Chapter

Whales as Indicators of Historical and Current Changes in the Marine Ecosystem of the Indo-Pacific Sector of the Antarctic

Yoshihiro Fujise and Luis A. Pastene

Abstract

We review the scientific information on whales that could be indicative of historical and current changes in the ecosystem in the Indo-Pacific sector of the Antarctic. The increased krill availability in the middle of the past century as a result of the heavy harvesting of the larger baleen whale species could have been translated into better nutritional conditions for the Antarctic minke whale, resulting in a decreasing trend in the age at sexual maturity and an increasing trend in recruitment rate and hence total population size between approximately 1940 and 1970. This nutritional condition has deteriorated more recently, as revealed by a decrease in energy storage and stomach content weight since the 1980's; these changes coincide with appreciable increases in the abundances of humpback and fin whales, which were heavily harvested in the first half of the past century. The historical demographic changes observed in the Antarctic minke whale are consistent with the pattern to be expected under the krill surplus hypothesis, with minke whales now again competing with other (recovering) baleen whale species for krill. However, these minke whales could also be using alternative feeding areas (e.g. polynias within the pack-ice) in response to the increase in abundance and geographical expansion of these other large whale species. This could provide an alternative explanation for indications from sighting surveys and population models of a decrease and then re-stabilisation of minke whale abundance in open water areas since the 1970s.

Keywords: East Antarctic, Antarctic minke whale, blue whale, fin whale, humpback whale, whaling, krill surplus hypothesis, abundance, biological parameters, nutritional condition

1. Introduction

The Antarctic ecosystem is very dynamic with changes in species composition and habitat occurring through time. Within this ecosystem, Antarctic krill

(*Euphausia superba*) is a key prey species, supporting different species of baleen whales, pinnipeds, birds and fish. Changes in the ecosystem can result from human interventions or from natural causes. One example of human intervention is the large-scale harvesting of whales in the first half of the 20th Century, which has been discussed by several authors [1, 2]. This harvesting started in the Antarctic Ocean in 1904. Several species of krill-eating large whales, such as the Antarctic blue (*Balaenoptera musculus intermedia*) and humpback (*Megaptera novaeangliae*) whales were heavily reduced in number by commercial whaling during the first half of the past century. Other species such as the fin whales (*B. physalus*) were reduced during the second half. Over more recent decades, the populations of some large whales have started to recover [3]. Changes in the biomass of whale species also seem to have had strong effects on the demography of other krill-eating predators in the Antarctic ecosystem [1, 2].

An example of the effects of natural causes is the increases in the chinstrap penguins (*Pygoscelis antarctica*) populations of the Scotia and Weddell Seas over the last four decades (1950's-1990's), which has been attributed to a gradual decrease in the frequency of cold years with extensive winter sea ice cover resulting from environmental warming [4]. However, more recent analyses in the Antarctic Peninsula and Scotia Sea conclude that the chinstrap penguin instead may be among the most vulnerable species affected by a warming climate [3].

In studying the changes in the Antarctic ecosystem, there needs to be differentiation between West and East Antarctic, as well between land-based and sea-based krill predators. The West Antarctic Peninsula represents one of the regions of the planet where the fastest warming has been observed in the last 50 years [5]. For this reason the studies documenting ecosystem changes in the West Antarctic have considered environmental variables in addition to demographic information on land-based krill predators (mainly penguin species) [3, 4], on which environmental factors could have a larger impact. Warming has not been reported for the East Antarctic, so that environmental factors would not be expected to play the predominant role in the ecosystem changes in this part of the Antarctic.

Here historical and current ecosystem changes in the Indo-Pacific sector of the Antarctic (involving mostly East Antarctic) are documented through the examination of biological and demographic parameters of sea-based predators (whales). These changes in parameter values are interpreted in the context of some established hypotheses.

2. Characterization of the research area

The present study is focused on the Indo-Pacific sector of the Antarctic, in the longitudinal range 35°E-145°W (**Figure 1**), south of 60°S, which is the approximate position of the Antarctic Convergence (AC). This longitudinal range includes International Whaling Commission (IWC) management Areas III (east part), IV, V and VI (west part) (**Figure 1**).

Prydz Bay is located at the west boundary of the research area while the Ross Sea is located at its east boundary. The research area is strongly influenced by the southern boundary of the Antarctic Circumpolar Current (SBACC), which interacts with the coastal East Wind Drift (EWD) in a series of fronts and eddies (**Figure 1**). A series of gyres link the EWD and the SBACC, e.g. the Prydz Bay and the Ross Sea gyres. Krill concentrations appear to track gyral systems off the East Antarctic, for example in the sectors between 30°-90°E or 80°-115°E [6].

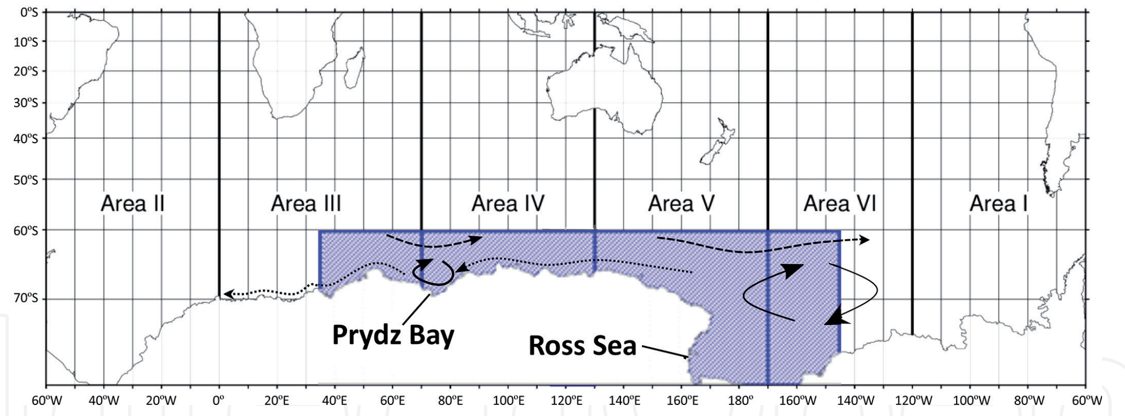

Figure 1.
Schematic representation of the research area (dashed in blue). The figure shows the Southern Hemisphere Areas that the International Whaling Commission (IWC) uses for the management and conservation of baleen whales (except the Bryde's whale, B. edeni). The research area is influenced by the southern boundary of the Antarctic Circumpolar Current (SBACC) (dashed arrow), which interacts with the coastal East Wind Drift (EWD) (dotted arrow) in a series of fronts and eddies.

3. Krill-eating baleen whale species in the Indo-Pacific sector of the Antarctic

Baleen whale species, except the Bryde's whale, migrate seasonally between low latitude breeding areas in winter to high latitude feeding areas in the Antarctic in summer. The main prey species of baleen whales such as Antarctic blue, fin, humpback and Antarctic minke (*B. bonaerensis*) whales (**Figure 2**) is the Antarctic krill. Therefore the summer migrations of these whales to the Antarctic are related to areas of krill concentrations, which in turn are associated with gyral systems.

3.1 Antarctic blue whale

This is the largest baleen whale species. The record for a whale killed in the Southern Hemisphere in the first half of the past century was a body length of more than 30 m and weigh of nearly 180 tons. During the austral summer Antarctic blue whales are distributed between the AC and the ice edge. There is limited information on the population structure of this species.

3.2 Fin whale

This is the second largest baleen whale species, with a maximum length of more than 27 m and weight of nearly 120 tons. During the austral summer, fin whales are found extensively south of 50°S, but most commonly north of 60°S. There is limited information on the population structure of this species.

3.3 Humpback whale

This species presents a maximum body length of 17 m and weight of 40 tons. During the austral summer humpback whales are distributed from south of the AC to the ice edge, but just to the north of the main distribution area for Antarctic minke whale. The IWC has identified seven populations of humpback whales in the Southern Hemisphere, which are denominated with alphabetic letters from 'A' to 'G' [7]. The populations occurring in the Indo-Pacific sector of the Antarctic are Populations 'C' (mainly in Area III), 'D' (mainly in Area IV), 'E' (mainly in Area V), and 'F'

Figure 2.
Krill-eating baleen whale species in the Indo-Pacific sector of the Antarctic. Top left: humpback whale; top right: Antarctic minke whale; bottom left: fin whale; bottom right: Antarctic blue whale.

(mainly in Area VI) (**Figure 1**). There are some spatial overlaps between adjacent populations in the Antarctic [8]. The breeding areas for Populations 'D' and 'E' are located in West and East Australia, respectively.

3.4 Antarctic minke whale

This is one of the smallest baleen whale species with a maximum body length of more than 10 m and weight of nearly 10 tons. During the austral summer, Antarctic minke whales are distributed mainly around the pack-ice. There are at least two populations of this species in the Indo-Pacific sector of the Antarctic, the Eastern Indian Ocean population in the western part of the research area (mainly the eastern part of Area III and Area IV) (**Figure 1**), and the Western South Pacific population in the eastern part of the research area (mainly the eastern part of Area V and Area VI) (**Figure 1**) [9, 10]. Both populations interact in a transition area between approximately 100° and 160°E (eastern part of Area IV and western part of Area V) (**Figure 1**) [11].

The biological and demographic studies summarized below are based on the approximate geographic limits of these 'populations' in the case of humpback and Antarctic minke whales, and on geographical areas for those species with limited information on population structure (Antarctic blue and fin whales).

4. Whale and environmental surveys in the Indo-Pacific sector

As explained briefly above, the causes of ecosystem changes in the Antarctic are complex. To determine those causes, long-term monitoring research programs focused on collecting biological data of krill predators, as well data on sea ice cover and environmental variables, are important. The kind of information which is used to monitor changes in the ecosystem through sea-based predators (whales) and their environment is shown in **Table 1**.

Most of the data in **Table 1**, which have been used in the studies summarized below, come from two main sources.

Parameter	How the information is obtained?	Relevance of monitoring
Krill biomass	Echo-sounder and net surveys	Krill is a key species in the Antarctic ecosystem. Changes in its abundance have effects on predators and the whole ecosystem
Whale abundance	Systematic sighting surveys	Fluctuations in the abundance of whales over time is important for their management. Different levels of whale abundance have different impacts on krill
Whale distribution	Systematic sighting surveys	Distributions of whale species can change with time in response to changes in abundance and/or changes in oceanographic conditions/krill abundance
Whale recruitment	Population dynamic models that use age and abundance information for whales	Same as above. Index of young whale abundance
Blubber thickness, fat weight and girth	Direct measurements from sampled whales	Index of body condition. Better nutritional condition (e.g. better availability through higher abundance of krill) will be reflected in thicker blubber, heavier fat and larger girth
Stomach content weight	Direct measurements from sampled whales	Index of body condition. Better nutritional condition will be reflected by heavier stomach contents
Age at sexual maturity (ASM)	Examination of the transition phase in earplugs; examination of ovaries and testis	Better nutritional conditions will be reflected in a shift of the ASM to younger ages, so that whales will be able to reproduce at younger ages
Pregnancy rate	Examination of ovaries and uterus	Better nutritional conditions will be reflected in higher pregnancy rates
Oceanographic conditions	Systematic oceanographic surveys based on CTD and XCTD	Changes in oceanographic conditions will affect the distribution and krill biomass, and in turn the abundance and distribution of whales. Changes in oceanographic conditions might be an effect of climate change

Table 1.
Biological and ecological parameters monitored for whales and their environment to investigate changes in the ecosystem.

4.1 JARPA and JARPAII programs

The Japanese Whale Research Program under Special Permit in the Antarctic (JARPA) was conducted in the austral summers from 1987/88 to 2004/05, and its second phase (JARPAII) from 2005/06 to 2013/14. Both programs conducted systematic surveys in the Indo-Pacific sector (35°E-145°W) of the Antarctic using both lethal (biological sampling of a limited number of Antarctic minke whales) and non-lethal (biopsy sampling and photo-identification of large whales, oceanographic and marine debris surveys, dedicated sighting surveys) approaches. The main objectives of these programs were related to the investigation of stock structure, biological parameters and feeding ecology of Antarctic minke whales, as well the investigation of environmental pollutants in whale tissue and the environment. These surveys were conducted in the open sea because the survey vessels were not ice strengthened. Data and research outputs from JARPA and JARPAII were reviewed by IWC-organized international workshop of specialists, and they are available in conjunction with the reports of those workshops [9, 12].

4.2 IWC's IDCR/SOWER programs

The IWC's International Decade for Cetacean Research (IDCR) undertook a series of Antarctic sighting cruises for assessment of Antarctic minke whales during the austral summers 1978/79–1995/96. From 1995/96 this was renamed the Southern Ocean Whale and Ecosystem Research (SOWER) program, and continued until the 2009/10 season. The primary aim of these programs was to conduct sighting surveys using the line transect method for estimating the abundance of Antarctic minke whales and other cetacean species. The survey programs have also enabled collection of biopsies, photo-identification, oceanographic and acoustic samples for studies on the ecosystem. As for JARPA and JARPAII, these surveys were conducted in the open sea because the survey vessels were not ice strengthened. Even though IDCR/SOWER surveys were conducted at a circumpolar level, it is the information from the surveys conducted in the Indo-Pacific sector, particularly in IWC Areas IV and V (see **Figure 1**), that is summarized here.

Some of the studies summarized below used biological data collected during former commercial whaling operations (by Japan and the former USSR) in the Indo-Pacific sector of the Antarctic.

5. Historical ecosystem changes revealed through whale demography

5.1 Trend in age at sexual maturity

Changes in the age at sexual maturity (ASM) indicate changes in the nutritional conditions for the whales, which in turn could indicate less or more food availability in the environment. Better nutritional conditions will be reflected by a shift of the ASM to younger ages, so that whales will be able to reproduce at younger ages and as a consequence the populations will grow faster. One of the methods for determining ASM in whales is through the examination of the 'transition phase' in the earplugs [13]. The earplugs of several baleen whale stocks exhibit seasonal growth layers which have been shown for some species to indicate the age of the animals. A transition from early, irregular layers to later, more regular layers can be seen in these earplugs (the 'transition phase'), and this has been shown to indicate the age at sexual maturity of the whale [13]. Historical changes in the ASM can be investigated through the analyses of cohorts (groups of whales born in the same year).

Earplugs of Antarctic minke whales were collected during the period of commercial whaling in the early 1970's, and during the JARPA/JARPAII surveys in the Indo-Pacific sector of the Antarctic for more than 25 years. A decline in the average age at transition in Antarctic minke whales in the Eastern Indian Ocean population from roughly 11 years for the cohorts of the 1950's to roughly 7 years for the cohorts of the 1970's was evident (**Figure 3**), and this trend was similar for females and males. The ASM remained stable until the 1980's cohorts [14]. This work was subsequently updated [15] by using a large number of samples, and those authors confirmed that the ASM remained stable until the 1998 cohort at least. The same pattern was observed for the Western South Pacific population.

5.2 Trend in recruitment rate and total population size

The Scientific Committee (SC) of the IWC has been applying statistical catch-at-age (SCAA) analyses to Antarctic minke whales since 2005. SCAA is a common method of fisheries stock assessment where age-structured catch data from a

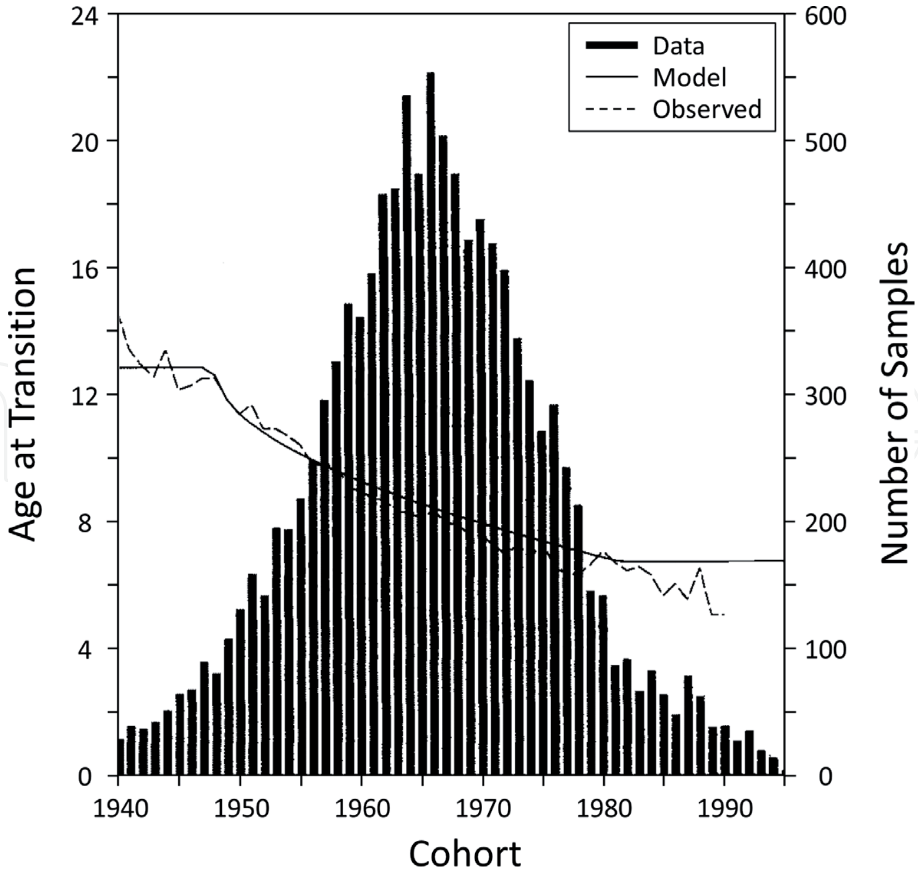

Figure 3.
Changes in the age at sexual maturity of Antarctic minke whale as determined from the transition phase, by cohort (Eastern Indian Ocean population). Histogram of the number of whales aged in each cohort is also showed. Age at sexual maturity changed from around 11 years in the 1950s cohorts to around 7 years in the 1970s cohorts (modified from [14]).

fishery are used to estimate quantities of interest, such as population size and natural mortality rates, employing the maximum likelihood estimation approach [16]. A summary history of the application of SCAA to Antarctic minke whale is provided in [17], and an assessment of this species using SCAA is reported in [18].

The data used when conducting assessment by SCAA on Antarctic minke whales consisted of catches, abundance estimates, length frequency data, and conditional age-at-length data. Different series of abundance estimates were used, i.e. those from the IWC's IDCR/SOWER and JARPA/JARPAII's dedicated sighting surveys in the Indo-Pacific sector of the Antarctic. The biological data mentioned above were available from the period of commercial whaling (Japan and the former USSR), and JARPA/JARPAII surveys in the Indo-Pacific sector of the Antarctic for more than 25 years.

The SCAA assessment on Antarctic minke whale included a 'reference' case and several sensitivity tests. These tests explored sensitivity to the weight assigned to the various data sources and penalties in the model fitting process, to assumptions related to vulnerability, natural mortality and catchability, and to the use or otherwise of the JARPA/JARPAII's abundance index data [18]. As in the estimation of the ASM, historical changes in recruitment and total population size can be investigated through the analyses of cohorts.

Figure 4 shows the temporal trend for the total size of the Eastern Indian Ocean population of Antarctic minke whales. Results presented here refer to the 'reference' case, and were robust to the sensitivity tests conducted. The population was estimated to have increased from 1930 until the early 1970's, with the population having declined subsequently and then staying stable. The increase in abundance

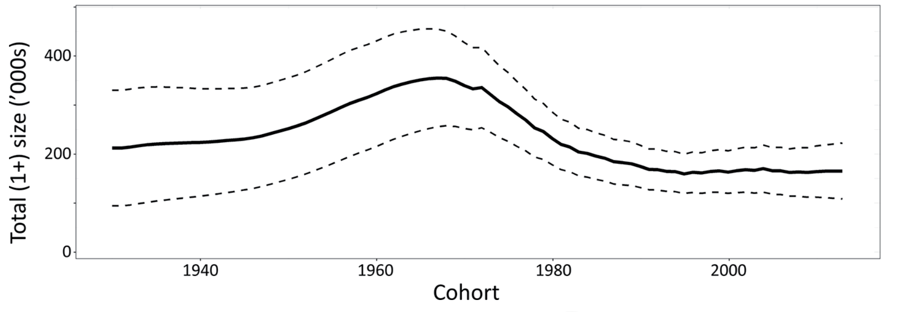

Figure 4.
Time trajectory of total (1+) population size for the Eastern Indian Ocean population of Antarctic minke whale (reference-case), by cohort. The dotted lines indicate 95% asymptotic confidence intervals (modified from [18]).

was due primarily to an increase in recruitment (**Figure 5**), arising in turn from an increase in carrying capacity [18], presumably due to an increase in the abundance of krill. A similar pattern was found for the Western South Pacific population.

It is interesting to note that the increase in total population size from 1930 to the 1970's coincided roughly with the period over which the ASM decreased.

5.3 Interpretation of results

The results of this section can be summarized as following:

- The average ASM of Antarctic minke whales declined from roughly 11 years for the cohorts of the 1950's to roughly 7 years for the cohorts of the 1970's; this trend was similar for females and males, and for the two populations occurring in the Indo-Pacific sector.

- The population of Antarctic minke whale increased from 1930 until the early 1970's, but declined subsequently and then re-stabilised. A similar pattern is evident for the two populations occurring in the Indo-Pacific sector.

- The increase in abundance was due primarily to higher recruitments resulting from an increase in carrying capacity with more food being available for these Antarctic minke whales during the middle decades of the last century.

These historical changes in the demography of Antarctic minke whale are consistent with expectations under the krill surplus hypothesis. The harvesting of large whales in the Antarctic Ocean started in 1904, and several species of large whales such as the Antarctic blue and humpback whales were heavily depleted by

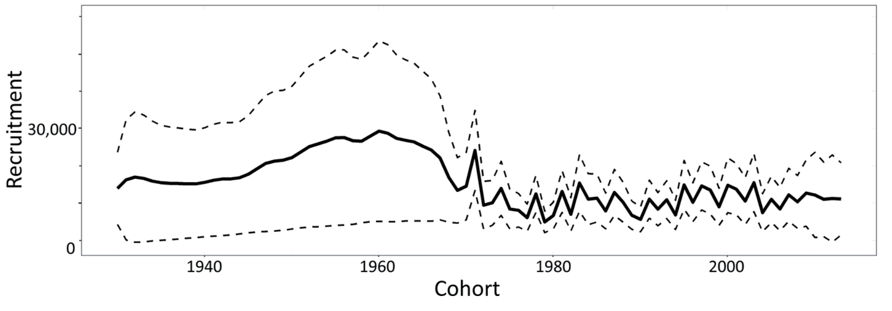

Figure 5.
Time trajectory of recruitment for the Antarctic minke whale of the Eastern Indian Ocean population (from 1930 and from 1975) for the reference case analysis, by cohort (modified from [18]).

the first half of the past century. Other species such as the fin whales were depleted during the second half of that century. Antarctic blue, fin and humpback whales were reduced to 5%, 21% and 2% of their original total sizes of 220,000, 490,000 and 130,000, respectively [19]. However, commercial harvesting of the Antarctic minke whales started only in the early 1970's, when the other baleen whale species were already depleted.

Some researchers have suggested that following the period of heavy harvesting of the large baleen whales in the Antarctic mainly during the middle decades of the past century, some 150 million tons of 'surplus' annual production of Antarctic krill became available for other krill predators, such as Antarctic minke whales, crabeater seals, fur seals, penguins and some albatrosses. These species then took advantage of this food surplus to increase their abundance. This is the so-called krill surplus hypothesis [1, 2].

The increased krill abundance around the middle of the past century could therefore have led to better nutritional conditions for some krill predators like the Antarctic minke whale. Although there is no direct observational evidence of improved nutritional conditions at that time, it is known that better nutritional conditions in whales may be reflected in a decrease in the age at sexual maturity. This was the case for Antarctic minke whales between approximately 1940 and 1970, which coincides with the period of depletion of some key krill-eating large whale species. This low age at sexual maturity led to an increase in the recruitment rate and total population size for minke whales over this period. The Antarctic minke whale perhaps rose to close to an increased carrying capacity resulting from a larger krill population by the 1970s, with the stock achieving this by stabilizing its age at sexual maturity at lower 7–8 years. The period of these demographic changes in Antarctic minke whales coincides with that characterized as 'favorable climate conditions and reduced competition for krill' and linked to penguin population changes [3].

6. Current ecosystem changes revealed through whale demography

Commercial whaling of humpback, Antarctic blue and fin whales in the Antarctic was suspended in 1963, 1964 and 1976, respectively. As an effect of these conservation measures, the abundance of these species have increased in recent decades, i.e. there have been recoveries from past commercial harvesting. The speed of recovery varies among species and populations. The increases in abundance of the recovering species will have effects on the ecosystem as a whole. In this section the current information on abundance and abundance trends of baleen whale species is examined, as well as some aspects of current nutritional conditions, feeding ecology and biological parameters of the Antarctic minke whale, a species which benefited from the krill surplus during the last century.

6.1 Abundance trend of baleen whales

Estimates of abundance of large whales in the Antarctic are based on systematic sighting surveys in open sea carried out under sampling methods advocated in DISTANCE [20], and the guidelines for surveys and analyses agreed by the IWC Scientific Committee (SC) [21]. Dedicated sighting surveys were carried out in the Indo-Pacific sector of the Antarctic under the JARPA/JARPAII programs using the IWC SC-agreed methodology and guidelines. Overall, the IWC SC carried out three circumpolar sighting surveys under the IDCR/SOWER programs (CPI, CPII and CPIII).

6.1.1 Humpback whales

Abundance and abundance trend estimates based on JARPA and JARPAII focused mainly in Areas IV (Population D) and V (Population E) (**Figure 1**). In Area IV the abundance was estimated in 29,067 whales (CV = 0.255) based on sighting data collected in 2007/08; in Area V the abundance was estimated in 13,894 whales (CV = 0.338) based on sighting data collected in 2008/09 [22].

Figure 6 shows the abundance trend of Populations D and E based on JARPA and JARPAII sighting data. For comparison purposes, the figure includes data from the IDCR/SOWER programs [23]. The figure shows a clear increasing trend, which is consistent for the JARPA/JARPAII and IDCR/SOWER survey data. Annual rate of increase was estimated at 13.6% (95% CI = 8.4–18.7%) and 14.5% (95% CI = 7.6–21.5%) for Areas IV and V, respectively, which were statistically greater than zero [22].

6.1.2 Antarctic minke whale

Abundance estimates and abundance trends of Antarctic minke whale for the Eastern Indian Ocean population (Area IV) and Western South Pacific population (Area V) have been conducted based on sighting surveys under JARPA [24]. Abundance estimates for the Eastern Indian Ocean population ranged from 16,562 (CV = 0.542) in 1997/98 to 44,945 (CV = 0.338) in 1999/00. Estimates for the Western South Pacific Ocean population ranged from 74,144 (CV = 0.329) in 2004/05 to 151,828 (CV = 0.322) in 2002/03.

Estimates of the annual rates of increase in abundance were 1.8% (95% CI: −2.5%, 6.0%) for the Eastern Indian Ocean population and 1.9% (95% CI: −3.0%, 6.9%) for the Western South Pacific population, which were not statistically greater than zero (**Figure 7**) [24].

The estimates based on IDCR/SOWER data were 55,237 (CV: 0.17) in Circumpolar II (CPII) and 59,677 (CV: 0.34) in circumpolar III (CPIII) for the Eastern Indian Ocean population (Area IV). For the Western South Pacific population (Area V) were 300,214 (CV: 0.13) in CPII and 183,915 (CV: 0.11) in CPIII.

6.1.3 Fin whales

For the purpose of the abundance estimates based on JARPA and JARPAII surveys, south of 60°S, the whole area was divided into a western area (Areas IIIE+IV) and eastern area (Areas V + VIW). For the western area the abundance was

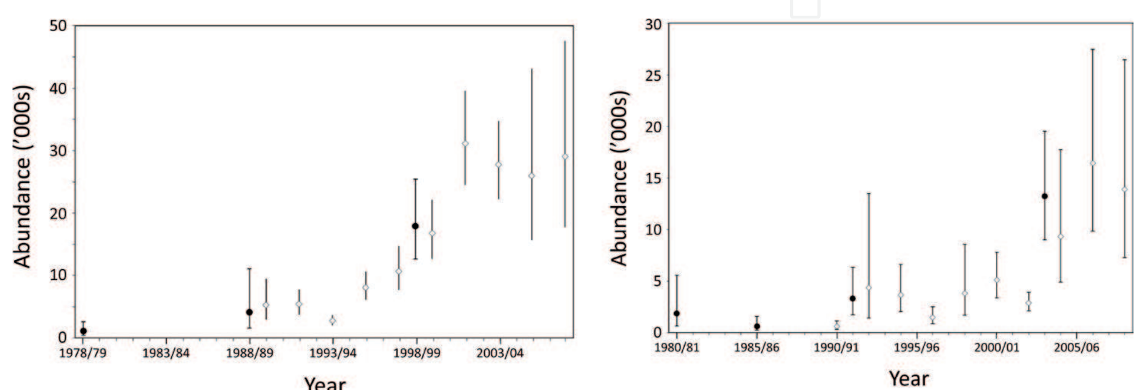

Figure 6.
Annual abundance trend for humpback whales in Areas IV (Population D) (left) and V (Population E) (right), south of 60°S. Estimates were based on sighting data collected by JARPA and JARPAII surveys primarily during January to February. Estimates from the IDCR-SOWER surveys [23] are shown for comparative purposes (filled circles). Vertical lines show 95% confidence intervals (modified from [22]).

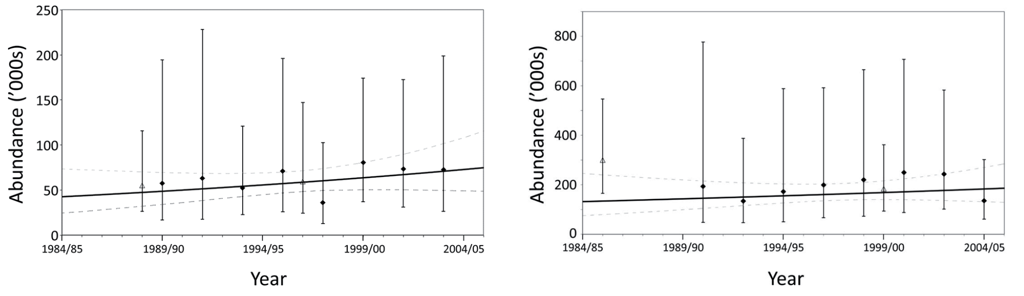

Figure 7.
Annual abundance trend for Antarctic minke whales of the Eastern Indian Ocean population (Area IV) (left) and Western South Pacific population (Area V) (right), together with their 95% CIs, based on sighting data from JARPA. The IDCR/SOWER estimates are shown for comparison (open triangles). The dashed curves indicate the 95% CIs for the exponential model applied to the JARPA estimates (modified from [24]).

estimated as 3,087 (CV = 0.191) in 1995/96, and 2,610 (CV = 0.285) in 2007/08. For the eastern area the abundance was estimated as 1,879 (CV = 0.226) in 1996/97, and 14,981 (CV = 0.298) in 2008/09. For the western area the increasing trend between 1995/96 and 2007/08 seasons was estimated at 8.9% (95%CI: -0.145%, 32.4%), while the trend in the eastern area between 1996/97 and 2008/09 was estimated at 12.0% (95%CI: 2.6%, 21.5%). The estimate for the eastern area was statistically greater than zero [25]. It should be noted that the JARPA/JARPAII surveys do not cover the latitudinal sector 50°-60°S, where fin whales distribute in large numbers in summer.

6.1.4 Antarctic blue whales

There is limited information on stock structure of Antarctic blue whales. Abundance of this species for the Indo-Pacific sector of the Antarctic (35°E-145°W), south of 60°S was 664 (CV = 0.328) in 2005/06 and 2006/07 seasons. The abundance was estimated at 1,223 whales (CV = 0.345) in the 2007/08 and 2008/09 seasons. The abundance trend was estimated at 8.2% (95% CI: 3.9%, 12.5%) between 1995/96 and 2008/09, which was not statistically greater than zero [25].

For most of the populations of these whale species were over-exploited in the past, but there is now scientific evidence of their recovery, although the speed of recovery is different among species and populations. The populations of Antarctic minke whale appear to be stable in recent years.

6.2 Changes in the distribution pattern of baleen whales

Substantial increases in the abundance of some species could have an implication on their pattern of distribution. Antarctic humpback whales from population D (Area IV) have increased substantially over recent decades, while the abundance of the Eastern Indian Ocean Population of Antarctic minke whale (Area IV) has been rather stable since the 1990s. We might expect some changes in the pattern of distribution of these two species. The spatial distribution of Antarctic minke and humpback whales was examined in the Indian sector (Area IV) based on JARPA/JARPAII sighting data for three periods: early (1989/1990, 1991/1992 and 1993/1994), middle (1995/1996, 1997/1998 and 1999/2000) and late (2001/2002, 2003/2004 and 2005/2006) [26]. Spatial distribution was estimated using generalized additive models (GAM). Presence or absence of whales was used as the response variable while seafloor depth, distance from shelf break and longitude were used as explanatory variables.

Mean probabilities of occurrence of Antarctic minke whales in the survey area in early, middle and late periods were 0.41, 0.46 and 0.41, while those of humpback whales were 0.14, 0.35 and 0.46. Occupied area indices (probabilities of occurrence of Antarctic minke whales less probabilities of occurrence of humpback whales) were also calculated. If the index is 1, only Antarctic minke whales were present in a grid cell, while only humpback whales were present if the index is −1. If the index is 0, probabilities of the presence of Antarctic minke whales and humpback whales in a grid cell were identical. Mean occupied area indices in early, middle and late periods were 0.28, 0.11 and – 0.07, respectively. The authors [26] concluded that the spatial distribution of humpback whales expanded to the south during the period investigated, while that of Antarctic minke whales remained stable. A summary of their results is presented in **Figure 8**.

The analyses were conducted based on sighting data obtained in the open sea. It should be mentioned that in the most recent period, Antarctic minke whales have also been observed frequently in polynias within the pack-ice [27], reflecting perhaps a response of this species to the geographical expansion of humpback whales to the south.

6.3 Changes in energy storage and stomach content weight

Nutritional condition in Antarctic minke whales has been investigated through different indices: blubber thickness under the assumption that the amount of lipids increase with the thickness of the blubber, girth and total fat. These data have been collected for more than 25 years during the JARPA and JARPAII surveys in the Indo-Pacific sector of the Antarctic (Areas IV and V). Regression analyses has shown that blubber thickness, girth and fat weight of sexually mature whales have been decreasing for nearly two decades [28]. The decrease per year was estimated at approximately 0.02 cm for mid-lateral blubber thickness and 17 kg for fat weight, corresponding to 9% for both measurements over the 18-year period (**Figure 9**).

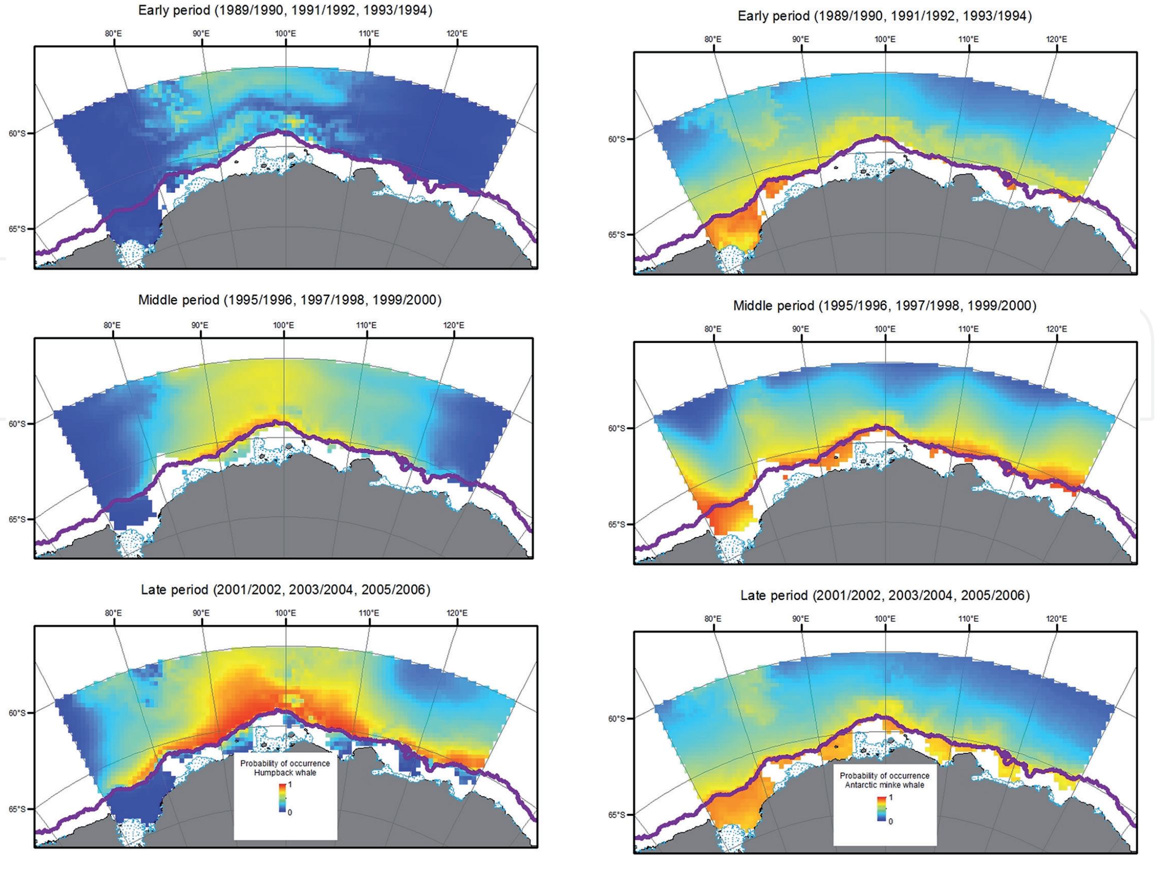

Figure 8.
Probability of occurrence of humpback (left) and Antarctic minke (right) whales in the Indian sector (Area IV) during three time periods [26]. Red indicates high probability of occurrence.

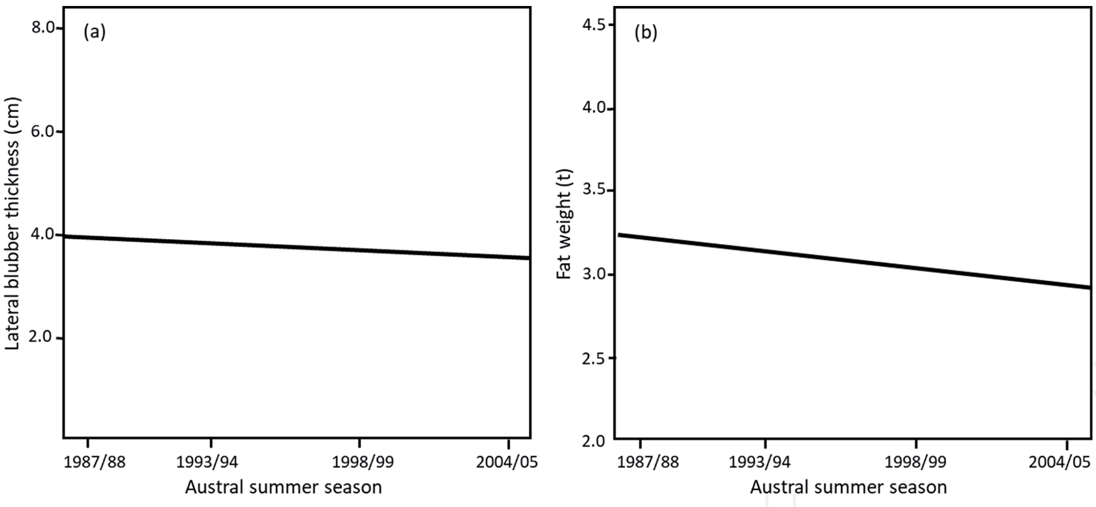

Figure 9.
Yearly trends in blubber thickness (a) and fat weight (b) for Antarctic minke whale in the Indo-Pacific sector of the Antarctic (modified from [28]).

Another study has reported the results of an analysis of temporal trend in stomach content weight in the Antarctic minke whale based on JARPA/JARPAII surveys [29]. A linear mixed-effects analysis showed a 31% (95% CI: 12.6–45.3%) decrease in the weight of stomach contents over the 20 years since 1990/91. A similar pattern of decrease was found for both males and females, except in the case of females sampled at higher latitudes in the Ross Sea (**Figure 1**). These results are consistent with the decline in energy storage reported above. Humpback whales are not found in the Ross Sea, where both Antarctic krill and ice krill (*E. crystallorophias*) are available, and where the authors [29] found no change in prey abundance for Antarctic minke whales.

The studies summarized above suggested a decrease in the abundance of krill for Antarctic minke whales, except in the Ross Sea.

6.4 Biological parameters

As indicated above, the ASM has remained stable at 7–8 years until the 1998 cohort (at least). The proportion of pregnant animals among mature females (PPF) for the Antarctic minke whale has been examined based on JARPA/JARPA surveys conducted between 1987/88 and 2010/11 [30]. The PPF for the Eastern Indian Ocean and Western South Pacific populations was high: 0.932 and 0.904, respectively, using data from all years combined. Linear regression analyses of the PPF over the years showed no significant temporal trend.

6.5 Interpretation of results

The results of this section can be summarized as following:

- The abundance of the once over-exploited large whale species such as the Antarctic blue, fin and humpback whales, has been increasing since the 1980's (at least). In particular, the increasing trends of Populations D and E of humpback whale and that of a population of fin whales in the eastern part of the research area were statistically significantly greater than zero.

- Since about 1990, the abundance of two populations of Antarctic minke whale has been rather stable as revealed by the SCCA analyses and abundance estimated by sighting surveys.

- Humpback whales from Population D (Area IV) have expanded their geographical distribution to the south in recent years, while the distribution of the Antarctic minke whales of the Eastern Indian Ocean population (Area IV) has remained stable in the open sea. Larger number of Antarctic minke whales are distributed in polynias within the pack-ice in recent years.

- The nutritional conditions of Antarctic minke whales has been deteriorating as evidenced by a decreasing trend of several nutritional indices.

- The ASM of Antarctic minke whale has remained low and stable around 7–8 years old until the 1998 cohort, and the PPF of Antarctic minke whale has remained high (over 0.9), and stable.

Deteriorating nutritional conditions of the Antarctic minke whales suggest less food available for this species in recent years. Less availability/abundance of Antarctic krill could be a response to environmental changes (e.g. global warming) and/or competition for food with the increasing large whale species such as Antarctic blue, fin and humpback whales. No evidence of global warming exists for the Indo-Pacific sector of the Antarctic [31], so competition for food could be a more plausible interpretation for the results of nutritional deterioration in the Antarctic minke whale. This reflects the end of the period of a krill surplus hypothesised during the past century. Nutritional deterioration as a consequence of competition is not entirely consistent with the low ASM and high APR of the Antarctic minke whale over more recent years. Under the competition hypothesis, this could be the result of a temporal phenomenon in that the response of ASM and APR to environmental changes producing a nutritional deterioration may be subject to time lags.

Direct competition occurs when two predators are present in the same area as a prey species, and may interfere with each other's access to the prey. Indirect competition may occur when two predators occur in different parts of the area of prey, but because the prey's production is limited, consumption by the one predator limits the production available for the other, and *vice versa* [32]. To investigate the plausibility of the competition hypothesis, estimates of krill biomass trends in the research area are required. There is some partial information on krill abundance based on dedicated krill surveys in the past, but the information is scattered and needs to be combined with that from new surveys in a comprehensive and consistent way so that time series data can be obtained. The period of these demographic changes in the Antarctic minke whales coincides with the post whaling era (1970's-) which has been characterized as 'unfavorable climate conditions and increasing competition for krill' [3].

Antarctic minke whales could also be using alternative feeding areas (e.g. polynias within the pack-ice) in response to the increase in abundance and geographical expansion of these other large whale species. This could provide an alternative explanation from sighting surveys and population models of a decrease and then re-stabilization of Antarctic minke whales abundance in open areas since the 1970's.

The increase of the Adelie penguins (*Pygoscelis adeliae*) in East Antarctic in recent decades [33] seems immediately not to be consistent with the competition hypothesis. The authors of the Adelie penguin study provided two explanations for the increase of this species: (i) harvesting of baleen whales, krill and fish across East Antarctic waters through the 20th century could have reduced competition between Adelie penguins and other predators for food, improving prey availability, and (ii) a proposed reduction in sea-ice extent in the mid-20 century may also have benefited Adelie penguins by enabling better access to the ocean for foraging. Since recovery of krill-eating large baleen whales has been reported since the 1980's, it is suggested that their explanation of environmental factors for the demographic changes of Adelie penguins since the

1980's is more plausible. Perhaps environmental changes have stronger effects on land-based predators such as the penguins than on sea-based predators such as whales.

7. Conclusions

This review of the scientific evidence for ecosystem changes in the Indo-Pacific sector of the Antarctic has highlighted the importance of long-time monitoring research programs focused on the collection of biological data for krill predators (both land-based and sea-based predators) as well as data on sea ice cover and environmental variables. The hypothesis proposed for the recent demographic changes found in whales is competition. To investigate this hypothesis further, estimates of krill abundance as well additional data collection of the predators and improved modelling analyses are required (see [34]). Also, oceanographic data obtained for more than 30 years in the Indo-Pacific sector of the Antarctic by JARPA/JARPAII surveys should be analysed to explore further the possible effect of global warming on the pattern of demographic changes found in whales.

In this context, Japan has started a new non-lethal research program to continue studying whales and the environment in the Indo-Pacific sector of the Antarctic. The program called JASS-A (Japanese Abundance and Stock structure Survey in the Antarctic) started in the austral summer of 2019/20, and will continue for at least eight years. It will conduct systematic sighting surveys for abundance estimates, biopsy sampling for genetic analysis of population structure, oceanographic and marine debris surveys, satellite tracking and photo-identification for studies on stock structure, distribution and movement of large whales, and Unmanned Aerial Vehicle (UAV) to observe whales outside of the main survey area. The analyses of the data to be collected will assist to examine the plausibility of the hypothesis proposed in this study further, in particular the observation that Antarctic minke whales have been moving into polynias within the pack-ice in recent years.

Acknowledgements

The authors thank the Fisheries Agency, Government of Japan for permits and funding for the whale surveys conducted in the Antarctic under the JARPA and JARPAII. They also thank the crew and researchers that participated in the surveys under the JARPA, JARPAII and IDCR/SOWER for collecting data and samples used in the analyses and studies summarized in this chapter.

Conflict of interest

The authors declare that there is no conflict of interest.

Author details

Yoshihiro Fujise and Luis A. Pastene*
Institute of Cetacean Research, Tokyo, Japan

*Address all correspondence to: pastene@cetacean.jp

References

[1] Laws RM. Seals and whales of the Southern Ocean. Philosophical Transactions of the Royal Society of London B. 1977;**279**:81-96

[2] Laws RM. The Ecology of the Southern Ocean. American Scientist. 1985;**73**:26-40

[3] Trivelpiece WZ, Hinke JT, Miller AK, Reiss CS, Trivelpiece SG, Watters GM. Variability in krill biomass links harvesting and climate warming to penguin population changes in Antarctica. PNAS. 2011;**108**(18):7625-7628

[4] Fraser WR, Trivelpiece WZ, Ainley DG, Trivelpiece SG. Increases in Antarctic penguin populations: reduced competition with whales or a loss of sea ice due to environmental warming? Polar Biology. *1992*;**11**:525-531

[5] Vaughan DG, Marshall GJ, Connolley WM, Parkinson CL, Mulvaney R, Hodgson DA, et al. Recent rapid regional climate warming on the Antarctic Peninsula. Climate Change. 2003;**60**:243-274

[6] Nicol S. Krill, currents, and sea ice: *Euphausia superba* and its changing environment. Bioscience. 2006;**56**(2):111-120

[7] International Whaling Commission. Report of the Workshop on the Comprehensive Assessment of Southern Hemisphere Humpback Whales. J. Cetacean Res. Manage. 2011;(special issue)**3**:1-50

[8] Kanda N, Goto M, Pastene LA. Stock structure of humpback whales in the Antarctic feeding grounds as revealed by microsatellite DNA data. Paper SC/F14/J31 presented to the Expert Workshop to Review the Japanese JARPAII Special Permit Research Programme, Tokyo, February 2014. 5pp. [Available from the IWC Secretariat]

[9] International Whaling Commission. Report of the Intersessional Workshop to Review Data and Results from Special Permit Research on Minke Whales in the Antarctic, Tokyo, 4-8 December 2006. J. Cetacean Res. Manage. 2008;**10**:411-445

[10] Pastene LA, Goto M. Genetic characterization and population genetic structure of the Antarctic minke whale *Balaenoptera bonaerensis* in the Indo-Pacific region of the Southern Ocean. Fisheries Science. 2016;**82**:873-886

[11] Kitakado T, Schweder T, Kanda N, Pastene LA, Walloe L. 2014. Dynamic population segregation by genetics and morphometrics in Antarctic minke whales. Paper SC/F14/J29 presented to the Expert Workshop to Review the Japanese JARPAII Special Permit Research Programme, Tokyo, February 2014. 20pp. [Available from the IWC Secretariat]

[12] International Whaling Commission. Report of the Expert Workshop to Review the Japanese JARPAII Special Permit Research Programme. J. Cetacean Res. Manage. 2015;**16**:369-409

[13] Lockyer C. The age at sexual transition of the southern fin whales (*Balaenoptera physalus*) using annual layer counts in the earplug. Journal du Conseil International pour l'Exploration de la Mer. 1972;**34**:276-294

[14] Thomson RB, Butterworth DS, Kato H. 1999. Has the age at transition phase of southern hemisphere minke whales declined over recent decades? Mar. Mamm. Sci. 1999;**15**(3):661-682

[15] Bando T, Kishiro T, Kato H. Yearly trend in the age at sexual maturity of Antarctic minke whales examined by transition phase in earplugs collected during JARPA and JARPAII surveys. Paper SC/F14/J8 presented to the Expert Workshop to Review

the Japanese JARPAII Special Permit Research Programme, Tokyo, February 2014. 10pp. [Available from the IWC Secretariat]

[16] Fournier D, Archibald CP. A general theory for analyzing catch at age data. Canadian Journal of Fisheries and Aquatic Sciences. 1982;**39**:1195-1207

[17] Punt AE. A summary history of the application of statistical catch-at-age analysis (SCAA) to Antarctic minke whales. J. Cetacean Res. Manage. 2014;**14**:81-92

[18] Punt AE, Hakamada T, Bando T, Kitakado T. 2014. Assessment of Antarctic minke whales using statistical catch-at-age analysis (SCAA). J. Cetacean Res. Manage. 2014;**14**:93-116

[19] Allen KR. Conservation and Management of Whales. Washington and Butterworths, London: Washington Sea Grand Publication; 1980 107p

[20] Buckland ST, Rexstad EA, Marques TA, Oedekoven CS. Distance Sampling: Methods and Applications. Springer International Publishing; 2015. 277p

[21] International Whaling Commission 2012. Requirements and Guidelines for Conducting Surveys and Analysing Data within the Revised Management Scheme. J. Cetacean Res. Manage. 2012;**13**:509-517

[22] Hakamada T, Matsuoka K. Estimates of abundance and abundance trend of the humpback whale in Areas IIIE-VIW, south of 60°S, based on JARPA and JARPAII sighting data (1989/90-2008/09). Paper SC/F14/J04 presented to the Expert Workshop to Review the Japanese JARPAII Special Permit Research Programme, Tokyo, February 2014. 36pp. [Available from the IWC Secretariat]

[23] Branch TA. Humpback whale abundance south of 60°S from three complete circumpolar sets of surveys. J. Cetacean Res. Manage. 2011;(special issue) **3**:53-69

[24] Hakamada T, Matsuoka K, Nishiwaki S, Kitakado T. Abundance estimates and trends for Antarctic minke whales (*Balaenoptera bonaerensis*) in Antarctic Areas IV and V based on JARPA sighting data. J. Cetacean Res. Manage. 2013;**13**(2):123-151

[25] Matsuoka K, Hakamada T. Estimates of abundance and abundance trend of the blue, fin and southern right whales in the Antarctic Areas IIIE-VIW, south of 60°S, based on JARPA and JARPAII sighting data (1989/90-2008/09). Paper SC/F14/J05 presented to the Expert Workshop to Review the Japanese JARPAII Special Permit Research Programme, Tokyo, February 2014. 36pp. [Available from the IWC Secretariat]

[26] Murase H, Matsuoka K, Hakamada T, Kitakado T. Preliminary analysis of changes in spatial distribution of Antarctic minke and humpback whales in Area IV during the period of JARPA and JARPAII from 1989 to 2006. Paper SC/F14/J18 presented to the Expert Workshop to Review the Japanese JARPAII Special Permit Research Programme, Tokyo, February 2014. 17pp. [Available from the IWC Secretariat]

[27] Ishikawa H, Goto M, Ogawa T, Bando T, Kiwada H, Isoda T, Kumagai S, Mori M, Tsunekawa M, Ohsawa T, Fukutome K, Koyanagi T, Kandabashi S, Kawabe S, Sotomura N, Matsukura R, Kato K, Matsumoto A, Nakai K, Hasegawa M, Mori T, Yoshioka S, Yoshida T. Cruise report of the Second Phase of the Japanese Whale Research Program under Special Permit in the Antarctic (JARPAII) in 2007/2008. Paper SC/60/O4 presented to the IWC Scientific Committee, Anchorage, June 2007. 19pp [Available from the IWC Secretariat]

[28] Konishi K, Tamura T, Zenitani R, Bando T, Kato H, Walløe L. Decline in energy storage in the Antarctic minke whale (*Balaenoptera bonaerensis*) in the Southern Ocean. Polar Biology. 2008;**31**:1509-1520

[29] Konishi K, Hakamada T, Kiwada H, Kitakado T, Walløe L. Decline in stomach contents in the Antarctic minke whale (*Balaenoptera bonaerensis*) in the Southern Ocean. Polar Biology. 2014;**37**:205-215

[30] Bando T, Hakamada T. Yearly trend in the proportion of pregnant animals among mature female Antarctic minke whales in the JARPA and JARPAII period. Paper SC/F14/J9 presented to the Expert Workshop to Review the Japanese JARPAII Special Permit Research Programme, Tokyo, February 2014. 6pp. [Available from the IWC Secretariat]

[31] Watanabe T, Okazaki M, Matsuoka, K. Results of oceanographic analyses conducted under JARPA and JARPAII and possible evidence of environmental changes. Paper SC/F14/J20 presented to the Expert Workshop to Review the Japanese JARPAII Special Permit Research Programme, Tokyo, February 2014. 10pp. [Available from the IWC Secretariat]

[32] International Whaling Commission. Report of the Scientific Committee. J. Cetacean Res. Manage. 2015;**16**:1-87

[33] Southwell C, Emmerson L, McKinlay J, Newbery K, Takahashi A, Kato A, et al. Spatially extensive standardized surveys reveal widespread, multi-decadal increase in East Antarctic Adelie penguin populations. PLoS One. 2015 http://dx.doi.org/10.1371/journal.pone.0139877

[34] Murase H, Palka D. Punt A, Pastene LA, Kitakado T, Matsuoka K, et al. Review of the assessment of two stocks of Antarctic minke whales (Eastern Indian Ocean and western South Pacific). J. Cetacean Res. Manage. 2020;**21**:95-122