

**Underwater vocal repertoire and their function in three
ice-breeding seals in the Arctic**

北極圏に生息する氷上繁殖型アザラシ 3 種の
水中音声レパートリーとその機能

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Chapter 1

General introduction

1.1. Current status of ice-associated seals in the Arctic

Recent loss of sea ice and snow resulting from climate change is expected to reduce the population of ice-associated seals (Moore and Huntington 2008) that largely rely on sea ice for their entire life history, including pupping, resting (molting), and feeding. There are three species of ice-associated seals in the Arctic: ringed (*Pusa hispida*) (Fig. 1.1), bearded (*Erignathus barbatus*) (Fig. 1.2), and ribbon seals (*Histiophoca fasciata*) (Fig. 1.3). Their distribution and seasonal movements are strongly associated with arctic sea ice (Moore *et al.* 2012; MacIntyre *et al.* 2013; Jones *et al.* 2014).

Based on the information including environmental changes, human impacts, and population trends of seals, the National Marine Fisheries Service (NMFS) listed the Arctic (*P. h. hispida*), Okhotsk (*P. h. ochotensis*), and Baltic (*P. h. botnica*) subspecies of ringed seals as threatened, and the Ladoga subspecies (*P. h. ladogensis*) as endangered in December 2012 (U.S. Endangered Species Act of 1973, 2012 (73 FR 16617)). At the same time, the NMFS listed the

distinct population segments of bearded seals in the Bering and Okhotsk Seas as threatened (U.S. Endangered Species Act of 1973, 2012 (75 FR 77496)).

For ribbon seals, the NMFS has determined that listing the ribbon seal as threatened or endangered under the ESA is not warranted at this time (U.S. Endangered Species Act of 1973, 2013 (78 FR 41371)) in 2013. Under the IUCN Red List, ribbon seals are currently listed as “data deficient” because available information on the abundance of seals is old (>20 years ago) and hence the current status of this species could not be evaluated sufficiently (Burkanov and Lowry 2008). For the management of these species, it is important to continuously monitor their distribution, abundance, and behaviors.

1.2. Passive acoustic monitoring for ice-associated seals

In recent years, passive acoustic monitoring, which monitor the presence of animals by recording vocalizations, have become popular to study marine mammals. Such methods have the advantages of recording sound continuously, thus even at night or in poor weather, when visual observations are impossible (Mellinger *et al.* 2007). Passive acoustic methods are indispensable in polar region, where visual observations are difficult mainly due to the poor accessibility of study

sites, which tend to be surrounded by the sea ice.

In aquatic-mating seals, most previous studies using passive acoustic monitoring have focused on the relationships between seasonal occurrence of seal's calls and environmental factors (e.g., sea ice thickness and/or extent; Miksis-Olds *et al.* 2011, Hannay *et al.* 2013; Jones *et al.* 2014; water temperature; MacIntyre *et al.* 2013, salinity; Moore *et al.* 2012; Miksis-Olds *et al.* 2014, or air-gun noise from a seismic survey; Moore *et al.* 2012), to assess the effects of recent environmental changes and human noise impact.

For acoustic monitoring to be successful, it is essential to be familiar with the vocal repertoire of each species to allow reliable identification of that species. Geographic variation in the vocalization within certain species is also important information for acoustic monitoring, which could be an indicator of distinctiveness among populations (e.g., Thomas *et al.* 1988; McDonald *et al.* 2006). Additionally, as Mellinger *et al.* (2007) have pointed out, it is necessary to understand the behavioral contexts of the vocalization. However, there is only limited information on vocal repertoire and behavioral contexts of the vocalization for ice-associated seals, mainly because direct observation is difficult and sound recording is possible for only a limited period of time due to the low accessibility to their wild habitat (Van Opzeeland *et al.* 2008).

1.3. Underwater vocalization in ice-associated seals

In pinnipeds that mate in the water, females are widely dispersed and actively feed even during the breeding season. Thus, males cannot monopolize females and must attract females prior to mating using courtship displays that often include vocalizations (*e.g.*, Van Parijs *et al.* 2003; Van Opzeeland *et al.* 2008).

All aquatic-mating pinnipeds produce various underwater vocalizations (Van Opzeeland *et al.* 2008), which have been suggested to function principally as territorial and/or courtship signals (Van Parijs *et al.* 2003). Of 13 aquatic-mating pinniped species, 10 inhabit polar regions and breed on ice (Stirling and Thomas 2003), where direct observation is difficult and sound recording is possible only for a limited time period. As a consequence, little is known about the behavioral contexts and/or the functions of vocalization in ice-associated seals.

1.4. Advantage of acoustic study in captivity

Studies on the vocalizations of captive aquatic-mating pinnipeds afford various advantages for understanding acoustic communications. For example, studies in captivity enable us

to obtain recordings during the non-breeding season, when the recording is generally difficult in the wild as individuals become widely dispersed. Serrano (2001) recorded in captive harp seals (*Pagophilus groenlandicus*) during the non-breeding season and found that the structures of the various call types differed from those of the breeding season, suggesting that vocal communication is important in the non-breeding season as well.

Studies on captive animals also enable direct and continuous observation of underwater behavior. Beier and Wartzok (1979) described the sequential underwater mating steps of captive spotted seals (*Phoca largha*), including vocalizations, and prior to this, mating had never been studied. Similarly, Rogers *et al.* (1996) analyzed the relationships between underwater vocalizations and the behavior of captive leopard seals (*Hydurga leptonyx*), and measured serum estrogen concentrations (reflecting the estrous condition of females). Notably, recorded calls in these studies could be assigned reliably to specific individuals of a species, which is generally difficult in the wild.

1.5. Aim of this study

In this study, I aimed to understand the vocal repertoire and estimate the function of these

underwater sounds by linking call types to caller's identity or sex, to seasonal occurrence of calling, and to the behavioral contexts in three species of ice seals (ringed, bearded, and bearded seals) in captivity. I described each call type and the associated underwater behavior, and then discuss the potential function of underwater vocalizations of seals.

Additionally, for ringed seals, I analyzed sound data recorded in the Southern Chukchi Sea to explore whether the call types of ringed seals recorded in captive study are also present in the wild recordings. Based on the result, I evaluated the applicability of sounds recorded in captivity to the monitoring of the behavior of wild ringed seals with passive acoustic recording.

For ribbon seals, I recorded underwater sounds of the species in the Southern Okhotsk Sea, where the vocal repertoire of this species is totally unknown. The vocal repertoire and the acoustic characteristics of sounds in the Okhotsk Sea were compared to those in the previous studies in the Bering and Chukchi Seas.

Finally, I will discuss how the present study for three ice-associated seals could be applied to the passive acoustic monitoring in the wild.

(a)



(b)

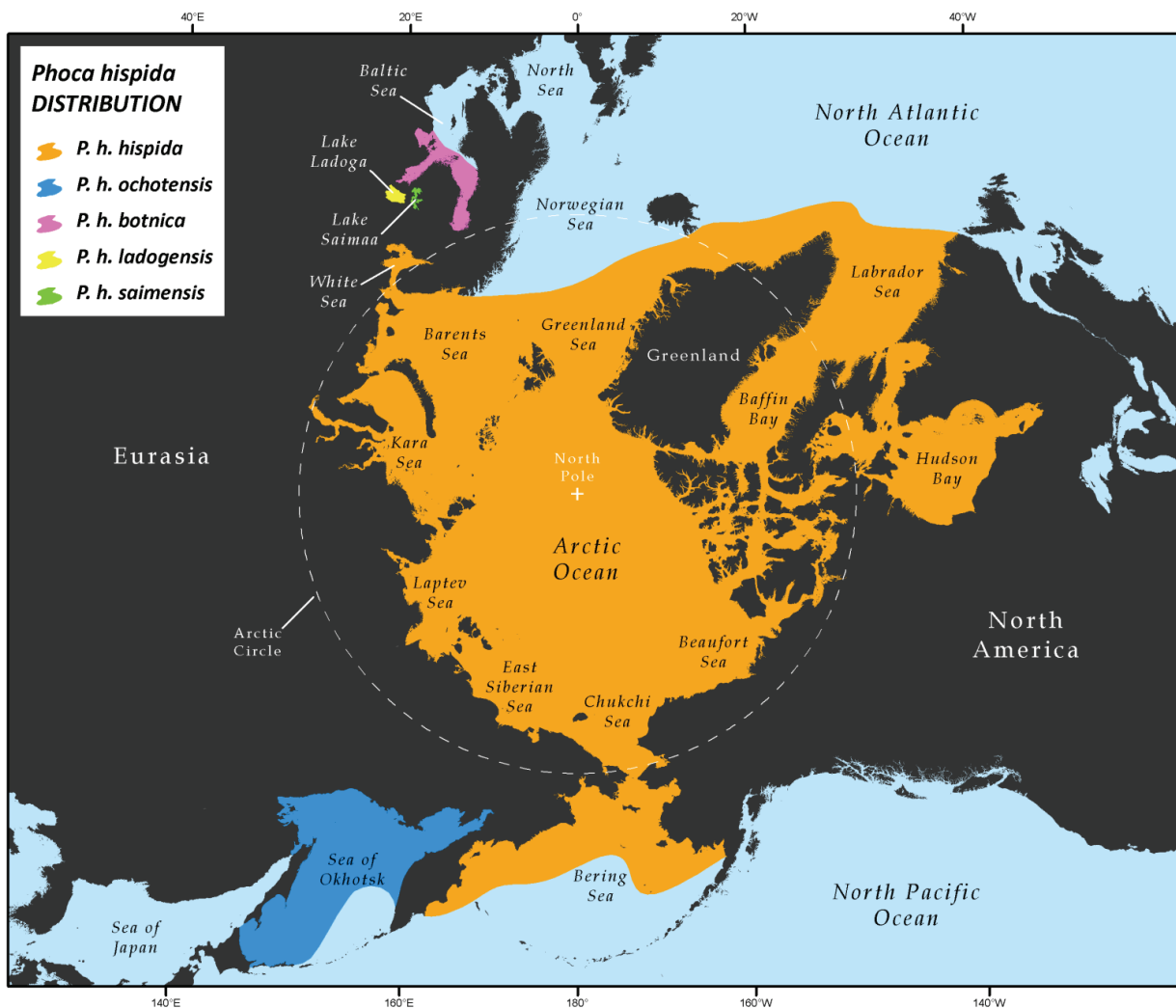


Fig. 1.1. (a) Photograph of a ringed seal (The image from Kelly *et al.* 2010) and (b) the distribution of five subspecies of ringed seals (The image from maps in Kelly *et al.* 2010)

(a)



(b)

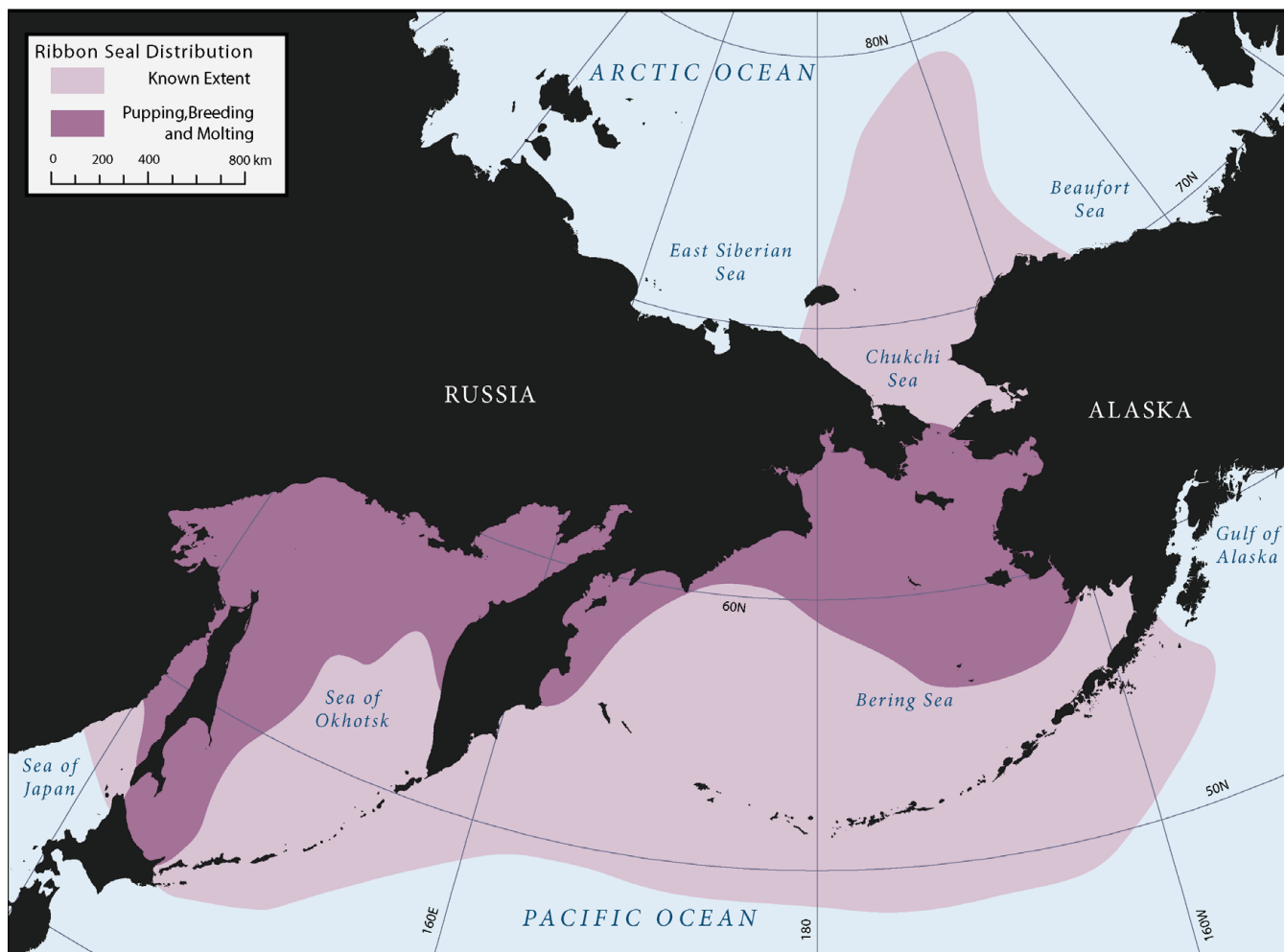


Fig. 1.3. (a) Photograph of a ribbon seal (The image from Boveng *et al.* 2013) and (b) the distribution of ribbon seals (The image from maps in Boveng *et al.* 2013)

Chapter2

General methods for captive studies

2.1. Study animals and facility

The behavioral observations and sound recordings were conducted in Otaru Aquarium, Hokkaido, Japan, from August 2011 to April 2015. Three subject species seals (ringed, bearded, and ribbon seals) were born in the aquarium or rescued from the coast of Hokkaido. The tank was filled with continuously circulating seawater from Ishikari Bay. The background noise (*e.g.*, from pumps, nearby people) during the recordings was low, such that vocalizations could be clearly distinguished from the noise. The aquarium keepers fed the seals once or twice a day, at around 0900 h and/or 1600 h.

2.2. Recording of underwater sounds

Sound Recordings

Recordings of sounds emitted by the seals were carried out continuously for 7–8 h in the daytime (0900–1700 h). Additional nighttime recordings were carried out for 10 h (1700–0300 h) as

possible.

Underwater sounds were recorded using an omni-directional hydrophone, (model SH 20k System Intech Co. Ltd, Tokyo, Japan) with a flat frequency response from 20 Hz to 20 kHz within 3 dB, connected to the amplifier (model aquafeelerIII, System Intech Co. Ltd, Tokyo, Japan), and a linear pulse code modulation (PCM) recorder model PCM D-50 (Sony Corporation, Tokyo, Japan) with a sampling rate of 48 kHz. The hydrophone was covered with a polyvinyl chloride pipe and deployed along the glass side of the tank with suction cups.

Data Analysis

The sound spectrograms of each call in the acoustic records were analyzed with Adobe Audition 3.0 (Adobe Systems, Inc.) with 1024, 2048, or 4096 points FFT size, and Hamming window. The acoustic characteristics (start, end, maximum and minimum frequency, and call duration) of each call were recorded only if these characteristics could be clearly identified. The recorded calls were classified into call types based on the differences in frequency and waveform of the sound spectrograms, referring to the call types reported in previous studies. For each call type, the seasonal and individual differences in the frequency of occurrence were analyzed.

2.3. Recordings of behaviors

Behavioral observation

Behavioral observations were conducted for 7–8 h during the daytime only (0900–1700 h) on the same day as the sound recordings. All occurrences of observed social behaviors (social interactions) were recorded (Altman 1974) for both the actor and recipient of the behavior. In addition, vocalizing individuals were identified by their unique posture, inflation of the throat and/or body, or the production of bubbles from the nostrils.

Data Analysis

The observed social behaviors were classified into behavior types, based on the postures and movement patterns of the actors. The seasonal and individual differences in the frequency of occurrence for each behavior type were analyzed. The behavior types were further classified into behavior categories based on the context of the behavior and assumed function. Finally, the associations between the call types and behavioral categories were analyzed to elucidate the functions of the underwater vocalizations.

2.4. Statistics

All statistical analyses were conducted using the software package R (Version 2.15.3; R Core Team 2015). The initial statistical significance level was set to $\alpha = 0.05$. The α -values for multiple comparisons were adjusted to $\alpha = 0.0167$ up to 0.05 using the sequential Bonferroni test (Holm's procedure) to control for type I family wise error rate (Holm 1979).

2.5. Ethical statement

This study was conducted following the “Ethical Guidelines on the Conduct of Research on Animals” established by Wildlife Research Center, Kyoto University, Japan. Permission for conducting this study was granted by Otaru Aquarium, Japan. All observations and recordings in this study were non-invasive and did not affect the welfare of seals.

Chapter 3: Study of underwater vocalizations in ringed seals

Section 3.1:

Underwater vocalizations and associated behavior in captive ringed seals

3.1.1. Introduction

The ringed seal (*Pusa hispida*), an aquatic-mating species, is the most numerous and widely distributed pinniped in the northern hemisphere. They are found in ice-covered waters either seasonally or permanently (Frost and Lowry 1981). Because of their completely ice-associated life history, including pupping in a birth lair made of ice and/or snow (Frost and Lowry 1981), ringed seals are called ice-obligated species, and hence, the recent loss of sea ice and snow resulting from climate change is expected to reduce their population (Moore and Huntington 2008). Five subspecies of ringed seals are reported in the Okhotsk Sea (*P. h. ochotensis*), the Bering and Arctic Ocean (*P. h. hispida*), the Baltic Sea (*P. h. botnica*), Lake Saimaa (*P. h. saimensis*), and Lake Ladoga (*P. h. ladogensis*), mainly based on morphological and genetic difference (Kelly *et al.* 2010). Three of five

subspecies (*P. h. ochotensis*, *P. h. hispida*, and *P. h. botnica*) in freshwater areas, while two subspecies (*P. h. saimensis* and *P. h. ladogensis*) live in salty water areas.

Among aquatic-mating pinnipeds, ringed seals belong to a group displaying relatively large vocal repertoires among its members (Rogers 2003). The seals produce at least eight types of underwater calls including yelps, barks, chirps, clicks, growls, burst pulses, knocking sounds (“knock–knock”), and woofs (Schevill *et al.* 1963; Stirling 1973; Stirling *et al.* 1983; Hyvärinen 1989; Kunnasranta *et al.* 1996; Rautio *et al.* 2009). Knocking sounds have not been reported among marine subspecies. However, as Rautio *et al.* (2009) discussed, this sound may be misidentified as a call made by other species (*e.g.*, walrus *Odobenus rosmarus*, or harp seal *P. groenlandicus*); it is often impossible to reliably assign a recorded call to specific species in the wild.

The functions of the various call types remain unclear. Vocalizations of ringed seals have been suggested to be associated with reproductive behavior, as occurrence of the call types increased during the mating season (late March to early April; Stirling *et al.* 1983). Some of the calls are thought to be used in certain social interactions, including those involved in the defense of breathing holes and interactions prior to mating (Stirling *et al.* 1983). However, the behavioral contexts of the vocalization remain poorly understood, because direct observation is difficult in the wild.

It can be hypothesized that sounds in non-breeding may also play an important role for ringed seals, as they remain in ice-covered areas throughout the fall, winter, and spring, maintaining breathing holes (Kelly *et al.* 2010), and hence social interaction will occur even in breeding season around the holes underwater. However, most of previous studies have been performed only during the breeding seasons. The one exception is a pilot study on a freshwater subspecies (*P. h. ladogensis*) inhabiting Lake Ladoga, Russia, in which underwater sounds of seals were recorded for 340 min in July, corresponding to the non-breeding season (Kunnasranta *et al.* 1996). Therefore, the vocal repertoires used during non-breeding seasons remain unclear.

In this chapter, I explored the functions of ringed seal underwater vocalizations by seasonality, sex, and behavioral context. I identified all call types, recorded the underwater behaviors of three captive seals, and explored whether seals made calls during the non-breeding season. I also explored sexual differences in the frequency of each vocalization and behavior, and the associations between call types and behavior, to estimate the functions of the sounds.

3.1.2. Methods

Study animals and facility

The behavioral observations and sound recordings were conducted in Otaru Aquarium, Hokkaido, Japan, from August 2011 to April 2012. Three subject seals (an adult male, an adult female, and a sub-adult female) were born in the aquarium or rescued from the coast of Hokkaido (Table 3.1.1). They were kept in the same tank (3.0 m × 2.8 m, 8.4 m² area, 1.8 m water depth) with surrounding ground covering an area of 11.3 m² (3.3 m × 3.4 m).

Data Sampling

Recordings of sounds emitted by the seals were carried out continuously for 7–8 h in the daytime (0900–1700 h) on August 22, September 9, 10, and 12–14, and December 19–24 in 2011; and March 1–6, and April 11 in 2012. Additional nighttime recordings were carried out for 10 h (1700–0200 h) on December 23 in 2011, and on March 4 and 5 in 2012. The recording periods were classified into ‘breeding season’ (December to April) and ‘non-breeding season’ (May to November) based on previous studies on wild ringed seals (Kelly *et al.* 2010) and a strong scent resembling gasoline exuding from the face of the adult male (Hardy *et al.* 1991, Ryg *et al.* 1992) also indicated

its rutting condition during the observation period from December to April. Sound recordings and behavioral observations were conducted following the general method (See Chapter 2).

Data analysis

The sound spectrograms had frequency resolutions of 46.9 Hz (Hamming window, 1,024 points, 48 kHz sampling rate), or 23.4 Hz (Hamming window, 2048 points, 48 kHz sampling rate).

The acoustic characteristics (start, end, maximum and minimum frequency, call duration, and number of harmonics) of each call were noted only if these characteristics could be clearly identified.

The recorded calls were classified into call types based on the differences in frequency and spectral pattern of the sound spectrograms, referring to the call types reported in previous studies (Hyvärinen 1989; Kunnasranta *et al.* 1996; Rautio *et al.* 2009; Schevill *et al.* 1963; Stirling 1973; Stirling *et al.* 1983). For each call type, the seasonal and individual differences in the frequency of occurrence were analyzed.

The observed social behaviors were classified into behavior types, based on the postures and movement patterns of the actors. The seasonal and individual differences in the frequency of occurrence for each behavior type were analyzed. The behavior types were further classified into

behavior categories based on the context of the behavior and assumed function. Finally, the associations between the call types and behavioral categories were analyzed to elucidate the functions of the underwater vocalizations.

Statistics

Differences in the frequencies of occurrence of the vocalizations and social behaviors between the breeding and non-breeding seasons, and those among individuals were analyzed using the log likelihood ratio test (*G*-test). In the *G*-test, we compared the observed frequency to the expected frequency of occurrence of calls/behaviors, which were balanced by recording hours.

3.1.3. Results

Vocal repertoire

The seals' vocalizations were recorded for a total of 162 h. The recorded sounds included 1,196 calls. Of these, 961 calls with lower noise levels were suitable for analyzing acoustic characteristics (Table 3.1.2). The analyzed calls could be classified into the following six call types: *long snorts*, *knocks*, *yelps*, *barks*, *clicks*, and *woofs* (Fig. 3.1.1). All types except the *long snort* were

identical to calls reported in previous studies on wild or captive ringed seals (Table 3.1.3).

Each call was matched to a type recorded in previous studies. We visually examined the spectral patterns of sound spectrograms and additionally referred to the other characteristics of each call described earlier. *Knocks* were the pulse-shape sounds (like door knocks) 500–900 ms in duration (Kunnasranta *et al.* 1996). The number of pulses observed in the present study (1–9) was similar to that of a previous study (2–8).

Yelps and *barks* often occurred in alternating series (Fig. 3.1.1g) as reported by Stirling (1973) upon analysis of Arctic recordings. *Yelps* and *barks* were similar in terms of both frequency and duration to those reported previously (Jones *et al.* 2014). The spectral patterns of *woofs* lacked high-frequency sidebands, and the frequencies were lower than those of *barks* (Stirling *et al.* 1983). We could not compare the acoustic parameters of the *woofs* made by our seals with those analyzed by Stirling *et al.* (1983), because the cited work lacked detailed data. However, the sound spectrograms of the cited report suggest that the duration and frequency range of *woofs* were similar to those of our animals. *Clicks* were pulse sounds of very short duration (2–20 ms) and rather low amplitude, as described in previous studies (Kunnasranta *et al.* 1996). *Clicks* were often difficult to identify by ear, and sound spectrographic analysis was required. The frequency range of clicks (700–

2,600 Hz) differed from that of ambient noises (e.g., pump motor noise) (< 300 Hz).

The *long snort* was newly described in the present study, which is easily distinguished from other call types by its long duration (4–12 s).

The frequencies of occurrence of call types were significantly different among the three individuals ($G = 568.4$, $P < 0.05$, G -test). *Knocks* were produced by all individuals but primarily by the adult male. *Long snorts* were produced by the adult male only, although the frequency of occurrence was low. *Yelps* and *barks* were mainly produced by the sub-adult female (Fig. 3.1.2). The adult female was relatively quiet and mainly produced *knocks*. It was impossible to identify the caller of the *clicks* because the amplitude was too low and no fluctuations of the throat or bubble production were observed in any individual when the clicks were recorded.

Vocalizations were more frequent in the breeding season than the non-breeding season ($G = 22.6$, G -test). *Long snorts*, *clicks*, and *woofs* were produced only in the breeding season (Fig. 3.1.3).

Social Behavior

The observations of underwater behaviors were conducted for a total of 131.1 h, and 174

underwater social behaviors were observed. These behaviors were classified into 12 types (Table

3.1.4). *Mount* was excluded from further analysis because the sample size was too small.

Based on the differences in sex and age between actors and recipients, behavior sequences, and seasonal changes, I categorized the behavior types into the following three behavioral categories: male's courtship, aggressive behavior, and submissive behavior.

Social behaviors were more frequent in the breeding season than the non-breeding season ($G = 40.944$, $P < 0.05$, G -test). *Gazing* and *face-to-face* were observed only in the breeding season (Fig. 3.1.4). *Small bubble*, *slow approach*, *gazing*, and *face-to-face* were only oriented from the adult male to the adult female (Fig. 3.1.5). Thus, these types of behavior were categorized as male courtship behavior. A typical sequence of such behavior was as follows: *small bubble* > *gazing* > *slow approach* > *face-to-face* > sound production of *long snorts* (Fig. 3.1.6).

In contrast, the *leave* behavior always occurred immediately after the *fast approach*, and the *body shake*, *jaw quiver*, *slap*, *burst bubble*, and *bite* were often observed before and/or after the *fast approach*. The *fast approach* and its accompanied behaviors were categorized as aggressive behaviors, while *leave* was categorized as submissive behavior. I defined the "submissive behavior" following the definition by Allan and Gilbert (1997): either active avoidance/escape behavior or

passive inhibition (which typically include particular body postures) behavior, and only active ones (avoidance/escape) were observed in this study.

Two typical agonistic interaction sequences were observed during the breeding season. In the first, the adult male made *burst bubble* and/or *slap* behavior and then showed *fast approach* to the sub-adult female, usually followed by *bite* or *body shake*; the sub-adult female showed submissive behavior, being driven out of the water for minutes or, sometimes, several hours. In the second sequence, the adult female exhibited aggressive behavior after courtship by the adult male; who then became submissive before commencing courtship once more. The adult male was never driven from the water.

Association between call types and social behaviors

All of the *long snorts* were associated with male courtship behaviors (Fig. 3.1.7). This call type was always produced by the adult male in the close vicinity of the adult female's face. *Knocks* were associated with either male courtship or aggressive behaviors, whereas most of the *yelps* and *barks* were associated with escape behaviors from the aggressor (Fig. 3.1.7). Alternating *yelps* and *barks* were produced principally by the sub-adult female and were associated with

submissive behavior. The *yelps* and *barks* were subordinated produced by the adult male to the adult female also during submissive behavior. During the sound production, neck or sometimes entire body of the caller vibrated simultaneously. I could not identify the caller of the *clicks*, but most of the *clicks* were recorded during non-social behaviors (*e.g.*, swimming, resting, and solo-playing) and few social behaviors were observed when the *clicks* were recorded. Of the 16 recorded *clicks*, 12 were recorded in the daytime (0.5 times/h) and 4 at night time (0.2 times/h). Only one *clicks* was recorded during feeding time.

3.1.4. Discussion

Vocal repertoires and their functions

Previous studies on vocalizations of wild ringed seals have reported at least eight call types. Of these, five (*yelp*, *bark*, *chirp*, *growl*, and *woof*) have been reported in ringed seals living in the sea (Stirling 1973, Stirling *et al.* 1983) and six (*yelp*, *chirp*, *growl*, *click*, *burst pulse*, and *knocks*) have been reported from seals living in freshwater lakes (Ladoga Lake, Russia by Kunnaranta *et al.* 1996, and Saimaa Lake, Finland by Hyvärinen 1989 and Rautio *et al.* 2009). As far as I know, there is only one report of the calls of a captive ringed seal, by Schevill *et al.* (1963), who recorded pairs

of pulses (*clicks*) from one captive adult male (2 years old and reared in a quiet pool) and discussed the possible use of active sonar by pinnipeds. There are no reports of other call types in ringed seals in captivity.

Five of the six call types identified in this study were identical to those reported by previous studies in the wild, suggesting that these call types are used in a similar way both in the wild and captive conditions. Because both the adult male and adult female were born in captivity to parents rescued from the coast of Hokkaido, this results indicate that ringed seals living in the sea may also produce *clicks* and *knocks*, although these call types have not been reported in sea populations in previous studies (Stirling 1973, Stirling *et al.* 1983). It is also possible that captive condition, where individuals are always at close range, made the individual interact more often than seals do in their wild habitat, and consequently the sound productions might be increased.

The *long snort* was described for the first time in this study. This call type is easily distinguished from other call types by its low-pitched constant frequency and long duration (>4.0 s), while the duration of other call types was shorter than 1.0 s. This call type has never been reported in the wild, possibly because it is used over a very limited area or limited time period for courtship display. It is also possible that *long snorts* have not previously been identified as a unique call type

produced by ringed seals, although previous recording data may have frequently included this call type.

The fact that *long snorts* were produced only by the adult male only during the breeding season during its courtship behavior toward the adult females, strongly suggests that this call type plays some role in courtship behavior. Although little is known about the courtship behavior of ringed seals, the *long snort* appears to be the male's acoustic signal for attracting females. This signal appeared to be directed toward the adult female, because the adult male vocalized this call in the vicinity of the female with a typical posture near the water surface (Fig. 3.1.6). Low-frequency sounds are possibly honest signals that reflect qualities of the individual such as body size or weight, that are made by various terrestrial large mammals (*e.g.*, Red deer *Cervus elaphus*; Charlton and McComb, 2007, domestic dog *Canis familiaris*; Taylor *et al.* 2010). The acoustic characteristics of the *long snort*, its low pitch and relatively loud sound, suggest a similar function. Additionally, the adult male vocalized this call type in the vicinity of the adult female (*i.e.*, the female may be able to measure the body size of the male visually), suggesting that this call type could indicate some other male's qualities rather than body size. For example, long duration of *long snorts* could be an indicator of diving ability of the seals (*i.e.*, oxygen storage capacity), which will critically affect the

survival rate fitness of individuals in pinnipeds.

Knocks were the most frequently recorded call type in this study. Kunnaranta *et al.*

(1996) identified knocking sounds by ringed seals for the first time using underwater recording in

Ladoga Lake, Russia, in summer. Then Rautio *et al.* (2009) reported similar call types in Saimaa

Lake during the breeding season. My study provides the first evidence that ringed seals from the

marine population also produce *knock* sounds like those from freshwater populations. *Knocks* have

not previously been reported in sea populations, possibly because these calls have been misidentified

as the calls of other species that have similar call types, such as walruses or harp seals, as suggested

by Rautio *et al.* (2009).

Knocks were produced by all three studied individuals mostly by the adult male, and

were often associated with aggressive behavior, suggesting that this call type was used as a threat

signal by the aggressor. The fact that the male's *knocks* were often associated with male courtship

behavior suggests that this call type also has a function as a male courtship signal. The association

with two different behavioral categories (aggression and male courtship) implies multiple functions

of this call type. *Knocks* were also recorded in ringed seals in Ladoga Lake, Russia, in association

with mother–pup pairs (Kunnasranta *et al.* 1996). Based on this fact, Van Opzeeland *et al.* (2008)

speculated that the knocking sounds were used for mother–pup communication during the lactation period because mothers continue to forage throughout the lactation period, leaving pups on the ice and probably need to communicate to locate their pups. This speculation also supported the multiple functions of knocks.

Yelps and *barks* represented the second most frequent call type in this study, and were mostly produced during submissive behavior, suggesting a function as submissive signals by the recipient of the aggression to decrease the risk of injury. Such submissive displays during agonistic interactions have been reported in other pinnipeds such as the northern elephant seal (Sandegren 1976). Stirling (1973) recorded the *yelps* and *barks* of wild ringed seals in the Arctic and also speculated that the *yelps* might represent a submissive signal because the *yelps* and *barks* were often uttered alternately during agonistic behavior. In the present study, the alternating yelps and barks were apparently produced by a single individual, mostly by the sub-adult female, with the neck or (sometimes) the entire body vibrating in synchrony with the call. Stirling (1973) considered that the *yelps* and *barks* were produced alternately by different individuals, and that *barks* might represent a threat signal by the aggressor. However, as both the *yelps* and *barks* were associated with submissive behavior, these call types might serve as submissive signals. In the wild, both male and female

ringed seals are believed to defend territories around breathing holes based on their strong loyalty to these sites and aggressive behavior around the sites (Smith and Hamill 1981). In the Arctic, ringed seals increase their aggressive behavior in April and young individuals are often kept from the water by adults and remain on land for a long period (Stirling, 1973). In such territorial contexts, submissive calls during agonistic interactions could play an important role underwater.

Click sounds have also been recorded in ringed seals in various locations (*e.g.*, Lake Ladoga, Russia: Kunnasranta *et al.* 1996; Lake Saimaa, Eastern Finland: Hyvärinen, 1989; and one captive study: Schevill *et al.* 1963). The *clicks* in each case had very short duration and inter-pulse intervals (2 to 20 ms), and their amplitudes were too low to hear without a hydrophone and amplifier. Although some previous studies have reported series of click pairs, I was only able to identify series of single *clicks*.

Some studies have speculated that pinnipeds perform echolocation using *clicks* (*e.g.*, Poulter, 1963; Renouf and Davies, 1982), mainly based on their ability to feed or to locate subject in darkness. However, Schusterman *et al.* (2000) suggested that sophisticated echolocation system is unlikely to exist in pinnipeds, mainly because they have not developed highly acute and high frequency sound production or reception systems in the water, being constrained by the obligate

amphibious auditory system. Instead of active sonar system, pinnipeds have evolved other sensory system including tactile (vibrissal touch), and high visual and hearing ability. This may also be the case in present study: the amplitude of *clicks* produced by ringed seals is relatively low and the frequency is not high like the ultrasonic sounds emitted by dolphins. *Clicks* were recorded less frequently than other call types and not associated with social behaviors or foraging activity. Hence, this call type seems to be unsuitable for study with an active sonar system. Further study is needed to better understand the function of this call type.

The *woofs* recorded in this study appeared to be identical to those reported by Stirling *et al.* (1983), who recorded the underwater sounds of ringed seal in the Canadian High Arctic. The spectral pattern of the *woofs* of the present study was similar to that of the *woofs* analyzed by Stirling *et al.* (1983); the pattern lacked high-frequency sidebands, and the woof frequencies were lower than those of *barks*. However, I could not compare the precise values of the acoustic parameters between the two sound types. *Woofs* were the least frequently recorded call type and were associated with all behavior categories. This call type seemed to be used in various contexts. Further study is needed to elucidate its function.

Behaviors associated with vocalizations

In land-breeding seal species, breeding behaviors are usually initiated without preliminary courtship. For example, Le Boeuf (1972) described how a northern elephant seal male directly approached a female and attempted intromission, biting her on the neck, and pulling her strongly toward him with his fore-flipper, without investigation or courtship display. In contrast, seal species that mate in the water are known to show some pre-copulation behavior, although only a few studies have described such behavior in detail, mainly because of the difficulty in observing their underwater behavior directly. Beier and Wartzok (1979) described the underwater mating behavior of captive spotted seals including their vocal behavior. The sequence of their pre-copulate behaviors included unique behaviors called ballooning and exchange breathing. As is also true of the spotted seals, the adult male ringed seal of present study displayed a typical behavior sequence, including *small bubbles*, *gazing*, *slow approach*, *face-to-face*, and *long snort* sounds directed toward the female only during the breeding season. This suggests that this behavior sequence is representative of the pre-copulation behavior of this species. However, I was unable to observe copulation in this study, probably because there were only two females, one of which was sexually immature; the other may not have been in estrus.

In previous studies on underwater behavior of seals, agonistic interactions have been reported more frequently than reproductive behaviors. Harp seals in the Gulf of St. Lawrence, Canada, were reported to emit sounds associated with air-bubble streaming from their naris and slapping with their fore-flippers in a threatening context (Merdsoy *et al.* 1978). The captive ringed seals of the present study also produced *burst bubble* and showed *slap* behavior with their fore-flipper in an agonistic context, suggesting that such behavior is commonly used among ice seals.

It is also noteworthy that the captive adult male of the present study often showed *fast approach* the sub-adult female (mostly followed by *bite* or *body shake* by the adult male) during the breeding season; the sub-adult female was driven from the water for minutes or sometimes several hours. Similar behaviors by adult males in the breeding season have been reported in the Arctic (Stirling 1973), suggesting that adult males of this species become territorial during the breeding season.

Application to passive acoustic monitoring

This study offers potential for the monitoring of wild ringed seals with passive acoustic

records by increasing target call types for this species and assessing not only the presence of the species but also its behavior. *Long snorts* were produced by adult male only in breeding season, suggesting that this call type could be applied to assess when and where the courtship behavior occurs. Such information is important to consider the effective management of this species to decide the place to conserve on a priority basis. On the other hand, *knocks*, *yelp*, and *barks* were produced during agonistic interaction, which could be an indicator of seasonal change in the degree of agonistic behavior for territorial defense and/or male–male competition. Previous study suggested that calling rates of ringed seals, including *yelps* and *barks*, increase as the breeding season progresses (Stirling *et al.* 1983), which also could be caused by increased agonistic interaction.

In conclusion, association between underwater vocalization and behavior were investigated for the first time for ringed seals and the function were estimated for each call type. This study could be applied to the monitoring of wild ringed seals with passive acoustic recordings to assess not only their distribution but also their behavior. Finally, I should note that in future studies it is necessary to increase the sample size to confirm the function of the underwater sounds. Playback experiments and endocrinological analyses would also be helpful to elucidate their function.

Table 3.1.1 Characteristics of the ringed seals living in the Otaru Aquarium

Name	Sex	Age (yrs)	State of maturity	Born/Capture place
<i>Wamoru</i>	Male	8	Adult	Born in Otaru Aquarium to parents rescued from the coast of Northern Hokkaido, Japan
<i>Ruru</i>	Female	4	Adult	Born in Otaru Aquarium to parents rescued from the coast of Northern Hokkaido, Japan
<i>Mint</i>	Female	3 (Estimated)	Sub adult	Rescued from coast of Northern Hokkaido, Japan in 2010

Table 3.1.2 Vocal parameters of each call type. The parameters were derived from the spectrograms produced with frequency resolutions of 46.9 Hz (Hamming window, 1,024 points, 48 kHz sampling rate) for *yelps*, *barks*, *long snorts*, and *clicks*, or 23.4 Hz (Hamming window, 2,048 points, 48 kHz sampling rate) for *knocks* and *woofs*.

(a) The fundamental frequency of each call type

(b) Other parameters of each call type. For *clicks*, “*n*” shows the total number of click trains (and that of individual pulses)

(c) Series parameters of each call type

(a)

Call type		Frequency (Hz)			
		Start	End	Maximum	Minimum
knocks	Mean±SD	89 ± 23	87 ± 21	173 ± 55	38 ± 13
	(Range)	(47 to 141)	(47 to 141)	(94 to 563)	(23 to 94)
yelp		934 ± 307	786 ± 255	1101 ± 331	710 ± 252
		(328 to 1593)	(328 to 1453)	(375 to 1828)	(281 to 1453)
bark		-	-	1727 ± 499	430 ± 293
		-	-	(281 to 2625)	(47 to 1031)
long snort		195 ± 63	164 ± 23	258 ± 52	109 ± 22
		(141 to 281)	(141 to 188)	(188 to 328)	(94 to 141)
clicks		-	-	2597 ± 281	731 ± 355
		-	-	(2203 to 4500)	(47 to 1031)
woof		78 ± 20	76 ± 10	138 ± 16	26 ± 7.8
		(47 to 141)	(70 to 94)	(117 to 164)	(23 to 47)

— Continued

(b)

Call type		Call duration (sec.)	Number of Pulses	Number of Harmonics	n
knocks	Mean ± SD	0.23±0.11	2.1±1.1	0	388
	(Range)	(0.027 to 0.82)	(1.0 to 9.0)	(0)	
yelp		0.13±0.067	1	0.64±0.77	262
		(0.034 to 0.44)	(1)	(1 to 2)	
bark		0.07±0.02	1	0	258
		(0.036 to 0.14)	(1)	(0)	
long snort		7.4±2.6	1	1.5±2.6	22
		(4.0 to 12)	(1)	(0 to 6)	
Clicks (Pulse)		0.002±0.001	4.0±0.63	0	16
		(0.002 to 0.003)	(3.0 to 5.0)	0	(43)
woof		0.61±0.27	1	0	15
		(0.20 to 1.1)	(1)	0	

(c)

Call type		Duration (sec.)	No. of repetitions	n
Series of knocks	Mean±SD	4.7±3.6	3.3±1.8	96
	(Range)	(0.045 to 22)	(1 to 12)	
Alternating series of yelp & bark		6.0±6.0	10±8.1	33
		(0.29 to 25)	(2 to 36)	
Click trains		0.12±0.03	-	16
		(0.06 to 0.15)	-	

Table 3.1.3 Descriptions of each call type

Name of call type	Reference	Definition
Long snort (captive)	–	Long duration, low-pitched, and constant frequency sound. Newly described in this study.
Knocks (wild)	Kunnasranta <i>et al.</i> 1996	Relatively low-pitched sound. Sounds like knocking at the door. Each call include 1 to 9 pulses. Often occurred in bouts repeating up to 12 times.
Yelp (wild)	Stirling 1973	Higher-pitched than bark and usually have harmonic components. Yelps more varied in frequency and duration than barks.
Bark (wild)	Stirling 1973	Lower-pitched and short duration (less than 0.2 seconds) sound. Yelp and bark often occurred in alternating series, similar to the sequence reported in the sound records from the Arctic (Stirling 1973) (Fig. 3.1g)
Clicks (wild and captive)	Kunnasranta <i>et al.</i> 1996 Schevill <i>et al.</i> 1963	Pulsed-shaped, wide frequency range sounds. Amplitude is quite low so it was not audible without a hydrophone and amplifier.
Woof (wild)	Stirling <i>et al.</i> 1983	Relatively narrow band and low-pitched sound without harmonics, though it was similar to barks. This call type was produced both underwater and at the water-surface.

Table 3.1.4 Descriptions of each behavioral type

Name of behavior	N	Definition
<u>Aggressive behavior</u>		
<i>Body shake</i>	18	Shaking the entire body keeping upright posture in the water toward another individual
<i>Jaw quiver</i>	5	Repeating small movements of the jaw with the mouth opened, looking at another seal
<i>Bite</i>	15	Biting or trying to bite (opening mouth) toward another seal
<i>Slap</i>	19	Hitting the water surface with a fore-flipper, or moving the a fore-flipper underwater rapidly to hit the other individuals
<i>Fast approach</i>	17	Swimming toward another individual at faster speed than usual speed when the seals are repeatedly circling around in the tank (approximately 0.7 m/s, estimated from video data)
<u>Submissive behavior</u>		
<i>Leave</i>	14	Swimming away from another individual at faster speed than usual, sometimes producing bubbles by slapping the water surface with fore-flippers
<u>Male's Courtship</u>		
<i>Slow approach</i>	14	Swimming toward another individual at slower speed than usual, mostly from the behind of the target individual
<i>Burst bubble</i>	16	Producing a large amount of bubbles at once from the nostrils
<i>Small bubble</i>	28	Producing small bubbles continuously from either or both nostrils
<i>Gazing</i>	19	Looking at another individual continuously keeping upright posture with its head directed toward another seal
<i>Face to face</i>	8	Touching or rubbing with its face to a face of another seal, sometimes holding the face of the other with fore-flippers
<u>(Other)</u>		
<i>Mount</i>	1	Mounting on the dorsal side of another seal, holding its back with fore-flippers.

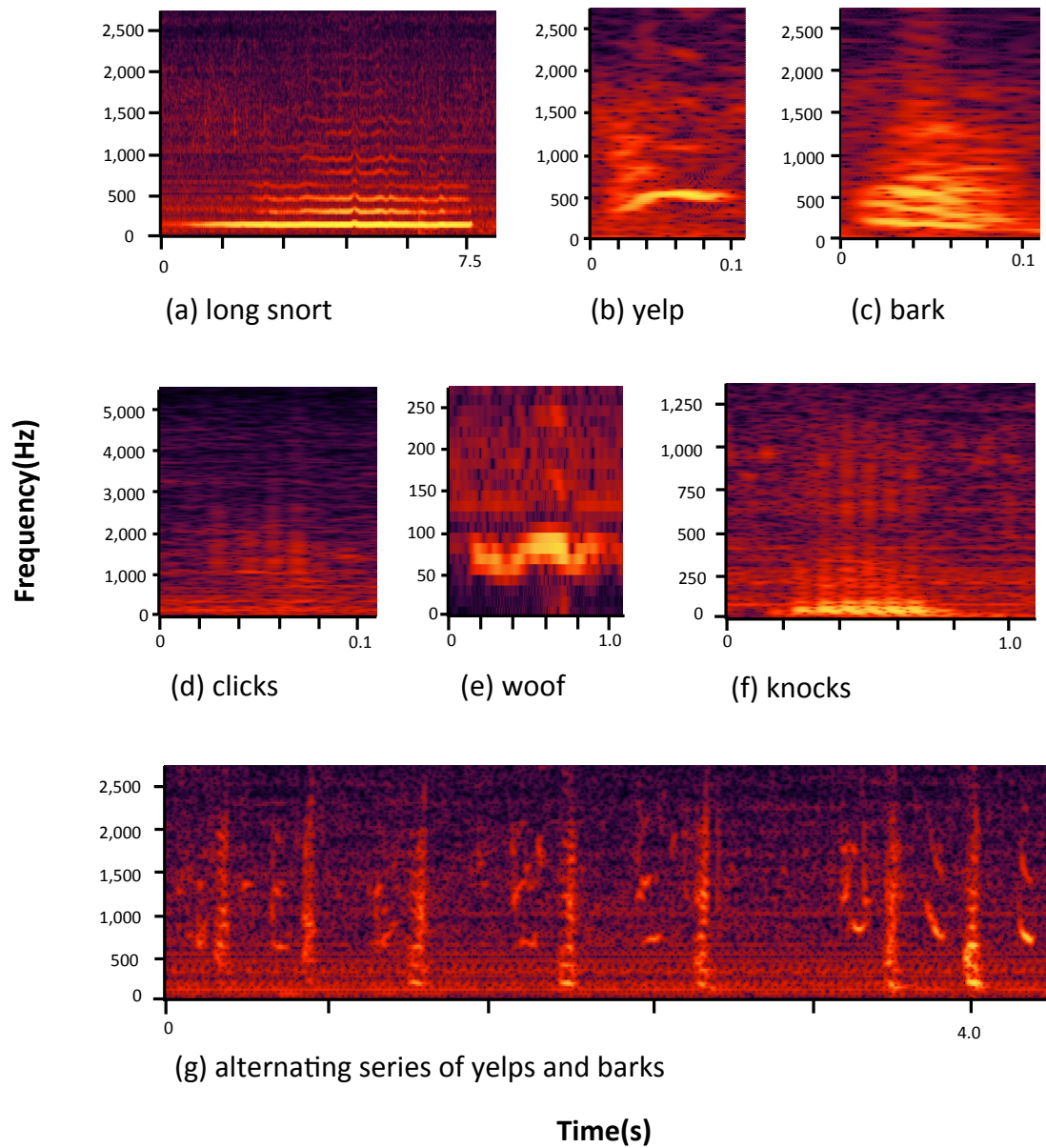


Fig. 3.1.1 Sound spectrograms of each call type of the ringed seals. All spectrograms were produced with frequency resolutions of 46.9 Hz (Hamming window, 1,024 points, 48 kHz sampling rate) for *yelps*, *barks*, *long snorts*, and *clicks*, or 23.4 Hz (Hamming window, 2,048 points, 48 kHz sampling rate) for *knocks* and *woofs*

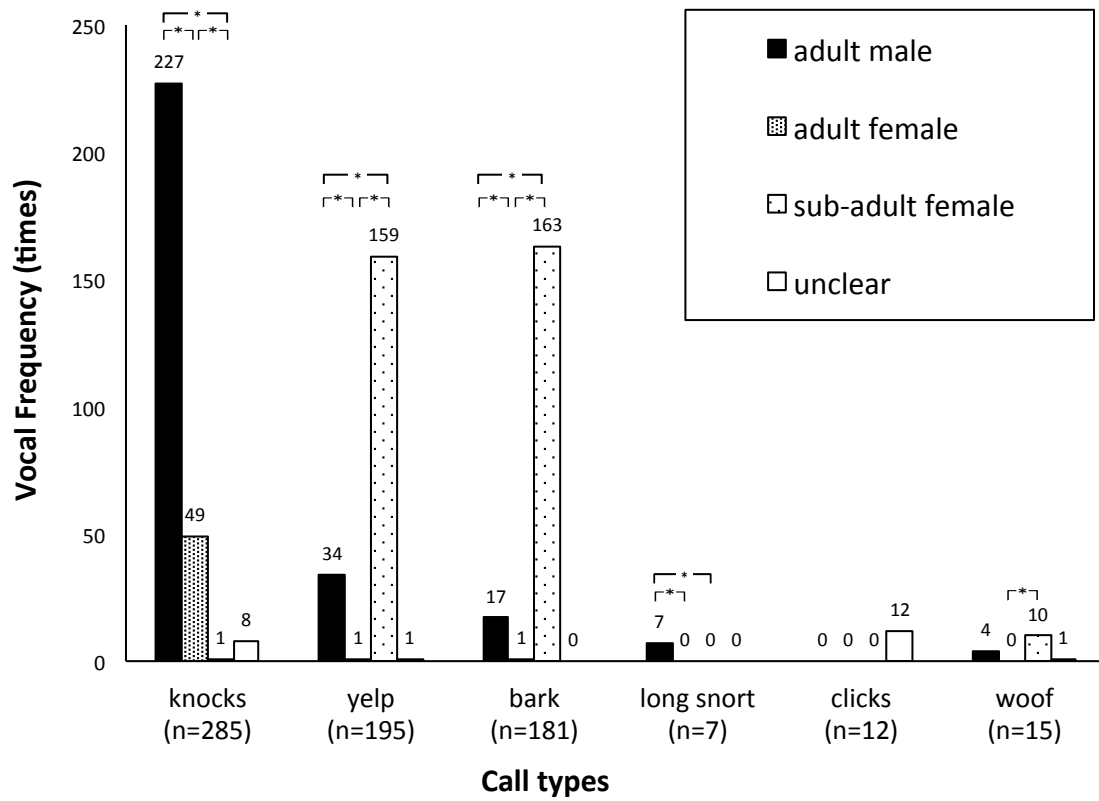


Fig. 3.1.2. The frequency of occurrence of each call type. Only daytime sound recordings were analyzed, because behavioral data were gathered only during the day (*: $P < \alpha$; the α -values were adjusted using Holm's method)

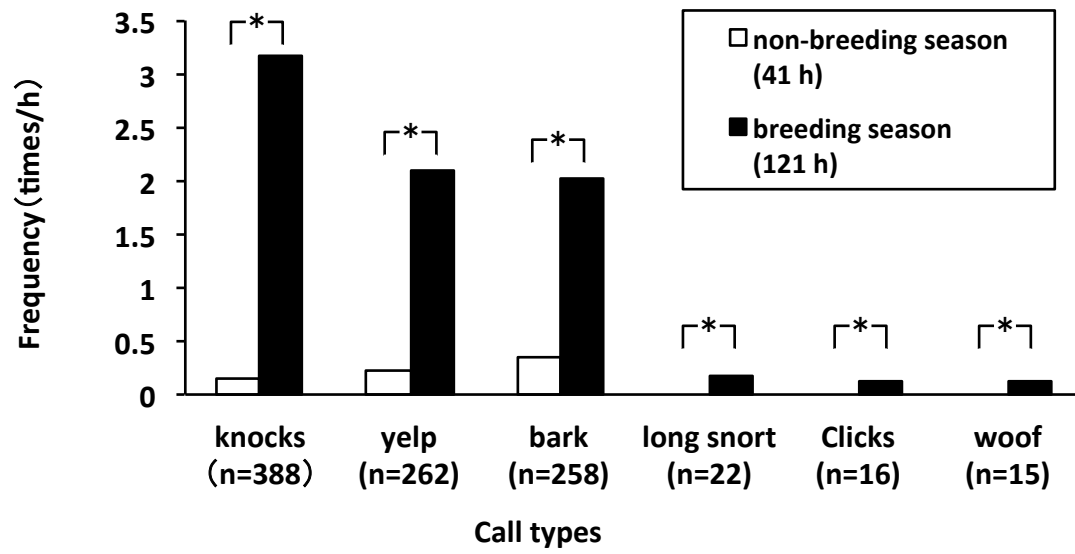


Fig. 3.1.3. Seasonal differences in the frequency of occurrence of each call type (* : $P < 0.05$)

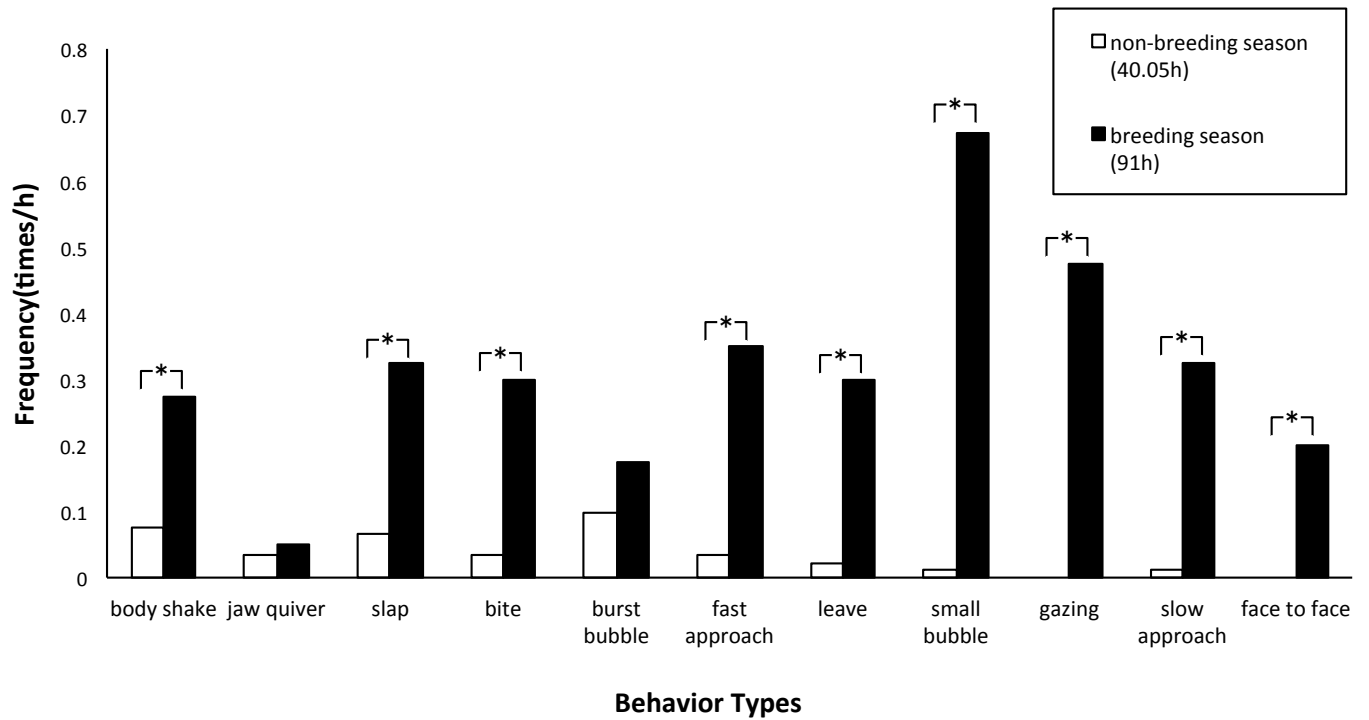


Fig. 3.1.4. Seasonal differences in the frequency of occurrence of all social behaviors in the three individuals (* : $P < 0.05$)

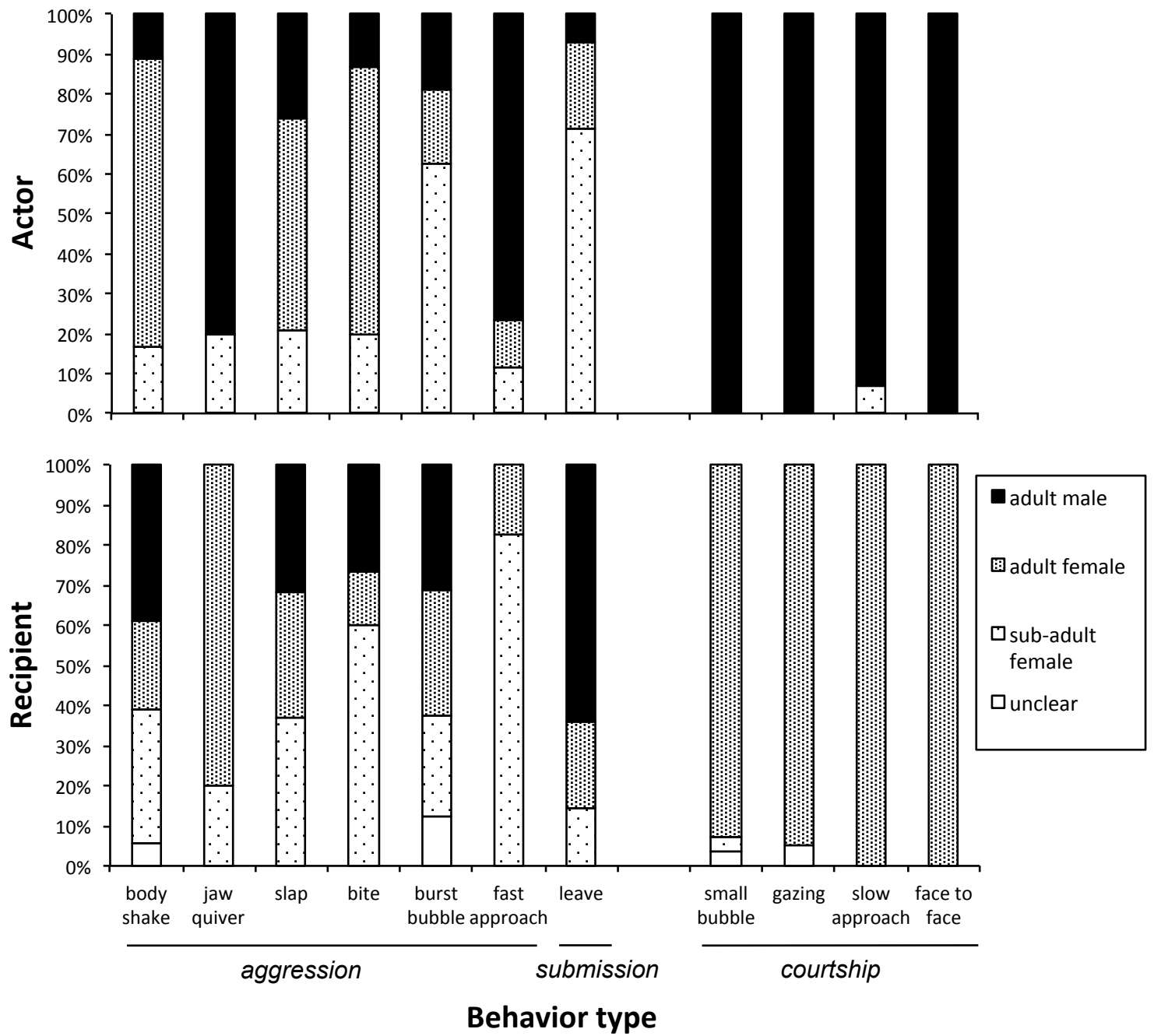


Fig. 3.1.5. The proportion of actor and recipient in each behavior type.

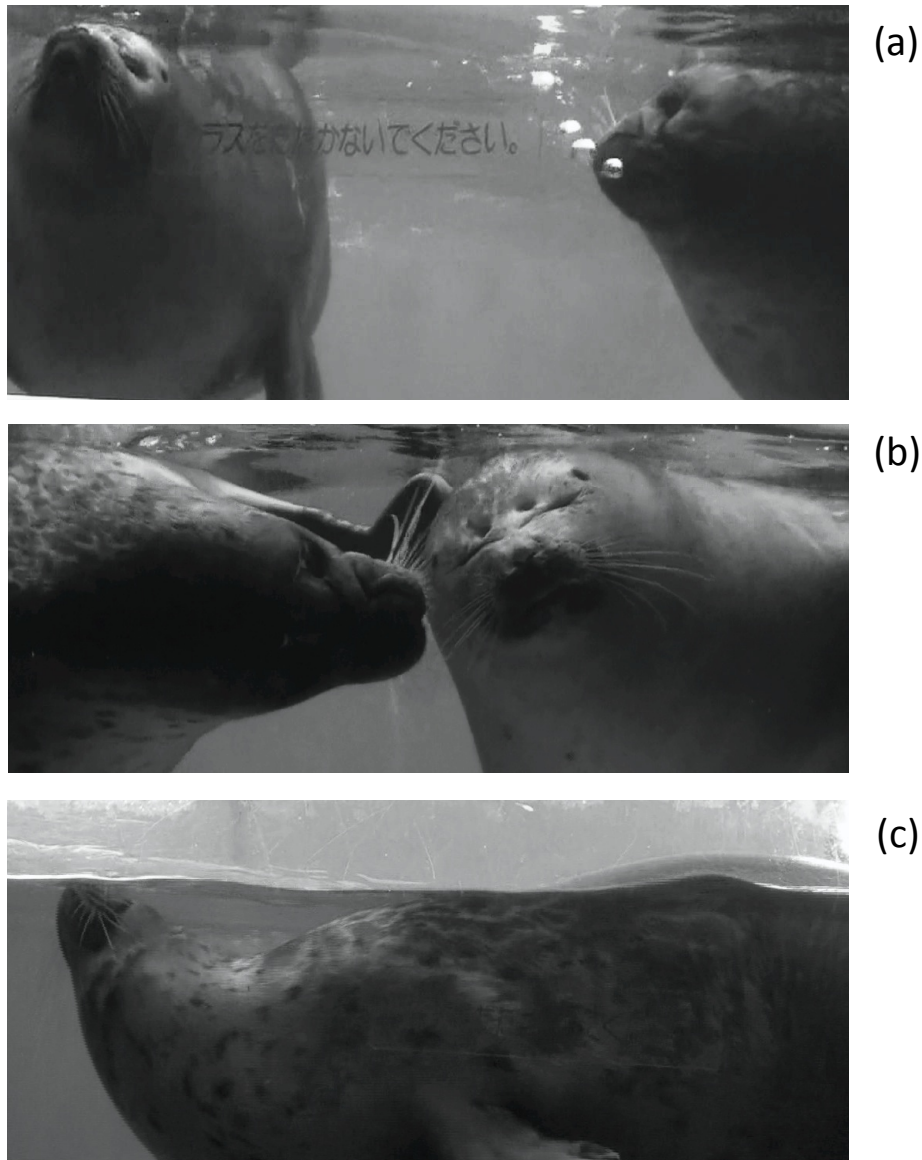


Fig. 3.1.6. A typical male courtship behavioral sequence. (a) Adult male (on the right in the photograph) produced small bubbles while gazing at the adult female (on the left in the photograph); and (b) then slowly approached the female (the male is on the left and the female on the right in the photograph), touched her face with his muzzle and fore-flipper; and (c) finally produced long snorting sounds while assuming a typical posture on the surface of the water near the female

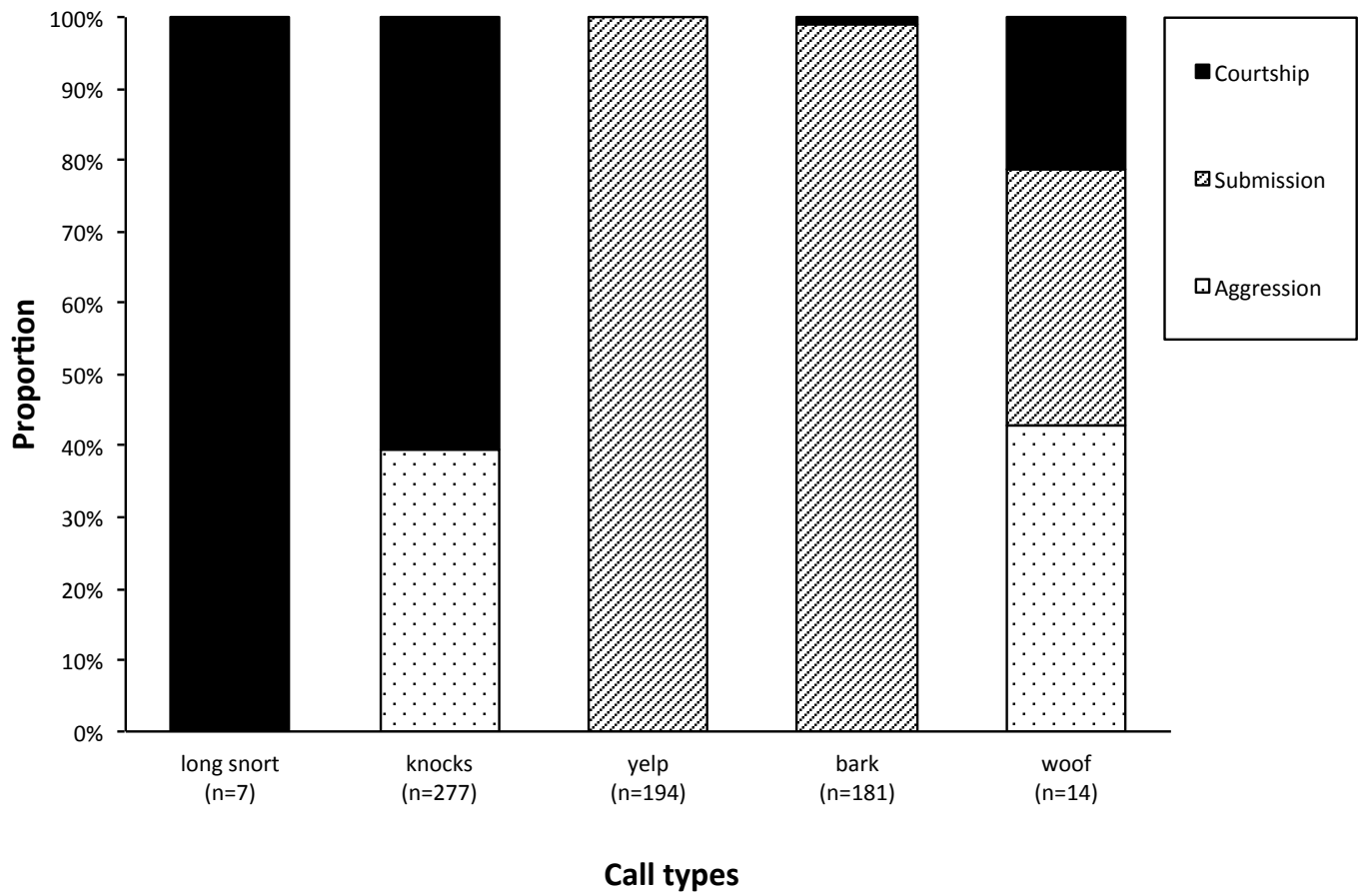


Fig. 3.1.7. Caller behavior associated with each call type. I analyzed only the calls for which callers were clearly identified

Section 3.2:

Application of captive study to passive acoustic monitoring for ringed seals in the wild (Pilot study)

3.2.1. Introduction

As discussed in Section 3.1, this study could be applied to the monitoring of wild ringed seals with passive acoustic records by increasing target call types and assessing their behaviors.

Several ringed seal calls (*e.g.*, *yelps*, *barks* and *growls*) had already been identified in passive acoustic records from the Arctic (Jones *et al.* 2014). I should note that some other calls identified in the present study in Section 3.1 (*e.g.*, *long snorts*, *knocks*) are possibly included in the data sets recorded in the wild. In this section, I analyzed sound data recorded in the Southern Chukchi Sea to explore whether the call types of ringed seals recorded in captive study are present also in the wild recordings.

3.2.2. Methods

As a pilot study, I analyzed sound data recorded in the Southern Chukchi Sea (67°43N,

168°50W; Fig. 3.2.1), using an autonomous recorder, AUSOMS V3.5 (Aquasound Inc., Kobe, Japan), with a 48 kHz sampling rate. I picked up the calls visually from sound spectrograms when the call seemed to be consistent with each call type in present study. Six-hour recordings on August 8th, 2012 (non-breeding season), and one-hour recordings on April 7th, 2013 (breeding season) were analyzed.

3.2.3. Results

A total of 103 *knocks* calls were identified in non-breeding season, and 43 *knocks* and 20 *long snorts* were identified in breeding season (Fig. 3.2.2). *Knocks* were basically within similar range in acoustic characteristics with those in captivity (Table 3.2.1) except that the maximum frequency of knocks is higher in Southern Chukchi Sea than that in captivity. The number of pulses within *knocks* ranged from 2 to 4, and approximately 90% of *knocks* sounds had 2 pulses within a call. *Long snorts* tended to have higher frequencies and shorter durations than those in captivity (Table 3.2.2). It is noteworthy that *knocks* and *long snorts* in the wild were often associating with alternating *yelps* and barks (Fig. 3.2.2c), which were previously identified as ringed seal calls in the wild (Stirling *et al.* 1983; Jones *et al.* 2014).

3.2.4. Discussion

Knocks were detected in the recordings in the wild habitat, whose acoustic characteristics were similar with those recorded in captivity, suggesting that wild ringed seals probably use similar call type as captive seals studied in the present study (Section 3.1). It is likely that these calls belong to ringed seals because no other species living in this region are reported to produce such sound types (walrus *Odobenus rosmarus*: Stirling *et al.* 1983, Stirling *et al.* 1987; bearded seal *Erignathus barbatus*: Stirling *et al.* 1983, Cleator *et al.* 1989, Risch *et al.* 2007). Additionally, association between *knocks/long snorts* and *yelps/barks* also supports that these sounds are made by ringed seals.

However, there were some considerable differences in the call types between wild and captive; number of pulses of *knocks* were mostly 2 in the wild while those were varied 1–9 in captive study, although the mean value were similar. Additionally, I can not conclude at this stage whether the difference in the acoustic characteristics (maximum frequency, especially) of *long snorts* between in captive and wild could be explained by within species variation. Further study is needed to explore the factor explaining such difference in vocalizations.

Although the sample size is highly limited at this stage, the *long snorts* were detected only in breeding season, which is consistent to the result of captive study. Thus, *long snorts* are possibly used to assess the reproductive behavior of this species. In conclusion, call types recorded in captive study could be applied to the passive acoustic monitoring in the wild habitat to monitor the behavior of the ringed seals.

Table. 3.2.1. Comparison of acoustic characteristics of the call type between the wild and captive.

The “*n*” indicate the number of calls used for measuring acoustic parameters.

Call type	Sea area	<i>n</i>		Frequencies (Hz)				Duration (sec.)	Number of pulses
				Start	End	Max	Min		
<i>Knocks</i>	Captive	388	Mean $\pm$ SD (Range)	89 $\pm$ 23 (47 to 141)	87 $\pm$ 21 (47 to 141)	173 $\pm$ 55 (94 to 563)	38 $\pm$ 13 (23 to 94)	0.23 $\pm$ 0.11 (0.027 to 0.82)	2.1 $\pm$ 1.1 (1.0 to 9.0)
	Chukchi	38		97 $\pm$ 16 (70 to 117)	75 $\pm$ 10.2 (70 to 94)	8205 $\pm$ 3305 (646 to 10034)	56.9 $\pm$ 11.8 (47 to 70)	0.22 $\pm$ 0.5 (0.13 to 0.26)	2.2 $\pm$ 0.5 (2.0 to 4.0)
<i>Long snort</i>	Captive	22		195 $\pm$ 63 (141 to 281)	164 $\pm$ 23 (141 to 188)	258 $\pm$ 52 (188 to 328)	109 $\pm$ 22 (94 to 141)	7.4 $\pm$ 2.6 (4.0 to 12)	–
	Chukchi	13		344 $\pm$ 17 (328 to 375)	263 $\pm$ 10 (258 to 281)	367 $\pm$ 20 (352 to 398)	250 $\pm$ 20 (234 to 281)	3.81 $\pm$ 1.3 (1.61 to 5.8)	–

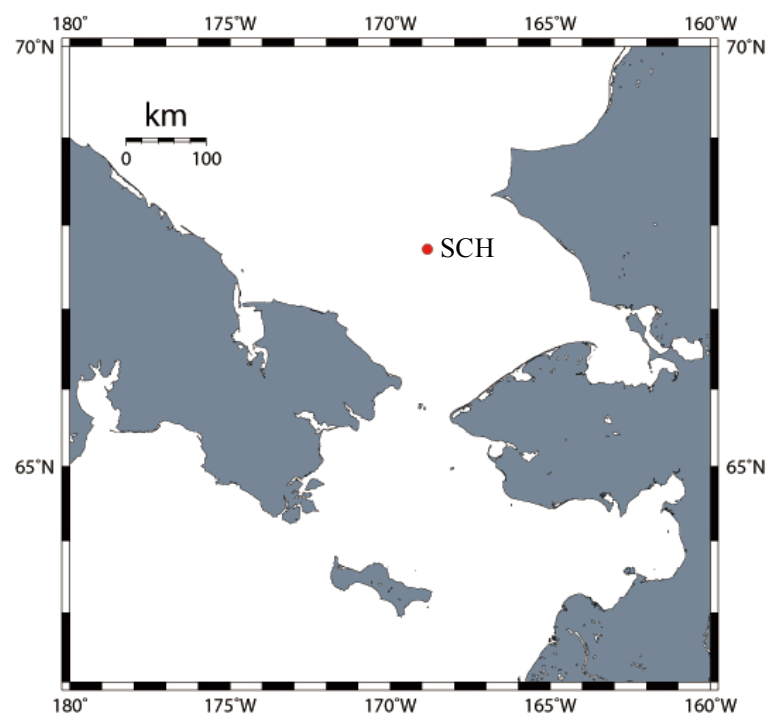


Fig. 3.2.1. The recording site in the Southern Chukchi Sea (SCH) in 2012 and 2013

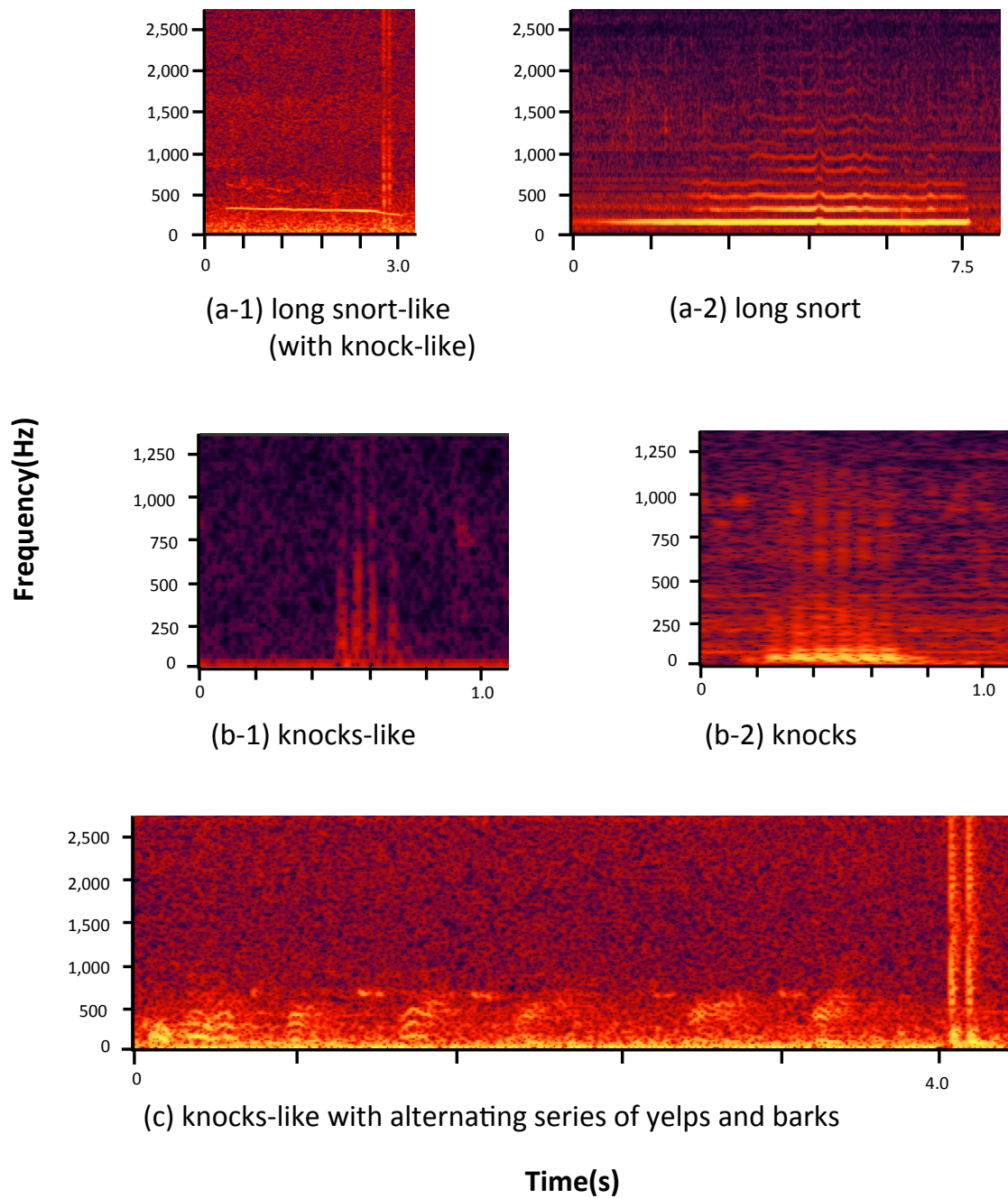


Fig. 3.2.2. Comparison of sound spectrograms of the call types between the wild and captive. All spectrograms were produced with frequency resolutions of 46.9 Hz (Hamming window, 1,024 points, 48 kHz sampling rate) for long snort-like in the wild (a-1), and long snort in captivity (a-2), or 23.4 Hz (Hamming window, 2,048 points, 48 kHz sampling rate) for knocks-like in the wild (b-1), knocks in captivity (b-2) and knocks-like sounds with alternating series of yelps and barks (c) barks.

Chapter 4:

Underwater vocalization and the behavioral contexts in captive bearded seals

4.1. Introduction

Ecology

The bearded seal (*Erignathus barbatus*) is the largest-sized species of northern ice-breeding seals (total length 2.0–2.5 m, body weight 260–60 kg), and females tend to be larger than males in some regions (Burns 1981a). They inhabit shallow water (<200 m deep) over continental shelf areas with sea ice in the Okhotsk, Bering, and Arctic Seas, where they feed primarily on benthic animals (Burns 1981a). Breeding and molting occur on ice floes between March and late June (Cameron *et al.* 2010). Bearded seals are basically solitary and widely dispersed (Burns 1981a). Therefore, direct observation is difficult and little is known about the behavioral aspects of this species.

Vocal repertoire of bearded seals

Vocalizations of bearded seals are basically classified into four call types (*trills*, *moans*, *ascents*, and *sweeps*), and *trills* were further classified into three subcategories, some of which are geographically specific (Risch *et al.* 2006). Additionally, Cleator *et al.* (1989) reported another distinctive low-pitched call type, *groan*, in the Ramsay Island but not in any other areas.

Frequency of occurrence of these call types are more frequent during breeding periods, and these calls are suggested to serve as advertisements of breeding condition and/or territorial maintenance (Cleator *et al.* 1989; Van Parijs *et al.* 2004). Although a considerable number of studies have suggested that these call types are produced only by males (*e.g.*, Davies *et al.* 2006; Van Parijs *et al.* 2003), the possibility of female vocalization cannot be excluded completely. Moreover, little is known about the behavioral context of these vocalizations, mainly because direct observation is difficult in the wild.

Aim of the study

Here, I aimed to investigate the functions of bearded seal underwater vocalizations by seasonality, sex, and behavioral context. As for ringed seals, I recorded underwater sound and social

behaviors of three captive seals. I also explored sexual differences in the frequency of each vocalization and behavior, and the associations between call types and behavior, to investigate the functions of the sounds.

4.2. Methods

The behavioral observations and sound recordings were conducted at the Otaru Aquarium, Hokkaido, Japan, from March 2012 to March 2015. Three subject seals (one adult male, two adult females) were rescued from the coast of Hokkaido (Table 4.1). They were kept in the same tank (7.8×6.0 m, 46.8 m^2 area, 1.0 m water depth) within a surrounding area covering 53.0 m^2 ($7.8 \text{ m} \times 6.8 \text{ m}$).

Continuous recordings of the sounds and behavior observations were conducted for 7–8 h during the daytime (0900–1700 h) continuously for 7–8 h in the daytime (0900–1700 h) on March 7, April 11–13, and December 26 in 2012; February 6–8, March 17–19, and April 15–17, May 26–28, September 28–30, October 21–23, November 18–20, and December 25–27 in 2013; January 28, 29, February 22–25, March 12–17, and October 15–17 in 2014; January 3–6, February 1–5, and March 8–13 in 2015. Sound recordings and behavioral observations were conducted following the general

method (See Chapter 2)

Data analysis

Classification and analysis of recorded sounds/behaviors were conducted following the general method (See Chapter 2). During the initial observations, as vocalizations of the adult male appeared to occur in a regular order, sequential analysis was conducted for male calls. First, the male calls were split into call bouts based on the bout criterion interval (BCI), which was measured by statistically objective method (Sibly *et al.* 1990) based on the frequency distribution of between individual vocal interval, defined as the interval from offset of the precedence call to onset of the following call (sec). Second, observed transition ratios, from one call type to others within call bouts, was calculated and compared with expected transition ratios assuming random transition, to test whether the male calls occurred in regular order or not. Third, song linearity index (S), which shows the complexity of ordering song (Scharff and Nottebohm 1991), was calculated from the number of call types and transition types as follows:

$$S = C/T$$

where, C indicate number of different call types per song and T indicate number of transition types

per song (*i.e.*, number of non-zero transition in the transition matrix; see Table 4.5). The linearity index score ranged from $1/C$ (completely random) to 1 (each call type has only one transition type). Thus, a lower linearity index indicates a more complex song.

4.3. Results

Vocal classification

Recordings were conducted for 442.1 hours in total, which included 3,586 calls. Of these recorded calls, 3,464 without overlap and/or high-level noise could be used for repertoire analysis. These calls were categorized into six call types (*trill*, *moan*, *high-moan*, *snort*, *bell*, and *groan*) (Table 4.2; Fig. 4.1). Three of the six call types (*trill*, *moan*, and *groan*) were consistent with those reported in the previous studies (Ray *et al.* 1969; Stirling *et al.* 1983; Cleator *et al.* 1989; Davies *et al.* 2006; and Risch *et al.* 2007). The other three call types (*high-moan*, *snort* and *bell*) are described for the first time in this study.

Each call was matched to a call type described in previous studies as follows (Table 4.3): *trills* were matched to those described previously, primarily based on their much longer duration (>5.0 s), and higher frequencies (>1 kHz) than those of any other call type, and the downward

sweeping of the frequency change (Cleator *et al.* 1989; Davies *et al.* 2006). *Moans* were basically unmodulated or showed fewer frequency modulations (Ray *et al.* 1969). *Groans* were the lowest-frequency sound among the call types of bearded seals (Cleator *et al.* 1989), mostly decreasing in frequency. The *groans* in this study were within similar ranges to those reported in a previous study (Cleator *et al.* 1989) in terms of frequency (<340 Hz), duration (0.2–1.7 s), and the number of repetitions (typically 3–6).

The *high-moan* was newly separated from the *moan* based on its higher frequency and longer duration (Fig. 4.2), with all five acoustic parameters being significantly different between the two ($P < 0.01$, Mann-Whitney U test). *Snort* and *bell* were newly described; these two call types were distinctive from other call types based on their relatively lower-pitched frequency than those of *trill*, *moan*, and *high-moan*, while higher-pitched frequency than those of *groans*. *Snorts* could be separated from *bells* by their longer duration and tonal spectral pattern, and *bells* were the only call type of bearded seals that had pulsed-shape spectral pattern.

During this study, only the adult male seal produced trill. On the other hand, only the adult female 1 made *snort* while the adult female 2 made *bell* and *groan*. Both sexes (the adult male and the adult female 2) shared *moan* and *high-moan* (Fig. 4.3).

Seasonal changes in vocalization

The male seal produced underwater sounds only during the period from December to the next April (Fig. 4.4a). The occurrence frequency of the vocalization varied by month ($\chi^2 = 13.2$, $P < 0.05$; Kruskal-Wallis rank sum test). The frequency of occurrence gradually increased from December, peaked in March, and then decreased until April.

The two females produced underwater sounds during a shorter period than did the male, who vocalized only in March (Fig. 4.4b). Either one of the two observed females vocalized for each year.

Sequential analysis of male vocalizations

As the three call types of the adult male seemed to follow a typical sequence (Fig. 4.1g), the sequence analysis was conducted. The “Bout criterion interval” (BCI) was determined to be 109.2 s, calculated from the x-coordinate at intersection of two regression lines (fast process and slow process; Fig. 4.5), whose composite curve explained variance of the data significantly higher than single regression line (Table 4.4). According to the calculated BCI value, a total of 2,032 calls

were split into 93 call bouts. The other 106 calls were categorized as single calls (*i.e.* Both BIIIs before/after the calls >109.2 sec). All of the single calls were trills. The average number $\pm$ SD of calls within bouts was 9.1 ± 19 (range: 2–355), and the average duration $\pm$ SD of bouts was 896 ± 1590 s (range: 15–9,222 s).

Second, the sequences within the bouts were analyzed. These bouts predominantly started with a *trill* (88 of 93) or a *high-moan* (5 of 93), and often ended with a *trill* (79 out of 93), although some ended with a *moan* (4 of 93) or a *high-moan* (10 of 93). The transition matrix from a call type to the next within a bout is shown in Table 4.5. The transition ratio was significantly different from those expected from random transition (Fig.4.6; $G = 1383.6$, $P < 0.001$, G -test). The occurrences of transitions from *trill* to *moan*, *moan* to *high-moan*, and *high-moan* to *trill*, were higher than those expected from random transition. Conversely, the occurrence of transitions from *moan* to *moan*, and from *high-moan* to *moan* were lower than those expected from random transition. Song linearity index of the male's vocal sequence was calculated as 0.38. Unlike the male vocalizations, female vocalization did not show any typical sequence.

Behaviors

The adult male did not show any social behaviors, nor did he approach the females during the period of observation (430.5 h in total). The adult male produced *column-like bubble* at the water surface when vocalizing. This bubbling was observed every time the adult male produced *moans* (635 of 635 cases) or *high-moans* (1,236 of 1,236 cases) but was rarely observed when it produced *trills* (73 of 1473 cases). This *column-like bubble* was not produced toward a specific female and hence was not regarded as “social” behavior.

The females showed *nuzzling* behavior toward the vocalizing individual ($n = 72$), which was the only social behavior observed in this study. Either of the two adult females showed *nuzzle* against the vocalizing adult male ($n = 70/72$) or against the vocalizing female ($n = 2/72$). The main body parts of the male nuzzled by females were the throat ($n = 27$), followed by the nose ($n = 21$) and other body parts: dorsal side of the body ($n = 9$), head ($n = 2$), ventral side of the body ($n = 1$), and unknown ($n = 10$). This behavior was observed only in March, consistent with the period during which the females produced sounds. *Nuzzle* of the adult females occurred just before its vocalization, and all *nuzzles* and associating sounds by females were observed within 1 min of the *trill* sounds produced by the male.

4.4. Discussion

Vocal repertoire and functions

Five types of underwater vocalization (*trills*, *moans*, *ascents*, *sweeps*, and *groans*) were reported in bearded seals (Risch *et al.* 2006; Cleator *et al.* 1989). Three of the five call types (*trill*, *moan*, and *groan*) observed in this study have been reported in previous studies (Ray *et al.* 1969; Stirling *et al.* 1983; Cleator *et al.* 1989; Davies *et al.* 2006; and Risch *et al.* 2007). The *high-moan* of the adult male was newly separated from the *moan* in this study, based on its higher frequency and longer duration. Risch *et al.* (2007) classified the bearded seal calls in the Arctic into four major call categories: *trill*, *ascent*, *sweep* and *moan*, based on the 16 acoustic parameters, but *moans* comprised only one group. This is possibly because that variations in acoustic parameters in moans are large within- and/or between-individuals and hence recordings made in the wild might pool the calls from various individuals with various frequencies or duration.

The *sweep* and *ascent* were not recorded in this study. This may be because these call types are geographically specific: the *ascent* has been reported only in Alaska and western Canada, and the *sweep* has been reported only in Svalbard and in the High Canadian Arctic (Risch *et al.* 2007).

This is the first report of vocalizations in female bearded seals. In this study, the females produced five call types, three of which (*high-moan*, *snort*, and *bell*) were described in this study for the first time. Although many studies have examined vocalizations in bearded seals (*e.g.*, Cleator *et al.* 1989; Davies *et al.* 2006; Van Parijs *et al.* 2003), no previous studies have reported on the vocalization in females. This may be because the females vocalize during a limited period (only in March), as shown in this study. Davies *et al.* (2006) observed ontogeny of vocal behavior in captive bearded seals (three males and three females). They reported that only males exhibited vocalization and, which might be because the observed females were young (<5 yrs) and hence not sexually receptive.

Basically, only males are known to produce vocalizations in species of aquatic-mating pinniped (Van Opzeeland *et al.* 2008). There are some reports, however, that female also vocalize (leopard seal *Hydrurga leptonyx*, Rogers *et al.* 1996; ringed seal *Pusa hispida*, Kunnasranta *et al.* 1996; harp seal *Pagophilus groenlandicus*, Serrano 2001; and Weddell seal *Leptonychotes weddellii*, Oetelaar *et al.* 2003). For recordings in the wild, it is often difficult to assign a recorded call to a specific individual with certainty, because other calling individuals may be nearby. Consequently, underwater sound production by females, whose vocal period tends to be shorter than that of males

(e.g., leopard seal, Rogers *et al.* 1996), could be overlooked in wild habitats.

The vocalization of the adult females occurred only during the breeding season and was associated with *nuzzle* behavior, mostly directed toward the adult male, suggesting that their vocalization might be used for courtship behavior, for example as a signal indicating their estrus and sexual receptivity. Rogers *et al.* (1996) suggested that adult female leopard seals use broadcast calls to advertise their sexual receptivity, based on the association between the presence of broadcast call and the high estradiol levels in the serum.

The relatively short vocalizing periods compared with those of the male could also reflect the short estrous cycle of the seals. During the breeding season, bearded seals are solitary and occur at low densities in the pack-ice areas (Burns *et al.* 1981a), and such pack-ice breeders have been reported to have short breeding periods (Riedman 1990). Consequently, they need to locate mates as effectively as possible. Under such conditions, vocalization could play an important role in the effective transmission of information. A similar function of female calls has been also suggested in the leopard seal (Rogers *et al.* 1996), which is also a solitary species and widely dispersed during the breeding season.

The function of the male call types remains unclear. However, the male bearded seal

produced sounds only around the breeding season, peaking in March, which is consistent with the mating season in the wild (Burns 1981a), suggesting that male vocalization is related to reproductive behavior. Although the vocalizations were not directed toward a specific female or associated with social behaviors, the adult females seemed to answer the male calls using vocalizations and *nuzzle* behaviors. Therefore, the male calls could be used for attracting females. Further study involving a larger number of males is needed to determine whether male vocalizations also function as territorial signals.

Sequence of male calls

The male bearded seal produced three call types in a typical sequence, starting and terminating with a trill, and three calls occurred in a regular order (*e.g.*, *trill* > *moan* > *high-moan* > *trill*) within a bout. Such sequential calls have been reported in pinnipeds (*e.g.*, Weddell seals; Terhune and Dell’Apa 2005, leopard seals; Rogers and Cato 2002) and other various vertebrates, including various birds (Catchpole and Slater, 1995, for review), primates (*e.g.*, Cowlshaw, 1996), and baleen whales (*e.g.*, Winn and Winn 1978). These sequential calls have often been referred to as “song” (defined as a series of different sounds in a fixed order produced repeatedly) and have been

suggested to function as reproductive and/or territorial signals (e.g., Catchpole and Slater, 1995).

The male bearded seal produced three call types in a typical sequence, starting and terminating with a trill, could be regarded as “song”, following the previous studies above.

The song linearity index, indicating the ordering complexity of call sequence, was calculated as $S = 0.38$, and the number of call types was $T = 3$. Currently, there are no comparable studies on complexity of call sequence in pinnipeds, but this score is close to that of domesticated Bengalese Finch in the previous study (*Lonchura striata* var. *domestica*; $S = 0.33$, $T = 5.3$) rather than white-backed munias, a wild form of the same species, (*Lonchura striata*; $S = 0.61$, $T = 5.3$) (Honda and Okanoya 1999). Another domesticated song-birds, Java sparrow *Lonchura oryzivora*, also showed similar score ($S = 0.35$, $T = 9.3$) (Hasegawa et al. 2011), though the number of call (note) types (T -values) are more than that of present study.

Honda and Okanoya (1999) suggested that songs of domesticated Bengalese finch have evolved to be more complex during domestication by female preference and by less constraints experienced in the wild predation such as predation. Thus, it is possible that song complexity of the bearded seal might also reflect the female choice and low predation risk. Further study is needed to compare the linearity index within- and between-species, or between captive/wild seals, to evaluate

such evolutionary constraints.

The function of the typical sequences of the male bearded seal calls is still unclear, but it is possible that complex sequential sounds are attractive for female and/or used for male–male competition. This is suggested to be the case for the songs of humpback whale (*e.g.* Winn and Winn 1978) and song birds (*e.g.*, Catchpole and Slater, 1995). This hypothesis could not be investigated in the present study as recordings from only one adult male were made. Further investigation is needed, and sound playback experiments of male sounds to adult females would enable to test this hypothesis.

Behaviors associated with vocalizations

No social behaviors were observed during the non-breeding season, possibly reflecting the fact that bearded seals do not have the opportunity to communicate with each other during other seasons, when they are widely dispersed (Burns 1981a). Unlike ringed seals, which maintain territories around breathing holes (Stirling *et al.* 1983) during both breeding and non-breeding season, bearded seals are widely dispersed around pack-ice area during non-breeding season. Thus, unlike ringed seals, bearded seals might have no need for agonistic interactions.

Nuzzle, the only social behavior observed in this study, was seen only during the breeding season. This behavior was observed mainly in females, suggesting that it may function as part of their courtship behavior, perhaps for example by advertising their estrous condition. Two cases of female-female nuzzling behavior were observed. It is possible that these *nuzzles* may function as submissive signals. Davies *et al.* (2006) reported that in *nuzzles* observed during male-male interactions, the subdominant male nuzzled against the dominant vocalizing male. Thus, this behavior seemed to have multiple functions.

Application to passive acoustic monitoring

As for ringed seals (see Chapter 3), the study of captive bearded seals could be applied to the passive acoustic monitoring of wild ringed seals by increasing the target call types for this species and assessing their behavior. Three call types (*high-moan*, *bell*, and *snort*) were newly described in this study, and these call types may be included in the recordings made in wild habitats. Some call types were produced by the male (*trill*), or only by females (*bell*, *snort*, and *groan*). These call types could be used for acoustic monitoring of each sex separately. Moreover, the fact that most of vocalizations occurred during the breeding season and were associated with female *nuzzle*, which

was observed only during the breeding season, suggests that these sounds could be an indicator of the reproductive behavior of this species.

Table 4.1. Characteristics of the bearded seals living in the Otaru Aquarium

Name	Sex	Age (yrs)	State of sexual maturity	Origin
<i>Paopao</i>	Male	>10	Mature	Rescued off coast of Northern Hokkaido, Japan
<i>Upa-upa</i>	Female	>13	Mature	Rescued off coast of Northern Hokkaido, Japan
<i>Non-non</i>	Female	>17	Mature	Rescued off coast of Northern Hokkaido, Japan

Table 4.2. Vocal parameters of each call type of bearded seal. The parameters were derived from the spectrograms produced with frequency resolutions of 46.9 Hz (Hamming window, 1,024 points, 48 kHz sampling rate) for trill, moan, high-moan, snort, and bell, or 11.7 Hz (Hamming window, 4,096 points, 48 kHz sampling rate) for groans. “*n*” indicates number of calls whose sound qualities were good and used for acoustic parameter analysis.

Call type		Frequency (kHz)				Duration(s)	n
		Start	End	Maximum	Minimum		
trill	Mean±SD	7.50±1.18	1.04±0.12	7.55±1.21	0.93±0.14	4.98±0.70	175
	(Range)	(4.09-10.33)	(0.94-2.53)	(1.03-10.33)	(0.56-2.44)	(1.73-7.32)	
moan		0.31±0.08	0.33±0.09	0.48±0.04	0.22±0.02	1.96±0.14	63
		(0.26-0.75)	(0.28-1.03)	(0.43-0.56)	(0.17-0.26)	(1.50-2.23)	
high-moan		0.64±0.12	0.48±0.12	0.75±0.12	0.41±0.12	3.78±2.06	57
		(0.43-0.90)	(0.30-0.81)	(0.56-1.03)	(0.17-0.73)	(1.41-9.63)	
snort		0.43±0.07	0.33±0.09	0.68±0.08	0.18±0.06	4.27±3.30	14
		(0.38-0.57)	(0.19-0.47)	(0.57-0.84)	(0.09-0.28)	(0.56-9.67)	
groan		0.077±0.024	0.071±0.011	0.10±0.02	0.064±0.0009	0.95±0.74	34
		(0.043-0.11)	(0.054-0.097)	(0.075-0.13)	(0.054-0.075)	(0.28-3.76)	
bell		—	—	2.86±0.63	1.50±0.20	1.76±0.96	72
		—	—	(2.15-4.00)	(1.20-1.73)	(0.92-3.63)	

Table 4.3. Description of each call type. “N” indicates total number of calls that were manually detected.

Name	N	Reference	Definition
<i>Trill</i>	1,473	Ray et al. 1969	Narrow band, frequency modulated calls, and in this study, only trills in descending frequencies were recorded. The start frequencies of trills vary from a 4.09 kHz to 10.3 kHz and the end frequencies were stable around 1.02 kHz in contrast.
<i>Moan</i>	635	Ray et al. 1969	Shorter duration and lower-pitched call compared to trill. Frequency is constant from start to the end.
<i>High-moan</i>	1,236	–	Newly distinguished from moan by acoustic characteristics: fundamental frequencies of high-moan were significantly higher and the duration was also significantly longer than moan. Frequency sweeps downward.
<i>Short</i>	14	–	Relatively low-pitched and the duration vary from 0.56 to 9.67 sec. Usually occurred in bouts and were repeated 2 to 5 times.
<i>Bell</i>	72	–	Pulsed sound including 8 to 40 pulses (Mean $\pm$ SD = 19 ± 9.2) within a call. Center frequency of the pulse is often downward in the latter of a call.
<i>Groan</i>	34	Cleator et al., 1989	The lowest frequency sound among the bearded seal call types. Usually occurred in bouts and were repeated 2 to 10 times.

Table 4.4. Comparison of ANOVA table between two regression analyses (1 process: single regression line, 2 process: composite curve of two regression lines). Table shows degree of freedom (DF), sum of squares (SS), mean square (MS), *F*-Value, and *P*-values of the two regressions and the added variances (from 2 process to 1 process).

	<i>df</i>	<i>SS</i>	<i>MS</i>	<i>F</i>	<i>P</i>
1 process	1	125.3	125.3	187.9	3.2405E-18
2 process	3	139.9	46.6	122.8	5.7788E-22
Added variance	2	14.6	7.3	19.2	8.5844E-07

Table 4.5. Transition matrix of the male 3 call types

Preceding call type	Following call type			Marginal Total
	trill	moan	h-moan	
trill	498	356	253	1107
moan	197	0	176	373
h-moan	438	14	100	552
Marginal Total	1133	370	529	2032

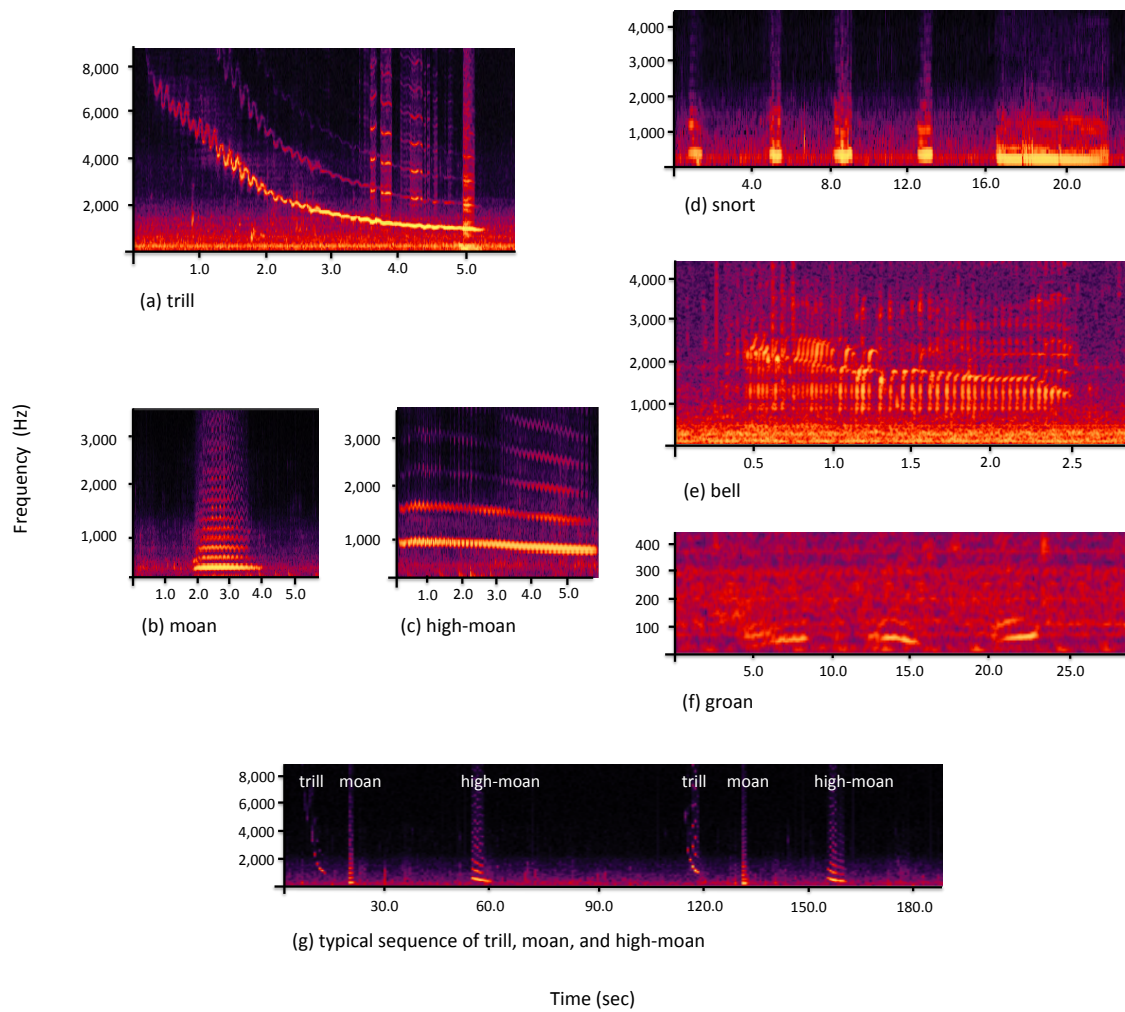


Fig. 4.1. Sound spectrograms of each call type of the ringed seals. All spectrograms were produced with frequency resolutions of 46.9 Hz (Hamming window, 1,024 points, 48 kHz sampling rate) for trill, moan, high-moan, snort, and bell, or 11.7 Hz (Hamming window, 4,096 points, 48 kHz sampling rate) for groans.

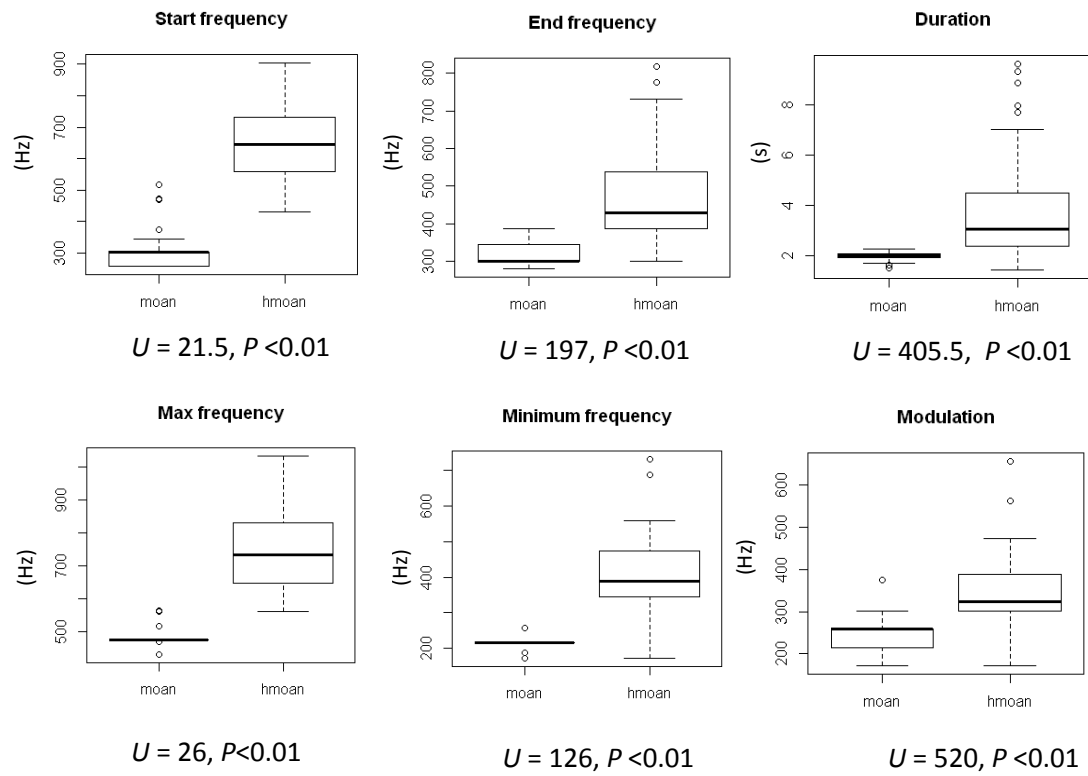


Fig. 4.2. Difference in the acoustic characteristics between moan and high-moan. U - and P - values were calculated by the Mann-Whitney U test.

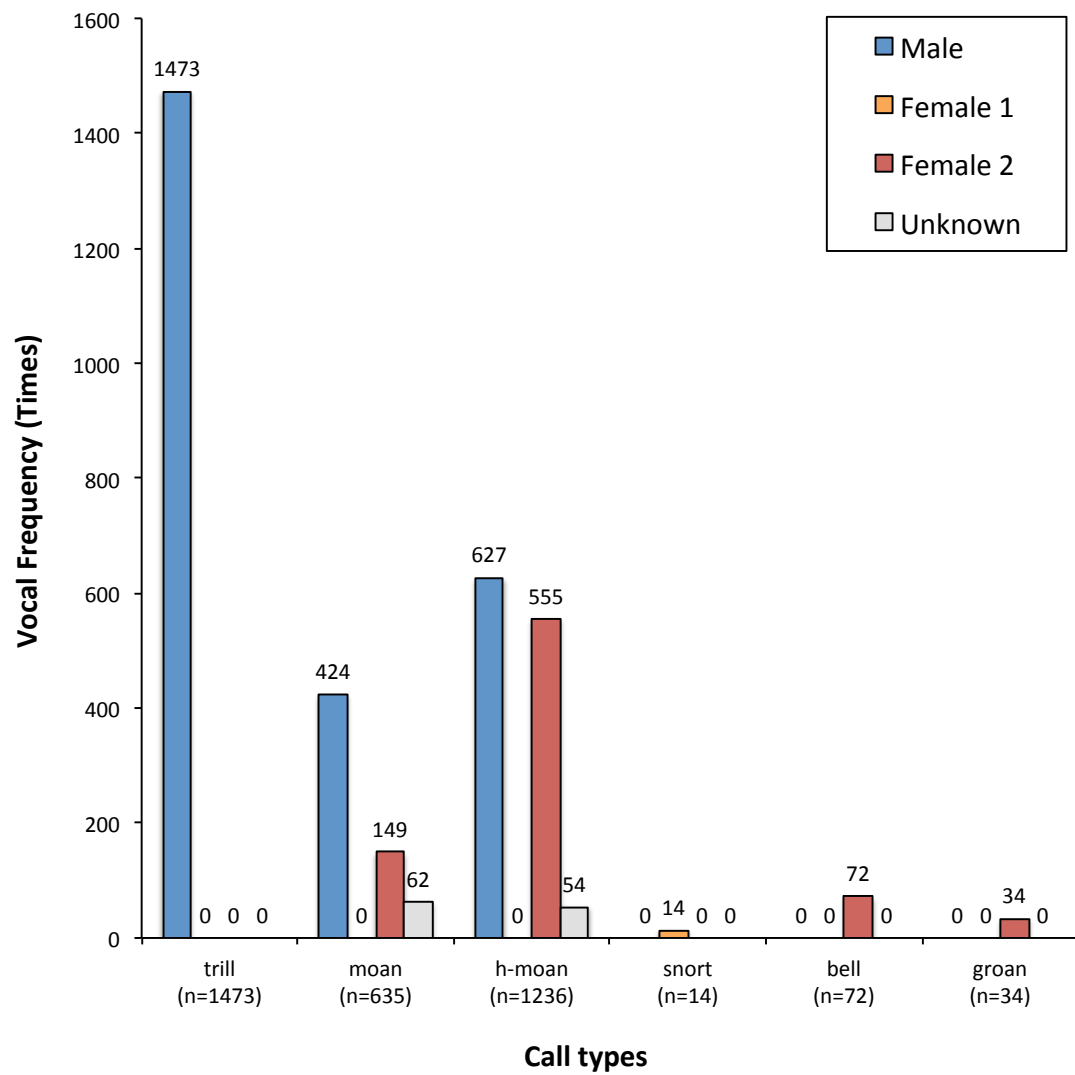


Fig. 4.3. Individual difference in frequencies of occurrence of the vocalizations by bearded seals

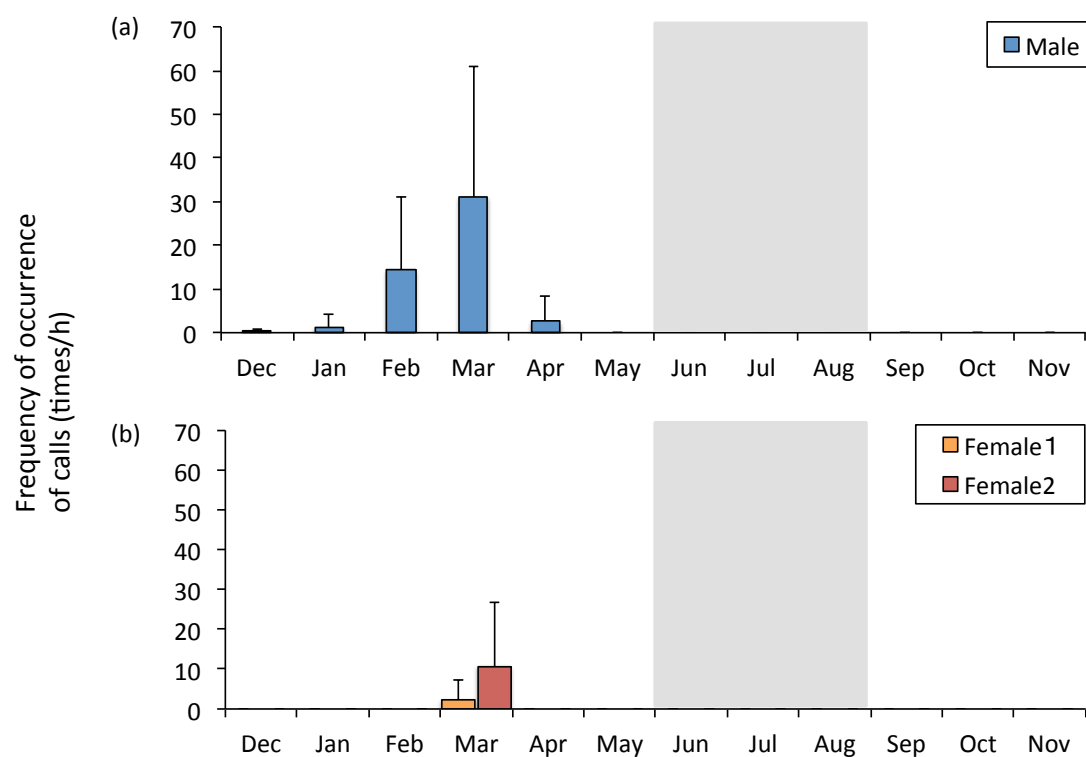


Fig. 4.4. Monthly presence of the vocalizations by 3 bearded seals (Mean value $\pm$ SD): (a) the adult male, and (b) the 2 adult females. Shaded areas indicate periods with no acoustic data.

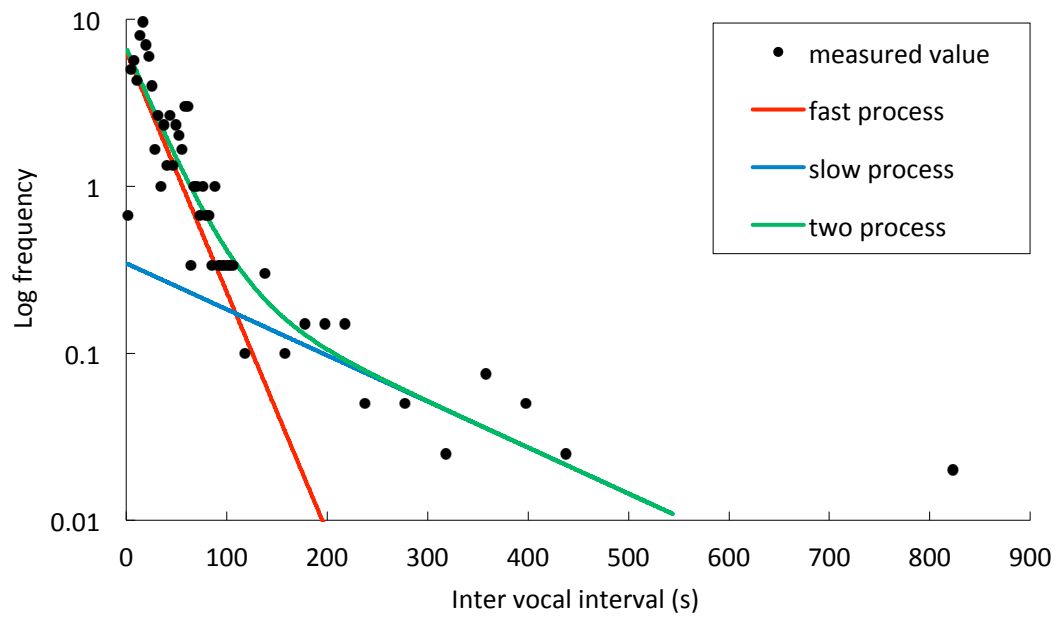


Fig. 4.5. Calculation of bout criterion interval following the method by Sibly *et al.* (1990). The plots show the relative frequency distribution of call intervals. The x-coordinate at intersection of two regression lines indicates the bout criterion interval.

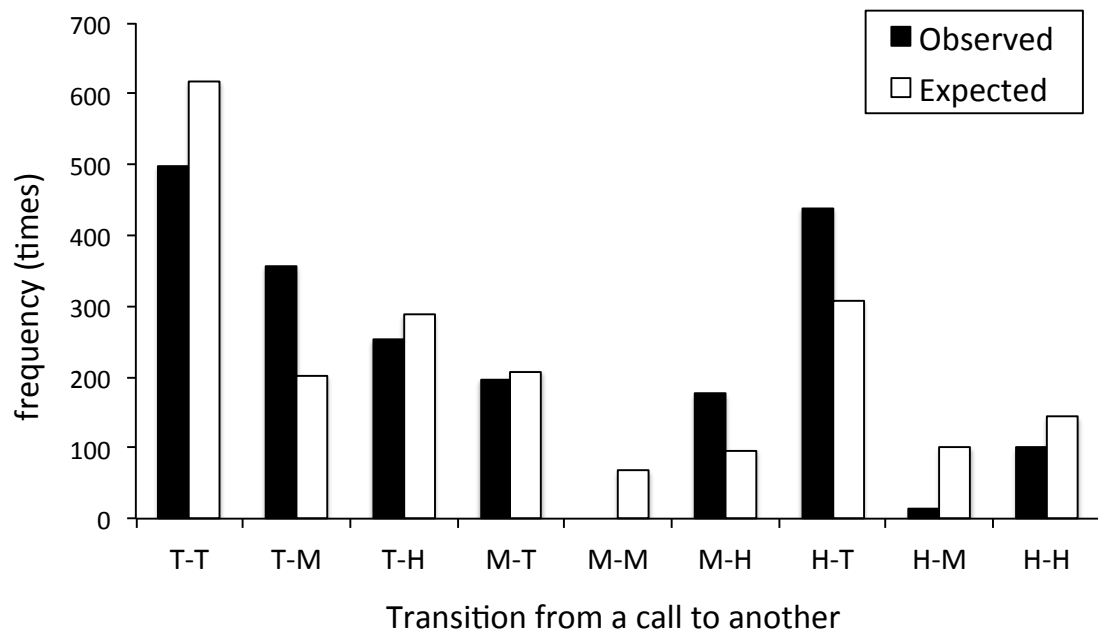


Fig. 4.6. Observed and expected frequency of the transition from a call to the next within a vocal bout by the adult male. The male produce 3 call type: trill (T), moan (M), and high-moan (H).

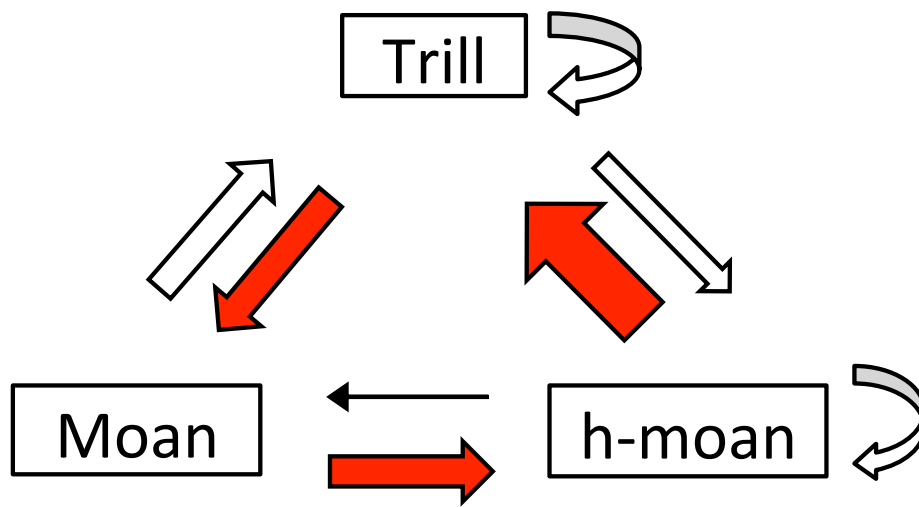


Fig. 4.7. Transition diagram within vocal bouts by the adult male. Wider arrows indicate the higher frequency of transition. Red arrows indicate that frequency of observed transition is higher than those of expected transition (see Fig. 4.6).

Chapter 5: Study of underwater vocalizations in ribbon seals

Section 5.1:

Acoustic recording and behavioral observation in captive ribbon seals

5.1.1. Introduction

Ecology

The ribbon seal (*Histiophoca fasciata*) is medium-sized species in the group of ice-associated seals in the North Pacific (Boveng *et al.* 2013). They are larger than ringed seals and smaller than bearded seals (150–175 cm in total length, and 70–90 kg in body weights; Burns 1981b, Fedoseev 2002). Males and females are reported to be similar in their sizes (Fedoseev 1973). This species inhabits ice-covered areas of the Okhotsk, Bering, and Chukchi Seas, where they feed primarily on cods or cephalopods in deeper (>200 m) sea areas (Burns 1981b). Breeding occurs on the ice floes peaking at the end of April to early May (Boveng *et al.* 2013). The breeding colonies have been reported in the Okhotsk and Bering Seas, but there is no clear evidence of population

distinction between the two (Boveng *et al.* 2013).

Vocal repertoire of ribbon seals

There are few studies on vocalization in the ribbon seal. Watkins and Ray (1977), who studied the species in ice-covered waters near St. Lawrence Island in the Bering Sea in May 1961, recorded two types of underwater sounds: “sweep” (*down sweep*) with intense downward frequency changes, and broadband “puffing” sounds. Miksis-Olds *et al.* (2011), who analyzed the ribbon seal sounds contained in passive acoustic monitoring records from the Bering Sea, further divided the puffing sounds into *roars* and *grunts*. Furthermore, Jones *et al.* (2014), who analyzed passive acoustic monitoring records from the Chukchi Sea, added three additional call types: *yowl*, *hiss*, and *growl*. Therefore, six call types (*down sweep*, *grunt*, *roar*, *yowl*, *hiss*, and *growl*) have been reported in the Bering and Chukchi Seas. Some other passive acoustic methods have also recorded ribbon seal vocalizations in the Bering (Miksis-Olds *et al.* 2014) and Chukchi Seas (Moore *et al.* 2012).

These sounds were speculated to function as reproductive and/or territorial signals (Watkins and Ray 1977) based on the seasonal occurrence of sounds. However, passive acoustic studies reported that ribbon seals vocalize even outside the breeding season in the Chukchi Seas

(Moore *et al.* 2012; Jones *et al.* 2014). Moreover, little is known about the behavioral context of the sounds mainly because the direct observation is difficult due to their entire pelagic life history.

In this chapter, I aimed to estimate the functions of underwater vocalizations in ribbon seals by seasonality and behavioral context of the sounds.

5.1.2. Methods

The behavioral observations and sound recordings were conducted in Otaru Aquarium, Hokkaido, Japan, from August 2011 to April 2012. Three subject seals (two adult females, and one sub-adult female) were rescued from the coast of Hokkaido (Table 5.1.1). They were kept in the same tank (5.7 m × 3.7 m, 21.2 m² area, 1.8 m water depth) with surrounding ground covering an area of 40.8 m² (11.0 m × 3.7 m). Recordings of sounds emitted by the seals and behavior observations were carried out continuously for 7–8 h in the daytime (0900–1700 h) on August 22, September 9, 10, 12, 13, and 14, and December 19, 20, 21, 22, 23, and 24 in 2011; and March 1, 2, 3, 4, 5, and 6, and April 10 in 2012. Additional nighttime recordings were carried out for 10 h (1700–0300 h) on December 23 in 2011 and April 10 in 2012. Sound recordings, behavioral observations, and consequent analysis were conducted following the general method (See Chapter 2).

5.1.3. Results

During the study period, three females of ribbon seals never vocalized nor showed any social behaviors neither in breeding and non-breeding seasons in the 19 recording days between Aug. 2011 to Apr. 2012 (129.3 hours in sound recording time and 122.8 hours in observation time) The three seals usually kept distances and rarely approached each other (Fig. 5.1.1).

5.1.4. Discussion

The three females never produced underwater sounds during the study period. It is possible that only male ribbon seals actively vocalize. Only adult males have developed air-sac attached to the lower end of the trachea (Abe *et al.* 1977), which is probably related to sound production and/or adding buoyancy (Burns 1981b), supporting the possibility of the male-specific sound production. Another possible explanation is that females also vocalize but only with the interaction with their mates and/or pups. My sampling periods were highly limited and hence further study is needed to confirm these possibilities.

Table 5.1.1. Characteristics of the ribbon seals living in the Otaru Aquarium

Name	Sex	Age(yrs)	State of sexual maturity	Origin
<i>Kurarisu</i>	Female	>8	Mature	Rescued off coast of Northern Hokkaido, Japan
<i>Kurara</i>	Female	>6	Mature	Rescued off coast of Northern Hokkaido, Japan
<i>Naporin</i>	Female	>3	Immature	Rescued off coast of Northern Hokkaido, Japan

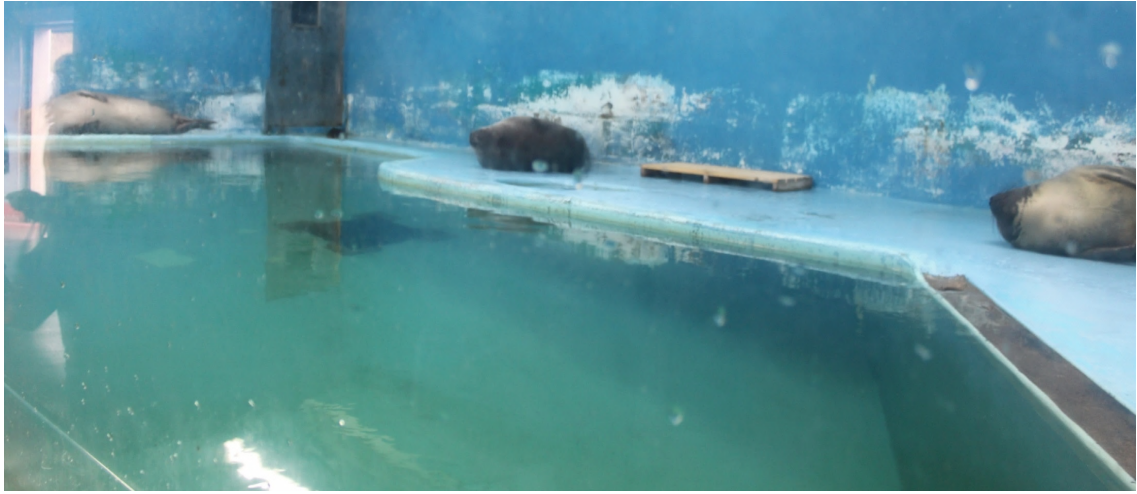


Fig. 5.1.1. Resting captive ribbon seals that always keep a distance from each other.

Section 5.2:

Geographically specific underwater vocalizations of ribbon seals (*Histiophoca fasciata*) in the Okhotsk Sea suggest a discrete population

5.2.1. Introduction

Marine mammal species are often separated into discrete populations, the evaluation of which is important in developing effective animal management strategies (Taylor 1997). To this end, for the species that vocalize distinctively, geographic variation in vocalization will indicate whether or not mixing among populations is occurring (Thomas *et al.* 1988; McDonald *et al.* 2006).

The ribbon seal (*Histiophoca fasciata*) is an ice-breeding species that inhabits ice-covered areas of the Okhotsk, Bering, and Chukchi Seas (Burns 1981b). Breeding colonies have been reported in the Okhotsk and Bering Seas, and the Biological Review Team in the National Oceanic and Atmospheric Administration (NOAA) judged that the threats of ribbon seal is more significant in the Okhotsk Sea than the Bering Sea, because of the sea ice loss and the regulation of petroleum development in the Okhotsk Sea (Boveng *et al.* 2013). However, there is currently no

clear evidence of population distinction between the two (Boveng *et al.* 2013).

Most seal species that mate in the water produce several call types (Stirling *et al.* 2003), but there are few studies on vocalization in the ribbon seal. Six call types (*down sweep*, *grunt*, *roar*, *yowl*, *hiss*, and *growl*) have been reported in the Bering and Chukchi Seas. Some other passive acoustic methods have also recorded ribbon seal vocalizations in the Bering (Miksis-Olds *et al.* 2014) and Chukchi Seas (Moore *et al.* 2012). However, there is no information on ribbon seal vocalization in the Okhotsk Sea.

Here, I record and analyze ribbon seal vocalizations in the Okhotsk Sea and compare their vocal repertoire and acoustic characteristics with those reported from the Bering and Chukchi Sea populations, to examine geographic variation in seal vocalization. I also discuss the possibility of a discrete population of ribbon seals in the Okhotsk Sea based on the vocal variation.

5.2.2. Methods

I recorded underwater sounds in the presence of ribbon seals off the coast of Rausu in the Okhotsk Sea, where the seals breed and molt from winter to spring in the presence of ice floes (Naito *et al.* 1979). Visual and audio recording surveys were conducted off the coast of Rausu (Nemuro

Strait, Fig. 5.2.1) from a boat named *Kamuiwakka-55* (13.30 m in total length, and inboard motor type) between March 22 and 26, 2013. The visual surveys were conducted only in good weather and sea conditions when I could identify seals within a distance of about 1 mile using binoculars (model Olympus EXWP I, 10×42). For each sighting, I recorded the group size, sex, growth stage (pup, sub-adult, or adult), and behavior (swimming or hauled-out).

When I sighted ribbon seals on the ice or in the water, I stopped the boat engine if possible and recorded underwater sounds using an omni-directional hydrophone, (model SH 20k System Intech Co. Ltd, Tokyo, Japan) with a flat frequency response from 20 Hz to 20 kHz within 3 dB, connected to the amplifier (model aquafeelerIII, System Intech Co. Ltd, Tokyo, Japan), and a PCM recorder (model PCM D-50, Sony Corporation, Tokyo, Japan) with a sampling rate of 48 kHz. The hydrophone was positioned <5 m below the sea surface when recording. The duration of the recordings varied from 2.0 to 94.1 min (Table 5.2.1) depending on sea ice movement; when sea ice neared the ship, I immediately stopped recording and moved away. Recordings were conducted at nine sites in total (Fig. 5.2.1).

The recorded sounds were analyzed using Raven Pro 1.4 (Cornell Lab of Ornithology). Acoustic characteristics (start, end, minimum and maximum frequencies, and duration) were

recorded for each call from the spectrogram (Fig. 5.5.2a). For the broadband and noisy calls, I did not record start and end frequencies (Fig. 5.2.2b). For the analysis of the acoustic parameters, I used only clear sound records in which the signal-to-noise ratio was >4 dB at the frequency of highest amplitude of the call in the 1/3 octave band analysis. The 1/3 octave band analyses were conducted using R (Version 2.15.3; R Core Team 2015). For the classification of call types, I mainly compared the spectral patterns of the recorded sounds with those of call types described in previous reports from the Bering (Watkins *et al.* 1977) and Chukchi (Jones *et al.* 2014) Seas (Table 5.2.2), additionally referring to the other characteristics described for each call types.

In particular, I precisely compared the *down sweeps* recorded in the Okhotsk Sea with those reported in previous studies in the Bering (Watkins *et al.* 1977) and Chukchi (Jones *et al.* 2014) Seas, focusing on the waveform of the sound spectrogram and the acoustic characteristics. During the initial analysis, as I found previously undescribed section (L2) in *down sweeps* connected behind the common section (L1), acoustic parameters of the two section were analyzed separately (Fig. 5.2.2 c). For the comparison of *down sweeps* among three areas, I used acoustic parameter data from Jones *et al.* (2014), who re-analyzed the records from Watkins *et al.* (1977) obtained near St. Lawrence Island during spring, and then compared these data with their own records from Pt.

Barrow, Alaska in the Chukchi Sea (Table 5.2.2).

Statistical analysis was performed using the software package R (Version 2.15.3; R Core Team 2015). Significance of the differences in duration and frequencies (start, end, minimum, and maximum frequencies) of *down sweeps* among 3 regions were tested using the Games-Howell test. The Games-Howell test was chosen because the acoustic parameters of *down sweep* showed normal distributions ($W = 0.99$, $P \geq 0.05$, Shapiro test), and the variances of the 3 data were not equal ($\chi^2 = 168.46$, $P < 0.05$, Bartlett's test). For *down sweeps* in the Bering and Chukchi Seas, as I only had the values of sample size, mean and standard deviation of each call characteristic (Jones *et al.* 2014), I simulated the data sets by generating random numbers from a normal distribution, whose mean and standard deviation values were set as those reported by Jones *et al.* (2014).

Additionally, acoustic characteristics of *down sweeps* were compared among 3 regions using principal component analyses (PCA), according to variations in their 4 acoustic parameters: duration in L1 part (sec), start frequency (kHz), end frequency (kHz), and presence/absence of L2 part (0/1). Maximum or minimum frequencies were not included for the PCA analysis because their values are mostly same as those of start and end frequencies, respectively.

5.2.3. Results

Sightings

I observed 16 ribbon seals during 12 sighting events and 14.8 h of visual observations (Table 5.2.1). Of the 16 seals, 4 were identified as males and 3 as females based on their body color patterns (Burns 1981b). I could not identify the remaining 9 seals because they were in the water and their body color patterns were not clearly seen. One of the observed females appeared pregnant because of her swollen belly, and I also saw a male–female pair on the ice. Therefore, my observation period appeared to coincide with the breeding season. During the boat trips for visual and audio recording, I also observed 18 spotted seals (*Phoca largha*) and 10 Baird’s beaked whales (*Berardius bairdii*), but these sightings did not overlap temporally or spatially with those of the ribbon seals.

Vocal repertoire

A total of 794 calls were recorded in the nine sessions, from 7.01 hours in the presence of ribbon seals. I concluded that these calls belonged to ribbon seals based on the following criteria:

- 1) I did not observe any other marine mammals in the vicinity (within 1 mile of the boat) when the

calls were recorded.

2) There have been no reports of other marine mammals observed in this survey emitting these call types (spotted seals, Beier *et al.* 1979; Baird's beaked whale, Dawson *et al.* 1998).

Of the 794 calls recorded, 786 in which I could identify wave-forms were classified into the following five call types (Fig. 5.2.3): *down sweep* ($n = 628$), *roar* ($n = 51$), *yowl* ($n = 73$), *grunt* ($n = 27$), and *hiss* ($n = 7$), with reference to Watkins and Ray (1977), Miksis-Olds *et al.* (2011), and Jones *et al.* (2014). The remaining eight calls were too weak for the wave-forms to be identified. Yowls and grunts frequently occurred in alternating series within the same bout as reported in Jones *et al.* (2014). I did not observe the *growls* reported in two previous studies (Watkins *et al.* 1977; Jones *et al.* 2014).

Each call was matched to a call type described in previous studies as follows (Table 5.2.2): *down sweeps* were matched to a previously described ones based on the intense downward frequency change of calls (Watkins *et al.* 1977). *Roars* were broadband and long duration signals as described in the previous studies (Miksis-Olds *et al.* 2011). Additionally, the duration of *roars* in present study was within the range of those reported in the previous study (Jones *et al.* 2014). *Grunts* were also broadband signals which had shorter duration and lower frequency than *roars*, as

described in previous studies (Miksis-Olds *et al.* 2011). *Yowls* were narrow band signals without harmonics as described in the previous study (Jones *et al.* 2014). *Yowls* and *grunts* frequently occurred in alternating series within the same bout as reported in Jones *et al.* (2014). *Hisses* could be separated from other call types by the higher frequency and longer duration as described in the previous study (Jones *et al.* 2014). I did not observe the *growls* reported in two previous studies (Watkins *et al.* 1977; Jones *et al.* 2014), which have 2 to 3 harmonics and a lower fundamental frequency than *barks*.

The call rate ranged from 0.1 to 6.6 calls/min. The four call types with the exception of *down sweeps* were recorded only when the ship engine was stopped (*i.e.*, engine noise was absent) (Table 5.2.1). The acoustic characteristics of these four call types were not remarkably different from those reported from other regions (Table 5.2.2), though the sample size in this study was relatively small because many calls were faint (a signal-to-noise ratio was <4 dB at the frequency of highest amplitude of the call in the 1/3 octave band analysis), and hence many of their acoustic parameters could not be measured.

Comparison of down sweeps

Down sweeps recorded in this study had two different acoustic characteristics from those reported in previous studies, as follows. First, most of the *down sweeps* analyzed had an undulating section in the last part of the call (Fig. 5.2.3a-1), whereas *down sweeps* reported from other regions had no such section, and instead continuously decrease in frequency (Fig. 5.2.3a-2). Most *down sweeps* recorded in the Okhotsk Sea could be separated into two sections based on frequency sweeps: a continuous downward section (L1) and an undulating section (L2) (as shown in Fig. 5.2.2c). Of 628 down sweeps recorded in the Okhotsk Sea, 588 had L2 sections. The remaining 40 *down sweeps* were very faint, with signal-to-noise ratios of the mean amplitude <1.0 . In addition, in the spectrogram of *down sweeps* with L2, the peak power of L2 was significantly lower than that of L1 (Mean $\pm$ SD = 68.4 $\pm$ 3.0 dB, and 70.4 $\pm$ 4.2 dB, respectively) ($P < 0.01$, Paired t -test), suggesting that L2 could be masked by noise more easily than L1. This result suggests that the L2 section would be present in most of down sweeps if the sounds were recorded close to the source.

Second, the duration of the L1 section of the *down sweeps* was significantly longer in the Okhotsk Sea than in previous recordings from the Bering ($t = 4.2$, $P < 0.01$, Games-Howell test) and Chukchi Seas ($t = 12.1$, $P < 0.01$, Games-Howell test), while the duration was not significantly

different between the Bering and Chukchi Seas ($t = 1.4$, $P = 0.34$, Games-Howell test) (Fig. 5.2.4)

In addition, all of the four frequency parameters of *down sweeps* were significantly higher in the Bering Sea than those in the Okhotsk/Chukchi Seas ($P < 0.01$, Games-Howell test).

There were also significant difference in the end and minimum frequencies between Okhotsk and Chukchi Seas ($t = 4.9$ and 5.0 , $P < 0.01$, Games-Howell test), while no significant difference was observed in the start and maximum frequencies between the two regions ($t = 0.51$ and 1.8 , $P = 0.86$ and 0.16 , respectively, Games-Howell test).

Principal component analyses showed that 36.7% of the variability in vocal parameters of *down sweeps* occurred within the PC1 axis, 26.7% in the PC2, and 20.8% in the PC3 (Table 5.2.3).

Presence of L2 part, L1 duration, and L1 end frequency was mostly correlated with the first, second, and third component axis (PC1, PC2, and PC3), respectively. A two-dimensional plot of the principal component axes separated the down sweeps in the Okhotsk Sea from those in the Bering/Chukchi Seas (Fig. 5.2.5).

5.2.4. Discussion

Vocal repertoire

This is the first report of the vocal repertoire of ribbon seals in the Okhotsk Sea. I found five of the six types of underwater vocalization reported in previous studies in the Bering and Chukchi Seas (Watkins *et al.* 1977; Miksis-Olds *et al.* 2011; Jones *et al.* 2014). However, my recordings captured no *growls*. *Growls* are the least frequent of ribbon seal vocalizations (Jones *et al.* 2014), and it is possible that I did not detect them because low-frequency sounds are more easily masked by the ship engine or other noises. Additionally, I recorded four of the five remaining call types, the exception being *down sweeps*, only when the ship engine was stopped (*i.e.*, engine noise was absent) (Table 5.2.1). This suggests that the intensity of *down sweeps* was higher than the other call types. To clarify ribbon seal vocal repertoire in this region, further sound sampling at reduced noise levels will be needed.

The acoustic characteristics of all call types other than *down sweeps* were not markedly different from those reported from other regions. The *down sweeps* recorded in the Okhotsk Sea, however, had two characteristics different from those reported in the Bering and Chukchi Seas: an undulating section (L2) at the end of the call, and longer duration. Although the sample size of

present study is limited and individual variation in the acoustic characteristics cannot be evaluated, the marked two characteristics are commonly found at all recording sites where I could record *down sweeps* during 4 recording days (Table 5.2.1), and hence these marked characteristics might be common among the individuals in the Okhotsk Sea. Therefore, I suggest that there is marked geographic vocal variation between the Okhotsk and Bering/Chukchi Seas.

The function of ribbon seal vocalizations is unclear. Recording period of present study (March 22 to 26) fell within the breeding season of ribbon seals in the Okhotsk Sea, which is from mid-March to April (Tikhomirov 1971). In addition, I found a pregnant female and a male-female pair. These observations suggest that some of the recorded call types were related to social interaction in a reproductive context. Watkins *et al.* (1977) also speculated that the vocalizations from ribbon seals in the Bering Sea have social functions in reproductive and/or territorial behavior, based on the seasonality of the vocalizations and an analogy with sounds made by other seals. However, recent passive acoustic methods demonstrated an acoustic presence of ribbon seals during the non-breeding season also in the Chukchi Sea (Moore *et al.* 2012, Jones *et al.* 2014). Further studies, focusing on the association between behavior and vocalizations, are needed to clarify the function of the vocalizations.

Possible factors affecting geographic variation

The marked variation observed in the *down sweeps* in the Okhotsk Sea might reflect limitation or lack of exchange of individuals between the populations of the Okhotsk Sea and those of the Bering/Chukchi Seas. Perry *et al.* (1999) suggested similar limitation of individual exchange between populations in harp seals based on the geographic variation in underwater vocalization; seals in the two herds in Canada (Gulf of St. Lawrence and the 'Front' ice east of Labrador) had common vocal repertoire and proportion in usage of call types, which differed from those in the third herd, Jan Mayen Island (east of Greenland). These findings were consistent to tagging studies indicating that the Gulf/Front herds may be interbreeding while both could be isolated from the Jan Mayen herd.

The limited exchange of individuals could be caused by geographic barriers and/or strong site fidelity by individuals. For spotted seals (*Phoca largha*), the Kamchatka Peninsula is thought to be a potential geographic barrier limiting the exchange of individuals between the Okhotsk and Bering Seas (Boveng *et al.* 2013). However, Boveng *et al.* (2013) suggested that it may be not the case with ribbon seals because of their pelagic life history, far out of the continental shelves. Although they found that seals tagged on the east coast of the Kamchatka Peninsula ($n = 10$) moved

to the central Bering Sea and the west coast of Alaska ($n = 41$), and vice versa, there is no clear evidence that ribbon seals move between the Okhotsk and Bering Seas. Further studies focusing on the movements of seals tagged on the west coast of the Kamchatka Peninsula or other parts of the Okhotsk Sea are needed to determine whether they move to the central Bering Sea or areas further northwest.

Site fidelity could limit the exchange of individuals, even in the absence of geographic barriers (Adams *et al.* 2006). Although I still have no information on site fidelity in ribbon seals, geographic vocal variation has been reported in several ice seal species with site fidelity, including the Weddell seal (*Leptonychotes weddellii*, Abgrall *et al.* 2003; Terhune *et al.* 2008), bearded seal (*Erignathus barbatus*, Risch *et al.* 2007).

Another possible factor affecting the geographic variation of *down sweeps* is environmental noise or sounds from other species. Some marine mammals change their acoustic characteristics according to sounds produced by other species (killer whale *Orcinus orca*, Mossbridge and Thomas 1999; Indo-Pacific bottlenose dolphin *Tursiops aduncus*, Morisaka *et al.* 2005; and beluga whale *Delphinapterus leucas*, Au *et al.* 1985). I detected no vocalizations from other species, nor any ice noises, while recording ribbon seal vocalizations in the Okhotsk Sea.

Similarly, in the Chukchi Sea, Jones *et al.* (2014) observed no temporal overlaps between the vocalizations of ribbon seals and those of other marine mammal species, and they detected ribbon seal vocalizations only during the open-water season, suggesting that little ice noise was recorded. In contrast, in the Bering Sea, several call types belonging to other species, including walrus (*Odobenus rosmarus*) and bearded seals (*Erignathus barbatus*), were detected while recording ribbon seal calls (January to May) (Miksis-Olds *et al.* 2011). Sea ice noise was likely included in these recordings because ribbon seal calls were detected only when the sea ice cover exceeded 80% (Miksis-Olds *et al.* 2011). This suggests that ambient environmental sound conditions during the recording periods were similar between the Okhotsk and Chukchi Seas, but differed between the Bering and Chukchi/Okhotsk Seas.

Such environmental factor in 3 regions could explain the difference in the start, end, minimum, and maximum frequencies between the Bering and Chukchi/Okhotsk Seas; calls in the Bering Sea have higher frequencies possibly to avoid the masking by other sound sources. Similar shift in vocal parameters has been reported in a beluga whale (*Delphinapterus leucas*) that increased the peak frequency and amplitude of echolocation sounds when it was exposed to snapping noise by shrimp (Au *et al.* 1985). In contrast, marked variation in the Okhotsk Sea (L2 part and longer

duration) is not likely to be explained by environmental noise or sounds from other species, because the *down sweeps* differed between the Okhotsk and Chukchi Seas while the sound environment was similar. In addition, the *down sweeps* were similar between the Bering and Chukchi Seas though the sound environment was different.

In conclusion, there was marked geographic variation in the underwater vocalizations of ribbon seals between the Okhotsk and Bering/Chukchi Seas. The factors underlying this variation remain unclear but might include the limited exchange of individuals between study regions. Therefore, the variation suggests the presence of a previously unknown discrete population in the Okhotsk Sea. Additional studies on morphological or genetic differences among populations would be useful to test this hypothesis.

Table 5.2.1. Information of observed seals and number of occurrence of call types during the recordings

Date	Group size	Male/ Female	Adult/Subadult /pup	Siwm /Haul out	Call Type							Ship Engine	Duration of the Recordings (min)
					Down sweep (with L2)	roar	yowl	grunt	hiss	others	Total		
130322	2	Unknown	Unknown	Haul out	24(13)	0	0	0	0	0	24	On	56.7
	2	Unknown	Unknown	Swim	76(72)	13	17	2	1	0	109	Off	50.2
	2	Unknown	Unknown	Swim	67(64)	2	0	0	0	8	77	Off	22.5
130324	1	Unknown	Unknown	Swim	419(399)	36	56	25	6	0	542	Off	81.6
130325	1	Unknown	Unknown	Swim	2(2)	0	0	0	0	0	2	On	8.0
	1	Male	Adult	Swim	-	-	-	-	-	-	-	-	
	1	Female	Adult	Haul out	7(7)	0	0	0	0	0	7	On	77.3
	2	Male&Female	Adult	Haul out	-	-	-	-	-	-	-	-	
	1	Male	Adult	Swim	3(3)	0	0	0	0	0	3	On	28.0
	1	Female	Adult	Haul out	-	-	-	-	-	-	-	-	
130326	1	Unknown	Unknown	Swim	0(0)	0	0	0	0	0	0	On	2.0
	1	Male	Adult	Haul out	30(30)	0	0	0	0	0	30	On	94.1
Total					628(588)	51	73	27	7	8	794		420.4

Table 5.2.2. Vocal parameters of each call type in the Okhotsk Sea and comparison of the acoustic parameters among three recording sites. (Acoustic parameters in the Bering Sea and the Chukchi Sea belong to Jones *et al.* 2014). (a) *Down sweeps*

(a)

Call type	Sea area	<i>n</i>		Frequencies (kHz)						Frequency sweep rate in L1 (kHz/s)	Duration (s)	
				Start	End_L1	End_L2	Min.	Max_L1	Max_L2		L1	L2
<i>Down Sweep</i>	Okhotsk	63	Mean $\pm$ SD	1.6 $\pm$ 0.3	0.3 $\pm$ 0.1	0.3 $\pm$ 0.09	0.3 $\pm$ 0.05	1.6 $\pm$ 0.3	1.6 $\pm$ 0.3	0.68 $\pm$ 0.13	1.94 $\pm$ 0.19	0.49 $\pm$ 0.07
			(Range)	(1.0 – 2.3)	(0.2 – 0.4)	(0.2 – 0.5)	(0.2 – 0.4)	(1.0 – 2.3)	(0.7 – 0.8)	(0.43 – 1.02)	(1.50 – 2.51)	(0.34 – 0.69)
	Bering	112		2.7 $\pm$ 1.4	0.6 $\pm$ 0.7	0.6 $\pm$ 0.8	0.6 $\pm$ 0.7	2.7 $\pm$ 1.4	2.7 $\pm$ 1.4	<i>ca.</i> 0.90	1.53 $\pm$ 0.97	N/A
				(0.7 – 9.8)	(0.03 – 2.3)	N/A	(0.02 – 2.3)	(0.7 – 10.2)	N/A		(0.53 – 6.38)	
	Chukchi	146		1.7 $\pm$ 0.6	0.4 $\pm$ 0.2	0.4 $\pm$ 0.3	0.4 $\pm$ 0.2	1.7 $\pm$ 0.6	1.7 $\pm$ 0.6	<i>ca.</i> 0.90	1.42 $\pm$ 0.41	N/A
				(0.8 – 4.1)	(0.1 – 1.4)	N/A	(0.1 – 1.4)	(0.8 – 4.1)	N/A		(0.57 – 2.94)	

Table 5.2.2. Vocal parameters of each call type in the Okhotsk Sea and comparison of the acoustic parameters among three recording sites (Acoustic parameters in the Bering Sea and the Chukchi Sea belong to Jones *et al.* 2014). (b): Other 5 call types

(b)								
Call type	Sea area	n		Frequencies(kHz)				Duration (s)
				Start	End	Min.	Max	
<i>Roar</i>	Okhotsk	9	Mean $\pm$ SD	-	-	0.6 $\pm$ 0.3	1.6 $\pm$ 0.2	0.9 $\pm$ 0.2
			(Range)	-	-	(0.2 – 0.8)	(1.4 – 2.2)	(0.5 – 1.3)
	Bering	38		0.4 $\pm$ 0.1	0.4 $\pm$ 0.2	0.3 $\pm$ 0.1	0.6 $\pm$ 0.2	0.8 $\pm$ 0.3
				(0.3 – 0.9)	(0.08 – 0.8)	(0.07 – 0.6)	(0.3 – 1.0)	(0.3 – 1.3)
	Chukchi	98		0.2 $\pm$ 1.5	0.4 $\pm$ 0.1	0.3 $\pm$ 0.1	1.6 $\pm$ 0.6	0.9 $\pm$ 0.3
				(0.2 – 1.5)	(0.1 – 0.8)	(0.09 – 0.6)	(0.5 – 3.0)	(0.3 – 1.6)
<i>Grunt</i>	Okhotsk	8		-	-	0.3 $\pm$ 0.05	0.7 $\pm$ 0.2	0.6 $\pm$ 0.02
				-	-	(0.2 – 0.3)	(0.6 – 0.9)	(0.6 – 0.7)
	Bering	173		0.4 $\pm$ 0.2	0.4 $\pm$ 0.2	0.3 $\pm$ 0.2	0.7 $\pm$ 0.3	0.4 $\pm$ 0.2
				(0.2 – 1.6)	(0.1 – 1.3)	(0.04 – 0.8)	(0.3 – 1.6)	(0.03 – 1.3)
	Chukchi	204		0.4 $\pm$ 0.2	0.4 $\pm$ 0.1	0.03 $\pm$ 0.1	1.1 $\pm$ 0.5	0.4 $\pm$ 0.2
				(0.2 – 1.1)	(0.2 – 1.0)	(0.07 – 0.7)	(0.3 – 2.6)	(0.1 – 1.1)
<i>Yowl</i>	Okhotsk	11		0.6 $\pm$ 0.05	0.6 $\pm$ 0.02	0.6 $\pm$ 0.02	0.7 $\pm$ 0.05	0.3 $\pm$ 0.06
				(0.6 – 0.7)	(0.6 – 0.6)	(0.5 – 0.6)	(0.6 – 0.7)	(0.2 – 0.8)
	Bering	54		0.7 $\pm$ 0.1	0.6 $\pm$ 0.1	0.6 $\pm$ 0.1	0.7 $\pm$ 0.1	0.5 $\pm$ 0.3
				(0.3 – 0.9)	(0.3 – 0.7)	(0.2 – 0.7)	(0.4 – 1.0)	(0.06 – 1.04)
	Chukchi	273		0.7 $\pm$ 0.2	0.6 $\pm$ 0.1	0.6 $\pm$ 0.1	0.7 $\pm$ 0.3	0.6 $\pm$ 0.3
				(0.2 – 2.2)	(0.2 – 1.3)	(0.2 – 1.2)	(0.2 – 2.6)	(0.1 – 1.9)
<i>Hiss</i>	Okhotsk	7		-	-	1.7 $\pm$ 0.4	2.1 $\pm$ 0.7	5.6 $\pm$ 3.0
				-	-	(1.1 – 2.3)	(1.3 – 3.2)	(2.6 – 8.9)
	Bering	20		1.3 $\pm$ 1.0	1.1 $\pm$ 1.1	0.9 $\pm$ 1.0	2.3 $\pm$ 2.3	4.4 $\pm$ 5.6
				(0.2 – 3.8)	(0.3 – 4.3)	(0.2 – 4.3)	(0.6 – 10.4)	(0.7 – 17.5)
	Chukchi	10		1.8 $\pm$ 0.1	1.7 $\pm$ 0.1	1.3 $\pm$ 0.3	2.2 $\pm$ 0.2	4.7 $\pm$ 2.8
				(1.7 – 1.9)	(1.4 – 1.9)	(0.5 – 1.6)	(1.7 – 2.3)	(0.4 – 7.5)
<i>Growl</i>	Okhotsk	-		-	-	-	-	-
				-	-	-	-	-
	Bering	4		0.2 $\pm$ 0.1	0.2 $\pm$ 0.1	0.2 $\pm$ 0.1	0.3 $\pm$ 0.2	0.3 $\pm$ 0.07
				(0.1 – 0.4)	(0.04 – 0.3)	(0.94 – 0.3)	(0.1 – 0.5)	(0.2 – 0.3)
	Chukchi	17		0.07 $\pm$ 0.02	0.08 $\pm$ 0.04	0.07 $\pm$ 0.02	0.5 $\pm$ 0.2	0.5 $\pm$ 0.2
				(0.04 – 0.1)	(0.05 – 0.2)	(0.05 – 0.1)	(0.3 – 0.8)	(0.2 – 0.8)

Table 5.2.3. Principal-component analyses of the 4 parameters of *down sweeps* of ribbon seals: duration in L1 part (sec), start frequency (kHz), end frequency (kHz), and presence/absence of L2 part (0/1).

	PC1	PC2	PC3
L1 Duration (s)	-0.427	0.699	-0.109
L1 Start Frequency (kHz)	0.463	0.533	-0.570
L1 End Frequency (kHz)	0.445	0.426	0.787
Presence/Absence L2 (1/0)	-0.636	0.216	0.209
Eigen Value	1.4	1.1	1.0
Cumulative Proportion of Variance (%)	36.7	63.4	84.2

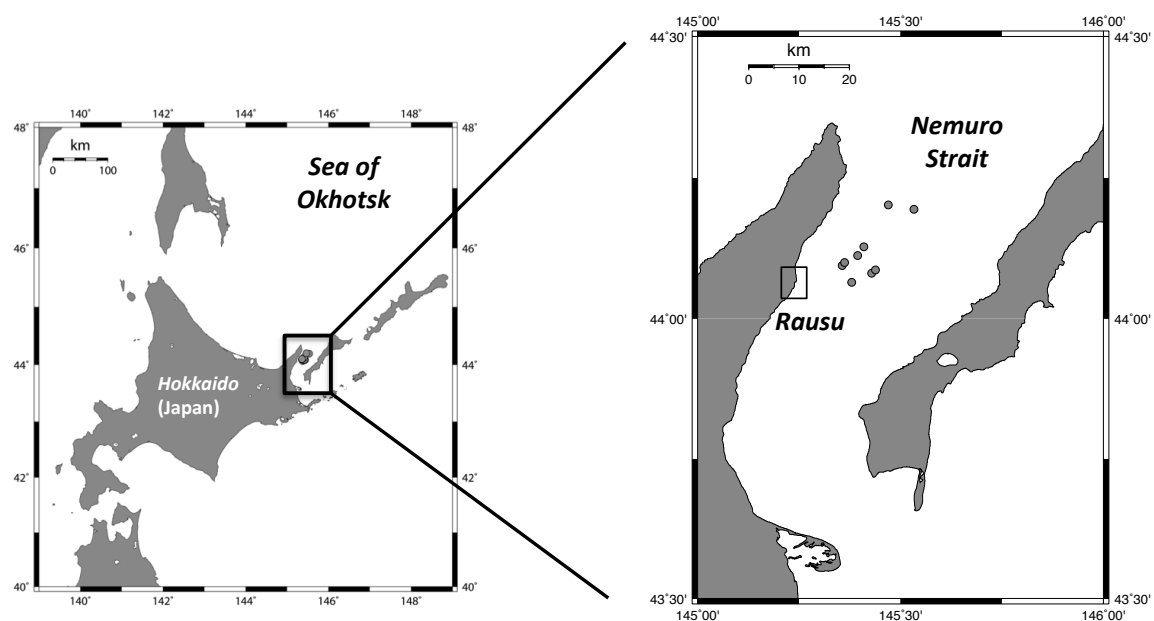


Fig. 5.2.1. Location of recording site. Each plot shows recording point in this study, where ribbon seal was sighted on the ice or in the water.

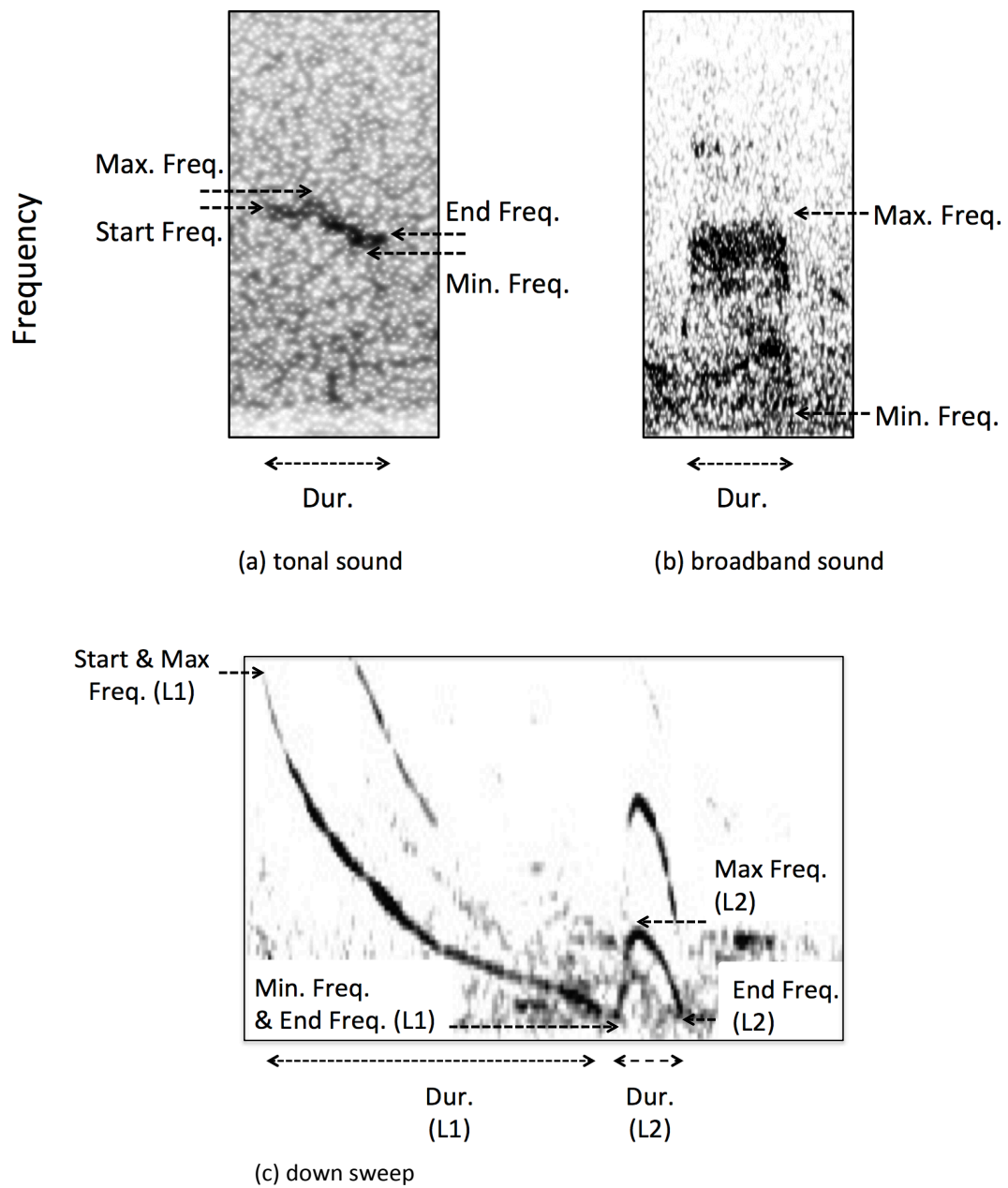


Fig. 5.2.2. Parameters measured for (a) tonal sound (*yowl*), (b) broad band and noisy sound (*roar*, *grunt*, and *hiss*), and (c) *down sweep* for the purpose of comparing the acoustic characteristics among sites.

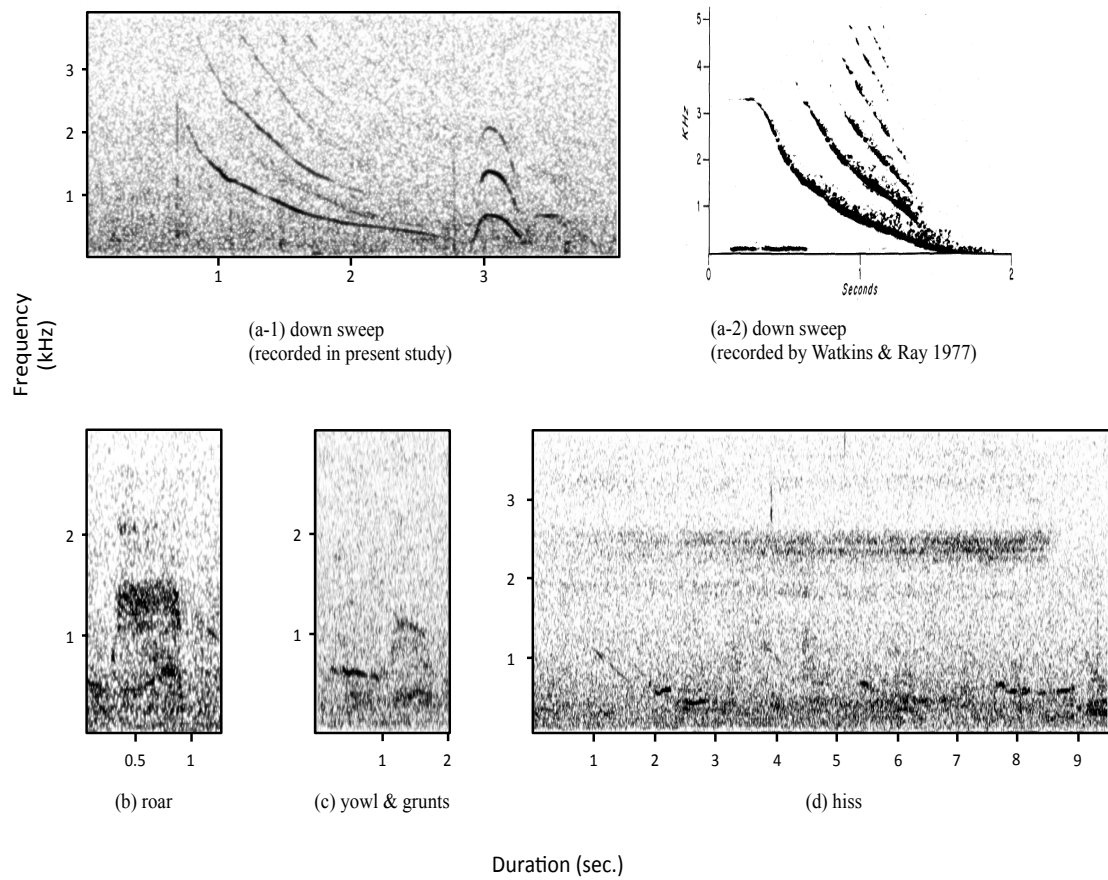


Fig. 5.2.3. Spectrograms of call types of ribbon seals: (a-1) *down sweep* recorded in present study, (a-2) *down sweep* recorded in the Bering Sea by Watkins and Ray 1977), (b) *roar*, and (c) *yowl* (left) and *grunts* (right), and (d) *hiss* (around 2.5 kHz) associated with alternating series of *yowl* and *grunts*. Spectrograms were made from 48 kHz sampling rate recordings with 2048 point FFT size, Hamming window, and 90 % overlap.

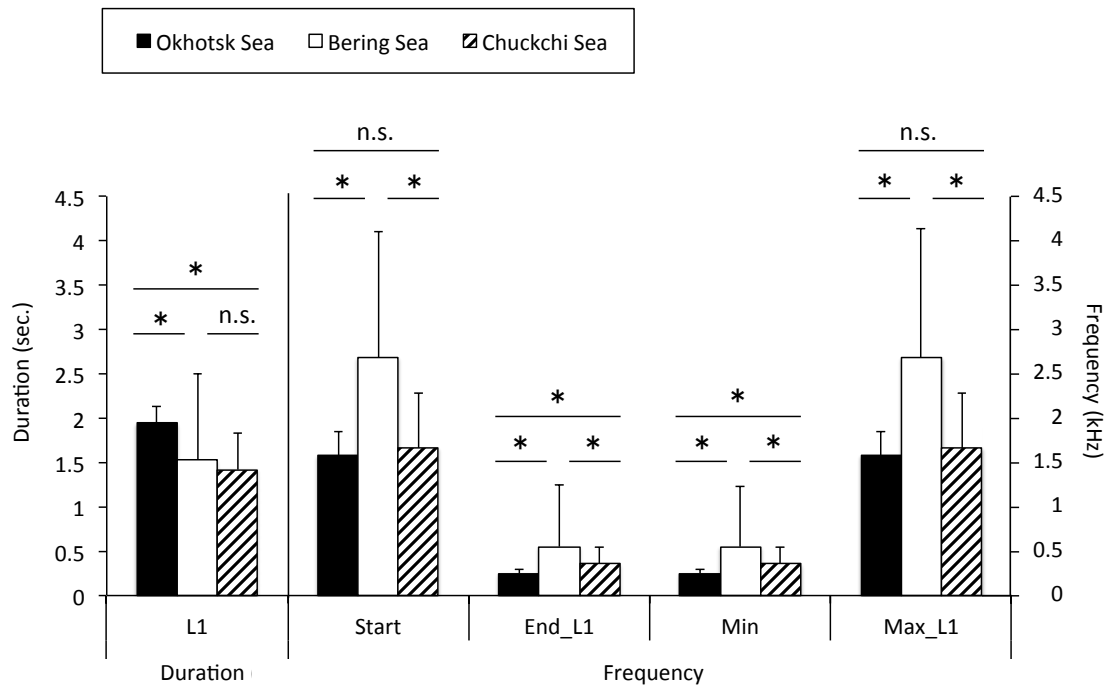


Fig. 5.2.4. Comparison of acoustic characteristics in *down sweeps* among three sites (*: $P < 0.05$, after adjusted using the Holm's procedure)

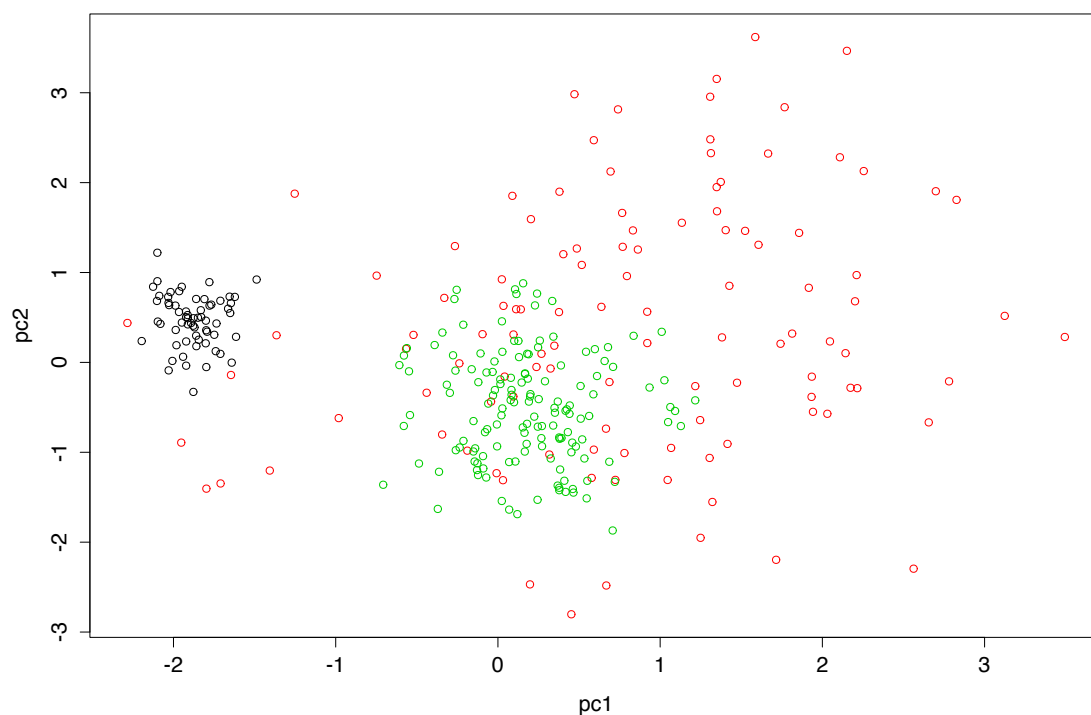


Fig. 5.2.5. A two-dimensional plot of the principal-component axes calculated from the 4 parameters of *down sweeps* in 3 regions for ribbon seals: duration in L1 part (sec), start frequency (kHz), end frequency (kHz), and presence/absence of L2 part (0/1). Plots for the Okhotsk Sea (black) are distinctive from those for the Bering (red), and the Chukchi (green) Seas, while there were some overlap between the Bering and Chukchi Seas.

Chapter 6:

General Discussion

6.1. Inter-specific comparison of vocal behavior

Relationship between underwater vocalization and ecological characteristics

Rogers (2003) categorized phocid seals into three groups based on their natural histories and acoustic characteristics. First group consist of the species in which estrus females are predictably distributed, and hence males can guard the estrus females. Most of the land-breeding seals belonged to this group and these seal species tend to be agonistic interaction. Contrary, most of the aquatic-mating seals (including ice-breeding seals) were placed in the second or third groups. In the second group, estrus females are predictably distributed but males cannot guard females (as females do not remain haul-out but actively swim for foraging), while in the third group, estrus females are not predictably distributed (widely dispersed) and hence males cannot guard females.

The ringed seal was placed in the second group consisting of the harp (*Pagophilus groenlandicus*), harbour (*Phoca vitulina*), and Weddell (*Leptonychotes weddellii*) seals. This group has the largest vocal repertoire of the three groups, including various types of sounds thought to be

used for short-range mate attraction and/or territory defense (Rogers 2003). Four of the six call types of ringed seals identified in the present study are thought to be used for short-range communication (*i.e.* contact with a specific individual) for mate attraction and/or agonistic interaction. The other two call types, woof and clicks, could not be analyzed because I could not identify the caller and/or the sample size (number of vocalizations) was too small.

In contrast, ribbon (*Histiophoca fasciata*) and bearded (*Erignathus barbatus*) seals were placed in the third group consisting of leopard (*Hydrurga leptonyx*) and ross (*Ommatophoca rossii*) seals. Species in this group produces sounds used in long-range communication (Rogers 2003). For example, captive leopard seals produce “broadcast” calls advertising their breeding condition to potential mates (Rogers *et al.* 1996). The 3 call types of male bearded seals identified in the present study also seemed to be used as long-range communication (*i.e.* sound with no social interaction and not toward a specific individual) in the same manner as leopard seals, while no such signals were identified in either my current or previous studies on the ringed seal. Although I did not observe any association between sound and behaviors of ribbon seals, the frequency-modulation in *down sweep* sounds may be easy to be localized by other individuals (May *et al.* 1986), suggesting that this species also use the sounds for long-range communication, as is the case in trill sounds of bearded

seals.

The difference in the acoustic behavior between the two groups seems to reflect their ecological characteristics. In the first group (including the ringed seal), most species are gregarious to some extent around the breathing hole of fast ice. In contrast, individuals of the second group (that including the bearded and ribbon seals) are widely dispersed in regions of pack-ice area (Rogers 2003). This ecological difference could cause the difference in the acoustic behavior among ice-associated seals.

Phylogenetic relationship was unlikely to explain the difference in the acoustic behavior, since phylogenically related species do not show acoustic similarity: for example, acoustic behavior of ribbon seal, which is solitary and vocalize primarily for reproduction, is quite different from its closest species, harp seal (Yonezawa *et al.* 2007), which is gregarious and have vocal repertoire for agonistic interaction. Instead, phylogenically-unrelated species often shows acoustic similarity: ringed seal and weddell seals, which use similar acoustic signals and show similar ecological characteristics (*e.g. gregarious and maintaining the breathing holes*) (Stirling and Thomas 2003).

Seasonality of vocalization

There was a difference in the seasonal occurrence of sounds between the ringed and bearded/ribbon seals: ringed seals vocalized both during breeding and non-breeding season, while bearded/ribbon seals produced sounds only during breeding season. This also seemed to reflect their ecological difference. Ringed seal is gregarious to some extent around the breathing hole throughout the year (Stirling *et al.* 1983), while bearded/ribbon seals become solitary and widely dispersed during non-breeding season (Burns 1981a,b), suggesting that only ringed seals need to social interactions (*e.g.* keeping territory around the breathing holes) even in the non-breeding season. However, I have to note that some passive acoustic studies showed the occurrence of sounds by bearded/ribbon seals in the Chukchi Sea outside the breeding season (Moore *et al.* 2012; MacIntyre *et al.* 2013; Jones *et al.* 2014), though the frequency of occurrence of sounds were much lower than those in breeding season.

6.2. Application to passive acoustic monitoring

Passive acoustic monitoring (PAM) is essential for ice-seals research in polar region, where direct and continuous observation of animals is difficult due to low accessibility by the sea ice and the seals' underwater movement in three-dimension. This study offers potential for the

monitoring of wild ice-seals with passive acoustic records in various aspects.

First, the number of target call types for PAM could be increased. For ringed seals, as suggested in Section 3.5, some of the calls identified in the present study (*e.g.*, long snorts, knocks) are likely to be included in the data sets recorded in the wild. Thus, present study could increase the repertoire size used for PAM of ringed seals, and could be applied to monitor the behavior of animals in the wild from the sounds. In the similar manner as ringed seals, bearded seal calls described in captivity could be detected in recordings in their wild habitat.

Second, some sounds could be used for monitoring the distribution of male and female seals separately. Some call types of bearded seals identified in present study were sex-specific (Ringed seals: long snort only by the adult male; Bearded seals: trills only by the adult male, and snort, bell, and groan only by the adult females). Especially, the female calls possibly indicate the presence of sexually active females, as these sounds were associated with possible reproductive behavior (nuzzling) during breeding season in captivity.

Third, the marked geographic variation in the underwater vocalizations of ribbon seals between the Okhotsk and Bering/Chukchi Seas could be an indicator of mixing among populations, which is important to understand the totally unknown population structure of this species.

Fourth, I can assess not only the presence of the species but also its behavior. Long snorts of ringed seals were produced by adult male only in breeding season, suggesting that this call type could be applied to assess when and where the courtship behavior occurs. On the other hand, knocks, yelp, and barks were produced during agonistic interactions, which could be an indicator of seasonal change in the degree of agonistic behaviors for territorial defense. For bearded seals, female vocalizations were associated with nuzzling behaviors, both of which were observed only in breeding season, suggesting that these sounds could be an indicator of the reproductive behavior of this species. Such information is essential to consider the effective management of the species to decide the place where to be conserved on a priority basis.

In most of passive acoustic studies for ice-seals, sound spectrograms are manually (visually) scanned by trained analysts, being compared to previously described call types for each species (*e.g.*, Miksis-Olds *et al.* 2011, MacIntyre *et al.* 2013, Jones *et al.* 2014). Currently, it seems difficult to set absolute criteria (time–frequency) for detecting target calls of the three species automatically, because there are many overlaps of the acoustic parameters among species. Thus, it is indicated that we should detect the call types mainly based on spectral patterns of spectrograms (see Table 3.1.3, Table 4.3, Fig. 3.1.1., Fig. 4.1, and Fig. 5.2.3).

Some automated detectors, however, have succeeded to detect target calls automatically.

Hannay *et al.* (2015) used automated detectors based on contour extraction for bearded seal calls and successfully detected the calls with 65% precision to the manual analyst. Such contour extraction would be applicable for tonal sounds (*e.g.*, *long snorts* of ringed seal, *trills*, *moans*, and *high-moans* of bearded seals, and *down sweeps* of ribbon seals), but not for the other pulsed or noisy sounds. As call types within species have several different functions, it is ideal that not only tonal sounds but also pulsed or noisy sounds should be detected manually by analysts, when monitoring the behavior of seals from sounds.

6.3. Conclusion and future research directions

I analyzed association between underwater vocalization and behavior of 3 ice-breeding seals in captivity and estimated the function of their sounds. Currently, little is known about the vocal behavior in most species of ice-breeding seals mainly due to the low accessibility to the natural habitat covered with sea ice. Accordingly, observation in captivity has great advantage to understand the behavioral context and function of their underwater vocalization. Captive studies could also be applied to other ice-breeding seals than my subject 3 species.

As I have limited number of individuals in the present study, future investigations are needed focusing on sexual and age differences in vocal behavior by increasing the target individuals in captivity. Additionally, the process of vocal learning also needs to be investigated in captivity, which I did not investigate currently due to the short study period.

Recent development of acoustic devices has enabled us to record the vocal activity longer duration in larger area. Present study in captivity offers potential for deriving more information from such recordings in the wild with passive acoustic records by increasing target call types and assessing not only the presence of the species but also its behavior.

Ice-associated seals largely rely on sea ice for their entire life history, including pupping, resting, and feeding, and hence recent dramatic climate change would negatively affect them. It is essential to continuously monitor how the behavior of animals will change according to current climate change. Monitoring of underwater behavior using sounds would be a strong way to assess such behavioral response of the ice-breeding seals and consider the effective management strategy.

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