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Prey selection of common minke (*Balaenoptera acutorostrata*) and Bryde's (*Balaenoptera edeni*) whales in the western North Pacific in 2000 and 2001

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ABSTRACT

A study of common minke and Bryde's whales was conducted in the western North Pacific in the 2000 and 2001 summer seasons to estimate prey selection of cetaceans as this is an important parameter in ecosystem models. Whale sighting and sampling surveys and prey surveys using quantitative echosounder and mid-water trawl were carried out concurrently in the study. Biomasses of Japanese anchovy, walleye pollock and krill, which were major prey species of common minke and Bryde's whales, were estimated using an echosounder. The results suggested that common minke whale showed prey selection for Japanese anchovy while they seemed to avoid krill in both the offshore and coastal regions and walleye pollock in the continental shelf region. Selection for shoaling pelagic fish was similar to that in the eastern North Atlantic. Bryde's whale showed selection for Japanese anchovy in August 2000 and July 2001, while it showed prey selection for krill in May and June in 2001.

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INTRODUCTION

A wide variety of prey species of common minke whales (*Balaenoptera acutorostrata*) in the western North Pacific was qualitatively described using commercial whaling data (Omura and Sakiura, 1956; Kasamatsu and Hata, 1985; Kasamatsu and Tanaka, 1992). These included Japanese anchovy (*Engraulis japonicus*), Japanese sardine (*Sardinops melanostictus*), sand lance (*Ammodytes personatus*), chub mackerel (*Scomber japonicus*), walleye pollock (*Theragra chalcogramma*), Pacific cod (*Gadus macrocephalus*), Pacific herring (*Clupea pallasi*), squid, krill and copepods. A quantitative feeding ecology study of minke whale was conducted from 1994 to 1999 in the Japanese Whale Research Program under Special Permit in the western North Pacific (JARPN) (Tamura and Fujise, 2002). The study showed a large variation of main prey species with area, season and year. The most important prey species in May and June was Japanese anchovy, and it changed to Pacific saury in July and August. Krill was the most important prey in September. Walleye pollock was also one of the important prey species in June and September in continental and shelf-edge waters off Hokkaido. Although Bryde's whale (*Balaenoptera edeni*)[1] fed on Japanese anchovy, Japanese sardine, horse mackerel (*Trachurus japonicus*), chub mackerel, lantern fish and krill (Nemoto, 1959), those data came from commercial whaling data and no quantitative analysis has been conducted. Because fishing effort was concentrated on the high-density area of the cetaceans, samples from commercial whaling had an inherent

[1]Nomenclature adopted by the International Whaling Commission (IWC) (Anonymous, 2001) was used. It contains more than one species but it is still unsettled in IWC.

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bias. Random sampling of cetaceans should be required to remove the bias.

Prey species of cetaceans have shown decadal fluctuations around Japanese waters. In the western North Pacific, commercial catch histories of pelagic fishes have shown drastic fluctuation and quasi-decadal species alterations, so-called species replacement since the 1950s (Yatsu *et al.*, 2001). Dominant species, were chub mackerel in the 1970s, Japanese sardine in the 1980s, and Pacific saury, Japanese anchovy and Japanese common squid in the 1990s. It is suggested that ocean-climate regime shifts have substantial impacts on the species replacement together with species interactions, although the mechanism of the replacement has not been clearly understood (PICES, 2004). Commercial catches of Pacific stock of walleye pollock were around 0.25 million tons from 1975 to 1985 but gradually declined to 0.15 million tons in 1996. It returned to 0.26 million tons in 1998 because of the presence of a strong cohort in 1995 but the catches declined again from 1999 to 0.11 million tons in 2002 (Fisheries Agency of Japan, 2004).

Fisheries scientists have been compelled to conclude that models that aim to contribute to the sustainable marine resources management have to take the ecosystem approach because of the recognition that exploited stocks are parts of ecosystems and that species usually interact (e.g. predator–prey relationship) (Sumaila *et al.*, 2000). Because common minke and Bryde's whales fed on target species of commercial fisheries and those target species of commercial fisheries showed year-to-year fluctuations, development of ecological models including cetacean in the western North Pacific is desirable from the marine living resources management and conservation perspectives. In such models, like the multispecies virtual population-based model, MULTISPEC (Bogstad *et al.*, 1997) and the mass balance model, ECOPATH (Pauly *et al.*, 2000), prey selection data are very important. To estimate prey selection using both food habit data of predator and prey availability data, the whale and the prey surveys must be conducted concurrently.

This paper presents the results of the first attempt to conduct concurrent whale and prey surveys in the western North Pacific in 2000 and 2001 as a part the Japanese Whale Research Program under Special Permit in the western North Pacific Phase II (JARPN II). The underlying question is whether common minke and Bryde's whales show any prey selection.

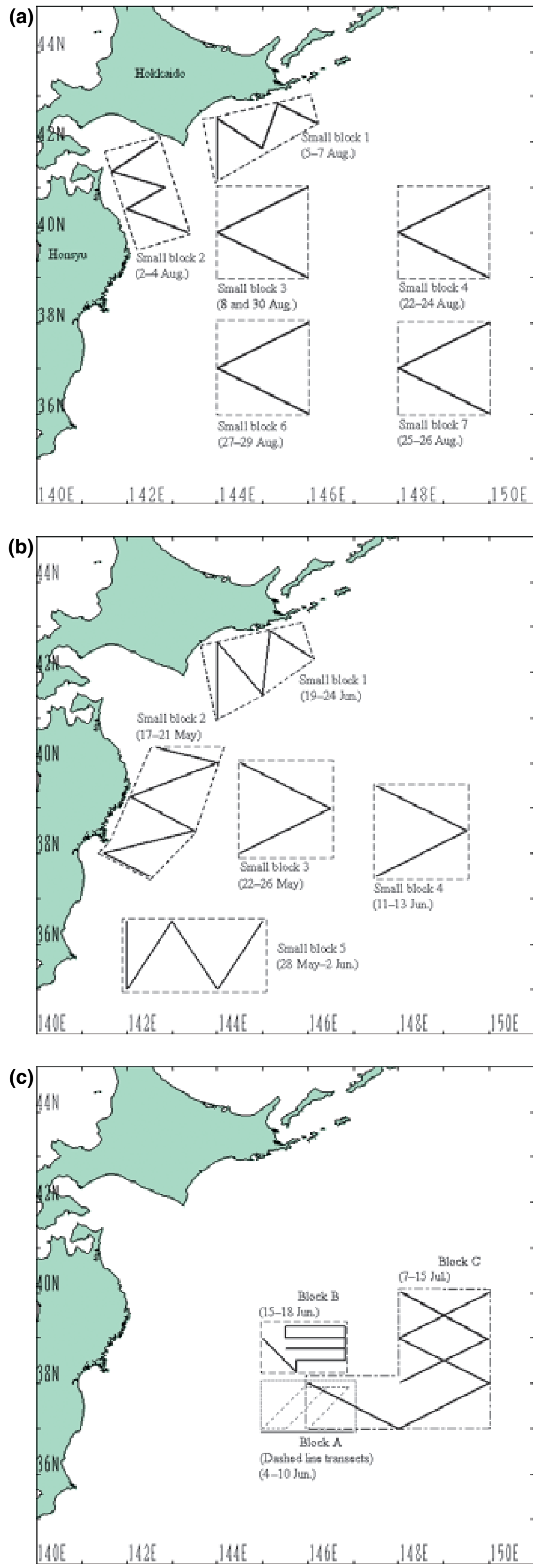


Figure 1. Research area, small blocks and planed track lines: (a) 2000, (b) 2001, and (c) 2001 (additional blocks).

In past discussions of food use patterns, the terms 'selection' and 'preference' have been used interchangeably, raising some confusion (Litvaitis, 2000). In this paper, preference is defined as the likelihood that an animal selects a particular resource given equal amounts of others, whereas selection is defined as the animal choosing a resource irrespective of amount of resources according to Johnson (1980).

MATERIALS AND METHODS

Survey area, period and vessels

The research area of the concurrent whale and prey surveys was off the Pacific coast of northern Japan (Fig. 1). The northern part of the research area was under the influence of Oyashio (cold low-salinity water) whereas the southern part of the area was under the influence of Kuroshio (warm high-salinity water). The area between Oyashio and Kuroshio is called the Kuroshio–Oyashio inter-frontal zone or transitional zone. As the first attempt to conduct concurrent whale and prey surveys in the western North Pacific, we mainly focused on a wide area coverage given the short survey periods to identify the conditions of cetacean feeding habitat in different water masses as well as bottom topography. To achieve our goal, small blocks were established within the survey area and the length of trackline in each small block was set to allow the survey to be completed in each small block within 2–5 days. Degree of coverage (d) defined by Aglen (1989) is commonly used to measure the sampling intensity of an echo sounder survey. Degree of coverage is written as $d = D/\sqrt{A}$ where D is the total length of the trackline and A is the size of the survey area. Although it is pointed out that a value of d more than 6 is an indication of sufficient coverage, priority was given to wide area coverage instead of degree of coverage. Seven small blocks (Blocks 1–7) were set within the area in 2000 but Block 5 was not surveyed because of logistical reasons. Five small blocks (Blocks 1–5) with an additional three blocks (Blocks A–C) were set in 2001. The small blocks were predetermined mainly based on the bottom topography and the information on the sea surface temperature just before the survey. Because sample sizes of Bryde's whales in the predetermined area in 2001 were small in number, the additional blocks were set adoptively to acquire more samples. Blocks 5 and A in 2001 were not

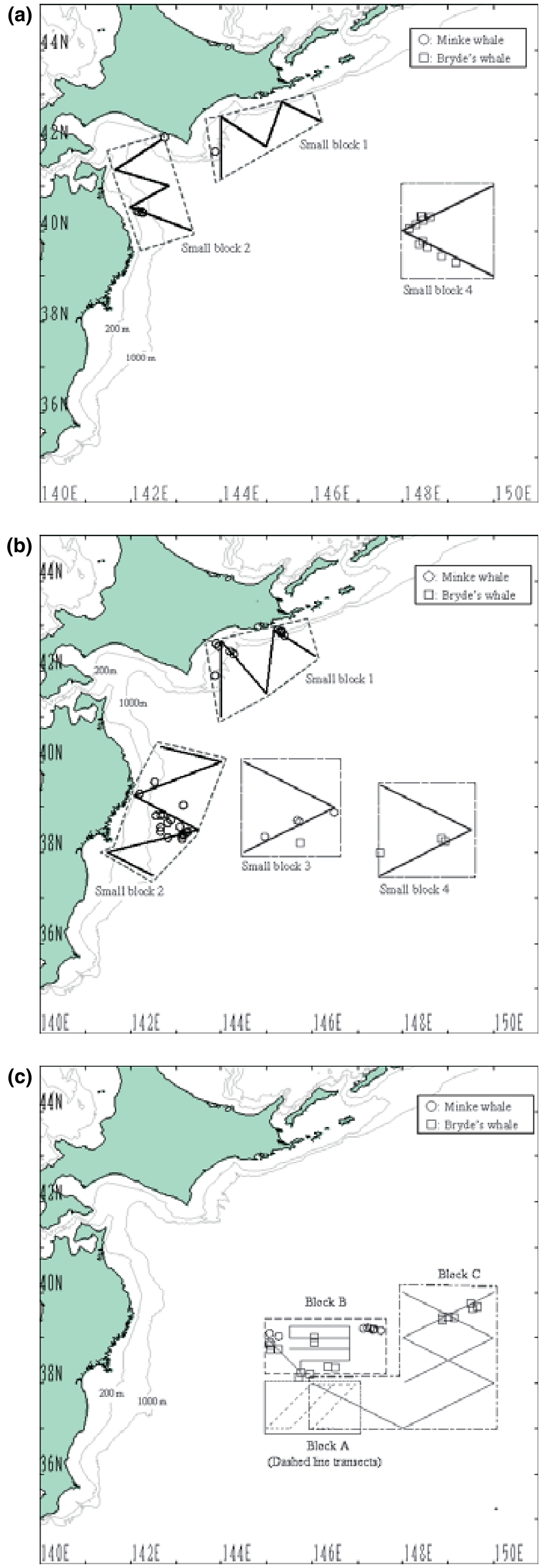


Figure 2. Sighting positions of sampled minke and Bryde's whales: (a) 2000, (b) 2001, and (c) 2001 (additional blocks). Thin lines showed 200 and 1000 m isobath.

Table 1. Summary of stomach contents of minke whales (a) and Bryde's whales (b) used in this analysis.

	Survey period				Stomach content						
					JA		WP		Kr		
Year	Prey	Cetacean	Block	Sampled animals (n)	n	wt (kg)	n	wt (kg)	n	wt (kg)	Total wt (kg)
(a)											
2000	5–7 August	7 August	1	1	1	26.3		–		–	26.3
	2–4 August	3–5 August	2	5	5	205.3		–		–	205.3
	19–24 June	19–23 June	1	10	5	110.0	8	403.8	2	35.2	549.1
2001	17–21 May	14–18 May 21–22 May	2	18	18	435.7		–		–	435.7
	22–26 May	22–27 May	3	4	1	162.6		–	3	13.9	176.5
	15–18 June	13–18 June	B	6	2	85.8		–	4	236.2	322.0
(b)											
2000	22–24 August	22–26 August	4	10	8	4288.7			3	191.1	4479.8
	22–26 May	22–27 May	3	1		–			1	215.4	215.4
2001	11–13 June	10–13 June	4	3		–			3	93.8	93.8
	15–18 June	13–18 June	B	12		–			12	1021.7	1021.7
	7–15 July	11–13 July	C	6	3	19.1			4	14.3	33.4

JA, Japanese anchovy; WP, Walleye Pollock; Kr, Krill. n, number of stomachs that contained given species; wt (kg), total weight of each prey species that was found in all sampled animals given survey block. Because some animals fed on two species simultaneously, number of sampled animals was not always equal to total number of n.

considered in the analysis because of insufficient survey coverage. The concurrent survey was conducted in August 2000 and from mid-May to mid-July in 2001. Three vessels, *Yushin-Maru* (YS1: 720GT), *Kyo-Maru No. 1* (K01: 812GT) and *Toshi-Maru No. 25* (T25: 739GT), were engaged in the whale survey consisting of sighting and sampling of whales. Stomach contents of sampled minke and Bryde's whales were examined on the research base ship, *Nisshin-Maru* (NM: 7575GT). Two vessels, *Kyoshin-Maru No. 2* (KS2: 368GT) and *Shunyo-Maru* (SYO: 396GT), were engaged in the prey survey in 2000. KS2 conducted the acoustic survey. SYO conducted the mid-water trawling to identify species compositions of acoustic backscattering. During the daytime, KS2 steamed at 10–11 knots along the track line. SYO followed KS2 at the distance of 1–2 nautical miles so that SYO could cast a mid-water trawl to identify the species of marks on the echosounder. *Torishima* (TOR: 426 GT) took over SYO in 2001.

Stomach content analysis

Common minke and Bryde's whales have a four-chambered stomach system. Because the forestomach contents only gives information about the last feeding event (e.g. Lindstrøm *et al.*, 1997), contents from only the forestomach were used in the analysis to avoid including prey species of whales which might have been consumed outside the survey area. Each forestomach content was weighed to the nearest 0.1 kg then subsamples were taken and frozen for laboratory analysis on the research mother ship. In the laboratory, prey species were identified to the lowest taxonomic level if possible. Ideally only undigested or moderately digested stomach contents should be used to reduce some of the main sources of uncertainty in reconstruction of stomach contents such as different passage and degradation rates by prey species and their sizes and accumulation of hard parts such as otolishs (Lindstrøm and Haug, 2001), but digested stomach contents were also used in this study to achieve sufficient sample sizes. The total weight of each prey species in the forestomach was estimated applying the weight ratio in the subsamples to the total weight of forestomach contents. Animals with empty stomachs and stomachs destroyed by the harpoon were not used in the analysis. Prey species less than 1% of total stomach content weights were not included in this analysis. Details of stomach content analysis were described in Tamura and Fujise (2002).

Estimation of prey biomass

A quantitative echo sounder (Simrad EK500 with software version 5.30) was operated during daytime on board KS2 to acquire acoustic data with operating frequency at 38 and 120 kHz. Calibrations were carried out in each year using the copper sphere technique described in EK 500 operation manual (Simrad, 1997).

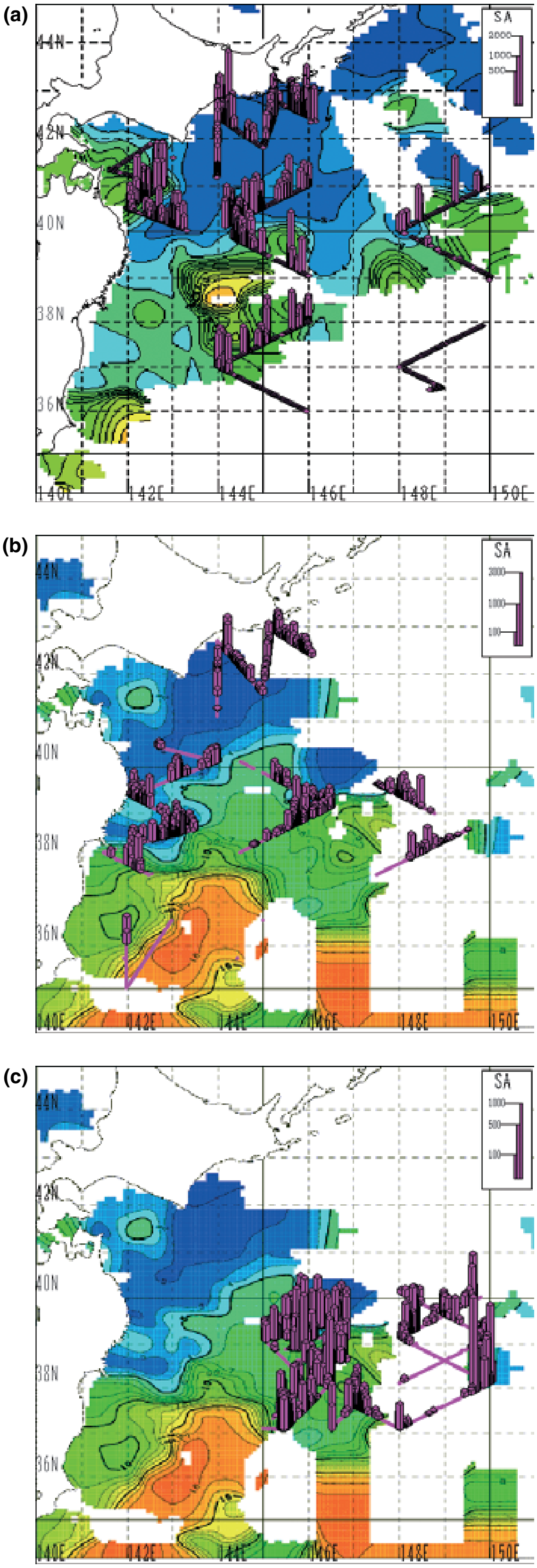


Figure 3. Distribution patterns and densities (S_A) of krill in 2000 (a), 2001 (b), and 2001 with additional blocks (c), were overlaid on water temperature maps. Maps published by Tohoku National Fisheries Research Institute (TNFRI) were modified. Water temperature maps at 200 m were used. August monthly map was used in 2000. June monthly map was used in 2001.

The targeting trawlings were made using a mid-water trawl net to identify fish species compositions of acoustical backscatter. The trawl net was towed at the depth of the backscatters. Towing speed was 3–4 knots. Trawl hauls were continued until target schools were captured though maximum trawling duration was set as 30 min. Catches were sorted into species and weighed. For the major species, 100 animals were sampled at random and the length was measured.

Acoustic data were analyzed with the aid of SonarData Echoview (version 2.10.51) software. In principle, species identifications of backscatterings were conducted based on the targeting trawling catches. In addition, reported school shapes of krill (Miyashita *et al.*, 1998), Japanese anchovy and walleye pollock (Ohshimo and Hamatsu, 1996) recorded on the echogram were also taken into account. For Japanese anchovy and walleye pollock, data collected at 38 kHz were used with the threshold set at −60 dB, and the depth range from 7 to 100 m in 2000 and from 10 to 250 m in 2001. For krill, data collected at 120 kHz were used with the threshold set at −80 dB. The analyzed depth range was from 12 to 250 m. It was reported that echoes were identified as krill if the difference of SV between 120 and 38 kHz fell between 10 and 15 dB (Miyashita *et al.*, 1997). The difference of SV was also taken into account in this study to identify krill. When the difference of SV was calculated, threshold of 38 kHz was set at −80 dB. Biomass estimation was conducted according to the method of Jolly and Hampton (1990). Details of the methods of the estimation of the resource abundance are described in Appendix A.

Prey selection analysis

Although there is no general agreement in the literature about which of several existing indices is the best measure of selection, the selection index of Manly *et al.* (2002) would appear to be one of the best indices of selection for most situations (Krebs, 1999). The standardized form of the selection index called Manly's α (Manly *et al.*, 1972), also known as Chesson's index (Chesson, 1978), was successfully applied to the North Atlantic stock of minke whale to reveal prey

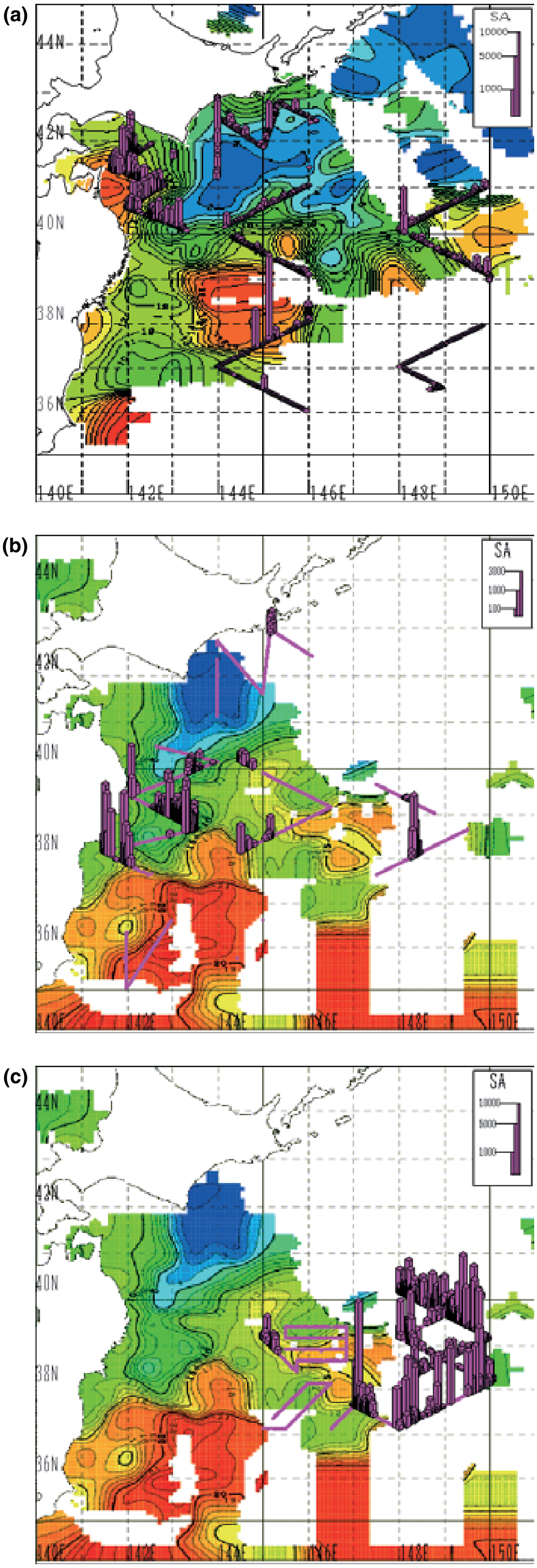


Figure 4. Distribution patterns and densities (S_A) of Japanese anchovy 2000 (a), 2001 (b), and 2001(additional blocks, c) were overlaid on water temperature maps. Maps published by Tohoku National Fisheries Research Institute (TNFRI) were modified. Water temperature maps at 50 m were used. August monthly map was used in 2000. June monthly map was used in 2001.

selectivity (Lindstrøm and Haug, 2001). Confidence intervals of the selection index were estimated as described below to test statistically whether whales randomly fed on prey species.

Assuming jth stomach contents with ith prey species are available, a total weight of prey species i used by all animals (u_{i+}) (kg) is

$$u_{i+} = \sum_{j=1}^{J} u_{ij} \tag{1}$$

where u_{ij} is weight of prey species i used by animal j.

The total weight of prey species used by animal $j(u_{+j})$ is

$$u_{+j} = \sum_{i=1}^{I} u_{ij}. \tag{2}$$

The total weight of all prey species used by all animals (u_{++}) is

Figure 5. Distribution pattern and density (S_A) of walleye pollock in 2001 was overlaid on water temperature map. A map published by Tohoku National Fisheries Research Institute (TNFRI) was modified. Water temperature map at 200 m in June was used.

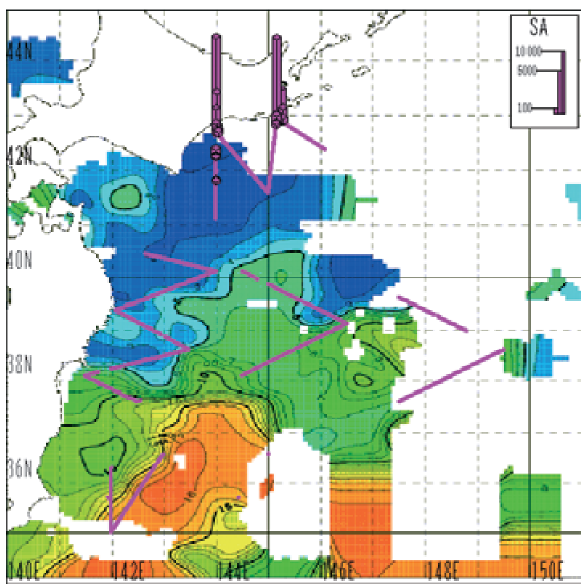


Table 2. Results of target trawlings. Catch weight (kg) at each trawling stations was shown.

Year	Block	Date	Trawling duration	Position	Sampling depth (m)	*Engraulis japonocus*	*Theragra chalcogramma*	Other fish species	*Todarodes pacificus*	Other squid species
2000	1	5 August	0:30	41–56.9N, 143–59.8E	0–30	64.6	0.0	0.2	29.0	0.0
	1	5 August	0:30	42–20.9N, 144–00.0E	0–30	367.0	0.0	+	+	0.0
	2	3 August	0:30	40–44.9N, 142–24.3E	0–30	41.0	0.0	0.0	0.2	+
	2	4 August	0:30	41–22.5N, 141–43.2E	0–30	9.0	0.0	0.2	0.0	0.0
	3	8 August	0:30	40–22.9N, 144–46.4E	0–30	2.1	0.0	0.0	3.2	0.0
	6	27 August	1:30	36–28.7N, 145–02.2E	0–30	5.2	0.0	+	0.0	0.0
	6	29 August	1:00	37–38.2N, 145–16.7E	0–30	43.8	0.0	+	0.0	0.0
2001	1	20 June	0:30	42–38.3N, 144–01.1E	70–100	0.0	94.6	0.0	+	+
	1	20 June	0:30	42–29.4N, 144–08.7E	0–30	0.0	12.4	+	2.0	0.0
	1	21 June	0:30	42–00.8N, 144–35.1E	0–30	0.0	0.0	+	+	0.0
	2	16 May	0:33	37–45.1N, 141–59.7E	0–30	400.8	0.0	+	0.0	0.0
	2	17 May	0:30	38–21.6N, 142–56.5E	0–30	50.0	0.0	+	0.0	0.0
	2	17 May	0:30	38–28.2N, 143–22.0E	0–30	749.2	0.0	9.6	3.4	0.0
	2	20 May	0:30	40–12.8N, 143–07.9E	30–60	1.0	0.0	0.0	0.0	0.0
	C	8 July	0:30	39–07.8N, 148–14.9E	0–30	0.9	0.0	+	0.0	0.0

The sign '+' represents catch weight less than 0.1 kg. Trawling stations which failed to capture the target backscattering were not included in the table.

$$u_{++} = \sum_{i=1}^{I}\sum_{j=1}^{J} u_{ij}. \quad (3)$$

Sample proportion of prey species i by weight used by all animals is

$$o_i = \frac{u_{i+}}{u_{++}}. \quad (4)$$

Sample proportion of available units in prey i is

$$\hat{\pi}_i = \frac{m_i}{\sum_{i=1}^{I} m_i} \quad (5)$$

where m_i is an amount of available units in prey i in a sample of available resource units. Manly's selection indices are

$$\hat{w}_i = \frac{o_i}{\hat{\pi}_i}. \quad (6)$$

Bonferroni confidence interval of $\hat{w}_i$ is given by

$$\hat{w}_i \pm z_{\alpha/(2i)}\mathrm{se}(\hat{w}_i). \quad (7)$$

If the confidence interval contains the value 1, whales feed on prey species randomly (Manly *et al.*, 2002). The value of α was set at 0.05.

Bonferroni confidence interval of the difference between two selection indices, $\hat{w}_i$ and $\hat{w}_k$, is written as:

$$(\hat{w}_i - \hat{w}_k) \pm z_{\alpha/\{2i(i-1)\}}\mathrm{se}(\hat{w}_i - \hat{w}_k). \quad (8)$$

If the confidence interval contains the value 0, difference between $\hat{w}_i$ and $\hat{w}_k$ is not statistically significant (Manly *et al.*, 2002). The value of α was set at 0.05. Details of statistical calculations are described in Appendix B.

Standardized Manly's selection index, Manly's α was written as:

$$\hat{B}_i = \frac{\hat{w}_i}{\sum_i \hat{w}_i}. \quad (9)$$

If $\hat{B}_i = 1/I$, species i is randomly selected; if $\hat{B}_i > 1/I$, species i is actively selected; if $\hat{B}_i < 1/I$, species i is avoided.

RESULTS

Stomach contents

A total of 44 minke and 32 Bryde's whales were used in the analysis. If only undigested stomach contents were selected, the numbers of available sample sizes were reduced to 26 individuals of minke and 16 individuals of Bryde's whales. Sighting positions of sampled animals are shown in Fig. 2. Sightings of minke whales were made in the northerly cold water region

Table 3. Vertical distributions of krill (Kr), Japanese anchovy (JA) and walleye pollock (WP) in each block in 2000 (a), 2001 (b) and 2001 (additional blocks) (c).

	Block 1		Block 2		Block 3		Block 4		Block 6		Block 7	
Depth	Kr	JA	Kr	JA	Kr	JA	Kr	JA	Kr	JA	Kr	JA
(a) 2000												
7–50 m	0.00	4.85	0.00	13.22	0.00	0.47	0.00	0.97	0.00	3.76	0.00	0.00
50–100 m	0.00	0.00	0.01	0.00	0.12	0.00	0.00	0.00	0.00	0.00	0.00	0.00
100–150 m	0.52	0.00	5.13	0.00	7.23	0.00	1.56	0.00	0.46	0.00	0.00	0.00
150–200 m	34.10	0.00	19.36	0.00	27.34	0.00	2.72	0.00	3.42	0.00	0.00	0.00
200–250 m	28.18	0.00	16.06	0.00	16.23	0.00	3.11	0.00	15.69	0.00	0.00	0.00

	Block 1			Block 2		Block 3		Block 4	
Depth	Kr	JA	WP	Kr	JA	Kr	JA	Kr	JA
(b) 2001									
7–50 m	4.98	0.62	0.05	1.25	11.38	3.01	1.28	0.94	0.19
50–100 m	2.97	0.00	2.03	1.43	1.47	0.03	0.00	0.17	0.97
100–150 m	3.55	0.00	1.60	1.13	0.03	0.33	0.00	0.12	0.05
150–200 m	0.62	0.00	0.07	5.06	0.00	4.49	0.00	1.27	0.00
200–250 m	0.22	0.00	0.06	4.07	0.00	7.74	0.00	6.06	0.00

	Block A		Block B		Block C	
Depth	Kr	JA	Kr	JA	Kr	JA
(c) 2001 (additional blocks)						
7–50 m	1.36	0.00	1.95	0.49	0.14	7.25
50–100 m	1.20	0.00	3.90	0.00	0.87	0.17
100–150 m	1.25	0.00	2.36	0.00	0.20	0.00
150–200 m	5.41	0.00	5.23	0.00	1.07	0.00
200–250 m	10.67	0.00	6.82	0.00	4.55	0.00

Nominal mean densities (t n.mile^{-2}) in each 50 m depth bin were shown in the tables.

whereas those of Bryde's were in the southerly Kuroshio–Oyashio transition zone. Summary of stomach contents is shown in Table 1. Ten minke whales and 17 Bryde's whales could not be used in the analysis because of either empty stomachs or because the stomachs had been damaged by the harpoon. Japanese anchovy was found in the stomachs of minke whales in all small blocks from late May to early August in each year. Thirty-two out of 44 animals fed on Japanese anchovy. Walleye pollock was found only in Block 1 in 2001 which is located off the coast of eastern Hokkaido. Eight animals fed on walleye pollock. Krill was found in three small blocks from May to June in 2001. Seasonal comparison can be made only in Block 2 in 2000 and 2001. Stomach contents were Japanese anchovy in May and August. The result suggested that Japanese anchovy was the most important prey in Block 2 although coverage was slightly different from 2000 to 2001. Five stomachs contained two prey species. One individual in Block 1 in 2001 fed on both walleye pollock and krill. The ratio was 3:7. Four individuals in Block 1 in 2001 fed on Japanese anchovy and walleye pollock. Ratios varied from 8:2 to 2:8.

Japanese anchovy was found in the stomachs of Bryde's whales in Block 4 in August 2000 and in Block C in July 2001. Krill was found in all small blocks from May to August in each year. Eleven stomachs contained Japanese anchovy while 23 stomachs contained krill. Two stomachs contained both Japanese anchovy and krill. Proportion of Japanese anchovy to total stomach contents was less than 1% in one animal while it was 30% in another.

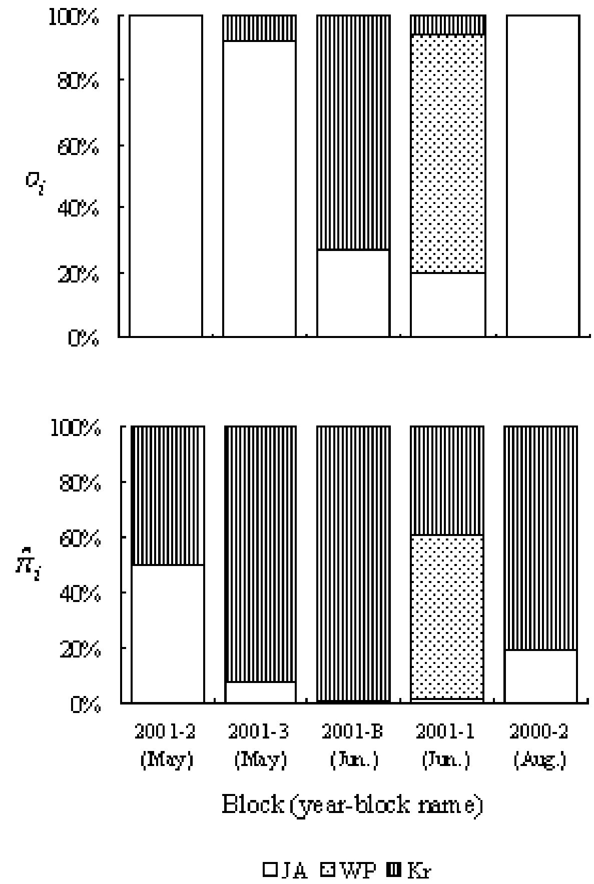
Distribution and biomass of prey species

Horizontal distributions of krill, Japanese anchovy and walleye pollock are shown in Figs 3–5, respectively. Results of the target trawlings are summarized in Table 2. Most of the krill was observed in the cold water area. Their distribution was well correlated with

Table 4. Summary of prey survey and biomass estimations of krill, Japanese anchovy and walleye pollock in each block.

Year	Block	Prey survey period	No. of trackline	No. of target trawl point	Distance covered by echo sounder (n.mile)	Survey area (n.mile^2)	Degree of coverage (*d*)	Krill Density (t n.mile^{-2})	Krill Biomass (10^3 t)	Krill CV	Japanese anchovy Density (t n.mile^{-2})	Japanese anchovy Biomass (10^3 t)	Japanese anchovy CV	Walleye pollock Density (t n.mile^{-2})	Walleye pollock Biomass (10^3 t)	Walleye pollock CV
2000	1	5–7 August	4	6	249	5,467	3.4	63.83	348.97	0.09	4.93	26.94	0.70	0.00	0.00	0.00
	2	2–4 August	4	3	219	5,108	3.1	43.33	221.33	0.63	10.55	53.88	0.56	0.00	0.00	0.00
	3	8 and 30 August	2	1	192	9,501	2.0	51.20	486.41	0.13	0.60	5.66	0.48	0.00	0.00	0.00
	4	22–24 August	2	2	206	7,736	2.3	7.39	57.14	0.57	0.97	7.47	0.21	0.00	0.00	0.00
	6	27–29 August	2	2	251	9,883	2.5	19.57	193.43	0.32	3.76	37.16	0.61	0.00	0.00	0.00
	7	25–26 August	2	1	167	9,883	1.7	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
2001	1	19–24 June	4	4	334	8,260	3.7	12.34	101.94	0.17	0.43	3.53	0.63	18.44	3.81	0.42
	2	17–21 May	5	4	414	12,473	3.7	12.93	161.30	0.25	12.87	160.59	0.48	0.00	0.00	0.00
	3	22–26 May	2	1	224	11,069	2.1	15.61	172.79	0.37	1.28	14.19	0.28	0.00	0.00	0.00
	4	11–13 June	2	1	193	11,057	1.8	8.56	94.61	0.32	1.21	13.41	0.52	0.00	0.00	0.00
	B	15–18 June	11	0	425	5,292	5.8	19.28	102.03	0.26	0.18	0.94	0.71	0.00	0.00	0.00
	C	7–12 July	4	1	668	22,849	4.4	6.82	155.82	0.32	7.42	169.49	0.57	0.00	0.00	0.00

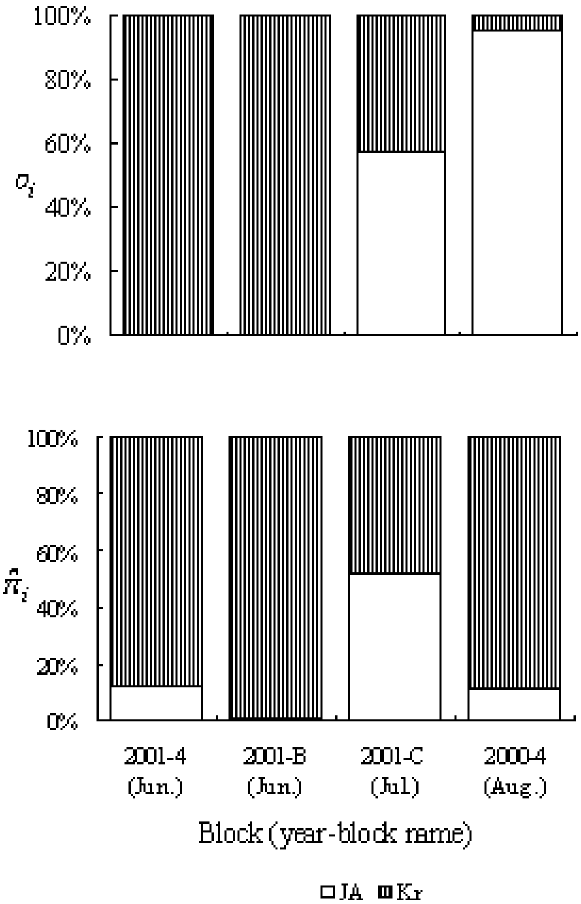
Figure 6. Relative frequency of prey species by weight in the minke whale stomach contents (o_i) and in the environment (π_i). JA, Japanese anchovy; WP, Walleye Pollock; Kr, Krill. Surveyed blocks were showed as 'surveyed year – block name'. For example Block 2 in 2001 was showed as '2001–2'.



water temperature at 250 m depth. Most of observed krill was considered as *Euphausia pacifica*. Krill was sporadically observed in the southern part of the survey area where krill consisted of several species other than *E. pacifica*. The distribution pattern of Japanese anchovy well reflected water temperature at 50 m depth. Japanese anchovy was scarce in the southern part of the survey area where the influence of Kuroshio was strong. It was abundant in Block 2 in August 2000 and May 2001. Japanese anchovy in Block 1 was abundant in 2000 but scarce in 2001. The difference might be explained by the seasonal migration to the north in August. Distribution of walleye pollock was only found in the continental slope-shelf zone in Block 1 in 2001.

Vertical distribution patterns of krill, Japanese anchovy and walleye pollock are summarized in Table 3. Most of the krill was concentrated at water depth

Figure 7. Relative frequency of prey species by weight in the Bryde's whale stomach contents (o_i) and in the environment (π_i). JA, Japanese anchovy; Kr, Krill. Surveyed blocks were showed as 'surveyed year – block name'. For example Block 4 in 2001 was showed as '2001–4'.



deeper than 150 m. An exception was found in Block 1 in 2001 where most of krill occurred shallower than 150 m water depth. In 2000, all Japanese anchovy schools were found shallower than 40 m depth. In 2001, most of Japanese anchovy schools were observed shallower than 50 m water depth, but some schools were observed from 50 to 150 m water depth especially in Blocks 2 and 4. Walleye pollock was abundant at depths deeper than 50 m and the peak was at depths between 100 and 150 m.

Estimated biomasses of Japanese anchovy, walleye pollock and krill are shown in Table 4. Degree of coverage in each block was less than 6 which was recommended by Aglen (1989). Krill was the most abundant in most of blocks except in the southern part of the survey area. Coefficient of variation (CV) of the biomass estimates for each species ranged between 0.1 and 0.7 in each small block.

Prey selection

Proportions of occurrence of prey species in stomachs of minke and Bryde's whales in each block are shown in Figs 6 and 7, respectively, with proportion of occurrence of prey species in the sea. Proportions of occurrence of prey species were not reflected in minke whale stomach contents. Manly's α indicated that minke whales showed selection for Japanese anchovy in all survey blocks regardless of season while they avoided krill although statistical analysis suggested that there was no prey selection for Japanese anchovy in Blocks 1, 3 and B in 2001 (Tables 5 and 6). In Block 1 in 2001, pairwise statistical comparison suggested that minke whales showed selection for walleye pollock and against krill. Bryde's whales showed contradictory results. Manly's α indicated that they showed selection for Japanese anchovy in August 2000 (Block 4) and July 2001 (Block C) although statistical analysis suggested that there was no selection for Japanese anchovy in Block C. In contrast, Bryde's whales selected krill in May and June in 2001 (Blocks 3, 4, and B).

DISCUSSION

Manly's α suggests that minke whale seem to select for Japanese anchovy. Selection for pelagic shoaling fish such as herring (*Clupea harengus*) and capelin (*Mallotus vilosus*) was observed in the northeast Atlantic (Haug *et al.*, 1996; Skaug *et al.*, 1997; Harbitz and Lindstrøm, 2001; Lindstrøm and Haug, 2001). Foraging success is measured by maximization of energy intake rate and minimization of time necessary to obtain nutrient (Schoener, 1971). Caloric values of Japanese anchovy, walleye pollock, and krill were 6402, 6192, and 3556 kJ kg^{-1}, respectively (Tamura and Fujise, unpublished data).[2] Japanese anchovy was concentrated shallower than 50 m water depth, while walleye pollock and krill

[2]The results were reported in the unpublished paper as follows: Tamura, T. and Fujise, Y. (2002). Daily and seasonal prey consumption by common minke whale and Bryde's whale in the western North Pacific. Appendix 4, pp. 85–96. *In*: Government of Japan (Y. Fujise, S. Kawahara, L.A. Pastene and H. Hatanaka, eds), Report of 2000 and 2001 feasibility study of the Japanese Whale Research Program under Special Permit in the western North Pacific-Phase II (JARPN II). Paper SC/54/O17 presented to the IWC Scientific meeting April 2002 [Available from the International Whaling Commission].

Table 5. Selection Index (w_i) and the results of statistical test, and Manly's α of minke and Bryde's whales in each small block in 2000 and 2001 surveys.

	Block 1		Block 2	
(a) Minke whale in 2000	Kr	JA	Kr	JA
w_i	0.000	13.954	0.000	5.108
CV(w_i)	–	–	–	–
Bonferroni CI (low)	–	–	–	–
Bonferroni CI (high)	–	–	–	–
Manly's α	0	1	0	1
1/*I*	0.5	0.5	0.5	0.5

	Block 1			Block 2		Block 3		Block B	
(b) Minke whale in 2001	Kr	JA	WP	Kr	JA	Kr	JA	Kr	JA
w_i	0.086	7.771	3.202	0.000	2.004	0.085	12.136	0.740	29.241
CV(w_i)	1.049	0.525	0.212	–	–	1.309	0.411	0.269	0.815
Bonferroni CI (low)	−0.130	−1.998	1.574	–	–	−0.165	0.946	0.294	−24.187
Bonferroni CI (high)	0.302	17.540	4.830	–	–	0.335	23.326	1.187	82.670
Manly's α	0.008	0.703	0.290	0.000	1.000	0.007	0.993	0.025	0.975
1/*I*	0.3	0.3	0.3	0.5	0.5	0.5	0.5	0.5	0.5

	Block 4	
(c) Bryde's whale in 2000	Kr	JA
w_i	0.049	8.281
CV(w_i)	0.761	0.224
Bonferroni CI (low)	−0.035	4.123
Bonferroni CI (high)	0.131	12.446
Manly's α	0.006	0.994
1/*I*	0.5	0.5

	Block 3		Block 4		Block B		Block C	
(d) Bryde's whale in 2001	Kr	JA	Kr	JA	Kr	JA	Kr	JA
w_i	1.082	0.000	1.142	0.000	1.009	0.000	0.895	1.096
CV(w_i)	–	–	–	–	–	–	0.604	0.466
Bonferroni CI (low)	–	–	–	–	–	–	−0.317	−0.049
Bonferroni CI (high)	–	–	–	–	–	–	2.107	2.242
Manly's α	1	0	1	0	1	0	0.449	0.551
1/*I*	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5

If the Bonferroni confidence interval of w_i contained the value 1, whales fed on prey species randomly. If Manly's α was equal to 1/*I*, species *i* is randomly selected. If Manly's α was greater than 1/*I*, species *i* is actively selected. If Manly's α was less than 1/*I*, species *i* is avoided.

were distributed deeper than 100 and 150 m water depth, respectively. Considering that usual foraging depth of minke whale was upper 100 m (Blix and Folkow, 1995), Japanese anchovy will be the first choice of prey to gain maximum energy intake with minimum dive time. The same kind of selection for epipelagic prey species was also observed in Dall's porpoises (*Phocoenoides dalli*) around Hokkaido, Japan (Ohizumi *et al.*, 2000). It should be noted that caloric values of prey species could be varied with their body sizes, season and year.

Although Manly's α showed prey selection of minke whales for Japanese anchovy, statistical test could not detect it in three Blocks (Blocks 1, 3 and B in 2001). High CVs of biomass estimates of Japanese anchovy in those blocks could be one of the reasons

Table 6. Pairwise comparisons of selection indices between prey species of minke and Bryde's whales. If the confidence interval contained the value 0, difference between $\hat{w}_i$ and $\hat{w}_k$ is not statistically significant.

	Block 1			Block 3	Block B
	Kr versus JA	Kr versus WP	JA versus WP	Kr versus JA	Kr versus JA
(a) Minke whale in 2001					
Bonferroni CI (low)	−18.462	−5.019	−7.198	−23.313	−82.334
Bonferroni CI (high)	3.092	−1.213	16.336	−0.788	25.332
					Block 4 Kr versus JA
(b) Bryde's whale in 2000					
Bonferroni CI (low)					−12.413
Bonferroni CI (high)					−4.059
					Block C Kr versus JA
(c) Bryde's whale in 2001					
Bonferroni CI (low)					−2.431
Bonferroni CI (high)					2.028

of the result of the statistical test. The survey in Block 1 was conducted off the coast of southeastern Hokkaido in June 2001. It was reported that Japanese anchovy was concentrated in the continental shelf zone of off southeastern Hokkaido in June 1991 (Mihara, 1998). Limited survey effort in the continental shelf zone in Block 1 could result in high CV of biomass estimate of Japanese anchovy. Blocks 3 and B in 2001 were located in the Kuroshio–Oyashio transition zone, where oceanographic conditions were complex. Those heterogeneities of oceanographic conditions could affect the distribution pattern of Japanese anchovy and could result in high CVs. Walleye pollock was mainly distributed in the continental slope zone (150–250 m water depth) and continental shelf zone (70–150 m water depth) off southeastern Hokkaido (Shida, 2002). The lower survey effort in the continental shelf-slope region could increase the CV of walleye pollock in Block 1. Finer scale consideration of oceanographic conditions and bottom topography will be required in future surveys to reduce CVs.

Krill was selected, avoided, or randomly selected in the eastern North Atlantic (Haug *et al.*, 1996; Skaug *et al.*, 1997; Harbitz and Lindstrøm, 2001; Lindstrøm and Haug, 2001). In the eastern North Atlantic, krill was well distributed in the upper 100 m water depth whereas it was distributed mainly deeper than 150 m water depth in this study. Because *E. pacifica* was mainly found at water temperature range 7–8 °C, it was mainly distributed in 200–300 m water depth range in daytime from June to February (Taki *et al.*, 1996). Availability of krill to minke whales may be varied because the vertical distribution pattern of krill depends on water temperatures.

Bryde's whales selected for krill in the early season (May and June) and then they selected for Japanese anchovy in the late season (July and August). Prey selection of Bryde's whale could change as the season progresses but because the survey coverage of each month was slightly different, it is difficult to distinguish between seasonal and geographical change of prey selection at this stage.

Lindstrøm and Haug (2001) pointed out four underlying assumptions of prey selectivity studies: (1) whale samples are randomly selected in the given survey area, (2) sampled whale feed in the survey area, (3) forestomach contents are reliably reconstructed, and (4) estimated prey biomass is reliable and constant during the survey period. Assumptions (1) and (2) were already considered in past surveys (Lindstrøm *et al.*, 1998; Tamura and Fujise, 2002). Ideally, only undigested stomach contents should be used to satisfy the assumption (3) but we have to trade reduced sample size with the accuracy of the weight of stomach contents. Because of the difficulty of obtaining the stomach contents of cetaceans, digested stomach contents were used to make good use of available samples in this study. Regarding assumption (4), considerations of the vertical distributions and the diurnal behavior of preys are necessary. Maximum depth of acoustic survey was set at 250 m because prey species of minke and Bryde's whales mainly occurred shallower than 250 m. It seemed that minke whales feed on prey shallower than 100 m (Blix and Folkow, 1995). No diving depth of Bryde's whale has been measured. It was pointed out that prey species such as Japanese anchovy (Ohshimo, 1996), walleye pollock (Abe *et al.*, 1999) and *Euphausia pacifica* (Taki *et al.*, 1996) showed diurnal vertical migration. Those species formed dense schools in daytime whereas they disperse at night. Because there was little diurnal change in the mean stomach content weight of minke whales during daytime, minke whales would feed on pelagic schooling prey species at the surface throughout the daytime (Tamura *et al.*, 1998). Given information on diurnal distribution patterns of prey species and the mean stomach content weight of minke whale in the daytime, prey survey conducting only during daytime is adequate. Because diurnal change of stomach content weight of Bryde's whale has not been reported, this point should be investigated in future surveys.

In the 2000 and 2001 surveys, we could not cover the autumn season when Pacific saury was abundant in the survey area. Because it was consumed by minke whales (Tamura and Fujise, 2002), whale and the concurrent prey surveys must be conducted in September and October to assess whether minke whale have preference for it. In the western North Pacific, biomass of pelagic fish such as Japanese sardine, Pacific saury, Japanese anchovy and chub mackerel has shown drastic fluctuations, so-called species replacement (Yatsu *et al.*, 2001). Stomach contents of minke whales reflected the historical change in dominant species in the survey area (Kasamatsu and Tanaka, 1992). Long-term concurrent monitoring of both whale stomach contents and the prey species abundance is critically important to develop ecosystem models that are suitable to the western North Pacific.

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APPENDIX A

Details of formulas used in acoustic data analysis

Mean backscattering area per square nautical mile of sea surface (S_A) by species for every 1 n.mile of survey transect over defined depth interval is calculated by the following formula:

$$S_A = 4\pi r_0^2 (1852)^2 \int_{r_1}^{r_2} s_V \, dr \left(\frac{m^2}{n.mile^2} \right) \qquad (A-1)$$

where r is depth from the sea surface, $r_0 = 1$ m representing the reference range for backscattering strength. A length–target-strength (TS) relationship for Japanese anchovy (Anonymous, 1990) is used;

$$\mathrm{TS} = 20\log\mathrm{TL} - 72.5 \qquad (A-2)$$

where TL is total length in cm. A length–weight relationship for Japanese anchovy (Anonymous, 1990) is used:

$$W = 0.004\,\mathrm{TL}^{3.09} \qquad (A-3)$$

where W is weight in gram.

A length–target-strength (TS) relationship for walleye pollock (Foote and Traynor, 1988) is used:

$$\mathrm{TS} = 20\log\mathrm{FL} - 66 \qquad (A-4)$$

where FL is folk length in cm.

A length–weight relationship for walleye pollock (Pereyra *et al.*, 1981) is used:

$$W = 0.0077\mathrm{FL}^{2.906} \qquad (A-5)$$

where W is weight in gram.

We assumed that all krill observed during two surveys was *Euphausia pacifica* and length and TS were 16.4 mm and −83.3 dB (Miyashita *et al.*, 1996), respectively, because no length–TS relationship for krill was available in this area. The average weight was 30.6 mg calculated using formula described by Odate (1987).

Average area biomass density (ρ) for each species is calculated as follows:

$$\overline{\rho} = \sum \frac{S_A}{\sigma} f_i W_i \qquad (A-6)$$

where f_i is the frequency distribution of ith length class. The acoustic cross section (σ) is converted from TS as follows:

$$\sigma = 4\pi(10)^{0.1\mathrm{TS}} \qquad (A-7)$$

Frequency distribution of each class (f_i) that is the acoustical contribution to the area backscattering for each length class (Ona, 1993):

$$f_i = \sum_{j=1}^{\infty} n_j L_j^2 \qquad (A-8)$$

where n_j is the number of individuals in size class j and the length is L.

Following procedures are adopted from Jolly and Hampton (1990). Weighted mean of S_A of each block is:

$$\overline{S_{Ak}} = \frac{\sum_{i=1}^{N_k} \overline{S_{Aki}}(n_{k_i})}{\sum_{i=1}^{N_k} n_{k_i}} \qquad (A-9)$$

where S_{Ak}= mean S_A in kth block, N_k= number of transects in kth block, S_{Aki}= mean S_A on the ith transect in kth block and n_{k_i}= number of 1 n.mile averaging intervals on the ith transect in kth block. In this formula, each transect is regarded as a single biomass density sample. Then variance of S_{Ak} is calculated with the formula (Jolly and Hampton, 1990):

$$\mathrm{Var}(\overline{S_{Ak}}) = \frac{N_k}{N_k - 1} \frac{\sum_{i=1}^{N_k} (\overline{S_{Aki}} - \overline{S_{Ak}})^2 n_{k_i}^2}{\left(\sum_{i=1}^{N_k} n_{k_i}\right)^2} \qquad (A-10)$$

$\bar{S}_A$ is converted to ρ using the above-mentioned formula. Biomass is estimated as;

$$B_k = A_k \hat{\rho}_k \qquad (A-11)$$

where B_k is density biomass in kth block and A_k is area of kth block. Variance of B_k is calculated with the following formula:

$$\mathrm{var}(B_k) = A_k^2 \mathrm{var}(\overline{\rho_k}) \qquad (A-12)$$

Coefficient of variation of B_k is calculated as:

$$\mathrm{CV}(B_k) = \frac{\sqrt{\mathrm{var}(B_k)}}{B_k} \qquad (A-13)$$

APPENDIX B

Details of statistical analysis procedures of prey selection analysis

Variances of $\hat{w}_i$s are calculated based on a formula of a ratio estimator

$$V(\hat{w}_i) \approx \frac{1}{u_{++}^2} \left\{ \frac{J}{(J-1)} \sum_{j=1}^{J} \left(\frac{u_{ij}}{\hat{\pi}_i} - \hat{w}_i u_{+j} \right)^2 + \hat{w}_i^2 \mathrm{CV}^2(\hat{\pi}_i) \sum_{j=1}^{J} u_{+j}^2 \right\}, \qquad (B-1)$$

(Cochran, 1977; Manly *et al.*, 2002). $\mathrm{CV}(\hat{\pi}_i)$ is estimated using variance of m_i based on a delta method (Seber, 1982) from

$$\mathrm{Var}(\pi_i) = \mathrm{Var}(m_i) \frac{m_{(-i)}^2}{(\Sigma m_k)^4} + \frac{m_i^2}{(\Sigma m_k)^4} \{\mathrm{Var}(m_1) + \cdots + \mathrm{Var}(m_{i-1}) + \mathrm{Var}(m_{i+1}) + \cdots + \mathrm{Var}(m_I)\} \qquad (B-2)$$

where $m_{(-i)} = m_1 + \cdots + m_i^{-1} + m_i^{+1} + \cdots + m_I$.

Variance of the difference between two selection ratios can be estimated as

$$V(\hat{w}_i - \hat{w}_k) = V(\hat{w}_i) + V(\hat{w}_k) - 2\mathrm{Cov}(\hat{w}_i, \hat{w}_k) \qquad (B-3)$$

Covariance of $\hat{w}_i$ and $\hat{w}_k$ can be estimated as

$$\mathrm{Cov}(\hat{w}_i, \hat{w}_k) \approx \frac{J}{\hat{\pi}_i \hat{\pi}_k u_{++}^2} \left\{ \frac{1}{(J-1)} \sum_{j=1}^{J} (u_{ij}u_{kj} - \hat{w}_i \pi_i u_{+j} u_{kj} - \hat{w}_k u_{ij} \pi_k u_{+j} + \hat{w}_i \hat{w}_k \pi_i \pi_k u_{+j}^2) + \frac{\hat{w}_i \hat{w}_k}{J} \mathrm{Cov}(\hat{\pi}_i, \hat{\pi}_k) \sum_{j=1}^{J} u_{+j}^2 \right\}. \quad (B-4)$$

where covariance of $\hat{\pi}_i$ and $\hat{\pi}_k$ can be estimated as

$$\mathrm{Cov}(\hat{\pi}_i, \hat{\pi}_k) = -\mathrm{CV}^2(m_i) \frac{m_{(-i)} m_i^2 m_k}{(\sum m_l)^4} - \mathrm{CV}^2(m_k) \frac{m_{(-k)} m_k^2 m_i}{(\sum m_l)^4} + \cdots + \sum_{l \neq i,k} \mathrm{CV}^2(\hat{m}_l) \frac{m_i m_k m_l^2}{(\sum m_l)^4} \quad (B-5)$$