Social structure in northern bottlenose whales: Stable relationships without stable groups

Sam F. Walmsley[1*], Laura J. Feyrer[1], Hal Whitehead[1]

[1] Department of Biology, Dalhousie University, Halifax, Nova Scotia, Canada.

Abstract

Uncovering the drivers and function(s) of social relationships across a wide range of species is key to understanding the ecology and evolution of social behaviour. Northern bottlenose whales have been identified as a particularly important case study for social evolution. Unlike other large, toothed whale species which live in kin-based social units, northern bottlenose whales appear to form fluid, fission-fusion communities. However, this understanding has not been revisited in over 20 years, and new lines of evidence suggest that female relationships may have been underestimated in previous work. Drawing on 35 years of photo-identification data, we used Bayesian social network and binomial mixture models to quantify social relationships between individuals. Northern bottlenose whale social networks had very low modularity but high social differentiation, indicating strong social preferences in the absence of stable groups or community partitions. Contrary to previous work, we found evidence for strong, long-lasting relationships among females, not just males. Though kinship had little influence on social relationships, age differences and residency influenced patterns of association. Broadly, this analysis supports the hypothesis that northern bottlenose whales exhibit a social system more similar to smaller, less sexually dimorphic toothed whales, such as dolphins. This work highlights the value of long-term ecological research for quantifying the social lives of long-lived species.

Keywords

Social relationships - Social networks - Whales - Relatedness - Kinship - Age differences - Residency – Social structure - Mixture model - *Hyperoodon ampullatus*

*Corresponding author: sam.walmsley@dal.ca

Introduction

Social relationships between individuals are increasingly recognized as essential to many species, with clear links to survival, reproduction, and well-being (Snyder-Mackler et al., 2020). And while it has been argued that sociality is ubiquitous across life (Frank, 2007), there remains enormous variation in how individuals, populations, and species rely on others. Understanding the ecological and evolutionary factors that underlie the formation of social relationships is a key goal for behavioural ecology. However, meeting this goal hinges on the quality of description of social behaviour across a wide range of species and populations. Studies on wild and less accessible animal populations are especially valuable, given the historical focus on "STRANGE" study species (e.g., individuals in captivity, or model species bred for lab research), which may exhibit atypical social behaviour (Webster & Rutz, 2020). In turn, these descriptions can offer insights into the functions of social behaviour and facilitate downstream comparative analyses to trace the phylogenetic history of social structure.

Kinship is often considered one of the most important factors underlying social relationships and shaping social structure across species (Lukas & Clutton-Brock, 2018; Smith, 2014). However, recent theoretical and empirical evidence suggests that even when relationships among genetic relatives are important, individuals may still opt to invest in relationships with non-kin. A review of kinship composition across 18 mammalian species found that nearly half lived in social units where they regularly interacted with non-kin (Pereira et al., 2023), while approximately 45% of cooperatively breeding bird species nest with non-relatives (Riehl, 2013). Longitudinal research has similarly shown that female rhesus macaques (*Macaca mulatta*) form strong (though somewhat less stable) relationships with non-kin, especially when they lack kin in their social environment (Cheng et al., 2024). Relationships with non-kin relationships may be beneficial simply in that they buffer against the risk of losing preferred kin partners, as described by the "social bet-hedging" hypothesis (Carter et al., 2017). Non-kin partners may also be able provide specific resources, information, or capacities that an individual's available kin cannot provide (Cheng et al., 2024). And while these types of relationships have generally received less attention than relationships among relatives, growing evidence suggests that they may be similarly important facets of social behaviour and its consequences.

Whales and dolphins (the cetaceans) have proven to be an excellent system for understanding the evolution and diversity of social behaviour in the context of kinship. Generally, larger toothed whales are thought to form social units based on maternal kin, centered on extended relationships between mothers and offspring (Rendell et al., 2019). Here, stable units of related females and offspring often live and travel together (e.g., sperm whales, *Physeter macrocephalus*). Smaller species are thought to form more fluid social networks (Weiss et al., 2021), often with fission-fusion grouping patterns and where kinship remains important, but a higher proportion of relationships are formed with non-kin. Toothed whale communities are generally thought to be female-centric (Rendell et al., 2019), though this may not be ubiquitous. Beluga whales (*Delphinapterus leucas*) often associate with unrelated or paternally-related individuals, upending the previous assumption that maternal kinship defines their social organization, as has been found in better-studied species (O'Corry-Crowe et al., 2020). Similarly, there is growing evidence that social relationships may be less tied to genetic relatedness than previously thought. For example, a study of Gray's beaked whales (*Mesoplodon grayi*) found that adults stranding together were exclusively non-relatives (Patel et al., 2017).

Little is known about the social behaviour of the beaked whales (family *Ziphiidae*), despite the fact that they comprise 24 of the nearly 80 species of toothed whales (Weiss et al., 2021). Blainville's beaked whale (*Mesoplodon densirostris*) and goose-beaked whales (*Ziphius cavirostris*) are considered less social generally (Baird, 2019), though do appear to dive collectively in relatively small groups (Alcázar-Treviño et al., 2021). Research on Blainville's beaked whales off Madeira Island found evidence for relatively short-term relationships involving females (e.g., up to 3.5 years but often less), and no evidence of long-term relationships among males. For this and other populations, female defense polygyny has been proposed as the mating system, whereby males compete and defend access to females. Research on Baird's beaked whales (*Berardius bairdii*) near the Commander Islands, Bering Sea, points to the presence of moderately differentiated relationships and some loose clustering into sub-groups (Fedutin et al., 2015). Though males and females were not distinguished, evidence of stronger relationships between more heavily scarred individuals raises the possibility of male-male coalitions (Fedutin et al., 2015). Baird's beaked whales also show potential evidence of culturally transmitted knowledge relating to foraging locations (Filatova et al., 2024).

Northern bottlenose whales may provide one of the most promising case studies for understanding the factors underlying whale social behaviour. While much remains to be learned, preliminary evidence from the Scotian Shelf population of northern bottlenose whales suggests that, unlike the female-centric societies of other deep-diving whales (e.g., sperm whales), they lack hierarchically structured social units (O'Brien, 2013; Weiss et al., 2019), and rarer long-term associations tend to be between males (Gowans et al., 2001; Gowans & Rendell, 1999), with few stable relationships occurring among females (O'Brien, 2013). However, a recent analysis of stable isotopes in northern bottlenose whale teeth indicates long weaning periods of 4 years (Feyrer et al., 2020), suggesting that sustained mother-calf relationships and potentially other social dynamics are yet to be understood for this population. Northern bottlenose whales are also highly interactive and exhibit pro-social behaviours, such as gathering around injured animals

(Gray, 1882). That these whales combine traits typical of female-centric, interdependent odontocete societies (e.g., extended weaning, group defense) with fluid social networks makes them a particularly interesting case study for understanding the form and function of social relationships. Furthermore, suggestions that differences in foraging ecology or site fidelity might also drive their unusual social behaviour (see Weiss et al., 2021), makes this Scotian Shelf population a particularly important system for advancing our understanding of odontocete sociality.

Here, we draw on individual-based data spanning 35 years to characterize the social relationships of northern bottlenose whales. With a much larger and longer-term dataset than previously available, and applying new analytic techniques, we aimed to provide a new description of social structure in the species, and specifically the Endangered population inhabiting the Scotian Shelf. Using a combination of Bayesian social network and social mixture models, we quantify the global structure of northern bottlenose whale relationships, test for the presence of long-term associations, and revisit the conclusion that females show no signal of differentiated relationships. We also explore how genetic relatedness, age differences, and residency patterns influence relationship formation. This expanded test of the idea that northern bottlenose whales have diverged in social structure from ecologically similar species advances an understanding of the factors influencing the evolution of social structure in whales and other mammals.

Methods

Study system and data collection

Northern bottlenose whales are deep-diving beaked whales found in several areas of the North Atlantic Ocean, and that primarily feed on squid, benthic fishes, and invertebrates (Moors-Murphy, 2018). Individuals in the present dataset are estimated to live up to approximately 37 years of age, and there has been some evidence that males live longer than females (Ellis et al., 2025). Northern bottlenose whales were photographed on the edge of the Scotian Shelf from ocean-going sailing vessels during 28 summers spanning 1988-2024 (Table S1). Research efforts were predominantly focused within the Gully submarine canyon (which became a Marine Protected Area in 2004). Smaller amounts of photographic data from other areas (e.g., Shortland and Haldimand canyons) were not considered in this analysis, though we did include photographs collected by other research vessels in the Gully during 2007-2009 and 2013. Film photography was replaced by digital technology starting in 2007, though all other procedures remained consistent across years. As photo-identifications are side-specific (i.e., left, or right side of the dorsal fin), and identity cannot always be linked across sides, we only considered left-sided identifications for our analysis. We also restricted our analysis to high-quality photographs (rating of 3 or above out of 4) to reduce heterogeneity in detection probabilities across individuals.

Visual sex classification was performed based on the shape of the melon (forehead) when photographs of melons and dorsal fins could be linked. Females tend to have smaller, rounded melons while males develop squarer, flatter, and often whiter melons over time. This means that younger males may sometimes be visually misclassified as females, which we accounted for in our analysis (See Robustness Checks). Sex classifications were only assigned if the observer was confident in melon characteristics. Biopsies and accompanying genetic sex and microsatellite data were collected for a subset of individuals in the population (N = 54 left-sided IDs). Bottlenose whales were biopsied during fieldwork using darts attached to a crossbow, and the tissue was stored in liquid nitrogen after retrieval. Microsatellite assays were applied to each biopsy sample (Feyrer et al., 2019). See (Feyrer & Walmsley, 2024) for additional details on photo-identification and the visual sex-classification of northern bottlenose whales. Simple age classes of calf, juvenile, and adult were also assigned for each individual in each year it was observed, based on relative body size, colouration, fin shape, and the presence of fetal folds (see Walmsley et al., 2024 for additional detail). Here, we restricted our analysis to individuals that were either visually classified as adults, or had a minimum age of 4 years old, which corresponds to the estimated weaning age for northern bottlenose whales (Feyrer et al., 2020). This allowed us to consider relationships among adults without the influence of potentially strong or consistent relationships between mothers and suckling offspring. Following (Walmsley et al., 2024), we calculated minimum age from the number of years that individuals were re-sighted in the photo-identification catalogue. Individuals classified as calves when first observed were assigned a minimum age of zero, while those classified as juveniles or adults when first observed were given a minimum age of one and three years, respectively.

Defining social associations

Similar to previous work on this population, we defined groups as photo-identifications within 10 minutes of one another (Gowans, 1999; O'Brien, 2013). This definition was transitive, i.e., if individual A was seen at 4:01 pm, B at 4:05 pm, and C at 4:12 pm, all three individuals would have been within a group. While northern bottlenose whales may spend variable amounts of time at the surface, has been shown that after approx. 10 minutes the probability of re-sighting the same animals decreases significantly (Gowans, 1999; O'Brien, 2013). When applied to the long-term dataset, this resulted in encounters with groups lasting 4.4 minutes on average (time between first and last photograph; SD of 7.3 minutes; range 0-74 minutes). Social associations were then defined based on group membership, i.e., we assumed that all group members were associated, following the "gambit of the group"(Whitehead & Dufault, 1999). For each group observation, we considered a social association to be possible between a pair of whales if at least one individual was present. This means that group observations were treated as sampling periods. When estimating dyadic relationships across years, we included an additional requirement that both whales were known to be alive. In other words, we excluded periods before the first, and after the final, year that each whale was photo-identified, so as not to confound our estimates of social relationships with demographic effects (especially birth and death).

Bayesian social network analysis

We used a Bayesian approach to generate posterior distributions of the strength of specific pairwise relationships between northern bottlenose whales. These are equivalent to "edge weights" in social network analysis. This approach allowed us to simultaneously track statistical uncertainty in the estimates for each relationship. We also used partial pooling, i.e., fitting relationship measures as a random effect, which should enhance the accuracy of our measures. We fit two types of network models: the first was a multi-year network incorporating data from all years and the aforementioned demographic restriction, and can be represented by the following equation:

$$\begin{aligned} Together_N &\sim Binomial(opportunities, p) \\ logit(p) &= \alpha_{overall} + \alpha_{[Dyad]} \\ \alpha_{[Dyad]} &\sim Normal(0, \sigma) \\ \alpha_{overall} &\sim Normal(-1.5, 1) \\ \sigma &\sim Exponential(1) \end{aligned}$$

Here, p represents the probability of a social association (binary) being observed between two animals. Here, $opportunities$ represents the number of group observations during which a social association between two animals was possible (see above), while $Together_N$ refers to the number of group observations when both individuals were detected. Crucially, α_{dyad} represents dyad-specific deviations from the mean $\alpha_{overall}$, which together allow us to estimate how often any given dyad is observed together (i.e., edge weight). The resulting multi-year network does not necessarily represent the social structure of the bottlenose whale community at any given time, but provides estimates of the strength of dyadic relationships across years.

Using the same model structure and priors as above, we also calculated annual networks. These were based on the same group association data, but only including individuals observed at least once in a given year. In other words, individuals lacking any detections in a given year would not be included in that year's network. To pool information about typical association rates across years, these annual networks were fit in a single model whereby dyads were treated completely independently (e.g., dyad A-B in 2021 was considered independent from dyad A-B in 2023). We then extracted each set of year-specific edge weights to create annual networks. These provided a better depiction of northern bottlenose whale social structure at a specific time point. Both network models were fit using the *brms* package in R (Bürkner, 2021).

Estimating global network properties

We calculated two metrics to characterize the social structure of northern bottlenose whales. Social differentiation (S) is the estimated coefficient of variation of the real association indices and is a measure of the variability in the strength of social relationships. Values less than 0.5 often interpreted as indicating homogenous associations while values greater than 2.0 indicate strong social preferences or "extreme" differentiation (Whitehead, 2009). Note that though this measure can provide similar insights to measures of Shannon complexity (also sometimes referred to as "S" and applied to animal communities), they are distinct measures. Modularity (Q) is a measure of the clustering or fragmentation of relationships into sub-units or groups. Ranging from 0 to 1, values of 0.3 or higher are generally interpreted as indicating non-trivial divisions (Newman, 2006; Whitehead, 2009).

All metrics were estimated within years, to avoid the influence of temporal or demographic changes influencing apparent network structure (Cantor et al., 2012). Both Q and S were estimated using the fitted annual Bayesian edge weight models. To propagate uncertainty in edge weights through these calculations, we constructed networks based on each of 1,000 randomly selected draws from the posterior of the edge weight model. We then calculated Q and S for each of these networks, resulting in a full posterior distribution for each annual measure. Q was calculated using the Louvain clustering algorithm in the *igraph* package in R (Csardi & Nepusz, 2006), while S was calculated as the coefficient of variation of edge weights for each network. Both measures were estimated using across all dyads taking edge weights into account, i.e., we did not restrict the calculation to dyads with an edge weight above a given threshold. However, we did not calculate modularity or social differentiation for two years during which just one pair of animals was observed (1991, 2009).

Exploring the duration of relationships

We used lagged association rate (LAR) analysis to quantify the duration of relationships in northern bottlenose whales. Given an observed social association between two animals, LARs represent the probability of another association being observed at a given time lag. Generalized across a community, visualizing change in LARs across time lags can provide insight into the formation and decay of social relationships. LARs were calculated using SOCPROG (Whitehead, 2009), based on associations within groups and using days as sampling periods. We ran separate analyses for all individuals, as well as sex-specific relationships (e.g., male-male, female-female, male-female). Because LARs are calculated from the perspective of a given focal animal, male-to-female and female-to-male dyads were analyzed separately. We also calculated a null association rate to determine the time lag at which dyadic relationships cease to differ from hypothetical random associations in the community. Jackknifing was used to estimate the precision of both LARs and null association rates.

Mixture models: Identifying types of social relationships

Mixture models can be a useful tool for distinguishing relationships of varying strength from a distribution of edge weights (Weiss et al., 2019). We fit a series of binomial mixture models to identify the number of "types" of relationships (i.e., components of mixture model) that northern bottlenose whales had, and whether this differs according to the sex composition of dyads (e.g., Female-Female, Male-Male, etc.). Models were fit using 1-5 components for different relationship types, and the Bayesian Information Criterion (BIC), which performs well at smaller sample sizes, was used to identify the best-fitting model (Ellis et al., 2021; Weiss et al., 2019). This approach also allowed us to directly estimate the complexity of social relationships, using Shannon entropy, where more even distributions of varied relationship strengths are considered most complex. Binomial mixture models were fit with the *SocMixMods* package in R (Ellis et al., 2021), using the same association data used for the social network model (i.e., only considering demographically possible associations), with the numerator as the number of sampling periods in which a given dyad was observed together, and the denominator as the number of sampling periods in which at least one of the individuals in the dyad was observed. We fit models specific to each sex combination, as well as an overall model that allowed us to incorporate additional data from individuals with unknown sex.

Modelling the drivers of social relationships

We used dyadic regression to explore how the formation of social relationships varied with several key predictors. The type of relationship (absent, weak, strong) assigned to each dyad by the mixture model approach was used as a response variable in these analyses, similar to (Ellis et al., 2021; Nielsen et al., 2023). This allowed us to estimate the relative probability of a given dyad forming an absent, weak, or strong social relationship across three key predictor variables: genetic relatedness, difference in minimum age, and residency (see below). This approach offered a straightforward and computationally feasible way to manage the otherwise large amount of absent or potentially avoidant relationships in the population (i.e., dyads with edge weights very close to zero). This also allowed specific types of relationships to vary in relation to predictor variables of interest, i.e., avoiding the implicit assumption that a predictor (e.g., relatedness) will influence the probability of forming weak or strong relationships in a similar fashion.

Separate models were fit for all individuals (including those of unknown sex), and for each dyadic sex combination where both sexes were known (male-male, female-male, female-female). We also included a multi-membership varying effect on the intercept, which accounts for the non-independence of specific animals being present in multiple dyads (Hart et al., 2022). We fit two versions of each model. The first version was fit using a single dataset where, for each dyad, we assigned their relationship type as the type with the highest probability in the mixture model results. These "hard label" assignments provided a best guess of each dyad's social relationship. The second versions were fit and pooled across 10 datasets where relationship assignments were drawn at random based on the dyad-specific probabilities from the mixture model results. This allowed us to assess the sensitivity of our results from the hard label models with an approach that incorporates the full uncertainty about each dyad's relationship type. We used Normal priors for slope terms with mean of 0 and standard deviation of 1 (while using standardized predictors), and verified that they were appropriate using prior predictive checks. Otherwise, we used default priors from *brms* in these models, which are only very weakly informative.

Genetic relatedness

We estimated the genetic relatedness between all biopsied individuals from the microsatellite data with the Wang estimator (Wang, 2002), implemented in the *related* package in R (Frasier et al., 2014). This estimator is designed to be robust to small sample sizes. It can also provide negative values, if pairs of individuals are less related than average given the sample. The resulting estimates of relatedness can simply be interpreted as a measure of genetic correlation between two individuals and are well-suited for analyses like generalized linear models where differences in relatedness across sampling units are of interest (Wang, 2017).

Differences in minimum age

Next, we explored how dyadic relationships varied as a function of *difference in minimum age*. Following Walmsley et al. (2024), we calculated the minimum age of individuals based on the year of first identification as well as their age class (calf, juvenile, adult) in that year. Absolute differences in these minimum age values were then used as a predictor of the formation and strength of dyadic relationships in northern bottlenose whales. As before, only "possible" dyads were considered, so we do not expect a negative relationship between difference in minimum age and the presence of social relationships to emerge simply because of births and deaths in the population.

Residency

Lastly, we explored how residency patterns impacted relationships between bottlenose whales. While this population shows strong site-fidelity to the Gully and year-round presence (Feyrer et al., 2024; Wimmer & Whitehead, 2005), some individuals have been repeatedly observed across decades (max. 34 years), while others are detected over much shorter time periods, i.e., within a single field season. Individuals were considered to exhibit *transient* behaviour if they only were detected in a single year (based on left-sided photoidentifications) that was not the first or last year of the study period (1988, 2024; as we would be unable to distinguish residency from demographic changes). While incomplete sampling of all individuals in each year will mean some misclassification of resident behaviour as transient, this provided a simple measure of residency patterns in the population. Similar measures have also been linked to behavioural differences in other beaked whales (Filatova et al., 2024). We used these classifications to compare social relationships across resident-resident, resident-transient, and transient-transient dyads.

Robustness checks

Northern bottlenose whales vary in the distinctiveness and permanence of their markings, which may affect our ability to re-identify individuals across multiple years. To address this issue, previous analyses of behaviour in this population have sometimes exclusively focused on individuals with more permanent markings (e.g., notches and back indentations; S. Gowans & Whitehead, 2001). While our photo-identification catalogue and protocol has been updated to focus on higher-quality photographs (which should reduce heterogeneity in re-identifications), we repeated key analyses with a restricted dataset to ensure that our findings were robust to the exclusion of less-distinctively-marked individuals. These checks included the re-analysis of global network measures, lagged association rates, mixture models, and multinomial GLMMs linking relatedness, age differences, and residency patterns to relationship types.

Additionally, sex classifications for individuals without genetic (biopsy) data may sometimes mistake younger males for females, as flatter, larger melons (foreheads) of males develop over time. To assess whether potential misclassifications could be influencing results for female-female dyads, we fit an additional multinomial GLMM to assess whether dyads of females with genetically confirmed sex differed in their distribution of social relationship types. For example, if strong relationships among "females" were in fact driven my misclassified males, "female-female" dyads lacking genetic sex confirmations should be less likely to form strong relationships. Aside from the lagged association rates, all analyses were conducted in R version 4.3.2, organized into a reproducible pipeline using the *targets* package (Landau, 2021; R Core Development Team, 2022), and are available at github.com/swalmsley/Bottlenose-Relationships. Models were assessed diagnostically using R-hat and effective sample size values prior to interpretation. Unless otherwise stated, we present 90% credible intervals (CIs) and effects are otherwise reported as the mean of the posterior of each coefficient alongside the associated probability of a directional effect (*pd*).

Ethical Note

Field research on northern bottlenose whales was approved by the Dalhousie University Committee on Laboratory Animals (UCLA), as well as the Department of Fisheries and Oceans (UCLA protocol number 24-017). This included permits from the Species at Risk Act Program and the Gully Marine Protected Area management team. The most invasive component of field research is biopsy collection, which involves collecting a small piece of skin using a sampling tip attached to either a crossbow bolt or a pole. This procedure has been shown to produce only moderate behavioural responses in biopsied whales, i.e., no severe reactions (Hooker et al., 2001). Less invasive procedures such as photo-identification and the presence of the research vessel are expected to have minimal impacts on the animals.

Results

In total, our analysis included 5,112 pairwise social associations (i.e., co-occurrence within groups) between 42,459 dyads of 623 individual northern bottlenose whales. Of these individuals, 110 were classified as male, 212 as female, and 301 as unknown sex. Groups included an average of 2.43 adult individuals (SD 1.89, range 1-27) and showed varying sex composition. While most groups consisted of individuals of a single sex, mixed sex groups were also common (35.7% of groups with at least 2 adults included males and females). Nearly half of groups with at least 2 adults included individuals of unknown sex (45.6%). Northern bottlenose whales formed a relatively fluid social community, with a mean posterior modularity of 0.28 (90% CI 0.17-0.38), calculated annually based on 1,000 draws of each network. This mean lies below the typical threshold of 0.3 for important divisions within a community (Whitehead, 2008), though there was a 35.5% posterior probability that modularity was above 0.3. Despite this lack of clear sub-units, social differentiation was high (mean 2.1, 90% CI 1.53-2.49), indicating the presence of differentiated relationships (Figure 1). Robustness checks excluding individuals with potentially less permanent markings returned very similar results, and we found no evidence that female dyads with genetically confirmed sex differed from those with visually confirmed sex, so here we focus solely on findings from our main analysis (See Supplemental Material for summary).

Most demographically possible dyads were never observed together in our sample (83%). Based on the multi-year network model, dyads that were observed associating at least once were detected together approximately 6% of time on average (i.e., mean edge weight of 0.06). However, relationships were highly variable. The mean maximum edge weight across individuals was 0.15, and the highest estimated edge weight was 0.59, suggesting little evidence of *very* strong associates or “constant companions”.

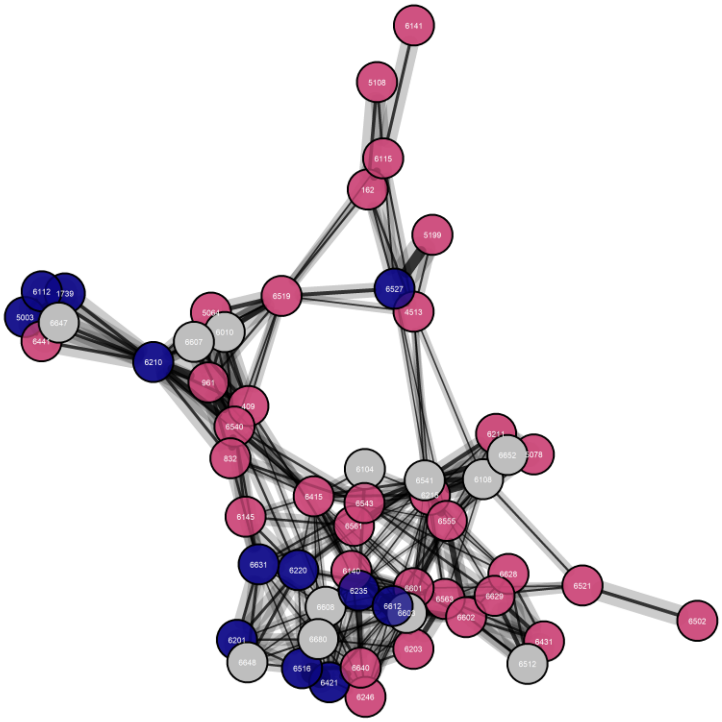

Figure 1 – Example of annual network based on data from 2023 showing relationships among northern bottlenose whales. Individuals (“nodes”) are represented by circles while the lines linking them represent estimates of the proportion of time that individuals are observed together (“edge weights”). The darker inner portion of each line represents the mean of the posterior of each edge weight (thicker lines implying a stronger relationship), while the outer grey bands represent the standard deviation. The blue circles or “nodes” represent males, the light red nodes represent females, and the grey nodes represent individuals of unknown sex. For visualization purposes, we only show edge weights with a mean of at least 0.02 (i.e., lines linking dyads that are estimated to be observed together at least 2% of the time).

Evidence for multiple types of social relationships

Social mixture models suggested that northern bottlenose whales formed at least 3 types of relationships, and potentially more. Based on BIC, the best model for female-female relationships included 4 categories, while the best model for male-male relationships included 5 categories. However, the categories with the highest association rates accounted for a very small proportion of possible relationships (< 1% for female-female relationships, < 3% for male-male relationships), and there was similar statistical support for models with 3 categories (Figure S1).

Accordingly, we carried out subsequent analyses based on the 3-category model for all sex combinations, allowing us to compare “absent or avoidant”, “weak”, and “strong” relationships across the population (Figure 2). These categories were based on the frequency of associations: absent or avoidant relationships involve dyads that were never or almost never observed together, weak relationships involved dyads that were detected together approximately 3% of the time, and strong relationships involved dyads detected together greater than 10% of the time. However, these rates and the proportion of dyads with each relationship type varied by sex (See Supplemental materials for summary tables). Note that while the very low association rates may result from an avoidant relationship, we cannot distinguish between avoidance and the simple lack of a preferred social relationship, so we use the term “avoidant/absent” to refer broadly to relationships with very few associations. It is also important to note that these rates will underestimate the true amount of time that dyads are together, as they rely on side-specific observations of individual whales in the wild, which will sometimes be missed. For example, a whale may not be photographed from both sides, or may not surface during photo-identification efforts. The complexity of associations, measured by Shannon entropy, varied by sex composition (female-female: 0.76, female-male: 0.86, male-male: 1.09). Shannon complexity increases as the number and evenness of relationship categories increase. Though there was some uncertainty in the mixture model’s assignment of specific relationship categories to dyads, the difference in probabilities of assignment between the first and second highest category was almost always greater than 30% (99% of dyads for model with all individuals).

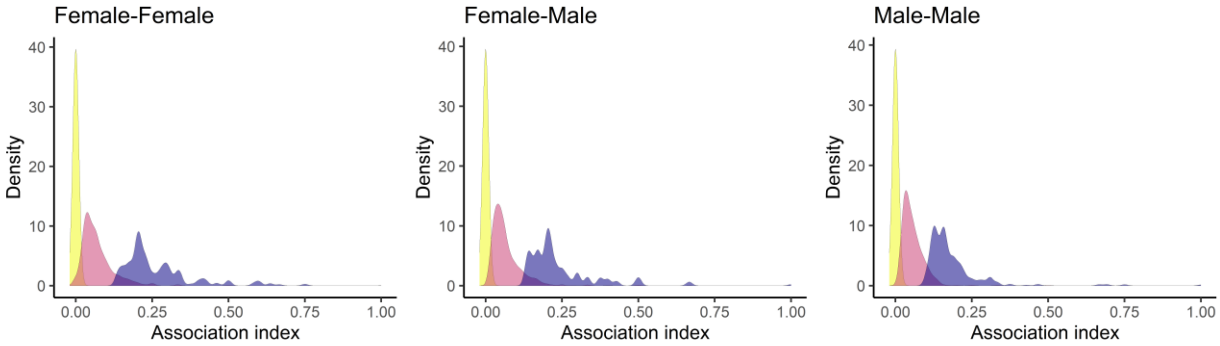

Figure 2 – Northern bottlenose whales have three types of relationships with others, regardless of the sexes of the dyad. These types represent dyads that very rarely interact (yellow), those that form weak relationships (red), and those that form strong relationships (purple). See Supplemental Materials for proportions and mean association index values for each category.

Evidence for strong bonds between females is of particular interest, as the previous understanding has been that females form weaker associations in this population (but see O’Brien, 2013). In fact, the mean association index of the “strong” relationship for female-female dyads was higher than that of male-male dyads, suggesting that they form the strongest relationships in terms of frequency of association. More generally, evidence for both weak and strong relationships in northern bottlenose whales runs counter to previous research which suggests that northern bottlenose whales have just two types of relationships (absent and weak; Weiss et al., 2019).

Long-term persistence of social relationships

Northern bottlenose whales formed extended social relationships, lasting more than a decade on average (Figure 3). Male-male relationships were particularly long-lasting (~15 years or more), while female-female relationships appeared to last approximately 10 years, based on the average point at which the lagged association rate crosses the null association rate (Figure 3). Relationships between males and females were shortest in duration, but were still unexpectedly long-lasting, only decaying to null association rates after approximately 3 years. While these reflect the average duration of social relationships across the community, our dataset included several examples of dyads seen together over periods of more than two decades (e.g., females "832" and "1336" were observed together in 1997 and 2021, while "102" and "409", a male-female pair, were observed together in 1996 and 2019), highlighting the extended history and familiarity between animals in this population. Results from the robustness check based on observations of individuals with more permanent markings were very similar, indicating that potential misidentifications were not influencing these patterns (Figure S3). Additionally, such misidentifications would likely result in underestimated relationship durations, meaning that we can be very confident that long-term relationships are present among these whales.

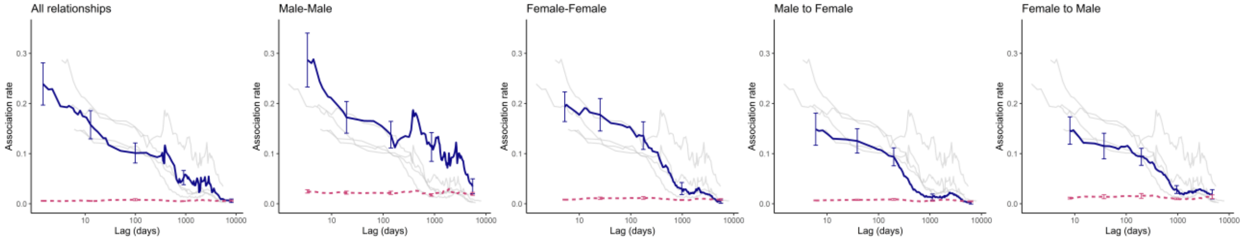

Figure 3 – Lagged association rates (LARs) reveal long-term relationships in northern bottlenose whales. Solid lines show LARs, which represent the probability of associated animals associating after a given time lag, while dashed lines represent the null association rate if no preferred relationships existed within the community. Error bars represent estimates of precision from jacknifing.

Factors influencing dyadic relationships in northern bottlenose whales

Effects of genetic relatedness on social relationships

We were able to estimate the relatedness of 431 dyads that overlapped in our long-term study and thus could have been socially associated. Estimates of relatedness ranged from -0.71 to 0.54, and were uncertain, with relatively wide confidence intervals. While this reduced our ability to be certain about specific genealogical relationships, we were still able to consider a range of relatedness estimates against social behaviour. Generally, relatedness did not appear to be a major driver of social relationships between northern bottlenose whales. This was true both when considering all individuals in the population, and when considering each sex combination in turn. For example, relative to absent relationships, the effect of relatedness on the probability of forming relationships was centered on zero for both weak relationships ($\beta = 2.50 \times 10^{-3}$, 90% CI: -1.02–1.1, pd= 51%), and strong relationships ($\beta = 0.1$, 90% CI: -1.45–1.62, pd = 54.6%). Similarly, we found little correlation between relatedness and Bayesian edge weights (Figure S2).

Effects of age differences on social relationships

Though we did not know the true ages of animals in the population, we estimated the minimum age of each individual based on age class (calf, juvenile, adult) and sightings records. Differences in minimum age appeared to negatively influence the probability of forming social relationships overall (weak relationships: $\beta = -0.2$, 90% CI -0.23–-0.16, pd = 100%; strong relationships: $\beta = -0.13$, 90% CI -0.24–-0.02, pd = 97.5%). These effects were much less certain when using multiple imputation to account for uncertainty in the assignment of relationship types to each dyad (weak relationships: $\beta = -4.90 \times 10^{-3}$, 90% CI -0.02–0.01, pd = 65.8%, strong relationships: $\beta = -4.10 \times 10^{-3}$, 90% CI -0.08–0.07, pd = 54.9%). However, male-male dyads specifically tended to form strong relationships with individuals of similar minimum ages ($\beta = -0.26$, 90% CI -0.48–-0.06, pd = 98.7%). This effect was detected regardless of whether we used multiple imputation, or a single dataset with the most likely relationship type assigned to each dyad. This contrasted with the strong relationships observed in female-female or female-male dyads, which were less common overall, but also largely independent of age differences (Figure 4).

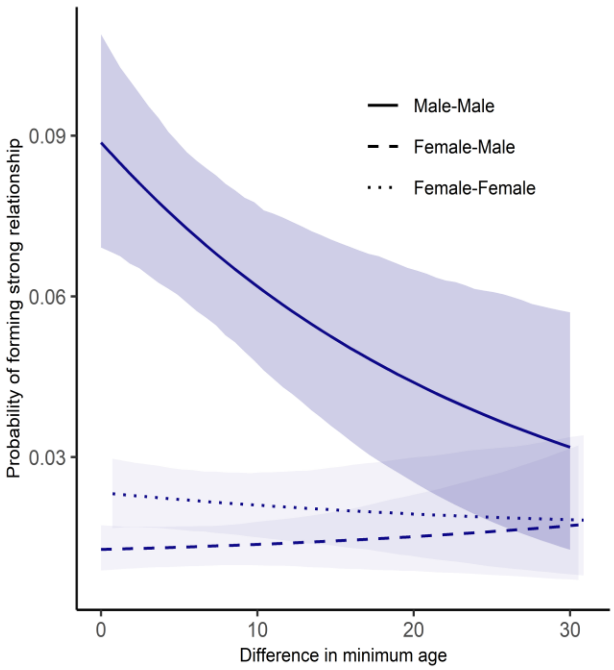

Figure 4 – The probability that a pair of whales forms a strong relationship depends on sex composition and age differences. For male-male pairs, strong relationships were more likely to occur within individuals of similar minimum ages.

Effects of residency on social relationships

Including individuals of unknown sex, most dyads in our analysis were composed of residents and transients (54%) or resident-resident pairs (34%), with fewer dyads of transient individuals (10%). Whales classified as transient were observed across shorter timespans *within* years as well (mean of 3.9 days between first and last observation), compared to residents (mean of 9.4 days between first and last observation). Social relationships, either weak or strong, were proportionally more common in resident-resident dyads than in resident-transient dyads (see Figure 5). This was true for male-male pairs (25% of resident dyads vs. 8% of resident-transient dyads), male-female pairs (14% vs. 6%), and for female-female pairs (15% vs. 8%). This pattern was reflected in GLMMs based on the most likely relationship type for each dyad (i.e., "hard labels"), where social relationships were less likely to occur for resident-transient (weak: β = -1.34, 90% CI -1.47–-1.2, pd = 100%; strong: β = -1.02, 90% CI -1.28–-0.76, pd = 100%) and also transient-transient dyads (weak: β = -0.99, 90% CI -1.26–-0.73, pd = 100%; strong: β = -1.4, 90% CI -1.92–-0.9, pd = 100%). However, we found no clear links between residency patterns and social relationships when using multiple imputed datasets (e.g., for resident-transient dyads, weak relationships: $\beta = 6.70 \times 10^{-4}$, 90% CI -0.04–0.04, pd = 50.3%; strong relationships: β = 0.04, 90% CI -0.1–0.19, pd = 65.5%). This likely resulted from the inherent uncertainty around relationships with "transient" whales, which by definition observed for shorter periods of time. Accordingly, we propose that these patterns be interpreted as only preliminary evidence of stronger relationships among resident dyads.

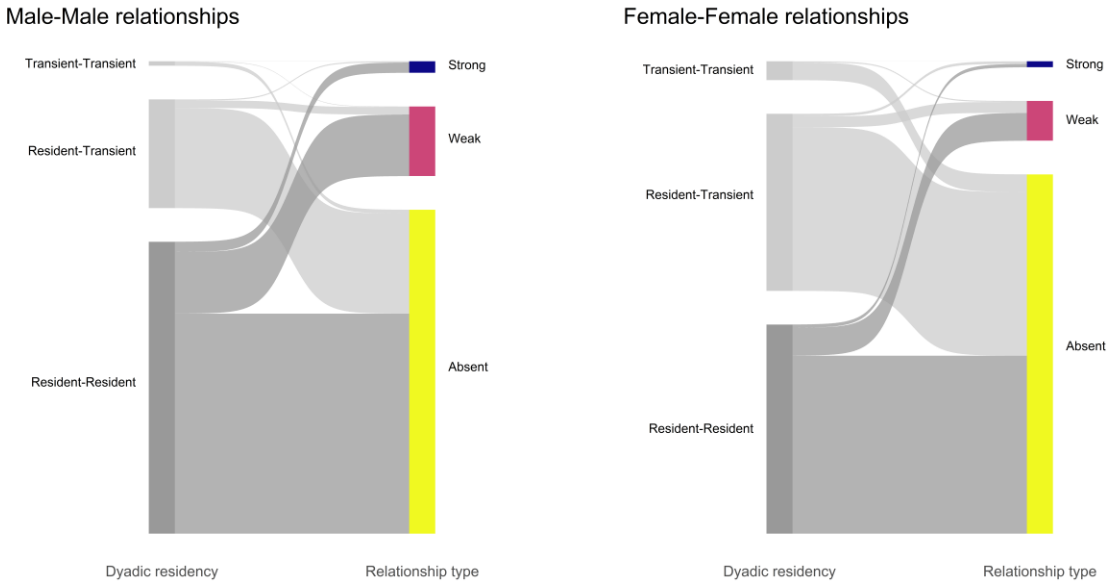

Figure 5 – Connections between residency patterns and relationship types for male-male and female-female dyads of northern bottlenose whales. The vertical width of grey and coloured bars represents the number of dyads of each type. Most female resident-transient pairs rarely interacted (with "absent" relationships), while male resident-transient pairs most often formed weak relationships.

Discussion

Northern bottlenose whales have been identified as an important species for understanding the diversity of social structures across toothed whales (Weiss et al., 2021; Whitehead, 2003). Our analysis supports this idea, demonstrating that strongly differentiated and long-lasting relationships can exist in the absence of stable groups. Toothed whales generally exist along a continuum of labile, fission-fusion dynamics to stable social groups centered around female kin (Rendell et al., 2019). Theory and comparative analyses indicate that these stable social systems are more likely to be found in toothed whales with "slower" life histories: larger body sizes, extended sexual maturity, and longer lifespans (Walmsley et al., 2025). These larger-bodied, more socially modular species are also expected to form relationships based on female kinship. Northern bottlenose whales provide a useful foil for these patterns (Gowans et al., 2001), by displaying many of the features more common to smaller species (e.g., dolphins) despite being among the largest beaked whales, and exhibiting deep-diving foraging behaviour, which has also been linked to the formation of stable social groups (Whitehead, 1996).

Most strikingly, we found no link whatsoever between kinship and the probability of forming a social relationship. This lies in clear contrast to populations where kinship is a principal driver of patterns of social association, as seen in many mammals (Archie et al., 2006), and more specifically to other large toothed whales, where matrilineal social units shape individual social environments (Rendell et al., 2019). While estimates of relatedness were uncertain and only available for a subset of possible dyads in our study, it also included several highly related dyads of various sex combinations with no evidence of social interaction whatsoever. For example, males "45" and "480" had an estimated Wang relatedness of 0.52 (CI 0.31-0.70) indicating they are likely brothers (based on similar minimum ages) or possibly father and son. However, they were *never* observed associating, despite overlapping in the dataset for 23 years, during which there were 77 group observations where one of the pair was seen. Similarly, two relatively closely related females "162" and "653" were not seen associating despite 8 years of overlap ($r = 0.45$, CI 0.17-0.63; 14 possible group observations). Thus, while we cannot rule out the possibility that kinship plays a more subtle role in structuring relationships (especially as we did not include very young animals in our analysis), northern bottlenose whales appear to diverge from species like sperm whales where social units are largely kin-based (Konrad et al., 2018). This is somewhat puzzling, as one might still expect animals lacking clear kin-based units to be exploiting the benefits of cooperation with kin present in their social environments (Walmsley et al., 2023).

Our findings also contrasted with previous research on northern bottlenose whales, revealing more social complexity overall, and especially for female-female relationships. Instead of forming loose networks of weak associations, females displayed a range of relationship types. These included the strongest relationships found across sex classes (based on mixture models with 3 classes), as well as absent or potentially avoidant dynamics between specific pairs (Figure 2). Thus, both males and females in the population form a diversity of relationships. This contrast with previous findings likely stems from the much larger and longer-term dataset (previous published analyses were based on 9 years of data spanning 1988-1997), which was likely important for detecting rarer, stronger female relationships. The contribution of new analytic techniques (e.g., social mixture models) may also be important, providing a quantitative approach to categorizing relationships. Given evidence of three or more general "types" of relationships in northern bottlenose whales, we hypothesize that different relationship types may offer different benefits, as predicted by the "Adaptive Relationships Framework" (De Moor & Brent, 2025). Though strong relationships may be more likely to involve high-risk help or cooperative behaviour, weak ties have also been shown to promote biological fitness in some species, potentially providing distinct benefits (McFarland et al., 2017). For example, weak relationships in this population could hypothetically provide benefits such as information about foraging opportunities (though we have no evidence of this to date). Regarding female-female bonds, in toothed whales with stable social units (e.g., sperm whales), strong female relationships allow for the shared care and defense of vulnerable offspring. It is possible that similar benefits underlie the formation of preferred relationships among females. A female with several strong relationships within the population may have relatively predictable access to help when necessary.

Demography appears to play some role in determining social relationships, particularly among males, which were more likely to form strong relationships with one another if they were more similar in estimated (minimum) age. This aligns with findings from male bottlenose dolphins that tend to form alliances within their age cohort as young animals, rather than bonding with relatives (Gerber et al., 2020). This suggests that familiarity with social partners may be important for the function(s) of male-male relationships in northern bottlenose whales. For example, male elephants also form relationships within age cohorts, which is thought to support "practice" for competitive behaviour (Chiyo et al., 2011). A greater capacity to form intergenerational relationships in females may also contribute to patterns of social ageing in the population. Older males, but not females, are less socially connected (Walmsley et al., 2024), which may in part be driven by the loss of preferred partners in a similar age cohort. It's not obvious that these long-lasting male relationships are coalitions or alliances as seen in some populations of bottlenose dolphins, however. While observations of jousting-like headbutting rituals raise the possibility of sexual conflict among males (Gowans & Rendell, 1999), preferred male-male relationships in northern bottlenose whales do not appear to be limited to one or two close partners (as in dolphins). Furthermore, male alliances are thought to be most beneficial when sexual size dimorphism is low, and when there is high local density. Neither of these seems to apply to northern bottlenose whales (O'Brien, 2013), which are sexually dimorphic (males are approximately 1.16 times as large as females), and densities, though likely higher in the Gully compared to other regions, aren't especially high compared to many other smaller cetaceans.

We found preliminary evidence that residency patterns influenced how northern bottlenose whales formed social relationships. More specifically, absent or possibly avoidant relationships were less likely to occur among residents (detected across multiple years) when compared to dyads involving "transient" whales. This was not unsurprising. For example, the finding that strong male-male relationships occurred among long-term residents aligns with our finding that they can last 15 or more years (Figure 3). Covariance between social relationships and a simple measure of residency supports the idea that social-spatial behaviour is not homogenous across the Scotian Shelf population. It also raises new questions regarding the social perceptions of the whales. Moffett argues that “societies” are based on mutual recognition of social membership (Moffett, 2024) – does the fact that resident whales may be less likely to interact with transient whales overall indicate a society of residents within the population? It is important to consider how our definition of “transient” behaviour might impact estimates of social association, however. For example, given that we only considered demographically possible associations, resident-transient dyads would necessarily have a single year of potential observations to draw from and may include years during which the resident was known to be alive but was not observed. We also found evidence that transient whales were detected across shorter timespans within years, meaning less opportunity for repeated interactions with preferred partners. While this is still a biologically meaningful indication of the lack of social association, it suggests that structural factors (e.g., broader-scale movements in and out of the Gully) could also be shaping the absence of relationships between residents and transients. Of course, these structural factors may themselves be a consequence (not cause) of the absence of a relationship.

Theory suggests that habitat configurations can play a major role in how animals form social relationships (He et al., 2019). The Gully – a localized and highly productive submarine canyon creates predictable access to potential social partners. Passive acoustic monitoring has revealed that northern bottlenose whales are effectively always present in the Gully, with less predictable presence in adjacent areas of the Scotian Shelf (Feyrer et al., 2024). Though the previous thinking was that this predictability may alleviate the need for females to form stronger relationships, new evidence suggests that females are socially selective about a smaller number of strong relationships. Additional long-term studies from other populations of northern bottlenose whales may help to identify the role of habitat in structuring beaked whale social structure, as other populations may have less localized habitats and individuals can travel long distances (Lefort et al., 2025). A study of northern bottlenose whales found between Jan Mayen Island and Iceland from 4 years of data identified preferred associations between males, but no preferences among a female-juvenile class of individuals (Jakobsdóttir, 2021).

The modularity of a social network and its social differentiation are expected to correlate, by definition, as the division into groups implies variability between within- and between-group relationships. There are also mechanistic reasons that social differentiation might promote modularity. A well-described strategy for forming new relationships is to adopt “friends of friends” – often referred to as triadic closure in network terminology (as a triangle of associations forms). Triadic closure is important in the social networks of humans and other species (e.g., hyenas, *Crocuta Crocuta*; Ilany et al., 2015), and has been proposed as a baseline mechanism influencing the formation of relationships (Davidsen et al., 2002). Crucially, closing social triangles may result in the formation of distinct groups (Asikainen et al., 2020), i.e., a more modular network. While simulation models would help to explore this further, the combination of differentiated relationships with limited modularity raises the question of whether simple social networking strategies like triadic closure are important for northern bottlenose whale relationships. More broadly, the lack of clear structural factors such as kinship determining “who associates with who” suggests that northern bottlenose whales may be forming relationships on subtler or more idiosyncratic factors, such compatibility between individual personalities, or perhaps the success of specific histories of cooperative exchange. For example, vampire bats (*Desmodus rotundus*) appear to “raise the stakes” to form new relationships, i.e., expanding from tolerance and grooming to higher-investment forms of interaction like food-sharing (Carter et al., 2020).

Understanding the social structure of offshore and deep-diving species like northern bottlenose whales is challenging, and as our findings have demonstrated, can require decades of consistent, long-term research. Nevertheless, our findings reinforce the idea that cetaceans provide compelling case studies for understanding the ecology and evolution of social relationships.

Data Availability

Data and analysis scripts are available here.

Acknowledgements

We thank all research assistants, students, volunteers, and skippers involved in collecting data for the Northern Bottlenose Whale Project since 1988. This includes many graduate students who collected and processed photo-identification data, including Annick Faucher, Shannon Gowans, Tonya Wimmer, Hilary Moors-Murphy, and Kristin O’Brien. We also thank Kristin O’Brien for her analyses and thesis work on similar questions in 2013, as well as Christine Konrad and Tim Frasier for advice on analyzing genetic data. We are grateful to Tony Einfeldt and Ian Paterson who conducted genetic analyses.

Funding Statement

Field research was funded by the Canadian Wildlife Federation, Natural Sciences and Engineering Research Council of Canada, Dalhousie University, the World Wildlife Fund Canada−Environment Canada Endangered Species Recovery Fund, the Canadian Whale Institute, the Island Foundation, the Whale and Dolphin Conservation Society, the National Geographic Society and the Department of Fisheries and Oceans Canada. Data analysis relevant to this paper was supported by the Department of Fisheries and Oceans Canada, the Natural Sciences and Engineering Research Council of Canada.

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