Narwhal communication and grouping behaviour: a case study in social cetacean research and monitoring

by

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Abstract

Narwhals (*Monodon monoceros*) are gregarious, toothed whales restricted to the Arctic, where habitats are changing and shipping traffic is increasing. Challenges associated with the remoteness of narwhal populations and the general difficulty of studying deep diving mammals have resulted in a lack of knowledge of narwhal social behaviour, which can only be rectified with intensive, direct and systematic observations. I studied the grouping patterns and vocal behaviour of narwhals using non-invasive methods and developed new statistical tools to analyse the data. The field work was conducted at Bruce Head, a peninsula at the mouth of Koluktoo Bay, Nunavut, during the summers of 2006-2008. Shore-based observations were used to delineate narwhal groups by sex and age class. Narwhals travelled in clusters of 1–25 individuals of mixed sex and age class. Narwhals entered the bay in larger groups than they exited. The coloration of narwhal's backs on photographs was used to estimate their age and investigate their association with individuals of similar age. To analyse these data, I developed statistical methods that examine the distribution of observations in time and their associated characteristics. Using these methods, I found that narwhals form groups with individuals of similar age. The variability and the context of usage of narwhal calls were examined from underwater recordings. Some physical characteristics of narwhal whistles seemed behaviour-specific. Both whistles and pulsed calls might serve in individual- or group-recognition. Finally, given that there is a need for sustained, local monitoring of narwhals, I explored the potential of passive acoustic methods for narwhal monitoring. An automated detector was able to correctly identify narwhal calls in a 25-day continuous recording. There was a correlation between the number of calls manually detected in non-continuous recordings and the number of narwhals observed during the recordings. Non-invasive methods can provide valuable insight into the social organization, communication and movement patterns of large numbers of non-disturbed cetaceans.

Résumé

Le narval (*Monodon monoceros*) est un cétacé grégaire arctique dont l'habitat est en train de se modifier rapidement. Les difficultés reliées à l'accès en Arctique et à l'étude des cétacés en haute mer expliquent le manque d'information sur le comportement social des narvals. Dans le cadre de mes études doctorales j'ai étudié les groupes sociaux des narvals ainsi que leur communication vocale en utilisant des méthodes de récolte de données non invasives. De plus, j'ai développé des méthodes statistiques pour l'analyse de ces données. Le travail de terrain s'est déroulé au cours des étés 2006 à 2008 dans la baie Koluktoo, au Nunavut. À partir d'observations faites de la côte, la composition et la taille des groupes de narvals ont été compilées. Les narvals se déplaçaient en groupes de 1 à 25 individus d'âge et de sexe variés et entraient dans la baie en groupes plus nombreux que lorsqu'ils en sortaient. La coloration sur le dos des narvals pris en photo a servi à estimer leur âge et à évaluer la formation de groupe en fonction de ces âges. Pour analyser ces données, j'ai développé des méthodes statistiques qui évaluent la distribution d'observations réparties dans le temps ainsi que des caractéristiques associées à chacune des observations. Cette analyse m'a permis de conclure que les narvals forment des groupes avec des individus d'âges similaires. La variabilité et le contexte de l'utilisation des vocalisations émises par les narvals ont par la suite été étudiés à partir d'enregistrements acoustiques sous-marins. Ainsi, certaines caractéristiques acoustiques des vocalisations semblent associées spécifiquement à certains comportements. De plus, certaines de ces vocalisations pourraient être uniques à chaque groupe. Finalement, j'ai exploré la faisabilité d'un programme de surveillance acoustique à long terme pour les narvals. Les vocalisations des narvals ont été correctement détectées par un détecteur automatique appliqué à un enregistrement continu sur 25 jours. Le nombre de narvals observés visuellement et le nombre de vocalisations entendues durant ces enregistrements non continus étaient corrélés. Ces méthodes non invasives

permettent d’étudier l’organisation sociale, la communication et les mouvements cétacés en grand nombre sans les perturber.

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Contribution of co-authors and remarks on style

The format of this thesis is manuscript-based and follows the guidelines of *Animal Behaviour*. I am the primary author of all the chapters of this thesis. Chapter 2 is co-authored with M. Auger-Méthé and M. M. Humphries and was published as an original paper in *Polar Biology*[1]. Chapter 3 is co-authored with G. Larocque, M. Auger-Méthé, P. Dutilleul and M.M. Humphries and has been accepted for publication as a commentary in *Animal Behaviour*[2]. This chapter does not contain an abstract because it is not required for commentaries in *Animal Behaviour*. Chapter 4 is co-authored with M. Auger-Méthé and M.M. Humphries and has been submitted as an original paper to *Marine Mammal Science*[3]. Chapter 5 is co-authored with M. Auger-Méthé, E. Chmelnitsky, S. Ferguson, and M.M. Humphries, and has been submitted as an original paper to *Arctic*[4]. The abstract of this chapter has been translated to French as required by the journal *Arctic*.

M. M. Humphries has provided academic supervision, ideas, statistical and editorial assistance for all chapters. M. Auger-Méthé assisted with data collection and was present in the field when all data were collected; she also contributed to the development of ideas, provided analytical help and comments for all chapters. G. Larocque has contributed to the method development and the writing of chapter 3. P. Dutilleul has provided statistical and editorial guidance for chapter 3. E. Chmelnitsky and S. Ferguson have provided data and editorial comments for chapter 5.

[1] **Marcoux, M., Auger-Méthé, M. & Humphries, M. M.** (2009) Encounter frequencies and grouping patterns of narwhals in Koluktoo Bay, Baffin Island. *Polar Biology,* 32, 1705-1716

[2]**Marcoux, M., Larocque, G., Auger-Méthé, M., Dutilleul, P. & Humphries, M. M.** (In Press) Statistical analysis of animal observations and associated marks distributed in time using Ripley's functions. *Animal Behaviour*

[3]**Marcoux, M., Auger-Méthé, M. & Humphries, M. M.** (submitted) Variability and context-specificity of narwhal (*Monodon monoceros*) whistles and pulsed calls. *Marine Mammal Science*

[4]**Marcoux, M., Auger-Méthé, M., Chmelnitsky, E., Ferguson, S. H. & Humphries, M. M.** (submitted) Local passive acoustic monitoring of narwhals in the Canadian Arctic. *Arctic*

Original contributions to knowledge

My thesis is the first detailed account of the grouping pattern and the vocal communication of narwhals. In addition, it provides novel methods for the study of social cetaceans and their monitoring.

Chapter 2: Encounter frequencies and grouping patterns of narwhals in Koluktoo Bay, Baffin Island

Most previously published research on narwhal behaviour involves remote tracking technologies or aerial surveys. These studies are often technologically and logistically challenging, and tend to disturb animals. Alternatively, shore-based studies allow for long-term direct observations of large numbers of undisturbed individuals, and, in other cetaceans, have provided major advances in the understanding of cetacean behaviour, including their foraging ecology, parental care and social organisation. This chapter describes an exceptional field site for shore-based observational research where I was able to consistently observe large numbers of narwhals passing in close proximity to the shore over multiple summers. The resulting observations represent the first data on the social grouping of narwhals, which indicates narwhals are sexually segregated with males forming bigger groups than females. Narwhal grouping patterns resemble grouping in belugas, the species with the distribution and biology the most similar to narwhals and in which groups are also sexually segregated. There are a few anecdotal accounts of the timing of narwhal movements in and out of bays with respect to the tidal cycle. I investigate this relationship using circular statistics. Although the analysis does not reveal strong patterns, it represents a novel approach to analyse the tidal cycle synchrony of marine mammal behaviour.

Chapter 3: Statistical analysis of animal observations and associated marks distributed in time using Ripley's functions

The grouping pattern of narwhals serves as a case study for the development of methods for the statistical analysis of observations distributed in time. Building on to the idea of using the percentage of white on the backs of photographed narwhals to estimate their age, I improve this approach by developing an automated routine to calculate narwhals' whiteness from digital images. I provide the first account of narwhal grouping pattern by age, revealing that narwhals are age-segregated, similar to other cetaceans with fusion-fission societies. Motivated by the lack of statistical methods to analyse temporal marked point patterns (i.e. irregularly-spaced observations distributed in time, in this case photographed narwhals, with characteristics associated with each observation, in this case the percentage of white on narwhals' backs, where both the distribution of observations and the distribution of marks is of interest). I review and refine available statistical techniques, emphasizing the Ripley functions, for the analysis of such data. In addition, I develop the similarity function which offers a new statistical method for the analysis of a quantitative mark associated with observations in time. Through this contribution, I promote the use of point pattern methods in a broad range of observational studies of animal such as, for example, birds captured at banding stations during migration, fish passing through a fish ladder, and pit-tagged small mammals feeding at station equipped with a receiver.

Chapter 4: Variability and context-specificity of narwhal (*Monodon monoceros*) whistles and pulsed calls

Prior to my thesis, knowledge of narwhal vocal communication was limited to three studies, two of them based on less than three hours of recordings and one of them based on recordings from only two narwhals. None of these studies investigated the behavioural context of narwhal calls. In this chapter, I present the first detailed description of narwhal vocal repertoire and examine the variability of their communication calls. I categorize narwhal whistles and pulsed calls using a state-of-the-art artificial neural network method rather than subjective manual categorization methods. The context of usage of narwhal calls is investigated for the first time suggesting that some of the acoustic characteristics of whistles are behaviour-specific. Thus, it is possible that whistles have specific functions associated with particular behaviours like the foraging-related bray calls in bottlenose dolphins and the social codas in sperm whales. I also provide the first evidence that narwhal whistles and pulsed calls are herd-or individual-specific. Group-specific calls are usually associated with stable matrilineal social organisations in other cetaceans.

Chapter 5: Local passive acoustic monitoring of narwhals in the Canadian Arctic

Community-based monitoring has been repeatedly suggested as an effective approach to monitor natural resources and has received a great deal of attention in recent years, especially in the context of monitoring in the Arctic. The current monitoring methods for narwhals are based on aerial and boat surveys, harvest data and traditional knowledge. This chapter establishes passive acoustic techniques as a viable alternative method for monitoring narwhals. I present evidence that narwhal calls can be detected on continuous recordings using an automated detector. The number of narwhal calls detected on a recording can be used to estimate the number of narwhals present during the recording. This chapter lays the foundation for the implementation of a local passive monitoring program for narwhals. In addition, this is the first time that passive acoustic approaches are suggested in the context of community-based monitoring of marine mammals.

Overall, my thesis contributes to the advancement of knowledge of an understudied species that plays an important role in the Arctic marine ecosystem. The results and approaches generated by this work have applications in broader fields of research such as development of non-invasive methods, statistical analysis of observational data, social organisation of cetaceans, and community-based monitoring.

Chapter 1

Introduction

Cetaceans are social animals that live in groups (Tyack 1986), which has important consequences for the fitness of individuals. In other species, group living improves resource acquisition (Creel and Creel 1995), vigilance and defence against predators (Bertram 1980), as well as enhances the care of the offspring (Clutton-Brock 2002). In some species, such as African elephants (*Loxodonta africana*; Wittemyer et al. 2005) and resident killer whales (*Orcinus orca*; Bigg et al. 1990), individuals form permanent groups that they keep for their entire life. Groups can differ in behaviours that affect their fitness, such as their food preferences and hunting techniques, or in the use of tools (Whiten et al. 1999). In some groups, older individuals possess ecological knowledge that they share only with the rest of their group, which gives fitness advantages to the members of that group (Payne 2003). Thus, group membership may ultimately affect individual survival and consequently fitness.

Cetaceans form groups that vary in their size and stability. For example, bottlenose dolphins (*Tursiops truncatus*) and bottlenose whales (*Hyperoodon ampullatus*) form fusion-fission groups that may last for a few hours (Würsig and Würsig 1977; Gowans et al. 2001) while sperm whales (*Physeter macrocephalus*) and killer whales form long term stable groups that may last a lifetime (Whitehead et al. 1991; Baird and Whitehead 2000). In general, odontocetes (toothed whales) are more gregarious than mysticetes (baleen whales), with the extreme case of pelagic dolphins forming groups of up to a few thousand individuals (Gowans et al. 2008). Although mysticetes seem to form smaller and less stable group than odontocetes, it is thought that their association ranges over a larger spatial scale. Their low cost of locomotion and their ability to communicate over long distances (Tyack and

Clark 2000) allow mysticetes to keep contact with individuals over several kilometers. In addition, during specific periods, mysticetes form tighter groups such as during migration (Brown and Corkeron 1995), breeding (Swartz et al. 2006) and feeding (Forcada et al. 1996). Thus, because of their social nature, both odontocetes and mysticetes are aggregated in time and space to different extents.

Communication is crucial to all social species as it helps to synchronize the behaviours of members of a group and allows for individual and/or group recognition. Individual recognition through vocal signatures is a widespread form of social communication across mammals (e.g. Goldman et al. 1995; Charrier et al. 2003; McComb et al. 2003) and vocal signatures may be used as contact calls to keep group cohesion in fluid fusion-fission groups (e.g. Connor et al. 2000b; Soltis et al. 2005). Group specific calls are common in cetaceans where individuals have strong, long-term bonds with other members of their group (e.g. Ford 1991; Rendell and Whitehead 2003). Thus, vocal characteristics and differences are closely linked to grouping patterns of cetaceans. In addition to social sounds, cetaceans rely on sound to navigate, either through echolocation for odontocetes (Norris 1969) or other types of calls for mysticetes (George et al. 1989). Therefore, cetaceans tend to be very vocal for both communication and navigation.

Given the importance of sociality and the social importance of acoustic communication in cetaceans, here I study the social behaviour and acoustic communication of an understudied Arctic cetacean: the narwhal (*Monodon monoceros*). In the next section, I review 1) methods for the study of cetaceans in general with an emphasis on methods related to social behaviour, 2) current knowledge about the biology of narwhals, in particular about their social and vocal behaviour, and 3) biological and physical aspects of the Arctic ecosystems that affect narwhals, as well as the relationship between narwhals and people living in the Arctic.

1.1 Literature review

1.1.1 The study of social cetaceans

The social nature of cetaceans poses multiple research challenges and opportunities. Cetaceans spend a great majority of their time underwater making them cryptic to above-water observers (Connor et al. 2000a). On the other hand, this is remedied partly by their gregarious nature as it is easier to detect a group than an individual. As a result, some research methods, such as count-based surveys (aerial or boat-based) must be adjusted for the clustering of the animals (Anderson et al. 1979) to account for bias in population estimates that may occur as a result of their gregariousness.

Historically, most research on cetacean was done on carcasses. This type of data is still currently available for a few species that are harvested and from stranded individuals. Studying carcasses provides a breadth of information about anatomy, some life history traits, contaminant burdens and population structure (e.g. Hay and Mansfield 1989; Muir et al. 1992; Sjare and Stenson 2010). In addition, insight about behaviour and social organisation might arise from studying carcasses. For example, Brodie (1969) proposed that prolonged lactation in odontocetes suggests social learning in this suborder. Genetic analysis of samples from harvested pods of long-finned pilot whales (*Globicephala melas*) in the Faeroes Islands revealed that this species possesses a matrilineal social organisation (Amos et al. 1991). While research on carcasses provides significant insight, information about behaviour is obviously limited.

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Technological improvements in acoustic recording and data storage are allowing scientists to take advantage of cetaceans' vocal nature in order to fill some gaps in marine mammal research and monitoring (Mellinger et al.

2007). Acoustic methods are often preferred to visual ones for the monitoring of cetacean as it can be used 24-hours a day, in rough weather conditions and over long periods of time. Moreover, the probability of detection of cetaceans is often much higher with acoustic than visual methods (Akamatsu et al. 2008; Kimura et al. 2009). Detection range can reach hundreds of kilometres, although it varies greatly among species and background noise conditions (Stafford et al. 2007). While it is often impossible to identify the individual emitting the sounds with a single recorder, the simultaneous use of several recording systems allows for the localisation of sound-emitting individual and for the study of acoustic communication at the level of the individual (Simard and Roy 2008).

Individual identification has also resulted in advances in the study of behaviour and social organisation in cetaceans. Most cetacean species have natural marks that allow for the identification of individuals through photo-identification (Hammond et al. 1990; Whitehead et al. 2000). Photo-identification can provide information on movement pattern as well as population size and dynamics. In addition, it may give insights into life history parameters (Hammond et al. 1990) and the social organisation of a species (Whitehead 1997). For example, the use of photo-identification of north bottlenose whales in the Scotian Slope south of Nova Scotia has revealed that individuals move between canons and that males have a higher rate of movement than females (Wimmer and Whitehead 2004). In sperm whales, photo-identification was used to identify allomaternal care of the calves (Gero et al. 2009).

More recently, tags equipped with data recorders have been deployed on cetaceans to record various information on dives, movement patterns, oceanography, and behaviour (Mate et al. 1997; Watkins et al. 2002). The transmission duration of tags varies greatly from a few hours in the case of VHF radios attached with suction cup tag (e.g. Baird et al. 2002) to over a year for satellite-linked tags bolted in the dorsal fin or the back of individuals (e.g. Laidre et al. 2004). Tags can provide detailed data that could not be obtained through visual observation (Laidre et al. 2003), however, price and logistical challenges limit the number of individuals that can be tagged. To bypass these challenges, new statistical techniques are being developed to translate the behaviour of one tagged individual to the behaviour of the herd that contains the individual.

The highly social nature of cetaceans makes them excellent candidates to study animal societies. Research constraints imposed by their marine habitat may be resolved by advances in techniques to study them. The use of non-invasive methods such as passive acoustics and photo-identification allows for the long term study of undisturbed individuals and has led to major breakthroughs in cetology. For example, photo-identification methods have allowed the delineation of several cetacean societies (Mann et al. 2000) and the use of passive acoustic approaches have led to the discoveries of culture in whales and dolphins (Rendell and Whitehead 2001).

1.1.2 Narwhal biology

Narwhals are strictly Arctic species commonly found between 70ºN and 80ºN (figure 1.1, Reeves and Tracey 1980; Hay and Mansfield 1989). Narwhals are the only species in the genus *Monodon* and one of the two species in the family Monodontidae, which also includes belugas (*Delphinapterus leucas*; Rice 1998). Both male and female narwhals undergo annual migrations from their wintering grounds in Baffin Bay or northern Davis Strait to summer ranges in the deep fjords of Greenland and Baffin Island (figure 1.1; Dietz et al. 2001), where they seem to return consistently (Heide-Jørgensen et al. 2003). During the spring migration, narwhals travel in groups of several hundred (Silverman 1979), however when in the fjords they are reported to form groups of about three individuals (Cosens and

Dueck 1991). Past research on the social behaviour of narwhals is limited to one unpublished Master's thesis (Silverman 1979) and more work is needed to further understand the delineation of groups by age and sex.

Narwhals spend half of the year in extremely dense pack ice (< 5%; Laidre and Heide-Jorgensen 2005b) and consequently, their movements and dive behaviour are influenced by ice coverage (Laidre et al. 2004). Narwhals feed primarily on their wintering ground and during late autumn and spring (Finley and Gibb 1982; Laidre and Heide-Jorgensen 2005a). Based on stomach content analysis, narwhals do not appear to feed in the fjords during the summer (Mansfield et al. 1975; Finley and Gibb 1982; Laidre and Heide-Jorgensen 2005a). Their late fall and winter diet is mainly comprised of squids *Gonatus fabricii* and Greenland halibut (*Reinhardtius hippoglossoides*), while the spring diet includes Polar (*Boreogadus saida*) and Arctic cod (*Arctogadus glacialis*) (Laidre and Heide-Jorgensen 2005a). Conception occurs in the spring (peaking in mid-April; Hay and Mansfield 1989) and most calves seem to be born in July and August (Mansfield et al. 1975; Hay and Mansfield 1989) after 15 months of gestation (Hay 1984) although newborns have been observed during the spring at the ice edge (Cosens and Dueck 1991).

Like other cetaceans, narwhals rely on sounds to communicate and navigate. Narwhals use echolocation clicks that can reach high frequency to scan their environment and find their preys (Møhl et al. 1990; Miller et al. 1995). They also emit whistles and pulsed calls that are believed to have a communication function (Ford and Fisher 1978; Shapiro 2006). The most complete examination of the vocal repertoire of narwhals is an unpublished report produced for a conservation agency and was motivated by the prospect of using narwhal calls repertoire as a stock identifier (Ford et al. 1986).

Narwhal are the only marine mammals that have a straight tusk (figure 1.2). The tusk erupts on the left side of the male upper jaw and represents a unique case of dental asymmetry (Hay and Mansfield 1989). The function of the tusk is still debated within the scientific community. The most accepted view is that it plays a role in male-male aggression (Silverman and Dunbar 1980; Best 1981). However, more recent work has shown that the tusk is covered by a high density of tubules that connect the surrounding environment to the pulp (Nweeia and Malkin 2005). With those tubules, the tusk could serve as a hydrodynamic sensor to detect gradients of salinity, temperature and pressure (Nweeia and Malkin 2005). More data on the behaviour and social organization of the narwhals may help to clarify the function of the tusk.

Narwhals are facing a rapidly changing environment that could affect their conservation status. Narwhals were ranked as one of the most sensitive Arctic and subarctic marine mammal species to climate changes based on an index calculated according to habitat requirements, and evidence for biological and demographic responses to climate change (Laidre et al. 2008). In addition, concerns have been raised about the effect of accelerated industrial exploitation of natural resources and its associated shipping traffic on Arctic cetaceans (Hovelsrud et al. 2008). Narwhals have been observed reacting to icebreaker presence by changing their behaviour and group size (Cosens and Dueck 1988). In other cetaceans, shipping traffic also alters the direction of travel (Bejder et al. 1999), behaviour (Lusseau 2006; Stockin et al. 2008), breathing patterns (Nowacek et al. 2001) and group spacing (Bejder et al. 1999; Nowacek et al. 2001). Moreover, when exposed to engine noise, belugas decreased their calling rate and changed the frequency range of their calls (Lesage et al. 1999).

Narwhals are protected nationally and internationally. They have been listed as “special concern” by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC 2004) and as “near threatened” by the International Union for Conservation of Nature (Jefferson et al. 2008). These statuses are mainly based on data deficiencies and uncertainties about narwhal numbers and trends. Additional protection for all cetaceans is provided by the Convention on International Trade in Endangered Species, which restricts trade of cetacean products regardless of their conservation status (CITES 2009).

Narwhals are currently hunted in northern Canada and Greenland during the summer, spring and fall (Priest and Usher 2004). The latest reported narwhal harvest for Canada was 425 ± 12 narwhals in 2001 (Priest and Usher 2004). In six Canadian Inuit communities, the hunt is currently co-managed by the Nunavut Wildlife Management Board (NWMB) and Department of Fisheries and Ocean of Canada (DFO; Armitage 2005). The NWMB regulates and monitors the hunt through local Hunter and Trapper Organisations (HTO) in each community. The NWMB reports the hunt to the DFO who, sequentially, advises them on sustainable hunting levels (Richard and Pike 1993). Hunting quotas were originally based on historical hunting levels (Strong 1988). Because some narwhals might migrate between Canada and Greenland, the Canadian and Greenlandic governments have created the Join Commission for the Conservation and Management of Narwhal and Beluga with a mandate to exchange information and organise joint research projects on shared narwhal and beluga stocks (Richard and Pike 1993).

Narwhals are currently monitored based on aerial and boat surveys as well as harvest data. Surveys are conducted regularly (roughly every 5 years) by DFO in different areas of Nunavut but never cover the entire range of the narwhal distribution (Richard et al. 1994; Innes et al. 2002; Richard et al. 2010). Survey counts must be adjusted for individuals that are underwater and for clusters of narwhals resulting in poor precision (Richard et al. 2010). The most recent assessment of narwhals in Canada estimates that the population is above 60,000 narwhals (Richard et al. 2010). Data from narwhal harvest is collected by local HTOs and includes the number of narwhals landed as well as the number of narwhals that were struck and lost (Armitage 2005). However, the estimation of population size and trend based on harvest data is biased by hunting effort and ice conditions (Nielsen 2009) as well as under-reporting of lost and struck narwhals. On occasion, tissues sample from harvested narwhals are sent by HTOs to the DFO for analyses of toxicology, diet and reproductive status (Finley and Gibb 1982; Hay and Mansfield 1989; Muir et al. 1992; Dietz et al. 2004).

1.1.3 The changing Arctic ecosystem and its impact on narwhals

The Arctic ecosystem inhabited by narwhals is mainly driven by its cryosphere. The sea-ice cover varies greatly seasonally, ranging from $\sim 6.5 \times 10^6$ km^2 in late summer to $\sim 14 \times 10^6$ km^2 in the late winter (Comiso 2006). The ice alters the exchange between the ocean and the atmosphere, as well as the sun absorption by the water (Horner 1989). Consequently, sea-ice governs the primary productivity, resulting in an Arctic marine food web characterised by a pulsative nature (Horner 1989). While low nutrient concentrations in the Arctic Ocean in general result in low productivity (Dunbar 1986), there are areas of high productivity associated with upwillings, ice edge and polynias where sea birds and marine mammals tend to gather (Bradstreet 1982; Stirling 1997). Thus, while in general food webs in the Arctic are relatively simple and short (Ainley and DeMaster 1990), specific productive areas can reach up to five levels (e.g. Lancaster Sound; Welch et al. 1992). Finally, the Arctic ecosystem is characterized by high levels of chemical contaminant such as organochlorines and heavy metals in higher trophic levels due to biomagnification through the food web and bioaccumulation in animal lipids (Macdonald and Bewers 1996; Muir et al. 1999).

The Arctic region is likely to experience pronounced climate changes as a result of ‘polar amplification’, defined as greater temperature increases in the Arctic compared to the earth as a whole due to feedbacks such as snow and ice albedo effects, reduction in the insulation by sea ice of the atmosphere from the Arctic Ocean and permafrost–methane hydrate feedbacks (McBean et al. 2005). Some consequences of climate change have already been reported such as a thinning of the sea-ice cover (Rothrock et al. 1999; Comiso 2002), a decrease in the extent of the sea-ice in the north pole region (Parkinson et al. 1999), and a shift in the distribution of the zooplankton and fish communities (Beaugrand et al. 2002; Perry et al. 2005). The Arctic summer sea-ice is predicted to disappear entirely by the middle or the end of the century (Johannessen et al. 2004; Holland et al. 2006; IPCC 2007). Simulations of an increased freshwater input to the ocean using a coupled ocean-atmosphere model predict a modification of the thermohaline circulation in the Atlantic (Manabe and Stouffer 1995) resulting in abrupt changes in sea surface temperature and salinity (Manabe and Stouffer 2000).

The impact of climate changes on marine mammals has been predicted based on knowledge of current distribution and habitat requirements, as well as direct observation of the impact of environmental change (Tynan and DeMaster 1997; Simmonds and Isaac 2007; Laidre et al. 2008; Moore and Huntington 2008; Whitehead et al. 2008). Changes of prey species distribution and population size are predicted to cause a shift in cetacean diet and/or distribution (Simmonds and Isaac 2007). For Arctic marine mammals, changes in ice regime are predicted to adversely affect species with high site fidelity and migration routes (Laidre et al. 2008). With reduced ice cover and increased sea temperature, the number of Arctic seasonal migrants is predicted to increase resulting in an increased competition between current Arctic species and summer migrants. Indeed, an increase in migrant species has already been noted in Hudson Bay where killer whale sightings have increased over the last 50 years (Higdon and Ferguson 2009). Furthermore, with the reduction of the sea-ice extent and the thinning of the ice, shipping traffic in the Arctic is expected to increase. Associated with this increase are increased risk of pollution and disturbance of cetacean habitats (Hovelsrud et al. 2008).

The narwhal is a species of high cultural and economical importance to northern communities. Narwhals have long been and are currently hunted by Inuit. Its skin and blubber (muktuk) are sources of protein, nutrients and vitamins and its ivory is sold intact or carved (Reeves 1992). The hunt is an important activity that allows members of the community to connect with the land, their traditions and each other. During interviews, elders and hunters from Pond Inlet have indicated that they highly value narwhals and hope to maintain their hunt (pers. observ.).

Although the international cetacean conservation movement and local subsistence whaling seem to have very divergent goals, they share several views and values related to whale conservation. Over the last few decades, international anti-whaling campaigns have worked to convince the general public of the special nature of whales, sometime referred to as the "super-whale" phenomenon (Kalland 1993). The impressive body size of some species, their intelligence (Marino 2002; Connor 2007), social complexity and culture (Connor et al. 2001; Rendell and Whitehead 2001), and the mysteries and myths related to their lives in the ocean, all contribute to make cetaceans very special in the eyes of the general public. Importantly, these views are also shared with native people. Whales and wildlife in general are associated with the survival of the ancestral and modern Inuit. They believe that whales are sentient beings that share their social space (Tyrrell 2007) and their special relationship is illustrated in legends central to their culture (Spalding 1979). As a consequence, Inuit must respect the whales by only harvesting animals that present themselves to be harvested, not harvesting more than required, using as much of each harvested whale as possible and sharing the harvest (Tyrrell 2007). Even though both the international conservation movement and the local Inuit share the same respect for whales, this respect translates into opposing opinions about the morality of killing whales. Interestingly, however, both groups share general objections to invasive whale research.

1.2 Rationale and objectives

Given the paucity of knowledge and studies on the social behaviour of narwhals and the importance of sociality for cetaceans in general, the broad objective of this thesis is to gain insight into the social behaviour of narwhals, specifically their grouping pattern and communication. Given the threats facing the narwhals and the tight connection between Inuit people and narwhal conservation, the possibility of community-based monitoring to track protected populations will be explored in this thesis.

Chapter 1 explores the grouping and movement patterns of narwhals on their summering grounds, with specific investigations of the size and sex composition of the groups. The behavioural observations related to this chapter provide foundations for the rest of the thesis. In chapter 2, I develop statistical methods to analyse behavioural observations in time and characteristics associated with each observation. This method is applied to the narwhal data to investigate the age composition of narwhal groups. Together, chapter 2 and 3 give insight into narwhal societies. Given that the vocal repertoire of cetaceans is in part shaped by their social organisation, chapter 4 investigates the variability and the context of usage of narwhal vocalisations. It provides insights into narwhal communication and the function of their calls, as well as investigates the possibility of group-specific calls. Finally, building on the acoustic results of chapter 4, chapter 5 explores the feasibility of a local monitoring program for narwhals using passive acoustic methods.

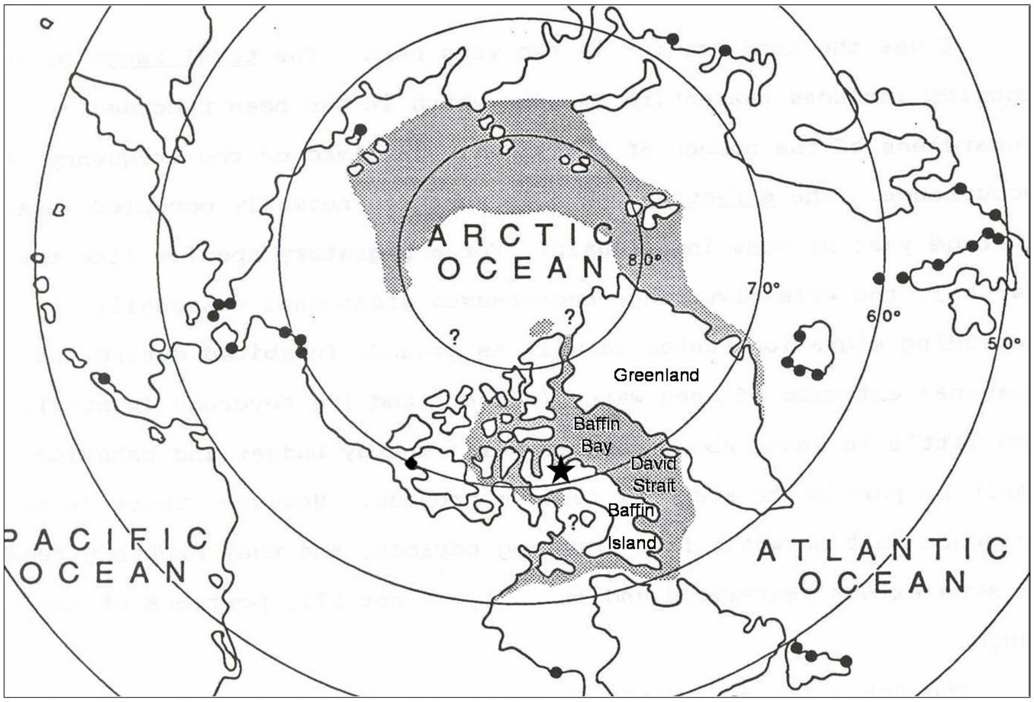

Figure 1.1. Map showing the distribution range of narwhals as modified from COSEWIC (2004). Shaded areas represent narwhals' general distribution, the dots indicate anecdotal reports and the star marks the fieldwork location.

Figure 1.2. Photograph of two male narwhals displaying their tusks with a third narwhal at Bruce Head, Koluktoo Bay, Nunavut (photo by Marie Auger-Méthé).

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Chapter 2

Encounter frequencies and grouping patterns of narwhals in Koluktoo Bay, Baffin Island

2.1 Abstract

The narwhal (*Monodon monoceros*) is a deep diving cetacean with a strictly Arctic distribution. The challenges associated with the remoteness of narwhals have resulted in a lack of knowledge of its social behaviour requiring direct, systematic observations. Bruce Head, a peninsula at the mouth of Koluktoo Bay (Nunavut), provides an exceptional site in Canada for nearshore observation of narwhals during the summer. In this study, we document the movement, timing and grouping patterns of narwhals observed from Bruce Head and how they relate to environmental factors such as the tide and the circadian cycle. Narwhals travelled in clusters of 1 to 25 individuals of mixed sex and age class. Narwhals entered the bay in bigger clusters than when they exited it. The clusters were part of herds that comprised up to 642 clusters. Narwhal movement patterns were not randomly distributed in time but did not consistently follow the tidal or circadian cycles across years. Bruce Head could host long-term behavioural studies of narwhals to unravel several unanswered aspects of narwhal biology.

Key words: circular statistics, Baffin Island, non-invasive methods

2.2 Introduction

Marine mammals, in general, and deep diving offshore cetaceans, in particular, are challenging research subjects because they spend most of their time underwater and far away from coastlines (Connor 2000; Schipper et al. 2008). Overcoming these challenges to advance understanding of a given species' behaviour, ecology and conservation requires the use of remote monitoring technology (Kooyman 2004; Hooker et al. 2007) or capitalizing on brief windows of direct observation opportunity generated by the species' behaviour and natural history (Baker and Herman 1981; Rugh et al. 2005).

Forms of remote monitoring technology frequently used in cetacean research include satellite telemetry (Mate et al. 1997; Laidre et al. 2004), time depth recorders (Laidre et al. 2002; Watkins et al. 2002), and acoustic monitoring (Stafford et al. 1998; Clark and Clapham 2004). Satellite telemetry and time depth recorders, in particular, have revolutionized marine mammal science because they provide detailed spatial and temporal data on behaviour and habitat use that cannot be obtained from direct observation (Laidre et al. 2003; Goldbogen et al. 2008). However, the expense of the technology, combined with the logistical challenges and invasiveness of attaching devices to free-ranging cetaceans, means that these approaches are most frequently employed by large, well-funded research programs and, yet, are usually limited to the monitoring of a small number of individuals (e.g. Goldbogen et al. 2008; Johnson et al. 2004).

Opportunities for direct observation generated by the species' behaviour and natural history are, by their very nature, selective and, as a result, may not be broadly representative of the species' behaviour and space use. However, they do permit detailed behavioural observation of many more individuals at much reduced cost, logistic complexity and levels of invasiveness. For example, much cetacean research has been conducted in near-shore areas from commercial whale watching vessels, including humpback whales (*Megaptera novaengliae*) in the Gulf of Maine (Clapham et al. 1993), resident killer whales (*Orcinus orca*) off the coast of British Columbia, Washington and Alaska (Baird 2000). More than 1,200 individually identified southern right whales (*Eubalaena australis*) have been observed from the cliffs of Peninsula Valdes, Argentina (Payne 1994). Extensive research has been conducted on bottlenose dolphins since 1970 in Sarasota, United-States (Irvine and Wells 1972) and since 1984 in Shark Bay, Australia (Connor and Smolker 1985). The deep near-shore waters off Kaikoura, New Zealand, has offered an ideal opportunity to study the behaviour and ecology of males sperm whales (*Physeter macrocephalus*; Childerhouse et al. 1995) and other marine mammals (e.g. dusky dolphins, *Lagenorhynchus obscurus*, Au and Wursig 2004; southern right-whale dolphins, *Lissodelphis peronii*, Visser et al. 2004). These studies of cetaceans in near-shore areas have provided key insights about cetacean behaviour, which have contributed to major advances over the last several decades in the behavioural ecology of marine mammal foraging, parental care, and social organization (Connor et al. 1992; Ford et al. 1998; Mann and Smuts 1999).

Studying Arctic marine mammals is associated with additional research challenges due to remoteness, ice cover, and the need for research approval by local community members. The narwhal (*Monodon monoceros*) is among the world's most difficult whales to study, primarily because of its year-round, high latitude distribution including occurrence in consolidated pack ice with less than 3% open water (Laidre and Heide-Jorgensen 2005b) throughout the dark, Arctic winter. Most research conducted to date on narwhals has involved radio-tracking of habitat use (e.g. Laidre et al. 2003; Laidre et al. 2004) and seasonal migration (e.g. Dietz et al. 2001; Heide-Jørgensen et al. 2003) as well as aerial surveys of population size and structure (e.g. Richard 1991; Heide-Jørgensen 2004). Narwhal samples from local harvests have been used to study diet (Finley and Gibb 1982; Laidre and Heide-Jorgensen 2005a), contaminant levels (Dietz et al. 2004; Wagemann and Kozlowska 2005) and genetic diversity (Palsbøll et al. 1997). In addition, acoustic devices have been used to record and study the underwater vocalisations of narwhals (e.g. Ford and Fisher 1978; Shapiro 2006). Despite these research efforts, narwhals have been identified as "special concern" by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC 2004) and as "near threatened" by the International Union for Conservation of Nature (Jefferson et al. 2008), largely because of data deficiencies (COSEWIC 2004) and uncertainties about numbers and trends (Jefferson et al. 2008). The lack of direct observational studies of narwhal behaviour means that very basic aspects of their feeding behaviour (Thiemann et al. 2008), the function of seasonal migration (Laidre et al. 2004), sexual selection (Reeves and Mitchell 1981) and social structure remain unknown (Whitehead 1998).

In the current paper, we describe a unique opportunity for shore-based, direct observation of narwhals by providing the first, published documentation of narwhal visitation to a near-shore area off Bruce Head (Iluviq: N 72° 04’, W 80° 32’), Koluktoo Bay, northern Baffin Island. Bruce Head is a rocky, elevated point that juts out into Milne Inlet, creating a 5 km wide entry into Koluktoo Bay that causes narwhals to swim close to the shore on their way into or out of the bay. The tendency for narwhals to frequent Koluktoo Bay has long been known by local Inuit hunters (Mary-Roussilière 1984-1985), who continue to harvest narwhals there. We are aware of two companies that are currently offering kayak-based whale watching tours at the site. In addition, we know of at least three narwhal research projects that were conducted at Bruce Head. Of the six narwhals captured by Newman (1971) for a captive display at the Vancouver Aquarium, five animals were captured at Bruce Head. During three summers, Mansfield et al. (1975) collected samples from narwhals captured in nets at strategic points in Koluktoo Bay to investigate growth, reproductive traits and stomach contents. Ford and Fisher (1978) spent five days in Koluktoo Bay to record narwhal vocalizations. Additionally, narwhal predation by killer whales has been observed in the bay (Campbell et al. 1988). Here, we document the number and temporal pattern of narwhal observations made from Bruce Head during two recent field seasons. We describe how the timing of narwhal observations relative to tidal and circadian cycles varied over the two years, as well as the size and composition of observed groups, and relate these to hypotheses about the function of groupings in odontocetes.

2.3 Methods

The study was conducted in Koluktoo Bay (Fig. 2.1), a 200-m deep bay, during the summers of 2007 (August 4-September 4) and of 2008 (August 1-23). Because of 24-hour summer daylight, we were able to gather data 24 hours per day during the two first weeks of each season. Observations were gathered from the shore on Bruce Head. Narwhals were observable up to 400-450 m from the shore which is about 8% of the width of the entrance of the bay. Maximum observable distance was calculated using the equations described by Lerczak and Hobbs (1998) to convert distances from angular readings taking into account the curvature of the earth. The parameters used were the distance between the two shorelines (5.2km), elevation of observations (30m AMSL), and the angular drop from the far shoreline to the boundary of the observation area (3.5-4°) estimated using half of the 7.5° field of view of 8x32 Celestron Noble 71204 binoculars. We only observed the narwhals while they passed in front of the peninsula since we were not able to follow them inside the bay. Narwhals are not always visible at the surface because they can spend more than half of their time underwater during the summer (Laidre et al. 2002). We increased our chances of detection by observing them through an angle of 75° located between two natural landmarks on the other side of the bay. To avoid recounting the same individuals twice, our effort was concentrated on one of the two halves of the angle depending on the direction of travel of the narwhal (i.e. on the half that was first crossed by narwhals entering the angle). Ninety-four percent of the narwhals observed were travelling in or out of the bay. Thus, we excluded narwhals exhibiting other behaviour (e.g., resting, socializing) for the analysis. All the observations were made with bare eye (to determine the size of the clusters) and binoculars (to determine the sex and age group of the members of the clusters). The observations were performed by MM and MA-M (90% of total clusters observed), as well as two field assistants, including one local Inuit present during the two field seasons. Observations from different observers were compared and cross-validated throughout the first day and intermittently during the remainder of the field season.

2.3.1 Grouping patterns

To quantify the gregarious nature of narwhal travelling behaviour, we documented the number, size and composition of clusters composing herds that entered and exited the bay. A cluster was defined as a group of narwhals in which an individual was within 10 body widths of another. Body width measurements are more reliable than direct measurements across variable distances (Mann 2000). When there was a high density of clusters travelling in front of Bruce Head at the same time (the number of clusters could reach up to 25 clusters per minute), we would only note the presence of clusters. For most of the clusters, we noted their size and when possible, we also noted their composition. Smaller narwhals of grey color were referred to as calves (up to two years of age; Hay and Mansfield 1989). Calves were differentiated from adults on the basis of being at least half the size of adults and usually close to a female in the "baby" or "echelon" position, and a more deliberate surfacing pattern (Mann and Smuts 1999). Larger narwhals with spotted patterns of black and white on their back were labelled as adults. We also labelled juvenile narwhals as adults. They were only slightly smaller than adults but did not show spotted patterns. When it was possible to observe the presence or absence of a tusk, we labelled adult narwhals with tusks as males and without tusks as females (Mansfield et al. 1975; Hay and Mansfield 1989). Females with tusks and males without tusks have been observed in harvested samples in low frequency (less than 5%; Hay 1984; Roberge and Dunn 1990). Since the presence and absence of the tusk was our only proxy for sex assignment, a few tusked females and tusk-less males could have been misclassified as males and females respectively. However given the low levels of occurrence of the two, we consider that they should not significantly alter our general results. A non-parametric Kolmogorov-Smirnov two sample test was performed to examine the difference in the size of the clusters of narwhals entering and exiting the bay.

We defined a “herd” as an aggregation of clusters of narwhals that passed in front of the peninsula. We determined the end of a herd when we did not see narwhals for more than 30 minutes. We noted the timing of the herds and the number of clusters within each herd. We compared the duration as well as the size of the herds that entered and exited the bay with non-parametric Kolmogorov-Smirnov two sample tests. To examine the distribution of different sex and age classes within herds, we divided the herds in four parts, each comprised of an equal number of clusters. We performed two sets of χ^2-tests to assess whether clusters containing calves or males were distributed equally or unequally among the four parts of the herds.

Finally, we investigated the synchrony of the clusters within a herd. We looked at the independence in time of consecutive clusters by comparing the distribution of the periods between two clusters against a Poisson distribution using a Chi-square test. The Poisson distribution is regularly used to evaluate the statistical significance of spatial or temporal aggregations (e.g. Sibly et al. 1990).

2.3.2 Environmental correlates of narwhal observations

To evaluate whether movements were correlated with environmental variables, we compared the timing of entries and exits of clusters and herds observed during two weeks of 24-hour observations (the two first weeks of each season) to the tidal cycle as well as the circadian cycle. Data on the timing of tides were obtained from the Canadian Hydrographic Service (http://www.tides.gc.ca/) which uses measurements from a buoy located in Koluktoo Bay (N72.31°, W80.57°). The tides lasted from 11 h 23 min to 13 h 48 min.

We used circular statistics to analyse the behaviour of narwhals around the tidal and circadian cycles. We transformed observations into angles in order to perform circular statistics. For the tidal data, we calculated the time between the observation of narwhals and the last high tide and divided it by the interval of time between the two consecutive high tides. This value was multiplied by 360 to obtain degrees. Therefore, an observation made at high tide would get a value of 0°, and an observation at low tide, a value of 180°. Angular values for the observations in accordance to the circadian cycle were calculated similarly; for example, observations done at midnight received a value of 0° and at noon, a value of 180°. Since the herds varied in duration, we used the time with the highest density of clusters as the time values for the herd.

We used a Watson's test for uniformity to evaluate the evenness of the movements around the tidal and the circadian cycle as well as a Watson's test for the von Mises distribution (Watson 1961) to evaluate the normality of the dataset. The von Mises is a symmetric unimodal circular normal distribution that is the most often used for circular datasets (Jammalamadaka and SenGupta 2001). The concentration of observations around the mode in the von Mises distribution is evaluated with the kappa value; values smaller than 2 indicate low concentration around the mode (Fisher 1993).

We performed a Watson's U^2 for two samples (Watson 1962) to test if the observations of clusters of narwhals entering and leaving the bay have the same distribution around the tidal cycle. We repeated similar tests for the circadian cycle. The statistical package "Circular" written for R was used for the circular analysis (Lund and Agostinelli 2007).

2.4 Results

2.4.1 Grouping patterns

An estimated 12,650 narwhals (8,750 in 2007 and 3,900 in 2008) grouped in 4,568 clusters were observed travelling into Kolutoo Bay (Fig. 2.2 and 2.3). The size of the 3,241 clusters of narwhals for which we could get complete count ranged from 1 to 25 individuals with an average of 3.5 individuals per cluster (Fig. 2.4a). Eighty-one percent of narwhals we observed were in a cluster of at least two individuals. Narwhals entered the bay in bigger clusters than when they exited (Kruskal-Wallis χ^2= 94.76, df = 1, p-value <0.001). Clusters composed of one female with one calf accounted for 52.2% (n=386) of the 740 clusters for which we were able to determine the sex and age class of all members (Fig. 2.5). However, our capacity to discriminate the members of a cluster was biased in favour of clusters of one female and one calf because of the ease of classifying them. Males and females rarely grouped together (1.5%, n=11) apart from when they were with calves (4.2% n=31). Among the clusters for which we were able to discriminate the sex and ages classes (n=740), 94% (n=696) were sexually segregated, including 15% (n=115) composed exclusively of males and 77.6% (n=581) composed of only females or females with calves. The largest groups we observed were mixed groups of males, females and calves (4.2%, n= 31, Fig. 2.5).

We observed 215 herds that lasted from 30 minutes to 10 hours 48 minutes. The herds of narwhals exiting the bay lasted longer than the herds entering the bay (3h49min and 2h29min respectively, Kolmogorov-Smirnov Two Sample Test P= 0.048). Herds comprised from 1 to 642 clusters (mean 22.4, Fig. 2.4b). There was no difference between the number of clusters per herd between herds entering and exiting the bay (Kruskal-Wallis chi-squared = 0.036, df = 1, p-value = 0.85). Clusters containing calves or males were distributed equally between the front, two central, and hind quarters of the herds (calves Pearson Chi-square=5.96, df=3, P=0.11; males Pearson Chi-square=4.41, df=3, P=0.22). For herds in which we were able to identify the sex of at least 10 individuals (n=43 herds), 79% comprised a mix of male and female.

The clusters entering and exiting the bay where highly aggregated in time (Fig. 2.3) even within a herd (Chi-square against Poisson distribution test statistic = 10053.3, df=8, lambda=2.518 p < 0.001) with 44% having less than a minute between two clusters.

2.4.2 Environmental correlates of narwhal observations

The correspondence between narwhal movements and the tidal cycle differed between the two years (Watson's Two-Sample Test of Homogeneity= 9.98, P-value<0.001) thus data from the two years were treated separately. In both years, the movements of clusters into and out of the bay were not distributed uniformly around the tidal cycle (2007: Watson’s Test for circular uniformity: 14.67, P-value < 0.01, 2008: test= 2.70, P-value < 0.01, Fig. 2.6) nor were they unimodal and normal (2007: Watson's Test for the von Mises Distribution=

2.29, P-value<0.01; 2008: Test = 1.02, P-value<0.01, Fig. 2.6). On average, entries in 2007 were concentrated shortly before the ebb tide (67.3°, kappa=1.26) but were broadly distributed across high, ebb and low tides with only flood tides generally avoided. In contrast, entries in 2008 were concentrated around flood tides (272.3°, kappa=0.5), with smaller peaks around high and low tides. In both years, exits were less frequently observed and more evenly distributed around the tidal cycle but tended to concentrate around low tide (2007: 165.6°, kappa=0.82 and 2008: 164.2°,kappa=0.62). However, kappa values < 2 indicate that entries were not unimodal, with high densities of entries and exits located not exclusively around the mean.

The distribution of the herds around the tidal cycle did not differ significantly between years (Watson's Two-Sample Test of Homogeneity= 0.026, P-value>0.1). Therefore, we pooled the data for the analysis. The herds were distributed uniformly around the tidal cycle (Watson's Test circular Uniformity = 0.024, P-value>0.1, Fig. 2.6) and followed the von Mises distribution (Watson's Test for the von Mises Distribution = 0.021, P-value > 0.1, mu=115.9 Fig. 2.6) but with a very low kappa value (k=0.10). The tidal conditions associated with narwhal herds entering the bay did not differ from those exiting the bay (Watson's Two-Sample Test of Homogeneity=0.088, P-value > 0.1. Fig. 2.6).

Since the circadian timing of cluster movements differed between the two years (Watson's Two-Sample Test of Homogeneity: 8.3018, P-value < 0.001, Fig. 2.7), we also treated the two years separately for the following analyses.

Narwhals entered the bay on average around 00:45h in 2007 (11.44°, kappa 0.73) and 09:30 h in 2008 (142.3°, kappa= 0.3534). There were several peaks in the times of entries of clusters. The clusters exited the bay on average around 19:00 h in both year (2007: 282.8°, kappa= 0.8193, 2008: 285.67°, kappa=1.768, Fig. 2.7). Similarly to the tidal cycle there was no difference between the circadian cycle of the herds entering and exiting the bay, when the data from 2007 and 2008 were pooled (refer to Table 2.1 and 2.2, Fig. 2.7).

2.4.3 Additional marine mammal observations

Other marine mammals observed from Bruce Head included 33 bowhead whale (*Balaena mysticetus*) sightings in groups of one or two individuals and 9 beluga (*Delphinapterus leucas*) sightings including a mother and calf pair. Around 70% of the bowhead whales and belugas sighted were within a narwhal herd. We also observed a pod of a minimum of 12 killer whales that entered the bay on August 12 2008 at 16:20; about five hours after a herd of approximately 135 narwhals went in the bay. At 19:45, we counted 61 narwhals exiting the bay. The killer whales exited the bay the following morning after staying around 14.5 hours in Koluktoo Bay.

2.5 Discussion

Bruce Head, at the entrance of Koluktoo Bay on northern Baffin Island, represents an exceptional locality for consistent observation of large numbers of narwhals from shore during the summer. Our estimated 8,750 narwhal sightings during four weeks in 2007 and 3,900 narwhal sightings during three weeks in 2008 likely under-represents the number of narwhals entering the bay, due to incomplete daily observation of narwhals (24 hrs per day for two weeks, but only 16 hrs per day for the other two weeks) and incomplete observational coverage of the channel entering Koluktoo Bay (maximum observation distance was 450 m, representing only 8% of the 5.2 km wide channel). On the other hand, we are very likely to have counted many of the same individuals two or more times. Preliminary analysis of photo-identification photographs (Auger-Méthé 2008) indicates at least two individuals were resighted entering the bay on multiple days. We observed more narwhal clusters entering than exiting the bay. If narwhals tend to swim farther from shore or spend more time underwater when they are exiting than entering the bay, this could simply be a result of our observation bias towards narwhals swimming close to shore and surfacing frequently. Alternatively, if we were equally likely to observe narwhals entering and exiting, then the higher number of narwhals observed entering could reflect an accumulation of narwhals in Koluktoo Bay over the course of the summer. The most recent estimates of the narwhal population in the Eclipse Sound area is 13,000-27,500 individuals (Richard et al. 2010). Assessing the proportion of this estimated regional population that visits Koluktoo Bay one or more times in a given summer awaits more comprehensive photo-identification analysis of the narwhals passing by Bruce Head, which we are currently pursuing.

The narwhals we observed were in clusters comprising 1 to 25 individuals with an average of 3.5 individuals per cluster. The clusters formed herds of 1 to 642 clusters with an average of 22.4 clusters per herd (corresponding to herds of 4 to 2247 individuals with an average of 78 individuals, estimated by multiplying the number of clusters per herd by the average cluster size). These observations are similar to the group size estimates from aerial surveys in Lancaster Sound (Cosens and Dueck 1991) and shore based surveys in Lancaster and Tremblay Sounds (Silverman 1979). The herds we observed were considerably larger than the 10 herds of 29 to 350 narwhals surveyed by Silveman (1979). In general, narwhal clusters and herds are bigger than the size reported for belugas (Michaud 2005), the species with the distribution and biology most similar to narwhals. Narwhals entered the bay in larger clusters than when they exited it. These larger clusters might be a by-product of the high densities of narwhals entering the bay in synchrony where two or more clusters could join and form a larger cluster to enter the bay. Thus, the size of the clusters of narwhals exiting the bay might be a better reflection of the typical size of stable groups of narwhals. For example, sperm whales form units that are stable for several years, but two or three units may join for a short period of time to form a larger group (Whitehead and Waters 1990).

There was an inverse relationship between cluster size and the degree of sexual segregation in narwhals as has been observed in other odontocetes. Small narwhal clusters were strongly sexually segregated, with 94% of clusters containing 2-9 narwhals composed exclusively of males or females with or without calves. However, the largest clusters and herds composed of many clusters almost always included a combination of males, females and calves. The occurrence of tusked females and tusk-less males might have altered our group composition observations and may result in an even greater degree of sexual segregation (if tusked narwhals in female groups were females and tusk-less narwhals in males groups were males). Observations of narwhals during spring migration also suggest a high degree of sexual segregation with males leading the migration (Greendale and Brousseau-Greendale 1976). Narwhal grouping behaviour resembles grouping in beluga, in which small groups are frequently sexually segregated but larger groups tend to mixed (Michaud 2005). More generally, sexual segregation is common in odontocetes (e.g. Connor et al. 1992; Whitehead and Weilgart 2000). Hypotheses explaining social sexual segregation in odontocetes invoke communal care for calves (Béland et al. 1990), defence or avoidance of predators (Arnbom et al. 1987), or resource selection and competition (Whitehead and Weilgart 2000). On the other hand, other cetacean species form groups of mixed composition regardless of group size (e.g. Karczmarski et al. 2005) and, in some cases, both sexes can remain with their natal group (Bigg et al. 1990; Ottensmeyer and Whitehead 2003). Elucidating inter-specific variation in patterns of sexual segregation in odontocete remains a challenge and cannot be explained by a single factor (Michaud 2005). Species, such as narwhals, characterized by variable degrees of sexual segregation, offer excellent opportunities to test, at an intra-specific level, these alternative hypotheses for drivers of sexual segregation

2.5.1 Environmental correlates of narwhal observations

Narwhals passed Bruce Head in pulses of several individuals and might use environmental cues to synchronize their movements. Narwhal entries and exits into the bay were not randomly distributed in time but did not consistently follow the tidal or circadian cycles across years. In 2007, narwhal clusters generally tended to enter the bay shortly before ebb tide after midnight while in 2008, they preferred entering at the rising tide in the late morning. Although the tendency for movements to coincide with particular environmental conditions in a given year (e.g., before ebb tide in 2007) could suggest narwhals use these conditions as cues to synchronize movements, the lack of inter-annual consistency in these cues indicates that they do not represent constraints. This possibility is also supported by Vibe's (1950) single year finding that narwhal entries at the head of Inglefied Bredning were associated with rising tide, which is similar to the tidal conditions we observed to be associated with movements in 2008. The reduced consistency and magnitude of circadian rhythmicity observed in this population of narwhals is similar to other mammals studied at high latitudes in summer (van Oort et al. 2005, Korslund 2006; but see Folk 2006) and the general pattern of reduced daily periodicity in marine mammals relative to terrestrial mammals (Watkins et al. 2002; Baird et al. 2008).

The fidelity of narwhals to the same fjords and bays each summer is a key feature of this species' behaviour, which allows us to observe large numbers of narwhals from Bruce Head; however, the reason why narwhals consistently visit the same fjords and bays is still under question. Feeding, escaping from predators and calving/rearing calves have been suggested to be drivers of site fidelity for other cetacean species (Rice et al. 1981; Simard and Lavoie 1999; Ford and Reeves 2008). Stomach content analyses clearly show that narwhals do not feed when they are in the bays and fjords during the summer (Finley and Gibb 1982; Laidre and Heide-Jorgensen 2005a). Narwhals tend to escape killer whale predation by moving into shallow waters close to shore (Steltner et al. 1984). Bays offer closer proximity to shoreline compared to the open water, which may allow the escape of narwhals to shallow waters. We observed narwhals swimming very close to the shore while exiting Kolutkoo Bay a few hours after a pod of killer whales entered the bay. The calving period of narwhals is from June to July (Hay and Mansfield 1989; Mansfield et al. 1975). The numerous mothers we observed with their calves were likely using the quiet waters of Koluktoo Bay to rear their calves. Knowledge of the context of aggregations of cetaceans in general is incomplete and understanding of the function of narwhal summer gatherings will contribute to further understand the habitat requirements of marine mammals.

There are two complementary approaches to the study of cetaceans in the wild. While remote technologies offer detailed spatial and temporal data that cannot be obtained from direct observations, non-invasive observational approaches allow research on larger numbers of undisturbed individuals. Bruce Head is a very promising site for applying non-invasive observational approaches as it provides the opportunity to frequently sight many individuals close to shore. The vertical contour of this peninsula facilitates the direct observation of narwhals, the deployment of underwater recording equipment, as well as the ability to take photographs of narwhals for photo-identification (e.g. Auger-Méthé 2008). In addition, Bruce Head provides an opportunity for counting narwhals and investigating population distribution and trends. However, limitations in the temporal and spatial extent of this study (i.e., partial observational coverage of narwhals entering one bay in the ice-free season) cannot be overlooked; like all wildlife research, results and applications must be interpreted in light of the study's particular spatial, temporal and methodological context. It has been highlighted that research in the Arctic should "*develop resident capacity and northern involvement in all stages of research in local, national and international issues"* (Graham and Fortier 2005). While studies using remote sensing technologies frequently involve northern residents for the capture, handling and instrumentation of narwhals (e.g. Dietz et al. 2001; Heide-Jorgensen et al. 2003), the non-invasive observational techniques described in this paper may be more readily approved and adopted by local Inuit communities (George 2006). The narwhal is a key species for monitoring the impacts of environmental change in high Arctic ecosystems and communities (Laidre et al. 2008). In conjunction with information obtained from remote technologies, data from the non-invasive techniques described above can contribute to the development of effective monitoring and conservation strategies for narwhals.

Table 2.1. Statistical tests on the movements of clusters around the tidal and circadian cycles.

	Watson test Uniformity	**Watson test Von Mises**
2007		
Tide	Test: 14.6699 P < 0.01	Test: 2.2883 P < 0.01 Mu=84.26° Kappa=0.84
Circadian	Test: 14.2424 P< 0.01	Test: 9.7108 P < 0.01 Mu=348.96° Kappa= 0.57
2008		
Tide	Test: 2.7013 P < 0.01	Test: 1.019 P < 0.01 Mu=255.4° Kappa=0.39
Time of day	Test: 1.7185 P < 0.01	Test: 1.363 P < 0.01 Mu=206.9° Kappa=0.17

Table 2.2. Statistical tests on the movements of herds around the tidal and circadian cycles

	Watson test Uniformity	**Watson test Von Mises**	**Watson Two Samples (in/out)**
Tidal cycle	Test: 0.0241 P >0.10	Test: 0.0208 P > 0.10 Mu=115.9° Kappa=0.099	Test: 0.0881 P > 0.10
Circadian cycle	Test: 0.1067 P > 0.10	Test: 0.0184 P > 0.10 Mu=292.8° Kappa=0.44	Test: 0.134 P > 0.10

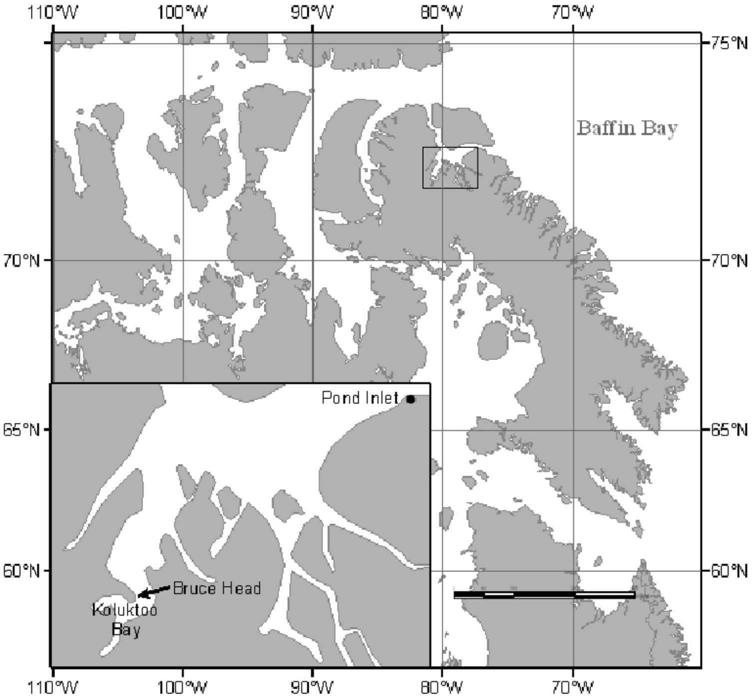

Figure 2.1. Map of the study site in northern Baffin Island.

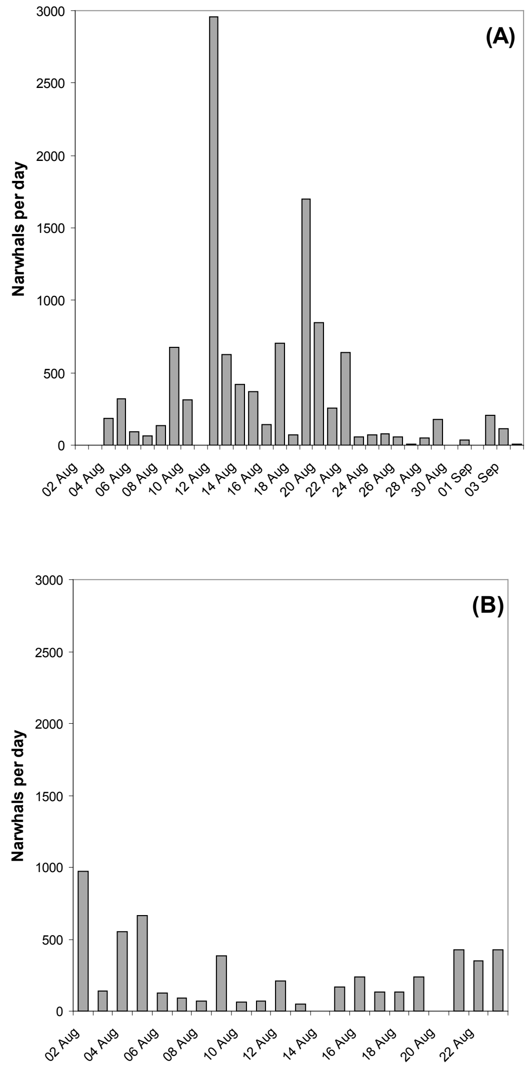

Figure 2.2. Average estimated number of narwhals sighted per day for a) 2007 and b) 2008. Since we were unable to determine the total number of individuals for all the clusters, we estimated the total number of narwhals seen by attributing the average cluster size (3.5 narwhals) to a cluster for which we did not know the size.

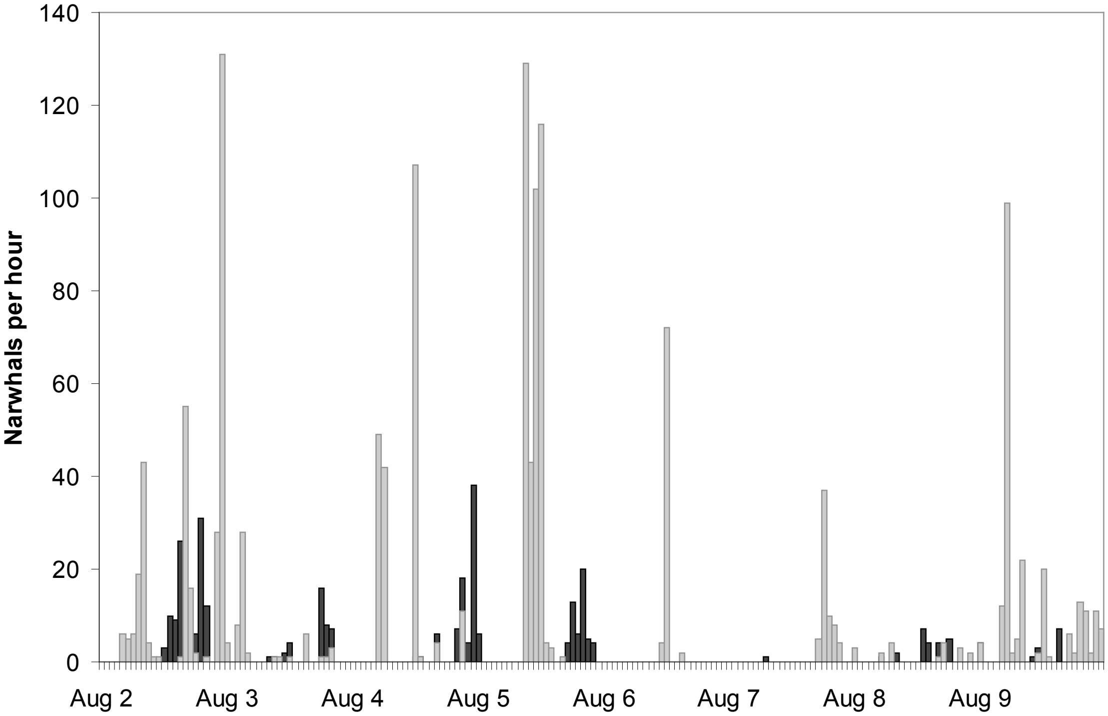

Figure 2.3. Sightings of narwhals entering (light grey) and exiting (dark grey) Koluktoo Bay viewed from Bruce Head during one week in 2008. The total number of narwhals was estimated as in figure 2.2.

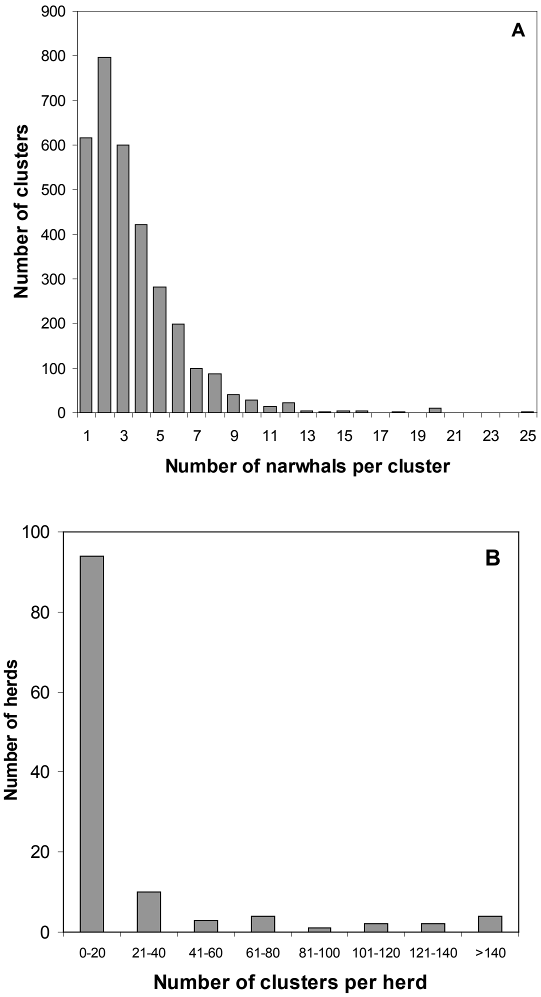

Figure 2.4. Distribution of the size of a) 3241 clusters and b) 215 herds of narwhals observed from Bruce Head in August 2007 and 2008.

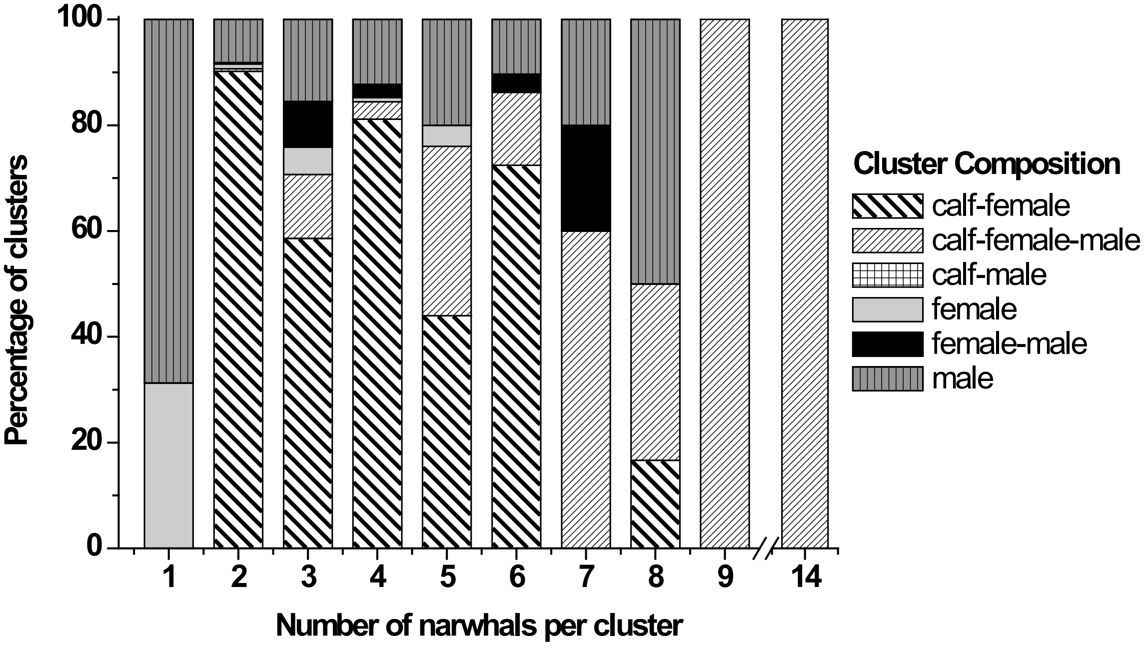

Figure 2.5. Composition of narwhal clusters of different sizes. Although we observed cluster sizes up to 25 individuals (fig. 2.2) we were able to identify the sex and age-class of 740 complete clusters ranging in size from 1-14.

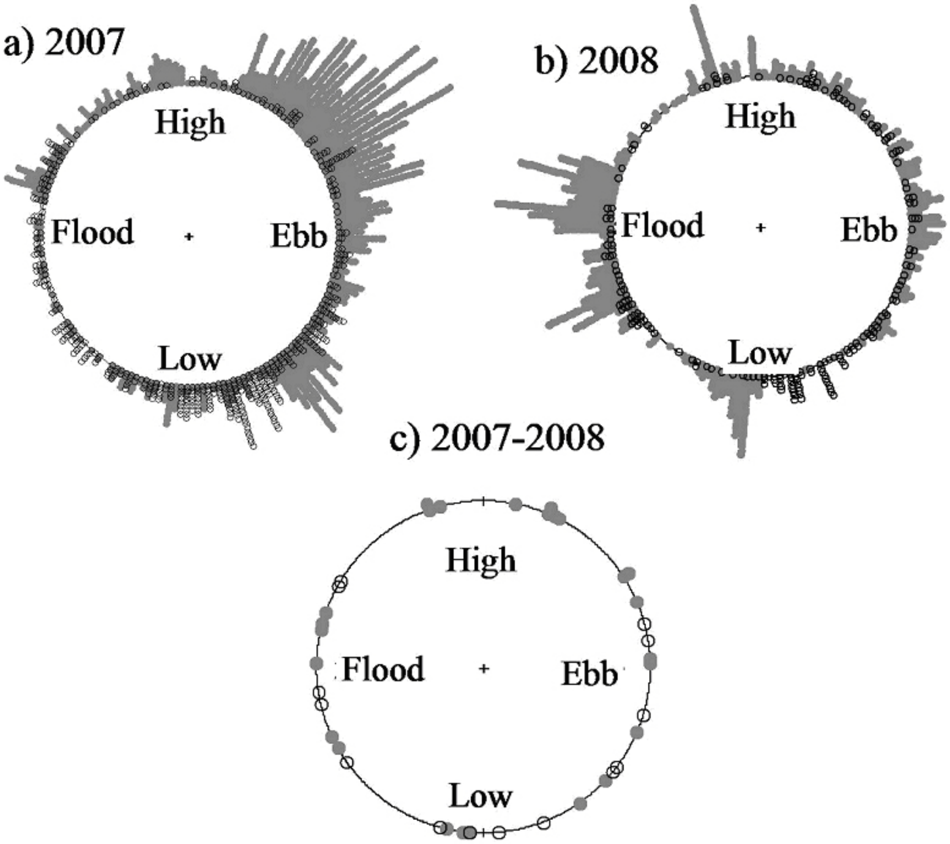

Figure 2.6. Entries (•) and exits (o) of clusters of narwhals around the tide cycle in a) 2007 and b) 2008. Entries (•) and exits (o) of herds of narwhals around the tide cycle in 2007 and 2008 combined. We used the period with the highest density of clusters to determine the timing of the herds.

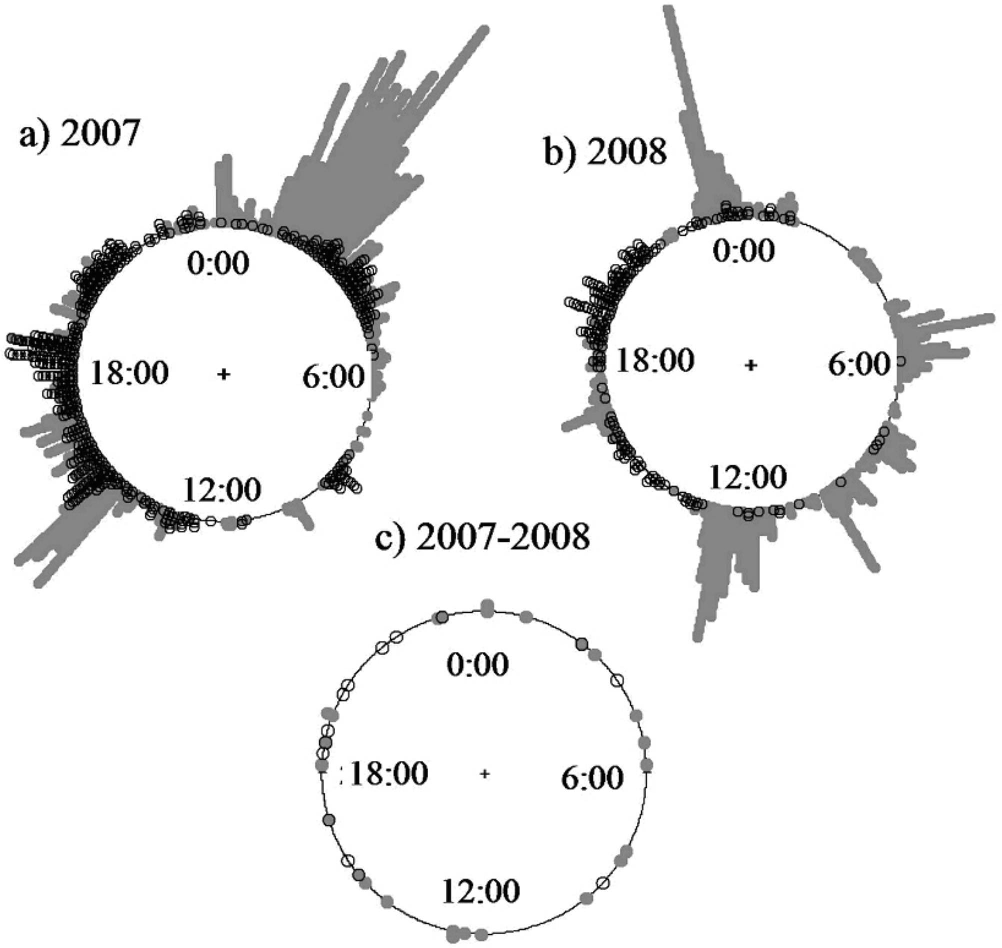

Figure 2.7. Entries (•) and exits (o) of clusters of narwhals around the circadian cycle in a) 2007 and b) 2008. Entries (•) and exits (o) of herds of narwhals around the circadian cycle in 2007 and 2008 combined. As in Fig 2.5. we used the period with the highest density of clusters to determine the timing of the herds.

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Linking statement

In the previous chapter, I explored the grouping pattern of narwhals based on visual observations. The definition of a group was set *a priori* based on the spatial distance between narwhals. In the next chapter, I develop a method to analyse photographs of narwhals distributed in time taken from an observation point. The photographs contain information about the age of individuals and the analysis allows for the delineation of narwhals groups according to their aggregation in time.

Chapter 3

Statistical analysis of animal observations and associated marks distributed in time using Ripley's functions.

3.1 Introduction

Biologists regularly collect behavioural observations of animals distributed in time from a fixed location. Examples include counts of migrating whales from an observation point (Marcoux et al. 2009), birds captured at banding stations during migration (Marra et al. 2005), measurements of fish passing through a fish ladder (Quinn et al. 1997) and characteristics of individuals captured by a camera trap (Karanth and Nichols 1998). The observer notes the time of passage of each individual. Additional characteristics might also be noted such as qualitative (sex, age group) or quantitative descriptors (size, weight) for each individual. This type of dataset is called a marked linear point pattern where each observation is traditionally referred to as an event or point and the characteristics of the observations are termed marks (Gatrell et al. 1996; Stoyan and Penttinen 2000). For the remainder of this paper, we will use the terms *observation* and *mark*.

Observations of travelling narwhals (*Monodon monoceros*) swimming past a fixed land location will be used through the remainder of the paper as an illustrative example of a marked linear point pattern. In this example, the observation is the passage of a narwhal and the mark is an index of age or age class of each individual. Like most whales, narwhals are a social species, such that individuals travel in groups. As a result, narwhal observations are often clustered in time (Marcoux et al. 2009). Furthermore, groups are likely to be composed of non-random aggregations of individuals of different ages and genders. By investigating the temporal distribution of observations and their associated marks, we gain insight into the size, composition and social organization of narwhal groups.

Unfortunately, point patterns such as these are difficult to analyse statistically because observations are sporadic and marks are temporally autocorrelated. The use of classical statistical methods in this context is problematic since the presence of autocorrelation in the marks violates the assumption of independence among observations (Diggle 1990). For example, a comparison of the average age of the narwhals among different seasons requires careful attention because the age of narwhals may be correlated at short time intervals. A number of methods available for the analysis of time series data are based on the premise that the observed pattern can be perceived as a surface pattern (Moran's I: Moran 1950; Geary's c: Geary 1954; variograms: Matheron 1962; spectral analysis: Bartlett 1963; Oden and Sokal 1986; Mantel's correlogram: Sokal 1986; time series analysis: Brillinger 1994;

e.g. wavelet analysis: Astafeva 1996). Some of these methods were developed to detect spatial autocorrelation in a spatially continuous phenomenon (Legendre and Legendre 1998), but can be readily applied to study temporal autocorrelation in a temporally continuous phenomenon such as climate and species abundance time series. However, these analyses are concerned with correlations in marks associated with each observation, not with the spatial or temporal distribution of observations (in space: Dutilleul and Legendre 1993; in time: Brillinger 1994). Since the latter is clearly of interest in the study of sporadic, non-continuous, animal observations, methods of surface pattern analysis are therefore not suited in the context described here. Fortunately, there are a limited number of techniques that have been developed largely in the context of spatial point patterns that can be applied to behavioural observations distributed in time, including nearest-neighbour analyses (Clark and Evans 1954; Diggle 1983) and Ripley's K and L functions (Ripley 1981). Methods based on nearest neighbours are only concerned with interactions between neighbours and thus suffer from their inability to characterise patterns beyond that scale (Perry et al. 2006). Ripley's K and L functions are concerned with the spatial or temporal distribution of observations and of their marks. Accordingly, we believe that the latter functions are the most suitable for the analysis of animal observations distributed in time.

With this commentary, we propose methods for the analysis of behavioural observations distributed in time, with a qualitative or quantitative mark, using modifications of Ripley's K and L functions. The general objective of the method is to understand the pattern of distribution of observations and associated marks at different scales (Ripley 1981; Diggle 1983). We propose three levels of analysis: 1) the temporal pattern of observations using Ripley's univariate K and L functions, 2) the temporal pattern of observations of individuals of different types using Ripley's cross K and L functions for bivariate data, and 3) the temporal pattern of marks, using a similarity function derived from the approach described by Stoyan (1984). When applied to our narwhal data, the shape of Ripley's K and L functions can provide insight into the size of narwhal aggregations and the scale dependence of the association of individuals with different marks. We investigate whether travelling narwhals are aggregated in time and whether narwhals of similar age classes are more or less likely to be observed travelling together than expected by chance. Through this contribution, we hope to promote the use of point pattern methods in animal behaviour studies by reviewing and refining available statistical techniques and providing Matlab (The MathWorks 2007) and R (R Development Core Team 2008) codes for evaluating the functions (Supplementary material). We highlight the need to address the mismatch between the prevalence of animal observations distributed in time and the rarity with which point pattern analyses have been performed in animal behaviour research.

3.2 Methods

3.2.1 Ripley's *K* and *L* functions for univariate data

Ripley's *K* and *L* functions (hereafter called the *K* and *L* functions) are typically used for the spatial analysis of point data, especially in forestry. Recent examples of applications of *K* and *L* functions include spatial patterns of barnacle recruitment (Munroe and Noda 2009), bark beetle attacks on pine trees (Rossi et al. 2009), spatial distribution of tree species (Rozas et al. 2009). The *K* and *L* functions have also been modified for one-dimensional spatial data (O'Driscoll 1998; Piou et al. 2009). Examples of temporal application of the *K* and *L* functions are uncommon but often involve spatio-temporal data (e.g. Stoyan and Penttinen 2000; Ma et al. 2006; Sebastian et al. 2006; Gardner et al. 2008; Lynch and Moorcroft 2008).

Here, we present an adaptation of the *K* and *L* functions for use with one-dimensional temporal data. The theoretical *K* function gives a description of a point process over a range of time scales, while *K* is the average number of observations for a given time lag divided by the rate of observations in the study period:

$$K(t) = \frac{E(t)}{\lambda} \tag{1}$$

where $E(t)$ is the expected (or average) number of observations for time lag t and λ is the overall mean rate of observations per time unit. The shape of the *K* function is of greater interest than the absolute numbers, with inflections in the function indicating scales of aggregations. A more intuitive quantity is

$E(t) = \lambda \cdot K(t)$, the expected number of observations within a time lag t before and after a typical observation, i.e. within a window of length $2t$ centered on the observation.

The simplest use of the *K* function is to test for complete temporal randomness (hereafter called temporal randomness), i.e. to test whether the observed distribution of observations follows a purely random process (or linear homogeneous Poisson process). Under the temporal randomness model, the density is constant at all *t* and the expected number of observations within time lag *t,* before and after a given observation, is equal to $E(t) = \lambda \cdot 2t$. Thus, when observations are randomly distributed in time, $K(t) = 2t$. The function *L*(t) is the normalized version of *K*(t). It is calculated as $L(t) = \frac{K(t)}{2} - t$, to allow $L(t)$=0 when observations are randomly distributed in time. When $K(t) > 2t$ and $L(t) > 0$*,* observations are more clustered in time than expected at random, indicating temporal aggregation. When $K(t) < 2t$ and $L(t) < 0$, observations are more evenly distributed in time than expected at random, and indicates temporal "avoidance" (for examples, see fig 4.18 in Illian et al. 2008; fig. 5 in Munroe and Noda 2009). In practical applications, λ is estimated with $\hat{\lambda} = n \cdot T^{-1}$, where *n* is the total number of observations and *T* is the duration of the study, and $\hat{K}(t)$ is estimated with $\hat{K}(t) = \frac{T}{n^2} \sum_i \sum_{i \neq j} I(d_{ij} < t)$, where d_{ij} is the time interval between observation *i* and *j. I*=1 if the time interval between *i* and *j* is smaller than the time lag t and I=0 if the interval is larger than the time lag t. The expected number of observations $E(t)$ is estimated with $\hat{E}(t) = \hat{\lambda} \cdot \hat{K}(t)$

Because the duration of the study is often arbitrary, some observations outside the temporal boundaries of the study may not be counted even if they are within a time lag t of an observation inside the duration of the study, leading to an underestimation of the function K. This edge effect must be corrected to facilitate the interpretation of the results. One possibility is to adjust for this by calculating the proportion w_{it} of the window of length $2t$ centered on observation i that falls within the duration of the study (O'Driscoll 1998). Windows that completely fall within the duration of the study are given a proportion of one and windows that partly fall outside the duration of the study are given a value less than one. For example, an observation made one minute before the end of the study period for the time lag t of five minutes would be given a proportion of $(5+1)/(2 \cdot 5) = 0.6$, since six minutes (five minute before and one minute after the observation) of the time window of 10 minutes (five minutes before and five minutes after the observation) are inside the study period. The proportion w_{it} is included in the denominator of the K function, giving more weight to observations that partly fall within the period (Ripley 1976):

$$\hat{K}(t) = \frac{T}{n^2} \sum_i \sum_{j \neq i} \frac{I(d_{ij} < t)}{w_{it}} \qquad (2)$$

The value of $\hat{K}(t)$ is calculated over different time lags arbitrarily determined by the user. However, it is common to consider only time lags that are smaller than a quarter of the duration of the study for the calculation of the $\hat{K}(t)$, as is often done in time series analysis (Dutilleul 1995).

Envelopes corresponding to the 0.025- and 0.975-quantile are calculated using a Monte Carlo simulation procedure, to assess the departure of the observed $\hat{K}(t)$ and $\hat{L}(t)$ functions from the expected functions under the null hypothesis. In general, the Monte Carlo simulation procedure distributes the observations in time randomly, to create datasets that have the same number of observations and the same overall mean rate of observations $\hat{\lambda}$ as the original dataset. Each simulation run can thus be seen as generating a partial realization of the homogeneous Poisson process (or random distribution). Functions $K(t)$ and $L(t)$ are evaluated for each simulated point pattern (Besag and Diggle 1977). At an approximate significance level of 5%, the null hypothesis that the observations are randomly distributed in time is rejected at the time lags t (scales) where the observed $\hat{K}(t)$ and $\hat{L}(t)$ functions fall outside the envelopes.

3.2.2 Ripley's cross K and L functions for bivariate analysis

In the previous section, we assessed if observations were distributed randomly in time or if they were aggregated or regular. It is also possible to test for the aggregation in time for observations of different types with themselves or with another type using the Ripley's cross K and L functions for bivariate data. Similarly to the univariate case, the theoretical cross *K* function (K_{ab}) is calculated as $K_{ab}(t) = E(t) \cdot \lambda_b^{-1}$, where $E(t)$ is the expected number of observations of type *a* within a time interval *t* before and after an observation of type *b* and λ_b is the overall mean rate of observation of type *b* per time unit.

In practice, the estimation with edge correction is:

$$\hat{K}_{ab}(t) = \frac{T}{n_a \cdot n_b} \sum_k \sum_l \frac{I(d_{a_k b_l} < t)}{w_{a_k t}} \tag{3}$$

where $d_{a_k b_l}$ is the length of time interval between the k^{th} observation of type *a* and the l^{th} observation of type *b, T* is the duration of the study, n_a and n_b are the numbers of observations of type *a* and *b*, and $w_{a_k t}$ is the proportion of a window of length 2*t*, centered on a_k, that falls within the duration of the study. When an edge correction is used, $\hat{K}_{ab}$ and $\hat{K}_{ba}$ are not equal but are positively correlated. A better estimation was obtained by Diggle and Milne (1983):

$$\hat{K}_{ab}(t) = \frac{\hat{\lambda}_b \hat{K}_{ab}(t) + \hat{\lambda}_a \hat{K}_{ba}(t)}{\hat{\lambda}_a + \hat{\lambda}_b} \tag{4}$$

There are three possible null hypotheses for bivariate point patterns: complete randomness, independence of populations and random labelling hypotheses (Diggle 1983). Under complete randomness, the null hypothesis states that the distributions of observations of the two types are completely random and that the two distributions are independent. The first part of this hypothesis, the complete randomness of the two distributions of observations, can be tested for each type with the univariate functions described above. If no pattern is found, testing for an interaction between the distributions of the two types of observations means testing for a relationship between two random point patterns, i.e. something that will rarely be encountered in practice. Under the hypothesis of independence of populations, the two types of observations belong to two different populations with different and independent temporal distributions (Lotwick and Silverman 1982). The null hypothesis then is that the temporal pattern of the two populations are independent of each other, i.e. $K_{ab}(t) = 2t$ and $L_{ab}(t) = \frac{K_{ab}(t)}{2} - t = 0$. When there are more observations of type *b* within the time lag of an observation of type *a* than expected, $K_{ab}(t) > 2t$ and $L_{ab}(t) > 0$, indicating association or attraction between the two populations. Conversely, $K_{ab}(t) < 2t$ and $L_{ab}(t) < 0$ indicate avoidance or repulsion between the two populations.

Envelopes for the estimated cross $\hat{K}$ and $\hat{L}$ functions can be created under the independence hypothesis by repeatedly shifting (a large number of times) all the times of occurrence of one type of observations by a random time lag (between zero and the time of the last observation of the study), while keeping the observations of the other type fixed (Lotwick and Silverman 1982); we used 10 000 shifts. The observations that fall outside the study period because of the shifting are relocated at the beginning of the study period as if the two ends were connected (similar to wrapping data into a torus in the case of two-dimensional data; Lotwick and Silverman 1982; Diggle 1983). Thus, the temporal pattern of the two types remains the same but their relative timing is randomly changed.

The random labelling hypothesis states that the type of the observations is independent of their time of occurrence (Diggle 1983), and assumes that observations of different types are from the same population. Thus, the observations might have a temporal distribution with some overall pattern, while the types of observations are randomly distributed. Hence, the *K* functions are invariant, i.e. $K_{ab}(t)=K_{aa}(t)=K_{bb}(t)=K_{ba}(t)=K(t)$ under the random labelling null hypothesis. In practice, the value of the pair difference $\hat{K}_{aa}(t)-\hat{K}_{ab}(t)$ can be used to indicate if, for example, a positive value indicates that observations of type *a* are more surrounded by observations of type *a* than of type *b*.

The significance of the estimated cross $\hat{K}$ and $\hat{L}$ functions can be assessed for random labelling using a Monte Carlo simulation procedure in which the type of observations is randomly changed, but not their timing (Diggle 1983). Thus, the temporal pattern of the observations and the number of observations of each type are not affected by the randomized re-labelling, and the envelopes have similar shapes as the univariate functions. With the random labelling hypothesis, the interest is in the temporal pattern of the qualitative type of an observation, but not the pattern of the observations.

3.2.3 Mark similarity function

As suggested by Stoyan (1984), Ripley's *K* and *L* functions can be modified to model a point pattern of observations with a mark, i.e. here a quantitative measurement for each observation. A measure of correlation between the marks of all pairs of observations is used in the calculation of the mark correlation function (Stoyan 1984). Here, we slightly modify Stoyan's function by using a measure of similarity instead of the measure of correlation. The similarity between the marks of each pair of observations (*i* and *j*) is calculated with the normalized equation (Legendre and Legendre 1998): $s_{ij} = 1 - abs((mark_i - mark_j)/(\max(mark) - \min(mark)))$. Thus, the most similar pair of individuals gets a value of 1 and the most dissimilar pair gets a value of zero. By replacing *I* in equation (2) by s_{ij}, we obtain:

$$\hat{K}_s(t) = \frac{T}{n^2} \sum_i \sum_{i \neq j} \frac{s_{ij}(d_{ij} < t)}{w_{it}} \qquad (5)$$

which represents the cumulative similarity between observations within a time lag *t*. There are at least two possible null hypotheses that can be tested with this mark similarity function: complete randomness and random labelling. Under complete randomness, the null hypothesis is that both the observations and the marks are randomly distributed in time. As mentioned above, the randomness of the distribution of observations can be tested with the univariate function. We consider that this hypothesis is too strong to apply to the mark similarity function.

The null hypothesis under random labelling is that marks associated with observations within a time lag are not more similar than expected by a purely random process. The significance of the function can be tested for random labelling by creating envelopes with random permutations of the marks without changing the times of observations. Thus, the temporal point pattern of the observations is not affected by the permutations, but the marks are. The shape of the envelopes should resemble the shape of the univariate $\hat{K}(t)$ function since the observation times are not changed. When the observed $\hat{K}_s(t)$ is above (below) the upper (lower) envelope, it indicates that the marks of observations within the time lag are more (less) similar than expected under the random labelling hypothesis.

An easier way to visualize $\hat{K}_s(t)$ is through $\hat{S}(t) = \frac{\hat{K}_s(t)}{\hat{K}(t)}$, which gives the average mark similarity between pairs of observations within a given window of time. As the time lag increases, $\hat{S}(t)$ should tend toward the average similarity between all the pairs of observations as the time lag tends toward including all pairs of observations. The envelopes for $\hat{S}(t)$ are computed by dividing the envelopes of $\hat{K}_s(t)$ by $\hat{K}(t)$.

3.2.4 Example: the narwhal dataset

The narwhal is a strictly Arctic toothed whale that spends its summers visiting the bays and fjords of Nunavut and Greenland for a few hours to a few days at a time (Dietz et al. 2001). Narwhals are highly gregarious and travel in herds of up to a few hundred individuals (Marcoux et al. 2009). The herds are divided into clusters of an average size of 3.5 individuals (Marcoux et al. 2009). During the summer of 2008, we took photographs of narwhals passing in front of a peninsula in Koluktoo Bay (N 72° 04' W 80° 32', Nunavut, Canada). Because of 24 hours summer daylight, we were able to photograph narwhals 24 hours per day. We used natural markings on the back of narwhals to identify individuals (Auger-Méthé et al. 2010) and only used one picture per individual for a given day to ensure that all observations used in the analysis correspond to different individuals. The research protocol for this project was approved by the McGill University Animal Care Committee (AUP 5147) according to Canadian Council for Animal Care guidelines.

Because narwhals change coloration with age, it is possible to use the amount of white on their skin as an index of age (Fig 3.1; Silverman 1979; Hay 1984; Hay and Mansfield 1989). Thus, we extracted from the photographs the proportion of white on a standardized area of the back as an age index (Appendix 1). A value of 0 was given to a young, dark grey narwhal, while a value close to 1 was given to an older, whiter narwhal, thereby creating an age index that is a continuous variable. To illustrate how Ripley's K and L functions can be used with bivariate (categorical) data, we also divided the narwhals in two age classes according to the percentage of white on their back: narwhals in the lower 50% of whiteness were categorized as "young" and narwhals in the higher 50% of whiteness were categorized as "old". Calves were not included in this analysis. The dataset includes 278 photographs of narwhals. Figure 3.2 illustrates an example of the dataset for Aug 2 2008.

3.3 Results

We tested for temporal aggregation of photographed narwhals at two different time ranges to illustrate the effect of changing the time scale. The first time range spans from zero to one day in two-hour intervals, and the second spans a maximum of 5 minutes in 30-second intervals (Fig. 3.3). Narwhals were more aggregated in time than expected for a random process at the two time scales investigated, as both the observed $\hat{K}$ and $\hat{L}$ functions lie well above their respective upper envelope.

We divided the dataset in two sub-datasets, one with young narwhals only (subscript y) and one with old narwhals only (subscript o), as described in the Methods section. We tested for temporal randomness in the two sub-datasets separately. The observed $\hat{K}$ function for each sub-dataset lies well above the upper envelope, indicating temporal aggregation when young and old narwhals are analysed separately (Fig. 3.4a and b). We calculated the cross $\hat{K}_{yo}$ and $\hat{L}_{yo}$ functions for time intervals from 0 to 5 minutes in increments of 30 seconds. We chose these time lags because we were interested in young and old narwhals swimming very close to each other, as they are likely to interact with each other. We tested for both the independence of population and the random labelling hypotheses.

For the independence of population hypothesis, the observed $\hat{K}_{yo}(t)$ and $\hat{L}_{yo}(t)$ fall well above the 0.975-quantile envelopes for all the time lags (Fig. 3.4c and 4d) indicating that the two sets of observations are not temporally independent. In other words, the number of young narwhals within a time lag of an old narwhal and the number of old narwhals within a time lag of a young are larger than expected under the independence hypothesis. Thus, the pattern of movement of young narwhals is synchronized to the pattern of movement of old narwhals, and vice versa, suggesting they are part of the same herds.

The two envelopes for the random labelling hypothesis are well above those for the independence hypothesis (Fig. 3.4c and d). The observed $\hat{K}_{yo}(t)$ and $\hat{L}_{yo}(t)$ fall below the lower envelope for the random labelling hypothesis for all the time lags (Fig. 3.4c and d) indicating that there is an apparent avoidance between young and old narwhals over short time lags. The pairwise differences $\hat{K}_{yy}(t)-\hat{K}_{yo}(t)$ and $\hat{K}_{oo}(t)-\hat{K}_{yo}(t)$ were used to explore this interaction further. Both $\hat{K}_{yy}(t)-\hat{K}_{yo}(t)$ and $\hat{K}_{oo}(t)-\hat{K}_{yo}(t)$ lie above the upper envelope, indicating that photographed narwhals are more aggregated in time with narwhals of their age class than narwhals of the other age class (Fig. 3.4e and f). This trend is significant only for intervals shorter than 2.5

minutes for the pairwise difference $\hat{K}_{oo}(t) - \hat{K}_{yo}(t)$. Thus, narwhals are more likely to group with individuals of their own age class.

We tested for the temporal aggregation of observations associated with a quantitative mark, the percentage of white on the back of each photographed narwhal. Similarly to the analysis of bivariate data, we used time intervals from 0 to 5 minutes in increment of 30 seconds. The $\hat{K}_s(t)$ function falls slightly above the upper envelope for time lags up to three minutes and lies between the two envelopes for larger time lags (Fig. 3.5a). It is easier to visualize the averaged function $\hat{S}(t)$, which also falls above the envelopes for time lags of 0 to 3 minutes (Fig. 3.5b). The dotted horizontal line represents the average similarity in the percentage of white on the back for all pairs of narwhals. Thus, narwhals that swim within less than three minutes of each other are more similar in whiteness, an index of age, than expected at random.

3.4 Discussion

Analysis of the temporal distribution of photographed narwhals swimming by a fixed location using K and L functions showed that narwhals were highly synchronized, especially narwhals of similar age. The general temporal distribution of narwhals was not random as narwhals were closer to each other in time than expected under temporal randomness. The shape of

$\hat{K}(t)$ and $\hat{L}(t)$ in Figure 3.3a and b provides a representation of the temporal distribution of photographed narwhals. The first inflection in the curve of $\hat{K}(t)$ is at the one-hour time lag, which indicates temporal aggregation of narwhals that are within one hour before or after each other, or within two hours in total. This corresponds to field observations of the average time it took for a herd of narwhals to pass in front of our observation point (Marcoux et al. 2009).

Young and old narwhals travelled synchronously (rejection of the independence hypothesis, Fig. 3.4c and d) but tended to aggregate with individuals of similar age class (rejection of the random labelling hypothesis, Fig. 3.4e and f). Narwhals that were within three minutes of each other were more similar in their age than the average, as approximated by the whiteness of their backs (Fig. 3.5a and b). Since narwhals horizontally swim at about 1.4 m s^{-1} (Dietz and Heide-Jørgensen 1995), their similarity in whiteness within three minutes before and after each other corresponds roughly to a distance of 250 m between individuals. Narwhals travel in herds of a few hundred individuals divided into smaller clusters of a few individuals swimming near each other in a coordinated way (Marcoux et al. 2009). The limited extent of time (3 min) and space (ca. 250 m) over which we detected non-random color patterns suggests that age-specific associations occur in narwhal clusters but not in herds.

Ripley's univariate and cross K and L functions, as well as the mark similarity functions, offer the possibility of testing for temporal aggregation with non-regularly spaced data which abound in observational studies of wild animals. We recommend to first test for temporal clustering of the observations (univariate functions), and then for the temporal pattern of the qualitative or quantitative mark of the animals (when applicable, bivariate and mark similarity functions). The methods described in this paper allow for missing observations under the assumption that the probability of missing an individual is constant throughout the study period and among all the individuals. For example, we could not photograph all the narwhals that passed at our observation point, but we assumed that the probability of photographing a narwhal was constant for all individuals. With this assumption, the general temporal pattern found should be similar to the pattern that would be found with the complete dataset. However, the number of observation that was estimated with $E(t) = \hat{\lambda} \cdot \hat{K}(t)$ is likely to be lower than the real one. For example, the average number of photographed narwhals that passed in front of the point within one hour before and after another narwhal (two hours, corresponding to the average duration of the passage of a herd) was 27.5, ($\hat{K}$ (1 hour) $\cdot$ $\hat{\lambda}$ = 55 $\cdot$ 0.5), which is much lower than the size of the typical herd we observed (around 80 narwhals; Marcoux et al. 2009). This shows that we observed more narwhals than the number of high-quality photographs that could be taken. Thus, caution is required when estimating group size from an estimated number of observations.

There are two main null hypotheses for Ripley's cross K and L functions, depending on the nature of the data. Since the calculated envelopes are different for the two hypotheses, the interpretation of results may lead to some confusion (Diggle 1983; Goreaud and Pelissier 2003). The main difference between the two hypotheses lies in the definition of the population. In the independence of population hypothesis, it is assumed that the observations of the two types arise from distinct populations or subgroups with unrelated temporal patterns. With the random labelling hypothesis, the observations are from the same population with one overall temporal pattern for the two types of observations. With the narwhal dataset, it was not clear whether young and old narwhals should be considered part of the same population or as two different sub-populations, as suggested by Goreaud and Pelissier (2003) for observations with different age categories. We first tested for independence assuming two sub-populations, and found that young and old narwhals were part of the same population. This is consistent with the fact that they travel together in large herds. Under the random labelling hypothesis, we found that the expected number of young narwhals within a time interval of an old narwhal (and vice versa) was smaller than expected. Thus, within the herds, young and old narwhals seem to avoid each other and aggregate with individuals of similar age class.

Ripley's K and L functions are cumulative functions (all pairs of observations at small lags are included in larger lags), which we prefer over their non-cumulative equivalent (only pairs of observations within a given time interval are used; pair-correlation function: Ripley 1981; O-ring statistics: Ripley 1981; Galiano 1982). Cumulative functions are less sensitive to sample sizes and to the choice of time interval classes (Wiegand and Moloney 2004). They are efficient at detecting patterns that operate up to a certain time interval (e.g. aggregation of travelling animals passing in front of a fixed observation point), while non-cumulative functions are better at detecting patterns operating at a specific time lag (e.g. the amount of time it would take for an animal to come back to the same feeding location; Perry et al. 2006). Non-cumulative functions might be appropriate depending on the biological questions of interest, but here, since we are interested in temporal aggregation of animals, we favour the cumulative functions.

In order to use the K and L functions described above, the stationarity assumption must be reasonable, i.e. it must be possible to assume that the statistical properties (the mean and variance) of the data are the same for the entire study period (Ripley 1981). For example, if increasing numbers of narwhals were passing by during the sampling period or if the nature of social aggregations changed during this time (i.e., group sizes became smaller or age-specific associations strengthened or weakened), then the assumption of stationarity would not be reasonable, preventing the use of the K and L functions without modification.

Although we were able to observe narwhals continuously during 24-hour daylight in the Arctic summer, many observational studies will be limited to periods of the day when animals are active and visible (e.g. Brodeur et al. 2008; Fortin and Fortin 2009; Ouattara et al. 2009). These intermittent datasets can be handled with an edge correction for each bout of continuous observation. In addition, the Monte Carlo simulation procedure for the complete randomness hypothesis should be used only to generate data within each bout of continuous observation (these modifications are included in the Matlab and R codes provided in the Supplementary material).

Here, we focused on the application of Ripley's functions to study the distribution of behavioural observations and their associated marks in time. The techniques involved have a broad range of application in biology and other fields where observations distributed in time are often irregularly spaced because the observer does not have control over their occurrence time. For example, this is the case with the occurrence of natural environmental phenomena such as storms or droughts. By definition, point patterns are composed of scattered observations in time (and one-, two- or three-dimensional space; Illian et al. 2008) so their analysis must exploit the spacing between their time of occurrence. Because the time lags between observations, and their associated characteristics, are often correlated, classical statistics are not always appropriate for their analysis. For all those reasons, we encourage biologists and behavioural ecologists to explore or re-explore their temporal datasets using Ripley's K and L functions and the variants presented here.

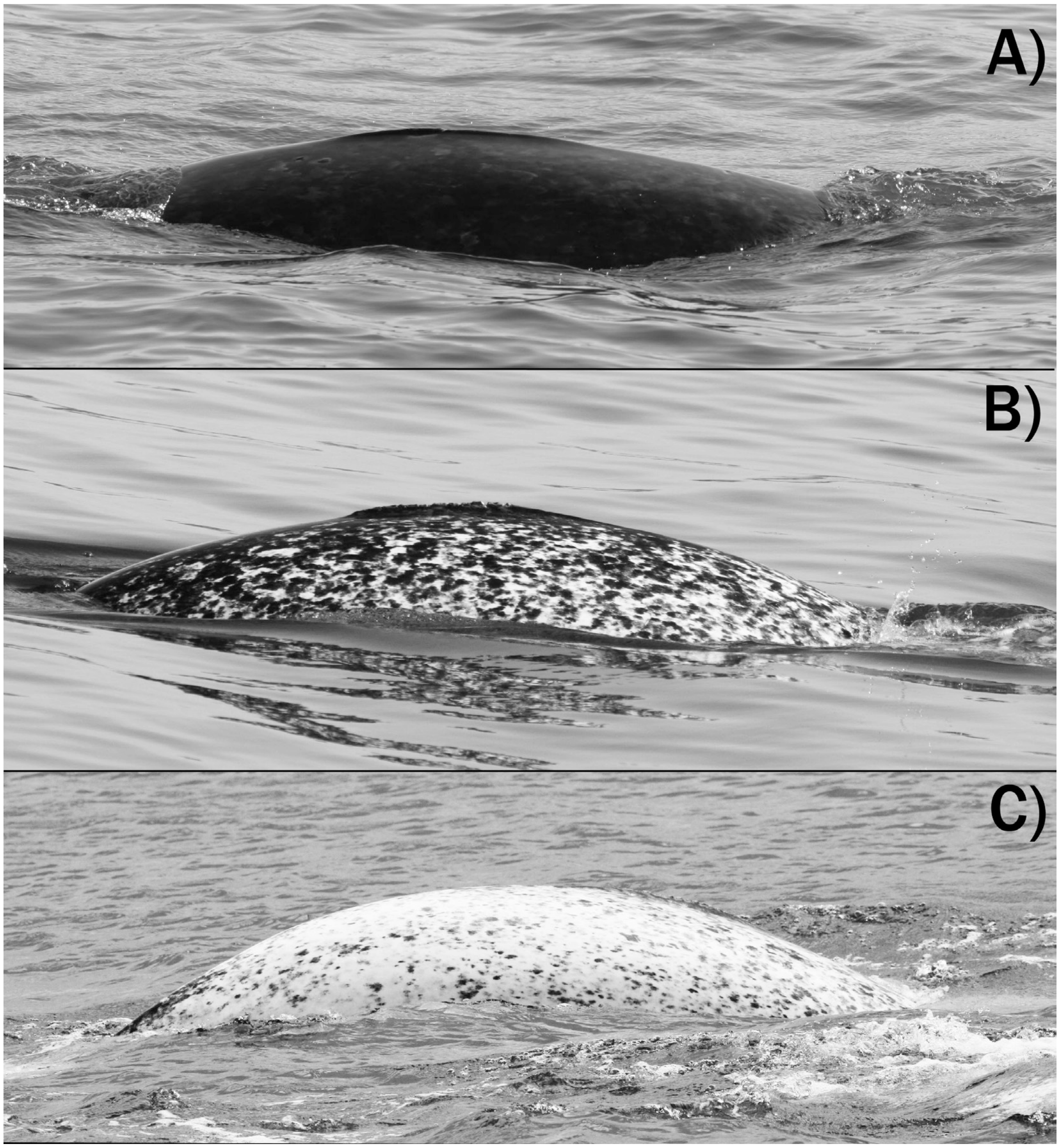
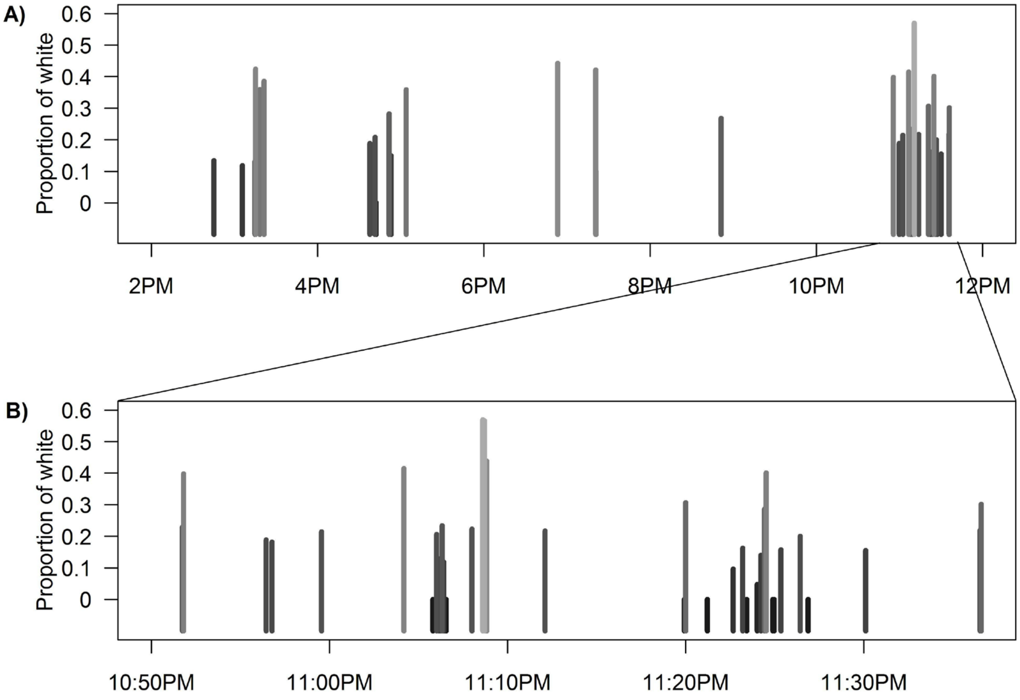


Figure 3.1. Photographs of narwhals with different amounts of white on their skin indicating different age classes: A) juvenile, B) adult, and C) old adult.


A)
B)
Proportion of white
0.6
0.5
0.4
0.3
0.2
0.1
0
2PM
4PM
6PM
8PM
10PM
12PM
10:50PM
11:00PM
11:10PM
11:20PM
11:30PM

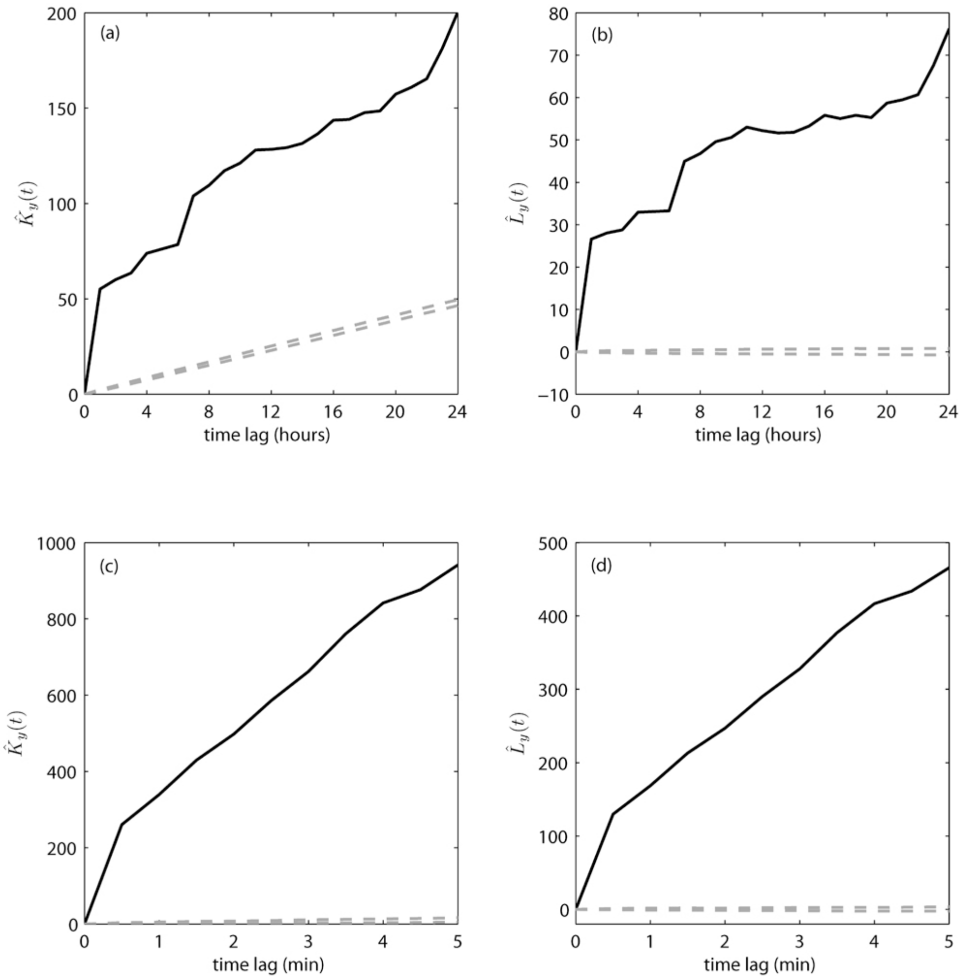


Figure 3.3. Univariate $\hat{K}(t)$ and $\hat{L}(t)$ for photographed narwhals at two different time scales A) and B) from 0 to 24 hours C) and D) from 0 to 4 minutes. Dashed lines represent lower and upper confidence envelopes obtained from the 0.025- and 0.975-quantile of 10 000 Monte Carlo simulations. All four plots indicate that the narwhals are more aggregated than expected under the randomness hypothesis at all time lags.

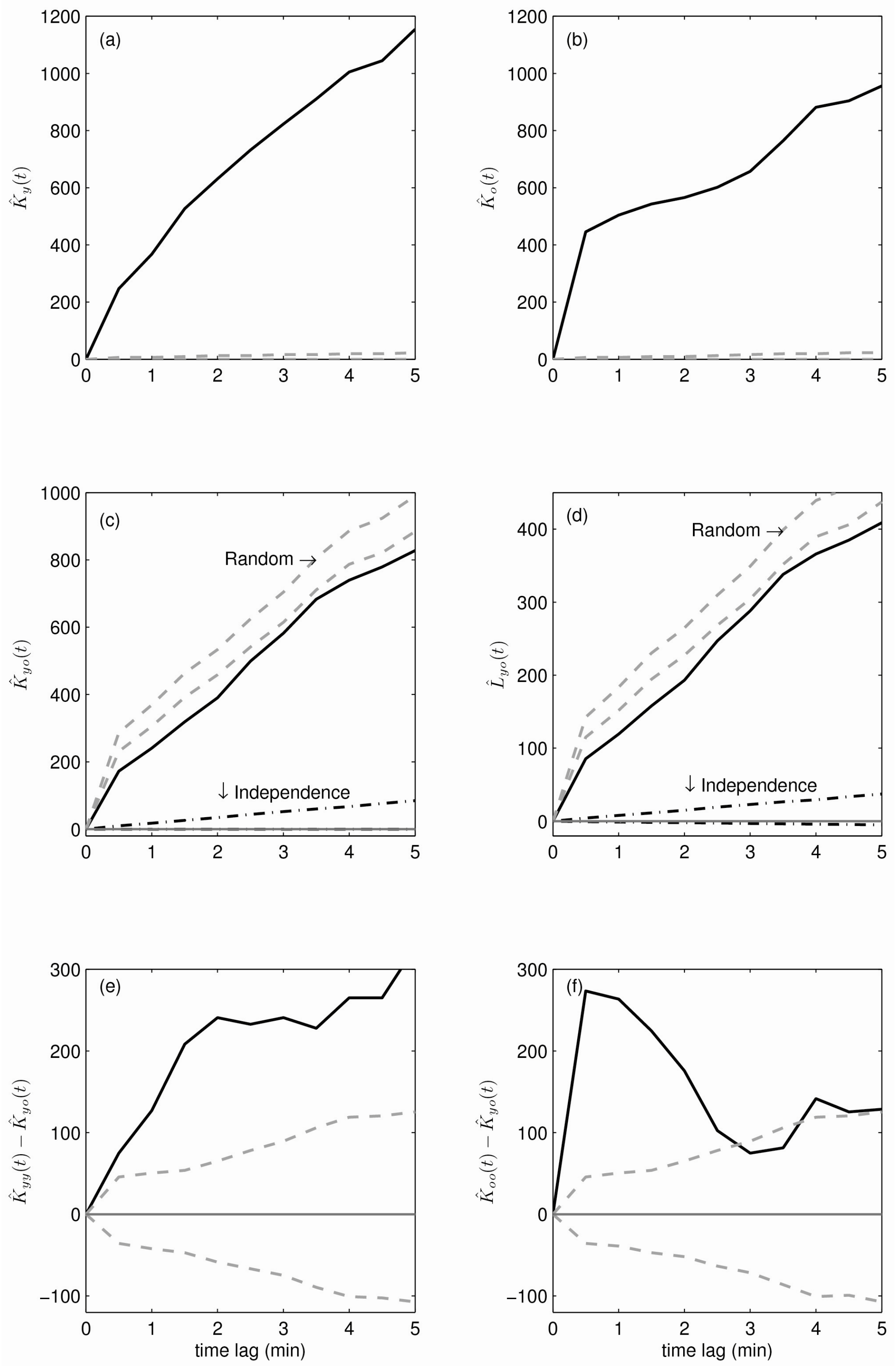

(a)
$\hat{K}_y(t)$
0
200
400
600
800
1000
1200
0
1
2
3
4
5
(b)
$\hat{K}_o(t)$
(c)
$\hat{K}_{yo}(t)$
Random →
↓ Independence
(d)
$\hat{L}_{yo}(t)$
Random →
↓ Independence
(e)
$\hat{K}_{yy}(t) - \hat{K}_{yo}(t)$
time lag (min)
(f)
$\hat{K}_{oo}(t) - \hat{K}_{yo}(t)$
time lag (min)
−100
100
300

Figure 3.4. A) Univariate $\hat{K}(t)$ of a subset of the data with young narwhals only (n=138). Dashed lines are 0.025- and 0.975-quantile from 10 000 Monte Carlo simulations. B) Univariate $\hat{K}(t)$ of a subset of the dataset with old narwhals only (n=14). C) and D) Cross $\hat{K}_{yo}(t)$ and $\hat{L}_{yo}(t)$ of photographed young and old narwhals. The solid line represents the functions $\hat{K}_{yo}(t)$ or $\hat{L}_{yo}(t)$ and black dashed-dotted lines are 0.025- and 0.975-quantile calculated from 10 000 Monte Carlo permutations for the independence of population hypothesis. Grey dashed lines are equivalent envelopes for the random labelling hypothesis (see text for more details about the permutations). The horizontal grey line at 0 provides a reference from the corresponding null hypothesis. E) Paired differences $\hat{K}_{yy}(t) - \hat{K}_{yo}(t)$ and F) paired differences $\hat{K}_{oo}(t) - \hat{K}_{yo}(t)$. Grey dashed lines are envelopes for the random labelling hypothesis.

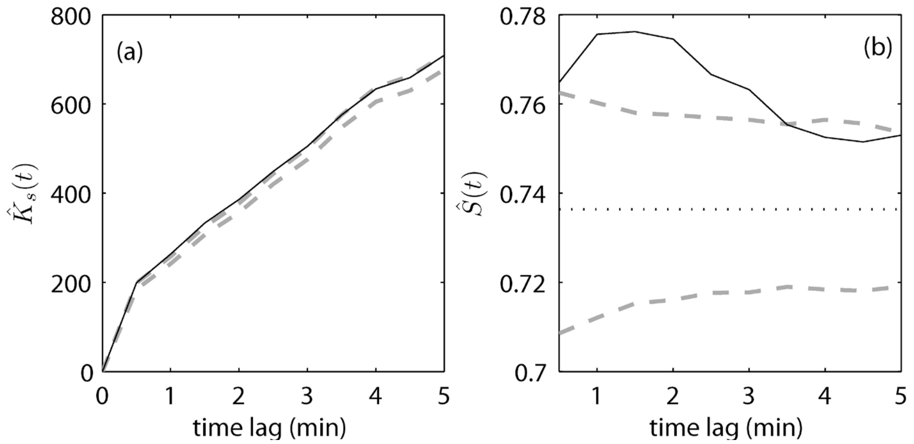


Figure 3.5 A) Mark similarity function $\hat{K}_s(t)$ and B) the average mark similarity function $\hat{S}(t)$ of the whiteness of photographed narwhals (solid lines). The dashed lines are 0.025- and 0.975- quantile estimated from 10 000 Monte Carlo random permutations of the mark (proportion of white). The horizontal dotted line in B) represents the average similarity of all pairs of observation. Both $\hat{K}_s(t)$ and $\hat{S}(t)$ fall outside the envelope for time lags smaller than three minutes indicating that narwhals that were within a interval of three minutes of each other were more similar in whiteness than expected under the randomness hypothesis.

3.5 Appendix

The usage of the percentage of white as an indicator of the age of narwhals.

As narwhals change in coloration with age (Silverman 1979; Hay 1984; Hay and Mansfield 1989), we used the percentage of white on the back of a narwhal as an estimation of the age (Auger-Méthé et al. 2010). We cropped each photograph to a standardized rectangular area located on the flank just under the dorsal ridge. The length of this rectangle was the same as the length of the dorsal ridge and the height was one eighth of its length. We created a routine that automatically calculates the proportion of white in the rectangle section. The routine maximizes the contrast of each photograph by subtracting the value of each pixel by the minimum value and dividing by the maximum value of the pixels of the rectangle. It transforms the rectangle to binary black and white using Otsu's (1979) gray scale function and calculates the proportion of white pixels in the rectangle. In order to prevent the program from including white patches that are not from the skin pattern, the method is not completely automated and a user has to decide if the binary black and white picture corresponds to the original picture. This way, we eliminated photographs of narwhals with glare on their back that was considered as a white spot by the program. We automatically gave a value of 0 to narwhals that were grey in color.

Validation

We validated the automated method by comparing this method with a random point estimating method similar to those used by ecologists to estimate percent cover (Meese and Tomich 1992). Fifty random points falling within the standard rectangle were selected and the colour of the pigmentation (black or white) for each of those points was visually inspected and noted. The amount of white of the skin was represented as the proportion of the 50 points that were white. In order to compare the degree of agreement between the two methods, we calculated the coefficient of correlation between the proportion of white calculated with the automated routine and by visual observation on 40 photographs. The agreement between the two method was satisfying (R-square= 0.6815) thus we use the semi-automated method for the analysis of all the pictures. We also tested the repeatability of the proportion of white from two photographs of different quality from 20 individuals. The pictures were taken a few seconds or minutes apart. The repeatability value (Lessells and Boag 1987) of the measure in the percentage of white was quite high (0.9814).

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Linking statement

The two previous chapters were concerned with the grouping patterns of narwhals and their analysis. Individuals in groups must communicate with each other to keep group cohesion and to assess group membership. In addition, the structure of cetacean groups often shapes their vocal repertoire. In chapter 4, I explore aspects of narwhal acoustic communication. I examine the context of usage of calls, their variability, and speculate about their potential function. In addition, I explore the hypothesis that narwhals have group-specific calls.

Chapter 4

Variability and context-specificity of narwhal (*Monodon monoceros*) whistles and pulsed calls

4.1 Abstract

The behavioral and environmental context of animal calls provides insights into their functions. Narwhals are a highly vocal species and, like other social cetaceans, rely on acoustic signals to communicate. We characterize and categorize narwhal whistles and pulsed calls, as well as investigate variation in these calls under different contexts (behavior, herd and year) using recordings made during the month of August, 2006-2008, in Koluktoo Bay (N 72° 04', W 80° 32'). We detected similarities among whistles but not pulsed calls that were produced under a similar behavioral context. Both whistles and pulsed calls recorded within the same herd were more similar than whistles and pulsed calls recorded within different herds. We did not find any type of whistle to be associated with a specific behavior although some acoustical features might be behavior specific. Both whistles and pulsed calls show properties that are consistent with the hypothesis that narwhals produce group- or individual-specific calls.

Keywords: Arctic; cetacean; dialect; Monodontidae; neural network; whale

4.2 Introduction

Many social animals rely on acoustic communication for several functions from recognizing individuals (Caldwell and Caldwell 1965) or groups (Ford 1989; Rendell and Whitehead 2003) to warning con-specifics about danger (Leger and Owings 1978). Assessing call function ideally requires knowing the identity and behavior of the emitter and the reaction of the receiver(s). However, the context of call usage as well as its variability among different individuals or groups can also provide insight into call function. For example, subantarctic fur seal (*Arctocephalus tropicalis*) pups recognize their mother "female attraction calls" that she emits when she returns back to the rookery after a foraging trip (Charrier *et al.* 2002).. The frequency with which bottlenose dolphins (*Tursiops aduncus*) emit sine whistles during traveling has been interpreted as evidence that the function of there calls involve group cohesion (Hawkins and Gartside 2010). In addition, calls can provide information about the emitter. For example, the inter-pulse interval of sperm whale (*Physeter macrocephalus*) clicks are correlated with body size (Rhinelander and Dawson 2004). Thus, the study of acoustic communication can provide insight into an animal's identity, group membership, physical characteristics, and behavior.

Cetaceans are social mammals that rely extensively on acoustic signals to communicate (Tyack 1986). Sound transmits better underwater than visual and olfactory cues, such that acoustic signals allow communication over long distance and at depths where there is no light (Janik 2005). Although acoustic communication is known to be highly important for cetaceans, our understanding of their communication systems is far less advanced than communication of terrestrial animals, mainly because of the challenges related to studying animals underwater (Janik 2009). Understanding of cetacean communication is based largely on captive studies and, more recently, recorder attachment to a few individuals in the wild. Studies combining behavioral observations with recordings from hand-held hydrophones in a few odontocete species in the wild have found behavior-specific calls (*Delphinapterus leucas*: Sjare and Smith 1986a; *Globicephala melas*: Weilgart and Whitehead 1990; *Physeter macrocephalus*; Whitehead and Weilgart 1991; *Tursiops truncatus*: Janik 2000; *Orcinus orca*: Simon et al. 2007), giving insight into the function of some calls. In addition, some cetacean species use acoustic communication to advertise group membership (Ford 1989; Rendell and Whitehead 2003) or individual identity (Caldwell and Caldwell 1965).

The narwhal (*Monodon monoceros*) is a loquacious, social cetacean (Odontoceti, Monodontidae) that is known to rely on sound to communicate (Ford and Fisher 1978) and to navigate (Miller et al. 1995). In general, narwhal acoustic communication is poorly understood, because the species is restricted to the high arctic and not present in captivity (Hay and Mansfield 1989). The two main kinds of communicative sounds narwhals are known to use are whistles (tonal sounds) and pulsed sounds (Ford and Fisher 1978). Whistles are narrow-band, frequency-modulated sounds between 300 Hz and 10 kHz (Ford and Fisher 1978). Pulsed sounds involve a short burst or long series of pulses (clicks) with a mean dominant frequency of 12- 20 kHz (Watkins et al. 1971), but can occasionally far exceed 100 kHz (Møhl et al. 1990). Some pulsed sounds with a high click repetition rate possess a tonal character with harmonically related sidebands (Ford and Fisher 1978) termed combined tonal/pulsed signals (Shapiro 2006). More recently, Shapiro (2006) has found differences in the characteristics of calls emitted by two narwhals fitted with recorders. However, it is not clear if these results are associated with individual- or group-specific differences (Shapiro 2006). In addition, there is no published data on context related variation in narwhal vocal behavior.

The objectives of this paper are three-fold. First, we characterize the variability of narwhal whistles and pulsed calls by quantifying physical characteristics of the calls. Second, we test if calls are context-specific by evaluating the similarity of calls among and between behavioral states, herds and years. Third, we evaluate if specific call types are associated with a behavioral state, herd, or year, by categorizing calls and investigating the context of usage for each call category.

4.3 Material and Methods

Fieldwork was conducted during the summers of 2006-2008 in Koluktoo Bay, Nunavut, Canada (N 72° 04', W 80° 32'). Recordings were collected from a peninsula at the entrance of the bay where narwhals swim near the shore when they enter and exit the bay (Marcoux et al. 2009). Based on general movement patterns of narwhals fitted with satellite-linked radio-transmitters (Dietz et al. 2001), narwhals are likely to stay in the bay for a few hours to a few days. A HTI-96 MIN series hydrophone (High Tech Inc, Gulfport, MS) with a frequency response from 2 Hz to 30 kHz was deployed either hanging from a buoy located at about 5 m from the shore in about 3 m depth (in 2006) or hanging from a pole at 1 m from the shore in 1 m water depth (in 2007 and 2008). Recorders used were either a Sony MiniDisc Player (in 2006) or Marantz PMD660 digital recorder (in 2006 to 2008), both at 44.1 kHz.

Narwhal behavioral state was observed from a natural high vantage point, 30 m above water. We noted the most prevalent behavioral state of visible narwhals within 450 m of the shore (Marcoux et al. 2009) using criteria derived from Mann and Smuts (1999): resting (moving slowly or stationary), travelling (moving steadily in a constant direction), or socializing (in physical contact with each other, including petting, rubbing, mounting, chases, tusk displays). Narwhals were divided into herds, defined as a group of narwhals that passed in front of the peninsula with a maximum time lag between individuals of 30 minutes (Marcoux et al. 2009).

The recording system used in this study had limitations related to attributing a call to a specific individual and detectable frequency range. We know neither the source level of narwhal calls nor their range of propagation at our site. Thus, we do not know the distance at which we can record narwhal calls with our recording system. We assume that vocalizations from narwhals closest to the hydrophone are louder on the recordings and are thus the most likely to be analyzed according to our selection criteria. Narwhals are very gregarious and the majority of our observations include two or more narwhals (Marcoux et al. 2009). Thus, it was impossible to attribute calls to a specific individual. Our recording devices only allowed us to measure frequencies from 2 Hz to 22.05 kHz (Nyquist frequency for a sampling rate of 44.1 kHz). It is therefore likely that we missed some calls that were emitted in the higher frequencies.

Recordings were visualized using Raven Pro 1.3 (Cornell Lab of Ornithology, Ithaca, NY) with a 10 second window view. Calls with signal to noise ratio higher than 10 dB were kept for analysis and saved as individual files. We analyzed both whistles and pulsed calls. Whistles were defined as pure tonal sounds, which may include harmonics that are only an integer multiple of the fundamental frequencies. Pulsed calls are a series of broadband pulses with a sideband structure and energy distributed in a broad range of frequencies. They often contain abrupt and patterned changes in pulse repetition rate, and usually have a tonal property because of their high pulse repetition rate (Ford 1989). Because we were interested in communication signals only, echolocation clicks characterized by broadband discrete clicks and slow repetition rate (Norris 1969) were not analyzed.

Individual whistles were opened with a custom Matlab (The Mathworks, Natick, MA, Release 2007) program to manually trace the frequency contour (similar to Watwood et al. 2004; Shapiro 2006). The user is provided with a spectrogram (window size of 256, overlap of 250 and fast Fourrier transform of 256 points) containing the whistle and uses a crosshair curser to select points along the contour (the fundamental frequency of the whistle over time). Once the contour is fully traced, the program interpolates between the points entered using a piecewise cubic Hermite interpolating polynomial (Fritsch and Carlson 1980). Finally, the program creates and saves a vector with a point at each 10 milliseconds. As a first exploration to characterize the whistles, the average, minimum, maximum, initial, and end frequencies were extracted together with the duration and the general slope (end frequency subtracted from initial frequency divided by duration).

Pulsed calls were digitized using another Matlab-based program that provides the user with a spectrogram (with the same parameters as for whistles). The user selects the frequency band where the signal is the most prominent, filtering out frequencies with most of the background noise. The power is summed for each interval of 0.136 milliseconds (window size of 256 points with overlap of 250 points) and plotted over time to identify peaks at each pulse. The user enters a moving threshold above which each peak is considered as an individual pulse. The pulse rate is calculated in Hertz by taking the inverse of the inter-pulse interval between two consecutive pulses. The pulse repetition rate is interpolated for the duration of the call using a piecewise cubic Hermite interpolating polynomial (Fritsch and Carlson 1980). The program saves a vector with the pulse repetition rate at intervals of 10 ms. Thus, the output is a pulse-rate contour. The average, minimum, maximum, initial and ending pulse repetition rates as well as the duration and the number of pulses were calculated.

In order to investigate if calls recorded under similar behavioral context are more similar than calls recorded under different behavioral contexts, we calculated a time-warped index of similarity between each pair of whistles and each pair of pulsed calls. The similarity index does not conserve the duration of the calls but warps them to maximize the similarity in the frequency domain (similar to Sakoe and Chiba 1978; Buck and Tyack 1993). The similarity between the calls *M* and *N* is calculated with:

$$s_{MN} = \frac{1}{m}\sum_{i=1}^{m}\frac{\min[M(i),N(i)]}{\max[M(i),N(i)]}$$

where *M(i)* and *N(i)* are the frequency or pulse-rate values for each 10 ms intervals *i*, and *m* is the number of 10 ms intervals for the call *M.* It is thought that similar to other mammals (Fay 1988), frequencies are perceived by cetaceans on a logarithmic scale (Cato and McCauley 2003; Deecke and Janik 2006). Thus, the similarity metric we used in the equation is a ratio which reflects relative differences. For example, a frequency difference of 5 Hz at low frequency (e.g. between 5 Hz and 10 Hz) is less similar (*s*=5/10=0.5) than a 5 Hz difference at higher frequency (e.g. between 100 Hz and 105 Hz; *s*=100/105=0.95). For the warping, parts of the call *M* were sped up or slowed down by a maximum factor of 3 to fit the frequency contour of call *N* (Deecke and Janik 2006). The similarity between the pair of calls *M* and *N* does not equal the similarity between the pair *N* and *M* (mainly because *M* and *N* differ in their number of 10 ms intervals, *m*), thus we measured the average of the two similarities.

In addition to calculating the time-warped index of similarity, we also calculated a more conservative similarity index, the shifted similarity, which keeps the duration of each call intact (Buck and Tyack 1993; Janik 1999). To calculate the shifted similarity index, we first calculated the dissimilarity between the two calls. The shorter call is slid along the longer call in order to maximize similarity in the frequency domain correcting for the probable imprecision of assessing the exact beginning and end of the calls. The dissimilarity between two calls *M* and N is calculated with:

$$d_{MN} = \frac{2}{m+n}\sum_{i=1}^{m} abs(M(i) - N(i))$$

where the sum of the absolute difference between the values at each 10 ms interval is divided by the average length of the two whistles so that whistles of very different length will have lower similarity. Once all the dissimilarities between pairs of calls are obtained, they are normalized from 0 to 100 by subtracting by the smallest value and then dividing by the range of values. We then obtained a similarity measure by subtracting them from 100. This similarity index measures absolute difference in frequency similar to other previously used measures (e.g., Buck and Tyack 1993; Janik 1999).

In order to assess the similarity of calls produced in different contexts, two binary matrices were built (one for whistles and one for pulsed calls), in which calls recorded under the same behavioral context received a ‘1’ and calls recorded under different behavioral context received a ‘0’. These matrices were overlaid with the similarity matrices and the average similarity of calls recorded under the same behavioral context (‘1’) was compared to that of calls recorded under different behavioral context (‘0’). To assess the significance of differences in similarity, we performed a Monte Carlo test (Manly 1997) in which the behavior was permuted 1000 times. The average similarity was calculated for each permutation. The same procedure was repeated to test for similarity within and among herds and years.

In order to categorize frequency contours of whistles and pulse-rate contours of pulsed calls, we used an adaptive resonance theory (ART) neural network developed by Deecke and Janik (2006). The network uses a vigilance parameter (critical similarity) to control the number of categories: a high vigilance results in many, fine scale categories while low vigilance results in few, general categories. When a call is entered in the network, a time-warped similarity index between the entering call and a set of reference calls already entered for each category is calculated as described above. If the vector is similar enough to the set of reference calls for the category (the similarity is larger than vigilance), it is added to that category. If it is not similar enough, a new category is created (Deecke and Janik 2006). Whistles and pulsed calls were analyzed separately.

A common problem in categorizing is deciding the optimal number of categories. The optimal number of categories should be the lowest number of categories that minimizes the within-category variance and maximizes the between-category variance (Milligan and Cooper 1985; Schreer et al. 1998). This principle was applied to assess the optimal number of categories of contours. Categorization was processed for 50 different vigilance values from 0% to 100% in steps of 2%. The ratio of the average within-category over the average between-category time-warped similarity was calculated and plotted against the number of categories obtained. Similar to the "variance ratio criterion" for clustering data (Caliński and Harabasz 1974), the optimal number of categories corresponds to where the ratio levels off.

To test the association between the call category (whistles and pulsed calls categorized separately) and the behavioral context in which the call was used, we built contingency tables with these two factors. We applied a Fisher exact test for count data with simulated p-values (based on 1e+05 replicates; Fisher 1935; Agresti 2002) to test the independence between the factors. Calls were included in the analysis only if all narwhals seen within one minute were exhibiting the same behavior. This test was repeated with the factors herd and year.

4.4 Results

A total of 172 whistles had a sufficient signal to noise ratio to be included in the analysis. The whistle frequencies averaged 5.2 kHz ranging from 405 Hz to 14.5 kHz and lasting from 0.04 to 3.56 s (Table 1, Fig. 4.1). Forty-six of the whistles analyzed were recorded while the narwhals were resting, 20 when they were socializing and 106 while they were traveling. The average time-warped similarity of whistles recorded within the same behavioral context was significantly higher than the average similarity among behavioral contexts (Monte Carlo, $P = 0.001$). The average time-warped similarity of whistles recorded within the same herd was also higher than the average similarity among herds ($P = 0.019$). There was no significant difference in the average time-warped similarity within a year and among years ($P = 0.576$, Table 2). Similar patterns were found with the shifted similarity index (except that similarity within herd was not significant, Table 2).

The analysis of pulsed calls included 147 calls that fulfilled our criteria. Pulse repetition rates averaged 683 Hz and ranged from 69 Hz to 2.43 kHz (Table 3). Pulsed calls lasted from 0.02 to 0.43 s and included 10 to 279 pulses (Table 3, Fig. 4.2). Eleven pulsed calls were associated with resting narwhals, 17 pulsed calls with socializing and 117 with traveling. Contrary to the whistles, the pulsed calls recorded in the same behavioral context were not more similar than pulsed calls recorded among different behavioral context (P = 0.80). Pulsed calls recorded within the same herd were marginally more similar than pulsed calls recorded among different herds ($P = 0.06$). The time-warped similarity of pulsed calls recorded during the same year was also higher than pulse calls recorded in different years ($P < 0.001$, Table 4). Similar patterns were found with the shifted similarity index (Table 4).

For whistles, the optimal ratio of within- to between-category similarity was obtained with eight categories, which corresponds to a vigilance of 18% (Fig. 4.3a,c,e). Whistles were separated into categories according to differences in duration and frequency (Fig. 4.4). Contingency analysis identified no association between whistle categories and behavior categories (Fisher's exact test $P = 0.29$). However, there was an association between whistle category and herd as well as between whistle category and year recorded (Fisher's exact test, $P = 0.005$ and $P = 0.002$ respectively).

The optimal ratio of within- to between-category time warped similarity of pulsed calls was attained with four categories and a vigilance of 10% (Fig. 4.3b, d, f). The pulsed calls were mainly categorized according to their duration (Fig. 4.5). Consistent with the similarity tests, contingency analysis indicated no association between pulsed call categories and behavioral categories (Fisher exact test, $P = 0.97$). There was an association between the pulsed call category and the herd as well as between the pulsed call category and the year it was recorded (Fisher exact test, $P < 0.001$ for both).

4.5 Discussion

This is the first study to explore and document correlations between narwhal vocalizations and behavior. We detected similarities among whistles but not pulsed calls that were produced under a similar behavioral context. Thus, it is possible that some narwhal whistles are behavior-specific. However, the similarities among whistles heard under similar behavioral context do not seem strong enough to support categorization of whistles according to behavior. Behavior-specific calls have been recorded in other cetacean species such as the foraging-related bray calls in bottlenose dolphins (Janik 2000) and the social codas in sperm whales (Whitehead and Weilgart 1991, Janik 2000). Nonetheless, most studies have found behavior-specific differences in call rate but not call type or call characteristics (Sjare and Smith 1986a; Weilgart and Whitehead 1990). Thus, although a lack of association between behavior and whistle type is not surprising, it remains possible that associations would have been detected if we had classified calls differently (i.e., in this study neural networks classified calls according to frequency, length and shape, but other forms of variation could be more behavior-specific), had a larger sample size, or were able to document a wider variety of vocalizations and behavior than what we observed among narwhals traveling to summer gathering sites.

Both whistles and pulsed calls recorded from the same herd were more similar than calls from different herds. This result is consistent with the possibility of group- or individual-specific calls in narwhals. Narwhal herds are composed of several smaller clusters (Marcoux et al. 2009). It is possible that narwhals that are part of the same cluster share similar calls, and that these calls are different from the ones shared within other clusters in the same herd. Thus, the similarity of calls heard from a herd might results from clusters having unique calls. In a study of two narwhals fitted with digital archival tags, Shapiro (2006) found that calls were more similar intra-individually than inter-individually and interpreted this as evidence that narwhals have individual- or group-specific calls. Individual- and group-specific calls are well-documented in other odontocete species

(*Lagenorhynchus obliquidens*, Caldwell and Caldwell 1965; *Orcinus orca*, Ford 1989; *Physeter macrocephalus*, Rendell and Whitehead 2003), but additional research on the vocalizations of larger samples of individually identified narwhals is needed to confirm whether narwhals have individual- and/or group-specific calls. Yearly variation in pulsed calls may reflect environmental variation. Narwhals may adjust the duration and the pitch of their pulsed calls to maximize sound propagation in varying acoustic environments (Lesage et al. 1999). Alternatively, different herds with group-specific pulsed calls might have visited the bay in different years, resulting in yearly variation.

Narwhals and belugas (*Delphinapterus leucas*) are closely related phylogenetically (Sharon and McGuire 1998) and have partially overlapping geographic range distributions (Innes et al. 2002). The two species also largely overlap in their vocal repertoire. The frequency range of narwhal whistles recorded in this study is comparable to the frequency range of beluga whistles, although some beluga whistles have a higher frequency (beluga whistles range from 0.2 to 18.1 kHz; Sjare and Smith 1986b; Karlsen et al. 2002; Belikov and Bel'kovich 2007). Narwhal whistles had similar duration as beluga whistles (Sjare and Smith 1986b; Karlsen et al. 2002; Belikov and Bel'kovich 2007). The average repetition rates of narwhal and beluga pulsed calls were similar, but beluga pulsed calls were longer (beluga pulsed call repetition rate from 0.20 to 1.30 kHz, total pulsed call duration from 0.04 to 1.52 sec; Sjare and Smith 1986b; Belikov and Bel'kovich 2008). Beluga whistles have been manually categorized into 16 categories (Sjare and Smith

1986b; Karlsen et al. 2002; Belikov and Bel'kovich 2007) based on categories developed for pilot whale whistles (Taruski 1979). While the difference in the categorization methods does not allow a direct comparison of the categories, a visual, qualitative inspection of the contours of narwhal and beluga whistles suggests that belugas may have more diversified whistle contours (see Table 1 in Sjare and Smith 1986b; Fig. 1 in Belikov and Bel'kovich 2007).

Acoustic monitoring is increasingly used and promoted as a non-invasive monitoring method (for a review see Mellinger et al. 2007). Given the loquacious nature of narwhals, this species seems a favorable candidate for acoustic monitoring programs (Marcoux et al. submitted). In addition, results from this study provide preliminary support for group- or potentially individual-specific calls in narwhals. This characteristic could potentially be used to differentiate between narwhal herds using acoustic recordings. Future studies at different locations and times of the year should provide a more extensive representation of narwhal vocal repertoire and its variability, and thus improve the detection of narwhal calls from recordings and possibly allow differentiation of narwhal populations, herds, and possibly individuals (Ford et al. 1986).

Table 4.1. Characteristics of the 172 whistle contours analysed in this study, recorded from narwhals in Koluktoo Bay, Nunavut.

	Average frequency (Hz)	**Minimum frequency (Hz)**	**Maximum frequency (Hz)**	**Frequency range (Hz)**	**Initial frequency (Hz)**	**End frequency (Hz)**	**Duration (sec)**	**Slope (Hz/sec)**
average	5235	4610	5891	1281	5132	5368	0.45	104
min	661	405	701	0	701	405	0.04	-31110
max	13706	11770	14511	119756	11940	14511	3.56	40060
standard deviation	3155	2816	3611	1787	3065	3432	0.38	7217
coefficient of variation	60.3%	61.1%	61.3%	139.5%	59.7%	63.9%	83.7%	69.4%

Table 4.2. Average time-warped and shifted similarities of narwhal whistle contours within and among behavioural context, herds and years. Significant values are bolded.

	time-warped similarity			shifted similarity		
	within	among	significance (p value)	within	among	significance (p values)
behaviour	**41.73**	**35.56**	**0.001**	**85.94**	**79.08**	**<0.001**
herd	**40.74**	**38.15**	**0.019**	80.02	79.10	0.064
year	38.41	38.83	0.576	79.08	79.44	0.659

Table 4.3. Characteristics of the 147 pulsed calls analysed in this study, recorded from narwhals in Koluktoo Bay, Nunavut.

	Average pulse rate (Hz)	**Minimum pulse rate (Hz)**	**Maximum pulse rate (Hz)**	**Initial pulse rate (Hz)**	**End pulse rate (Hz)**	**Duration (sec)**	**# pulses**
average	683	390	947	578	591	0.12	77.4
min	152	69	190	69.	70	0.02	10
max	1769	1131	2436	2436.	1787	0.43	279
standard deviation	279	235	415	371	326	0.07	44.2
coefficient of variation	40.9%	60.3%	43.8%	64.2%	55.3%	56.2%	57.1%

Table 4.4. Average time-warped and shifted similarities of narwhal pulsed calls within and among behavioural context, herds and years. Significant values are bolded.

	time-warped similarity			shifted similarity		
	within	among	significance (p value)	within	among	significance (p value)
behaviour	51.38	54.26	0.80	47.54	48.76	0.782
herd	54.58	51.74	0.06	**49.83**	**47.45**	**0.007**
year	**55.41**	**49.58**	**<0.001**	**49.62**	**46.44**	**<0.001**

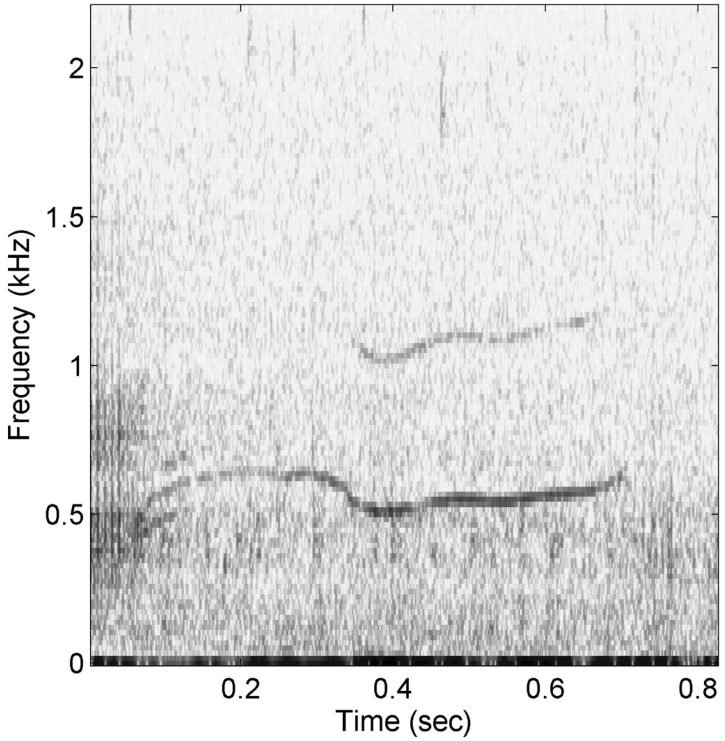

Figure 4.1. Sample spectrogram of a narwhal whistle recorded from Bruce Head, Koluktoo Bay, Nunavut on 22 August 2006.

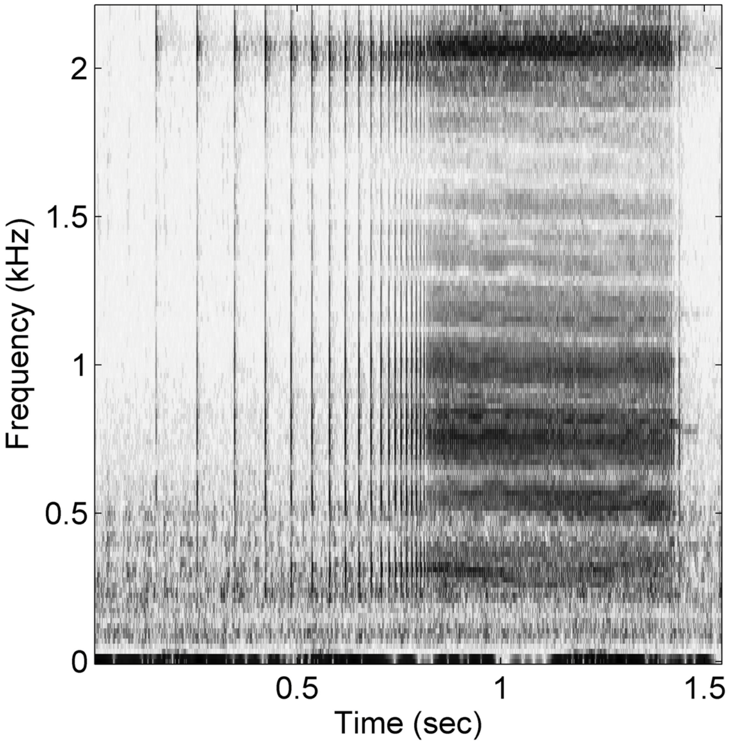

Figure 4.2. Sample spectrogram of a narwhal pulsed call recorded from Bruce Head, Koluktoo Bay, Nunavut on 2 August 2008.

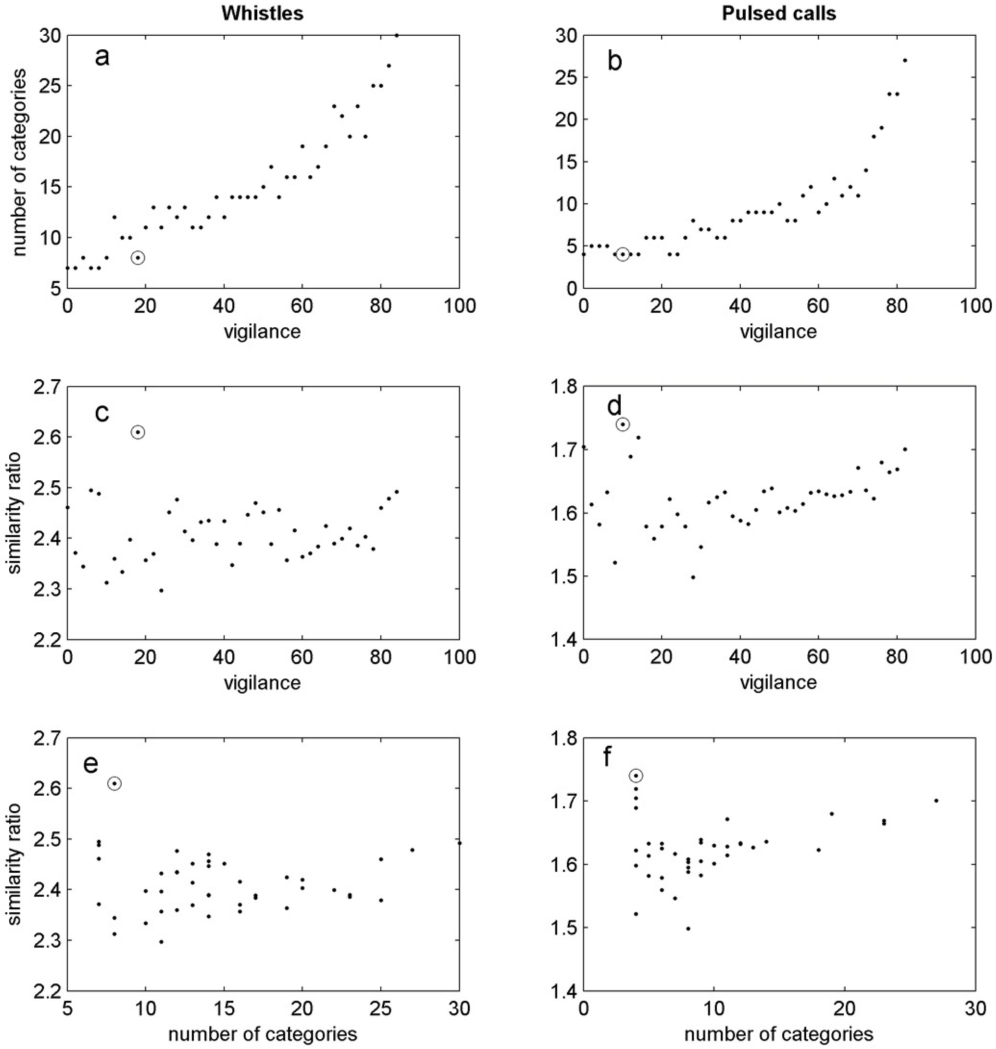

Figure 4.3. Increasing number of categories obtained from neural network analysis with increasing vigilance for narwhal whistles (a) and pulsed calls (b), as well as the increase in the within-category to between-category similarity ratios with increasing vigilance for whistles (c) and pulsed calls (d). For whistles, the optimal within-category to between-category similarity ratio corresponds to eight categories with a vigilance of 18% and is circled (e). For pulsed calls, the optimal within-category to between-category similarity ratio at four categories which corresponds to a vigilance of 10% and is circled (f). Circles in other panels indicate the corresponding category numbers (a and b) and similarity ratios (c and d).

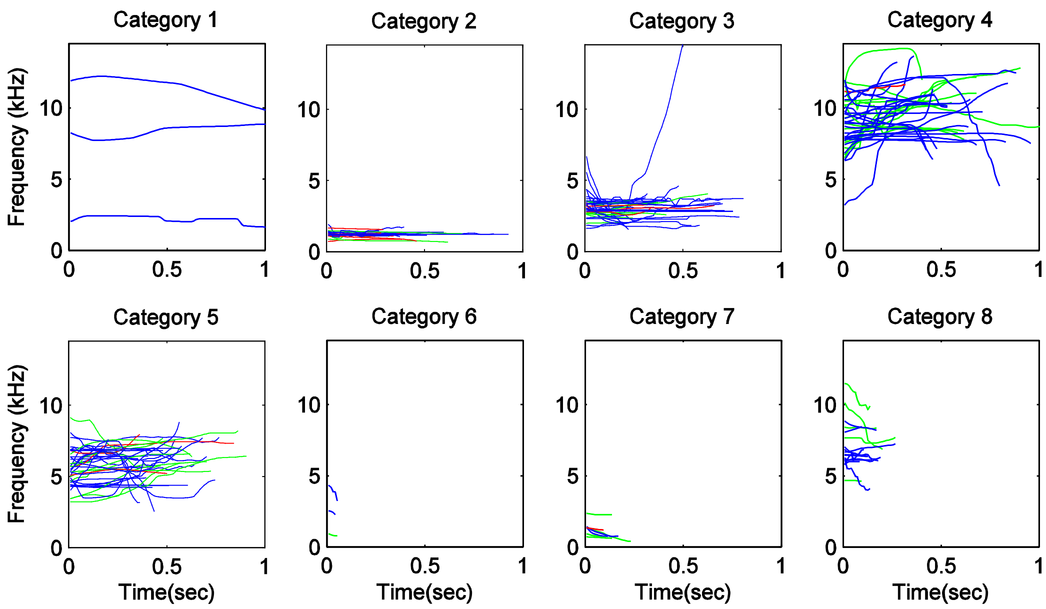

Figure 4.4. Narwhal whistle frequency contours categorized according to neural network analysis, color coded by behavioural state (solid grey=travelling, solid black=resting, dashed black=socializing). Whistles of category one were cut to fit the same scale as the other categories (original duration of 1.58, 2.85 and 3.56 seconds).

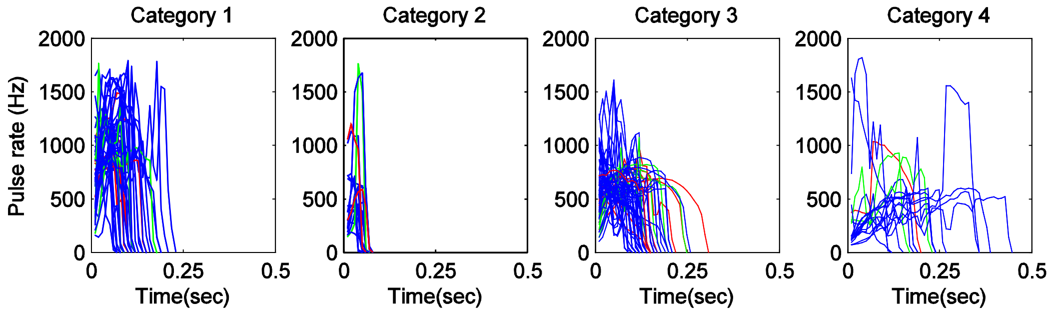

Figure 4.5. Pulse repetition rates of narwhal pulsed calls categorized according neural network analysis, color coded by behavioural state (solid grey=travelling, solid black=resting, dashed black=socializing).

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Linking statement

In the chapter 4, I have characterized and categorized narwhal vocalisations. These findings can be applied to passive acoustic monitoring of narwhals, which is the focus of chapter 5. The vocal repertoire described in chapter 4 serves as baseline information for the detection of narwhal calls.

Chapter 5

Local passive acoustic monitoring of narwhals in the Canadian Arctic

5.1 Abstract

The habitat of narwhals (*Monodon monoceros*) is being altered by climate change and increasing anthropogenic activities in the Arctic. Narwhals are socially, culturally and economically important to Inuit who rely on them for food and livelihood. There is a need for long-term community-based monitoring of narwhals. We examine the suitability of passive acoustics for local monitoring of narwhals using data gathered in the Canadian Arctic from an autonomous acoustic recorder (2006) and an on-site digital recorder (2006-2008). Recordings combined with behavioural observations permitted evaluation of the relationship between the number of narwhals present and the number of calls heard. In addition, we explore appropriate settings and assess the performance of an automated detector used to localize narwhal vocalizations over long recording periods containing significant non-target sound. Collectively, these results suggest that combining passive acoustic sampling with automated call detection offers a useful approach for local

monitoring of the presence and relative abundance of narwhals and other marine mammals.

5.2 Résumé

Le narval (*Monodon monoceros*) vit dans un habitat en rapide transformation à cause des changements climatiques et de l'augmentation de l'activité humaine en Arctique. Cette espèce représente des intérêts culturels, sociaux et économiques pour les Inuits qui en dépendent pour leur alimentation et le commerce. Le besoin d'un programme communautaire de surveillance des narvals est réel et évident. Nous explorons la pertinence d'un programme de surveillance par acoustique passive pour les populations de narvals à partir de données récoltées à l'aide d'une enregistreuse autonome (2006) et d'une enregistreuse non autonome (2006-2008). L'utilité d'un détecteur de vocalisations de narval automatique est évaluée en calculant la performance de plusieurs paramètres de détection. Des enregistrements accompagnés d'observations sur le terrain nous permettent d'évaluer la corrélation entre le nombre de vocalisations entendues et le nombre de narvals observés. Le détecteur automatique a détecté les vocalisations de narvals avec succès donnant la possibilité d'appliquer les résultats de la corrélation pour évaluer le nombre de narvals présents.

5.3 Introduction

Like other Arctic marine mammals, narwhals (*Monodon monoceros*) are experiencing a rapidly changing environment including a changing climate (Laidre and Heide-Jorgensen 2005; Laidre et al. 2008) and an increase in anthropogenic activities (Moore and Huntington 2008). Narwhals are culturally and economically important to local Inuit residents (Reeves 1992; Priest and Usher 2004). The narwhal has been listed as "near threatened" by the International Union for Conservation of Nature (IUCN, Jefferson et al. 2008) and as "special concern" by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC 2004). The rationale behind these listings is uncertainty related to some life-history traits such as generation time and longevity, population trends and structure, the future state of Arctic marine ecosystems during a period of rapid climate change, as well as increasing resource exploitation in the Arctic (COSEWIC 2004; Jefferson et al. 2008). Current monitoring and management efforts of narwhal populations are informed by harvest reporting (Armitage 2005a), aerial surveys (Richard et al. 2010), and Traditional Ecological Knowledge (Westdal et al. 2010).

Effective ecological monitoring in the Canadian Arctic requires multiple indicators and scales of observation. One on hand, monitoring programs are made more effective by explicit objectives, identification of inexpensive, unbiased and generalizable indicators, and rigorous statistical interpretation (Yoccoz et al. 2001). On the other hand, the degree to which selected indicators resonate with local observations, community priorities and potential anthropogenic impacts is an important determinant of their relevance to co-management perspectives and decision making (Dowsley and Wenzel 2008). Marine mammals are especially challenging in this regard because their size and mobility means they range over large spatial areas, while their long generation time and low reproductive rates contribute to lagged and latent population responses and recovery times (Lewison et al. 2004). As a result, local observations can differ widely from larger scale assessments and responses observed over the short-term may not be reflected in longer-term trends (Richard and Pike 1993). In these circumstances, where impacts and responses occurring locally or more globally over shorter or longer timescales are of interest to different stakeholders, a plurality of monitoring approaches can help to bridge the gap between the observations and interests of stakeholders (Mallory et al. 2006; Berkes et al. 2007).

Community-based (also called participatory) monitoring has been repeatedly suggested as an effective approach to sample natural resources (Wismer and Mitchell 2005). Community-based monitoring involves local people in multiple steps of the process (Holck 2008) and, in so doing, contributes to local stewardship and capacity building as well as public education and outreach (Conrad and Daoust 2008). By using local expertise and resources, community-based monitoring is usually less expensive and longer lasting (Danielsen et al. 2005). In addition, community-based monitoring is often very relevant to residents because it is more likely to focus on locally important resources and places (Pearce et al. 2009). However, many past community-based monitoring efforts performed by non-scientists have focused on qualitative rather than quantitative measures (Berkes et al. 2007) and have sometimes focused on easy and inexpensive indicators rather than those that are of most direct local relevance and importance, like wildlife. As the research capacity of northern communities expands and community-researcher alliances strengthen (Berkes et al., 2007; Tremblay et al., 2008), the breadth of approaches and technologies that are compatible with community-based monitoring expands. Technologically and statistically-involved wildlife monitoring techniques are compatible with community-based monitoring programs, as long as these approaches are developed in partnership with communities and incorporate rather than exclude local methods of observation.

Passive acoustic monitoring has been suggested as an effective and low cost monitoring technique for marine mammals, with the capacity to sample 24 hours per day, in poor weather conditions and over long periods (see review by Mellinger et al. 2007). Most acoustic monitoring programs simply note the presence of calls by species of interest (e.g., Johnston et al. 2008; Todd et al. 2009). However, some attempts have been made to estimate marine mammal abundance using acoustic monitoring; notably, these estimates are improved by information about the average call rates of individuals and how this varies with group size and behavioural state (Van Parijs et al. 2002; Mellinger et al. 2007; Kimura et al. 2009). Specific acoustic monitoring programs have advanced knowledge of several cetaceans species such as sperm whale presence in the Gulf of Alaska during the winter, when boat-based surveys cannot be conducted (Mellinger et al. 2004), extended breeding period of humpback whales on their feeding ground (Clark and Clapham 2004) and night foraging behaviour of beaked whales (Johnston et al. 2008).

Here, we conduct a pilot study of the feasibility of passive acoustic monitoring for narwhals presence and relative abundance in the Canadian Arctic. Specifically, we deployed an autonomous recording system for 25 days in an area known to be frequented by narwhals, then tested the usefulness of an automated detector to extract narwhal vocalisations from the audio file. We then combined behavioural observations and passive on-site digital recordings from a second site to relate the number of narwhals and their behavioural state to the number of vocalizations recorded.

5.4 Methods

5.4.1 Characteristics of narwhal vocalisation

The narwhal is a vocal species that emits echolocation clicks, as well as pulsed calls and whistles (Ford and Fisher, 1978; Shapiro, 2006). The frequency of narwhal clicks might be well above 100 kHz and maximum source levels can reach 218 dB re 1 μPa (Møhl et al. 1990). Pulsed sound frequencies are usually between 0.5 to 24 kHz, while whistles are between 300 Hz and 10 kHz (Watkins et al. 1971; Ford and Fisher 1978). Source levels of narwhal whistles and pulsed calls are not known (Shapiro 2006). A detailed description of narwhal vocalisations is provided elsewhere (Marcoux et al. Submitted).

5.4.2 Recordings and behavioural observations

We tested the feasibility of detecting narwhal vocalisations with an automated detector using data from Repulse Bay, Nunavut (66° 20' N, 86° 0' W, Fig. 5.1). Recordings were obtained using an autonomous recorder (AURAL M2, Multi-Électronique Inc, Rimouski Québec) deployed in approximately 30 m of water from 9 August to 2 September 2006. The AURAL contains a HTI-96 MIN series hydrophone (High Tech Inc http://home.att.net/~hightechinc/) with a frequency response from 2 Hz to 30 kHz. The sampling rate was 32.77 kHz and it recorded segments of 32 minutes 33 seconds at the beginning of each hour for a total of 302 hours. Our recording system did not allow us to determine the detection range of narwhal calls. Behavioural observations could not be obtained at this site, so comparison of acoustic recordings with narwhal observations required research at a second site.

We determined how the number of vocalizations recorded on audio files was related to the number and behavioural state of narwhals present in Koluktoo Bay, Nunavut (72°04' N, 80°32' W, Fig.5.1), near the Hamlet of Pond Inlet. The fieldwork occurred in the summers of 2006 to 2008. Technical failure of a continuous autonomous recorder at this site prevented replication of the recording and analytical procedures used for Repulse Bay recordings. Instead, we used a hand-held digital recorders (Sony MiniDisc Player in 2006 and Marantz PMD660 from 2006 to 2008, both with recording rates of 44.1

kHz), with a hydrophone similar to the one described above (HTI-96) either hanging from a buoy approximately 5 meters from the shore in about 3 meters depth (in 2006) or hanging from a pole from the shore in 1 meter depth (in 2007 and 2008). Due to limited availability of power and data storage, recordings were initiated after we detected narwhals and stopped before or immediately after narwhals were out of sight. In addition, we noted the wind force measured according to the Beaufort scale as an indication of the background noise that could mask narwhal vocalisations. As in the previous dataset, the detection range of narwhal calls could not be determined.

Behavioural observations were performed from the Bruce Head peninsula with a viewing area approximately 30 meters above water level (Marcoux et al. 2009). We noted the number of narwhal groups (individuals within 10 body widths of each other) that swam within 400 m of the hydrophone (distance at which narwhals were observable; Marcoux et al. 2009). The average size of the groups was 3.5 individuals (Marcoux et al. 2009) with a median group size of three and a standard deviation of 2.6 individuals. We used the number of groups instead of the absolute number of narwhals because we were not able to obtain accurate counts for each group. We also noted the prevalent behavioural state of narwhals in each group as one of the following: resting (group moving slowly or stationary), travelling (group moving steadily in a constant direction), or socializing (group in physical contact with each other; similar to Mann and Smuts 1999).

5.4.3 Analysis

We used the sound analysis software Raven Pro 1.3 (Cornell Lab of Ornithology 2003-2008) to produce spectrograms, a two-dimension grid representing a sound file with the time on the abscissa, the frequency on the ordinate, and the intensity of the sound as a color gradient. The spectrogram used a Hann Window, with a Fast Fourier Transform size of 256 samples and 50% overlap. This provides a 64 Hz frequency resolution and a 7.8 ms time resolution, selected to optimize the trade-off between resolution in time and frequency domains.

Automated detection

The *Repulse Bay* recordings were used to test the feasibility of detecting narwhal calls with an automated detector. We used the sound analysis software XBAT (Figueroa 2007) based on the signal processing toolbox in Matlab (The MathWorks 2007). Within this software we used the data template option under the detector menu. This detector uses reference calls (templates) to be detected in an audio file. Then it calculates a time series of cross-correlations between the call template and the sound files. The user sets a threshold value above which peaks in the cross-correlation time series are logged as detections. We targeted the detection of pulsed calls (the most abundant call type in all our recordings) with peak frequency between 1030 and 3110 Hz; 85% of all manually detected pulsed calls were within this frequency range (see section "Relationship between the number of calls and the number of narwhals"). To eliminate false detection of noise events, we selected non-target sounds identified by the detector and set them as templates for rejections. These non-targeted sounds were mostly mechanical noise caused by the friction between parts of the mooring.

We tested 16 detector settings with different combinations of call templates for detection and noise templates for rejection. These settings were applied to a subset of 10 hours 51 minutes of recording (20 segments of 32.5 minutes). This subset was also examined visually and aurally to detect and count narwhal vocalisations based on a range of narwhal pulsed call types described by Marcoux et al. (Submitted). The number of calls and vocalisation events (defined as a recording segment of 32.5 min containing at least five calls) identified by each detector setting was compared to the number of pulsed calls and vocalisation events identified manually in subset.

Adjusting the detector settings to minimize the number of missed calls invariably led to an increase in false detections, such that it was impossible to simultaneously achieve an acceptably low number of missed calls and false detections. Thus, fully automated call detection, involving the use of a detector to extract the exact number of calls present in a recording sequence is not currently possible, because of the trade-off between minimizing the number of false detections and the number of missed calls (Munger et al. 2005; Mellinger et al. 2007).

As an alternative, we employed the call detector as a screening device used to identify recording sequences that potentially contained narwhal calls and therefore required manual examination. When used as a screening device, the priority is for the detector to minimize missed vocalization events, even though this will increase the number of false detections (false detections result in more of the recording being manually examined but do not cause noise to enter the dataset as mistaken calls, since all potential calls are verified manually). We tested the 16 detector settings using the 10 hours 51 minutes subset known to contain four vocalization events and selected a detector setting that successfully detected all four vocalisation events and did not generate false detections. This detector setting was based on templates of a pulsed call with peak frequency of 2688 Hz (Fig. 5.2a) and of three non-target sounds (e.g. Fig. 5.2b). We applied this detector to the entire 302 hr recording sequence, then conducted a manual assessment of the detected segments to confirm whether they did in fact contain narwhal calls.

Relationship between the number of calls and the number of narwhals

To test the relationship between the number of calls identified on a recording and the number of narwhals present during the recording we used the *Koluktoo* recordings. We counted calls produced during a one-minute period in the middle of five-minute calling segment (similar to Van Parijs et al. 2002). Only recordings for which narwhal calls were loud enough (10 db above background noise) were retained for analysis (Boisseau 2005; Díaz López 2010). The number of whistles and pulsed sounds were counted in each one-minute bout. We did not investigate echolocation clicks since they are difficult to isolate and count, and tend to have higher frequencies than the range of our recordings. Spectrograms were visualized in 10-second increments. To facilitate detection, we adjusted the contrast of the spectrogram view and/or amplified the sound file.

A backward stepwise regression (Crawley 2005) was used to construct a model with the total number of detected calls in one-minute period in the middle of five-minute calling segment as the dependent variable. The independent variables were 1) the number of groups and 2) their predominant behavioural state, observed within the same five-minute bout, 3) the year (which also accounted for the different recording setups) and 4) the Beaufort wind force scale during the recording. The selection criteria was p-value<0.1 for the F-test on the type III sum of square. The analysis was performed with the package "Car" (Fox 2002) written in R (R Development Core Team 2008).

5.5 Results

The use of the automatic detector as a screening device reduced the recording sequence that had to be manually inspected from 302 hours to 22 hours. The detector identified 41 segments with detections in the entire *Repulse* dataset, of which, after manual inspection, 17(41%) contained at least five narwhal calls, and thus were classified as vocalisation events.

Narwhal vocalisation events occurred on nine of the 24 days that were monitored (Fig. 5.3), but more than half of the events were concentrated within a single two- day period. Recordings on other days involved discrete detections, concentrated around 2h00 and 16h00. Collectively, these results indicate precisely when narwhals were present in this locality and distinguish between periods of nearly continuous presence and occasional passages.

For the *Koluktoo* dataset, we analysed 63 one-minute recording segments from 12 different days in 2006 to 2008. There was a positive and significant relationship between the number of groups observed visually and the number of calls (pulsed and whistles) identified on recordings (Fig. 5.4, Table 1). The number of calls identified also declined with increasing wind force (Table 1). The model accounted for 33% of the variation in the total number of calls identified (adjusted R^2-squared= 0.33, F(2,59)= 15.97, p <0.001, Fig. 5.4). The variables 'behavioural state' (Fig. 5.5) and 'year' were excluded from the model as non-significant (p>0.1). Thus, we did not find any effect of the behavioural state or year on the rate of vocalisation of narwhals. Generally, narwhal calls were present in our recordings whenever we visually observed narwhals in the bay.

In addition to detecting narwhals, we could monitor for the presence of other marine mammal species and shipping traffic. On 2 August 2008 and 4 August 2008, we detected bowhead whale (*Balaena mysticetus*) vocalisations in our *Koluktoo* recordings that coincided with visual observations in the bay.

Bowhead whale calls are differentiable from narwhals calls because they are emitted at a lower frequency range (Clark and Johnson 1984). Although we observed killer whales (*Orcinus orca*) in Koluktoo Bay on two different days, we could not identify vocalisations in 50 minutes of recordings when they were present. Finally, ships travelling in and out of Koluktoo Bay could also be identified in our recordings, highlighting the potential for monitoring the effect of shipping on marine mammal habitat use, which is of significant interest in the Arctic (Hovelsrud et al. 2008) and globally (Tyack 2008).

5.6 Discussion

Passive acoustic recording is a promising technique for local monitoring of narwhals in Nunavut. Narwhal calls can be automatically detected on recordings made by autonomous recorders. Additionally, an index of narwhal numbers can be derived from the number of calls manually detected on recording bouts corrected for the appropriate covariate (Beaufort Wind force). Presence only data and/or relative abundance data are commonly used in population monitoring (Pollock et al. 2002; Royle and Nichols 2003; Joseph et al. 2006). For narwhals, acoustic monitoring indicates presence and also provides information about relative abundance. Thus, acoustic monitoring has the potential to provide information about narwhal movement patterns, habitat selection, and daily and seasonal visitation patterns.

Acoustic monitoring programs provide the opportunity to match the design of the monitoring with ecological knowledge and local relevance. Decisions about the location of the recorders and the timing of the monitoring can be guided by local knowledge. For example, our work in Koluktoo Bay was based from Bruce Head, a traditional hunting site, simultaneously represents a site of known high narwhal abundance but also of high local value for hunting (Mary-Roussilière 1984-1985). In this way, ecological knowledge of local residents informs the design of monitoring programs (Gagnon and Berteaux 2006), which increases relevance to the local community (Pearce et al. 2009). In addition, already-existing integrated ocean observing systems (IOOS) use biophysical mooring to monitor marine ecosystems and the impact of climate change on them. By including acoustic monitoring in their design, IOOSs offer an opportunity to integrate information about marine mammal movements with biophysical data (Stafford et al. 2010).

Estimating narwhal numbers from recorded vocalizations requires calibration with visual and behavioural observations and environmental measurements (e.g., wind speed). We found a correlation between the number of narwhals observed and the number of calls manually detected on the audio recording. Because each site has unique physical acoustic characteristics and sound transmission rates depending on the water column depth, sea floor composition and geometry, water temperature and salinity (Richardson et al. 1995; Madsen and Wahlberg 2007), this relationship is likely to be specific to the site and depth where the hydrophone is located. Thus, we could not apply the correlation found in Koluktoo Bay to the recordings from Repulse Bay.

Counts of narwhals in the vicinity of the recorder are required for each specific recorder location to obtain an index of narwhal numbers. Wind speed negatively affected our ability to detect narwhal vocalisations, probably through increased wave noise. Thus, estimation of narwhal numbers should be corrected with wind speed measurements from an anemometer *in situ*. Calibrating the relationship between narwhal calls and observations and anemometer deployment introduce opportunities for local involvement.

Once autonomous recorders are retrieved, recordings must be downloaded and calls detected manually or with an automated detector. We have shown that narwhal vocalisations can be detected with a cross-correlation detector (Figueroa 2007) providing presence/absence data. But our inability to identify detector settings that avoid both missed calls and false detections, means detectors can only be used as screening devices used to identify potential calls that must be then manually verified and counted. Combining automated detection of vocalization bouts followed by manual call verification and counting is still preferable to an entirely manual evaluation, since the automated screening step greatly reduces the volume of recordings that must be examined. Most of the detector settings we tested were sensitive to the noise produced by the mooring system of the recording device, resulting in a high rate of false positive detections. Improvements to the mooring to minimize mechanical noise would greatly improve automated detection. In addition, new detectors are currently being developed which could significantly improve the efficacy of detecting narwhal vocalisations (e.g. Erbe and King, 2008; Adam, 2008).

The scale and precision of an acoustic monitoring program depends mainly on the acoustic device used, on their numbers and location (Mellinger et al. 2007; Van Parijs et al. 2009). Our pilot study was limited to one autonomous recorder in one location for 25 days. Thus the spatial and temporal coverage of this study is very limited. However, the use of several recorders would allow for broader spatial coverage, more precise spatial localization, and more information about group size and number. For example, detection distance for beluga (*Delphinapterus leucas*) whistles in the mouth of the Saguenay fjord was estimated to be 3 km under low noise condition, equivalent to a coverage of 28.3 km^2 per hydrophone (Simard et al. 2010). An array of four hydrophones covered the study area and permitted estimation of the number of belugas present from the number of whistles (Simard et al. 2010). To increase coverage for narwhal monitoring, hydrophones could also be placed in strategic locations, for example, in known narwhal migration routes. The measures developed in this paper provide an index of narwhal abundance, but not absolute numbers. As with other long-term monitoring projects, repetition of the same protocol over several years is crucial to to estimate temporal trends in local presence or abundance. Data collected from fixed acoustic devises are easier to standardize over time since they do not involve spatial variation (Evans and Hammond 2004).

Acoustic monitoring offers a useful addition to existing forms of narwhal monitoring based on aerial surveys and harvest data. Visual and photographic surveys from aircraft or boats are widely used to estimate the size and distribution of narwhal populations (e.g. Innes et al. 2002; Heide-Jørgensen 2004; Richard et al. 2010). Harvest data is also used to monitor narwhal populations. As part of the co-management agreement in six communities in Nunavut, all landed, lost or struck narwhals must be reported (Armitage 2005b). Occasionally, the sex and size of harvested narwhals are reported and tissue samples are collected for further analyses examining diet, contaminants, reproductive status and population condition (Finley and Gibb 1982; Hay and Mansfield 1989; Roberge and Dunn 1990; Muir et al. 1992; Dietz et al. 2004; Wagemann and Kozlowska 2005). Although all of these methods of narwhal research and monitoring have different emphasis, strengths and limitations, all clearly contribute to our knowledge of the species and its management status. Acoustic monitoring certainly cannot substitute for harvest monitoring and aerial surveys, which yield important and spatially extensive information about population size, population distribution and harvest intensity. Nonetheless, the technique does offer relatively low-cost and low-observer-intensity information about local presence and relative abundance of narwhals over time at discrete locations. Within this diverse but logistically constrained realm of narwhal monitoring approaches, acoustic monitoring offers an additional, independent, low cost and low effort method for local monitoring of narwhal populations.

Passive acoustic monitoring provides complementary and novel insight into questions related to the ecology and conservation of narwhals. For example, more exhaustive information on the timing and intensity of specific habitat usage can be examined through passive acoustic methods. Narwhals are known to visit fjords in the summer, but neither the spatial extent, nor the temporal duration of their presence in the fjords is well known (Dietz et al. 2001). Moreover, the seasonal extent of narwhals' presence in their known wintering grounds could be explored in more detail (Heide-Jørgensen et al. 2002; Laidre et al. 2003). Passive acoustic monitoring could also determine if harvesting activities or shipping traffic causes narwhals to leave an area, and if so, also determine the duration of the avoidance response. In addition, acoustic monitoring could document the rare occurrences of other marine mammal species in particular localities and whether these coincide with the presence or absence of more common species. Finally, this technique may be use to evaluate the impacts of weather and tidal cycles on narwhal movement patterns.

Table 5.1. Parameters of the model selected by the stepwise regression to predict the number of narwhal calls detected in a one-minute recording bout.

	estimate	Sum of Squares	df	F value	P value
Intercept	26.88	9787.1	1	125.83	<0.0001
Number of groups	0.93	981.5	1	12.31	0.0009
Beaufort	-3.46	650.8	1	8.15	0.006
Residuals		4625.6	58		

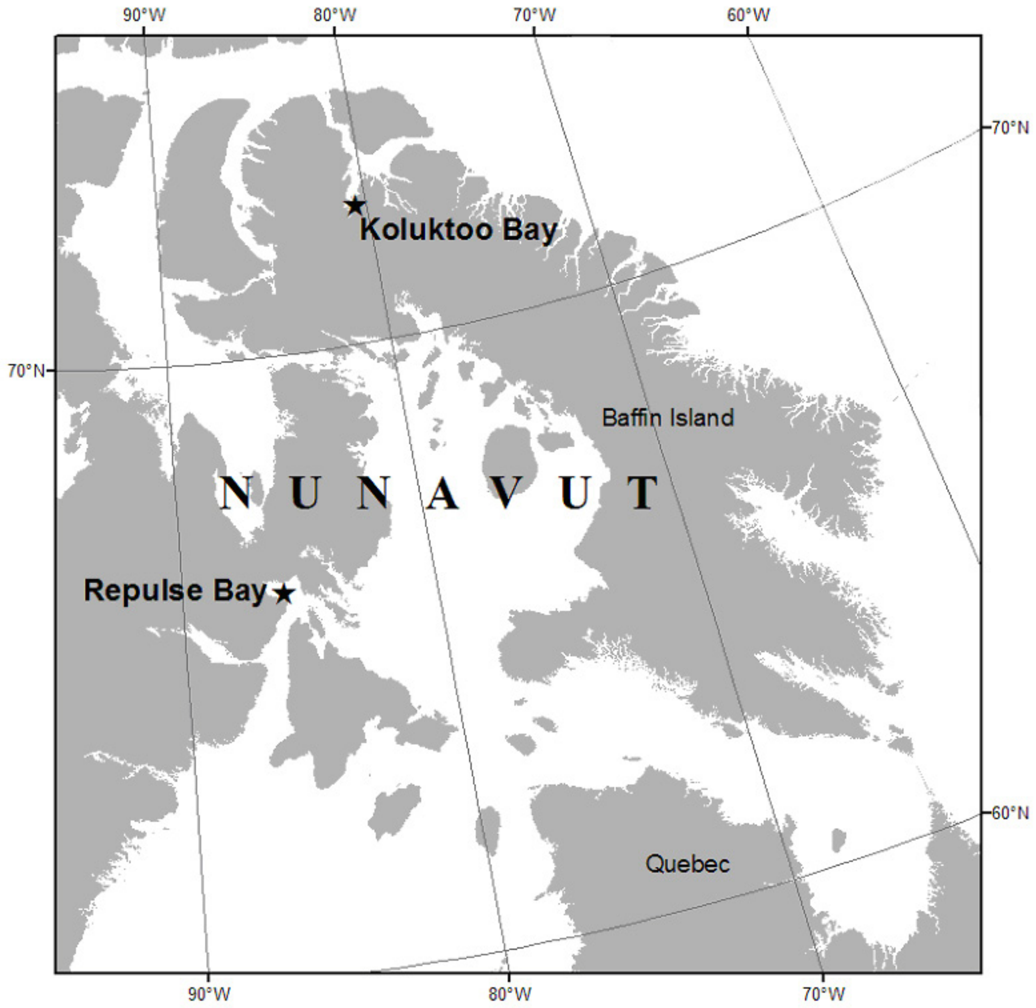

Figure 5.1. Map of Nunavut with the stars representing the two study sites.

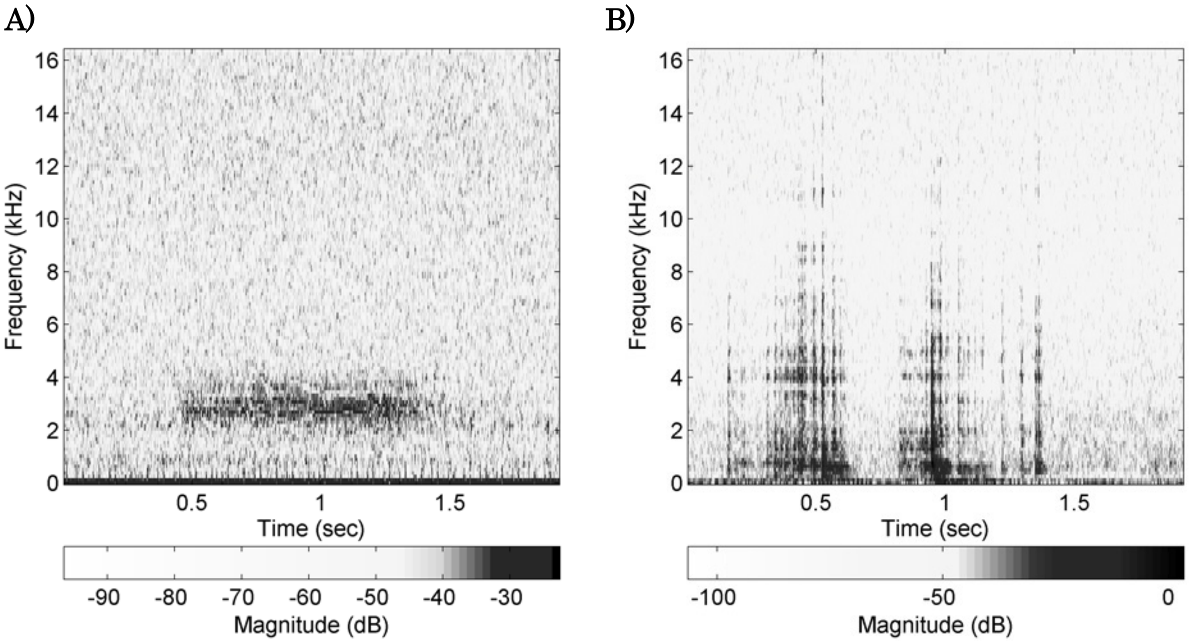

Figure 5.2. A) Template of narwhal pulsed call selected for the setting of the automated detector. B) Example of noise selected for rejection for the setting of the automated detector

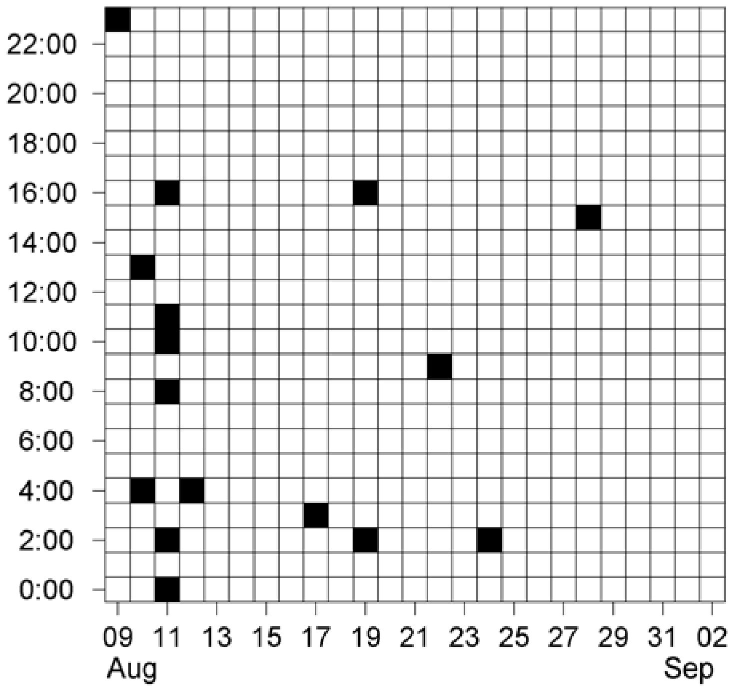

Figure 5.3. Acoustic detections of narwhals in the entire *Repulse* data set. Each grid represents an hour and black filled grids represent a detection event during that hour.

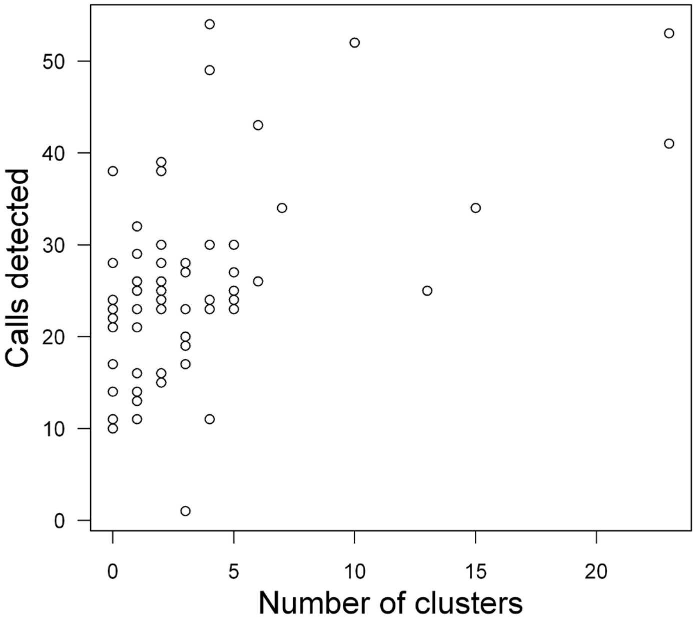

Figure 5.4. Regression between the number of calls detected in five-minute recording bouts and the associated number of narwhal groups observed.

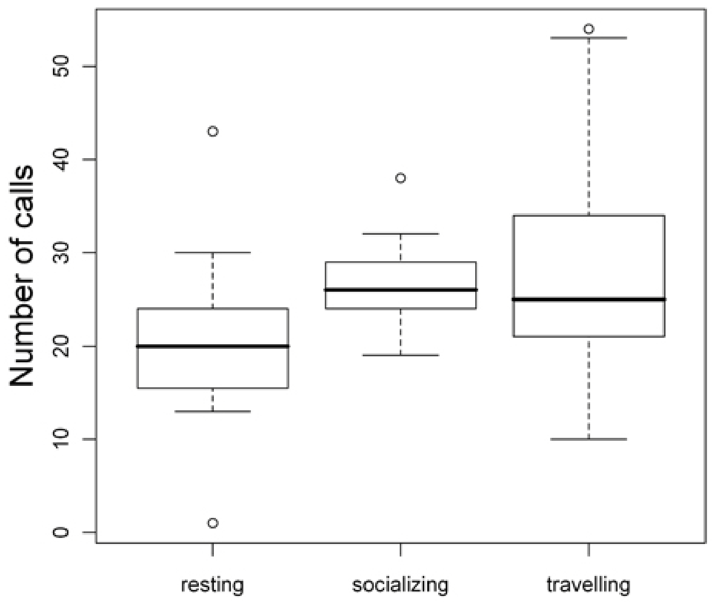

Figure 5.5. Number of calls detected in five-minute recording bouts in relation to narwhal behavioural states. The bottom and top of the box represent, respectively, the first and third quartile, the middle represent the median, the whiskers represent 95th percentile of the data and open circles are outliers. The number of call detected did not significantly different among behaviours.

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Summary and final conclusions

I studied the social and vocal behaviour of narwhals using non-invasive methods. In addition, I developed statistical methods for the study of behavioural observations and suggested an alternative method for the local monitoring of narwhals. My thesis provides new insights and applications to 1) the social organisation of cetaceans, 2) cetacean communication, 3) community-based monitoring, and 4) narwhal research.

6.1 Social organisation

The grouping pattern of narwhals resembles the grouping pattern of other cetaceans with fusion-fission societies. Results from chapters 2 and 3 document that narwhals are segregated by sex and by age, and that males form bigger groups than females. This grouping pattern is similar to the fusion-fission grouping pattern of bottlenose dolphins (*Tursiup truncatus*), the world's best studied cetacean (Connor et al. 2000b). Male bottlenose dolphins form stable alliances with other males to herd females (Connor et al. 1992). Some female bottlenose dolphins are almost always solitary while females with calves of similar age tend to associate with each other (Smolker et al. 1992). Narwhal societies might be similar to bottlenose dolphin societies where male narwhals could form alliances to herd females. Male narwhals are the only cetaceans with a tusk, which is likely used for sexual display or during aggressive encounters between males (Silverman and Dunbar 1980). Consequently, there seems to be competition between males for reproductive females. In other cetaceans, males form alliances to herd females if females are clustered, if the rate of encounter with females is low, or if the average number of males per receptive female is low (Connor et al. 2000a; Whitehead and Connor 2005). These conditions are met in narwhals, where females are found in a clumped distributions and are receptive only once every three years (Hay and Mansfield 1989). Thus, the grouping pattern of narwhals and the competition between males to access females meet some of the conditions for a fusion-fission society and male alliance formation.

6.2 Cetacean communication

The analyses in chapter 4 provide evidence that narwhal calls might be individual- or group-specific. The vocal communication of cetaceans is tightly related to the structure of their social organization (Tyack 1986). Bottlenose dolphins have signature whistles that function as cohesion calls (Janik and Slate 1998). Given the similarities between the grouping pattern of narwhals and of bottlenose dolphins, it would not be surprising that narwhals also produce signature whistles. This hypothesis has been suggested by Shapiro (2006) who showed that narwhal calls possess acoustical characteristics for individual recognition. I found that narwhal calls recorded within a herd were more similar that calls recorded among different herds. Because I was not able to attribute calls to specific individuals, I could not determine if this similarity is a characteristic of individuals or herds. While individual-specific calls are common in fusion-fission societies in cetaceans, group-specific calls are consistent with communication in cetaceans forming matrilineal groups (Ford 1991; Rendell and Whitehead 2003).

6.3 Community-based monitoring

Passive acoustic is a promising way of monitoring narwhals allowing for active involvement of local communities. Scientist in the Arctic are sometimes considered by locals as “ground squirrels” as they “appear suddenly, usually in the summer months, scurry around on the tundra doing who knows-what, and then disappear just as quickly without anyone's knowing exactly what they were up to" (Gearheard and Shirley 2007). The development of research partnerships between universities and northern communities is essential for the long-term sustainability of research in the Arctic (Pearce et al. 2009). Establishing research focus and objectives in partnership greatly improves the quality and relevance of the research. Passive acoustic monitoring is a promising method to integrate scientific research with local needs and involvement. In addition, acoustic methods are compatible with Inuit traditional values since they are non-invasive, do not involve handling of animals and have a low environmental impact.

6.4 Narwhal research

The future of narwhal research should involve more *in situ* research. Most of the recent research on narwhals entails a minimum of time spent in the field (e.g. Dietz et al. 2008; Heide-Jørgensen et al. 2008; Richard et al. 2010; Westdal et al. 2010). For example, with satellite tags, the only time spent in the field is for the instrumentation of the animal during which behavioural observation are biased since the animal is experiencing stressful conditions. Similarly to major advances in primatology that were achieved through long-term observation of primates in the wild (Cheney et al. 1987), many breakthroughs in cetology have been achieved through observing wild cetaceans (e.g. Rendell and Whitehead 2001). In addition, the use of non-invasive techniques was central to major advances in cetology (Payne and McVay 1971; Ford 1991). For example, photo-identification methods have allowed the delineation of several cetacean societies (Mann et al. 2000) and the use of passive acoustic have let to the discoveries of culture in whales and dolphins (Rendell and Whitehead 2001). Methods for photo-identification of narwhals have been recently developed, which open the examination of several new research questions (Auger-Méthé 2008). For instance, a natural next step for this thesis involves getting better insight into the stability of narwhal groups through mark-recapture methods. When applied to narwhal research, new technological and statistical approaches to the study of animal behaviour in the wild are likely to advance our understanding of this unique whale and of cetaceans in general.

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