ASSOCIATION PATTERNS AND SOCIAL DYNAMICS OF KILLER WHALES (*Orcinus orca*) IN GREATER PUGET SOUND

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"people...seem to treat cetaceans as if the whole group somehow fell from Mars, behaviorally, rather than being normal products of evolution; as if they cannot be expected to show behavioral traits typical of other social mammals, such as dominance hierarchies, territoriality, collective defence, prolonged parental care and so on"... K. Pryor (1986, p.91).

INTRODUCTION

Most dolphins are highly social mammals which spend their lives as members of a mobile school with complex intra-school relationships (Norris & Dohl 1980a; Würsig 1986). Recent studies of wild aggregations have shown variations among dolphin species in the permanence, size, and individual or subgroup membership of schools. Many of the smaller species of dolphin, especially bottlenose dolphins (_Tursiops truncatus_), exhibit both group fluidity and short-term subgroup stability (Würsig & Würsig 1977, 1979, 1980; Norris & Dohl 1980a; Wells et al. 1980, 1987; Connor & Norris 1982; Johnson & Norris 1986; Shane et al. 1986; Wells 1986). Larger dolphins, such as killer whales (_Orcinus orca_) and pilot whales (_Globicephala_ spp.), form stable social units (Bigg 1982; Balcomb et al. 1982; Kasuya & Marsh 1984). Killer whales indigenous to the inland marine waters of the Pacific Northwest exhibit an especially stable social system (S.L. Heimlich-Boran 1986; Bigg et al. 1987; Bain 1988).

Killer whales in Greater Puget Sound are long-lived (Bigg 1982; Bigg et al. 1987). Females may live to at least 60 years of age and some have been estimated to reach 80 years. First parturition occurs at about 14 years and females typically produce 4 to 6 offspring over a 25 year span, usually born singly at intervals ranging from 3 to 8 years (Bigg et al. 1987; Heyning & Dahlheim 1988). Gestation is estimated at 15 months, with lactation lasting about 12 months and an additional period of calf dependency of at least 2 years. Annual pregnancy rates are estimated at about 13.7 % (Heyning & Dahlheim 1988), with large differences in fecundity between females (Balcomb & Bigg 1986). Reproductively senescent females may live an additional 20 or more years after their last birth. Males appear to have a higher mortality rate than females, with average life-spans reaching at least 30 years of age and maximum longevity of about 50 years (Bigg et al. 1987). They begin secondary dorsal fin growth at about age 7, reach sexual maturation at 14 years, but do not reach full adult size until about age 20 (J. Heimlich-Boran 1986a; Bigg et al. 1987).

Killer whales live in social groups with overlapping generations (Bigg 1982; S.L. Heimlich-Boran 1986; Matkin & Leatherwood 1986; Bigg et al. 1987; Bain 1988). Specific groups, commonly referred to as "pods," associate together as closed communities. Bigg et al. (1987) have identified three socially isolated communities in the inland marine waters of Washington and British Columbia: a northern resident community totalling 16 pods off northern Vancouver Island; a southern resident community of 3 pods off southern Vancouver Island and Washington; and a transient community of 30 pods which occur sporadically throughout the entire region. No interactions have been observed between communities, and numerous lines of evidence suggest residents and transients differ in patterns of distribution, seasonal occurrence, acoustic dialects, and prey choice (Ford & Fisher 1982, 1983; Felleman 1986; J. Heimlich-Boran 1988; Felleman et al. In press), as well as apparently inherited pigmentation patterns and dorsal fin morphology (Bigg et al. 1987, Baird & Stacey In Press). Additionally, the two resident communities have different sex and age class distributions. During the 1960's and 1970's, several maturing males and females were removed from the sounthern resident community for display in aquaria (Bigg 1982). Whereas the nothern resident community has a sex ratio of one adult female per adult male and a fairly even distribution of animals of all ages, the sex ratio of the southern community is 3 adult females per adult male and many potential breeders were lost from the population (Olesiuk & Bigg 1988).

Residents appear to have complex social relationships (S.L. Heimlich-Boran 1986; Bigg et al. 1987). Female killer whales form close-knit kin-based relationships. Offspring associate with their mother well into maturity (S.L. Heimlich-Boran 1986; Bigg et al. 1987). Extremely close affiliations exist between these maternal groups and non-reproductive adult females (probably older, post-reproductive females who are possibly grandmothers or aunts of the offspring: S.Heimlich-Boran 1986, Bigg et al. 1987). Two or more maternal subgroups form permanent associations as pods. Some pods have subpods within them which may not always travel together (Bigg et al. 1987).

When either community or pod dissociation occurs, individual whales consistently return to their own pod and subgroup (Balcomb et al. 1980; S.L. Heimlich-Boran 1986; Bigg et al. 1987). This stabilty in group membership and consistency in social patterns has been exhibited for 15 years of study (S.L. Heimlich-Boran 1986; Bigg et al. 1987).

This paper expands upon the initial examination of the cohesive structures that maintain pod membership in the southern community of killer whales in Greater Puget Sound (S.L. Heimlich-Boran 1986). This study re-evaluates associations occurring at the surface of the water between members of each pod and between members of differing pods. I assumed that the occurrence of two or more whales travelling at the surface alongside one another indicates a social affiliation or bond between them. This assumption has been the foundation for a number of very diverse studies: lions (Schaller 1972), elephants (Douglas-Hamilton & Douglas-Hamilton 1975; Moss & Poole 1983), eland (Underwood 1981), elk (Knight 1970), and several cetacean species (Würsig 1978; Taber & Thomas 1982; S.L. Heimlich-Boran 1986; Wells 1986; Ballance 1987). Three factors which may affect associations within pods and between pods are examined: the influences of sex and age on associations between individuals; the influences of specific behaviors on over-all affiliations between sex and age classes; and the influences of kinship.

I will show that although there are some effects from sex and age factors, kinship remains the over-riding influence on association trends within the resident killer whale community of Greater Puget Sound. I will also show that the resulting social system is a multilevel society centered around core groups of maternally related kin similar in some ways to that described for pilot whales (Kasuya & Marsh 1984), elephants (Douglas-Hamilton & Douglas Hamilton 1975; Dublin 1983), baboons (Kummer 1968; Stammbach 1987), hyaenas (Kruuk 1972), buffaloes (Jarman &

Jarman 1979) and some human communities (Gough 1962; Irons 1983; Waterhouse 1983; Wasser & Barash 1983).

METHODS

Data Collection and Definitions

Sampling Methods

Killer whales were observed in the inland marine waters of Washington and British Columbia, between 47.0 degrees and 49.3 degrees north latitude (Fig. 1), from 21 March to 16 November 1982, and from 21 January to 29 November 1983. The majority of research occurred in Haro Strait in the San Juan Islands. Whales were usually first located via sightings from shore stations on San Juan Island or from sightings phoned in by the public to a toll-free sighting report system. Whales were followed in 5 m motorboats and occasionally in larger sailboats.

All whales were individually identifiable from naturally occurring marks and scars on the dorsal fin and back. Bigg et al. (1987) assigned names to each whale; pods were named alphabetically and individuals numerically within their pod (e.g. A1, B15, etc.). Many whales were identified visually in the field with the aid of a photographic guide to individuals (Bigg et al. 1987).

Photographs of the dorsal fin and back of all individuals were taken with 35 mm cameras using 200-300 mm lenses.

Data collection concentrated on group composition and spacing, identification and associations of all whales present, and the recording of the dominant behavior occurring at that time. Pairs or groups of whales were defined as in association when surfacing within one adult body length (about 8 meters) of each other.

Sampling was conducted on a continuous basis. However, for analysis, observations were standardized as frequency counts of 15 minute interval scan samples (Altmann 1974). This regime was used to counteract any errors in field observations resulting from two primary sources: 1) surfacing intervals of associating whales were more sequential rather than synchronous, and occurred over several minutes; and 2) not all whales within an associating group were easily identified, and confirmed identification often required many observations over several minutes. Data samples were only included in this study if there were photographically-confirmed identifications of the whales occurring at that time. These sampling criteria were fairly rigorous and reduced the data base. Based on previous reports on the distribution of whale observations in the study area

(Balcomb, Boran & Heimlich 1982; Osborne 1986; J. Heimlich-Boran 1988), I believe that the samples used in my analyses accurately represent the overall distribution of whale observations during the study.

Sex and Age Class Definitions

The sex/age classes considered in this analysis were adult males, barren adult females, mothers, adolescents, and immatures. Ages were determined from observed years of birth for whales less than 15 years old, and estimated for whales greater than 15 years old, based on assumptions from Bigg et al. (1987) and records at The Whale Museum, Friday Harbor, Washington. Adult males were defined as whales of 15 or more years of age with large dorsal fins and approaching full adult size. Adult females were females of 15 or more years of age. Barren adult females were those with no observed births since 1974, the onset of killer whale studies in this region, and which have been presumed of post-reproductive age (Bigg et al. 1987). Mothers were adult females with known calves. Adolescents were sub-adult whales and included both sexes from 7 to 14 years of age, an average based on the initiation of allometric dorsal fin growth in males (J. Heimlich-Boran 1986a) and the average age of first birth in females (Bigg et al. 1987). Immatures included males, females and calves of undetermined sex from newborn to 6 years of age. Sexes were pooled in both sub-adult classes in order to increase group size for statistical analyses.

Study Population

Seventy-two whales identified in 1982 and 1983 comprised the study population (Table 1). This included: 19 whales comprising J pod (3 adult males, 3 barren adult females, 5 mothers, 3 adolescents and 5 immature whales); 10 whales comprising K pod (2 adult males, 2 barren adult females, 3 mothers, 2 adolescents and 1 immature whale); 5 whales comprising L-sub pod (2 adult males, 2 barren adult females and 1 mother); and 38 L pod whales (5 adult males, 4 barren adult females, 13 mothers, 10 adolescents and 6 immature whales).

An additional 8 whales from L-pod were observed with the pod during this time period (Bigg et al. 1987), but they were not photographically documented in this study and may have been missed during my observations. L pod has a frequent habit of splitting into independent sub-groups (Balcomb et al. 1982; Bigg et al. 1987). Until recently, L-sub pod has been considered a discrete sub-group of L pod. However, Bigg et al. (1987) currently suggest that it is actually a sub-group of K pod, based on acoustic simlarities between the two groups and the frequent associations between them. However, for this study, "L-sub" will remain the term in use for this group of whales.

Behavioral Definitions

Behaviors were categorized from combinations of quantifiable parameters of group composition, spacing of individuals, speed and direction of travel, and the occurrence of specific behaviors such as leaps, tail slaps, penile erections, etc. (Osborne 1986). Observations of prey were used as confirmation of feeding behaviors. Osborne (1986) analyzed these parameters and defined eight functional categories of behavior. The functions of the behaviors proposed by Osborne have been confirmed through a variety of methods (Felleman 1986; J. Heimlich-Boran 1986b, 1988; Felleman et al. In press). I pooled behaviors into four major groups: feeding, travel, rest and social/sexual behaviors.

Feeding behavior included milling, foraging and percussive foraging. Milling was defined as non-directional swimming by a majority of group members, lasting longer than 15 minutes and when prey were observed being actively pursued by whales (Osborne 1986, Felleman 1986; Felleman et al. In press). Foraging was defined as directional movement (travel) interspersed with short bouts of milling, implying whales were searching areas and feeding when prey were encountered (J. Heimlich-Boran 1988; Felleman et al. In press). Percussive foraging was defined as foraging behavior interspersed with bouts of percussive behaviors such as slapping tails and flippers on the surface of the water. Percussive behaviors create loud underwater noises that are thought to aid in the herding of fish prey (Norris & Dohl 1980a; Würsig 1986).

Travel behavior included directional, uninterrupted movement at speeds of 2.0 to 4.0 knots, and movement at speeds greater than 4.0 knots interrupted by percussive behaviors such as "porpoising" or high-speed leaping out of the water. Percussive travel may simply be a boisterous (or energy efficient: Blake 1983) means to get from one place to another, a means of communication for dispersed groups (Norris & Dohl 1980a; Whitehead 1985), or an aid to prey herding (Norris & Dohl 1980a; Würsig 1986) since it quite often appears to end at favored feeding areas (J. Heimlich-Boran 1988).

Rest behavior was defined as slow, directional travel in tightly clumped groups breathing synchronously. Osborne (1986) noted this behavior occurred in bouts of 0.5 hrs to 6.6 hrs, averaging 1.8 hrs.

There were three behaviors pooled as social/sexual behaviors: play, intermingling and active sexual displays. Play behavior was defined by the repetitious occurrence of behaviors serving no obvious practical function, such as full-body leaping out of the water (breaching) or interacting with floating objects (e.g. drifting kelp). Both calves and adults played (Osborne 1986). Intermingling behavior was a rare behavior characterized by tightly clumped groups of whales in body contact, often rolling around and lifting each other out of the water. This behavior primarily occurred when two pods met after being separated (Osborne 1986), and may function similarly to "rallying" groups of spinner dolphins gathering prior to foraging (Norris & Dohl 1980b; Norris et al. 1985), to "greeting ceremonies" of African wild dogs before the hunt (Estes & Goddard 1967; Frame et al. 1979), or to greetings of African elephants from neighboring family groups (Moss & Poole 1983). Sexual behavior was strictly defined by the observation of a male surfacing with an erect penis. This behavior occurred in a wide variety of contexts and the term is not meant to imply that the behavior always involved breeding. There is great difficulty in isolating the social aspects of sexual behavior from its reproductive function in cetaceans (Norris & Dohl 1980a; Wells 1984) as well as in other mammals (Hanby 1976). Hanby (1976) recommended calling these behaviors "socio-sexual" behaviors.

Analytical Methodology

Behavioral Analysis

The four major behavioral categories were examined for both their distribution during the study period and occurrence in multi-pod and single-pod groups. Behavior distributions for different pod groupings were tested for significant variations using a chi-square analysis (Zar 1984). The intrinsic null hypothesis was that the distribution of behaviors for different pod groupings should be similar to the overall distribution of behaviors (J. Heimlich-Boran 1988). Chi-square tables were subdivided to determine which behaviors or which pod groupings were responsible for significant differences.

Pod Interactions

I compared the number of hours each whale pod was observed, alone or with other pods (termed "pod hours") to determine broad-scale differences in the sociality of the four main whale groups. The compositions of multi-pod groups were then compared to examine preferences in across-pod affiliations.

Basic Format for Analysis of Associations

Analyses for association patterns were performed on two basic categories of data, associations within pods and associations between pods. Analysis of associations within pods considered two sub-sets of data: 1) associations between all whales, including documented kin (mother/calf and sibling pairs); and 2) associations between whales which were not documented kin (termed "non-kin"). This sub-division was a means of factoring out possible influences of kinship, assuming that related whales associated differently than non-related whales.

Associations between Individuals

Associations between individuals, both within pods and across pods, were examined at several levels. Variation in the number of associates of individual whales was examined by counting the number of different whale pairs and comparing these as a percentage of the number of all possible pair occurrences. The frequency of associations between individuals was examined using a coefficient of association that normalized data to adjust for differences in sighting frequencies of individual whales resulting from the unequal distribution of observation time of the four pods (Schaller 1972; Morgan et al. 1976; Lehner 1979; S.L. Heimlich-Boran 1986; Wells 1986):

$$\text{Coefficient of Association} = 2J/(A+B)$$

where J = the number of sightings of whale A and whale B together

A = the total number of sightings of whale A, alone or with other whales

B = the total number of sightings of whale B, alone or with other whales

Coefficients were calculated for all possible pairs of identified whales and ranged from zero for two whales that were never seen within one adult body length of eachother, to 0.86 for pairs that were seen together most frequently. No pair achieved a value of 1.00, which would indicate they were always sighted together. Pairs with values of zero were not included in further analyses.

Coefficients of association between individual whales were employed to examine trends in associations of pods as well as of sex/age classes. Groups of pair association coefficients were tested for differences using the non-parametric tests of Kruskal-Wallis rank ANOVA and Dunn's multiple comparisons (Wells, 1986). Single-link cluster analyses were performed on the coefficients of association between individuals in each pod to determine their relative association within the overall pod structure (Morgan et al. 1976; Lehner 1979).

Associations between Sex/Age Classes

Chi-square analyses were conducted on the frequencies of joint occurrences of classes, testing the null hypothesis that associations were evenly distributed across all classes. Expected values were generated in proportion to the number of possible associates in each class. The chi-square analyses were subsequently subdivided for analysis of the relative contributions of particular classes to overall significant differences.

Coefficients of association were also calculated for each class (termed "class association coefficient") based on the frequencies of joint pair occurrences pooled by class (Wells, 1986). These were employed as a descriptive method to examine relative association patterns between the five sex/age classes during feeding, travel, rest and social/sexual behaviors. They were not tested for statistical significance. Two modifications of the basic equation were required:

$$\text{Coefficient of Association between two classes} = Nij/(ni+nj)-Nij$$

where ni = the total number of pairs including class i (eg: the occurrence of adult males with all classes)

nj = the total number of pairs including class j (eg: the occurrence of mothers with all classes)

Nij = the total number of pairs where the two classes occurred together.

Coefficient of Association within one class = Nii/Nij

where Nii = the total number of pair occurrences within class i (e.g. the occurrence of adult males together)

Nij = the total number of pair occurrences between class i and all other classes (e.g. the occurrence of adult males with all classes).

RESULTS

The Data Base

Distribution of Whale Observations

Seventy-two resident whales from four major pods were seen in 98 encounters for 120.75 hours of observation, 69.25 (57%) hours in 1982 and 51.50 (43%) hours in 1983. The mean number of 15 minute scan samples per whale was 44.5 (SD = 44.29, N = 72, Range = 1 - 188), or about 11.11 hrs per whale.

Whales were observed in all but two months of the study period. Three-fourths of the observations were during June through September, with a peak in August (Fig. 2). J pod was seen in all but three months of the study. K pod was observed predominantly June through November. L pod was also seen predominantly June through November, but with greatest frequency in September. L sub-pod observations were most abundant June through August.

Sighting effort decreased during winter due to poor weather conditions which required hauling boats out of the water. However, reports from other sighting sources show similar seasonal distribution patterns and suggest that in spite of limited winter observations, pods occur in the study area predominantly during spring to fall (J.R. Hemlich-Boran 1986, Felleman et al. 1988). Bigg et al. (1987) suggested the range of these whales extends to the Pacific coast of Vancouver Island and Washington state and this may be their primary wintering area.

Composition of Groups

Groups of whales were composed of two or more animals from either one pod (single-pod groups), or from two or more pods (multi-pod groups). Single-pod groups were seen during 70.50 hours (58%) of observation, predominantly through spring and early summer. Multi-pod groups were seen during 50.25 hours (42%) of observation, primarily in late summer and fall (Fig. 2).

J, K, L and L-sub pods were observed for 193 pod hours (Fig. 2). J pod accounted for 46% of all pod hours and was seen approximately equally in single and multi-pod groups. K pod acounted for 26% of the total pod hours and was more often observed in multi-pod groups than in single-pod groups. L and L-sub pods accounted for 11% and 17% of the total pod hours, respectively. Whereas L whales were seen in multi-pod groups slightly more than in single-pod groups, L-sub whales were predominantly observed in multi-pod groups.

Groups composed of J and K whales were the most frequently observed multi-pod groups (Table 2). J,K and L-sub multi-pod groups were also frequently observed, yet L-sub whales were more often observed with J whales than with K whales. L pod whales were observed in multi-pod groups in approximately equal amounts with whales from other pods.

Behavioral Budget

The distribution of behaviors for the entire study period is shown in Table 3. Feeding behavior comprised almost half of the whales' time. Rest and travel occurred with approximately equal frequency and comprised about one quarter of the whales' time. Social/sexual behavior was rarely observed. The overall proportions of these behaviors in single and multi-pod groups were not significantly different than expected.

Comparison of the distributions of these behaviors for each pod to the above overall distribution yielded significant differences for only L pod whales and L-sub pod whales (Chi-square = 10.150, df = 3, P <0.025 and Chi-square = 10.916, df = 3, P < 0.025, respectively).

In L pod, only social/sexual behavior occurred significantly more than expected. This behavior was exhibited predominantly when L whales were in multi-pod groups rather than in groups with their own pod members (Chi-square = 10.002, df = 3, P < 0.025).

In L-sub pod, rest behavior was observed more than expected. As in L pod, this behavior was more predominant when L-sub whales occurred in multi-pod groups than when they were in single-pod groups (Chi-square = 14.496, df = 3, P <0.005)

Composition of Pairs

The distribution of pair combinations within pods (intra-pod) and across pods (inter-pod) is shown in Table 4. Individual whales were seen with a variety of associates. Every whale in J, K, and L-sub pods was seen at least once with every other member of its own pod; thus, 100% of all possible intra-pod pair-wise combinations occurred in these pods. In contrast, just over one quarter (27%) of all possible pair-wise combinations were observed in L pod. This suggests greater disassociation in this pod, the largest of all pods in the community.

Just over one-eighth (13%) of all possible pair-wise combinations across pods occurred. Pair-wise combinations did not conform to the dynamics of group formation. A greater percentage of all possible pair-wise combinations of K/L-sub whale pairs were observed than J/L-sub pairs; although multi-pod groups composed of J and L-sub whales occurred more frequently than groups of K and L-sub whales. Although multi-pod groups composed of J and K whales were the most frequently-occurring of all multi-pod groups, less than half of the corresponding possible pair-wise combinations were observed. This suggests selectivity in inter-pod associations between individual whales. The lowest percentages of possible inter-pod pairwise combinations were those involving L pod whales, indicating greater association between J,K, and L-sub pods and little association between these pods and L pod.

In addition to this variability in numbers of associates, whales also showed variation in the frequency of association with particular individuals. The frequency of association, as described by coefficients of association, showed variation with pod affiliations. Coefficients of association also showed some variation with sex and age, as well as behavior.

Associations Within Pods

Comparison of Pair Associations by Pod

The coefficients of pair associations within pods, including mother/calf and sibling relationships, ranged from 0.04 to 0.86 (Mean = 0.21, SD =.147, N = 415). The range of values excluding these kin relationships was 0.04 to 0.63 (Mean = 0.18, SD = 0.110, N = 380).

Figure 3 shows the distribution of association coefficients for pairs of whales in each of the 4 pods. Kruskal-Wallis rank ANOVA and Dunn's multiple comparison testing revealed few significant differences between the coefficients of association within the four pods. Association coefficients for pairs of whales in L pod were lower than those in the other pods, but only significantly different ($P < 0.05$) than those for J pod and K pod. Figure 3 shows that this pattern was the same for the groups of coefficients excluding known mother-offspring and sibling pairs.

Pod values pooled associations between sex/age classes, which may have masked the contribution of particular classes to the overall variability between the four pods. Therefore, differences between the classes of the pods were examined (Table 5).

Analysis of association coefficients including mother/offspring and sibling pairs showed that there were no significant differences between pods in the coefficients of barren adult females or sub-adults. Interpretation of tests on adult male coefficients was problematic. Rank ANOVA showed that the coefficients of adult males were significantly different ($H= 8.054$, $df = 3$, $N = 156$, $P < 0.05$), yet multiple comparison testing failed to locate any significant differences between them. However, the greatest variation (at $P < 0.10$) was between the values of L pod adult males and those of K pod adult males. The values of L pod mothers were significantly ($P < 0.05$) lower than those of both J pod mothers and K pod mothers. This suggests fewer overall associations by L pod mothers with pod members than mothers in the other pods.

Examination of non-kin association coefficients (i.e. the groups of values excluding known mother-offspring and sibling pairs) showed little variation from the above results. The coefficients of association between L-pod mothers and all other non-kin pod members were again significantly lower ($P < 0.05$) than those of J and K mothers. The association coefficients of J pod immature whales were significantly ($P < 0.05$) higher than the association coefficients of L pod immature whales.

Overall, dissimilarity between pods was not wide-spread. Differences in associations between mothers and whales in their own pods contributed almost exclusively to the divergence of L pod from the others. The comparatively low coefficients of L pod pair associations, particularly those of mothers, parallels the trends in pair-wise occurrence within the pod and may reflect greater dissociation within L pod. The divergence of L pod from the others also parallels the trends of group and pair-wise occurrences and may also reflect a relative dissociation from the community at large. However, since differences between pods were not extreme, pair associations from all four pods were pooled for further analysis of sex/age classes.

Comparison of Pair Associations by Sex and Age Class

Table 6 shows the distribution of association coefficients amongst the five sex/age classes. The association coefficients of all adult males with all whales of their own pods were lowest as compared to the coefficients for all barren adult females, mothers, adolescents and immatures. However, multiple comparison testing revealed that the only significant ($P < 0.05$) differences were between the coefficients of adult males and those of barren adult females, adolescents and immatures; values of the former were lower than those of the latter three groups.

Examination of non-kin coefficients of association revealed secondary differences. The coefficients of mothers were significantly ($P < 0.05$) less than those of barren adult females. The coefficients for adult males remained significantly ($P < 0.05$) lower than those of barren adult females, but were not significantly different from the coefficients of mothers or either of the two sub-adult classes.

These two analyses indicate that adult males and barren adult females associate outside the norm within their own pods, adult males tending towards lower coefficients and barren adult females towards higher coefficients. Additionally, the associations of mothers and calves to whales of their own pods are dominated by their associations with kin; low associations between mothers and non-offspring are more on a par with pair associations of adult males.

Class values pooled associations between whales of all classes. This may have masked the contribution of particular sex/age classes to the overall variability between classes. Therefore, the associations of each class were examined.

There were no significant differences in coefficients of intra-pod pair associations between adult males or barren adult females, and whales of other sex/age classes, including associations with whales of their own class. This indicated that association efforts of these two classes with members of their own pod were fairly uniform.

Associations of mothers with members of their own pods (including their offspring) showed some significant variability. Associations between mothers and immatures ranked highest, but were only significantly ($P < 0.05$) higher than associations between mothers and adult males and associations between mothers and themselves. Coefficients of association between mothers and adolescents ranked the next highest but were not significantly different from associations between mothers and other classes. Examination of non-kin association coefficients (coefficients of association between whales other than mothers and offspring or siblings) revealed no significant differences in pair coefficients of association between mothers and any sex/age class of their own pods (like the association patterns of adult males and barren adult females). This suggests that the differential association effort exhibited by mothers is primarily due to their close relationships with their immature offspring.

Coefficients of association between adolescents and barren adult females ranked highest of all adolescent association coefficients. However, they were only significantly ($P < 0.05$) higher than those between adolescents and adult males. Coefficients of association between adolescents and barren adult females remained highest-ranking in the analysis of coefficients of association between adolescents and non-kin whales. They ranked significantly ($P < 0.05$) higher than associations between adolescents and adult males, and associations between adolescents and non-related mothers. This indicates adolescents have little affinity for adult males and great affinity for barren adult females. Adolescent whales' affinities for these females may be equal to, or even greater than, affinities for their own mothers. As shown in previous studies (S.L. Heimlich-Boran 1986; Bigg et al. 1987), the barren adult females with which adolescents have highest coefficients of association are the same barren adult females with which their mothers also have high values. This strongly suggests that the associations between adolescents and barren adult females may very well be relationships between kin.

Coefficients of association between immatures ranked highest of all associations between immatures and pod members (including known mothers and siblings). However, they were only significantly ($P < 0.05$) higher than those between immatures and adult males. Coefficients of association between immatures and mothers were also significantly higher ($P < 0.05$) than coefficients of association between immatures and adult males. Coefficients between non-kin immatures also ranked highest of all associations between immatures and non-kin whales. They again ranked significantly ($P < 0.05$) higher than coefficients of association between immatures and adult males. Coefficients of association between immatures and barren adult females were also significantly ($P < 0.05$) higher than those between immatures and adult males. This indicates immature whales have primary associations with cohorts and mothers, secondary affiliation with barren adult females, and comparatively little affiliation with adult males. This secondary affinity for barren adult females is often with the same females which have high values with their mothers. As with adolescents, this indicates that associations between immatures and barren adult females are kin relationships.

In summary, each class appears to associate with each other sex/age class somewhat differently and there are some basic patterns in associations between sex/age classes.

The paucity of significant variability within each class suggests that each tends to have a rather even distribution of association effort with whales within their own pod. This appears to be more so for adult whales than sub-adult whales, suggesting that association effort of whales evens out after maturation. Aside from associations between mothers and their youngest offspring, there was no significant variability in the assocations of adult classes with other classes. Sub-adult associations with barren adult females were quite different from their associations with adult males. This accounted for most of the variability, particularly in adolescents. Although each class appears to have its own trend, the overall lack of significant variability in the pair association coefficients within and between age and sex classes indicates that associations do not strictly follow a hierarchy based on sex or age parameters.

Class Associations

Chi-square analyses, conducted on the frequencies of joint occurrences of classes, indicated that only the mother and adolescent classes associated non-randomly (Chi-square = 14.49, df = 4, $P < 0.005$ and Chi-square = 10.94, df = 4, $P < 0.05$, respectively). Subdivision of Chi-square showed that for both classes, association with adolescents was less than expected and accounted for the overall significant difference. Chi-square analyses based on the frequencies of joint occurrences of classes excluding mother-calf and sibling pairs showed some further distinctions. Mothers associated with non-related adolescents as well as non-related immatures less than expected (Chi-square = 23.07, df = 4, $P < 0.001$; Chi-square = 9.82, df = 4, $P < 0.05$, respectively). Adolescents associated with non-related adolescents less than expected (Chi-square = 15.87, df = 4, $P < 0.005$).

Class association coefficients were not evenly distributed across all classes nor in the behavior categories of foraging, travel, rest and social/sexual activity (Figs. 4 and 5). All classes except mothers shared their highest intra-pod class association coefficient (inclusive of mother/calf and sibling relationships) with mothers; mothers shared theirs with immatures (Fig. 4). All classes except immatures had least affiliation with their own class; affiliations between immatures and adult males were low. (Fig. 4). This pattern was found in feeding, travel, and rest behaviors. Affiliations were dramatically different in social/sexual behavior for all classes except adolescents. Adult males shared their highest class association coefficient with their own class. Barren adult females had equal affiliation with mothers and adult males. Mothers had greatest affiliation with barren adult females. Immatures were closest affiliates.

Secondary preferences were found for only some classes with examination of class values excluding mother/calf and sibling relationships (Fig. 5). Mothers affiliated most with adult males and, in general, least with non-related sub-adults. Immatures affiliated most with barren adult females and least with non-related adolescents. Adolescents had secondary affiliation with adult males and barren adult females. These results appear to conflict with the results of the previous analyses of pair association coefficients between individual adolescents and other whales, which indicated great preference for barren adult females and little affinity for adult males. However, whereas adolescent affinity for adult males was found only in travel and rest behaviors (representing 23% and 25% of the sampling time, respectively), their preference for barren adult females was greatest during foraging and social/sexual behaviors (representing 44% and 8% of the sampling time, respectively).

Secondary affiliations were again most different in social/sexual behavior. Mothers affiliated most with barren adult females. Immatures affiliated most with non-related immatures. This was most probably influenced by the inclusion of play activity as part of the broader social/sexual category. Immature whales engaged in play most often in the company of other immatures. Adolescent affiliations with barren adult females were equal to their affiliations with non-related immatures.

Cluster Groups within Pods: Individual Associations

Predominant associations between individuals had a major effect on the distribution of pair associations and class association patterns. For example, the significantly higher coefficients of association between adolescent whales and barren adult females were based on associations between specific individuals (i.e. not all adolescents have high association coefficients with all barren adult females). Examination of individual associations revealed clusters, or sub-groups, within the general pod structure (Figs. 6 and 7).

J pod (Fig. 6) comprised four sub-groups and one mother/calf pair. All sub-groups contained a mother and her immature and adolescent offspring. Two of these maternal sub-groups had a barren adult female and an adult male as additional sub-group members. One included only a barren adult female, and another included just one adult male as its additional sub-group member. The mother/calf pair were members of another sub-group through their association with the barren adult female.

K pod (Fig.6) comprised one distinct maternal sub-group with a barren adult female as an additional member, one mother/calf pair, one barren adult female/adolescent pair and three comparatively "independent" whales. The mother/calf pair was most closely associated with the extended maternal sub-group through the association between the mothers. One of the independent whales was a mother (of the adolescent in the non-maternal pair) who was most closely associated with the extended group through her association with the barren adult female. The other independent whales were males who were most closely affiliated with this independent mother. The barren adult female/adolescent pair were the most distantly associated whales in the pod.

The diminutive L-sub pod (Fig. 6) had no confirmed mother/offspring relationships. It comprised two groups: a trio composed of a mother, barren adult female and adult male; and barren adult female/adult male pair.

L pod (Fig.7), the largest of the four pods, comprised roughly six sub-groups, two relatively independent mother/calf pairs, and six relatively independent individual whales. Sub-group membership was more varied in L pod than in the other pods. All included at least one maternal group but many included more than one. Several included more than one barren adult female and one included three adult males but no barren adult female. A few included single mothers whose calves were not observed during the study. Three of the independent whales were adolescents: two males ages 9 (L44) and 11 years (L14) and one 13 year-old female (L22); L44 and L22 are siblings. The other independent whales were adult females: two barren adult females (L12 and L09) and one mother (L23). L44 and L22 were most closely affiliated with L28, a barren adult female who was a member of a sub-group which did not include their mother (L32); L12 was most closely affiliated with an adolescent in this same sub-group. L14 is the son of L23, yet they had little affiliation; she had the least affiliation with other pod members.

In summary, a common "formula" was prevalent. All sub-groups within pods comprised a mother and her immature and/or adolescent offspring. Generally, a barren adult female was an additional sub-group member, with high coefficients of association with the mother or one or more of her offspring. An adult male was also often included, having his highest coefficient of association with one of these members, usually the mother. In each pod, there were one or two clusters whose members had equitable association coefficients to some whales in other clusters, indicating that co-membership was not uncommon.

Associations Across Pods

Comparison of Pair Associations Across Pods

Coefficients of pair association across pods (inter-pod) ranged from 0.01 to 0.13 (Mean = 0.03, SD = 0.021, N = 461). Associations across pods were not as easily examined as associations within pods. Limitations in number of pair occurrences (only 13% of all possible pairs) and frequency of occurrence of these few pairs restricted analyses.

Inter-pod associations were not the same in all four pods. Although coefficients of association were extremely low, Kruskal-Wallis rank ANOVA and Dunn's multiple comparison testing revealed some significant variability. The values between K and L-sub pod members (Mean = 0.05, SD = 0.024, N = 42) ranked highest. They were significantly greater ($P < 0.05$) than those between J and L-sub pod members (Mean = 0.03, SD = 0.020, N = 56) and those between K and J pod members (Mean = 0.03, SD = 0.019, N = 85). This followed the trend in pair occurrences amongst these whales. Coefficients of association between J and L-sub pod members were also significantly ($P < 0.05$) lower than those between L pod and L-sub pod members (Mean = 0.04, SD = 0.018, N =19); although a greater percentage of all possible J/L-sub whale pairs were observed. J and L pod had the least amount of affiliation (Mean = 0.02, SD = 0.009, N = 17) but coefficients were not significantly less than coefficients between K and L pods (Mean = 0.03, SD = 0.014, N = 42), or L-sub and L pods.

The contribution of particular classes to the overall variability in associations across pods was not addressed. Table 7 shows that in many cases, the number of pair occurrences (and corresponding coefficients of association) between classes from different pods was insufficient for rank analysis of variance or Chi-square tests. Therefore, across-pod associations of classes were pooled from all pods for further analyses on the effect of sex and age on associations between whales from different pods.

Comparison of Pair Associations by Sex and Age Class

Comparison of the across-pod association coefficients of adult males, barren adult females, mothers, adolescents and immatures revealed no siginificant differences between them. However, separate examination of the associations of each class revealed some significant differences.

Coefficients of across-pod associations between adult males were the highest of all adult male coefficients (Mean = 0.05, SD = 0.034, N = 20), but only significantly higher ($P < 0.05$) than those between adult males and adolescents from different pods (Mean = 0.02, SD= 0.011, N =20). This indicates some differential association effort and an affinity of adult males for others outside their own pod.

Inter-pod coefficients of pair associations between individual barren adult females and other whales were not significantly different, indicating equal effort in associations with whales of different classes across pods.

Coefficients of association between mothers and whales from other pods showed little variation. Coefficients of association for mothers with barren adult females (Mean = 0.04, SD = 0.021, N = 37) were significantly higher ($P < 0.05$) than those between mothers of different pods (Mean = 0.03, SD = 0.030, N = 15), indicating differential effort and some affinity between these two classes in across-pod interactions.

The inter-pod coefficients of association between sub-adults and whales of other sex/age classes from different pods were not significantly different from each other.

Comparison of Class Association Coefficients

Chi-square analyses, conducted on the frequencies of joint occurrences of classes across pods, showed that adult whale classes associated non-randomly (adult males Chi-square = 18.529, df = 4, P < 0.001; barren adult females Chi-square = 16.786, df = 4, P < 0.005; mothers Chi-square = 22,126, df = 4, P < 0.001). In contrast, associations of sub-adults were random. Subdivision revealed that adult males associated with each other more than expected (Chi-square = 18.53, df = 4, P < 0.001) and with barren adult females more than expected (Chi-square = 10.48, df = 3, P < 0.025). A lack of association with adolescents (Chi-square = 16.79, df = 3, P < 0.005) accounted for the significant differences for barren adult females. Mothers associated more than expected with barren adult females (Chi-square = 22.13, df = 3, P < 0.001) and adult males (Chi-square = 13.48, df = 2, P < 0.005).

Class association coefficients calculated for interactions between pods were not evenly distributed across all classes (even non-existent) nor in the behavioral categories of feeding, travel, rest, and social/sexual activity (Fig. 8).

Adult males had greatest affiliation with other adult males and least with sub-adult whales. This trend was found in all behavioral categories except travel, where their primary affiliation was with barren adult females (which ranked comparatively low in all other behaviors). Adult male affiliation with mothers ranked second-highest in all behaviors except social/sexual, where their affiliation with barren adult females was equal to their affiliations with mothers. Additionally, they showed no affiliation with immature whales in this behavior.

Barren adult females had most affiliation with mothers and least with sub-adult whales and other barren adult females. The affiliations of barren adult females with adult males ranked second-highest. This trend was found in all behaviors except travel, where barren adult affiliations with adult males were equal to their affiliations with mothers, and affinity for other barren adult females increased. During social/sexual activity, barren adult females had no affiliations with sub-adults and their affiliations with other barren adult females ranked second-highest.

Affiliations of mothers exhibited trends which seem partially conflicting with the results of analyses of their pair associations. Whereas their pair associations with barren adult females ranked highest, their class affiliation with barren adult females ranked second to their affiliations with adult males, overall. However, figure 8 shows that these class coefficients are almost equal. Preference for adult males was found only in feeding and rest behaviors. Mothers showed preference for the barren adult female class primarily during travel and secondarily during rest and social/sexual behaviors. Although mothers' pair associations with other mothers ranked lowest, their class affiliations with sub-adult classes were lowest. Nevertheless, they had most affiliation with "non-pod" adolescents during social/sexual behavior.

Sub-adult class association coefficients with whales from other pods were, in general, unvaried and extremely low, suggesting a general lack of association with whales from other pods; coefficients were lacking in some behaviors (Fig. 8) Adolescents exhibited the greatest variability. During travel and social/sexual behaviors their class association coefficients with non-pod mothers were comparatively higher than in other behaviors. Immatures had the least variability in class association coefficients and the least amount of across-pod interactions. Any suggestion of trends or preferences for classes (or whales) in other pods is inappropriate.

Individual Associations

Unlike associations within pods, associations across pods did not fall into discrete clusters. Rather, associations between particular individuals were responsible for consistent ties across pods. Although the mean across-pod coefficient of association was 0.03, with a standard deviation of 0.02, association coefficients less than 0.10 will not be described in this section. The highest across-pod coefficient of association between J and K pod was between two mothers, J04 and K07 (0.13); the highest of all inter-pod coefficients. The highest coefficients of association between J and L-sub pod were between the adult males L17 and J03 (0.11), and L17 and J06 (0.10). The highest coefficients of association between K and L-sub pods were also between adult males: K01 and L19 (0.11), and K05 and L17 (0.10). All other links between pods were coefficients of association that fell below 0.10.

DISCUSSION

The data from 1982-1983 correspond to earlier work (S.L. Heimlich-Boran 1986; Bigg et al. 1987) and support the hypothesis of a stable, multilevel social system centered around core groups of maternally related kin. Although familial relationships appear to provide the structural basis of this society, frequencies of association within pods and across pods were not altogether independent of sex, age and behavioral factors.

Social Structure Summary

Associations Within Pods

In general, associations occurred between members of all sex/age classes within pods. Although only mothers and adolescent whales had fewer associates than expected, all classes exhibited distinctly different trends in associations.

Adult whales exhibited less variation in association than sub-adults. Adult males had fairly similar and comparatively low levels of individual association with whales in all classes, indicating a peripheral position within the pod structure. Within this overall trend, adult males exhibited relatively more preference for mothers than for other whales. Barren adult females also had fairly similar but comparatively high levels of individual association across all classes, suggesting a central position within the pod structure. They also exhibited relatively more preference for mothers, with secondary affinity for adult males. The associations of mothers were closest with their immature offspring, as would be expected. Mothers had significantly fewer partnerships with both related and non-related adolescents, as well as non-related immatures. At a secondary level, mothers had relatively more preference for adult males and barren adult females and little affinity for other mothers. Aside from relationships with their offspring, mothers' levels of individual association were comparatively low across all classes. This suggests that mothers' centralized positions within the pod structure are kin-based and, without offspring, peripheral to barren adult females.

Sub-adults exhibited the most distinct variations in associations. Adolescents had significantly fewer partnerships with other adolescents, both related and non-related, indicating a lack of cohort formation. Their individual associations were greatest with barren adult females and least with adult males. Adolescent class affinities did not follow this pattern and are difficult to interpret. They exhibited preference for their mothers and secondary affinity for barren adult females and adult males. Without a statistical guide to these class interactions, emphasis should be placed on their significantly high preference for barren adult females during individual associations. Immatures' associations were greatest with their mothers, as would be expected.

They also exhibited secondary association with other immatures, related and non-related, indicating a tendency towards cohort formation. Associations between non-related immature whales and a lack of association between mothers indicates that cohort formation is independent from adult relationships. The longevity of affiliations formed between immature whales appears to be comparatively short-term and not carried through adolescence (as evidenced by the lack of a corresponding adolescent cohort formation). Aside from known kin relationships, they exhibited strong preference for barren adult females; specifically the preferred associates of their mothers. As already suggested, the associations between sub-adults and barren adult females may represent kin relationships.

Several conclusions can be drawn. In general, adult whales exhibit a different mode of association with pod members than sub-adult whales. Aside from associations between mothers and their youngest calves, association effort for adults is fairly uniform, with preference for other adults. Adolescent whales and immature whales associate differently and age appears to be the influential factor. As mothers direct the greatest proportion of their effort to their youngest calves, their adolescent offspring associate almost exclusively with the barren adult female associates of their mothers. Indeed, it appears that aside from these relationships, they have comparatively little interaction with other pod members and are essentially set apart from the rest of the commmunity, depending on barren adult females to maintain some level of social integration. Immature whales will also favor the adult female associates of their mothers, but are more socially integrated with the rest of the pod through their strong associations with their mothers.

Associations Between Pods

The small number of pair-wise combinations of whales from different pods indicates selectivity in associations between pods. Associations were not totally independent of sex and age: interactions were primarily between adults.

Adult males had significantly more adult male associates from other pods than expected. Adult male frequencies of association were highest with other adult males and lowest with adolescents from other pods. Additionally, the associations of adult males ranked second-highest in comparison to the associations of other classes. This indicates that association interest and effort of adult males with whales from other pods is concentrated almost exclusively on other adult males and apparently integral to interactions between pods. Barren adult females had significantly fewer adolescent associates from other pods than expected. However, their associations were fairly similar across all classes and were comparatively the highest of all classes, indicating a central position in across-pod interactions. They exhibited slightly greater preference for mothers than adult males. Mothers had more barren adult female and adult male associates from other pods than expected; their class affinities for these two other adult classes were almost equal. Their individual associations were greatest with barren adult females, least with mothers from other pods and ranked third-highest when compared to the associations of the other classes. This suggests that their position in across-pod interactions is peripheral to barren adult females; simliar to within-pod interactions.

Sub-adults exhibited variation in associations with whales from other pods. Their values ranked comparatively low and there was often a total lack of association with specific classes, indicating a more random pattern of across-pod association. This suggests that their associations are peripheral to, and perhaps even independent of, interactions occurring between adults from different pods. On a relative scale, as a class, both adolescents and immatures had extremely little variation in their class affiliations. However, adolescents generally exhibited more interest in mothers from other pods.

In conclusion, like associations within pods, adults and sub-adults have quite different modes of association. Interactions between pods are primarily between adults, with sub-adults being satellites to the adult activity. Adolescents exhibit some interest in whales from other pods, yet their associations are not an integral component of interactions between pods.

Effects of Behavior

In general, feeding, travel and rest behaviors had little effect on the general mode of associations between whales within pods. Social/sexual behavior, however, had substantial effect on class affiliations. In this behavior, affiliations were extremely different from the general trend. Adult class affiliations closely resembled those of adult whale interactions across pods. Adult males affiliated predominantly with other adult males and secondarily with adult females. Barren adult females and mothers affiliated primarily with each other and secondarily with adult males. Immatures' greatest affiliations were with each other rather than with mothers. Interactions of adolescents varried more with behavior than did the other classes. In social/sexual behaviors, adolescents' affiliations were primarily with their mothers and secondarily with barren adult females and immatures.

Inter-pod affiliations varied more with behavior than did intra-pod affiliation. In general, class affiliations across pods during social/sexual activity were not different from class affiliations within pods duirng this behavior. Mothers presented the exception, having primary affiliations with adolescent whales and secondary affiliations with barren adult females from different pods.

Active socializing in these whales, including sexual displays, probably serves to stabilize social bonds, either through friendly appeasement or through assertion of dominance hierarchies. This behavior may be between competing individuals, or may maintain friendships. Ritualized social/sexual behavior between adult males is common to many mammalian species, notably ungulates (Geist 1966, 1971; Clutton-Brock et al. 1982), primates (Ploog & McClean 1963; Ploog 1967; Hanby 1976; Smuts 1985; Dunbar 1986; Goodall 1986), canids (Mech 1970; Kruuk 1972; Wilson 1975; Frame et al. 1979; elephant seals (Le Boeuf 1974) and cetaceans (Silverman & Dunbar 1980; Darling 1983; Wells 1984). Active socializing between adult female killer whales may also serve similar competitive functions, as it does for primates (Alvarez 1973; Hanby 1976; Hrdy 1977;

Rowell 1978; Dunbar & Dunbar 1977; Dunbar 1979, 1980; Wasser 1983), canids (Frame & Frame 1976; Frame et al. 1979; Packard & Mech 1980) and elephants (Dublin 1983). However, it may serve to reaffirm kinship ties, both within pods and across pods, as observed in lions (Schaller 1972), primates (Hrdy 1977; Dunbar 1986; Goodall 1986; Stewart & Harcourt 1987; Gouzoules & Gouzoules 1987) and elephants (Moss 1988). Adolescent affiliations may exhibit greater variability with behavior because of their comparatively ostracized position in the social structure. Their affiliations may actually be more random or they may be tolerated by certain classes more than others during particular behaviors, as seen in some canids (Mech, 1970; Bertram 1979) and primates (Hanby 1976; Wasser 1983; Goodall 1986; Smuts 1987b; Walters 1987; Gouzoules & Gouzoules 1987). The affiliations between immature whales within pods during social/sexual behavior are most probably specifically due to play activity and its inclusion in the broader behavioral category of social/sexual behavior. Their interactions with whales from other pods are probably due only to their associations with their mothers.

Behavior also varied with the number of pods present. Rest, social/sexual and feeding behaviors occurred in approximately equal proportions of single pod hours and multi-pod hours. In contrast, travel behavior occurred approximately twice as much in single pod hours as in multi-pod hours. This suggests that single pods tend to do more travelling and multi-pod groups tend to do more feeding, resting and socializing. J. Heimlich-Boran (1988) and Felleman et al. (In press) showed that multiple pods engage in cooperative prey herding and suggested that coordinated feeding strategies improve the ability to locate and capture prey. This is not unlike cooperative hunting exhibited by other social carnivores, notably lions (Schaller 1972; Caraco & Wolf 1975; Bertram 1978, 1979; Packer 1986), wolves (Mech 1970), wild dogs (Estes & Goddard 1967; Frame et al. 1979) and spotted hyenas (Kruuk 1972). Osborne (1986) and Jacobsen (1986) noted that resting killer whale groups exhibited synchronous, coordinated movements also requiring cooperative effort. Norris et al. (1985) suggested that in resting groups of spinner dolphins, information from the environment is integrated (at low levels) by each individual in consort with other group members, implying that sensory integration by several animals during a semi-aware state provides more complete information about their environment. Thus, killer whale pods may come together during times when a larger number of individuals is most beneficial, and the community dissociates when co-operation is less neccessary.

Pod Units

Associations in J pod (19 whales) were the most stable. Subgroups were discrete with non-fluid membership. Interactions between sub-groups were stable. The pod was always observed in its entirety, even when occurring with whales from other pods. It was observed with other pods almost as much as it was observed alone.

Associations in K pod (10 whales) and L-sub pod (5 whales) were not as stable as in J pod. Subgroup memberships were less distinct and interactions appeared to be between individuals rather than discrete sub-groups. Both pods were always observed in their entirety, yet both exhibited group flexibility. K pod was seen more often with other pods than it was obvserved alone. L-sub pod was rarely observed alone. Rest behavior was observed more than expected in L-sub pod and occurred more than expected in the company of whales from other pods. K and L-sub pods were most closely affiliated with each other. Bigg et al. (1987) suggested that "L-sub" is a misnomer resulting from observations made in the first years of study, and they include the five L-sub pod whales as a discrete sub-pod within K pod. However, in this study L-sub pod was also frequently observed with J and L pod, suggesting the original delineation for l-sub pod was not incorrect.

Associations in L pod (38 whales) were the least stable. Mother/offspring pairs or groups comprised the most discrete sub-groups. Additional sub-group membership was more varied than in the other pods. Bigg et al. (1987) determined 12 maternal sub-groups within L pod and grouped these into 3 larger sub-pods. L pod was seldom observed in its entirety and frequently split into these sub-pods (and often into the smaller sub-groups), indicating that interactions between sub-groups were not stable. Mothers, in particular, had less association with other pod members than mothers in J,K and L-sub pods. L pod was observed slightly more with other pods than alone, indicating that subroups were not completely interactive with whales from other pods. Indeed, J,K and L-sub pods had more affiliation with each other than with L pod.

In conclusion, the four pods comprising the southern community exhibit distinctly different modes of associations, both within pods and between pods. Bigg et al. (1987) suggest that these pods are separate lineages within one clan, based on the similarity of their acoustic dialects; J pod and K pod (which includes L-sub pod) are most closely related. Each pod may further represent a different phase of population stability. J pod best fits the general trends and may typify a steady-state population. L pod least fit the general mode and may be typical of a fissioning population; J pod may eventually begin to show similar trends with growth in population. K and L-sub pods exhibited both similarities to and differences from the general mode and may be typcial of a growing population. Differences may be a result of pod size, or more social aspects (such as: 1) the degree of relatedness within and between sub-groups; 2) the number, age, and sex of offspring; 3) the amount of non-kin pair-bonding carried over from calf-hood), or an interplay between the two. K and L-sub pods may be different from the norm because their small group size requires greater association with each other (or other whales) to benefit most from cooperative behaviors (e.g. rest, feeding and social activities). In contrast, L pod may split into smaller sub-groups to reduce possible competition for resources.

The Regional Killer Whale Social System in Perspective

There appear to be a number of unique features to killer whale social systems in this region. In most mammal and bird species, one sex or the other disperses from its natal group, apparently to avoid inbreeding with close relatives, but also to find better feeding and mating opportunities elsewhere (Packer 1979; Pusey 1980; Greenwood 1980, 1983; Shields 1982, 1983; Moore & Ali 1983; Pusey & Packer 1987). However, during 14 years of observation, there have never been any observations of emigration or immigration in the killer whales of the Pacific Northwest (Bigg 1982; Balcomb & Bigg 1986; Bigg et al. 1987). Both males and females have shown total natal philopatry, remaining in the social groups of their mothers until well into maturity. If we assume that pressures on these whales are the same as in terrestrial systems (inbreeding avoidance etc.), their natal philopatry suggests that mating does not occur within pods. Rather, mating may occur with whales from other pods.

Competition between individuals plays a critical role in the maintenance of a social system (Darwin 1871; Alexander 1974; Wilson 1975). The form and frequency of competition both between and within the sexes is either overt or limited to highly ritualized displays which may not result in scars or other visible signs of actual battle (Lorenz 1966; Norris 1967). The marked sexual dimorphism of killer whales (males can weigh twice as much as females: Matkin & Leatherwood 1986) and female-biased sex ratios (Bigg 1982) suggest a polygynous mating system with sexual selection creating competition between males for access to females (Darwin 1871; Emlen & Oring 1977). However, there have been no observations of overt male-male, or female-female, competition to date. Group living species often resolve this competition in the form of dominance hierarchies (Dewsbury 1982a; Vehrencamp 1983), and dominance hierarchies have been observed in captive groups of related dolphin species (Tavolga & Essapian 1957; Norris 1967; Bateson 1974).

The most overt hierarchy exhibited by these whales is one based on differential fecundity in females. Females having greatest reproductive success could be considered "alpha" females, as in some species of canids (Mech 1970; Packard & Mech 1980; Beckoff et al. 1981). Females with lifespans beyond the reproductive period may continue to interact sexually to maintain some type of social status with males and other females, as seems to be true for some primates (Hanby 1976; Hrdy & Whitten 1987). Reproductively senescent females exist in long-finned pilot whales, Globicephala macrorhynchus (Kasuya & Marsh 1984), and some primate species (Hrdy & Whitten 1987). Kasuya and Marsh (1984) found that some barren female pilot whales were still lactating, implicating a role of nursemaid. Reproductively senescent killer whales may have switched their efforts from their own calf-bearing to aiding other females (probably kin) in calf-rearing. Thus, these barren adult females may be considered pod matriarchs in the same sense as in elephant societies (Douglas-Hamilton & Douglas-Hamilton 1975; Dublin 1983; Moss & Poole 1983; Moss 1988).

Sexual behavior (specifically, the observation of an erect penis) in male killer whales often may be highly ritualized displays between competing individuals. Penile erection displays are common in squirrel monkeys (Samiri _sciureus_) and can represent "demanding, self-assertion, courting, and the desiring of closer contact" (Ploog & McClean 1963; Ploog 1967). Other evidence suggests it is an attempt to obtain "social approval" (Hinde & Stevenson-Hinde 1976) or as a greeting to maintain male-male friendships (Smuts 1985). Ploog (1967) found that the rate of penile displays was higher in squirrel monkey groups which were undergoing challenges to existing dominance relationships. Of course, there is also the possibility that vocalizations may serve some role in dominance displays. Encounters between neighboring groups of monkeys are often limited solely to calling bouts (Cheney 1987). Competing male ungulates (Clutton-Brock et al. 1982), male lions (Schaller 1972), and male elephant seals (Le Boeuf 1974) all have roaring and bellowing contests. Darling (1983) suggested that the songs of humpback whales serve a similar purpose.

The supporting evidence that killer whale males are subject to higher levels of competition and stress than are female whales, is the higher male mortality rate (Bigg 1982; Balcomb & Bigg 1986; Bigg et al. 1987). This results in a lack of surplus males and female-biased sex ratios, especially in the community of killer whales resident to Greater Puget Sound. The variability of male reproductive success in these social groups is still completely unknown.

The results from this study suggest the following hypothesis about the social organization of the killer whales resdient to Greater Puget Sound. As a whale ages, it moves from an integrated position within the community, based on its relationship with its mother, to a less integrated period during adolescence in which social ties remain primarily through the older female generation. With full adulthood, dependency upon these "allo-mothers" (N.J. Haenel 1986) declines and direct affiliations with mothers are re-established. Adult whales remain with the maternal sub-group and associations with other pod members become more equal. However, there are subtle differences dependent on sex. Females appear to achieve a more central position in the pod. This is most probably due to a greater dependency on their mothers or elder sisters as they enter the reproductive pool and require (or receive) aid in raising offspring. Close associations between adult whales therefore appear to be based on relationships between direct kin. With age, mothers become reproductively senescent and enter the older female generation which provides the "glue" for both the pod unit and the larger community of pods.

Fission from the main maternal subgroup and establishment of separate subgroups is probably the result of an interplay of several factors including the age of the older female and the number, ages and sex of her offspring. Several scenarios are possible. An older female with several offspring may stay with her youngest daughter (and her offspring), continuing to function as an "allo-mother," while her older, more experienced adult daughters (and their offspring) disengage from the larger maternal group and form separate subgroups. Bigg et al. (1987) suggest that most maternal subgroups within a pod are closely related, either mothers, sisters, daughters or cousins. An older female having only one or two adult daughters may stay closely associated with both, maintaining direct contact throughout her lifetime. In both situations, any adult sons stay with their mother. When these older females die out, siblings or cousins may eventually separate more permanently, forming new lineages or pods.

Much research has shown the influence of environmental pressures on mammalian social systems, notably resource dispersion, con-specific competition for resources, and predation (Crook 1970; Eisenberg et al. 1972; Jarman 1974; Caraco & Wolf 1975; Crook et al. 1976; Emlen & Oring 1977; Macdonald 1983; Wrangham & Rubenstein 1986; Wrangham 1987; Clutton-Brock & Harvey 1978). Because predation is not a considerable problem for killer whales, the distribution of food resources and the competition for those resources are the major environmental pressures on their social systems. The multilevel social structure centered around matrifocal units of killer whales resident to Greater Puget Sound undoubtedly results from the overall productive stability of this esturine habitat.

Established fish populations provide patchy but seasonally abundant, tidally-predictive food resources for the four resident whale pods (Felleman 1986; J. Heimlich-Boran 1988; Felleman et al. In press). Consequently, these whales aggregate during summer months in the same locale; Osborne (1986) noted these pods split up during the winter months. Large, cooperative groups increase the feeding efficiency on large schools of fish prey. Würsig (1986) speculated that groups of intimate individuals can pool experiences and memories of previous feeding success. This could be crucial in exploiting patchy prey resources like salmon. In comparison, transient killer whales move through the area in seasonally unpredictable patterns, in generally smaller groups which do not coalesce into larger aggregations (Bigg et al. 1987). Their primary food resources are other marine mammals, mostly pinnipeds which occur in patches throughout the area (Felleman et al. In press). Smaller cooperative groups are more efficient at capture of such prey. This mode is also seen in killer whales off Patagonia, Argentina, where indvidual whales will often beach themselves as they rush towards pinnipeds on shore (Lopez & Lopez 1985).

Socializing behaviors in killer whale groups which aggregate on a regular basis on feeding grounds would seem to increase the efficiency of the groups through reaffirmation of intimate community relationships. It seems logical that over time, a fairly intricate social system would evolve in such regularly-occurring groups. J. Heimlich-Boran (1988) showed the development of specific localized areas for specific behavioral purposes. Ford and

Fisher (1982, 1983) suggested acoustic dialects are most likely learned and Bain (1988) showed that a captive killer whale from Iceland learned the acoustic repetoire of its killer whale companion from British Columbia. Barash (1982) noted "many animals acquire information by observational or imitative learning." Bonner (1980) suggested that the transfer of information by such behavioral means can be considered as passed in a cultural fashion and accumulated in the form of knowledge and tradition. In long-lived animals, such as the resident killer whales in Greater Puget Sound, accumulation of cultural knowledge undoubtedly occurs through the maintenance of inter-generational bonds (Bonner 1980; Nishida 1987).

In this particular community of killer whales, such bonds are maintained through matrilines. Sex, age and behavior do have some influence on bonds within the familial architecture of this social system. The social patterns described in this paper for the killer whales resident to Greater Puget Sound certainly suggest the possiblity of, and mechanisms for, the transmission of cultural knowledge. However, this social system may be unique to the killer whales in Greater Puget Sound. The different sex ratios and age distributions of the northern resident killer whale community (Bigg et al. 1987; Bain 1988) probably causes some variation. The northern community, having experenced less impact from human activities, may better represent the ultimate "steady-state" population for killer whales in the Pacific Northwest. Thus, the southern resident community is possibly in a phase of an evolving social system and may eventually show much similarity to the northern community. Further comparative studies will be required before we can give a general hypothesis for the social behavior of killer whales. It is likely that their high degree of behavioral flexibility probably results in variable forms of social organization specific to different habitats world-wide.

Table 1. The Study Population. All ages greater than 15 years are estimates based on assumptions from Bigg et al. 1987 and records at The Whale Museum, Friday Harbor, Washington.

POD	SEX		IDENTIFICATION	AGE 1983	MOTHER
J	Adult Males		J01	31	
			J03	29	
			J06	26	
	Barren Adult Females		J02	75	
			J08	51	
			J09	58	
	Mothers		J04	24	
			J05	45	
			J07	50	
			J10	19	
			J12	48	
	Adolescents	Males	J16	11	J07
		Females	J11	11	J04
			J14	9	J12
	Immatures	Males	J18	5	J10
		Females	J17	6	J05
			J19	4	J04
		Unknown	J20	2	J10
			J21	1	J04
K	Adult Males		K05	29	
			K01	27	
	Barren Adult Females		K08	53	
			K11	50	
	Mothers		K07	77	
			K04	50	
			K03	26	
	Adolescents	Females	K12	12	K04
			K13	11	K07
	Immatures	Males	K14	6	K03
L	Adult Males		L19	31	
sub			L17	15	
	Barren Adult Females		L30	70	
			L40	22	
	Mothers		L18	32	

Table 1 continued. The Study Population. All ages greater than 15 years are estimates based on assumptions from Bigg et al. 1987 and records at The Whale Musuem, Friday Harbor, Washington.

POD	SEX		IDENTIFICATION	AGE 1983	MOTHER
L	Adult Males		L01	23	
			L10	23	
			L06	21	
			L33	19	
			L38	17	
	Barren Adult Females		L28	58	
			L09	56	
			L12	51	
			L25	51	
	Mothers		L04	45	
			L07	45	
			L21	45	
			L02	34	
			L03	33	
			L32	31	
			L37	50	
			L26	25	
			L11	24	
			L35	24	
			L23	49	
			L27	17	
			L05	17	
	Adolescents	Males	L14	11	L23
			L42	10	L11
			L50	10	L35
			L39	8	L02
			L44	9	L32
		Females	L22	13	L32
			L43	11	L37
			L60	11	L26
			L51	10	L03
			L47	9	L21
	Immatures	Males	L41	6	L11
			L54	6	L35
		Unknown	L53	6	L07
			L52	3	L26
			L55	6	L04
			L56	5	L32

Table 2. Frequency distribution of multi-pod observations

GROUP COMPOSITION	HOURS	%
J and K whales	15.00	30
J and L-sub whales	8.25	16
J and L whales	.75	2
K and L-sub whales	3.50	7
K and L whales	1.50	3
L and L-sub whales	1.00	2
J,K and L-sub whales	13.25	26
J,L and L-sub whales	1.75	3
K,L and L-sub whales	1.25	3
J,K and L whales	2.25	5
J,K,L-sub and L whales	1.75	3
TOTAL	50.25	100

Table 3. Behavioral time budget of whale observations

BEHAVIOR	SINGLE POD HOURS	MULTI POD HOURS	TOTAL	%
Feeding	32.00	20.50	52.50	44
Travel	18.75	9.00	27.75	23
Rest	15.00	15.25	30.25	25
Social/Sexual	4.75	5.50	10.25	08
All	70.50	50.25	120.75	100

Table 4. Within- and across-pod pair associates as percentages of all possible pair combinations. There were: N(N-1)/2 possible intra-pod combinations; N1 + N2 number of whales for combined pods; and N1 x N2 possible inter-pod combinations.

POD COMBINATIONS	NUMBER OF WHALES	NUMBER OF POSSIBLE PAIRS	NUMBER OF OBSERVED PAIRS	%
INTRA-POD				
J/J	19	171	171	100
K/K	10	45	45	100
L-sub/L-sub	5	10	10	100
L/L	38	703	191	27
INTER-POD				
J/K	29	190	85	45
J/Lsub	24	95	56	59
J/L	62	817	17	02
K/Lsub	15	50	42	84
K/L	53	430	12	03
L/Lsub	48	215	19	09
TOTAL	77	1797	231	13

Table 5. Within-pod coefficients of association comparing the sex/age class values of each pod. All = the group of coefficients including known mother/offspring & sibling pairs. Non-kin = the group of coefficients excluding mother/offspring & sibling pairs.

CLASS	MEAN	SD	N	RANGE
ADULT MALES				
J Pod	0.17	0.107	51	0.35 - 0.42
K Pod	0.20	0.064	17	0.10 - 0.29
L Pod	0.15	0.104	81	0.04 - 0.59
L-sub Pod	0.23	0.151	7	0.05 - 0.46
BARREN ADULT FEMALES				
J Pod	0.24	0.146	51	0.05 - 0.63
K Pod	0.24	0.069	17	0.14 - 0.40
L Pod	0.18	0.096	43	0.04 - 0.43
L-sub Pod	0.25	0.175	7	0.07 - 0.47
MOTHERS: all				
J Pod	0.23	0.168	80	0.04 - 0.70
K Pod	0.24	0.091	24	0.09 - 0.50
L Pod	0.18	0.169	112	0.04 - 0.86
L-sub Pod	0.23	0.209	4	0.05 - 0.47
Mothers: non-kin				
J Pod	0.17	0.103	72	0.04 - 0.62
K Pod	0.23	0.072	21	0.09 - 0.34
L Pod	0.14	0.101	97	0.04 - 0.59
ADOLESCENTS: all				
J Pod	0.23	0.168	80	0.03 - 0.65
K Pod	0.24	0.091	24	0.13 - 0.50
L Pod	0.18	0.169	112	0.04 - 0.86
Adolescents: non-kin				
J Pod	0.17	0.103	72	0.03 - 0.50
K Pod	0.23	0.072	21	0.13 - 0.40
L Pod	0.14	0.101	97	0.04 - 0.57
IMATURES: all				
J Pod	0.24	0.171	80	0.04 - 0.70
K Pod	0.21	0.074	9	0.10 - 0.37
L Pod	0.24	0.225	34	0.04 - 0.86
Immatures: non-kin				
J Pod	0.19	0.102	71	0.04 - 0.63
K Pod	0.23	0.072	21	0.10 - 0.27
L Pod	0.14	0.075	24	0.04 - 0.32

Table 6. Within-pod coefficients of association between sex/age classes. Reciprocal values between classes are listed for the first class but not the second. All = the group of coefficients including mother/offspring & sibling pairs. Non-kin = the group of coefficients excluding mother/offspring & sibling pairs.

CLASS		MEAN	SD	N	RANGE
Adult Males with:					
All pod members		0.16	0.105	156	0.03 - 0.59
Adult males		0.18	0.112	14	0.05 - 0.42
Barren Adult Females		0.20	0.109	27	0.04 - 0.46
Mothers		0.16	0.112	56	0.04 - 0.59
Adolescents		0.16	0.099	33	0.03 - 0.39
Immatures		0.14	0.088	26	0.04 - 0.36
Barren Adult Females with:					
All pod members		0.22	0.124	118	0.04 - 0.63
Barren Adult Females		0.17	0.680	7	0.06 - 0.27
Mothers		0.20	0.129	41	0.05 - 0.62
Adolescents		0.25	0.122	24	0.07 - 0.50
Immatures		0.24	0.146	19	0.12 - 0.63
Mothers with:					
All pod members		0.21	0.164	220	0.04 - 0.86
Non-kin pod members		0.17	0.105	194	0.04 - 0.62
Mothers		0.15	0.097	35	0.06 - 0.50
Adolescents:	all	0.23	0.182	48	0.05 - 0.86
	non-kin	0.17	0.091	34	0.05 - 0.57
Immatures:	all	0.29	0.229	40	0.07 - 0.86
	non-kin	0.17	0.067	28	0.07 - 0.29
Adolescents with:					
All pod members		0.22	0.149	141	0.03 - 0.86
Non-kin pod members		0.19	0.100	120	0.03 - 0.57
Adolescents:	all	0.22	0.056	8	0.16 - 0.32
	non-kin	0.22	0.060	7	0.16 - 0.32
Immatures:	all	0.23	0.165	28	0.06 - 0.75
	non-kin	0.18	0.064	22	0.06 - 0.31
Immatures with:					
All pod members		0.24	0.181	124	0.04 - 0.86
Non-kin pod members		0.18	0.096	104	0.04 - 0.63
Immatures:	all	0.29	0.168	11	0.15 - 0.69
	non-kin	0.22	0.062	9	0.15 - 0.34

Table 7. Number of pair occurrences between sex/age classes from one pod with whales from different pods

	J POD	K POD	L-sub	L POD
J POD				
Adult Males	-	22	15	2
Barren Adult Females	-	14	6	0
Mothers	-	25	16	12
Adolescents	-	8	6	3
Immatures	-	16	13	0
K POD				
Adult Males	20	-	10	2
Barren Adult Females	14	-	8	5
Mothers	30	-	12	3
Adolescents	14	-	10	1
Immatures	7	-	2	1
L-sub				
Adult Males	27	17	-	6
Barren Adult Females	8	18	-	11
Mothers	11	7	-	2
L POD				
Adult Males	3	3	3	-
Barren Adult Females	2	2	3	-
Mothers	3	4	9	-
Adolescents	7	3	4	-
Immatures	2	0	0	-

Figure 1. Map of the study area.

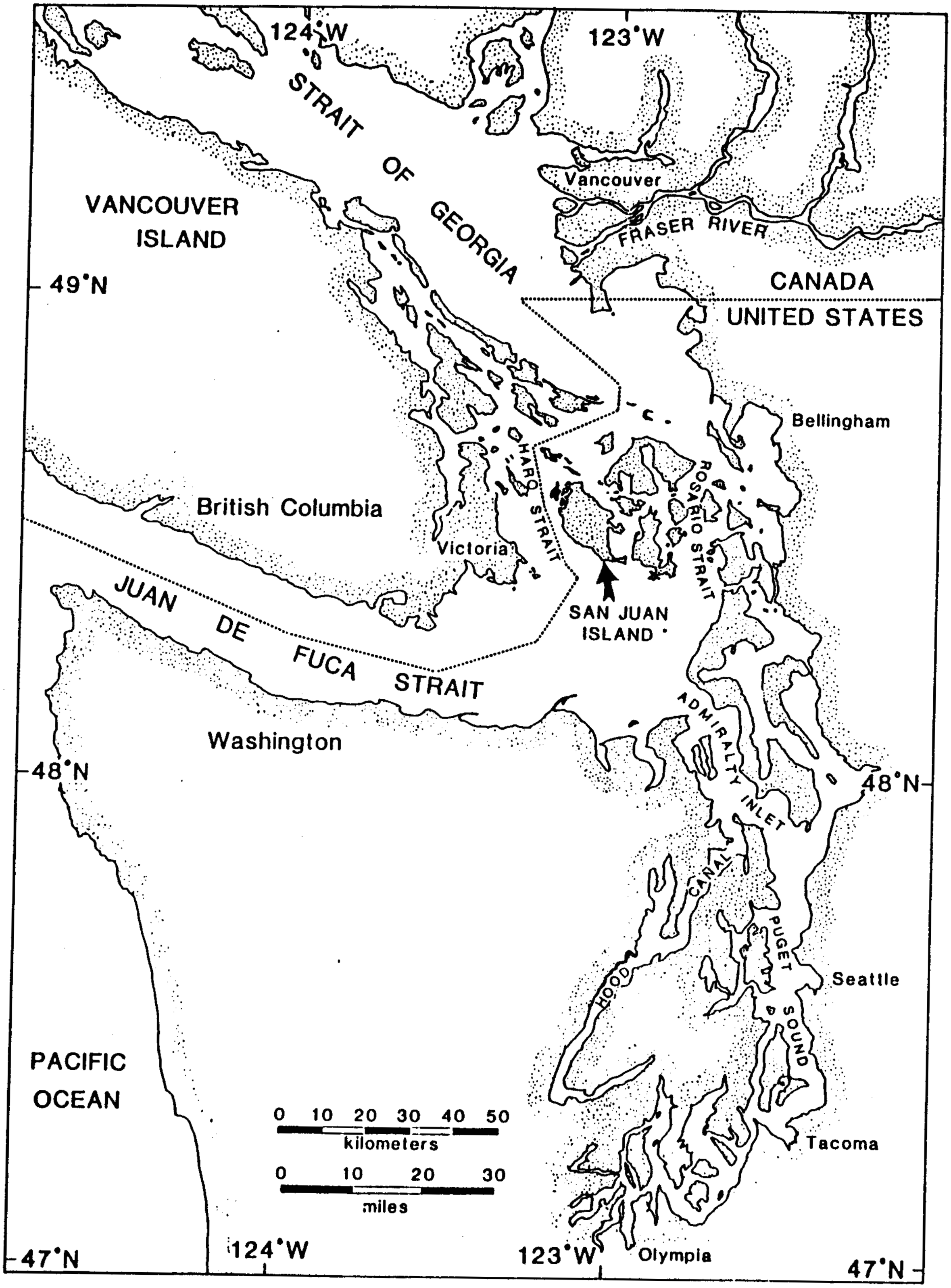

124°W
123°W
STRAIT OF GEORGIA
VANCOUVER ISLAND
Vancouver
FRASER RIVER
49°N
CANADA
UNITED STATES
Bellingham
HARO STRAIT
ROSARIO STRAIT
British Columbia
Victoria
SAN JUAN ISLAND
JUAN DE FUCA STRAIT
Washington
ADMIRALTY INLET
48°N
48°N
HOOD CANAL
PUGET SOUND
Seattle
PACIFIC OCEAN
0 10 20 30 40 50
kilometers
0 10 20 30
miles
Tacoma
47°N
124°W
123°W
Olympia
47°N

Figure 2. Seasonal distribution of pod hours for observations of pods J,K,L and L-sub during the 1982-1983 study period. Percent hours per month are derived by dividing the number of hours alone (and the number of hours with other pods) by the total number of observation hours.

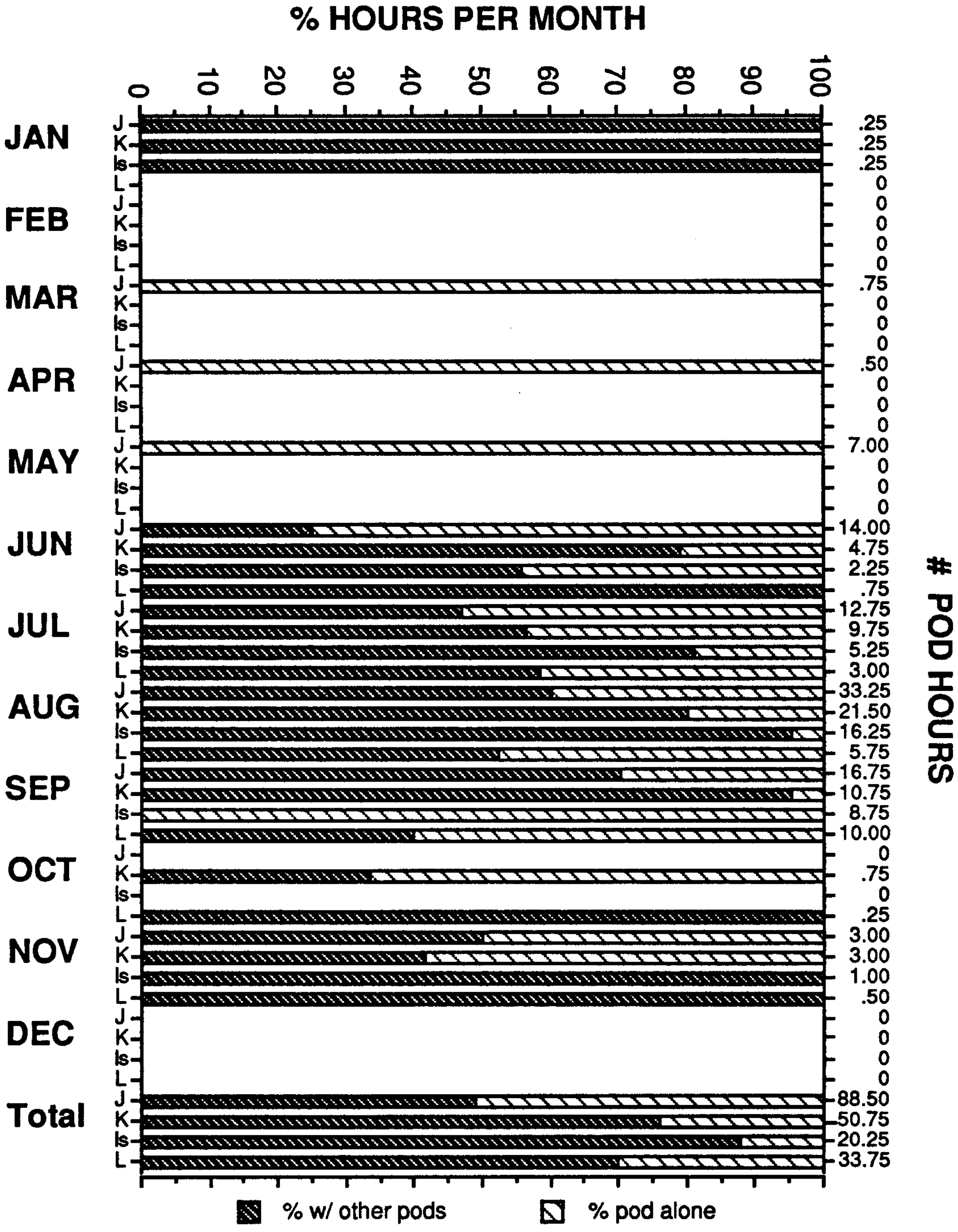
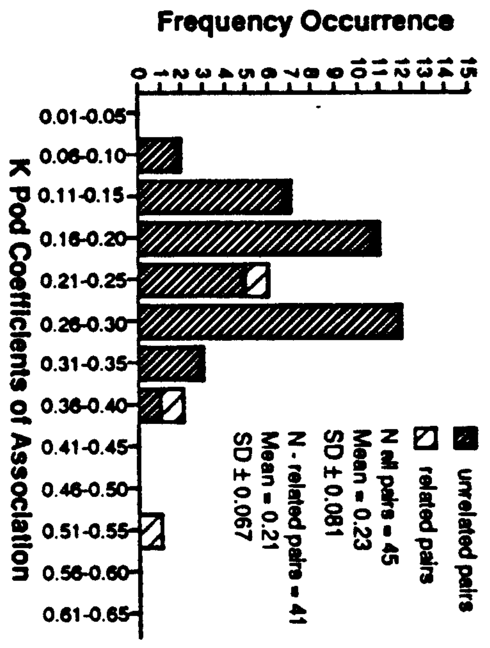
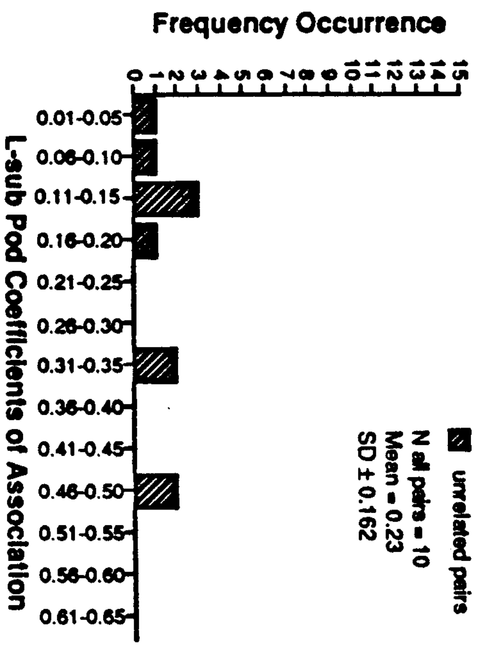
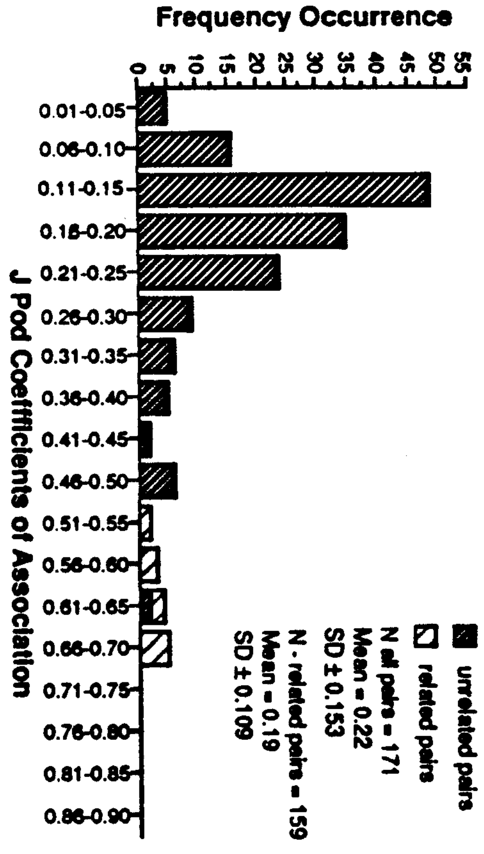

% HOURS PER MONTH
0
10
20
30
40
50
60
70
80
90
100
POD HOURS
JAN
J .25
K .25
ls .25
L 0
FEB
J 0
K 0
ls 0
L 0
MAR
J .75
K 0
ls 0
L 0
APR
J .50
K 0
ls 0
L 0
MAY
J 7.00
K 0
ls 0
L 0
JUN
J 14.00
K 4.75
ls 2.25
L .75
JUL
J 12.75
K 9.75
ls 5.25
L 3.00
AUG
J 33.25
K 21.50
ls 16.25
L 5.75
SEP
J 16.75
K 10.75
ls 8.75
L 10.00
OCT
J 0
K .75
ls 0
L .25
NOV
J 3.00
K 3.00
ls 1.00
L .50
DEC
J 0
K 0
ls 0
L 0
Total
J 88.50
K 50.75
ls 20.25
L 33.75
▩ % w/ other pods
▨ % pod alone

Figure 3. Distribution of coefficients of association between individual whales in each of the four pods comprising the southern Resident Community. "All pairs" includes "related pairs" (confirmed mother/offspring and sibling relationships)


Frequency Occurrence
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
0.01-0.05
0.06-0.10
0.11-0.15
0.16-0.20
0.21-0.25
0.26-0.30
0.31-0.35
0.36-0.40
0.41-0.45
0.46-0.50
0.51-0.55
0.56-0.60
0.61-0.65
K Pod Coefficients of Association
▨ unrelated pairs
☐ related pairs
N all pairs = 45
Mean = 0.23
SD ± 0.081
N - related pairs = 41
Mean = 0.21
SD ± 0.067


Frequency Occurrence
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
0.01-0.05
0.06-0.10
0.11-0.15
0.16-0.20
0.21-0.25
0.26-0.30
0.31-0.35
0.36-0.40
0.41-0.45
0.46-0.50
0.51-0.55
0.56-0.60
0.61-0.65
L-sub Pod Coefficients of Association
▨ unrelated pairs
N all pairs = 10
Mean = 0.23
SD ± 0.162


Frequency Occurrence
0
5
10
15
20
25
30
35
40
45
50
55
0.01-0.05
0.06-0.10
0.11-0.15
0.16-0.20
0.21-0.25
0.26-0.30
0.31-0.35
0.36-0.40
0.41-0.45
0.46-0.50
0.51-0.55
0.56-0.60
0.61-0.65
0.66-0.70
0.71-0.75
0.76-0.80
0.81-0.85
0.86-0.90
J Pod Coefficients of Association
▨ unrelated pairs
☐ related pairs
N all pairs = 171
Mean = 0.22
SD ± 0.153
N - related pairs = 159
Mean = 0.19
SD ± 0.109

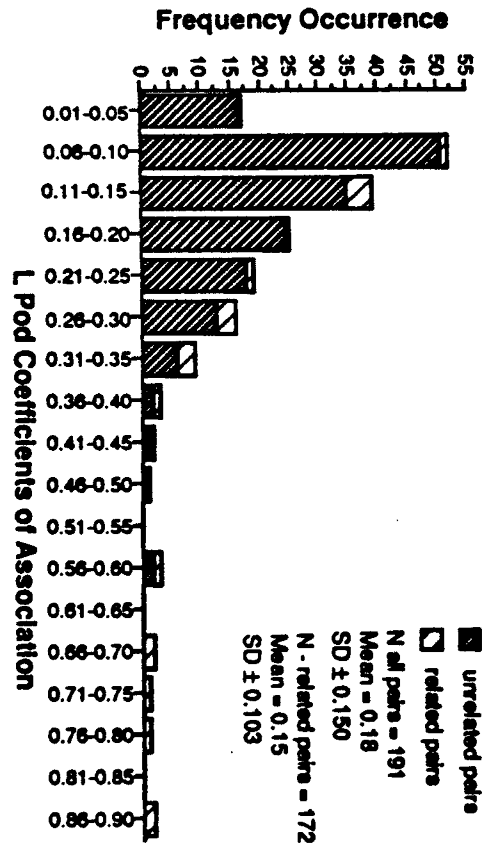

Frequency Occurrence
0
5
10
15
20
25
30
35
40
45
50
55
0.01-0.05
0.06-0.10
0.11-0.15
0.16-0.20
0.21-0.25
0.26-0.30
0.31-0.35
0.36-0.40
0.41-0.45
0.46-0.50
0.51-0.55
0.56-0.60
0.61-0.65
0.66-0.70
0.71-0.75
0.76-0.80
0.81-0.85
0.86-0.90
L Pod Coefficients of Association
▨ unrelated pairs
☐ related pairs
N all pairs = 191
Mean = 0.18
SD ± 0.150
N - related pairs = 172
Mean = 0.15
SD ± 0.103

Figure 4. Distribution of sex/age class association coefficients within pods, including known mother/offspring and sibling pairs. Feed = feeding behavior; Trav = travel behavior; Rest = rest behavior; Soc = social/sexual behaviors.

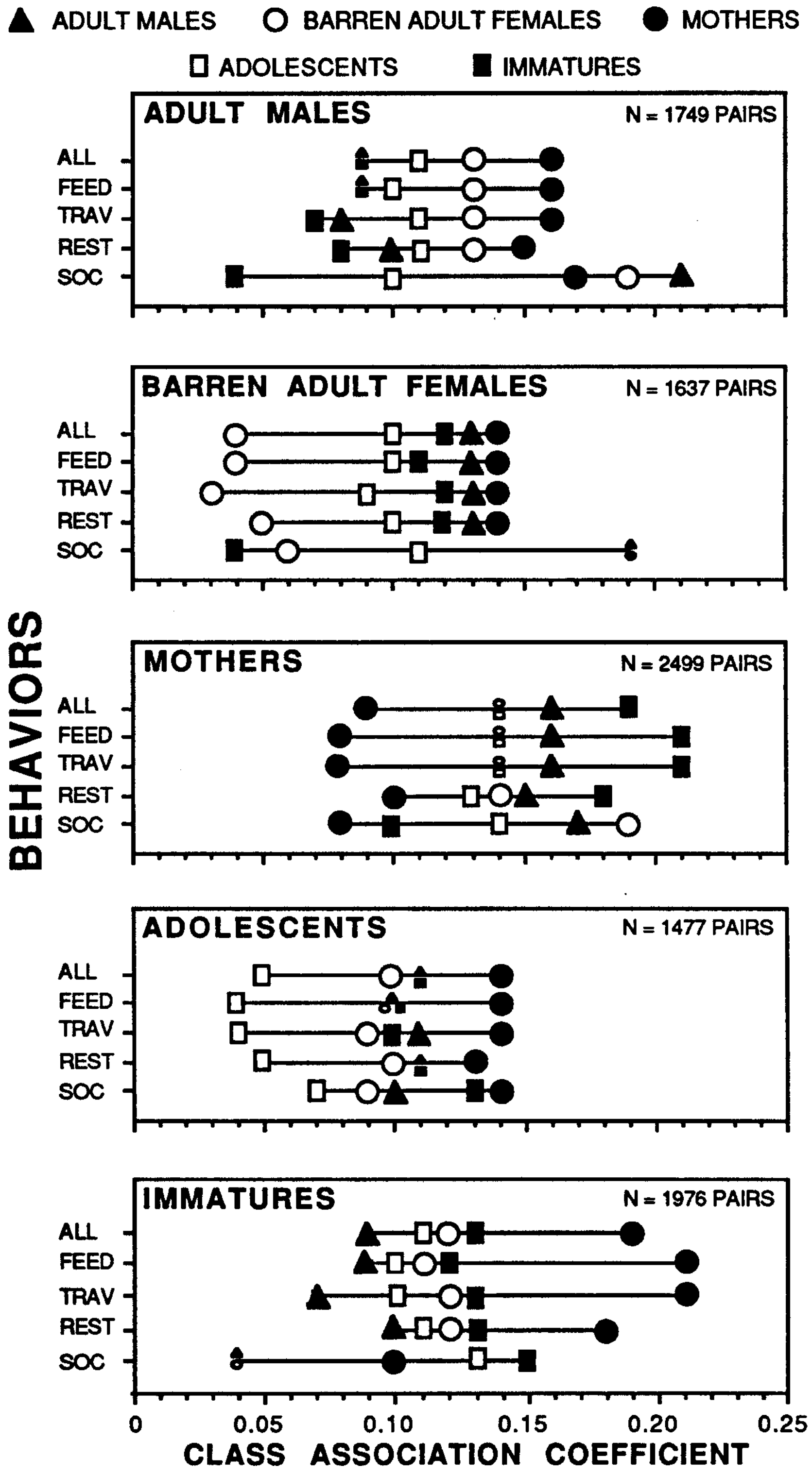

▲ ADULT MALES
○ BARREN ADULT FEMALES
● MOTHERS
☐ ADOLESCENTS
■ IMMATURES
ADULT MALES
N = 1749 PAIRS
BARREN ADULT FEMALES
N = 1637 PAIRS
MOTHERS
N = 2499 PAIRS
ADOLESCENTS
N = 1477 PAIRS
IMMATURES
N = 1976 PAIRS
ALL
FEED
TRAV
REST
SOC
BEHAVIORS
0
0.05
0.10
0.15
0.20
0.25
CLASS ASSOCIATION COEFFICIENT

Figure 5. Distribution of class association coefficients between whales within pods, excluding known mother/offspring and sibling pairs. Feed = feeding behavior; Trav = travel behavior; Rest = rest behavior; Soc = social/sexual behaviors.

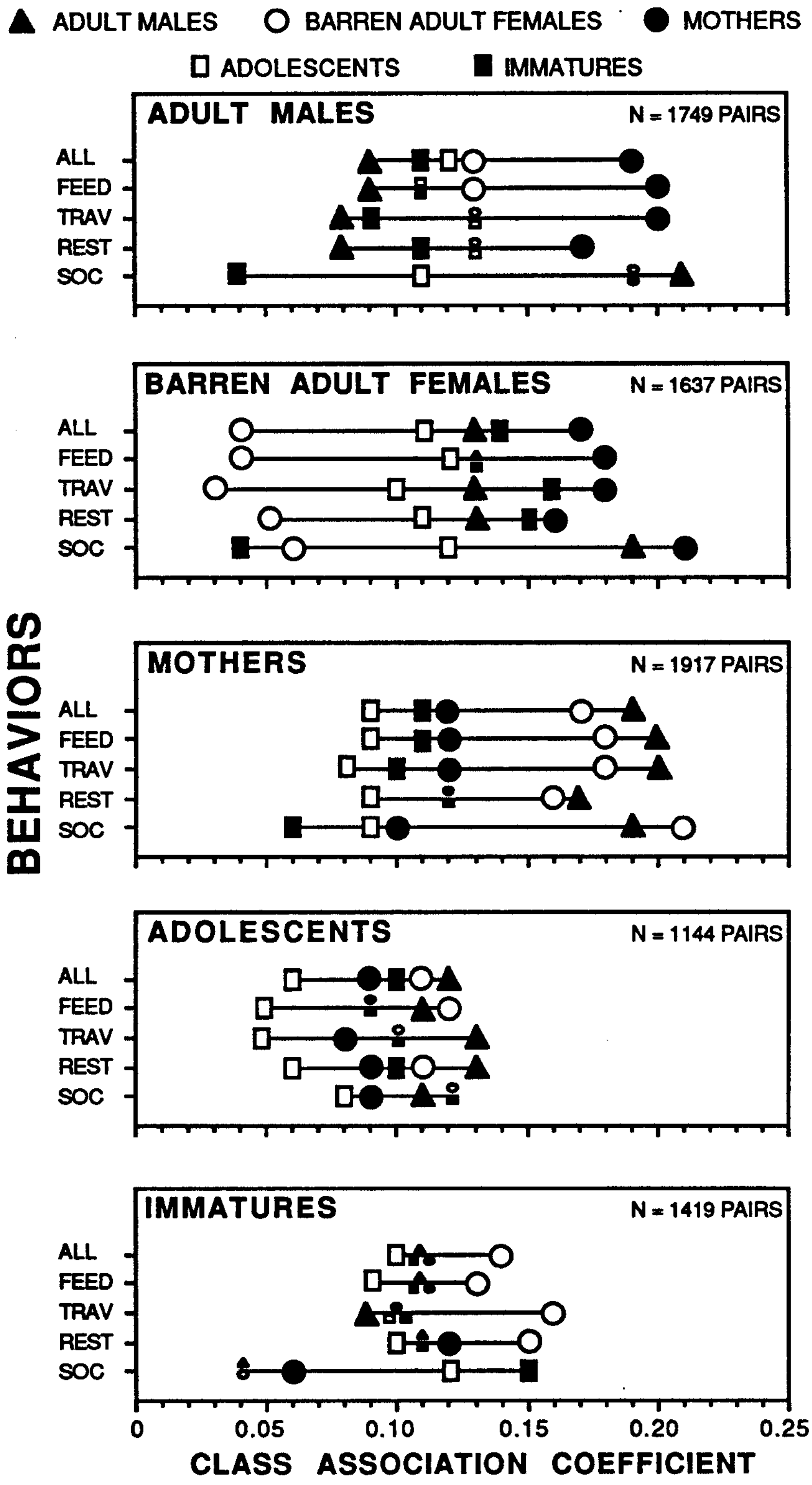

▲ ADULT MALES
○ BARREN ADULT FEMALES
● MOTHERS
☐ ADOLESCENTS
■ IMMATURES
ADULT MALES
N = 1749 PAIRS
BARREN ADULT FEMALES
N = 1637 PAIRS
MOTHERS
N = 1917 PAIRS
ADOLESCENTS
N = 1144 PAIRS
IMMATURES
N = 1419 PAIRS
ALL
FEED
TRAV
REST
SOC
BEHAVIORS
0
0.05
0.10
0.15
0.20
0.25
CLASS ASSOCIATION COEFFICIENT

Figure 6. Dendrogram for associations in J, K, and L-sub pods showing clusters of individuals forming long-term sub-groups. Aml = adult males; Baf = barren adult females; Mos = mothers; Ado = adolescents; Imm = immature whales.

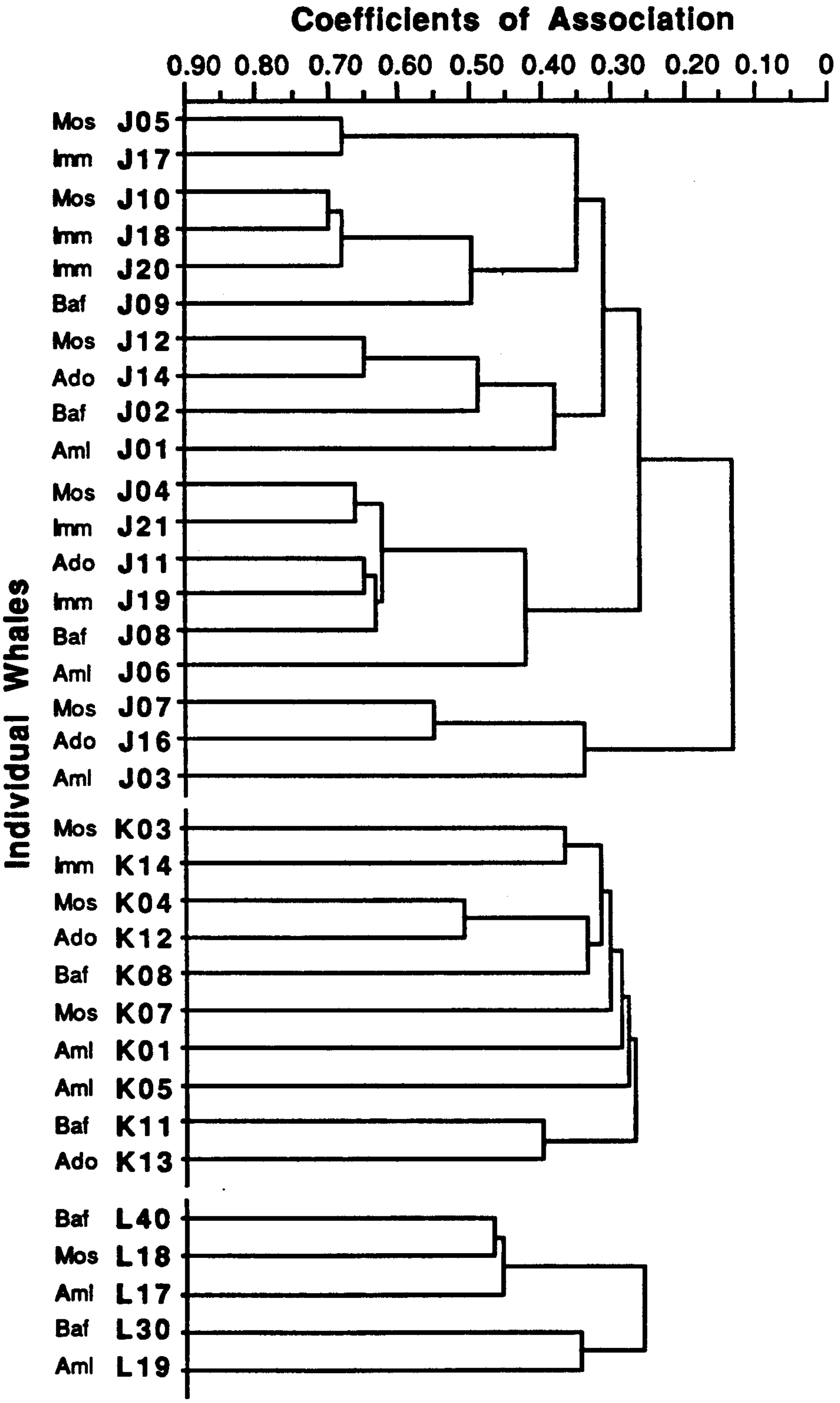

Coefficients of Association
0.90
0.80
0.70
0.60
0.50
0.40
0.30
0.20
0.10
0
Individual Whales
Mos J05
Imm J17
Mos J10
Imm J18
Imm J20
Baf J09
Mos J12
Ado J14
Baf J02
Aml J01
Mos J04
Imm J21
Ado J11
Imm J19
Baf J08
Aml J06
Mos J07
Ado J16
Aml J03
Mos K03
Imm K14
Mos K04
Ado K12
Baf K08
Mos K07
Aml K01
Aml K05
Baf K11
Ado K13
Baf L40
Mos L18
Aml L17
Baf L30
Aml L19

Figure 7. Dendrogram for associations in L pod showing clusters of individuals forming long-term sub-groups. Aml = adult males; Baf = barren adult females; Mos = mothers; Ado = adolescents; Imm = immature whales.

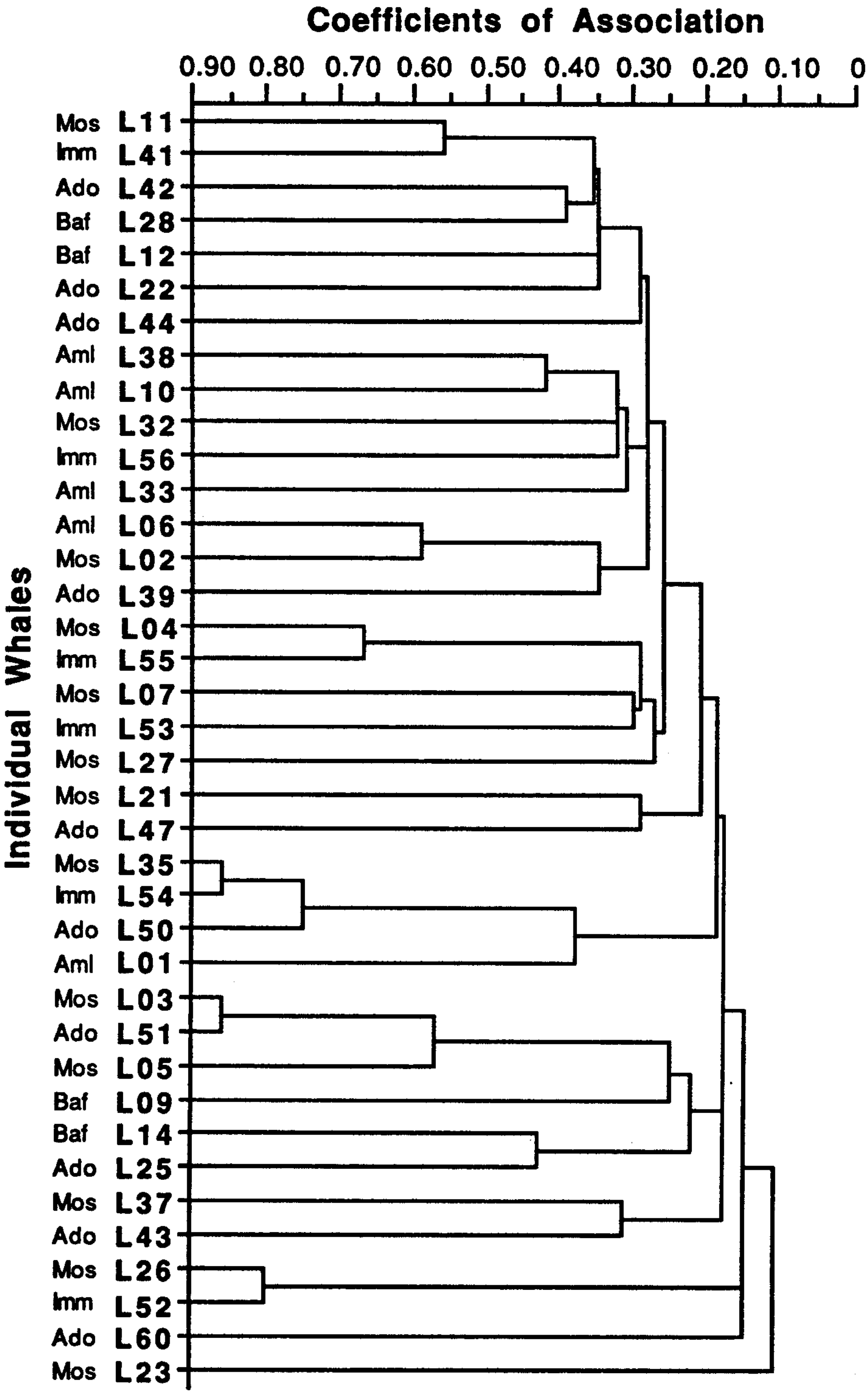
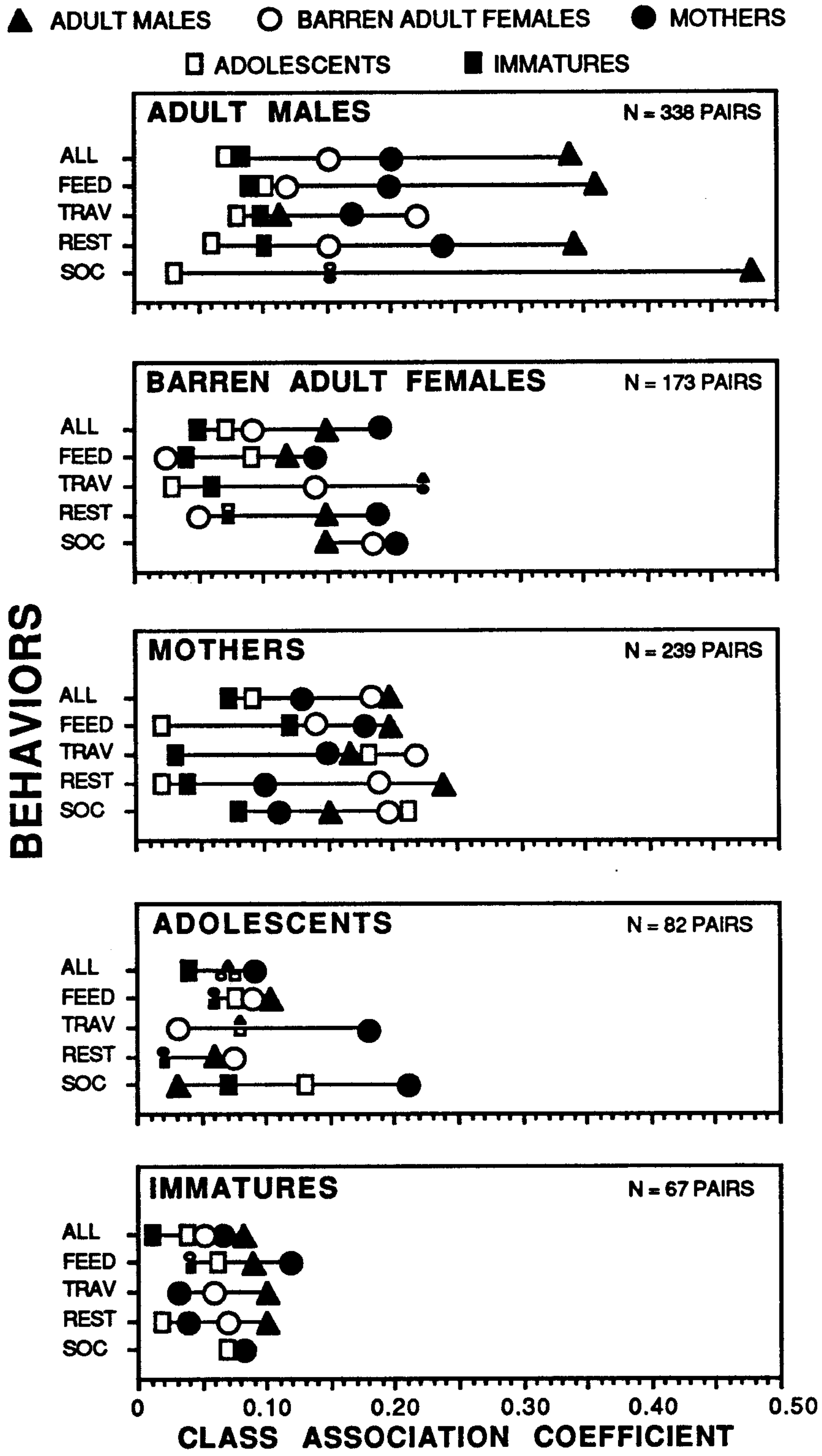

Coefficients of Association
0.90 0.80 0.70 0.60 0.50 0.40 0.30 0.20 0.10 0
Individual Whales
Mos L11
Imm L41
Ado L42
Baf L28
Baf L12
Ado L22
Ado L44
Aml L38
Aml L10
Mos L32
Imm L56
Aml L33
Aml L06
Mos L02
Ado L39
Mos L04
Imm L55
Mos L07
Imm L53
Mos L27
Mos L21
Ado L47
Mos L35
Imm L54
Ado L50
Aml L01
Mos L03
Ado L51
Mos L05
Baf L09
Baf L14
Ado L25
Mos L37
Ado L43
Mos L26
Imm L52
Ado L60
Mos L23

Figure 8. Distribution of class association coefficients between whales from different pods. Feed = feeding behavior; Trav = travel behavior; Soc = social/sexual behaviors.


▲ ADULT MALES
○ BARREN ADULT FEMALES
● MOTHERS
□ ADOLESCENTS
■ IMMATURES
ADULT MALES
N = 338 PAIRS
BARREN ADULT FEMALES
N = 173 PAIRS
MOTHERS
N = 239 PAIRS
ADOLESCENTS
N = 82 PAIRS
IMMATURES
N = 67 PAIRS
ALL
FEED
TRAV
REST
SOC
BEHAVIORS
0
0.10
0.20
0.30
0.40
0.50
CLASS ASSOCIATION COEFFICIENT

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