

Causes and consequences of female centrality in cetacean societies

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“The evolution of female-biased kinship in humans and other mammals” Mattison et al. (Eds)

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Abstract

Cetaceans are fully aquatic predatory mammals that have successfully colonized virtually all marine habitats. Their adaptation to these habitats, so radically different from those of their terrestrial ancestors, can give us comparative insights into the evolution of female roles and kinship in mammalian societies. We provide a review of the diversity of such roles across the Cetacea, which are unified by some key and apparently invariable life-history features. Mothers are uniparous, while paternal care is completely absent as far as we currently know. Maternal input is extensive, lasting months to many years. Hence, female reproductive rates are low, every cetacean calf is a significant investment, and offspring care is central to female fitness. Here strategies diverge, especially between toothed and baleen whales, in terms of mother-calf association and related social structures, which range from ephemeral grouping patterns to stable, multi-level, societies in which social groups are strongly organised around female kinship. Some species exhibit social and/or spatial philopatry in both sexes, a rare phenomenon in vertebrates. Communal care can be vital, especially among deep-diving species, and can be supported by female kinship. Female-based sociality, in its diverse forms, is therefore a prevailing feature of cetacean societies. Beyond the key role in offspring survival, it provides the substrate for significant vertical and horizontal cultural transmission, as well as the only definitive non-human examples of menopause.

1. Introduction

When cetacean ancestors severed all ties with terrestrial habitats, capable of completing their entire lifecycle without recourse to any solid ground, they became subject entirely to the selective forces engendered by the marine habitat. This was the beginning of an evolutionary experiment on how a terrestrial heritage of mammalian sociality would respond to the diverse and sometimes radically different nature of oceanic ecosystems. In this review, we summarise how this natural experiment provides deep comparative insights into social evolution, especially the role of female kinship, and how both flexibility and constraint interact in the evolution of female social roles. While we know a lot about some species, we know almost nothing about the social structure of most of the 80+ cetacean species, which means most of these potential insights remain untapped. Given both the strong parallels and key differences between primate and cetacean social systems—including brain size, life history, and diversity in social bonds—comparative analysis of female social roles in cetaceans can inform our understanding of female social roles in primate societies, including our

own. This has important implications for understanding socio-cultural changes in modern human societies, where for example a comparative understanding of female social roles can guide thinking about sources and solutions to the problem of underrepresentation of women in positions of leadership [1]. Therefore, in this paper we review the behavioural ecology literature on cetacean social structure to provide a synthesis of the varied, and sometimes very pronounced, forms of female-based kinship found in this taxon, and try to identify broad principles to organise this diversity. We hope this will help researchers aiming to understand similar variation across both aquatic and terrestrial mammalian societies, including that between human societies.

We shall explain how things are different for a mammal in the ocean, but does this mean that the social evolution predictions formulated over decades of research in terrestrial mammals do not apply to cetacean societies? A recent analysis of mammalian social complexity and kinship by Lukas & Clutton-Brock [2] shows how the distribution of different aspects of social complexity is strongly related to average within-group female relatedness. However, lack of data meant only one cetacean species was included, so here we assess how well our understanding of cetacean sociality matches qualitatively with these predictions. Furthermore, the traditional view of female sociality in primates has centred on the competition for food, as delineated by the distribution of resources (e.g. [3]), but the nature of such competition can be radically different in a fluid three-dimensional environment where travel costs can be low and resources can be impossible to defend. So can we readily apply such views to cetaceans?

The key message of our treatment is a conceptual relationship, laid out in Figure 1, between modularity of social structure (i.e. the extent to which associations are concentrated within rather than between long-term social groups) and the degree to which those social organisations are biased toward females. Where cetacean species have a modular social structure, that modularity is always centred around lineages of close female relatives. Organisation into sets of highly connected individuals (i.e. a modular social structure) is associated with a tendency of maternally-related individuals to interact among themselves. This ranges from systems described as ‘matrifocal’, a loosely defined term largely reflecting statistical population genetic findings of increased maternal relatedness with social groups compared to between [e.g. 4], up to true matrilineal kinship structure, in which long-term groups strictly contain individuals related through a recent female ancestor. This relationship differs between baleen and toothed whales. The social systems of baleen whales tends to be generally unstructured (here illustrated by the highly connected, non-modular social network of humpback whales with a weak matrilineal influence) while the social systems of toothed whales are more variable, with variation across species loosely correlating with body size.

The social structures of small species range from low to intermediate levels of both modularity and influence of matrilineal kinship (here, illustrated by the modular social network of bottlenose dolphins in which females apparently occupy more central positions). Such modularity as exists in the better known small toothed whales seems to be driven by a variety of other social (e.g. homophily and learning [5]) and non-social mechanisms (e.g. home-range and temporal overlap [6]) and although matrilineal kinship may organize social relationships (e.g. [7]) the organisational bias is not strong enough to create discrete social modules. In contrast, both modularity and the strength of female-biased kinship organisation peak among the larger toothed whales, illustrated by the social structures of sperm and killer whales, characterized by lifetime division into social modules of highly-related individuals.

We first discuss how and why things are different, ecologically and socially, for mammals in the ocean. We then provide an overview of female kinship organisation in cetaceans, structuring our treatment along the most significant taxonomic division in the group, between the baleen and toothed whales. For each, we outline what is known about female kinship and how this relates to foraging ecology and mating systems, but are biased toward the toothed cetaceans, where we see diverse forms of female-biased kinship. In particular, we develop a case study of killer whales, *Orcinus orca*, because it potentially informs us about key aspects of human evolution, such as the evolution of menopause. Finally, we synthesise these findings in to an assessment of how well cetaceans fit within the current models of female sociality outlined above.

2. Mammals in the ocean

Cetaceans comprise a diverse collection of animals in terms of length, habitat, life-history strategies and social systems [8]. Body sizes vary from the 1.3m vaquita, *Phocoena sinus*, to the >30m adult blue whale, *Balaenoptera musculus*. They are distributed nearly from pole to pole, inhabiting the coldest to the warmest seas, and from shallow riverine and coastal waters to offshore pelagic zones. The most profound differences, both phylogenetically and socioculturally, lie between the generally larger, long-lived 14 species of the suborder Mysticeti and the disparate group of ~76 species that comprise the suborder Odontoceti (henceforth baleen and toothed whales, respectively). They all occupy intermediate to top trophic levels but have evolved quite different primary feeding adaptations, filter-feeding baleen and echolocation respectively. These lead to major divergences in anatomy, foraging behaviour and life style. Baleen whales typically migrate to tropical breeding grounds in winter and temperate or polar feeding grounds in summer, where they filter large, dense schools of small planktonic crustaceans and schooling fish from the water. Toothed whales do not

follow such strict migration schedules. While their varied life styles match the diversity of their body sizes and habitats, all use their echolocation to hunt prey ranging from a wide diversity of fish and cephalopods, to other marine mammals.

Like all mammals [9], cetacean females play the pivotal role in reproduction and the survival of offspring, including gestation, lactation, weaning, post-weaning care. Currently we know of no species in which paternal participation extends beyond copulation. In the thermodynamically challenging aquatic habitat, female reproduction is even more energetically expensive than on land. Cetaceans expend considerable energy to regulate body temperature, and females must help newborns to quickly grow and insulate their bodies with blubber layers. Females universally give birth to a single, large precocial calf after long gestation periods, and subsequently produce extremely lipid-rich milk [10]. Young cetaceans take time to achieve behavioural and energetic independence, and so cetaceans are unusual in the ocean where parental care is uncommon. Since their mating systems are, wherever known, polygynous or polygynandrous, such care falls almost entirely on the mothers, who will nourish the young until they learn to feed for themselves, and may go on to protect and accompany them well into their adult lives. Female cetaceans are therefore slow offspring producers with long somatic and reproductive lifespans, and long gestation and maturation periods (Figure 2), ramping up the scale of investment represented by each calf, and turbocharging the divergent selective pressures on males and females. The mother-calf bond is therefore the cornerstone of cetacean societies.

Outside the mother-calf pair, cetaceans are typically gregarious animals, but show a large diversity in observed group size, from pairs to pelagic dolphin shoals that number thousands [11]. They form groups that are tightly clustered spatially. Individuals are usually within a few body lengths of one another, and if not, still within easy communication range [12]. While the groups vary considerably in number of members and stability, cetaceans actively form and maintain these groups by coordinating behaviour with group mates. In several, perhaps most, species, there is substantial sexual segregation, so females primarily accompany other females [13,14]. The drivers of this segregation are not fully understood, but likely reflect the two sexes having divergent ecological and social needs for reproductive success (for example, male sperm whales, *Physeter macrocephalus*, accessing high-latitude food sources to attain competitive size or male bottlenose dolphins, *Tursiops* spp., increasing mating opportunities by joining alliances [11]). From the perspective of observers, and perhaps for the animals themselves, the most salient attribute of groups is association—the animals are close together and coordinate their movements. This may bring them a number of benefits, including protection against predators and the communal discovery of food, but the

association itself may be an important part of maintaining bonds [12]. Repeated observations of associations between individuals leads researchers to think about the relationships underlying the associations, and in female cetaceans we see a diversity in the strength of such bonds such that there is a parallel diversity in the terminology used to describe collections of individuals who regularly associate - groups, units, pods, herds, and so forth. Partly this reflects a somewhat haphazard historical approach to terminology in the field. For example, stable groups of maternally-related mid-sized toothed whales tend to be referred to as 'pods', while in sperm whales, the largest toothed whales, they are 'units', for reasons that initially appear simply historical (it is also possible to see 'pod' used as a default term for assemblages of cetaceans, regardless of association strength or relatedness). But this also reflects the fact that in many species we observe relationship patterns that are unique, and do not readily extend across multiple species or even populations, so for example killer whale pods in some populations can be extremely stable, less so in others [15], while there is evidence of membership change in sperm whale units [16]. Here, we use terms that reflect the original literature and try where possible to bring through the original definitions of those terms in order that readers can appreciate the underlying diversity. The diversity is unified however by the idea that bonded females can increase mutual fitness through cooperative hunting, alloparental care (care provided by individuals other than the biological parents), and communal defence of each other and their calves, as well as through sharing information. For female cetaceans, we argue, the ramping up of divergent selection pressures has made these benefits even more important and thereby strongly favoured female-biased kinship organisation.

Relationships between female cetaceans need not be universally mutualistic of course, but aggression and dominance seem rare—for example, female-female aggression is very rare in the best-studied population of bottlenose dolphins in Shark Bay, Australia [17]. Female dominance hierarchies have been described in captivity, but took years to identify, being based on a handful of 'flinches' per year, and these animals were in forced proximity [18]. Interestingly, the hierarchy that emerged among females was based on age, not size. There is little evidence for such hierarchies in the wild however, as female can readily avoid each other in fission-fusion societies [19].

Furthermore, resource defence is very different in marine habitats. Often it is simply impossible, if not pointless, because of the abundance of resources – even in a shallow water coastal dolphin population, where resource defence might be more plausible, 32 years of study have yielded just one observation of prey stealing (JM, pers obs) and females are completely tolerant of others closely inspecting their prey catches [20]. Thus competition between females seems to be largely indirect.

3. Maternal kinship in baleen whales

The baleen whales are among the largest animals that ever lived, with the relatively recent evolution of present gigantism coincident with increases in intense but ephemeral primary productivity resulting from wind-driven upwelling starting in the Pliocene, around 4.5 Ma [21]. Baleen whale lives reflect their reliance on dense aggregations of small, low trophic level prey that are highly abundant only seasonally [22], inducing most species to undertake long, regular feeding/breeding migration cycles [23]. They accumulate energy for reproduction during an intense half-year feeding season during the summer, taking advantage of seasonal resource abundance driven by blooms in primary productivity in temperate and high latitude waters. For the other half of the year they largely fast, and migrate to warmer, low-latitude winter breeding grounds. There, males provide their brief reproductive contribution while females engage in the costly tasks of gestation, parturition, lactation, and/or offspring protection. Combined, these female life-history processes tend to be fast relative to other cetaceans [10], notable in relatively fast offspring growth during short gestation and lactation periods (Figure 2). Most baleen whales are therefore capital breeders. Lactation is short, 6-8-mo, with calves typically weaned in their first year after extraordinary energy transfers—blue whales for example transfer about 220 kg of milk per day to their calves [24]. Post-weaning maternal care is very limited [25]. Females take about a year to replenish body reserves, breeding every other or every third year, which makes the full reproductive cycle rather short for such large, long-lived mammal [10,22].

Groups of baleen whales are typically small and temporary, formed by individuals aggregating in feeding and reproductive contexts and then parting ways once the activity is over [10,22]. An individual whale may associate with many others during its lifetime, forming dense, yet weakly connected social networks (Figure 1). The exception amongst the generally short-lived and unstructured social interactions is the mother-calf bond [10]. However, this general picture is based on extremely sparse knowledge, and at least in some cases there is evidence for subtle longer-term social effects, especially in the relatively well studied humpback whale, *Megaptera novaeangliae*, on which our discussion primarily focusses. Furthermore, nearly all baleen whale populations were severely impacted by whaling, and only some have recovered to anything like their pre-hunt densities. We expect most mammals to show some degree of flexible responses to ecological conditions, including conspecific density, so we cannot really know the extent to which our current

picture of baleen whale sociality is of a markedly shifted baseline as opposed to the conditions under which it primarily evolved (e.g. [26,27]).

While the mother-calf bond is relatively short compared to toothed whales, it is the one form of female kinship organisation that most profoundly affects baleen whale populations. During their first year calves accompany their mothers on a migration cycle to the feeding grounds before returning back to the breeding area. Calves apparently learn the route in so doing, and consequently both males and females show fidelity to this migration pathway, restricting gene flow between populations that utilize different seasonal habitats. Multiple studies of the maternally-inherited mitochondrial DNA at the global [28–30], ocean basin [31], and single population [32] scale confirm that this basic element of female kinship creates migratory traditions in this species that have profound consequences for the genetic structure of its populations. Similar results have been presented for southern right whales, *Eubalaena australis*, suggesting this may be the case across many migratory baleen whale species [33]. Furthermore, it seems that these traditions conform to more than just general feeding or breeding areas, as returning calves are more likely to return to local habitat features on scales of ~50km [34,35], suggesting that female-based population structure also occurs on a fine scale. A consequence of this second, female-based inheritance system for migratory knowledge is that in the post-whaling era it is far from certain that all historical breeding populations will be able to recover properly if they lack adequate habitat knowledge [33].

Data on longer term social bonds that might support female-based kinship are patchy at best, and again largely confined to the relatively well-studied humpback whales. One study of southern hemisphere migrating humpback whales showed that once mother-calf pairs were excluded, then there were no obvious relatedness patterns in animals that were sampled either associated during migration or on the same day in the same area [36]. This study therefore suggests that there is little obvious social role for female-based kinship among adult females. However, on a northern hemisphere feeding ground, more stable associations have been documented, lasting up to 79 days and with pairs of animals re-associating in multiple years [37]. Genetic sampling in this population subsequently showed that when mother-calf pairs were excluded, females were still on average 1.7 times more likely to form social associations with maternally-related individuals (i.e. sharing the same mitochondrial DNA haplotype) than by chance, while there was no such evidence for males [38]. This suggests that we are yet to fully understand fine-scale female kinship organisation in these populations. Importantly, these associations appear to have fitness consequences in that there appear to be significant variations in fecundity between matrilineal lines [39]. Similarly, while on a feeding ground in the Gulf of St. Lawrence, Canada, pairs of similar aged non-lactating females were seen

associated together for up to six successive summers, and females in the pairs that had the longest history of association also had the highest reproductive output [40]. It therefore seems highly plausible that maternal kinship does affect humpback whale social associations, but in ways that are still too subtle for our current knowledge to detect.

Humpback whales can however share more than simply migratory knowledge within their populations. In well-studied populations, evidence for important social learning effects is clear. For example, in the humpback whale population that feeds in the Gulf of Maine a novel-foraging technique, lobtail feeding, spread through cultural transmission in response to an ecological shift leading to a switch of primary prey species [41]. There was no evidence that females or males were more likely to learn the technique, nor that calves whose mothers used the technique were more likely to acquire it themselves, suggesting a broadly horizontal social transmission pattern. There is circumstantial evidence however that, like migration, these foraging preferences and techniques might sometimes pass within maternal lines. It comes from an unusual mortality event in the late 1980s caused by whales eating mackerel (*Scomber scombrus*) contaminated by neurotoxins from an algal bloom [42]. Ten whales that died were sampled, and all had one of two mitochondrial DNA haplotypes, sufficiently rare in the broader population to make it statistically implausible to be a chance pattern. Since humpback whales eating mackerel is not common, the authors suggested this shared prey preference could represent foraging preferences transmitted culturally down matriline just like migratory knowledge [42]. Such preferences could be one mechanism underlying fecundity variation between matriline. We have also known for some time that in some regions, such as the waters off Southeast Alaska, humpback whales cooperate very closely to gather and concentrate shoals of prey (e.g. [43]), but the relationships between members of these cooperating groups are poorly known. Whales in this region are also quick to exploit new resources—in the past decade they have increasingly targeted juvenile salmon released from hatcheries [44] but again, we lack the necessary corollary information to understand any role of female kinship in the spread of the behaviour. We therefore still have much to learn about baleen whale sociality and the role that female kinship organisation might play in it, but the hints are there that it might be a significant factor, largely mediated by the transmission of knowledge within the mother-calf bond.

4. Maternal kinship in toothed whales

Toothed whales are a more speciose and more heterogeneous taxon than the baleen whales. Species vary more in size, habitat use and trophic niche, and life history strategies are not tied to strict migratory schedules. They inhabit riverine, coastal and oceanic ecosystems [8], and exploit a diverse

range of niches. Their echolocation apparatus makes them efficient predators on a wide range of sometimes fast-moving prey in all these habitats.

Similarly, social structures among toothed whales tend to be more varied in number, type and stability than in the baleen whales [11]. Most of the smaller species form groups that frequently respond to the risks and resources by adapting their size, membership, and cohesion [45]. Smaller pelagic toothed whales typically form loose social networks, whether within the small (ca. 2-10 members) groups of beaked whales to the large aggregations (10's to 1,000's) of pelagic dolphins. But many species also engage in long-lasting social relationships [12,45]. The emergent social structures in toothed whales roughly mirror this contrast between smaller and larger species in the incidence and stability of social modules—sets of individuals that interact more often and more strongly with one another (Figure 1). Social stability and influence of females peaks among the larger species along with sexual dimorphism—notably in killer and sperm whales [46,47]—which are arranged in stable social groups with a marked influence of female kinship.

Female body size also influences the speed of life-history processes (Figure 2). Smaller species mature sooner, have slightly shorter gestation, lactation and calf-rearing periods than the larger species, in which pregnancy lasts >1 year and lactation can last anywhere from 8 months to 8 years or more in some species [10,48,49]. The reproductive cycles of toothed whales often take longer than 2 years to complete. In contrast to baleen whales, most toothed whales are income breeders that build nutritional supplies simultaneously with reproduction, thus compensating for slower prenatal growth rates with extended post-weaning care [25]. This care, sometimes provided by groupmates, allows the young to rely on their mother's rich milk while they progressively develop independent foraging skills (e.g. [50]). Often these skills, such as location, identification, capture and processing of prey, are learned, typically from the mother (e.g. [51,52]).

Mother and calf are the core unit of every cetacean society, but this is accentuated in toothed whales because maternal investment is so extensive. Lactation lengths are probably grossly underestimated in the literature, as longitudinal studies find much longer lengths than fisheries (bycatch or harvested animals) or cross-sectional studies report [10,24]. Most studies use interbirth intervals as a proxy, but these are only useful when restricted to intervals following a surviving offspring. For example, killer whale calving intervals average 4.9 years between viable calves, although there are some 2-year intervals [53], indicating that lactation can almost completely overlap with the next pregnancy. Among the largest toothed whales with stable matrilineal units, offspring of at least one sex remain with their mothers for a lifetime. Among the smaller toothed

whales with highly dynamic fission-fusion societies, maternal kin maintain strong bonds in the social network (e.g., *Tursiops* spp.: [54–58]). Post-weaning maternal investment and influence is also extensive in a number of species. These effects are likely born from the longer-term nature of the mother-calf bond, with toothed whale mothers hunting through the extensive lactation period. This sets up dramatic trade-offs between direct maternal care and foraging, but it also helps explain vertical transmission of social and foraging tactics among toothed whales.

Immediately after birth, neonates tag alongside their mothers in echelon position—which is a hybrid of the ‘follower’ and ‘carrying’ strategies of terrestrial mammals in that it imposes energetic costs (hydrodynamic drag) on the mother while boosting the calf’s swimming [59,60]. Within months, the calf transitions from mostly echelon to mostly infant position, under the mother’s abdomen and tail, which provides protection, hydrodynamic benefits and nursing access, again at an energetic cost to the mother [59,60]. In Shark Bay, bottlenose dolphin calves average 39% (range 10-80%) of their time in infant position from the 4th month of life until weaning [61].

Early calf care is intense. Unlike terrestrial mammals, cetaceans have unihemispheric sleep. Newborn calves hardly sleep at all and newly parturient mothers also forgo rest [62,63] and hunt minimally in the early days [64]. But lactating females must increase their food intake by more than 40% [65,66], so diving and separating from the calf for brief periods becomes necessary. Mothers shorten their dive times or spend more time at the surface to accommodate limited calf diving ability (e.g., bottlenose dolphins [67]; beluga whales [68]). Mother-calf separations are prolonged in some deep-diving species, although allomaternal support can compensate for the mother’s absence in some species (e.g. sperm whales [69,70]) but not others (such as northern bottlenose whales [71] and other beaked whales [72]).

While low levels of relatedness among associated individuals are a common occurrence among baleen whales, the extent of association among parent, offspring, and other female kin, varies over a broad spectrum in toothed whales. The range encompasses the relatively loose fission-fusion networks of bottlenose dolphins, species like narwhal (*Monodon monoceros*) that have been described as ‘matrifocal’ [73], through to various forms of matrilineal social structure from social ‘units’ containing multiple matrilines in sperm whales (e.g. [74]) and the extreme case of bisexual social philopatry seen in the fish-eating ‘resident’ ecotype of killer whales found in the waters of the NE Pacific (e.g. [75]).

Towards one end of this spectrum (Figure 1), we find the bottlenose dolphins, and likely other small toothed cetaceans (e.g. [76]). Bottlenose dolphins exhibit both sexual segregation and a highly

dynamic fission-fusion social structure [14,77–79]. While there is some variation among populations around the globe, females have strong bonds with their offspring, but particularly their daughters [54,80], and form female-dominated social networks within their community [5,64,77]. In contrast, males often form small, long-term alliances that compete with other alliances to sequester females [81–84].

We have recently begun to understand more about the key role of female kinship organisation in bottlenose dolphin societies. For example, a recent study shows a clear sex-bias in maternal accommodation of limited calf diving ability [67]. Specifically, Shark Bay bottlenose dolphin mothers shortened their dives only when young daughters, but not young sons, were close-by. There was no sex difference when the calves were tens of meters away and unable to observe maternal behaviour directly. This pattern suggests that mothers were affording their daughters more learning opportunities with respect to foraging than sons, a pattern consistent with the sex biases in foraging tactics in Shark Bay [52,85]. Although offspring of both sexes engage in maternal foraging tactics pre-weaning [51], daughters are more likely to retain these tactics well into adulthood [86,87]. While more than 20 distinct foraging tactics have been observed in Shark Bay, females specialize in the rare tactics (those exhibited by a small subset of the population), ranging from sponge tool use, to strand-foraging/beaching to trevally hunting [85,86]. Non-genetic processes of social inheritance, specifically strong vertical cultural transmission and maternal effects [5,7] are heavily implicated in these ecological patterns. This inheritance also includes vertical transmission of social tactics, with high mother-calf similarity, although again more so for daughters than sons [5,88,89]. Female dolphins, more so than males, inherit their mother's social network [7]. Such matrilineal bonds prove critical, as female calving success is linked to having a network of successful mothers [55], and male juvenile survival also depends on the maternal network [90].

Narwhal are an arctic species which appears to occupy an intermediate position both in terms of modularity of their social structures and the degree of matrilineal social structure. They occur in 'herds', aggregations of hundreds of individuals [91]. Herds are composed of several small clusters (between 3-20 individuals) that tend to be segregated based on age and sex [91,92]. Genetic evidence shows that animals sampled on different summer feeding grounds vary in mitochondrial DNA haplotype frequencies [73]. This suggests a role for female based kinship in structuring the population during summer, presumably through passing habitat knowledge down the female line, while on winter breeding grounds it seems the different lineages mix much more readily. Thus apparently while not strictly matrilineal, this social structure is described as 'matrifocal' [73], which we understand to mean reflecting a general tendency for shared maternal ancestry, while noting

that there is still much detail to be discovered about the social structure of the species. While narwhal social dynamics and kinship are difficult to study, their vocal diversity is consistent with individual- and/or group-specific calls [93], suggesting more social complexity than is currently understood.

The beluga whale, *Delphinapterus leucas*, is another circumpolar species for which more is known. There are at least 16 recognized stocks of beluga whale around the world, distinguished primarily by their summer habitat, but also differing in morphology, behaviour, and genetics [94]. Among the most studied are the three stocks in Hudson Bay, Canada, which show clear differentiation among both sexes in their mitochondrial, but not nuclear, DNA [95,96]. This pattern could stem from both sexes showing matrilineal site fidelity to summer grounds [95,97,98], or a stable matrilineal group structure with bisexual social philopatry [99]. Such structure would facilitate allonursing, which has been observed in captive belugas [100]. Furthermore, during migration female belugas in particular travel with close kin, and within migrating herds, close kin are, on average, more likely to be proximate in space and time [4,98]. While males do not appear to disperse geographically, sexual segregation occurs in which males typically remain with their kin as juveniles but then leave to associate mostly with other mature males, often farther north and in deeper waters [4,101,102], resulting in modest male dispersal [98]. Beluga populations are therefore strongly structured by fidelity to maternally inherited migratory culture and female kin relationships, resulting in populations that retain demographic and evolutionary independence despite partial sympatry [98].

In the open ocean pelagic habitat, both long- and short-finned pilot whales (*Globicephala melas* and *G. macrorhynchus*) exhibit bisexual natal philopatry according to genetic evidence [103,104]. Social analyses across multiple study sites suggest that long-finned pilot whales live in stable 'units' containing up to 30 animals of both sexes, which regularly interact to form larger, but temporary, 'groups' [105–108]. Recent genetic evidence based on mass strandings suggests that these larger groups contain multiple matrilineal units as well as distant relatives, consistent with the presence of multiple matrilineal units [109]. Within groups calves regularly associate with non-maternal females, and this does not appear to be limited to unit members [110], although more data are needed to confirm alloparental care. These patterns of social structure and kinship appear to be mirrored in the congeneric, but typically more tropically distributed, short-finned pilot whale [104,111,112].

Nearing the other end of the spectrum, sperm whales are the most sexually dimorphic cetacean in terms of body size and allometry, and live in a society that is strongly sexually segregated post-maturity. Females live in a multi-levelled society which has at its base social 'units' - technically

defined as animals identified together on multiple occasions at least 30 days apart or in multiple years [16,113], but in practise remaining stable over decades [114], units are groups of females and immatures that travel together. They are largely, but not rigidly, defined by kinship, often contain multiple matriline, and their members communally raise and defend their offspring [16,69,70,114,115]. Males leave their natal units in their early teens. Units form temporary 'groups' with other units that share the same vocal dialect. All units that share a dialect are members of the same 'clan' [116,117]. Clans exhibit variation in behavioural repertoire that appears to affect fitness [118–121]. Kinship among female sperm whales seems to drive associations, but not fully explain them, particularly those between units within clans [122,123]. It also is closely related to allocare in the form of babysitting and allonursing [124]. There also appears to be significant variation in social structure between ocean basins. In the Pacific, units are larger and composed of multiple matriline, while units in the Eastern Caribbean are smaller and based on closer kin, typically single matriline [125]. One hypothesis for these differing patterns of kinship relates to differences in prey species affecting optimal group size, as appears to be the case among killer whales [126], while another is varying levels of predation threat from killer whales in the two places [125].

Finally, killer whales are the most extreme example among the cetaceans of how matrilineal kinship can structure societies. In some populations both sexes exhibit natal philopatry to the matrilineal 'pods' into which they are born (pods here are defined as groups containing related matriline that are associated during more than 50% of sightings [75]). Their global population is divided into 'ecotypes' which differ not only genetically, but also morphologically and behaviourally [127]. The current hypothesis is that ecotypes result of culturally-driven ecological specialisation through vertical social learning within matrilineally-based social groups, followed by reproductive isolation through behavioural and possibly genetic mechanisms [127–129]. The strong fidelity to particular ecological specialisations likely results from the high investment in learning needed to acquire the complex, often cooperative, and sometimes highly risky nature of the foraging tactics involved (e.g. [130]).

While killer whales are among the most globally distributed species, the various ecotypes show considerable variation in social organization and behaviour, particularly in relation to foraging specialization. While many ecotypes have highly specialized diet preferences, others are more generalized [127]. There are at least ten recognized ecotypes of killer whales—five each in the northern and southern hemispheres, and there is still debate about their status as species or subspecies [131]. The two best studied forms are the Bigg's (formerly 'transient') mammal eating ecotype and the resident or fish eating ecotype found in sympatry in the northeastern Pacific Ocean.

Fish-eating, resident type killer whales have larger social units, and unlike Bigg's killer whales, exhibit bisexual natal philopatry. Post-reproductive resident females are known to physically lead their matriline around, particularly when prey abundance is low, suggesting that the ecological knowledge of the elder females can boost the fitness and survival of her matriline or pod [132,133]. Mammal-eating, Bigg's type killer whales form small social units of less than six members that are generally composed of a reproductive female and her offspring. In this ecotype, there is evidence that offspring of both sexes sometimes disperse either permanently or temporarily [134], which leads to significantly different kinship structure among and within pods compared to the resident type. While it remains unclear if post-reproductive lifespans have evolved among Bigg's killer whales [135], there is a documented case of infanticide among this ecotype [136] where a post-reproductive female and her mature male offspring cooperatively killed the calf of an unrelated female in the same population. This may represent an extreme case of late-life helping, driven by inclusive fitness and likely sexual selection [136], illustrating how highly modular social structure organised around female kinship structure can draw boundaries across which rather direct competition can be selected for. In killer whales then, we have the opportunity to explore the consequences of some of the most extreme forms of female-based kinship structure in mammals.

5. Consequences and perspectives

The nature of the interactions and relationships between female cetaceans, most notably the strong transitive bonds within the social units of the large matrilineal odontocetes, are the consequence of ecological pressures and evolutionary histories. But there is feedback, and these female-female relationships have, in turn, consequences for ecology and evolution.

Cetaceans are big players in the ecology of the ocean [137,138]. The female-centred societies of the whales and dolphins have an important role in this. Most obviously, cetaceans can use complex cooperative foraging techniques to efficiently exploit, and sometimes expand, their prey base [139–141]. However, in none of these remarkable cases are the sexes of the animals recorded, so we do not know whether the cooperation is just among females, driven by females, or not sexually biased. There is some suggestion that one such technique, cooperative mud-ring feeding in which animals take specific roles in stirring up sediment to create barriers against which to herd fish, but the small sample sizes preclude certainty [142]. We do know that some individually-based foraging techniques are passed through the female line, as recorded in detail for the bottlenose dolphins in Shark Bay [51,85], and can be inferred from the differential isotope-ratio profiles of sympatric clans of sperm whales [119] as well as the distinctive foraging specialisations of different killer whale types [46,127].

In the case of the killer whales, the ecological implications of their female-based sociocultural structure are likely profound. Social learning within matrilineal groups likely drove the deep division of killer whales into sometimes-sympatric, but highly ecologically distinctive and specialized, ecotypes [127]. Models suggest that this culturally-driven ecological specialization, while adaptive in the short term, leaves ecotypes vulnerable to extirpation, while reducing overall population size and resource abundance [129].

The female-based sociocultural structure of cetacean societies also influences who is available to eat what. Beluga whales have not recolonized habitats from which they were extirpated by whaling despite migration routes of extant populations passing nearby, and this is likely a result of the stability of matrilineally-transmitted knowledge about habitat and migration [95]. This will have affected the distribution and abundance of their prey, as will have the dynamics of space-use by different clans of sperm whales [143].

Evolution—be it the evolution of phenotypes, genotypes or cultures—needs heritability. For cetaceans, indeed for most mammals, a disproportionate amount of heritability runs through the female line. While males provide half the nuclear genes, females do that as well as transmitting all the mitochondrial DNA, maternal effects, many epigenetic effects [144], and, perhaps especially in cetaceans, being the primary conduit for culture [145].

Interactions between female-to-offspring or female-to-female transmissions of genes and culture have set up population structures in cetaceans at scales ranging from a few kilometres (e.g. bottlenose dolphins in Shark Bay, Australia [146]) to a few thousand kilometres (e.g. southern right whales [33]). These patterns result primarily because females give their offspring not only genes but also socially learned information, including foraging strategies (in the case of the bottlenose dolphins) and migration routes (in the case of the right whales).

The parallel transmission of genes and culture has effects beyond population structure. Gene-culture hitchhiking is a process by which diversity at a neutral genetic locus is reduced due to selection on culturally-inherited traits that are being transmitted in parallel with the genes. This is a plausible mechanism for the very low mitochondrial DNA diversities of the large matrilineal toothed whales [147]. The basic scenario is of matrilineally-structured social groups possessing characteristic cultures as well as characteristic distributions of mitochondrial haplotypes. The haplotypes residing in groups with selectively advantageous cultural elements will prosper at the expense of those haplotypes that are primarily restricted to groups with less well-tuned behaviour. This process reduces overall mitochondrial DNA diversity.

When important transmission processes run through a female-centred social network, selection may work to improve their efficiency. An unusual case of this is the evolution of menopause, the typical cessation of reproduction in females long before the end of life. Found only in several species of matrilineal whale and humans [135], the evolution of menopause is an evolutionary puzzle, but comparisons of female social organisation partly stimulated by findings in cetaceans have borne fruit in recent years. Theory [148], as well as some empirical evidence [132], suggests that in species where females are increasingly related to their group-mates as they age and have increasing levels of ecological knowledge with experience, then the inclusive fitness benefits of assisting and leading group members may outweigh the direct fitness of reproduction. This is apparently augmented in killer whales by the competitive consequences of lifelong associations between female kin when mothers and daughters breed at the same time in the same group [149,150]. Selection is expected to favour increased investment in competition in younger females, and indeed calves of older females co-breeding with their daughters suffer much higher mortality than those of their daughters in the same groups [149]. The importance of studying female sociality in cetaceans is underlined by these elegant—and unique outside humans—descriptions of how cooperation and conflict between female kin can explain the evolution of a striking feature of human life history.

6. Closing remarks

Kinship may drive complexity in cetacean societies differently among species. Lukas and Clutton-Brock [151] distinguish two concepts of social complexity: organizational social complexity is a reproductive division of labour between breeders and non-breeders, while relational complexity constitutes “conflicts of interest between group members and the social traits associated with them, including well-defined dominance hierarchies, competitive alliances and other behavioural tactics used to maintain social status”. Organizational complexity might be higher among the larger toothed whales in which killer whale and sperm whales exhibit high levels of alloparental care and defence and in which multileveled societies might impose upon individual preferences. In contrast, within the looser female networks of dolphins, relational complexity is likely higher such that conflicts of interest might arise and be dealt with through fission-fusion dynamics and individually specific long-term bonds confer a range of social and reproductive benefits. However, to understand this properly it is clear that we need more quantitative data from cetacean studies so that they can be included in these types of large-scale analyses.

Explaining the diversity of female-biased kinship structures in cetaceans remains a significant challenge. It seems clear that there is no simple phylogenetic explanation for these differences: the

family Delphinidae include exemplars from both ends of the toothed whale social spectrum from fission-fusion to stable kin-based groups (bottlenose dolphins and killer whales, respectively). However, there is perhaps a tipping point as kin structures become increasingly modular, where female relatedness becomes sufficiently high within groups (compared to between them) that inclusive fitness benefits from increased cooperation and reduced conflicts among group members become an important driver of life history and cultural evolution in some species. Cooperative care of calves emerges from our treatment as a major factor driving some of this diversity, associated with stronger female bias in kinship organisation, but movement ecology, foraging specialisations, and perhaps size-based refugia from predation may also interact to produce a complex selective landscape. This spectrum among cetaceans, from weak social bonds outside the mother-calf pair, through various forms of matrifocal and partially matrilineal societies, through to strictly matrilineal structures, provides a potentially powerful opportunity to test these hypotheses going forward. We therefore anticipate many insights into the evolution of sociality driven by female kinship from future studies of cetaceans.

Data accessibility. This article has no additional data.

Competing interests. We declare we have no competing interests.

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Figure captions

Figure 1. Social and matrilineal kinship structure in cetaceans - a conceptual organisation.

Cetacean societies across the Mysticeti (baleen whales) and Odontoceti (toothed whales) span a continuum between low and high modularity, increasingly structured into sets of highly connected individuals with the tendency of maternally-related individuals to interact among themselves (female kinship organisation ranging from matrifocal to more strictly matrilineal). Networks depict empirical data from long-term studies (after [152]) on photo-identified individuals (red nodes = females, blue nodes = males, yellow nodes = calves) connected by association (vertex thickness is proportional to association index).

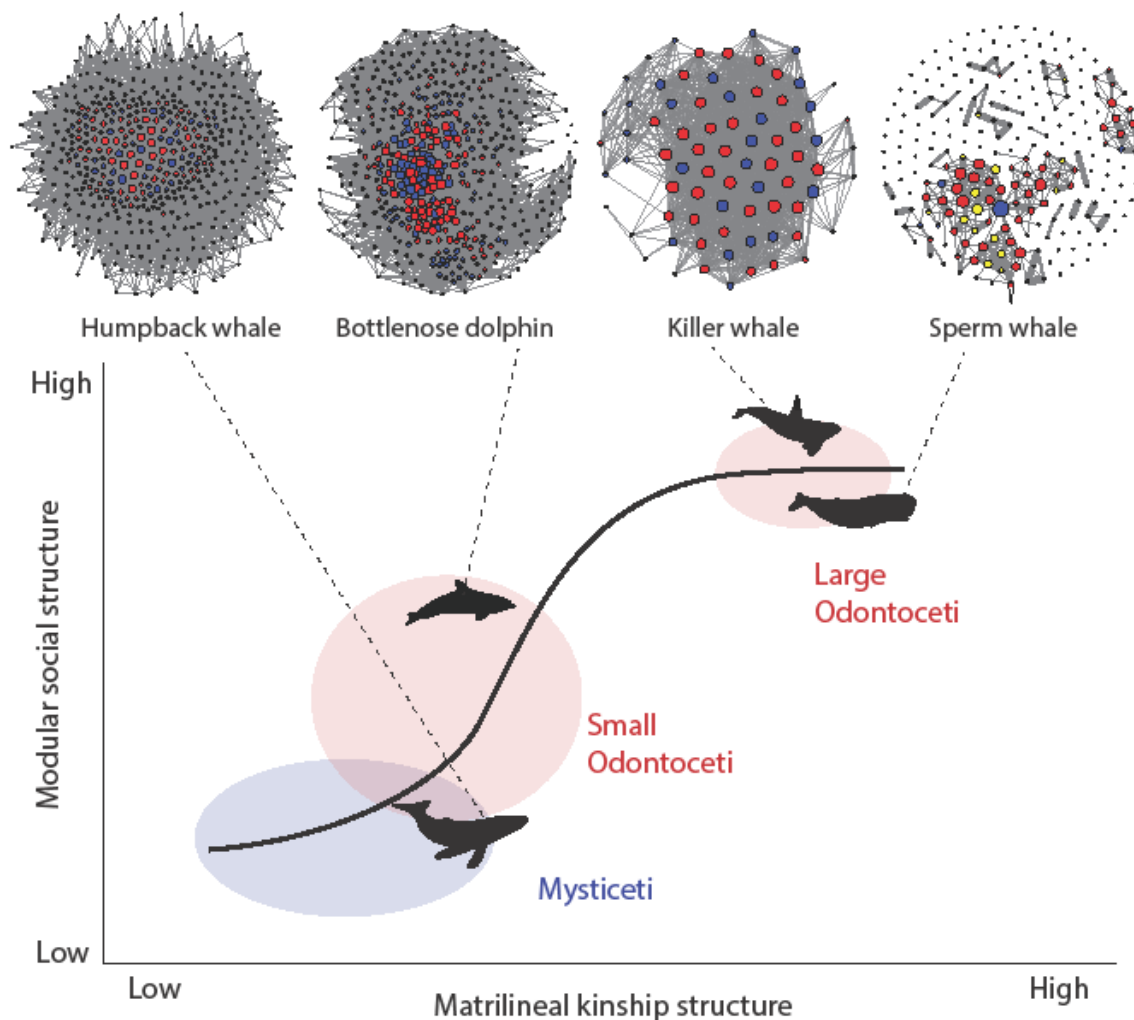


Figure 2. Life-history processes and the central role of females as mothers in cetacean societies.

(A) Duration of key life-history processes of female toothed whales (Odontoceti) and baleen whales (Mysticeti). Split violin plots indicate the probability distributions of log-transformed length of gestation and lactation (mean), inter-birth interval (mode), maturity (mean age at first birth), and longevity (maximum lifespan) across 13 Mysticeti species (red) and 43 Odontoceti species (blue). Dashed lines within violins indicate mean values. (B) Speed of female life-history processes relative to body length between toothed and baleen whales. Age at sexual maturity correlates highly with all other life history traits and thus is used here as a summary measure of the other life-history processes. Shaded circles represent species of Odontoceti (red) and Mysticeti (blue) and solid icons indicate the mean values for each taxonomic family to which data was available. Icon sizes are suggestive of the average body length. Data and estimation methods in [10].

