Abstract.—The social structure and genealogical relationships of resident killer whale pods in Prince William Sound, Alaska, are inferred from association analysis and direct observation. During 1984–95 a total of 2444 hours of observation were made and 36,009 photographs were taken of identifiable killer whales. Cole's association index and a point correlation coefficient index were used to test the statistical significance and strength of associations between individuals, and a clustering procedure was used to delineate group structure. A total of 202 whales were grouped into 9 pods. Genealogical relationships were inferred from the strength of bonds among pod members. Genealogical trees suggested that intrapod groups were matrilineal in structure. Splitting of one pod (AN pod) was observed during the study; however, there was no splitting of matrilineal groups.

Association patterns and inferred genealogies of resident killer whales, *Orcinus orca*, in Prince William Sound, Alaska

Craig O. Matkin
North Gulf Oceanic Society
P.O. Box 15244
Homer, Alaska 99603
E-mail address: comatkin@xyz.net

Graeme Ellis

Peter Olesiuk
Department of Fisheries and Oceans
Pacific Biological Station
Nanaimo, British Columbia, Canada V9R 5K6

Eva Saulitis
North Gulf Oceanic Society
P.O. Box 15244
Homer, Alaska 99603

Manuscript accepted 14 December 1998.
Fish. Bull. 97: 900–919 (1999).

It is well established that individual killer whales can be recognized by unique marks, scars, and pigmentation patterns (Bigg et al., 1987; Heise et al., 1992). During the past 25 years a number of studies have used this fact to investigate the life history, behavior, population dynamics, vocalizations, abundance, and movements of killer whales in coastal waters of the eastern North Pacific including Prince William Sound, Alaska (Balcomb et al., 1982; Bigg et al., 1990; Olesiuk et al., 1990; Ford, 1991; Matkin et al., 1994). As a result of these studies, at least two forms of killer whale, termed "resident" (fish-eating) and "transient" (mammal-eating), have been described in the nearshore waters of Puget Sound, British Columbia, and southern Alaska (Bigg, 1982; Leatherwood et al., 1990; Morton, 1990; Ford et al., 1998; Saulitis et al., in press). Although resident and transient killer whales occur sympatrically, they are considered separate populations owing to genetic variation in mtDNA haplotypes (Stevens et al., 1989; Hoezel and Dover, 1991) and microsatellite variation in nuclear DNA (Hoezel et al., 1998). Mating between the two forms has not been observed and resident and transient killer whales have not been seen traveling together (Morton, 1990; Saulitis, 1993; Matkin et al., 1994). Studies in British Columbia and Washington indicate that resident whales of both sexes remain in their natal pods for life, whereas transients appear to have a more fluid social structure (Bigg et al., 1990).

The social organization of resident killer whales in Prince William Sound has been previously described from direct observation of associations among individuals (Leatherwood et al., 1984; Heise et al., 1992). These studies name pods on the basis of observation of groups of individuals that repeatedly traveled together. Each identifiable whale is assigned an alphanumeric code (Leatherwood et al., 1984;

Ellis, 1987; Heise et al., 1992). The first letter in the code (A) designates Alaska, followed by a letter (A–Z) indicating the animal's pod as determined by observational data. Individuals within a pod are assigned sequential two-digit numbers. Pods that result from an observed splitting of a pod share letter designations, i.e. AN10 and AN20 pod.

In this study, we tested the hypothesis that Prince William Sound resident killer whales form nonrandom associations by examining the structure of some of the extensively studied pods in greater detail. Bond strength was established by direct observation of the proximity of whales to one another and by statistical analysis of the association of individuals in photographic sequences. We used statistical analyses to evaluate whether association patterns were random and used clustering techniques to describe underlying association patterns. Subsequently, we inferred genealogical relationships as an explanation for observed association patterns.

An understanding of social organization and genealogy is a prerequisite for studies of the sociology, life history, and population dynamics of Prince William Sound resident killer whales.

Materials and methods

Field methods

Field observations and photographs used in this analysis were collected from 1984 to 1995 in Prince William Sound, Alaska, and adjacent waters. Data were obtained throughout the Sound, although the study was centered in the southwestern portion. Field work occurred from April to October, but the greatest effort and the majority of encounters with resident pods occurred in July, August, and September. Vessels used to approach the whales to obtain photographs ranged in length from 4 to 9 m and in power from 50 hp outboard motors to 185 hp diesel inboard–outboard engines.

The techniques used to approach and photograph individuals were consistent over the duration of the study. During each encounter, individual whales were typically photographed several times from a distance of 15–30 m. Individual photographs were taken of the left side of each whale, showing details of the dorsal fin and gray saddle patch, with the technique developed by Bigg et al. (1986). An effort was made to move systematically through the pod and to obtain lateral-aspect photographs of individuals, such that each filled at least 50% of the frame. Photographs were taken during all behavioral modes and when whales were tightly grouped (i.e. resting) as well as when they were spread over a considerable distance (i.e. feeding). Encounters lasted until all whales were photographed or until weather or darkness (or both) made photography impracticable.

In the early years of the study we used a 35-mm SLR Nikon FM2 camera with an autowinder mounted on a shoulder brace. Later this setup was replaced by a 35-mm SLR Nikon 8008 autofocus camera with a shoulder brace. In all years a 300-mm lens was used and Ilford HP5 35-mm film was exposed and processed at ISO 1600.

Data recorded during each encounter with killer whales included date, time, duration, and location of the encounter. The total number of individuals present, the identity of individuals that could be immediately recognized, and the general behavior of the whales (i.e. feeding, resting, traveling, socializing, and milling) were also noted. Whales were considered associated on the basis of direct observation when they were seen traveling in the same direction and at the same speed for a period of greater than a few minutes and for a distance less than several body lengths.

Analysis of photographs

Throughout the study, each photographic frame was examined numerous times with a dissecting microscope to insure that all individuals were correctly identified (Bigg et al., 1987). Mothers of new calves were identified on the basis of consistent close association of calves with a specific female (Bigg et al., 1990). Identified individuals were recorded in a standard format to facilitate computer analyses, and uncertain identifications were excluded from the analysis.

Data analysis

In order to test the hypothesis that killer whales form nonrandom associations, associations between individuals were examined by using statistical analysis of photographic data. Photographs were placed in the order in which they were taken, and the identity of all individuals in each frame was tallied for each encounter. The analytical program examined associations between animals within photographic frames and in immediately adjacent frames. Photographic sequences that contained less than two individuals were deleted because they provided no information on association among individuals. Data from the remaining frames were accumulated in a 2×2 contingency table for each pair of whales for all years in which both individuals were photographed:

		First whale		
		Present	Absent	Total
Second whale	present	a	b	$a + b$
	absent	c	d	$c + d$
	total	$a + c$	$b + d$	n

where $(a + c)$ and $(a + b)$ denote the total number of occurrences of the first and second individuals respectively, a the number of joint occurrences, and d the total number of frames in which neither whale occurred in years in which both were photographed.

First, the degree of association between all individuals was measured by using Cole's (1949) association index (CAI):

$$CAI = \frac{ad - bc}{(a+b)(b+d)} \quad \text{for } ad > bc,$$
$$SE = \frac{(a+c)(c+d)}{n(a+b)(b+d)}$$

$$CAI = \frac{ad - bc}{(a+b)(a+c)} \quad \text{for } bc > ad \text{ and } d > a,$$
$$SE = \frac{(b+d)(c+d)}{n(a+b)(a+c)}$$

$$CAI = \frac{ad - bc}{(b+d)(c+d)} \quad \text{for } bc > ad \text{ and } a > d,$$
$$SE = \frac{(a+b)(a+c)}{n(b+d)(c+a)}.$$

The index was expressed as a percentage ranging from 100 to –100, with 100% indicating that the joint number of occurrences of each whale equaled the number of occurrences of the least-photographed individual. Zero percent indicated that the individuals were randomly distributed among photographs, and –100% indicated that the two individuals were never photographed together. The statistical significance of CAI values was evaluated according to their standard errors using Student's t test (Cole, 1949).

The CAI provides a measure of complete association (rather than absolute association) in that a value of 100% occurs only when the joint number of occurrences equals the number of occurrences of the less frequently photographed individual (see Cole, 1949, for details and a review of association indices). An index of complete association was deemed more appropriate for an analysis of patterns of association between individuals because not all individuals were equally identifiable (see Bigg et al., 1990) as was especially the case for cow–calf pairs, in which the often well-marked mother was generally identified in more photographs than her usually indistinct young calves even though they always traveled together.

Only CAI values for all years' combined were used to determine intrapod groups. CAI values were later calculated for the periods 1984–88 and 1989–95 and used to examine changes in bond strength between mothers and female offspring as the offspring matured and produced their own calves. The relationship between age of males and the bond strength with their mothers was also examined with these CAI values.

Groupings of individuals were identified from dendrograms constructed with an agglomerative average single-link algorithm (Johnson, 1967; see Fig. 1) In this procedure, CAI values for all possible pairs of individuals were compared and the pair with the highest CAI was linked. Then the pair of unlinked individuals with the highest CAI was linked, or an unlinked individual with a higher mean CAI value with previously linked individuals was linked to that pair, and so on until the mean CAI dropped to 20%. By this point, the vast majority of individuals had been linked into intrapod groups and we switched to an analysis with the point correlation coefficient (PCC):

$$PCC = \frac{ad - bc}{\sqrt{[(a+b)(a+c)(b+d)(c+d)]}},$$

where a represents the number of photographs containing one or more members of both groups, b and c represent the numbers containing members of only one or the other of the groups, and d represents the number containing no members of either group.

The PCC index, a measure of absolute association, was used to examine associations among intrapod groups determined by CAI analysis because each group was considered equally identifiable. The PCC index varies from 100% to –100%, with 0 indicating a random distribution. An index of absolute association was deemed to be more appropriate for intrapod groups because all groups contained readily identifiable animals; therefore observation of one group in the absence of another group indicated that each group was traveling independently of one another. The relationships among intrapod groups were examined from dendrograms constructed from PCC values with an agglomerative average single-link algorithm (see Fig. 2). Linkages with a positive PCC

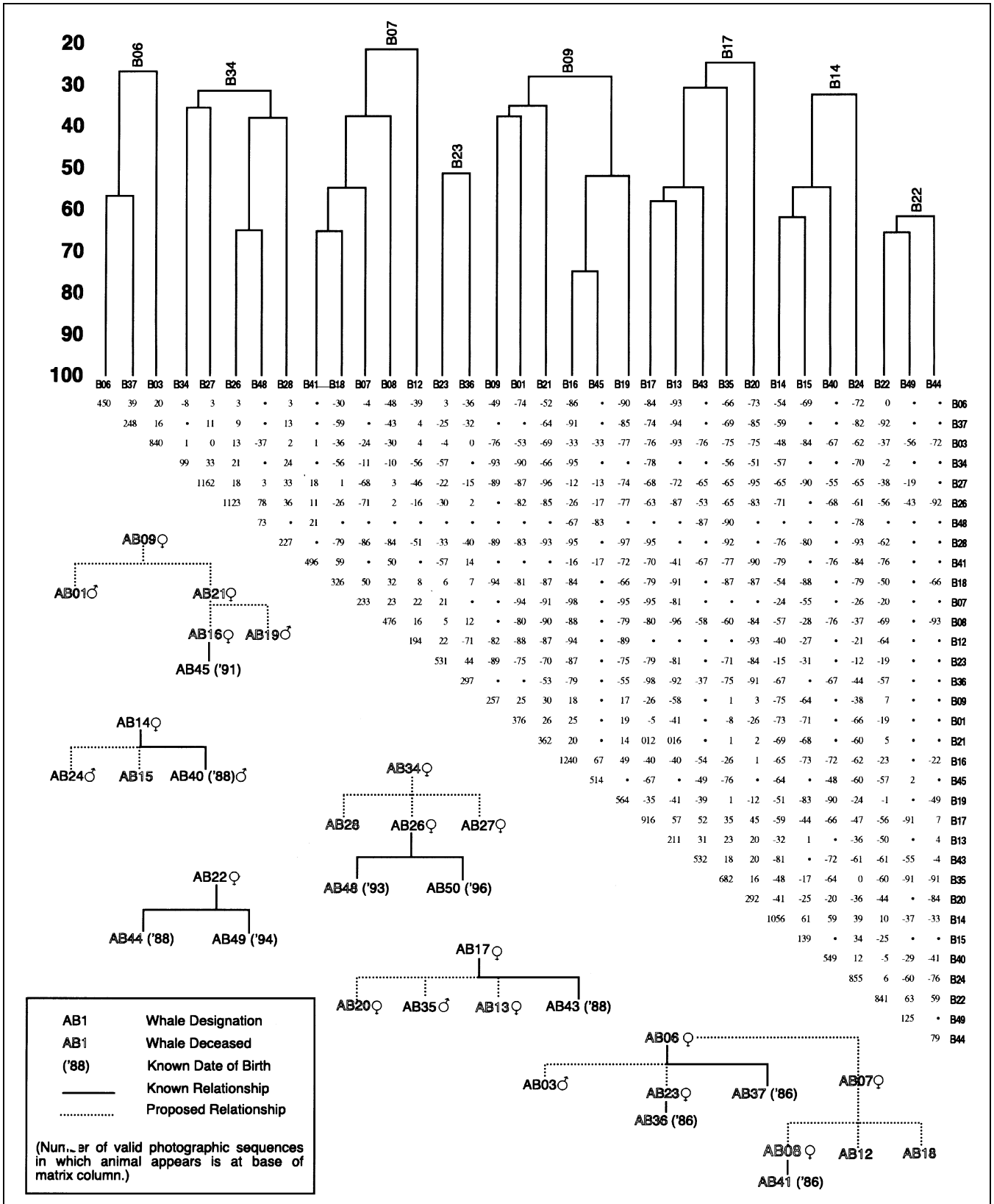

Figure 1

Top: dendrogram illustrating intrapod groups and relationships among individuals with CAI values calculated at the population level. (Relationships among intrapod groups are shown in Fig. 2.) Middle: matrix of CAI values between pairs of individuals calculated at the pod level for AB pod, AB17 subpod. Numbers at the base of each column in the matrix are the number of valid photo sequences in which that individual appears. Bottom: inferred genealogical trees.

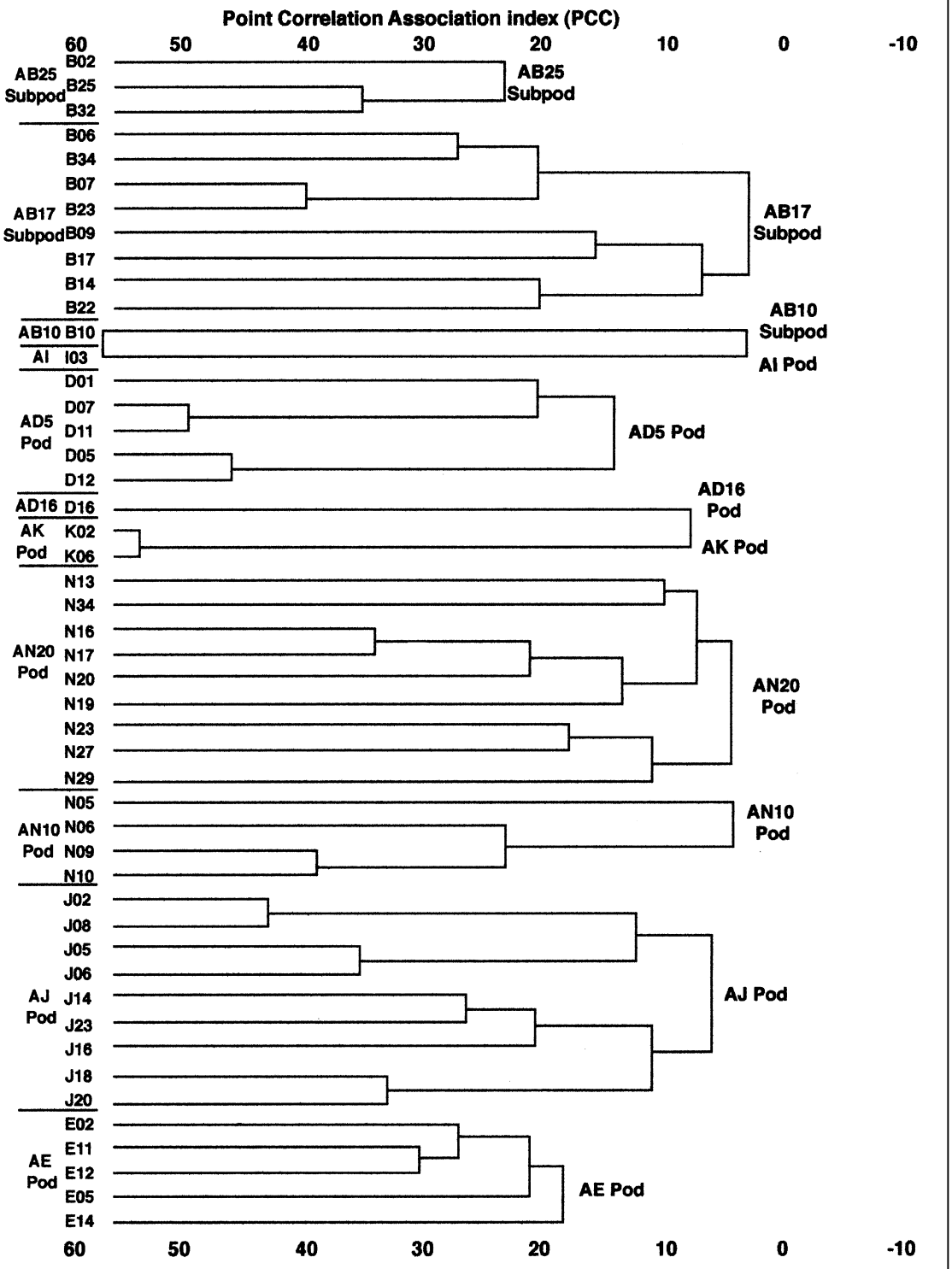

Figure 2

Dendrogram illustrating the relationships among intrapod groups (see top of Fig. 1 and Figs. 3–12) with values derived from PCC analysis.

association value (PCC>0) were designated as pods (Fig. 2). Groups were designated as subpods rather than pods when PCC values between them did not exceed zero but direct observation and photographic

summaries of encounters indicated that designated subpods traveled together as a single pod over 50% of the time.

Determination of sex and age

Sexually mature males were differentiated from females and immature males by their higher dorsal-fin height-to-width ratio (HWR), which typically exceeds 1.4 by 15 years of age (Olesiuk et al., 1990). Mature females were identified when they gave birth and were accompanied by a new calf. The sex of most juveniles could not be determined except in cases where the penis or the unique pigmentation pattern of the genital region was observed (Bigg et al., 1990; Olesiuk et al., 1990).

Actual ages could be determined for whales born during the study on the basis of their birth year. The ages of whales that were immature at the beginning of the study were estimated when they were first seen on the basis of relative size of the whale and size of the dorsal fin (Bigg et al., 1990). The approximate year of birth for whales that matured during the study was estimated by subtracting the mean age of maturity (15 years for both sexes) from the year they matured. Females were considered to have matured in the year they gave birth to their first viable calf, and males in the year in which their dorsal fin attained an HWR of 1.4 (Bigg et al., 1990; Olesiuk et al., 1990). The year of birth of males that were sexually but not physically mature at the start of the study was estimated by subtracting the mean age of physical maturity from the year their dorsal fin attained a HWR of 1.6–1.8, indicating physical maturity. Males that were physically mature and had a dorsal fin HWR of 1.6–1.8 at the beginning of the study were considered to be at least 21 years of age at that time. The minimum age of females that were mature at the beginning of the study was estimated by subtracting 15 years from the estimated birth year of their eldest offspring. This was a minimum estimate because a female's elder offspring may have died before the start of the study. Females that had not given birth for a decade or more were considered postreproductive (Olesiuk et al., 1990).

Construction of genealogical trees

Because statistical analysis indicated that whales associated in stable groups (or pods), CAI values were recalculated for all individuals within each pod and displayed in a matrix to show the relative strength of association among pod members (Fig. 1). We postulated that associations within pods reflected genealogical relationships and used them in conjunction with data on known relationships, sex and age data, and direct observations to infer genealogical relationships (Fig. 1).

Possible maternal genealogical trees were constructed in three steps (Bigg et al., 1990). Individuals to be incorporated into the tree as offspring were selected beginning with those born during the study, followed by those that were juvenile at the start of the study, and finally by those that were mature at the start of the study. Second, their potential mothers were identified. All mature females in the same pod were considered, providing that they could have been at least 12 years (minimum age of maturity) older. An individual's own mature daughters were excluded as potential mothers. Third, the relative strength of bonds as indicated by CAI values between the individual and all its potential mothers was examined. The potential mother with which the individual was most closely bonded was assumed to be its mother. An individual not strongly bonded to any potential mother was not assigned a mother. Matrices were cross-checked to insure that mother–offspring assignments created sibling groups that demonstrated reasonable linkage by CAI values. Direct observation was used to supplement statistical analysis to construct genealogies in instances where individuals and groups were less frequently photographed and where there was some ambiguity in the numerical analysis.

Results

A total of 2444 hours of direct observation of whales was logged from 1984 to 1995 (Table 1), during which 36,009 frames of film were exposed that were suitable for use in statistical analysis of association patterns (more than one individual appeared in the photographic sequence). A total of 202 whales photographed between 1984 and 1995 were included in the association analysis. According to direct field observations and inspection of photographs, these had previously been assigned to 9 pods (Table 2; Heise et al., 1992). Another 158 whales were tentatively grouped into 5 pods by field observation and visual inspection of photographs (pod AX, 54 whales; pod AY, 11 whales; pod AS, 17 whales; pod AF, 48 whales; pod AG, 28 whales). These pods were not included in the association analysis because there were insufficient photographs. The individuals listed in Table 2 represent the cumulative membership of pods over all years of the study. In all pods and most groups, the numbers of individuals varied over the course of the study as members died or were born during the study.

Table 1
Hours of direct observation and number of usable film frames by year.

Year	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	Total
Frames	6,076	1,284	2,967	1,326	1,400	3,549	5,940	3,701	3,641	2,333	1,662	2,130	36,009
Hours	307	154	127	91	92	268	423	246	255	127	120	234	2444

Statistical analysis indicated that individual whales did not associate randomly with one another. For individuals seen together at least once, 38.5% of all CAI values from the initial analysis of all individuals in all years were significantly less than 0 at a 5% confidence level (30.1% at a 1% level) and 27.5% were significantly greater than 0 at a 5% level (23.2% at a 1% level) (see Cole, 1949). Because these values are far greater than expected owing to chance, we rejected the null hypothesis that association patterns were random. The various animals positively associated with a particular individual tended to be positively associated themselves. These groups were also indicated by the agglomerative cluster analysis. A dendrogram showing associations among all 202 individuals included in the analyses was too large to exhibit here as a single figure; it appears split into pods along with matrices of CAI values and proposed genealogical trees for each pod (Figs. 1, and 3–12)

In nearly all cases, intrapod groups of individuals linked by association analysis at greater than 20% CAI reflected groupings established by direct observation. Direct observation also indicated that these intrapod groups virtually always traveled together. Most intrapod groups were centered around a reproductive or postreproductive female, which led us to suspect that these groups reflected matrilineal genealogies. However, in four cases single males (AE14, J02, N19, and D01) were not joined to other intrapod groups (CAI>20%) and in two cases pairs of males (AD02 and AD12, and AB02 and AB29) were linked to each other but not to other intrapod groups (CAI>20%). The nine pods examined contained 48 intrapod groups, including male singles and pairs (Figs. 1 and 3–12). With the exception of AB pod, pods comprised 1–9 intrapod groups. Two pods (AI and AD16) contained only one intrapod group. The three subpods of AB pod contained a total of 12 intrapod groups. Intrapod groups were composed of 1–9 individuals.

Patterns of association between intrapod groups, as indicated by statistical analysis, generally supported the pods constructed by direct observation. Forty-six of the 48 intrapod groups (190 of 202 individuals) were linked at the zero level of association into their respective pods (Fig. 2). There were two exceptions; repeated direct observations were used to clarify separations into intrapod groups. First, the AB10 subpod was linked in the dendrogram with AI pod (PCC=4) before it was linked with the other subpods of AB pod. Second, AK pod and AD16 pod formed distinct clusters as expected but were joined at the PCC = 8 level, which was greater than the zero level adopted to define the other pods.

Table 2
Pods and individual whales used in this analysis.

Pod	Cumulative membership
AB	AB01-AB51
AI	AI01-AI07
AJ	AJ01-AJ38
AE	AE01-AE20
AK	AK01-AK14
AN10	AN01-AN03, AN05-AN12, AN35,AN38, AN40-AN41, AN45-AN51
AN20	AN04, AN13-AN34, AN36-AN37, AN39, AN42-AN44
AD05	AD01-AD12, AD19,AD21-AD27
AD16	AD13-18, AD20

On the basis of direct observation, AN10 pod and AN20 pod were considered a single pod (AN pod) until 1989, when they began traveling separately a majority of the time. AN whales were encountered on 46 occasions during 1984–88; the AN10 and AN20 groups were observed together in 35 (76%) of these encounters. In contrast, during 1989–95 they were observed together in only 3 of 65 (5%) encounters where AN whales were present. After 1992 they were not seen traveling together and were thus designated as separate pods. The association analysis supported their designation as separate pods (Fig. 1). AD pod was also considered a single pod early in the study on the basis of direct observation during a few encounters. From more recent direct observation and the results of the association analysis, it is now designated as two pods (AD5 and AD16 pods).

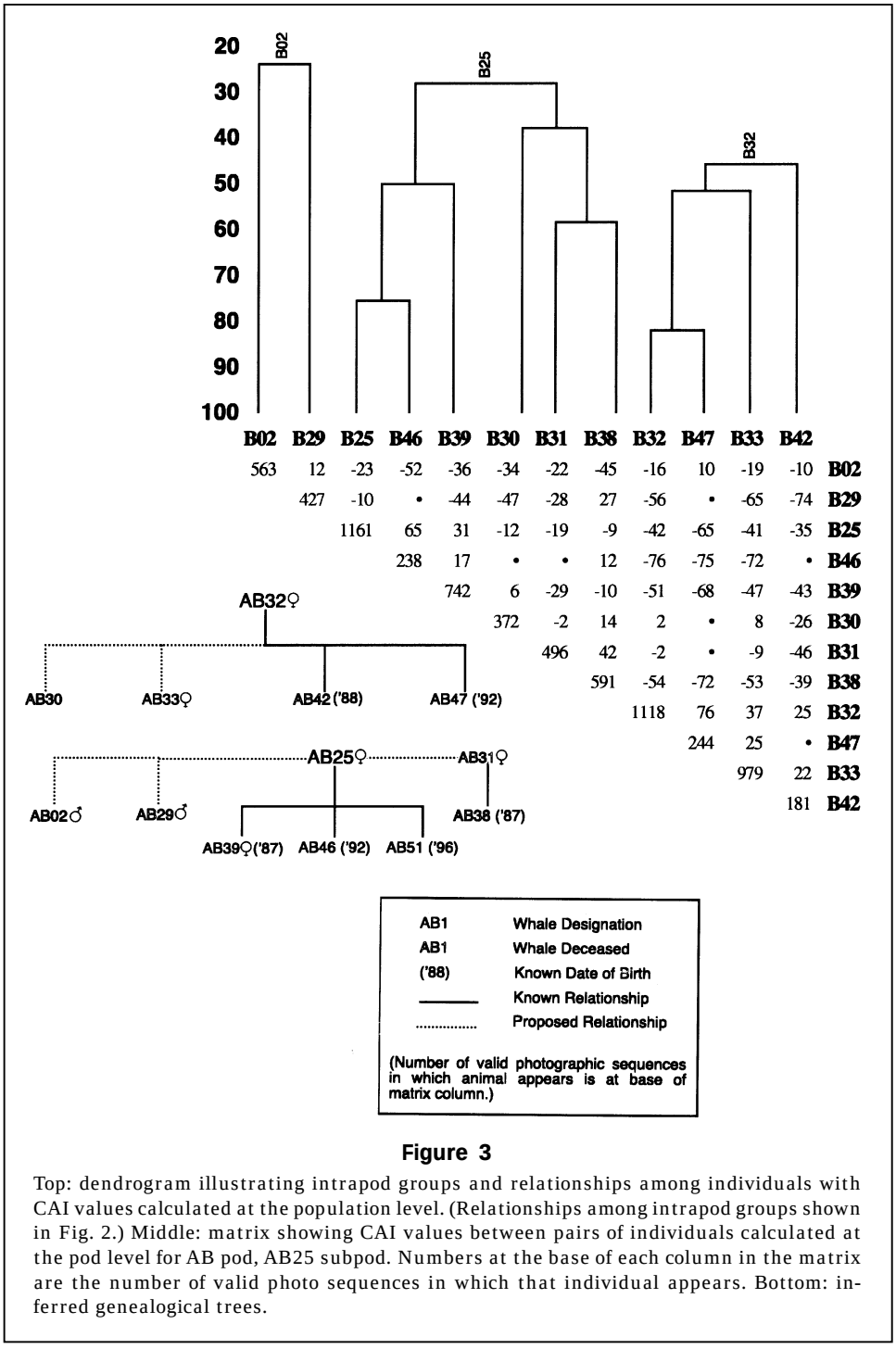

Figure 3

Top: dendrogram illustrating intrapod groups and relationships among individuals with CAI values calculated at the population level. (Relationships among intrapod groups shown in Fig. 2.) Middle: matrix showing CAI values between pairs of individuals calculated at the pod level for AB pod, AB25 subpod. Numbers at the base of each column in the matrix are the number of valid photo sequences in which that individual appears. Bottom: inferred genealogical trees.

On the basis of lack of linkage in the PCC dendrograms above the zero level, AB pod was divided into three subpods (AB10, AB17, AB25), although prior to 1994, direct field observations indicated that these subpods very rarely traveled separately. However, even when traveling together, the subpods typically traveled as cohesive units within the pod. Since 1994, direct observation has indicated that the AB25 subpod has split off and travels mainly with AJ pod. Other than those established for AB pod, no other subpods were identified in the study.

To explain association patterns within intrapod groups, we postulated that these represented matrilineal groups and that genealogical relationships

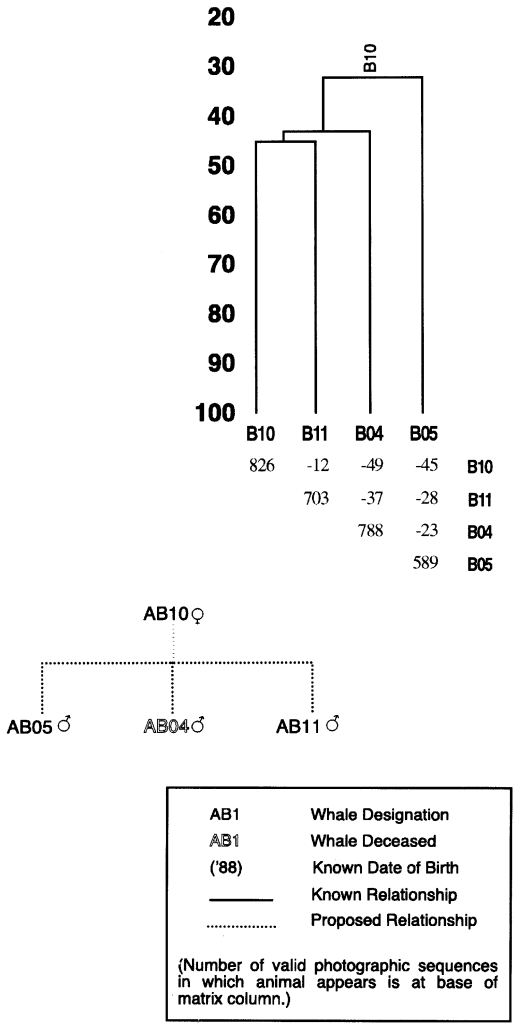

Figure 4

Top: dendrogram illustrating intrapod groups and relationships among individuals with CAI values calculated at the population level. (Relationships among intrapod groups shown in Fig. 12.) Middle: matrix showing CAI values between pairs of individuals calculated at the pod level for AB pod, AB10 subpod. Numbers at the base of each column in the matrix are the number of valid photo sequences in which that individual appears. Bottom: inferred genealogical trees.

could be deduced by examination of bond strengths within these groups. CAI values were calculated between all individuals of each pod and dendrograms of the CAI values were constructed to reveal the structure of associations between the members of each pod (Figs. 1, and 3–12).

The individuals in the nine pods examined in the second CAI analysis were placed in 39 postulated

Table 3

Cole's association index (CAI) values for mothers and female offspring that produced their first calf in 1987 or later.

Reproductive offspring	Year of first calf	Mother	CAI 1984–1988	CAI 1989–1995
AJ3	1990	AJ8	28	13
AJ4	1994	AJ8	57	20
AJ13	1992	AJ14	40	33
AK7	1993	AK6	51	24
AN10	1987	AN9	22	-20
AN11	1992	AN9	30	23
AN26	1990	AN23	53	34
AN31	1990	AN20	28	19
AN35	1988	AN9	29	2

maternal genealogical trees on the basis of linkages established in association analysis. An additional four newborn calves were observed in 1996 and placed in the genealogical trees on the basis of field observations only. Genealogical trees were constructed by first establishing all known mother–offspring relationships from field observations. There were 58 offspring born during the study that appeared in the photographs used for association analysis. In all but one case (AB41 and mother AB8), the CAI values between offspring and their known mothers was higher than for any other pairings of individuals. Direct observation also indicated that offspring maintained their strongest bonds with their known mothers throughout the study period. The three offspring born at the beginning of the study were still most strongly bonded to their mothers after 12 years. These were mother–offspring pairs AI3 and AI4 (CAI=27); AK6 and AK8 (CAI=34); and AE11 and AE13 (CAI=46).

The strength of the bond between females and their mothers declined in the nine cases in which females became reproductive during the study and their mothers remained alive throughout the study (Table 3). A paired *t* test of CAI values for 1984–88 and CAI values for 1989–95 showed that the tendency for associations to decline after female offspring become reproductive was statistically significant (t=4.88, P=0.0012).

There were 31 juveniles (estimated age 10 years or less in 1984) at the beginning of the study. Association analysis indicated that all but five of these whales remained most closely bonded to the whales judged by direct observation to be their mothers. Three of these exceptions were females that produced calves (AK7 and calf AK12; AN8 and calves AN41

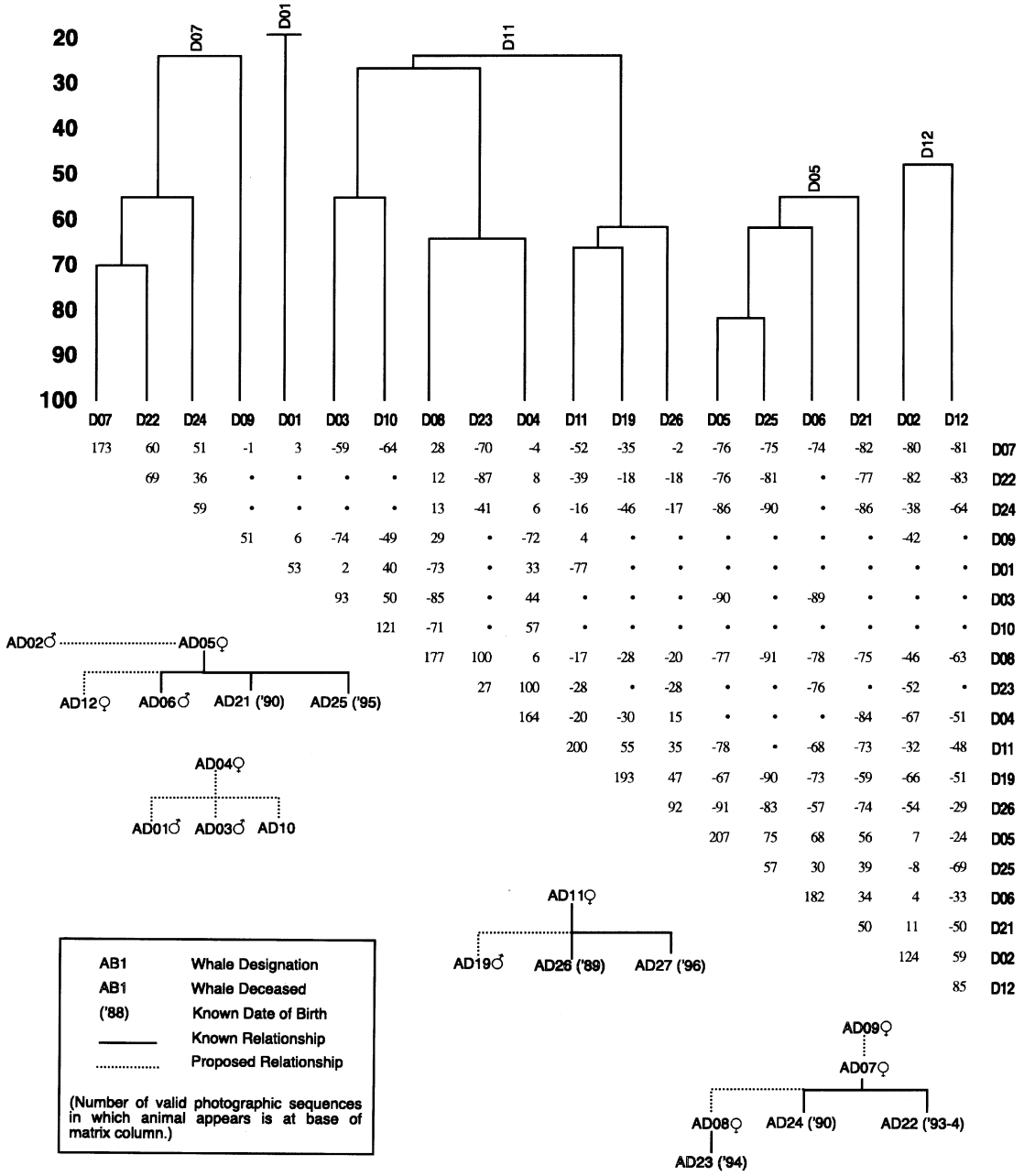

Figure 5

Top: dendrogram illustrating intrapod groups and relationships among individuals with CAI values calculated at the population level. (Relationships among intrapod groups shown in Fig. 2.) Middle: matrix showing CAI values between pairs of individuals calculated at the pod level for AD5 pod. Numbers at the base of each column in the matrix are the number of valid photo sequences in which that individual appears. Bottom: inferred genealogical trees.

and AN48; AN11 and calves AN47 and AN49). These females became most closely bonded to their own calves rather than to their mothers. One juvenile male, AN19, had a stronger bond with apparent juvenile sibling AN18 (CAI=16) than with his apparent mother, reproductive female AN17 (CAI=4). The juvenile AB18 had a stronger bond (CAI=58) with a young calf, AB41, in his intrapod group than with his apparent mother, reproductive female AB7 (CAI=22). However, in the cases of all five of these whales, the strongest bond with an adult female remained with their apparent mothers.

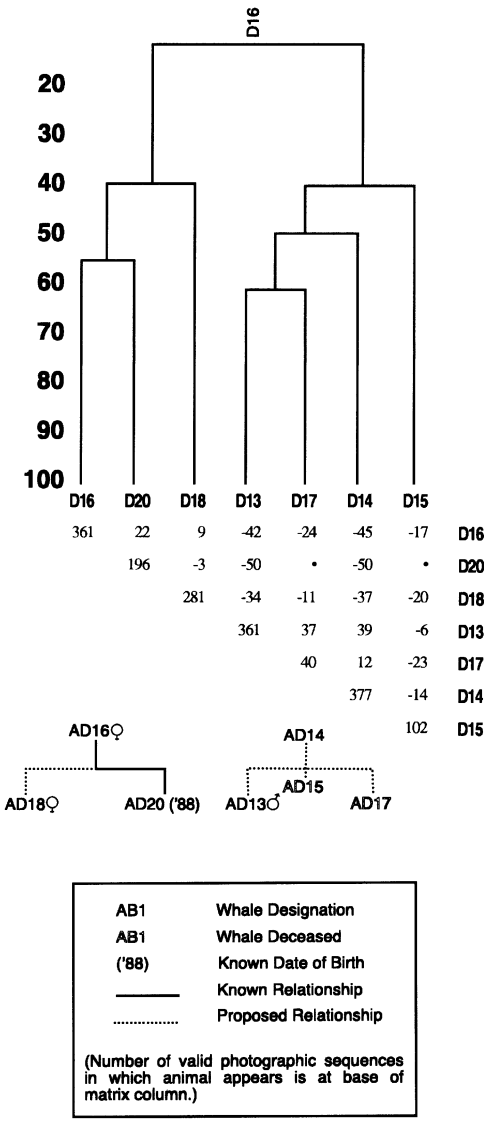

Figure 6

Top: dendrogram illustrating intrapod groups and relationships among individuals with CAI values calculated at the population level. (Relationships among intrapod groups shown in Fig. 2.) Middle: matrix showing CAI values between pairs of individuals calculated at the pod level for AD16 pod. Numbers at the base of each column in the matrix are the number of valid photo sequences in which that individual appears. Bottom: inferred genealogical trees.

The strength of bonds between male offspring and their mothers was highly variable (Table 4). Simple regression analysis indicated that the strength of bonds tended to diminish with age, but not significantly ($F_{1,27}$=1.62; P=0.215).

Table 4

Cole's Association Index (CAI) values for male killer whales and their mothers. Ages estimated as described in methods; ages over 20 years are mimimum ages.

Whale	Estimated approx. age (yr)	CAI Value	Whale	Estimated approx. age (yr)	CAI Value
AB1	33	25	AJ9	18	32
AB3	30	20	AJ16	27	48
AB24	25	39	AJ17	29	18
AB35	19	35	AJ21	19	31
AJ25	22	48	AK4	27	29
AD3	27	50	AK1	27	20
AE1	32	25	AN3	32	31
AE3	18	21	AN7	24	17
AE6	16	38	AN14	19	47
AE14	19	24	AN21	25	54
AE9	32	31	AN24	15	55
AJ1	31	39	AN25	24	28
AJ2	27	21	AN30	16	54
AJ7	19	55	AN33	23	41
AN1	32	66			

Of the 45 proposed maternal lineages (Figs. 3–12), 25 included two generations, 16 included three generations, and four had four generations. In all but one of the four-generational trees, the oldest matriarch died during the study. We identified four matrilineal intrapod groups that appeared destined to die out. These were the single adult male, AB3 (Fig. 4); the AB10 subpod which consisted of the apparently postreproductive female AB10 and 3 adult male sons, AB4, AB5, and AB11 (Fig. 6); the apparently postreproductive AJ12 and her adult male son, AJ16 (Fig. 9); and the apparently postreproductive AN 34 and her adult male son, AN21 (Fig. 10). Three of the remaining matrilineal groups had produced two reproductive females in one generation and were growing, and eight had produced one reproductive female and were relatively stable. The fate of the other matrilineal groups will be determined later as offspring born during the study mature and their reproductive potential is realized.

Discussion

Direct observations indicated that resident killer whales in Prince William Sound do not associate randomly with one another, but rather tend to associate with specific individuals. Statistical analysis of associations in photographic sequences supports this

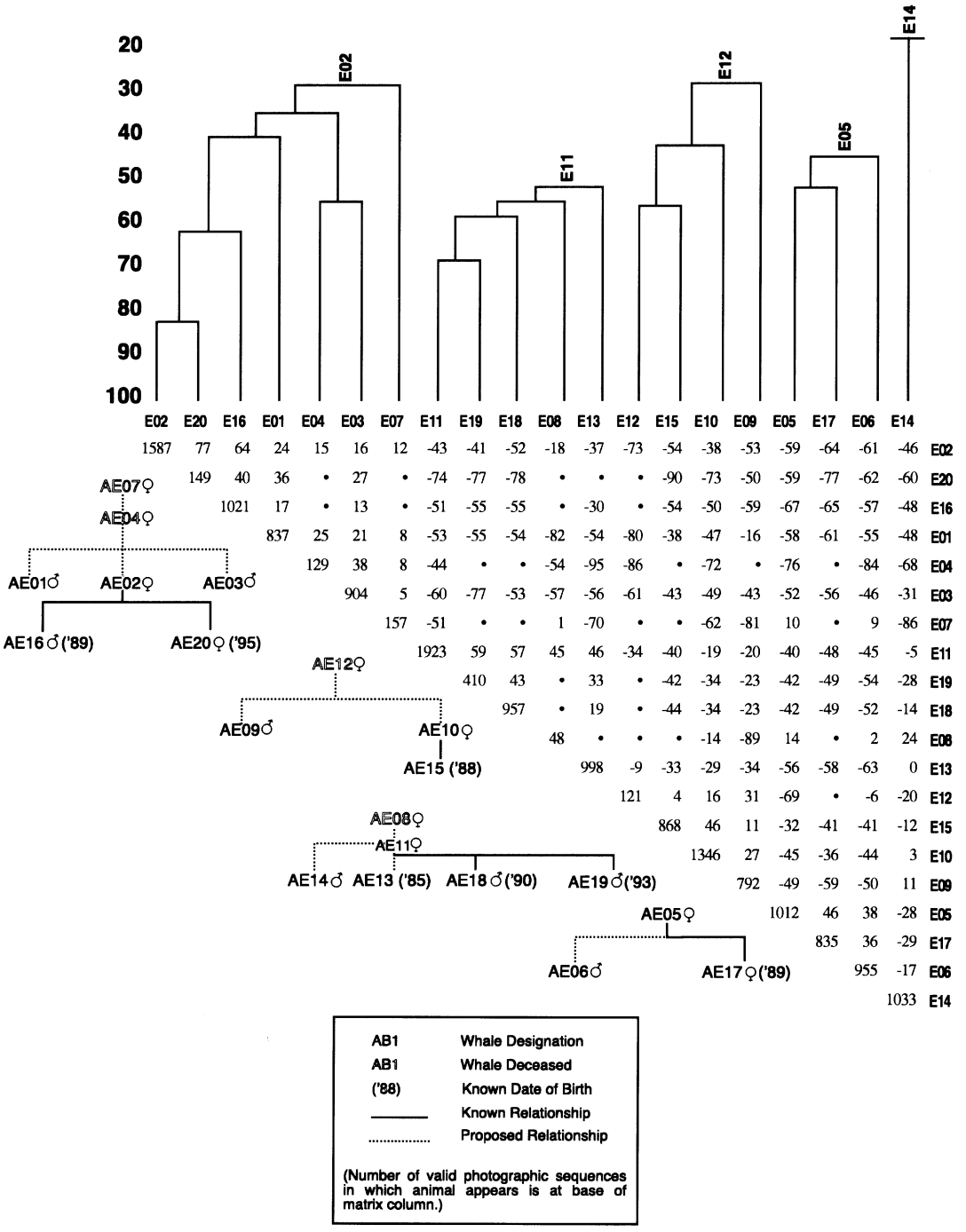

Figure 7

Top: dendrogram illustrating intrapod groups and relationships among individuals with CAI values calculated at the population level. (Relationships among intrapod groups shown in Fig. 2.) Middle: matrix showing CAI values between pairs of individuals calculated at the pod level for AE pod. Numbers at the base of each column in the matrix are the number of valid photo sequences in which that individual appears. Bottom: inferred genealogical trees.

observation. It is important to appreciate that in this analysis (Fig. 1 and subsequently Figs. 3–12), results were obtained by using a continuous clustering process in which all whales were treated as individuals

and were linked into progressively larger groups until they formed a single large group. This analysis examines the relationships between individuals in the entire population.

We postulate that the significant long-term associations observed were based on genealogical relationships. Judged from known relationships (mothers and offspring born during the study), the strength of bonds among individuals within pods appeared directly correlated with their degree of relatedness.

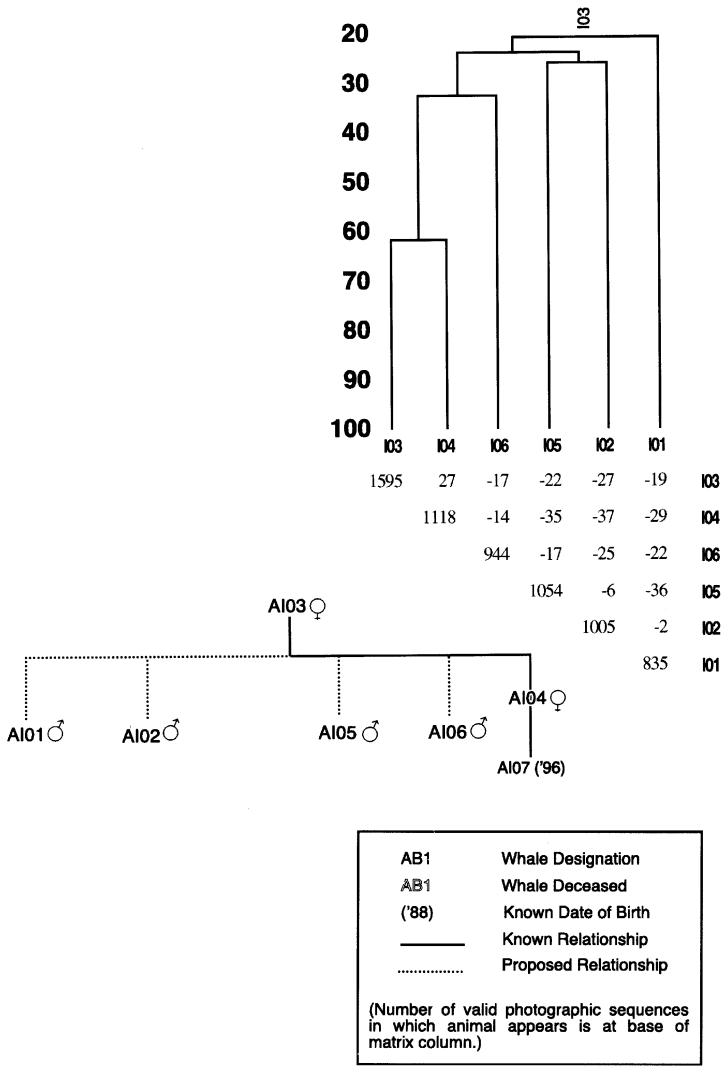

Figure 8

Top: dendrogram illustrating intrapod groups and relationships among individuals with CAI values calculated at the population level. (Relationships among intrapod groups shown in Figure 2.) Middle: matrix showing CAI values between pairs of individuals calculated at the pod level for AI pod. Numbers at the base of each column in the matrix are the numbers of valid photo sequences in which that individual appears. Bottom: inferred genealogical trees.

Our findings that resident killer whales in Prince William Sound are organized in statistically identifiable pods and intrapod groups are similar to results from studies of resident killer whales in British Columbia and Washington State (Heimlich-Boran, 1986; Bigg et al., 1990). Bigg et al. (1990) defined a pod as a group of individuals that traveled together at least 50% of the time. All the resident pods described in Prince William Sound fit that definition. Pod membership is also supported by pod-specific vocal dialects in both areas (Bigg et al., 1990; Ford, 1991; Ford[1]).

Pod delineations based on direct observation were supported by association analysis in all but two cases. Both discrepancies appeared in the final stages of the agglomerative linking procedure. Although each pod was a distinct cluster, AD16 pod was found to be linked to AK pod with a PCC value of eight, at somewhat higher than the level of linkage between other pods. This was not supported by direct observation and was apparently an artifact of small sample size. AD16 pod was infrequently photographed and was often part of multipod groups that included AK pod.

The AB10 subpod was linked with AI pod (PCC=4) before being linked with other members of AB pod. AI pod frequently traveled with AB pod early in the study, and we suspect that AI pod (7 whales in 1996) was in the final stages of a gradual split from the then 35-member AB pod when the study began in 1984. AI pod traveled more independently of AB pod in later years. The pod-specific dialects for AI and AB pods are very similar (Ford[1]), supporting this hypothesis. The preponderance of adult males in AI pod (4 out of 7 whales in 1996) may have contributed to the independence of this matrilineal group. Bigg et al. (1990) found that matrilineal groups with a high percentage of males tend to travel more independently. This was also evident for the AB10 subpod, in which 3 out of 4 members were adult males. AB10 subpod often traveled a distance away from the remainder of AB pod.

Direct observation and photographic analysis also indicated that some males

[1] Ford, J. K. B. 1997. Vancouver Public Aquarium, P.O. Box 3232, Vancouver, B.B., Canada. Personal commun.

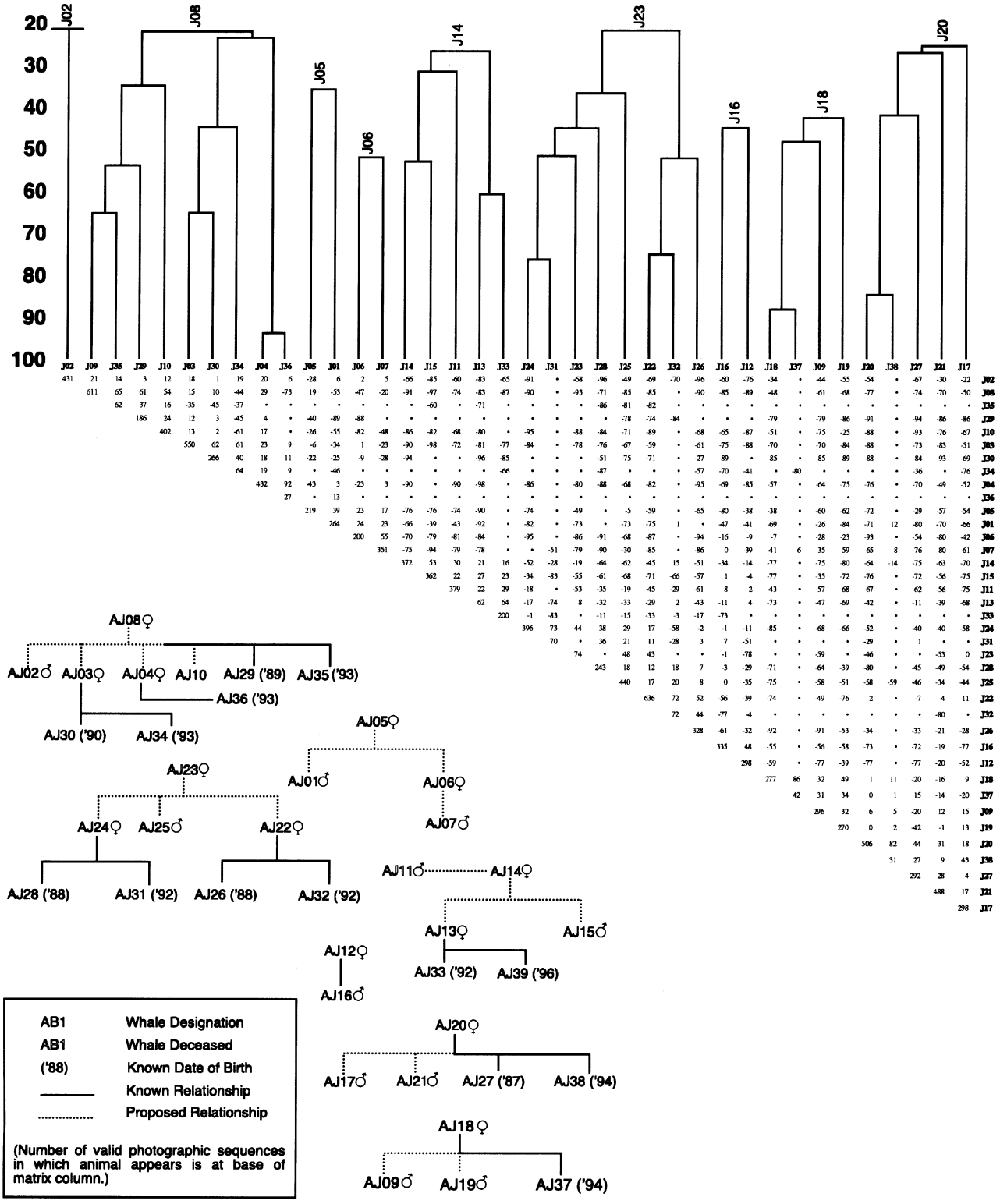

Figure 9

Top: dendrogram illustrating intrapod groups and relationships among individuals with CAI values calculated at the population level. (Relationships among intrapod groups shown in Fig. 2.) Middle: matrix showing CAI values between pairs of individuals calculated at the pod level for AJ pod. Numbers at the base of each column in the matrix are the number of valid photo sequences in which that individual appears. Bottom: inferred genealogical trees.

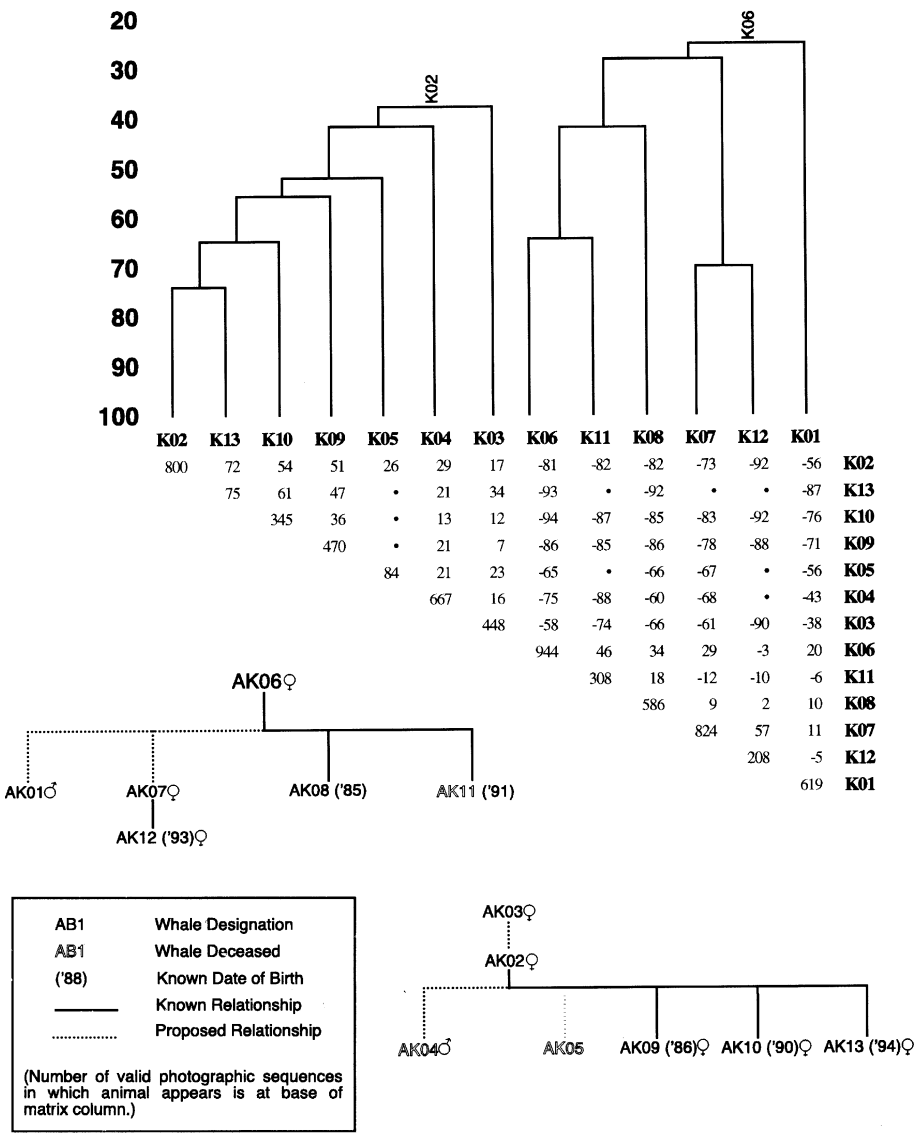

Figure 10

Top: dendrogram illustrating intrapod groups and relationships among individuals with CAI values calculated at the population level. (Relationships among intrapod groups shown in Fig. 2.) Middle: matrix showing CAI values between pairs of individuals calculated at the pod level for AK pod. Numbers at the base of each column in the matrix are the number of valid photo sequences in which that individual appears. Bottom: inferred genealogical trees.

occasionally traveled with other adult or juvenile males or traveled independently, particularly during the multipod encounters observed in July and August (Matkin et al., 1997). In two cases, pairs of males were more highly associated with each other than with any other intrapod groups.

We witnessed the splitting of one pod (AN pod into AN10 and AN20 pods) during the course of the study. This was not a gradual occurrence, as suggested by Bigg et al. (1990) for A04, C01, and D01 pods in British Columbia but appeared to be a rather abrupt event around 1989. The pod split along intrapod (matrilineal) groups, while all 13 of the intrapod groups in the two pods remained intact. AN pod numbered 35 whales at the time it split and was the largest pod in the study at that time.

Bigg et al. (1990) defined subpods as fragments of pods that occasionally split and traveled separately

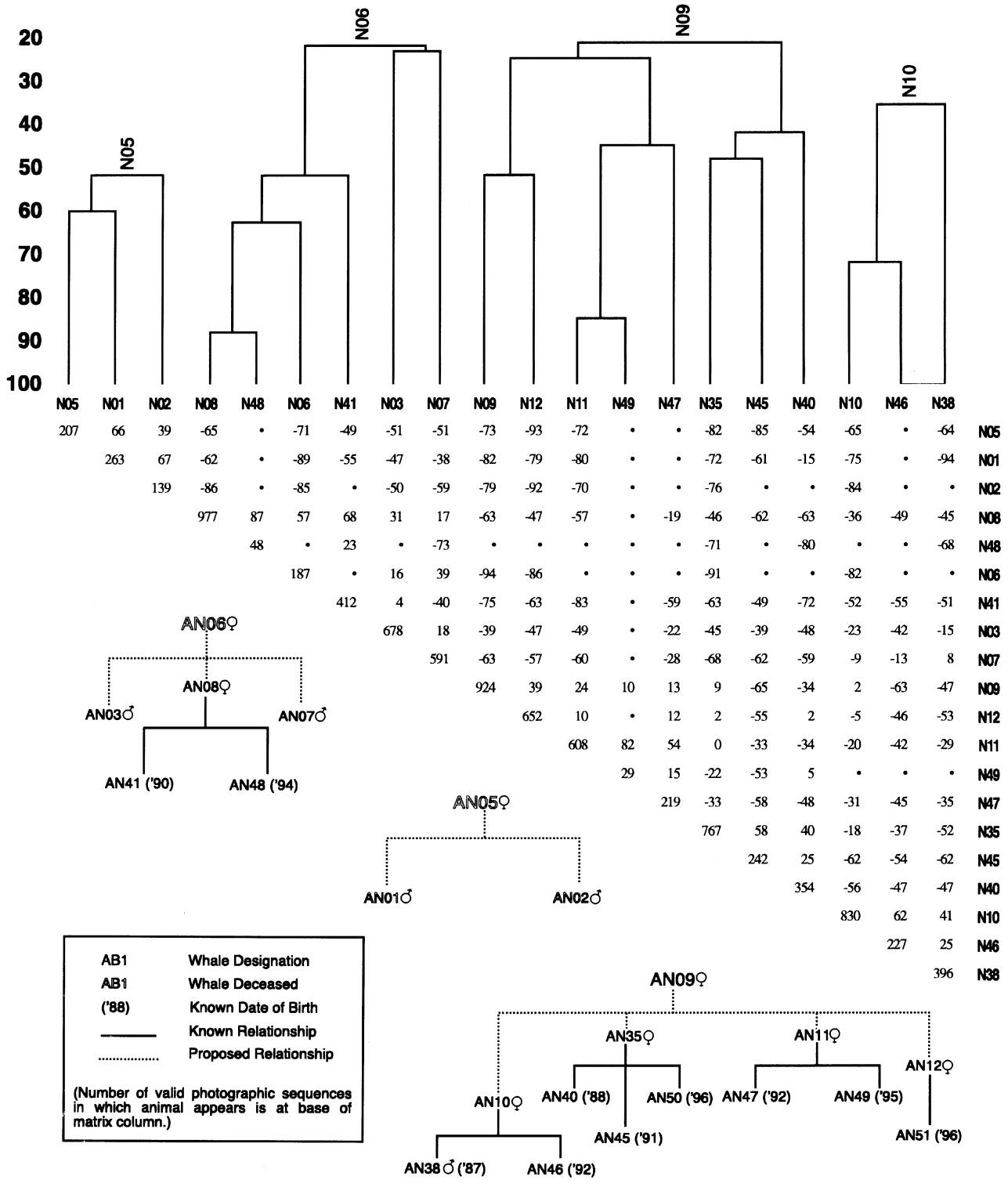

Figure 11

Top: dendrogram illustrating intrapod groups and relationships among individuals with CAI values calculated at the population level. (Relationships among intrapod groups shown in Fig. 2.) Middle: matrix showing CAI values between pairs of individuals calculated at the pod level for AN10 pod. Numbers at the base of each column in the matrix are the number of valid photo sequences in which that individual appears. Bottom: inferred genealogical trees.

from their pods. Through association analysis, we expanded this definition to include groups that travel in unison with their pod but rarely mix with other groups within the pod. This latter situation occurred only for AB pod, which was divided into three subpods. By direct observation and examination of

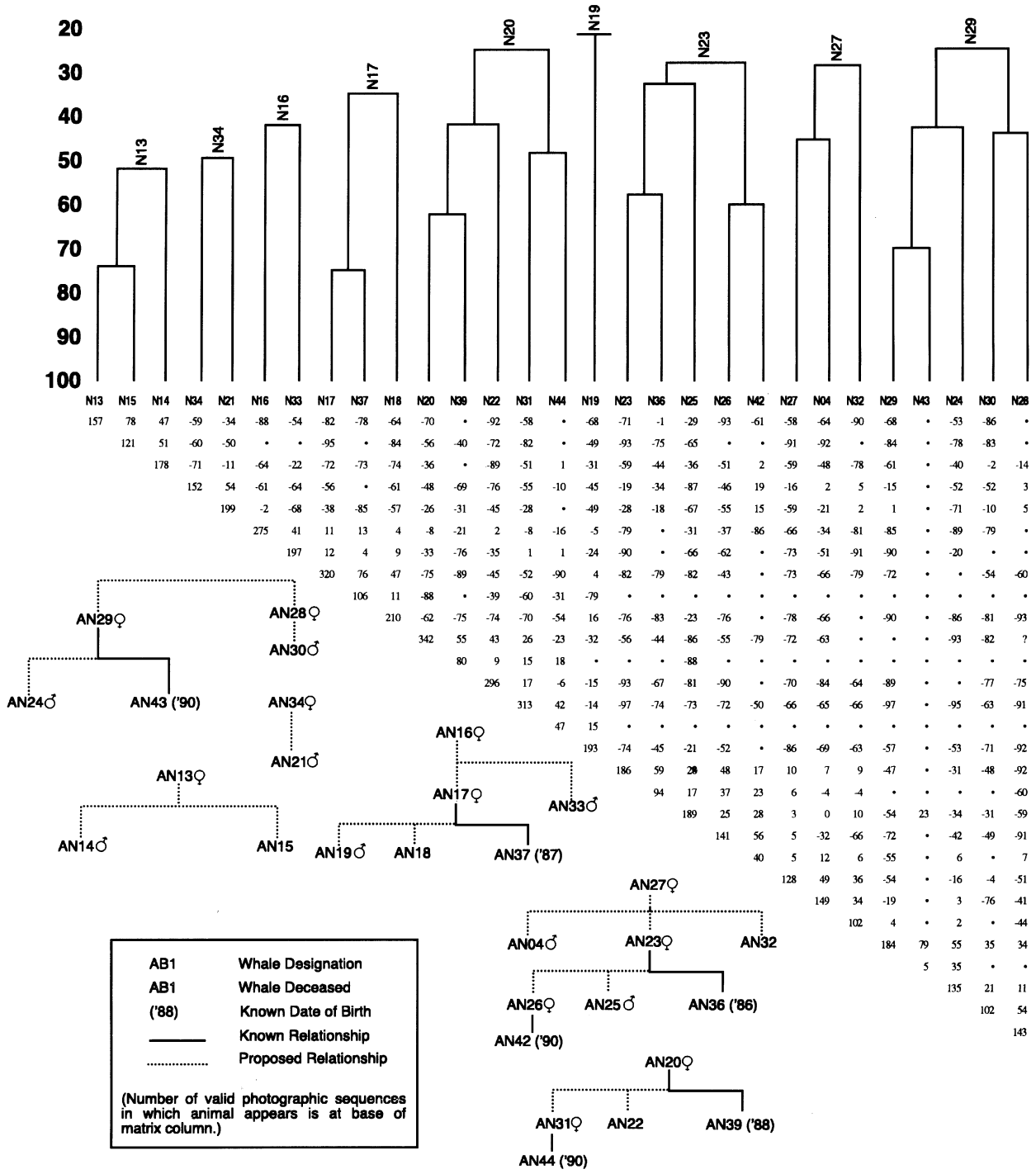

Figure 12

Top: dendrogram illustrating intrapod groups and relationships among individuals with CAI values calculated at the population level. (Relationships among intrapod groups shown in Fig. 2.) Middle: matrix showing CAI values between pairs of individuals calculated at the pod level for AN20 pod. Numbers at the base of each column in the matrix are the number of valid photo sequences in which that individual appears. Bottom: inferred genealogical trees.

photographs of this pod, it was determined that AB pod nearly always traveled as a unit; however, in the dendrogram linking intrapod groups (Fig. 2) it appeared as three separate groups (PCC>0). This finding indicated that although they were traveling together, the subpods tended not to mix with the rest of the pod.

Communities were described by Bigg et al. (1990) as closed populations of pods that associated with one another. They described two geographically distinct communities of resident killer whales (northern and southern residents) that had separation in range near the middle of Vancouver Island, British Columbia. We found no separation of pods into communities by this definition in our area, although our study discerned matrilineal (intrapod) groups, subpods, and pods. Resident whales from AF and AG pods photographed regularly in southeastern Alaska were observed swimming with the pods described in this study (Matkin et al., 1997). One of the pods described in this paper, AD5 pod, was photographed off Kodiak Island. It thus appears that geographic boundaries do not delineate communities for resident killer whales from southeastern Alaska to Kodiak Island.

The association analysis for individuals within pods strongly suggested that strength of bond was directly correlated to degree of relatedness. There was only one case in which statistical analysis indicated that offspring born during the study did not maintain the strongest bond with its mother. The mother AB8 and her sibling AB18 both died at the time of the Exxon Valdez oil spill. AB8 left her year-old offspring, AB41 (born 1988). Association analysis indicated that AB41 was more closely linked (CAI=58) to its mother's apparent sibling, AB18, than to its mother, AB8 (CAI=50); the young whale AB41 died several years later (1993–4).

Five whales that were juveniles at the beginning of the study were most closely associated with whales other than their mothers. Three were females, AK07, AN08, and AN11, each of which produced offspring during the study. Following these births, they were more closely bonded to their offspring rather than to their own mothers. This finding demonstrates that new mothers, when they produce calves, develop distance from their own mothers (Table 4). The tendency of females with offspring to travel farther from their mothers than the distance prior to first reproduction suggests a process of separation that may also be basic to new pod formation.

Our proposed genealogical trees suggest that intrapod groups are matrilineal groupings of mothers and their descendants (Figs. 1 and 3–12). There was no immigration or emigration of male or female offspring from these natal groups over the course of our study. These extremely stable matrilineal groups appear to be the foundation of resident pod social structure in Prince William Sound. This is similar to results from studies in British Columbia and Washington State (Bigg et al., 1990).

We were most confident in genealogical trees for pods that were most frequently photographed, such as AE and AK pods, and less confident in trees for the much less frequently observed AD5 and AD16 pods. The large number of mortalities in AB pod also made construction of genealogical trees more difficult. The greatest potential source of error in genealogical assignment was the death of the mother of a young whale prior to the study, in which case the young whale would likely travel with its closest female relative. However, since the annual natural mortality rate for reproductive females is extremely low (0.0048 according to Olesiuk et al., 1990), this source of error was probably insignificant except following disasters such as the high loss of reproductive females after the Exxon Valdez Oil Spill (Matkin et al., 1994).

In all but one of the resident pods we examined, the total number of whales increased over the period of the study, indicating that a majority of matrilineal groups have been growing or dividing (or doing both) over the past decades. The exception was AB pod, which declined during this period from 35 to 23 whales (28 deaths; 16 births). Six of the mortalities occurred during 1985 and 1986 when there was a conflict with the sablefish (*Anaplopoma fimbria*) fishery (Matkin et al., 1994). During this period apparent bullet wounds were observed in 16 whales.

Fourteen of the mortalities in AB pod occurred in the year and a half following the 1989 Exxon Valdez oil spill (Matkin et al., 1994). Some of the matrilineal groups in the pod are nearly extinct as a result of these deaths. An adult male, AB03, appears to be the last member of a once-large matrilineal group linked by the apparent sisters AB06 and AB07 (Fig. 1; AB03 has since died). Another large matrilineal group (matriarch AB09) has been reduced to a single orphaned 5-year-old, AB45. Many of the mortalities have been those of juveniles (13) or reproductive females (4) and have severely reduced the reproductive potential of the pod.

The statistical support for the existence of intrapod groups and the apparent lack of emigration or immigration into these groups allows for determination of demographic changes, both natural and induced, within resident killer whale populations. The detailed delineation of social structure in resident killer whales provides a unique opportunity for monitor-

ing and modeling of these populations. This situation appears to be unique among social mammals (e.g. the lack of male dispersal), with the possible exception of the long-finned pilot whale. In that species, molecular typing revealed that pod members also form extended family groupings from which individuals do not disperse (Amos et al., 1993). Molecular typing of individual whales described in this study is currently in progress (Barrett-Lennard[2]).

Acknowledgments

Work from 1989–92 was funded as part of the damage-assessment program of the Exxon Valdez Oil Spill (EVOS) Trustee Council. The EVOS Trustee Council also provided funds in 1995 for field work and analysis as part of the oil-spill restoration program. Work in 1984 was supported by Hubbs Sea World Research Institute, and fieldwork in 1986 was supported by Alaska Sea Grant and the National Marine Mammal Laboratory. Data for killer whale pods in Prince William Sound in 1985, 1987, 1988, 1993, and 1994, and in March 1989 following the EVOS, were provided by the North Gulf Oceanic Society. The Society was funded by private donations, the Alaska State Legislature, the Sail Alaska Foundation, and the Alaska Sea Grant program.

The project would not have been possible without the participation of L. Barrett-Lennard, K. Heise, O. von Ziegesar, and K. Balcomb-Bartok, who led field efforts at various times. Field assistance or other substantial contributions were made by R. Angliss, L. Daniel, K. Englund, F. Felleman, M. Freeman, B. Goodwin, M. Hare, M. James, L. Larsen, J. Lyle, E. Miller, L. Saville, C. Schneider, R. Blancato, S. A. Sikema, K. Turco, and E. Weintraub. E. Miles of Miles Photo Lab provided all photographic development and printing services.

Literature cited

Amos, B., C. Schlotterer, and Diethard Tautz.
1993. Social structure of pilot whales revealed by analytical DNA profiling. Science (Wash. D.C.) 260:670–672.

Balcomb, K. C., J. R. Boran, and S. L. Heimlich.
1982. Killer whales in Greater Puget Sound. Rep. Int. Whal. Comm. 32:681–686.

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

Bigg, M. A., G. M. Ellis, and K. C. Balcomb III.
1986. The photographic identification of individual cetaceans. Whalewatcher: J. Am. Cetacean Soc. 20:10–12.

Bigg, M. A., G. M. Ellis, J. K. B. Ford, and K. C. Balcomb III.
1987. Killer whales: a study of their identification, genealogy and natural history in British Columbia and Washington State. Phantom Press, Nanaimo, British Columbia, 79 p.

Bigg, M. A., P. F. Olesiuk, G. M. Ellis, J. K. B. Ford, and K. C. Balcomb III.
1990. Social organization and genealogy of resident killer whales (*Orcinus orca*) in the coastal waters of British Columbia and Washington State. Rep. Int. Whal. Comm. Spec. Issue 12:386–406.

Cole, L. C.
1949. The measurement of interspecific association. Ecol. 30:411–24.

Ellis, G. M.
1987. Killer whales of Prince William Sound and Southeast Alaska: a catalogue of individuals photoidentified, 1976–1986. Hubbs Sea World Res. Inst. Tech. Rep. 87–200, 76 p.

Ford, J. K. B.
1991. Vocal traditions among resident killer whales (*Orcinus orca*) in coastal waters of British Columbia. Can. J. Zool. 69:1454–1483.

Ford, J. K. B., G. M. Ellis, L. G. Barrett-Lennard, A. B. Morton, R. S. Palm, and K. C. Balcomb.
1998. Dietary specialization in two sympatric populations of killer whales (*Orcinus orca*) in coastal British Columbia and adjacent waters. Can. J. Zool. 76(8):1456–1471.

Heimlich-Boran, S. L.
1986. Cohesive relationships among Puget Sound killer whales. *In* B. C. Kirkevold and J. S. Lockard (eds.), Behavioral biology of killer whales, p. 251–284. Alan R. Liss, New York, NY.

Heise, K., G. Ellis, and C. Matkin.
1992. A catalogue of Prince William Sound killer whales, 1991. North Gulf Oceanic Society, Homer, AL, 51 p.

Hoezel, A. R., Dahlheim, M., and Stern, S. J.
1998. Low genetic variation among killer whales (*Orcinus orca*) in the eastern North Pacific and genetic differentiation between foraging specialists. Heredity 89:121–128.

Hoezel, A. R., and G. A. Dover.
1991. Genetic differentiation between sympatric killer whale populations. Heredity 66:191–195.

Johnson, S. C.
1967. Hierarchical clustering schemes. Psychometrika 32:241–54.

Leatherwood, S., K. C. Balcomb III, C. O. Matkin, and G. Ellis.
1984. Killer whales (*Orcinus orca*) in southern Alaska. Hubbs Seaworld Res. Inst. Tech. Rep. 84–175, 54 p.

Leatherwood, S., C. O. Matkin, J. D. Hall, and G. M. Ellis.
1990. Killer whales, *Orcinus orca*, photo-identified in Prince William Sound, Alaska, 1976 through 1987. Can. Field-Nat. 104(3):362–371.

Matkin, C. O., G. Ellis, M. Dahlheim, and J. Zeh.
1994. Status of killer whales in Prince William Sound, 1984–1992. *In* T. Loughlin (ed.), Marine mammals and the Exxon Valdez, p. 141–162. Academic Press, San Diego, CA.

Matkin, C. O., D. Matkin, G. M. Ellis, E. Saulitis, and D. McSweeney.
1997. Movements of resident killer whales between southeastern Alaska and Prince William Sound, Alaska. Mar. Mamm. Sci. 13(3):469–475.

[2] Barrett-Lennard, L. 1998. Dep. Zoology, Univ. British Columbia, Vancouver, B.C., Canada. Personal commun.

Morton, A. B.
1990. A quantitative comparison of the behavior of resident and transient forms of killer whale off the central British Columbia coast. Rep. Int. Whal. Comm. Spec. Issue 12:245–248.

Olesiuk, P. F., M. A. Bigg, and G. M. Ellis.
1990. Life history and population dynamics of resident killer whales (*Orcinus orca*) in the coastal waters of British Columbia and Washington State. Rep. Int. Whal. Comm. Spec. Issue 12:209–244.

Saulitis, E.
1993. The behavior and vocalizations of the AT group of transient killer whales in Prince William Sound, Alaska. Master's thesis, Univ. Alaska, Fairbanks, AK, 113 p.

Saulitis, E. L., C. O. Matkin, L. Barrett-Lennard, K. Heise, and G. Ellis.
In press. Foraging behavior of transient killer whales (*Orcinus orca*) in Prince William Sound, Alaska. Mar. Mamm. Sci.

Stevens, T. A., D. A. Duffield, E. D. Asper, K. G. Hewlett, A. Bolz, L. J. Gage, and G. D. Bossart.
1989. Preliminary findings of restriction fragment differences in mitochondrial DNA among killer whales (*Orcinus orca*). Can. J. Zool. 67:2,592–2,595.