Group size and composition of northern bottlenose whales (*Hyperoodon ampullatus*) between Iceland and Jan Mayen

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15 eininga ritgerð sem er hluti af
Baccalaureus Scientiarum gráðu í Líffræði

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Útdráttur

Þekking á félagsgerð og atferli andarnefja (*Hyperoodon ampullatus*) er verulega ábótavant, sérstaklega í norðausur Atlantshafi. Flestar rannsóknir á félagsgerð og atferli andarnefja hafa farið fram á landgrunninu út af Nova Scotia í Kanada, nánar tiltekið í neðansjávargilinu, The Gully, og á nærliggjandi svæðum. Á árunum 2013-2016 var farið í leiðangra milli Íslands og Jan Mayen og gögnum safnað um adarnefjur á svæðinu. Þessi gögn voru notuð í þessari rannsókn til að athuga atferli andarnefja með tilliti til fjölda einstaklinga í hjörð. Einnig voru ljósmyndir sem teknar voru í leiðöngrunum notaðar til að greina einstaklinga í flokka eftir aldri og kyni og var hlutfall þessara flokka innan hjarðar rannsakaður. Sjónrænt mat (n=621)á fjölda einstaklinga var notað til að áætla stærð hjarðar. Meðalstærð hjarðar reyndist vera þrír einstaklingar auk þess sem hjarðir með fleiri en sex einstaklinga voru sjaldséðar. 19,6% einstaklinga sem greindir voru í aldurs-kyn flokka reyndust vera kynþroska karldýr (MM) og 80,4% kvendýr-ungdýr (FJ). Einstaklingar greindir sem kynþroska karldýr virtust frekar sækjast í að vera með öðrum kynþroska karldýrum í hjörð fremur en einstaklingum sem flokkaðir voru sem kvendýr-ungdýr. Líkurnar á því að einstaklingur yrði flokkaður sem kynþroska karldýr voru hærri ef önnur kynþroska karldýr voru til staðar í hjörðinni (58%) heldur en þegar engin önnur kynþroska karldýr voru til staðar (4%). Einstaklingar sem voru flokkaðir sem kvendýr-ungdýr sýndu ekki greinileg tengsl við ákveðna flokka. Einnig virðist ekki vera samband milli hlutfalls aldurs-kyn flokka og stærð hjarðar þar sem hlutföll flokkanna breyttust ekki með fjölda einstaklinga í hjörð. Niðurstöður þessarar rannsóknar sýna því að andarnefjur í norðaustur Atlantshafi virðast hafa svipaða félagsgerð og atferli og andarnefjur á landgrunninu út af Nova Scotia.

Abstract

Information on social structure and behaviour of northern bottlenose whales (*Hyperoodon ampullatus*) is very scarce, especially in the northeast Atlantic. Most research on social behaviour of northern bottlenose whales has focused on a subpopulation of the species around the Gully, a submarine canyon on the eastern Scotian Shelf in Canada. In this study the group size and composition of northern bottlenose whales between Iceland and Jan Mayen was examined. Data collected in the summers of 2013-2016 was analysed. Analysis on visual estimates (n=621) showed that the average group size for northern bottlenose whales was three and that groups of six or more were uncommon. Using photographic age-sex classification 19.6% of individual were classified as mature male (MM) and 80.4% as female-juvenile (FJ). Analysis on group composition showed that individuals classified as mature males preferred associations with other individuals of the same age sex class. The probability of an individual being classified as mature male was considerably higher if other mature males were present in the group (58%) compared to when other mature males were absent from the group (4%). Individuals classified as female-juvenile did not seem to have preferences regarding associations and group size did not seem to affect group composition. The results of this study are in line with previous studies on the Scotian Shelf population indicating that the social structure of northern bottlenose whales in the northeast Atlantic resembles that of the northwest Atlantic.

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1 Introduction

Northern bottlenose whales (*Hyperoodon ampullatus*) are toothed wales belonging to the family Ziphiidae (or, beaked whales). Northern bottlenose whales were heavily hunted by whalers from 1882-1920 and again in 1930-1973. After these two excessive whaling periods the northern bottlenose whale populations showed evidence of depletion. In 1977 the International Whaling Commission categorized the species as provisionally protected stock with allowable quota of zero animals (Mead, 1989). The effects from this extensive whaling on the species as well as its status today is uncertain (Whitehead & Hooker, 2012).

1.1 Distribution

Northern bottlenose whales are most commonly found in cold, Arctic and subarctic waters and generally keep to deep waters (>500m) (Moors-Murphy, 2018). Northern bottlenose whales in the northeast Atlantic prey mainly on cephalopods, but other prey are crustaceans and fish. Deep-sea cephalopods of the species *Gonatus fabricii* and *G. steenstrupi* make up a large portion of their diet (Santos et al., 2001; Lick & Piatkowski, 1998). It has been suggested that the distribution of northern bottlenose whales likely reflects the distribution of this preferred prey (Fernandez et al., 2014; Bloch et al., 1996). Northern bottlenose whales in the north-east Atlantic are most abundant in deep waters around the Faroe Islands, Iceland and Jan Mayen (Leonard & Øien, 2020; Pike et al., 2019).

Northern bottlenose whales have been divided into two stocks for management purposes, the northeast and the northwest Atlantic stock. The stocks are separated by Cape Farwell in southern Greenland. Historically, six areas of concentration have been detected for northern bottlenose whales and these areas were used as different fishing grounds during the whaling era. These six areas are (Whitehead & Hooker, 2012);

1. Eastern Scotian Shelf, Canada
2. Off northern Labrador, Canada, and southern Baffin Bay
3. East Greenland, Iceland, Jan Mayen and the Faroe Islands
4. South west of Svalbard (Spitzbergen)
5. Off Andenes in northern Norway
6. Off Møre in western Norway

Sightings of northern bottlenose whales off mainland Norway (locations 5 and 6) are very rare nowadays (Øien & Hartvedt, 2011; Leonard & Øien, 2020).

Whitehead et al, (1997) reported that the whales in the Gully, a submarine canyon off the coast of Nova Scotia, were morphologically different from the whales off Labrador and they seemed to breed at a different time than the whales off Labrador (Whitehead et al., 1997). Furthermore, comparison of nuclear and mitochondrial markers of northern bottlenose whales from the Gully, north of Iceland and off the coast Labrador showed that the Gully population is distinct from the Labrador population and Icelandic population, indicating that northern bottlenose whales on the Eastern Scotian shelf, including the Gully, form a separate subpopulation (Dalebout et al, 2006). Panmixia between the Labrador and Icelandic stock could not be rejected and could therefore indicate dispersal between the two stocks. However, this can also be explained by the small sample size of the Icelandic stock (n=23) used in the study (Dalebout et al, 2006).

1.2 Sexual dimorphism

Northern bottlenose whales are sexually dimorphic. The males are larger than females as well as the shape and size of the head differs. Mean body length at sexual maturity for females is 6.9 meters and 7.5 meters for males. Mature males have a relatively larger head than females and the slope of their melon becomes steeper making the forehead look flat (Gray, 1882; Mead, 1989). The function of this morphological difference is uncertain but may be related to head-butting behaviour, which is thought to be a form of male-male aggression (Gowans & Rendell, 1999). From the melon morphology the whales have been categorized into three age-sex classes; juvenile/female, subadult male and mature male (Gowans et al. 2000). Genetic analysis along with melon-profile photographs showed that 9 out of 10 whales were categorized correctly into age-sex classes, indicating that melon morphology can be used to effectively determine the sex of individuals. However, of the 10 individuals none belonged to the subadult age-sex class (Gowans et al., 2000). Furthermore subadult males and females can be difficult to tell apart from the shape of the melon.

1.3 Social structure

The social structure of northern bottlenose whales is poorly understood. In the north-east Atlantic they are often seen in groups of 1-5 individuals (Pike et al., 2019). Surveys on cetacean abundances in the northeast Atlantic have estimated an average group size of 2.12-3.00 depending on survey block (Leonard & Øien, 2020). Large groups of 16 or more whales have been spotted, however it is rare. Solitary individuals have also been reported and seem to be common. Solitary animals are often young, however solitary old males have also been spotted (Benjaminsen & Christensen, 1979). Northern bottlenose whales in the Gully, Canada, were found to stay in small groups of 3 on average (Gowans et al., 2001).

Photo-identification methods can be used to analyse behaviour and social structure of northern bottlenose whales. Marks such as fin notches and back indentations are stable and persistent enough to be used to identify individuals long term. Other markings such as patches and scars can be used to identify individuals within the same season or adjacent years (Freyrer et al, 2021). Photo-identification methods have been used to analyse social structure of northern bottlenose whales in the Gully. The research showed that individuals changed groups often and that individuals belonging to the mature male age-sex class were more likely to form long-term (1-2 years) associations with each other than individuals classified as female-juvenile. Individuals classified as female-juvenile also showed no preferred age or sex when forming associations with other individuals. Neither did they show preference to specific individuals. Therefore, the associations made between individuals of northern bottlenose whales indicated a fission-fusion society (Gowans et al., 2001). Migration patterns and other life history events (e.g. timing of the calving season) were found to differ between the relatively small Scotian Shelf population (fewer than 150 individuals) and other, poorer understood populations of northern bottlenose whales (Whitehead & Hooker, 2012). It is therefore unknown whether the association patterns observed in the Gully are representative for those of other populations.

1.3.1 Social structure of related species

The social structure of other related species is also poorly understood. The social structure of Baird‘s beaked whales (*Berardius bairdii*) around Commander Islands has been studied. Some individuals showed long-term associations with other whales spanning several years (Fedutin et al., 2014). However that research did not look into group composition regarding sex and age. It has been suggested that Blainville’s beaked whales (*Mesoplodon densirostris*) form groups of mixed sex where one dominant adult male protects the females from other male competitors. Occasionally two adult males have been sighted with a group of females, however in that case one male had more tooth rake scars and lager teeth than the other, indicating a dominant and a subservient male. They also stayed spatially separated. The social structure of Blainville’s beaked whales has been described as fluid and individuals had numerous social patterns forming short term associations with other individuals ranging from weeks to months. Blainville’s beaked whales form small groups of 3.5 individuals on average. For Cuvier’s beaked whales (*Ziphius cavirostris*) two males accompanying a group of females has also been recorded, but the social structure for the species is less known than that of Blainville’s beaked whales. Cuvier’s beaked whales in Hawaii formed smaller groups of 2.6 individuals on average and are more often seen solitary (McSweeny et al., 2007).

1.4 Objective

Information about the group composition and social behaviour of the northern bottlenose whale is very deficient (Whitehead & Hooker, 2012). Most of the research on the species has focused on the north-west Atlantic, more specifically the Scotian continental slope including the Gully (e.g. Hooker et al, 2019; Gowans et al, 2001; Gowans et al, 2000; Dalebout, 2006). From the years 2008-2021 the northern bottlenose whale was classified as “data deficient” according to the IUCN red list (Taylor et al., 2008). Recently the global status of the species was re-evaluated and it is now categorized as “near threatened” (Whitehead et al, 2021).

The overall objective of this study is to increase the understanding of social structure and group composition of northern bottlenose whale in the northeast Atlantic. This study will focus on answering the following research questions:

- Do northern bottlenose whales in the northeast Atlantic more commonly associate with individuals within their age-sex class?

- What is the group size in which these whales are encountered?

- Are variations in their group composition (age-sex classes) linked to group size?

2 Methods

2.1 Data set available to the project

Data collected on four cruises between Iceland and Jan Mayen in the summers of 2013, 2014, 2015 and 2016 were made available by the HYPMO project. During these research cruises northern bottlenose whales were photographed as well as visual observations of group size (low, best, high number representing the minimum, best and maximum estimate, respectively), whether or not the group was seen before (i.e. a resighting), and other parameters were recorded for each encounter (Miller, Wensveen et al., 2016; Miller, Narazaki et al., 2015; Kvadsheim et al., 2014). From the photographs individuals had been identified based on markings on the dorsal fin area to form a photo ID catalogue (Neubarth & Wensveen, 2021; see also https://hypmo.org/catalogue/). The main objectives of these research cruises were to investigate body condition of whales and their behavioural response to navy sonar (Miller, Kvadsheim et al., 2015; Miller, Narazaki et al 2016; Wensveen et al, 2019); therefore, the photographs were collected opportunistically and mostly concurrent with tagging and biopsy sampling effort.

Biopsy samples were taken from 22 live animals in the years of 2014 and 2016, with 12 samples from 2014 and 10 from 2016 (Miller & Hall, 2018). Sex was determined from genetic analysis of part of the skin collected with the biopsy sample (Rosel, 2003). Pregnancy was determined based upon progesterone concentrations in the blubber of the biopsy samples (Trego et al., 2013).

2.2 Data processing and analysis

2.2.1 Age-sex classification

All photos of individuals in the “left side” dorsal photo-ID catalogue were visually inspected as well as photos of individuals that biopsy samples were taken from. If the melon of the animal was visible in the photographs, the best photo was selected per individual and added to the melon catalogue. Photos in the melon catalogue were imported to digiKam and photos were assigned melon IDs and quality (Q) rated following Feyrer et al (2020) (figure 2-1):

- Q=4 stars: the entire melon is visible, and the water line is just above the beak or lower.

- Q=3 stars: at least half of the melon is visible

- Q=2 stars. Less than half of melon is visible. The rounded edge of the melon is still visible.

- Q=1 star: the melon is not visible, the rounded edge of the melon is submerged.

If the observer/camera is at an angle other than perpendicular (90°) to the orientation of the whale it can cause errors in the age-sex analysis. Therefore, the initial quality rating above was adjusted for the angle from the photographer to the whale according to the following criteria:

- One star is subtracted from the rating if the observer is at a 45°-75° or 105°-135° angle to the whale (both in the horizontal and vertical plane).

- Two stars are subtracted from the rating if the observer is at an angle <45° or >135°

Figure 2-1: Quality rating examples. A: 1 star quality rating. B: 2 stars quality rating. C: 3 stars quality rating. D: 4 stars quality rating.

Juveniles cannot be distinguished from females in photographs since the melon profile is similar for both ages regardless of the sex of the juvenile. Consequently, females and juveniles must be assigned to the same age-sex class. Photographs with quality rating of 2 stars or more were assigned to one of two age-sex classes: mature male (MM) or female-juvenile (FJ) following a systematic qualitative analysis of the shape of the melon (Feyrer et al, 2020). The subadult male class originally proposed by Gowans et al. (2000) was not used (see Discussion for rationale). A reviewer confidence level following Feyrer et al (2020) (figure 2-2) was also assigned during the age-sex assessments:

- 2: Not confident

- 3: Fairly confident

- 4: Very confident

Figure 2-2: Examples of confidence levels for sex-age classes. Female- juvenile class (FJ) on left. Mature male (MM) on right.

Whereas the quality rating is a well-defined metric based on how much of the melon was above the water surface and the angle to the photographer, the reviewer confidence score is a more subjective metric and can incorporate other factors like light conditions.

Fisher's exact test (social science statistics, 2021) was used to determine if the male to female ratio based on the genetic sex determination was significantly different between the two age-sex classes determined from the photographic analysis.

2.2.2 Group size

Visual sighting data, including group size estimates, stored in Access databases were exported to one excel table for all four Jan Mayen cruises. The low, best and high estimates of group size were used from the first sighting of each group, i.e. resightings were excluded. Kruskal-Wallis tests were used to statistically compare these group size estimates as well as between years for best group size estimate only. Each Kruskal-Wallis test showing significant results was followed by a post hoc Dunn's test including a Bonferroni correction of the significance level (α=0.05/number of tests) to determine which comparison was significant.

2.2.3 Group composition

Field notes and systematically collected visual observations, in combination with detailed inspection of the raw photographs taken in the field, were used to determine group composition of groups that included individuals from the melon catalogue. Metadata was extracted from Melon ID photographs using R (R Core Team, 2021) and time stamps ("date taken") were used to link data from photographs to the visual sighting data. Group IDs were assigned for all individuals that were part of the age-sex analysis and/or were biopsied. Other individuals in these groups that had their melon photographed were added to the melon catalogue. Group size was taken as the 'best estimate' from the visual sighting database or field notes, except when more individuals could be identified from the photographs. In that case the new estimate based on the photos was used in the group composition analysis.

To determine whether or not individuals preferred to associate with the same age-sex class or the other age-sex class, or whether age-sex classifications depended on group size, binomial Generalised Linear Models (GLMs) with logit link function were fitted in R (R core team, 2021). Backwards model selected based on the p-values in the ANOVA table (Type II) was used to select the best, most parsimonious model. The response variable was age-sex class (MM or FJ) and the full model included four explanatory variables: presence/absence of (other) MM in the group, presence/absence of (other) FJ in the group, presence/absence of unknown (i.e. whales without age-sex classification) in the group, and group size. Interactions were not tested due to sample size limitations. To assess how well the model fitted the data partial residual plots and R2 were used. Akaike information criterion (AIC) was used to select the best link function (logit, probit, complementary log-log or cauchy). For the best model, covariate significance was assessed using Walt tests.

The data set included all analysed individuals from groups with at least two age-sex classifications from photos of $Q \geq 3$ (appendix B). As a sensitivity check, the procedure was repeated on a data set that also included age-sex classifications from photos of $Q=2$.

3 Results

3.1 Group size

The visual estimates of group size showed that northern bottlenose whales around Jan Mayen were most often seen in groups of three, and groups of six or more were uncommon (figures 3-1 and 3-2). A Kruskal-Wallis test showed that there was significant difference between the low-, best- and high- estimates ($p<0.001$; $\chi^2=101.7$). A Dunn's test revealed that there was significant difference between best number and high number group size estimate ($p<0.001$; $Z=-6.9$) as well as between high number and low number group size estimates ($p<0.001$; $Z=9.9$), but not between best number and low number group size estimates ($p> 0.05$; $Z=3.5$) (figure 3-2). Another Kruskal-Wallis test revealed that there was no significant difference in the best estimate values between years ($p>0.05$; $\chi^2=2.9$). Furthermore, a group size of three was the most common in each year, with most groups being of a size of 2-4 according to the best estimate of group size (figure 3-3).

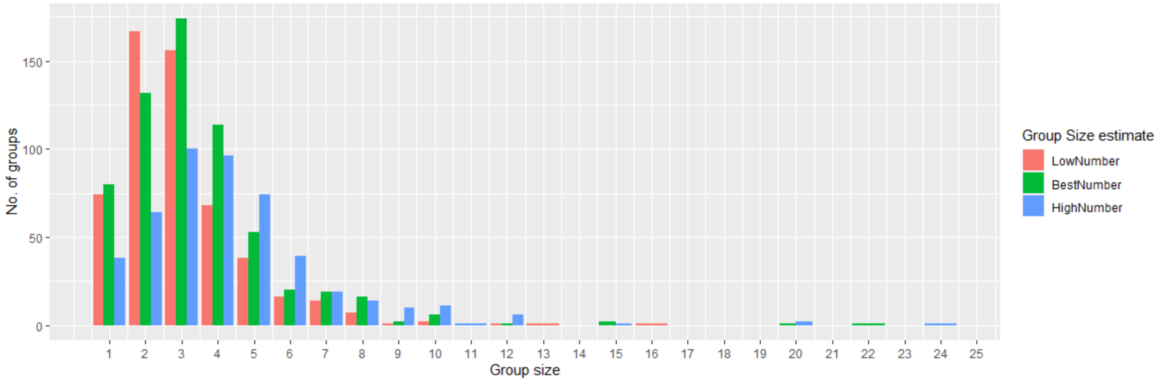

Figure 3-1: Group size estimates for all years (2013-2016).

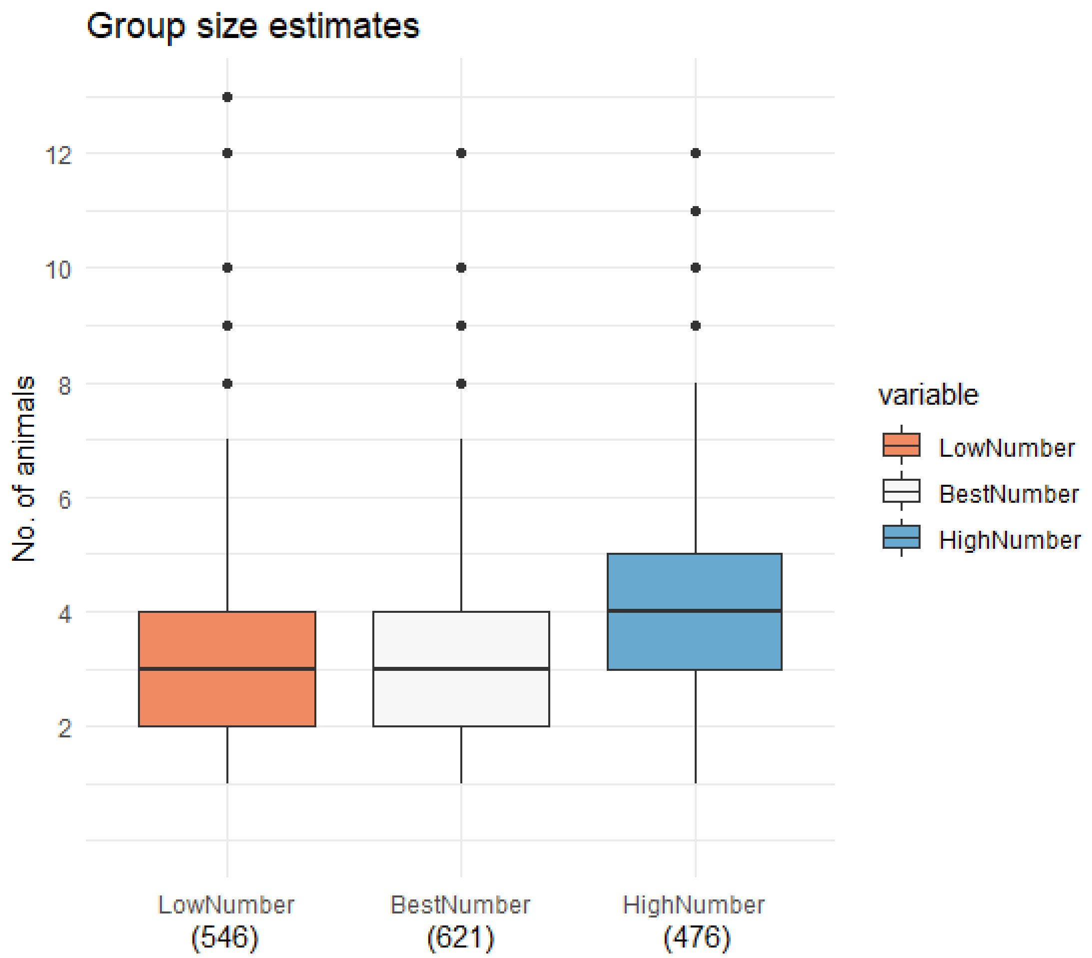

Figure 3-2: Boxplot of group size estimates of all four years (2013-2016). Numbers on X-axis indicate sample sizes. Groups larger than n=13 are not shown.

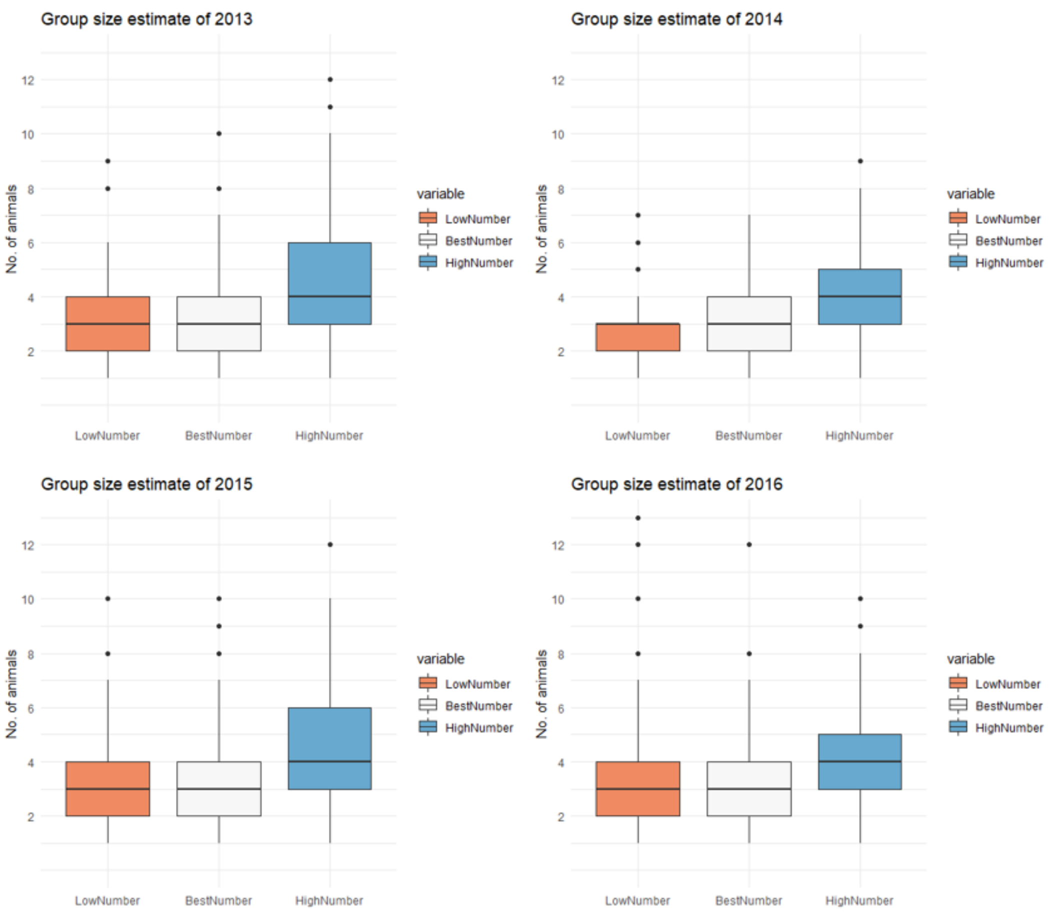

Figure 3-3: Low, best and high group size estimates for each year. Group size values higher than 13 are not shown (sample sizes: n=199 groups in 2013, n=149 groups in 2014, n=194 groups in 2015 and n=165 groups in 2016).

3.2 Age-sex classification

A total of 165 melon-profile photos were analysed of which 12 were quality (Q)=1, 52 were Q=2 (thereof 52 had the lowest confidence score, 2), 68 were Q=3 (thereof 17 confidence 2) and 33 were Q=4 (thereof 0 confidence 2). From the melon catalogue 30 animals were classified as mature males (19,6%) and 123 animals as female-juvenile (80,4%).

Sex was determined by genetic analysis of biopsy samples from a total of 22 animals. This analysis identified 6 animals as male (27,3%) and 16 as female (72,7%). Out of the 22 animals 15 individuals were also in the melon catalogue, thus providing a means to cross-validate the photographic method. Three of these 15 individuals were determined to be male (20,0%) and 12 (80,0%) to be female. Photographic age-sex classification indicated that 2 whales were mature males (MM) (13,3%) and 13 female-juvenile (FJ) (86,7%). The one whale assigned to the female- juvenile age-sex class but determined male was judged to be adult in the field and had a melon-profile photo quality of 2 (table 3-1, appendix A). Thus, the whale may have been a juvenile male and thus without the flattened forehead, or an adult male that was misclassified due to photo quality. The results of Fisher’s exact test indicated that there was a significant ($p<0.05$) difference in the female to male ratio between the two sex-age classes, suggesting the photographic method was accurately classifying the whales.

Table 3-1: Age-sex classifications based on photographic analysis for individuals that were biopsied. Age class refers to the visual observations made in the field.

AgeSex	BiopsySex	Quality rating	Age class
FJ	Male	2	Adult
FJ	Female	4	Adult
FJ	Female	4	Sub-adult
MM	Male	4	Sub-adult
FJ	Female	3	Adult
FJ	Female	3	Adult
FJ	Female	4	Adult
FJ	Female	4	Adult
FJ	Female	3	
MM	Male	3	
FJ	Female	3	Sub-adult
FJ	Female	3	Sub-adult
FJ	Female	2	Sub-adult
FJ	Female	3	
FJ	Female	4	Sub-adult

3.3 Group composition

A total of 51 groups were identified which included a total of 224 individuals (mean group size: 4.5) (appendix C). From these, 107 individuals where assigned age-sex classes (47.8%), 92 individuals with melon-profile photos of Q≥3 (39.7%), and 117 individuals of unknown age-sex class (52.2%) (appendix C). Of the 92 individuals classified in age-sex classes (Q≥3), 73 were classified as female-juvenile (79.3%) and 19 as mature male (20.7%) (appendix C). The minimum proportions in the group averaged 0.08 (SD=0.18) for MM and 0.35 (0.24) for FJ, and the proportion of unknowns averaged 0.56 (0.19) (appendix C). Analyses for the effects of covariates on age-sex class were performed using data from 26 groups with 65 individuals.

The selected model included the presence/absence of MM in the group (Walt test: $Z=3.97$, $p<0.001$), but not the presence/absence of FJ or unknown in the group, or group size. This model with a logit link function explained about half of the variation in the data ($R^2=0.47$) and no difference in AIC was found with models with other link functions. This indicated that the probability of an individual being classified as female-juvenile or mature male depended on the presence of (other) mature males in the group (figure 3-4). The probability of an individual being classified as mature male was determined to be 0.58 if other mature males were present and 0.04 if no other mature males were present. The probably of an individual being classified as FJ was also higher when other FJ were present (0.71) than not (0.14) (figure 3-4); however, this difference was not statistically significant.

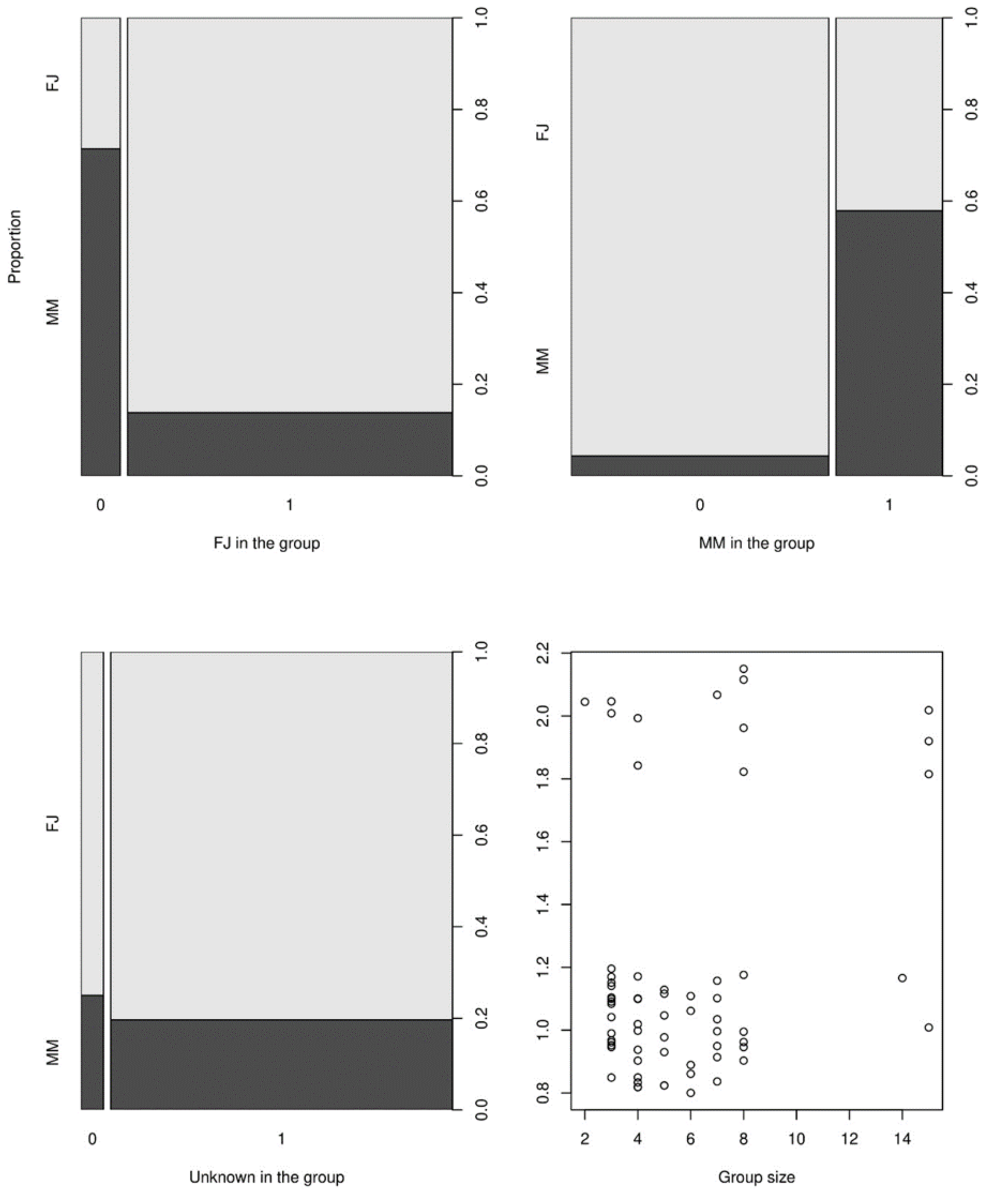

Figure 3-4: Proportions of female-juvenile (FJ) and mature male (MM) age-sex classifications for the different group parameters investigated. Top left: absence (0) and presence (1) of (other) FJ in the group. Top right: absence (0) and presence (1) of (other) MM in the group. Bottom left: absence (0) and presence (1) of unknown in the group. Bottom right: Group size. In the factor covariate plots the horizontal width of the bars represent the difference in sample size between factor levels. In the plot for group size, data points above 1.5 on the Y-axis represent MM and datapoints below 1.5 represent FJ.

4 Discussion

4.1 Group size

Dunn's test revealed that the maximum group size estimates were significantly different from the minimum and best estimates, indicating that observers generally felt that they could have missed an individual while estimating group size at the surface. There was no significant difference in the best group size estimates between years, suggesting that group sizes did not change from year to year and data could be pooled to investigate group composition.

According to the results the average group size of northern bottlenose whales north off Iceland and around Jan Mayen is 3 individuals in group (figure 3-2 and 3-3). These results relate well to previous findings. An average group size of 3 has been reported for northern bottlenose whales in the Gully (Gowans et al, 2001) and an average group size of 2-4 individuals has been reported for northern bottlenose whales in the north-east Atlantic (Benjaminsen & Christensen, 1979).

Large group sizes did occur but were not common. Largest group sizes recorded where 24 (highest maximum estimate), 22 (highest best estimate) and 15 (highest minimum estimate) (figure 3-2). Large groups of northern bottlenose whales have been recorded before but are considered rare (Benjaminsen & Christensen, 1979). A fission-fusion society has been suggested for northern bottlenose whales (Gowans et al., 2001) and therefore it is likely that the largest groups recorded in the visual data consisted of two or more groups temporally coming together at the surface.

4.2 Sex ratio

Low ratio of males was detected from genetic analysis of biopsy samples. Six out of the 22 animals genetically analysed were identified as male, i.e. 27,3 % of the individuals were identified as male and 72,7 % as female. This ratio is not alike the sex ratio reported in the Scotian Shelf population. From genetic analysis of biopsy samples taken from 20 free swimming whales in the Gully 45% were identified as male and 55% as female (Gowans et al., 2000).

Photographic age-sex classification revealed that 79.3% of the individuals assigned age-sex classes were classified as female-juvenile (FJ) (n=73) and 20.7% were classified as mature male (MM) (n=19). The same type of analysis based on data from the Gully resulted in comparable rates of mature males: 28,1% (n=64) (Gowans et al. 2001) and 20,2% (n=168) (Gowans et al., 2000). However, both studies included the subadult male age-sex class which was not included in this study. The subadult male class was described as having a melon-profile intermediate to mature males and female-immature classes. Because of inconsistencies in classification of the subadult male class, the photographic age-sex classification used by the "Whitehead lab" at Dalhousie University has been revised and consists now of two age-sex classes, female-juvenile (FJ) and mature male (MM) (Feyrer et al, 2020). Therefore, individuals belonging to the subadult male class could have been classified as mature males with low confidence rating or as female-juvenile in this study.

The low rate of mature males in this study is therefore similar to previously reported values and could be the result of mature males only being classified in that category since the melon-profile has not changed in immature males. However low rates of males from genetic analysis of biopsy samples indicates low rates of males of all ages in the area, especially since it does not compare to previous study. On the other hand the small sample size in this study (n=22) and in the previous study (n=20) (Gowans et al, 2000) could cause a bias and not be representative of the population.

4.3 Group composition

Individuals classified as mature male seemed to prefer associations with other mature males. The probability of an individual being classified as mature male was considerably higher if other mature males were present in the group (58%) compared to when other mature males were absent from the group (4%). This corresponds well with the only other study available for northern bottlenose whales, from the Gully. Gowans et al (2001) found that subadult- and mature males were more likely to prefer associations of other males of the same age-sex class but individuals classified as female-juvenile showed no preference to age-sex classes (Gowans et al, 2001).

In this study other female-juveniles in group and group size did not seem to effect group composition. Individuals classified as female-juvenile showed a tendency to from groups with other individuals of the same age-sex class (figure 3-4). However, there was not a significance affect for (other) female-juvenile in the groups and therefore it can not be assumed that individuals belonging to the female-juvenile class prefer to make associations with other individuals of the same age-sex class. Likewise, no significance was detected for group size indicating that the ratio of age-sex classes in groups does not vary with group size (figure 3-4).

The social behaviour and group composition of northern bottlenose whale does not seem to resemble that of Cuvier's beaked whales. Cuvier's beaked whales form small groups with usually only one adult male accompanying few females (McSweeney, et al. 2007). A recent study found that adult Cuvier's beaked whale males showed more synchrony when diving than other pairs (adult male and another animal of a different age and/or sex) and that synchrony for male pair lasted from days to weeks. On the other hand the sample size of the study was small (13 individuals in 8 groups) (Cioffi et al., 2021) thus further studies might be needed.

4.4 Future prospects

The results of this study indicate that group size and composition of northern bottlenose whales in the northeast Atlantic resembles that of the northwest Atlantic population, more specifically the subpopulation near the continental shelf off Nova Scotia. Nonetheless, further research could continue to deepen the understanding of social behaviour and structure of northern bottlenose whales in the northeast Atlantic. Geographical segregation has been suggested between male and female bottlenose whales based on whaling data (Benjaminsen & Christensen, 1979), therefore further studies including spatial effects on group composition in the northeast Atlantic might be of interest to explore segregation within the species.

Genetic studies using microsatellites have shown that the Scotian shelf population likely represents a defective subpopulation (Dalebout et al, 2006; Feyrer et al, 2019). Genetic studies have also detected the possibility of migration of individuals between southern Labrador, Iceland, Davis Strait and off the coast of Newfoundland (Feyrer et al, 2019). Therefore genetic analysis on individuals of the northeast Atlantic population might be of interest and shed an important light on relation of northern bottlenose whales between areas, migration and potential subpopulations of the species.

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Appendix A

Appendix A: Overview of individuals in group catalogue. ID refers to dorsal ID from the ID catalogue; IDs starting with 5 are from the low distinctiveness catalogue. All IDs are from left side catalogue except for RID0376 (right side ID).

Melon-ID	Group-ID	Biopsy ID	ID	Gruop Size	Melon Rating	Age-Sex	Biopsy Sex	Time First Photo
20	55		ID5040	3	3	FJ3		10/06/2014 9:36
22	31		ID0036	6	3	FJ2		11/06/2014 12:20
23	31		ID5046	6	4	FJ4		11/06/2014 12:20
24	32		ID5034	4	4	FJ4		11/06/2014 16:13
25	32		ID5035	4	4	FJ4		11/06/2014 16:13
26	56		ID0039	4	4	MM2		12/06/2014 11:11
27	56		ID0040	4	4	MM4		12/06/2014 11:11
28	57		ID0043	3	4	MM4		12/06/2014 11:24
30	2		ID0046	4	3	FJ2		12/06/2014 12:55
32	33		ID0051	4	3	FJ2		14/06/2014 13:48
33	34		ID5067	2	4	FJ4		14/06/2014 14:36
35	35		ID0053	7	4	FJ4		15/06/2014 8:10
36	5		ID0054	3	4	FJ4		15/06/2014 8:14
39	36		ID5083	5	3	FJ3		22/06/2014 14:20
40	37		ID0059	2	3	MM2		22/06/2014 19:40

Appendix A (continued): Overview of individuals in group catalogue. ID refers to dorsal ID from the ID catalogue; IDs starting with 5 are from the low distinctiveness catalogue. All IDs are from left side catalogue except for RID0376 (right side ID).

44	7		ID5062	4	4	MM4		23/06/2014 15:03
46	38		ID0065	5	3	FJ3		24/06/2014 15:54
49	39		ID0068	3	3	FJ3		15/06/2015 19:08
50	40		ID0069	4	3	FJ2		15/06/2015 19:57
51	41		ID0082	4	3	FJ4		18/06/2015 2:57
52	42		ID0083	3	2	FJ2		18/06/2015 4:23
53	42		ID0084	3	3	FJ3		18/06/2015 4:23
55	43		ID0080	4	3	MM3		18/06/2015 6:58
56	44		ID0081	3	3	FJ3		18/06/2015 19:03
57	45		ID5088	7	3	FJ3		20/06/2015 15:20
59	45		ID5090	7	3	FJ3		20/06/2015 15:20
60	45		ID5091	7	4	MM4		20/06/2015 15:20
61	46		ID0100	3	3	FJ3		21/06/2015 4:19
62	46		ID0099	3	3	FJ3		21/06/2015 4:19
64	47		ID0101	3	4	MM4		21/06/2015 6:55
65	48		ID0104	2	4	MM4		22/06/2015 11:07
67	49		ID0113	3	3	FJ2		22/06/2015 12:20

Appendix A (continued): Overview of individuals in group catalogue. ID refers to dorsal ID from the ID catalogue; IDs starting with 5 are from the low distinctiveness catalogue. All IDs are from left side catalogue except for RID0376 (right side ID).

69	50		ID5152	9	4	FJ4		22/06/2015 13:41
71	51		ID0124	8	3	FJ2		23/06/2015 10:16
73	51		ID0117	8	3	FJ3		23/06/2015 11:44
74	52		ID5125	3	3	FJ3		24/06/2015 4:19
76	53		ID0127	3	3	FJ3		28/06/2015 13:43
78	54		ID5181	4	4	FJ4		01/07/2015 22:04
80	9	1602	ID0133	8	3	FJ2	Female	06/06/2016 9:00
81	9	1603	ID0135	8	3	MM3	Male	06/06/2016 8:56
82	17		ID0150	2	3	FJ3		09/06/2016 10:57
85	18		ID0141	3	3	FJ3		09/06/2016 16:59
86	19		ID0157	4	3	FJ3		14/06/2016 11:58
89	20		ID5219	4	3	FJ3		15/06/2016 19:48
95	21		ID0172	8	4	FJ4		16/06/2016 3:27
96	11	1605	ID0175	4	3	FJ3	Female	16/06/2016 11:20
100	22		ID0182	4	3	FJ2		17/06/2016 8:49
101	23		ID5240	3	4	FJ4		17/06/2016 15:41
102	24		ID5243	4	3	FJ2		17/06/2016 18:41

Appendix A (continued): Overview of individuals in group catalogue. ID refers to dorsal ID from the ID catalogue; IDs starting with 5 are from the low distinctiveness catalogue. All IDs are from left side catalogue except for RID0376 (right side ID).

103	13		ID0162	5	3	FJ3		18/06/2016 7:00
105	25		ID0193	3	3	FJ3		20/06/2016 9:17
107	15		ID0130	6	3	FJ3		21/06/2016 9:01
110	15		ID0204	6	3	FJ3		21/06/2016 9:05
112	27		ID5266	5	4	FJ4		21/06/2016 14:19
113	28		ID0195	7	4	FJ4		21/06/2016 16:16
114	29		ID0217	4	4	FJ4		22/06/2016 19:54
115	29		ID0216	4	3	FJ3		22/06/2016 19:17
117	30		ID0219	15	3	MM3		25/06/2016 21:35
119	2	1402	ID0044	4	2	FJ2	Male	12/06/2014 12:55
120	5	1405		3	4	FJ4	Female	15/06/2014 8:22
121	6	1406		3	4	FJ4	Female	23/06/2014 7:29
122	7	1407	ID0061	4	4	MM4	Male	23/06/2014 15:07
123	8	1408		7	3	FJ3	Female	24/06/2014 22:29
124	8	1409		7	3	FJ3	Female	24/06/2014 22:51
125	8	1410		7	4	FJ4	Female	25/06/2014 0:10
126	8	1411		7	4	FJ4	Female	25/06/2014 0:39

Appendix A (continued): Overview of individuals in group catalogue. ID refers to dorsal ID from the ID catalogue; IDs starting with 5 are from the low distinctiveness catalogue. All IDs are from left side catalogue except for RID0376 (right side ID).

127	10	1604	RID0376	3	3	FJ3	Female	06/06/2016 11:41
129	13	1607		5	3	FJ4	Female	18/06/2016 7:02
130	15	1609	ID0201	6	4	FJ4	Female	21/06/2016 9:01
131	15			6	3	FJ3		21/06/2016 9:01
132	15			6	2	FJ2		21/06/2016 9:08
133	27			5	3	FJ2		21/06/2016 13:56
134	28			7	2	FJ2		21/06/2016 16:16
135	30			15	3	MM3		25/06/2016 20:18
136	9			8	3	FJ2		06/06/2016 9:21
137	30			15	4	MM4		25/06/2016 21:38
138	30			15	3	FJ3		25/06/2016 21:43
139	30			15	4	MM4		25/06/2016 21:51
140	17			2	2	FJ2		09/06/2016 10:58
141	20			4	4	FJ4		15/06/2016 20:00
142	21			8	3	MM2		16/06/2016 3:32
143	21			8	3	MM4		16/06/2016 3:32
144	21			8	3	MM3		16/06/2016 3:32

Appendix A (continued): Overview of individuals in group catalogue. ID refers to dorsal ID from the ID catalogue; IDs starting with 5 are from the low distinctiveness catalogue. All IDs are from left side catalogue except for RID0376 (right side ID).

145	21			8	2	FJ2		16/06/2016 3:33
146	22			4	4	FJ4		17/06/2016 8:51
150	31			6	3	FJ4		11/06/2014 12:29
151	32			4	3	FJ3		11/06/2014 16:14
152	57			3	3	MM3		12/06/2014 11:26
156	2			4	2	FJ2		12/06/2014 12:52
157	5			3	4	FJ4		15/06/2014 8:21
158	7			4	2	FJ2		23/06/2014 15:06
159	38			5	4	FJ4		24/06/2014 16:27
160	18			3	3	FJ3		09/06/2016 17:00
161	23			3	2	FJ2		17/06/2016 15:41
162	48			2	2	MM2		22/06/2015 11:10
163	49			3	2	MM2		22/06/2015 13:20
164	49			3	3	FJ2		22/06/2015 13:20
165	51			8	2	FJ2		23/06/2015 10:08
166	52			3	2	FJ2		24/06/2015 4:20
167	42			3	3	FJ3		18/06/2015 4:14

Appendix A (continued): Overview of individuals in group catalogue. ID refers to dorsal ID from the ID catalogue; IDs starting with 5 are from the low distinctiveness catalogue. All IDs are from left side catalogue except for RID0376 (right side ID).

168	**45**			**7**	**3**	**FJ3**		**20/06/2015 20:46**
169	11			4	2	FJ2		16/06/2016 11:27
170	11			4	4	FJ4		16/06/2016 11:27
171	11			4	3	FJ3		16/06/2016 11:29
172	10			3	3	FJ3		06/06/2016 11:41
173	10			3	2	FJ2		06/06/2016 11:41
174	6			3	3	FJ3		23/06/2014 7:29

Appendix B

Appendix B: Group composition data based on identified individuals (Q≥3) in group, showing number of other individuals (Q≥3) classified as female-juvenile (#FJ), number of other individuals (Q≥3) classified as mature male (#MM) and number of other individuals with unknown age-sex class (#Unk).

GroupID	MelonID	Age-sex	Group Size	#FJ	#MM	#Unk
2	30	FJ	4	0	0	3
5	120	FJ	3	2	0	0
5	36	FJ	3	2	0	0
5	157	FJ	3	2	0	0
6	121	FJ	3	1	0	1
6	174	FJ	3	1	0	1
7	122	MM	4	0	1	2
7	44	MM	4	0	1	2
8	123	FJ	7	3	0	3
8	124	FJ	7	3	0	3
8	125	FJ	7	3	0	3
8	126	FJ	7	3	0	3

Appendix B (continued): Group composition data based on identified individuals (Q≥3) in group, showing number of other individuals (Q≥3) classified as female-juvenile (#FJ), number of other individuals (Q≥3) classified as mature male (#MM) and number of other individuals with unknown age-sex class (#Unk).

9	80	FJ	8	1	1	5
9	81	MM	8	2	0	5
9	136	FJ	8	1	1	5
10	127	FJ	3	1	0	1
10	172	FJ	3	1	0	1
11	96	FJ	4	2	0	1
11	170	FJ	4	2	0	1
11	171	FJ	4	2	0	1
13	129	FJ	5	1	0	3
13	103	FJ	5	1	0	3
15	130	FJ	6	3	0	2
15	107	FJ	6	3	0	2
15	110	FJ	6	3	0	2
15	131	FJ	6	3	0	2
17	82	FJ	2	0	0	1

Appendix B (continued): Group composition data based on identified individuals (Q≥3) in group, showing number of other individuals (Q≥3) classified as female-juvenile (#FJ), number of other individuals (Q≥3) classified as mature male (#MM) and number of other individuals with unknown age-sex class (#Unk).

18	85	FJ	3	1	0	1
18	160	FJ	3	1	0	1
19	86	FJ	4	0	0	3
20	89	FJ	4	1	0	2
20	141	FJ	4	1	0	2
21	95	FJ	8	0	3	4
21	142	MM	8	1	2	4
21	143	MM	8	1	2	4
21	144	MM	8	1	2	4
22	100	FJ	4	1	0	2
22	146	FJ	4	1	0	2
23	101	FJ	3	0	0	2
24	102	FJ	4	0	0	3
25	105	FJ	3	0	0	2
27	112	FJ	5	1	0	3

Appendix B (continued): Group composition data based on identified individuals (Q≥3) in group, showing number of other individuals (Q≥3) classified as female-juvenile (#FJ), number of other individuals (Q≥3) classified as mature male (#MM) and number of other individuals with unknown age-sex class (#Unk).

27	133	FJ	5	1	0	3
28	113	FJ	7	0	0	6
29	114	FJ	4	1	0	2
29	115	FJ	4	1	0	2
30	117	FJ	14	1	3	10
30	135	MM	15	1	3	10
30	137	MM	15	1	3	10
30	138	FJ	15	0	4	10
30	139	MM	15	1	3	10
31	22	FJ	6	2	0	3
31	23	FJ	6	2	0	3
31	150	FJ	6	2	0	3
32	24	FJ	4	2	0	1
32	25	FJ	4	2	0	1
32	151	FJ	4	2	0	1

Appendix B (continued): Group composition data based on identified individuals (Q≥3) in group, showing number of other individuals (Q≥3) classified as female-juvenile (#FJ), number of other individuals (Q≥3) classified as mature male (#MM) and number of other individuals with unknown age-sex class (#Unk).

33	32	FJ	4	0	0	3
34	33	FJ	2	0	0	1
35	35	FJ	7	0	0	6
36	39	FJ	5	0	0	4
37	40	MM	2	0	0	1
38	46	FJ	5	1	0	3
38	159	FJ	5	1	0	3
39	49	FJ	3	0	0	2
40	50	FJ	4	0	0	2
41	51	FJ	4	0	0	3
42	53	FJ	3	1	0	1
42	167	FJ	3	1	0	1
43	55	MM	4	0	0	3
44	56	FJ	3	0	0	2
45	57	FJ	7	2	1	3

Appendix B (continued): Group composition data based on identified individuals (Q≥3) in group, showing number of other individuals (Q≥3) classified as female-juvenile (#FJ), number of other individuals (Q≥3) classified as mature male (#MM) and number of other individuals with unknown age-sex class (#Unk).).

45	59	FJ	7	2	1	3
45	60	MM	7	3	0	3
45	168	FJ	7	2	1	3
46	61	FJ	3	1	0	1
46	62	FJ	3	1	0	1
47	64	MM	3	0	0	2
48	65	MM	2	0	1	0
49	67	FJ	3	1	0	1
49	164	FJ	3	1	0	1
50	69	FJ	9	0	0	8
51	71	FJ	8	1	0	6
51	73	FJ	8	1	0	6
52	74	FJ	3	0	0	2
53	76	FJ	3	0	0	2
54	78	FJ	4	0	0	3

Appendix B (continued): Group composition data based on identified individuals (Q≥3) in group, showing number of other individuals (Q≥3) classified as female-juvenile (#FJ), number of other individuals (Q≥3) classified as mature male (#MM) and number of other individuals with unknown age-sex class (#Unk).

55	20	FJ	3	0	0	2
56	26	MM	2	0	1	2
56	27	MM	2	0	1	2
57	28	MM	3	0	1	1
57	152	MM	3	0	1	1

Appendix C

Appendix C: Overview of groups and group composition. Group composition based on photos with Q≥3, showing number of individuals classified as mature males (#MM), number of individuals classified as female- juvenile (#FJ) and number of individuals with unknown age-sex class (#UNK). Group composition based on photos with Q≥2, showing number of individuals classified as mature males (#MM-all), number of individuals classified as female- juvenile (#FJ-all) and number of individuals with unknown age-sex class (#UNK-all). Proportions of age-sex classes and unknown individuals calculated based on age-sex classification of photos with Q≥3 (pMM, pFJ and pUNK).

GroupID	Group Size	#MM	#FJ	#UNK	#MM-all	#FJ-all	#UNK-all	pMM	pFJ	pUNK
2	4	0	1	3	0	3	1	0,00	0,25	0,75
5	3	0	3	0	0	3	0	0,00	1,00	0,00
6	3	0	2	1	0	2	1	0,00	0,67	0,33
7	4	2	0	2	2	1	1	0,50	0,00	0,50
8	7	0	4	3	0	4	3	0,00	0,57	0,43
9	8	1	2	5	1	2	5	0,13	0,25	0,63
10	3	0	2	1	0	3	0	0,00	0,67	0,33
11	4	0	3	1	0	4	0	0,00	0,75	0,25
13	5	0	2	3	0	2	3	0,00	0,40	0,60
15	6	0	4	2	0	5	1	0,00	0,67	0,33
17	2	0	1	1	0	2	0	0,00	0,50	0,50
18	3	0	2	1	0	2	1	0,00	0,67	0,33
19	4	0	1	3	0	1	3	0,00	0,25	0,75
20	4	0	2	2	0	2	2	0,00	0,50	0,50
21	8	3	1	4	3	2	3	0,38	0,13	0,50
22	4	0	2	2	0	2	2	0,00	0,50	0,50
23	3	0	1	2	0	2	1	0,00	0,33	0,67
24	4	0	1	3	0	1	3	0,00	0,25	0,75
25	3	0	1	2	0	1	2	0,00	0,33	0,67
27	5	0	2	3	0	2	3	0,00	0,40	0,60

Appendix D (continued): Overview of groups and group composition. Group composition based on photos with Q≥3, showing number of individuals classified as mature males (#MM), number of individuals classified as female- juvenile (#FJ) and number of individuals with unknown age-sex class (#UNK). Group composition based on photos with Q≥2, showing number of individuals classified as mature males (#MM-all), number of individuals classified as female- juvenile (#FJ-all) and number of individuals with unknown age-sex class (#UNK-all). Proportions of age-sex classes and unknown individuals calculated based on age-sex classification of photos with Q≥3 (pMM, pFJ and pUNK).

28	7	0	1	6	0	2	5	0,00	0,14	0,86
29	4	0	2	2	0	2	2	0,00	0,50	0,50
30	15	4	1	10	4	1	10	0,27	0,07	0,67
31	6	0	3	3	0	3	3	0,00	0,50	0,50
32	4	0	3	1	0	3	1	0,00	0,75	0,25
33	4	0	1	3	0	1	3	0,00	0,25	0,75
34	2	0	1	1	0	1	1	0,00	0,50	0,50
35	7	0	1	6	0	1	6	0,00	0,14	0,86
36	5	0	1	4	0	1	4	0,00	0,20	0,80
37	2	1	0	1	1	0	1	0,50	0,00	0,50
38	5	0	2	3	0	2	3	0,00	0,40	0,60
39	3	0	1	2	0	1	2	0,00	0,33	0,67
40	4	0	1	3	0	1	3	0,00	0,25	0,75
41	4	0	1	3	0	1	3	0,00	0,25	0,75
42	3	0	2	1	0	3	0	0,00	0,67	0,33
43	4	1	0	3	1	0	3	0,25	0,00	0,75
44	3	0	1	2	0	1	2	0,00	0,33	0,67
45	7	1	3	3	1	3	3	0,14	0,43	0,43
46	3	0	2	1	0	2	1	0,00	0,67	0,33
47	3	1	0	2	1	0	2	0,33	0,00	0,67
48	2	1	0	1	2	0	0	0,50	0,00	0,50
49	3	0	2	1	1	2	0	0,00	0,67	0,33
50	9	0	1	8	0	1	8	0,00	0,11	0,89
51	8	0	2	6	0	3	5	0,00	0,25	0,75
52	3	0	1	2	0	2	1	0,00	0,33	0,67

Appendix E (continued): Overview of groups and group composition. Group composition based on photos with Q≥3, showing number of individuals classified as mature males (#MM), number of individuals classified as female- juvenile (#FJ) and number of individuals with unknown age-sex class (#UNK). Group composition based on photos with Q≥2, showing number of individuals classified as mature males (#MM-all), number of individuals classified as female- juvenile (#FJ-all) and number of individuals with unknown age-sex class (#UNK-all). Proportions of age-sex classes and unknown individuals calculated based on age-sex classification of photos with Q≥3 (pMM, pFJ and pUNK).

53	3	0	1	2	0	1	2	0,00	0,33	0,67
54	4	0	1	3	0	1	3	0,00	0,25	0,75
55	3	0	1	2	0	1	2	0,00	0,33	0,67
56	4	2	0	2	2	0	2	0,50	0,00	0,50
57	3	2	0	1	2	0	1	0,67	0,00	0,33
Average	**4,48**	**0,38**	**1,46**	**2,64**	**0,42**	**1,72**	**2,34**	**0,08**	**0,35**	**0,56**
SD	**2,31**	**0,85**	**0,99**	**1,89**	**0,88**	**1,13**	**2,00**	**0,18**	**0,24**	**0,19**
Total	**224**	**19**	**73**	**132**	**21**	**86**	**117**			