Temporal and geographic variation in the social structure of female sperm whales

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Received February 25, 1992
Accepted May 15, 1992


The social structure of female sperm whales (Physeter macrocephalus) was examined from data collected during studies of identified individuals off the Galápagos Islands in 1985, 1987, and 1989, off the Seychelles Islands in 1990, and off mainland Ecuador in 1991. Three levels of social organization were examined in the Galápagos Islands studies. “Units,” permanent associations between individuals, showed no significant deviation from a mean size of 13 individuals. “Groups,” temporary associations between units lasting a few days, had a mean size of 24 individuals. Group size was lower in 1987 (an “El Niño” year) than in 1985 or 1989, but this difference was not statistically significant. “Aggregations” of groups in the same general area lasting periods of hours were significantly larger in 1985 (mean of 77 individuals) than in 1987 (mean of 47 individuals). There are significant differences between areas in aggregation sizes but not in group sizes. Groups appear to aggregate frequently off the Galápagos Islands, occasionally off mainland Ecuador, and very rarely off the Seychelles Islands. These temporal and geographic differences in sizes of groups and aggregations in sperm whales are probably caused by variations in the distribution and abundance of their food, but responses to recent exploitation may also be a factor.


[Traduit par la rédaction]

Introduction

Female sperm whales (Physeter macrocephalus) are clearly social. They are often seen in interactive groups at the surface (Caldwell et al. 1966; Whitehead and Weilgart 1991; Kahn 1991), and associations between individual females can persist over periods of years (Ohsumi 1971; Gordon 1987; Whitehead et al. 1991).

Using individual photographic identifications and other data collected between 1985 and 1989 off the Galápagos Islands, we have examined the social organization of the female sperm whales and their accompanying offspring in those waters in some detail (Whitehead and Weilgart 1990; Whitehead et al. 1991). From that research, we recognize three hierarchical levels of association among female and immature sperm whales:

Units: These consist of animals who are constant companions over periods of several years, and perhaps throughout their lives (Whitehead et al. 1991). Animals within units may be related (Arnbom and Whitehead 1989). Off the Galápagos Islands, individuals were members of units containing a mean of approximately 13 animals, although there seemed to be considerable variation (Whitehead et al. 1991).

Groups: A few units may associate in an integrated fashion for a period of several days, appearing to feed and rest together. Off the Galápagos Islands, individual whales were members of groups containing a mean of about 23 animals, or roughly two units, and having a half-life, before splitting, of about 6.5 days (Whitehead et al. 1991). A group of whales travelling together sometimes contained just one unit.

Aggregations: Groups were often found in the same general area. These temporary aggregations varied considerably in the number of whales present (they might consist of just one group) and in their compactness. Whitehead and Weilgart (1990) derived an acoustic measure of aggregation size in which the rate at which the distinctive clicks of the sperm whale were heard through a hydrophone was related to the number of whales within acoustic range (approximately 5 km with our acoustic equipment and techniques of measuring click rates). Off the Galápagos Islands the mean size of tracked aggregations (as defined by the number of whales within range of our hydrophone) was 43 whales, or roughly two groups, although aggregations often consisted of just one group (Whitehead and Weilgart 1990).

The plasticity of animal social organizations has attracted considerable interest in recent years (e.g., Magurran and Seghers 1990). Animal social organizations are generally seen as the result of interactions between proximate ecological forces and social traditions or “culture” (Wrangham and Rubenstein 1986). The manner in which a social organization
varies temporally and geographically may indicate the significance of different environmental factors and, possibly, how their effects are mediated by culture.

Our analyses of the units, groups, and aggregations of the Galápagos sperm whales suggested some year-to-year variation in the sizes of these structures off the Galápagos Islands (Whitehead and Weilgart 1990; Whitehead et al. 1991). Here we look in more detail at this variation, as well as at differences in social organization between different geographical regions.

**Methods**

**Field studies**

Field studies were carried out off the Galápagos Islands (2°S–1°N, 89°–93°W) in February–April 1985, January–June 1987, May 1988, and January–May 1989; off the Seychelles and Amirantes islands (2°–8°S, 51°–57°E) in February–May 1990; and off mainland Ecuador (3°S–2°N, 80°–83°W) in January–March 1991. We used 10- to 18-m auxiliary sailing vessels that spent 10–25 days at sea between port calls. Whales were located and tracked both acoustically, using a directional hydrophone, and visually for continuous periods of days (Whitehead and Gordon 1986).

During daylight, the flukes (tails) of the diving whales were photographed using 35-mm cameras equipped with 300-mm lenses. These photographs allowed us to identify individuals (Arn bom 1987). Standard 5-min recordings of the sounds of the whales were made through Benthos AQ17 omnidirectional hydrophones, Barcus–Berry ‘Standard’ or Ithaco 453 preamplifiers, and Uher 4000, Nagra IV-SJ, Sony TC770, or Sony WM-D6C Professional Walkman tape recorders.

While whales were being followed, these recordings were made each hour, on the hour, during the 1985 and 1987 Galápagos studies. Off mainland Ecuador in 1991 recordings were made each hour on the hour for 4 h, followed by 11 h without recording. During the 1990 Seychelles study, recordings were made on a more irregular schedule during encounters and while tracking sperm whales.

**Analysis**

The mean time spent searching for whales was used as a rough indicator of the abundance of aggregations of whales (Table 1). Standard errors for mean search times were estimated using negative exponential distribution theory.

We used the mean click rate as a measure of the mean aggregation size for the different studies. Click rates were calculated by digitizing a 16- or 8-s section of each recording session and then using a computer routine described by Whitehead and Weilgart (1990) to count the number of clicks in the section and calculate the click rate. We converted click rates into estimates of the mean number of animals within range of the hydrophone, the aggregation size, using the overall mean individual click rate (1.22 clicks/s) calculated by Whitehead and Weilgart (1990). For the Seychelles whales, we adjusted this to account for the longer interval between consecutive clicks of the same individual, a median of 0.75 s (Kahn 1991) compared with 0.50 s for the Galápagos whales (Whitehead and Weilgart 1990). The overall mean individual click rate for the Seychelles whales was thus 0.82 clicks/s.

As click rates show considerable autocorrelation at lags of up to 13 h (Whitehead and Weilgart 1990), means and standard errors of aggregation sizes off the Galápagos Islands were estimated from the click rates of recordings made at 07:00 (an hour of the day with a mean click rate similar to the overall mean). There were 20 recordings made at 07:00 in 1985 and 35 in 1987. Tests for significant differences between click rates in 1985 and 1987 also used this reduced data set. For the Seychelles and mainland Ecuador studies, only click rates calculated from recordings 14 h or more apart were used in estimating means and standard errors (39 recordings for the Seychelles Islands and 21 for mainland Ecuador).

To make aggregation sizes comparable with group and unit sizes, the mean aggregation size per individual whale (i.e., the mean number of whales present in an aggregation with a particular whale) was calculated from the unautocorrelated measured aggregation sizes, $A(i)$, by

$$ \frac{\sum A(i)^2}{\sum A(i)} $$

The social bonds between individuals were examined using the individual identification photographs. These were processed as described by Arn bom (1987) and Whitehead et al. (1991). Photographs of insufficient quality for individuals to be identified with certainty, and photographs of mature males, who sometimes accompany the groups of females, were not used in the analysis.

Data are insufficient for it to be profitable to fit the full model of social organization used by Whitehead et al. (1991) to the identifications from different years of the Galápagos study or to the data from the Seychelles or mainland Ecuador studies. However, a modification of that technique allowed mean group and unit sizes to be estimated for some of these studies. By “group size” and “unit size” we mean the number of companions an individual has at any time that are in the same group or unit. These will tend to be larger than the mean sizes of groups or units as they are encountered by observers (e.g., Underwood 1981).

As in Whitehead et al. (1991), we considered two whales to be known associates at a particular time if they were photographed within 2 h of one another. To estimate the sizes of the short-term groupings, we examined associations over periods of a few days or less. For each day of each study the first 10 identified individuals that were also seen on another day were considered “key” whales. This procedure largely removes any bias caused by oversampling large and thus perhaps less stable, groups. If animals are found in groups of size $M+1$, then the probability that a particular identified associate of key whale X is whale Y, given that X and Y are members of the same group at that time, is $1/M$. Then, if key whale X has $N(X,t)$ identified companions at time $t$, and $N(X,t+d)$ at time $t+d$, and if there is no change in group composition between these times, the expected number of repeat companions of X between the two occasions is approximately $N(X,t) \cdot N(X,t+d)/M$. So, as in eq. 1 of Whitehead et al. (1991), the expected number of identified associations repeated $d$ time units apart, where groups retain their membership over $d$ time units, is

$$ C(d) = \frac{\sum N(X,t) \cdot N(X,t+d)}{2 \cdot M} = \frac{S(d)}{M} $$

where $S(d) = \sum N(X,t) \cdot N(X,t+d)/2$. If associations were independent, then $C(d)$ would be binomially distributed. They are clearly not independent (as repeat associations between A and B and A and C over a particular pair of days would make a repeat association between B and C more likely). However, we might reasonably expect the variance of $C(d)$ to be approximately proportional to $S(d)$. Assuming this, and also that the data for different time intervals $d$ are approximately independent (see Whitehead et al. 1991), we estimated $M+1$ and its standard error from eq. 1, using the SYSTAT nonlinear estimation module (Wilkinson 1987). Off the Galápagos Islands, the mean half-life for groups was estimated to be 6.5 days (Whitehead et al. 1991). Therefore, only time periods during which it was likely that groups retained their membership ($d = 2$ days, 1 day, and 4–13 h) were used to estimate $M+1$. Differences between the estimated group sizes from different data sets were tested using Kruksal–Wallis nonparametric analysis of variance on estimates of $M$ calculated for each of the three time intervals separately.

Over periods much greater than 6.5 days, so that all temporary groups would have broken up but individuals would still be associating with members of their permanent units, the expected number of repeat companions of key whale X between $t$ and $t+d$ is approxi-
(N(X,t) - n/M) - N(X,t + d)/M, where n + 1 is the unit size, as n/M is the probability that the photographed whale is a member of X's permanent unit. Then, over these long time intervals

\[ C(d) = \frac{S(d) \cdot n}{M^2} \]

We used this equation, and the previous estimate of \( M \) (from eq. 1), to estimate \( n + 1 \), the unit size, by means of nonlinear estimation as before, but this time with \( d = 21-40, 41-80, \) and \( 81-1500 \) days. The output standard error for \( n + 1 \) was adjusted to incorporate uncertainty associated with the estimate of \( M \).

The estimates of mean group size (22.1 animals) and mean unit size (13.6 animals) produced by these techniques for the whole Galápagos data set are very similar to those obtained by Whitehead et al. (1991) through the fitting of a more comprehensive model of social organization to the identification data (group size = 23.0 animals, unit size = 13.0 animals).

### Results

#### Temporal variability in social organization off the Galápagos Islands

There is clearly no significant variation in unit or group sizes between the 3 years of the Galápagos study, although groups had smaller estimated mean sizes in 1987 than in 1985 and 1989 (Table 1). The mean aggregation size, as indicated by click rates recorded at 07:00, was significantly higher in 1985 than in 1987 (Kruskal-Wallis test statistic = 474, \( P = 0.030 \)). There is no significant difference between the rates of finding sperm whales in the 3 years (likelihood ratio \( G = 2.90, 2 \text{ df}, P > 0.1 \)).

#### Geographical variability in social organization

There were insufficient reidentifications of whales over periods of more than 20 days, a criterion that has only been achieved for the Galápagos Islands as yet. Whitehead et al. (1991), following Best (1979), have suggested that communal calf care (alertness for, and protection against, predators, communal suckling, etc.) may be the primary function of permanent units. If this is true, we might expect relatively little geographical variation in unit size, unless predation pressure differs significantly between areas (see Kahn 1991) or food resources in some areas are insufficient for 13 whales travelling together.

<table>
<thead>
<tr>
<th>Region and period</th>
<th>Whales identified in &gt;1 day</th>
<th>Unit size</th>
<th>Group size</th>
<th>Aggregation size</th>
<th>Search time (h)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>n</td>
<td>Mean SD</td>
<td>Mean SD</td>
<td>Mean SD</td>
<td>Mean SD</td>
</tr>
<tr>
<td>Galápagos Islands</td>
<td>1985</td>
<td>76</td>
<td>11.9 5.2</td>
<td>26.5 8.5</td>
<td>77.4 9.9</td>
</tr>
<tr>
<td></td>
<td>1987</td>
<td>118</td>
<td>11.2 6.2</td>
<td>20.0 1.0</td>
<td>47.3 4.7</td>
</tr>
<tr>
<td></td>
<td>1989</td>
<td>124</td>
<td>13.9 5.3</td>
<td>25.1 6.4</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>1985–1989</td>
<td>359</td>
<td>13.6 1.4</td>
<td>22.1 1.3</td>
<td>61.3 4.7</td>
</tr>
<tr>
<td>Seychelles</td>
<td>1990</td>
<td>51</td>
<td>-</td>
<td>18.0 3.2</td>
<td>15.7 1.6</td>
</tr>
<tr>
<td></td>
<td>1991</td>
<td>42</td>
<td>-</td>
<td>27.2 3.2</td>
<td>49.2 5.5</td>
</tr>
<tr>
<td>Mainland Ecuador</td>
<td>1985</td>
<td>118</td>
<td>11.2 6.2</td>
<td>20.0 1.0</td>
<td>47.3 4.7</td>
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</tr>
</tbody>
</table>

The results summarized in Table 1 suggest little temporal variation in the sizes of units off the Galápagos Islands. It would be surprising if this were not the case, since units are defined as being “permanent” in membership, so little variation in size would be expected over time. Geographical variation in unit size would be most interesting to examine, but estimating unit size requires many reidentifications of individuals over periods of more than 20 days, a criterion that has only been achieved for the Galápagos Islands as yet. Whitehead et al. (1991), following Best (1979), have suggested that communal calf care (alertness for, and protection against, predators, communal suckling, etc.) may be the primary function of permanent units. If this is true, we might expect relatively little geographical variation in unit size, unless predation pressure differs significantly between areas (see Kahn 1991) or food resources in some areas are insufficient for 13 whales travelling together.

For the three study areas, there are clear differences in aggregation sizes off the Galápagos Islands in 1985 and 1987. Differences in group size were smaller and not significant, but were similar in direction to changes in aggregation size. Nineteen eighty-seven was an “El Niño” year in which the unusual oceanographic conditions, including raised sea-surface temperatures (about 2.5°C higher than in 1985 and 1989), apparently decreased sperm whale feeding success (Whitehead et al. 1989). The reduced aggregation size in 1987 may have been a response to changes in prey distribution and abundance.

Several environmental factors could account for these
differences. The most obvious of these is the distribution and abundance of the sperm whales’ prey. Unfortunately, little is known about the distribution and abundance of mesopelagic squid, particularly of the genus *Histioteuthis*, which are the primary prey of the sperm whales in all three areas (Kahn 1991; Papastavrou 1987; Smith 1992). However, sperm whale distribution and abundance are generally correlated with primary productivity (Berzin 1971), which is high off the Galápagos Islands and mainland Ecuador, and lowest off the Seychelles Islands (Berger 1989). This correlation, plus our finding that aggregations in the Galápagos were smallest during an “El Niño” year indicates that the whales aggregate more in areas and at times of greater food abundance.

Another potential determinant of social and spatial organization is hunting. Between 1950 and 1985, the population off mainland Ecuador, which is contiguous to the Peruvian whaling grounds, was hunted heavily (Ramirez 1989). Sperm whales off the Seychelles Islands were hunted sporadically by Soviet whalers on their way to the Antarctic (Kahn 1991). They may also have been taken off South Africa, if this is part of their range (Kahn 1991). In contrast, the animals off the Galápagos Islands were, as far as we know, virtually untouched, although some have been found to migrate to the Peruvian whaling grounds (Ivashin 1978; S. Dufault and H. Whitehead, unpublished data). Whaling could potentially decrease group sizes as members of the constituent units are removed, or increase them if the whales respond to predation through greater aggregation, as suggested by Melville (1851). Our results, with the largest groups being found in the most heavily exploited population, might appear to support this latter hypothesis. However, since the smallest groups were found in a moderately exploited population, the differences in group sizes between areas are not statistically significant, and there are other potential confounding factors, this support must be tentative.

In general, our results suggest that lower levels of sperm whale social organization are less variable temporally and geographically than upper levels. This is consistent with the lower levels (units) being concerned with calf care and the upper levels (aggregations) being short-term responses to prevailing ecological conditions.

**Acknowledgements**

The Galápagos and mainland Ecuador studies were principally funded by the Natural Sciences and Engineering Research Council of Canada, the International Whaling Commission, M. Clark, the Green Island Foundation, the Whale and Dolphin Conservation Society, and the Dalhousie University Research Development Fund. Ilford Canada provided photographic film. The World Wildlife Fund, David Day, and Dieter Plage kindly loaned equipment. We are very grateful to T. Lyholm, who contributed identifications of individual whales that he photographed off the Galápagos Islands in 1988 and 1989. The Seychelles study was partially funded by the Cetacean Society International and sponsored by Canadian Airlines International and Kodak Canada. We are most grateful to those who collected the data at sea, especially T. Arnborn, M. Barbeau, S. Brennan, A. Brooks, D. Day, M. Dillon, G. Faure, L. Fawcett, K. Gonzalez, C. Hendrickson, N. Jaquet, Y. James, M. Jones, B. Lambert, Y. Leleengboto, K. Lohr, K. Lynch, G. Merlen, V. Papastavrou, H. Reyes, K. Richard, T. de Roy, R. Smith, S. Smith, C. Smythe, J. Staniforth, S. Staniforth, S. Waters, and L. Weilgart. We thank H. G. Kahn, who made his sailboat available for the Seychelles study, the Armada of Ecuador, and the government of the Republic of the Seychelles for permission to carry out the research. During the field projects we received considerable assistance from G. Davis, G. Merlen, N. Shah, The Charles Darwin Foundation, and the Charles Darwin Research Station. We especially thank S. Dufault, Y. James, P. McKenna, S. Waters, and L. Weilgart for their major parts in analyzing the data. The manuscript benefited from improvements suggested by S. K. Katona, T. Lyholm, K. R. Richard, and an anonymous reviewer.


