Social structure of male sperm whales

(*Physeter macrocephalus*)

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General Introduction

Male sperm whales (*Physeter macrocephalus*) seem to form unique societies among mammals. The factors promoting the society of male sperm whales may be quite different from those in other species. Although, in general, reproduction and kinship have a great influence on the formation of society and males' bonds (Wrangham 1983), male groups of sperm whales are not kin-based (Bond 1999; Autenrieth et al. 2018), and relationships between males seem to be promoted by a different factor other than mating. Thus, an investigation of the social structure of male sperm whales, which is unique among mammals, contributes not only to reveal the social structure of this species but also examines how ecological factors other than reproduction and kinship affect the formation of society.

The sperm whale is the largest toothed whales (odontocetes) and is distributed all over the world, from the equator to the ice edge (Rice 1989). This species shows the greatest sexual dimorphism of all cetaceans (Whitehead 2003). Mature males, at 15-18 meters in length and 40-50 metric tons, are approximately 1.5 times as long and 3 times as heavy as mature females (Best 1979). Both sexes are segregated in separate geographical areas (Whitehead 2003 data from Rice 1989).

Since the social studies based on photo-identification developed (e.g., Gordon 1990; Whitehead and Weilgart 1991), the social structure of female sperm whales became one of the best-understood of all cetaceans. The most basic element of sperm whale society is the social unit, consisting of about 8-12 females and their offspring (Christal et al. 1998; Whitehead 2003). Most females stay in their natal units throughout their life. Although social units are often consisting of related females, they may contain one, two, or more matrilines (Christal 1998). Researchers sometimes observed transfers between units as well as merges, and splits of a social unit, although they seemed rare (Christal et al. 1998). Two or more units may travel together for a few days as a cohesive group of about 20 animals to socialize and forage together (Christal & Whitehead 2001). Communal care such as allo-suckling (suckling calves who are not their calves) and babysitting near the surface during foraging dives were observed within social units (Best et al. 1984; Gordon 1987). Codas which are click trains including 3-20 clicks lasting 0.2-2.0 seconds (Watkins & Schevill 1977) are often heard when groups of females and juveniles are socializing. Codas are believed to function as social communication signals (e.g., Watkins & Schevill 1977, Weilgart & Whitehead 1993). Groups of females have distinctive repertoires of codas. In the Pacific and in the Eastern Caribbean, groups are delineated clearly into clans by distinctive coda repertoires (Rendell & Whitehead 2003; Gero et al. 2016). Coda repertoires appear to be acquired culturally from within family units. Thus, the female sperm whale is a highly-social animal.

In contrast with females which stay in their natal unit, male sperm whales leave the unit before sexual maturity (~6-16 years) and are found within “bachelor school” consisting of males of about the same size, generally at high latitudes outside the females’ range (Gaskin 1970; Ohsumi 1971; Best 1979). The researchers found a negative correlation between the number of animals within a “bachelor school” and the mean body length of the school members, suggesting that the sizes of schools became smaller as members grew up (Gaskin 1970; Best 1979). The number of males within the “small bachelor schools” consisting of young animals which are smaller than 12.8 meters on average is about 12-15 or multiple of it, and finally, mature males were often found alone (or in pairs) in higher latitude areas (Best 1979). Considering the reproductive cycle of females (about 5 years, Best 1984) and the genetic analyses of the mass-stranded male group (Bond 1999; Autenrieth et al. 2018), the male group is not based on kinship. Information about the "bachelor school" is mainly based on the observation and specimens caught by large-scale modern industrial whaling, thus, it is still unknown how the “bachelor schools” were formed and why they decrease in group size as individuals get older.

Little information about the social structure of male sperm whales has been reported since the end of modern whaling in the late 1980s. Limited referable studies suggested that the males rarely form the large-scale cohesive group such as “bachelor school” and are found within the aggregation across 10-30 kilometers (e.g., Gillespie 1997; Leaper & Scheidat 1998). Interactions between males were not observed (Christal & Whitehead 1997), and there is no evidence about preferred and long-term relationships among males within aggregation (Letteval et al. 2002). On the other hand, coordinated movement within aggregations observed by Christal & Whitehead (1997) and mass-stranding of groups consisting of only males (e.g., Rice 1989) might imply the presence of social bond among male sperm whales. There is a serious gap in knowledge about males’ society between the past and recent studies, and the social structure of male sperm whales after leaving the natal unit is still poorly known.

Nemuro Strait, Hokkaido, Japan, is a summer feeding ground for male sperm whales (Uni 2006) and has been used for commercial whale watching during which long-term photo-identification has been conducted. This photo-identification project that Ms. Hal Sato started in 2006, provides a valuable dataset to understand the ecology and social structure of male sperm whales. In 2013, we found the habitat of male sperm whales in Goto Submarine Canyon, Nagasaki, Japan. Males in this area are younger than animals in Nemuro Strait and other study areas abroad, and little is known about the ecology of such young males globally.

My dissertation aimed to reveal the social structure of male sperm whales using a large photo-identification dataset from two study areas: Nemuro Strait and Goto Submarine Canyon. In Chapter 1, to obtain the background information for social analyses, I investigated the trend in residence patterns and the abundance of male sperm whales in Nemuro Strait. In Chapter 2, I examined association patterns (preference and temporal patterns of association) to reveal whether social relationships exist among male sperm whales. In Chapter 3, I examined the correlation between body length and association indices and network measures of individuals to reveal the change in relationships as males age. Finally, I summarized the social structure of male sperm whales and discussed ecological factors driving the social relationships among males.

Chapter 1 Residence Pattern and Abundance

1.1 Introduction

The ecology of male sperm whales after they leave their natal group is still poorly understood (Whitehead 2003). Their extended home ranges make it difficult to understand the population size, movement patterns on a global scale, and social structure. An understanding of key ecological information such as abundance, which reflects the state of population (e.g., Gero & Whitehead 2016), and residence patterns, that can help determine temporal patterns of association (Whitehead 2008) on a local scale, is important for the conservation and management of any animal population.

It is well-documented that female sperm whales form stable social units, which rarely change membership apart from births, deaths, and the dispersal of juvenile males (Christal et al. 1998). Most females stay within their mother's unit for the duration of their lives (Christal et al., 1998). In contrast, males leave their natal unit before sexual maturity at about the age of 6 years or later (Best 1979; Richard et al. 1996). What little is known about the lives of male sperm whales comes from snippets of data collected at mating grounds and a few study areas in higher latitude. There is not much evidence for structured male groups within this species and males tend to be solitary when documented in aggregations (Whitehead 2003). Although the scale of these aggregations varies widely, they are usually made up of several males spanning an area from 10 to 30 km across found during visual and acoustic survey (e.g., Gillespie 1997; Leaper & Scheidat, 1998). The residency of male sperm whales in aggregations has been studied in some detail at four study sites: off the Galápagos (Christal & Whitehead 1997; Christal 1998); the Gully off Nova Scotia

(Whitehead et al. 1992); Andenes, Norway (Ciano & Huele 2001); and Kaikoura, New Zealand (Childerhouse et al. 1995; Jaquet et al. 2000). However, in some areas of these listed areas, data are still insufficient and there is large geographical and individual variation in mean residence time and abundance among such aggregations (Lettevall et al. 2002). To assess and mitigate human impacts on sperm whales, not only seasonal occurrence, population parameters, and residency must be understood for each area of interest because the scale of influence can vary greatly depending on the number of animals and their residency times.

Nemuro Strait, Hokkaido, Japan, which is a relatively narrow strait between the Shiretoko Peninsula, northeast of Hokkaido, and Kunashir Island, is a summer habitat for male sperm whales (Uni 2006). This area is also used extensively by both commercial fishing and whale-watching industries, so whales using this area are exposed to high levels of potentially disruptive human activities. Sperm whale abundance and residency patterns have not been examined in Nemuro Strait, hindering our ability to understand the impact of these activities on the local sperm whale population. In this paper, I describe the residency patterns and abundance of male sperm whales in Nemuro Strait using mark-recapture methods (Seber 1982). I will further the general pattern of foraging area use and compare with similar information from other areas.

1.2 Methods

Field methods

Fieldwork was conducted in Nermuro Strait (43.580°N, 145.100-145.150°E, 44.200°N, 145.230-145.350°E; Fig. 1-1) between May (except in 2006) and October over a 12-year period (from 2006 to 2017, a total of 1,513 days).

Photo-identification data were collected during field surveys aboard five commercial whale-watching boats in the strait. Each cruise lasted approximately 2.5 hr, with tours operating twice a day when weather conditions allowed. During the cruise, I searched for whales visually with binoculars and acoustically using a hydrophone, and the information was shared among all of the whale-watching boats. Although the cruise route differed slightly from day to day (depending on the weather and ocean conditions or on the presence of whales), in most cases, whales were found in the central part of the strait (Fig. 1-1; 500-1,500 m deep, about 5-15 nautical miles from Rausu Fishing port). To assist in determining the sex of animals, I estimated the body length of individuals photogrammetrically following the procedures of Gordon (1990), and Jaquet (2006). All whales were presumed to be male as no animals were seen with a calf and none were less than 12 m long, the documented maximum length of female sperm whales (Best 1969).

Individual identification

Sperm whales, as well as many other cetacean specie, can be identified individually based the shape, coloration and marks on their flukes or dorsal fins (Hammond et al. 1990). In previous sperm whale studies, 90% of encountered individual could be reliably identified this way (Whitehead & Gordon 1986). Photographs of the flukes of diving sperm whales were taken using an APS-C digital single-lens reflex camera (Canon EOS 40D, 7D, Nikon D7000) equipped with a 70-300 mm zoom lens. A total of 3,137 photographs were matched to an identification catalog following the methods of Arnbom (1987). A quality rating (Q) between 1 and 5 was assigned to each photograph based on focus, tilt, exposure, orientation, and percent of fluke visible (Arnbom 1987). Only high-quality photos with a $Q \geq 4$ (2,969 photos) were used for analyses. Photo-identification data was not collected blindly (i.e., we often knew the identities of the animals that we were photographing) because this study involved observations of focal animals in the field.

Residency in Nemuro Strait

The residency of individuals in the strait was determined by calculating lagged identification rates using Socprog 2.8 (Whitehead 2017). The lagged identification rate for a particular lag τ is the probability that an individual identified at any time 0 is reidentified in a photograph taken at τ units later (Whitehead 2001):

$$\mathrm{R}(\tau) = \frac{P(\tau)}{N}$$

where $\mathrm{R}(\tau)$ is the lagged identification rate for time lag τ; $\mathrm{P}(\tau)$ is the probability that the individual is still in the study area after time lag τ; and N is the abundance in the study area. Lagged identification rates were estimated by

$$\mathrm{R}(\tau) = \frac{\sum_i \sum_{j:t_j=t_i+\tau} m_{ij}}{\sum_i n_i \sum_{j:t_j=t_i+\tau} n_j}$$

where n_i is the individual identified at time t_i; m_{ij} is the number of individuals identified at both time ti and time t_j. Mortality was considered to be zero in this analysis as deaths were unlikely to occur over the sampling period. Three models of residency were fitted to the residency rate (Whitehead 2001), and the Akaike information criterion (AIC; Akaike 1973; see Burnham & Anderson, 2002) was used to determine the best model (Whitehead 2009). Jack-knife techniques (Efron & Stein 1981) were used to calculate 95% confidence interval error bars and standard errors for each model parameter.

The three models were:

(1) “Closed” (no changes in the individuals present in Nemuro Strait):

$$\mathrm{R}(\tau) = \left(\frac{1}{N}\right)$$

(2) “Emigration” (individuals could leave Nemuro Strait, but never return):

$$\mathrm{R}(\tau) = \left(\frac{1}{N}\right) e^{-\tau/I}$$

(3) “Temporary emigration” (individuals could enter and leave Nemuro Strait, then reenter the strait; Whitehead 1990):

$$R(\tau) = \frac{O \times e^{-\tau\left(\frac{1}{O}+\frac{1}{I}\right)} + I}{(I + O)N}$$

where N is the number of individuals in Nemuro Strait; I is the mean time spent inside the strait; and O is the mean time spent outside the strait (Whitehead 2009).

Population analysis

Mark-recapture analyses were conducted using Program MARK (White & Burnham 1999). Pollock’s Robust Design (Kendall et al. 1995; 1997) was applied to assess abundance and emigration pattern. A year was considered as the primary sampling period and months within each year were set as the secondary occasion. The modifications on Robust Design by Kendall et al. (1997), which allow for an animal in the population to be unavailable for capture at a given time, were used to estimate temporary emigration.

The Robust Design models were composed of these parameters: Φt: the apparent survival probability from primary occasion t to t + 1; pt, ct: the probability that an individual available for capture in occasion t would be recaptured in the secondary samples, s, of the primary occasion t; γ’t, γ”t: the probability that an individual would be unavailable for capture during primary occasion t given that it was unavailable or available in the previous occasion.

Abundance (N) was estimated using the full parameterization of maximum likelihood available in Program MARK (White & Burnham 1999). Three models were designed using the notation provided by Kendall et al. 1997: Markovian movement (γ’, γ”), where the probability of availability depends on whether the animal was available for capture; random movement (γ’ = γ”), where the probability of availability is completely random; and models with no emigration (γ’ = γ” = 0). The robust design module in Program MARK (White & Burnham 1999) includes the classical closed population model (Otis et al. 1978). The AIC (Akaike 1973; see Burnham & Anderson 2002) was used to assess the relative model fit and the model with the lowest AIC was selected as the model with the most support.

1.3 Results

From 2006 to 2017, sampling was performed on a total of 1,513 days (average 126 days per year; from 58 days in 2006 to 148 days in 2010; Table 1-1) and we encountered sperm whales on 890 of these days during the months of May to October. Most animals (87.3%) were found from July to September. A total of 225 unique individuals were identified photographically. The average number of individuals identified in one season was 36 animals (SE = 2.55, Fig. 1-2). Of the 225 individuals, 89 animals (39.6%) were identified over multiple years, with these animals being resighted between two and nine times. Only 18 individuals (8.0%) were encountered over a period of five or more years (Fig. 1-3). The number of new individuals identified each year varied from 5 in 2016 to 30 in 2017. The reidentification rate increased from 2007 to 2012 and generally declined from 2013 onwards (Fig. 1-2). The mean resighting rate was 48.8% (SE = 6.36), although this fluctuated between years.

The “Emigration + reimmigration” model was selected as the best model for lagged identification rate based on the lowest AIC. The best supported mean residency time in Nemuro Strait was 769 (SE = 372.4, 95%CI: 30.4-1,010.4) days, approximately 2 years (Table 1-2, Fig. 1-4a). Lagged identification rate decreased 40-150 days after the initial sighting of an individual, but increased again approximately 200 days later. The result of an analysis limiting the maximum time lag to 120 days showed that male sperm whales stayed in the study area for a mean duration of 48 days (SE = 8.36, 95%CI: 35.9-71.2; Fig. 1-4b). Pollock’s Robust Design models that did not account for emigration (Table 1-3, models 9, 10) fit the data poorly, and emigration probabilities seemed to follow a random or Markovian movement model (Table 1-3, models 1, 2). The model with most support had random and constant emigration probabilities, constant survival and time-dependent capture probability between and within primary occasions (Table 1-3, model 1). Under this best-supported model, temporary emigration from the study area to neighboring regions was the same for a given emigrant remaining outside of the study area ($\gamma'' = \gamma' = 0.483$, SE = 0.04, 95%CI: 0.404-0.563). Thus, the probability of whales remaining in the study area between capture occasions ($1 - \gamma''$) and the return rate of temporary emigrants to the study area were equal ($1 - \gamma'' = 1 - \gamma' = 0.517$). The apparent survival rate for the whales was 0.965 (SE = 0.004, 95%CI: 0.956-0.971). Annual abundance varied from 28 individuals (SE = 4.49, 95%CI: 24-37 in 2015; SE = 4.49, 95%CI: 24-37 in 2016) to 66 individuals (SE = 6.50, 95%CI: 57-84) in 2011 (Table 1-1).

1.4 Discussion

This study shows that male sperm whales were present in Nemuro Strait predominantly during the months of June to September. This is similar to what has been observed in other areas where male sperm whale abundance and residency has been studied. In Andenes, Norway, male sperm whales are similarly found in a submarine canyon during the summer (Lettevall et al. 2002; Rødland & Bjørge 2015). Likewise, males are observed during summer months (June–August) in the Gully, Nova Scotia, Canada (Whitehead et al. 1992). Sperm whales off Kaikoura also shift their habitat seasonally (Jaquet et al. 2000), but on a different spatial scale (Childerhouse et al. 1995). In general, male sperm whales in mid or high latitude migrate seasonally, although the temporal and spatial scale of this migration varies by area.

Results of this study indicated that new individuals continued to be recruited to the area throughout the study period (Fig. 1-2). This suggests that the population of sperm whales in Nemuro Strait is either open or represents only a portion of a closed population that covers a wider geographic area. Thus, recruitment to the population may represent immigration or simply be captures of individuals that had not been photographed previously. When considering whales in Nemuro Strait as a population on a geographic level, immigration explains these results best as most whales encountered had unique marks on their flukes and were identified from several whale-watching boats, making it unlikely that the identification of most whales using the area for the first time was missed.

Lettevall et al. (2002) examined the residency of male sperm whales in aggregations at the four study areas: Kaikoura, Andenes, Galápagos, and Nova Scotia. Mean residence times within aggregations ranged from a few days to a few weeks. Off Kaikoura, Andenes, and Nova Scotia, sperm whale distribution is strongly associated with the bathymetry: deeper waters of a prominent submarine canyon (Ciano & Huele 2001; Jaquet et al. 2000; Lettevall et al. 2002). In each study area, males spent most of the time foraging within aggregations (Christal & Whitehead 1997; Jaquet et al. 2000; Madsen et al. 2002; Whitehead et al. 1992). An aggregation can be regarded as a set of animals that is present in the foraging area, and as the definition of an aggregation remains the same between geographic regions where male sperm whales have previously been studied, these earlier findings are appropriate for comparisons with our results. Nemuro Strait, which has similar geological features, is also a foraging area of male sperm whales. At 48 (SE = 8.36) days, residency of male sperm whales in Nemuro Strait is approximately the same as other areas; Kaikoura 42.0 (SE = 10.3), Andenes 13.6 (SE = 3.6), Galápagos 27.3 (SE: no data) days, with the exception of the Gully 2.9 (SE = 3.6) days. Hence, male sperm whales may move from one feeding area to a neighboring area every few weeks, although there is some difference among areas or individuals (e.g., Childerhouse et al. 1995).

Individual identifications and the lagged identification rate show that most individuals identified in Nemuro Strait (86.7%) did not use the study area for very long (<4 years). In Bleik Canyon, Norway, male sperm whales were also seen on average for only 1 or 2 years (Rødland & Bjørge 2015). Therefore, in general, it appears males may shift their foraging range gradually every few years. That being said, it has been noted that some individuals returned to the study area repeatedly (e.g., Ciano & Huele 2001; Jaquet et al. 2000). In

Nemuro Strait, one male (NS-PM033) also was observed for nine consecutive years from 2006 to 2014.

The abundance of sperm whales in Nemuro Strait varied greatly from year to year. While there was no consistent (upward or downward) trend, I noted that some years (in 2015 and 2016) had an estimated abundance significantly lower than those found during other years. Given this information, it is important to continue to study abundance dynamics in this area in order to better understand these variations and the reasons behind them.

Although it is still unknown as to whether human activity plays a negative role as a factor affecting sperm whale abundance, in Nemuro Strait, these anthropogenic influences are worth investigating as potential threats to this population. Nemuro strait is the site of various fishing operations including bottom gillnets, with catches of several fish species continuing to decline since the late 2000s. For example, the total catch of walleye pollock (*Theragra chalcogramma*) has decreased by 55% between 2006 and 2017 despite maintained fishing effort (Rausu Fishermen's Association, personal communication, 17 February 2018). Although I have no data available on the feeding habits of sperm whales in this area, their prey abundance is likely decreasing as the result of overfishing or bycatch. Further studies are vital for understanding the role that local fisheries might have on sperm whale prey abundance. Another threat to whales is the influence of disturbance from whale-watching boats. Commercial whale watching in Nemuro Strait started in 1998, with four companies currently running tours. The number of cruises has increased in recent years, particularly since July 2006, when Shiretoko was listed on the UNESCO World Heritage List (UNESCO World Heritage Centre, n.d.). As of 2012, the total number of cruises from

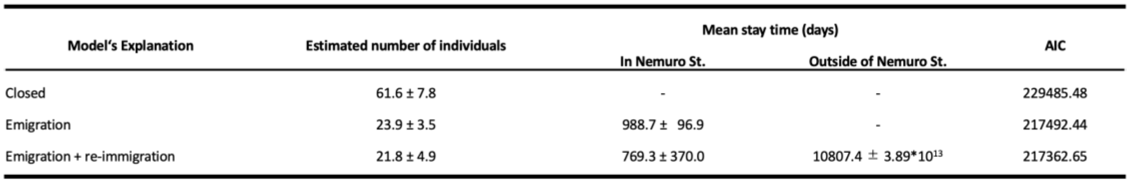
July to September is about 500 (Fig. 1-5). In Kaikoura, New Zealand, research has shown that sperm whales respond to whale-watching activities by changing ventilation and vocalization patterns (Richter et al. 2006). Studies such as this have not yet been conducted in Nemuro Strait. Although our research over the last decade has revealed no significant growth or decline in the sperm whale population in the strait, it is necessary to continue to monitor the trend of abundance as estimates in some years have been significantly lower than those of average years.

This study provides comparative knowledge of abundance and residency on a local scale, which will contribute to our research on movement patterns, and social structure of male sperm whales in Nemuro Strait. Further comparative studies are needed to reveal the general pattern and geographical variation of their ecological habits. It is also necessary to assess the potential human influences in the area, as it is used extensively for fisheries and whale-watching, to find solutions for local industries to coexist with sperm whales while minimizing disturbance for this species over the long-term.

1.5 Tables and Figures

Table 1-1. Estimated residency parameters (±SE) for all individuals in all years

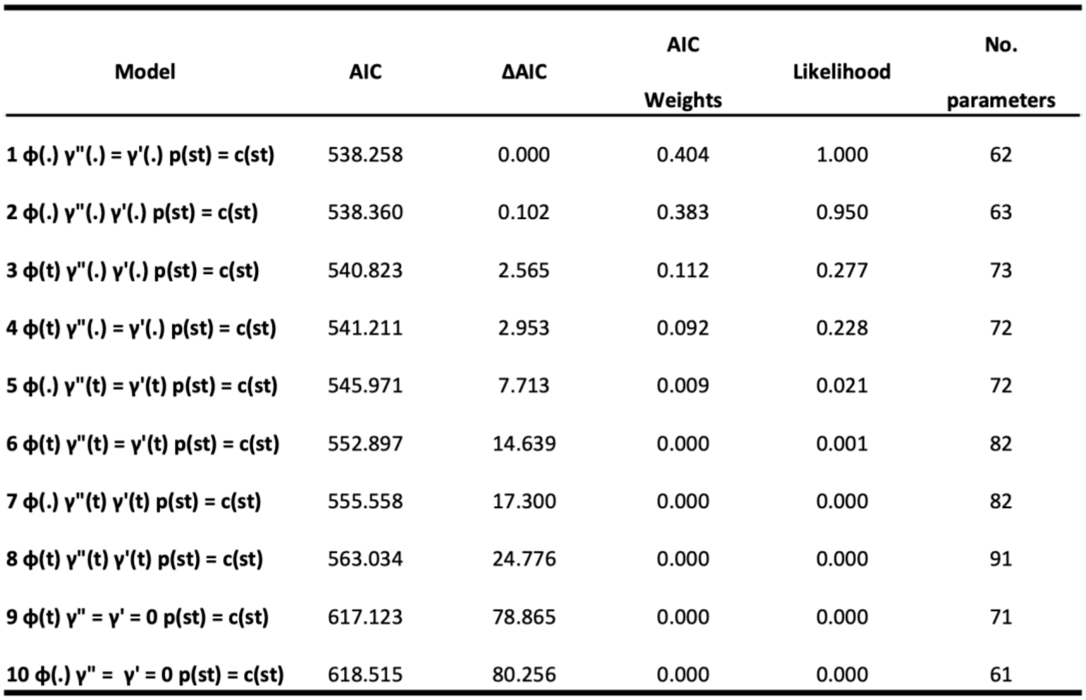
Model with best support based on Akaike Information Criterion (AIC) are given in Bold.



Model's Explanation	Estimated number of individuals	Mean stay time (days)		AIC
		In Nemuro St.	Outside of Nemuro St.	
Closed	61.6 ± 7.8	-	-	229485.48
Emigration	23.9 ± 3.5	988.7 ± 96.9	-	217492.44
Emigration + re-immigration	21.8 ± 4.9	769.3 ± 370.0	10807.4 ± $3.89*10^{13}$	217362.65

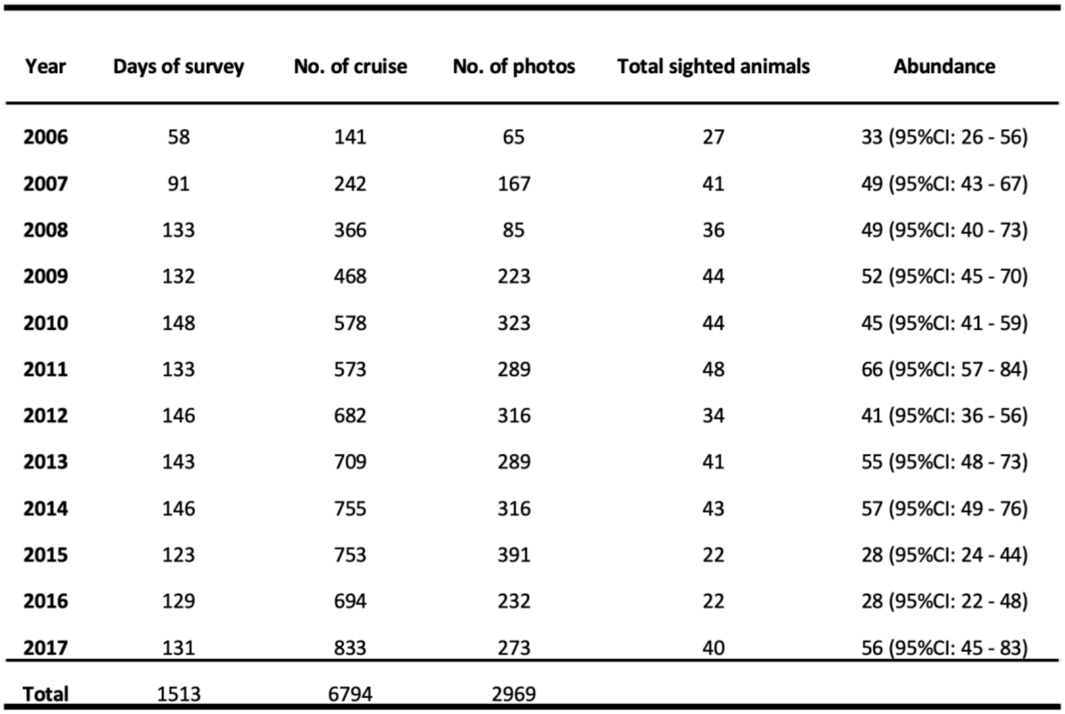
Table 1-2. Pollock’s Robust Design models for survival (φ), temporary emigration (γ), capture (p), and recapture probabilities (c) ranked by the lowest AIC

AIC weight indicates the strength of evidence for a given model. Model notation: no emigration (γ” = γ’ = 0); Markovian emigration (γ”, γ’); random emigration (γ” = γ’); constant parameter (.) or time-dependence (t, s).



Model	AIC	ΔAIC	AIC Weights	Likelihood	No. parameters
1 ϕ(.) γ"(.) = γ'(.) p(st) = c(st)	538.258	0.000	0.404	1.000	62
2 ϕ(.) γ"(.) γ'(.) p(st) = c(st)	538.360	0.102	0.383	0.950	63
3 ϕ(t) γ"(.) γ'(.) p(st) = c(st)	540.823	2.565	0.112	0.277	73
4 ϕ(t) γ"(.) = γ'(.) p(st) = c(st)	541.211	2.953	0.092	0.228	72
5 ϕ(.) γ"(t) = γ'(t) p(st) = c(st)	545.971	7.713	0.009	0.021	72
6 ϕ(t) γ"(t) = γ'(t) p(st) = c(st)	552.897	14.639	0.000	0.001	82
7 ϕ(.) γ"(t) γ'(t) p(st) = c(st)	555.558	17.300	0.000	0.000	82
8 ϕ(t) γ"(t) γ'(t) p(st) = c(st)	563.034	24.776	0.000	0.000	91
9 ϕ(t) γ" = γ' = 0 p(st) = c(st)	617.123	78.865	0.000	0.000	71
10 ϕ(.) γ" = γ' = 0 p(st) = c(st)	618.515	80.256	0.000	0.000	61

Table 1-3. The sampling effort (days of survey, number of cruises and photos) and abundance estimate of sperm whales in Nemuro Strait based on Pollock's Robust Design model with best support



Year	Days of survey	No. of cruise	No. of photos	Total sighted animals	Abundance
2006	58	141	65	27	33 (95%CI: 26 - 56)
2007	91	242	167	41	49 (95%CI: 43 - 67)
2008	133	366	85	36	49 (95%CI: 40 - 73)
2009	132	468	223	44	52 (95%CI: 45 - 70)
2010	148	578	323	44	45 (95%CI: 41 - 59)
2011	133	573	289	48	66 (95%CI: 57 - 84)
2012	146	682	316	34	41 (95%CI: 36 - 56)
2013	143	709	289	41	55 (95%CI: 48 - 73)
2014	146	755	316	43	57 (95%CI: 49 - 76)
2015	123	753	391	22	28 (95%CI: 24 - 44)
2016	129	694	232	22	28 (95%CI: 22 - 48)
2017	131	833	273	40	56 (95%CI: 45 - 83)
Total	1513	6794	2969		

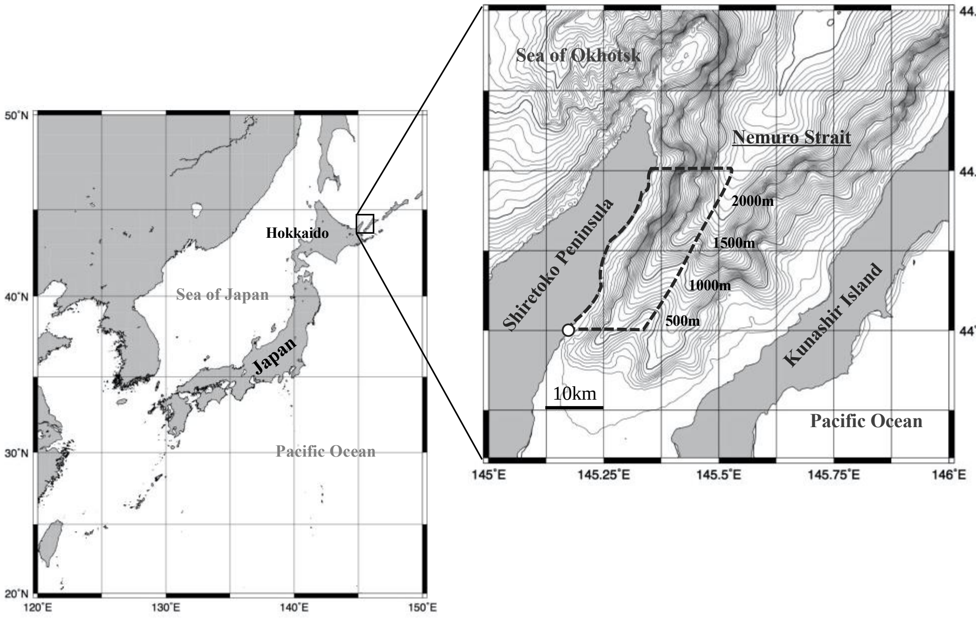


Fig. 1-1. Study area in Nemuro Strait, Hokkaido, Japan

Broken line shows the range of study area, and red mark represent the area where the most whales were found. ○ indicates position of "Rausu fishing port" (departure point of whale-watching boat).

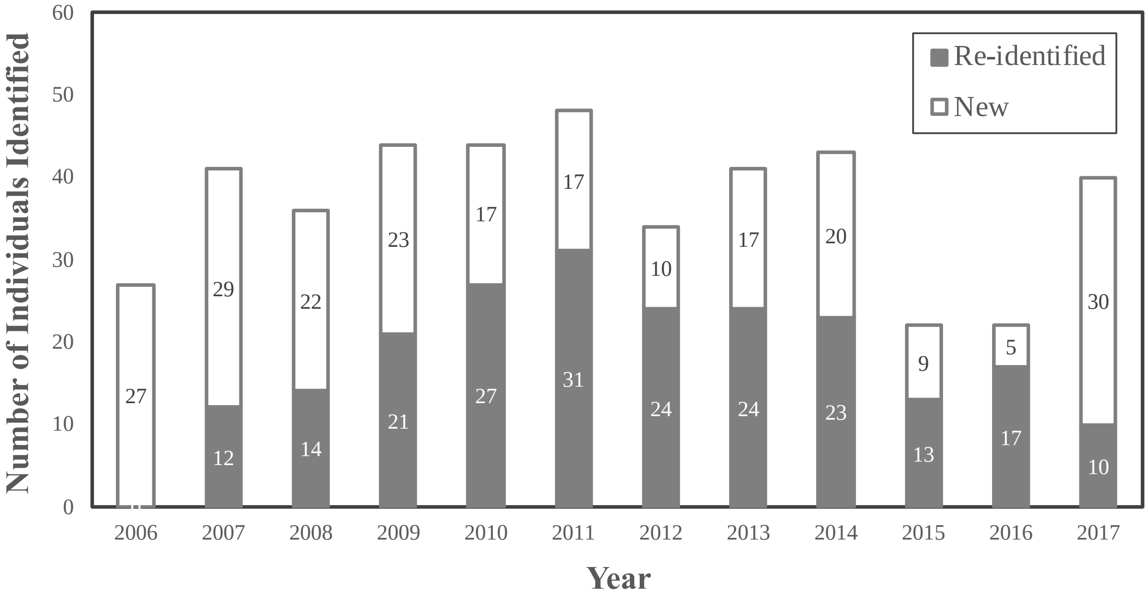


Fig. 1-2. Number of individuals identified and re-identified in Nemuro Strait in the period 2006 - 2017

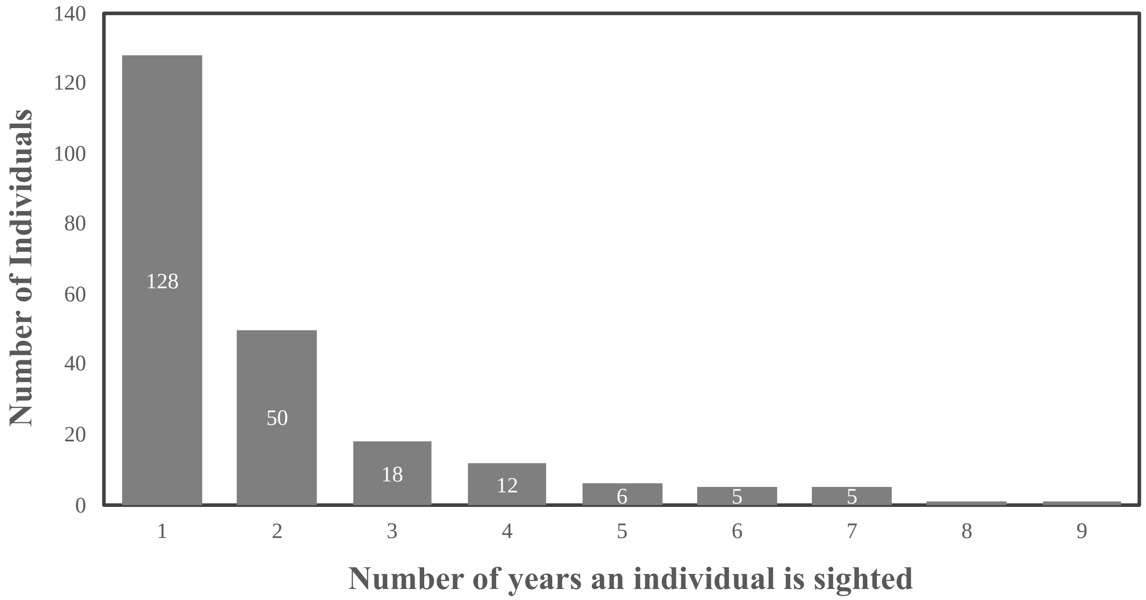


Fig. 1-3. Number of individuals sighted in a particular number of years in Nemuro Strait in the period 2006-2017

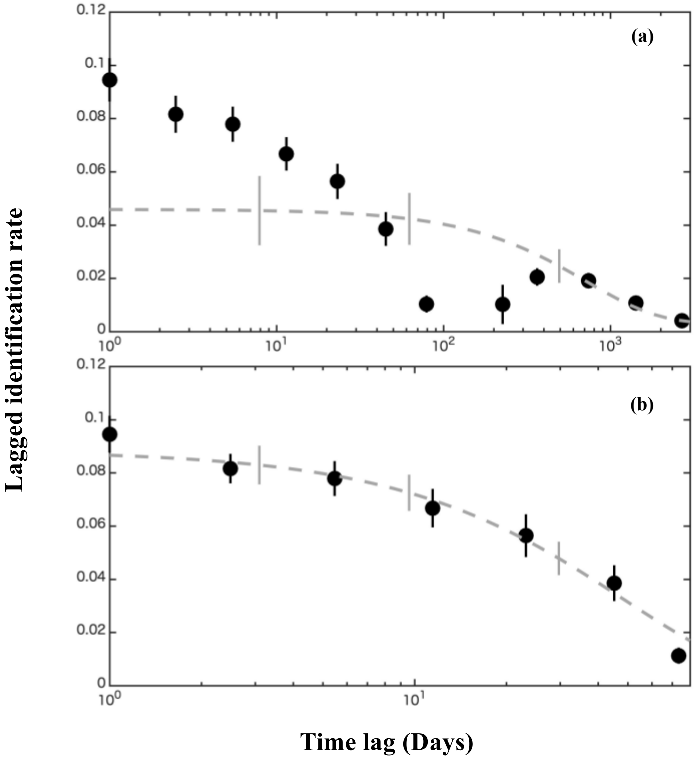


Fig. 1-4 (a). Lagged identification rate (probability of re-identifying an animal after a certain time lag) of male sperm whales in Nemuro Strait over the whole study period, and (b). within 120 days (about 1 research season)

Points (●) show observation data and the broken line is the Best-fitting model. Error bars represent standard error estimated using jack-knife methods.

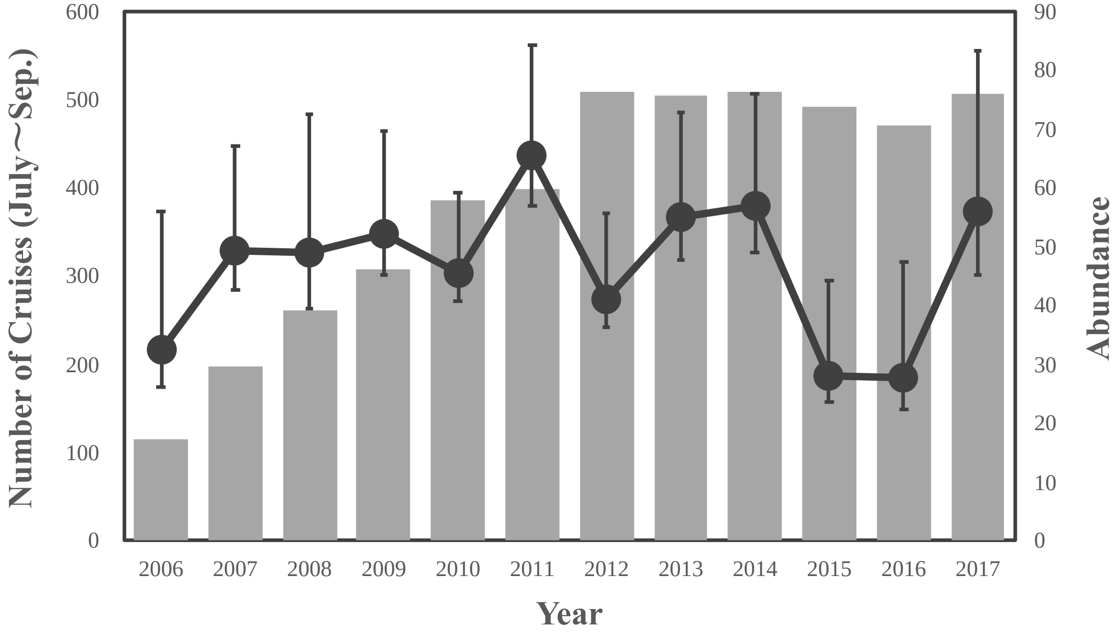


Fig. 1-5. Number of whale-watching cruises (bar) and abundance of sperm whales (closed circles) in Nemuro Strait from 2006 to 2017

Error bars represent 95% confidence intervals.

Chapter 2 Long-term Social Relationships

2.1 Introduction

Among mammals, male relationships tend to be competitive (van Hooff & van Schaik 1994), and consistently strong association rates are relatively rare. In some species, males form strong relationships to defend estrous females, or access to female groups or territory (e.g., chimpanzee *Pan troglodytes*: Mitani et al. (2000); bottlenose dolphin *Tursiops sp.*: Connor et al. (1992); lion *Panthera leo*: Packer & Pusey (1982); cheetah *Acinonyx jubatus*: Caro & Collins (1987)). Most of these associated males are kin. Although male sperm whales form all-male groups, the factors promoting group formation among males may be quite different from those in species where males associate with related males to improve mating success.

Female sperm whales and their offspring live in stable social units at low or mid-latitudes (Whitehead 2003), and most females remain within their natal unit throughout their life (Christal et al. 1998). In contrast, males leave their natal unit before sexual maturity (~6-16 years) and are described as forming “bachelor schools” consisting of males of about the same age, generally at high latitudes outside the females’ range (Best 1979). The sizes of bachelor schools have a negative correlation with mean body length within the school suggesting diminishing sociality with age (e.g., Gaskin 1970, Ohsumi 1971, Best 1979). Finally, males, in their forties and older, may be seen alone in high latitude areas including near the ice edges, as well as in lower latitude areas where they migrate to mate (Whitehead 2003, Whitehead & Weilgart 2000). Therefore, from what we know, male relationships within bachelor schools of sperm whales are quite different from those in alliances or coalitions which relate to defense of females or territory as no females are present, or even nearby, at these higher latitudes. However, little is known about the extent of sociality in bachelor schools.

Mass stranding events –when two or more animals beach themselves at the same place and time- suggest that male sperm whales can form cohesive male groups. Mass-strandings are commonly reported for highly social odontocetes such as short-finned pilot whales *Globicephala macrorhynchus*, long-finned pilot whales *Globicephala melas* and false killer whales *Pseudorca crassidens* (Sergeant 1982). Sperm whales sometimes also mass-strand, and some mass stranding consist only of males (e.g., Rice 1989; Whitehead 2003). For instance, Rice (1989) reported a total of thirteen all-male strandings including 3 to 37 animals (mean 12.5 animals). These events suggest that there may be strong associations among males. However, there is no information about their associations before stranding. Bond (1999) found that among two all-male mass-strandings on the coast of Scotland, most animals were genetically unrelated to one another. Autenrieth et al. (2018)'s genetic analysis suggested that the 27 male sperm whales that stranded together in the North Sea were not maternally related individuals but instead included assemblages of individuals from different natal geographic regions. Schnitzler et al. (2018) also reported evidence for at least two cohorts with different origins among 24 of these males based on contaminant and genetic analyses. Considering the long calving intervals of individual females (every 4-6 years, Best et al. 1984; Rice 1989) and the size of female family units (~10, Whitehead 2003), it would be almost impossible to form an all-male group consisting of more than very few related males of approximately the same age. Taken together, these results suggest factors other than kinship structure male relationships.

Despite observations of “bachelor schools” (e.g., Gaskin 1970) and mass strandings of nonbreeding males (Sergeant 1982, Rice 1989), there is little evidence from modern studies of living sperm whales that males form groups with preferred association (Whitehead 2003). In visual and acoustic surveys at high latitudes, aggregations of males spanning from 10 to 30 km are commonly found (e.g., Gillespie 1997, Leaper & Scheidat 1998). Such aggregations were also described by whalers (Caldwell & Caldwell 1966). Christal & Whitehead (1997) found male sperm whales swimming alone within aggregations of males spreading over 20 km across off the Galapagos Islands. Members of the male aggregations usually showed consistent heading mostly within about 20° of the modal heading of the aggregation on the same day, but interactions between members were not observed (Christal & Whitehead 1997). Therefore, it is unclear whether the males’ coordinated movements were a response to external factors such as the distribution of prey or geographical features (such as the presence of canyons) or reflected social bonds between the males themselves.

Lettevall et al. (2002) reported no evidence of preferred companionship or long-term relationships among photo-identified males from 4 study areas: Andenes (Norway); The Gully (Nova Scotia, Canada); off Galapagos Islands (Ecuador); Kaikoura (New Zealand). Thus, among males, there is no evidence of the long-term relationships, or social units, that are characteristic of females and their dependent young. However, in these studies, identification data were fairly sparse and perhaps insufficient to detect some forms of long-term social structure. Moreover, Lettevall et al. (2002) also mentioned the possibility of more social groups consisting of relatively small and young males based on heading coordination within aggregations and mass strandings. Thus, the social relationships between male sperm whales are still poorly known.

Here, I try to fill this gap in knowledge by investigation the social associations among nonbreeding male sperm whales in the Nemuro Strait, Hokkaido, Japan. This area is a summer feeding ground for male sperm whales and has been used extensively for commercial whale watching during which photo-identification has been conducted since 2006. I used this photo-identification dataset to characterize the nature of male relationships and show that males have consistent long-term associations.

2.2 Methods

The field methods and individual identification methods are as described in detail in Chapter 1. Identification data of sperm whales were collected in the Nemuro Strait (Fig. 2-1) between 2006 and 2017. Only photographs of $Q \geqq 4$ were included in the following analyses.

Data Analysis

In the framework proposed by Hinde (1976), the social structure of a population is a synthesis of the pattern of the relationships among its members, which in turn are described by the nature and quality of their interactions (Whitehead & Weilgart 2000; Whitehead 1997; 2008). In most cetacean species, social interactions occur under the sea surface which makes them difficult to quantify. Because of this, many researchers studying social structure in cetaceans make an assumption called “the gambit of the group”: individuals are assumed to be interacting if they are found in the same location at the same time (Whitehead & Dufault 1999). Thus, the relationships between pairs of individuals can be described by the characteristics and temporal patterning of their associations (Hinde 1976; Whitehead 1995; 2008).

Previous sperm whale studies have quantified associations two ways: either spatially by assuming that individuals within a cluster (within 3 body lengths of each other and coordinating movements, Gero et al. 2013) are associating (e.g., Whitehead et al. 2012; Cantor & Whitehead 2015; Gero et al. 2015) or temporally by assuming that sperm whales identified within 10 min (e.g., Christal & Whitehead 2001), 2 hour (e.g., Lettevall et al. 2002; Whithead & Weilgart 1991; Whitehead et al. 1992; Konrad et al. 2018) or in same day (e.g., Lettevall et al. 2002; Konrad et al. 2018) are associating. Whales in clusters are assumed to be associating since they are in visual, and sometimes physical, contact with each other while whales encountered within 2 hours are assumed to be associating since they are in acoustic contact with each other (the audible range through hydrophones is 16 km for “usual clicks” (searching echolocation clicks) and 60 km for “slow clicks” (clicks used by males) (Whitehead 2003 data from Madsen 2002). Previous studies (e.g., Christal et al. 1998; Gero et al. 2015) also showed that using stronger measures of association (such as “in a cluster together” and 10 min criterion), as compared to those with looser criteria, did not affect the outcome of permutation tests for preferred associations.

In this study, I considered whales identified within 1 hour of each other from the same boat to be associated. Associated whales were observed 2,841 ± 1,961 m (mean ± SD) apart on average (n = 758, Fig. 2-2). In the Strait, sperm whales dispersed over wider ranges: in land-based visual surveys an average of 5.5 animals were identified per hour, with an average horizontal distance of 5,778 ± 3,786 m (mean ± SD, n = 9,790; Supplement 2-1) between them. This distance is twice as wide as that between associated animals identified from the research vessels. Thus, associating whales (sighted within 1 hour) are proximate animals in the foraging area, and are likely to be within acoustic contact of each other.

To quantify the strength of associations between individuals, I used the half-weight index (HWI). An HWI equal to zero indicates that the dyad never associated -as per our definition of association- and an HWI equal to one indicates that the members of the dyad were always observed within 1 hour of each other (Whitehead 2008). The sampling period (unit of analysis) was 1 day, so that the association dataset indicates which individuals were associating on which days.

Preferred Associations

A permutation test examined the null hypothesis that associations between individual males were random given the temporal pattern of each individual's identifications. In this test, I permuted associations within samples. The association matrices for each day were randomized 10,000 times with 10,000 flips per permutation maintaining the number of associates of each individual on each day, with HWIs being calculated after each permutation, at which point the P-values stabilized (Whitehead 2009). If some pairs of animals were preferentially associating with or avoiding one another over different days, then this would increase variation among the HWIs. Thus, if the standard deviation or the coefficient of variation of the observed association indices was significantly higher than those calculated from the randomly permuted data, the null hypothesis (no preferential associates over days) was rejected (Whitehead 2008).

Temporal Pattern

Temporal change in association was examined by calculating the standardized lagged association rates (SLAR) for associations with identification data from 225 individuals. The standardized lagged association rate is an estimate of the probability that if two individuals are associated at any time, then, after a given time lag, the second individual will be a randomly chosen associate of the first (Whitehead 1995). The SLAR was compared to the standardized null association rates (SNAR): that is the expected SLAR if individuals associated at random. Four exponential models were fitted to SLAR to describe the temporal patterning of male associations in Nemuro Strait: the first model had no decay and suggests permanent associations; the second model had a decay down to zero and suggests that associations decrease until complete disassociation; the third model had a decay that levelled off and suggesting both long-lasting and temporary associations; and the fourth model had two decays and suggested two levels of disassociation, at a shorter and longer time lags respectively (Whitehead 2008). The standard error of the SLAR was estimated using jackknife methods (Whitehead 2008). The best fitting model was chosen based on the lowest Quasi Akaike Information Criterion (QAIC). All social analyses were carried out in the SOCPROG 2.8. software (Whitehead 2009).

Cluster

Clusters are sets of sperm whales observed at the surface within 3 body lengths of one another and swimming in the same direction (Gero et al. 2013). During social or resting periods, it is typical for females and immatures to cluster (Whitehead 2003). Therefore, clusters can be regarded as a signal of social interaction among sperm whales. In contrast to females, most nonbreeding males are seen alone at the surface (Lettevall et al. 2002), however, these males do sometimes actively cluster (Caldwell & Caldwell 1966). Thus, when I encountered a cluster, I recorded the cluster size, the behavioral mode (surfacing between dives, socializing, resting), and identified the individual members of the cluster whenever possible.

2.3 Results

I obtained 2,968 identifications of 226 individual male sperm whales on 608 different days in the Nemuro Strait. 44 photographs (out of a total of 3012, 1.5%) could not be identified due to the absence of marking on the sperm whales' flukes. The discovery curve for individuals is still increasing steadily as new individuals are identified every year (Supplement 2-2). 127 individuals (56.2%) were identified over multiple years (2-9 times). Individuals were identified on a mean of 14 days each, and on each day had a mean of 1.4 associates (identified within 1 hour). The mean association index was 0.130. The mean cluster size (including single animal clusters) in Nemuro Strait was 1.07 individuals (cluster size range: 1-7), so that males were usually seen alone.

The standard deviation and the coefficient of variation of the association indices were significantly higher for the observed than for the randomized data ($P < 0.01$, Table 1). Thus, the null hypothesis that there are no preferential associations among males between sampling periods (days) was rejected.

The SLAR was higher than the SNAR for time lags less than approximately 1700 days (Fig. 2-3). Therefore, some pairs of individuals were more often associated than expected if association was random for periods of up to about 5 years. The SLAR was highest for short time lags, and decreased after approximately 100 days, indicating that many associations between individuals last for at least 3 months, the approximate duration of a field season. A model with a simple term of exponential decay in relationship strength best fitted the SLAR data (Table 2-2). The mean duration of association estimated from the best model is 968 days (inverse of exponential parameter; Table 2-2).

Twenty dyads were observed associated over more than two years (Table 2-3). The individual males NS-PM101 and NS-PM118 have been observed associated on 29 days over 4 different years (2011, 2013, 2015, and 2016). For 55 clusters with two or more individuals, I could identify all the individuals composing the cluster. Forty-one clustered pairs were identified, 6 of which formed a cluster more than once. These pairs were observed association over more than 2 years, and 5 of the 6 pairs observed in the same cluster multiple times had at least twice the mean association index of all dyads. The individuals NS-PM099 and NS-PM101 were observed associated on 19 different days in 3 different years and were observed in clusters together on 7 different days. On two of those occasions, August 27 and September 13, 2013, the whales NS-PM099 and NS-PM101 rubbed and rested together at the surface (Fig. 2-4).

2.4 Discussion

Long-term associations among male sperm whales

This study suggests that male sperm whales can form long-term associations. I note, however, that associations between male sperm whales in the Nemuro Strait (mean index = 0.130) are much lower than those within female social units (e.g., off the Galapagos Islands the mean index is 0.399, Christal & Whitehead 2001). This is despite the fact that the Galapagos study used a tighter definition of association for females (identified within 10min, Christal & Whitehead 2001). These findings strongly reinforce conclusions from previous studies that males are less social than females (e.g., Christal & Whitehead 1997, Lettevall et al. 2002).

On the other hand, the results also suggest that, although low, associations among some males in Nemuro Strait are not random. Male sperm whales are feeding relatively close to their preferred associates within the foraging ground where multiple males are dispersed. Letteval et al. (2002) found that association patterns of male sperm whales in 4 research areas were not significantly different from random. However, this does not necessarily mean that males in these study areas are not social. Considerable identification data are needed to detect preferred companionships (Whitehead 2007), especially when the rate of associations is low. Therefore, the apparent discrepancy between our results and those of

Letteval et al. (2002) may reflect the smaller dataset of the earlier study. Differences between sperm whales of different regions could also play a part. Whitehead et al. (2012) revealed a clear contrast in the social structures of female sperm whales between the eastern Pacific and North Atlantic Oceans, likely due to differences in predation pressure between the ocean basins (Whitehead et al. 2012). In addition, further investigation is needed to reveal whether the social structure varies geographically in males as well.

I also found that the male sperm whales associate for about 2.7 years on average. The timing and pattern of decline in their rates of association is similar to that of the lagged identification rate (probability that an animal is still in a study area after different time lags; Whitehead 2001; 2008) which indicated that the males stay for a mean of 2.1 years in the Strait (Kobayashi & Amano 2020). This suggests that the decline of association rates is unlikely to be caused only by dis-association among dyads, but instead is primarily caused by death or emigration to other areas by one member of the pairs. Therefore, preferred relationships among males could last for longer periods, more than 2.7 years, perhaps for 5 years, considering our findings that the empirical association rates were higher than the null expectancy for lags of about 5 years. Taken together, these results suggest that while male sperm whales are not as social as females, they have long-term relationships, preferred associations and forage in close spatial proximity.

In mid and high-latitude areas, males make repeated foraging dives lasting about 40 minutes, separated by about 7 minutes breathing at the surface (e.g., Whitehead et al. 1992, Jaquet et al. 2000, Wahlberg 2002). During those foraging dives, the usual echolocation clicks and slow clicks (thought to be communicative vocalizations of males) are produced (e.g., Wahlberg 2002; Madsen & Møhl 2000). Madsen and Møhl (2000) estimated that sperm whales may be able to hear each other at ranges of 16 km for usual clicks, and up to 60 km for slow clicks. Thus, pairs of males deemed to be associated were within the presumed audible range of echolocation clicks, and males might obtain information about prey distribution or feeding success from the echolocation clicks of others. Synchrony of horizontal movement among males in Nemuro Strait (Amano & Kobayashi, personal observation) and heading coordination within aggregations of males as reported by Christal and Whitehead (1997) may also be caused by such interaction among neighboring males while foraging. Christal and Whitehead (2001) suggested that a possible value of long-term relationship among females is communal sharing of information about resources of high uncertainty over their large home ranges. A similar function of "ecological enhancement" may also promote the long-term social relationships among males. However, since there are few observations of direct interactions during foraging dives between males, further study is needed to test this hypothesis.

Although pairs of male sperm whales which preferentially associate for long periods tend to be observed in close spatial proximity, most individual whales identified in Nemuro Strait are kilometers apart from one other. Males within long-term preferred social relationships sometimes gather and rest with their companions at the surface as females do. The association indices of pairs displaying such relationships tended to be higher. However, this cannot be rigorously statistically tested because the data are limited and there is a structural correlation between association index and frequency of clustering. Nevertheless, the data on identifications within clusters identified, while sparse, provide further evidence of social relationships between males across years.

Previous studies of male sociality from 4 different areas reported males usually alone at the surface with few clusters of 2 or more whales. Compared to our study, repeated resighting of clusters consisting of the same pair of individuals was much rarer and the interval of observations between these repeat clusters were quite short-term: from several tens of minutes to 3 days (Lettevall et al. 2002). Although further research is needed to explain the discrepancies between my results and these, one possible explanation for the low frequency of cluster resights is that whales clustered at the surface are often hard to identify since they often do not fluke up following social interactions as they do during foraging dives.

Female sperm whales form clusters near the surface almost every day to socialize and rest with members of their social units and with others within a larger, temporary group (Gordon 1987; Whitehead & Weilgart 1991). These behaviors may be important for maintaining the social bonds between members of a social unit after dispersion during foraging dives (Whitehead & Weilgart 1991). Though the frequency of forming clusters is lower than among females, males may also form clusters to maintain social bonds, suggesting that social life is still significant for males.

Cluster formation by males may also have a function as anti-predation behavior. Curé et al. (2013) reported that large males over 15 m long interrupted their foraging or resting dives and formed clusters with other males or produced coda vocalizations in response to playbacks of vocalizations from their major natural predator, the killer whale, *Orcinus orca*

(Whitehead 2003). Codas play a major role in communication among sperm whales, but codas have only rarely been recorded in the high latitude habitats of males (Wahlberg 2002; Madsen 2000; Madsen et al. 2002). These experimental results suggest that large males are not completely solitary and interact with neighboring males when threatened by predators. Cluster formation by resting whales may also have an anti-predator function (Whitehead 2003). Hence, predation pressure, probably by killer whales, may play an important role in promoting social relationships between males. In addition, cohesive bachelor schools observed by whalers and scientists during the modern whaling period (e.g., Gaskin 1970; Ohsumi 1971; Best 1979) might have a similar root, with animals responding to the presence of whaling ships. In recent centuries, the most dangerous predators for sperm whales have been humans not killer whales. At sperm whaling's peak, over 20,000 animals per year were caught globally (from Best 1983), and about 2,000 animals were also killed every year by Japanese coastal whaling during the late 1960s (Kasuya 1999). Although many scientists (e.g., Gaskin 1970; Ohsumi 1971; Best 1979) and whalers described cohesive "bachelor schools" of male sperm whales, there have been few observations of such groupings during studies of living animals following the whaling period (Lettevall et al. 2002). Hunting has likely affected not only sperm whale populations but also their behavior.

Long-term associations in male mammals

This study found social relationships among non-breeding male sperm whales and suggests that they may be important. Long-term relationships between non-reproductive (and generally unrelated) males are rare among mammals. Often, in non-solitary mammalian species, reproductive-age males live with females, either as monogamous pairs (e.g., prosimians, gibbons), as members of well-structured closed groups (e.g., most primates, lions, horses), or larger, looser, more promiscuous groupings (e.g., some larger ungulates, dolphins) (Clutton-Brock1989). The males within groups may have relationships, sometimes strong and important relationships, but they are thought to be based on the enhancement of reproductive success (e.g., chimpanzees: Mitani et al. 2000). When males live largely apart from females, there may also form strong bonds which function during breeding attempts, for instance as alliances (e.g., bottlenose dolphins: Connor et al. 1992). However, strong relationships among non-breeding males without females being present or in prospect seem rare especially when males are unrelated.

A possible exception is the African elephant (*Loxodonta africana*) which has a similar life history to the sperm whale (see Best 1979, Weilgart et al. 1996), although the motivation of association between males may be much different from that of sperm whales. After leaving their maternal units, male elephants tend to associate with males about the same age sometimes acting as sparring partners, or with older bulls who may be reservoirs of social and ecological knowledge within breeding herds (Evans & Harris 2008). Male elephants' associations are positively correlated with genetic relatedness (Chiyo et al. 2011) unlike sperm whales which associate with unrelated males of the same size. These difference show that associations among non-breeding male elephants may more directly function in increasing mating success than is the case with sperm whales where geographical segregation between the sexes is much more extreme (1,000s km for sperm whales; 10s km for elephants).

Conclusion

Beyond mammals, I know of no evidence of long-term bonds between unrelated non-breeding males in birds, reptiles or amphibians. Some instances may have been missed by scientific studies, or by us when surveying the literature. However, such cases are almost certainly very rare. Sperm whales seem to be an unusual species in which male bonds are not based on reproduction or kinship. This sociality may be promoted by the importance of cooperation in a pelagic habitat (likely for cooperative foraging or anti-predation) and the extreme spatial separation of the two sexes for prolonged periods in a species which is otherwise highly social. To understand the social structure of male sperm whales more deeply, relationships between male sperm whales should be examined for longer periods of time, in additional study sites, over a wider range of ages, and in more behavioral detail.

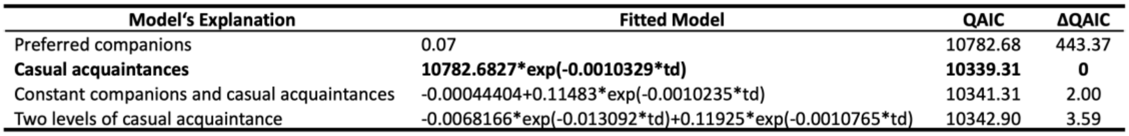
2.5 Tables and Figures

Table 2-1. Permutation test for preferential association between single day periods

	Observed data	Random data	P-value
SD of mean association index	0.03248	0.03134	0.0071
CV of mean association index	8.69431	8.42104	0.0002

Table 2-2.Exponential decay models fitted to the standardized lagged association rate among male sperm whales in the Nemuro Strait

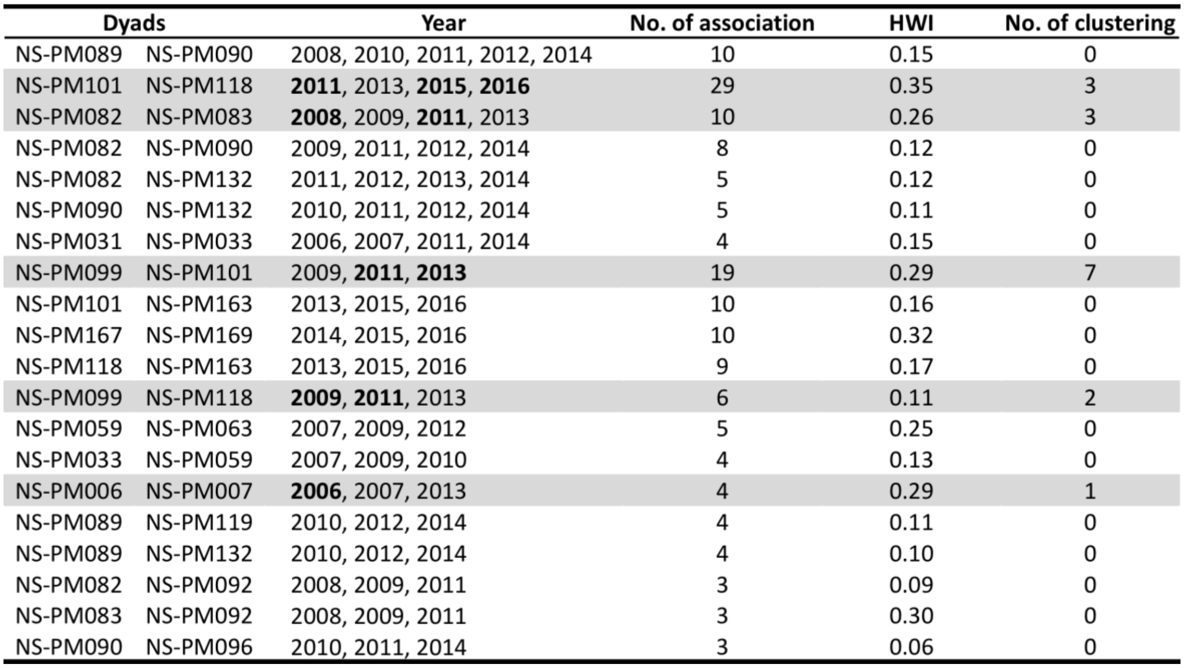
The lowest Quasi Akaike Information Criterion value (QAIC) indicates the best-fitted model. ∆QAIC is the difference between the QAIC for the current model and best-fitted model. Duration of association estimated from the best model is 968 days.



Model's Explanation	Fitted Model	QAIC	∆QAIC
Preferred companions	0.07	10782.68	443.37
Casual acquaintances	**10782.6827*exp(-0.0010329*td)**	**10339.31**	**0**
Constant companions and casual acquaintances	-0.00044404+0.11483*exp(-0.0010235*td)	10341.31	2.00
Two levels of casual acquaintance	-0.0068166*exp(-0.013092*td)+0.11925*exp(-0.0010765*td)	10342.90	3.59

Table 2-3. Twenty dyads observed associated during more than 2 years

Bold shows years which the dyads were observed in the same cluster.



Dyads		Year	No. of association	HWI	No. of clustering
NS-PM089	NS-PM090	2008, 2010, 2011, 2012, 2014	10	0.15	0
NS-PM101	NS-PM118	**2011**, 2013, **2015**, **2016**	29	0.35	3
NS-PM082	NS-PM083	**2008**, 2009, **2011**, 2013	10	0.26	3
NS-PM082	NS-PM090	2009, 2011, 2012, 2014	8	0.12	0
NS-PM082	NS-PM132	2011, 2012, 2013, 2014	5	0.12	0
NS-PM090	NS-PM132	2010, 2011, 2012, 2014	5	0.11	0
NS-PM031	NS-PM033	2006, 2007, 2011, 2014	4	0.15	0
NS-PM099	NS-PM101	2009, **2011**, **2013**	19	0.29	7
NS-PM101	NS-PM163	2013, 2015, 2016	10	0.16	0
NS-PM167	NS-PM169	2014, 2015, 2016	10	0.32	0
NS-PM118	NS-PM163	2013, 2015, 2016	9	0.17	0
NS-PM099	NS-PM118	**2009**, **2011**, 2013	6	0.11	2
NS-PM059	NS-PM063	2007, 2009, 2012	5	0.25	0
NS-PM033	NS-PM059	2007, 2009, 2010	4	0.13	0
NS-PM006	NS-PM007	**2006**, 2007, 2013	4	0.29	1
NS-PM089	NS-PM119	2010, 2012, 2014	4	0.11	0
NS-PM089	NS-PM132	2010, 2012, 2014	4	0.10	0
NS-PM082	NS-PM092	2008, 2009, 2011	3	0.09	0
NS-PM083	NS-PM092	2008, 2009, 2011	3	0.30	0
NS-PM090	NS-PM096	2010, 2011, 2014	3	0.06	0

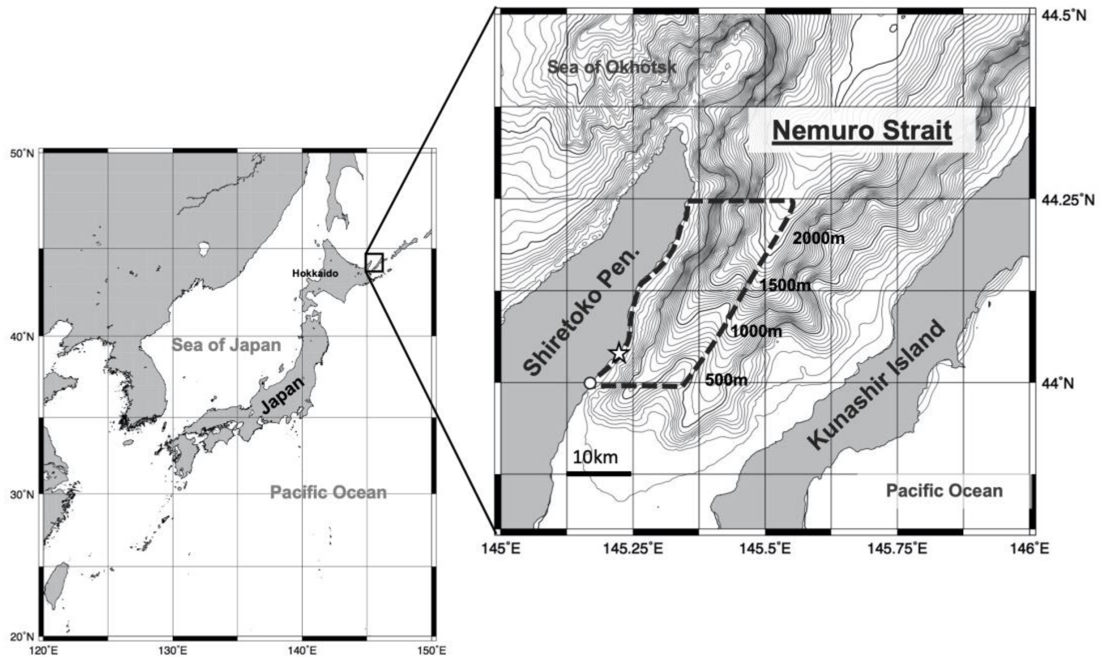


Fig. 2-1. Map of the location of Nemuro Strait, Hokkaido, Japan

Broken line shows the range of study area, and open circles indicates position of "Rausu Fishing Port" (departure point of whale-watching boat). Open star shows the "Whale View Park" (theodolite station, see S1 Figure). The maps were created by using GMT: The Generic Mapping Tools (ver. 5.4.5; https://www.generic-mapping-tools.org/, Wessel et al. 2013), and the depth contours were created on GMT based on "500m Gridded Bathymetry Data" provided by Japan Coast Guard (https://jdoss1.jodc.go.jp/vpage/depth500_file.html).

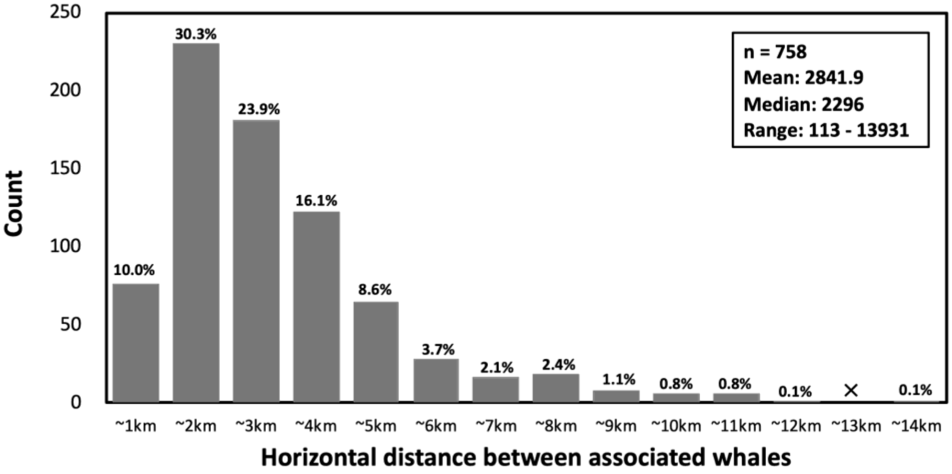


Fig. 2-2. Distribution of horizontal distance between locations of observations of associating whales (identified within 1 hour) from the research vessel

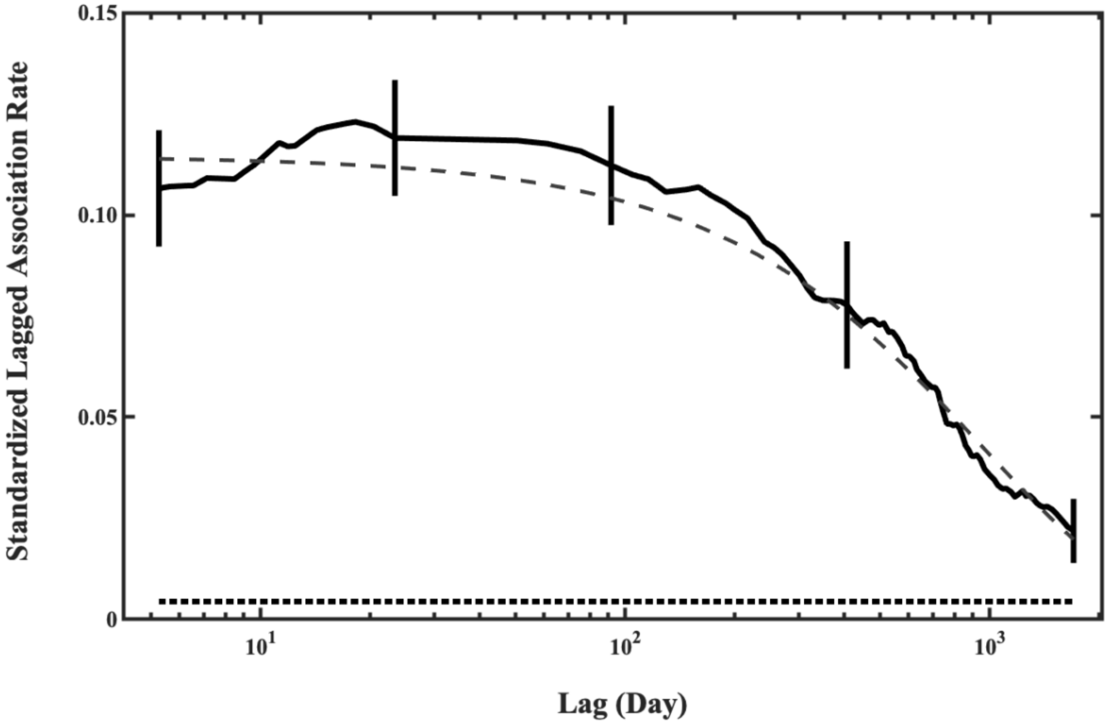


Fig. 2-3. Standardized lagged association rate for males in the Nemuro Strait, with jack-knifed estimates of precision

The SLAR (black line), SNAR (dot line; the theoretical SLAR if the individuals are randomly associated) and best-fitting model (broken line) are shown for the males in Nemuro Strait.

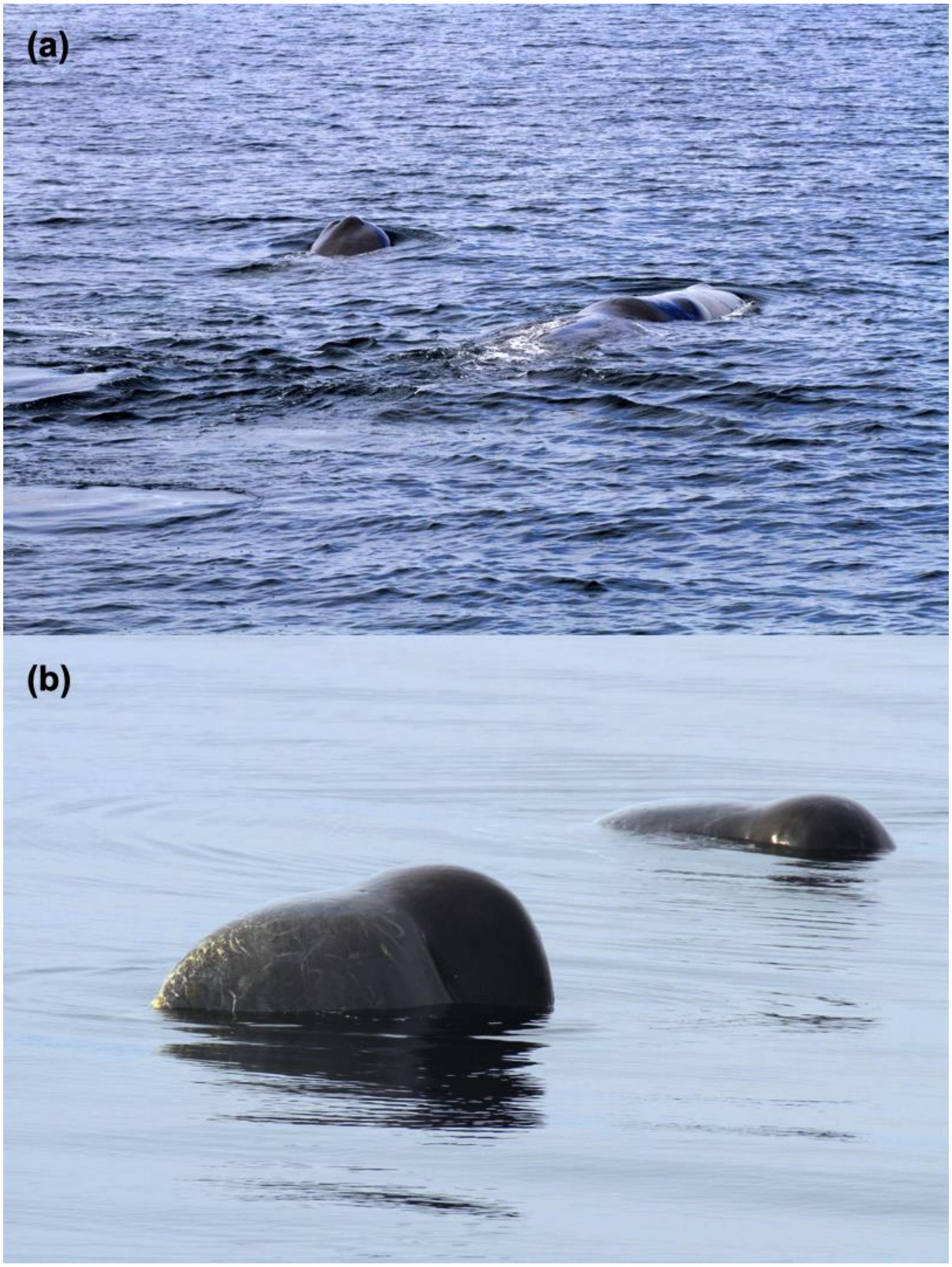
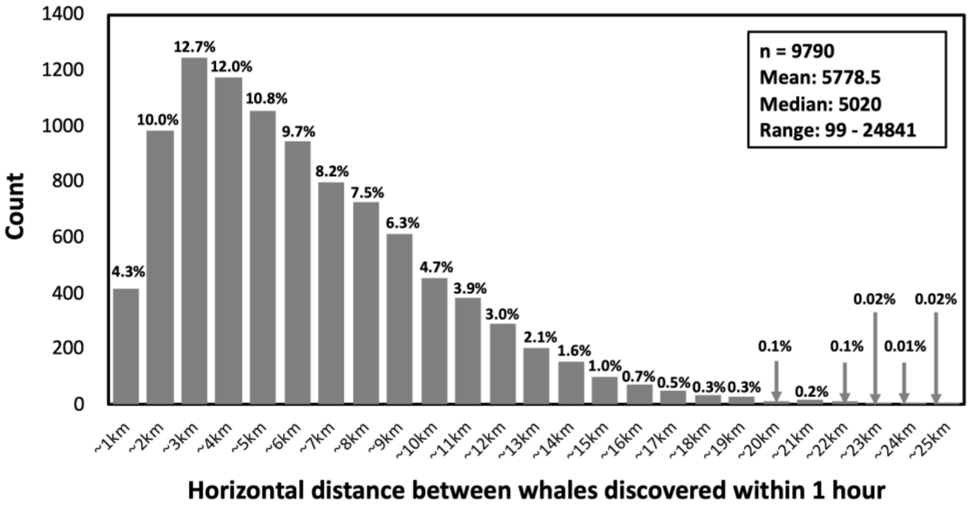
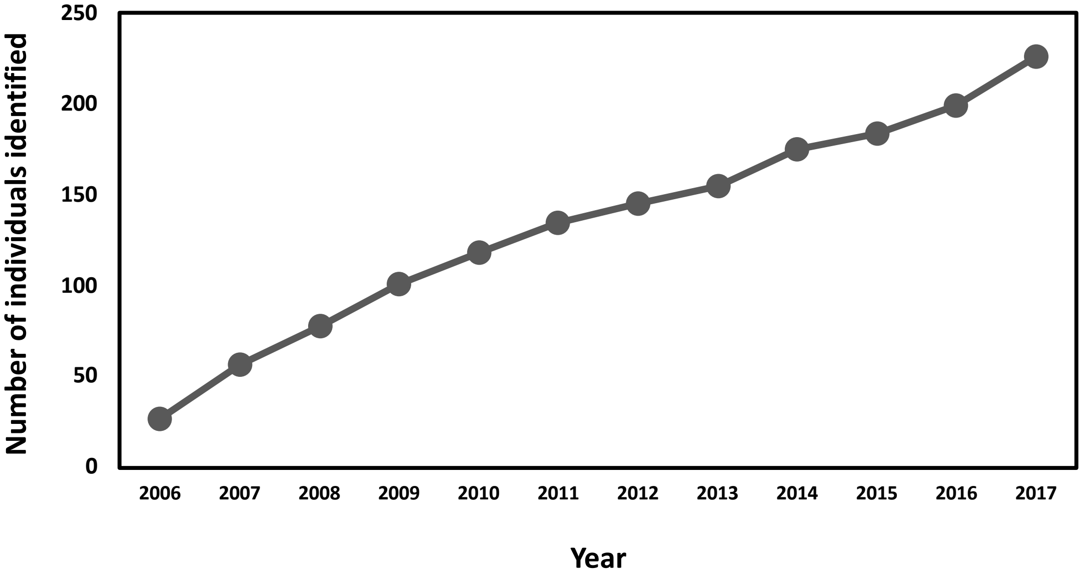


Fig. 2-4. Two resting male sperm whales (NS-PM099 and NS-PM101) photographed on (a) August 27 and (B) September 13, 2013



Supplement 2-2. The distribution of horizontal distance between whales observed within 1 hour from land-based survey

Surveys were carried out from the Whale View Park in Rausu Town, Hokkaido, Japan (44°02'N, 145°13'E; 73 m above sea level) on 256 days from 2010 to 2019. Observation range is about 15 nmi, which substantially coincides with the range of photo-identification research. Four observers search for whales using binoculars (Nikon MONARCH 12×42) and the position of each whale was recorded using digital theodolite (SOKKIA DT5). The distances between whales identified within 1 hour were calculated using the data collected during the 139 days for which the visibility was over 10 nmi and Beaufort Wind Scale was less than 5).



Supplement 2-2. Discovery curves for individuals identified in Nermuro Strait between 2006 and 2017

Chapter 3   Decreasing Sociality with Body Size

3.1 Introduction

Strong and stable social bonds between males have been reported in some promiscuous mammals as a way of increasing access to females (e.g., lions: Packer & Pusey 1982; cheetahs: Caro & Collins 1987; Marnewick & Cilliers 2006) or defending estrous females (chimpanzee: Mitani et al. 2000; bottlenose dolphins: Connor et al. 1992). However, in general, male relationships tend to be competitive (van Hooff & van Schaik 1994). Although males of polygynous mammals such as several ungulates species (e.g., bighorn sheep, *Ovis canadensis*: Mooring et al. 2003; white-tailed deer, *Odocoileus virginianus*: Kie & Bowyer 1999) and primates (e.g., hanuman langurs, *Semnopithecus entellus*: Sugiyama et al. 1996) form all-male groups, the relationships between males within the groups are typically looser and more labile than within mixed-sex groups of the same species. This may result from these all-male groups being primarily a temporary residence for males who are currently unable to breed, and the benefit of this group formation is not particularly significant. Long-term associations within labile all-male groups (e.g., African elephants: Douglas-Hamilton et al. 2001) and stable all-male group (e.g., mountain gorilla, *Gorilla gorilla beringei*: Yamagiwa 1987) are reported in a few species.

Sperm whales also seem to form stable all-male groups not directly related to reproduction. Males leave their natal social unit before sexual maturity (~6-16 years old) and are found in all-male groups (Best 1979; Whitehead 2003). The relationships within the all-male groups may be quite different from those in alliances or coalitions which relate to defense of females or territory, because males do not seem to play an active role in reproduction until at least their late twenties, and before that age are generally well separated from groups of females (Best et al. 1984; Whitehead 2003). During the modern whaling period, scientists and whalers (e.g., Gaskin 1970; Ohsumi 1971; Best 1979) described all-male groups of the sperm whales which they called “bachelor schools”. Bachelor schools consist of animals about the same size; the differences in length between the biggest animal and the smallest animal in a bachelor school were typically within 1.8 m (Best 1979). The number of animals within a bachelor school was found to be negatively correlated with the mean body length of the school members suggesting that the sizes of bachelor schools became smaller as members grew older, until finally (over 20 years after leaving their natal unit) males were often found alone or in pairs (Best 1979). These conclusions about the sociality of non-breeding male sperm whales were based on brief observations from the board of whaling vessels and analyses of whales caught during the whaling period, therefore results of previous studies might not be reflected the nature of males’ group. The fact that there are few data about cohesive male group from present-day studies of living sperm whales (Whitehead 2003) also suggest what was observed during whaling might not be natural. More recently, male sperm whales have been observed repeating foraging dive dispersed over large areas (over a few km between neighboring individuals on average) and are found most often alone at the surface. Thus, we do not yet have a good understanding of the nature of bachelor schools, including how the group sizes of bachelor schools change with the size of their members. Long-term studies of individually-identified animals are required to understand the true nature of male society. In Chapter 3, I found the changes in social relationships with growth among male sperm whales and discuss explanations for why the size of these unusual all-male groups decreases with age.

3.2 Methods

Field methods

(i) Nemuro Strait, Hokkaido, Japan

Field work was conducted in Nemuro Strait (43.580°N, 145.100-145.150°E, 44.200°N, 145.230-145.350°E; Fig. 3-1) during summer field seasons (mainly between July and September) over 12 years (from 2006 to 2017, a total of 890 days). Individual identification and body length data of male sperm whales were collected during field surveys aboard five commercial whale-watching boats in the Strait.

(ii) Goto Submarine Canyon, Nagasaki, Japan

I also carried out a photo identification survey in Goto Submarine Canyon (32.017°-32.050° N, 128.100°-129.000° E, Fig. 3-1), which is about 50 km south of Goto Islands, Nagasaki Prefecture. Male sperm whales migrate to this area from March to August. Research cruises were carried from 2013 to 2017 using “*Kakuyo-maru*” (training ship of Nagasaki University Faculty of Fisheries, 63 m long) and “*Miu*” (dive boat, 16 m long).

Individual identification

The individual identification methods are as described in detail in Chapter 1. Only photographs of Q≧4 were included in the following analyses.

Body length measurement

Whales were measured using single-camera photogrammetric methods (see Gordon 1990; Jaquet 2006). To estimate the fluke width and head (blowhole-dorsal fin) length, I measured the distance from the camera to whale using laser-rangefinder (Bushnell Pro 1600, Bushnell Inc.). The body or fluke length in the image were measured using Image J ver. 1.51 (U. S. National Institutes of Health, Bethesda, Maryland, USA, https://imagej.nih.gov/ij/, see Rasband 1997). The total length of the whales was estimated based on proportion of each part to total length (Total length = 0.3875 + 1.679 * Head - 0.015 * Head^2, Gordon 1990, Log (Total length) = 0.9268 * Log (Fluke width) + 0.605, Jaquet 2006). Because these photogrammetric methods tend to underestimate size (Jaquet 2006), I used the maximum estimated body length of animals from which body length estimates were made more than once within two years from the last observation.

Data Analysis

In this chapter, I considered whales associated if they were identified within 1 hour of each other from the same boat (see Chapter 2). A one-day sampling period was used along with the half-weight index (HWI, Whitehead 2008), as this measure of association accounts best for observer biases that are common when using basic photo-identification techniques. To describe male sociality, we calculated the maximum association index (a measure of how well associated a whale was with its most common associate), and association strength (a measure of gregariousness, closely related to the typical group size). These measures are defined by previous studies (Whitehead 2008; Whitehead 2009; Lusseau et al. 2008). All social analyses were conducted with SOCPROG 2.8 (Whitehead 2009), and I performed Spearman's rank correlation test between each statistic and body length using R version 3.47 (R Development Core Team 2013).

3.3 Results

I obtained 2,969 identifications of 226 male sperm whales on 608 different days in Nemuro Strait, and 275 identifications of 24 individuals on 29 different days in Goto Submarine Canyon. A total of 58 animals (49 animals from Nemuro Strait; 9 animals from Goto Submarine Canyon) were measured for body length. The mean size among males in Nemuro Strait was 15.8 m (minimum = 12.4 m, maximum = 18.6 m), and in Goto Submarine Canyon was 11.6 m (minimum = 9.5 m, maximum = 14.6 m).

Data from 45 animals (40 animals from Nemuro Strait, and 5 animals from Goto Submarine Canyon), that were identified on more than 5 days and had their body length measured more than once, were used in the following analyses. The association strength (a measure of gregariousness, closely related to the typical group size) and maximum association indices (a measure of how well associated a whale was with its most common associate) were calculated based on HWI for each individual. We found significant negative correlation between association strength and body length (Spearman's rank correlation: ρ= -0.474, p = 0.001; Fig. 3-2a), with marginal significance among males larger than 14 m (Spearman's rank correlation: ρ= -0.306, p = 0.055; Fig. 3-2b). Maximum association index also decreased with body length (Spearman's rank correlation: ρ= -0.333, p = 0.026; Fig. 3-3a), but this relationship was no longer significant for animals larger than

14 m (Spearman's rank correlation: ρ= -0.177, p = 0.275; Fig. 3-3b). The average of association strength is 1.89 among males less than 14 m and 1.05 among males over 14 m.

3.4 Discussion

I found that the association strength of male sperm whales was negatively correlated with body length. This indicates that male associations weaken with growth. Although we had a few data for males less than 14 m in length, association strengths of young males were in a similar range as females and calves within their natal social unit (Gero et al. 2013). This suggests that immature or maturing males have close relationships. The decline of association strength was likely to start around the length of 13 m. Best (1969) found that males sperm whales reach puberty at a length of approximately 39 ft (= 11.9 m) and sexual maturity at a length of around 45 ft (= 13.7 m) based on a histological study of the testis, thus the results suggest that male sperm whales become less social, especially just around sexual maturity.

Fig. 3-2 also showed that the number of approximate associates reduced from two (when less than 14 m) to one (when 16 m or larger). Although we cannot directly compared the gregariousness estimates based on temporal association with the group size of bachelor school observed directly on board because the size and spatial scale of group were different, this study confirmed a decrease in group size of male sperm whales with members' growth as reported by multiple authors during the whaling period.

The decline of maximum association indices showed that the relationships between males associated most frequently were also weaken, however the indices were uncorrelated with body length after sexual maturity. Kobayashi, Whitehead, & Amano (in press, see Chapter 2) found that large males in Nemuro Strait did not randomly associated with other males, and the preferred associations between males may remain stable for at least 3 years (and probably more than 5 years). The low correlation between maximum association indices and body length in large males may reflect these long-term associations between mature males.

Although the drivers behind this decrease in male sperm whale sociality are still unknown, here I discuss possible scenarios. As the body length at which this change happens approximately coincides with the body length at sexual maturity, some endocrinal change, such as the rise of testosterone levels, may be implicated in the decline in sociality (Best 1969; Whitehead & Weilgart 2000). Testosterone induces spermatogenesis (Brown & Follett 1977), the development of some secondary sexual characteristics (Wingfield & Farner 1980) and changes in behaviors (Balthazart 1983). There has been much study of male reproductive function and competition among males in relation to testosterone level (e.g., Anestis 2006); high testosterone levels may affect dominance and social relationships through aggression (Muller & Wragham 2004). However, in sperm whales there is a gap of more than 10 years between sexual maturity and sociological maturity (when males become prime breeders) (Best 1979; Whitehead 2003), and no females are found at or near study sites. Thus, mating competition cannot directly explain my finding of decreasing sociality.

As male sperm whales grow, the cost-benefit balance of sociality will change. In the Chapter 2, I suggested that associations among male sperm whales may function to enhance foraging through cooperation, cooperative foraging being a frequent benefit of group living.

On the other hand, competition for food resources is the most obvious cost of group formation and seems to explain group size in various mammal species including primates (Janson & Goldsmith 1995), and cetaceans (Baird & Dill 1996). Sperm whales show a typical two-stage growth pattern (Best 1970), and secondary growth around puberty may raise the cost of group living. Maturing male sperm whales need high energetic returns from foraging to obtain and maintain their great size, which may ultimately determine their access to females on the breeding grounds (Whitehead 1994). It is estimated that sperm whales eat 3-4 % of their body weight per day (Rice 1989). Assuming that body weights of sperm whales 10 m (immature or maturing) and 15 m (sexually mature) long (Best 1984) are 9.1 t, and 32.9 t (based on mass (kg) = 0.000137 Length (ft) $^{3.18}$, Omura 1950), daily prey consumptions are about 272.1 kg, and 987.7 kg respectively (Fig. 3-4). This suggests that mature males need more than three times as much prey as younger males who have recently left their natal group. Sexual maturity might, therefore, exacerbate foraging competition between males and thus induce a reduction in sociality.

In addition to these increasing costs, a decrease in the benefits of group-living and the need for cooperation may also influence group size. Male sperm whales grow rapidly after puberty, with the differential growth and development of the head being significant (Nishiwaki et al. 1963). Adipose tissue, the “spermaceti organ”, inside the large head functions as a resonance chamber to make the very powerful and highly directional clicks (Madsen 2002; Cranford 1999). A larger head can produce a louder sound (Cranford 1999), and so the large male may be able to search for prey more widely using these strong echolocation clicks. The increasingly powerful search capabilities of growing males reduce the benefits of cooperation. Furthermore, migrating to more productive high latitudes and developing efficient foraging dive behavior (Teloni et al. 2008) may also promote independence.

Another benefit of group living that likely decreases with size is cooperative defense (Birkhead 1977) and the dilution effect (Foster & Treherne 1981) when faced by predators. The primary natural enemy of sperm whales is the killer whale (Rice 1989; Jefferson et al. 1991). There are no reports of attacks by killer whales on adult male sperm whales, which may relate to their size and/or the power of their acoustic systems. However, playback of sounds of mammal-feeding killer whales sounds induced social interactions between male sperm whales over 15 m long (Curé et al. 2013). Hence, large males may not be completely freed from predation risks from the killer whale. However, smaller males would have much higher predation risk than that of large bulls. Hence, a decrease in the predation risk associated with secondary growth may also influence the sociality of male sperm whales.

In this study I described the decrease in sociality of male sperm whales after sexual maturity, which corresponds to the reduction of group size reported by whalers. At the proximate level, this decrease of sociality might be caused by physiological maturation and changing hormone levels. Functional drivers likely relate to changing costs and benefits of group living (especially in relation to cooperative foraging) that accompany the secondary growth spurt. Additional data on young males before sexual maturity would help understanding of these changes.

3.5 Tables and Figures

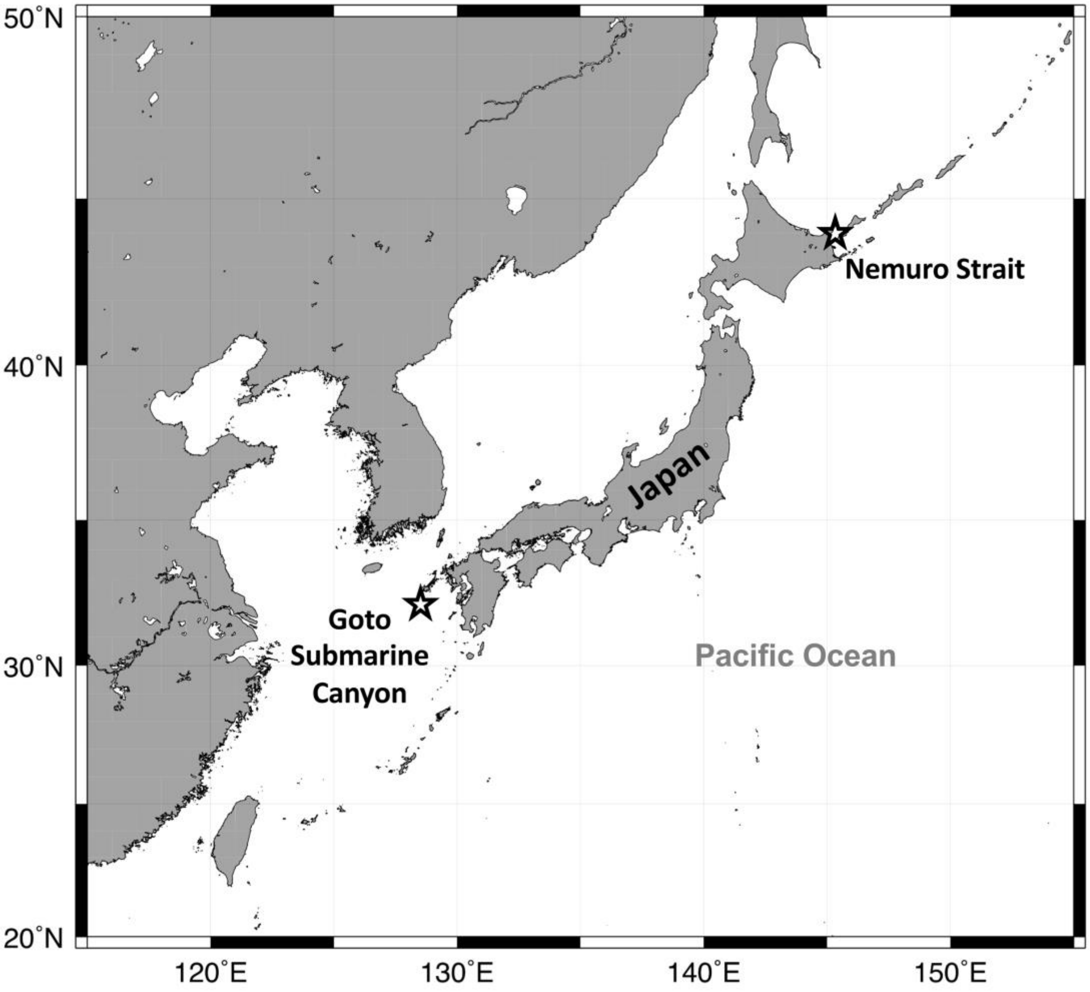


Fig. 3-1. Study area showing the location of Nemuro Strait and Goto Submarine Canyon study sites

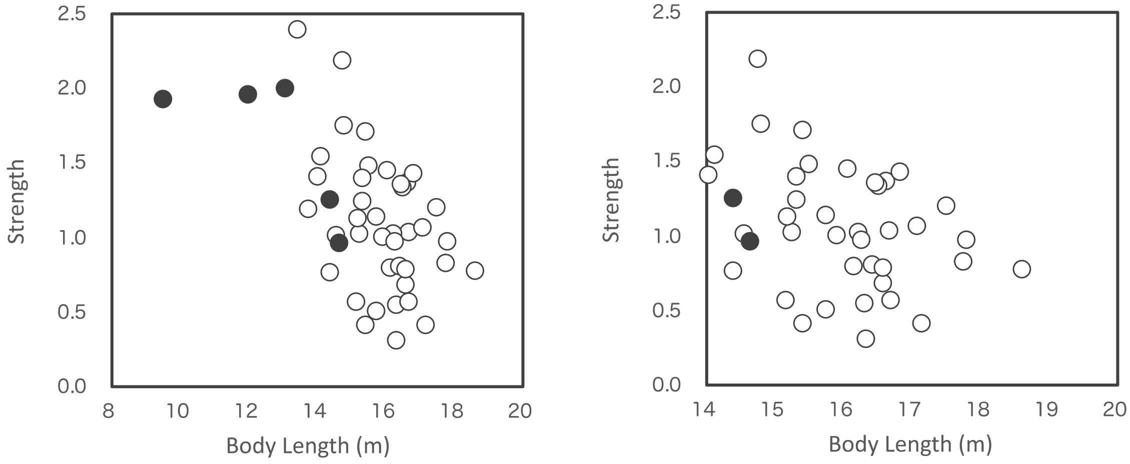


Fig. 3-2. Relationships between body length and association strength among (a) all males (Spearman's rank correlation: ρ= -0.474, p = 0.001) and (b) large males (Spearman's rank correlation: ρ= -0.306, p = 0.055)

The filled circles (●) are males in Goto Submarine Canyon and open circles (○) are males in Nemuro Strait.

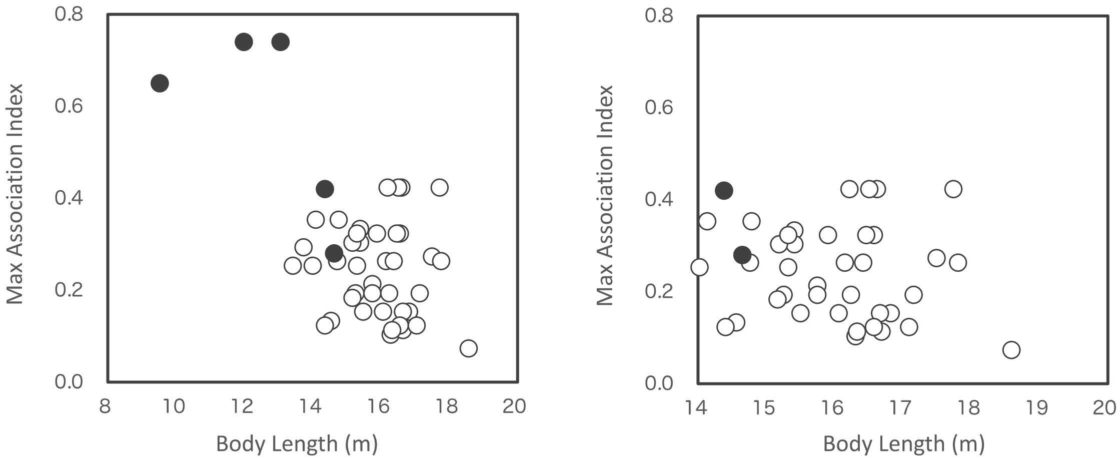


Fig. 3-3. Relationships between body length and maximum association indices among (a) all males (Spearman's rank correlation: ρ= -0.333, p = 0.026) and (b) large males (Spearman's rank correlation: ρ= -0.177, p = 0.275)

The filled circles (●) are males in Goto Submarine Canyon and open circles (○) are males in Nemuro Strait.

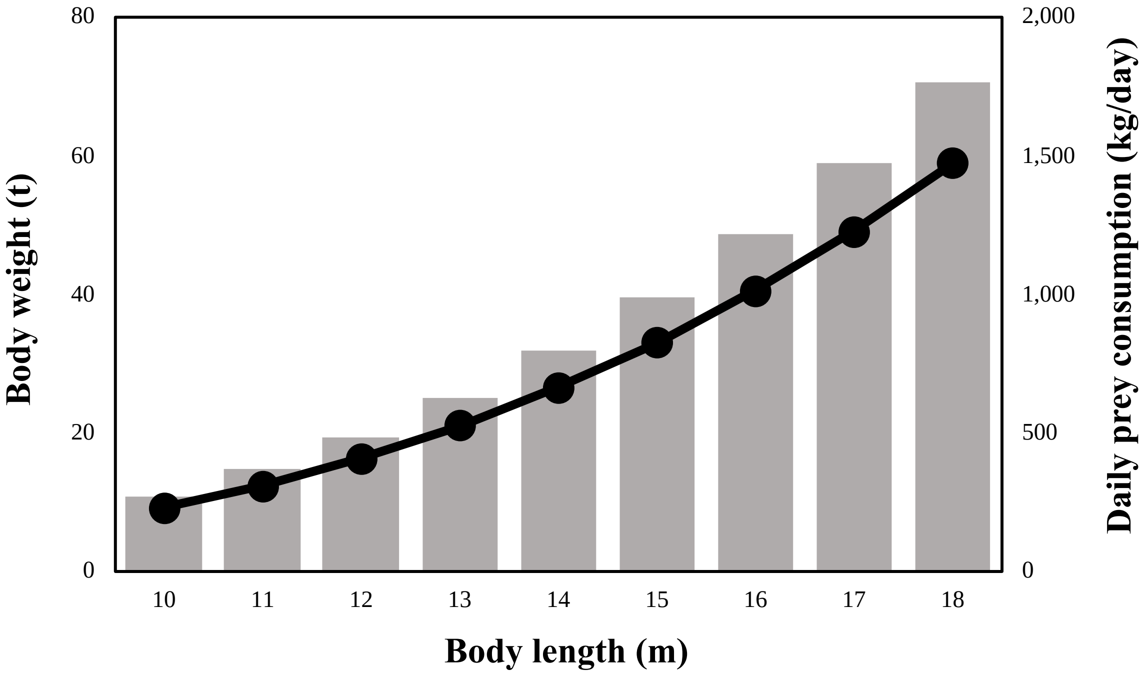


Fig. 3-4. Relationships between body length, body weight, and daily prey consumptions.

Body weight was calculated using Omura (1950)'s formula, and daily prey consumption was estimated as 3% of body weight (Rice 1989).

Chapter 4 GENERAL DISCUSSION

4.1 A Review of Results

In this study, I examined the residence patterns (Chapter 1), preference and temporal patterns of association (Chapter 2), and changes in relationships with age (Chapter 3) in male sperm whales in the Nemuro Strait and Goto Submarine Canyon, Japan, to understand their social structure.

In chapter 2, I examined the association patterns among males using long-term photo-identification data obtained in Nemuro Strait. I found that the association index among males is lower than that of females. This suggests that, in this context, male sperm whales are less social than females. On the other hand, the results also show that males in close spatial proximity have preferred companionships and, therefore, that males tend to dive and forage near preferred associates. Temporal pattern of association models (standard lagged association rates) suggest that the preferred association between males last for at least 2.7 years on average, 5 years maximum. The mean duration of associations approximately coincides with residence time in the study area (as suggested in Chapter 1). This indicates that the decline of SLARs is unlikely to be caused by dis-association among dyads, but instead, is primarily caused by emigration to other areas by one or both members of the pairs. Therefore, the preferred association among males lasts at least throughout their residence time in the study area, with potential for longer relationships in the order of decades. In addition, although the data is limited and sparse, males with long-term preferred companionships have been observed occasionally interacting directly at the surface and resting together within their cluster, which suggest that social interactions occur among members of such associations.

In chapter 3, I examined the correlation between body length and association indices and network measures using photo-identification data from two study sites (Goto Submarine Canyon and Nemuro Strait). The results show that immature or maturing males have strong relationships but that gregariousness rapidly decreases around sexual maturity. The strength of association between males also frequently decreased, although, the indices were uncorrelated with body length after sexual maturity. These results suggest that males leaving natal social units form male groups with long-term social relationships, but that the strength of those relationships and the size of those groups decrease around sexual maturity. Such decline does not appear to be caused by members’ death by predation or disease but instead increased asociality.

4.2 Social Structure of Male Sperm Whales

The results of my dissertation suggest that some relationships among male sperm whales are not temporal or accidental but persist over several years, perhaps a decade or longer. Such long-term relationships seem to be at the core of male sperm whale society. Long-term pairs lasting for a long time sometimes form a cluster. However, the frequency of cluster formation is clearly lower than that of females. The clustering seems to be more frequent among young males and they often interact directly within the cluster (Kobayashi et al. personal observation).

Although further studies are needed, I presume that male groups typically consist of a few animals, since the number of associates suggested by gregariousness is one or two (Chapter 3). It is possible that males also interact acoustically with other males who are farther away within the study area, resulting in larger group sizes than reported here, but this is unlikely. Other studies around the world corroborate these results. For example, Letteval et al. (2002) documented small male cluster sizes of two or three individuals. In Nemuro Strait, modal cluster size is two and maximum cluster size was seven until 2017 (an exceptionally large cluster was observed in 2019, more on this in following sections). Altogether this suggests that the group size of long-term male associates is small, at least at or after sexual maturity. This is similar to results from the whaling period (e.g., Best 1979). Therefore, multiple long-lasting groups (or pairs) may be present within males observed in our study areas on the same day or within aggregation reported previously. Although further studies are needed to reveal group interactions and potential hierarchal social structure, display of coordinated movement from members of the group (or pair) suggest that they may fulfill a certain function. Immature or maturing males may form larger groups than matured males since younger males show higher gregariousness. However, such groups may not be as large as “bachelor schools”, which consist of 12-15 males (Best 1979). Bachelor school might comprise multiple inner groups too, associating temporarily. This will be discussed in the following section.

4.3 Ecological factors driving the long-term relationships between males

In this section, I will try to discuss potential ecological factors driving the formation of long-term relationships among male sperm whales. Considering the life history and sexual segregation of sperm whales, group formation likely serves a purpose in increasing survival until the onset of mating opportunities (their thirties or later) rather than short-term reproductive success. Here, I discuss two potentially important factors: feeding success and anti-predation.

(1) Feeding success

Sperm whales spend most of their time (about 75% of the day, e.g., Amano & Yoshioka 2003; Watwood et al. 2006; Aoki et al. 2007) performing foraging dives. Although diving patterns differ across regions (e.g., Aoki et al. 2007), and cultural clans (Cantor et al. 2015), dives are often performed in a u-shaped pattern at depths over 400 meters for about 40-60 minutes. Around 90 seconds after the start of the dive, when the whale is about 200 meters deep (Johnson and Tyack 2003), sperm whales start producing echolocation clicks called “usual clicks”. Inter-click interval (ICI) is the time from one click to the next (Au et al. 1993). It is a good indicator for the maximum search range (Verfuβ 2005) as it correlates to search distance. The maximum search range of females or juveniles estimated from ICI is 380-490 meters (Whitehead 2003).

During foraging, groups of females and offspring often spread out in line. This is usually called “rank” or “feeding rank”, and, in most cases, the angle of “rank” is vertical to the direction of movement (Whitehead 1989; 2003). The length of the “rank” is about 1 kilometer (Whitehead 2003). It is considered that females share information about prey distribution through the forming the "rank" (Whitehead 1989).

In contrast, males are found in aggregation across 10-30 kilometers (e.g., Gllespie 1997; Leaper and Scheidat 1998; Letteval et al. 2002) and seem to generally forage independently (Whitehead 2018). However, males within aggregation tended to move coordinately and showed consistent heading, mostly within about 20°of the modal heading of the aggregation on the day (Christal 1998). It is unclear whether males' coordinated movements are a response to external factors such as the distribution of prey or geographical features. In Nemuro Strait, coordinated horizontal movement among males across the entire study area was observed (personal observation). Nemuro Strait is a feeding ground for male sperm whales, and, in the strait, males repeat 40-60 minute foraging dives between surfacing of 7-8 minutes. The mean horizontal distance between males assumed to be associated (identified within 1 hour from the same boat) is about 2.8 km and it is much shorter than the mean distance among all males detected from the land using digital theodolite within 1 hour (Chapter 2). The findings that neighboring males were preferred associates suggest that males tend to feed nearby preferred associates, thus, some interaction or cooperation which relates to foraging may be present among males.

However, remains the question of how male sperm whales interact or cooperate during foraging. My dissertation (Chapter 2) and previous studies (e.g., Letteval et al. 2002; Whitehead et al. 1991) showed that males are often observed alone in the study area. Mean horizontal distance between males assumed associated is 2.8 km, and fewer observation of males within 1 km (Chapter 2, Fig. 2-2) suggest that male sperm whale foraging strategy is unlikely to be the same as the prey-chasing cooperative foraging of pelagic dolphins (e.g., Benoit-Bird & Au 2009) and the “bubble-net feeding” of humpback whales (e.g., Friedlaender et al. 2011). The audible range of a hydrophones is 16 km for “usual clicks” and 6 km for “creaks” (Whitehead 2003 data from Madsen 2002). Male sperm whales can hear clicks from individuals beyond this area and, therefore, males assumed to be associated are well within audible range of not only usual clicks, but also creaks, which are a signal of prey capture. Therefore, males may use the clicks and creaks of others to obtain information about prey distribution, prey abundance, and the feeding success of other males.

Madsen et al. (2002) suggested that males sperm whales can use eavesdropping to locate the prey patches. Although eavesdropping can appear to be one-sided, and therefore not require interactions in the short-term, it could promote the formation of aggregations of male sperm whales and cause coordinate headings. Fais et al. (2015) examined the relationship between diving depth and ICI, by attaching the D-tag to Norwegian male sperm whales. They suggested that male sperm whales determine the diving depth at the onset of the dive and change their searching behavior depending on the dive depth. In this study, the authors emphasized that sperm whales select their new foraging layer based on, not their neighbors’ echolocation, but their own foraging success in previous dives and their outstanding echolocation ability which can search a wide range and multiple prey patches. Inter-individual distance of a few kilometers seems too wide for a detailed communal share of prey information. However, it may be sufficiently useful in sharing the rough information regarding the feeding area, with males obtaining information on the quality of foraging from neighboring individuals. Too short an inter-individual distance may have the disadvantage of reducing searching efficiency and increasing competition in prey patches. In Nemuro Strait, males seem to arrange the distance between individuals (about 2 km) so that they do not get too close, while still allowing communication (Kobayashi and Amano unpublished). Schakner et al. (2014) suggested that depredation from longline fishing by male sperm whales may be transmitted through social learning by examining the spread pattern of depredation behavior in the Gulf of Alaska. Although the exact mechanism responsible for the spread of the depredation behavior is still up for debate, it seems to support my hypothesis that males share prey information with their associates.

The results of Chapter 3 suggest that male sperm whales which have just left their natal unit have close relationships, but that these relationships decrease in number and strength when they are sexually mature. It is thought that this decrease in gregariousness is caused by an imbalance between the benefits and costs of group formation with members' growth. The most basic cost of group formation is competition for food resources. Previous studies suggest that mature males need more than three times as much prey as younger males who have recently left their natal group (see Chapter 3). This increase in energy demand might cause foraging competition between males and worsen the relationships among them.

Besides the increase in prey consumption, improvement in search efficiency may also weaken the social bonds and spatial cohesion among male sperm whales. The large male may be able to search for prey more widely using these strong echolocation clicks. Therefore, it is possible that the gregariousness of large males decrease in response to the increased ability to survey a larger area alone. As males grow up, they also move to higher latitude areas and use the habitats such as canyon (Jaquet & Whitehead 1996) and shallow shelf waters (Scott & Sadove 1997) which are relatively close to the shore and rarely used by female groups. Foraging in the highly productive areas and efficient foraging dive behavior may also promote independence.

Based on the results of this and previous studies, I suggest that interactions and cooperation relating to foraging are important drivers of long-term relationships in male sperm whales. The benefits of such interactions may be important, especially in the early stage after leaving their natal unit. As males grow up, the imbalance between cost and benefit between foraging efficiency and group formation will become significant, and the group finally split.

(2) Anti-predation

Anti-predation can also promote (or be a benefit of) long-term relationships among male sperm whales. Potential sperm whale predators are killer whales (Rice 1989; Jefferson et al. 1991), false killer whales (Palacios & Mate 1996), pilot whales (Weller et al. 1996), and large sharks (Best et al. 1984). Among them, only the killer whale has been reported to kill sperm whales (Whitehead 2003). Blackfish, such as pilot whales, sometimes harass groups of female sperm whales but they are significantly different in length from adult female sperm whales and, thus, are unlikely to have as serious of an impact on the survival of sperm whales as killer whales.

Predation pressure is considered to be an important factor in the formation of female society and their life history (Whitehead 2003). The presence of predators may be a serious threat to female groups as they include smaller individuals and vulnerable calves. The loss of a calf is larger in females than in males. Females appear to actively protect their calves, which are dependent on them for about 5 year, through communal care. Females often stagger the timing of their dives so that the calf is not alone at the surface during foraging (Whitehead 1996; 2018). When they encounter predators, females display a formation of group defense called the "Margaret formation" (Nishiwaki 1962; Whitehead 2003). The "Marguerite formation" is a formation in which the members of the group radiate out like a marguerite flower with their head facing inward and their flukes outward, with claves in the middle to keep predators at bay and protect vulnerable calve (Whitehead 2003).

Although there are no direct observations of male sperm whales being attacked by killer whales, smaller males will have a higher predation risk than larger males in general. Thus, males who have just left their mother's patronage and social unit may be more likely to be attacked than mature individuals. In 2019, I observed a large group of male sperm whales in Nemuro Strait (Kobayashi et al. 2020). Approximately 30 individuals, within a range of about 1 nautical mile, were observed moving, diving and surfacing in a coordinated fashion. The sperm whales formed clusters of various sizes (from 2 to 18 individuals) when they came to the surface. The cluster of 18 animals is the largest cluster recorded in Nemuro Strait since the start of the survey in 2006. The body length of all of the individuals found near the boat was about 10 m long, which is smaller than the minimum estimated body size in this area. During this encounter, males made a formation similar to the “Marguerite formation” twice. Although killer whales were not recorded on that day, two days later pod of mammal-eating killer whales and a cluster consisting of 5 male sperm whales were observed in the strait. Thus, it is possible that males also form large groups to protect themselves from predators. This anecdotal observation indicates that young males may form cohesive clusters when they encounter predators.

Predation risk may decrease with age. When males reach sexual maturity their body length is larger than that of physically mature females (>12 meters), with mature males reaching over 15 meters. Therefore, predation risk is likely to reach its minimum when males become less social. On the other hand, several previous studies (Curé et al. 2013; 2016) suggested that playback of killer whales' sound interrupted the diving of sperm whales and elicited grouping behaviors. This suggests that male sperm whales (even mature males) cannot completely ignore predators, and mature males are not fully solitary.

The most significant predator of sperm whales is humans aboard whaling ships (Whitehead 2003). Unlike killer whales, whalers have caught males, often targeting the larger size individuals. This pressure is particularly different from the natural condition factors, and it may have influenced the behavior and group composition of male sperm whales. The waxing and waning of whaling could explain why large and cohesive groups of males like “bachelor schools” are rarely observed in recent studies. As shown by my observation (Kobayashi et al. 2020), it seems that large male groups do occur under natural situations, but such scenarios are likely to be rare. Actually, the group size of “bachelor school” observed during the whaling period (12-15 animals or multiple of it) is apparently larger than the cluster size observed by recent research (mostly two or three animals). Thus, the “bachelor schools” may have included not only long-term male associates, but also other groups that share the same area.

In this study, I found that male sperm whales, which were previously thought to be solitary and asocial, have long-term relationships lasting for at least several years. Such male relationships are very rare among mammals and may be promoted by the importance of cooperation (mainly communal sharing of information and prey resources and anti-predation) in pelagic habitats. These factors are basically the same as that drive the evolution of female sperm whale's sociality but, among males, the necessity of cooperation against the predators is likely to be less than females which have vulnerable calves. On the other hand, males need to maintain their larger body size and grow up earlier for future mating success. Hence, for males, foraging success is more important and it may be the main function of long-term relationships between males.

4.4 Remaining issues and future studies

(1) Interaction between male sperm whales

This study suggests that male sperm whales have long-term social relationships which might contribute to increased foraging efficiency and lower predation risk. However, it is still unclear how males interact with each other. Interactions and cooperation during foraging is only circumstantial evidence. To reveal male relationships and their functions in detail, we will have to investigate their interactions over long time scales. It may be hard work (that is why we have to assume “the gambit of group”), but we should continue our efforts for an accumulation of information about their interactions. The survey combined the acoustic and bio-logging techniques and Unmanned Aerial Systems may able to describe cetaceans interaction which has been difficult to observe.

(2) Effects of endocrinal changes on relationships

The results of this study showed that the decline in sociality seems to occur during sexual maturity. Asociality may be caused by some endocrinal change such as the rise of testosterone levels that makes males aggressive. However, the body size at sexual maturity was estimated based on analyses from whaling catch data, an indirect estimate. To reveal the effects of endocrinal changes we need to examine the correlation between testosterone levels and association indices or other measures using the biopsy samples obtained from the individuals for which we have long-term association data.

(3) Reconsideration of genetic relatedness within the group

Previous studies examining the relatedness among the mass-stranded males (e.g., Bond 1990), and the long reproductive cycle of females (about 5 years) suggested that males within the group are unrelated. However, other studies using samples obtained from mass-stranded males suggested that the relationship before stranding is unknown, thus it is still not well known whether males' associations were based on kinship. I will investigate the relatedness among male sperm whales observed associating for multiple years to reconsider the genetic structure of male sperm whale society.

4.5 Tables and Figures

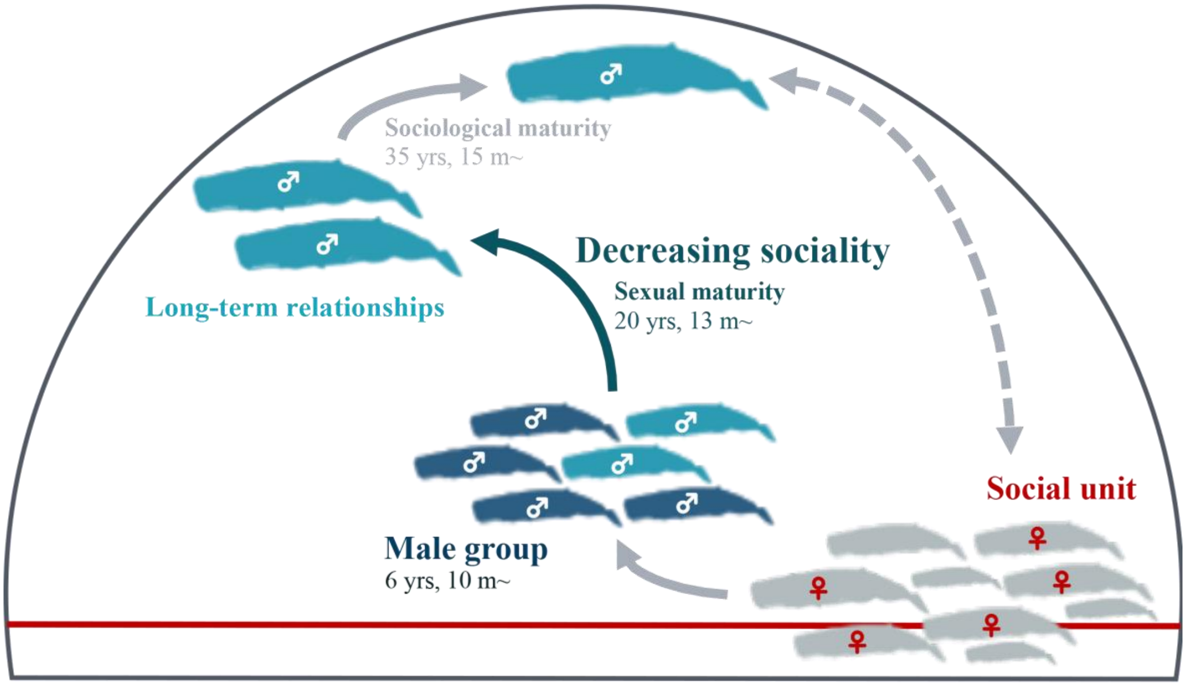


Fig. 4-1. Life history and social structure of male sperm whales

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ABSTRACT

Male sperm whales (*Physeter macrocephalus*) form the rare type all-male groups consisting of unrelated non-reproductive males. Investigation of the social structure of male sperm whales, which is unique among mammals, contributes not only to our understanding of the social structure of this species but also allow us to examine how ecological factors other than reproduction and kinship affect the formation of society. However, little information about the social structure of male sperm whales has been reported after the end of modern commercial whaling. My dissertation aimed to reveal the social structure of male sperm whales using a large photo-identification dataset from two study areas: Nemuro Strait, Hokkaido, and Goto Submarine Canyon, Nagasaki, Japan.

In Chapter 1, to obtain the background information for social analyses, I investigated the trend in residence patterns and the abundance of male sperm whales in the Nemuro Strait. The best model for a lagged identification rate suggests that residence time around the strait is 2.1 years, with individuals staying in the strait about 48 days each year. These findings, along with previous studies, suggest that males move from one feeding area to another neighboring area every several weeks, shifting their home ranges gradually over a period of a few years.

In Chapter 2, I examined association patterns (preference and temporal patterns of association) to reveal whether social relationships exist among male sperm whales in Nemuro Strait. The results suggest that male sperm whales, which were thought to be solitary and asocial previously, have preferred associations lasting for at least 2.7 years, 5 years maximum. Since the timing of dis-association approximately coincides with the

residence time in one foraging area, thus, male relationships may actually persist for 5 years or more. Such associations may function to enhance foraging or combat predation in pelagic habitats.

In Chapter 3, I examined the correlation between body length and association indices and network measures of individuals to reveal the change in relationships with male’s age. I found that young males smaller than 13 meters show high association indices comparable to those of female groups, while these measures rapidly decrease between body lengths of 13 and 14 meters at around attaining sexual maturity. The imbalance between the benefits and costs of forming a group due to the growth spurt after puberty may be the main cause of this decline of sociality.

This study found that male sperm whales, which were previously thought to be solitary and asocial, have long-term relationships lasting for at least several years. Such relationships may contribute to their survival until sociological maturity through cooperative feeding and anti-predation behavior and drive the formation of non-reproductive male groups. The costs from competition for resources may outweigh the benefits from cooperation in foraging and protection against predators for larger animals, and which may reduce male’s sociality following the spurt of secondary growth with sexual maturity.