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Vol. 3

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for the Cetacean Population Studies
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PREFACE

The first issue of the *Cetacean Population Studies (CPOPS)*, created with the aim of promoting cetacean research not only in Japan, but also internationally, was published in December 2018, carrying on the spirit of the *Scientific Reports of the Whales Research Institute*, which had ceased publication in 1988. The centerpiece of this effort was the late Dr. Seiji Ohsumi, who unfortunately passed away on November 2, 2019, as we previously announced in this journal. He was very keen to see this journal flourish, but as it was still in the early days since publication of our first issue, I felt truly overwhelmed when I realized that we could not show him the day.

At the "Memorial Service in Honor of the late Dr. Seiji Ohsumi" held on December 23, 2019, people from home and abroad gathered to commemorate him, and many scientists from around the world also sent heartwarming messages. There was a spontaneous outpouring of voices from various people present there who wanted to leave these messages as a remembrance of Dr. Ohsumi.

This CPOPS Vol. 3, in addition to the usual collection of research papers, includes such messages and several chapters looking back at Dr. Ohsumi's accomplishments as a memorial issue dedicated to him. After finishing the editing, I reaffirmed my conviction that, while Dr. Seiji Ohsumi left many research achievements in various fields, the starting point was that of a cetacean biologist deeply rooted in field research. I can only hope that the foundation of this journal will remain the same. And I sincerely hope that this volume will reach Dr. Osumi in heaven.

In addition to the members of the publishing and editorial boards, many national and international scientists have helped edit this volume. I am deeply grateful for their scientific contributions. I would also particularly express my sincere gratitude to Dr. Gabriel Gomez Diaz, Ms. Tomoko Kuba and Ms. Kuniko Takata of the CPOPS secretariat.

October 1, 2021

Hidehiro Kato
Chairman
Publication Committee for the Cetacean Population Studies

Foreword*

Remarkable evolution in cetacean studies in recent decades owes much to major journals that have made significant contribution to the development of modern cetology: Discovery Reports, published by the National Institute of Oceanography in the United Kingdom, and Norwegian Whaling Gazette in Norway, as well as The Scientific Reports of the Whales Research Institute in Japan.

The Scientific Reports of the Whales Research Institute was first published in 1948, a year after the Whales Research Institute was established. Aiming to share valuable research findings and scientific knowledge worldwide, the publication was formatted in English since its beginning, quite an ambitious attempt in Japan still recovering from the devastation of World War II.

Since its first publication, a total of 246 scientists contributed 419 scientific papers to The Scientific Reports of the Whales Research Institute. It is widely acknowledged and appreciated that these scientific papers were the foundation for the development of cetacean studies worldwide, and in today's terms, it was a research journal that had a significant impact factor, or high number of citations. Regrettably, however, The Scientific Reports of the Whales Research Institute was discontinued in 1988 with the 39th volume after the institute was reorganized into the Institute of Cetacean Research.

In the 30 years since then, various types of journals on cetacean studies have been published globally, each offering different perspectives on scientific research outcomes. As for Japan, no research journal matching The Scientific Reports of the Whales Research Institute in its quality has been published. It is probably because many domestic cetologists have sought to publish their papers in international research journals based outside Japan.

As the global environment surrounding the issue of whaling became increasingly complex, we have observed a shift in publishing policies among these journals, rejecting papers whose findings are based on specific research methods such as lethal sampling. Because of this, no small numbers of papers submitted by biological scientists using samples collected through lethal surveys, even just for some parts, have been denied proper reviews. While we agree that animal ethics should be given high priority when writing a research paper, if a paper, the research method of which is allowed under domestic and international rules, is rejected, it is a decision made beyond scientific judgment.

Our new journal for cetacean population studies intends to follow the scientific policy of The Scientific Reports of the Whales Research Institute, that is, to contribute to global development of cetacean studies. As long as submitted papers conform to scientifically-accepted animal ethics, we do not make distinctions based on research methods. At the same time, to maintain the journal's neutrality in the complex global environment surrounding whaling issues, the journal will be published from a newly organized committee, rather than as a bulletin type scientific report from a specific research institute. The title of the new journal will be Cetacean Population Studies to be abbreviated CPOPS, and we aim to keep our door wide-open for researchers worldwide, contribute to the scientific development of resource studies for marine mammals especially focusing on cetaceans, and nurture many aspiring scientists.

Seiji Ohsumi

Seiji Ohsumi, Ph. D.
Chairman
Publication Committee for the Cetacean Population Studies

December 31, 2018

*Introductory declaration by the former Chairman of the Cetacean Population Studies Publication Committee on the occasion of the launching of this journal.

RELEVANCE OF THE SCIENTIFIC WORK ON CETACEANS OF DR. SEIJI OHSUMI

Luis A. PASTENE and Hidehiro KATO

Institute of Cetacean Research, Toyomi-cho 4–5, Chuo-ku, Tokyo 104–0055, Japan

Dr. Seiji Ohsumi, 'Seiji' as he was known by colleagues and friends, passed away on 2 November 2019 at the age of 89 years. It was a sad day for his family, friends and for all of us who knew and worked with him; without a doubt it was a sad day for cetacean science as well. During his memorial service held on 23 December 2019, many messages were received from colleagues and friends from both Japan and abroad. Most of those messages mentioned Seiji as a kind and true gentleman, a person that enjoyed meeting people at social events, a great cetacean scientist, and a person whose energy and enthusiasm for research remained undiminished until the end. We agree with that characterization of Seiji very much.

Seiji was a skilled debater with a deep command of the scientific issues. His opinions were always based on updated knowledge and good scientific information, and he strongly defended his ideas. During the meetings, people could have passionate discussions and disagreements with him over some issues. However, he never became angry and it was common to see Seiji outside the meetings displaying great courtesy to those same colleagues. Seiji enjoyed social events including parties very much, and saw those events as opportunities to hear and learn from people from different research areas, cultures or countries. At the very domestic level he saw the small parties as an opportunity for younger people to express their opinions, knowing that they were unable to express such opinions in more formal meetings.

Here we would like to focus on the scientific work conducted by Seiji. First, we briefly outline his professional career and then we highlight some of his most relevant scientific contributions.

Brief outline of professional career

- Born on 12 July 1930 in Gunma Prefecture, Japan.
- Graduated in 1948 from the Science Course at the Niigata Public High School under the former educational system.
- Completed pre-graduate studies in 1951 at the Faculty of Agriculture, the University of Tokyo.
- Published his first study in English in 1954 in collaboration with some colleagues. The study was titled 'On the sexual maturity of the sei whale of the Bonin waters' under his original name Seiji Kimura (Nishiwaki *et al.*, 1954).
- Completed post-graduate studies in 1958 at the Faculty of Agriculture, the University of Tokyo. The title of his doctoral dissertation was 'A study on age determination of the fin whale' (Ohsumi, n.d.).
- Became a member of the Whale Research Institute (WRI) in 1958. In his early days at the WRI, Seiji was mainly engaged in field work at numerous places where commercial whaling occurred as well in laboratory work and analyses of samples he collected. In this period, he worked under the supervision of the late Prof. Masaharu Nishiwaki and Dr. Hideo Omura.
- Became a member of the Population Dynamics and Statistics Division of the Tokai Regional Fisheries Research Laboratory in 1966.
- Became Head of the Unit for Cetacean Population Studies at the government's Far Sea Fisheries Research Laboratory (FSFRL) in 1967.
- Became Director General of the FSFRL between 1988 and 1991.
- Became a member of the board of directors of the Institute of Cetacean Research (ICR) in 1991.
- Became Director General of the ICR between 1995 and 2003.

- Became a Senior Scientific Adviser of the ICR in 2004.
- Became Adviser Emeritus at the ICR from 2015 until he passed away in 2019.

Scientific contributions

Seiji was a prolific researcher with over 700 scientific articles and publications on cetacean biology and ecology, conservation and management, and whaling issues, among other subjects. He regularly presented his work at scientific meetings as well as in public forums.

Apart from his specialized scientific publications and lectures in the field of natural and applied science that targeted scientists, he considered it important that the general public was aware of cetacean conservation and management, and consequently spent considerable time preparing articles and talking to the general public on those topics. He was especially skilled at writing and talking in a way that was understandable for different kinds of audiences. This is reflected in the large number and diversity of his written publications and articles on cetaceans, whaling, whale conservation and management, and whale food culture, prepared during his productive life (see also his bibliography in this issue):

- Specialized papers published or presented at scientific meetings: 286
- Books and book contributions: 58
- Reports and booklets: 40
- Geiken Tsushin (Whales Research Institute/Institute of Cetacean Research (WRI/ICR) Quarterly Newsletter published in Japanese since 1948): 100
- Miscellaneous: 257

Some relevant studies

The scientific work of Seiji was mainly focused on the assessment and management of large whales as well as with the natural history of this group of animals.

Seiji conducted the work on assessment and management largely in the context of the work of the Scientific Committee of the International Whaling Commission (IWC/SC), the international organization in charge of the conservation and management of the large whales. The IWC/SC is recognized as the most skilled group of specialists in the field of whale assessment and management, and Seiji was one of its leading members for over five decades. Seiji was engaged in the assessment and management of several large whale species, including fin (*Balaenoptera physalus*), sei (*B. borealis*), Bryde's (*B. edeni*), common minke (*B. acutorostrata*), Antarctic minke (*B. bonaerensis*), and sperm (*Physeter macrocephalus*) whales of both hemispheres. Seiji's contributions to the biological knowledge and assessment of these species were enormous, and these contributions are reflected in many publications in the specialized journal of the IWC.

As in other groups of marine living resources, age and reproductive data are essential for assessment through the application of population dynamic models. Seiji not only applied models to assess different populations and species of large whales but also investigated the scientific basis of some of the essential data used in those models. One of the most remarkable examples is the work he conducted to determine the age of fin whales based on their earplugs (Ohsumi, 1964).

By the time of the publication of this work, several approaches were available to estimate the age of the fin whale, namely body length, stage of growth, number of ovulations, white scars (Mackintosh and Wheeler, 1929); baleen plates (Ruud, 1940); crystalline lens (Nishiwaki, 1950), and earplugs (Purves, 1955). Seiji believed that the laminations found in the core of earplugs were the best approach to determine age because the laminations were considered to form periodically and were present in both males and females throughout the whale's lifespan and earplugs are relatively easy to collect and prepare for reading (Ohsumi, 1964).

The main scientific question at that time was on the frequency of deposition of the earplug laminations, which was considered to be biannual (Laws and Purves, 1956). Seiji examined this matter in further detail by using biological material of a number of fin whales taken in both the Antarctic and the North Pacific. He used three approaches to address the question above: examination of age characters from recaptured whales (mark-recaptured whales), comparison of results among different approaches, and an examination of the population dynamics on the age composition based on earplug laminae readings.

After detailed analyses and examination he stated the following: that 'it will be concluded that the annual accumulation rate of earplug lamination must be less than two, probably near one, and average annual ovulation rate will be under one, probably near 0.5, although there are individual and racial variations. In addition, the average age at sexual maturity will be older than 5 years, probably 9–11 years. Of course, there are individual variations in the age of sexual maturity' (Ohsumi, 1964).

The conclusions above regarding the annual deposition rate of earplug laminations had strong implications for the assessment and management not only of fin whales but of several other balaenopterid species where earplugs were subsequently used for determining the age, e.g., Antarctic minke whales. In his 1964 publication, Seiji recommended that 'the standardization of the reading of earplug lamination should be established….'. Subsequent work on Antarctic minke whales and other species have benefited from the early studies of Seiji, and standardization has been conducted thoroughly in recent years. Age data based on earplugs have also been very useful in the calibration of molecular methods being developed to determine age in the Antarctic minke whales.

In the field of natural science there are many contributions from Seiji not only on large baleen whales but also on odontocetes. Here we would like to highlight the investigation he made on the school structure of sperm whales (Ohsumi, 1971).

Ohsumi (1971) studied the structure of sperm whale using biological information obtained from three complete schools taken in coastal waters of Japan (1) and pelagic waters of the Southern Hemisphere (2). Information examined included the number of whales forming a school, size distribution, sex ratio, sexual maturity, physical maturity, age distribution and sexual condition of whales which form a school.

Based on detailed analyses, Seiji proposed the following hypothesis on the formation of sperm whale schools, in which the behavioral foundation of sperm whales is considered to be a maternal family group.

- The fundamental form of a sperm whale school is the 'nursery school,' which is composed of mature females and calves nursed by mature females.
- Immature males and females are also nursed by mature females until the time of sexual maturity.
- The average size of school was estimated to be 27.1 whales, and half of them are mature females.
- A nursery school moves as a tightly united school and remains as a family for long time.
- Some immature whales leave the nursery school after weaning to form 'juvenile schools.'
- After attainment of puberty, all males gradually leave the nursery school. Males at puberty form 'bachelor schools.'
- Socially mature males or bulls form a small 'bull school' or live alone. Most bulls are considered to live as solitary animals.
- Bulls struggle with each other to join a nursery school in the breeding season, and the winning bull and the nursery school form the so-called 'harem.'

Seiji also estimated that the number of mature females served by a bull in a harem was 14 on average.

This study was not only important in understanding the natural history of sperm whales but it was also useful for their assessment. In particular, parameters important for assessment include the number of mature females with which a bull mates and the ratio of number of males/mature females; information on both was obtained in Seiji's study (Ohsumi, 1971).

Special awards

His scientific and dissemination work on cetaceans and whaling was recognized with numerous awards including the following:

- The Order of the Sacred Treasure, Gold Rays with Rosette (2002).
- The Royal Norwegian Order of Merit (2006).
- Special Award of the Mammal Society of Japan (2011).

Some final thoughts

Seiji's scientific contribution to the knowledge of cetaceans is enormous. He made contributions not only in the field of basic biology and ecology of cetaceans but also contributed substantially in the assessment of several species, which was translated into appropriate policies of conservation and management. He was a hard worker in the field, in the laboratory (Fig. 1), in the analyses, and in the preparation of scientific communications. He was very skilled at expressing his ideas and studies through written and oral presentations, which were understandable to different audiences. We were fortunate not only to share with him the same institute and discuss together research plans and results, but also share social events that Seiji enjoyed very much. In particular many colleagues and friends with Japanese knowledge appreciated his beautiful Japanese sentence expressions. His enthusiasm for the study of cetaceans was evident throughout his life as he was assisting the ICR until the very last moment before his death. His enthusiasm, energy, productivity and courtesy should be an example for the younger cetacean scientists, especially for those working at the ICR.

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Fig. 1. Dr. Seiji Ohsumi counting growth laminae in a whale earplug at ICR (August 5, 2010).

RECOLLECTIONS OF DR. SEIJI OHSUMI

RECOLLECTIONS OF SEIJI OHSUMI

Yong-Rock AN

Cetacean Research Institute, National Fisheries Research and Development Institute,
139–29, Maeam-dong, Nam-gu, Ulsan, Republic of Korea

It is a great honor to remember the life of the late Dr. Oshumi. We have lost the extraordinary life of this remarkable man who devoted his whole life to Cetology.

The first time I met him was when we entered Ishinomaki Port after the JARPN II research cruise in 2003. My first impression of him was that of a very gracious and gentle man, but when we talked about whale research, his eyes were full of energy.

I understand that he and my Japanese leaders and colleagues fully supported me to prepare my post-doctoral study on Cetology. But I gave up the great opportunity to study whales in Japan because at about the same time I got a job as a whale researcher of the Cetacean Research Institute (CRI) in Korea. Nevertheless, he still congratulated and encouraged me.

Dr. Oshumi was always energetic and very active when I met him at the IWC Scientific Committee or the related workshops. He was my great teacher with more extensive experience and deeper knowledge on Cetology than anyone else. Also, he was very interested in the policies and issues of whaling in Korea as well as my research activity.

The citizens of Ulsan, the venue for the 57th IWC meeting in 2005, know him very well because he participated in the Whale Festival several times and gave valuable lectures on Cetology and whaling culture. I believe their thoughts and prayers are with his bereaved family and colleagues.

Great man, great loss. I will always be grateful for his contributions to whale research and mentorship. I am missing already his smile and clapping in Kanto style.

Rest in peace Oshumi-sensei.

IN MEMORY OF DR. SEIJI OHSUMI

Arne BJØRGE and Tore HAUG

Institute of Marine Research, Nordnesgaten 50, Bergen, Norway

It was with great sadness that we received the message that Dr. Seiji Ohsumi passed away November 2, 2019. We learned to know and admire Dr. Ohsumi at the Scientific Committee (SC) of the International Whaling Commission (IWC), where he participated as a leading scientist over a period of more than half a century and chaired the Japanese delegation in the 1990's.

Dr. Ohsumi had an interest in, and great knowledge of, a variety of scientific aspects of the biology, ecology and management of cetaceans. He published strange details and curiosities such as the finding of visible hind limbs in striped (*Stenella coeruleoalba*) and bottlenose (*Tursiops truncatus*) dolphins (Ohsumi, 1965; Ohsumi and Kato 2008) and the virginal membrane in large rorquals (Ohsumi; 1969). But his most important achievements were on the life history, in particular age determination, of a number of species (e.g., Nishiwaki, Hibiya and Ohsumi, 1958a, 1958b; Ohsumi, Kasuya and Nishiwaki, 1963; Ohsumi, 1964) and his revolutionary studies into the social life of the sperm whale (*Physeter macrocephalus*, Ohsumi, 1971). In recent years during the special permit whaling, his interests were also devoted to the ecological role of cetaceans, especially their feeding habits and consumption, and their role in the ecosystem (Tamura and Ohsumi 2000; Fujise, Hatanaka, and Ohsumi 2010). His publication record spans more than six decades and covered species from the small Dall's porpoise (*Phocoenoides dalli*) to the great blue whale (*Balaenoptera musculus*).

Dr. Ohsumi was one of the most respected members of the IWC/SC. Although members of the SC could have different views on a number of issues, all participants listened carefully when Dr. Ohsumi spoke. His impressive publication record and his life-long experience from surveys at sea, laboratory work and advanced theoretical studies in the office, made him an authority within the SC. His knowledge combined with a well-developed sense of humour made him also one of the best debaters in the SC. And we all loved his funny speeches every year at the traditional dinner party following the closing session of the SC. Dr. Ohsumi will be deeply missed.

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REMEMBERING DR. SEIJI OHSUMI

Robert L. BROWNELL Jr.

Former Chair of the IWC Scientific Committee, Southwest Fisheries Science Center, NOAA, USA

Seiji lived a wonderful life and was a great scientist. When Dr. Omura died, I attended his service and there were many people present, including Seiji. During the service, Seiji said to me that "I hope that when I die this many people will attend my service 'to pick my bones'". As it turned out, the number of people at the memorial ceremony for Seiji on 23 December 2019 far exceeded the number that attended Omura's service. Seiji was a great help to me when I was doctoral student at the Ocean Research Institute, University of Tokyo. So that I could survive as a non-working student in 1974, Seiji arranged for me to be Visiting Biologist at the Far Seas Fisheries Research Laboratory in Shimizu via a Japanese Government Research Award for Foreign Specialists.

RECOLLECTIONS OF SEIJI OHSUMI

Doug BUTTERWORTH

Professor Emeritus, Department of Mathematics and Applied Mathematics, University of Cape Town, South Africa

I first met Seiji in late 1980 at an IWC workshop held in Seattle, during which he invited me to partake in what was my first sushi meal. The workshop was held to discuss how best to develop estimates of whale abundance from sighting surveys. This topic had come into prominence as a key component of the IWC's International Decade of Cetacean Research, whose flagship programme was annual minke whale assessment surveys in the Antarctic. Seiji was co-convenor of the programme together with my own colleague, Peter Best, and this soon led to many visits to Japan to participate in the meetings that planned these surveys. Seiji would chair these in his customary friendly style, but also took responsibility for organising hospitality for the foreign guests outside meetings' hours. Thus, it was Seiji who took me on my first "tourist trip" around Tokyo, including Tokyo Tower and the Meiji Shrine, and the evenings would often encompass a visit to his favourite robatayaki bar in Shinjuku with its large badger statue outside. Seiji was a great host, and when on one occasion some on my relatives accompanied me on a visit to Tokyo, he insisted on according us the rare privilege of a visit to his own home in Shinjuku. Fortunately, on that occasion we managed to get there without becoming lost in the cavernous underground malls of Shinjuku station, something even Shinjuku-resident Seiji would admit had sometimes happened indeed to him.

For many decades Seiji served as the leading Japanese whale scientist, representing his views and country faithfully and effectively in the cauldron that was the IWC Scientific Committee during those times, as well as tabling the outcomes of his often-substantial studies in that forum. In debates there he frequently clashed with arch-anti-whaler Sidney Holt on a host of issues, gamely responding in interchanges that would play on the subtleties of the English language which, unlike for him, was the mother tongue of his opponents and gave them an undue advantage.

My abiding recollection of Seiji will be of his unchanging pleasant and friendly nature. After his retirement, he would still come through regularly to his work-space at the Institute of Cetacean Research. A visit there would always include catching up with him, when he'd enthusiastically explain what research issue he was working on at the time. Like the late John Bannister, with whom he shared so many IWC/SC meetings, he was the epitome of a gentleman.

CONDOLENCES ON THE PASSING OF DR. SEIJI OHSUMI

Phillip CLAPHAM

Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 7600 Sand Point Way NE, Seattle, WA, USA

On behalf of my wife and myself, please accept our sincere condolences for the passing of the great Seiji Ohsumi. It is a very sad day. Seiji's scientific contributions were large, but I will always remember him for his gentle nature and his kindness. We often disagreed at the IWC, but my wife and I always enjoyed our conversations with him, and he always displayed a great courtesy to everyone.

He will be missed.
Very sincerely,

Phillip Clapham and Yulia Ivashchenko

REMEMBERING DR. SEIJI OHSUMI

Doug DEMASTER

Former Chair of the IWC Scientific Committee, and Director, Alaska Fisheries Science Center, NOAA, USA

In the Alaska Native culture, elders are greatly respected for their wisdom and civility. At the IWC Scientific Committee, while I was chair, I greatly appreciated Dr. Ohsumi's contributions to our deliberations. He was one of our elders. His comments reflected considerable experience and knowledge regarding whales and whaling. He was an elder to be respected. I was very grateful to him for his consistent support of Alaska Native subsistence hunters.

With my deep regards,

Doug DeMaster

CONDOLENCES ON THE PASSING OF DR. SEIJI OHSUMI

Greg DONOVAN

Former Head of Science, International Whaling Commission, Cambridge, UK

I was so sorry to hear of the news of the death of Seiji. He was a great man and one of the kindest senior scientists as I began my cetacean career 42 years ago and remained a true gentleman throughout the years. His knowledge of cetacean biology, especially of the large whales was unparalleled and his energy and enthusiasm remained undiminished until the end—an example to all of us. Please pass my sincere condolences to all my Japanese colleagues and especially those at ICR.

With best wishes

Greg

HOMAGE TO DR. SEIJI OHSUMI

Yoshihiro FUJISE

Director General, Institute of Cetacean Research, 4–5 Toyomi, Chuo-ku, Tokyo, Japan

Dr. Seiji Ohsumi joined the Institute of Cetacean Research (ICR) in 1991, and from December 1995 to January 2004 he was in charge of the operation of the Institute and the guidance of the staff as its director-general. In addition to his scientific accomplishments as a researcher with more than 700 papers, he was interested in everything related to whales, including whale culture and whales as food, and attended many relevant meetings and never stopped being interested in these things. Especially on the research side, he constantly inspired young researchers with various ideas. Further, the spirit of taking good care of food has been passed on to the institute's staff with the catchphrase "You would be scolded by Dr. Ohsumi if you leave the food you are served." In addition to paying homage to the teacher who pursued his dream throughout his life, I think many of us would like to live such a life.

Ohsumi-sensei, I'm really thankful to you.

MEMORIES OF SEIJI OHSUMI

Ray GAMBELL

Former Secretary to the International Whaling Commission (1976–2000),
Green End, Landbeach, Cambridge, CB25 9FD, UK

Seiji Ohsumi was already an important figure in the world of whale research when I entered this field in the early 1960s. It was a time of great international pressure to halt the over-catching and decline of whale populations, particularly in the Antarctic. Research on the basic biology and lives of the great whales had been carried out by scientists, mainly from the whaling nations, since the beginning of the Antarctic whaling industry at the beginning of the century. Thus, Japan had a history of such endeavours, and Seiji built on and expanded this knowledge base by his own research.

I was fortunate therefore to work with Seiji, and whale biologists from a rather small group of countries, to bring together the research we carried out on these fascinating and commercially valuable animals. We met at the annual meetings of the Scientific Committee of the International Whaling Commission, at special meetings and working groups around the world, to bring together our knowledge on specific species or populations. We also socialised outside the working hours!

The new science of fisheries population dynamics and the regulation of fisheries was brought to bear on the whaling problem in the 1970s. This required all the available catch statistics and relevant biological information such as growth, age and mortality of the different species and populations to be combined together for analysis. Seiji joined with scientists from other nations to pool these data and prepare them for mathematical analysis.

Despite the pressures of these meetings, Seiji was always a charming and approachable colleague. We kept in touch after I retired in the year 2000 and exchanged cards and news at Christmas. His last message to me was “I go into the office every day—I have no other interest.”

SOME WORDS FOR DR. SEIJI OHSUMI

John "Craig" GEORGE

Wildlife Biologist (retired), North Slope Borough, Department of Wildlife Management, Utqiaġvik, Alaska, USA

It is an honor to offer some words for Dr. Seiji Ohsumi. Like many classically trained whale biologists of his time, Ohsumi understood whales "inside and out." He was knowledgeable about their anatomy, physiology, population dynamics, marine ecology, whaling history and more.

While editing and writing the recently published book "The Bowhead Whale: Biology and Human Interactions"[1] I carefully reviewed the report *Black Right Whales of the North Pacific* by Ohsumi and colleagues[2]. I was astonished at the detail and sheer volume of work they did on this species. I was also impressed that the North Pacific right whales are more similar anatomically to their bowhead cousins than I previously realized; this has important implications to the bowheads' response to climate warming.

Equally important to being an outstanding whale biologist, Seiji Ohsumi was a gentleman. His conduct at the IWC Scientific Committee (SC) meetings was always dignified and respectful even during the many heated debates. I particularly valued his insights on the feeding ecology, reproductive biology, and health assessment of large whales.

I always enjoyed his words at the SC banquet and was impressed by his uncanny oratory skills in English which were far better than my own. He would give a toast or tell a story usually following John Bannister's silly Australian "dunny" joke. He would often say, "I don't understand British humor, but I enjoyed your story nonetheless." Thanks for your honesty, Seiji, no one really understands British humor!

At the IWC meeting in Anchorage he indicated that would like to taste bowhead whale. With the help of an Inupiat friend, we shared some *agviq* (bowhead) Japanese style with soy sauce and wasabi. It was a nice moment as he expressed his impressions and reverence for the whale. I considered Seiji a great friend and greatly miss him. I feel honored to carry on the type of work he did on large whale biology.

[1] George, J. C. and Thewissen, J. G. M. (Eds.), 2020. The Bowhead Whale, *Balaena mysticetus*: Biology and Human Interactions. 1st Edition. Elsevier/Academic Press, 668 pp.

[2] Omura, H., Ohsumi, S., Nemoto, T., Nasu, K., and Kasuya, T. 1969. Black right whales in the North Pacific. *Sci. Rep. Whales Res. Inst.* 21: 1–78.

REMEMBERING DR. SEIJI OHSUMI

Hiroshi HATANAKA

Adviser Emeritus, Institute of Cetacean Research, 4–5 Toyomi, Chuo-ku, Tokyo, Japan

Dr. Ohsumi was a man who walked the straight and narrow path of whale research. He used to say that "my occupation is whale research and my hobby is also whale research" and he never gave a second thought to this path. Nearly 30 years ago, I got to work with whales under the guidance of Dr. Ohsumi, and I was amazed at the breadth and depth of his knowledge of whales. I had the opportunity to travel abroad with him and he was highly regarded and respected by foreign scientists as well.

In the midst of post-war food shortages, we Japanese were on the verge of starvation and, ever since, Dr. Ohsumi kept consistently conducting and leading research to promote the use of cetacean resources to provide animal protein and establish their sustainable use on a scientific basis.

Now that Dr. Ohsumi has passed away, I am immersed in a sense of loss of an excellent leader and a feeling of loneliness for losing an unparalleled friend.

MOURNING DR. SEIJI OHSUMI

Yoshihiro HAYASHI

Former President, National Museum of Nature and Science, 7–20 Ueno Park, Taito-ku, Tokyo, Japan

Dr. Ohsumi was a person who never wavered. Although he was 16 years my senior, whenever we met, he always had a smile on his face and spoke in a way that made me feel no age difference. The fact that we studied at the same university, though we were in different departments, and that our birthdays were on the same day, July 12, may have been the reason why I felt particularly close to him. Likewise, Dr. Ohsumi's doctoral dissertation was on the establishment of an age assessment method for fin whales, while my theme was the geographical variation of wild boars, and I needed an accurate age assessment to compare wild boars from different regions. It is said that the age of whales can be accurately estimated even at 100 years old by the annual rings formed on their earwax plugs, but wild boars' age can only be read up to 10 years at most due to the annual rings formed in the cementum of their posterior molars. However, since both fin whales and wild boars are mammals, I remember Dr. Ohsumi's thesis being very helpful for my research.

It was only after I was dispatched to the Southern Ocean as a veterinarian during the 1978–79 whaling season, when the International Whaling Commission (IWC) asked the Fisheries Agency for "an accurate estimation of killing time of Antarctic minke whales" that I became able to talk closely with Dr. Ohsumi. He was always present in the Japanese delegation's waiting room at the annual IWC meetings held at Cambridge University in the UK, Germany, St. Kitts and Nevis, Mexico, and so on. It is thanks to our predecessors that Japan has been able to play an active role in the international community as a sound, unwavering whaling nation, and Dr. Ohsumi was undoubtedly one of our country's foremost figures in this field.

May he rest in peace.

RECOLLECTION OF SEIJI OHSUMI

Kazuhiko HIRAMATSU

Associate Professor, Atmosphere and Ocean Research Institute, The University of Tokyo, 5–1–5 Kashiwanoha, Kashiwa, Chiba, Japan

When I got a job at the National Research Institute of Far Seas Fisheries in April 1984 and was assigned to the High Latitudes Oceanography Section, Oceanography and Southern Ocean Resources Division, the division leader was Dr. Seiji Ohsumi. He was my boss's boss. I did not have much opportunity to talk to him because he was promoted to the Research Planning and Coordination Division in a little over a year, but I was impressed with his aggressive appearance. He was already in his mid-50s at that time.

After that, he was the Director General of the National Research Institute of Far Seas Fisheries and there was not much contact between an ordinary researcher and the director. But one day, I was called into the director's office and wondered what was going on. He introduced me to a matchmaking. I declined politely because the marriage was decided just before, but it seems that there was also an aspect of taking care of staff who are unlikely to get married. After he moved to the Institute of Cetacean Research, there was a little interaction, such as attending a meeting when I was involved with research on cetaceans for a short time, and participating in the Fisheries Resources Management Colloquium at the Institute of Cetacean Research. In retrospect, I have had a long relationship with him since I started as a researcher.

TWO MEMORIES OF DR. OHSUMI

Koichi KAJI

Professor Emeritus, Tokyo University of Agriculture and Technology,
Director of Wildlife Management Research Center, 940 Aogakicho, Sawano, Tamba, Hyogo, Japan

There are two things that left a strong impression in my memories of Dr. Ohsumi. One is a letter of compassionate encouragement and an expectation that I received from Dr. Ohsumi when I moved from a research institute in Hokkaido to Tokyo University of Agriculture and Technology (TUAT) in April 2006. Every time I encountered a difficult situation, I was able to return to my original intension by rereading the letter many times.

The other is the event at the whaling seminar co-hosted with Professor Hidehiro Kato of Tokyo University of Marine Science and Technology (TUMSAT) in July 2007. In that year, I focused on the whaling controversy in my seminar for six first-year students. As the final touch on the seminar, Professor Kato kindly arranged a joint seminar titled “On the Whaling Issue.” This was an exceptional seminar in which graduate students of the TUMSAT commented on the presentation by the TUAT first-year students, and a scientist from the Institute of Cetacean Research (ICR) gave a summary and comment. Dr. Ohsumi, an adviser of the ICR, also participated in the joint seminar and gave warm comments on the three presentations on the “History of Whaling” in Part 1.

However, Dr. Ohsumi seriously argued, “I don’t think so,” in response to the opposition’s allegations in Part 2, “The Controversy over Whaling.” Participants praised the student for making such a good presentation that Dr. Ohsumi would seriously argue. I felt the sincerity of the academic discipline when I saw Dr. Ohsumi sincerely facing the presentation of the first grader. I would like to cherish Dr. Ohsumi’s message that it is science-based words that can transcend the conflict of values.

RECOLLECTION OF SEIJI OHSUMI

Toshio KASUYA

Retired Professor, Mie University and Teikyo University of Science and Technology, Nagayama, Tama-shi, Tokyo, Japan

In the autumn of 1960 Dr. Masaharu Nishiwaki of the Whales Research Institute (WRI; Director Hideo Omura) invited me to pursue my graduation thesis in his laboratory, where I met Dr. Seiji Ohsumi. The next year I joined WRI as a research staff and received trainings from Ohsumi for cetacean biologists. These included photo film development, photo printing and creating block copies for papers. I also learned from him processing of cetacean gonads and ageing of whales. The experiences at WRI, including two North Pacific and an Antarctic pelagic whaling cruises, formed the foundation of my later activities. Before modern tools such as personal computer and word processor became available in the early 1980s, we biologists used abacus, slide rule, table of logarithms for data analyses, and typewrote manuscript. Recent biologists have an easier work environment and tend to create a flood of papers often with complicated statistical analyses of value I don't know.

After spending 5 years at WRI, I was invited by Nishiwaki to the Ocean Research Institute, University of Tokyo, and worked mainly on biology of Japanese small cetaceans and river dolphins of the world. Then in 1983 Ohsumi invited me to the Cetacean Division of the Far Seas Fisheries Research Laboratory. With the cooperation of my staff, I enjoyed 14 years (1983–1997) of my life in the Laboratory working on the biology and management of cetaceans around Japan. I believe that Ohsumi worked for us during the period as a buffer between our cetacean group and the Fisheries Agency.

After my retirement from educational jobs at Mie (1997–2001) and Yamanashi (2001–2006), I was fortunate to resume regular contacts with Ohsumi with drinking at a buckwheat noodle shop in Shinjuku, usually twice a year. The last was on 10 July 2019, when we talked about inviting some elderly cetacean biologists, but it did not happen.

FOLLOWING SEIJI OVER 40 YEARS

Hidehiro KATO

Professor Emeritus, Tokyo University of Marine Science and Technology,
Advisor, Institute of Cetacean Research, 4–5 Toyomi-cho, Chuo-ku, Tokyo, Japan

I first met Dr. Seiji Ohsumi (I would refer to him hereafter as "Seiji" for the sake of friendliness) when I was a PhD student majoring in pinnipeds such as seals and sea lions. For some days 40 years ago, Seiji chaired a session at the marine mammal symposium, and I was sitting in the backmost row of the hall. I was intently watching him from the back of the room, and his unique way of speaking in his later days, which you are all familiar with, was already there. Even now, when I close my eyelids, the impressions of that time immediately come to mind. The image brings me back memories!

Although it did not occur to me at the time of the symposium, later on I was hired as a researcher at the former Whales Research Institute, where Seiji had also worked in the past, through the intermediary of the late Dr. Hideo Omura and others, and later moved to the Far Seas Fisheries Laboratory in Shimizu, where I followed Seiji. Even if we continued our research at different institutions for a while, we kept working closely together in the research itself, and after my retirement from Tokyo University of Marine Science and Technology in 2018, I had the honor of working with him as an advisor at ICR.

Seiji's written Japanese was flowing and elegant, beautiful, and grammatically correct. Overseas scientists cannot imagine that one of Seiji's articles on whale enlightenment was used in one of the chapters of a Japanese language textbook selected for junior high school. On the night before Seiji's death, we exchanged passionate opinions as usual about the ideal whale research and their stock management. His face was calm, but full of intelligence. Seiji's education was different from the education that we, the younger generation, had. Seiji inherited the liberal arts principles based on the deep philosophical insights of the old high school under the prewar education system. As well as being a preparatory course to enter the imperial university, it was the essence of elite education that has already been lost in Japan. Seiji was from the last student generation to graduate from the old Niigata Public High School in 1949 and went on to the old University of Tokyo, where he met his respected supervisor, the late Professor Masaru Nishiwaki, and Seiji was initiated in cetacean sciences by him there. The image of Seiji singing his favorite dormitory song loudly at the dormitory song festival of the old high school which, like many others in Japan is now closed, is always overlapping in my mind with the image of him at the symposium.

Fig. 1. Dr. Seiji Ohsumi at the time of the old Niigata Public High School, 17 or 18 years old. *Courtesy of Seiji's family*.

May he rest in peace.

MEMORIAL REMINDER OF THE LATE DR. SEIJI OHSUMI

Akito KAWAMURA

Professor Emeritus, Mie University, 1577 Kurimamachi Yacho, Tsu, Mie, Japan
8–9–8 Nanae-cho, Kameda-gun, Hokkaido 041–1111, Japan

More than fifty years ago Dr. Seiji Ohsumi initiated a bio-ecological research on the Antarctic minke whales. During the 1967/68 whaling season a total of 597 minkes were caught by our whaling fleets, and some essentially important biological data were obtained. With these together with some past knowledge and sighting records having been done from time to time, Dr. Ohsumi was very aware of the importance toward establishing a well-designed model for stock management. At that time Dr. Ohsumi foresighted coming future days of minke whale fisheries in the Southern Ocean and reported one of the basic data on the stock of this species while the amount of related data and/or evidence was still very limited. The report was: Stock of the Antarctic Minke Whale. *Sci. Rep. Whales Res. Inst.*, No. 22, (1970).

In this report he estimated the population size of the Antarctic minke whale to be 70,000, mainly based on sighting records obtained. Although the number itself was about one tenth of the later understandings, he suggested that introduction of latitudinal and longitudinal unit areas was undoubtedly possible an important key for stock management in the future. With hope for developing more modernized regulations for whaling fisheries together with what he aimed and described in the report, the story as a whole was full of suggestions.

As one of the younger alumni disciples of the old Whales Research Institute (WRI) I am very proud of him, having co-authored the report mentioned above. At the same time I hope that Ohsumi's foresighted and precursory work on whale stock management and whale fisheries would be reminded widely on this occasion.

We lost a true man of whales and whale fisheries. Recollections around activities and the old WRI always accompany the late Dr. Seiji.

May his soul rest in peace.

Ohsumi, S., Masaki Y., and Kawamura, A. 1970. Stock of the Antarctic minke whale. *Sci. Rep. Whales Res. Inst.* 22: 75–125.

RETROSPECT OF THE LATE DR. SEIJI OHSUMI

Zang Geun KIM

Senior Scientist, Fisheries Resources Management, National Fisheries Research and Development Institute,
408–1 Shirang-ri, Gijang-Up, Gijang-Gun Busan, Republic of Korea

As a person who was once in charge of cetacean research in Korea, I would like to honor the memory of the late world-renowned whale scientist, Dr. Seiji Ohsumi.

He admitted me as a trainee on cetacean research in the Far Sea Fisheries Research Institute for three months. When I arrived at Shizuoka Station in summer 1988, he came to pick me up and guided me to the Institute and assigned an employee apartment for my accommodation. During the training period there, I met with Drs. Tomio Miyashita and Hidehiro Kato and other colleagues.

Since 1993, Korea and Japan have established scientific cooperation through agricultural and fisheries cooperation as well as science and technology cooperation, as mandated in the Article 65 of the UNCLOS. This, in certain way led to the start of systematic cetacean research in Korea and inspired the establishment of the Cetacean Research Institute (CRI, NFRDI) in 2004. I wish this harmonious friendship may continue (Fig. 1).

I met him for more than 20 years in multiple opportunities such as on the occasion of the IWC meetings or social events and exchange programs (Fig. 2) until I left the Cetacean Research Institute of Korea in 2009. One of the precious memories that comes to my mind is that he liked the Korean soybean paste soup in my house and travelled with me to many places in Korea.

With all these memories, my family and I pray that the deceased may have a rest of peace at God's mercy.

I would like to express my sincere congratulation on the establishment of the Cetacean Research Institute in this very historical city of whaling in Korea as an old cetologist from the next country.

Korean and Japanese scientists have been working cooperatively for the sake of rational utilization and management of cetacean resources, and I hope more tight relationship will be built by use of this good chance.

I wish your Institute will develop steadily and largely as a splendid center of cetacean research in Korea!

大隅清治
Seiji Ohsumi
The Institute of Cetacean Research, Tokyo

Fig. 1. The message of Dr. Ohsumi to the opening of CRI in 2005.

Fig. 2. Group photo at the symposium on cetacean research in the Fisheries Research and Development Institute, February 14, 2001.

REMEMBERING DR. SEIJI OHSUMI

Toshiya KISHIRO

Deputy Director, Highly Migratory Resources Division, Fisheries Resources Institute, National Research and Development Agency, Japan Fisheries Research and Education Agency, 2–12–4 Fukuura, Kanazawa-ku, Yokohama, Kanagawa, Japan

I met Dr. Ohsumi for the first time when I joined the National Research Institute of Far Seas Fisheries after graduation in 1989. At that time, he was the director of the Institute, and I received rudimentary guidance as a researcher from him as a newcomer to the Cetacean Lab. He was engaged not only in pursuing research on whales, but also worked to organize research on other international fishery resources sections such as tuna and salmon and nurtured many researchers at the National Institute. In addition, despite his busy schedule, he had written many books on whales aimed for the general public and contributed to the dissemination of whale knowledge in Japanese society. All of us admired his vitality and inclusive, straight personality. After his retirement in 1991, he moved to the Institute of Cetacean Research, and continued to work and enthusiastically guide our cetacean research for many years. He had been literally a living dictionary and a spiritual pillar for us. On behalf of our Institute, I express sincerely respect for his achievements, and deep gratefulness for his leadership and encouragements for us. I feel that he continues to encourage the future progress of the cetacean population studies even after he’s gone.

I pray from the bottom of my heart that his soul may rest in peace.

RECOLLECTIONS OF SEIJI OHSUMI

Rebecca LENT* and Iain STANILAND**

**Secretary, International Whaling Commission*
***Secretariat Lead for Science, International Whaling Commision*
The Red House, 135 Station Road, Impington, Cambridge, UK

Dr. Seiji Ohsumi was a stalwart of the IWC Scientific Committee (SC) because of his long-standing, valued and active participation in the committee. He will be remembered fondly and appreciated for his years of dedication to scientific research and his contributions to the IWC. Between 1967 and 2010 Dr. Ohsumi authored and co-authored 182 papers[3] submitted to the SC collaborating with scientists from all over the world. This impressive body of work spanned a wide range of subject areas, including stock assessments, mathematical modelling, reproduction, feeding, and genetics, and contributed to our knowledge of baleen whales and small cetaceans alike. There are few who have contributed as much to the SC as Dr. Ohsumi.

Dr. Ohsumi was also committed to supporting early career researchers providing mentoring of their studies and research. His legacy lives on in the IWC as many of his former students and collaborators continue to serve with us today. His passing is a great loss to cetacean science and he is already greatly missed by the IWC community.

[3] Editor's Note:
CPOPS received with these recollections note from the IWC Office an extensive list of works by Dr. Ohsumi related to the Scientific Committee of the IWC. This list was collated and incorporated into Seiji Ohsumi's bibliography presented in the following section of this issue.

PERSONAL TRIBUTE TO DR. SEIJI OHSUMI

Christina LOCKYER

Research Director, Age Dynamics, Huldbergs Alle 42, Kongens Lyngby, Denmark

My first recollection of Seiji Ohsumi was in 1972 when I attended the IWC Scientific Committee for the first time. The IWC SC was a very different body to that existing today with only about two dozen participants from Australia, Canada, Iceland, Japan, Norway, USSR, South Africa, UK, USA and FAO. Seiji was very smart, dark suited, clean-shaven and jet-black hair. He was then in his early 40s. Then in my mid-20s, I looked up to him as a senior scientist. He seemed very inscrutable and I was a little in awe. He was very interested in my age estimation techniques in baleen whales and arranged for me to visit the Far Seas Fisheries Laboratory in Shimizu in 1977 for 3 months to read ear plugs and teach some students. He organised everything for me, right down to the Japanese style apartment. I recall being very sick during a national holiday when I lost much weight. Seiji was concerned and insisted on taking me for a sushi dinner with Suntory whisky to help me recover and lift my spirits. It really worked, and since then he always showed great kindness and hospitality to me. We met many times over the decades we were both active whale scientists, and I visited Japan for research several times when he often invited me to his home and took me sight-seeing (Fig. 1). When working on ear plugs in Tokyo in December 2009, he was a grand host and invited me to dine together with his wife, herself a prominent professor (Fig. 2). In late September 2019, I visited Japan for a first vacation cruising around Japan. We met before I departed and enjoyed a pleasant time together (Figs. 3 and 4). I did not know he would leave us forever some weeks later. Our last contact was by e-mail 2 days before he died, when he wished me a good recovery from breast cancer. He was a special man, and my recollections of him are very personal; now more as a friend and colleague than about his work achievements which were themselves awesome. He became the respected and very kind friend that I knew for 47 years. May he rest in peace.

Fig. 1. Seiji acting as tour guide for me on a personal tour of Kamakura.

Fig. 2. Dining out with Seiji and his wife in December 2009. I remember this place had a lovely garden where we walked.

Fig. 3. Outside a dinner venue in Tokyo, September 2019.

Fig. 4. Seiji during a walkabout with me near the Ginza in September 2019.

IN REMEMBRANCE OF DR. SEIJI OHSUMI

Koji MATSUOKA

Research Executive Director, Institute of Cetacean Research, 4–5 Toyomi-cho, Chuo-ku, Tokyo 104–0055, Japan

I first met Dr. Seiji Ohsumi when I joined the Institute of Cetacean Research (ICR) back in 1992, while he was the Executive Director there. For the first ten years or so of my working at the Institute, I was constantly shuttling back and forth between the North Pacific and the Antarctic Oceans. Dr. Ohsumi never forgot to encourage us young researchers, often asserting that the field was the basis of whale research and that it was important to write papers even on small topics. During those intense day and night sessions at the annual IWC/SC meetings, we received from him sometimes harsh and sometimes warm guidance on the legitimacy of research whaling and the importance of its continuation. The International Decade of Cetacean Research Program (IDCR) which he helped to launch in 1978/1979, was succeeded by the Southern Ocean Whale and Ecosystem Research Program (IWC/SOWER) and now by the ongoing International Whaling Commission/Pacific Ocean Whale and Ecosystem Research (IWC-POWER). Since my joining ICR, I went to the Antarctic Ocean as much as 15 times, and because of that, every time I had to be away for the New Year festivities. I will never forget that Dr. Ohsumi invited my family to his home on each of those occasions, thus warmly guarding my home front while I was away. I sincerely pray for the repose of his soul.

IN MEMORY OF DR. OHSUMI

Tsukasa MURAYAMA

Professor, Department of Marine Biology, School of Marine Science and Technology, Tokai University, 3–20–1 Orido, Shimizu Ward, Shizuoka City, Shizuoka, Japan

I first met Dr. Seiji Ohsumi when I was in my first year of university, participating in a seminar on cetaceans held in Shimizu City (now Shimizu ward), Shizuoka Prefecture. On the second day of the seminar, we visited the Far Seas Fisheries Research Laboratory, where Dr. Ohsumi talked to us about various topics. He was still a young man, but he explained many things to us, fledgling researchers, while holding a handful of materials in front of him. While Dr. Ohsumi had already made many achievements since the 1960s and 1970s, contributing greatly to cetacean research in Japan, at that time I did not know anything about research nor did I know much about him. However, from that day on, I often found the name “S. Ohsumi” in a number of international journals, and as I stumbled upon books written by Dr. Ohsumi in bookstores, I remember being surprised when I realized he was such an outstanding person.

After that, I went on to pursue cetacean research, and we had more opportunities to talk, and I was indebted to him in many ways, which did not change after he moved on to the Institute of Cetacean Research. When I went to visit him at the Institute with my doctoral thesis after receiving my doctorate, he welcomed me with a calm expression and congratulated me.

Dr. Ohsumi also keenly tried to spread the word about his research and whales to young people and the general public who liked natural science. For example, he often visited the activities of groups of people who were interested in dolphin and whale research, and gave them advice on the ecology of cetaceans and their research. He also participated in almost every symposium I organized every year in Tokyo, and gave presentations at some of them. After the symposium, he always talked to the participants, students who had just started their research, and aquarium staff, not only about whales, but also about the sea and ships, including his own experiences. He was never pompous as a great authority on cetacean research, and the young people also entertained friendly feelings toward him.

No matter what I asked him, he always responded with an affable smile and an amiable manner, and I regret and feel sad that I will never see him again.

I sincerely pray for the repose of his soul.

RECOLLECTION OF DR. SEIJI OHSUMI

Tomio MIYASHITA

Associate Researcher, Fisheries Resources Institute, National Research and Development Agency, Japan Fisheries Research and Education Agency, 5–7–1 Orido, Shimizu, Shizuoka, Japan

I have been indebted to Dr. Ohsumi for his help and support in both my work and private life since I started working at the Far Seas Fisheries Research Laboratory in 1980. When I joined the Laboratory, Dr. Ohsumi was the head of the cetacean resources section, and he taught me about marine mammals, starting with their scientific names, even though I had no connection with those animals. In addition, when I saw him directly typing English documents in preparation for the IWC SC meeting that was just around the corner, he would crack up day and night, typing away on his IBM electric typewriter, and I feel that he taught me by example how to approach my work with a strict attitude. He always asked me "Why?" in response to my doubts. There were times when I was at a loss for an answer, but I believe that I was taught to pursue the truth through these experiences. When I look at the many papers and writings that Dr. Ohsumi has left behind, I am once again amazed at the scientific contributions he has made. He loved to drink, and I was invited by him to drink at many occasions in the past. When I look at the photos, I remember those events such as 'Hanami' to see cherry blossoms and 'Imonikai' to eat boiled taro. He was also from Gunma Prefecture, and when my wife and I were married, he served as our matchmaker. We are very grateful to him for his help in dealing with the situation. Now, we are filled with sadness at the loss of Dr. Ohsumi. May he rest in peace.

CONDOLENCES ON THE PASSING OF DR. SEIJI OHSUMI

Sally MIZROCH

Retired Research Biologist, Alaska Fisheries Science Center, NOAA, USA

I met Seiji the very first time I attended the meeting of the International Whaling Commission's Scientific Committee in 1980. I was a new member of the US delegation and Seiji was the head of the Japanese delegation. Back in those days, even though the US and Japanese delegations had very different views on commercial whaling, we enjoyed spending time together after hours singing and drinking. We developed close and long-lasting personal friendships.

I was a young female scientist, one of maybe four women in attendance during those early years, and Seiji was always very supportive of all of us and of me personally. Seiji had an affinity for many young scientists, male and female, and his support contributed to our own growth as scientists.

Seiji and I genuinely enjoyed each other's company each time we met. He was my thoughtful tour guide during my many visits to Japan and we respected each other's viewpoints even when we disagreed.

I also enjoyed Seiji's long great friendship with my friend and long-time collaborator Dale Rice. One of my fondest early memories was sitting with Seiji on a bus ride from Reykjavik to the Icelandic whaling station in 1987 when he told me that he and Dale were exactly the same age. He and Dale Rice were part of a remarkable generation of biologists whose analyses advanced our knowledge of cetacean biology in a breathtaking fashion. Now they are together again. I miss them both very much and was lucky to be friends and collaborators with them.

I've attached a photo of Seiji, Dale, and Gordon Pike from 1963 (Dale Rice's photo collection), a photo of Seiji with a Discovery mark logbook showing mark recovery data for a sei whale Dale had marked off California in 1965, and some recent photos of Seiji when I spent time with him in Tokyo and in Kamakura City.

So sadly,

Your old friend Sally

Fig. 1. Seiji Ohsumi, Dale Rice and Gordon Pike (right) having coffee break during the IWC Sperm Whale Workshop in Seattle, WA (1963).

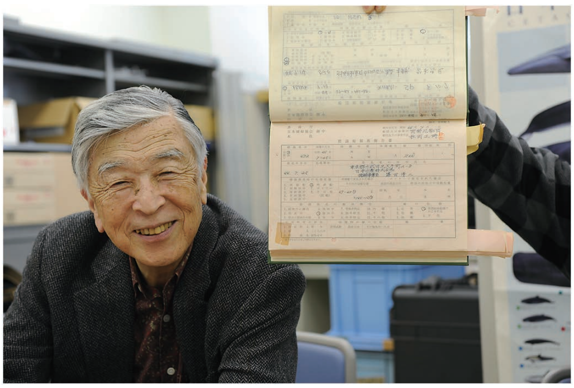

Fig. 2. Seiji with the Discovery Mark recovery logbook showing the recovery of a sei whale Dale Rice's marked off southern California in 1965 (2012).

Fig. 3. Seiji as tour guide in Kamakura City in 2012.

Fig. 4. Seiji and I the last time we met in Tokyo. He is wearing a souvenir hat I gave him in 2012 from my favorite baseball team, the Seattle Mariners (September 4, 2014).

MEMORIES OF DR. SEIJI OHSUMI

Joji MORISHITA

Professor, Department of Marine Policy and Culture, Tokyo University of Marine Science and Technology, 4–5–7-Konan, Minato-ku, Tokyo, Japan

When I became a government official at the Fisheries Agency of the Government of Japan in 1982, Dr. Ohsumi was one of the most knowledgeable scientists about whales and whaling. When I attended my first-time International Whaling Commission (IWC) meeting in 1992 held in Glasgow, UK, he was already regarded as a legendary figure in the whale/whaling community of the world. Since then, we attended so many meetings together and travelled around and into many corners of the world (Figs. 1 and 2). Every one of them is memorable and I learned a lot from Dr. Ohsumi.

Two stories among so many remind me of who Dr. Ohsumi was.

He told me that he was criticized by Japanese whalers as anti-whaling when he, as a young scientist, reported to the IWC Scientific Committee about the poor stock status of some whale stocks and supported whaling restrictions targeting those stocks. He was smiling when he told me of this story, but I am sure it was not a pleasant episode for him. However, it was clear to me that his conscience as a scientist was always the most important guiding principle of his activities and statements.

Another story is very much consistent with the above. Dr. Ohsumi had held many important and responsible positions through his professional life, including that of Director General of the National Research Institute of Far Seas Fisheries (NRIFSF, Shimizu Laboratory), and Director General of the Institute of Cetacean Research (ICR), to name a few. But he was most happy when he passed all these responsibilities to his successors and told me then that he finally became one simple scientist again that can contribute to science. He actually contributed to the advancement of science till the last day of his life.

He was stubbornly a pure scientist even when the results of his research and analysis were against the interests of whalers. While he was an excellent manager of the organizations he had led, he preferred to be a simple scientist. He hated “political scientists.” He often said to young scientists to be a scientist rather than a scientific technician.

It was my great honor and privilege to have worked with Dr. Ohsumi. His legacy will remain with all of us who met him.

Fig. 1. During a Japan-Russia scientific planning meeting in Moscow (June 1999).

Fig. 2. During a trip to Norway to finalize the blue whale skeleton lease contract to Shimonoseki city (July 1999).

ONWP

Hideki MORONUKI

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Ohsumi-sensei was not just a scientist but also a man of vital spirit and warm heart. Everybody knows that he was one of the pioneering whale scientists in Japan, who supported Japan's whaling industry from top to bottom. He is also well known to many of us as a "militant" pursuing the sustainable use of whale resources. However, this was not only for the benefit of Japan, but also for all over the world, specifically for developing countries. He advocated his own humanitarian whaling plot where sustainable whaling would be conducted for ample whale resources in the Antarctic Ocean and whale products obtained therefrom would be distributed to developing countries severely suffering from food crisis (Ohsumi's New Whaling Plot). In order to materialize his plot, he devoted himself to the resumption of science-based sustainable whaling and thereby encouraged young scientists, industry colleagues and Government officials to fight together.

On 1 July 2019, more than 31 years after the introduction of the so-called Moratorium on Commercial Whaling, Japan resumed the sustainable whaling based on the best scientific information available. Fortunately, we were able to celebrate the resumption of the sustainable whaling together with you, Ohsumi-sensei. However, it was not in time to materialize your plot. We still have a lot of things to do and a lot of obstacles to overcome before your dream may become true. However, you do not need to worry about it too much, Ohsumi-sensei. Please remember that you brought up so many pupils and followers who will make the most of your will to meticulously seek a way to move your plot forward. Please therefore look forward to a future big news about the sustainable whaling in the Antarctic Ocean being resumed and that the food shortage in some developing countries is being mitigated through ONWP: Ohsumi's New Whaling Plot.

APPRECIATE THAT I COULD SHARE TIME WITH A GREAT SCIENTIST

Gen NAKAMURA

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In my childhood, I occasionally saw the name of Dr. Seiji Ohsumi in some books. But the first contact with him was not until 2006, when I started my Cetology studies at the university. After that, 13 years have passed. I guess it might be a very short time in his life, but it was a very meaningful period for me. Even after he retired, he energetically attended the conferences or meetings and delivered innovative opinions to us, based on his vast knowledge. I feel very sorry that I was unable to talk and discuss with him, but I leverage that with his papers, books, and memories for my life as a researcher. I really appreciate you, Ohsumi-sensei.

A FEW WORDS IN MEMORY OF DR. SEIJI OHSUMI

Luis A. PASTENE

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Seiji was an important person during several stages of my life. The first time I met him was in 1981 during a workshop on cetacean reproduction in the United States. At that time, I was a pre-graduate student at the Concepcion University in Chile. Knowing my interest in cetacean research, he kindly provided information on scholarships and encouraged me to carry out postgraduate studies in Japan. Furthermore, in 1985 he helped me secure a scholarship that allowed me to travel to Japan in October of that year. Then I started postgraduate studies at the Ocean Research Institute (ORI) of the University of Tokyo. Seiji was supportive of me both personally and professionally as I adapted to living in Japan. In 1992, I became a member of the Institute of Cetacean Research (ICR) where Seiji was Executive Director, and we continued to work together at ICR until he died on 2 November 2019. He always supported my research activities in ICR and provided strict but fair criticism of my studies. I was impressed by Seiji's enthusiasm and dedication to cetacean and whaling research, and to the ICR. Until the very last week, he came to the institute almost every day, actively participating in our domestic meetings and providing useful advice and suggestions. I think many colleagues and friends will agree with me that Seiji can be characterized as a great cetacean scientist, a true gentleman and a very enthusiastic person for research and social-related activities. I feel happy that our last work interaction in 2019—on Chilean blue whale research—was a very positive one with Seiji supporting and agreeing with my conclusions on that particular study. I feel a deep respect and gratitude to the memory of Seiji.

MOURNING THE PASSING OF DR. SEIJI OHSUMI

Kazumi SAKURAMOTO

Professor Emeritus, Tokyo University of Marine Science and Technology,
4–5–7 Konan, Minato-ku, Tokyo, Japan

I would like to express my heartfelt condolences on the passing away of Dr. Seiji Ohsumi, who devoted his life to the study of whales and was a world-renowned authority on whale research.

I have been fortunate enough to be involved in cetacean research since 1982, and from then until his demise, I had the opportunity to receive guidance from Dr. Ohsumi both in private and public life. The first meeting of the International Whaling Commission (IWC) that I attended was the Minke Whale Ageing Workshop held in Cambridge, England in April 1983. At that time, the only researchers who participated from Japan were Dr. Seiji Ohsumi, Dr. Hidehiro Kato and myself, but I still remember vividly the gentle and strict guidance I received from him even as a newcomer. Since then, we attended together many meetings of the IWC Scientific Committee while Dr. Ohsumi continued his research activities as Director General of the Institute of Cetacean Research (ICR) and later on as Adviser Emeritus to the ICR, and gave me much guidance until just before he became ill. I also recall with deep emotion the many enjoyable conversations we had at social gatherings.

The image of Dr. Ohsumi that is etched in my mind is his big smile and his gentle gaze. The sadness of losing a great leader and the image of Ohsumi-sensei will never leave my heart. I sincerely pray for the repose of his soul.

CONDOLENCES ON THE PASSING OF DR. SEIJI OHSUMI

Hawsun SOHN

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First of all, please accept my deepest and heartfelt condolences.

In the face of Dr. Seiji Ohsumi's obituary, all Korean colleagues could not hide their sorrow of losing the great pioneer. Dr. Ohsumi's research has been a valuable reference of information on cetacean for researchers in Korea where the study was still in its early stages but also in Northeast Asia as well. Even after his retirement, we could feel his special affection and warm kindness toward young colleagues at the meeting room. He used to say Hello in Korean, 안녕하세요 (Annyunghaseyo) whenever he met young Korean researchers.

On one side of the lobby in the Cetacean Research Institute, there is a letter written by him, who hopes for a joint cooperation research between Korea and Japan.

Korea remembers Dr. Ohsumi's great achievements and warm heart.

Please rest in peace.

IN MEMORY OF DR. SEIJI OHSUMI

Tsutomu TAMURA

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The first time I met Dr. Ohsumi was when I was still a graduate student about to participate in one of Japan's whale research program cruises, and he had just become Director General of the Institute of Cetacean Research (ICR). I remember how nervous I was when he said, "I hope you will do your research well", while handing me the researcher's letter of appointment.

Several years later, after completing my doctoral course, I joined the ICR and immediately found myself having lots of work to do. It was the task of collecting all the resource abundance information on cetaceans in the world available then and estimating the amount of their predation. He gave me heaps of advice as I had just joined the Institute and didn't know from my right to my left.

As a result, we were able to report that the world's whale predation amounted to about 300 to 500 million tons, equivalent to three to five times the world's marine fisheries catch at that time. In retrospect, I think it was the inclusion in the paper of the name and essence of the renowned whale scientist Dr. Seiji Ohsumi, that created such a big buzz around the world. Back then, there was a lot of criticism that our whale prey consumption estimation was overrated, but Dr. Ohsumi said that this was because of the great interest that this field of research was arousing worldwide. Recently, other scientists have shown that whales may be eating even larger amounts of prey[4] than our original estimations, and I am glad that my research with Dr. Ohsumi has come back into the spotlight.

In addition, at our repeated drinking parties he would always emphasize to us that "A full-fledged researcher must be able to go into the field, write a paper, and do both". The last time I saw him, glowing with enthusiasm he spoke about his passion for research, and I never thought I would have to say goodbye so suddenly.

I pray for the repose of his soul.

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RECOLLECTION OF SEIJI OHSUMI

Ralph TIEDEMANN

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In the course of my fruitful collaboration with Japanese scientists, I was so lucky (and happy) to have had the opportunity to repeatedly travel to Tokyo in order to work at ICR. At ICR, I very regularly met Seiji Ohsumi who was still doing cetacean research, despite of his age. Seiji always gave me a very warm and friendly welcome in Japan in general and at ICR in particular. It was enlightening to discuss with him cetacean science as well as IWC matters, as he had a rare combination of several decades' research experience, up-to-date-knowledge, and thoughtfully balanced arguments. He was even following the latest genetic technologies in population studies, as I could witness first-hand during a scientific lecture of mine at ICR, which Seiji attended and actively participated during discussion. Most memorable though, is a non-science moment with Seiji: I was invited to a superb sushi restaurant in Tsukiji where I enjoyed the company of my Japanese colleagues and friends and had the privilege to sit next to him (Fig. 1). We were chatting the whole evening about everything but science. I will never forget his deep insights into many aspects of human life, including the history back to the middle of the last century. Many facts and facets I was hardly aware of being within his personal experience and remembrance, and he communicated them with his unique enlightening and whole-hearted attitude. I was deeply impressed. I will miss Seiji.

Fig. 1. A non-science moment with Seiji and colleagues.

REMEMBERING DR. SEIJI OHSUMI

Senzo UCHIDA

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When I was a senior member of the Ito Aquarium in the 1970s, staff scientists of the Whales Research Institute (WRI), led by Director Dr. Hideo Omura including Drs. Masaharu Nishiwaki, Seiji Ohsumi, Tadayoshi Ichihara, Keiji Nasu and some others, visited the aquarium on a comfort trip organized by WRI. At the aquarium, there was also an accommodation facility that relocated the inn where I grew up in Ito Onsen hot spring, and everyone held a big banquet after the duties. Dr. Teruo Tobayama, the head of the aquarium, and Uchida (myself) served as hosts as well and offered a lot of beer and sake for them. At that time, everyone was drinking a lot and making a big fuss.

The next day at a different high-class inn also located in Ito Onsen, it seemed that it was even more than that, and Seiji appeared to have been very active there too. The following day, the president of the inn, an intellectual gentleman, called me and said, “I didn’t see that coming!”

It was a long time ago, a long time ago.

RECOLLECTIONS OF SEIJI OHSUMI

Gísli A. VÍKINGSSON

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I met Seiji Ohsumi for the first time in 1988, at my first annual meeting of the Scientific Committee (SC) of the International Whaling Commission (IWC). At that time, I had worked on cetacean research for only two years, after completing my thesis on quite a different subject, behavioural ecology of greylag geese! Although naive in this branch, I had learned enough to know the name of Dr. Seiji Ohsumi and I felt a kind of starstruck when Seiji approached me on the first day of the meeting and welcomed me to the Committee with his specially charming and warm attitude. This was the first of many conversations I had with Seiji over the next three decades, mostly within the context of the IWC. Despite all the tensions and politics associated with some discussions taking place within the SC, in particular those concerning the scientific activities of Japan (and sometimes also Iceland and Norway), I always sensed the great respect that Seiji had among almost all the scientists in the SC, irrespective of their position in the often-heated debate. To outsiders, such respect for opponents in a scientific debate could seem a matter of course in a scientific forum, but this could not be taken for granted during some periods of extreme polarization within the Committee.

Dr. Ohsumi was a remarkable scientist that continued to explore new fields in science throughout his career. The great legacy of Seiji Ohsumi as a pioneer in whale research is evident from his large amount of scientific works produced over 60 years, and the memories of a great colleague, and a mentor to many, will live long into the future.

REMEMBERING SEIJI OHSUMI

Lars WALLØE

Professor Emeritus, Department of Physiology, University of Oslo, Norway

I met Seiji Ohsumi for the first time in the IWC Scientific Committee meeting in San Diego in 1988, and since then we have met at every IWC/SC meeting and every IWC Commission meeting until quite recently. In addition, I have visited Japan more than 50 times over the last 30 years, and nearly each time I have had the opportunity to discuss whale scientific questions and the related political questions with him. Only during 2019, I met with Seiji in ICR three times, in late February, in mid-June and in July. Every time we had interesting discussions. In the 1990s, he once accompanied me to Taiji and showed me the whale museum there, and he travelled with me to other local communities to meet the local whalers and for them to show me their boats and whaling equipment. We travelled together in Norway also. I wanted to show him our local communities and wanted him to meet our whalers. Together we and Masayuki Komatsu managed to establish a semi-permanent loan of a blue whale skeleton from the university museum in Tromsø to the aquarium in Shimonoseki and with fiber-glass copies of the skeleton on display in four other places in Japan, among them Taiji.

What was my impression of Seiji Ohsumi? Seiji was eight years older than me, and when we met in 1988, he had a life-long experience in whale science. I also had an extensive scientific background, but whale science was new to me. My experience with the subject was about two years old. Despite this difference in age and experience, Seiji from the first meeting treated me as an equal and did never use his longer experience as an argument when we had some small disagreements. Compared to the Norwegian society, the Japanese is in general very hierarchical, but Seiji definitely did not fit into this picture of the Japanese society. He had authority based on knowledge and experience, not on his position in an administrative hierarchy. When he lacked knowledge in a particular scientific discipline, he admitted it; he did not try to bluff, but listened to others who had the knowledge.

Most of the years we interacted, Seiji was head of the Japanese delegation to the IWC/SC, and I was head of the Norwegian delegation. Since our two countries had attitudes to whaling different from most other countries, we had to collaborate. For me this collaboration was a great pleasure. We both had the same attitude and opinions about whaling, and I think we learned a lot from each other. I shall miss Seiji Ohsumi in the future, but I am very happy to have known him.

RECOLLECTIONS OF SEIJI OHSUMI

Yuri YAKOVLEV

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I met Seiji Ohsumi on the voyage of the *RV Akademik Oparin* in 1993. This expedition was one of the few with scientists from different countries, mostly from Japan. The Tokyo cable TV group, TBS, was also on board. Much attention was paid to underwater photography and video, in which I participated as a professional diver and zoologist. At that time I was not yet engaged in the study of whales, and I saw the work of Japanese cetacean researchers for the first time. In fact, right away I came to the conclusion that this is a very hard work, against the background of which underwater diving seemed to me already an easy and exciting entertainment.

Having participated in many expeditions, I immediately noticed a man whose appearance indicated that he was a scientist with tremendous experience in field research, so I was not at all surprised to learn that he was the foremost expert on the whales of the Pacific Ocean, Professor Ohsumi. It so happened that from the first days of the voyage I became friends with Tsuneo Nakamura, a well-known wildlife and sailing photographer, who taught me the peculiarities of whale photography from the *Achilles* boat (Fig. 1). After work or in inclement weather, Tsuneo and I very often accepted the professor's invitation to stop by his quarters. Such gatherings sometimes ended late. The topics of conversation were very diverse, but not whale-oriented. Unfortunately, the weather conditions on that cruise were extremely unfavourable for whale sightings and we tried not to discuss this circumstance. I remember well as being said in the conversation that whaling in the post-war years made it possible to supply the younger generation with animal protein and keep our countries' populations healthy. Plans were made to carry out regular expeditions on the then numerous ships of the Far Eastern Branch of the Russian Academy of Sciences in subsequent years to the north, to the Arctic. However, these quite realistic projects could not be implemented due to the inept policy of the scientific fleet management.

Later, when I started studying gray whales, I had the opportunity to meet with Professor Ohsumi only at conferences. He said that if I needed his support, I could freely turn to him. But, as they say in Russia, the certainty of getting help from a friend is much more valuable than the help itself.

Fig. 1. Tsuneo Nakamura (Volvox Inc.), Yuri M. Yakovlev (Institute of Marine Biology, Vladivostok), Dr. Seiji Ohsumi (ICR). North Kuril Islands, 1993. On board the *RV Akademik Oparin*.

IN A LAB WITHIN SIGHT OF MOUNT FUJI

Motoi YOSHIOKA

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Evoking the first time I met Dr. Ohsumi, I wrote the following in a manuscript submitted to a journal in 1990: "*I went to visit Dr. Seiji Ohsumi at the Far Seas Fisheries Research Laboratory in Shimizu to see if there was any way I could make a breakthrough in my research. Dr. Ohsumi gave me a lot of advice in his laboratory which had a beautiful view of Mt. Fuji from the window, but his comment about my work on hormones being* '*quite interesting*' *was a great encouragement to me afterwards.*" I was 24 years old then, and unsure whether I would be able to continue my research on dolphin reproductive hormones in graduate school. He gave me words of encouragement for my research which I had been conducting from a viewpoint that so far had not existed in cetacean research in Japan. However, if I had not visited Dr. Ohsumi that day, I might have given up my research on cetaceans soon after. My encounter with Dr. Ohsumi was a major event at such a crucial moment for me. Forty years have passed since then. During this period, I received from him much scientific advice and guidance from the viewpoint of population biology and reproductive biology, which was his field of specialty, when I became involved in the research of Dall's porpoises and Bryde's whales. However, what left the greatest impression on me during my association with him is that he was very open to students who had just started their cetacean research —just as he was to me when I visited Shimizu, at research meetings and other occasions, and always looked at us warmly and gave us encouragement.

In the days when information on cetacean research was not readily available as it is now on the internet, his many books, translations, and articles were very valuable materials for students to learn. Dr. Ohsumi, who devotedly made many research achievements in whale research contributing greatly to the management of whale resources and the continuation of the whaling industry in Japan, was always thinking about the future of cetacean research in Japan and giving light to us students who did not know what kind of life they would lead in the future. Looking back on my current self as a university faculty member who has been studying whales and dolphins with students for over 30 years, I wonder to what extent I have been able to train the next generation of researchers. I hope I can spend my remaining time as a professor so that I may reduce that doubt as much as possible.

I would like to once again express my deepest gratitude to Dr. Ohsumi for his continuous interest in whales and to young people wanting to study them, and I sincerely pray for the repose of his soul.

CONDOLENCES ON THE PASSING OF DR. SEIJI OHSUMI

Alexandre ZERBINI

Chair of the IWC Scientific Committee, Cooperative Institute for Climate, Ocean, and Ecosystem Studies, University of Washington & Alaska Fisheries Science Center, NOAA, USA

Indeed, a rich life and major contributions to cetacean science. Our community lost one of the best and my thoughts and prayers are with his family and friends.

Best wishes, Alex

MEMORIES OF MY FATHER, DR. SEIJI OHSUMI

Noriko OSUMI

Vice President, Tohoku University; Professor, Tohoku University School of Medicine, 2–1 Seiryo-machi, Aoba-ku, Sendai, Miyagi, Japan

In my mind, I still haven't sorted out my father's passing. When I rushed to the hospital on November 2, 2019, he was already out of it and I didn't get to spend his last hours with him. The last time I saw my father before he died was on October 4, 2019, which I could trace from my Google Calendar records. On that day, I had dinner with my high school classmates and visited my parents in Shinjuku late, so we only exchanged a few words before my returning to Sendai the next morning. That day, he said he had plans to go to a gathering of the old Niigata High School, and he showed me his old school cap, laughing as he told me that he was going to wear it and sing the dormitory song.

I can barely remember my childhood. My father had been working alone at the National Research Institute of Far Seas Fisheries (formerly Far Seas Fisheries Research Laboratory) in Shimizu since my early elementary school. I used to complain that I could spend more time with my father if he took the Shinkansen when he came back from Zushi, where we lived at the time. However, after joining the Tohoku University as a professor, I came to realize how difficult it is, physically and financially, for those who work alone to return home to their families every week. Now I understand how much he loved my mother, and me. When my father taught me to play Go and Shogi, he would not let me win, which made me dislike those games. I think my habit of reading books came from watching my father. As a scientist, my father was very strict about the use of words, so from a young age, he would ask me, "What is the definition of that?". Accordingly, I became a very logical child and was rather shunned by other classmates. My mother also worked at Japan Women's University, so weekends were complete rest for my father and mother, while family vacations were rare. However, there were other rare occasions when foreign researchers came to our house as guests. For me, English was not a subject to study for exams, but a means of communication. This experience has helped me in my current career as a neuroscientist. After entering graduate school, I learned that my father's dissertation was on "A study on age determination of the fin whale," and I was depressed at the difference in scale from my own first dissertation. I hoped that it would catch someone's attention, so after my father passed away, I got a copy from the National Diet Library and had it published by the University of Tokyo Repository[5].

In 1992, when the International Whaling Commission annual meeting was held in Glasgow, UK, I stayed at the same hotel with my father because I also had to attend an international conference that was held at the same time there. My father's snoring was so bad that I didn't want to go with him again, but I was more shocked by the fact that anti-whaling activists were demonstrating around the hotel. I had heard about it indirectly from my father, but it meant a lot to me to know it in real life. I think this experience, in addition to the general books written by my father, was a major factor in my developing a great interest in science communication; scientists in every field need to communicate with the public. Before my father passed away, in August of 2017, I happened to bump into him at the gate of Narita Airport. He was going to visit the Faroe Islands in Denmark, where whales are fished, with a group including Mr. Kazutaka Sangen, the mayor of Taiji, where the Whale Museum is located; my father was the honorary director of the museum at the time. I was going to Sweden via Copenhagen for an international meeting. My father and I never informed each other of our business trip plans in advance, so it must have been a coincidence that God brought us together. I really wish I could have learned more things from my father. He was blessed with the wonderful people around him. I hope that my father's passion for sustainable whaling will lead you to take your own actions.

Rest in peace, my father.

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BIBLIOGRAPHY OF THE PUBLISHED WORKS OF DR. SEIJI OHSUMI

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Abstract

The published works of the late Dr. Seiji Ohsumi (Gunma, 1930–Tokyo 2019) are presented here as a modest contribution to the perpetuation of his memory. This bibliography was compiled so as to include both his scholarly works and other popular publications targeted toward a general audience. It is grouped into the following four categories: 1. Scientific journal papers (including unpublished works presented to the International Whaling Commission Scientific Committee (IWC/SC)); 2. Books and book contributions (authored works, translations and other contributions such as editorial supervision, commentary, editing and editorial advice); 3. Reports and booklets, and 4. Others. The latter group comprises works published in the *Geiken Tsuushin* Whales Research Institute/Institute of Cetacean Research (WRI/ICR) Quarterly Newsletter, and other miscellaneous writings such as essays and articles that appeared in various magazines, newsletters and other organizations' periodicals, most of them in Japanese. Some interviews and website articles are also included as he made it a point to record them among his written works. Scientific works are listed by year of publication and, on the same year, alphabetically by author. Other publications are presented chronologically by group.

During a span of 65 years, he authored and coauthored the 741 works listed in this compilation. Their numbers, by category, are: 286 scientific papers, 58 books and book contributions, 40 reports and booklets, and 357 works in other categories (100 in *Geiken Tsuushin* and 257 miscellaneous).

Key words: cetacean biology, cetacean ecology, resource management, whaling, whale food culture, whale stock assessment.

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COLLECTION OF MOMENTS

Compiled by Gabriel GOMEZ DIAZ

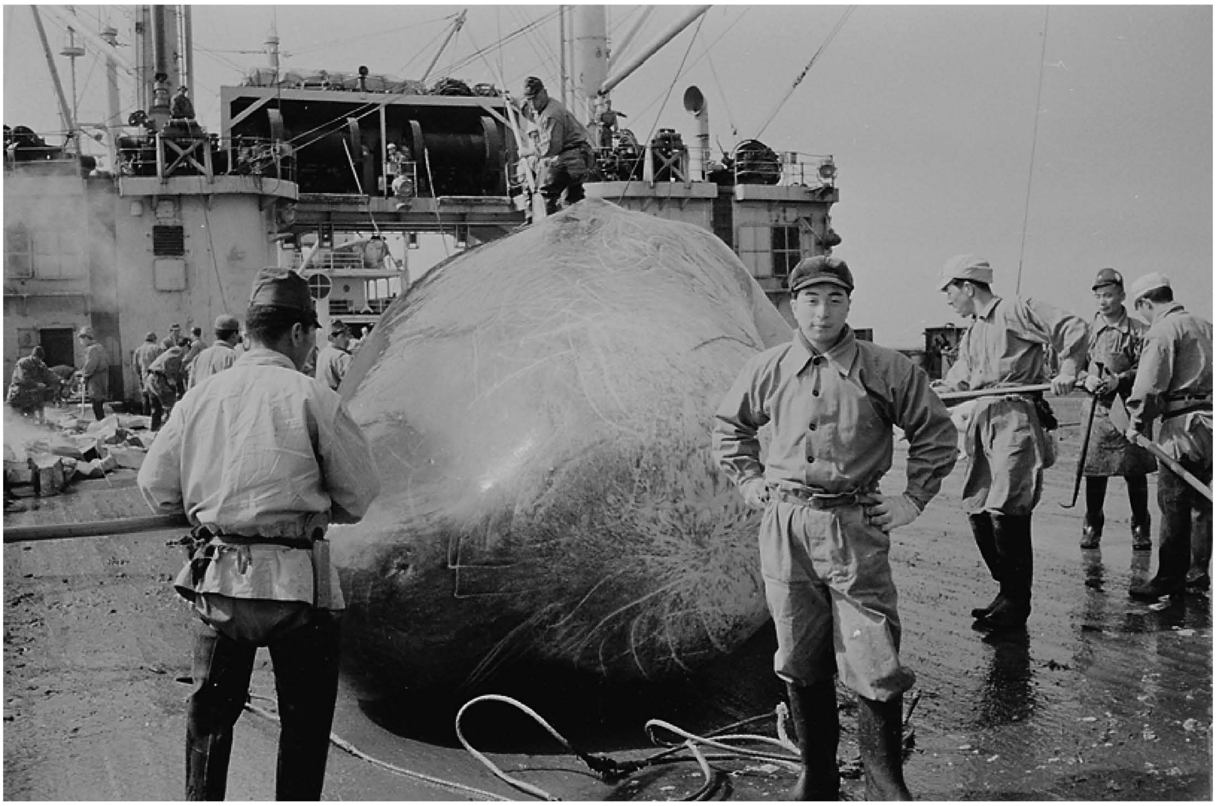

Fig. 1. In 1954 Seiji went for the first time on a Mothership whaling operation: the *Kinjo-Maru* western North Pacific whaling ground exploratory survey. At the time he was a master's degree student and was hired as a temporary employee of the Fisheries Agency to work as a junior fisheries supervisor, also participating in biological research of captured whales. He was 23.

Fig. 2. Seiji on the deck of the whaling Mothership *Tonan-Maru* before departure (1950s).

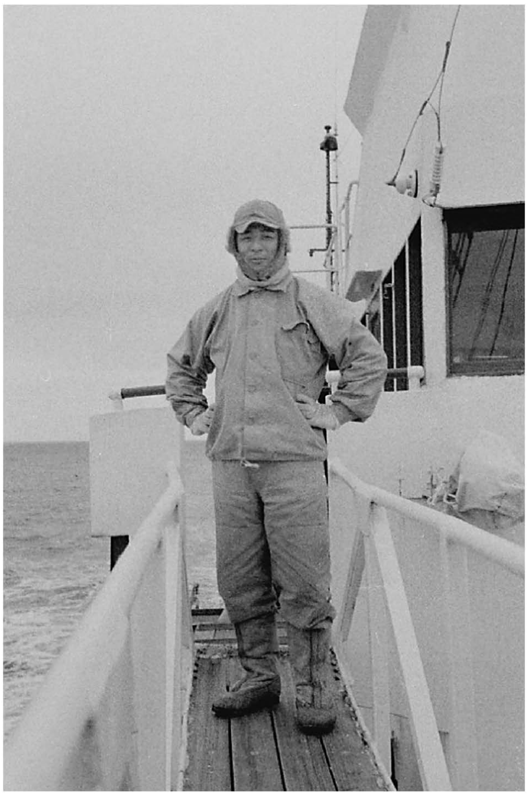

Fig. 3. On a whale catcher boat in the Antarctic (1972).

Fig. 4. Dr. Seiji Ohsumi (right end, front row) posing with Dr. Hideo Omura (right end, back row), Prof. Masaru Nishiwaki (fourth from the right end, back row) and fellows during a Whales Research Institute (WRI) member trip to Yugawara Onsen hot spring resort facility (1960s).

Fig. 5. In Tsukishima at the entrance of the WRI during a visit by Dr. David E. Gaskin (center, front row). Dr. Ohsumi is second from left, back row. We can see also Drs. Hideo Omura, Keiji Nasu, Toshio Kasuya and Tadayoshi Ichihara among other WRI staffs.

Fig. 6. At the Mombetsu (Hokkaido) flensing platform. Right whale special permit sampling personnel. From left to right: Drs. Hideo Omura, Seiji Ohsumi, Saburo Machida, Akito Kawamura and Toshio Kasuya (1961).

Fig. 7. Special Meeting of the IWC/SC in La Jolla, CA. Seiji (9th from left) posing together with Drs. Roy Chapman, Edward D. Mitchell, Michael Tillman, Åage Jonsgaard, Ray Gambell, John Bannister, Hideo Omura, James G. Mead, Mikhail V. Ivashin and other important members at the time (December 1974).

Fig. 8. Seiji with Dr. Omura at a gathering.

Fig. 9. During a meeting in the United States.

Fig. 10. With Prof. Doug Butterworth and other colleagues, 1994 IWC/SC meeting.

Fig. 11. A gathering during the Aging Seminar by Dr. Christina Lockyer (center, front) with many scientists and students at Tokyo University of Marine Science and Technology, December 2009.

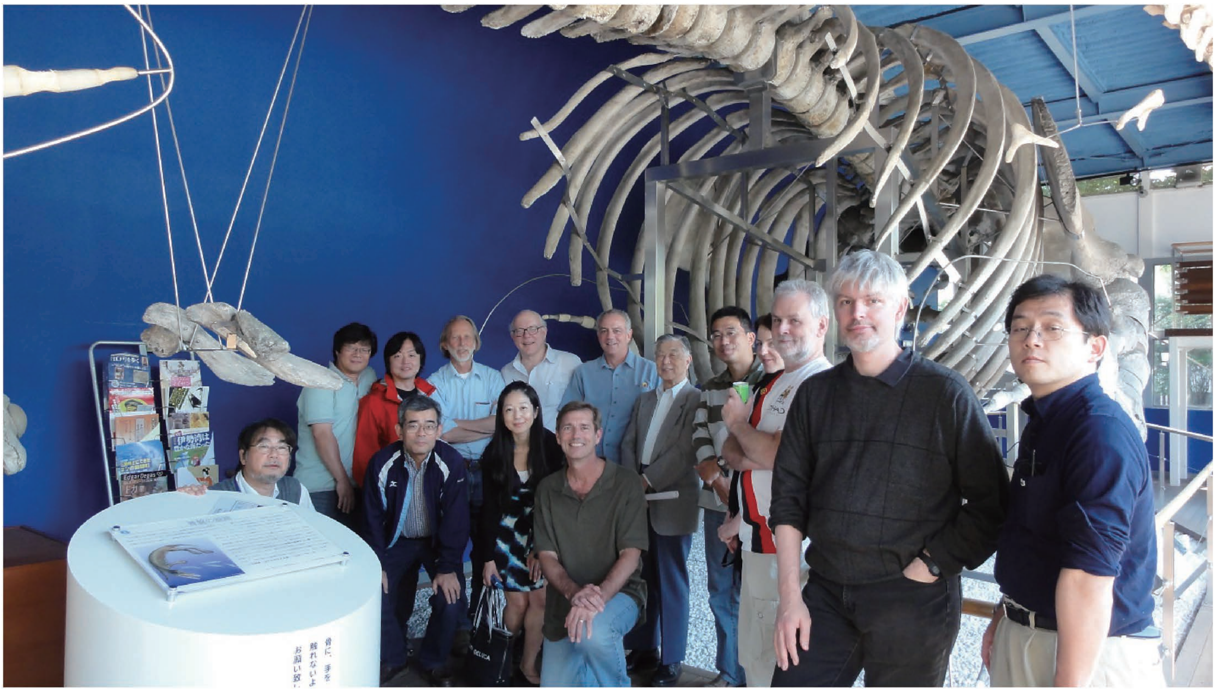

Fig. 12. 2010 POWER planning meeting in Tokyo. Posing with colleagues next to the right whale skeleton originally sampled by Seiji in 1961, on display at the Marine Science Museum, Tokyo University of Marine Science and Technology.

Fig. 13. 2010 POWER planning meeting in Tokyo. Next to Seiji is Dr. Bob Brownell. We can see Drs. Greg Donovan, Phil Clapham, Yulia Ivashchenko, Sharon Hedley, Toshihide Kitakado, Rock An, Yoshihiro Fujise, Koji Matsuoka, Tomio Miyashita, Toshiya Kishiro and Hidehiro Kato among other relevant participants.

Fig. 14. Memorial party to pay tribute to the memory of Peter Best. Front row, from left to right: Keiko Sekiguchi, Greg Donovan, Seiji Ohsumi, John Bannister, Hidehiro Kato, Kazuo Yamamura and Tomio Miyashita (2015).

Fig. 15. Memorial party to remember and honor the late John Bannister, held at Hotel Fukuracia Harumi, Tokyo, in October 2018.

Fig. 16. Dr. Seiji Ohsumi having a normal working day—like on this 19 February 2019 morning, we often found him perusing some of the IWC/SC working documents kept at the Institute of Cetacean Research (ICR).

Full Paper

A blue whale just after blowing, Antarctic.

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DWARF MINKE WHALES: MORPHOLOGY, GROWTH AND LIFE HISTORY BASED ON SAMPLES COLLECTED FROM THE HIGHER LATITUDES IN THE SOUTHERN HEMISPHERE

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Abstract

This study examined the morphology, growth and life history of dwarf minke whales to identify and confirm any differences from other minke whale species and subspecies. The study was based on biological samples and data obtained from 16 whales (3 males and 13 females) collected through the 1987/88 to 1992/93 austral summer seasons by the Japanese Whale Research Program under Special Permit in the Antarctic (JARPA). The whales were collected between latitudes 58°23′S and 65°04′S in the Antarctic area between 90°E and 180°. Mean body length at physical maturity was estimated to be 7.16 m for females, approximately 1.5 m to 2.0 m smaller than equivalent values of Antarctic minke whales and North Pacific common minke whales. The characteristic feature of a white shoulder/flipper patch was confirmed and some variations in the overall color pattern was found. Skeletal observations confirmed the previously reported characteristic features on the vertex of the skull. In addition, this study found a longer rostrum, deeply curved mandible, and narrower nasal bone in dwarf minke whales in comparison with other minke whales. All pregnant females had conceived in mid-austral winter (middle of June to early August). Females are likely to attain sexual maturation at 6–6.5 m and at around 7–10 years of age. Stomach contents indicated that dwarf minke whales mainly fed on lantern fishes around the Antarctic Convergence in summer. Analyses by ANCOV revealed significant differences in both external body and skull morphology among different species and subspecies. Furthermore, cluster analyses on the skull morphology revealed differentiation between dwarf minke whales and other common minke whales but they are more closely related to North Atlantic common minke whales. These analyses concurred with previous genetic analyses results. The results of this study provided support for the proposed subspecific status of dwarf minke whales.

Key words: dwarf minke whale, diminutive minke whale, minke whale clade, morphology, life history parameters.

Introduction

Early reports suggested the existence of a different form of minke whale from the typical southern minke whale (now known as the Antarctic minke whale, *Balaenoptera bonaerensis*) in the Southern Hemisphere (Kasuya and Ichihara, 1965; Gaskin, 1976; Wada and Numachi, 1979; Best, 1982; Baker, 1983; Singrajah, 1983). Subsequently, Best (1985) described two morphological forms of southern minke whale as being the ordinary and the small (diminutive) forms based on material collected from both the South African coast and the Antarctic. He also documented differences in shoulder/flipper coloration, type of baleen as well as other differing external morphological features between the two forms: the smaller ('dwarf' or diminutive) and the larger ordinary (*B. bonaerensis*) forms.

Arnold *et al.* (1987) further examined the morphology of the small form of minke whales in the Australian coastal area which he called 'diminutive' minke whales. They conducted some preliminary osteological examination and found some characteristic skull features and distinctive pigmentation which were additional to those reported in Best (1985). However, their sample sizes were too small and geographically restricted to reach any definitive conclusions on their taxonomic status. Subsequently some additional studies were conducted on the Australian diminutive form e.g., Arnold *et al.* (2005).

The Japanese Whale Research Program under Special Permit (JARPA) started in the 1987/88 austral summer season and continued until the 2004/05 season. The target species for the sampling was the southern 'ordinary' minke whale. However, at the end of the first survey in 1987/88, a minke whale, having a noticeably clear white patch on the shoulder (Fig. 1) was sampled on 23 March 1988. Fifteen additional whales with a similar characteristic were sampled in subsequent JARPA surveys until the 1992/93 season. Those whales were associated with the dwarf minke whales reported by Best (1985) and Arnold *et al.* (1987). The total 16 dwarf minke whales were examined by two of the authors (Kato and Fujise) on the deck of the research base vessel. Materials from these dwarf minke whales were first reported by Kato and Fujise (2000), and some of the biological data from their report was used in Perrin and Brownell (2002, 2009) for their description of different types of minke whales.

Wada *et al.* (1991) and Pastene *et al.* (1994) conducted the first genetic analyses of dwarf minke whales sampled by the JARPA, based on mitochondrial DNA. They found substantial differences among southern 'ordinary,' North Pacific and dwarf minke whales. Their phylogenetic analyses suggested that dwarf minke whales were closer to the North Pacific minke whale than to the southern ordinary minke whale. North Atlantic minke whale samples were not available for genetic analysis at that time and the authors recommended additional genetic and non-genetic analyses to elucidate the taxonomy of the minke whale. Based on the genetic and non-genetic studies summarized above and the recompilation of Rice (1998), the Committee of Taxonomy of the Society for Marine Mammalogy (SMM, marinemammalscience.org) listed the following species and subspecies of minke whale:

Antarctic minke whale, *Balaenoptera bonaerensis* Burmeister, 1867 also known as ordinary southern minke whale, Southern Hemisphere minke whale, ordinary form of minke whale, dark shoulder

Fig. 1. A dwarf minke whale (88/89-013) sampled under the JARPA program in the Antarctic, in the 1988/89 season.

form of minke whale.

Common minke whale, *B. acutorostrata* Lacépède, 1804 having three separate subspecies as below:

North Atlantic minke whale, *B. a. acutorostrata* Lacépède, 1804.

North Pacific minke whale, *B. a. scammoni*, Deméré, 1986.

Dwarf minke whale, *B. a. un-named* subsp. [Rice, 1998] also known as diminutive minke whale, dwarf form of minke whale.

More recent genetic analyses using samples of minke whale worldwide provided further evidence for the separation of the two species, and at least three subspecies of the common minke whale using mtDNA sequences (Pastene *et al.*, 2007, 2010) and microsatellite DNA (Glover *et al.*, 2013). These studies indicated that dwarf minke whales are more closely related to the North Atlantic common minke whale (see also relevant sections in Murase *et al.*, 2020).

The biological samples and data of dwarf minke whales taken by the JARPA were further analyzed in the present study following the initial analyses conducted by Kato and Fujise (2000) while it is still a small sample size. The aim of the study is to compare the biological features, including external and skeletal morphologies, with those of other species and sub-species of minke whales in an attempt to elucidate the taxonomic status of the dwarf minke whale. Also, the study provided an opportunity to test the hypothesis derived from recent genetic studies that dwarf minke whales are more closely related to the North Atlantic common minke whale.

Materials and methods

The present paper examined biological features of the dwarf minke whales taken by the Japanese Whale Research Program under Special Permit in the Antarctic (JARPA). Preliminary results of the previous analyses of these samples were presented to the IWC Scientific Committee meeting in 2000 (Kato and Fujise, 2000). The biological features, including external and skeletal morphologies, were compared in the present study with those of other species and sub-species of minke whales in an attempt to elucidate the taxonomic status of the dwarf minke whale.

Biological materials

The present study primarily used biological samples and information collected from the 16 dwarf minke whales (3 males and 13 females) sampled under JARPA through 1987/88 to 1992/93, at which time the dwarf minke whale was not recognized as a different taxon from the Antarctic minke whale, at least at the species level. No dwarf minke whales were sampled after the seasons of 1992/1993. Table 1 summarizes primary biological information used in the present study. The following data were collected onboard the research base vessel according to the field and laboratory protocols provided in Kato *et al.* (1989): body length to the nearest cm, sex, number and length of fetus, testes weight, number of corpora in both ovaries, thickness of blubber, and stomach contents.

Sexual maturity was examined by standard methods based on ovary and testis examination. Females were determined as sexually mature animals by the presence of at least one *corpus albicans* or a *corpus luteum* in both ovaries.

Sexual maturity in males was determined by histological examination of the testis. Tissues were collected from the center of the heavier testis by cutting out a 5 mm square sample. After fixation with 10% neutral buffered formalin solution, the tissues were sliced to a thickness of 3 μm. Subsequently they were stained by Eosin Hematoxylin solution and examined under a light microscope with 400× magnification scale. Taking account of the timing of samplings, which were conducted outside of the likely breeding season, sexual maturity was determined by the presence of spermatids in addition to sperm. If there were neither sperm nor spermatids in the seminiferous tubules, size of the open lumen (minor axis) in the seminiferous tubules was considered, as in other studies for balaenopterids (North

Table 1. Primary biological information of the sixteen dwarf minke whales which were examined in the present study, listed by order of their body lengths.

Sample No.	Body length (m)	Body weight (t)	Sex	Stomach contents*			Foetus			Age and at its transition phase (Tp**)		Testis wt. (g)		no. ovulation, corpus luteum (CL) and albicans (CA)		Sexual status after present examination	Blubber thickness at lateral side below dorsal fin (cm)	Girth at umbilicus (cm)
				Type	Volume	Size	no.	Sex	Length (cm)	Age	Tp	Left	Right	CL	CL+CA			
92/93-108	3.53	0.65	Female	—	0	—	0			1				0	0	Immature	3.3	92
90/91-002	3.83	0.7	Female	Eu	1	S	0			1				0	0	Immature	3.1	114
89/90-002	4.29	0.85	Female	Fish	1	—	0			3						Immature	3	115
88/89-005	4.45	1	Female	—	0	—	0			—				0	0	Immature	3.3	126
88/89-070	5.94	2.25	Female	Fish	1	—	0			7				0	0	Immature	2.4	150
90/91-014	6.61	4.3	Female	Fish	1	—	1	F	98.6	19	9			1	10	Mature	4.1	204
90/91-118	6.82	5.05	Female	Fish	1	—	1	F	111.7	22	5			1	6	Mature	4.6	214
88/89-013	6.99	4.2	Female	Fish	1	—	1	M	119	23	11			—	—	Mature	3.7	203
88/89-227	7.02	4	Female	Fish	1	—			Lost***	10	4					Mature	5.6	192
92/93-107	7.04	3.79	Female	—	0	—	1	F	83.8+****	17	9			?****	5+****	Mature	4	178
89/90-215	7.07	4.55	Female	Fish	2	—	1	M	115	—				1	10	Mature	3.6	196
92/93-330	7.17	5.5	Female	Fish	1	—	1	F	169.6	19	6			1	4	Mature	5.4	214
90/91-012	7.47	4.45	Female	Fish	1	—	1	M	102.8	26	6			1	13	Mature	3.1	189
89/90-199	5.41	2.05	Male	Fish	1	—				—		57	53			Immature	3.3	153
88/89-014	6.6	2.95	Male	Fish	2	—				10		195	182			Mature	3.6	165
87/88-273	7.01	4.66	Male	Fish	1	—				21	11	540	530			Mature	3.7	201

*: Recorded according to BIWS (Bureau of International Whaling Statistics) format. Eu: Euphasiids.
**: Tp represents age at sexual maturity.
***: Left ovary and foetus lost by harpoon.
****: Ovaries and foetus partly damaged by harpoon.

Pacific sei whale, Masaki, 1976; Antarctic minke whale, Kato, 1986; Inoue *et al.*, 2014). The measurements on the minor axis of the respective seminiferous tubules using the ocular micrometer were taken by randomly choosing 25 tubules from the respective samples.

Age was determined by counting growth layers on the bisected core surfaces in earplugs under a stereoscopic microscope, as detailed by Lockyer (1984), under the assumption that one growth layer (a pair of pale and dark laminae) was deposited per year, as well as establishing the position of a transition phase in the earplug (Locker, 1972; Kato, 1985).

In addition, external measurements (76 points), were obtained according to the protocol of Kato *et al.* (1992), and comparison of sexually mature individuals was carried out among 10 dwarf minke, 704 Antarctic minke and 161 North Pacific common minke whales (from the ICR data base for JARPA and the Japanese Whale Research Program under Special Permit in the North Pacific (JARPN).

Skeletal measurements were compared among dwarf, Antarctic minke and North Pacific common minke whales. Skeletal measurements (21 points) from eight dwarf minke whales and five Antarctic minke whales were made based on the protocol of Omura (1975). For North Pacific common minke whales, skeletal measurements from Nakamura (2012), which followed the same principal method of Omura (1975), were used.

To compare biological aspects of the dwarf minke whales with other minke whale species and sub-species, published biological information with equivalent quality was used. Details are given in the relevant sections.

Sighting information of sampled whales

While sighting information was available from 1987/88 onwards under the JARPA program, for the present study, only sightings of the dwarf minke whales sampled from 1987/88 to 1992/93 were used. All dwarf minke whales sighted and recorded during the shipboard surveys were identified from their characteristic white shoulder/flipper patches, which could be easily observed during closing mode surveys (also see Kato *et al.*, *in press*).

Table 2. Sighting information of the dwarf minke whales used in the present study.

Year/Month/ Date sighted	School ID no.	Sighting time	Location						School size	Estimated B.L. at sea	Sample no.
			Latitude			Longitude					
1988/3/23	5002	14.47	58	23	S	111	26	E	2	6.8, 6.0	87/88-273
1989/1/13	8014	14.24	55	22	S	178	10	E	1	5.5	88/89-005
1989/1/17	5001	10.27	62	4	S	177	28	E	1	6.2	88/89-013
1989/1/17	8003	11.42	62	7	S	177	2	E	1	6.1	88/89-014
1989/2/4	5004	8.43	60	38	S	175	7	E	1	5.0	88/89-070
1989/3/19	1001	8.13	61	54	S	177	55	E	1	6.0	88/89-227
1989/12/6	8004	17.24	55	59	S	97	17	E	1	5.0	89/90-002
1990/1/12	1001	7.4	61	30	S	128	6	E	1	6.0	89/90-199
1990/1/15	1002	9.41	60	59	S	116	6	E	1	8.3	89/90-215
1990/12/29	1001	6.16	65	4	S	178	12	E	1	4.5	90/91-002
1991/1/3	1001	8.13	61	9	S	175	21	W	1	7.0	90/91-012
1991/1/3	5003	11.5	60	40	S	176	34	W	1	8.5	90/91-014
1991/1/26	8001	9.08	60	34	S	146	49	E	1	7.5	90/91-118
1993/1/10	1004	18.00	60	51	S	167	42	E	1	6.5	92/93-107
1993/1/11	8001	15.02	60	31	S	166	5	E	1	3.0	92/93-108
1993/3/22	8003	15.28	61	49	S	143	16	E	1	6.5	92/93-330

Results

Sighting position of sampled whales

Table 2 indicates relevant sighting information regarding the dwarf minke whales sampled during the present study.

Fig. 2 plots the 16 dwarf minke whales sampled based on locations of their sightings during the JARPA surveys from 1987/88 to 1992/93, and by reproductive category. No specific difference in location between reproductive categories was observed. In the longitudinal sector, searched between 97°17′E and 173°33′W, dwarf minke whales occurred from 48°42′ to 65°04′S. Most animals (75%; n=12 animals) were seen around latitudes 60° to 62°S, but it should be noted that there was limited sighting effort north of 60°S. Therefore, this result does not necessarily mean they were rare north of 60°S. Rather, these records should be interpreted to represent the likely southern limit for dwarf minke whale distribution in summer. Within the area surveyed there were three regions of relatively high concentration: 125°–128°E, 141°–146°E, and 177°–179°E at 60–62°S. These areas were located off the concaved continental coastlines of Antarctica such as the Ross Sea.

In terms of segregation from Antarctic minke whales, it is noticeable that dwarf minke whales were distributed in more northern waters than the Antarctic minke whales in summer (Fig. 1). Sightings of Antarctic minke whales by JARPA surveys from the early 1990s to the present were distributed south of 60°S with their density much higher from 63°S to the ice edge zone (e.g., Hakamada *et al.*, 2005).

Throughout the surveys of the IDCR/SOWER[1] programmes, a total of 54 dwarf minke whales, comprised of two pairs and 50 singletons, were sighted (Kato *et al.*, in press). These sightings were only 0.13% of the total number of Antarctic minke whale (*B. bonaerensis*) sightings (41,854 individuals) made during the same searching effort.

Body size and growth

As summarized in Table 1, the 16 dwarf minke whales collected from 1987/88 to 1992/93 comprised three males and 13 females. The smallest (3.53 m) and largest (7.47 m) individuals were both females. Of the three males, two were sexually mature and their mean body length was 6.81 m. Of the

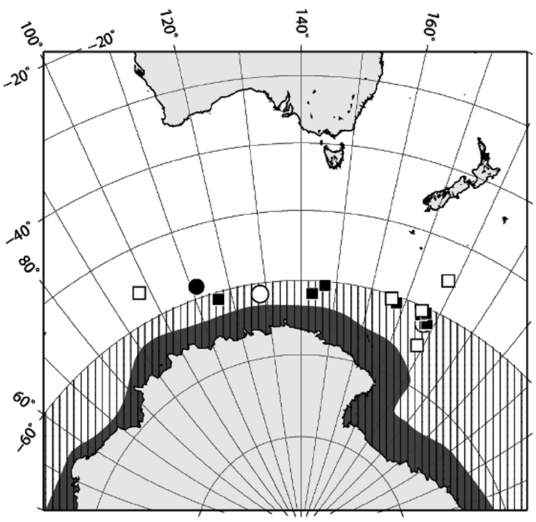

Fig. 2. Sighting locations of the dwarf minke whales sampled during JARPA surveys from 1987/88 to 1992/93 and showing the approximate range of Antarctic minke whale in summer (hatched, with darker area indicating higher sighting density). Immature male (○), mature male (●), immature female (□), mature female (■).

[1] International Whaling Commission International Decade for Cetacean Research (IDCR), Southern Ocean Whale and Ecosystem Research (SOWER).

13 females, eight individuals were sexually mature with a mean body length of 7.02 m (SD: 0.249).

Of the 16 animals, the age was successfully determined for 13 (two males and 11 females). Resultant age readabilities were 0.67 (2/3) and 0.85 (11/13) for males and females, respectively. The mean growth curve of the dwarf minke whales together with that of Antarctic minke whales (Zenitani *et al.*, 1997) and North Pacific common minke whales (Maeda, 2012) are shown in Fig. 3 for both sexes. Female dwarf minke whales appeared to grow to 3.5–3.7 m at age one and then rapidly reach 6 m at age 10, with an asymptote at around 7.0 m (or slightly more) in body length at about age 20.

Fitting the von Bertalanffy growth model to the available data produced the following formula for female dwarf minke whales:

$$Lt = 7.16(1 - e^{(-0.19(t+2.69))}) \quad (1)$$

where Lt is body length in meters at age (t).

If the asymptotic length from the equation is taken as a proxy for the mean body length at physical maturity, then an interim value of 7.16 m for female dwarf minke whales is obtained. Allowing for possible errors due to the characteristics of the growth formulae used here and the limitations of the data (especially small sample size among older animals), a comparison with Antarctic minke whales (Zenitani *et al.*, 1997; Bando *et al.*, 2006) and North Pacific common minke whales (Maeda, 2012) was carried out using von Bertalanffy growth formulae as below:

$$Lt = 9.16(1 - e^{(-0.23(t+2.13))}) \text{ Antarctic minke whale} - \text{Female} \quad (2)$$

$$Lt = 8.61(1 - e^{(-0.27(t+2.00))}) \text{ Antarctic minke whale} - \text{Male} \quad (3)$$

$$Lt = 8.66(1 - e^{(-0.11(t+7.60))}) \text{ North Pacific common minke whale} - \text{Female} \quad (4)$$

$$Lt = 7.49(1 - e^{(-0.41(t+0.90))}) \text{ North Pacific common minke whale} - \text{Male} \quad (5)$$

From the above equations as well as from Fig. 3, it is concluded that dwarf minke whales are significantly smaller in body length at least in females than both Antarctic minke whales and North Pacific common minke whales throughout all age classes. The mean asymptotic lengths estimated from the growth formulae above indicated that fully grown female dwarf minkes were about 2.0 m shorter than Antarctic minke whales (Zenitani *et al.*, 1997; Bando *et al.*, 2006) and about 1.5 m shorter than North Pacific common minke whales (Maeda, 2012). Thus far, under the present analysis, those differences were statistically significant (t-test; $p<0.001$).

Due to the small sample size in all age classes, it was not possible to estimate the mean asymptotic

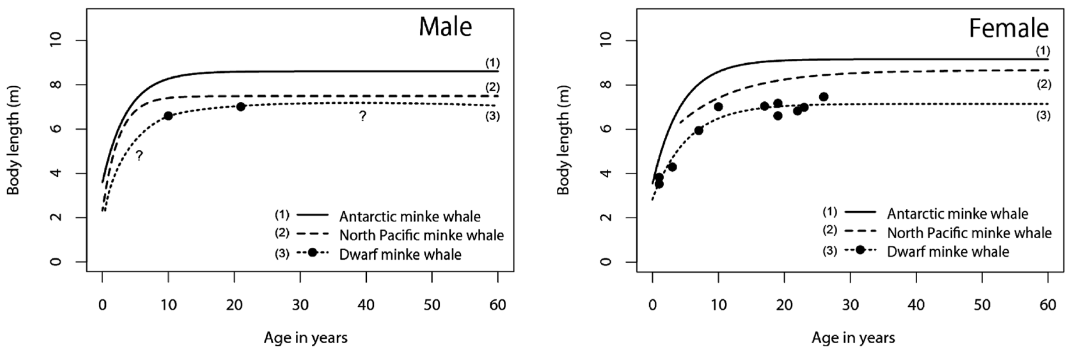

Fig. 3. Plots of body length at age and growth curves of dwarf minke whales by sex (closed circle, dotted line), in comparison with mean growth curves (length at age) of Antarctic minke whales (solid line) from Zenitani *et al.* (1997) and of North Pacific common minke whales (broken line) from Maeda (2012). All the resultant growth curves were fitted by the von Bertalanffy growth formulae.

length or the length at physical maturity of males under the present study.

Under such limitation of the data, an attempt was made to obtain the range of body length at physical maturity for males by using values from other minke whales. The ratios of asymptotic body length of males to those of females are 0.94 (8.61/9.16 m) and 0.86 (7.49/8.66 m) in the Antarctic minke whales and the North Pacific common minke whales, respectively. These ratios were applied to the dwarf minke whales using the value for females (7.16 m), and the values of 6.73 m and 6.16 m were obtained from the Antarctic minke whales and the North Pacific common minke whales, respectively. It is considered inappropriate to narrow down these values further given the limitations of the data. Thus, mean body length at physical maturity for males in the dwarf minke whales is likely to be around 6.2–6.7 m.

Body length-weight relationship

Two male and 13 female dwarf minke whales were weighed both before and after flensing (Table 3). Whole body weights before flensing varied from 0.650 tons (3.53 m) to 5.50 tons (7.47 m). For females, the relationship was examined by fitting an exponential regression of whole-body weight on body length, as follows:

$$W = 0.01235L^{3.007} \quad (r = 0.9922, \mathrm{n} = 13) \qquad (6)$$

where W is whole-body weight in tons and L is body length in meters.

The slope of the regression provides an indication of the relative fatness of the animal shape. The body weight-length relationship for female Antarctic minke whales (Fujise *et al.*, unpublished), obtained through the same procedure as the present study using whole body weight during the feeding season, was as follows:

$$W = 0.019304L^{2.792} \quad (r = 0.9741, \mathrm{n} = 1{,}113) \qquad (7)$$

The coefficient for the slope (2.792) was significantly smaller than that for dwarf minke whales

Table 3. Body weights of dwarf minke whales by weighing their whole body before flensing and in parts after flensing.

Sample No.	Body length (m)	Body weight* (t)	Sex	Foetus number	Blubber** (kg)	Blubber** (%)	Muscle** (kg)	Muscle** (%)	Bone** (kg)	Bone** (%)	Viscera** (kg)	Viscera** (%)	Other** (kg)	Other** (%)	Total** (kg)	Total** (%)
92/93-108	3.53	0.65	F	None	146	26.3	234	42.4	94	17.0	72	13.0	7	1.3	552	100
90/91-002	3.83	0.70	F	None	174	25.7	333	49.3	92	13.7	68	10.0	9	1.3	676	100
89/90-002	4.29	0.85	F	None	212	25.8	391	47.4	112	13.7	90	11.0	17	2.1	823	100
88/89-005	4.45	1.00	F	None	225	21.2	599	56.6	133	12.6	91	8.6	10	0.9	1,057	100
88/89-070	5.94	2.25	F	None	401	19.1	1,264	60.2	277	13.2	150	7.1	6	0.3	2,098	100
90/91-014	6.61	4.30	F	1	967	23.0	2,350	55.9	447	10.6	392	9.3	45	1.1	4,201	100
90/91-118	6.82	5.05	F	1	1,054	21.7	2,816	58.0	463	9.5	495	10.2	30	0.6	4,857	100
88/89-013	6.99	4.20	F	1	950	21.9	2,505	57.8	403	9.3	401	9.3	73	1.7	4,331	100
88/89-227	7.02	4.00	F	Lost	984	24.9	2,278	57.7	411	10.4	263	6.7	13	0.3	3,948	100
92/93-107	7.04	3.79	F	1	834	22.5	2,142	57.8	435	11.8	284	7.7	10	0.3	3,705	100
89/90-215	7.07	4.55	F	1	975	22.0	2,452	55.2	478	10.8	454	10.2	84	1.9	4,442	100
92/93-330	7.17	5.50	F	1	1,149	21.3	3,073	56.9	511	9.5	517	9.6	148	2.7	5,397	100
90/91-012	7.47	4.45	F	1	957	21.9	2,378	54.4	562	12.9	409	9.4	62	1.4	4,368	100
89/90-199	5.41	2.05	M		399	20.4	1,156	59.2	211	10.8	165	8.4	22	1.1	1,952	100
88/89-014	6.60	2.95	M		662	22.6	1,652	56.5	327	11.2	234	8.0	47	1.6	2,922	100
87/88-273	7.01	—	M		960	20.5	2,897	61.9	495	10.6	306	6.5	26	0.5	4,684	100

*: Whole body weighted using a large scale before flensing.
**: Percentage figures are the proportions to the sums of all parts after flensing.

(3.007), which suggests that dwarf minke whales tended to be stockier than other minke whale types, despite both being sampled at the peak of their feeding seasons. This is also endorsed by nature in Fig. 6, which indicates proportion to body length of the dwarf minke whales is higher than of other minkes at the measurement point P17 of girth at umbilicus.

The proportion of the sum of parts to the whole-body weight before flensing ranged from 0.851 to 1.058[2] with a mean of 0.973, indicating an average of only 2.7% weight loss during flensing. Muscle occupies almost half or more of the sum of parts (mean: 54.58%), with the proportion being higher in the larger animals, while the proportions of blubber (mean: 22.87%) and bone (mean: 11.92%) were higher among the smaller animals.

Morphology

External appearance in terms of discriminating the dwarf minke whale from other species and subspecies of minke whales

Previous authors have reported that dwarf minke whales have distinctive external characteristics, primarily a white shoulder patch. This distinguishes dwarf minke whales from all other types of minke whales at sea (Best, 1985; Arnold *et al.*, 1987, Kato and Fujise, 2000). Additional features have been described for dwarf minke whales such as the dark throat patch and a thorax blaze (Arnold *et al.*, 2005).

From field examinations during this study, the following three points by which dwarf minke whales can be easily distinguished from other types of minke whales were identified (Fig. 4A and additional images given in Fig. 4B):

Characteristic (a): A dark throat patch usually extends ventrally as a peninsula of pigmentation on

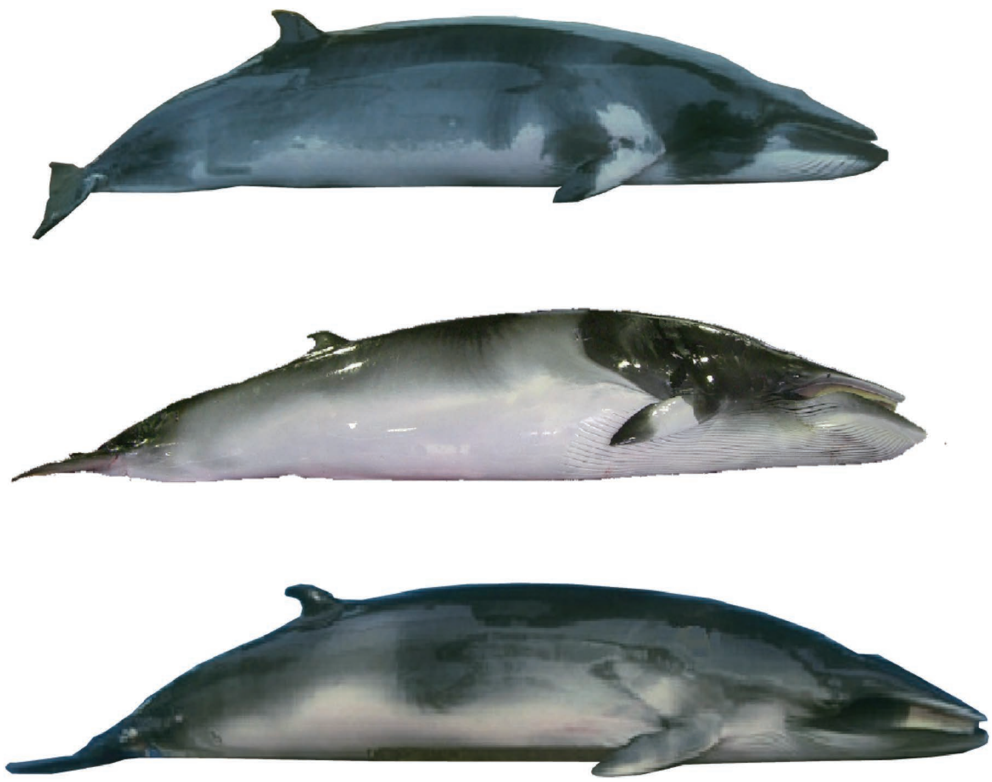

Fig. 4A. Lateral views of different types of minke whales scaled down to the same size; **upper**: dwarf minke whale (DWM); **middle**: North Pacific common minke whale (NPM); **bottom**: Antarctic minke whale (ATM). Alphabetical symbols in the upper picture correspond to the explanation of characteristics above.

[2] It is unlikely that the value exceeds 1.0, which may be due to logistic errors during the measurement.

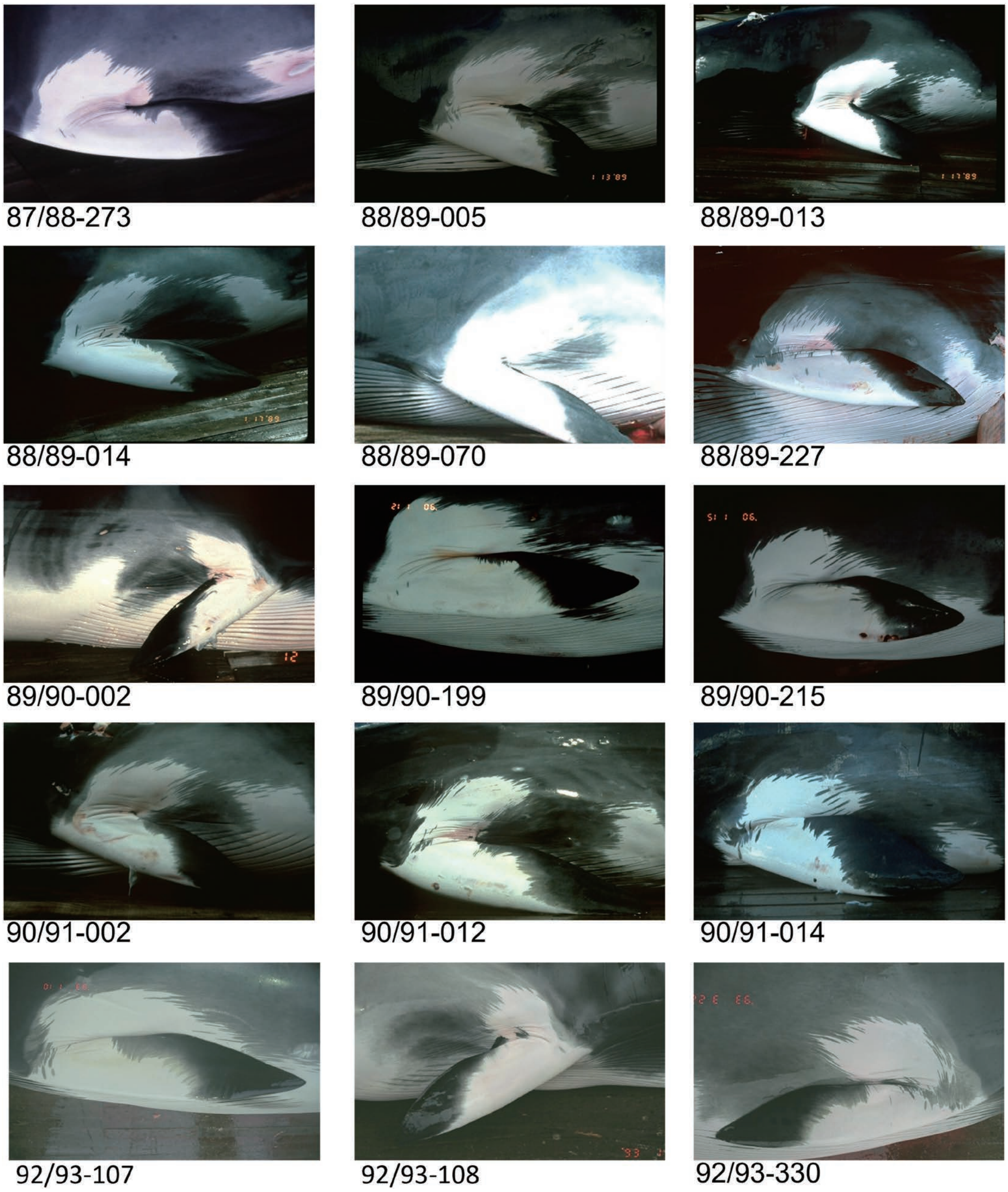

Fig. 4B. Variation of shoulder/flipper coloration on the body surface for 15 of the 16 dwarf minke whales examined in the present study. No photography was taken of 90/91–118 (see also Table 2).

the ventral grooves restricted to the region between the flipper insertion and the angle of the gape. In the samples for the present study, this dark patch was symmetrically arranged on both sides.

Characteristic (b): Fig. 4B shows the variation in shoulder/flipper pigmentation among the 16 specimens. Best (1985) reported that dwarf minke whales have an entire white patch on the shoulder/flipper regions. On the other hand, Arnold *et al.* (1987) found an elongated dark oval patch within it and hidden when the flipper is held against the body, which they called the "flipper oval." However, there is much variation in this pattern as illustrated in Fig. 4B. The flipper ovals certainly existed in their approximate position in all specimens, but the 'arch like white bands' surrounding the dorsal margin of the flipper oval were sometimes incomplete so that the white patch on the shoulder region was cut into two in all but one case. Only one animal (90/91–118) had a complete white patch above the flipper oval on the shoulder region. Unfortunately, no photograph was available in Fig. 4B for this animal.

Characteristic (c): The thorax blaze/patches were principally located above the white patch on the flippers, usually in a somewhat triangular shape. As in Fig. 4B, there were some variations in the pattern of connection between the flipper oval and the thorax blaze/patches being totally connected or separated by splashed pigmentations.

The present study confirmed the three characteristics noted above as consistent keys to distinguishing dwarf minke whales from other minke whales (Fig. 4A). In addition, the present samples provided some additional information on blowhole streaks, which Best (1985) reported in a small dwarf minke whale (about 4 m) from South Africa but were not seen in any dwarf minke whales off Australia (Arnold *et al.*, 1987, 2005). In the specimens examined in the present study, the blowhole streaks were absent or obscure. However, all of the six fetuses larger than 98.6 cm listed in Table 1 had very distinctive parallel streaks in the posterior region of the blowhole. This may indicate changes in coloration with respect to age that is more distinct in younger stages, or possibly more visible in living animals or when underwater (Arnold *et al.*, 2005).

Baleen plate coloration

Fig. 5 (A and B) shows a typical baleen plate coloration of dwarf minke whales, which was shared by all the specimens in the present study. As both Best (1985) and Arnold *et al.* (1987) noted, the outside view of the baleen plate series is two-tone, being creamy white anteriorly and dark gray or brown posteriorly. The darker coloration in the posterior portion of the series is due to a thin dark outer border of the plates. As in Fig. 5(B), this baleen plate coloration is different from the other minke whales. The external view of the baleen plate series of Antarctic minke whales is predominantly black on the left side and creamy white in 1/3 of the anterior portion and black in 2/3 of the posterior portion on the right side while it is usually entirely creamy white for North Pacific common minke whales (though there are rare cases where animals have plates with a thin dark outer border in the posterior parts of the series). Thus, it is evident that the dark outer border is much wider in Antarctic minke whales than in dwarf minke whales (Best, 1985).

Kato *et al.* (1992) suggested that the occurrence of a dark outer border to the baleen had some growth-specific nature in North Pacific common minke whales, therefore the proportion of anterior creamy white plates and posterior black outer margined plate in dwarf minke whales was examined. According to similar statistics (Table 4), the length of the creamy white portion varied from 24 to 115 cm (mean: 67.29, SD: 21.15) and 28–94 cm (mean: 63.21, SD: 16.98) on right and left sides respectively, or 31–85% (mean 53, SD: 13) and 36–85% (mean: 50, SD: 12) of the total length of the baleen plate series, respectively. The ratio of right side to the left side was 1.06 (SD: 0.13), thus the creamy white portion of the right side was slightly longer than that of the left, but not significantly so. As to growth specific changes in proportion of the plates having black outer margin, the samples were not clear enough for detecting such nature.

In summary, the external view of a baleen plate series of dwarf minke whales is mostly bilaterally symmetrical in coloration with a creamy white anterior portion that extends for almost half of the en-

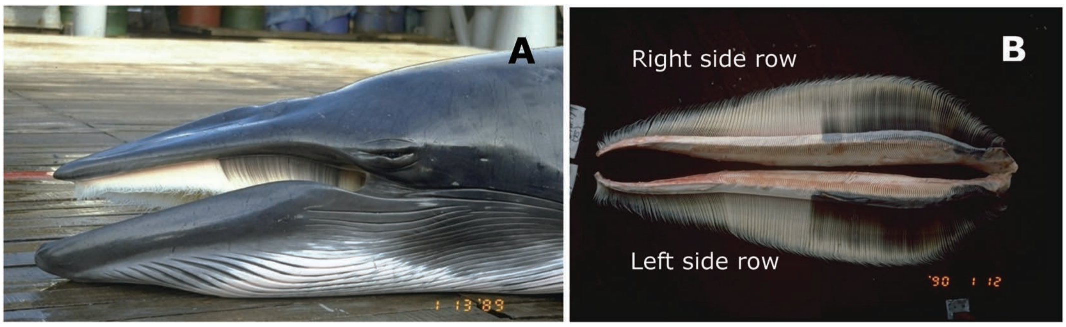

Fig. 5. **A**: Lateral view of left side of dwarf minke whale head showing baleen plates exposed in its slightly opened mouth. **B**: Labial view of the baleen plate series removed from both sides of the upper jaw.

Table 4. Baleen plate series of the dwarf minke whales having measured data, especially the proportion of baleen series of the plate with creamy white coloured outer margin to the total length of baleen. See also Fig. 5B.

Sample no.	Sampling date	Body length (cm)	Sex	Baleen plate series, length (cm) at outer margin						% of Right side of creamy white margin R (w/t)/L (w/t)
				Right side series			Left side series			
				Total	creamy white	R (w/t)*	Total	creamy white	L (w/t)*	
87/88-273	1988/3/23	701	Male	145	72	0.50	142	72	0.51	0.98
88/89-005	1989/1/13	445	Female	88	41	0.47	89	37	0.42	1.12
88/89-013	1989/1/17	699	Female	147	65	0.44	148	78	0.53	0.84
88/89-014	1989/1/17	66	Male	134	45	0.34	130	48	0.37	0.91
88/89-070	1989/2/4	594	Female	118	73	0.62	118	71	0.60	1.03
88/89-227	1989/3/19	702	Female	148	79	0.53	148	71	0.48	1.11
89/90-002	1989/12/6	429	Female	86	73	0.85	86	73	0.85	1.00
89/90-199	1990/1/12	541	Male	112	60	0.54	112	59	0.53	1.02
89/90-215	1990/1/15	707	Female	152	86	0.57	152	76	0.50	1.13
90/91-002	1990/12/29	383	Female	77	24	0.31	78	28	0.36	0.87
90/91-012	1991/1/3	747	Female	163	115	0.71	166	94	0.57	1.25
90/91-014	1991/1/3	661	Female	142	83	0.58	141	70	0.50	1.18
92/93-118	1991/1/26	682	Female	139	65	0.47	139	51	0.37	1.27
92/93-107	1993/1/10	704	Female	135	61	0.45	135	57	0.42	1.07
				Mean	67.29	0.53		63.21	0.50	1.06
				S.D.	21.15	0.13	S.D.	16.98	0.12	0.13

*: Proportion of creamy white length per total length of baleen plate row in each side.

tire length of the baleen plates. With this characteristic, they differ from both Antarctic minke whales (bilaterally asymmetric baleen coloration) and North Pacific common minke whales (usually all creamy white baleen). In comparison, dwarf minke whales have an intermediate coloration.

External body proportion

Prior to the statistical analyses, the general characteristics of the external body proportions of dwarf minke whales were examined in comparison with Antarctic minke whales (n=507) and North Pacific common minke whales (n=91). Fig. 6 shows the body proportions (expressed as a percentage of the body length from tip of snout to notch of tail flukes) for dwarf minke whales, Antarctic minke whales and North Pacific common minke whales. The rostrum of the dwarf minke whale is elongated in a V shape, typical of minke whales. On average the head (P19) comprised 22.90% (min. 21.20–max. 24.10) of the body length. The average length from the tip of snout to the center of the blowhole (P2) comprised 14.50% (12.80–15.60); to the center of the eye (P3) 17.60% (15.50–17.60); and to the external auditory meatus (P4) 22.70% (20.20–24.10) of the body length. The average length from the tip of snout to the posterior end of the ventral grooves (P6) comprised 51.00% (49.10–53.10), to the umbilicus (P7) 54.90% (53.10–56.00), the center of the genital aperture (P8) 71.00% (67.00–72.60), and to the anus (P9) 74.80% (73.80–75.70) of the body length.

The pectoral fin is also an elongated oval shape with tapering tip typical of balaenopterids and its length (P12, tip to anterior insertion) and breadth (P14) were 16.10% (15.00–17.50) and 4.10% (3.60–4.30), respectively. The dorsal fin is falcate with a tapering tip of which the height (P11) was 4.30% (3.30–4.30). The tail flukes are leaf-like in shape with a rather straight posterior margin and tapering tips at both ends, while their width (P16) was relatively broad at 28.10% (24.90–31.10) and depth (P15) was 7.00% (6.40–7.50).

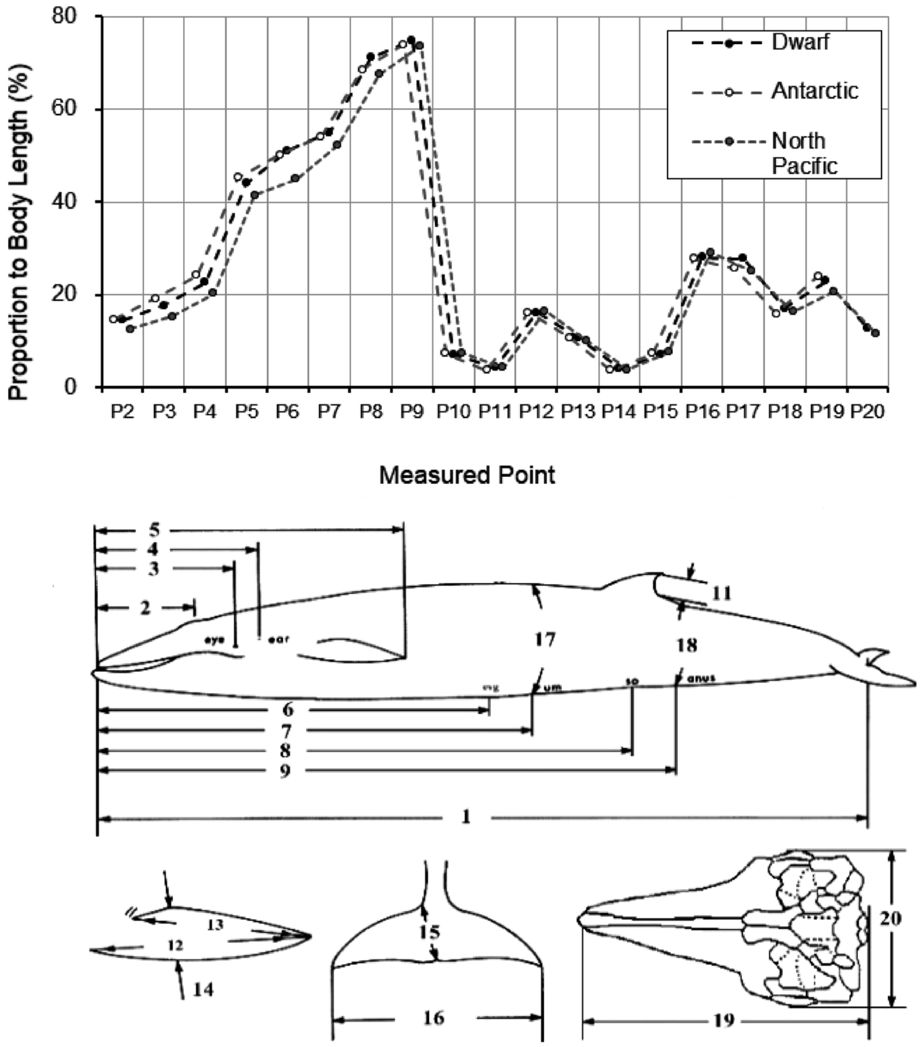

Fig. 6. Mean external measurements (P2–P20) of sexually mature dwarf (closed circle), Antarctic (open circle) and North Pacific minke whales (gray colored circle), expressed as respective proportion to the body length. Abbreviations of respective measurement points correspond to the numbered locations in the illustration.

All the body proportion measurements in the anterior half of the body were highest for Antarctic minke whales and lowest for North Pacific common minke whales, with dwarf minke whales being intermediate between the two but somewhat closer to Antarctic minke whales. On the other hand, the relative proportions of the appendages were remarkably close to each other among the three types of minke whales. Those aspects are further examined by statistical analyses in the later section.

Skeletal features

Skeletal observations were taken from all 16 animals collected, but data from eight sexually mature animals were to be the base for the present analyses especially on skull, to minimize possible growth dependent changes. Those observations were appropriately compared and verified with other type of minke whales in some cases.

1. Skull

Firstly, before the statistical analyses, general aspects of the skeleton are presented in this section. See also details of the skeleton in Appendix 1.

Fig. 7 shows the dorsal view of the skull of a dwarf minke whale as compared to those of North Pacific common minke whales and Antarctic minke whales. The diagnostic differences in skull mor-

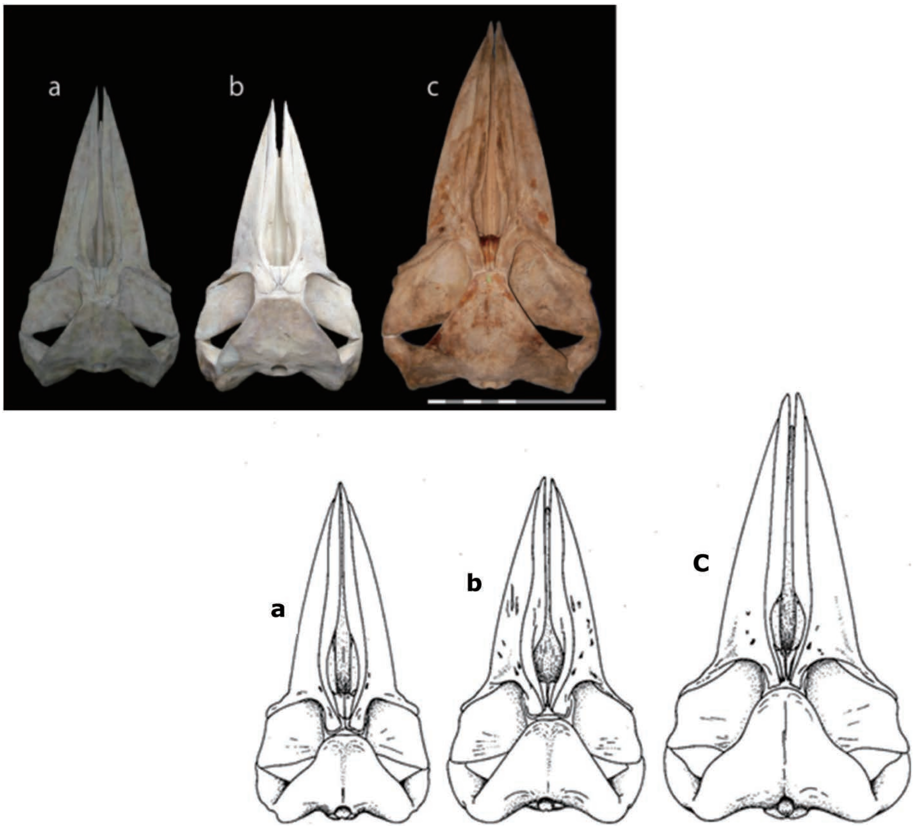

Fig. 7. Dorsal view of skulls by photographing (upper) and corresponding contour drawings (bottom) of the dwarf (**a**: 87/88-273), the North Pacific (**b**: 08NPCK-M030) and the Antarctic minke whale (**c**: 93/94-AM287) showing the principal differences in morphology among the three different types of minke whales of which were fully grown animals. The attached bar on the photos is 1.0 m long with a 10 cm scale interval.

phology can be seen among them. As an example of the skeletal specimens, multidimensional views of the entire skeleton, including skull and other skeletal parts of a male dwarf minke whale of 7.10 m in body length registered as specimen MTUM-DW273, are shown in Appendix 1. Details of the skull measurements are given in Appendix 2.

The vertex of the skull is considered an important taxonomic trait. A distinct interparietal bone was present in dwarf minke whales (Arnold *et al.*, 1987; Kato and Fujise, 2000). This characteristic has been identified in North Pacific common minke whales and in Antarctic minke whales (Nakamura, 2012). Further, the presence of the interparietal in the vertex has also been identified in North Atlantic minke whales (Fig. 8). In dwarf minke whales, the posterior end of the nasal bone and the posterior end of the premaxilla are more extended toward the vertex compared with those of North Pacific common minke whales. As a result, the nasal bone of dwarf minke whales is more elongated than in North Pacific common minke whales, resulting in a significantly larger ratio of the length of the nasal bone relative to the anterior width of the nasal bone. In dwarf minke whales, proportional length of maxilla and premaxilla to the skull were significantly larger than those in North Pacific common minke whales. On the other hand, the width of the orbit, width and height of the occipital condyle, and the length and width of the palatine relative to the skull length were all smaller than in North Pacific common minke whales.

In terms of absolute measurement values, the maximum length and maximum width of the tympanic bullae of dwarf minke whales (7.9 ± 0.3 cm and 6.1 ± 0.2 cm, respectively) were approximately 10% smaller than in North Pacific common minke whales (9.0 ± 0.4 cm and 6.9 ± 0.3 cm, respectively) and Antarctic minke whales (9.2 ± 0.6 cm and 7.1 ± 0.3 cm, respectively), whereas their maximum width was close to North Atlantic common minke whales (8.2 ± 0.2 cm).

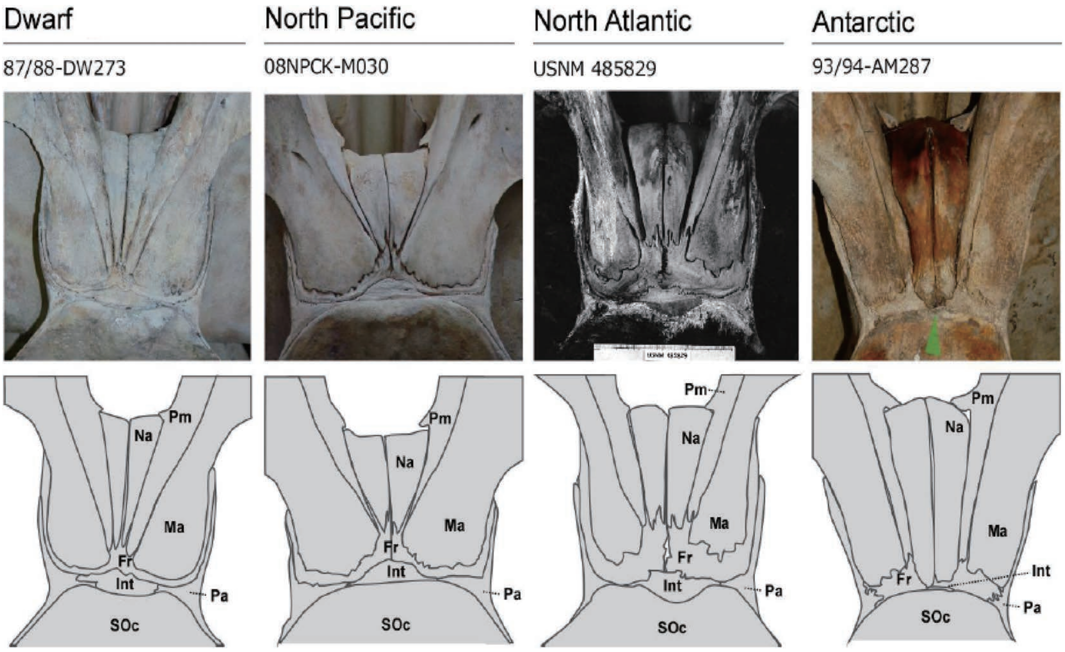

Fig. 8. Morphological comparison of the vertex region on the skulls among dwarf, North Pacific, North Atlantic common minke whales and the Antarctic minke whales. Abbreviations represent: **Fr**, frontal; **Int**, interparietal; **Ma**, ascending process of maxilla; **Na**, nasal; **Pa**, parietal; **Pm**, premaxilla.

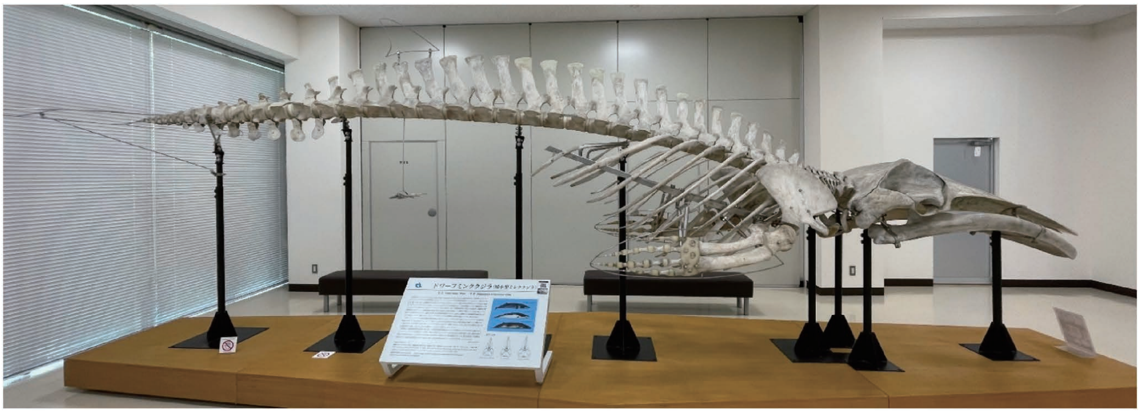

Fig. 9. Lateral view of mounted complete skeleton of the dwarf minke whale (museum specimen No. MTUM DW273; field sample ID No. 87/88-273). The specimen was mounted under supervision by Kato and is displayed at the Museum of Marine Science, Tokyo University of Marine Science and Technology, Tokyo.

An entire lateral view of the dwarf minke whale skeleton (87/88-273) is shown in Fig. 9.

2. Vertebral number

The total number of vertebrae in the dwarf minke whales examined ranged from 47 to 50 with a mean of 48.6 (SD: 0.9). The ranges were 47–51 with a mean of 49 (SD: 0.9) and 47–51 with a mean of 48.8 (SD: 0.80) in Antarctic minke whales and North Pacific common minke whales, respectively. Thus, the total number of vertebrae is virtually identical in all three minke whale species or sub-species (Table 5).

The vertebral formula for the dwarf minke whale was C7+D10–11+L11–14+Ca18–20=47–50, and for the mean values C7+D10.6+L11.7+Ca19.2=48.6 (SD: 0.9). Again, this formation is the same, or within the known range, to those of other minke whale species and sub-species.

Table 5. Mean and range of number of vertebrae in each section of the vertebral colum by different type of minke whales.

	Dwarf (n=16)	Antarctic (n=42)	North Pacific (n=200)	North Atlantic (n=1)
Cervical (C)				
Mean	7	7	7	7
SD	0	0	0	0
Range	7	7	7	7
Dorsal (D)				
Mean	10.6	10.7	10.5	11
SD	0.5	0.5	0.5	0
Range	10–11	10–12	10–11	11
Lumbar (L)				
Mean	11.7	11.8	12.1	12
SD	0.9	0.8	0.6	0
Range	11–14	10–14	11–13	12
Caudal (Ca)				
Mean	19.2	19.4	19.3	18
SD	0.8	0.9	0.8	0
Range	18–20	17–22	17–23	18
Total				
Mean	48.6	49.0	48.8	48
SD	0.9	0.9	0.8	0
Range	47–50	47–51	47–51	48

3. Number of ribs

For the dwarf minke whales examined, the ribs are relatively thin and broad, and their numbers are 10–11 on each side, with the mean number of ribs being identical on each side as 10.7 (SD: 0.48). These are slightly fewer than in the Antarctic minke whales (10–12, mean 11.1 (SD: 0.45)) and North Pacific common minke whale (10–12, mean 10.8 (SD: 0.4)), but not significantly so. No floating rib was found among the present specimens of dwarf minke whales.

4. Shape of sternum

Three types of sternum shape are observed in species and sub-species of minke whales: Y-shape (looks like a ginkgo leaf), T-shape and an intermediate shape (Fig. 10). The T-shape sternum is common among dwarf minke whales, Antarctic minke whales and North Pacific common minke whales; the manubrium parts were rather larger in the North Pacific common minke whales. The Y-shape was only confirmed in dwarf minke whales with the presence of a hole in the center of the sternum in some whales. The Y-shape sternum is likely to be rare among balaenopterids and is possibly exhibited only in dwarf minke whales and must be closely related to the shape of the associated ribs. This characteristic may suggest some differences in feeding behavior, but more samples and further examinations are required to confirm this.

Life history parameters

Females

1. Reproductive status

While ovaries were unfortunately lost from the three females, six of the 13 females of dwarf minke whales were firstly confirmed to be sexually mature and four were confirmed as immature based

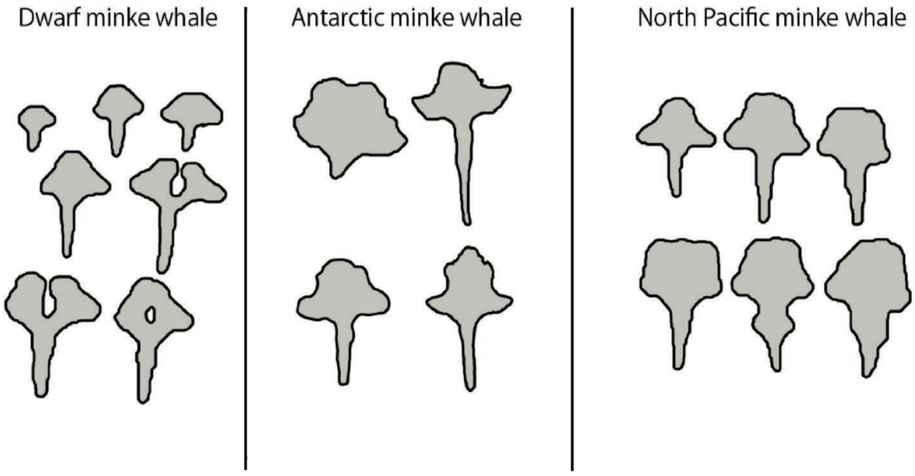

Fig. 10. Variations in shape of the sternum among dwarf, Antarctic and North Pacific common minke whales based on contours of the actual sternums in each type of minke whale.

on gonad examination. Of the remaining three females one (88/89-013) was to be mature because of having a fetus, another (88/89-227) was thought to be mature given its size (7.02 m) and age (10 years old) as well as the presence of a transition phase as a mark of attainment of sexual maturity in the ear plug, and the third (89/90-002) likely to be immature from its size (4.29 m) and age (3 years old), as summarized in Table 1. Resultant sexual status of the present samples was five sexually immature versus eight mature. All sexually mature females excepting one missing the uterine horns were confirmed to be pregnant, apparently indicating a 100% pregnancy rate. This figure should be, however, treated with caution because of the small sample size and possible segregation or timings of migration associated with reproduction.

The transition phase in the earplug was used as an indicator of age at sexual maturity while an annual rate of growth layer deposition was assumed (Lockyer, 1972; Kato, 1982). The mean annual ovulation rate after attainment of sexual maturity was estimated as follows:

$$no.corpora/(total\ age - transition\ phase) \quad (8)$$

Values from four females having both transition phase and number of corpora ranged from 0.31 to 1.00 with a mean of 0.58, which are understood to be annual ovulation rate leading to maximum value of annual pregnancy rate. This result suggests that the apparent 100% pregnancy rate might be too high as an annua1 pregnancy rate (true pregnancy rate) and this high value was possibly due to reproductive segregation in relation to latitude, i.e., pregnant females migrate further south as in the case of Antarctic minke whales (Masaki, 1979; Kato, 1982).

None of the mature females was lactating, but possible milk remnants consisting of transparent yellowish liquid were found in the mammary gland of one female (sample ID number: 92/93-107), suggesting this animal was sampled just after weaning her calf.

2. Fetus and breeding season

The sex ratio in the fetus samples was 3 males to 4 females, and the mean litter size was 1.0 (n=7). The lengths of the fetuses were relatively similar, ranging from 98.6 to 119 cm with one at 169.6 cm (Table 6).

To investigate the timing and duration of the breeding season, conception dates were estimated by back-calculating from fetus length and date of capture, and applying the fetal growth rate formula for Antarctic minke whales (Kato and Miyashita, 1991; Kato, 1995), as follows:

$$t = 1.622L^{0.892} + 74 \quad (9)$$

Table 6. Estimated conception date for the pregnant dwarf minke whales based on back-calculating by the fetal growth curve estimated by Kato (1995).

Season	Specimen no.	Date	Fetal length (cm)	Days after concept.	Estimated concept. date*
90/91	012	3 Jan, 1991	102.8	175	13 Jul, 1990
90/91	014	3 Jan, 1991	98.6	171	17 Jul, 1990
92/93	107	10 Jan, 1993	84.0	158	6 Aug, 1992
89/90	215	15 Jan, 1990	115.0	186	14 Jul, 1989
88/89	013	17 Jan, 1989	119.0	189	13 Jul, 1988
90/91	118	26 Jan, 1991	111.7	183	28 Jul, 1990
92/93	330	22 Mar, 1993	169.6	232	3 Aug, 1992

*: Mean=22 July.

where t is time (days) passed since conception and L is fetal body length in cm (Table 6).

Estimated conception dates were concentrated in a very narrow band from the middle of July to early August, that is, over a 25-day period. Thus, provided that southbound migration is not dependent on reproductive segregation, even with the small sample size, it appears that the breeding season of the dwarf minke whale likely occurs over a few weeks in mid-winter with a peak in middle to late July. This contrasts with the case of Antarctic minke whales where the breeding season extends over six months with a weak peak in September/October (Kato, 1995).

3. Body Length and age at sexual maturity

With the present small sample size, it was difficult to estimate lengths or ages at sexual maturity with accuracy, especially for males.

For females, the smallest mature individual was 6.61 m and the largest immature individual was 5.94 m in length (Table 1), from which body length at sexual maturity is likely to be around these values or around 6.0–6.5 m. In a separate study, Kato (1987) examined the density dependent nature of temporal changes for parameters related to sexual maturity in Antarctic minke whales and concluded that the length at sexual maturity remained constant over time, while age at sexual maturity declined with density dependence. Thus, length at sexual maturity is a reliable threshold parameter for species- or subspecies-specific sexual maturity. For other minke whales, estimates are:

North Pacific common minke whales, female, 7.1 m (Kato, 1992),

North Atlantic common minke whales, female, 7.1–7.5 m (Jonsgard, 1951; Christensen, 1981; Larsen and Kaple, 1982),

Antarctic minke whales, female, 8.1 m (Best, 1982; Kato, 1982; Zenitani *et al.*, 1997; Bando *et al.*, 2006).

In females, values for dwarf minke whales were much smaller (approximately 1.0–2.0 m smaller) than the those for Antarctic and North Pacific common minke whales.

The age of the youngest sexually mature female was 10 years and that of the oldest immature female was 7 years. Therefore, their average age at sexual maturity is likely in the range of 7–10 years (Table 1). This result is consistent with the age at sexual maturity estimated from the transition phase (Table 1), which was 4–11 years with a mean of 7.14 years (SD: 1.05).

4. Maximum life span

The oldest whale in the sample was a 26-year-old female (Table 1). This is most likely to be an under-estimate of longevity due to the small sample size. This parameter can be estimated using the equation of Ohsumi (1979) which was derived from fitting both baleen and toothed whales as below:

$$T = 31.277e^{0.05480L} \qquad (10)$$

where T is maximum life span in years and L is body length at physical maturity in meters.

The above equation was applied to the estimated length at physical maturity (asymptotic length for females, 7.16 m) in the present study to estimate the approximate value of the maximum life span. The result was 47 years. This is not so different from those of other minke whale species and sub-species derived from the same equation, e.g., 50 years for the Antarctic minke whale and 48 years for the North Pacific common minke whale. It is emphasized here that this is an interim value.

Males

It was difficult to estimate any life history parameters in males because of the limited number of specimens (Table 1). It was considered that the 5.41 m dwarf minke whale with testes weighing 53 and 57 g was an immature animal. The other two whales, a 7.01 m male (age 21) with testes weighing 530 and 540 g (hereafter 87/88–273) and a 6.6 m male (age 10) with testes of 182 and 195 g (hereafter 88/89-014) were presumed to be mature animals. For these two cases, additional analyses based on histological examinations of the testes were conducted.

Histological sections for those testes are shown in Fig. 11. It was confirmed that numerous spermatocytes were present in most of the seminiferous tubules of both males, but no sperm was present in both males. The reason why there were no sperm among almost all of the seminiferous tubules is not a surprising event even for fully sexually mature males. It is thought to be due to timing of the samplings of the testes (January to March which did not overlap with the likely breeding season in July–August inferred from conception timing calculated backward from the fetus frequencies in the above section.

However, it was further noted that some spermatids existed in the seminiferous tubules of the larger male. Some examples of these are shown by the arrows in Fig. 11(B). This suggests the male was

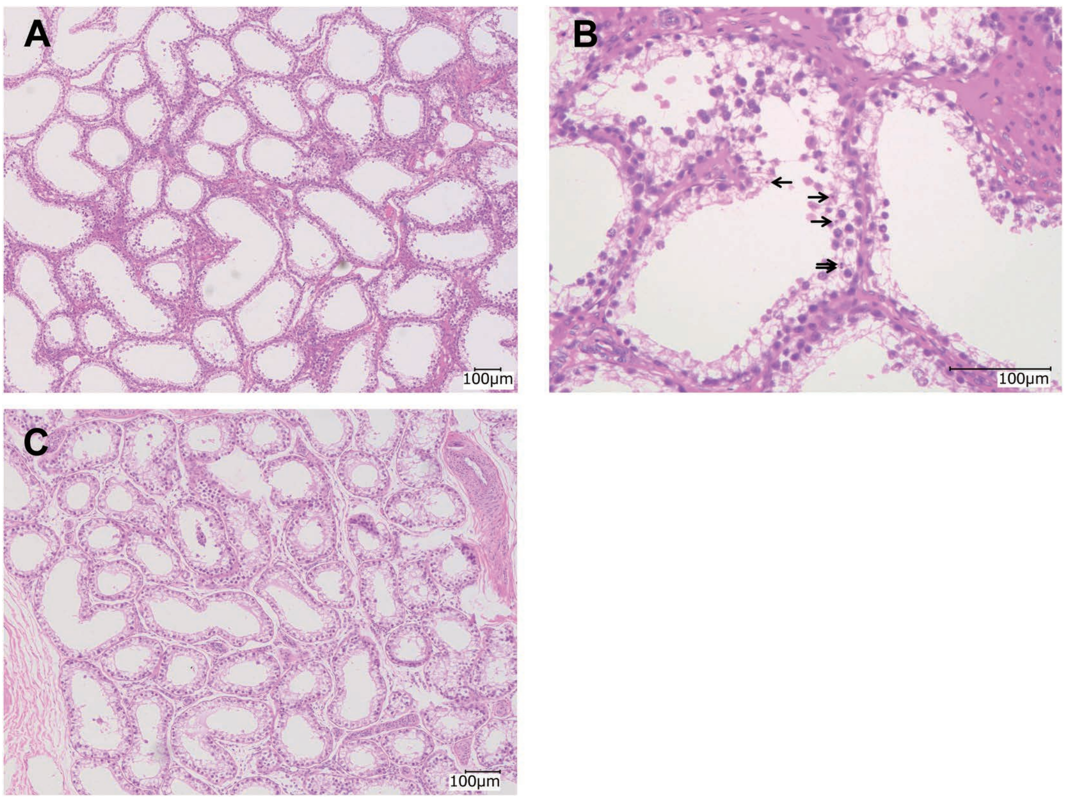

Fig. 11. Histological section images of the seminiferous tubules for the males examined. Bars in all three images represent 100 μm. **A**: large male (87/88-273), body length 7.01 m and age 21 years. **B**: magnified view of the 87/88-273 seminiferous tubules indicating spermatids with arrows. **C**: the second large male (88/89-014) whose body length was 6.60 m and age 6 years.

in a somewhat sexually active status even if out of the main breeding season. Thus, the larger male (87/88-273) was definitely a mature animal. For the second larger male (88/89-014), spermatids could not be confirmed in any of its seminiferous tubules during the present microscopic observation.

Another measure of male sexual maturity was the size of the seminiferous tubules. Masaki (1976) examined the diameter (minor axis) of seminiferous tubules in sei whales and found significant correlation in relation to sexual maturity. Kato (1986) also found a similar relationship between the diameter and sexual maturity in Antarctic minke whales. The threshold value for sexual maturity was mostly 100μm. Inoue *et al.* (2018) examined the minor axis of the seminiferous tubules in North Pacific common minke whales and found that over 100μm would be enough to determine sexual maturity even when the samples were collected in the non-breeding season. According to the present measurement of seminiferous tubules, those were 177.6μm (n=25, SD: 29.49) and 124.4μm (n=25, SD: 13.71) for the larger male (87/88-273) and the second larger male (88/89-014) respectively. They were wider than the threshold value of 100μm of sexual maturity in other minke whale types even in non-breeding season. Another measure for sexual maturity in males is the presence of the open lumen within the respective seminiferous tubules. Masaki (1976) reported that the presence of the open lumen could be used as a criterion for sexual maturity in North Pacific sei whales. In our analyses, as evident in Fig. 11(B), the open lumen can be seen in the majority of the seminiferous tubules for the two males.

From the above examinations, it can be confirmed that the two large males (87/88-273, 88/89-014) were sexually mature.

Food and feeding habits

The stomach contents of 16 dwarf minke whales were examined. 13 individuals contained food, while the remainder were empty or contained only traces of food (Table 7).

Table 7. Stomach contents, weights and prey species eaten by dwarf minke whales in relation to sampling location and time.

Sample no.	Location						Sampling time	BIWS stomach record			Content weight in kg**	Prey species identified
	Latitude			Longitude				Item	Relative richness*	Size		
87/88-273	58	23	S	111	26	E	15.24	Fish	1	—	22.7	Myctophidae
88/89-005	55	22	S	178	10	E	14.55	—	0	—	4.9	
88/89-013	62	4	S	177	28	E	10.54	Fish	1	—	38.3	Myctophidae
88/89-014	62	7	S	177	2	E	12.50	Fish	2	—	33.9	Myctophidae
88/89-070	60	38	S	175	7	E	9.00	Fish	1	—	5.6	Myctophidae
88/89-227	61	54	S	177	55	E	8.40	Fish	1	—	6.8	Myctophidae
89/90-002	55	59	S	97	17	E	18.23	Fish	1	—	15.6	Myctophidae
89/90-199	61	30	S	128	6	E	9.20	Fish	1	—	14.0	Myctophidae
89/90-215	60	59	S	116	6	E	10.51	Fish	2	—	47.3	Myctophidae
90/91-002	65	4	S	178	12	E	7.29	Eu	1	small	3.4	Euphausiids
90/91-012	61	9	S	175	21	W	8.38	Fish	1	—	29.1	Myctophidae
90/91-014	60	40	S	176	34	W	12.36	Fish	1	—	20.7	Myctophidae
90/91-118	60	34	S	146	49	E	9.43	Fish	1	—	2.6	Myctophidae
92/93-107	60	51	S	167	42	E	18.26	—	0	—	0.0	
92/93-108	60	31	S	166	5	E	16.16	—	0	—	2.5	
92/93-330	61	49	S	143	16	E	15.53	Fish	1	—	35.7	*Krefftichthys anderssoni*

*: Relative richness by the BIWS format: 0, empty; 1, 25%; 2, 26–50%; 3, 51–75%; 4, 76–100%.
**: Combined value for the first (fore) and second (main) stomachs.

Stomach contents weighed between 2.6 kg and 47.3 kg (n=13) and the contents were partially digested. The species composition of the contents was mainly uniform within each stomach, thus the food in the stomachs would have been representative of food organisms typically consumed by dwarf minke whales.

Sampling locations were spread out latitudinally and longitudinally. Except for one sampled further north from the Antarctic Convergence (with empty stomach), the majority of dwarf minke whales were sampled in the vicinity of the Antarctic convergence (58–62°S). The species identification of food organisms was referred to Mr. Hiromasa Furuhashi (Hokkaido University) a specialist of morphology and taxonomy of myctophid fish. Observations were made by placing the photophore pattern over the fish body surface, a method which is widely used for species identification of myctophid fishes. The specialist inferred that there were remnants of myctophids, including *Krefftichthys anderssoni*. This clarified that these dwarf minke whales fed mainly on small fish in the vicinity of the Antarctic Convergence.

On the other hand, euphausiids (probably *Euphausia superba*) were found in the stomach of one dwarf minke whale sampled at 65°S, which is further south of the Antarctic Convergence and where dwarf minke whales are known not commonly occur (Kato *et al.*, in press). Euphausiids such as *E. superba* are known to be abundant in this region. Thus, it cannot be automatically determined that the dwarf minke whale is a fish-feeder. It appears that the dwarf minke whale is more of an opportunistic feeder and utilizes organisms which are available in abundance as food.

From the above, it can be summarized that dwarf minke whales feed mainly on small gregarious fish species such as myctophids in their normal summer habitat, while dwarf minke whales in lower latitudes off Brazil feed on euphausiids (Secchi *et al.*, 2003) on an opportunistic basis.

Morphometric analysis

External body proportions

A total of 21 external measurements collected from 16 dwarf minke whales were compared statistically with those from 507 Antarctic minke whales and 91 North Pacific common minke whales. All measurements were log-transformed prior to the analysis.

The morphometric comparison for the three species and sub-species of minke whales was carried out using three methods. The first was the analysis of covariance (ANCOV). This assumes that the allometric relationship between body length (V01) and each of the remaining measurements holds irrespective of age, while body length was used as a covariate to the other measurements (Jover, 1992; Tanaka and Tarumi, 1986). Secondly, measurements showing no significant regression with body length were also used for the multivariate analysis of variance (MANOVA) (Jover, 1992; Tanaka *et al.*, 1990). The third method was the canonical discriminant analysis (DA) using component scores from a principal component analysis (PCA) (Tanaka *et al.*, 1984a, 1984b; Christensen *et al.*, 1990).

To evaluate morphometric differences between males and females, 14 measurements of the dwarf minke whales were analyzed using MANOVA, and a significant difference (Wilks' $\Lambda=0.17026$, $p<0.01$) was detected. ANCOV was also carried out using 20 measurements (V02-V09, V11-V20 and V31-V32) of the dwarf minke whales with body length as a covariate. The analysis indicated no sexual difference except for one characteristic (V08: from tip of snout to sexual aperture), which is known to be sexually dimorphic.

To evaluate differences in external body proportion for dwarf minke whales, Antarctic minke whales and North Pacific common minke whales, MANOVA was carried out using the 14 measurements, and a significant difference was detected (females: Wilks' $\Lambda=0.17026$, $p<0.01$; males: Wilks' $\Lambda=0.24714$, $p<0.01$). ANCOV was conducted using 20 measurements from females. The analysis revealed that 14 of the measurements were significantly correlated with body length (Table 8) while some of the measurements differed significantly in that dwarf minke whales showed larger values in the posterior parts of the body (V08 and V09), flipper, and dorsal fin (V11 and V12). Antarctic minke

Table 8. Results of ANCOV of body proportion with body length (V01) as a covariate for three types of minke whale: dwarf (DWM), Antarctic (ATM) and North Pacific (NPM) minke whales. **Upper**, for female; **bottom** for male.

Female

	Sample size			Result of ANCOV	Estimated value at mean covariate with 95% CF		
	DWM	ATM	NPM		DWM	ATM	NPM
	n	n	n		Mean+95%	Mean+95%	Mean+95%
V02	13	270	40	p<0.01	4.732+0.035	4.761+0.007	4.665+0.020
V03	13	270	34	p<0.01	4.940+0.031	5.024+0.006	4.847+0.018
V04	13	268	9	p<0.01	5.188+0.023	5.258+0.005	5.113+0.027
V05	13	257	40	p<0.01	5.856+0.018	5.866+0.004	5.795+0.010
V06*	13	270	33	p<0.01			
V07*	13	269	33	p<0.01			
V08	13	267	18	p<0.01	6.345+0.009	6.328+0.002	6.311+0.007
V09	13	270	43	P<0.01	6.369+0.008	6.357+0.002	6.348+0.005
V11	13	259	30	p<0.01	3.461+0.067	3.362+0.014	3.402+0.042
V12	13	264	36	p<0.01	4.850+0.051	4.732+0.011	4.681+0.029
V13*	13	267	18	p<0.01			
V14*	13	269	33	p<0.01			
V15	13	270	25	p<0.05	4.038+0.043	4.052+0.009	4.013+0.029
V16	13	266	21	p<0.01	5.405+0.039	5.384+0.008	5.440+0.029
V17*	13	270		p<0.01			
V18*	13	270	29	p<0.01			
V19	13	265	14	p<0.01	5.192+0.022	5.243+0.005	5.084+0.022
V20	13	264	17	p<0.01	4.607+0.025	4.635+0.005	4.460+0.023
V31	11	216		p<0.01	5.128+0.027	5.169+0.006	
V32	12	247		p<0.05	5.120+0.035	5.164+0.007	

Male

	Sample size			Result of ANCOV	Estimated value at mean covariate with 95% CF		
	DWM	ATM	NPM		DWM	ATM	NPM
	n	n	n		Mean+95%	Mean+95%	Mean+95%
V02	3	236	48	p<0.01	4.723+0.082	4.725+0.009	4.654+0.021
V03	3	235	41	p<0.01	4.931+0.055	4.986+0.006	4.859+0.015
V04	3	233	15	p<0.01	5.170+0.042	5.220+0.005	5.072+0.021
V05	3	229	45	p<0.01	5.837+0.043	5.832+0.005	5.758+0.012
V06	3	237	36	p<0.01	5.969+0.041	5.955+0.005	5.857+0.012
V07*	3	237	36	p<0.01			
V08	3	237	30		6.266+0.019	6.253+0.002	6.255+0.006
V09	3	237	48	p<0.01	6.352+0.016	6.344+0.002	6.335+0.004
V11	3	229	40	p<0.05	3.525+0.134	3.370+0.015	3.411+0.038
V12	3	231	41	p<0.01	4.849+0.078	4.728+0.009	4.774+0.022
V13*	3	232	9	p<0.01			
V14	3	235	41	p<0.01	3.450+0.063	3.330+0.007	3.360+0.018
V15	3	237	40		3.973+0.075	4.012+0.008	3.994+0.022
V16	3	236	33	p<0.01	5.382+0.068	5.365+0.008	5.412+0.021
V17	3	237			5.327+0.066	5.334+0.007	
V18*	3	237	44	p<0.01			
V19	3	236	19	p<0.01	5.156+0.041	5.210+0.005	5.078+0.018
V20	3	233	20	p<0.01	4.572+0.048	4.613+0.005	4.401+0.021
V31	3	199			5.098+0.043	5.136+0.005	
V32	3	218			5.095+0.045	5.138+0.005	

*: As the results showed no correlation with body length as a covariate, a multivariated analysis of variance was adopted.

whales showed larger values in measurements related to head proportion (V03, V04, V19, V31, V32). North Pacific common minke whales showed wider flukes (V16). In spite of the small sample size, similar results were observed for males (Table 8).

The result of PCA showed that the first Principal Component (PC1) is related to growth, with a positive value observed for all variables. The PC2 seems to be correlated to body appendages such as flipper, dorsal fin, and flukes. The values were positive for girth (V11) and flukes (V15 and V16) while negative values were observed in anterior parts of the body (from V02 to V09). Principal component scores from PCA were examined using the canonical discriminant analysis (DA). Eigenvalues and eigenvectors derived from DA are shown in Table 9 by each canonical variate (CAN) with and without PC1. Plots of the first two variates are shown in Fig. 12 for both sexes. For males, irrespective of whether PC1 was included or not, the three forms are visibly separate from each other. These results indicate significant differences in external morphology among the three types of minke whale.

Skull measurements

1. ANCOV analyses

Comparative skull morphology analyses were carried out based on 76 skull measurements from 15 dwarf minke whales, 33 Antarctic minke whales, 27 North Atlantic common minke whales and 29 North Pacific common minke whales. The measurements were log-transformed prior to the analyses. Because of the small sample size, the analysis was conducted by combining data of both sexes.

The same methods of analysis as those for external morphometry were conducted: MANOVA, ANCOV, PCA, and DA. In ANCOV, condylo-premaxillary length (SK01) was used as the covariate.

Table 10 shows the results of ANCOV. Fifty-nine measurements indicated a significant regression with the SK01. Of these, 46 were significantly different among the four species and sub-species of minke whales. For five measurements (indicated by ** in Table 10) that had no significant slope in the regression line taking the SK01 as a covariate, MANOVA were applied instead of ANCOV, indicating that measurements related to rostrum (SK03, SK05, SK06, SK07, SK08, SK09, SK19, SK21) are

Table 9. Eigenvectors and eigenvalues derived from the canonical discriminant analysis using the PC scores of PCA for each sex.

Female					Male				
Principal Component	PC1-PC14		PC2-PC14		Principal Component	PC1-PC14		PC2-PC14	
	CAN1	CAN2	CAN1	CAN2		CAN1	CAN2	CAN1	CAN2
PC1	−1.0647	1.0367			PC1	1.2805	−0.7460		
PC2	5.8434	−1.8680	4.5469	3.9497	PC2	−5.8619	1.8779	5.4162	2.5298
PC3	14.1278	−0.6006	12.4648	5.6995	PC3	−13.4996	−1.0185	12.7377	0.1822
PC4	1.7539	6.3519	3.9619	−5.6118	PC4	0.7162	−6.3630	−0.3579	−6.7861
PC5	4.9272	3.2111	5.6326	−1.3752	PC5	5.3022	−2.4817	−4.8601	−3.1148
PC6	−4.7839	−4.6171	−6.0319	2.8102	PC6	8.5320	0.8708	−8.0618	0.1251
PC7	−2.0632	0.9634	−1.4914	−1.6930	PC7	−2.2883	0.1613	2.1421	0.3836
PC8	1.0791	−8.8291	−2.3480	9.0719	PC8	0.8390	9.7660	−1.2719	10.2354
PC9	15.2995	3.0035	14.8688	2.5732	PC9	−19.5342	−4.2379	18.5691	−2.6552
PC10	16.0063	28.5834	25.1179	−22.3201	PC10	−13.2718	−18.5866	13.3946	−18.3927
PC11	14.2007	13.2371	17.7122	−7.9283	PC11	−2.2114	14.2976	1.3674	15.3041
PC12	11.7966	21.5350	18.7129	−16.8394	PC12	18.7030	4.3906	−17.7983	2.8929
PC13	−13.6419	35.3312	1.0133	−39.6776	PC13	12.6217	−30.3189	−10.3333	−33.1692
PC14	−12.6909	15.0742	−5.6906	−19.3782	PC14	−14.0194	−2.3797	−13.3009	−1.2024
Eigenvalue	2.0810	0.9049	1.6351	0.5091	Eigenvalue	2.4671	0.1671	1.7534	0.1430

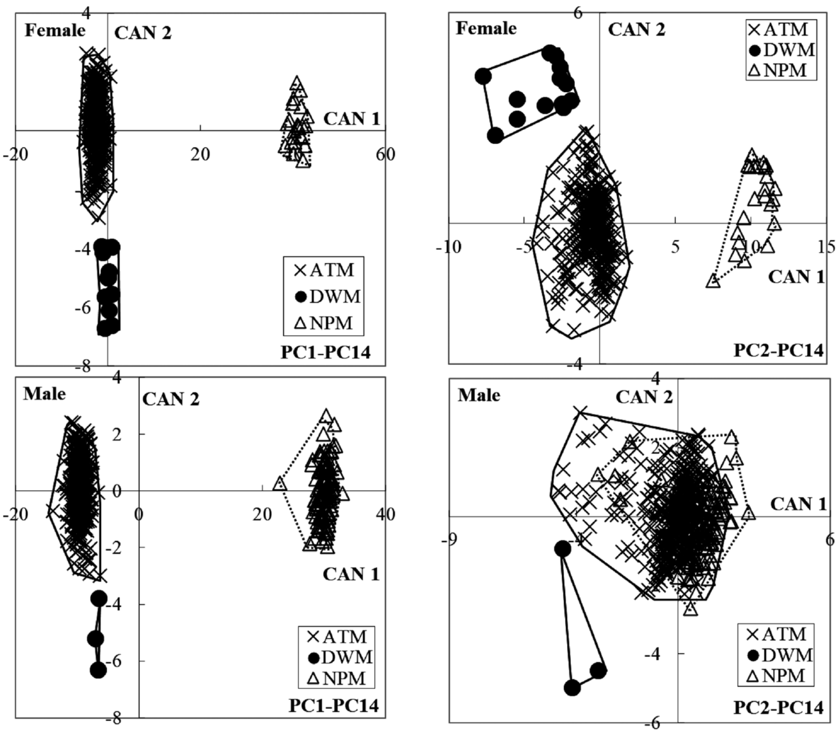

Fig. 12. Scatter plots of scores on the first and second canonical variates derived from external body proportions of dwarf minke whales (DWM), Antarctic minke whales (ATM) and North Pacific common minke whales (NPM), for females (upper) and males (lower).

smaller in Antarctic minke whales, i.e., Antarctic minke whales seem to possess a relatively shorter and narrower rostrum, and a larger mouth cavity. The analysis also shows that Antarctic minke whales have a somewhat larger occipital portion of skull (SK30, SK32, and SK63).

From the results of PCA, eigenvalues and eigenvectors were calculated using DA for each canonical covariate CAN (Table 11) with and without PC1. Plots of the first two CANs are shown in Fig. 13. Irrespective of whether PC1 was included or not, skull morphology differed among dwarf minke whales, Antarctic minke whales and North Pacific common minke whales.

CLUSTER analyses for skull morphology

Although the following analysis is not necessarily the most effective approach to advance the investigation on differences in skull morphology among taxa, cluster type analyses were carried out using skull data of sexually mature whales, comprising eight dwarf minke whales (present study), 14 North Atlantic common minke whales (present study and from Tomilin (1967)), five Antarctic minke whales (from Nakamura, 2012), and 47 North Pacific common minke whales (from Nakamura, 2012).

In earlier analyses, statistical differences were identified in 29 of 44 proportions among minke whale taxa. Furthermore, reliable measurements, which are potentially less subject to technical measuring error, were extracted. These included (1) CBL (condylobasal length), (2) length of tympanic bulla, (3) pre-maxilla length as proportion of CBL, (4) maxillary length as proportion of CBL, (5) mandible length along its outer margin as proportion of CBL, (6) occipital length as proportion of CBL.

Among the six variables chosen, (3), (4) and (5) had growth dependent changes in relative values. For this comparison, only the data obtained from sexually mature animals or those from animals with a CBL $>$145 cm, which were known to be independent of growth dependent changes, were used. The values of the respective variants are given in Appendix 2.

In the next step to evaluate degree of similarity among the different taxa, the parameter S was esti-

Table 10. Results of ANCOV of skull measurements with skull length (SK01) as a covariate for minke whales in four types: dwarf form (DWM), North Atlantic (NA), North Pacific (NPM) and Antarctic (ATM) minke whales.

Item	Sample size				Result of ANCOV	Estimated value at mean covariate with SE			
	DWM	NA	NPM	ATM		DWM	NA	NPM	ATM
	n	n	n	n		Mean+SE	Mean+SE	Mean+SE	Mean+SE
SK02	15	5	29	32	0.450	4.715+0.009	4.703+0.014	4.700+0.006	4.696+0.007
SK03	13	8	25	31	0.000	4.845+0.008	4.845+0.009	4.831+0.005	4.785+0.006
SK04	13	1	26	31	0.000	4.857+0.008	4.835+0.026	4.842+0.006	4.797+0.006
SK05	12	5	25	28	0.000	4.802+0.008	4.818+0.012	4.793+0.005	4.748+0.006
SK06	12	2	24	26	0.000	4.804+0.080	4.814+0.019	4.795+0.005	4.749+0.007
SK07	13	1	27	25	0.000	4.851+0.009	4.876+0.027	4.841+0.006	4.799+0.007
SK08	13	1	27	25	0.000	4.857+0.009	4.891+0.026	4.844+0.006	4.796+0.007
SK09	14	1	29	28	0.000	4.872+0.008	4.908+0.024	4.865+0.005	4.810+0.006
SK10	15	7	29	29					
SK11	12	1	23	25	0.048	2.098+0.047	2.370+0.135	2.204+0.032	2.127+0.037
SK12	12	1	23	24	0.000	2.152+0.043	2.551+0.122	2.236+0.028	2.079+0.034
SK13	15	4	28	32	0.041	4.204+0.017	4.163+0.029	4.233+0.012	4.194+0.013
SK14*	13	27	28	29					
SK15*	15	1	26	30					
SK16*	14	5	26	29					
SK17*	15	9	28	32					
SK18	14	5	25	29	0.045	4.432+0.028	4.439+0.038	4.412+0.019	4.333+0.022
SK19	15	11	28	33	0.000	4.110+0.017	4.033+0.017	4.052+0.011	3.975+0.013
SK20*	15	11	28	32					
SK21	14	—	25	25	0.000	2.727+0.068		2.838+0.044	2.271+0.056
SK22	13	—	11	27	0.527	2.211+0.055		2.284+0.054	2.235+0.040
SK23*	13	8	25	28					
SK24	14	3	24	28	0.967	2.728+0.030	2.750+0.054	2.731+0.020	2.743+0.023
SK25	13	—	20	24	0.244	0.991+0.150		0.987+0.107	0.678+0.122
SK26*	13	5	27	32					
SK27	13	5	28	32	0.000	2.815+0.028	3.025+0.042	2.851+0.018	2.917+0.021
SK28*	14	3	27	31					
SK29*	14	—	28	30					
SK30	14	—	28	30	0.000	2.328+0.019		2.421+0.013	2.479+0.015
SK31	13	3	28	31	0.009	2.834+0.051	2.679+0.101	2.650+0.033	2.633+0.039
SK32	15	4	27	29	0.000	3.695+0.017	3.842+0.030	3.763+0.012	3.830+0.014
SK33	14	—	28	30	0.000	2.085+0.026		2.148+0.018	1.913+0.021
SK34*	14	—	28	28					
SK35	11	1	20	26	0.000	2.096+0.019	2.181+0.051	2.239+0.014	2.200+0.015
SK36**	11	1	22	26	0.000	1.793+0.017	1.758+0.057	1.945+0.012	1.965+0.011
SK37**	10	1	20	26	0.000	2.040+0.018	2.140+0.057	2.220+0.013	2.235+0.011
SK38**	10	1	19	26	0.000	1.808+0.016	1.705+0.049	1.952+0.011	1.973+0.010
SK39**	10	1	19	26	0.000	1.808+0.016	1.705+0.049	1.952+0.011	1.973+0.010
SK40**	14	6	28	27	0.004	3.316+0.070	3.056+0.106	3.325+0.049	3.475+0.050
SK41	12	2	23	28	0.001	2.595+0.039	2.736+0.078	2.581+0.026	2.767+0.029
SK42	14	—	26	26	0.000	4.967+0.005		4.946+0.003	4.966+0.004
SK43	14	—	24	24	0.000	4.926+0.005		4.908+0.003	4.927+0.004
SK44*	14	2	26	25					
SK45	14	—	25	22	0.000	4.927+0.006		4.900+0.004	4.919+0.005
SK46	13	—	24	23	0.000	4.637+0.010		4.571+0.006	4.640+0.008
SK47	13		24	24	0.000	4.640+0.010		4.582+0.006	4.650+0.008
SK48	14	21	28	26	0.159	3.692+0.069	3.525+0.058	3.658+0.046	3.667+0.061
SK49*	14	21	28	26					
SK50*	13	3	28	30					
SK51*	13	3	21	26					
SK52	14	2	29	27	0.000	4.696+0.008	4.698+0.018	4.655+0.005	4.712+0.007
SK53	13	2	25	24	0.000	4.702+0.008	4.711+0.016	4.653+0.005	4.706+0.006
SK54	13	4	26	30	0.010	4.991+0.006	5.006+0.009	4.978+0.004	4.990+0.004
SK55	12	4	21	27	0.010	4.994+0.005	5.010+0.007	4.980+0.003	4.991+0.004
SK56*	15	2	29	30					

Table 10. Continued.

Item	Sample size				Result of ANCOV	Estimated value at mean covariate with SE			
	DWM	NA	NPM	ATM		DWM	NA	NPM	ATM
	n	n	n	n		Mean+SE	Mean+SE	Mean+SE	Mean+SE
SK57	14		28	28	0.224	2.899+0.044		2.871+0.029	2.788+0.036
SK58	14	4	28	32	0.050	3.018+0.040	3.032+0.070	3.028+0.027	2.894+0.032
SK59	15	6	27	32	0.000	5.179+0.011	5.215+0.015	5.150+0.008	5.143+0.009
SK60	15	3	28	32	0.095	5.164+0.019	5.238+0.040	5.147+0.013	5.120+0.015
SK61	15	5	27	32	0.011	5.125+0.010	5.148+0.015	5.111+0.007	5.091+0.008
SK62	15	3	28	32	0.093	5.111+0.015	5.168+0.031	5.107+0.010	5.076+0.012
SK63	14	2	28	31	0.000	3.129+0.015	3.170+0.037	3.103+0.010	3.195+0.012
SK64	14	6	29	30	0.000	3.131+0.015	3.117+0.021	3.103+0.010	3.184+0.012
SK65	14	2	29	31	0.708	2.821+0.026	2.770+0.062	2.802+0.017	2.828+0.021
SK66	14	5	28	31	0.576	2.829+0.026	2.810+0.040	2.793+0.018	2.819+0.021
SK67	8	—	27	22	0.027	2.571+0.038		2.589+0.020	2.481+0.028
SK68	8	—	25	22	0.035	2.551+0.040		2.586+0.021	2.482+0.029
SK69	6	—	23	24	0.002	2.506+0.084		2.750+0.045	2.927+0.050
SK70	6	—	25	24	0.006	2.573+0.071		2.759+0.037	2.890+0.043
SK71	6	—	25	25	0.000	1.870+0.072		2.186+0.037	2.031+0.043
SK72	6	—	26	25	0.000	1.883+0.061		2.177+0.031	2.036+0.037
SK73	7	—	26	26	0.004	3.039+0.032		3.044+0.015	2.946+0.018
SK74	7	—	24	26	0.009	3.057+0.033		3.051+0.016	2.960+0.019
SK75	6	—	26	25	0.136	0.957+0.076		0.931+0.034	1.052+0.042
SK76	6	—	25	25	0.058	0.952+0.075		0.928+0.033	1.071+0.040

*: Parallel test indicated no significance.
**: As the result showed no correlation with skull length as a covariate, a multivariated analysis of variance was adopted.

Table 11. Eigenvectors and eigenvalues derived from the canonical discriminant analysis using the PC scores of PCA.

Principal Component	PC1-PC5		PC2-PC5	
	CAN1	CAN2	CAN1	CAN2
PC1	−1.5129	0.4102		
PC2	1.1734	0.7607	1.2413	0.3346
PC3	−0.0517	0.8427	0.5924	−0.6666
PC4	0.6007	−0.3278	0.1062	0.7068
PC5	0.0859	−0.3668	−0.1870	0.5102
Eigenvalue	3.2417	0.7854	1.0365	0.3831

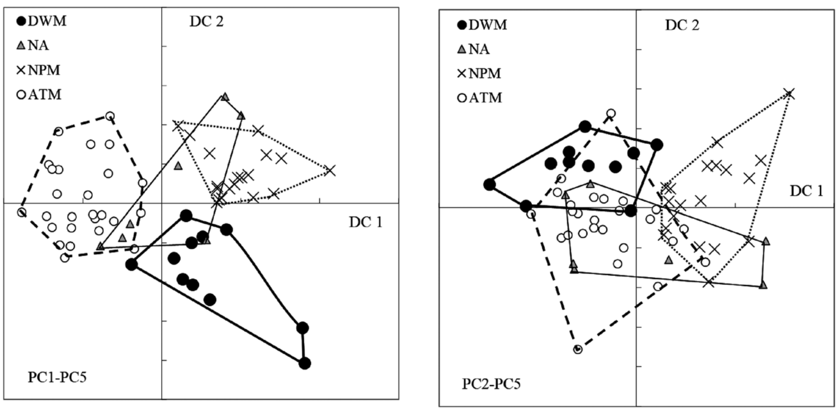

Fig. 13. Scatter plots of scores on the first and second canonical variates derived from skull measurements of dwarf (DWM), North Atlantic (NA), North Pacific (NPM) and Antarctic minke whales (ATM).

Table 12. Estimated value of correction coefficient *r* and degree of similarity *S* in the cluster analysis on the skull between different types of minke whales.

Type	Estimated (*r*/*S*)			
	Antarctic	North Pacific	Dwarf	North Atlantic
Antarctic				
North Pacific	0.9922 0.0078			
Dwarf	0.9833 0.0167	0.9983 0.0017		
North Atlantic	0.9825 0.0175	0.9972 0.0028	0.9983 0.0017	

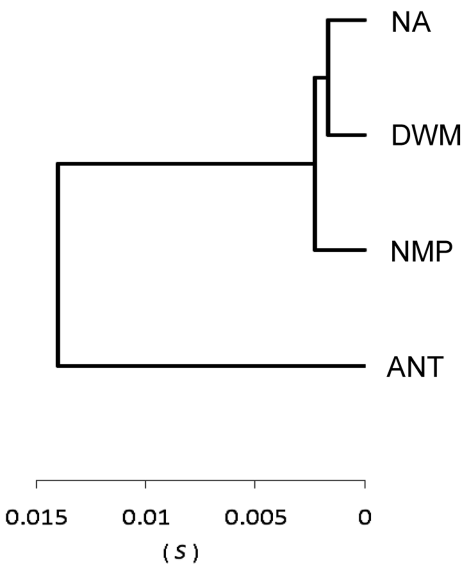

Fig. 14. Dendrogram showing the degree of similarity among the minke whale clade based on cluster analyses on the skull morphology. ANT, Antarctic minke whale; NPM, North Pacific common minke whale; NA, North Atlantic common minke whale; DWM, dwarf minke whale. *S*, see below.

mated as defined below:

$$S = 1 - r \tag{11}$$

where *S* represents the degree of similarity, *r* being the correlation coefficient on the variants between different types of minke whales.

Table 12 gives the estimated values for correlation coefficient and degree of similarity for each pairwise comparison. A dendrogram was produced through cluster analyses using the values from the group average method. These represent the interrelationships in different minke whale taxa by weighing the degree of similarity (Fig. 14). From this dendrogram it was clear that the Antarctic minke whales were most distant, and secondly, the North Pacific common minke whales were relatively distant from the North Atlantic common minke whales and dwarf minke whales. In conclusion, in the present cluster analysis, the dwarf minke whales were closest morphologically to the North Atlantic common minke whales. This was also genetically supported by the previous analyses such as Pastene *et al.* (2007).

Discussion

First of all, throughout this study, the scarcity of available samples has become an issue, however, as it is almost impossible to obtain further samples of the same quality, we had to proceed with the analyses, bearing in mind this sample limitation. Thus, the shortage of an adequate number of samples should be recognized as a potential problem in all analyses during this study.

There are currently many reports on the occurrence of dwarf minke whales from coastal waters in low and middle latitudes in the Southern Hemisphere, mainly Brazil and Australia (Zerbini *et al.*, 1996; Acevedo *et al.*, 2006; Meirells *et al.*, 2011, etc.). In higher latitudes, data on dwarf minke whales has only been from sightings (Kato and Fujise, 2000, Acevedo *et al.*, 2011, Kato *et al.* in press). Until the present study there was no information on the biology of dwarf minke whales in higher latitudes. Arnold *et al.* (1987) reported a considerable number of the dwarf minke whale strandings and sporadic sightings in the austral winter. The 80% of sightings were in the waters off Queensland, Australia, in June and July (Arnold, 1997), which would be consistent with the north-south seasonal movements exhibited by other austral balaenopterids. However, there have also been mid-summer strandings of dwarf minke whales on the southeast coast of Australia (Arnold *et al.*, 1987; Zerbini *et al.*, 1996; Kemper, pers. comm.) and sightings off Brazil (at 23°S) during the month of January (Hassel *et al.*, 2003). Therefore, it is possible that migrations are dispersed seasonally but not undertaken by all individuals.

The relative distributions of dwarf minke whales and Antarctic minke whales in winter are not well known, although dwarf minke whales were found closer inshore than Antarctic minke whales in the waters off both Brazil as well as the east coast of South Africa (Best, 1985; Zerbini *et al.*, 1996). Published information (Arnold, 1997; Arnold *et al.*, 2005) suggested that a large proportion of dwarf minke whales remain in lower to mid-latitudes during summer, even though they can be found as far south as the Antarctic Convergence. Kato *et al.* (in press) examined all of dwarf minke whale sightings made during the 1994/95 to 2003/04 IDCR/SOWER cruises and reached almost the same conclusion as the present study in terms of sighting distribution. Further sighting information, combined with experiments such as photo-identifications, will provide a clearer understanding on their distributions and movements.

The migration of dwarf minke whales as far south as the Antarctic Convergence in summer is latitudinally of a much wider range than generally expected, as dwarf minke whales are thought to prefer coastal zones in low and middle latitudes. However, this may not be unnatural when considered as an adaptive radiation process of the minke whale clade.

In both hemispheres, minke whales are widely distributed from the ice edge to tropical waters while developing or dividing into closely related species or subspecies. In this interpretation, they might further adapt this cline along the allopatric speciation. The minke whale is one of the most cosmopolitan groups and has a clear morphological cline from North Pacific or North Atlantic common minke whales to Antarctic minke whales. Dwarf minke whales may have evolved in an ecological niche between Northern Hemisphere common minke whales and Antarctic minke whales. Inferring from this relationship, it can be said that the same interpretation is also true morphologically and perhaps behaviorally for food and feeding habits. Those of the dwarf minke whales are somewhere between North Pacific or North Atlantic common minke whales and Antarctic minke whales. Both Best (1985) and Arnold *et al.* (1987) indicated dwarf minke whales have distinct morphological features and they bear a closer morphological resemblance to Northern Hemisphere common minke whales rather than to Antarctic minke whales. The present study also identified these characteristics in-depth with a larger sample size and the use of morphometric analyses.

Pastene *et al.* (2007) provided mtDNA sequence evidence for the separation of the two species, the Antarctic minke whale and the common minke whale, and at least three sub-species of the common minke whale. They hypothesized that the two species diverged in the Southern Hemisphere less than

5 million years ago, and that the current subspecies of the common minke whale diverged after the Pliocene some 1.5 million years ago. Furthermore, Pastene *et al.* (2010) provided mtDNA sequence evidence for the genetic separation of the dwarf minke whale in the Southern Hemisphere. The study used samples from JARPA in the western South Pacific sector of the Antarctic, Tonga and New Zealand (western South Pacific: WSP), as well as from Brazil, Chilean Patagonia and Antarctic Peninsula (western South Atlantic: WSA). They found phylogenetic differences between dwarf minke whales in the WSP and WSA, with dwarf minke whales from the WSA being closer to North Atlantic common minke whales than to dwarf minke whales from the WSP. Glover *et al.* (2013) provided microsatellite DNA evidence for the separation of the two species and three subspecies of the common minke whale. These genetic analyses used the dwarf minke whale specimens from this study.

Nakamura *et al.*, (2018) showed that there were clear morphological differences in the white patch of the flipper between North Pacific and North Atlantic common minke whales, which have been recently recognized as two distinctively separate subspecies. Further, the length between the tip of flipper to the proximal border of white patch relative to the total flipper length was significantly larger in the North Atlantic (74.31%) as compared to the North Pacific (63.62%) common minke whales. Also, the mean angle between the proximal boundary line of the white patch and the longitudinal axis of the flipper was significantly different between the North Atlantic (70.05 degrees) and the North Pacific (92.29 degrees) common minke whales. Therefore, a numerical comparison of the white patch on the flipper/shoulder should be conducted in the future for the three sub-species of common minke whales.

Morphometric analyses on both the body proportion and the skull revealed at least three types of common minke whale clade can be distinguished. Also, the flipper/shoulder portion is a consistent and reliable characteristic for distinguishing the three types. As examined by Nakamura *et al.* (2018), the white patch of the flipper/shoulder portion is wider in the following order; dwarf minke whale＞North Atlantic common minke whale＞ North Pacific common minke whale. This is an additional indication that the dwarf minke whale is closer to the North Atlantic common minke whale. While it is still inconclusive due to small sample size, the cluster analyses on body proportion and skull morphometry (Fig. 12) in the present study supports this hypothesis. Before reaching the final conclusion on the taxonomic status of dwarf minke whales, there are some outstanding issues to be pursued. Numerical comparison of the white patch between the dwarf minke whale and the North Atlantic common minke whale needs to be conducted. In addition, in light of the genetic differences suggested by several studies, morphological and morphometric comparative analyses among dwarf minke whales from different locations of the Southern Hemisphere should be carried out.

However, there is little doubt that the dwarf minke whales have diverged from other common minke whales, at least at the subspecies level. Morphometric comparison in both external body and skull proportions in the present study provided reliable evidence to identify and confirm the differences among the minke whale clade. The separation of dwarf minke whales from other common minke whale sub-species is further supported by genetic evidence. Based on such convincing evidence, dwarf minke whales from the Indo-Pacific sector of the Antarctic examined in this study should be formally described as an independent sub-species or species from other common minke whales.

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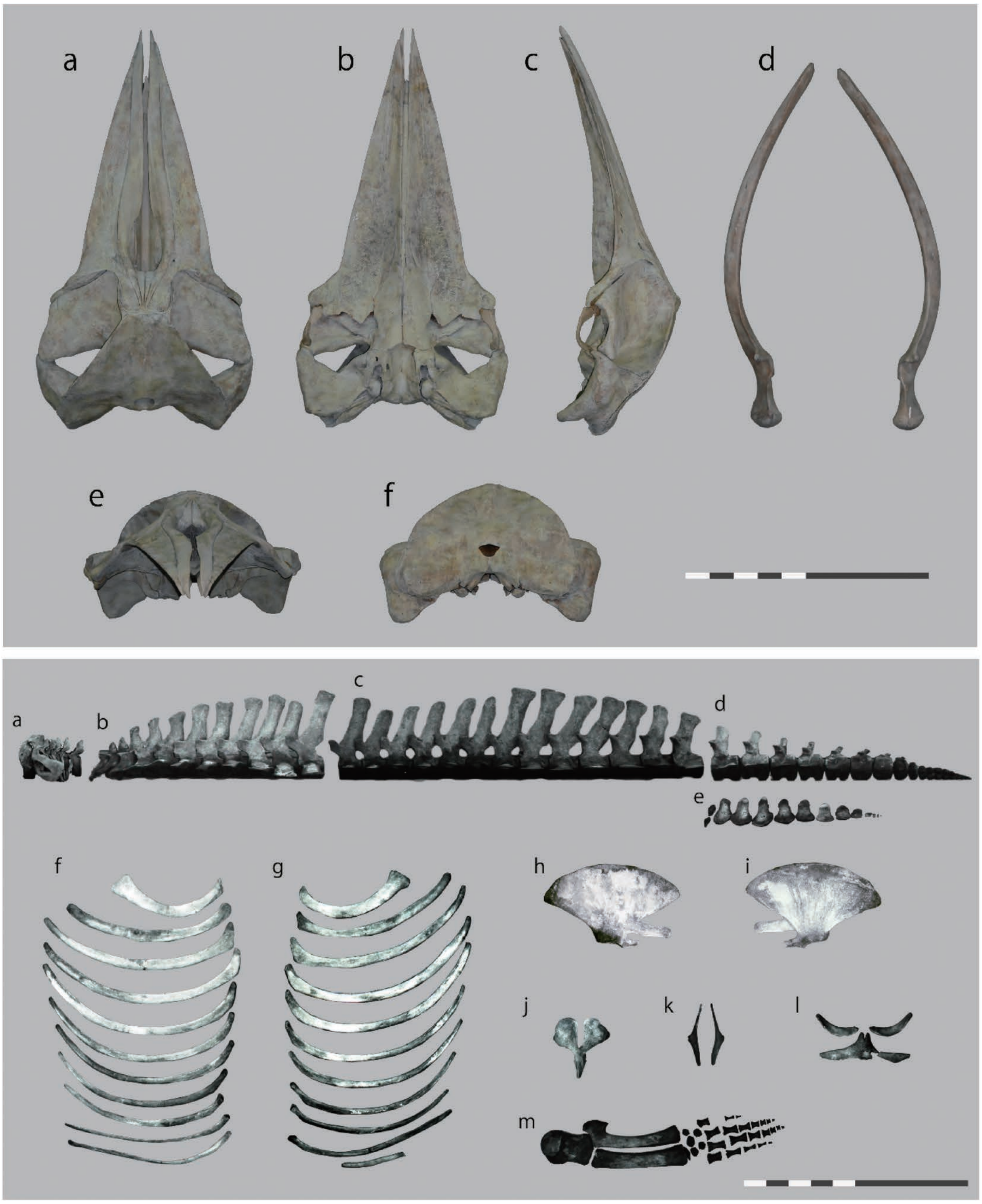
Appendices

Appendix 1. **Upper**: Skull and mandible of the dwarf minke whale (MTUM-DW273); **a)** skull dorsal view, **b)** skull ventral view, **c)** skull lateral view, **d)** mandibles dorsal view, **e)** skull frontal view, **f)** backward view. **Bottom**: other bones of the same skeleton; **a)** cervical, **b)** dorsal, **c)** lumber, **d)** caudal vertebrae, **e)** chevron, **f, g)** left and right ribs with lateral surface and **h, i)** coastal surface of right and left scapula, **j)** sternum, **k)** pelvic bone, **l)** hyoid, **m)** humerus, radius, ulna and manus on the left flipper. Scale bars are 1.00 m size marked with 0.1 m intervals.



Appendix 2. List of skeletal measurements by the standard measuring method for all dwarf minke whales examined in the present skeletal analysis.

Measurement points	Specimen ID	87/88 273		88/89 013		88/89 014		88/89 070		89/90 199		88/89 227		89/90 215		92/93 330		Mean±S.D. %
	Body length (m)	7.01		6.99		6.6		5.94		5.41		7.02		7.07		7.17		
	Sex	M		F		M		F		M		F		F		F		
		cm	%	cm	%	cm	%	cm	%	cm	%	cm	%	cm	%	cm	%	
Condylobasal length		159.7		163.4		149.0		133.1		122.3		164.7		169.2		156.1		
Length of rostrum		101.4	63.5	106.0	64.9	97.7	65.6	83.4	62.7	81.6	66.7	111.0	67.4	112.0	66.2	106.8	68.4	65.7±1.94
Length of premaxillary (L)		119.3	74.7	119.4	73.1	109.8	73.7	97.9	73.6			120.0	72.9	122.8	72.6	119.8	76.7	73.9±1.44
Length of premaxillary (R)		120.0	75.1	121.3	74.2	109.3	73.4	98.5	74.0	92.0	75.2	120.8	73.3	122.4	72.3	120.2	77.0	74.3±1.44
Length of maxillary (L)		117.2	73.4	114.3	70.0	105.5	70.8	94.3	70.8			115.2	69.9	119.3	70.5	111.4	71.4	71±1.18
Length of maxillary (R)		117.3	73.5	114.8	70.3	105.0	70.5	94.1	70.7			115.4	70.1	119.3	70.5	112.8	72.3	71.1±1.26
Tip of premaxillary to tip of maxillary (L)		4.5	2.8	8.4	5.1	8.3	5.6	8.7	6.5			10.7	6.5	9.6	5.7	10.3	6.6	5.5±1.33
Tip of premaxillary to tip of maxillary (R)		4.9	3.1	9.8	6.0	9.2	6.2	5.7	4.3			10.7	6.5	8.3	4.9	10.5	6.7	5.4±1.34
Tip of premaxillary to nares, anterior		109.0	68.3	106.2	65.0	96.8	65.0	85.9	64.5	82.2	67.2	109.1	66.2	110.4	65.2	104.2	66.8	66±1.31
Tip of premaxillary to vertex		123.7	77.5	126.5	77.4	116.0	77.9	103.7	77.9	96.3	78.7	128.3	77.9	131.7	77.8	125.5	80.4	78.2±0.98
Tip of premaxillary to palatine, anterior (L)		99.5	62.3	102.3	62.6	97.8	65.6	85.8	64.5			108.2	65.7	108.0	63.8	100.2	64.2	64.1±1.33
Tip of premaxillary to palatine, anterior (R)		99.8	62.5	105.2	64.4	97.8	65.6	86.9	65.3	78.7	64.3	107.6	65.3	108.3	64.0	100.1	64.1	64.5±1
Tip of premaxillary to palatine, posterior (L)		134.5	84.2	137.4	84.1	128.1	86.0	111.7	83.9			142.2	86.3	145.3	85.9	135.2	86.6	85.3±1.16
Tip of premaxillary to palatine, posterior (R)		134.5	84.2	139.2	85.2	127.6	85.6	111.7	83.9	102.8	84.1	141.3	85.8	143.2	84.6	135.5	86.8	85±1.01
Tip of premaxillary to pterygoid process (L)		144.0	90.2	146.3	89.5	134.6	90.3	119.7	89.9			150.3	91.3	153.8	90.9	143.1	91.7	90.5±0.76
Tip of premaxillary to pterygoid process (R)		143.8	90.0			134.8	90.5	119.3	89.6	108.4	88.6			152.3	90.0	143.3	91.8	90.1±1.04
Tip of premaxilla to posterior edge of occipital bone (L)		170.0	106.4	165.7	101.4	156.8	105.2	139.1	104.5			173.4	105.3	177.8	105.1	165.3	105.9	104.8±1.63
Tip of premaxilla to posterior edge of occipital bone (R)		169.4	106.1	166.1	101.7	155.9	104.6	138.7	104.2	127.4	104.2	172.0	104.4	176.8	104.5	165.3	105.9	104.4±1.35
Tip of premaxilla to posterior edge of temporal bone (L)		164.2	102.8	168.7	103.2	153.5	103.0	136.5	102.6			169.4	102.9	172.2	101.8	162.7	104.2	102.9±0.74
Tip of premaxilla to posterior edge of temporal bone (R)		164.8	103.2	171.2	104.8	152.2	102.1	136.5	102.6	124.0	101.4	168.2	102.1	170.7	100.9	162.7	104.2	102.7±1.34
Breadth of maxillary, posterior edge		19.0	11.9	14.2	8.7	14.3	9.6	14.0	10.5	11.6	9.5	19.0	11.5	15.3	9.0	17.9	11.5	10.3±1.24
Breadth of premaxillary, posterior edge		3.0	1.9	3.4	2.1	3.2	2.1	2.1	1.6	1.3	1.1	4.8	2.9	3.2	1.9	3.0	1.9	1.9±0.52
Tip of premaxillary to anterior end of vomer, median		21.2	13.3	17.7	10.8	18.3	12.3	19.3	14.5	17.9	14.6	21.7	13.2	18.5	10.9	16.3	10.4	12.5±1.65
Length of vomer		122.4	76.6	131.3	80.4	116.2	78.0	107.0	80.4	93.7	76.6	127.6	77.5	136.5	80.7	126.1	80.8	78.9±1.86
Breadth of rostrum at base		55.1	34.5	50.7	31.0	51.2	34.4	49.2	37.0	43.8	35.8	53.8	32.7	59.3	35.0	58.2	37.3	34.7±2.1
Breadth of premaxillary at base		17.3	10.8	15.4	9.4	12.8	8.6	11.7	8.8	11.3	9.2	13.7	8.3	12.8	7.6	13.2	8.5	8.9±0.97
Breadth of rostrum at middle		31.4	19.7	30.7	18.8	30.5	20.5	28.7	21.6	23.7	19.4	34.2	20.8	36.4	21.5	34.8	22.3	20.6±1.21
Breadth of premaxillary at middle		12.6	7.9	12.7	7.8	12.7	8.5	11.8	8.9	9.8	8.0	15.2	9.2	16.5	9.8	15.4	9.9	8.7±0.83
Greatest breadth of premaxillary		22.2	13.9	20.2	12.4	19.2	12.9	17.4	13.1	15.9	13.0	22.3	13.5	22.0	13.0	22.8	14.6	13.3±0.7
Breadth of cranium, maxillaries		79.1	49.5	76.0	46.5	73.8	49.5	65.9	49.5	57.6	47.1	78.7	47.8	82.8	48.9	80.5	51.6	48.8±1.62

Appendix 2. (Continued.)

Measurement points	Specimen ID / Body length (m) / Sex	87/88 273 7.01 M		88/89 013 6.99 F		88/89 014 6.6 M		88/89 070 5.94 F		89/90 199 5.41 M		88/89 227 7.02 F		89/90 215 7.07 F		92/93 330 7.17 F		Mean±S.D. %
		cm	%	cm	%	cm	%	cm	%	cm	%	cm	%	cm	%	cm	%	
Breadth of cranium, anterior edge of zygomatic process		89.1	55.8	84.5	51.7	80.8	54.2	72.8	54.7	64.7	52.9	86.3	52.4	91.5	54.1	89.4	57.3	54.1±1.82
Breadth of cranium, middle of orbital foramen		80.1	50.2	77.5	47.4	72.3	48.5	66.7	50.1	58.6	47.9	77.7	47.2	83.0	49.1	80.4	51.5	49±1.51
Breadth of occipital bone		69.5	43.5	63.3	38.7	59.3	39.8	51.2	38.5	49.4	40.4	66.4	40.3	62.6	37.0	61.7	39.5	39.7±1.9
Breadth of cranium, middle of zygomatic process		89.3	55.9	82.1	50.2	79.4	53.3	71.8	53.9	64.6	52.8	85.3	51.8	88.5	52.3	87.7	56.2	53.3±2.01
Length from upper ridge of foramen magnum to superior part of occipital bone		40.4	25.3	40.4	24.7	36.4	24.4	31.4	23.6	27.7	22.6	40.2	24.4	43.2	25.5	37.3	23.9	24.3±0.93
Greatest breadth of palatine		24.8	15.5	23.3	14.3	23.8	16.0	21.8	16.4	18.5	15.1	22.7	13.8	26.5	15.7	25.3	16.2	15.4±0.93
Length of palatine (L)		36.8	23.0	37.4	22.9	32.3	21.7	28.3	21.3	26.6	21.7	36.2	22.0	37.8	22.3	37.7	24.2	22.4±0.94
Length of palatine (R)		37.1	23.2	36.1	22.1	32.3	21.7	27.3	20.5	27.0	22.1	35.8	21.7	36.4	21.5	37.1	23.8	22.1±1.02
Breadth of palatine, posterior		25.3	15.8	22.8	14.0	23.1	15.5	21.3	16.0	21.7	17.7	27.3	16.6	27.7	16.4	26.7	17.1	16.1±1.14
Breadth across hamular processes of pterygoid		12.9	8.1	12.7	7.8	11.7	7.9	11.3	8.5	11.6	9.5	13.8	8.4	14.4	8.5	12.8	8.2	8.3±0.54
Length of orbit (L)		17.0	10.6	15.0	9.2	16.5	11.1	15.5	11.6	14.5	11.9	16.5	10.0	16.5	9.8	16.5	10.6	10.6±0.92
Length of orbit (R)		16.5	10.3	16.0	9.8	15.5	10.4	15.5	11.6	14.0	11.4	17.0	10.3	16.0	9.5	16.5	10.6	10.5±0.74
Height of cranium				50.0	30.6	45.1	30.3	34.3	25.8	37.2	30.4	49.4	30.0	51.5	30.4	53.4	34.2	30.2±2.45
Length of nasals		14.9	9.3	16.3	10.0	14.5	9.7	14.0	10.5	10.8	8.8	17.8	10.8	18.7	11.1	17.8	11.4	10.2±0.89
Breadth of nasal, posterior		1.1	0.7	2.0	1.2	1.3	0.9	1.1	0.8	0.8	0.7	2.6	1.6	1.2	0.7	1.9	1.2	1±0.33
Breadth of nasal at middle		4.4	2.8	5.8	3.5	4.9	3.3	4.5	3.4	3.3	2.7	7.1	4.3	6.5	3.8	5.3	3.4	3.4±0.53
Minimum breadth of parietal bones		18.5	11.6	16.4	10.0	15.3	10.3	16.5	12.4	12.8	10.5	20.1	12.2	19.4	11.5	20.0	12.8	11.4±1.05
Height of foramen magnum		6.4	4.0	5.9	3.6	7.3	4.9	6.6	5.0	6.3	5.2	6.3	3.8	6.3	3.7	6.7	4.3	4.3±0.61
Breadth of foramen magnum		8.2	5.1	7.8	4.8	6.0	4.0	7.3	5.5	7.4	6.1	7.1	4.3	6.5	3.8	7.3	4.7	4.8±0.75
Breadth across occipital condyles		17.0	10.6	16.7	10.2	15.7	10.5	15.8	11.9	13.3	10.9	14.3	8.7	16.8	9.9	17.2	11.0	10.5±0.93
Breadth of occipital condyle (L)		6.8	4.3	7.0	4.3	6.2	4.2	6.6	5.0	5.3	4.3	6.8	4.1	6.7	4.0	6.3	4.0	4.3±0.31
Breadth of occipital condyle (R)		6.9	4.3	7.0	4.3	6.5	4.4	6.2	4.7	5.3	4.3	6.3	3.8	6.5	3.8	6.8	4.4	4.2±0.28
Height of occipital condyle (L)		10.9	6.8	9.8	6.0	10.1	6.8	9.2	6.9	8.6	7.0	8.8	5.3	10.0	5.9	9.8	6.3	6.4±0.6
Height of occipital condyle (R)		11.1	7.0	10.0	6.1	10.0	6.7	9.2	6.9	8.4	6.9	8.9	5.4	10.0	5.9	9.8	6.3	6.4±0.56
Length of tympanic bulla (L)		8.3	5.2	8.2	5.0	7.9	5.3	8.2	6.2	7.3	6.0	7.7	4.7	8.3	4.9	7.6	4.9	5.3±0.53
Minimum breadth of tympanic bulla (L)		4.8	3.0	5.1	3.1	4.9	3.3	5.2	3.9	4.5	3.7	5.1	3.1			4.8	3.1	3.3±0.35
Greatest breadth of tympanic bulla (L)		6.1	3.8	6.3	3.9	6.1	4.1	6.2	4.7	5.7	4.7	5.9	3.6			5.9	3.8	4.1±0.43
Thickness of tympanic bulla at middle (L)						4.3	2.9	4.5	3.4	3.8	3.1	4.3	2.6	4.2	2.5	4.0	2.6	2.8±0.35
Skull height				50.0	30.6	45.1	30.3	34.3	25.8	37.2	30.4	49.4	30.0	51.5	30.4	56.4	36.1	30.5±3.01
Minimum width of the skull at squamous temporal				17.4	10.6	15.8	10.6	14.9	11.2	13.6	11.1	17.1	10.4	14.8	8.7	17.2	11.0	10.5±0.84

Appendix 2. (Continued.)

Measurement points	Specimen ID	87/88 273		88/89 013		88/89 014		88/89 070		89/90 199		88/89 227		89/90 215		92/93 330		Mean±S.D. %
	Body length (m)	7.01		6.99		6.6		5.94		5.41		7.02		7.07		7.17		
	Sex	M		F		M		F		M		F		F		F		
		cm	%	cm	%	cm	%	cm	%	cm	%	cm	%	cm	%	cm	%	
Occipital bone width at jugal process				36.8	22.5	36.2	24.3	36.2	27.2	21.7	17.7	46.6	28.3	43.3	25.6	41.3	26.5	24.6±3.56
Length of mandible, straight (L)		164.5	103.0	167.0	102.2	155.0	104.0	140.0	105.2	127.0	103.8	170.8	103.7			165.0	105.7	104±1.2
Length of mandible, straight (R)		155.4	97.3	157.4	96.3	146.0	98.0	133.5	100.3	120.7	98.7	161.0	97.8			154.8	99.2	98.2±1.3
Length of mandible, curved (L)		156.2	97.8	158.0	96.7	145.8	97.9	133.5	100.3	121.5	99.3	162.0	98.4	167.0	98.7	154.5	99.0	98.5±1.1
Length of mandible, curved (R)		164.5	103.0	166.4	101.8	154.0	103.4	139.9	105.1	126.0	103.0	170.8	103.7	167.5	99.0	165.5	106.0	103.1±2.12
Breadth of mandible at middle (L)		7.0	4.4	6.8	4.2	6.4	4.3	6.0	4.5	4.7	3.8	7.5	4.6	6.8	4.0	6.8	4.4	4.3±0.24
Breadth of mandible at middle (R)		7.0	4.4	7.1	4.3	6.5	4.4	6.2	4.7	4.7	3.8	7.3	4.4	6.8	4.0	7.0	4.5	4.3±0.26
Height of mandible at middle (L)		10.4	6.5	10.0	6.1	9.8	6.6	9.7	7.3	7.6	6.2	11.1	6.7	11.8	7.0	10.6	6.8	6.7±0.38
Height of mandible at middle (R)		10.5	6.6	10.3	6.3	10.2	6.8	9.5	7.1	7.7	6.3	11.2	6.8	12.0	7.1	10.7	6.9	6.7±0.32
Height of mandible at coronoid process (L)		21.5	13.5	21.0	12.9	19.3	13.0	18.4	13.8	16.0	13.1	23.3	14.1	23.2	13.7	21.4	13.7	13.5±0.46
Height of mandible at coronoid process (R)		21.4	13.4	21.2	13.0	19.4	13.0	18.5	13.9	16.3	13.3	23.2	14.1	23.7	14.0	21.6	13.8	13.6±0.44
Height of mandible at coronoid (L)		16.8	10.5	16.1	9.9	14.3	9.6	14.4	10.8	12.1	9.9	18.3	11.1	17.3	10.2	17.7	11.3	10.4±0.63
Height of mandible at coronoid (R)		16.4	10.3	16.1	9.9	14.8	9.9	14.4	10.8	12.3	10.1	18.5	11.2	18.3	10.8	17.3	11.1	10.5±0.54
Breadth of mandible at coronoid (L)		10.2	6.4	10.0	6.1	9.4	6.3	9.3	7.0	7.7	6.3	10.7	6.5	11.5	6.8	11.7	7.5	6.6±0.46
Breadth of mandible at coronoid (R)		11.0	6.9	9.9	6.1	9.3	6.2	9.1	6.8	8.0	6.5	10.7	6.5	11.3	6.7	11.2	7.2	6.6±0.36

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GENETIC MATCHES OF SOUTHERN RIGHT WHALES IN THE INDIAN SECTOR OF THE ANTARCTIC: A CONTRIBUTION TOWARDS UNDERSTANDING THEIR MOVEMENT AND SITE-FIDELITY

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Abstract

Genetic analyses were conducted to investigate the individual identification (and matching) of southern right whales (*Eubalaena australis*) from samples collected in the austral summer in the Indian Ocean sector of the Antarctic (between 80°–135°E, south of 60°S). The study was conducted to evaluate the utility of this approach for studies on site fidelity and range. In total, 157 skin biopsy samples were collected from free-ranging whales during fourteen summer surveys. The DNA was extracted from each biopsy sample, genotyped at fourteen microsatellite loci, sequenced for 381 nucleotides of the mtDNA control region, and the sex determined by the presence of a Y-chromosome specific locus. Eight matches were detected (four males and four females) using individual matching by multi-locus genotypes supported by mtDNA haplotype and sex determination. Where photographs were available, two matches were confirmed by photo-identification. These eight re-samples show that at least some males and females returned to the same feeding grounds across years. The average longitudinal dispersal ranges, latitudinal dispersal ranges and average direct distances between marks and recaptures were: 13°06′ and 7°15′; 1°23′ and 0°47′; and 361 n.miles and 199 n.miles for males and females, respectively. The time spans ranged from 3–13 years with an average of 6.7 and 7.8 years for males and females, respectively. Sampling and matching occurred in an area where visual surveys showed aggregations of southern right whales associated with high krill concentration. The study confirms the feasibility of the genetic approach, but more definitive inferences on site fidelity and movement ranges will require a large number of biopsy samples genotyped, from both south and north of 60°S.

Key words: southern right whales, Antarctic, genetic tagging, site fidelity, movement, distribution.

Introduction

Baleen whales are important components of the Antarctic marine ecosystem as top predators. Substantial changes in their abundance and distribution, for example due to past whaling or more recently climate change, affects the entire ecosystem. For this reason, systematic monitoring of baleen whale abundance, pattern of movement and distribution in Antarctic waters is important.

A substantial amount of biological and ecological information on large whales and their environment was obtained in the Indo-Pacific sector of the Antarctic (35°E–145°W) by the 'Japanese Whale

Research Program under Special Permit in the Antarctic' Phases I and II (JARPA, JARPAII) and the subsequent 'New Whale Research Program in the Antarctic' (NEWREP-A). These were conducted annually under the auspices of the Government of Japan between the 1987/88 and 2018/19 austral summer seasons under Article VIII of the International Convention for the Regulation of Whaling (ICRW). Most of the demographic and ecological analyses conducted under these research programs targeted the Antarctic minke whale (*Balaenoptera bonaerensis*) and other Balaenopterid species (see summaries of results in Murase *et al.* (2020) and Fujise and Pastene (2021)). In the context of this paper, southern right whale (*Eubalaena australis*) sightings were recorded and where possible, photo-identification and genetic samples were collected.

A further important source of information from Antarctic waters is the sightings, photo-identification and biopsy data collected at the circumpolar level by the International Whaling Commission-International Decade for Cetacean Research/Southern Ocean Whale and Ecosystem Research (hereafter IWC-IDCR/SOWER) surveys conducted between the 1978/79 and 2009/10 austral summer seasons. Photo-identification data and biopsy samples of species including southern right whales were collected opportunistically during the IDCR/SOWER.

This study focuses on the southern right whales. The species has a circumpolar distribution. They spend the austral winter in inshore waters of South America, South Africa and Australasia; in spring whales move south to spend the austral summer feeding in waters around Antarctic before returning north in the autumn (Reeves *et al.*, 2002). They can reach a maximum body length of 17 m and the body length at birth is 4–4.6 m. They are believed to live more than 70 years and calves are produced every 3–5 years (Reeves *et al.*, 2002). The primary breeding grounds are located at South Africa, South West Australia, Argentina, and New Zealand Sub-Antarctic (IWC, 2001; 2013; Carroll *et al.*, 2016). Research effort to investigate stock structure, distribution and abundance trend has focused mainly on the breeding grounds, and limited information exists on the distribution, site fidelity and movements in the feeding grounds, and on the connection between breeding grounds in low latitude waters and higher latitude feeding grounds.

Migration patterns, movements and feeding ground destinations have been studied using direct approaches including photo-identification and more recently, telemetry as well as indirect approaches such as visual surveys and historic whaling records. Telemetry has been used to investigate movement patterns of South African right whales (Mate *et al.*, 2011) and western South Atlantic right whales (Zerbini *et al.*, 2016; 2018). The telemetry and photo-identification (e.g., Best *et al.*, 1993) studies in the Argentina and South African breeding grounds show that southern right whales are found throughout large areas of the South Atlantic Ocean and visit several potential feeding areas each season.

The focus of the present paper is the Indian Ocean sector of the Antarctic, between 80°–135°E, south of 60°S. Previous studies have shown that animals from that sector are associated with breeding grounds in the Australasian region (e.g., IWC, 2001; 2013). For example, Bannister (2001) reviewed the distribution and movement of 'Australian' southern right whales based on historical whaling data, recent sighting surveys, 1960s Soviet catch data and photo-identification data. The review confirmed the traditional view of seasonal movements to and from coastal breeding grounds in warm waters and feeding grounds in colder waters. In terms of direct evidence, he presented two photo-identification matches, the first made between whales identified of either Western Australia or South Australia in winter/spring and waters around 40°–44°S; 116°–125°E where a sighting of 35 animals had been made in December–January 1995–96 (Bannister *et al.*, 1997). The other evidence was a southern right whale photographed at 64°26′S; 114°54′E in February 1996, which had been identified over a period of 18 years on the coast of Western Australia (Bannister *et al.*, 1999). These data suggest that at least some of the summer feeding aggregation of southern right whales in the Antarctic Indian Ocean sector belong to the South West Australian population.

Most recently, Mackay *et al.* (2020) presented telemetry information of six animals tagged in Australasian wintering grounds. They suggested at least three probable foraging grounds: to the southwest of Western Australia, the Subtropical Front and Antarctic waters—the Subtropical Front appearing to be a feeding ground for animals from both New Zealand and Australian waters. They also suggested that the observed variable population growth rates between wintering grounds in Australasia might reflect fidelity to different quality feeding grounds. Thus, similar to results from the South African and Argentina breeding grounds, Australasian animals appear to visit multiple potential feeding areas each season.

A high concentration of sightings of southern right whales was observed in the Indian sector (80°–135°E) of the Antarctic Ocean during various austral summer season cruises of JARPA and JARPAII (Matsuoka and Hakamada, 2020) and the IWC-IDCR/SOWER cruises. Biopsy samples collected opportunistically during the IDCR/SOWER and JARPA/JARPAII surveys in that sector were used in the present study on genetic matching based on microsatellite DNA (msDNA). The main objective of the individual identification based on genetic matching was to evaluate the utility of this approach to study site fidelity and ranges in this species. The use of genetic markers (‘tags’) has long been shown to represent a viable alternative/supplement to photographic methods of individual recognition—such markers are permanent in all individuals (Palsbøll *et al.*, 1997a).

Materials and methods

Samples

A total of 157 skin/blubber biopsy samples were obtained opportunistically from free-ranging southern right whales along the sighting surveys of JARPA/JARPAII (n=108) and IWC-IDCR/SOWER (n=49) in the Antarctic Indian sector (80°–135°E), south of 60°S from the 1993/94 to 2015/16 austral summer seasons. A variety of collection systems was used including crossbows, air guns and modified shot guns, all using modified collection darts that took a small sample of skin and blubber. The geographical distribution of the southern right whales sampled is shown in Fig. 1.

DNA extraction

Genomic DNA was extracted from approximately 0.05g of the outer epidermal layer of the skin tissue using standard phenol/chloroform protocols (Sambrook *et al.*, 1989) or using Gentra Puregene kits (QIAGEN). Extracted DNA was stored in TE buffer (10mM Tris-HCl, 1mM EDTA, pH 8.0).

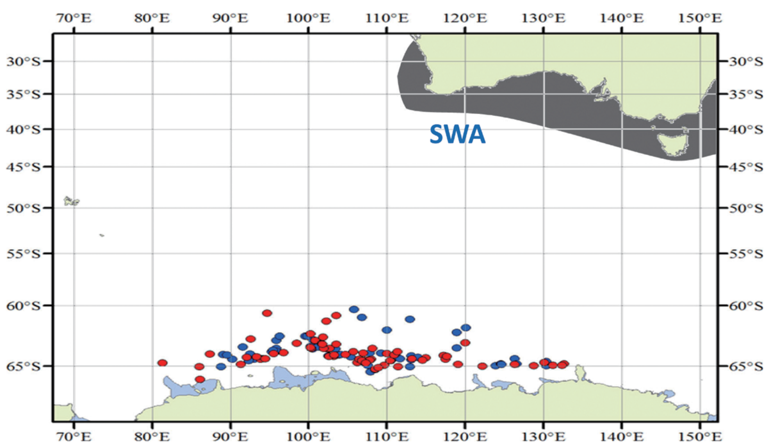

Fig. 1. Geographical distribution of southern right whales in the Indian Ocean sector of the Antarctic examined in this study. Red: females; Blue: males. SWA: South West Australia. Light blue shading shows the ice configuration.

Laboratory procedure for msDNA

Genetic variation was examined at 14 msDNA loci: EV1, EV14, EV21, EV37, EV94 (Valsecchi and Amos, 1996), GT23, GT211, GT310 (Bérubé *et al.*, 2000), GATA28 (Palsbøll *et al.*, 1997b), Dl-rFCB17 (Buchanan *et al.*, 1996), TR3G2, TR2G5, TR2F3 and TR3F2 (Frasier *et al.*, 2006). Details of the laboratory work for msDNA are provided in Pastene and Goto (2016).

Laboratory procedure for mtDNA

Mitochondrial DNA (mtDNA) control region sequences were used as one way to confirm individual identification by nuclear markers. Samples sharing a same genotype should also share a same haplotype.

The first 470 base pairs (bp) at the 5′ end of the mtDNA control region were amplified by polymerase chain reaction (PCR). Details of the laboratory work for mtDNA sequencing are provided in Pastene and Goto (2016).

Laboratory procedure for sex determination

Sex determination is important both to examine potential sex-specific patterns of movement as well as an additional way to confirm individual msDNA matching. Samples sharing the same genotype should be of the same sex. The SRY locus located on the Y chromosome was used for sex determination following the method of Abe *et al.* (2001) with a slight modification (see Milmann *et al.*, 2021).

Analytical procedure

MtDNA

Variable sites and unique sequences (haplotypes) were identified using the program MacClade (Maddison and Maddison, 1989).

MsDNA

The computer program MICRO-CHECKER (van Oosterhout *et al.*, 2004) was used to check for null alleles and reading/typing errors. The probability that two unrelated individuals have identical genotype (i.e., an identical genetic 'tag') is negatively correlated with the number of loci analysed and the degree of variation at each locus (Palsbøll, 1999). For this reason, it is important the estimations of the nuclear DNA diversity of southern right whales at each msDNA locus, as well the probability of identity (I). The latter is the probability that two unrelated individuals from the same panmictic population have an identical composite genotype (see Paetkau and Strobeck, 1994). The I was estimated per locus and across loci. The number of alleles per locus, inbreeding coefficient (F_{IS}) and expected heterozygosity (H_E) per locus was calculated using FSTAT 2.9.3 (Goudet, 1995). Statistical tests for the deviations from expected Hardy–Weinberg genotypic proportions were conducted using GENEPOP 4.0 (Rousset, 2008), both by each locus and for all loci combined. Individuals with identical multi-locus genotypes sampled during the same sighting (duplicates) were investigated, and one from each duplicate was removed for subsequent analyses.

Results

Final dataset

There were four cases of biopsies with identical multi-locus genotypes sampled during the same sighting (duplicates). There were two cases of mother-offspring pairs, which were deduced from observations at the field and from genetic data. After removing four duplicates, the sample sizes for the msDNA analyses on individual identification was 153 (76 males and 77 females).

Level of msDNA diversity and probability of identity

No evidence of null alleles and typing/reading errors was found. Table 1 shows the estimated msDNA diversity indices. The number of alleles per locus ranged from 2 to 14 (average 7.5), and the H_E ranged from 0.07 to 0.89 (average 0.65). The F_{IS} in each locus ranged from −0.035 to 0.162 (average 0.007). There was no significant deviation from the Hardy–Weinberg genotypic proportion. *I* for each locus ranged from 0.022 at DlrFCB17 to 0.861 at EV21, which was estimated to be 1.95×10^{-10} when all loci were combined.

Genetic matching

As shown in Table 2, eight matches were detected (four males and four females). The multi-locus genotype matches were supported by mtDNA (same haplotype), sex determination (same sex), and, in the two cases where pictures were available, by photo-identification matches (Fig. 2).

Site-fidelity and movement range

Figs. 3A–B show the geographical distribution of the matches of female and male southern right whales, respectively. Table 2 summarises the matches and associated data. The elapsed time between sample and re-sample ranged between 3 and 13 years (average 7.25 years). In the case of females, the range was 3–11 years (average 7.75 years) and, in the case of males 4–13 years (average 6.75 years). The average longitudinal dispersal ranges were 13°06′ and 7°15′ in males and females, respectively. The average latitudinal dispersal ranges were 1°23′ and 0°47′ in males and females, respectively (Table 2). The average direct distances between sample and re-sample positions were 361 n.miles and 199 n.miles for males and females, respectively (Table 2). A statistical test showed no significant differences between females and males in the direct distances between samples and re-samples ($W=14$, Mann-Whitney, $p=0.114$).

Table 1. Indices of microsatellite DNA diversity in southern right whales from the Indian sector of the Antarctic: A: number of alleles; H_E: expected heterozygosity; HW: *P*-value for the test of Hardy-Weinberg equilibrium; F_{IS}: inbreeding coefficient; and *I*: probability of identity.

Microsatellite loci	A	H_E	HW	F_{IS}	*I*
EV1	14	0.87	0.25	0.010	0.025
GT310	6	0.62	0.05	0.057	0.205
GT23	8	0.81	0.96	0.024	0.059
EV94	5	0.41	0.78	−0.021	0.401
EV14	10	0.76	0.14	0.006	0.076
GT211	10	0.82	0.08	0.077	0.055
EV37	11	0.82	0.95	−0.017	0.046
GATA28	10	0.77	0.28	0.006	0.090
EV21	3	0.07	0.10	0.162	0.861
DlrFCB17	13	0.89	0.54	−0.019	0.022
TR2F3	2	0.49	0.62	0.044	0.379
TR3G2	8	0.77	0.52	−0.035	0.093
TR2G5	2	0.50	0.14	−0.123	0.376
TR3F2	3	0.48	0.68	0.055	0.361
Overall		0.65	0.21	0.007	1.95e-10

Table 2. Cases of sample/re-sample in southern right whales from the Indian sector of the Antarctic determined by microsatellite DNA genotyping. All genotype matches were supported by the mtDNA analysis (same haplotypes) and by the results of sex determination (same sex). Cases 2 and 3 (the only ones for which photographs were available) were confirmed by photo-identification, SR: sample/resample; ID: label of the whale; S: sex; BL: body length determined visually by researchers from the vessels (in meters); ET: elapsed time (year) between samples and re-samples; DD: direct distance between the positions of samples and re-samples (in n. miles); LAR: latitudinal dispersal range between samples and re-samples; LOR: longitudinal dispersal range between samples and re-samples.

	SR	ID	S	BL	Date (D/M/Y)	Position		ET	DD	LAR	LOR
1	Sample	93IVR004	M	14.3	05/03/1994	64°14′S	113°04′E	5	377	1°34′	13°34′
	Re-sample	98SWR046	M	14.3	31/01/1999	62°40′	99°30′				
2	Sample	97IVR007	M	11.9	15/01/1998	62°55′	100°28′	4	241	1°41′	8°13′
	Re-sample	01IVR023	M	12.9	15/02/2002	64°36′	92°15′				
3	Sample	99IVR012	F	16.4	10/02/2000	64°35′	114°31′	8	303	0°19′	11°46′
	Re-sample	07IVR56	F	15.3	01/03/2008	64°54′	126°17′				
4	Sample	98SWR140	F	13.4	05/02/1999	63°19′	103°28′	3	265	1°11′	9°38′
	Re-sample	01IVR018	F	13.3	14/02/2002	64°30′	93°50′				
5	Sample	01IVR024	M	13.2	15/02/2002	64°36′	92°15′	13	490	0°31′	18°47′
	Re-sample	14AJ4R036	M	13.7	28/02/2015	64°05′	111°02′				
6	Sample	98SWR137	F	13.1	02/02/1999	63°00′	100°50′	9	157	1°03′	5°21′
	Re-sample	07IVR49	F	12.8	22/02/2008	64°03′	95°29′				
7	Sample	98SWR141	F	12.8	07/02/1999	63°55′	105°42′	11	69	0°36′	2°16′
	Re-sample	09SWR011	F	13.2	29/01/2010	64°31′	107°58′				
8	Sample	09SWR008	M	13.2	24/01/2010	64°27′	111°38′	5	335	1°47′	11°51′
	Re-sample	14AJ4R004	M	12.7	22/02/2015	62°40′	99°47′				

Discussion

Previously Carrol *et al.* (2016) carried out successfully a genetic matching study in southern right whales of the New Zealand nursery ground. The study presented here is the first of such kind in southern right whales of the Indian sector of the Antarctic. Results of the Hardy–Weinberg equilibrium test suggest that whales in this sector belong to the single putative 'South Western Australia' population earlier identified by the IWC Scientific Committee (IWC, 2001; 2013) based upon *inter alia* results of photo-identification matches (Bannister *et al.*, 1999; Bannister, 2001). Individual identification by genetic matching has the potential to contribute to studies on movement and site fidelity in this population. Here, some relevant aspects of this approach and its utility for southern right whales are discussed.

Utility of genetic matching for individual identification of southern right whales

The number (n=14) of msDNA loci used in the present study and the degree of polymorphism (see Table 1) proved to be appropriate for the purpose of individual identification in southern right whales. There was a very low estimated probability of identity i.e., two unrelated individuals having an identical composite genotype. The eight cases of genotyping matching were supported by the mtDNA analyses (same haplotype) and sex determination (same sex). In addition, for the two cases where photographs were available, genotyping matching was supported by photo-identification. The authors conclude that the eight cases of genotyping matching corresponded to matching of the same individual whales and thus confirms the utility of genetic matching to identify individuals (see also Carrol *et al.*, 2016).

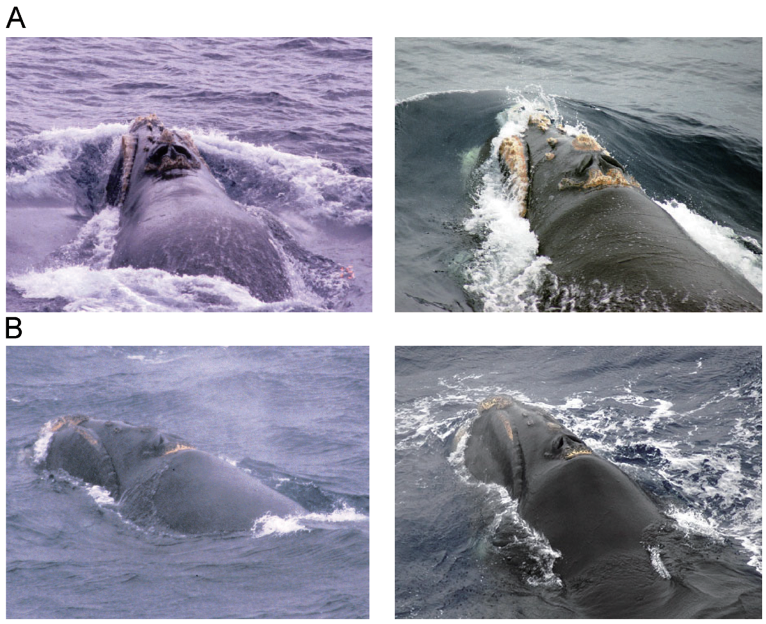

Fig. 2 **A**: A southern right whale sighted in the Indian sector of the Antarctic on 15 January 1998 (left) and re-sighted in the same sector on 15 February 2002 (right) (Matching No. 2 in Table 2). **B**: A southern right whale sighted in the Indian sector of the Antarctic on 10 February 2000 (left) and re-sighted in the same sector on 1 March 2008 (right) (Matching No. 3 in Table 2).

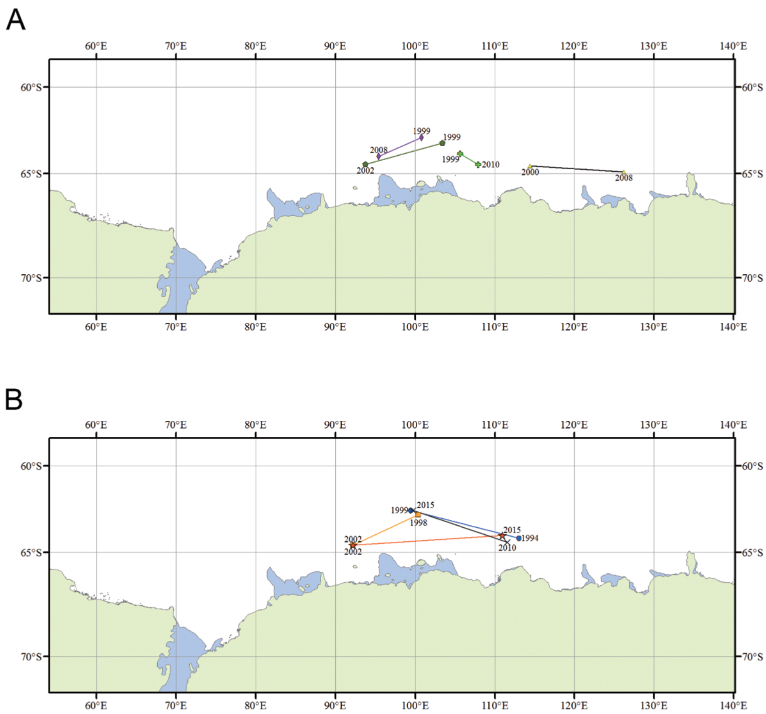

Fig. 3. Maps showing sample/re-sample positions referred to in the text. **A**: females–note that match 2002–2008 was also confirmed by photographs. **B**: males–note that match 1998–2002 was also confirmed by photographs. Light blue shading shows the ice configuration.

Utility for studies on site fidelity and movement ranges of southern right whales

The eight matches here show that at least some females and males visit the same feeding ground in the Indian sector of the Antarctic south of 60°S in summer. The total samples and the matches both were close to 1 : 1 males and females. Although the direct distances between sample and re-sample by sex were statistically non-significant, this probably relates to the small sample size. Qualitatively (Table 2 and Fig. 3), the results are not in conflict with the findings of Carroll *et al.* (2011) that males are more mobile than females.

As explained earlier, telemetry data from southern right whales tagged in breeding grounds in Australasia (Mackay *et al.*, 2020), South Africa (Mate *et al.*, 2011) and Argentina (Zerbini *et al.*, 2016; 2018) suggested that individuals may visit several feeding grounds within the same season e.g., in middle latitudes and high latitudes, and this aspect of southern right whale's ecology should be considered when discussing site fidelity. The abundance of southern right whales in the Indian sector of the Antarctic was estimated as 910 in 1988/89 from sightings data (95% CI: 409–2,026) (Matsuoka and Hakamada, *in press*) and the number of individuals identified in this study was 145 (153 minus eight individuals re-sampled). This corresponds to about 16% (range between about 1–36% of the estimated total population). The low number of matches limits the applicability of inferences on relative site fidelity and the pattern of longitudinal dispersal to the total population. The comparison above should be seen with caution. The 1988/89 estimate has wide confidence intervals and the biopsy sampling is pretty wide and carried out after the abundance estimates.

Whilst the present study confirms the feasibility of the approach, it is clear that more definitive inferences on site fidelity and movement ranges will require a larger number of biopsy samples, from both south and north of 60°S (all the samples in this study were obtained south of this latitude).

Food availability in the area of genetic matching

Recognizing the limited number (and sampling distribution) of samples, the present results allow the formulation of the following ecological inferences for further investigation. The Indian Ocean sector of Antarctic waters south of 60°S represents one of the several possible feeding grounds for the South West Australia population (e.g., see Mackay *et al.*, 2020). Our results show that at least some southern right whales of both sexes return to the same sector at some point in their lives, presumably for feeding. Matches were found in a broad area that has shown consistent annual aggregations of southern right whales (e.g., Matsuoka and Hakamada, 2020) and that were seen in areas of high krill concentrations (e.g., Murase *et al*, 2002; Matsuoka *et al.*, 2003; Nicol, 2006).

Qualitative analyses of food consumption of southern right whales in the Antarctic Indian sector could be investigated by stable isotope analyses of the same biopsy samples used in the present study. Information on prey species consumed by southern right whales will assist in confirming the ecological inference aforementioned.

Finally, genotyping data in this study can be used for other purposes, for example to estimate abundance and other demographic parameters (e.g., survival rates) of this species within a mark-recapture context (e.g., Wade *et al.*, 2010).

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EVALUATION OF A PATERNITY METHOD BASED ON MICROSATELLITE DNA GENOTYPES FOR ESTIMATING THE ABUNDANCE OF ANTARCTIC MINKE WHALES (*BALAENOPTERA BONAERENSIS*) IN THE INDO-PACIFIC REGION OF THE ANTARCTIC

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Abstract

This study describes a paternity method based on microsatellite DNA genotypes to estimate the abundance of mature male Antarctic minke whales (*Balaenoptera bonaerensis*) in the Indo-Pacific region of the Antarctic using a maximum likelihood approach. The analyses were based on biological and genetic (microsatellite DNA at 12 loci) data from Antarctic minke whales collected by surveys of the Japanese Whale Research Program under Special Permit in the Antarctic-Phase II (JARPAII) in the Indo-Pacific region of the Antarctic. A total of 2,126 Antarctic minke whales taken in the austral summer seasons 2006/07, 2008/09, 2009/10, 2010/11 and 2011/12 from locations 35°E to 145°W were used in the analyses. The abundance of mature males estimated by this method was then extrapolated to estimate total abundance for comparison with results for abundance obtained using conventional line transect methods in the research area. The total abundance derived from the paternity method (ca. 210,000–220,000) was generally lower than that obtained by the line-transect method (ca. 260,000–410,000), although the figure from the line-transect method was within the 90% confidence interval of the estimates by the paternity method, and the area covered by both methods was slightly different. Additionally, the geographical locations of mother/fetus–father pairs provided the opportunity to evaluate the current hypothesis on population structure of this species in the Indo-Pacific region. Results for the geographical distribution of mother/fetus–father pairs were generally consistent with the hypothesis of separate Eastern Indian Ocean and Western South Pacific Ocean populations, because 8 of 10 pairs were found in the expected areas of distribution of either populations. However, two pairs were found in distant areas. As a whole, the results from the present study demonstrated the utility of the paternity method for estimating the abundance of Antarctic minke whales and for assisting the interpretation of population structure hypotheses.

Key words: Antarctic minke whale, paternity analysis, population structure, microsatellite DNA.

Introduction

Population abundance and trajectories provide key information required for effective conservation and management of wildlife. In the case of whaling, the International Whaling Commission (IWC) developed and adopted the Revised Management Procedure (RMP), a single-species management procedure[1] for calculating commercial catch limits for whaling of baleen whales (Anon, 1994; Punt and Donovan, 2007). The RMP consists of a series of rules to manage whaling (including multi-stock scenarios), based largely upon catches determined by a simple generic *Catch Limit Algorithm* (*CLA*), that requires two kinds of information: a time series of abundance estimates and catch-history data. The key to the approach is that the *CLA* was rigorously tested by simulation to ensure that it is robust to inevitable scientific uncertainty, while the implementation of the RMP in specific multi-stock situations is also tested by simulation to ensure robustness to evaluate uncertainty in key parameters (known as *Implementation Simulation Trials*, *ISTs*). The catch limits set by the *CLA* take into account the uncertainty in the abundance estimates and thus it is important to obtain abundance estimates with good precision. Abundance information about whales is also required for the development of ecosystem models and multi-species management procedures.

In recent decades, visual surveys using 'Distance sampling' approaches (e.g., Buckland *et al.*, 2001) have been the most common method for estimating the abundance of cetacean species. Amongst other assumptions, this approach depends upon an assumption that all animals on the trackline are seen (or can be corrected for the actual detection probability on the trackline—the so-called g(0) value). It is also assumed that, for estimating trends in a population (rather than trends within a geographical area), the full population is surveyed each time (difficult for wide-ranging species such as cetaceans). A good example of the complexity in the use of the line-transect method was the assessment of Antarctic minke whales by the IWC Scientific Committee (SC), based on three Antarctic circumpolar surveys conducted under the International Decade of Cetacean Research and Southern Ocean Whale and Ecosystem Research (IDCR/SOWER) programs. Obtaining robust abundance estimates from these surveys and then interpreting the results triggered a decade-long discussion in the IWC SC about the method of estimating g(0) and possible distributional shifts of whales over time e.g. to unsurveyed areas beyond the ice-edge of the survey region that prevents vessels entering (IWC, 2013).

Mark–recapture methods based on internal marks (Discovery type, e.g., see Buckland and Duff, 1989) or individual identification by photographic matching (e.g., Hammond *et al.*, 1990) can be used to estimate some marine mammal population sizes (Sobtzick, 2010). However, in the case of Antarctic minke whales the former method is not possible because there are no current catches of this species. Obtaining sufficient photographs for photographic identification and then matching them is considerably more difficult for Antarctic minke whales than say, humpback, right and blue whales.

Given the limitations mentioned above, alternative methods are being investigated for estimating the abundance of whales. Mark–recapture approaches based on genetic individual identification from biopsy samples have been used to estimate population abundance and to examine the migration patterns of whales (e.g., Palsbøll, 1999). Whilst valuable for smaller populations, the logistics of obtaining a sufficiently large sample size make it often impractical for large populations.

The most promising recent technique involves paternity testing. For paternity analyses, DNA profiles of mother/fetus, usually from a set of microsatellite loci, are used to look for potential fathers of the fetuses within the sample population. If their fathers are found, the number of matches can be used in traditional mark–recapture analyses (e.g., see Skaug and Øien, 2004). Paternity analysis and close-kin mark–recapture methods based on genetic data have been used to estimate the abundance of North Atlantic humpback whales (Palsbøll *et al.*, 1997; Nielsen *et al.*, 2001).

This study describes a paternity method based on microsatellite DNA genotypes to estimate the abun-

[1] Sometimes in fisheries the term 'management strategy' is used.

dance of mature male Antarctic minke whales in the Indo-Pacific region of the Antarctic using a maximum likelihood approach. Mature male abundance is extrapolated to total abundance and the estimates compared with those obtained from conventional line-transect methods in the same research area. The paper also identifies additional research required to improve the precision of the paternity method for abundance estimate purposes. Finally, the geographical locations of mother/fetus–father pairs are used to evaluate the current hypothesis on population structure of this species in the Indo-Pacific region of the Antarctic.

Materials and methods

Samples

Samples from a total of 2,126 Antarctic minke whales were available from the surveys of the Japanese Whale Research Program under Special Permit in the Antarctic-Phase II (JARPAII) in the austral summer seasons 2006/07, 2008/09, 2009/10, 2010/11 and 2011/12. The surveys were conducted in the Indo-Pacific region of the Antarctic, in the IWC Management Areas (see Donovan, 1991) IIIE (35°–70°E), IV (70°–130°E), V (130°E–170°W) and VIW (170°–145°W) (Fig. 1). For each sampled whale, the following information was available: sample ID, sampling date, sampling location (latitude and longitude), sex and maturity, occurrence of fetus, age and the quality of the age estimation.

The details of the samples used in the analyses are presented in Table 1.

Microsatellite DNA

Each sample (including fetuses) was genotyped using 12 microsatellite DNA loci: EV1, EV104, GT211, DlrFB14, GT195, GT23, AC045, AC082, AC087, AC137, CA234 and GT129. The details of the laboratory work for DNA extraction and microsatellite DNA genotyping were reported by Pastene and Goto (2016). Loci CA234 and GT129 were excluded from the present analyses because of the existence of null alleles and genotyping errors. Individuals with missing allele data on some loci (576 animals) and some mother/fetus pairs that had mismatching alleles (37 animals) were also excluded from the statistical analysis.

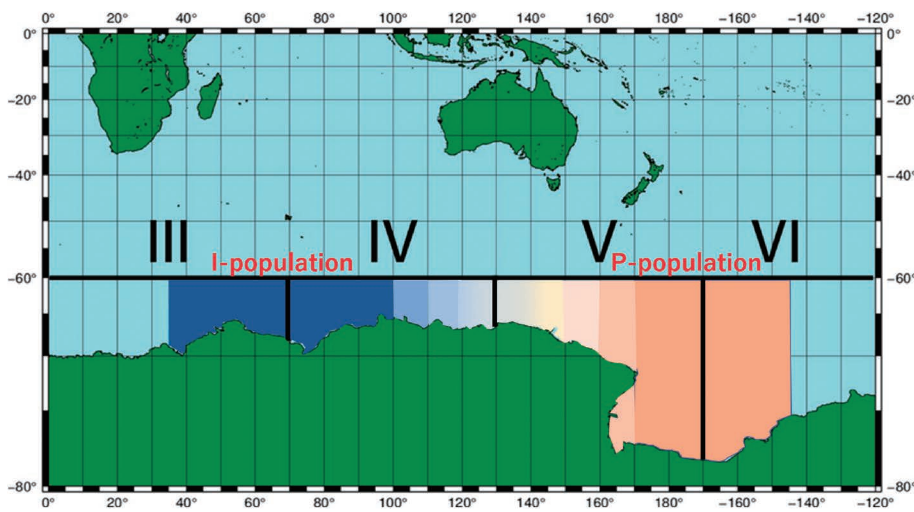

Fig. 1. IWC management Areas IIIE, IV, V and VIW where the study was conducted. The figure also shows a schematic representation of the hypothesis of population structure of Antarctic minke whale in the Indo-Pacific region of the Antarctic. At least two populations occur in this region, the Eastern Indian Ocean Population (I) and the Western South Pacific Ocean Population (P), which overlap in a transition area.

Table 1. Number of sampled individuals used in the analysis. Individuals which had missing data for one or more loci were excluded from the analysis.

		Area	2006/07	2008/09	2009/10	2010/11	2011/12
Female	With fetus (Mother/fetus pair)	IIIE–VW	0	0	156	0	12
		VE–VIW	242	43	0	78	79
	Immature or mature but without fetus	IIIE–VW	0	3	71	0	38
		VE–VIW	106	63	0	30	38
Male	Mature male	IIIE–VW	133[1]				
		VE–VIW	265[1]				
		IIIE–VW		150[2]			
		VE–VIW		145[2]			
		IIIE–VW			151[3]		
		VE–VIW			79[3]		
		IIIE–VW				33[4]	
		VE–VIW				83[4]	
		IIIE–VW	0	5	120	0	36
		VE–VIW	128	71	0	46	37
	Immature male	IIIE–VW	0	5	46	0	13
		VE–VIW	24	31	0	16	13

[1] The total number of mature males aged ≥6 years in 2006/07; [2] The total number of mature males aged ≥6 years in 2008/09; [3] The total number of mature males aged ≥6 years in 2009/10; [4] The total number of mature males aged ≥6 years in 2010/11.

Assumptions on population structure

Abundance estimates developed using the paternity method are presented here under two assumptions: (i) no population structure; and (ii) population structure based on the hypothesis proposed by Pastene and Goto (2016). Regarding (ii), the IWC SC (IWC, 2008) has agreed that there are at least two genetically distinct populations in this region, one in the east (Pacific or P-population) and the other in the west (Indian or I-population) with a 'soft' boundary between these populations in Areas IVE and VW, which changed by year and sex. For practical purposes, the present study assumes that the I-population is distributed from Area IIIE to Area VW, and the P-population from Area VE to Area VIW. Fig. 1 shows a schematic representation of the population structure of Antarctic minke whales in the Indo-Pacific region, and its relation with IWC Management Areas.

Identification of father from mother/fetus genotype profiles

The first step in the process of using the paternity method to estimate abundance is to examine the microsatellite DNA profiles of the mother/fetus pairs to look for potential fathers within the total sample. The probability of the fetus's genotype at each locus, given the mother's and potential father's genotype, was calculated following Marshall *et al.* (1998). Table 2 shows the conditional probabilities for all compatible mother/fetus–potential father pairs. The possibility of a male being the true father is rejected when the probability of the fetus's genotype is 0. In this study, 10 loci were used for the estimation, and the 10 probabilities for the fetus's genotype multiplied. When the results are greater than 0, the potential father is considered the true father.

To aid interpretation, the sexual maturity of the males was considered. Males aged six years old or older were defined as mature males (Tamura and Konishi, 2014; Murase *et al.*, 2020) and the sensitivity of the results to using definitions of seven and eight years old was also examined.

The geographical positions of mother/fetus and true father pairs were mapped using Generic Map-

Table 2. Conditional probabilities for all compatible mother/fetus–potential father pairs.

Fetus's genotype (g_o)	Potential father's genotype (g_p)	Mother's genotype (g_m)	$\Pr(g_o \mid g_m, g_p)$	$\Pr(g_o \mid g_m)$
BB	*BB*	*BB*	1	*b*
BB	*BX*	*BB*	1/2	*b*
BB	*BB*	*BX*	1/2	*b*/2
BB	*BX*	*BX*	1/4	*b*/2
BC	*BB*	*CC*	1	*b*
BC	*BX*	*CC*	1/2	*b*
BC	*BB*	*CY*	1/2	*b*/2
BC	*BX*	*CY*	1/4	*b*/2
BC	*BB*	*BC*	1/2	$(b+c)/2$
BC	*BY*	*BC*	1/4	$(b+c)/2$
BC	*BC*	*BC*	1/2	$(b+c)/2$

X represents any allele other than *B*; *Y* represents any allele that is neither *B* nor *C*. The frequencies of alleles *B* and *C* are denoted *b* and *c*. $\Pr(g_o \mid g_m, g_p)$ is the probability of the fetus's genotype given the mother's and alleged father's genotypes and $\Pr(g_o \mid g_m)$ is the probability of the fetus's genotype given the mother's genotype (Marshall *et al.*, 1998).

ping Tools (GMT[2]) (Fig. 2).

Likelihood function for estimating the number of mature males

The likelihood function for the abundance of mature males was obtained as described by Nielsen *et al.* (2001). Assuming $I_j\,(i)$ is the event that the *j*th potential father is the true father of the *i*th fetus, $I_0\,(i)$ is the event that the potential father is not in the samples, $\boldsymbol{M_i}$ is the *i*th maternal genotype, $\boldsymbol{O_i}$ is *i*th associated genotype of the fetus, $\boldsymbol{F_j}$ is the genotype of the *j*th potential father, $\boldsymbol{A}$ is the matrix of allelic frequencies for all loci, *N* is the abundance of mature males in the area and *n* is the number of sampled mature males, then the likelihood function for *N* is expressed as:

$$\begin{aligned} L(N) &\propto \prod_i \Pr(\boldsymbol{O_i} \mid \boldsymbol{M_i}, \boldsymbol{F}, \boldsymbol{A}, N) \\ &= \prod_i \left(\frac{(N-n)}{N} \Pr(\boldsymbol{O_i} \mid \boldsymbol{M_i}, \boldsymbol{A}) + \frac{1}{N} \sum_{j=1}^{n} \Pr(\boldsymbol{O_i} \mid \boldsymbol{M_i}, \boldsymbol{F_j}) \right) \\ &= \prod_i \left(\frac{(N-n)}{N} \Pr\big(\boldsymbol{O_i} \mid \boldsymbol{M_i}, \boldsymbol{A}, I_0(i)\big) + \frac{1}{N} \sum_{j=1}^{n} \Pr\big(\boldsymbol{O_i} \mid \boldsymbol{M_i}, \boldsymbol{F_j}, I_j(i), \boldsymbol{A}, N\big) \right) \text{ for } N > n. \quad (1) \end{aligned}$$

Here, $\Sigma_{j=1}^{n} \Pr(\boldsymbol{O_i} \mid \boldsymbol{M_i}, \boldsymbol{F_j})$ refers to the sum of the probabilities that the father of the *i*th fetus is the *j*th potential father when the *i*th maternal genotype and the *j*th potential father are given, and $\Pr(\boldsymbol{O_i} \mid \boldsymbol{M_i}, \boldsymbol{A})$ refers to the probability of the *i*th fetus's genotype given the *i*th mother's genotype. The point estimate of *N* was computed by maximizing the logarithm of $L(N)$, and the 90% confidence interval of *N* was calculated by the likelihood profile as $\{N;\ \log L(N) \geq \log L(\hat{N}) - 0.5\chi^2\ (0.10)\}$, where $\chi^2\ (0.10)$ is the 10th upper percentile of chi-square distribution with the degree of freedom 1.

To estimate the total abundance of Antarctic minke whales, the total was prorated based upon the proportions of males and females, and immature and mature whales, from the sampled data, under the assumption that the sample was representative of the true population (by assuming an equal selectivity from the population(s)). The proportion of male whales was 0.436 for the case of a single population, and 0.491 and 0.407 for I- and P-populations, respectively. Also, the proportion of immature whales

[2] https://www.generic-mapping-tools.org/

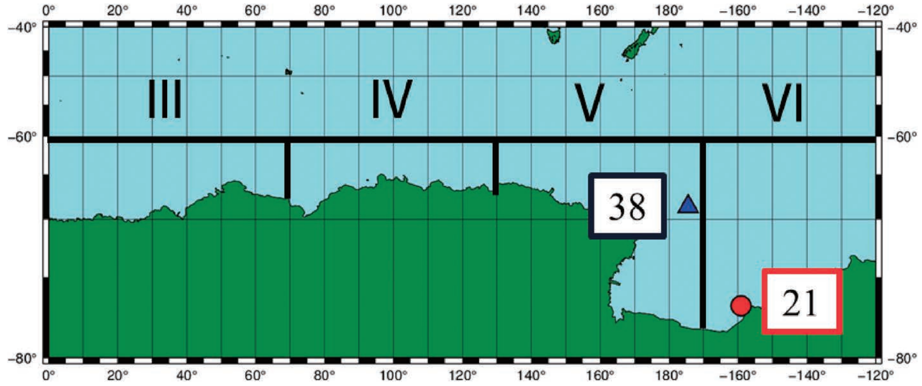

Fig. 2A. Positions of a mother-fetus pair and its true father. The circle indicates a female caught in 2006/07 and the triangle indicates a male caught in 2006/07. The red and blue boxed numbers are the ages of female and male, respectively.

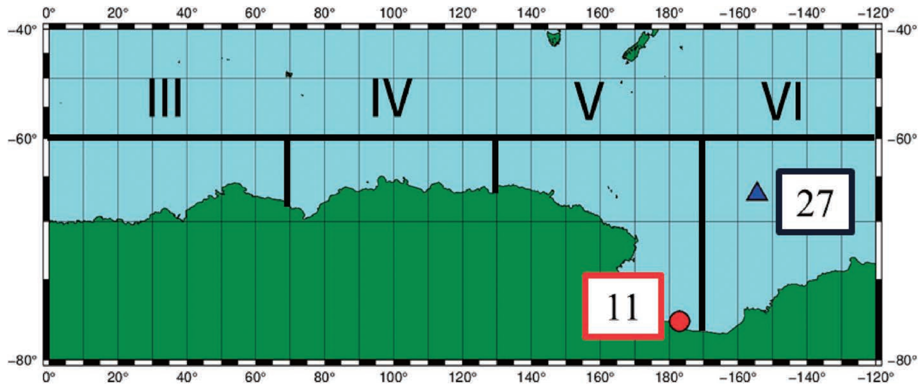

Fig. 2B. Positions of a mother-fetus pair and its true father. The circle indicates a female caught in 2006/07 and the triangle a male caught in 2008/09.

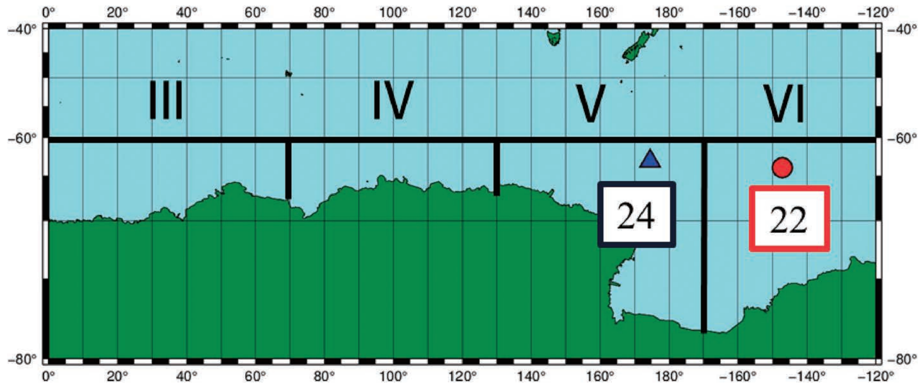

Fig. 2C. Positions of a mother-fetus pair and its true father. The circle indicates a female caught in 2006/07 and the triangle a male caught in 2010/11.

under the assumption of knife-edge maturity-at-age six years old was 0.254 for a single population, and 0.299 and 0.225 for I- and P-populations, respectively. For a sensitivity test, eight years old was used as the maturity age. In this case the immature proportion was 0.317 for a single population, and 0.366 and 0.286 for I- and P-populations, respectively.

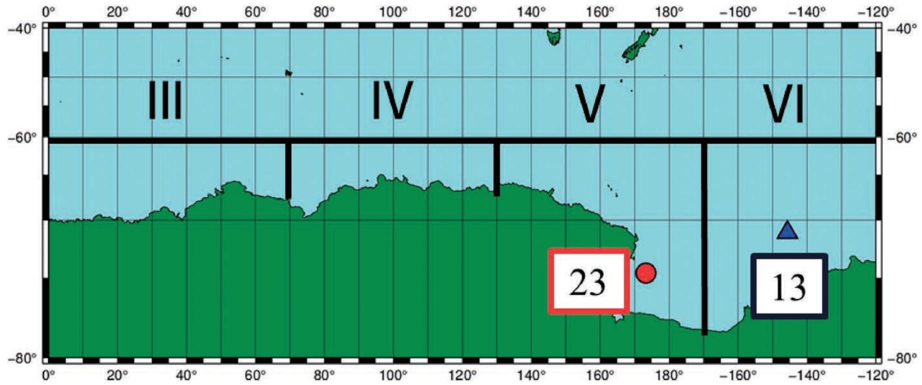

Fig. 2D. Positions of a mother-fetus pair and its true father. The circle indicates a female caught in 2006/07 and the triangle a male caught in 2011/12.

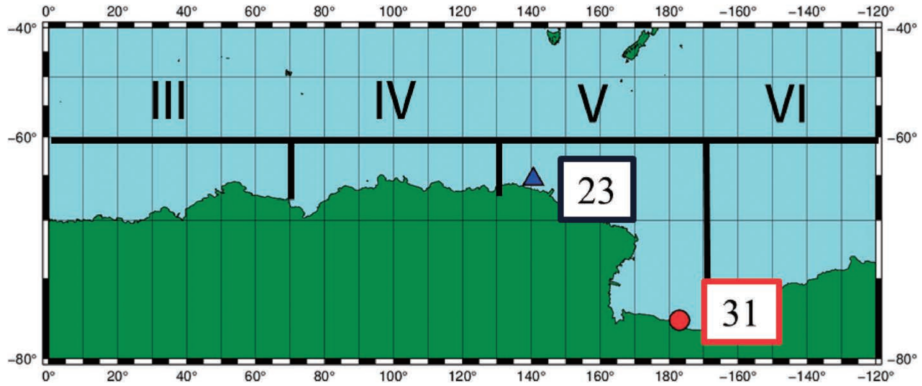

Fig. 2E. Positions of a mother-fetus pair and its true father. The circle indicates a female caught in 2006/07 and the triangle a male caught in 2011/12.

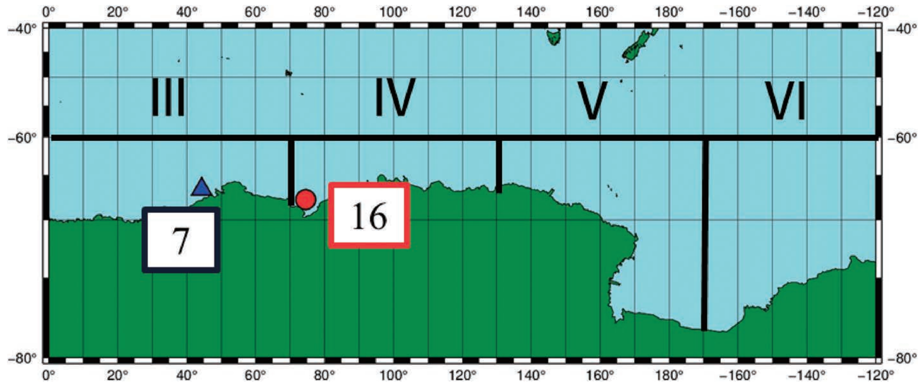

Fig. 2F. Positions of a mother-fetus pair and its true father. The circle indicates a female caught in 2009/10 and the triangle a male caught in 2009/10.

Results

Mother/fetus and mature male pairs

A total of 10 mother/fetus–father pairs were identified under the assumption of a maturity age of six years old. There were no cases of multiple fathers for one fetus. True fathers were found for five mothers/fetuses caught in 2006/07 and five mothers/fetuses caught in 2009/10.

The location of the matching pairs is shown in Figs. 2A–J. Eight pairs occurred in nearby geographical locations (Figs. 2A–H) while two pairs occurred in distant locations (Figs. 2I, J).

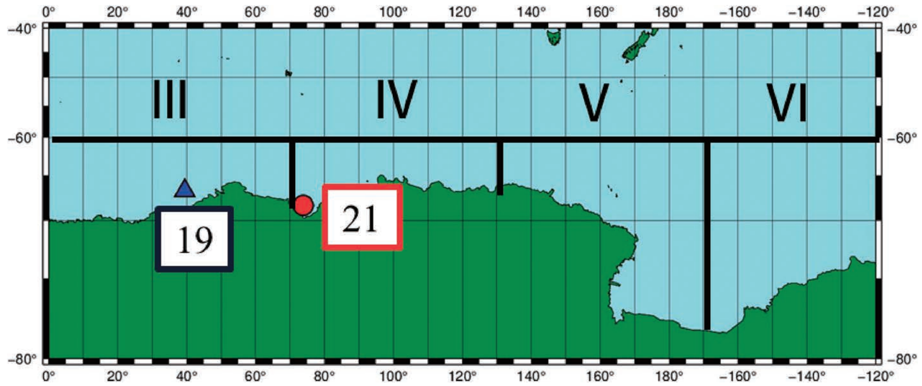

Fig. 2G. Positions of a mother-fetus pair and its true father. The circle indicates a female caught in 2009/10 and the triangle a male caught in 2009/10.

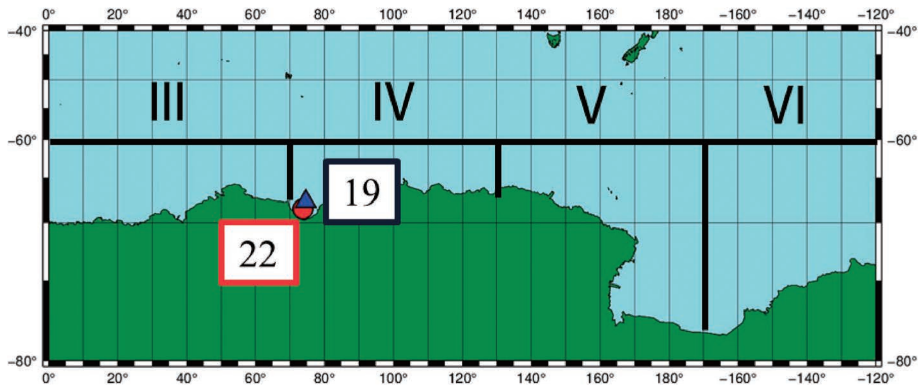

Fig. 2H. Positions of a mother-fetus pair and its true father. The circle indicates a female caught in 2009/10 and the triangle a male caught in 2009/10.

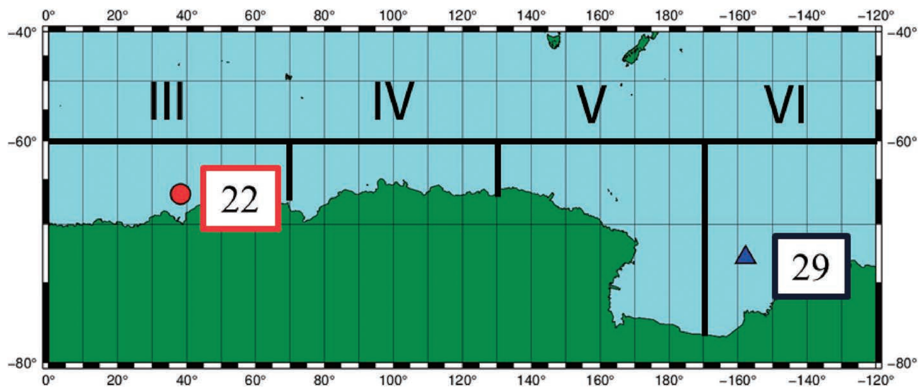

Fig. 2I. Positions of a mother-fetus pair and its true father. The circle indicates a female caught in 2009/10 and the triangle a male caught in 2011/12.

The abundance of mature males (population structure information not considered)

Combining data for all years, $\hat{N}_{\text{mature male}}$ was estimated to be 68,874 (90%CI=42,625–122,779). The likelihood profile is shown in Fig. 3. Using the ratios of males to females and immature to mature whales to estimate the total population, the total population size, $\hat{N}$, was estimated as 211,600 (90%CI=130,954–377,210).

The abundance of mature males (population structure information considered)

For the I-population and using data from the two relevant years (2009/10 and 2011/12), the estimat-

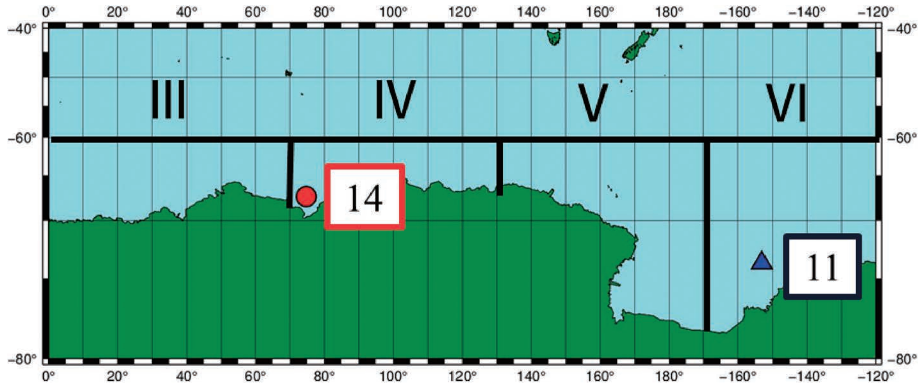

Fig. 2J. Positions of a mother-fetus pair and its true father. The circle indicates a female caught in 2009/10 and the triangle a male caught in 2011/12.

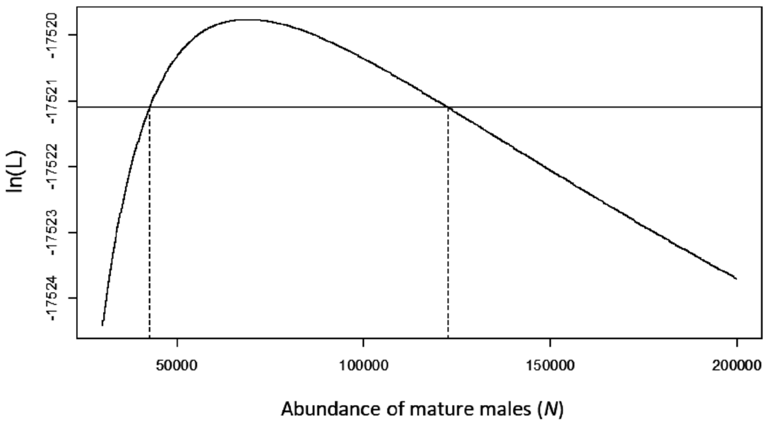

Fig. 3. The likelihood profile for $\hat{N}_{\text{mature male}}$ using 10 loci and five years of mother-fetus pairs and mature males for analysis without considering population structure (assumption of single population).

ed abundance of mature males $\hat{N}_{\text{mature male}}$ was 10,478 (90%CI=4,662–32,212), and the total population $\hat{N}$ was 30,432 (90%CI=13,540–93,556). The likelihood profile is shown in Fig. 4A.

For the P-population (2006/07, 2008/09, 2010/11 and 2011/12), the estimated abundance of mature males $\hat{N}_{\text{mature male}}$ was 59,961 (90%CI=28,853–161,155), and $\hat{N}$ was 189,946 (90%CI=91,401–510,506). The likelihood profile is shown in Fig. 4B.

There were 9 pairs when the age of sexual maturity in males was changed from six to eight years old. Therefore, six years old was used for the subsequent analysis of abundance. Comparison of abundance estimates are summarized in Table 3.

Discussion

The main objective of this study was to apply a new paternity method based on maximum likelihood to estimate the abundance of the Antarctic minke whale in the Indo-Pacific region of the Antarctic, and to evaluate this method by comparing the results with those obtained by line-transect methods in the same region.

Estimates from the paternity methods

There are some technical issues that need to be considered with respect to the paternity method estimates presented here. A key factor relates to the issues that resulted in the exclusion of a considerable amount of data due to the following reasons:

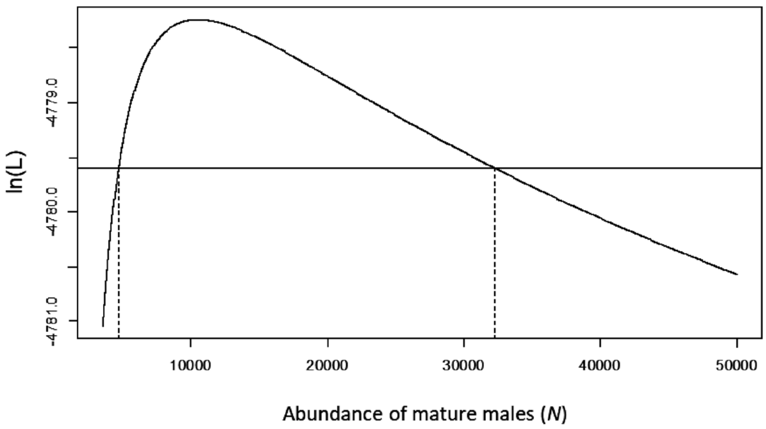

Fig. 4A. The likelihood profile for $\hat{N}_{\text{mature male}}$ using 10 loci in Areas IIIE, IV and VW using five years of mother-fetus pairs and mature males for analysis (I-population under the assumption of two populations).

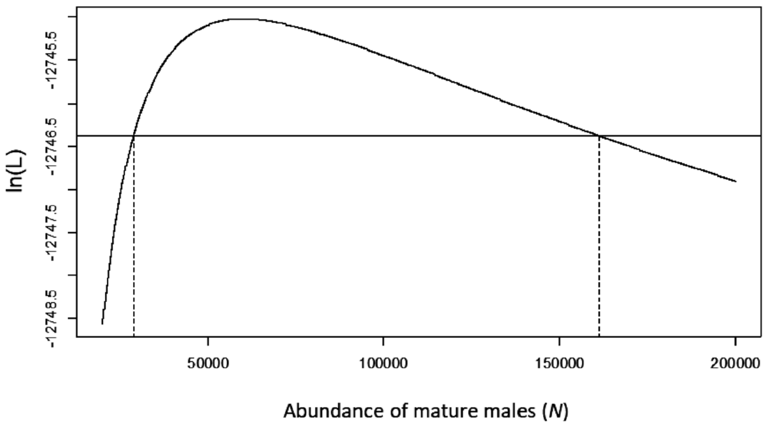

Fig. 4B. The likelihood profile for $\hat{N}_{\text{mature male}}$ using 10 loci in Areas VE and VIW using five years of mother-fetus pairs and mature males for analysis (P-population under the assumption of two populations).

(1) genotyping errors indicated by mother/fetus pairs with clearly different genotypes (37 pairs);
(2) missing allele information for some loci (576 individuals), indicating a genotyping error; and
(3) two loci with a high null allele frequency.

Presence of such genotyping errors and null alleles could cause reduction of matching cases, and therefore the estimated abundance tends to be positively biased. Such errors and allelic dropout can be considered in statistical models. However, such technical drawbacks in the DNA experiment should also be examined and, where possible, corrected so that updated data can be used in future analyses. Data collected after the 2011/12 austral summer season should be also used.

For practical reasons, the assumption of population structure considered a hard boundary between the I and P-populations. Refined analyses should consider the probability of assignment of each individual to each population in the overlap area.

Finally, this method considered only the relationship between mother/fetus and father. If other relative categories such as siblings are incorporated into the analyses, then the estimation performance (precision and accuracy) could be improved (Bravington *et al.*, 2016a; b).

Comparison with estimates from line-transect surveys

The preliminary results on abundance can be summarized as follows: i) there were no substantial differences in abundance under the two assumptions on population structure; ii) there was a slight difference in I-population estimate depending on the assumption for maturity age used, which gave an impact on the candidate fathers and successful pairs; and iii) the abundance derived from the paternity

Table 3. Results of abundance estimates for the Antarctic minke whales derived from the paternity analysis (in this paper) and a comparison with the estimates obtained using the line-transect method from the IWC SOWER programme (IWC, 2013, p.27) and JARPA/JARPAII (Hakamada and Matsuoka, 2014).

Method	Assumption/Data	IWC Management Area							Remarks
		Area III		Area IV	Area V		Area IV		
		III–W	III–E		V–W	V–E	VI–W	VI–E	
Paternity analysis with single population	Base case			211,600 (90%CI=130,954–377,210)					Maturity age=6 yrs old
	Sensitivity case			228,478 (90%CI=137,936–422,368)					Maturity age=8 yrs old
Paternity analysis with I- and P-populations	Base case			30,432 (90%CI=13,540–93,556)		189,946 (90%CI=91,401–510,506)			Maturity age=6 yrs old
	Sensitivity case			45,637 (90%CI=17,359–192,539)		182,458 (90%CI=87,924–488,166)			Maturity age=8 yrs old
Line transect method	IDCR/SOWER (1992/93–2003/04, IWC 2013)	93,215 (CV=0.35)		55,237 (CV=0.49)	183,915 (CV=0.36)		80,835 (CV=0.37)		All the estimates were corrected by g(0) estimates. The CVs include the additional variance.
	JARPA/JARPAII (1989/90–2008/09, Hakamada and Matsuoka 2014)			56,699* (30,585–95,725)	207,012* (132,431–299,433)				All the estimates were corrected by g(0)estimates. The interval in brackets is a range of time series estimates.

*An average (and the range in brackets) of a series of abundance estimates in Hakamada and Matsuoka (2014).

method was similar or somewhat lower than that obtained by the line-transect method (Table 3). It should be noted that this comparison was not straightforward because the research areas covered by the two methods are not identical (for example, the western part of Area III and eastern part of Area VI were not covered by the paternity method). The figure from the line-transect method, however, tends to be within the 90% confidence interval of the estimates by the paternity method.

Possible advantage of the paternity analysis over the line transect method is a less demanding requirement of the coverage of the habitat area. In the line transect method, the survey is assumed to cover the whole habitat area while the genetic tagging does not require this condition strongly as far as the sampling is randomly conducted. However, in the paternity analysis, false positive and/or false negative in matching between mother/fetus and father is crucial, and therefore the method is subject to over- or under-estimation depending on the quality of matching. Also, if the number of matching is quite low and the population size is large, “recapture probability” and “actual number of recapture” might be so low and it could cause a large extent of uncertainty in the abundance estimation. In fact, in our analyses, the matching occurred only in 10 pairs for hundreds of thousands of population size, and hence the 90% CI tends to be wide. To increase the recapture probability, other kinship definitions such as half-sibling can be used for improving estimation performance. This warrants further extension of methods to simultaneously account for different kinship types and population structure.

Inference of results for population structure hypotheses

The study offered the opportunity to compare the information obtained from this study with the current population structure hypotheses for the Indo-Pacific region. The geographical positions of mother/fetus–true father pairs are broadly consistent with the hypothesis of separate I- and P-populations. A total of 8/10 pairs was found in the expected areas of distribution of either I- or P-population. For example, five pairs were found in the expected area of distribution of the P-population while three pairs were found in the expected area of distribution of the I-population. In two cases, however, mother/fetus–true father pairs were found in quite different feeding areas. In the first case, the mother/fetus was caught in the expected area of I population while the true father was found in the expected area of the P-population. In the second case, the mother/fetus was caught in the expected feeding area of the I-population while the true father was found in the expected area of the P-population. These two examples are not inconsistent with the hypothesis of I- and P-populations, because it is expected that some whales move longitudinally within the feeding grounds, wherever they breed, and that such movements are more marked in males (Kitakado *et al.*, 2014; Murase *et al.*, 2020).

Conclusion

The results from this study have demonstrated the utility of the paternity method for obtaining abundance estimates of the Antarctic minke whale because the estimates are compatible with those obtained using the line-transect method. A number of ways to improve the estimates have been identified.

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NEW INSIGHTS INTO THE GENETIC STRUCTURE OF SEI WHALES (*BALAENOPTERA BOREALIS*) AT THE INTER-OCEANIC SCALE

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Abstract

To describe global genetic diversities and genetic structure of sei whales, population genetic and phylogenetic analyses were performed using mitochondrial DNA (mtDNA) control region sequence (480 bp) data from specimens collected in three oceanic regions: North Pacific (NP: $n=39$), North Atlantic (NA: $n=84$) and Southern Hemisphere (SH: $n=6$). Microsatellite DNA (msDNA) analyses were also performed using genotype data at seventeen loci in a sub-set of samples ($n=39$ in NP and $n=4$ in SH). The haplotype (h) and nucleotide (π) diversities were higher in NP ($h=0.92$ and $\pi=0.009$) and SH ($h=1.00$ and $\pi=0.012$) than in NA ($h=0.68$ and $\pi=0.002$). The haplotype frequency was significantly different among the three oceanic regions, and the conventional pairwise F_{ST} estimates support the difference between NA and the other two populations. Furthermore, except for one haplotype, there were no other shared haplotypes among the three oceanic regions, suggesting contemporary migration and gene flow would be strongly restricted at inter-oceanic scales. This inference was also supported by the msDNA analyses. The haplotype genealogy reconstructed by the maximum-likelihood approach strongly supported two clusters, the first consisting of NA haplotypes, and the second consisting of NP and SH haplotypes. This genealogy was supported by the statistical parsimony haplotype network. These results indicated hierarchical genetic structuring of sei whales globally, in which whales in SH are genetically closer to NP whales than to NA whales. Based on a comparison of the inter-oceanic genetic structure and phylogeny of the sei whales with those of fin whales, which is another cosmopolitan baleen whale species, it is suggested that the genetic structure of sei whales reflects occasional gene flow between the Northern and Southern hemispheres and/or incomplete lineage sorting, similar to the case of fin whales.

Key words: sei whale, stock structure, control region, worldwide, phylogeography.

Introduction

The sei whale, *Balaenoptera borealis*, is one of the large baleen whales inhabiting all the major open oceans, except the northern Indian Ocean (Horwood, 1987; Rice, 1998). Sei whales live up to sixty years and their body length reaches up to 20 m. It is believed that they migrate from low-latitudes winter breeding grounds to summer feeding grounds in high-latitudes, although little is known about the migratory routes and the exact location of breeding grounds of this species. This migration pattern, coupled with asynchronous seasonal breeding cycles between the Northern and Southern hemispheres, should favor reproductive isolation and resultant genetic divergence of sei whales between the hemispheres, as observed in other cosmopolitan baleen whales, *e.g.*, fin whale, *Balaenoptera physalus* (Archer *et al.*, 2013) and humpback whale, *Megaptera novaeangliae* (Jackson *et al.*, 2014). Furthermore, the continental masses separating the North Atlantic from the North Pacific have probably prevented gene flow of sei whales between the two oceans since the closure of the Panama Seaway, which is believed to have occurred during the Pliocene (Coates *et al.*, 1992).

Previous published population genetic work of sei whales is limited, despite their global distribution. Pioneering work was carried out by Wada and Numachi (1991) based on allozymes. This study revealed allele frequencies of three polymorphic allozymes to be significantly different between Antarctic and North Pacific sei whales, without any further differentiation within the oceans. The genetic homogeneity within the western North Pacific was supported by the subsequent work by Kanda *et al.* (2006) using microsatellite DNA (msDNA) polymorphisms at seventeen loci. The most recent study used mitochondrial DNA (mtDNA) control region sequences and msDNA genotypes. The study found evidence of genetic structuring between North Pacific and North Atlantic sei whales, but not within the North Atlantic (Huijser *et al.*, 2018). Taking these previous findings together, it is highly possible that sei whales are genetically differentiated among North Pacific (NP), North Atlantic (NA) and oceans of the Southern Hemisphere (SH).

The objective of this study was to describe global genetic diversities and genetic structure of sei whales using mtDNA control region sequences and msDNA genotype data of this species worldwide. This is the first study to incorporate sei whale samples from the NP, NA and SH.

Materials and Methods

Laboratory procedures

Samples and DNA extraction

A total of 44 tissue samples of sei whales (Fig. 1) was collected from three sources: (1) whaling under the second phase of the Japanese Whale Research Program under Special Permit in the western North Pacific (JARPNII) in 2002 (n=39); (2) biopsy sampling under the Japanese Whale Research Program under Special Permit in the Antarctic (JARPA) in 2000/01 (n=3) and 2002/03 (n=1); (3) stranding at southern Brazil in 2015 (n=1, export and import CITES permits 18BR030112/DF and 18JP000006/TI, respectively). Note that the 39 samples collected in the western North Pacific were the same as those used in the previous msDNA analyses (Kanda *et al.*, 2006), but their nucleotide sequences at mtDNA control region were determined for the first time in the present study.

Sampled skin tissues were preserved in 99% ethanol or stored frozen at −20°C until use. Total genomic DNA was extracted from 0.05 g of skin tissue using either the standard phenol-chloroform method (Sambrook *et al.*, 1989) or the Gentra Puregene kits (QIAGEN). Extracted DNA was stored in TE buffer (10mM Tris-HCl, 1mM EDTA, pH 8.0).

MtDNA sequencing

For all samples subjected to the DNA extraction, 534 base pairs (bp) of the mtDNA control region were amplified by the polymerase chain reaction (PCR) using the set of primers MT4 (Árnason *et*

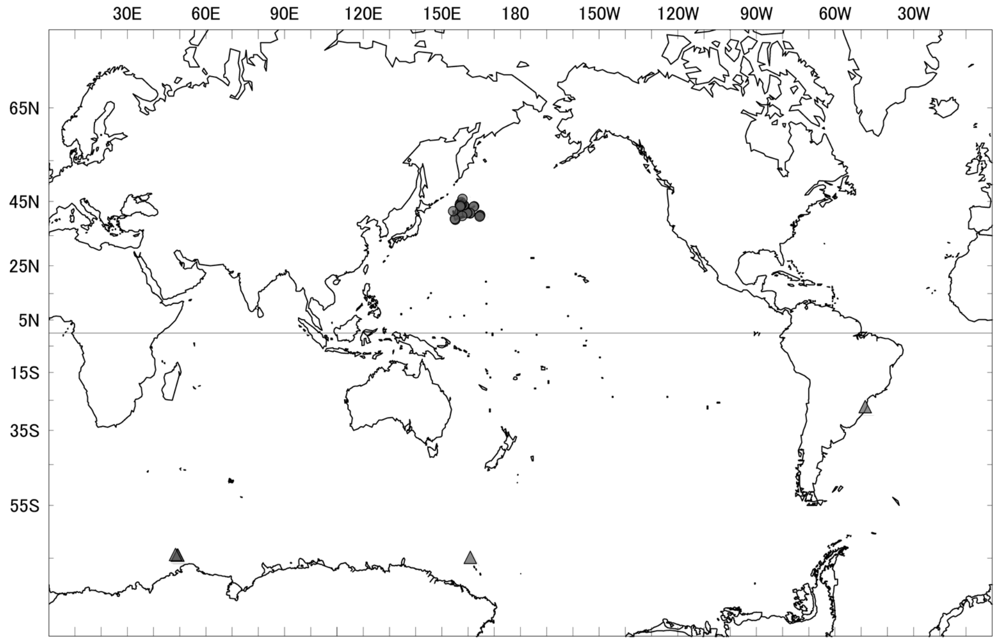

Fig. 1. Geographical position of samples newly sequenced and/or genotyped in the present study. Symbol shape indicates sample population: circle (NP, n=39), triangle (SH, n=5).

al., 1993) and Dlp5R (5′-CCATCGAGATGTCTTATTTAAGGGGAAC-3′). PCR was carried out in a 25 μL reaction mixture containing 10–100 ng of template DNA, 0.2 mM of dNTPs, 0.1 mM of each primer, 0.5 units of *EX Taq* DNA polymerase (TaKaRa), and 1× PCR buffer. Each reaction was performed with an initial denaturation step at 95°C for 5 minutes, followed by 30 cycles of 30 seconds at 94°C, 30 seconds at 50°C and 30 seconds at 72°C, with a final extension step at 72°C for 10 minutes. PCR products were purified using MicroSpin S-400HR columns (Pharmacia Biotech). Cycle sequencing was performed using BigDye terminator cycle sequence Kit (Applied Biosystems) and the PCR primers, following the protocols of the manufacturer. The cycle sequencing products were purified using AutoSeq G-50 spin Columns (Pharmacia Biotech). The labeled sequencing fragments from tissue samples from JARPNII and JARPA were resolved using an ABI PRISM 377, while the fragment of the stranding sample was sequenced with ABI3500 Genetic Analyzers (Applied Biosystems).

MsDNA genotyping

Three samples collected under the JARPA in 2000/01 and one stranding sample collected in southern Brazil in 2015 were genotyped at 17 nuclear msDNA loci, *i.e.*, EV1, EV14, EV21, EV94, EV104 (Valsecchi and Amos, 1996), GT011 (Bérubé *et al.*, 1998), GT23, GT211, GT271, GT310, GT575 (Bérubé *et al.*, 2000), GATA28, GATA53, GATA98, GATA417, GGAA520 (Palsbøll *et al.*, 1997), and DlrFCB17 (Buchanan *et al.*, 1996), in three multiplex fluorescent PCRs. Each of the multiplex PCRs was carried out in a 10 μL reaction mixture, containing 10–100 ng of template DNA, 5 μL of 2× Type-it Multiplex PCR master mix (QIAGEN), and 1 μL of primer mix (2 μM each primer), at 95°C for 5 minutes, followed by 28 cycles at 95°C for 30 seconds/54, 58 or 59.5°C for 90 seconds/72°C for 30 seconds, and a post-cycling extension at 60°C for 30 minutes. PCR products were electrophoresed on an ABI3500 DNA Analyzer (Applied Biosystems), and allele sizes were determined using a 600 LIZ size standard (Applied Biosystems) and GeneMapper v. 4.0 (Applied Biosystems).

Dataset

In order to investigate the global genetic structure, mtDNA and msDNA data were divided into three oceanic regions: (1) North Pacific (NP); (2) North Atlantic (NA); (3) Southern Hemisphere (SH).

MtDNA

Combining the 44 mtDNA control region sequences newly sequenced in this study with the 85 sequences generated in the previous studies (of which, 84 were from the Gulf of Maine, Iceland and Azores (Huijser *et al.*, 2018) and one from the Antarctic Ocean (Sasaki *et al.*, 2005)) resulted in a total of 129 mtDNA sequences of sei whales from NP (n=39), NA (n=84) and SH (n=6) (Table 1).

MsDNA

Combining msDNA genotypes of the four new individuals from SH (three from the Antarctic and one from Brazil), with a subset of genotype data in NP generated by Kanda *et al.* (2006), resulted in a total of 43 genotype set of sei whales from NP (n=39) and SH (n=4) (Table 1). The newly obtained msDNA scores were standardized to the previous scores, which Kanda *et al.* (2006) generated using the BaseStation100 DNA fragment analyzer (Bio-Rad), by comparing the scores of the same samples between the present and previous platforms.

Data analyses

MtDNA

Haplotype (h) and nucleotide (π) diversities with sample standard deviations (Nei, 1987) were estimated using the program ARLEQUIN v. 3.5.2.2 (Excoffier and Lischer, 2010).

The difference in mtDNA haplotype frequency among oceanic regions was tested using the Monte Carlo simulation-based chi-square test of independence with 10,000 replicates (Roff and Bentzen, 1989) in R (R Core Team, 2016). The conventional F_{ST} estimates between oceanic regions were calculated using 10,000 random permutations of the original dataset, as implemented in ARLEQUIN. The FDR correction (Benjamini and Hochberg, 1995) was used to adjust the statistical significance level in the pairwise estimates.

The mtDNA haplotype genealogy of sei whales was reconstructed using the maximum-likelihood approach (ML-tree) with 10,000 bootstrap resampling in the program MEGA ver. 10.0.5 (Kumar *et al.*, 2018). The best-fit nucleotide substitution model was determined based on the Bayesian Information Criterion using MEGA, and Tamura 3-parameter model (Tamura, 1992) with G=0.487 and I=0.747 was selected. Two sequences of *Balaenoptera edeni* (GenBank accession number: X72196) and *Balaenoptera brydei* (unpublished data) were used as outgroups in the analysis. The statistical parsimony network (Clement *et al.*, 2000) of mtDNA control region haplotypes was also depicted using the program PopART (Leigh and Bryant, 2015).

MsDNA

The departure from Hardy–Weinberg equilibrium (*HWE*) was tested and the inbreeding coefficient (F_{IS}; Weir and Cockerham, 1984) was estimated, using GENEPOP (Raymond and Rousset, 1995; Rousset, 2008). The number of alleles (A), allelic richness (AR) and expected heterozygosity (H_E)

Table 1. Numbers of mitochondrial (mt) and microsatellite (ms) DNA data used in this study. The mtDNA nucleotide sequences in NP were newly obtained from the same samples used for msDNA analyses in Kanda *et al.* (2006).

Oceanic region		MtDNA		MsDNA	
		n	Reference	*n*	Reference
North Pacific	(NP)	39	This study	39	Kanda *et al*. (2006)
North Atlantic	(NA)	84	Huijser *et al*. (2018)	–	
Southern Hemisphere	(SH)	5	This study	4	This study
		1	Sasaki *et al*. (2005)		
Total		129		43	

Table 2. Summary of mtDNA variations of sei whales and haplotype frequency in each of and across the oceanic regions. Numbers in 'Variable site' represent nucleotide positions corresponding to 'H01' deposited in DDBJ under the accession no. LC629100. See Table 1 for abbreviations of the oceanic region.

Haplotype	Variable site																															Accession No.	Reference	Haplotype frequency			
	64	78	92	103	107	110	111	112	139	191	207	247	251	257	260	264	272	278	283	289	294	295	296	297	299	309	340	371	404	407	408			NP	NA	SH	Global
H01	T	T	G	C	T	C	A	C	A	T	T	T	A	A	T	C	C	A	C	G	C	T	G	T	C	A	T	T	C	T	C	LC629100	This study	1	0	0	1
H02	.	.	.	.	.	.	.	.	G	.	.	.	.	.	.	.	T	G	.	A	.	.	.	C	.	.	C	.	.	C	.	LC629101	This study	1	0	0	1
H03	.	.	.	.	.	.	.	.	G	.	.	.	.	.	.	.	T	G	.	A	.	.	.	C	.	.	C	.	.	.	.	LC629102	This study	8	0	0	8
H04	.	.	.	.	.	.	.	.	G	.	C	.	.	.	.	.	T	.	.	.	T	.	A	C	T	.	C	.	.	.	.	LC629103	This study	2	0	0	2
H05	.	.	.	.	.	.	.	.	G	.	.	.	.	.	.	.	T	.	.	A	.	.	.	C	T	.	C	C	.	.	.	LC629104	This study	2	0	0	2
H06	.	.	.	.	.	.	.	.	G	.	.	.	.	.	.	.	T	.	.	.	T	.	A	.	T	G	.	.	.	.	.	LC629105	This study	1	0	0	1
H07	.	.	.	.	.	.	.	.	G	.	C	.	.	.	.	.	T	G	.	.	.	.	A	.	.	.	C	.	.	.	.	LC629106	This study	7	0	0	7
H08	.	.	.	.	.	.	.	.	G	.	.	.	.	.	.	.	T	.	.	.	.	.	A	.	.	G	.	.	.	.	.	LC629107	This study	4	0	0	4
H09	.	.	.	.	.	.	.	.	G	.	.	.	.	.	.	.	T	.	.	A	.	.	.	C	.	.	C	.	.	.	.	LC629108	This study	3	0	0	3
H10	.	.	.	.	.	.	.	.	G	.	C	.	.	.	.	.	T	.	.	.	T	.	A	.	T	.	C	.	.	.	.	LC629109	This study	1	0	0	1
H11	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.	.	.	.	.	.	.	.	.	C	.	.	.	.	LC629110	This study	1	0	0	1
H12	.	.	.	.	.	.	.	.	G	.	.	.	.	.	.	.	T	.	.	.	.	.	.	C	.	.	C	.	T	.	.	LC629111	This study	1	0	0	1
H13	.	.	.	.	.	.	.	.	G	.	.	.	.	G	.	.	.	.	.	A	.	.	.	.	.	.	C	.	.	.	.	LC629112	This study	1	0	0	1
H14	.	.	.	.	C	.	.	.	G	.	.	.	.	.	.	.	T	.	.	A	.	.	.	.	.	.	G	.	.	.	.	LC629113	This study	1	0	0	1
H15	.	.	.	.	.	.	.	.	G	C	C	.	.	.	.	.	T	G	.	.	.	.	A	.	.	.	C	.	.	.	.	LC629114	This study	1	0	0	1
H16	.	.	.	.	.	.	.	.	G	.	.	.	.	.	.	.	.	.	.	A	.	.	.	C	.	.	C	.	.	.	.	LC629115	This study	1	0	0	1
H17	.	.	.	.	.	.	.	.	G	.	.	.	.	.	.	.	T	.	.	A	.	.	.	.	.	.	C	.	.	.	.	LC629116	This study	1	0	0	1
H18	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.	.	.	.	.	.	.	.	.	.	.	.	.	LC629117	This study	1	0	0	1
H19	.	.	.	.	.	.	.	.	G	.	C	.	.	.	.	.	T	.	.	.	.	.	A	.	.	.	C	.	.	.	.	LC629118	This study	1	0	0	1
H87	.	.	.	.	.	T	.	.	G	.	.	.	.	.	.	.	T	.	.	A	.	C	A	.	.	.	C	.	.	.	T	LC629119	This study	0	0	1	1
H88	.	.	.	.	.	T	.	.	G	.	.	.	.	.	.	T	T	.	.	A	T	.	A	.	.	.	C	.	.	.	.	LC629120	This study	0	0	1	1
H89	.	.	.	.	.	.	C	.	G	.	.	C	G	.	.	.	T	.	.	A	T	C	A	.	.	.	.	.	.	.	.	LC629121	This study	0	0	1	1
H90	.	.	.	.	.	T	.	.	G	.	.	.	.	.	.	T	.	.	.	A	T	.	A	.	T	.	C	.	.	.	.	LC629122	This study	0	0	1	1
SH1	.	.	.	.	.	.	.	T	G	.	.	.	.	.	.	.	T	.	.	.	.	.	A	.	T	.	C	.	.	.	.	NC_006929.1	Sasaki *et al*. (2005)	0	0	1	1
NA1	C	C	C	T	.	.	.	.	G	C	.	.	.	.	G	.	T	.	.	C	.	C	A	.	T	.	C	C	.	.	.	MH035689	Huijser *et al*. (2018)	0	9	0	9
NA2	.	C	C	T	.	.	.	.	G	C	.	.	.	.	G	.	.	.	.	C	.	C	A	.	T	.	C	C	.	.	.	MH035690	Huijser *et al*. (2018)	0	10	0	10
NA3	.	C	C	T	.	.	.	.	G	C	.	.	.	.	G	.	T	.	.	C	.	C	A	.	T	.	C	C	.	.	.	MH035691	Huijser *et al*. (2018)	0	43	0	43
NA4	.	C	C	T	.	.	.	.	G	.	.	.	.	.	G	.	T	.	.	C	.	C	A	.	T	.	C	C	.	.	.	MH035692	Huijser *et al*. (2018)	0	16	0	16
NA5	.	C	C	T	.	.	.	.	G	C	.	.	.	.	G	.	T	.	T	C	.	C	A	.	T	.	C	C	.	.	.	MH035693	Huijser *et al*. (2018)	0	2	0	2
NA6	.	.	.	.	.	T	.	.	G	.	.	.	.	.	.	T	.	.	.	A	T	C	A	.	.	.	C	.	.	.	.	MH035694	Huijser *et al*. (2018)	0	1	1	2
NA7	.	C	C	T	.	.	.	.	G	C	.	.	.	.	G	.	T	.	.	C	.	C	A	.	.	.	C	C	.	.	.	MH035695	Huijser *et al*. (2018)	0	3	0	3
																																	Total	39	84	6	129
																																	Number of haplotypes	19	7	6	31
																																	Haplotype diversity *(s.d.)*	0.92 (0.03)	0.68 (0.04)	1.00 (0.10)	0.86 (0.02)
																																	Nucleotide diversity *(s.d.)*	0.009 (0.005)	0.002 (0.002)	0.012 (0.008)	0.013 (0.007)

were estimated using the program FSTAT ver. 2.9.3.2 (Goudet, 1995).

Bayesian clustering analysis was performed to infer the most likely number of clusters using STRUCTURE 2.3.4 (Pritchard *et al.*, 2000). The analysis was conducted with ten independent runs for $K=2$–3. All runs were performed with 100,000 Markov chain Monte Carlo repetitions and 10,000 burn-in length using the admixture model with correlated allele frequencies. The web-based program STRUCTURE HARVESTER (Earl and von Holdt, 2012) was used to estimate the mean posterior probability of the data. Additionally, principal component analysis (PCA) was performed in R using the '*dudi.pca*' function in the *ade4* package (Chessel *et al.*, 2004; Dray *et al.*, 2007).

Results

Genetic variations

MtDNA

The mtDNA control region sequences (480 bp) of 129 sei whales from the three oceanic regions contained 31 variable nucleotide sites and a single indel (1 bp) defining 31 haplotypes, of which 23 were novel (deposited in GenBank with accession numbers: LC629100–LC629122) (Table 2). Apart from haplotype 'NA6', none of the haplotypes were shared among oceanic regions. Haplotype 'NA6' was shared between NA and SH (Table 2). The h and π for the total samples were 0.86 and 0.013, respectively (Table 2). These estimates were higher in SH (1.00 and 0.012) and NP (0.92 and 0.009) than in NA (0.68 and 0.002).

MsDNA

All 17 msDNA loci were polymorphic in a total of 43 sei whales in NP and SH, with locus-specific allele numbers from 3 alleles at GATA53 and GT271 to 17 alleles at DlrFCB17 (Table 3). The *AR* was higher in SH than in NP. No significant deviations from *HWE* were observed in each locus or across the loci of NP and SH (Table 3). Although the significant departure from *HWE* was detected at GATA417 when the two populations were combined (Table 3), the global test did not support the statistical significance.

Table 3. Summary statistics of 17 msDNA loci of sei whales: A, the number of alleles; AR, allelic richness; H_E, expected heterozygosity; F_{IS}, inbreeding coefficient; HWE, p-value of the Hardy-Weinberg equilibrium test. F_{IS} and HWE at GT011 in SH were incomputable since one of two alleles was represented by only one copy. See Table 1 for abbreviations of the oceanic region. Bold text indicates the statistical significance at $\alpha=0.05$.

Locus	NP (n = 39)					SH (n = 4)					Total (n = 43)				
	A	AR	H_E	F_{IS}	HWE	A	AR	H_E	F_{IS}	HWE	A	AR	H_E	F_{IS}	HWE
DlrFCB17	15	5.42	0.87	0.026	0.686	6	6.00	0.92	-0.091	1.000	17	5.45	0.87	0.010	0.565
EV1	12	4.65	0.81	0.015	0.455	6	6.00	0.92	0.182	0.466	15	4.99	0.84	0.054	0.225
EV14	14	5.35	0.87	-0.063	0.913	7	7.00	0.96	-0.043	1.000	14	5.49	0.88	-0.057	0.749
EV21	6	3.35	0.64	-0.085	0.754	4	4.00	0.75	0.000	1.000	7	3.59	0.68	-0.029	0.831
EV94	6	3.20	0.61	-0.087	1.000	6	6.00	0.92	0.182	0.446	8	3.59	0.67	-0.015	0.443
EV104	5	3.80	0.75	-0.064	0.730	5	5.00	0.83	-0.200	1.000	5	3.90	0.76	-0.069	0.681
GATA28	10	4.73	0.82	0.001	0.749	6	6.00	0.92	-0.091	1.000	11	4.85	0.83	-0.005	0.761
GATA53	3	2.17	0.35	0.123	0.241	2	2.00	0.58	0.571	0.426	3	2.25	0.37	0.191	0.075
GATA98	6	3.70	0.73	0.119	0.454	2	2.00	0.50	-0.500	1.000	6	3.60	0.71	0.084	0.482
GATA417	7	4.00	0.76	0.023	0.143	5	5.00	0.79	0.053	0.775	10	4.49	0.80	0.072	**0.007**
GGAA520	8	4.26	0.80	0.098	0.190	4	4.00	0.79	0.368	0.302	8	4.33	0.80	0.132	0.062
GT011	4	2.59	0.47	0.021	0.572	2	2.00	0.25	–	–	5	2.59	0.46	0.028	0.660
GT023	6	2.80	0.49	-0.040	0.380	5	5.00	0.88	-0.143	1.000	7	3.01	0.54	-0.029	0.177
GT211	4	2.11	0.33	0.069	0.249	4	4.00	0.79	-0.263	1.000	5	2.39	0.41	0.081	0.141
GT271	3	1.55	0.15	-0.051	1.000	2	2.00	0.58	0.571	0.429	3	1.78	0.23	0.297	0.073
GT310	3	2.14	0.39	-0.256	0.275	4	4.00	0.71	-0.412	1.000	5	2.42	0.43	-0.245	0.499
GT575	4	2.51	0.56	-0.006	0.913	4	4.00	0.79	-0.263	1.000	6	2.85	0.61	0.011	0.422
Average			0.61	-0.004	0.884			0.76	-0.010	1.000			0.68	0.020	0.070

Table 4. Conventional pairwise F_{ST} estimates between oceanic regions for mtDNA. Asterisks show the statistical significance after FDR correction: *$p<0.05$, **$p<0.01$, ***$p<0.001$. See Table 1 for abbreviations of the oceanic regions.

Oceanic region	NP	NA	SH
NP			
NA	***0.210		
SH	0.048	**0.206	

Table 5. Summary of STRUCTURE analyses showing the average ln Pr(X|K) for each of *K*, and respective probability.

K	ln Pr(X|K)	Variance	P(K|X)
1	-2122.47	53.79	~1.00
2	-2138.42	193.24	~0.00
3	-2233.04	436.19	~0.00

Genetic differentiation and structure

MtDNA

The haplotype frequency was significantly different among the three oceanic regions ($\chi^2=246.48$, $p<0.001$). Conventional pairwise F_{ST} estimates were significantly different from zero in the pairs of NP and NA as well as SH and NA, but no significant difference was seen between SH and NP (Table 4).

MsDNA

The STRUCTURE analyses conducted for different sampling partitions without information on their geographic origins presented the highest probability at $K=1$ (Table 5). However, the four sei whales from the SH were distinguishable from NP whales by high posterior probabilities ($q>0.8$) of belonging to a particular cluster at $K=2$ (Fig. 2).

In PCA analysis, the first (PC1) and second (PC2) principal components explained 9.81% and 6.95% of the total variation, respectively. This analysis suggests that the 43 sei whales could be divided into two distinct clusters (NP and SH) along the PC1 axis (Fig. 3).

Phylogenetic analyses

The ML-tree showed two clusters supported by high bootstrap values (Fig. 4a), one which consisted of haplotypes found in NA and the other of haplotypes found in NP and SH. Within the NP/SH cluster, the ML-tree also showed a sub-cluster containing four of the six haplotypes found in SH, *i.e.*, ‘NA6’, ‘H87’, ‘H88’ and ‘H90’. However, this cluster had a low bootstrap value (Fig. 4a).

The statistical parsimony network showed the two clusters were separated by six mutational steps, which consisted of a star-like genealogy of haplotypes found in NA, and more complex structures in NP and SH (Fig. 4b). The haplotype network also showed that all haplotypes found in SH were separated from those in NP by several mutational steps.

The haplotype ‘NA6’ found in both NA and SH was located in the NP/ SH cluster in each topology (Fig. 4).

Discussion

This is the first population genetic study of sei whales worldwide. In particular, analyses using msDNA has never been reported in SH sei whales. Notwithstanding the small number of samples used from SH, the preliminary findings of this study provide some new insights into the genetic structure and phylogeography of this species.

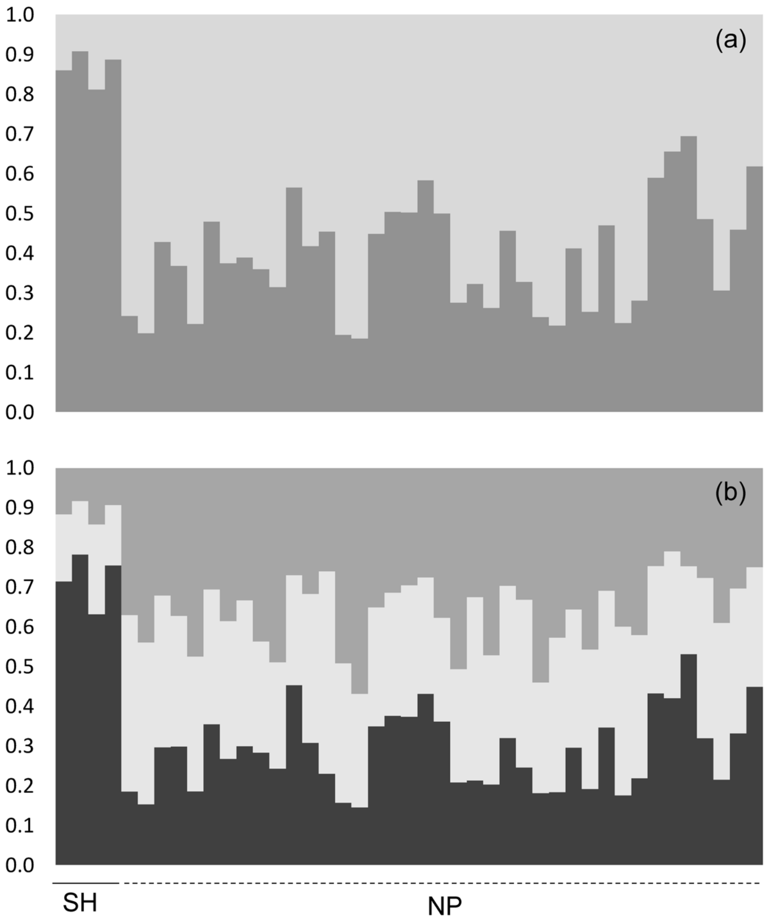

Fig. 2. Bar plot of posterior probabilities in STRUCTURE analyses for sei whales in oceans of the Southern Hemisphere (SH) and the North Pacific (NP): (a) $K=2$ and (b) $K=3$. Each individual is characterized by a thin vertical line, which is divided into K colored segments on the basis of the individual's membership fractions in K clusters.

Genetic structure

The haplotype frequency of sei whales was significantly different among the three oceanic regions, and the conventional pairwise F_{ST} estimates suggested the genetic differentiation of this species between NA and the other two oceanic regions. This observation is consistent with the pattern of genetic differentiation of sei whales between NP and NA presented by Huijser *et al.* (2018). Although the F_{ST} estimates did not support a genetic difference between NP and SH, given no haplotype sharing, the insignificant result was likely to be caused by the small sample size in SH. In fact, Wada and Numachi (1991) using a larger number of samples demonstrated the significant genetic differentiation between NP and SH sei whales. Furthermore, this inference was supported by the msDNA analyses. The STRUCTURE analysis suggested that the most likely number of populations at Hardy-Weinberg/linkage equilibrium in the data set consisting of sei whales in SH and NP was one, which was consistent with no deviations from *HWE* in each of and across populations. However, despite the small sample size in SH, the four SH sei whales were distinguishable from the NP whales by high posterior probabilities ($q>0.8$) when $K=2$ was assumed. This was also supported by the result of multivariable analysis, *i.e.*, PCA, separating the four sei whales from other NP whales along the first PC axis.

The PCA analysis also showed a large genetic variation of SH cluster consisting of samples collected across the vast oceanic region, *i.e.*, the western South Atlantic and the Antarctic Ocean. This, coupled with high h in SH, might be suggestive of an inclusion of samples derived from multiple breeding populations in a single sample population. Given the genetic structuring shown in other SH

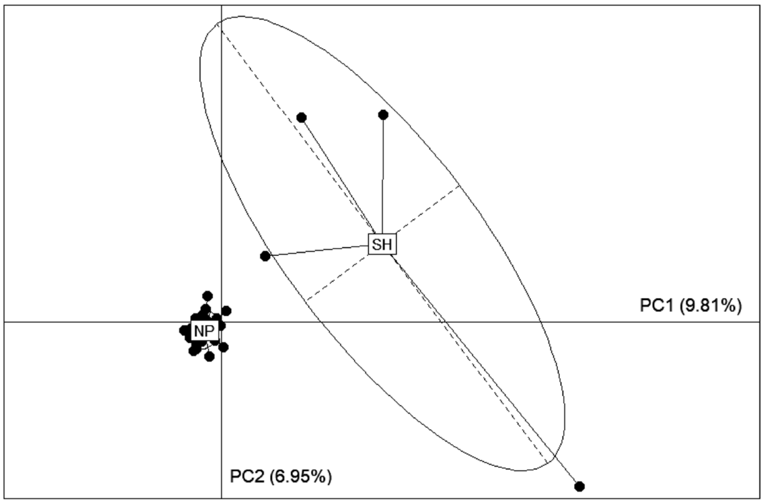

Fig. 3. Result of PCA analysis on genotypes at seventeen msDNA loci. See Table 1 for abbreviations of the oceanic regions.

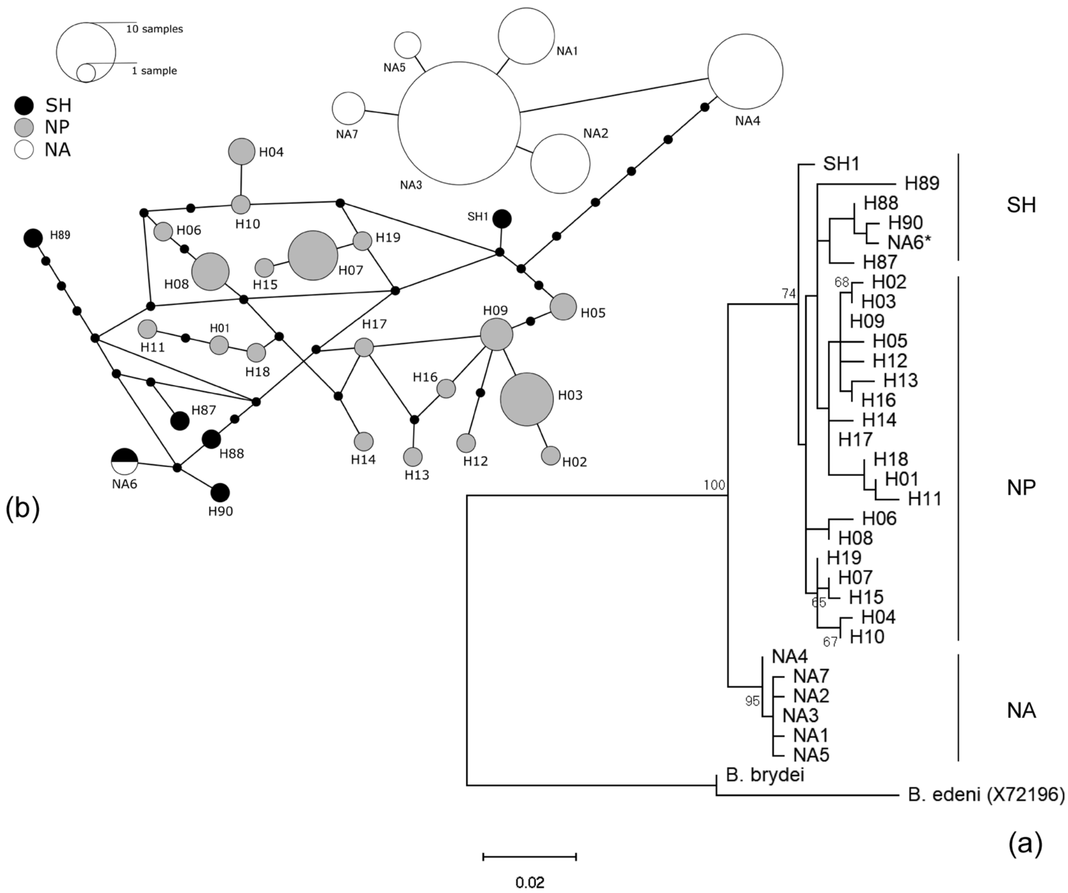

Fig. 4. Genealogy reconstructed by the maximum-likelihood approach (a), and statistical parsimony network (b) of mtDNA control region haplotypes of sei whales. The phylogenetic tree was rooted by outgroup of *B. brydei* and *B. edeni*, which was drawn to scale with branch lengths measured in the number of substitutions per site. Only bootstrap values above 60% are shown. Asterisk shows haplotypes shared among oceanic regions. Circles of the haplotype network represent different haplotypes. The colors and sizes of circles refer to the geographical origin and abundance of haplotypes, respectively. Small black circles indicate intermediate haplotypes not found in this study. See Tables 1 and 2 for abbreviations of the geographical origin of haplotypes and haplotype information, respectively.

baleen whales (*e.g.*, humpback whales, Olavarría *et al.*, 2007; Antarctic minke whales, Pastene and Goto, 2016), that possibility could not be excluded at this stage.

The haplotype network and ML-tree strongly supported the divergence of haplotypes found in NA from those in NP and SH, as shown by Huijser *et al.* (2018). The haplotype network further showed that all haplotypes found in SH were separated from those in NP by several mutational steps. The ML-tree revealed a sub-cluster containing most of the haplotypes found in SH, however, there was no significant bootstrap support. These results are indicative of ocean-specific mitochondrial lineages, which are compatible with the observed difference in the degrees of the pairwise F_{ST} estimates among sei whales from the three oceanic regions.

Taking all the present and previous findings together, sei whales appear to be significantly differentiated among oceanic regions hierarchically, and whales in SH are more closely related to whales in NP than to whales in NA. Except for haplotype 'NA6', there were no other haplotypes that were shared among the three oceanic regions, which suggests that contemporary migration and gene flow would be strongly restricted at inter-oceanic scales.

Interestingly, the pattern of inter-oceanic genetic structuring observed in the present study was similar to that in fin whales with the lower F_{ST} estimates between NP and SH (mtDNA, 0.005–0.106; single-nucleotide polymorphisms (SNPs), 0.098) than between NA and NP (mtDNA, 0.018–0.198; SNPs, 0.1668) as well as between NA and SH (mtDNA, 0.017–0.121; SNPs, 0.1447) (Archer *et al.*, 2019). This, coupled with genealogical concordance between fin and sei whales described below, suggests that the pattern of genetic structuring in sei whales could be attributed to historical events, *i.e.*, recent occasional gene flow between the Northern and Southern hemispheres and/or incomplete lineage sorting (ILS).

Phylogeographic inferences

The ML-tree found no evidence of divergence of SH haplotypes from NP ones, despite the inference of genetic differentiation between the two oceanic regions. ILS and/or recent occasional gene flow may explain this observation, because they can be the cause of shared genetic variations among populations after their divergence. The mtDNA phylogenetic study of fin whales demonstrated a polyphyletic pattern of NP and SH haplotypes (Archer *et al.*, 2013), which was similar to that of the sei whale. The study also suggests the possibilities of a relatively recent introgression between the two oceans and/or retention of ancestral polymorphisms due to ILS of the large whale species.

Huijser *et al.* (2018) inferred that an expansion of the North Atlantic sei whale population occurred after the last glacial maximum (LGM, 26.5–19 thousand years ago; Clark *et al.*, 2009) based on phylogeographic analyses. The star-like genealogy of haplotypes and lower genetic diversities observed in NA in the present study would be attributed to this historical event in the case of the NA sei whales. On the other hand, SH and NP haplotypes showed more complex structures with a high number of haplotypes of intermediate frequency on the network. Given the inferences of ILS with high h in NP and SH, the result could reflect ancestral polymorphisms of NP and SH whales in a large long term effective population size. It seems that they have been separated long enough to be void of shared haplotypes, but not long enough to have evolved reciprocal mitochondrial monophyly. Such reciprocal monophyly is indeed observed among NA and the combined NP/SH cluster, suggesting a considerably more ancient divergence.

In the present study, there are also signs of recent or contemporary occasional inter-oceanic migration/dispersal events, one from SH to NA (NA6) and one from NP to SH (SH1). This inference is compatible with the restricted but rare inter-equatorial gene flow inferred in humpback whales (*e.g.*, Jackson *et al.*, 2014) and fin whales (Cabrera *et al.*, 2019). So far, there is no direct evidence for trans-equatorial gene flow in sei whales. However, this seems probable in this species, given its high mobility as demonstrated by tagging studies (*e.g.*, Olsen *et al.*, 2009) and continuous distribution across the equatorial waters inferred from stranding records along the northern coast of Brazil (*e.g.*, Costa *et al.*, 2017; Mayorga *et al.*, 2020; Milmann *et al.*, 2020).

Conclusion

Notwithstanding the small sample size used from SH, the present study demonstrated the hierarchical genetic structuring of sei whales globally for the first time, with high genetic diversity in SH/NP, in which whales in SH are genetically closer to NP whales than to NA whales. These findings, coupled with the previous findings in sei whales as well as in other cosmopolitan baleen whales, suggested the following phylogeographical scenarios of this species: (1) a shorter history of divergence among SH and NP, leading to retention of ancestral polymorphisms due to ILS in SH and NP, (2) occasional gene flow between the Northern and Southern hemispheres.

Extended genetic analyses using larger sample sizes across the oceans and more genetic loci have to be conducted in this species to investigate finer genetic structure and demographic estimates, *e.g.*, migration rate and effective population size.

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EVIDENCE OF WINTER MIGRATION OF HUMPBACK WHALES TO THE HACHIJO ISLAND, IZU ARCHIPELAGO OFF THE SOUTHERN COAST OF TOKYO, JAPAN

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Abstract

In the western North Pacific Ocean, humpback whales (*Megaptera novaeangliae*) migrate to the Okinawa (26°13′N, 127°41′E) and Ogasawara (27°04′N, 142°13′E) islands of Japan for breeding. The Hachijo Island (33°06′N, 139°47′E) is located in the Izu Archipelago —further north from known wintering grounds of those whales. In the 2015–16 winter, humpback whales were sighted around the Hachijo Island in significant numbers. This led to a monitoring project of whales around the island that was initiated from the 2016–17 winter to elucidate their migration. Here, we report the results of monitoring over two subsequent winter seasons (2016–17 and 2017–18). A survey was conducted within 5 nautical miles of the coast of the island using a dedicated vessel (12GT) for respectively 32 and 34 days in the first and second season from November to April. Humpback whales were sighted from November to March in the first season and from November to April in the second season, and a total of sightings of respectively 205 and 397 whales were recorded in the 2016–17 and 2017–18 seasons. Characteristic behaviors in the wintering grounds, such as singing and forming competitive groups, were confirmed in both seasons. Moreover, around 15% of the whales were repeatedly sighted during the same season, and six individuals observed in the first season were resighted in the second season. These results suggest that waters around the Hachijo Island are part of the winter migration grounds of humpback whales, and their migration to waters off the Hachijo area is expected to continue in the future. Long-term monitoring focusing on the social composition of groups is necessary, and additional photo-identification and genetic data should be collected to shed light on the habitat use and causes of sudden occurrence of humpback whales around this island.

Key words: Hachijo Island, humpback whale, wintering ground, Photo-ID, residency, site fidelity.

Introduction

Humpback whales (*Megaptera novaeangliae*) belong to the family Balaenopteridae of the suborder Mysticeti (Fig. 1). They undergo seasonal migration, staying in highly productive feeding grounds at high latitudes during the summer and autumn and migrating to breeding grounds at temperate low latitudes in winter (Dawbin, 1966; Baker *et al.*, 1986; Clapham, 2000). In the North Pacific Ocean,

Fig 1. Humpback whale. This Photo was taken in 22 January, 2017 at Hachijo Island.

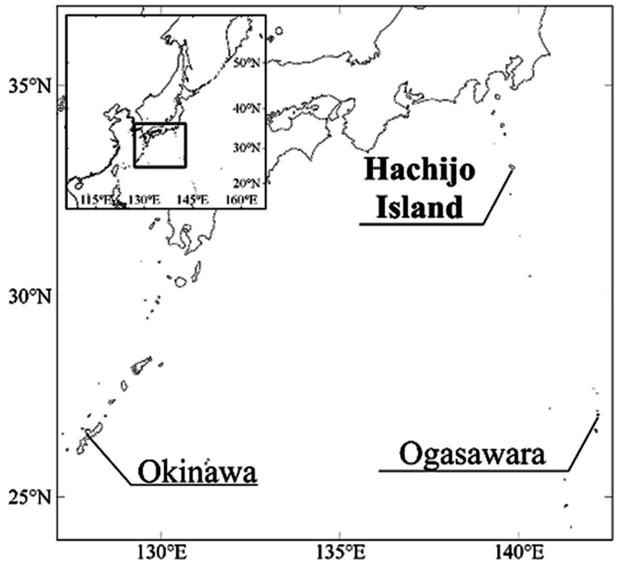

Fig. 2. Map of Hachijo Island and two other major wintering grounds of humpback whales known in Japan.

some wintering grounds have been reported, namely the coasts of Mexico, Revillagigedo Archipelago (Urbán and Aguayo, 1987), Hawaii (Baker and Herman, 1981), the Philippines (Acebes *et al.*, 2007), Ogasawara Islands (Darling and Mori, 1993), Okinawa (Nishiwaki, 1959; Kobayashi *et al.*, 2016), and Mariana Archipelago (Hill *et al.*, 2020). The occurrence peak of humpback whales in the wintering ground of the North Pacific Ocean generally lasts from February to March (Urbán and Aguayo, 1987; Mobley *et al.*, 1999; Kobayashi *et al.*, 2016). In the wintering grounds, some behaviors related to the mating of humpback whales were observed. Male humpback whales sing long complex songs (Payne and McVay, 1971; Baker and Herman, 1984), and males compete physically among multiple male whales for mating opportunities with females (Tyack and Whitehead, 1983; Baker and Herman, 1984; Clapham, 2000).

In November 2015, we received a report from diving companies that an unusually large number of humpback whales appeared around the Hachijo Island (Kono E. and Yamakoshi, pers. comm.). The Hachijo Island is located south of Tokyo in the southern part of the Izu Archipelago (33°06′N, 139°47′E), approximately 700 km north of the Ogasawara Islands, which is one of the known primary wintering grounds of humpback whales in Japan (Fig. 2). According to Uda (1954), the waters around the Hachijo Island have not been previously reported as the whaling grounds of humpback whales. Furthermore, there has been no scientific monitoring of large whales in this region. Therefore, there are not any previous formal records which mention whether humpback whales migrated to this region seasonally or not. Before this sudden migration in 2015, only five sporadic sightings of humpback whales around this island were reported, including once each in April 2005 and May 2010 and thrice in March 2013 (Tokyo Metropolitan Government Park Association Hachijo Visitor Center, pers. comm.).

Therefore, on December 23, 2015, the Japan Broadcasting Corporation (NHK) and the Laboratory of Cetacean Biology, Tokyo University of Marine Science and Technology (TUMSAT) collaborated to visually survey the coastal area of Hachijo Island. In this preliminary survey, 37.4 nautical miles were searched along the coast of the island and at least 10 humpback whales belonging to five social groups were sighted in the southwest part of the island in water depths less than 200 m. Moreover, a song was confirmed and recorded.

To examine whether the migration of a significant number of whales around the Hachijo Island is temporary and to collect photo-identification data for investigating the migratory connections to other areas, a shipboard survey has been conducted around the island by the local government and TUMSAT throughout the breeding season (November to April) since 2016. The present study reports the results of monitoring over two subsequent seasons (2016–17 and 2017–18) and explores the importance of waters around the Hachijo Island as wintering grounds of western North Pacific humpback whales based on occurrence, behavior, and photo-identification data.

Materials and Methods

Field Survey

We conducted surveys within five nautical miles of the coast of the Hachijo Island, departing from and arriving at the Yaene Port (33°06′N, 139°46′E). In the field the *Aki-Maru*, a small dedicated research vessel of 12 GT (length, aprox. 15 m; width, 2.5 m) with a single inboard diesel-powered engine was used. Three researchers on board visually searched for whales with the naked eye from the observation platform (3 m above sea level). The survey was conducted from 9:00 to 15:00, and the search speed of the vessel was set at 8–9 knots. When whales were sighted, one researcher recorded the time and position of the vessel (latitude and longitude) using a global positioning system (Garmin eTrex10J). When the vessel reached the estimated location at which the whales were spotted, one researcher recorded the time, position, and sea surface temperature (SST), and two other researchers attempted to take photographs for identification. In addition, the behavior and group size of the whales were observed and recorded. The researchers lowered a hydrophone (OKI Whalephone II) at least once per day to evaluate whether the whales were singing.

Photo-identification

Humpback whales can be identified based on the pattern of pigmentation on the ventral fluke and the shape of its edge (Katona and Whitehead, 1981). When humpback whales were sighted, the vessel immediately followed the target group, and the researchers took photographs for identification using a NIKON D7000 camera with a 55–300 mm lens (AF-S DX NIKKOR 55–300 mm f/4.5–5.6 GED) and a NIKON D7500 camera with a 19–300 mm lens (AF-S DX NIKKOR 18–300 mm f/3.5–5.6 GED). Two types of surveys were conducted—one was circling around the island, and the other was staying in the waters where sightings were expected. In both types of surveys, we attempted to take as many photographs as possible.

After the surveys were completed in each season, the resightings were compiled to assess the residency around the island during a season. In the present study, the good-quality photographs that were in focus and clearly showing the pattern of pigmentations on the ventral fluke and the shape of its edge were used. We printed the photographs obtained during each season and sequentially compared them by visual examination to identify the individuals. Each of the three researchers performed the above steps, and the final identification results were compiled as resightings. The individuals re-photographed at intervals of 1 or more days within the same season were considered resightings. Moreover, photographs were compared between the 2016–17 and 2017–18 seasons to assess whether the same individuals migrated to areas around the Hachijo Island in the following season.

Results and Discussion

Survey effort and sightings

Table 1 summarizes the results of the survey effort and sightings during the 2016–17 and 2017–18 seasons. The survey was conducted for respectively 32 and 34 days from November to April in the 2016–17 and 2017–18 seasons. Table 2 summarizes the monthly survey effort for each season. In both seasons, a large amount of effort was devoted to February and March when the occurrences of whales were generally expected to be high in order to obtain more Photo-ID (Urbán and Aguayo, 1987; Mori *et al.*, 1998; Mobley *et al.*, 1999; Kobayashi *et al.*, 2016). The survey area and track lines during each season are illustrated in Fig. 3. In the 2016–17 season, we covered 986.0 nautical miles in total, and the first sighting of a humpback whale in the season was recorded on November 20, 2016. From that day until March 19, 2017, 205 whales belonging to 136 social groups were sighted. In the 2017–18 season, we covered 835.6 nautical miles in total and sighted 397 whales belonging to 232 social groups from November 28, 2017, to April 9, 2018. The mean sighting rate in the 2017–18 season (11.7 whales per day) was approximately two times the rate in the 2016–17 season (6.4 whales per day). Fig. 4 presents the monthly changes in sighting per unit effort (SPUE; number of whales sighted per day) in both seasons. The temporal trend of occurrences in a season is one of the critical indicators to clarify the habitat use of humpback whales during the winter. In Okinawa (Kobayashi *et al.*, 2016) and Ogasawara (Mori *et al.*, 1998), the period of the most frequent occurrence of whales was from February to March, with a single peak. The trend observed in eastern Australia, which is considered a migration corridor, frequently occurs in the early stages of the season; this is followed by a decline and then an increase in number of whales at the end of the season (Burns, 2010).

Table 1. Survey period, survey effort (number of days surveyed and total search distance in nautical miles), total number of sightings, and sightings per unit effort (SPUE) in each winter season.

Season	Start survey (yyyy/mm/dd)	Finish survey (yyyy/mm/dd)	Survey effort (days)	Survey effort (nautical miles)	Sightings (groups/whales)	SPUE (whales/days)
2016/17	2016/11/18	2017/04/24	32	986.0	136/205	6.4
2017/18	2017/11/28	2018/04/23	34	835.6	232/397	11.7

Table 2. The number of survey days and searching distance per month in each season. The study was designed to increase survey efforts in February and March as the frequency of humpback whale occurrence in the wintering ground was expected to be high.

Season	Survey effort							
	Unit	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	Total
2016/17	Days	3	5	4	7	9	4	32
	Nautical miles	134.4	169.5	103.1	182.3	233.5	163.2	986.0
2017/18	Days	2	6	5	9	8	4	34
	Nautical miles	61.5	137.3	127.3	214.3	192.1	103.2	835.6

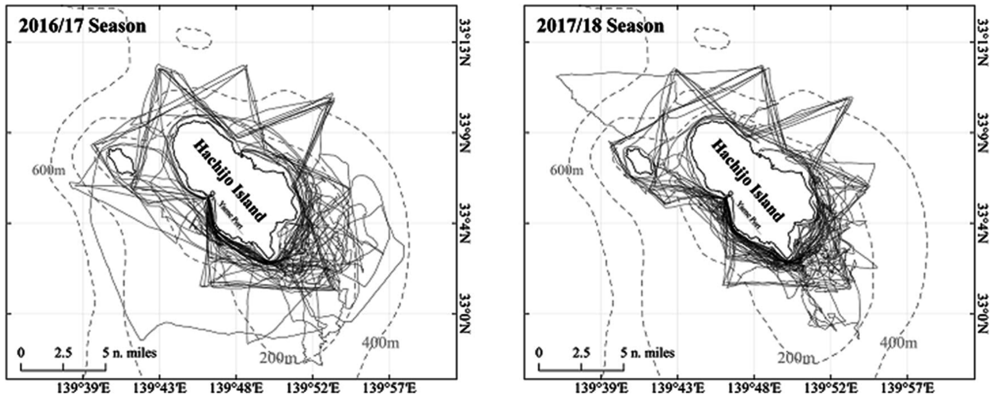

Fig. 3. Survey track lines in the 2016–17 (left) and 2017–18 (right) winter seasons. The survey was conducted within 5 nautical miles from the coast of Hachijo Island in both seasons.

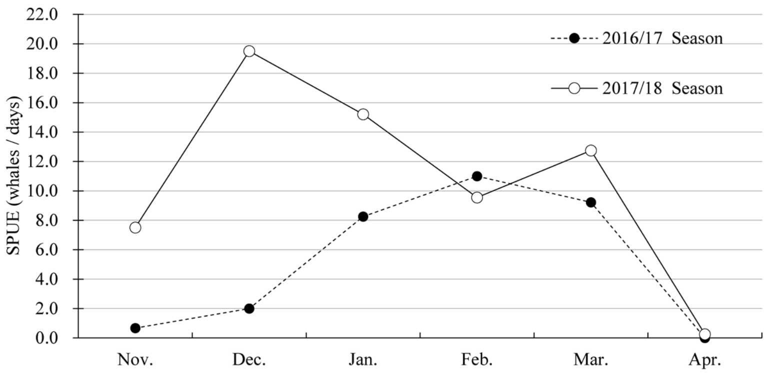

Fig. 4. Monthly sightings per day from November to April in the 2016–17 and 2017–18 seasons. SPUE: Sightings per unit of effort.

In the first season, a single peak of occurrences around the Hachijo Island was recorded in February; however, in the second season, SPUE decreased after a peak in December and then increased in March. The Kuroshio Current path is one of the possible reasons for these differences in the temporal trends of whale occurrence between the two seasons. The Kuroshio large meander was underway since August 2017, and the current path around the Hachijo Island (around 140°E) significantly differed between the first and second seasons (Qiu, 2019). In the Southern Hemisphere Madagascar wintering grounds in, humpback whales swim along strong currents during non-migratory offshore movements (e.g., travel between breeding sites or short-term offshore travel) (Trudelle *et al.*, 2016). Assuming that humpback whales behave in the same manner around the Hachijo Island, they might swim near the island or offshore depending on the Kuroshio Current path. This may have also affected the number of annual sightings in the survey area. However, detailed investigation to elucidate the above is not possible with data collected for only 2 winter season surveys. In addition, the unevenness in the amount of effort in each month of the season raises the possibility that the SPUE of some months does not adequately reflect the relative abundance of whales. Based on the above, the present study results do not allow us to determine when the peak in the number of migrating whales to Hachijo Island occurs, and it is not possible to conclude whether the use of the area by humpback whales is similar to that of Okinawa and Ogasawara. Therefore, continuous field surveys and long-term monitoring of individuals through satellite telemetry are necessary to understand the trend of occurrence of humpback whales around Hachijo Island. However, as humpback whales were continuously sighted around Hachijo Island from November to March for the two consecutive seasons, it is reasonable to assume that this species uses this area for winter migration.

Characteristic behaviors

Humpback whale singing behavior was confirmed from mid-January to late March in 2016–17 and from late November to late March in 2017–18. Singing behavior is considered to play specific roles; as such, songs serve as an acoustic display to attract females, a threat behavior during intrasexual competition, and a spacing function among males (Clapham, 2000). Furthermore, on March 5, 2017, a group of four whales and another group of two whales merged to form a six-whale group. The whales of this group swam violently. For instance, one individual hit its head on the water surface, while another pushed other whales with its head. These behaviors were consistent with the competitive behaviors reported in the wintering grounds by Tyack and Whitehead (1983) as well as by Baker and Herman (1984). Such competitive behaviors were observed respectively two and three times in the 2016–17 and 2017–18 seasons. Based on the observations of singing and competitive behaviors, humpback whales likely use the areas around the Hachijo Island as a mating ground.

Photo-identification

A total of 203 individuals were identified during both seasons. Respectively 58 and 151 individuals were identified in the 2016–17 and 2017–18 seasons, and six individuals were identified in both seasons. Table 3 summarizes the results of photo-identification in the same season, and Tables 4a and 4b summarize the survey dates and the dates when individuals were resighted for each season. In the 2016–17 season, 10 of the 58 individuals (17.2%) were resighted within the same season. Nine of ten individuals were resighted once, while one individual was resighted twice, and the period between the first and the last sighting (or occupancy) ranged from 1 to 40 days (mean: 9.5 days; SD: 13.7 days). In the 2017–18 season, 21 of the 151 individuals (13.9%) were resighted within the same season. Thirteen of the 21individuals were resighted once, six were resighted twice, and one individual was resighted each three and four times, respectively; and the occupancy ranged from 1 to 52 days (mean: 10.6 days; SD: 15.4 days). Thus, in both seasons, most of the individuals were not resighted and around 15% were resighted within the same season.

The proportion of individuals resighted during a season provides basic information on the residency of humpback whales. For instance, a high proportion indicates that individuals are likely to be resighted in a certain area and tend to stay there for a long period, whereas a low proportion indicates that individuals are less likely to be sighted in a certain area and tend to move around instead of staying. The frequency of resighting in the Hawaiian waters (off Kauai) was 5%–14% (Cerchio, 1998), and similar values have also been reported in Silver Bank (9.1%) (Mattila *et al.*, 1989), Samana Bay (15.8%) (Mattila *et al.*, 1994), Ecuador (12.9%) (Scheidat *et al.*, 2000), and Abrolhos Bank (13%) (Wedekin *et al.*, 2010). Values of approximately 10%–15% indicate that individuals do not stay in the same area for a long period and tend to move widely within each wintering ground. This observation is also supported by the reports using satellite telemetry of extensive local movements in Hawaii (Mate *et al.*, 1998), Silver Bank (Kennedy *et al.*, 2014), and Ecuador (Guzmán and Félix, 2017). In contrast, the frequency of resighting in the feeding grounds has been reported to be as high as 77.3% in the Gulf of Maine (Clapham *et al.*, 1993) and as low as 2.1% along the east coast of Australia, which is believed to be a migration corridor (Burns, 2010). Of note, these proportions depend on the survey

Table 3. Number of individuals photo-identified and resighted in each season, and the minimum and maximum period between the first and last sighting of the resighted individuals in the same season.

	Number of Photo-IDs	Number of individuals resighted (%)	The minimum period between first and last sighting (days)	The maximum period between first and last sighting (days)
2016/17	58	10 (17.2%)	1	40
2017/18	151	21 (13.9%)	1	52

Table 4a. The survey dates and dates when individuals were resighted in the 2016–17 season. Black circle indicates the date an individual was sighted.

ID #	Month	Nov.			Dec.					Jan.				Feb.						Mar.									Apr.				Number of resighting
	Day	18	20	29	3	12	13	25	26	17	18	20	22	4	5	8	25	26	27	4	5	8	9	17	18	19	20	23	5	6	23	24	
IH-004								●	●																								1
IH-007										●	●							●															2
IH-008										●	●																						1
IH-025															●						●												1
IH-029															●		●																1
IH-037																	●	●															1
IH-039																	●	●															1
IH-043																	●	●															1
IH-059																				●	●												1
IH-061																				●	●												1

Table 4b. The survey dates and the dates when individuals were resighted in the 2017–18 season.

ID #	Month	Nov.		Dec.						Jan.					Feb.									Mar.								Apr.				Number of resightings
	Day	28	29	9	10	18	20	21	23	7	8	20	21	22	8	9	10	17	18	19	20	21	22	3	4	13	14	15	26	27	28	9	10	22	23	
IH-108				●	●								●																							2
IH-101				●			●																													1
IH-049				●									●	●																						2
IH-117					●			●																												1
IH-127						●	●		●																											2
IH-159										●	●																									1
IH-166												●				●	●			●						●										4
IH-169												●		●																						1
IH-176													●	●																						1
IH-200															●		●																			1
IH-201															●		●																			1
IH-203																●							●													1
IH-207																●	●						●													2
IH-212																●	●																			1
IH-237																					●		●													1
IH-265																										●	●	●								2
IH-276																											●	●								1
IH-279																											●	●								1
IH-281																											●	●		●						2
IH-282																											●	●	●		●					3
IH-303																													●	●						1

effort and population size. In the present study, since 80% of the resighted individuals were sighted within three days of their first sighting, the proportion of resighting may have been underestimated due to 1–2 weeks interval between the survey dates. However, considering the short gap between resighting and the rare sighting of individuals, such as IH-166, for two months, possibly few individuals remain in the vicinity of Hachijo Island for an extended period, suggesting that the residency of humpback whales around Hachijo Island is comparable to that in other wintering grounds.

Interestingly, 6 of the 58 individuals identified in the first season returned to the waters around the Hachijo Island in the subsequent season (Fig. 5). According to Calambokidis *et al.* (2001), few individuals migrate to different wintering grounds every year, and each population has a specific wintering ground.

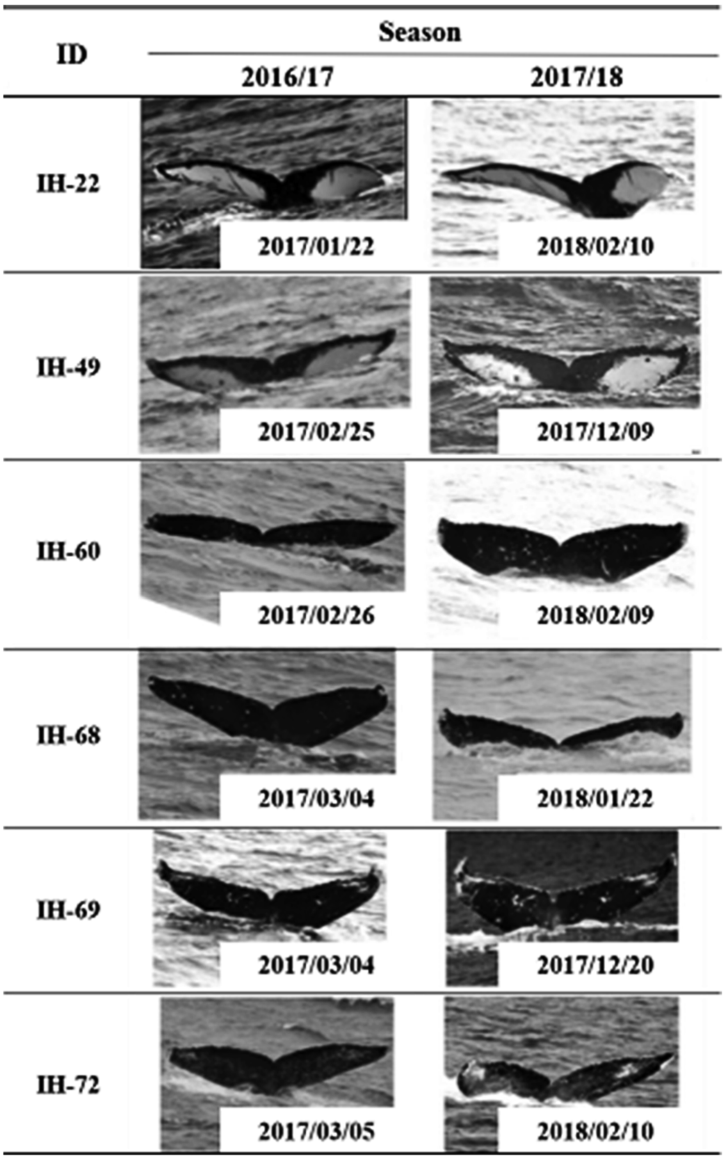

Fig. 5. Tail photographs of whales that were observed around the Hachijo Island in two consecutive seasons. Dates indicate the day on which each individual was photographed in each season (all copyrights are reserved to TUMSAT).

Calambokidis *et al.* (2001) assessed the site fidelity for North Pacific wintering grounds using the Match index (Equation 1), which reflects the size of the overall population sampled and the degree of site fidelity.

The Match index is expressed by the following:

$$I_{i \to j} = [m_i / (a_i n_j)] \times 1{,}000 \quad (1)$$

where,

a_i = number of marked releases at time 1 in region i (i=1, …, R)
n_j = number examined for marks at time 2 in region j
m_i= marked recaptures in region j, originally marked in region i

The frequency of identification of the same individual in different wintering grounds during different years was low, and the Match index was 0.015 between Mexico and Hawaii, 0.010 between Hawaii and Japan (Okinawa and Ogasawara), and 0.000 between Mexico and Japan; however, frequency of reidentification of the same individual in the same wintering grounds but during different years was relatively high, and the Match index was 0.257 for Hawaii, 0.518 for Mexico, and 2.365 for Japan (Calambokidis *et al.*, 2001). Around the Hachijo Island, 58 individuals were marked in the first season (a_i), 151 individuals were examined for marks in the subsequent season (n_j), and 6 individuals were recaptured (m_i). Based on these counts, the Match index was 0.685, indicating that site fidelity for the Hachijo Island is similar to that reported for Hawaii and Mexico.

Considering that the residency and site fidelity for the Hachijo Island were comparable to those for the other wintering grounds, the same population likely migrates to the areas around the island annually and uses it as some parts of their wintering grounds. In other words, this area is as important as other wintering grounds for the migration of humpback whales, and migration to waters off the Hachijo area is expected to continue in the future.

Absence of mother–calf pairs

Newborn calves (typically approximately 4 m long) were not sighted in both seasons. In Okinawa and Ogasawara, mother–calf pairs have been observed during winter (Darling and Mori, 1993; Kobayashi *et al.*, 2016). Generally, the SST at the wintering grounds of humpback whales is above 21.0°C (Rasmussen *et al.*, 2007). However, according to daily measurements near the Yaene Port (33°06′N, 139°50′E) by the Tokyo Metropolitan Islands Area Research and Development Center for Agriculture, Forestry and Fisheries, the mean SST from November to April was 19.0°C (SD: 3.1°C; range: 13.6–25.8°C) in the 2016–17 season and 19.9°C (SD: 1.9°C; range: 15.4–24.1°C) in the 2017–18 season. This relatively low SST may be unsuitable for nursing. However, based on a personal communication (Kato, H., Akama, N. and Kono, E., pers. comm.) a mother-calf pair was observed in the southeastern part of the island in March 2016, which may have been missed in our survey.

The results of the present study provide novel insights into the annual migration of humpback whales to the waters around the Hachijo Island and their distinct breeding behavior in winter. However, we cannot conclude whether the waters around the Hachijo Island indeed serve as a breeding ground for these whales, similar to Okinawa and Ogasawara, given the absence of newborn calves. The objective of migration to the areas around the Hachijo Island remains debatable, and several hypotheses have been put forth, such as these areas being part of a migration corridor or this being a temporary migration. If the waters around the Hachijo Island are established as a breeding ground in the future, mother–calf pairs should be sighted frequently around the island. Therefore, long-term monitoring focusing on the composition of the social groups should be conducted to reveal the habitat use. Moreover, in humpback whales, the timing of migration to wintering ground varies depending on the sex and reproductive status (Dawbin, 1966; Brown *et al.*, 1995) of individuals. Therefore, the sex and sexual maturity of whales sighted around the Hachijo Islands should be determined and compared with those of whales reported in other wintering grounds to clarify the habitat use of the waters around this island.

Causes of sudden appearance

The abundance of humpback whales in the North Pacific Ocean declined from approximately 15,000 in 1905 to 1,000 in 1965 because of catch in commercial whaling (Johnson and Wolman, 1984). Following the prohibition of commercial whaling of this species in 1966 by the International Whaling Commission, the number of humpback whales increased. More recently, the abundance of humpback whales in the North Pacific Ocean was estimated to be 21,063, which is greater than the estimates of pre-whaling abundance (Barlow *et al.*, 2011). This explosive increase in the number of humpback whales in the North Pacific Ocean may be one of the reasons for the sudden appearance of these whales around the Hachijo Island in winter. In fact, the expansion of the wintering grounds of humpback whales with the recovery of their population in the Hawaiian waters has been reported (Mobley *et al.*, 1999). Similarly, expansion of the wintering grounds was confirmed near

Peru (Guidino *et al.*, 2014). However, there are no data on the abundance of humpback whales in the western North Pacific Ocean after the "Structure of Populations, Levels of Abundance, and Status of Humpbacks" (SPLASH) study (Barlow *et al.*, 2011). Further, the population dynamics around 2015, when humpback whales appeared around Hachijo Island, must be clarified to prove this hypothesis. Currently, the stock structure of the population migrating to the Hachijo Island remains unclear. Therefore, the migratory connections between the Hachijo Island and other wintering grounds in the North Pacific Ocean and feeding grounds at high latitudes must be established based on photo-identification and genetic data. To clarify the cause of the sudden appearance of humpback whales around the Hachijo Island, continuous monitoring at a local scale around the island, and at a broader scale, is imperative.

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GROWTH-RELATED CHANGES IN CRANIUM OF KILLER WHALES IN THE WESTERN NORTH PACIFIC

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Abstract

One of the crucial questions for using the skull morphology for classification purposes in cetaceans is whether the skull features have growth-dependent differences. This question was addressed by examining cranial specimens collected from killer whales in different localities of the western North Pacific. The present study is the first to investigate developmental change in the skull morphology of western North Pacific killer whales. A total of 24 cranial measurement characters were examined from 22 animals collected between 1937 and 2011. Two kinds of analyses were conducted 1) the relationships between body length (BL) and cranium length (condylobasal length CBL), and 2) between CBL and each measurement character. For these analyses, an allometric equation was used. The relationship between BL and CBL showed a negative growth pattern, consistent with previous studies in delphinid species. The length of the lacrimal bone and the width of the internal nasal cavity showed isometric change. Therefore, these characters can be used as criteria for sex and/or species/subspecies classification as their proportions are free from relative change with respect to skull growth in CBL. Regarding ontogenic growth, this study showed that the anteroposterior length of the temporal fossa, the zygomatic process and the space where the temporal muscle passes became proportionally larger as their skull grows. The development and activity of temporal muscles would produce these changes. On the morphometric features involved in the generation and modification of acoustic signals, this study found the following changes: the width of the posterior regions of the rostrum and preorbital bone became wider; the ventral surface of the preorbital process became thick and sturdy, and the maxillary crest became more apparent with the skull growth. Therefore, these morphometric features might be used to characterize species/subspecies of the killer whales, which have highly divergent foraging behavior and vocalization.

Key words: killer whale, skull morphology, growth-related change, western North Pacific.

Introduction

The skull is an anatomical feature that consistently and compellingly displays species-specific characteristics and is an essential tool to study morphological differentiation (Miyazaki, 1994). Hence, the skull size and shape can be essential as classification criteria. Studies on small cetaceans showed that the shape and size of the skull could provide information on geographical distribution of the species, intraspecific subpopulations with different ecological characteristics such as feeding ecology and acoustic properties, and social behavior, e.g., Van Waerebeek (1993), Yoshida *et al.* (1995), Galatius and Gol'din (2011), Costa *et al.* (2016). Kitchener *et al.* (1990) studied the skull morphology of false killer whale *Pseudorca crassidens* from three ocean basins, Australia ($n=34$), Scotland ($n=58$), and South Africa ($n=53$), showing considerable divergence among localities, including sexual dimorphism in the skull morphology. They considered this helpful information for the conservation and management of the species.

Comparative analyses of skull morphology require large sample sizes; however, the availability of samples and data for such studies is limited for most cetacean species, including the killer whales *Orcinus orca*. Killer whales are distributed throughout all oceans and contiguous seas, from equatorial regions to the polar pack-ice zones. Still, they are most numerous in coastal waters and cooler areas where productivity is high (Rice, 1998). Their wildly divergent diet preferences, cultural practices, and external morphological characteristics seem incongruent with their current categorization as a single taxon (Heyning and Dahlheim, 1988; Pitman and Ensor, 2003; Foote *et al.*, 2009; Morin *et al.*, 2010; Pitman *et al.*, 2011). Resident, transient and offshore killer whale ecotypes have been well characterized since the 1980s in the eastern North Pacific (Bigg *et al.*, 1990).

Further west of the North Pacific, a report identified multiple killer whale subpopulations throughout the Aleutian Islands: one subpopulation in the eastern and one in the central Aleutian Islands, and a third subpopulation ranging from the western Aleutians to Kamchatka and the Kuril Islands, Russia (Parsons *et al.*, 2013). Recent colonization/re-colonization of the western North Pacific by small groups of killer whales originating from the central/eastern North Pacific has been suggested (Filatova *et al.*, 2018). Although the information on this species around Japan is limited, catch records between 1948 and 1957 indicated killer whales were distributed in the coastal waters off Japan from Hokkaido to the Okinawan islands. Researches in different oceans have revealed the existence of sympatric populations displaying morphological, dietary, and genetic diversification e.g., in the Antarctic (Pitman and Ensor, 2003; LeDuc *et al.*, 2008) and the North Atlantic oceans (Foote *et al.*, 2009, 2010; Morin *et al.*, 2010). Currently, the taxonomic status of killer whales is undergoing scrutiny and possible revision (Krahn *et al.*, 2004; LeDuc *et al.*, 2008; Morin, 2010; Bruyn *et al.*, 2013).

One important question for using the skull morphology for classification purposes is whether the skull features have a nature of growth-dependent differences. In the present study, this question was addressed by examining cranial specimens of killer whales collected from different localities in the western North Pacific. This study is the first one to investigate a developmental change in the skull morphology of killer whales.

Materials and methods

Samples

The list of samples used in the present study is shown in Table 1. Skull samples of killer whales were available from different museums, aquariums and other institutions in Japan. Killer whales were from different localities of the Pacific coast of Japan, the Okhotsk Sea, and around the Okinawan Islands. A total of 22 skulls of killer whales (seven females, eight males, and seven individuals with no sex information) were available. Body length information was available for 14 whales.

Morphometric feature

Cranial measurements are given in Table 2. Crania were measured in a straight line using an anthropometer to the nearest 0.1 cm. We did not include the mandible bone in this study because it was lost in several individuals. A total of 24 measurements was used in the statistical analysis (Table 2, Fig. 1). Most of those measurements have been used previously in taxonomic and population identity studies of Delphinidae species (Perrin, 1975; Kitchener *et al.*, 1990). In this study the measurements were identified using the prefix 'Vx' (see Table 2). The body length and sex information were obtained from each museum, aquarium or university storing a specimen when possible. The observation of genital organs determined sex.

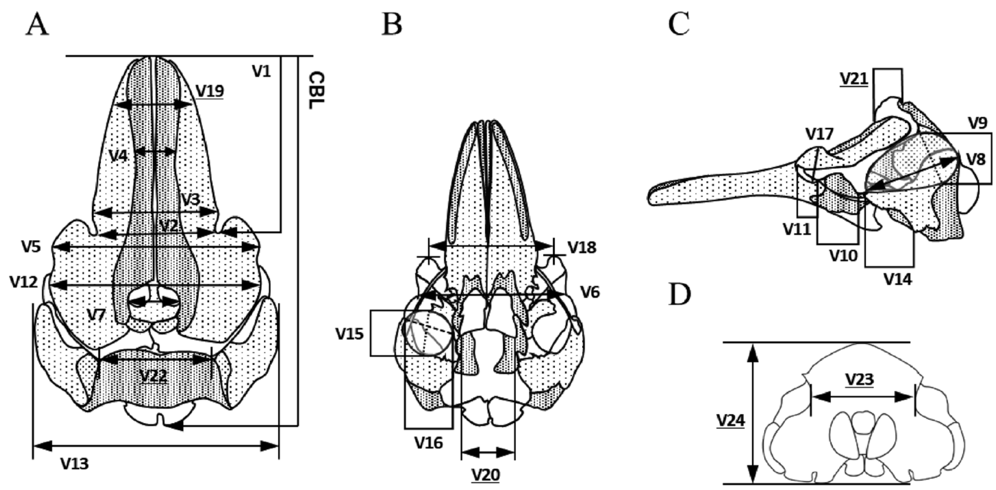

Fig. 1. Killer whale *Orcinus orca* cranial measurement points. **A**: Dorsal view of the cranium, **B**: ventral view, **C**: lateral view, and **D**: posterior view. Measurement points were determined following Perrin (1975) and Kitchener *et al.* (1990) and are abbreviated according to Table 2.

Statistical analysis

The relationships between body length and skull length, and between skull length and each length measurement were examined using the following allometric equation:

$$y = \beta x^{\alpha} \tag{1}$$

where x is body/skull length, y is skull length/each length measurement, β is the intercept of the line on the y-axis, and α is the slope of the line, also known as the allometric coefficient. The allometric coefficients (α) at each measurement site were examined using a t-test for classification of three different growth patterns: positive allometry (α significantly greater than 1), isometric allometry, and negative allometry (α significantly smaller than 1). Analyses by sex were not conducted because of the limited number of whales with identified gender. Although the range of sampling years was vast, we treated them as one sample collection because of the limited number of specimens available.

Results

Relationship between body length (BL) and skull length (condylobasal length CBL)

The relationship between BL and CBL (Fig. 1) was examined in a subset of 14 killer whale samples for which body length data were available. The BLs in these whales ranged from 218 cm to 785 cm, which had CBLs of 43.8 cm and 121.7 cm, respectively (samples No. 15 and 8, respectively in Table 1). The CBL showed a negative growth pattern ($y=-0.37x^{0.78}$, $P<0.001$) (Fig. 2), indicating that CBL growth is relatively slower than that of BL.

Relationship between skull length (CBL) and other cranial measurements

Table 2 shows the results of the allometric analyses for the relationship between CBL and each cranial measurement (see also Appendix).

Skull width, rostral length and width

Four of the five skull width characters (V5, V6, V12, and V13 in Fig. 1 and Table 2) showed a positive growth pattern, though the width at the tip of the antorbital process of the maxilla (V18) was isometric. The rostral width characters (V2–4 and V19) also exhibited positive allometry with the growth of CBL (Table 2). These results showed the braincase becoming relatively shorter, the rostral length

Table 1. List of specimens of the killer whales from western North Pacific examined in this study, by sex, age, and locality of sampling. Body length (BL) and skull (condylobasal) length (CBL) are also shown.

Sample no.	Sex	BL (cm)	CBL (cm)	Age	Location	Year obtained	Sample ID	Sample holder
1	F	547	98.5	—	East China Sea, Okinawa	1988	M67 (nago-B)	Nago Museum
2	F	600	99.2	17*	Nemuro Strait, Rausu	2005	kaitaku-AKW6	Hokkaido Museum
3	F	654	108.6	29*	Nemuro Strait, Rausu	2005	rakuno-AKW9	Rakuno Gakuen University
4	F	614	103.8	—	Pacific Ocean, Kii Peninsula, Taiji	2008	1.2.7	Port of Nagoya Public Aquarium
5	F	589	99.7	>28**	Pacific Ocean, Kii Peninsula, Taiji	2011	Taiji-6	Taiji Whale Museum
6	F	563	98.3	13*	Nemuro Strait, Rausu	2005	AMP-R20-AKW2	Ashoro Museum of Paleontology
7	F	550	99.8	—	Okinawan Island, Japan	1994	SUM071	Okinawa Churashima Foundation
8	M	785	121.7	—	Seto Inland Sea, Hyogo	1957	Suma-K01	Suma Aqualife Park
9	M	700	110.7	—	East China Sea, Okinawa	1988	M66 (nago-A)	Nago Museum
10	M	704	118.2	—	Soya Strait, Wakkanai	2010	SNH10057	Okhotsk Museum Esashi
11	M	660	107.9	—	Pacific Ocean, Kii Peninsula, Taiji	1978	Taiji-2	Taiji Whale Museum
12	M	—	122.0	—	Okhotsk, Sakhalin Island, Gulf of Patience	1937	KPM-NF1002979	Kanagawa Prefectural Museum of Natural History
13	M	690	120.6	—	Pacific Ocean, Kii Peninsula, Taiji	1966	Taiji-1	Taiji Whale Museum
14	M	410	85.1	—	Boso Peninsula, Japan		O-15	Tobayama's Cetacean Collection/TUMSAT***
15	M	218	43.8	—	Boso Peninsula, Japan		O-11	Tobayama's Cetacean Collection/TUMSAT***
16	Uk	—	96.5	—	Toyokoro-cho, Hokkaido, Japan	2005	AMP-R26	Ashoro Museum of Paleontology
17	Uk	—	96.2	—	Taiki-cho, Hokkaido, Japan	2005	AMP-R27	Ashoro Museum of Paleontology
18	Uk	—	104.2	—	Japan		ICR-001	Institute of Cetacean Research
19	Uk	—	106.8	—	Kii Peninsula, Japan		Taiji-3	Taiji Whale Museum
20	Uk	—	104.9	—	Kii Peninsula, Japan		Taiji-4	Taiji Whale Museum
21	Uk	—	103.4	—	Kii Peninsula, Japan		Taiji-5	Taiji Whale Museum
22	Uk	—	104.6	—	Okinawan Island, Japan		Okinawa-1	Okinawa Churashima Foundation

*: Age information quoted from Amano *et al.* (2011).
**: Rearing period.
***: Tokyo University of Marine Science and Technology.

(V1) somewhat longer, and the braincase width relatively more comprehensive (Fig. 3). The zygomatic process of the squamosal bone became laterally more protrusive with CBL growth, in qualitative observation, as the space where the temporal muscle passes (the ventrolateral opening of the temporal fossa) was getting more enlarged compared to those of the newborn calf (Fig. 4).

Braincase

In this study, the braincase was defined as the regions directly covering the brain, including the frontal, maxilla, premaxilla, ethmoid, sphenoid, squamosal, parietal, interparietal and occipital bones (Uekusa *et al.*, 2018). The measurements indirectly describing the braincase size (V22, V23, and V24) showed negative allometry or isometry, though the length of squamosal (V14), which is not directly

Table 2. Relative growth coefficients and growth patterns of each killer whale skull region.

Region	Site no.	Measurement character	n	Based on condylobasal length (CBL) α	Based on condylobasal length (CBL) $\ln\beta$	P-value†	Relative growth pattern	Adj. R square
Skull width	V13	Greatest width of skull	22	1.13	−1.04	**	positive	0.99
	V5	Greatest preorbital width	22	1.18	−1.44	**	positive	0.97
	V6	Least supraorbital width	22	1.24	−1.75	**	positive	0.98
	V12	Greatest width of maxillaries	21	1.34	−2.19	**	positive	0.91
	V18	Width at tip of anterior process of maxilla	21	1.31	−2.14	0.075	isometry	0.76
Rostral length and width	V1	Length of rostrum	22	1.13	−1.23	*	positive	0.98
	V2	Width of rostrum at base	22	1.28	−2.49	**	positive	0.98
	V3	Width of rostrum at 60 mm anterior to the base of rostrum	21	1.35	−2.78	**	positive	0.89
	V4	Width of premaxillaries at midlength of rostrum	22	1.59	−4.93	**	positive	0.91
	V19	Width of rostrum at 3/4 length, measured from posterior end	20	1.91	−5.81	**	positive	0.93
Braincase	V22	Greatest parietal width at the posterior section of the frontal	21	0.75	0.14	*	negative	0.75
	V23	Greatest occipital width within temporal fossa	20	0.95	−0.76	0.795	isometry	0.54
	V24	Height of skull	11	1.15	−1.52	0.458	isometry	0.79
	V14	Length of zygomatic process of squamosal (right)	22	1.28	−2.95	**	positive	0.98
Temporal fossa	V8	Greatest length of right temporal fossa, measured to external margin of raised suture	22	1.20	−2.01	**	positive	0.97
	V9	Greatest width of right temporal fossa at right angles to greatest length	21	1.07	−1.91	0.744	isometry	0.57
	V15	Anteroposterior diameter of the ventrolateral opening of the right temporal fossa	20	1.35	−3.37	*	positive	0.87
	V16	Lateral diameter of the ventrolateral opening of the right temporal fossa	21	1.40	−3.60	0.054	isometry	0.72
Nasal area	V7	Greatest width of external nares	21	0.85	−1.27	0.398	isometry	0.55
	V20	Greatest width of internal nares	20	0.95	−1.52	0.32	isometry	0.95
	V21	Distance from foremost end of junction between nasals to hindmost point of margin of supraoccipital crest	19	0.76	−1.19	0.08	isometry	0.65
Orbital region	V10	Length of right orbit from apex of preorbital process of frontal to apex of postorbital process	22	0.53	0.08	**	negative	0.70
	V11	Length of antorbital process of right lacrimal	22	1.17	−3.12	0.307	isometry	0.72
	V17	The antorbital process thickness: the distance from the ventral surface of the lacrimal to the dorsal surface of the maxilla (right-side)	21	1.84	−5.90	**	positive	0.79

†: The significance of deviation of each relative coefficient from a value of 1 (*: $P<0.05$, **: $P<0.01$).

related to the braincase size, showed positive allometry (Table 2). According to qualitative observations, the parietal bones in the newborn calf's temporal crest were laterally curved convex in posterior view, and the greatest parietal width within the temporal fossa was wide as long as the greatest width of the skull (Fig. 3). However, the temporal surface of the parietal bones concavely curved with CBL growth and development of the temporal crest.

Temporal fossa

The anteroposterior length (V8) and the dorsoventral width (V9) of the temporal fossa showed positive allometry and isometry, respectively (Table 2). Hence, the temporal fossa size became rela-

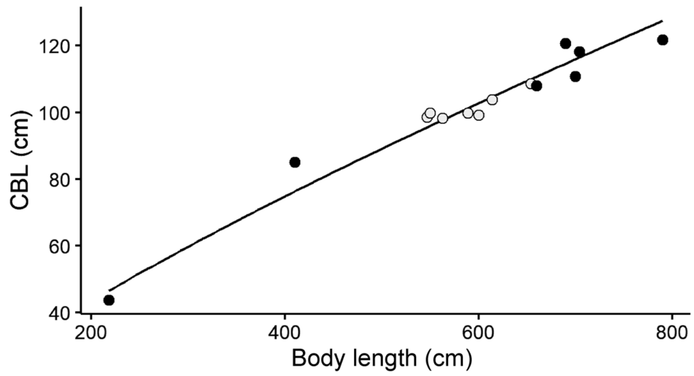

Fig. 2. Relationship between body length and condylobasal length (CBL). Black and white circles indicate males and females, respectively. The solid line indicates the prediction line from allometry analysis.

tively broader with CBL growth (i.e., horizontally with a long, elliptic shape) (Fig. 4). In qualitative observations, the dorsal and lateral views of the skulls showed that the posterior ends of the temporal crest are located far anterior to the posterior end of the occipital condyles in the newborn calf (Fig. 3). However, along with the growth of the CBL, the posterior ends of the temporal crest were extended in a posterior direction, and the crest of the temporal fossa clearly developed, becoming thick and conspicuously ridged.

The anteroposterior diameter (V15) and the lateral diameter (V16) of the ventrolateral opening border of the temporal fossa showed positive allometry and isometry, respectively. These growth patterns represented an extension of the space where the temporal muscle passes (Fig. 4). The posterior view of the skull clearly showed the development of the temporal crests and an exoccipital and squamosal extension with CBL growth (Fig. 3).

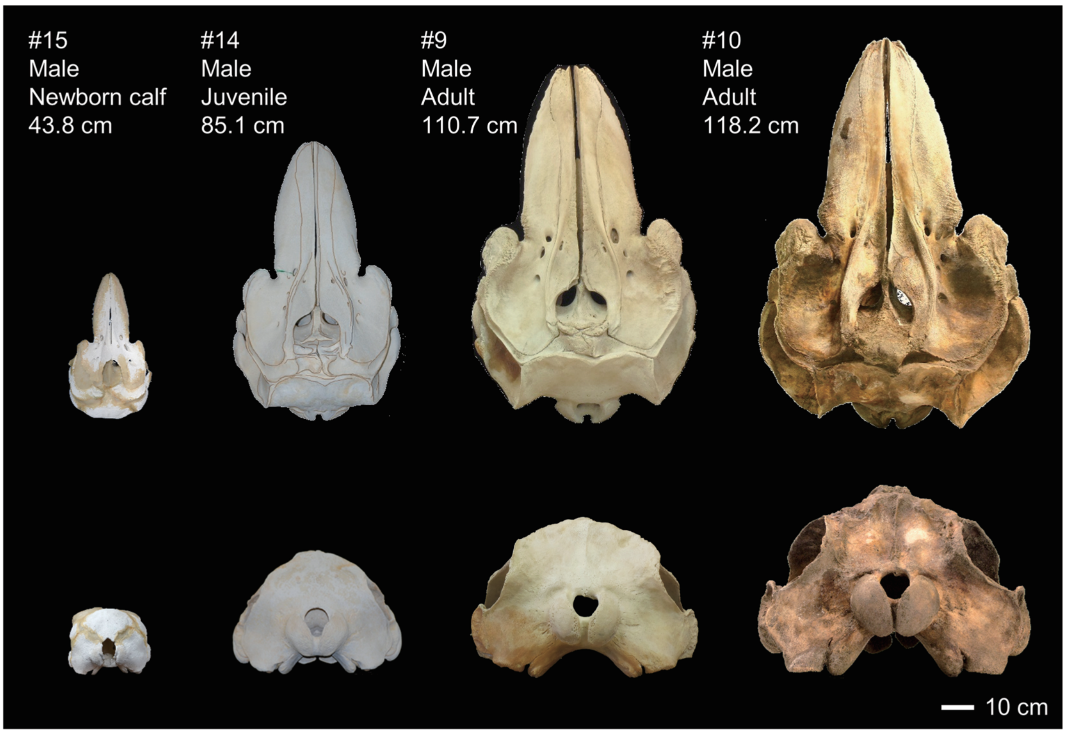

Fig. 3. Dorsal (upper) and posterior (lower) view of four male killer whale crania. Condylobasal length (CBL) and width of these crania scaled to the actual length.

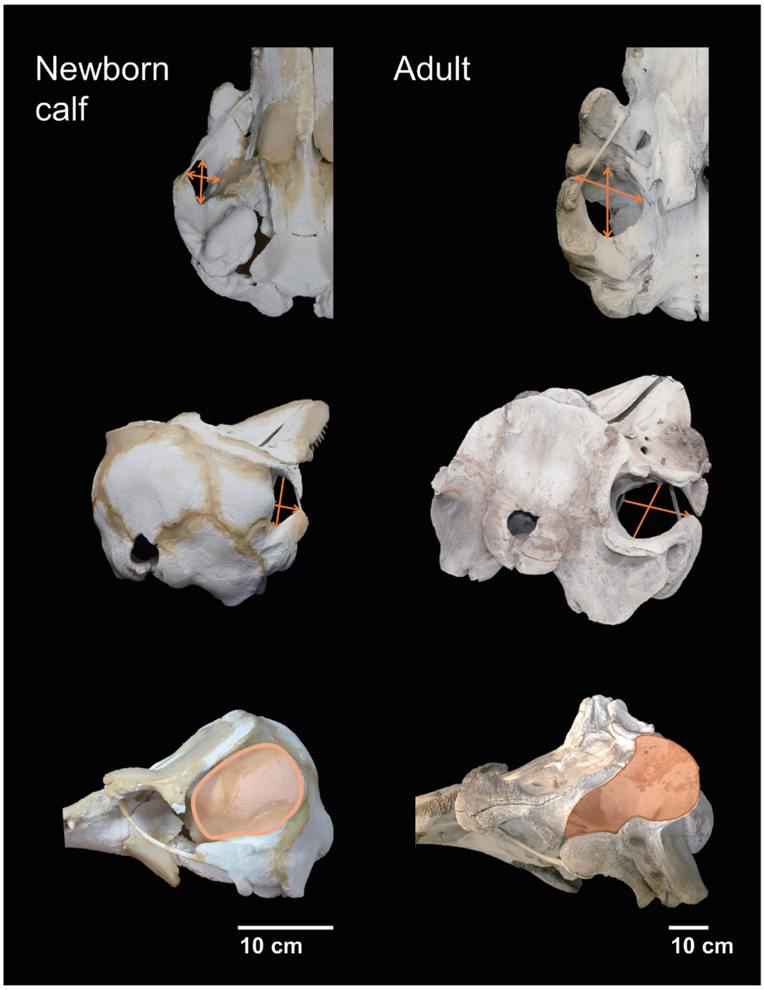

Fig. 4. Ventral (upper), diagonally right rear (middle) and lateral (lower) views of the newborn calf and adult killer whale cranium. Orange arrows show the measurement points of the ventrolateral opening border of the temporal fossa, which consists of the zygomatic process of the squamosal bone posteriorly and the postorbital process of the frontal bone anteriorly (V15 and V16 in Table 2 and Fig. 1). Orange shades cover the estimated area where the temporal muscle is attached.

Nasal area

The width of the nares (V7 and V20) and the anterior junction of nasal to posterior margin of supraoccipital crest length (V21) displayed isometry (Table 2). According to qualitative observations, the adult animals' nasal and surrounding areas (frontal, parietal, and occipital bones) were particularly protruded in a dorsal direction, which differed from those of the newborn calf (Fig. 4). Frontal and intraparietal bones were hardly visible as they were covered by maxillary and supraoccipital bones.

Orbital region

The orbit length from the apex of the preorbital process of the frontal bone to the apex of the postorbital process, represented by V10, exhibited negative allometry (Table 2). The antorbital process thickness defined as the distance from the ventral surface of the lacrimal to the dorsal surface of the maxilla (V17) indicated positive allometry (Table 2). The relative length of the antorbital process of the lacrimal bone (V11) showed isometry with CBL growth, and it was thick and sturdy throughout the growth of a newborn into an adult whale (Fig. 4). The surface of the antorbital process, represented by the maxilla bone, remarkably developed in a dorsal direction.

Discussion

Relationship between CBL and BL

The ratio of CBL to BL of killer whales declined with growth, and negative allometry was detected (Fig. 2). According to previous studies, the growth rate of some delphinid species' skull decreases with growth, and they stop growing when their BL reaches a plateau at a certain age (Perrin, 1975; Ito and Miyazaki, 1990; Kitchener *et al.*, 1990; Miyazaki and Amano, 1994). Therefore, the results of the present study agree with those previous studies. Differences in physical maturity of BL between sexes are known in some whale species (e.g., short-finned pilot whale *Globicephala macroryhnchus* (Miyazaki, 1990), false killer whale *Pseudorca crassidens* (Baird, 2002; Ferreira *et al.*, 2014)). Killer whales exhibit a difference in size according to sex (adult males are longer than females). Sexual dimorphism (especially in external morphology) is evident in the killer whales. For example, profound sexual dimorphism was observed in the dorsal fin and flipper size (males have larger structures) (Heyning and Dahlheim, 1988). Therefore it is expected that such sex differences in the relationship between CBL and BL also occur in the killer whales, and future studies should consider comparisons between females and males.

Utility of skull measurements as classification criteria

Isometric changes in some particular skull measurements mean that such measurements can be employed as criteria for sex and/or species/subspecies classification as they are not affected by changes in the skull size. While other measurements also showed an isometric character, the authors consider that the best candidates to be used as taxonomical classification criteria are the lacrimal bone length (V11) and the width of the internal nasal cavity (V20) because these measurements showed isometry (Table 2).

Lacrimal bone length (V11)

The proportion of V11 to the CBL did not change from newborn calf to adult, thus showing that it might be helpful for sex prediction analysis in all age stages. A previous study that used only adult killer whales from the western North Pacific reported that the lacrimal bone length was useful for sex prediction in this species (Takahashi *et al.*, 2019). The study used linear discriminant analysis and a Random forest algorithm. However, the authors recommended caution in interpreting their results as the true sexual dimorphism for the population because the number of samples used in the study was limited. The present study used a comparatively larger sample size, adding calf killer whales and gaining results to support this measurement character's utility for classification criteria: e.g., sex classification. Kitchener *et al.* (1990) reported a significant difference in this measurement between sexes in the false killer whale *P. crassidens*. This would be collateral evidence supporting our results. Therefore, we conclude that the killer whale lacrimal bone length might be useful for sex prediction regardless of specimen age.

Width of the internal nasal cavity (V20)

The width of the internal nasal cavity presented an isometry pattern with a high adjusted R square value (>95%). This measurement character might be used as novel criterion to discriminate species and subspecies of killer whales because 1) the measurement presented a low individual variance, and 2) the proportion of the measurement never changes with growth. Point 2) makes possible that all available samples can be used for discriminatory purposes. With larger sample sizes, this measurement character might be helpful to discriminate between sexes as well.

Maturity and sex information are usually used in studies on taxonomy based on morphometry. The body shape (not only the skull shape) of immature animals usually differs from that of mature animals. Such studies require a considerable number of samples to deal with several factors (e.g., sex, maturity). However, materials of this kind are hard to obtain in cetaceans. For this reason, the information on growth-independent changes of some skull measurements in the present study is essential for future taxonomical studies of the killer whales.

Effect of ontogenetic growth on cranial shape

The allometry of the cranium of the killer whale was examined to clarify the effects of size (i.e., ontogenic growth) on cranium shape. Only the width at the posterior section of the frontal bone (V22) showed clearly negative allometry, although other features related to skull width (e.g., V13) showed positive allometry. The analyses suggest that the upper maxillaries width (V12) indicates negative allometry while it represents the dorsal part of the braincase, i.e., it is restricted by the brain size. In contrast, the skull width (V13) and the horizontal diameter of temporal fossa proper (V16), which are not determined by brain size, showed positive allometry, creating space for the temporal muscle to pass. In other words, the temporal muscle can be developed with CBL growth.

The temporal muscle is a fan-shaped muscle situated within the temporal fossa of the skull. The primary function of this muscle is to produce the movements of the mandible at the temporomandibular joint and thus facilitate the act of mastication. In the case of cetaceans, the temporal muscle is also known as one of the most developed muscles for mouth-closing (Seagars, 1982; Herring, 2007; Kim *et al.*, 2018). A site of origin for the temporal muscle is the temporal fossa represented by V8 and V9 in our study. Although the width of the temporal fossa in a dorsoventral direction (V9) had no positive allometry, the length in an anteroposterior direction (V8) showed a high development with CBL growth without being limited in a space produced by brain size. By qualitative observation, the posterior ends of these bones consisted of the temporal fossa extending in a posterior direction, over the posterior end of the braincase. These results indicate an extension of the surface and the crest where the temporal muscle originates (Fig. 4). In addition, the results showed that the space where the temporal muscle passes were expanded with positive allometry and isometry (V15, 16; Fig. 4). Therefore, the temporal fossa and temporal crest expansion may be caused by the development of muscle thickness. Especially, the posterior extension of the temporal crest might also increase the length of the muscle itself and increase the area of temporal muscle attachment. In the case of the bottlenose dolphin, the allometry of the temporal fossa implies the development of the temporal muscle with CBL growth, and similar trends in the allometry of these characters between mature and immature specimens indicate that the development of temporal muscle occurs not only in ontogeny but also in larger specimens among mature individuals (Kurihara and Oda, 2009). In other words, the feeding habit affects this morphological feature during both the immature and mature stages. This previous study speculated that the same tendency might occur in the killer whales since they have a habit of catching and shearing/biting prey (Ford, 2018). Therefore, if this tendency also occurs in mature killer whales having different feeding habits (i.e., ecotype), this morphological feature should be further examined for a more sophisticated understanding and increased application in taxonomy.

Killer whale's rostral length and width characteristics showed positive allometry in this study, which appears to be related to the development of the feeding apparatus. Several studies using a sufficient number of skull samples, e.g., bottlenose dolphin (Kurihara and Oda, 2009), baleen whales (Nakamura *et al.*, 2012), have concluded that the positive allometry of rostral length is related to the feeding apparatus, i.e., it reflects the growth for extension of the range for prey catching (Costa *et al.*, 2016). For the rostral width, it might have been affected by the development of the lateral rostral muscles inserted at the lateral side at the rostrum. Mead and Fordyce (2009) concluded that the posterior areas of the rostrum (V2 and V3 in this study) and its attached rostral muscles are involved in the feeding apparatus. Hence these features can reflect differences in feeding habits between populations.

In addition to the width of the rostrum, the present study results suggested that the width from the ventral surface of the lacrimal bone (i.e., ventral surface) to the top of the maxillae bone showed positive allometry. Also, the surrounding area, i.e., the antorbital process of the maxillae bone and the preorbital process of the frontal bone, became thick, tough, sturdy, and the maxillary crest became more remarkable with CBL growth. The posterior areas of the rostrum and the area surrounding the antorbital process of the maxilla are suggested that it is involved in the generation and modification of acoustic signals (Mead, 1975; Huggenberger *et al.*, 2009). These portions are covered by the anterointernus muscle and *M. maxillonasolabialis anteroexternus*, relating the nasal apparatus structure (Huggenberger *et al.*, 2009). Huggenberger *et al.* (2009) concluded that these muscles might exert a pulling force on the connective tissue dorsal to the anterior nasofrontal sac and the rostral bursa cantantis. The lateral region of the *M. maxillonasolabialis anterointernus* attaches to connective tissue dorsal to the angle and the inferior vestibulum and may control air movement and pressure in the angle and the nasofrontal sac.

Moreover, Cranford *et al.* (2011) concluded that all extant toothed whales generate sonar signals using phonic lips and these muscles and tissues. In the killer whales, various and high-frequency acoustic behaviors are known, and they can be considered as one of the survival strategies or habits by population/ecotype (Miller and Bain, 2000; Deecke *et al.*, 2005, 2011; Simon *et al.*, 2006). Therefore, the apparent developmental change in this area might be considered one of the crucial features of each killer whale population/ecotypes, and combining previous studies and our morphological report could provide valuable evidence on taxonomic studies.

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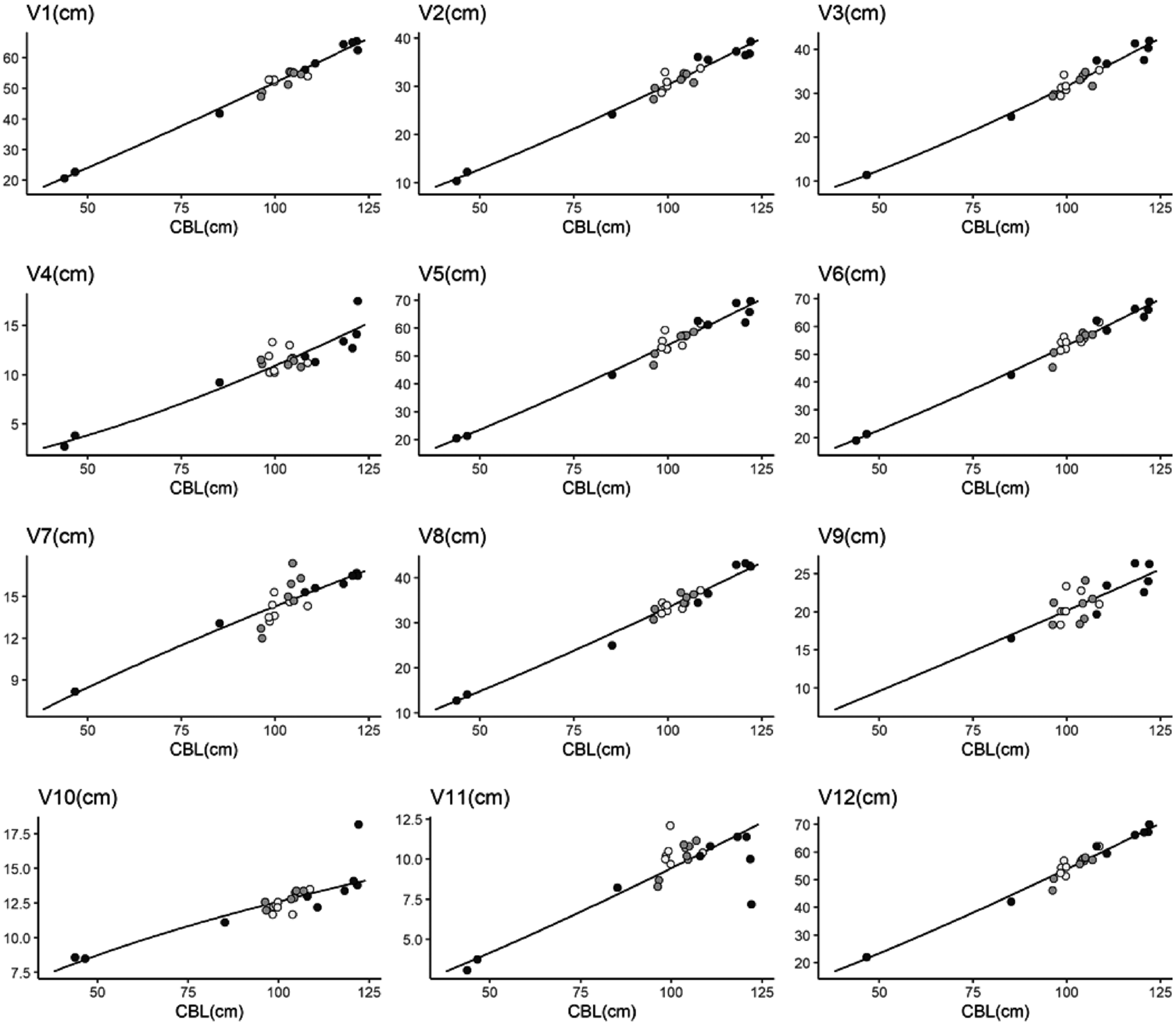
Appendix

Changes in the proportion of each measured character to the CBL of killer whales in the western North Pacific. Black, white, and gray indicate male, female, and sex-unknown, respectively. The solid line indicates the prediction line from allometry analyses. Skull morphometric feature measurements are abbreviated according to Table 2.



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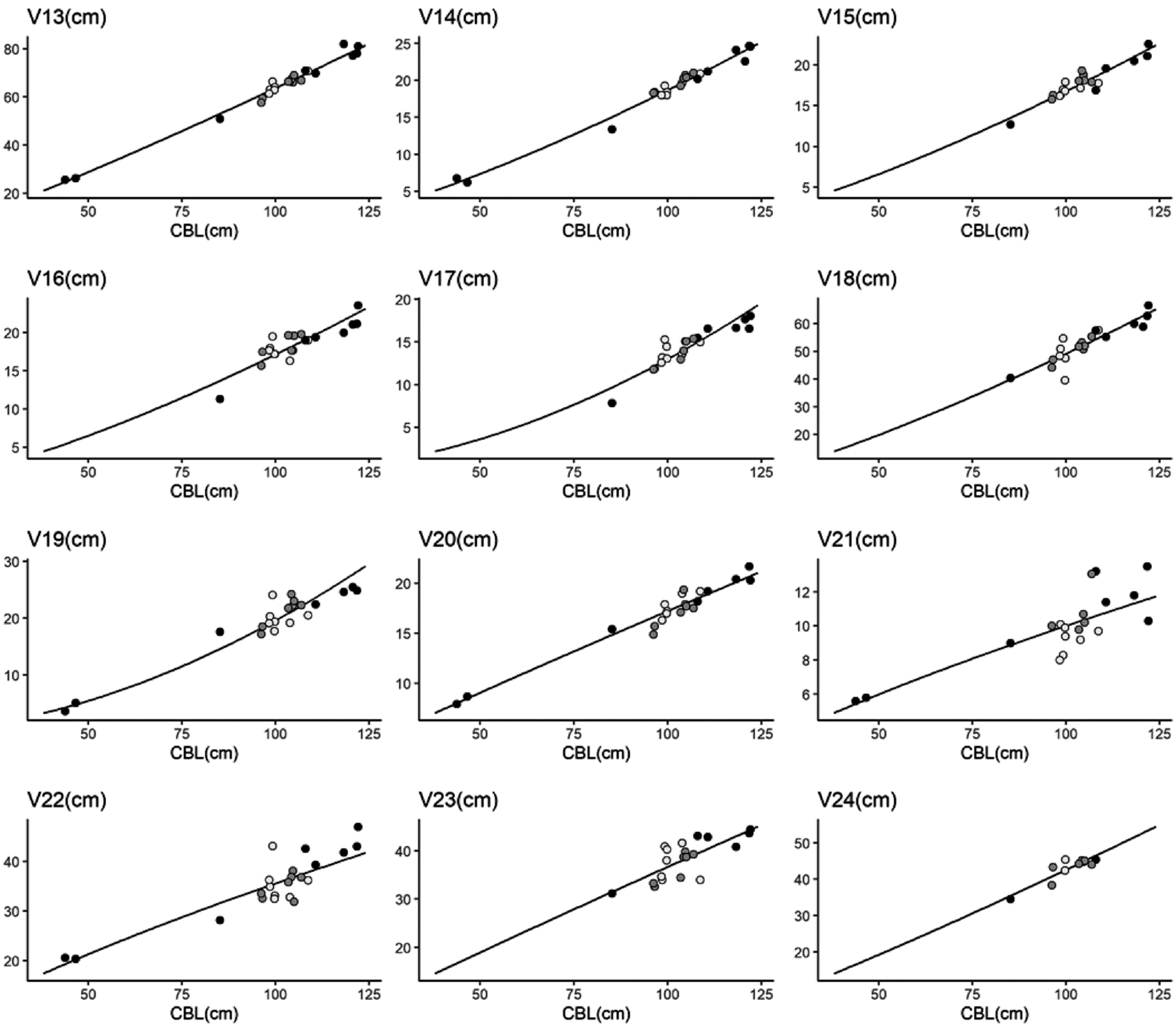

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AGE ESTIMATION FROM TEETH IN LONGMAN'S BEAKED WHALES (*INDOPACETUS PACIFICUS*) STRANDED IN NEW CALEDONIA (SOUTH PACIFIC)

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Abstract

Seven Longman's beaked whales mass stranded in New Caledonia in November 2013, of which 4 ultimately died, in a first worldwide event reported for this poorly known Ziphioid species. Teeth were extracted, collected and thoroughly cleaned of gum tissue from 3 females ranging from juvenile to adult and one adult male. These were sectioned (crown-root) and prepared using two different methods and examined under microscope magnification when Growth Layer Groups (GLGs) in both dentine and cement were successfully identified. The methods employed for aging included 1) sectioning centrally at approx. 150 μm through crown and root on an Isomet circular diamond saw and examining under a microscope using both transmitted polarised light and plain light; and, 2) thick sectioning (wafering) at approx. 2.5 mm and subsequent decalcification in RDO™ (a proprietory brand, Illinois, USA) and then thin sectioning the wafer at 10–25 μm and staining with Ehrlich's acid haematoxylin. GLGs were investigated in both dentine (25 micron) and cementum (10–15 μm). Layering was evident in both tissues but higher counts were more evident in thin stained sections of cementum. Although dentinal GLGs in untreated tooth sections have been used successfully for aging in Ziphioid species *Hyperoodon ampullatus* (Christensen 1973, Feyrer *et al.*, 2020), it is believed this is the first time that teeth have been used for estimating age from GLGs in this tropical species.

Key words: Age estimation, Ziphioid whales, *Indopacetus pacificus*, teeth.

Introduction

Longman's beaked whale (*Indopacetus pacificus*), first described as a large species of the genus *Mesoplodon* (Longman, 1926) from a beachcast skull found in northern Queensland, Australia, was later assigned to its own genus, *Indopacetus*, after comprehensive morphological evaluation (Moore, 1968) and the discovery of a second skull in Somalia (Azzaroli, 1968). This species has long been considered one of the rarest and least known of all whales. Groups of *Indopacetus* are encountered with some regularity in the tropical Indian and Pacific Oceans (Anderson *et al.*, 2006; Afsal *et al.*, 2009; Yamada *et al.*, 2012), and there have been occasional reports of strandings (<20 stranded animals to date, Yamada *et al.*, 2012) most of which have been singletons, with the exception of a cow-calf pair in Taiwan (Yao *et al.*, 2012). More recently, a stranding was reported off the Phillipines (Acebes *et al.*, 2019), and two separate strandings were reported off Okinawa, Japan, including a neonate (Kobayashi *et al.*, 2021, 2021a).

This paper focuses on tooth material and relevant data from a mass stranding of Longman's beaked whales in New Caledonia in the southwest Pacific Ocean, and describes the details of the aging methods used, which may be helpful for researchers investigating more precise age in other beaked whales. Among the samples collected from three females ranging from juvenile to adult and one adult male, were the paired teeth, extracted and thoroughly cleaned of gum tissue. The details of the stranding event are described by Garrigue *et al.* (2016) when seven animals came ashore together on the south coast of the Grande Terre on 16 November 2013, four of which ultimately died. Only a brief account of the age estimation was reported at this time. This is believed to be the first worldwide mass stranding event for this poorly known species, and the first time tooth layering has been investigated for Longman's beaked whale.

Methods

Age was estimated using a single tooth from each of the four animals examined and was determined without other detailed biological information apart from sex and body length. The remaining tooth was retained untouched for other analyses. Two methods of aging were applied to investigate which might be more informative, and are detailed here. Although aging methods have been detailed for other beaked whales—Northern Bottlenose whale *Hyperoodon ampullatus* (Christensen, 1973; Feyrer *et al.*, 2020)—Longman's beaked whale is a tropical species, and in general little is known about aging in beaked whales.

Fig. 1 shows the size and shape of a tooth. Each tooth was thoroughly cleaned of gum tissue and 2–3 sections, *ca.* 150 μm thick, were cut centrally through the crown and root of each tooth, using an Isomet

a) b) c) d)

Fig. 1. The series of photos shows the size and dimensions of a tooth from specimen #4: a) and b) the length of the tooth in different aspects; c) the greatest width of the tooth; d) the elliptical open pulp cavity at the root. Only the top 10 mm of the tooth crown are exposed above the gum line which is clearly visible from the darker colour.

Fig. 2. Buehler Isomet low-speed diamond saw for sectioning teeth. The chuck and wood block mount for the tooth are shown. The tooth is affixed to the wood block using a standard hobby glue gun employing glue sticks. The glue is easily removed after cutting and can be made easier by soaking the tooth sections and block in water for some minutes.

Fig. 3. A portable benchtop freezing microtome used for sectioning decalcified teeth. Note the horizontal cutting plane, the fixed freezing stage and the mobile blade. The specimen is frozen by means of a Peltier device with flowing water in counter current. The blade is not cooled and the microtome is operated at room temperature. The temperature of the freezing stage is generally around −12°C and can be adjusted by altering the water flow to the device.

slow-speed circular diamond saw (see Fig. 2). These thin sections were examined under a binocular dissecting microscope at magnification x7–x40 using alternately transmitted plain light and polarized light, focusing on Growth Layer Groups (GLGs) in both dentine and cementum (see Perrin and Myrick Jr., 1980; Lockyer *et al.*, 2016 for GLG definition). Each GLG observed was assumed to have been deposited over a 1-year period as validated in other odontocetes *e.g. Physeter macrocephalus* (Gambell, 1977), *Globicephala melas* (Lockyer, 1993), *Tursiops truncatus* (Hohn *et al.*, 1999), *Delphinapterus leucas* (Lockyer *et al.*, 2016), and various mammal species (Read *et al.*, 2018). In addition, a thicker central section (wafer) (2–2.5 mm) was removed from each tooth, again through crown-root axis adjacent to the first thin section, and decalcified in a rapid decalcifying solution RDO™ (a proprietory brand, Illinois, USA) for up to 15 h. Thin sections of (10–25 μm) of this central wafer were then made using a freezing microtome (see Fig. 3) and stained with Ehrlich's Acid Hæmatoxylin (EAH) as described for other species (Lockyer, 1993; Lockyer and Braulik 2014; Read *et al.*, 2018). The thinnest sections were destined for cemental examination and the thicker sections for dentinal study. In this instance, the thin decalcified sections were placed in large histo-cassettes in an agitated ripe solution of EAH for up to 45 min until stain uptake was deemed optimal. The sections were then transferred to water in the histo-cassettes and rinsed thoroughly of excess stain for several minutes. Subsequently, the sections were transferred into a weak ammonia solution (just a few drops of ammonia in the solution enough to turn the pH alkaline) and soaked here for about 3 min. until the sections had turned uniformly from deep red to purple-blue. After a second rinsing in water, the sections were then examined wet under a microscope and the best sections were removed for mounting. Sections used for age estimation were floated onto 5% gelatin-coated microscope slides under water and arranged with a maximum of 2 sections per slide. The slides were then carefully blotted, section downwards, on absorbent paper (a type that does not shed fibres) and then air-dried in a fume cupboard for about 30 min. and permanently mounted under glass cover slips with DPX, a fast drying mixture of distyrine (a plasticizer) and xylene. The slides were then allowed to completely dry in the fume cupboard for several days before examination. Plain transmitted light was then used for examination under a microscope as for the unstained thick sections. Age data estimated from both preparation methods were recorded in both dentine and cement.

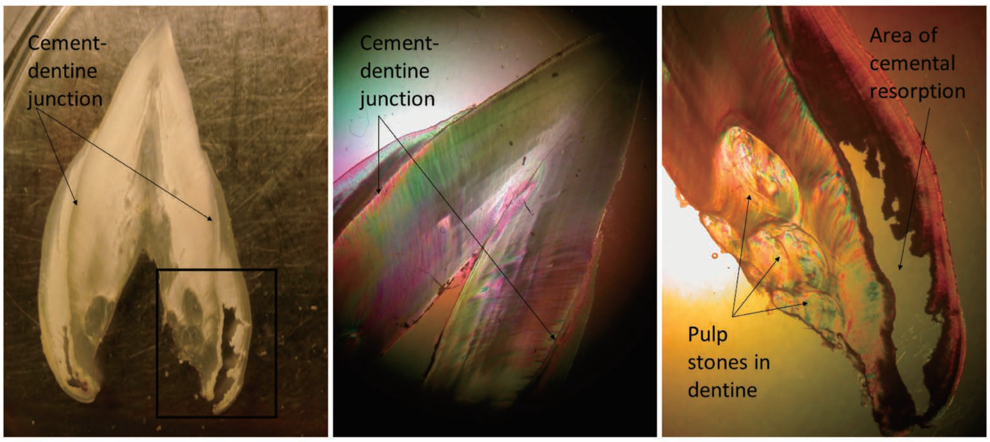
Results

The ages estimated from the different sections are presented in Table 1 where both stained and untreated sections are recorded as well as GLGs in both the dentine and cementum. The first point to note is that for all specimens, the stained sections are generally providing higher GLG counts in both dentine and cementum, with the exception of the dentine in specimen #6 where no identifiable GLGs could be seen in the stained section. The other point is that cementum is generally providing higher counts and greater clarity than the dentine. The most consistent ages for both the adult female #6 and adult male #2 were estimated as 20–22 and >20–26 GLGs respectively, which by analogy with GLG deposition rate in other cetaceans may be equivalent to years (see review in the Methods). Ages of the sub-adult females #4 and #5 were less clear, but #4 was estimated as 8–9 GLGs and #5 as 14–17 GLGs. Figs. 5–7 incl. show the untreated and stained sections of cementum for specimens #2, #5 and #6, respectively. In each case, more GLGs appear to be visible in the stained than in the untreated sections. The GLGs identified are those that fall in the range shown for cementum in Table 1. At this stage when the method of age estimation is experimental, it is unclear whether some of the identified

Table 1. Age estimates for four whales based on the examination of dentinal and cementum Growth Layer Groups (GLGs) under two different treatments (After Garrigue *et al.*, 2016).

Specimen number	Age-sex class	Treatment	No of GLGs[2] observed		Overall Age[1] Estimate (GLGs)[2]
			Dentine	Cementum	
#2[a]	Adult M, length 590 cm	unstained stained	7+++[3] 20	20+ 26	20–26 (range 7++ to 26)
#4[b]	Sub adult F, length 564 cm	unstained stained	8 9–12	5++[3] 8+[3]	8–9 (range 5++ to 12)
#5[c]	Sub adult F, length 590 cm	unstained stained	8++[3] 12+[3]	14 17[3]	14–17 (range 8++ to 17)
#6[d]	Adult F, length 618 cm	unstained stained	12++[3] no GLGs visible	20 22	20–22 (range 12++ to 22)

[1] Overall age was based on the modal age from several counts.
[2] One GLG is assumed to be equal to one year but this requires future validation.
[3] Addition symbol (+) indicates that more GLGs were present, but were too indistinct to be counted, and multiple+symbols reflect the relative amount of indistinct GLGs. In addition, the following comments relate to individual teeth.
[a] Crown worn down. Some GLGs may be missing. Dentinal resorption in root.
[b] The presence of pulp stones interfered with the GLG pattern in the dentine such that it was difficult to count at the base. Cement poorly stained and ill-defined. Dentinal resorption or decay in the root.
[c] GLGs had poor definition, including double laminae. Dentinal resorption, or decay in root.
[d] No dentinal resorption in root.



a) b) c)

Fig. 4. Untreated section 150 microns thickness, of specimen #4: a) complete section examined under plain transmitted light showing central dentine, surrounding cementum, and large areas of resorption at the dentine-cementum junction in the root; b) dentine examined under polarised filters, showing GLGs; c) close up of the resorption area from a) examined under polarised filters showing pulp stones in the dentine root.

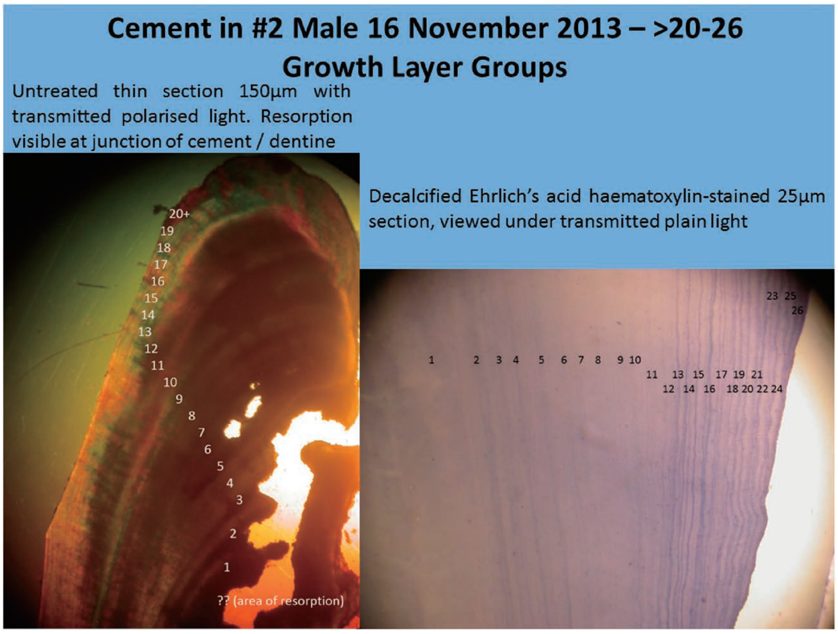


Fig. 5. Comparison of cementum in untreated and decalcified stained sections of specimen #2.

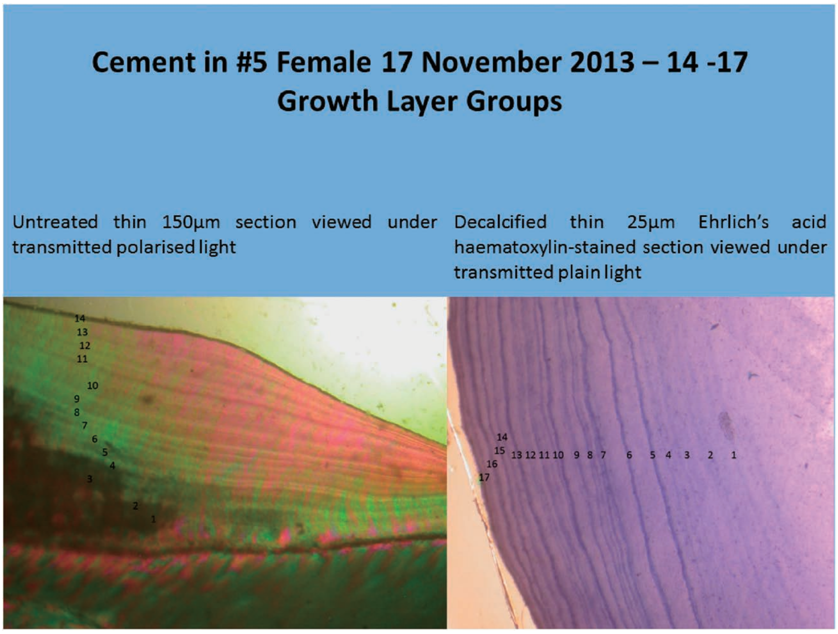


Fig. 6. Comparison of cementum in untreated and decalcified stained sections of specimen #5.

GLGs might actually be accessory lines. Figs. 5–7 all show identified GLGs in the decalcified and stained cementum, but it is clear that some are darkly stained and others paler; in addition, sometimes the spacing between layers is not regular but very close appearing double (for example, see GLGs 19 and 21, Fig. 7) suggesting possible accessory lines. The untreated cementum in Fig. 7 shows identifies only 20 GLGs, indicating that staining may highlight other ultrastructures in addition to GLGs. Read *et al.* (2018) discuss the significance and possible causes of accessory lines in marine mammalian teeth under the topic of tooth anomalies, including periodic changes in nutrition, hormonal levels and environmental factors. Presently it is difficult to identify likely factors for this tropical species, not knowing much about the life history.

The specimens #2, #4 and #5 all had evidence of extensive mineral resorption at the dentine-cemen-

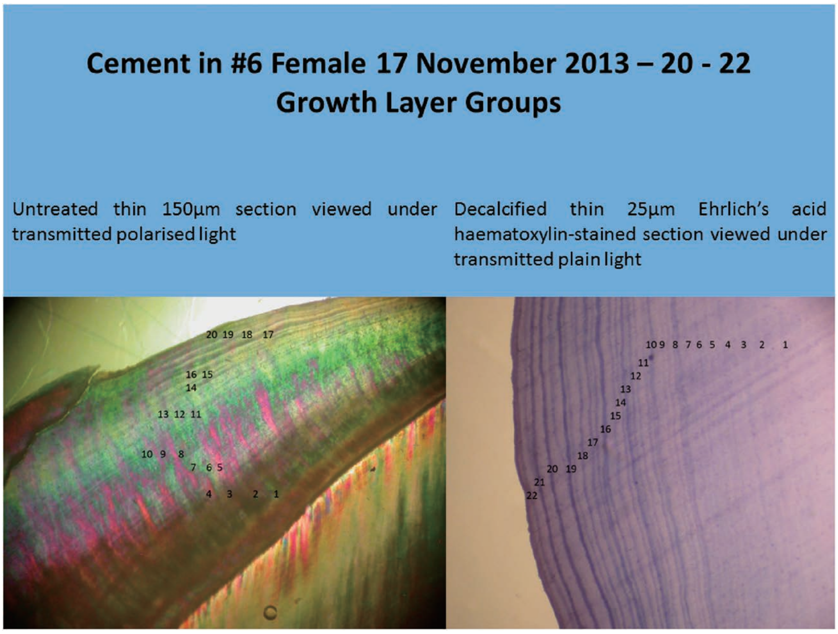


Fig. 7. Comparison of cementum in untreated and decalcified stained sections of specimen #6.

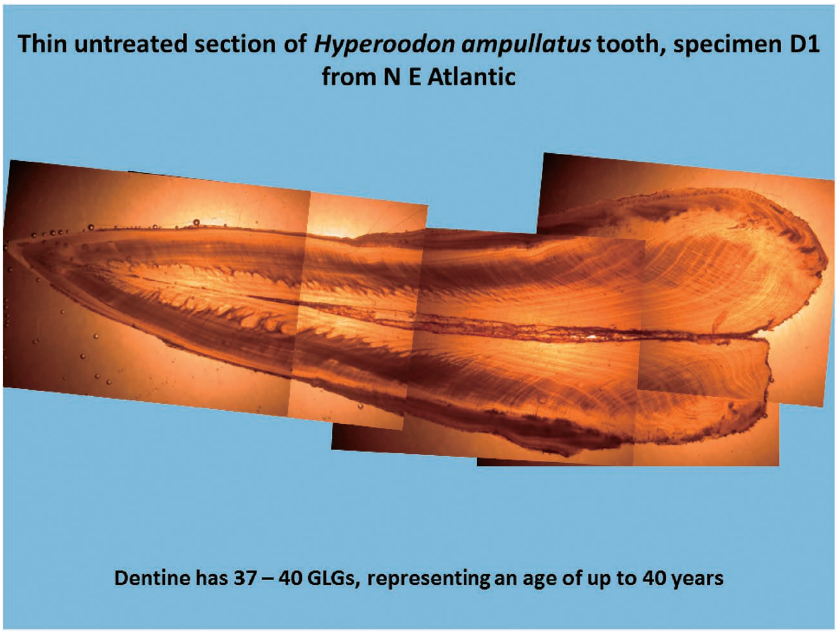


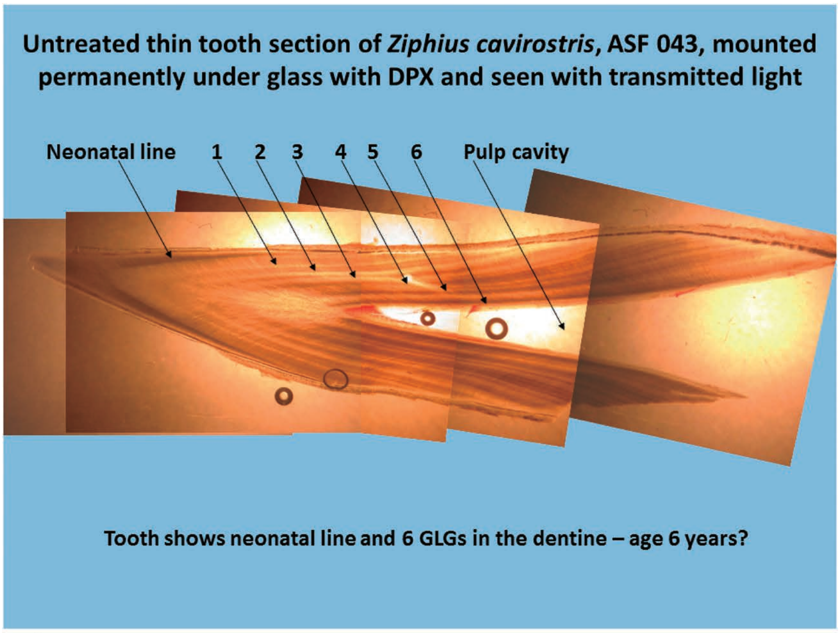
Fig. 8. Dentinal GLGs in an untreated section of a tooth of *Hyperoodon ampullatus*.

tum junction in the root region (Fig. 4a, c), while #6 had no such condition.

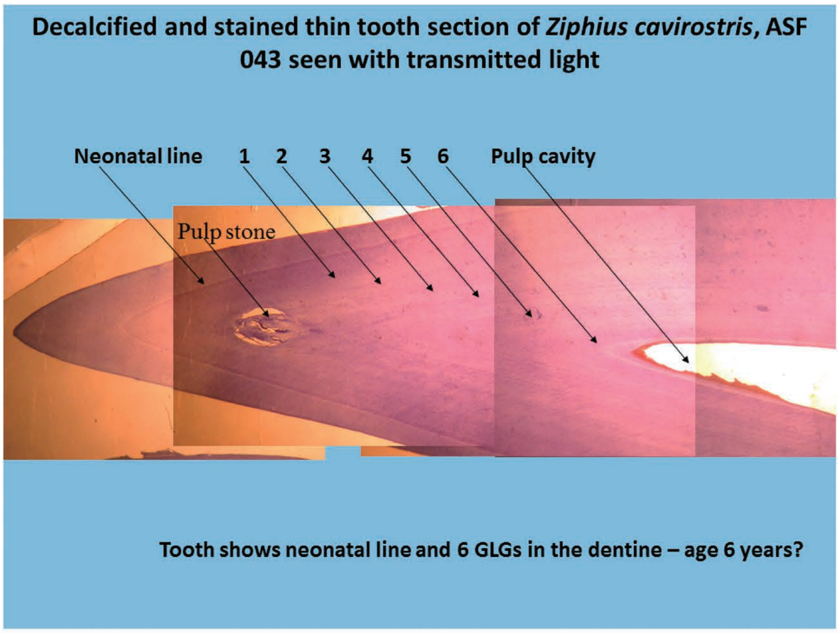
Discussion and conclusions

Both methods of preparation detailed here were adequate for identifying GLGs in cementum, with slightly higher counts in stained sections. Generally, GLGs were difficult to identify in the dentine which presented a lower age count than cementum. Thus cemental GLGs would appear to be the preferred tissue for age estimation in Longman's beaked whale. Stained sections tended to produce higher GLG counts, but at the moment it is unclear whether accessory lines may be highlighted and what time period a GLG represents. However, as suggested above, the norm in most mammals is an annual deposition of GLGs (Gambell, 1977; Lockyer 1993; Hohn *et al.*, 1999; Lockyer *et al.*, 2016; Read *et al.*, 2018). In this study, the dentine did not provide clear differentiation of GLGs so that this tissue must be regarded as unreliable for total age estimation in this species, based on this limited investigation.

Generally, dentinal GLGs are preferred for aging in cetacean teeth (Stewart and Stewart 2014; Read *et al.*, 2018). In *Hyperoodon ampullatus*, the dentinal GLGs in untreated tooth sections are the preferred aging tool, as noted earlier (Christensen, 1972; Feyrer *et al.*, 2020). This is demonstrated in Fig. 8 where an untreated section (prepared in the same manner as *Indopacetus* teeth) shows up to 40 dentinal GLGs. There is no wear at the crown so that all GLGs are represented. There is limited information about aging in Ziphioid whales, and the authors note that teeth of *Ziphius cavirostris* (prepared



a)



b)

Fig. 9. Comparison of dentinal GLGs in a) untreated and b) decalcified stained sections of teeth of *Ziphius cavirostris*.

in a similar manner as *Indopacetus pacificus* teeth) presented good GLG resolution in both untreated and decalcified stained sections of dentine (Fig. 9). It should be noted however, that the cementum in both *Ziphius* and *Hyperoodon* is thinner and less conspicuous than in *Indopacetus* (compare Fig. 4). Additionally, unlike *Ziphius* and *Hyperoodon*, for which there have been past fisheries (Japan, Norway) when some life history information was learned, there is almost nothing known about *Indopacetus*, including the extent of its distribution outside tropical waters, if at all. All that can be drawn from the methods tried presently is that cementum appears to be the best tissue to use for aging, and decalcifiying and staining the tissue tends to reveal more detail and thus higher counts than the untreated sections.

With respect to the presence of mineral resorption in the roots of the teeth of *Indopacetus*, the cause is unknown (Fig. 4a, c). It is reported that high levels of cadmium (Cd) in the body can lead to interference in bone mineral structure, specifically calcium (Kazantsis, 2004; Sughis *et al.*, 2011). Garrigue *et al.* (2016) reported high concentrations of Cd in the kidneys and liver of #4, #5 and #6, but coincidentally noted that the lowest concentration was observed in #6, the only animal with no resorption. In addition #4 had many pulp stones present in the dentine (Fig. 4b, c), the cause of which is again unknown. However, the presence of these structures made reading the dentinal GLGs very difficult. Such inclusions do not occur in cementum.

It is believed this is the first time that teeth have been used for estimating age from GLGs in this species, *Indopacetus*. These initial results are very promising and may be helpful to others who may encounter similar specimens. The method may also be helpful in investigating some other beaked whale species.

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SPATIAL AND TEMPORAL DISTRIBUTION OF FLOATING MARINE MACRO DEBRIS IN THE INDO-PACIFIC REGION OF THE ANTARCTIC

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Abstract

Marine debris can affect marine species including whales through ingestion and entanglements. Surveys of marine debris in the Antarctic waters are very limited. This study investigated the floating marine macro debris occurring in the Indo-Pacific sector of the Antarctic (35°E–145°W), south of 60°S, based on Japanese sighting surveys conducted between the austral summer seasons 1991/92 and 2018/19. In order to examine the spatial differences in distribution and density, the marine macro debris data were divided into IWC management Areas IIIE, IV, V and VIW as well as into CCAMLR Convention Areas. Furthermore, to investigate temporal differences, the data were divided into two periods: 1991/92–2004/05 and 2005/06–2018/19. A total of 175 objects were found, consisting mainly of metal and polymer products. Buoys/floats constituted the most frequent sightings, representing 67% of all marine macro debris found. The density indices (number of marine macro debris observed by 100 n.miles) increased from the first to the second period in all Areas. The increase in the number of marine macro debris between the first and second periods was statistically significant in Areas IV and V. The larger number of marine macro debris in the second period (represented predominantly by buoys/floats) coincides with an increase in fishing activities in the surveyed area. However, the overall number of floating marine macro debris in the Indo-Pacific sector of the Antarctic is low and much lower than that reported for the North Pacific and North Atlantic, and this result is consistent with the low incidence of marine macro debris found in the stomach of Antarctic minke whales reported for the same sector. Continued monitoring of floating marine macro debris is recommended given the increasing trend in the number of fisheries and tourist activities in the Antarctic.

Key words: Antarctic, Japanese sighting survey, marine macro debris, fishing buoy.

Introduction

Marine pollution is defined as the introduction by man, directly or indirectly, of substance or energy into the marine environment (including estuaries) resulting in such deleterious effects as harm to living resources, hazards to human health, hindrance to marine activities including fishing, impairment of quality for use of sea water and reduction of amenities (GESAMP, 1991). Marine debris, also known as marine litter, is a kind of pollutant including, among many others, man-made objects such as polymer bags, buoys, rope, lost fishing lines and nets. Once in the sea, such debris becomes mobile and their movement, distribution and accumulation pattern depend on oceanic currents and gyres. A workshop of the International Whaling Commission Scientific Committee (IWC/SC) agreed that marine debris, and its contributions to entanglements, exposures including ingestions, and associated impacts, including toxicity, is both a welfare and a conservation issue for cetaceans on a global scale (IWC, 2014). Naturally, marine debris can affect other pelagic species as well.

The problem of pollution by marine debris is more frequent and critical in populated areas. Evidence from remote oceanic islands suggests a southward-decreasing, strong latitudinal gradient in litter densities from subtropical and temperate waters through the subtropical convergence to the Antarctic Polar Front and beyond. That is, there is a clear decreasing trend in marine debris accumulation with latitude (Gregory and Ryan, 1997; Barnes, 2005). However, in recent years, marine debris has been recorded in remote places such as sub-Antarctic and Antarctic regions (Barnes *et al.*, 2010; Ivar do Sul *et al.*, 2011). The sources of this pollutant in the Antarctic could be global oceanic debris drifting across the Antarctic Polar Front or debris from tourism and fisheries activities, which have been increasing in sub-Antarctic and Antarctic areas (Lamers *et al.*, 2008; CCAMLR, 2012).

As indicated above, floating marine debris could be a threat affecting the welfare and conservation of large whales migrating to the Antarctic each austral summer for feeding. Such threats could be through entanglements, ingestions, and associated impacts, including toxicity (IWC, 2014; Baulch and Perry, 2014). For this reason, it is important to monitor the type, number and distribution of floating marine debris in the Antarctic feeding grounds. Unfortunately, previous studies of this kind are very scarce in the Antarctic. Suaria *et al.* (2020) investigated the abundance of floating plastics around the Southern Ocean from a survey conducted during the Antarctic Circumnavigation Expedition in 2016/17, and the authors confirmed the Southern Ocean as the region with the lowest concentration of plastic globally. The IWC International Decade for Cetacean Research-Southern Ocean Whale and Ecosystem Research (IDCR-SOWER) conducted observations on floating macro debris in 1987/88 (Matsuoka *et al.*, 2003) and up to 2009/10 when the survey was completed (Murase *et al.*, 2020). Although a brief summary was presented in Murase *et al.* (2020), analyses of the data collected are yet to be conducted. The authors found low occurrence of marine macro debris in the Antarctic.

The main objective of this study was the investigation of the spatial and temporal distribution of floating marine macro debris in the Indo-Pacific sector of the Antarctic. The study is based on observations conducted from systematic vessel-based sighting surveys of the former research programs JARPA/JARPAII (Japanese Whale Research Program under Special Permit in the Antarctic, Phases I and II) (Government of Japan, 1987, 1989, 2005) and NEWREP-A (New Scientific Whale Research Program in the Antarctic Ocean) (Government of Japan, 2015), over a period of 28 years. Outputs from this study could provide valuable information for the development of conservation policies of whales and the Antarctic ecosystem.

Materials and methods

Research area

The marine macro debris observations were conducted along the surveys of the JARPA, JARPAII and NEWREP-A, which had as the main objective the systematic collection of sighting and biological data of whales in IWC Antarctic management Areas III (0°–70°E), IV (70°–130°E), V (130°E–170°W) and VI (170°–120°W). The marine macro debris data analyzed in this study were from the eastern part of Area III (IIIE) (35°–70°E), Area IV, Area V and the western part of Area VI (VIW) (170°–145°W), from 60°S to the ice edge, from where data for a longer period were available (Figs. 1A and 1B). The marine macro debris data were also summarized according to the Convention Areas of the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR). Figs. 1A and 1B show the geographical boundaries of the IWC and CCAMLR management areas used for the analyses in this study. IWC Area IIIE overlaps partially with CCAMLR Divisions 58.4.2–4; Area IV with Divisions 58.4.1–3; Area V with Division 58.4.1 and Sub-area 88.1; and Area VIW with Sub-area 88.2. In

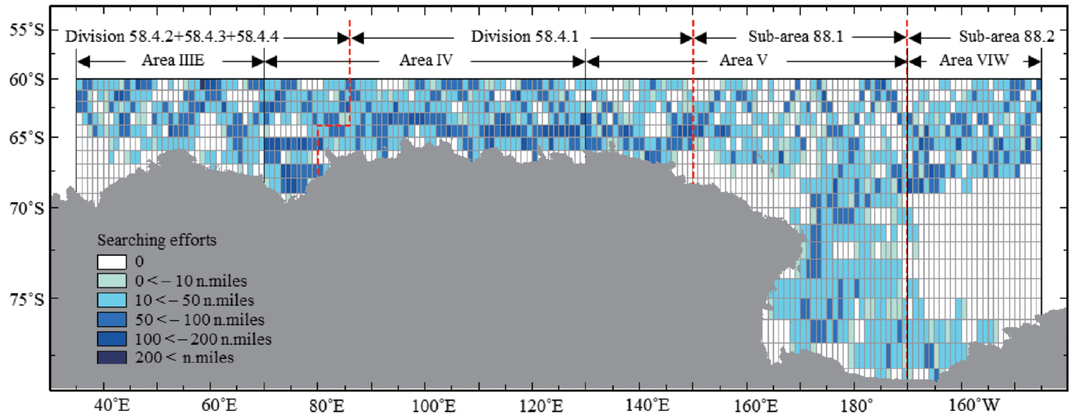

Fig. 1A. The sighting effort (n.miles surveyed by Lat. 1°×Long. 1° square) of the JARPA survey in the Indo-Pacific sector of the Antarctic during the austral summer seasons 1995/96 to 2004/05 (first period, a total of 50,476 n.miles surveyed). The figure also shows the geographical boundaries of the IWC and CCAMLR management areas used for the analyses in this study.

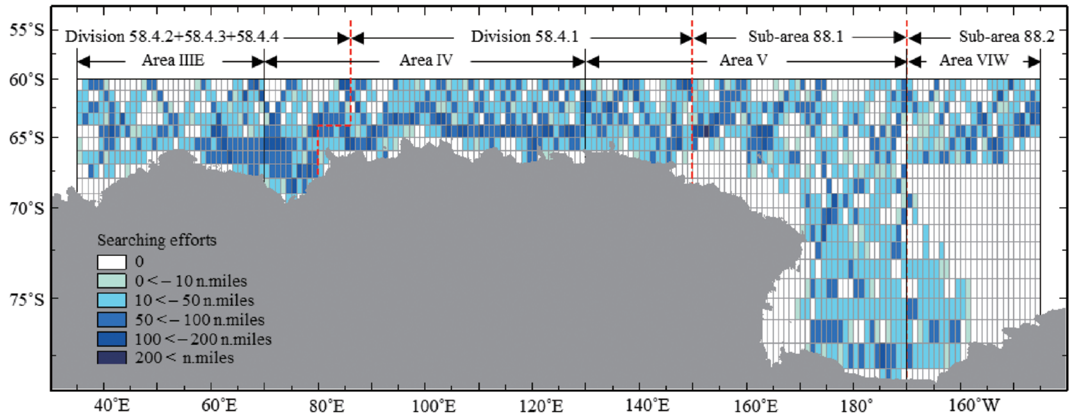

Fig. 1B. The sighting effort (n.miles surveyed by Lat. 1°×Long. 1° square) of the JARPAII and NEWREP-A surveys in the Indo-Pacific sector of the Antarctic during the austral summer seasons 2005/06 to 2018/19 (second period, a total of 52,328 n.miles surveyed). The figure also shows the geographical boundaries of the IWC and CCAMLR management areas used for the analyses in this study.

this regard, the data of marine macro debris collected in the Indo-Pacific sector of the Antarctic can be useful for these two international organizations. CCAMLR management areas involve the terminology 'Areas,' 'Divisions' and 'Sub-areas.' For practical purposes, in this study these are referred simply as CCAMLR 'Areas.'

As the surveys were limited to waters south of 60°S, i.e., south of the Antarctic Polar Front, which acts as a barrier of debris movement from lower latitude waters to the Antarctic (see above), the emphasis of this study was on longitudinal differences in the distribution of marine macro debris, given the wide longitudinal span of the surveys in the Indo-Pacific sector.

Research period

Marine macro debris surveys were conducted mainly during January–February, in the austral summer seasons between 1991/92 and 2018/19.

Survey procedure

Observation of marine macro debris was carried out from the platform of sighting vessels participating in JARPA, JARPAII and NEWREP-A. The main objective of the sighting vessels was the collection of sighting data of whales for abundance estimation purposes. Although the protocol of the surveys included the observation of floating marine macro debris along the track-lines, they could not be considered as dedicated marine macro debris surveys. Details of the general sighting survey procedures can be found in Nishiwaki *et al.* (2006) and Nishiwaki *et al.* (2014). Basically, the sighting vessels followed a pre-determined zig-zag track-line at a speed of 11.5 knots. The sighting surveys involved two observers on the top platform (19 m high from the sea level) and five observers on the upper bridge platform (11 m high from the sea level). Sighting surveys, including the observations of marine macro debris on the sea surface, were carried out from the platforms using a scaled binocular developed by the Institute of Cetacean Research and FUJINON (FUJINON 7×50 FMT-SX; 7×50 mm, ICR model). The vessel did not deviate from the track-line when an item of marine macro debris was sighted.

Marine macro debris data were recorded separately for sighting surveys conducted ‘on effort’ (primary observers were present at the relevant observation platforms) and ‘off effort’ (marine macro debris recorded during drifting, transit and experiments). For each observation, the type of marine macro debris, the sighting date and the geographical position were recorded. When feasible, pictures were taken.

The surveys focused on marine macro debris objects of sizes approximately 300 mm or larger (estimated visually by experienced observers). It should be noted that the sighting probability of small objects decreases with distance from the vessels. As a consequence, some small objects occurring at long distances could have been missed. However, the survey procedures were exactly the same for each annual survey in the 28-year period, so the comparison of density indices (see below) between temporal strata is still a valid approach in relative terms.

Data analysis

To examine geographical differences in distribution, marine macro debris data were grouped by IWC management Area and CCAMLR Convention Areas. To investigate temporal trends in the Areas, marine macro debris data were grouped into two periods: 1991/92–2004/05 (first period) and 2005/06–2018/19 (second period). This temporal division was made so that the sighting effort (searching nautical miles) was evenly distributed between the two periods. In making this temporal division it was also considered that fishery and tourist activities in the Antarctic had increased from the 2000’s (see Fig. 1 in Lamers *et al.*, 2008 and Figs. 6 and 7 in CCAMLR, 2012), and therefore an increase in the number of marine macro debris was expected for the second period.

No sighting survey was conducted in the seasons 2010/11, 2011/12 and 2013/14. Observations of marine macro debris between the seasons 1991/92 and 1994/95 were made under both ‘on effort’ and ‘off effort,’ however, the type of effort was not recorded. Therefore data in this period were not used when the density indices (see below) were calculated.

The density index (the number of marine macro debris observed per 100 n.miles) was calculated for each management Area in each of the two periods, based on the marine macro debris data collected under ‘on effort’ mode. The number of marine macro debris per unit area is an alternative method to assess its geographical and temporal distribution. Given the number and complexity of each IWC and CCAMLR area examined, the density index was selected for practical purposes.

A chi-square test was used to assess the differences in the number of marine macro debris between periods based on the expected frequency of 50 : 50.

Results

Sighting effort

Figs. 1A and 1B show the sighting effort expressed in nautical miles, surveyed in the first and second periods, respectively. The searching effort was similar in both periods, 50,476 n.miles and 52,328 n.miles in the first and second periods, respectively.

Floating marine macro debris

Tables 1A–1C show the number of marine macro debris in the whole (A), first (B) and second (C) periods, respectively, grouped by the IWC Areas. A total of 175 observations of marine macro debris were recorded between 1991/92 and 2018/19 (15 metallic objects, 159 polymer products and one object of unknown material). Buoys/floats made of polymer (Fig. 2) accounted for 67% of all marine macro debris. Most buoys/floats observed were single objects. The total numbers of marine macro

Table 1A. Summary of floating marine macro debris recorded during systematic sighting surveys in the Indo-Pacific sector of the Antarctic by JARPA, JARPAII and NEWREP-A between the austral summer seasons 1991/92 and 2018/19, by IWC Area and effort (on and off).

Type of marine macro debris	Metal (Total number=15)				Polymer products (Total number=159)														Other (Total number=1)		Sub total		Total
	Can		Drum (≦200L)		buoy /float*		Bottle		Container		Fender		Net		Other polymer products **		Styrofoam products		Other products ***				
IWC Area / effort	on	off	on	off	on	off	on	off	on	off	on	off	on	off	on	off	on	off	on	off	on	off	
Area IIIE	0	0	1	0	5	2	1	2	0	0	0	0	0	0	0	0	1	0	0	0	8	4	12
Area IV	0	0	2	4	30	11	0	1	1	0	0	1	1	0	1	3	8	2	1	0	44	22	66
Area V	2	0	2	3	45	12	3	0	2	0	5	1	2	0	1	0	2	0	0	0	64	16	80
Area VIW	0	0	1	0	8	5	0	0	0	0	0	0	0	0	3	0	0	0	0	0	12	5	17
Total	2	0	6	7	88	30	4	3	3	0	5	2	3	0	5	3	11	2	1	0	128	47	175

*Observed on the surface as single objects, however, at least in eight cases, several objects were observed; those cases were counted as a single observation. Material of buoys/floats was considered to be polymer, in addition to Styrofoam and rubber.
**Two ropes, two tanks, one ball, one sheet, and two unknown products.
***A squared box of unknown material.

Table 1B. Summary of floating marine macro debris recorded during systematic sighting surveys in the Indo-Pacific sector of the Antarctic by JARPA, between the austral summer seasons 1991/92 and 2004/05 (first period), by IWC Area and effort (on and off).

Type of marine macro debris	Metal (Total number=9)				Polymer products (Total number=39)														Other (Total number=0)		Sub total		Total
	Can		Drum (≦200L)		buoy /float		Bottle		Container		Fender		Net		Other polymer products		Styrofoam products		Other products				
IWC Area / effort	on	off	on	off	on	off	on	off	on	off	on	off	on	off	on	off	on	off	on	off	on	off	
Area IIIE	0	0	1	0	2	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	3	1	4
Area IV	0	0	1	2	5	1	0	0	1	0	0	0	0	0	0	1	6	1	0	0	13	5	18
Area V	2	0	1	1	7	3	3	0	0	0	1	0	0	0	0	0	0	0	0	0	14	4	18
Area VIW	0	0	1	0	4	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	3	8
Total	2	0	4	3	18	7	3	1	1	0	1	0	0	0	0	1	6	1	0	0	35	13	48

Table 1C. Summary of floating marine macro debris recorded during systematic sighting surveys in the Indo-Pacific sector of the Antarctic by JARPAII and NEWREP-A, between the austral summer seasons 2005/06 and 2018/19 (second period), by IWC Area and effort (on and off).

Type of marine macro debris	Metal (Total number=6)				Polymer products (Total number=120)														Other (Total number=1)		Sub total		Total
	Can		Drum (≦200L)		buoy /float		Bottle		Container		Fender		Net		Other polymer products		Styrofoam products		Other products				
IWC Area / effort	on	off	on	off	on	off	on	off	on	off	on	off	on	off	on	off	on	off	on	off	on	off	
Area IIIE	0	0	0	0	3	2	1	1	0	0	0	0	0	0	0	0	1	0	0	0	5	3	8
Area IV	0	0	1	2	25	10	0	1	0	0	0	1	1	0	1	2	2	1	1	0	31	17	48
Area V	0	0	1	2	38	9	0	0	2	0	4	1	2	0	1	0	2	0	0	0	50	12	62
Area VIW	0	0	0	0	4	2	0	0	0	0	0	0	0	0	3	0	0	0	0	0	7	2	9
Total	0	0	2	4	70	23	1	2	2	0	4	2	3	0	5	2	5	1	1	0	93	34	127

Fig. 2. Example of a single floating marine macro debris observed at two distances from the vessel at position 67°S, 179°W (IWC Area V; CCAMLR Sub-area 88.1) during the 2013/14 austral summer season. Picture by one of the authors (KM).

Table 2A. Summary of floating marine macro debris recorded during systematic sighting surveys in the Indo-Pacific sector of the Antarctic by JARPA, JARPAII and NEWREP-A between the austral summer seasons 1991/92 and 2018/19, by CCAMLR Area and effort (on and off).

Type of marine macro debris	Metal (Total number=15)				Polymer products (Total number=159)														Other (Total number=1)		Sub total		Total
	Can		Drum (≦200L)		buoy /float		Bottle		Container		Fender		Net		Other polymer products		Styrofoam products		Other products				
CCAMLR Area / effort	on	off	on	off	on	off	on	off	on	off	on	off	on	off	on	off	on	off	on	off	on	off	
58.4.2+58.4.3+58.4.4	0	0	1	0	15	4	1	2	1	0	0	0	0	0	0	1	1	1	0	0	19	8	27
58.4.1	0	0	3	7	34	15	1	1	1	0	5	2	2	0	2	2	9	1	1	0	58	28	86
88.1	2	0	1	0	31	6	2	0	1	0	0	0	1	0	0	0	1	0	0	0	39	6	45
88.2	0	0	1	0	8	5	0	0	0	0	0	0	0	0	3	0	0	0	0	0	12	5	17
Total	2	0	6	7	88	30	4	3	3	0	5	2	3	0	5	3	11	2	1	0	128	47	175

Table 2B. Summary of floating marine macro debris recorded during systematic sighting surveys in the Indo-Pacific sector of the Antarctic by JARPA, between the austral summer seasons 1991/92 and 2004/05 (first period), by CCAMLR Area and effort (on and off).

Type of marine macro debris	Metal (Total number=9)				Polymer products (Total number=39)														Other (Total number=0)		Sub total		Total
	Can		Drum (≦200L)		buoy /float		Bottle		Container		Fender		Net		Other polymer products		Styrofoam products		Other products				
CCAMLR Area / effort	on	off	on	off	on	off	on	off	on	off	on	off	on	off	on	off	on	off	on	off	on	off	
58.4.2+58.4.3+58.4.4	0	0	1	0	6	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	8	1	9
58.4.1	0	0	1	3	3	2	1	0	0	0	1	0	0	0	0	1	6	1	0	0	12	7	19
88.1	2	0	1	0	5	2	2	0	0	0	0	0	0	0	0	0	0	0	0	0	10	2	12
88.2	0	0	1	0	4	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	3	8
Total	2	0	4	3	18	7	3	1	1	0	1	0	0	0	0	1	6	1	0	0	35	13	48

Table 2C. Summary of floating marine macro debris recorded during systematic sighting surveys in the Indo-Pacific sector of the Antarctic by JARPAII and NEWREP-A, between the austral summer seasons 2005/06 and 2018/19 (second period), by CCAMLR Area and effort (on and off).

Type of marine macro debris	Metal (Total number=6)				Polymer products (Total number=120)														Other (Total number=1)		Sub total		Total
	Can		Drum (≦200L)		buoy /float		Bottle		Container		Fender		Net		Other polymer products		Styrofoam products		Other products				
CCAMLR Area / effort	on	off	on	off	on	off	on	off	on	off	on	off	on	off	on	off	on	off	on	off	on	off	
58.4.2+58.4.3+58.4.4	0	0	0	0	9	4	1	1	0	0	0	0	0	0	0	1	1	1	0	0	11	7	18
58.4.1	0	0	2	4	31	13	0	1	1	0	4	2	2	0	2	1	3	0	1	0	46	21	67
88.1	0	0	0	0	26	4	0	0	1	0	0	0	1	0	0	0	1	0	0	0	29	4	33
88.2	0	0	0	0	4	2	0	0	0	0	0	0	0	0	3	0	0	0	0	0	7	2	9
Total	0	0	2	4	70	23	1	2	2	0	4	2	3	0	5	2	5	1	1	0	93	34	127

debris were 48 and 127 in the first and second periods, respectively. The buoys/floats were the main marine macro debris in both periods but its percentage was higher in the second period (52% and 73% in the first and second period, respectively).

A similar pattern was observed when the data were grouped by CCAMLR Areas (Tables 2A–2C).

Geographical distribution of marine macro debris

Figs. 3A and 3B show the geographical distribution of marine macro debris in the first and second periods, respectively, in both IWC and CCAMLR Areas. In the first period, the marine macro debris (mainly buoys/floats) were concentrated near the borders between IWC Areas but they were more widely distributed through the CCAMLR Areas. In the second period, the distribution of marine macro debris (mainly buoys/floats) was notably wider in both IWC and CCAMLR Areas, and they were concentrated mainly in Areas IV (CCAMLR Areas 58.4.1–3) and V (CCAMLR Areas 58.4.1 and 88.1), reflecting perhaps the larger searching effort spent in those Areas.

The most southerly marine macro debris sighting was a buoy in the Ross Sea, at position 76°S, 171°W (IWC Area V, CCAMLR Area 88.1).

Density index

Tables 3A–3C show the density indices in the whole (A), first (B) and second (C) periods, respec-

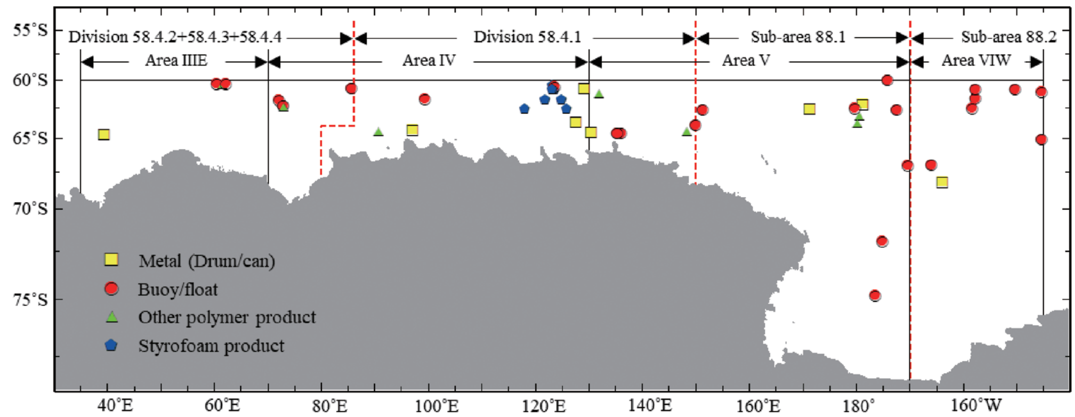

Fig. 3A. Distribution of marine macro debris sighted by JARPA survey in the Indo-Pacific sector of the Antarctic during the austral summer seasons 1991/92 to 2004/05 (first period) (on and off effort), by IWC and CCAMLR management areas.

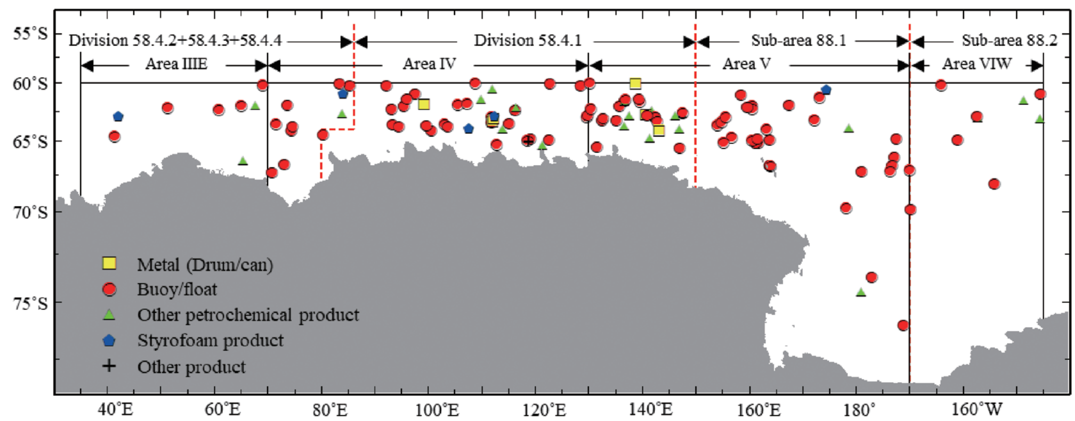

Fig. 3B. Distribution of marine macro debris sighted by JARPAII and NEWREP-A surveys in the Indo-Pacific sector of the Antarctic during the austral summer seasons 2005/06 to 2018/19 (second period) (on and off effort), by IWC and CCAMLR management areas.

tively, grouped by the IWC Areas. The index for all Areas and period was 0.12. The largest index was in Area V and the smallest in Area IIIE. The density indices increased between the first and second period in all Areas. A chi-square test resulted in significant temporal differences in the number of marine macro debris in Areas IV (chi-square=7.36, df=1, p=0.007) and V (chi-square=20.25, df=1, p<0.001). However no significant differences were found between periods when the density indices were used. It is likely that the values of density are too low to detect any difference. No significant differences were found in the number of marine macro debris between the first and second periods in Areas IIIE (chi-square=0.50, df=1, p=0.480) and VIW (chi-square=0.33, df=1, p=0.564).

Tables 4A–4C show the density indices in the whole (A), first (B) and second (C) periods, respectively, grouped by the CCAMLR Areas. The pattern found is very similar to the analysis of IWC Areas. The largest index was in Area 58.4.1 and the smallest in Area 58.4.2–4. The density indices increased between the first and second periods in all Areas. A chi-square test resulted in significant temporal differences in the number of marine macro debris in Area 58.4.1 (chi-square=19.93, df=1, p<0.001) and 88.1 (chi-square=9.26, df=1, P=0.002). However no significant differences were found between the two periods when the density indices were used. No significant differences in the

Table 3A. The searching distance (n.miles), number of marine macro debris and density indices (number of marine macro debris observed per 100 n.miles) during JARPA, JARPAII and NEWREP-A surveys in the Indo-Pacific sector of the Antarctic during the austral summer seasons 1995/96 to 2018/19, by IWC Area (data for the period 1991/92–1994/95 were not used for the reasons explained in the 'Data analysis' section).

IWC Area	Searching distance	Number of marine macro debris	Density index
Area IIIE	15,576	8	0.05
Area IV	36,408	44	0.12
Area V	38,488	64	0.17
Area VIW	12,331	12	0.10
Total	102,804	128	0.12

Table 3B. The searching distance (n.miles), number of marine macro debris and density indices (number of marine macro debris observed per 100 n.miles) during JARPA survey in the Indo-Pacific sector of the Antarctic during the austral summer seasons 1995/96 to 2004/05 (first period), by IWC Area (data for the period 1991/92–1994/95 were not used for the reasons explained in the 'Data analysis' section).

IWC Area	Searching distance	Number of marine macro debris	Density index
Area IIIE	7,300	3	0.04
Area IV	18,912	13	0.07
Area V	17,684	14	0.08
Area VIW	6,579	5	0.08
Total	50,476	35	0.07

Table 3C. The searching distance (n.miles), number of marine macro debris and density indices (number of marine macro debris observed per 100 n.miles) during JARPAII and NEWREP-A surveys in the Indo-Pacific sector of the Antarctic during the austral summer seasons 2005/06 to 2018/19 (second period), by IWC Area.

IWC Area	Searching distance	Number of marine macro debris	Density index
Area IIIE	8,276	5	0.06
Area IV	17,496	31	0.18
Area V	20,804	50	0.24
Area VIW	5,752	7	0.12
Total	52,328	93	0.18

Table 4A. The searching distance (n.miles), number of marine macro debris and density indices (number of marine macro debris observed per 100 n.miles) during JARPA, JARPAII and NEWREP-A surveys in the Indo-Pacific sector of the Antarctic during the austral summer seasons 1995/96 to 2018/19, by CCAMLR Area (data for the period 1991/92–1994/95 were not used for the reasons explained in the 'Data analysis' section).

CCAMLR Area	Searching distance	Number of marine macro debris	Density index
58.4.2+58.4.3+58.4.4	26,510	19	0.07
58.4.1	34,756	58	0.17
88.1	27,304	39	0.14
88.2	14,234	12	0.08
Total	102,804	128	0.12

Table 4B. The searching distance (n.miles), number of marine macro debris and density indices (number of marine macro debris observed per 100 n.miles) during JARPA survey in the Indo-Pacific sector of the Antarctic during the austral summer seasons 1995/96 to 2004/05 (first period), by CCAMLR Area (data for the period 1991/92–1994/95 were not used for the reasons explained in the 'Data analysis' section).

CCAMLR Area	Searching distance	Number of marine macro debris	Density index
58.4.2+58.4.3+58.4.4	12,720	8	0.06
58.4.1	17,773	12	0.07
88.1	12,637	10	0.08
88.2	7,347	5	0.07
Total	50,476	35	0.07

Table 4C. The searching distance (n.miles), number of marine macro debris and density indices (number of marine macro debris observed per 100 n.miles) during JARPAII and NEWREP-A surveys in the Indo-Pacific sector of the Antarctic during the austral summer seasons 2005/06 to 2018/19 (second period), by CCAMLR Area.

CCAMLR Area	Searching distance	Number of marine macro debris	Density index
58.4.2+58.4.3+58.4.4	13,790	11	0.08
58.4.1	16,984	46	0.27
88.1	14,667	29	0.20
88.2	6,887	7	0.10
Total	52,328	93	0.18

number of marine macro debris were found between the first and second periods in Areas 58.4.2–4 (chi-square$=$0.47, df$=$1, p$=$0.491) and 88.2 (chi-square$=$0.33, df$=$1, p$=$0.564).

Discussion

The present study summarized the spatial and temporal distribution of marine macro debris in the Indo-Pacific sector of the Antarctic based on data collected systematically over a period of 28 years. The data were organized based on the management areas of two international organizations in charge of the conservation and management of Antarctic marine living resources, the IWC and the CCAMLR. Although similar surveys have been conducted previously in the Antarctic (e.g., Matsuoka *et al.*, 2003; Suaria *et al.*, 2020), the present study is the first to report marine macro debris information which were collected along systematic sighting surveys in the same region (Indo-Pacific sector of the Antarctic) over a long period of time (28 years).

Marine debris has been increasing worldwide and one of the main concerns is the negative effect of this kind of pollutant on marine species through ingestion and entanglements (see reviews by Panti *et al.*, 2019; IWC, 2020). Emphasizing the importance of this subject, two international workshops were held recently to discuss the interaction between marine mammal and marine debris, and to define future research plans (Panti *et al.*, 2019; IWC, 2020).

The main results of the present study can be summarized as follows: i) the occurrence of floating marine macro debris in the Indo-Pacific sector of the Antarctic is low, and much lower in comparison with the occurrence in other oceans of the world; ii) buoys/floats made of polymer were the main marine macro debris found in this sector of the Antarctic, comprising 67% of all marine macro debris observed; iii) the largest density indices were found in IWC Areas IV and V (and CCAMLR Areas 58.4.1 and 88.1); and iv) there is an increasing temporal trend of marine macro debris (particularly buoys/floats) in all Areas, which was statistically significant in IWC Areas IV and V (and CCAMLR Areas 58.4.1 and 88.1).

Regarding i) above, the results of low occurrence of marine macro debris in the Antarctic are consistent with the results of Suaria *et al.*, (2020) and the preliminary results of IWC/IDCR-SOWER (Murase *et al.*, 2020). Matsumura and Nasu (1997) reported floating marine macro debris in the North Pacific Ocean and its adjacent waters for the period 1987–1991. Their surveys covered approximately 926,000 n.miles and recorded 136,338 pieces of marine macro debris (including natural objects). About 60% of marine macro debris were polymer products (e.g., fishing gear, Styrofoam products, and other polymer products). Total densities expressed in number of objects observed per 1 n.mile^2 were 20–40 in coastal waters, 0.2 in the north equatorial current area (5°–15°N, across the central Pacific), and 1–3 in the subarctic boundary area (35°–45°N). Barnes and Milner (2005) reported the results of floating marine macro debris across the entire latitudinal range from the Antarctic to the North Atlantic. Densities of marine macro debris ranged from 0 to 5 items/km^2 in sub-Antarctic and Antarctic waters. Marine macro debris density values have a peak of 10 to 100+ items/km^2 in the North Atlantic (English Channel). Clearly, the number of marine macro debris in the Indo-Pacific sector of the Antarctic is much lower than those observed in the North Pacific and North Atlantic oceans, although it should be noted that the density index used in the present study is not directly comparable with the densities reported in other studies.

Points ii), iii) and iv) above are related with the occurrence of buoys/floats, the main marine macro debris observed in the Indo-Pacific sector of the Antarctic. Buoys/floats accounted for about 67% of all sighted floating marine macro debris and its density indices increased between the first and second periods. It should be noted that Barnes *et al.* (2010) recorded three pieces of marine macro debris (a polymer cup and two fishing buoys) in the Dumont d'Urville and Davis Seas (i.e. Areas IV and V) during a survey conducted in the 2007/08 austral summer season. Figs. 4A and 4B show the annual trend of the density indices for buoys/floats in each of the management Areas of IWC and CCAMLR, respectively. An increasing trend is observed, particularly in IWC Area IV and V (Fig. 4A); and in CCAMLR Areas 58.4.1 and 88.1 (Fig. 4B), after the 2005/06 austral summer season. It is important to investigate the source of the buoys/floats observed and the reasons for the increasing trend in density after this season.

Oceanic fronts, such as the subtropical Convergence and Antarctic Polar Front, act as barriers for the movement of marine debris from low latitude waters to polar areas (Gregory and Ryan, 1997). Although these barriers are considered permeable by some authors (e.g. Gregory, 2009), the hypothesis that all buoys/floats observed in the Indo-Pacific sector of the Antarctic were transported from lower latitudes has a low plausibility. Since the season 2004/05, licensed longline vessels have conducted exploratory fishery for Antarctic toothfish (*Dissostichus mawsoni*) in CCAMLR Area 58.4.1, which overlaps partially with IWC management Areas IV and V. The number of licensed vessels in Area 58.4.1 was four to seven in 2004/05 to 2007/08 seasons, however it decreased to one to three in 2008/09 to 2014/15 seasons (SC-CAMLR, 2012a; CCAMLR, 2013, 2014, 2015). In Area 88.1, which

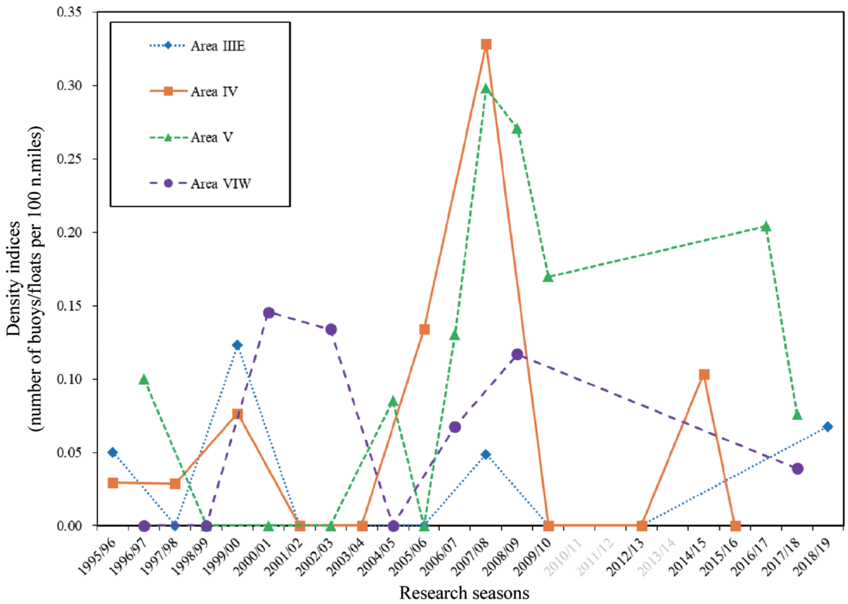

Fig. 4A. The trend of the density indices of sighted buoys/floats by austral summer season and IWC Area, between 1995/96 and 2018/19 (data for the period 1991/92–1994/95 were not used for the reasons explained in the 'Data analysis' section).

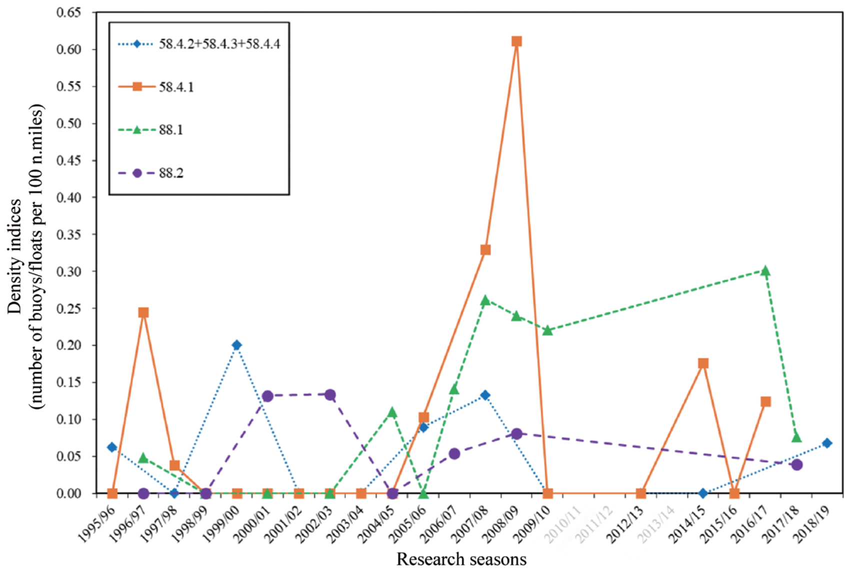

Fig. 4B. The trend of the density indices of sighted buoys/floats by austral summer season and CCAMLR Area, between 1995/96 and 2018/19 (data for the period 1991/92–1994/95 were not used for the reasons explained in the 'Data analysis' section).

overlaps partially with IWC management Areas V, one to three licensed longline vessels fished in the exploratory fishery for *Dissostichus* spp. from 1996/97 to 2001/02 (except 10 vessels in 2000/01). This number increased to more than 10 in 2002/03 to 2011/12 (SC-CAMLR, 2012b), 16 in 2016/17 and 25 in 2017/18 (CCAMLR, 2017, 2018). The number of sighted buoys/floats increased significantly in Areas IV and V after the 2005/06 season, peaked in the 2007/08 season, and then decreased. However, the decrease in Area V was less prominent than in Area IV (Fig. 4A). The pattern exhibited in Figs. 4A and 4B mimics the fluctuations of longline fishing operations in these Areas. In addition to this, operations by IUU (illegal, unreported and unregulated) vessels have been reported in these areas (SC-CAMLR, 2012a, 2012b). Therefore, it is likely that the buoys/floats debris observed in the present study come from fishing vessels operating in Areas 58.4.1 and 88.1. Although not statistically significant, the density index increased between the first and second period in Area 88.2, where fishing activities were also reported (see Fig. 1 in Brooks *et al.*, 2020). It should be noted that a loss of fishing gears from bottom longline fisheries targeting Antarctic toothfish operating in Areas 88.1 and 88.2 was reported in Webber and Parker (2012).

Fishing operations are a source of marine macro debris in the Antarctic, contributing not only to direct fishing-related debris but also miscellaneous debris items (Ivar do Sul *et al.*, 2011). Webber and Parker (2012) recommended that fishing vessels and/or the CCAMLR observers should record detailed information on gear loss, in order to estimate unaccounted fishing mortality and to reduce the loss of fishing gear. Such information is also essential to understanding the interaction among whales, fisheries and marine debris.

Despite the increasing trend observed in some areas, the overall number of floating marine macro debris in the Indo-Pacific sector of the Antarctic is very low, and this result is consistent with the low incidence of marine macro debris and entanglements found in the stomach of Antarctic minke whales in the same sector of the Antarctic (see Isoda *et al.*, this issue).

Conclusions

This study provided the results of the first systematic and comprehensive surveys of floating marine macro debris in the Indo-Pacific sector of the Antarctic conducted for a period of 28 years. The occurrence of floating marine macro debris (metal and polymer products mainly) was generally low. The level of occurrence was substantially lower in comparison with the information reported for other oceanic basins, and this result is consistent with the low incidence of marine macro debris and entanglements found in the stomach of Antarctic minke whales in the same sector of the Antarctic. The main floating marine macro debris was fishing buoys/floats, which increased during the second half of the survey period. The probable source of the buoys/floats are fishing vessels operating in the Antarctic. Long-term surveys (e.g., JARPA, JARPAII and NEWREP-A) proved to be very useful for collecting information of marine debris in the Antarctic. This monitoring of marine macro debris is continuing in the same region under the Japanese Abundance and Stock-structure Surveys in the Antarctic (JASS-A) program (Government of Japan, 2019) since the 2019/20 season. It is recommended that periodical analyses of marine macro debris are conducted and reported in the future.

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Short note

Surface feeding of a sei whale, North Pacific.

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SKELETAL MEASUREMENTS ON SOME LARGE CETACEAN SPECIES DONE BY SCIENTISTS OF TUMSAT AND ICR

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Abstract

In the present paper, detailed measurements of the cranium and mandible of the following large cetacean species and subspecies have been assembled: Antarctic minke whale (*Balaenoptera bonaerensis*; $n=7$), dwarf minke whale (*B. acutorostrata* subsp.; $n=8$), North Pacific common minke whale (*B. a. scammoni*; $n=15$), sei whale (*B. borealis*; $n=1$), Bryde's whale (*B. edeni*; $n=1$) and gray whale (*Eschrichtius robustus*; $n=5$).

Key words: skeletal measurement, Balaenopteridae, Eschrichtiidae, morphometric, large whale.

The head of an animal contains indispensable organs for survival, such as the feeding apparatus, sensory and respiratory organs. Because the skeleton supports and protects these organs, its shape provides a lot of information about the lifestyle of an animal. Furthermore, the skeleton remains as a fossil for hundreds of millions of years and can be used for phylogenetic studies. Therefore, the characteristics of the skeleton, particularly the cranial skeleton, are very important for taxonomical, morphological, anatomical, and paleobiological studies (Miyazaki, 1994). However, skeletal specimens of large whales are quite scarce globally owing to difficulties in acquiring the dead bodies of large whales, high cost and longtime involved in their preservation compared with other mammals, and the large space required for their preservation and storage. In addition, the skeletal specimens of large whales that are available are often assembled and hung in very high places in museums, such as in exhibition halls, making it difficult for scientists to gain access to them for observation.

Dr. Hideo Omura, ex-director of the Whales Research Institute (WRI), vigorously collected skeletal specimens of large whales from the 1950s onward and published many papers on his findings (e.g., Omura and Sakiura, 1956; Omura, 1957, 1975; Omura *et al.*, 1962, 1969, 1970, 1981). The authors of this paper inherited his techniques of skeletal measurements that were directly or indirectly adapted from those he had developed and would like to make the datasets on the skeletal measurements of the following large whale species and subspecies available to others: Antarctic minke whale (*Balaenoptera bonaerensis*; $n=7$), dwarf minke whale (*B. acutorostrata* subsp.; $n=8$), North Pacific common minke whale (*B. acutorostrata scammoni*; $n=15$), sei whale (*B. borealis*; $n=1$), Bryde's whale (*B. edeni*; $n=1$) and gray whale (*Eschrichtius robustus*; $n=5$).

The Antarctic and dwarf minke whales were collected from the Japanese Whale Research Program under Special Permit in the Antarctic (JARPA), which was conducted in the Antarctic Ocean (35°E–145°W) between 1987/88 and 2004/05. The common minke and sei whales were collected from the Japanese Whale Research Program under Special Permit in the Western North Pacific (JARPN) and the Japanese Whale Research Program under Special Permit in the Western North Pacific-Phase II (JARPN II), which were conducted in the North Pacific during 1994–2016. These surveys were conducted in accordance with Article VIII of the International Convention for the Regulation of Whaling and all relevant Japanese regulations, and the study protocol was approved by the Government of Japan (2004). The surveys were planned and conducted by the Institute of Cetacean Research, the National Research Institute of Far Seas Fisheries, and the Fisheries Research Agency (IWC, 2001; 2008; 2017).

After external measurements and predetermined observations had been made, the carcasses were buried in the ground for approximately 2–3 years for the removal of the soft tissues attached to the skeletons. Subsequently, skeleton was dug out and washed to remove any soil and remaining soft tissues on it. It was then dried, fixed with stainless steel straps, and impregnated with resin to prevent it from curving. Then, measurements were made, and the methodology and measurement points determined by Omura (1975) as well as some additional points (Figs. 1, 2) were utilized for further assessments. The cranium was oriented so that the tip of the premaxilla and the right and left squamosals touched the ground, as shown in Fig. 1f, and the straight length of the mandible was measured with the mandible set flat. Measurements were taken as the distance from point to point down to the nearest millimeter scale. A stainless-steel caliper was used for straight distances <50 cm, a large 3.5 m anthropometer was used for straight distances >50 cm, and a measuring tape was used for curved lengths.

We provided the measurements of the craniums and mandibles of the Antarctic minke whales, dwarf minke whales, common minke whales, sei whale and gray whales (Tables 1–5). In each table, the specimen ID is the number that was assigned to the specimen by the institute or museum storing the skeleton and the body length is the distance from the tip of the snout to the notch of the flukes.

Skeletal measurements of the gray whales were collected from the animals, stranded or bycaught around the Japanese coast. These measurements were cited from Nakamura and Kato (2014) with some minor corrections.

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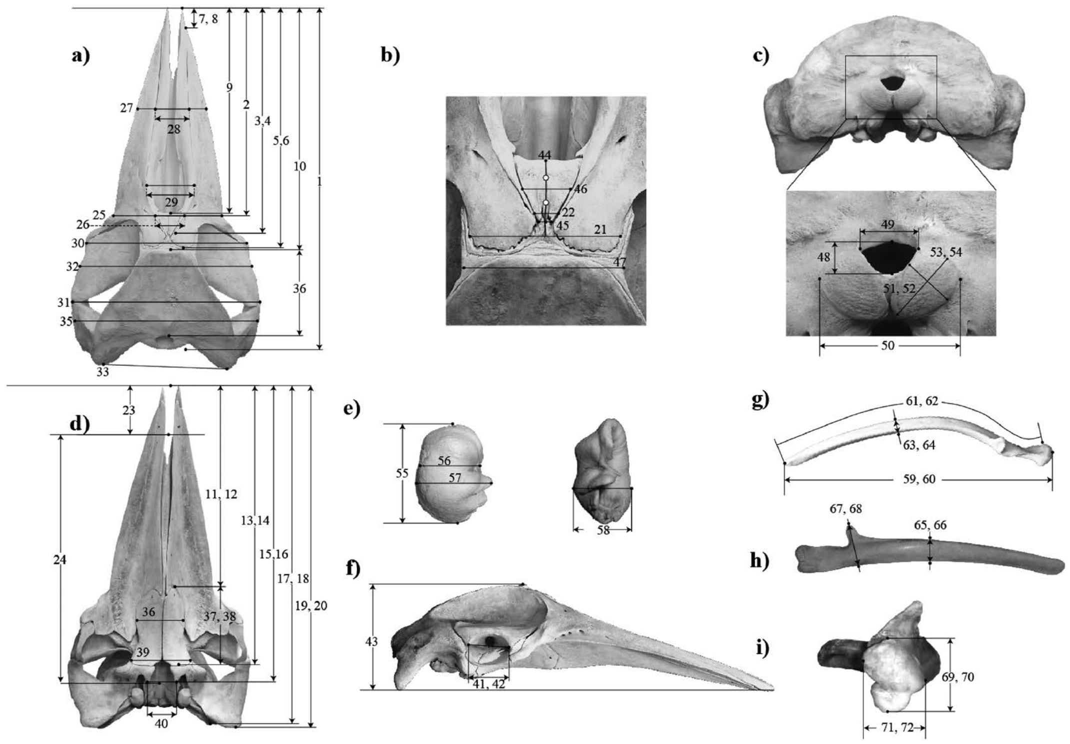


Fig. 1. Measurement points of the cranium and mandible of balaenopterid species. a) dorsal view of cranium, b) vertex of cranium, c) caudal view of cranium, d) ventral view of cranium, e) tympanic bullae, f) lateral view of cranium, g) dorsal view of mandible, h) lateral view of mandible, i) caudal view of mandible.

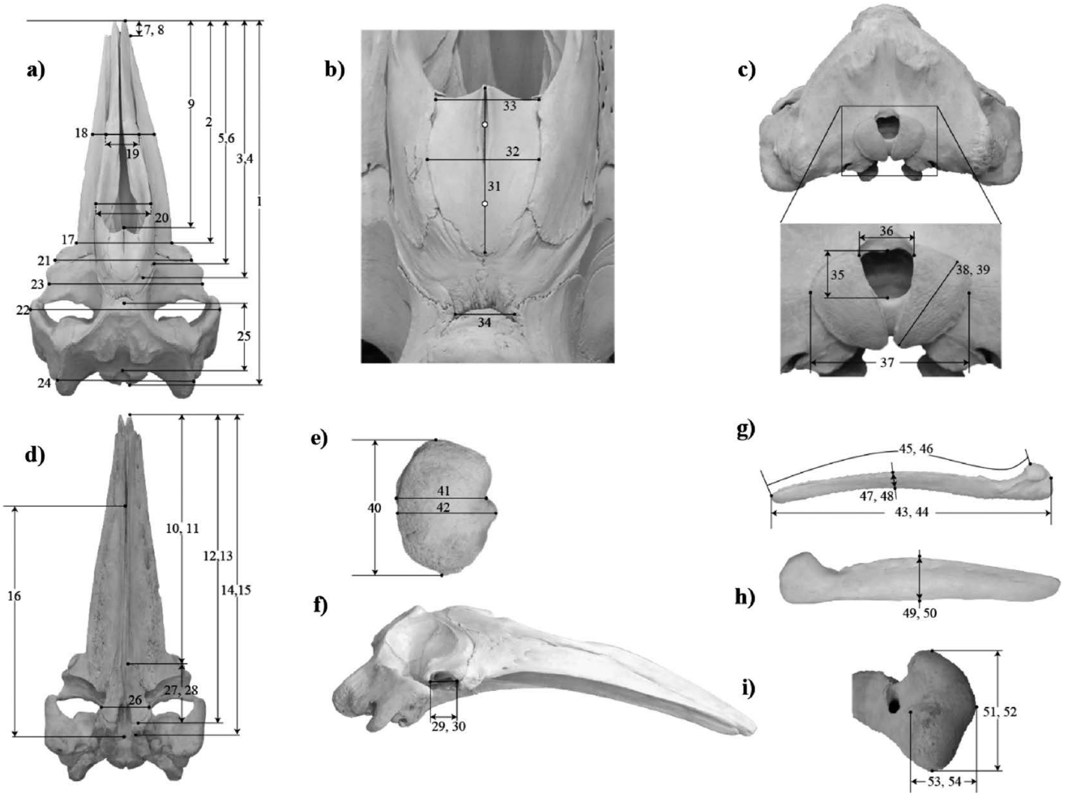


Fig. 2. Measurement points of the cranium and mandible of gray whales. a) dorsal view of cranium, b) vertex of cranium, c) caudal view of cranium, d) ventral view of cranium, e) tympanic bullae, f) lateral view of cranium, g) dorsal view of mandible, h) lateral view of mandible, i) caudal view of mandible.

Table 1. Measurements on cranium and mandible with some biological information on Antarctic minke whales.

Scientific name	*Balaenoptera bonaerensis*						
Locality	Antarctic						
Body length (m)	8.88	8.05	8.53	9.38	9.08	9.28	8.97
Sex	M	M	M	M	M	F	F
Current affiliation*	ICR	ICR	ICR	NA	ICR	NA	ICR
Specimen number	87/88 053	87/88 102	87/88 229	89/90 272	93/94 287	89/90 292	01/02 039
1. Condylobasal length	217.8	186.3	213.6	226.4	208.2	223.7	216.3
2. Length of rostrum	146.0	115.6	136.9	152.4	135.0	145.2	143.4
3. Length of premaxillary (L)	159.0	135.3	151.3	165.3	149.7	161.7	155.0
4. Length of premaxillary (R)	159.2	133.6	151.9	166.0	148.3	162.5	155.5
5. Length of maxillary (L)	149.4	130.6	144.8		139.9	148.9	147.0
6. Length of maxillary (R)	148.1	131.8	142.3	158.2	138.0	152.6	144.1
7. Tip of premaxillary to tip of maxillary (L)	11.7	7.3	8.7		12.3	10.7	11.6
8. Tip of premaxillary to tip of maxillary (R)	8.9		8.7	13.0	10.3	10.1	13.8
9. Tip of premaxillary to nares, anterior	148.2	118.2	134.9	151.0	132.6	143.0	136.8
10. Tip of premaxillary to vertex	157.8	135.6	153.9	169.2	150.8	167.1	157.9
11. Tip of premaxillary to palatine, anterior (L)	154.2	119.3	142.6	148.0	140.3	151.7	146.2
12. Tip of premaxillary to palatine, anterior (R)	154.3	121.6	143.2	146.9	139.2	151.4	146.4
13. Tip of premaxillary to palatine, posterior (L)	191.5	160.8	184.9	196.2	178.8	198.1	188.4
14. Tip of premaxillary to palatine, posterior (R)	191.8	160.2	185.2	196.1	177.0	198.4	189.0
15. Tip of premaxillary to pterygoid process (L)	198.6	168.0	193.6	205.6	187.5	206.0	196.0
16. Tip of premaxillary to pterygoid process (R)	198.6	169.0	193.8	205.3	185.4	205.7	195.7
17. Tip of premaxilla to posterior edge of occipital bone (L)					216.0		224.5
18. Tip of premaxilla to posterior edge of occipital bone (R)					214.2		224.3
19. Tip of premaxilla to posterior edge of temporal bone (L)					207.0		216.5
20. Tip of premaxilla to posterior edge of temporal bone (R)					205.3		216.2
21. Breadth of maxillary, posterior edge		21.6	17.4	19.1	16.5	21.2	17.0
22. Breadth of premaxillary, posterior edge	4.6	3.6	3.5	2.7	5.3		3.7
23. Tip of premaxillary to anterior end of vomer, median		24.9	30.6	28.2	25.3	21.5	30.9
24. Length of vomer					167.6		170.9
25. Breadth of rostrum at base	64.7	65.7	63.6	69.7	67.4	68.5	64.7
26. Breadth of premaxillary at base	11.3	14.0	13.1	18.9	14.4	18.5	12.7
27. Breadth of rostrum at middle	38.5	44.2	41.6	44.2	43.3	46.8	39.2
28. Breadth of premaxillary at middle	16.6	16.4	15.9	19.1	19.5	17.8	17.6
29. Greatest breadth of premaxillary	25.7	25.8	24.8	26.1	25.8	25.5	24.2
30. Breadth of cranium, maxillaries	98.9	97.6	101.7	105.6	103.3	107.6	98.3
31. Breadth of cranium, anterior edge of zygomatic process	110.5	106.6	108.5	119.5	116.6	114.9	109.3
32. Breadth of cranium, middle of orbital foramen	101.4	100.1	104.0	108.9	107.3	106.9	99.4
33. Breadth of occipital bone	91.3	81.6	85.9	101.8	90.3	81.9	81.8
34. Breadth of cranium, middle of zygomatic process	111.1	108.9	110.8	121.4	114.7	118.3	111.7
35. Length from upper ridge of foramen magnum to superior part of occipital bone	60.0	53.9	61.2	63.6	62.4		61.1
36. Greatest breadth of palatine					28.2		27.7
37. Length of palatine (L)	42.3	46.1	46.4		43.0	49.5	47.4
38. Length of palatine (R)	41.7	45.6	46.6		42.8	49.0	47.9
39. Breadth of palatine, posterior	31.8	35.1	33.3		34.4	32.6	30.4
40. Breadth across hamular processes of pterygoid	18.4	19.2	14.3	18.8	21.9	22.0	19.8
41. Length of orbit (L)	19.3	19.6	18.8	18.7	21.5	20.9	20.0
42. Length of orbit (R)	19.0	19.3	19.1	19.0	20.5	20.8	20.0
43. Height of cranium					60.8		59.6
44. Length of nasals	14.0	17.7	16.3	14.8	19.5	20.3	20.7
45. Breadth of nasal, posterior	4.6	3.5	3.4	2.7	1.8	1.1	1.5
46. Breadth of nasal at middle	8.6	6.8	5.7	8.4	8.0	7.3	

Table 1. Continued.

Specimen number	87/88 053	87/88 102	87/88 229	89/90 272	93/94 287	89/90 292	01/02 039
47. Minimum breadth of parietal bones	24.6	22.4	20.6		16.3	22.2	18.7
48. Height of foramen magnum	8.6	6.6	9.3		8.5		9.0
49. Breadth of foramen magnum	9.0	6.9	8.6		8.1		6.6
50. Breadth across occipital condyles	21.5	19.6	22.8	23.0	22.7	20.3	21.4
51. Breadth of occipital condyle (L)		8.1	9.9		8.9		9.8
52. Breadth of occipital condyle (R)		8.7	10.2		9.5		9.5
53. Height of occipital condyle (L)	14.9	11.8	12.7	12.6	12.8	14.1	14.5
54. Height of occipital condyle (R)	14.5	12.2	12.0	13.3	13.0	12.9	14.4
55. Length of tympanic bullae (L)	10.2	9.1	8.4	9.7	8.9	9.3	9.4
56. Minimum breadth of tympanic bullae (L)					5.5		5.7
57. Greatest breadth of tympanic bullae (L)	7.4	7.6	6.9	7.5	6.8	7.5	6.8
58. Thickness of tympanic bullae at middle (L)					4.8		4.9
59. Length of mandible, straight (L)	222.0	195.0	218.5	231.1	215.5	227.0	217.0
60. Length of mandible, straight (R)	211.0	184.7	206.4	212.0	201.6	220.0	206.0
61. Length of mandible, curved (L)	210.8	185.1	207.2	215.6	200.0	219.2	206.5
62. Length of mandible, curved (R)	218.8	192.8	217.4	227.9	213.5	228.3	216.0
63. Breadth of mandible at middle (L)		8.0	8.0	8.8	8.1	8.3	7.6
64. Breadth of mandible at middle (R)		8.1	8.2	8.9	8.3	8.3	7.6
65. Height of mandible at middle (L)		16.2	15.8	16.9	17.7	16.0	16.1
66. Height of mandible at middle (R)		15.8	16.7	17.4	17.7	16.4	15.6
67. Height of mandible at coronoid process (L)	26.4	29.3	30.4	30.7	29.3	31.6	28.8
68. Height of mandible at coronoid process (R)	27.7	29.4	30.5	31.1	29.2	30.9	29.1
69. Height of mandible at coronoid (L)	19.6	18.9	20.8	20.2	19.4	22.4	21.3
70. Height of mandible at coronoid (R)	20.1	19.3	20.9	19.5	19.1	21.5	21.3
71. Breadth of mandible at coronoid (L)	14.5	14.3	14.2	14.8	14.7	15.1	16.1
72. Breadth of mandible at coronoid (R)	15.3	13.9	15.3	16.2	14.0	14.5	15.2

* ICR: Institute of Cetacean Research, NA: Nagoya Public Aquarium

Table 2. Measurements on cranium and mandible with some biological information on dwarf minke whales.

Scientific name	*B. acutorostrata* subsp.							
Locality	Antarctic							
Body length (m)	7.01	6.60	5.41	6.99	7.02	5.94	7.07	7.17
Sex	M	M	M	F	F	F	F	F
Current affiliation*	TUMSAT	ICR	ICR	ICR	ICR	ICR	ICR	ICR
Specimen number	87/88 273	88/89 014	89/90 199	88/89 013	88/89 227	88/89 070	89/90 215	92/93 330
1. Condylobasal length	159.7	149.0	122.3	163.4	164.7	133.1	169.2	156.1
2. Length of rostrum	101.4	97.7	81.6	106.0	111.0	83.4	112.0	106.8
3. Length of premaxillary (L)	119.3	109.8		119.4	120.0	97.9	122.8	119.8
4. Length of premaxillary (R)	120.0	109.3	92.0	121.3	120.8	98.5	122.4	120.2
5. Length of maxillary (L)	117.2	105.5		114.3	115.2	94.3	119.3	111.4
6. Length of maxillary (R)	117.3	105.0		114.8	115.4	94.1	119.3	112.8
7. Tip of premaxillary to tip of maxillary (L)	4.5	8.3		8.4	10.7	8.7	9.6	10.3
8. Tip of premaxillary to tip of maxillary (R)	4.9	9.2		9.8	10.7	5.7	8.3	10.5
9. Tip of premaxillary to nares, anterior	109.0	96.8	82.2	106.2	109.1	85.9	110.4	104.2
10. Tip of premaxillary to vertex	123.7	116.0	96.3	126.5	128.3	103.7	131.7	125.5
11. Tip of premaxillary to palatine, anterior (L)	99.5	97.8		102.3	108.2	85.8	108.0	100.2
12. Tip of premaxillary to palatine, anterior (R)	99.8	97.8	78.7	105.2	107.6	86.9	108.3	100.1
13. Tip of premaxillary to palatine, posterior (L)	134.5	128.1		137.4	142.2	111.7	145.3	135.2
14. Tip of premaxillary to palatine, posterior (R)	134.5	127.6	102.8	139.2	141.3	111.7	143.2	135.5
15. Tip of premaxillary to pterygoid process (L)	144.0	134.6		146.3	150.3	119.7	153.8	143.1
16. Tip of premaxillary to pterygoid process (R)	143.8	134.8	108.4			119.3	152.3	143.3
17. Tip of premaxilla to posterior edge of occipital bone (L)	170.0	156.8		165.7	173.4	139.1	177.8	165.3
18. Tip of premaxilla to posterior edge of occipital bone (R)	169.4	155.9	127.4	166.1	172.0	138.7	176.8	165.3
19. Tip of premaxilla to posterior edge of temporal bone (L)	164.2	153.5		168.7	169.4	136.5	172.2	162.7
20. Tip of premaxilla to posterior edge of temporal bone (R)	164.8	152.2	124.0	171.2	168.2	136.5	170.7	162.7
21. Breadth of maxillary, posterior edge	19.0	14.3	11.6	14.2	19.0	14.0	15.3	17.9
22. Breadth of premaxillary, posterior edge	3.0	3.2	1.3	3.4	4.8	2.1	3.2	3.0
23. Tip of premaxillary to anterior end of vomer, median	21.2	18.3	17.9	17.7	21.7	19.3	18.5	16.3
24. Length of vomer	122.4	116.2	93.7	131.3	127.6	107.0	136.5	126.1
25. Breadth of rostrum at base	55.1	51.2	43.8	50.7	53.8	49.2	59.3	58.2
26. Breadth of premaxillary at base	17.3	12.8	11.3	15.4	13.7	11.7	12.8	13.2
27. Breadth of rostrum at middle	31.4	30.5	23.7	30.7	34.2	28.7	36.4	34.8
28. Breadth of premaxillary at middle	12.6	12.7	9.8	12.7	15.2	11.8	16.5	15.4
29. Greatest breadth of premaxillary	22.2	19.2	15.9	20.2	22.3	17.4	22.0	22.8
30. Breadth of cranium, maxillaries	79.1	73.8	57.6	76.0	78.7	65.9	82.8	80.5
31. Breadth of cranium, anterior edge of zygomatic process	89.1	80.8	64.7	84.5	86.3	72.8	91.5	89.4
32. Breadth of cranium, middle of orbital foramen	80.1	72.3	58.6	77.5	77.7	66.7	83.0	80.4
33. Breadth of occipital bone	69.5	59.3	49.4	63.3	66.4	51.2	62.6	61.7
34. Breadth of cranium, middle of zygomatic process	89.3	79.4	64.6	82.1	85.3	71.8	88.5	87.7
35. Length from upper ridge of foramen magnum to superior part of occipital bone	40.4	36.4	27.7	40.4	40.2	31.4	43.2	37.3
36. Greatest breadth of palatine	24.8	23.8	18.5	23.3	22.7	21.8	26.5	25.3
37. Length of palatine (L)	36.8	32.3	26.6	37.4	36.2	28.3	37.8	37.7
38. Length of palatine (R)	37.1	32.3	27.0	36.1	35.8	27.3	36.4	37.1
39. Breadth of palatine, posterior	25.3	23.1	21.7	22.8	27.3	21.3	27.7	26.7
40. Breadth across hamular processes of pterygoid	12.9	11.7	11.6	12.7	13.8	11.3	14.4	12.8

Table 2. Continued.

Specimen number	87/88 273	88/89 014	89/90 199	88/89 013	88/89 227	88/89 070	89/90 215	92/93 330
41. Length of orbit (L)	17.0	16.5	14.5	15.0	16.5	15.5	16.5	16.5
42. Length of orbit (R)	16.5	15.5	14.0	16.0	17.0	15.5	16.0	16.5
43. Height of cranium		45.1	37.2	50.0	49.4	34.3	51.5	53.4
44. Length of nasals	14.9	14.5	10.8	16.3	17.8	14.0	18.7	17.8
45. Breadth of nasal, posterior	1.1	1.3	0.8	2.0	2.6	1.1	1.2	1.9
46. Breadth of nasal at middle	4.4	4.9	3.3	5.8	7.1	4.5	6.5	5.3
47. Minimum breadth of parietal bones	18.5	15.3	12.8	16.4	20.1	16.5	19.4	20.0
48. Height of foramen magnum	6.4	7.3	6.3	5.9	6.3	6.6	6.3	6.7
49. Breadth of foramen magnum	8.2	6.0	7.4	7.8	7.1	7.3	6.5	7.3
50. Breadth across occipital condyles	17.0	15.7	13.3	16.7	14.3	15.8	16.8	17.2
51. Breadth of occipital condyle (L)	6.8	6.2	5.3	7.0	6.8	6.6	6.7	6.3
52. Breadth of occipital condyle (R)	6.9	6.5	5.3	7.0	6.3	6.2	6.5	6.8
53. Height of occipital condyle (L)	10.9	10.1	8.6	9.8	8.8	9.2	10.0	9.8
54. Height of occipital condyle (R)	11.1	10.0	8.4	10.0	8.9	9.2	10.0	9.8
55. Length of tympanic bullae (L)	8.3	7.9	7.3	8.2	7.7	8.2	8.3	7.6
56. Minimum breadth of tympanic bullae (L)	4.8	4.9	4.5	5.1	5.1	5.2		4.8
57. Greatest breadth of tympanic bullae (L)	6.1	6.1	5.7	6.3	5.9	6.2		5.9
58. Thickness of tympanic bullae at middle (L)		4.3	3.8		4.3	4.5	4.2	4.0
59. Length of mandible, straight (L)	164.5	155.0	127.0	167.0	170.8	140.0		165.0
60. Length of mandible, straight (R)	155.4	146.0	120.7	157.4	161.0	133.5		154.8
61. Length of mandible, curved (L)	156.2	145.8	121.5	158.0	162.0	133.5	167.0	154.5
62. Length of mandible, curved (R)	164.5	154.0	126.0	166.4	170.8	139.9	167.5	165.5
63. Breadth of mandible at middle (L)	7.0	6.4	4.7	6.8	7.5	6.0	6.8	6.8
64. Breadth of mandible at middle (R)	7.0	6.5	4.7	7.1	7.3	6.2	6.8	7.0
65. Height of mandible at middle (L)	10.4	9.8	7.6	10.0	11.1	9.7	11.8	10.6
66. Height of mandible at middle (R)	10.5	10.2	7.7	10.3	11.2	9.5	12.0	10.7
67. Height of mandible at coronoid process (L)	21.5	19.3	16.0	21.0	23.3	18.4	23.2	21.4
68. Height of mandible at coronoid process (R)	21.4	19.4	16.3	21.2	23.2	18.5	23.7	21.6
69. Height of mandible at coronoid (L)	16.8	14.3	12.1	16.1	18.3	14.4	17.3	17.7
70. Height of mandible at coronoid (R)	16.4	14.8	12.3	16.1	18.5	14.4	18.3	17.3
71. Breadth of mandible at coronoid (L)	10.2	9.4	7.7	10.0	10.7	9.3	11.5	11.7
72. Breadth of mandible at coronoid (R)	11.0	9.3	8.0	9.9	10.7	9.1	11.3	11.2

* ICR: Institute of Cetacean Research, TUMSAT: Tokyo University of Marine Science and Technology

Table 3. Measurements on cranium and mandible with some biological information on common minke whales from the North Pacific.

Scientific name	*B. a. scammoni*								
Locality	North Pacific								
Body length (m)	7.31	7.38	7.25	7.53	7.65	7.52	7.51	7.70	4.49
Sex	M	M	M	M	M	M	M	M	M
Current affiliation*	ICR	ICR	ICR	ICR	ICR	KCM	HM	AMP	AMP
Specimen number	94NP 011	94NP 009	94NP 012	97NP 068	97NP 070	05NPCK M001	08NPCK M030	10NPCK M047	10NPCK M054
1. Condylobasal length	145.3	149.8	154.3	160.0	156.7	154.5	152.4	160.2	95.9
2. Length of rostrum	90.7	93.5	88.4	104.4	99.3	96.8	97.0	108.4	59.0
3. Length of premaxillary (L)	107.0	106.8	105.2	116.8	113.9	109.8	109.7	119.3	64.4
4. Length of premaxillary (R)	107.0	106.9	103.9	116.2	113.1	109.9	109.5	119.2	64.0
5. Length of maxillary (L)	101.3		100.7	111.3		103.5	104.3	113.2	63.4
6. Length of maxillary (R)			98.4	112.3	108.3	103.4	105.5	114.5	63.0
7. Tip of premaxillary to tip of maxillary (L)	8.3		11.6	10.1	10.6	9.3	9.6	8.7	5.2
8. Tip of premaxillary to tip of maxillary (R)			9.0	9.5	9.0	9.2	8.2	7.7	6.2
9. Tip of premaxillary to nares, anterior	94.2	95.2	91.3	106.3	103.2	95.6	97.8	107.5	57.2
10. Tip of premaxillary to vertex	113.0	113.0	110.5	122.0	119.3	114.0	117.1	125.0	70.9
11. Tip of premaxillary to palatine, anterior (L)	87.2	94.3	90.6	100.9	99.8	93.4	93.0	98.6	55.3
12. Tip of premaxillary to palatine, anterior (R)	88.7	92.8	92.0	101.3	99.4	93.8	93.0	99.4	55.0
13. Tip of premaxillary to palatine, posterior (L)	120.6	125.4	127.2	135.7	133.0	129.4	127.2	134.6	76.0
14. Tip of premaxillary to palatine, posterior (R)	121.1	125.0	128.0	135.4	133.1	129.6	126.9	136.0	76.0
15. Tip of premaxillary to pterygoid process (L)	128.1		134.9	142.0	140.6	137.3	135.1	143.2	82.0
16. Tip of premaxillary to pterygoid process (R)	128.8		136.0		140.5	138.3	135.0	140.0	81.6
17. Tip of premaxilla to posterior edge of occipital bone (L)	154.0	157.1		167.6	166.4		162.7	171.9	98.4
18. Tip of premaxilla to posterior edge of occipital bone (R)	155.7	157.6		166.8	166.0		161.4	172.8	98.0
19. Tip of premaxilla to posterior edge of temporal bone (L)	150.0	153.4		163.7	162.3		159.0	167.0	96.2
20. Tip of premaxilla to posterior edge of temporal bone (R)	151.5	153.6		162.4	162.3		158.0	167.9	95.4
21. Breadth of maxillary, posterior edge	18.7	15.9	15.5	19.4	14.7		22.0	17.0	7.2
22. Breadth of premaxillary, posterior edge	5.7	2.8	3.2	4.3	3.8	2.3	2.9	3.0	2.1
23. Tip of premaxillary to anterior end of vomer, median	23.9	19.3	20.3	34.7	27.7	23.3	31.4	33.3	15.8
24. Length of vomer	108.5	116.3		111.8	114.9		108.6	112.5	69.5
25. Breadth of rostrum at base	50.7	51.1	47.8	54.6	48.6	49.6	50.1	55.0	30.5
26. Breadth of premaxillary at base	17.2	16.7	16.7	16.7	14.8	16.6	17.2	12.8	7.3
27. Breadth of rostrum at middle	29.0	28.7	29.4	29.2	28.3	24.5	33.5	32.3	18.4
28. Breadth of premaxillary at middle	12.3	12.3	15.7	12.5	12.4		14.9		8.7
29. Greatest breadth of premaxillary	20.9	21.3	21.1	21.7	20.2	20.2	22.0	21.6	13.0
30. Breadth of cranium, maxillaries	75.2	71.8	73.9	79.4	72.5	71.6	77.7	80.9	44.0
31. Breadth of cranium, anterior edge of zygomatic process	87.3	83.2	85.9	89.6	83.8	80.7		89.0	50.5
32. Breadth of cranium, middle of orbital foramen	77.6	75.3	77.8	80.9	76.7	74.0	80.4	82.5	44.5
33. Breadth of occipital bone	68.8	63.7	66.7	62.7	67.3	63.1	66.7	70.0	39.2
34. Breadth of cranium, middle of zygomatic process	87.4	83.4	84.7	89.3	84.7	82.8	86.6	87.9	49.5
35. Length from upper ridge of foramen magnum to superior part of occipital bone	41.3	37.8	43.0	41.6	39.8	40.5	39.2	42.1	26.0
36. Greatest breadth of palatine	24.7	20.7	23.6	24.8	24.0	22.4	23.3	24.4	14.0
37. Length of palatine (L)	37.4	34.4	39.0	37.0	36.8	39.1	36.8	38.6	21.7
38. Length of palatine (R)	36.6	35.0	37.5	36.2	37.2	37.7	35.9	38.5	22.6

Table 3. Continued.

Specimen number	94NP 011	94NP 009	94NP 012	97NP 068	97NP 070	05NPCK M001	08NPCK M030	10NPCK M047	10NPCK M054
39. Breadth of palatine, posterior	28.7	27.6	28.9	25.7	26.9	30.9	28.5	32.7	16.6
40. Breadth across hamular processes of pterygoid	13.0		10.5		14.3	12.9			
41. Length of orbit (L)	18.0	16.0	17.4	17.7	19.5	17.1		17.9	13.4
42. Length of orbit (R)	18.0	16.0	17.6	17.5	19.0	17.9	16.5	17.9	13.4
43. Height of cranium	49.8	44.4		48.5	45.9				
44. Length of nasals	13.8	12.8	14.3	11.4	11.8	13.2	13.0	14.5	7.7
45. Breadth of nasal, posterior	3.5	1.3	2.5	2.4	2.0	1.4	1.8	2.1	1.0
46. Breadth of nasal at middle	7.1	5.4	6.0	7.8	5.9	5.9	8.7	6.5	3.8
47. Minimum breadth of parietal bones	19.8	19.3	17.2	21.6	17.7	15.2	24.2	19.5	10.4
48. Height of foramen magnum	7.3	7.1	9.7	7.7	6.7		6.4	7.2	5.5
49. Breadth of foramen magnum	7.6	7.3	8.0	7.0	7.0		8.0	7.4	6.9
50. Breadth across occipital condyles	18.3	18.3	18.5	17.7	16.7	17.9	20.1	18.0	13.7
51. Breadth of occipital condyle (L)	7.1	6.9	7.6	7.0	6.3	7.9	8.1	7.7	5.2
52. Breadth of occipital condyle (R)	6.7	7.1	7.5	7.2	6.7	7.6	7.8	7.6	5.5
53. Height of occipital condyle (L)	10.3	10.7	11.0	10.9	9.5	10.4	10.9	11.2	8.7
54. Height of occipital condyle (R)	10.3	10.8	10.9	10.7	9.7	10.7	10.7	10.8	9.0
55. Length of tympanic bullae (L)	8.7	9.1	9.3	9.2	8.8	8.9	9.1		9.2
56. Minimum breadth of tympanic bullae (L)	5.3	5.8		5.7	5.6		5.8		5.7
57. Greatest breadth of tympanic bullae (L)	6.5	6.9		6.2	6.7	6.9	7.0		7.1
58. Thickness of tympanic bullae at middle (L)	4.9	5.0		4.8	4.8				
59. Length of mandible, straight (L)	148.0	152.5	148.8	160.0	159.4	154.5	155.0	161.5	96.0
60. Length of mandible, straight (R)	142.0	145.8	149.0	151.8	153.2	152.0	148.7	155.0	92.6
61. Length of mandible, curved (L)	142.2	146.0	155.4	152.4	152.8	151.5	149.8	154.0	92.2
62. Length of mandible, curved (R)	149.0	152.6	153.2	160.4	158.8	156.0	154.6	162.5	95.6
63. Breadth of mandible at middle (L)	6.2	6.3	6.3	7.0	6.2	6.3	6.4	7.1	4.2
64. Breadth of mandible at middle (R)	6.1	6.1	6.9	7.0	6.3	6.3	6.6	7.2	4.1
65. Height of mandible at middle (L)	11.4	10.3	10.8	11.2	10.2	11.4	11.3	11.7	6.4
66. Height of mandible at middle (R)	11.7	10.3	10.3	11.2	10.3	11.5	11.5	11.8	6.5
67. Height of mandible at coronoid process (L)	20.7	19.0	20.2	21.0	21.0	20.2	22.0	20.4	13.4
68. Height of mandible at coronoid process (R)	20.1	18.6	20.6	20.7	21.2	20.9	22.1	20.1	13.3
69. Height of mandible at coronoid (L)	14.6	15.3	15.4	14.4	14.6	13.3	15.7	14.7	8.9
70. Height of mandible at coronoid (R)	14.2	15.5	15.6	14.7	14.8	13.7	15.5	14.0	9.3
71. Breadth of mandible at coronoid (L)	11.3	10.6	11.5	10.3	9.8	10.3	10.3	10.4	6.8
72. Breadth of mandible at coronoid (R)	11.3	10.7	11.2	10.0	10.2	10.8	10.3	10.4	6.8

* ICR: Institute of Cetacean Research, HM: The Hagi Museum, AMP: Ashoro Museum of Paleontology

Table 4. Measurements on cranium and mandible with some biological information on common minke, sei and Bryde's whale from the North Pacific.

Scientific name	*B. a. scammoni*						*B. borealis*	*B. edeni*
Locality	North Pacific						North Pacific	
Body length (m)	8.09	7.60	7.75	7.31	7.30	7.11	13.37	12.41
Sex	F	F	F	F	F	F	M	F
Current affiliation *	ICR	ICR	ICR	ICR	ICR	ICR	MBIK	MBIK
Specimen number	94NP 021	95NP 048	97NP 078	99NP 063	99NP 073	99NP 098	03NP SE045	00NP B006
1. Condylobasal length	167.3	156.7	166.8	161.4	161.5	151.9	306.5	297.6
2. Length of rostrum	101.4	105.7	107.5	103.0	102.8	95.8	203.9	195.8
3. Length of premaxillary (L)	119.5	119.2	123.1	117.8		112.1	233.8	
4. Length of premaxillary (R)	119.7	119.8	122.3	118.7	118.7	113.0		
5. Length of maxillary (L)	115.2	112.6		110.5	113.3	106.3	226.3	225.2
6. Length of maxillary (R)	115.0	112.6	117.2	111.6	112.0	106.5	224.3	225.0
7. Tip of premaxillary to tip of maxillary (L)	7.9	10.2		10.4		9.3	17.3	8.2
8. Tip of premaxillary to tip of maxillary (R)	8.1	10.6		10.2	9.0	9.3	16.7	
9. Tip of premaxillary to nares, anterior	107.6	104.4	111.6		104.6	98.8	213.5	212.2
10. Tip of premaxillary to vertex	123.2	125.3	129.8	123.8	123.8	117.3	238.3	235.3
11. Tip of premaxillary to palatine, anterior (L)	104.0	98.4	103.8	99.8		92.7	213.1	207.8
12. Tip of premaxillary to palatine, anterior (R)	104.7	98.0	104.9	101.4	100.8	92.1	211.0	207.6
13. Tip of premaxillary to palatine, posterior (L)	142.4	135.3	139.0	136.3		126.9	267.7	256.4
14. Tip of premaxillary to palatine, posterior (R)	143.3	135.4	139.3	137.3	135.8	127.7	266.2	257.4
15. Tip of premaxillary to pterygoid process (L)	150.6	143.3	146.6	143.8		134.0	281.5	275.0
16. Tip of premaxillary to pterygoid process (R)	150.7	143.6	147.1	144.3	144.5	134.7	279.9	274.9
17. Tip of premaxilla to posterior edge of occipital bone (L)		170.6	173.6	170.1		154.3		
18. Tip of premaxilla to posterior edge of occipital bone (R)		170.9	172.6	170.7	167.2	154.3		
19. Tip of premaxilla to posterior edge of temporal bone (L)		168.9	169.9	164.8		158.6		
20. Tip of premaxilla to posterior edge of temporal bone (R)		169.0	168.3	165.2	163.2	159.0		
21. Breadth of maxillary, posterior edge	17.6	13.3	18.7	15.2	14.3	16.4	27.8	24.0
22. Breadth of premaxillary, posterior edge	5.4	3.2	5.2	2.4		3.1		
23. Tip of premaxillary to anterior end of vomer, median	24.6	24.6	27.6	25.8	30.0	29.4	22.8	33.4
24. Length of vomer		119.7	123.8	119.0	118.2	108.1	265.3	241.3
25. Breadth of rostrum at base	53.3	60.3	53.1	53.4	50.3	48.3	92.2	94.2
26. Breadth of premaxillary at base	22.3	14.5	21.6	17.6	15.3	17.2	27.9	22.1
27. Breadth of rostrum at middle	32.2	34.7	32.1	32.7	29.2	26.7	51.9	55.8
28. Breadth of premaxillary at middle	13.8	14.8	14.9	15.0	12.3	10.7	28.4	17.6
29. Greatest breadth of premaxillary	25.8	24.6	25.3	22.7	21.3	20.3	34.5	24.0
30. Breadth of cranium, maxillaries	80.1	85.4	77.7	79.4	75.8	73.7	130.0	128.8
31. Breadth of cranium, anterior edge of zygomatic process	92.8	96.5	90.5	87.7	83.4	83.0	148.9	136.6
32. Breadth of cranium, middle of orbital foramen	85.9	89.3	81.4	80.8	76.0	74.4	134.4	131.2
33. Breadth of occipital bone	65.5	72.4	67.3	68.6	61.7	61.8	105.6	100.3
34. Breadth of cranium, middle of zygomatic process	92.4	94.6	91.8	86.5	83.3	81.4	154.1	142.6
35. Length from upper ridge of foramen magnum to superior part of occipital bone	44.6	39.3	42.9	39.2		36.3	78.4	67.5
36. Greatest breadth of palatine	28.0	27.4	26.8	23.8	22.6	21.8	31.7	37.4
37. Length of palatine (L)	41.1	40.2	37.8	38.8		37.3	62.5	52.5
38. Length of palatine (R)	41.6	39.7	36.7	38.4	36.8	38.2	63.3	53.0
39. Breadth of palatine, posterior	30.2	29.4	29.5	28.4		25.8	41.9	41.4
40. Breadth across hamular processes of pterygoid	13.4	14.3	14.3	13.1	14.8	13.8	26.3	23.0
41. Length of orbit (L)	17.9	16.0	17.5	17.5	17.0	16.0	23.9	23.8
42. Length of orbit (R)	18.4	16.5	17.5	17.5	17.0	16.0	24.8	23.0
43. Height of cranium		54.4	52.2	51.4	48.5	47.8		
44. Length of nasals	13.7	16.0	13.9	13.1	14.7	13.8	22.4	
45. Breadth of nasal, posterior	3.9	1.3	1.3	1.5	1.8	0.8	2.6	

Table 4. Continued.

Specimen number	94NP 021	95NP 048	97NP 078	99NP 063	99NP 073	99NP 098	03NP SE045	00NP B006
46. Breadth of nasal at middle	8.3	5.7	8.1	5.5	5.3	6.0	10.6	
47. Minimum breadth of parietal bones	21.5	16.4	21.5	17.2	16.5	19.4	29.7	26.3
48. Height of foramen magnum	12.0	6.6	6.3	6.6	6.7	7.0	7.5	6.5
49. Breadth of foramen magnum	10.0	6.8	6.7	7.3	7.1	7.8	7.0	5.9
50. Breadth across occipital condyles	19.6	16.6	18.3	17.5	16.2	17.0	28.0	26.5
51. Breadth of occipital condyle (L)	7.7	6.8	7.0	7.1	7.3	6.4	13.6	11.7
52. Breadth of occipital condyle (R)	7.7	6.7	7.0	7.1	7.3	6.4	13.2	11.1
53. Height of occipital condyle (L)	11.3	10.5	10.9	10.7	10.7	9.8	16.7	18.1
54. Height of occipital condyle (R)	11.2	10.4	10.8	10.8	10.7	9.9	17.0	17.9
55. Length of tympanic bullae (L)	9.3		9.0	9.3		9.3	12.1	12.1
56. Minimum breadth of tympanic bullae (L)			5.8	5.2		5.8	7.1	
57. Greatest breadth of tympanic bullae (L)	7.3		7.0	6.8		7.0	9.0	7.9
58. Thickness of tympanic bullae at middle (L)			4.7	5.3		5.2	5.8	
59. Length of mandible, straight (L)	164.6	168.5	168.0	163.5	160.4	155.0	302.0	287.5
60. Length of mandible, straight (R)	164.0	161.6	159.0	158.0	153.0	147.5	292.3	286.9
61. Length of mandible, curved (L)	170.4	163.0	159.5	158.0	154.5	148.0	293.3	305.5
62. Length of mandible, curved (R)	170.0	167.5	167.8	164.5	159.5	154.0	301.0	306.5
63. Breadth of mandible at middle (L)	7.1	7.1	6.7	7.1	6.3	6.2	12.3	13.6
64. Breadth of mandible at middle (R)	7.2	7.1	6.7	7.0	6.4	6.3	12.2	14.8
65. Height of mandible at middle (L)	12.5	13.5	11.1	11.7	10.3	10.0	23.3	21.0
66. Height of mandible at middle (R)	12.6	13.7	11.2	11.6	10.7	10.2	23.1	19.8
67. Height of mandible at coronoid process (L)	21.2	23.3	20.2	21.4	20.0	20.5	38.2	34.6
68. Height of mandible at coronoid process (R)	21.2	23.3	20.3	21.8	20.6	20.1	38.6	35.4
69. Height of mandible at coronoid (L)	15.0	15.4	16.5	16.0	16.0	15.8	27.4	25.0
70. Height of mandible at coronoid (R)	16.1	17.4	16.1	15.3	16.3	15.4	27.3	24.7
71. Breadth of mandible at coronoid (L)	13.6	12.0	11.9	10.2	10.7	10.3	22.5	18.4
72. Breadth of mandible at coronoid (R)	12.0	11.9	11.6	10.0	10.6	10.3	22.1	18.4

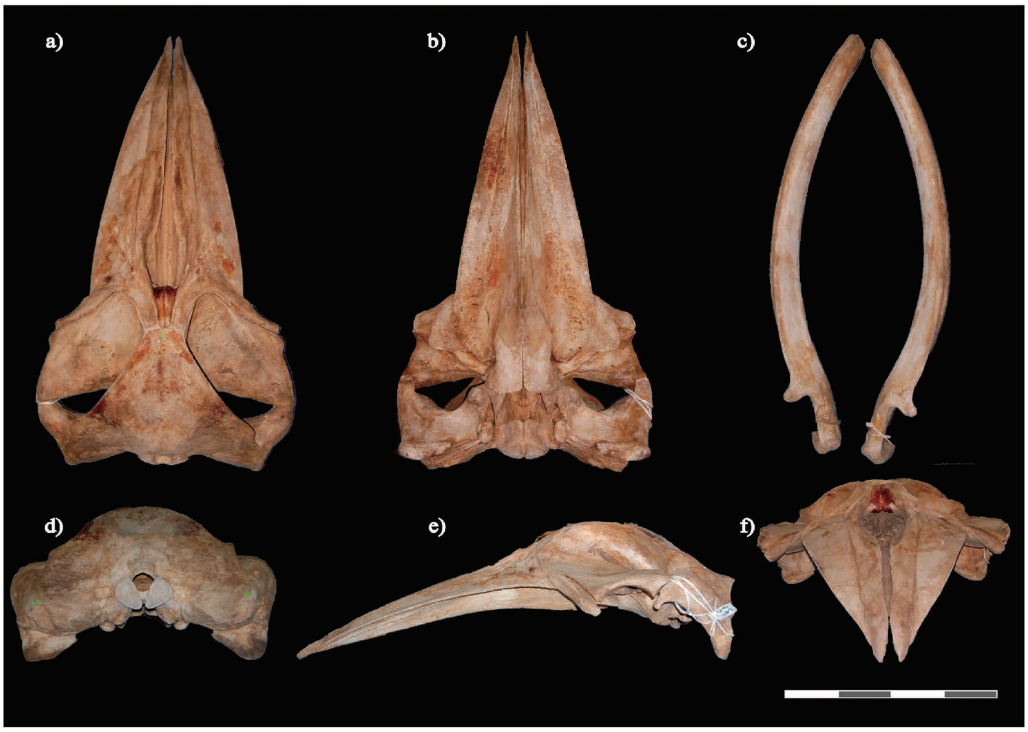
* ICR: Institute of Cetacean Research, KCM: Kushiro City Museum, MBIK: Marine Biodiversity Institute of Korea

Table 5. Measurements on cranium and mandible with some biological information on gray whales.

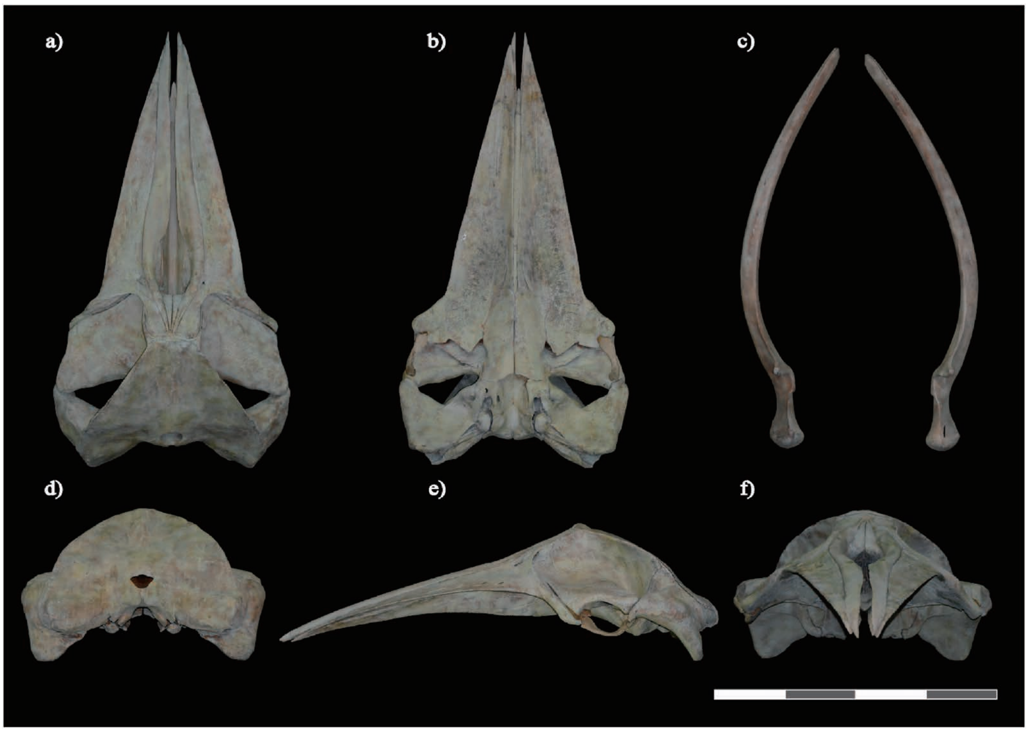
Scientific name	*Eschrichtius robustus*				
Locality	Enoshima, Onagawa, Miyagi pref.		Toyokoro, Obihiro, Hokkaido	Kohzu, Kanagawa pref.	Miyazaki beach, Miyazaki pref.
Sex	F	F	F	M	UNK
Body length (m)	12.79	7.75	9.50	8.00	Est. 7.7
Current affiliation*	TUMSAT	Ishinomaki city	AMP	KPM	NZM
ID	M804A	M804B	AMP-R9	KPM-NF1001969	NZM-159
1. Condylo-basal length	259.5	146.1	187.5	145.8	
2. Length of rostrum (median)	181.9	91.1	125.3	89.3	
3. Length of premaxillary (L)	213.4	112.1	146.2	105.0	
4. Length of premaxillary (R)	212.4	111.7	149.5	103.8	
5. Length of maxillary (L)	190.0	98.3	137.9		
6. Length of maxillary (R)	192.8	98.4	135.4		
7. Tip of premaxillary to tip of maxillary (L)	11.7	6.0	6.0	4.2	
8. Tip of premaxillary to tip of maxillary (R)	10.1	5.8	7.4	2.5	
9. Tip of premaxillary to nares, anterior	179.4	94.3	126.5	88.8	
10. Tip of premaxillary to palatine, anterior (L)	180.5	91.0	126.6	89.1	
11. Tip of premaxillary to palatine, anterior (R)	182.3	90.7	125.9	90.9	
12. Tip of premaxillary to palatine, posterior (L)	219.3	116.5	157.8	117.4	
13. Tip of premaxillary to palatine, posterior (R)	220.4	117.5	158.3	117.8	
14. Tip of premaxillary to pterygoid process (L)	231.2	124.8	166.2	123.0	
15. Tip of premaxillary to pterygoid process (R)	230.2	124.1	166.0	122.6	
16. Length of vomer	177.0	91.3	128.5		
17. Breath of rostrum at base	61.5	34.7	42.9	35.0	
18. Breath of rostrum at middle	39.7	20.2	26.2	22.8	
19. Breath of premaxillary at middle	15.6	12.3	11.6	13.1	
20. Greatest width of premaxilla	34.8	20.4	27.3	22.4	
21. Breadth of cranium, maxillaries	87.6	50.7	64.1	52.0	
22. Breadth of cranium, anterior edge of zygomatic process	120.5	72.2	83.4	71.2	80.3
23. Breadth of cranium, middle of orbital foramen	96.8	50.8	67.8	55.7	65.3
24. Breadth of occipital bone	87.6	51.0	63.7	50.6	57.9
25. Length from upper ridge of foramen magnum to superior part of occipital bone	53.6	34.7	43.7	34.7	38.8
26. Greatest breadth of palatine	36.0	22.6	26.1	25.1	
27. Length of palatine (L)	43.9	28.9	36.6	27.2	
28. Length of palatine (R)	41.8	28.4	36.6	27.0	33.9
29. Length of orbit (L)	17.5	13.5	15.6	13.8	
30. Length of orbit (R)	17.1	13.0	15.7	14.6	14.7
31. Length of nasals, curved	34.0	16.8	24.4	20.3	
32. Breadth of nasal at middle	18.2	7.7	11.2		
33. Breadth of nasal, anterior	18.9	10.8	16.8	11.6	13.8
34. Minimum breadth of parietal bones	24.7		22.6	17.1	
40. Height of foramen magnum	10.4	7.7	12.0	8.1	9.9
41. Breadth of foramen magnum	10.4	9.0	9.9	6.9	8.9
42. Breadth across occipital condyles	30.5	20.5	25.2	19.5	23.3
43. Height of occipital condyle (L)	20.9	15.4	17.8	14.9	17.8
44. Height of occipital condyle (R)	21.0	15.6	17.4	14.5	18.2
45. Length of tympanic bullae (L)	10.5	9.0	9.5	9.1	10.8
46. Minimum breadth of tympanic bullae (L)	7.8				
47. Greatest breadth of tympanic bullae (L)	9.8	8.4	8.3	8.3	9.2
48. Length of mandible, straight (L)	249.8	133.5	173.2	138.4	156.5
49. Length of mandible, straight (R)	246.6	131.5	173.7	139.5	158.9
50. Length of mandible, curved (L)	253.6	136.0		138.5	157.2
51. Length of mandible, curved (R)	254.0	136.0		139.8	155.6
52. Breadth of mandible at middle (L)	10.4	5.8	7.3	5.3	6.9
53. Breadth of mandible at middle (R)	12.3	5.6	6.9	5.1	6.8
54. Height of mandible at middle (L)	33.8	13.8	18.5	15.3	17.6
55. Height of mandible at middle (R)	33.3	14.1	18.0	15.3	16.7
56. Height of mandible at coronoid (L)	44.3	23.2	31.4	21.5	26.2
57. Height of mandible at coronoid (R)	45.4	23.4	30.8	22.1	26.5
58. Breadth of mandible at coronoid (L)	20.9	10.1	14.7	10.4	11.8
59. Breadth of mandible at coronoid (R)	21.3	10.2	15.3	10.8	12.0

*TUMSAT: Tokyo University of Marine Science and Technology, AMP: Ashoro Museum of Paleontology, KPM: Kanagawa Prefectural Museum of Natural History, NZM: Miyazaki Prefectural Museum of Natural History

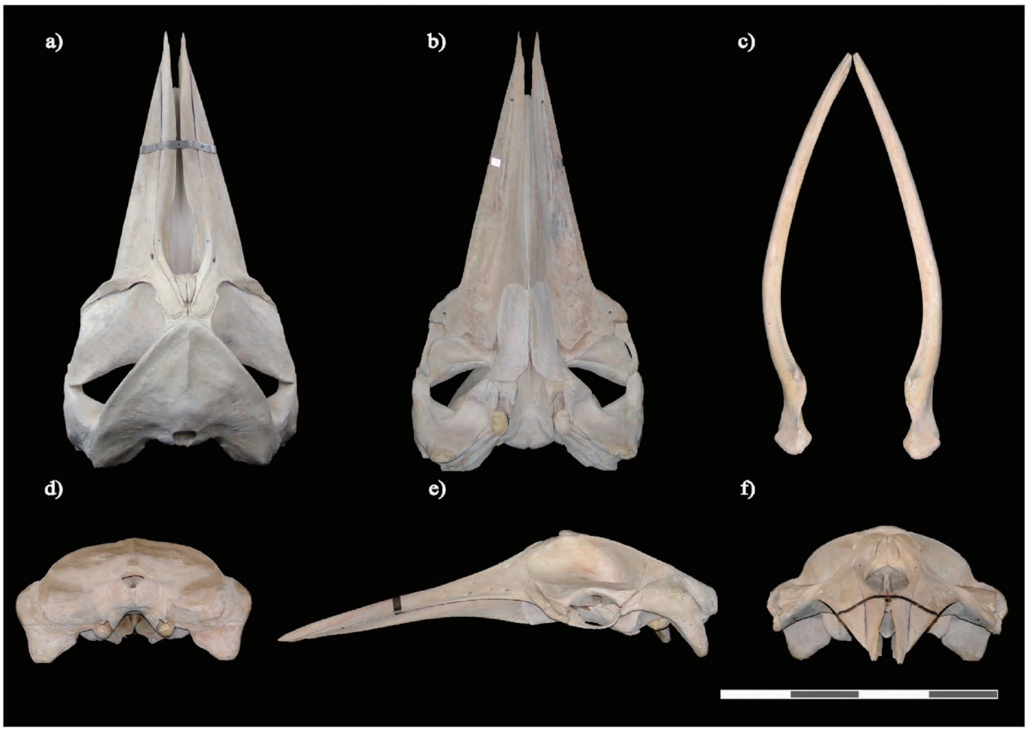
Appendix 1. Photographs of the cranium and mandible of Antarctic minke whale (93/94–287). a) dorsal view of cranium, b) ventral view of cranium, c) dorsal view of mandibles, d) caudal view of cranium, e) lateral view of cranium and f) frontal view of cranium. Scale bar indicates one meter.



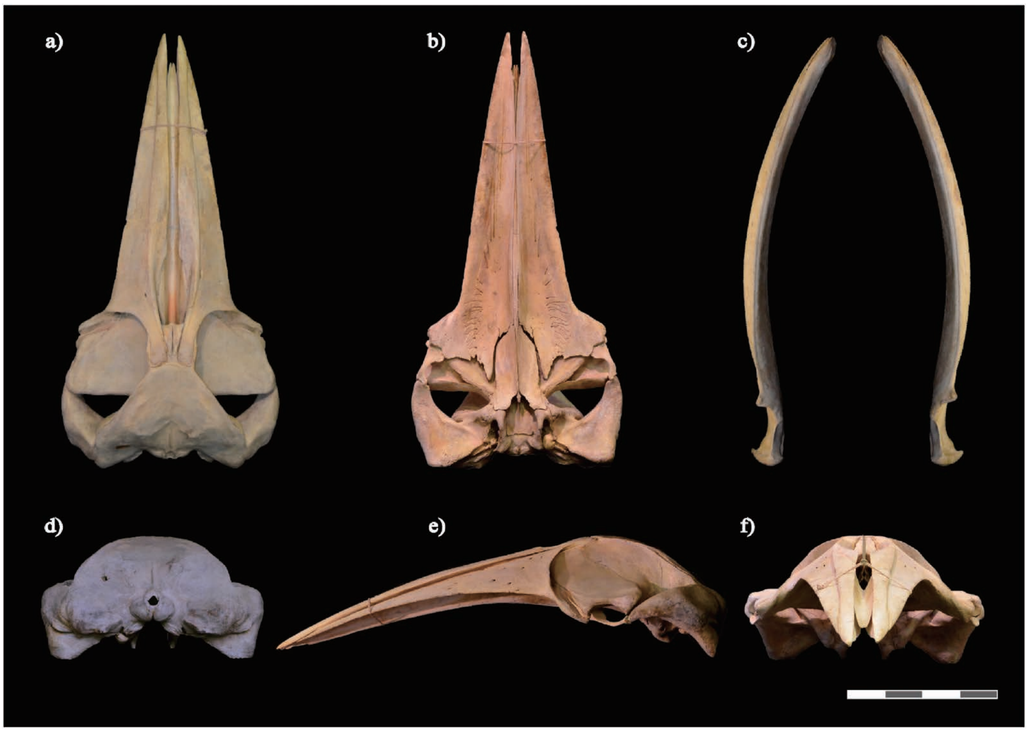
Appendix 2. Photographs of the cranium and mandible of dwarf minke whale (87/88–273). a) dorsal view of cranium, b) ventral view of cranium, c) dorsal view of mandibles, d) caudal view of cranium, e) lateral view of cranium and f) frontal view of cranium. Scale bar indicates one meter.



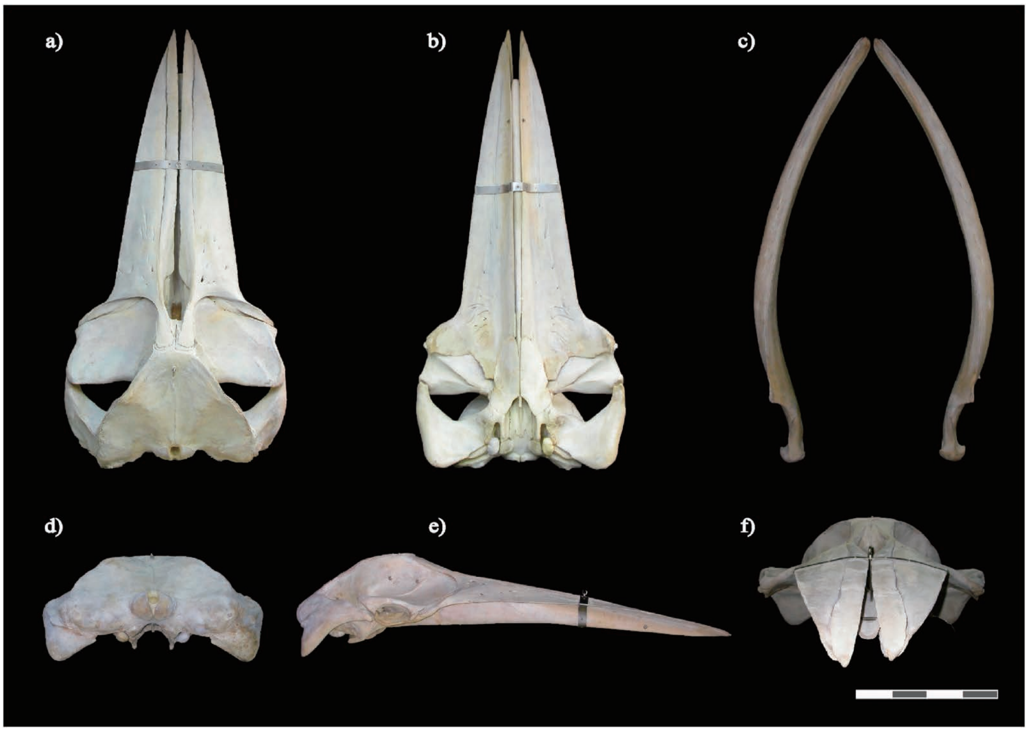
Appendix 3. Photographs of the cranium and mandible of common minke whale from the North Pacific (05NPCK-M001). a) dorsal view of cranium, b) ventral view of cranium, c) dorsal view of mandibles, d) caudal view of cranium, e) lateral view of cranium and f) frontal view of cranium. Scale bar indicates one meter.



Appendix 4. Photographs of the cranium and mandible of sei whale from the North Pacific (03NP-SE045). a) dorsal view of cranium, b) ventral view of cranium, c) dorsal view of mandibles, d) caudal view of cranium, e) lateral view of cranium and f) frontal view of cranium. Scale bar indicates one meter.



Appendix 5. Photographs of the cranium and mandible of Bryde's whale from the North Pacific (00NP-B006). a) dorsal view of cranium, b) ventral view of cranium, c) dorsal view of mandibles, d) caudal view of cranium, e) lateral view of cranium and f) frontal view of cranium. Scale bar indicates one meter.



Appendix 6. Photographs of the cranium and mandible of gray whale (M804A). a) dorsal view of cranium, b) ventral view of cranium, c) dorsal view of mandibles, d) caudal view of cranium, e) lateral view of cranium and f) frontal view of cranium. Scale bar indicates one meter.

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FETAL DEVELOPMENT IN TAIL FLUKES OF THE ANTARCTIC MINKE WHALE

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Abstract

Tail flukes of the Antarctic minke whale fetuses were studied to expand the available knowledge on fetal development, which is relatively understudied, as previous studies are qualitative in nature. Seven measurement points on the tail flukes of 122 fetuses (after conception 12.9 to 259.5 days) were recorded. We quantitatively defined the developmental stages based on the measurements. Tail flukes formed after an estimated fetal age of 57.8 days (9.4 cm) and retained almost the same shape as postnatal at 124.6 days (47.3 cm). The results also revealed that the growth rates differed at each measurement point and each developmental stage.

Key words: Antarctic minke whale, Balaenopteridae, embryology, fetus, fluke, ontogeny.

Several descriptive studies on the morphological changes in tail flukes (hereafter, flukes) during intrauterine development were conducted on mysticetes (Ogawa, 1953; Ohsumi, 1960; Roston *et al.*, 2013) and odontocetes (Ogawa, 1953; Nishiwaki *et al.*, 1963; Amano and Miyazaki, 1993; Štěrba *et al.*, 2000; Thewissen, 2018). However, quantitative studies—measurements and statistical analysis—on the developmental changes of flukes which is one of the most attractive and drastic changes are expected during the intrauterine period, are limited as obtaining a sufficient number of fetal samples for such an analysis is difficult.

This paper provides such quantitative information as above on the development of fetal flukes in cetaceans using the Antarctic minke whales (*Balaenoptera bonaerensis*) and measurements obtained from the New Scientific Whale Research Program in the Antarctic Ocean (NEWREP-A) operation in 2017/18 under the special permit issued by Government of Japan in accordance with the International Convention for Regulation of Whaling (ICRW) (Bando *et al.*, 2018). Samples were collected from the Pacific sector of the Antarctic area bounded by 170°W, 120°W, 60°S, and sea ice edge (or coastline), which corresponds to Area VI as defined by the International Whaling Commission (IWC).

NEWREP-A commenced in the austral summer of 2017/18 and the seasons after with the first author, Kim Y. as well as Bando T. and Nishimura F., on board the research base R/V *Nisshin Maru* in that year (8,030 GT). Through the sampling exercises, 122 fetuses from 122 pregnant females were examined by Kim alongside Bando and Nishimura.

Measurements, including the body length and fluke morphometrics with five measurement points, namely, *total span* (*TS*), *maximum span* (*MS*), *depth of flukes* (*DF*), *anterior length* (*AL*), and *posterior length* (*PL*) as defined in Fig. 1, derived from Ohsumi (1960) for fin whales (*B. physalus*) and Amano and Miyazaki (1993) for Dall's porpoises (*Phocoenoides dalli*), were made during the field survey. *TS* and *MS* were treated as the same for fetuses with less than 47.3 cm in body length because the fetal flukes have indistinguishable tips during the initial developmental stages as their skin lobes are rounded. The body length was measured parallel to the body axis, from the tip of the upper jaw to the notch of the flukes to the nearest 0.1 cm. Body lengths of small fetuses with bent heads and tails were mea-

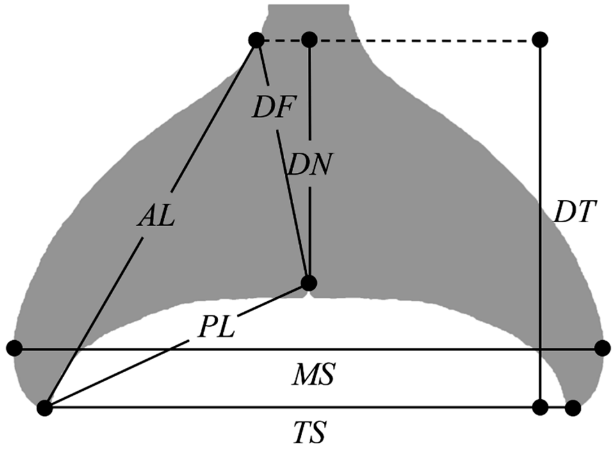

Fig. 1. Measurement points of flukes from the Antarctic minke whale fetuses: *total span* (*TS*), from left tip to right tip; *maximum span* (*MS*), from left ridge to right ridge; *depth of flukes* (*DF*), from anterior insertion, the most anterior point of skin lobes which was visually determined by the first author, to notch; *anterior length* (*AL*), from anterior insertion to tip; *posterior length* (*PL*), from notch to tip; *distance to notch* (*DN*), from the left anterior insertion and right anterior insertion lines to the notch; and *distance to total span* (*DT*), from left anterior insertion and right anterior insertion lines to *TS*.

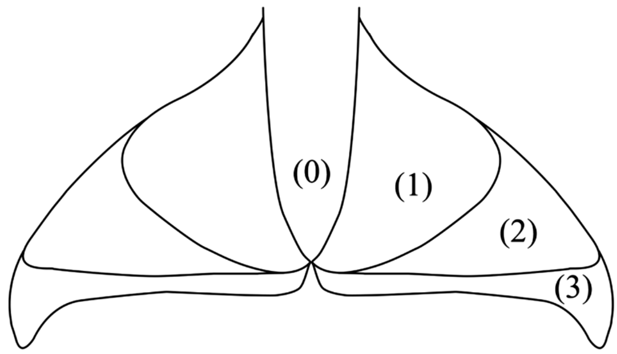

Fig. 2. Developmental stages of the flukes as the Antarctic minke whale fetuses develop: Stage (0), *tail shape*; Stage (1), *diamond shape*; Stage (2), *triangle shape*; Stage (3), *boomerang shape*.

sured along the curved body axis. These measurement points were measured to three decimal places along a straight line from point to point using 30 or 40 cm vernier calipers. Two additional measurement points, namely, *distance to notch* (*DN*) and *distance to total span* (*DT*), were measured. Because the flukes' tips are curved ventrally and both points could not be measured accurately in the field, both measurement points were measured to three decimal places using digital photographs of flukes in the laboratory using the ImageJ software developed by Schneider *et al.* (2012). Fetal age (number of days after conception) was estimated from the body length of the Antarctic minke whale using methods devised by Kato and Miyashita (1991) and seconded by Bando (2017) (see Appendix for the details).

The developmental stages of the fetal flukes were categorized based on Ohsumi (1960) and were conventionally defined as follows (Fig. 2): Stage (0), *tail shape*, with a completely tail-like shape with no skin lobes on both sides; Stage (1), *diamond shape*, when skin lobes form on both sides and flukes have a diamond-like shape (*DT* is less than or equal to half of *DN*); Stage (2), *triangle shape*, when flukes become triangular in shape (*DT* is more than half of *DN*); and Stage (3), *boomerang shape*, when both of the flukes' tips are pointed and the flukes take a boomerang-like shape (*DT* is more than *DN*). The typical shapes of the Antarctic minke whale flukes during their developmental stages [(0)–(3)] are exemplified as in Fig. 3. We also incorporated the allometric equation (Huxley, 1950). Growth pattern analyses were evaluated using *t*-test. Mean values of the ratios of each measurement point to

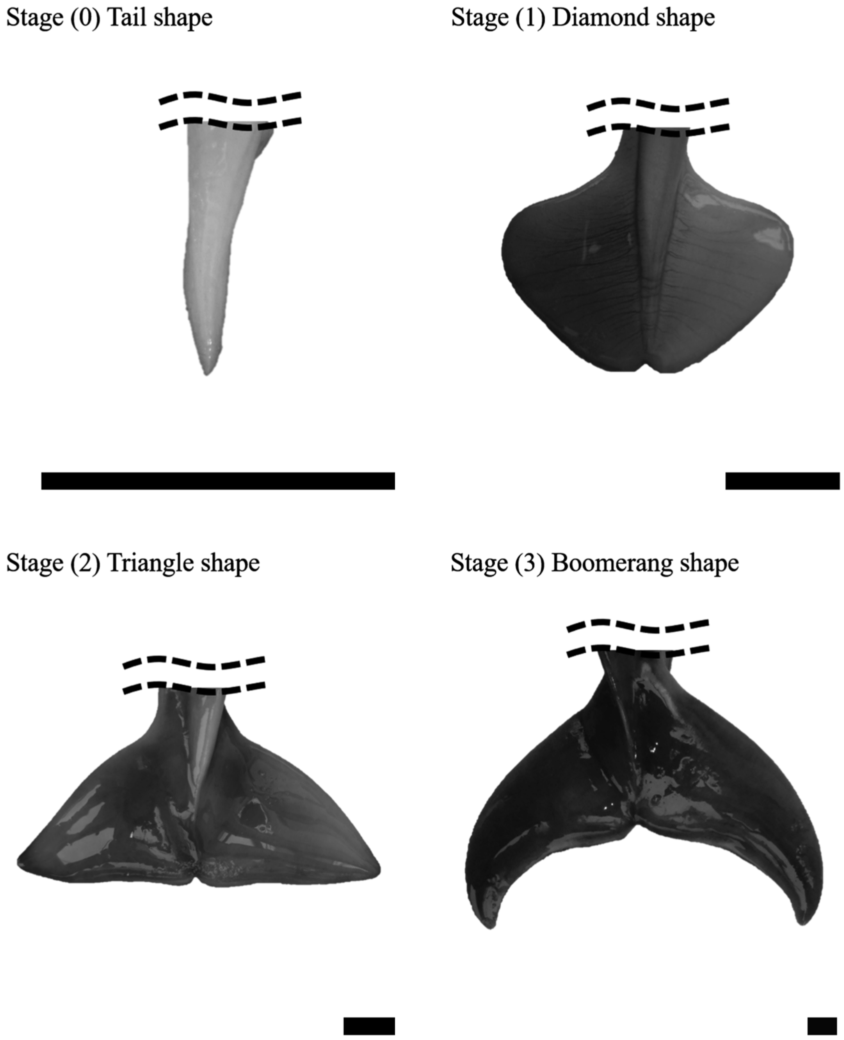

Fig. 3. Photographs of the flukes of the Antarctic minke whale fetuses at each developmental stage. Stage (0), *tail shape* (4.3 cm, 26.4 days, sex unknown); Stage (1), *diamond shape* (17.1 cm, 94.4 days, male); Stage (2), *triangle shape* (34.5 cm, 112.2 days, female); and Stage (3), *boomerang shape* (53.1 cm, 130.1 days, female). Black scale bar indicates 1.0 cm, respectively.

the body length at each developmental stage were evaluated using Mann–Whitney U test. Significant levels of both statistical tests were set at 0.05.

The *MS*/*DF* and *AL*/*PL* ratios indicate the flukes' aspect and diagonal ratios, respectively. These ratios increased as fetuses develop with the following results (Fig. 4): Stage (1), the *MS*/*DF* and *AL*/*PL* ratios increased from 1.0 to 1.4 and from 0.4 to 0.9, respectively; Stage (2), *MS*/*DF* increased from 1.7 to 2.9, and *AL*/*PL* increased from 0.8 to 1.3; and Stage (3), *MS*/*DF* leveled and increased from 2.2 to 3.2, and *AL*/*PL* increased from 1.2 to 1.7. At the beginning of Stage (1), *MS* and *DF* were almost the same. However, *MS* became larger than *DF* as the fetal flukes developed and elongated along the transverse axis direction. Meanwhile, at this stage, *AL* was less than half of *PL*. This changed late in Stage (2) when *AL* became larger than *PL*. This means that the anterior edge of flukes grows faster than their posterior part.

The result of this study showed that fetal age which corresponded to the developmental stages were 12.9–41.8 days in Stage (0), 57.8–96.0 days in Stage (1), 99.0–118.0 days in Stage (2), and 124.6–259.5 days in Stage (3) (Table 1). The flukes started developing skin lobes 57.8 days after conception.

The growth patterns of each measurement point to body length are shown in Table 2. In Stage (1), four measurement points showed positive growth patterns relative to the body length. These were *TS*,

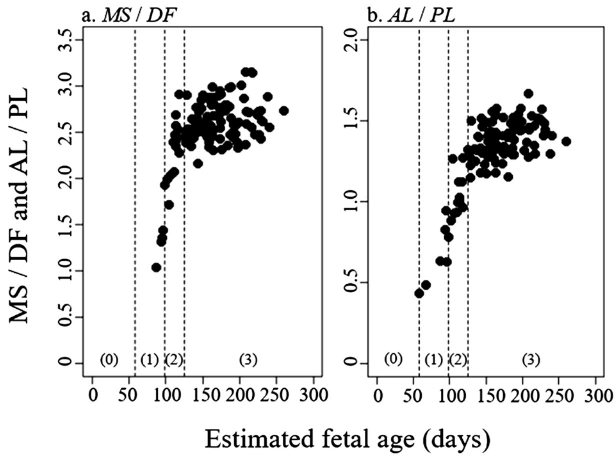

Fig. 4. The relationship between two ratios of fetal flukes (y axis) and estimated fetal age (x axis) at developmental stages of the Antarctic minke whale. The aspect ratio of the flukes, *MS*/*DF* (a), and the diagonal ratio of the outer edges, *AL*/*PL* (b). The dotted lines indicate the starting point of each developmental stage of fetal flukes, from the left to the right: (0), (1), (2), and (3). Stage (0), *tail shape*; Stage (1), *diamond shape*; Stage (2), *triangle shape*; and Stage (3), *boomerang shape*.

Table 1. The body length and estimated fetal age of the Antarctic minke whale at each developmental stage of fetal flukes.

Developmental stage	*N*	Body length (cm)		Estimated fetal age (days)	
		Range	Mean (SD)	Range	Mean (SD)
(0)	3	2.1–6.8	4.4 (2.4)	12.9–41.8	27.0 (14.5)
(1)	9	9.4–18.6	14.5 (3.0)	57.8–96.0	84.7 (13.3)
(2)	14	21.5–40.5	33.1 (5.8)	99.0–118.0	110.8 (5.8)
(3)	96	47.3–203.0	105.1 (35.3)	124.6–259.5	176.6 (30.8)

Stage (0), *tail shape*; Stage (1), *diamond shape*; Stage (2), *triangle shape*; Stage (3), *boomerang shape*.

MS, *AL*, and *PL* ($P<0.01$). Isometric growth patterns were found in the other three points—*DF*, *DN*, and *DT* ($P>0.05$). Positive growth patterns were observed in *TS*, *MS*, *AL*, *PL*, and *DT* in Stage (2) ($P<0.05$), while *DF* and *DN* showed isometric growth patterns to body length ($P>0.05$). In Stage (3), *AL*, *PL*, and *DT* showed positive growth patterns ($P<0.01$), and isometric growth patterns were produced at *MS*, *DF*, and *DN* ($P>0.05$). Negative growth pattern to body length were observed at *TS* ($P<0.05$). In all developmental stages, positive patterns were observed at *AL* and *PL*, while *DF* and *DN* showed isometric patterns. As the flukes developed from Stage (2) to (3), the growth patterns of *TS* and *MS* changed. In Stage (2), the growth patterns to body length of both measurement points were positive, but in Stage (3), those two measurement points were different. In Stage (3), a negative growth pattern was observed at *TS*, and an isometric growth pattern was observed at *MS*. The growth pattern of the *DT* changed from isometric in Stage (1) to positive in Stage (2).

The changes in ratios of each measurement point of the fetal flukes relative to their body length at each developmental stage are as follows (Table 3, Fig. 5). Each ratio was compared using the average values, and the standard deviations were shown with the average values. *TS* and *MS* ratios were 11.1±4.0% in Stage (1) and increased to 22.4±2.6% in Stage (2) ($P<0.01$). In Stage (3), while *TS* is constant at 22.0±2.5% ($P>0.05$), *MS* increased to 24.3±1.9% ($P<0.01$). The *DF* ratio ranged from 9.7±0.6% to 10.8±1.0% for Stage (1) and (2) ($P>0.05$). In Stage (3), DF decreased to 9.2±0.5% ($P<0.01$). The *AL* and *PL* ratios increased with the developmental stages. *AL* increased from 5.8±2.1% to 11.7±1.9% when the developmental stage became from Stage (1) to Stage (2) ($P<0.01$).

Table 2. The growth patterns of fetal flukes at developmental stages of the Antarctic minke whale.

Developmental stage	Measurement point	N	α[1]	ln β[1]	Growth pattern[2]	r^2	P-value
	TS	7	2.605	0.001	Positive	0.980	**
	MS	7	2.605	0.001	Positive	0.980	**
	DF	4	0.883	0.149	Isometric	0.319	n.s.
(1)	*AL*	6	2.341	0.002	Positive	0.934	**
	PL	6	1.423	0.028	Positive	0.995	**
	DN	7	0.787	0.178	Isometric	0.902	n.s.
	DT	7	0.937	0.049	Isometric	0.778	n.s.
	TS	14	1.544	0.033	Positive	0.956	**
	MS	14	1.544	0.033	Positive	0.956	**
	DF	14	0.940	0.120	Isometric	0.889	n.s.
(2)	*AL*	14	1.737	0.009	Positive	0.921	**
	PL	14	1.366	0.032	Positive	0.904	*
	DN	13	1.068	0.079	Isometric	0.944	n.s.
	DT	14	1.970	0.003	Positive	0.884	**
	TS	79	0.921	0.313	Negative	0.882	*
	MS	92	1.034	0.208	Isometric	0.957	n.s.
	DF	96	0.982	0.100	Isometric	0.973	n.s.
(3)	*AL*	92	1.176	0.076	Positive	0.974	**
	PL	91	1.095	0.080	Positive	0.949	**
	DN	65	0.990	0.102	Isometric	0.931	n.s.
	DT	65	1.316	0.036	Positive	0.944	**

[1] α and ln β are the allometric coefficient and constant, respectively. The asterisk indicates the significance levels of each allometric coefficient from a value of 1 (t-test: *, $P<0.05$; **, $P<0.01$, n.s., no significant difference). Stage (0), *tail shape*; Stage (1), *diamond shape*; Stage (2), *triangle shape*; and Stage (3), *boomerang shape*.

[2] The allometric equation $y=\beta x^{\alpha}$ was used to determine the growth curves and patterns in each developmental stage, where x is the body length (cm), y is the length of the measurement point (cm), α is the allometric coefficient, and β is the allometric constant. The growth patterns of each measurement point were classified into three based on the significance (t-test) of the allometric coefficients applied: positive when the allometric coefficient was significantly larger than 1, isometric when the allometric coefficient was not significantly different from 1, and negative when the allometric coefficient was significantly smaller than 1. All statistical analyses were made using R version 3.5.1 (R Core Team, 2018) running on RStudio version 1.1.456 (RStudio Team, 2016). Since no significant differences (ANCOVA, $P>0.05$) were observed in the growth patterns of all measurement points (results are not shown here) between males and females, they were not separated in our analysis.

In Stage (3), *AL* showed 17.2±1.5% ($P<0.01$). On the other hand, *PL* increased from 8.7±1.0% in Stage (1) to 11.5±1.2% in Stage (2) and to 12.4±1.2% in Stage (3) ($P<0.05$). The *DN* ratio ranged from 9.8±0.8% to 10.2±0.8% for all the developmental stages ($P>0.05$). The *DT* ratio increased through all the stages and ranged 4.2±0.5% in Stage (1), 7.7±1.6% in Stage (2), and 15.3±2.1% in Stage (3) ($P<0.01$). The ratios of each measurement point to body length varied depending on the developmental stage. Exceptionally, *DN* stayed within a certain range regardless of the developmental stages. As the flukes developed, the measurement points with increasing ratios were *MS*, *AL*, *PL*, and *DT*. The ratios of the other measurement points (*TS* and *DF*) changed with developmental stages.

Several authors have examined the fetal development of flukes, including Štěrba *et al.* (2000) for common dolphins (*Delphinus delphis*), pantropical spotted dolphins (*Stenella attenuata*), spinner dolphins (*S. longirostris*), and harbor porpoises (*Phocoena phocoena*), Nishiwaki *et al.* (1963) for sperm whales (*Physeter macrocephalus*), and Ohsumi (1960) for fin whales. This paper is the first attempt to incorporate a quantitative measure of fetal growth into drawing the morphological development of fetal flukes of the Antarctic minke whale.

Table 3. The ratios of fetal flukes to body length of the Antarctic minke whale at the developmental stages.

Developmental stage	Measurement point	*N*	The ratios of fetal flukes to body length (%)		*P*-value	
			Range	Mean (SD)	(2)	(3)
(1)	*TS*	7	5.3–15.5	11.1 (4.0)	**	
	MS	7	5.3–15.5	11.1 (4.0)	**	
	DF	4	9.5–11.8	10.8 (1.0)	n.s.	
	AL	6	3.1–8.6	5.8 (2.1)	**	
	PL	6	7.1–9.7	8.7 (1.0)	**	
	DN	7	9.2–11.7	10.2 (0.8)	n.s.	
	DT	7	3.5–4.7	4.2 (0.5)	**	
(2)	*TS*	14	17.9–26.6	22.4 (2.6)		n.s.
	MS	14	17.9–26.6	22.4 (2.6)		**
	DF	14	8.8–10.6	9.7 (0.6)		**
	AL	14	8.3–15.3	11.7 (1.9)		**
	PL	14	9.4–13.6	11.5 (1.2)		*
	DN	13	9.3–11.2	10.1 (0.5)		n.s.
	DT	14	5.1–10.3	7.7 (1.6)		**
(3)	*TS*	79	16.7–28.0	22.0 (2.5)		
	MS	92	20.4–30.1	24.3 (1.9)		
	DF	96	8.1–10.9	9.2 (0.5)		
	AL	92	13.3–20.7	17.2 (1.5)		
	PL	91	9.9–15.8	12.4 (1.2)		
	DN	65	7.5–12.0	9.8 (0.8)		
	DT	65	10.5–20.2	15.3 (2.1)		

The asterisk indicates the significance levels of difference to the average value of each ratio between the consecutive developmental stages (Mann–Whitney U test: *, $P<0.05$; **, $P<0.01$, n.s., no significant difference). Stage (0), *tail shape*; Stage (1), *diamond shape*; Stage (2), *triangle shape*; and Stage (3), *boomerang shape*.

Ohsumi (1960) showed the growth patterns of fin whale fetal flukes (*DF* and *PL* in our study) to body length. Their *DF* changed from a negative growth pattern to a positive one as the fetuses developed. This positive growth pattern was observed at the *PL*. Nishiwaki *et al.* (1963) observed the ratios to body length of three measurement points of sperm whale's fetal flukes, which correspond to the *TS*, *DF*, and *PL* in our study. They found that the *TS* and *PL*/body length ratios increased, while *DF* decreased. The growth patterns and ratios of the fetal flukes of the Antarctic minke whale indicated a rapid growth along the transverse axis direction during the fetal development. The results suggest that the growth rates of cetacean fetal flukes at these measurement points vary from species to species.

Štěrba *et al.* (2000) compared the fetal age development of flukes of four dolphin species: the common dolphin, the pantropical spotted dolphin, the spinner dolphin, and the harbor porpoise. They found that the flukes from each species started developing 32–42 days after conception, while we found that the Antarctic minke whale flukes began to develop at fetal age of 57.8 days. These results are evidence that the development of the Antarctic minke whale flukes begins about 15 days later than that of the dolphins, which would be key for comparing relative ratio to total gestation period and the methodological differences between previous studies and this study, which we plan to do in future investigations.

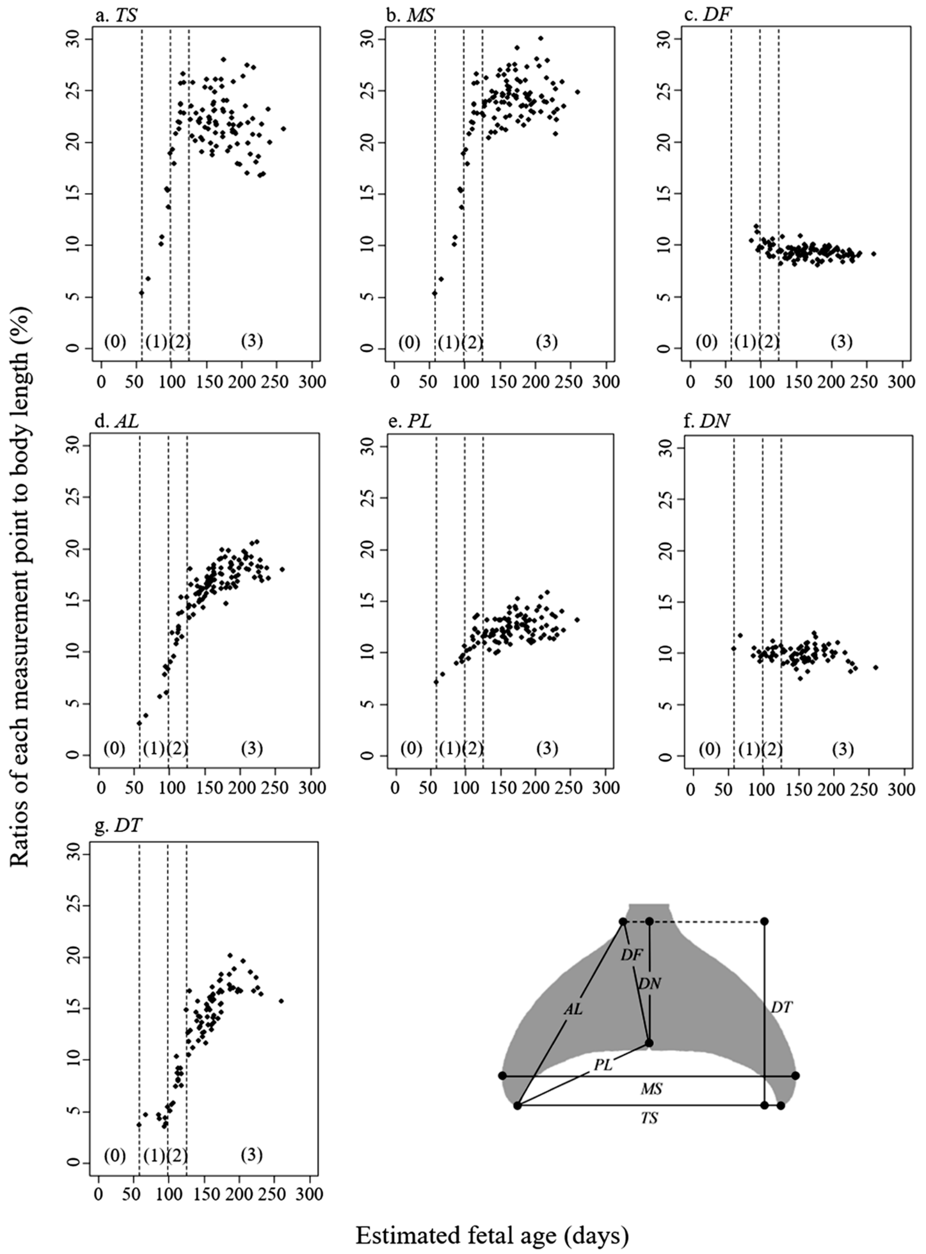

Fig. 5. The relationship between ratios of fetal flukes to body length (y axis) and estimated fetal age (x axis) of the Antarctic minke whale. *TS* (a), *MS* (b), *DF* (c), *AL* (d), *PL* (e), *DN* (f), *DT* (g). The dotted lines indicate the starting points of each developmental stage of fetal flukes, from the left to the right: (0), (1), (2), and (3). Stage (0), *tail shape*; Stage (1), *diamond shape*; Stage (2), *triangle shape*; Stage (3), *boomerang shape*.

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Appendix

Formulas for estimating fetal age of the Antarctic minke whale

We used formula (1) based on Kato and Miyashita (1991) to estimate the fetal age (t, expressed in days) when the body length was 15 cm or more. The growth rate of the fetus changes with the formation of the placenta (Laws, 1961). The placenta of this species is formed when the body length is 15 cm (Kato and Miyashita, 1991). Bando (2017) studied Bryde's (*B. edeni brydei*) and sei whales (*B. borealis*) fetuses, and assumed that days after conception (i.e., fetal age) of fetuses with a body length of less than 15 cm were proportional to their body length. This study made a similar assumption. First, we calculated the fetal age at 15 cm in body length using formula (1) and estimated it at 92.2 days. Subsequently, we adapted $t=aL$ to estimate the growth coefficients (a), which we calculated as 6.147. Formula (2) was used when the body length was less than 15 cm.

$$t = 1.622\,L^{0.892} + 74 \tag{1}$$

$$t = 6.147\,L \tag{2}$$

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

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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.

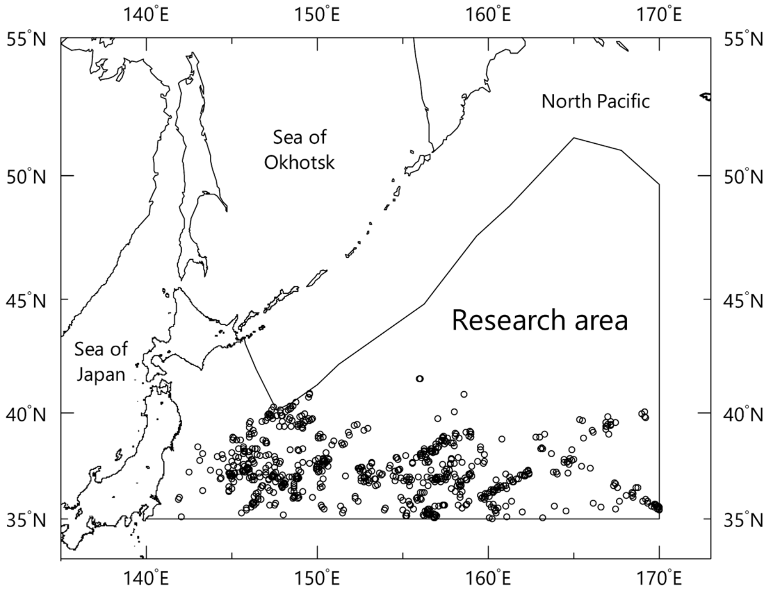

Fig. 2. Research area of the second phase of the Japanese Whale Research Program under Special Permit in the Western North Pacific (JARPNII) and location of sightings of Bryde's whales sampled during 2000–2016 surveys.

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

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

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):

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

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

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):

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

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

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

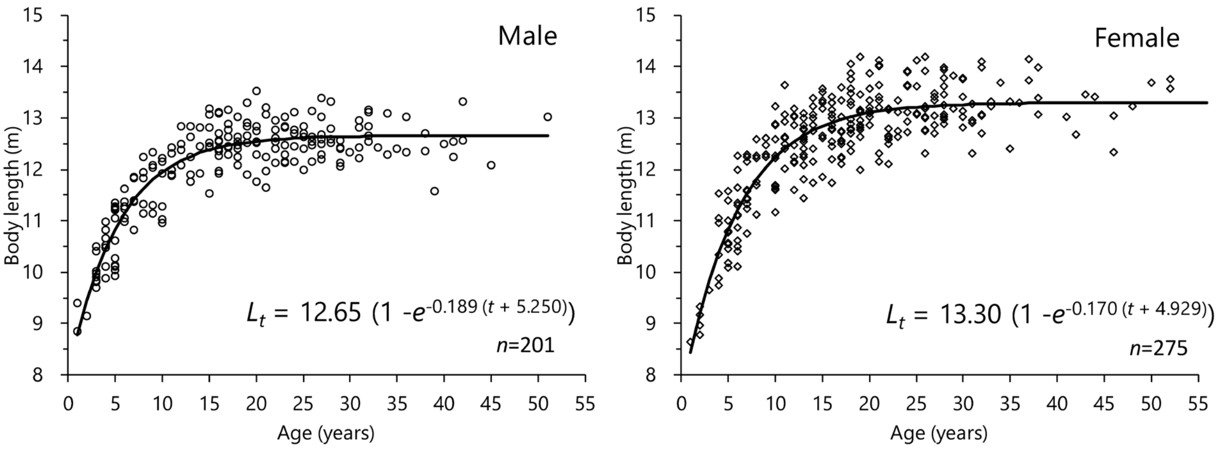

Fig. 3. Relationship between body length and age in Bryde's whale. The solid lines show the von Bertalanffy growth curves.

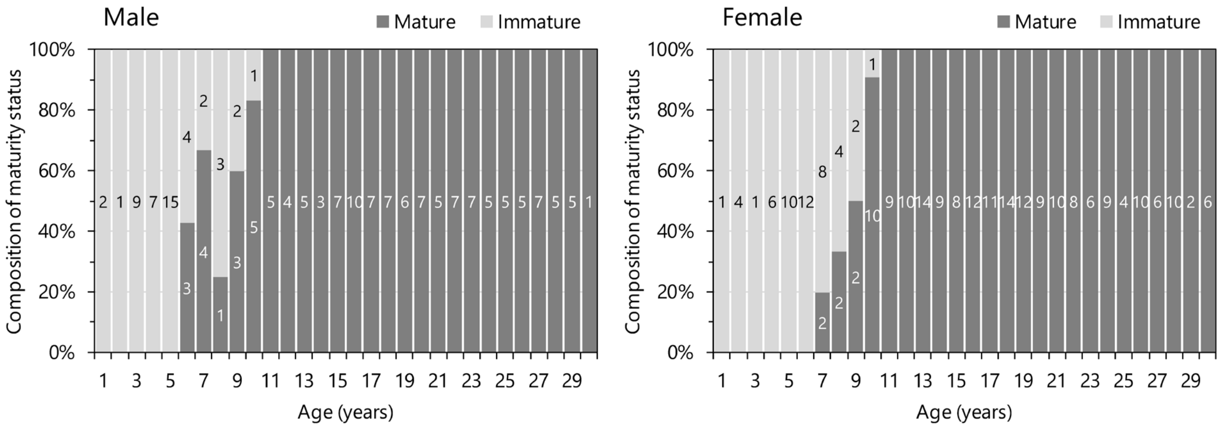

Fig. 4. Sexual maturity status by age and sex in Bryde's whale. Numbers in the bars are the numbers of samples examined.

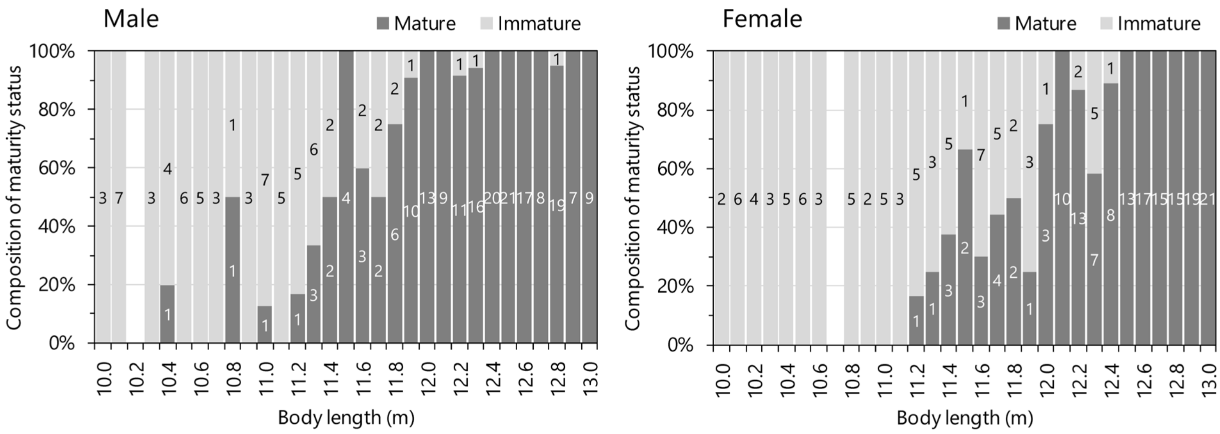

Fig. 5. Sexual maturity status by body length and sex in Bryde's whale. Numbers in the bars are the numbers of samples examined. Body length values were rounded to 0.1 m.

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

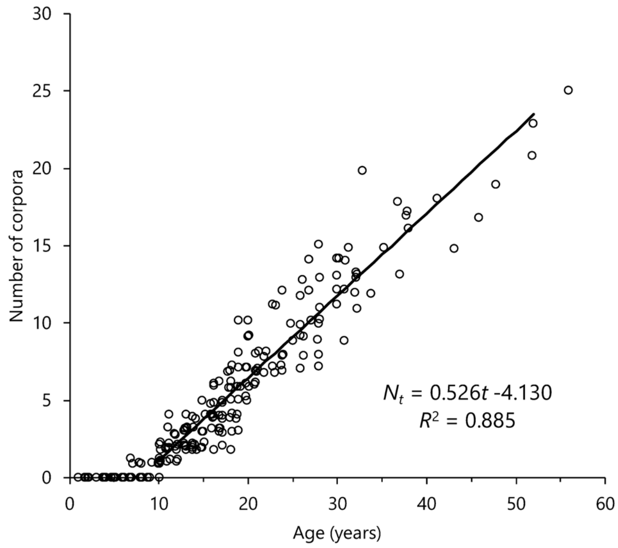

Fig. 6. Jitter plot showing the relationship between age and number of corpora lutea and corpora albicantia in Bryde's whale. The linear regression line was fitted to ages 10 years and more.

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.

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SEASONAL CHANGES IN THE EARPLUG GERMINAL LAYERS OF NORTH PACIFIC COMMON MINKE WHALES

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Abstract

We investigated the annual accumulation rate of the most recently formed layer of earplugs, the germinal layer (GL), of the North Pacific common minke whales, which is important for age estimation. The pale GLs from Kushiro in September and October were found to be significantly thicker than those from Ayukawa in April and May. The results suggest that the pale lamina accumulated during an approximately six-month period from spring to autumn in their feeding season. This was consistent with the hypothesis that one pale and one dark lamina, comprising one growth layer group, are formed annually in this species.

Key words: earplug, common minke whale, age determination, germinal layer, accumulation rate.

The earplugs of baleen whales were first considered to show aging characteristics by Purves (1955). The external auditory meatus lumen is flattened dorso-ventrally, so that the dorsal and ventral epidermis walls are in apposition forming a "blind" section (Purves, 1955). Because of this, the earplug will never fall out throughout a whale's life. The earplug is composed of a "core" and an "outer covering" (Fig. 1). The core of the earplug (b in Fig. 2), where the growth layer group (dark lamina and pale lamina) is formed, is composed of exfoliated and keratinized epidermis of a finger-sack-like tissue called the glove finger (Fig. 1). It is surrounded by a layer of wax-like material from the external auditory canal membrane (outer covering, a in Fig. 2).

Currently, earplugs are used in age estimation for several species of baleen whales (Lockyer, 1984a; Gabriele *et al.*, 2010; Nielsen *et al.*, 2012; Kitakado *et al.*, 2013; Maeda *et al.*, 2016). Many baleen whales are known to migrate seasonally, breeding in low-latitude waters in winter and feeding in high-latitude waters in summer. It is thought that this annual cycle is reflected in earplug growth layers, with a pale lamina forming during the summer feeding season and a dark lamina forming during the winter breeding season (Fig. 2); therefore, one growth layer group represents one year (Roe, 1967;

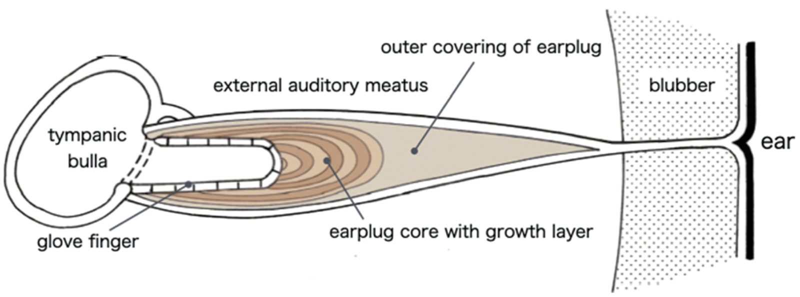

Fig. 1. Diagram showing the anatomical position of the earplug in a typical baleen whale. After Purves (1955).

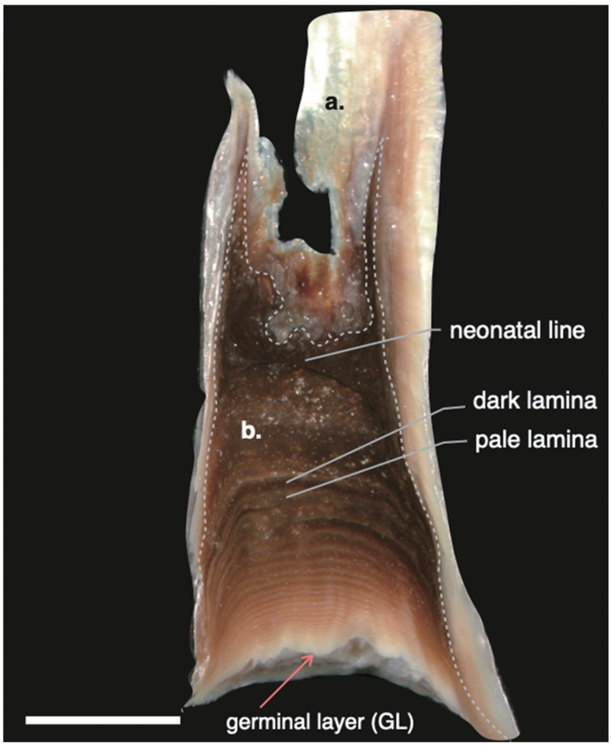

Fig. 2. Bisected surface of an earplug of a common minke whale. **a**: (outside the dotted line), outer covering; **b**: (inside the dotted line), core with growth layers. Scale bar represents: 5 mm.

Lockyer, 1972, 1984b). Fat content tends to be lower in the dark lamina and higher in the pale lamina according to histological observations of fin whale (*Balaenoptera physalus*) earplugs (Roe, 1967). Many other studies have examined whale earplugs; for example, Ohsumi (1964) investigated the annual accumulation rate of earplugs in southern-hemisphere fin whales using the mark-recapture method, and Gabriele *et al.* (2010) conducted a comparative study of the earplug growth layer and long-term individual identification in North Pacific humpback whales (*Megaptera novaeangliae*).

Previously, age estimation from the earplugs of the common minke whale (*B. acutorostrata*) was generally thought to be difficult and impractical because of the softness of the earplugs and the poor formation of growth layers (Sergeant, 1963; Mitchell and Kozicki, 1975; Christensen, 1981; Larsen and Kapel, 1983; Christensen *et al.*, 1990; Kato, 1992; Auðunsson *et al.*, 2013). Under the Japanese Research Program and a special permit in the Western North Pacific (JARPNII), common minke whale earplugs were carefully collected using the gelatinized extraction method (Maeda *et al.*, 2013) and attempts were made to read the growth layer groups. Maeda *et al.* (2016) reported age readability and age estimation errors in common minke whales and concluded that the earplugs of this species can be used as a valid age estimation tool.

However, the annual accumulation rate of growth layers has not been analyzed for North Pacific common minke whales, and age estimation was conducted on the assumption that one growth layer group is formed per year as in other baleen species. In the case of the common minke whale, it is important to understand the periodicity of growth layer formation for age estimation. In this study, we focused on the recently formed layer, the germinal layer (GL), of the earplug and aimed to determine the periodicity of growth layer formation based on seasonal changes in the GL (Fig. 2).

Earplugs obtained from JARPNII Coastal Components from 2003 to 2016 were used. These surveys were conducted off Ayukawa (the Pacific coast of northern Honshu; within a 50-mile radius of Ayukawa Port 38°17′N, 141°30′E) in April and May and off Kushiro (the Pacific coast of eastern Hokkaido; within a 50-mile radius of Kushiro Port 42°59′N, 144°22′E) in September and October (Fig. 3).

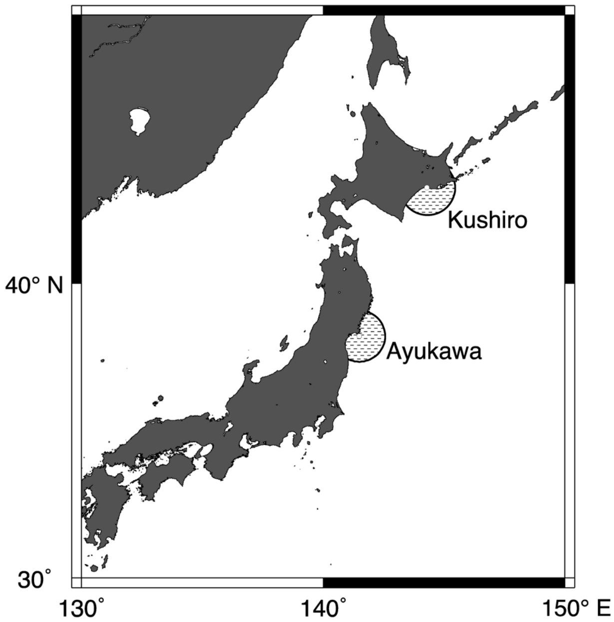

Fig. 3. Survey areas off Ayukawa (the Pacific coast of northern Honshu; within a 50-mile radius of Ayukawa Port 38°17′N, 141°30′E) in April and May, and off Kushiro (the Pacific coast of eastern Hokkaido; within a 50-mile radius of Kushiro Port 42°59′N, 144°22′E) in September and October.

Table 1. Pale and dark ratio of germinal layer (GL) of the earplug of common minke whales in Ayukawa and Kushiro.

	Number of individuals	Pale (%)	Dark (%)	Unknown (%)
Ayukawa (April to May)	175	111 (63.4)	63 (36.0)	*1 (0.6)
Kushiro (September to October)	185	185 (100)	0 (0.0)	0 (0.0)

*The GL was very thin and the type of the color could not be classified.

The earplugs were preserved in 10% neutral buffered formalin solution. In the laboratory, after cutting flat along the central axis of the earplug by using a sharp blade, the earplug was ground on a wet stone under running water to expose the neonatal line and growth layers (Fig. 2). Growth layers were counted underwater using a stereoscopic microscope (magnification: 3.2–31.5). The age in years was defined as one growth layer group comprising a pair of pale and dark laminae in the core. The earplugs of 360 individuals with clear growth layers from the neonatal line to the GL were selected and observed to determine whether the GL was pale or dark (Ayukawa: 175 individuals; Kushiro: 185 individuals; age range: 1 to 44 years). For 204 of these individuals, the thickness of the pale GL was measured using an image analysis software (ImageJ, a public domain, Java-based image processing program, National Institute of Health, USA).

Pale GLs were observed in 63.4% of the earplugs from Ayukawa in April and May and in 100% from Kushiro in September and October (Table 1). For the pale GLs, the mean thickness from Ayukawa was 0.21 mm, while that from Kushiro was 0.40 mm (Fig. 4A). The pale GLs from Kushiro were significantly thicker than those from Ayukawa (t-test; $p<0.05$).

Since the thickness of the GL is expected to compress as the number of growth layers increases, the thicknesses of the pale GLs from Ayukawa and Kushiro were compared with the number of growth layers. The GL thickness from both Ayukawa and Kushiro decreased as the number of growth layers increased, but the Kushiro GLs were thicker than the Ayukawa GLs in all growth layer number classes (Fig. 4B). In growth-layer classes 1–5, 6–10 and 11–15, the pale GLs from Kushiro were significantly thicker than those from Ayukawa (t-test; $p<0.05$).

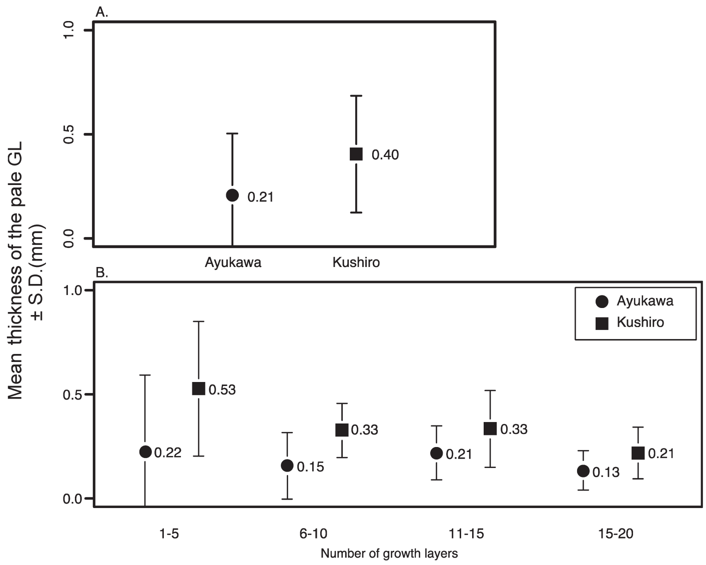

Fig. 4. **A**: Comparison of mean thickness of the pale GL (mm) between Ayukawa in April to May and Kushiro in September to October. **B**: Comparison of mean pale GL thickness (mm) between Ayukawa in April to May and Kushiro in September to October by type of growth layers.

Maeda *et al.* (2013) measured the length of earplugs in the North Pacific common minke whale and examined the growth of the earplug (the core and the outer covering) with age, and found that the outer covering that covers the core was not present in younger earplugs, but it became thicker with age. In younger individuals (with fewer layers), the outer covering has not yet formed and there is more space in the ear canal; the wax pushed out of the glove finger is not compressed and forms a thicker layer (although younger individuals have a better metabolism). However, as the number of layers increases, it was considered that the outer covering developed and the core of the earplug becomes larger; there is less space in the ear canal and the thickness of the GL formed by extrusion from the glove finger becomes thinner.

Lockyer (1972) examined fin whales from the southern hemisphere and observed a distinctly spaced growth layer that diminished suddenly, which was called the transition phase. The transition phase in the earplug, where widely spaced growth layers abruptly become much closer together, indicates the age at sexual maturity. Maeda *et al.* (2017) reported the transition phase could be identified in the North Pacific common minke whale and the mean age at transition phase was about 7 years old for both males and females. While some individuals showed the transition phase (rapid narrowing of the layer interval) as early as 4 years of age (Maeda *et al.*, 2017), the large number of young individuals with relatively wide stratum widths suggests that the SD were greater in the 1–5 years old group.

Hatanaka and Miyashita (1997) reported that immature minke whale individuals are distributed along the northern Pacific coast in early summer; mature females are abundant in high-latitude waters (Sea of Okhotsk) in summer; and mature males are distributed south of mature females in summer, mainly east of the Kuril Islands, and are abundant off eastern Hokkaido at the end of summer. To examine seasonal changes in the accumulation of the growth layers, the feeding season migration route of minke whales was assumed to be as follows. In early summer, minke whales migrate northward along the northern Pacific coast to feed, then migrate to Sanriku off Ayukawa in April and May, which is the early feeding season, and then further northward to their main feeding grounds. They then migrate southward to the waters off Kushiro in September and October, which is the latter half of the feeding season.

While individuals with dark GLs were observed in the early feeding season in Ayukawa, no individuals with dark GLs were observed in the late feeding season in Kushiro. The pale GL was significantly thicker in Kushiro than in Ayukawa, suggesting that a pale layer accumulated during the feeding season from spring to autumn, which lasts approximately six months. This was consistent with the hypothesis that the growth layer (one pair of pale and dark laminae) is accumulated once a year in common minke whales, as in fin whales and other species.

In this study, earplugs with clear growth layers were used. However, Maeda *et al.* (2016) reported that age readability of North Pacific common minke whale was 45.2% for male, 41.2% for female, and most of unreadable earplugs of mature animals had growth layers with unclear formation such as irregular lamination and partially-formed growth layers. Individuals with irregular growth layer groups may not have a clear seasonal migration, and this point requires further investigation.

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A NOTE ON RECENT SURVEYS FOR RIGHT WHALES *EUBALAENA JAPONICA* IN THE WESTERN NORTH PACIFIC

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Abstract

The information of the North Pacific right whale in the western North Pacific was summarized based on the data collected by the Institute of Cetacean Research (ICR: 1994–2016) and the Fisheries Resources Institute (NRIFSF: 1982–2011 including recent Japanese and Russian joint cruise data) with a total of 599,596.7 nautical miles of research distance. North Pacific right whales were distributed north of 42°N in the western North Pacific, including 10 mother and calf pairs during April to September. Two main high-density areas were observed north of 45°N in the area to the far offshore southeast of Kamchatka Peninsula (north of 45°N to 51°N, between 158°E and 168°E) and the central part in the Sea of Okhotsk. There were no sightings in the Sea of Japan during 1982 to 2016. A total of 60 individuals were photographed and 28 biopsy samples were collected. It appears that this species has been showing signs of increase since 1990's, but it is necessary to carefully monitor this population in the future to check the trend. Further surveys, analysis and international collaboration are required to improve our understanding of this species.

Key words: western North Pacific, sighting survey, distribution, North Pacific right whale, *Eubalaena japonica*.

The North Pacific right whale (*Eubalaena japonica*) mainly feeds on copepods and other small invertebrates, such as krill and copepods and they migrate annually between low-latitude winter breeding grounds and colder summer feeding grounds (Nishiwaki, 1966; Kawamura, 1982). In the western North Pacific, according to the plotted spatial distribution of American whaling, based mainly on the original data in the studies of Maury (1852) and Townsend (1935), the right whales were concentrated on either side of the North Pacific, and there were also seasonal changes in distribution, with whales occurring on both sides of the North Pacific in the periods March–May and June–August (Smith *et al.*, 2012). Because they are a slow-swimming whale that floats after death and provided considerable quantities of commercially valuable whale oil and baleen, they were a highly desirable target species (Omura *et al.*, 1969; Omura, 1986). For this reason, they were taken extensively by whaling in the 19th and 20th centuries. Additionally, this species was targeted by illegal Soviet whaling in the 1960's (Ivashchenko *et al.*, 2017).

In the Sea of Okhotsk, according to earlier studies in the 1980's–90's, right whales occurred in small numbers in the central and northeastern parts, and also in few sightings to the southeast of Sakhalin Island and by the Sea of Okhotsk side of the central Kuril Islands (Berzin and Vladimirov, 1986). There have been no observations of right whales in the northern Sea of Japan by Russian vessels since the early the 1960's (Vladimirov, 1993).

In the western North Pacific outside of the Sea of Okhotsk, it was also noted that the Kuril Islands, the Kamchatka coasts and offshore areas are likely to be major summer feeding areas, based on his-

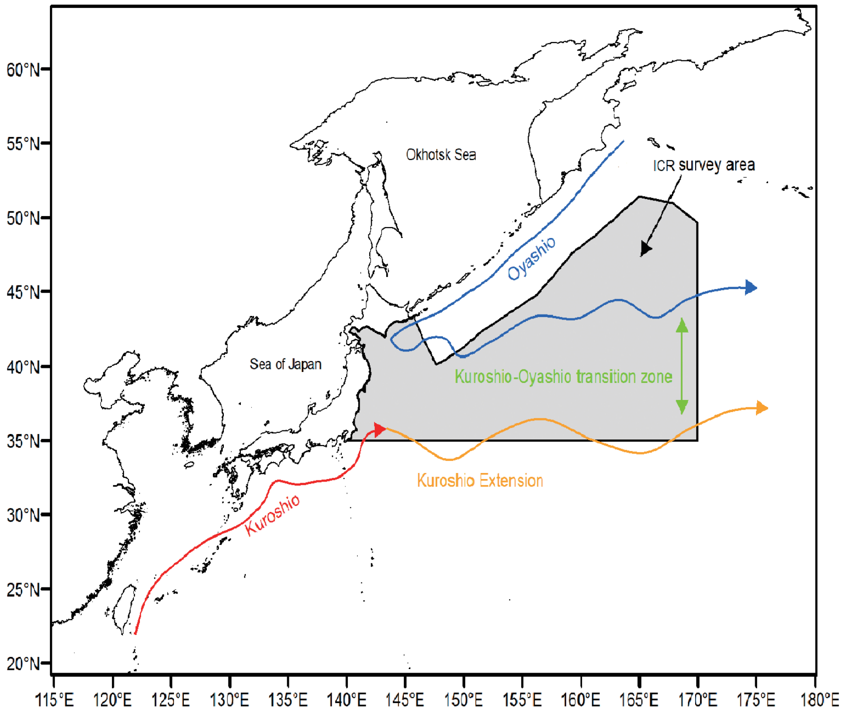

Fig. 1. Schematic map of oceanographic conditions around western North Pacific. The northern part of the ICR survey area is under the influence of the Oyashio (a subarctic western boundary current with cold, low-salinity water) whereas the southern part is under the influence of the Kuroshio and its extension (the subtropical western boundary current with warm, high-salinity water) (after Okazaki *et al.*, 2016).

Table 1. Summary of North Pacific right whale sightings during the JARPN/JARPNII (1994–2016) from April to September, describing the year in which the right whale was sighted. Sch.: Number of the primary sightings of schools. Ind.: Number of the primary sightings of individuals. Calf: Number of calves including Ind. Mss: observed mean school size (Ind./Sch.). SST: Range of surface temperature of the sighting position. Photo-ID: number of individuals, Biopsy sample: number of samples.

Year	Western North Pacific						
	Sch.	Ind.	Calf	Mss	SST (°C)	Photo-ID	Biopsy sample
1994	1	2	1	2.00	17.0	2	0
1995	2	2	0	1.00	6.8–13.2	1	0
1997	2	3	0	1.50	3.5–7.5	1	0
1998	4	6	2	1.50	3.3–13.3	5	0
2001	2	3	1	1.50	12.0–16.9	3	0
2002	2	2	0	1.00	13.4–16.0	0	0
2003	5	6	1	1.20	3.0–15.7	4	1
2004	2	4	0	2.00	10.3–12.7	3	2
2005	2	4	2	2.00	12.3–16.6	2	2
2006	11	15	0	1.40	7.8–10.3	11	2
2007	1	1	0	1.00	13.3	0	0
2008	5	6	1	1.20	8.8–15.1	4	4
2009	1	1	0	1.00	7.5	1	0
2011	13	20	2	1.54	2.7–4.2	18	14
2012	2	2	0	1.00	8.3–13.9	2	1
2013	1	1	0	1.00	13.4	1	0
2014	1	1	0	1.00	13.5	1	0
2015	3	4	0	1.33	2.3–2.4	1	2
Total	60	83	10	1.38	2.3–17.0	60	28

torical records (e.g., Omura, 1986; Vladimirov, 1993; Brownell *et al.*, 2001; Clapham *et al.*, 2004; Josephson *et al.*, 2008). The distribution pattern was reported using the Japanese Scouting Vessel (JSV) data (5°×5° square analyses), and there were no sightings outside the Sea of Okhotsk in August between 1964 and 1990 (Miyashita *et al.*, 1995). Recent sighting information has been limited (e.g., Matsuoka *et al.*, 2016). The *R/V Oshoro-Maru* also reported few sightings in the east of the Kurile Islands in June in 2012 and 2013 (Sekiguchi *et al.*, 2014). In this note, we examined the North Pacific right whale distribution pattern using a combination of two major sighting datasets in the western North Pacific and the Sea of Okhotsk covering the years 1982 to 2016.

The Institute of Cetacean Research (ICR) conducted the Japanese Whale Research Program under special Permit in the North Pacific (JARPN: 1994–1999), and JARPN Phase II (2000–2016) which included systematic whale sighting surveys with and without sampling activity. The research areas of this program were the western North Pacific waters north of 35°N (Fig. 1). All whale species were recorded during the sighting surveys. When a school that seemed to be of large cetacean was sighted, the ship approached to the school to identify the species, estimate the school size, and obtain other information (e.g., the number of calves, sea surface temperature at sighting position etc., and conducted opportunistically photo-ID and biopsy sampling). As for the results, North Pacific right whale is the rarest baleen whale sighted. Table 1 summarizes the primary whale sightings during the JARPN/JARPNII surveys from April to September. A total of 213,425.4 n.miles were surveyed and 60 schools (83 individuals including 10 calves, 16.6% of the schools were mother & calf pair during 23 years) were observed. The observed mean school size was 1.38 individuals (n=60). The surface temperature ranged from 2.3°C to 17.0°C.

The National Research Institute of Far Seas Fisheries (NRIFSF; formerly Far Seas Fisheries Re-

Table 2. Summary of North Pacific right whale sightings during the NRIFSF sighting surveys (1984–2003), describing the year in which the right whale was sighted. Sch.: Number of the primary sightings of schools. Ind.: Number of the primary sightings of individuals. Mss: observed mean school size (Ind./Sch.). SST: Range of surface water temperature of the sighting position. Data after 2004 are undergoing analysis.

Year	Sea of Okhotsk and western North Pacific			
	Sch.	Ind.	Mss	SST
1984	2	4	2.00	16.9–17.3
1990	2	5	2.50	8–12.9
1991	1	1	1.00	17.0
1992	17	26	1.53	8.9–11.8
2003	13	16	1.23	3.8–13.4
Total	35	52	1.49	3.8–17.3

Table 3. Summary of North Pacific right whale sightings during Japanese–Russian cruises listing the year the survey was conducted between 1998 and 2011 in the Sea of Okhotsk during May to September. Sch.: Number of the primary sightings of schools. Ind.: Number of the primary sightings of individuals. Calf: Number of calves including Ind. Mss: observed mean school size (Ind./Sch.). SST: Range of surface temperature of the sighting position.

Year	Sea of Okhotsk				
	Sch.	Ind.	Calf	Mss	SST
1998	2	2	—	1.00	—
2000	3	3	—	1.00	—
2003	16	20	—	1.25	—
2009	17	29	0	1.71	7.4–15.7
2010	3	4	1	1.33	8.4–14.3
2011	1	1	0	1.00	5.8

search Laboratory) started dedicated whale sighting surveys in the North Pacific in the early 1980's from July to September (1982–2012) including the Japanese–Russian cruises (1998–2011) in the Sea of Okhotsk (Tables 2 and 3). The sighting method and procedure were based on the International Whaling Commission (IWC) Southern Hemisphere cetacean sighting surveys (e.g., Miyashita and Kato, 1998). These procedures are almost the same as the JARPN/JARPNII II surveys described above, except that some vessels did not have a top barrel. A total of 386,171.3 miles were surveyed. Generally, right whales were distributed north of 50°N in the central part of the Sea of Okhotsk after April when the sea ice disappears, although there was not enough effort in the northern part for logistical reasons. The observed mean school size was 1.49 individual (n=35). The surface temperature ranged from 3.8°C to 17.3°C.

As a result, Fig. 2 shows the combined density index (by Lat.1°×Long.1°square analyses; number of primary sightings of individuals/100 n.miles) of North Pacific right whales by the JARPN/JARPNII and NRIFSF data (1982–2016) during April to October. A total of 599,596.7 n.miles were surveyed. New sightings confirm that there are two high-density areas observed north of 45°N in the far offshore southeast of the Kamchatka Peninsula (from north of 45°N to 51°N, between 158°E and 168°E), and north of 50°N in the Sea of Okhotsk. These high-density areas seemed to be their feeding grounds and coincided with previous large-scale distribution patterns based on catches (Smith *et al.*, 2012) and sightings (Miyashita *et al.*, 1995). On the other hand, there were no sightings in the Sea of Japan, although there were two migration routes along both sides of the main Japanese island, based on historical whaling data (Omura, 1986).

The low number of sightings compared to other baleen whales confirms the rarity of this species in the western North Pacific, and reinforces the belief that both historical and illegal whaling in the 1960's devastated the population. It appears that this species has been showing signs of recovery since the 1990's, but it is necessary to continue monitoring this population to assess its trend in the future. Photo-ID data and biopsy samples were collected opportunistically during JARPN/JARPNII surveys

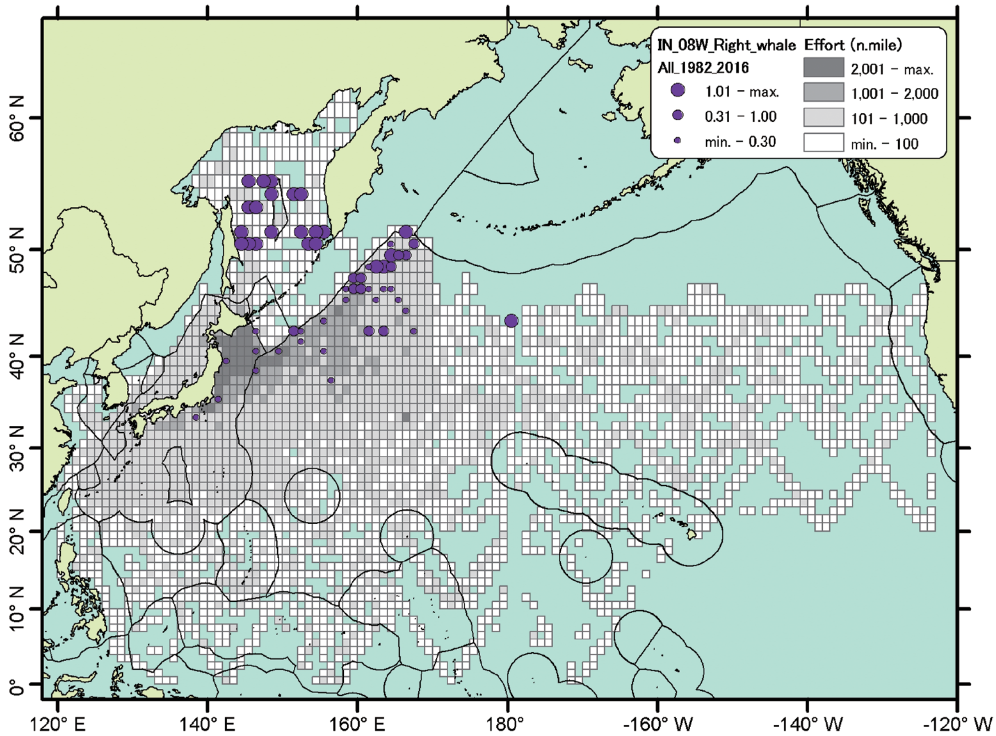

Fig. 2. The map shows combined Density Index (primary sightings of individuals/100 n.miles) of North Pacific right whales comprising the whole ICR (1994–2016) and NRIFSF (1982–2003) datasets from April to October by Lat.1°×Long.1°square, including the Japanese and Russian joint cruises (1998–2011) in the Sea of Okhotsk.

(Table 1, Figs. 3a–3c). Sixty individuals were photographed, and matching work is ongoing. Also, a total of 28 biopsy samples were collected and analyzed including the samples collected in the eastern side of the Pacific under international collaboration (Pastene *et al.*, in review). Further survey, analysis and international collaboration are required to improve our understanding on the seasonal distribution, migration pattern and abundance estimation of this rare species.

Fig. 3a. A head of North Pacific right whale sighted in the western North Pacific on 2 August 2006 (left), and a long white scars on the caudal peduncle keel of a right whale sighted in the western North Pacific on 1 August 2006 (right).

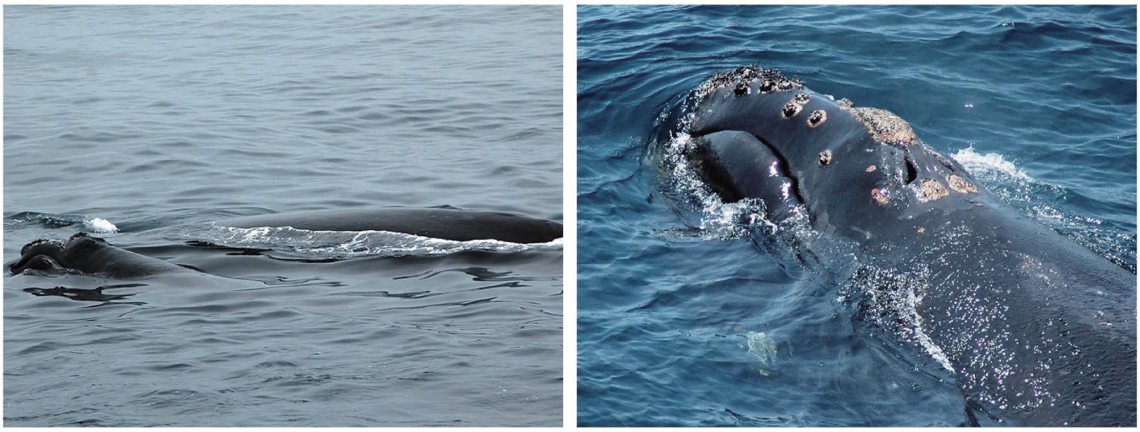

Fig. 3b. A North Pacific right whale mother and calf pair sighted in the western North Pacific on 2 August 2008 (left), and surfacing individual, sighted in the western North Pacific on 31 May 2012 (right).

Fig. 3c. A white spot on the right side of the lower jaw of a right whale sighted in the western North Pacific on 29 May 2011 (left), and scars on the back of an individual sighted in the western North Pacific on 6 June 2012 (right).

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CETACEANS OFF GABON BASED ON A 2011 SIGHTING SURVEY, WITH A PRELIMINARY DENSITY ESTIMATE OF THE HUMPBACK WHALE *MEGAPTERA NOVAEANGLIAE*

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Abstract

Results of a cetacean sighting survey in coastal Gabon waters from September 4 to 9, 2011 are reported. Four whale species humpback (30 schools/191 individuals), Bryde's (1 school/2 individuals), sei (1 school/6 individuals), and sperm (2 schools/2 individuals), and 3 species of dolphin (pantropical spotted (1 school/150 individuals), Atlantic spotted (1 school/40 individuals) and bottlenose (1 school/25 individuals)) were observed over 232.1 nm of transect lines (26% of planned transects, covering 878.0 nm). Based on these survey data, using distance sampling methods, we estimate the density of humpback whales in this region to be 0.481 individuals/nm^2 (CV=0.477).

Key words: Gabon, humpback whale, distance sampling, density estimation, line transect.

Humpback whales *Megaptera novaeangliae* occur worldwide in all major oceans (Clapham, 2018). The Scientific Committee of the International Whaling Commission (IWC/SC) identified seven breeding stocks (A–G) of this species in the Southern Hemisphere (IWC, 2005), with waters off Gabon including part of stock B. From 1912–1930, 7,883 humpback whales were landed at whaling stations in Gabon (Harmer, 1928; Best, 1994), and a further 7,080 animals were landed in 9 whaling seasons between 1934 and 1959 (Budker and Collignon 1952; Budker 1952, 1953; Budker and Roux 1968; Weir, 2010). While commercial humpback whaling in the Southern Hemisphere was banned by the IWC in 1963 (IWC, 2011), after more than 50 years it is thought that stocks of this species may have recovered. A comprehensive assessment of Southern Hemisphere humpback whales was completed in 2015. An assessment model was conducted then using abundance estimates by mark-recapture methods provided in Collins *et al.* (2010); the depletion level (i.e., abundance per initial population size) of the humpback whale breeding stock off Gabon was estimated to be 74% in 2015 (IWC, 2016).

Three cetacean sighting surveys have been completed in COMHAFAT (La Conférence Ministérielle sur la Coopération Halieutique entre les Etats Africains Riverains de l'Océan Atlantique) coastal zone waters. The first cetacean sighting survey in Gabon coastal waters occurred in 2011; a second survey took place in the Gulf of Guinea in 2013, covering the Côte d'Ivoire, Ghana, Togo and Benin (Diallo and Bamy, 2013). A third survey was conducted in coastal waters of Guinea, Sierra Leone and Liberia in 2018 (Diallo *et al.*, 2018). A fourth proposed (2019) survey was scheduled for coastal waters off Guinea, but it has yet to be done. During the 2019 IWC/SC68a meeting in Nairobi, Kenya, the plan for this fourth survey in the COMHAFAT coastal zone was presented. The IWC Standing Working

Group on Abundance Estimates, Status of Stocks, and International Cruises (ASI) encouraged that abundance estimates of cetacean species sighted in the COMHAFAT coastal zone be presented to the future IWC/SC meeting to determine how they could be used for the Revised Management Procedure (RMP) or for other cetacean studies in this region (IWC, 2020). For this reason, we report hitherto unpublished estimates of humpback whale abundance data from the 2011 survey off Gabon.

The 2011 survey was conducted during the dry season in waters off Gabon (when rain is scarce and wind is weak). Because many cetacean species migrate into waters off Gabon during the austral winter (Weir, 2010), we performed this survey during this period. The main objective was to obtain information on the abundance and distribution of cetaceans in the coastal zone of Gabon (Diallo and Bamy, 2013). The survey was performed by the Centre National des Sciences Halieutiques of Boussoura (CNSHB) under the auspices of COMHAFAT, with collaboration from some African fisheries institutions and fisheries research centers, such as the Direction Générale des Pêches (DGP) in Gabon, Centre de Recherches Océanologiques (CRO) of Abidjan in Côte d'Ivoire, Institut Mauritanien de Recherche Océanographique et des Pêches (IMROP) of Nouadhibou in Mauritania, Centre de Recherche Océanographique de Dakar Thiaroye (CRODT) of Dakar in Senegal, Direction des Pêches (DP) of Cotonou in Benin, Marine Fisheries Research Division (MFRD) of Tema in Ghana, Fisheries and Oceanography Research Station (SRHOL IRAD) of Limbé in Cameroon, and the Center for Applied Fisheries Research (CIPA) of Bissau in Guinea-Bissau.

The *N/O General Lansana Conté*, a research vessel of Guinean nationality, 29.93 m in length, 3.25 m in draught, of 1400 CV horsepower and 198 GRT (Fig. 1), was used for the survey. Further survey details are provided in Diallo and Bamy (2013). A 10-day survey period was scheduled in September 2011, as per the itinerary shown in Table 1.

The study area was in the Gabonese EEZ including the isobaths from 200 m to 1,000 km, and excluded shallow waters and areas around oil fields. Six survey blocks were identified (left panel, Fig. 2) comprising three offshore (ON, OM, OS) and three coastal (CN, CM, CS) blocks. Within blocks, zigzag track lines of 878.0 nm total length were set (right panel, Fig. 2). Survey participants included 10 vessel crew and 9 research staff; 2 Guinean researchers conducted the survey, with researchers from each of 6 African countries (1 from each of Mauritania, Senegal, Ghana, Benin, and Togo, and 2 from Gabon) also participating. The cruise leader, Samba Diallo, entered data onto a computer during the survey; other scientists helped identify schools of cetaceans and count numbers of individuals.

The survey used a line-transect method (Burnham *et al.*, 1980) authorized by the Scientific Com-

Fig. 1. The *N/O General Lansana Conté* used for COMHAFAT cetacean sighting surveys.

Table 1. Itinerary of the 2011 cetacean sighting survey in Gabon coastal waters.

Date	Event
August 29	Vessel left Conakry to Libreville
August 28–30	Participants arrived in Libreville
August 31	Pre-survey meeting was held in Libreville
September 2	Vessel arrived at Libreville
September 3	Vessel left Libreville to survey area
September 4	Survey was started
September 9	End of the survey
September 10	Vessel arrived in Libreville
September 11	Vessel left Libreville to Conakry
September 12	Post-survey meeting was held in Libreville
September 13–14	Participants left Libreville
September 14	Vessel arrived at Conakry

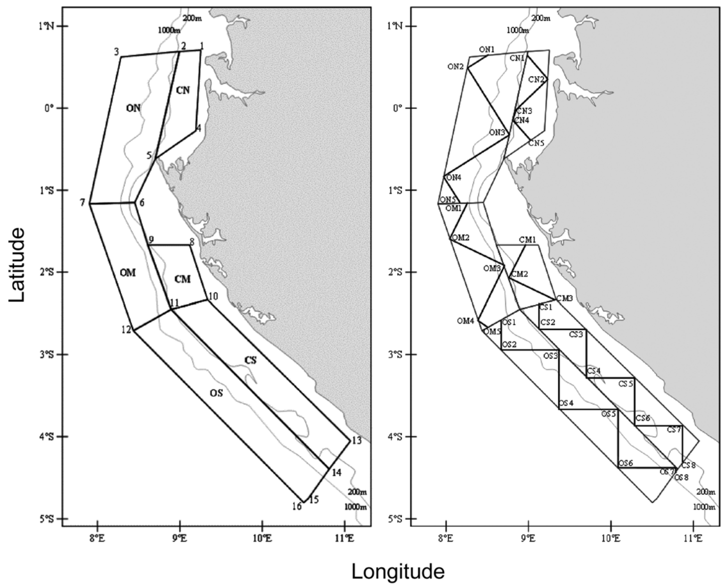

Fig. 2. Gabon coastal water research areas: 2011 survey blocks conducted by COMHAFAT (left panel) and survey zig-zag track lines of 878.0 nm length set in survey blocks (right panel) (after Diallo and Bamy, 2013).

mittee of the IWC, following procedures and protocols in the requirement and guidelines for sighting surveys (IWC, 2012). Surveys occurred during daylight from 30 min after sunrise to 30 min before sunset, in good weather conditions (Beaufort scale ≤ 4, visibility >2 nm). A normal closing mode survey was performed for all encountered cetacean species; for further details of sighting procedures see Diallo and Bamy (2013). Angles to sightings were measured using angle boards situated in front of observers. To calibrate the distances to and angle measurements of sightings, distance and angle measurement experiments were performed during the survey (to adjust measurement error if necessary).

During the survey, sighting effort and weather data were recorded. All data, including photographs belong to the COMHAFAT, with copies stored at the CNSHB in Guinea, and the Fisheries Resources Institute, Japan Fisheries Research and Education Agency, in Japan.

To estimate humpback whale density, we used data for 13 primary (ship on-effort) sightings for this species, and effort data. For detection function estimation, conventional distance-sampling methods were used, including multi-covariate distance sampling, where detection on the track line is assumed as certain (i.e. $g(0)=1$). The covariate to be considered for possible inclusion in the detection function is school size. Missing values for other candidate covariates (such as Beaufort scale and visibility) precluded our considering them in detection functions.

We used the Multiple Covariate Distance Sampling (MCDS) Engine in the mrds package in R for calculations (Thomas *et al.*, 2010). The Hazard rate and Half normal models are fitted as candidate models for the detection function. The full model of the detection function is provided by:

$$\text{Hazard rate: } g(x,z) = 1 - \exp\left[-\left\{ x \Big/ a\exp(Size) \right\}^{-b}\right] \tag{1}$$

$$\text{Half normal: } g(x,z) = \exp\left[-x^2 \Big/ 2a^2 \exp\{2(Size)\}\right] \tag{2}$$

where x is the perpendicular distance from the track line to the sighting, z is a vector of covariates (i.e., *Size*), a ($a>0$) and b ($b\geq 1$) are coefficients to be estimated, and *Size* is observed school size.

Density estimation is the second step used in the distance-sampling method. The analytical method follows that of Buckland *et al.* (2015). For analysis we assumed that all schools of cetaceans on the track line were detected. Density and its variance were estimated based on a Horvitz–Thompson like estimator of abundance, as expressed in equations (3) and (4), respectively:

$$D = \frac{1}{2WL}\sum_{i=1}^{n}\frac{s_i}{p(x_i, z_i)} \tag{3}$$

where D is the density estimate, W is the truncation distance, L is the searching effort, s_i is the size for ith school, and $p(x_i, z_i)$ is the probability of detection at a perpendicular distance x_i and covariate z_i.

$$\mathrm{var}(D) = \left(\frac{1}{2WL}\right)^2 \left\{ \frac{1}{L(K-1)}\sum_{k=1}^{K} l_k \left(\frac{P_{Ck}}{l_k} - \frac{P_C}{L}\right)^2 + \sum_{j=1}^{r}\sum_{m=1}^{r}\frac{\partial P_C}{\partial \theta_j}\frac{\partial P_C}{\partial \theta_m}H_{jm}^{-1}(\theta) \right\} \tag{4}$$

where K is the number of transect, l_k is searching distance in kth transect, P_{Ck} is the abundance estimate in the covered region on the kth transect, P_C is the abundance estimate in the covered region, and $H_{jm}^{-1}(\theta)$ is the jmth element of the inverse of the Hessian matrix of detection function with respect to the vector of the coefficients θ.

Akaike information criterion (AIC) values were compared to select the best model to estimate the probability of a school being detected $p(z_i)$ given the covariate z_i, which is expressed by the following equation (5) using the detection function $g(x, z_i)$ (see equations (1) and (2)). The detection function with the minimum AIC is selected as the best model among the candidate models.

$$p(z_i) = \frac{1}{W}\int_0^W g(x, z_i)\,dx = \frac{1}{W}\hat{f}\left(0|z_i\right) \tag{5}$$

The 2011 survey in coastal waters of Gabon covered 232.1 nm over 6 days—only 26% of the planned searching distance. Although 10 survey days had been initially scheduled, only the ON, CN and CM blocks out of 6 blocks could be covered within available time (Fig. 3). During this survey, 30 schools of humpback whales (191 individuals), 2 schools of sperm whales (*Physeter macrocephalus*) (both with 1 ind.), and 1 school of each of Bryde's (*Balaenoptera edeni*) (2 ind.) and sei (*B. borealis*) (6 ind.) whales, and 1 school of pantropical spotted (*Stenella attenuata*) (150 ind.), 1 school of Atlantic spotted (*S. frontalis*) (40 ind.), and 1 school of bottlenose (*Tursiops truncatus*) (25 ind.) dolphins were detected (Table 2). Sighting positions for (a) humpback whales, (b) Bryde's, sei, and sperm whales, and (c) dolphins are shown in Fig. 3. No feeding behavior was observed during the survey.

The best model of estimated detection function fitted to the relative frequency of detected schools by perpendicular distance intervals as a function of perpendicular distance from the track line to a humpback whale sighting using 2011 survey data is depicted in Fig. 4. A density estimate of

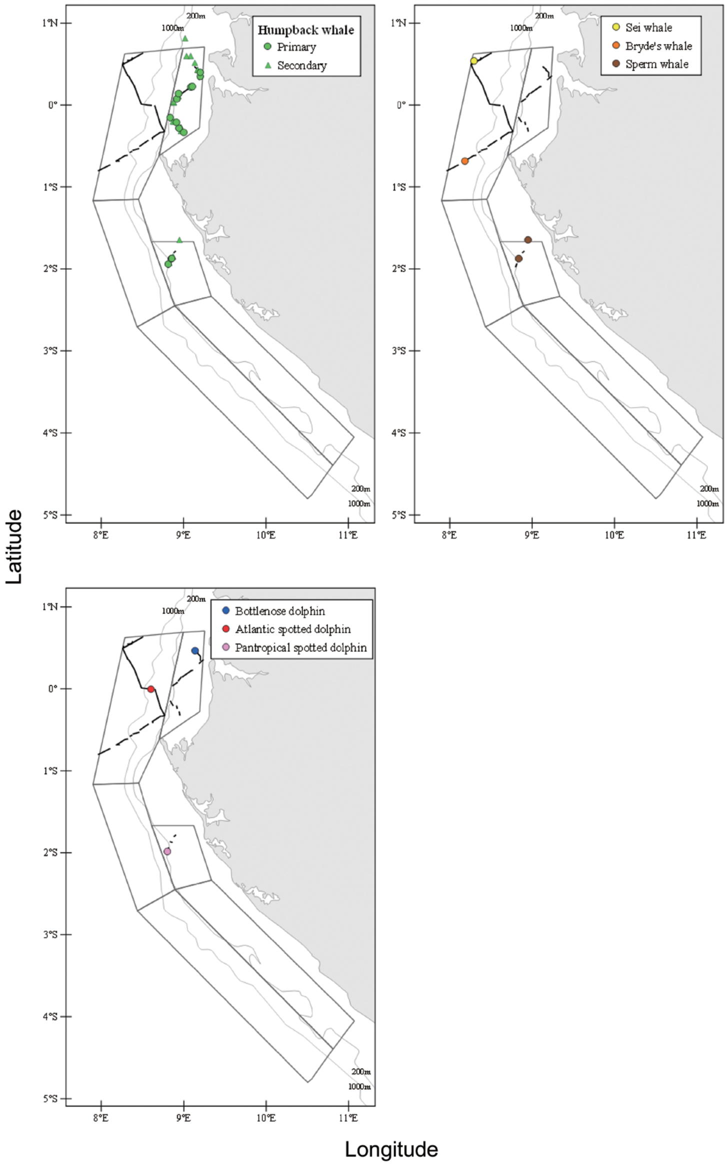

Fig. 3. Map of the 2011 survey area, blocks, line transects, and sighted schools of humpback whales (upper left panel), Bryde's, sei and sperm whales (upper right panel), and dolphins (lower panel).

Table 2. Primary and secondary sightings during the 2011 cetacean sighting survey.

Species name	Primary		Secondary		Total	
	Sch.	Ind.	Sch.	Ind.	Sch.	Ind.
Humpback whale	13	50	17	141	30	191
Sperm whale	1	1	1	1	2	2
Sei Whale	0	0	1	6	1	6
Bryde's whale	1	2	0	0	1	2
Pantropical spoted dolphin	0	0	1	150	1	150
Atlantic spotted dolphin	1	40	0	0	1	40
Bottlenose dolphin	1	25	0	0	1	25
Unidentified whale	2	2	6	13	8	15
Unidentified dolphin	3	15	1	10	4	25

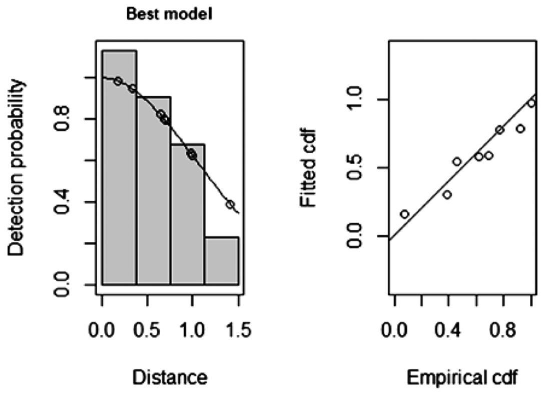

Fig. 4. Plot of the best model of estimated detection function fitted to relative frequency of schools as a function of perpendicular distance (nm) from the track line to a humpback whale sighting based on 2011 survey data. Cdf in the caption for the right panel is the abbreviation for cumulative distribution function.

0.481 ind./nm^2 (CV=0.477) from this model has a low AIC of 11.437. Branch (2011) estimated humpback whale abundances in feeding grounds in Antarctic waters south of 60°S during the austral summer to be 4.36×10^{-5} ind./nm^2 (CV=0.53) in 1992/93 between 0° and 40°E, and 2.55×10^{-4} ind./nm^2 (CV=0.75) in 1996/97 between 30°W and 0°. Branch (2011) considered that estimates of abundance in breeding stock B were greater than in the assumed corresponding feeding area (20°W–10°E) in Antarctic waters because humpback whales in their southern migration migrated to waters north of 60°S. It is therefore likely that most humpback whales from this breeding stock do not migrate as far south as 60°S to reach that area covered by the International Decade of Cetacean Research/Southern Ocean Whale and Ecosystem Research Programme (IDCR/SOWER) surveys. Japanese Sighting Vessel (JSV) data identify a high density area north of 60°S (Miyashita *et al.*, 1995), with many sightings of this species in 2005/06 during the IWC SOWER survey (Ensor *et al.*, 2006). Another possibility is that animals in breeding stock B migrate to a different longitudinal sector, supported by genetic evidence that breeding stock B does not differ significantly in Areas II and III, in longitudinal sectors 60°W–70°E (Loo *et al.*, 2011).

Because more humpback whales were sighted in CN and CM than in ON blocks, more survey effort could be allocated to coastal as opposed to offshore blocks in future surveys (to more accurately estimate humpback whale abundance). Buckland *et al.* (2015) and the IWC (2012) suggested allocating increased effort to known high density strata. If more primary sightings occur in future COMHAFAT surveys, further analyses of abundance estimates could be performed for other species from the 2011 survey data (i.e., sei, Bryde's and sperm whales, and pantropical spotted, Atlantic spotted, and bottlenose dolphins).

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HISTORICAL JAPANESE WHALE SIGHTING SURVEYS IN THE CHUKCHI SEA

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Abstract

Before *the T/S Oshoro Maru* surveys in 2007 and 2008, three Japanese research vessels had conducted whale sighting surveys in the Chukchi Sea, in 1937 (*R/V Kaihou Maru* and *Yūki Maru*) and 1958 (*R/V Fumi Maru No.16*). However, their results are not well-known. The author found four references about these voyages and compared the results with *T/S Oshoro Maru* data from the 2007 and 2008 voyages. Despite the long period separating these surveys (about 20 years and then 50 years), the whale distributions in this region were somewhat similar.

Key words: Chukchi Sea, Japanese whale sighting survey, large whale species.

Despite its biological importance, the Chukchi Sea is one of the least surveyed regions. This region is closed down for a long period by winter ice, and often covered by deep fog during summer. However, at least three Japanese research vessels managed to conduct oceanographic and biological surveys in the Chukchi Sea, including shipboard cetacean sighting surveys. *R/V Kaihou Maru* (the Ministry of Agriculture and Forestry, 1064 gross tonnage) and *Yūki Maru* (Hokuyou-Hokei Co., 350 gross tonnage) carried out surveys from the end of July to the beginning of August, 1937, and the *R/V Fumi Maru No.16* (Taiyo Fisheries Co., 598 gross tonnage) survey was conducted in the summer of 1958. This author found four cruise reports in Japanese about these cruises (Nasu, 1960a, 1960b; Yamaguchi, 1961; Tatou, 1985). The cruise report of *R/V Yūki Maru* has not been found, and thus its data were extracted from Nasu (1960a) and Tatou (1985). The author had an opportunity to conduct cetacean sighing surveys in the Chukchi Sea from *T/S Oshoro Maru* (Hokkaido University, Japan; 72.8 m length and 1,779 gross tonnage) as a part of the International Polar Year (IPY) special research in summer 2007 and 2008. It seems that these historical cruises did not have systematically organized track lines in the way our *Oshoro Maru* cruises did; however, their data are very important for describing the distribution of whales in this region in the past. In this Short Note, the author would like to compare sighting results among those historical cruises and the *T/S Oshoro Maru* cruises, in order to investigate any change in whale occurrence in the Chukchi Sea.

R/V Kaihou Maru and *Yūki Maru* survey in summer 1936

The *R/V Kaihou Maru* entered the Chukchi Sea on 26 July, 1937 and reached the furthest north point (71°12′N, 174°50′W) by a Japanese vessel in 29 July. The vessel continued its survey westward along the ice edge and then on 1st August headed back along the Russian coast line. Their survey covered the entire western part of the Chukchi Sea (Fig. 1) and Table 1 shows the summary of their cetacean sightings extracted from Yamaguchi (1961). Six species of large whales were sighted: blue whale *Balaenoptera musculus*, fin whale *B. physalus*, humpback whale *Megaptera novaeangliae*, right whale *Eubalaena japonica*, minke whale *B. acutorostrata* and sperm whale *Physeter macrocephalus*.

On the other hand, the *R/V Yūki Maru* sailed along the entire coast line of the Chukchi Sea in about the same period (26 July to 3 August, 1937) (Fig. 2, from Nasu, 1960a). The main purpose of the *R/V Yūki Maru* voyage was the investigation of possible new whaling grounds and thus it is presumed that the vessel had professional observers. Unfortunately, no detailed data could be found for this *Yūki*

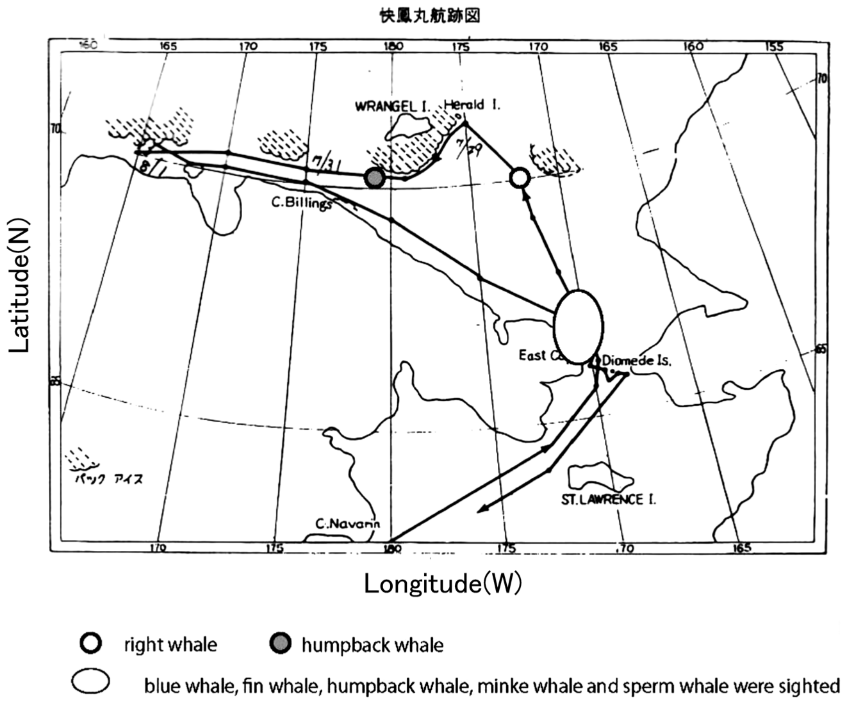

Fig. 1. The track line and whale sighting locations of *R/V Kaihou Maru* in summer 1937 (the figure was converted from Fig. 2 in Yamaguchi, 1961). Sighting location data are from Table 1.

Table 1. Sighting summary for *R/V Kaihou Maru* survey in summer 1937. Data were extracted from Table 1 in Tatou (1985).

Sighting location	Species					
	Blue whale	Fin whale	Humpback whale	Sperm whale	Right whale	Minke whale
66°36′N, 169°43′W		15–16				
66°42′N, 169°49′W						1
67°20′N, 170°08′W			11			
70°00′N, 173°05′W					1	
69°50′N, 179E50′W			6			
67°05′N, 171°05′W	15–16					
67°00′N, 170°55′W		8				
66°50′N, 170°35′W		about 200				
66°42′N, 170°35′W	11	about 100		50		
66°38′N, 170°15′W			about 100			
66°25′N, 169°52′W			2			

Maru survey (Table 2), but Nasu (1960b) described that "many" fin whales were sighted near the coast of Siberia (66°40′N, 170°W), at least one humpback whale, and a rather unusual sighting of a right whale and a sperm whale.

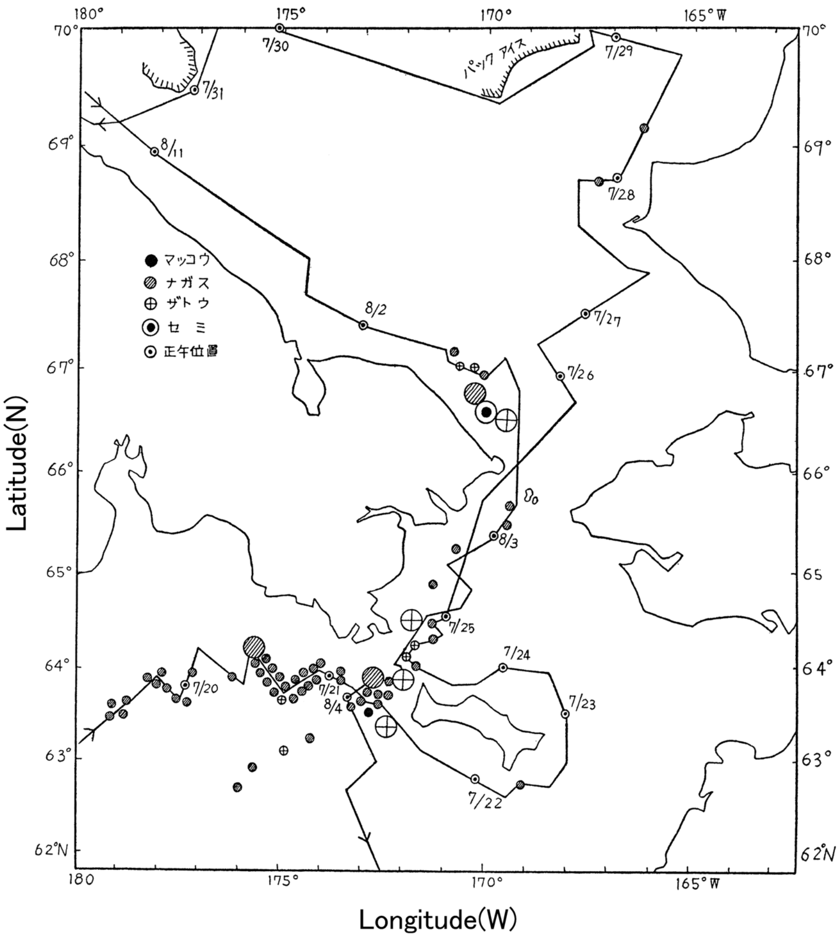

Fig. 2. The track line and sighting positions by *R/V Yūki Maru* in 1937 summer (from Fig. 5 in Nasu, 1960a). Symbols explanation: sperm whale (closed circle); fin whale (hatched circle); humpback whale (crossed circle); right whale (circle with a big black dot). Circles with a small dot indicate vessel position at noon.

Table 2. Sighting summary from *R/V Yūki Maru* during the 1937 summer cruise, based on data from Nasu, 1960a and Tatou, 1985.

Species	Total no. of animals	Approximate sighting location
Fin whale	“many”	66°40′N, 170°W
Humpback whale	1?	66°40′N, 170°W
Right whale	1?	66°30′N, 170°W
Sperm whale	?	66°30′N, 170°W

R/V Fumi Maru No.16 survey in summer 1958

The *R/V Fumi Maru No.16* surveyed the Chukchi Sea between 16 and 20 August 1958. Fig. 3 shows the track line and Fig. 4 indicates whale sighting locations (figures from Nasu, 1960a). A total of 86 animals were sighted. Most were gray whales *Eschrichtius robustus* (82 animals), but there were also two right whales, one fin whale, and one unidentified whale (Table 3; data from Nasu, 1960a).

T/S Oshoro Maru survey in summer 2007 and 2008

The *T/S Oshoro Maru* conducted two IPY oceanographic and biological research cruises in the Chukchi Sea. In 2007, the survey started from 5 August and ended on 15 August at Nome, AK. In 2008, the cruise schedule was a month earlier, starting from Nome on 6 July and ending at Dutch Harbor, AK on 17 August. Details of course lines and oceanographic observations are available in data

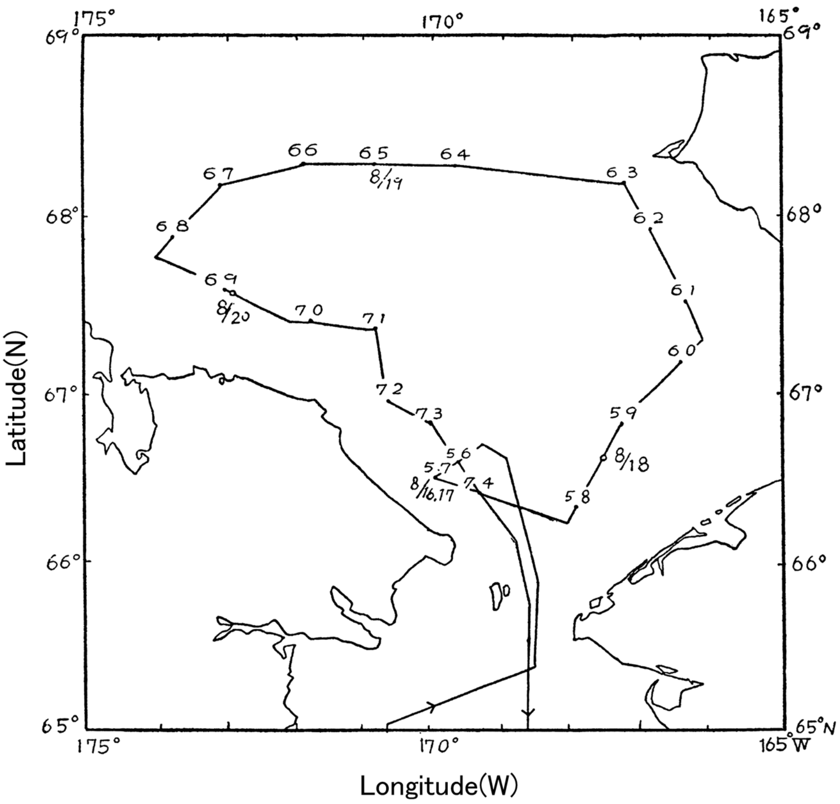

Fig. 3. The track line of *R/V Fumi Maru No.16* survey in summer 1958 (from Fig. 1 in Nasu, 1960a).

books from Hokkaido University (Faculty of Fisheries Sciences, Graduate School of Fisheries Sciences, School of Fisheries Sciences, Hokkaido University 2008, 2009). Table 4 summarizes sighting results in the Chukchi Sea and Fig. 5 shows track lines and cetacean sighting positions. A total of six cetacean species were identified: bowhead whale *Balaena mysticetus* (30 animals in 2007), humpback whale (three in 2007 and one in 2008), minke whale (three in 2007 and nine in 2008), gray whale (212 in 2007 and 16 in 2008), killer whale *Orcinus orca* (five in 2007) and harbor porpoise *Phocoena phocoena* (one in 2007 and six in 2008).

These five relevant cetacean surveys were done a long time apart (about 20 years, then 50 years respectively); however, sighting locations are rather similar, the main locations being just after the Bering Strait and off Point Hope. Russian–American aerial and shipboard surveys between 1968 and 1982 also indicated gray whale aggregations just after the Bering Strait (Berzin, 1984). It seems these large whale species utilized the Chukchi Sea region as their summer feeding area, well before the area was widely freed from ice because of “global warming”.

Table 5 summarizes the presence/absence of large whale species sighted in the Chukchi Sea survey areas by the five cruises. Only *R/V Kaihou Maru* sighted six species of large whales, blue, fin, humpback, right, minke and sperm whales, but not gray whales, in the Chukchi Sea surveyed area (also see Table 1). Nasu (1960a) assumed poor sightings from *R/V Fumi Maru No.16* were caused by bad visibility (dense fog) and the whale migration period. The second year (2008) of the *T/S Oshoro Maru* Chukchi Sea survey also encountered very poor visibility condition and thus the total sighting was much less than in the previous year (Table 4). Poor visibility for the *R/V Fumi Maru No.16* survey might have caused a lack of humpback whale sightings as well. Humpback whales were sighted in large numbers (about 120? animals in total, Table 1) by *R/V Kaihou Maru*, at least one animal by *R/V Yūki Maru* (Table 2) and one school in each of the *T/S Oshoro Maru* 2007 and 2008 surveys (Table 4).

Although no fin whales were sighted by the *T/S Oshoro Maru* 2007 and 2008 surveys, animals were sighted in the three surveys in 1936 and 1958 (Tables 1, 2, 3 and 5; Figs. 1, 2, and 4). Fin whales were

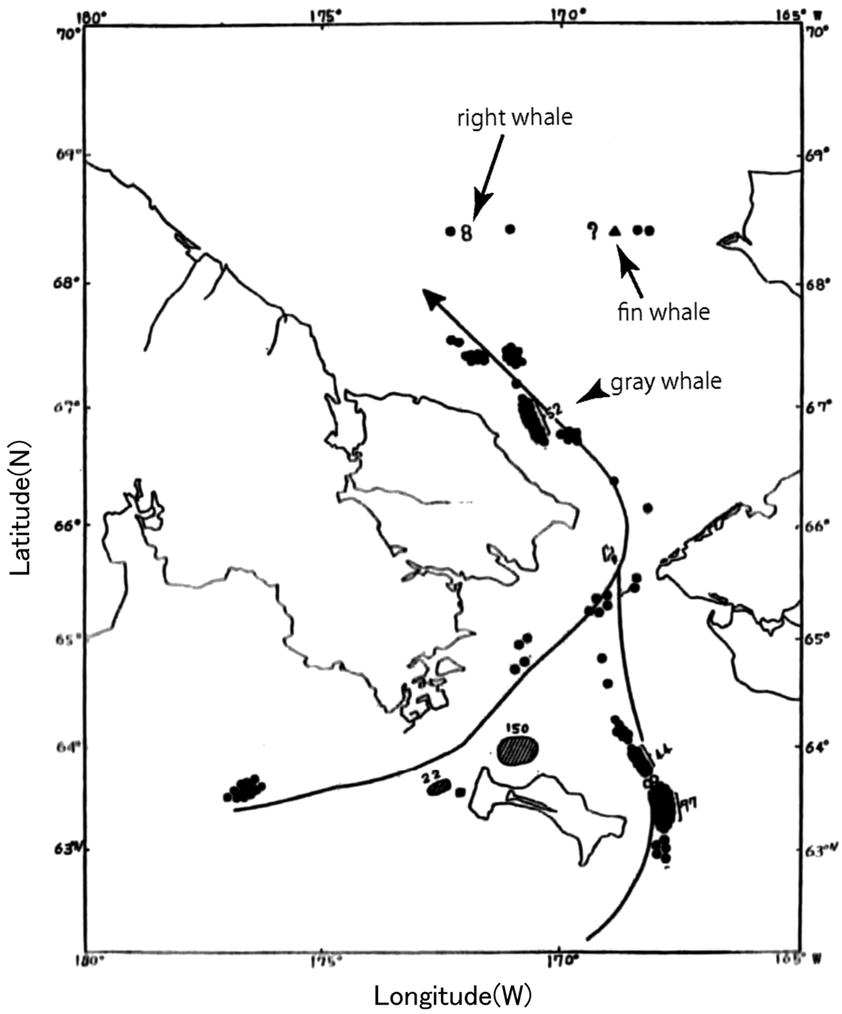

Fig. 4. Whale sighting positions during the *R/V Fumi Maru No.16* survey in summer 1958 (from Fig. 4 in Nasu, 1960a).

Table 3. Sighting summary from *R/V Fumi Maru* No. 16 during the 1958 summer cruise, based on data from Nasu, 1960a and Tatou, 1985.

Species	Total no. of animals	Approximate sighting location
Fin whale	1	50 nm off Point Hope
Right whale	2	off Point Hope?
Gray whale	78	67°N, 170°W
	2	off Point Hope
	2	?
UnID whale	1	?

sighted off the Bering Strait and Point Hope, and even at the far north ice edge (66°36′N, 169°43′W; Table 1; Fig. 1). Fin whales were often sighted in the Bering Sea during the *T/S Oshoro Maru* 10-year cruises (a total of 399 fin whales in 174 groups, Table 1 in Sekiguchi, 2015). Before the North Pacific fin whaling ban in 1976, the fin whale summer geographical distribution might have extended further into the Chukchi Sea. Berzin and Rovnin (1966) and Tomilin (1967) also noted the occurrence of fin whales in the Chukchi summer.

Sightings of right whales by *R/V Kaihou Maru*, *Yūki Maru* and *Fumi Maru No.16* were rather unusual. Tomilin (1967) reported the record at Cape Prince of Wales and the possible further north distri-

Table 4. Sighting summary from the *T/S Oshoro Maru* IPY surveys in summer 2007 and 2008.

Species	2007		2008	
	Total numbers of		Total numbers of	
	School	Individuals	School	Individuals
Bowhead whale	1	30	0	0
Humpback and like-humpback whale	1	3	1	1
Minke and like-minke whale	2	3	6	9
Gray and like-gray whale	12	212	5	16
Killer whale	1	5	0	0
Harbor porpoise	1	1	3	6
UnID large baleen whale	9	35	2	2
UnID large whale	1	2	1	1
UnID small whale	2	2	2	2
UnID whale	1	2	5	5
UnID dolphin	1	1	0	0
Dead whale	1	1	1	1
Total	33	297	26	43

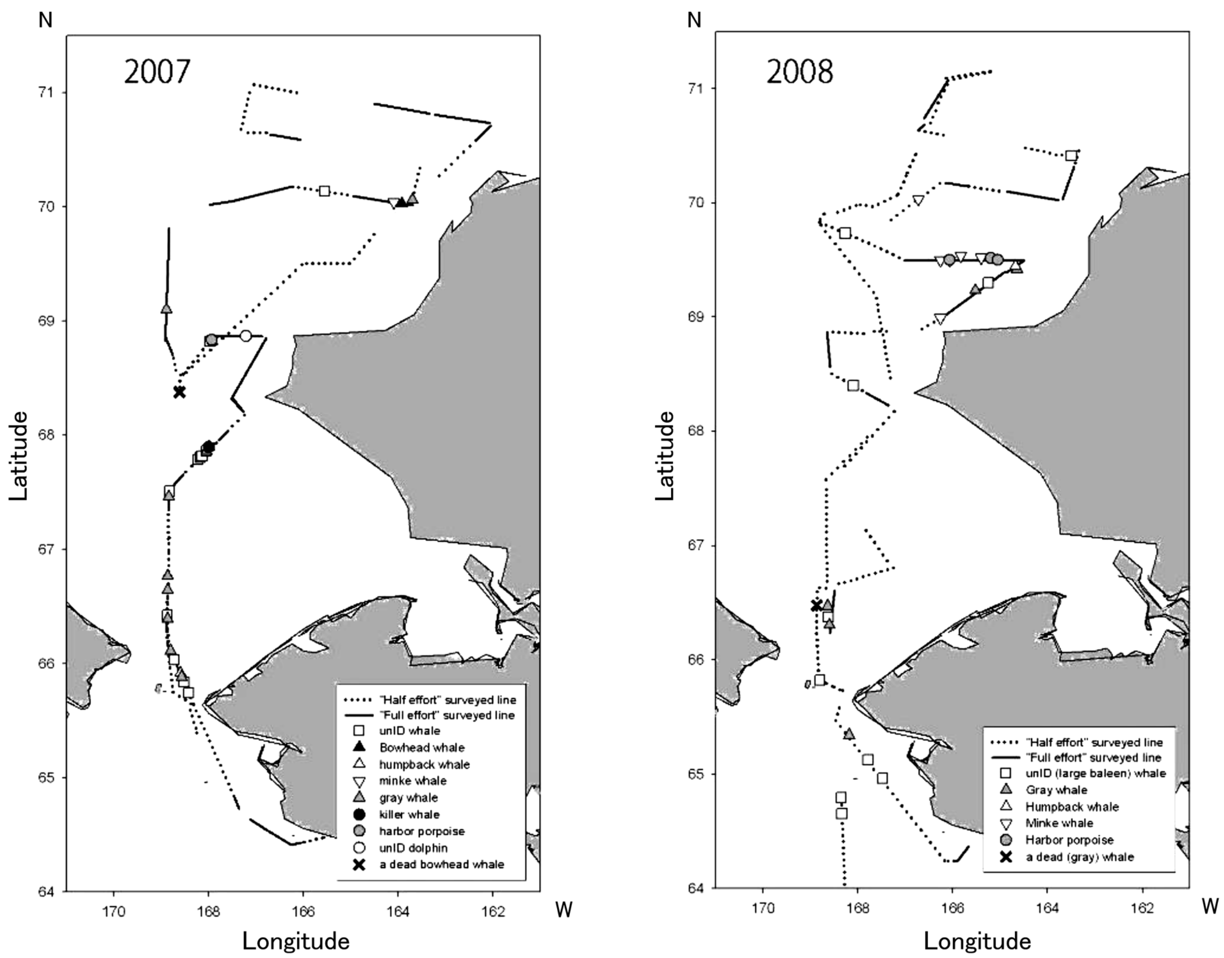

Fig. 5. Cetacean sighting positions by the *T/S Oshoro Maru* in summer 2007 and 2008.

Table 5. The summary of sighted whale species for each survey in the Chukchi Sea (present (✓) or absent (abs)).

Survey year	1937	1937	1958	2007	2008
Research vessel	*Kaihou Maru*	*Yūki Maru*	*Fumi Maru*	*Oshoro Maru*	*Oshoro Maru*
Bowhead/NP right whale	✓	✓	✓	✓	abs.
Blue whale	✓	abs.	abs.	abs.	abs.
Fin whale	✓	✓	✓	abs.	abs.
Humpback whale	✓	✓	abs.	✓	✓
Minke whale	✓	abs.	abs.	✓	✓
Gray whale	abs.	abs.	✓	✓	✓
Sperm whale	✓	✓	abs.	abs.	abs.

bution, but at present no other record of right whales in the Chukchi Sea has been found. The *T/S Oshoro Maru* 2007 survey encountered a school of bowhead whales off Point Hope, where *R/V Kaihou Maru* and *Fumi Maru No.16* sighted right whales. It is possible that they might have mistaken right whales for bowhead whales.

Gray whales have been known to be abundant in the Chukchi Sea for years (Nikulin, 1946; Berzin and Rovnin, 1966; Tomilin, 1967; Berzin, 1984; Sekiguchi, 2015), however, no sightings were reported from the 1937 cruises (Table 5). This might be related to the migration period of gray whales, since their cruise period was a bit earlier than those of the *R/V Fumi Maru* and *T/S Oshoro Maru*.

The two 1937 cruises had sightings of sperm whales (Tables 1, 2, and 5). There is no official record of sperm whales in the Chukchi Sea, although Berzin and Rovnin (1966) wrote about sighting reports of this species. Sperm whale sightings could be due to a misidentification, but it is hard to believe whaling professionals made such a mistake for sperm whales. If there is an original cruise report for the *R/V Yūki Maru* voyage, it may provide the answer.

To conclude, these old Japanese whale sighting survey data are important for investigating the change in whale distribution in the Chukchi Sea over the years. It is necessary to look for the detailed sighting data for the *R/V Yūki Maru*, which are missing from this study.

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The author thanks all crews of *T/S Oshoro Maru* and research participants during the 2007 and 2008 IPY summer cruises for their help. Professor Seiichi Saito, Hokkaido University, invited the author on the *T/S Oshoro Maru* cruises. Very special acknowledgement goes to the late Dr. Seiji Ohsumi, the Institute of Cetacean Research, who brought the *R/V Yūki Maru* and other Japanese voyages to the Chukchi Sea to my attention. Without his deep knowledge of the history of Japanese whale surveys, the author would never have noticed these important works as presented in this Short Note. Dr. John W. Menzies, South Africa Astronomical Observatory, kindly checked the English. The comments of reviewers helped to improve this manuscript.

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SEXUAL DIMORPHISM IN THE DORSAL FIN OF PACIFIC WHITE-SIDED DOLPHINS (*LAGENORHYNCHUS OBLIQUIDENS*) FROM COASTAL WATERS OFF JAPAN

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Abstract

Records of external measurements of 35 male and 40 female Pacific white-sided dolphins collected from 1970 to 2020 were examined for the shape change of the dorsal fin and the difference between males and females. For mature individuals based on a body length of 200 cm, which is an approximate guideline for maturity, a significant difference was detected in the ratios of the front edge length and the tip height which were 3.8 on average with a maximum value of 5.6 in males, and 2.8 (average) and 3.1 (maximum value) in females, respectively. It was concluded that sexually mature males could be distinguished by measuring the shape of the dorsal fin.

Key words: allometry, dorsal fin, growth, morphology, Pacific white-sided dolphin.

The Pacific white-sided dolphin (*Lagenorhynchus obliquidens*) is an endemic species of the North Pacific Ocean, and even a mature individual is relatively small, with a body length of 2.5 m or less. Length at birth is reported to be about 80–95 cm. The distribution area on the western side of the Pacific Ocean is along the Sea of Japan and the Pacific coast of Japan on the western Pacific Ocean (Leatherwood and Reeves, 1982, Brownell *et al.*, 1999). Hayano *et al.* (2004) identified a distribution gap around the longitude of 150°E or between Japanese coastal waters and the offshore western and central North Pacific, and concluded that samples from these two geographical areas came from different populations. The authors suggested that the low genetic difference could be due to the short time since reproductive isolation between the two geographical populations off Japan. The origin of the Japanese name "Kama-iruka" is that the dorsal fin resembles a "sickle" (Kasuya, 2017).

Regarding individual identification of dolphins and whales, the dorsal fin is one of the most obvious traits to consider whether in the wild or in captivity. The dorsal fin shape, size, color, scratches, and cuts are used to identify an individual. Killer whales (*Orcinus orca*) are known as an example where individual identification and identification by sex and maturity status is possible by observing the dorsal fin. The male dorsal fin (height to width ratio) could be readily distinguished from that of a female, and a height to width ratio of 1.4 or greater was indicative of a mature male (Olesiuk *et al.*, 1990, 2005).

In the case of the Pacific white-sided dolphin dorsal fin morphology, it has been found that sexually mature males have a pronouncedly curved and round dorsal fin (Walker *et al.*, 1986). Furthermore, Kasuya and Yoshida (1990) and Kasuya (2017) clarified that the tip of the dorsal fin hangs down in mature males from the point of measurement of the height of the tip of the dorsal fin and the overall height. Attempts have been made to identify sexually mature males from photographs of the dorsal fins of wild Pacific white-sided dolphin herds using this method (Morton, 2006). However, there are no studies that have examined the body length and dorsal fin measurements of this species in comparison with the sex.

In this study, we investigated changes in dorsal fin shape and curvature using proportion measurements of Pacific white-sided dolphins collected in the waters of both the Pacific Ocean side and the Sea of Japan side of Honshu, Japan, over the past 50 years from 1970 to 2020. The purpose of this study was to clarify the difference in dorsal fin shape between males and females with changes in body length, and to contribute to the biological database of Pacific white-sided dolphins.

The measurements used in this study are shown in Fig. 1. The proportion measurement records of 35 males and 40 females were used. These measurement records include post-mortem measurements (bycatch or after death in captivity) and live individuals' latest measurements data at Kamogawa Sea World (KSW). It is a characteristic of Pacific white-sided dolphins distributed in the coastal waters of Japan that individual differences in body length are large in all age ranges. The range shared by sexually mature and immature individuals was 180–234 cm for males and 195–209 cm for females (Kasuya, 2017). From this, the guideline for sexually mature body length was roughly set to 200 cm in this paper.

The following allometric equation was used to extract growth patterns at each point:

$$y = \beta x^{\alpha}$$

where x defines the body length; y, the length (cm) of the measurement points; α, the allometric coefficient; and β is a constant. The t-test was conducted using allometric coefficients to reveal growth patterns at each measurement point, and the data were grouped into three different growth patterns: positive allometry (hyperallometry) when the allometric coefficient was significantly greater than 1, isometric allometry and negative allometry (hypoallometry) when the allometric coefficient was less than 1. These statistical analyses were conducted by using the packaged tools in the statistical software R (R Core Team, 2021). Fig. 2 shows the obtained body length plotted against each measurement point of dorsal fins for males and females. The body length (measurement point No. 1, Fig. 1) ranged from 71 cm (fetus) to 231 cm for males and 70.5 cm (fetus) to 225 cm for females. As the body length increased, each measured value also increased, and the slope of the graph increased. For differences between males and females in each graph, the length of dorsal fin base (measurement point No. 2, Fig. 1) differed between males and females. The maximum value was 49.0 cm for males and 41.0 cm for females. However, the height of the dorsal fin tip (measurement No. 3) was conspicuously narrower in individuals of body length 200 cm or more for both males and females (Fig. 2). In other words, the tip of the dorsal fin tended to hang down as individuals sexually matured in both males and

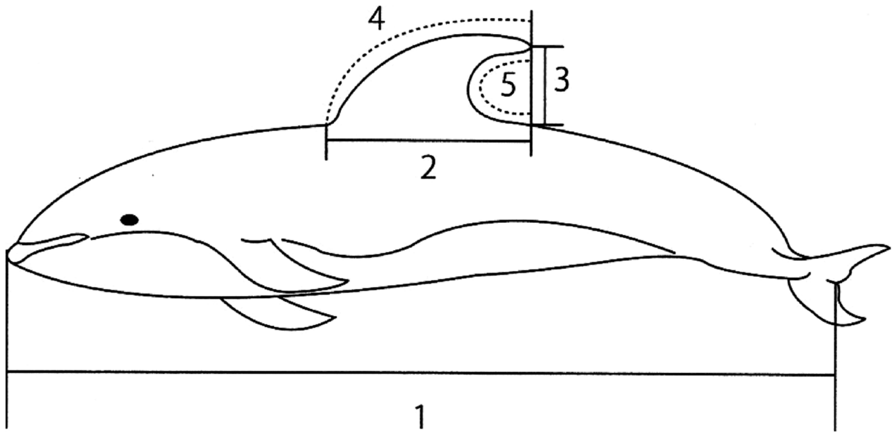

Fig. 1. External measurement points of Pacific white-sided dolphin used in the present study: **No. 1**, from the tip of the upper jaw to notch in the tail fluke (body length); **No. 2**, length of dorsal fin base; **No. 3**, height of dorsal fin tip; **No. 4**, length from the front edge to fin tip and **No. 5**, length from fin tip to trailing edge.

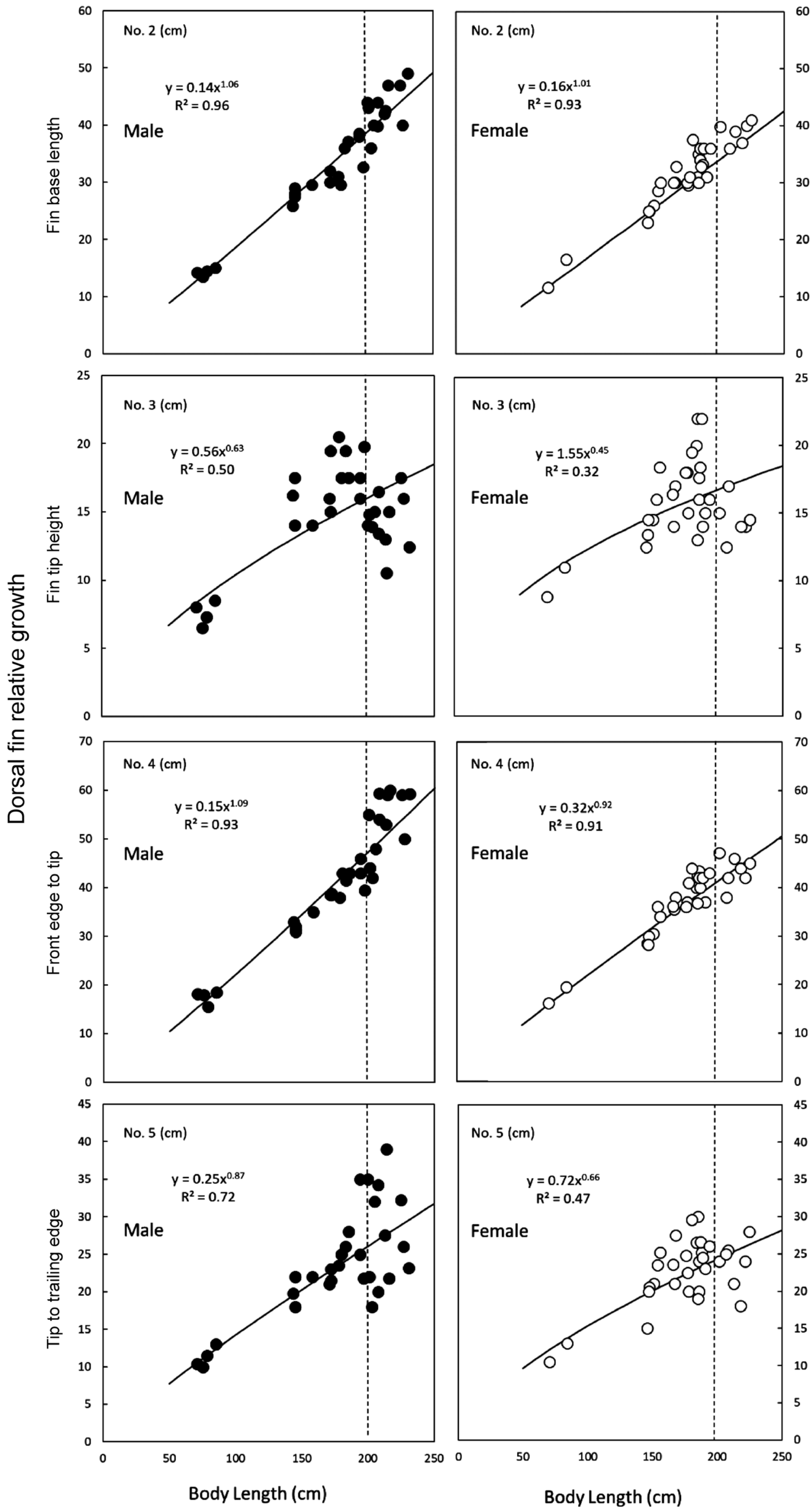

Fig. 2. Relative growth of measured points in dorsal fin and body length of the Pacific white-sided dolphin. Closed circles (left) represent males and open circles (right) represent females, respectively. The dotted line indicates the approximate body length of a sexually mature (200 cm) individual.

females. The front edge length (measurement point No. 4, Fig. 1) was also different between males and females. For individuals with a body length over 200 cm, dorsal fins grew longer in males than in females. The maximum value was 59.4 cm for males and 47.5 cm for females. The dorsal fin trailing edge length (measurement point No. 5) values varied widely for both males and females. This may be due to the variety of trailing edge shapes. The maximum value was 39.0 cm for males and 29.6 cm for females.

Table 1. Allometry of the length of dorsal fin measurement points and body length of Pacific white-sided dolphin males and females.

Male	Measurement points	α	β	R^2	Growth pattern	P-value
No. 2	Length of dorsal fin base	1.06	0.14	0.96	isometric allometry	0.135
No. 3	Tip height	0.63	0.56	0.50	negative allometry	0.003**
No. 4	Front edge length	1.09	0.15	0.93	isometric allometry	0.097
No. 5	Trailing edge length	0.87	0.25	0.72	isometric allometry	0.204

Female	Measurement points	α	β	R^2	Growth pattern	P-value
No. 2	Length of dorsal fin base	1.01	0.16	0.93	isometric allometry	0.782
No. 3	Tip height	0.45	1.55	0.32	negative allometry	0.000**
No. 4	Front edge length	0.92	0.32	0.91	isometric allometry	0.137
No. 5	Trailing edge length	0.66	0.72	0.47	negative allometry	0.010**

** indicates a statistically significant difference ($p<0.01$) between sexes in the length of dorsal fin measurement points and body length (see also Fig. 2).

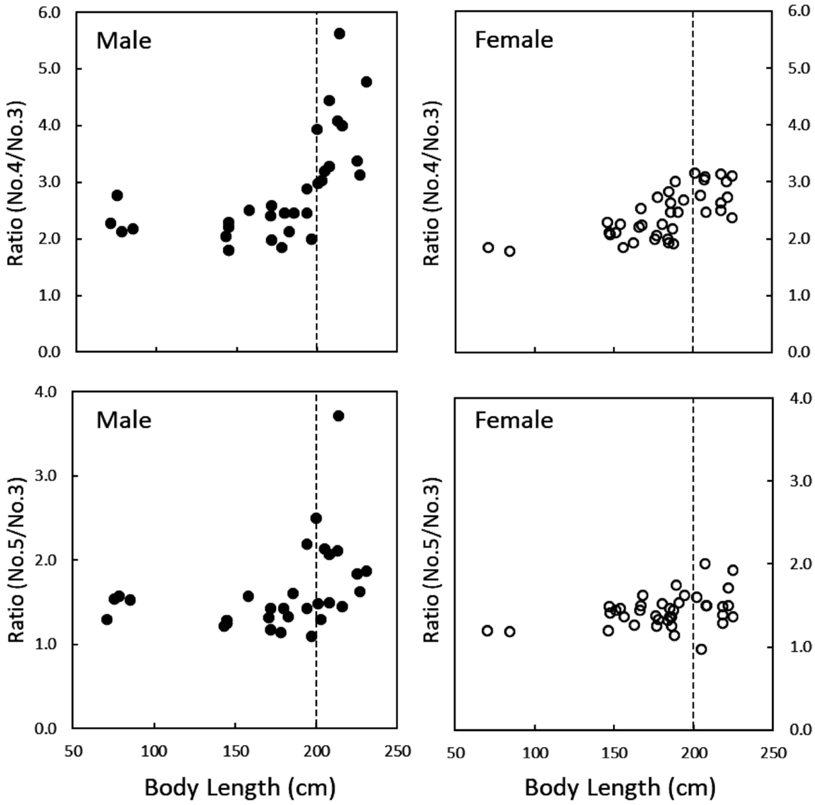

Fig. 3. Pacific white-sided dolphin dorsal fin growth-related ratio change No. 4/No. 3 shows front edge length to tip height ratio and No. 5/No. 3 shows trailing edge length to tip height ratio. Closed circles (left) represent males and open circles (right) represent females, respectively. The dotted line indicates the approximate body length of a sexually mature (200 cm) individual.

Table 1 shows the values applied to the relative growth curve (relationship between the length of dorsal fin measurement points and body length) for males and females. Tip height in males, and tip height and front edge length in females showed negative allometry.

Fig. 3 shows front edge length to tip height (No. 4/No. 3) and trailing edge length to tip height (No. 5/No. 3) ratios by body length for males and females. The ratio rises sharply after a body length of 200 cm in males, while on the other hand such a change is not observed in females.

Fig. 4 shows the front edge length to tip height (No. 4/No. 3) and the trailing edge length to tip height (No. 5/No. 3) ratios of individuals over 200 cm in body length. The ratios of front edge length to tip height were significantly higher in males (3.8±0.2, mean±SE, $n=12$) than in females (2.8±0.1, $n=10$) (t-test, $p<0.01$). No significant difference was found in the trailing edge length to tip height ratios.

This study found that the dorsal fins of Pacific white-sided dolphins inhabiting the coastal waters of Japan differ in shape and size between males and females. Especially in length of dorsal fin base (measurement point No. 2) and front edge length (measurement point No. 4), males clearly grew more than females. When the ratio of dorsal fin was examined using these measurements (Fig. 1), a significant difference was found in the front edge length to tip height ratio (No. 4/No. 3). This difference in the shape of the dorsal fins of males and females was effective for individual identification of wild Pacific white-sided dolphins and identification of sexually mature males. Suzuki *et al.* (2020) suggested that there are at least two forms on the coastal waters of Japan, and from the result of genetic structural analysis of 64 Pacific white-sided dolphins kept at aquariums in Japan, they concluded that in the Japanese coastal waters, genetic exchange between populations with different genetic backgrounds seems

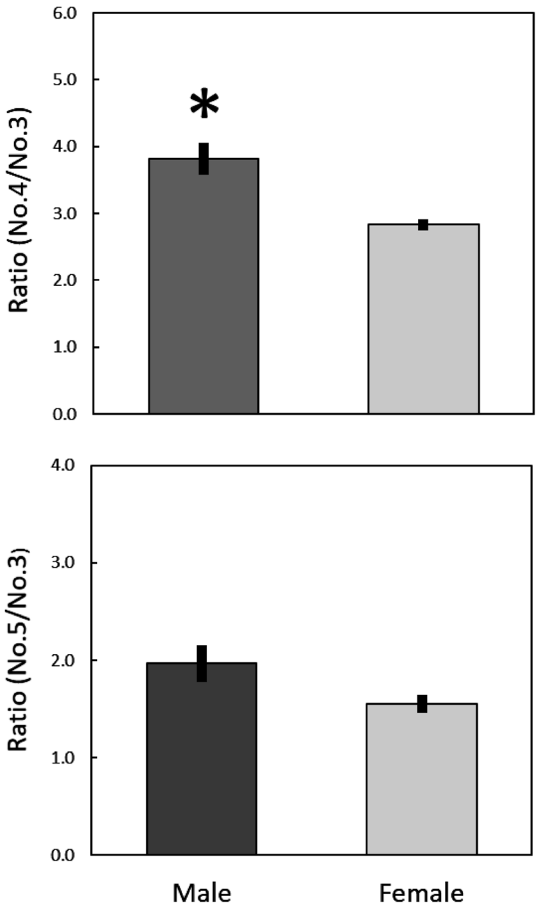

Fig. 4. Comparison of the dorsal fin ratios between mature males and females. No. 4/No. 3 shows front edge length to tip height and No. 5/No. 3 shows trailing edge length to tip height. The vertical black bars indicate the average error and * indicates a statistically significant difference (p<0.01) between sexes.

to occur in the wild. In the future, it is hoped that differences in body length and external morphology between individuals of the forms identified by genetic structural analysis will be investigated.

As a conclusion, we compared the measured values of the dorsal fin for the Pacific white-sided dolphin using records from the coastal waters of Japan. It was shown that the ratio of the dorsal fin can be used to identify sexually mature males. Their dorsal fin (front edge length to tip height ratio) could be readily distinguished from that of females, and a ratio of 3.8 or greater was indicative of a sexually mature male.

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We would like to express our deep gratitude to all the staff who have been involved in the continuous care of dolphins, and the measurement of proportions and the storage of records for over 50 years at Kamogawa Sea World. We would like to thank Masayuki Muramatsu and Naoko Suhara for their cooperation in preparing the figures and the significance test. Finally, we deeply appreciate the anonymous reviewers for their helpful suggestions.

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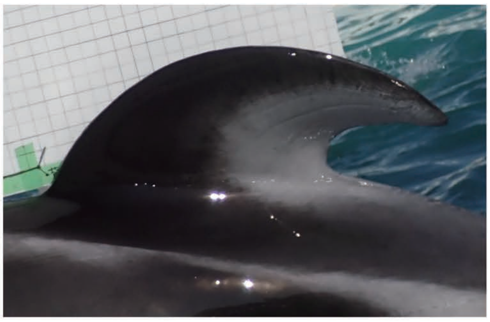
Appendix

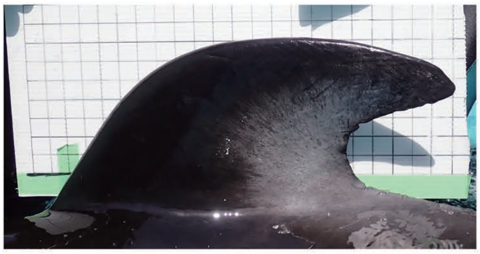
Dorsal fin shape photos; ID, sex, sexual status, body length.

The photos are shown based on body length left to right, from top to bottom by male (this page) and female (next page). The individuals in the photos have been kept at KSW and confirmed to be mature and immature by reproductive history, sex hormones, and semen collection in the case of males.

ID 055: male, mature, 231 cm

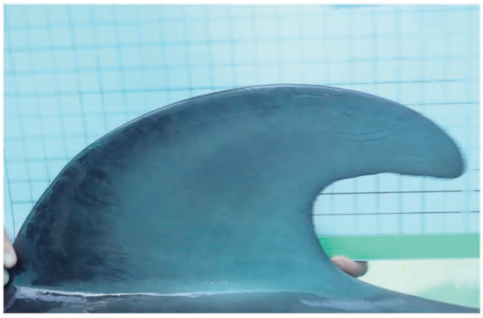


ID 054: male, mature, 214 cm



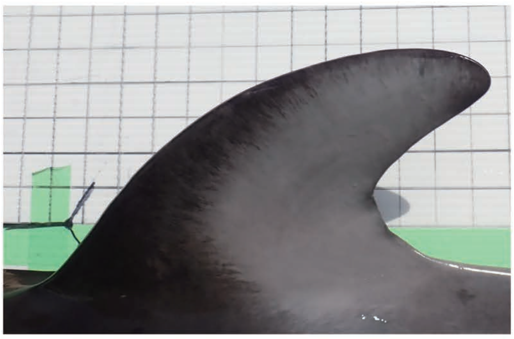
ID 032: male, mature, 213 cm

ID 062: male, mature, 205 cm



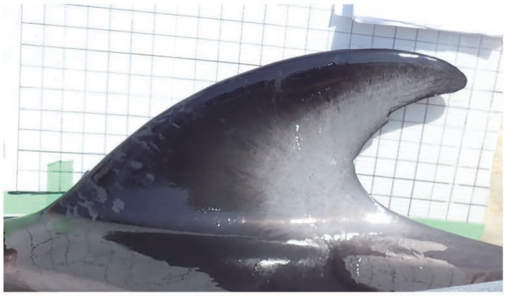
ID BL1: male, mature, 200 cm

ID 063: male, immature, 183 cm

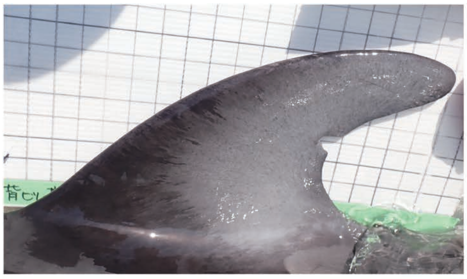


ID 065: male, immature, 158 cm

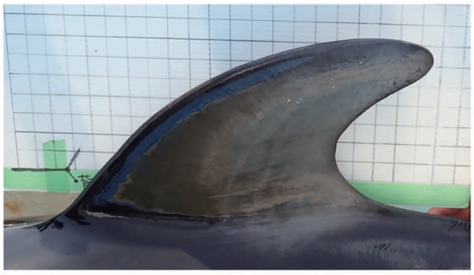
Appendix (Continued.)



ID 056: female, mature, 225 cm



ID 061: female, mature, 207 cm



ID 052: female, mature, 194 cm

ID 046: female, mature, 195 cm

ID 060: female, immature, 205 cm

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PRELIMINARY USE OF NEAR-INFRARED SPECTROSCOPY TO ESTIMATE THE BIOCHEMICAL COMPONENTS OF THE MUSCLES OF THE ANTARCTIC MINKE WHALE *BALAENOPTERA BONAERENSIS*

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Abstract

The energetic condition of whales is an important information to understand their energy demand to sustain their migration and reproductive success. However, basic energetic information based on biochemical components (protein, lipid, sugar, and water) and calorimetric data are limited, particularly in small baleen whales such as the minke whale. This study reports the biochemical components of the muscle tissues of 61 Antarctic minke whales (*Balaenoptera bonaerensis*) of different sexes and sexual maturity using near-infrared (NIR) spectroscopy. Prior to sample analysis, a calibration curve based on a standard chemical analysis was installed in the NIR analytical equipment. The dorsal muscle tissues from Antarctic minke whales contain approximately 0.5%–0.6% lipid, 26% protein, and 73% water, suggesting that the dorsal muscle contains a small amount of lipid and a high proportion of water. These proportions were similar between sexes and sexual classes. The proportions of lipids in the dorsal muscle of Antarctic minke whales are likely to be lower than those of other baleen whales, such as sei (*B. borealis*) and fin (*B. physalus*) whales, and this requires further investigation.

Key words: lipid contents, nutritional condition, muscle tissue, Antarctic minke whale.

The information about the nutritional indices of baleen whales is important to evaluate their energetic conditions and energy demand to sustain their migration and reproductive success. The information on their biochemical components, such as protein, lipid, sugar, and water, and calorimetric data are necessary to estimate the total energy deposit of individuals and evaluate their nutritional indices. The biochemical components of large whales, such as fin (*Balaenoptera physalus*) and sei (*B. borealis*) whales, were previously reported (Arai and Sakai, 1952; Lockyer *et al.*, 1984, 1985; Aguilar and Borrell, 1990).

This biochemical composition differs among whale species, and it also varies with the season, body size, reproductive status, and organs (Lockyer *et al.*, 1984, 1985; Aguilar and Borrell, 1990). Therefore, species-specific biochemical information is needed to estimate their energy deposits using tissues that function as a lipid deposit. However, little information is available for Antarctic minke whales (*B. bonaerensis*). The biochemical components and lipid contents of Antarctic minke whales were previously reported from the aspect of food nutrition (Ito *et al.*, 1993, 1998; Iida *et al.*, 1998). The biochemical components of the "red meat" from three Antarctic minke whales (a mature male, an immature female, and a >30-year-old female) were reported by Iida *et al.* (1998). The lipid contents of the dorsal muscle at the level of the dorsal fin (regarded as red meat) and tail (regarded as lipid-rich "tail meat") were examined in 29 males and 23 females (Ito *et al.*, 1998). Although fat tissue such as blubber function as lipid deposit, muscle mass represents a greater proportion in terms of weight

Fig. 1. Near-infrared spectrometer CA-HM (Joy World Pacific Co. ltd.) and a terminal PC. The solid muscle samples were homogenized using a food processor and a portion the (approximately 25 g) was set for analysis on a saucer at the lower right slot.

(Gunnlaugsson *et al.*, 2020). Therefore, it is important to determine the biochemical components of their muscle tissues to calculate the total energy contents and their function for energy storage.

In this study, near-infrared (NIR) spectroscopy was used to determine the biochemical components of the muscle tissues of Antarctic minke whales. While conventional methods analyze the samples only for a single component, NIR spectroscopy allows simultaneous measurements of multiple biochemical components, optimizing the use of samples. However, this NIR technique needs a calibration based on a regression model to predict the biochemical properties based on spectral data (Prieto *et al.*, 2017).

The NIR technique was used to estimate the biochemical components of the muscle tissues from 61 Antarctic minke whales sampled during the austral summer of 2016/17 under NEWREP-A (New Scientific Whale Research Program in the Antarctic Ocean). Muscle tissues were sampled from the dorsolateral muscle at the level of the dorsal fin. To reduce the seasonal effect on the analyses of the biochemical components during the summer feeding period, the samples from a limited time period in the survey season were used (December 15–January 5). The samples involved 25 immature males, 14 mature males, 17 immature females, and five pregnant females.

The muscle samples were scanned using an NIR spectrometer, CA-HM (Joy World Pacific Co., Ltd.; Fig. 1). Before the analysis, a calibration curve set for whale muscles was prepared (Fig. 2). This figure shows the plots of the values of protein, lipid, and water components from conventional chemical analyses and NIR spectroscopy. The muscle tissues from Antarctic minke whales and North Pacific sei whales were used for this calibration. This calibration curve was fit using these values and installed in the spectrometer.

The muscle samples were homogenized using a food processor, and a sub-sample (approximately 25 g) was set on a saucer dedicated for NIR spectroscopy (Fig. 3). In both conventional chemical analyses and NIR spectroscopy, the white fibrous parts, such as perimysium, were not removed from the muscle sample since these are muscle components. However, the results were expected to vary slightly by homogenizing the muscle samples.

The summary of the NIR analysis of the dorsal muscle at the level of the dorsal fin of Antarctic

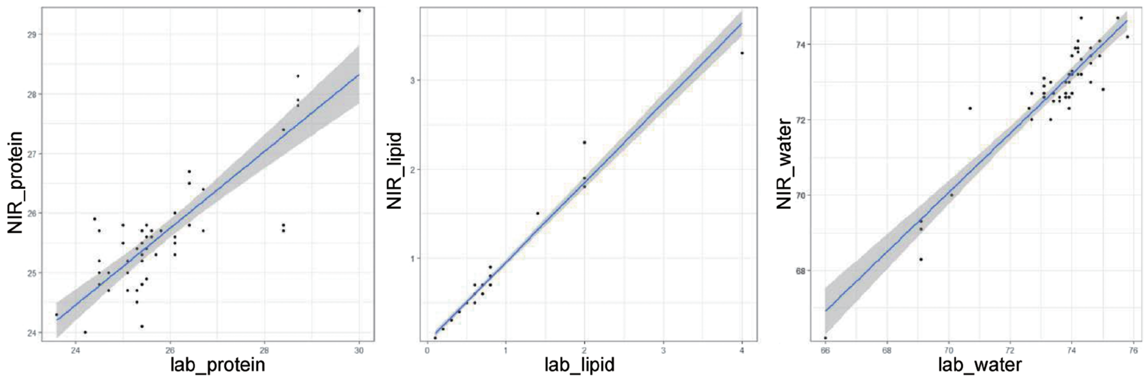

Fig. 2. Comparisons of biochemical components between laboratory-based and near-infrared (NIR) analyses to set a standard curve of the whale muscles for NIR spectroscopy. Left, protein; center, lipid; right, water. The muscle samples from Antarctic minke and North Pacific sei whales were used. The gray bands represent the 95% confidence intervals.

Fig. 3. Homogenized muscle of an Antarctic minke whale set on a saucer before analysis on the near-infrared spectrometer. The white fibrous parts were included in the analysis.

minke whales is listed in Table 1. On average, the muscle tissues contain approximately 0.5%–0.6% lipid, 26% protein, and 73% water, showing that the muscle consists of a very small amount of lipid and a high percentage of water in all maturity stages. The lipid compositions are similar among sexes and sexual maturity/classes. The results of Iida *et al.* (1998) are similar to the results of this study (Table 1). Ito *et al.* (1998) also showed that the lipid content of the dorsal muscle at the level of the dorsal fin was approximately 1.1% in Antarctic minke whales sampled in the austral summer of 1990/91 (Table 1). This lipid content in muscle tissues was slightly higher compared to the results of the present study. However, the energy storage differs among years and seasons (Konishi *et al.*, 2008; Konishi and

Table 1. Summary of the calorie content and biochemical components (per 100 g) of the muscles of Antarctic minke whales. For comparative purposes, the data from the results of Iida *et al.* (1998) and Ito *et al.* (1998) based on conventional analyses are also indicated.

	Immature male		Mature male		Immature female		Pregnant female		Iida *et al.* (1998)			Ito *et al.* (1998)			
	mean	SD	mean	SD	mean	SD	mean	SD	Mature male	Immature female	Mature female	Male	SD	Female	SD
Calorie (kcal)	106.03	3.54	107.05	6.22	104.18	2.28	107.61	3.33	—	—	—	—	—	—	—
Protein (g)	25.08	0.45	25.58	0.82	24.82	0.35	25.45	0.47	24.10	24.00	24.40	—	—	—	—
Lipid (g)	0.59	0.22	0.48	0.37	0.50	0.15	0.60	0.17	0.70	0.30	0.36	1.14	0.57	1.11	0.5
Sugar (g)	0.10	0.00	0.10	0.00	0.10	0.00	0.10	0.00	0.15	0.36	0.14	—	—	—	—
Water (g)	73.23	0.63	72.84	1.13	73.58	0.43	72.85	0.63	74.40	74.60	74.50	—	—	—	—
Ash	—	—	—	—	—	—	—	—	0.92	1.65	0.90	—	—	—	—
Lateral blubber thickness at the level of dorsal fin (cm)	3.33	0.61	3.41	0.44	3.22	0.47	3.10	0.66	—	—	—	—	—	—	—
Half girth at the level of umbilicus (cm)	163.28	18.27	212.00	10.70	166.29	19.14	214.20	9.91	—	—	—	—	—	—	—
Sample size	25		14		17		5		1	1	1	29		23	

Walløe, 2015), and this difference may suggest a possible seasonal and yearly variation of lipid contents in the muscles of Antarctic minke whales.

The lipid contents of the dorsal muscles of fin and sei whales exceeded 3% on average. The muscles in the anterior body part at the level of the flippers have less accumulated lipids compared to those in the middle and posterior parts of the body (Lockyer *et al.*, 1985). Given this, the muscles of Antarctic minke whales seem to have less lipid contents than those of large baleen whales. However, to confirm this, further comparative analyses among baleen whale species should be conducted using the same methodology while strictly considering the body parts from where the muscle samples are obtained.

The application of NIR spectroscopy to estimate the biochemical components of whale tissues is useful and practical to determine the basic information about the energetics of baleen whales. The use of techniques, such as NIR, which allows analysis of multiple components from a single sample, is of particular utility in the case of baleen whale samples, which are limited and difficult to access.

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INGESTION OF MARINE DEBRIS AND EVIDENCE OF ENTANGLEMENTS INVOLVING ANTARCTIC MINKE WHALES (*BALAENOPTERA BONAERENSIS*) SAMPLED IN THE INDO-PACIFIC SECTOR OF THE ANTARCTIC

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Abstract

This study presents the results of an examination of marine macro debris ingested by Antarctic minke whales (*Balaenoptera bonaerensis*) in the Indo-Pacific sector of the Antarctic in the period 1987/88–2018/19. Whales used in this study were sampled by surveys of the former Japanese whale research programs under special permit in the Antarctic. Also, this study examines evidence of past and present entanglements around the body of the animals. Of a total of 11,992 whales examined, 19 had ingested macro debris (0.16%) such as polymer products and wood. Only four cases of entanglements were recorded in the 11,992 whales examined (0.03%). Of 5,215 whales examined from the period of 2005/06 onward, six whales presented body marks associated with past entanglements (0.12%). It was concluded that the frequency of macro debris ingested as well as the number of entanglement cases involving Antarctic minke whales sampled in the Indo-Pacific sector of the Antarctic are extremely low in comparison with whales in the North Atlantic. These low frequencies of ingested debris and entanglements are unlikely to have a negative effect on the conservation of the Antarctic minke whale populations in this sector of the Antarctic.

Key words: Antarctic, Antarctic minke whale, marine macro debris, ingestion, entanglements.

Marine debris is a kind of pollutant affecting marine wildlife. Among the marine debris types, plastics have a more negative impact on marine wildlife than others. Plastics include microplastic particles (with a diameter <5 mm, Arthur *et al.*, 2009) and macroplastic particles (>20 mm, Barnes *et al.*, 2009). Such marine debris could cause disease or be ingested and lead to starvation (Gregory, 2009). Recently, two workshops (Panti *et al.*, 2019; IWC, 2020) were held to discuss the current status of the interaction between marine debris and marine mammals. The objectives of the workshops were to identify negative effects on the animals; to identify possible areas of research to assess the impact of marine debris on this group of animals; and to propose ways to alleviate the problem. So far, detection of debris interactions in cetaceans has largely depended on data collected from small sample sizes provided by stranded animals. Therefore it has been difficult to determine the implications of debris interactions at a population level (Baulch and Perry, 2014).

The present study focuses on the Antarctic, one of the most isolated places on earth where the effect of human activities and the occurrence of marine debris are assumed to be limited (see also Isoda *et al.*, this issue). There is limited information regarding interaction between marine debris and whales in the Antarctic. This study investigates the occurrence of marine macro debris ingested by Antarctic minke whales (*Balaenoptera bonaerensis*) based on whales sampled over a period of more than 30 years in the Indo-Pacific sector of the Antarctic by surveys of the former JARPA/JARPAII (Japanese

Table 1. Number of macro debris ingested by Antarctic minke whales and frequencies (number of whales with debris ingestion per 100 Antarctic minke whales) in the Indo-Pacific sector of the Antarctic in the austral summer seasons 1987/88–2018/19 (JARPA, JARPAII and NEWREP-A). In parentheses are the numbers of marine debris found in the forestomach and main stomach when only those two compartments were examined in the 2005/06–2013/14 seasons (JARPAII).

Research season	Sample size	Number of whales with debris ingestion	Marine debris*								Number of whales with debris ingestion per 100 Antarctic minke whales
			Wood		Polymer product		Others		Total		
1987/88	272	1	0	(0)	1	(0)	0	(0)	1	(0)	0.37
1988/89	236	0	0	(0)	0	(0)	0	(0)	0	(0)	0.00
1989/90	326	0	0	(0)	0	(0)	0	(0)	0	(0)	0.00
1990/91	323	0	0	(0)	0	(0)	0	(0)	0	(0)	0.00
1991/92	288	2	1	(0)	1	(0)	0	(0)	2	(0)	0.69
1992/93	327	2	1	(0)	1	(0)	0	(0)	2	(0)	0.61
1993/94	330	2	1	(0)	1	(0)	0	(0)	2	(0)	0.61
1994/95	330	0	0	(0)	0	(0)	0	(0)	0	(0)	0.00
1995/96	439	0	0	(0)	0	(0)	0	(0)	0	(0)	0.00
1996/97	440	0	0	(0)	0	(0)	0	(0)	0	(0)	0.00
1997/98	438	0	0	(0)	0	(0)	0	(0)	0	(0)	0.00
1998/99	389	2	1	(0)	1	(0)	0	(0)	2	(0)	0.51
1999/00	439	3	1	(0)	2	(0)	0	(0)	3	(0)	0.68
2000/01	440	3	2	(2)	1	(0)	0	(0)	3	(2)	0.68
2001/02	440	0	0	(0)	0	(0)	0	(0)	0	(0)	0.00
2002/03	440	2	0	(0)	1	(1)	1	(0)	2	(1)	0.45
2003/04	440	1	0	(0)	0	(0)	1	(1)	1	(1)	0.23
2004/05	440	1	1	(0)	0	(0)	0	(0)	1	(0)	0.23
2005/06	853	0	0	(0)	0	(0)	0	(0)	0	(0)	0.00
2006/07	505	0	0	(0)	0	(0)	0	(0)	0	(0)	0.00
2007/08	551	0	0	(0)	0	(0)	0	(0)	0	(0)	0.00
2008/09	679	0	0	(0)	0	(0)	0	(0)	0	(0)	0.00
2009/10	506	0	0	(0)	0	(0)	0	(0)	0	(0)	0.00
2010/11	170	0	0	(0)	0	(0)	0	(0)	0	(0)	0.00
2011/12	266	0	0	(0)	0	(0)	0	(0)	0	(0)	0.00
2012/13	103	0	0	(0)	0	(0)	0	(0)	0	(0)	0.00
2013/14	250	0	0	(0)	0	(0)	0	(0)	0	(0)	0.00
2014/15	-	-	-	-	-	-	-	-	-	-	-
2015/16	333	0	0	(0)	0	(0)	0	(0)	0	(0)	0.00
2016/17	333	0	0	(0)	0	(0)	0	(0)	0	(0)	0.00
2017/18	333	0	0	(0)	0	(0)	0	(0)	0	(0)	0.00
2018/19	333	0	0	(0)	0	(0)	0	(0)	0	(0)	0.00
Total	11,992	19	8	(2)	9	(1)	2	(1)	19	(4)	0.16

* All items found in stomach and duodenal ampulla except one polymer product found in the anus of one whale. Category 'others' includes one small black piece of carbonized object (research season: 2002/03) and one small rubber piece (research season: 2003/04).

Research Program under Special Permit in the Antarctic, Phases I and II) and NEWREP-A (New Scientific Whale Research Program in the Antarctic Ocean). The Antarctic minke whale is a small baleen whale species, which migrates between low latitude winter breeding grounds and high latitude summer feeding grounds in the Antarctic where it is widely distributed (Kasamatsu *et al.*, 1995). The species feed mainly on Antarctic krill (*Euphausia superba*) but also on ice krill (*E. crystallorophias*)

Fig. 1. A piece of polymer product found in the stomach of an Antarctic minke whale sampled during the 2002/03 austral summer season at position 76°S; 175°E (IWC Area V; CCAMLR sub-area 88.1).

Table 2. Ingestion of macro debris by Antarctic minke whales by sex and sexual maturity in the Indo-Pacific sector of the Antarctic in the austral summer seasons 1987/88–2018/19 (JARPA, JARPAII and NEWREP-A). In parentheses are the sample sizes examined by sex and sexual maturity.

	Female		Male		Total
	Immature	Mature	Immature	Mature	
Marine debris	(1,962)	(3,970)	(1,385)	(4,673)	(11,992)*
Wood	0	3	0	5	8
Polymer product	1	1	0	7	9
Others	0	0	1	1	2
Total	1	4	1	13	19

* Includes one male and one female of unknown sexual maturity status.

in some areas of the Antarctic (Ichii and Kato, 1991; Tamura and Konishi, 2009). It has been assumed that these whales ingested debris mixed in with food during the austral summer feeding period in the Antarctic waters.

This study also examines the body surface of the whales to identify entanglements, i.e., objects attached to the body (from the period of JARPA, JARPAII and NEWREP-A) or evidence from scars and marks of past entanglement events (from the period of JARPAII and NEWREP-A when more detailed photographic records were available). This is a unique study because it examines ingestion and entanglements in the Antarctic minke whale based on a series of surveys conducted over 31 years, and it is the first study to provide a summary of information regarding interaction between marine macro debris and whales in the Antarctic.

The surveys were conducted during the austral summer seasons from 1987/88 to 2018/19. Table 1 shows the details of the survey years and the number of samples for each year. The research area comprised the Indo-Pacific sector of the Antarctic, specifically the International Whaling Commission (IWC) Antarctic Management Areas III East (IIIE) (35°–70°E), IV (70°–130°E), V (130°E–170°W) and VI West (VIW) (170°–145°W), south of 60°S (JARPA and NEWREP-A) and south of 62°S (JAR-

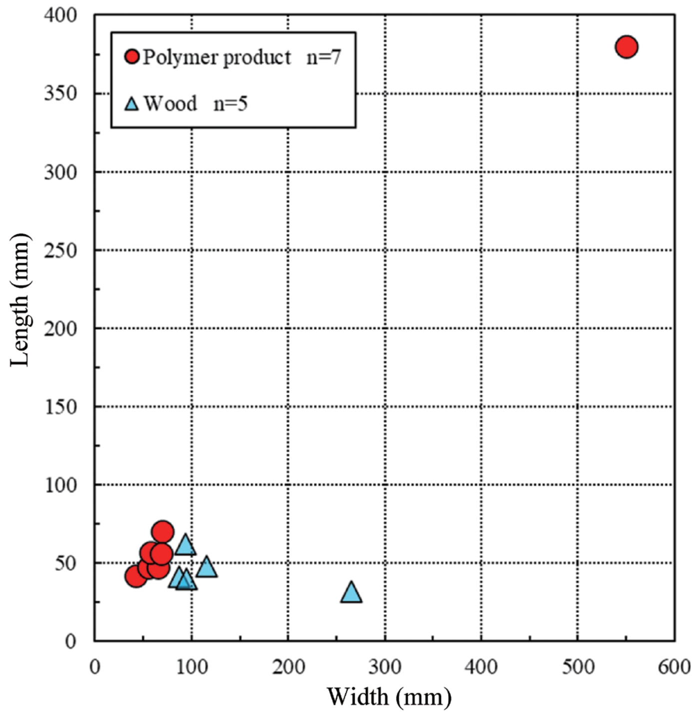

Fig. 2. Size of marine debris ingested by Antarctic minke whales in the Indo-Pacific sector of the Antarctic (1987/88–2004/05). The sample size of debris in this figure is different from that in Table 1 (no size information was available for two polymer products and three wood pieces).

PAII). These areas overlap partially with the Convention Areas of the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR): Area IIIE with Divisions 58.4.2–4, Area IV with Divisions 58.4.1–3, Area V with Division 58.4.1 and sub-area 88.1, and Area VIW with sub-area 88.2.

In order to obtain samples representative of the populations, Antarctic minke whales were sampled randomly on predetermined track-lines (Nishiwaki *et al.*, 2006; Nishiwaki *et al.*, 2014). Sampled whales were examined onboard of the research base vessel where several biological measurements and samples were collected. Body length was measured to the nearest 1 cm from the tip of snout to the deepest part of the notch of the flukes along a straight line parallel to the body axis. Body weight was obtained using a large weighing scale installed on the flensing deck. Sex of the whales was determined by researchers on board. Sexual maturity in females was determined by the presence of at least one corpus luteum or albicans in the ovaries and for males a single testis weight of 400 g or more was used as a criterion (Kato, 1982).

The stomachs of 11,992 Antarctic minke whales were examined. Examination of macro debris was conducted during the routine analysis of stomach contents following established protocols (Tamura and Konishi, 2009). The three stomach chambers and the duodenal ampulla were examined macroscopically during the period 1987/88–2004/05 (JARPA) and 2015/16–2018/19 (NEWREP-A). Only the fore and main stomachs were examined during the period 2005/06–2013/14 (JARPAII). Macro debris and objects other than preys were recorded. The sizes of solid objects were estimated from scaled photographic records.

Out of the 11,992 Antarctic minke whales examined, a total of 19 whales had ingested macro debris (Table 1). None of the whales had multiple marine debris in their stomachs. Fig. 1 shows an example of marine debris (polymer product) found in the stomach of an Antarctic minke whale. There were nine cases of polymer product ingestion and eight cases of wood ingestion. Macro debris ingestion was not observed after the 2005/06 season and there was no temporal increasing trend over the re-

Table 3. List of entanglement cases in the Antarctic minke whales in the Indo-Pacific sector of the Antarctic in the austral summer seasons 1987/88–2018/19 (JARPA, JARPAII and NEWREP-A) (see Fig. 3).

Research season	Date	Latitude	Longitude	Body length(m)	Body weight(t)	Sex	Stomach contents	Entanglement objects	Fig. 3
1995/96	22 Dec. 1995	62°48'S	68°55'E	7.5	4.7	M	Empty	Fishing hook	a
2003/04	10 Dec. 2003	63°10'S	54°56'E	5.7	2.1	M	Krill	Monofilament fishing line	b
2005/06	6 Jan. 2006	64°26'S	72°40'E	7.8	N/A	F	Krill	Rope	c
2005/06	5 Mar. 2006	63°56'S	103°46'E	5.7	N/A	M	Krill	Packing band	d

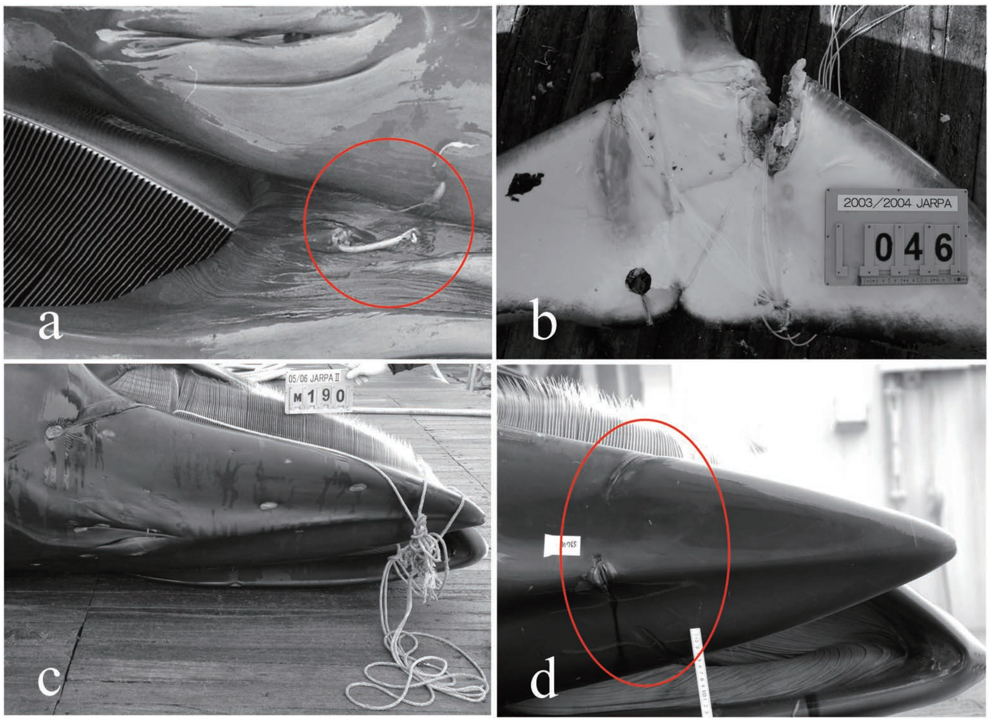

Fig. 3. Four cases of entanglement in the Antarctic minke whales in the Indo-Pacific sector of the Antarctic in the austral summer seasons 1987/88–2018/19 (JARPA, JARPAII and NEWREP-A). **a**: fishing hook; **b**: monofilament fishing line; **c**: rope; **d**: packing band (the band was lost when the whale was transported to the research base vessel).

search period. The frequency of stomachs with debris per 100 Antarctic minke whales examined was very low (0.16%) and the frequency of polymer products was 0.08%. Around 68.4% of all macro debris was ingested by mature males (Table 2). Most macro debris (75.0%) was less than 100 mm in size (Fig. 2). There were three debris, one polymer bag and two small wood pieces with sizes of more than 100×100 mm. Apart from debris, stones were found in six whales (in six austral seasons) and feathers in 37 whales (in thirteen austral seasons).

The frequency of ingested debris per 100 Antarctic minke whales was very low in comparison with debris found in whales from the North Atlantic. For example, six of 82 Icelandic fin whales (*B. physalus*) examined had debris in their stomachs while on the eastern coast of the United States, three of 19 mysticetes examined contained synthetic objects in their gut (Sadove and Morreale, 1990). The frequencies of marine debris ingestion obtained from stranded animals in the UK were 2.2% in the harbour porpoise (*Phocoena phocoena*) and 2.3% in the short-beaked common dolphin (*Delphinus delphis*) (Deaville and Jepson, 2010). For the Indo-Pacific sector of the Antarctic, our study found that only 19 Antarctic minke whales out of 11,992 examined had macro debris in their stomachs (0.16%).

The Antarctic minke whale is a filter feeder species with swallowing behavior (Nemoto, 1970), and

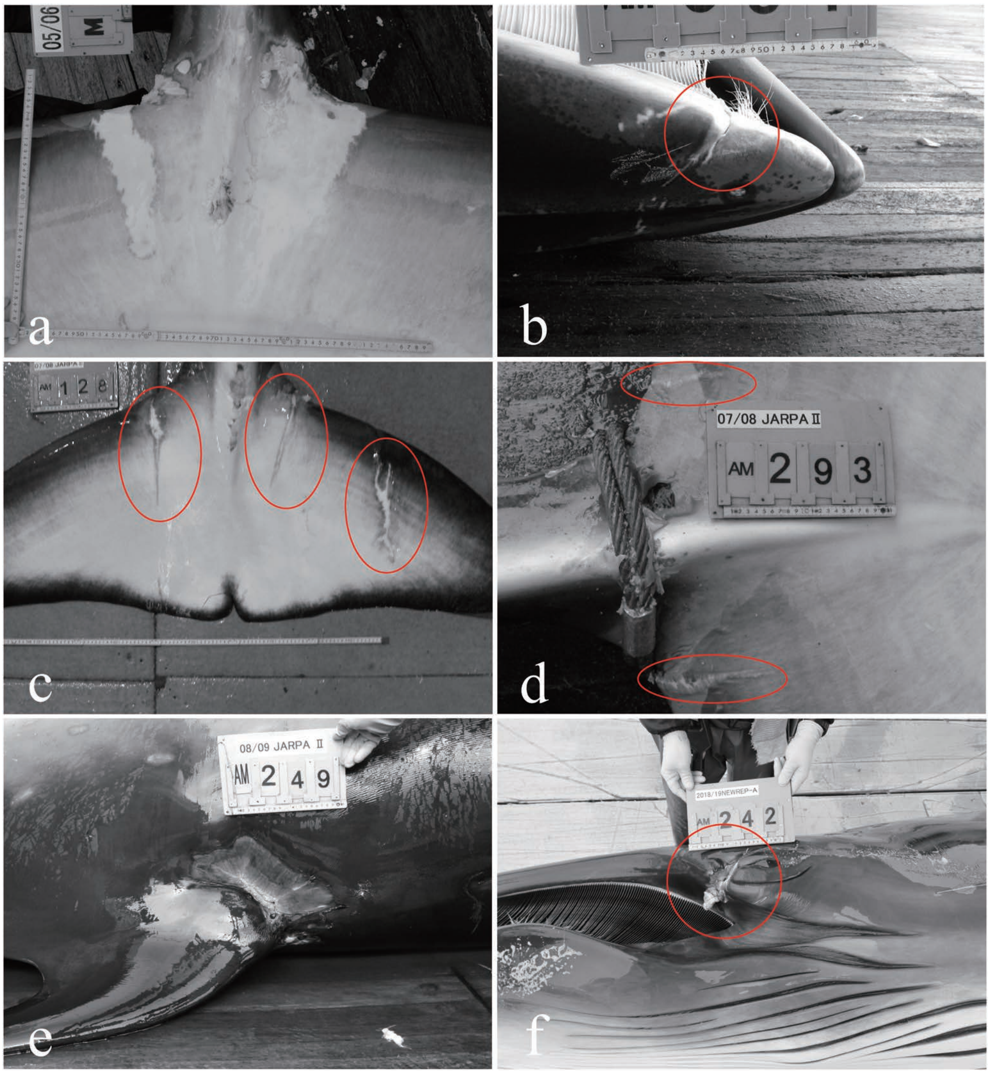

Fig. 4. Six cases of Antarctic minke whales in the austral summer seasons 2005/06–2018/19 (JARPAII and NEWREP-A) presenting marks and scars possibly produced by past entanglements. **a**: healed injury of flukes; **b**: healed injury of snout; **c**: healed injury of flukes; **d**: healed injury of flukes (rope used in the whale processing is also shown); **e**: healed injury of dorsal fin; **f**: unhealed injury of head.

this foraging behavior of Antarctic minke whales is associated with shallow waters (less than 100 m in depth) (Friedlaender *et al.*, 2014), which increases the chance of ingesting debris floating on the surface or in layers just under the surface.

Regarding entanglements, only four cases were found in the total sample of 11,992 whales (0.03%) (Table 3, Fig. 3). These included a fishing hook, a monofilament fishing line, a rope and a packing band. Six out of 5,215 Antarctic minke whales examined from the period of 2005/06 onward presented scars and marks likely to be associated with past entanglements (0.12%) (Fig. 4). It was assumed that scars were healed injuries (five cases) while unhealed marks were considered as injuries (one case). The unhealed injury was observed during the most recent survey under NEWREP-A. The possibility of these scars being produced by attacks from killer whales (*Orcinus orca*) is low. Scars observed in the present study were not consistent with the dentition of killer whales which comprise linear, parallel scars spaced 2.5–5.0 cm apart (Naessig and Lanyon, 2004). As in the case of debris, cases of entanglements with dangerous objects were extremely low in the Antarctic minke whales from the Indo-Pacific sector of the Antarctic when compared to the North Atlantic. For example, along the eastern coast of the United States and Canada during 2002–2006, 27 and 77 cases of entanglements

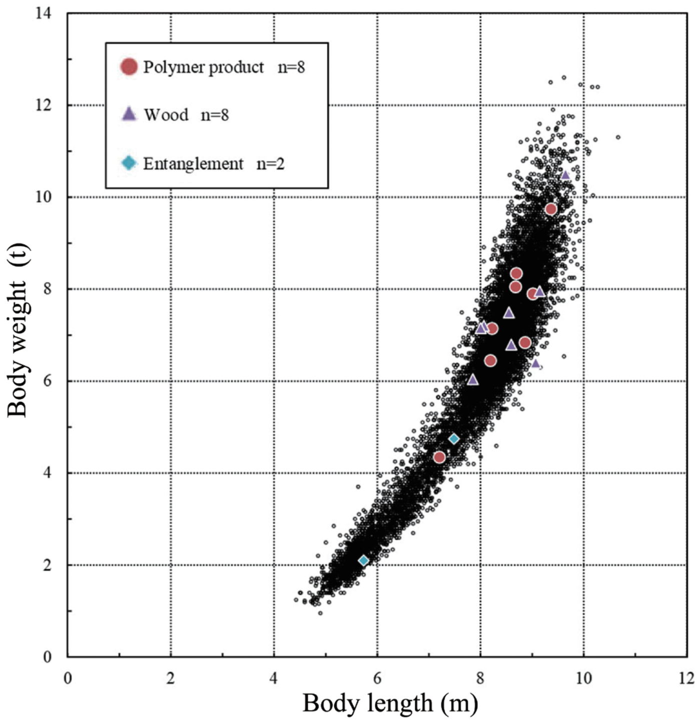

Fig. 5. Relationship between body length and body weight in the Antarctic minke whales (n = 10,037) including whales ingesting debris and cases of entanglement. The sample size in this figure is different from those in Tables 1 and 3 (no body weight was available for one animal that ingested polymer product and two entangled animals).

were reported for common minke whales (*B. acutorostrata*) and humpback whales (*Megaptera novaeangliae*), respectively (Glass *et al.*, 2008). In Iceland, five of 95 fin whales examined showed signs of previous entanglements (Sadove and Morreale, 1990). It was reported that entanglement of Antarctic fur seals (*Arctocephalus gazella*) was caused mostly by loop shaped debris such as packing bands (Croxall *et al.*, 1990; Arnould and Croxall, 1995). Similar cases were reported for common minke whales in the Atlantic (Gill *et al.* 2000). In the present study, one of the four cases of entanglement in the Antarctic minke whale was from a packing band (Fig. 3d). CCAMLR has prohibited the discharge of plastics and restricted the use of packing bands on fishing vessels through Conservation Measure 26–01 (CCAMLR, 2006). Fishing gear is the most significant source of entanglements for whales and such entanglements have been reported in various waters (Laist, 1997; Simmonds, 2012). In the Antarctic, reports of mortality of whales attributed to entanglements related to fisheries operations are rare. One of those reports informed of the mortality of a sperm whale and another one possibly of an Antarctic minke whale (SC-CAMLR 2004; 2012). In the present study, only three cases of entanglements occurred, possibly from fishing gears (derelict or active) (Fig. 3).

In the cases involving both macro debris ingested and entanglements, it was shown that whales were not emaciated according to the usual body-length-weight relationship (Fig. 5). In conclusion the frequencies of marine macro debris ingested as well the cases of entanglements involving Antarctic minke whales in the Indo-Pacific sector of the Antarctic are extremely low, and much lower in comparison with cases reported in the North Atlantic. These low frequencies of ingested debris and entanglements are unlikely to have a negative effect on the conservation of the populations of Antarctic minke whales in the Indo-Pacific sector of the Antarctic.

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Review

Blowing of a juvenile fin whale, North Pacific.

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A SHORT REVIEW OF ACOUSTIC MONITORING OF LARGE WHALES IN JAPANESE WATERS

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Abstract

Passive acoustic monitoring studies of large whales in the Japanese EEZ are reviewed in this paper. Submarine cables to monitor seismic events have been installed on the Pacific Ocean side of Japan because of the risk of earthquake strikes. Low frequency fin whale *Balaenoptera physalus* calls have been detected mostly in winter time. Many fin whale calls were observed in the waters off Kushiro in the northern part of Japan. A scientific submarine cable in Sagami Bay, 100 km west of Tokyo, revealed frequent presence of sperm whales *Physeter macrocephalus* year around. In the Ogasawara and Okinawa archipelagos, known as breeding grounds of humpback whales *Megaptera novaeangliae*, songs were recorded using stationed or boat-based recordings.

Key words: passive acoustic monitoring, fin whale, sperm whale, humpback whale, underwater sound.

Introduction

As is well known, baleen whales produce low frequency sounds during the breeding season. For example, blue whales produce frequency modulated sounds as low as 15.3 Hz (Stafford *et al.*, 2001), which is similar to the frequency range of earthquake vibrations. In the early 90's, underwater sound data received by military submarine cables was made available for scientific purposes to monitor baleen whales passively. Earlier, Dr. Ohsumi suggested application of passive acoustic monitoring for a survey of baleen whales (Ohsumi, 1994), referring to SOSUS and SURTASS systems (Nishimura and Conlon, 1994). Passive acoustic monitoring is the method of observing animals by receiving their vocalizations. Especially in the ocean, passive acoustic monitoring is a powerful method to identify presence, location, and movement of phonating animals in the water.

However, the passive acoustic method was not widely used in Japanese waters until recent years. Most of the Japanese studies are not accessible from outside of Japan or not yet published. As those studies are not well known internationally, there is the mistaken impression of a "vacuum zone" of passive acoustic monitoring of large whales in the western Pacific Ocean. This paper briefly introduces passive acoustic monitoring studies of large whales in Japanese waters. In contrast, passive acoustic monitoring of small odontocetes has been extensively conducted in Japanese and Asian waters. Many of these scientific papers appeared in international journals, which can be found by searching "A-tag" and "porpoise":

https://scholar.google.com/scholar?hl=0%2C5&q=A-tag+porpoise.

Review

Japan is located at the edge of the Pacific Rim and has suffered severe earthquake strikes many

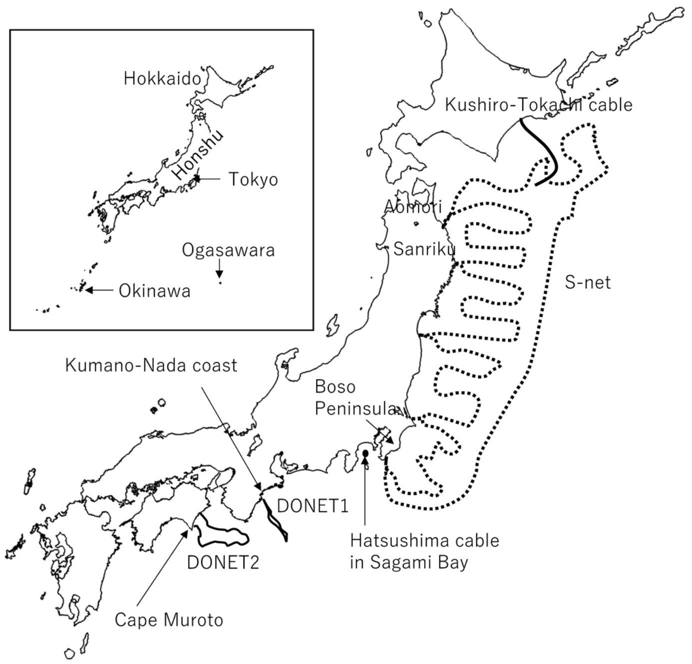

Fig. 1. Location of submarine cables in the Japanese EEZ and two breeding grounds of humpback whales (Okinawa and Ogasawara). Hatsushima cable is for scientific research purposes. The other four cables (Kushiro-Tokachi, DONET1, DONET2 and S-net) are deployed to observe seismic events nearby the trench shafts. The S-net shown in dotted line has seismometers, which provides water acceleration associated with low frequency sounds; no hydrophone data is available.

times. To monitor seismic events, submarine cables have been installed in the Japanese EEZ (exclusive economic zone), as shown in Fig. 1. For example, the Kushiro-Tokachi cable off Hokkaido was deployed in 1999 (Hirata *et al.*, 2002). S-net is the newly installed 5,500 km submarine cable in operation since 2016, which covers the eastern side of Honshu Island from off Hokkaido, Aomori, Sanriku and the Boso Peninsula (https://www.seafloor.bosai.go.jp/S-net/). The installation of DONET1 (Dense Ocean Floor Network System for Earthquakes and Tsunamis) observational equipment on 20 stations at Kumano-Nada was completed in 2011 (https://www.jamstec.go.jp/donet/e/cable/). In addition, DONET2 was deployed off Cape Muroto. DONET systems are currently operated by the National Research Institute for Earth Science and Disaster Resilience (https://www.seafloor.bosai.go.jp/). Hatsushima cable in Sagami Bay has recorded a human audible range of underwater sounds since 1993 (Iwase *et al.*, 2001). These cable systems have hydrophones or seismometers to record underwater sound pressure or water acceleration.

Passive acoustic monitoring of fin whales *Balaenoptera physalus*

Low frequency calls of fin whales were detected in winter time off Hokkaido by the Kushiro-Tokachi cable (Matsuo *et al.*, 2017). Four stations (DSO, OBS1, OBS2, OBS3) with hydrophones are located between 41°40.050′N–42°15.168′N, 144°20.454′E–145°3.372′E and 2,124 m–3,428 m in depth. Over a total of 2,981 recording days, 2,865,403 calls were identified by an automatic detector designed for this study. Clear seasonal differences were observed, being high during October and February, and low in the summertime. The number of calls received in a month showed a double peak structure in October and January. Call detection did not show a diurnal pattern. Nishida *et al.* (2018) developed a web system to visualize detections of fin whale calls. Yoshida (2017) independently analyzed Kushiro-Tokachi cable data and reached a similar conclusion of the seasonal presence of fin whales.

Ocean bottom seismometer data of S-net well supported the above results. Using 150 points of S-net observatory data, Nakamura (2020) documented the frequent call detections during October to

April. In areas off Kushiro and Aomori, the number of detections were high during December to January. After January, the area of the highest reception shifted to the south-west, in waters off Aomori and Sanriku. In addition, calls were detected on the shore side of the trench shaft, approximately 200 km off Honshu Island. The seismometers in the southern part of S-net located off Boso Peninsula received fin whale calls in winter time, although the number of received calls was far smaller compared with those observed off Kushiro.

According to the DONET1 data, no fin whale calls were identified year round (Ikuo Matsuo, pers. comm.). The location of DONET1 is approximately 400 km southwest of Boso Peninsula. This area might not be a breeding ground of fin whales. For DONET2, data analysis of baleen whale sounds has not been conducted.

Passive acoustic monitoring of sperm whales *Physeter macrocephalus*

Hatsushima Island Cabled Observatory (Hatsushima cable) is located on the seafloor at a depth of 1,175 m about 7 km southeast off Hatsushima Island in the western part of Sagami Bay, which is approximately 90 km southwest of Tokyo. Iwase (2012) retrieved audio sounds recorded from the soundtrack of videotape, which was received by the hydrophone of this observatory. Sperm whale clicks including creaks (series of very rapid clicks, inter-click intervals less than about 0.2 second) were observed. Iwase (2012) reported that no seasonality of the detections of sperm whale clicks was observed during the 1994–2012 period. The data suggested that sperm whales appeared around Hatsushima cable all year.

Amano *et al.* (2014) recorded sperm whale sounds by towed or suspended hydrophone off the Kumano-Nada coast and Ogasawara waters. Statistical differences in the number of clicks and inter-click intervals were identified. They suggested different vocal clans in the two study sites.

Passive acoustic monitoring of humpback whales *Megaptera novaeangliae*

Since Payne and McVay (1971) reported the songs of humpback whales, song structure of baleen whales produced in the breeding season is one of the major subjects of underwater bioacoustics. Maeda's (2002) doctoral dissertation at Nagasaki University gives a systematic description of the song structure of humpback whales in Okinawa waters. Using boat-based recordings during 1991–1998, unit structure and unit sequence in a phrase were analyzed. Individual variations and year-by-year change of song structure were reported. In addition, Maeda (2002) compared song recordings between Okinawa and Ogasawara waters during 1992–1995 and found no significant difference in song structures of humpback whales. As Darling and Mori (1993) reported, the same humpback whales were identified in both waters, consistent with the comparisons of acoustic features.

In recent years, singing behavior and the location of humpback whales in Ogasawara waters were examined to assess the effect of ship noise (Tsujii *et al.*, 2018). They installed two fixed underwater recorders separated by 3.0 km. Recorders were exchanged every two or three weeks before their batteries ran out. Each recorder had a stereo hydrophone. This monitoring method enabled localization of singers by triangulation from the two locations, simultaneously with the recording of song structure. Fewer whales sang nearby, within 500 m, of the shipping lane. Humpback whales reduced sound production after a ship passed, when the minimum distance to the whale from the ship trajectory was 1,200 m.

Discussion

Passive acoustic monitoring is a powerful method to observe presence, location, and movements of cetaceans. Even density can be estimated when phonating intervals, directionality, and source level are available. In Japanese waters, several already-existing submarine cables are available. Most of the data is available for research purposes judged to be conducive to the management of baleen whales in the Japanese EEZ. To accelerate passive acoustic studies of large whales, several future directions can be suggested.

1. Encourage open data policy of underwater sounds. Data classification and masking will be needed to avoid conflict with national security in the low frequency range. For high frequency sounds of sperm whales and other large odontocetes, this constraint will be relaxed.
2. For automatic detection and classification of species or families, collections of species' annotated sounds are required to ensure acceptable performance of machine learning applications.
3. Improvement of density estimation models will serve for abundance estimation of offshore baleen whale populations. In the winter time when survey vessels are difficult to operate, the area of breeding grounds of large baleen whales will be an appropriate target for passive acoustic monitoring studies.

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IMPACT OF WHALE RESOURCE MANAGEMENT RESEARCH ON SIKA DEER MANAGEMENT

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Abstract

Sika deer population management in Hokkaido has been strongly influenced by whale resource management research in monitoring frameworks and management approaches. The whale survey consisted of five pillars: catch statistics, visual observations, tag-recovery surveys, biological surveys from whaling, and special catch surveys. In references to the whale monitoring, sika deer monitoring was constructed involving capture information (SPUE, CPUE), visual observations (spotlight census, aircraft survey), radio telemetry surveys, genetic surveys, and biological surveys from hunting and culling for assessing age structure and the reproductive characteristics of female deer. We adopted the Revised Management Procedure (RMP) for whaling to Hokkaido sika deer population as feedback management because there was uncertainty in estimating population size. Feedback management incorporated into deer management in the eastern part of Hokkaido became the pioneer of science-based wildlife management in Japan. It influenced the establishment of the Specified Wildlife Conservation and Management Plan by amending the Wildlife Protection and Hunting Act in 1999. Feedback management is almost synonymous with adaptive management in a broad sense. The large-scale feedback management of sika deer in Hokkaido is a practical example of adaptive management of deer ahead of the world.

Key words: Adaptive management, feedback management, revised management procedure, sika deer, monitoring, whale.

Introduction

Hokkaido Government established the Hokkaido Institute of Environmental Sciences (HIES) in 1991, when I started to work as a researcher for sika deer (*Cervus nippon*) management. Until then, monitoring of terrestrial large animals was not carried out except for Japanese serow (*Capricornis crispus*), a species designated as a nation's Special Natural Monument. Sika deer population management in Hokkaido has been strongly influenced by whale resource management research in monitoring frameworks and management approaches. As a result, it has played a leading role in science-based wildlife management in Japan.

Review

Monitoring

In 1991, when I was planning sika deer monitoring all over Hokkaido, Dr. Hidehiro Kato kindly sent me a book entitled "Study on Whale Stock Management" (Sakuramoto *et al.*, ed. 1991). This book, covering all aspects of whale resource management involving theory and practice, attracted me very much. The whale resource management research was ideal for researchers on large mammal population dynamics. Dr. Seiji Ohsumi reviewed the method and its system in Chapter 1 (Ohsumi, 1991), which was particularly useful for constructing the baseline of sika deer monitoring.

The whale survey consisted of five pillars: catch statistics, visual observations, tag-recovery surveys, biological surveys from whaling, and special catch surveys. The biological surveys were conducted for three purposes: genetic analysis for separation of lineages, estimation of biological parameters, and elucidation of cetaceans' ecosystems.

In references to the whale monitoring, I constructed sika deer monitoring using capture information (SPUE: Sighting per Unit Effort, CPUE: Catch per Unit Effort) per each 5 km×5 km grid, and visual observations (spotlight census, aircraft survey) over a wide area to grasp the rough population trend. To determine the management unit for sika deer, my research team and I conducted radio telemetry surveys and genetic surveys in Eastern Hokkaido. We also worked on age determination from the individuals captured by hunting and culling and analyzed the reproductive characteristics of female deer.

Seasonal migration, the genetic structure of populations

To determine management units for sika deer population, we examined seasonal migration and habitat use by installing dozens of VHS radio transmitters in the deer population in eastern Hokkaido (Uno and Kaji, 2000, Igota *et al.*, 2004). We also studied changes in the populations' genetic structure in recovering the distribution from near extinction (Nagata *et al.*, 1998) and expanding the distribution to the saturation period (Ou *et al.*, 2014). These findings were significant for considering the management unit for developing sika populations in Hokkaido.

Population dynamics: its processes and mechanisms

As model survey sites for closed habitats, I chose Nakanoshima Island in Lake Toya, where deer have been artificially introduced, and Cape Shiretoko, where deer colonized. I set up two places for an open environment: Onbetsu town and Ashoro town in Eastern Hokkaido. The population survey method depended on the region; drive count method on Nakanoshima Island, aerial survey at Cape Shiretoko, spotlight count at Onbetsu town, and cohort analysis by age determination of a total of 17,549 individuals captured in Ashoro town over 12 years. Then, we analyzed the process and pattern of population fluctuation and its mechanism.

These studies revealed that the natural increase rate of sika deer was around 20% without harvesting or predator, that explosive increases occur, even when they are introduced into the island or naturally colonizing, and even in settled populations with original habitat. Large-scale population crash repeatedly occurred in closed habitat (Nakanoshima Island and Cape Shiretoko) (Kaji, 2018). Thus, in the absence of predators and harvesting, the populations would not be in equilibrium with plants and substantially impacted the vegetation. These clearly showed that aggressive culling for female deer was necessary to reduce the overabundant sika deer population.

Feedback Management

From the hunting season in 1994, female deer hunting was allowed in Hokkaido for the first time in 72 years. However, there were many objections in fear that overharvesting in the Meiji era would lead to extinction. We recognized the increasing trends of the deer population in eastern Hokkaido. However, there was uncertainty in estimating population size, so it was impossible to determine how many deer we should harvest at that time.

We invited Dr. Hiroyuki Matsuda, an expert in mathematical ecology and fishery resource management, as a lecturer and held a resource management study session for sika deer to consider breakthrough measures. Dr. Matsuda proposed feedback management of sika deer (Matsuda *et al.*, 1999) following the Revised Management Procedure (RMP) for whaling (Tanaka, 1982). Feedback management incorporated into deer management in the eastern part of Hokkaido became the pioneer of science-based wildlife management in Japan. It influenced the establishment of the Specified Wildlife Conservation and Management Plan by amending the Wildlife Protection and Hunting Act in 1999. The Ministry of the Environment adopted a Feedback management approach in the deer management manual.

Towards adaptive management

Adaptive management is suitable for managing wildlife populations and natural resources that obtain insufficient and uncertain data and continuously improves management policies and practices through adaptive learning and feedback management (Walters, 1986). On the other hand, feedback management is a management policy for sustainable use at the optimum level based on uncertain information on natural resources (Tanaka, 1982), which is almost synonymous with adaptive management in a broad sense.

Adaptive management is considered the best way to solve the biological and policy dilemma of deer management in US national parks; however, there are limited cases in practice (Porter and Underwood, 1999). In France, adaptive management using indicators of ecological change is adopted for the management of small scale and well-defined population of roe deer (Morellet *et al.*, 2007). Therefore, the large-scale feedback management of sika deer in Hokkaido is a practical example of adaptive management of deer ahead of the world.

Conclusion

On October 25, 2001, I had the opportunity to report on the feedback management of sika deer in Hokkaido at the Institute of Cetacean Research seminar. Dr. Shoichi Tanaka, who advocated feedback management, and Dr. Ohsumi, the Institute of Cetacean Research director, attended the venue.

In the seminar, I explained that the deer management goal in Europe and the United States was maintaining maximum sustain yield (MSY) by managing the population around K/2 of the MSY curve. However, K/2 was too high to prevent damages to agriculture and forestry and ecosystem of cervid populations with weak density dependence like sika deer (Kaji *et al.*, 2010). Avoiding severe deer damages, maintaining the population considerably lower than the carrying capacity was required. The sika deer management goals of our program were: (1) to keep the population at moderate density levels preventing population irruption, (2) to reduce damage to crops and forests, and (3) to sustain a reasonable yield of hunting without endangering the population. We developed a threshold harvesting approach as feedback management involving three threshold levels of relative population size, four levels of hunting pressure, with a choice of four corresponding management actions by sex-specific hunting, based on the estimates of relative population size (Matsuda *et al.*, 1999).

I concluded that harvesting was the only operational experiment, essential for population abundance estimation and density dependency detection. Hunting was a large-scale ecological experiment since it was impossible to conduct repetitive experiments in nature and manipulate the natural environment. Drs. Ohsumi and Tanaka were pleased to listen to my presentation, which encouraged me to progress science-based wildlife management for sika deer.

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Others

Snouting of an old Bryde's whale, North Pacific.

Historical Records

AN ANALYSIS OF JAPANESE WHALE KILLING DATA WITH SPECIAL EMPHASIS ON THE USE OF THE ELECTRIC LANCE AS A SECONDARY KILLING METHOD[1)]

Lars WALLØE[2)]

Abstract

During the IWC Workshops on whale killing methods in 1992 and 1995 Japanese whalers were criticized for the use of the electric lance as a secondary killing method. It was claimed, especially by Australian scientists, that the use of the electric lance resulted in long survival times and much suffering. The times to death for 891 whales were analysed by logistic regression and Cox regression. For 560 of these a secondary killing method was used; the electric lance was used in 326 cases, and a cold harpoon in 234 cases. The median killing time for the electric lance was 40 s and for the cold harpoon 4.7 minutes. The analyses showed that the electric lance killed the whales much faster than the cold harpoon. At the time, Japanese laws did not allow the crew to keep firearms on board fishing or whaling vessels. These laws have been changed, and today the use of a shot from a rifle through the brain of the whale is the preferred secondary killing method.
(This abstract was prepared in August 2021 in accordance with request from the Publication Committee for the Cetacean Population Studies (CPOPS)).

Key words: electric lance, whale killing methods, minke whales, Kaplan-Meier plots, Cox regression.

Preamble

The present paper was prepared for the IWC Commission meeting in Aberdeen in 1996. The work was supported by the late Seiji Ohsumi, who was head of the Japanese delegation to the IWC Scientific Committee, and Mr. Kazuo Shima, the Japanese Commissioner to the IWC at the time. Although the main results were presented orally and discussed during the Commission meeting, and copies of the manuscript were distributed to the participants, the article was never properly published. Killing methods for whales were not considered part of the terms of reference for the IWC Scientific Committee, and the manuscript could therefore not be published in its series of scientific papers. On the occasion of publication of the memorial volume for the late Seiji Ohsumi, we have now tried to retrieve it.

[1)] The present scientific article was originally prepared for the IWC Commission meeting as document (IWC/48/WK 2—1996) in Aberdeen, Scotland, in 1996. The paper is reproduced here in accordance with the request from the CPOPS Publication Committee, to commemorate the days when Dr. Seiji Ohsumi was active at the IWC Scientific Committee.

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IWC/48/WK 2—1996

AN ANALYSIS OF RECENT JAPANESE WHALE KILLING DATA WITH SPECIAL EMPHASIS ON THE USE OF THE ELECTRIC LANCE AS A SECONDARY KILLING METHOD

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Introduction

Killing methods for minke whales have improved considerably during the past 15 years (IWC/47/18-1995). The IWC held its first workshop on the topic in 1980 ('Workshop on humane killing techniques for whales' —IWC/33/15). The workshop made a number of recommendations for future research and development, and also recommended a set of criteria which should be used to measure time to death in whales. These were the time "taken for the mouth to slacken, the flipper to slacken and all movement to cease." The workshop recognised that these criteria probably overestimated the time to death, since work on dolphins had shown that these animals, like other mammals, may have agonal reflex movements.

Workshops on whale killing methods in 1992 (IWC/44/REPHK) and 1995 (IWC/47/18) evaluated the progress made since 1980 and made new recommendations. Although a wide range of views was expressed at these workshops, the data presented seemed to indicate that the killing methods currently being used for minke whales by Japanese and Norwegian whalers compared favourably in efficiency with those used in the hunting of large terrestrial animals in Europe and North America (Lockyer –IWC/47/WK1; Øen and Walløe—IWC/47/WK9).

However, some of the participants at these two workshops, especially in 1995, strongly criticised the use of the 'electric lance' as a secondary killing method (e.g. Blackmore IWC/47/WK2). On the other hand, the Japanese Government presented a paper to the 1995 workshop which appeared to indicate that the electric lance killed whales very rapidly (IWC/47/WK 11). Unfortunately, the paper did not give much information except for the mean times to death for some subgroups.

During the workshop, I received the impression that the participants did not understand the content of the paper properly, and that its claim that the mean time to death was only 44 seconds when the lance was used was not believed. I therefore proposed to my Japanese colleagues that I should reanalyse the Japanese data on killing times, using statistical methods which I had previously used on similar data from Norwegian whaling operations (Øen and Walløe 1995). The present paper contains the main results of this analysis.

Materials and Methods

The primary data for the present analysis consist of the killing times and a number of covariates for all whales included in the Japanese scientific catches of minke whales in the Southern Ocean and in the North Pacific respectively during the last two hunting seasons.

In all 891 minke whales were taken: 330 in 1994–95 and 440 in 1995–96 in the Antarctic Ocean, and 21 in 1994 and 100 in 1995 in the North Pacific. All whales were taken by the same whaling vessel and by and large by the same crew of whalers. Only 6 different gunners operated the harpoon gun during these two years.

The killing time, i.e. the time from a strike by the penthrite grenade harpoon until the whale was declared dead according to the criteria established by the IWC (IWC/33/15 1980), was recorded using a stop-watch. If a whale died instantaneously or within a few minutes, no secondary killing method was used. But if the whale showed signs of life after the first hit, the crew prepared to use one of the two available secondary killing methods. The first of these was to shoot a second (cold) harpoon into the whale. This operation could be repeated. The second method available was to use electrical stunning.

The following is a short description of electrical stunning as carried out by Japanese minke whalers. The whale is pulled up to the catcher boat and two electrodes (‘electric lances’) are inserted through the blubber into the muscular tissue underneath, one in front of the heart and one behind. The whale is killed by sending alternating current between the electrodes. The mechanism responsible for the death of the animal is probably fibrillation of the heart, causing complete cessation of circulation. When the current is switched on, the animal body usually undergoes convulsive muscular contractions, and it is not possible to apply the IWC death criteria. The current is therefore switched off at regular intervals. The duration of each bout of current is reported to be about 10 seconds.

The electric lance was sometimes used in addition to a cold harpoon if the first (or second) cold harpoon failed to kill the animal.

In most cases the whalers chose the secondary killing method they considered most suitable in the circumstances. If, for instance, the whalers considered that the first harpoon was in danger of being pulled out, a second harpoon was used. On the other hand, if the whale was close to the boat, it was often not possible to shoot it with a second harpoon, but the electric lance could conveniently be applied.

In some cases either secondary killing method could be used with an equal chance of success as judged by the whalers. During the Antarctic whaling operations, the use of the cold harpoon or electric lance as the secondary killing method was randomised for 123 of these animals, 61 during the 1994–95 season and 62 during the 1995–96 season. This group of whales is designated the ‘experimental’ group.

In addition to the time to death the data file contained the following covariates for each whale: a letter identifying the gunner, the body weight, the body length, ‘experimental’ or not, (first) secondary method (none, harpoon, lance), number of cold harpoons, voltage and amperage of electric current, time to firing of (first) cold harpoon, time to use of lance, loss/recapture, and in addition a serial number which could be used to obtain additional information about individual whales if desired. All 891 records were complete.

The data were analysed by conventional statistical methods. Since many of the variables have empirical statistical distributions with long tails to large values (e.g. time to death), non-parametric tests and estimation methods were used. Most of the results are presented as survival plots. For some variables, survival analysis with censoring was used, and the survival distributions were estimated by product-limit (Kaplan-Meier) methods (BMDP1L). The influence of covariates on time to death was investigated by Cox regression (proportional hazard) and by a combination of logistic regression for whales killed instantaneously (<10 s) and Cox regression for whales surviving more than IOs (BMDP2L+BMDPLR). To investigate possible differences between gunners and seasons, a general mixed model analysis of variance including gunners as a random variable was used (BMDP3V).

Results

Fig. 1 presents the distribution of times to death for all 891 whales which are included in the analysis. Two whales which were first lost and later recaptured survived for 96 and 130 minutes respectively and are not represented on this graph (but are included in the statistics). 26% of the whales died instantaneously. The median survival time was 4.8 minutes, 9.5% of the whales lived for more than 10 minutes, and 3.1% for more than 15 minutes. Thirty five whales were lost and later recaptured using grenade or cold harpoons, 32 because the harpoon pulled out and 3 because the fore-runner broke. All whales with survival times longer than 20 minutes were from this group of 35 lost and recaptured whales.

Fig. 2 shows that there were only minor differences between the results obtained from dif-

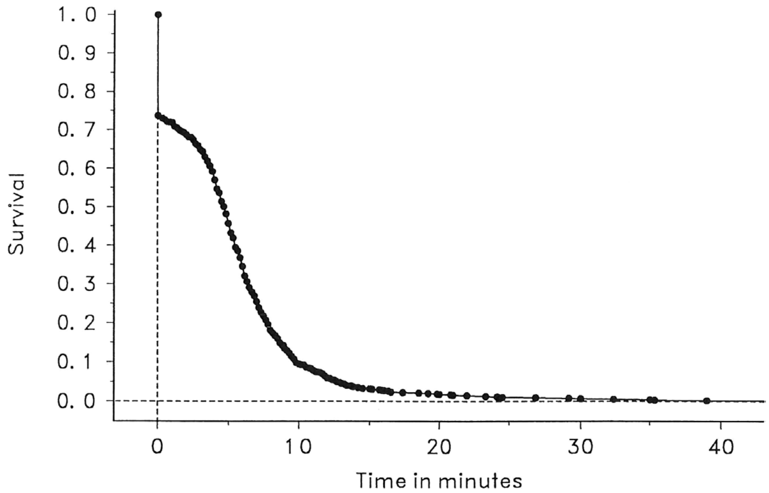

Fig. 1. Survival plot for all 891 minke whales caught during Japanese scientific whaling in the two-year period from April 1994 to April 1996. Abscissa: Time in minutes after the whale was hit by a grenade harpoon. Ordinate: Fraction of whales still showing signs of life. Each dot represents the time of death of one or more whales. Two whales which were lost and recaptured survived for 96 and 130 minutes, respectively and are excluded from the graph (but not from the statistical calculations). Median survival time: 4.8 minutes.95% confidence interval for the median: (4.5–5.0) minutes.

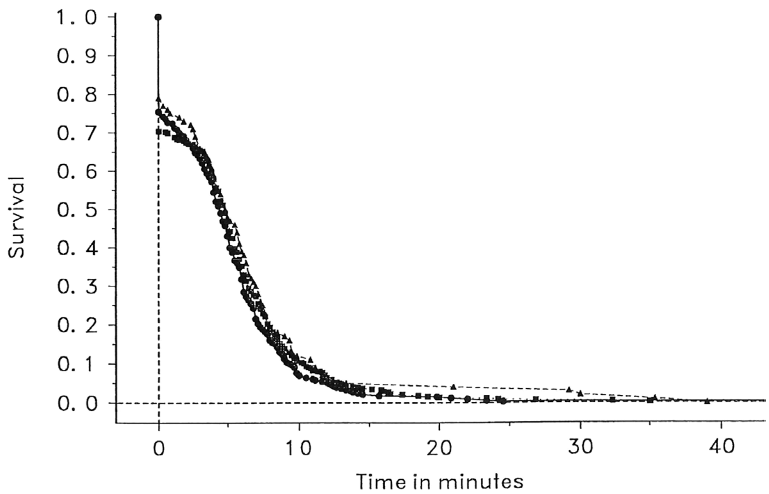

Fig. 2. Survival plots for whales caught in the North Pacific in 1995 (100—triangles), in the Antarctic Ocean in 1994–95 (330—circles), and in the Antarctic Ocean in 1995–96 (440—squares). Axes as in Fig. 1.

ferent oceans and years.

In addition to the 233 whales which died instantaneously, 98 whales died before a secondary killing method could be used. The survival plot for these 331 whales is shown in Fig. 3. The death rate for whales which were not killed instantaneously was 1.8% per minute when no secondary killing method was used.

For the remaining 560 whales (63%), a secondary killing method was used; the electric lance was used in 326 cases, and a cold harpoon in 234 cases. Only 111 of the 234 whales for which cold harpoons were chosen as the secondary killing method actually died as a result of being hit by this harpoon. The remaining 123 were finally killed by the electric lance. Thus, 449 whales in all were killed by the electric lance. In 326 cases the electric lance was used immediately after the grenade harpoon, and in 123 cases after one or more cold harpoons had failed to kill the animal.

Fig. 4 presents the distribution of total times to death for whales for which secondary killing methods were used, divided into two groups: 326 whales which were stunned with the elec-

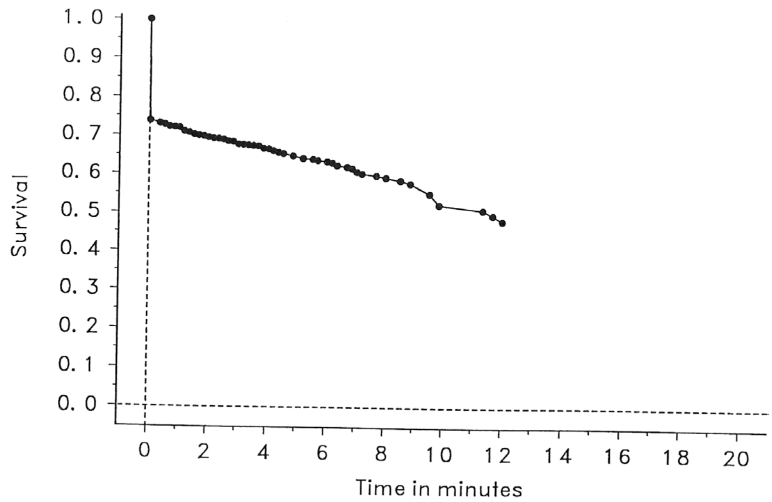

Fig. 3. Survival plot for the 331 whales which were killed by the grenade harpoon alone. Axes and symbols as in Fig. 1.

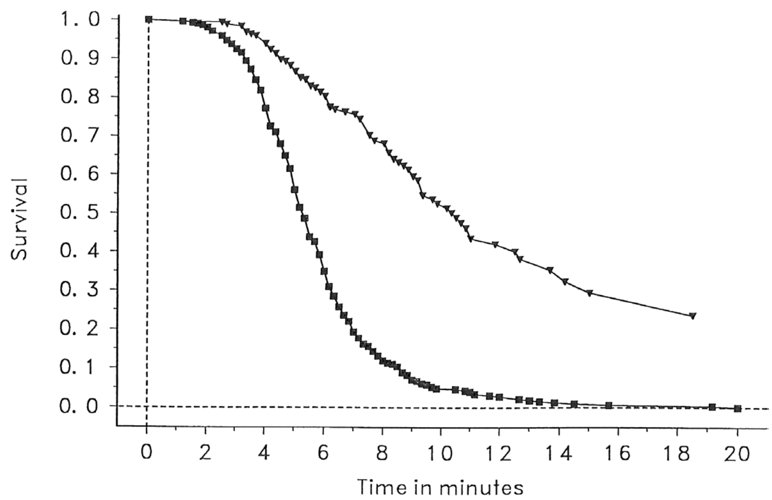

Fig. 4. Survival plots for whales for which the electric lance was used as the only secondary killing method (squares—n=326), and for whales which were shot with a cold harpoon (triangles, lost/recaptured excluded—n=199). The later were censored if and when the electric lance was used (53% censored). Median survival time for lanced whales: 5.3 (5.2–5.5) minutes, for whales that were cold harpooned 10.4 (9.3–12.5) minutes.

tric lance after being hit by a penthrite grenade, and 199 whales which were shot with a cold harpoon. Whales were censored from this plot if and when the electric lance was used after a cold harpoon. The 35 lost and recaptured whales have been excluded from this plot. If they had been included, the tail of the cold harpoon curve would have been lifted somewhat (so that survival at 15 minutes would have been 37.5% instead of 29.4% as in Fig. 4). Both curves in Fig. 4 display a plateau during the first few minutes due to the delay between the hit of the grenade harpoon and the use of the secondary killing method. The median delay was 5.8 minutes for harpooning and 4.3 minutes for lancing.

Fig. 5 presents a similar comparison between the two secondary killing methods, but only for the 123 whales which were randomised between the two methods. The median survival time for the harpooned whales was 8.4 minutes and for the lanced whales 6.1 minutes. The difference is statistically significant at the 1% level.

Fig. 6 shows the survival curve after application of the electric lance in the lanced group

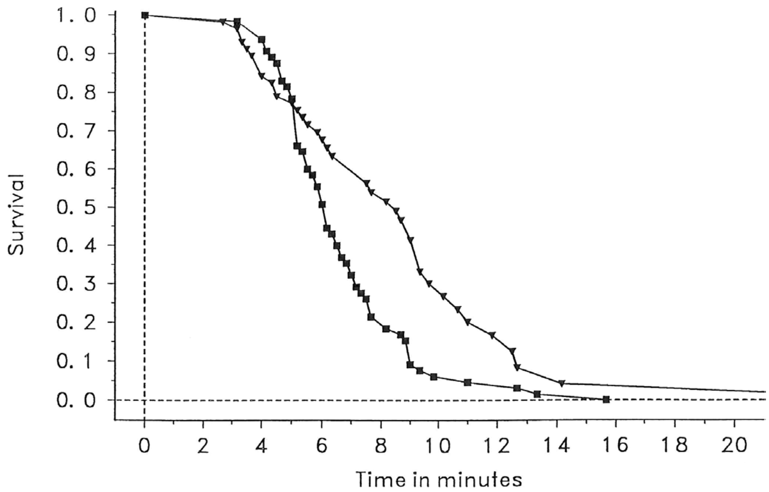

Fig. 5. Survival plots comparing the harpoon and lance as secondary killing methods as in Fig. 4, but only for the 123 whales which were randomised between the two methods. Median survival time for the harpooned group (n=58): 8.4 (7.5–9.3) minutes, for the lanced group (n=65): 6.1 (5.5–6.7). The difference between the two survival curves is statistically significant (p=0.002, Mantel-Cox test, two-sided).

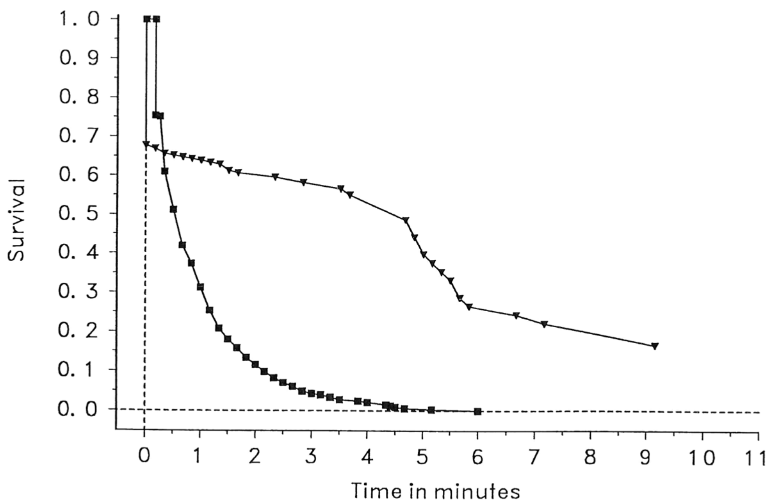

Fig. 6. Survival plots displaying the killing times for the two secondary killing methods. The abscissa is the time after the application of the secondary killing method. The median survival time for the lance was 0.7 (0.5–0.7) minutes (n=326). The median survival time for the cold harpoon was 4.7 (3.5–5.2) minutes (n=234). Harpoon whales were censored if and when the electric lance was applied (53 censored).

and the survival curve after being hit by the cold harpoon for the harpooned group. Harpooned whales were censored if and when the electric lance was used. The median killing time for the electric lance was 40 seconds. The cold harpoon killed 32% of the whales instantaneously, but even so the median killing time was 4.7 minutes. Removal of lost and recaptured whales from the harpooned group (35 whales) or addition of killing times in cases where the lance was used following one or more cold harpoons (123 whales) did not change the median survival times or their 95% confidence intervals, nor were there any noticeable changes in the survival plots.

Fig. 7 is identical to Fig. 6, except that only times to death for the 123 randomised whales are plotted. Results from the same 123 whales are also plotted in Fig. 8, the only difference being that harpooned whales which were later stunned by the lance have not been cen-

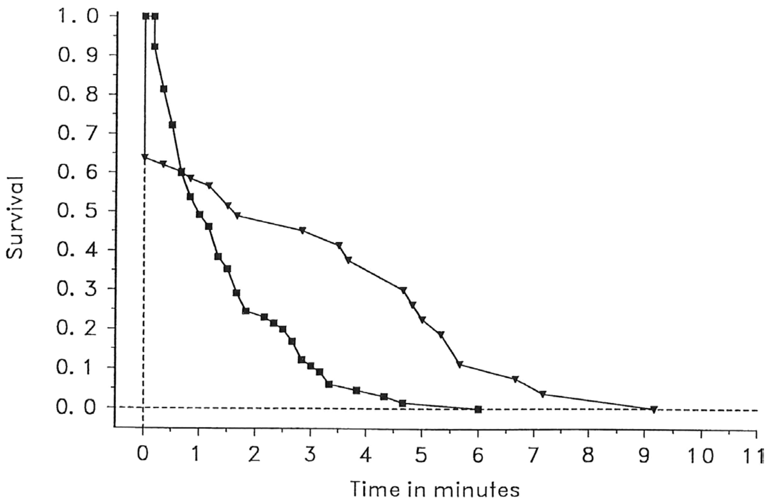

Fig. 7. Survival plots comparing the killing times for harpoon and lance as in Fig. 6, but only for the 123 whales which were randomised between the two methods. Harpooned whales were censored as in Fig. 6 (17 whales—29%). Median killing time for the cold harpoon was 1.6 (0.3–4.7) minutes (n=58), and for the electric lance 1.0 (0.7–1.5) minutes. The difference between the two survival curves is statistically significant (p=0.01, Mantel-Cox test, two-sided).

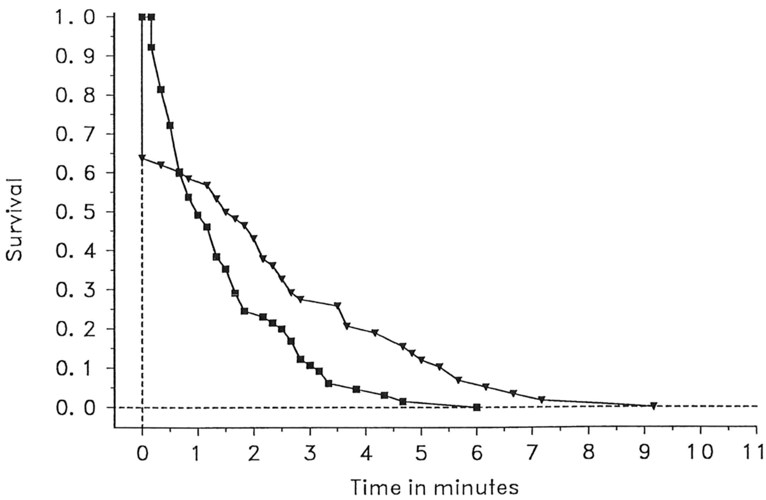

Fig. 8. Survival plots comparing harpoon and lance as in Fig. 7, but without censoring. Some of the whales in the harpooned group were therefore in reality killed by the electric lance after the cold harpoon had been used. Median killing time for the cold harpoon was 1.5 (0.3–2.3) minutes (n=58), and for the lance 1.0 (0.7–1.5) minutes (as in Fig. 7). The difference between the two survival curves is statistically significant (p=0.02, Mantel-Cox test, two-sided).

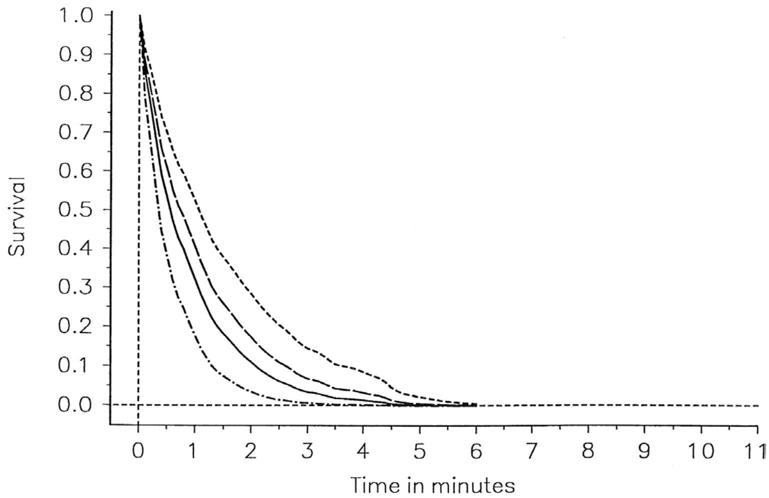

Fig. 9. Estimated survival curves after the onset of electrical stunning based on Cox regression for selected values of three covariates (whale length, voltage and amperage).
Solid line: 5 m, 110 V, 5 A.
Long dash: 5 m, 110 V, 10 A.
Dot—dash: 5 m, 220 V, 5 A.
Short dash: 10 m, 110 V, 5 A.

sored, but contribute the actual times of death to the statistics. This comparison corresponds to what is known as 'intention to treat' in medical applications of statistics. The differences displayed in both figures are statistically significant at the 1% level.

Whale length was the only covariate which influenced both the time to death from a hit by a grenade harpoon and the time to death from either a hit by a cold harpoon or from the onset of electrical stunning. The strength of this influence was similar in all subgroups and for both secondary killing methods, and is illustrated in Fig. 9. This figure also reveals the effect of voltage and amperage on the time to death from the onset of stunning. None of the other covariates recorded had any influence on the time to death, or on the fraction of whales which were killed instantaneously by a grenade harpoon. Nor were there any significant differences in killing efficiency between the six gunners.

Discussion

About one quarter of the whales taken in Japanese scientific whaling operations during the last two years died instantaneously from a hit by a grenade harpoon. Most of the remaining whales died within 15 minutes, either from injuries caused by the grenade or after the use of one of the two secondary killing methods available to the whalers, i.e. to shoot a cold harpoon into the whale or to use the electric lance.

The percentage of whales killed instantaneously is certainly an underestimate. There is general agreement that the death criteria for whales agreed in 1980 (IWC/33/15) are too strict (IWC/47/18), since there is no reason to believe that minke whales do not show agonal movements caused by spinal reflexes, seizures and convulsions similar to those in other mammals. Thus, some whales may very well have been dead or at least unconscious before a secondary killing method was used.

The similarity between the results obtained in different seasons and regions (Fig. 2) shows that the efficiency of Japanese killing methods is not much affected by differences in hunting conditions and environment.

Fig. 3 suggests that the death rate for whales which survived the first hit would have been very low if no secondary killing method had been employed.

Fig. 4 clearly shows that given the way the secondary killing used by the whalers, the lance kills whales much faster than the cold harpoon. However, the difference between the two curves may be caused entirely or partly by selection bias. In Fig. 5 the difference is smaller, but it is still present and statistically significant. In this 'experimental' group of whales the animals were randomised between the two secondary killing methods. We may therefore safely conclude that the lance kills the whales faster than the cold harpoon.

The lance curve in Fig. 5 ('experimental' group) is very similar to the lance curve in Fig. 4, but delayed by about one minute. This may be because whales which were too close to the boat could not be shot with a cold harpoon and were therefore excluded from the experimental (randomised) group.

A clear difference between the two methods is also revealed in Figs. 6, 7 and 8, which show plots of survival against the time from firing the cold harpoon or switching on the current. Again, the plots show that the electric lance kills the whales faster than the cold harpoon.

The most interesting result presented in these figures, however, is how fast the electric lance kills whales. The median time to death is about 40 s, and only some 5% of the animals survive more than 3 minutes (n=326, but n=449 gives the same result). The Japanese Government reported a mean time to death of 44 s based on 92 of these whales (IWC/47/WK11), which is in full agreement with the results from the present analysis.

The effect of covariates on the time to death from the onset of electrical stunning is illustrated in Fig. 9. The figure shows that the expected median killing time for a 10 m minke whale is about twice that for a 5 m whale, if the values of the other covariates are the same. This dependence on the size of the whale is not unexpected.

The electric lance operates as a constant voltage system, which means that the amperage is mainly determined by the resistance between the two electrodes. Fig. 9 shows that the killing time decreases as the voltage increases. The effect of amperage is perhaps more unexpected, as the killing time increases with increasing current between the electrodes. A possible explanation is that a high amperage is a result of current shunts between the electrodes in the seawater on the outside of the whale (or in seawater in the thorax and abdomen), which cause less current to flow through the tissues.

In last year's Workshop on Whale Killing Methods, Blackmore claimed that the electric lance could not "cause cardiac fibrillation except in a small minority of cases" (IWC/47/WK 2 and IWC/47/18), and recently New Zealand and the United Kingdom have repeated this claim in a note to IWC commissioners (1996) and in a summary (IWC/48/WK 1) of a paper in press (Blackmore et al. 1996), which refers to another paper in press by the same group of authors (Barnes et al. 1996). Although Blackmore's electrical measurements on carcasses and theoretical calculations may be of interest in some contexts, they are not relevant to an analysis of the effectiveness of the electric lance. The empirical evidence that the lance kills quickly is overwhelming.

Acknowledgements

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REMEMBERING DR. SEIJI OHSUMI: A DREAM FOR ESTABLISHING A RESEARCH CENTER OF MARINE MAMMALS IN THE INDIAN OCEAN

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Dr. Hiran Wasantha Jayewardene, adviser to the Minister of Strategic Planning and Development in the Democratic Socialist Republic of Sri Lanka invited me and Dr. Seiji Ohsumi to the International Workshop of Marine Mammals to be held at Colombo in Sri Lanka during 5–9 April 2003. He, the nephew of Mr. Junius Richard Jayewardene who was the second President of Sri Lanka, had a chal-

Fig. 1. International Workshop of Marine Mammals held in Colombo, Sri Lanka during 5–9 April 2003.

Fig. 2. Group photo taken with staff of the Sri Lanka National Aquatic Resources Research and Development Agency (NARA).

Fig. 3. Photo taken with Mr. Tyronne Fernando, Minister Foreign Affairs of Sri Lanka: Author, Minister of Foreign Affairs of Sri Lanka, Dr. Ohsumi, and Dr. Jayewardene (left to right).

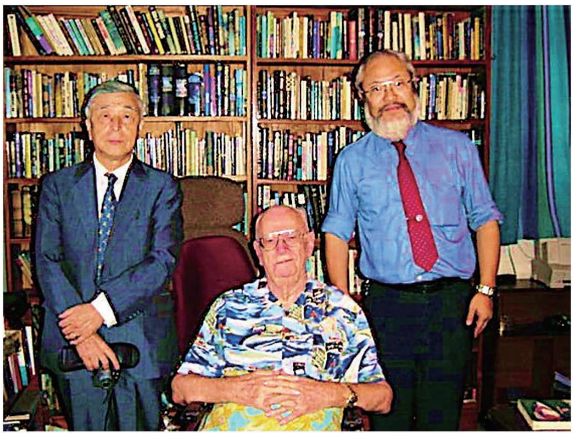

Fig. 4. Photo taken with Sir Arthur Charles Clarke: Dr. Ohsumi, Sir Clarke, and Author (left to right).

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lenging idea to improve the economy through ecotourism such as whale watching and to establish peace and stability at Trincomalee in the northeastern Sri Lanka, where a lot of refugees had illegally moved from neighboring India.

Sri Lanka is located in one of the most valuable and important areas for geopolitical and scientific study in the Indian Ocean. Thus the establishment of a "Research Center of Marine Mammals in the Indian Ocean" would be very useful for mutual collaboration in marine science between Japan and Sri Lanka. In the workshop, we exchanged significant scientific information on the behavior of marine mammals and their environmental condition and discussed a cooperative research plan and education system for young scientists between Japan and Sri Lanka (Fig. 1).

Since the Conference on the Treaty of Peace with Japan was held in San Francisco on 4 September 1951, Japan has had a close relationship with the Democratic Socialist Republic of Sri Lanka (then known as Ceylon). In spite of attack by the Japanese navy to Colombo and Trincomalee in 1942, Mr. Junius Richard Jayewardene, who participated in the conference as a representative of Ceylon, made a historically impressive speech including the following words: "Hatred ceases not by hatred but by love" and "Sri Lanka didn't receive any war reparation from Japan", and did not officially request to Japan for the World War II Reparations. Up to this day, the Japanese government has been continuing strong support Sri Lanka through the program of Official Development Assistance (ODA).

After the workshop on marine mammals, Dr. Hiran W. Jayewardene took us on a trip to Trincomalee, where many species of marine mammals such as sperm whales and blue whales often came close to the coast of this area and the people enjoyed whale watching from the cliff on a hill. In addition, as this place is close to the naval station of Sri Lanka, this area is considered to be the best location for improving marine science including whales' observation and their environmental study in the Indian Ocean. This area is also a memorial place for us, where the late Professor Masaharu Nishiwaki, Director of the Ocean Research Institute of the University of Tokyo, attended the International Conference of *Dugong dugon* in 1972. On the way back to Colombo, we visited the National Aquatic Resources Research and Development Agency (NARA), where a lot of skull and skeleton samples of the stranded marine mammals were preserved and discussed future research of marine science there (Fig. 2).

In order to encourage research activity of marine science with mutual collaboration between Japan and Sri Lanka, Dr. Ohsumi, Dr. Jayewardene and I officially met Mr. Tyonne Fernando, the Minister of Foreign Affairs at the time (Fig. 3). Through fruitful discussion with him, we obtained a good feeling for the future research plan on marine mammals with mutual collaboration of both countries. As the support program of ODA was one of the most useful ways for establishing our plan, Mr. Seiichiro Otsuka, Ambassador of Japan, advised us to submit our research plan to the Japanese government through the government of Sri Lanka. However, in 2005 the government of Sri Lanka started to fiercely fight again against the anti-government group of Tamil (LTTE), thus our plan had to be stopped unfortunately. Now, as the Democratic Socialist Republic of Sri Lanka becomes a peaceful and politically stable country, it is just time for establishing the cooperative research plan on marine mammals between Japan and Sri Lanka.

Finally, we met the late Sir Arthur Charles Clarke, a famous writer of science fiction and fantasy, and talked about our dream (Fig. 4). He had great interest in the "Biologging Science", through which we can obtain wonderful knowledge of marine mammals and their environmental condition without killing animals. He strongly recommended that we should improve the new science and supply the fantastic knowledge to the public people in not only both countries but also all over the world. Now, it is just time to realize our dream of establishing a "Research Center of Marine Mammals in the Indian Ocean" under the brilliant spirit of the late Dr. Seiji Ohsumi.

Press hands in prayer.

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