Behavioural evidence for social units in long-finned pilot whales

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Abstract: In general, mammal species show geographic or social dispersal by one or both sexes. Long-term behavioural observations and genetic evidence have confirmed that fish-eating *resident* killer whales, *Orcinus orca*, are a rare exception. Female and male offspring travel with their mothers for their whole lives: this is natal group philopatry. It is suspected that pilot whales, *Globicephala* spp., also follow this social pattern, but longitudinal data on the social structure of live long-finned pilot whales, *Globicephala melas*, are rare. We observed *G. melas* through July and August of 1998–2000 off northern Nova Scotia, Canada. Estimated group sizes ranged from 2 to 135 (mean = 20, SD = 17, median = 15, n = 249). We distinguished 322 individuals on the basis of distinctive marks on the dorsal fin, with estimated mark rates of 0.336 (proportion) (SE = 0.041) and 0.352 (mean of estimates) (SE = 0.036). Permutation testing rejected the null hypothesis of random association between individuals ($p < 0.0005$). The best fit model of the standardized lagged association rate suggests short-term associations of individuals over hours to days and long-term associations with a subset of those individuals over years. When scaled according to mark rate, sets of long-term associates average approximately 11–12 individuals, a much lower estimate than that presented previously from drive-fishery data from the Faroe Islands. Genetic sampling of behaviourally studied individuals is recommended.

Résumé : Les espèces de mammifères ont en général une dispersion géographique ou sociale qui implique l'un ou les deux sexes. Des observations du comportement sur de longues périodes et des données génétiques confirment que les épaulards, *Orcinus orca*, des piscivores *sédentaires* sont l'une des rares exceptions. Les petits mâles et femelles se déplacent en compagnie de leur mère durant toute leur vie (philopatrie du groupe natal). Les globicéphales, *Globicephala* spp., suivent, croit-on, ce même pattern social, mais les données suivies sur la structure sociale du globicéphale noir, *Globicephala melas*, sont peu nombreuses. On trouvera ici des observations sur le globicéphale noir faites en juillet et août 1998–2000 au large du nord de la Nouvelle-Écosse, Canada. Les tailles estimées des groupes varient de 2 à 135 (moyenne = 20, écart type = 17, médiane = 15, n = 249). Trois cent vingt-deux individus ont pu être identifiés grâce à des marques distinctes sur leur nageoire dorsale et les taux de marquage estimés sont de 0,336 (erreur type = 0,041) et 0,352 (erreur type = 0,036). Des tests de permutation permettent de rejeter l'hypothèse nulle d'une association aléatoire entre les individus ($p < 0,0005$). Le modèle le mieux ajusté du taux standardisé d'association avec décalage montre l'existence d'associations d'individus de courte durée sur des périodes d'heures et de jours, ainsi que des associations de longue durée sur des périodes d'années pour un sous-ensemble de ces individus. Une fois cadrés par les taux de marquage, les ensembles d'individus à associations de longue durée contiennent environ 11–12 baleines, un nombre estimé bien inférieur à celui obtenu antérieurement à partir des données de chasse à la baleine par rabattage aux îles Féroé. Un échantillonnage génétique des individus dont on a étudié le comportement serait intéressant à faire.

[Traduit par la Rédaction]

Introduction

Dispersal from the natal group by neither male nor female offspring (natal group philopatry) is extremely rare among mammals (Greenwood 1980). The only well-supported example of strict natal group philopatry is the *resident* form of the killer whale, *Orcinus orca*, found off the northwest coast of North America (Bigg et al. 1990; Barrett-Lennard 2000). Comparison with another species in which natal group philopatry exists could aid in understanding the evolution of this social system. Natal group philopatry has been sus-

pected in the two species of pilot whales, *Globicephala* spp. (Heimlich-Boran 1993; Connor et al. 1998), 5–6 m long members of the Delphinidae. Yet, while behavioural studies of the short-finned pilot whale, *Globicephala macrorhynchus*, have been and are being conducted (e.g., Shane and McSweeney 1990; Heimlich-Boran 1993), the genetic relationships of individuals have not been studied in detail. In the long-finned pilot whale, *Globicephala melas*, tissue samples from drive fisheries have been analyzed by many means (e.g., Andersen 1988; Amos et al. 1993*b*; Caurant et al. 1994; Fullard 2000), but behavioural studies of social struc-

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ture have not been carried out. Hence, in both cases, our view of pilot whale social structure is limited.

In the traditional drive fishery off the Faroe Islands, long-finned pilot whales are herded as a group to coastal drive sites by small boats and killed on shore (Bloch et al. 1993). The whales are spotted quite close to shore, (0.9 naut. mi., on average, and always <4 naut. mi.; Bloch et al. 1990) and it is highly unusual for individuals to escape the herding (Amos 1995).

Pedigree analysis of grinds (the word used by the Faroese to describe a set of whales hunted together, and the hunt itself) shows that multigenerational sets of maternally related males and females are captured together, and that breeding within the grind is rare or nonexistent (Amos et al. 1993a, 1993b; Fullard 2000). In addition, significant differences in protein polymorphisms (Andersen 1988, 1993), tissue concentrations of organochlorines (Aguilar et al. 1993) and trace metals (Caurant et al. 1993, 1994), and communities of parasitic intestinal helminths (Balbuena and Raga 1994) between some grinds have been found.

The presence of related individuals within grinds and the differences between some grinds mentioned above have been interpreted to imply that grinds are persistent entities (e.g., Andersen 1988; Fullard 2000). However, inferences are limited by the cross-sectional nature of the grind data and the difficulty in distinguishing extended relatives from unrelated individuals. To date, it has not been conclusively shown that grinds are single social units.

Social structure has been defined as the pattern of relationships between individuals; these relationships are described using observations of behavioural interactions (Hinde 1976). In studies of living cetaceans, social structure is usually deduced from patterns of affiliation among photographically identified individuals (Würsig and Jefferson 1990). Unfortunately, it can be difficult to make repeat observations of the same individual pilot whales, let alone their associations, given their wide-ranging behaviour (Mate 1989a, 1989b) and large groups (e.g., Sergeant 1962; Zachariassen 1993; Cañadas and Sagarminaga 2000). In addition, there is no proven, reliable method to sex and age individual pilot whales by surface observation at sea. Nonetheless, behavioural observations provide a means to investigate short-term (hours to months) patterns of affiliation and an alternative method to genetic work for evaluating hypotheses about long-term grouping patterns.

In this study, we tracked the grouping structure of wild long-finned pilot whales at the individual level, using photo-identification techniques across a 2-year span. Our main goals were to use behavioural evidence to quantify the social structure of long-finned pilot whales and to compare these findings with the social scenario previously generated through the drive fishery.

Methods and materials

Field methods

All observations were made off the northernmost coast of Cape Breton Island, Nova Scotia, Canada (47°02′N, 60°29′W), from a 10.6 m long commercial whale-watch vessel. Throughout July and August of 1998–2000, three 2.5- to 3-h trips were conducted daily, weather permitting. The study site spanned ~85 km^2, although only one-half to two-thirds might be covered in a given trip. In the western North Atlantic Ocean, short-finned pilot whales are seen only as far north as New Jersey (Mercer 1973) and have never been recorded from the Canadian east coast (Stacey and Baird 1993). Hence, all pilot whales sighted in this study were considered to be long-finned pilot whales. When sighted, pilot whales were approached slowly to within ~50 m. In general, the vessel would either travel parallel with pilot whales moving together in a distinct direction, or remain, motor off, with a stationary set of whales. In 1998, C.A.O. was the only researcher on board. During 1999 and 2000, photographic and note-taking duties were divided between C.A.O. and a field assistant.

An "encounter" was the base spatiotemporal unit by which we delineated group membership. All encounters started when pilot whales were first sighted. An encounter was terminated when observation effort ceased if the vessel had to return to port, or 10 min from the last sighting if all pilot whales submerged for more than 10 min, or when the vessel moved from one set of pilot whales to another with at least 200 m between the nearest individuals of the two sets. All pilot whales photographed during the same encounter were considered to be members of the same group. "Group" will be used throughout to mean individuals in an encounter.

One observer counted the members of a group every 10 min from the start of an encounter. We defined group size for each encounter as the largest of these counts. The calves, distinguished by their grey colour and small size, were also counted during each encounter.

We took photographs of the dorsal fin of individual pilot whales on black and white Ilford 400 ASA film using a Canon Elan IIe camera with databack (printing time, to the minute, on each exposure) and an autofocus 300-mm lens. Photographs were taken opportunistically, without regard to the presence or absence of an individual's distinguishing marks and regardless of whether the photographer had already taken a photograph of that individual during the encounter, except during trips when a shortage of film caused the collection protocol to change to obtaining a good photograph of all individuals present.

Analysis of photographs and encounters

Individual pilot whales were identified from the silhouette of the dorsal fin viewed in the negatives. A quality rating (Q) on a scale of 1 to 5 (poor to ideal) assigned to each fin image (by C.A.O.), based on image suitability in terms of five characteristics: focus, size, orientation, exposure, and the percentage of the fin image that was visible in the frame (see Arnbom 1987; Dufault and Whitehead 1993, 1995). The mark points (MP), simple nicks or internal corners in large notches, on the dorsal-fin silhouette in each fin image were also counted. Only images that rated $Q \geq 3$, containing fins with $MP \geq 3$, were included in the analyses, to increase the certainty of matches and the ability to recognize individuals if additional marks were acquired.

Fins were matched within encounters by viewing the negatives on a light table with a 10× magnifying loupe. Fins were matched between encounters using digital copies of the whale images (~530–590 kilobytes, black and white, tif format, generated by a Nikon LS2000 negative scanner), facili-

tated by the fin-matching program Finscan[3] (Araabi et al. 2000). All decisions about matches were made by C.A.O. Uncertain matches were verified by a second individual experienced in photo-identification.

In some analyses, encounters with the poorest photographic coverage were excluded. These were defined as encounters in which the number of photographs taken was smaller than the number of individuals counted as present (group size), or in which it was noted in the field that it was not possible to photograph the entire group. The remaining encounters are designated "coverage > 0". Analyses that excluded encounters based on the poorest coverage likely give a more consistent assessment of individual presence or absence than those in which all encounters were used, but may be biased towards smaller groups, since it was difficult to photograph all individuals in very large groups within the time constraints of the trips. In some analyses, selecting encounters in which the number of photographs taken was at least twice the group size should give an even more consistent and higher quality assessment of individual presence or absence. These encounters are designated "coverage ≥ 2".

We estimated the proportion of the whales observed that were sufficiently well marked to be included in the analyses in two ways. First, an overall proportion was calculated as follows: (number of good-quality fin images ($Q \geq 3$) of well-marked individuals (MP ≥ 3)) / (number of good-quality fin images ($Q \geq 3$) of all individuals). This estimate assumes that, on average, the same numbers of good-quality photographs were taken of well-marked individuals as of poorly marked or unmarked ones. The mark rate was calculated using photographs of encounters with coverage ≥ 2 only, and in which photographic effort was opportunistic for all individuals. A standard error for the overall mark rate was estimated, using the mark rate calculated for each of the three study seasons as separate estimates, as in Gowans et al. (2000).

Additionally, we divided the number of well-marked individuals identified in an encounter by the group size and then averaged the encounter estimates. To minimize uncertainty in the group size, only groups estimated to have 10 or fewer members were included. As with the previous estimate, only encounters with coverage ≥ 2 were included.

Associations

The strength of the behavioural relationships between dyads was represented using two indices of the frequency of co-occurrence: the half-weight association index and the simple ratio association index (Cairns and Schwäger 1987; Ginsberg and Young 1992). However, as the inferences drawn were the same for the two indices, only values of the half-weight association index will be presented. Individuals photographed during the same encounter (group) at least once during a day were considered associated for the day (the sampling period). To illustrate the association patterns of those whales sighted most often, average-linkage cluster analyses (Manly 1994) were constructed using animals sighted on 4 or more days and including only encounters with coverage > 0.

We used permutation tests (Bejder et al. 1998; Whitehead 1999) to test whether the association patterns observed were different from what might be expected at random, given the population size and residency patterns of the population. An observed standard deviation of the pairwise association indices that is significantly larger than those from permuted data sets is taken as evidence that individuals have preferred or avoided companions (Whitehead 1999). Individuals sighted on 3 or more days were included to give a larger sample size than that analyzed in the cluster analysis. All encounters were included, 20 000 permutations were generated for each test, and to ensure that p values were stable, six runs of the permutation test were generated using the simple ratio and half-weight association indices in three runs each.

We used the standardized lagged association rate (SLAR) to model temporal aspects of social structure (Whitehead 1995, 1997). The SLAR is the average probability, given that individuals A and B are associated at time 0, that B will be identified later in a photograph of a randomly chosen group member at a time lag τ when A is also present (Whitehead 1995). The SLAR is estimated by calculating

[1] $\hat{g}(\tau) = \Sigma_A\Sigma_t c(A, t, \tau)/[\Sigma_A\Sigma_t N(A, t){\cdot}N(A, t + \tau)]$

where $c(A, t, \tau)$ is the number of associates that were seen with individual A at both time t and time $t + \tau$, and $N(A, t)$ is the number of associates seen with individual A at time t. The SLAR is compared at all time lags with the null association rate, i.e., the SLAR expected if all individuals are associating at random, given the population size:

[2] $\hat{g}(\tau) = 1/(P - 1)$

where P is the number of well-marked individuals in the analysis. Sampling periods were individual hours and the analysis was restricted to only those encounters with coverage ≥ 2. All individuals photo-identified within an encounter were considered to be associated. Standard errors were estimated by jackknife methods (Efron and Gong 1983). Mathematical models representing simulated social structures (Whitehead 1995) were fit to the SLAR (Table 1). The best fit model was chosen as that which minimized Akaike's (1974) Information Criterion.

The preceding analyses of association patterns were conducted in MATLAB 5.2.1 using SOCPROG statistical modules (Whitehead 1999).

Unit membership

To investigate whether "units" that were stable in the long term existed, we followed a procedure similar to that of Christal et al. (1998). Individuals sighted on at least 4 days, each sighting separated from the preceding one by a gap of at least 30 days, were identified as "key" individuals. According to this rule, key individuals must have been sighted in more than one season (as the maximum length of the study season was 2 months) and were likely to have been seen in all 3 years of the study. Individuals sighted at any time on the same day as the key individual for at least 3 days, each sighting separated from the preceding one by a gap of at least 30 days, were selected as constant compan-

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[3] Finscan was developed at the University of Texas Medical Branch, the Texas A&M Marine Mammal Project, and the Texas A&M Electrical Engineering Department with support from the National Science Foundation, and was provided to the authors by Dr. Gil Hillman.

Table 1. Fit of social-system models to the standardized lagged association rate (SLAR).

Description of model	Model formula	Maximum-likelihood values for parameters	Jackknifed standard errors for parameters	No. of parameters	AIC[a]
Constant companions (CC)	$g(\tau) = a_1$	$a_1 = 0.0504$	0.0187	1	4392
Casual acquaintances (CA)	$g(\tau) = a_2 e^{(-a_1\tau)}$	$a_1 = 5.14 \times 10^{-5}$	5.12×10^{-5}	2	4363
		$a_2 = 0.0599$	0.0281		
Rapid disassociates + CC	$g(\tau) = a_2 + (1 - a_2)e^{(-a_1\tau)}$	$a_1 = 2.91$	0.800	2	4360
		$a_2 = 0.0459$	0.0194		
CA + CC	$g(\tau) = a_2 + a_3 e^{(-a_1\tau)}$	$a_1 = 0.0476$	0.106	3	**4311**
		$a_2 = 0.0414$	0.0196		
		$a_3 = 0.0664$	0.0326		
Two levels of CAs	$g(\tau) = a_3 e^{(-a_1\tau)} + a_4 e^{(-a_2\tau)}$	$a_1 = 0.00212$	0.149	4	4408
		$a_2 = -6.59 \times 10^{-5}$	1.47×10^{-4}		
		$a_3 = 0.0784$	1.10		
		$a_4 = 0.0178$	1.05		

[a]The value in boldface type is for the best fit model, according to Akaike's Information Criterion (AIC).

ions of the key individual. A unit was defined as a key individual and all of its constant companions (if a unit consisted of more than two individuals, all individuals had to be constant companions of at least two of the others).

As stated above, unit membership was defined through sightings of members *on the same day*. However, individuals were often sighted during encounters with individuals both inside and outside their own unit. We tested the null hypothesis that individuals showed no short-term preference for members of their own unit over other individuals against the alternative hypothesis that individuals associated preferentially with members of their own unit. We used a sign test, considering each unit as a distinct case (as in Christal and Whitehead 2001). For each unit, encounters were selected in which (*i*) coverage > 0, (*ii*) photographs were taken opportunistically, with no cease in photographic effort, (*iii*) at least two members of the same unit were photo-identified, and (*iv*) at least one well-marked animal outside the unit was photo-identified. For this analysis, individuals were considered to be associated if they were photographed *within 2 min of each other* at least once during the encounter. Hence, pairs of individuals were either associated (1) or not associated (0) for each encounter. For each unit, the ratio of the number of observed pairwise associations between members of the same unit (observed associations within the unit; OAU) to the number of observed pairwise associations between a unit member and an individual not in that unit (observed associations with animals not in the unit; OANU) was calculated, summing each quantity over all suitable encounters (*i*):

[3]   observed ratio $= \sum_i OAU_i / \sum_i OANU_i$

This ratio was compared with the ratio of the potential number of within-unit associations (potential associations within the unit; PAU) to the potential number of associations between a unit member and an individual not in that unit (potential associations with animals not in the unit; PANU), each summed over all suitable encounters (*i*):

[4]   expected ratio $= \sum_i PAU_i / \sum_i PANU_i =$
$1/2 \cdot \{\sum_i [(MU_i)(MU_i - 1)]\} / \sum_i [(MU_i)(MNU_i)]$

where MU_i is the number of members of the unit and MNU_i is the number of well-marked animals not in the unit that were present during suitable encounter *i*.

The sign test considered only whether the observed ratio was larger (+) or smaller (–) than the expected ratio for each unit. To calculate the statistical significance, the number of + signs was assumed to be binomially distributed, under the null hypothesis that there was no preference for individuals inside versus outside the unit (i.e., the probability of obtaining a + for any unit is 0.5). This is a conservative test that does not require independence of the units.

Results

Group sizes

In total, 327 trips were made on 141 different days. Long-finned pilot whales were encountered on 253 occasions, totaling 154.6 observation hours. Group-size estimates averaged 20 (SD = 17, range = 2–135, median = 15, $n = 249$ encounters for which group size was estimated; Fig. 1). The proportion of groups observed to contain calves was 78.3% (198/253 groups). Groups containing calves ranged in size from 5 to 135 (mean = 23, median = 18, SD = 18, $n = 197$ encounters for which group size was estimated).

Marked individuals

Overall, an estimated percentage of 33.6% (SE = 4.1%) of individuals carried 3 or more MP on the dorsal fin. When calculated by encounter, for groups of 10 or fewer individuals, the mean of the estimates was 35.2% (SE = 3.6%), although the mark rate ranged from 0% to 67% ($n = 27$, median = 30%). In all, 322 individuals were distinguished by 3 or more MP. Of these, 41.0% (132) were sighted on more than 1 day. The maximum number of days on which an individual was sighted was 15 (ID No. 302). The majority of individuals (72.4%) were sighted in only one field season, 19.3% in two seasons, and 8.4% in all three seasons. New individuals were continually being discovered throughout the study. There does not appear to be a resident population that uses the study area exclusively, nor is it likely that all well-marked individuals who pass through the area have been captured photographically to date (Ottensmeyer 2001).

Fig. 1. Observed group sizes of long-finned pilot whales (*Globicephala melas*), July–August 1998–2000. Bins for group sizes include the value of the label (e.g., 1–5, 6–10, etc.).
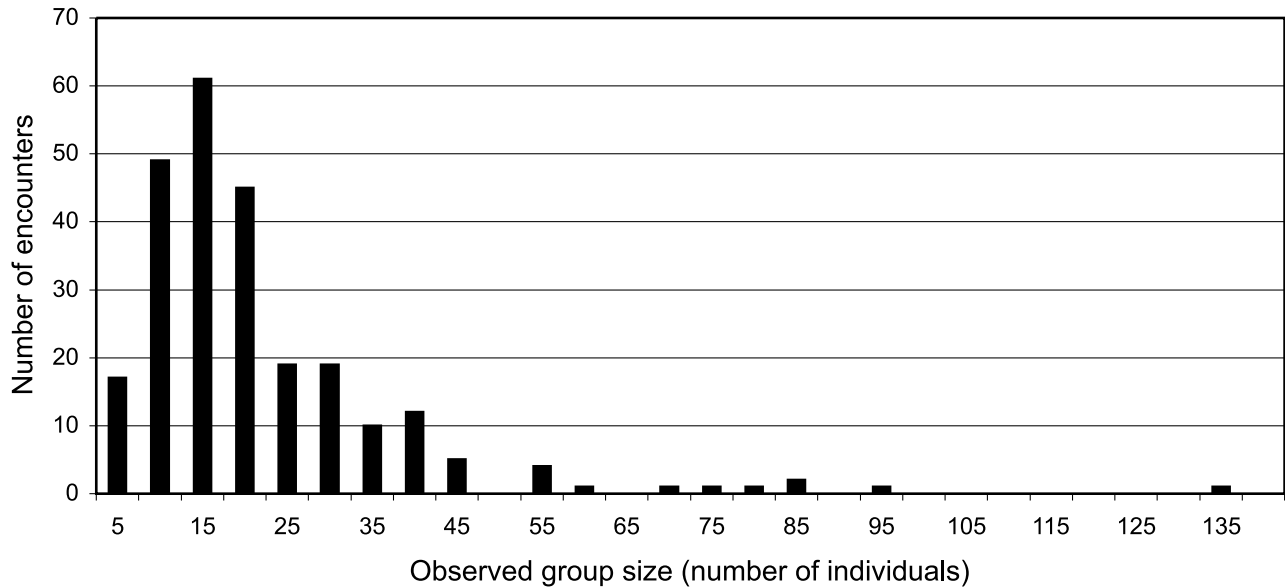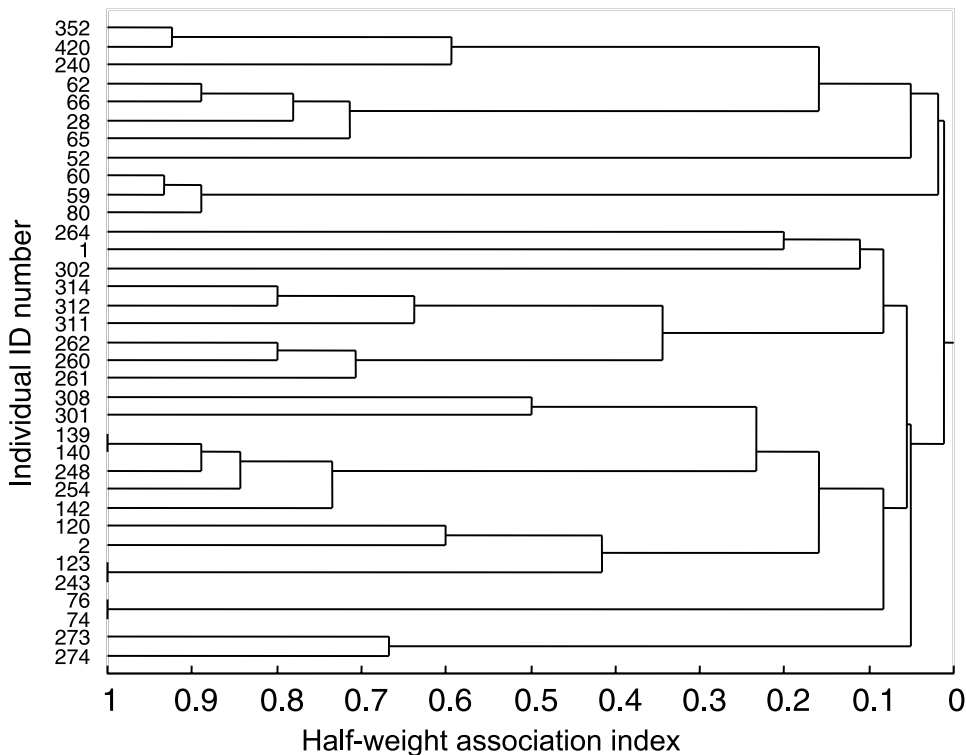

Fig. 2. Average-linkage cluster analyses of associations between well-marked individuals seen on ≥4 days, using only encounters with coverage > 0.
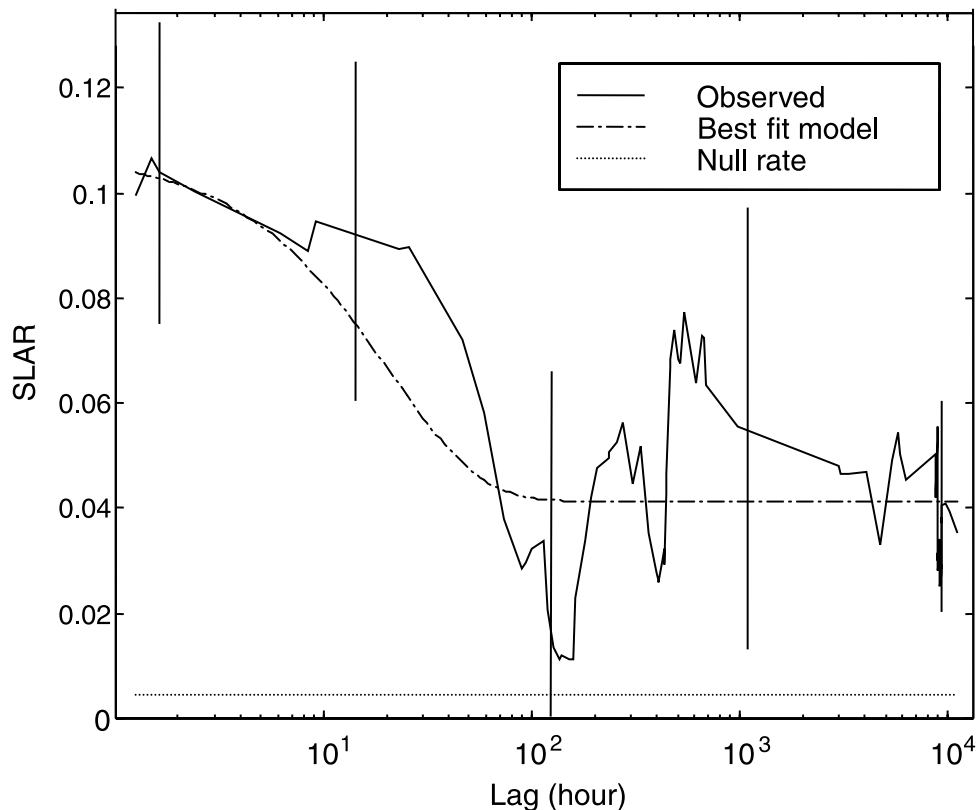

Associations of individuals

The cluster diagram (Fig. 2) shows that most individuals who had been sighted repeatedly (on 4 or more days) were frequently sighted with particular companions, some pairs never being sighted apart (e.g., ID Nos. 74 and 76; 123 and 243; 139 and 140). Of the 35 individuals sighted on ≥4 days, 33 (92%) were linked to another individual or cluster of individuals at a half-weight index value of ≥0.5. Because of incomplete photographic coverage during encounters, it is difficult to distinguish the absence of an individual from a failure to photographically capture that individual in a given encounter. Hence, the estimates of association reported here are likely negatively biased.

The standard deviation of the observed pairwise association indices was significantly higher than those from permuted data sets (simple ratio index: $p < 0.0003$; half-weight

Fig. 3. Standardized lagged association rate (SLAR) for all well-marked individuals sighted in encounters with coverage ≥ 2. Approximate error bars were generated by jackknife techniques (±1 standard error). The moving average over 1000 associations is shown. The maximum-likelihood best fit model represents associations with casual acquaintances and constant companions. The null association rate represents the theoretical SLAR if individuals associated randomly.

index: $p < 0.0005$). Thus, we could reject the null hypothesis that individuals associated randomly.

Over short time scales, the SLAR (Fig. 3) fell (to approximately 1 week), but appeared to stabilize above the rate expected if individuals were associating at random (the null association rate) between the scales of 1 and 14 months. Owing to the restrictions of encounter quality (coverage ≥ 2), only one encounter from 1998 was included. Hence, it was not possible and not appropriate to estimate the SLAR at time lags beyond 14 months. The coverage restriction limited this analysis to sightings of 221 well-marked individuals. Since the estimated SLAR appears to stabilize above the null rate at longer time lags, long-term relationships appear to exist.

The SLAR drops to quite a low level at time lags of approximately 5–7 days (~120 to ~160 h). In fact, the error bar estimated at a time lag of approximately 120 h (5 days) crosses the null association rate. However, close inspection of the resightings of individuals at time lags of 5–7 days revealed that 10 of the 20 time spans of those lags involved encounter 2110, by far the largest of the encounters included in the SLAR (group size was 75, all others were <45). Since previous and subsequent resightings of the individuals in encounter 2110, in more typical group sizes, would form a small proportion of this large group, just by virtue of the difference in group size, the low SLAR at these time lags appears to be largely an artifact of this single large encounter.

Hence, the overall persistence of relationships at longer time lags appears reasonable.

The social-system model that fit the curve best describes two levels of associates: casual (short-term) acquaintances and constant (long-term, consistent) companions (Table 1). The model curve fell until lags lasted approximately 100 h (~4 days). This suggests that typically, individuals remained with a set of associates over periods of hours to days (a mix of casual acquaintances and constant companions), but by the end of a few days, they had largely disassociated from all individuals except a smaller number of constant companions. This subset was resighted with the individual for periods up to at least 14 months. Information on units presented below suggests that these relationships actually persist for longer than can be predicted by the SLAR. This analysis cannot express how much time passed before a set of constant companions met with another set of individuals, but suggests that their stay with the new associates was brief as well. The error bars on the SLAR are quite large. Hence, it should be noted that these are general trends and cannot predict the association pattern of all groups at all times.

At very short time lags (i.e., seconds), the probability that an individual is still with the associates it had at time zero is theoretically 1 (100%). Given the standardization of the lagged association rate, the level at which the observed SLAR curve is expected to cross the y axis represents the reciprocal of the number of short-term companions of a ran-

Fig. 4. Sightings of all key individuals and their constant companions. Symbols denote photographic capture at least once on a particular day; ●, key individuals in the unit; ■, non-key individuals in the unit; *, key individuals who are constant companions of only one unit member; ×, non-key individuals who are constant companions of only one unit member. ID numbers in boldface type denote probable mature males, ID numbers in italics denote probable mature individuals (possibly females), and underlined ID numbers denote likely mothers. Other individuals are as yet unclassed. Ticks along the *x* axis indicate individual days in each field season. Note that according to the rules of unit membership, unit C includes only ID Nos. 243, 123, and 120.

Number of days in field season
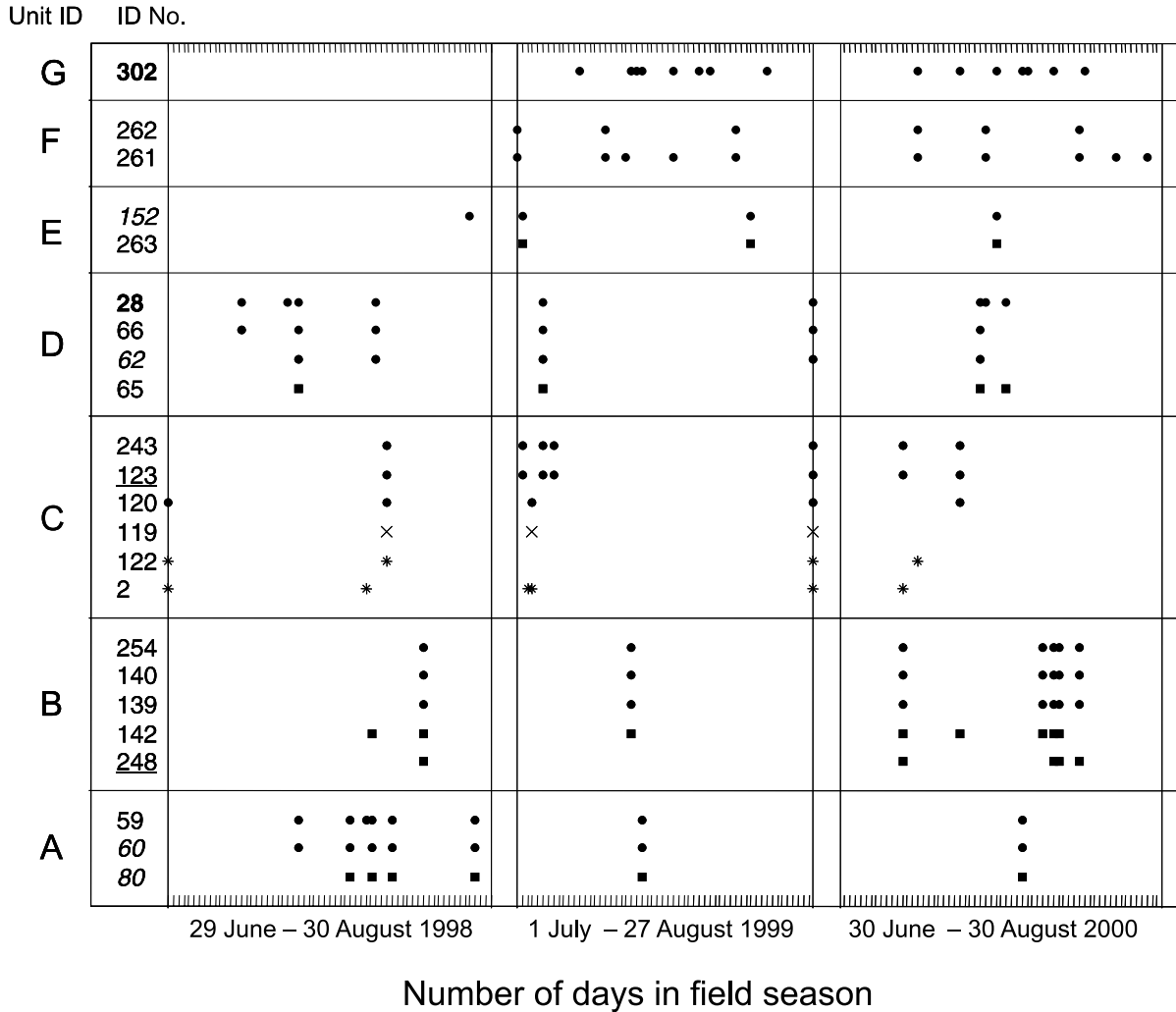
domly chosen individual (probability 1 divided by the mean number of other individuals present; Whitehead 1995). The value of the best fit curve when τ was set to 0 was 0.108. This suggests that the average number of well-marked whales remaining with an individual from one second to the next is nine. This provides two alternative estimates of the mean observed group size (scaled by the mark rate 0.336 or 0.352, plus 1 for the individual): 29 and 27. It is reasonable that these estimates are larger than the mean observed group size (20), given the difficulties in making accurate visual counts of cetaceans. Counts, particularly when groups are large, are generally underestimates.

The level at which a lagged association rate stabilizes (if it does so) relative to its maximum may be interpreted as the proportion of the total number of whales present in the short term that actually remain with a given individual (Whitehead 1995). The model that best fits the observed SLAR stabilizes at a value of 0.041, or 38% of the maximum SLAR. This suggests that some 40% of the individuals sighted at a given time with a given individual will be its long-term companions. This corresponds to ~3.6 well-marked constant companions for that individual, which suggests that a stable set of individuals (the number of constant companions, scaled by the mark rates, plus 1) typically consists of 11 or 12 individuals. There is additional variability in these estimates from both the mark rate and the fit of the SLAR model. Hence, these estimates should be viewed as centres of a distribution rather than constant figures.

Unit membership

The sighting record of all key individuals and all of their constant companions is plotted in Fig. 4. Sets of individuals exist whose members were, with few exceptions, sighted exclusively on the same days as the other members. Seven units were delineated by the rules set out in the methods. Further investigation of the timing of the photographs of unit

Table 2. Analysis of short-term association patterns by unit members.

| Unit ID | No. of suitable encounters | Ratio of associations within unit to associations with animals outside unit | | |
		Observed	Expected	Percent difference
A	3	0.40	0.33	+21
B	3	0.65	0.33	+97
C	5	0.19	0.14	+36
D	2	0.70	0.31	+126
E	1	0.25	0.06	+317
F	6	0.28	0.20	+40

Note: See the text for details of calculations.

members on those days revealed that on almost all occasions, key individuals were photographed within 45 min of all of their constant companions, and frequently within 5 min (Ottensmeyer 2001). ID No. 302 is included as a unit (G). Given the low mark rate of the population, it is possible that ID No. 302 had constant companions who bear fewer than the 3 MP required for inclusion in the analysis. Preliminary matching of individuals with 1 or 2 MP suggests that ID No. 302 does indeed have constant companions.

The mean unit size is three well-marked individuals ($n = 7$, SD = 1.3, median = 3). When scaled by the mark-rate estimates (0.336 and 0.352), the mean unit size becomes eight (95% confidence intervals of the mean: (8.0–8.9), (7.7–8.6)). These estimates of the mean size of a stable set of long-term companions are likely negatively biased. There are likely other well-marked individuals who are constant companions of the units presented here who have been disqualified as a result of the strict nature of the definition and the fact that in many cases photographic coverage was not complete.

Using the criterion of being photographed *within 2 min* as a measure of association between two individuals, individuals associated with others both within and outside their unit during an encounter. However, given the number of well-marked individuals in each encounter, the preference of individuals for members of their unit was significant ($p = 0.0313$; see Table 2), despite the low power of the sign test to reject the null hypothesis (sample size = 6 units). The amount by which the observed ratio was greater than the expected ratio varied from unit to unit. However, in all cases, the direction of the difference is consistent. The cases (units) should be nearly independent, since only 2 of the 18 encounters deemed suitable for this analysis were considered in the calculations twice (in encounter 1005, two members of unit C and both members of unit E were among the 11 well-marked individuals present; in encounter 2028, all five members of unit B and two members of unit C were among the 10 well-marked individuals present). No encounters from the first season (with only a single observer) satisfied all of the selection criteria for this sign test. Hence, the ability to track associates based on a definition of a 2-min association should be consistent through the encounters used in this analysis. Despite the small sample size, this evidence suggests that in general, members of the same unit prefer to associate in very close temporal and presumably spatial proximity while the unit is aggregated with other whales.

Discussion

Across a maximum span of 26 months, we observed 253 groups of long-finned pilot whales, from which 322 individuals were identified. Groups observed in the study area appeared to be short-term amalgams of long-term subsets of individuals, here termed units. Even in short-term encounters, individuals showed some preference for members of their own unit over other individuals.

Mark rate

The mark rates estimated in this study show variability among groups, at least among small encounters, and are meant as guidelines. If there was heterogeneity of photographic-capture probability among individuals that was linked to their probability of being well marked, the mark-rate estimates presented here may be biased in unclear ways. The second method of mark-rate estimation (for small encounters) does not assume that similar numbers of photographs were taken of well-marked as of poorly marked individuals, and, if we assume close to complete photographic coverage, may be less affected by this heterogeneity. The similarity of mark-rate estimates obtained using the two methods lends support to their being reasonable average estimates. We know of no other mark rates estimated for long-finned pilot whales. However, estimates for short-finned pilot whales off Santa Catalina Island, California (33.5%–35.0%; Shane and McSweeney 1990), are remarkably similar to those found here. The same authors found a mark rate of 45.3% amongst short-finned pilot whales off Kona, Hawai'i, although they could not determine the reason for the difference. Miyashita et al. (1990), studying the northern form of short-finned pilot whales off Japan, found identifying characters in all photographs (including notches, the saddle pattern behind the dorsal fin, and surface scars), implying a mark rate of 100%. Heimlich-Boran (1993) calculated a mark rate of ~85% for short-finned pilot whales off the Canary Islands, using notches in the fin and surface characteristics such as scars. Since surface scars, in particular, likely do not persist over years, they were not utilized as identifying features in the current study. Their inclusion in the mark rates from Japan and the Canary Islands renders these estimates not strictly comparable to the estimates presented here.

Since surface marks are acquired over time, older individuals are more likely to be considered "well-marked" than younger individuals. No calves were individually identifiable, and it is likely that juveniles are underrepresented as well. It is also likely that males acquire more marks than females of a similar age and may be overrepresented. Since there is no reliable method to determine sex or age from regular surfacings at sea, it is not possible to determine whether the association pattern described here is representative of all segments of the population. Groups appeared to be of mixed sizes and sexes (Ottensmeyer 2001), yet the size–sex classifications were difficult to corroborate, and this observation does not illuminate the longevity of associations. Perhaps in the future, the use of the saddle pattern will allow a greater proportion of the population to be distinguished. This, combined with genetic sampling of known individuals, will greatly increase the resolution of association patterns and

confirm whether the extrapolations in group sizes made here are appropriate.

Unit sizes

The average size of the defined units (about 8 individuals) is likely an underestimate, since we chose a deliberately restrictive unit definition. That the standardized lagged association rate (which has no such deliberate bias) generated a higher estimate (11 or 12 individuals) is expected. Heimlich-Boran (1993) delineated "pods" of short-finned pilot whales by means of a cluster diagram to link individuals with a high frequency of co-occurrence. Clusters that he interpreted as meaningful pods are likely the closest entity that might be equivalent to a unit in this study, since they were defined by the repeated, common presence of individuals in an observed group. The pod sizes he reported ranged between 3 and 33, the majority of pods being composed of 9 or fewer identified individuals (Heimlich-Boran 1993). Given his calculated mark rate of ~85%, the majority of pods would have been composed of 11 or fewer individuals. This size of pods of short-finned pilot whales is similar to that found for units of long-finned pilot whales in the present study.

What is a unit?

Among cetaceans, some general patterns of social structure have been found, three of which include long-term relationships. In sperm whales, *Physeter macrocephalus*, females maintain multiyear associations with other females, their daughters, and immature sons (Christal and Whitehead 2001) as well as unrelated individuals (Mesnick 2001), while mature males appear to rove singly between sets of females, or form temporary multimale groups (Whitehead and Weilgart 2000). In contrast, male bottlenose dolphins, *Tursiops aduncus*, in Shark Bay, Australia, maintain "alliances" with other males for many years (Connor et al. 1992), while females in the same area have a looser network of primarily female associates (Smolker et al. 1992). *Resident* killer whales off northwestern North America are rare in that male and female offspring maintain potentially lifelong associations with their mothers. *Resident* killer whale pods typically encompass 1–3 related matrilineal units, each consisting of roughly two to nine individuals (Bigg et al. 1990; Ford et al. 2000). Given the lack of information on the sex of individuals in the current study, and since we have likely been able to generalize about only the most obvious relationships, it is not yet possible, using this study alone, to distinguish between the different social scenarios. Both likely mature males and likely mature females appear to be unit members (Fig. 4). However, this type of evidence is sparse.

To determine what units represent biologically, the best clues likely come from extensive genetic studies conducted on the long-finned pilot whales hunted in the Faroese drive fishery (Amos et al. 1991*a*, 1991*b*, 1993*a*, 1993*b*; Fullard 2000). The culmination of these studies is a series of pedigree diagrams in which mother–calf relationships are linked (Fullard 2000). "Strict matrilines" (called family groups by Fullard 2000) within each grind were identified, consisting of an average of 4.5 individuals (range 2–27, found from 11 grinds), including between two and four generations of whales. Both adult male and adult females were present with their mothers, and mating within the grind is rare or nonexistent. Although it is not possible to track directly the persistence of relationships between whales that have been hunted, the high proportion of related individuals of varying ages found within grinds is strong evidence that in general, maternally related individuals spend a substantial portion of their lives together. This is the best available evidence that natal group philopatry occurs in long-finned pilot whales. The mean *strict matriline* size is smaller than the estimated size of the long-term units identified in this study. However, Fullard (2000) suggested that the missing links of recent ancestors would likely have joined strict matrilines already identified within each grind. This is a very plausible scenario and if it is true, the set of individuals found together who represent an "extended matriline", i.e, a set of individuals related directly to each other through parent–offspring relationships and recent ancestors, would increase.

We propose that units of long-finned pilot whales found off Nova Scotia typically represent extended matrilines. If this is true, it would seem that Nova Scotian matrilineal units (related individuals who maintain long-term behavioural relationships) are generally smaller than most of the grinds studied in the Faroe Islands.

Relationships between units

The behavioural work presented here suggests that the groups of long-finned pilot whales typically sighted off Nova Scotia are ephemeral structures, and that constituent units disassociate after a few hours or days. Unfortunately, since sightings of individuals on consecutive days are rare, it is difficult to track the timing of that dissociation directly, although the SLAR gives average estimates of this process. The work on long-finned pilot whales hunted in the Faroe Islands has been interpreted as suggesting that entire grinds (often large groups of 80–100 or more) represented long-term entities, and that all herded individuals were related (e.g., Amos et al. 1993*b*; Fullard 2000).

It would not be surprising if social structure varied within a species. Unfortunately, since the methodologies used at the two study sites are so different, it is difficult to discern whether the apparent difference in long-term group size is real or a product of the biases of each method. Recent analysis of the structure of the long-finned pilot whale population in the North Atlantic Ocean has shown some genetic differences between samples collected in Cape Cod, the Faroe Islands, and the U.K., and especially between west Greenland and the other sites (Fullard et al. 2000). Rather than being geographically based, the differences found were linked to differences in sea-surface temperature between areas. Given the substructure found, it may be that genetic differences exist between the pilot whales sighted off Nova Scotia and those hunted off the Faroe Islands. However, without a genetic comparison, this is difficult to determine. Indeed, the maps provided by Fullard et al. (2000) indicate that sea-surface temperatures may be even more similar between Nova Scotia and the Faroe Islands than between Cape Cod and the Faroe Islands. Hence, it is unclear whether there is any genetic reason to suspect that social structures in the area in the current study and the Faroe Islands are similar or different.

A morphometric comparison of pilot whales taken by the former drive fishery in Newfoundland and those taken in the Faroe Islands revealed differences in body proportions between individuals at those sites, which may indicate geographic isolation (Bloch and Lastein 1993). However, given sea-surface temperatures (Fullard et al. 2000), the Newfoundland samples may have more in common with the west Greenland samples than with those from Nova Scotia. A recent investigation of the correlates of group size in delphinids showed that pilot whales tended to form smaller groups when they fed more on mesopelagic fish and less on cephalopods (Gygax 2002). However, studies of stomach contents from individuals in both the Faroe Islands and off the Atlantic coast of North America show that squid form, by far, most of the diet in both locations (Desportes and Mouritsen 1993; Gannon et al. 1997a, 1997b).

Is it possible that the social structures of long-finned pilot whales in both locations are more similar than they appear? Further collection of behavioural data will be necessary to confirm the generality of the observations presented here. Given the difficulty of photographically capturing entire groups, especially when they are large, and the potential for variability in the mark rate, refinement of the typical unit size would be desirable. The data collected from the drive fishery may be biased by the cross-sectional nature of the data collection and our ability to determine relatedness of extended relatives. Perhaps it is useful to review the evidence that the grind is a behavioural unit.

Fullard (2000) presented the most recent data, with the highest genetic resolution of relationships between individuals found in grinds. Her evaluation of the relatedness of "old" females (aged ≥25 years) within grinds showed a marginal degree of relatedness above that of "old" females in different grinds (Fullard 2000). This could suggest that the strict matrilines already identified within grinds are themselves related. However, when only those grinds in which the best resolution of relatedness is available are included in the analysis, there was no difference in relatedness between "old" females within a grind and randomly chosen "old" females outside the grind. While it is likely that some "strict" matrilines within grinds are related to each other, we believe that it is not clear that all would be.

Amos (1993; Amos et al. 1993b) found a positive correlation between age and a grind-specific genotype frequency index for two grinds (containing 90 and 103 individuals). That the alleles of older individuals were common in the grind implied relatedness within the grind. Amos (1993) simulated the genotypes of pilot whales in grinds, varying grind size, reproductive rate, the number of alleles at a single locus, and whether the grind was founded by a single individual or a set of closely related individuals. The observed age–genotype frequency index correlations were closer to the mean correlations of the simulations with a single founder than to the mean correlations of simulations with multiple founders. This too has been interpreted to mean that entire grinds on the order of 100 whales were single extended matrilines. However, the observed correlations fell within the 95% confidence intervals of all the simulated grinds, and the highest correlations from the simulations with multiple founders were well above the observed values. Indeed, as Fullard (2000) pointed out, the two grinds sampled by Amos (1993) had unusually large strict matrilines (identified by pedigree analysis as consisting of close to 30 individuals). In addition, the "old" females within these two grinds were not related to any greater degree than they were to "old" females outside their grind (Fullard 2000). It may be that the large matrilines within the grinds were responsible for the high correlations observed, and that entire grinds are not always single or even extended matrilines.

Other analyses showed significant differences between some grinds in protein polymorphisms (Andersen 1988, 1993), tissue concentrations of organochlorines (Aguilar et al. 1993) and trace metals (Caurant et al. 1993, 1994), and communities of parasitic intestinal helminths (Balbuena and Raga 1994). These lines of evidence support the idea of the grind as a behavioural unit. However, because in most of these studies, the vast majority of grinds were only partially sampled, it is difficult to discern the extent to which the calculated differences between grinds could be created when a high proportion of a grind's samples come from a single extended matriline within the grind. In addition, significant differences between some grinds do not necessarily imply the similarity within grinds that one would expect if all individuals really were long-term associates.

We find that the data currently available cannot, as yet, resolve the difference between the social structure of long-finned pilot whales inferred in this study through behavioural means and that found through the drive fishery in the Faroe Islands. Variation in social structure between these two geographic areas is entirely possible, but is not clear. To refine our view of pilot whale social structure, further research is necessary, possibly in the form of longer behavioural follows of particular individuals (on the order of days to weeks), extension of the longitudinal study of individuals, and genetic sampling of behaviourally studied populations.

Acknowledgments

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