Social structure and mating system of sperm whales off northern Chile

Amanda K. Coakes and Hal Whitehead

Abstract: We studied the social structure and mating system of sperm whales (*Physeter macrocephalus* L., 1758) off northern Chile over 10 months in 2000, photographically identifying 898 individuals. The mean size of encountered groups of females with immatures was about 23 animals, while the estimated mean size of units (sets of females and immatures with permanent relationships) was 11 animals. About 4% of the population consisted of large mature males, although this varied seasonally. Groups of females and immatures, as well as large males, spent only a matter of days within the study area at a time. There was no evidence for preferred ranges for the males, for males consistently accompanying particular groups, or for males forming coalitions. Males roved between the groups of females and immatures. Both mature males and females or immatures appeared to take the initiative in maintaining or breaking close associations. These results are similar to those from studies off the Galápagos Islands, even though the habitat, nonsocial behaviour, and relative abundance of mature males were quite different in the two areas.

Résumé : Nous avons étudié la structure sociale et le système d'accouplement chez des cachalots (*Physeter macrocephalus* L., 1758) au large du nord du Chili sur un période de 10 mois en 2000 et nous avons identifié 898 individus à l'aide de photographies. La taille moyenne des groupes de femelles et de jeunes observés est d'environ 23 animaux, alors que la taille estimée des unités (ensembles de femelles et de jeunes qui ont des liens permanents) est de 11 animaux. Les grands mâles à maturité représentent environ 4 % de la population, mais ce nombre varie avec les saisons. Les groupes de femelles et d'immatures, tout comme les grands mâles, ne passent que quelques jours dans la zone d'étude à chacune de leurs visites. Il n'y a pas d'indication que les mâles aient des aires de répartition préférées, qu'il accompagnent systématiquement certains groupes, ni qu'ils forment des coalitions. Les mâles vont d'un groupe à l'autre de femelles et d'immatures. Le maintien et le bris des associations étroites peuvent se faire à l'initiative à la fois des mâles et des femelles adultes ou alors des immatures. Ces résultats sont semblables à d'autres obtenus au large des îles Galápagos, bien que l'habitat, les comportements non-sociaux et l'abondance relative des mâles matures soient très différents dans les deux régions.

[Traduit par la Rédaction]

Introduction

Species are often considered to have characteristic social structures and mating systems, but both of these frequently vary spatially, and sometimes temporally. For example, both the social structure and mating systems of bottlenose dolphins (genus *Tursiops* Gervais, 1855) vary among study areas (Connor et al. 2000). These variations may be due to differences in predation risk, resource distribution, or other factors (Connor et al. 2000).

Describing such variation is important. Interspecific comparisons are often used to study selective forces in social evolution (e.g., Clutton-Brock 1989). Representing the trait of a whole species using results from one study area will degrade such analyses if there is intraspecific spatial variation. Furthermore, intraspecific variation itself gives valuable insight into selective forces, as in the case of the bottlenose dolphins (Connor et al. 2000). An understanding of intraspecific differences in sociality and mating behaviour between sites is important in formulating sound conservation policies, as both characteristics are important elements of population structure in many species (Sutherland 1998).

The sperm whale (*Physeter macrocephalus* L., 1758) is a species for which the influence of social behaviour on population biology has been a special concern (Best 1979). In particular, it has been suggested that the elimination of large mature males by whaling has led to a reduction in female fertility through a reduction in conception rates (Clarke et al. 1980; Whitehead et al. 1997), the degree of reduction being strongly dependent on the form of the mating and social systems (May and Beddington 1980; Whitehead 1987).

We have a basic understanding of the organization of these animals' social lives, mainly from studies off the Galápagos Islands (Whitehead 2003). Sperm whales are slow-growing, long-lived animals (Rice 1989), which allows for the formation of long-term bonds between individuals. Off the Galápagos Islands, female and immature sperm whales live in stable assemblages of about 10 individuals, called

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units (Christal et al. 1998). Members of units stay together over periods of years or more, although some individuals have been known to transfer between units (Christal et al. 1998). Units seem to generally consist of two or more unrelated matrilines (Whitehead 2003). When females and immatures are encountered in the wild they are usually in groups of about 20 animals, consisting of two or more units, which move in a coherent manner and stay together for a few days (Whitehead 2003).

Not only are sperm whales exceptionally sexually dimorphic, with mature males growing to approximately 18 m compared with about 11 m for females (Rice 1989), but they are also highly sexually segregated. At the age of approximately 6 years, a male leaves its natal unit and begins to move towards higher latitudes (Best 1979). The largest males can be found near the ice edge at both poles. Nonbreeding males show little sign of social structure (Letteval et al. 2002). After about age 27, males journey back to the tropical and subtropical breeding grounds on an unknown schedule (Best 1979). Off the Galápagos Islands, breeding males move between the groups of females and immatures, spending only a few hours, or less, with any group at any time (Whitehead 1993).

While the breeding behaviour and social structure of females and immatures has been studied off mainland Ecuador, the Seychelles, Sri Lanka, and the southeast Caribbean (Gordon 1987; Gordon et al. 1998; Whitehead and Kahn 1992), effort has been much less than off the Galápagos Islands. As a result, our conception of sperm whales' social behaviour is largely based upon results from this one location. This bias is particularly problematic for research on male mating behaviour, as very little information on this topic has been collected from any other area. Furthermore, the abundance of mature males off the Galápagos Islands was abnormally low during the period of the behavioural studies (Whitehead 1993), thereby restricting the amount of data that could be collected and also raising concerns about the generality of results, as mating systems may vary with effective sex ratio (Clutton-Brock 1989).

To investigate the generality of the results from the Galápagos Islands not only on the social structure of female and immature sperm whales, but more particularly on the breeding behaviour of males, we here analyse data collected in the waters off the coast of northern Chile in 2000 (Fig. 1). Compared with studies in other parts of the world, this field project comes much closer to providing a data set comparable in size to that from the Galápagos Islands, especially with reference to the behaviour of the large mature males, as these were relatively common during the Chile 2000 study (see below).

Although sperm whales are common to both the Galápagos Islands and northern Chile (Townsend 1935), the habitats and nonsocial behaviour of the whales show several important contrasts between the two areas:

- *Bottom topography*. The Galápagos Islands are volcanic, so the habitat in this area consists of islands, or sets of islands connected by shelf area, rising from deep water. In contrast, the topography off Chile is simpler and rather linear (Fig. 2).
- *Productivity*. Estimates of surface chlorophyll concentration off the Galápagos Islands are high for a tropical area (0.62–6.3 mg/m^3; Houvenaghel 1978) but are still generally lower than in the highly productive upwellings off northern Chile (0.60–24.8 mg/m^3; Escribano and McLaren 1999).
- *Sea-surface temperature*. While the waters off the Galápagos Islands are cool for equatorial waters (the annual

Fig. 1. Areas of research on sperm whales (*Physeter macrocephalus*) off northern Chile and the Galápagos Islands.

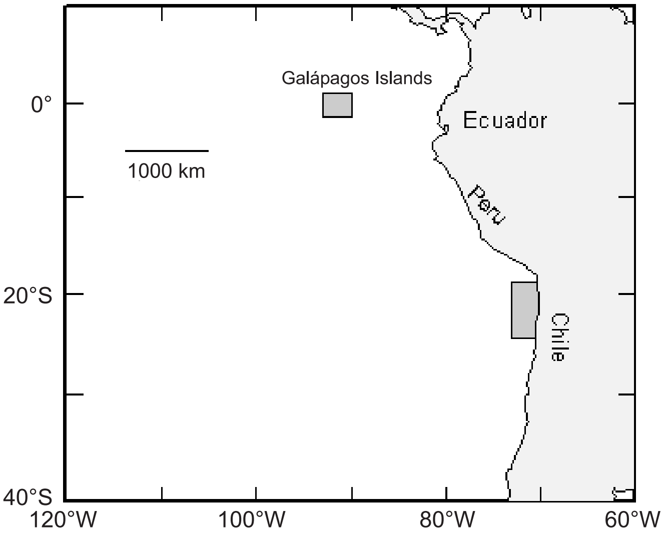
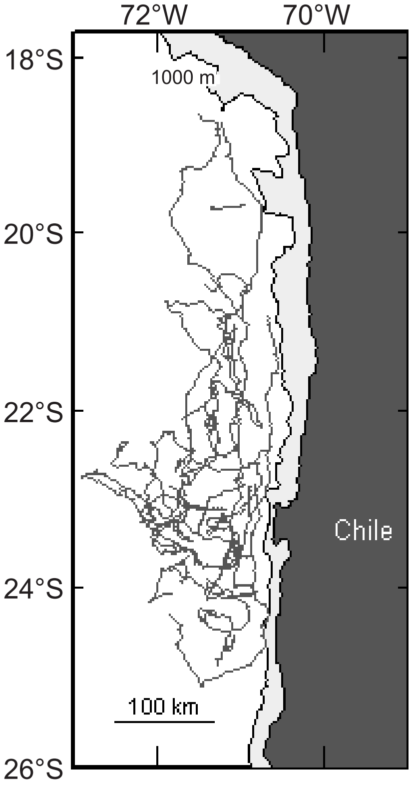


Fig. 2. Track of research vessel while following groups of female and immature sperm whales off northern Chile. Waters shallower than 1000 m are light-shaded (modified from Whitehead 2003).



mean sea-surface temperature at 0600 during our studies was 22–26 °C), they are warmer than off northern Chile (the sea-surface temperature at 0600 during our studies was 15–21 °C), where temperatures were close to the lower limit for female sperm whales (~15 °C; Rice 1989).

- *Diet*. There is considerable uncertainty about the specifics of sperm whales' diet in both locations. However, off the Galápagos Islands the predominant diet seems to be histioteuthid squid of about 300 g (Smith and Whitehead 2000), whereas Chilean sperm whales were found to feed principally upon the much larger (~20 kg), and more muscled, ommastrephid squid *Dosidicus gigas* D'Orbigny, 1835 (Clarke et al. 1976, 1988).
- *Movements*. Movements also differed between the areas. Over a range of time intervals, the straight-line distance moved by sperm whales off Chile was about 50% greater than that moved by the more sedentary animals off the Galápagos Islands (Whitehead 2003).

All of these factors have the potential to affect, directly or indirectly (e.g., through predator or prey abundance or patch size), social behaviour and mating systems. But do they? In this study of the social and mating systems of the Chilean sperm whales, we used as far as possible the same methods as in previous work in the Galápagos Islands (especially as described by Christal et al. 1998; Whitehead 1993, 2003), to allow the results to be directly comparable. Also for comparability, data from Galápagos Islands studies subsequent to 1991 were omitted from most analyses, as densities of females and immatures around the islands became very low in the 1990s, leading to rather atypical measures of social structure (Christal 1998).

Methods

Field methods

Research was conducted from a 12-m sailing vessel between March and December 2000 in the waters off the coast of northern Chile (18–23°S to 70–73°W; Fig. 2). Ten trips were conducted lasting from 12 to 21 days each. Sperm whales were located and followed both acoustically, using hydrophones, and visually (Whitehead and Gordon 1986). Encounters, defined as uninterrupted time periods during which sperm whales were either heard or seen, lasted from a few minutes to a maximum of 11 days.

During daylight while following whales, identification photographs were taken of the whales' flukes as they dived (Arnbom 1987), using a Canon EOS Elan II 35-mm camera with a data-back recorder, 300-mm lens, and Ilford HP5 black and white film.

As each photograph was taken, the cluster size and cluster composition (i.e., numbers of mature males, females or immatures, and calves present) were recorded. We also recorded whether photographs were of large males or females/immatures. Animals that swam in the same direction, at the same speed, and within one body length of each other were considered to be in the same cluster.

Photo-identification

Individual sperm whales were identified using unique markings on the trailing edge of their tail flukes. A quality rating was assigned to each photograph ranging from $Q = 1$ (poor) to $Q = 5$ (high), based on focus, exposure, orientation of the fluke in the frame, percentage of the frame covered by the fluke, and fluke angle relative to the water surface (Arnbom 1987). Only high-quality ($Q > 2$) photographs were used for further analyses.

Photographs were matched to each other and to a catalogue of others identified in the South Pacific by eye and using a computer-assisted matching program modified from that described by Whitehead (1990*a*).

Group-size estimation

Almost always, only one group was followed during daylight hours of a particular day. The group size for a particular day was estimated using the identification data. Each day's identifications were divided into two sets, before and after midday, or the first and second half of the identifications (Whitehead 2003), and group size for that day was then estimated using a Petersen mark–recapture estimator:

$$[1] \qquad g = (n_1 + 1)(n_2 + 1)/n_{12} - 1$$

where g is the estimated the group size, n_1 is the number of individuals identified in the first set of identifications, n_2 is the number identified in the second set, and n_{12} is the number identified in both sets. We estimated the coefficient of variance (CV) of each day's group-size estimate (from Seber 1982):

$$[2] \qquad \mathrm{CV} = [(n_1 + 1)(n_2 + 1)(n_1 - n_{12})(n_2 - n_{12})/(n_{12} + 1)^2(n_{12} + 2)]^{1/2}/g$$

As in Whitehead (2003), two sets of group-size estimates were generated, those with $\mathrm{CV} < 0.25$ and a more inclusive set with $\mathrm{CV} < 0.40$. We used two levels of precision because the precision of these group-size estimates decreases as group size increases. Therefore, including only the most precise estimates may lead to group sizes that are biased low (Whitehead 2003).

The group sizes calculated above are as experienced by an outside observer, such as a predator or a researcher surveying the animals. However, the group sizes that individual whales experience are generally larger, as relatively more of them are in larger groups (Jarman 1974). The group sizes experienced by members of groups are called "typical group sizes" and their mean is estimated as

$$[3] \qquad g_t = \Sigma g(i)^2/\Sigma g(i)$$

where $g(i)$ are the estimates of group size from eq. 1.

Temporal stability of associations

The standardized lagged association rate (SLAR) is the probability that if two animals are associated at any time, one will be a randomly chosen associate of the other after a given time lag (Whitehead 1995), and indicates the temporal stability of social bonds. SLARs were estimated for a variety of lags using the formula

$$[4] \qquad h(d) = \frac{\Sigma\Sigma\, c(A, j, d)}{\Sigma\Sigma\, N(A, j, t_{A,j,d})N(A, j, t_{A,j,d} + d)}$$

Table 1. Estimates of group sizes (g) and typical group sizes (g_t) of sperm whales (*Physeter macrocephalus*) off Chile and in other areas of the southeast Pacific (Whitehead 2003), calculated using the Peterson mark–recapture method with a day's individual identification data split in half.

	Estimates with CV < 0.25			Estimates with CV < 0.40		
Location	n	g	g_t	n	g	g_t
Chile (2000)	26	23.6 (12.9)	30.4 (16.7)	51	29.2 (26.8)	53.3 (49.1)
Galápagos Islands (1985–1999)	97	18.8 (10.0)	24.8 (11.0)	139	23.8 (15.5)	35.5 (19.6)
Ecuador/Peru (1991, 1993)	15	26.2 (7.4)	28.8 (6.4)	20	30.0 (13.5)	37.6 (18.3)

Note: Values are given as the mean with SD in parentheses.

where the summations are over A and j, and

A are individuals

d is the time lag between identification periods

j is a list of pairs of identification periods separated by d time units on both of which A was identified

$t_{A,j,d}$ is the first of the pair of the identification periods in the list specified by A,j,d

$c(A,j,d)$ is the number of associates that were seen with individual A at both time period $t_{A,j,d}$ and time period $t_{A,j,d} + d$

$N(A,j,t_{A,j,d})$ is the number of associates seen with individual A at time period $t_{A,j,d}$

$N(A,j,t_{A,j,d}+d)$ is the number of associates seen with individual A after a time lag d from $t_{A,j,d}$

At various time lags, we calculated jackknife standard error bars for the SLAR estimate by sequentially omitting data from 30-day periods (Whitehead 1995).

We fitted a model to the SLAR estimates that had previously been shown to fit the Galápagos Islands data successfully (Whitehead 1995). This model was reparameterized to aid interpretation, and fitted to both the data from Chile in 2000 and those from the Galápagos Islands prior to 1992, restricting attention to lags less than 1 year for comparability. The model fitted was

$$[5] \qquad h(d) = \frac{[u_t - 1 + (g_t - u_t)\,\mathrm{e}^{-ad}]}{(g_t - 1)^2}$$

where u_t is the mean typical unit size and a is the rate at which units disassociate. The model was fit using the SOCPROG programs (Whitehead 2003), and gave estimates and estimated standard errors for the three parameters g_t, u_t, and a. This is equivalent to the "constant companions" (unit members) plus "casual acquaintances" (members of the group but not of the unit) models of previous analyses (e.g., Whitehead et al. 1992). Other models of the exponential family (Whitehead 1995) fit the Chile data less well than this (see Coakes 2003).

Group membership and male associations

All photographs taken on 1 day were assumed to be from the same group. To determine whether the groups were the same on different days, the following criterion was used (as in Weilgart and Whitehead 1997). If n_X animals were identified on day X and n_Y were identified on day Y, with m_{XY} common to both days, then data from the 2 days were considered to be from the same groups if

$$[6] \qquad m_{XY} > 0.25 \cdot \text{minumum}\,\{n_X, n_Y\}$$

Large mature males were never photo-identified away from groups of females and immatures, and so were considered associated with the groups being followed on the days that they were photo-identified.

Results

Photo-identification data

We encountered sperm whales 48 times during the 10 months, over which we took 1971 photo-identification photographs (with $Q > 2$). From these we identified 898 individuals.

Social structure of females and immatures

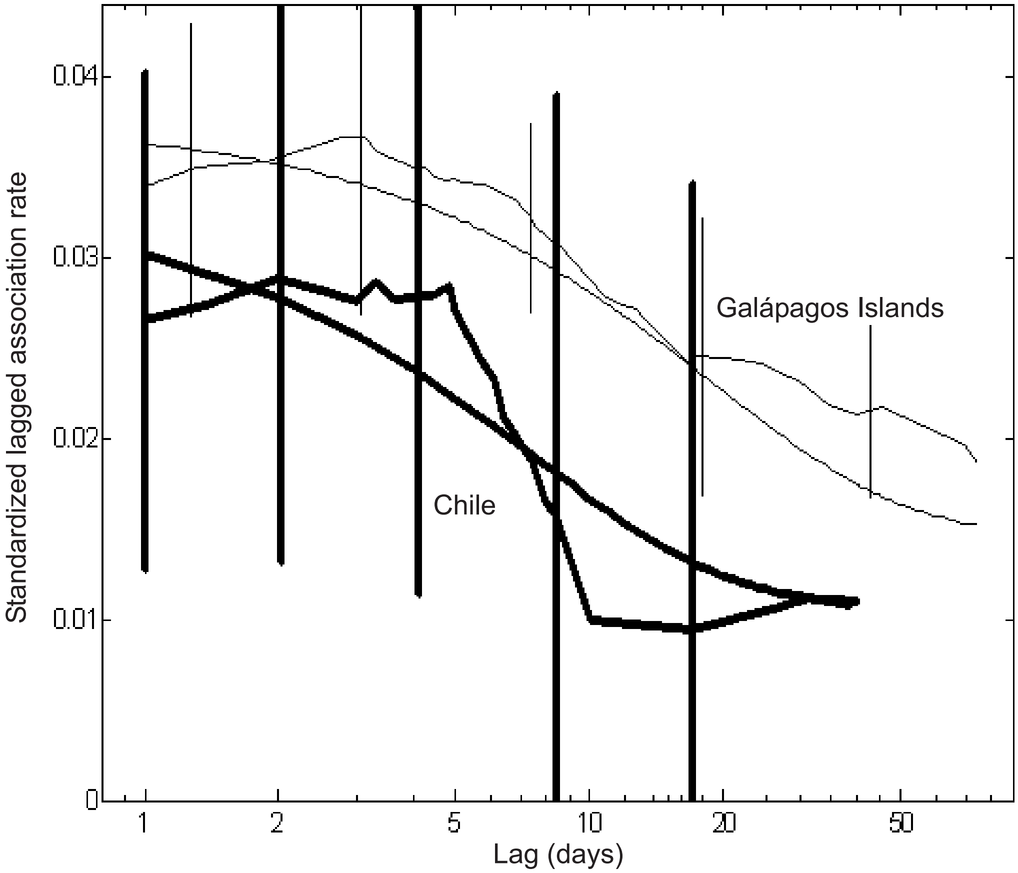
Estimated mean group sizes for females and immatures were not significantly different whether the data were divided in half or split before and after noon (paired t test, $P > 0.1$). Group-size estimates, calculated by splitting the data in half for each day, for our study in Chile in 2000 are compared with those from earlier studies off the Galápagos Islands and Ecuador/Peru in Table 1. Although there was much variation, group sizes in all three areas were about 20–30 animals, with typical group sizes somewhat larger. The particularly large mean typical group-size estimate for Chile in 2000 for CVs < 0.4, 53.3 animals, is especially imprecise (SD = 49.1), owing to some very large and imprecise daily estimates, perhaps because more than one group was followed on those days. Estimates for Chile were similar to those for Ecuador/Peru and slightly larger than those obtained off the Galápagos Islands (Table 1), but not significantly so (for both CV < 0.25 and CV < 0.40; t tests, $0.05 < P < 0.1$).

The pattern of SLARs from Chile is similar to that from the Galápagos Islands (Fig. 3), although the rates are somewhat lower and decline at smaller lags. This suggests larger typical group sizes, and less stable groups, off Chile. These differences are reflected in the parameters for the fitted models (Table 2), although the confidence intervals of the estimated parameters for the two areas overlap. Estimated typical group sizes from this methodology agree with those from the daily group-size estimates (Table 2). Estimated typical unit sizes were almost identical for the two areas, although precision was low, especially for Chile, where data were fewer (Table 2).

Abundance, seasonality, residence, and ranging of mature males

Off Chile in 2000, photographs of mature males constituted 5.5% of the total of high-quality photographs ($Q > 2$), and 3.6% of animals identified from high-quality photo-

Fig. 3. Standardized lagged association rates for female and immature sperm whales off northern Chile in 2000 (thick lines) and the Galápagos Islands in 1985–1991 (thin lines), with fitted models (smooth curves; see Table 2). Vertical lines show approximate standard errors from the jackknife procedure.



graphs were mature males. Both these rates are higher than those found off the Galápagos Islands prior to 1992 (Table 2).

Off Chile the relative abundance of large males was greater in July–September than in other months (Fig. 4). There was a break in the field research during much of August, so most of our data on the period of high male abundance come from July. Although the estimated relative abundance of males in March was also high compared with other months, confidence is low, as only one male was identified during this month and there were only 17 identifications overall.

Off Chile in 2000, 24 of the 33 mature males (73%) were photographed on a single day. Mean residency (the span between the first and last days identified) was 1.27 days, and the maximum residency was 13 days. When only those individuals identified on more than 1 day were included, residency increased to 4.5 days. Mature males were identified on a mean of 1.6 different days (range 1–7 days) off Chile during the 10-month field season. This was less than the residency off the Galápagos Islands (a mean of 2.6 days; Whitehead 1993) but did not differ significantly (*t* test, $P > 0.20$) from that of the female and immature whales off Chile, which were identified on a mean of 1.4 different days (range 1–9 days). Particular mature males were identified on 39% of the field days between their first and last identifications. None of the identified males from Chile in 2000 had been previously identified in other studies in the South Pacific.

As off the Galápagos Islands (Whitehead 1993), there was no evidence that mature males had preferred ranges or defended territories within the Chile study area, as identifications of the same male on more than 1 day were not clumped in their distribution (Fig. 5).

During the 10-month field project off Chile, mature males were never visually observed more than 10 km from groups of females and immatures.

Associations between males and females/immatures

Off Chile between March and June 2000, female and immature groups were not accompanied by large males on most of the days that we tracked them (0.16 males per group per day). The few cases when males were observed involved identifications of only a single male on any day. However, during the period between 1 July and 2 August, when males were most abundant, all but 1 of the 14 groups tracked were seen with at least one male (a mean of 2.64 males per group per day (range 0–6); Table 3). Furthermore, groups 3 and 5 did not have males with them when they were first identified on 7 April and 10 April, respectively, but they did have males associated with them when they were resighted in July. After August the number of males with groups de-

Table 2. Densities, social structure, and male behaviour of sperm whales inferred from studies carried out off northern Chile and the Galápagos Islands.

	Chile (2000)	Galápagos Islands (1985–1991)
No. of encounters	48	61
No. of photo-identifications ($Q > 2$)	1971	4475
No. of animals identified	898	1548
Densities		
No. of encounters/h	0.028	0.036
Photographs of large males (%)	5.5	2.5
Identifications of large males (%)	3.6	1.3
Time of peak male abundance	July–September	April–May[a]
Female/immature social structure		
Group size (daily data; $CV < 0.25$)[b]	23.6 (12.9)	18.8 (10.0)[c]
Typical group size (daily data; $CV < 0.25$)[b]	30.4 (16.7)	24.8 (11.0)[c]
Typical group size (SLAR estimates)[d]	31.3 (18.7)	27.7 (8.1)
Typical unit size (SLAR estimates)[d]	11.0 (18.0)	11.5 (6.3)
Rate of disassociation of groups (day^{-1}; SLAR estimates)[d]	0.134 (0.185)	0.053 (0.065)
Residency and ranging of individual males		
Median days identified[e]	1 (1–7)	2 (1–5)[f]
Median span of identifications (days)[e]	0 (0–13)	1 (0–70)[f]
Preferred ranges or territories	No evidence	No evidence[f]
Associations between males and females/immatures		
Males move between groups?	Yes	Yes[f]
Groups seen with several males?	Yes	Yes[f]
Duration of male association with group	Hours	Hours[f]
Individuals clustered with several males?	Yes	Yes[f]
Females/immatures have different association rates with males	No significant trend	No significant trend[f]

Note: SLAR, standardized lagged association rate.

[a] Whitehead et al. (1989).

[b] Values in parentheses show SD.

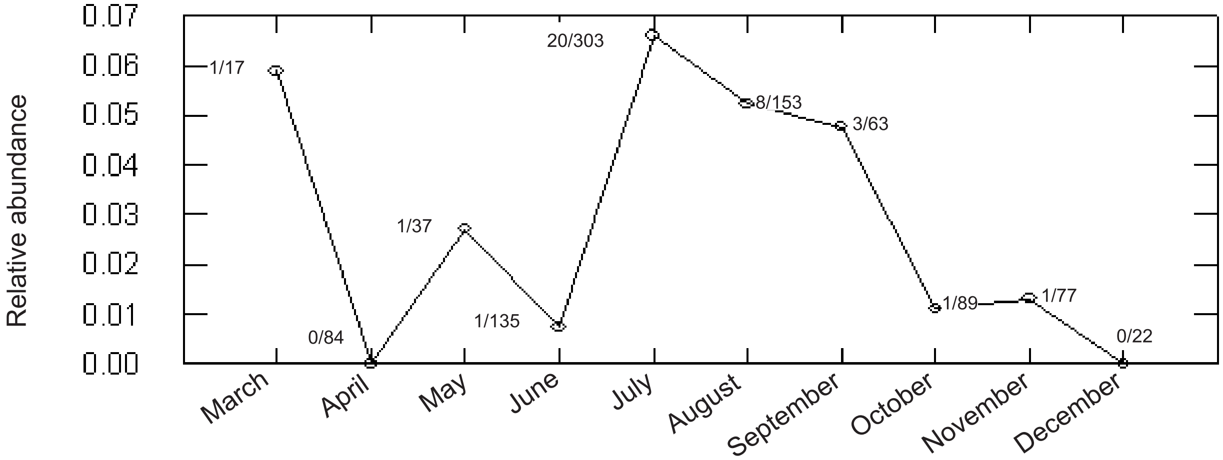
[c] Whitehead (2003).

[d] Values in parentheses show SE.

[e] Values in parentheses show the range.

[f] Whitehead (1993).

Fig. 4. Seasonal relative abundance of male sperm whales off the coast of northern Chile, calculated as a proportion of the total number of identifications each month that were of adult males. The numbers beside the data points give the number of large males / total number of individuals for each month.



clined once again (a mean of 0.35 males per group). This reflects the seasonal variation in the relative abundance of males. There was no sign in the Chile data that certain groups were more or less likely to be visited by males, depending on the season (Table 3). There was also little sign of preferential associations between particular groups of females and immatures and particular males (Table 3). Males appeared to spend a matter of minutes to hours with a partic-

Fig. 5. Distributions of individual mature males. Points represent the location of the first identification of a mature male on a particular day and each symbol represents one individual. (*a*) Males identified on more than 1 day. (*b*) Males identified on more than 3 days.

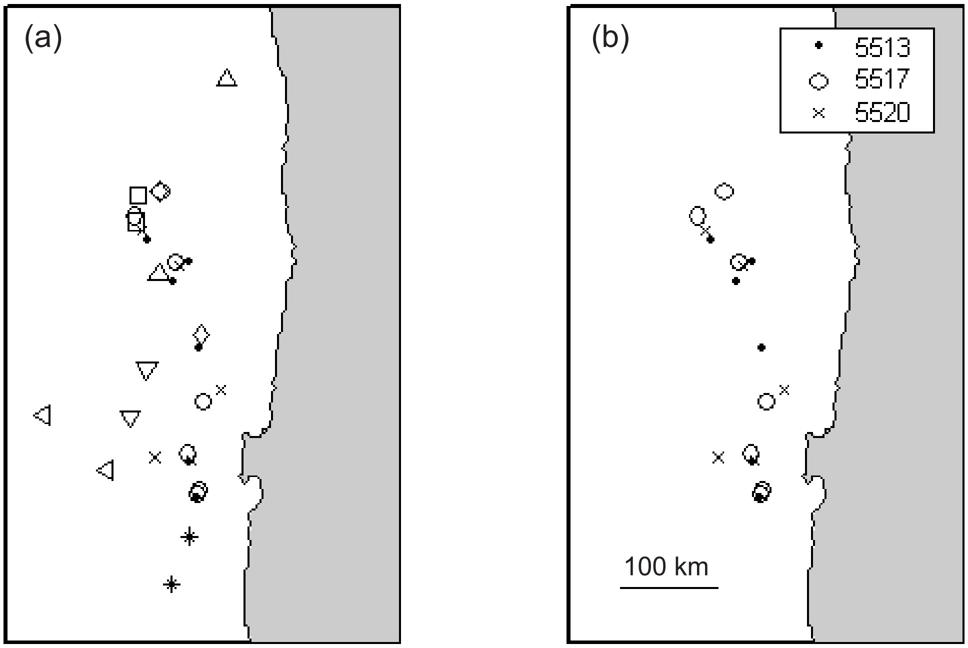


Table 3. Number of days on which particular males and particular groups of females and immatures were identified together during the period of high male abundance, 1 July to 2 August 2000.

	Female/immature group No.														
Male ID No.	3	5	18	19	20	21	22	23	24	25	26	27	28	29	Total
5503			1												1
5504				1											1
5505					1										1
5507					1										1
5508					1										1
5509					2										2
5510					1										1
5511					1										1
5512						1									1
5513		1						1	3					1	6
5515								2							2
5516								1							1
5517	1	1						2			1		1	1	7
5518								1	1						2
5519									1						1
5520	1	1						1	1			1			5
5521			1												1
5522										1					1
5523									1						1
5525									1						1
5526												1			1
5527														1	1
5528														1	1

ular group of females and immatures before moving on, but were sometimes found to revisit the same group over several days (Table 3).

At the individual level, 16 females or immatures identified off Chile were clustered with males on more than one occasion. Five of these females or immatures were identified with only one particular male, eight with two males, and three with three different males (over periods of 3–6 days). This demonstrates that over the course of a few days, a female or immature may cluster with a number of different males. Some females or immatures were photographed clustered with two different males on the same day, and sometimes clusters contained more than one male. We used the same method as in Whitehead (1993) to see whether some females or immatures were identified with males more frequently than others during the period of intense male visitation, 1 July to 2 August 2000. Of the 95 females or immatures identified on more than one day during this period, nine clustered with males on both the first 2 days they were identified, 27 clustered with males on only one or other of the days, and 59 were identified clustered with males on neither day. As with the Galápagos Islands data (Whitehead 1993), these proportions were not significantly different from those expected from a binomial distribution under the null hypothesis that all females and immatures had the same probability of being accompanied by males (*G* test, P = 0.134), although rather more animals were identified with males on 2 days (9) than expected under the null hypothesis (5.3).

Within clusters containing both males and females or immatures, females or immatures dived before their male companions 53% of the time, suggesting that both sexes played a role in maintaining contact with the other. No copulation was observed, although the observation conditions would make this difficult to see.

Associations between mature males

On four occasions two males were identified clustered together off Chile in 2000. Three times on 1 July, males 5503 and 5521 were photographed in the same cluster and once, on 5 July, males 5507 and 5508 were identified in the same cluster. However, when the definition of association is extended to include pairs of animals identified within 2 h of one another, the number of occasions two males were associated increased to nine, with three males associated with one another on two occasions. However, there were no repeat associations between individual mature males over more than 1 day, even under this relaxed definition of association.

During the study off Chile in 2000 we observed a brief fight between two mature males. This interaction (at 1410 on 21 July 2000) began with two whales, a presumed female and a mature male, swimming side by side. The female repeatedly made shallow dives, coming up alternately on either side of the male. After a few minutes, another male approached quickly, lobtailing (thrashing its flukes) at the surface. When the two males came together, there was much splashing and one male's tail emerged with the other male's jaws around it. One male (we do not know which) quickly left the area and the other remained with the female (for a more detailed account see Whitehead 2003).

Discussion

Sperm whales off Chile

We began field research off Chile in 2000 partly because the female and immature sperm whales that we had been studying off the Galápagos Islands had deserted the region around the islands over the 1990s (Whitehead et al. 1997), eliminating the possibility of further studies of social structure in this area. Many of the sperm whales originally studied off the Galápagos Islands were reidentified off the mainland of the Americas, especially Ecuador and Peru (Whitehead 2003). Among the 898 animals identified off Chile in 2000, only one was known from the Galápagos Islands catalogue and eight from research off mainland Peru (Coakes 2003). The other 889 were new, indicating that the animals encountered off Chile were largely distinct from the subjects of the Galápagos Islands studies. Thus, our results largely pertain to a different set of animals from those in the earlier Galápagos Islands research.

During the research off Chile, sperm whales were fairly abundant and thus we were able to accumulate a set of data not that much smaller than that collected off the Galápagos Islands (Table 2). Hence, for the first time we can assess, with reasonable power, whether the Galápagos Islands results pertain to another area and another set of animals. Relative densities of males were approximately twice as high off Chile (Table 2), giving relatively greater power to this part of the analysis as well as the potential for identifying variations in mating that relate to the effective sex ratio.

It has been proposed that the remarkably low density of mature males off the Galápagos Islands between 1985 and 1995 was due to the effects of intense male-biased whaling in the region between 1958 and 1981 (Whitehead et al. 1997). The relatively higher male density off Chile could, then, be explained by some regrowth in the proportion of mature males in the southeast Pacific during the 1990s, or by the favourable position of the Chilean grounds: at higher latitudes, and on a possible migration route, the Humboldt Current, more large males may reach northern Chile than the equatorial waters off the Galápagos Islands.

Social system

Overall, results on the social and mating systems of the sperm whales off Chile were similar to those from the Galápagos Islands, despite the differences between the environments of the two sites, and some contrasts in the nonsocial behaviour of the whales (see Introduction). This indicates that the environment is not a short-term driver of sperm whale social systems. We think that these results (see discussions in Coakes 2003; Whitehead 2003) support the consensus perspective on the function of female sociality (Best 1979; Gordon 1987; Pitman et al. 2001; Whitehead 2003): that predation risk, probably especially from killer whales (*Orcinus orca*), is a more fundamental driver of grouping in female and immature sperm whales than foraging factors, as predators are a constant threat, while prey types are ephemeral and very variable (e.g., Kawakami 1980).

Mating system

Clarke et al. (1964) estimated that the peak mating season for sperm whales off the coast of Chile was between June and December. The peak in male abundance reported here, between July and September, fits within this time frame, but suggests a more concentrated season. This difference may be due to the fact that we estimated the breeding season more directly from when males were actually present on the breeding grounds, whereas Clarke et al. (1964) estimated the breeding season indirectly from the size and presence of foetuses in whaled animals. There may be more imprecision in this technique due to variable foetal growth and long gestation periods (14–15 months; Best et al. 1984).

Most mature males, like most females, seemed to spend only a few days within our Chilean study area. Photo-identifications indicate shorter residence times of both sexes off Chile, compared with the Galápagos Islands (Table 2). This could be an artifact of the physically larger study area off Chile (about 3 times larger; Fig. 1), so that animals within it were less likely to be identified during any period.

Results from Chile confirm the model of the sperm whale mating system inferred from the results from the Galápagos Islands, where relative male densities were much lower (Whitehead 1993): mature males rarely, if ever, hold territories, form coalitions with other males, or accompany groups of females and immatures, defending them against other males. Instead they rove between groups of females and immatures, usually spending a few hours or less with any group at a time, but sometimes revisiting the same group repeatedly over a few days.

Despite this confirmation of these aspects of the mating system, it is still unclear what determines paternity in this hugely dimorphic species (mature males are roughly 3 times the mass of females; Rice 1989). Physical combat seems to be part of the picture, as attested to by the observation of fighting during this study, as well as the scars on mature males from each other's teeth (Kato 1984). However, male combat seems to be quite rare (Whitehead 2003), and we frequently observed two or more males peacefully attending the same group together (also seen off Dominica, West Indies, by Gordon et al. 1998), as well as both females and large males taking the initiative to join or leave clusters. Such observations indicate that dominance hierarchies among males and (or) female choice may be significant elements of the mating system of the sperm whale. Other results also indicate an important role for dominance or female choice: higher than expected levels of paternal relatedness within groups (Christal 1998; Richard et al. 1996); and low female fertility off the Galápagos Islands despite large males attending groups of females and immatures about once per day during the breeding season (Whitehead 2003).

Conclusion

This study suggests that the social and mating systems of sperm whales off northern Chile and the Galápagos Islands are quite similar despite substantial differences in latitude, habitat structure, sea surface temperature, movement patterns, and probably diet. This indicates that sperm whale sociality is primarily driven by other factors. It seems likely that the reduction of predation risk on females or their calves may be the primary function of most elements of the social structure of the females and immatures (Best 1979; Gordon 1987; Pitman et al. 2001; Whitehead 2003), and, in turn, that the distribution and social structure of the females have largely driven the evolution of the male mating strategy (Clutton-Brock 1989; Whitehead 1990*b*). While the Galápagos Islands and northern Chile study areas are about 3500 km apart (Fig. 1), they are in the same oceanic basin and current system; it may be that sperm whales in other parts of the world organize their societies differently. For instance, group sizes off the Seychelles Islands in the Indian Ocean seem to be smaller (Whitehead and Kahn 1992). We encourage similar studies of sperm whale social structure in other areas.

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