First attempt of estimation of feeding impact on krill standing stock by three baleen whale species (Antarctic minke, humpback and fin whales) in Areas IV and V using JARPA data

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ABSTRACT

To assess the magnitude of the interspecific competition among three baleen whale species, Antarctic minke, humpback and fin whales, for their major prey krill, impact of feeding of three baleen whales on krill was estimated in Areas IV and V using JARPA data. Three data sets, whale abundance, daily krill consumption rate of whales and krill biomass, were used in the analysis. All data used in this analysis were collected in situ except daily krill consumption rate of humpback and fin whales because of lack of biological information. Three baleen whales consumed 10-21% and 31% of krill standing stock in Area IV and V, respectively. In Area IV, humpback whales consumed krill twice to three times of Antarctic minke whales. The results indicated that krill surplus for Antarctic minke whales could be now ended because of increase of humpback whales in Area IV though this point should be investigated quantitatively in future using multi-species model including both baleen whales and krill.

INTRODUCTION

In the Antarctic, intensive commercial whaling on large baleen whales, blue (*Balanoptera musculus*), fin (*B. physalus*) and humpback whales (*Megaptera novaeangliae*) between early and mid 20th century resulted in increasing in amount of available food, Antarctic krill (*Euphausia superlba*), to other krill feeder such as Antarctic minke whales (*B. bonaerensis*). Although neritic krill species, ice krill (E. crystallorophias), is a food item of Antarctic minke whales in some part of the Antarctic waters such as the Ross Sea and Prydz Bay, the contribution to the total food consumption of Antarctic minke whales is low in comparison with Antarctic krill (Tamura et. al. 2006). This phenomenon is called as “krill surplus” (Laws, 1977) and it has been a central theorem of the Antarctic ecosystem study. In response to the krill surplus, the decline of mean age at sexual maturity of minke whales was observed (Kato, 1987). But after the ban of commercial whaling of large whales in 1987, abundance of those species appears to increase in recent years. For example, abundance of blue whales increase 8% per year at the circumpolar level (Branch et al., 2004) though the abundance was still low comparing with pre-exploitation population size. Humpback whale Breeding stock D (Area IV) have been showed remarkable increasing rate of abundance (Matsuoka et al., 2006) and recover to near pre-exploitation level (Johnston and Butterworth, 2005). Given such information of recovery of abundance of large baleen whales, we have to revisit the krill surplus theorem and reconsider the current magnitude of interspecific competition of baleen whales for krill. To assess the magnitude of interactions between krill and baleen whales in multi-species model, estimation of feeding impact of baleen whales on krill is critically important. It had recognized that study of interspecific competition among baleen whales had been precluded because of lack of good data on whale abundance, food consumption of mysticetes and euphausiid biomass

(Clapham and Brownell, 1996). However, multi-disciplinary studies combing surveys on cetacean, krill and oceanography were conducted in the Antarctic waters in recent years to solve the questions. For instance, feeding impact of baleen whales to standing stock of krill was estimated in the South Atlantic region of the Southern Ocean (Reilly et al., 2004) but it lacked the in-situ biological information to estimate the krill consumption rate of baleen whales.

Data from the Japanese Whale Research Program under Special Permit in the Antarctic (JARPA) provided us opportunity to investigate the feeding impact of baleen whales on krill using in-situ cetacean sighting and biological data as well as krill biomass data which were collected concurrently. JARPA has been conducted every year since the 1987/88 in compliance with Article VIII of the International Convention for the Regulation of Whaling (ICRW). One of the primary objectives of the JARPA is elucidation of the role of whales in the Antarctic marine ecosystem through the study of whale feeding ecology. To achieve the study objectives, cetacean sighting and biological survey has been conducted from the beginning of JARPA. The JARPA interim review meeting took place in May, 1997. In the meeting, it was pointed out that concurrent studies on the distribution and abundance of prey species was required to achieve the objective. In response to that point, echo sounder survey to examine distribution and abundance of krill has been conducted concurrently with cetacean survey in later years of JARPA.

This paper presented the results of estimation of feeding impact of three baleen whale species, Antarctic minke, humpback and fin whales, on krill standing stock in Area IV and Area V.

MATERIALS AND METHODS

General

Two baleen whale management area defined by the International Whaling Commission (IWC), Area IV (70°E-130°E) and Area V (130°E-170°W), were surveyed alternative years in JARPA. In addition to two Areas, eastern part of Area III and western part of Area VI were also surveyed alternative years. The echo sounder data from 1999/2000 to 2002/2003 were considered as suitable for this analysis after the biomass estimation of krill using the echo sounder data was conducted. Intra-annual variability in krill abundance was well known around the Antarctic. For example, krill abundance early (December) and late (March) austral summer was significantly lower than that in January around South Georgia (Brierley, et al., 2002). Though echo sounder data were corrected in 1998/1999 in Area V, the survey timing and coverage were different from rest of two years (2000/2001 and 2002/2003). Higher Krill biomass in 1998/1999 than rest of two years could indicate such intra-annual variability. By the same reasoning, Area V in 2004/2005 was not considered because poor weather condition impeded data recording in northwestern part of Area V. Eastern part of Area III and Western part of Area VI were surveyed in either/both December or/and March. Because intra-annual variability of krill biomass could be one of the confounding factors to interpret inter-annual differences of feeding impact of baleen whales on krill, data from Area V in 1998/99 and 2004/2005, Eastern part of Area III and Western part of Area VI were not considered in this paper.

Abundance estimation of whales

Methodology of abundance estimation of whales used in this study was described by Burt and Stahl (2000) which is the standard methodology adopted by IWC. The program DISTANCE (Buckland et al., 1993) was used for abundance estimation. Details of abundance estimation methods of Antarctic minke whales and, humpback and fin whales were described in Hakamada et al. (2006) and Matsuoka et al. (2006), respectively. For Antarctic minke whale abundance estimates, correction methods developed by Haw (1991) were applied to estimate the degree of under-estimate of the abundance because of closing mode.

Prey consumption estimation of whales

We estimated the total prey consumption of krill by three baleen whale species. For Antarctic minke whale, we estimated the total prey consumption of krill consumed by different maturity stages of

Antarctic minke whales in Areas IV and V based on the abundance data of Antarctic minke whale and composition of maturity stages of Antarctic minke whales sampled during JARPA surveys (Tamura et al., 2006). For humpback and fin whale, we estimated the total prey consumption of krill using Method 2 of Tamura et al. (2006). We assumed mean body masses of 30,400 kg and 55,600 kg for humpback and fin whale, respectively (Trites and Pauly, 1998). The average field metabolic rate used in these calculations was obtained from Blix and Folkow (1995). The value of 80 kJ/kg per day is based on indirect determination of oxygen consumption from studies of the respiratory rates. The total muscle, internal organs fat and blubber masses of humpback and fin whale did not calculated. We assumed that they need 71.3 % of field metabolic rate as muscle, internal organs fat and blubber deposition. We assumed that humpback and fin whales spend about 120 days during the austral summer in the Antarctic (Lockyer, 1981).

Krill biomass estimation

Echo sounder surveys to estimate the krill biomass were conducted concurrently with cetacean sighting survey. An EK500 scientific echo sounder (Simrad, Norway) with software version 5.30 operating frequency at 38 and 120 kHz on board the cetacean survey vessel was used to collect data. We applied the acoustic data analysis described by Hewitt and Demer (1993) and Demer and Hewitt (1995). Details of the analysis were described in Murase et al. (2006).

RESULTS

Results of the abundance estimation and the krill consumption of Antarctic minke, humpback, and fin whales and the biomass of krill were summarized in Table 1. Humpback whales fed krill more than Antarctic minke whales in Area IV. In 2001/02, humpback whales fed krill twice to three times of Antarctic minke whales. Fin whales fed about same amount of krill as Antarctic minke whales in 2001/2002. In contrast, Antarctic minke whales fed 21-25% of krill standing stock in Area V whereas humpback and fin whales fed less than 10%. Three baleen whales fed 11-20% and 31% of krill standing stock in Areas IV and V, respectively.

DISCUSSION

Matsuoka et al. (2006) and Johnston and Butterworth (2005) suggested that humpback whales in Area IV have increased rapidly in recent years. In conjunction with it, long term trend of age at sexual maturity of Antarctic minke whales were remained constant for 7-8 years in recent years in Area IV (Zenitani et al. 2006). As the number of predators increase, intraspceicifc and interspecific competition for krill would increase. As the results, the decreasing trend of age of sexual maturity of Antarctic minke whales could be suspended. In addition to the constant trend of age at sexual maturity, it was indicated that blubber thickness of Antarctic minke whales getting thinner and thinner in recent years (Konishi et al. 2005). The present analysis suggested that amount of krill consumed by humpback whales was about twice to three times of Antarctic minke whales. Together with those analysis results, interspecifc competition between humpback and Antarctic minke whales for krill in Area IV could already occur but the magnitude would not be too high because the trend of age at sexual maturity of Antarctic minke whales were remained constant at this stage.

Aside from yearly trend, it was indicated that year to year food availability fluctuation could be occurred. The blubber thickness of Antarctic minke whales in 1999/2000 was higher than 2001/2002 (Konishi and Tamura, 2005). In 1999/2000, abundance of humpback whales was lower than 2001/2002 (Matsuoka et al. 2006). As the results, feeding impact of humpback whales on krill was lower in 1999/2000. Such a year to year abundance fluctuation of humpback whales could affect the biological parameters of Antarctic minke whale though actual mechanism is still open to the question.

In contrast, because abundances of large baleen whales were still in low levels in Area V, Antarctic minke whales appeared to be dominated over krill but blubber thickness of Antarctic minke whales getting thinner and thinner in recent years (Konishi and Tamura, 2005). The result could indicate the intraspecific competition of Antarctic minke whales in Area V.

Though feeding impact of fin whales on krill appeared to be low in survey area, one should bear in mind that main distribution area of fin whales is far north of the survey area. Abundance of blue whales in Area IV and V in years considered in this paper was in low level (143-317 individuals) (Matsuoka et al., 2006) though it increases at the circumpolar level (Branch et al., 2004). Although feeding impact of blue whales on krill is still low at this stage, effect of the increase of abundance of blue whales could intensify the interspecific competition among baleen whales in the future. In this paper, krill predators other than baleen whales were not considered because of lack of reliable abundance estimates for those species. Though it is ideal to consider all krill predators to assess the feeding impact on krill, minimum realistic approach considering only baleen whales is realistic at this stage. The results of such excises can be updated if the abundances of other krill predators are available.

Production to biomass (P/B) ratio of Antarctic krill was ranged from 0.8 to 2.27 (Siegel, 2000 for review). Given the P/B ratio of Antarctic krill, feeding impact of baleen whales on standing stock of krill reported in this paper could not be too high. Krill density showed both short and long term changes. In short term, krill biomass showed large year to year fluctuation at decadal scale in response to environmental variability such as sea ice extent and oceanographic conditions (e.g. Pakhomov, 2000; Hewitt and Demer, 2003). It was reported that krill biomass have showed statistically significant decreasing trend in the southwest Atlantic since 1976 (Atkinson et al. 2004) though the magnitude of decrease should be studied further to draw the conclusion because wide varieties of net types were used in the analysis. Because the P/B ratio could change in response to the environmental variables in both short and long term, feeding impact of baleen whales on standing stock of krill could be different year to year.

Recent study suggested that baleen whale consumed 4-6% of krill biomass in the South Atlantic sector of the Southern Ocean (50°S-65°S, 20°W-70°W) (Reilly et al., 2004). Large discrepancy between their result and our result could be explained by following reasons. As pointed by Reilly et al. (2004), large proportions of Antarctic minke whales in the South Atlantic sector of the Southern Ocean may migrate to the ice edge zone during the survey period. It was well known that the ice edge zone is important feeding habitat of Antarctic minke whales (Ichii, 1990; Murase et al., 2002). There was no pack ice in the South Atlantic sector of the Southern Ocean in austral summer. Thus, few presences of Antarctic minke whales could contribute lower krill consumption rate. Inclusions of sightings in poor weather conditions and ambiguous species identification sightings in abundance estimation in Reilly et al. (2004) added large uncertainty to estimation of amount of krill consumed by cetaceans. It was reported that Antarctic minke whales distributed in the pack ice region where normal cetacean sighting survey vessels could not access (e.g. Naito, 1982; Ensor, 1989). Krill biomass under sea ice was significantly higher than that in open sea (Brierley et al., 2002). Because sea ice is not retreated to the Antarctica in most of portion of Area IV and Area V, within pack ice distribution of Antarctic minke whales and krill could affect the estimation of krill consumption rate by baleen whales in both negative and positive directions. Krill consumption by humpback and fin whales could have either positive or negative biases because the estimates had many assumptions. To assess the adequacy of estimated krill consumption rate of baleen whales, simulation study of multispecies model such as Mori and Butterworth (2006) could be useful to predict the dynamics of both krill and baleen whales.

It should be noted that Demer and Conti (2005) proposed the new TS for *E. supreba* using Stochastic Distorted-Wave Born-Approximation (DSDWBA) model. If the new TS applied to our results, krill biomass would be 2.5 times higher than the current estimates. Even though feeding impact of baleen whales on krill in this paper was estimated using best scientific knowledge at the time of the analysis, the values should be revaluated once the new reliable scientific facts are available in the future.

A combination of several analyses including presented in this paper indicated that krill surplus situation could be changed. But it is not clear whether the trajectory of the Antarctic marine system could go to the pristine state or to the new equilibrium at this stage. Long term data collection of baleen whales and krill is necessary to monitor the change in the Antarctic marine ecosystem. Following points should be considered to improve the estimate of the rate of krill consumption by baleen whales in future: 1) long term concurrent cetaceans and their prey survey should be conducted in peak abundance season of krill and whales (January and February) to minimize seasonal effect, 2) the survey should be conducted in same area in same survey timing to interpret yearly changes and 3) biological information of humpback and fin whales will improve the krill consumption estimation by those two species.

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Table 1. Summary of abundances and krill consumption of Antarctic minke, humpback and fin whales and, krill biomass in Area IV and V in each survey year.

Area	Year	Abundance (inds.)	Krill consumption (milliont t)	Krill biomass (ten thousand ton)	(Whale %)
・Antarctic minke whale					
IV	1999/00	44,931	1.19	34.20	3.5
	2001/02	48,280	1.33	34.10	3.9
V	2000/01	164,789	4.48	20.70	21.6
	2002/03	201,883	5.73	22.60	25.4
・Humpback whale (1,108.8 kg/day)					
IV	1999/00	16,751	2.23	34.20	6.5
	2001/02	31,134	4.14	34.10	12.1
V	2000/01	5,130	0.68	20.70	3.3
	2002/03	2,873	0.38	22.60	1.7
・Fin whale (2,027.9 kg/day)					
IV	1999/00	1,565	0.38	34.20	1.1
	2001/02	5,861	1.43	34.10	4.2
V	2000/01	5321	1.29	20.70	6.2
	2002/03	3210	0.78	22.60	3.5
・Total					
IV	1999/00	-	3.8	34.20	11.1
	2001/02	-	6.9	34.10	20.2
V	2000/01	-	6.5	20.70	31.2
	2002/03	-	6.9	22.60	30.5