Behavioral Ecology and Sociobiology (2026) 80:14
https://doi.org/10.1007/s00265-025-03630-3

REVIEW

Beluga societies: the social and cultural lives of an enigmatic odontocete

Jaclyn A. Aubin[1,2] · **Daniel J. Mennill**[1] · **Robert Michaud**[3] · **Valeria Vergara**[2]

Received: 27 January 2025 / Revised: 18 July 2025 / Accepted: 21 July 2025 / Published online: 20 January 2026
© The Author(s), under exclusive licence to Springer-Verlag GmbH Germany, part of Springer Nature 2026

Abstract

Beluga whales live in complex societies, but their social structure and cultural lives are poorly described compared to those of some other cetaceans. In this review, we summarize the evidence for fission-fusion social dynamics, sexual segregation, male alliances, female social structure, multilevel sociality, and cultural traditions among belugas. We compile evidence of atomistic, individual-based social dynamics within beluga societies. We show that most beluga societies are sexually segregated, although there is considerable intra-specific variation in the social structure of belugas. Our review of research on male beluga sociality reveals that males sometimes associate closely, and that these associations can last for weeks to months. Further research is needed to determine whether these associations are stable and long-lived, as in other cetaceans. Our examination of female beluga sociality, including our assessment of the influence of maternal kinship, reveals equivocal findings. Growing evidence suggests that female beluga sociality is partly driven by maternal kinship, and that the degree to which female belugas associate with kin may vary seasonally. Therefore, female beluga sociality may be best defined as "matrifocal" rather than "matrilineal". We review the evidence supporting a multilevel social structure among belugas and suggest four possible social levels: the mother-calf dyad, the group, the herd, and the community. Finally, we discuss migratory and vocal culture among belugas. Our review showcases the complex social lives of this enigmatic species and highlights important areas for future research.

Keywords *Delphinapterus leucas* · Fission-fusion · Matrifocal · Matrilineal · Sociality · Social structure

Introduction

Odontocetes, the toothed whales, have been widely recognized as highly social animals where cultural traditions play an important role in ecology and behavior. Toothed whales possess a broad range of social structures (Mann et al. 2000) and the evidence of cultural traditions among toothed whales has attracted much attention from the research community (Rendell and Whitehead 2001; Norris 2002; Cantor and Whitehead 2013). As we strive to better understand the social and cultural lives of odontocetes, certain species, such as the bottlenose dolphin (*Tursiops* sp.), the sperm whale (*Physeter macrocephalus*), and the killer whale (*Orcinus orca*) have garnered much attention and have come to be well-characterized (Connor et al. 1998; Beck et al. 2012; Connor and Krützen 2015; Whitehead et al. 2024). Others, like the beluga, remain relatively poorly understood, possibly due to the challenges inherent in observing marine animals in remote, often inhospitable habitats.

Belugas are circumpolar, occupying Arctic regions of Canada, Alaska, and Russia, although their distribution extends into temperate regions in some parts of the world (DFO 2023). They were initially thought to have a lifespan of 30–35 years, but they are now known to reach 75–80 years of age in the wild (Lesage et al. 2014; Waugh et al. 2018). Belugas rely on seasonally available prey such as capelin (*Mallotus villosus*) and Arctic cod (*Boreogadus saida*), but are generally opportunistic consumers of various fishes, cephalopods, molluscs, and other marine

Communicated by S. Parks

✉ Jaclyn A. Aubin
jaclyn.a.aubin@gmail.com

[1] Department of Integrative Biology, University of Windsor, Windsor, ON N9B3P4, Canada

[2] Raincoast Conservation Foundation, Sidney, BC, Canada

[3] Groupe de Recherche et d'Éducation sur les Mammifères Marins, Québec, QC, Canada

invertebrates (Loseto et al. 2009; Kelley et al. 2010; Lesage et al. 2020). Killer whales (*Orcinus orca*) and polar bears (*Ursus maritimus*) are the primary predators of belugas, although some populations have no natural predators (Freeman 1973; Westdal et al. 2017). Most beluga populations undergo long seasonal migrations, generally summering in coastal areas, and wintering in more open-water areas when coastal areas become ice-bound (COSEWIC 2014). Even resident beluga populations show seasonal movements within their estuarine habitats (DFO 2014). There are currently eight recognized beluga populations in Canada, although our understanding of their population structure is dynamic and subject to frequent revision (COSEWIC 2020; DFO 2022). Several populations are known to interbreed on common wintering grounds, suggesting that some populations may eventually be reassessed, while others were only recently recognized as distinct units, and more may be recognized in the future (DFO 2022; Parent et al. 2023).

In this review, we synthesize the available evidence for fission-fusion dynamics, sexual segregation, male social dynamics, matrifocality, multilevel social structure, and culture in belugas. We begin by examining the evidence for fission-fusion dynamics and sexual segregation in this species. We then delve into the social dynamics of male and female belugas, addressing controversies about whether female beluga societies are matrilineal. Next, we examine the evidence of multilevel social structure among belugas. Finally, we review the evidence of culture in belugas. Throughout this review, we identify avenues for future research and techniques and technologies that will be crucial to further our understanding of beluga sociality and culture. As predominantly Arctic animals, belugas face diverse conservation challenges, many of which stem from anthropogenic activities. To implement appropriate conservation measures, it is imperative for us to better understand their social structure and culture. For example, evidence suggests that belugas show vertical transmission of migratory routes and summering areas (Colbeck et al. 2013), which may make them particularly vulnerable to anthropogenic disturbance in the changing Arctic. By deepening our understanding of beluga societies and culture, we also come to better appreciate precisely what is at stake in our conservation efforts: the uncertain future of a socially-complex, highly cultural species.

A note on within-species variation

Although it may be tempting to assume that all beluga populations share similar social structures and cultural behaviours, studies of other whales and dolphins teach us that this assumption may be incorrect. For example, different ecotypes of killer whales exhibit drastically different behaviors and social structures (Baird 2000). While beluga populations are not recognized to represent different ecotypes, they are nonetheless genetically distinct; some populations have been separated for over 30,000 years (O'Corry-Crowe et al. 2010) and exhibit differences in migratory behaviour (De March et al. 2002; Postma 2017). Bottlenose dolphins and sperm whales also exhibit compelling examples of within-species social variation (Whitehead et al. 2012; Gowans 2019). Population differences may manifest in different cultural traditions. For example, the resident Cook Inlet and St. Lawrence beluga populations are short-distance migrants and likely do not possess the same degree of migratory culture as beluga populations that undergo long-distance migrations. As such, we are careful throughout this review to specify sampling locations and the populations being discussed. Where relevant, we comment on apparent differences between populations and discuss possible evolutionary explanations for such differences. In supplementary Table S1, we also outline the populations that show evidence of the phenomena being discussed. It is likely that future research will show us that different beluga populations exhibit different social strategies and unique cultural identities. Given the current lack of a general synthesis of beluga sociality and culture, we attempt in this review to sketch its broad outlines, with the hope that future researchers will refine our linework and color in the blank spaces.

Fission-fusion societies and beluga whales

Broadly, a fission-fusion society is any society where group size and composition changes quickly and periodically (Gowans 2019). While this definition has limitations, which are discussed in the penultimate paragraph of this section, it provides a useful starting point for examining beluga social structure. The term "fission-fusion" was first used to describe the social dynamics of non-human primates (Kummer 1971), but has since been adopted to describe the social structure of Asian elephants (*Elephas maximus*; de Silva et al. 2011), bottlenose dolphins (Connor et al. 2000), Bechstein's bats (*Myotis bechsteinii*; Kerth et al. 2011), modern humans (Marlowe 2005), crows (*Corvus* ssp.; Uhl et al. 2019), common ravens (*Corvus corax*; Loretto et al. 2017), and other animals. Fission-fusion societies are likely widespread due to the evolutionary advantages of flexible grouping patterns. Although living in social groups carries considerable advantages, it also carries important costs, such as increased competition, increased detectability by predators, and increased disease and parasite transmission (Dunbar 1989). By adjusting their grouping patterns dynamically, animals that live in fission-fusion societies are able to modulate the trade-offs of social living by adjusting group size and membership (Kelley et al. 2011; Jordaan et al. 2021). Although belugas have been repeatedly characterized as a fission-fusion species (Karenina et al. 2013; Hill and Campbell 2014; Michaud 2014; O'Corry-Crowe et al. 2020; Mayette et al. 2022), no single study provides definitive evidence of such a social structure. In this review, we present two lines of evidence that support the widespread idea that belugas live in fission-fusion societies. First, beluga group sizes are highly variable and second, individuals have been observed moving between groups.

The terminology used by cetacean researchers to describe the social structure of whales is diverse. For example, killer whale researchers use terms such as "matriline" and "pod" (Baird 2000), whereas sperm whale researchers prefer "unit" and "group" (Whitehead and Weilgart 2000). There is currently no such widely accepted terminology among beluga researchers. In this review, we use the terms "group" and "herd". Following Lemieux Lefebvre et al. (2018), we define a group as two or more individuals that are in relatively close proximity to each other and engaged in similar behaviours, and a herd as an assemblage of distinct groups, where the distance between individuals in a group is small, but the distance between groups is relatively large. These terms are functional definitions, largely based on visual observations of whales from boat decks and drones and may not fully capture the whales' full social experience (see Box 1 for a discussion on defining groups in whales and dolphins). Despite their limitations, these terms serve as a stepping stone to a more cohesive understanding of beluga sociality. Other authors have defined these terms differently, and we are therefore careful in interpreting these words in previously published works (for example, Colbeck et al.'s (2013) "groups" are defined as animals captured at the same site on the same day and are therefore likely more similar to our "herds".) To preserve clarity, we use the term "aggregation" when discussing assemblages of belugas in a looser, more colloquial sense, unless citing authors that specifically use the term "group" in their published works.

Several authors have noted that belugas can be found alone or in small groups (Finley et al. 1982; Mayette et al. 2022), or in herds that can reach thousands of animals (Sergeant 1962; Sergeant and Brodie 1975; Ognetev 1981; Seaman 1981). These observations suggest that individuals and smaller aggregations periodically merge to form large aggregations. In their influential monograph on belugas, Bel'kovitch and Sh'ekotov (1993) report on thousands of hours of observations of belugas in the White Sea and Amur River estuary. They found that belugas frequently formed ephemeral groups of 2–8 animals which sometimes joined to form groups of 15–20 animals (Bel'kovitch and Sh'ekotov 1993), quite similar to what was found in the St. Lawrence with average group sizes varying between 2 and 5 individuals and average herd sizes between 6 and 65 (Michaud 1993). Habitat and activity appear to impact beluga grouping patterns, with smaller groups and herds found in sheltered coastal habitats and larger gatherings forming during socializing and foraging activity (Michaud et al. 1990; Lemieux Lefebvre et al. 2018). In the White Sea, the largest beluga herds are typically observed in May through September (Krasnova et al. 2012). In the St. Lawrence estuary, scattered groups of belugas reunite into large herds in the fall (Vladykov 1944; Pippard 1985).

Box 1 Defining groups in belugas and other whales and dolphins

Group size in whales and dolphins is often defined by chain rules (Mann and Smuts 1998; Gero et al. 2016; Connor et al. 2017; Fig. 1). Various chain rules have been used to define groups in belugas and narwhals, including a 10-metre chain rule (Mayette et al. 2022), a one-to-two-body-length chain rule (Cosens and Dueck 1991), and a one-body-length chain rule (Ausen et al. 2023). Within these frameworks, individuals are often considered to be alone if they are more than one to two body lengths away from other individuals. However, given that sound travels so effectively underwater, covering large distances at a speed over 4 times as fast as in air, animals may be in close acoustic contact even when separated by much more than one body length. Therefore, although these chain rules are widely used in cetacean literature, they may reflect our biases as a visual, terrestrial species, and fail to reflect the Umwelten of the beluga and other cetaceans. Adult beluga contact calls were found to have a median communication range of 6.7 km in quiet environments, and 2.9 km in noisy environments (Vergara and Mikus 2021). With this in mind, it may be worthwhile to use more liberal chain rules, such as the 200m chain rule that Augusto et al. (2017) used to define groups in long-finned pilot whales, chain rules based on acoustic ranges (Parsons et al. 2009; Foster et al. 2012), or chain rules that include a behavioural component, similar to those used by Lemieux Lefebvre et al. (2018) to define cetacean groups.

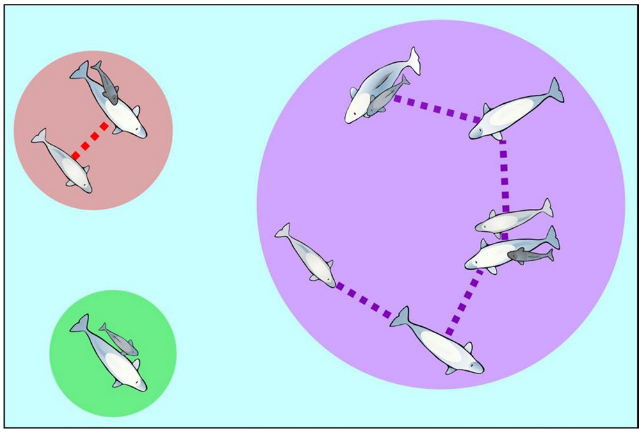

Fig. 1 Example of a one-body-length chain rule being used to define beluga groups. In each group, every individual is less than one body length away from another group member. In this example, three groups are shown, represented in red, purple, and green. Every individual in each group is more than one body length away from all individuals in the other groups

Direct observations of individuals joining and separating from other individuals also provides anecdotal evidence that belugas live in fission-fusion societies. In a reproductive gathering in the White Sea, an adult with individually distinguishing scars was observed twice alone, and three times as a member of three different groups (Alekseeva et al. 2013). In the same population, males have been observed temporarily joining aggregations of females with young (Kleinenberg et al. 1964), and juveniles have been observed moving between kindergarten groups and hunting groups (Bel'kovitch and Sh'ekotov 1993). In the St. Lawrence Estuary, "social congregating", the meeting and interchange of groups, has also been observed (Pippard and Malcolm 1978).

Identity calls and social organization

In cetacean societies, the nature of identity-related information provided in contact calls is linked to social organization (Tyack 2000), and we may gain insight into beluga social behaviour by considering features of acoustic signals. Identity signals can either be individually unique or collectively shared. Shared contact calls that signal social membership tend to be favored in species characterized by long-term social stability (Tyack 2000) such as killer whale pods (Ford 1991) and sperm whale units (Rendell and Whitehead 2003). Conversely, in socially dynamic species that maintain long term relationships in the context of fission-fusion social systems, contact calls tend to be individually distinctive, as in the well-studied bottlenose dolphin signature whistles (Sayigh et al. 1998; Tyack 2003). Individual vocal signatures are well-adapted to fission-fusion sociality because they allow individuals to keep track of each other, especially in aquatic environments where vision is often ineffective (Sayigh et al. 1998; Tyack 2003; Vergara and Mikus 2019).

Belugas have been suggested to have distinctive vocal signatures in their contact calls (Morisaka et al. 2013; Mishima et al. 2015; Vergara and Mikus 2019; Panova and Agafonov 2023). These calls, important in social cohesion, can be biphonal, including both a rapid broadband pulse train, and an overlapping tonal or pulsed element that potentially serves as an acoustic signature element (Vergara and Mikus 2019). Although the pattern of the pulse train appears to be individually distinctive (Mishima et al. 2015), the potential signature element described by Vergara and Mikus (2019) is a more compelling candidate as a true vocal signature. True vocal signatures represent distinctive, learned acoustic features that are unlikely to arise from morphological variation in voice characteristics (Boughman and Moss 2003). While subtle differences in voice characteristics are often effective for individual recognition, this may be insufficient in aquatic settings due to challenges like depth-induced alterations in the nasal sound-production complex of diving odontocetes and high background noise in marine environments (Tyack 2000; Ridgway et al. 2001). To overcome these obstacles and enhance individual distinctiveness, learning to modify acoustic characteristics of calls becomes crucial (Tyack 1997). In temporary natural beluga entrapments in Cunningham Inlet, the number of contact call types with unique elements was strongly correlated with the number of animals being recorded (Vergara and Mikus 2019). Similarly, among all-male groups in the White Sea, the number of unique contact call types recorded was strongly correlated with the number of animals observed (Panova and Agafonov 2023).

If belugas have individual vocal signatures, this suggests that they possess a communication system well-adapted to fission-fusion social dynamics. However, further research is needed to determine whether beluga contact calls represent individual or familial vocal signatures. Some evidence from captive belugas suggests that contact call types may be shared between related individuals (Vergara et al. 2010; Ames and Vergara 2020). Yet this may also arise from mimicry of the vocal signatures of others, as has been observed in bottlenose dolphins, who can copy the individually distinctive whistles of close associates (Tyack 1986; King et al. 2013; King and McGregor 2016). Therefore, the potential for individual vocal signatures in belugas requires further investigation.

Nuances in fission-fusion dynamics

The term 'fission-fusion society" has been criticized for being needlessly dichotomous (Aureli et al. 2008). Some societies that have not been traditionally considered to be fission-fusion societies exhibit fission-fusion dynamics, while other societies that are described as fission-fusion societies can vary drastically in the degree of fission-fusion dynamics. For example, the societies of bottlenose dolphins (*Tursiops* sp.) and chimpanzees (*Pan troglodytes*), which live in very flexible groups that may change membership over short time spans (Lehmann and Boesch 2004; Wiszniewski et al. 2009), and the stable matrilineal social units of female sperm whales and African elephants (*Loxodonta africana*), which may nonetheless join with other social units for short periods (Whitehead et al. 1991; de Silva and Wittemyer 2012), all possess some degree of fission-fusion dynamics. Some authors have attempted to remedy this problem. Rodseth et al. (1991) suggested that fission-fusion societies can be described as "atomistic", where individuals are the smallest social unit that may leave and join others, or "molecular", where stable, long-term groups are the smallest social unit that may leave and join others. Another characterization of fission-fusion societies focuses on the relative importance of the group. For example, van

Schaik (1999) defined "group-based fission-fusion" societies as those where individuals live in permanent groups that can undergo fission, and "individual-based fission-fusion" societies as societies where individuals are often alone or in small groups, and the society itself can only be recognized on the basis of all association patterns. Aureli et al. (2008) suggest that fission-fusion dynamics should be ranked along three axes: (1) temporal variation in spatial cohesion, (2) temporal variation in group size, and (3) temporal variation in group composition. Societies that score highly on all three dimensions have higher-fission-fusion dynamics, while societies that score low on all dimensions have lower fission-fusion dynamics. This system has some limitations; both territorial, solitary species, and highly stable societies would be characterized as having lower fission-fusion dynamics, despite presenting important social differences.

Which characteristics best describe the fission-fusion sociality of belugas? We might recognize that atomistic societies generally tend to have individual-based, higher (sensu Aureli et al. 2008) fission-fusion dynamics, while molecular societies tend to have group-based, lower fission-fission dynamics. In the White Sea, lone belugas are sometimes observed in offshore areas (Kleinenberg et al. 1964). In the Beaufort Sea and in the St. Lawrence Estuary, large percentages of belugas observed during aerial surveys were considered to be alone (i.e., no other animals nearby; Michaud 1993; Mayette et al. 2022). Considered together with the aforementioned evidence of fission-fusion dynamics in belugas, these findings suggest that beluga sociality is more similar to the higher fission-fusion dynamics (as defined by Aureli et al. 2008) seen in bottlenose dolphins, chimpanzees, and spider monkeys, *Ateles* sp. (Chapman 1990; Connor et al. 2000; Lehmann and Boesch 2004), than to the lower fission-fusion dynamics seen in animals with stable social structure, such as sperm whales and African elephants (Whitehead et al. 1991; de Silva and Wittemyer 2012). Further investigations, using a variety of techniques and technologies, will be needed to fully characterize beluga societies (Fig. 2). In particular, photo-identification, passive acoustic monitoring, and acoustic tags will be helpful in disentangling the fission-fusion social dynamics of belugas.

Sexually-segregated societies and beluga whales

Sexually segregated societies are common among sexually-dimorphic social mammals, including ungulates (Clutton-Brock et al. 1987; Ruckstuhl and Neuhaus 2000), primates (Chapman 1990; Surbeck et al. 2017), and cetaceans (Michaud 2005a; Morteo et al. 2014). Sexually-segregated societies show sex differences in social behaviour or space-use patterns, where individuals segregate themselves with other individuals of the same sex outside of the breeding period (Main et al. 1996; Michaud 2005a). Many hypotheses have been suggested to explain such patterns, including sex differences in predator avoidance, energetic requirements, foraging strategies, avoidance of intraspecific competition, and social preferences for same-sex interactions, often due to male aggression and harassment (Main et al. 1996; Ruckstuhl and Neuhaus 2002; Galezo et al. 2018).

Biologists have long suggested that belugas live in sexually-segregated societies (Vladykov 1944; Sergeant 1962; Kleinenberg et al. 1964; Brodie 1971; Pippard 1985). As early as 1944, Vladykov noted that, in summer, females of the St. Lawrence Estuary population primarily inhabit shallow inlets, while males concentrate in deeper waters. A clear spatial segregation was also described between all-adult herds, presumed to be mostly males, and herds of adults accompanied by young in the St. Lawrence Estuary (Michaud 1993; Ouellet et al. 2021). Richard et al. (1998) found sex differences in the movement patterns of six satellite-tagged belugas in the Canadian High Arctic: while four females remained near the tagging site, two tagged males both traveled north from the tagging site. In the Eastern Beaufort Sea, Richard et al. (2001) found that tagged males and females occupied different habitats during the summer. Similarly, female and male belugas in the Chukchi and Beaufort Seas were found to select different habitats (Hauser et al. 2017). In addition, during subsistence hunts around Hudson Bay, animals captured together tended to be of the same sex (Colbeck et al. 2013). Evidence from captive animals also supports the idea that belugas tend to congregate with members of the same sex. Among captive belugas, males were found to associate with other males seven times more often than they associated with females, while females were often alone (Hill et al. 2018).

Beyond sex, segregation in belugas appears to be partially determined by reproductive state. In the St. Lawrence Estuary, lactating females with young frequently segregated themselves from males and other females (Sergeant 1986). Similarly, in the Canadian High Arctic, nursing females and presumed older female offspring were found to select estuarine habitats, while large males rarely frequented estuaries, and females with older calves and subadult males frequented ice-edge habitat (Smith et al. 1994). Use of estuaries and shallow bays by females with calves in the summer is widespread, and has been reported in multiple beluga populations, including the St. Lawrence Estuary population (Pippard 1985), the Eastern Beaufort Sea population (Hauser et al. 2017), and the White Sea population (Krasnova et al. 2014). Several explanations have been put forth regarding the use of shallow estuaries by females with calves, including predator avoidance, prey access, and

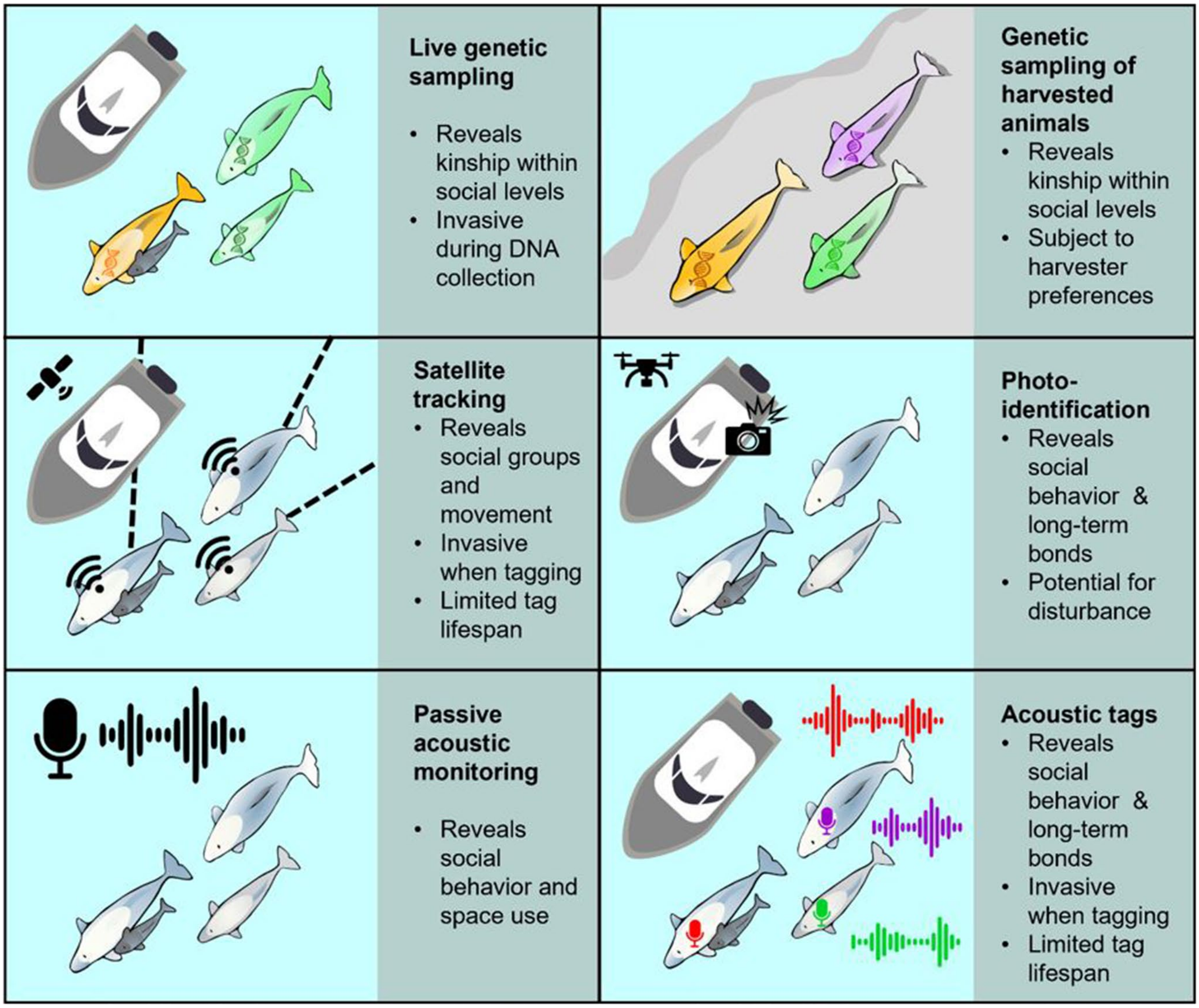
Live genetic sampling
Reveals kinship within social levels
Invasive during DNA collection
Genetic sampling of harvested animals
Reveals kinship within social levels
Subject to harvester preferences
Satellite tracking
Reveals social groups and movement
Invasive when tagging
Limited tag lifespan
Photo-identification
Reveals social behavior & long-term bonds
Potential for disturbance
Passive acoustic monitoring
Reveals social behavior and space use
Acoustic tags
Reveals social behavior & long-term bonds
Invasive when tagging
Limited tag lifespan

Fig. 2 Field methods that provide insight into beluga social structure and culture. Each method is associated with several advantages and disadvantages, some of which are listed above

thermal stress mitigation (Sergeant 1973; Fraker et al. 1979; Noel et al. 2022).

Other studies, in contrast, have found an absence of sexual segregation among belugas. Using stable isotope analysis of male and female belugas, Kelley (2014) found evidence of dietary overlap between male and female belugas outside of the breeding season in the Western Hudson Bay. However, males and females may be socially segregated and still show dietary overlap. In the same population, two estuaries showed no evidence of segregation between adults with young, juveniles, and adults without young, suggesting that both estuaries were used by both males and females (Westdal et al. 2022). Similarly, a multi-year photo-identification study of Cook Inlet belugas found no evidence of broad-scale sexual segregation during the ice-free season: males and females were frequently photographed in the same areas, and in the same groups (given the reported sizes of these groups, they likely correspond to what we refer to as herds; McGuire et al. 2020). Intriguingly, adult males were seen in herds with calves almost as often as adult females in the Cook Inlet population (McGuire et al. 2020). It is unclear whether sexual segregation occurs in this population outside of the ice-free season.

Although it is evident that sexual segregation is a key feature of some beluga populations, it may be premature to generalize this social structure to all beluga populations. Different beluga populations may exhibit different social structures, possibly due to different evolutionary pressures including prey availability, predation pressure, or population density. However, we are not aware of any ecological pressures that consistently align with the presence or absence of sexual segregation in the populations described here, although this represents a rich area for future investigation. The lack of segregation described in some beluga populations may reflect differences in methodology and terminology, or seasonal changes in beluga behaviour (see Fig. 4). While sexual segregation may not be ubiquitous among belugas, it is certainly widespread, and accordingly, it is worthwhile to evaluate male and female beluga social structures separately.

Females beluga societies: matrilineal, matriarchal, or matrifocal?

In many animal species, older females are socially central or dominant. These societies are variably described as matrilineal, matriarchal, or matrifocal (Brown Gladden et al. 1997; Palsbøll 1997; Marcoux et al. 2006; Whitehead et al. 2017). These terms are often used interchangeably to describe female-dominated societies, without specific definitions. In Box 2, we define these terms and present examples of matrifocal, matrilineal, and matriarchal societies. One uniting feature of matrifocal societies is that females form strong connections with their daughters, but also with more distant kin and non-kin, resulting in societies where maternal kin tend to interact with each other, but where associates are not exclusively or primarily maternal kin (Rendell et al. 2019). Matrilineal societies, however, are composed of one or a few matrilines (Rendell et al. 2019). Matriarchal societies, whereby elder females are socially dominant or hold a leadership role can be matrilineal or matrifocal (McComb et al. 2001; Brent et al. 2015; see Box 2 for more details).

The task of assigning these labels to different animal species is not always straightforward. For example, is a species truly matrilineal if groups include unrelated males, as is often the case in species with male-biased dispersal? Some killer whale ecotypes show the unusual phenomenon of bisexual natal philopatry, such that matrilines, the first social level, are composed of a matriarch, her sons, daughters, and her daughters' offspring (Ford 2019). Similarly, in pilot whales (*Globicephala* sp.) both males and females show natal philopatry, and groups are typically composed of multiple matrilines, although the degree of relatedness between matrilines is unclear (Alves et al. 2013; Nichols et al. 2020). In the cases of sperm whales and elephants, mature males leave their mothers to roam or associate with other males, such that female social units are composed of matrilines of females and their immature offspring (McComb et al. 2001; Coakes and Whitehead 2004). In some species, social interactions are structured by maternal kinship, but societies are characterized by fission-fusion dynamics rather than stability, as in the case of giraffes (*Giraffa camelopardalis* sp.; Bercovitch and Berry 2013). Are these examples of matrifocality, matrilineality, or something else? A broad range of social structures have been described as matrilineal. We suggest that matrifocality and strict matrilineality exist on a continuum, and that most species described as matrifocal or matrilineal can be placed somewhere along this continuum (Box 2, Fig. 3). Examples of species that can be broadly grouped as matrifocal include giraffes (Bercovitch and Berry 2013), bottlenose dolphins (Smolker et al. 1992; Frère et al. 2010; Tsai and Mann 2013), and narwhals (*Monodon monoceros*; Palsbøll 1997), all of which live in societies that are structured around maternal kin yet don't live in stable matrilineal societies (Fig. 3). Species that can be classified as strictly matrilineal include resident killer whales (Ford 1991), and perhaps, pilot whales (Alves et al. 2013; Nichols et al. 2020). Other, less strictly matrilineal species include sperm whales (Coakes and Whitehead 2004), pilot whales (Alves et al. 2013; Nichols et al. 2020), African elephants (McComb et al. 2001), spotted hyenas (*Crocuta crocuta*; Holekamp et al. 2012), and meerkats (*Suricata suricatta*; Griffin et al. 2003; Fig. 3).

Along a continuum from matrifocality to matrilineality, where do matriarchal societies belong, societies where older females tend to be socially dominant or hold leadership roles (Wittemyer et al. 2005; McHugh 2019)? We suggest that matriarchy is a quality of matrifocal and matrilineal societies, rather than a type of society onto its own (Fig. 3). Examples of species known to be matriarchal include African elephants (McComb et al. 2001), giraffes (Berry and Bercovitch 2015), spotted hyenas (Smith et al. 2015), and killer whales (Brent et al. 2015). These species have also been described as matrilineal (elephants, killer whales, and hyenas) or matrifocal (giraffes). For many species, it appears that the question of whether a species is matriarchal has never been explored (Fig. 3).

By living with relatives, individuals can easily cooperate with kin and benefit from kin selection (Hamilton 1964; Wild 2023). Many forms of cooperation have been observed in matrifocal and matrilineal societies, including food sharing (Wright et al. 2016), collaborative defense (Graw and Manser 2007; Ponnampalam 2016), alarm calling (Rauber and Manser 2021), and offspring care (i.e., allocare; English et al. 2010; Konrad et al. 2019). A female living with maternal kin might receive assistance with offspring rearing, as the survival and reproductive success of her offspring would increase the inclusive fitness of her associates. For animals such as odontocetes with extremely protracted periods of offspring dependence, such assistance from kin is likely an important factor driving the emergence of matrifocal and matrilineal societies (Rendell et al. 2019).

Box 2 Matrifocal, matrilineal, and matriarchal societies

Matrifocal (from the Latin focus for fireplace, hearth, i.e., a point of convergence)

Definition: A matrifocal society is one where mothers and female kin represent a point of social convergence. In matrifocal societies, social interactions tend to be structured around maternal kinship, although groups are not composed exclusively of maternal kin.

Examples: Giraffes live in fission-fusion societies where kin, particularly mother-offspring pairs, have the strongest associations, and kinship plays an important role in herd composition (Bercovitch and Berry 2013).

Female bottlenose dolphins appear to be weakly matrifocal; females tend to associate more with females from the same maternal lineage, and sometimes continue to associate with their mothers well into adulthood, although social interactions are also structured by home-range overlap and paternal kinship (Smolker et al. 1992; Frère et al. 2010; Tsai and Mann 2013). Similarly, narwhals are thought to live in fission-fusion societies (Breed et al. 2017), and genetic analyses suggest a matrifocal social structure, with maternal kin migrating to specific summering areas (Palsbøll 1997). Similar migration patterns are known in belugas.

Comments: It is noteworthy that many matrifocal societies show atomistic, individual-based fission-fusion dynamics, while many matrilineal societies show more stable group structure, or molecular, group-based fission-fusion dynamics (Fig. 3). Animals in matrifocal societies may benefit from both preferential kin associations and highly flexible grouping patterns.

Matrilineal (from the Latin linea for line)

Definition: A matrilineal group is one where group members belong to the same maternal lineage and can be traced back to a recent maternal relative (Rendell et al. 2019). In most cases, groups described as matrilineal are composed of multiple matrilines.

Examples: Resident Killer whale matrilines are composed of a female, her adult and immature male and female offspring, and her daughters' offspring, and offspring remain with their family group for life (Ford 2019). Groups of closely related matrilines that frequently travel and forage together are known as pods (Ford 2019). Short-finned pilot whales are similar in that both males and females remain in their natal groups which are typically composed of multiple related matrilines (Alves et al. 2013; Nichols et al. 2020). Animals that are not strictly matrilineal, but are often described as such, include African elephants, sperm whales, spotted hyenas, and meerkats. African elephant families and sperm whale units are composed of adult females and their offspring although adult females are not always closely related (McComb et al. 2001; Coakes and Whitehead 2004). Spotted hyenas (*Crocuta crocuta*) and meerkats (*Suricata suricatta*) societies are often composed of a single matriline, but also include unrelated males due to male-biased dispersal (Griffin et al. 2003; Holekamp et al. 2012).

Comments: In contrast to matrifocal societies, matrilineal societies are often composed of stable groups. Stable group structure is a prerequisite for matrilineal societies. A wide range of societies can be described as matrilineal, including societies composed of multiple related matrilines and societies that include unrelated males (Fig. 3). Nonetheless, the term "matrilineal" remains a useful term for distinguishing these societies from matrifocal societies and societies that are not structured by maternal kinship.

Matriarchal (from the Greek root ἀρχή (chief, leader, ruler)

Definition: A matriarchal society is one where mothers and older females hold a leadership role or are socially dominant (Wittemyer et al. 2005; McHugh 2019, 2015).

Examples: Among African elephants, the presence of older females improves the reproductive success of their families, likely due to the social and ecological knowledge of older matriarchs (McComb et al. 2001, 2011).

Other examples of species where older females hold a leadership role include spotted hyenas (Smith et al. 2015) and Thornicroft's giraffe (*Giraffa camelopardalis thornicrofti*; Berry and Bercovitch 2015).

Comments: We consider that matriarchy is a quality of matrifocal and matrilineal societies, rather than a separate social category. It seems likely that many matrifocal and matrilineal species are also matriarchal; however, in many cases, questions of social dominance and leadership remain unexamined (Fig. 3).

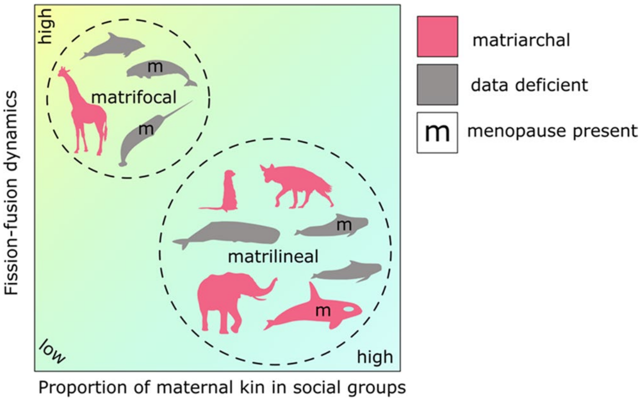

Fig. 3 Matrifocal and matrilineal societies: a conceptual organization centering the influence of fission-fusion dynamics and the proportion of maternal kin in groups. Matriarchal societies are found among both matrifocal and matrilineal societies, and animals in both matrifocal and matrilineal societies show evidence of menopause

The social bonds and organization of female belugas remain a topic of much interest, particularly their long-term stability. Anecdotal evidence suggests that female belugas prefer to affiliate with specific individuals, and associations between individuals other than mothers and dependent calves can be long-lived. In the St. Lawrence Estuary, one adult female was repeatedly observed traveling with another adult of unknown sex and immature individuals (Pippard and Malcolm 1978). In addition, a large adult female and a large sub-adult female satellite-tagged together in Cunningham Inlet were found to have travelled together for at least 21 days (Smith et al. 1994). Preliminary analyses of decades of photo-identification effort in the St. Lawrence Estuary also indicated that females have preferred companions (Michaud 1999, 2005b). It is not known whether these associates were maternal kin, such as a mother and a mature daughter, or non-kin.

The question of whether belugas live in matrilineal societies has sparked controversy. O'Corry-Crowe et al. (2020) noted that some authors have mistakenly used the model of a "stable, matrilineal group" as a cornerstone of beluga society, citing works by Palsbøll et al. (2002), Krasnova et al. (2014), and Vergara and Mikus (2019). Palsbøll et al. (2002) found a high degree of genetic heterogeneity in Baffin Bay belugas, which they suggest might arise from a matrilineal pod structure similar to killer whales, a reasonable interpretation of the data presented. Krasnova et al. (2014) described a "relatively stable community structure", with females and their calves forming the "stable core of the group". However, they later state that the structure of Solovetsky belugas is "labile and unstable", where belugas "periodically form groups followed by their disjoining and rearrangement". Similarly, Vergara and Mikus (2019) state that "large summering herds are assemblages of matrilineal groups of females, calves, and older female offspring", but also note that "individuals from the various family groups regularly join and split". Thus, both Krasnova et al. (2014) and Vergara and Mikus (2019) emphasize the fission-fusion dynamics of belugas, rather than emphasizing stable matrilineal societies. Palsbøll et al. (2002) meanwhile, only suggest that their observations could be consistent with a stable matrilineal social structure. Overall, while the idea of a stable matrilineal social structure in belugas has been suggested, it remains contentious and is far from widely accepted as a cornerstone of beluga society, highlighting the need for further research on female social behaviour.

Do belugas associate with maternal kin?

A compelling, data-rich picture of beluga social structure was presented by O'Corry-Crowe et al. (2020). Using genetic data from 10 different beluga populations, they found that different types of groups show different degrees of maternal relatedness. As expected, mother-calf dyads were almost always parent-offspring pairs, while groups composed of multiple mother-calf dyads showed intermediate relatedness (O'Corry-Crowe et al. 2020). Other types of groups, such as juvenile-only, adult male-only, and mixed-age, showed low relatedness. Groups were routinely composed of more than one matriline, and individuals sharing the same mitochondrial DNA lineage were not always closely related (O'Corry-Crowe et al. 2020). Overall, O'Corry-Crowe et al.'s (2020) findings are largely aligned with the majority of the available literature on beluga social structure, with one notable exception: groups of females with calves were no more closely related than groups of males.

The finding that groups of females with calves are no more closely related than groups of males (O'Corry-Crowe et al. 2020) is surprising. If daughters associate with their mothers beyond the period of offspring dependence, we should expect to find high relatedness among females. O'Corry-Crowe et al. (2020) did find that close maternal kin regularly interact and associate. However, they also regularly associate with non-kin, paternal relatives, and distant relatives. O'Corry-Crowe et al.'s (2020) findings clearly show that beluga societies are not strictly structured around maternal kinship. In this respect, belugas may be similar to bottlenose dolphins in the sense that adult daughters occasionally associate with their mothers, but groups maintain high fission-fusion dynamics (Tsai and Mann 2013). As with bottlenose dolphins, beluga mother-daughter bonds may be socially important, without resulting in a matrilineal social structure. Like bottlenose dolphins and narwhals, beluga societies may be best defined as matrifocal, rather than matrilineal (Fig. 3).

Other findings by O'Corry-Crowe et al. (2020) are broadly aligned with previous observations of beluga sociality. Given that belugas show male-biased social dispersal (Colbeck et al. 2013; O'Corry-Crowe et al. 2018), we would not necessarily expect male belugas to associate with maternal kin. Similar patterns of low relatedness have been reported among bachelor groups of male sperm whales (Bond 1999) and bottlenose dolphin male alliances (Connor et al. 2011). Interestingly, adult male bottlenose dolphins appear to avoid associating with their mothers, despite often occupying overlapping home ranges (Tsai and Mann 2013). O'Corry-Crowe et al. (2020) also note that large herds of belugas are not composed exclusively of maternal kin. This is expected if herds represent assemblages of matrilines, rather than single matrilines, as suggested by Colbeck et al. (2013) and authors of earlier studies (Kleinenberg et al. 1964; Bel'kovitch and Shekotov 1993).

The strength and relative stability of the mother-daughter bond among belugas remains a topic of considerable interest. Several studies have suggested that mothers might associate with offspring of various ages beyond the period of offspring dependence. Kleinenberg et al. (1964) reported the capture of a juvenile with an adult female and dependent calf. All three animals shared the same rare feature, the presence of a fifth digit, suggesting that the juvenile may have been the female's older offspring. This would imply that older offspring sometimes remain associated with their mother, even after the birth of a younger sibling. More broadly, Kleinenberg et al. (1964) remarked on the typical presence of small migrating groups of 2–4 individuals, usually one adult and 2–3 younger animals. The authors suggested that these small assemblages are maternal families, and that they are likely maintained for several years. Sergeant (1962) also commented on the presence of small groups composed of an adult female with 2–3 offspring of various ages, presuming that these represent familial units.

It is worth noting that these authors lacked the genetic data to substantiate such inferences.

Genetic data suggest that beluga societies may be structured around female kinship, at least some of the time. As previously stated, Baffin Bay belugas sampled at the same sites across years showed significant levels of genetic variability, which could arise as a result of a matrilineal social structure, although other explanations are also plausible (Palsbøll et al. 2002). Colbeck et al. (2013) found that belugas, particularly females, tend to associate with kin during migration, but not after migration. In addition, Elharram (2011) found that females in one area of the St. Lawrence Estuary were highly related, suggesting maternally-directed philopatry. Given these findings, and other lines of evidence presented above, it seems likely that daughters continue to associate with their mothers, but not necessarily as a stable dyad.

Whether or not mature daughters associate with their mothers might depend on the mother and daughter's reproductive state, given the link between reproductive state and habitat selection previously discussed. Patterns of association also appear to vary seasonally. Colbeck et al. (2013) found that female belugas tend to associate with kin during migration, but not after migration. O'Corry-Crowe et al.'s (2020) genetic samples from 10 populations were obtained from a wide range of contexts, including summer and fall aggregations, migratory groups, resident populations, temporary entrapments, and mass-stranding events. It would be illuminating to investigate how maternal relatedness varies across these different seasonal and environmental contexts, and across populations. Given the growing body of genetic data, it may be possible to determine how the relatedness of aggregations change across seasons and contexts. Given Colbeck et al.'s (2013) findings, we might expect to find higher relatedness among aggregations of mothers and calves during migration versus during the summer.

Menopause in matrifocal odontocetes

Belugas, like humans, are one of a few species that show evidence of menopause (Ellis et al. 2018). Other odontocetes with post-reproductive lifespans include killer whales, short-finned pilot whales, false killer whales, and narwhals (Photopoulou et al. 2017; Ellis et al. 2018). Interestingly, both killer whales and short-finned pilot whales live in stable matrilineal societies (Baird 2000; Alves et al. 2013). Many of the hypotheses for the evolution of post-reproductive lifespans require that daughters remain closely associated with their mothers (Johnstone and Cant 2010). Older females may forego reproduction because they can increase their fitness more effectively by providing care and guidance to their existing offspring and grandchildren than by producing new offspring themselves (Hawkes et al. 1998; Brent et al. 2015). Another hypothesis proposes that older females may forego reproduction in order to avoid competing with their daughters (Lahdenperä et al. 2012; Croft et al. 2017). These hypotheses are not mutually exclusive; both factors may theoretically contribute to the emergence of menopause in the same population. Recent research suggests that odontocetes evolved menopause through a lengthening of lifespan uncoupled from a lengthening of the reproductive lifespan (Ellis et al. 2024). Ellis et al. (2024) emphasize that such an extended post-reproductive lifespan is beneficial when grandmothers provide intergenerational help or avoid intergenerational reproductive conflict, requiring extensive social contact with maternal kin. However, our review suggests that such conditions are not only found in matrilineal societies with stable, long-term groups, but also in societies with fission-fusion dynamics, such as belugas.

The presence of menopause in a matrifocal species with fission-fusion dynamics underscores that stable matrilineal societies are not a prerequisite for menopause to evolve. For example, caring for grand-offspring may be more conducive to fitness than producing new offspring, even when grandmothers are not constant companions to their grand-offspring (Ellis et al. 2024). Allomaternal care has been observed in wild belugas (Aubin et al. 2021), but it is still unclear who provides allocare to offspring. In captivity, allonursing was reported when an unrelated adult female and a juvenile half-sister both began lactating and nursed a calf (Leung et al. 2010). In the St. Lawrence Estuary, one observation of an older, presumably post-reproductive female who was still lactating at an estimated age of 68 years (according to modern aging techniques, i.e., 1 growth-layer group per year, Waugh et al. 2018) suggests that grandmothers may sometimes nurse their grand-offspring (McAlpine et al. 1999). As emphasized by Ellis et al. (2024), menopause can evolve under various social contexts, and not only in stable matrilineal societies.

Post-menopausal females may be particularly likely to assume matriarchal roles. Post-reproductive female resident killer whales tend to lead collective movements, particularly in years of low salmon abundance (Brent et al. 2015). This suggests that post-menopausal females may hold important knowledge about the distribution and preferred habitats of prey species. Post-menopausal female resident killer whales also protect their adult sons from social conflict; adult males living with their post-menopausal mothers sustained fewer social injuries than males whose mothers were pre-menopausal or deceased (Grimes et al. 2023). Given that both belugas and narwhals can be described as matrifocal and show evidence of post-reproductive lifespans, we propose that these species may also be matriarchal, with older, post-menopausal females acting as matriarchs. Beluga matriarchs could play important roles within their societies, possibly contributing to the maintenance of migratory routes (Brennin et al. 1997; Colbeck et al. 2013) and using their ecological knowledge to avoid deadly ice entrapments (McHugh 2019). Future studies should examine the roles of post-menopausal females in beluga societies.

Male beluga societies

Evidence suggests that belugas show male-biased dispersal; mature males leave their mothers to associate with other males (Colbeck et al. 2013; O'Corry-Crowe et al. 2018, 2020). However, whether these groups represent loose associations or stable alliances, as has been observed in male bottlenose dolphins (Connor and Krützen 2015), remains unclear. Conference presentations based on decades of photo-identification efforts in the St. Lawrence Estuary suggest that males form long-lasting associations (Michaud 1999, 2005b). These data, though unpublished, raise the possibility that belugas form long-term male-male affiliations. Hill et al. (2018) note that there is no published evidence that beluga males display male-male alliances. This is an important area for further careful study, possibly involving animals with tags that facilitate quantification of the stability and duration of male-male associations (Fig. 1).

Published accounts of male social structure support the idea that males, at least sometimes, form distinct aggregations. In Northern Québec, belugas can be found in "bachelor groups," i.e., aggregations of large white individuals, presumed to be male, that are "tightly cohesive" and "strikingly compact" (Finley et al. 1982). Smith et al. (1994) also commented on the presence of close-knit groups of 10–15 males in Cunningham inlet, while Sergeant (1962) remarked on the presence of groups of 10–20 large animals, presumably males, that remained segregated from other animals in the Canadian Arctic. In the White Sea, male-only aggregations comprised of dozens of animals have been observed (Kleinenberg et al. 1964). Whether these aggregations, and the relationships that structure them, are stable, remains to be determined through careful field studies.

Evidence from satellite-tagged males suggests that male aggregations may be stable at times, but that social stability may vary seasonally or be context-dependent. Three males captured in the same herd in the Eastern Chukchi Sea and equipped with satellite tags remained together while traveling through heavy ice for up to 29 days and then separated upon arrival in areas of open water and looser ice (Suydam et al. 2001). Similarly, three males tagged together in Svalbard travelled together for up to 120 days thereafter (Lydersen et al. 2001). Such long-lasting associations in males do not appear to be based on kinship (O'Corry-Crowe et al. 2020). These findings, together with the aforementioned photo-identification data, suggest that male belugas sometimes form long-lasting associations.

Strong male-male bonds have been documented in some odontocete species. Bottlenose dolphins in Western Australia provide the most well-studied example, where pairs or trios of males form alliances that can last for several decades (Connor and Krützen 2015). These alliances frequently persist until the presumed death of partners (Connor and Krützen 2015), and partners show convergence in the structure of their signature whistles over time (Smolker and Pepper 1999). These partnerships are thought to facilitate mating opportunities: in a three-dimensional, underwater environment, it would be difficult for a lone male to control access to a female, but two or three males may be able to influence her movements (Connor and Krützen 2015). Male sperm whales also appear to form bonds with other males, although these bonds are not as long-lived (Whitehead and Weilgart 2000). Upon dispersing from their natal groups, young sperm whales form loose associations of similarly aged males sometimes called "bachelor schools" (Best 1979). However, as males age, these bachelor schools dissolve and males begin to avoid other breeding males (Whitehead and Weilgart 2000). It remains unclear whether the associations of male belugas are more similar to bottlenose dolphins, sperm whales, or other species. Studies using photo-identification data, satellite tracking, and acoustic monitoring (both from passive hydrophones and acoustic tags) will be instrumental in assessing the stability of male bonds, while genetic studies will reveal the influence of kinship on male-only aggregations (Fig. 2).

Do belugas live in multilevel societies?

Multilevel societies emerge through the hierarchical nesting of associations, where the fission and fusion of progressively larger social levels contribute to the overall social structure of a population (Grueter et al. 2012, 2020; Cantor et al. 2015). There is some disagreement over the precise definition of a multilevel society. Grueter et al. (2012, 2020) consider that a primary stable social unit is a pre-requisite for the formation of multilevel societies, while others suggest that multilevel societies can emerge in the absence of well-defined, stable social units (VanderWaal et al. 2014). Multilevel societies have been identified in African elephants (Wittemyer et al. 2005), killer whales (Tavares et al. 2017), sperm whales (Rendell and Whitehead 2003), plains zebras (*Equus burchelli*; Rubenstein and Hack 2004), bottlenose dolphins (Connor and Krützen 2015), and humans (Hamilton et al. 2007). Multilevel societies have been suggested to emerge through various mechanisms, including cultural transmission (in sperm whales; Cantor et al. 2015), as a means of protection from intruding males (in non-human primates; Grueter et al. 2012), through sexual selection (in plains zebras; Rubenstein and Hack 2004), and as a result of limits to cognitive capacity (in non-human primates; Grueter et al. 2012). Although belugas have been suggested to live in multi-level societies (O'Corry-Crowe et al. 2020; Panova and Agafonov 2023), the precise levels of beluga society have not been defined. Here, we propose four possible nested beluga social levels that may represent levels of a multilevel society (Fig. 4).

First level: the mother-calf dyad

There is no doubt that the mother-calf relationship is central to beluga sociality. When belugas were hunted in the St. Lawrence Estuary, hunters were known to target young calves in order to secure their mothers, because mothers would not leave their wounded young (Vladykov 1944). Similarly, hunters in Churchill, Canada often preferentially targeted nursing females, because they swim more slowly and less erratically, presumably to ensure that they do not become separated from their calves (Douglas 1951). In the eastern Canadian Arctic, most beluga calves were found to be weaned between 1 and 3 years of age, although one sampled individual was weaned at 4 years of age (Matthews and Ferguson 2015). In Cook Inlet, offspring were typically observed alongside their mothers for up to 5 years, but one offspring was consistently photographed with its mother over a period of 8 years (McGuire et al. 2020). In captivity, one juvenile female continued to nurse until six years of age, while her half-brother was still nursing at 3 years of age (Leung et al. 2010). Our own observations in the St. Lawrence Estuary suggest that older, large juveniles continue to nurse, or attempt to nurse from their mothers (JAA pers. obs.). Young calves are dependent on their mothers for several years, and are almost always at the sides of their mothers (Brodie 1971; Krasnova et al. 2014). In and around Hudson Bay, a significant proportion of herds sampled throughout the year were found to contain mother-offspring pairs (Colbeck et al. 2013). Taken together, these findings suggest that the mother-calf dyad is a relatively stable social unit that typically persists over several years. Similar to African elephants (Wittemyer et al. 2005), we suggest that the mother-calf unit represents the core unit of beluga social hierarchy (Fig. 4).

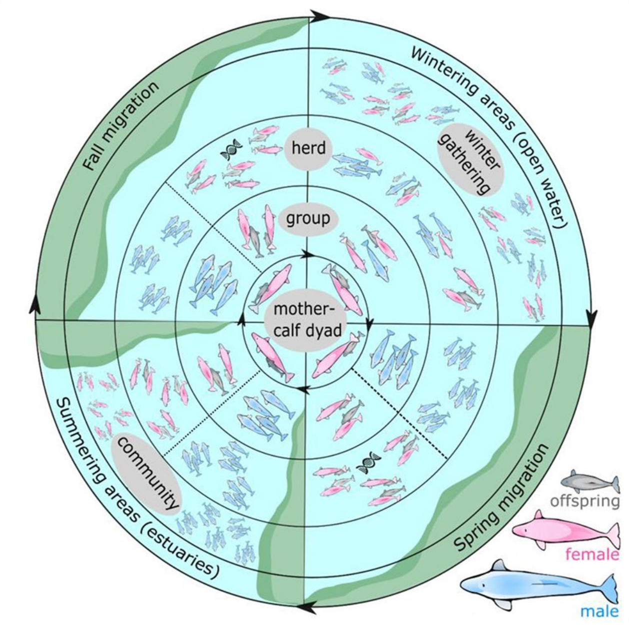

Fig. 4 Conceptual model of the levels of beluga multilevel sociality across the seasons. First level (center): the mother-calf dyad is the first-level and core unit of beluga social structure. Second level (innermost ring): the group represents a second level of beluga social structure. Male and female groups tend to be sexually-segregated throughout most of the year, except possibly in winter. Third level (middle ring): the herd is an assemblage of groups. Herds tend to be sexually-segregated during the summer and are likely not sexually-segregated during the winter. Female herds tend to be closely related during migration. Sexual-segregation also appears to be present during migration. Fourth level (outermost ring): social aggregations differ seasonally. In the summer, communities are thought to coalesce through natal philopatry of individuals to particular estuarine habitats. Although belugas show clear patterns of sexual segregation during the summer, it is unclear how the sexes differ in their community compositions, including in migration. Winter gatherings can be composed of individuals from multiple populations wintering in the same open-water areas. It is unclear whether social levels higher than the herd occur during spring and fall migrations

Second level: the group

Beluga groups tend to be relatively small: in some areas of the St. Lawrence Estuary, 99% of groups are composed of 5 animals or fewer (Michaud 1993). Female groups are typically composed of several mother-calf dyads, along with older offspring, and females not accompanied by offspring, some of which may be pregnant, and some of which may be post-reproductive (Bel'kovitch and Sh'ekotov 1993; Ellis et al. 2018; O'Corry-Crowe et al. 2020). We argue that the mother-offspring dyad is a building block of the female group. However, female groups are not stable and do not represent fixed social units as is seen among female sperm whales and killer whales. Instead, as we have discussed above, these groups undergo frequent fission and fusion, with animals moving from one group to another. How the relatedness of female groups might change with seasonal context and with reproductive state is an intriguing area for future research. As previously described, male groups are typically composed of several unrelated adult males (O'Corry-Crowe et al. 2020). Belugas show male-biased dispersal; mature males disperse from their natal groups to associate with other mature males (Colbeck et al. 2013; O'Corry-Crowe et al. 2018, 2020). How male groups might change in composition seasonally remains unknown.

Third level: the herd

As we have previously discussed, herds are assemblages of groups (Lemieux Lefebvre et al. 2018). While groups are typically composed of fewer than 5 animals, herds can number a hundred animals or more, and even thousands of animals in some parts of the world (Sergeant and Brodie 1975; Michaud 1993; Chernetsky et al. 2011). Due to strong fission-fusion dynamics, belugas frequently move between groups within a herd. It is unclear whether herds are socially determined, or represent the congregation of groups to advantageous areas (i.e., areas that are safe from predators, or rich in prey). It seems likely that the congregation of groups into herds results from both social and environmental factors. In the St. Lawrence Estuary, three types of herds have been identified: adult-only herds (presumed to be herds of males), herds of adults with young (presumed to be herds of females with their offspring), and mixed herds (presumed to be composed of both sexes; Michaud 1993). In the summer months, different areas of the St. Lawrence are frequented by different herd types, with a strong sexual segregation in herds apparent in most areas (Michaud 1993; Ouellet et al. 2021). Herds appear to vary in size seasonally: in the White Sea, the largest beluga herds are typically observed in May through September (Krasnova et al. 2012) while in the St. Lawrence Estuary the largest herds are observed in the fall (Vladykov 1944; Pippard 1985). Evidence suggests that the relatedness of herds also varies seasonally. Most beluga populations are migratory, undertaking migrations between the open water areas where they winter and the estuarine habitats where they summer (Sergeant and Brodie 1975; Fraker et al. 1979). Evidence from subsistence hunts during migration suggests that herds tend to be composed of female kin (Colbeck et al. 2013). However, for belugas sampled in summering areas, there was significantly higher than expected proportion of parent-offspring pairs, but not close-kin pairs. Colbeck et al. (2013) offer two explanations for this pattern: (1) closely-related females (with the exception of mother-offspring pairs) disband upon arrival to the summering grounds and regroup before leaving again, or (2) migratory herds join with other herds on the summering grounds. Both explanations could be consistent with multilevel sociality.

Fourth level: the community

One of the most notable characteristics of belugas is their tendency to aggregate in estuaries during the summer months (Smith et al. 1994; Brennin et al. 1997; COSEWIC 2020). For example, belugas summering in the Mackenzie River estuary consistently congregate into concentration areas during the summer calving season (Fraker et al. 1979). Cumberland Sound belugas enter the estuarine waters of the sound in the summer and these concentration sites have not changed in over 50 years (Brodie et al. 1981). Similarly, the belugas of Northern Quebec use traditional estuarine habitats in the summer (Finley et al. 1982), the belugas of Western Hudson Bay summer in the Nelson, Churchill, and Seal River estuaries (Smith et al. 2017), and the belugas of the sea of Okhotsk summer in various estuaries (Meschersky et al. 2018). Aggregating in estuaries during the summer calving season likely carries several important benefits. Warm estuarine waters may be less metabolically stressful to calves, which are born in and near estuaries during the summer (Sergeant 1973; Noel et al. 2022). Many estuaries are also rich in prey (Watt et al. 2016), and their use may reflect a predator avoidance strategy (Simard et al. 2014). Brackish warm waters and abrasive substrates may also facilitate epidermal moulting, a phenomenon observed in belugas in many estuaries during the summer (Aubin et al. 1990; Smith et al. 1992).

Genetic analyses of belugas summering in the Gulf of Alaska, the Bering-Chukchi-Beaufort Seas, and the Sea of Okhotsk reveal direct evidence that belugas are philopatric to their summering grounds (O'Corry-Crowe et al. 2018). Belugas sampled at 12 locations across Canada were found to show clear differentiation in their mitochondrial genotype, suggestive of maternally-directed philopatry to summering grounds (Brennin et al. 1997). Similarly, in the St. Lawrence Estuary population, evidence from 18 years of photoidentification suggests the presence of three clusters that preferentially frequent three different portions of the population's summer range (Bonnell et al. 2022). It seems likely that migratory routes and traditional summering areas are passed down from mother to offspring, an example of maternally-directed philopatry (Colbeck et al. 2013). We suggest that the belugas sharing these traditional areas represent communities. Both fission-fusion dynamics and sexual segregation have been observed within beluga communities during the summer months (Kleinenberg et al. 1964; Krasnova et al. 2012; Alekseeva et al. 2013). The relationship of communities to herds is perhaps not strictly hierarchical: while herds are temporary assemblages of individuals in constant fission and fusion, the community is a stable assemblage of individuals seasonally sharing a geographic location. Further research emphasizing long-term monitoring of individual movement and social behaviour is needed to disentangle the social dynamics of herds and communities and better understand the nature and function of these communities. We suggest that the community, an aggregation of kin and non-kin that share seasonal fidelity to the same area could represent a high level of a multilevel beluga society.

A possible fifth level: the winter gathering

Much of the research on beluga sociality has focused on their behavior within summering areas and during migration, with little attention to their behavior during winter. The reasons for this are likely logistical: belugas winter in particularly remote areas, in particularly harsh conditions for the biologists who monitor them. Intriguingly, some beluga populations show clear differentiation in their mitochondrial DNA, but no differentiation in their nuclear DNA (De March and Postma 2003; Turgeon et al. 2012) suggesting that maternal kin show fidelity to summering areas but breed with males from different populations on their wintering grounds (Brown Gladden et al. 1999). Therefore, in some areas, winter gatherings may represent a social level higher than population. In such cases, winter gatherings may represent multiple populations coming together. For example, populations wintering in the Hudson Strait include the Western Hudson Bay, Eastern Hudson Bay, and Ungava Bay populations (DFO 2022). Researchers are in the process of disentangling the population structure of Northern Canadian belugas, and redefining important conservation units (e.g., Parent et al. 2023). The concept of the winter gathering may offer important biological insights and serve as a valuable framework for advancing our understanding of beluga population structure.

Further research is needed to investigate the nature and functions of the social structures that we have outlined above. We emphasize the need for long-term, multi-year datasets examining the bonds between individuals and their relatedness. Genetic sampling, satellite tracking, photo-identification, and acoustic monitoring studies could expand our understanding of beluga social structure and multilevel sociality (Fig. 2).

Culture in belugas

Although various definitions of culture exist (see Rendell and Whitehead 2001), here we use the definition proposed by Boyd and Richerson (1996) and rephrased by Rendell and Whitehead (2001): “culture is information or behaviour acquired from conspecifics through some form of social learning”. We argue that belugas are cultural animals showing evidence of both migratory and vocal culture. Furthermore, the importance of socially-acquired traits, and the long period of offspring dependence seen in this species suggests that belugas may also possess other forms of culture still unknown to us and calling out for further investigation.

Migratory culture

Several lines of evidence suggest that beluga migratory routes and summering areas are culturally transmitted. Using data from satellite-tagged whales, Smith and Martin (1994) found that belugas in the Canadian High Arctic show similar patterns of movement across years, suggestive of specific migratory routes. Among Hudson Bay belugas, individuals, particularly females, tend to migrate with kin (Colbeck et al. 2013). Colbeck et al. (2013) found that mothers and offspring tended to associate closely during and after migration, suggesting that migratory routes, as well as summering areas, may be culturally transmitted from mother to calf. The protracted period of offspring dependence among belugas (Brodie 1971; Krasnova et al. 2014; Matthews and Ferguson 2015; McGuire et al. 2020) means that each calf undergoes multiple migrations with their mother, thereby facilitating the transmission of the migration route from mother to calf. Belugas sampled at 12 locations across Canada were found to show clear differentiation in their mitochondrial DNA, suggestive of maternally-directed philopatry to summering grounds (Brennin et al. 1997). More recently, using genetic data from belugas in three different populations, O’Corry-Crowe et al. (2018) found evidence of natal philopatry to summering areas with limited dispersal from these areas, suggestive of migratory culture in belugas in the Gulf of Alaska, Bering-Chukchi-Beaufort Seas, and the Sea of Okhostk. In the St. Lawrence Estuary, several decades of research suggest that belugas form multiple clusters of individuals each using preferentially using restricted areas (Bonnell et al. 2022) and using predictable transit corridors to move between habitats (Pippard 1985; Ouellet et al. 2021). If these routes and spatial preferences are acquired through social learning, they may be further evidence of culture in belugas (Fig. 5).

Vocal culture

There is no doubt that belugas are capable of vocal learning, a prerequisite for vocal culture. Belugas are exceptional vocal imitators, and have demonstrated the ability to imitate heterospecifics, including bottlenose dolphins (Panova and Agafonov 2017) and humans (Eaton 1979; Ridgway et al. 2012). Their aptitude for mimicry is striking: a male captive beluga was found to be able to imitate human speech and computer-generated sounds (Murayama et al. 2014). But what of vocalizations learned socially, as our definition of culture requires? It seems likely that the beluga’s aptitude for mimicry stems from the importance of social vocal learning in this species. Evidence from captive whales also suggests that belugas acquire vocalizations from conspecific animals. In captivity, both a male beluga calf, Tuvaq, and

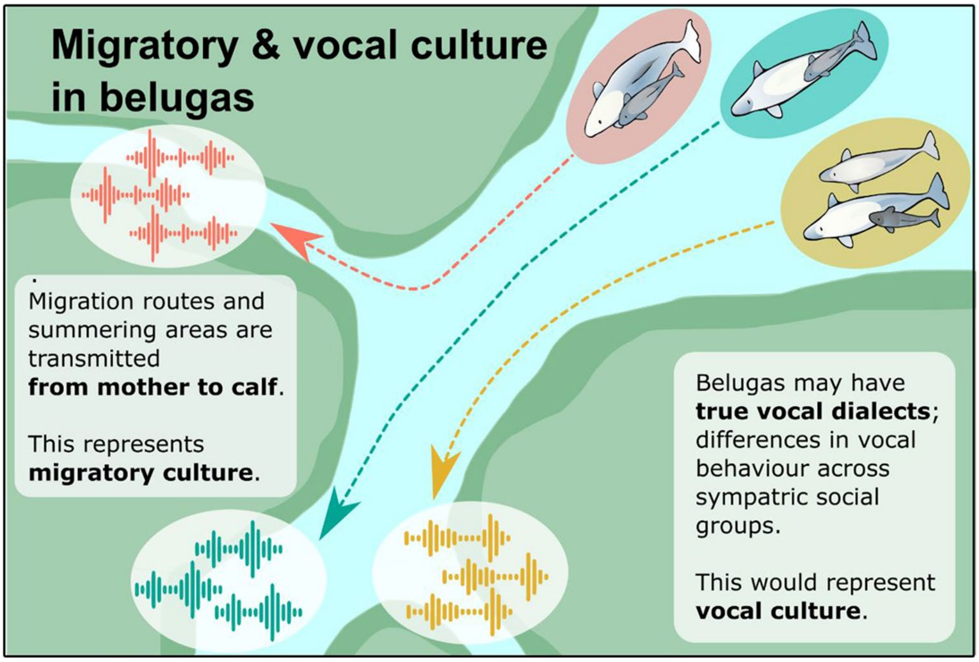
Migratory & vocal culture in belugas
Migration routes and summering areas are transmitted from mother to calf.
This represents migratory culture.
Belugas may have true vocal dialects; differences in vocal behaviour across sympatric social groups.
This would represent vocal culture.

Fig. 5 Migratory and vocal culture in belugas. Evidence suggests that belugas possess migratory culture in the form of well-established migratory routes and summering areas that are passed down from mother to calf. Preliminary evidence also suggests that belugas may possess vocal culture in the form of vocal dialects, although definitive evidence of dialects in belugas is still lacking

his half-sister appear to have acquired one of their mother's calls (Vergara and Barrett-Lennard 2008). However, in this case it is difficult to determine whether the vocalization was learned or genetically inherited. Compellingly, Tuvaq also acquired one of his father's calls, but only after being held in the same tank as his father, suggestive of social vocal learning (Vergara and Barrett-Lennard 2008).

Some evidence also suggests that belugas may possess vocal dialects, similar to those of killer whales (Ford 1991), sperm whales (Weilgart and Whitehead 1997), and short-finned pilot whales (Van Cise et al. 2018; Fig. 5). Vocal dialects are a compelling example of culture in wild animals, and are thought to arise as a result of vocal learning, among other factors (Marler and Tamura 1962). Following Conner (1980) we define dialects as vocal differences between neighbouring, potentially interbreeding animals. This differs from geographic vocal variation, which arise as a result of geographic distance between animals and reproductive isolation. Belugas in Canada and Russia are known to display geographic vocal variation (Panova et al. 2016; Booy et al. 2023), and some vocal differences have been identified among the belugas of the White Sea, although it is unclear whether the animals sampled represent geographically isolated or potentially interbreeding groups (Panova et al. 2019). Intriguingly, belugas were first suggested to possess dialects in 1979. In the first recorded beluga playback study, Morgan (1979) found that playback of non-local beluga sounds to belugas did not elicit a response, whereas playback of local sounds did. Morgan (1979) suggested that this may be due to belugas possessing different dialects. Further study is required to determine whether belugas show evidence of vocal variation consistent with dialects.

Beluga culture and conservation

Our understanding of beluga culture may help inform conservation strategies for beluga populations. Although belugas, as a species, are currently listed as "least concern" on the IUCN Red List (Lowry et al. 2017), many populations are endangered, including the Cook Inlet (Hobbs et al. 2008), Cumberland Sound, Ungava Bay, and St. Lawrence Estuary populations (COSEWIC 2014, 2020). Climate change is likely to negatively impact beluga populations worldwide (Watt et al. 2016; Noel et al. 2022).

Horizontally-transmitted culture- culture transmitted within generations- may facilitate more rapid adaptation to changing environments than vertically or obliquely-transmitted culture (Whitehead et al. 2004). Understanding how culture is transmitted in belugas may therefore provide insight into the resilience of different beluga populations. In addition, distinct communities may possess different cultural traits that that influence their vulnerability to anthropogenic threats (Brakes et al. 2021). For example, beluga populations whose traditional migratory routes overlap with areas of heavy marine traffic may have a greater exposure to disturbance than populations traveling along quieter routes (Chion et al. 2021). The degree to which belugas adhere to their migratory routes might in turn impact how they respond to new shipping routes in the changing Arctic.

In addition, if belugas possess regional dialects, vocal differences between communities may be shaped by local levels of anthropogenic noise, with some dialects potentially being more resilient to increasing anthropogenic noise. Beyond practical matters, by recognizing belugas as cultural beings, we better appreciate the inherent value of each individual, group, herd, and community. The field of conservation is increasingly recognizing the inherent value of both individuals (Ferraro et al. 2023) and non-human cultures (Brakes et al. 2019). As cultural beings ourselves, we are well-equipped to understand what is at stake: the loss of each beluga population represents not just a decline in numbers but the irrevocable loss of a distinct culture, including its vocal traditions, migratory knowledge, and other cultural traits yet unknown to us.

Conclusion and future research directions

In this review, we have summarized the literature on beluga social structure and culture. We conclude that there is ample evidence of fission-fusion dynamics within beluga societies, and that these dynamics may be characterized as atomistic, individual-based fission-fusion dynamics. Future research should examine whether fission-fusion dynamics differ between the sexes, and whether the fission-fusion dynamics of females differ with reproductive activities. We found that most beluga societies, though not all, are sexually segregated. As such, belugas may provide an interesting study system to investigate the emergence of sexual segregation. Our examination of existing studies of male beluga sociality reveals that male belugas often associate closely with each other, and that these associations can be stable. However, further work is needed to quantify the stability and longevity of male associations, similar to research on male bottlenose dolphins. The question of whether female belugas live in matrilineal societies can be clarified by precisely defining the terms "matrilineal", "matrifocal", and "matriarchal". We attempted to clarify these definitions (Box 2), and suggest that female belugas live in matrifocal, but not matrilineal societies. These societies are partly structured by female kinship, and mothers and older females are socially central. The existence of older, post-reproductive females also suggests that belugas may be matriarchal. The evolution of menopause in this species represents a compelling avenue for ongoing research, as we strive to better understand the evolution and significance of female post-reproductive lifespans. We show that there is ample evidence of multilevel social structure among belugas and suggest four possible social levels: the mother-calf dyad, the group, the herd, and the community. Further work is needed to understand how sexual segregation operates across these social levels, and how the social levels change seasonally. Finally, we note that there is strong evidence that belugas possess migratory culture, and moderate evidence that belugas possess vocal culture. Further investigation is needed to determine whether belugas possess vocal dialects. As highly gregarious social learners with protracted periods of offspring dependence and long post-reproductive lifespans, belugas may also possess many other forms of culture that are yet unknown to us.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00265-025-03630-3.

Acknowledgements We thank the many researchers who have made this review possible. We thank two anonymous reviewers for feedback that improved the manuscript. For silhouettes in Fig. 2.1, we thank Chris Huh, Cathy, and Sarah Werning through licenses from creativecommons.org and public domain images from phylopic.org.

Author contributions Conceptualization, investigation, visualization, and writing (original draft) were performed by JAA. Validation and writing (review and editing) were performed by RM. Funding acquisition, supervision, validation, and writing (review and editing) were performed by DJM and VV.

Funding This work was supported by the Natural Sciences and Engineering Research Council of Canada (NSERC) through a scholarship to JAA and a grant to DJM.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

References

Alekseeva YI, Panova EM, Bel'kovich VM (2013) Behavioral and acoustical characteristics of the reproductive gathering of Beluga whales (*Delphinapterus leucas*) in the vicinity of myagostrov, golyi sosnovets, and Roganka Islands (Onega bay, the White Sea). Biol Bull 40:307–317

Alves F, Quérouil S, Dinis A, Nicolau C, Ribeiro C, Freitas L, Kaufmann M, Fortuna C (2013) Population structure of short-finned pilot whales in the oceanic Archipelago of Madeira based on photo-identification and genetic analyses: implications for conservation. Aquat Conserv 23:758–776

Ames AE, Vergara V (2020) Trajectories of vocal repertoire development in beluga (*Delphinapterus leucas*) calves: insights from studies a decade apart. Aquat Mamm 46:344–366

Aubin JA, Michaud R, Vander Wal E (2021) Prospective evolutionary drivers of allocare in wild Belugas. Behaviour 518:1–30

Augusto JF, Frasier TR, Whitehead H (2017) Social structure of long-finned pilot whales (Globicephala melas) off northern Cape Breton Island Nova Scotia. Behaviour 154(5):509–540

Aureli F, Schaffner CM, Boesch C et al (2008) Fission-fusion dynamics: new research frameworks. Curr Anthropol 49:627–654

Ausen EL, Barber DG, Basu A, Ehn J, Walker D, Dalman L, MarcouxM (2023) River-influenced beluga (Delphinapterus leucas)summer habitat use in western Hudson Bay, Canada. Arctic Sci 00:1–17

Baird RW (2000) The killer whale: foraging specializations and group hunting. In: Mann J, Connor RC, Tyack PL, Whitehead H (eds)

Cetacean societies: field studies of whales and dolphins. University of Chicago Press, Chicago, pp 127–153

Beck S, Kuningas S, Esteban R, Foote AD (2012) The influence of ecology on sociality in the killer whale (*Orcinus orca*). Behav Ecol 23:246–253

Bel'kovitch VM, Sh'ekotov MN (1993) The Belukha whale: natural behavior and bioacoustics. Woods Hole Oceanographic Institution, Falmouth

Bercovitch FB, Berry PSM (2013) Herd composition, kinship and fission–fusion social dynamics among wild giraffe. Afr J Ecol 51:206–216

Berry PSM, Bercovitch FB (2015) Leadership of herd progressions in the Thornicroft's giraffe of Zambia. Afr J Ecol 53:175–182

Best PB (1979) Social organization in sperm whales, physeter macrocephalus. In: Winn FE, Olla BL (eds) Behavior of marine mammals: current perspectives in research. Vol. 3, cetaceans. Plenum, New York, pp 227–289

Bond JM (1999) Genetic analysis of the sperm whale (*Physeter macrocephalus*) using microsatellites. Dissertation, University of Cambridge

Bonnell TR, Michaud R, Dupuch A, Lesage V, Chion C (2022) Extracting spatial networks from capture–recapture data reveals individual site fidelity patterns within a marine mammal's spatial range. Ecol Evol 12:e8616

Booy KV, Vergara V, Loseto L, Mikus M-A, Marcoux M (2023) Geographic variation in simple contact calls of Canadian Beluga whales (*Delphinapterus leucas*). Mar Mamm Sci 40:e13095

Boughman JW, Moss CF (2003) Social sounds: vocal development of mammal and bird calls. In: Simmons AM, Fay RR, Popper AN (eds) Acoustic communication: springer handbook of auditory research, vol 16. Springer, New York, pp 138–224

Boyd R, Richerson PJ (1996) Why culture is common, but cultural evolution is rare. Proc Br Acad 88:77–93

Brakes P, Dall SRX, Aplin LM et al (2019) Animal cultures matter for conservation. Science 363:1032–1034

Brakes P, Carroll EL, Dall SRX et al (2021) A deepening Understanding of animal culture suggests lessons for conservation. Proc R Soc B 288:20202718

Breed GA, Matthews CJD, Marcoux M, Higdon JW, LeBlanc B, Petersen SD, Orr J, Reinhart NR, Ferguson S (2017) Sustained disruption of Narwhal habitat use and behavior in the presence of Arctic killer whales. P Natl Acad Sci USA 114:2628–2633

Brennin R, Murray BW, White BN, Clayton JW, Friesen MK, Maiers LD (1997) Population genetic structure of Beluga whales (*Delphinapterus leucas*): mitochondrial DNA sequence variation within and among North American populations. Can J Zool 75:795–802

Brent LJN, Franks DW, Foster EA, Balcomb KC, Cant MA, Croft DP (2015) Ecological knowledge, leadership, and the evolution of menopause in killer whales. Curr Biol 25:746–750

Brodie PF (1971) A reconsideration of aspects of growth, reproduction, and behavior of the white whale (*Delphinapterus leucas*), with reference to the Cumberland sound, Baffin island, population. J Fish Res Board Can 28:1309–1318

Brodie PF, Parsons JL, Sergeant DE (1981) Present status of the white whale (*Delphinapterus leucas*) in Cumberland sound. Rep Int Whale Commn 31:579–582

Brown Gladden JG, Ferguson MM, Clayton JW (1997) Matriarchal genetic population structure of North American Beluga whales *Delphinapterus leucas* (Cetacea: Monodontidae). Mol Ecol 6:1033–1046

Brown Gladden JG, Ferguson MM, Friesen MK, Clayton JW (1999) Population structure of North American Beluga whales (*Delphinapterus leucas*) based on nuclear DNA microsatellite variation and contrasted with the population structure revealed by mitochondrial DNA variation. Mol Ecol 8:347–363

Cantor M, Whitehead H (2013) The interplay between social networks and culture: theoretically and among whales and dolphins. Phil Trans R Soc Lond B Biol Sci 368:20120340

Cantor M, Shoemaker LG, Cabral RB, Flores CO, Varga M, Whitehead H (2015) Multilevel animal societies can emerge from cultural transmission. Nat Commun 6:8091

Chapman CA (1990) Association patterns of spider monkeys: the influence of ecology and sex on social organization. Behav Ecol Sociobiol 26:409–414

Chernetsky AD, Krasnova VV, Bel'kovich VM (2011) Studies of the structure of the Solovetsky reproductive gathering of Beluga whales (*Delphinapterus leucas*) in the white sea using the photo identification method. Oceanology 51:275–280

Chion C, Bonnell TR, Lagrois D, Michaud R, Lesage V, Dupuch A, McQuinn IH, Turgeon S (2021) Agent-based modelling reveals a disproportionate exposure of females and calves to a local increase in shipping and associated noise in an endangered beluga population. Mar Pollut Bull 173:112977

Clutton-Brock TH, Iason GR, Guinness FE (1987) Sexual segregation and density-related changes in habitat use in male and female red deer (*Cervus elaphus*). J Zool 211:275–289

Coakes AK, Whitehead H (2004) Social structure and mating system of sperm whales off Northern Chile. Can J Zool 82:1360–1369

Colbeck GJ, Duchesne P, Postma LD, Lesage V, Hammill MO, Turgeon J (2013) Groups of related belugas (*Delphinapterus leucas*) travel together during their seasonal migrations in and around Hudson Bay. Proc R Soc B-Biol Sci 280:20122552

Cosens SE, Dueck LP (1991) Group size and activity patterns of belugas (Delphinapterus leucas) and narwhals (Monodon monoceros) during spring migration in Lancaster Sound. Can J Zool 69(6):1630–1635

Conner DA (1980) Dialects versus geographic variation in mammalian vocalizations. Anim Behav 30:297–298

Connor RC, Krützen M (2015) Male dolphin alliances in Shark Bay: changing perspectives in a 30-year study. Anim Behav 103:223–235

Connor RC, Mann J, Tyack PL, Whitehead H (1998) Social evolution in toothed whales. Trends Ecol Evol 13:228–232

Connor RC, Wells RS, Mann J, Read AJ (2000) The bottlenose dolphin: social relationships in a fission–fusion society. In: Mann J, Conner RC, Tyack PL, Whitehead H (eds) Cetacean societies: field studies of dolphins and whales. University of Chicago Press, Chicago, pp 91–126

Connor RC, Watson-Capps JJ, Sherwin WB, Krützen M (2011) A new level of complexity in the male alliance networks of Indian Ocean bottlenose dolphins (*Tursiops* sp). Biol Lett 7:623–626

COSEWIC (2014) COSEWIC assessment and status report on the Beluga whale, *Delphinapterus leucas*, st. Lawrence estuary population, in Canada. Committee on the Status of Endangered Wildlife in Canada, Ottawa

COSEWIC (2020) COSEWIC assessment and status report on the Beluga whale, *Delphinapterus leucas*, Eastern high Arctic-Baffin Bay population, Cumberland sound population, Ungava Bay population, Western Hudson Bay population, Eastern Hudson Bay population and James Bay population in Canada. Committee on the Status of Endangered Wildlife in Canada, Ottawa

Connor RC, Cioffi WR, Randićć S, Allen SJ, Watson-Capps J, Krüützen M (2017) Male alliance behaviour and mating access varies with habitat in a dolphin social network. Sci Rep 7(1):46354

Croft DP, Johnstone RA, Ellis S, Nattrass S, Franks DW, Brent LJN, Mazzi S, Balcomb KC, Ford JKB, Cant MA (2017) Reproductive conflict and the evolution of menopause in killer whales. Curr Biol 27:298–304

De March BGE, Postma LD (2003) Molecular genetic stock discrimination of Belugas (*Delphinapterus leucas*) hunted in Eastern Hudson bay, Northern quebec, Hudson strait, and Sanikiluaq

(Belcher Islands), Canada, and comparisons to adjacent populations. Arctic 56:111–124

De March BGE, Maiers LD, Friesen MK (2002) An overview of genetic relationships of Canadian and adjacent populations of belugas (*Delphinapterus leucas*) with emphasis on Baffin Bay and Canadian Eastern Arctic populations. NAMMCO Sci Publ 4:17–38

de Silva S, Wittemyer G (2012) A comparison of social organization in Asian elephants and African Savannah elephants. Int J Primatol 33:1125–1141

de Silva S, Ranjeewa AD, Kryazhimskiy S (2011) The dynamics of social networks among female Asian elephants. BMC Ecol 11:17

DFO (2014) Status of Beluga (*Delphinapterus leucas*) in the st. Lawrence river estuary (Canadian science advisory secretariat research document 2013/076). Department of Fisheries and Oceans, Mont-Joli, Quebec

DFO (2022) Harvest advice for Eastern Hudson Bay and James Bay Beluga (*Delphinapterus leucas*). (Canadian science advisory secretariat research document 2022/024). Department of Fisheries and Oceans, Mont-Joli, Quebec

DFO (2023) Abundance and population trajectory of st. Lawrence Beluga (Canadian science advisory secretariat research document 2023/024). Department of Fisheries and Oceans, Mont-Joli, Quebec

Douglas CW (1951) Report on Beluga investigations at Churchill in 1950. J Fish Res Board Can 485:1–33

Dunbar RIM (1989) Social systems as optimal strategy sets: the costs and benefits of sociality. In: Standen V, Foley RA (eds) Comparative socioecology: the behavioural ecology of humans and other mammals. Blackwell Scientific, Oxford, pp 131–149

Eaton RL (1979) A beluga imitates human speech. Carnivore 2:22–23

Elharram M (2011) Population genetic structure and habitat use of the St. Lawrence beluga whales (Delphinapterus leucas). MSc thesis, Trent University

Ellis S, Franks DW, Nattrass S, Currie TE, Cant MA, Giles D, Balcomb KC, Croft DP (2018) Analyses of ovarian activity reveal repeated evolution of post-reproductive lifespans in toothed whales. Sci Rep 8:12833

Ellis S, Franks DW, Lybkaer M, Nielsen K, Weiss MN, Croft DP (2024) The evolution of menopause in toothed whales. Nature 627:579–585

English S, Nakagawa S, Clutton-Brock TH (2010) Consistent individual differences in cooperative behaviour in meerkats (*Suricata suricatta*). J Evol Biol 23:1597–1604

Ferraro KM, Ferraro AL, Arietta AZA, Sommer NR (2023) Revisiting two dogmas of conservation science. Conserv Biol 37:e14101

Finley KJ, Miller GW, Allard M, Davis RA, Evans CR (1982) The Belugas (Delphinapterus leucas) of Northern quebec: distribution, abundance, stock identity, catch history and management. Can Tech Rep Fish Aquat Sci 1123:Winnipeg

Ford JKB (1991) Vocal traditions among resident killer whales (*Orcinus orca*) in coastal waters of British Columbia. Can J Zool 69:1454–1483

Ford JKB (2019) Killer whales: behavior, social organization, and ecology of the oceans' apex predators. In: Wursig B (ed) Ethology and behavioral ecology of odontocetes. Springer International Publishing, Cham, pp 239–259

Foster EA, Franks DW, Mazzi S, Darden SK, Balcomb KC, Ford JKB, Croft DP (2012) Adaptive prolonged postreproductive life span in killer whales. Science 337:1313

Fraker MA, Gordon CD, Ford JKB, Cambers G (1979) White Whale (*Delphinapterus leucas*) distribution and abundance and the relationship to physical and chemical characteristics of the Mackenzie estuary. Fish & Mar Serv Tech Rep 863, Winnipeg

Freeman MMR (1973) Polar bear predation on Beluga in the Canadian Arctic. Arctic 26:162–163

Frère CH, Krützen M, Mann J, Watson-Capps JJ, Tsai YJ, Patterson EM, Connor R, Bejder L, Sherwin WB (2010) Home range overlap, matrilineal and biparental kinship drive female associations in bottlenose dolphins. Anim Behav 80:481–486

Galezo AA, Krzyszczyk E, Mann J (2018) Sexual segregation in Indo-Pacific bottlenose dolphins is driven by female avoidance of males. Behav Ecol 29:377–386

Gero S, Bøttcher A, Whitehead H, Madsen PT (2016) Socially segregated, sympatric sperm whale clans in the Atlantic Ocean. RSoc Open Sci 3(6):160061

Gowans S (2019) Grouping behaviors of dolphins and other toothed whales. In: Würsig B (ed) Ethology and behavioral ecology of odontocetes. Springer International Publishing, Cham, pp 3–24

Graw B, Manser MB (2007) The function of mobbing in cooperative meerkats. Anim Behav 74:507–517

Griffin AS (2003) A genetic analysis of breeding success in the cooperative meerkat (*Suricata suricatta*). Behav Ecol 14(4):472–480

Grimes C, Brent LJN, Ellis S, Weiss MN, Franks DW, Ellifrit DK, Croft DP (2023) Postreproductive female killer whales reduce socially inflicted injuries in their male offspring. Curr Biol 33:3250–3256

Grueter CC, Chapais B, Zinner D (2012) Evolution of multilevel social systems in nonhuman primates and humans. Int J Primatol 33:1002–1037

Grueter CC, Qi X, Zinner D et al (2020) Multilevel organisation of animal sociality. Trends Ecol Evol 35:834–847

Hamilton WD (1964) The genetical evolution of social behaviour. J Theor Biol 7:17–52

Hamilton MJ, Milne BT, Walker RS, Burger O, Brown JH (2007) The complex structure of hunter–gatherer social networks. Proc R Soc Lond B 274:2195–2203

Hauser DDW, Laidre KL, Stern HL, Moore SE, Suydam RS, Richard PR (2017) Habitat selection by two Beluga Whale populations in the Chukchi and Beaufort seas. PLoS One 12:e0172755

Hawkes K, O'Connell JF, Jones NGB, Alvarez H, Charnov EL (1998) Grandmothering, menopause, and the evolution of human life histories. P Natl Acad Sci USA 95:1336–1339

Hill HM, Campbell CA (2014) The frequency and nature of allocare by a group of Belugas (*Delphinapterus leucas*) in human care. Int J Comp Psychol 27:501–514

Hill HM, de Silva-Gruber ODG, Noonan M (2018) Sex-specific social affiliation in captive Beluga whales (*Delphinapterus leucas*). Aquat Mamm 44:250–255

Hobbs RC, Shelden KEW, Rugh DJ, Norman SA (2008) Status review and extinction risk assessment of cook Inlet Belugas (Delphinapterus leucas). AFSC processed rep. 2008-02, Alaska fish sci cent. NOAA Natl Mar Fish Serv, Seattle, WA

Holekamp KE, Smith JE, Strelioff CC, Van Horn RC, Watts HE (2012) Society, demography and genetic structure in the spotted hyena. Mol Ecol 21:613–632

Johnstone RA, Cant MA (2010) The evolution of menopause in cetaceans and humans: the role of demography. Proc R Soc Lond B 277:3765–3771

Jordaan RK, Reisinger RR, Oosthuizen WC, de Bruyn PJN (2021) Seasonal fission and fusion of killer whale, *Orcinus orca*, social structure at sub-Antarctic Marion Island. Anim Behav 177:223–230

Karenina K, Giljov A, Glazov D, Malashichev Y (2013) Social laterality in wild Beluga whale infants: comparisons between locations, escort conditions, and ages. Behav Ecol Sociobiol 67:1195–1204

Kelley TC (2014) Linking feeding and reproductive ecology in beluga (*Delphinapterus leucas*) and narwhal (*Monodon monoceros*) Dissertation, University of Manitoba

Kelley TC, Loseto LL, Stewart REA, Yurkowski M, Ferguson SH (2010) Importance of eating capelin: unique dietary habits of Hudson Bay Beluga. In: Ferguson SH, Loseto LL, Mallory ML (eds) A little less arctic: top predators in the world's largest inland sea, Hudson Bay. Springer, Dordrecht, pp 53–69

Kelley JL, Morrell LJ, Inskip C, KrauseJ, Croft DP (2011) Predation risk shapes social networks in fission-fusion populations. PLoS One 6:e24280

Kerth G, Perony N, Schweitzer F (2011) Bats are able to maintain long-term social relationships despite the high fission–fusion dynamics of their groups. Proc R Soc Lond B 278:2761–2767

King SL, McGregor PK (2016) Vocal matching: the what, the why and the how. Biol Lett 12:20160666

King SL, Sayigh LS, Wells RS, Fellner W, Janik VM (2013) Vocal copying of individually distinctive signature whistles in bottlenose dolphins. Proc R Soc Lond B Biol Sci 280:20130053

Kleinenberg SE, Yablokov AV, Belkovich BM, Tarasevich MN (1964) Beluga (*Delphinapterus leucas*) an investigation of the species. Academy of sciences of the USSR, the A. N. Severtsov Institute of Animal Morphology, Moscow

Konrad CM, Frasier TR, Whitehead H, Gero S (2019) Kin selection and allocare in sperm whales. Behav Ecol 30:194–201

Krasnova VV, Chernetsky AD, Kirillova OI, Bel'kovich VM (2012) The dynamics of the abundance, age, and sex structure of the Solovetsky reproductive gathering of the Beluga Whale *Delphinapterus leucas* (Onega bay, white Sea). Russ J Mar Biol 38:218–225

Krasnova VV, Chernetsky AD, Zheludkova AI, Bel'kovich VM (2014) Parental behavior of the Beluga Whale (*Delphinapterus leucas*) in natural environment. Biol Bull 41:349–356

Kummer H (1971) Primate societies: group techniques of ecological adaptation. Aldine/Atherton, Chicago

Lahdenperä M, Gillespie DOS, Lummaa V, Russell AF (2012) Severe intergenerational reproductive conflict and the evolution of menopause. Ecol Lett 15:1283–1290

Lehmann J, Boesch C (2004) To fission or to fusion: effects of community size on wild chimpanzee (*Pan troglodytes verus*) social organisation. Behav Ecol Sociobiol 56:207–216

Lemieux Lefebvre S, Lesage V, Michaud R, Humphries MM (2018) Classifying and combining herd surface activities and individual dive profiles to identify summer behaviours of Beluga (*Delphinapterus leucas*) from the st. Lawrence estuary, Canada. Can J Zool 96:393–413

Lesage V, Measures L, Mosnier A, Lair S, Michaud R, Béland P (2014) Mortality patterns in st. Lawrence estuary Beluga (*Delphinapterus leucas*), inferred from the carcass recovery data, 1983–2012. DFO Canadian Science Advisory Secretariat Research Document 2013/118, Mont-Joli, Quebec

Lesage V, Lair S, Turgeon S, Béland P (2020) Diet of st. Lawrence estuary Beluga (*Delphinapterus leucas*) in a changing ecosystem. Can Field-Nat 134:21–35

Leung ES, Vergara V, Barrett-Lennard LG (2010) Allonursing in captive belugas (*Delphinapterus leucas*). Zoo Biol 29(5)

Loretto M-C, Schuster R, Itty C, Marchand P, Genero F, Bugnyar T (2017) Fission-fusion dynamics over large distances in raven non-breeders. Sci Rep 7:380

Loseto LL, Stern GA, Connelly TL, Deibel D, Gemmill B, Prokopwicz A, Fortier L, Ferguson SH (2009) Summer diet of Beluga whales inferred by fatty acid analysis of the Eastern Beaufort Sea food web. J Exp Mar Biol Ecol 374:12–18

Lowry L, Reeves R, Laidre K (2017) Delphinapterus leucas. The IUCN Red List of Threatened Species 2017: e.T6335A50352346. http://dx.doi.org/10.2305/IUCN.UK.2017-3.RLTS.T6335A50352346.en

Lydersen C, Martin A, Kovacs K, Gjertz I (2001) Summer and autumn movements of white whales *Delphinapterus leucas* in svalbard, Norway. Mar Ecol Prog Ser 219:265–274

Main MB, Weckerly FW, Bleich VC (1996) Sexual segregation in ungulates: new directions for research. J Mammal 77:449–461

Mann J, Smuts BB (1998) Natal attraction: allomaternal care and mother–infantseparations in wild bottlenose dolphins. An Beh 55(5):1097–1113

Mann J, Connor RC, Tyack PL, Whitehead H (eds) (2000) Cetacean societies: field studies of dolphins and whales. University of Chicago Press, Chicago

Marcoux M, Whitehead H, Rendell L (2006) Coda vocalizations recorded in breeding areas are almost entirely produced by mature female sperm whales (*Physeter macrocephalus*). Can J Zool 84:609–614

Marler P, Tamura M (1962) Song dialects in three populations of white-crowned sparrows. Condor 64:368–377

Marlowe FW (2005) Hunter-gatherers and human evolution. Evol Anthropol 14:54–67

Matthews CJD, Ferguson SH (2015) Weaning age variation in Beluga whales (*Delphinapterus leucas*). J Mammal 96:425–437

Mayette A, Loseto L, Pearce T, Hornby CA, Marcoux M (2022) Group characteristics and spatial organization of the Eastern Beaufort Sea Beluga whale (*Delphinapterus leucas*) population using aerial photographs. Can J Zool 100:363–375

McAlpine DF, Kingsley MCS, Daoust P-Y (1999) A lactating record-age st. Lawrence Beluga (*Delphinapterus leucas*). Mar Mamm Sci 15:854–859

McComb K, Moss C, Durant SM, Baker L, Sayialel S (2001) Matriarchs as repositories of social knowledge in African elephants. Science 292:491–494

McComb K, Shannon G, Durant SM, Sayialel K, Slotow R, Poole J, Moss C (2011) Leadership in elephants: the adaptive value of age. Proc R Soc Lond B 278:3270–3276

McGuire TL, Himes Boor GK, McClung JR, Stephens AD, Garner C, Shelden KEW, Wright B (2020) Distribution and habitat use by endangered cook Inlet Beluga whales: patterns observed during a photo-identification study 2005–2017. Aquat Conserv 30:2402–2427

McHugh K (2019) Odontocete social strategies and tactics along and inshore. In: Würsig B (ed) Ethology and behavioral ecology of odontocetes. Springer International Publishing, Cham, pp 165–182

Meschersky IG, Chernetsky AD, Krasnova VV, Solovyev BA, Udovik DA, Shpak OV, Glazov DM, Rozhnov VV (2018) Mitochondrial lineages of the Beluga Whale *Delphinapterus leucas* in the Russian Arctic. Biol Bull 45:147–154

Michaud R (1993) Distribution estivale du Béluga du Saint-Laurent: synthèse 1986–1992. Rapp tech can sci Halieut Aquat 1906. Pêches et Océans Canada, Québec, Québec

Michaud R (1999) Social organization of the St. Lawrence beluga, *Delphinapterus leucas*. In: 13th Conference on the Biology of Marine Mammals, Society for marine mammalogy, Maui, Hawaii

Michaud R (2005a) Sociality and ecology of the odontocetes. In: Ruckstuhl K, Neuhaus P (eds) Sexual segregation in vertebrates. Cambridge University Press, Cambridge, pp 303–326

Michaud R (2005b) Complex social structure in beluga whales: Do males form alliances? Are males territorial? In: Delphinid and Primate Social Ecology Conference, Kyoto, Japan

Michaud R (2014) St. Lawrence estuary Beluga (*Delphinapterus leucas*) population parameters based photo-identification surveys 1989–2012. DFO Can Sci Advis Sec Res Doc 2013/130, Québec

Michaud R, Vézina A, Rondeau N, Vigneault Y (1990) Annual distribution and preliminary characterization of beluga habitats in the St. Lawrence. Can Tech Rep Fish Aquat Sci 1757, Quebec

Mishima Y, Morisaka T, Itoh M, Matsuo I, Sakaguchi A, Miyamoto Y (2015) Individuality embedded in the isolation calls of captive Beluga whales (*Delphinapterus leucas*). Zool Lett 1:1–27

Morgan DW (1979) The vocal and behavioral reactions of the beluga, *Delphinapterus leucas*, to playback of its sounds. In: Winn HE, Olla BL (eds) Behavior of marine animals: current perspectives in research, vol 3. Cetaceans. Plenum, New York, pp 391–423

Morisaka T, Yoshida Y, Akune Y, Mishima H, Nishimoto S (2013) Exchange of signature calls in captive Belugas (*Delphinapterus leucas*). J Ethol 31:141–149

Morteo E, Rocha-Olivares A, Abarca-Arenas LG (2014) Sexual segregation of coastal bottlenose dolphins (*Tursiops truncatus)* in the Southwestern Gulf of Mexico. Aquat Mamm 40:375–385

Murayama T, Iijima S, Katsumata H, Arai K (2014) Vocal imitation of human speech, synthetic sounds and Beluga sounds, by a Beluga (*Delphinapterus leucas*). Int J Comp Psychol 27:369–384

Nichols HJ, Arbuckle K, Fullard K, Amos W (2020) Why don't long-finned pilot whales have a widespread postreproductive lifespan? Insights from genetic data. Behav Ecol 31:508–518

Noel A, Iacozza J, Devred E, Marcoux M, Hornby C, Loseto LL (2022) Environmental drivers of Beluga Whale distribution in a changing climate: a case study of summering aggregations in the Mackenzie estuary and Tarium Niryutait Marine Protected Area. Arct Sci 8:1305–1319

Norris N (2002) Creatures of culture? Making the case of cultural systems in whales and dolphins. Bioscience 52:9–14

O'Corry-Crowe G, Lydersen C, Heide-Jørgensen MP, Hansen L, Mukhametov LM, Dove O, Kovacs KM (2010) Population genetic structure and evolutionary history of North Atlantic Beluga whales (*Delphinapterus leucas*) from West greenland, Svalbard and the white sea. Pol Biol 3:1179–1194

O'Corry-Crowe G, Suydam R, Quakenbush L et al (2018) Migratory culture, population structure and stock identity in North Pacific Beluga whales (*Delphinapterus leucas*). PLoS One 13:e0194201

O'Corry-Crowe G, Suydam R, Quakenbush L, Smith TG, Lydersen C, Kovacs KM, Orr J, Harwood L, Litovka D, Ferrer T (2020) Group structure and kinship in beluga whale societies. Sci Rep 10:11462

Ognetev GN (1981) Studies on the ecology and the taxonomy of the white Whale (*Delphinapterus leucas* pall. 1776) inhabiting the Soviet Arctic. In: Thirty-First Report of the International Whaling Commission International Whaling Commission, London, pp 515–520

Ouellet J-F, Michaud R, Moisan M, Lesage V (2021) Estimating the proportion of a Beluga population using specific areas from connectivity patterns and abundance indices. Ecosphere 12:e03560

Palsbøll PJ (1997) Population structure and seasonal movements of narwhals, *Monodon monoceros*, determined from MtDNA analysis. Heredity 78:284–292

Palsbøll PJ, Heide-Jørgensen MP, Bérubé M (2002) Analysis of mitochondrial control region nucleotide sequences from Baffin Bay beluga, (*Delphinapterus leucas*): detecting pods or sub-populations? NAMMCO Sci Publ 4:39

Panova EM, Agafonov AV (2017) A beluga whale socialized with bottlenose dolphins imitates their whistles. Anim Cogn 20:1153–1160

Panova EM, Agafonov AV (2023) Possible occurrence of contact calls in all-male groups of free-ranging Beluga whales. J Zool 320:29–41

Panova EM, Belikov RA, Agafonov AV, Kirillova OI, Chernetsky AD, Bel'kovitch VM (2016) Intraspecific variability in the vowel-like sounds of Beluga whales (*Delphinapterus leucas*): intra- and interpopulation comparisons. Mar Mamm Sci 32:452–465

Panova EM, Agafonov A, Belikov R, Melnikova F (2019) Characteristics and microgeographic variation of whistles from the vocal repertoire of Beluga whales (*Delphinapterus leucas*) from the white sea. J Acoust Soc Am 146:681–692

Parent GJ, Mosnier A, Montana L, Cortial G, St-Pierre AP, Bordeleau X, Lesage V, Watt C, Postma L, Hammill MO (2023) Re-examining populations of Beluga in the Hudson Bay-Strait complex and assessing the impact on harvests in Nunavik and Sanikiluaq management units. DFO Can Sci Advis Sec Res Doc 2023/004, Ottawa

Parsons KM, Balcomb KC, Ford JKB, Durban JW (2009) The social dynamics of Southern resident killer whales and conservation implications for this endangered population. Anim Behav 77:963–971

Photopoulou T, Ferreira IM, Best PB, Kasuya T, Marsh H (2017) Evidence for a post-reproductive phase in female false killer whales *Pseudorca crassidens*. Front Zool 14:30

Pippard L (1985) Status of the st. Lawrence river population of Belugas *Delphinapterus leucas*. Can Field-Nat 99:439–450

Pippard L, Malcolm H (1978) White whales (*Delphinapterus leucas*). Observations on their distribution, population and critical habitats in the st. Lawrence and Saguenay rivers. Department of Indian and Northern Affairs, Ottawa

Ponnampala LS (2016) No danger in sight? An observation of sperm whales (*Physeter macrocephalus*) in Marguerite formation off muscat, Sultanate of Oman. Aquat Mamm 42:162–167

Postma LD (2017) Genetic diversity, population structure and phylogeography among belugas (*Delphinapterus leucas*) in Canadian waters: Broad to fine-scale approaches to inform conservation and management strategies. Dissertation, University of Manitoba

Rauber R, Manser MB (2021) Effect of group size and experience on the ontogeny of sentinel calling behaviour in meerkats. Anim Behav 171:129–138

Rendell L, Whitehead H (2001) Culture in whales and dolphins. Behav Brain Sci 24:309–324

Rendell LE, Whitehead H (2003) Vocal clans in sperm whales (*Physeter macrocephalus*). Proc R Soc Lond B 270:225–231

Rendell L, Cantor M, Gero S, Whitehead H, Mann J (2019) Causes and consequences of female centrality in cetacean societies. Phil Trans R Soc Lond B Biol Sci 374:20180066

Richard PR, Heide-Jørgensen MP, St. Aubin D (1998) Fall movements of belugas (*Delphinapterus leucas*) with satellite-linked transmitters in Lancaster sound, Jones sound, and Northern Baffin Bay. Arctic 51:5–16

Richard PR, Martin AR, Orr JR (2001) Summer and autumn movements of Belugas of the Eastern Beaufort Sea stock. Arctic 54:223–236

Ridgway SH, Carder DA, Kamolnick T, Smith RR, Schlundt CE, Elsberry WR (2001) Hearing and whistling in the deep sea: depth influences whistle spectra but does not attenuate hearing by white whales (*Delphinapterus leucas*) (Odontoceti Cetacea). J Exp Biol 204:3829–3841

Ridgway S, Carder D, Jeffries M, Todd M (2012) Spontaneous human speech mimicry by a cetacean. Curr Biol 22:860–861

Rodseth L, Wrangham RW, Harrigan AM et al (1991) The human community as a primate society [and comments]. Curr Anthropol 32:221–254

Rubenstein DI, Hack M (2004) Natural and sexual selection and the evolution of multi-level societies: insights from zebras with comparisons to primates. In: Kappeler PM, van Schaik CP (eds) Sexual selection in primates, 1st edn. Cambridge University Press, Cambridge, pp 266–279

Ruckstuhl KE, Neuhaus P (2000) Sexual segregation in ungulates: a new approach. Behaviour 137:361–377

Ruckstuhl KE, Neuhaus P (2002) Sexual segregation in ungulates: a comparative test of three hypotheses. Biol Rev 77:77–96

Sayigh LS, Tyack PL, Wells RS, Solow AR, Scott MD, Irvine AB (1998) Individual recognition in wild bottlenose dolphins: a field test using playback experiments. Anim Behav 57:41–50

Seaman GA (1981) Preliminary results of recent studies of Belukhas in Alaskan waters. Rep Int Whal Commn 31:567–573

Sergeant DE (1962) The biology and hunting of Beluga or white whales in the Canadian Arctic. Fish Res Board Can, Fisheries and Oceans Canada, Montreal

Sergeant DE (1973) Biology of white whales (*Delphinapterus leucas*) in Western Hudson Bay. J Fish Res Board Can 30:1065–1090

Sergeant DE (1986) Present status of white whales *Delphinapterus leucas* in the st. Lawrence estuary. Nat Cancer 113:61–81

Sergeant DE, Brodie PF (1975) Identity, abundance, and present status of populations of white whales, *Delphinapterus leucas*, in North America. J Fish Res Board Can 32:1047–1054

Simard Y, Loseto LL, Gautier S, Roy N (2014) Monitoring beluga habitat use and underwater noise levels in the Mackenzie Estuary: Application of passive acoustics in summers 2011 and 2012. Can Tech Rep Fish Aquat Sci 3068, Fisheries and Oceans, Mont-Joli - Quebec

Smith TG, Martin AR (1994) Distribution and movements of belugas, *Delphinapterus leucas*, in the Canadian high Arctic. Can J Fish Aquat Sci 51:1653–1663

Smith TG, St Aubin DJ, Hammill MO (1992) Rubbing behaviour of belugas, *delphinapterus leucas*, in a high Arctic estuary. Can J Zool 70:2405–2409

Smith TG, Hammill MO, Martin AR (1994) Herd composition and behaviour of white whales (Delphinapterus leucas) in two Canadian Arctic estuaries. In: Born EW, Dietz R, Reeves RR (eds) Studies of white whales (*Delphinapterus leucas*) and narwhals (*Monodon monoceros*) in Greenland and adjacent waters. Meddr Grønland, Biosci 39:175–184

Smith JE, Estrada JR, Richards HR, Dawes SE, Mitsos K, Holekamp KE (2015) Collective movements, leadership and consensus costs at reunions in spotted hyaenas. Anim Behav 105:187–200

Smith AJ, Higdon JW, Richard P, Orr J, Bernhardt W, Ferguson SH (2017) Beluga whale summer habitat associations in the Nelson River estuary, Western Hudson Bay, Canada. PLoS One 12:e0181045

Smolker RA, Pepper JW (1999) Whistle convergence among allied male bottlenose dolphins (delphinidae, *tursiops* sp). Ethology 105:595–617

Smolker RA, Richards AF, Connor RC, Pepper JW (1992) Sex differences in patterns of association among Indian Ocean bottlenose dolphins. Behaviour 123:38–69

St Aubin DJ, Smith TG, Geraci JR (1990) Seasonal epidermal moult in Beluga whales (*Delphinapterus leucas*). Can J Zool 68:359–367

Surbeck M, Girard-Buttoz C, Boesch C, Crockford C, Fruth B, Hohmann G, Langergraber KE, Zuberbühler K, Wittig RM, Mundry R (2017) Sex-specific association patterns in bonobos and chimpanzees reflect species differences in cooperation. R Soc Open Sci 4:16108

Suydam RS, Lowry LF, Frost KJ, O'Corry-Crowe GM, Pikok D (2001) Satellite tracking of Eastern Chukchi Sea Beluga whales into the Arctic Ocean. Arctic 54:237–243

Tavares SB, Samarra FIP, Miller PJO (2017) A multilevel society of herring-eating killer whales indicates adaptation to prey characteristics. Behav Ecol 28:500–514

Tsai YJ, Mann J (2013) Dispersal, philopatry, and the role of fission-fusion dynamics in bottlenose dolphins. Mar Mamm Sci 29:261–279

Turgeon J, Duchesne P, Colbeck GJ, Postma LD, Hammill MO (2012) Spatiotemporal segregation among summer stocks of Beluga (*Delphinapterus leucas*) despite nuclear gene flow: implication for the endangered Belugas in Eastern Hudson Bay (Canada). Conserv Genet 13:419–433

Tyack PL (1986) Whistle repertoires of two bottlenosed dolphins, *Tursiops truncatus*: mimicry of signature whistles? Behav Ecol Sociobiol 18:251–257

Tyack PL (1997) Development and social functions of signature whistles in bottlenose dolphins *tursiops truncatus*. Bioacoustics 8:21–46

Tyack PL (2000) Functional aspects of cetacean communication. In: Mann J, Connor RC, Tyack PL, Whitehead H (eds) Cetacean societies: field studies of whales and dolphins. University of Chicago Press, Chicago, pp 270–307

Tyack PL (2003) Dolphins communicate about individual-specific social relationships. In: de Waal FBM, Tyack PL (eds) Animal social complexity: intelligence, culture, and individualized societies. Harvard University Press, Cambridge, pp 342–361

Uhl F, Ringler M, Miller R, Deventer SA, Bugnyar T, Schwab C (2019) Counting crows: population structure and group size variation in an urban population of crows. Behav Ecol 30:57–67

Van Cise AM, Mahaffy SD, Baird RW, Mooney TA, Barlow J (2018) Song of my people: dialect differences among sympatric groups of short-finned pilot whales in hawai'i. Behav Ecol Sociobiol 72:193

van Schaik CP (1999) The socioecology of fission-fusion sociality in orangutans. Primates 40:69–86

VanderWaal KL, Wang H, McCowan B, Fushing H, Isbell LA (2014) Multilevel social organization and space use in reticulated giraffe (*Giraffa camelopardalis*). Behav Ecol 25:17–26

Vergara V, Barrett-Lennard LG (2008) Vocal development in a Beluga calf (*Delphinapterus leucas*). Aquat Mamm 34:123–143

Vergara V, Mikus M-A (2019) Contact call diversity in natural Beluga entrapments in an Arctic estuary: preliminary evidence of vocal signatures in wild Belugas. Mar Mamm Sci 35:434–465

Vergara V, Michaud R, Barrett-Lennard L (2010) What can captive whales tell Us about their wild counterparts? Identification, usage, and ontogeny of contact calls in belugas (*Delphinapterus leucas*). Int J Comp Psychol 23:278–309

Vergara V, Wood J, Lesage V, Ames A, Mikus M-A, Michaud R (2021) Can you hear me? Impacts of underwater noise on communication space of adult, sub-adult and calf contact calls of endangered st. Lawrence Belugas (*Delphinapterus leucas*). Polar Res 40:5521

Vladykov VV (1944) Etudes Sur les mammifères aquatiques III.-chasse, biologie et Valeur économique du marsouin blanc Ou Béluga (*Delphinapterus leucas*) du fleuve et du Golfe Saint-Laurent. Contrib Dep Fish Que 14:5–I94

Watt C, Orr J, Ferguson S (2016) A shift in foraging behaviour of Beluga whales *Delphinapterus leucas* from the threatened Cumberland sound population may reflect a changing Arctic food web. Endanger Species Res 31:259–270

Waugh DA, Suydam RS, Ortiz JD, Thewissen JGM (2018) Validation of growth layer group (GLG) depositional rate using daily incremental growth lines in the dentin of Beluga (*Delphinapterus leucas* (Pallas 1776)) teeth. PLoS One 13:e0190498

Weilgart L, Whitehead H (1997) Group-specific dialects and geographical variation in coda repertoire in South Pacific sperm whales. Behav Ecol Sociobiol 40:277–285

Westdal KH, Davies J, McPherson A, Orr J, Ferguson SH (2017) Behavioural changes in Belugas (*Delphinapterus leucas*) during a killer Whale (*Orcinus orca*) attack in Southwest Hudson Bay. Can Field-Nat 130:315

Westdal KH, Davies J, Ferguson SH (2022) Assessing seasonal spatial segregation by age class of Beluga whales (*Delphinapterus leucas*) in Western Hudson Bay estuaries. PLoS One 17:e0255756

Whitehead H (2024) Sperm whale clans and human societies. R Soc Open Sci 11:231353

Whitehead H, Weilgart L (2000) The sperm whale: social females and roving males. In: Mann J, Connor RC, Tyack PL, Whitehead H (eds) Cetacean societies: field studies of whales and dolphins. University of Chicago Press, Chicago, pp 154–173

Whitehead H, Waters S, Lyrholm T (1991) Social organization of female sperm whales and their offspring: constant companions and casual acquaintances. Behav Ecol Sociobiol 29:385–389

Whitehead H, Rendell L, Osborne RW, Würsig B (2004) Culture and conservation of non-humans with reference to whales and dolphins: review and new directions. Biol Conserv 120:427–437

Whitehead H, Antunes R, Gero S, Wong SNP, Engelhaupt D, Rendell L (2012) Multilevel societies of female sperm whales (*Physeter macrocephalus*) in the Atlantic and Pacific: why are they so different? Int J Primatol 33:1142–1164

Whitehead H, Vachon F, Frasier TR (2017) Cultural hitchhiking in the matrilineal whales. Behav Genet 47:324–334

Wild G (2023) Pillars of biology: the genetical evolution of social behaviour, I and II. J Theor Biol 562:111430

Wiszniewski J, Allen SJ, Mööller LM (2009) Social cohesion in a hierarchically structured embayment population of Indo-Pacific bottlenose dolphins. An Beh 77(6):1449–1457

Wittemyer G, Douglas-Hamilton I, Getz WM (2005) The socioecology of elephants: analysis of the processes creating multitiered social structures. Anim Behav 69:1357–1371

Wright BM, Stredulinsky EH, Ellis GM, Ford JKB (2016) Kin-directed food sharing promotes lifetime natal philopatry of both sexes in a population of fish-eating killer whales, *Orcinus orca*. Anim Behav 115:81–95

Publisher's note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Springer Nature or its licensor (e.g. a society or other partner) holds exclusive rights to this article under a publishing agreement with the author(s) or other rightsholder(s); author self-archiving of the accepted manuscript version of this article is solely governed by the terms of such publishing agreement and applicable law.