Seasonal fission and fusion of killer whale, *Orcinus orca*, social structure at sub-Antarctic Marion Island

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Highlights

- Seasonal changes in food distribution and abundance are common.
- Fusion of killer whale social structure occurs when food is abundant.
- Fission occurs during periods of low prey abundance.
- Resource abundance is therefore an important driver of social structure.

Variation in the distribution and abundance of food resources are key factors affecting animal sociality. In environments with variable resources, dynamic social organization, such as the fission and fusion of groups, is thought to increase the benefits of group living, while reducing the costs. We investigated the relationship between social organization and prey abundance in a highly social predator, the killer whale. This was achieved by analysing 12 years (2006–2018) of seasonally delineated (coinciding with high and low prey abundances) association data obtained from nearly 90 000 identification photographs of killer whales in-shore at Marion Island in the sub-Antarctic Indian Ocean. Association network measures were compared between periods using randomized association matrices. Half-weight association index, degree, number of modules and group size were all greater during periods of high prey abundance while mean distance, centrality and modularity were lower during this same period. Results suggest that killer whales at Marion Island were more social, formed larger groups and had more associations during periods of high prey abundance. During periods of lower prey abundance, fewer interactions, stronger clustering and more division in the association network were observed. These results indicate that the social organization of this population of killer whales is seasonally dynamic, with increased sociality measures coinciding with periods of higher prey abundance. These results are similar to those of other social species, emphasizing the importance of resource abundance as a driver of social structure in animal societies.

Keywords: association; delphinid; network; prey abundance; seasonality; sociality

Annual variations in meteorological conditions (e.g. rainfall, temperature, ocean currents and wind patterns) result in climatic seasonality and associated periodicity in the distribution of resources, such as food, water and nutrients, that are essential for animal survival (Boyce, 1979). Animals respond to seasonal variation in the distribution of resources in various ways, including behavioural variation (Creel & Winnie, 2005).

Some animals respond to changes in resource distribution and availability through fine-scale changes in their social structure (Whitehead & Kahn, 1992). One such response is a process called 'fission–fusion', where individuals join and leave social groups dynamically, thereby increasing foraging efficiency and resource exploitation while maintaining the benefits of group living (Krumer, 1971). Fission–fusion dynamics occur over both short (e.g. hours) and long (e.g. years) time frames (Whitehead & Kahn, 1992; Archie, Moss, & Alberts, 2006) and are found in numerous taxonomic groups, including birds (Aplin, Farine, Morand-Ferron, & Sheldon, 2012), fish (Croft et al., 2003) and mammals (e.g. bats, Kerth, Perony, & Schweitzer, 2011; spotted hyaenas, *Crocuta crocuta,* Holekamp et al., 1997; lions, *Panthera leo*, Mbizah et al., 2020). Fission–fusion dynamics have, however, been best studied in animals typically considered highly cognitive, such as primates (Smuts, Cheney, Seyfarth, Wrangham, & Struhsaker, 1987), elephants (Archie et al., 2006) and dolphins (Wiszniewski, Allen, & Möller, 2009).

Fission–fusion dynamics are associated with costs and benefits at the individual level. When smaller groups are formed (i.e. fission), individuals experience greater predation pressure and reduced ability to cooperatively defend resources (Manson & Wrangham, 1991; Beauchamp, 2017). However, fission can be beneficial as it reduces local resource competition and manages social conflicts (Asenio et al., 2008; Smith, Kolowski, Graham, Dawes, & Holekamp, 2008). Conversely, an increase in group size (i.e. fusion) has the potential to create conflict between individuals and can increase foraging costs (Aureli & Schaffner, 2007). Fusions can, however, be beneficial as individuals in larger groups experience reduced predation pressure, increased hunting efficiency and are better able to cooperatively defend resources from smaller groups (Beauchamp, 2017; Manson & Wrangham, 1991). Resource abundance is therefore an important determinant of fission–fusion dynamics; the costs associated with fusion events, resulting in larger groups, are lowest when resources are abundant (see Macdonald & Johnson, 2015 for review).

Seasonal resource variation is particularly evident in high-latitude environments such as the Southern Ocean, where broad- and fine-scale spatial and temporal fluctuations in various physical properties of regional water masses occur (Rintoul, Donguy, & Roemmich, 1997). These fluctuations influence the distribution, diversity, abundance and phenology of biological communities occupying this ocean (Rodhouse & White, 1995; Arrigo, Worthen, Schnell, & Lizotte, 1998; Field, Bradshaw, Burton, & Hindell, 2007; Lascara, Hofmann, Ross, & Quetin, 2007). Southern Ocean marine predators such as seals, penguins and flying seabirds often breed ashore in colonies during the short milder spring and summer season. In the case of Marion Island in the sub-Antarctic Indian Ocean, the peak abundance of breeding seals and penguins occurs between September and December (du Plessis, van Heezik, & Seddon, 1994; Crawford, Cooper, & Dyer, 2003; Kirkman et al., 2004; Hofmeyr et al., 2007). This period is also associated with increased inshore abundance of killer whales at Marion Island in response to the influx of breeding seals and penguins (Condy, van Aarde, & Bester, 1978; Reisinger, de Bruyn, Tosh, et al., 2011).

Despite their abundance peaking between September and December, killer whales are observed foraging in the inshore waters at Marion Island throughout the year (Condy et al., 1978; Keith, Bester, Bartlett, & Baker, 2001; Reisinger et al., 2011). These killer whales prey mainly on seals (southern elephant seals, *Mirounga leonina*, and Subantarctic fur seals, *Arctocephalus tropicalis*) and penguins (king penguins, *Aptenodytes patagonicus*, and macaroni penguins, *Eudyptes chrysolophus*) when foraging in-shore. Additionally, they likely feed on Patagonian toothfish, *Dissostichus eleginoides,* when not at Marion Island (Reisinger et al., 2011, 2016).

Social groups of killer whales at Marion Island range in size from one to 16 individuals with a modal group size of three (Tosh, de Bruyn, & Bester, 2008; Reisinger, Beukes (née Janse van Rensburg), Hoelzel, & de Bruyn, 2017). Superficially, this makes them socially and ecologically similar to killer whales at the Galápagos Archipelago (mean group size = 4, range 1–15), which prey opportunistically on a range of species (Denkinger et al., 2020), killer whales in the Atlantic (mean = 5, range 1–15), which hunt both seal and herring, *Clupea harengus* (Beck, Kuningas, Esteban, & Foote, 2012), and the 'Bigg's' (formerly 'transient') killer whales of the Eastern North Pacific (ENP; mean = 2.4, range 2–10), which feed on marine mammals (Ford et al., 1998; Baird & Whitehead, 2000; Ford, 2000; Tavares et al., 2018). Relatively small group sizes, as observed in these populations, are thought to be the most energy efficient per capita when preying on relatively large animals such as marine mammals. In ENP 'Bigg's' killer whales, group sizes are consistent with the 'maximization of energy intake' hypothesis where the risk of energy shortfall is minimized while foraging (Baird & Dill, 1996). An increase or decrease in group size from the mean would presumably decrease the per capita energy intake of killer whales in these populations. However, group sizes in killer whales and other social predators are sometimes larger than the predicted optimum size, likely to better protect offspring, defend kills, when resource abundance is greater (resulting in increased energy intake) and for other social functions (Arnbom, Papastavrou, Weilgart, & Whitehead, 1987; Baird & Dill, 1996; Carbone, Du Toit, & Gordon, 1997; Alava et al., 2013). For example, larger than optimum group sizes are observed in lions and African wild dogs, *Lycaon pictus*, since the risk of kleptoparasitism by spotted hyaenas decreases as hunting group size in these predators increases (Caraco & Wolf, 1975; Carbone et al., 1997).

A change in resource abundance may therefore lead to fine-scale changes in social structure such as the increase and decrease in group size, which will affect the number and nature of social relationships among group members Tavares et al., 2017. A better understanding of these changes provides insight into the potential ecological drivers of fission–fusion dynamics. We addressed this subject using data from a highly social top predator, the killer whale. We investigated the 'seasonality' of social structure (group size and measures of association) of killer whales at Marion Island, that is, how social structure changes between periods of high and low seasonal prey abundance. Some aspects of killer whale social structure at Marion Island have been investigated (Tosh et al., 2008; Reisinger et al., 2017) but differences in social structure between seasons are not yet known. Short-term fission–fusion has, however, been suggested to be present in this population due to the presence of unrelated individuals within the same social groups indicating a lack of philopatry (Reisinger et al., 2017).

Methods

Ethical Note

The Animal Ethics Committee (AEC) of the Faculty of Veterinary Science, University of Pretoria provided ethics clearance for this study (EC077-15).

Study Area

Marion Island is the largest island (296 km^2) in the Prince Edward Islands archipelago (46˚54′S, 37°45′E) and lies approximately 22 km southwest of neighbouring Prince Edward Island (45 km^2) in the sub-Antarctic Southern Indian Ocean. The archipelago is situated some 1800 km southeast of South Africa, 2300 km north of Antarctica and 950 km west of Îles Crozet, the nearest landfall.

Data Collection

Between May 2006 and April 2018, identification photographs of killer whales were collected during land-based observations at Marion Island (Jordaan, Oosthuizen, Reisinger, & de Bruyn, 2020). Photographs were taken during opportunistic sightings while doing other fieldwork or during dedicated observation sessions where trained observers would search for killer whales at a location for a predetermined, uninterrupted, period of 2–10 h. Dedicated observations were performed throughout the year at various locations around the island, covering areas of the coastline most frequented by killer whales (Keith et al., 2001; Reisinger, Keith, Andrews, & de Bruyn, 2015). During all sightings, the observer would attempt to photograph the dorsal fins and saddle-patches of all individuals in the group for as long as the group was in photographic range. Additionally, the groups' size, age/sex composition and movement direction were estimated and later confirmed after photographic identification. Age classes used in this study were calf (male and female: 0–3 years), juvenile (male: 3–13 years; female: 3–10 years) and adult (male > 13 years; female > 10 years; Olesiuk, Bigg, & Ellis, 1990; Best, Meÿer, & Lockyer, 2010). Sexes were only assigned to individuals that had reached sexual maturity or where sex-specific ventral markings were clearly observed. Sexual maturity was determined when females gave birth to calves or when no growth in fin size over a 5-year period was evident (Olesiuk et al., 1990).

Photographic Identification

Individual killer whales were identified through careful examination of any nicks, notches or mutilations in dorsal fins and saddle patches (Bigg et al., 1987) and through comparison to individuals in existing photographic identification catalogues (Reisinger & de Bruyn, 2014; Jordaan, Reisinger, & de Bruyn, 2019). A quality score, ranging from 1 (poor) to 5 (excellent), was assigned to all photographs and was based on the size, level of obscurity and angle of the dorsal fin in the photograph as well as lighting, exposure and focus. Analyses were done using only identifications of killer whales obtained from photographs with a quality score ≥3 (Reisinger, de Bruyn, & Bester, 2011). To further strengthen the analyses, we excluded individuals (*N* = 15) that were seen fewer than four times during the study period (Tosh et al., 2008).

Social Analysis

Social structure refers to a set of interactions between individuals that combine to form community dynamics (Hinde, 1976). A social network is a measure of social structure and consists of nodes (representing individuals, groups or other entities) and edges (the relationships that connect nodes). Edges typically represent the manner and magnitude of how nodes associate or interact and may have numeric values (weighted edges) describing the strength of the relationship (Farine & Whitehead, 2015). To determine measures of association for killer whales at Marion Island, we performed social network analyses in R (R Core Team, 2020) with the packages ‘asnipe’ (Farine, 2019) and ‘igraph’ (Csardi & Nepusz, 2006).

The data format for these analyses was an individual identification matrix where each row represented a group and each column an individual (i.e. node). In each row, a value of 1 represented an individual that was observed to be present in the given group and a value of 0 represented individuals that were not observed in the group (Farine, 2013). Individuals were considered to be part of the same group when they were photographically identified in the same group. In the field, a group was defined as all individuals within visual range of the observer that were in the same behavioural state (e.g. foraging, travelling, resting, etc.) and moving in the same direction (Ford, 1989). Individuals within the same group were assumed to be associated according to ‘gambit of the group’ (Whitehead & Dufault, 1999). Group delineation was easily achievable in our study due to the spatial and temporal separation between nearly all sightings. For analyses, calendar days were defined as sampling periods, and we assumed that observed associations were maintained for the entire day. If an individual was observed in multiple groups during a sampling period (day), it was included in each group that it was observed in for that sampling period. The data were subdivided into two periods across all years, representing periods within the year when killer whale and prey abundance was greatest (September - December: ‘peak’) and lowest (January - August: ‘off-peak’; Reisinger et al., 2011).

We calculated the following measures of association for the weighted association networks obtained for peak and off-peak periods.

Dyad level metrics. (1) Half-weight association index (HWI): an estimate of the proportion of time that two individuals spend together (Cairns & Schwager, 1987). This index was chosen as it reduces bias when not all members of a group are observed/identified during a sampling period. (2) Strength: the sum of the weights of the adjacent associations for each individual in the association network. The greater the strength, the more closely associated individuals are (Barrat, Barthelemy, Pastor-Satorras, & Vespignani, 2004). (3) Degree: the total number of associations per individual in the association network.

Network level metrics. (4) Mean distance: the average path length in the association network determined by calculating the shortest paths between all pairs of individuals in the network. The smaller the mean distance, the shorter the average distance and the closer the association between individuals (West, 1996). (5) Centrality (closeness centrality): a measure of network level centralization determined by the sum of the distances between one individual and all other individuals in the association network. If this distance is small, the closeness centrality is high (Beauchamp, 1965; Wasserman & Faust, 1994). (6) Modularity: a function to detect the quality of module division within the association network by calculating the leading non-negative eigenvector of the modularity matrix of the graph (Newman, 2006). The greater the modularity, the greater the strength of division of the association network. (7) Number of modules: the number of social modules within the association network determined by Newman's (2006) eigenvector-based function for modularity. (8) Lagged association rate (LAR): a measure of the probability that an individual is observed re-associating with another individual at a given time lag (Whitehead, 2008).

To test the null hypothesis that there is no variation between peak and off-peak periods, a set of ‘random’ association matrices was created to compare to the real (observed) matrix for each period (Whitehead, Bejder, & Ottensmeyer, 2005). This ‘random’ set of association matrices was created through randomizations of the data stream, which involved assigning each group a season identifier (peak or off-peak) and randomizing these sets of labels within each year while controlling for group size. This method keeps the number of groups within each season constant but permutes during which period specific groups occur (Franz & Alberts, 2015).

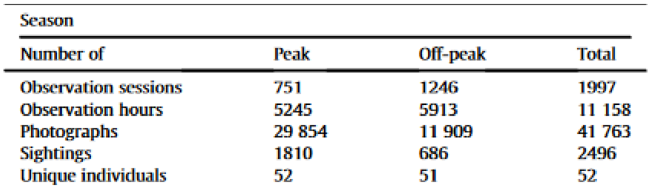
We randomized the data stream 1000 times. Measures of association were calculated for random networks of each period and the difference between periods (peak minus off-peak) was compared to observed differences (peak minus off-peak). Statistical significance (*P* values) was calculated as the proportion of times the test statistics of the permuted data (i.e. ‘random’ association matrices) were more extreme than the test statistics of the real data (i.e. observed matrices; Whitehead et al., 2005).

Data (igraph objects) were converted to 'GEXF' (Graph Exchange 'XML' Format) graph files using the ‘rgexf’ package (Vega Yon, 2020). Plots were constructed in Gephi (Bastian, Heymann, & Jacomy, 2009) using the Louvain method (Blondel, Guillaume, Lambiotte, & Lefebvre, 2008) for layout and nodes are coloured according to Newman's (2006) eigenvector-based function for modularity. Differences in group size between periods were compared with a Welch two-sample *t* test (Welch, 1938).

Results

We conducted 1997 dedicated killer whale observation sessions totalling 11 158 h from May 2006 to April 2018. Throughout this time, 89 792 photographs were taken across 2668 sightings occurring during observation sessions (0.24/h) and during 2071 opportunistic sightings. A total of 41 763 suitable photographs (quality score ≥3) were obtained from 2496 sightings with 1810 of these sightings occurring within the peak period and 686 occurring during the off-peak period (Table 1, Fig. 1a). Fifty-two individual killer whales were seen at least four times; 16 of these were calves born to known individuals during the study.

Table 1. Observation effort of killer whale research at Marion Island from 2006 to 2018



Season			
Number of	Peak	Off-peak	Total
Observation sessions	751	1246	1997
Observation hours	5245	5913	11 158
Photographs	29 854	11 909	41 763
Sightings	1810	686	2496
Unique individuals	52	51	52

Only photographs with a quality score ≥3 and sightings that included these photographs are shown.

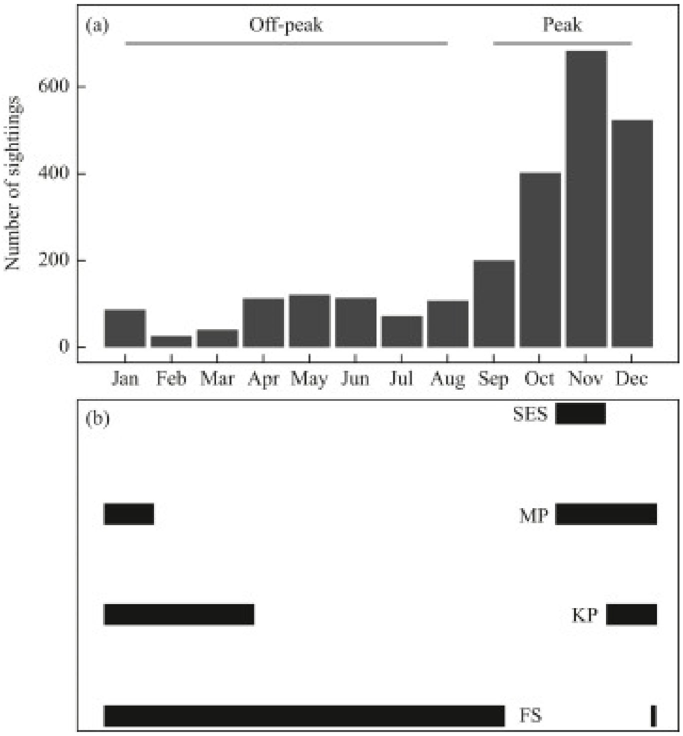


Figure 1. (a) The total number of killer whale sightings per month at Marion Island between 2006 and 2018, and (b) the reproductive period of seal and penguin species at Marion Island. The reproductive period for southern elephant seals (SES; Kirkman et al., 2004) and Subantarctic fur seals (FS; Hofmeyr et al., 2007) is the time between the median pupping and weaning dates. For king penguins (KP; du Plessis et al., 1994) and macaroni penguins (MP; Crawford et al., 2003) the reproductive period is between the median date of adult penguin arrival and median crèching date. See Table 1 for observational effort data.

Association network analyses indicated variation between network statistics measured during different periods of the year (Table 2) with significant differences in HWI, strength, centrality, modularity and number of modules between peak and off-peak periods (Table 3). Despite being significant, the permuted difference was greater than the observed difference for HWI and strength while opposite differences (i.e. positive versus negative) were observed for centrality, modularity and the number of modules (Table 3). In the peak period, LAR was initially more stable than that in the off-peak period which steadily declined. Initially, LAR during the off-peak period was higher than that for peak but both peak and off-peak LAR gradually decayed to similar levels before sharp declines after 900 days (Fig. 2). Group size during the peak period (mean = 3.74; 95% confidence interval (CI) = 3.68–3.81; range 1–17) was significantly greater than the mean group size during the off-peak period (mean = 2.98; CI = 2.90–3.05; range 1–10; $t_{3903.9} = 15.22$, $P < 0.001$; Table 2, Fig. 3).

Table 2. Social structure measures of killer whales at Marion Island, from 2006 to 2018

	Peak		Off-peak	
	Mean	SD	Mean	SD
HWI	0.029	0.099	0.022	0.087
Mean distance	1.45	–	2.35	–
Strength	1.53	0.78	1.13	0.55
Centrality	0.20	–	0.47	–
Degree	26.81	11.12	9.80	5.54
Modularity	0.64	–	0.68	–
Number of modules	12	–	10	–
Group size	3.74	2.25	2.98	1.52

Measures are summarized into Peak (September to December across all years) and Off-peak (January to August across all years). Means ±SD are presented only for half-weight association index (HWI), strength, degree and group size as these are the only measures that were determined per dyad and not for the association network as a whole.

Table 3. Difference in social structure measures of Marion Island killer whales between peak (September to December) and off-peak (January to August) resource availability periods from 2006 to 2018

Statistic	Observed difference (peak - off-peak)	Permutated difference (peak - off-peak)	*P*
HWI	0.007	0.014	**< 0.001**
Mean distance	-0.900	-0.870	0.37
Strength	0.398	0.754	**< 0.001**
Centrality	-0.271	0.430	**0.045**
Degree	17.004	16.033	0.11
Modularity	-0.048	0.019	**0.006**
Number of modules	2	-3.87	**0.01**

Observed difference is the difference between actual values obtained for each period (peak minus off-peak). Permuted difference is the difference between the mean values obtained from random networks permuted 1000 times for each period (peak minus off-peak). Statistical significance was calculated as the proportion of times the test statistics of the permuted data were more extreme than the test statistics of the real data (i.e. observed difference). Significant *P* values (< 0.05) are in bold.

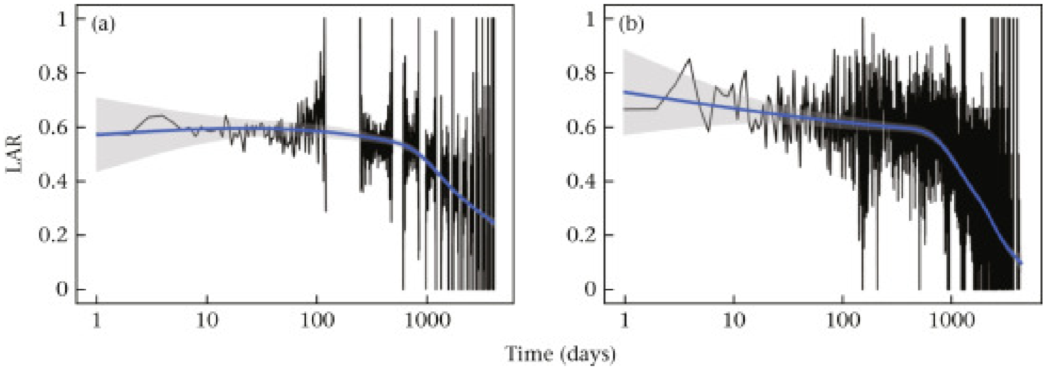


Figure 2. Lagged association rates (LAR) of killer whales at Marion Island for (a) all peak periods (September to December) and (b) all off-peak periods (January to August) from 2006 to 2018. LAR is a measure of the probability that an individual is observed reassociating with another individual at a given time lag (Whitehead, 2008). Regression lines (and 95% confidence intervals represented by the shaded area) are drawn.

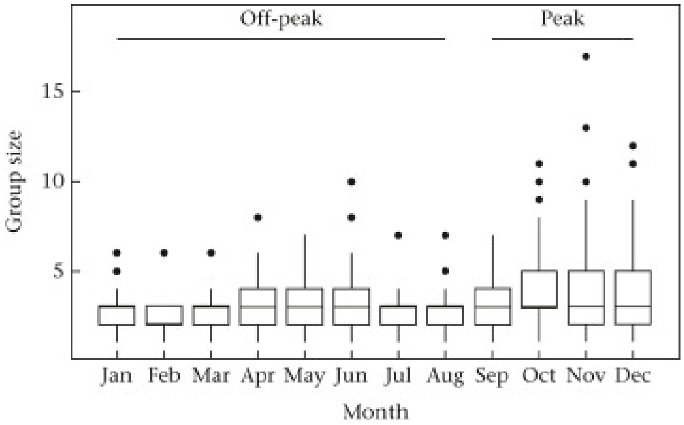


Figure 3. Variation in monthly killer whale group size at Marion Island during 2006–2018. The box plots show the median and 25th and 75th percentiles; the whiskers indicate the values within 1.5 times the interquartile range and the circles are outliers.

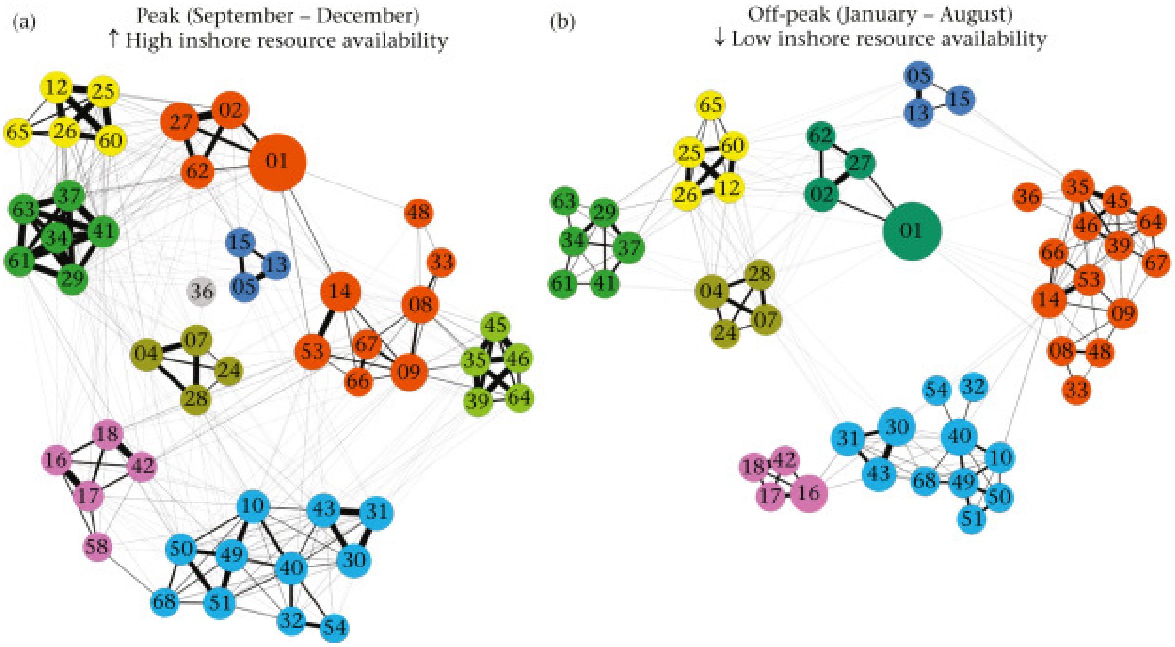


Figure 4. Network plots for Marion Island killer whales over (a) all peak periods (September - December) and (b) all off-peak periods (January - August) during 2006–2018. Each node (coloured circle) represents an individual killer whale and each vertex/edge (line between two nodes) represents the association between two killer whales. Numbers in nodes indicate the unique ID code for each individual but 'M0' was omitted from node labels (e.g. M001 is labelled as 01). The size of the node represents 'betweenness' centrality (how social, or gregarious, the killer whale is) with larger nodes reflecting more social individuals. Edges are weighted by the half-weight association index (HWI; higher HWI indicated with darker lines) and only weights > 0.01 are shown. Individuals were grouped into social units, represented by different colours, using the Louvain method for community detection (Blondel et al., 2008).

Peak and off-peak network plots (Fig. 4) show the differences in network and module structure between periods, as indicated by the network statistics. These plots show fewer nodes and fewer connections between nodes in the off-peak than the peak period. Group composition associations differed between periods. This can be seen with M014 et al. who combined with M001 et al. during the peak period and M045 et al. during the off-peak period. M001 et al. and M045 et al. formed separate groups during the off-peak and peak periods, respectively, illustrating different fission–fusion tactics between social groups. As a whole, more division in the network can be seen in the off-peak period, with stronger within clustering of groups.

Overall, HWI, strength and the number of modules were greater during the peak period while centrality and modularity were lower during the peak period. These differences suggest that killer whales were more social during the peak period as individuals had higher probabilities of socializing (HWI), formed stronger associations (strength), the population was less divided (number of modules, centrality and modularity) and groups were larger (group size).

Discussion

Killer whale social structure at Marion Island varied significantly between seasons with fission–fusion dynamics evident. During 'peak' periods when killer whale and prey abundance is greatest in-shore at Marion Island, killer whales were more social and formed a fluid association network consisting of more and larger groups. Killer whales spent more time with other killer whales (evidenced by higher HWI) and formed stronger associations (strength) during peak periods. There were also more subgroups within the network (number of modules) and the average group size of associating individuals was greater (group size) during peak periods. Stronger clustering and division and fewer interactions between social groups were observed in the association network during the off-peak period. There was a decrease in centrality and modularity during the peak period, indicating that the sum of all distances between individuals (i.e. the broadness of the network) increased (centrality) and the strength of division in the association network decreased (modularity).

Ultimately, these results indicate that in this killer whale population, fission and fusion of the social network occurs during off-peak and peak periods, respectively, with fission occurring when resources are constrained and fusion when resources are high (Wittemyer, Douglas-Hamilton, & Getz, 2005). Killer whales are known to benefit from fusion and larger group sizes in the presence of larger and/or more abundant prey, as their net rate of energy intake is then maximized (Baird & Whitehead, 2000; Tavares et al., 2017). Although prey may be more likely to detect larger groups of killer whales (Baird & Dill, 1996), hunting success may increase through cooperative hunting strategies (Baird & Whitehead, 2000). Cooperative hunting strategies also benefit other social predators such as wolves, *Canis lupus*, which increase group size when targeting large, difficult to hunt species such as bison, *Bison bison*, resulting in an increased hunting success rate (MacNaulty et al., 2014). Similarly, killer whales in the Galápagos, Punta Norte and ENP ('Bigg's') occasionally increase group size to hunt cetaceans with greater success (Hoelzel, 1991; Alva et al., 2013; Baird & Whitehead, 2000; Denkinger et al., 2020).

Reduced competition and maximized net rate of per capita energy intake are likely the main benefits that Marion Island killer whales experience by fission events and a reduction in group size when prey abundances are lower (January - August). Similar results were reported for 'southern residents' in the ENP where the social network was less interconnected during years of low Chinook salmon, *Oncorhynchus tshawytscha*, abundance (Foster et al., 2012). Lower prey availability results in increased time spent searching for prey and further travel distances, therefore decreasing opportunities for social interactions, leading to smaller group sizes with less interconnectivity (Felleman, Heimlich-Boran, & Osborne, 1991; Nichol & Shackleton, 1996; Parsons, Balcomb, Ford, & Durban, 2009). Smaller groups of killer whales have the benefit of reduced probability of detection by prey and less potential for social conflicts, but they sacrifice potential cooperative hunting opportunities and calf defence (Baird & Dill, 1996; Baird & Whitehead, 2000; Smith et al., 2008; Tavares et al., 2018).

The abundance of the Marion Island killer whale populations' primary prey is likely the main driver of their fission–fusion dynamics. However, seasonal variation in diet composition, not only absolute prey abundance, likely influences these social dynamics too. For example, different groups of Atlantic killer whales in the same social network show different levels of association dependent on prey, with groups hunting seals being smaller and displaying lower levels of association compared to larger, more closely associated groups that hunt herring (Beck et al., 2012). Similarly, in wolves from Yellowstone National Park, smaller packs (two to six individuals) hunted elk, *Cervus elaphus*, while larger packs (9–13 individuals) hunted bison (MacNaulty et al., 2014). Similar patterns may be present in Marion Island killer whales. However, to what extent, or if, there is fine-scale temporal variation in the diet of social groups at Marion Island is uncertain. Furthermore, even less is known about social structure and potential fission–fusion dynamics of social groups when they are not observed inshore at Marion Island, when they are potentially foraging for Patagonian toothfish or other prey (Reisinger et al., 2015, 2016).

Although seasonal fissions and fusions of killer whale social structure were evident at Marion Island, these dynamics may potentially also be driven by primary factors other than per capita energy maximization. Additional explanations for observed seasonal fusion, and observed differences in fission–fusion strategies between social groups, may include fusions for social reasons such as mating, calf protection and alloparental care, although these are difficult to observe and measure in cetaceans (Packer, Scheel, & Pusey, 1990; Beauchamp, 2017). For example, when facing increased predation threats, sperm whales, *Physeter macrocephalus*, increase group size to protect calves (Arnbom et al., 1987). Similarly, in lions, larger group sizes offer greater protection for their young and the increased ability to defend territories for long periods (Packer et al., 1990). Lastly, the social network characteristics we observed may have been influenced by our inclusion of all age classes in the analyses (Whitehead, 2008) although this should not account entirely for the observed differences between periods, since any biases should be similar in both periods.

Greater levels of association and increases in group size shown by killer whales at Marion Island during periods of greater prey availability are comparable to the responses made by other social species under similar situations (e.g. spotted hyaenas, Smith et al., 2008; lions, Mbizah et al., 2020; wolves, MacNaulty et al., 2014; sperm whales, Whitehead & Kahn, 1992). Therefore, fission–fusion events are likely largely driven by the net rate of energy gain per capita, particularly in this population of killer whales.

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