ALLOCARE IN ST. LAWRENCE ESTUARY BELUGAS: PATTERNS, PROSPECTIVE DRIVERS, AND POTENTIAL BENEFITS

by

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ABSTRACT

Allocare, care provided to offspring by non-parents, challenges our understanding of how animals should allocate their time and energy. The evolution and maintenance of allocare in populations suggests that alloparents receive fitness benefits from allocare. In many species, recipient offspring also receive important benefits from alloparents. My research represents the first in-depth investigation of allocare in wild belugas. By examining patterns of allocare, I seek to understand why beluga allomothers provide care to the offspring of others. My findings suggest that allocare in St. Lawrence Estuary belugas may be driven by kin selection and reciprocation. I also investigate potential benefits of allocare for recipient offspring by examining variables associated with variation in offspring risk, energetic costs, and group sociality. Patterns of allocare were not consistent with protective, energetic, or social benefits to offspring. However, patterns of calf allocare were influenced by herd movement pattern and tidal phase. .

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LIST OF ABBREVIATIONS AND SYMBOLS

ΔAIC – Change in Akaike’s Information Criterion

AIC – Akaike’s Information Criterion

BaP – Benzo(a)pyrene

BSM – Baie-Ste-Marguerite

COSEWIC – Committee on the Status of Endangered Wildlife in Canada

DDT - Dichlorodiphenyltrichloroethane

DFO – Department of Fisheries and Oceans

ER – Evidence Ratio

GREMM – *Groupe de Recherche et d’Éducation sur les Mammifères Marins*

INRS – *Institut National de Recherche Scientifique*

PBDE – Polybrominated diphenyl ethers

PCB – Polychloricated biphenyls

SARA – Species At Risk Act

SÉPAQ – Société des Établissements de Plein Air du Québec

SLE – St. Lawrence Estuary

SSLMP – Saguenay St. Lawrence Marine Park

WWF – World Wildlife Fund

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CHAPTER 1: A BRIEF HISTORY OF BELUGAS IN THE ST. LAWRENCE

1.1 Overview of beluga biology

1.1.1 Arctic adaptations

Belugas (*Delphinapterus leucas*) are an arctic-adapted cetacean with circumpolar arctic distribution (COSEWIC, 2004). Belugas and narwhals (*Monodon monoceros*), their closest living relatives, are the only two species of the family Monodontidae. Monodonts are characterized by unfused cervical vertebrae, allowing independent movement of the head, and a cartilaginous "dorsal ridge" in place of a dorsal fin (Stewart & Stewart, 1989). This dorsal ridge allows monodonts to break sea ice up to 20 cm in thickness to form breathing holes (Sergeant, 1973). To maintain thermal homeostasis in arctic waters, both species possess a thick layer of blubber, up to 27 cm in thickness and accounting for up to 43% of total body mass for belugas (Sergeant & Brodie, 1969). Belugas and narwhals can be easily distinguished by their colouration. While narwhals are grey with white dappling, adult belugas are pure white, providing cryptic colouration against snow and ice floes (Vladykov, 1944). However, newborn beluga calves are typically pale brown in colour, gradually turning grey in the first year of life and only turning pure white after reaching sexual maturity (Sergeant, 1986). In recent years, there has been some controversy over the correct method of aging belugas from dental growth layers, leading to dramatic underestimates in the longevity of the species (Lockyer et al., 2007). It is now generally agreed that belugas can live up to 70 years in the wild (Luque & Ferguson, 2010).

1.1.2 Migratory behaviour

Belugas are migratory, travelling from open ocean wintering grounds to coastal waters and estuaries in the summer (Sergeant, 1973). Shallow estuaries are likely advantageous for foraging, epidermal moulting, and predator avoidance. Estuaries tend to have a high abundance of beluga prey, such as capelin, smelt, cod and benthic invertebrates (Vladykov, 1944; Watt, Orr, & Ferguson, 2016). Belugas are also observed rubbing against abrasive estuarine substrates, a behaviour which likely facilitates the annual moulting of the whales' epidermis (Smith, St. Aubin, & Hammill, 1992;). Use of estuaries could also reflect predator avoidance (Sergeant, 1973; Simard et al., 2014), particularly orcas (*Orcinus orca*; Lowry, Nelson, & Frost, 1987; Ferguson, Kingsley, & Higdon, 2012) and polar bears (*Ursus maritimus*; Freeman, 1973; Lowry et al., 1987). Migration routes may be culturally transmitted from mothers to their calves. Female belugas show strong philopatry, returning every year to the same summering grounds, and likely transmit knowledge of these migration routes to their dependent offspring (Colbeck et al., 2013).

1.1.3 Acoustic behaviour

Like other odontocetes, belugas are a highly vociferous species. Renowned for their vast vocal repertoire, belugas have long been known as "sea canaries" (Sergeant & Fisher, 1957). Beluga sounds can be broadly classified in two categories: pulsed sounds and frequency modulated sounds (Au, 1993; Herzing 2000). Pulsed sounds are used for echolocation, and both pulsed sounds and frequency modulated sounds are used for social communication (Vergara & Mikus, 2019). Belugas are highly social, maintaining long-term social bonds with conspecifics (Michaud, 2005; Alekseeva, Panova, & Bel'kovich, 2013; Krasnova et al., 2014). Given the limited visibility of marine environments, these social bonds are mainly maintained through acoustic communication. Recent work by Vergara & Mikus (2019) suggests that, like bottlenose dolphins, belugas use signature calls, calls specific to individuals or groups, which animals use to advertise their presence or group membership. Acoustic communication is also vitally important to the mother-calf bond. Mothers and calves use highly stereotyped contact calls to communicate and maintain proximity (Vergara, 2010). Birth events in the wild and in captivity are characterized by an outburst of such calls, likely directed by the mother towards her newborn calf (Vergara, 2010).

1.1.4 Reproduction and sex differences

Beluga reproductive behaviour remains poorly understood, although evidence suggests a promiscuous mating system (Kelley et al., 2015). Mating is likely seasonal, occurring in late winter or early spring in most populations (Brodie, 1971; Glabicky, DuBrava, & Noonan, 2010). Females gestate for 14-15 months, typically giving birth during the summer (Sergeant, 1973). Offspring are weaned between one and three years of age (Matthews & Ferguson, 2015). Reproductive females typically produce a single calf every three years (Sergeant, 1973). Both male and female offspring remain closely associated with their mother for several years after weaning (Colbeck et al., 2013). Males are larger than females, reaching up to 5.7 meters in length, compared to a maximum length of 4.7 meters for females (Vladykov, 1944). Females reach sexual maturity between 8 to 14 years of age, compared to 16 to 18 years of age for males (Lemieux Lefebvre et al., 2012). For most of the year, males and females are spatially segregated

(Loseto et al., 2006; Lemieux Lefebvre et al., 2012). These segregation patterns may reflect variation in foraging strategies or responses to predation risk between males and females (Galezo et al., 2017). Sexual segregation may also reflect female avoidance of males, possibly due to the risk of infanticide (Michaud, 2005; Loseto et al., 2006).

1.1.5 Evidence for male infanticide

Infanticide by males occurs in multiple odontocete species (Dunn et al., 2002; Bowler et al., 2018; Towers et al., 2018), although it has never been directly observed in belugas. Observations by seasoned researchers studying belugas in the St. Lawrence Estuary support the possibility of infanticide by males. Robert Michaud (pers. comm.), head researcher of the *Groupe de Recherche et d'Éducation sur les Mammifères Marins* (GREMM), reports that males are sometimes observed violently tossing calves in the air, an action reminiscent of confirmed infanticides by bottlenose dolphins (*Tursiops* sp.; Dunn et al., 2002) and orcas (*Orcinus orca*; Towers et al., 2018). In contrast to these agonistic encounters, other interactions between males and calves appear altruistic in nature. In one case, a calf was observed under the care of three males over the course of several hours (Robert Michaud, pers. comm.). Such a long separation of a calf from its mother suggests that the calf was likely orphaned. In another case, a confirmed orphan calf was briefly escorted by a group of males after an attempt to reintroduce the calf into a social group (Robert Michaud, pers. comm). Taken together, these observations support a nuanced interpretation of associations between males and offspring.

1.1.6 Female sociality

Beluga sociality is thought to be structured by fission-fusion dynamics characterized by long-term bonds and labile group membership (Alekseeva, Panova, & Bel’kovich, 2013; Krasnova et al., 2014). Evidence suggests that females associate preferentially with kin. During migration, groups of females tend to closely related, while groups of males tend to be closer in age but more distantly related (Colbeck et al., 2013). Along with short-finned pilot whales (*Globicephala macrorhynchus*), orcas, and humans, belugas are one of few species with post-reproductive female lifespans (i.e. menopause; Ellis et al., 2018). While most species show a gradual decline in fertility with age, these species show a sudden cessation of reproductive ability, with females typically spending a large portion of their lives in a post-reproductive state (Croft et al., 2015). According to the grandmother hypothesis, post-reproductive female lifespans may evolve when older females can gain greater fitness by helping their young female kin care for offspring than from continuing to produce offspring themselves (Sear & Mace, 2008). Post-reproductive lifespans may be particularly adaptive when older females compete with their offspring for resources, potentially leading to reproductive conflict (Croft et al., 2017). Alternately, post-reproductive lifespans may reflect the importance of ecological knowledge possessed by older females, allowing matriarchs to continue helping their adult offspring (Greve, Kierdorf, & Kierdorf, 2009; Brent et al., 2015).

1.2 Current status of beluga populations in Canada

The Committee on the Status of Endangered Wildlife in Canada (COSEWIC) recognizes seven beluga designatable units (i.e. populations) in Canada (COSEWIC, 2004). Many of these populations are harvested by indigenous communities in northern Canada, Alaska, and Greenland. Given prohibitively expensive food costs, the availability of beluga meat is crucial to food security for many northern communities (Tyrrell, 2007; Kenny et al., 2018). Beluga hunting is also a meaningful practice which allows communities and individuals to express their cultural identity and transmit traditional knowledge (Tyrrell, 2007). Since the 1980s, the Department of Fisheries and Oceans (DFO) has worked in concert with First Nation partners to set whaling quotas, with such harvest management representing the bulk of conservation effort for most populations (Tyrrell, 2008). Beluga populations in Canada are genetically distinct (de March, Maiers, & Friesen, 2001; de March & Postma, 2003) and defined by non-overlapping summer ranges, although the winter ranges of many populations overlap (Fig. 1.1). Of seven Canadian populations, six are currently considered to be at risk of extinction.

1.2.1 Eastern Beaufort Sea population – "Not at Risk"

This population is conservatively estimated to number over 39,000 individuals (National Marine Fisheries Service, 2002). Approximately 186 animals are harvested every year by the Inuvialuit and indigenous Alaskan communities (Harwood et al., 2002). Current harvest levels are considered to have little impact on the population (DFO, 2000).

1.2.2 Eastern High Arctic - Baffin Bay population – "Special Concern"

This population is estimated to number over 21,000 individuals, but differences in wintering patterns suggest that this unit may represent two distinct populations (Innes et al., 2002). One group, numbering around 17,000 animals, winters in the Baffin-Bay North Water area (Innes & Stewart, 2002). This group appears stable, with annual harvests well below maximum sustainable yield. However, the other group of approximately 7,900 animals which migrate to the Western Greenland Coast in winter has shown a notable decline since 1981 (Heide-Jørgensen & Acquarone, 2002). Winter harvests along the Western Greenland Coast could be as high as 941 individuals annually (Heide-Jørgensen & Rosing-Asvid, 2002), well above the maximum sustainable harvest for this group (Innes & Stewart, 2002).

1.2.3 Western Hudson Bay population – "Special Concern"

Despite being the largest beluga population in Canada, and perhaps the largest beluga population worldwide, the Western Hudson Bay population is designated as "special concern", as hunting has increased considerably in recent years (COSEWIC, 2004). Population estimates from 2015 suggest a population of 54,500 animals (DFO, 2018a). Total catches, including struck-and-lost animals, were estimated at 584 animals in 2015, currently well within maximum sustainable yield for this population (DFO, 2018a). To preserve this population, it will be necessary to ensure that total catches do not continue to increase unchecked.

1.2.4 Eastern Hudson Bay population – "Endangered"

Aerial surveys suggest that the Eastern Hudson Bay population declined by almost 50% between 1985 and 2001 (Gosselin et al., 2002), but has currently stabilized at approximately 3400 individuals (DFO, 2018a). Although attempts were made to limit harvesting of this population, previously recommended harvest limits are now considered to have been too high (Lesage, Doidge, & Fibich, 2001). Management of this population is complicated by harvesting along its migration route and within its winter range.

Genetic evidence shows that Eastern Hudson Bay belugas represent a significant portion of animals harvested by Nunavut and Nunavik communities (de March & Postma, 2003). DFO (2018a) estimates that approximately 60 animals are harvested each year. Continued harvesting at this rate is associated with a 50% chance of recovery of the population in the next 50 years (DFO, 2018a).

1.2.5 Cumberland Sound population – "Threatened"

Initially numbering about 5000 animals, the Cumberland Sound population was reduced to fewer than 1000 animals in the 1970s (Brodie, Parsons, & Sergeant, 1981; Mitchell & Reeves, 1981). This decline is attributed to a large-scale commercial beluga hunt by the Hudson Bay Company from 1868 to 1939. The population is currently estimated at 1009 individuals (DFO, 2019). The community of Pangnirtung is currently allowed an annual quota of 41 animals, but continued harvesting at this rate carries a 96% probability of population decline in the next 10 years (DFO, 2019).

1.2.6 Ungava Bay population – "Endangered, possibly extirpated"

An aerial survey in 2001 did not sight any belugas in Ungava Bay (Gosselin et al., 2002). From sightings made outside of transect lines, Kingsley (2000) estimated that the population could number as few as 50 individuals. There has been a marked decline in the median age of belugas taken by the Nunavik communities of Northern Quebec, suggesting a shift in the age structure of the population (Lesage et al., 2001). The Inuit of Kangirsuk report a noticeable population decline and mention noise disturbance as a possible factor (COSEWIC, 2014). This population may be extirpated, although overlap with the winter ranges of other populations complicates this assessment (COSEWIC, 2004).

1.2.7 St. Lawrence Estuary population – “Endangered”

This population is currently estimated to number 889 individuals (Mosnier et al., 2014). The St. Lawrence Estuary (SLE) beluga population was historically decimated by hunting, and a ban on hunting in 1979 has resulted in little to no population recovery (DFO, 2013). The failure of this population to recover from hunting pressure has been attributed to exposure to environmental pollutants (Ménard, & Hammill, 2014; Martineau et al., 2002; Lebeuf et al., 2004; Lebeuf, Measures et al., 2014; Lebeuf, Raach et al. 2014), disturbance from marine traffic (Blane & Jaakson, 1994; Scheifele et al., 2005; DFO, 2014; Finley & Davis, 1984; Ménard et al., 2014), and other environmental factors (Plourde et al., 2014; Starr et al., 2017). The impact of these threats on SLE belugas suggests that harvest management may be insufficient to ensure the continued survival of belugas in Canadian waters.

As the Arctic warms and human activities encroach further onto previously-undisturbed beluga habitat, environmental pollutants and marine traffic are becoming increasingly problematic for Arctic beluga populations (de Wit, Herzke, & Vorkamp, 2010; Muir & de Wit, 2010; McWhinnie et al., 2018). Here, we discuss historical and current social contexts responsible for the decline and stalled recovery of the St. Lawrence Estuary beluga population, in hopes of informing increasingly urgent attempts to protect endangered wildlife in Canada.

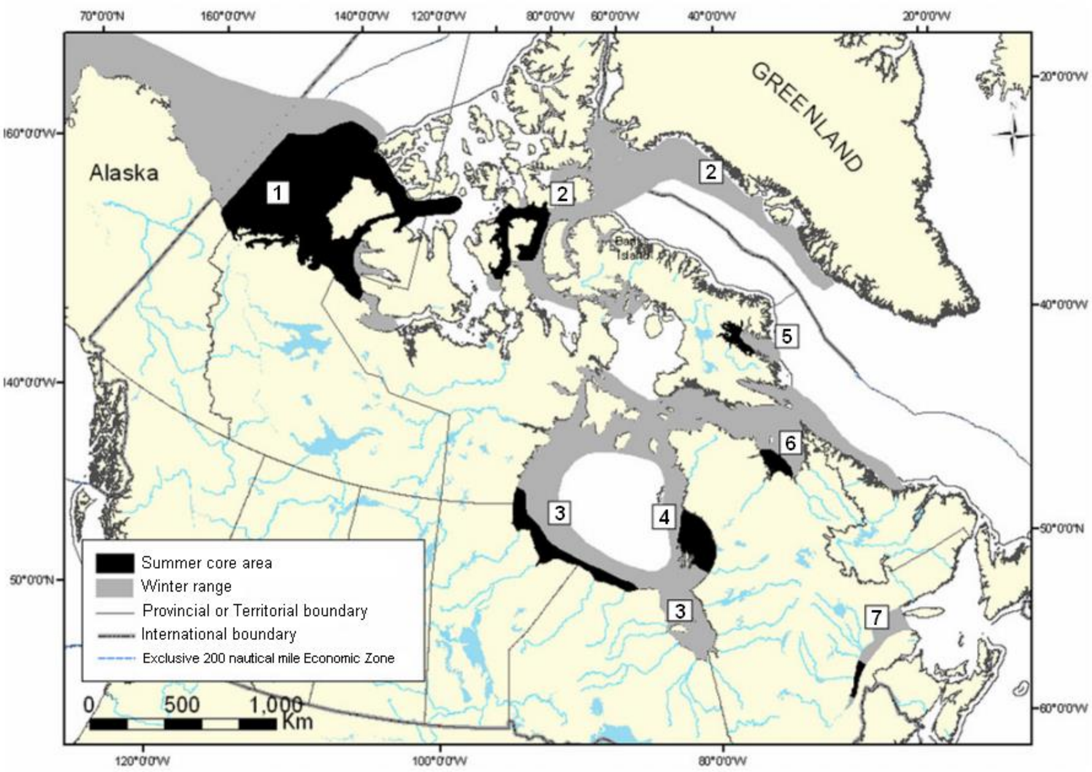

Figure 1.1. Summer and winter ranges of Canadian beluga populations: 1) Eastern Beaufort Sea population, 2) Eastern High Arctic - Baffin Bay population, 3) Western Hudson Bay population, 4) Eastern Hudson Bay population, 5) Cumberland Sound population, 6) Ungava Bay population, 7) St. Lawrence Estuary population. Modified from DFO, 2016.

1. 3 Historical human impacts on SLE belugas

1.3.1 Post-glacial relicts

The ancestors of SLE belugas immigrated to the Champlain Sea, a temporary inlet of the Atlantic Ocean created by glacial retreat at the end of the last Ice Age, approximately 12,000 years ago (Harington, 1977). At its peak, the Champlain Sea extended as far west as modern-day Ottawa, as evidenced by an extensive marine fossil record (Harington, 1977). The best-preserved beluga fossil from this period, radiocarbon dated to 10,700 ± 90 years ago, was uncovered in St-Felix-de-Valois in 2001 (Harington et al., 2006). Further examination of the specimen, dubbed “Felix”, showed that the animal was male, and died at approximately 60 years of age (Harington et al., 2006). As the land rebounded from glacial compression, the Champlain Sea receded, confining a population of belugas to the newly formed St. Lawrence Estuary approximately 10,000 years ago (Harington, 1977). SLE belugas are geographically isolated and genetically distant from Arctic beluga populations (Gladden et al., 1999). Historically, the SLE beluga population is estimated to have numbered up to 10,000 individuals and ranged from Quebec City to the Gaspé coast (Vladykov, 1944).

1.3.2 Historical whaling in the St. Lawrence Estuary

Archaeological evidence shows that the Iroquois first began hunting belugas in the St. Lawrence over 1500 years ago (Tremblay, 1993). In an account from 1535, the sons of Donnaconna, chief of Stadaconna, refer to belugas as *adhothuys*, and describe them as a favoured prey animal which prefers brackish waters (Cartier, 1535 as cited in Biggar, 1924). The world’s first commercial whalers, the Basques, operated in the St. Lawrence as early as 1510 (Bélanger, 1971). Although Basque whalers mainly targeted the large, blubber-rich Bowhead whale (*Balaena mysticetus*), other whales, including belugas, were also harvested opportunistically (McLeod et al., 2008). With the signing of the Treaty of Utrecht in 1713, the Basques were banned from the St. Lawrence, allowing French colonists to monopolize exploitation of the still-abundant beluga (Aguilar, 1986). Belugas were locally known as *marsouins blancs,* white porpoises. Many coastal communities, particularly Rivière-Ouelle, supported thriving beluga "fisheries" (Mailloux, 1879). While some whalers continued to employ the "Basque method", harpooning animals from vessels, others maintained elaborate weirs (Vladykov, 1944). Possibly first invented by the Iroquois, weirs are made up of a long series of "harts", saplings driven into the sediment over several hundred meters in a curved shape (Mailloux, 1879). Belugas were funneled into the weir at high tide and remained trapped on the shore as the tide ebbed. Planted about a meter apart, the weirs allowed ample space for belugas to slip through. However, the vibration of the harts in the currents and wind produced low frequency sounds that panicked and repelled trapped belugas (Vladykov, 1944). Contemporary accounts report that, on one occasion, 500 belugas were taken in a weir during a single tide at l'Île-aux-Coudres (Casgrain, 1896).

1.3.3 Beluga products

Belugas taken in weirs or in open waters were hauled ashore and skinned. Their blubber was stripped away and melted to produce oil. An exceptionally large beluga can produce as many as 500 liters of oil, although most average between 150 to 190 liters (Vladykov, 1944). Beluga oil was locally used as a cooking oil but was especially valued for its use as lamp oil (Casgrain, 1896). In Canada, beluga oil was mainly used to light the lamps of lighthouses (Fortin, 1868). The exceptionally fine oil extracted from the head, known as "jaw oil" was particularly valuable as a commercial lubricant for fine mechanisms, such as watches, typewriters, and firearms (Vladykov, 1944). Beluga hides were tanned to produce a famously resilient leather marketed as *peau de marsouin* (Casgrain, 1896). Contemporary accounts do not mention uses for the flesh of belugas, suggesting that beluga meat carried little economic or cultural importance for French Canadian colonists.

1.3.4 The first belugas in captivity

A small number of SLE belugas were also captured alive. Stored in crates lined with seaweed, these animals were trucked to the United States for public exhibition (Casgrain, 1896). In 1861, one of the first captive whale exhibits was constructed by Phineas T. Barnum. The showman arranged for the construction of a small pool in the basement of his American Museum and purchased two belugas for his new attraction (Barnum, 1866). Both whales died after only two days of captivity. From 1861 to 1868, several SLE belugas were exhibited at various P. T. Barnum establishments. All met with grim fates, succumbing to suffocation, hyperthermia, pulmonary infection, and multiple museum fires (Mather, 1899). Despite the short lifespans of captive belugas, the exhibitions proved profitable. In 1871, a female beluga from Rivière-Ouelle was shipped across the Atlantic for exhibition at the Royal Aquarium of London, but survived only four days upon arrival. This short exhibition was considered successful, "clearing more than enough to pay for the animal and all expenses" (Mather, 1899).

1.3.5 Efforts to eradicate SLE belugas

In 1928, an unusually high abundance of belugas in the St. Lawrence coincided with poor catches in local cod and salmon fisheries (Vladykov, 1944). Fishers were quick to blame belugas for their empty nets. A newspaper article from the time declares: “Porpoises [sic] are the cause of a great famine” ("*Les Marsouins Sont Cause d'une Grande Famine*", 1926). Initially, the Quebec Minister of Fisheries implemented population control measures by systematically bombing herds of belugas ("*La Chasse aux Marsouins*", 1931). These efforts were considered insufficient. In 1931, in response to mounting public pressure, the Quebec government issued a $50 bounty (approximately $850 in today’s currency) on each beluga killed in the St. Lawrence ("*Nouvelle Prime aux Pêcheurs*", 1931). In 1932, this bounty was reduced to $15 (approximately $260 in today’s currency; "*Phoques et Marsouins*", 1932). The subsidized beluga hunt continued until 1938, when doubts were raised over the actual impact of belugas on the fisheries ("*Le Père Gabriel Bouliane nous parle...*", 1938). To settle the question, the Minister of Fisheries hired Dr. Vadim Vladykov, a well-known ichthyologist, to undertake a detailed study of SLE belugas. Vladykov’s (1946) findings showed that, contrary to popular belief, belugas did not consume large quantities of salmon or cod, and suggested that the decline in fisheries was likely due to a hydrological anomaly. From 1932 to 1937, 1897 beluga bounties were collected (Vladykov, 1944). The number of animals killed prior to 1931, particularly those impacted by systematic bombings, remains unknown.

1.3.6 The end of the beluga hunt

In the 1940s, the cheapness and availability of petroleum products lead to the obsolescence of whale oil, and the subsequent collapse of the commercial whaling industry (Vladykov, 1944). By 1955, all commercial beluga hunting had ceased in the St. Lawrence (Lesage & Kingsley, 1995). Some whalers attempted to institute a recreational beluga hunt, with limited success ("*Pourquoi se rendre…",* 1950). In 1962, the inhabitants of l'Île-aux-Coudres raised their long-neglected weir to preserve local knowledge of the traditional beluga hunt. However, belugas were scarce, and the weir was only modestly successful. One trapped juvenile would become the last SLE beluga sold into captivity. These events are chronicled in the documentary *Pour la Suite du Monde* ("Of Whales, the Moon, and Men"), by Michel Breault and Pierre Perreault (1963). By the late 1970s, the general public began to turn against beluga hunters. Locals and government scientists began to notice a dramatic decline in the abundance and range of SLE belugas, raising questions about the health of the population (Sergeant & Hoek, 1988). The first aerial survey of the population in 1973 estimated 500 to 1000 individuals (Sergeant and Brodie 1975), but surveys using a different method by Pippard and Malcolm in 1975 and 1977 estimated a population of no more than 350 (Pippard 1985). In 1979, beluga hunting in the St. Lawrence Estuary was officially banned under the Fisheries Act (DFO, 2012).

1.4 Early SLE beluga conservation efforts

1.4.1 Endangered designation and early response

COSEWIC designated the SLE beluga population as Endangered in 1983 (Cook & Muir, 1984). In 1986, DFO formed an ad hoc committee for the conservation of SLE belugas (Kingsley, 1991). The committee highlighted environmental contamination and anthropogenic disturbance as possible threats, and emphasized the need to gain more knowledge on SLE belugas. The committee's recommendations lead to the Interdepartmental Action Plan to Favour the Survival of the St. Lawrence Beluga and the development of the Research Plan for the Beluga of the St. Lawrence in 1988 (DFO, 1990). As part of the Research Plan, a new standard for aerial transect population surveys was implemented, including a conservative 15% correction factor for submerged animals (Kingsley, 1991). Between 1988 and 1993, population surveys consistently reported between 500 and 590 individuals, less than 10% of the estimated population in 1886 (DFO, 1990; Lesage & Kingsley, 1995). Sergeant and Hoek (1988) estimated that the annual production rate for SLE belugas was less than half that of other Canadian beluga populations. While the initial decline in the population was caused by overhunting, depressed birth rates suggested that the population faced ongoing pressures (Lesage & Kingsley, 1995). In 1995, DFO and the World Wildlife Fund (WWF) produced the first St. Lawrence Beluga Recovery Plan (Bailey & Zinger, 1995).

1.4.2 Ongoing threats: Environmental contamination

In 1983, researchers began to systematically recover and necropsy beluga carcasses from the St. Lawrence. Concerning trends arose. Martineau et al. (1987) noted that all carcasses sampled were highly contaminated with organochlorine compounds, such as polychlorinated biphenyls (PCBs) and dichlorodiphenyltricholoethane (DDT). By 1993, 120 carcasses had been sampled, of which 45 were necropsied. In addition to PCBs and DDT, SLE belugas showed much higher levels of lead, mercury, “Mirex”, and benzo[a]pyrene (BaP) than Arctic belugas (Béland et al., 1993). These contaminants, originating from industries in the Great Lakes and the broader St. Lawrence river basin, were either inadvertently or intentionally offloaded into the river system, eventually permeating the St. Lawrence Estuary and its food webs (Martineau et al., 2002). Béland (1996) noted that, due to high levels of PCBs, SLE beluga carcasses qualify as hazardous toxic waste. Females showed lower contaminant loads than males, due to offloading of toxins to offspring during gestation and nursing (Gauthier et al., 1998; Martineau et al, 1987). Many carcasses, particularly calves, showed contaminant levels known to be carcinogenic, immunosuppressant, or otherwise reproductively impairing (DeGuise, Martineau, Beland, & Fournier, 1995; Martineau et al., 1994). Pathologies were widespread: 40% of carcasses had tumours, 53% had lesions in the digestive tract, 40% of adult females had mammary gland lesions, and many carcasses showed tooth loss, periodontitis and evidence of immunosuppression (Béland et al., 1993). Two carcasses showed intersexed genitalia, the first and only examples of intersexed cetaceans (DeGuise, Lagacé, & Béland, 1994). Taken together, these findings suggest intense contamination of the SLE beluga food chain over an extended period, resulting in population-level health consequences.

1.4.3 Ongoing threats: Disturbance from marine traffic

Along with environmental contamination, anthropogenic disturbance was one of the factors initially cited as a potential threat to SLE belugas. Pippard (1985) noted that belugas once regularly frequented Tadoussac Bay, but abandoned the area following construction of a marina in the 1970s. Similarly, Cap St-Etienne, identified as a beluga high residency area before 1990, was no longer frequented by belugas in 1992 (Michaud & Chadenet, 1990; Michaud, 1993). It was feared that, if anthropogenic development in the estuary continued unabated, other areas representing critical beluga habitat might also be abandoned (Ménard, 1997). Since the 1980s, a successful whale watching industry developed in the St. Lawrence Estuary (DFO, 1987). In the late 1980s, an estimated 600 whale watching excursions originated from Tadoussac and Baie Ste-Catherine every year (Blane & Jaakson, 1994). While operators were discouraged from targeting belugas for observation, DFO lacked the legislation to implement regulations (DFO, 1987). In addition to whale-watching excursions, ferry crossings, pleasure boats, and cargo ships contributed to the high density of marine traffic within the range of SLE belugas (Kingsley, 1999). The St. Lawrence Seaway, an international shipping corridor connecting the Atlantic Ocean to the Great Lakes, must, by necessity, pass through the range of SLE belugas (COSEWIC, 2014). In 1980, approximately 8800 cargo ships traveled the St. Lawrence seaway, a rate of approximately one passage per hour (Maltais & Pelletier, 2018).

1.4.4 Reassessment of the population

In 1997, COSEWIC reaffirmed the St. Lawrence beluga's Endangered designation (DFO, 2012). However, in 1998, results from aerial surveys suggested a conservative estimate of 600-700 individuals and a slightly increasing population (Kingsley, 1998). The St. Lawrence Beluga Recovery Plan was seemingly producing results: many of its recommendations had been followed, leading to reductions in the levels of some environmental contaminants (Lesage & Kingsley, 1998). However, marine traffic continued to be problematic. Evidence of disturbance of belugas by vessels was mounting. Blane & Jaakson (1994) found that belugas alter their behaviour in the presence of small vessels, while Lesage et al. (1999) found alterations in the vocal behaviour of belugas exposed to vessel noise. It became increasingly apparent that government agencies lacked the legislative power to properly address threats to SLE belugas.

1.4.5 Creation of the Saguenay St. Lawrence Marine Park

In 1998, after nearly a decade of consultations, the Saguenay-St. Lawrence Marine Park (SSLMP) was created. Located at the confluence of the Saguenay Fjord and the St. Lawrence River, the SSLMP aims to protect all marine species within its boundaries, including its flagship species, the SLE beluga (Maltais & Pelletier, 2018). The SSLMP covers 1425 km^2 and encompasses a large portion of SLE beluga habitat (Kingsley, 1999). In 2002, a set of regulations within the boundaries of the SSLMP were signed into law. These regulations state that small vessels must maintain a distance of 400 meters from belugas at all times, and that vessels cannot remain stationary within less than half a nautical mile (926 meters) of belugas (Goverment of Canada, 2002).

1.4.6 SARA listing and designation change

After the proclamation of the Species At Risk Act (SARA) in 2003, the status of SLE belugas was downgraded from “Endangered” to “Threatened” based on estimates which suggested a larger population than previously determined (COSEWIC, 2004; Kingsley, 1999). Under SARA, the critical habitat for listed species must be identified and protected. The SLE beluga’s new recovery strategy included a description of critical habitat, determined from the summer distribution of females with young (DFO, 2012).

1.5 Latest threats against SLE belugas

1.5.1 Elevated calf mortality in 2008, 2010, 2012

By 2012, unusual mortality trends among SLE belugas were causing widespread concern. The summers of 2008, 2010, and 2012 saw unusually high mortality for belugas calves. During the first 24 years of the carcass recovery program, between 0 and 3 newborn calves were recovered annually, but 8 were found in 2008, 8 more in 2010, and an additional 16 newborn calf carcasses were recovered in 2012 (DFO, 2013). Many factors seemed to contribute to calf mortality. While the first peak observed in 2008 was attributed to a toxic algal bloom, there was no evidence of algal blooms in 2010 and 2012 (Ménard et al., 2014; Starr et al., 2017). However, in 2012, the Gulf of St. Lawrence experienced an extreme warm-water perturbation event which caused a catastrophic breeding failure among Norther Gannets, likely due to low forage fish availability (Montevecchi et al., 2013). This warm-water perturbation also resulted in unusual behaviour among marine mammals (Montevecchi et al., 2013), and may have negatively impacted SLE belugas. More broadly, researchers also found evidence of an environmental regime shift from 1998 to 2012, characterized by a decrease in ice cover and low prey availability which may have impacted calf survival (Plourde et al., 2014). Finally, it was suggested that high densities of marine traffic, particularly whale watching boats and pleasure crafts, during the summer calving season may negatively impact newborn calves. Mothers and calves maintain contact acoustically through contact calls (Vergara & Barrett-Lennard, 2008). However, calf contact calls are easily masked by low-frequency noises such as those produced by boat engines, such that calves may become more easily separated from their mothers in noisy environments (the "mother-calf separation hypothesis", Vergara et al., in prep). Ménard et al. (2014) found that years of elevated calf mortality coincide with years of peak boating activity, suggesting a link between anthropogenic disturbance and calf mortality.

1.5.2 Perinatal complications and female mortality

Further analyses suggested that calf mortality was possibly linked to elevated mortality among reproductive females. From 1983 to 1999, male and female adult mortality was not significantly different, but from 2000 to 2012, adult females were disproportionately represented in carcasses recovered (Lair, Martineau, & Measures, 2014). This pattern was partially explained by high rates of perinatal mortality, females dying while, or immediately after, giving birth (Lesage et al., 2014). Extremely rare among other cetaceans, such perinatal complications may be linked to the elevated contaminant load of St. Lawrence beluga mothers and calves, persistent disturbance by vessels, or both (Lair et al., 2014). While levels of other contaminants in belugas remained stable or decreased slightly after 1987, levels of polybrominated diphenyl ethers (PBDEs) rose dramatically from 1987 to 1995, and remain elevated (Lebeuf et al., 2014). PBDEs are known have endocrine disrupting effects, particularly for fetuses, and may contribute to high rates of perinatal complications. In domestic animals, the detrimental effects of disturbance on parturition are well-documented (Mee, 2004; 2008). SLE belugas suffer high rates of anthropogenic disturbance, particularly in the summer calving season (Lair et al., 2014). Therefore, findings of elevated calf mortality in years with higher marine traffic are consistent with both the perinatal disturbance hypothesis and the mother-calf separation hypothesis (Ménard et al., 2014).

1.5.3 Population decline and demographic shift

Recent population modelling efforts, informed by decades of data from surveys and recovered carcasses, showed further cause for concern. Mosnier et al. (2014) found a 12.6% decline in the population from 2000 to 2012, with a model estimate of 889 [95% CI: 672 -1167] individuals in 2012. In response, COSEWIC once again designated the population as Endangered (COSEWIC, 2014). The model also showed major demographic shifts in the population, with highly variable inter-year calf mortality and pregnancy rates, and a decline in the proportion of juveniles in the population (Mosnier et al., 2014). These findings stress the importance of implementing conservation measures which support the health of reproductive females. Elevated mortality in reproductive females is incompatible with population recovery, particularly for belugas, a slow maturing species with low reproductive rates (Mosnier et al., 2015).

1.5.4 Research and conservation response

Recognizing reproductive females as an important segment of the population, recent studies and conservation strategies have specifically targeted females and offspring. Baie Ste-Marguerite has long been recognized as an important area for SLE belugas. Every summer, groups of females travel up the Saguenay Fjord to the secluded bay with newborn calves (Busque, 2006; Michaud, 1992; Pippard & Malcolm, 1978). To reduce disturbance of these groups, boating restrictions were implemented in Baie-Ste-Marguerite in the summer of 2018 (Ménard, Conversano, & Turgeon, 2018). From 2016 to 2018, Vergara et al. (in prep.) undertook a study examining the effects of acoustic disturbance in Baie-Ste-Marguerite on mother-calf communication and separations. My research occurred in parallel to this project.

1.5.5 Thesis Objectives

Rather than examining the mother-calf bond, I examined bonds between offspring and other female group members through the lens of allocare. Allocare occurs when non-parent group members (i.e., alloparents) provide care to offspring (Blaffer Hrdy, 1976). While allocare has been described anecdotally in wild belugas (Bel'kovitch & Sh'ekotov, 1990; Krasnova et al., 2014), and observed within a captive group (Leung, Vergara, & Barrett-Lennard, 2010; Hill & Campbell, 2014), it has not been quantitatively described in a wild beluga population until now. In populations where females care for offspring cooperatively, allomothers can contribute to the survival of offspring (Lee, 1987; Stanford, 1992; Ross & MacLarnon, 2000). Notably, in populations with allocare, orphans are more likely to be adopted by group members and survive to adulthood

(Riedman, 1982). I examined the benefits of allocare for both allomothers and recipient offspring to contribute to our understanding of a previously unknown aspect of SLE beluga behavioural ecology. My findings may inform future management decisions, such as whether to euthanize stranded belugas calves or encourage allomaternal adoptions through relocation (DFO, 2018b).

1.5.6 The future of SLE belugas

Under the umbrella of the St. Lawrence Beluga Project, many teams are currently working to promote the welfare of SLE belugas. Collaborators include the GREMM, the St. Lawrence National Institute of Ecotoxicology, the *Université de Montreal* faculty of veterinary medicine, the *Réseau Québécois d'Urgence pour les Mammifères Marins*, teams at Trent University and Saint Mary's University, Toxen, the Ocean Wise conservation group, the Shedd Aquarium, DFO, Parks Canada, and the *Société des Établissements de Plein Air du Québec* (SÉPAQ). Despite a multi-decade attempt to promote the recovery of SLE belugas, the population's future remains precarious. Like so many endangered populations in Canada, SLE belugas are threatened by ongoing economic developments. Three industrial port development projects in the St. Lawrence Estuary are currently in the final stages of development (Arianne Phosphate, 2019; BlackRock Metals Inc., 2018; Énergie Saguenay, 2019), with two new marine terminals planned in the upstream section of the Saguenay Fjord. These new terminals are expected to triple shipping traffic in the Saguenay Fjord, and threaten the recovery of the St. Lawrence beluga (DFO, 2018c). By providing empirical evidence to support population management decisions, and through continued pressure on governments, we hope to ensure the continued survival of the SLE beluga population and all other sympatric species within the St. Lawrence Estuary.

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1.7 Co-authorship Statement

Chapters 2 and 3 of this thesis were co-authored with Dr. Eric Vander Wal and Robert Michaud. I was the principal contributor to the design, data analyses and manuscript preparation for all chapters of this thesis. For Chapters 2 and 3, Dr. Eric Vander Wal provided critical assistance with study design, analysis, and manuscript preparation, and Robert Michaud provided crucial guidance and feedback relating to the ecology of the study system. Chapter 2 will be submitted to Behaviour and Chapter 3 will be submitted to Marine Mammal Science. It was necessary to repeat information pertaining to data collection in Chapters 2 and 3, in addition to information pertaining to the study species.

CHAPTER 2: PATTERNS AND PROSPECTIVE DRIVERS OF ALLOCARE IN ST. LAWRENCE ESTUARY BELUGAS

2.1 Abstract

Allocare, investment in offspring from non-parents, poses an evolutionary enigma. While the fitness trade-offs driving parental care are universal, the evolutionary mechanisms driving alloparents to provide care are diverse and variable across taxa. Among bottlenose dolphins (*Tursiops* spp.), allocare is driven by the need for young females to acquire parenting skills ("learning-to-parent") and an indiscriminate attraction towards infants ("natal attraction") while allocare in sperm whales (*Physeter macrocephalus*) is best explained by kin selection and reciprocation. Among belugas (*Delphinapterus leucas)*, allocare has been reported in wild and captive populations, but its underlying mechanisms remain untested. Using drone footage, we quantified allomaternal associations in St. Lawrence Estuary (SLE) belugas to determine which proposed mechanisms are consistent with patterns of allocare in this population. We observed significantly more adult than subadult allomothers ($P < 0.001$), inconsistent with the learning to parent hypothesis. We also observed that allomaternal investment remained constant across offspring age classes, inconsistent with both the learning-to-parent and the natal attraction hypotheses. While mothers provided less care to older offspring, there was no significant difference in the amount of allocare provided to the three offspring age classes. As the observed patterns of allocare are inconsistent with both the learning-to-parent and natal attraction hypotheses, we suggest that allocare in SLE belugas is likely driven by kin selection, reciprocation, or a combination of both.

2.2 Introduction

Parental care is a limited resource, and allocations of care therefore reflect an evolutionary trade-off (Trivers, 1972). However, in some species offspring receive care from parents as well as other group members, through allocare (Riedman, 1982). Among mammals, these non-parent caregivers are typically female, and referred to as allomothers (Isler & van Schaik, 2012). Allomothers provide care through allonursing, food-provisioning, infant-carrying, allogrooming, and protection from predators and hostile conspecifics (Blaffer Hrdy, 1976). For example, female wedge-capped capuchins (*Cebus oliveceus*) nurse each other's young (O'Brien & Robinson, 1991), female African elephants (*Loxodonta africana*) assist, comfort, and protect all calves within their family unit (Lee, 1987), and sperm whales (*Physeter macrocephalus*) take turns escorting calves during maternal foraging dives (Whitehead, 1996). Like parental care, allocare is understood to reflect an evolutionary trade-off. However, while mothers provide care to promote their own direct fitness, this is not always the case for allomothers.

Several hypotheses seek to explain the adaptive value of allocare for allomothers. Of these, three hypotheses can be considered ultimate explanations for allocare: kin selection, reciprocation, and group augmentation. The kin selection hypothesis suggests that allomothers should provide care to related offspring as long as the inclusive fitness benefit of doing so is greater than the cost to their future reproduction (Hamilton, 1964; Trivers, 1972). The reciprocation hypothesis suggests that allomothers provide care to unrelated offspring with the expectation of receiving some benefit in exchange (Trivers, 1971, 2006). The exact conditions necessary for reciprocation behaviour to occur have been extensively debated since the phenomenon was first proposed (Rothstein & Pierotti, 1988; Symons, 1989; Carter, 2014). Here we consider that any assistance or benefit which allomothers receive from others as a result of care provided are reciprocal benefits. Finally, allocare may be adaptive when group members have improved fitness in larger groups, such that allomothers benefit by helping the offspring of others reach maturity, a form of delayed reciprocation (Kokko, Johnstone, & Clutton-Brock, 2001).

In contrast to the ultimate hypotheses described above, the learning-to-parent and the natal attraction hypotheses seek to understand allocare as a by-product of proximate mechanisms for parental care. That is, allocare is not adaptive itself, but it may make allomothers better parents. The learning-to-parent hypothesis suggests that, to become good mothers, females must first learn how to care for offspring, particularly highly vulnerable newborns (Paul & Kuester, 1996). Therefore, young females provide care to the offspring of others to gain future fitness benefits. In this case, any benefit to offspring is incidental, a form of by-product beneficence (Rothstein & Pierotti, 1988). Similarly, the natal attraction hypothesis suggests that allocare results from an indiscriminate attraction towards infantile traits (Quiatt, 1979). In this case, natal attraction favours maternal behaviour, but sometimes results in females providing care to unrelated offspring.

Although the evolutionary mechanisms underlying allocare among primates have been closely examined in past decades (e.g.: Blaffer Hrdy, 1976, 2011; Lancaster, 1971; Quiatt, 1979; Fairbanks, 1990), allocare among social odontocetes, i.e. toothed whales, remains a comparatively neglected topic. Based on numerous anecdotal observations and reports, allocare is apparently common among toothed whales, such as bottlenose dolphins, (*Tursiops* spp.; Mann & Smuts, 1998), Atlantic white-sided dolphins (*Lagenorhynchus acutus*; Simard & Gowans, 2004), harbour porpoises (*Phocaena phocaena;* Anderson, 1969), orcas (*Orcinus orca;* Haenal, 1986), sperm whales (Whitehead, 1996), and belugas (*Delphinapterus leucas;* Bel'kovitch & Sh'ekotov, 1990; Krasnova et al., 2014). However, the factors motivating allocare have only been examined in two of these species. Among sperm whales, allocare is primarily driven by kin selection and reciprocation (Gero, Gordon, & Whitehead, 2013; Konrad et al., 2018), while allocare among bottlenose dolphins is driven by natal attraction and learning-to-parent (Mann & Smuts, 1998; Stanton, Gibson, & Mann, 2011). These conflicting findings suggest that odontocete allomothers are driven by a mosaic of possible benefits, and that a host of pressures could have driven the evolution of allocare in odontocetes. Among belugas (*Delphinapterus leucas*), allocare has been described in captive animals (Leung et al., 2010; Hill & Campbell, 2014), and anecdotally reported in wild populations (Bel'kovitch & Sh'ekotov, 1990; Béland, Faucher, & Corbeil, 1990; Krasnova et al., 2014), suggesting that belugas are prime candidates to further explore the diversity of evolutionary pressures driving allocare.

Although many aspects of beluga ecology remain shrouded, decades of research have provided a basic understanding of some aspects of their lives. Observations of belugas in the wild and measurements of beluga reproductive tracts suggest a promiscuous mating system (Kelley et al., 2015). Females typically give birth during the summer (Sergeant, 1973). Offspring are highly dependent on their mothers, weaning between 1 and 3 years of age (Matthews & Ferguson, 2015), but remain closely associated with their mothers for several years afterwards (Colbeck et al. 2013). For most of the year, adult males and females are spatially segregated (Loseto et al. 2006; Lemieux Lefebvre et al., 2012). Beluga sociality is structured by fission-fusion dynamics, characterized by long-term social bonds and labile group membership (Alekseeva, Panova, & Bel'kovich, 2013; Krasnova et al., 2014). Evidence suggests that females associate preferentially with kin (Colbeck et al. 2013), although social bonds with non-kin may also be important (O'Corry-Crowe, 2020).

Among odontocetes, both maternal care and allocare are frequently described in the context of formation locomotion: dyadic formations between adult "escorts" and offspring which are hydrodynamically costly to escorts, but advantageous to offspring (Weihs, 2004; Hill & Campbell, 2014). Analogous to infant-carrying in terrestrial animals, formation locomotion represents the second most energetically costly odontocete maternal behaviour after lactation (Altmann & Samuels, 1992; Noren, 2008). Two types of formation locomotion are typically described among odontocetes: echelon position, where offspring are maintained in close proximity to the escort's mid-lateral flank (Noren et al., 2008, Fig. 2.1A) and infant position, where offspring swim directly beneath the escort's tail (Noren & Edwards, 2011, Fig. 2.1B). Although echelon position greatly facilitates offspring locomotion, it is highly costly to escorts. A bottlenose dolphin calf in echelon receives 60% of its thrust from the escorting individual, which in turn sees its maximum swim speed reduced by 24% due to additional drag (Weihs, 2004; Noren, 2008). In contrast, infant position confers only minimal hydrodynamic benefits to offspring and is relatively energetically economical for escorts, but may function to camouflage offspring from predators, provide comfort in high-stress situations, and facilitate nursing (Noren & Edwards, 2011).

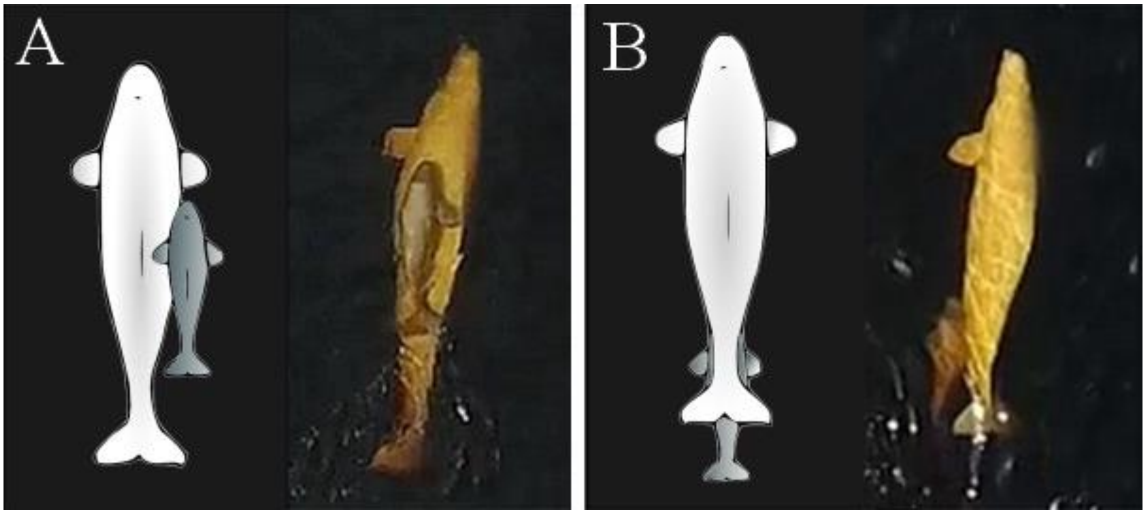


Figure 2.1: Formation locomotion positions typical of offspring care among belugas and other social odontocetes, depicted as dorsal-facing diagrams and as seen from uncrewed aerial vehicle (UAV) footage. A) Female beluga with offspring in echelon position, an energetically costly maternal care behaviour. B) Female beluga with offspring in infant position, a relatively less costly maternal behaviour offering social and anti-predator benefits.

The mechanisms underlying the evolution of allocare can be glimpsed through a species' behavioural ecology. For example, group augmentation is unlikely to drive allocare in belugas, as belugas do not live in stable groups. The fission-fusion dynamics of beluga sociality do not permit offspring to be retained within a stable group structure, one of the pre-requisites of the group augmentation hypothesis (Kokko et al., 2001). However, the relative importance of the learning-to-parent and natal attraction hypotheses can be weighed by examining how allocare varies with both allomother age and recipient offspring age (Blaffer Hrdy, 1976; Quiatt, 1979; Maestripieri, 1994; Bădescu et al., 2015).

2.2.1 Predictions for the learning-to-parent hypothesis

When allocare results in future fitness benefits for allomothers through learning-to-parent, we expect that most allomothers should be subadults, given that caring for infants typically only improves the fitness of reproductively inexperienced females (Fairbanks, 1990). Simultaneously, these subadult allomothers should favour infants, as contact with infants, but not older offspring, is expected to improve a female's parenting skills and future reproductive success (Mann & Smuts, 1998).

2.2.2 Predictions for the natal attraction hypothesis

In contrast, natal attraction places no particular constraint on allomother age, as females of any age or reproductive state can experience natal attraction (Mann & Smuts, 1998). However, natal attraction allocare should decrease as offspring age, due to the progressive loss of infantile traits as offspring mature (Bădescu et al., 2015).

2.2.3. The kin selection and reciprocation hypotheses

Finally, kin selection and reciprocation allocare can benefit allomothers at any age, but require that offspring receive tangible benefits from allocare (Blaffer Hrdy, 1976). In the case of kin selection, allomothers can only benefit if allocare provides a fitness benefit to related offspring (Hamilton, 1964). Similarly, allomothers can only expect reciprocal benefits if they first provide benefits to recipient offspring (Trivers, 1971). In some species, allocare is most beneficial to infants (Stanford, 1992; Konrad et al., 2018), while in others, allocare is more beneficial for older offspring (Altmann, 1980; O'Brien & Robinson, 1991). Therefore, we cannot generate informative predictions for the kin selection and reciprocation hypotheses based on the ages of allomothers and recipient offspring.

2.2.4 Hypotheses and predictions for the evolution of allocare in SLE belugas

Through a sustained effort targeting groups of females with offspring in the St. Lawrence Estuary (SLE) beluga population, we quantified allomaternal associations to identify whether allocare among SLE belugas is consistent with the learning-to-parent and natal attraction hypotheses. We characterized allomothers as either subadult or adult. We also examined how allomaternal investment, estimated as a function of the duration of (a) allomaternal associations, (b) echelon swims and (c) infant swims with allomothers, varied with offspring age. Echelon swimming and infant swimming are mutually exclusive, and reflect high and low-cost behaviours, respectively. Therefore, we expected that a decrease in association duration and echelon swim, coupled with an increase in infant swimming would reflect a decrease in allocare. We then compared the proportion of subadult and adult allomothers, and the observed relation between offspring age and allomaternal investment to those predicted by the learning to parent, natal attraction hypotheses (Table 2.1). Here, we combine the kin selection and reciprocation hypotheses, as they are observationally equivalent. Neither of these hypotheses can be tested by examining the ages of allomothers and recipient offspring. However, kin selection and reciprocation are well-established drivers of allocare among odontocetes (Gero et al. 2013, Konrad et al. 2018) and other mammals (Briga, Pen, & Wright, 2012; Blaffer Hrdy, 2012), and therefore we include them here as a biological null hypothesis.

Table 2.1. Four proposed hypotheses for the evolution of allocare among St. Lawrence Estuary belugas. We predicted the prevalence of subadult allomothers, and relation between allomaternal investment and offspring age for each hypothesis. 1) The learning-to-parent hypothesis predicts that most allomothers will be subadults, and that allomaternal investment will decline with offspring age, as evidenced by a decrease in association duration and echelon swim duration, and an increase in infant swim duration. 2) The natal attraction hypothesis predicts that most allomothers will not be subadult, and that allomaternal investment will decline as offspring age. 3) The kin selection and reciprocation hypotheses are observationally equivalent and offer no specific predictions. Allomaternal investment was estimated by association duration, echelon swim duration, and infant swim duration.

		Metrics for allomaternal investment		
Hypotheses for evolution of allocare	Most allomothers subadult?	Association duration	Echelon swim duration	Infant swim duration
1. Learning-to-parent	Yes	-	-	+
2. Natal attraction	No	-	-	+
3. Kin selection & Reciprocation	No	-/+	-/+	-/+

2.3 Methods

2.3.1 Obtaining footage of female belugas with young

We conducted fieldwork in the summers of 2016 to 2018 (Table 2.2). Using uncrewed aerial vehicles (UAV; Phantom 4 and Phantom 4 Pro, DJI, Shenzhen, China) we obtained footage of groups of female SLE belugas with offspring. Sampling occurred in the Saguenay Fjord, between the mouth of the Fjord and Baie Ste-Marguerite, in Quebec, Canada (Fig. 2.2). Baie-Ste-Marguerite represents a portion of the SLE beluga summer range heavily used by females with young in the summer (Pippard & Malcolm, 1978; Michaud, 1993). During the 2016 field season and the early 2017 field season, the UAV was launched from the deck of an 8 m rigid-hulled inflatable vessel. At the midpoint of the 2017 field season, a scaffolding tower was constructed in Baie-Ste-Marguerite to be used as a fixed launch point. The UAV was launched from this structure for the remainder of the 2017 field season and the entire duration of the 2018 field season. Construction and use of the tower represented a conscious effort to reduce the ecological impact of our study, as noise from watercraft are an important source of disturbance to odontocetes in general (Erbe, 2002; Williams, Trites, & Bain, 2006), and SLE belugas specifically (Lesage et al., 1999; Scheifele et al., 2005).

2.3.2 Ethical note

Our fieldwork methods were reviewed and approved by the Memorial University Animal Care Committee (Animal Use Protocol: 20190640). Our research, and specifically, the use of research UAVs in the Saguenay St. Lawrence Marine Park was covered by research permit SAGMP-2018-28703 issued by Parks Canada and QUE-LEP-001-2018 issued by Fisheries and Oceans Canada. At all times, we maintained the UAV at an altitude greater than 20 m to avoid disturbing the study subjects.

Table 2.2. Summary of sampling effort of allomaternal associations among belugas in the St. Lawrence Estuary, showing the sampling period for each year, the number of sampling days, the total number of UAV flights per year, mean video duration by year, and the total duration of footage obtained per year.

Year	Start date	End date	# Sampling days	# UAV videos	Mean video duration ± SD (min.)	Total footage duration (h)
2016	07/16	09/22	18	61	13.4 ± 5.5	13.7
2017	06/25	08/12	16	58	15.6 ± 4.4	14.4
2018	07/08	08/19	22	60	17.8 ± 3.2	16.9
Total	-	-	56	179	15.6 ± 4.8	45.0

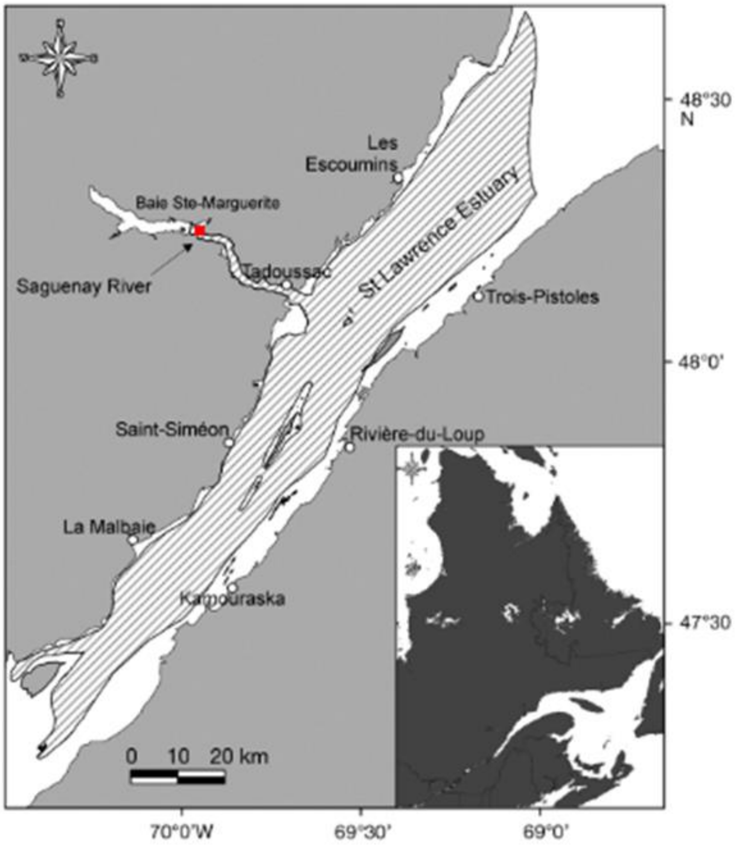


Figure 2.2: Summer distribution of St. Lawrence Estuary belugas in Quebec, Canada. In 2016 and 2017, sampling occurred in the Saguenay river, between Tadoussac, and Baie Ste-Marguerite. Sampling in 2018 occurred in Baie Ste-Marguerite exclusively. The red square denotes the approximate location of the BSM research tower. Modified from Lemieux Lefebvre et al. (2012).

2.3.3 Continuous behavioural focal sampling of beluga offspring

Following Altmann's (1974) recommendations for continuous behavioural focal sampling, we conducted focal follows for all offspring recorded in UAV footage. Offspring were sorted into three age classes: calves (~0-4 months, Fig. 2.3A), yearlings (~12-16 months, Fig. 2.3B), and juveniles (~2-5 years, Fig. 2.3C). We also differentiated subadults (~6-12 years) from adults (Fig. 2.3D). Seen from our UAV footage, belugas lack individually distinguishing features, so each new observation of offspring (calf, yearling, or juvenile) was recorded as a new focal individual. This inevitably resulted in some resampling, which we attempted to control for in our models. A focal follow consisted of the entire duration of time that a focal individual remained in sight or could be distinguished from other individuals. Focal follows lasting less than 10 seconds were discarded. To verify that we were not resampling the same animals each day, we checked the frequency of re-observation of photo-identified individuals in the study site during the study period (Appendix A). We conducted behavioural analysis of focal follows with the event recorder JWatcher 1.0 (Blumstein & Daniel, 2007).

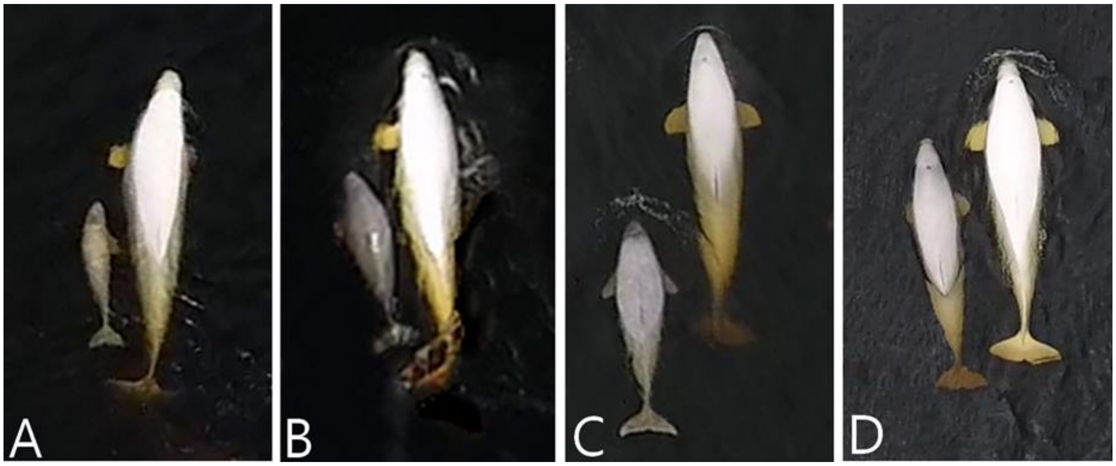


Figure 2.3. Comparing four age classes of immature St. Lawrence Estuary belugas relative to adult females. **A)** Calf, approximately one third adult length, pale brown in colour with pigmentation surrounding blowhole, fetal folds visible behind pectoral fin. **B)** Yearling, approximately half adult length, dark grey in colour (although some individuals much paler), plump, barrel-like profile. **C)** Juvenile, over half adult body length, pale grey in colour, tailstock elongated relative to yearling but retains plump profile. **D)** Subadult, typically showing a slimmer profile and smaller body size compared to adults. Subadults have not yet reached a pure white colour, and so can be distinguished from adults even when adults are not available for size comparison.

2.3.4 Quantifying maternal and allomaternal associations

To quantify allomaternal associations, we recorded associations between focal individuals and group members, and defined these associates as “escorts” if they provided care by escorting offspring in formation locomotion. According to Weihs (2004), bottlenose dolphin calves benefit from echelon position when the distance between mother and calf is less than the sum of half of the mother’s thickest cross-section and half the calf’s thickest cross-section. We considered offspring to be in echelon position if they were roughly within this distance of an escort, with synchrony in directional change. Infant position required no such limiting distance, as offspring always appeared to be in physical contact with the escort, often directly beneath her tailstock. We counted the number of escorts associated with each offspring, maintaining a conservative estimate by counting a new escort only when previously observed escorts were still visible and no longer associated with the offspring. We calculated the duration of each escorted association, and the duration of echelon swims and infant swims during associations.

2.3.5 Assigning mothers and allomothers

Given the difficulties in assigning maternity to any one escort, we relied on certain assumptions to identify which escorts were most likely to be mothers, and which were most likely to be allomothers. We categorized all subadult escorts as allomothers, as these individuals were likely sexually immature. When offspring only associated with a single adult escort, we assigned maternity to this escort. When offspring associated with multiple adult escorts, we assigned maternity to the escort that spent the greatest proportion of the focal follow with the offspring. We designated all other adult escorts as allomothers, based on the assumption that offspring should spend more time in association with mothers than with allomothers (Gordon, 1987; Hill et al., 2013). While most individuals were impossible to distinguish using our methods, we were fortunate to repeatedly observe a mother and juvenile which could always be identified. Céline was first observed in the St. Lawrence Estuary in 1987. She can be easily recognized by a deep scar on her left flank. In 2014, Céline gave birth to a calf with a distinctive spinal deformity. In 2017, we observed this juvenile six times over two sampling days. In all focal follows, our assumptions allowed us to correctly identify Céline as the juvenile's mother. On average, the juvenile spent 3 minutes and 13 seconds with Céline, and only 51 seconds with allomothers. The juvenile typically swam away from its mother for short periods to swim with other females, only to return to her side for the remainder of the focal follow. We noted that most instances classified as allocare followed a similar pattern.

2.3.6 Interobserver reliability analysis

To ensure the reliability of the main observer (JAA), we trained two additional observers to re-analyze a subset of the videos. These observers respectively analyzed 11 and 17 videos, for a total of 28. For all variables of interest, their observations were then compared to JAA's observations. See Appendix B for more details on the interobserver reliability analysis.

2.3.7 Comparing adult and subadult allomothers

To obtain a representative estimate of the number of potential adult and subadult allomothers available to offspring, we counted how many times we observed subadults and adults in all groups (including those which did not include offspring) during the 2017 sampling season. In 2017, we recorded 107 observations of subadults and 1,230 observations of adults. We therefore consider that subadults represent approximately 8.0% of available allomothers. We used a chi-squared goodness of fit test to determine whether the observed proportion of subadult allomothers differs from the proportion of subadult allomothers predicted from availability alone (8.0%).

2.3.7 Comparing maternal and allomaternal investment across age classes

We constructed three generalized linear mixed models to compare the impact of offspring age on the duration of escort associations, echelon swims, and infant swims, for both maternal and allomaternal associations (Table 2.3). Maternal associations were included in the models to verify that the metrics used to describe investment showed the expected pattern of declining maternal investment as offspring aged (Trivers, 1972). Residuals for all three models were checked for normality and found to be acceptable. We conducted Tukey post-hoc tests to check for significant differences between age classes, for both mothers and allomothers, for all three models. We then used the obtained intercept and coefficients for each model to estimate the duration of each behaviour for each combination of offspring age and escort type. All analyses were carried out in the R environment (version 3.4.3, R. Core Team, 2013) with the lme4 package (Bates et al., 2015).

Table 2.3: Generalized linear mixed models used to test how maternal and allomaternal investment in SLE belugas vary with offspring age class. We included year as a random effect to account for variation in sampling strategies across years. We included video as a random effect because conditions tended to be similar within videos, and individual offspring were most likely to be re-sampled within videos. We included focal follow as a random effect because focal individuals that associated with both mothers and allomothers appeared multiple times in the dataset. We used scaled focal follow duration as an offset to account for variations in the observability (i.e., time spent at surface) of different age classes. This variable was scaled (by subtracting the mean and dividing by the standard deviation) to control for overdispersion. All three models were identical except for the response variable.

	Models		
	Association	Echelon	Infant
Response variable	Duration of association (s)	Duration of echelon swim (s)	Duration of infant swim (s)
Fixed effects	Offspring age (calf, yearling, or juvenile), Escort type (mother or allomother)		
Interaction	Offspring age * Escort type		
Random effects	Year, Video, Focal follow		
Offset	Scaled focal follow duration		

2.4 Results

2.4.1 Inter-observer reliability analysis

The interobserver analysis suggested that JAA's observations were reliable. For the 28 videos analyzed, all variables compared showed moderate to excellent agreement between JAA and the two observers. Koo & Li (2016) consider that an intraclass correlation coefficient value lower than 0.5 reflects poor reliability, values between 0.5 and 0.75 represent moderate reliability, values between 0.75 and 0.9 reflect good reliability, and values greater than 0.9 reflect excellent reliability. The lower bound of all our intraclass correlation coefficients 95% confidence intervals were greater than 0.5 and are therefore acceptable under these guidelines (Table 2.4). For more details, see Appendix B.

Table 2.4. Correlation coefficients with confidence intervals comparing JAA's observations to JB and AKE's observations across a subset of 28 videos. The lower bound of all intraclass correlation coefficient confidence intervals are greater than 0.5 and are therefore considered acceptable by Koo & Li (2016).

Variable of interest	Intraclass correlation coefficient [95% CI]
Association duration	0.91 [0.79, 0.96]
Echelon swim duration	0.84 [0.64, 0.93]
Infant swim duration	0.81 [0.57, 0.91]
Number of calves	0.93 [0.84, 0.97]
Number of yearlings	0.89 [0.77, 0.95]
Number of juveniles	0.81 [0.60, 0.91]
Number of escorts	0.87 [0.71, 0.94]

2.4.2 Mothers and allomothers

In total, from 176 UAV videos, we recorded and analyzed 1866 focal follows of calves, yearlings, and juveniles in the St. Lawrence Estuary beluga population from 2016 to 2018. Of 1866 focal follows, 258 (13.8%) showed evidence of allocare, with offspring either associating with subadult females, or with multiple adult females. Associations between mothers and focal offspring lasted on average 63 seconds, while associations with allomothers lasted 27 seconds. When we excluded associations where mothers were identified on the basis of being the sole escort (ie, focal follows when no secondary escorts were identified), maternal associations were considerably longer, 111 seconds on average compared to 27 seconds for allomothers.

Table 2.5. Summary of all focal follows analysed. The low number of yearlings observed is likely due to low first-year survival among SLE belugas. Most, but not all focal follows included a maternal association. The long average duration of calf focal follows, and proportionally high number of allomaternal associations observed is likely due to the poor diving ability of calves, which results in greater observability. More juveniles were observed as this age class includes multiple year cohorts. Note that standard deviations are greater than the mean in all measurements of duration, demonstrating high variability in the observability and duration of associations even within age classes. These data are not suitable for non-parametric testing, as each focal follow does not represent an independent observation. To account for resampling of individuals within sampling days, and possible differences between sampling years, the video number and year of each focal follow must be taken into account.

			Maternal		Allomaternal	
	Number of focal follows	Mean focal follow duration (s)	Number of associations	Mean association duration ± SD (s)	Number of associations	Mean association duration ± SD (s)
Calf	465	132.8 s ± 162.6 s	431	97.2 ± 121.6	107	26.9 ± 38.3
Yearling	211	86.7 ± 105.8	195	60.2 ± 66.9	20	22.6 ± 25.0
Juvenile	1190	69.7 ± 81.5	1058	48.9 ± 57.5	130	17.9 ± 23.3
All age classes	1866	87.4 ± 113.2	1684	62.5 ± 82.4	257	22.0 ± 30.8

2.4.3 Role of subadult allomothers

In focal follows were allocare occurred, 309 allomothers were observed, of which 300 were adult females, and only 9 were subadult females. Subadults were not commonly observed in groups with focal individuals. On average, each focal group (group containing a focal offspring) included 5.8 adults and only 0.2 subadults. This suggests that subadults may associate preferentially with other subadults or groups without offspring. We previously found that subadults represented 8% of available allomothers to offspring. Results from the chi-squared goodness of fit test showed that the observed number of subadult allomothers was significantly smaller than the predicted number of subadult allomothers ($\chi^2 = 11.55$, $P < 0.001$).

2.4.4 Impact of offspring age class on maternal and allomaternal investment

Results from the Association model, the Echelon model, and the Infant model show that offspring age impacted the duration of maternal behaviours, but not allomaternal behaviours. Output from the models show how the levels of each fixed categorical variable and their interactions influenced the duration of behaviours, relative to the interaction between calf and mother, randomly chosen as the intercept (Table 2.4). For the Association and Echelon models, the intercept was significantly different from the interaction between yearling and mother (Association: $Z = -6.96$, $P < 0.001$, Echelon: $Z = 10.0$, $P < 0.0001$). For every model, the intercept was significantly different from the interaction between juvenile and mother (Association: $Z = -12.66$, $P < 0.001$, Echelon: $Z = -19.0$, $P < 0.001$, Infant: $Z = 3.62$, $P < 0.001$). Along with the results of the Tukey post-hoc test, these results confirm that the duration of maternal behaviours varied significantly with offspring age class (Fig. 2.4A, B, C). Results from the Tukey post-hoc tests showed that allomaternal behaviour duration did not vary significantly among age classes. For all models, differences in allomaternal behaviour duration were insignificant (Fig 2.4D, E, F).

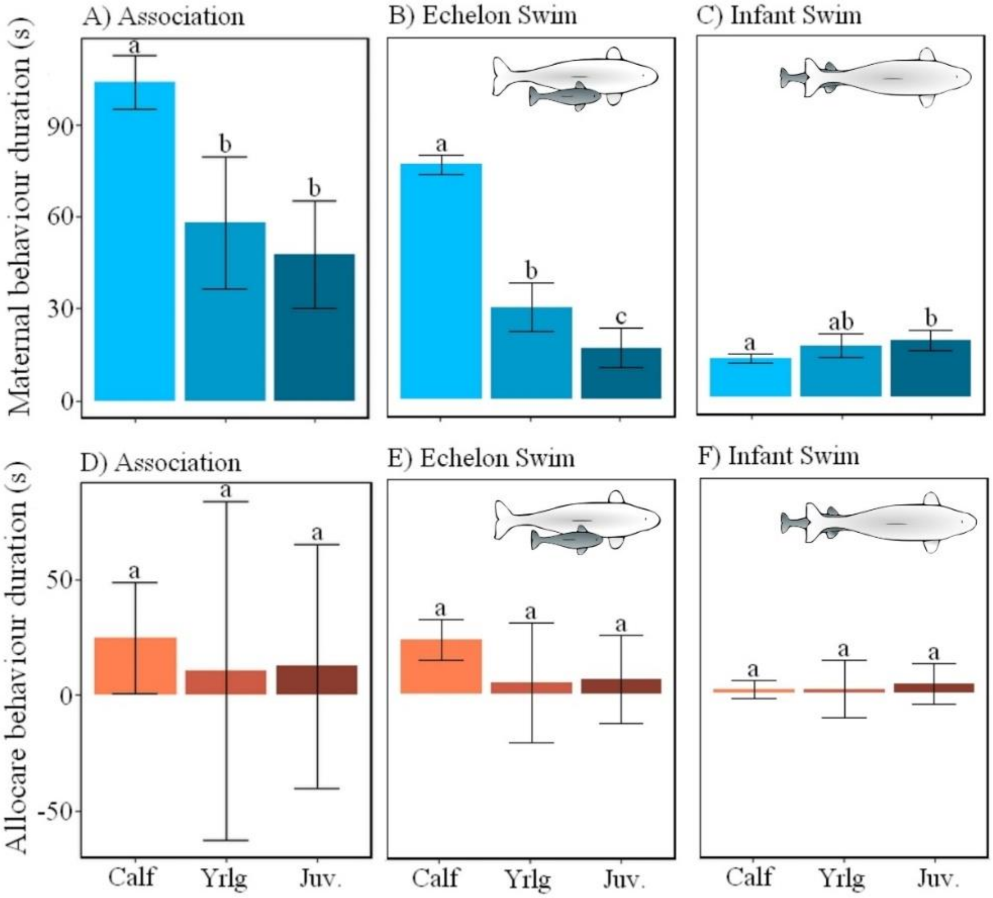
Table 2.6: Association model, Echelon model, and Infant model describing the duration of offspring-care behaviours in the St. Lawrence Estuary beluga population as a function of escort type (mother or allomother) and offspring age class (calf, yearling, or juvenile) and their interaction. 95% confidence intervals for each estimate included in brackets. Bolded estimates were significant (*P* < 0.05).

		Models		
		Association	Echelon	Infant
Response variable		Duration of association (s)	Duration of echelon swim (s)	Duration of infant swim (s)
Fixed effects	Intercept (Calf*Mother)	**103.6 [94.9, 112.3]**	**76.7 [70.5, 83.0]**	**12.6 [9.5, 15.6]**
	Type: Allomother	**-78.8 [-94.0, -63.5]**	**-53.2 [-64.2, -42.2]**	**-10.8 [-15.6, -6.0]**
	Age: Yearling	**-45.6 [-58.4, -32.8]**	**-46.6 [-55.8, -37.3]**	4.2 [-0.5, 9.0]
	Age: Juvenile	**-56.0 [-64.8, -47.2]**	**-59.8 [-66.1, -53.6]**	**5.9 [2.7, 9.1]**
	Yearling*Allomother	31.5 [-5.1, 68.2]	**28.1 [4.0, 52.4]**	-3.6 [-15.8, 7.6]
	Juvenile*Allomother	**43.8 [23.5, 64.1]**	**42.8 [28.9, 56.7]**	-4.2 [-10.1, 2.9]
Marginal R^2 (fixed effects only)		0.11	0.17	0.04
Conditional R^2 (fixed and random effects)		0.24	0.28	0.45

2.4.5 Estimating maternal and allomaternal behaviour duration from the models

For each combination of escort type (mother or allomother) and offspring age class (calf, yearling, or juvenile) we summed the model intercepts and relevant slopes to obtain estimates of the duration of each behaviour for each combination (Fig. 2.4). We then used the results of the post-hoc tests to indicate whether differences between combinations were significant. Overall, maternal association and echelon swim duration decreased with offspring age (Fig. 2.4A, B), while maternal infant swim duration increased with offspring age (Fig. 2.4C). Allomaternal behaviour durations showed no such trends: neither allomother association, echelon swim, nor infant swim duration varied significantly between age classes (Fig 2.4D, E, F). To verify that the significant differences between age classes for maternal associations were not an artifact of large sample sizes, we repeated the analysis using only the subset of focal follows that had both maternal and allomaternal associations. When maternal and allomaternal associations shared a similar sample size, we found no change in our results.

Figure 2.4. Estimate of the durations of maternal-care behaviours (shades of blue, panels A, B, C) and allocare behaviours (shades of orange, panels D, E, F) calculated from the Association model (panels A, D), Echelon model (panels B, E), and the Infant model (C, F). Age classes sharing the same letter within the same panel were not significantly different, while age classes with different letters were significantly different (P < 0.05). Note that some estimates carry very large confidence intervals, sometimes ranging below zero. While negative duration is impossible, these large confidence intervals reflect the high variability in behaviour duration observed even within age class-escort type combinations. Age classes were only compared within, and not among, panels.



2.5 Discussion

Using focal observations of beluga offspring in the St. Lawrence Estuary, we attempted to determine which hypotheses for allomaternal benefit, i.e., kin selection, reciprocation, learning-to-parent, and natal attraction, are consistent with allocare in the population. We found that subadult allomothers were under-represented in the dataset, suggesting that allocare is mainly provided by adult females in the SLE beluga population. We also found that maternal investment tended to decline as offspring aged, as shown by a decrease in maternal association and echelon swim duration, coupled with an increase in the duration of infant swim. However, allomaternal investment did not vary with offspring age. Neither the duration of allomaternal associations, echelon swims, or infant swims varied significantly with offspring age class.

2.5.1 Patterns of maternal investment

The observed pattern of maternal investment is consistent with Trivers' (1972) parental investment hypothesis, as well as existing literature on maternal investment in belugas and bottlenose dolphins (Mann & Smuts, 1998; Noren & Edwards, 2011; Stanton et al., 2011; Matthews & Ferguson, 2015). As offspring aged, mothers spent less time with offspring, and replaced high cost maternal behaviours with lower cost behaviours. This is consistent with a gradual reduction of parental investment, aimed at minimizing costs to future reproduction while maximizing survival of current offspring (Trivers, 1972). A similar pattern of declining maternal investment is apparent in belugas of the eastern Canadian arctic that show gradual weaning, with offspring diet progressively shifting from exclusively milk, to exclusively solid foods across a multi-year span (Matthews &

Ferguson, 2015). Maternal investment, defined by the same metrics used in our study, also showed a similar decline among the bottlenose dolphins of Shark Bay. In this population, offspring gradually spent less time in association with their mothers as they age (Stanton et al., 2011), and the predominant behaviour of mother-offspring dyads shifted from echelon position to infant position as offspring age (Mann & Smuts, 1999; Noren & Edwards, 2011). This confirms that the metrics used to approximate allomaternal investment accurately captured variation in maternal investment across age classes. The observed patterns of allomaternal investment are likely sufficiently robust to infer patterns of allocare.

2.5.2 The learning-to-parent hypothesis

Through the learning-to-parent hypothesis, allocare has been suggested to improve direct fitness of allomothers, by allowing young nulliparous females to acquire experience with infant-handling before producing their own offspring (Lancaster, 1971). By caring for infants, young nulliparous females can improve their future reproductive success, likely due to improvements in their maternal abilities (Tardif, Richter, & Carson, 1984; Bădescu et al., 2015). If allocare in the SLE beluga population persists as a low stakes parenting exercise, we predicted that most allomothers would be young, nulliparous females, and that allocare would decline as offspring aged. Given that the majority of observed allomothers in the St. Lawrence estuary were adult females, and that allocare did not vary with offspring age, we found no support for the learning-to parent hypothesis. This contrasts with observations of allocare in bottlenose dolphins, where immature females frequently attempt to separate newborn calves from their mothers to engage in echelon swims (Mann & Smuts, 1998). Among primates, the learning-to-parent hypothesis tends to receive strong support. Across taxa, juvenile and subadult females interact with offspring more than non-parent adults (Maestripieri, 1994). For example, among ursine colobus (*Colobus vellerosus*) subadult females carry both related and unrelated offspring for long periods of time (Brent, Teichroeb, & Sicotte, 2008; Bădescu et al., 2015).

2.5.3 The natal attraction hypothesis

Natal attraction, an indiscriminate attraction towards infantile traits perceived to be "cute", has been suggested to be a major driver of parental and prosocial behaviours in group-living animals (Silk, 1999; Archer & Monton, 2011; Stark et al., 2016). Despite being sometimes described as a "reproductive error", natal attraction does not imply that animals are unable to recognize their own offspring, but rather that certain traits have been selected to elicit care-giving behaviours (Riedman, 1982; Silk, 1999). Given that older offspring possess fewer infantile traits than infants, natal attraction typically ceases as offspring age (MacKinnon, 2011). In SLE belugas, we found that allomaternal investment in SLE belugas was constant across age classes, inconsistent with the natal attraction hypothesis. Although adult females are also prone to natal attraction (Mann & Smuts, 1998; Silk, 1999), immature females seem particularly sensitive to infantile traits. Indeed, many examples in nature link natal attraction and learning-to-parent allocare. Both immature bottlenose dolphins and ursine colobus females are most strongly attracted to infants (Mann & Smuts, 1999, Bădescu et al., 2015). However, among Barbary macaques (*Macaca sylvanus*), allomothers tend to be immature females, but participation in allocare does not improve first-born survival for these females (Paul & Kuester, 1996), suggesting that natal attraction can persist without learning-to-parent benefits for allomothers.

2.5.4 The kin selection & reciprocation hypotheses

In contrast to the learning-to-parent and natal attraction hypotheses, both the kin selection and reciprocation hypotheses require that offspring and mothers derive benefit from the actions of allomothers. When allocare is kin-selected, offspring, mothers, and allomothers all share in the benefits of allocare through their shared genes (Hamilton, 1964; Rose et al., 2007). Similarly, when allocare is driven by reciprocation, the benefits imparted to offspring and mothers by allomothers are expected to be proportional to the reciprocal benefits received by allomothers (Trivers, 1971, 2006). Therefore, allocare occurring under these hypotheses requires only that some benefit be imparted to recipients, without imposing constraints on the age of allomothers, or the age of recipient offspring. Given that allomaternal investment did not vary with age, and that subadult allomothers did not predominate, we can exclude both the learning-to-parent and natal attraction hypotheses, but not the kin selection and reciprocation hypotheses. Among the sperm whales of the Caribbean and Sargasso seas, evidence shows that allocare is driven by kin selection and reciprocation, perhaps similarly to SLE belugas (Gero et al., 2009; Gero et al., 2013; Konrad et al., 2018). In these populations, adult allomothers preferentially cared for closely related offspring. In one case, reciprocation of allocare between two mothers was observed after a one-year delay (Gero et al., 2013). Similar patterns of allocare are seen in capped langurs (*Presbutis pileate*), where allomothers are almost exclusively adult, parous females, and allocare occurs primarily between kin and reciprocating females (Stanford, 1992).

Kin selection and reciprocation both appear to be consistent with beluga social structure. Evidence suggests that belugas live in highly dynamic fission-fusion societies structured by long-term social bonds (Smith, Hammill, & Martin, 1994; Loseto et al. 2006; Krasnova et al., 2012). Some aspects of beluga life history hint at the importance of maternal kinship. Belugas are one of few species with post-reproductive female lifespans (Ellis et al., 2018), suggesting that grandmothers may play an important role as caregivers. In addition, observations of high relatedness within female groups during migration support the kin selection hypothesis (Colbeck et al., 2013). However, other findings suggest that beluga sociality is not exclusively kin-dependent: O'Corry-Crowe (2020) found that all beluga groups examined included both related and unrelated individuals, and that most groups tended to have low relatedness. This suggests that long-term bonds among belugas, rather than being exclusively shaped by kinship, might also result from cooperative and reciprocative behaviour.

2.5.5 Patterns of extended allocare

Allocare often seems to mirror parental care, with alloparents offering younger offspring more care than older offspring. While consistent with learning-to-parent allocare and natal attraction, this pattern is also apparent in populations where allocare is driven by kin selection and reciprocation, e.g., sperm whales (Konrad et al., 2018) and capped langurs (Stanford, 1992). This suggests that allocare is primarily directed towards infants because infants need more care to survive. More rarely, allocare either increases with offspring age or remains constant, similar to SLE belugas. We define these exceptions as “extended” allocare. Among capuchins, constant levels of allocare are maintained as maternal care declines: for offspring aged 4-6 months, allomaternal interactions outnumber maternal interactions (O’Brien & Robinson, 1991). Such extended allocare results in offspring receiving high levels of care until they reach independence. While infant-directed allocare promotes infant survival during the period of highest mortality, extended allocare likely provides less critical, but still important benefits.

2.5.6 Prospective offspring benefits of extended allocare

We suggest that, among SLE belugas, extended allocare could be important to the weaning and social development of offspring. As a result of parent-offspring conflict, mothers and offspring typically disagree over weaning timing (Trivers, 1974), and this conflict can result in considerable stress for offspring (Malm & Jensen, 1997; Mandalaywala et al., 2014). Arctic beluga females typically give birth every three years (Brodie, 1971), while juvenile belugas in Arctic populations continue to nurse until three years of age (Matthews & Ferguson, 2015). Although evidence that allomothers mediate weaning conflict is scarce, in one study the presence of an unrelated adult was found to reduce the frequency of weaning-related distress behaviours in domestic horse foals (Henry et al., 2012). This suggests that allomaternal intervention during weaning might buffer the deleterious effects of weaning stress. Among SLE belugas, this may partially explain why allocare does not vary with age. Perhaps some allomothers focus their attentions on vulnerable infants, while others direct care towards weaning-stressed older siblings.

Extended allocare may also impart important social benefits to offspring by allowing offspring to acquire social skills and develop social bonds with allomothers. Several studies have shown that early connectivity in social networks can lead to improved outcomes for offspring (McDonald, 2007; Nunez, Adelman, & Rubenstein, 2015). Among bottlenose dolphins, maternal separations allow offspring to broaden their social networks and form long-lasting relationships with conspecifics from an early age (Stanton et al., 2011). Given that the social dynamics of belugas may resemble the fission-fusion social dynamics of bottlenose dolphins (Alekseeva et al., 2013; Krasnova et al., 2014), allocare could allow SLE beluga offspring to form important social bonds from an early age. In this case, the hydrodynamic benefits of allocare could be secondary to its social benefits, particularly for older offspring.

2.5.7 Prospective maternal benefits of extended allocare

By caring for older offspring as well as infants, SLE beluga allomothers may also allow mothers to focus their energy on future reproduction rather than current offspring. In species with high levels of allocare, offspring tend to grow rapidly, and wean earlier than offspring from species without allocare (Ross & MacLarnon, 2000). In many cases, earlier weaning results in shorter birth intervals. Among vervet monkeys (*Chlorocebus pygerythrus*), mothers which received assistance from allomothers had shorter birth intervals than mothers who reared their offspring alone (Fairbanks, 1990). Additionally, among humans (*Homo sapiens*), birth intervals are significantly shorter than those of other great apes of similar body size, and this discrepancy has been attributed to the role of allocare in human child-rearing (Sear & Mace, 2008). As cetacean offspring age, both nursing and swimming in echelon position become more costly to mothers due to the increased energetic requirements and increased body size of offspring (Lee, Majluf, & Gordon, 1991; Mann & Smuts, 1999), suggesting that allocare may become increasingly valuable to mothers as offspring age. By investing in older offspring as well as in infants, SLE beluga allomothers could provide relief to mothers at a time when maternal care becomes particularly costly and detrimental to future reproduction.

2.5.8 Limitations

While our observations allowed us to refute the learning-to-parent and natal attraction hypotheses, we were unable to test predictions related to kin selection and reciprocation. To provide strong evidence of the kin selection hypothesis, we would need to demonstrate that allomothers and recipient offspring share more genes than expected by chance. We would also have to demonstrate that recipient offspring have improved fitness, resulting in inclusive fitness benefits for allomothers. To provide strong evidence for the reciprocation hypotheses, following Gero et al. (2009), we would require multi-year data on the identity of mother and allomothers to verify whether individuals engage in reciprocation. Unfortunately, these goals were outside of the scope of this project.

Another limitation of this studies was that we were unable to positively identify mother-offspring relationships from UAV footage. We operated under the assumption that a focal offspring’s “main adult escort”, the adult female with whom the offspring spent most of a focal follow, was its mother. However, during shorter focal follows it is possible that we misidentified allomother as mothers, or mothers as allomothers. While we validated our assumptions for a single highly recognizable mother-offspring pair, this single case does not necessarily mean that our definitions correctly identified all mothers. Due to our limited knowledge of allocare among belugas, we attempted to be conservative in defining allomothers. Patterns of allocare in wild belugas should be further examined with marked individuals to determine whether our assumptions were valid.

2.6 Conclusions and future directions

From observations of maternal and allomaternal associations in the SLE beluga population, we found that allomaternal investment remained constant across age classes, inconsistent with the natal attraction and learning-to-parent hypotheses. Adult allomothers predominated over subadult allomothers, further discounting the learning-to-parent hypothesis. While we were unable to test the kin selection and reciprocation hypotheses, these are the only remaining evolutionary hypotheses for the evolution of allocare consistent with patterns of allocare among SLE belugas. Given that both these hypotheses require some benefit to mothers and offspring, we explored the potential benefits of extended allocare for offspring and mothers. We suggest that extended allocare in SLE belugas could improve the survival of calves and provide weaning stress relief and social benefits to yearlings and juveniles. Allocare for older offspring also likely benefits mothers through shortened birth intervals. These hypotheses suggest that, while allomaternal investment in SLE belugas did not vary across age classes, allomaternal motivation likely did. Future work should focus on exploring these motivations by determining the social and environmental contexts in which allocare occurs in the SLE beluga population, and whether these contexts vary across age classes. By further examining how a socially and cognitively complex cetacean species cooperates though allocare and other expressions of altruism, we will expand our understanding of prosocial behaviour across taxa.

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CHAPTER 3: IMPACT OF ENVIRONMENTAL AND SOCIAL CONDITIONS ON ALLOCARE IN ST. LAWRENCE ESTUARY BELUGAS

3.1 Abstract

Allocare, care for offspring from non-parental group members, can carry important fitness benefits for offspring. We examined potential benefits of allocare to recipient offspring by examining the environmental and social conditions in which allocare occurred among St. Lawrence Estuary belugas. We hypothesized that allomothers provide calves (ie, neonates) with protective and energetic benefits, while providing social benefits to juveniles. We predicted that calf allocare would mainly occur in risky and energetically costly conditions, while juvenile allocare would occur in highly social conditions. We quantified boat traffic and the presence of male belugas as proxies for risk, tidal phase and directional herd movements as proxies for energetic cost, and group size and milling herd movements as proxies for group sociality. We found evidence that tidal phase and herd movement pattern influenced patterns of allocare. Notably, calf allocare was never observed in herds moving directionally during the flow tide, suggesting that calves do not rely on allomothers in energetically costly contexts. Indeed, none of our findings supported the hypothesis that beluga allomothers provide protective, energetic, or social benefits to offspring. We suggest that patterns of allocare may be driven by the needs of mothers, rather than the needs of offspring.

3.2 Introduction

In some species, offspring are highly dependent on care provided by parents, as well as other group members (Riedman, 1982). These group members are known as alloparents, and the care they provide is referred to as allocare, from the Greek *allos*, meaning “other” (Blaffer Hrdy, 2011). Allocare is, therefore, care from “other” parents. Like parental care, allocare offers a suite of benefits to offspring, including protection from threats, energetic advantages, and social benefits. When offspring are in particularly risky situations, alloparental supervision and intervention can contribute to offspring survival. Sperm whales (*Physeter macrocephalus*) in a social unit stagger their dives such that vulnerable calves are never left alone at the surface during maternal foraging bouts (Whitehead, 1996). Similarly, blue monkey (*Cercopithecus mitis*) allomothers actively defend infants against aggressive conspecifics and retrieve infants during predator alarm calls (Förster & Cords, 2005). Allomothers also provide offspring with energetic benefits through food-sharing, allonursing, and by facilitating travel (Ross & MacLarnon, 2000). Primate allomothers often carry infants (Altmann & Samuels, 1992), while cetacean allomothers can travel with offspring in formation locomotion (Noren et al., 2008, Hill & Campbell, 2014). Allocare may also facilitate the formation of social bonds between offspring and group members, allowing offspring to acquire important social skills (Lancaster, 1971; Blaffer Hrdy, 1976; Fairbanks, 1990; Stanford, 1992). Early social initiation is likely particularly important in species with long-term social bonds and labile group membership, such as belugas (*Delphinapterus leucas;* Michaud, 2005; O’Corry-Crowe et al. 2020).

Allocare has been observed in both captive and wild belugas (Bel’kovitch & Sh’ekotov, 1990; Hill & Campbell, 2014; Leung, Vergara, & Barrett-Lennard, 2010). Most recently, we reported the occurrence of allocare in St. Lawrence Estuary (SLE) belugas and found that patterns of allocare in this population are most consistent with kin selection and reciprocation (Chapter 2). From an evolutionary perspective, allocare driven by kin selection or reciprocation must provide benefits to recipient offspring in order to persist within populations (Silk, 1999). The benefits of allocare may vary as offspring age as a function of their changing needs. Beluga calves are relatively altricial at birth, struggling to reach the surface to breathe without the help of their mother (Béland, Faucher, & Corbeil, 1990). For many weeks after birth, calves remain in formation with mothers and allomothers, as they lack the muscle tone and coordination required for group travel (Krasnova, Bel’kovich, & Chernetskiĭ, 2006; Hill, 2009). By two years of age, most juveniles consume prey items in addition to milk, and frequently leave their mother’s side (Smith, St. Aubin, & Hammill, 1992; Matthews & Ferguson, 2015). However, these developmental changes do not result in reduced attention from allomothers. We previously found that allomaternal investment remained constant across three age classes of beluga offspring (calves; 0-4 months, yearlings; 12-16 months, juveniles; 2-5 years), even as maternal investment declined (Chapter 2). Although we found no variation in allomaternal investment, the nature of allocare may change as offspring age. Specifically, we expected that allocare likely offers protective and energetic benefits to calves, and social benefits to juveniles.

To determine the benefits of allocare to SLE beluga offspring, we examined the occurrence and duration of allocare provided to two offspring age classes, calves (0-4 months), and juveniles (2-5 years). We noted that allocare occurred in 17% (224/1288) of SLE beluga offspring focal follows. To determine whether these 17% of focal follows shared common conditions, we investigated environmental and social variables related to various benefits to offspring. When allocare did occur, we noted that the duration of associations between offspring and allomothers was highly variable, so we also investigated whether environmental and social variables impact the duration of allocare.

3.2.1 Protection: Offspring risk

Given that allomaternal offspring defense should primarily occur when offspring are at risk, we identified two variables likely to increase risk to offspring: boat traffic, and the presence of males.

3.2.1.2 Offspring risk: Boat traffic

The Saguenay Fjord receives considerable marine traffic from shipping vessels and pleasure boats (Ménard et al., 2014). The deleterious effects of marine traffic and noise pollution on odontocetes are well documented (for a review see Weilgart, 2007). Specifically, group cohesion and mother-offspring communication may be negatively compromised in noisy environments (Parijs & Corkeron, 2016; Vergara et al., in prep.), and ship strikes are a potentially deadly threat to all marine mammals in the St. Lawrence Estuary (Ménard et al., 2014; Chion et al., 2018;). If allomothers protect offspring from such threats, we expect that allocare will increase as boat traffic increases.

3.2.1.3 Offspring risk: Male presence

Infanticide by males has been reported in numerous odontocete species (Dunn et al., 2002; Zheng et al., 2016; Bowler et al., 2018; Towers et al., 2018). While infanticide has never been observed among belugas, Loseto et al. (2006) suggest that patterns of sexual segregation among belugas are consistent with a risk of infanticide by males. An increase in allocare in the presence of males would be consistent with a protective function for SLE beluga allocare.

3.2.2 Energetic benefits: Offspring energetic costs

If the primary function of allocare is to increase energetic resources available to offspring, allocare should increase when offspring's energetic costs are high. We considered that offspring's energetic demands should vary as a function of herd movement patterns and tidal phase.

3.2.2.1 Herd movement pattern

Beluga herds present multiple surface movement patterns which can be summarized as "milling", circular movement resulting in low net displacement, "directional" continuous unidirectional movement, and "multidirectional", directional movement with frequent deviations (Lemieux Lefebvre et al., 2017). Travel through water is particularly challenging and energetically costly for cetacean offspring (Noren et al. 2008). As persistent directional movement is synonymous with travel, an increase in allocare during directional movement would suggest that allomothers provide energetic benefits to offspring. By "carrying" offspring during travel, allomothers could considerably reduce energetic costs for recipient offspring (Noren et al., 2008).

3.2.2.1 Offspring energetic costs: Tidal phase

Twice every day, the Saguenay Fjord undergoes dramatic tidally-driven changes which can result in tidal fluctuations reaching 6 m (Belzile, Galbraith, & Bourgault, 2016). During the ebb tidal phase, the Saguenay Fjord's seaward flow can reach up to 1.7e^{4} m^{3}/s (Saucier & Chassé, 2000). However, as the tide rises, the Fjord's seaward surface currents are counteracted by an influx of cold, high salinity water from the St. Lawrence Estuary flowing over a shallow sill at the mouth of the Fjord (Saucier & Chassé, 2000). Simard et al. (2014) have suggested that belugas in the Mackenzie River may exploit the flow tide current to facilitate upstream travel. Similarly, Busque (2006) noted that most beluga arrivals in Baie-Ste-Marguerite occurred during the flow tide, suggesting that belugas prefer to travel from the St. Lawrence to Baie-Ste-Marguerite (a roughly 25 km journey) during the flow tide. Therefore, an increase in allocare during the flow tide phase, particularly in herds travelling directionally, would suggest that allomothers provide energetic benefits to offspring by providing assistance during long distance travel.

3.2.3 Group sociality

If SLE beluga allocare mainly provides offspring with social benefits, we considered that allocare should increase in settings conducive to sociality. We measured group sociality as a function of herd movement pattern (Lemieux Lefebvre et al. 2017) and group size (Sarabia, Heithaus, & Kizska, 2018).

3.2.3.2 Group sociality: Herd movement pattern

"Milling", a herd movement pattern defined as circular movement resulting in low net displacement, is suggested to reflect either feeding or social behaviour (Lemieux

Lefebvre et al., 2017). As milling herds are likely to engage in social behaviour, an increase in allocare in milling herds would be consistent with allocare providing social benefits to offspring.

3.2.3.1 Group sociality: Group size

Sarabia et al. (2018) found that social behaviour in wild bottlenose dolphins, defined by high rates of body contact, play, and sexual behaviours occurred in larger groups than other behaviours such as travel. Although the relationship between group size and social behaviour has not been examined in wild belugas, the similar social structures shared by belugas and bottlenose dolphins (Wells, Scott, & Irvine, 1987; O'Corry-Crowe, 2020) suggest that the frequency of social behaviours among belugas may also increase in larger groups. Therefore, an increase in allocare in larger groups would be consistent with allocare playing a role in the socialization of offspring.

3.2.4 Hypotheses and predictions

Given the changing needs of offspring as they age, we expected that allocare would occur in different conditions for beluga calves and juveniles (Table 3.1). We hypothesized that allomothers mainly provide calves with protection and energetic assistance, and therefore predicted that calf allocare would increase in risky and energetically costly conditions. We hypothesized that juveniles mainly gain social benefits from allocare and predicted that juvenile allocare would increase in highly social situations.

Table 3.1. Predicting how variables measuring offspring risk (boat traffic and male presence), energetic costs (herd movement pattern, tidal phase) and group sociality (herd movement pattern, group size) will impact the occurrence and duration of allocare among St. Lawrence Estuary belugas, based on hypothesized benefits of allocare for calves and juveniles.

Benefit to offspring	Age class	Conditions	Variables	Impact on allocare
Protection	Calf	Offspring risk	Boat traffic	Increase
			Male presence	Increase
Energetic benefits	Calf	Offspring energy costs	Herd mvmt pattern	Increase during directional mvmt
			Tidal phase	Increase during flow tide, particularly during directional mvmt
Social benefits	Juvenile	Sociality	Herd mvmt	Increase during milling herd mvmt
			Group size	Increase

3.3 Methods

3.3.1 Obtaining footage of females with offspring

We collected footage of groups of female belugas with offspring in the Saguenay Fjord, in the Saguenay-St. Lawrence Marine Park in Quebec, Canada using uncrewed aerial vehicles (UAV; Phantom 4 and Phantom 4 Pro, DJI, Shenzhen, China) in the summers of 2016, 2017, and 2018. We recorded footage of belugas from the mouth of the Saguenay Fjord to Baie-Ste-Marguerite (Fig. 3.1). Baie-Ste-Marguerite is a portion of the SLE beluga summer range heavily used by females with young in the summer (Pippard & Malcolm, 1978; Michaud, 1992). During the 2016 and early-2017 field seasons, the UAV was launched from the deck of an 8m rigid hulled inflatable vessel. At the midpoint of the 2017 field season, a stationary UAV launch-tower was constructed in BSM with the goal of eliminating acoustic disturbance caused by the research vessel. Afterwards, all sampling occurred within Baie-Ste-Marguerite. We obtained a total of 156 videos of approximately 15 minutes each.

3.3.2 Ethical note

Our fieldwork methods were reviewed and approved by the Memorial University Animal Care Committee (Animal Use Protocol: 20190640). Our research, and specifically, the use of research UAVs in the Saguenay St. Lawrence Marine Park was covered by research permit SAGMP-2018-28703 issued by Parks Canada and QUE-LEP-001-2018 issued by Fisheries and Oceans Canada. At all times, we maintained the UAV at an altitude greater than 20 m to avoid disturbing the study subjects.

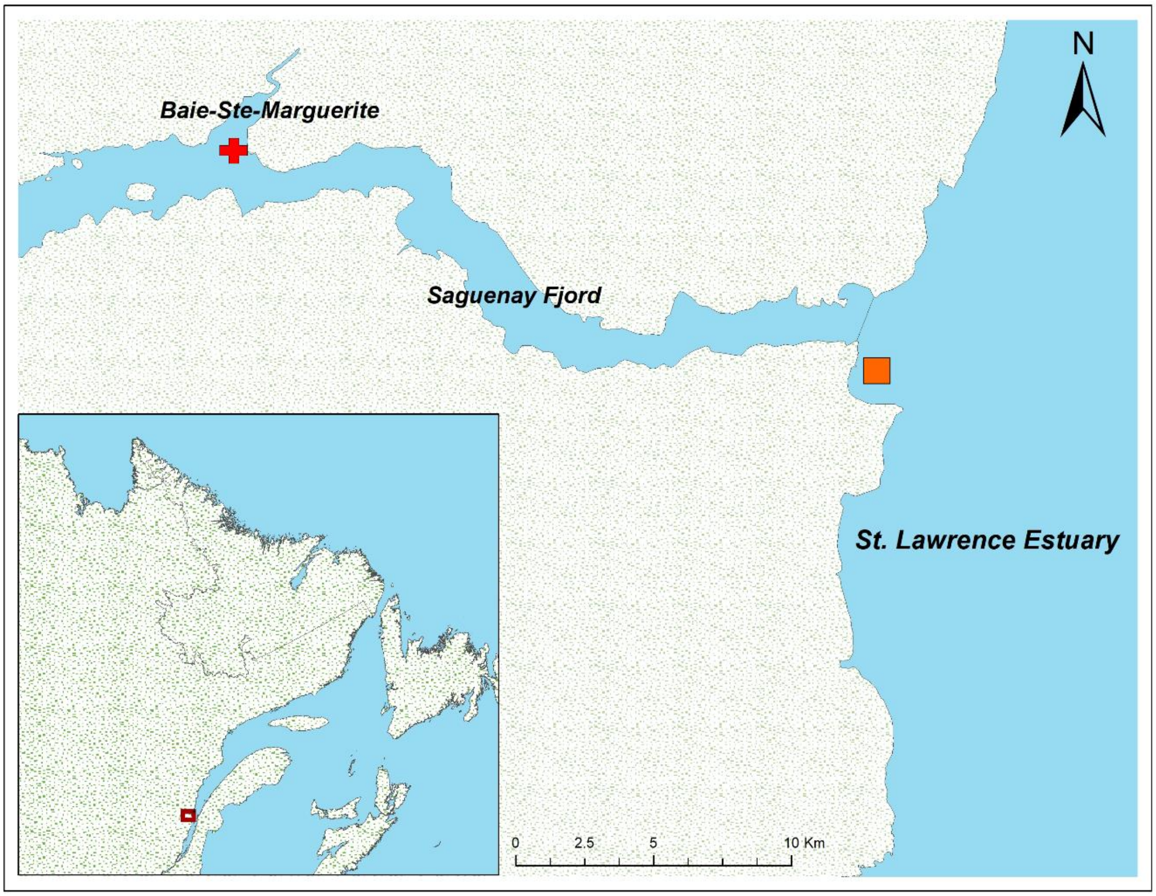

Figure 3.1. Study site in the Saguenay-St. Lawrence Marine park, Quebec, Canada. Sampling occurred from Baie-Ste-Marguerite to the mouth of the Saguenay Fjord in 2016 and 2017. Sampling occurred exclusively in Baie-Ste-Marguerite in 2018. Approximate location of the Baie-Ste-Marguerite research tower shown by red cross. Approximate location of water level readings used to determine tidal phase shown by orange square.

3.3.3 Continuous behavioural focal sampling of offspring

For all beluga offspring in UAV videos, we conducted continuous behavioural focal sampling following Altmann (1974), using the event recorder JWatcher 1.0 (Blumstein & Daniel, 2007). Focal offspring were classified as calves, yearlings or juveniles based on colour, size, and morphology (Fig. 3.2). As our UAV system was not specialized for photo-identification, we were unable to differentiate between individuals. Each new observation of a beluga offspring was recorded as a new focal individual. Each focal follow consisted of the entire duration of time that an offspring remained in sight or could be distinguished from other offspring. We later controlled for resampling of the same individuals by including video and date as random factors in all models. Focal follows lasting less than 10 seconds were discarded.

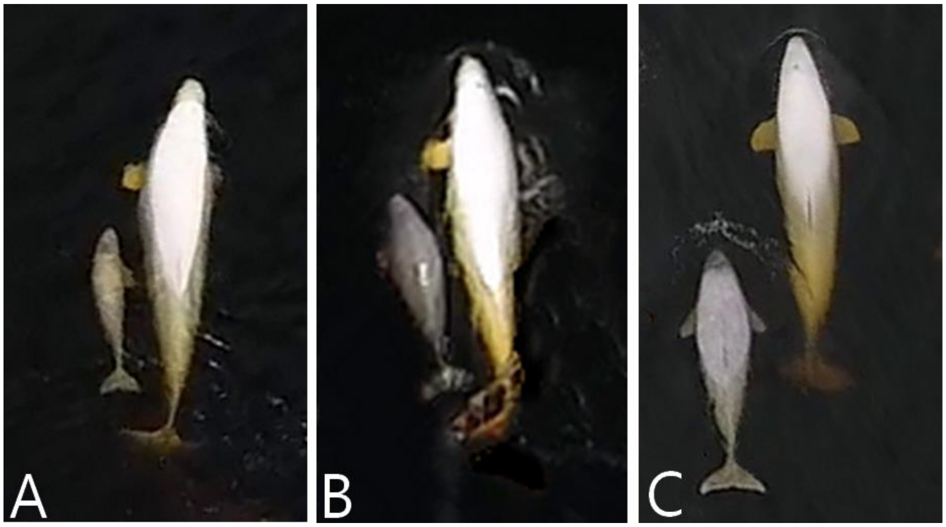

Figure 3.2. Comparing St. Lawrence Estuary beluga offspring age classes relative to adult females. **A)** Calf, approximately one third of adult length, pale brown in colour with pigmentation surrounding blowhole, fetal folds visible behind pectoral fin. **B)** Yearling, approximately half of adult length, dark grey in colour (although some individuals much paler), plump, barrel-like profile. **C)** Juvenile, over half of adult body length, pale grey in colour, tailstock elongated compared to yearling.

3.3.4 Occurrence and duration of allocare

For all focal follows, we recorded the occurrence and duration of allomaternal associations. Following Hill & Campbell (2014), we considered that allocare occurred when offspring swam in formation locomotion with multiple females. In these focal follows, we assigned maternity to the adult female which spent the greatest proportion of time associated with the focal offspring, and defined all other females as allomothers (Gordon, 1987; Hill & Campbell, 2014). Formation locomotion was considered to represent allocare due to energetic costs to allomothers coupled with energetic benefits to offspring (Noren, 2008; Noren & Edwards, 2011). While formation locomotion allocare is defined by its energetic benefits, the physical proximity between allomothers and offspring is also consistent with offspring defense and social interaction. For each focal follow we recorded whether allocare occurred, and when it did, we recorded the duration of the focal follow spent in allocare.

3.3.5 Interobserver reliability analysis

To ensure the reliability of the main observer (JAA), we trained two additional observers to re-analyze a subset of the videos. These observers respectively analyzed 11 and 17 videos, for a total of 28. We then compared their observations to JAA’s observations for all variables of interest. See Appendix B for further details.

3.3.6 Inferring offspring risk, energetic costs, and group sociality

Variables used to estimate offspring risk, offspring energetic costs and group sociality were measured in the field and during video analysis, or retrieved after video analysis.

3.3.6.1 Offspring risk: Boat traffic

During fieldwork, the number of boats within 2 km of the center of the beluga herd was noted approximately every 30 minutes. While 2 km may seem a considerable distance, Erbe (1997) showed that propeller cavitation noise from an ice breaker can mask beluga calls over a radius of 22 km. While no ice breakers were present in the Saguenay Fjord, Erbe (2002) also showed that whale watching boats can mask the calls of orcas (*Orcinus orca*) from up to 14 km away. All focal follows within a video were assigned the boat count nearest in time to the start of the video. When the UAV was launched from a research vessel in 2016 and 2017, the research vessel was included in the boat count. Therefore, all focal follows in 2016 and early 2017 include at least one boat within 2 km of the herd.

3.3.6.2 Offspring risk: Male presence

We devised a method to use qualitative observations to quantitatively assess the presence of male belugas in UAV footage. This method relied on morphological and size differences to differentiate males from females, in addition to cues obtained from group composition and social behaviour (Vladykov, 1944; Smith, Hammill, & Martin, 1994; Glabicky, DuBrava, & Noonan, 2010; O'Corry-Crowe et al, 2020; Appendix C). This method produced a Male Presence (MP) score between 0 (unlikely that males were observed in a video) to 1 (high certainty that males were observed). All focal follows within a video shared the same MP score.

3.3.6.3 Offspring energetic costs & Group sociality: Herd movement patterns

During herd observations in the field, we assessed and noted herd movement patterns approximately every 30 minutes. Following the *Groupe de Recherche et d'Éducation sur* *les Mammifères Marins's* (GREMM) standard sampling protocol, a herd is considered to include all animals within a radius of 2 km and is typically composed of multiple smaller groups. Therefore, herd movement patterns broadly describe the behaviour of multiple groups. Each video was assigned the herd movement pattern (milling, directional, or multidirectional) noted nearest in time to the start of the video.

3.3.6.4 Offspring energetic costs: Tidal phase

Water level measurements were obtained in Baie Ste-Catherine (denoted by orange square in Fig. 3.1) every 15 minutes over the time span of the study (Canadian Hydrographic Service, 2020). These measurements were used to determine the peak high tide and low tide nearest in time to the start of each video. The tidal phase at the beginning of each video was classified as "ebb tide" or "flow tide".

3.3.6.5 Group sociality: Group size

During behavioural analysis, we recorded the number of individuals in each focal offspring's group. A group was defined as all animals within one body length, using chain rule (Smolker et al., 1992). As group size tended to vary over the course of a focal follow, we estimated mean group size for each focal follow. Importantly, herd movement pattern was assessed for the entire herd, and not for the individual groups referred to here.

3.3.7 Constructing the model sets

Using an information theoretic approach, we constructed a series of models incorporating various combinations of the risk, energetic, and social variables described above (Table 3.2). We first used chi-squared tests and regression models to ensure that none of the explanatory variables of interest were correlated. Yearlings were underrepresented in the dataset and did not provide enough data points to construct meaningful models. Using Akaike's Information Criterion (AIC), we ranked all models to determine which fit the data most parsimoniously (Burnham & Anderson, 2002; 2004). We used a two-step approach, first examining which variables influenced the likelihood of allocare occurring, and for cases when allocare did occur, examining variables influencing the duration of allocare. We used scaled allocare duration (by subtracting the mean and dividing each value by the standard deviation) to account for overdispersion in allocare duration. Separate model sets were constructed for each step, for both calves and juveniles, resulting in four model sets.

To control for resampling of focal individuals within the same video and on the same date, we included video and date as random effects, nesting video within date. We also included focal follow duration as an offset, to account for variations in observability of each focal offspring. This was particularly important to account for differences between age classes. Calves typically spend more time at the surface than juveniles, and so we tended to observe more allomaternal associations for calves simply because they were observed for longer. We scaled focal follow duration in all models to account for overdispersion. All model sets included a null model, which incorporated only the random effects and the offset, and a global model, which incorporated the random effects, offset and all fixed variables (Table 3.2).

3.3.8 Testing the models

Here, we used a conservative approach, considering that only models with ΔAIC < 2 showed evidence of explanatory ability (Burnham & Anderson, 2002). We used the obtained ΔAIC to calculate the evidence ratio (ER) of models relative to the top ranked model. For the top ranked models in each model set, we examined the proportion of variance in the data set explained by the fixed effects of each model by calculating marginal R^2 values. We examined the effect sizes for each fixed variable by examining the beta coefficients associated with each variable and their confidence intervals. All analyses were carried out in the R environment (version 3.4.3, R. Core Team, 2013) with packages “lme4” (Bates et al., 2015), “MuMIn” (Barton, 2017), and “sjstats” (Ludecke, 2019).

Table 3.2: Fixed effects, interaction, random effects, and offset included in models for each model set. All models include the video and date as nested random effects and the scaled duration of focal follow as an offset. We included a null model, incorporating no fixed effects, and a global model incorporating all fixed effects. Male Presence (MP) score describes the likelihood that males are present.

	Fixed effects					**Interaction**	**Random**	**Offset**
Model	Boats in 2km	MP score	Herd mvmt	Tidal phase	Group size	Tidal*Mvmt	Video:date	Focal follow duration
Null							X	X
Global	X	X	X	X	X		X	X
Boats + Males	X	X					X	X
Boats	X						X	X
Males		X					X	X
Herd mvmt + Tide			X	X			X	X
Tide				X			X	X
Herd mvmt*Tide			X	X		X	X	X
Group size + Herd mvmt			X		X		X	X
Group size					X		X	X

3.4 Results

3.4.1 Inter-observer reliability analysis

The interobserver analysis suggested that JAA was reliable in identifying the occurrence of allocare and the duration of allomaternal associations. For the 28 videos analyzed, all variables compared showed moderate to excellent agreement between JAA and the two observers. Koo & Li (2016) consider that an intraclass correlation coefficient value lower than 0.5 reflects poor reliability, values between 0.5 and 0.75 represent moderate reliability, values between 0.75 and 0.9 reflect good reliability, and values greater than 0.9 reflect excellent reliability. The lower bound of all our intraclass correlation coefficients 95% confidence intervals were greater than 0.5 and are therefore acceptable under the guidelines above (Table 2.4). For more details, see Appendix A.

Table 3.3 Correlation coefficients with confidence intervals comparing JAA's observations to JB and AKE's observations across a subset of 28 videos. The lower bound of all intraclass correlation coefficient confidence intervals are greater than 0.5 and are therefore considered acceptable by Koo & Li (2016).

Variable of interest	Intraclass correlation coefficient [95% CI]
Association duration	0.91 [0.79, 0.96]
Echelon swim duration	0.84 [0.64, 0.93]
Infant swim duration	0.81 [0.57, 0.91]
Number of calves	0.93 [0.84, 0.97]
Number of yearlings	0.89 [0.77, 0.95]
Number of juveniles	0.81 [0.60, 0.91]
Number of escorts	0.87 [0.71, 0.94]

3.4.2 Response variables

We obtained a total of 369 calf focal follows and 919 juvenile focal follows. We expected to observe more juveniles as this age class includes multiple year-cohorts. On average, calf focal follows lasted 147 seconds and juvenile focal follows lasted 76 seconds. Calves have weak diving abilities compared to juveniles, and therefore spend more time at the surface and are easier to observe. Allocare occurred in 101 calf focal follows (27%) and 123 juvenile focal follows (13%). Once we took focal follow duration (i.e., observability) into account, the difference between calf and juvenile allocare occurrence was insignificant (see Chapter 2). Associations between allomothers and calves lasted on average 30 seconds, with a standard deviation of 42 seconds. Associations between allomothers and juveniles lasted on average 19 seconds, with a standard deviation of 25 seconds.

3.4.3 Explanatory variables

On average, we recorded 1.6 boats within 2 km of the beluga group, but boat count ranged from 0 to 23. We observed 552 focal follows with an MP score of 0, 374 focal follows with an MP score of 1, and 362 with an intermediate MP score. We observed 589 focal follows in herds that were milling, 499 in herds that were multidirectional, and 293 in herds that were directional. Group size ranged from 3 to 52, with an average of 10.7 individuals per group. We observed 640 focal follows during the tidal ebb phase and 717 focal follows during the tidal flow phase.

3.4.4 Model selection: Calf allocare occurrence

Results from AIC analysis show that tidal phase, herd movement pattern, and their interaction best explained the occurrence of calf allocare (Table 3.4). The Tide *Movement model was 10 times more likely than the Tide + Movement model, which did not include an interaction, and 200 times more likely than the Global model. In addition, the Tide*Movement model explained 90% of the marginal variance in calf allocare occurrence (Table 3.5). However, none of the beta coefficients of the model were statistically significant (Table 3.5). It is unusual that, despite explaining a large portion of the variance in the data, the model did not include any statistically significant variables. While this can occur as a result of correlation between explanatory variables, our preliminary Pearson's chi-squared tests showed no correlation between tide state and herd movement pattern ($\chi^2 = 1.4$, $P = 0.51$).

We proceeded to examine the raw data. We found that calf allocare never occurred in herds travelling directionally during the flow tide (Fig. 3.4). Indeed, the proportion of calf focal follows in directionally travelling herds during flow tide in which allocare did not occur (32/268) was significantly different from the proportion of focal follows in which allocare did occur (0/101, $\chi^2 = 11.7$, $P = 0.0006$). For all other combinations of herd movement pattern and tidal phase, we found no significant difference between the proportion of calf focal follows where allocare occurred compared to those where allocare did not occur.

Table 3.4: Top ranked models predicting the occurrence of calf (n = 369) and juvenile (n = 919) allocare and the duration of calf (n = 98) and juvenile (n = 123) allocare in SLE belugas. Top models and models within 2 ΔAIC of the top model are bolded and considered to be equally likely. All models (including the null model) include an offset (focal follow duration), and video (nested within date) as random effects. AIC weight (AIC*w*) represents the probability that a given model is the most parsimonious, while the evidence ratio (ER) compares the strength of evidence of the top model relative to a given model.

	Calf				Juvenile			
	Top 5 models	ΔAIC	AIC*w*	ER	Top 5 models	ΔAIC	AIC*w*	ER
Allocare occurrence	**Tide*Mvmt**	**0.0**	**0.91**	**1**	**Global**	**0.0**	**0.89**	**1**
	Temp + Mvmt	4.7	0.09	10.3	Tide*Mvmt	5.0	0.08	11.9
	Global	10.6	0.01	2.0e2	Tide + Mvmt	6.5	0.04	25.5
	Tide	22.8	0.00	8.9e4	Tide	20.0	0.00	2.2e4
	Mvmt	102.4	0.00	1.7e22	Grp size + Mvmt	136.7	0.00	4.7e29
Allocare duration	**Tide + Mvmt**	**0.0**	**0.59**	**1**	**Tide**	**0.0**	**0.42**	**1**
	Tide*Mvmt	**0.9**	**0.38**	1.6	**Tide + Mvmt**	**0.2**	**0.38**	**1.1**
	Grp size + Mvmt	6.1	0.03	20.6	**Tide*Mvmt**	**1.5**	**0.20**	**2.1**
	Boats	13.6	0.00	8.8e2	Global	10.4	0.00	1.8e2
	Boats + Males	43.4	0.00	2.5e9	Null	29.2	0.00	2.1e6

Table 3.5. Top ranked models predicting calf allocare occurrence and calf and juvenile allocare duration in SLE belugas. Conditional R^2 (cR^2) considers the proportion of variance explained by both fixed and random effects, while marginal R^2 (mR^2) considers only fixed effects. Note that the confidence intervals of all β coefficients overlap zero and are therefore not statistically significant.

Response variable		**Top model**	**mR^2**	**cR^2**	**Fixed effects**	**β**	**95% CI**
Allocare occurrence	Calf	Tide*Mvmt	0.90	0.91	Flow/milling (intercept)	-1.09	[-2.3, 0.14]
					Ebb	0.11	[-1.4, 1.6]
					Multidirectional	-0.57	[-2.1, 1.0]
					Directional	-17.6	[-585.6, 550.4]
					Ebb/multidirect.	0.66	[-1.2, 2.6]
					Ebb/milling	18.0	[-550.0, 586.1]
Allocare duration	Calf	Tide + Mvmt	0.02	0.07	Flow/milling (intercept)	-0.29	[-0.92, 0.34]
					Multidirectional	0.22	[-0.43, 0.86]
					Directional	0.44	[-0.31, 1.19]
					Ebb	0.04	[-0.62, 0.71]
	Juvenile	Tide	0.02	0.02	Flow (intercept)	-0.29	[-0.69, 0.11]
					Ebb	0.34	[-0.18, 0.80]

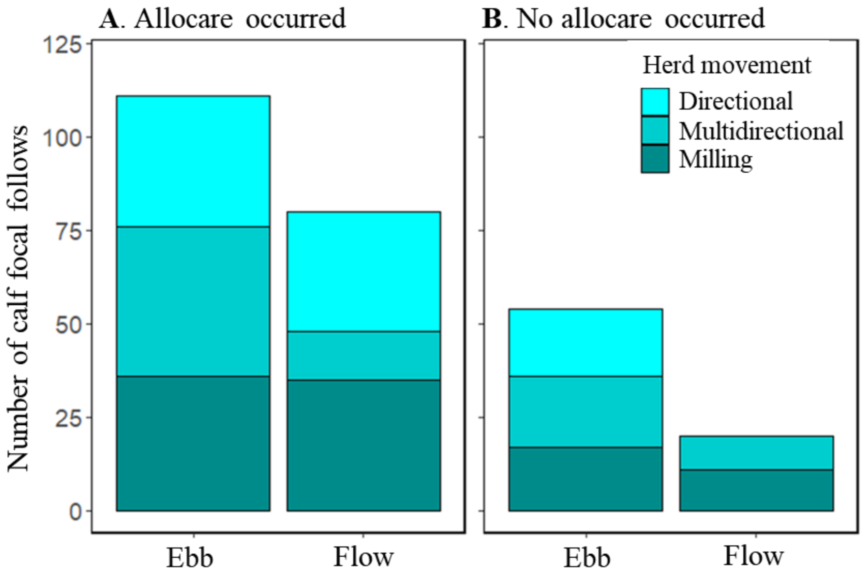

Figure 3.3. Number of calf focal follows in each combination of herd movement and tidal phase. Panel A shows focal follows where allocare occured and panel B shows focal follows where allocare did not occur. Calf allocare never occurred in herds travelling directionally during the flow tide, revealing a significant difference between focal follows where allocare did and did not occur (χ2 = 11.7, P = 0.0006). For all other combinations of herd movement pattern and tidal phase, we found no significant difference between the proportion of calf focal follows where allocare occurred compared to those where allocare did not occur.

3.4.5 Model selection: Juvenile allocare occurrence

Our analysis shows that the Global model best explained the occurrence of juvenile allocare (Table 3.4). The Global model performed 12 times better than the Tide*Movement model, 25 times better than the Tide+Movement model, and 2200 times better than the Tide model. Since no model outperformed the Global model, we conclude that none of the variables examined can explain patterns of juvenile allocare occurrence in a satisfactory manner.

3.4.6 Model selection: Calf allocare duration

The Tide+Movement model and the Tide*Movement model outcompeted all other models in explaining the duration of calf allocare (Table 3.4). The Tide+Movement model was 1.6 times more likely that the Tide*Movement model, suggesting that the interaction term included in the Tide*Movement model was not particularly informative. However, the Tide+Movement model only explained 2% of the marginal variance in calf allocare duration (Table 3.5). In addition, the confidence intervals of all beta coefficients overlapped zero, suggesting that none of the variables tested were statistically significant (Table 3.5).

3.4.7 Model selection: Juvenile allocare duration

For juveniles, allocare duration was best explained by the Tide model, the Tide+Movement model, and the Tide*Movement model (Table 3.4). Since all three models include the tidal phase variable, it’s likely that the herd movement variable and the interaction term did not contribute much to the explanatory power of the models. The Tide model was 180 times more likely than the Global model. However, the Tide model only explained 2% of the marginal variance in the juvenile allocare duration, and none of the explanatory variables appear significant upon examination (Table 3.5).

3.5 Discussion

We hypothesized that St. Lawrence Estuary beluga calves and juveniles receive different benefits from allocare: protective and energetic benefits for calves, and social benefits for juveniles. We found that calf allocare never occurred in herds travelling directionally during the flow tidal phase, contrary to our prediction that calf allocare would increase in herds traveling directionally and during the flow tide. Indeed, none of our predictions were met. Calf allocare did not increase in risky and energetically costly contexts, and juvenile allocare did not increase in contexts conducive to sociality. This suggests that allocare among belugas is not primarily driven by its benefits to offspring, or that we were unable to adequately measure variables related to offspring risk, energetic costs, and group sociality. Overall, our findings failed to explain broader patterns of allocare, but offered some insight into the role that beluga allomothers might play.

3.5.1 Offspring energetic costs

We found evidence that herd movement pattern and tidal phase influenced the likelihood of calf allocare. Indeed, calf allocare never occurred in herds traveling directionally during the flow tidal phase. Based on the hypothesis that beluga allomothers provide energetic benefits to calves, we predicted that calf allocare would increase during directional herd movement. Our findings do not align with this prediction. Crucially, we found that it was specifically the interaction between herd movement pattern and tidal phase which influenced the likelihood of calf allocare. Due to the hydrological characteristics of the Saguenay Fjord (Saucier & Chassé, 2000; Belzile et al. 2016), it is energetically advantageous for belugas to restrict their upstream movements to the flow tidal phase. Due to this limitation, herds moving directionally during the flow tide are likely to be travelling up the Saguenay Fjord to Baie-Ste-Marguerite, an approximately 25 km journey. Therefore, we predicted that allomothers would be more likely to care for calves during the flow tide, particularly in herds traveling directionally. However, we found that allomothers never provided care to calves during the flow tide in herds moving directionally. This finding suggests that calves rely primarily on their mothers during travel, rather than receiving energetic assistance from allomothers. Additionally, while tidal phase and herd movement patterns influenced whether or not calf allocare occurred, we did not find strong evidence that it impacted the duration of calf allocare, nor the occurrence and duration of juvenile allocare.

3.5.2 Offspring risk

3.5.2.1 Boat traffic

We detected no relationship between the number of boats sharing space with belugas and the occurrence or duration of allocare. We predicted that calf allocare would increase with boat traffic, due to a risk of communication disruption and boat strike, but we observed no such trend. Alternately, we might also have predicted that allocare would decrease when boat traffic increased. While allomothers sometimes protect the offspring of others against threats, even an experienced allomother may not be as protective as an offspring's own mother. This may explain why, in some species such as yellow baboons (*Papio* *cynocephalus*), mothers only allow allocare to occur once offspring survive the highly vulnerable neonatal period (O'Brien & Robinson, 1991). However, we detected no relationship, neither positive nor negative, between the number of boats sharing space with belugas and the occurrence or duration of allocare.

While it is possible that the belugas in this study were habituated to such disturbances, boat traffic is known to negatively impact cetaceans in general, and SLE belugas specifically. Scheifele et al. (2005) found that SLE belugas increase the amplitude of their calls to compensate for increased noise levels, an indication of a first-order response to acoustic disturbance. In addition, Blane & Jaakson (1994) showed that SLE belugas spend more time underwater and increase their speed to avoid boats, and that these reactions become more acute as boat traffic increases. Boat traffic is also known to negatively impact foraging and social cohesion in belugas and other odontocetes (Finley & Davis, 1984; Aguilar Soto et al., 2006; Parijs & Corkeron, 2016). While our findings suggest no link between allocare and disturbance by boats, they certainly show a high degree of disturbance. We noted that, during one particular focal follow, 23 boats were recorded within 2 km of the herd. Given the ease with which sounds travels through water, our findings highlight the intensity of acoustic disturbance experienced by belugas in Baie-Ste-Marguerite and the Saguenay Fjord. Unfortunately, these areas could see a large increase in marine traffic in the near future. Three industrial port development projects are currently in final stages of development (BlackRock Metals Inc., 2018; Arianne Phosphate, 2019; Énergie Saguenay, 2019), with two new marine terminals planned in the upstream section of the Saguenay Fjord. These new terminals are expected to triple shipping traffic in the Saguenay Fjord (DFO, 2018).

3.5.2.3 Offspring risk: Male presence

Contrary to our predictions, we failed to find a relationship between male presence and the occurrence or duration allocare. We predicted that calf allocare would increase in the presence of males, reflecting possible risks of infanticide. Alternately, we could have predicted that mothers would tend to keep calves closer in the presence of males, leading to a reduction in allocare. However, neither prediction is supported by our findings. Among both belugas and bottlenose dolphins, female habitat selection is consistent with avoidance of males, possibly due to risks posed by infanticidal males (Michaud, 2005; Loseto et al., 2006; Galezo et al., 2017). While infanticide undoubtedly occurs among odontocetes (Dunn et al., 2002; Towers et al., 2018), further investigation of odontocete male behaviour suggests that males also have many neutral and positive interactions with offspring. Male bottlenose dolphins associate with calves in captivity (Levengood & Dudzinski, 2016) and occasionally in the wild (Mann & Smuts, 1999). While males may sometimes present a risk to offspring, infanticide may be a relatively rare event rather than a constant threat.

3.5.3 Group sociality

3.5.3.1 Herd movement pattern

We hypothesized that allocare provides juvenile belugas with social benefits, and therefore predicted that juvenile allocare would increase in highly social contexts. As our data collection did not include any explicit measures of social behaviour, we used herd movement patterns and group size as measures of group sociality. Because the herd movement pattern defined as “milling” has been associated with social behaviour

(Lemieux Lefebvre et al. 2017), we predicted that juvenile allocare would increase in herds engaged in milling. However, we found no relationship between milling movement patterns and patterns of allocare, for neither calves nor juveniles.

3.5.3.1 Group size

Under the hypothesis that allocare provides juveniles with social benefits, we also predicted that juvenile allocare would increase as a function of group size. Social behaviours among belugas and other odontocetes typically include such behaviours as body contact, rubbing, play, and socio-sexual behaviour (O'Corry-Crowe et al. 2009). In a study on wild bottlenose dolphins in the Florida coastal Everglades, Sarabia et al. (2018) found that socializing groups were significantly larger than traveling groups (although not significantly larger than foraging groups). We found that group size had no impact on the occurrence or duration of allocare for neither juveniles nor calves.

It is possible that measuring group size did not provide a sufficient proxy for group sociality in belugas. Halteman & Ryan (2019) found that the frequency of social behaviours in a captive beluga group increased when a new male was added to a group composed of two females and one male. However, the frequency of social behaviours remained high when a female was subsequently removed from the group, suggesting that group composition may be more important than group size in modulating social behaviour among belugas. It remains unclear, however, to what degree the social dynamics of artificially formed captive groups reflect the social dynamics of free-living belugas.

It is nonetheless noteworthy that allocare did not increase as a function of group size. While increasing group size might increase the frequency of social behaviours, it also undoubtedly increases the number of available allomothers. Across taxa, sociality is heavily structured by kinship and familiarity, particularly in social species characterized by long-term bonds such as social odontocetes (Wiszniewski, Lusseau, & Möller, 2010; Wizniewski, Brown, & Moller, 2012; Titcomb, O'Corry-Crowe, & Hartel, 2015). One study of captive dolphins showed that calves with greater access to kin were more social than calves in groups with fewer relatives (Levengood & Dudzinski, 2016). In sperm whales, allomothers preferentially associate with the offspring of closely related, or reciprocally cooperative group members (Gero, Gordon, & Whitehead, 2013; Konrad, Frasier, Whitehead, & Gero, 2018). Our finding that allocare did not increase with group size suggests that beluga allomothers are similarly choosy about the offspring they care for, perhaps selecting recipient offspring based on kinship or familiarity with mothers.

3.5.4 Allocare as maternal relief

As we were unable to determine any potential benefits of allocare to beluga offspring based on environmental and social variables, we suggest that beluga allomothers may be more concerned with the needs of mothers than the needs of offspring. Indeed, maternal care is extremely energetically costly, and offspring are cumbersome. Offspring may hamper their mother's foraging attempts, preventing them from attaining optimal nutritional intake (Stanton et al., 2011). Among sperm whales, females stagger their foraging dives to ensure that vulnerable calves are never left alone at the surface (Whitehead, 1996). While dive staggering provides protective benefits to sperm whale calves, it also permits their mothers to forage more freely. We also suggest that allomothers might provide relief to mothers by caring for offspring during weaning conflict, although this hypothesis has never been explicitly tested. Regardless of the exact mechanism involved, maternal relief can strongly impact reproductive output. In species with high levels of allocare, offspring tend to grow rapidly and wean at an early age, possibly leading to reduced interbirth intervals and enhanced maternal fitness (Ross & MacLarnon, 2000). Among vervet monkeys (*Chlorocebus pygerythrus*), mothers that received help from allomothers had shorter interbirth intervals than mothers that did not benefit from allocare (Fairbanks, 1990).

These benefits can resonate across evolutionary timescales. Despite a famously protracted period of offspring dependence, humans have much shorter interbirth intervals than other great apes, likely due to the ubiquity of allocare in child-rearing (Sear & Mace, 2008; Blaffer Hrdy, 2011). From an evolutionary perspective, these maternal fitness benefits may dwarf the protective, energetic, and social benefits of allocare for offspring. Rather than responding to contexts impacting offspring, allomothers may instead respond to the needs of mothers. If a mother needs to forage to maintain her milk supply, or requires assistance during weaning conflict with her offspring, an allomother may provide care, regardless of the risk, energetic, or social conditions involved. Further exploring SLE beluga allocare through the lens of maternal benefit may provide insights which offspring benefit could not provide.

3.6 Conclusions and future directions

We found that tidal phase and herd movement patterns partially explained the occurrence of allocare among SLE beluga calves. Indeed, we noted that allocare never occurred in herds moving directionally during the flow tidal phase. However, none of the variables examined adequately explained calf allocare duration, nor patterns of juvenile allocare. Our hypothesis that calves received energetic and protective benefits from allocare, while juveniles received social benefits, was not supported. During energetically costly activities such as travel, calves seem to rely primarily on their mothers rather than receiving assistance from allomothers. We have successfully ruled out many plausible variables which may have impacted allocare in this population. We found that the frequency of allocare was not impacted by boat traffic nor the presence of males. Our findings also show that the frequency of allocare does not increase with group size, suggesting that allomothers may be choosy about which offspring they provide care to. Future work should focus on exploring the benefits of allocare for mothers and investigating how social and genetic relationships structure patterns of allocare among St. Lawrence Estuary belugas.

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CHAPTER 4: CONSERVATION AND BEHAVIOURAL ECOLOGY FOR AT-RISK ANIMAL POPULATIONS

4.1 Introduction

St. Lawrence Estuary (SLE) belugas are a geographically isolated, genetically distinct population (Gladden et al., 1999) listed as endangered under the Species at Risk Act (COSEWIC, 2014). As residents of the St. Lawrence, these belugas have suffered increasing anthropogenic disturbance over the past several centuries. Human impacts on the riverscape include a legacy of overexploitation and environmental contamination, intensive development of the shoreline, and high densities of marine traffic (Pippard, 1985; Martineau et al., 2002; DFO, 2014). Efforts to protect the SLE beluga population have been ongoing since the 1980s (DFO, 1990). Through various measures, the impacts of older contaminants have been mitigated, only for new toxins to appear in beluga tissues (Lebeuf et al., 2014; Simond et al., 2017). While a high prevalence of tumours and lesions once represented the principal health concern for the population, perinatal complications and elevated neonate mortality have recently arisen as conspicuous obstacles to population recovery (Martineau et al., 1994; Lair, Martineau, & Measures, 2014; Lesage et al., 2014). Such complications may be caused by elevated contaminant loads in gestating females and their offspring (Gauthier et al., 1998; Lesage et al., 2014), an environmental regime shift (Plourde et al., 2014), algal blooms (Starr et al., 2017), disturbance from marine traffic (Ménard et al., 2014), or a combination of multiple factors. High rates of perinatal mortality among reproductive females are incompatible with population recovery (Mosnier et al., 2014). Recognizing the sensitivity of this segment of the population, research interests have recently focused on the behavioural ecology of beluga females and their dependent offspring.

4.2 Chapter 2 summary

Using footage of groups of females with young, I examined the occurrence of allocare, or cooperative offspring care, among SLE belugas. Allocare had previously been anecdotally reported in wild beluga populations (Bel’kovitch & Sh’ekotov, 1990, Krasnova et al., 2009) and observed in captive belugas (Leung et al., 2010; Hill & Campbell, 2014). My work represents the first quantification of allocare in a wild beluga population. In addition to confirming that SLE belugas care for offspring cooperatively, I examined the evolutionary drivers of allocare in this population. Allocare poses an evolutionary enigma: why should animals expend time and energy caring for the offspring of others? The answer to this question varies across taxa. Among bottlenose dolphins (*Tursiops* spp.), allocare is driven by the need for young females to acquire parenting skills (“learning-to-parent”) and an indiscriminate attraction towards infants (“natal attraction”) (Mann & Smuts, 1998). In contrast, allocare in sperm whales (*Physeter macrocephalus*) is best explained by kin selection and reciprocation (Gero, Gordon, & Whitehead, 2013; Konrad et al., 2018).

By examining the age classes of allomothers, we found evidence to refute the learning-to-parent hypothesis for this population. From a total of 309 allomaternal association observed, only 9 (2.9%) involved subadult allomothers. Statistical testing showed that this difference was unlikely to have arisen by chance ($\chi^2 = 544.3$, $P <$

0.0001). Because individuals identified as adults were likely to have previously reared calves, these allomothers were unlikely to see any benefit from participating in allocare as a parenting exercise (Fairbanks, 1990).

By examining the relationship between offspring age and allomaternal investment, we further refuted the learning-to-parent hypothesis and provided evidence refuting the natal attraction hypothesis. When examining maternal associations, we found that mothers spent less time in association with older offspring, and replaced a high-cost care behaviour (echelon swimming) with a low-cost care behaviour (infant swimming). This pattern reflects the expected pattern of decreasing maternal investment with offspring age (Trivers, 1972). However, we detected no such pattern for allomaternal investment. Neither the duration of allomaternal associations, echelon swimming, nor infant swimming varied significantly with offspring age class. The learning-to-parent hypothesis predicts that most recipients of allocare will be infants, as this represents the most crucial learning period for immature females gaining parenting skills (Mann & Smuts, 1998). Similarly, the natal attraction hypothesis predicts that most recipients of allocare will be infants, due to the influence of natal traits of female behaviour (Bădescu et al., 2015).

As we were unable to refute the kin selection and reciprocation hypotheses, we suggest that SLE beluga females likely provide allocare to relatives, or as a form of reciprocation. Our findings hint at the cooperative nature of female beluga societies. Findings from Arctic populations suggest that belugas sociality may be structured by maternal kinship (Colbeck et al., 2013), consistent with the kin selection hypothesis. Recent findings show that belugas (along with orcas, short-finned pilot whales, and humans) are one of few species with female post-reproductive lifespans (i.e., menopause: Marsh & Kasuya, 1984; Ellis et al., 2018). In the context of allocare, these findings suggest the opportunity to test how grandmothers contribute to the welfare of offspring in a non-human animal (Hawkes et al., 1998; Johnstone & Cant, 2010).

4.3 Chapter 3 summary

In the second chapter of this thesis, I explored how offspring benefit from allocare. Both the kin selection and reciprocation hypotheses imply that mothers, offspring, or both, will receive fitness benefits from allocare. In the case of kin selection, this benefit occurs due to the genes shared by allomothers, mothers, and offspring (Hamilton, 1964; Konrad et al., 2018). Alternately, when reciprocation drives allocare, allomothers are expected to provide benefits with the goal of receiving reciprocal compensation (Trivers, 1971; 2006). In Chapter 2, I showed that allocare among SLE belugas may be driven by kin selection and reciprocation. In addition, I found that allomaternal investment did not vary across offspring age classes. Beluga calves are relatively altricial at birth but gain some independence after reaching one year of age (Krasnova et al., 2009). This suggests that allocare directed towards calves might serve a different function than allocare directed towards juveniles. Specifically, I hypothesized that calf allocare would occur in risky or energetically costly conditions, while juvenile allocare would occur in socially conducive conditions.

I used environmental and social variables measured in the field or during video analysis, and categorized these variables as relating to risk (presence of males, boat traffic), energetic costs (herd movement pattern, tidal phase), and social context (herd movement pattern, group size). I predicted that calves, the youngest age class, would receive more allocare in risky and energetically costly conditions, reflecting the protective and energetic benefits of allocare. In contrast, I predicted that juveniles, the oldest dependent age class, would receive more allocare in highly social conditions, reflecting the social benefits of allocare for older offspring. I used these variables to model the occurrence and duration of allocare and used the Akaike Information Criterion (AIC) to assess which models best fit the data.

I found that patterns of calf allocare were influenced by tidal phase and herd movement pattern. Indeed, calf allocare never occurred in herds travelling directionally during the flow tide. As directional movement during the flow tide is consistent with upstream travel, this finding ran contrary to our prediction that calf allocare would increase in energetically costly conditions. Rather, this finding suggests that calves are more likely to rely on mothers for assistance during travel. However tidal phase and herd movement pattern did not seem to influence calf allocare duration, nor any patterns in juvenile allocare. None of the other variables tested influenced patterns of allocare in calves and juveniles, suggesting that patterns of allocare among belugas may not be driven by protective, energetic, or social benefits for offspring.

Indeed, I may have failed to measure the most important variables predicting the occurrence and duration of allocare in this population. For example, if allocare among SLE belugas is kin selected, allocare may only occur within highly related social groups. Similarly, reciprocal allocare may only occur in conditions conducive to reciprocation. Therefore, occurrence of allocare may depend more on the presence of suitable allomothers than on any other environmental or social conditions. It is also possible that I did not have sufficient data to make robust assessments about conditions conducive to allocare. Alternately, it is possible that the occurrence of allocare in SLE belugas is more strongly tied to maternal benefit than offspring benefit. Further investigations of allocare in belugas should consider maternal relief as a possible motive for allomothers.

4.4 Behavioural ecology and conservation

Over the past twenty years, many have called for increased integration of the fields of animal behaviour and conservation (Curio, 1996; Caro, 1999; 2007). For various reasons, this nascent field, termed “conservation behaviour” has failed to be widely embraced (Caro & Sherman, 2013; Fernández-Juricic & Schulte, 2016). While behavioural studies of at-risk population might be considered impractical and unnecessary, an in-depth understand of a population’s behavioural ecology is crucial to developing effective conservation strategies (Buchholz, 2007). Here, we provide two examples where knowledge of animal behaviour was successfully integrated into conservation decision-making.

Semel, Sherman, & Byers' (1988) findings on wood duck (*Aix sponsa*) egg-dumping provide a classic example of how behavioural ecology must be considered in conservation decisions. The authors found that installing highly visible nest boxes lead to increased nest abandonment and decreased hatching success, due to the wood duck’s propensity for nest parasitism. Cryptic nest boxes at low densities, however, were found to decrease egg dumping and favour hatching success. Thanks in part to these efforts, wood duck populations are now thriving. More recently, Shier (2006) found that preserving family groups during translocation of black-tailed prairie dogs resulted in improved outcomes for this special concern keystone species. Black-tailed prairie dogs that were translocated as part of a family group were five times more likely to survive one-year post-release and had higher reproductive fitness than individuals translocated with unrelated individuals.

In both these cases, a consideration of a population's behavioural ecology, egg-dumping among wood ducks, and social bonding in black-tailed prairie dogs, was essential to the development of effective conservation strategies. Of course, there are considerable gaps in our understanding of the behavioural ecology of many animals. Cetaceans, as large, highly mobile animals living in a hostile (to us) environment, pose unique challenges for behavioural studies (Nowacek et al., 2016). Like many management decisions, those involving SLE belugas must often be made without a definitive understanding of many aspects of their behavioural ecology, but rather using the best available information.

4.5 Relocation of stranded beluga calves

Over the past four years, five live strandings of newborn beluga calves have been reported in the St. Lawrence Estuary (DFO, 2018a). Of these five, three were recovered from the shoreline and rapidly relocated to groups of females with offspring, in hopes that the infant would be adopted and survive. Unfortunately, the fate of these animals is unknown, as post-release tracking was limited. Recently, the Department of Fisheries and Oceans (DFO, 2018a) issued an advisory report stating that future calf strandings will result in euthanasia rather than attempts at relocation. This decision rests on two main points. First, that the likelihood of relocations resulting in successful adoptions is nil. In order to survive, calves must resume nursing within hours of relocation, in addition to surviving the physiological stress of stranding and relocation (Hammill & Lesage, 2018). Therefore, euthanasia is suggested as the only reasonable solution. Second, it was determined that, even if successful, such interventions are irrelevant to the recovery of the population. DFO (2018a) found that 12 to19 stranded calves would need to be successfully relocated and adopted every year to halt the decline of the population.

While orphan adoption is rare in nature, it has been reported in over 120 mammal species (Riedman, 1982). Riedman (1982) suggests that the mechanisms driving adoption are similar to those driving allocare. While adoption has never been observed among wild belugas, one study reports spontaneous lactation and allonursing in a captive group. When a captive female gave birth, her two tankmates, a daughter and an unrelated female both spontaneously lactated and nursed her calf (Leung et al., 2010). However, as spontaneous lactation does not occur instantaneously (Ridgway et al., 1995), a stranded beluga calf would need to nurse from a previously lactating female. Beluga offspring are typically weaned between 1.5 and 3 years of age, with most offspring consuming both milk and prey items during the second year of life (Matthews & Ferguson, 2015). Therefore, any given group of females is likely to include many lactating females with offspring at various stages of development. Carcasses of SLE belugas show that some females continue to lactate until 63 years of age, despite the fact that no pregnancies have been observed in animals older than 51 (Lair et al., 2014). This suggests that post-reproductive females may allonurse the offspring of others or continue to nurse their mature offspring.

These observations, along with my documentation of allocare in the SLE beluga population, suggest that orphan adoption may be consistent with the behavioural ecology of belugas. Counter to DFO's assessment, I suggest that stranded calf relocations may be successful, given ideal conditions.

Population modelling supports DFO's assessment that, even if successful, orphan relocations are extremely unlikely to contribute to the recovery of the SLE beluga population (Hammill & Lesage, 2018). As a late maturing species with relatively high first-year mortality, a rescued beluga calf would still need to survive until sexual maturity to contribute to the recovery of the population (Mosnier et al., 2014). However, I suggest that population recovery should not be the only factor considered when intervening on behalf of individuals from at-risk populations.

According to Hammill & Lesage (2018), previous relocation efforts were not motivated by population conservation issues, but rather out of concern for the welfare of individual animals. When wild animals are harmed by human activities, many argue that we have a moral obligation to intervene. Whether this intervention results in relocation or euthanasia should be carefully determined based on risks and benefits, with a strong consideration for individual welfare (Moore et al., 2007). While the direct cause of calf strandings has not been determined, human impacts on the SLE beluga population suggest that humans are likely at fault, either directly or indirectly (Martineau et al., 2002; Lair et al., 2014; Lesage et al., 2014; Ménard et al., 2014). Therefore, if relocation of stranded calves carries a reasonably high chance of success, relocation may be warranted, regardless of its impact on the population's recovery.

If relocation is in the best interest of stranded calves, other potential benefits arise. Notably, future strandings would provide the opportunity to investigate orphan adoption in a wild cetacean. If we hypothesize that orphan adoption occurs in species with behavioural traits such as allocare, spontaneous lactation, and delayed weaning, then future relocations of stranded calves offer a natural experiment to test this hypothesis. Documenting an orphan adoption in a wild cetacean population would provide insight into offspring care and altruism in socially and cognitively complex mammals.

Relocating stranded calves could also indirectly benefit the population by increasing public awareness of current threats facing SLE belugas. As charismatic megafauna, belugas capture the public imagination in a way that few other species can. However, despite professing appreciation for SLE belugas, the Canadian public has shown minimal concern towards recent industrial port developments which threaten their survival. The planned construction of two new marine terminals is expected to triple marine traffic in the Saguenay Fjord, increasing acoustic disturbance in a sensitive portion of beluga habitat (DFO, 2018b). This is particularly concerning, as underwater noise has been linked to reproductive suppression in cetaceans (Wright et al., 2007, Nabi et al., 2018). In addition, these developments will place belugas and other marine species at risk of toxic spills (DFO, 2018b). In the past, calf relocations in the St. Lawrence Estuary have garnered considerable public interest. In 2014, CBC’s *The Nature of Things* produced a documentary entitled “Call of the Baby Beluga”, which examined the attempted relocation of a stranded female calf. Future calf relocations would provide the opportunity to engage the public in a compelling narrative contextualizing the ongoing plight of the population. Public action on behalf of SLE belugas, and other sympatric species in the St. Lawrence Estuary will likely be favoured when the public are exposed to images of a vulnerable individual in distress.

4.6 Limitations

The methods we employed constrained us to make certain assumptions in our interpretations. While the studies described in Chapters 2 and 3 boast a reasonably large sample size, it is important to note that a sample size of 1500 focal follows is not equivalent to 1500 animals sampled. Except in rare cases, it was impossible to assign multiple focal follows to a single offspring. The resolution offered by the uncrewed aerial vehicle's (UAV) camera did not allow for photoidentification of most individuals. As belugas rarely remain visible in UAV footage for longer that a few minutes, individuals were inevitably resampled within the same video. Animals were also likely resampled over the course of each summer, and possible across years as well. To help control for re-sampling within videos and days, we included video and date as random effects in all our models. We also analyzed the frequency of relocation of photo-identified individuals (Appendix A), which suggested that we did resample the same small group of animals on each sampling day.

Another limitation of these studies was that we were unable to positively identify mother-offspring relationships from UAV footage. We operated under the assumption that a focal offspring's "main adult escort", the adult female with whom the offspring spent most of a focal follow, was its mother. Additional adult escorts were identified as allomothers under the assumption that offspring should spend more time with their mother than with allomothers. It should be noted, however, that Konrad et al. (2018) found that this assumption does not always hold true for sperm whale allocare: in one case, a sperm whale calf's "main escort" was genetically ruled out as its mother. Such cases, however, are likely rare in nature. We validated our assumptions for a single highly recognizable mother-offspring pair, but this single case does not necessarily mean that our assumptions correctly identified all mothers. Therefore, we were conservative in identifying allomaternal associations and may have underestimated the relative importance of allocare in beluga societies.

While we were unable to refute the kin selection and reciprocation hypotheses for allocare, this does not amount to strong evidence for these hypotheses. To provide strong evidence of the kin selection hypothesis, we would need to demonstrate that allomothers and recipient offspring share more genes than expected by chance. We would also have to demonstrate that recipient offspring have improved fitness, resulting in inclusive fitness benefits for allomothers. To provide strong evidence for the reciprocation hypothesis, following Gero et al. (2009), we would require multi-year data on the identity of mothers and allomothers to verify whether individuals engage in reciprocation. Unfortunately, these goals were outside of the scope of this project.

4.7 Future directions

Our findings provide insight to the cooperative nature of female beluga societies. However, to further expand our ability to test hypotheses on the behavioural ecology of belugas, future studies should pair visual behavioural monitoring with acoustic monitoring and genetic analysis. Belugas are a highly acoustic species, relying on sound to navigate their environment, detect prey, and communicate with conspecifics (Turl, 1998). Studies using only visual data are therefore limited in their ability to draw inferences on beluga behaviour. In addition, without genetic data, evolutionary questions relating to kin selection and fitness can only be addressed peripherally.

Further work on SLE belugas should focus on examining the social behaviour and space use of females in the population. Reproductive females are a particularly sensitive segment of the population, yet we know very little about their social structure and fine-scale space use (Mosnier et al., 2014). Evidence suggests that belugas employ individually or group-specific vocal signatures (Morisaka et al., 2013; Mishima et al., 2015; Vergara & Mikus, 2019). These vocal signatures may be transmitted from mothers to offspring through vocal learning (Vergara & Barrett-Lennard, 2008). By acoustically monitoring distinctive signature calls across the range of SLE belugas, we will gain insight on the social structure and ranges of groups of females.

By constructing a catalogue of distinctive signature calls through acoustic and visual monitoring, we could develop a passive acoustic monitoring tool for SLE belugas similar to those used to monitor orca (Holt, Noren, & Emmons, 2013) and bottlenose dolphin (Gerstein et al., 2011) populations. Compared to other survey methods, passive acoustic monitoring is extremely cost-effective, and can provide exceptionally fine-scale data for population monitoring. By continuing to promote the union of conservation and behavioural ecology, we may yet provide the tools and knowledge needed to ensure the survival of St. Lawrence Estuary belugas.

4.8 Thesis summary

Allocare challenges our understanding of how animals should allocate their time and energy. My research represents the first in-depth investigation of allocare in wild belugas. By examining patterns of allocare, I sought to understand why beluga allomothers provide care to the offspring of others. My findings suggest that allocare in St. Lawrence Estuary belugas may be driven by kin selection and reciprocation. Some aspects of beluga life history hint at the importance of maternal kinship. Belugas are one of few species with post-reproductive female lifespans (Ellis et al., 2018), suggesting that grandmothers may play an important role as caregivers. The discovery that post-reproductive females can continue to lactate (Lair et al, 2014) suggests that allocare from grandmothers could be extensive. In addition, observations of high relatedness within female groups support the kin selection hypothesis (Colbeck et al., 2013). Alternately, reciprocation may occur between both kin and familiar non-kin. As long-lived and highly social animals, belugas likely form long-lasting, strong social bonds with both kin and non-kin (O’Corry-Crowe et al., 2020).

I also investigated potential benefits of allocare for offspring by examining variables associated with variation in offspring risk, energetic costs, and group sociality. None of our predictions related to protective, energetic, and social benefits of allocare were supported, suggesting that patterns of allocare in belugas are not strongly driven by the needs of offspring. Instead, allomothers may be more concerned with the needs of mothers, as described by the maternal relief hypothesis. Taken together, my findings hint at the importance of female cooperation in cetacean societies. The ties that bind female belugas and structure their daily lives have yet to be fully revealed. Allocare likely represents a single facet of the complex relationships between daughters, mothers, grandmothers, aunts, and friends.

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APPENDIX A. CHAPTER 2: FREQUENCY OF RE-OBSERVATION OF KNOWN INDIVIDUALS

Since 1985, the GREMM has led an extensive effort to photograph and catalogue SLE belugas. Over hundreds of cumulative hours, the GREMM's researchers have followed herds of belugas and attempted to photograph all individuals encountered. The photographs are then scrutinized to identify persistent scars, discolorations, and malformations, and matched to previous photographs of the same animal. Known animals are issued an alphanumeric code and re-observed year to year. To date, the GREMM has successfully catalogued several hundred animals, approximately 15-20% of the total population.

As our UAV footage was not optimized to allow individual recognition of animals, we did not have a good estimate of the true number of animals sampled. Over our 2016, 2017, and 2018 field seasons, we observed belugas over 69 sampling days. The observed herds numbered, on average 26.3 ± 16.3 individuals, and ranged in size from 1 to 80 individuals. To ensure that we were not always observing the same small subset of the population, we calculated the frequency of re-observation of photo-identified individuals. Photoidentification protocols were carried out in our study site (Baie Ste-Marguerite and the Saguenay Fjord) over 77 sampling days from 2016-2018.

In total, we observed 60 known animals in the study area during the 2016-2018 field seasons. In 2016, 36 known individuals were photographed during 28 sampling days. On average, individuals were observed on 2.6 ± 2.2 sampling days (Table B1). Of the 28 known individuals observed in 2016, 21 were observed on more than one sampling day. For these recurring individuals, we were interested in calculating the frequency of re-observation, to determine whether animals tended to use the study area intensely for short durations or returned throughout the summer. In 2016, within-season recurring individuals were re-observed on average every 6.2 ± 4.6 sampling days (Table B1).

In 2017, we observed a total of 22 known individuals over 19 sampling days. These 22 individuals included 15 animals that had been identified in 2016 and 7 animals that had not. On average, known individuals in 2017 were observed on 2.5 ± 1.5 sampling days (Table B1). Of the 22 known individuals observed in 2016, 15 were observed on more than one sampling day. These within-season recurring individuals were re-observed on average every 5.8 ± 4.1 sampling days.

In 2018, we observed a total of 29 known individuals over 30 sampling days. These 29 individuals included 14 animals that were also observed in 2016 and 15 animals that were also observed in 2017. Only 9 known individuals were re-observed every field season. On average, known individuals were observed on 2.4 ± 1.6 sampling days in 2018 (Table A1). Of the 29 known animals observed in 2018, 16 were observed on more than one sampling day. On average, these individuals were observed every 6.3 ± 5.3 sampling days (Table A1).

Our findings support the notion that the study area is frequented by a well-mixed subset of the population. None of the known individuals were consistently re-observed on every sampling day of any field season. In 2018, one known individual was re-observed on five sequential sampling days, but there were an unusual occurrences. Most known individuals were only observed a few times per field season. For known animals that were observed more than once in a field season, patterns of re-observation suggest that most animals don't remain in the study area or return consistently for several days at a time. This has implications for the true sample size of this study. While it is inevitable that certain focal individuals were resampled, our findings do not suggest that every sampling day consisted of resampling the same mothers and offspring.

Table A.1: Results of photo-identification effort over the course of the 2016-2018 field seasons. For individuals that were observed in multiple years, each year's observations were tabulated separately. Within-season recurring individuals refers to animals that were observed on more than one sampling day within a field season.

	2016	2017	2018
Sampling days	28	19	30
Known individuals	36	22	29
Mean number of sampling days observed	2.6 ± 2.2	2.5 ± 1.5	2.4 ± 1.6
Within-season recurring individuals	21	15	16
Re-observation interval of within-season recurring individuals	Every 6.2 sampling days ± 4.6	Every 5.8 sampling days ± 4.1	Every 6.3 sampling days ± 5.3

APPENDIX B: INTEROBSERVER ANALYSIS

To ensure the reliability of the main observer (JAA), we trained two additional observers (BJ and AKE) to re-analyze a subset of the videos using the event recorder JWatcher 1.0 (Blumstein & Daniel, 2007). We reanalyzed 28 videos from a total of 156. BJ and AKE analyzed 11 and 17 videos, respectively, for a total of 28 (Table B.1). JWatcher's "Analysis" function was used to summarize the observer's observations and produce files which we imported into the R environment (version 3.4.3, R. Core Team, 2013) for further analysis. As we were only interested in assessing JAA's reliability, we pooled the observations of the two observers. As the videos contained multiple overlapping focal follows, we were unable to compare observations by focal follow. Instead, we summed all behaviour durations and counts of interest within a video and compared all variables by video. We compared all variables analyzed in Chapters 2 and 3 (Table B1). By comparing the number of offspring of each age class identified, we tested whether JAA could reliably differentiate between the three age classes. By comparing the number of escorts identified, we tested whether JAA could reliably determine when allocare occurred. We used the intraclass correlation coefficient with a two-way mixed effects model to assess the reliability of JAA's observations using the ICC function of the psych package (Revelle, 2018).

Following Koo & Li (2016), we considered that an intraclass correlation coefficient from 0 to 0.5 showed poor agreement between the observers, 0.5 to 0.75 showed moderate agreement, 0.75 to 0.9 showed good agreement, and 0.9 to 1.0 showed excellent agreement. For the 28 videos analyzed, all variables of interest showed moderate to excellent agreement between JAA and the two observers.

Table B.1 Correlation coefficients with confidence intervals comparing JAA's observations to JB and AKE's observations across a subset of 28 videos. The lower bound of all intraclass correlation coefficient confidence intervals are greater than 0.5, and are therefore considered acceptable by Koo & Li (2016).

Variable of interest	Intraclass correlation coefficient [95% CI]
Association duration	0.91 [0.79, 0.96]
Echelon swim duration	0.84 [0.64, 0.93]
Infant swim duration	0.81 [0.57, 0.91]
Number of calves	0.93 [0.84, 0.97]
Number of yearlings	0.89 [0.77, 0.95]
Number of juveniles	0.81 [0.60, 0.91]
Number of escorts	0.87 [0.71, 0.94]

B.1 References

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APPENDIX C. CHAPTER 3: ASSESSING THE PRESENCE OF MALE BELUGAS

We devised a method to use qualitative observations to quantitatively assess the presence of male belugas in UAV footage of groups of females with offspring. This method relies on various characteristics of males and male groups to determine the likelihood that males are in close proximity to focal offspring.

C.1 Criteria

We chose four criteria which could be assessed in a binary manner for each video. Each video was viewed, and the likely of males being observed was rated based on whether or not the four criteria were fulfilled.

C.1.1 Morphology

To the trained eye, adult male and female belugas can be distinguished visually based on certain morphological differences (Vladykov, 1944). Females tend to be more rotund, while males have a more tapered shape. Males also have well-developed lateral muscles, resulting in a well-defined neck and head region (Smith, Hammill, & Martin, 1994). Females tend to have a softer contour, with the blubber of the head flowing smoothly into the body. The prominence of the male's head is further emphasized when the melon grows enlarged during periods of excitement (Krasnova et al., 2014).

C.1.2 Size

Adult males are considerably larger than females, reaching up to 5.7 meters in length in the SLE population, compared to only 4.7 meters for females (Vladykov, 1944). As such, fully grown males are usually easily recognized when footage allows for side-to-side comparison. However, in cases where multiple animals are not available for visual size assessment, or when males are not fully grown, it is more difficult to recognize males based on size alone.

C.1.3 Group composition

Belugas are sexually segregated for most of the year (Loseto et al., 2006). Males tend to group together, while females and offspring form their own groups (Stewart & Stewart, 1989). As offspring are dependent on their mothers for several years (Krasnova et al., 2014), even small groups of females typically include at least one dependent offspring. Therefore, groups which include only adults are typically groups of males (O'Corry-Crowe et al., 2020).

C.1.4 Behaviour

Groups of males and females can sometimes be distinguished based on behaviour (Krasnova et al., 2014). Males tend to swim in close proximity to each other, closely coordinating their movements, whereas groups of females tend to be more loosely associated. In addition, males display high rates of socio-sexual behaviour which includes pelvic thrusting and rubbing (Glabicky, DuBrava, & Noonan, 2010; Hill et al., 2015), both of which are easily observed in UAV footage.

C.2 Weighing the criteria

While all four criteria are valuable in assessing the presence of males, we considered that each should not be weighed equally. For example, a single male in a group of females may obviously fulfil the size and morphology criteria, while failing to meet the group composition and behaviour criteria. Similarly, it is possible to observe a group of females without offspring, or a group of males not engaging in socio-sexual behaviour. As such, we considered that size and morphology were the most reliable criteria in assessing the presence and males, and that group composition and behaviour were less reliable. Therefore, we assigned a weight of 0.4 to size and morphology, and a weight of 0.1 to group composition and behaviour.

C.3 The Male Presence score

By multiplying each criterion's 0 or 1 value by its weight and summing the products across all four criteria, we produced a score between 0 (unlikely that males were present in the footage) and 1 (high certainty of male presence). We define this as the Male Presence (MP) score.

For example, if a video shows animals consistent with male size and morphology, but not consistent with male group composition and behaviour (Fig. C.1B), we obtain an MP score of 0.8: $(1*0.4) + (1*0.4) + (0*0.1) + (0*0.1) = 0.8$. Figure C.1A shows a group of females with offspring. If this was the only group present during a video, that video would receive an MP score of 0, as there are no animals with male size and morphology, there are offspring in the group, and no male-typical behaviours are present. In contrast, Figure C.1C shows a group of large animals with male-typical morphology, group composition, and behaviour, and would therefore receive an MP score of 1.

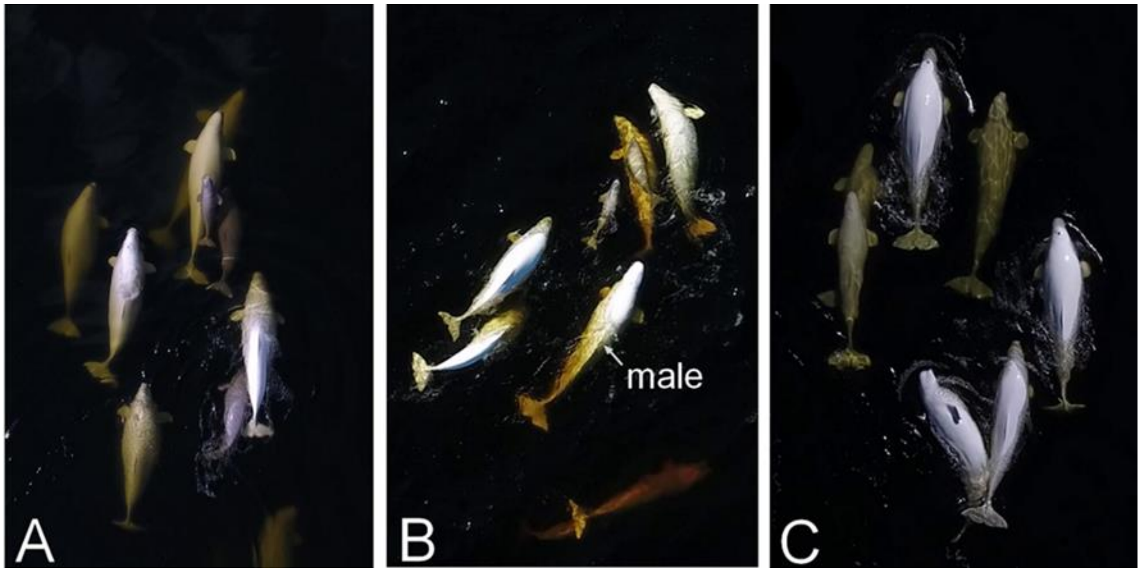

Figure C.1 A) Group of females with calf and juveniles, Male Presence (MP) score = 0. B) Group of females with two calves and a presumed male; MP score = 0.8. Note the large body size, well-defined neck and wedge-shaped body typical of males. C) Group of males; MP score = 1.0. Note the absence of offspring and presence of socio-sexual behaviour.

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