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Social structure of long-finned pilot whales (*Globicephala melas*) off northern Cape Breton Island, Nova Scotia

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Abstract
Cetacean social structures include fluid and stable elements. Long-finned pilot whales (*Globicephala melas*) live in units that interact forming labile groups. In this study conducted off Cape Breton Island, between 1998–2011, we confirm unit membership predicts associations between individuals. We determine how units are structured and interact. We delineated 21 nearly-stable social units, with an average 7 members. For units where multiple individuals are sexed, both sexes are present. Most units showed long-term stability, while one showed evidence of splitting. Three units shared individuals with the largest unit (K, average size = 29). Splitting is likely triggered by size and difficulties maintaining associations between all individuals. Pilot whales face many pressures driving sociality at a range of temporal and social scales producing a multilevel society. While we have produced a more detailed model of long-finned pilot whale social structure, there are still unanswered questions, particularly whether units are strict matrilines.

Keywords
social structure, pilot whale, unit, fission, associations.

1. Introduction

Social structure can be defined in a variety of ways (Whitehead, 2008). Definitions can be ethological (e.g., Hinde, 1976; Kappeler & van Schaik, 2002), based on behavioral-ecological studies (e.g., Wilson, 1971; Michener, 1974), on mating systems (e.g., Emlen & Oring, 1977; Clutton-Brock, 1989) or on

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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 & Whitehead, 2003; Augusto et al., 2012; Gero et al., 2014). There also may be a feedback loop between individuals and their social system (Kappeler & van Schaik, 2002): social structure shapes the individual's behaviour, and its behaviour influences the population's social structure.

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 by 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).

The social structure of long-finned pilot whales (*Globicephala melas*), 5–7-m delphinids which we will refer to as pilot whales, has been studied in three coastal locations: the Faeroes, Cape Breton Island and Gibraltar (Amos et al., 1991, 1993; Ottensmeyer & Whitehead, 2003; de Stephanis et al., 2008). In the Faroes, groups of animals containing tens to over 100 individuals, called "grinds", were driven ashore together. These grinds contained related individuals of both sexes, and so it was suggested that this was a case of bisexual natal phylopatry to the grind (Amos et al., 1991, 1993). However, the Faeroe studies do not provide data on the temporal variation of associations between individuals on any scale. The population off Cape Breton

Island has been studied using photoidentification (Ottensmeyer & Whitehead, 2003), revealing a society composed of stable units containing about 8 animals. Units interact regularly with each other, forming labile groups. In Ottensmeyer & 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, following Amos et al.'s (1991, 1993) suggestion for the Faeroes. The social structure of the Gibraltar resident population is similar in social structure to that in Cape Breton, but on a smaller scale, with small units (2–3 identified 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., 2008). 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) in that stable units form labile groups. This form of social structure has been well studied in killer and sperm whales and is believed to be an important driver of life history evolution and cultural evolution in these species (Brent et al., 2015; Whitehead & Rendell, 2015).

Here we study the social structure of the Cape Breton pilot whale population in greater depth than previous studies. We had three 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 as well as the temporal stability of this structure. The third was to describe how units interact with each other. We expect unit size to be comparable with Ottensmeyer & Whitehead's (2003) results, that units will be comprised of both males and females, and have stable membership over the period of the study. We also analyzed within-unit structure to assess any indications of unit fission. Following results from killer and sperm whales (Bigg et al., 1990; Gero et al., 2015), we expect that units may show preferences in their associations with other units. The structure and integrity of social units, as well as interactions among social units, over a range of time scales, are important elements of social structure, as well as determinants of how social structure affects the evolution of culture and life history (Whitehead & Rendell, 2015; Croft et al., 2017).

2. Methods

2.1. Behavioural and photographic data collection

Data were collected in July and August, from 1998 to 2000 and from 2002 to 2011, from 13-m whale-watching vessels off the northwest coast of Cape Breton Island, NS, 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). The harbours are 46 km apart. Up to five trips were conducted daily, lasting a maximum of 2.5 h 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 was less than 20 knots.

Usually, two researchers collected behavioural and photographic data on each trip. Behavioural data collected included estimates of group size and number of calves present. The waters were scanned for the presence of pilot whales, and when a group was sighted the vessel approached it slowly and kept parallel to the movement of the whales 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 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. The chain rule was used to estimate group size, meaning each whale within a group had to be less than 200 m from another whale. Whales that were farther than 200 m away from the boat or too far to reliably estimate group size and behaviour 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 & 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. *Photoidentification*

Photoidentification pictures of the dorsal fin area (Auger-Methe & 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 300 mm autofocus lens, and a Canon EOS-10D (digital) or Canon 30D (digital) with a 200 mm or 300 mm 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 & Whitehead, 2003; Auger-Methe & Whitehead, 2007). Photoidentification was performed using Finscan (Araabi et al., 2000) on photographs with $Q > 2$ showing dorsal fins with MP $\geqslant 2$. We also updated the estimate of the mark rate of the population, the proportion of individuals with MP $\geqslant 2$, to include both film and digital camera data. To do so we calculated how many of the $Q > 2$ photographs of individuals had MP $\geqslant 2$ (e.g., if there were 50 photographs of individuals with $Q > 2$, but only 25 of them had individuals with MP $\geqslant 2$, the mark rate was 0.50), for both film and digital data.

2.3. *Biopsy sampling*

Tissue was collected by remote biopsy sampling in July and August of 2010 to 2012 off Pleasant Bay harbour from a semi-rigid 4.5-m inflatable boat, as in Kowarski et al. (2014). 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 the harbour, 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 the photo-identification 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 11 August 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 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).

2.4. Molecular analysis

Molecular analyses were used to determine sex. DNA was extracted using the phenol:chloroform extraction method described in Sambrook & Russel (2001) and Wang et al. (2008). Sex of individuals was determined using a multiplex PCR of two primer pairs: one that amplifies an approx. 400 bp portion of the ZFX/ZFY gene (present on both sex chromosomes) and one that amplifies an approx. 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 1 × *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.

2.5. What is the turnover in this population?

For the following analyses only encounters with 'coverage > 0', photographs with $Q > 2$, and individuals with $MP \geqslant 2$ 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 during 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 whether there were turnover differences between the sexes we repeated the analysis for both males and females separately.

2.6. How stable are relationships in this population?

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

Sampling periods were days, and individuals were 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 with 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 & 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.

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 (MM, FF, FM) 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.

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

Units were 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 & 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 re-sightings 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 analysed 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.

2.8. *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.

2.9. *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 behaviourally 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.

2.10. How do units relate to one another?

When analysing 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 min. 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.

3. Results

3.1. Photo-identification and molecular sexing

There were 1231 individuals with MP $\geqslant 2$ identified on 485 days from $Q > 2$ photos. The mean number of days that these individuals were identified was

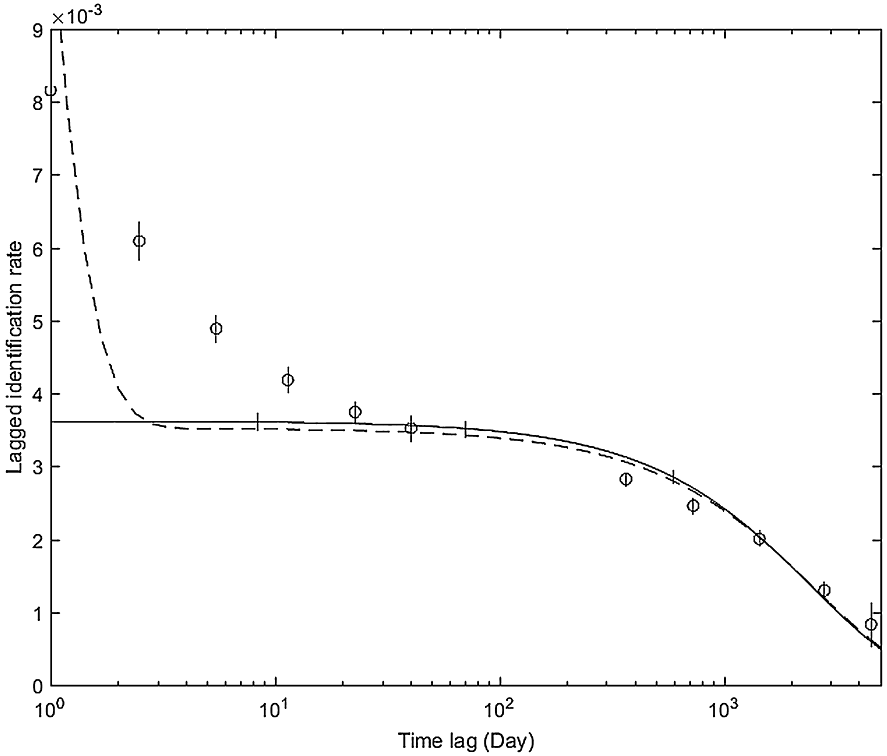


Figure 1. Lagged Identification Rate (LIR). Error bars were calculated using the jackknife technique. The maximum-likelihood model that performed best with the SLAR is represented with a solid line. The maximum-likelihood best fit model is represented with a dashed line.

5.6 (range 1–66). Reidentification rates fell after about 3 years (Figure 1). The mark rate for film was 0.48, while for digital photographic data it was 0.54. Overall, the updated mark rate for this population was 0.51, so 51% of the population was identifiable. A total of 76 individuals were sexed, 75 of which had been photo-identified. Of these, 33 were females and 42 were males.

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 decreased with time (Figure 1). We fitted the model type emigration/mortality (a_1 = emigration rate; $1/a_2 = N$) $g(\tau) = a_2 e^{(-a_1\tau)}$, 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 $a_1 = 0.000400$ day^{-1} (SE $= 4.2\text{e}{-}05$), which is equal to 0.1460 year^{-1}. The best fit model for the LIR was Emigration + reimmigration + mortality ($a_1 = N$; $a_2 =$ mean time in study area; $a_3 =$ mean time out of study area; $a_4 =$ mortality rate) $g(\tau) = a_3\text{e}^{(-a_1\tau)} + a_4\text{e}^{(-a_2\tau)}$ had $a_1 = 0.000384$ day^{-1} (SE $= 4.866\text{e}{-}05$), which is equal to 0.1382 year^{-1}. The decline values for emigration/mortality (0.1460 year^{-1}) and emigration + reimmigration + mortality (0.1382 year^{-1}) were very similar, which indicates that individuals seemed 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). For the female LIR, the model type emigra-

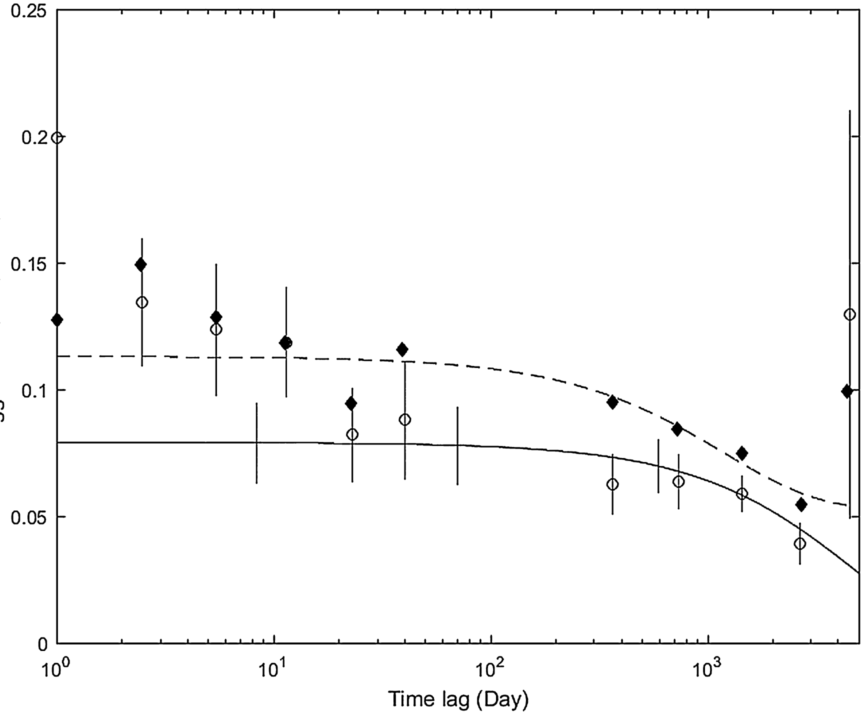


Figure 2. Lagged Identification Rate (LIR) for individuals of different sexes. Males are represented by empty circles, females by full diamonds. Error bars were calculated using the jackknife technique. The maximum-likelihood best fit model is represented with a solid line for males and dashed for females.

tion + reimmigration $g(\tau) = a_2 + a_3\mathrm{e}^{(-a_1\tau)}$ best fitted to the data showed $a_1 = 0.000834$ (SE = 0.041) or 0.3044 year^{-1}. For the male LIR, the model type emigration/mortality $g(\tau) = a_2\mathrm{e}^{(-a_1\tau)}$ best fitted to the data showed $a_1 = 0.000211$ (SE = 9.4705e−05) or 0.07702 year^{-1}. Given these results, males appeared 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 units A, B and E (Table 1 in the Supplementary data in the online edition of this journal, which can be accessed via http://booksandjournals.brillonline.com/content/journals/1568539x) where only one individual from the original unit was identified in the later years. We then compared photographs of those seen in the same encounter as the remaining unit individual during the later years with its previous companions in the earlier years (Table 2 in the Supplementary data in the online edition of this journal, which can be accessed via http://booksandjournals.brillonline.com/content/journals/1568539x). In both unit A and B it was not possible for the original unit IDs to have gained marks that would make them 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 were influencing the decline of the LIR.

3.3. How stable are relationships in this population?

The association rate between individuals decreased with time (Figure 3). The SLAR and error bars crossed the null association rate at about 25 years. The best fit model for the data was characterized as 'casual acquaintances and constant companions' (Table 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}, SE = 4.2e−05), indicating demography, and SLAR (0.000793 day^{-1}, SE = 5.9e−05), indicating association, were similar enough to suggest that demography may explain a good deal of the association rate decline.

The parameters of the best fit model suggest an average typical group size of 32 identified individuals ($1/a_2$). (Typical group size is the group size typically experienced by a member of the population (Whitehead, 2008)). Scaling this value to take non-identifiable individuals into account (Ottensmeyer & Whitehead, 2003), and the SE of the mark rate, average typical

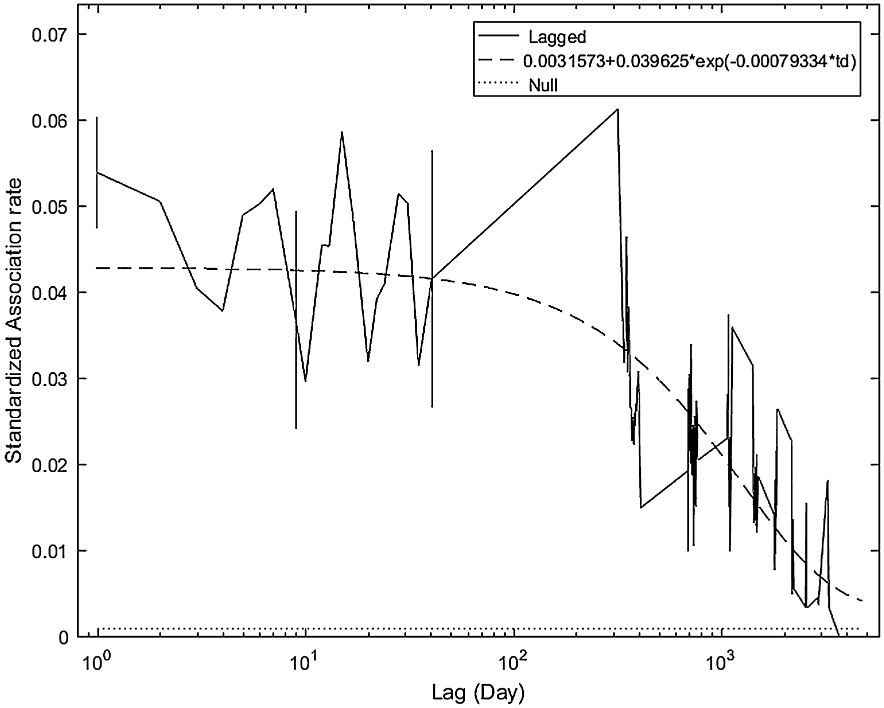


Figure 3. Standardized lagged association rate (SLAR). Error bars were calculated using the temporal jackknife technique. The null association rate represents the theoretical SLAR if individuals associated randomly. The maximum-likelihood best fit model represents casual acquaintances.

group size increased to 59 individuals. This is similar to our at sea group size estimates (Ottensmeyer & 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 (Table 3 in the Supplementary data in the online edition of this journal, which can be accessed via http://booksandjournals.brillonline.com/content/journals/1568539x). 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 120 000 permutations, indicated differences in association rates between-versus-within sexes (Matrix correlation $= -0.00398$, $p = 0.0498$). The negative matrix correlation indicates that individuals preferred to associate with members of the other sex, but the low

Table 1.
Fit of social models to the standardized lagged association rate for the population.

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)	47 906.40	1252.46
Casual acquaintances (CA)	$g(\tau) = a_2 \mathrm{e}^{(-a_1\tau)}$	$a_1 = 0.000654$ day^{-1} (SE 5.60e−05) $a_2 = 0.0419$ day^{-1} (SE 0.00388)	46 656.81	2.87
CA + CC	$g(\tau) = a_2 + a_3 \mathrm{e}^{(-a_1\tau)}$	$a_1 = 0.000793$ day^{-1} (SE 0.000264) $a_2 = 0.0316$ day^{-1} (SE 0.00236) $a_3 = 0.0396$ day^{-1} (SE 0.00411)	*46 653.94*	
Two levels of CA	$g(\tau) = a_3 \mathrm{e}^{(-a_1\tau)} + a_4 \mathrm{e}^{(-a_2\tau)}$	$a_1 = 0.000653$ day^{-1} (SE 21.0) $a_2 = 0.000653$ day^{-1} SE (0.0253) $a_3 = -0.0113$ day^{-1} (SE 8.07) $a_4 = 0.0531$ day^{-1} (SE 0.703)	46 660.81	6.87

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 italics.

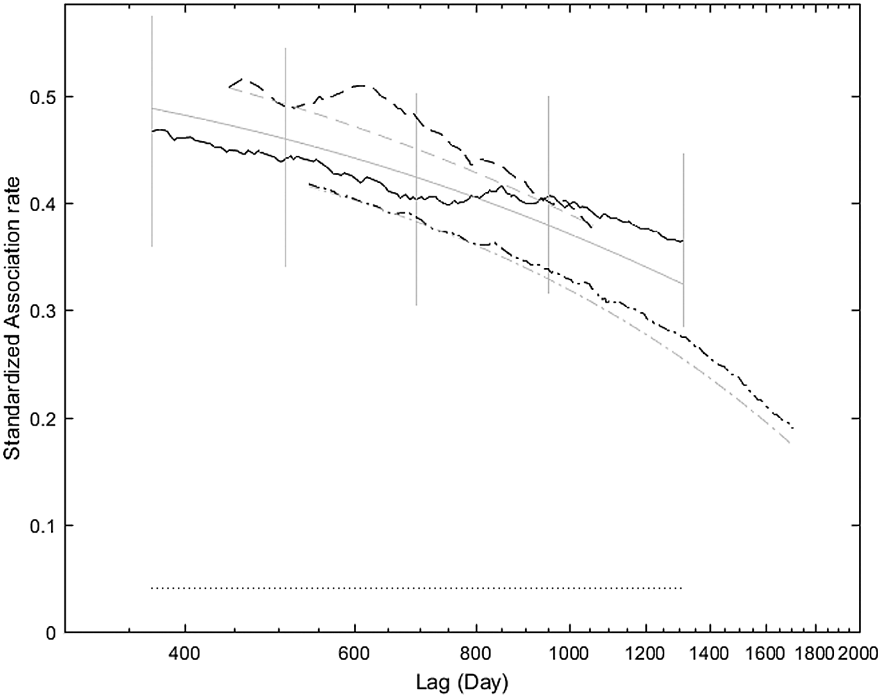


Figure 4. Standardized lagged association rate (SLAR) for individuals of different sexes. MF: Male to Female, FF: Female to Female, FM: Female to Male. Error bars were calculated using the temporal jackknife technique. The null association rate represents the theoretical SLAR if individuals associated randomly. The maximum-likelihood best fit models are noted for each sex.

value shows a very small effect. The temporal pattern of associations also did not vary much according to the sex of the dyad (Figure 4, Table 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.

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

Twenty one units were identified (Table 1 in the Supplementary data in the online edition of this journal, which can be accessed via http://booksandjournals.brillonline.com/content/journals/1568539x), 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

Table 2.
Fit of social models to the standardized lagged association rate for the associations between females (FF), from female to male (FM) and male to female (MF).

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)	$g(\tau)=a_2\mathrm{e}^{(-a_1\tau)}$	$a_1=0.000475$ day^{-1} (SE 0.0834) $a_2=0.627$ day^{-1} (SE 0. 423)	*259.04*	
CA + CC	$g(\tau)=a_2+a_3\mathrm{e}^{(-a_1\tau)}$	$a_1=5.72$ 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	$g(\tau)=a_3\mathrm{e}^{(-a_1\tau)}+a_4\mathrm{e}^{(-a_2\tau)}$	$a_1=1.03$ 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 (CA)	$g(\tau)=a_2\mathrm{e}^{(-a_1\tau)}$	$a_1=0.000703$ day^{-1} (SE 0.000110) $a_2=0.556$ day^{-1} (SE 0.0740)	*651.52*	
CA + CC	$g(\tau)=a_2+a_3\mathrm{e}^{(-a_1\tau)}$	$a_1=2.14\mathrm{e}{-05}$ day^{-1} (SE 10.69) $a_2=-9.36$ day^{-1} (SE 166.0) $a_3=9.89$ day^{-1} (SE 2278.0)	*636.59*	

Table 2.
(Continued.)

Description of Model	Model formula	Maximum likelihood values for parameters (Jackknifed standard errors for parameter)	QAIC	ΔQAIC
Two levels of CA	$g(\tau) = a_3 e^{(-a_1\tau)} + a_4 e^{(-a_2\tau)}$	$a_1 = 0.167$ day^{-1} (SE 0.639) $a_2 = 0.000759$ day^{-1} (SE 0.000119) $a_3 = 0.316$ day^{-1} (SE 0.284) $a_4 = 0.598$ day^{-1} (SE 0.0795)	671.17	19.65
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)	$g(\tau) = a_2 e^{(-a_1\tau)}$	$a_1 = 0.000434$ day^{-1} (SE 0.000142) $a_2 = 0.573$ day^{-1} (SE 0.125)	*624.00*	
CA + CC	$g(\tau) = a_2 + a_3 e^{(-a_1\tau)}$	$a_1 = 0.0136$ day^{-1} (SE 26.0) $a_2 = 0.357$ day^{-1} (SE 0.184) $a_3 = 0.346$ day^{-1} (SE 240.1)	631.97	7.97
Two levels of CA	$g(\tau) = a_3 e^{(-a_1\tau)} + a_4 e^{(-a_2\tau)}$	$a_1 = 0.496$ day^{-1} (SE 3.47) $a_2 = 0.000402$ day^{-1} (SE 0.000159) $a_3 = 0.474$ day^{-1} (SE 0.809) $a_4 = 0.552$ day^{-1} (SE 0.135)	626.10	2.1

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 italics.

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 & Whitehead, 2003), we decided to simplify the dataset and omitted these individuals.

Unit identification varied through the years (Figure 4 in the Supplementary data in the online edition of this journal, which can be accessed via http://booksandjournals.brillonline.com/content/journals/1568539x). 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 the years 1998, 2000, 2002–2008 and 2011).

Units appear quite well differentiated (Figure 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

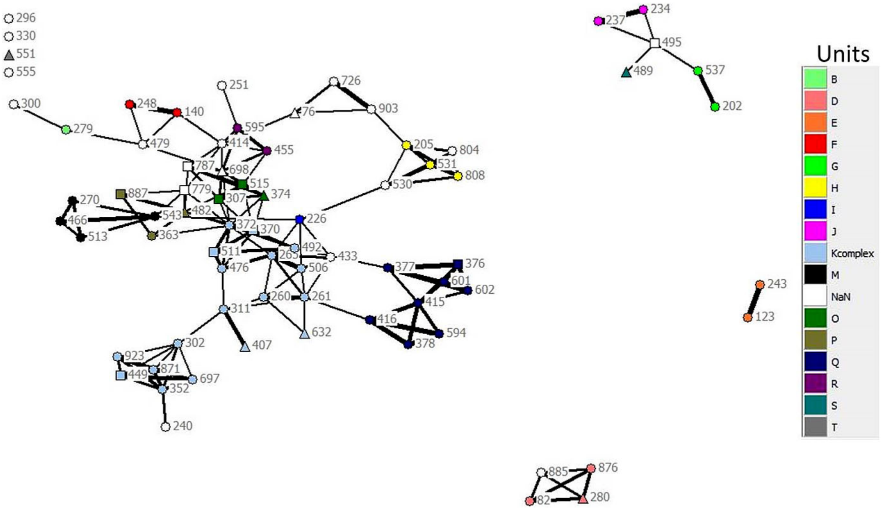


Figure 5. Network of individuals seen more than 20 times during the sampling period, with CoA $\geqslant 0.1$. Different colours represent different units (individuals not assigned to a unit are marked as NaN) and different symbols sexes. Circles — non identified sex, Squares — Females, Triangles — Males.

without the *K* complex (Figure 4 in the Supplementary data in the online edition of this journal, which can be accessed via http://booksandjournals.brillonline.com/content/journals/1568539x).

Fifteen units had more than one individual identified in at least 6 years (Figure 5 in the Supplementary data in the online edition of this journal, which can be accessed via http://booksandjournals.brillonline.com/content/journals/1568539x), 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 (Table 6 in the Supplementary data in the online edition of this journal, which can be accessed via http://booksandjournals.brillonline.com/content/journals/1568539x). 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.

3.5. What is the size and sex-ratio of units?

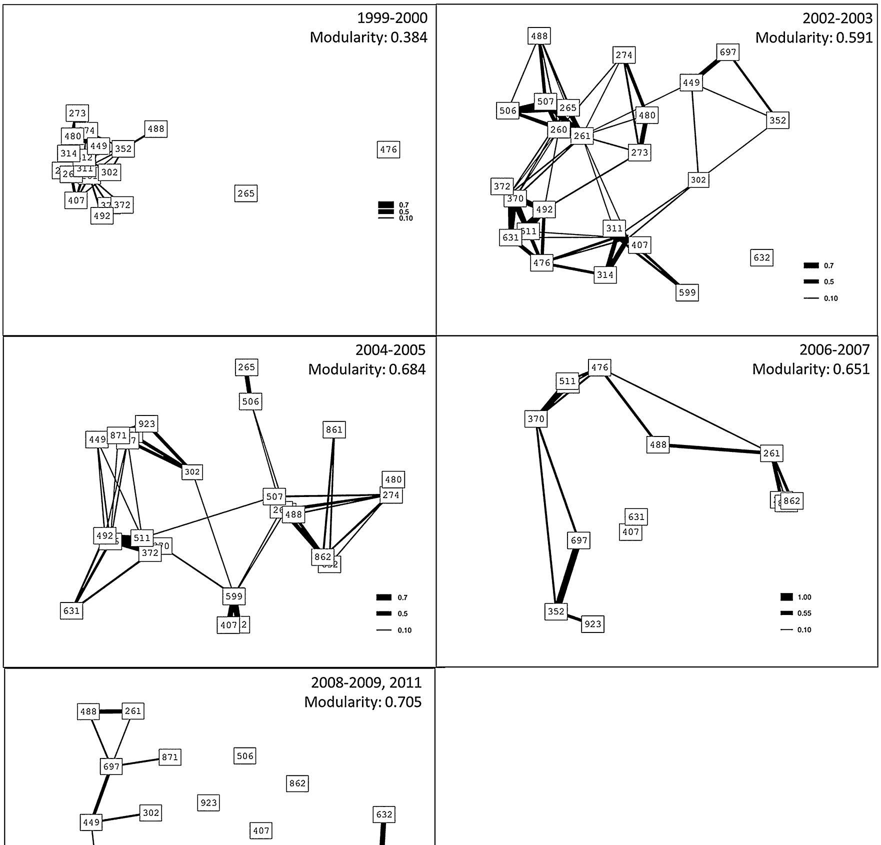
Mark rate of units varied between 0.33 and 0.73 (Table 1 in the Supplementary data in the online edition of this journal, which can be accessed via http://booksandjournals.brillonline.com/content/journals/1568539x). When corrected for the each specific unit mark rate, average unit size varied between 3 and 29 individuals. Mean unit size for the population was 6.83.

Individuals in 7 different units were sexed (Table 1 in the Supplementary data in the online edition of this journal, which can be accessed via http://booksandjournals.brillonline.com/content/journals/1568539x). 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).

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 (Table 7 in the Supplementary data in the online edition of this journal, which can be accessed via http://booksandjournals.brillonline.com/content/journals/1568539x). Units B and Q were divided into 2 clusters each and the K complex into 5 clusters (Table 8 in the Supplementary data in the online edition of this journal, which can be accessed via http://booksandjournals.brillonline.com/content/journals/1568539x).

To examine the dynamics within the K complex, we analysed the network diagrams and modularity in different years (Figure 6). Individuals in the



1999-2000
Modularity: 0.384

2002-2003
Modularity: 0.591

2004-2005
Modularity: 0.684

2006-2007
Modularity: 0.651

2008-2009, 2011
Modularity: 0.705

Figure 6. Network diagrams for the K complex across different years of the study. Modularity was calculated using Newman's (2006) eigenvector method.

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.

3.7. How do units relate to one another?

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

The K complex appeared at the centre in the 'all units' network diagrams (Figure 9 in the Supplementary data in the online edition of this journal, which can be accessed via http://booksandjournals.brillonline.com/content/journals/1568539x). Different individuals from the K complex connected to different units, but their highest associations were with others within the K complex. After removing the K complex from the analysis, no other unit replaced it although several units showed somewhat central positions in the network (Figure 10 in the Supplementary data in the online edition of this journal, which can be accessed via http://booksandjournals.brillonline.com/content/journals/1568539x). When looking at dyads within units it becomes more obvious that there was not a central, all-connecting, unit when the K complex was removed. Each individual associated with a maximum of one or two different units at HWI > 0.1 (Figure 10 in the Supplementary data in the online edition of this journal, which can be accessed via http://booksandjournals.brillonline.com/content/journals/1568539x). Associations between pairs of individuals within the K complex were heterogeneous, with some dyads in near constant association while others barely associated (Figure 11 in the Supplementary data in the online edition of this journal, which can be accessed via http://booksandjournals.brillonline.com/content/journals/1568539x).

4. Discussion

4.1. The study population

The pilot whale population that summers off Cape Breton has been the subject of a long term study since 1998. The first analysis of its social structure (Ottensmeyer & Whitehead, 2003) was performed using data from 1998 to

Table 3.
Associations between units.

Sampling	All units		
	Day	Hour	Encounter
Metrics			
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			
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			
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)

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.

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 & 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.

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 & 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 (Figure 12 in the Supplementary data in the online edition of this journal, which can be accessed via http://booksandjournals.brillonline.com/content/journals/1568539x).

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/year is entirely due to mortality.

Identification change is very likely happening in this population, and a part of the reason behind the LIR decline (Table 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 & 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 & 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 to 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 analyse 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.

The low re-sighting rate over time, the relatively small number of sexed individuals (79), and the possibility of mark change all reduce the power of our analysis to meet its objectives. However, by the standards of studies of cetacean social structure, the data set is large both in the number of individuals identified and the time scale. Thus, we can make valuable inferences that advance our knowledge of pilot whale social structure.

4.2. Does social unit membership explain the greatest part of how individuals associate?

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 & Whitehead, 2003; de Stephanis et al., 2008). A total of 123 individuals were affiliated to quite well-delineated units, although there are linkages between units and uncertainties. This total 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.

From the twenty-seven units identified in this study, six of the seven identified by Ottensmeyer & Whitehead (2003) were present (Table 4). Unit E was not identified due to the stricter unit-membership 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 4.
Comparison between units identified by Ottensmeyer & Whitehead (2003) with data collected between 1998 and 2000, and this study with data collected 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	

Units were calculated using the original protocol from Christal et al. (1998) between 1998 and 2000, and the modified protocol from 1998 to 2011.

4.3. How are units structured?

The structure of a social unit contains several properties. Most basic are the number of individuals, and the distribution of these members into classes, primarily sex. A unit may or may not be sub-structured into somewhat self-contained subunits, or clusters. All these properties can change over time. Furthermore, they tend to be related: larger units may be more likely to show substructure, to split, and to show dynamic membership (e.g., Christal et al., 1998).

Ottensmeyer & Whitehead (2003) estimated a mean unit size of 7 for the Cape Breton population, similar to our results. All units had less than 12 individuals, except unit K which had 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 different for the long-finned pilot whale population off Gibraltar (de Stephanis et al., 2008), with smaller line units of 2–3 identifiable individuals. With a correction factor for non-identifiable individuals of about 1.5 (de Stephanis et al., 2008), mean line unit size becomes roughly 2–5. The Gibraltar animals form 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. Pilot whales then appear to share similar pod/unit size with resident killer whales and with sperm whales, where, in each case, mean unit size is also quite similar 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., 2008). 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 — members of each cluster preferentially associating with other members of the same cluster — 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. 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. 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 & Poole, 1983; Moss & Lee, 2011). In these species, fission events usually occur along matrilines, with each matriline becoming a new group.

4.4. Interactions among units

Units frequently associated with one another to form groups. Comparing unit and group size, we can see that groups contain on average about 5 units. The average typical group size was considerably different than the one estimated by Ottensmeyer & Whitehead (2003) for this population. The typical group size increased from 29 to 57–62 individuals. It is 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.

Units appear to have association preferences among the other 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.

4.5. Conclusions

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 the social dynamic. We now know that Cape Breton units have a mean size of 7, 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 that one unit held a central role in the network of associations among units. Without the K complex unit associations between units would be much fewer. This is a concept that would also be interesting to explore in other populations. 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.

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