J-STAGE Advance published date: January 31, 2021

IMPROVED ESTIMATES OF SOME LIFE-HISTORY PARAMETERS OF THE PELAGIC SUBSPECIES OF BRYDE'S WHALE IN THE WESTERN NORTH PACIFIC

Takeharu BANDO

Institute of Cetacean Research, 4–5 Toyomi-cho, Chuo-ku, Tokyo 104–0055, Japan
Corresponding author: bando@cetacean.jp

Abstract

Estimates of several life-history parameters of the pelagic subspecies of Bryde's whale (*Balaenoptera edeni brydei*) in the western North Pacific were made based on samples collected from the second phase of the Japanese Whale Research Program under Special Permit in the Western North Pacific (JARPNII) from 2000 to 2016. A total of 730 individuals were sampled in the western North Pacific, between the Japanese coast and 170°E and between 35°N and approximately 42°N. Age information was obtained from earplugs of 475 individuals (65.2%). The growth curves were estimated as $L_t = 12.65\ (1 - e^{-0.189\ (t+5.250)})$ and $L_t = 13.30\ (1 - e^{-0.170\ (t+4.929)})$ for males and females, respectively. The mean age at sexual maturity was estimated as 7.72 (SE=0.49) and 8.56 (SE=0.39) years, and the mean body length at sexual maturity was estimated as 11.41 m (SE=0.25) and 11.75 m (SE=0 .23) for males and females, respectively. The annual ovulation rate was estimated as 0.526/year. Increased readability of earplug age in the JARPNII resulted in improved estimates of age-related life-history parameters for the western North Pacific Bryde's whale compared with those based on samples collected during the past commercial whaling period.

Key words: life-history parameter, Bryde's whale, earplugs, western North Pacific.

Bryde's whale is widely distributed throughout the world, especially in waters with temperatures of 20°C or more (Kato and Perrin, 2017). Two types of Bryde's whale are found around Japan, one along the coast of the southwestern part of Japan and the other on pelagic waters in the Pacific side of Japan (Kishiro, 1996; Yoshida and Kato, 1999). Some authors (e.g., Wada *et al.*, 2003) recognize these two types as separate species, a smaller coastal species *Balaenoptera edeni* Anderson, 1879 (Eden's whale) and a larger pelagic species *B. brydei* Olsen, 1913 (Bryde's whale). Other authors (e.g., Kershaw *et al.* 2013; Kato and Perrin, 2017) assign these species a subspecific status: *B. edeni edeni* and *B. edeni brydei*. This study focused on the larger, pelagic subspecies of Bryde's whale (Fig. 1).

The second phase of the Japanese Whale Research Program under Special Permit in the Western North Pacific (JARPNII) started in 2000, under a permit issued by the Government of Japan. The pelagic subspecies of Bryde's whale was selected as one of the target species for sampling. Biological investigations, such as body length measurements and sampling of reproductive organs and earplugs, were conducted on whole animals in order to estimate life-history parameters. The JARPNII was completed in 2016, and a total of 730 Bryde's whales (314 males and 416 females) were sampled during the 17 year survey period.

Age data are important for assessment of stock and management of large whales. Age estimation based on the number of growth layers accumulated in the earplugs is considered the most reliable tool for age determination in baleen whales (Lockyer, 1984a; Maeda *et al.*, 2016). During the JARPNII,

Fig. 1. Pelagic subspecies of Bryde's whale in the western North Pacific. Note the three distinct ridges in the head, which are characteristic of this species.

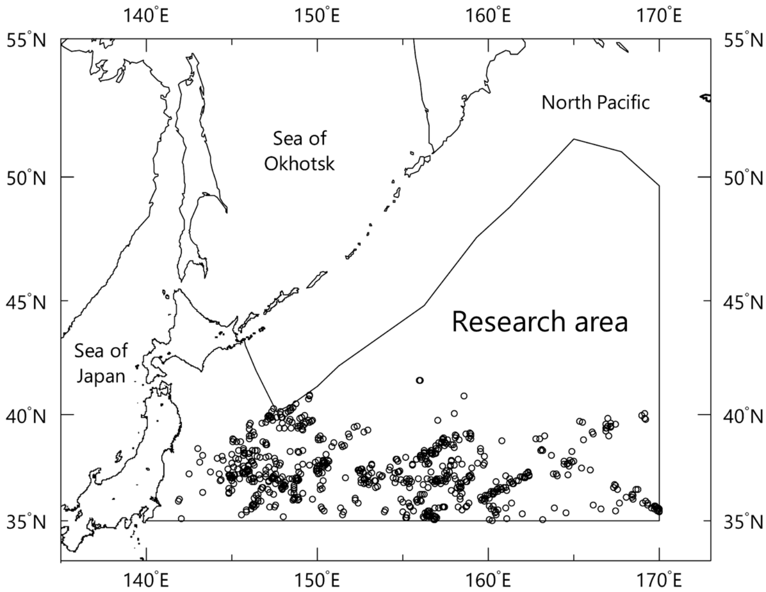

Fig. 2. Research area of the second phase of the Japanese Whale Research Program under Special Permit in the Western North Pacific (JARPNII) and location of sightings of Bryde's whales sampled during 2000–2016 surveys.

earplugs were collected carefully from each whale by experienced biologists.

Age-related life-history parameters are important for monitoring the status of stocks and can be used in various analyses, including population dynamics models (e.g., the statistical catch-at age model; Punt *et al.*, 2014). Previous estimates of life-history parameters of Bryde's whale were based on samples collected during the commercial whaling period (Kato and Yoshioka, 1995; Ohsumi, 1977). However, samples from commercial whaling are not representative of the stock, as whaling operations targeted large individuals and a legal size limit was imposed in some operations. Therefore, some life-history parameters estimated from these samples, such as age at sexual maturity are thought to be biased (Kato, 1982; Kato and Yoshioka, 1995; Ohsumi, 1977). JARPNII collected samples randomly, regardless of body length or age, resulting in less biased estimates (Bando *et al.*, 2016).

This article summarizes the results of estimation of several life-history parameters in the pelagic subspecies of Bryde's whale in the western North Pacific based on randomly collected samples, which should be more representative than those obtained in past commercial whaling.

Whales were sampled between the Japanese coast and 170°E, and between 35°N and approximately 42°N (Fig. 2). Two biological stocks of the pelagic subspecies of Bryde's whale have been suggested for the western North Pacific, one between the Japanese coast and approximately 165°E and the other east of 180°, with a transition area between 165°E and 180° (IWC, 2018). Analyses were conducted on the assumption that all samples were from the western stock because it is difficult to identify stocks for each individual and the number of samples from east of 165°E was not large (Fig. 2) (IWC, 2018).

Body length was measured to the nearest 1 cm in a straight line from the tip of the snout to the notch of the flukes using stainless steel measuring tapes. Sexual maturity in males was determined by examination of a histological sample from the testis. Males with seminiferous tubules over 100 μm diameter and spermatid or open lumen in the tubules were considered to be sexually mature (Nishiwaki *et al.*, 1954; Lockyer, 1984b). Sexual maturity in females was determined by the presence or absence of corpora lutea and albicantia in the ovaries. If there was at least one corpus luteum or corpus albicans in the ovaries, the female was considered to be sexually mature (Nishiwaki *et al.*, 1954; Lockyer, 1984b).

Earplugs were collected from all sampled animals, following the method developed for baleen whales (Omura, 1963; Maeda *et al.*, 2016). The left and right earplugs were collected carefully and immediately fixed in 10% formalin. In the laboratory, the surface along the central axis of the earplug was cut using a sharp blade, and was placed on a wet stone to expose the growth layers. The growth layers were counted under water using a stereoscopic microscope. A growth layer group was defined as one pair of light and dark laminae in the core and was considered to indicate 1 year of age. All earplugs were read by the author.

To estimate the growth curve, the von Bertalanffy growth model was fitted to body length and age as

$$L_t = L_\infty \left(1 - e^{-K\,(t - t_0)}\right) \quad (1)$$

where L_t is the body length at age t, L_∞ is the asymptotic length, K is the growth rate coefficient and t_0 is the theoretical time at zero length.

Age at sexual maturity (t_m) was estimated by the following equation (Cooke, 1984):

$$T_m = g - 0.5 + \sum_{a=g}^{h} \left(\frac{I_a}{N_a} \right) \quad (2)$$

$$\mathrm{var}\,(t_m) = \sum_{a=g}^{h} \frac{M_a I_a}{N_a^2 (N_a - 1)} \quad (3)$$

where
M_a is the number of mature animals of age a,
I_a is the number of immature animals of age a,
N_a is the total number of animals of age a,
g is the age of the youngest mature animal in the sample, and
h is the age of the oldest immature animal in the sample.

Body length at sexual maturity (l_m) was estimated by the following equation (Cooke, 1984; Kato, 1992) (body length was rounded to 0.1 m):

$$L_m = j - 0.05 + 0.1 \sum_{b=j}^{k} \left(\frac{I_b}{N_b} \right) \quad (4)$$

$$\mathrm{var}\,(l_m) = 0.1 \sum_{b=j}^{k} \frac{M_b I_b}{N_b^2 (N_b - 1)} \quad (5)$$

where
M_b is the number of mature animals of body length b,
I_b is the number of immature animals of body length b,
N_b is the total number of animals of body length b,
j is the body length of the smallest mature animal in the sample, and
k is the body length of the largest immature animal in the sample.

The annual ovulation rate was estimated by applying linear regression analysis between age and the total number of corpora (corpora lutea and corpora albicantia). The regression line was fitted to ages 10 years and older because almost all animals were mature at the age of 10 years.

The readability of earplugs varied depending on the maturity status of the individual. The readability of earplugs of sexually immature individuals was 43.8% for males and 40.8% for females. The readability of earplugs of sexually mature individuals was higher than that of immature individuals: 74.0% for males and 76.4% for females. The readability of all samples was 65.2% (Table 1). Although the proportion of immature individuals with lower earplug readability was higher in JARPNII samples than in commercial whaling samples from the 1970s (30.9% vs. 14.3%) (Ohsumi, 1977), the proportion of samples from which age could be determined increased drastically from commercial whaling samples (17.4%; Ohsumi, 1977) to JARPNII samples.

The relationship between age and body length is shown in Fig. 3. For both sexes, the growth rate was high at younger ages and stabilized after the age of 20 years. The following von Bertalanffy growth curves were estimated:

$$\text{Male:} \quad L_t = 12.65\left(1 - e^{-0.189\,(t+5.250)}\right)$$
$$\text{Female:} \quad L_t = 13.30\left(1 - e^{-0.170\,(t+4.929)}\right).$$

Table 1. Readability of earplugs of Bryde's whales for determination of age according to sex and sexual maturity status.

Status	Male			Female			Total		
	Number of whales	Readable earplugs	Readability (%)	Number of whales	Readable earplugs	Readability (%)	Number of whales	Readable earplugs	Readability (%)
Immature	105	46	43.8	120	49	40.8	225	95	42.2
Mature	208	154	74.0	296	226	76.4	504	380	75.4
Total	313	200	63.9	416	275	66.1	729	475	65.2

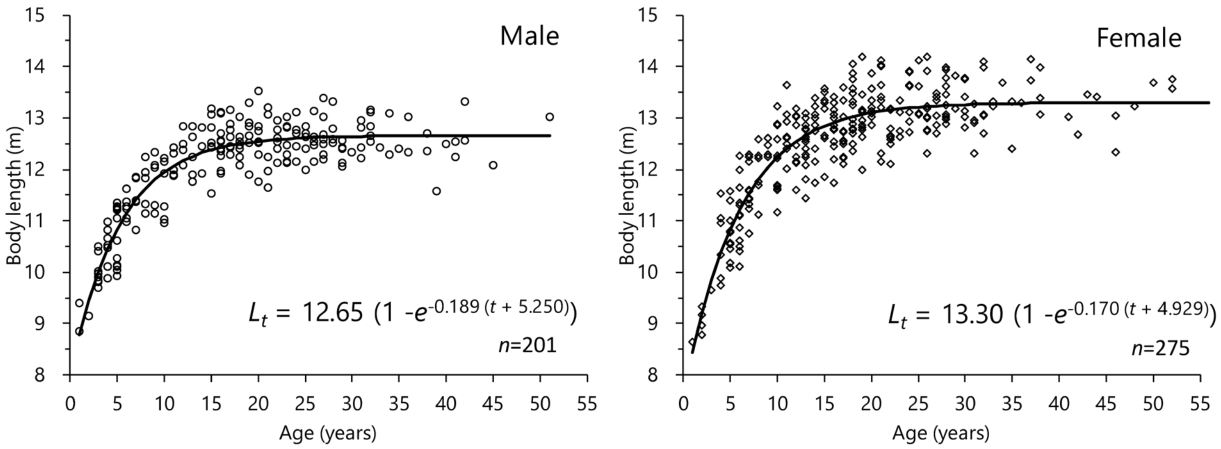

Fig. 3. Relationship between body length and age in Bryde's whale. The solid lines show the von Bertalanffy growth curves.

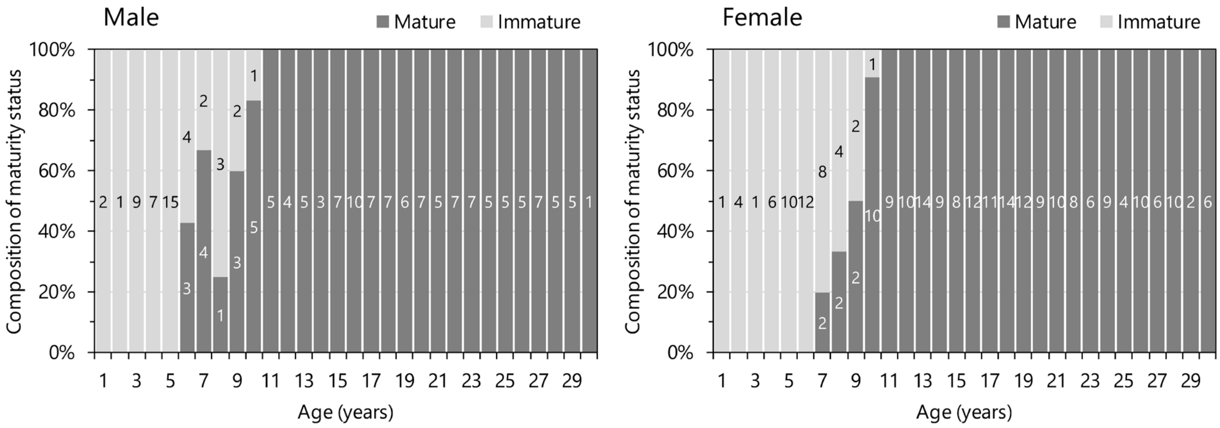

Fig. 4. Sexual maturity status by age and sex in Bryde's whale. Numbers in the bars are the numbers of samples examined.

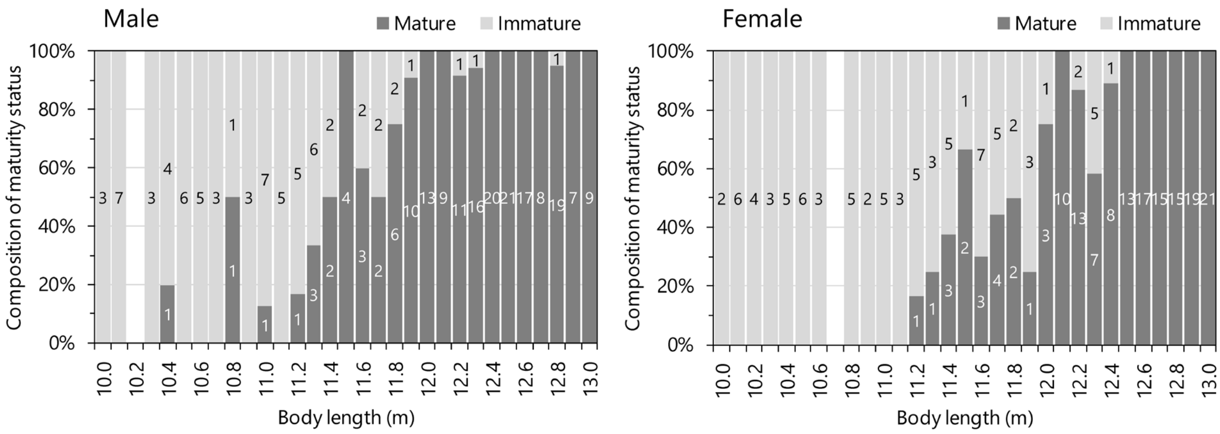

Fig. 5. Sexual maturity status by body length and sex in Bryde's whale. Numbers in the bars are the numbers of samples examined. Body length values were rounded to 0.1 m.

Figs. 4 and 5 show sexual maturity status by age and body length. Males first reached sexual maturity at the age of 6 years, and all males were sexually mature by the age of 11 years (Fig. 4). The mean age at sexual maturity (t_m) for males was estimated as 7.72 years (SE=0.49). Females first reached sexual maturity at the age of 7 years, and all females were sexually mature by the age of 11 years. T_m was estimated as 8.56 years (SE=0.39).

Males first reached sexual maturity at a body length of 10.4 m, and all males with a body length of 12.9 m or greater were sexually mature (Fig. 5). The mean body length at sexual maturity (l_m) was estimated as 11.41 m (SE=0.25). Females first reached sexual maturity at a body length of 11.2 m, and all females with a body length of 12.5 m or greater were sexually mature. L_m was estimated as 11.75 m (SE=0.23).

The corpora lutea and corpora albicantia first appeared at the age of 7 years and the number of corpora increased linearly after the age of 10 years (Fig. 6). The annual ovulation rate was estimated as 0.526.

The life-history parameters of the western North Pacific Bryde's whale have been estimated by several authors using commercial whaling samples. Ohsumi (1977) estimated the growth curves of Bryde's whales based on commercial whaling samples from the western North Pacific in the 1970s. The results were preliminary because of the small numbers of younger individuals in the samples due to the small numbers of young individuals in the catch and difficulty in collecting, preparing, and counting the number of layers in the earplugs of young animals (Ohsumi, 1977).

Ohsumi (1977) reported the age at sexual maturity of Bryde's whales collected by commercial whaling in the western North Pacific as 10 years for males and 8 years for females. Although the estimated

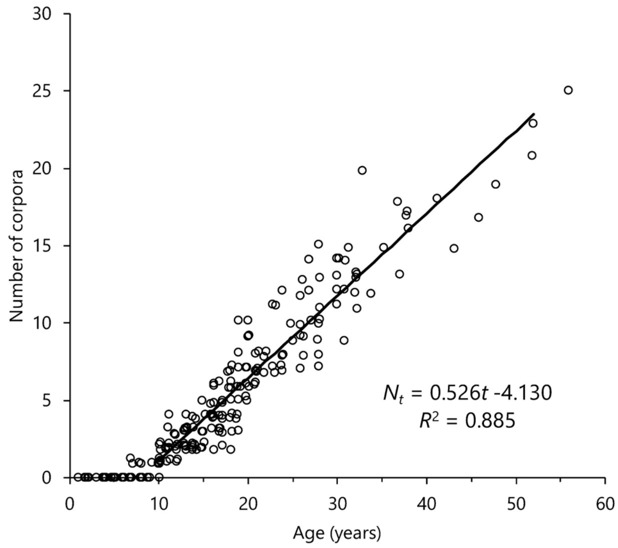

Fig. 6. Jitter plot showing the relationship between age and number of corpora lutea and corpora albicantia in Bryde's whale. The linear regression line was fitted to ages 10 years and more.

values in the present study are similar to the estimates from commercial whaling, consideration should be given to the possibility of bias arising from legal size limits and the selection of large animals during commercial whaling. Large whales were preferred and individuals of the same age but large body length, which has high probability of maturity, are caught among the younger whales during commercial whaling, which leads to overestimation of the sexual maturity rate of younger individuals and underestimation of the age at sexual maturity. Further analysis including other parameters that are free from bias, such as age at first ovulation, is needed to determine whether any changes in the age at sexual maturity have occurred between the period of commercial whaling and the period of the JARPNII program.

Kato and Yoshioka (1995) reported body length at sexual maturity of Bryde's whales collected by the commercial whaling in the coastal region of the western North Pacific in the 1970s as 11.4 m and 11.8 m for males and females. These results are comparable to the results of the present study. In Kato and Yoshioka's study, testis weight was used as a criterion of male sexual maturity. The present study used histological examination of the testis, which is more desirable than testis weight as a criterion of male sexual maturity (Lockyer, 1984b), and which would enhance the credibility of the estimated value.

The annual ovulation rate was estimated as 0.455 from the 1970s commercial whaling samples (Ohsumi, 1977), which was lower than the value estimated in this study (0.526). As in the case of age at sexual maturity, there may be an underestimation bias in estimates from commercial whaling samples. In commercial whaling, whales with the same age but large body length, which would grow and reached sexual maturity faster and have more corpora lutea and albicantia, are caught among the younger whales, which leads to underestimation of the annual ovulation rate.

In conclusion, in this study improved estimates of some life-history parameters are derived for the pelagic subspecies of Bryde's whale in the western North Pacific from randomly collected samples of animals with a wide range of ages and body lengths. Further analysis, including examination of yearly trends will contribute to understanding and management of this whale stock.

Acknowledgements

My sincere thanks are due to all researchers and crews that collected data and samples during the JARPNII surveys. I also thank Dr. Tsutomu Tamura and colleagues of the Institute of Cetacean Research for useful suggestions and help in conducting laboratory work. Dr. Yoshihiro Fujise, director-general of the Institute of Cetacean Research, provided the original idea for this analysis. Dr. Hidehiro Kato, Professor Emeritus of Tokyo University of Marine Science and Technology gave me the opportunity to conduct this study. Finally, I greatly appreciate the anonymous reviewers for their valuable suggestions.

References

Bando, T., Yasunaga, G., Tamura, T., Matsuoka, K., Murase, H., Kishiro, T. and Miyashita, T. 2016. Methodology and survey procedures under the JARPNII—offshore component—during 2008 to 2014 with special emphasis on whale sampling procedures. Paper SC/F16/JR4 presented to the JARPNII special permit expert panel review workshop, Tokyo, February 2016 (unpublished). 14 pp. [Available from the secretariat of IWC].

Cooke, J.C. 1984. The estimation of mean ages at sexual maturity from age sample. Paper SC/36/O22 presented to IWC Scientific Committee, 1984 (unpublished). 8 pp. [Available from the IWC Secretariat].

Government of Japan. 2000. Research plan for cetacean studies in the western North Pacific under special permit (JARPNII) (Feasibility study plan for 2000 and 2001). Paper SC/52/O1 presented to the IWC Scientific Committee, 2000 (unpublished). 68 pp. [Available from the secretariat of IWC].

International Whaling Commission. 2018. Report of the Workshop on the Implementation Review of western North Pacific Bryde's whales. *J. Cetacean Res. Manage*. *(Suppl.)* 19: 561–593.

Kato, H. 1982. Some biological parameters for the Antarctic minke whale. *Rep. Int. Whal. Commn.* 32: 935–945.

Kato, H. 1987. Density dependent changes in growth parameters of the southern minke whale. *Sci. Rep. Whales Res. Inst.* 38: 47–73.

Kato, H. 1992. Body length, reproduction and stock separation of minke whales off northern Japan. *Rep. Int. Whal. Commn.* 42: 443–453.

Kato, H. and Perrin, W.F. 2017. Bryde's whales *Balaenoptera edeni/brydei*. pp. 158–163. In: B. Würsig, J.G.M. Thewissen and K. Kovacs (eds.) *Encyclopedia of marine mammals, Third Edition.* Academic Press, San Diego. 1190 pp.

Kato, H. and Yoshioka, M. 1995. Biological parameters and morphology of Bryde's whales in the western North Pacific, with reference to stock identification. Paper SC/47/NP11 presented to the IWC Scientific Committee, 19 pp. (unpublished). 19 pp. [Available from the secretariat of IWC].

Kershaw, F., Leslie, M.S., Collins, T., Mansur, R.M., Smith, B.D., Minton, G., Baldwin, R., LeDuc, R.G., Anderson, R.C., Brownell, R.L. and Rosenbaum, H.C. 2013. Population differentiation of 2 forms of Bryde's whales in the Indian and Pacific Oceans. *J. Hered.* 104 (6): 755–764.

Kishiro, T. 1996. Movements of marked Bryde's whales in the western North Pacific. *Rep. Int. Whal. Commn.* 46: 421–428.

Lockyer, C. 1984a. Age determination by means of the earplug in baleen whales. *Rep. Int. Whal. Commn.* 34: 692–696.

Lockyer, C. 1984b. Review of baleen whale (Mysticeti) reproduction and implications for management. *Rep. Int. Whal. Commn. (Special Issue 6)*: 27–50.

Maeda, H., Bando, T., Kishiro, T., Kitakado, T. and Kato, H. 2016. Basic information of earplug as age character of common minke whales in western North Pacific. Paper SC/F16/JR53 presented to the JARPNII special permit expert panel review workshop, Tokyo, February 2016 (unpublished). 10 pp. [Available from the secretariat of IWC].

Nishiwaki, M., Hibiya, T. and Kimura, S. 1954. On the sexual maturity of the sei whales of the Bonin waters. *Sci. Rep. Whales Res. Inst.* 8: 165–177.

Ohsumi, S. 1977. Bryde's whales in the pelagic whaling ground of the North Pacific. *Rep. Int. Whal. Commn. (Special Issue 1)*: 140–148.

Ohsumi, S. 1986. Yearly change in age and body length at sexual maturity of a fin whale stock in the eastern North Pacific. *Sci. Rep. Whales Res. Inst.* 37: 1–16.

Omura, H. 1963. An improved method for collection of earplugs from baleen whales. *Norsk Hvalfangst-Tidende* 10: 279–283.

Punt, A.E., Hakamada, T., Bando, T. and Kitakado, T. 2014. Assessment of Antarctic minke whales using statistical catch-at-age analysis. *J. Cetacean Res. Manage*. 14: 93–116.

Wada, S., Oishi, M. and Yamada, T. 2003. A newly discovered species of living baleen whale. *Nature* 426: 278–281.

Yoshida, H. and Kato, H. 1999. Phylogenetic relationships of Bryde's whales in the western North Pacific and adjacent waters inferred from mitochondrial DNA sequences. *Mar. Mamm. Sci*. 15: 1269–1286.

Received: October 31, 2019
Accepted: September 16, 2020
Published online: January 31, 2021