Diet records and stock structure of minke whales *Balaenoptera acutorostrata* around Japan examined by $\delta^{13}C$ and $\delta^{15}N$ analyses

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ABSTRACT

Carbon and nitrogen stable isotope ratios of mature male minke whales *Balaenoptera acutorostrata* inhabiting around Japan were analyzed to estimate recent diet records and to elucidate its stock structure. We extracted 21 baleens, 44 muscles and 44 livers from the whales obtained from JARPN surveys conducted in 1996, 1998 and 1999. One or two $\delta^{15}N$-depletion peaks were formed in the baleens of the whales caught in the sub-areas 7 and 8 and they were considered to be formed in early summer. The growth rate of baleen was estimated to be about 130mm/year, thus it was assumed that approximately 1.5 years of diet record would remain in the baleen plates of the mature minke whales. The isotopic values in $\delta^{13}C$ - $\delta^{15}N$ maps showed different distribution pattern between the area groups caught in the western North Pacific (sub-areas 7 and 8) and the southern Okhotsk Sea (sub-area 11) in every kind of tissues, while there was not local difference between sub-areas 7 and 8 in the western North Pacific. Some of the whales, identified as O stock from genetic analyses, showed the isotopic values characteristic of sub-areas 7 and 8 in spite of its being caught in the sub-area 11. It suggests the mixing of the O stock whales among the sub-areas 7, 8 and 11. These results are consistent with the hypothetical population structure having been presented by genetic analyses and do not support the W stock hypotheses.

INTRODUCTION

The analysis of $\delta^{13}C$ and $\delta^{15}N$ of consumer and prey tissues is a valuable method to examine the trophic relationship and feeding habit of aquatic animals. $\delta^{15}N$ of animals is enriched by 3.4±1.1‰ per trophic level (Minagawa and Wada, 1984), whereas a small enrichment of about 1‰ was found for $\delta^{13}C$ (DeNiro and Epstein, 1978; Rau et al., 1983; Fry, 1988). Consequently, $\delta^{15}N$ is a possible indicator of the trophic level of the animal examined and $\delta^{13}C$ can be used to identify a primary producer at the base of a food chain to which the animals belong. The $\delta^{13}C$ - $\delta^{15}N$ map in an ecosystem can thus show an isotopic food web structure on a corresponding food base.

On the other hand, $\delta^{13}C$ and $\delta^{15}N$ of local food webs often have wide variations among different areas, mainly reflecting the isotopic variations of primary producers. Such local variations of stable isotope ratios were recently utilized to study the migration characteristics and population structure of fish and birds (Hesselein et al., 1991; Minami and Ogi, 1997; Takai and Sakamoto, 1999) and it was also shown that the stable isotopic oscillations along the length of the baleen plates would reflect the annual migratory information of bowhead whales *Balaena mysticetus* and southern right whales *Eubalaena australis* (Schell et al., 1989a, b; Best and Schell, 1996; Hobson and Schell, 1998). Since minke whale is supposed to do wide latitudinal migration in the North Pacific (Ohsumi, 1983; Hatanaka and Miyashita, 1997), similar characteristics of isotopic variations are expected to appear in baleen plates of this species inhabiting around Japan. Thus in this study, $\delta^{13}C$ and $\delta^{15}N$ of minke whales in the western North Pacific and the southern Okhotsk Sea were analyzed in order to clarify the diet records, migration characteristics and stock structure of this species around Japan. Especially, we focused on the matured males for simplifying the comparison among the groups caught in the different habitat areas.

MATERIAL AND METHODS

Sampling

Baleen plates (n=21), muscles and livers (n=44) were extracted from mature male minke whales caught in the western North Pacific (sub-areas 7 and 8) and the southern Okhotsk Sea (sub-area 11) during JARPN surveys conducted in 1996, 1998 and 1999 (Tables 1 and 2). As prey species of the whales, Japanese anchovy *Engraulis japonicus* and krill *Euphausia pacifica* were collected in the same areas (Table 2). These sample were kept at –20℃ until stable isotope analysis.

$\delta^{13}C$ and $\delta^{15}N$ analysis

The baleen plates were sampled for isotopic analysis at 7 or 14mm intervals along their outside edge with a punch. The baleen plates, muscles, livers and prey species samples were all dried at 60℃ and ground to a fine powder. Lipids were removed with a chloroform-methanol (2:1) solution. Powdered samples (0.5 to 1.0mg) were put into tin cups and the isotope ratios of carbon and nitrogen were measured by a Delta-S mass spectrometry (Finnigan MAT, Germany) coupled with the elemental analyzer (Carlo Erba, Italy). $\delta^{13}C$ and $\delta^{15}N$ were expressed as the per mill deviation (‰) from the standard as defined by the following equation:

$$\delta^{13}C \text{ or } \delta^{15}N = \{R\,(\text{sample}) / R\,(\text{standard}) - 1\} \times 1000\ (‰)$$

where $R = {}^{13}C/{}^{12}C,\ {}^{15}N/{}^{14}N$

Belemenite (PDB) and atmospheric nitrogen were used as the carbon and nitrogen isotope standards, respectively. The analytical precision for the isotopic analyses was ±0.3‰ for both $\delta^{13}C$ and $\delta^{15}N$.

RESULTS

Baleen plates, muscles and livers

The isotopic values in baleens of male minke whales ranged from –19.6 to –16.6‰ in $\delta^{13}C$ and from 8.4 to 15.0‰ in $\delta^{15}N$ (Table 1). The average isotopic values of the baleens from sub-area 11 were lower by 0.3 - 0.5‰ in $\delta^{13}C$ and higher by 0.6 - 0.9‰ in $\delta^{15}N$ than those from sub-area 7 and 8 (Fig. 1, Table 2), while there was little difference (<0.3‰) between sub-areas 7 and 8. Similar characteristics appeared in the $\delta^{13}C$ - $\delta^{15}N$ maps of muscles and livers as well (Figs. 2 and 3). The average isotopic values of the muscles and livers from sub-area 11 were lower by 0.3 - 0.5‰ in $\delta^{13}C$ and higher by 0.7 – 1.3‰ in $\delta^{15}N$ than those from sub-areas 7 and 8 (Table

2).

Prey species

The mean isotopic values of the Japanese anchovy sampled from gut contents of minke whale (No. 98097) caught in sub-area 8 were -19.0±0.8‰ in $\delta^{13}C$ and 8.6±0.8‰ in $\delta^{15}N$ (n=4), while the fish captured in Usujiri, Pacific side of Hokkaido showed higher values, –17.8‰ in $\delta^{13}C$ and 10.2‰ in $\delta^{15}N$ (n=2) (Fig. 4, Table 3). The $\delta^{13}C$ of krill was more depleted in the Okhotsk Sea (-20.6‰) than off Sanriku in the Pacific Ocean (-18.5‰), while the $\delta^{15}N$ values were homogeneous between the both areas ranging from 8.5 to 8.7‰.

Oscillation patterns of $\delta^{13}C$ and $\delta^{15}N$ in baleen plates

The $\delta^{15}N$ records of six whales caught in sub-areas 7 and 8 in May and June (Nos. 98008, 98050, 98085, 98092, 98097 and 98100) showed $\delta^{15}N$-depletion peaks of 8.4 to 9.5‰ occurring 120 to 140mm from the base of baleen (Figs. 5a, b). As for No.98092, 1.6‰ depletion of $\delta^{15}N$ was found at the recently-formed strata (14mm from the base of baleen). The other five whales, Nos. 96051, 96054, 98003, 98027 and 98081, showed various oscillation patterns of $\delta^{15}N$. No. 98003 caught in early May showed twin $\delta^{15}N$-depletion peaks occurring at the tip of baleen (220mm) and 100mm from the base of baleen. In the case of No.96051 caught in late August, $\delta^{15}N$-depletion peak appeared far away from the base (160mm) relative to the other whales caught in May and June. In the baleen of No.96054, caught on the same day as No.96051, $\delta^{15}N$ depleted at the tip of baleen (170mm) and $\delta^{15}N$-depletion peak was found at 20mm from the base. Nos. 98027 and 98081 showed higher $\delta^{15}N$ values relative to the other whales from sub-areas 7 and 8 though the recently-formed strata of No.98081 was depleted.

There were three oscillation patterns of $\delta^{15}N$ values in the baleens from sub-area 11 (Fig. 5c). (I) No. 96034 had a $\delta^{15}N$-depletion peak occurring at 120 to 140mm from the base as well as the whales from sub-areas 7 and 8, though its $\delta^{15}N$ values were higher by 1.6‰ than the $\delta^{15}N$ of the latters. (II) Nos. 96035, 99057, 99077, 99082 and 99085 showed a weak $\delta^{15}N$-depletion peak at 100 to 150mm from the base and the second decrease of $\delta^{15}N$ at the recently formed strata, although No. 99085 showed higher $\delta^{15}N$ values relative to the other whales from sub-area 11. (III) The $\delta^{15}N$ values in the baleen of the other whales (Nos. 96023, 96045, 99074 and 99088) changed 0.9 to 1.5‰ only and notable oscillations were not detectable.

Such oscillation patterns were not found in $\delta^{13}C$ and the isotopic values were homogenous in every stratum of the baleens ranging 1.7‰ or less (Figs. 5a-c)

DISCUSSION

Growth rate of baleen plates and period of accumulated diet records

All of nine minke whales caught in early summer (May or June) in sub-areas 7 and 8 had no $\delta^{15}N$-depletion peaks at the recently-formed strata except No.98092 and No.98081 (Figs. 5a, b). On the other hand, a clear $\delta^{15}N$-depletion peak was found at the recently formed strata (20mm from the base) of No. 96054 caught in late summer (August)(Fig. 5a). This indicates that the $\delta^{15}N$-depletion peak may be formed in early summer.

Nos. 98003 and 98092 had two $\delta^{15}N$-depletion peaks in the baleen and their inter-peak intervals were both approximately 130mm. It means that the growth rate of the baleen may be 130mm per year in minke whales, on the basis of the premise that the $\delta^{15}N$-depletion peak would be annually formed in a particular season. Baleen plates of adult whales were reported to grow 200mm or less per year in bowhead whales (Schell et al., 1989a, b) and 270mm per year in southern right whales (Best and Schell, 1996). It indicates slow growth of the baleen plates of minke whales relative to these two species. Since the length of baleen plates of minke whales was averaged 186±22mm in this study, it seems that diet records during about 1.5 years remained in the baleen plates of the mature minke whales inhabiting around Japan.

Baleen plates of minke whale showed only one or two striking $\delta^{15}N$-depletion peaks, while total of the peaks were over 20 in the $\delta^{13}C$ of bowhead whales and seven in both $\delta^{13}C$ and $\delta^{15}N$ of southern right whales (Best and Schell, 1996; Schell et al., 1989). The latter two species have the longest baleen plates of 2-4m long in Mysticeti, relative to the plates of only about 0.2m long in minke whales. In this species, the friction between baleens and lower jaws and the consequent abrasion of baleens do not allow them to lengthen over 0.2m because of the specific structure of oral cavity. Also the small number of the $\delta^{15}N$-peaks in the baleens would be explained by this specific character.

Recorded prey species

In the western North Pacific, minke whales mainly feed on Japanese anchovy in early summer (May and June), and Pacific saury *Cololabis saira* in middle to late summer (July to September)(Tamura, 1998, 2000). It was thus assumed that the $\delta^{15}N$-depletion peaks would be formed in the season when Japanese anchovy was fed on as a main prey species, though difference in isotopic value between anchovy and saury is not clear at present.

Nails, whiskers, and hairs of seals are enriched by 3‰ in both $\delta^{15}N$ and $\delta^{13}C$ relative to their preys (Hobson et al., 1996). This enrichment factor may apply to the baleen of the whales, since it is a keratinous tissue as well. It predicts that the isotopic values of the whales exclusively feeding on Japanese anchovy would be 11‰ in $\delta^{15}N$ and -16‰ in $\delta^{13}C$ in sub-area 8. However, the whale $\delta^{15}N$ ranged from 8 to 9‰ and $\delta^{13}C$ from -19 to -18‰ around the strata of $\delta^{15}N$-depletion peak. This discrepancy may be attributable to the insufficiency of the sample number of the fish. Temporal variability in stable isotope ratios is greater at lower levels of aquatic ecosystem (Cabana and Rasmussen, 1996). Our observed value might not represent the isotopic values of Japanese anchovy consumed by minke whales because of the seasonal isotopic change of the fish. $\delta^{13}C$ and $\delta^{15}N$ of the prey species and another lower consumers must be analyzed for sufficient samples in the future.

In the southern Okhotsk Sea, minke whales feed on krill exclusively in middle to late summer (July and August)(Tamura, 2000). But several types of oscillation patterns in isotopic values were detected in the baleen plates of minke whales caught in sub-area 11. If whales fed on krill exclusively throughout the summer in this area, different oscillation patterns in the $\delta^{15}N$ values would not be formed. This may indicate that whales have several migration patterns in the southern Okhotsk Sea and that they come from the area outside of sub-area 11.

The difference of stable isotope ratios between sub-areas

Livers are supposed to have more rapid turnover rates than muscles and hairs and thus be an indicator of more recent feeding information, while muscles and keratinous tissues such as baleens are assumed to reflect long term feeding records (Tiezen et al., 1983; Hobson et al., 1992). All of these tissues showed similar $\delta^{13}C$ - $\delta^{15}N$ maps: The isotopic values from the whales caught in the sub-areas 7 and 8 were 0.3 to 0.5‰ higher in $\delta^{13}C$, and 0.6 to 1.4‰ lower in $\delta^{15}N$ than those from sub-area 11 in all three tissues (Figs. 1-3). This distinct different value between the sub-areas in every kind of tissues suggests that there would be different habitat area groups in the sub-areas 7+8 and 11.

Comparison with genetic analyses on stock structure

According to genetic analyses, two distinct stocks are assumed to occur in the western North Pacific: one in the Sea of Japan (what is called J-stock) and the other in the Pacific side of Japan and the Okhotsk Sea (O-stock) with a spacial/temporal mixing of stocks in the southern part of Okhotsk Sea in April and August (reviewed in Pastene et al. (2000)). The baleens of Nos. 96023 and 96035 showed the isotopic values characteristic of the whales in sub-areas 7 and 8, although they were caught in the sub-area 11 (Fig. 1, Table 1). It means that these two whales might have migrated to the area from sub-area 7 or 8 recently. On the other hand, baleen and muscle of No. 98027 showed the isotopic values characteristic of the whales in sub-area 11 in spite of its being caught in the sub-area 7 (Figs. 1 and 2, Table 1). This whale might have migrated from sub-area 11, contrary to Nos. 96023 and 96035. The haplotype of these whales were all specific to O stock (Goto, unpublished data) and thus it was indicated that the mixing of the O stock whales would exist among the sub-areas 7, 8 and 11.

In this study, the $\delta^{13}C$ - $\delta^{15}N$ maps of baleens, muscles and livers showed different distribution pattern between the western North Pacific (sub-areas 7 and 8) and the southern Okhotsk Sea (sub-area 11), while there was not a local difference between sub-areas 7 and 8 in the western North Pacific. It suggests that there would be two area groups of the whales inhabiting different areas around Japan. On the other hand, it was also suggested that there would be mixing of O stock whales among the two areas, since some whales caught in the southern Okhotsk Sea showed the isotopic values characteristic of the whales from the western North Pacific. These results are contradictory to the W stock hypotheses and thus negate its reliability.

ACKNOWLEDGEMENTS

We would like to thank all captains, crews and researchers, who were involved in JARPN surveys in 1996 – 1999. T. Meguro and T. Kanehisa of the Department of Fishery, University of Hokkaido, provided the krill samples from southern Okhotsk Sea. K. Taki of Mixed Water Region Fisheries Oceanography Division, Tohoku National Fisheries Research Institute provided the krill samples from western North Pacific. We thank the staff of the Center for Ecological Research, Kyoto University for their help for our analyses. We also thank to H. Hatanaka of the National Research Institute of Fisheries Science for kindly review the manuscript.

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Table 1. Sampling data and stable isotope ratios for mature male minke whales whose baleen plates were measured along their length for $\delta^{13}C$ and $\delta^{15}N$ values (mean±S.D.; ‰).

Sample No.	Date	Location	Body Length(m)	$\delta^{13}C$(‰) Mean±S.D.	$\delta^{13}C$(‰) Range	$\delta^{15}N$(‰) Mean±S.D.	$\delta^{15}N$(‰) Range	n
Sub-area 7								
98003	1998.5.5	39°49.6′ N 145°40.0′ E	7.5	-17.4±0.3	-18.2 to -17.0	10.7±0.6	9.3 to 11.6	18
98008	1998.5.7	40°6.8′ N 149°8.8′ E	8.1	-17.7±0.4	-18.3 to -17.0	10.7±0.6	8.9 to 11.2	15
98027	1998.5.11	39°19.0′ N 145°36.6′ E	7.6	-17.9±0.2	-18.3 to -17.6	12.3±0.4	11.7 to 12.8	14
98050	1998.5.24	40°17.5′ N 149°53.3′ E	7.1	-17.7±0.4	-18.4 to -17.0	11.0±0.7	9.5 to 12.0	13
96051	1996.8.26	41°9.6′ N 143°14.7′ E	7.4	-16.9±0.2	-17.3 to -16.6	11.5±0.5	10.2 to 12.0	16
96054	1996.8.26	41°14.2′ N 143°14.0′ E	7.1	-17.5±0.2	-17.9 to -17.2	10.3±0.6	9.3 to 10.8	13
Sub-area 8								
98081	1998.6.7	40°26.6′ N 150°6.3′ E	7.6	-16.8±0.2	-17.2 to -16.6	14.4±0.6	12.9 to 15.0	13
98085	1998.6.7	40°24.8′ N 150°1.8′ E	8.0	-17.7±0.4	-18.4 to -16.8	10.3±0.7	8.4 to 11.2	24
98092	1998.6.10	40°13.6′ N 151°35.2′ E	7.7	-18.0±0.3	-18.7 to -17.5	9.8±0.6	8.4 to 10.5	24
98097	1998.6.10	40°37.4′ N 151°45.1′ E	7.5	-17.9±0.3	-18.3 to -17.4	9.8±0.6	8.6 to 10.7	14
98100	1998.6.13	40°24.0′ N 150°14.6′ E	7.6	-18.1±0.3	-18.6 to -17.5	9.9±0.6	8.5 to 10.9	26
Sub-area 11								
96023	1996.8.17	44°30.1′ N 144°26.9′ E	7.1	-17.4±0.3	-17.9 to -16.8	10.7±0.5	9.7 to 11.2	14
96034	1996.8.19	45°3.4′ N 144°35.8′ E	7.6	-18.1±0.4	-18.8 to -17.7	11.8±0.6	10.7 to 12.6	27
96035	1996.8.19	45°3.1′ N 144°31.2′ E	7.2	-17.1±0.3	-17.9 to -16.6	11.1±0.5	10.0 to 11.7	24
96045	1996.8.21	44°32.4′ N 143°40.8′ E	7.3	-18.3±0.2	-18.7 to -18.0	11.2±0.3	10.8 to 11.7	13
99057	1999.7.7	45°13.6′ N 143°23.1′ E	7.0	-18.8±0.3	-19.5 to -18.3	11.9±0.5	10.7 to 12.4	16
99074	1999.7.9	44°34.5′ N 143°56.1′ E	7.3	-17.8±0.3	-18.2 to -17.4	11.5±0.3	11.0 to 12.1	16
99077	1999.7.10	44°57.7′ N 144°37.4′ E	7.2	-18.6±0.3	-19.3 to -18.1	11.7±0.4	11.0 to 12.1	15
99082	1999.7.11	44°45.7′ N 144°58.0′ E	7.7	-19.1±0.3	-19.6 to -18.6	11.8±0.8	10.0 to 12.8	14
99085	1999.7.12	44°24.3′ N 144°36.2′ E	7.7	-17.4±0.2	-18.1 to -17.1	14.1±0.5	13.0 to 14.6	15
99088	1999.7.13	44°38.0′ N 145°3.5′ E	7.9	-17.5±0.1	-17.7 to -17.3	11.6±0.4	10.8 to 12.1	18

Table 2. Stable isotope ratios (mean±S.D.; ‰) measured for muscle, liver and average of baleen plate of mature male minke whales from sub-areas 7, 8 and 11.

Locality	Year	Muscle		Liver			Average of baleen plate		
		$\delta^{13}C$(‰)	$\delta^{15}N$(‰)	$\delta^{13}C$(‰)	$\delta^{15}N$(‰)	n	$\delta^{13}C$(‰)	$\delta^{15}N$(‰)	n
Sub-area 7	1998	-18.2±0.5	10.4±0.9	-18.3±0.5	10.9±0.6	14	-17.5±0.4	11.1±0.7	6
Sub-area 8	1998	-18.3±0.5	10.1±1.4	-18.2±0.4	10.7±0.7	10	-17.7±0.5	10.8±2.0	5
Sub-area 11	1999	-18.6±0.5	11.1±1.1	-18.7±0.5	12.0±0.6	20	-18.0±0.7	11.7±1.0	10

Table 3. Sampling data, $\delta^{13}C$ and $\delta^{15}N$ of prey species of minke whale.

Species	Locality	Date	Sampling methods	$\delta^{13}C$(‰)	$\delta^{15}N$(‰)
*Engraulis japonicus**	Sub-area 8	1998/6/10	No.98097 gut contents	-18.0	9.4
				-19.8	8.0
				-19.1	9.0
				-19.3	7.8
	Usujiri, Hokkaido	1999/10/4	set net	-17.6	10.5
				-18.0	9.9
*Euphausia pacifica***	Off Sanriku	1999/10/11-21	larval net	-18.4	8.7
				-18.6	8.7
	Southern Okhotsk Sea	1999/9/30	flame trawl	-20.5	8.6
				-20.7	8.5

*: measured for the muscle tissue.

**: 20 individuals were mixed.

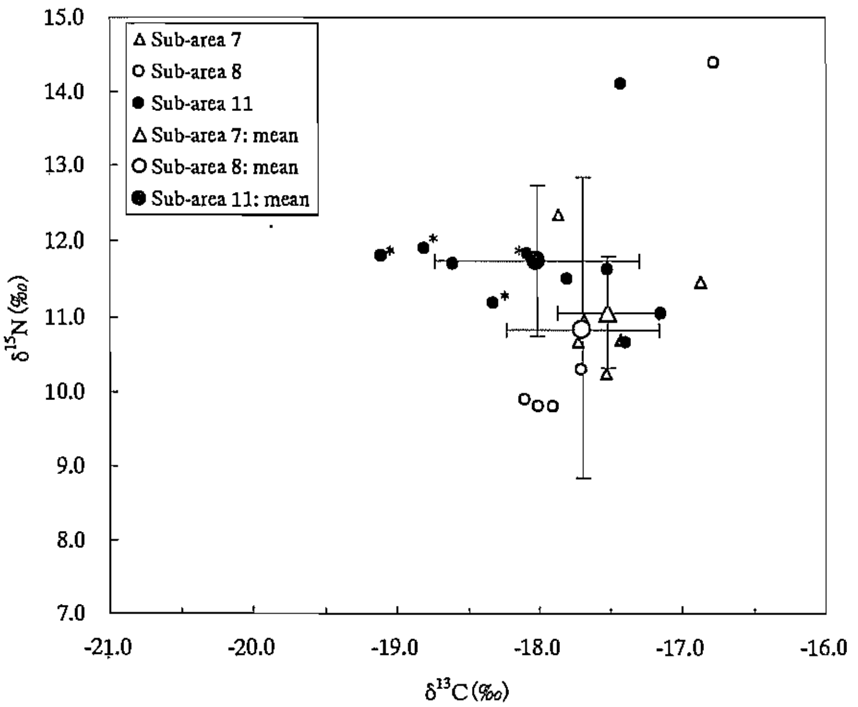

Fig. 1. The $\delta^{13}C$ - $\delta^{15}N$ map of baleen of western North Pacific minke whales.
(*: identified as J stock from genetic analyses (Goto unpublished data))

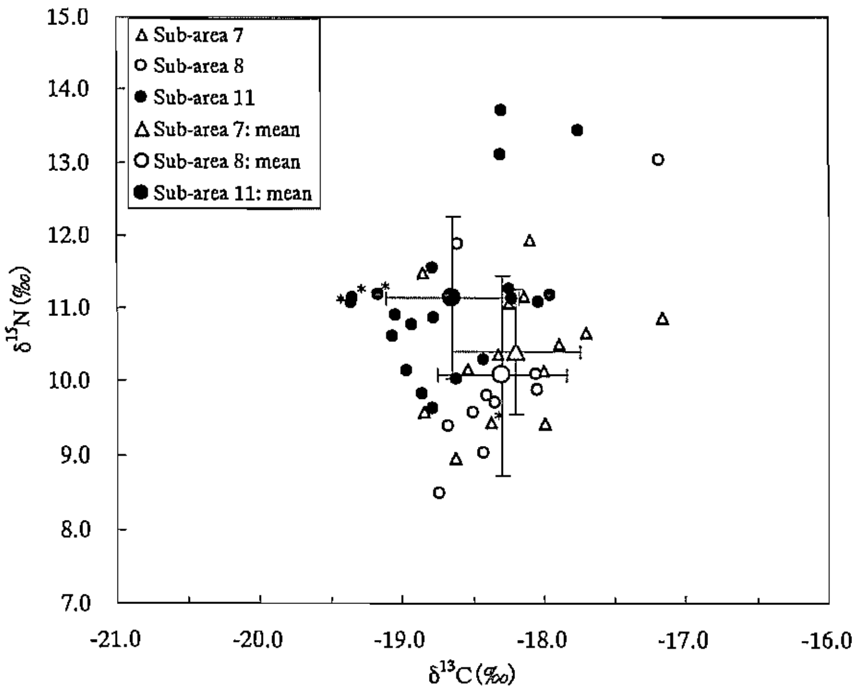

Fig. 2. The $\delta^{13}C$ - $\delta^{15}N$ map of muscle of western North Pacific minke whales.
(*: identified as J stock from genetic analyses (Goto unpublished data))

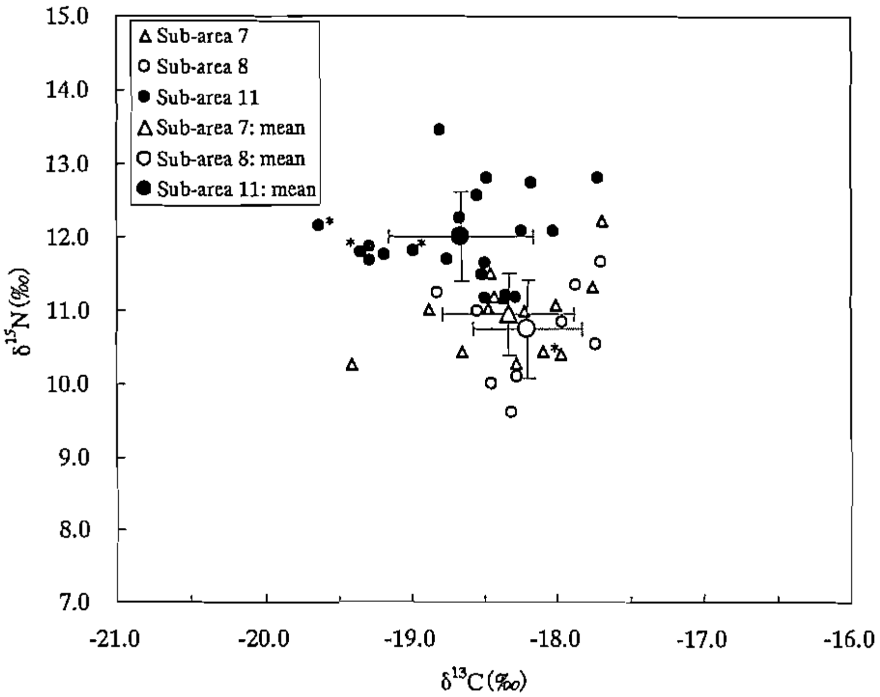

Fig. 3. The $\delta^{13}C$ - $\delta^{15}N$ map of liver of western North Pacific minke whales.
(*: identified as J stock from genetic analyses (Goto unpublished data))

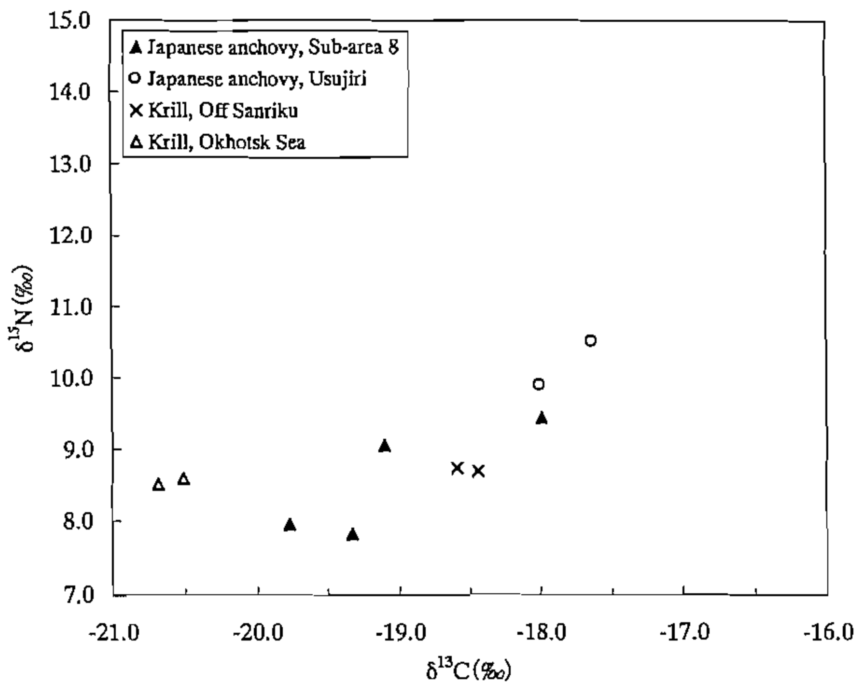

Fig. 4. The $\delta^{13}C$ - $\delta^{15}N$ map of preys of western North Pacific minke whales.

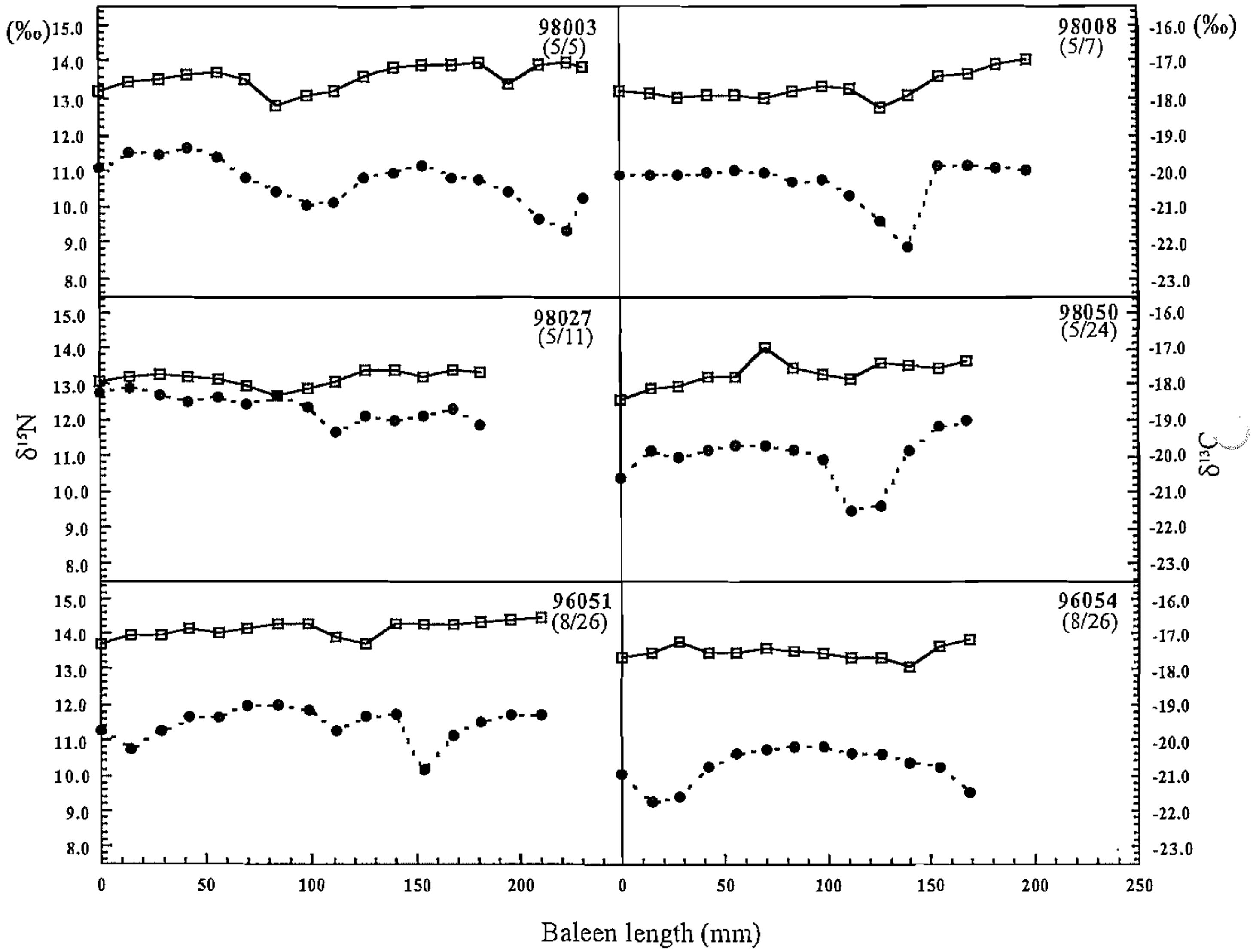

Fig. 5a. Nitrogen (●) and carbon (□) isotope ratios along the length of the baleen plates of minke whales from sub-area 7. Catch date of each individual is shown in parenthesis.

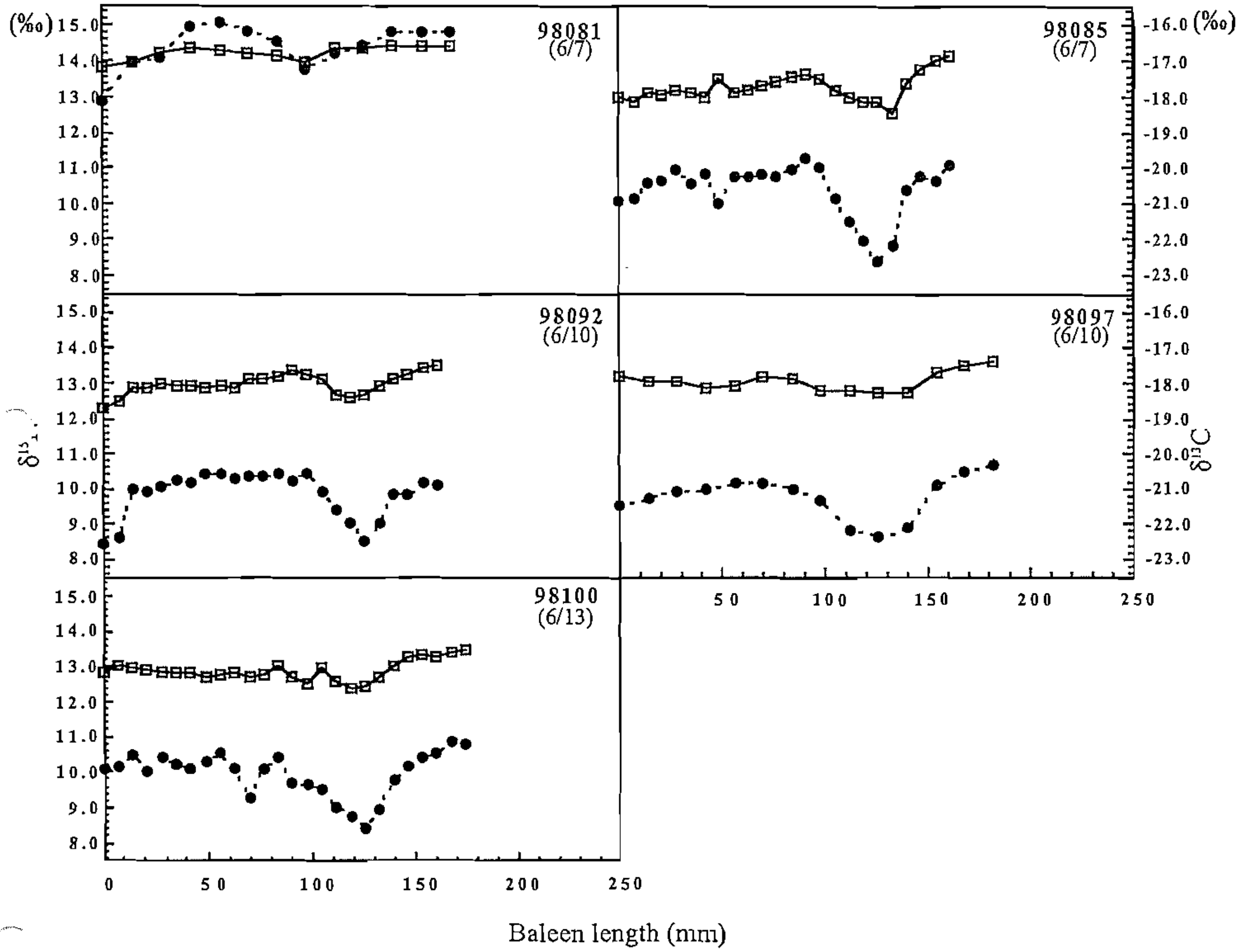

Fig. 5b. Nitrogen (●) and carbon (□) isotope ratios along the length of the baleen plates of minke whales from sub-area 8. Catch date of each individual is shown in parenthesis.

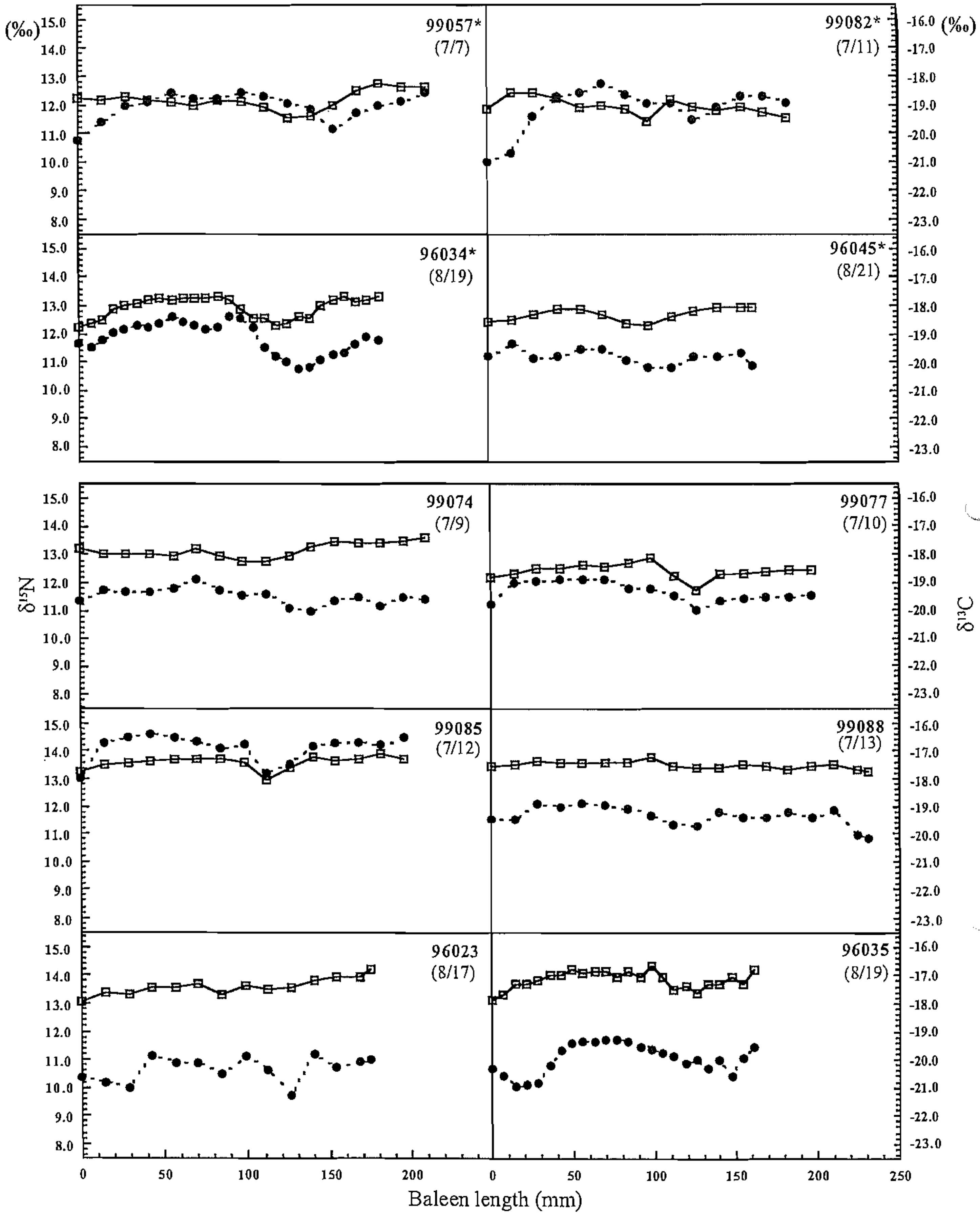

Fig. 5c. Nitrogen (●) and carbon (□) isotope ratios along the length of the baleen plates of minke whales from sub-area 11. Catch date of each individual is shown in parenthesis.
(*: idntified as J stock from genetic analysis(Goto unpublished data))