J. Zool.*, **66**, 565–578.

Hoelzel, A. R. & Osborne, R. W. 1986. Killer whale call characteristics: implications for cooperative foraging stragies. In: *Behavioral Biology of Killer Whales* (Ed. by B. Kirkevald & J. S. Lockard), pp. 373–406. New York: A. R. Liss.

Hoyt, E. 1984. *The Whale Called Killer.* 2nd edn. New York: E. P. Dutton.

Jacobsen, J. K. 1986. The behaviour of *Orcinus orca* in the Johnstone Strait, British Columbia. In: *Behavioral Biology of Killer Whales* (Ed. by B. Kirkevald & J. S. Lockard), pp. 135–186. New York: A. R. Liss.

Jewell, E., Fiscus, G. & Pratt, D. 1971. *Forecasts of the 1971 Puget Sound Salmon Runs and Management Proposals for the Commercial Net Fisheries.* Seattle, Washington: Washington Department of Fisheries.

Lamprecht, J. 1978. The relationship between food competition and foraging group size in some larger carnivores. *Z. Tierpsychol.*, **49**, 260–284.

Norris, K. S. & Dohl, T. P. 1980. The structure and function of cetacean schools. In: *Cetacean Behavior* (Ed. by L. M. Herman), pp. 211–261. New York: John Wiley.

Osborne, R. W. 1986. A behavioral budget of Puget Sound killer whales. In: *Behavioral Biology of Killer Whales* (Ed. by B. Kirkevald & J. S. Lockard), pp. 211–250. New York: A. R. Liss.

Rodman, P. S. 1981. Inclusive fitness and group size with a reconsideration of group sizes of lions and wolves. *Am. Nat.*, **118**, 275–283.

Stasko, A. B., Horral, R. M. & Hasler, A. D. 1976. Coastal movements of mature Fraser River salmon (*Oncorhynchus nerka*) observed by ultrasonic tracking. *Trans. Am. Fish. Soc.*, **105**, 64–71.

Stasko, A. B., Horral, R. M., Hasler, A. D. & Stasko, D. 1973. Coastal movements of mature Fraser River pink salmon (*Oncorhynchus gorbuscha*) as revealed by ultrasonic tracking. *J. Fish. Res. Bd Can.*, **30**, 1309.

Wursig, B. 1986. Delphinid foraging strategies. In: *Dolphin Cognition and Behavior: A Comparative Approach* (Ed. by R. Schusterman, R. Thomas & F. G. Wood), pp. 347–359. Hillsdale, New Jersey: Lawrence Erlbaum.

Wursig, B. & Wursig, M. 1980. Behavior and ecology of the dusky dolphin, *Lagenorhynchus obscurus*, in the South Atlantic. *Fishery Bull.*, **77**, 871–890.

Zimen, E. 1976. On the regulation of pack size in wolves. *Z. Tierpsychol.*, **40**, 300–341.