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Cetaceans as indicators of historical and current changes in the Antarctic ecosystem

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ABSTRACT

Changes in the Antarctic ecosystem are triggered by anthropogenic and natural factors. This paper reviews the scientific information on whales produced mainly by the Institute of Cetacean Research (ICR), that could be indicative of changes in the Antarctic ecosystem in the context of two hypotheses, the 'krill surplus' hypothesis in the middle of the past century, and the hypothesis of recovery of krill-eater large whales since the 1980's. The information in the Indo-Pacific region of the Antarctic (70°E–170°W) showed that the increased krill availability in the middle of the past century could have been translated into better nutritional conditions for some krill predators like the Antarctic minke whale, resulting in a decreasing trend in the age at sexual maturity and an increasing trend in the recruitment rate and total population size of this species between approximately 1940 and 1970. The evidence available since the 1980's showed a sharp increase in the abundance of some species such as the humpback and fin whales, which had been heavily exploited in the first half of the past century. The evidence also showed that, in parallel to this increase, the nutritional condition of Antarctic minke whales has deteriorated as revealed by a decrease in energy storage and stomach content weight since the 1980's. This observation is consistent with the stable trend of age at sexual maturity, recruitment and abundance of this species after the 1980's. Therefore the historical demographic changes observed in the Antarctic minke whale are consistent with the pattern expected under the 'krill surplus' hypothesis, while the demographic and ecological changes observed in recent years are consistent with the changes expected under the reverse of the 'krill surplus' hypothesis.

INTRODUCTION

The Antarctic ecosystem is a very dynamic one with changes in species composition and habitat occurring through time. Within this ecosystem the Antarctic krill (*Euphausia superba*) is a key prey species supporting different species of baleen whales, pinnipeds, birds and fish. Changes in the ecosystem can be derived from human interventions or from natural causes. One example of the former is the large-scale exploitation of whales in the first half of the 20th Century, which has been discussed by several authors, notably by Laws (1977; 1985). Exploitation of large whales in the Antarctic Ocean started in 1904. Several species of krill-eater large whales such as Antarctic blue (*Balaenoptera musculus intermedia*) and humpback (*Megaptera novaeangliae*) whales were heavily depleted by commercial whaling by the first half of the past century. Other species such as the fin (*B. physalus*) whales were depleted during the second half of the 20th Century. Large changes in the biomass of some whale species had a strong effect on the demography of other krill-eater predators in the Antarctic ecosystem (Laws 1977; 1985).

One example of the latter are the environmental changes reported in recent years for some parts of the Antarctic. For example Fraser *et al.* (1992) suggested that the increase in chinstrap penguin populations in the last four decades (1950's–1990's) were due to a gradual decrease in the frequency of cold years with extensive winter sea ice cover resulting from environmental warming. Their observation was supported by a multidisciplinary winter expedition to the Scotia and Weddell seas, satellite images of ocean ice cover, and the analysis of long-term surface temperature records and penguin demography. Less ice cover means wider open waters available for penguin's feeding on krill. This observation contradicted the hypothesis that the increases in the penguin population resulted from an increase in prey availability brought on by the decrease in baleen whale stocks. They cited modeling work that predicted that the

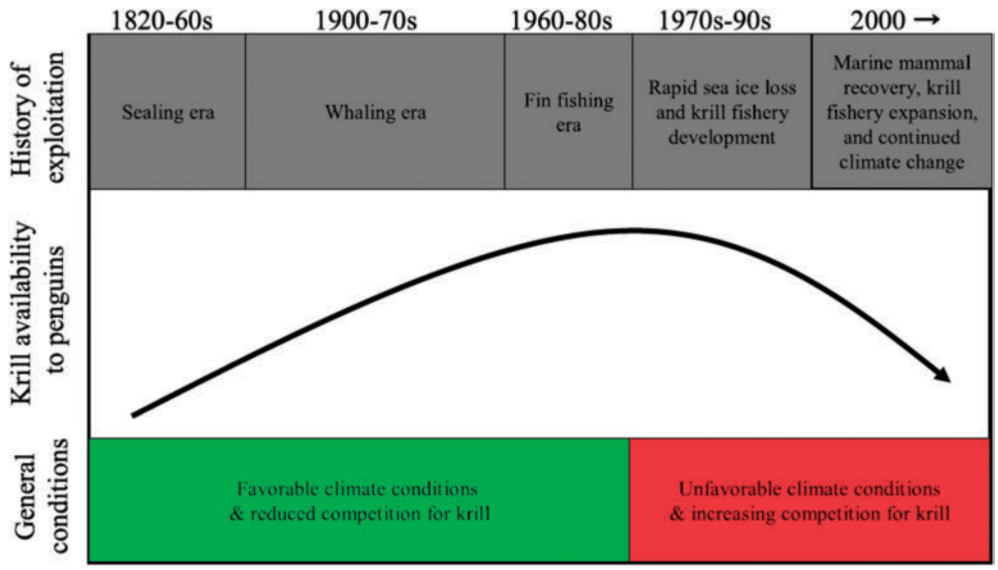

Figure 1. Schematic diagram of ecosystem perturbation in the Scotia Sea (after Trivelpiece *et al.*, 2011).

Table 1

Biological and ecological parameters monitored from whales and their environment to investigate change in the ecosystem.

Research 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	Fluctuation of abundance of whales through time is important for their management. Different levels of whale abundance have different impacts on krill.
Whale distribution	Systematic sighting surveys	Distribution of whale species can change with time in response to changes in abundance and/or changes in oceanographic conditions/krill availability.
Whale recruitment	Population dynamic models that use age and abundance information from 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 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 in heavier stomach contents.
Age at sexual maturity (ASM)	Examination of transition phase in earplugs; examination of ovaries and testis.	Better nutritional conditions will be reflected in a shift of the ASM to younger ages e.g. 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 distribution and krill biomass and in turn the abundance and distribution of whales. Changes in oceanographic conditions might indicate an effect of climate changes.

benefits of a reduction in baleen whales would have been most directly conferred to predators of similar size and behavior, namely, other whales (Fraser *et al.*, 1992). However more recent analyses in the Antarctic Peninsula and Scotia Sea concluded that the chinstrap penguin instead may be among the most vulnerable species affected by a warming climate (Trivelpiece *et al.*, 2011).

Trivelpiece *et al.* (2011) presented a very informative diagram of ecosystem perturbation in West Antarctic (Scotia Sea) due to both, anthropogenic reasons such as the commercial over-exploitation of marine resources (sealing from 1820 to the 1960′s, whaling from 1900 to 1970; fishing for ice fishes and Notothenids from 1960–1980), and natural reasons (climate-change effects from the 1970′s). They noted that a pelagic trawl fishery for krill also developed from the 1970′s, and that in the 2000′s, the once-depleted marine mammal populations had recovered or were recovering, that the krill fishery was expanding, that climate change was progressing and that Adelie and chinstrap penguin populations were decreasing (Figure 1). The causes of ecosystem changes in the Antarctic are therefore complex, and to understand those causes, long-term monitoring research programs focused on collecting biological data of krill predators as well as data on sea ice cover and environmental variables, are important.

Previous studies have documented ecosystem changes in West Antarctic, and have considered environmental variables and demographic information of land-based krill predators. The objective of this study was to review the scientific evidence for expected changes in the Indo-Pacific region of the Antarctic, in the context of some established hypotheses. The evidence is based mainly on biological and ecological data of baleen whales, sea-based predators, collected by ICR. Table 1 shows the data monitored in whales and their environment, which are informative of changes in the ecosystem.

KEY BALEEN WHALES IN THE ANTARCTIC ECOSYSTEM

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 of baleen whales such as Antarctic blue, fin, humpback and Antarctic minke (*B. bonaerensis*) whales is the Antarctic krill therefore their summer migrations to the Antarctic are related to areas of krill concentrations as those shown in Figure 2. Breeding areas of the humpback whales occurring in the Antarctic research area are located in both Western and Eastern Australia.

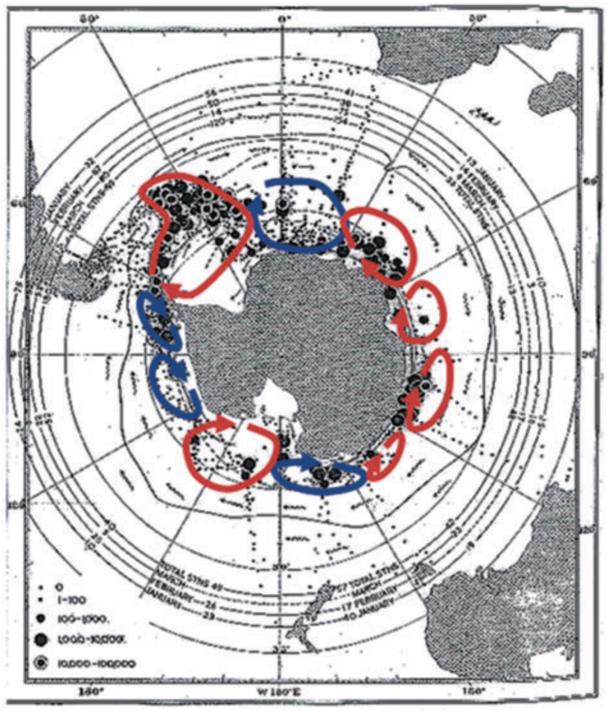

Figure 2. Areas of krill distribution in the Antarctic associated with gyres (after Nicol, 2006).

Breeding areas for the other species are assumed to be in low latitudes of the eastern Indian and western South Pacific Oceans.

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 that 30 m and weight of nearly 180 tons. During the austral summer season blue whales are distributed mainly above the Antarctic Convergence to the ice edge. Current abundance in all of the Antarctic is approximately 3,000 animals.

Fin whale

This is the second largest baleen whale species with a maximum length of 27.1 m and weight of 120 tons. During the austral summer season fin whales are found extensively south of 50°S, most commonly north of 60°S (Branch and Butterworth, 2001). In the Antarctic fin whales feed on krill. The existing estimates from limited parts of the range covered are of the order of several thousand animals.

Humpback whale

This is a highly migratory species with a maximum body length of 17 m and weight of 40 tons. During the austral summer season it is distributed south of the Antarctic Convergence to the ice edge but just north of the main distribution area of Antarctic minke whale. In the Antarctic, humpback whales feed on krill. The total current Southern Hemisphere abundance is probably at least 60,000.

Antarctic minke whale
This is one of the smallest baleen whale species with a maximum body length of 10.7 m and weight of 10 tons. During the austral summer season it is distributed mainly around the pack-ice and feeds on krill. Abundance of Antarctic minke whale in the Antarctic was estimated at 515,000 animals (IWC, 2013).

RESEARCH AREA

The review was focused on the Indo-Pacific region of the Antarctic, in the longitudinal sector between 70°E and 170°W, south of 60°S, including both Indian (Area IV according to International Whaling Commission (IWC) terminology, 70°–130°E) and Pacific (Area V according to IWC terminology, 130°E–170°W) sectors. The research area includes Prydz Bay as its western boundary and the Ross Sea as the eastern boundary.

CHANGES IN THE ANTARCTIC ECOSYSTEM

The review of evidence of changes in the Indo-Pacific region of the Antarctic is treated in two periods, historical and current. The former corresponds to the period approximately from the start of commercial whaling in the Antarctica in 1904 until approximately 1970′s, which Trivelpiece *et al.* (2011) characterized as ʻfavourable climate conditions and reduced competition for krillʼ (Figure 1). The latter corresponds to the period from the 1970′s–1980′s to recent years, which those authors characterized as ʻunfavorable climate conditions and increasing competition for krillʼ (Figure 1).

Historical changes
The ecological effect of the large-scale exploitation of whales in the first half of the 20th Century has been discussed by several authors, notably by Laws (1977; 1985). Exploitation of large whales in the Antarctic Ocean started in 1904. Several species of large whales such as blue and humpback whales were heavily depleted by the first half of the past century (Figure 3). Other species such as the fin and sei whales were depleted during the second half of the 20th Century. Commercial exploitation of the Antarctic minke whale started in the early 70′s when all other baleen whale species were already depleted. Table 2 shows the original and current (by 1980) abundance of large whales exploited in the Southern Hemisphere (mainly Antarctic). In the Southern Hemisphere the abundance of large whale species such as the blue and humpback whales decreased to a minimal percentage of the original abundance before exploitation. In the case of the Antarctic minke whales, which were not exploited during the first half of the past century, the current abundance has not changed with regard the original abundance.

As noted earlier, the Antarctic krill is a key prey species in the Antarctic ecosystem supporting different species of baleen whales, pinnipeds, birds and fish. Some researchers have suggested that following the main exploitation period of large baleen whales in the Antarctic (approximately at the middle of the past century) some 150 million tons of ʻsurplusʼ annual production of Antarctic krill (Figure 4) became available for other krill predators, such as Antarctic minke whales, crabeater seals, fur seals, pen-

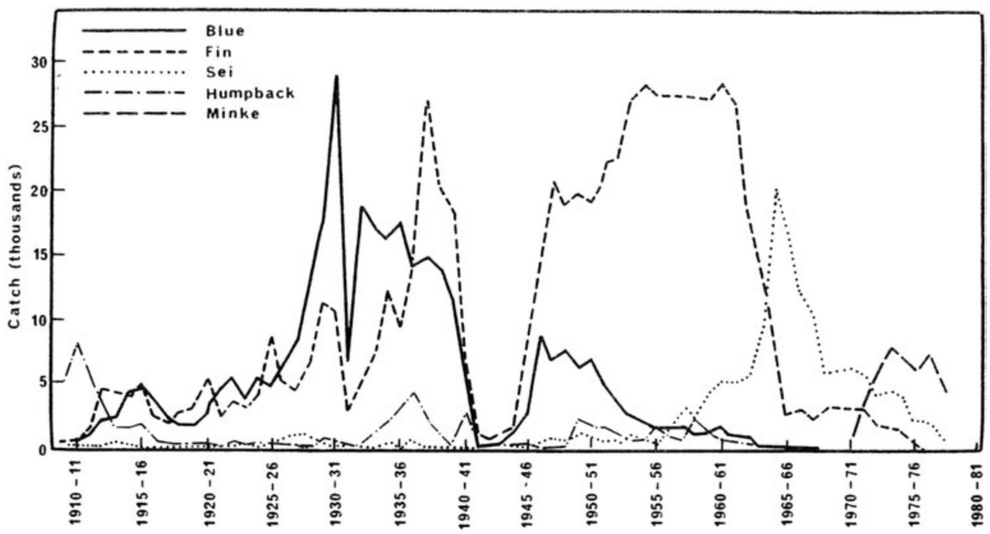

Figure 3. Catches of baleen whales in the southern Hemisphere, 1910–1977 (after Allen, 1980).

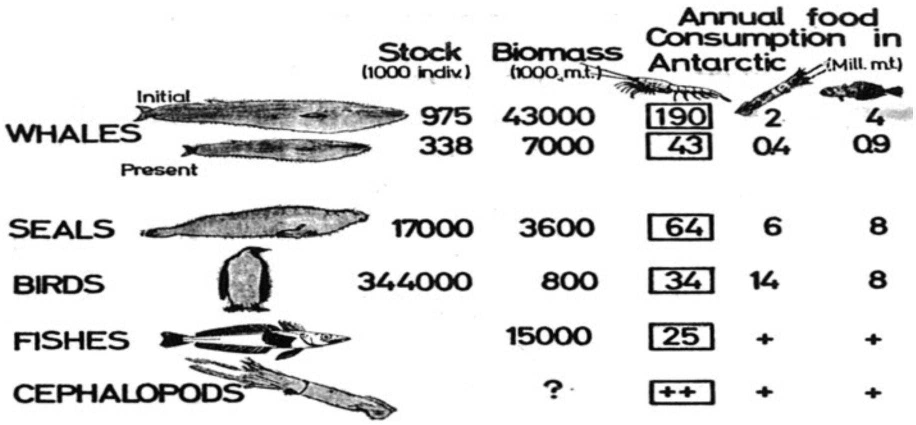

Figure 4. Initial and present (1970′s) biomass and annual krill consumption of exploited large baleen whale species and other predators in the Antarctic (after Laws, 1977; Sahrhage, 1984).

Table 2

Original and current (by 1980) abundance of exploited large whales in the Southern Hemisphere (modified of Allen, 1980).

	SPERM Male	SPERM Female*	RIGHT	BOWHEAD	GRAY	HUMPBACK	BLUE	FIN	SEI	BRYDE'S	MINKE
TOTAL POPULATIONS**											
Southern Hemisphere											
Original	625	625	(100+)	—	—	130	220	490	191	(30)	205
Current	460	510	(3²)	—	—	3	11	103	37	(30)	205
%	74	82	(3)	—	—	2	5	21	19	100	100

guins and some albatrosses which took advantage of this food surplus to increase their abundance. This is the so-called ′krill surplus′ hypothesis (Laws, 1977; 1985).

Inter-specific effects of the surplus hypothesis

Antarctic minke whale

As shown in Table 2, Antarctic minke whales were not exploited in the first half of the past century and the commercial exploitation of this species only started in the 1970′s at a moderate scale under management of the IWC. The expectation here was that the krill surplus by the middle of the past century translated to better nutritional conditions, which should have been reflected in changes in demographic parameters of this species. In particular we focus here on the information on age at sexual maturity and total abundance.

Changes in the age at sexual maturity (ASM) indicate change in nutritional conditions of the whales, which in turn could indicate less or more food availability in the environment. Better nutritional conditions will be reflected in a shift of the ASM to younger ages e.g. whales will be able to reproduce at younger ages and as a consequence the populations will growth faster (Table 1). One of the methods for determining age at sexual maturity in whales is examination of the ′transition phase′ in the earplugs. 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, and this is thought to indicate the age at maturity of the whale (Thomson *et al.*, 1999). Historical changes in the age at sexual maturity can be investigated when the analyses are carried out on 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 Japanese whale research in the Indo-Pacific region of the Antarctic (JARPA and JARPAII), for more than 25 years. Thomson *et al.* (1999) showed a decline in the average age at transition in Antarctic minke whales in the Indian sector from roughly 11 for the cohorts of the 1950′s to roughly 7 for those of the 1970′s, and the trend was similar for females and males. This work was updated by Bando *et al.* (2014) by using a large number of samples, and analyses conducted on two biological stocks, one mainly distributed in the Indian Ocean sector and the other in the Pacific Ocean sector.

These results suggested that the nutritional conditions were optimal for Antarctic minke whales after a period in which other krill-predators species such as the Antarctic blue and humpback whales were already depleted (Figure 3).

The Scientific Committee (SC) of the IWC has been applying statistical catch-at-age (SCAA) analyses on Antarctic minke whales since 2005. A summary history of the application of SCAA to this species was presented by Punt (2014), and an assessment of Antarctic minke whales using SCAA was reported by Punt *et al.* (2014).

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 e.g. those from the IWC SC's International Decade of Cetacean Research/Southern Ocean Whale and Ecosystem Research (IDCR/SOWER) as well as those from Japanese dedicated sighting surveys in the Indo-Pacific region of the Antarctic. Biological data were available from the period of commercial whaling (Japan and the former Soviet Union), and from Japanese whale research in the Indo-Pacific region of the Antarctic (JARPA and JARPAII), for more than 25 years.

The SCAA assessment on Antarctic minke whale involved a 'reference' case and several sensitivity tests. These sensitivity tests explored sensitivity to the weight assigned to the various data sources and penalties, the assumptions related to vulnerability, natural mortality and catchability, and to the use or otherwise of the Japanese research's index data (Punt *et al.*, 2014).

Results presented here refer to the 'reference' case in Punt *et al.* (2014), which was robust to the sensitivity tests conducted (Figure 6 for the Indian sector). As shown in Figure 6, the stock was estimated to have increased from 1930 until the early 1970's, with the stock having declined subsequently thereafter. The increase in abundance was due primarily to an increase in recruitment owing in turn to an increase in carrying capacity (Punt *et al.*, 2014).

For historical changes examined in this section, it is interesting to note that the increase from 1930 to 1970's roughly coincided with the period in which the age at sexual maturity decreased. Again these results suggested that the nutritional conditions were optimal for Antarctic minke whales after a period in which other krill-predator species such as the Antarctic blue and humpback whales were already depleted (Figure 3).

Summary

According to the 'krill surplus' hypothesis, the increased krill availability was translated into better nutritional conditions for some krill predators like the Antarctic minke whale. In the case of this species this resulted in some

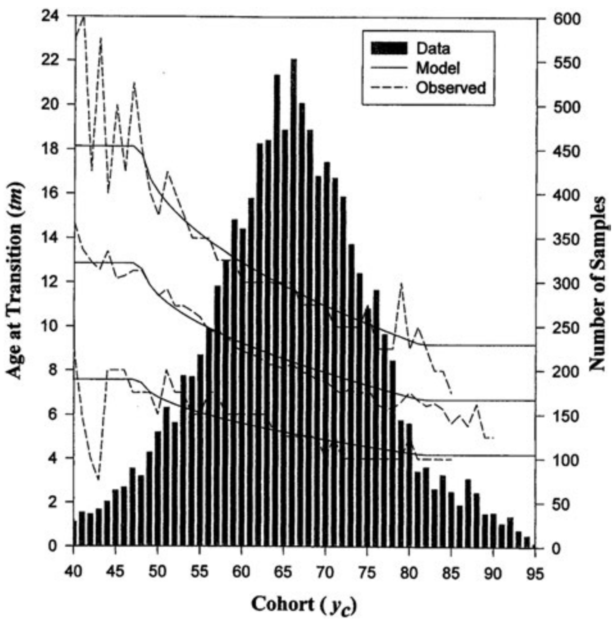

Figure 5. Changes in the age at sexual maturity of Antarctic minke whale, by cohort (Indian Ocean sector). Age at sexual maturity changed from around 11 years in 1950s cohorts to around 7 years in 1970s cohorts (middle curve) (after Thomson *et al.*, 1999).

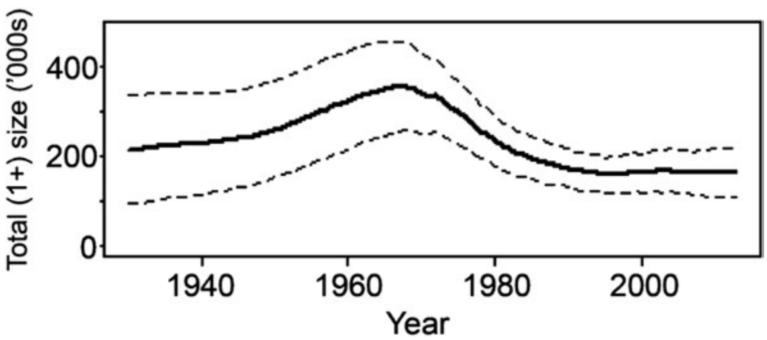

Figure 6. Time trajectories of total (1+) population size of Antarctic minke whales in the Indian sector (base-case). The dotted lines indicate 95% asymptotic confidence intervals (after Punt *et al.*, 2014).

biological changes such as the observed decreasing trend in the age at sexual maturity between approximately 1940 and 1970 (Figure 5), which coincide with the period of depletion of some key krill-eater large whale species (Figure 3). A low age at sexual maturity favored an increase in the recruitment rate and total population size in a similar period (Figure 6).

The Antarctic minke whale perhaps reached the increased maximum carrying capacity by the late 1960s, and then the stock responded by stabilizing the age at sexual maturity at 7–8 years old (Figure 5). This biological process should have resulted in a stable continuous high rate of newborns after 1970 since the recruitment was rather stable after 1970 (Figure 6). The trend in recruitment is consistent with the trend in total abundance of Antarctic minke whale estimated by sighting data which has been broadly stable since the 1980′s.

Finally it should be noted that the period of demographic changes observed in Antarctic minke whales coincides with the period 1900–70′s (′whaling era′) in Trivelpiece *et al.* (2011), which they characterized as ′favorable climate conditions and reduced competition for krill′ (Figure 1). Such conditions allowed for rapid growth and increase in populations of the Antarctic minke whale and other krill-eater predators in that period.

Current changes

Commercial whaling of humpback, Antarctic blue and fin whales in the Antarctic was banned in 1963, 1964 and 1976, respectively. As an effect of these conservation measures, the abundance of these species increased in recent decades, which points toward a recovery from past commercial exploitation. The speed of recovery varies among these species and among stocks within these species. The increase in the abundance of large whale species that feed on krill in the Antarctic means less food available for species like the Antarctic minke whale that once benefited from the surplus of krill. It was expected that these conditions, which correspond to the ′reverse′ of the krill surplus hypothesis, should have some effect on the nutritional conditions and on demographic parameters of Antarctic minke whale and other species that once benefited from the surplus of krill.

Evidence for the increase in abundance of large whales in the Indo-Pacific region of the Antarctic

To estimate abundance of large whales in the Antarctic, systematic sighting surveys have been carried out under the DISTANCE sampling method (Buckland *et al.*, 2015), and the guidelines for surveys and analyses agreed by the IWC SC (IWC, 2012). The IWC SC carried out three circumpolar sighting surveys under the IDCR/SOWER programs. Japanese researchers also carried out dedicated sighting surveys in the Indo-Pacific region using the same methodology and guidelines.

Matsuoka *et al.* (2011) reported abundance estimates and abundance trends for two populations of the humpback whales, stock D in the Indian sector (Area IV) and stock E in the Pacific sector (Area V). Results showed that the abundance of both stocks has been increasing in the last decades. Abundance and population growth rates of humpback whale in the Indian sector and in the Pacific sector were 31,000 (16.4% increase by year with 95% CI: 9.5–23.3%) and 9,000 (12.1% increase by year with 95% CI: 1.7–22.6%), respectively. The current abundance of the stock in the Indian sector is close to that at its pre-exploitation level. Figure 7 shows the abundance trend

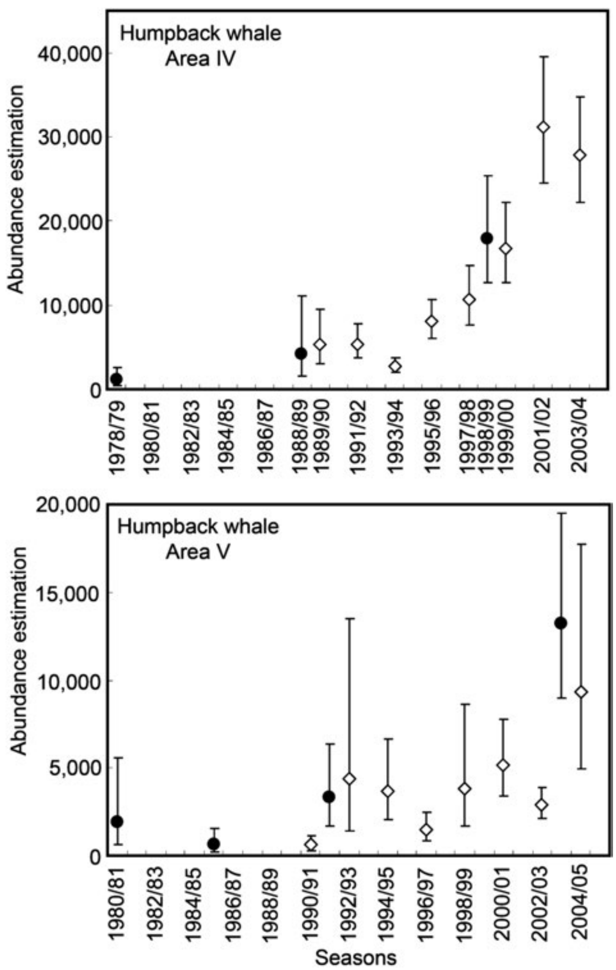

Figure 7. Abundance trend of humpback whale in the Indian sector (Area IV) and Pacific sector (Area V) based on Japanese dedicated sighting surveys. Black dots are abundance estimates based on the IDCR/SOWER surveys, which are consistent with those from the Japanese surveys (after Matsuoka *et al*, 2011).

of this stock in the Indian and Pacific sectors for the period 1989/90–2003/04, and compares it with the trend estimated using IDCR/SOWER sighting data (Matsuoka *et al.*, 2011). There is a clear increasing trend that is consistent between both Japanese and IDCR/SOWER surveys (see Figures 7).

The abundance and annual population growth rates of fin whales in the Indian sector and Pacific sector based on Japanese dedicated sighting surveys were estimated at 6,514 (16.0% CV: 0.78 increase rate) and 5,241 (12.8% CV: 0.60 increase rate) for the period 1989/90–2004/05, respectively (Matsuoka *et al.*, 2005). It should be noted that abundance estimates for fin whales were made based on data obtained south of 60°S because the Japanese dedicated sighting surveys did not cover the main distribution area of fin whales in the austral summer, which is north of 60°S.

The circumpolar abundance of the Antarctic blue whales based on IDCR/SOWER surveys was estimated at 1,700 (95% Bayesian interval 860–2,900) in 1996. Although this figure corresponds to less than 1% of the original levels, blue whales are increasing at 7.3% per annum (95% Bayesian interval 1.4–11.6%) (Figure 8) (Branch *et al.*, 2004).

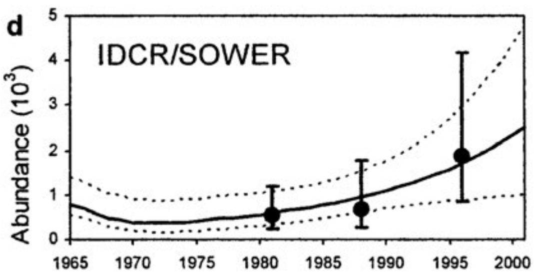

Figure 8. Posterior abundance trajectory (and 95% interval) from 1965, and the IDCR/SOWER abundance estimates for blue whales in the Antarctic (d) (after Branch *et al.*, 2004).

Possible inter-specific effects of the recovery of large whales

Antarctic minke whale

Trend in abundance

Hakamada *et al.* (2013) estimated abundance and abundance trends of Antarctic minke whale in the Indian sector (Area IV) and Pacific sector (Area V) based on Japanese dedicated sighting surveys (JARPA and JARPAII), under the assumption of g(0)=1. Abundance estimates for the Indian sector range from 16,562 (CV=0.542) in 1997/98 to 44,945 (CV=0.338) in 1999/00, while those for the Pacific sector range 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 are 1.8% with a 95% CI of [−2.5%, 6.0%] for the Indian sector and 1.9% with a 95% CI of [−3.0%, 6.9%] for the Pacific sector. Adjustments to allow for the g(0) being less than 1 were made by the application of a regression model, developed from the results of the Okamura-Kitakado (OK) method estimate of minke whale abundance from the IDCR-SOWER surveys, which provides estimates of g(0) from the statistics of the minke whale school size distribution in a stratum. With this adjustment, abundance estimates increased by an average of 32,333 (106%) for the Indian sector and 89,245 (86%) for the Pacific sector, while the estimates of annual rates of increase and their 95% CIs changed slightly to 2.6% [−1.5%, 6.9%] for the Indian sector and 1.6% [−3.4%, 6.7%] for the Pacific sector. See Figure 9 for the abundance trends in the two sectors.

In 2012 the IWC SC agreed to a new best abundance estimate for Antarctic minke whale in Antarctic open waters south of 60°S, based on IDCR/SOWER sighting data. The estimates were 720,000 based on the sighting data collected during the CPII (1985/86–1990/91) with 95% CI (512,000, 1,012,000), and 515,000 based on the sighting data collected during the CPIII (1992/93–2003/04) with

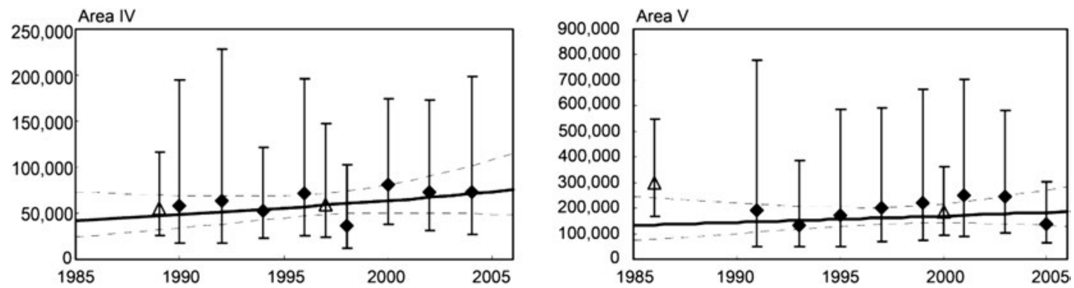

Figure 9. The best case estimates of annual abundance of Antarctic minke whale in the Indian sector (Area IV) and Pacific sector (Area V) together with their 95% CIs. The IDCR/SOWER estimates for a common northern boundary for CPII and CPIII are shown by the open triangles. Confidence intervals include allowance for additional variance. The dashed curves indicate the 95% Cis for the exponential model (after Hakamada *et al.*, 2013).

95% CI (361,000, 733,000). No significant statistical differences were found between the CPII and CPIII estimates (IWC, 2013).

The estimates in the Indian sector (Area IV) were 55,237 (CV: 0.17) in CPII and 59,677 (CV: 0.34) in CPIII. In the Pacific sector (Area V) were 300,214 (CV: 0.13) in CPII and 183,915 (CV: 0.11) in CPIII.

By considering the 95% CIs of the estimates it can be suggested that the stocks of Antarctic minke whales are broadly stable with at most a slight decline.

Changes in spatial distribution

Figures 10 and 11 show the temporal changes in whale species composition in the Indian sector (Area IV) and Pacific sector (Area V) based on Japanese dedicated sighting surveys. In the Indian sector, humpback whales were more frequently observed than Antarctic minke whales in recent years (Figure 10). In the Pacific sector Antarctic minke whale is still the predominant species (Figure 11).

The increase in abundance of the large whales once depleted by commercial whaling implies changes in the spatial distribution of whale species. Murase *et al.* (2014) examined Japanese dedicated sighting survey data to study the spatial distribution of Antarctic minke whales and humpback whales in the Indian sector (Area IV) during 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). 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 minus 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 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 concluded that the spatial distribution of humpback whales expanded during the period investigated while that of Antarctic minke whales remained stable. The results suggested the possibility that competition between humpback and Antarctic minke whales for habitat in the Indian sector (Area IV) during the period studied could have been intensified as abundance of humpback whales increased. A summary of the results are presented in Figure 12.

It should also be mentioned here that Antarctic minke

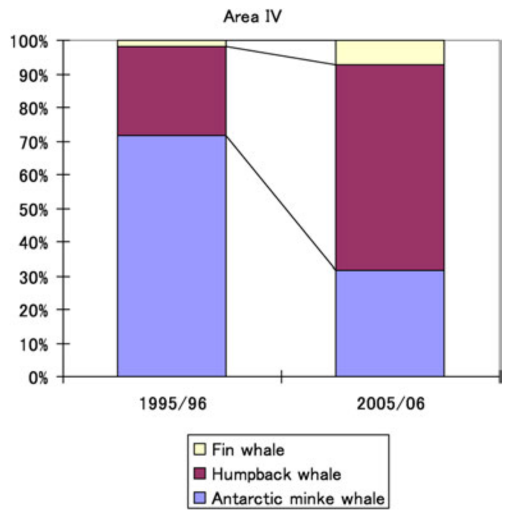

Figure 10. Sighting composition of Antarctic minke, humpback and fin whales in the Indian sector (Area IV) for two Japanese dedicated sighting surveys, 1995/96 and 2005/06. Note that humpback whales are more frequently observed than Antarctic minke whales in recent years (see explanation of data source in Pastene *et al.*, 2014).

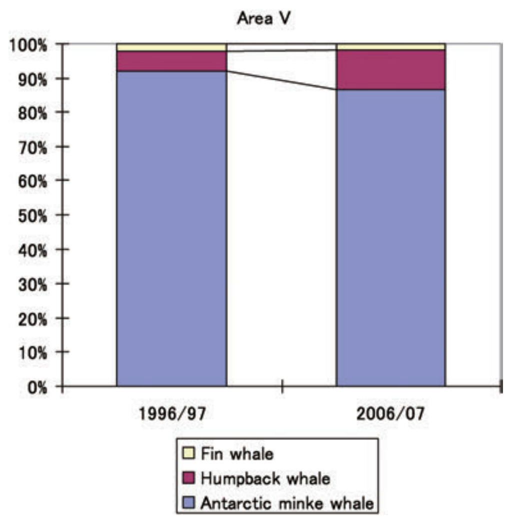

Figure 11. Sighting composition of Antarctic minke, humpback and fin whales in the Pacific sector (Area V) for two Japanese dedicated sighting surveys, 1996/97 and 2006/07. Note that Antarctic minke whale is still the predominant species. The composition of humpback whales in the total sighting have increased but at a slower pace compared to the Indian sector (see explanation of data source in Pastene *et al.*, 2014).

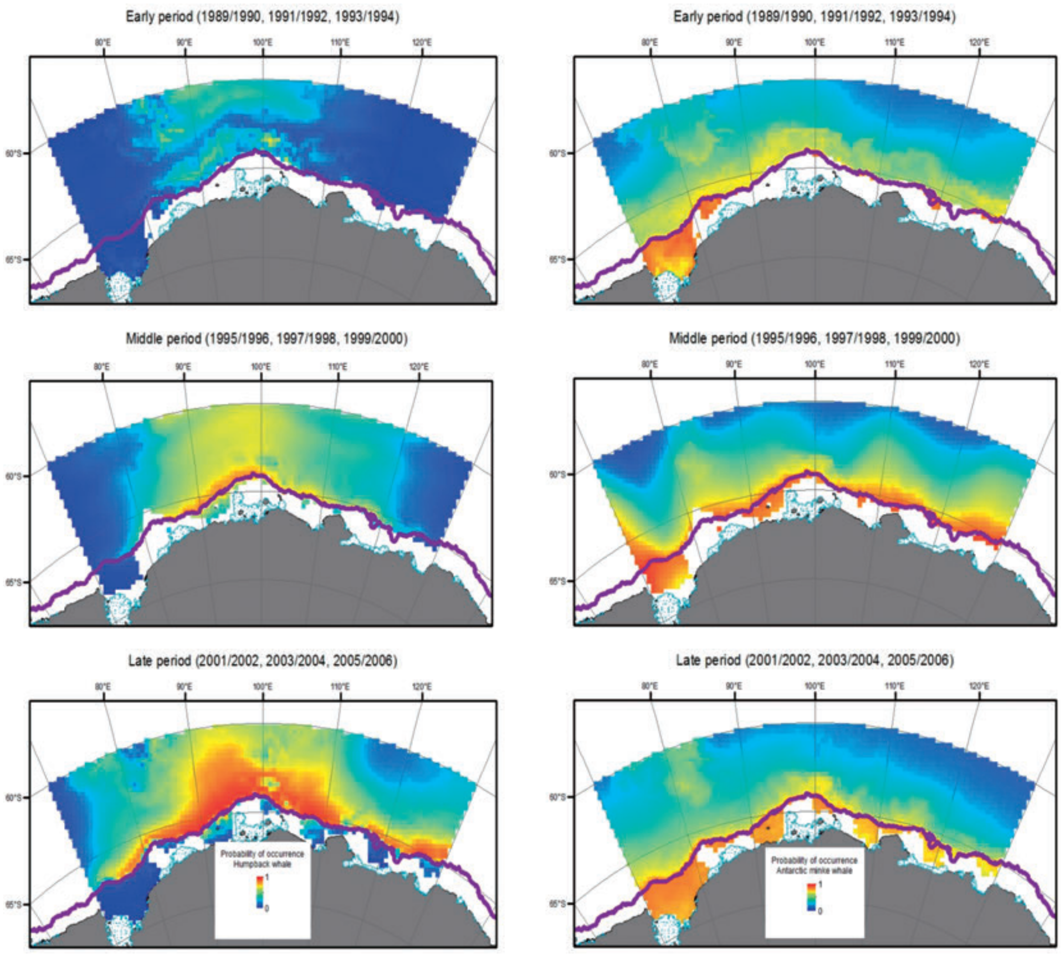

Figure 12. Probability of occurrence of humpback (left) and Antarctic minke (right) whales in the Indian sector (Area IV) in three periods: early, middle and late (after Murase *et al.*, 2014). Red indicate high probability of occurrence.

whales have been observed more frequently in polynias within the pack-ice in recent years (Matsuoka, pers. comm. 2016), reflecting perhaps a response to the geographical expansion of humpback whales.

Nutritional conditions

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 by Japanese research (JARPA and JARPA II) in the Indo-Pacific region of the Antarctic (Areas IV and V).

Konishi *et al.* (2008) showed the results of the annual trend in energy storage in sexually mature Antarctic minke whales based on data collected for a period of 18 years in the Indo-Pacific region. Regression analyses clearly showed that blubber thickness, girth and fat weight have been decreasing for nearly two decades. 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 13).

Konishi *et al.* (2014) reported the results of an analysis of temporal trend in stomach content weight in the Antarctic minke whale in a 20-year period. 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 in both males and females, except in the case of females sampled at higher latitude in the Ross Sea. These results were 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 found no change in prey availability for Antarctic minke whales.

These studies suggested a decrease in the availability of krill for Antarctic minke whales.

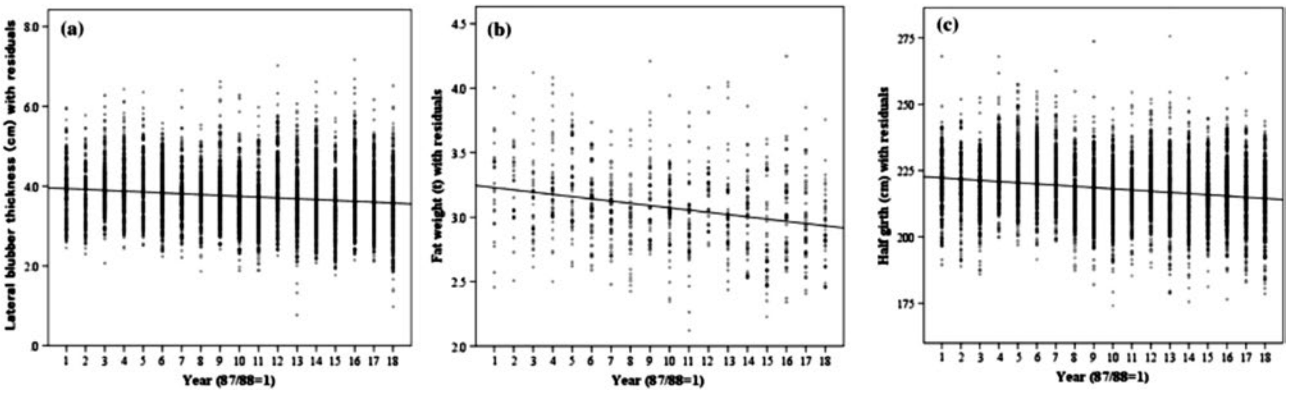

Figure 13. Yearly trends in blubber thickness (a), fat weight (b) and girth (c) in Antarctic minke whale in the Indo-Pacific region of the Antarctic from 1987/88 to 2004/05 (after Konishi *et al.*, 2008).

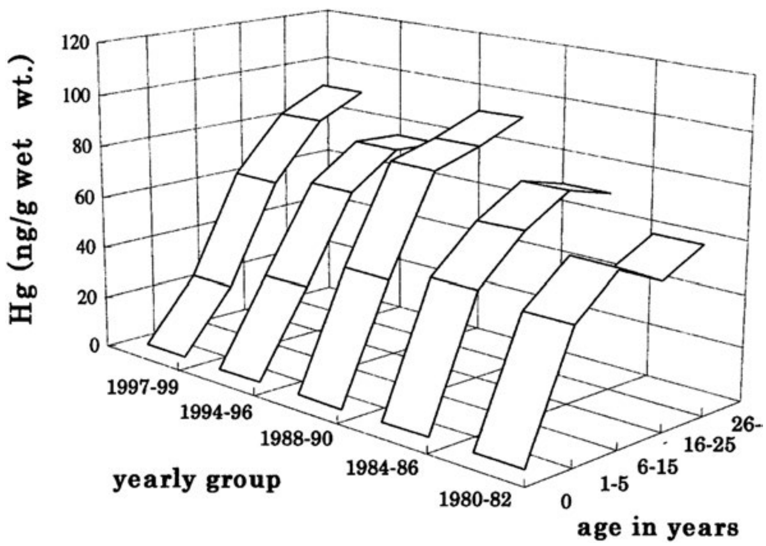

Figure 14. Yearly age-related changes of hepatic Hg concentrations in the Antarctic minke whale (after Honda *et al.*, 2006).

Pollutant loads

Honda *et al.* (2006) studied yearly age-related accumulations of Hg in the Antarctic minke whales collected in the period 1980–1999 in the Indo-Pacific region. One of the relevant results was that of Hg levels and growth rates in young age-groups (1–5 years old): Hg levels and body weights for the 1997/99 season groups were significantly lower than those for the 1988/90 groups. On the other hand they examined the Hg levels in krill from the whale stomach, and no yearly significant differences were found. They concluded that the differences in Hg levels in younger age groups was due to differences in the amount of food intake by the whale i.e. whale are consuming less food in recent years (Figure 14). These results are consistent with the decrease in stomach contents weight in Antarctic minke whales in recent years.

Demographic parameters

As shown in Figure 5 the age at sexual maturity for Antarctic minke whales has stabilized or slightly increased since the 1970′s and 1980′s. The recruitment has consistently been broadly stable since the 1970′s and the total abundance estimated by SCAA has been stable or slightly decreasing (Figure 6). These observations are consistent with the observation of deteriorated nutritional conditions since the 1980′s.

Other species

A recent study showed that the regional population of the krill-eater Adelie penguin have almost doubled in abundance since the 1980′s and have been increasing since the earliest counts in the 1960′s. These results of decadal-scale change were based on a combination of extensive new population survey data, new population estimation methods, and re-interpretation of historical survey data (Southwell *et al.*, 2015).

Summary

Evidence available since the 1980′s has shown that the nutritional conditions for Antarctic minke whales have not been optimal as revealed by the decrease in energy storage and stomach content weight since the 1980′s. This observation is consistent with the observations that age at sexual maturity has stabilized or slightly increased in the 1970′s and that the recruitment was stable after 1970. The stable trend in recruitment is consistent with the total abundance of Antarctic minke whale estimated by sighting data which has been broadly stable since the 1980′s.

The observations above suggest less availability of krill for Antarctic minke whales. Less availability of krill for this species could result from competition with other recovering krill-eater large whale species, e.g. the reversal of Laws′ ′krill surplus′ hypothesis. The implication of these ′deteriorated′ nutritional conditions is the possibility of a decrease of Antarctic minke whale abundance in the near future.

Southwell *et al.* (2015) provided two explanations for the increase of the Adelie penguins in East Antarctica. The first was that 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, and improved prey availability. The second was that 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 a strong recovery of krill-eater large baleen whales has been reported since the 1980′s, it can be suggested that environmental factors are more plausible for explaining the increase of Adelie penguins since the 1980′s. Probably environmental changes have stronger effects on land-based predators such as the penguins than on sea-based predators such as whales.

CONCLUDING REMARKS

The review of scientific evidence for ecosystem changes in the Indo-Pacific region of the Antarctic has highlighted the importance of long-time monitoring research programs focused on the collection of biological data of krill predators (land-based and sea-based predators) as well as data on sea ice cover and environmental variables. Evidence of environmental changes are more marked in West Antarctic than East Antarctic. An implication of this is that in East Antarctic (Indo-Pacific region), competition for space and food could better explain the pattern of changes in biological and demographic parameters observed among sea-based krill predators. However to further investigate the plausibility of this hypothesis it will be necessary to obtain information on krill biomass trends in the research area. There is some partial information based on dedicated krill surveys in the past but the information is scattered and needs to be combined with new surveys in a comprehensive and consistent way so that time series data can be obtained.

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