POPULATION STATUS AND SOCIAL STRUCTURE OF NORTHERN BOTTLENOSE WHALES *(HYPEROODON AMPULLATUS)* ON THE SCOTIAN SHELF

by

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For my Mom,
I remember the excitement of watching you finish your Master’s degree when I was 11 years old, and I am so proud to be following in your footsteps.

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ABSTRACT

I examined the dynamics of an endangered population of northern bottlenose whales over a 23-year period during which its prime habitat, the Gully canyon, was made a Marine Protected Area (MPA). Using mark-recapture techniques on photo-identifications I estimate a current population of 116 animals (95% CI=101-130). The population size and sex-ratio have remained stable since before the MPA designation suggesting this population is persisting. I used photo-identifications and high definition videography to examine the social organization of northern bottlenose whales, including behavioural synchrony. Relationships are highly variable; most associations are short-lived, but there are also long-term preferred associations lasting from several years (female/immature dyads) to over a decade (mature male dyads). I found little, if any, division of the social community. Synchronized breathing is common, precise, and appears to vary with behaivoural context. Although speculative, synchronized breathing might play a role the maintenance of general social relationships within this population.

LIST OF ABBREVIATIONS AND SYMBOLS USED

AIC	Akaike Information Criterion
X^2	Chi square statistic
CCC	Cophenetic Clustering Coefficient
CI	Confidence Interval
COSEWIC	Committee on the Status of Endangered Wildlife in Canada
CV	Coefficient of Variation
DFO	Department of Fisheries and Oceans Canada
F	Female/immature
G	Modularity
Het	Heterogeneity
HWI	Half-weight Index of Association
ID	Identifiability
IQR	Interquartile Range
IUCN	International Union for Conservation of Nature
τ	Lag, with respect to Lagged Association Rates
L	Left
n	number (sample size)
P	Probability
MM	Mature Male
MPA	Marine Protected Area
Q	Quality (rating)
QAIC	Quasi-Akaike Information Criterion
R	Right
S	Spearman's rank correlation coefficient test statistic
SARA	Species At Risk Act
SD	Standard Deviation
SE	Standard Error
SLAR	Standardized Lagged Association Rate
SLR	Single Lens Reflex

ρ	Spearman’s rank correlation coefficient (rho)
SM	Subadult Male

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CHAPTER 1
INTRODUCTION

In the face of accelerating rates of species extinctions, it is becoming critical that we understand how to effectively conserve threatened and endangered wildlife. For example, among vertebrates, one out of five species are currently threatened (not even including those species that are considered data deficient), and this proportion is continuing to grow (Hoffmann *et al.,* 2010). Despite the ongoing loss of biodiversity, there is fortunately an increasing number of examples of conservation success. This thesis presents the status of an endangered population of northern bottlenose whales off Nova Scotia, Canada. With a particular emphasis on conservation, it also provides a current example of endangered cetacean monitoring and management.

1.1 STUDY SPECIES–THE NORTHERN BOTTLENOSE WHALE

The northern bottlenose whale *(Hyperoodon ampullatus)* is a species of beaked whale (family Ziphiidae) that inhabits the North Atlantic Ocean. Northern bottlenose whales have pronounced melons (foreheads) and beaks, and display sexual dimorphism in melon shape and body length. They are relatively large beaked whales; males have a body length of up to 9.8 m and females up to 8.5 m (Benjaminsen, 1972). Males have melons that become white and square in profile as they mature (Reeves *et al.*, 1993). Northern bottlenose whales are deep-diving cetaceans, making regular dives up to1450 m (Hooker and Baird, 1999), and off Nova Scotia they feed primarily on deep water squid of the genus *Gonatus* (Hooker *et al.*, 2001).

Compared to most marine mammals, very little is known about the biology of beaked whales. They are often elusive–living far off shore and surfacing rather briefly (Cox *et al.*, 2006). Much of the current research on beaked whales has focused on their extreme sensitivity to underwater noise, including the frequencies that are often used for geophysical exploration and defense sonar (Barlow and Gisiner, 2006). Exposure to such frequencies is thought to cause physiological changes such as gas-bubble disease as well as behavioural changes which may result in beaked whale strandings and mortality (Cox *et al.*, 2006). This has raised concern for beaked whale conservation globally, particularity in light of the fact that so little is known about the general biology and local scale distribution of beaked whales. Additionally, there are also concerns about by-catch in fisheries and ship strikes (Ledwell *et al.*, 2005; Whitehead and Hooker, 2012).

Commercial whalers documented northern bottlenose whales that were taken across the North Atlantic. Their whaling records showed there are populations off Labrador, Nova Scotia, Iceland, Norway and the Azores (Benjaminsen, 1972; Reeves *et al.*, 1993; Dalebout *et al.,* 2006). Migration between these populations seems to be quite low. The population off Nova Scotia (referred to as the Scotian Shelf northern bottlenose whale population) appears to be genetically distinct from populations off Labrador and Iceland (Dalebout *et al.,* 2006). The Scotian Shelf northern bottlenose whale population is the only population of northern bottlenose whales in the world with long-term photo-identification data, allowing studies on population biology, movements and social structure (Whitehead *et al.*, 1997b; Gowans *et al.,* 2001; Wimmer and Whitehead, 2004; Whitehead and Wimmer, 2005). This ongoing long-term research program has been conducted by the Whitehead lab., Dalhousie University, since 1988.

1.2 STUDY SITE AND POPULATION–THE SCOTIAN SHELF

Northern bottlenose whales along the Scotian Shelf are consistently found in a submarine canyon called the Gully (Figure 1.1), which lies approximately 200 km offshore Nova Scotia on the edge of the Scotian Shelf (Hooker *et al.*, 2002). Northern bottlenose whales also move between the Gully and adjacent Shortland and Haldimand canyons, which also occur on the Scotian Shelf (Wimmer and Whitehead, 2004). As a small and isolated population, the Scotian Shelf northern bottlenose whales were assessed as Endangered by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) in 2002, and under the Species At Risk Act (SARA) in 2006. The Gully, which is critical habitat for this population, was designated a Marine Protected Area (MPA) in 2004.

The Gully submarine canyon was designated an MPA in part because of its importance as habitat for at least 11 species of cetaceans, including this endangered population of northern bottlenose whales and another rare species of beaked whale, Sowerby's beaked whale, *Mesoplodon bidens* (Hooker *et al.,* 1999). Submarine canyons can be very productive due to different oceanic and biophysical processes that act to funnel and trap nutrients into the deep water and benthos. For example, in the Kaikoura Canyon off New Zealand, biomass within the canyon was found to be 100 times greater than in non-canyon habitats of similar depth (De Leo *et al.*, 2010). The Gully submarine canyon off Nova Scotia is the largest canyon in the entire northwest Atlantic, making it unique both as an oceanic feature, but also in terms of its biodiversity. As an MPA, this habitat now protects the resident population of northern bottlenose whales and many other marine species including cold-water corals and fish (DFO, 2008).

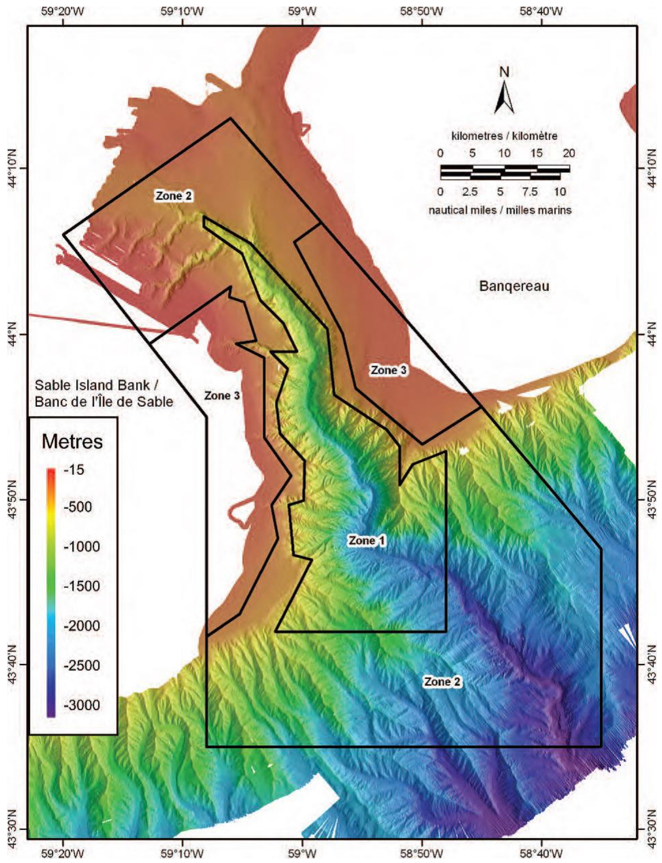


Figure 1.1 Map of the Gully Marine Protected area showing management Zones 1-3 (From DFO, 2008). The deep water (>500 m) habitat in Zone 1 is completely off-limits to commercial fisheries and any seismic activity, in order to provide protection for the northern bottlenose whales and other deep water species. This image was used with permission of the Department of Fisheries and Oceans Canada, Dartmouth, NS.

There are several anthropogenic threats to northern bottlenose whales, including those that use the Gully (Whitehead and Hooker, 2012). Before the moratorium on commercial whaling which was put in place in 1986, northern bottlenose whales were targeted by commercial whaling fleets on the Scotian Shelf. Whether they have since recovered from past exploitation is uncertain (Whitehead and Hooker, 2012). Northern bottlenose whales are also thought to be sensitive to modern human activities such as underwater noise, interactions with fishing activities, or vessel collisions (Hooker *et al.*, 1999; Whitehead and Hooker, 2012). The deep waters of the Gully (>500 m known as Zone 1) are completely protected from commercial fisheries. However, restricted fisheries are still allowed in specific marginal areas of the Gully (Zones 2 and 3; DFO, 2008), and the whales move outside the MPA where they receive no specific protection. Commercial shipping traffic is advised to avoid the MPA, and although tourism is starting to develop in the Gully, at present very few tourists visit the Gully. The efficacy of these changes to the Gully habitat in protecting northern bottlenose whales has not previously been assessed. Chapter 2 of this thesis addresses the success of the MPA and conservation initiatives as they relate to the population of northern bottlenose whales in the Gully, by using photo-identification and mark-recapture techniques.

1.3 METHODS BACKGROUND–PHOTO-IDENTIFICATION

Photo-identification techniques are a non-invasive and often useful way to obtain data to investigate the population dynamics, movements and social structure of cetaceans (Würsig and Jefferson, 1990), including species such as bottlenose dolphins (*Tursiops* spp.; Würsig and Würsig, 1977), pilot whales (*Globicephala melas*; Shane and McSweeney, 1990), and sperm whales (*Physeter macrocephalus*; Dufault and Whitehead, 1995). Northern bottlenose whales exhibit variation in natural markings including notches on their dorsal fins making each individual distinct. The feasibility and success of photo-identification as a means to study northern bottlenose whales in the Gully has been previously demonstrated (Whitehead *et al.*, 1997b; Gowans *et al.,* 2001; Gowans and Whitehead, 2001).

The primary goal for photo-identification of northern bottlenose whales in the Gully continues to be monitoring population size and trends (*e.g.* Whitehead *et al.*, 1997b; Whitehead and Wimmer, 2005). The Whitehead lab., Dalhousie University, has established a catalogue of identified northern bottlenose whale individuals and just prior to the establishment of the MPA in 2004, there were an estimated 163 individuals on the Scotian Shelf, with no substantial or significant population trend discernible since the start of studies in 1988 (Whitehead and Wimmer, 2005). Chapter 2 of this thesis uses data collected in 2010-2011 to examine population size and combines it with earlier photo-identification data (since 1988) to estimate population trends in the period from 1988 to 7 years after the MPA was established.

1.4 METHODS BACKGROUND–SOCIAL STRUCTURE

Chapters 3 and 4 focus on the social structure of northern bottlenose whales in the Gully. Social structure is a description of how the social relationships among different individuals in a population are organized (Hinde, 1976). The social structure of northern bottlenose whales was examined by Gowans (1999) and Gowans *et al.* (2001), who found evidence for fission-fusion social structure with long-term preferred associations among males, and no long-term preferred associations between females. Gowans *et al.* (2001) proposed that northern bottlenose whales may have a similar social structure to coastal populations of another cetacean species, the bottlenose dolphin. The social structure of coastal bottlenose dolphins has been well documented for many populations. The similarities between bottlenose whale and bottlenose dolphin social structures, as well as the potential areas of similarity which had not been studied prior to this thesis, are outlined in Appendix 3. The primary parallel Gowans *et al.* (2001) found between these species was long-term preferred associations between males but not females, although this pattern could have also arisen if there were insufficient data in the past to detect long-term preferred associations between females. In Chapter 3, I re-examine the description of northern bottlenose whale social structure by Gowans *et al.* (2001) using data inclusive of 1988-2011, which represents a much larger data set and thus more powerful analysis.

I then apply techniques that are novel to the study of northern bottlenose whale social structure including network analysis to examine division of the social network into distinct social communities (hereby referred to as ‘community division’). In Chapter 4, I examine social structure on a finer scale than has previously been done, by describing the patterning of associations over small temporal (breathing synchrony) and spatial (relative positions within dyads) scales. Spatial position within dyads and synchrony are associated with social bonds in bottlenose dolphins (Connor *et al.,* 2006; Sakai *et al.,* 2010), and may be used as social signals (Connor, 2007), or a means to reduce intra-alliance tension (Connor *et al.,* 2006), and thus may also be important in the maintenance of social bonds among northern bottlenose whales.

Among endangered wildlife, there are many examples of how an understanding of social structure is important for effective conservation. A classic example is the passenger pigeon, *Ectopistes migratorius*. Human activities were originally responsible for a dramatic decrease in abundances, but according to the estimated birth rates for this species, the remnant populations should have recovered once hunting was banned. Passenger pigeons once formed breeding flocks composed of millions of individuals, and these aggregations were important as the birds were social foragers (Halliday, 1980). As a consequence of both human exploitation and the need for many conspecifics in order to increase foraging success, as colonies became smaller and smaller the breeding success of pairs likely decreased. Eventually, birth rates were too low to allow their recovery. If the natural social facilitation in breeding was what accelerated the decline of this species after their abundance was artificially lowered, then social factors might have been what ultimately drove them to extinction (Halliday, 1980).

For highly social large mammals, when populations are reduced in size there is further potential for the loss of socially learned knowledge. This may happen if there are not enough role models left from whom to acquire the learned behaviours and the transmission of social learning becomes disrupted (Reed, 1999). This may in part explain the absence of right whales in the waters off Labrador (Whitehead *et al.*, 2004). Right whales were once abundant in this area, but became decimated by commercial whaling.

Whitehead *et al.* (2004) suggest that the loss of cultural knowledge about how to use the waters off Labrador might be the reason why right whales have yet to return.

The two main components of this thesis, population size and social structure, can be quite integrated, especially for species that are social, long-lived and have slow reproductive rates. For example, we may be able to estimate parameters such as mortality using the population models I apply in Chapter 2, but to understand the biological significance of this mortality, we must understand how removing a few individuals will affect the rest of society. Even low rates of mortality can greatly affect a population, if key individuals with important social roles are removed from a social network. For example, in African elephant (*Loxodonta africana*) societies, older matriarchs possess enhanced social knowledge which can increase the reproductive success of other elephants in their groups (McComb *et al.,* 2001). Because older females are larger, they are often targeted by hunters. As a result, the young females in a group can suffer fitness implications if their tie to an older matriarch in their social network is lost. Unfortunately, our current understanding of beaked whale societies is much more limited than those of the African elephant. Quantifying how populations change is in the essence of monitoring endangered species, but including an understanding of their social structure paints a more complete picture of how management practices may impact a social species such as the northern bottlenose whale.

1.5 APPLICATIONS OF THESIS RESEARCH

This thesis provides population level information including a current estimate of population size, population trends, and sex-ratios, which are objectives outlined in the DFO recovery strategy mandate for the Scotian Shelf northern bottlenose whale population. Furthermore, it aims to better understand social structure of this population, and processes such as spatial and temporal patterns in the interactions of individuals, which may drive the overall patterns of social organization. A better knowledge of social structure will help inform management decisions for bottlenose whales in the Gully, and possibly other beaked whale populations as well. The utility of this thesis research is not just limited to beaked whales; rather, it contributes to our general knowledge of the conservation of small, endangered populations. In both marine and terrestrial systems, the applications of this thesis may be particularly relevant to understanding population dynamics and efficacy of current management practices for those species that that are long-lived and slow reproducing.

CHAPTER 2
POPULATION ANALYSIS OF ENDANGERED NORTHERN BOTTLENOSE WHALES *(HYPEROODON AMPULLATUS)* ON THE SCOTIAN SHELF, SEVEN YEARS AFTER THE ESTABLISHMENT OF A MARINE PROTECTED AREA

The work presented in Chapter 2 has been accepted for publication (Appendices 1-2): O'Brien, K. and H. Whitehead. In Press. Population size, population trends and demographics of endangered northern bottlenose whales *(Hyperoodon ampullatus)* on the Scotian Shelf, Nova Scotia, Canada, seven years after the establishment of a Marine Protected Area. Endangered Species Research dx.doi.org/10.3354/esr00533

2.1 INTRODUCTION

Species extinctions are occurring at alarming rates around the world (Pimm *et al.*, 1995), and as a consequence, there is a growing need to monitor and protect endangered wildlife (Campbell *et al.*, 2002). In many countries, the protection of vulnerable marine species and habitats is increasingly being tackled through the implementation of Marine Protected Areas (MPAs) (Wood *et al.*, 2008). However, the efficacy of MPAs as a conservation tool has been debated (Jameson *et al.*, 2002; Kareiva, 2006). Nonetheless, there does seem to be consensus that ongoing evaluations are important for the success and improvement of MPAs (Pomeroy *et al.*, 2005; Thompson *et al.*, 2008; Ojeda-Martínez *et al.*, 2009), and biophysical indicators such as focal species abundance can be measured to determine whether MPA objectives are being met (Pomeroy *et al.*, 2005).

I examined the abundance and population trends of an endangered beaked whale population in the Gully, a recently established MPA located on the Scotian Shelf, offshore Nova Scotia. The availability of long-term data collected decades before and after the establishment of the Gully MPA makes this population an appropriate point of focus to examine changes in abundance coinciding with MPA implementation.

The northern bottlenose whale *(Hyperoodon ampullatus)* is a species of beaked whale (family Ziphiidae) that inhabits the North Atlantic Ocean. Northern bottlenose whales forage in deep waters such as submarine canyons where they can dive to 1450 m (Hooker and Baird, 1999) to feed on deep water squid (Reeves *et al.*, 1993). One canyon where northern bottlenose whales are regularly sighted is the Gully submarine canyon located on the edge of the Scotian Shelf (Reeves *et al.*, 1993) about 50 km from Sable Island. It is the largest underwater canyon in the northwest Atlantic. Deep waters of the Gully (depths >500 m) have been identified as critical habitat for this resident population of northern bottlenose whales, and provide a productive habitat for a diversity of marine organisms including other cetaceans (DFO, 2008).

Northern bottlenose whales are also found outside of the Gully, in nearby canyons on the Scotian Shelf such as Shortland canyon (Figure 2.5). Thus the Gully contains an open population, where whales immigrate and emigrate between the MPA and elsewhere on the Scotian Shelf (Wimmer and Whitehead, 2004). At any one time, the majority of all northern bottlenose whales on the Scotian Shelf (referred to as the Scotian Shelf population) are found in the Gully. Population dynamics of northern bottlenose whales within the Gully have been studied since 1988 and a population estimate made prior to the creation of the MPA suggested that approximately 163 northern bottlenose whales used this and other habitat on the Scotian Shelf (Whitehead and Wimmer, 2005).

Small populations often have lower resilience to natural catastrophes and demographic, environmental, and genetic stochasticity (Shafer, 1981). Together, these destabilizing factors can act on small populations to result in reduced evolutionary potential (Frankham, 1996) and increased likelihood of extinction (Shafer, 1981). Because long-lived, slow reproducing animals with stable social and breeding systems are especially vulnerable to extinction (Lacy, 2000), conservation has been a major impetus toward furthering our understanding of the population dynamics of northern bottlenose whales on the Scotian Shelf. Eighty-seven northern bottlenose whales from the Gully were taken by commercial whalers operating out of Blandford, Nova Scotia during the 1960s (Reeves *et al.*, 1993). Whaling off Nova Scotia ended several decades ago, but unfortunately without a baseline population estimate prior to the emergence of commercial whaling, it is difficult to assess the impacts of whaling on this species.

The genetic distinctiveness of Gully northern bottlenose whales from neighbouring populations (Dalebout *et al.*, 2006), the small population size (Whitehead *et al.*, 1997b) and the suspected vulnerability to environmental degradation (Reeves *et al.*, 1993) contributed to the Scotian Shelf northern bottlenose whales being assessed as Endangered by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) in 2002, and the Species at Risk Act (SARA) in 2006. In 2004, critical habitat of the northern bottlenose whale within the Gully was designated a Marine Protected Area (DFO, 2008).

In addition to past exploitation, there are several modern human activities which could potentially have negative impacts on this population. Northern bottlenose whales are thought to be vulnerable to entanglement in fishing gear and noise pollution from shipping and seismic testing such as that related to oil and gas exploration (Hooker *et al.*, 1999; Gowans *et al.*, 2000b; Whitehead and Hooker, 2012). Tourism is also an emerging industry in the Gully MPA, and the future effects of offshore whale watching activities on whales and their habitat are uncertain.

The Gully MPA regulations that were put in place in 2004 prevent seismic exploration activities within the MPA and recommend that commercial shipping vessels avoid the area. However, the sounds of seismic surveys outside the MPA can be heard inside it (McQuinn and Carrier, 2005). At present, there are only low levels of ship traffic in the Gully (DFO, 2009). Fishing is not allowed in the core area of the MPA which has been identified as northern bottlenose whale critical habitat, although restricted fishing activities and gear are permitted in peripheral areas of the MPA (DFO, 2008) and sets of drifting fishing gear have been observed within the MPA boundaries on at least two occasions (K. O'Brien and H. Whitehead, unpublished data). The core area and boundaries of the Gully MPA are illustrated in Figure 2.5.

Understanding whether this bottlenose whale population is stable, growing, or in decline, is a current conservation priority (DFO, 2009). Before the MPA no significant trends were identified, suggesting the population was stable (Whitehead and Wimmer, 2005). This study evaluates population trends in the context of the management changes that were implemented when the Gully became an MPA. Because bottlenose whales are long-lived, slow reproducing animals (Benjaminsen, 1972), growth is very difficult to detect over the relatively short time span since the Gully MPA was established. Thus the examination of population trends is likely a more appropriate tool to detect population decline, which could potentially occur more rapidly than population growth.

In addition to changes in abundance, whaling could have altered the sex-ratio if whalers specifically targeted mature males as was done with sperm whales hunted off Peru (Whitehead *et al.*, 1997a). Whaling on the Scotian Shelf took place between 1962 and 1967, during which period records show 87 northern bottlenose whales were killed, although likely more were injured or lost (Reeves *et al.*, 1993). Mature males could have been targeted because they are larger than females and so would produce more oil, and because females do not have spermaceti (Reeves *et al.*, 1993). Altering the age and sex-ratios by hunting has been shown to have strong effects on the population growth rates of many ungulates and terrestrial carnivore populations (Milner *et al.*, 2007). By comparing the past and current sex-ratios, I examined whether the population demographics of northern bottlenose whales in the Gully have changed over the last 23 years, in order to understand the implications of altered demography on this population's recovery.

The goals of this study were: (1) to determine the population size of northern bottlenose whales in the Gully, (2) to examine population trends to understand how the population may have changed since the establishment of the MPA and (3) to examine how the sex-ratio has changed over time. Because early studies did not include effort in canyons other than the Gully, all long-term analyses are restricted to only those whales observed in the Gully (referred to as the Gully northern bottlenose whale population). As the unit of management is the Scotian Shelf population, I also produce a current population estimate for the entire Scotian Shelf. Together, the descriptions of population abundance, trends and demographics for the Gully northern bottlenose whale population since the establishment of the MPA will indicate whether present mitigation measures have been sufficient to protect this endangered beaked whale population from decline.

2.2 METHODS

2.2.1 Photograph Collection

A total of four surveys, each three weeks in duration, were conducted from the 12 m auxiliary sailing vessel *Balaena* during the summer months of 2010 and 2011. Survey effort rotated between the Gully, and neighbouring canyons (Shortland and Haldimand), with the greatest effort concentrated in the Gully. When northern bottlenose whales were encountered, photographs of both the left and right sides of dorsal fins and melons were taken, and individuals were photographed at random, irrespective of whether or not they had previously been photographed or how well marked they were. Digital photographs were taken with Canon 50D and Canon 20D SLR cameras, each fitted with a fixed 300 mm lens. Similar field methods for collecting photo-identification data on northern bottlenose whales using film photography have been used since 1988, and are described in detail by Gowans *et al.* (2000b) and Whitehead and Wimmer (2005).

2.2.2 Photograph Analysis

Photographs were ranked by quality (Q) based on criteria established by Gowans and Whitehead (2001). These criteria were originally designed to quality-rate film photographs, so I modified them slightly to allow for the digital photographs (Figure 2.1). Criteria for focus, orientation and proportion of the body visible were quality-rated irrespective of individual markings. Exposure was of less consequence, as images could be adjusted in this respect digitally. Additionally, the proportion of the frame occupied by the dorsal fin was not included as a criterion for digital images, because they were of much higher resolution than film photographs. Digital images were instead magnified until the dorsal fin occupied at least ¼ of the frame, after which the sharpness of focus was used to determine the quality of the photograph.

To ensure that even subtly marked individuals could be identified, I restricted the data set to high quality photographs (Gowans and Whitehead, 2001). If a photograph was ranked poor in one or more criteria it was given a $Q \leq 3$. $Q=4$ photographs were good in all criteria, $Q=5$ were of excellent quality for all criteria, however only the dorsal fin was visible, and $Q=6$ had excellent quality for all criteria with the dorsal fin plus the flank

(± one dorsal fin width) visible. To avoid biasing toward highly identifiable individuals, only photographs rated *Q*≥4 were included in all analyses.

The highest quality photograph of each individual identified in each year (2010 and 2011) was used to match between 2010 and 2011 sampling periods (Figure 2.1), and then matched by eye to a printed film catalogue (1988-2009), assisted using an 8X magnifying glass. All matches were confirmed by K. O'Brien.

Figure 2.1 Comparison of the best film and the best digital photograph of the same individual northern bottlenose whale *(H. ampullatus)*. Digital photographs are high resolution colour images, and thus contain additional information that can aid in matching.

Figure 2.2 The same northern bottlenose whale *(H. ampullatus)* individual resighted after one year. Individual whales are distinguished by unique marks such as scars on the flank and notches on the dorsal fin.

2.2.3 Statistical Analyses

2.2.3.1 Population Size

Two-sample Petersen mark-recapture estimates using Seber modifications (Seber, 1982) were conducted for the Scotian Shelf northern bottlenose whale population (the Gully, Shortland and Haldimand) as well as for just the Gully population, on the digital photo-identification data from 2010 and 2011. The following equation was used where N_g = population size, n_1 = the number of individuals identified in 2010, n_2 = the number of individuals identified in 2011, and m = the number of individuals identified in both 2010 and 2011:

$$N_g = \left(\frac{(n_1 + 1)(n_2 + 1)}{(m + 1)} \right) - 1$$

All mark types were used to identify individuals over the 12 month period, with the exception of diatom patches seen on the skin because the shape of these patches changed rapidly. Left and right dorsal fin side data were analysed separately, and the mean estimates of N_g were averaged. Estimates of SE for each side were calculated following Seber (1982), and averaged. CI were calculated assuming the lognormal distribution (Whitehead, 2009), and averaged across both sides.

2.2.3.2 Population Trends

Open population models were fit to the photo-identification data in order to examine population trends since 1988. Open population models differ from simpler closed population estimates such as the Petersen mark-recapture estimates described above, because open models include additional parameters such as mortality, reimmigration, heterogeneity in identification and/or mortality, and a linear population trend. Some of these models, including those that incorporate heterogeneity in parameters, are described by Whitehead and Wimmer (2005); other more complex models such as those with quadratic or piecewise trends and their equations are listed in Table 2.1.

Piecewise trends were included to examine scenarios where population trends differed before and after a given year. This transition year was either specified in the model as a year when major environmental changes occurred such as 1999 (when the highest seismic noise was recorded on the Scotian Shelf; COSEWIC, 2011), 2003 (when several oil spills occurred near Sable Island; Hooker *et al.*, 2008), and 2004 (when the Gully became a MPA). If the year was not specified it was estimated by parameterization. Thirty-five candidate models were fit to the northern bottlenose whale photo-identification data and model preference was determined by AIC, which evaluates how well a model is supported by the data, while compensating for the inclusion of additional parameters (Burnham and Anderson, 2002). Parameter values and 95% confidence intervals (CI) were estimated using maximum likelihood.

To prevent bias in effort between locations (the Gully was surveyed since 1988 whereas visits to Shortland and Haldimand began in 2003), I only included data that were collected in the Gully in the trend analysis. Due to the long time span of the analysis (23 years), the assumption that animals do not lose their marks between sampling periods was met by restricting long-term analyses to reliably marked individuals, those with notches in the dorsal fin, back indents, and/or mottled patches which have been shown to persist over many years (Gowans and Whitehead, 2001).

Open population modelling analyses were conducted only on reliably marked individuals, and estimates of population size for marked individuals (Nm) were then scaled to account for the proportion of the population without reliable marks, by multiplying N_m by h, the proportion of reliably marked individuals within the entire population (Whitehead and Wimmer, 2005). I estimated h as the ratio of all high quality photographs ($Q \geq 4$) to those photographs of reliably marked whales (left and right photographs combined). After calculating this ratio separately for each year, I calculated the mean h across all years. I estimated the coefficient of variation CV(h) by dividing the standard deviation weighted by the number of high quality photographs, by the sample mean. The mean population estimate for the total population of whales (reliably and unreliably marked) in the Gully

(N_t) and upper and lower 95% CI from the best supported model for each fin side were determined using the following equation adapted from Whitehead and Wimmer (2005):

$$CI\ (N_t) = N_t \pm 1.96\ N_t \sqrt{CV(h)^2 + \left\{ \frac{\left[CI\ (N_m) - N_m \right]}{1.96\ N_m} \right\}^2}$$

As open population modeling provides estimates of population size for each year, I was most interested in determining the most recent estimate, for 2011. Estimates for N_t and CI (N_t) from right and left side dorsal fin photographs were then averaged. All population modelling was done using the statistical software SOCPROG (Whitehead, 2009).

2.2.3.3 Changes in the Sex-Ratio Over Time

I examined the melon photographs of all individuals identified from high quality dorsal fin photographs in 2010 and 2011. Melon photographs were quality-rated and assigned to one of three age/sex classes based on secondary sexual characteristics (Figure 2.3), following the methods described by Gowans *et al.* (2000a). The first class included immature whales (male and female) and adult females (F) because they have melon characteristics that are indistinguishable from each other. The second class comprised subadult males (SM) which had begun to develop secondary sexual characteristics including flattening of the anterior melon. The third class consisted of mature males (MM), the melons of which were square in profile and white in colour.

Figure 2.3 Example of variation in melon shape and colouration for the female/immature (F), subadult male (SM), and mature male (MM) age/sex classes of northern bottlenose whales.

For each year (1988-2011), I expressed the number of whales in each sex class as a ratio of the total number of whales for which the sex was determined. I then tested how well the term ‘year’ predicted the above ratio for each sex class using a generalized linear model with a binomial distribution, performed in R (R Development Core Team, 2013). The AIC values for null and complete models were compared by stepwise regression to determine if ‘year’ was a useful predictor of the sex-ratio. I analysed photographs of the left and right sides of melons separately, and there was agreement between the two sides.

2.3 RESULTS

2.3.1 Population Size

For the Scotian Shelf population, a total of 4147 high quality photographs from 2010 and 2011 were of sufficient quality to include in the analyses, from which 127 (right) and 121 (left) unique individuals were identified. Petersen mark-recapture estimates from 2010 and 2011 data were 150 animals (95% CI=135-165 animals) from the analysis of right dorsal fin side photographs, and 136 animals (95% CI=125-147 animals) using left side photographs. The average estimate of northern bottlenose whales on the Scotian Shelf was 143 animals (SE=7.9, 95% CI=129-156 animals). In total, 89% (95% CI=81-98%) of the estimated total population has been photographed.

For the population that uses the Gully, a total of 3272 high quality photographs from 2010 and 2011 were included, from which 94 (right) and 92 (left) unique individuals were identified. Petersen mark-recapture estimates from 2010 and 2011 data were 121 animals (95% CI=105-137 animals) and 110 animals (95% CI=98-122 animals) from photographs of right and left dorsal fin sides (respectively). The average estimate of northern bottlenose whales in the Gully was 116 animals (SE=8.7, 95% CI=101-130 animals), of which 81% (95% CI=72-93%) of the animals have been photographed.

2.3.2 Population Trends

In total, 3153 left and 2960 right dorsal fin side photographs collected between 1988 and 2011 were of sufficient quality to include in the analyses (of which 1227 left and 1219 right dorsal fin side photographs were collected between 2010 and 2011). A complete list of all 35 models with associated AIC and ΔAIC values, scaled population estimates and estimated trend parameters is provided in Table 2.1. The models with the lowest AIC values, and that therefore were best supported by the photo-identification data, included the parameters mortality and heterogeneity in identifiability (right side photographs), and heterogeneity in mortality and identifiability (left side photographs) (parameters in bold, Table 2.1). Parameter estimates from the best supported open population models are listed in Table 2.2.

Similar to closed population models, open population models also generate estimates of population size. The most recent population estimate (2011) of reliably marked individuals within the population were the same for both dorsal fin sides, at 107 animals (95% CI=92-128 animals). The proportion of high quality photographs to those showing individuals with reliable marks was 1.46 (CV=0.12), yielding scaled estimates of total population size for the Gully northern bottlenose whale population of 158 animals (95% CI=114-205 animals) from right side photographs, and 157 animals (95% CI=113-205 animals) from left side photographs. After averaging both dorsal fin sides, the estimate for the entire Gully population was 157 animals (95% CI=113-205) animals. Because population estimates for open and closed models differed, they were plotted side-by-side on Figure 2.4 for comparison.

Table 2.1 A complete list of candidate open population models for northern bottlenose whales *(H. ampullatus)* in the Gully with support for each model indicated by lowest ΔAIC values. The best supported models are in bold, and all candidate models have associated scaled population estimates (N_t), AIC values, ΔAIC values, and trends estimated by parameterization (two trends are given for piecewise models). Models were fitted using identifications made from right and left sides of dorsal fins separately. Heterogeneity (Het) and identifiability (ID) are abbreviated, and example general equations for models with trends represented with asterisks (*) are listed below the table.

	Left side photographs				**Right side photographs**			
Model	**Nt**	**AIC**	**ΔAIC**	**trend(s) %/year**	**Nt**	**AIC**	**ΔAIC**	**trend(s) %/year**
Mortality	128	1114.78	34.66		133	1163.98	38.07	
Mortality + trend	124	1115.25	35.13	-0.01	133	1165.88	39.96	0.00
Reimmigration	119	1108.62	28.50		116	1149.57	23.66	
Reimmigration + mortality	117	1109.31	29.19		117	1149.99	24.07	
Het in mortality	119	1102.05	21.93		126	1158.47	32.56	
Het in mortality + trend	114	1102.21	22.09	-0.01	126	1160.46	34.55	0.00
Het in identifiability	**157**	**1080.37**	**0.25**		**157**	**1125.91**	**0.00**	
Het in ID + trend	157	1082.37	2.25	0.00	157	1127.91	1.99	0.00
Het in ID + het in mortality	**157**	**1080.12**	**0.00**		**158**	**1127.27**	**1.35**	
Het in ID + het in mortality + trend	157	1082.12	2.00	0.00	157	1129.24	3.33	0.00
Quadratic trend*	128	1116.90	36.78		139	1167.17	41.26	
Stable until year *y* then increasing with trend *q***	141	1117.25	37.13	-0.01	135	1167.54	41.63	-0.02
Stable until 2004 then increasing with trend *q*	130	1115.39	35.27	-0.03	135	1165.64	39.72	-0.01
Stable until 2003 then increasing with trend *q*	130	1115.47	35.35	-0.02	135	1165.66	39.75	-0.01
Stable until 1999 then increasing with trend *q*	131	1115.16	35.03	-0.02	135	1165.62	39.70	-0.01
Decreasing with trend *q* until year *y* then stable***	107	1117.25	37.13	0.01	127	1167.88	41.96	0.00
Decreasing with trend *q* until 2004 then stable	114	1115.52	35.40	0.01	132	1165.96	40.05	0.00
Decreasing with trend *q* until 2003 then stable	115	1115.55	35.43	0.01	132	1165.97	40.06	0.00
Decreasing with trend *q* until 1999 then stable	121	1116.15	36.03	0.01	135	1165.95	40.03	0.00
Piecewise (*y* estimated)****	123	1119.03	38.91	-0.04 0.00	147	1169.31	43.40	-0.04 -0.01
Piecewise (*y*=2004)	122	1117.18	37.06	-0.02 0.01	143	1167.48	41.57	-0.02 -0.01
Piecewise (*y*=2003)	122	1117.21	37.09	-0.02 0.01	142	1167.53	41.61	-0.02 -0.01
Piecewise (*y*=1999)	128	1117.10	36.97	-0.01 0.00	141	1167.32	41.41	-0.01 -0.01
Het in ID + quadratic trend	166	1083.78	3.66		167	1129.13	3.22	
Het in ID + stable until year *y* then increasing with trend *q*	157	1084.32	4.20	-0.00	159	1129.67	3.76	-0.01
Het in ID + stable until 2004 then increasing with trend *q*	157	1082.29	2.17	-0.01	158	1127.79	1.88	-0.01

Table 2.1 Continued.

	Left side photographs				Right side photographs			
Model	**Nt**	**AIC**	**ΔAIC**	**trend(s) %/year**	**Nt**	**AIC**	**ΔAIC**	**trend(s) %/year**
Het in ID + stable until 1999 then increasing with trend *q*	157	1082.31	2.19	0.00	158	1127.77	1.85	-0.01
Het in ID + decreasing with trend *q* until year *y* then stable	160	1084.32	4.19	0.00	164	1128.94	3.02	-0.03
Het in ID + decreasing with trend *q* until 2004 then stable	160	1082.35	2.23	0.00	158	1127.91	1.99	0.00
Het in ID + decreasing with trend *q* until 2003 then stable	159	1082.36	2.23	0.00	159	1127.90	1.99	0.00
Het in ID + decreasing with trend *q* until 1999 then stable	161	1082.29	2.17	-0.01	162	1127.77	1.86	-0.01
Het in ID + piecewise (*y* estimated)	183	1085.65	5.53	-0.09 -0.01	155	1131.91	5.99	0.00 0.00
Het in ID + piecewise (*y*=2004)	169	1084.14	4.01	-0.02 -0.01	170	1129.61	3.70	-0.02 -0.01
Het in ID + piecewise (*y*=2003)	165	1084.24	4.11	-0.01 -0.01	168	1129.66	3.74	-0.01 -0.01
Het in ID + piecewise (*y*=1999)	164	1084.16	4.04	-0.01 -0.01	168	1129.41	3.50	-0.01 -0.01

Model* $\exp(q_1.t + q_2.t^2)$

Model** $\exp((t>y).q.(t-y))$

Model*** $\exp((t<y).q.(y-t))$

Model**** $\exp((t>y).\ q_1.(t-y)+(t<y).q_2.(y-t))$

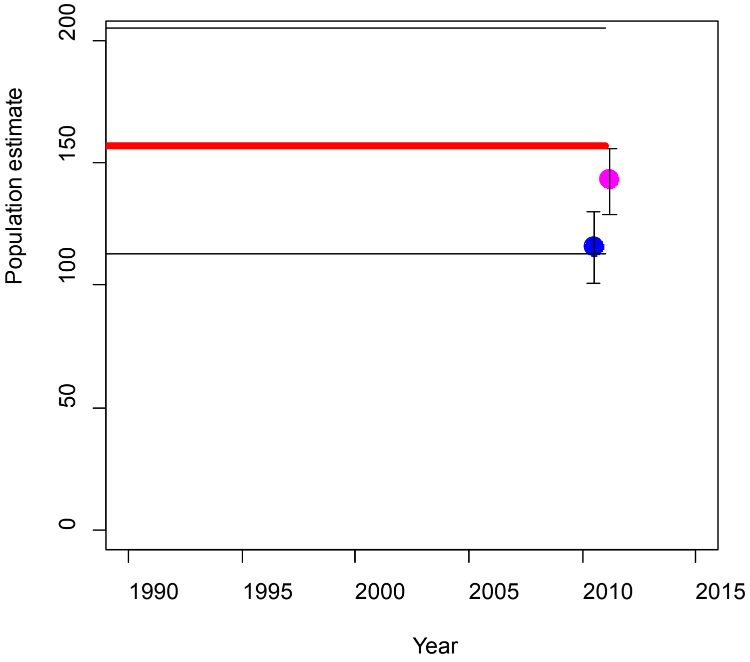


Figure 2.4 Side-averaged mean population estimates of northern bottlenose whales *(H. ampullatus)* in the Gully, comparing the open population estimate from 1988-2011 (red) and closed population estimate 2010-2011 (blue). The Scotian Shelf closed population estimate (magenta) is jittered for clarity. Black horizontal (1988-2011) and vertical (2010-2011) lines represent 95% confidence intervals, and the dotted green line shows when the Gully MPA was established in 2004.

Table 2.2 Parameter estimates for the best supported models from left and right side dorsal fin photo-identifications of northern bottlenose whales in the Gully, as well as side-averaged parameter estimates. Parameter estimates are presented as mean (likelihood 95% CI).

Parameter	**Right dorsal fins**	**Left dorsal fins**	**Averaged parameter estimate**
Mortality rate	0.09 (0.07–0.11)	0.13 (0.08–0.18)	0.11 (0.07–0.15)
Estimated proportion of low-mortality/low-identifiability individuals	0.68 (0.52–0.85)	0.71 (0.51–0.86)	0.70 (0.51–0.85)
Estimated mortality of low-mortality individuals	n/a	0.07 (0.03-0.11)	n/a

Regardless of the dorsal fin side, the same two models described in Table 2.2 were best supported by the photo-identification data. The second best models for each side had moderate support, indicated by only a small difference in AIC values compared to the best supported models (ΔAIC of 0.24 for left sides, and 1.35 for right sides). There was much less support for all models that included linear, quadratic or piecewise trends, as indicated by higher AIC values. Adding a linear population trend to the parameters of the simplest and best supported candidate model, the estimated population trends using left and right side photo-identifications (respectively) were -0.08% per year and -0.01% per year, and averaging these trends (as well as their respective 95% CI) yielded a side-averaged trend of -0.05% per year (95% CI= -2.0 to 2.0% per year).

2.3.3 Changes in the Sex-Ratio Over Time

The most abundant age/sex class was females/immatures (Figure 2.5). The sex-ratios were also quite similar between the Gully and Shortland canyon, except for subadult males who were more common in the Gully (Figure 2.5).

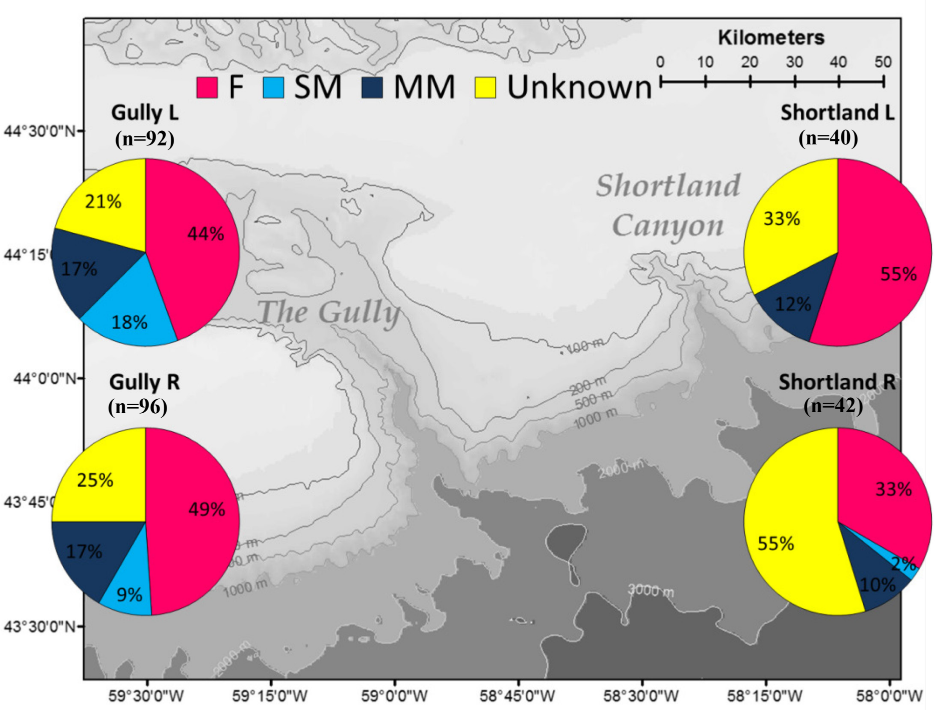


Figure 2.5 Current (based on 2010-2011 data) age and sex structure of whales found in the Gully and Shortland canyons. The background map was provided by H. Moors-Murphy. Separate analyses were conducted using photo-identification data from left (L) and right (R) dorsal fin sides, and results for both sides were presented for comparison. Age/sex classes are abbreviated as females/immatures (F), subadult males (SM), and mature males (MM).

The term 'year' did not appear to be a useful predictor of the number of individuals of any sex class across time (*P* >0.05, Table 2.3). Also, models that included the variable 'year' as a predictor generally had less support than their corresponding null models, as indicated by lower AIC values (Table 2.3). This suggests the sex-ratio has not changed significantly between 1988 and 2011. In two cases the models with the term 'year' had higher support than the null models (F~Year for left side photo-identification data, and SM~Year for right side photo-identification data). However, these patterns were not consistent between left and right side photo-identification data, and *P* values for the parameter 'year' were relatively high, which overall suggests little support for a significant change in the ratio of age/sex classes over time.

Table 2.3 Fit of models for each age/sex class predicted by year, compared to the fit of the corresponding null models. Support for models with year as a predictor are indicated by a lower ΔAIC compared to the null model. *P* values are estimates of the probability that a parameter was included in a model by chance, and thus indicates the utility of including that parameter in the model.

Fin side	**Left Models**	**AIC**	**ΔAIC**	**Coefficients for models with year as the predictor variable**			
				Term	**Estimate**	**SE**	***P* value**
Left	F~Year	68.391	0	(Intercept)	36.266	24.475	0.138
	null	68.514	0.123	Year	0.018	0.012	0.145
	MM~Year	69.250	0.022	(Intercept)	42.117	31.031	0.175
	null	69.228	0	Year	-0.022	0.016	0.163
	SM~Year	61.757	0.625	(Intercept)	48.036	43.412	0.269
	null	61.127	0	Year	-0.025	0.022	0.249
Right	F~Year	72.151	0.914	(Intercept)	25.535	23.907	0.285
	null	71.237	0	Year	0.012	0.012	0.297
	MM~Year	69.086	1.857	(Intercept)	9.856	28.995	0.734
	null	67.229	0	Year	-0.005	0.015	0.706
	SM~Year	59.774	0	(Intercept)	82.966	45.592	0.069
	null	61.469	1.695	Year	-0.043	0.023	0.062

2.4 DISCUSSION

Using closed population models, I estimate the current population size of northern bottlenose whales in the Gully is 116 animals (SE=8.7, 95% CI=101-130 animals). The population size estimate based on open population models (157 animals, 95% CI=113-205) was greater, although less precise (Figure 2.4). These estimates are both consistent with past studies of this population that used open population models (Whitehead *et al.*, 1997b; Gowans *et al.*, 2000b; Whitehead and Wimmer, 2005). While open population models are useful for exploring temporal trends, population size is often estimated with greater uncertainty. The closed population estimates presented in this study are more precise than the open population estimates largely as a result of high survey effort in 2010 and 2011 combined with higher quality and greater numbers of digital photographs which increased the likelihood of capturing excellent images of each individual. High quality digital photographs allowed fine details of nicks and marks to be resolved, and so for the closed population estimates of the Gully and Scotian Shelf populations, all of the individuals in high quality photographs could be identified. Thus in contrast to the open models, there was no need to scale the closed population estimates to account for non-marked individuals. As a result, uncertainty around closed population estimates was not confounded by error introduced by scaling. Finally, a very high proportion of the Scotian Shelf population was actually observed (89%; 95% CI=81-98%), and Petersen mark-recapture analyses have very little bias at such high sample sizes (Robson and Regier, 1964). In general, photographs of calves seemed to have low quality-ratings, often because of poor focus or exposure which made it impossible to see subtle marks and scars on the skin. Thus calves may have been underrepresented, and it is possible this estimate of population size could be slightly conservative as a result.

Because northern bottlenose whales in the Gully are part of a larger Scotian Shelf population (which includes the Gully, Shortland and Haldimand canyons), I estimated the population size of whales on the entire Scotian Shelf, 143 animals (SE=7.9, 95% CI=129-156 animals). This greater than the Gully estimate, but shows that a large portion of the northern bottlenose whales on the Scotian Shelf have been observed within the Gully MPA. Since the Scotian Shelf population is not fully mixed (Wimmer and Whitehead, 2004) and whales can enter and leave the Gully MPA, current legislation within the MPA will not protect them at all times. However, Hooker and Gerber (2004) note that MPAs can be beneficial even if a marine predator does not remain exclusively within the MPA boundaries, by reducing the frequency an animal encounters anthropogenic threats.

To examine population trends in long-term data (since 1988), open population models were explored as they account for mortality, births, immigration and emigration; dynamics which cannot be ignored over multiple decades. Conventional mark-recapture techniques (such as the Petersen mark-recapture closed population model used in this chapter) often assume homogenous capture and recapture probabilities among all individuals in a population. However, heterogeneity in the identifiability of individuals resulting from individual variation in behaviour or morphology is thought to be common if not ubiquitous among mark-recapture studies of cetaceans (Hammond, 1986; 1990). Heterogeneous capture probabilities among other cetacean populations have been documented, for example humpback whales in the Gulf of Maine (Hammond, 1990) and sperm whales off the Azores (Matthews *et al.*, 2001).

I attempted to account for heterogeneity in identifiability in three ways. First, I only used high quality photographs, so that even subtly marked individuals could be identified. Second, I restricted the analysis to include only individuals with mark types that are retained over many years, and third, I built models that accounted for any remaining heterogeneity in identifiability. Factors such as age-specific biases in mortality can lead to violation of the assumption that mortality rates are homogenous, especially when mark-recapture analyses are applied over longer temporal scales (Hammond, 1986). I included candidate models in this analyses that incorporated heterogeneity in identifiability and/or mortality by dividing the population into two groups, and allowing the probability of mortality or identification to differ between groups but not within groups. Similar to past research on this population (Whitehead and Wimmer, 2005), the models that included heterogeneity in identifiability and/or mortality best fit the data. Although incorporating heterogeneity in such analyses is potentially useful, it still can only account for limited heterogeneity in capture probabilities which remains a possible source of bias in the population estimates presented in this chapter.

Before the MPA, there was no detectable population trend in the Gully (Whitehead and Wimmer, 2005). The inclusion of data collected since 2004 added a substantially greater time span over which to examine population trends, and considerably increased power to detect non-linear trends. The fact that none of the complex models incorporating a linear or non-linear trend were selected for, despite including more data and thus presumably greater statistical power to detect a trend, provides further support that the current population size of northern bottlenose whales in the Gully is stable. The best supported model with a trend had a 95% CI of -2.0 to 2.0% per year, suggesting that while stable, the population could be decreasing or increasing within a net range of ± 3 animals per year.

The estimated mortality rate was 11% (95% CI=7-15%), which seems unrealistic given northern bottlenose whales are long-lived cetaceans (and thus recruitment rate is likely low) and overall, this cetacean population appears stable. Overestimated rates of mortality could have been the result of violating the assumption that ‘reliable’ marks do not change over time, which could occur if a ‘reliable’ mark became obscured by a new mark. Such changes would not affect the estimate of population size, but would inflate the estimate of mortality. It is possible, however, that activities outside of the MPA (*e.g.* fishing, ship traffic or underwater noise) could influence mortality given the whales can move in and out of the MPA.

Since survey effort focused only on the Gully in years 1988-2002, the results of these models, including estimates of population trends and mortality, are limited to the Gully and are not generalized for the Scotian Shelf population as a whole. However, the Gully is the only part of the Scotian Shelf northern bottlenose whale habitat that has been protected as a MPA, and thus provides an appropriate scale to examine the effectiveness of current conservation initiatives.

It is still unclear why the population size of northern bottlenose whales in the Gully is so small. It is possible the small population size is due to depletion from past whaling (Reeves *et al.*, 1993), current anthropogenic factors depressing population growth, or that the population has recovered from past exploitation and has stabilized at or near the carrying capacity of the Gully environment (DFO, 2009). Genetics have provided support that the population size was small even before the emergence of commercial whaling in this region (Dalebout *et al.*, 2006). Understanding the mechanisms regulating population size will likely only be resolved with long-term monitoring of this population beyond the scope of this study.

Based on the current age/sex structure of the Scotian Shelf population, the Gully appears to be important habitat for groups of bottlenose whales comprised of mature males, females and subadult males, whereas areas outside of the MPA may be used less by subadult males. Assigning individuals to qualitative age/sex classes based on melon shape is inherently subjective, although classification of all whales in 2010-2011 was determined by a single observer. Thus observer bias cannot explain the fewer sightings of subadult males in Shortland canyon. There is however a greater proportion of whales of unknown age/sex in Shortland canyon, indicating the pattern that was observed warrants further study.

While classifying the sex of whales, I noticed two individuals (#2013 and #293) who were classified as mature males in 2011 based on melon shape (square in profile) and despite being relatively old their melons had not yet turned white. Individual #2013 was first identified in 2002 and again seen in 2011, so he was at least 9 years old (and could be much older). Individual #293 was first identified in 1990, so he was at least 21 years old when he was resighted in 2011. This seemed to contradict the general description of mature male bottlenose whales as having melons that are white in colour (Reeves *et al.*, 1993). Benjaminsen and Christensen (1979) estimated that male northern bottlenose whales caught off Labrador matured between 7-11 years, and whales older than this were considered sexually mature males. Their measurements were determined by examining the histology of testes from whales hunted in this region. My examination of melons revealed that either mature males develop white melon colouration at a later age than was previously thought or that not all mature males acquire this characteristic.

Similar to the findings for population abundance, there was no evidence that the sex-ratio has changed significantly over time, despite whaling losses in the past. Humans often selectively hunt animal populations (Milner *et al.*, 2007), for example, by removing large males in sexually dimorphic species (Whitehead *et al.*, 1997a). Two thirds of the northern bottlenose whales that were taken by whalers off Nova Scotia, and that were sexed, were males (Reeves *et al.*, 1993). The results of this chapter suggest that either whaling did not destabilize the sex-ratio prior to this study (starting in 1988) or any that deviations in the sex-ratio had already equilibrated by 1988.

My study set out to investigate whether conservation objectives of the Gully MPA are being met under the present level of habitat protection. The conservation goal for northern bottlenose whales on the Scotian Shelf is to maintain at least a stable population (DFO, 2009). These results suggest that both the population size and demographics have been stable since before the establishment of the MPA, and remain so. However, future events, whether stochastic or related to climate change (Hoegh-Guldberg and Bruno, 2010), could have the potential to affect this population and put the effectiveness of this MPA to further test.

CHAPTER 3
THE SOCIAL STRUCTURE OF AN ENDANGERED POPULATION OF NORTHERN BOTTLENOSE WHALES (*HYPERDOODON AMPULLATUS*) ON THE SCOTIAN SHELF, NOVA SCOTIA

3.1 INTRODUCTION

In light of the well documented link between low densities and low per capita birth rates known as the Allee effect, small populations are often regarded as conservation concerns (Lamont *et al.,* 1993; Kuussaari *et al.,* 1998; Somers *et al.,* 2008). The Allee effect can operate via many mechanisms such as inbreeding depression, reduced opportunities for cooperation, and fluctuations in sex-ratios known as demographic stochasticity (Courchamp *et al.,* 1999). Allee effects can lead small populations to extinction, and social species may be particularly vulnerable because of the many benefits they may derive from the presence of conspecifics such as communal knowledge (*e.g.* African elephants, *Loxodonta* spp.; McComb *et al.,* 2001) or communal infant care (*e.g.* sperm whales, *Physeter macrocephalus*; Whitehead, 1996; Gero *et al.,* 2009). Furthermore, not all social behaviours positively affect fitness, and if certain behaviours limit birth rates or increase mortality, then social structure can also have important implications for population persistence beyond those relating to the Allee effect (Reed, 1999; Blumstein, 2010). For example, mating systems which are an element of all social systems (Kappeler and van Schaik, 2002) can have a profound influence on the effective population size (Parker and Waite, 1997). This point is well illustrated among marmoset monkeys, were the presence of a dominant female can result in the reproductive suppression of subordinate females (Abbott, 1987). The relationship between sociality and population viability should be an important consideration in the conservation of social species and especially small endangered populations.

In Chapter 2, discussion was focused on the conservation of an endangered population of northern bottlenose whales *(Hyperoodon ampullatus)* in the context of external factors that could threaten population persistence. I demonstrated that northern bottlenose whales in the Gully are stable, both in terms of the total population abundance and the sex-ratio.

A goal of the Gully Marine Protected Area was to protect the critical habitat of these whales, and by extension, protect the animals from extrinsic threats such as noise pollution, commercial shipping traffic and potential interactions with fisheries activities (DFO, 2008). The MPA regulations may help protect this population from many environmental or external threats, but current conservation measures should also consider intrinsic factors such as demographic stochasticity, to which small populations are especially vulnerable (Legendre *et al.,* 1998; Melbourne and Hastings, 2008). This chapter focuses on social structure, a possible intrinsic factor that could also potentially influence population persistence.

Social or group living can enable individuals to maximize their ability to forage, avoid predation and reproduce (van Schaik and van Hoof, 1983), thus there is great motivation for mammals to live in societies. Diverse social systems have been documented within class Mammalia, and have been studied extensively among primates (*e.g.* van Schaik and van Hoof, 1983; Kappeler and van Schaik, 2002) and cetaceans (*e.g.* Whitehead, 1996; Connor *et al.,* 1998; Bräger *et al.,* 2004). In this study, I follow the definition of social structure provided by Hinde (1976), where social structure is the overall patterns that emerge from the way social relationships are organized within a society (Hinde, 1976): how individuals interact with each other, the nature of these interactions, and how they are patterned over time. The terms social systems, structure and organization are often used synonymously, although social structure is sometimes distinguished from social organization, as social structure describes the composition of societies by determining class membership (*e.g.* age, sex, pregnant), whereas social organization describes how class structures are maintained within society (Box, 1973).

Data collected on northern bottlenose whales since 1988 present the opportunity to examine social relationships (associations) between individuals across multiple decades. The overall goal of this study is to piece together a more detailed understanding of social structure, using recently collected data to address the following questions about social relationships: *(1) How does association strength vary within and between age/sex classes? (2) How variable are associations among individuals? (3) How large are* *aggregations of whales? (4) Does gregariousness vary among individuals overall, and in their rates of association with different age/sex classes? (5) Is there evidence for short-term preferred associations? (6) Is there evidence for long-term preferred associations? (7) How do relationships change over time? (8) Can the social structure be represented as a set of hierarchically nested tiers, or separate social communities?*

Since social structure is based on the interactions between individuals (Hinde, 1976), these questions allow us to better understand the types, patterns and longevity of social interactions (*Questions* 1, 2, 5 and 6). Because the above questions use statistics to quantify different types of relationships, and ultimately I wish to understand the nature not just the presence of different social relationships, I also examine some case studies of specific individuals in the population. In addition, investigating group size and gregariousness (*Questions* 3 and 4) may indicate environmental pressures such as predation (which tends to increase group size) or food limitations (which tend to decrease group size) in the Gully. Finally, I explored whether the social network of the Gully northern bottlenose whales is divided into distinct social communities (hereby referred to as 'community division') because effective management of endangered populations such as the northern bottlenose whales on the Scotian Shelf may require that social community division be accounted for (*Question* 8). Distinct social communities within a single population have been documented for bottlenose dolphins (Lusseau *et al.,* 2006). Understanding whether there is social community division could be important when deciding at which scale management is being applied, at the level of species, population, or social community.

From a social evolutionary perspective, this study also provides a model of beaked whale social organization. Factors such as niche, habitat or phylogeny have been suggested as potential drivers for the social evolution of different social structures. I will compare species that share similar ecological constraints to help identify commonalities and differences in the evolution of social structure in northern bottlenose whales, bottlenose dolphins (*Tursiops* spp.) and sperm whales. Past studies indicated that the deep-diving northern bottlenose whales of the Gully have a social system completely unlike that of the species with most ecological similarity, the sperm whale. Instead, they appear to share similarities with shallow-water populations of bottlenose dolphins (Gowans *et al.,* 2001).

Since little is known about beaked whale social systems in general, previous work on the social structure of northern bottlenose whales has looked at other cetacean species such as bottlenose dolphins, to provide a mode for social structure. Coastal bottlenose dolphin societies have been studied around the world, with similar social patterns documented in many different populations (Appendix 3). Gowans *et al.* (2001) found that bottlenose whale and bottlenose dolphin societies both have groups that are often composed of only a few individuals (on average 3 animals), long-term preferred associations among males, and a loose network of associates among females. Groups constantly form and break up in order to balance the costs and benefits of group living, a social organization described as fission-fusion. Gowans *et al.,* (2001) also proposed that the long-term preferred associations among male northern bottlenose whales may be similar in nature to the well-known male alliances composed of pairs and occasionally trios of male dolphins that have been noted in several different bottlenose dolphin societies (Smolker *et al.,* 1992; Bräger *et al.,* 1994; Connor *et al.,* 1996; Bearzi *et al.,* 1997; Chilvers and Corkeron, 2002; Lusseau *et al.,* 2006). Past studies of northern bottlenose whale societies have not found long-term preferred associations between females (Gowans, 1999; Gowans *et al.,* 2001), although it is possible there were simply not enough data previously to be able to these preferred associations.

By comparing northern bottlenose whale societies to other species such as the sperm whale and coastal bottlenose dolphin, I hope to advance our overall understanding of bottlenose whale social structure. More specifically, this research expands our knowledge of the nature of long-term preferred associations, the existence of tiers (in a hierarchical society), and whether or not the social network of this population is divided into distinct social communities.

3.2 METHODS

3.2.1 The Data Set

Photo-identification data were collected in the Gully, on the edge of the Scotian Shelf, during the period 1988-2011. Individuals were distinguished based on characteristics of their dorsal fins and flanks (discussed in detail in Chapter 2). Photo-identifications can be made using either the left or right side of the dorsal fin, and because I could not always tell if photographs taken from the left and right side of an animal were in fact from the same individual, separate catalogues were maintained for each side. All analyses were also carried out separately based on left and right photo-identifications. For simplicity, when results from both sides were in agreement, I present only the results of the left dorsal fin side data (results from the right dorsal fin side data are included as Appendix 4). When possible, the sex of individuals was determined from characteristics of the melon or forehead (described in Chapter 2); adult females and immature whales of both sexes have the same melon shape and cannot be distinguished from melon profiles alone. Subadult males have some flattening of the anterior melon, and mature males have melons that are square and often white in colour (Reeves *et al.,* 1993).

3.2.2 Associations

Behavioural interactions among individuals are the basis of cetacean social structure (Hinde, 1976). However, associations may be used as a proxy for interactions when interactions themselves are difficult to observe (Whitehead and Dufault, 1999). Associations are often defined by proximity and coordination of behaviour between pairs of individuals (dyads), or groups of individuals (Whitehead, 2008a). Assuming that animals are associating when they are spatially clustered is common practice in studies of animal social structure, and has been termed the "gambit of the group" (Whitehead and Dufault, 1999). In this study, I defined association as membership to a *cluster, group*, or *encounter* (see definitions below).

Cluster: A *cluster* was a transitive set of individuals (in the mathematical sense, if individuals A and B are associated, and B and C are associated, then A and C are also associated) observed at the surface either together or alone, so long as surfacings were no more than 2 minutes apart. All individuals observed at the surface in a single *cluster* were assumed to be associating.

Group (Gowans, 1999): A *group* was a set of (or lone) individual(s) observed at the surface, so long as consecutive surfacings among group members were no more than 10 minutes apart. When whales were not seen at the surface for more than 10 minutes, I assumed they made a deep foraging dive, and considered the next individuals that were encountered to be a new *group*. *Groups* were transitive; for example, individual A may have surfaced at 10:15, A and B at 10:18 and C at 10:26. A, B, and C would be considered to be in the same *group*. All individuals identified in the same *group* were considered to be associating.

Encounter: If a new *cluster* began less than 30 minutes after the last *cluster* ended, I assumed these were likely the same whales and so considered both of these *clusters* to be in the same *encounter*. Each *encounter* consisted of one or more *clusters*. For example, if *cluster* 1 contained individual A at 10:10, and *cluster* B contained individuals B and C at 10:25, then individuals A, B, and C were included in the same *encounter*. I also set spatial restrictions on a single encounter. If the whales being observed near the boat dove, and the next whales to surface were >1000 m away, I was not confident these would be the same whales and assigned them to a new *encounter*. All individuals observed within a single *encounter* were considered associated under this definition of association.

The operational definition of *group* follows Gowans (1999), who found that a 10 minute cut-off was appropriate based on her observation that if whales were not observed for 10 minutes, they generally were not observed again for a long time. Because arbitrary definitions of group have the potential to influence how associations are interpreted, I also looked at finer scale associations; I selected a 2 minute cut-off of no observations, which I considered appropriate to distinguish repeated surface dives (often less than a minute apart) from deeper dives (several minutes apart). In addition, I examined broader associations (30 minute temporal cut-off, and 1km spatial cut-off) to account for possible autocorrelation between consecutive sightings of groups. All 3 operational definitions are somewhat arbitrary, and so to better understand how the definition of association might influence the interpretations of social relationships, whenever possible, analyses were repeated using all three different definitions of association (*i.e. clusters, groups*, and *encounters*).

Because the operational definitions *encounters* and *clusters* were only recently included in the data collection protocol (to examine how interpretations vary with our definition of association), for all data collected prior to 2010, only *groups* were recorded. For this reason, only *groups* could be examined as the unit of association to examine social structure for all long-term analyses (1988-2011). Also, because long-term analyses required that individuals be identified across decades, the long-term data set was restricted to only those individuals with markings that would not disappear over time (referred to as reliably marked individuals; Gowans and Whitehead, 2001). Reliable mark types included dorsal fin notches, back indents and mottled patches (Gowans and Whitehead, 2001). Since this restriction greatly reduced the sample size, whenever possible analyses were repeated using only the recent data (2010-2011). Because of the short time span and high quality of digital images from 2010 and 2011, all individuals photographed in high quality images in these years could be included in the analyses (not only those with reliable marks). Furthermore, the 2010-2011 data set had the additional advantage that demographic changes (deaths, births, and transitions between age classes) were few and likely not of major consequence.

Using the following calculation for half-weight association indices (HWI) below, I estimated association indices between each pair of individuals (dyad), using each definition of association. The calculation of association indices and all social analyses were carried out using SOCPROG (Whitehead, 2009).

Half-weight association index (HWI) between individuals *A* and *B* (Whitehead, 2008a):

$$\frac{x}{x + y_{AB} + 1/2\,(y_A + y_B)}$$

$x =$ number of sampling periods (days) *A* and *B* were observed associated, $y_A =$ number of sampling periods *A* was identified without *B*, $y_B =$ number of sampling periods *B* was observed without *A*, and y_{AB} = number of sampling periods *A* and *B* were both observed but not associated with each other.

Whitehead (2008a) reviewed the advantages and limitations of several indices of association commonly used in the study of animal social structures. When studying northern bottlenose whales in the wild, I could not always identify all of the individuals in a *cluster*, *group*, or *encounter* (sometimes an individual was not photographed, or the photographs were of low quality). Individuals may have been missed that were underneath the surface of the water and hidden from view. As a result, the estimates of individuals seen alone (y_A or y_B) could be inflated and x would be underestimated. Half-weight association indices take half the sum of y_A and y_B to compensate for this inflation, and so provide less-biased estimates of the true proportion of time that individuals spend associated at the surface. For all analyses other than permutation tests (*Questions* 4-6), associations were either *clusters*, *groups*, or *encounters*, and sampling periods were calendar days, as in Gowans *et al.* (2001) to account for autocorrelation between subsequent *clusters*, *groups*, or *encounters* observed on the same day.

The correlation coefficients between true association indices (the actual proportion of time individuals spend together that I am trying to estimate) and calculated association indices (calculated from the raw data), and their associated measures of SE were estimated using a maximum likelihood estimator as an indicator of the power of the analysis (Whitehead, 2008b). For this calculation as well as when addressing *Questions* 1-3, I used an observation threshold (Croft *et al.,* 2008) to restrict individuals included in the analyses to those who had been identified in least 15 sampling periods. I chose 15 sampling periods because the largest values of maximum association indices between any individual and all other individuals were very different using 0, 5, or 10 sampling periods as the observation threshold, but became stable when I used 15 or 20 sampling periods. Using a threshold of 15 sampling periods, there were enough long-term (1988-2011) data that measures between classes could be compared, while also describing the maximum association indices for any individual with all others with reasonable accuracy. The short-term data set (2010-2011) consisted of fewer sampling periods, and there were not enough data to use the same restriction threshold. As a result, the analyses for *Questions* 1-3 were carried out on the long-term data set only.

3.2.3 Research Questions

3.2.3.1 *Question (1) How does association strength vary within and between age/sex classes?*

Mantel tests were used to test the null hypothesis that association rates were similar between and within age/sex classes for data collected within the Gully MPA. For each age/sex class, I calculated the mean (over all individuals) of the mean, maximum, and sum of association indices with other individuals. These indicate the average probability that any two individuals were associated in any sampling period, the probability of observation of association of any individual with its closest associate in any sampling period (within the restricted data set), and the average number of individuals (within the restricted data set) observed associated with any individual in any sampling period.

3.2.3.2 *Question (2) How variable are associations among individuals?*

Social differentiation describes how varied the relationships are within a society. In statistical terms, it has been defined by Whitehead (2008a) as the coefficient of variation (CV) of the ‘true’ association indices (the actual proportion of time individuals spend together). Low measures of social differentiation (near zero) are indicative of undifferentiated societies, whereas high measures (close to or greater than one) suggest relationships are heterogeneous (Whitehead, 2008a). I calculated social differentiation using maximum likelihood and bootstrapped SE for the population as a whole, as well as within separate age/sex classes following the methods of Whitehead (2008b).

3.2.3.3 *Question (3) How large are aggregations of whales (clusters, groups or encounters)?*

I estimated the number of associating individuals observed together, using three definitions: *clusters*, *groups* and *encounters*. The number of whales in each *cluster* was counted during field observations, irrespective of which whale or how many were identified afterwards by photo-identification. Using the maximum number of individuals for any *cluster* in a single *encounter* to estimate the size of each *encounter*, I also estimated the mean *encounter* size. Because *group* size was not recorded in the field during the years 2010 and 2011, I estimated mean *group* size from the photo-identification data. These data included only those individuals identified from high quality photographs without applying a threshold of observation. Mean *group* size was estimated by calculating the mean, over all individuals, of the sum of association indices as a measure of gregariousness (how many associates on average, a randomly chosen individual would have) and adding one (the randomly chosen individual itself) to estimate the typical *group* size (Whitehead, 2008a).

3.2.3.4 *Question (4) Does gregariousness vary among individuals overall, and in their rates of association with different age/sex classes?*

Unequal gregariousness means that some individuals are consistently found with greater or fewer associates, and, in this case, in *encounters* that are generally large or small. As a measure of variability in gregariousness within and between classes, I examined the standard deviation (SD) of the typical *encounter* sizes by calculating the number of associates each individual had in each encounter, determining the mean number of associates across encounters for each individual, and estimating the SD of these means across all individuals. Unequal gregariousness was indicated by a significantly high SD of typical *encounter* sizes of raw data describing northern bottlenose whale associations, compared to randomly permuted data. Analyses were made both within classes (*e.g.* did females differ in the number of females they associated with?) as well as between classes (*e.g.* did males differ in the number of females they associated with?). Analyses were only carried out on the short-term data set (2010-2011) to reduce the chance that an individual may switch classes during the analysis (such as from the subadult male class to the mature male class).

3.2.3.5 *Question (5) Is there evidence for short-term preferred associations?*

Following Gowans *et al.* (2001), I tested for preferred associations among individual northern bottlenose whales in the Gully using both the long-term (1988-2011) and short-term (2010-2011) data sets. Associations were defined as individuals belonging to the same *group* for the long-term data set, and the same *encounter* or *cluster* for the short-term data set. To test for short-term (within 5 day sampling periods) preferred associations, I generated an association matrix and permuted groups within samples while keeping constant the number of *clusters*, *groups*, or *encounters* in which each individual was observed, as well as the number of animals in each *cluster*, *group,* or *encounter*. This analysis required the population to be closed within sampling periods; therefore 5 day sampling periods were chosen (Gowans, 1999), a small enough sampling period so that birth, mortality, immigration and emigration were unlikely, but large enough to have enough groups during that period that permutations were possible. One possible disadvantage of this method is that it does not account for differences in gregariousness between individuals, which could lead to the null hypothesis of equal association rates being erroneously rejected (which is another reason I tested for differences in gregariousness between individuals in *Question* 4).

3.2.3.6 *Question (6) Is there evidence for long-term preferred associations?*

To test for long-term (between sampling periods) preferred associations, I permuted associations within samples, while keeping the number of associations of each animal in each sampling period constant (Whitehead, 2008a). This method makes fewer assumptions (for example it does not assume equal gregariousness) than permuting *groups*, *clusters* or *encounters* within samples and is therefore preferable for testing long-term preferred associations. Associations were defined as individuals belonging to the same *group* for the long-term data set, and the same *encounter* or *cluster* for the short-term data set. This method tested the null hypothesis that associations are random against the alternative that some pairs of individuals may have preferentially associated or not associated over the long-term. To ensure I was detecting preferred associations rather than avoidances I checked all instances where the association strength between two individuals was significantly different from expected, to make sure the association strengths were particularly high (rather than particularly low).

3.2.3.7 *Question (7) How do relationships change over time?*

Understanding relationships in a society hinges on mapping the temporal component to association (Hinde, 1976). Lagged association rates are often calculated for social systems to better understand how the patterns of associations change over time (Whitehead, 1995). The lagged association rate, at lag τ, is the probability that two associating individuals are also associating τ time units later (Whitehead, 2008a). Using the long-term data on northern bottlenose whale associations from photo-identifications spanning 1988-2011, I examined general lagged association rates and within-class lagged association rates. A version of the lagged association rate, the standardized lagged association rate, is preferable when not all associates are observed (Whitehead, 2008a), which is the case with this data set. Standardized lagged association rates (g') were calculated using the equation below.

Standardized lagged association rates (g') (Whitehead, 2008a):

$$g'(\tau) = \frac{\sum_{j,k|(t_k - t_j)=\tau} \sum_X \sum_{Y \neq X} a_j(X,Y) \cdot a_k(X,Y)}{\sum_{j,k|(t_k - t_j)=\tau} \sum_X \left(\sum_{Y \neq X} a_j(X,Y) \right) \cdot \left(\sum_{Y \neq X} a_k(X,Y) \right)}$$

Where: τ =5 days (Gowans *et al.,* 2001) and *X* and *Y* represent two individuals, and *j* and *k* represent sampling periods. The term $a_j(X,Y)$=1 if individuals *X* and *Y* associated in sampling period *j*, and 0 if they did not.

When calculating lagged association rates, there was no observation threshold to restrict individuals. Standardized lagged association rates (g') were calculated for the population in general as well as for the female/immature and mature male classes separately. There were not enough data to calculate lagged association rates for subadult males. I attempted to fit to the standardized lagged association rate data to several models described in detail in Whitehead (2008a). They include: $SLAR_1: g' = a$, $SLAR_2: g' = a \cdot e^{-b\tau}$, $SLAR_3: g' = a + c \cdot e^{-b\tau}$, and $SLAR_4: g' = a \cdot e^{-b\tau} + c \cdot e^{-d\tau}$, where *a, b, c* and *d* are constants. These exponential form models indicate different ways in which association can diminish with time. Models were then fit to standardized lagged association rate data, and model fit was indicated by low *Q*AIC values (Whitehead, 2007). Jackknife techniques were used to estimate the SE of model parameters.

3.2.3.8 *Question (8) Can the social structure be represented as a set of hierarchically nested tiers, or separate social communities?*

To yield a more accurate representation of the social data, I applied an observation threshold to the association data of 5 sampling periods. This meant that dyads observed in less than 5 sampling periods, and for whom there was very little data to examine social relationships, were excluded. Using this threshold, there were also enough data to examine how the three definitions of associating animals (those found in the same *cluster, group,* or *encounter*)*,* influenced the results.

To test whether society is hierarchically structured, I used hierarchical cluster analysis to represent the relationships between individuals using a tree diagram, and calculated the Cophenetic Clustering Coefficient (CCC) as a measure of support for a hierarchical model. The CCC describes how well data can be represented hierarchically. Measures of CCC>0.8 are generally interpreted as a good representation of the data (Whitehead, 2008a).

To examine social community structure, I explored whether there were substructures of the social network, where individuals were more densely linked to each other than they were to the rest of the animals in the network. I considered a social community to be a collection of individuals which behave in a self-contained way, so that most interactions and associations occur within the community (Whitehead, 2008a). Social communities were found by maximizing modularity (Newman, 2004). Modularity is a way to quantify the number of edges (which represent social relationships) within a social community, relative to the total number of edges that could be linked throughout the social network if edges were drawn at random. To calculate modularity, I used the modifications for weighted networks described by Whitehead (2008a) as Modularity-G, which controls for the gregariousness of individuals. Modularity values can range from 0-1, and modularity values between 0.3-0.7 represent substantial community division (Newman and Girvan, 2004).

The network data were restricted to ensure divisions were the result of social factors, and not temporal or spatial division. Temporally restricting the network analyses to 2010-2011 also reduced any demographic effects, such as mortality or births during the study period. Spatial restrictions limited the networks to within a single canyon (the Gully).

3.3 RESULTS

3.3.1 The Data Sets

Using the long-term data set, 215 individuals from 612 *groups* were identified from high quality photographs of the left sides of dorsal fins in the period 1988-2011 in the Gully MPA. There were 28 individuals and 328 *groups* seen in at least 15 sampling periods (days).

From the short-term data set, 92 individuals were identified from 95 different *encounters*. Some encounters had multiple *clusters*, and as such, there were 219 *clusters*. The data sets are summarized in Table 3.1. As a reference, the data restrictions are indexed by research questions (1-8). Correlation coefficients between true association indices and calculated association indices were approximately 0.4 suggesting the descriptions of social structure presented in this study, which are based on association indices, are somewhat representative of the true measures of association (Table 3.2).

Table 3.1 Summary of data sets. The data sets and data restrictions for each research question are described below. In the Gully, 215 sides of individuals have been identified since 1988 (these include left and right sides so some individuals may be represented twice). Associations are defined as membership to the same *cluster, group* or *encounter* depending on the research question, location and span of analysis (long or short-term).

Location	Years	Observation threshold	# Individuals	# Groups	# Clusters	# Encounters
Gully	1988-2011	none	215	612	-	-
		15 *(Questions 1-2)*	28	328	-	-
	2010-2011	none	92	-	219	95
		5 *(Question 8)*	44	-	187	83
Shortland canyon	2010-2011	none	40	-	44	8
		5 *(Question 8)*	5	-	12	6
Scotian Shelf	2010-2011	none	121	-	262	103

Table 3.2 Estimated correlation coefficients between true association indices and calculated association indices with bootstrapped SE. Associations were defined by membership to the same *group.* Estimates are presented for the population in general, as well as each separate age/sex class.

Class	Correlation coefficient (SE)
All	0.43 (SE=0.041)
Female/immature	0.44 (SE=0.073)
Subadult male	No estimate (too few data)
Mature male	0.44 (SE=0.072)

3.3.2 Research Questions

3.3.3.1 *Question (1) How does association strength vary within and between age/sex classes?*

The majority (greater than 70%) of all association indices were near zero (Figure 3.1), in other words any randomly chosen pair of whales spent very little time with one another. The mean over all individuals of the maximum association indices was 0.23 (SE=0.10) showing that in general, individuals spend only about 20% of their time with their strongest associate. The largest value of any association index was 0.42 suggesting that none of the dyads were constant companions. This is further illustrated in the case studies I present later in this chapter which indicate that associations were not constant across years (Tables 3.13-3.15). No individual had a sum of association index of zero, meaning none of the whales observed in this study were completely solitary. The mean value of the mean association indices for mature males was higher than for females, and for all between-class measures (Figure 3.2); although the overlapping SE bars indicate this difference was not significant.

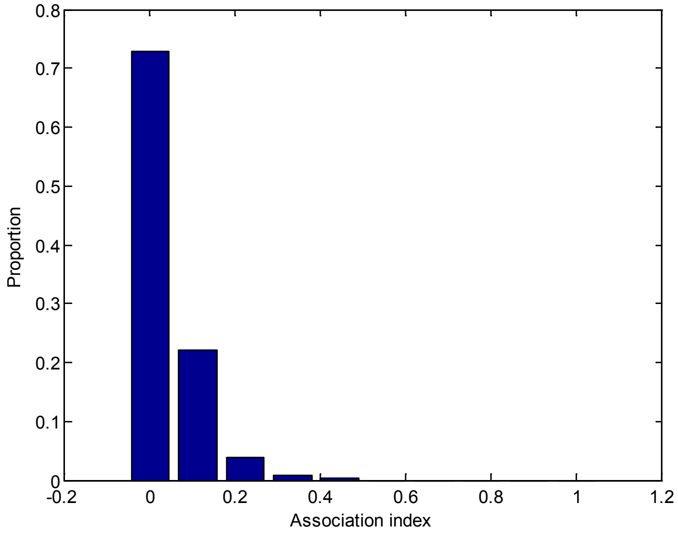


Figure 3.1 The distribution of half-weight association indices for northern bottlenose whales in the Gully. These results are restricted to individuals which were identified in at least 15 sampling periods.

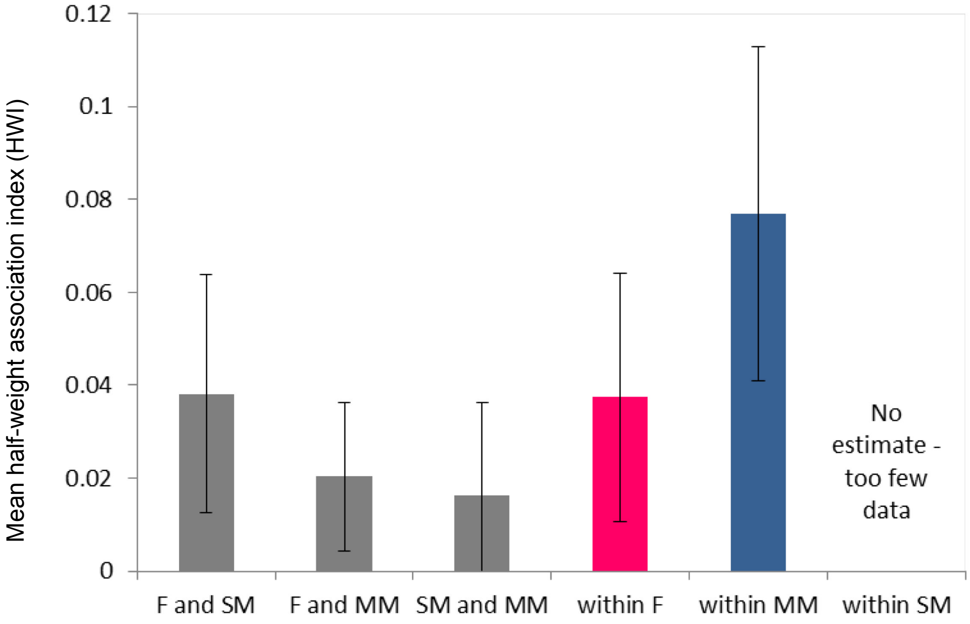


Figure 3.2 Within class (pink or blue) and between class (grey) measures of the mean (over all individuals) of the mean association indices. Error bars are SE. Classes are abbreviated as females/immatures (F), subadult males (SM) and mature males (MM).

Patterns of associations between and within classes were different (Mantel test, t=5.093; P<0.001). Mean association indices and sum of association indices were generally higher within classes than between them, showing that individuals associated more with members of their own class (Table 3.3). This is also evident in the case studies (Tables 3.13-3.15); for example the focal female #45 had many repeated associations with other females, and the focal subadult male #5158 had many repeated associations with other subadult males.

Table 3.3 Measures of within and between class half-weight association indices (SD).

Class	Mean	Sum	Maximum
Within	0.052 (0.040)	1.58 (0.483)	0.192 (0.137)
Between	0.021 (0.011)	0.37 (0.206)	0.131 (0.059)
Overall	0.035 (0.019)	1.95 (0.507)	0.228 (0.100)

3.3.3.2 *Question (2) How variable are associations among individuals?*

Regardless of which side the photo-identification data were based on (right or left) or the class (female/immature or mature male) high measures of social differentiation (>0.5) suggested a well differentiated society (Table 3.4). There were not enough data to measure social differentiation for subadult males. Social differentiation measures between females and males differed by more than twice the sum of the SE, which indicates females had significantly higher measures of social differentiation. This relates to differences in the distribution of association indices (Figure 3.3). Association indices were mostly zeros among females (about 90% of the association indices), with a very small proportion of non-zero association indices. In contrast, males had a more even distribution of association indices ranging from 0-0.4.

Table 3.4 Measures of social differentiation estimated using maximum likelihood with bootstrapped SE. Estimates are presented for the population in general, as well as each separate age/sex class.

Class	Social differentiation measure (SE)
All	0.81 (0.05)
Female/immature	0.93 (0.09)
Subadult male	No estimate (too few data)
Mature male	0.52 (0.10)

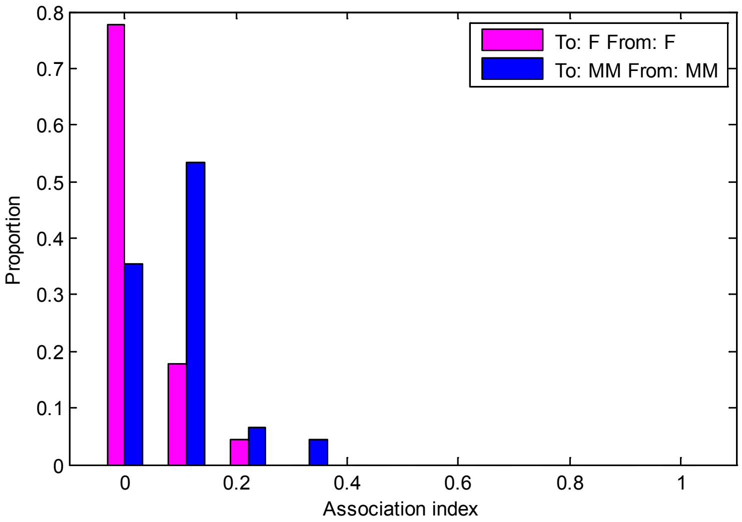


Figure 3.3 Differences in the distribution of half-weight association indices for male and female northern bottlenose whales in the Gully. These results are restricted to individuals who were identified in at least 15 sampling periods.

3.3.3.3 *Question (3) How large are aggregations of whales (clusters, groups, or encounters)?*

The number of individuals found associating together was approximately 3-4 whales (SD=2-3) regardless of how associations were defined (membership to the same *cluster, group* or *encounter*; Table 3.5).

Table 3.5 Mean size of aggregations of whales that were observed associating together, and estimates of SD.

Definition of association	Mean group size (SD)
Cluster	3.33 (1.94)
Group (left side photo-identification data)	3.84 (2.72)
Group (right side photo-identification data)	4.04 (3.11)
Encounter	4.23 (2.25)

3.3.3.4 *Question (4) Does gregariousness vary among individuals overall, and in their rates of association with different age/sex classes?*

In this study the gregariousness of an individual is defined as the mean number of other individuals associated with that individual during a 5-day sampling period. Between classes, it is, for example, the mean number of males associated with a particular female during a sampling period. I found evidence of significant differences in gregariousness between individuals, suggesting some individuals have more associates and some individuals have fewer associates (Table 3.6). This was also the case when female/immature whales and subadult males were compared. Females differed in the number of associates they had in general, as well as the number of subadult male associates they had. Mature males also differed in the number of female associates and subadult male associates they had, but not in the number of other males they associated with.

Table 3.6 Differences in gregariousness between individuals. The following results are based on left side photo-identifications (unless significant results were found only for right side photo-identification data, in which case they were included in parentheses). Associations were defined as individuals observed in the same *encounter* using the short-term (2010-2011) data set. Significant *P* values are indicated by an asterisk. Classes are abbreviated as female/immature (F), subadult male (SM) and mature male (MM).

Class	**n**	**Number of permutations**	**SD of typical *encounter* size**		***P* value of SD**
			Real data	**Random data**	
All	121	60 000	34.6	30.2	0.001*
Within F	69	60 000	21.4	16.9	<0.001*
F to SM	69 13	10 000	16.8	10.3	<0.001*
F to MM	69 13	20 000	20.4	15.8	0.058
Within SM	13	40 000	10.4	7.9	0.126
SM–F	13 69	20 000	8.8	6.7	0.004*
SM–MM	13 13	30 000	3.5	3.5	0.114
	(10 18)	(10 000)	(4.3)	(3.9)	(0.042*)
Within MM	13	10 000	3.4	4.9	>0.999
MM–F	13 69	20 000	5.3	4.7	0.129
	(18 5)	(30 000)	(6.2)	(4.9)	(0.005*)
MM–SM	13 13	10 000	4.7	2.0	0.001*

3.3.3.5 *Question (5) Is there evidence for short-term preferred associations?*

There was evidence for short-term (within 5-day sampling periods) preferred associations for all age/sex classes (Table 3.7). This was indicated by higher mean association indices of the real data compared to the randomly permuted data. The same overall patterns were observed for both the restricted long-term data (1988-2011) and the higher resolution recent data set from 2010-2011(data for *encounters* are given in Table 3.7). This showed that regardless of which dataset was examined, there are general patterns across all age/sex classes that individuals preferentially associate with other individuals over 5 day time spans.

Table 3.7 Results from permutation tests for short-term preferred associations within classes. The following results are based on left side photo-identifications (unless significant results were found only for right side photo-identification data, in which case they were included in parentheses). Significant *P* values are indicated by an asterisk.

Data set	**Class**	**n**	**Number of permutations**	**Mean Association index**		***P* value**
				Real data	**Random data**	
1988-2011	Female/immature	81	40 000	0.016	0.017	0.009*
	Subadult male	19	10 000	0.039	0.040	0.288
		(20)	(60 000)	(0.022)	(0.029)	(0.005*)
	Mature male	32	20 000	0.026	0.029	0.025*
2010-2011	Female/immature	69	60 000	0.12	0.13	0.026*
	Subadult male	13	40 000	0.20	0.21	0.182
		(10)	(10 000)	(0.18)	(0.20)	(0.047*)
	Mature male	13	10 000	0.15	0.16	0.050*

3.3.3.6 *Question (6) Is there evidence for long-term preferred associations?*

There was also evidence that both mature males and females have long-term preferred associations (Table 3.8), as indicated by the CV of real association indices being significantly greater than the CV of the randomized data. Long-term preferred associations were not detected among subadult males; however, failure to reject the null hypothesis of random associates could be due to low sample size. Examples of long-term preferred associates from the case studies I present later in this chapter would be individuals #45 and #251 (both mature females; Table 3.13), or individuals #606 and #3 (both mature males; Table 3.14).

Table 3.8 Results from permutation tests for long-term preferred associations. The following results are based on left side photo-identifications (unless significant results were found only for right side photo-identification data, in which case they were included in parentheses). Significant *P* values are indicated by an asterisk.

Data set	**Class**	**n**	**Number of permutations**	**CV of Association index**		***P* value of CV**
				Real data	**Random data**	
1988-2011	Female/immature	81	10 000	4.56	4.27	<0.001*
	Subadult male	19	30 000	3.30	3.31	0.837
	Mature male	32	30 000	2.76	2.75	0.457
		(37)	(5 000)	(3.10)	(2.94)	(0.003*)
2010-2011	Female/immature	69	10 000	1.94	1.76	<0.001*
	Subadult male	13	40 000	1.08	1.07	0.387
	Mature male	13	30 000	1.51	1.46	0.137
		(18)	20 000	(1.54)	(1.50)	(0.019*)

3.3.3.7 *Question (7) How do relationships change over time?*

General patterns of standard lagged association rate (SLAR) data indicate that associations diminished exponentially over time (Table 3.9). The equation and parameter estimates (SE) for the best supported model were $g'(\tau) = a \cdot e^{-b\tau}$ where $g'(\tau)$= standardized lagged association rate at lag τ in days, a =0.0467 (SE=0.0096), and b =0.0005 (SE=0.0001). Results from the right side photo-identification data were similar, although suggested that dissociation may have occurred at two time scales (Table A3.3). These levels could be the short and long-term associations that were detected using permutation tests. For the population in general, standardized lagged association rates were above null for roughly 5000 days or 13 years (Figure 3.4). This suggests some preferred relationships were maintained over a decade, but that all preferred associations eventually dissociated over time. Short and long-term preferred associations were also evident in the case studies (Tables 3.13-3.15), all of which eventually ended and none of the individuals that were examined had any constant companions across years.

Table 3.9 Comparison of model fit for SLAR models to describe associations for the population in general. Best support for model fit is indicated by the lowest ΔQAIC.

Model	*Q*AIC	Δ*Q*AIC	Support
$SLAR_1 : g' = a$	2219.3	85.5	None
$SLAR_2 : g' = a \cdot e^{-b\tau}$	**2133.8**	**0.00**	**Most**
$SLAR_3 : g' = a + c \cdot e^{-b\tau}$	2134.9	1.06	Some
$SLAR_4 : g' = a \cdot e^{-b\tau} + c \cdot e^{-d\tau}$	2136.5	2.66	Some

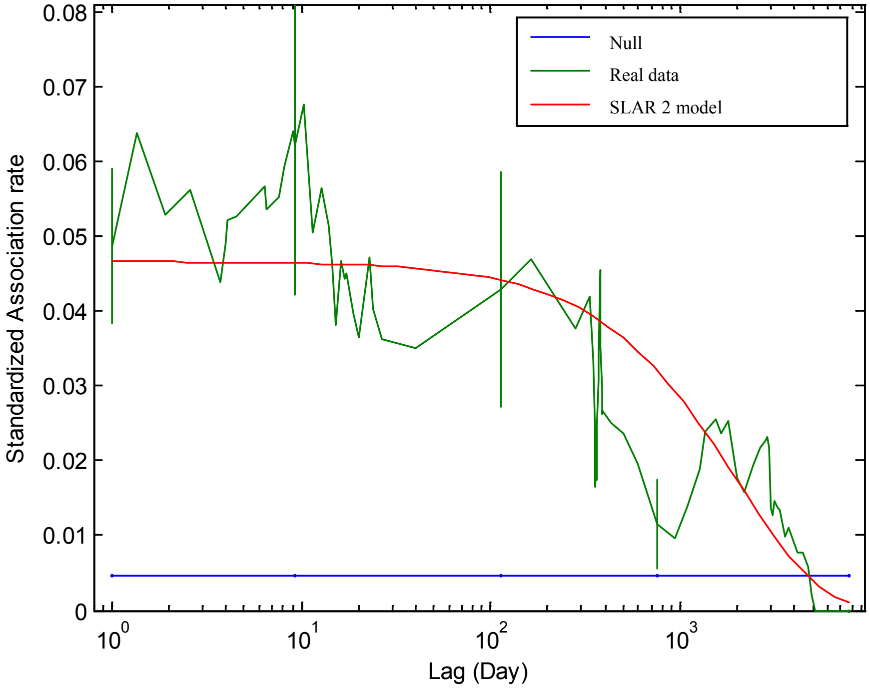


Figure 3.4 Real and modelled standardized lagged association rate data showing that in general, preferred associations diminish and reach roughly random levels after approximately 5000 days (more than a decade).

Standardized lagged association rates were only calculated for the mature male and female/immature classes, as there were not enough data to examine the subadult male class. Similar to the patterns of SLAR data that were noted for the population in general, data for the female/immature class also best supported models where associations dissociated exponentially over time (Table 3.10). The equation and parameter estimates (SE) for the best supported model were $g'(\tau) = a \cdot e^{-b\tau}$, a=0.0970 (SE=0.0330), and $b = 0.0014$ (SE=0.0012). Again, right side photo-identification data indicated dissociation may occur on two time scales (Table A3.4). Most of the preferred associations between females lasted less than 2000 days (roughly 5 years) as seen in Figure 3.5. All preferred associations eventually dissociated.

Data for mature males also best supported the model where associations diminish exponentially over time (Table 3.11 and Table A3.5). The equation and parameter estimates (SE) for this model were $g'(\tau) = a \cdot e^{-b\tau}$, a =0.130 (SE=0.0498), and $b = 0.0002$ (SE=0.0001). Mature males showed evidence for the longest preferred associations. The standardized lagged association index exceeded the null rate for approximately 5000 days or 13 years (Figure 3.6).

Table 3.10 Comparison of model fit for SLAR models to describe associations within the female/immature class. Best support for model fit is indicated by the lowest ΔQAIC.

Model	***Q*AIC**	**Δ*Q*AIC**	**Support**
$SLAR_1 : g' = a$	654.9	32.9	None
$SLAR_2 : g' = a \cdot e^{-b\tau}$	**622.1**	**0.00**	**Most**
$SLAR_3 : g' = a + c \cdot e^{-b\tau}$	623.1	1.02	Some
$SLAR_4 : g' = a \cdot e^{-b\tau} + c \cdot e^{-d\tau}$	626.0	3.93	Less

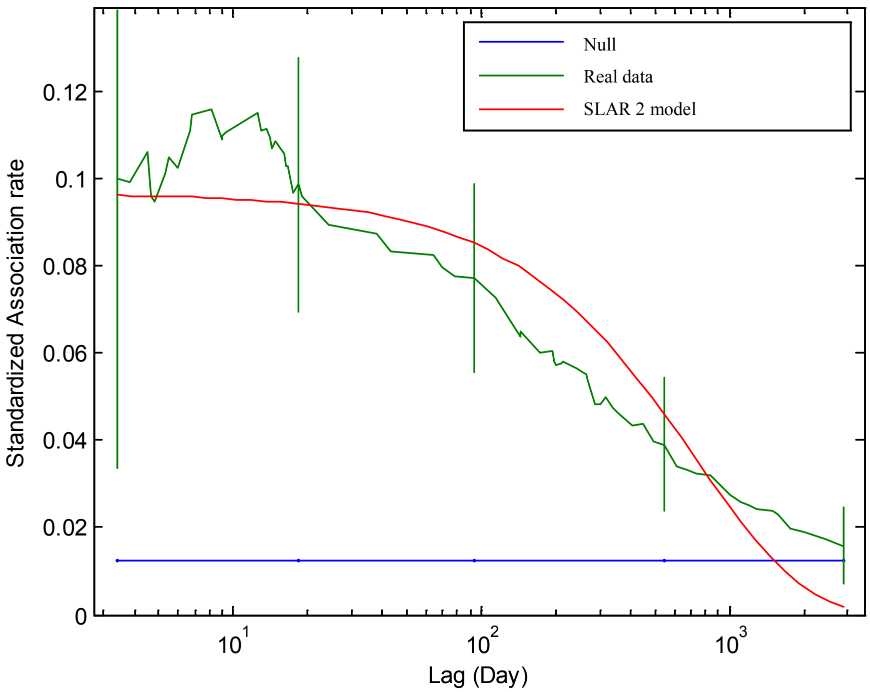


Figure 3.5 Real and modelled standardized lagged association rate data showing that preferred associations among female and immature northern bottlenose whales diminish and reach random levels after about 2000 days (over 5 years).

Table 3.11 Comparison of model fit for SLAR models to describe associations within the mature male class. Best support for model fit is indicated by the lowest Δ*Q*AIC.

Model	***Q*AIC**	**Δ*Q*AIC**	**Support**
$SLAR_1 : g' = a$	199.7	1.81	Less
$SLAR_2 : g' = a \cdot e^{-b\tau}$	**197.9**	**0.00**	**Most**
$SLAR_3 : g' = a + c \cdot e^{-b\tau}$	198.0	0.09	Strong
$SLAR_4 : g' = a \cdot e^{-b\tau} + c \cdot e^{-d\tau}$	201.5	3.62	Less

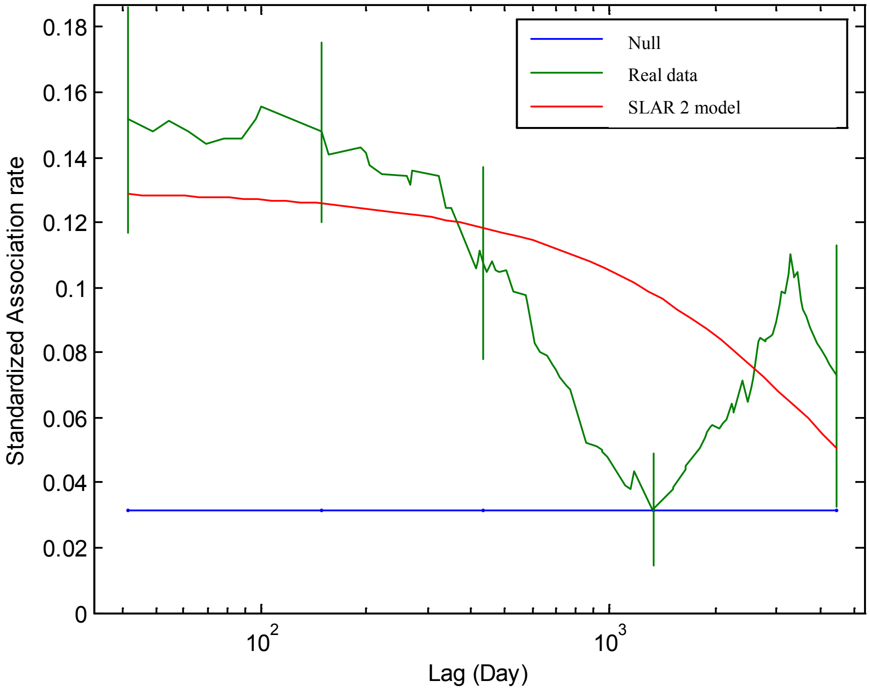


Figure 3.6 Real and modelled SLAR data showing that preferred associations among mature males diminish but do not reach random levels at 5000 days (over a decade). Apparent large-scale oscillations are probably spurious (due to low sample size and high seasonality of data collection).

Table 3.12 shows some of these long-term preferred associations in further detail. For example, mature males #1 and #3 preferentially associated over a span of 11 years. Table 3.12 also illustrates two important aspects of the long-term preferred associations that were observed among mature males. Preferred associations among mature males are not restricted to pairs or trios, as they are with bottlenose dolphins. For example, in 1989 strong association indices were recorded between individual #1 and several other mature males. Also, preferred associates were not constant companions; they were seen together in some years and seen apart in others.

Table 3.12 A closer look at long-term preferred associations between mature males. Annual variation in association strength was measured for individual #1 (a mature male) and several of his preferred associates, during the years in which he was observed.

Dyad	**1989**	**1990**	**1994**	**1996**	**1998**	**1999**	**2001**	**2003**
1 and 3	0.57	0.67	0.00		0.36	0.00	1.0	0.00
1 and 10	0.33	0.00		0.00	0.25	0.00		
1 and 33	0.00			0.00	0.40	0.00	0.00	
1 and 37	0.25	0.00		0.00	0.40	0.00	0.00	
1 and 76	0.00	0.33		0.00				
1 and 120	0.33			0.00		0.00		0.00
1 and 225				0.67			0.00	0.50

3.3.3.7.1 Case Studies

All of the statistical analyses conducted so far provide information about the presence or absence of different patterns of relationships, but do not necessarily indicate their nature. Following Gowans (1999), I have included three case studies to provide more tangible examples of some of the complex social patterns I have described for the population. Unfortunately, because not all of the whales seen in past years were observed recently, I could only reexamine one of the three animals selected by Gowans (1999) in her case studies. I present information on the relationships of a female (#45), a mature male (#606) and a subadult male (#5158). Because individuals are highly variable, these case studies are not necessarily representative of their respective age/sex classes. Also, when calculating association indices for the case studies I did not apply an observation threshold, so values for association strength (HWI) are likely inflated, and thus are less reliable than those presented in earlier analyses. I included these HWI values to demonstrate the ranking rather than the magnitude of relationship strengths between the individuals in the case studies and their associates.

I repeated the case study of individual #45, a female northern bottlenose whale, whose associations were originally examined by Gowans (1999). This updated case study of female whale (#45) illustrates several characteristics of the long-term preferred associations between females: they involve multiple individuals (are not restricted to pairs or trios), they may span years but eventually the preferred associations end, and associates are not constant companions but are seen together in some years and apart in others. Between 1989 and 1998, Gowans noted that #45 was repeatedly found in the same *group* as #1, a mature male. I re-examined the associations of #45 including more recent data (Table 3.13). I did not observe further associations between #45 and #1; however, #45 was in the same *group* as another mature male (#824) on several occasions between 1997 and 2003. Individual #45 associated with all classes (females/immatures, subadult males, and mature males). She also repeatedly associated with specific females both within years and across years. The maximum associate of #45 was #131 (another female) with a half-weight association index of 0.27. Individual #45 was observed in 32 sampling periods (30 of which were high quality photographs of the left side of the dorsal fin and thus included in the HWI calculations), individual #131 was observed in 15 (high quality left photographs) and they were both observed in 6 sampling periods.

Individual #606 (Table 3.14) is a mature male and was first identified in 1989. His case study illustrates that long-term preferred associations among males are similar to those described above among females: males can have more than one or two preferred associates, their preferred associations last from several years to a decade but eventually end, and although preferred associates are repeatedly seen together, they are not constant companions (they are sometimes observed apart). Male #606 associated with all age/sex classes, and the majority of the repeated associations within and across years were with other mature males. For example, he was seen with #3 in 1990 and again in 2002; he was also observed in the same *group* as #606 on four occasions between 2010 and 2011. Most associations with subadult males were not repeated. Associations with females were often repeated within years, and occasionally across years (*e.g.* he associated with females #89 and #5112 in both 2010 and 2011). The maximum associate of mature male #606 was actually a female (#5112) with a half-weight association index of 0.55 even though she was only observed in the same *group* as #1148 in recent years (2010 and 2011). Individual #5112 was seen in 6 sampling periods, individual #606 has been observed in 19 (although only 5 were of high quality and the left side of the dorsal fin, and thus included in calculations of association indices). The pair was observed together in 3 sampling periods.

Individual #5158 (Table 3.15) is a subadult male. His case study illustrates how northern bottlenose whale associations were often stronger within classes, than between them. Subadult male #5158 associated with all age/sex classes, however associations with females were generally not repeated and only one association spanned from 2010 to 2011 (#5003). Similarly, only one mature male (#5075) was repeatedly observed in the same *group* as #5158 between 2010 and 2011. In contrast, the majority of associations with other subadult males were repeated several times between 2010 and 2011. The maximum associate of #5158 was a mature male #5075, with a half-weight association index of 0.67. These associates were both seen across many sampling periods; individual #5158 was seen 6 times, #5075 was seen 9 times, and the pair was observed together in 5 sampling periods. Because the distinction between subadult males and mature males is somewhat subjective, the fact that the pattern of associations of #5075 seemed more like those of the other subadult male associates could indicate that #5075 was a relatively young mature male.

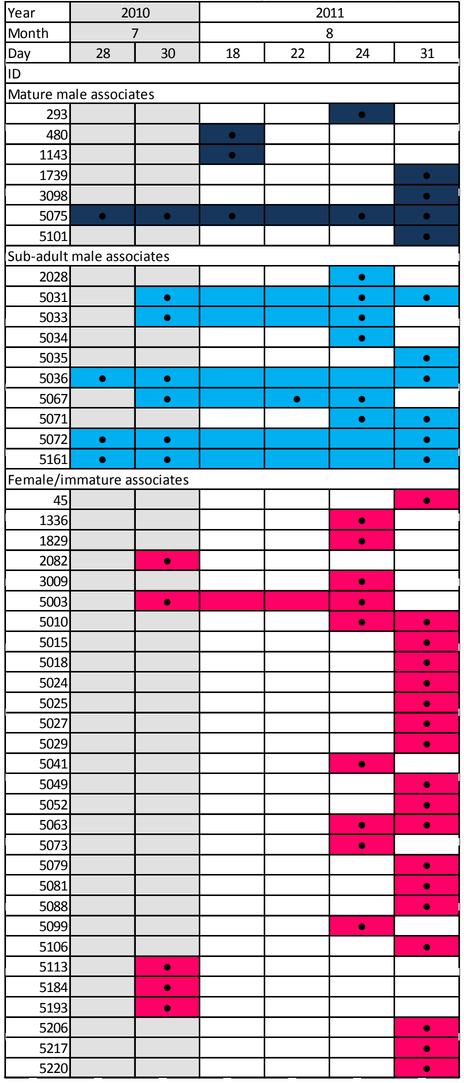
Table 3.13 Associations of a female northern bottlenose whale (individual #45) observed between 1989 and 2011. This table was adapted from Gowans (1999) who examined associations of the same individual from 1989-1998. The time periods over which single or repeated associations were documented are highlighted in colours that correspond to the age/sex class of the associate (dark blue for mature males, light blue for subadult males, and pink for females/immatures).

Year	1989		1990			1993	1994		1995	1996	1997						1998									1999		2002	2003		2010	2011
Month	8		7		8	7	8		8	6	8						7				8					8		8	8		7	8
Day	3	10	28	29	5	15	12	13	29	22	4	12	14	16	18	25	14	26	27	28	9	10	11	15	16	12	18	19	28	29	21	31
ID																																
Mature male associates																																
1	●	■	●	●	●	■	■	●	■	■	■	■	■	■	■	■	■	●	●													
3	●	■	●	●	●	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	●								
10																		●														
33																		●	●													
37																			●													
71															●																	
118																				●												
225																														●		
290				●																												
413																			●													
480													●																			
508							●	●																								
549																		●														
824															●	■	■	■	■	●	■	■	■	■	■	■	■	■	■	●		
1039														●	■	●																
1143																			●												●	
1292															●																	
1422																			●													
1424																				●												
2023																															●	
2102																																●
5101																																●
Sub-adult male associates																																
28	●	●	■	■	■	■	■	■	■	■	■	■	■	■	●																	
32	●																															
51	●																															
102					●																											
120										●																						
124													●																			
406				●																												
1507																								●								
5071																																●
5158																																●
Female/immature associates																																
47	●																															
54	●	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	●	
56													●	●	■	●																
131																●	■	●	■	●	●	●	●	●	●							
251								●	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	●	●	●	●		
390								●																								
409						●	■	●																								
418			●																													
440				●																												
531							●	●	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	●					
633						●	■	●	●																							
653							●	●	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	●					
804																●	■	■	●													
832																											●					
952																											●					
961												●	●	■	■	■	●															
1019																		●	■	●	●	■	●	●	●	■						
1155																				●												
1239											●																					
1332																		●														
1334																		●														
1404																									●							
1470																											●					
1617																										●						
1618																										●						
1630																											●					
1634																											●					
1645																											●					
1651																											●					
1904																															●	
3043																															●	●
5905																															●	
5907																															●	
5908																															●	

Table 3.14 Associations of a mature male (individual #606) observed between 1989 and 2011. The time periods over which single or repeated associations were documented are highlighted in colours that correspond to the age/sex class of the associate (dark blue for mature males, light blue for subadult males, and pink for females/immatures).

Year	1989		1990			1996	1997	2002		2010			2011						
Month	8		7	8		6	6	8		7		8	8						
Day	4	13	28	8	9	18	11	8	27	24	31	27	15	18	21	22	23	24	25
ID																			
Mature male associates																			
1		●	●																
3			●	■	■	■	■	■	●										
16													●	■	■	●	■	●	
120						●	●	■	●										
225													●	■	■	●			
293																●			
413			●																
480													●	■	■	●	■	●	
1143										●	●	■	●	■	■	●			
1739																●			
5039											●								
5075															●	■	■	●	
5137												●							●
Sub-adult male associates																			
13			●																
28				●															
59			●																
152			●																
420			●																
531					●									●					
2028																●			
2095											●	■	●	■	■	●			
5030																●			
5031																●			
5034																●			
5035																●			
5044											●								
5059															●				
5069													●						
5071															●				
5161																●			
Female/immature associates																			
17															●				
61	●	●																	
89											●	●	■	■	■	●			
102													●	■	■	■	■	●	
162																●			
316			●																
418			●																
518				●															
677								●											
1829															●				
3016																		●	
3033												●							
4117															●				
4102											●								
4203											●								
5018																●	●		
5019																●			
5020																●			
5022																●	●		
5026																●			
5027													●						
5028													●	■	■	●			
5029													●	■	■	●			
5032											●								
5049																●	●		
5052													●						
5073																		●	
5081													●						
5089																●			
5090																●			
5092																		●	
5106																●			
5112											●	●	■	■	■	■	■	■	●
5121																	●		
5223										●	●								

Table 3.15 Associations of a subadult male (individual #5158) observed between 2010 and 2011. The time periods over which single or repeated associations were documented are highlighted in colours that correspond to the age/sex class of the associate (dark blue for mature males, light blue for subadult males, and pink for females/immatures).



Year	2010		2011			
Month	7		8			
Day	28	30	18	22	24	31
ID						
Mature male associates						
293					●	
480			●			
1143			●			
1739						●
3098						●
5075	●	●	●		●	●
5101						●
Sub-adult male associates						
2028					●	
5031		●			●	●
5033		●			●	
5034					●	
5035						●
5036	●	●				●
5067		●		●	●	
5071					●	●
5072	●	●				●
5161	●	●				●
Female/immature associates						
45						●
1336					●	
1829					●	
2082		●				
3009					●	
5003		●			●	
5010					●	●
5015						●
5018						●
5024						●
5025						●
5027						●
5029						●
5041					●	
5049						●
5052						●
5063					●	●
5073					●	
5079						●
5081						●
5088						●
5099					●	
5106						●
5113		●				
5184		●				
5193		●				
5206						●
5217						●
5220						●

3.3.3.8 *Question (8) Can the social structure be represented as a set of hierarchically nested tiers, or separate social communities?*

I applied hierarchical cluster analysis to examine community structure, using the short-term (2010-2011) data. Average linkage was selected as it produced the lowest CCC, while single, complete and Ward link functions showed less support. CCC values for all classes were less than 0.8, suggesting hierarchical models did not appropriately describe the social data. In some cases, values of CCC were near 0.8, however temporal elements of sampling, rather than social factors, could have produced this pattern. For example, apparent hierarchical patterns could be due to the temporal structure of data (divided between years and days) rather than a reflection of social processes. There was some indication of division within the social network into separate social communities, but low measures of modularity suggest at most only weak support (Table 3.16).

Table 3.16 Social community division was explored using hierarchical cluster analysis and network modularity. Cophenetic Clustering Coefficient (CCC) values >0.8 indicate data are well represented by a hierarchical model, and modularity values between 0.3-0.7 indicate substantial community division.

Location	**Association defined by whales in the same**	**CCC**	**Modularity (G)**
Gully	*Encounter*	0.717	0.209
	Cluster	0.792	0.394

3.4 DISCUSSION

There were five main results of this chapter. (1) Most associations are short-lived and consistent with a fission-fusion social organization, although associations are variable. (2) Long-term preferred associations are not restricted to mature males, but are also found among female/immature whales. (3) The nature of these preferred associations may be somewhat different than the male alliances described in bottlenose dolphin societies, as long-term preferred associations among northern bottlenose whales change over time and can involve several animals (not just pairs or trios). Furthermore, since females also had preferred associates, long-term preferred associations do not necessarily reflect a male mating strategy. (4) There is some indication subadult males associate with each other, and while speculative, groups might be analogous to young male bachelor herds described in sperm whale societies. (5) There is no hierarchical structuring and little, if any, community division among northern bottlenose whales within the Gully MPA.

Over all, this study drew several of the same conclusions as Gowans (1999) and Gowans *et al.* (2001) who first examined the social structure of northern bottlenose whales in the Gully. These include a fission-fusion social structure in which associations are labile, strong preferences for within-class associations, and long-term preferred associations between mature males. In this study, the finding of preferred associations both on short and long-term time scales among female/immature whales is likely a reflection of more data, and thus greater statistical power to detect relationships that are significantly stronger than one would expect by chance alone. Gowans *et al.* (2001) suggested the preferred associations among mature males may be similar in nature to the male alliances seen in bottlenose dolphins. The nature of preferred associations among female/immature whales, and the lack of any hierarchical structuring or community division, have not previously been examined for this (or any) population of northern bottlenose whales.

Since the closest relatives of northern bottlenose whales, other beaked whale species, are among the least known of all marine mammals, it is not helpful to look to other beaked whale species to help explain these social patterns. Therefore, I discuss other cetaceans with ecological and social similarities, primarily the coastal bottlenose dolphin, to help understand why northern bottlenose whales in the Gully evolved their particular social structure.

3.4.1 Long-Term Preferred Associations Among Males

One of the main areas of social structure I hoped to advance was the nature of long-term preferred associations among males. Gowans et al. (2001) first noted these long-term preferred associations, and in my thesis, I found evidence these preferred associations are maintained up to over a decade. Beaked whale social structure is not well understood, however in Blainville’s beaked whales (*Mesoplodon densirostris*) and Cuvier’s beaked whales (*Ziphius cavirostris*), groups of animals usually only have one male (McSweeney *et al*., 2007). Therefore, the presence of long-term preferred associations among northern bottlenose whales might be unusual for beaked whales.

Gowans *et al.* (2001) noted that the social structure of northern bottlenose whales closely resembles that of coastal bottlenose dolphin populations, in which the females generally live in a labile fission-fusion network, whereas male pairs and occasionally trios form long-lasting tight alliances [*e.g.* Shark Bay, Australia (Smolker *et al.,* 1992; Connor *et al.,* 1996); Queensland, Australia (Chilvers and Corkeron, 2002); Northern Adriatic Sea (Bearzi *et al.,* 1997); Texas, USA (Bräger *et al.,* 1994); Moray Firth, Scotland (Lusseau *et al.,* 2006)], with one exception being a small population geographically isolated in Doubtful Sound, New Zealand (Lusseau *et al.,* 2003). The Doubtful Sound population appears to be atypical among bottlenose dolphins, and is discussed in more detail below. In general, strong bonds between mature males are important in bottlenose dolphin mating systems, and are thought to function as a way to increase male reproductive success (Connor *et al.,* 1992). Male alliances cooperate to herd females that are potential mates, and to defend females from other male alliances (Connor *et al.,* 1992; 1996; Parsons *et al.,* 2003).

Since female northern bottlenose whales also form long-term preferred associations, male reproductive strategies cannot be the only function of long-term preferred associations in this species. Furthermore, long-term preferred associations among mature male northern bottlenose whales have some differences from the constant male alliances that have been described for bottlenose dolphins (*e.g.* Connor *et al.,* 1992; Smolker *et al.,* 1992; Krützen *et al.,* 2003). The preferred long-term associations among mature bottlenose whales are not continuous throughout time; after several years or up to a decade later, they all eventually end. In this study, I also found the association strength between male northern bottlenose whales (at most approximately 0.4) was much lower than those noted for bottlenose dolphin male alliances (0.8-1; Connor *et al.,* 1992). In other words, even closest male bottlenose whale companions only spent at most 40% of their time together. Northern bottlenose whales often had several strong associates in a given year, and were not organized into pairs or trios like they are in bottlenose dolphin societies (Connor *et al.,* 1992). In addition, I did not observe males "herding" females, a behaviour often seen among male alliance pairs of bottlenose dolphins that attempt to monopolize mating opportunities with a female (Connor *et al.,* 1992).

Since male northern bottlenose whales have more than 1 or 2 preferred associates, it seems unlikely they form pair and trio alliances. However, an alternate explanation is that pairs/trios preferentially associate with other alliances (which would also produce a pattern where each male has several preferred associates). Such second-order, and even third-order alliances have been described among male bottlenose dolphins in Shark Bay, Australia (Connor *et al.,* 2011). It is unlikely that relationships among male bottlenose whales in the Gully are organized into primary (pairs and trios), secondary, or even tertiary levels of male alliances, as social structure in the Gully did not appear to be hierarchically organized.

Although male alliance pairs or trios are commonly observed among bottlenose dolphin populations, male alliance formation is not the only pattern observed in bottlenose dolphin societies. In a population of bottlenose dolphins near New South Wales, Australia, there are mature male dolphins which form alliances, as well as those which have several (less strong) preferred associations with many mature males (Wiszniewski *et al.,* 2012). The authors noted that dolphin populations where male alliances are most prevalent have two common characteristics: high population density and a low degree of sexual dimorphism. They noted these factors make it more difficult for a single male to monopolize a potential mate, and thus could favor the formation of male alliances.

The Gully is not a dense population; as discussed in Chapter 2 the size of the population of northern bottlenose whales that use the Gully is relatively small and whales can move between canyons. Furthermore, northern bottlenose whales are highly sexually dimorphic in body size (the maximum body size for males is 1.3 m greater than for females; Benjaminsen, 1972). Thus based on low density and a high degree of sexual dimorphism in body size, it may not be surprising that male northern bottlenose whales do not appear to form alliances composed of pairs and trios of animals who are constant (or nearly constant) companions, as is commonly observed among male bottlenose dolphins. Therefore, while long-term preferred associations among males appear to be an important characteristic of both northern bottlenose whale and coastal bottlenose dolphin social organizations, the nature of these relationships appears to be somewhat different between the two species.

3.4.2 Long-Term Preferred Associations Among Females

As mentioned above, preferred associations between individuals were not a characteristic exclusive to the mature male class. Short-term preferred associations (several days) were found among all classes of northern bottlenose whales (subadult male, mature male and female/immature whales), and long-term preferred associations were detected among dyads of mature males (lasting over a decade) and female/immature whales (lasting around 5 years), alike. Among Cuvier's and Blainville's beaked whales, repeated associations spanning many years have been documented among females (McSweeney *et al.,* 2007). However, for these other beaked whale species, groups are often composed of many females and a single male, and there is some indication their group structure reflects the mating system described as female defense polygygy (McSweeney *et al.,* 2007). Because northern bottlenose whale groups often contain multiple males, it is not likely they share similar mating systems.

One possible explanation for long-term preferred associations within the female/immature class is that some of the long-term preferred associations that were detected within the 'female' class were mother and offspring pairs. Preferred associations lasting up to 4 years have been documented among mother/calf pairs of bottlenose dolphins in Shark Bay (Smolker *et al.,* 1992). Immature northern bottlenose whales could have been included in the 'female' class as they cannot be visually distinguished from mature females using only melon shape. The case study of a female bottlenose whale (Table 3.13) illustrates, however, that individuals which repeatedly associated were likely not necessarily restricted to pairs (there can be several preferred female/immature associates), were not constant across years (association strength varied annually), and maximum association indices were rather low (less than 0.4) which means there were no constant companions. Together, these findings suggest the long-term preferred associations between female/immature northern bottlenose whales were not restricted to mother/calf pairs. Furthermore, unpublished genetic analysis using 17 Gully animals (6 males and 11 females) found negative and non-significant correlations between genetic relatedness (as indicated by microsatellites), and association index, with three putative parent-offspring pairs among females and juveniles having no recorded associations (M. Dalebout, D. Ruzzante, and H. Whitehead, unpublished data).

Interestingly, there is one population of bottlenose dolphins in New Zealand for which preferred associations among females has been documented. Doubtful Sound, New Zealand, is a fjord environment and thus has ecological similarities to the Gully (Lusseau *et al.,* 2003). Both fjords and submarine canyons are environments characterized by deep water with steep slopes. Despite environmental similarities, the cetacean populations in these habitats have several major differences. Doubtful Sound is a closed population, whereas whales move between the Gully and neighbouring Shortland and Haldimand canyons. Also, dolphins in Doubtful sound commonly have constant companions across 6 month periods, and the mean association index was approximately 0.47 (Lusseau *et al.,* 2003), which is more than an order of magnitude higher than the mean association index value for northern bottlenose whales (approximately 0.04). Thus both the physical and social environments of these two populations are very different, and could have potentially led to some of the observed differences between these species in the long term preferred associations among female/immature animals.

Among primates, whose societies are probably the best documented of any mammals apart from humans, the evolution of sociality among females is thought to have been driven primarily to maximize their access to resources (Silk, 2002), especially food. If female preferred associations among northern bottlenose whales are not related to mother/calf pairing as they often are in dolphin societies (Mann and Smuts, 1999), or communal infant care (alloparenting or allosuckling) as in species such as sperm whales, it is possible they are somehow a strategy to optimize foraging efficiency.

Continuous associations have been recorded among pregnant female humpback whales off Maine, USA (Weinrich, 1991), some lasting almost 3 months. Weinrich (1991) proposed that the function of these associations might be to benefit from cooperative feeding and thus to increase fat stores necessary for lactation. Among female/immature northern bottlenose whales, long-term preferred associations are fairly infrequent, and only a few individuals are likely pregnant at the same time. Therefore, it seems possible that the underlying function of female long-term preferred associations could be related to reproductive status as it is in humpback whales off Maine. However, it does not explain why these associations would last up to 5 years, which is well beyond the gestation and nursing period of a northern bottlenose whale. Additionally, northern bottlenose whales forage at depth, so associations at the surface do not necessarily reflect associations when foraging, and there has yet to be any evidence of cooperative foraging among bottlenose whales.

3.4.3 Subadult Male Groups

While I did not detect long-term preferred associations among subadult males, this may have been due to low sample sizes. Like all age/sex classes, subadult males likely have stronger associations within their own age/sex class; this pattern is illustrated in the case study of a subadult male (Table 3.15). One possible benefit to subadult males grouping together in the Gully could be protection from aggressive mature males. In other beaked whale species, linear tooth scars are often seen along the body of whales as a result of aggressive interactions between males (Heyning, 1984). While less linear scarring is generally seen in northern bottlenose whales than other beaked whales such as *Mesoplodon* spp., head-butting between males has been observed which could indicate intraspecific agonism (Gowans and Rendell, 2006). Mature male bottlenose whales have flattened melons and large body size (Benjaminsen, 1972; Reeves *et al.,* 1993), and so could potentially present formidable opponents for a subadult male.

3.4.4 Lack of Social Community Division

In addition to describing how relationships vary between classes, and between individuals within classes, I also examined how society was organized on broader scales. Lusseau *et al.* (2006) described a dolphin population where distinct social communities overlapped in their spatial range, and cautioned that recognizing these separate social communities could be important in conservation as each may require separate management protocols. As a whole, there was only weak support for division of the social network into distinct social communities. This suggests there is some degree of connectedness between individuals within the population of bottlenose whales that use the Gully. This seems probable given the population is relatively small, and the fission-fusion dynamics results in groups readily forming and dissociating.

3.4.5 Social Evolution

Comparing social structures of related or ecologically similar species can facilitate an understanding of the common selective pressures on social systems (Croft *et al.,* 2008). Gowans (1999) and Gowans *et al.* (2001) demonstrated that northern bottlenose whales have very different social structures from deep-diving sperm whales, despite their ecological similarities. For sperm whales, the need for females to make deep foraging dives while dependent calves remained vulnerable at the surface was likely a factor in the evolution of stable matrilineal units which could provide babysitting services (Whitehead, 1996; Gero *et al.,* 2009). The social structure of northern bottlenose whales has been shaped very differently, despite the fact that they also make deep dives. Beaked whale calves are born with a relatively large body size compared to sperm whale calves (Huang *et al.,* 2011). This may enable beaked whale calves to begin making full dives sooner and follow their mothers on deep foraging dives (Huang *et al.,* 2011). Perhaps morphological characteristics that allow for early diving abilities have permitted northern bottlenose whales to escape the constraints of leaving calves at the surface unprotected, and consequently, the evolution of stable social units.

Fission-fusion systems can allow aggregations of individuals to balance the costs and benefits of group living by aggregating for specific tasks such as predator protection or adjust group size to limit feeding competition (van Schaik and van Hooff, 1983). The average size of aggregations (regardless of the definition as *cluster*, *group*, or *encounter)* was approximately 3-4 whales (SD=2-3 animals). Small group size could be due to factors such as relatively low predation or small food patches in the Gully (Gowans *et al.,* 2007). The pressures on group size may also differ between classes, for example, if subadult males have greater competition from mature males, or a stronger need to group together for protection.

The long-term preferred associations I observed were fairly infrequent. Consistent with the fluid social structures of coastal bottlenose dolphins (*e.g.* Bräger *et al.,* 1994) associations were generally quite weak, although there were a few strong associations (Figure 3.1). Both male dyads and female dyads were found to form long-term preferred associations, thus if these alliances are related to their mating system, the function of these long-term preferred associations must be different than with bottlenose dolphins.

In order for a description of social structure to be useful, the definition of associating individuals should accurately reflect socially or biologically meaningful units. I explored several ways to define associations. In all analyses, regardless of whether associations were defined based on *clusters*, *groups*, or *encounters,* the same general trends were observed (although at slightly different magnitudes). This suggests the underlying processes described in this study were not influenced greatly by the definition of associating individuals. Based on the correlation coefficients I calculated between the true association indices and calculated association indices (Table 3.2), the descriptions are at least somewhat representative of the social structure for northern bottlenose whales.

3.4.6 Conclusions

The northern bottlenose whales of the Gully appear to have evolved a social structure unlike the other deep-diving whales examined, which could be related to their unusual habitat. The Gully is the largest underwater canyon in the entire northwest Atlantic (DFO, 2008), and likely imposes an interesting set of constraints on social evolution. As more is discovered about other beaked whale species, such as Sowerby's beaked whales (*Mesoplodon bidens*) which are also found in the Gully, or beaked whales in canyons elsewhere, it will be interesting to see if the patterns of social structure of the northern bottlenose whales in the Gully are shared among other populations of beaked whales.

Using knowledge of social structure in the management of whales in the Gully is not a recent endeavour. Commercial whalers were among the first to realize how useful knowledge of social structure was in our interactions with this species. Whalers exploited the tendency for northern bottlenose whales to protect injured group members, and used this information to draw entire groups within the range of harpoons (Reeves *et al.,* 1993). The social cohesion among groups of northern bottlenose whales demonstrated by their willingness to defend their associates seems even more remarkable when you consider that most associations are weak and short-lived. Since the population of northern bottlenose whales that use the Gully is relatively small, individuals likely interact frequently. Despite our best attempts to elucidate the complex patterns of social relationships within this population, we cannot evaluate the capacity of whales to identify and remember community members.

The primary goal of this study was to advance our understanding of northern bottlenose whale social structure on the Scotian Shelf, and provide information that could be useful for the effective conservation of this endangered population. My hope is that understanding northern bottlenose whale social structure will prove as valuable a tool for modern conservation as it was for historical exploitation. Just as coastal bottlenose dolphins in many ways served as a model for this northern bottlenose whale society, the descriptions of social structure for the Scotian Shelf population presented in this chapter may provide an informative model for other less studied populations of northern bottlenose whales elsewhere, or even other beaked whale species, for which very little is known.

CHAPTER 4
SYNCHRONOUS BREATHING AND ITS ROLE IN THE SOCIAL ORGANIZATION OF NORTHERN BOTTLENOSE WHALES *(HYPEROODON AMPULLATUS)* ON THE SCOTIAN SHELF

4.1 INTRODUCTION

When the pattern or rate of a normal behaviour is altered due to the presence of another individual (and not strictly a response to external stimuli), it is said to be the result of social facilitation (Clayton, 1978). Synchronized egg laying and communal displays among certain bird species and synchrony of estrus in some species of primates, bovids and felids are all thought to involve socially facilitated behaviours (Clayton, 1978). Many studies have examined whether the temporal clustering of behaviour is socially facilitated. These include synchronous movements of social spiders (*Anelosimus eximius;* Krafft and Pasquet, 1991), coordinated singing of duets by pairs of singing birds such as manakins (*Chiroxiphia linearis*; Trainer *et al.*, 2002), and synchronized surface breathing among several families of air breathing fish species (Kramer and Graham, 1976). These examples all involve multiple individuals performing the same actions at (nearly) the same time.

Socially facilitated synchronous behaviours can be found among diverse animal taxa and social organizations, indicating they may be an important element of social interactions. In the dairy cow (*Bos taurus*) industry, synchronized behaviour is such an integral part of the social lives of animals in the herd, that the degree to which cows synchronize their lying and feeding has been used to assess animal welfare when comparing different holdings such as outdoor pastures and indoor cells (O'Driscoll *et al.*, 2008). Synchronous movement and sound in the form of dance and music have been proposed as important factors in the evolution of human sociality and culture (Hagen and Bryant, 2003).

Several functions of socially facilitated synchronous behaviours have been proposed including predator avoidance and serving as a social signal. Kramer and Graham (1976) suggested that the process of animals synchronizing movements in time is analogous to schooling fish that synchronize movement in space. In their study of air breathing fish, the authors suggested that by synchronously breathing at the surface, even though fish were spaced apart. They speculated that individuals might reduce predation by confusing aerial predators or by causing ripples at the surface of the water that would make it more difficult for aerial predators to see the fish below the surface of the water. Thus animals may benefit from reduced predation as a result of coordinating their movements in time. In addition, the signal hypothesis for the function of synchronous behaviour in humans and bottlenose dolphins proposes that animals can use synchronous displays to advertise the strength of their social bonds with other animals (Clayton, 1978; Hagen and Bryant, 2003; Connor *et al.*, 2006). Thus by serving as a signal, synchronous behavioural displays may be an important element of group cohesion.

Some of the strongest evidence for the latter function proposed for behavioural synchrony, the signal hypothesis, comes from human societies. Humans are unrivaled in the animal kingdom in the degree to which genetically unrelated groups of individuals form cooperative alliances (coalitions), and the coordinated actions involved in music and dance may have served as the signalling system allowing individuals to assess the quality of coalitions (Hagen and Bryant, 2003). Music and dance are considered to be credible signals because these displays take a lot of time and practice and therefore would indicate the length of time a coalition has been associated (Hagen and Bryant, 2003). For example, in human warfare, music could not only demonstrate alliance membership, but can indicate military power: how well coalition members could coordinate actions and work together (Hagen and Bryant, 2003). By serving as a signal for coalition strength, coordinated displays can allow attacking parties to assess their competitors before they interact, and avoid fights they are likely to lose. Advantages such as this demonstrate how the use of social signals could have direct fitness benefits, and thus could be favoured in the social evolution of animal societies.

There is also evidence from non-human animals that show how synchronous behaviour can serve as an effective social signal of coalition strength. Experiments with pairs of male duetting Australian magpie-larks (*Grallina cyanoleuca*) have demonstrated empirically that highly coordinated duets are perceived as a greater threat, and that established pairs coordinate duets much more precisely than new pairs (Hall and Magrath, 2007). The experiments of Hall and Magrath (2007) were novel for non-human animals, in that they demonstrated the duets served as a signal for strength of the coalition, rather than just an advertisement of coalition size.

Because of the link demonstrated between synchronous behaviours and social relationships, synchronous behaviour has received recent attention as a potential tool to study social organizations, particularly among cetaceans. One of the difficulties of studying cetaceans is that they spend only a small portion of their lives at the surface where they can be easily observed, and so it is often difficult to collect enough data to accurately describe social relationships. If information on breathing or diving synchrony can offer insight into animal societies, it is an appealing method because many data can be collected in a relatively short amount of time (Sakai *et al.*, 2010). There are some studies of synchronous actions of long-finned pilot whales (*Globicephala melas;* Senigaglia and Whitehead, 2012) and sperm whales (*Physeter macrocephalus*; Whitehead, 2003), but among marine mammals synchrony has been most extensively studied in populations of bottlenose dolphins (*Tursiops* spp.*; e.g.* Conner *et al.*, 2006). For bottlenose dolphin societies, similar to humans, there is strong evidence that synchrony may be used as a social signal and a way to reduce tension within male alliances, and that is important in the maintenance of male alliance relationships (Connor *et al.*, 2006; Connor, 2007).

Studies of synchronized behaviour have also been used as a tool for cetacean conservation. Synchronous breathing among dolphins has been shown to increase in response to anthropogenic stressors (Hastie *et al.*, 2003; Tosi and Ferreira, 2009), and so synchronous breathing appears to be a promising tool to examine direct short-term effects of anthropogenic stress on cetaceans (Tosi and Ferreira, 2009). For example, increased synchrony as a measurable short-term behavioural change has been examined to help understand potential cumulative consequences of boat traffic on a small population of bottlenose dolphins within a candidate Special Area of Conservation (Hastie *et al.*, 2003).

In this thesis chapter I examine breathing synchrony in an endangered population of northern bottlenose whales (*Hyperoodon ampullatus*) off Nova Scotia. The purpose of this study was to explore whether this behaviour is socially facilitated and thus could yield insight into northern bottlenose whale social structure. In addition, I wanted to evaluate whether measures of synchronous behaviour could potentially serve as a research tool to study social relationships. I collected high definition video recordings of the surface activities of groups of animals, and analysed the video recordings to discern the patterning of associations over temporal (synchrony) and spatial (relative positions within dyads) scales. The following questions are addressed: *(1) Do pairs of northern bottlenose whales synchronize their surface breathing? (2) Can the degree of synchrony be used to infer social structure (association index or age/sex class)? (3) Can the degree of synchrony be explained by other variables including physical (water transparency, swell height, or canyon location) and biological (group size, group behaviour, spatial proximity, the presence of other cetacean species, or the need to prepare to dive) variables?* The latter questions aim to help understand the possible stimuli for synchronized breathing among northern bottlenose whales and whether or not this behaviour is socially facilitated.

Northern bottlenose whales on the Scotian shelf are a small, genetically distinct, and endangered population (listed by COSEWIC in 2002 and SARA in 2006). Examining behavioural synchrony could potentially inform us further about the social organization of this population, and benefit our conservation efforts. Furthermore, I evaluate whether synchronous breathing among northern bottlenose whales could be a useful tool to reveal age/sex classes, or the different types of bonds that are found between individuals. Types and strengths of social relationships among northern bottlenose whales have traditionally been studied using long-term observations of association patterns (Gowans, 1999; Gowans *et al.*, 2001; Chapter 3). The study of synchronous breathing could potentially reveal similar information about social relationships over a much shorter observation period. For this reason, I consider the feasibility of using measures of breathing synchrony as a tool to study populations of northern bottlenose whales elsewhere (such as the Labrador-Davis Straight population, or those off north western Europe) for which much less is known about population and social structure.

4.2 METHODS

4.2.1 Video Collection

High definition video recordings were collected for groups of northern bottlenose whales at the surface from the Gully and Shortland canyons on the Scotian Shelf between July 24th and August 31st, 2011. In this chapter, I use the term ‘group’ to define whales seen together at the surface on a given video recording (note: in Chapter 3 the term *group* was used in a different context and was italicized for clarity). Filming was done using a Canon Vixia HFS30 from the crow’s nest of the 12 m auxiliary sailing vessel *Balaena*, with a camera height of approximately 10 m above sea level. Video was collected concurrently with the photo-identification studies described in Chapter 2. As defined in Chapter 3, video recording started at the beginning of a *cluster* (a transitive set of individuals observed at the surface either together or alone, so long as surfacings were no more than 2 minutes apart). Video recordings ended when whales dove. If the whales surfaced within 2 minutes of a dive, the next video to be recorded would also be of the same *cluster*. If the whales dove for longer than 2 minutes but less than 30 minutes, the next video would be of a different *cluster* within the same *encounter.* If whales dove for more than 30 minutes, or the next set of animals surfaced over 1 km away, the next video recording would be of a new *encounter* (see Chapter 3 for a more detailed discussion of *clusters* and *encounters*). Groups and individuals close to the vessel were filmed irrespective of their behaviour or markings, and effort was made to include all whales at the surface in the video when possible.

4.2.2 Video Analysis

When a northern bottlenose whale breathes at the surface, the exhalation forces water out of the blowhole which is visible to an observer. Exhalations were the cue used to examine breathing synchrony among animals, and so analyses were restricted to video recordings where the whales were within approximately 200 m of the boat, which I estimated was the farthest distance that exhalations could be accurately recorded (Senigaglia and

Whitehead, 2012). Because I was interested in whether breathing was socially facilitated, I also restricted videos to recordings where group size was at least 2 whales. The videos analysed in this study represent a subset of the videos that were collected in the field. The subset was chosen by noting the number of whales that were identified from photographs taken at the same time, and analysing videos where the group size on the video was less than or equal to the number of whales that had been identified during that period of surface activity (*cluster*). For example, if I knew that only 3 individuals (*e.g.* #5052, #5003 and #606) had been identified from photographs taken of a given *cluster*, I would only analyse videos recorded from that *cluster* where the group size was 3 or fewer whales. Since animals were generally more easily identified from the photo-identification photos than the video, this restriction ensured I was likely to be able to identify the whales in the videos, and thus analysed the subset of videos that were most useful towards understanding social relationships.

4.2.3 Measuring Synchronous Breathing from Videos

Following Lafortuna *et al.* (2003) and Senigaglia and Whitehead (2012), for each individual, the start of each exhalation was measured as when white foam first appeared at the blowhole. A rare exception to this occurred when individuals were resting and exhaled without any visible foam, because the blowhole had remained above the water for several consecutive breaths. In these instances, the start of the exhalation was measured as when the blowhole first began to open. The start time of all exhalations was measured in frames numbered from the start of the video (1 frame =1/30 s).

In similar studies of synchronous breathing among cetaceans, such as Connor *et al.* (2006), the observers had prior knowledge of the social bonds between animals before they examined synchronous breathing in the field, and thus the researchers could focus observations on specific pairs of whales and relate synchrony to those types of relationships (*e.g.* comparing measures of synchrony between alliance pairs and non-alliance pairs). Since prior knowledge of the social relationships between whales was not available during the fieldwork in this study, attempts were made to quantify the observations of breathing synchrony for all the individuals at the surface at a given time.

As groups could include up to 20 animals, and trying to keep track of every possible combination of pairs of animals would be extremely difficult when group size was large, measurements were restricted to paired surface exhalations between nearest neighbours. This was necessary to ensure data were collected in a simple and consistent manner, although I acknowledge a possible drawback of this method is that any synchronization of breathing between animals that were not nearest neighbours would have been missed.

On each video, whenever an animal exhaled, the time lag between exhalations of that animal and its nearest neighbour (spatially closest companion) was measured. The time lags were the principal data used for all analyses; lags were positive if the focal animal surfaced before its nearest neighbour or negative if the focal animal surfaced after its nearest neighbour. When deciding which whale was the nearest neighbour, the following criteria were used:

1. The nearest neighbour was the whale closest in proximity, *e.g.* Figure 4.1 (left): A is the nearest neighbour of B, B is the nearest neighbour of A, and B is the nearest neighbour of C.
2. Consecutive exhalations were only considered to be paired if the two individuals were nearest neighbours, *e.g.* Figure 4.1 (left): if A exhaled and was followed by C, the paired breathing would not be analysed because C is not the nearest neighbour of B.
3. If an animal had two nearest neighbours that were equally close, the exhalation of the temporally closest neighbour was chosen to estimate the lag, *e.g.* Figure 4.1 (right): if whales D, E, and F exhaled at frames 1, 2, 8 (respectively), then the nearest neighbour of E would be D (who exhaled within 1 frame of E) rather than F (who exhaled within 8 frames of E).
4. If a whale exhaled, and its nearest neighbour exhaled both before and after it (thus there were two possible lags describing the paired exhalation event), the shorter of the lags was used, *e.g.* Figure 4.1 (left): if B exhaled at frame 2, and A was the nearest neighbour who exhaled at frame 1 and at frame 30, the exhalation at frame 1 was used for the time of the nearest neighbour's exhalation as it was temporally closest to the exhalation of B.

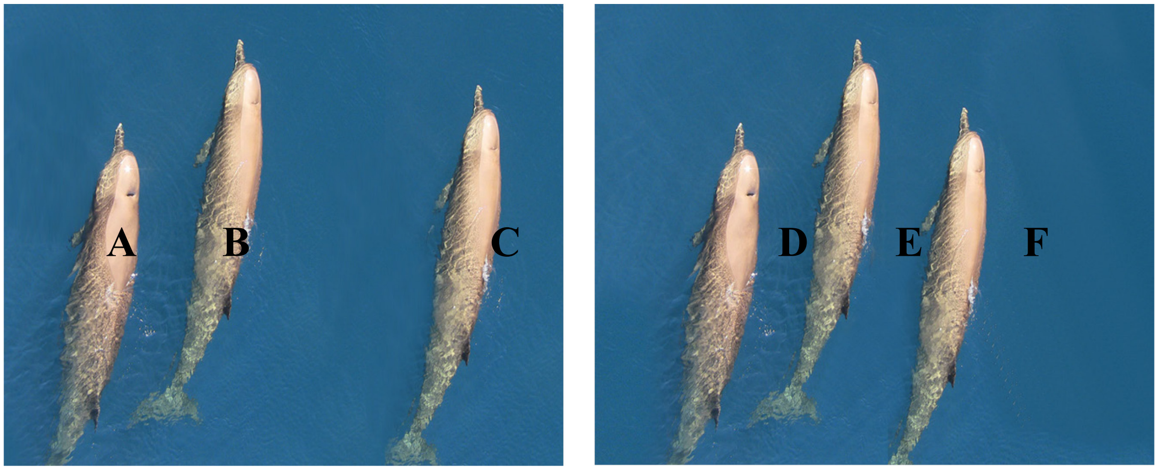


Figure 4.1 Relative positions of northern bottlenose whales (individuals A-E) at the surface, to provide clarification for the definitions of a nearest neighbour.

In total, 2791 paired surface breaths (and thus 2791 lags) were identified from 249 video recordings. When the absolute value of the lags (the difference in time between the exhalations of nearest neighbour pairs) was low, I considered the degree of synchrony to be high. For the analyses, I defined three measures of synchrony: the median of the absolute value of lags, the proportion of lags ≤1 s and the proportion of lags ≤100 ms (the latter two thresholds for synchronous breathing events were based on the distribution of lag data; Figure 4.2).

4.2.4 Classifying the Type and Strength of Social Relationships

When possible, the identity and age/sex class were noted for known animals on the video recordings. Age/sex classes include female/immatures (F), subadult males (SM) and mature males (MM). In 410 paired surfacings, both whales were identified and in 374 paired surfacings the age/sex class of both whales were estimated. When the identity of both whales in a paired surfacing was known, the association strength was estimated based on their half weight association index (HWI). Association indices are estimates of the proportion of time whales spend together (Whitehead, 2008a). The HWI calculations were based on association data from 1988-2011, were restricted to high quality photographs (Q>3), and used a sample period of 1 day. To generate association matrices, I used identifications from either the left or right dorsal fin sides (if both sides were observed for the pair, then the mean of the left and right dorsal fin side HWI values were used). This accounted for the high incidence of whales that have separate identification numbers for the left and right sides of their dorsal fins. As a result, both whales in a paired surfacing had to be travelling in the same direction, so that identifications were made from the same side. In only 5 cases out of over 400, the animals in a paired surfacing moved in opposite directions and these data were excluded from the analysis.

4.2.5 Measuring Physical Variables

To determine whether environmental variables affect synchrony, I measured water transparency each day at noon (weather permitting) using a Secchi disk to measure the Secchi depth (m) at sea. Swell height (m) was also estimated every 3 hours at sea. The location (either the Gully or Shortland submarine canyon) where the video was collected was also noted.

4.2.6 Measuring Biological Variables

To examine whether spatial proximity affects synchrony, and to evaluate the possibility that synchronized surfacing results in hydrodynamic advantages, I measured the spatial positioning of animals during paired exhalations using the measures distance and stagger [Connor *et al.*, 2006; synonymous with lateral and longitudinal distances by Sakai *et al.* (2010)]. Distance describes how far apart individuals are in the dimension perpendicular to their bodies and is measured in body widths. Stagger describes how far ahead (as a positive integer) or behind (as a negative integer) an animal is relative to its nearest neighbour, and is measured in body lengths.

The group's surface behaviour was recorded as one of three mutually exclusive states (Gowans, 1999). These included travelling, when whales move quickly in the same direction, milling where whales move slowly with movement not focused in any particular direction, or logging when whales stop moving and line up parallel to each other to rest. Group size was recorded as the maximum number of whales observed on a single video recording.

Because of the possibility that synchrony might serve as a signal for group cohesion, and group cohesion may be influenced by the presence of other cetacean species, I also examined whether breathing synchrony varied with the occurrence of polyspecific associations. On several occasions, northern bottlenose whales were observed within several body lengths of other cetacean species including Sowerby's beaked whales (*Mesoplodon bidens*), or long-finned pilot whales. I noted all cases in which a polyspecific association occurred during the *cluster* from which a video was recorded.

Finally, I was interested in investigating whether whales increased their synchrony in preparation for diving. Northern bottlenose whales make deep foraging dives to feed on deep water squid (Hooker and Baird, 1999), and thus synchronized breathing at the surface seems plausible as a means to prepare to synchronize diving activities underwater. In general, video recordings ended when the whales dove. To measure when in the video a surfacing occurred (*e.g.* early, midway or near the end of the recording), I divided the time at which each surfacing occurred (measured relative to the start of the video), by the last recorded surfacing on each video. In following text, this proportion is referred to as the 'nearness to dive' measure. Proportions near zero would indicate the paired exhalation was near the start of the recording, and a proportion equaling one would mean the breathing event was the last exhalation before the whales dove.

4.2.7 Statistical Analyses and Research Questions

Even after logarithmically transforming the lag data, neither the full data set (known and unknown whales) nor the HWI data set (restricted to known individuals of known age/sex class) were normally distributed (full data set: Shapiro-Wilk normality test, W=0.945, $P<0.001$; HWI data set Shapiro-Wilk normality test, W=0.908, $P<0.001$). Thus non-parametric tests were used for statistical analyses to address the questions below.

4.2.7.1 *Question (1) Do pairs of northern bottlenose whales synchronize their surface breathing?*

The absolute values of lags between paired surfacings were compared to a distribution that would be expected if lags were randomly assigned. The random distribution was calculated by dividing the sample size of the raw data (the total number of lags) by the number of possible values each lag could have between -300s to 300 frames. As a result, the expected frequency of lags with a value of zero frames, was the sample size * 1/601. Similarly, the expected frequency of lags with an absolute value of 1 (and thus include lags of 1 or -1 frames) would be the sample size * 2/601. The medians and interquartile ranges (IQR) of distance and stagger were calculated for highly synchronous surfacings (where lags were ≤1 s and ≤100 ms).

4.2.7.2 *Question (2) Can the degree of synchrony be used to infer social structure (association index or age/sex class)?*

To determine if synchrony was significantly associated with relationship type, I used a Kruskal Wallis test to examine whether synchrony was significantly related to the age/sex classes of the whales. Since there were multiple data for each pair, I used median values of lags, proportion of lags ≤1 s and proportion of lags ≤100 ms for pairs of known whales (and known age/sex class) as the unit of analysis to avoid pseudo-replication.

To determine whether synchrony was significantly associated with relationship strength, I calculated Spearman's rank correlation between the median absolute value of lags between dyads of known individuals and their association indices. As erroneously high or low association indices can be the result of too few sightings of the two individuals, I applied observation thresholds to the analysis, so that whales included were those seen in at least 5, 10 or 15 sampling periods (Croft *et al.*, 2008).

Five pairs of individuals were each observed in two different videos, allowing the opportunity to examine consistency across video recordings. Ideally, it would be useful to know if specific pairs consistently had higher or lower synchrony than the other whales in their groups. However, due to small sample size, the analyses were limited by low power. It was possible, however, to test whether *all* 5 pairs were significantly more or less synchronous than other members of their respective groups and in both their respective videos. To do this, for each pair I calculated the measure of synchrony for that dyad, and the measure of synchrony between all the other whales on the same video. This was repeated for all pairs, and both videos in which each pair was observed. For each pair, the probability of having higher or lower measures of synchrony than the rest of the whales in both videos is 0.5 under the null hypothesis that pairs do not show consistently characteristic levels of synchrony. Thus for a total of 5 pairs, the probability that *n* pairs had measures of synchrony that were higher or lower than the other whales in both their respective videos, $P(n)$, can be expressed as the equation: $P(n) = \frac{5! / [(5-n)! \cdot n!]}{2^5}$

4.2.7.3 *Question (3) Can the degree of synchrony be explained by other physical and biological variables?*

To determine whether synchrony was significantly related to any of the physical or biological explanatory variables, I used two nonparametric tests: the Spearman's rank correlation test (for continuous predictor variables) and Kruskal Wallis test (for categorical predictors). For these tests, lag data were not restricted to known individuals because social relationships were not part of these analyses. Since there were multiple lag data for the daily Secchi depth measurements, locations and median daily swell height estimates, I used median values for days as the unit of analysis to avoid pseudo-replication. Similarly, since there were multiple data for videos (and videos within the same *encounters* were likely autocorrelated), for tests involving predictor variables of group size, group behaviour, polyspecific association, distance, stagger and 'nearness to dive' measures, I used median values for *encounters* as the unit of analysis to avoid pseudo-replication. All statistical analyses were performed in R (R Development Core Team, 2013).

4.3 RESULTS

4.3.1 *Question (1) Do pairs of northern bottlenose whales synchronize their surface breathing?*

The distribution of time lags between consecutive surfacings of nearest neighbours (truncated at 300 frames) had a distribution that looked very different from the distribution expected if lags were assigned a value between -300 and 300 frames at random (Figure 4.2). The higher than expected number of paired surfacings with very short time lags indicates northern bottlenose whales synchronize surface breathing. There is a marked increase in lags up to 100 ms (3 frames). These highly synchronous surfacings (n=175) most often occurred when individuals were approximately side by side (median stagger=0, IQR=0) and one body width apart (median distance=1, IQR=1) as indicated in Figure 4.3. The median and IQR of distance and stagger were the same when synchronous breathing was defined as lags up to 1 s (n=1043).

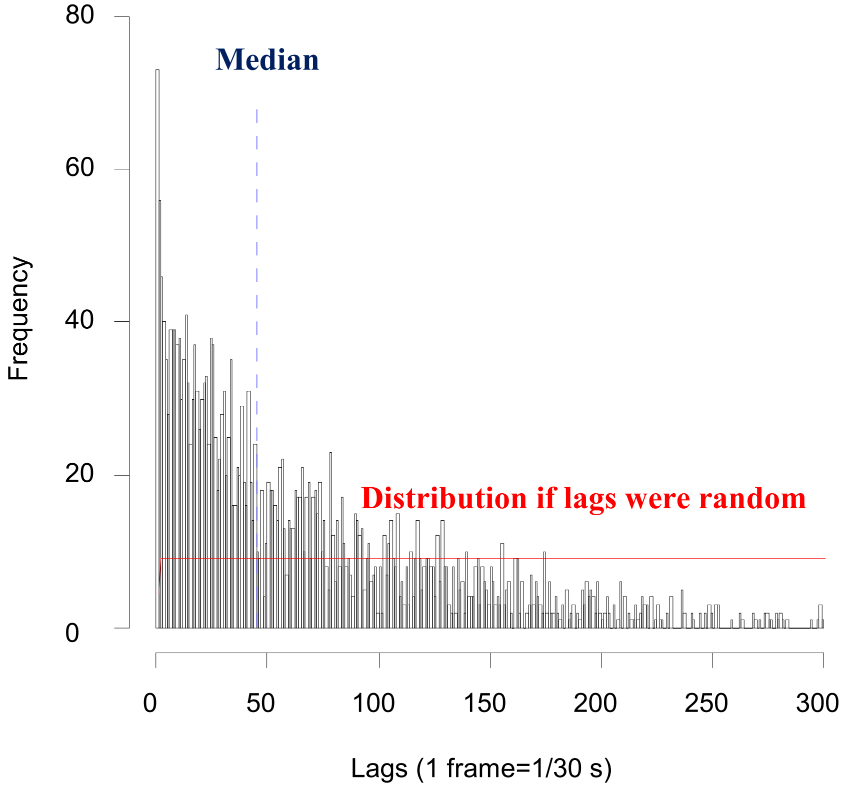


Figure 4.2 Distribution of lags (in frames) between consecutive exhalations of pairs of northern bottlenose whales.

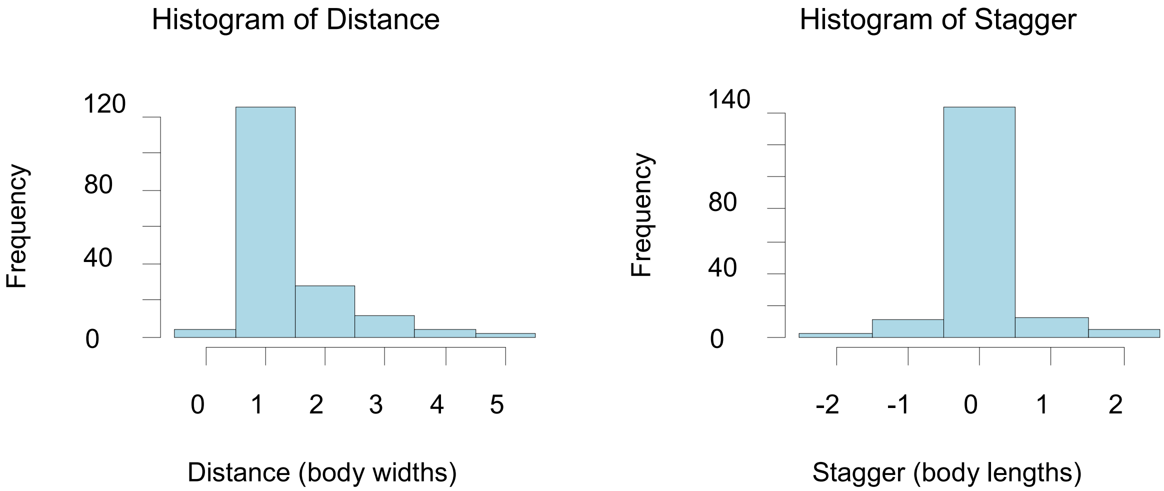


Figure 4.3 When northern bottlenose whales surface within 100 ms of their nearest neighbour, they are most often one body width apart (median distance=1) and side by side (median stagger=0).

4.3.2 *Question (2) Can the degree of synchrony be used to infer social structure (association index or age/sex class)?*

There was no significant relationship between synchrony and the strength (HWI), or type (age/sex classes) of relationship, regardless of the threshold of observations used or the definition of synchrony (Table 4.1; Figure 4.4).

Table 4.1 Tests for significant relationships between synchrony and relationship strength (HWI) or type (age/sex classes). Rho (ρ) is the Spearman's rank correlation coefficient, S is the test statistic for the Spearman's rank correlation test, X^2 is the Kruskal-Wallis rank sum statistic, df= the degrees of freedom of the approximate chi-squared distribution of the test statistic, and Obs specifies the threshold of observations for analyses where there were restrictions on the minimum number of observations per dyad.

Explanatory Variable	**Measure of synchrony**	**Test statistics**	***P* value**
HWI	Obs≥5	$S=1.11*10^7$, $\rho=0.034$	0.494
	Obs≥10	$S=4.27*10^3$, $\rho=0.218$	0.232
	Obs≥15	$S=5.10*10^2$, $\rho=-0.402$	0.173
Age/sex class	Median lag	Kruskal-Wallis $X^2=3.253$, df=5	0.661
	Proportion lags ≤1s	Kruskal-Wallis $X^2=7.463$, df=5	0.188
	Proportion lags ≤100 ms	Kruskal-Wallis $X^2=3.460$, df=5	0.630

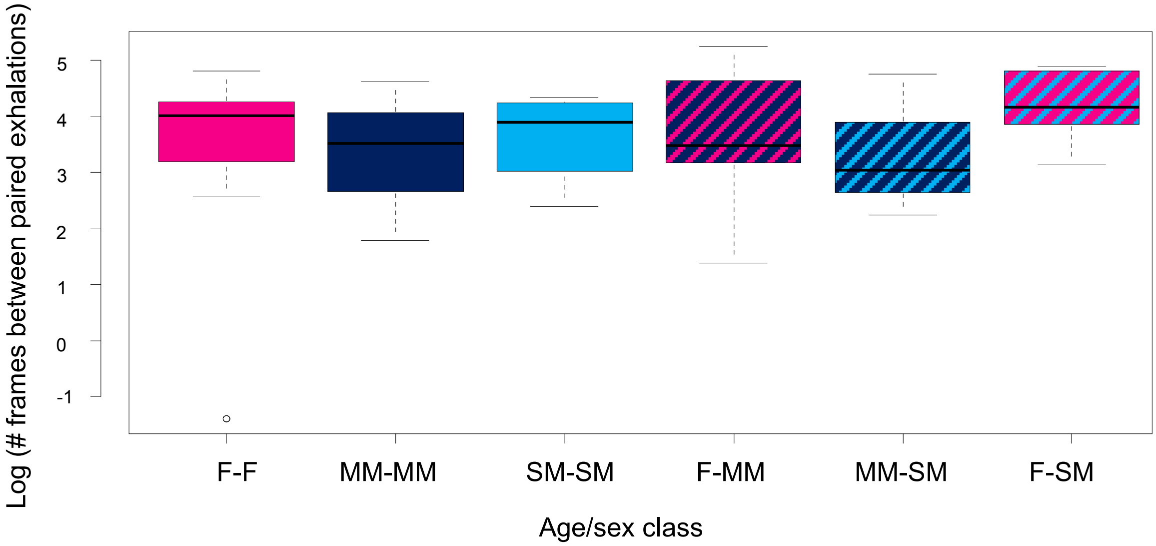


Figure 4.4 Synchrony (median lags between paired surfacings) did not differ significantly depending on the age/sex classes of the whales.

The following 5 pairs of whales were each observed in two different videos: individuals #106/#102 (MM/F), #5019/#5028 (F/F), #5027/#5029 (F/F), #5029/#5089 (F/F), #5071/#45 (SM/F). All pairs had consistently higher synchrony than other whales in their groups, in both their respective videos, except for one dyad (#2027/#5029) which had higher synchrony than other group members in one video, but lower synchrony in the other video. There was insufficient evidence to reject the null hypothesis that pairs do not show consistently characteristic levels of synchrony, across all three measures of synchrony: median lag (*P*=0.156), proportion of lags ≤1 s (*P*=0.313) and proportion of lags ≤100 ms (*P*>0.999). This indicates synchrony may vary between pairs, or between video recordings, which likely represent different social or environmental contexts.

4.3.3 *Question (3) Can the degree of synchrony be explained by other physical and biological variables?*

Synchrony was not significantly associated with any of the environmental variables that were examined (Table 4.2). There was also no indication that whales increase synchrony towards the end of videos, as one might expect if they were preparing to dive (Table 4.3). Of the other biological variables (Table 4.3), the proportion of lags ≤100 ms strongly and significantly differed with group behaviour (Figure 4.5) but this was not as clearly the case for the proportion of lags ≤1 s. There was a slightly negative correlation between the absolute value of lags and group size (and thus a slightly positive relationship between synchrony and group size). The statistical test for this correlation yielded a fairly low *P* value, although it was not statistically significant (P=0.090).

Table 4.2 Tests for significant relationships between synchrony and physical predictors: Secchi depth (m), median daily swell height (m) and canyon (Gully or Shortland). Rho (ρ) is the Spearman's rank correlation coefficient, S is the test statistic for the Spearman's rank correlation test, X^2 is the Kruskal-Wallis rank sum statistic, and df= the degrees of freedom of the approximate chi-squared distribution of the test statistic.

Measure of synchrony	**Variable**	**Test statistics**	***P* value**
Median lag	Secchi	S=240, ρ=-0.091	0.789
	Swell	S=301, ρ=-0.385	0.242
	Canyon	Kruskal-Wallis X^2=0.739, df=1	0.390
Proportion ≤1 s	Secchi	S=244, ρ=-0.110	0.748
	Swell	S=163, ρ=0.257	0.446
	Canyon	Kruskal-Wallis X^2=0.739, df=1	0.390
Proportion ≤100 ms	Secchi	S=231, ρ=-0.050	0.883
	Swell	S=180, ρ=0.183	0.589
	Canyon	Kruskal-Wallis X^2=0.046, df=1	0.830

Table 4.3 Tests for significant relationships between synchrony and biological predictors including group size, group behaviour (logging or milling), polyspecific associations with pilot whales or Sowerby's beaked whales, distance (body widths), stagger (body lengths) and nearness to dive. Rho (ρ) is the Spearman's rank correlation coefficient, S is the test statistic for the Spearman's rank correlation test, X^2 is the Kruskal-Wallis rank sum statistic, and df= the degrees of freedom of the approximate chi-squared distribution of the test statistic.

Measure of synchrony	**Variables**	**Test statistics**	***P* value**
Median lag	Group size	S=5363, ρ=-0.321	0.090
	Group behaviour	Kruskal-Wallis X^2=0.016, df=1	0.899
	Polyspecific associations	Kruskal-Wallis X^2=1.678, df=2	0.432
	Distance	S=3179, ρ=0.217	0.258
	Stagger	S=4244, ρ=-0.045	0.816
	Nearness to dive	S=3502, ρ=0.137	0.477
Proportion lags ≤1s	Group size	S=3997, ρ=0.015	0.936
	Group behaviour	Kruskal-Wallis X^2=2.496, df=1	0.114
	Polyspecific associations	Kruskal-Wallis X^2=0.455, df=2	0.797
	Distance	S=3577, ρ=0.119	0.539
	Stagger	S=2868, ρ=0.294	0.122
	Nearness to dive	S=3758, ρ=0.074	0.701
Proportion lags ≤100 ms	Group size	S=3343, ρ=0.177	0.359
	Group behaviour	Kruskal-Wallis X^2=4.846, df=1	0.028*
	Polyspecific associations	Kruskal-Wallis X^2=0.462, df=2	0.794
	Distance	S=3536, ρ=0.129	0.505
	Stagger	S=2909, ρ=0.284	0.136
	Nearness to dive	S=4305, ρ=-0.060	0.756

Figure 4.5 The proportion of highly synchronous surfacings (lags ≤100 ms) differed significantly with the type of behaviour (milling and logging). There were insufficient data to evaluate the third behaviour type, travelling.

4.4 DISCUSSION

There are three main results of this chapter. (1) Northern bottlenose whales often synchronize surface exhalations with their nearest neighbours. (2) Synchronous breathing does not vary significantly with relationship type (age/sex classes) or relationship strength (association indices), but does vary significantly with behavioural state. (3) Although inconclusive, the findings of this chapter suggest synchronous breathing is not related to environmental variables but could be related to social variables such as group behavior. Thus it is possible that synchronous breathing could be a socially facilitated behaviour. If synchronous breathing does play a role in maintaining social bonds, as is thought to be the case for bottlenose dolphins, the results of this chapter suggest synchronous breathing might play a role in the maintenance of general social bonds within this tight knit community in the Gully.

Synchronized breathing appears to be a common phenomenon among northern bottlenose whales. Individuals often surface within 100 ms of each other, which is slightly less than synchronous male bottlenose dolphins which surface approximately 120-150 ms apart (Connor *et al.*, 2006). The breathing synchrony measured in this study is also similar to that of pilot whales off Cape Breton (Senigaglia and Whitehead, 2012). For pilot whales, given that whales surface within 3 seconds of each other, they surface within the same second approximately 50-60% of the time, and within 2 seconds of each other 30-40% of the time (Senigaglia and Whitehead, 2012). For northern bottlenose whales, these estimates are very similar: 51.5% and 28.6% (respectively). Northern bottlenose whales appear to synchronize behaviour very precisely compared to other cetacean species. For example, sperm whale terminal dives appear to be somewhat synchronous, however, the measured time lags between individual dives are much greater. Clusters of sperm whales usually synchronize dive times (measured by the fluke ups) within 10 s of each other, and often within 2 s (Whitehead, 2003). Since my study examined all breaths, and not just terminal dives, direct comparisons are not possible between studies of sperm whale terminal dives and syncrhonous breathing in bottlenose whales in this chapter. It seems possible, however, that because sperm whales are much larger than northern bottlenose whales, their precision of synchrony might be less. Also, because sperm whale age/sex classes are dimorphic in body length (differences between calves, females, immature males) it may be that animals initiate the dives or surface breaths with precise synchrony, but because of differences in body lengths they become less coordinated by the time flukes are raised.

One possible bias in this analysis arises from the condition that if two neighbours are spatially near, I selected the lag that was temporally smallest. This could potentially bias towards shorter lags, although it was necessary to make simple and consistent measurements of the nearest neighbours (nearest in space, and then nearest in time). A potential consequence of this bias would be that in Figure 4.2, the red line showing expected lag frequencies if whales were to breathe at random relative to each other, may start to decline at higher lags rather then remain level. This would be the result of slightly lower probabilities for some of the longer lags. This bias would not change the high frequency of lags that were very small <1s or <100ms, nor should it influence the comparison of synchrony across variables, such as group size or behaviours. Thus this bias, while acknowledged, should be of little consequence on the main results of this chapter. Northern bottlenose whales appear to exhibit some of the most precise synchronous displays among cetaceans. I review 8 different possible factors (which are not mutually exclusive) that could select for this behaviour, and discuss the support for each below:

4.4.1 Possible Factors that Select for Synchronous Breathing

4.4.1.1 Factor 1. Synchrony at the Surface Allows Whales to Synchronize Movements Underwater (Connor *et al.*, 2006)

This explanation seems especially plausible for deep-diving cetaceans such as northern bottlenose whales, as deep-diving activities would be directly linked to respiration because of oxygen demands. Northern bottlenose whales regularly dive to depths of 1450 m (Hooker and Baird, 1999). Therefore, I expected synchrony would increase towards the end of the videos (videos ended when whales dove, although I could not distinguish between shallow dives or deep dives). I found no evidence to support this explanation, as there was no significant correlation between the proportion of highly synchronous lags, or the median lag, and when (early or late) in the video the paired exhalation occurred.

4.4.1.2 Factor 2. Synchrony Varies with Environmental Stimuli (Hastie *et al.*, 2003)

Synchrony did not vary significantly with the physical variables that I measured (water transparency and swell height). It is possible that the time scale over which these physical variables were measured (several hours to a day) may have been too broad to correlate to variation in synchrony, which was measured at the scale of seconds. Alternatively there could be other external stimuli that were not accounted for (*e.g.* underwater noise). Hastie *et al.* (2003) proposed that increased synchrony in bottlenose dolphins could be a way to strengthen social cohesion in acoustically loud environments, where other forms of communication were more difficult. Beaked whales (family Ziphiidae, which includes northern bottlenose whales) are very sensitive to underwater noise, including the frequencies used for geophysical exploration and defense sonar (Barlow and Gisiner, 2006). Since I did not measure underwater noise in this study, I cannot rule out that the acoustic environment (as a stressor or as a stimulus) affects breathing synchrony among northern bottlenose whales.

In addition to physical variables, anthropogenic factors in the environment may promote synchrony. Increased breathing synchrony in response to boat traffic has been documented in bottlenose dolphins (Hastie *et al.*, 2003) and estuarine dolphins (*Sotalia guianensis*; Tosi and Ferreira, 2009), although boat traffic within the Gully MPA is very low and is likely not a major source of stress for northern bottlenose whales within the MPA (DFO, 2009). In addition, there is likely more ship traffic in Shortland canyon than within the Gully MPA, but I did not detect any difference in the median lags, or proportions of synchronous surfacings between canyons. Since the research platform is a boat, it is possible the presence of the research vessel is the stimulus for synchronous breathing. I do not believe this to be the case, as whales often approach our vessel, and even rest right beside our research boat. The research platform is also fairly small (12 m), a sailboat (although when we are with whales, the vessel is often under power using a diesel engine), and we travel at low speed (<5 knots) within the Gully MPA both to minimize noise and as a caution for driving around the whales.

Anthropogenic stressors are not the only source of disturbance; predation risk may also promote behavioural synchrony. In several families of air breathing fish, many individuals synchronize their surface breaths, likely as a means to reduce predation (Kramer and Graham, 1976). Two killer whale (*Orcinus orca)* attacks on northern bottlenose whales have been documented (Jefferson *et al.,* 1991), although killer whales are rarely observed in the Gully (Whitehead, 2013). Predation is likely a major driver for groups to form among marine mammals, and sperm whale group defense behaviours in response to killer whale predation have been observed off California (Pitman *et al.*, 2001). Sperm whales defend themselves from killer whale attacks by forming a rosette pattern; the sperm whales arrange themselves in a circle around a calf or injured animal with their powerful tails facing outwards toward their attackers (Pitman *et al.*, 2001). Although speculative, it seems possible that synchronized activities such as breathing could signal to predators that group members are able to work in a coordinated fashion if attacked. The use of synchronous breathing in northern bottlenose whales as a response to predation pressures could be investigated through the use of acoustic playback experiments with killer whale sounds. Since this population is endangered and resides within a MPA, the ramifications of disturbing the whales likely outweighs the direct benefits for this population that would be gained from such studies.

4.4.1.3 Factor 3. Synchrony is a Function of Group Size (Hastie *et al.*, 2003; Senigaglia and Whitehead, 2012)

There was a slightly negative correlation (ρ= -0.321) between group size and the median absolute value of lags (which indicates a positive relationship between group size and synchrony) that was near to, but not, statistically significant (*P*=0.090). This relationship was even weaker when the measure of synchrony was the proportion of synchronous lags rather than the median lag. These results could have been influenced by sampling methods, especially if the method by which the nearest (spatially closest) neighbour was interpreted in this study did not reflect the true pairs of synchronizing whales. When there are only two whales, the nearest neighbour is always clear, but as group size increases deciding the nearest neighbour becomes more subjective.

Alternatively, this correlation between synchrony and group size could be genuine; similar relationships have been documented in other cetacean populations. Bottlenose dolphins in the Moray Firth, Scotland, showed a positive relationship between group ("school") size and synchrony (Hastie *et al.*, 2003), although the authors noted this could have been due to an underlying effect where larger sample sizes have a higher clustering probability (Speakman *et al.*, 1992). Pilot whales have also been shown to increase synchrony when group size reaches 30 or more individuals (Senigaglia and Whitehead, 2012). Senigaglia and Whitehead (2012) reasoned that larger group size may create a more stressful and complicated social environment, which may lead to increased synchrony (consistent with factor 2). Interestingly, I found that synchronous breathing by northern bottlenose whales did not vary significantly with the occurrence of polyspecific associations with Sowerby's beaked whales or pilot whales, which also seem like complex social environments.

4.4.1.4 Factor 4. Synchrony Varies Between Behavioural States (Connor *et al.*, 2006)

The proportion of highly synchronous surfacing (lags up to 100 ms) differed substantially between behavioural states (milling and logging). Behaviours such as swimming in circles around our research vessel, animals rolling on their sides or hanging upside down just below the surface of the water, blowing bubbles, and on rare occasions even head-butting (Gowans and Rendell, 2006) are observed during bouts of milling. Thus when milling, interactions between individuals can be highly variable, and could include both agonistic and affiliative behaviours. In contrast, during logging whales tend to line up parallel to each other and “bob” at the surface as they rest. If milling represents a more hectic social environment than logging, these results again indicate support for factor 2. Connor *et al.* (2006) also found that bottlenose dolphin male alliance members synchronize exhalations more often during social behaviour than nonsocial behaviour.

4.4.1.5 Factor 5. Synchrony is an Adaptation to Reduce Drag (Connor *et al.*, 2006)

As Senigaglia and Whitehead (2012) noted with pilot whales that breathe synchronously, most synchronous pairs are side by side, a situation where they would not incur advantages of decreased drag. The positions most favourable for forward propulsion are obliquely in front or behind of another whale (Weihs, 2004). Conversely, the same argument has been used as support that synchrony *is* related to drag, and the side-by side positioning of synchronous pairs may ensure neither partner gains a hydrodynamic advantage (Connor *et al.*, 2006).

When northern bottlenose whales are logging, they are generally moving much too slowly for drag to be an issue, but there could potentially be hydrodynamic advantages from synchrony with behaviours such as milling or travelling. In this study, since northern bottlenose whales had a higher proportion of highly synchronous surfacings when milling compared to logging (Figure 5), it was interesting to find that these whales were more synchronous in situations where hydrodynamic advantages(although limited since they are moving slowly) could be gained. Additionally, there was no significant association with swell height which would also likely relate to the need for hydrodynamic advantages when swimming at the surface. Thus overall, there is no strong support for synchrony as an adaptation to reduce drag in this species.

4.4.1.6 Factor 6. Synchrony is a Function of Close Spatial Proximity (Connor *et al.*, 2006)

There was no indication that whales swimming close to each other have a higher probability of surfacing together, as synchrony was not significantly associated with the distance between individuals.

4.4.1.7 Factor 7. Synchrony Varies with Age/Sex Classes (Perelberg and Schuster, 2008) and/or Social Relationships (Sakai *et al.*, 2010)

Among bottlenose dolphins off Japan, when female pairs of dolpins breathe, there is a shorter time lag between paired exhalations than for pairs of male dolphins, and subadult pairs less than adults. Thus the degree of synchrony of exhalations has be related to the age/sex classes of the dolphins. In contrast, synchronous breathing among northern bottlenose whales does not appear to vary with age/sex class. Also, since I did not film any young northern bottlenose whale calves, the patterns of synchrony that I observed cannot be explained as the similar, highly synchronous surfacings that have been described for mother-calf pairs of bottlenose dolphins (Mann and Smuts, 1999). It is possible some northern bottlenose whales in this study were immature animals, but they cannot be reliably distinguished from adult females (Gowans *et al.*, 2000a).

Synchronous breathing varying with the type and strength of social relationships, as it appears to be with dolphins, is related to factor 2. One might expect that those relationships which are strongest (for example long-term preferred associations among mature males) may be those that require the most social cohesion. Synchronous breathing among male alliance pairs has been noted in bottlenose dolphins and is more common during social behaviours with females (Connor *et al.*, 2006). However, there was no indication in my study that breathing synchrony was related to the strength of northern bottlenose whale social relationships. As a result, measuring synchronous breathing does not appear to be an informative tool to reveal the type or strength of social relationships within populations of northern bottlenose whales on the Scotian Shelf.

4.4.1.8 Factor 8. Synchrony is a Social Signal (Connor *et al.*, 2006)

Connor *et al.* (2006) proposed that humans and dolphins may share a relatively uncommon social characteristic, that synchrony could function to signal coalition quality. In bottlenose dolphin societies, these signals are related to male alliances. There is some evidence in this study that synchronized breathing in northern bottlenose whales may also serve as a signal, although alliances similar to those of bottlenose dolphins have only been proposed among mature male bottlenose whales (Gowans *et al.*, 2001), and even those alliances are not as long-lasting (Chapter 3). The social structure of northern bottlenose whales in the Gully does involve long-term preferred associations among dyads of females, and dyads of mature males, which can last several years. Also, animals in the Gully appear to be organized as a single community without any discernible community division (Chapter 3). Therefore, there may be a general need for the reinforcement of social bonds for animals who live in a well-integrated community such as the Gully.

Support for the signal hypothesis to reinforce social bonds among bottlenose dolphins, includes variation in synchronous displays, for example with behaviour context (Connor *et al.*, 2006). Such variation with behavioural state was also observed among northern bottlenose whales. Additionally, if there is a fitness benefit to pairs of animals who preform synchronous displays, then it seems logical that animals without social ties would try to mimic this signal and essentially “cheat”; any two animals could make a display and incur the fitness benefits, without necessarily having to spend the time or practice involved in maintaining social bonds. This is thought to be why signals of coalition strength take a lot of practice and are often very complex (Hagen and Bryant, 2003; Hagen and Hammerstein, 2009). For example, the duets sung by coalition pairs of male long-tailed manakins are thought to take years to develop (Trainer *et al.*, 2002), thus providing an accurate signal that the partnerships are longstanding. Bottlenose dolphin male alliances have evolved elaborate displays including aerial leaps in addition to synchronous breathing or surfacing, and humans have developed complex and intricate songs as well as dances and marching.

If coordination takes considerable time investment or practice to be perceived as a longstanding relationship, then for synchronous events to be a signal, they should be very highly coordinated. As a byproduct of choosing three different criteria to define synchrony, I was able to examine the proportion of synchronous surfacings at two different scales of precision: surfacings of ≤1 s apart, as well as those ≤100 ms. If synchrony does in fact serve as a signal for the reinforcement of bonds among community members of northern bottlenose whales in the Gully, such a signal could have evolved to become extremely precise. This could explain why significant variations in lags across behaviours were only detected when the criteria used to define synchrony was more precise (100 ms rather than 1 s). Additionally, it could in part account for why breathing synchrony in northern bottlenose whales appears to be among the most precise of coordinated actions reported among cetaceans; in some cases even more precise than synchronized breathing reported for bottlenose dolphin male alliance pairs (Connor *et al.*, 2006).

4.3.2 Conclusions: Synchrony to Promote Short-Term Social Bonds

Although I found no indication that synchrony was related to environmental stimuli, the range of external stimuli I measured was very limited. There was some support for factors 2, 3, 4, 5 and 8 which all involve social facilitation to explain the occurrence of synchronized breathing, but overall the evidence for social facilitation of breathing synchrony among northern bottlenose whales remains weak. While speculative, of the factors investigated in this study, these results indicate northern bottlenose whales might synchronize their breathing to increase group cohesion, possibly by using synchrony to signal mutual cooperation (Connor *et al.*, 2006). Situations where breathing synchrony and group cohesion may be most important probably reflect environmental stressors including complex social environments. There are numerous examples of how relationships between individuals are based on behavioural interactions, and they are not just limited to the temporally clustering of behaviour. From social grooming in primates and greeting ceremonies in spotted hyenas (*Crocuta crocuta*; Smith *et al.*, 2011) to the singing of national anthems, the use of social behaviours to reinforce social bonds within groups of animals is widespread.

There are many similarities in the patterns of social relationships (and thus social structure) between bottlenose whales and bottlenose dolphins, and it appears synchronous breathing might be another element of sociality shared by these two cetacean species. While the support remains speculative, it may not be surprising that the factors proposed to explain breathing synchrony in these two species might overlap: promoting group cohesion (possibly by reducing tension) and signalling cooperation (Connor *et al.*, 2006). What I did not expect is that these explanations better apply to the fleeting, ephemeral group cohesion or general community cohesion among northern bottlenose whales than the long-term relationships (years-decades) maintained by preferred associates. Synchrony does not appear to be a useful tool to indicate the nature or strength of relationships among northern bottlenose whale societies, and at present, long-term photo-identification studies prove the most informative means to understand long-term social bonds.

Behavioural synchrony may however, offer insight towards the importance of reinforcing ephemeral group membership, or day-to-day interactions, which appear to be an important aspect of northern bottlenose whale social structure. Northern bottlenose whales in the Gully live in a fission-fusion society, where all animals belong to the same community, but group membership changes frequently. Despite the ephemeral nature of these groups, there is still cooperation. In Chapter 3, I mention how even though whales are constantly changing groups and associates, whalers noted their tendency to defend injured group members, often being killed themselves in the process (Reeves *et al.*, 1993). Integrated behaviours such as synchronized breathing are becoming more frequent in their application to the study of animal social structure (Whitehead, 2008a; *e.g.* Hastie *et al.*, 2003; Connor *et al.*, 2006; Senigaglia and Whitehead, 2012). This research of northern bottlenose whales on the Scotian Shelf further illustrates how the study of synchronous behaviour can be used to advance our understanding of cetacean societies.

Future research including a wider range of external stimuli, examining these environmental variables at finer scales, may offer more concrete evidence as to whether or not synchronous breathing in northern bottlenose whales is in fact, a product of social facilitation.

CHAPTER 5
CONCLUSIONS

My thesis research makes new contributions to science in two principal ways: applied research to assess the population status and address the knowledge gaps for an endangered cetacean population, and within a theoretical framework to further our understanding of the social organization of a member of one of the least known families of marine mammals, the beaked whales. Below, I discuss the main findings of my thesis on the population status and social organization of northern bottlenose whales (*Hyperoodon ampullatus*) in the Gully, as well as the implications on local (the conservation of this population on the Scotian Shelf) and broader (other populations and beaked whale species) scales.

5.1 POPULATION STATUS

As northern bottlenose whales on the Scotian Shelf are endangered, there is a Recovery Strategy in place to organize conservation efforts and prevent their local extinction. The overall goals of the Recovery Strategy are "*to achieve a stable or increasing population and to maintain, at a minimum, current distribution"* (DFO, 2009). The Gully population has been stable since 1988 and has remained so up to 2011 (Chapter 2). Over the 23 year period that this study addresses, the Gully submarine canyon went from being unprotected, to a candidate MPA, to a full MPA. This thesis was not an experiment to test the effect of the MPA on population size, which would require controls and replicates that were not feasible. Instead, this study aimed to examine whether conservation objectives are being met for this endangered population under the current management regime.

Chapter 2 of my thesis provided current information addressing Objective 2, and the corresponding identified knowledge gaps listed in the Recovery Strategy for the Northern Bottlenose Whale *(Hyperoodon ampullatus)*, Scotian Shelf population, in Atlantic Canadian Waters (DFO, 2009):

"*Objective 2. Improve understanding of the population size, trend and distribution"* (DFO, 2009).
Based on the most recent data available on northern bottlenose whales on the Scotian Shelf (up to and including 2011), estimates were produced for both the current population size of northern bottlenose whales in the Gully as 116 animals (SE=8.7, 95% CI=101-130 animals), and the entire Scotian Shelf as 143 animals (SE=7.9, 95% CI=129-156 animals). With the use of digital photography in this study, a greater proportion of the population was photo-identified, and this led to more precise estimates of population size and trends than previous assessments.

Knowledge gap: "estimates of vital rates (e.g., birth and death rates) are required for modelling population, dynamics and the determination of recovery reference points" (DFO, 2009).
In this study, the best supported population model with a trend had a 95% CI of -2.0% to 2.0% per year. This suggests that while stable, the Gully population could be decreasing or increasing within a net range of ± 3 animals per year.

Knowledge gap: "the age and sex class structure for the Scotian Shelf population and how they are distributed within and use Shortland and Haldimand canyons" (DFO, 2009).
The current age/sex structure of the Scotian Shelf population (Gully and Shortland canyons) is depicted in Figure 2.5. There were insufficient data to assess the age/sex class structure of the animals in Haldimand canyon. The Gully habitat is used by groups of bottlenose whales comprised of mature males, females and subadult males, whereas canyons outside of the MPA may be used less by subadult males.

Knowledge gap: "the sex-ratio in the Scotian Shelf ... population" (DFO, 2009).
Over the 23 year period the Gully population was examined, there was no evidence that the sex-ratio has changed significantly over time.

The stable population size, absence of a decreasing population trend, and indication that sex-ratios have not changed over the last 23 years, all provide support that this population is persisting. These findings are generally consistent with previous assessments, and thus probably do not imply that there needs to be an immediate change in our management efforts with respect to this population. It is encouraging, however, to know that the objective of maintaining at minimum a stable population is currently being met.

No significant increases in population size have been detected since the MPA was established in 2004, although it seems probable that the implementation of MPA regulations have positively influenced this population, and will continue to do so in the future. This study shows that this population could be increasing (or decreasing) up to a maximum of 2% per year, thus I am likely examining this situation too early to detect any benefits of MPA regulations on population growth. Off New Zealand, Gormley *et al.* (2012) have documented an increased growth rate for a resident population of endangered Hector's dolphins (*Cephalorhynchus hectori*) over a 24 year span since their habitat became protected as an MPA. The work of Gormley *et al.* (2012) not only it illustrates the success of area-based management for an endangered cetacean population, but it also shows the benefit of long-term monitoring to evaluate MPA efficacy.

5.2 SOCIAL ORGANIZATION

Northern bottlenose whales, like most cetaceans, are social animals. They have a complex repertoire of social behaviour that ranges from agonistic behaviours (such as head-butting; Gowans and Rendell, 2006) to affiliative behaviour (such as resting their chin on a neighbour's back). They also commonly interact with other species such as Sowerby's beaked whales (*Mesoplodon bidens*). Thus social interactions are an important component of their daily lives. This thesis aimed to further our understanding of the social organization of northern bottlenose whales in the Gully. Specifically, I wanted to add some detail to our knowledge of long-term preferred associations among dyads of female/immature whales and dyads of mature males, apply network statistics to examine community division, and incorporate the use of high definition video recordings to explore breathing synchrony.

Summarizing the principal results on the social organization of northern bottlenose whales in the Gully: they have a fission-fusion social system, associations are strongest within rather than between age/sex classes, and while most associations are weak there are some long-term preferred associations. These long-term preferred associations are maintained over a span of many years (some dyads of females) up to over a decade (some dyads of males), but these preferred associations all eventually ended and thus, at least among the animals that I studied, are not maintained for life. Northern bottlenose whales synchronize their surface breathing, and if the underlying function of this behavior is similar to that of bottlenose dolphins, synchronous breathing could perhaps play a role in the maintenance of social relationships. At present, there remains insufficient evidence to draw any conclusions about the function of synchronous breathing, although it does appear to vary with behavioural context and thus might be related to social factors.

The Gully habitat is a unique oceanographic feature, and has likely contributed to some of the distinct characteristics of northern bottlenose whale social organization. Even though the Gully is the largest underwater canyon in the northwest Atlantic, the approximately 116 northern bottlenose whales that use the Gully share a relatively small habitat. The canyon measures 40 x 16 km, and in some areas it is over 3 km deep (DFO, 2008). Submarine canyons have steeply sloping walls, so the horizontal aspect of the Gully is even smaller at increasing depths, where northern bottlenose whales spend a great deal of time foraging. Consequently, the spatial constraints of the Gully habitat likely drive individuals to interact frequently. To draw an analogy from my own society, the northern bottlenose whales of the Gully may be similar to the residents of a small town; everyone knows everyone else, but they are not all necessarily preferred associates. This general recognition of other members of the population could help explain why group members appeared to demonstrate social cohesion when they were attacked by whalers, even though in general, most associations appear to be weak and fleeting. Unfortunately, our current descriptions of social structure cannot evaluate the capacity of whales to recognize and remember past associates. Although speculative, it is possible that the general associations of the tight knit community of northern bottlenose whales in the Gully may, in part, be maintained by synchronized breathing.

There are likely many different factors which have shaped the social structure of northern bottlenose whales on the Scotian Shelf. The Gully environment may have played an important role, but not all cetaceans of the Gully have the same social structure. For example sperm whales (*Physeter macrocephalus*) also use the Gully, but their societies have evolved sexual segregation, permanent social units composed of females and immature animals, and communal infant care. Thus environment alone cannot account for the social structure of northern bottlenose whales in the Gully. Phylogeny likely also plays a role in social evolution. Beaked whales have relatively large calves (Huang *et al.,* 2011), which may mean they are able to reach diving capability sooner, and thus they could have bypassed the need for the evolution of cooperative infant care. Northern bottlenose whales and coastal bottlenose dolphins (*Tursiops* spp.) have many aspects of social structure in common (Gowans, 1999, Gowans *et al.*, 2001), but these species also have many differences (Chapter 3). Environment, ancestry and morphology have likely all played important roles in social evolution of northern bottlenose whales in the Gully.

The northern bottlenose whales of the Scotian shelf are the most extensively studied of all identified populations for this species. Descriptions of the population structure and social structure for the Scotian Shelf population may help us better understand many other populations that have not been the subject of long-term photo-identification studies, including those populations in regions off eastern Canada (northern Labrador, and in southern Baffin Bay), as well as the eastern North Atlantic [waters off Greenland, Iceland, Jan Mayen and the Faeroe Islands, and Norway including Svalbard (Spitzbergen); Whitehead and Hooker, 2012]. In addition, as more light is shed on the social structures of related beaked whale species such as the southern bottlenose whale (*Hyperoodon planifrons*) or the tropical bottlenose whale (also known as Longman's beaked whale, *Indopacetus pacificus*), it will be interesting to see if these close relatives share similar patterns of social relationships.

The social structure research in this thesis is primarily driven by questions about social evolution; however, it also has relevance for the conservation of threatened and endangered species. On a broader scale, the methods used in this thesis have proved useful in the study of another beaked whale species listed as Special Concern (COSEWIC), Sowerby's beaked whale, which is also commonly observed in the Gully. The methods outlined in Chapters 2 and 3 have provided a starting point to apply photo-identification methods to the study of the population structure and social organization of this sympatric beaked whale species. On a local scale, the apparent lack of community division in the Gully (Chapter 3) supports managing the northern bottlenose whales of the Gully as a single well-integrated community. As whales enter and leave the MPA to visit other canyons, there is the potential for human activities outside the MPA to affect this population. At present Shortland and Haldimand canyons are being considered for offshore petroleum exploration, including the use of seismic activities (CNSOPB, 2013). The Gully, Shortland, and Haldimand canyons lie not far apart along the edge of the Scotian Shelf. If such activities prohibit the movement of whales between the canyons, and thus create artificial community division, there is potential for social network of the Gully community to be altered.

5.3 CONCLUSIONS AND DIRECTIONS FOR FUTURE RESEARCH

Small populations are thought to be at greater risk of extinction (Shafer, 1981), thus continued monitoring of this very small and endangered population of northern bottlenose whales will be critical in future years to help ensure that if population decline occurs, it can be detected early so that mitigation strategies can be adapted. A portion of this population has been sampled using genetic techniques (Gowans *et al.*, 2000a; Dalebout *et al.*, 2001; Dalebout *et al.*, 2006) and future work using biopsy samples could yield considerable insight toward discerning the sex of individuals as well as their relatedness, movements, diet and reproductive status, and links to other populations. Such information could further our understanding of this small population of northern bottlenose whales and their recovery. Additionally, as more data is collectedd on lesser known beaked whale species, we may soon be able to evaluate the utility of northern bottlenose whales as a model for beaked whale social structure in general.

The Gully MPA was created for broad-scale ecosystem and biodiversity conservation (Westhead *et al.,* 2012). While the results of this dissertation research are limited to understanding the status of one cetacean species in this ecosystem, marine predators such as cetaceans may be especially useful focal species to indicate wide-scale ecosystem change (Hoyt, 2011) and thus studies of the northern bottlenose whale, the most iconic species of the Gully, will provide insight as we strive to conserve this unusual and productive marine habitat.

APPENDIX 1
PUBLICATIONS

The work presented in Chapter 2 has been accepted for publication:
O'Brien, K. and H. Whitehead. In Press. Population size, population trends and demographics of endangered northern bottlenose whales *(Hyperoodon ampullatus)* on the Scotian Shelf, Nova Scotia, Canada, seven years after the establishment of a Marine Protected Area. Endangered Species Research dx.doi.org/10.3354/esr00533

Appendix 2
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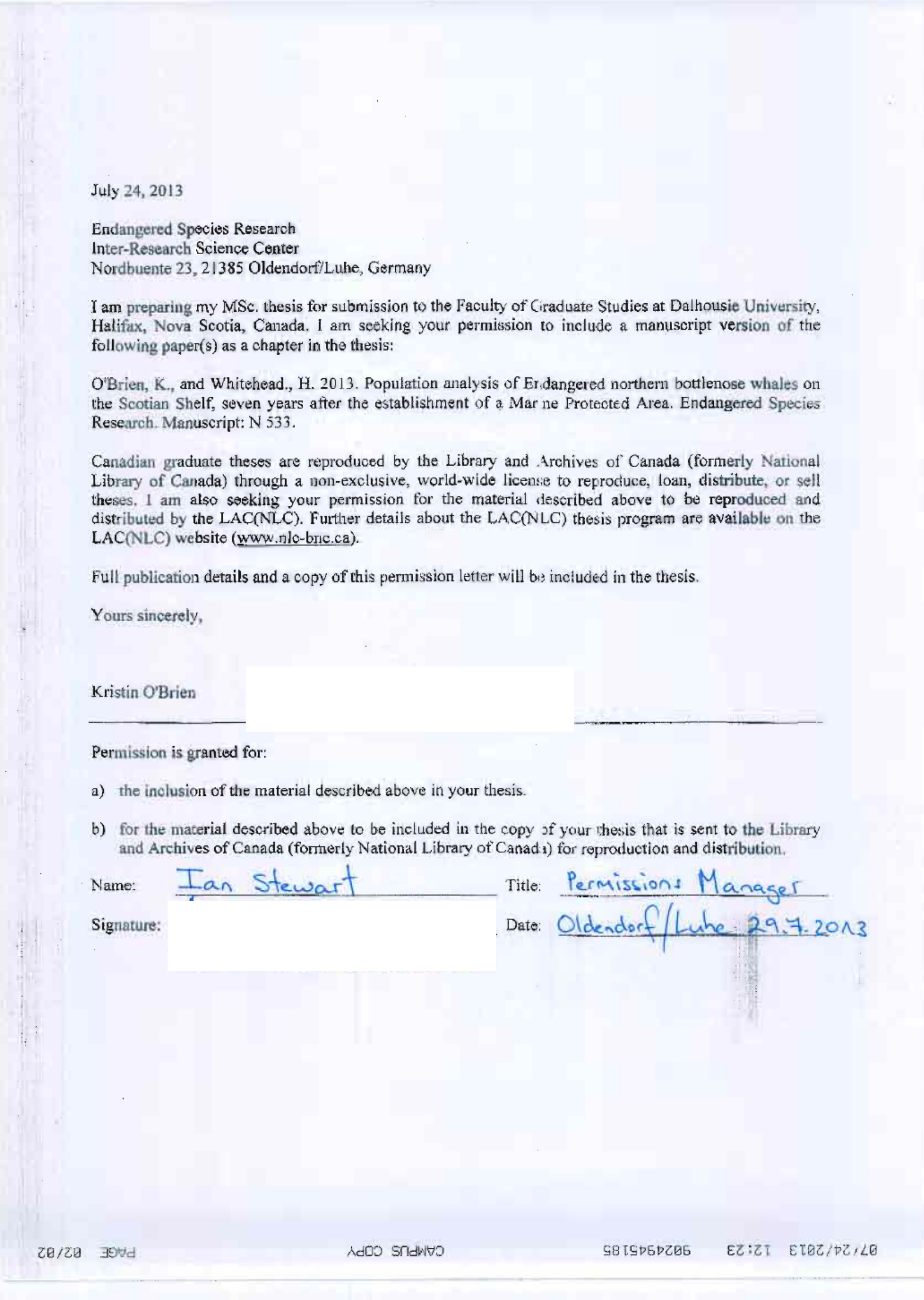

July 24, 2013

Endangered Species Research
Inter-Research Science Center
Nordbuente 23, 21385 Oldendorf/Luhe, Germany

I am preparing my MSc. thesis for submission to the Faculty of Graduate Studies at Dalhousie University, Halifax, Nova Scotia, Canada. I am seeking your permission to include a manuscript version of the following paper(s) as a chapter in the thesis:

O'Brien, K., and Whitehead., H. 2013. Population analysis of Endangered northern bottlenose whales on the Scotian Shelf, seven years after the establishment of a Marine Protected Area. Endangered Species Research. Manuscript: N 533.

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APPENDIX 3

TABLE A3.1 COMPARISON OF SOCIAL STRUCTURE BETWEEN NORTHERN BOTTLENOSE WHALES (*HYPEROODON AMPULLATUS*) AND COASTAL BOTTLENOSE DOLPHIN (*TURSIOPS* SPP.) POPULATIONS PRIOR TO THIS THESIS

Aspect of social structure	**Bottlenose dolphins**	**Northern bottlenose whales**
Fission-fusion societies	Shark Bay, Australia (Smolker *et al.,* 1992; Connor *et al.,* 1996), Queensland, Australia (Chilvers and Corkeron, 2002), Northern Adriatic Sea (Bearzi *et al.,* 1997), Texas, USA (Bräger *et al.,* 1994), Moray Firth, Scotland (Lusseau *et al.,* 2006).	Gully: fission-fusion with group membership changing frequently (Gowans *et al.,* 2001). Revisited in Chapter 3.
Group size	Shark Bay, Australia: mean of 4.8 (Smolker *et al.,* 1992), Northern Adriatic Sea: mean of 7 and mode of 2 (Bearzi *et al.,* 1997), Texas, USA: mean of 4.4 (Bräger *et al.,* 1994).	Gully: 3.0 (Gowans *et al.,* 2001). Revisited in Chapter 3.
Associations among males are stable; females form a loose network of associations	Shark Bay, Australia: male associations are stable over decades (Connor *et al.,* 1992; Smolker *et al.,* 1992; Krützen *et al.,* 2003; Connor *et al.,* 2006; Connor, 2007).	Gully: male associations can last 1-2 years (Gowans *et al.,* 2001). Revisited in Chapter 3.
Strong mother-calf bonds	Cedar Keys, Florida (Quintana-Rizzo and Wells, 2001), Shark Bay, Australia (Smolker *et al.,* 1992).	Not studied.
Community division	Doubtful Sound, New Zealand (Lusseau and Newman, 2004), Moray Firth, Scotland (Lusseau *et al.,* 2006), Tampa Bay, Florida (Urian *et al.,* 2009).	Addressed in Chapter 3.
Motor synchrony	Shark Bay, Australia: male alliances exhibit synchrony especially when a female is present (Connor *et al.,* 2006). Tokyo, Japan: synchrony occurs within sex-age classes, and between mother-calf pairs and escort-calf pairs (Sakai *et al.,* 2010). Moray Firth, Scotland: synchrony is not associated with feeding, negatively associated with the presence of calves, and positively associated with boat traffic (Hastie *et al.,* 2003).	Addressed in Chapter 4.
Distance and stagger within dyads	Shark Bay, Australia: increased synchrony is correlated with decreased distance between individuals (Connor *et al.,* 2006). Tokyo, Japan: the distance between synchronous pairs is smallest for mother-calf dyads, and there is less distance between pairs of females than pairs of males (Sakai *et al.,* 2010).	Addressed in Chapter 4.

Appendix 4
SOCIAL STRUCTURE ANALYSES FROM CHAPTER 3 REPEATED USING RIGHT DORSAL FIN SIDE DATA

Table A4.1 Results from right side photo-identifications for the correlation coefficients between true association indices and calculated association indices with bootstrapped SE. Associations were defined by membership to the same *group.* Estimates are presented for the population in general, as well as each separate age/sex class.

Class	Correlation coefficient (SE)
All	0.392 (SE= 0.031)
Female/immature	0.404 (SE= 0.048)
Subadult male	No estimate (too few data)
Mature male	0.576 (SE= 0.050)

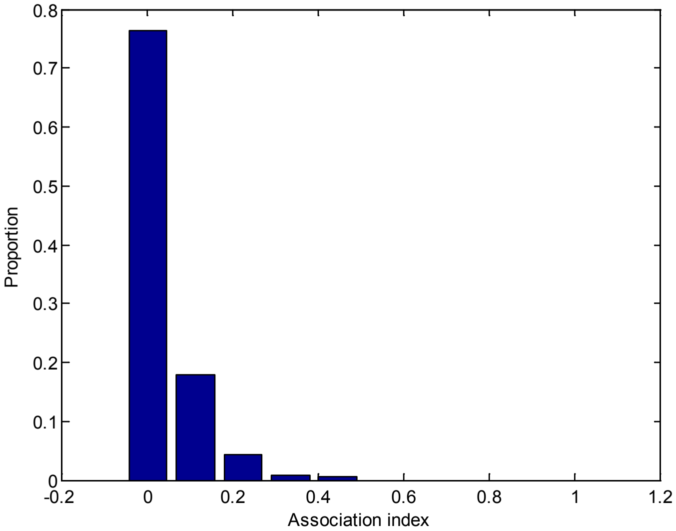

Figure A4.1 The distribution of half-weight association indices for northern bottlenose whales in the Gully based on right side photo-identifications. These results are restricted to individuals who were identified in at least 15 sampling periods.

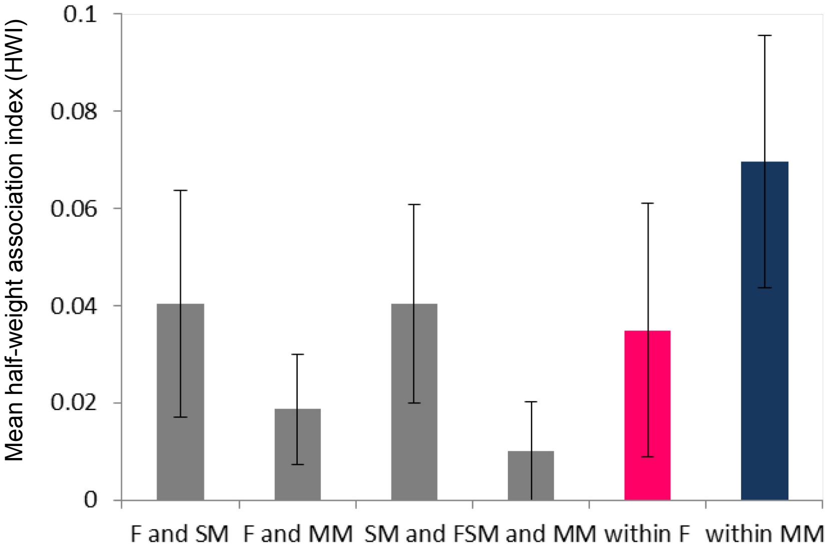

Figure A4.2 Within class (pink or blue) and between class (grey) measures of the mean (over all individuals) of mean association indices based on right side photo-identifications. Error bars are SE. Classes are abbreviated as females/immatures (F), subadult males (SM) and mature males (MM).

Table A4.2 Measures of within and between class half-weight association indices (SD) from right side photo-identification data.

Class	**Mean**	**Sum**	**Max**
Within	0.0478 (0.0338)	1.53 (0.410)	0.208 (0.154)
Between	0.0193 (0.0122)	0.336 (0.218)	0.135 (0.0604)
Overall	0.0319 (0.0147)	1.86 (0.398)	0.247 (0.110)

Table A4.3 Measures of social differentiation estimated using maximum likelihood with bootstrapped SE for right side photo-identifications. Estimates are presented for the population in general, as well as each separate age/sex class.

Class	**Social differentiation measure (SE)**
All	0.83 (0.04)
Female/immature	0.91 (0.10)
Subadult male	No estimate (too few data)
Mature male	0.82 (0.06)

Table A4.4 Differences in gregariousness between individuals that were based on right side photo-identifications, and were consistent with results presented in Table 3.6 and left out for simplicity. Significant *P* values are indicated by an asterisk. Classes are abbreviated as female/immature (F), subadult male (SM) and mature male (MM). All results presented here were from associations based on animals in the same *encounter*, results based on *clusters* were similar.

Class	**n**	**Number of permutations**	**SD of typical group size**		***P* value of SD**
			Real data	**Random data**	
All	127	60 000	26.0	23.7	0.017*
Within F	55	40 000	11.4	7.5	0.001*
F to SM	55 10	20 000	10.0	9.1	0.027*
F to MM	55 18	10 000	8.4	8.6	0.510
Within SM	10	10 000	4.3	2.3	<0.001*
SM–F	10 55	10 000	4.4	3.6	<0.001*
Within MM	18	10 000	6.8	6.7	0.449*
MM–SM	18 10	30 000	10.3	9.3	0.204

Table A4.5 Results from permutation tests for short-term preferred associations within classes that were based on right side photo-identifications, and were consistent with results presented in Table 3.7 and left out for simplicity. Significant *P* values are indicated by an asterisk. Associations were defined as members of the same *group* for long-term analyses (1988-2011) and *encounters* for short-term (2010-2011) analyses. Analyses where associations were defined by membership to the same *cluster* were similar.

Data set	**Class**	**n**	**Number of permutations**	**Mean Association Index**		***P* value**
				Real data	**Random data**	
1988-2011	Females/immatures	79	60 000	0.017	0.017	0.152
	Mature males	37	60 000	0.029	0.031	0.015*
2010-2011	Females/immatures	55	40 000	0.090	0.095	0.003*
	Mature males	18	10 000	0.152	0.149	0.714

Table A4.6 Results from permutation tests for long-term preferred associations within classes that were based on right side photo-identifications, and were consistent with results presented in Table 3.8 and left out for simplicity. Significant *P* values are indicated by an asterisk. Associations were defined as members of the same *group* for long-term analyses (1988-2011) and *encounters* for short-term (2010-2011) analyses. Analyses where associations were defined by membership to the same *cluster* were similar.

Data set	**Class**	**n**	**Number of permutations**	**CV of Association index**		***P* value**
				Real data	**Random data**	
1988-2011	Females/immatures	79	40 000	4.608	4.393	0.021*
	Subadult males	20	-	-	-	-
2010-2011	Females/immatures	55	5 000	2.194	1.995	<0.001*
	Subadult males	10	20 000	1.271	1.221	0.167

Table A4.7 Comparison of model fit for SLAR models to describe associations for the population in general. Results are based on right side photo-identifications. Best support for model fit is indicated by the lowest Δ*Q*AIC.

Model	***Q*AIC**	**Δ*Q*AIC**	**Support**
$SLAR_1 : g' = a$	2729.2	60.41	Less
$SLAR_2 : g' = a \cdot e^{-b\tau}$	2673.0	4.22	Less
$SLAR_3 : g' = a + c \cdot e^{-b\tau}$	2672.9	4.10	Less
$SLAR_4 : g' = a \cdot e^{-b\tau} + c \cdot e^{-d\tau}$	**2668.8**	**0.00**	**Most**

The equation and parameter estimates (SE) for the best supported model describing group dynamics for all northern bottlenose whales in the Gully were: $g'(\tau) = a \cdot e^{-b\tau} + c \cdot e^{-d\tau}$, where $g'(\tau)$= standardized lagged association rate at lag (τ), τ = 1 day, a =0.0950 (SE=0.0977), $b = 1.133$ (SE=0.827), $c = 0.0351$ (SE=0.00962), and $d = 0.000320$ (SE=7.77 e^{-005}).

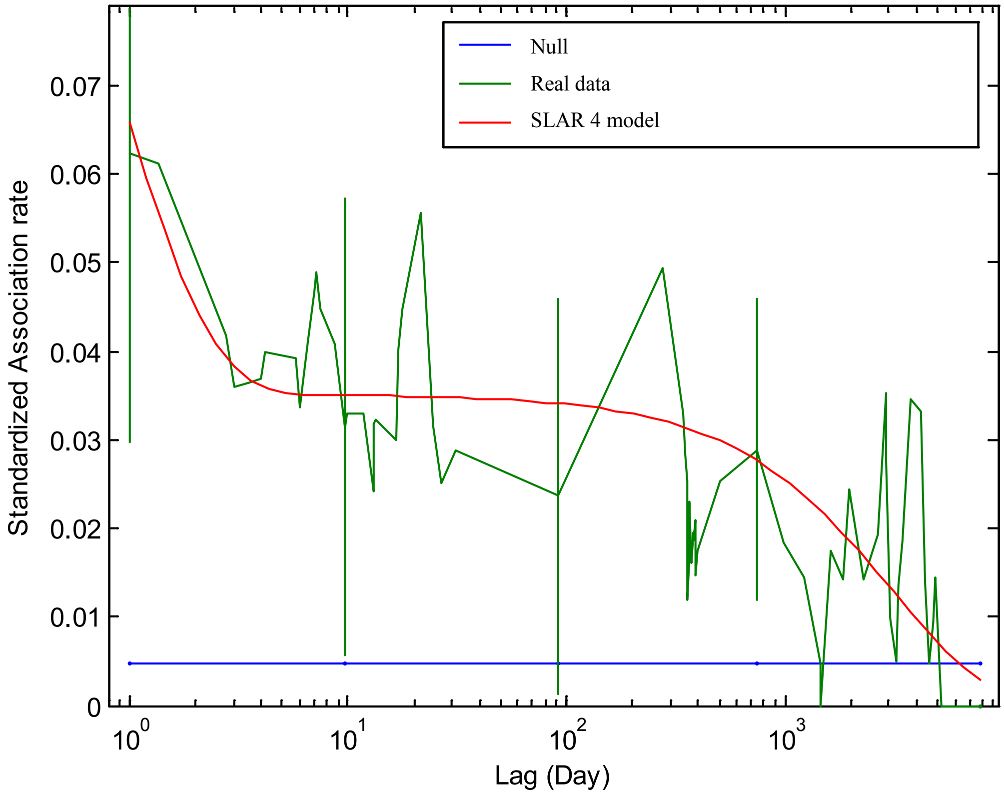

Figure A4.3 Real and modelled standardized lagged association rate data showing that preferred associations among northern bottlenose whales diminish and reach random levels after approximately 5000 days (over 13 years). The following results are based on right side photo-identifications only.

Table A4.8 Comparison of model fit for SLAR models to describe associations within the female/immature class based on right side photo-identifications. Best support for model fit is indicated by the lowest Δ*Q*AIC.

Model	*Q*AIC	Δ*Q*AIC	Support
$SLAR_1 : g' = a$	601.39	35.24	Less
$SLAR_2 : g' = a \cdot e^{-b\tau}$	566.44	0.29	Some
$SLAR_3 : g' = a + c \cdot e^{-b\tau}$	566.34	0.19	Some
$SLAR_4 : g' = a \cdot e^{-b\tau} + c \cdot e^{-d\tau}$	**566.15**	**0.00**	**Most**

The equation and parameter estimates (SE) for the best supported model describing group dynamics for female and immature northern bottlenose whales in the Gully were: $g'(\tau) = a \cdot e^{-b\tau} + c \cdot e^{-d\tau}$ where $g'(\tau)$= standardized lagged association rate at lag (τ), $\tau = 1$ day, a =0.313 (SE=4.17), $b = 1.01$ (SE=4.17), $c = 0.0966$ (SE=1.07), and $d = 0.000971$ (SE=0.297).

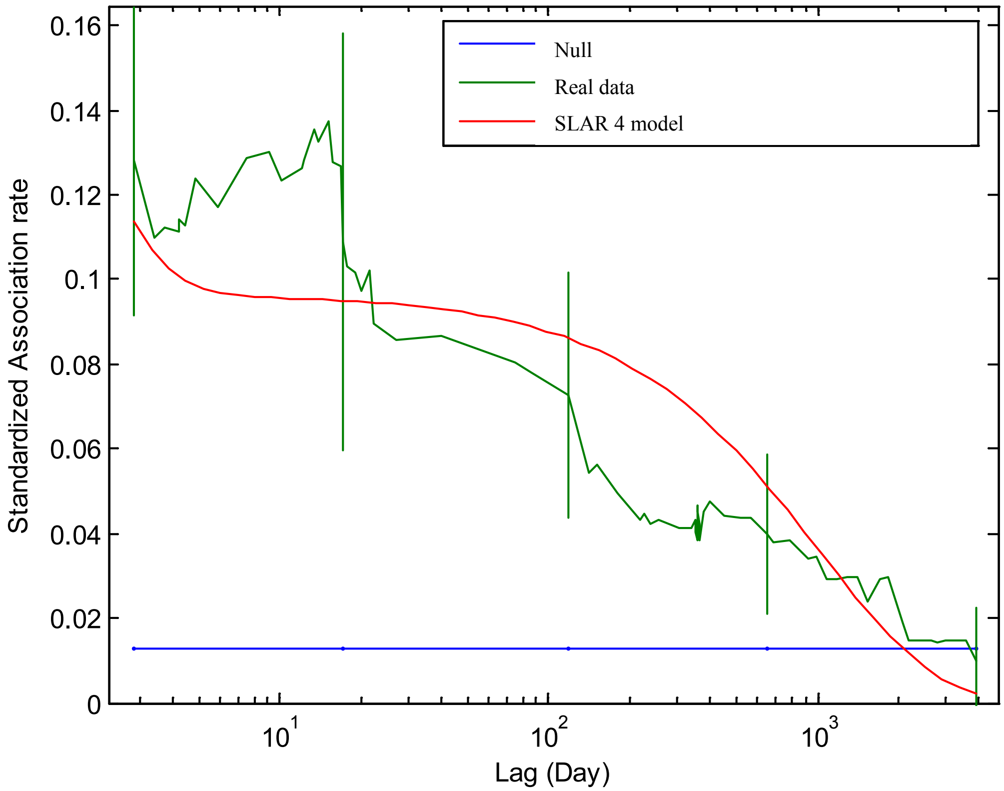

Figure A4.4 Real and modelled standardized lagged association rate data showing that preferred associations among female and immature northern bottlenose whales diminish and reach random levels after approximately 3000 days (over 8 years). The following results are based on right side photo-identifications only.

Table A4.9 Comparison of model fit for SLAR models to describe associations within the mature male class based on right side photo-identifications. Best support for model fit is indicated by the lowest Δ*Q*AIC.

Model	***Q*AIC**	**Δ*Q*AIC**	**Support**
$SLAR_1 : g' = a$	970.63	10.38	Less
$SLAR_2 : g' = a \cdot e^{-b\tau}$	**960.25**	**0.00**	**Most**
$SLAR_3 : g' = a + c \cdot e^{-b\tau}$	964.20	3.95	Less
$SLAR_4 : g' = a \cdot e^{-b\tau} + c \cdot e^{-d\tau}$	963.06	2.81	Less

The equation and parameter estimates (SE) for the best supported model describing group dynamics for female and immature northern bottlenose whales in the Gully were: $g'(\tau) = a \cdot e^{-b\tau}$ where $g'(\tau)$= standardized lagged association rate at lag (τ), $\tau = 1$ day, a =0.137 (SE=0.0496), and b =0.000152 (SE=0.000111).

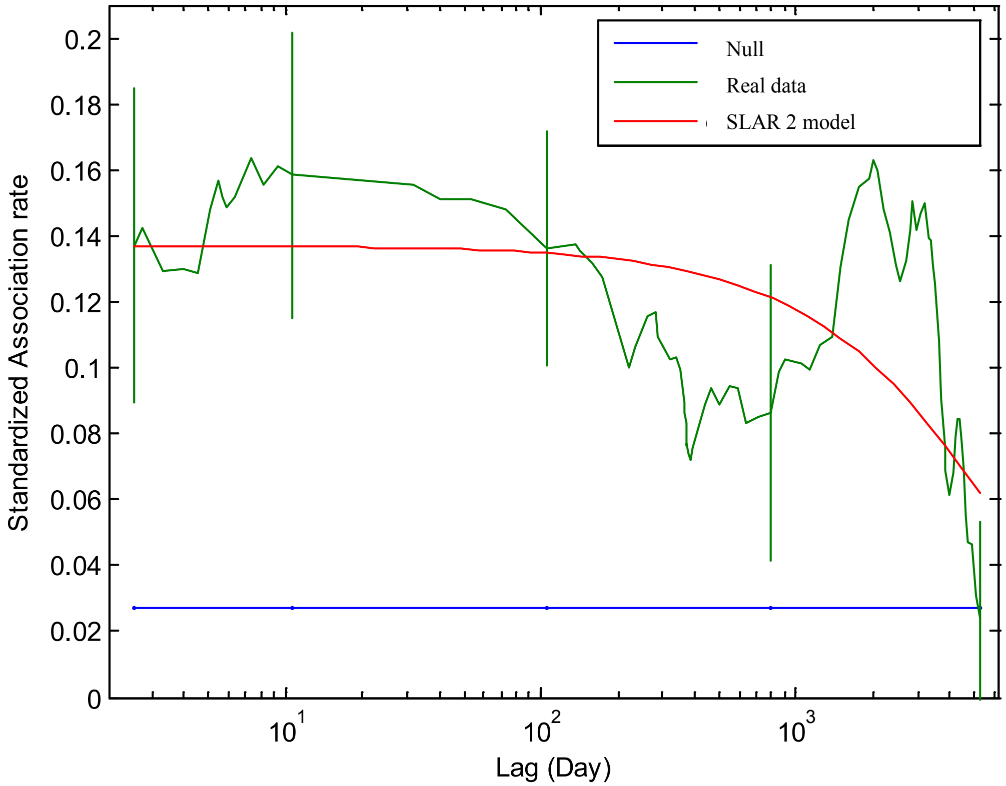

Figure A4.5 Real and modelled standardized lagged association rate data showing that preferred associations among mature male northern bottlenose whales diminish and reach random levels after a maximum of 4000 days (over 10 years). The following results are based on right side photo-identifications only.

Table A4.10 Community division was explored using hierarchical cluster analysis and network modularity. These results are based on right side photo-identifications only. Cophenetic Clustering Coefficient (CCC) values >0.8 indicate data are well represented by a hierarchical model, and modularity values between 0.3-0.7 indicate substantial community division.

Location	**Association defined by whales in the same:**	**CCC**	**Modularity (G)**
Gully	*Encounter*	0.692	0.273
	Cluster	0.771	0.416

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