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## Multilevel Societies of Female Sperm Whales (*Physeter macrocephalus*) in the Atlantic and Pacific: Why Are They So Different?

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**Abstract** We can examine the evolution of multilevel societies using comparative studies. Intraspecific comparisons are valuable because confounding factors are reduced. Female sperm whales live in multilevel societies. However, studies at several locations have found substantial and consistent differences in social structure between the eastern Pacific and North Atlantic Oceans, even though nuclear DNA shows no significant differentiation between the populations. In the Pacific, female sperm whales live in nearly permanent social units that typically contain about 11 females and immatures of multiple unrelated matrilineal units. These units form temporary groups with other units for periods of days, apparently exclusively with other units from the same cultural clan. Clans contain thousands of females, are not distinct in nuclear DNA, but are sympatric and have distinctive culturally determined vocalizations and movement patterns. In the North Atlantic social units rarely group with other units, and there is no evidence for sympatric cultural clans. Possible drivers of these contrasts include oceanographic differences, predation, the effects of whaling, and culture. We suggest that protection against predation by killer whales is the primary reason for grouping in the Pacific, and as killer whales do not seem such a threat in the Atlantic, social units there rarely form groups, and have not evolved the clans that primarily function to structure interunit interactions. This analysis highlighted several factors that may influence the evolution of multilevel societies,

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ranging from the attributes of resources, to predation, anthropogenic effects, culture, and even the cultures of other species.

**Keywords** Culture · Oceanography · *Physeter* · Predation · Society · Sperm whale · Whaling

## Introduction

By multilevel (or multitier) societies we mean the nesting of two or more levels of social organization so that an individual is a member of a social structure, e.g. group, unit, ... *A*, which is itself a member of another structure, e.g. band, clan, ... *X*, which in turn could be a part of another structure at a higher tier of social organization. While multilevel societies are best known in terrestrial mammals and especially primates (see other contributions to this special issue), they are also prominent features of the social systems of some cetaceans (Connor *et al.* 1998). As these societies evolved in a radically different environment from that of the terrestrial mammals, this suggests that there is no direct environmental driver of the multilevel phenomenon; it may be instead a secondary consequence of other social and psychological characteristics. We can examine the evolution of this important, and somewhat unusual, social phenomenon using comparative studies among and between phylogenetic groups, such as orders of mammals, and habitats, such as marine and terrestrial. This special issue, with its articles focused on various species, provides a major resource for such comparative perspectives. For instance, some primates seem to have come to a multilevel society through preferred relationships among smaller core units and others through differentiation of larger core units (Grueter and Zinner 2012). The former, amalgamation, route, seems to be prevalent in the Cetacea, as we discuss in the text that follows.

We can also look at intraspecific variation in social structure. Because potentially confounding factors are fewer than in interspecific studies, these comparisons can be particularly informative. We here compare multilevel sperm whale (*Physeter macrocephalus*) societies in the Atlantic and the Pacific, a comparison we find particularly intriguing because there are few if any systematic differences in nuclear DNA between sperm whales in the two oceans (Lyrholm *et al.* 1999), yet, as we show, there are substantial differences in the social systems that are consistent over large spatial scales within each ocean. To set the scene, we first summarize knowledge of multilevel societies in cetaceans, and then give a general picture of sperm whale society. For more detailed, although sometimes dated, information about cetacean societies in general see Mann *et al.* (2000), and for sperm whale societies see Whitehead (2003b).

There have been detailed studies of the social systems of only a few species of Cetacea. However, some clear general trends have emerged. Among the baleen whales (Mysticeti), there is no indication of multilevel societies (Gowans *et al.* 2007). Bottlenose dolphins (*Tursiops* spp.) are by far the best studied cetaceans (Connor *et al.* 2000). Their social systems have been described in a number of coastal locations around the world. The general picture that emerges is of females possessing a network of associates within communities, while males, in some areas, form closely

integrated permanent alliances (Gowans *et al.* 2007). However, in one study area, Shark Bay, Australia, alliances form alliances with each other (Connor *et al.* 1992, 2010) when competing for access to females so there is a multilevel society among these male bottlenose dolphins. Multilevel male alliance structure may well exist in other bottlenose dolphin populations or in those of other small, inshore cetaceans, but we currently lack evidence.

The most tiered multilevel society so far discovered in the ocean is that of the killer whale (*Orcinus orca*). In the North Pacific, northeast Atlantic and Antarctic oceans, at least, killer whales are segregated into “ecotypes” (Baird 2000; Foote *et al.* 2009; Pitman and Ensor 2003). The ecotypes are morphologically, genetically, culturally, and ecologically distinct, even though they may share the same waters. Some molecular-genetic studies suggest that the ecotypes should be considered as separate subspecies, or perhaps species (Morin *et al.* 2010), although Pilot *et al.* (2010) find evidence for male-mediated gene flow between ecotypes. Thus it is not clear whether ecotype itself should be considered a level of the multilevel society of killer whales.

The best known of the ecotypes are the “resident” fish-eating killer whales of the eastern North Pacific. These whales, which eat mainly salmon (Salmonidae), live in stable matrilineal groups containing an older female and all her living offspring, both male and female; there is no dispersal between groups (Ford *et al.* 2000). Vocal repertoires appear to play a major role in their social structure. Matrilineal groups that have similar vocal repertoires spend the majority of their time traveling together as members of the same pod, and distinctive vocal repertoires can be used to identify pod membership unambiguously (Yurk *et al.* 2002). Pods that share some parts of their repertoires are members of the same clan, and one to three clans form a community. Communities have largely distinct ranges, and show small but consistent genetic differences. Mating seems to usually occur between clans but within communities (Barrett-Lennard 2000), except when there is only one clan in the community (as with the “southern resident” community). There are characteristic behaviour patterns linked to various elements of this hierarchical social system, such as the clan-specific vocal signals and community-specific greeting ceremonies (Yurk 2003).

The “transient” killer whale ecotype of the North Pacific, whose members eat marine mammals and not fish, are found in the same waters as the “residents.” The transients also have a matrilineally based social structure, but it is less stable and much less clearly multilevel than that of the residents (Baird 2000).

The sperm whale, the largest toothed whale, is a deepwater predator, feeding principally on cephalopods at depths below 300 m. It is an animal of extremes, possessing the largest brain on Earth, the most powerful natural sonar system, and, possibly, the greatest biomass of any mammal before human population expansion over the last two millennia (Whitehead 2003b). The sexes lead very different lives. Males leave their mothers at very approximately age 10 and then gradually move to cold waters, growing very large. They form ephemeral “bachelor groups,” but as they grow older and larger they are often seen alone (Whitehead 2003b). In their late 20s they start to return periodically to the tropical and subtropical habitat of the females and immatures to mate (Best 1979). On the breeding grounds, breeding males generally spend only a matter of hours or less with any one social unit of females (Whitehead 1993).

The fundamental level of the social structure of female sperm whales is the social unit. A social unit consists of *ca.* 10 females and immatures that travel

together (up to *ca.* 100 km/d), care for and suckle each other's offspring, and defend themselves communally (Christal *et al.* 1998; Gero *et al.* 2009; Ortega-Ortiz *et al.* 2011; Pitman *et al.* 2001; Whitehead 1996a). While most females spend their lives in the same social unit, and so the units have a matrilineal structure, there are occasional transfers between units, as well as unit fission and fusion (Christal *et al.* 1998). Thus, at least in the Pacific, units frequently contain several matrilineal lines (Mesnick 2001), and there appears to be some social structuring within them; e.g., social affiliation between pairs correlated with relatedness in one well-studied unit in the Atlantic in which all females were closely related (Gero *et al.* 2008). Units can coalesce into groups that travel together over periods of hours to days (Whitehead *et al.* 1991). Groups may contain 1–3 units, and so about 5–50 animals. The members of a group can be tightly clustered, sometimes touching, when socializing. However, when foraging, the individuals spread out over scales of hundreds of meters to kilometers. The whales return to the surface to breathe for *ca.* 7 min between foraging dives of about 40 min singly or in clusters of two or three individuals (Whitehead 2003b). When groups contain two or more units, association is generally greater between members of the same unit, compared with that between individuals of different units (Christal and Whitehead 2001).

Units do not form groups randomly with other units; there are preferences (Whitehead 2003b). Off Dominica in the Atlantic, certain pairs of units that use the same area are much more likely to form groups than other pairs (S. Gero, *unpubl. data*). Pacific units also have preferences in group formation (Whitehead 2003b). Most tellingly, these Pacific units have been documented to form groups only with other units of their own vocal clan, even though two or more clans may use the same waters (Rendell and Whitehead 2003). Clans can be identified through their distinctive vocalization patterns, span thousands of kilometers, and may contain thousands of members (Rendell and Whitehead 2003). They have characteristic movement patterns and use of habitat, as well as differences in diet, feeding success, and, seemingly, reproductive success (Marcoux *et al.* 2007a; b; Whitehead and Rendell 2004;). The population structure of female sperm whales in the Pacific is defined more by cultural clan than geography (Rendell *et al.* 2012).

Although the initial study of the social structure of living female sperm whales took place in the Indian Ocean (Gordon 1987), and there has been one other published Indian Ocean study (Whitehead and Kahn 1992), all other results come from either the eastern Pacific or North Atlantic. The Mediterranean Sea contains a small, isolated, and somewhat strange—for instance, with a very low diversity of coda vocalization patterns—population of sperm whales (Engelhaupt *et al.* 2009; Pavan *et al.* 2000), and is not considered here. However, in both the eastern Pacific and main body of the North Atlantic, researchers have studied female sperm whales in several locations (Fig. 1), using somewhat similar methods. In the Atlantic these locations are the Azores, the Sargasso Sea, off Dominica (in the Caribbean Sea), and in the northern Gulf of Mexico. Pacific locations are the Gulf of California and the waters off the Galápagos Islands, mainland Ecuador, and northern Chile. As we show, in some respects there are consistent and notable differences between the social structures of female sperm whales in these Atlantic and Pacific locations.



**Fig. 1** Map showing study locations, Gulf Stream, and Humboldt Current.

## Sperm Whale Social Structures in the Atlantic and Pacific

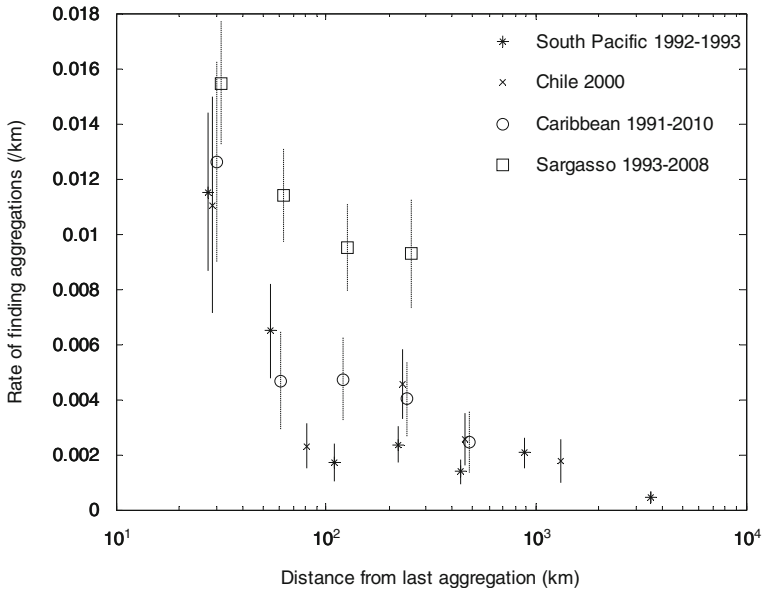
### Large-Scale Spatial Structure: Density and Variation in Density

In acoustic surveys for sperm whales, using the same boat and methods, we encountered aggregations of whales (separated by  $>20$  km) two to three times more frequently in the western North Atlantic than in the South Pacific (Table I). Even in the productive waters off northern Chile, encounter rates were substantially lower than in the Caribbean or Sargasso Seas. Unfortunately, we do not have estimates of the number of whales in aggregations in both the Atlantic and Pacific.

The spatial organization of the aggregations of whales also appears different (Fig. 2). The ranges at which the rate of encountering aggregations declines suggests that whale concentration in the Pacific is more patchy than in the Atlantic. In the Pacific, the whales seem concentrated at scales of *ca.* 50 km, with a low probability of

**Table I** Rates of encountering sperm whale aggregations acoustically in four study areas (excluding first 20 km of each search)

| Area                            | Years     | Encounters/km | Encounters | km     | Author                           |
|---------------------------------|-----------|---------------|------------|--------|----------------------------------|
| Pacific                         |           |               |            |        |                                  |
| South Pacific                   | 1992–1993 | 0.0018        | 70         | 39,072 | Jaquet 1996                      |
| Northern Chile                  | 2000      | 0.0033        | 44         | 13,492 | H.Whitehead, <i>unpubl. data</i> |
| Atlantic                        |           |               |            |        |                                  |
| Caribbean Sea                   | 1991–2010 | 0.0070        | 124        | 17,628 | H.Whitehead, <i>unpubl. data</i> |
| Sargasso Sea ( $<40^{\circ}$ N) | 1993–2008 | 0.0047        | 244        | 52,315 | S. Wong, <i>unpubl. data</i>     |



**Fig. 2** Rates of encountering sperm whales with range from previous encounter during a survey of the South Pacific in 1992–1993, research off northern Chile in 2000, and various surveys in the Sargasso Sea (latitudes  $<40^{\circ}\text{N}$ ) and Caribbean Sea (SEs shown by vertical lines).

encountering aggregations as distance from the previous aggregation increases. By contrast, in the Atlantic, especially in the Sargasso Sea, aggregations of whales are more evenly dispersed, being concentrated over scales of *ca.* 200 km. This represents the concentration of sperm whales in the northwest Sargasso Sea. Densities in the southeast Sargasso Sea, *ca.* 500 km away, are much lower (S. Wong, *unpubl. data*).

Genetic data suggest fair uniformity in sperm whale genotypes across large areas of the Pacific (Lyrholm and Gyllensten 1998; Lyrholm *et al.* 1999; Whitehead *et al.* 1998), although recent work indicates that the California Current region supports a demographically independent population of whales (Mesnick *et al.* 2011). Further genetic structure in the Pacific may become evident with more powerful modern techniques. In the Atlantic, however, there is strong differentiation in maternally transmitted mitochondrial DNA (mtDNA) between the whales in the Gulf of Mexico and those in the western North Atlantic (Engelhaupt *et al.* 2009), a thousand or so kilometers away (Fig. 1). Photoidentification and satellite tracking data lend support to the genetic evidence. In the North Atlantic, movements of females between the Caribbean and Sargasso Sea seem to be rare, as there are no photoidentification matches between 194 photoidentified individuals in the Caribbean and 161 in the Sargasso Sea, 1800 km to the north (Gero *et al.* 2007). Females tracked using satellite tags for weeks to more than a year remained in the northern Gulf of Mexico and had ranges spanning 200–700 km (Ortega-Ortiz *et al.* 2011). Mark-recapture studies of photoidentifications indicate quite small populations in the Caribbean (*ca.* 145, Gero *et al.* 2007) and the waters around the Azores (*ca.* 300–800; Matthews *et al.* 2001), in contrast to roughly 1245 whales estimated to be using the waters off the Galápagos Islands in the Pacific in the 1980s and 1990s (Whitehead *et al.* 1997). In contrast, there are several photoidentification matches between the waters of the Gulf of



California—even more enclosed than the Gulf of Mexico—and the Galápagos Islands, 4000 km away, in the Pacific (Whitehead *et al.* 2008). Indeed, the ranges of female sperm whales in the eastern tropical Pacific regularly span 1000 km and occasionally >4000 km (Whitehead *et al.* 2008). Thus it seems that female sperm whales in the eastern Pacific range further and their populations are less geographically and genetically structured than those in the Atlantic.

### Presence of Clans

Sperm whales produce short, stereotyped patterns of clicks, called codas, often in social contexts but also at the beginning and end of foraging dives (Schulz *et al.* 2008; Watkins and Schevill 1977; Whitehead and Weilgart 1991). The coda repertoire of individual whales is mostly shared among social unit members (Schulz *et al.* 2010), although some coda types appear to contain also individually specific information (Antunes *et al.* 2011). Coda repertoires of units seem to be temporally stable (Rendell and Whitehead 2005). In the Pacific, sperm whale social units can be assembled into vocal clans based on the most common coda types in their repertoires (Rendell and Whitehead 2003). Social units from different clans are often sympatric and share many mtDNA haplotypes, which suggests that vocal clans are the result of cultural transmission. In addition to the strong interclan variation, repertoires also show a weaker geographic variation, possibly reflecting regional vocal dialects maintained at the scale at which sperm whale units disperse in their habitat (Rendell and Whitehead 2005).

In the North Atlantic, differentiation between the coda repertoires of social units in the same area is much less marked than in the Pacific. Codas can be compared using a multivariate similarity metric (Rendell and Whitehead 2003). Hierarchical clustering of the Pacific Ocean codas using this metric separates social unit repertoires into clans with good support from a bootstrap procedure. In contrast, the same procedure applied to the North Atlantic tends to separate repertoires into geographic regions but with less support (Antunes 2009). Also, the mean repertoire similarity in the North Atlantic is higher than the mean values found between clans in the Pacific but lower than that found within clans (Antunes 2009). Hence, it seems there is a marked contrast between vocal repertoire variation in two ocean basins with strong differentiation among sympatric units in the Pacific and no evidence for anything similar in the North Atlantic.

### Group and Unit Sizes

In the Pacific, the mean typical group size is consistently *ca.* 28 individuals in all study areas, whereas in the Atlantic it is about 8 individuals (Table II). Typical group size is the mean group size experienced by a member of the population (Jarman 1974). It is generally larger than the group size experienced by outside observers, such as researchers or other members of the whales' ecosystem.

Mean unit size is consistently about 11 individuals in the Pacific, meaning that groups usually contain *ca.* 2–3 units. In the Atlantic the unit size is generally similar to the group size, indicating that groups usually consist of just one unit. In seven seasons of detailed studies off Dominica, only rarely were groups of more than one unit observed (S. Gero, *unpubl. data*). Units may also be a little smaller in the Atlantic compared with the Pacific, especially off Dominica and in the Gulf of Mexico (Table II).

**Table II** Estimates of typical group size and social unit size (excluding calves) for sperm whales in study sites in the Atlantic and Pacific

| Area               | Typical group size±SE | Unit size±SE | Authors  |
|--------------------|-----------------------|--------------|--|
| Pacific            |                       |              |  |
| Galápagos          | 27.7±8.1              | 11.5±6.3     | Coakes and Whitehead 2004  |
| Gulf of California | 28.4±6.4              | 12.5±4.5     | Jaquet and Gendron 2009  |
| Ecuador            | 27.2±3.2              | —            | Whitehead and Kahn 1992  |
| Northern Chile     | 31.3±18.7             | 11.0±18.0    | Coakes and Whitehead 2004  |
| Atlantic           |                       |              |  |
| Gulf of Mexico     | 7.4±4.0               | 5.2±3.5      | Jaquet and Gendron 2009  |
| Azores             | 11.5±1.0              | 12.2±1.4     | Antunes 2009   |
| Dominica           | 6.6±1.5               | 6.4±0.6      | Gero <i>et al.</i> 2009 for groups; S. Gero, <i>unpubl. data</i> for units |
| Sargasso Sea       | 12.0±6.6              | —            | Gero <i>et al.</i> 2009  |

### Group/Unit Matrilineal Structure

We can use molecular genetic data to examine the kinship structure within groups or units. For quite a number of sperm whale groups, and a very few units, mitochondrial haplotype data exist for several whales within the group or unit. If we assume that individuals from the same matriline possess the same haplotype, and that individuals from different groups are rarely from the same matriline, then we can estimate the probability that two individuals in the same group are members of the same matriline:

$$q = [P(\text{share hapl.}|\text{same group}) - P(\text{share hapl.}|\text{different group})] / [1 - P(\text{share hapl.}|\text{different group})]$$

This measure is closely related to Jost's (2008)  $D$ , which estimates interpopulation differentiation rather than intrapopulation similarity.

We used data from 140 individuals sampled from 38 groups in the Gulf of Mexico (Ortega-Ortiz *et al.* 2011; only groups in which the number of sampled females exceeded the number of sampled males), 11 individuals from 2 groups in the Sargasso Sea (S. Gero, D. Engelhaupt, *unpubl. data*), and 194 individuals from 30 groups in the Pacific (Rendell *et al.* 2012). For each study area, we estimated the standard error of  $q$  using the nonparametric bootstrap (resampling groups with replacement 1000 times). Estimates were:

$$\begin{aligned} q(\text{Pacific}) &= 0.422 + \text{SE } 0.101 \\ q(\text{Gulf of Mexico}) &= 0.486 + \text{SE } 0.164 \\ q(\text{Sargasso Sea}) &= 0.525 (\text{SE unavailable; too few groups}) \end{aligned}$$

These numbers indicate, but do not conclusively show, that group members in the Atlantic are more likely to be from the same matriline than those in the Pacific.

Mitochondrial genetic data have been published for only four known units. All seven members of a unit sampled off Dominica, West Indies, possessed the same

mitochondrial haplotype (Gero *et al.* 2008), as did 12–15 sampled members (level of duplication unclear in a few cases) of a Galápagos unit containing 17 individuals (Christal 1998). However, also off the Galápagos, 2 haplotypes were present in 5 individuals sampled from a unit containing 9 members, and also in samples from 3 individuals in a 5-member unit (Christal 1998; Mesnick 2001).

Thus there are indications that matrilineality is a more pronounced feature of sperm whale social structure in the Atlantic compared with the Pacific at both the group and unit level. Geographic or clan-based structuring of populations could affect these metrics, but we found little sign of this in the Pacific where we had clan information.

### Spatial Spread of Groups

We do not have direct measurements of the spatial spread of groups, but used an indirect method to measure the spatial dispersion of foraging groups, thus investigating the impression of one of us (H. Whitehead) that foraging groups of female sperm whales are more dispersed spatially in the Atlantic than in the Pacific. The method is basically that used by Christal and Whitehead (2001), with some modifications. It uses data on the photographs of the flukes of diving, i.e., foraging, sperm whales together with GPS-recorded positions of the photographs. We used only high-quality photographs with Arnobom's (1987)  $Q \geq 3$ , in which female or immature whales were individually identified. We removed repeat photographs of the same individual within 10 min, and considered focal photographs with at least five other identifications taken within 2 h, of which at least one had to be taken before the selected photograph and one after it (and excluding photographs taken at the same time as the focal photograph). We then used these before and after identifications to estimate the mean track of the group, from quadratic regressions of latitude against time and longitude against time. From this track we calculated the left/right displacement of the focal identification from the mean track of the group (see Fig. 1 of Christal and Whitehead 2001), with left displacements being positive, and right displacements being negative, excluding displacements  $> 2$  km which seemed to result from problems with the track-fitting regressions. We considered the standard deviations of these left/right displacements as a measure of the spatial dispersion of the group.

We calculated these standard deviations for three studies in the Pacific and four in the Atlantic. There is no indication (Table III) that displacements about the track line were greater in the Atlantic, in fact there is a slight trend for the reverse. These displacements might have been confounded with group size, but there is almost no correlation between SD (left/right displacement) and estimated group size ( $r=0.069$ ;  $P=0.407$ ) among the 147 d on which the displacement was estimated for at least five identifications and for which we could estimate the group size with a CV  $< 0.3$  (using the mark-recapture method of Whitehead 2003b, pp. 216–217). Thus the spatial spread of individuals within groups seems similar in the Atlantic and Pacific.

### Social Structure of Units

Gero *et al.* (2008) examined the internal social structure of a well-studied unit off Dominica, in the Atlantic, and found substantial heterogeneity in the association

**Table III** Estimates of the spatial dispersion of individuals from the mean track within groups of sperm whales in the Pacific and Atlantic oceans, as indicated by the standard deviation of the left/right displacement of identified dive locations of individual sperm whales from the estimated mean trackline of the group's movement

| Ocean    | Study             | Number of focal photoidentifications | SD (left/right displacement, km) |
|----------|-------------------|--------------------------------------|----------------------------------|
| Pacific  | Galápagos 1995    | 316                                  | 0.69                             |
|          | Galápagos 1999    | 367                                  | 0.68                             |
|          | Chile 2000        | 1175                                 | 0.54                             |
| Atlantic | Sargasso Sea 2004 | 28                                   | 0.69                             |
|          | Dominica 2005     | 257                                  | 0.53                             |
|          | Dominica 2008     | 289                                  | 0.49                             |
|          | Dominica 2010     | 830                                  | 0.48                             |

strengths between non-calf unit members. In contrast, Christal and Whitehead (2001) found little evidence for preferred or avoided affiliations within 14 Galápagos social units from the Pacific, except in two large and relatively unstable units. We examined this apparent contrast by calculating the social differentiation within units during study years, thus avoiding heterogeneity that could be due to recruitment, mortality, emigration, or immigration. The social differentiation is the estimated coefficient of variation (standard deviation divided by mean) of the true association indices, i.e., the actual proportion of time associated, between members of the unit. A social differentiation of 0 is completely homogeneous, whereas if the social differentiation is  $>1.0$  there is considerable diversity among the relationships among the pairs of individuals (Whitehead 2008). We estimated social differentiation, using a simple ratio association index, defining association as diving within 10 min, and using daily sampling periods as in Christal and Whitehead (2001), by the likelihood method described by Whitehead (2008), and its standard error (SE) using the nonparametric bootstrap with sampling periods chosen randomly with replacement for each of 100 bootstrap samples. We compare the means of estimated social differentiation for those unit-year combinations with an estimated SE  $<0.2$ .

The mean social differentiation for the Galápagos (Pacific) was  $0.41 \pm \text{SE } 0.16$  ( $N=5$ ), and for the waters off Dominica (Atlantic)  $0.59 \pm \text{SE } 0.10$  ( $N=10$ ). There was no statistically significant difference between these values (Mann–Whitney  $U$ -test statistic 35.5;  $P=0.20$ ).

### Calving Rates and Care of Calves

It has been hypothesized that the evolution of communal care for calves was the driving force toward sociality in sperm whales (Best 1979; Whitehead 2003b). As a result, the presence and abundance of calves are likely factors influencing the particular social structures observed in either ocean.

Studies of the care of calves are more detailed in the Atlantic compared with the Pacific (there is also some information from the Indian Ocean; Gordon 1987). Sperm whales in the Sargasso Sea and off Dominica show somewhat different patterns of

calf care. The two systems differ both in the quantity and quality of allocare (typically by escorting calves at the surface while the mother was feeding at depth) provided by the escorts. Although all or most of the unit members in Dominica escorted calves in their units at some point, in each unit one nonmaternal female, which shared a strong bond with each calf, provided most of the allocare. In the Sargasso Sea, a small proportion of the larger groups escorted the calves and each calf had multiple females that nursed it (Gero *et al.* 2009). In the Pacific, published information on the details of calf care is limited to observations off the Galápagos that two particular females/immatures were identified escorting different calves at different times, and that one identified calf was observed being escorted by three different individually identified females/immatures at different times (Arnbom and Whitehead 1989). However, a statistical analysis of dive data collected off the Galápagos showed that, compared with groups without calves, groups that contained calves had less synchronous dive behavior, and thus shorter periods without females at the surface (Whitehead 1996a). No such study has been carried out in the Atlantic, partially because groups without calves are very scarce in most Atlantic study locations.

Off the Galápagos, the abundance of first-year calves as a proportion of observations of females and other immatures was 0.031 (685/22070 observations; 1985–1999), off mainland Ecuador 0.012 (60/5209; 1985–1993), and off Chile 0.007 (59/8475; 1993, 2000) (H. Whitehead, *unpubl. data*). In the North Atlantic, the abundance of known calves as a proportion of adults and immatures identified was 0.296 (48/162) off Dominica (2005–2010; S. Gero, *unpubl. data*), 0.182 (18/99) in the Sargasso Sea (2004 only; S. Gero, *unpubl. data*), and 0.124 (30/241) in the Gulf of Mexico (2002–2005; Jochens *et al.* 2008). Even with a slight difference in the methods used to calculate the values in the two oceans, it becomes apparent that calving rates are much lower in the Pacific, although some of this difference could be due to differences in calf mortality at, or soon after, birth. Also, it should be noted that calving rates from the Pacific are calculated from data collected between 1985 and 2000, and they may be higher now, especially if they were depressed by the effects of modern whaling that ended in 1982 (see later and Whitehead *et al.* 1997).

Thus, the primary difference between the oceans in regard to calves and calf care between the Atlantic and Pacific is in the number of calves, with calves being generally much more abundant in the Atlantic. A useful comparison of potential differences in calf care will have to wait until comparable studies of this phenomenon are conducted in the two oceans.

## Discussion

We have considered a number of measures (listed in the first column of Table IV) of the social lives of female sperm whales from the eastern tropical Pacific and North Atlantic. A few measures, such as the spatial dispersion of groups, showed no clear distinction. We collected the data for alloparental care in an asymmetrical manner, with different research foci in the different oceans. These methodological differences were themselves the result of a clear and strong contrast: the much higher preponderance of calves in the Atlantic. In consequence, we cannot at this time usefully compare patterns of calf care between the oceans. The statistical power of the analysis

**Table IV** Features of the social systems of female sperm whales of Atlantic and Pacific oceans that are considered in this article, together with assessments of the strength of evidence for contrasts between the oceans, and the potential of four driving factors

| Attribute   | Atlantic/Pacific contrast   | Strength of evidence for difference | Possible explanations:     |           |         |         |
|---|---|-------------------------------------|----------------------------|-----------|---------|---------|
|   |   |                                     | Oceanography/<br>resources | Predation | Whaling | Culture |
| Aggregation density   | Two- to threefold higher in Atlantic  | Good                                | XX                         | O         | XX      | X       |
| Scale of concentration  | Pacific: <i>ca.</i> 50 km<br>Atlantic: <i>ca.</i> 200 km                          | Fair                                | X                          | O         | O       | X       |
| Population structure  | Pacific: <i>ca.</i> 2000 km<br>Atlantic: <i>ca.</i> 500 km                        | Indication                          | X                          | O         | O       | X       |
| Clans   | Pacific: important<br>Atlantic: absent  | Good                                | X                          | X         | O       | XX      |
| Group size  | Pacific: <i>ca.</i> 28<br>Atlantic: <i>ca.</i> 8                                  | Good                                | X                          | XX        | X       | X       |
| Unit size   | Pacific: <i>ca.</i> 11<br>Atlantic: <i>ca.</i> 8                                  | Fair                                | O                          | X         | X       | X       |
| Group/unit genetic structure                                    | More matrilineal in Atlantic than in Pacific                                      | Indication                          | O                          | O         | X       | X       |
| Spatial spread of groups (SD displacement from mean track line) | Little difference:<br>Pacific: <i>ca.</i> 0.6 km<br>Atlantic: <i>ca.</i> 0.6 km   | Poor                                | —                          | —         | —       | —       |
| Intraunit social differentiation                                | No significant difference:<br>Pacific: <i>ca.</i> 0.4<br>Atlantic: <i>ca.</i> 0.6 | Indication                          | O                          | X         | X       | X       |
| Proportion of calves  | Pacific: <i>ca.</i> 0.015<br>Atlantic: <i>ca.</i> 0.18                            | Good                                | X                          | X         | XX      | X       |
| Allomaternal care   | Present in both oceans  | None                                | —                          | —         | —       | —       |

XX=most likely factor; X=potentially significant factor; O=unlikely to be important; —=no indication of contrast between oceans

of the kinship structure of groups was low, again restricting the scope of our conclusions. However, in other respects the social lives of female sperm whales within their multilevel societies are clearly different in the two oceans. Compared with Atlantic sperm whales, those in the Pacific have generally larger ranges and form much larger groups. They are also members of culturally defined sympatric clans, which do not seem to be present in the Atlantic (Table IV).

We consider four potential explanations for these differences: oceanography as a driver of resource availability, predation, patterns of whaling, and culture. We explain how each factor differs between the oceans and how these differences might have impacted social structure. In Table IV we make a rough assessment of the potential for each factor being the cause of the observed differences in social structure. These factors are not necessarily mutually exclusive, and may work in consort, e.g., if

individuals develop cultural traditions to deal with local oceanographic or predation issues.

### Oceanographic Contrasts and Resource Availability

The Atlantic and Pacific oceans differ systematically in several ways, including the Pacific being much larger, generally deeper, with narrower continental shelves and steeper continental slopes. There is also a systematic difference in the study sites, in that those in the Pacific are on the eastern side the ocean basin, and those in the Atlantic on the western side of the ocean basin or, in the case of the Azores and the Sargasso Sea study areas, in the central ocean gyre (Fig. 1). Eastern boundary currents found on the east side of ocean basins in temperate waters flow toward the equator and are cold, broad, slow, and generally productive. The Humboldt Current strongly affects the waters of our Chile, Ecuador, and Galápagos study areas. By contrast, the western boundary currents found on the west side of ocean basins (such as the Gulf Stream) are warm, narrow, rapid, deep, and generally unproductive currents that flow poleward from the tropics (Garrison 2007) (Fig. 1). The gyres are particularly unproductive. These Atlantic/Pacific and eastern/western contrasts mean that study sites in the Atlantic are generally warmer and less productive than those in the Pacific. However, in other respects, there are similarities between our study sites in the different oceans: Dominica, Azores, and Galápagos are all close to steep islands of volcanic origin; those near the Sargasso Sea, mainland Ecuador and northern Chile, are broader areas off fairly linear continental shelf breaks; and the Gulf of California and Gulf of Mexico are both nearly enclosed water bodies well separated from the main ocean.

It seems most unlikely that any of these physical oceanographic traits directly affects sperm whale social structure in any appreciable way. However, they will affect the overall abundance and spatial and temporal availability of resources for the sperm whale, particularly the deepwater cephalopods upon which they largely subsist (Kawakami 1980). Unfortunately, we know little about the ecology and life history of these cephalopods, making it difficult to examine directly any relationships between sperm whale density and distribution with that of their prey (for an exception see Jaquet and Gendron 2002). The effects of oceanography on sperm whales through resource availability are therefore speculative. However, oceanic fronts, currents, and bathymetry are some factors influencing the distribution and abundance of squid (Bakun and Csirke 1998; O'Dor 1992). Thus physical oceanographic processes could lead to differences in the types and densities of squid available to sperm whales, as well as the spatial and temporal variation of these densities. As sperm whales almost certainly compete with each other for food in some circumstances and at some scales, and may be able to cooperate with one another in other circumstances and over other scales (Whitehead 2003b), these differences in oceanography could drive differences in social structure.

For instance (Table IV), a higher density of sperm whale aggregations in the Atlantic could result from a greater overall density, or differences in the aggregative structure, of cephalopod prey. Oceanography could also drive sperm whale movements (Whitehead 1996b) and thus potentially their population structure via the spatial and temporal scale and stability of concentrations of their squid prey. Prey

abundance may be more predictable in the Atlantic than in the Pacific, where the El Niño Southern Ocean phenomenon seems to have a large effect on sperm whale feeding success and migrations (Ramirez and Urquizo 1985; Smith and Whitehead 1993). Sperm whale clans in the Pacific have distinctive movement strategies and feeding success (Whitehead and Rendell 2004). The evolution and persistence of the clan structure may be related to the diversity and temporal variability of sperm whale resources (Antunes 2009). For instance, if there are consistently two or more rather different types of prey available, and specialization generally pays, then culturally propagated feeding traditions, which expand into other areas of behavior, may evolve in communities of interacting animals (Estes *et al.* 2003; Sargeant and Mann 2009). Similarly cultural traditions may relate to methods of dealing with variability over large or small scales of space or time.

Differences in resource availability can easily be seen as drivers of differences in group size. If the main disadvantage of grouping is competition for food, then larger groups will be penalized more in areas with less concentrated food (Krause and Ruxton 2002). With generally less primary productivity in the Atlantic study areas (Antunes 2009), we might expect lower cephalopod densities and thus smaller groups, the pattern observed. However, the higher reproductive success of Atlantic sperms would seem to indicate better feeding. This apparent contradiction might be explained by scale: if cephalopods in the Pacific are hard to find but occur in large temporary gluts, whereas those in the Atlantic are spread more evenly spatially or temporally, then the result might be smaller groups but greater reproductive success in the Atlantic.

## Predation

Although sharks may scavenge sperm whale carcasses, and medium-sized cetaceans such as pilot whales (*Globicephala* spp.), may harass the living individuals, it seems unlikely that any of these species are a serious mortality risk to sperms (Whitehead 2003b). In contrast, the considerably larger killer whales have been observed attacking and killing sperm whales (Whitehead 2003b). Sperm whales defend themselves against these attacks socially and communally, usually but not always successfully (Pitman *et al.* 2001). Defending themselves and their young against killer whales may be the primary function of the sociality of female sperm whales (Pitman *et al.* 2001; Whitehead 2003b). However, of all 10 descriptions of attacks by killer whales on sperm whales in the scientific literature (Brennan and Rodriguez 1994; Jefferson *et al.* 1991; Pitman *et al.* 2001; Whitehead 2003b), none were in the North Atlantic, while 6 were in the eastern Pacific (the other 4 are from the Southern Ocean). This is despite the fact that more time has been spent observing living sperm whales in the North Atlantic than in Pacific, and that killer whales have been known to attack other large whales in the North Atlantic (Whitehead and Glass 1985). Three of us (H. Whitehead, S. Gero, L. Rendell) observed killer whales and sperm whales in the same place at the same time in the North Atlantic (May 7, 2004; 40°5'N 63°50'W): the two species seemed to ignore one another, an unusual occurrence in the Pacific, where sperm whales often react dramatically to the presence of killer whales (Arnbom *et al.* 1987; Brennan and Rodriguez 1994; Pitman *et al.* 2001). Part of the reason for the lack of observations of killer whales attacking sperm whales in the Atlantic may be a lower



density of killer whales than in the Pacific; they are very rarely sighted in any of our Atlantic study sites, whereas there are a number of sightings from the Pacific counterparts. However, another factor seems to be at work. Killer whales are very much creatures of habit, with each set of killer whales having a few species of clearly preferred prey, while other potentially nutritious food is ignored (Ford and Ellis 2006; Ford *et al.* 1998; Pitman and Durban 2011). The potential explanation for these observations then is that sperm whales, while being a potential prey item for some Pacific killer whales, are not on the regular menu for most or all North Atlantic members of that species, despite perhaps being a more attractive prospect, with smaller groups defending larger numbers of calves. If so, this difference in risk could explain the smaller sizes of the groups, and perhaps units, in the Atlantic. Killer whale danger might also promote clan formation if members of the clans have developed different methods of protecting themselves against killer whales. If killer whales are killing a fair number of infants then this difference in predation rate could also explain the relative scarcity of young calves in the Pacific (Table IV), although there is no evidence that killer whales do kill a substantial number of sperm whale calves.

## Whaling

Sperm whaling came in two phases, each with its characteristic technology. Open boat whaling started in 1712, peaked in the 1840s, with about 6000 sperm whales being killed per year (Starbuck 1878), declined in the later years of the 19th century, and had marginal significance in the 20th century (Rice 1989). The whalers used sails and oars, caught the whales with hand-thrown harpoons, and killed them with hand-held lances. Many whaling ships were based in New England ports such as Nantucket and New Bedford. During the 18th century almost all their whaling was in the North Atlantic, and they continued to sail through the grounds of the northwest Atlantic on their voyages to and from other oceans in the 19th century. Thus the whales using our Atlantic study areas were particularly heavily targeted by the open-boat whalers in the 18th and 19th centuries.

Modern mechanized whaling, with catcher boats and harpoon guns, began in the late 19th century, started to target sperm whales seriously in the 1920s, peaked in the 1960s, with *ca.* 25,000 sperm whales being killed per year, and virtually ended in the 1980s with the International Whaling Commission's (IWC) moratorium on commercial whaling (Tønnessen and Johnsen 1982). This type of whaling was carried out all over the world, except in the warmer waters of the western North Atlantic, so female sperm whales in our Atlantic study areas were virtually unaffected. In contrast, between the 1950s and early 1980s mechanized sperm whaling was particularly intense in the eastern tropical Pacific. The whales were targeted by shore-based operations in Peru and Chile (Ramirez 1989), as well as by pirate whalers (Tønnessen and Johnsen 1982), all operating outside the regulations of the IWC. Thus, the populations using our Pacific study areas were heavily affected by quite recent whaling.

This contrast in recent whaling experience could explain some of the differences between Atlantic and Pacific social systems. The destruction of social units in the Pacific may have made them less matrilineal, led to increased unit or group size, and

increased social homogeneity within units, if remnant social structures merged after the slaughter. Such mergers may have constituted attempts to maintain necessary social services, such as sufficient numbers of individuals within units for effective communal defensive against killer whales, as well as social arrangements for rearing and protecting calves, or sharing knowledge. The exploitation may also have lowered the birth rate, either by changing the sex ratio—large mature males were targeted particularly heavily—or because reproductive success, and successful calf-rearing, was lowered for females in social units that had lost important members (Whitehead *et al.* 1997), as has been found with elephants (*Loxodonta africana*) that have a social structure similar to that of sperm whales (McComb *et al.* 2001; also see de Silva and Wittemyer 2012). Finally, sperm whale populations in the Pacific may have undergone dramatic range shifts, after removal of individuals along the productive coastal waters of South America opened an ecological opportunity for groups previously occupying less productive central gyre waters to the west (Whitehead *et al.* 1997). These movements may have brought previously allopatric groups into sympatry, resulting in the sympatric behavioral variation we observe today in the Pacific but not the Atlantic.

## Culture

The differences between the vocalizations, habitat use, and movement strategies of the clans of female sperm whales in the Pacific are almost certainly culturally determined: the whales learn these behavioral patterns from their mothers or other members of their unit/group/clan (Rendell and Whitehead 2003; Whitehead and Rendell 2004). However, there may be much more to their cultures than this (Whitehead 2003b). Their culture could include, directly or indirectly, how they aggregate and move, whether they form clans, or how groups or units should be structured (Table IV). There is evidence that Pacific clans have differential reproductive success (Marcoux *et al.* 2007a), which suggests that differences in calving rates between Atlantic and Pacific female sperms might also be partially a consequence of cultural differences between the behaviour of the whales—e.g., foraging or defensive behavior—in the different oceans. Unfortunately culture, although easy to speculate about and thus appearing prominently in Table IV, is hard to pin down (Laland and Janik 2006), so there is little we can say definitively on this, apart from again noting that the apparent lack of major genetic divergence between the two oceans is at least consistent with the notion of a cultural component to the observed variation in social behavior.

## The Multilevel Societies of Sperm Whales: Evolution and Function

For some time sperm whale scientists have suggested that the complex matrilineally based, multilevel societies of female sperm whales are largely driven by their deep-diving behavior and the potential for predation, especially on their calves (Best 1979). Female sperm whales must dive deep to feed (Whitehead 2003b) and their calves cannot, or do not, follow. Thus, they are left at the surface, vulnerable to predators. The presence, at or near the surface, of other members of the calf's social unit or group provide safety through vigilance, as well as individual and communal defence. From this perspective, one might expect the larger the group or unit the better (Krause and Ruxton 2002).

There are other potential benefits, as well as costs, of groups or units. Whitehead (2003b) considers the potential foraging benefits of forming a group, concluding them to be likely fairly small for predators of deepwater cephalopods in most instances. However, over longer time scales, the permanence of the social units provides a potential benefit in communal knowledge, either pooled among the females (Johnstone and Cant 2010) or transmitted from the most experienced to the least, as in the congruently structured elephant societies. The most obvious downside of this communal living is competition for food, which will increase with group and unit size. This competition will be at the level of the group of individuals that forage in the same space, which will be the same as the unit size if there is no grouping of units. Group and unit sizes are expected to evolve generally to maximize the differences between their benefits and costs (Krause and Ruxton 2002). The antipredation benefits could be at either the level of the group, if sheer numbers are what count when protecting a female or calf against predators, or at the level of the unit if experience working together is important when dealing with the threats. In contrast, the communal knowledge benefits will be at the level of the unit.

Could this framework explain the Atlantic/Pacific contrasts? Some aspects of the social structure of female sperm whales—especially group size and the presence of clans—are so consistently and compellingly different between the Atlantic and Pacific that they signal one of the major factors that differ between the oceans as a driver. Oceanography does differ systematically between the Atlantic and Pacific sites, and this may affect foraging ecology, and so drive social systems, as suggested in the preceding text. However, the data that we have assembled do not appear consistent with this scenario, at least at a superficial level. If feeding success was better in the Atlantic, then why are groups smaller? If feeding success was better in the Pacific, then why is calving success lower? As noted previously, differences in the scales of the benefits and costs might produce the observed pattern. However, in the Pacific, feeding success varies considerably between years at the same location (Smith and Whitehead 1993), without much obvious change in social structure (Whitehead and Kahn 1992). At different locations in the Pacific, and at different times, whales can be eating very different kinds of cephalopods: small (*ca.* 0.4 kg), sluggish histioteuthids off the Galápagos (Smith and Whitehead 2000) vs. large (*ca.* 30 kg), mobile, and aggressive *Dosidicus gigas* in the Gulf of California (Jaquet and Gendron 2002). Thus, although oceanographic differences between the oceans may account for larger scale phenomena such as scales of sperm whale concentration through their influence on cephalopod distribution, there seems less support for them as drivers of the social differences at levels of social groups and units.

In contrast, if units are largely about communal knowledge, and groups function mainly in defence against killer whales, then the fairly similar-sized units in the two oceans, but much larger groups in the more dangerous Pacific make sense. Further, the members of these large Pacific groups may be paying for their safety with competition-induced reductions in feeding success, which might have consequences for reproductive rates, partially explaining that contrast between the oceans. The low incidence of calves in the Pacific groups may explain the indicated reduction in social differentiation, as intraunit social structure of at least one Dominica unit is based around the presence and care of calves (Gero *et al.* 2008).

Antunes (2009), noting that social units in the Atlantic rarely form groups with other social units whereas those in the Pacific usually do (Table II), suggests that the formation of clans may be a response to this. Units form groups with other units that possess similar behavior, and these preferences led to the development of symbolically marked (using the coda vocalizations, and perhaps other signals) clans. In the Atlantic, with much lower predation risk, grouping is less frequent and less critical, so clans did not develop.

Although the different balances between defense against predators—seemingly a large issue in the Pacific but not in the Atlantic—and resource competition may explain the most obvious contrasts in social structure of female sperm whales in the two oceans, the other factors listed in Table IV may also have roles. Consistent differences in oceanographic processes may, through their effects on cephalopod distributions, have led to ocean-specific larger scale patterns at the level of aggregations. At the smaller scale, quite recent heavy whaling in the Pacific may have had an important role in changing the kinship and social structure of units, making them less matrilineal but more socially homogeneous. It is also a likely factor in the much lower incidence of calves in the Pacific, which, as we have noted, has large implications for small-scale social structure. Culture, our fourth factor, is rather a black box. It could explain any of the contrasts in Table IV because culture can easily produce strange and sometimes nonadaptive patterns in large-scale behavior (Richerson and Boyd 2005). For instance, there are many clear systematic differences between the social behavior of humans in Europe and eastern Asia. These contrasts are fairly consistent across a wide range of environmental conditions on both continents, and are the products of cultural evolution. Similar processes may have happened with sperm whales, or other cultural species. However, they will be very hard to pin down as culture is so difficult to study in wild animals, especially when they live in the deep ocean. Ironically, in the predation-based scenario that we have outlined for the evolution of consistent differences between sperm whale social systems in the Atlantic and Pacific, the fundamental distinction between the oceans is in the culturally driven behavior of killer whales, for which sperm whales are on the menu in the Pacific, but not in the Atlantic. This, apparently arbitrary, difference in the cultures of killer whales in the two oceans then may have had a large role in shaping the multilevel social systems of the sperms.

We have presented a scenario for the differences in social measures between sperm whales in the two oceans that have emerged from much field work. It seems plausible but may well be wrong. Sperm whale social systems are difficult to study. There is much to learn. Goals should include fine-scale studies of social behavior, such as the work of Gero *et al.* (2009) on calf care, in both oceans, detailed analysis of the kinship structure of groups and units using molecular genetics, and the study of culture at all levels of their societies.

### Comparison Between Species

A major difference between the multilevel societies of sperm whales, as well as killer whales, and those of primates, is the role of males. In these whale species, adult males are either not present in the primary social units—sperm whales—or have rather peripheral roles—killer whales. In contrast, relationships between adult males and

females, and interactions among adult males, are prominent features of primate multilevel societies and have been hypothesized to drive their formation (Grueter and Van Schaik 2010; Grueter and Zinner 2012). This primary difference between cetaceans and primates is likely related to increased difficulty in defending anything, whether resources or females, in the fluid, three-dimensional ocean (Whitehead 2003a).

Hill *et al.* (2008) found a consistent scaling ratio between the group sizes at successive layers of a multilevel social structure. It is close to three in several primate species, elephants, and resident killer whales. The sperm whales in the Pacific seem a major exception, with unit sizes of *ca.* 11, group sizes of *ca.* 28 (although sperm whale groups, being ephemeral are not really a level of social structure), and clan sizes in the thousands. The clans are hundreds of times larger than groups or units, so, unless there are multiple levels of sperm whale social structure that we have not identified, sperm whales do not abide by the universal scaling factor of 3.

## Conclusion

The social system of female and immature sperm whales in the North Atlantic is based around the social unit, about 6–12 often matrilineally related individuals that move together, raise their calves communally, and likely share important knowledge. These units very occasionally form groups with other units. In the Pacific, grouping with other units is the norm perhaps, we suggest, as a response to predation by killer whales. The frequency and importance of group formation in the Pacific then seems to have led to, or at least contributed to, the evolution of the most remarkable level of sperm social structure: very large, sympatric, cultural clans. Extremely heavy modern whaling in the Pacific may have destroyed the integrity of many units, as well as affecting the adult sex ratio. The consequences either directly, or indirectly because of a consequent drop in reproductive rate, may be less matrilineal and socially differentiated social units than in the Atlantic. Systematic differences in oceanography between the oceans likely affect their aggregation patterns at larger scales.

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