Growth and Reproduction in Harbour Porpoise (*Phocoena phocoena*) Inhabiting Hokkaido, Japan

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Abstract

Growth and maturity parameters of harbour porpoises (*Phocoena phocoena*) around Japanese waters were summarized using samples and information from 214 individuals stranded and bycaught along the coast of Hokkaido from 2009 to 2019. We estimated ages from dental growth layer groups (GLGs), made more accurate by independently determining the mean date when layers are established. Gompertz growth curves were fitted, predicting asymptotic lengths of 136.9 cm for males and 158.5 cm for females. Sexual dimorphism was present from 3 years of age, with females larger than males as reported in other subpopulations. Length at sexual maturity (LSM) and age at sexual maturity (ASM) were estimated as 143.1 cm and 7.7 years, respectively, for males, and 154.4 cm and 7.3 years, respectively, for females. In comparison with other studies that examined stranded and bycaught harbour porpoises in other locations, foetuses and neonates comprised a very small proportion of samples. Differences from other populations in the age distributions of pregnant females also indicated that the coastal area of Hokkaido is not used as an area for parturition. This study uses data from the past 10 years to provide basic information on growth and reproduction of animals in and around Hokkaido, which is part of the North Pacific subpopulation of harbour porpoises.

Key Words: growth, maturity, western Pacific Ocean, harbour porpoise, *Phocoena phocoena*

Introduction

Harbour porpoises (*Phocoena phocoena*) inhabit most of the coastal waters of the Northern Hemisphere (Gaskin, 1984; Read, 1999; Jefferson et al., 2015). Their distribution in the eastern Atlantic extends from coastal areas of the Western Sahara to the Barents Sea, including the Faroe Islands, Iceland, and Greenland, and in the western Atlantic from North Carolina to the Gulf of Maine. In the Pacific Ocean, they are found from California and the northern part of Japan to the Bering Sea, the Sea of Okhotsk, and the Sea of Japan (International Union for Conservation of Nature [IUCN], 2020). They are subjected to various interactions with human activities but, because of their inshore distribution, their presence as bycatch is the most significant threat to this species and has been reported from most habitats (Jefferson & Curry, 1994). In some areas, bycatch affects population abundance because of high unintentional mortality (Caswell et al., 1998; Vinther & Larsen, 2004; Moore & Read, 2008).

Life history parameters such as reproductive status, pregnancy, growth rate, and growth curve are required to assess potential effects of a decrease in population abundance (Eberhardt & Siniff, 1977; DeMaster, 1984; Learmonth et al., 2014). These parameters are influenced by regional prey abundance, density-related intraspecific competition, environmental changes, and anthropogenic influences. For example, Börjesson & Read (2003) noted that the timing of conception was similar among the Kattegat, Skagerrak, and North Sea populations but was significantly earlier than the Baltic Sea population. They suggested that these differences in mating seasons were related to seasonal patterns in the distribution and behaviour of prey. The growth curves of the populations in the Gulf of Maine and Bay of Fundy changed between the 1970s and 1980s, and in 1993 were considered to be threatened by population declines due to bycatch (Read & Gaskin, 1990). Kesselring et al. (2017) concluded that

the shortened lifespan of the Baltic Sea population was linked to the artificial influence of rising bycatch mortalities.

Three major reproductively isolated populations of *P. phocoena* are recognised—*P. p. vomerina* in the eastern North Pacific, *P. p. phocoena* in the North Atlantic, and *P. p. relicta* in the Black Sea and the Sea of Azov—and several population units have been identified within these three populations based on genetic studies (Chivers et al., 2002; Culik et al., 2011; Bjørge & Tolley, 2018). In the North Pacific Ocean, some studies suggested that the population around Japan was a subspecies of the North Pacific population "*P. p. subsp.*" (Gaskin, 1984; Rice, 1998; Taguchi et al., 2010b; Culik et al., 2011), although this has not been officially recognized. Amano & Miyazaki (1992) argued that western Pacific animals differ sufficiently from those in the eastern Pacific in the morphology of their skulls to warrant subspecific separation. Genetic structure and phytogeography of harbour porpoises in the North Pacific demonstrated substantial genetic divergence between the northwest (Strait of Georgia, Alaska, and Japan) and southeast (Monterey–British Columbia) group (Taguchi et al., 2010b). If the eastern Pacific population is a subspecies, some differences in morphology, habitat, and life history will be apparent. Previous studies have provided some differences, but information on life history has not often been reported.

The life history of *P. p. phocoena* in the North Atlantic has been studied more intensely than that of other subspecies—for example, in coastal waters of the North Sea, the Baltic Sea, West Greenland, Denmark, the Bay of Fundy, and the Gulf of Maine (Lockyer, 1995, 2003; Read & Hohn, 1995; Lockyer & Kinze, 2003; Ólafsdóttir et al., 2003; Learmonth et al., 2014). In contrast to the North Atlantic population, limited information has been reported for the North Pacific population. In the Northwest Pacific, Gaskin et al. (1993) examined the biology of Japanese harbour porpoises, including their distribution, life cycle, and reproductive status using 60 stranded and bycaught individuals. Taguchi et al. (2010a) estimated their seasonal distribution around Japan by using 240 stranding and bycatch records but did not examine their life history.

The Hokkaido coast of Japan, which is located in the northwest Pacific Ocean, has the highest number of stranded harbour porpoises in Japan. In the present study, sexual maturation of harbour porpoises around Hokkaido are examined using samples and data from stranded and bycaught harbour porpoises, and currently available information regarding their life history parameters are summarized.

Methods

Postmortem Examinations

Between 2009 and 2019, 214 harbour porpoises were reported as stranded or bycaught by the Stranding Network Hokkaido (SNH). Basic information, including date found, location (latitude and longitude), and whether they were bycaught or stranded, was recorded for all individuals. Necropsies were conducted on 152 animals. Porpoises were considered bycatch when they were found in a fishing net. Locations were classified as occurring along the coast of either the Sea of Japan, Sea of Okhotsk, or Pacific Ocean (Figure 1). The 152 necropsied harbour porpoises were classified into five stages of carcass condition: alive, freshly dead, moderate decomposition, advanced decomposition, or mummified/skeletal (Perrin & Geraci, 2009). Body length (cm), body weight (kg), and cause of death were recorded as accurately as possible.

Captive Harbour Porpoises

Observations of captive harbour porpoises were used to supplement size-at-age data obtained from postmortem examinations. The Otaru Aquarium houses four harbour porpoises (two males and two females) that were bycaught in set nets and rescued (by the authors) in Hakodate, Hokkaido, Japan. One of the female porpoises has given birth three times under human care. Birth dates and body lengths of these calves were recorded and incorporated into growth model estimates. The birth records of "Atsuko" at the Otaru Aquarium are summarized in Table 1. Based on these data, average body length at birth were determined to be 82 and 88 cm for females and males, respectively.

Counting of Growth Layer Groups

Age determinations were conducted on teeth collected from 80 individuals. Toothed whales have monophyodont teeth. Counting the growth layer groups (GLGs), which represent annual depositions of the dentine and cementum (Perrin & Myrick, 1980; Bjørge et al., 1995), has been accepted as the most reliable method of age determination. Teeth were removed from the middle mandibular region and sectioned parallel to the mandible at about 30 μm thickness. The section that included the crown and central pulp cavity was selected for each tooth and stained with Mayer's haematoxylin. Both dentinal and cemental GLGs were counted using a binocular microscope (10-50x), based on methods from Bjørge et al. (1995). Counts were made blind—that is, without knowledge about the sex, body length, or reproductive status of each animal—on at least two separate occasions. If the two age estimates did not correspond, the sections were independently
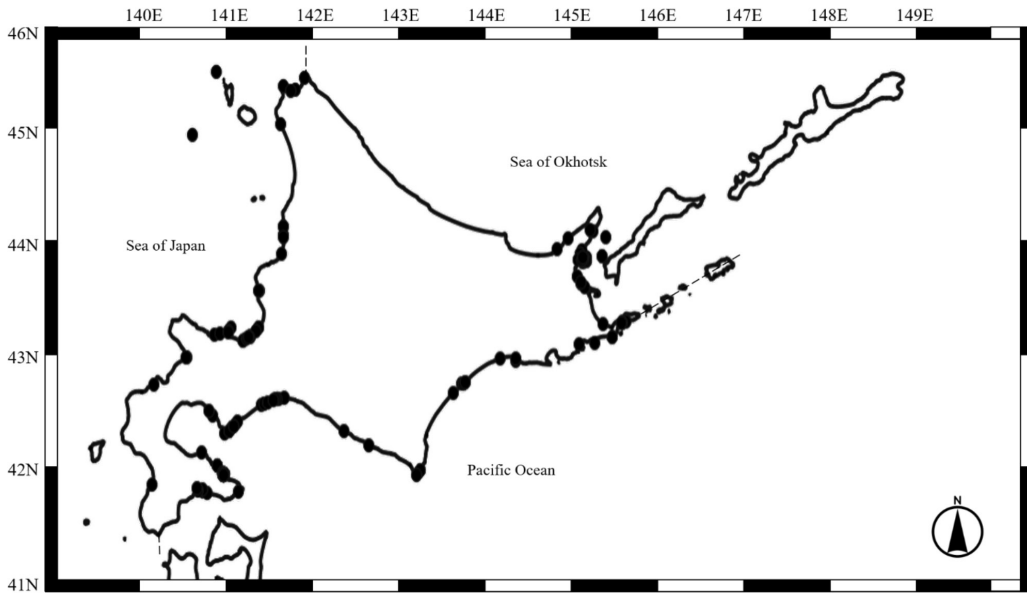
Figure 1. Definition of locations on the coast of the Sea of Japan, the Sea of Okhotsk, and the Pacific Ocean

Table 1. Birth record of the captive female harbour porpoise (Atsuko) and her neonates

	Date of Birth (d/mo/y)	Sex	Body length (cm)	Weight (kg)	Note
1st time	14/1/2011	Unknown	40	--	Miscarriage
2nd time	15/5/2015	Male	88	--	Died 9 min after birth
3rd time	30/5/2017	Female	82	9.28	Died 2 wks after birth

re-examined. If two of the three readings agreed, they were used for the age determination.

Age Estimation

To estimate more specific ages (t_i) at the date of death, we first had to establish the standard date of the GLG increment in reference to a calendar year (i.e., when the increment started/ended). Harbour porpoises were categorized by the number of GLGs, and those showing one to three GLG(s) were used for estimating the standard date because younger individuals have high growth rates and their ages were more readily determined from their body lengths.

First, a provisional d_S was assumed to provide an initial value of the standard date of the GLG increment. The value of d_S was in years starting from 1 January (i.e., if the standard date was 1 July, d_S was set as 0.5). Then, the age of an individual (i) was calculated from the number of GLGs (n), the date of death (d_i), and d_S, as follows:

$$t_i = \begin{cases} n + d_i - d_S + 1 & \text{for } d_S \geq d_i \\ n + d_i - d_S & \text{for } d_S < d_i \end{cases} \quad (1)$$

If d_S corresponds to the real date of the GLG increment, estimated age t_i and body length l_i will show a strong positive correlation because of their rapid growth. However, if d_S is incorrect, the estimated age would lead to a weaker or even negative correlation with body length (Figure 2). A d_S value of 0.56 (corresponding to 25 July; r^2 = 0.44) provided the highest correlation and was used as the standard date.

Finally, "years of age" of each individual (i) was estimated using equation (1) with $d_S = 0.56$. Note that in this article, "years old" is equivalent to the number of GLGs and is given as an integer, whereas "years of age" is used to express the estimated age in decimal years.
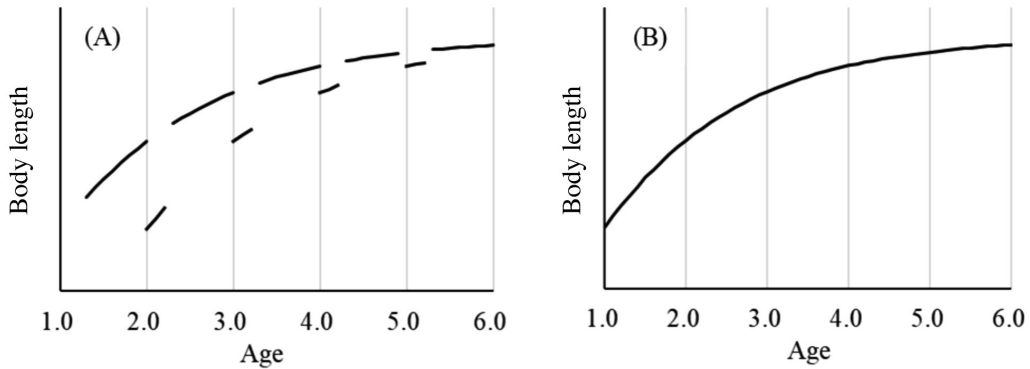
Figure 2. Explanation of the estimation of the standard day of the GLG increment d_S with (A) an example of poor estimation where d_S was set at 2 mo before the GLG increment and (B) a correct estimation.

Reproductive Status

Left and right ovaries were removed from 29 female harbour porpoises and preserved in 10% neutral buffered formalin. The presence or absence of lactation or a foetus in the uterus were recorded during postmortem examination of all female porpoises. If a foetus was found, sex, body length, and weight were measured. The ovaries were cut into approximately 1-mm-thick slices which were then dehydrated and embedded in paraffin, sectioned at 10 to 30 μm, and stained with haematoxylin-eosin. The presence or absence of *corpora lutea* (CL) and *corpora albicantia* (CA) was recorded. Female reproductive maturity was classified either immature (no *corpus* present) or mature (at least one CL or CA present, or the female was pregnant or lactating). These criteria for female reproductive status were based on Perrin et al. (1984) and other studies (e.g., Kasuya & Marsh, 1984; Lockyer, 1995, 2003; Read & Hohn, 1995; Learmonth et al., 2014).

In males, both right and left testes were removed and preserved in 10% neutral buffered formalin. The testes of 53 individuals were weighed during dissection. Tissue samples taken from the middle of the testis were prepared for histology as described for the ovaries. The status of sexual maturity in males was determined using two standards. In the first, based on criteria used by Gaskin et al. (1993) who studied porpoises in Japanese waters, individuals whose single testis weighed less than 90 g were considered immature. The second criterion following Learmonth et al. (2014) was based on histological observation of the mean diameters of the seminiferous tubules and of spermatogenesis. This method defined three categories of maturity: (1) immature (abundant interstitial tissue and Sertoli cells, primary spermatogonia present, and diameter of seminiferous tubules < 60 μm),

(2) pubescent (reduction in density of interstitial tissue and Sertoli cells; some production of spermatocytes but < 80 μm), and (3) actively mature (abundant spermatogonia, spermatocytes, spermatids, and spermatozoa > 80 μm). Sections of 30 μm were prepared for histological examination and observed using a USB digital microscope (Model MJ-MS302; Sato Shoji Co., Ltd., Kanagawa Prefecture, Japan). The diameters of the seminiferous tubules were averaged from five micrographs taken from each individual with 20 measurement points per micrograph.

The 50% age at attainment of sexual maturity (ASM) and length at sexual maturity (LSM) were estimated based on Learmonth et al. (2014). Binomial GLMs (with logit link function) were fitted to data of sexual maturity with respect to age or length in both sexes. The LSM for females was calculated from the mean of the maximum length of immature individuals and the minimum length of mature individuals because the range of the immature and mature individuals did not overlap and binomial GLMs were not applicable.

Gompertz Growth Model

The Gompertz growth curve (Fitzhugh, 1976) was applied to predict the growth pattern of each sex separately as follows:

$$L_t = L_\infty e^{(-ce^{-Kt})}$$

where L_t is a body length (cm), L_∞ is the asymptotic value, c is a constant, K is the growth rate constant, and t is age. Following Akamine (2004), differences in growth between males and females were tested.

Table 2. Collated information on samples used in this study

		Male	Female	Unknown	Total
Total		103	70	41	214
Bycaught		75	48	4	127
Stranded		28	22	37	87
Necropsied		78	57	17	152
Released		19	9	1	29
Sample not collected		6	4	23	33
Location	Sea of Japan	13	5	14	32
	Sea of Okhotsk	45	34	7	86
	Pacific Ocean	45	31	20	96
The state of decomposition	Alive	21	12	3	36
	Freshly dead	56	38	5	99
	Moderate decomposition	10	15	10	35
	Advanced decomposition	14	5	9	28
	Mummified/skeletal	1	0	13	14
	Not recorded	1	0	1	2
Recorded data	Body length	81	60	16	157
	Weight	35	27	0	62
	Gonads	53	29	0	82
	Teeth	50	29	1	80
Foetus		1	0	0	1
Neonates/calves		0	0	2	2

Results

Sample Collection

Table 2 summarizes the basic information used in this study. Between 2009 to 2019, 214 stranded or bycaught harbour porpoises were recorded. One individual (SNH12002) found stranded alone on the beach was considered a foetus because its body length (37 cm) was obviously smaller than that of neonates. Two individuals were regarded as neonates because their body lengths were < 90 cm or because one of them was stranded with a larger (> 140 cm) female porpoise. Most of the bycaught individuals were collected in April, but reports (including stranded porpoises) were recorded throughout all seasons (Figure 3).

Age Determination

Individuals in the sample ranged from 1.02 to 12.01 y of age. Of the 80 harbour porpoises, 57 (71.3%) were below 5.0 y of age (Figure 4). The oldest female was 12.01 y of age, and the oldest male was 10.9 y of age. Two neonates (0.0 y of age) under human care at Otaru Aquarium are included.

Growth Model

The Gompertz model provided optimally fitted curves for body length vs age for males and females (Figure 5). The equations of the curves were as follows:

Males: $L_t = 136.9e^{(-0.45e^{-0.959t})}$

Females: $L_t = 158.5e^{(-0.60e^{-0.463t})}$

The growth rate of males decreased with age, and, on average, they grew 27.3 cm/y until 1.0 y of age, 12.9 cm/y between 1.0 and 2.0 y of age, and 5.4 cm/y between 2.0 and 3.0 y of age. There was little change in body length after 4.0 y of age in males, but the growth of females continued after 4.0 y of age. Females grew 5.20 cm/y between 4.0 and 5.0 y of age, but growth decreased to less than 1.0 cm/y after 8.0 y of age. There was an obvious sexual dimorphism in growth patterns present between males and females, and the asymptotic length was also larger in females (F-test, $p < 0.05$).
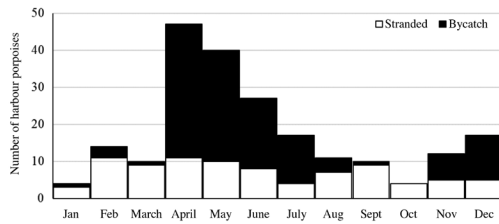
Figure 3. The number of harbour porpoises (*Phocoena phocoena*) stranded or in bycatch by month. Black bars represent stranded individuals, and white bars represent bycaught individuals.
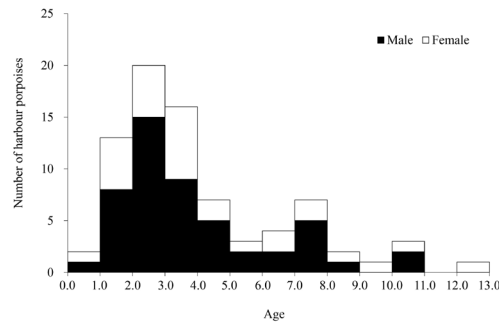

Figure 4. Age distribution of harbour porpoises in this study around Hokkaido, Japan

Reproductive Status

Two males (SNH16053 and SNH18014) were excluded because their organs were decomposed and their histological status could not be assessed. Testis mass was available for 51 animals assessed using the first standard based on Gaskin et al. (1993). Nine males in which the left testis weight was greater than 90 g were classified as mature. The oldest immature male was 7.8 y of age, and mature males ranged from 2.7 to 11.0 y of age. Using the second standard of assessment, 42 individuals were considered immature (104.5 to 154.6 cm), three were pubescent (141.3 to 143.0 cm), and three were mature (141.8 to 155.7 cm). The testes weights of three mature individuals were greater than 200 g. Two of the three pubescent individuals had testis weights of 91 and 98 g, respectively (Table 3).

Three females were reported as pregnant because a foetus was present, and no female was lactating. Female SNH19008-1 was stranded with a neonate (SNH19008-2) and was therefore regarded as mature. We were unable to measure the body length of SNH19008-2 because it had disappeared when researchers arrived at the stranding site. The presence of a CL and a CA was

confirmed in four individuals. Thus, in total, eight females were definitively determined as mature.

Length at Sexual Maturity and Age at Attainment of Sexual Maturity

LSM and ASM for males were estimated as 143.1 cm ($n = 48$) and 7.7 y of age ($n = 45$), respectively. LSM and ASM for females were 154.4 cm ($n = 30$) and 7.3 y of age ($n = 22$), respectively. Note that the male LSM was greater than the asymptotic length, which will be addressed in the "Discussion" (Figure 6).

Discussion

Parturition Area

In contrast to studies in other regions, we suggest that the coastal area of Hokkaido is not used for giving birth. The distribution of ages of foetuses, neonates, pregnant females, and mature females was quite different from that observed in other studies. In the present study, 5.0% (7 of 214) of harbour porpoises were foetuses and neonates, including porpoises whose teeth could not be collected but whose body length was obtained. In contrast, 41% (87 of 210) of harbour porpoises in British waters were under 1 y of age (Lockyer, 1995). Nevertheless, in contrast to British waters, young individuals were dominant in Hokkaido. In our study, individuals between 1 to 4 y of age comprised 73% (103 of 141), while 59% (123 of 210) of individuals were greater than 2 y old in British waters.

Foetuses or neonates accounted for just 1.4% (3 of 214) of samples in the present study, but 10% (98 of 944) in UK waters (Learmonth et al., 2014). We observed a rate of pregnancy in females of 2% (4 of 214) compared with 11% (96 of 879) in UK waters. In the present study, mature harbour porpoises of both sexes comprised 21% (17 of 80) compared with 34 to 55% around European waters (Lockyer et al., 2003; Ólafsdóttir et al., 2003; Learmonth et al., 2014).

It is possible that parturition of harbour porpoises around Hokkaido takes place in the northern part of the Sea of Okhotsk, but we are unaware of information that supports this. Further investigations are therefore needed concerning the conservation of this putative subspecies.

The Asymptotic Length and Length at Sexual Maturity

Males—The estimated length of sexually mature males (143.1 cm) was greater than the estimated asymptotic length (136.9 cm). If this were true, most of the population around Hokkaido would not reach sexual maturity, and the population would become extinct. This result might be caused
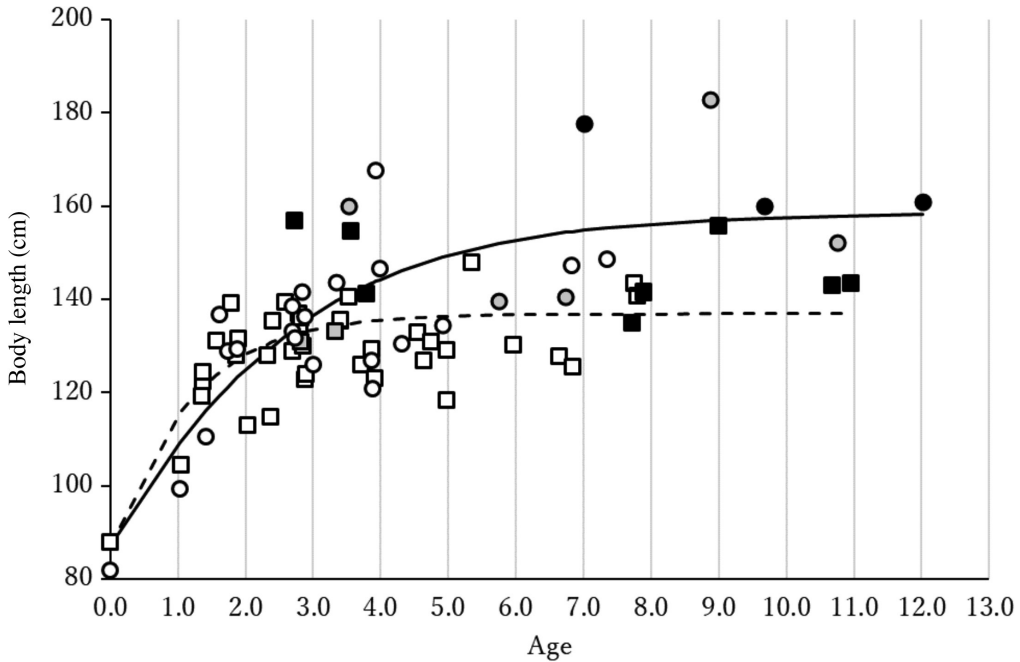
Figure 5. Age at length for male and female harbour porpoises around Hokkaido, Japan. White symbols represent immature individuals, grey symbols represent individuals for which we were unable to determine sexual maturity, and black symbols represent mature individuals. The solid line shows the Gompertz curve for females, and the dashed line shows the Gompertz curve for males. Circles represent females, and squares represent males.

Table 3. Measurements of body length in immature and mature harbour porpoises

		n	Body length (cm)				Testis weight (g)
			Min	Max	Mean	SD	Mean
Male (by testis volume) n = 51	Immature	42	104.5	147.9	128.8	9.4	18.9
	Mature	9	135.0	157.0	145.2	7.0	353.4
Male (by histological examination) n = 48	Immature	42	104.5	154.6	127.4	17.5	29.3
	Pubescent	3	141.3	143.0	141.9	0.9	94.5
	Mature	3	141.8	155.7	147.0	7.6	772.0
Female n = 30	Immature	22	99.3	148.6	134.2	12.4	--
	Mature	4	161.0	177.8	166.7	6.1	--
	Pregnant	4	160.1	174.6	167.7	7.4	--

by biased sampling from the whole population. If most of the mature males leave the coastal area of Hokkaido, the sample would be biased towards immature individuals, and the estimated growth curve and LSM would be unreliable. Therefore, based solely on our samples, the LSM of male individuals remains unknown. Samples from the parturition area will be essential for the accurate estimation of the growth curve and LSM and will require further collaborative studies.
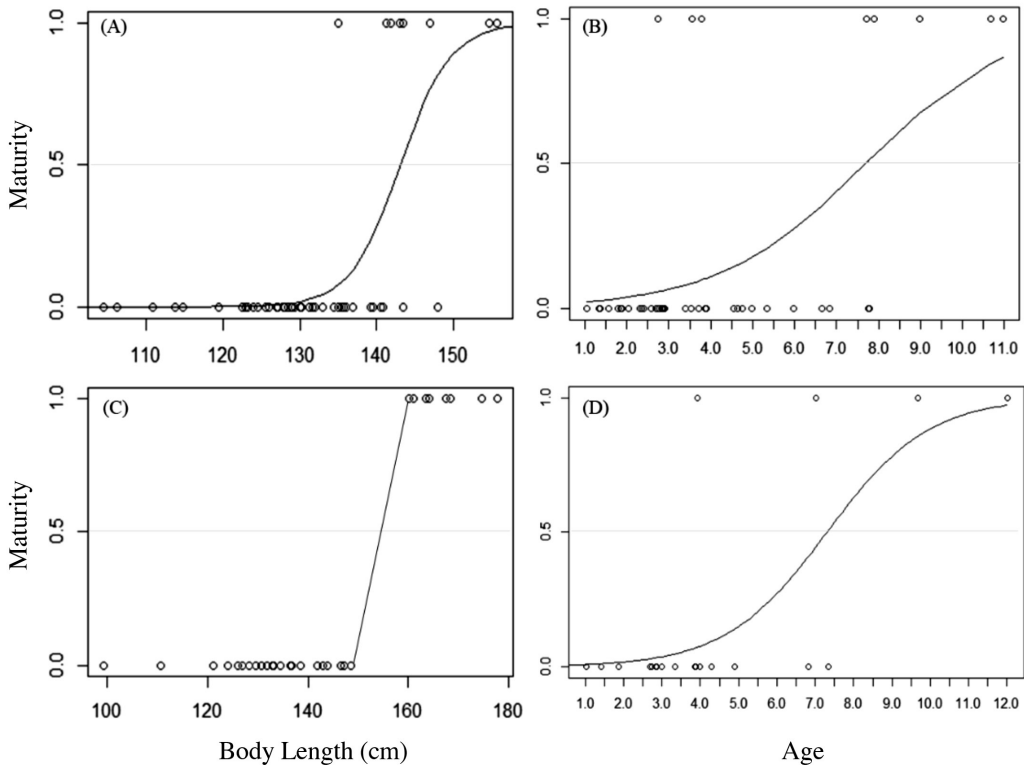
Figure 6. Binomial regressions to estimate LSM and ASM in male (A, B) and female (C, D) harbour porpoises. (A) and (C) show relationships between body length (cm) and sexual maturity, and (B) and (D) show relationships between age and sexual maturity. Note that in (C) the length range of immature and mature females does not overlap.

Females—The estimated female asymptotic length (158.5 cm) was very similar to the estimated minimum mature female length (160.1 cm). It is reasonable that physical maturity coincides with the length at which they become fertile. In contrast to previous studies in the other populations, LSM of females was about 10 cm greater than that of males (Table 4).

Body size varies among subpopulations and geographic locations. Maximum body length was recorded as 186.5 cm for females in the present study, which is similar to what has been reported in Spanish and Portuguese waters (Sequeira, 1996; Lens, 1997). These populations are distributed within similar latitudinal zones and photoperiodic regimes. In contrast, larger female asymptotic lengths were recorded for the waters of Great Britain, the Bay of Fundy, West Greenland, and Denmark, implying that female LSMs are also larger in these regions.

Sexual Dimorphism
The difference in body lengths between the sexes was apparent at almost 3 y of age, based on estimates from the Gompertz growth model (Figure 5), indicating a sexual dimorphism in which females are larger than males. Similar observations have been reported in many previous studies (e.g., Gaskin, 1984; Yurick & Gaskin, 1987; Read, 1999; Lockyer, 2003; Learmonth et al., 2014).

Typically, sexual dimorphism in mammals results in males that are larger than females. Female harbour porpoises may need a larger body size to give birth to bigger calves to help both calf and mother to survive in colder water (Stuart & Morejohn, 1980; Read & Tolley, 1997; Galatius, 2005). An alternative explanation is that males are engaged in sperm competition to ensure the production of offspring (Gaskin, 1984). This hypothesis implies that the shorter body lengths of males might increase their reproductive success by ending physical growth at an earlier age thus allowing earlier investment in testicular development.

Table 4. Estimated length at sexual maturity of harbour porpoises in each geographic area in the current and previous studies

Subpopulation	Location	LSM Female (cm)	Male (cm)	References
P. p. phocoena	Bay of Fundy (1969-1973)	147.0	134.0	Read & Gaskin, 1990
	Bay of Fundy (1985-1988)	143.0	?	Read, 1990
	Newfoundland and Labrador	146.4	135.1	Read & Hohn, 1995
	West Greenland	138.0-142.0	127.0	Lockyer et al., 2001
				Lockyer et al., 2003
	Iceland	146.0	135.0	Ólafsdóttir et al., 2003
	British waters	140.0-145.0	130.0-135.0	Lockyer, 1995
	Danish waters	143.0	135.0	Lockyer & Kinze, 2003
				Sørensen & Kinze, 1994
	Scottish (UK) waters	138.8	132.2	Learmonth et al., 2014
P. p. reclita	Black Sea	143.5	132.0	Gol'din, 2004
P. p. vomerina	Hokkaido	154.4	143.1	This study

Age Estimation

Age is generally estimated to the nearest 0.5-y interval in cetaceans. For example, Ólafsdóttir et al. (2003) considered that a new cycle can be assumed to start at the beginning of June because GLGs, which consist of two layers, were sometimes already closed by the formation of a new opaque layer in March and April. Gaskin (1977) described the formation of the translucent layer from January to September and the opaque layer from June to February. However, it was difficult to estimate to 0.5-y intervals in this study because we did not know when the layer was formed; poor data were available before and after giving birth. Therefore, in this study, we estimated the age of harbour porpoises using d_S, the estimated standard date of the GLG increase. This was calculated to be 25 July, implying that this study has a similar cycle to that reported by Ólafsdóttir et al. (2003).

Conclusion

Our study is important in being the first to provide basic information on the growth and reproduction of harbour porpoises around Hokkaido, which are part of the North Pacific subpopulation, using data and samples from the past 10 y. Harbour porpoises in the northwest Pacific Ocean have access to a wider area than only Hokkaido. Further wide-ranging studies will help scientists to understand the biology of these animals, including their taxonomy, habitat, and ecology, thereby contributing to the conservation of this population.

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