SOCIAL STRUCTURE OF THE PILOT WHALES (*GLOBICEPHALA MELAS*) OFF CAPE BRETON, NOVA SCOTIA, CANADA

by

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I dedicate this thesis to my grandparents:

To my grandma Rosalina, for helping me understand the value of kindness.

To my grandpa Gualdino, for making me believe I could do whatever I put my heart into.

TABLE OF CONTENTS

LIST OF TABLES ..... **viii**

LIST OF FIGURES ..... **x**

ABSTRACT ..... **xii**

LIST OF ABBREVIATIONS AND SYMBOLS USED ..... **xiii**

ACKNOWLEDGEMENTS ..... **xvi**

CHAPTER 1: INTRODUCTION **1**

1.1 WHY DO SOME ANIMALS LIVE IN GROUPS? 1

1.2 SOCIAL STRUCTURE 1

1.3 CETACEAN SOCIAL STRUCTURE 4

1.4 WHAT AFFECTS SOCIAL STRUCTURE 5

1.5 SOCIAL STRUCTURE AND ALLOCARE 7

1.6 PILOT WHALES 10

1.6.1. Life history *10*

1.6.2 Ecology *11*

1.6.4 Distribution *12*

1.6.7 Social structure *12*

1.7 OBJECTIVES 14

CHAPTER 2: SOCIAL STRUCTURE OF PILOT WHALES OFF NORTHERN CAPE BRETON ISLAND, NOVA SCOTIA **16**

2.1 INTRODUCTION 16

2.2 METHODS 18

2.2.1 Behavioral and Photographic Data collection *18*

2.2.1 Photoidentification *20*

2.2.2 Biopsy sampling *20*

2.2.3 Molecular analysis *21*

2.2.4 What is the turnover in this population? *22*

2.2.5 How stable are relationships in this population? *22*

2.2.6 Are there stable long-term social units in the population? *23*

2.2.7 What is the size and sex-ratio of units? *24*

2.2.8 Is there within-unit structure? *25*

2.2.9 How do units relate to one another? *25*

2.3 RESULTS 26

2.3.1 Photoidentification and molecular sexing *26*

2.3.2 What is the turnover in this population? *27*

2.3.3 How stable are relationships in this population? *30*

2.3.4 Are there stable long-term social units in the population? *36*

2.3.5 What is the size and sex-ratio of units? *38*

2.3.6 Is there within-unit structure? *38*

2.3.7 How do units relate to one another? *40*

2.4 DISCUSSION 41

2.4.1 How do individuals associate with each other and are units the best way to describe it? *41*

2.4.2 How are units structured and how do they associate with each other? *46*

CHAPTER 3: THE INFLUENCE OF BEHAVIOURAL STATE ON PILOT WHALE (*GLOBICEPHALA MELAS*) SOCIAL STRUCTURE 49

3.1 INTRODUCTION 49

3.2 METHODS 51

3.2.1 Behavioural and Photographic Data collection *51*

3.2.2 Photo Identification *53*

3.2.3 Do associations between individuals vary with behavioural state? *53*

3.2.4 Are associations between units affected by behavioural state? *55*

3.3 RESULTS 55

3.3.1 Do associations among individuals vary with behavioural state? *58*

3.3.2 Are associations between units affected by behavioural state? *60*

Are association preferences between units changing with different behavioural states? *61*

3.4. DISCUSSION 63

3.4.1 Limitations *63*

3.4.2 Do associations among individuals vary with behavioural state? *64*

3.4.3 Are associations between units affected by behavioural state? *66*

3.4.4. Conclusion *68*

CHAPTER 4: KINSHIP PATTERNS OF LONG FINNED PILOT WHALE S (*GLOBICEPHALA MELAS*) OFF NORTHERN CAPE BRETON ISLAND, NOVA SCOTIA **69**

4.1. INTRODUCTION 69

4.2. METHODS 71

4.2.1 Biopsy sampling *71*

4.2.2 Photographic data collection and photoidentification *73*

4.2.3 Sexing individuals *74*

4.2.4 Estimating relatedness *74*

4.2.5 Comparison of kinship and association patterns *76*

4.2.6 Analysis of mitochondrial DNA *78*

4.3. RESULTS 79

4.3.1 Molecular data *79*

4.3.2 Comparison of kinship and association patterns *82*

4.3.3 Are units comprised of one or more matrilines? *85*

4.4. DISCUSSION 85

4.4.1 Comparison of kinship and association patterns *85*

4.4.2 Are units comprised of one or more matrilines? *88*

CHAPTER 5: USING PHOTOGRAPHY TO DETERMINE SEX IN PILOT WHALES (GLOBICEPHALA MELAS) IS NOT POSSIBLE: MALES AND FEMALES HAVE SIMILAR DORSAL FINS **90**

CHAPTER 6: CHARACTERIZING ALLOPARENTAL CARE IN THE PILOT WHALE POPULATION THAT SUMMERS OFF CAPE BRETON **101**

6.1 INTRODUCTION 101

6.2 METHODS 104

6.2.1 Data collection *104*

6.2.2 Identification of Closest Companions *105*

6.2.3 Identification of calves *106*

6.2.4 Characterizing alloparental care *108*

6.2.5 Characterizing alloparents *110*

6.3 RESULTS 111

6.3.1 Data collection *111*

6.3.2 Identification of calves and closest companions *111*

6.3.3 Characterizing alloparental care *112*

6.3.4 Characterizing alloparents *118*

6.4 DISCUSSION 120

6.4.1 Methodological limitations *120*

6.4.2 Characterizing alloparental care *121*

6.4.3 Characterizing alloparents *123*

6.4.4 Why does alloparental care happen? *124*

6.4.5 Conclusion *126*

CHAPTER 7: CONCLUSION **128**

OVERVIEW OF RESULTS 129

Chapter 2 – Pilot whales form social units, which break apart when they become too large *129*

Chapter 3 – Individuals show association preferences according to behavioural state *129*

Chapter 4 – Bisexual natal phylopatry is not the most likely dispersal pattern for this population *130*

Chapter 5 – Dorsal fin shape is not correlated with the pilot whales' gender *131*

Chapter 6 – Alloparental care is common in this population *131*

PILOT WHALE SOCIALITY 132

IMPORTANCE OF RESEARCH AND FUTURE DIRECTIONS 134

REFERENCES 136

APPENDICES 151

LIST OF TABLES

Table 2.1 – Fit of social models to the standardized lagged association rate for the population. τ, time in days; QAIC, quasi-Akaike information criterion; ΔQAIC, variation of QAIC between the current model and the best fit; g, SLAR. The best model with lowest QAIC is marked in bold. *31*

Table 2.2 - Fit of social models to the standardized lagged association rate for the associations between Females (FF), from Female to Male (F-M) and Male to Female (M-F). τ, time in days; QAIC, quasi-Akaike information criterion; ΔQAIC, variation of QAIC between the current model and the best fit; g, SLAR. The best model with lowest QAIC is marked in bold. *34*

Table 2.3 - Associations between units. S – Estimate of social differentiation using the maximum likelihood method. S < 0.3 – homogeneous society, S > 0.5 – well differentiated society, S > 2.0 – extremely differentiated society. SE – Standard Error. *40*

Table 2.8 - Comparison between units identified by Ottensmeyer and Whitehead (2003) with data collected between 1998 and 2000, and this study with data collected from 1998 to 2011. Units were calculated using the original protocol from Christal et al. (1998) between 1998 and 2000, and the modified protocol from 1998 to 2011. ..... *45*

Table 3.1 – Observations under each behavioural state. Encounters – number of encounters where only one behavioural state was recorded; Identifications – total number of distinct individuals or units identified per behavioural state. *56*

Table 3.2 - Membership (well-marked individuals) in social units which were defined using a protocol modified from Christal et al. (1998). *57*

Table 3.3 - Results for associations between pairs of individuals. Mark rate for the population 0.51. Sampling period: day; group association: encounter. Estimate of social differentiation using the maximum likelihood method. S < 0.3 – homogeneous society, S > 0.5 – well differentiated society, S > 2.0 – extremely differentiated society. Average gregariousness is calculated using individual gregariousness, the sum of an individual's association indices, for the population. Associations are considered non-random when p-value of CV < 0.01, and are marked in bold. *58*

Table 3.4 –Associations between pairs of units. Sampling period: day; group association: encounter. Estimate of social differentiation using the maximum likelihood method. 62

Table 4.1 - Sampled individuals affiliated with units. Sex was determined using a multiplex PCR of two primer pairs, ZFX/ZFY and SRY. Haplotype was determined using a consensus region of 200 bp of a variable region of mtDNA.....80

Table 4.2 – Comparison of haplotypes found in individuals affiliated to units and previously published research in the North Atlantic.....82

Table 5.1 - Summary of results from the Principal Component Analysis on the coefficients of the Elliptic Fourier descriptors. 96

Table 6.1 - Summary of calf types identified in 2009, 2010, and 2011. Calves "Analyzed" refers to calves seen in more than one encounter with an identifiable CC, therefore able to be used in this study. 112

Table 6.2 - Number of calves in relation to number of encounters and number of CCs they were identified with. Data set for 2009-2011 with only identifiable CCs accounted for. 113

Table 6.3 - Maternity test adapted from Grellier et al. (2003) for 2009, 2010, and 2011. Significant test results are marked in bold ($z_{0.05}$ = 1.64). A1 High: CC with the highest simple ratio index (SI_1) with the calf; A2 High, CC with the second highest simple ratio index with the calf; n1, total number of times A1 High and calf were seen together; n2, total number of times A2 High and calf were seen together; z, unicaudal z-test result. Only cases with enough resightings to apply the method are shown.....114

Table 6.4 - Closest companions identified in several years, and in which role they were identified in. CM – confirmed mother, CC - closest companion (when mother was not confirmed),or A – Alloparent (CC when the mother is known as another individual) 116

Table 6.5 - Closest companions (CCs) that were affiliated with a unit or genetically sexed 119

LIST OF FIGURES

Figure 2.1 – Lagged Identification Rate (LIR). Error bars were calculated using the jackknife technique. The maximum-likelihood model that performed best with the SLAR is represented with a solid line. The maximum-likelihood best fit model is represented with a dashed line. 27

Figure 2.2 – Lagged Identification Rate (LIR) for individuals of different sexes. Males are represented by empty circles, females by full diamonds. Error bars were calculated using the jackknife technique. The maximum-likelihood best fit model is represented with a solid line for males and dashed for females. 29

Figure 2.3 - Standardized lagged association rate (SLAR). Error bars were calculated using the temporal jackknife technique. The null association rate represents the theoretical SLAR if individuals associated randomly. The maximum-likelihood best fit model represents casual acquaintances. 30

Figure 2.4 – Standardized lagged association rate (SLAR) for individuals of different sexes. MF: Male to Female, FF: Female to Female, FM: Female to Male. Error bars were calculated using the temporal jackknife technique. The null association rate represents the theoretical SLAR if individuals associated randomly. The maximum-likelihood best fit models are noted for each sex. 33

Figure 2.5 –Network of individuals seen more than 20 times during the sampling period, with CoA ≥0.1. Different colours represent different units (individuals not assigned to a unit are marked as NaN) and different symbols sexes. Circles - non identified sex, Squares - Females, Triangles – Males 37

Figure 2.6 – Network diagrams for the K complex across different years of the study. Modularity was calculated using Newman's (2006) eigenvector method. 39

Figure 3.1 – Plots comparing the HWI of dyads of individuals between behavioural states. The diagonal represents the case where dyads would be expected to fall if behavioural state had no relationship with strength of association.....60

Figure 3.2 – Plots comparing the HWI of dyads of units between behavioural states. The diagonal represents the case where dyads would be expected to fall if behavioural state had no relationship with strength of association.....63

Figure 4.1 – Distribution of estimated relatedness between pairs of individuals. Relatedness was calculated using Wang's (2007) estimator.....81

Figure 4.2 – Distribution of estimated relatedness between pairs of females within and between units. Relatedness was calculated using Wang's (2007) estimator. N=14 pairs 83

Figure 4.3 – Distribution of estimated relatedness between pairs of different sexes within and between units. Relatedness was calculated using Wang's (2007) estimator. N=574 pairs. 84

Figure 5.1 - Photograph of a pilot whale dorsal fin, illustrating the line that runs from the anterior to the posterior insertion point of the dorsal fin.....92

Figure 5.2 - Examples of saddle patch density. Saddle patches are within the rectangle. The left most picture represents a dense saddle patch, the center picture a medium saddle patch and the right most picture a sparse saddle patch. 95

Figure 5.3 - Dorsal fins of sampled individuals. Males are on the inside of the polygon, females on the outside.....97

Figure 5.4 - Variation in dorsal fin shape, explained by the first two components of the PCA. PC1 represents the first component and PC2 the second component. Mean represents the mean shape for the component, -2 SD the mean shape minus standard deviation, and +2 SD the mean plus standard deviation. The leftmost sketch is the overlap of shapes for each component.....98

Figure 5.5 - Saddle patch density of males (M) and females (F) in the sampled population. 98

Figure 5.6 - Frequency of the number of mark points (MPs) possessed by males (M) and females (F) in the sampled population. 100

Figure 6.1 - Identification of calf age using photography. NB - Newborn, FF - Foetal Fold, GC - Grey Calf .108

ABSTRACT

The long-finned pilot whale (*Globicephala melas*) is an intensely social species. I describe the social structure of the population off Cape Breton, Nova Scotia, using 12 years of individual association and behavioural data, adding molecular analyses and investigating alloparental care. Previous studies on the social structure of the species point to pilot whales being organized into social units that associate in labile groups. Units were thought to be matrilineal and comprised of both males and females, with individuals showing bisexual phylopatry. So, social structure for this species was thought to be similar to that of 'resident' killer whales (*Orcinus orca*) in the northwest Pacific. The results of my research suggest a somewhat different structure.

I confirmed that pilot whales live in social units comprised of both sexes. I found 21 units in this population, with an average size of 7 individuals. One of the units, the K complex, became very large and started breaking apart over the duration of the study. I found that, over and above membership of the same unit, behavioural state influences how individuals associate with each other.

Genetic analysis of microsatellites found no greater relatedness of individuals within the same unit rather than in different units. It seems that unit membership is more fluid than previously thought. I could not assess matrilineality using analysis of mitochondrial DNA due to low haplotype diversity, with only 3 haplotypes identified.

I tried to create a model to sex individuals based on dorsal fin shape and photo identification characteristics, but found no correlation between any of those identifiers and individuals' gender.

Alloparental care is common in this population, with more than half the calves being cared for by non-parents. Both sexes care for calves, and carers and calves can be from different social units. There were no cases of reciprocal care, although it is possible reciprocity is occurring outside of the studied 3-year time frame.

In conclusion, this population showed some features of social structure that were expected, including the existence of social units, their size and the prevalence of alloparental care. The study also highlighted aspects that were not expected, such as dispersal between units shown by the microsatellite data and a broad distribution of potential alloparental carers for a calf.

LIST OF ABBREVIATIONS AND SYMBOLS USED

A – Alloparent

aF – Age at maturity for females

aM – Age at maturity for males

b – Birth rate per mature female per year at low population size

bp – Base pairs

C – Celsius

CA – Casual acquaintance

CC – Closest companion

cm – Centimeters

CM – Confirmed mother

CoA – Coefficient of Association

d – Days

DFO – Department of Fisheries and Oceans, Canada

DMSO – Dimethylsulphoxide

EDTA – Ethylenediaminetetraacetic acid

EFD – Elliptical Fourier Description

F – Female

hr – Hour

HWI – Half Weight Index

ID – identification

K – Rough equilibrium population size

Kg – Kilograms

Km – Kilometers

LIR – Lagged Identification Rate

m – Meters

M – Male

mF – Mortality per year for females

$MgCl_2$ – Magnesium chloride

mL – Millilitre

mM – Mortality per year for males

MP – Mark Points

mtDNA – Mitochondrial DNA

ng - Nanograms

PCR – Polymeras Chain Reaction

PM – Possible mother

Q – Quality rating

QAIC – Quasi-Akaike Information Criterion

s – Seconds

S – Social differentiation

SD – Standard Deviation

SE – Standard Error

SI – Simple Index

SLAR – Standardized Lagged Association Rate

T – Number of years of permutation

u – Mean unit size

yr – Year

μL – Microliter

τ – Time in days

σ – SE of relatedness estimate

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CHAPTER 1: INTRODUCTION

1.1 WHY DO SOME ANIMALS LIVE IN GROUPS?

While some animals lead fairly solitary lives, others live in groups. Living in a group has benefits and costs. For group living to persist, benefits for the individual need to outweigh costs. Costs can be caused by competition between group members for resources or an increased probability of receiving parasites and diseases, while benefits are related to increased resource acquisition rates and social learning, and diminished predation (Gowans *et al.* 2007). Living in a group might also decrease predation and increase access to resources (Alexander 1974).

1.2 SOCIAL STRUCTURE

Social structure can be defined in different ways (Whitehead 2008). Definitions can be ethological (*e.g.* Hinde 1976; Kappeler and van Schaik 2002), based on behavioural-ecological concepts (*e.g.* Wilson 1971; Michener 1974), on mating systems (*e.g.* Emlen and Oring 1977; Clutton-Brock 1989), or social niches (Flack *et al.* 2006). Different definitions are usually applied to different *taxa*. Definitions of social structure have also evolved over time, influenced by different areas of research. Concepts from anthropology, human psychology (Roney and Maestripieri 2003), and social network theory (Flack *et al.* 2006) have been incorporated.

Behavioural-ecology definitions of social structure are mostly used in studies of social insects. The most used social definitions are from the Michener-Wilson (M-W) framework (Wilson 1971; Michener 1974). This framework was built using a small taxonomic range as a base, the Hymenoptera and Isoptera. There are several levels in this framework, according to the criteria:

- Solitary – don't show any of the traits listed below;
- Subsocial – adults care for larvae or nymphs for a period of time;

- Communal – members of the same generation aggregate but do not cooperate in brood care;
- Quasisocial – as Communal, but members cooperate in brood care;
- Semisocial – as Quasisocial, but reproductive division of labour also occurs;
- Eusocial – as Semisocial, but with generation overlap and offspring assist their parents.

There are also two general terms that are used in this framework. *Presocial* refers to any level that is not Eusocial, and *Parasocial* refers to all states in which members of the same generation interact. There is much debate about the definition of eusocial (Costa and Fitzgerald 2005), with eusociality currently being used in two very different contexts (Lacey and Sherman 2005). On one hand it's been used as a general definition capable of uniting very different taxa, where alloparental care and reproductive skew exist (Sherman *et al.* 1995; Lacey and Sherman 2005), while on the other hand, it's been used to separate different societies based on the presence/absence of castes (Crespi and Yanega 1995; Crespi 2005) or phylogenetic histories (Wcislo 2005).

In species that mostly form aggregations to breed, like pinnipeds and amphibians, social structure studies are focused on mating behaviour and classified according to mating systems. These are classified according to ecological variables, which influence the intensity of sexual selection and, in turn, influence the form of mating systems. In birds, females are free to choose mating partners based on their phenotype or territory quality. Their mating systems can be divided in three classes, according to how many mates each sex has during a breeding season: *monogamy*, when each sex only takes on one mate; *polygyny*, when males mate with several females; and *polyandry*, when females mate with several males (Emlen and Oring 1977). For mammals, the framework differs, since females do not usually disperse too far from their natal

area. Female groups tend to stay together over several generations and males impose themselves over pre-existing groups of females (Clutton-Brock 1989). To the three basic mating systems described by Emlen and Oring (1977), one more is added (Clutton-Brock 1989). *Promiscuity* happens when males or females mate with different mates during the breeding season and then show no bond with them after the mating has occurred. Females also present two distinct type of monogamy: *long-term monogamy*, when mating bonds are exclusive with one male through most of the females' lifetime, or *serial monogamy* when the mating bonds are exclusive to one male during one or more breeding season, but a female can have different partners in the course of a lifetime.

A new approach to social structure, based on social network theory, has emerged in recent years. Social organization is defined as the union of social niches. Social niches are the behavioural connections of an individual across several, overlapping social networks. Instead of focusing on dyadic relationships, this definitions focus on individual characteristics (Flack *et al.* 2006). This relative new approach has not been used very much, but as social network theory becomes more commonly applied in studies of sociality it will probably become more widespread. It seems to have potential to become widely used in sociality studies (Whitehead 2008).

The ethological approach is used in some studies of the social structure of birds and mammals, particulary primates (*e.g.* Kappeler and van Schaik 2002) and cetaceans (*e.g.* Ottensmeyer and Whitehead 2003). Hinde's (1976) framework is commonly used, particularly in marine mammal studies. This framework is comprised of interactions, relationships and surface structure (*i.e.* social structure (Whitehead 2008)). Hinde (1976) considered interactions directed behaviours from one individual to another, which are limited in time. Interactions are defined in terms of

what individuals are doing together – content – and how they do it – quality. Relationships integrate the interactions between pairs of individuals adding the patterns associated with time and previous interactions. Social structure deals with the same three features – pattern, content and quality – but of relationships within a population (Hinde 1976). Hinde (1976) also identified factors that can influence the different levels of the framework, such as psychological and physiological variables, age and sex classes, and kinship.

1.3 CETACEAN SOCIAL STRUCTURE

Many cetaceans live in groups, and their social structures contain elements that vary from fluid to stable. An example of a largely fluid social structure is the fission-fusion society of bottlenose dolphins (*Tursiops* sp.), where affiliations between individuals in groups changes from minutes to hours, although some pairs of males can stay together over a number of years (Connor *et al.* 2000, Parsons *et al.* 2003). How individuals associate is influenced by several factors, such as age, sex, relatedness, reproductive condition and the formation of coalitions (Connor *et al.* 1992; Wells and Scott 1994; Connor and Whitehead 2005; Whitehead and Connor 2005). Risso's dolphins (*Grampus griseus*) display a social structure that is less fluid than that of bottlenose dolphins, but not completely stable. In these societies, individuals can live in stable pairs, which belong to larger units, or simply not show strong long term associations with others (Hartman *et al.* 2008). The two best known cases for stable societies in cetaceans are sperm whales (*Physeter macrocephalus*) and "resident" orcas (*Orcinus orca*) in the North East Pacific, which have a matrilineal basis. Sperm whales live in units comprised of female and their young. When they reach adulthood, females stay with their unit but males do not (Whitehead 2003; Gero *et al.* 2007). In "resident" orca societies, both males and females stay with their natal pods, which are sets of individuals that spend more than half of their time together (Bigg *et al.* 1990). This is one of the few known cases of bisexual natal phylopatry.

1.4 WHAT AFFECTS SOCIAL STRUCTURE

For cetaceans, group living is influenced by specific costs and benefits. The benefits are related to predator protection, parasites and prey availability; while costs are related to travel, feeding competition and phylopatry (Connor 2000).

The main predators for cetaceans are killer whales, sharks and, in some cases, humans. Living in a group might increase protection from predators, mainly by *dilution* – a larger group means that each individual is less likely to be attacked. It might work similarly with parasites. And many species of whales and dolphins work cooperatively to find and trap prey (Connor 2000).

The extent to which animals migrate or become resident is broadly related to resource availability. According to Gowans *et al.* (2007), when resources are stable and predictable over time, delphinid populations tend to remain resident, while when resources are variable they tend to increase their range. Resources are distributed in a 3D environment, which makes it unlikely that any individual can exclude others from accessing those resources. In this case scramble-type competition prevails, and equal resource sharing is promoted, which influences group size.

Resource availability also plays a role in stabilizing social structure. There are two populations of resident bottlenose dolphins that have more stable societies than is general for this species: Doubtful Sound in New Zealand (Lusseau *et al.* 2003) and the Sado estuary in Portugal (Augusto *et al.* 2012). Both populations are small and phylopatric, but are influenced by different resource availability. In Doubtful Sound the complex fjord habitat makes resource distribution patchy and difficult for individuals to access, promoting phylopatry and long lasting associations between individuals and knowledge sharing to assist access to the resources (Lusseau *et al.* 2003). In the Sado estuary, on the other hand, the high resource availability compared with the outlying areas

promotes not only phylopatry, but reduces competition between individuals, promoting large groups with high associations between individuals (Augusto *et al.* 2012).

Anthropogenic pressures can also affect animal social structure, as may be the case with sperm whales. The Caribbean sperm whale units typically comprise only one matriline (Gero *et al.* 2007), while in the Pacific units usually contain two or more (Whitehead 2003). This difference is thought to be related to whaling pressure (Whitehead *et al.* 2012). While the Caribbean whales were not intensively whaled by modern whalers, the Pacific sperms suffered massive population losses due to whaling efforts. These losses might have reduced units to such small sizes that fusions occurred to maintain social services, such as predator defense, leading to multi-matrilineal units.

Social structure is also affected by sex-biased dispersal. In birds and mammals, females are usually phylopatric, tending to stay with their group, while males disperse (Greenwood 1980). But for most species, even the phylopatric sex disperses in small numbers (Handley and Perrin 2007). Sex-biased dispersal is largely influenced by two selective pressures: mating systems and inbreeding avoidance strategies. For instance, male dispersal is expected in female-defense systems, since male competition is usually higher than the limiting resource of female availability. In this case, males tend to disperse to avoid kin competition. In the case of inbreeding avoidance, if one sex disperses for this purpose, the other sex tends to remain phylopatric since the risk of inbreeding is minimized (Handley and Perrin 2007).

In rare cases both sexes stay with their natal groups – bisexual natal phylopatry. For this to happen selective pressures to remain in the group have to outweigh the pressures to disperse. This has to be the case for both sexes. The selective pressures that favour dispersal are resource availability, kin competition and inbreeding avoidance (as mentioned above), and pressures to

stay include increased risk for mortality outside the natal group, familiarity with the natal area and kin cooperation (Handley and Perrin 2007). So, for both sexes not to disperse, pressures to stay have to be high: individuals that disperse may have lower fitness than the ones that stay; individuals may explore the resources of their environment in a complex way, which means familiarity with the natal area increases survival; and/or kin cooperation between individuals in the natal group may grant an advantage, especially in social species (Handley and Perrin 2007). Pressures to disperse have to be weak or be avoided: resources in the group's home range must support individuals; the resource availability and/or kin cooperation should be enough to outweigh kin competition; and kin recognition mechanisms and available non-kin in the group's range should be enough to avoid inbreeding depression.

1.5 SOCIAL STRUCTURE AND ALLOCARE

One fairly common behavioural pattern associated with mammal social structure is allocaring. Allocare can be defined as a non-parent helping to raise young (Woodroffe and Vincent 1994). These individuals are referred to as allocarers, and can be siblings, other relatives or even individuals unrelated to the young (Kleiman and Malcolm 1981; Riedman 1982; Jennions and MacDonald 1994; Woodroffe and Vincent 1994). Allocare changes the patterns of how individuals interact with each other and, therefore, has the potential to be one of the factors that shape social structure.

Allocare has costs and benefits for the allocarer. These costs vary in a continuum. In some cases it is not very costly, as with elephants (*Loxodonta* sp., Lee and Moss 1986; Lee 1987) and sperm whales (Whitehead 1996). Elephants allocare by comforting calves in distress (Lee 1987), which does not take them much time from doing other activities, such as foraging. Sperm whales babysitters change their dive synchrony to stay with calf at the surface, but it does not seem to

affect their feeding rates, so it should not be very costly (Whitehead 1996). In other cases the cost is higher, as with meerkats (*Suricata suricatta*, Dooland and MacDonald 1996, 1997; Clutton-Brock *et al.* 1998). When meerkats are babysitting, they usually do not eat, and may lose up to 2% body weight during a babysitting day. If, instead of babysitting, individuals were foraging they would be able to maintain, or even gain, body weight (Clutton-Brock *et al.* 2001). In rare cases the cost is extremely high, with individuals adopting unrelated young (*e.g.* red howler monkey, *Alouatta seniculus*, Agoramoorthy and Rudran 1992; Indo-Pacific bottlenose dolphin, *Tursiops aduncus*, Sakai *et al.* 2016).

In the case of negligible costs, allocare can evolve as a by-product of the evolution of social structure. In most cases allocare does present a cost, so an adaptive mechanism has to be in place for it to evolve. Mechanisms can be divided in to two types of system (Wright 1997, 1999): *investment systems*, where the allocarers help young with the expectation that the young will help them when they are older, which include reciprocal altruism, kin selection and group augmentation; and *signaling systems*, where allocare is performed as a signal to other individuals in the population; these include “pay to stay” systems and social prestige.

Reciprocal altruism happens when the allocarer performs an action that is detrimental to its own inclusive fitness, but beneficial to another individual. There is the expectation that the action will be reciprocated, even though reciprocity does not have to be instantaneous (Trivers 1971; Axelrod and Hamilton 1981). This mechanism is thought to be in play with African elephant allocare (Lee 1987). The majority of allocarers in elephants are juvenile females from the same unit. Since mother-daughter bonds stay strong through elephants’ lives, younger weaned females tend to live in close proximity to their mothers in the same unit and consequently spend time with their siblings. A female that has been allocared for by a sibling will be between 5 to 10

years old when that female sibling has her own calf, and will allocare for it, displaying delayed reciprocity (Lee, 1987). With kin selection the allocarer helps its kin, expecting that it will increase the probability to pass on their common genes to the next generations (Hamilton 1964a, b). This is thought to be one of the mechanisms involved in sperm whale allocare (Gero *et al.* 2013), with units being matrilineal and preferred babysitters being related to the mother. With group augmentation, the allocarers help with the expectation that young will survive and stay in the same group. This maintains, or increases, the benefits of living in a well-functioning group (Brown 1987; Kokko *et al.* 2001). Meerkats are an example of this mechanism in play (Clutton-Brock 2002). In this species group size is related to success in foraging, breeding, growth and overall survival of group members. Larger groups do considerably better than smaller groups on all accounts. In pay-to-stay systems, allocarers are subordinate to a dominant reproducing pair, and allocare is a way to pay rent to stay in the group (Gaston 1978; Kokko *et al.* 2002). Pay to stay is mostly common in fish (*e.g.* Balshine-Earn et al 1998; Bergmüller *et al.* 2005), but has also been hypothesized in moustached tamarins (*Saguinus mystax*; Löttker *et al.* 2007). In this species grooming is used as a way to encourage individuals to stay in the group and, ultimately, pay rent by helping care for the young. Social prestige happens when a male takes handicap (*i.e.* does an action that is costly to its fitness) to advertise that it has a high mating quality or fitness (Zahavi 1975, 1995). In this particular case the handicap would be helping care for young the male is not related to. This model is based on the behaviour of Arabian babblers (*Turdoides squamiceps*), but has been questioned since it has been presented (Wright 1999). There have not been any documented cases of this evolutionary pathway for allocare in mammals.

1.6 PILOT WHALES

Long finned pilot whales (*Globicephala melas*), which I will be referring to as pilot whales from here on, are sexually dimorphic medium-sized delphinids. The only other member of their genus is the short finned pilot whale (*G. macrorhynchus*), with a more temperate distribution. Adult males can reach up to 6.1 m while females can reach up to 4.7 m (Sergeant 1962). They are black or dark grey in colour, with lighter coloured areas, which vary from white to cream: an anchor shaped patch on their throat, which extends ventrally; a post-orbital eye blaze; and a saddle patch on their back, posterior to the dorsal fin.They have a distinctive bulbous melon, which was the source of their common name, pothead whales, in Newfoundland (Sergeant 1962). Their dorsal fin is located forward in the body, and is larger for males since it grows isometrically with body size (Bloch *et al.* 1993). Dorsal fin shape might also be different between sexes, with males showing a thicker edge, a more rounded contour and a more rounded tip (Sergeant 1962).

1.6.1. Life history

Pilot whale females can live up to 60 years, while males usually only live up to 45 years (Kasuya *et al.* 1988; Bloch *et al.* 1993). There has been some evidence that females outlive their reproductive potential (Sargeant 1962), although a long post-reproductive life span has not been proven. Sexual maturity is achieved at different ages according to sex, and also varies with location. In the western North Atlantic females reach maturity between 6 and 7 years, and males around 12 years (Sargeant 1962). It takes long to reach sexual maturity in east North Atlantic waters, with females reaching maturity at 9 years and males at 17 years (Bloch *et al.* 1993; Desportes *et al.* 1993). The cause for this difference has not been investigated. Mating and calving usually happens during summer, and the gestation period is between 12 and 14 months (Martin and Rothery 1993). Calves are nursed for at least two years (Sargeant 1962), but can stay

close to their mothers for longer than that. Average reproductive cycles vary with location. In western North Atlantic waters average cycles have been estimated to average 3.3 years (Sargeant 1962), while in the eastern North Atlantic an estimated average is 5.1 years (Martin and Rothery 1993).

1.6.2 Ecology

Pilot whales feed mostly on cephalopods, such as the long-finned and short-finned squids (*Loligo pealei* and *Illex illecebrosus*, respectively). They also consume smaller crustaceans and fish, such as Atlantic mackerel (*Scomber scombrus*) and Atlantic cod (*Gadus morhua*) (Sergeant 1962; Desportes and Mouritsen 1993; Abend and Smith 1997; Gannon *et al.* 1997).

Given that pilot whales feed on species that are caught for human consumption, they are sometimes subjected to incidental catches. There are only two current cases of directed fisheries: in Greenland and the Faroe Islands (Taylor *et al.* 2008). Greenland catches are small and opportunistic, while the Faroe catches – grinds or *grindadráp* – are larger and more organized. In the grinds, fishermen drive large groups of whales, sometimes above a hundred individuals, ashore to be slaughtered. The meat is then distributed to the village. The grinds are considered a tradition in the Faroe Islands, although they seem to be diminishing primarily due to mercury and PCB contamination in the whales' meat and blubber, which makes it unfit for safe human consumption. There has also been international pressures to end the grinds over the last decades (Dam and Bloch 2000; Fielding 2011; Singleton 2016).

Pilot whales are also known to strand (*e.g.* Geraci and St. Aubin 1977; Gannon *et al.* 1997; Beatson *et al.* 2007; Bogomolni *et al.* 2010; Gales *et al.* 2012). It has been thought that each mass stranding was composed of related individuals, but in New Zealand strandings can be comprised of several matrilines and unrelated individuals (Oremus *et al.* 2013).

1.6.4 Distribution

Pilot whales show an antitropical distribution in the North Atlantic and Southern Oceans (Olson and Reilly 2002). North and South populations are isolated from each other (Bernard and Reilly 1999). Population sizes in both hemispheres are not well known (Taylor *et al.* 2008), with the North Atlantic having an estimated very roughly 750,000 individuals (Buckland *et al.* 1993). This uncertainty is the main reason they are considered data deficient by the IUCN Red List (Taylor *et al.* 2008). They are found in oceanic waters, restricted seas such as the North Sea and Gulf of Saint Lawrence (Abend and Smith 1999) and coastal waters in the Mediterranean. While most are migratory, the Gibraltar Strait contains both migratory and resident pilot whales (Cañadas and Sagarminaga 2000; Verborgh 2005).

1.6.7 Social structure

Different methodological approaches have been used to understand pilot whale social structure. The first studies date back to the 1990's, (Amos *et al.* 1991; Amos *et al.*1993; Balbuena and Raga 1994; Andersen and Siegismund 1994), using data from the fisheries in the Faroe Islands. Necropsies of grinds allowed biological sampling and the data collected was applied to social structure studies. These were focused on two pods, one with 103 and another with 90 individuals (Amos *et al.* 1991; Amos *et al.* 1993). Results show that pods consist of both male and female individuals, genetically related to each other (Amos *et al.* 1991; Amos *et al.* 1993) and sharing common parasites (Balbuena and Raga 1994). It was also discovered that males do not sire offspring within their own pod (Amos *et al.* 1991; Andersen and Siegismund 1994) and that they associate only briefly with the pod where they fertilize females (Amos *et al.* 1991). These studies pointed at the possibility of pilot whales presenting bisexual natal phylopatry. It was also hypothesized that pods were stable units, where individuals remained together for extended

periods of time. Since it was impossible to determine any patterns of associations across time, the stability of pods in this study was not assessed.

A behavioural approach to this species' social structure was undertaken more recently with the migrant population of pilot whales found off Cape Breton, Canada in the summer (Ottensmeyer and Whitehead 2003). The association analysis revealed that observed groups of about 2-135 individuals are labile structures, that last only hours to days. Groups are comprised of one or more stable units, which are long-term structures. Units are comprised of about 11 to 12 individuals and it has been hypothesized that they are extended matrilines, *i.e.* mothers, their offspring and recent ancestors. Unfortunately, no molecular data on the individuals was collected, rendering it impossible to determine the relationships between individuals, their sexes and the possibility of bisexual natal phylopatry at unit level.

The same behavioural protocol was used to study the resident pilot whales in the Strait of Gibraltar and contiguous waters (de Stephanis *et al.* 2008a), but in this study genetic sexing of individuals was performed. The results show a slightly different social structure than the one found in Cape Breton. Individuals form small units – dubbed *line units* – which vary from 2 to 3 identified individuals. Associations in these line units seem to be constant from ten days up to six years. These are comprised of both males and females, possibly with natal phylopatry, which seem to have characteristic feeding patterns (de Stephanis *et al.* 2008b). There are also units that are formed by consistent aggregations of line units. The social structure for this population includes aggregations of units and line units into pods, which are similar to the groups in Cape Breton. Pods aggregated temporarily to feed or breed, reaching up to 150 individuals in the same area, for less than ten days (de Stephanis *et al.* 2008a).

The major difference between this population and the one off Cape Breton is at the unit level. The smaller size of the line units, in the Gibraltar population, may mean that these represent mother-offspring relationships (de Stephanis *et al.* 2008a) instead of extended matrilines, as is hypothesized in Cape Breton. It is also possible that the units in Gibraltar are larger than was determined, since the presence of unidentified individuals was not taken into account (in the Cape Breton population approximately 66% of individuals were not identifiable using the methods employed by Ottensmeyer and Whitehead (2003)). If this is the case, units may be similar structures in both sites.

Each study of this species shows a slightly different representation of pilot whale social structure. It is possible that social structure varies among populations of the same species (Ottensmeyer and Whitehead 2003), especially when comparing migrant to resident populations, since the ecological pressures differ (Gowans *et al.* 2007). It is also possible that differences between methodological approaches in studying the populations may be the cause. While in the studies of Ottensmeyer and Whitehead (2003) and de Stephanis *et al.* (2008a) the temporal variation of associations could be assessed, in those studies on the Faroese population using grinds it could not. The pods described in the Faeroes could be aggregations of different groups, more similar to communities than units, but the methodology of those studies made that impossible to discern.

1.7 OBJECTIVES

Given the information above, I expect that pilot whale social structure, for the Cape Breton population, comprises units which aggregate to form groups and, on a larger scale, communities. I expect units to comprise extended matrilines, to which individuals are bisexually phylopatric. Knowing that units in Gibraltar are segregated by feeding patterns, I expect to see differential

association of units when they are feeding in comparison to other behavioural states. Considering morphological studies, I hope to be able to differentiate between adult males and females using dorsal fin photos. Finally, given this population's stable social structure, I expect to see young being allocared for. These hypotheses will be tested in the following five data chapters:

Chapter 2 - The social structure of pilot whales off Northern Cape Breton Island, Nova Scotia

Chapter 3 – The influence of behavioural state on pilot whale (*Globicephala melas*) social structure

Chapter 4 – Kinship patterns of long finned pilot whale (*Globicephala melas*) off Northern Cape Breton Island, Nova Scotia

Chapter 5 – Using photography to determine sex in pilot whales (*Globicephala melas*) is not possible: males and females have similar dorsal fins

Chapter 6 – Characterizing alloparental care in the pilot whale population that summers off Cape Breton

CHAPTER 2: SOCIAL STRUCTURE OF PILOT WHALES OFF NORTHERN CAPE BRETON ISLAND, NOVA SCOTIA[1][2][3]

2.1 INTRODUCTION

Social structure can be defined in a variety of ways (Whitehead 2008). Definitions can be ethological (*e.g.* Hinde 1976, Kappeler and van Schaik 2002), based on behavioral-ecological studies (*e.g.* Wilson 1971, Michener 1974), on mating systems (*e.g.* Emlen and Oring 1977, Clutton-Brock 1989) or on social network theory (Flack *et al.* 2006). For this study we defined social structure using Hinde's (1976) three-tier framework (interactions, relationships and social structure). This framework is built upon the interactions between pairs of individuals (dyads). Interactions are defined in terms of what dyads are doing together (content) and how they do it (quality). Relationships integrate the interactions between dyads in terms of content, quality and patterns associated with time and previous interactions. Social structure deals with the same three features but of relationships within a population. This is the most commonly used definition in cetacean studies (*e.g.* Connor *et al.* 2000, Ottensmeyer and Whitehead 2003, Augusto *et al.* 2012, Gero *et al.* 2014). There also may be a feedback loop between individuals and their social system (Kappeler and van Schaik 2002): social structure shapes the individual's behavior, and its behavior influences the population's social structure.

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[1] This chapter has been accepted with major revisions in Behaviour. The full reference is: Augusto, J. F., Frasier, T.R. & Whitehead, H. (2017). Social structure of long finned pilot whales (*Globicephala melas*) off Northern Cape Breton Island, Nova Scotia. Behaviour. DOI 10.1163/1568539X-00003432

[2] Authors' contributions: Joana F. Augusto (JFA), Hal Whitehead (HW): Developed the research idea; JFA collected the behavioural data 2009 onwards and HW contributed with previous data; Timothy R. Frasier (TRF) collected skin biopsies with JFA; JFA analyzed the data with contributions from HW and TRF; JFA wrote the manuscript; HW and TRF contributed with comments and edits on the manuscript; JFA reviewed the manuscript during the peer-review process

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Social structure in group living cetaceans varies from fluid to stable societies. One example of a fluid society is that of some coastal bottlenose dolphins (*Tursiops sp.*). These are found in spatio-temporal communities of up to 100 individuals (Parsons *et al.* 2003) and are organized into fission-fusion societies, characterized rapidly changing associations, but also stable associations between pairs that can last for years (Connor *et al.* 2000). On the opposite end of the spectrum, with stable societies, are sperm whales (*Physeter macrocephalus*) and killer whales (*Orcinus orca*), in which females, and sometimes males, live in stable units that have a matrilineal basis (Bigg *et al.* 1990, Christal *et al.* 1998, Gero *et al.* 2007). Risso's dolphins (*Grampus griseus*) show an intermediate form of social structure: individuals can live associated in pairs, belong to units or simply not have any strong long term associations (Hartman *et al.* 2008).

Long-finned pilot whales (*Globicephala melas*), which we will refer to as pilot whales, are medium-sized delphinids. Their social structure has been studied in three coastal locations; the Faeroes, Cape Breton Island and Gibraltar (Amos *et al.* 1991, 1993, Ottensmeyer and Whitehead 2003, de Stephanis *et al.* 2008a). These studies suggest that the populations in these locations show similar societal structure. In the Faroes groups of animals containing just over 100 individuals, "grinds" were diven ashore together. These grinds contained related individuals of both sexes. It was suggested this was a case of bisexual natal phylopatry (Amos *et al.* 1991, 1993). However, these studies do not provide data on the temporal variation of associations between individuals. The population off Cape Breton has been studied using photoidentification (Ottensmeyer and Whitehead 2003), revealing a society composed of stable units containing about 8 animals. Units interact regularly with each other, forming labile groups. In Ottensmeyer and Whitehead's (2003) study, no information on relatedness was available. The authors hypothesized that units are extended matrilines and that pilot whales show bisexual natal phylopatry to their units, as suggested by Amos *et al.* (1991, 1993). The Gibraltar resident

population social structure is similar in social structure to that in Cape Breton, but on a smaller scale, with small units (2-3 individuals, referred to as line units) that interact forming labile pods (up to 14 individuals). Line units are comprised of both sexes, but no relatedness analysis has been performed (de Stephanis *et al.* 2008a). Social structure of the congeneric and more tropical short-finned pilot whale (*Globicephala macrorhynchus*) seems similar to that of the long-finned pilot whales (Heimlich-Boran 1993, Mahaffy 2012, Alves *et al.* 2013, Servidio 2014, Mahaffy *et al.* 2015).

Here we study the social structure of this pilot whale population in greater depth than previous studies. We had two primary objectives. The first was to confirm that social unit membership explains the greatest part of how individuals associate with each other. The second objective was to determine how units are structured and how they interact with each other. We expect unit size to be comparable with Ottensmeyer and Whitehead's (2003) results, and that units will be comprised of both males and females. We also analyzed within-unit structure, to assess any indications of unit fission.

2.2 METHODS

2.2.1 Behavioral and Photographic Data collection

Data were collected in July and August, from 1998 to 2000 and from 2002 to 2011, from 13-meter whale-watching vessels off the northwest coast of Cape Breton Island, Nova Scotia, Canada. From 1998 to 2000, the vessel departed from Bay St. Lawrence harbor (47°02' N 60°29'W), and from 2002 to 2011 it departed from Pleasant Bay harbor (46° 49' N, 60° 47' W). The harbors are 46 km apart. Up to five trips were conducted daily, lasting a maximum of 2.5 hours each, and covering up to 40 km south to 30 km north of the harbor, and a maximum of 8 km offshore. Trips were only performed when the wind was less than 20 knots.

Usually, two researchers collected behavioral and photographic data on each trip. Behavioral data collected included estimates of group size and number of calves present. The waters was scanned for the presence of pilot whales, and when a group was sighted the vessel approached it slowly and kept parallel to their movement or stayed stationary with the motor on idle or turned off.

Data were collected and organized by encounters using the same protocol over all the study years. Encounters began when a whale was sighted and ended when the vessel had to leave the whale or group by either returning to port or by moving to another group that was more than 200 meters away. Encounters also ended if the group was submerged for more than ten consecutive minutes. All individuals in an encounter were considered to be in the same group. The chain rule was used to estimate group size, meaning each whale within a group has to be less than 200m from another whale. Whales that are farther than 200m away from the boat or too far to reliably estimate group size and behavior were considered distinct groups. Researchers photographed individuals in a group regardless of whether they would be identifiable or not, and strived to not consecutively photograph the same individuals, but rather to cover all adult individuals present. Photographs of both left and right sides of animals were collected whenever possible. Encounters were classified according to photographic coverage (Ottensmeyer and Whitehead 2003): 'coverage = 0' if the number of individuals present exceeded the number of photographs, 'coverage > 0' if the number of photographs exceeded individuals, and 'coverage > 2' if the number of photographs exceeded twice the number of individuals.

2.2.1 Photoidentification

Photoidentification pictures of the dorsal fin area (Auger-Methe and Whitehead 2007) of individuals not identified as calves were collected using a Canon EOS Elan IIe (film) or Canon Rebel G (film) between 1998 and 2003 with a 300mm autofocus lens, and a Canon EOS-10D (digital) or Canon 30D (digital) with a 200mm or 300mm autofocus lens from 2004 onward. Each photograph was quality rated (Q) from 1 to 5 according to the attributes of focus, size, orientation, exposure and percentage of fin visible. Individuals were identified using the number and position of mark points (MP), *i.e.* nicks and internal corners of notches of dorsal fins (Ottensmeyer and Whitehead 2003, Auger-Methe and Whitehead 2007). Photoidentification was performed using Finscan (Araabi *et al.* 2000) on photographs with Q>2 showing dorsal fins with MP>2. We also updated the mark rate of the population, the proportion of individuals with MP>2, to include both film and digital camera data. To do so we calculated how many of the Q > 2 photographs of individuals had MP ≥ 2 (*e.g.*, if there were 50 photographs of individuals with Q>2, but only 25 of them had individuals with MP ≥ 2, the mark rate was 0.50), for both film and digital data.

2.2.2 Biopsy sampling

Tissue was collected by remote biopsy sampling in July and August of 2010 to 2012 off the Pleasant Bay Harbor from a semi-rigid 4.5 meter inflatable zodiac, as in Kowarski *et al.* (2014). Sampling was extended to 2012 due to poor weather conditions and consequent low number of samples collected in 2011. Up to two sampling trips were performed daily in the mornings and evenings. No trips were performed when conditions were above 4 on the Beaufort Scale. Sampling trips covered up to 40 km south to 30 km north of harbor, while remaining less than 8 km offshore.

The collection protocol described in Kowarski *et al.* (2014) was followed. This included scanning possible individuals for identifying marks that could be used to match them to photoidentification database and ensure they were not previously sampled, before the darts were deployed. Two crossbows were used in the sampling. An Excalibur Vixen II crossbow with a draw weight of 68 kg until August 11, 2012; and an Excalibur Apex with a draw weight of 40 kg for the remainder field season. The change in draw weight reduced the damage to the arrows and the force hitting the sampled individuals. Sampling darts were obtained from CETA-DART (Denmark; Palsbøll *et al.* 1991). All sampling protocols were approved by the Saint Mary's University Animal Care Committee, and appropriate permits were obtained from Fisheries and Oceans Canada (DFO).

2.2.3 Molecular analysis

Molecular analyses were used to determine sex. DNA was extracted using the phenol:chloroform extraction method described in Sambrook and Russel (2001) and Wang *et al.* (2008). Sex of individuals was determined using a multiplex PCR of two primer pairs: one that amplifies a ~400 bp portion of the ZFX/ZFY gene (present on both sex chromosomes); and one that amplifies a ~200 bp portion of the SRY gene (only on the Y-chromosome) (Gilson *et al.* 1998). PCR was performed on 20 ng of purified DNA in a 20 µL reaction volume that contained 1X Taq polymerase PCR buffer, 0.2 mM each dNTP, 1.5 mM $MgCl_2$, 0.3 µM of each primer, 0.16 µg/mL BSA, and 0.05 U/µL Taq polymerase (Promega). PCR cycles were performed as follows: the first step at 94°C for 5 min; followed by 30 cycles comprised of denaturation at 94°C for 30 s, annealing at 55°C for 1 min, and extension at 72°C for 1 min. A final extension step was performed at 60°C for 45 min. The PCR products were then separated and visualized using agarose gel electrophoresis in 1.5% agarose gels stained with ethidium bromide.

2.2.4 What is the turnover in this population?

For the following analyses only encounters with 'coverage > 0', photos with Q > 2, and individuals with MP≥2 were used. To determine the turnover pattern of individuals in the population we calculated the Lagged Identification Rates (LIR) (Whitehead 2001) in SOCPROG 2.6 (Whitehead 2009). The LIR analysis estimates the probability that an individual identified in a particular time period is identified again "τ" units of time later, and so indicates demographic changes in use of the study area. To determine if there are demographic differences between the sexes we repeated the analysis for both males and females separately.

2.2.5 How stable are relationships in this population?

Coefficients of association (CoAs) between dyads were calculated using the half-weight index (Cairns and Schwager 1987) in SOCPROG 2.6 (Whitehead 2009).

Sampling periods are days, and individuals are considered associated for the day if they were identified in the same encounter at least once during the day. To model how these associations varied in time, we calculated standardized lagged association rates (SLAR) (Whitehead 1995) in SOCPROG 2.6 (Whitehead 2009) with day as the sampling period, using all identified individuals. For lag τ, this rate estimates the probability that if two individuals, A and B, are associated at a particular time then τ units of time later, a randomly chosen associate of individual A will be B. The SLAR obtained was then compared with theoretical models representing different types of social structure (Whitehead 1995). To assess which model generated values most similar to our data, the quasi-Akaike information criterion (QAIC) was calculated. The model that minimized this criterion was considered the best fit (Whitehead 2007). The fit of the other models was also assessed using differences in QAIC between a model and that of the best fitting model (ΔQAIC). If ΔQAIC is between 0 and 2 there is substantial support for the model, if it is between 4 and 7 it has considerably less support, and if it is larger than 10 it has essentially no support (Burnham

and Anderson 2002). We repeated the analysis for individuals sexed as males and females separately.

To determine whether variation in the association rates with time lag could be explained by the demographically-induced changes in identification rates with time lag we used the model that performed best with the SLAR to create a best fit model for the LIR (full population and different sexes separately), and compared parameters from the models of the two processes. We also determined the best overall fit model as a comparison.

To explore whether associations vary within versus between sexes we used a Mantel test (Mantel 1976, Whitehead 2007) in SOCPROG 2.6 (Whitehead 2009). The null hypothesis states that mean association indices within and between sexes are similar. A SLAR analysis was then used for each pair of sex classes (M-M, F-F, F-M) to examine how the temporal patterns of association differed among the pairs of classes.

To visualize how individuals associate, we used Network analysis in SOCPROG 2.6 (Whitehead 2009) and NetDraw (Borgatti 2002). The nodes in the network are individuals and ties reflect the strength of association—*i.e.* the association index (HWI)—between them. We restricted the network to individuals identified on more than 20 days. In the network diagram, link width is proportional to the HWI for those dyads with CoA > 0.2.

2.2.6 Are there stable long-term social units in the population?

Units are defined as sets of individuals in nearly permanent mutual association, and are comprised of key individuals and their closest companions (CCs). According to the method used by Christal *et al.* (1998) and Ottensmeyer and Whitehead (2003) key individuals are identified on at least three days, each of these sightings separated by at least 30 days. CCs of key individuals are individuals seen on the same day as the key individual during at least two days; these

sightings are also separated by at least 30 days. We used a modification to this method, by increasing the minimum number of days to four for key individuals and to three for CCs. Given the extensive nature of the data spanning more than ten years, parameters had to be stricter (*i.e.*, more demanding conditions for individuals to be considered members of the same unit). This aimed at decreasing the likelihood of including individuals in the same unit with low resightings between years and the likelihood of having unit size inflated by them. In order to identify any temporal changes in the units, we compared when (month and year) individuals in units were seen together.

To test the long term stability of associations within units we analyzed the associations between dyads of individuals identified over at least 6 years. We compared the last sightings of the two individuals to the last sighting of the dyad. Associations were considered stable when the last sighting of the dyad in the same encounter was in the same year as the last sighting of at least one of its individuals.

2.2.7 What is the size and sex-ratio of units?

Given that not all individuals in the population are identifiable and that the number of non-identifiable individuals in each unit might differ, we calculated unit-specific mark rates. For this we used the same method as calculating the mark rate for the population, but restricted to encounters where only the unit in question was identified. This method provides us with a unit-specific mark rate which was then used to scale the number of identifiable animals in each unit to an estimate of its real size. Identification change and recruitment/mortality of individuals is possible in the span of this study. Enumerating all individuals assigned to a unit in any year will then artificially increase its size. To counteract that effect we calculated the average unit size per

year for units identified in more than 3 days during a year. For all units in which more than one individual was sexed we noted how many males and females were identified and sexed.

2.2.8 Is there within-unit structure?

To assess whether there is structure within units we used network analysis to delineate clusters within units by maximizing modularity. Modularity measures how well a network is divided into clusters – sets of individuals that are largely behaviorally self-contained over all relevant time scales, so that nearly all interactions and associations occur within, rather than between, clusters (Newman 2004). Modularity was maximized using Newman's (2006) eigenvector method in SOCPROG 2.6 (Whitehead 2009). Modularity values greater than 0.3 are a good indicator of division in the network.

2.2.9 How do units relate to one another?

When analyzing associations between units we considered three different scenarios: including all units, removing the K complex (Units K, L, N and U), and the K complex separately. For each scenario Gero *et al.*'s (2005) method was followed in SOCPROG 2.6 (Whitehead 2009): we chose three different metrics of association that correspond to increased spatio-temporal coordination: 'day' (members from the different units identified on the same day), 'hour' (identified within the same hour), and 'encounter' (identified in the same encounter). We used three sampling periods: 'year', 'day', and 'hour' that focus on different aspects of social structure. A 'year' sampling period informs us of long-term associations between units; a 'day' sampling period reflects our sampling process of working in daylight hours; and an 'hour' sampling period approximates the maximum time we have spent in an encounter in the field, which can last between 5 and 40 minutes. Combinations of when sampling period is smaller or equals the metric were removed from the analysis. Each combination of sampling period and metric was subjected to a permutation test to examine the hypothesis of randomness of

associations (Bejder *et al.* 1998, with modifications described by Whitehead *et al.* 2005). Social differentiation was then calculated (Whitehead 2008). Social differentiation is estimated by the coefficient of variation (CV) of the true association indices. It reflects how varied the social system is: homogenous (below about 0.3), well differentiated (above 0.5) and extremely well-differentiated (above 2). Associations between units were visualized using network diagrams.

2.3 RESULTS

2.3.1 Photoidentification and molecular sexing

There were 1231 individuals with MP ≥ 2 identified on 485 days from Q > 2 photos. The mean number of days that these individuals were identified was 5.6 (range 1-66). Reidentification rates fell after about 3 years (Figure **2**.**1**). The mark rate for film is 0.48, while for digital data is 0.54. Overall, the updated mark rate for this population was 0.51, so 51% of the population was identifiable. A total of 79 individuals were sexed, 75 of which were photoidentified. Of these, 32 were females and 43 were males.

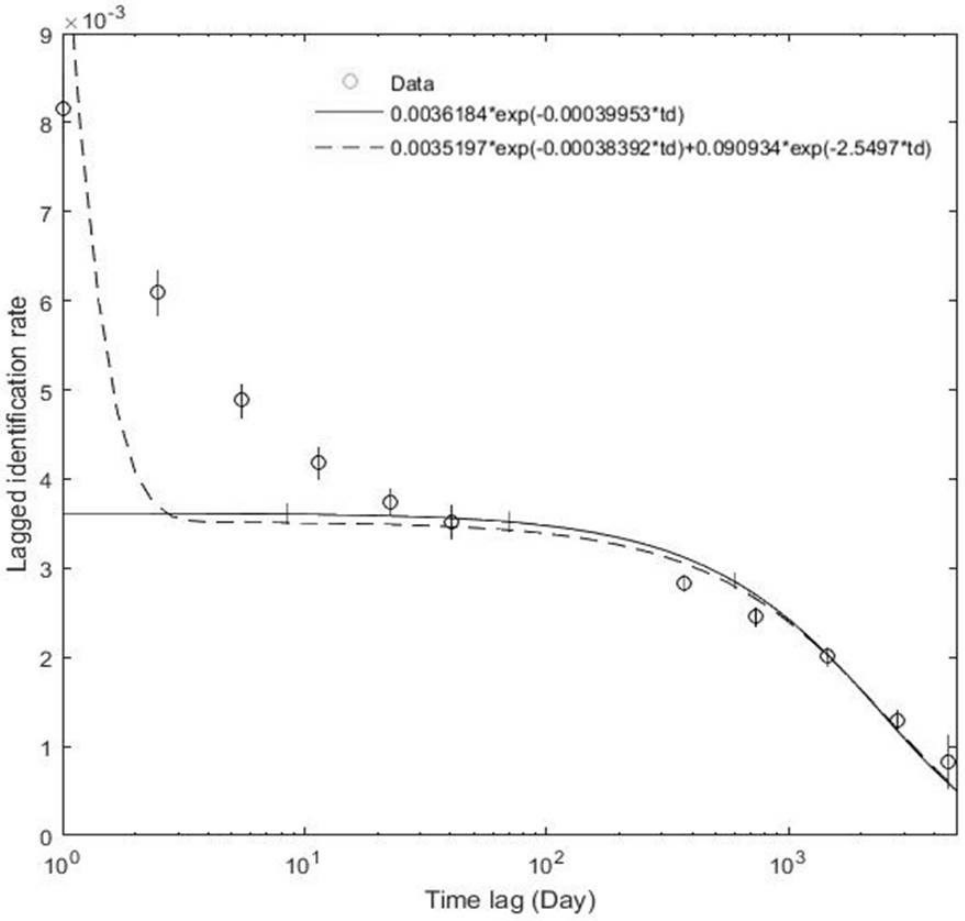

Figure 2.1 – Lagged Identification Rate (LIR). Error bars were calculated using the jackknife technique. The maximum-likelihood model that performed best with the SLAR is represented with a solid line. The maximum-likelihood best fit model is represented with a dashed line.

2.3.2 What is the turnover in this population?

The Lagged Identification Rate (LIR) declined with time lag. This means that the probability of an individual being identified in the population after the first sighting decreases with time (Figure **2**.**1**). We fitted the model type Emigration/mortality (a1=emigration rate; 1/a2=N) $g(\tau) = a2\exp(-a1\tau)$, to the LIR to test if the decline was similar between the LIR and Standardized Lagged Association Rate (SLAR). If so, the LIR decline could explain, at least partially, the SLAR decline.

The Emigration/mortality fitted to the LIR data with a1= 0.000400 day-1 (s.e. 4.2e-05), which equals to 0.1460 yr-1. The best fit model for the LIR was Emigration + reimmigration + mortality (a1=N; a2=Mean time in study area; a3=Mean time out of study area; a4=Mortality rate) $g(\tau) = a3\exp(-a1\tau)+a4e(-a2\tau)$ had a1 = 0.000384 day-1 (s.e. 4.866e-05), which equals to 0.1382 yr-1. The decline values for Emigration/mortality (0.1460 yr-1) and Emigration + reimmigration + mortality (0.1382 yr-1) were very similar, which means individuals seem to leave the population after a mean of about 7 years.

Looking at sexes separately, the LIR for both males and females also showed a decline (Figure **2**.**2**). For the female LIR, the model type Emmigration + reimmigration $g(\tau) = a2+a3e(-a1\tau)$ best fitted to the data showed a1 = 0.000834 (s.e. 0.041) or 0.3044 yr-1. For the male LIR, the model type Emmigration/mortality $g(\tau) = a2e(-a1\tau)$ best fitted to the data showed a1 = 0.000211 (s.e. 9.4705e-05) or 0.07702 yr-1. Given these results, males appear to be more likely to be re-identified in the population than females.

To test whether the decline of identification rates could be caused by individuals gaining enough new marks so as to render them new identifications, we looked at 3 units (Supplementary Material **1**) where only one individual from the original unit was identified in the later years: units A, B and E. We then compared who was seen in the same encounter as the remaining unit individual with its previous companions (Supplementary Material **2**). In both unit A and B it was not possible for the original unit IDs to have gained marks that would make them become similar to the new individuals observed, but in Unit E 4 individuals could have. None of these individuals were genetically sexed. So, it is possible that individuals gaining new IDs are influencing the decline of the LIR.

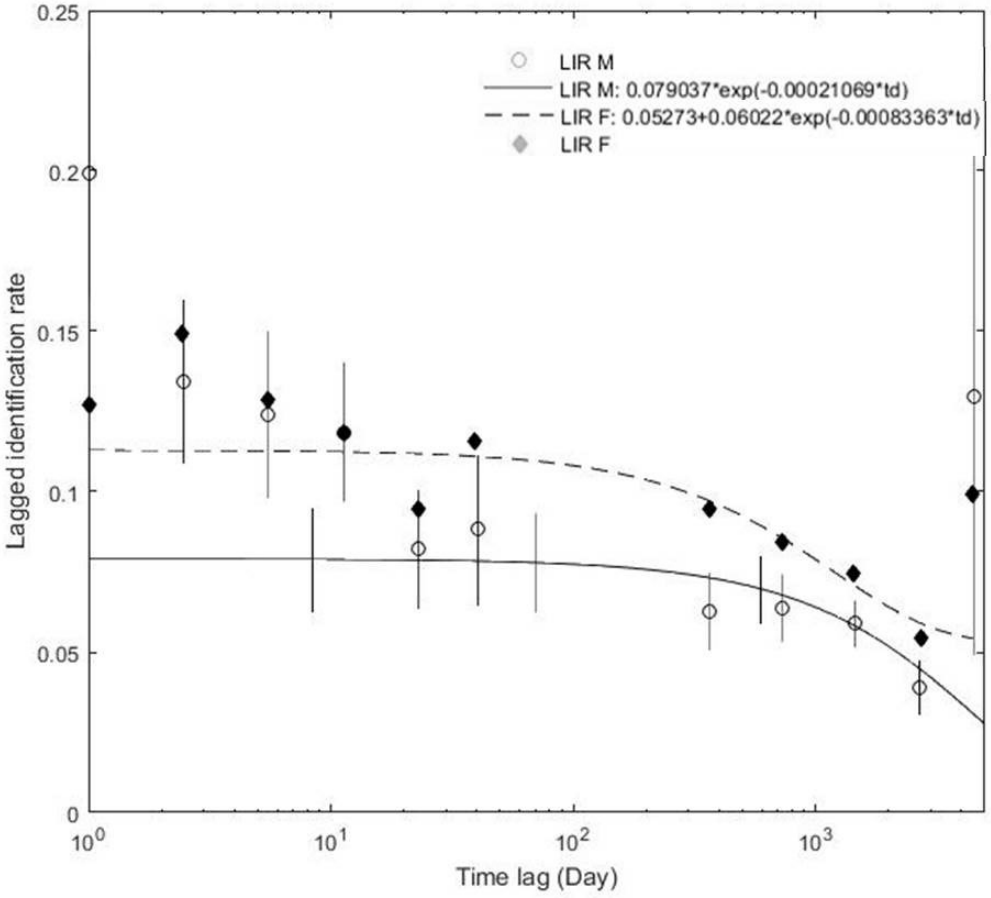

Figure 2.2 – Lagged Identification Rate (LIR) for individuals of different sexes. Males are represented by empty circles, females by full diamonds. Error bars were calculated using the jackknife technique. The maximum-likelihood best fit model is represented with a solid line for males and dashed for females.

2.3.3 How stable are relationships in this population?

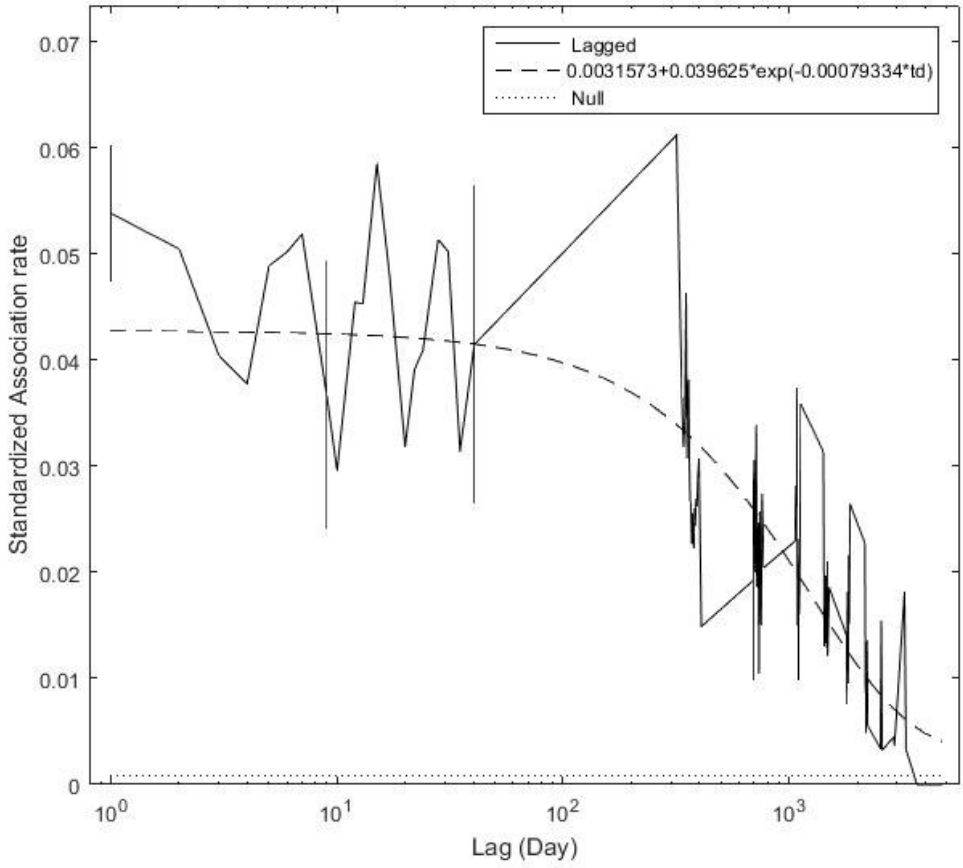

Figure 2.3 - Standardized lagged association rate (SLAR). Error bars were calculated using the temporal jackknife technique. The null association rate represents the theoretical SLAR if individuals associated randomly. The maximum-likelihood best fit model represents casual acquaintances.

The association rate between individuals decreases with time (Figure **2**.**3**). The SLAR and error bars cross the null association rate at about 25 years. The best fit model for the data was characterized as 'casual acquaintances and constant companions' (**Table 2.1**; model descriptions are not prescriptive: different social systems can be fitted by the same statistical model (Whitehead 2008)). The rate of decline of the best fit models of LIR (0.000400 day-1, s.e. 4.2e-05), indicating demography, and SLAR (0.000793 day-1, s.e. 5.9e-05), indicating association, are

similar enough, indicating that demography may explain a good deal of the association rate decline.

Table 2.1 – Fit of social models to the standardized lagged association rate for the population. τ, time in days; QAIC, quasi-Akaike information criterion; ΔQAIC, variation of QAIC between the current model and the best fit; g, SLAR. The best model with lowest QAIC is marked in bold.

Description of Model	Model formula	Maximum likelihood values for parameters (Jackknifed standard errors for parameters)	QAIC	ΔQAIC
'Constant companions' (CC)	$g(\tau) = a_1$	$a_1 = 0.0253\ day^{-1}$ (SE 0.00241)	47906.40	1252.46
'Casual acquaintances' (CA)	$g(\tau) = a_2 e^{(-a_1 \tau)}$	$a_1 = 0.000654\ day^{-1}$ (SE 5.60e-05) $a_2 = 0.0419\ day^{-1}$ (SE 0.00388)	46656.81	2.87
CA + CC	$g(\tau) = a_2 + a_3 e^{(-a_1 \tau)}$	$a_1 = 0.000793\ day^{-1}$ (SE 0.000264) $a_2 = 0.0316\ day^{-1}$ (SE 0.00236) $a_3 = 0.0396\ day^{-1}$ (SE 0.00411)	**46653.94**	
'Two levels of CA'	$g(\tau) = a_3 e^{(-a_1 \tau)} + a_4 e^{(-a_2 \tau)}$	$a_1 = 0.000653\ day^{-1}$ (SE 21.0) $a_2 = 0.000653\ day^{-1}$ SE (0.0253) $a_3 = -0.0113\ day^{-1}$ (SE 8.07) $a4 = 0.0531\ day^{-1}$ (SE 0.703)	46660.81	6.87

The parameters of the best fit model suggest an average group size of 32 identified individuals (1/a2). Scaling this value to take non-identifiable individuals into account (Ottensmeyer and Whitehead 2003), and the SE of the mark rate, average group size increases to an interval of 57

to 62, with an average of 59 individuals. This is similar to our at sea group size estimates (Ottensmeyer and Whitehead 2003).

Maximum associations, *i.e.* the association between an individual and its closest measured associate, varied between below 0.1 and 1.0. The maximum associations within and between sexed individuals reflected this variation (Supplementary Material **3**). There were only a few cases where both individuals with mutual maximum association were sexed, two mixed sex and one only female dyad. A Mantel test, with 120000 permutations, indicated differences in association rates between- versus-within sexes (Matrix correlation =-0.00398, p = 0. 0498). The negative matrix correlation indicates that individuals prefer to associate with members of the other sex, but the low value shows a very small effect. The temporal pattern of associations also did not vary much according to the sex of the dyad (Figure **2**.**4**, Table **2**.**2**). Associations between the sexes appeared to fall slightly faster than among females, but this is a small difference. There were not enough data to calculate the temporal pattern of associations among males.

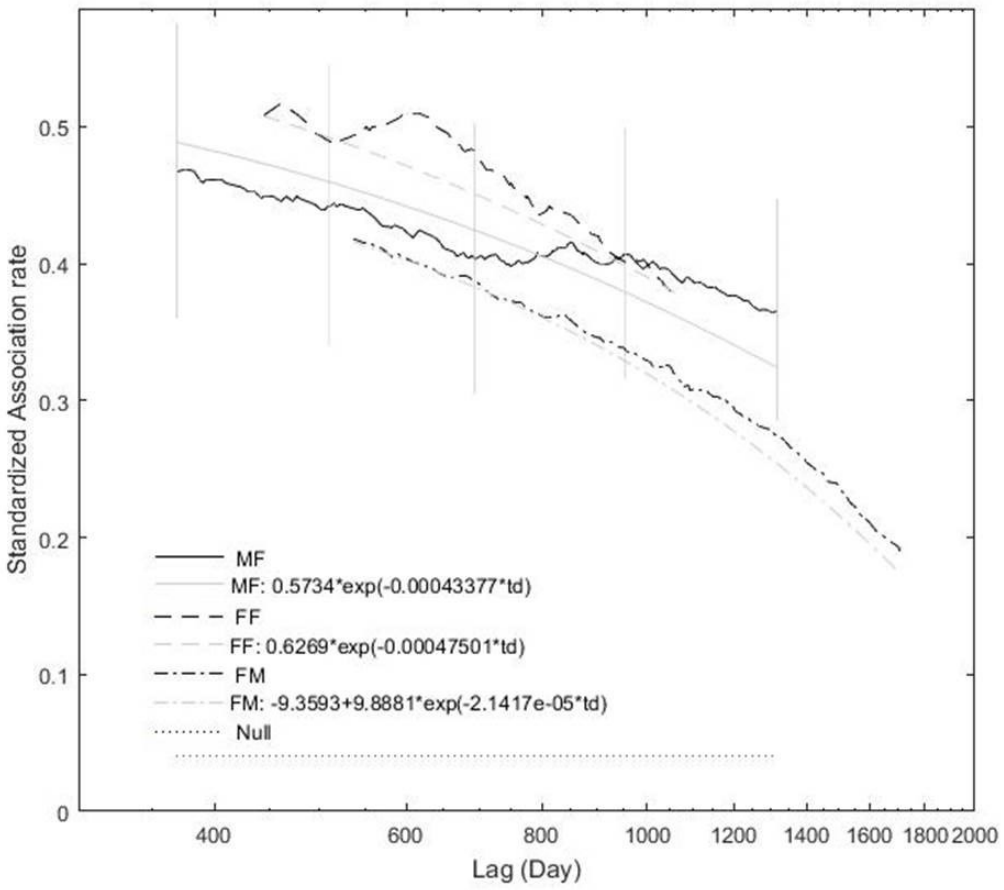

Figure 2.4 – Standardized lagged association rate (SLAR) for individuals of different sexes. MF: Male to Female, FF: Female to Female, FM: Female to Male. Error bars were calculated using the temporal jackknife technique. The null association rate represents the theoretical SLAR if individuals associated randomly. The maximum-likelihood best fit models are noted for each sex.

Table 2.2 - Fit of social models to the standardized lagged association rate for the associations between Females (FF), from Female to Male (F-M) and Male to Female (M-F). τ, time in days; QAIC, quasi-Akaike information criterion; ΔQAIC, variation of QAIC between the current model and the best fit; g, SLAR. The best model with lowest QAIC is marked in bold.

Description of Model	Model formula	Maximum likelihood values for parameters (Jackknifed standard errors for parameter)	QAIC	ΔQAIC
		Female – Female (FF)		
'Constant companions' (CC)	$g(\tau) = a_1$	a_1 = 0.452 day^{-1} (SE 0.202)	269.83	10.79
'Casual acquaintances' (CA)	$g(\tau) = a_2 e^{(-a_1 \tau)}$	a_1 = 0. 000475 day^{-1} (SE 0. 0834) a_2 = 0. 627 day^{-1} (SE 0. 423)	**259.04**	
CA + CC	$g(\tau) = a_2 + a_3 e^{(-a_1 \tau)}$	a_1 = 5.72 day^{-1} (SE 4.14) a_2 = 0. 457 day^{-1} (SE 0.21) a_3 = -139.6 day^{-1} (SE 677.3)	271.09	12.05
'Two levels of CA'	$g(\tau) = a_3 e^{(-a_1 \tau)} + a_4 e^{(-a_2 \tau)}$	a_1 = 1.03 day^{-1} (SE 4.66) a_2 = 0. 000497 day^{-1} (SE 0. 130) a_3 = 1.0351 day^{-1} (SE 1.39) a_4 = 0. 641 (SE 0. 243)	499.17	240.13
		Female – Male (FM)		
'Constant companions' (CC)	$g(\tau) = a_1$	a_1 = 0. 302 day^{-1} (SE 0. 0670)	730.97	79.45
'Casual acquaintances'	$g(\tau) = a_2 e^{(-a_1 \tau)}$	a_1 = 0. 000703 day^{-1} (SE 0. 000110) a_2 = 0. 556 day^{-1} (SE 0. 0740)	**651.52**	

(CA)				
CA + CC	$g(\tau) = a_2 +$	a_1 = 2.14 e-05 day^{-1} (SE 10.69)		
	$a_3^{e(-a_1\tau)}$	a_2 = *-9.36* day^{-1} (SE 166.0)	*636.59*	
		a_3 = 9.89 day^{-1} (SE 2278.0)		
'Two levels of CA'	$g(\tau) = a_3e^{(-a_1\tau}$	a_1 = 0. 167 day^{-1} (SE 0.639)		
	$) + a_4e^{(-a_2\tau)}$	a_2 = 0. 000759 day^{-1} (SE 0. 000119)	671.17	19.65
		a_3 = 0.316 day^{-1} (SE 0.284)		
		a_4 = 0. 598 day^{-1} (SE 0. 0795)		
		Male – Female (MF)		
'Constant companions' (CC)	$g(\tau) = a_1$	a_1 = 0. 413 day^{-1} (SE 0. 100)	653.48	29.48
'Casual acquaintances' (CA)	$g(\tau) = a_2e^{(-a_1\tau}$ $)$	a_1 = 0. 000434 day^{-1} (SE 0. 000142) a_2 = 0. 573 day^{-1} (SE 0. 125)	**624.00**	
CA + CC	$g(\tau) = a_2 +$	a_1 = 0.0136 day^{-1} (SE 26.0)		
	$a_3^{e(-a_1\tau)}$	a_2 = 0. 357 day^{-1} (SE 0. 184)	631.97	7.97
		a_3 = 0. 346 day^{-1} (SE 240.1)		
'Two levels of CA'	$g(\tau) = a_3e^{(-a_1\tau}$	a_1 = 0. 496 day^{-1} (SE 3.47)		
	$) + a_4e^{(-a_2\tau)}$	a_2 = 0. 000402 day^{-1} (SE 0. 000159)	626.10	2.1
		a_3 = 0. 474 day^{-1} (SE 0.809)		
		a_4 = 0. 552 day^{-1} (SE 0. 135)		

2.3.4 Are there stable long-term social units in the population?

Twenty one units were identified (Supplementary Material **1**), with membership varying from 2 to 26 well-identified individuals. Six individuals belonging to unit K, the largest unit, (260, 261, 265, 506, 632 and 862) also belonged to up to three other units (L, N and U), with individual 261 belonging to all. We will henceforth refer to units K, L, N and U as the 'K complex', since there were several shared individuals between K and the other units.

During our analysis we also identified 81 key individuals that had no identified closest companions and so did not generate units. Although it is possible they have CCs that are not identifiable (Ottensmeyer and Whitehead 2003), we decided to simplify the dataset and omitted these individuals.

Unit identification varied through the years. While some units were sighted across the whole study, others were more confined to specific years. There were cases of individuals within units that disappeared after a certain number of years, in concordance with the LIR model, but there were others who reappeared after a gap of some years (*e.g.* individual 345 from unit B identified in years 1999, 2003-2008 and 2011), and 248 from unit F identified in years 1998, 2000, 2002-2008 and 2011).

Units seem quite well differentiated (Figure **2**.**5**) in the network diagram. The exception is the K complex, which seems to have a connective role between units. This is apparent when looking at the network diagram of units without the K complex (Supplementary Material **4**).

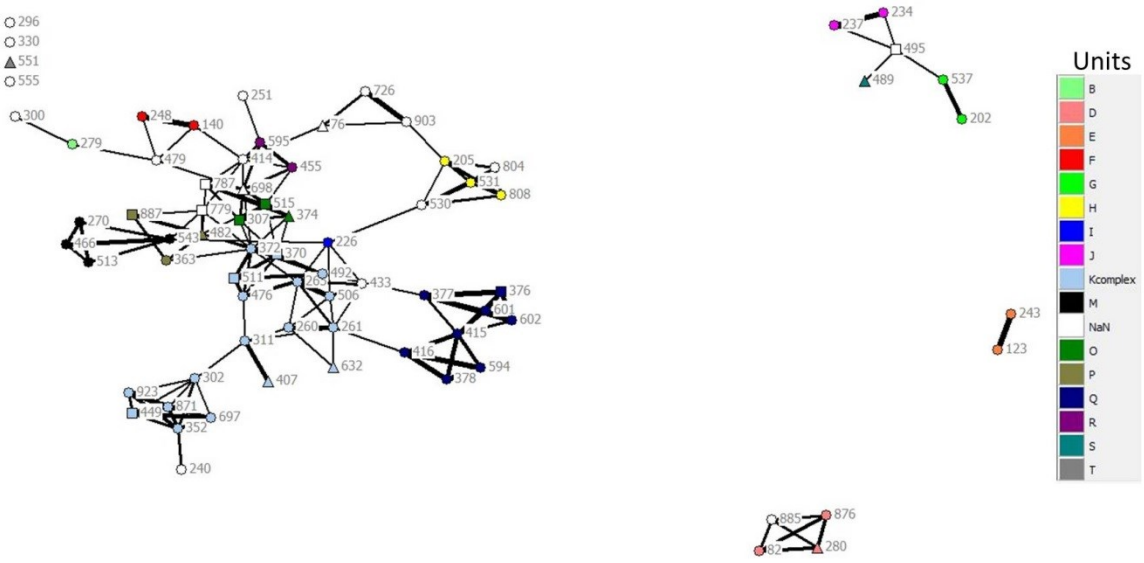

Figure 2.5 –Network of individuals seen more than 20 times during the sampling period, with CoA ≥0.1. Different colours represent different units (individuals not assigned to a unit are marked as NaN) and different symbols sexes. Circles - non identified sex, Squares - Females, Triangles – Males

Fifteen units had more than one individual identified in at least 6 years (Supplementary Material **5**), which allowed us to assess the stability of dyadic relationships. Relationships were considered stable when the last year where both individuals in that dyad were seen coincided with the last time at least one of them was seen. If that was not the case, the dyadic relationship was considered unstable. Outside the K complex stability rates were high, with 80% of relationships being stable. In the K complex stability was much lower, signifying the complex and dynamic structure of this social entity.

The mean number of days per year that units were identified varied between 2.6 for unit T and 20.9 for the K complex (Supplementary Material **6**). Even though the K complex was seen more often than the other units, it is likely this is related to the number of individuals included within it. When looking at the mean number of days each individual was seen per year, individuals in the K complex were similar to individuals of other units.

2.3.5 What is the size and sex-ratio of units?

Mark rate of units varied between 0.33 and 0.73 (Supplementary Material **1**). When corrected for the each specific unit mark rate, average unit size varied between 3 and 29 individuals. Mean unit size for the population was 6.83.

Individuals in 7 different units were sexed (Supplementary Material **1**). Only three cases had more than one sexed individual per unit, but all of them were mixed sex (F:M): K complex (3:2), O (2:2), and P (1:1).

2.3.6 Is there within-unit structure?

Only units B, Q and the K complex showed apparent within-unit structure, in the sense of having at least two clusters within the unit and a modularity greater than 0.3 (Supplementary Material **7**).Units B and Q were divided into 2 clusters each and the K complex into 5 clusters (Supplementary Material **8**).

To examine the dynamics within the K complex, we analyzed the network diagrams and modularity in different years (Figure **2**.**6**). Individuals in the network became less connected from 1999 to 2011, and modularity steadily increased from 0.384 in 1999-2000 to 0.705 in 2008-2011. This shows an increase in intra-complex structure with time.

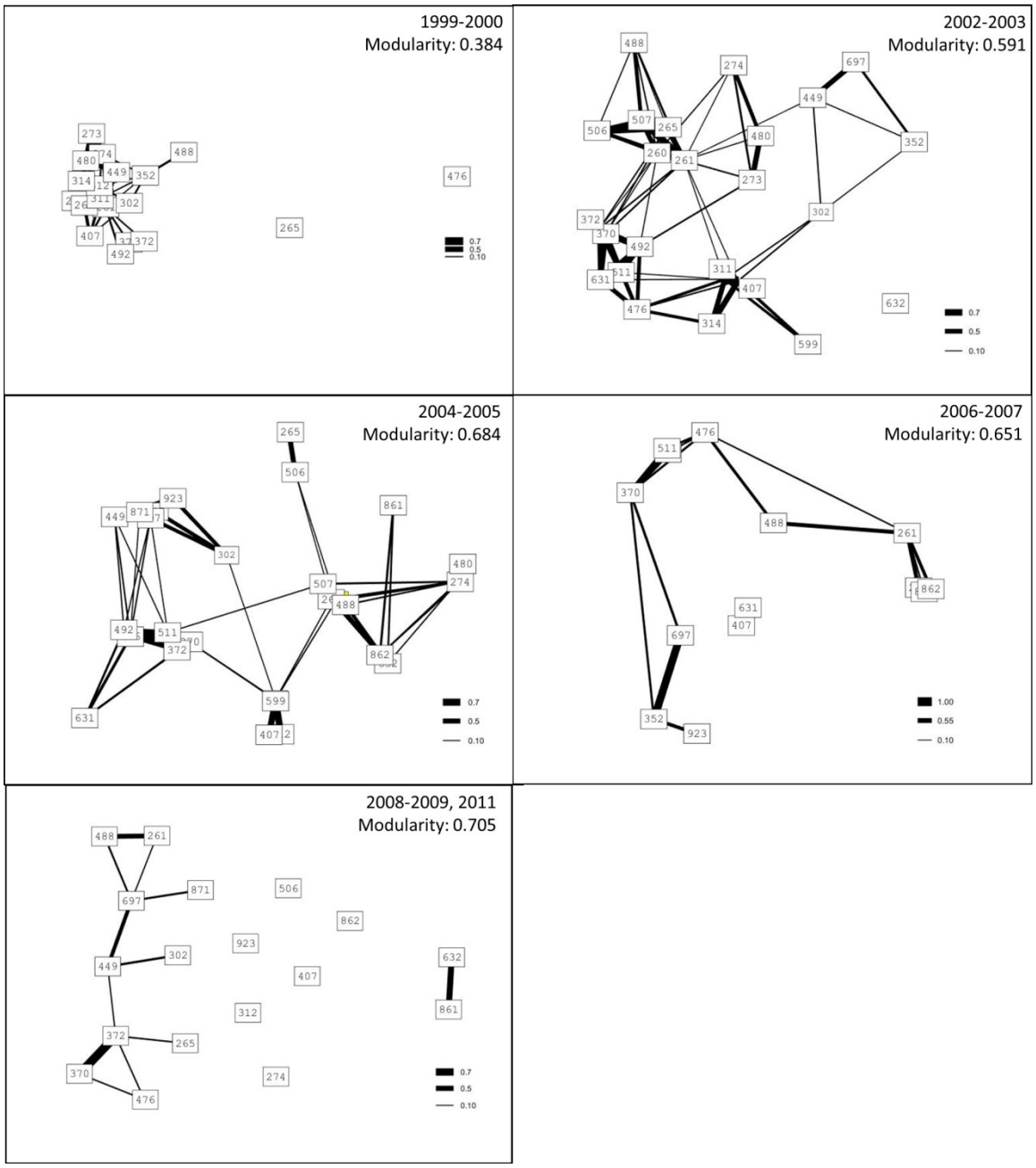

Figure 2.6 – Network diagrams for the K complex across different years of the study. Modularity was calculated using Newman's (2006) eigenvector method.

2.3.7 How do units relate to one another?

Table 2.3 - Associations between units. S – Estimate of social differentiation using the maximum likelihood method. S < 0.3 – homogeneous society, S > 0.5 – well differentiated society, S > 2.0 – extremely differentiated society. SE – Standard Error

All units			
Sampling	Metrics		
	Day	Hour	Encounter
Year	S = 0.342 (SE = 0.131)	S = 0.000 (SE = 0.118)	S = 0.564 (SE = 0.246)
Day	-	S = 1.288 (SE = 0.102)	S = 1.320 (SE = 0.136)
Hour	-	-	S = 0.834 (SE = 0.121)
No 'K Complex'			
	Day	Hour	Encounter
Year	S = 0.000 (SE = 0.176)	S = 0.000 (SE = 0.122)	S = 0.000 (SE = 0.332)
Day	-	S = 0.550 (SE = 0.098)	S = 0.462 (SE = 0.140)
Hour	-	-	S = 0.408 (SE = 0.181)
Within 'K Complex'			
	Day	Hour	Encounter
Year	S = 0.603 (SE = 0.153)	S = 0.066 (SE = 0.223)	S = 1.309 (SE = 0.169)
Day	-	S = 2.017 (SE = 0.117)	S = 2.042 (SE = 0.133)
Hour	-	-	S = 1.551 (SE = 0.149)

All the scenarios looking at between-unit structure suggested well or very well differentiated societies, except for the combination: sampling period: Year and metric: Hour in all scenarios, and sampling: Year metric: Day for no 'K complex'. In these scenarios the societies appeared homogenous (Table **2**.**3**).

The K complex appeared at the center in the 'all units' network diagrams (Supplementary Material **9**). Taking a closer look at dyads within units, different individuals from the K complex connect to different units, but their highest associations are with others in the same complex. When removing the K complex from the analysis, no other unit replaces it although several units show somewhat central positions in the network (Supplementary Material **10**). When looking at dyads within units it becomes more obvious that there is not a central, all-connecting unit, when the K complex is removed. Each individual associates with maximum of one or two different units at HWI>0.1 (Supplementary Material **10**). Associations between pairs of individuals within the K complex are heterogeneous, with some dyads in near constant association while others barely associate (Supplementary Material **11**).

2.4 DISCUSSION

2.4.1 How do individuals associate with each other and are units the best way to describe it?

The pilot whale population that summers in Cape Breton has been a part of a long term study since 1998. The first analysis of its social structure (Ottensmeyer and Whitehead,2003) was performed using data from 1998 to 2000. This dataset was increased to include 11 sampling years with this study. This increase gives us more detailed information on this population's social structure. The total number of individuals identified reflects this, with an increase from 332 individuals identified by Ottensmeyer and Whitehead (2003) to the current 1231. From these

individuals, 38.8% were seen only once and 63.2% were seen in three or less encounters. Thus the resighting rate for this population is quite low. We were also able to sex 79 individuals.

The decline of the identification rate, observed for both males and females, has a threefold potential explanation: emigration from the area, high mortality/recruitment rates and/or individuals gaining new identification codes due to an increase in mark points or better photographic technology.

Emigration from the population, in this case, can mean that individuals have left the area or that they are still in the general area, but not identified during the study period. There could be dispersal to areas nearby, but outside the boundaries of our vessel-of-opportunity-limited study area, or anywhere else in the northern North Atlantic. Individuals may not return to the study area because of ecological changes, especially of prey type or availability (*e.g.*, Reilly 1990, Simmonds and Eliott 2009). In such cases it is more likely that we would stop seeing complete units instead of just a few select individuals, given the nature of the associations among unit members. This happened with some of the units in our study population. For instance, no individuals from unit J were identified between 2007 and 2009, and from unit M in 2007 (Supplementary Material **12**).

There are no estimates for mortality for this population, but there are some estimates of female survival gathered from the Faroese drive fishery (Bloch *et al.* 1993, Foote 2008). Unfortunately, these results are not directly comparable to the LIR, so that we might assess the extent to which mortality might be influencing identification rates. However, long-finned pilot whales are long-lived animals (Bloch *et al.* 1993, Foote 2008) and it seems unlikely that a lagged identification rate decline of 0.146/yr is entirely due to mortality.

Identification change is very likely happening in this population, and a part of the reason behing the LIR decline (**Table 2.2**). New marks can be gained through injuries (Sergeant 1962, Bigg *et al.* 1987), interactions with other individuals, predators, boats or fishing gear. The rate of gain for ID marks in the dorsal outline has been estimated at 0.0848 and 0.0182 per year for notches and protruding pieces, respectively (Auger-Methe and Whitehead 2007). This means that in ten years an individual is very likely to have a mark change. Size of the marks also has to be taken into account. The gain of just one notch, if large enough or in a location that removes previous marks, can be enough for the individuals to be identified with a new ID.

We also have to take into account that this study was started with film data collection (1998-2003) and then moved to digital (2004-2011). Our ability to detect mark changes probably increased due to that change (Mazzoil *et al.* 2004) and, in some cases, smaller marks or more detail of larger notches seen on digital photos, not visible in film photographs, might have led to individuals gaining a new identification in the catalogue. This is indicated in the increase in the identification rate from 0.34, when only using only film data (Ottensmeyer and Whitehead 2003), to 0.51 when adding digital images.

There also seems to be a difference in the identification rates between sexes, with male LIR falling more slowly than that of the females. Given that the number of MPs is not significantly correlated with sex (Augusto *et al.* 2013), it is possible that this difference is related with male size. Pilot whales are sexually dimorphic (Sergeant 1962), and since dorsal fins grow isometrically (Bloch *et al.* 1993), males also present larger dorsal fins. This might make it easier to photograph male rather than female dorsal fins.

The perceived temporal change in association rate indicated by the SLAR is heavily influenced by the decline in the identification rate, which happens for both males and females. This decline

makes it more difficult to analyze this population's social structure. With the SLAR model being so heavily influenced by changes in the identification rate with time through mortality/recruitment, emigration/immigration and/or mark change, it is not possible to usefully estimate the stability of associations over the decadal period of this study. It also influenced our unit analysis, with ID change possibly inflating our estimates of unit size; or even affecting who is considered a key individual or constant companion, since it generally decreases the overall time span of identifications for individuals.

Social unit membership seems to describe a large part of the pattern of associations between individuals, as expected from previous studies (Amos *et al.* 1991, 1993, Ottensmeyer and Whitehead 2003, de Stephanis *et al.* 2008a). A total of 123 individuals were affiliated to units. This comprises 10% of the individuals identified in the population, but as noted before, 63.2% of all identified individuals were sighted in less than 3 encounters, and would automatically be excluded from inclusion in units with our stricter requirements. Individuals affiliated to units comprised 27.2% of this restricted set.

From the twenty-seven units identified in this study, six of the seven identified by Ottensmeyer and Whitehead (2003) were present (Table 4). Unit E was not identified due to the stricter unit rules employed in this study, with individuals in unit E only being seen 3 times with a 30 day gap between sightings. Two individuals from the original unit C were removed from the unit for the same reason. Three units remained stable between the two different time periods, with additions of newly identified individuals in two cases. Units F and G were not as stable. All individuals in the two units now belong to unit K, but 261 also belongs to units L, N and U. This seems to be related to the stability of unit K and the K complex, not an intrinsic problem with the method itself.

Table 2.4 - Comparison between units identified by Ottensmeyer and Whitehead (2003) with data collected between 1998 and 2000, and this study with data collected from 1998 to 2011. Units were calculated using the original protocol from Christal *et al.* (1998) between 1998 and 2000, and the modified protocol from 1998 to 2011.

Unit ID 1998-2000	ID individuals	Unit ID currently	Changes in membership
A	59 60 80	C	None
B	254 140 139 142 248	F	Addition: 701
C	243 123 120 119 122 2	E	Removal: 119, 122
D	28 66 62 65		Addition: 279, 345
E	152 263	Not in analysis	

F	262	K
	261	K, L, N, U
G	302	K

2.4.2 How are units structured and how do they associate with each other?

The average typical group size is considerably different than the one estimated by Ottensmeyer and Whitehead (2003) for this population. The typical group size increased from 29 to 57-62 individuals. But it is also possible that the previous study might have been biased towards smaller groups due to the restrictions of group coverage allied with the use of film photography.

On the other hand, Ottensmeyer and Whitehead (2003) estimated a mean unit size of 7, similar to our results. All units have less than 12 individuals, except unit K which has 29. So, while with a larger sampling size we can identify more individuals belonging to units, the average size does not seem to change, pointing toward a common unit size. Common unit size is also similar in short-finned pilot whales, with numbers varying between 12 in Hawai'i (Mahaffy, 2012, Mahaffy *et al.* 2015), 11 in Tenerife (Heimlich-Boran 1993) and 15 in Madeira (Alves *et al.* 2013). Unit size seems very different for the long-finned pilot whale population off Gibraltar (de Stephanis *et al.* 2008a), with smaller line units of 2-3 individuals. It is possible that these line units might be larger when non-identifiable individuals are taken into account (de Stephanis *et al.* 2008a). This is also a smaller, resident population, while the other populations have more variable residency patterns. It seems possible that pilot whales (*Globicephala spp.*) have a tendency for unit size to be around 10 individuals. Comparing unit and group size, we can see that groups contain on average about 5 units.

Pilot whales then appear to share common pod/unit size with resident killer whales and with sperm whales, where, in each case, unit size is quite stable across populations. Resident killer whale pods vary between 2-9 individuals in the NE Pacific (Bigg *et al.* 1990) and between 4-8 individuals in the NW Pacific (Ivkovich *et al.* 2010). These pods are very stable, and rarely gain or lose individuals by means other than births and death (Bigg *et al.* 1990, Ivkovich *et al.* 2010). Sperm whale mean unit size varies from 5-13 across study areas in the North Atlantic and eastern Pacific (Whitehead *et al.* 2012).

In the three units for which we have multiple individuals sexed, there are both males and females present. This confirms the results from the Faroe Islands (Amos *et al.* 1991, 1993) and Gibraltar (de Stephanis *et al.* 2008a). Pilot whale populations seem to be organized into units comprised of both sexes.

We found three apparent cases of within-unit structure. Units B and Q were divided into two clusters, which appeared related to temporal changes in unit-membership. The K complex, on the other hand, shows a more complex structure. It was divided into 5 clusters, which bear some resemblances with the original units that are connected in the complex. What is likely happening with the K complex is a loss of stability and possible fission event, as seen by the increase in modularity through the years. There are several matrilineally-based species in which this phenomenon has been observed, such as sperm whales (Christal *et al.* 1998), killer whales (Bigg *et al.* 1990, Ford *et al.* 1994, Parsons *et al.* 2009) and elephants (*Loxodonta sp.*; Moss and Poole 1983, Moss and Lee 2011). Fission events usually occur along matrilines, with each matriline splitting into a new group.

It seems likely that, due to demographic changes, possibly its large size and consequent difficulty in maintaining associations between all individuals, the K complex is breaking apart into smaller units.

The K complex it is at the center of all the association diagrams, and when it is removed from the analysis no other unit takes a similar central position. Remaining units tend to only associate with a small number of others. This might be related to the sheer size of the K complex, with 29 individuals. This is much larger than any other unit, so there are more opportunities for individuals of other units to associate with K complex individuals. If the cohesiveness of the complex is decreasing and fission is happening, its clusters might be associating more with individuals outside of the K complex.

In conclusion, this expanded dataset gave us a clearer, and richer, picture of pilot whale society. While the notion that they live in stable social units still stands, we have deepened our understanding of its dynamic. We now know that units have a common size of 8, may be comprised of adults of both sexes and can go through fission events when they reach a certain size due to difficulty in maintaining social bonds. Both pilot whale species (*Globicephala spp.*) show a common unit size around 10 individuals, with both males and female present. Fission events had not previously been described in the species and should be explored in other populations. We also found a unit that plays a central role in how units associate. Without the K complex unit associations between units would be much lower. This is a concept that would also be interesting to explore in other populations. But, there are still unanswered questions, both on the dynamics of within-unit associations, such as fission events, and the relationship between individuals in units, specifically how genetically related they are and if they belong to the same matriline. The latter will be addressed in subsequent studies.

CHAPTER 3: THE INFLUENCE OF BEHAVIOURAL STATE ON PILOT WHALE (*GLOBICEPHALA MELAS*) SOCIAL STRUCTURE

3.1 INTRODUCTION

In chapter 2 I established that I would use Hinde's (1976) definition of social structure to study pilot whale society. This framework comprises of three levels: interactions, relationships and surface structure (*i.e.* social structure (Whitehead 2008)). Hinde (1976) considered interactions as limited in time and as directed behaviours from one individual to another. Interactions are thus defined in terms of content (what individuals are doing together) and quality (how they do it). Relationships integrate the interactions between pairs of individuals with content, quality and patterns associated with time and previous interactions. Lastly, social structure deals with the same three features – pattern, content and quality – but of relationships within a population (Hinde 1976). Hinde (1976) also points out several factors that can influence social structure at different levels, such as psychological and physiological variables, age and sex classes, and kinship. We now know, for instance, that the social structure of zebras (*Equus burchelli*) is influenced by the social status of males (Fischhoff *et al.* 2009); by reproductive state in elephants (*Loxodonta africana*, Goldenberg *et al.* 2014); by age and sex in northern long-eared bats (*Myotis septentrionalis*, Patriquin *et al.* 2010); and behavioural states in meerkats (*Suricata suricatta*, Madden *et al.* 2011) and bottlenose dolphins (*Tursiops truncatus*, Gero *et al.* 2005; Gazda *et al.* 2015).

But why do we expect social structure to change with behavioural state? Goldenberg *et al.* (2014) hypothesized that if male elephants used sexually inactive periods to create and maintain bonds with other males, allowing them to share knowledge, there might be preferred companions during that period. This would only be possible to determine when social structure

was studied separately for sexually active and inactive periods. For meerkats, on the other hand, there was evidence that individuals interacted with each other differently in social groups according to different classes, such as age, mass, social status and sex (*e.g.* Jordan 2007, Brotherton *et al.* 2001, Clutton-Brock *et al.* 2004). Madden *et al.* (2011) hypothesized that these differences would vary according to behavioural state, and thus affect social structure. In the bottlenose dolphins of Shark Bay, adult males tend to form alliances of two to three individuals (Connor *et al.* 1992), while adult females congregate in larger groups, more related to reproductive status. Gero *et al.* (2005) hypothesized that these differences would lead individuals to have different opportunities to interact depending on sex, while juveniles being less constrained might show more behaviourally specific associations. It is important to note that in both cases there were changes in association preferences with behavioural state, not just a changes in group size.

Long-finned pilot whales (*Globicephala melas*), which I will be referring to as pilot whales from here on, are known to live in stable social units (Ottensmeyer and Whitehead 2003; de Stephanis *et al.* 2008a). The population that summers off Cape Breton, NS, Canada, lives in units with a mean size of 7 individuals (Ottensmeyer and Whitehead 2003; Chapter 1). Individuals affiliated with units tend to stay together for at least several years. These units interact to form groups, which are labile. Until now there have been no studies on how behavioural state can influence the way group form or break apart, or if unit association preferences change under different behavioural states. In this study I investigate two hypotheses. The first is that individuals show different preferred associations according to behavioural states. There is evidence of this happening in other species that live in stable social groups, such as elephants (Goldenberg *et al.* 2014) and meerkats (Madden *et al.* 2011), so it is possible this also happens in long-finned pilot whales. The second hypothesis is that units show different preferred associations according to

behavioural states. Units associate with each other in groups where affiliation changes from hours to days. Pilot whale units in the Straits of Gibraltar have different C and N signatures (de Stephanis *et al.* 2008a), and therefore specific feeding preferences. It is possible this also happens in the Cape Breton population. In this case, I expect to see units with similar feeding preferences feeding on the same resources, hence showing preferred associations during feeding. Given that social behaviour includes mating, I expect associations between units to be more diverse in this state. Not much is known about this population's movement patterns within the Gulf of Saint Lawrence. If units have preferred travel routes within the Gulf (whether they prefer to travel at certain distances from shore or at different times during the summer), it is possible that they associate more with other units travelling on the same routes.

Given the socially-complicated K complex of several intertwined units, described in Chapter 2, I expect it to have high association rates with other units. It is then possible that it will affect the analysis of how associations among units vary in different behavioural states. I will take that into account when analysing and discussing the data.

3.2 METHODS

3.2.1 Behavioural and Photographic Data collection

Data were collected in July and August, from 1998 to 2000 and 2002 to 2010 from 13-metre whale watching vessels off the northwest coast of Cape Breton Island, Nova Scotia, Canada. From 1998 to 2000, the vessel departed from Bay St. Lawrence harbour (47°02' N 60°29'W), and from 2002 to 2011 it departed from Pleasant Bay harbour (46° 49' N, 60° 47' W). Up to five trips were conducted daily, lasting a maximum of 2.5 hours each, and covering up to 40 km south to 30 km north of the harbour, and a maximum of 8 km offshore. Trips were only performed when the wind strength was less than 20 knots.

Usually, two researchers collected behavioural and photographic data on each trip. The area was scanned for the presence of pilot whales, and when a group was sighted the vessel approached it slowly and kept parallel to their movement or stayed stationary with the motor on idle or turned off.

Data were collected and organized by encounters. Encounters began when a whale was sighted and ended when the vessel had to leave the group by either returning to port or by moving to another group which was more than 200 m away. Encounters also ended if the group was submerged for more than ten consecutive minutes. All individuals in an encounter were considered to be in the same group and therefore will be referred to as groups. Researchers photographed individuals in a group regardless of whether they would be identifiable or not, and strived to not consecutively photograph the same individuals, but rather to cover all individuals present. Groups were classified according to photographic coverage. When the number of photographs in an encounter was smaller than the number of individuals estimated to be present (*e.g.* due to difficult photographing conditions such as big swells or unpredictable movement patterns of the individuals) the encounter was considered to have poor coverage, considered 'coverage < 0'. Encounters where the number of photographs exceeded the number of individuals were considered 'coverage > 0' and encounters in which the number of photographs were at least double the number of individuals estimated to be present are considered 'coverage ≥ 2'.

Encounters were classified according to four behavioural states: feeding (F), resting/milling (R), travelling (T) and socializing (S). Groups were considered to be *feeding* when individuals showed prolonged or tail-out dives, with no directional movement, little active surface behaviour and individuals surfacing mostly alone. Groups were considered *resting/milling* when individuals

tend to be logging (floating at the surface without moving) the majority of the time, or travelling slowly, below the idle speed of the boat (ca 4.5 km/hr). In this state dives tended to be short. Groups were considered to be *travelling* when individuals show steady directional movement, faster than boat's idle speed. There is a mix of short and longer (under a minute) dives. Groups were considered to be *socializing* when individuals did not present directional movement, dive time was short (<10 seconds) and there were active surface behaviours, such as tail or flipper slaps and flops, where the individual clears part of its body from the water and lands on different parts of its body. Body contact was also common when socializing. Only encounters that were classified with a single behavioural state were used for the analysis in this chapter, encounters identified with multiple behavioural states (*e.g.* F/S) were removed from the dataset.

3.2.2 Photo Identification

Photoidentification photographs of the dorsal fin area (Auger-Methe and Whitehead 2007) were collected using a Canon EOS Elan IIe (film) or Canon Rebel G (film) between 1998 and 2003 with a 300mm autofocus lens, and a Canon EOS-10D (digital) or Canon 30D (digital) with a 200mm or 300mm autofocus zoom lens from 2004 onward. Each photograph was quality rated and identified using the same protocol followed in Chapter 1.

3.2.3 Do associations between individuals vary with behavioural state?

Are association rates changing with different behavioural states?

The coefficients of association (CoAs) between dyads were calculated for each behavioural state, for only coverage ≥2 encounters only, using the half-weight index (Cairns and Schwager 1987) in SOCPROG2.6 (Whitehead 2009):

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

Where *x* corresponds to the number of sampling periods where the individuals, A and B, were identified as associated; y_{AB} corresponds to the number of sampling periods where the individuals, A and B, were both identified but not associated *;* y_A the number of sampling periods where individual A was identified but not individual B; and y_B the number of sampling periods where individual B was identified but not individual A.

Sampling periods are months, and individuals are considered associated if they were identified in the same encounter at least once during the day. The CoAs were organized into association matrices for each behavioural state.

I investigated two hypotheses as to how social structure might change with behavioral state:

1. Variation in association rate/group size. For each behavioural state I calculate mean group (*i.e.* encounter) size, and also the mean gregariousness (sum of association indices for an individual).

2. Variation in association preference. I calculated the social differentiation (measure of how variable dyadic associations are, Whitehead 2008) for each behavioural state. I also calculated the observed and expected (using permutation methods, Bejder *et al.* 1998; Whitehead 2008) CVs of the association matrices as measures of preference in association for each behavioural state, and tested these against the null hypothesis that there was no preference.

Are association preferences changing with different behavioural states?

In order to assess how the strength of association between individuals was influenced by behavioural state, I plotted the CoAs for each dyad of units, under each behavioural state, against each other (Whitehead 1997). The diagonal of the plot represents cases in which the strength of association does not vary with behavioural state.

3.2.4 Are associations between units affected by behavioural state?

Are association rates between units changing with different behavioural states?

In chapter 1, units are defined as sets of individuals in nearly permanent mutual association. Unit affiliation was assessed using a modification of the method employed by Christal *et al.* (1998) and Ottensmeyer and Whitehead (2003). I followed the same protocol as above to determine associations between units in different behavioural states, but replacing individual identity with the corresponding unit. Only individuals identified as members of units were used for this analysis.

Are association preferences between units changing with different behavioural states?

In order to assess if the strength of association between units is influenced by behavioural states, I plotted the CoAs for each pair of units, under each behavioural state, against each other (Whitehead, 1997). The diagonal of the plot represents cases in which the strength of association does not vary with behavioural state.

3.3 RESULTS

The numbers of encounters are tabulated for each behavioural state for the individual and the unit analysis (Table 3.1). Encounters where individuals were travelling were the most common, while socializing was the least observed. The number of individuals observed under each behavioural state varied between 250 and 780.

Table 3.1 – Observations under each behavioural state. Encounters – number of encounters where only one behavioural state was recorded; Identifications – total number of distinct individuals or units identified per behavioural state.

	Individuals		Units	
	Encounters	Identifications	Encounters	Identifications
Foraging	601	695	309	18
Resting	224	400	109	16
Socializing	117	250	57	18
Travelling	904	780	496	18

Twenty one units have been identified in this population (Table **3.2**). The K complex is comprised of individuals of units K, L N and U, which frequently affiliated with one another. The K complex was considered as one unit in this analysis, lowering the total number of units to 18. All units were observed while feeding, socializing and travelling, while only 16 were observed resting (Table **3.1**).

Table 3.2 - Membership (well-marked individuals) in social units which were defined using a protocol modified from Christal *et al.* (1998).

Unit	Individuals
A	1, 246
B	28, 62, 65, 66, 279, 345
C	59, 60, 80
D	82, 280, 719, 876
E	2, 120, 123, 243
F	139, 140, 142, 248, 254, 701
G	202, 537
H	205, 496, 531, 808
I	226, 483, 679
J	234, 237, 346, 894
K Complex	260, 261, 262, 265, 273, 274, 302, 311, 312, 314, 352, 370, 372, 407, 449, 476, 480, 488, 492, 506, 507, 511, 599, 631, 632, 697, 861, 862, 871, 923
M	270, 466, 473, 513, 543, 569, 617
O	307, 374, 508, 515, 517, 518, 570, 637
P	363, 482, 887, 889

Q	375, 376, 377, 378, 415, 416, 594, 601, 602, 674
R	455, 595
S	489, 490
T	550, 551

3.3.1 Do associations among individuals vary with behavioural state?

Group size did not vary significantly between behavioural state (ANOVA, $p = 0.593$). Gregariousness was similar between all behavioural states (Table 3.3). Social differentiation was highest when travelling, although all behavioural states show well differentiated societies (Table 3.3). Individuals associated non-randomly under all behavioural states.

Table 3.3 - Results for associations between pairs of individuals. Mark rate for the population 0.51. Sampling period: day; group association: encounter. Estimate of social differentiation using the maximum likelihood method. S < 0.3 – homogeneous society, S > 0.5 – well differentiated society, S > 2.0 – extremely differentiated society. Average gregariousness is calculated using individual gregariousness, the sum of an individual's association indices, for the population. Associations are considered non-random when p-value of CV < 0.01, and are marked in bold.

Behaviour	Mean group size (S. D.)	Mean group size with mark rate updated	Social differentiation	Gregariousness (S. D.)	CV of HWI	Permuted CV of HWI	p-value of CV of permuted HWI
Feeding	3.00 (2.42)	5.88 (4.75)	4.92	4.19 (2.45)	10.97	10.87	**0.001**
Resting/Milling	3.0 (2.48)	5.88 (4.86)	2.98	4.73 (3.14)	9.05	9.02	**0.001**
Socializing	3.11 (2.46)	6.10 (4.82)	1.80	4.72 (2.70)	7.16	7.15	**0.001**
Traveling	3.18 (2.59)	6.24 (5.07)	7.10	4.29 (2.51)	10.76	10.39	**0.001**

Do association preferences between individuals change with different behavioural states?

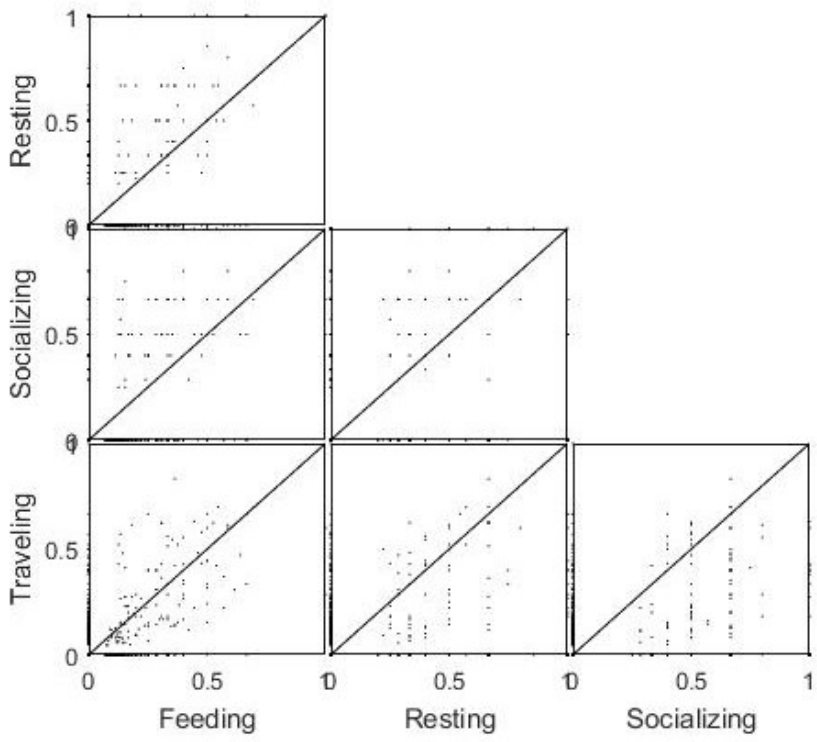

Figure 3.1 – Plots comparing the HWI of dyads of individuals between behavioural states. The diagonal represents the case where dyads would be expected to fall if behavioural state had no relationship with strength of association.

There were cases where dyads were only observed associated in one of the behavioural states (Figure 3.1). Dyadic associations tended to be higher when resting or socializing compared with travelling or feeding (Figure **3.1**).

3.3.2 Are associations between units affected by behavioural state?

The number of units in a group does not vary significantly between behavioural state (ANOVA, p = 0.172). Gregariousness was similar between all behavioural states (Table 3.4). While the estimates of social differentiation all suggest well-differentiated societies at the unit level, there

was no evidence for preferred or avoided associations between units for any behavioural state (Table 3.4).

Are association preferences between units changing with different behavioural states?

Associations between dyads of units were generally low, with some cases having no relation between behavioural state and strength of association. There were many cases where pairs of units were only observed associated in one behavioural state. Associations were higher when socializing (Figure **3.2**).

Table 3.4 –Associations between pairs of units. Sampling period: day; group association: encounter. Estimate of social differentiation using the maximum likelihood method.

Behaviour	Mean group size (S. D.)	Social differentiation	Gregariousness (S. D.)	CV of HWI	Permuted CV of HWI	p-value of permuted HWI
Feeding	2.05 (1.41)	1.41	1.58 (0.24)	1.78	1.78	0.492
Resting/Milling	2.03 (1.22)	1.24	1.38 (0.28)	2.80	-	-
Socializing	2.21 (1.65)	0.62	1.59 (0.44)	2.52	2.52	0.407
Traveling	2.26 (1.57)	1.54	1.37 (0.18)	1.55	1.53	0.172

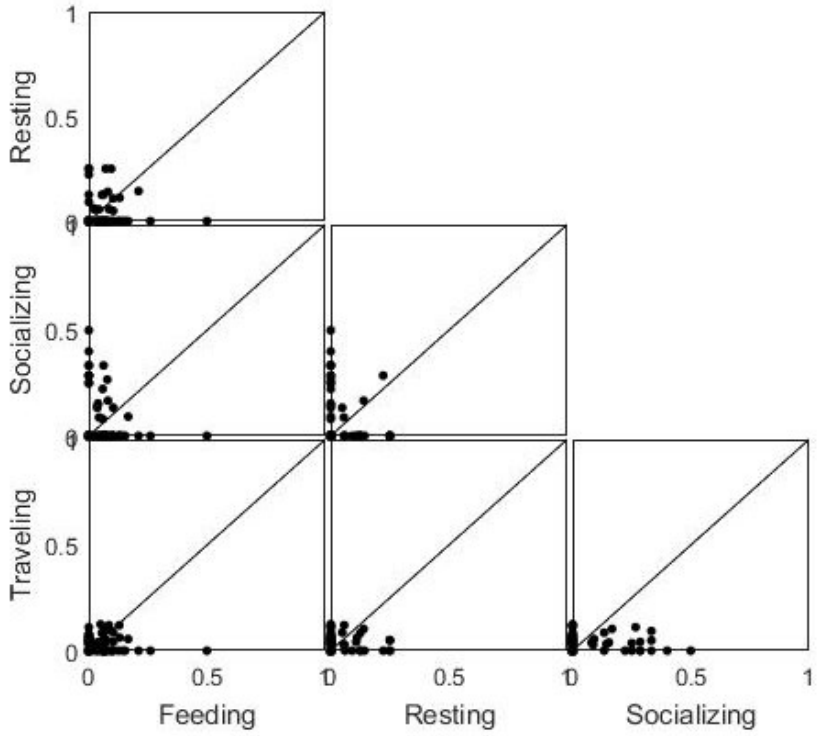

Figure 3.2 – Plots comparing the HWI of dyads of units between behavioural states. The diagonal represents the case where dyads would be expected to fall if behavioural state had no relationship with strength of association.

3.4. DISCUSSION

3.4.1 Limitations

Encounters where individuals were resting and socializing were less common in the analysis due to poor coverage. In both behavioural states it is more difficult to collect quality photos for identification, and hence to reach good coverage, and so inclusion in the data set. When individuals are resting they tend to log at the surface, and in most cases the water partially obscures the dorsal fin. The same happens when the speed is very slow and the dorsal fin barely

breaks the surface of the water. There are similar issues with socializing. When individuals perform aerial behaviours it is difficult to collect good identification photographs, and the same happens when there is body contact between individuals. There were also many encounters where socializing was one of several behavioural states recorded; these multiple records were removed from the analyses. For instance, in the feeding/socializing case, individuals might show prolonged tail-out dives, as well as many active behaviours with body contact when at the surface. This is a source of ambiguity, hence the removal of encounters with multiple behavioural states from the analyses.

3.4.2 Do associations among individuals vary with behavioural state?

Mean group size was similar among all behavioural states. When comparing these values with the ones obtained for all behavioural states combined in chapter 1, they are much smaller. This is due to the removal of encounters with several recorded behavioural states, which tend to include more animals than encounters with only one behavioural state. This is particularly the case for feeding/social encounters.

Group size and gregariousness are closely related, given that gregariousness is defined as the tendency for an individual to form associations (Pepper *et al.* 1999). Similar group sizes between behavioural states translate into similar average gregariousness for individuals between behavioural states. This means that there is no change is association rates between behavioural states.

It was not unexpected to find preferences and avoidances between individuals under different behavioural states, since we know this to be case overall (Ottensmeyer and Whitehead 2003; Chapter 1). While all behavioural states show well-differentiated societies, travelling shows a much higher social differentiation than other states. According to my hypothesis, I would expect

feeding to have a higher social differentiation if units tended to have specific feeding patterns. Given the high social differentiation for feeding this is still very possible, although the preferences seem to be more distinct while travelling.

The individuals that show highest associations (HWI>0.75) within behavioural states are not the same across different states. This denotes a preference for individuals to associate differently according to behavioural states, showing the possibility of varying associations across behavioural states.

Most individuals with high associations within a behavioural state belong to the same unit. There are several cases of individuals not attributed to units that show high associations with each other. Some are key individuals that have no identified closest companions, while others have not been identified enough times during the study period to be considered key individuals or closest companions. There are only three cases of individuals in a unit having a high association with an individual not affiliated to a unit: Individual 59 (Unit C) with 155 and 252 while resting; and individual 808 (unit H) with 660 while feeding. Individuals 155 and 255 do not have enough observations to be considered for the unit analysis. Both individual 155 and 252 were only seen in 3 encounters while resting, all of them with 59. Individual 660 is a key individual, but with no identified closest companions. It was only identified in 3 encounters while feeding, two of them with 808, the third with no other unit. Attributes such as sex or age mould association preferences in other species. For instance, in bottlenose dolphins adult females show lower associations with each other, and may be considered acquaintances; adult males show higher associations with other adult males, and may be considered affiliates; while juveniles base their associations more on short term or specific behavioural needs, since they are less constrained by social organization than adult individuals (Gero *et al.* 2005). However, in meerkats, sex and social

status have no influence on which individuals groom or get groomed. Individuals of different ages and masses groom each other, regardless of social status or sex (Madden *et al.* 2011). Unfortunately, demographic information is not available for our pilot whale population.

3.4.3 Are associations between units affected by behavioural state?

The mean number of units in a group was also similar for all behavioural states, with each group having a mean of two units present. I am probably encountering the same source of error as with individuals, by discarding large encounters with several behavioural states, and an underrepresentation of socializing. As with individuals, units have similar gregariousness across behavioural states, due to the similarity of the two definitions. This again reflects the lack of change in association rates between behavioural states.

Comparing the social differentiation values for individuals and for units, the latter are much lower. I believe the high social differentiation of individuals can be explained by the structure in the population caused by individuals associating in units. When looking at units only, it informs us much better on the differences caused by behavioural states. These are quite similar across behavioural states between units, in contrast to between individuals across behavioural states. Socializing has a lower social differentiation, but still within the range of a well-defined society ($S > 0.5$, Whitehead 2008). This aligns with the hypothesis that associations while socializing are quite diverse. Feeding, travelling and resting pilot whale units, on the other hand, form well-defined societies with similar social differentiations.

I uncovered no statistically significant preferred/avoided associations between pairs of units across behavioural states. This might be due not having enough data to detect these patterns, or that units show no distinct preferences when associating. It seems more likely that there are not enough data to detect these.

We know from chapter 1 that the K complex serves as connecting role between units. This is possibly due to its size, which facilitates interacting with more individuals, and consequently with more units. Hence, I was expecting to see higher association rates with other units, which was not the case. The K complex shows similar mean and maximum associations to other units across behavioural states.

Given that pilot whale units in the Straits of Gibraltar have different C and N signatures (de Stephanis *et al.* 2008a), and hence feeding preferences, I hypothesized that if we are faced with a similar scenario in this population we would see dyads of units showing feeding preferences. The associations of units while feeding was generally low, with the only dyad with a high association (HWI ≥ 0.5) being C and A. This dyad was only seen together in two encounters while feeding. Unit B was present in one of the encounters, and unit G in the other. The high association coefficient is due to unit C only being seen in one other encounter in this behavioural state, and without any other units.

Since socializing includes mating behaviour, I hypothesized that associations between units in this behavioural state would be more diverse. Associations in this state both vary more widely and show higher maxima than in any other state. This reveals a preference for units to socialize when they meet. This is after removing all mixed state encounters from the analysis, in which socializing is featured prominently. The spread of associations between units in this behavioural state indicates that it is possible, although not cerain, that my hypothesis is correct.

With travelling, I hypothesized the possibility of units sharing preferred travelling routes. These routes might be related to *where* units travel (*e.g.* some units my prefer to travel close to shore, while others prefer to travel between 1 and 2 km offshore); or to *when* units travel (*e.g.* some units my prefer to spend time inshore during the day and travel offshore during the evening,

while other prefer the opposite). In this case, there should be dyads of units with high associations while travelling, while others were closer to zero. All associations between units in this behavioural state were quite low, with no dyads standing out as higher than the rest. It seems highly unlikely that units share preferred travelling routes in this population at this scale.

3.4.4. Conclusion

In conclusion, association preferences between individuals vary according behavioural state. Some of this variation can be explained by structure caused by units, but not all of it. It would be interesting to reassess this information when demographic information, such as age class and sex, for more individuals in the population is available. There seems to be some evidence for association preferences between units, but not across all behavioural states. Unfortunately units had rather few identifications together, which made patterns hard to discern.

CHAPTER 4: KINSHIP PATTERNS OF LONG FINNED PILOT WHALE S (*GLOBICEPHALA MELAS*) OFF NORTHERN CAPE BRETON ISLAND, NOVA SCOTIA

4.1. INTRODUCTION

Kinship, or how individuals are related, plays an important role in the social structure of mammals. It influences whether individuals live in groups and, if they do, which individuals stay with their natal group (phylopatry) and which disperse. Mammals usually show sex-biased dispersal, with females being phylopatric, while males disperse (Greenwood 1980). There are four evolutionary models that explain this pattern, all related to kinship patterns: inbreeding avoidance; kin selection; local mate competition; and cooperative behaviour among kin (reviewed by Handley and Perrin (2007)). Within these models there are selective pressures that can favour dispersal or phylopatry. The main selective pressures that are thought to favour dispersal from the natal group are related to resource availability, kin competition and inbreeding avoidance. Selective pressures that do not favour dispersal are related to increased risk of mortality outside the natal group, familiarity with the natal area and kin cooperation (Handley and Perrin 2007). The pattern of dispersal seems to be influenced by social complexity. Differences in dispersal between sexes are more marked in highly social mammals that are polygynous and live long lives (Greenwood 1980, Pusey 1987, Smale *et al.* 1997).

Female phylopatry can produce matrilineal socially stable groups, marked by high intra-group kinship, as in elephants (*Loxodonta* sp, Moss and Lee 2011) and sperm whales (*Physeter macrocephalus*, Christal *et al.* 1998; Gero *et al.* 2007). In some matrilineal societies, unrelated males accompany groups and breed with the females, for a certain amount of time, as is the case with lions (*Panthera leo*, Schaller 1972) and meerkats (*Suricatta suricata*, Doolan and

Macdonald 1999). But female phylopatry does not always result in matrilineality. Bottlenose dolphins (*Tursiops truncatus*) live in fission-fusion societies (Connor *et al.* 2000) even though some populations have male-biased dispersal (Krützen *et al.* 2004; Bilgmann *et al.* 2007; Wiszniewski *et al.* 2010). Dispersal happen from their natal groups, so even though male home ranges can still overlap with their mother's, they don't spend most of their time in the same groups. Bottlenose dolphin groups can present a mix of related and unrelated individuals.

Long finned pilot whales (*Globicephala melas*), henceforth referred to as pilot whales, live in stable social units (Amos *et al.* 1991, 1993; Ottensmeyer and Whitehead 2003; de Stephanis *et al.* 2008a, Chapter 1). In the Faroe Islands, social structure was studied using grinds – groups of whales that are driven ashore by fisherman for slaughter. These groups are quite large, up to over a hundred individuals of both sexes, which are all related, although the males present did not sire the calves in the group (Amos *et al.* 1991, 1993). This was the first suggestion of *bisexual natal phylopatry* for this species. Bisexual natal phylopatry is defined as both sexes staying with their natal groups, which means there is little to no dispersal of males or females.

In the population of long-finned pilot whales off Cape Breton several stable units were identified (Ottensmeyer and Whitehead 2003, Chapter 2). Units interact forming labile groups that break apart after hours to weeks. It has been hypothesized that units are extended matrilines, and the possibility of bisexual natal phylopatry was again brought up by Ottensmeyer and Whitehead (2003), but no molecular studies had been performed in this population at that point. The resident population off Gibraltar was also found to comprise of social units (de Stephanis *et al.* 2008a), as with the population off Cape Breton, but on a small scale. *Line units* are about half the size of the Cape Breton units, and come together to form pods. Line units contain males and females, but matrilines and relatedness patterns were not investigated.

Bisexual natal phylopatry, from a social point of biew, is extremely rare in mammalian societies. It was first verified in *resident* orcas (*Orcinus orca*) in the Eastern North Pacific. Orca pods are cohesive groupings of individuals that stay together for more than half the time they are observed. The resident orcas are matrilineal, where both males and females stay with their natal pod (Bigg *et al.* 1990; Baird 2000). The resident-type orcas in the northwest Pacific show a similar structure, with matrilineal units where at least some individuals of both sexes present phylopatry (Ivkovich *et al.* 2010). Pods are very stable, where births and deaths are usually the only way to gain or lose individuals (Bigg *et al.* 1990; Ivkovich *et al.* 2010). Bisexual natal phylopatry has also been suggested for brown long-eared bats (*Plecotus auritus*), when returning to their summer colonies after winter hibernation (Burland *et al.*, 1999; Burland *et al.*, 2001); and for Bornean orangutans (*Pongo pygmaeus*), although in this case it might be the result of habitat fragmentation that is preventing the males from dispersing, as is customary in this species (Goossens *et al.*, 2006).

In this chapter I investigate the relationship between pilot whale kinship and association patterns. I expect to find that individuals in units are more related to each other than to individuals outside of their units. I also expect to find both males and females in units. These conditions would point toward bisexual natal phylopatry at the unit level, as hypothesized by Amos *et al.* (1991, 1993) and Ottensmeyer and Whitehead (2003). If matrilineality is present, I also expect to see only one mitochondrial haplotype per unit.

4.2. METHODS

4.2.1 Biopsy sampling

Sample collection was by remote biopsy sampling, during July and August of 2010 to 2012, off Pleasant Bay harbour (46° 49' N, 60° 47' W), Cape Breton, from a semi-rigid 4.5-m inflatable

zodiac. Up to two sampling trips were performed daily, in the mornings (06:00am to 09:30am) and evenings (07:00pm to 09:30pm). Times were chosen to not conflict with commercial whale watching trips, while having sufficient daylight to work. No sampling trips were made when Beaufort Sea State was higher than 4. Trips covered up to 40 km south to 30 km north of Pleasant Bay harbour, while remaining less than 8 km offshore.

Once a group of pilot whales was sighted the vessel approached it parallel to the group's direction of movement. Individuals were scanned for identifying marks on their dorsal fin that could be used to (1) match it to the photoidentification database and (2) to insure they were not previously sampled. If there were no identifiable and unsampled individuals in a group we resumed the searching for a different group. When an individual was chosen to be sampled, the vessel kept travelling parallel to it and approached to an approximate 7 metre range. The dorsal fin of the chosen individual was photographed and when a good quality photograph had been collected we deployed a sampling dart, which collected skin and blubber. The shooter aimed at the dorsal-lateral region directly below, and slightly posterior to, the dorsal fin. Sampling was only attempted when the chosen individual was behaving in a predictable manner and when a clear shot was possible. Video footage of sampled individuals was collected before, during and after sampling to assess behavioural responses (Kowarski *et al.* 2014).

Two crossbows were used in the sampling. An Excalibur Vixen II crossbow with a draw weight of 68 kg until August 11, 2012; and an Excalibur Apex with a draw weight of 40 kg for the remainder of the field season. The change in draw weight reduced the damage to the arrows and the force hitting the sampled individuals. Sampling darts were obtained from Finn Larson (CETA-DART, Denmark) (Palsbøll *et al.* 1991). Darts were equipped with a 2 cm × 0.7 cm three-pronged sampling tip which prevented the loss of samples, and a hole for air escape. A

compressed foam collar followed the tip, preventing the tip from penetrating the skin more than necessary; allowing the dart to rebound on impact with the whale; and acting as a flotation device for easier retrieval. Between sampling events tips were cleaned and sterilized. To avoid contamination, tips were individually wrapped in tin foil, which was only removed once the tip was screwed on to the dart and the shooter was ready to sample a new individual.

4.2.2 Photographic data collection and photoidentification

Data were collected in July and August, from 1998 to 2000 and 2002 to 2010 from 13-metre whale watching vessels off the northwest coast of Cape Breton Island, Nova Scotia, Canada. From 1998 to 2000, the vessel departed from Bay St. Lawrence harbour (47°02' N 60°29'W), and from 2002 to 2011 it departed from Pleasant Bay harbour. Up to five trips were conducted daily, lasting a maximum of 2.5 hours each, and covering up to 40 km south to 30 km north of the harbour, and a maximum of 8 km offshore. Trips were only performed when Beaufort Sea State was below 6.

Usually, two researchers collected behavioural and photographic data on each trip. The area was scanned for the presence of pilot whales, and when a group was sighted the vessel approached it slowly and kept parallel to the whales' movement or stayed stationary with the motor on idle or turned off.

Photoidentification photographs of the dorsal fin area (Auger-Methe and Whitehead 2007) were collected using a Canon EOS Elan IIe (film) or Canon Rebel G (film) between 1998 and 2003 with a 300mm autofocus lens, and a Canon EOS-10D (digital) or Canon 30D (digital) with a 200mm or 300mm autofocus zoom lens from 2004 onward.

Photographs were rated according to focus, size, orientation and exposure. Finscan (Araabi *et al.* 2000) was used to find a match in the project database. Individuals were identified using the number and position of mark points (MP), *i.e.* nicks and internal corners of notches, of dorsal fins (Ottensmeyer and Whitehead 2003; Auger-Methe and Whitehead 2007). This populations' mark rate - the proportion of individuals that were identifiable was estimated to be 0.51 (Chapter 2). In the case of biopsied individuals, only the best photograph of each individual was used to match with the database.

4.2.3 Sexing individuals

DNA was extracted using the phenol:chloroform extraction method described in Wang *et al.* (2008). Sex of individuals was determined using a multiplex PCR of two primer pairs: one that amplifies a ~400 bp portion of the ZFX/ZFY gene (present on both sex chromosomes); and one that amplifies a ~200 bp portion of the SRY gene (only on the Y-chromosome) (Gilson *et al.* 1998). PCR was performed on 20 ng of purified DNA in a 20 µL reaction volume that contained 1X Taq polymerase PCR buffer, 0.2 mM each dNTP, 1.5 mM $MgCl_2$, 0.3 µM of each primer, 0.16 µg/mL BSA, and 0.05 U/µL Taq polymerase. PCR cycles were performed as follows: the first step at 94°C for 5 minutes, followed by 30 cycles comprised of denaturation at 94°C for 30 seconds, annealing at 55°C for 1 minute, and extension at 72°C for 1 minute. A final extension step was performed at 60°C for 45 minutes. The PCR products were then separated and visualized using agarose gel electrophoresis in 1.5% agarose gels stained with ethidium bromide.

4.2.4 Estimating relatedness

Kinship patterns were studied using a measure of relatedness. To determine relatedness between individuals I used microsatellite analyses. Twenty-two loci that are known to amplify in a wide number of marine mammals (Wang *et al.* 2008; Rooney *et al.* 1999) were tested with the

dataset (Supplementary Material **13**). Each loci was tested separately, with no multiplex reactions performed. For each loci PCR was performed on 20 ng of purified DNA in a 20 µL reaction volume that contained 1X Taq polymerase PCR buffer, 0.2 mM dNTP, 1.5 mM $MgCl_2$, 0.3 mM of each primer, 0.16 µg/mL BSA, and 0.05 U/µL Taq polymerase. PCR cycles were performed as follows: the first cycle at 95°C for 4 minutes, followed by 30 cycles comprised of denaturation at 95°C for 30 seconds, annealing at variable temperatures of 50°C, 55°C and 60°C for 30 seconds, and extension at 72°C for 30 seconds. A final cycle was performed at 72°C for 10 minutes. The PCR products were then separated and visualized using agarose gel electrophoresis in 1.5% agarose gels stained with ethidium bromide. The best annealing temperature were determined for each amplified loci.

Each individual was genotyped for the amplified loci in an ABI DNA sequencer (Applied Biosystems). I used GeneMarker® (Liu *et al.* 2011) to score loci for each individual. Loci were considered not variable when all individuals presented the same allele score. When scores varied across individuals, the loci were considered variable. Variable loci were used to determine relatedness between individuals.

Relatedness is defined as the probability that two individuals share an allele due to recent common ancestry. It can be estimated from genetic data using various mathematical equations – estimators. I used the R package 'related' (Pew *et al.* 2015) to determine which estimator is best for my dataset. This package allows me to calculate relatedness using seven estimators (Queller and Goodnight 1989; Li *et al.* 1993; Ritland 1996; Lynch and Ritland 1999; Wang 2002; Milligan 2003; Wang 2007). It creates a simulated dataset of pairs of individuals with known relatedness using the real allele frequency data, and uses this information to determine what estimator is

most adequate for my dataset, and thus to construct a matrix of estimates of relatedness between individuals.

4.2.5 Comparison of kinship and association patterns

To compare kinship and association patterns I used data on both the coefficients of association (associations) and unit affiliation (Chapter 2). In chapter 2, I defined units as sets of individuals (key individuals and their constant companions) in nearly permanent mutual association. Unit affiliation was assessed using a modification of the method employed by Christal *et al.* (1998) and Ottensmeyer and Whitehead (2003). Key individuals are identified on at least four days, each of these sightings separated by at least 30 days. Constant companions of key individuals are individuals seen on the same day as the key individual during at least three days, these sightings also separated by at least 30 days.

The data provided by the best relatedness estimator was used in a set of Mantel tests (Mantel 1976) in SOCPROG2.6 (Whitehead 2009). Mantel tests allowed me to test if the values in two square association matrices are correlated. The null hypothesis for Mantel tests is no correlation between values.

To test whether relatedness and general unit affiliation were correlated, I compared the relatedness matrix with a general unit affiliation binary matrix. This matrix indicates if individuals belong to the same unit (1) or not (0). The null hypothesis was that individuals in the same unit are as related as individuals in different units.

To test whether associations were correlated with relatedness, I compared the relatedness matrix with the coefficient of association matrix from chapter 2. The coefficient of association

matrix was restricted to only individuals that were genetically tested. The null hypothesis was that relatedness and associations were not correlated.

To test for female dispersal I compared relatedness of females within and between units using histograms, due to the low number of observations. The null hypothesis is that females are no more related to females in their own units than to females in other units. To test for male dispersal I compared relatedness between sexes within and between units using the same method. The null hypothesis is that males are no more related to females in their own units than to females in other units.

4.2.5.1 Testing the power of within/between units relatedness

To test the power of the relatedness analysis, I used an agent-based simulation of pilot whale demography, developed by Hal Whitehead (Supplementary Material **14**). This allowed me to create simulated populations that I could sample in the same manner as my actual genetic data: 3 units with only one individual sampled, 2 units with two individuals sampled, 1 unit with three individuals sampled and 1 unit with five individuals sampled. Each simulation of 500 years outputted population size, number of units, matrix correlation between relatedness and membership of the same unit, and p-value of Mantel test of this relationship. I could then compare the results from the simulated data with those from the real data, so assessing the power of the analysis.

I ran the first set of simulations with what was considered the most likely set of parameters for our population:

- K = 6000 rough equilibrium population size
- m_F = 0.068 mortality per year for females

- m_M = 0.078 mortality per year for males
- a_F = 7 age at maturity for females
- a_M = 12 age at maturity for males
- b = 0.3 birth rate per mature female per year at low population size
- u = 7 mean unit size
- T = 500 number of years of permutation
- σ = 0.103 SE of relatedness estimate

Each simulation was run 10 times with the same set of parameters (steps 1-4 in Supplementary Material **14**) and their results averaged. I then tried different sets of parameters, in order to find conditions that would align with my actual results (Supplementary Material **15**).

4.2.6 Analysis of mitochondrial DNA

To test whether units comprise of one or more matrilines I amplified and sequence a portion of the variable control region of mtDNA for individuals identified as members of units. Amplification used a multiplex PCR of two primer pairs, t-proM13F and Primer-2M13R, according to the BigDye® Direct kit (Thermo Fisher Scientific). PCR was performed on 10 ng of purified DNA in a 7.5 µL reaction volume that contained BigDye PCR Master Mix and 0.8µM of each primer. PCR cycles were performed as follows: the first step at 95°C for 10 minutes, followed by 35 cycles comprised of denaturation at 96°C for 3 seconds, annealing at 62°C for 15 seconds, and extension at 68°C for 30 seconds. A final extension step was performed at 72°C for 2 minutes. Product was then subject to cycle sequencing: the first step at 37°C for 15 minutes, followed by a second step at 80°C for 2 minutes, a third step at 96°C for 1 minute, and by 25 cycles comprised of denaturation at 96°C for 10 seconds, annealing at 50°C for 5 seconds, and extension at 60°C for 75 seconds. Product was then de-salted using ethanol precipitation (Brown 2006) and each

individual was sequenced on an ABI DNA sequencer (Applied Biosystems). Sequences were confirmed and trimmed using Chromas v2.6 (Technelysium Pty Ltd) and aligned in MEGA7 (Kumar *et al.* 2016) using Clustal-W (Larkin *et al.* 2007). The National Center for Biotechnology Information (NCBI) BLAST (Altschul *et al.* 1990) was used to query GenBank to confirm that sequences were pilot whale mtDNA and to compare with published haplotypes.

Under the hypothesis that units are strictly matrilineal, each unit should only contain one mtDNA haplotype (sequence).

4.3. RESULTS

4.3.1 Molecular data

Seventy six individuals were biopsy sampled, 72 of which had been photo-identified in the project database. Of the identified individuals, 15 were affiliated with units (Table 4.1). The sexing loci amplified for 75 of the 76 samples analyzed. Females comprised 44% of the data (n = 33), while males comprised 56% (n = 42).

Of the 22 microsatellite loci tested, 20 amplified for the species and 13 were variable within the 76 individuals sampled (Supplementary Material **16**). The R package 'related' suggests the best-supported relatedness estimator for this dataset is the one presented by Wang (2007), with a correlation coefficient between observed and expected values of 0.736. Relatedness values varied between 0 and 1, with more than half of the values below 0.10 (Figure 4.1).

Table 4.1 - Sampled individuals affiliated with units. Sex was determined using a multiplex PCR of two primer pairs, ZFX/ZFY and SRY. Haplotype was determined using a consensus region of 200 bp of a variable region of mtDNA.

Individual	Unit	Sex	Haplotype
82	D		A
280	D	M	A
370	K	F	A
407	K	M	A
449	K	F	A
511	K	F	A
632	K, U	M	B
307	O	F	A
374	O	M	A
515	O	F	A
482	P	M	A
887	P	F	A
376	Q	F	C
489	S	M	A
551	T	M	A

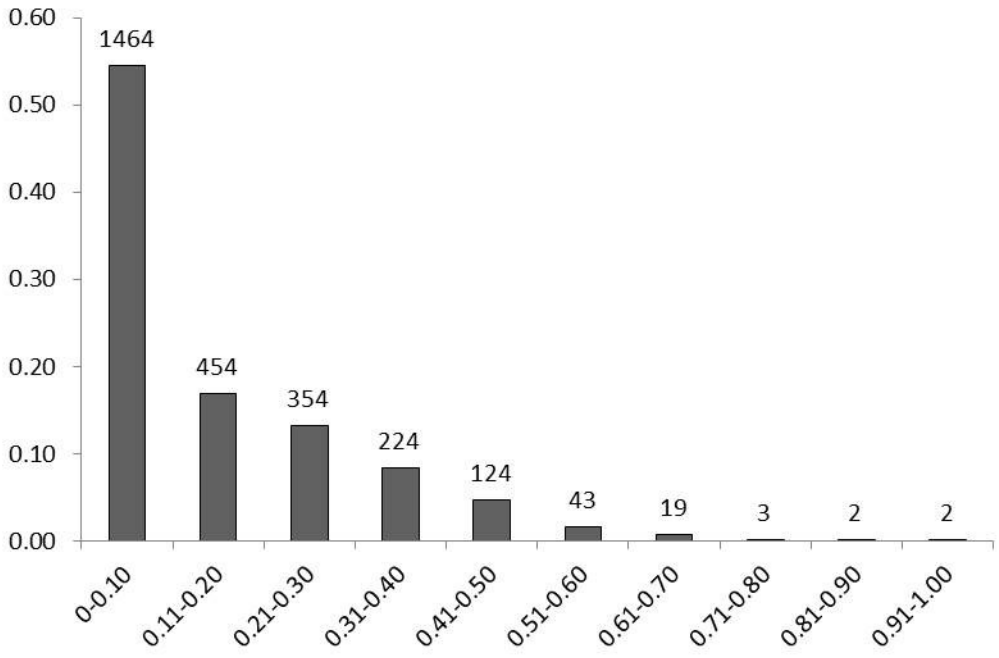

Figure 4.1 – Distribution of estimated relatedness between pairs of individuals. Relatedness was calculated using Wang's (2007) estimator.

The control region of the mtDNA was sequenced for all 15 individuals affiliated with units, with sequences varying in size. Sequences were truncated to a variable consensus region of 200 bp. A total of three haplotypes were found (Table 1). When compared with previously published results, haplotype A was found in Sable Island (Siemman 1994; Oremus *et al.* 2009); haplotype C was found in North East USA (Siemman 1994; Oremus *et al.* 2009; Monteiro *et al.* 2015); and haplotype B was not found on GenBank (Table 4.2). There were 13 individuals with haplotype A and one individual each with haplotypes B (#632) and C (#280).

Table 4.2 – Comparison of haplotypes found in individuals affiliated to units and previously published research in the North Atlantic (Siemman 1994; Oremus *et al.* 2009; Monteiro *et al.* 2015).

Haplotype	Variable location in sequences			Individuals	Found in the world
	32	50	52		
A	G	C	A	13	Sable Island
B	A	C	A	1	Not seen before
C	G	T	G	1	"Cape Cod"

4.3.2 Comparison of kinship and association patterns

A Mantel test comparing relatedness and whether individuals belong to the same unit (14 individuals) showed no significant correlation (1000 permutations, matrix correlation = -0.0123, p = 0.95). For the three units in which more than one individual was sexed, there were both males and females present (Table 1). Within-unit relatedness between pairs of individuals for units were R_K = -0.0251 for unit K, R_O = 0.121 for unit O and R_P = 0.182 for unit P. Mean relatedness within units is 0.103, and between units 0.113.

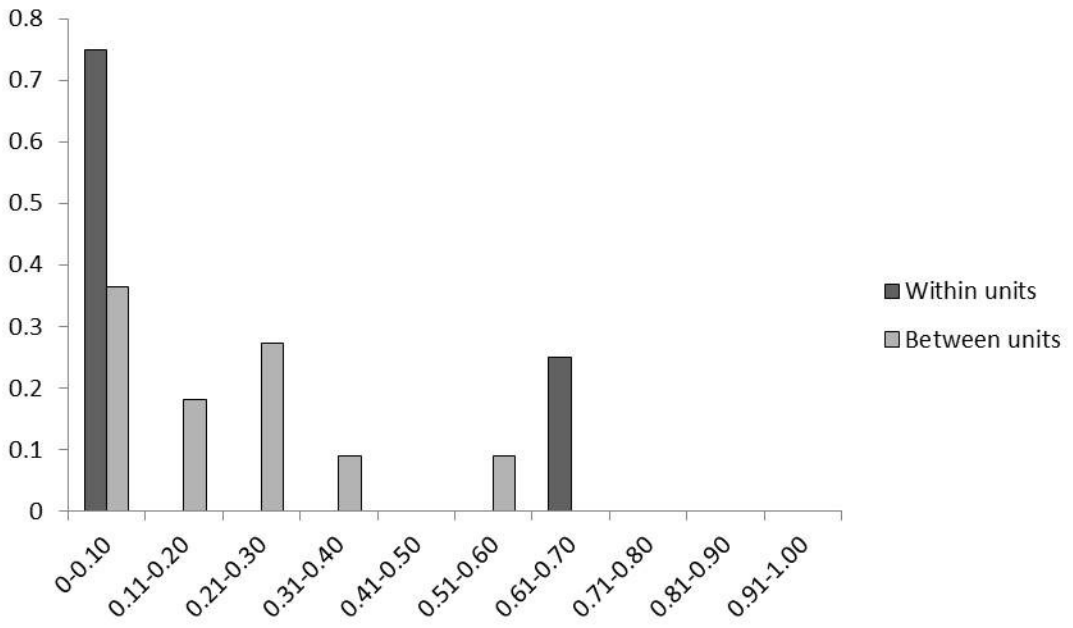

Figure 4.2 – Distribution of estimated relatedness between pairs of females within and between units. Relatedness was calculated using Wang's (2007) estimator. N=14 pairs

A Mantel test comparing the relatedness and association indices (62 individuals) showed no significant correlation (matrix correlation = 0.0252; 1000 permutations, p = 0.36). Associations between females within units and between units seem similar (Figure 4.2), as do associations between sexes (Figure 4.3).

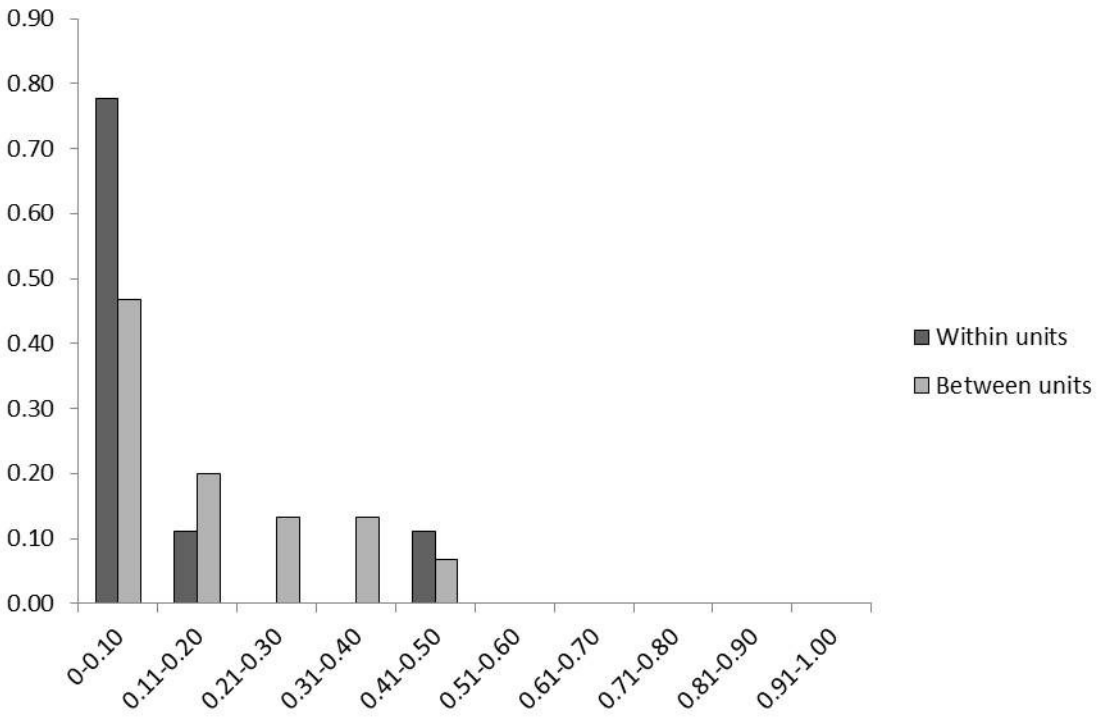

Figure 4.3 – Distribution of estimated relatedness between pairs of different sexes within and between units. Relatedness was calculated using Wang's (2007) estimator. N=574 pairs.

4.3.2.1 Assessing results using the demographic model

This modeling specifically assessed the result of no significant relationship between membership of the same unit and kinship. The initial set of parameters represents best estimates for the demography of this population. If the results were similar to those from the real data (*i.e.* often no significant relationship between kinship and co-unit membership), this would mean that these unexpected results could have been a result of low sampling effort so that the power of my analyses was too low to obtain the expected significant result. However, the results obtained were quite different between my analysis and the model.

With these initial parameters, the mean matrix correlation between unit membership and kinship was much higher for the model, at 0.462, compared to -0.0123 for the actual data. The p-

values are also different, with a mean significant p-value of 0.008 for the model while the p-value for my analysis was non-significant at 0.95. Thus the modeled populations showed a significant correlation between relatedness and unit-membership when sampled in the same manner as the real population, while the real population did not.

This means that, even with my small sampling pool, if the population had the demographic structure expected, there would have been a clear relationship between unit-membership and relatedness. This suggests the power of my analyses is sufficient and that the demographic/social structure of the pilot whale population does not fit the presumed model.

I then ran the model with a range of other combinations of demographic parameters to see whether I could replicate the actual results (Supplementary Material **15**). There was only one scenario in which the non-significant real result was replicated, when the population size was lowered to 500 individuals and unit size increased to 15-20 individuals.

4.3.3 Are units comprised of one or more matrilines?

Mitochondrial DNA data are consistent with the units being matrilineal (Table 4.1), with the possible exception of the K complex. However this analysis has little power due to the near ubiquity of haplotype A in the Cape Breton population.

4.4. DISCUSSION

4.4.1 Comparison of kinship and association patterns

Previous studies on pilot whale social structure (Amos *et al.* 1991, 1993; Ottensmeyer and Whitehead 2003; de Stephanis *et al.* 2008a) have introduced the hypothesis that pilot whales show bisexual natal philopatry at the unit level. For this hypothesis to be tenable units have to be comprised of both males and females; individuals within units, both males and females, have

to be more related to each other than to individuals outside of their unit; males and females both have to show low dispersal.

While we had a small number of individuals in units sampled, in all cases where there were multiple individuals sexed in a unit there were both male and females. Hence, the first condition is met. Results are similar to those for populations in the Faroe Islands (Amos *et al.* 1991, 1993), where grinds were found to contain both males and females, and off Gibraltar (de Stephanis *et al.* 2008a) where line units also contained both sexes. However, I found no evidence of correlation between how much time individuals spend together and how related they are, nor that individuals in units are more related to each other than with any other individual in the population.

Even though 76 individuals were sampled for this study, and most of them identified in the database, only a fraction of them were affiliated with units. Of the 15 individuals in units, three were the only individual identified in that unit. Only units D, K, O and P had multiple individuals genetically analyzed. This low sampling rate limits the power of my analyses when comparing associations and kinship patterns. So do my findings of no more relatedness within rather than between units mean something? An agent-based model was created to address this issue, which shows that if individuals within units were more related to each other than between units, my sampling would have shown it. This means that the low relatedness in individuals between units is not an artifact of low sampling. There is only a small set of parameters for which a data set, and methodology, like mine would produce non-significant correlations between unit co-membership and kinship. There are three primary scenarios that could explain these results:

Associations between individuals are random

One explanation for relatedness and associations to be unrelated is that associations between individuals are random within the population, and so that social units do not exist. This seems highly unlikely, given the results found for this species in the Faroe Islands (Amos *et al.* 1991, 1993), Gibraltar (de Stephanis *et al.* 2008a) and in this population (Ottensmeyer and Whitehead 2003, Chapter 2). In all these population there is evidence of the existence of social units.

Units are larger than expected, and population size is lower

One set of parameters which produce non-significant relationships between estimates of kinship and unit membership are those with a much lower population size, at 500 individuals, and larger units with 15-20 individuals. Results were non-significant only when both conditions were met. This explanation also seems unlikely, since it contradicts information known about pilot whale units in the population (Ottensmeyer and Whitehead 2003, Chapter 2). Pilot whale units in this population average 7 individuals, a number that seems common across the species, and at least 1231 individuals have been photoidentified in the study area over the study period.

Individuals move between units and form clans

Another explanation for the results found is that units are not completely stable over long periods of time. This would mean there is some mobility of individuals between units. This possibility is plausible given what was found previously in Chapter 2. There is evidence that the K complex is a unit that has become too large to maintain social bonds and is breaking apart. Individuals from the K complex could be creating their own units or associating with units that were already formed. But there may also be other processes, such as individuals or sets of individuals sometimes changing units.

However, my results seem to conflict with those of Amos *et al.* (1991, 1993), where individuals in grinds were found to be related and show bisexual natal phylopatry. Nonetheless, grinds were much larger than units, at around 100 individuals, and their temporal stability was not assessed due to the nature of the sampling events. It is possible that what Amos *et al.* (1991, 1993) was describing as a grind was not a single unit, but something like what can be considered a *clan* in killer or sperm whales. Clans are usually defined using acoustic parameters (*e.g.* Ford 1991, Yurk *et al.* 2002, Rendell and Whitehead 2003), but we can use a definition from social networking. A clan can be defined as a set of units that tend to interact more with each other than with others outside of that clan, the same definition as social clusters (Newman 2006). Hence, membership of units could still be labile across large periods of time, thus increasing between-unit relatedness, while individuals maintain phylopatry to the larger social entity of the clan. Applying this concept to this population, it is possible that the twenty one units found in this study are a part of a clan that uses the Cape Breton area.

4.4.2 Do units comprise of one or more matrilines?

Pilot whales are known for having low mtDNA haplotype diversity. Siemann (1994) found three haplotypes in the North Atlantic, Oremus *et al.* (2009) found 14 haplotypes world-wide but only six across the North Atlantic, and Monteiro *et al.* (2015) found six in the North Atlantic, but only one of them off the eastern USA. I found three haplotypes in individuals affiliated with units, which agrees with previous studies. Unfortunately, this low diversity makes it impossible to confirm if units are matrilineal. It has to be noted that one individual in unit K has a different haplotype than all other four individuals sampled in the same unit. But, since it is only one case, it gives us very little information.

The most interesting finding about haplotypes does not pertain to social structure, but to population structure. This population summers in Cape Breton, but where it spends the remainder of the year has not been studied. Only haplotype B, found in one individual, is a match to the "Cape Cod" whales (Siemann 1994). Thirteen of the fifteen individuals analyzed belong to haplotype A, which matches with 3 animals stranded in 1991 on Sable Island on the Scotian Shelf (Siemann 1994). This is strong evidence that these whales belong to a Scotian Shelf/ Gulf of St Lawrence population. The latest size estimates, through aerial surveys, are of around 6000 individuals (Lawson and Gosselin 2009) for the Scotian Shelf and Gulf of St Lawrence.

Not all individuals in the sampling pool were sequenced for mtDNA, only the ones affiliated with units. Subsequent studies on this population should focus on determining the haplotypes of the remaining individuals and performing population analyses. This is especially important given that pilot whales are considered *Data Deficient* by IUCN (Taylor *et al.* 2008), and not much is known about their population structure in the North Atlantic.

In conclusion, the lack of correlation between kinship and relatedness patterns makes it difficult to assess the notion of bisexual natal phylopatry at the unit level for this population. It does provide interesting insights on sociality, with the most likely explanation for the patterns observed being the movement of individuals between social units, instead of completely discreet units, over time. I could not assess matrilineality due to low haplotype variability. But mtDNA analyses provided us with new information about population structure, linking the Cape Breton population with those on the Scotian

CHAPTER 5: USING PHOTOGRAPHY TO DETERMINE SEX IN PILOT WHALES (GLOBICEPHALA MELAS) IS NOT POSSIBLE: MALES AND FEMALES HAVE SIMILAR DORSAL FINS[4][5][6]

Photo-identification is used to study populations, movements and social structure (*e.g.*, Bigg *et al.* 1987, Ottensmeyer and Whitehead 2003, Oremus *et al.* 2007). All of these analyses are more informative if the sexes of the identified individuals are known. In a few ideal cases the identification photograph itself contains a strong indicator of sex. For instance the great sexual dimorphism in the size and shape of the dorsal fin in adult killer whales (Orcinus orca) allows sex to be determined together with individual identity from photographs (Bigg *et al.* 1987).

Long-finned pilot whales (Globicephala melas) are delphinids, almost entirely black or dark colored. They present three lighter areas of skin, varying from cream to white: the saddle patch, located posterior to the dorsal fin; the post-orbital eye blaze, located above the eyes; and an anchor shaped patch on the throat area, extending ventrally (Sergeant 1962). Adult size length can reach up to 4.72 m for females and 6.10 m for males (Sergeant 1962). The sexual dimorphism of the species is also present in the size of the dorsal fin. Because dorsal fin size increases isometrically with body length, adult males have bigger dorsal fins than females (Bloch *et al.* 1993). It has also been suggested that dorsal fin shape differs between the sexes, with males showing a thicker edge, a more rounded contour and a more rounded tip (Sergeant 1962).

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[4] This chapter has been published as a note in Marine Mammal Science. The full reference is: Augusto, J. F., Frasier, T.R. & Whitehead, H. (2013). Using photography to determine sex in pilot whales (Globicephala melas) is not possible: Males and females have similar dorsal fins. Marine Mammal Science 29(1): 213–220. DOI: 10.1111/j.1748-7692.2011.00546.x

[5] Authors' contributions: Joana F. Augusto (JFA), Hal Whitehead (HW): Developed the research idea; JFA collected the behavioural data 2009 onwards and HW contributed with previous data; Timothy R. Frasier (TRF) collected skin biopsies with JFA; JFA analyzed the data with contributions from HW and TRF; JFA wrote the manuscript; HW and TRF contributed with comments and edits on the manuscript; JFA reviewed the manuscript during the peer-review process

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Shape can be analysed using digital photography and shape analysis methods, such as the elliptical Fourier descriptor analysis (Kuhl and Giardina 1982). This method has been widely used to describe shape in different taxa, such as petals of Japanese primrose (*Primula sieboldii*) (Yoshioka *et al.* 2004), roots of Japanese radish (*Raphanus sativus* L.) (Iwata *et al.* 1998), wings of mosquitoes (*Ritera culicidae*) (Rohlf and Archie 1984), fish otoliths (Reig-Bolano *et al.* 2010) and dorsal fins of bottlenose dolphins (*Tursiops truncatus*) (Rowe and Dawson 2009). This method also has the advantage of analyzing shape independently of size (Kuhl and Giardina 1982).

The population of pilot whales that summers off Cape Breton, Nova Scotia, Canada has been the subject of study since 1998 (Ottensmeyer and Whitehead 2003). Individual pilot whales have been identified using photo-identification, based on the number and location of mark points in their dorsal fins (Auger-Methe and Whitehead 2007). Saddle patch color and density were also found to be useful when identifying individual pilot whales. Although, given the high number of individual pilot whales identified in this population, the amount of photographic data collected each year, and that saddle patch pattern is not included in any photo-identification software, it has not been used as a photo-identification trait for this population.

Following Sergeant's (1962) suggestion, we investigated whether pilot whale dorsal fin shape, coupled with the photo identification traits saddle patch and number of mark points, were different enough between sexes for us to be able to predict sex based on photographic data.

Data were collected during July and August 2010 off Pleasant Bay, Cape Breton, Canada. Skin biopsies of 20 individuals were collected using a crossbow (Excalibur Vixen) from a distance from 10 to 30 m to the individual. Bolts with a compressed foam stop collar were used so that penetration would not be deeper than the tip (25 mm), allowing it to rebound on impact and enabling it to float. These were fired to the mid lateral region, below and caudal to the dorsal

fin. Skin samples were stored in solution of 20% DMSO solution saturated with salt (Seutin *et al.* 1991). Photographic data were collected prior to and during biopsy using a Canon EOS 400D with a 70-300 mm lens. Only individuals that were identified in the population catalogue and seen for more than two years in the area were sampled.

DNA was extracted using the phenol:chloroform extraction method (Sambrook and Russel 2001). Sex of individuals was determined using a multiplex PCR of two primer pairs: one that amplifies a ~400 bp portion of the ZFX/ZFY gene (present on both sex chromosomes); and one that amplifies a ~200 bp portion of the SRY gene (only on the Y-chromosome) (Gilson *et al.* 1998). PCR was performed on 20 µg of purified DNA in a 20 µL reaction volume that contained 1X Taq polymerase PCR buffer, 0.2 mM dNTP, 1.5 mM $MgCl_2$, 0.3 mM of each primer, 0.16 µg/mL BSA, and 0.05 U/µL Taq polymerase. PCR cycles were performed as follows: the first cycle at 94°C for 5 min, followed by 30 cycles comprised of denaturation at 94°C for 30 s, annealing at 55°C for 1 min and extension at 72°C for 1 min. A final cycle was performed at 60°C for 45 min. The PCR products were then separated and visualized using agarose gel electrophoresis in 1.5% agarose gels stained with ethidium bromide.

Figure 5.1 - Photograph of a pilot whale dorsal fin, illustrating the line that runs from the anterior to the posterior insertion point of the dorsal fin.

Photo-identification pictures collected during the biopsy protocol were classified in terms of focus, size, exposure, percentage of dorsal fin visible in the frame, and orientation of the dorsal fin according to the camera. Special attention was given to orientation of the dorsal fin, since dorsal fin shape would be distorted if the dorsal fins were not perpendicular to the axis of the camera lens. Pictures with the greatest total classification values for each individual were considered the best pictures. Dorsal fin images were extracted from the background, cropped at the base of the fin, flipped so that they were all facing the right side, and rotated so the base was horizontal (Adobe Photoshop CS5). Dorsal fin base was defined as the line than runs from the anterior to the posterior insertion point of the dorsal fin (Figure 5.1). The anterior insertion point is marked as the bottom of the concavity formed by the junction of dorsal fin and body. A reference line was then drawn following the main axis of the back, and the posterior insertion point was marked when it reached the dorsal fin (Rowe and Dawson 2009). All of the photographs were processed by the same person for consistency (by J. F. A.).

Dorsal fin shape was analyzed through Elliptical Fourier Description (EFD), using the software package SHAPE (Iwata and Ukai 2002). For each image, the contrasting areas between the white background and the dark dorsal fin were used to convert the image from RGB to black and white, facilitating shape detection. A closed contour of the dorsal fin was then extracted by edge detection and recorded as chain code (Freeman 1974). Each dorsal fin contour was saved as a set of sequential points, each a pair of x and y coordinates, measured counter-clockwise from an arbitrarily set starting point (Yoshioka *et al.* 2004).

EFD coefficients were calculated from the chain-coded contours by discrete Fourier transformation (Kuhl and Giardina 1982). These were normalized to be invariant according to size, rotation and starting point of the contour (Ywata and Ukai 2002). There are two methods of

normalization the first based on the ellipse of the first harmonic (Kuhl and Giardina 1982); the second based on the longest radius – the farthest point from the centroid to the contour (Ywata and Ukai 2002). The longest radius method allows manual alignment of the contours so it was chosen for the normalization, allowing the dorsal fin bases to be horizontal during the remaining analysis.

Shape of dorsal fin was determined based on the normalized EFDs using a sum of trigonometric functions – harmonics. Each contour was approximated using the first 20 harmonics. Results were summarized in a PCA (Rohlf and Archie 1984), based on the variance-covariance matrix of the EFD coefficients. The variance explained by each component was also visualized (Furuta *et al.* 1998). The coefficients of the EFDs were recalculated, making the score for each PCA to be equal to the mean plus or minus two times the standard deviation, and the scores of the remaining components to be zero. Then, an inverse Fourier transformation was applied to create the contour corresponding to each component.

To determine whether dorsal fin shape varied according to sex of the individuals, a discriminant analysis and multivariate variance analysis (Minitab 15) were performed using the statistically significant ($P<0.05$) PCA scores.

The saddle patch is a band of light pigmentation, located behind the dorsal fin (Sergeant 1962), that does not vary once individuals reach maturity. It can vary in color and pigmentation level (Auger-Methe and Whitehead 2007) between individuals. The pigmentation levels – sparse, medium, and dense – were assessed for each individual, based on the best pictures (Figure 5.2). A permutation test (R 2.12.2) was use to determine if the distribution of pigmentation level was related to sex of the individuals. Color – gray, white and cream – was not tested because it did not seem consistent between photographs of the same individual in different lighting conditions.

Figure 5.2 - Examples of saddle patch density. Saddle patches are within the rectangle. The left most picture represents a dense saddle patch, the center picture a medium saddle patch and the right most picture a sparse saddle patch.

Mark points are defined as nicks and internal corners of larger notches present in the dorsal fin trailing edge (Ottensmeyer and Whitehead 2003, Auger-Methe and Whitehead 2007). They are the basis for the photo identification of different individuals in the population. The number of mark points for each individual was determined, and a Mann-Whitney U test (Minitab 15) was applied to test whether the number of mark points was related to sex of the individuals. From the 18 individuals sexed, 11 were males and 7 females (Figure 5.3). The dorsal fin photographs of these individuals were used to calculate the standardized Elliptic Fourier coefficients. Dorsal shape variability was well summarized well by the first two principal component axes that explained more than 80% of the total variance (Table 5.1).

How each component affects dorsal fin shape is indicated in Figure 5.4. The mean shape sketched for each component separately (Mean), and the mean minus (-2 SD) and plus the standard deviation (+2 SD) are presented. The left most sketches represent the overlap between the three, illustrating the variability of the component. The non-overlapping areas represent where variability is largest.

Table 5.1 - Summary of results from the Principal Component Analysis on the coefficients of the Elliptic Fourier descriptors.

Component	Eigenvalue (10^{-4})	Proportion of variance (%)	Cumulative variance (%)
1	85.9	58.2569	58.2569
2	33.2	22.4907	80.7476
3	12.5	8.4585	89.2061
4	6.52	4.4229	93.6289
5	3.64	2.4703	96.0992
6	2.45	1.6643	97.7635

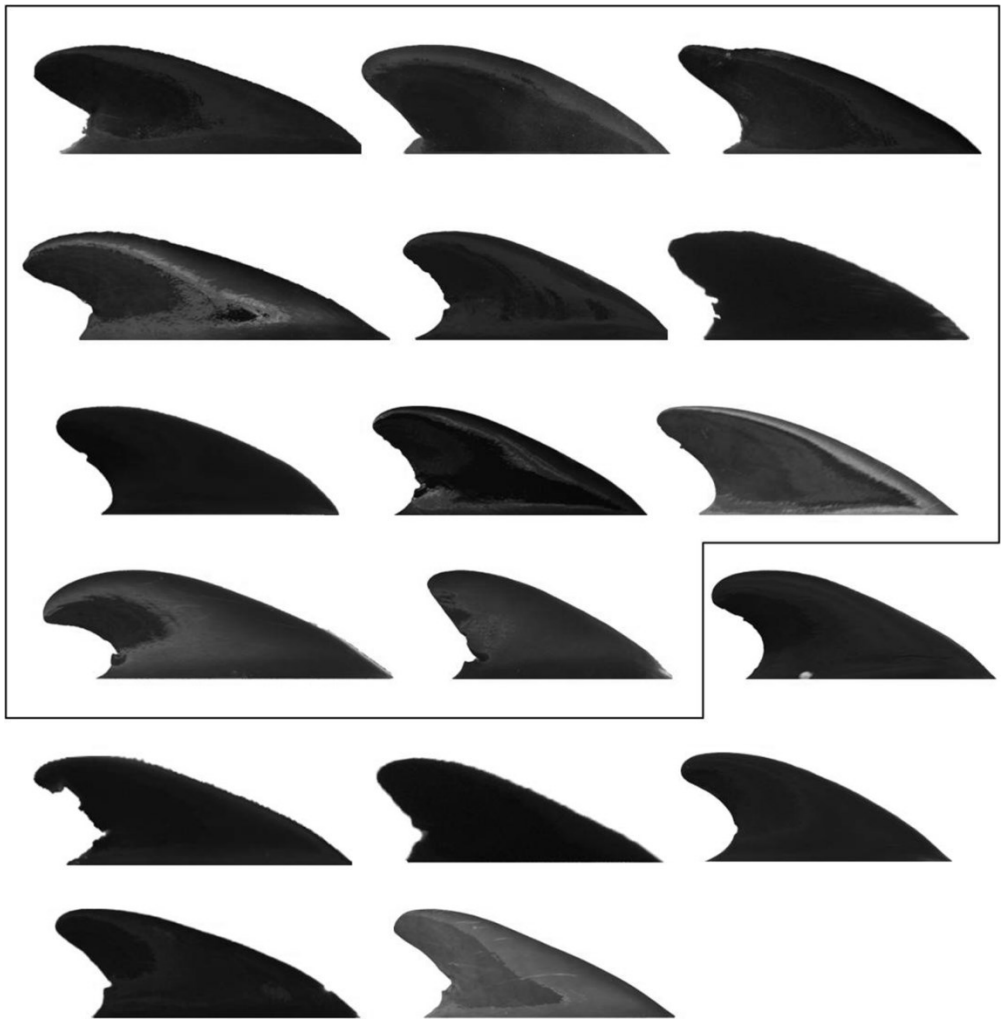

Figure 5.3 - Dorsal fins of sampled individuals. Males are on the inside of the polygon, females on the outside.

The first component relates to the height of the dorsal fin and distance from the tip to the anterior insertion point. The second component relates to the hang of dorsal fin tip relative to the anterior insertion point and how falcate the anterior area of the dorsal fin is.

The discriminant function analysis, with cross-validation, correctly classified only 56% (with linear response) and 44% (with quadratic response) of the individuals according to the first six principal components for dorsal fin shape. Variance analysis found no significant differences between sexes for the six first principal components (MANOVA, Wilk's Lambda = 0.52, F = 2.25, df = 5, 12, P = 0.119).

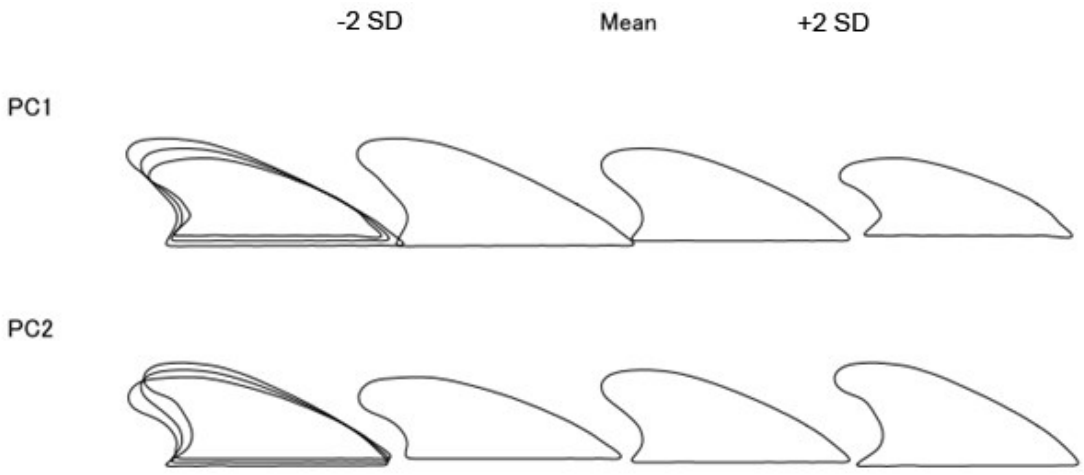

Figure 5.4 - Variation in dorsal fin shape, explained by the first two components of the PCA. PC1 represents the first component and PC2 the second component. Mean represents the mean shape for the component, -2 SD the mean shape minus standard deviation, and +2 SD the mean plus standard deviation. The leftmost sketch is the overlap of shapes for each component.

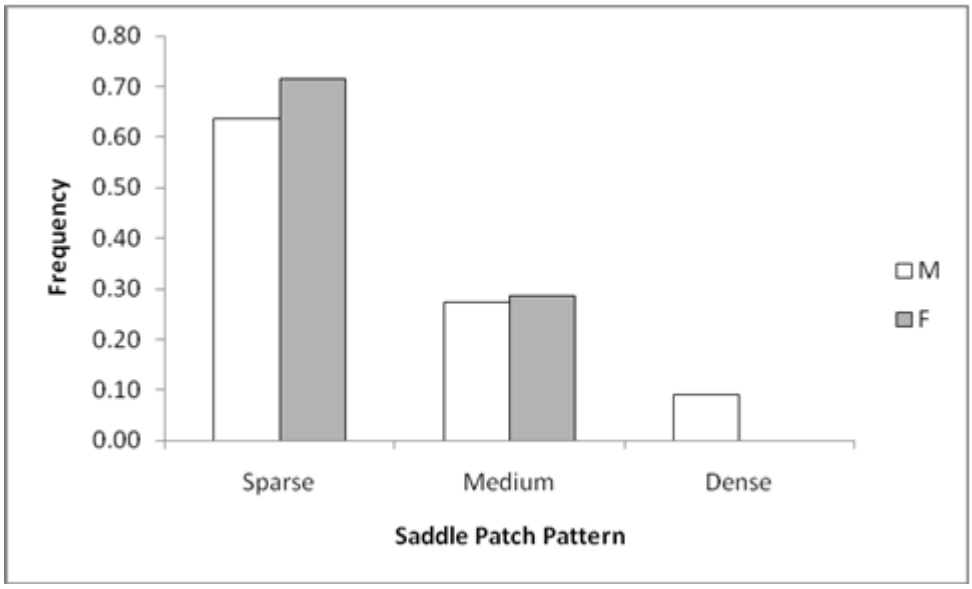

Figure 5.5 - Saddle patch density of males (M) and females (F) in the sampled population.

There was no relation between the distribution of saddle patch density and sex (permutation test, P=0.17; Figure 5.5).

Given that only individuals previously identified for this population were sampled, and only individuals with more than 2 mark points are identifiable (Ottensmeyer and Whitehead 2003), all individuals have at least two mark points. There was no significant difference between number of mark points for males and females (P=0.23; Figure 5.6). Contrary to prior suggestions (Sergeant 1962), male dorsal fins do not have a significantly more rounded contour or a more rounded tip. Male pilot whales do have larger dorsal fins than females (Sergeant 1962, Bloch *et al.* 1993) and human perception of shape can be altered by size factors (Yoshioka *et al.* 2004), s

o it is possible that the characteristics said to be typical of male fins appeared more prominent to the human eye because of a larger dorsal fin size. Elliptical Fourier descriptors analyze shape independently of size, so they can determine the variation in dorsal fin shape without the same biases as human perception. The number of mark points and the saddle patch density, traits used for photo-identification of individuals, also did not vary significantly between males and females.

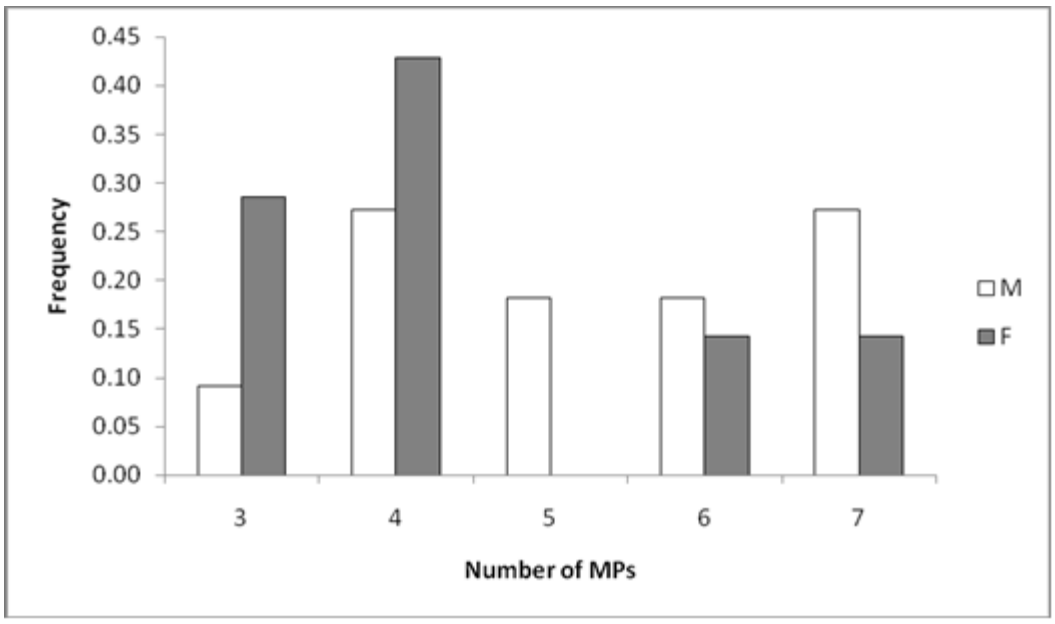

Figure 5.6 - Frequency of the number of mark points (MPs) possessed by males (M) and females (F) in the sampled population.

In summary, we found no substantial or significant difference between males and females in any of the analyzed parameters: dorsal fin shape, saddle patch density and number of mark points. Even though our sample size was small, if dorsal fin characteristics varied with sex as markedly as referred by Sergeant (1962), that variation would have been detected. Instead, we found that dorsal fin characteristics vary within sex. It does not seem possible, given the parameters used, to identify the sex of individuals using photo-identification photographs.

CHAPTER 6: CHARACTERIZING ALLOPARENTAL CARE IN THE PILOT WHALE POPULATION THAT SUMMERS OFF CAPE BRETON[7][8][9]

6.1 INTRODUCTION

In mammals, the care of young is mostly provided by the mothers (Kleiman and Malcolm 1981), but in some species others may also help: fathers, siblings or even unrelated individuals (Kleiman and Malcolm 1981, Riedman 1982, Jennions and MacDonald 1994, Woodroffe and Vincent 1994). These are considered alloparents. Alloparental care can be defined as any nonparent taking part in the process of raising young, by engaging in behaviors that benefit the young (Woodroffe and Vincent 1994). Alloparental care is linked to group living and sociality (*e.g.*, Konig 1997). It is often used as a synonym of cooperative breeding (Fernandez-Duque *et al.* 2009), although cooperative breeding can be defined more strictly as a proportion of females in the group not reproducing regularly, and instead helping to care for the young of others (Boomsma 2007, Cornwallis et al. 2010, Lukas and Clutton-Brock 2012). Alloparental care can be divided into two forms, direct and indirect (Kleiman and Malcolm 1981). In direct alloparental care there is an interaction with the young, which can increase its survival probability, such as grooming, huddling or providing food. When the behavior is not directed towards the young, but still influences its survival, it is considered indirect alloparental care, for example shelter construction and maintenance, or sentinel behavior (Kleiman and Malcolm 1981).

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[8] Authors' contributions: Joana F. Augusto (JFA), Hal Whitehead (HW): Developed the research idea; JFA collected the behavioural data 2009 onwards and HW contributed with previous data; Timothy R. Frasier (TRF) collected skin biopsies with JFA; JFA analyzed the data with contributions from HW and TRF; JFA wrote the manuscript; HW and TRF contributed with comments and edits on the manuscript; JFA reviewed the manuscript during the peer-review process

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Babysitting is a particular case of direct alloparental care, where the carer purposefully changes its behavior to stay close to the young to its benefit (Whitehead 1996). For example, meerkat (*Suricatta suricata*) pups are babysat in their natal burrow, while mothers leave the colony to forage with other members of their group. Each nursery has one or two babysitters that stay behind to care for the babies. While the babysitters are caring for the babies, they usually do not eat, and may lose up to 2% body weight during the babysitting day. If, instead of babysitting, individuals were foraging they would be able to maintain, or even gain, body weight (Clutton-Brock *et al.* 2001). Costs of behavior are not always this high with all species. For instance, Sperm whales (*Physeter macrocephalus*) babysit by changing their dive synchrony and take care of the calf at the surface, which likely has a very small cost (Whitehead 1996).

For alloparental care to happen, the costs for the alloparent need to be balanced by its benefits. When costs are negligible, alloparental care can be a byproduct of the evolution of sociality. Indirect alloparental care and communal broods or colonies will often fit into this category. When alloparental care is costly, it has to be maintained by an adaptive mechanism. These mechanisms can be divided into two different types of systems: investment, where the alloparents' rewards are based on the behavior of the young they helped previously when they reach maturity; and signaling, where alloparental care is performed for other individuals in the population to know about (Wright 1997, 1999).

Investment mechanisms include reciprocal altruism, kin selection, and group augmentation. Reciprocal altruism happens when the alloparent performs a beneficial action to another individual, which is detrimental to its fitness, with the expectation that it will be reciprocated (Trivers 1971, Axelrod and Hamilton 1981). Reciprocation does not have to be instantaneous, if individual recognition mechanisms are in place. Kin selection occurs when the alloparent helps

its kin, in the expectation that it will help to increase the possibility to pass on their commonly-held genes to subsequent generations (Hamilton 1964a, b). In group augmentation alloparents help young, even if unrelated, with the expectation that they will stay in the group, increasing or maintaining the benefits of living in a large, well-functioning group (Brown 1987, Kokko *et al.* 2001). Signaling systems include pay to stay and social prestige. In pay to stay subordinate alloparents assist the dominant breeding pair as a way to pay rent to stay in the group (Gaston 1978, Kokko *et al.* 2002). In social prestige males care for young other than their own as a way to advertise their mating quality (Zahavi 1975, 1995).

Several cetacean species are known or suspected to engage in alloparental care. Bottlenose dolphins (*Tursiops* spp., Caldwell and Caldwell 1966, Mann and Smuts 1998) and killer whales (*Orcinus orca*, Bigg *et al.* 1987) are known to escort calves, a form of babysitting; sperm whales also babysit (Whitehead 1996, Gero *et al.* 2009); and sperm whales and belugas (*Delphinapterus leucas*) allonurse, *i.e.*, nurse calves that are not their own (Best *et al.* 1984, Leung *et al.* 2010). All these species live in social groups, of different types including labile fission-fusion and stable matrilineal units, as well as combinations of these elements (Rendell and Gero 2014).

Long-finned pilot whales (*Globicephala melas*) live in social units that coalesce to form ephemeral groups (Ottensmeyer and Whitehead 2003, de Stephanis *et al.* 2008a), but little more is known about their social dynamics. Genetic studies on groups of pilot whales driven ashore in the Faeroe Islands, “grinds”, found that the large groups that compose the grinds contain individuals of both sexes, but none of the males are the fathers of the calves in the same grind (Amos *et al.* 1991, 1993). Unfortunately, these studies do not give us information on how associations between individuals change over time. The Cape Breton, Canada (Ottensmeyer and Whitehead 2003) and Strait of Gibraltar (de Stephanis *et al.* 2008a) populations show the above

mentioned social structure of stable social units. The Strait of Gibraltar units are comprised of males and females (de Stephanis *et al.* 2008a), while molecular sexing had not been performed in the Cape Breton population until this study (Ottensmeyer and Whitehead 2003). It has been hypothesized that units correspond to extended matrilines (Ottensmeyer and Whitehead 2003).

We examined patterns of escorting, *i.e.*, accompanying calves, and investigated several hypotheses, including: whether it is possible to identify who the likely mothers of the calves are due to their predominate accompaniment of the calf, given that in other cetacean species where alloparental care happens calves still spend a much larger amount of time with their mothers when compared to other carers; that given this species' cohesive social structure accompaniment of the calf by nonmothers, *i.e.*, alloparental care, happens at all developmental stages of the calf; and that alloparents are predominantly females in the same unit as the mother, which would allow for reciprocity of the behavior, as well as perhaps kin selection, driving the alloparental care.

6.2 METHODS

6.2.1 Data collection

Data were collected in July and August, from 2009 to 2011 from a 13-meter whale watching vessel off the northwest coast of Cape Breton Island, Nova Scotia, Canada. . Up to five trips were conducted daily, departing from Pleasant Bay Harbor (46° 49' N, 60° 47' W) and lasting a maximum of 2.5 h each, covering up to 40 km south to 30 km north of the Harbor, and a maximum of 8 km offshore. Trips were only performed when the wind strength was less than 20 knots.

Usually, two researchers collected behavioral and photographic data on each trip. In the rare case where only one researcher was available, priority was given to photographic coverage. The area was scanned for the presence of pilot whales, and when a group was sighted the vessel approached it slowly and kept parallel to their movement or stayed stationary with the motor on idle or turned off.

Data were collected and organized by encounters. Encounters began when a whale was sighted and ended when the vessel left the group by either returning to port or by moving to another group that was more than 200 m away. Encounters also ended if the group was submerged for more than ten consecutive min. All individuals in an encounter were considered to be in the same group. Calves were counted and photographed. Adults escorting them – closest companions – were also photographed, so they could be identified later. Escorting is defined as accompanying the calf in close proximity, less than 1 calf body length, while at the surface. Only one animal could escort a calf at any time. When several individuals are close to the calf, the one that surfaced within the least amount of time to the calf was considered the escort.

Tissue from adult individuals was collected by remote biopsy sampling in July and August of 2010 to 2012, off the Pleasant Bay Harbor, from a semi-rigid 4.5 m inflatable zodiac, as in Kowarski *et al.* (2014).

6.2.2 Identification of Closest Companions

Closest companions were identified through pictures of the dorsal fin area (Auger-Méthé and Whitehead 2007). These were collected using a Canon 30D (digital) with a 200 mm or 300 mm autofocus lens. Each photograph was quality rated (Q) from 1 to 5 according to the attributes of focus, size, orientation, exposure, and percentage of fin visible. Individuals were identified using the number and position of mark points (MP), *i.e.*, nicks and internal corners of notches, of

dorsal fins (Ottensmeyer and Whitehead 2003, Auger-Méthé and Whitehead 2007). Photo identification within each year was performed by eye by J. F. Augusto on photographs with Q>2 showing dorsal fins with MP>2. Individuals with less than three MPs were deemed unidentifiable. Identifiable CCs were numbered within in each year using a year specific code (*e.g.*, 2009_a1, 2011_a3), matched between years and identified in the project catalogue (identification numbers: *e.g.*, 235, 580) using Finscan (Araabi *et al.* 2000). In cases where I did not find a match for the adults in the project catalogue they remained identified with their within-year number (*e.g.*, 2009_a1, 2011_a3). When one of those adults was identified in several years, the identifying number of its first year was used (*e.g.*, 680, in both 2009 and 2011).

6.2.3 Identification of calves

Calves were identified individually (*e.g.*, c100, c70) using several different types of markings: pigmentation patterns, including the saddle patch and foetal folds, linear marks, tooth rakes, patches, white scars (Auger-Méthé and Whitehead 2007) and, when existing, MPs in the trailing edge of the dorsal fin (Ottensmeyer and Whitehead 2003; Auger-Méthé and Whitehead 2007). MPs and white scars are the only markings that remain constant with time (Auger-Méthé and Whitehead 2003). How clearly saddle patches can be observed increases with age and size of the individual (Bloch *et al.* 1993b), but saddle patches do not disappear with time. The light coloration of calves and juveniles may make it harder to identify the saddle patch in animals of these age classes. The loss rate for the remaining markings (foetal folds, linear marks, tooth rakes and patches) varies between 0.4/yr and 1/yr (Auger-Méthé and Whitehead 2003). Since the field season lasts two months at the same time each year, and most of the markings used to identify individuals last less than a year, identifications were only possible within the field seasons, not between different field seasons, except for those individuals with three or more MPs in the dorsal fin or other markings that remained unchanged. Calves with one or more MPs

on their dorsal fin or body could be identified between seasons. MPs are rare in calves, so it should be possible to identify individuals with a low number of MPs.

Calves were classified according to their age and morphology. Newborn calves have foetal folds and a bent over dorsal fin. Calves with foetal folds are younger than one year. Gray calves are older than one year, are gray and have lost their foetal folds (Figure 6.1; Slooten and Dawson 1988, Herzing 1997, Grellier *et al.* 2003, Auger-Méthé and Whitehead 2007).

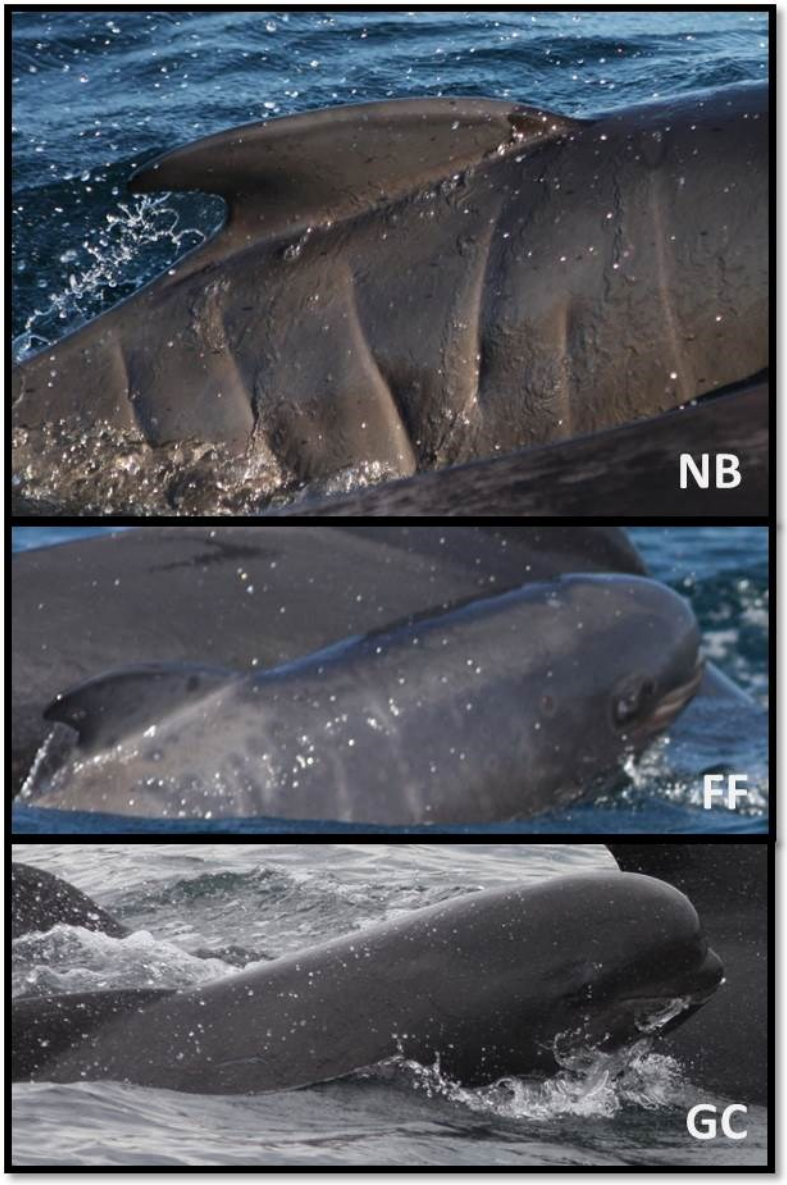

Figure 6.1 - Identification of calf age using photography. NB - Newborn, FF - Foetal Fold, GC - Grey Calf

6.2.4 Characterizing alloparental care

Only calves that were identified in at least two encounters with identifiable CCs were included in the analysis. Instances of alloparental care happened when one calf was identified with more than one CC during the sampling period. Here, the assumption is that the observed close

association is representative of alloparental care, even if specific care-giving behaviour was not observed.

We assumed that the CC predominantly associated with a calf was its mother (see Grellier *et al.* (2003) for justification). When a calf was only observed with one CC, it was considered its mother. When calves were seen with multiple CCs I used an adaptation of the method described in Grellier *et al.* (2003) to assign the mother. We used the photographic records to calculate the coefficients of association between calves and CCs using the simple ratio index

$$SI = \frac{x}{n}$$

where *x* is the number of frames the calf and the CC were identified in the same, or consecutive photographs in the same surfacing event, and *n* the total number of frames either the calf or the CC were identified.

We then used a one tailed z-test to compare the CC with the highest *SI* for each calf *(SI1)* and the CC with the second highest *SI (SI2)*.

$$z = \frac{SI_1 - SI_2}{\sqrt{SI(1-SI)(\frac{1}{n_1} + \frac{1}{n_2})}}$$

Where$SI_1 = \frac{x_1}{n_1}$, $SI_2 = \frac{x_2}{n_2}$ and $SI = \frac{(x_1+x_2)}{(n_1+n_2)}$. This approach is only considered good when n1 + n2 > 12.The null hypothesis for this test is that the SIs are similar between the two CCs. When z<z0.05 the null hypothesis is accepted, which means both CCs spent a similar amount of time with the calf. In this case, the maternity of the calf remains undetermined. When z ≥ z0.05 the null hypothesis is rejected, which means individual 1 spent more time with the calf. In this case,

individual 1 is considered the mother of the calf. This method is only applicable when the mother has enough mark points to be identifiable.

We did not apply this method when the calf was seen in more frames with unidentified CCs than with identified CCs. Since mothers tend to spend a much larger amount of time with the calf than alloparents (Whitehead 1996, Grellier *et al.* 2003) it was possible that the mother was an unidentified CC.

Reciprocal alloparental care happens when two mothers care for each other's calves. To determine whether this occurred within the population I determined which mothers cared for other calves, and who the mothers of those calves were. This analysis was performed within and between years.

6.2.5 Characterizing alloparents

We characterized alloparents according to two characteristics, whether they were members of the same unit as the calves they were escorting and their sex. We defined units as sets of individuals in nearly permanent mutual association, comprised of key individuals and their close companions. Unit membership was assessed using a modification of the method employed by Christal et al. (1998) and Ottensmeyer and Whitehead (2003). Key individuals were those identified in at least four sampling days, with these days separated by at least 30 days. Close companions were those identified on the same day as key individuals, for at least three sampling days, and with sightings separated by at least 30 days. Calves were assumed to be in the same unit as their mothers.

To determine the sex of individuals I used molecular methods. DNA was extracted using the phenol:chloroform extraction method (Sambrook and Russel 2001). Sex of individuals was

determined using a multiplex PCR of two primer pairs: one that amplifies a ~400 bp portion of the ZFX/ZFY gene (present on both sex chromosomes); and one that amplifies a ~200 bp portion of the SRY gene (only on the Y-chromosome) (Gilson *et al.* 1998). PCR was performed on 20 ng of purified DNA in a 20 µL reaction volume that contained 1X Taq polymerase PCR buffer, 0.2 mM dNTP, 1.5 mM MgCl2, 0.3 µM of each primer, 0.16 mg/mL BSA, and 0.05 U/µL Taq polymerase. PCR cycles were performed as follows: the first cycle at 94°C for 5 min, followed by 30 cycles of denaturation at 94°C for 30 s, annealing at 55°C for 1 min, and extension at 72°C for 1 min. A final extension step was performed at 60°C for 45 min. The PCR products were then separated and visualized using agarose gel electrophoresis in 1.5% agarose gels stained with ethidium bromide.

6.3 RESULTS

6.3.1 Data collection

Data were collected in a total of 661 encounters of pilot whale groups, 85.9% of which contained calves. In 2009 there were 239 encounters, 87.0% with calves; in 2010 there were 245 encounters, 86.9% with calves; and in 2011 there were 177 encounters, 83.1% with calves.

6.3.2 Identification of calves and closest companions

A total of 356 calves were identified with MP>2 between 2009 and 2011 (Table 6.1). Gray calves were more common than calves with foetal folds, and only one newborn was identified. Ninety two calves were identified with more than one CC in two encounters and considered for the alloparental care analysis. This comprised 50% of all calves identified in 2009, 28% in 2010 and 18% in 2011 (Table 6.1). Two calves from 2010, c24 and c106, were removed from the maternity

analysis due to a high number of identifications with CC that were not identifiable. A total of 90 calves were used for the following analyses.

Table 6.1 - Summary of calf types identified in 2009, 2010, and 2011. Calves "Analyzed" refers to calves seen in more than one encounter with an identifiable CC, therefore able to be used in this study.

	Year	2009	2010	2011
Identified	Total	56	129	171
	Newborns	1	0	0
	Foetal Folds	17	16	30
	Gray Calves	38	113	141
Analyzed	Total	28	34	30
	Newborns	1	0	0
	Foetal Folds	10	5	10
	Gray Calves	17	29	20

6.3.3 Characterizing alloparental care

The number of CCs in relation to the developmental stage of the calves was not very variable. In 2009 and 2010, calves with foetal folds and gray calves both had a median of two CCs. Calves with foetal folds had between one and four CCs. In 2009, gray calves had between one and five CCs, and between one and four in 2010. In 2011 calves with foetal folds had a median of three CCs and grey calves of one CC.

Some calves were identified with only one CC: 14.3% in 2009, 19.4% in 2010 and 36.7% in 2011 (Supplementary Material 18). There is a weak but positive relationship between the number of encounters in which a calf was identified and the number of identified CCs (Table 6.2, Spearman's rho: 0.242) While most calves were identified with more than one CC, there were several cases where only one CC was identifiable, so no further analysis were conducted.

Table 6.2 - Number of calves in relation to number of encounters and number of CCs they were identified with. Data set for 2009-2011 with only identifiable CCs accounted for.

		Number of CCs each calf was seen with					Total number of calves per encounter	Mean number of CCs per encounter
		1	2	3	4	5		
number of encounters each calf was identified in	2	23	32	8	1	0	64	1.80
	3	6	3	7	0	1	17	2.24
	4	1	0	4	2	0	7	3.00
	5	0	0	1	0	0	1	3.00
	6	3	0	0	1	0	4	1.75
	11	0	1	0	0	0	1	2.00
	Total	33	36	20	4	1	94	

There were apparent discrepancies in some results. In 2009 individual 1245, which is a male, was the only identifiable individual identified with calf c33. Also in 2009, individual 1353, another male, was identified as the individual that spent most time with both calves c18 and c20. Finally, in 2011 individual 717 was identified as the mother of two calves, c293 and c232.

Table 6.3 - Maternity test adapted from Grellier *et al.* (2003) for 2009, 2010, and 2011. Significant test results are marked in bold ($z_{0.05}$ = 1.64). A1 High: CC with the highest simple ratio index (SI_1) with the calf; A2 High, CC with the second highest simple ratio index with the calf; n1, total number of times A1 High and calf were seen together; n2, total number of times A2 High and calf were seen together; z, unicaudal z-test result. Only cases with enough resightings to apply the method are shown.

2009						
Calf	A1 High	SI_1	A2 High	SI_2	n1+n2	z
c15	**1550**	0.62	113	0.17	**39**	**2.86**
c23	**2009_a61**	0.73	1075	0.2	**30**	**2.93**
c8	**474**	0.67	1570	0.14	**16**	**2.10**
patch	2009_a1	0.58	2009_a2	0.42	**48**	1.15
c14	861	0.31	1034	0.23	**26**	0.34
c24	1525	0.57	575	0.29	**14**	1.08
C28	517	0.5	2009_a79	0.5	**16**	0
c6	1448	0.43	1347	0.29	**14**	0.56
2010						

Calf	A1 High	SI_1	A2 High	SI_2	n1+n2	z
c128	**1283**	1.00	2010_a40	0.08	**18**	**3.76**
c89	2010_a12	0.25	312	0.11	**13**	0.64
c97	1438	0.28	2009_a61	0.27	**29**	0.03
c143	312	0.36	2010_a40	0.17	**23**	1.07
c153	312	0.25	2010_a23	0.25	**16**	0
c154	2009_a81	0.33	2009_a106	0.14	**17**	0.79
c184	2010_a43	0.4	2010_a20	0.38	**13**	0.09
			2011			
Calf	A1 High	SI_1	A2 High	SI_2	n1+n2	z
c386	**2011_a25**	0.71	2009_a81	0.07	**22**	**3.18**
c387	**2009_a101**	0.50	2009_a81	0.14	**20**	**1.69**
c213	**2011_a53**	0.71	1050	0.14	**14**	**2.16**
c222	**1379**	0.67	2010_a2	0.18	**20**	**2.20**
c284	1161	0.5	113	0.5	**16**	0

The Grellier *et al.* (2003) method assigned mothers in three cases in 2009, one case in 2010 and four cases in 2011 (Table 6.3). There were 12 cases in 2009 and 2011, and 14 cases in 2010 where there were too few resightings for the method to be useful.

Table 6.4 - Closest companions identified in several years, and in which role they were identified in. CM – confirmed mother, CC - closest companion (when mother was not confirmed),or A – Alloparent (CC when the mother is known as another individual)

Adult ID	**Calf id in 2009**	**Role**	**Calf id in 2010**	**Role**	**Calf id in 2011**	**Role**
2009_a2	Patch	CC	Patch	CC	Patch	CC
2009_a28	c12	CC	c229	CC	-	
113	c14 c15	A A	-	-	c284	A
1086	c14 c15	A A	c162 c163	CC CC	-	-
2009_a45	c18	CC	c69	CC	-	-
808	c20	CC	c143	A	-	-
228	c21	**CM**	c61	CC	-	-
2009_a61	c23	**CM**	c97	CC	-	-
575	c24	CC	-		Patch	CC

517	c28	CC	c76	CC	-	-
2009_a81	c31	CC	c154	CC	c239 c306 c307	**CM** A A
2009_a101	c46	**CM**	-	-	c307	**CM**
637	c47 c56	CC CC	c132 c159	CC **CM**	c266	CC
2009_a106	c48	CC	c126 c154	CC CC	c268	CC
1283	c48	CC	c128	**CM**	-	-
1449	c6	CC	c178	CC	-	-
2010_a2	-	-	c57	CC	c216 c222	CC A
1455	-	-	c69	CC	c189	CC
1438	-	-	c88 c97 c98	CC A **CM**	c311 c222	CC A

595	-	-	c90	**CM**	c231	**CM**
1037	-	-	c131	CC	c131	CC

Twenty one adults were seen escorting calves in multiple years (Table 6.4, Supplementary Material 19). The calf "Patch" was consistently identified throughout the three years with the same adult, 2009_a2, and with her more frequently than other CCs, so I considered her its mother. Two adults were assigned as mothers during several years. Adult 2009_a101 was assigned as mother to calf c46 in 2009 and to calf c397 in 2011; adult 595 was assigned as mother to calf c90 in 2010 and c231 in 2010. Unfortunately, the calves were identified using different sides of their dorsal fins in different years, and presented no MPs, so matching them was not possible.

No instances of reciprocal alloparental care within or between years were found (Supplementary Material **20**). Three adults identified as mothers escorted calves of other mothers. Adult 1438 escorted the calf of 1379, which escorted the calf of an unidentified mother. Adult 2011_a25 escorted the calf of 2009_a10, which escorted the calf of 595. Adult 595 was not observed to escort any calf other than its own.

6.3.4 Characterizing alloparents

There were only two cases where calves were seen with multiple CCs assigned to a unit. Neither of these belong to the same social unit. Calf c78 had CCs from units Q and K, L, N and U; and calf c143 had CCs in units K and H (Supplementary Material **19**).

A total of 75 adults were sexed, 32 females and 43 males, but only 5 of these were identified as CCs. From these five CCs, four were males and one a female. None of these CCs accompanied

the same calf, so genetic relatedness between the mother and CCs, or among CCs, could not be assessed (Table 6.5).

Table 6.5 - Closest companions (CCs) that were affiliated with a unit or genetically sexed

CC	Unit	Sex
261	K, L, N, U	
280	D	M
312	K	
517	O	
543	M	
602	Q	
637	O	
808	H	
861	U	
1162		F
1245		M
1353		M
1441		M

6.4 DISCUSSION

6.4.1 Methodological limitations

There are several methodological limitations to be considered in this study. The first one lies with the identification of calves. While with adults I use MPs to identify individuals, calves rarely possess these types of marks (Auger-Méthé and Whitehead 2007). MPs can be gained by injuries (Sergeant 1962, Bigg *et al.* 1987), interacting with other individuals, predators, boats or fishing gear. Pilot whale calves are born with unmarked or with very small marks on their fins. This means that for most calves I have to use other, more temporary, markers to identify individuals. Marks can be found on both dorsal fin and body (Auger-Méthé and Whitehead 2007), but are usually restricted to one side of the individual. This makes it harder to identify both sides of a calf, and to identify it over several years. This unfortunately hampers our ability to look at multi-year alloparental care patterns for this population.

The second methodological issue is that the proportion of animals with MP>2 is only about 0.34 for this population (Ottensmeyer and Whitehead 2003). While this proportion is enough for studying some aspects of social structure (Ottensmeyer and Whitehead 2003), it means that a large percentage of individuals escorting calves cannot be identified. These can be either mothers or companions. This is the case of the mother of calf c33, for instance. The only identifiable individual escorting calf c33 was individual 1245, which was a male. This presumably means the mother was an individual without enough MPs to be identified. There were also cases where individuals were not identified in the population catalogue and remained with their within-year codes (*e.g.*, 2009_a2).

The third methodological issue is the low number of repeated observations of the companions with the same calf. There are several reasons for this. The study population is in the thousands.

Data are collected from an opportunistic vessel, giving limited encounter durations. Also, groups are not often seen repeatedly on different trips on the same day. Likewise, the photographic data are difficult to collect for both calf and companion simultaneously. The percentage of identified calves used in the study varies from 50% to 18% of calves over different years. In many cases when I collected a Q>2 picture of a calf, I did not also collect a Q>2 photo of the companion, or vice versa. There is also a biological factor that might be influencing the low number of repeated observations of a particular individual accompanying a particular calf. With escorts and calves being members of the same group, but not necessarily of the same unit, and groups being ephemeral it might be that different individuals escort the same calf over time. With our opportunistic sampling strategy we might not be able to study the same group enough times to see repeated alloparental care events by the same individuals before the group breaks up.

6.4.2 Characterizing alloparental care

Given the limitations stated above, it was only possible to assign mothers to calves in a small number of cases. Grellier *et al.*'s (2003) method yielded results assigning mothers when more than one CC was present (Table 6.3), but for many cases there were not enough data for the analysis to be used reliably. But even with our methodological limitations it is possible to detect alloparental care.

We operationally defined alloparental care as taking place when a calf was being escorted (accompanying a calf at less than 1 calf body length, while at the surface) by only one individual, who was not the calf's mother. It was not straightforward to discriminate mothers from other escorts (CCs). However, in observations between 2009 and 2011, more than 50% of all calves

identified were seen with more than one companion, at least one of whom was not the mother. This constituted alloparental care according to our definition.

It is reasonable to assume that a calf is safer if accompanied by an adult than on its own. Hence, escorting should be considered alloparental care. This definition also aligns with those in some other species. For instance, in African elephants (*Loxodonta* spp.) individuals are considered caring when they greet and investigate calves, or when they provide assistance to a calf in distress (Lee 1987). In cetaceans, definitions are usually based on how close calves are to potential alloparents. With bottlenose dolphins, an individual is considered to be an alloparent if it is seen next to a calf (*e.g.*, Mann and Smutts 1998, Grellier *et al.* 2003). Similarly, with killer whales individuals are considered alloparents when accompany calves (Bigg *et al.* 1990). With sperm whales, when mothers deep dive, the allocarer is the individual that stays close to the calf at the surface (Whitehead 1996).

Given that pilot whale social structure is built upon stable units (Ottensmeyer and Whitehead 2003, de Stephanis *et al.* 2008a) this result is not unexpected. Members of other cetacean species that live in unit-focused societies, such as sperm whales and killer whales, are known to show alloparental care for each other's calves (Bigg *et al.* 1990, Gero *et al.* 2009). In sperm whales calves are even thought to be central to unit stability and alloparental care to be the primary function for units (Gero *et al.* 2013).

In our study, calves under a year old have roughly as many different escorts as calves over a year old. Due to the difficulties of finding enough markings on newborns to identify them, there are not enough data on newborn calves to test whether they are cared for by more or fewer individuals than older calves. Newborn calves are cared for by alloparents in other species. In sperm whales, for instance, there is alloparental care for calves when they are still newborns,

under two months old (Gero *et al.* 2009). In meerkats alloparental care also occurs when calves are quite young. From their third week, pups are babysat by one or two alloparents in the natal burrow while the remainder of the group forages (Clutton-Brock *et al.* 1998).

6.4.3 Characterizing alloparents

Given the strong associations between members of the same unit, I expected to find alloparental care preferentially happen within units. However, I found that alloparental care for a particular calf is being performed by individuals not in the same unit as each other or as the mother of the calf. In fact, I found no cases of individuals of the same unit caring for the same calf, so alloparental care is happening at the group level. Groups are much more ephemeral than units, lasting from hours to days (Ottensmeyer and Whitehead 2003). So, alloparental caring events should also be more ephemeral and with less opportunities for individuals to reciprocate.

Four out of the five sexed CCs were male, which indicates that male pilot whales perform alloparental care under our definition. This happens in some other species, such as killer whales (Bigg *et al.* 1990), bottlenose dolphins (Lusseau 2007), Atlantic spotted dolphins (*Stenella frontalis*, Weinpress and Herzing 2015), spectral tarsiers (*Tarsius tarsier*, Gursky 2000) and black snub-nosed monkeys (*Rhinopithecus bieti*, Xiang *et al.* 2010). Unlike killer whale males, which care for related calves within their own pod, male pilot whales are, at least sometimes, caring for calves outside of their units. In bottlenose dolphins, male alliances can escort females and young, which might be an alloparental caring strategy to prevent infanticide of their descendants (Lusseau 2007). In Atlantic spotted dolphins males discipline young, promoting behaviors more desired in group living, and hence their fitness (Weinpress and Herzing 2015). Spectral tarsier juvenile and adult males both groom and play with young (Xiang *et al.* 2010). In these last two cases it is possible that young are learning from their male carers how to behave

socially. Social norms and behaviors are very important in group living. It is possible that male pilot whales are also providing important social experience for calves.

6.4.4 Why does alloparental care happen?

If escorting is costly – Showing alloparental care for another's calf can have costs for the alloparent, such as increased risk of predation by protecting the calf (*e.g.*, canids, Woodrof and Vincent 1994) and energetic costs by decreasing foraging time (*e.g.*, meerkats, Clutton-Brock *et al.* 2000). If escorting is costly, there have to be evolutionary mechanisms in place for it to have evolved. Given that alloparental care is happening outside of units, it seems to preclude alloparental care being driven by kin selection (Hamilton 1964a, b). Given that groups are known to be ephemeral on a short time scale, separating in a matter of hours or days (Ottensmeyer and Whitehead 2003), group augmentation (Brown 1987) also seems an extremely unlikely mechanism to be acting in this population.

Reciprocal altruism (Trivers 1971) could be an explanation for alloparental caring behavior within groups. With altruistic interactions, an individual behaves in a way that is detrimental to itself, but beneficial to another. Altruism can evolve as a strategy due to the expectation that the selfless behavior will be reciprocated in the future – reciprocal altruism (Trivers 1971, Axelrod and Hamilton 1981). We did not find any cases of alloparental caring reciprocity either within or between years in this study. Given that I cannot identify all the mothers of the calves studied, reciprocity is hard to determine. But, in the two cases where I could follow two mothers and their calves across years (2009_a2 and 595) neither was observed to provide alloparental care for any other calf. Reciprocity may be occurring at a different time scale than our study can identify. Since alloparental care is happening within groups, which are ephemeral structures, it is possible that there are not many opportunities for individuals to reciprocate alloparental care

within a small time scale. This reciprocity might only be happening when units congregate in groups after long periods of time. Also, it is possible that alloparental care is delayed until the calf is not dependent on its mother. We know that delayed reciprocity can happen with sperm whales (Gero *et al.* 2013) and African elephants (Lee 1987). Mothers might care for others during their interbirth interval or, possibly, after becoming reproductively senescent (Sergeant 1962). Given that there is no technique to age live pilot whales, the reproductive senescence hypothesis is currently impossible to test.

If alloparental care is mostly happening when escorting individuals don't have calves of their own, it is also possible that immature females also serve as carers. In this case reciprocity would not necessarily need to happen, since the females are gaining other benefits from alloparental caring, such as learning how to take care of young. It is hypothesized that this is the case with bottlenose dolphins (Mann and Smuts 1998) and with vervet monkeys (*Chlorocebus pygerythrus*, Fairbanks 1993).

It has been suggested that some male bottlenose dolphins in Doubtful Sound, New Zealand, continuously associate with new mothers and their offspring because they recognize calves as their own (Lusseau 2007). We know from Amos *et al.* (1991, 1993) that male pilot whales do not sire offspring in their "grinds", but due to the ephemeral natural of groups it is unlikely that male pilot whales find related calves for which to provide alloparental care in the different groups that they associate with. It is possible that males are providing alloparental care as a way to show their mating potential to females, a strategy known as social prestige (Zahavi 1975, 1995). According to this theory, males take on a handicap, *i.e.*, a costly behavior, as a way to advertise their mating potential to females. This handicap would be too expensive for a male with inferior

mating potential to take. In this specific case, the handicap would be displaying the altruistic behavior of alloparental caring for calves that are not their offspring.

If escorting is not costly – If escorting is not costly, then there is no need for an evolutionary mechanism to be in play for it to emerge in the population. So, escorting would not be an altruistic act, but an act without cost to the individual's fitness. This could happen if the energetic and other requirements of escorting are negligible. In that case the individual would be able to behave in the same manner when escorting or not escorting a calf, or the differences would be negligible. This is supported by the ubiquity of alloparental caring events in our study. They do not appear to be associated with any particular behavior on the part of the carers, and carers do not seem to change their behavior during an event. These events are also not linked with any obvious costly behavior, such as food provisioning, which has an effect on individual fitness. Alloparental care in sperm whales, for instance, probably has a low cost since the individual only has to change dive synchrony, which likely has a low effect on its fitness (Whitehead 1996). We could not find a published case of alloparental care with no cost. What is probably happening in this population is that the cost of escorting is so low that it is negligible. This would also explain why males provide alloparental care outside of their natal unit. If escorting has little to no impact, either proximately or ultimately, on the fitness of the adults, males should not actively deter calves from approaching and being escorted by them. Calves may, for various proximate (*e.g.*, curiosity) and/or ultimate (*e.g.*, increased protection from predators) reasons be attracted to swimming next to a variety of adults, including males.

6.4.5 Conclusion

In conclusion, alloparental care behavior happens frequently in the Cape Breton pilot whale population. Alloparental care is performed by individuals not in the same social unit as the

mothers of the calves, and is also performed by males. Even though I did not find any cases of within or between year alloparental care reciprocity in this three year frame, I hypothesize it is possible that delayed reciprocity is happening on a larger time scale. It is more likely, though, that alloparental care by escorting calves has a negligible cost to the carer's fitness, so there is no evolutionary mechanism associated with the behavior, and alloparental care is a byproduct of this species' social structure.

CHAPTER 7: CONCLUSION

The purpose of this thesis was to increase knowledge of pilot whale social structure by studying a large, primarily photoidentification, dataset from the population that summers off Cape Breton, Nova Scotia, and adding molecular information to it. Previous studies of social structure in this species (Amos *et al.* 1991, 1993, Ottensmeyer and Whitehead 2003, de Stephanis *et al.* 2008a) pointed toward a social structure similar to sperm whales (*Physeter macrocephalus*, Christal *et al.* 1998, Gero *et al.* 2007) or killer whales (*Orcinus orca*, Bigg *et al.* 1990), in which matrilineality is key. It was hypothesized that pilot whales display bisexual natal phylopatry, which is very uncommon in mammals. This was a primary hypothesis that I set out to test, and I intended to learn more about a species with such an unusual dispersal pattern. The results of my research suggest that the social structure of the Cape Breton pilot whales is rather different from these expectations.

I also tried to increase the power of my dataset by looking into the possibility of sexing individuals using photographic data. Unfortunately that did not prove to be possible, but I debunked the widespread idea that sexes present differently-shaped dorsal fins.

Finally, I looked into an important component of any social animal's life: the care of young, and how it may be shared by non-parents. This is a key component in sperm whale social structure (Gero *et al.* 2013) and widespread in killer whale societies (Bigg *et al.* 1987), the species with social systems that seemed very close to the pilot whales'. I found allocare to be common in this population but, again, the specifics were not what I expected.

With this thesis I paint a clearer picture of the social dynamics of the pilot whales that summer in Nova Scotia, revealing interesting and unexpected features, and raising intriguing further questions.

OVERVIEW OF RESULTS

Chapter 2 – Pilot whales form social units, which break apart when they become too large

I identified a total of 1,231 individuals in this study. Resighting rates were low, with 38.8% seen only once and 63.2% were seen in three or fewer encounters. A hundred and three individuals could be assigned to 21 different social units. The units contained both males and females, with an average total size of 7 individuals. This size seems to be common across different populations of pilot whales. Unit identification patterns varied: some units were sighted across the whole study, while others were restricted to specific years. Social units can go through fission events when they become too large to maintain social bonds. This was the case of the K complex, which I found to be breaking apart during the 12 years of the study. The K complex also seems to play an important role connecting units, possibly due to its large size.

Chapter 3 – Individuals show association preferences according to behavioural state

I found differences in association preferences between individuals under different behavioural states. Pairs of individuals with highest associations (HWI>0.75) within a behavioural state were typically not the same across behavioural states. Most of these patterns can be explained by individuals in the same units spending more time together, but not all. There were 3 cases of individuals not belonging to the same unit that showed high associations under only one behavioural state. Unfortunately, the lack of demographic information, such as age class and sex, made it impossible to analyse these patterns in more depth.

Looking at associations between units, there seems to be some evidence for association preferences, but not across all behavioural states. Given the low number of units identified together, the patterns were hard to identify.

Chapter 4 – Bisexual natal phylopatry is not the most likely dispersal pattern for this population

Amos *et al.* (1991, 1993) presented the hypothesis of bisexual natal phylopatry for this species. If social units were the object of this dispersal hypothesis, it predicted that I should find units comprising both sexes; that individuals in units would be more closely related to each other than to individuals of other units, for both sexes; and both sexes would have rates of low dispersal from their natal units. Of these predictions, only the first one was met, which means that bisexual natal phylopatry within units is unlikely for this population. I tested the power of my relatedness analysis using an agent-based model that simulated different demographic scenarios under which I could find results similar to my analysis. Of the scenarios examined, the most likely one may be that unit membership is more fluid than previously thought, with some individuals switching units within what could described, following the killer whale (Ford 1991, Yurk *et al.* 2002) and sperm whale (Rendell and Whitehead 2003) models, as social clans. In this scenario, bisexual natal phylopatry might hold but within clans, not social units. Haplotype diversity was low, with only 3 haplotypes found in units. The ubiquity of haplotype A across units made it impossible to assess matrilineality.

Chapter 5 – Dorsal fin shape is not correlated with the pilot whales' gender

In one of the first publications describing pilot whale morphology, Sergeant (1962) suggested that males and females showed different dorsal fins, with females' being more triangular-like and males more hook-like. I tested that hypothesis, adding the possibility that other identification traits (saddle patch morphology and number of mark points) were also influenced by gender. The intent of this chapter was to build a model that would allow me to predict the gender of an individual using only photographic data. Unfortunately, I found no correlation between any of the measures used and the gender of the individuals. There was variability in all characteristics within each gender, making it impossible to determine an individual's gender based solely on photographic data.

Chapter 6 – Alloparental care is common in this population

Given the pilot whales' social structure, I expected that alloparental care was occurring in this population. I confirmed this, with calves often being accompanied by an individual who was not their mother. However, the details of how alloparental care happens were different from what I anticipated. I expected to see alloparental care being performed mostly by females in the same social unit as the mother of the calf. I expected to see reciprocity, and possibly kin selection, as evolutionary mechanisms driving alloparental care. This was not the case. I found both sexes caring for calves, care being given by individuals outside of the calf's social unit and no instance of reciprocal care during the study's three year time frame.

In terms of reciprocity, it is still possible that it is happening outside of the study's time frame. On one hand, groups of social units are ephemeral structures, so opportunities to reciprocate care might only be possible on a larger time scale. On the other hand, it is also possible that

reciprocity is delayed until the calf is not dependent on its mother, which might take longer than the three years I studied. But, more plausibly, it seems likely that reciprocity and kin selection are not very important evolutionary mechanisms behind alloparental care in this population of pilot whales. The most likely explanation for the pattern I observed is that the cost of alloparental care is low, having a negligible impact on the carer's fitness. This means that there need be no specific evolutionary mechanisms associated with alloparental care, but instead that it is as a byproduct of pilot whale sociality: calves perhaps associating actively with animals nearby whatever their kinship or social relationship.

PILOT WHALE SOCIALITY

Animals tend to live in groups when it makes resource acquisition easier and/or when group living reduces predation risk (Alexander 1974, Bertram 1978). To form long-term social group, such as the social units of pilot whales, individuals need to be able to recognize each other and remember past interactions, but there also need to be specific ecological pressures (Handley and Perrin 2007). Individuals tend to leave their natal group when resource availability is low, there is high kin competition and as a strategy to avoid inbreeding depression. Individuals tend to stay with their natal group when there is high mortality outside of their natal group, kin cooperation is high and when familiarity with the natal area is helpful to acquire resources. Pilot whales presumably form semi-permanent units, instead of ephemeral groups, because the pressures to stay are stronger than the pressures to disperse.

Unit size is about 7 in this population, and similar across other populations. It seems to be a size where social interactions between all individuals can be maintained, with increase resource acquisition and lowered predation risk. If units become too small, due to stranding events, low

birth rates or low survival of young, or simple stochasticity, fusion with another unit might provide an increase in protection from predators, decreasing mortality. Fusion might also provide an increase in cooperation between individuals, if there are enough resources in the environment. On the other hand, when units become too large individuals cannot maintain social interactions with all others. This leads to unit fission. It is also possible that competition between individuals in large units increases and, if resource availability and mortality outside of the unit is low, it can lead to individuals dispersing.

Movement of individuals between units can be caused by the fission or fusion of units, but there can also be other explanations. When units become too large, before they fission, certain individuals might choose to leave their units in order to decrease competition and have a better chance at acquiring resources in a smaller unit. When there are sole survivors of stranding events, these individuals might become floaters. In elephants (*Loxodonta* sp.; Moss and Poole 2011), floaters are usually individuals left without a family due to poaching, that try to join other families. Even when they are accepted by a family, their associations are much looser and they tend to hop between different families. Floaters could also happen when individuals were being hunted. Pilot whales were hunted intensely in Newfoundland until 1972 (Dickinson and Sanger 2005), but our knowledge as to how that population is connected to the Cape Breton animals that I studied is very limited. There was only one individual with sequenced mtDNA from Newfoundland (Siemman 1994), and that haplotype did not match any found in the Cape Breton population. It is possible, that if pilot whales form clans similar to those found in killer and sperm whales (Ford 1991, Yurk *et al.* 2002, Rendell and Whitehead 2003), that dispersal happens between units of the same clan.

Finally, pilot whales' social structure produced the alloparental care patterns observed, with individuals of both sexes caring for calves, outside of their units. It is also possible that alloparental care is happening between individuals of the same clan, instead of between individuals of the same unit. This is impossible to assess at this point, and would be an interesting question to study in this population, together with its geographical neighbours.

IMPORTANCE OF RESEARCH AND FUTURE DIRECTIONS

Overall, my thesis provided a deeper look into this pilot whale population's social structure. The fact that I found social units was expected, given previous studies (Amos *et al.* 1991, 1993, Ottensmeyer and Whitehead 2003, de Stephanis *et al.* 2008a). Finding a unit in the process of fission was not unexpected either, given that it has been documented in other species with similar social structures (sperm whales (Christal *et al.*, 1998), killer whales (Bigg *et al.,* 1990; Ford *et al.*, 1994, Parsons *et al.*, 2009) and elephants (Moss and Poole, 1983; Moss and Lee, 2011), but it was the first time that it had been described in this species. The same can be said for the alloparental care, not unexpected based on social structure, but described for the first time in the species. The most important finding for this population was that bisexual natal phylopatry within social units might not be the best descriptor for dispersal patterns, as has been thought for decades (Amos *et al.* 1991, 1993), but there is some fluidity in unit membership.

The fact that units are not as stable as previously thought poses interesting challenges moving forward. This instability could have many forms ranging between temporary (over maybe months) movement of individuals between units, permanent dispersal of a few or many individuals between units, floater individuals, quite labile mixing or even temporary fusion and consequent fission of units.

Temporary movement of floaters between units could be studied using focal follows of units over time, depending on the time frame. It would be possible to follow a unit until an individual moved away, over a period of days, and then change the focus to that individual. Permanent dispersal and fusion-fission between units would be more difficult to study. Both would need a long term database within which it was possible to identify individuals assigned to units several times during the same year. Individuals would also need to have a high reidentification rate between years. Then it would be possible to identify who individuals were spending more time with, and at what scale did those preferences change.

Finally, in this study I only determined relatedness for a small number of individuals in units. In order to confirm my results, a larger biopsying event would also need to take place, focusing on sampling most individuals in known social units. This would increase our knowledge not just of relatedness between individuals, but increase our chances of recognizing more haplotypes in the population giving us a better insight into matrilineality. Another possibility would be to sequence a larger portion of the mtDNA, in search of other sites that would have enough variability, or even do whole mtDNA sequencing.

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APPENDICES

Supplementary Material 1 - Affiliation of individuals to units. Unit memberships were assigned using the modified protocol from Christal et al. (1998). Average size was calculated averaging the number of individuals identified in units for all the years that unit was seen for 3 or more days. Mark rate correction factor was calculated specifically for each unit using the Ottensmeyer and Whitehead (2003) method. When there was not enough data to calculate specific unit mark rates, the general mark rate for the population was used, 0.51*. Size correction was applied using each unit's correction factor for unidentifiable individuals. Total IDs are the IDs identified for unit. Key individuals are seen during at least four days, each of these sightings separated by at least 30 days. Sex – M, males; F, Females; blank – unknown.

Unit	Average size	Mark rate correction factor	Average size with correction	ID	Key Individual?	Sex
A	2	0.33	6	1	Yes	
				246	Yes	
B	4.29	0.40	11	28	Yes	
				62	Yes	
				65	Yes	
				66	Yes	
				279	Yes	
				345	No	
C	2	0.70	3	59	Yes	
				60	Yes	
				80	Yes	
D	2.78	0.41	7	82	Yes	
				280	Yes	M
				719	No	
				876	Yes	

				2	No	
				120	No	
E	3.20	0.70	5			
				123	Yes	
				243	Yes	
				139	Yes	
				140	Yes	
				142	Yes	
F	3.83	0.64	6			
				248	Yes	
				254	Yes	
				701	Yes	
				202	Yes	
G	1.63	0.51*	3*			
				537	Yes	
				205	Yes	
				496	Yes	
H	3.14	0.51*	6*			
				531	Yes	
				808	Yes	
				226	Yes	
I	2.14	0.73	3	483	Yes	
				679	No	
				234	No	F
				237	No	
J	3.2	0.51	6			
				346	No	
				894	No	

				260	Yes	
				261	Yes	
				262	Yes	
				265	No	
				302	Yes	
				311	Yes	F
				312	Yes	
				314	Yes	
				352	Yes	
				370	Yes	F
				372	Yes	
				407	Yes	M
K	14.45	0.51	29	449	Yes	F
				476	Yes	
				488	Yes	
				492	Yes	
				506	No	
				507	Yes	
				511	Yes	F
				599	Yes	
				631	No	
				632	No	M
				697	Yes	
				862	No	

				871	Yes	
				923	Yes	
L	2	0.49	4	261	No	
				265	Yes	
				506	Yes	
M	4	0.43	9	270	Yes	
				466	Yes	
				473	Yes	
				513	Yes	
				543	Yes	
				569	Yes	
				617	Yes	
N	2.75	0.55	5	261	No	
				273	Yes	
				274	Yes	
				480	Yes	
O	5.33	0.51*	11*	307	Yes	F
				374	Yes	M
				508	No	
				515	Yes	F
				517	Yes	
				518	Yes	
				570	No	
				637	No	

				363	Yes	
				482	Yes	M
P	2.22	0.51*	4*			
				887	Yes	F
				889	No	
				375	No	
				376	Yes	F
				377	Yes	
				378	Yes	
				415	Yes	
Q	6.30	0.60	11			
				416	Yes	
				594	Yes	
				601	Yes	M
				602	Yes	
				674	Yes	
				455	Yes	
R	1.75	0.51*	3*			
				595	Yes	
				489	Yes	M
S	1.75	0.51*	3*			
				490	Yes	
				550	Yes	
T	1.33	0.51*	3*			
				551	Yes	M
				260	No	
				261	No	
U	3.11	0.51*	6*			
				632	Yes	M
				861	No	

	862	Yes

Supplementary Material 2 – Testing the possibility of identification change due to gaining of new marks using units A, B and F. All individuals are identified by their numerical ID code. No – not possible that individual seen is the same previously identified in the unit; Maybe

Unit A: Individuals 1 & 246	
2007	
1 seen with	Could it be 246?
482	No
918	No
476	No
1033	No
428	No

Unit B: Individuals 345 & 28, 62, 65 & 279				
2008				
345 seen with	Could it be 28?	Could it be 62?	Could it be 65?	Could it be 279?
1458	No	No	No	No
1459	No	No	No	No

Unit E: Individuals 243 & 123, 120, 2			
2009			
243 seen with	Could it be 123?	Could it be 120?	Could it be 2?
1511	No	No	No
263	*Maybe*	*Maybe*	No
1501	No	*Maybe*	No
2011			
243 seen with	Could it be 123?	Could it be 120?	Could it be 2?

1460	No	*Maybe*	No
677	*Maybe*	*Maybe*	No
1668	*Maybe*	No	No
376	No	No	No

Supplementary Material 3 - Information on maximum associates for sexed individuals. ID – individual identification; Max. Assoc. – Maximum association for individual, Max. Assoc. ID – ID with maximum association with the individual; Sex – sex of Max. Assoc. ID, M – Male, F – Fem

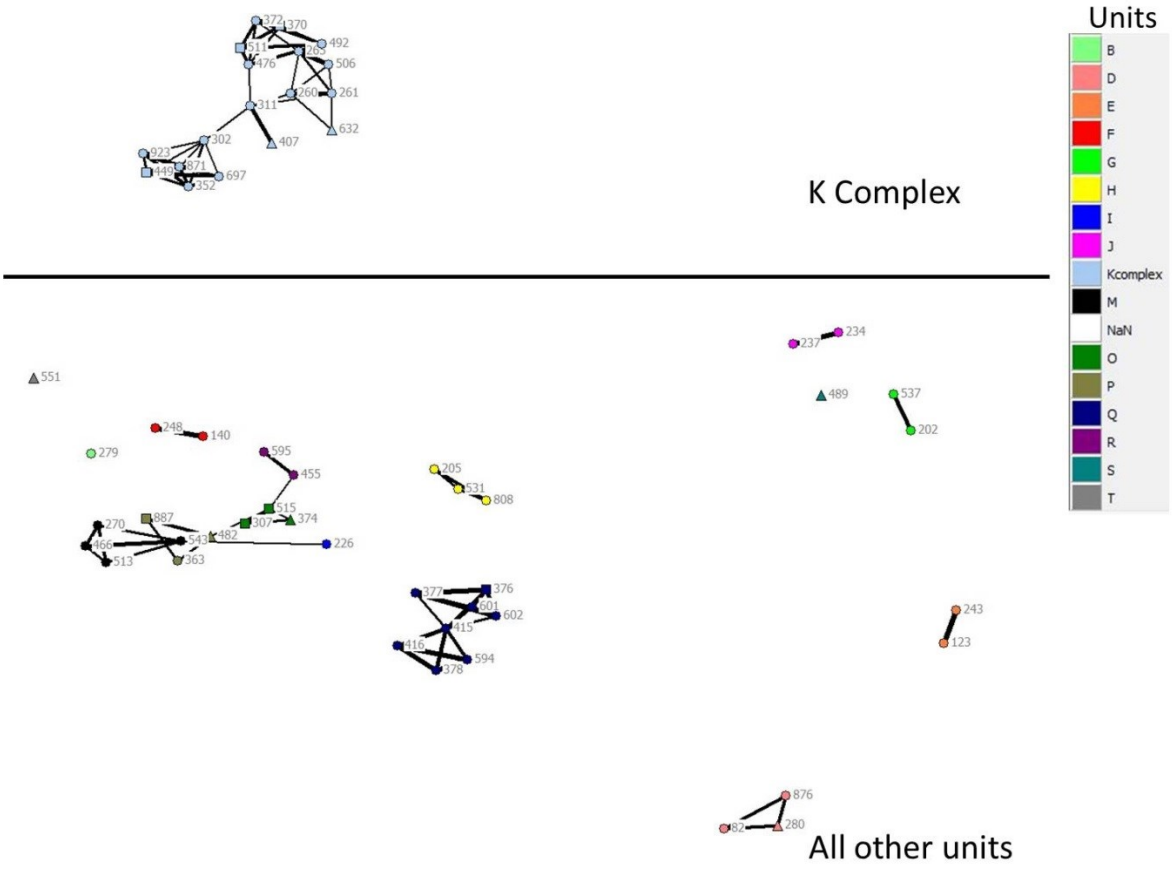
ID	Max. Assoc.	Max. Assoc. ID	Sex
		Females	
234	0.63	346, 237	
307	0.55	515	
311	0.50	407	M
370	0.79	372	
376	0.67	377	
434	0.40	357	
449	0.48	697	
511	0.47	372	
588	0.50	545	
687	1.00	688	
702	0.25	408	
787	0.45	637	
798	1.00	792, 797	
887	0.39	482	
931	0.67	1163	
934	0.59	578	
1031	1.00	1030, 1032	
1068	1.00	1065, 1067	
1145	0.50	1397, 1399	

1162	0.67	1163, 1538, 1539, 1540	1539 F
1211	0.67	1212	
1435	0.50	1678	
1440	0.63	1439	
1539	1.00	1538, 1540, 1541	

Males			
76	0.48	463	
235	0.40	1060	
280	0.41	82, 876	
374	0.42	518	
407	0.50	311	F
417	0.40	225, 323	
478	0.42	479	
489	0.63	490	
505	0.50	981	
574	0.11	569	
601	0.59	674	
628	0.40	514	
632	0.57	862	
670	0.80	668	
682	0.83	1019	
698	0.33	455	
903	0.68	726	
1053	0.59	336	

1078	0.05	302	
1148	0.67	1146, 1147	
1234	0.20	893	
1245	0.33	1498	
1353	0.67	1460, 1461	
1361	0.50	1586, 1587, 1282	
1398	0.67	1397, 1399, 1673, 1680	
1403	1.00	1399, 1402	
1412	0.32	376	F
1466	0.40	1468	
1477	0.50	1446, 1448	
1516	0.67	1335	
1522	1.00	1512	
1650	0.50	1140	
1666	1.00	554	

Supplementary Material 4 - Comparison of differentiated and connected units. Network of individuals seen more than 20 times during the sampling period. Different colours represent different units.



Supplementary Material 5 - Investigating the stability of dyadic associations within units, for individuals seen for at least six years. For each dyad the last year they were identified was compared to the last year they were identified in the same encounter. In stable associat

Unit	First Year individuals were seen	Last year individuals were seen	Dyad	First year dyad was seen together	Last year dyad was seen together	Stable association?
A	1-1998	1-2007	1-246	2000	2005	Yes
	246-1998	246-2005				
B	65-1998	65-2005	65-66	1998	2003	No
	66-1998	66-2007	65-279	1999	2005	Yes
	279-1999	279-2006	65-345	2005	2005	Yes
	345-1999	345-2011	66-279	1999	2006	Yes
			66-345	2004	2009	No
			279-345	2005	2006	Yes
D	82-1998	82-2011	82-280	2002	2009	Yes
	280-1999	280-2009	82-876	2004	2009	Yes
	876-2004	876-2009	280-876	2004	2009	Yes
E	2-1998	2-2005	2-123	1999	2003	No
	123-1998	123-2004	2-243	1999	2003	No
	243-1998	243-2009	123-243	1999	2004	Yes
F	140-1998	140-2009	140-248	1998	2007	No
	248-1998	248-2011	140-701	2003	2008	Yes
	701-2003	701-2008	248-701	2003	2008	Yes

H	205-1998	205-2008	205-531	2003	2008	Yes
	531-2002	531-2011	205-808	2003	2008	Yes
	808-2003	808-2009	531-808	2003	2009	Yes
I	226-1998	226-2011	226-483	2003	2007	Yes
	483-2000	483-2007				
J	234-1998	234-2011	234-237	2000	2011	Yes
	237-1998	237-2011	234-346	1999	2006	Yes
	346-1999	346-2006	237-346	2002	2006	Yes
K complex	260-1999	260-2006	260-261	1999	2006	Yes
(K, L, N, U)	261-1999	261-2009	260-274	2000	2004	No
	274-1999	274-2009	260-302	2002	2005	No
	302-1999	302-2009	260-311	1999	2005	Yes
	311-1999	311-2005	260-312	2000	2004	No
	312-1999	312-2009	260-352	2000	2004	No
	352-1999	352-2007	260-370	2002	2005	No
	370-1999	370-2011	260-372	2002	2004	No
	372-1999	372-2011	260-407	2002	2004	No
	407-2000	407-2011	260-449	2000	2006	Yes
	449-2000	449-2011	260-476	2002	2003	No
	476-2000	476-2008	260-488	2003	2004	No
	488-2000	488-2009	260-511	2008	2004	No
	511-2002	511-2007	260-632	2004	2006	Yes
	632-2002	632-2011	260-697	2003	2004	No
	697-2003	697-2009	260-871	2004	2004	No

871-2004	871-2011	261-274	2000	2004	No
		261-302	1999	2009	Yes
		261-311	1999	2005	Yes
		261-312	1999	2004	No
		261-352	1999	2004	No
		261-370	2000	2008	No
		261-372	2000	2008	No
		261-407	2000	2004	No
		261-449	2000	2008	Yes
		261-476	2000	2007	No
		261-488	2002	2009	Yes
		261-511	2003	2004	No
		261-632	2004	2009	Yes
		261-697	2003	2009	Yes
		261-871	2004	2004	No
		274-302	2000	2004	No
		274-311	-	-	-
		274-312	2000	2000	No
		274-352	2000	2004	No
		274-370	-	-	-
		274-372	2000	2000	-
		274-407	-	-	-
		274-449	2000	2000	No
		274-476	-	-	-

	274-488	2000	2004	No
	274-511	2002	2002	No
	274-632	-	-	-
	274-697	-	-	-
	274-871	2004	2004	No
	302-311	1999	2005	Yes
	302-312	1999	2005	No
	302-352	1999	2007	Yes
	302-370	2005	2008	No
	302-372	2005	2008	No
	302-407	2000	2005	No
	302-449	2003	2008	Yes
	302-476	2005	2005	No
	302-488	2004	2009	Yes
	302-511	2002	2005	No
	302-632	-	-	-
	302-697	-	-	-
	302-871	2004	2005	No
	311-312	1999	2005	Yes
	311-352	1999	1999	No
	311-370	2005	2005	Yes
	311-372	-	-	-
	311-407	2000	2005	Yes
	311-449	-	-	-

	311-476	2002	2003	No
	311-488	2002	2004	Yes
	311-511	2003	2003	No
	311-632	2004	2004	No
	311-697	-	-	-
	311-871	-	-	-
	312-352	1999	2000	No
	312-370	-	-	-
	312-372	-	-	-
	312-407	2004	2005	Yes
	312-449	2000	2000	No
	312-476	-	-	-
	312-488	2004	2004	No
	312-511	-	-	-
	312-632	2004	2004	No
	312-697	-	-	-
	312-871	2005	2005	No
	352-370	2006	2007	Yes
	352-372	2006	2006	No
	352-407	-	-	-
	352-449	2000	2005	Yes
	352-476	2006	2006	No
	352-488	2000	2004	No
	352-511	2004	2006	No

	352-632	2004	2004	No
	352-697	2003	2007	Yes
	352-871	2004	2005	Yes
	370-372	1999	2011	Yes
	370-407	-	-	-
	370-449	2005	2011	Yes
	370-476	2000	2008	Yes
	370-488	2004	2004	No
	370-511	2003	2007	Yes
	370-632	2004	2009	No
	370-697	2006	2008	No
	370-871	2006	2006	No
	372-449	2004	2011	Yes
	372-476	2000	2008	Yes
	372-488	2004	2007	No
	372-511	2003	2007	Yes
	372-632	2004	2009	No
	372-697	2004	2008	No
	372-871	2004	2006	No
	407-449	2002	2002	No
	407-476	2002	2007	Yes
	407-488	2002	2004	No
	407-632	2004	2004	No
	407-871	2005	2005	No

			449-476	2004	2005	No
			449-488	2002	2003	No
			449-511	2004	2005	Yes
			449-632	2004	2004	No
			449-697	2003	2008	Yes
			449-871	2004	2005	No
			476-488	2007	2007	No
			476-511	2003	2006	No
			476-697	2004	2006	No
			476-871	2004	2006	No
			488-511	2004	2004	No
			488-632	2004	2004	No
			488-697	2003	2009	Yes
			488-871	2004	2004	No
			511-632	2004	2004	No
			511-697	2004	2006	No
			511-871	2004	2006	Yes
			632-697	2004	2004	No
			632-871	2004	2004	No
			697-871	2004	2008	No
M	270-1999	270-2005	270-473	2002	2005	Yes
	473-2000	473-2008	270-513	2002	2005	Yes
	513-2002	513-2009	270-543	2002	2005	Yes
	543-2002	543-2011	270-617	2002	2005	Yes

	617-2002	617-2009	473-513	2002	2008	Yes
			473-543	2002	2005	No
			473-617	2002	2008	Yes
			513-543	2002	2005	No
			513-617	2002	2009	Yes
			543-617	2002	2005	No
O	307-1999	307-2011	307-374	2002	2008	Yes
	374-1999	374-2008	307-515	2002	2011	Yes
	515-2002	515-2011	307-517	2002	2009	Yes
	517-2002	517-2009	307-518	2002	2007	Yes
	518-2002	518-2007	307-637	2003	2005	No
	637-2002	637-2011	374-515	2002	2008	Yes
			374-517	2002	2005	No
			374-518	2002	2007	Yes
			374-637	2003	2005	No
			515-517	2002	2009	Yes
			515-518	2002	2005	No
			515-637	2003	2005	No
			517-518	2002	2005	No
			517-637	2003	2005	No
			518-637	2003	2005	No
P	363-1999	363-2006	363-482	2000	2006	Yes
	482-2000	482-2011	363-887	2004	2006	Yes
	887-2004	887-2011	482-887	2006	2001	Yes

Q	376-1999	376-2011	375-377	1998	2003	Yes
	377-1999	377-2006	375-378	1999	2003	Yes
	378-1999	378-2005	375-415	2003	2003	Yes
	415-2000	415-2011	375-416	2003	2003	Yes
	416-2000	416-2011	375-601	2002	2003	Yes
	601-2002	601-2008	375-602	2002	2003	Yes
	602-2002	602-2011	377-378	1999	2004	No
			377-415	2003	2005	No
			377-416	2003	2003	No
			377-601	2002	2006	Yes
			377-602	2002	2006	Yes
			378-415	2000	2005	Yes
			378-416	2002	2005	Yes
			378-601	2003	2004	No
			378-602	2003	2004	No
			415-416	2000	2006	No
			415-601	2003	2008	Yes
			415-602	2003	2011	Yes
			416-601	2003	2007	No
			416-602	2003	2003	No
			601-602	2002	2008	Yes
R	455-2000	455-2009	455-595	2002	2003	No
	595-2002	595-2011				
S	489-2000	489-2009	489-490	2000	2008	No

	490-2000	490-2011

Supplementary Material 6 - Mean number of days each unit was seen per year.

Unit	Mean number of days each unit was seen per year	Total number of individuals in unit	Mean number of days per individual per year
A	2.8	2	2.27
B	3.8	6	2.20
C	2.8	3	2.22
D	5.9	4	4.34
E	3.0	4	2.02
F	3.5	6	2.35
G	4.8	2	4.11
H	3.9	4	2.58
I	3.9	3	2.81
J	3.8	4	2.80
K complex	20.9	30	3.45
M	5.9	7	3.27
O	6.5	8	2.49
P	3.9	4	2.92
Q	7.4	10	3.67
R	3.6	2	3.20
S	2.7	2	2.52
T	2.6	2	2.06

Supplementary Material 7 - Structure within units. Clusters were assigned by maximizing modularity using Newman's (2006) eigenvector method. Modularity > 0.3 is considered to indicate useful division and units divided in this way are marked in bold.

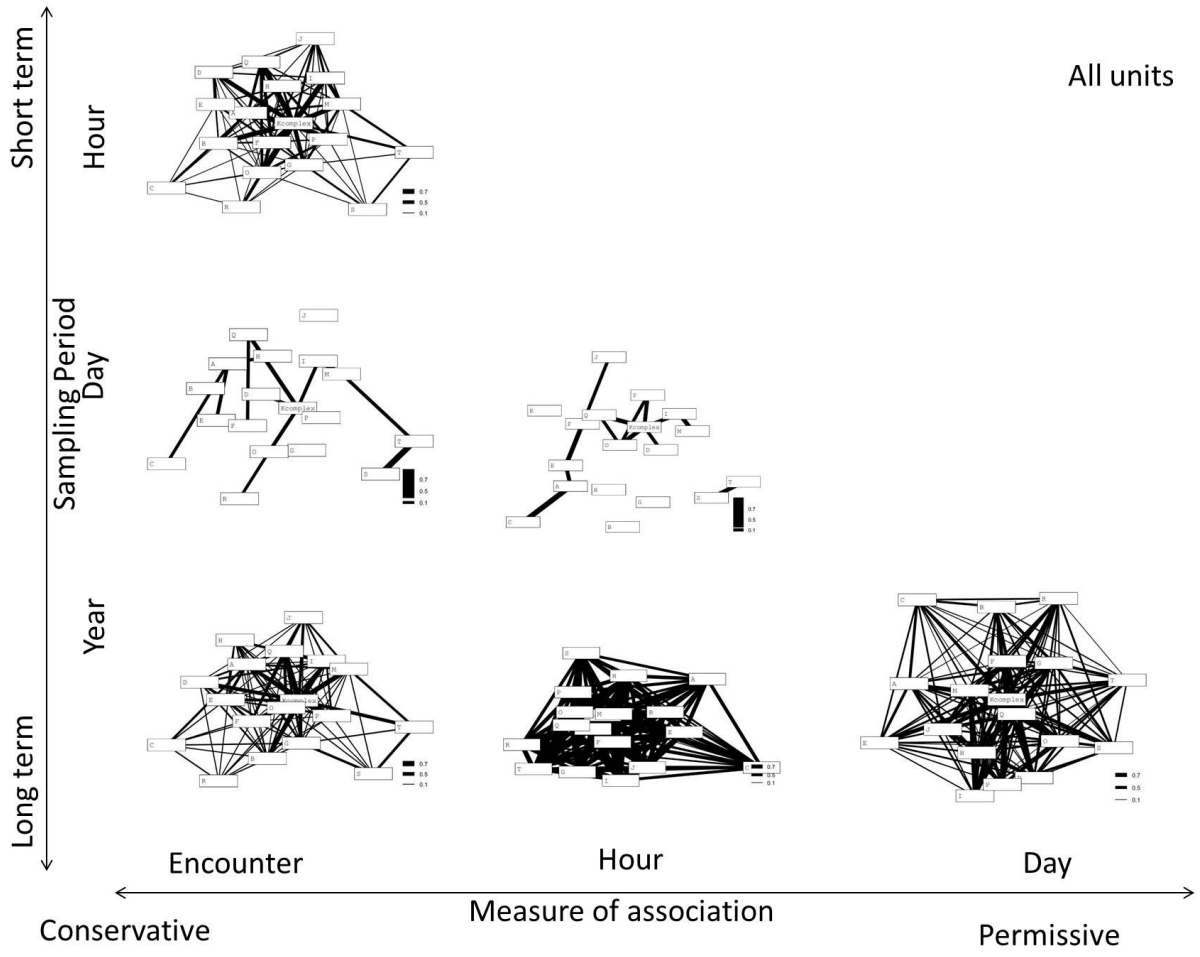
Unit	Clusters within unit	Modularity
A	1	0.500
B	2	**0.303**
C	1	0.334
D	1	0.269
E	1	0.260
F	2	0.234
G	1	0.500
H	1	0.252
I	1	0.344
J	1	0.253
K Complex	5	**0.614**
M	2	0.167
O	2	0.184
P	2	0.253
Q	2	**0.433**
R	1	0.500
S	1	0.500
T	1	0.500

Supplementary Material 8 - Comparison between the individuals in the K complex clusters and composing units.

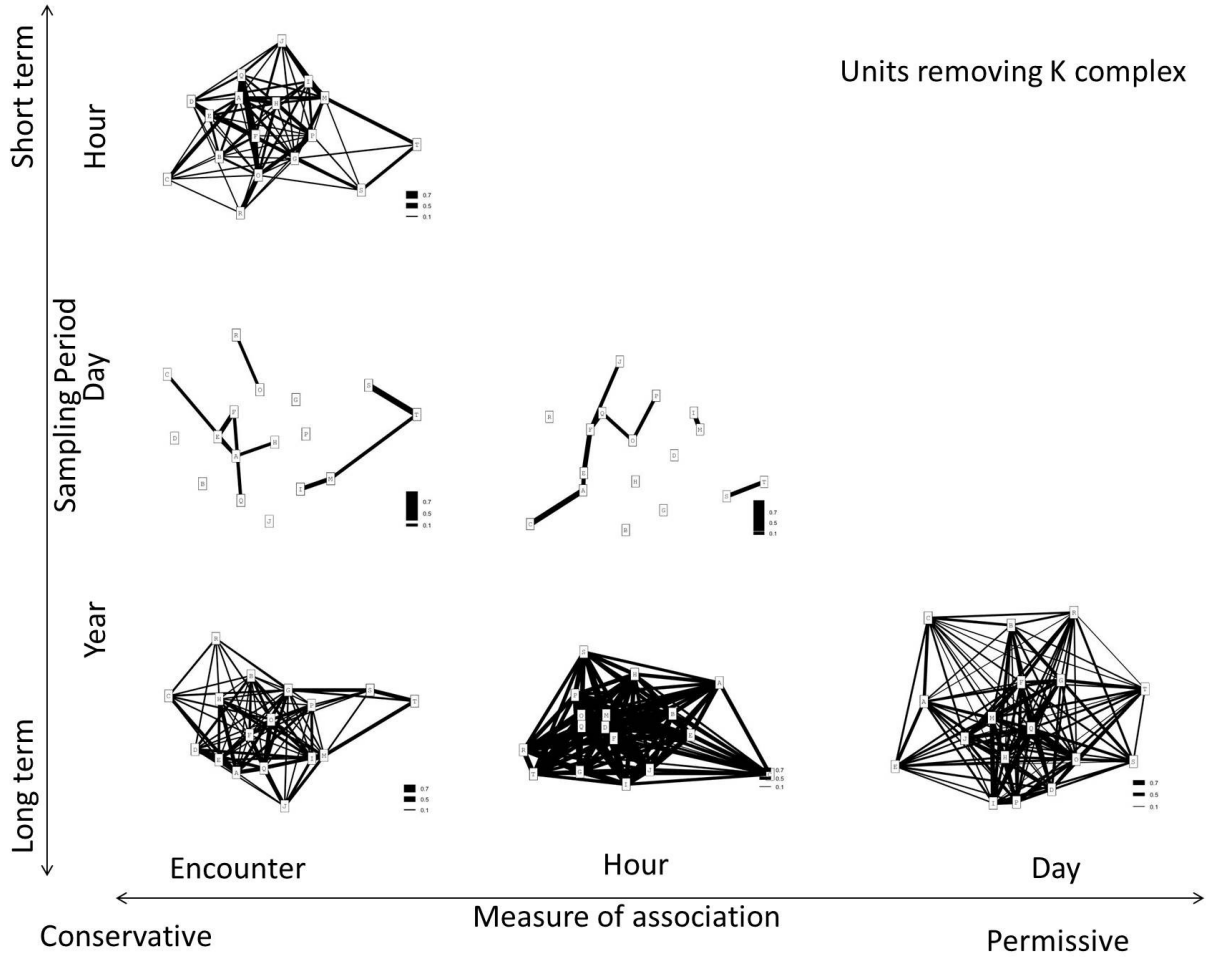
Individual	Cluster	Unit
261	1	K, L, N, U
311	1	K
312	1	K
314	1	K
407	1	K
599	1	K
302	2	K
352	2	K
449	2	K
697	2	K
871	2	K
923	2	K
260	3	K, U
262	3	K
265	3	K, L
488	3	K
506	3	K, L
507	3	K
632	3	K, U
861	3	U
862	3	K, U
370	4	K

372	4	K
476	4	K
492	4	K
511	4	K
631	4	K
273	5	N
274	5	N
480	5	N

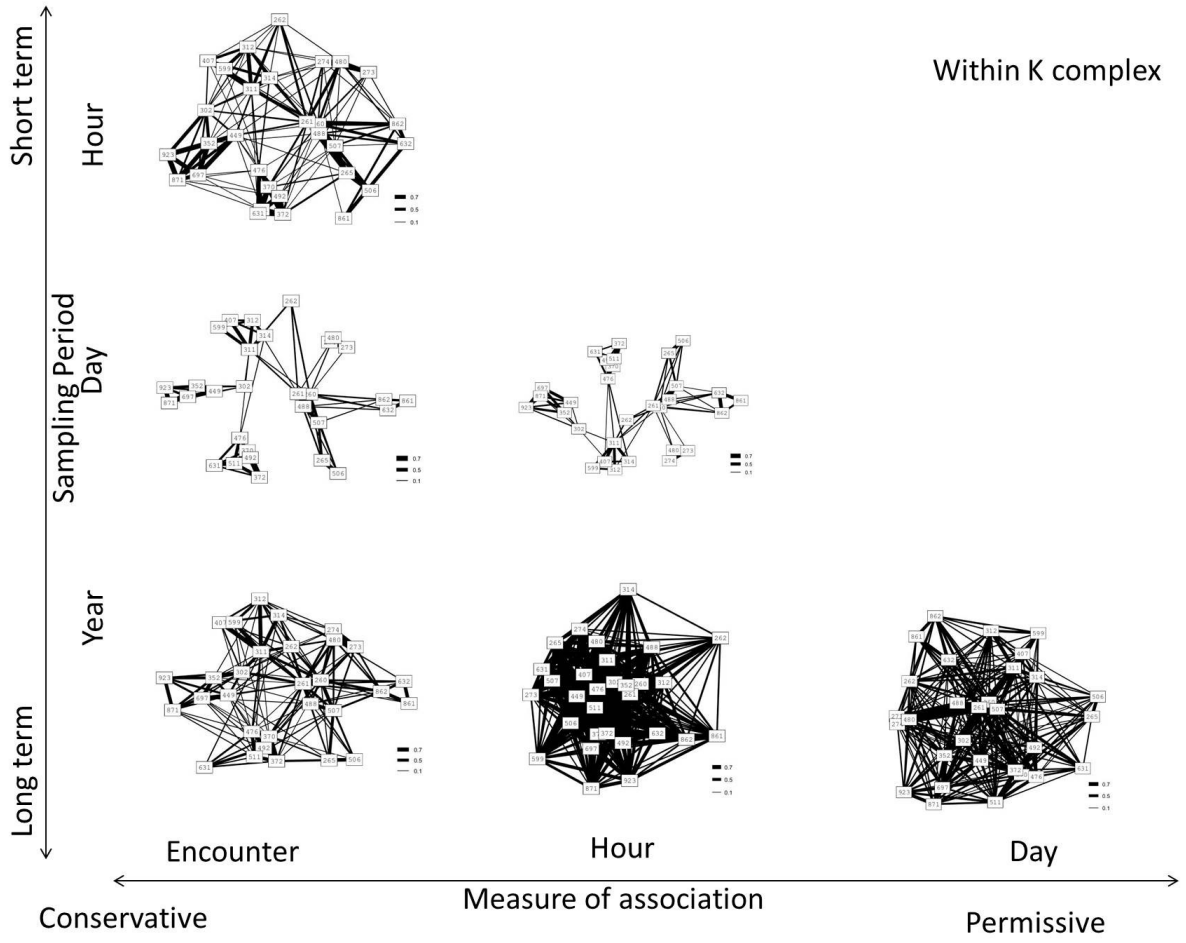
Supplementary Material 9 - Sociograms of how all units associate based on the CoA, varying across the pairings of different sampling periods and measures of association. Only CoA > 0.1 is shown. Sampling period increases while moving down the picture, and measure of association



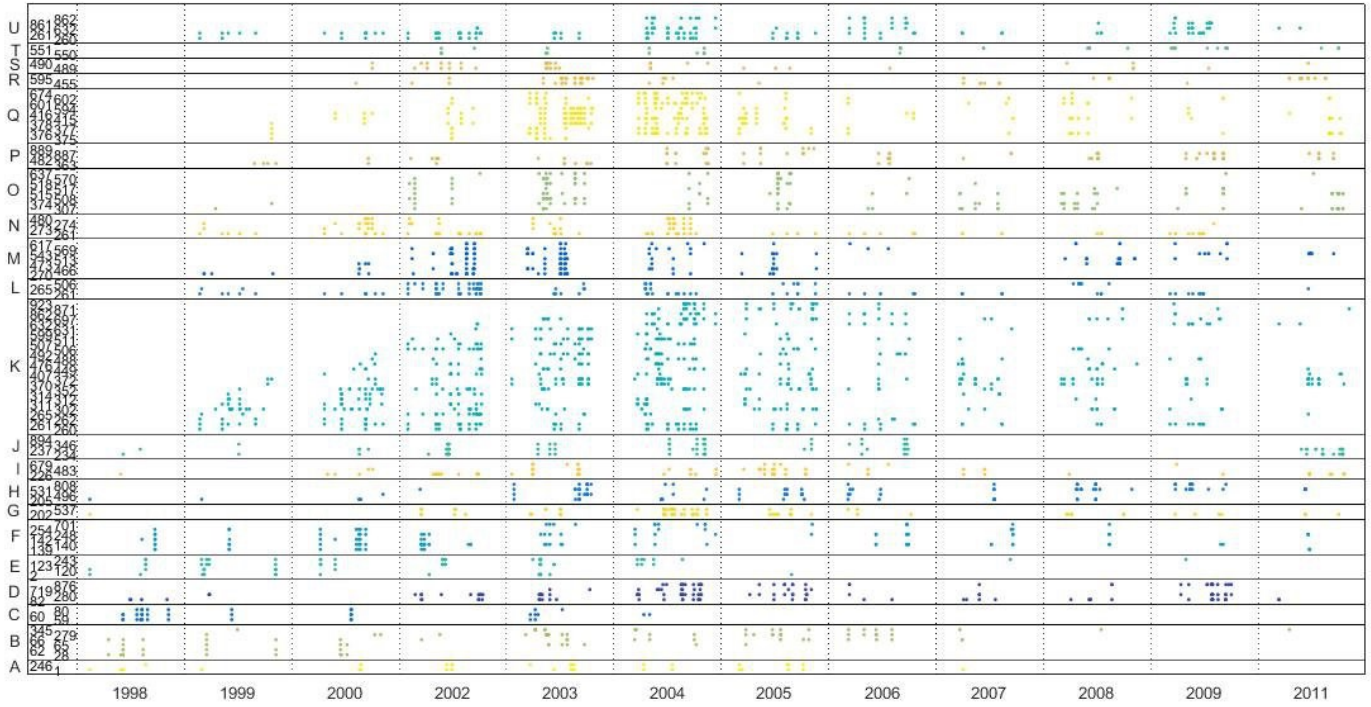
Supplementary Material 10 - Sociograms of how units associate, while not taking the K complex into account, based on the CoA, varying across the pairings of different sampling periods and measures of association. Only CoA > 0.1 is shown. Sampling period increases while moving do



Supplementary Material 11 - Sociograms of how individuals within the K complex associate based on the CoA, varying across the pairings of different sampling periods and measures of association. Only CoA > 0.1 is shown. Sampling period increases while moving down the picture, and



Supplementary Material 12 - Temporal distribution of individuals in units. The x axis represents days individuals were seen in different years. The y-axis represents individuals and which units they are affiliated with. The x-axis shows July and August for each year.



Supplementary Material 13 – Microsatellite loci tested and and their primer sequence.

Locus	Primer sequence (5'-3')	Reference
EV104Mn	TGGAGATGACAGGATTTGGG	Valsecchi and Amos (1996)
EV14Pm	TAAACATCAAAGCAGACCCC CCAGAGCCAAGGTCAAGAG	Valsecchi and Amos (1996)
EV1Pm	CCCTGCTCCCCATTCTC ATAAACTCTAATACACTTCCTCCAAC	Valsecchi and Amos (1996)
EV37Mn	AGCTTGATTGGAAGTCATGA TAGTAG AGCCGTGATAAAGTGC	Valsecchi and Amos (1996)
EV5Pm	AGCTCCTTAGACTCAACCTC TATGGCGAGGGTTCCG	Valsecchi and Amos (1996)
EV94Mn	ATCCTATTGGTCCTTTTCTGC AATAGATAGTGATGATGATTCACACC	Valsecchi and Amos (1996)
FCB1	TGCATCTCCATGGTATGTCTTATCC AGCCTCTGCTATGCCTGGAACGC	Buchanan *et al.* (1996)
FCB14	CTACATTTGCCTCTTATAGACATAGC AAGTTGTCTTAGTTAGTCTGTGCTC	Buchanan *et al.* (1996)
FCB4	CCTGTCAGGAGAATTGAGGTATCC GGATAAGGCCATTAGCCTCCACC	Buchanan *et al.* (1996)
FCB5	CTCCTCATGGTCAGACTCCCAG	Buchanan *et al.* (1996)

	GTACATTTACCCATTCAGAACTTTGG	
GATA028	AAAGACTGAGATCTATAGTTA CGCTGATAGATTAGTCTAGG	Palsbol *et al.* (1997)
GATA098	TGTACCCTGGATGGATAGATT TCACCTTATTTTGTCTGTCTG	Palsbol *et al.* (1997)
GATA417	CTGAGATAGCAGTTACATGGG TCTGCTCAGGAAATTTTCAAG	Palsbol *et al.* (1997)
GT023	CATTTCCTACCCACCTGTCAT GTTCCCAGGCTCTGCACTCTG	Berube *et al.* (2000)
IGF1	GGGTATTGCTAGCCAGCTGGT CATATTTTTCTGCATAACTTGAACCT	Barendse *et al.* (1994)
RW34	AGCCCCATAACGGCGCATA GGGAGCCAGAACCTGATAC	Waldick *et al.* (1999)
RW48	CCAATGACTTTTCCCTGTA GATACCGCAGTGTGTCCTG	Waldick *et al.* (1999)
SW10	ACCTAAGGATGGACATG ATTCCCAGGTCTCCAA	Richard *et al.* (1996)
SW13	ACCTGTCITAATGAAATCCC ACCT AAATGATGCTCTT	Richard *et al.* (1996)
TexVet5	GATTGTGCAAATGGAGACA TTGAGATGACTCCTGTGGG	Rooney *et al.* (1999a)

SW19	CTAGTTTCTTTAACAGTAATC ACTTCTGGGCTTTTCACCTA	Richard *et al.* (1996)
FCB1	TGCATCTCCATGGTATGTCTTATCC AGCCTCTGCTATGCCTGGAACGC	Buchanan *et al.* (1996)
FCB17	TCAGCCTCTATAACGTCCTGAGC ATGGGGACTGCCTATATTAGTCAG	Buchanan *et al.* (1996)
RW31	TATTCATGGAGTGCTTTGG CCTAGAGTCCAGTGTGGTA	Waldick *et al.* (1999)

Supplementary Material 14- agent-based simulation of pilot whale demography model, developed by Hal Whitehead.

The parameters for the model, as are as follow:

- K: rough equilibrium population size
- m_F: mortality per year for females
- m_M: mortality per year for males
- a: age at maturity (assumed same for males and females)
- a_F: age at maturity for females
- a_M: age at maturity for males
- b: birth rate per mature female per year at low population size
- u: mean unit size
- σ: SE of relatedness estimate

The attributes of individuals are as follow:

At the start of each year, t, there are n(t) animals. Each living animal, i, has the following attributes:

- g(i,t) age in years
- s(i) sex (male/female)—does not change
- u(i,t) unit number—does not change, except if unit splits
- R(i,j) relatedness value with each other animal in population (expected proportion of shared genes through descent). R(i,j)=R(j,i); R(i,i)=1

The model is described as:

1. Initially, t=0, there are K/2u units, each with u members, giving N(1)=K/2 individuals. Individuals have equal probability to be male or female, and have an age randomly chosen on the interval [0 1/m]. All individuals are unrelated, except to themselves (R(i,j)=0; R(i,i)=1).
2. At each year, t, the following steps happen, in the following order:
    2.1. Mortality. All N(t) individuals die with probability m_F, m_M for females and males respectively. Dead individuals are removed from further steps of the simulation, leaving w(t) individuals alive.
    2.2. Aging. All living animals grow 1 year older.
    2.3. Birth. All nmoth(t) females over the age of female maturity give birth to one offspring with probability b·K/(K+N(t)·(nmoth(t)·b /(N(t)-w(t))-1)) [negative values become 0]. This gives density dependence, and a population stabilizing near K.
        2.3.1. Each newborn, i, has equal probability to be male or female (s(i)=0/1), and has age zero (g(i,t)=0).
        2.3.2. The newborn belongs to the same unit as its mother (u(i)=u(mother(i)).
        2.3.3. Its father is chosen randomly, with replacement (so a male can potentially be the father of two or more newborns), from all living males over the age of male maturity but not members of the mother's unit.
        2.3.4. The relatedness between a newborn, i, and any other member of the population, j, is given by: R(i,j) = R(j,i) = [R(mother(i),j) + R(father(i),j)]/2, and R(i,i) = 1
    2.4. Any unit with size larger than 2u members splits, with members being randomly assigned to either of the daughter units.
3. After T years, the simulation stops.
4. We wish to check the within/between-unit patterns of relatedness in a sample of 4 units from which we sample 2, 5, 3, and 2 individuals respectively.

4.1. Randomly choose 4 units, whose sizes are at least 2, 5, 3 and 2 animals respectively.

4.2. From these units, select 2, 5, 3, 2 individuals respectively.

4.3. Add estimation error (normal random variable with SD=σ) to relatedness values for these individuals

4.4. Work out, for this set of 12 individuals:

4.4.1. Mean within-unit relatedness (R)

4.4.2. Mean between-unit relatedness

4.4.3. Matrix correlation of R with same unit (1), different unit (0), matrix

4.4.4. Mantel test of R with same unit (1), different unit (0), matrix

4.5. Do steps 4.1-4.3 10 times, and work out means of measures 4.3.1-4.3.4.

Supplementary Material 15 – Results of the agent-based simulation of pilot whale demography model. All parameters were run using 500 years of permutations, mortality per year for females of 0.068, mortality per year for males 0.078, age at maturity for females of 7 and at males of 12, and birth rate per mature female per year at low population size of 0.3, SE of relatedness estimate 0.103. Parameters inputted: K - rough equilibrium population size; u – mean unit size. Parameter outputted: Pop – average population size; N Units – average number of units; Matrix r – average matrix correlation between relatedness and associations; Mantel p – average p-value associated with matrix r; relatedness within – average relatedness between of pairs of individuals within the same unit; relatedness between – average relatedness between of pairs of individuals between different units.

K	u	Pop	N Units	Mean Unit Size	Matrix r	Mantel p	Relatedness within	Relatedness between
6000	7	5983	976.4	6.13	0.462	0.008	0.178	0.013
2000	7	2031	331.2	6.13	0.443	0.009	0.186	0.031
500	7	489	80.4	6.08	0.413	0.014	0.265	0.123
6000	14	6047	517.6	11.69	0.322	0.049	0.115	0.011
6000	21	6002	349	17.20	0.278	0.073	0.097	0.009
500	21	498	28	17.82	0.217	0.154	0.193	0.122

Supplementary Material 16 – Loci tested for pilot whales that amplified during PCR, visualized in 1.5% agarose gel, and showed variability between individuals, and their preferential amplification temperature.

Loci	Amplification temperature (°C)
EV104Mn	60
EV14Pm	60
EV1Pm	55
EV37Mn	60
EV94Mn	50-60
FCB1	55-60
FCB14	60
FCB5	50-60
GATA098	50
IGF1	50-60
RW34	50-60
RW48	50
SW10	55

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Supplementary Material 18 – Calves identified with only one CC in 2009, 2010 and 2011. Enc. – number of encounters the calf was identified with the CC. None of the CCs were sexed.

2009			2010			2011		
Calf	CC	Enc.	Calf	CC	Enc.	Calf	CC	Enc.
c2	1447	2	c90	595	2	c191	929	2
c21	228	2	c95	2010_a54	2	c225	1308	2
c3	2009_a8	3	c98	1438	3	c231	595	3
c46	2009_a101	2	c110	602	2	c233	661	2
			c159	637	2	c265	2011_a17	2
			c160	2010_a20	2	c286	1217	2
			c165	1156	2	c293	*717*	3
						c212	2011_a49	3
						c232	*717*	2
						c239	2009_a81	3
						c240	2011_a8	2

Supplementary Material 19 - Calves identified with several closest companions in 2009, 2010 and 2011. CC – Closest Companions, when accompanied by "+" at least one other unidentified individual was also seen, Encounters – number of encounters calves and CCs were identified in, Sex – sex of closest companion, Unit – Social Unit to which the closest companion belongs to, when in italics units belong to the K complex. Confirmed mothers are bolded and italicized.

2009					2010					2011				
Calf	CC	Encounters	Sex	Unit	Calf	CC	Encounters	Sex	Unit	Calf	CC	Encounters	Sex	Unit
Patch+	2009_a1	6	-	-	c57	2010_a1	1	-	-	c189	1455	1	-	-
	2009_a2	7	-	-		2010_a2	1	-	-		1276	1	-	-
c11+	2009_a120	1	-	-	c60	2010_a3	1	-	-		2009_a4	1	-	-
	1162	2	F	-		2010_a4	1	-	-	c216	2010_a2	2	-	-
c12	543	1	-	M	c61	2010_a5	1	-	-		1037	1	-	-
	680	1	-	-		228	1	-	-	c268	2011_a17	1	-	-
	2009_a28	2	-	-	c69	1455	1	-	-		2009_a106	1	-	-
	1447	1	-	-		2010_a66	1	-	-	c277	2011_a19	1	-	-
c14	861	2	-	*U*		2009_a45	1	-	-		2011_a21	1	-	-

	113	1	-	-		602	1	-	Q		2011_a22	1	-	-
	1086	1	-	-	c78	2010_a50	1	-	-	c306+	2009_a81	1	-	-
	1034	1	-	-		261	1	-	*K, L, N, U*		***2011_a25***	2	-	-
	1550	1	-	-	c80+	2010_a52	1	-	-		2009_a81	1	-	-
	113	2	-	-		2010_a53	1	-	-	c307	2011_a25	1	-	-
c15	1086	1	-	-		2010_a30	2	-	-		***2009_a101***	1	-	-
	1550	3	-	-	c88+	1438	1	-	-		1438	1	-	-
	2009_a37	1	-	-		2010_a58	1	-	-	c311	2011_a27	1	-	-
c16	2009_a38	1	-	-		312	1	-	*K*		2011_a30	1	-	-
	609	1	-	-	c89	2010_a12	1	-	-	c335	938	1	-	-
	1353	2	M	-		280	2	M	D		1379	1	-	-
c18+					c97+					c340+				
	2009_a45	1	-	-		2009_a61	4	-	-		1470	1	-	-

	1460	1	-	-		1438	1	-	-		2009_a2	1	-	-
c19+														
	347	2	-	-		2010_a65	1	-	-	Patch	575	1	-	-
	347	1		-		2009_a28	1	-	-		351	1	-	-
					c100+									
c20	1353	1	M	-		2010_a15	1	-	-		1160	2	-	-
										c214+				
	808	1	-	H		***1283***	2	-	-		2011_a40	1	-	-
					c128+									
	1439	1	-	-		2010_a40	1	-	-		2011_a41	1	-	-
										c215+				
c23	***2009_a61***	4	-	-		1451	1	-	-		543	1	-	M
	1075	1	-	-	131+	1037	2	-	-		1161	2	-	-
										c284				
	1525	3	-	-		2010_a61	1	-	-		113	1	-	-
c24+	575	1	-	-		637	1	-	O		351	1	-	-
										c221				
	660	1	-	-	c132+	2010_a42	2	-	-		2011_a48	2	-	-
c26+	466	2	-	M		2010_a62	1	-	-	c266	637	1	-	O

	1162	1	F	-		2010_a12	2	-	-		1308	1	-	-
					c133									
	517	2	-	O		2010_a41	1	-	-		1276	1	-	-
c28														
	2009_a79	2	-	-		2010_a19	1	-	-		***2011_a53***	2	-	-
					c137+									
	1243	2	-	-		1441	1	M	-	c213+	1050	1	-	-
c32+														
	1529	1	-	-		312	3	-	*K*		985	1	-	-
	1439	1	-	-	c143	2010_a40	1	-	-		***1379***	2	-	-
c47	1551	1	-	-		808	1	-	H	c222	1438	1	-	-
	637	1	-	O		312	1	-	*K*		2010_a2	1	-	-
					c153+									
	2009_a106	1	-	-		2010_a23	1	-	-	c253+	1767	3	-	-
c48														
	1283	1	-	-		2010_a24	1	-	-	c285+	918	3	-	-
					c154+									
	642	1	-	-		2009_a106	1	-	-					
c50														
	1498	2	-	-	c161	2010_a27	1	-	-					

c56	637	1	-	O		2010_a28	1	-	-
	1548	1	-	-	c162+	1086	1	-	-
	1449	2	-	-		2010_a46	1	-	-
c6+	531	1	-	H		2010_a41	1	-	-
	1716	1	-	-	c163+	1086	1	-	-
	1347	1	-	-		817	1	-	-
c8	***474***	3	-	-		1351	1	-	-
	1570	1	-	-	c181+	2010_a30	1	-	-
c31+	2009_a81	2	-	-		2010_a31	1	-	-
c33+	1245	2	M	-	184	2010_a43	1	-	-
c34+	2009_a89	2	-	-		2010_a20	2	-	-
c4+	1529	2	-	-	c76+	517	2	-	O

c126+	2009_a106	7	-	-
c127+	2010_a40	3	-	-
c129+	2010_a55	4	-	-
c178+	1499	2	-	-
Patch+	2009_a2	4	-	-

Supplementary Material 20 – Reciprocity between known mothers of calves in 2009, 2010 and 2011. NI – not identified

2009				
Mother	Calf	Calf's allopar ents	Mother alloparental cared for calves	Alloparental cared calves' mother
1447	C2	-	C12	NI
228	C21	-	c61	NI
2009_a8	C3	-	-	-
2009_a101	C46	-	c307	2009_a101
1550	C15	113, 1086	C14	NI
2009_a61	C23	1439, 1075	c97	NI
474	C8	1570	-	-
2010				
Mother	Calf	Calf's allopar ents	Mother alloparental cared for calves	Alloparental cared calves' mother
595	c90	-	c231	595
2010_a54	c95	-	-	-
1438	c98	-	c88	NI

			c89	NI
			c311	NI
			c222	1379
602	c110	-	c78	NI
637	c159	-	C47	NI
			C56	NI
2010_a20	c160	-	c184	NI
1156	c165	-	-	-
1283	c128	2010_a40	C48	NI
2011				
Mother	Calf	Calf's allopar ents	Mother alloparental cared for calves	Alloparental cared calves' mother
929	c191	-	-	-
1308	c225	-	c266	NI
661	c233	-	-	-
2011_a17	c265	-	c268	NI
1217	c286	-	-	-
717	c231	-	-	-

	c293			
2011_a49	c212	-	-	-
2011_a8	c240	-	-	-
2011_a25	c306	2009_a81	c307	2009_a10
2009_a10	c307	2009_a81 2011_a25	c231	595
2011_a53	c213	1050 985	-	-
1379	c222	1438 2010_a2	c340	NI

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