Trophic relationships in early spring along the Okhotsk coast of Hokkaido, Japan, as traced by stable carbon and nitrogen isotopes

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Abstract: We measured stable carbon and nitrogen isotope ratios (13C/12C and 15N/14N) of organic matter sources and consumers, including fishery resources, along the Okhotsk coast of northern Hokkaido, Japan, in early spring to characterize the food web. Phytoplankton and benthic detritus, including ice algae, fecal pellets, and benthic microalgae, constituted the main food sources for primary consumers (zooplankton and small benthic invertebrates, respectively); seagrass and terrestrial plant debris served no trophic function for consumers. Planktivorous and benthivorous fish species could be differentiated using stable carbon isotope ratios. Differences in stable nitrogen isotope ratios revealed species-specific feeding habits of crustacean groups: copepods were separated into three groups as herbivorous, omnivorous, or omnivorous-carnivorous, and benthic amphipods were divided into two groups as either omnivorous or omnivorous-carnivorous. We distinguished four levels of both pelagic and benthic trophic linkages. The δ13C values were enriched by 0.9–1.3‰ at the linkage between each pelagic trophic level except between the 1st and 2nd levels; δ15N values were enriched by 2.2–2.9‰ at each level. For benthic trophic linkages, the enrichment for δ13C and δ15N values between each level ranged from 0.6‰ to 1.0‰ and from 1.6‰ to 2.6‰, respectively. Trophic positions of copepod, mysids, and sand lance appeared between pelagic and benthic linkages. This suggests that those species have fed on both pelagic and benthic diets.

Key words: Okhotsk coast, organic matter sources, stable isotopes, trophic linkages

Introduction

Fishery resources, such as salmon, scallops, crabs, and flatfishes, are abundant along the Okhotsk coast of northern Hokkaido, Japan (Mizushima 2003, Kudo et al. 2006). Most of these fishery resources are sustained by a food web that starts with a spring bloom of diatoms following the retreat of sea ice in April (Tanaka et al. 2003). We also previously observed that overwintering benthic gammaridean individuals growing in size appeared abundantly nearshore along the Okhotsk coast during May (Hiwatari et al. 2004) and that a food supply in the form of large numbers of ice algae cells and abundant fecal pellets from zooplankton, such as euphausiids, settled from seasonal sea ice off the Okhotsk coast (Hiwatari et al. 2008). From these observations of the pelagic and benthic trophic linkages, we assumed that the food supply for the fishery resources and the benthic crustacean population was associated not only with the spring diatom bloom but also with the flux of organic matter during the period with seasonal sea ice.

As many pelagic and benthic invertebrates and fishes inhabit the entire Okhotsk coastal area (Hiwatari et al. 2004, Suda et al. 2004), it is important to understand not only the source of organic matter for these animals but also the trophic structure of the food webs in the area ecosystems. The integrated analysis of carbon and nitrogen stable isotopes is a powerful technique for distinguishing sources of organic matter and the trophic positions of consumers (Michener & Schell 1994). The technique is based on the
predictable isotopic fractionation from one trophic level to the next. The $\delta^{13}C$ composition of consumers reflects the composition of assimilated food, with slight enrichment ($\sim 1\%$; Fry & Sherr 1984). In contrast, the $\delta^{15}N$ composition undergoes a consistent enrichment ($\sim 3.5\%$) from prey to predator and can be used to determine the trophic position of an organism (Minagawa & Wada 1984).

The use of stable carbon and nitrogen isotopes for the trophic study of ecosystems along the Okhotsk coast of northern Hokkaido has been limited to the effects of salmon on material transport to the terrestrial ecosystem (Kaeriyama & Minagawa 2008), and to the study of diet patterns in cultured marine bivalves (Aya & Kudo 2007, 2010); studies of the trophic structure in the nearshore zone and offshore along the Okhotsk coast are scarce. Therefore, the objectives of this study are to: (1) investigate $\delta^{13}C$ and $\delta^{15}N$ differences in organic matter sources and consumers, including fishery resources; (2) identify the sources of organic matter supporting consumers; (3) reveal species-specific differences in feeding habits in crustacean groups; and (4) clarify the pelagic and benthic ecosystem trophic linkages nearshore and offshore along the Okhotsk coast of northern Hokkaido in the early spring. Furthermore, in this context, we discuss: (1) processes of $\delta^{13}C$ enrichment of benthic organic matter sources; (2) relationships between shape of mouth parts and species-specific feeding habits of crustacean groups; (3) number of trophic levels and those values of $\delta^{13}C$ and $\delta^{15}N$ in both pelagic and benthic trophic linkages; and (4) mutual relationships among producer and consumer groups with abundant biomass in ecosystem of the Okhotsk coast based on the results of both pelagic and benthic linkages.

Materials and Methods

Study area

This study was primarily conducted at two sites: a nearshore site at Yasshushinai along the Mombetsu coast and an offshore site (Fig. 1) that is subject to seasonal sea ice (Hiwatari et al. 2008). Two rivers, Mombetsu River and Yasshushinai River, reach the Mombetsu coast near the study area. In the autumn, large quantities of grasses cut from farms upstream accumulate at the mouth of the Mombetsu River (Hiwatari et al. 2004). Sediments along the Mombetsu coast consist of coarse sands, and the seagrass Zostera marina Linnaeus is interspersed throughout the nearshore zone at depth of 8–10 m.

From May to October 2003 (except for July, when no field survey was conducted), water temperatures at the Yasshushinai site ranged from 6.9°C (May) to 18.7°C (September), salinity ranged from 33.10 psu (May) to 33.71 psu (September), and chlorophyll $a$ concentrations ranged from 0.5 $\mu g L^{-1}$ (June and August) to 2.0 $\mu g L^{-1}$ (May) in surface water (10 m depth) (Hiwatari et al. 2004). On 12 April 2004 when the present study was conducted, water temperature, salinity, and chlorophyll $a$ concentration were 4.6°C, 30.73 psu, and 4.0 $\mu g L^{-1}$, respectively, at the surface water (10 m depth) at the Yasshushinai site where there was a spring bloom of phytoplankton (Hiwatari unpubl. data)

There are important fishery grounds offshore from the Mombetsu coast, one being a seabed sowing and cultivation ground for scallops at around 40 m depth and the other the hair crab (Erimacrus isenbeckii (Brandt)) fishery ground, which is more than 80 m in depth. The hair crab cage fishery is conducted every year soon after the retreat of sea ice. Salmon (Oncorhynchus gorbuscha (Walbaum)) and O. keta (Walbaum)) run up both rivers in the autumn, and their larvae hatch and return to the sea in early spring, appearing in the nearshore zone along the Mombetsu coast.

The fauna in the nearshore zone along the Mombetsu coast from June 2002 to April 2004 as revealed by a sledge net (60 cm wide, 40 cm high, 2 m long, 800 $\mu m$ mesh) was composed of eight phyla and 12 classes, including five orders of Crustacea, two suborders of Amphipoda, and three suborders of Decapoda; the major taxa throughout the study period were Mysidae and Amphipoda (Hiwatari et al. 2003, 2004). The ichthyofauna captured along the Mombetsu coast by an experimental beach seine from May 2003 to April 2004 consisted of 5,914 individuals of both pelagic and demersal fishes belonging to 22 families and 47 species. The families, in order of species abundance, were Pleuronectidae (eight species), Cottidae (seven species), and three species each of Osmeridae, Hexagrammidae, Agonidae, and Stichaeidae (Suda et al. 2005, 2008). Gut content analysis of representative pelagic and demersal species showed that the major diet of the pelagic fishes was copepods and that of demersal fishes was mysids and amphipods (Suda et al. 2008, Shiino 2008, Fuzawa 2009).
Sampling collection and processing

Sampling collection data are summarized in Table 1. Phytoplankton was collected by towing a phytoplankton net with a mesh of 130 μm for about 10 min. A particulate organic matter (POM) sample was obtained by using a sampling bottle. Ice algae were sampled from sea ice. Terrestrial plant debris and seagrass Zostera marina were collected by a sledge net. Macroalgae attached on the side of a pier in Mombetsu Harbor was collected by hand. Organic matter in seabed sediment was collected by a SCUBA diver. Benthic microalgae growing on the underwater observational window (8 m depth) of the Okhotsk Tower were collected by scraping the algae from the surface of the pane. Pelagic invertebrate samples were collected by towing a zooplankton net with a mesh of 330 μm. Samples of benthic invertebrates—including amphipods, except Paralorchesistes sp., and mysids and decapods, except for the hair crab Erimacrus isenbeckii—were collected in a sledge net and kept frozen. Adult scallops were collected by fishery dredge from the seabed at the planting site. Amphipods were collected by a beach seine net. Three demersal fishes were collected in a sledge net.

Sample procedures for isotopic analysis are also summarized in Table 1. The phytoplankton sample was sieved through a 330 μm mesh screen to remove zooplankton, and filtered onto a precombusted (450°C, 4 h) Whatman GF/F filter (47 mm in diameter). The filter was then exposed to HCl vapor for 4 h to remove carboxylates and kept frozen. After the filter sample was divided into three pieces, the three subsamples were freeze-dried for analysis. POM, ice algae, and benthic microalgae samples were subsequently filtered and processed in the same way as the phytoplankton sample. The surfaces of terrestrial plant debris, seagrass, and macroalgae samples were cleaned by brushing to remove the epiphyte components, and then the samples were washed with 1.2 N HCl, rinsed with distilled water, dried at 60°C, and ground into powder. In processing of the organic matter in seabed sediment, the upper 2 cm of the sediment was dried at 60°C and ground was then soaked in 1.2 N HCl overnight to remove carbonate. The samples on filters and of whole bodies of zooplankton were freeze-dried using freeze dryer equipment and the ground samples placed in tin capsules for analysis. All samples were analyzed for carbon and nitrogen stable isotope ratios using a Finnigan isotope-ratio mass spectrometer (MAT252A, Finnigan, Germany) coupled to a Fisons element analyzer (EA-1108, Fisons Instruments). Raw stable isotope measurements are normalized to values for our laboratory working standard material: L-alanine (δ13C = −21.12±0.06‰ [n = 12], δ15N = −0.04±0.08‰ [n = 12]), measured by Elemental Analyzer-Isotope Ratio Mass Spectrometer (EA-IRMS), which has been calibrated against known isotopic reference materials, International Atomic Energy Agency (IAEA)-NBS19 (limestone, δ13CVPDB = +1.95‰) and IAEA-N1 (ammonium sulfate, δ15NART = +0.4±0.2‰) distributed from National Institute of Standards and Technology (NIST) as Reference Materials (RM) 8544 and RM 8547, respectively. Stable isotope ratios are expressed in conventional δ notation as per mil (‰) according to the following equation:

\[ \delta X = \left( \frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right) \times 1000, \]

where X is 13C or 15N and R is the corresponding 13C/12C or 15N/14N ratio.

Results

Producers: organic matter sources

The δ13C of organic matter sources at the Yashushushina site ranged from −27.7±2.8‰ for terrestrial plant debris to −14.8±1.0‰ for the seagrass Zostera marina (Table 2).
Table 1. Sampling date, site, method, depth and processing for isotopic analysis.

| Sample | Date       | Site | Method | Depth | Processing for isotopic analysis | Procedure | No. of samples | No. of analyses |
|--------|------------|------|--------|-------|---------------------------------|-----------|----------------|----------------|
| **Producers (organic matter sources)** |            |      |        |       |                                 |           |                |                |
| Phytoplankton | 12 Apr. 04 | Ya.* | PN     | Surface | freeze-dried | 50¹ | 3           |
| Particulate organic matter | 24 Mar. 05 | Off     | Bottle | Surface | freeze-dried | 23¹ | 3           |
| Ice algae | 4 Mar. 05 | Off | Sea ice | Surface | freeze-dried | 50¹ | 3           |
| Terrestrial plant debris | 12 Apr. 04 | Ya, | SN* | 4–10 m | dried 60°C, ground | 16² | 3           |
| Macroalgae: Callophyllum sp. | 12 Apr. 04 | MH | Hand | Surface | dried 60°C, ground | 24³ | 3           |
| Macroalgae: Laminaria sp. | 12 Apr. 04 | MH | Hand | Surface | dried 60°C, ground | 50¹ | 3           |
| Zostera marina | 12 Apr. 04 | Ya | SN | 8–10 m | dried 60°C, ground | 30¹ | 3           |
| Sediment organic matter | 14 Mar. 05 | Okhotsk Tower | Core sample | 10 m | dried 60°C, ground | 15¹ | 3           |
| Benthic microalgae | 14 Mar. 05 | Okhotsk Tower | Bottle | 8 m | freeze-dried | 2            |
| **Consumers: invertebrates** |            |      |        |       |                                 |           |                |                |
| Copepods | A. sp. | 12 Apr. 04 | Ya | ZN     | Surface | freeze-dried | 20¹ | 3           |
| Calanus glacialis | 5 Mar. 04 | Off | ZN | Surface | freeze-dried | 6¹ | 3           |
| C. glacialis | 12 Apr. 04 | Ya | ZN | Surface | freeze-dried | 16² | 3           |
| Eurytemora herdmani | 12 Apr. 04 | Ya | ZN | Surface | freeze-dried | 50¹ | 3           |
| Neocalanus cristatus | 5 Mar. 04 | Off | ZN | Surface | freeze-dried | 19¹ | 3           |
| Pseudocalanus sp. | 12 Apr. 04 | Ya | ZN | Surface | freeze-dried | 15¹ | 3           |
| Amphipods | Themisto japonica | 5 Mar. 04 | Off | ZN | Surface | freeze-dried | 20¹ | 3           |
| Euphausiids | T. inermis juvenile | 5 Mar. 04 | Off | ZN | Surface | freeze-dried | 6¹ | 3           |
| T. inermis adult | 5 Mar. 04 | Off | ZN | Surface | dried 60°C, ground | 10⁰ | 3           |
| Gastropods | Clione limacina | 5 Mar. 04 | Off | ZN | Surface | freeze-dried | 4¹ | 3           |
| Sagitta elegans | 5 Mar. 04 | Off | ZN | Surface | freeze-dried | 5¹ | 3           |
| Bivalves | M. yessoensis juvenile | 9 June 05 | Off | HCC | 20 m | dried 60°C, ground | 20¹ | 9           |
| M. yessoensis adult | 15 Mar. 05 | Off | HCC | 30 m | dried 60°C, ground | 3 | 9           |
| Amphipods | Atylus sp. | 12 Apr. 04 | Ya | SN | 4–10 m | dried 60°C, ground | 16² | 3           |
| Monoculodes sp. male | 12 Apr. 04 | Ya | SN | 8–10 m | dried 60°C, ground | 24³ | 3           |
| M. sp. female | 12 Apr. 04 | Ya | SN | 8–10 m | dried 60°C, ground | 20¹ | 3           |
| Paraliochebus sp. | 19 Mar. 05 | Utoro | HN | Sea ice | dried 60°C, ground | 6³ | 3           |
| Pontogeneia sp. | 12 Apr. 04 | Ya | SN | 4–10 m | dried 60°C, ground | 6³ | 3           |
| Mysids | Arcanomysis ochotensis | 12 Apr. 04 | Ya | SN | 4–6 m | dried 60°C, ground | 20¹ | 3           |
| Euxanthomyxys japonica | 12 Apr. 04 | Ya | SN | 8–10 m | dried 60°C, ground | 16² | 3           |
| Decapods | Crangon sp. | 12 Apr. 04 | Ya | SN | 4–10 m | dried 60°C, ground | 8¹ | 3           |
| C. sp. | 12 Apr. 04 | Ya | SN | 4–10 m | dried 60°C, ground | 4¹ | 3           |
| C. sp. | 12 Apr. 04 | Ya | SN | 4–10 m | dried 60°C, ground | 3 | 3           |
| C. sp. | 12 Apr. 04 | Ya | SN | 4–10 m | dried 60°C, ground | 2 | 3           |
| Hair crab Telmessus cheiragonus juvenile | 12 Apr. 04 | Ya | SN | 8–10 m | dried 60°C, ground | 1 | 3           |
| Erimacrus isenbeckii adult | 28 Mar. 05 | Off | CT | 80 m | dried 60°C, ground | 3 | 9           |
| **Consumers: fishes** |            |      |        |       |                                 |           |                |                |
| Pelagic | Larvae | 12 Apr. 04 | Ya | ZN | Surface | freeze-dried | 50¹ | 3           |
| Oncorhynchus gorbuscha juvenile | 16 Apr. 04 | MH | HN | Surface | dried 60°C, ground | 8¹ | 3           |
| Oncorhynchus keta juvenile | 16 Apr. 04 | MH | HN | Surface | dried 60°C, ground | 6¹ | 3           |
| Ammodytes personatus young | 16 Apr. 04 | Ya | BSN | 0–5 m | dried 60°C, ground | 15 | 5           |
| Clupea pallasi Valenciennes juvenile | 16 Apr. 04 | Ya | BSN | 0–5 m | dried 60°C, ground | 15 | 5           |
| Demersal | Brachyopsis rostrata | 12 Apr. 04 | Ya | SN | 8–10 m | dried 60°C, ground | 1 | 3           |
| Pallastina barbata young | 12 Apr. 04 | Ya | SN | 8–10 m | dried 60°C, ground | 1 | 3           |
| Pleuronectes pectinatissimus young | 12 Apr. 04 | Ya | SN | 8–10 m | dried 60°C, ground | 3 | 9           |

*Ya.: Yashushinai site; Off: Offshore site; MH: Mombetsu Harbor; PN: Phytoplankton net; SN: Sledge net; ZN: Zooplankton net; HCC: Hanging culture cage; FD: Fishery dredge; HN: Hand net; CT: Cage trap; BSN: Beach seine net; Plural individuals picked up from number in parenthesis were used to obtain a single analysis; Number in parenthesis indicates the number of individuals combined to powder.
Table 2. Values of $\delta^{13}C$ and $\delta^{15}N$ and C:N ratios for organic matter sources along the Okhotsk coast of Hokkaido, Japan. Values are means±SD (for n=3) or ranges (for n=2).

| Sample                  | $\delta^{13}C$ (‰) | $\delta^{15}N$ (‰) | C:N (mol/mol) |
|------------------------|---------------------|---------------------|---------------|
| Phytoplankton          | -22.2±0.1           | 4.9±0.3             | 5.7±0.1       |
| Particulate organic matter | -24.1              | 5.9                 | 6.2           |
| Ice algae              | -22.3 to -21.5      | 6.5 to 7.2          | 7.5 to 8.2    |
| Terrestrial plant debris | -27.7±2.8           | 2.7±1.0             | 36.5 to 15.2  |
| Macroalgae: Callophyllis sp. | -21.7±0.0       | 6.9±0.0             | 7.0±0.3       |
| Macroalgae: Laminaria sp. | -20.5±0.1          | 5.5±0.2             | 9.4±0.5       |
| Seagrass Zostera marina | -14.8±0.1           | 8.0±0.7             | 17.6±0.8      |
| Sediment organic matter | -24.8±0.1           | 5.4±1.6             | 13.3±0.1      |
| Benthic microalgae     | -21.1 to -20.7      | 5.2 to 5.6          | 7.0 to 7.2    |

Particulate organic matter (POM) at the offshore site on 24 March 2005 showed a more depleted carbon isotopic signature than that of phytoplankton during the spring bloom at the Yashushinai site on 12 April 2004. The $\delta^{13}C$ signatures of benthic microalgae (-21.1 to -20.7‰) was more enriched than that of phytoplankton.

The $\delta^{15}N$ of organic matter sources ranged from 2.7±1.0‰ for terrestrial plant debris to 8.0±0.7‰ for seagrass Z. marina (Table 2). Among phytoplankton, POM, ice algae and benthic microalgae, the phytoplankton from the spring bloom on 12 April 2004 at the Yashushinai site had the most depleted $\delta^{15}N$ value (4.9±0.3‰), whereas ice algae was the most enriched (6.5 to 7.2‰).

The molar carbon : nitrogen ratios ranged from 5.7±0.1 for spring bloom phytoplankton to 36.5±15.2 for terrestrial plant debris.

Consumers: invertebrates

Of the pelagic invertebrate taxa, the copepod Acartia sp. was the most depleted $\delta^{13}C$ (-24.9±0.1‰), whereas the copepod Eurytemora herdmani Thompson was the most enriched (-21.0‰) (Table 3). The $\delta^{13}C$ values of copepods were significantly different between species (Kruskal–Wallis test, p<0.05). The $\delta^{13}C$ values for other groups, such as amphipods, euphausiids, gastropod, and chaetognath, were within the range of values for the copepods (Table 3).

$\delta^{15}N$ ranged from 6.5‰ in the copepod Pseudocalanus sp. to 13.1±0.1‰ in Sagitta elegans (Verrill), which typically is carnivorous. Both the $\delta^{13}C$ and $\delta^{15}N$ signatures were similar for adults and juveniles of the euphausiid Thysanoëssa inermis (Krøyer).

In the benthic taxa, the amphipod Parallochistes sp. collected from the bottom of sea ice showed the most depleted $\delta^{13}C$ signature (-21.2‰), whereas the largest Crangon sp. (body length 55.2 mm) was the most enriched (-16.8±0.3‰) (Table 3). Although the scallop Mizuhopecten yessoensis (Jay) is a suspension feeder, the adults from the seabed cultivation area showed an enriched $\delta^{13}C$ signature (-18.1‰), as did the deposit feeders, such as amphipods. Both the $\delta^{13}C$ and $\delta^{15}N$ of adult scallops were more enriched than those of juveniles (Mann–Whitney U-test; p<0.01 and p<0.05, respectively).

Values for $\delta^{15}N$ ranged from 8.1±0.2‰ in the amphipod Atylus sp. to 12.9±0.1‰ in the hair crab Erimacrus isenbeckii, the stomach contents of which included fragments of decapods and polychaetes (Hiwatari, unpubl. data). Both the $\delta^{13}C$ and $\delta^{15}N$ signatures of the largest Crangon sp. (body length 55.2 mm) were more enriched than those of the smaller individuals (body length 18.3–41.1 mm; Mann–Whitney U-test, p<0.05).

Fishes

There was a significant difference between the $\delta^{13}C$ of pelagic fishes excluding larvae (mean −20.9‰) and the demersal fishes (mean −17.0‰) (Mann–Whitney U-test, p<0.001) (Table 4). In contrast, the $\delta^{15}N$ values were not significantly different between the fish groups (Mann–Whitney U-test, p=0.859).

Species-specific differences in $\delta^{15}N$ signatures of crustacean groups

The $\delta^{15}N$ signatures of organisms reflect their trophic position because of differences in their feeding habits. Differences in the $\delta^{15}N$ for species in three crustacean groups are shown in Fig. 2.

The $\delta^{15}N$ values of copepod species revealed three trophic groups (Kruskal–Wallis test, p<0.001). Pseudocalanus sp. and Neocalanus cristatus (Krøyer) were the most depleted group, with $\delta^{15}N$ signatures of 6.5 and 7.4‰, respectively. Eurytemora herdmani had an intermediate $\delta^{15}N$ value (9.2‰), and Acartia sp. and Calanus glacialis Jaschnov were the most enriched group (10.5 and 11.2‰, respectively).

Benthic amphipods fell into two trophic groups (Mann–Whitney U-test, p<0.01). Atylus sp., Pontogeneia sp., and Parallochistes sp. had $\delta^{15}N$ values of 8.1–8.5‰, whereas...
Table 3. Body length, wet weight, $\delta^{13}$C and $\delta^{15}$N values, and C:N ratios for pelagic and benthic invertebrates collected along the Okhotsk coast of Hokkaido, Japan. Values are means±SD (for $n\geq 3$).

| Sample | Body length | Wet weight | $\delta^{13}$C | $\delta^{15}$N | C:N |
|--------|-------------|------------|----------------|----------------|-----|
|        | (mm)        | (g)        | %o             | %o             | mol/mol |
| Pelagic |             |            |                |                |     |
| Coccolithophores |        |            |                |                |     |
| Acartia sp. | 1.4±0.2 | 0.2±0.1 | 1.2±0.1 | 1.1±0.1 | 0.00 | 0.00 |
| Calanus glacialis | 2.0±0.2 | 0.2±0.1 | 1.2±0.1 | 1.1±0.1 | 0.00 | 0.00 |
| C. glacialis | 2.5±0.6 | 0.6±0.1 | 1.2±0.1 | 1.1±0.1 | 0.00 | 0.00 |
| Eurytemora herdmani | 2.0 | 0.2 | 1.2±0.1 | 1.1±0.1 | 0.00 | 0.00 |
| Paraschizops longipes | 2.0 | 0.2 | 1.2±0.1 | 1.1±0.1 | 0.00 | 0.00 |
| Neocalanus cristatus | 2.0 | 0.2 | 1.2±0.1 | 1.1±0.1 | 0.00 | 0.00 |
| Pseudocalanus sp. | 2.0 | 0.2 | 1.2±0.1 | 1.1±0.1 | 0.00 | 0.00 |
| Amphipods | 2.0 | 0.2 | 1.2±0.1 | 1.1±0.1 | 0.00 | 0.00 |
| Themisto japonica (Bozellius) | 2.0 | 0.2 | 1.2±0.1 | 1.1±0.1 | 0.00 | 0.00 |
| Euphausiids | 2.0 | 0.2 | 1.2±0.1 | 1.1±0.1 | 0.00 | 0.00 |
| Thysanoosura inermis (Kröyer) | 2.0 | 0.2 | 1.2±0.1 | 1.1±0.1 | 0.00 | 0.00 |
| T. inermis | 2.5±0.2 | 0.2±0.1 | 1.2±0.1 | 1.1±0.1 | 0.00 | 0.00 |
| Gastropods | 2.0 | 0.2 | 1.2±0.1 | 1.1±0.1 | 0.00 | 0.00 |
| Clione limacina (Phipps) | 2.0 | 0.2 | 1.2±0.1 | 1.1±0.1 | 0.00 | 0.00 |
| Chaetognath | 2.0 | 0.2 | 1.2±0.1 | 1.1±0.1 | 0.00 | 0.00 |
| Sagitta elegans (Verrill) | 2.0 | 0.2 | 1.2±0.1 | 1.1±0.1 | 0.00 | 0.00 |
| Benthic | 2.0 | 0.2 | 1.2±0.1 | 1.1±0.1 | 0.00 | 0.00 |
| Bivalve | 2.0 | 0.2 | 1.2±0.1 | 1.1±0.1 | 0.00 | 0.00 |
| Scallop Mizuhopecten yessoensis (Jay) | 2.0 | 0.2 | 1.2±0.1 | 1.1±0.1 | 0.00 | 0.00 |
| M. yessoensis adult | 2.0 | 0.2 | 1.2±0.1 | 1.1±0.1 | 0.00 | 0.00 |
| Amphipods | 2.0 | 0.2 | 1.2±0.1 | 1.1±0.1 | 0.00 | 0.00 |
| Atylus sp. | 2.0 | 0.2 | 1.2±0.1 | 1.1±0.1 | 0.00 | 0.00 |
| Monoculodes sp. | 2.0 | 0.2 | 1.2±0.1 | 1.1±0.1 | 0.00 | 0.00 |
| M. sp. female | 2.0 | 0.2 | 1.2±0.1 | 1.1±0.1 | 0.00 | 0.00 |
| Paralochestes sp. | 2.0 | 0.2 | 1.2±0.1 | 1.1±0.1 | 0.00 | 0.00 |
| Pontogeneia sp. | 2.0 | 0.2 | 1.2±0.1 | 1.1±0.1 | 0.00 | 0.00 |
| Mysids | 2.0 | 0.2 | 1.2±0.1 | 1.1±0.1 | 0.00 | 0.00 |
| Archaeomysis ochotensis (Hanamura) | 2.0 | 0.2 | 1.2±0.1 | 1.1±0.1 | 0.00 | 0.00 |
| Exacanthomysis japonica (Murano) | 2.0 | 0.2 | 1.2±0.1 | 1.1±0.1 | 0.00 | 0.00 |
| Decapods | 2.0 | 0.2 | 1.2±0.1 | 1.1±0.1 | 0.00 | 0.00 |
| Crangon sp. | 2.0 | 0.2 | 1.2±0.1 | 1.1±0.1 | 0.00 | 0.00 |
| C. sp. | 2.0 | 0.2 | 1.2±0.1 | 1.1±0.1 | 0.00 | 0.00 |
| C. sp. | 2.0 | 0.2 | 1.2±0.1 | 1.1±0.1 | 0.00 | 0.00 |
| Hair crab Telmessus cheiragonus (Tilesius) | 2.0 | 0.2 | 1.2±0.1 | 1.1±0.1 | 0.00 | 0.00 |

Monoculodes sp. (males and females) was the most enriched (10.8‰). Mysids species were divided into two trophic groups: Archaeomysis ochotensis (Hanamura) with a $\delta^{15}$N of 9.4‰ and Exacanthomysis japonica (Murano) with a $\delta^{15}$N of 11.6‰.

**Discussion**

**Organic matter sources**

In this study, the most depleted $\delta^{13}$C values were in terrestrial plant debris (−27.7‰), whereas the seagrass Zostera marina had the most enriched value of −14.8‰ (Table 1). The terrestrial CO2 fixation pathway in photosynthesis principally involves C3 and C4 plants (O’Leary 1988). The difference in C3 and C4 photosynthetic mechanisms results in a difference in isotope fractionation during carbon fixation in C3 and C4 plants. Accordingly, C3 plants have $\delta^{13}$C values of approximately −28‰, whereas C4 plants are approximately −14‰ (O’Leary 1988). Both C3 and C4 plants also inhabit marine habitats. Most phytoplankton have C3 CO2 fixation. As phytoplankton take up CO2 not only through the diffusion of dissolved CO2 but...
also through the active transport of HCO$_3^-$, the phytoplankton show more enriched $\delta^{13}$C values of approximately $-22\%$ (France 1995) compared to terrestrial plants, whereas Zostera spp. as C$_4$ plants have $\delta^{13}$C values ranging from $-15.8\%$ to $-9.2\%$ (Hemminga & Mateo 1996). The $\delta^{13}$C values of both terrestrial plant debris and Z. marina found in this study fell within the ranges of $\delta^{13}$C values for terrestrial plant and seagrass in previous studies.

In this study, the phytoplankton sample was obtained using a net with a mesh of 130 $\mu$m, and then sieved through a 330 $\mu$m mesh screen to remove zooplankton. As most uni-cell phytoplankton are smaller in size than 130 $\mu$m, they would pass through the 130 $\mu$m mesh net, whereas the spring bloom of diatom Chaetoceros sp., with a chain-like shape longer than 130 $\mu$m, occurred on the sampling date; therefore, the phytoplankton sample would consist mainly of the Chaetoceros sp. like chain. However, besides the phytoplankton, microzooplankton, larger than 130 $\mu$m and less than 330 $\mu$m, would be retained in the phytoplankton sample. Therefore, it is necessary to take the ‘phytoplankton’ sample into consideration to discuss the differences between the phytoplankton and POM for $\delta^{13}$C, $\delta^{15}$N, and carbon:nitrogen ratio values. The $\delta^{13}$C value of $-24.1\%$ for POM on 24 March 2005 at the offshore site was more depleted than the value of $-22.2\%$ for the phytoplankton on 12 April 2004 at the Yassushinai site, whereas the $\delta^{15}$N of 5.9‰ for POM was only slightly enriched relative to 4.9‰ for the phytoplankton (Table 2). Low temperatures are known to result in the depletion of $\delta^{13}$C of marine plants (Rau et al. 1989, Hemminga & Mateo 1996, Vizzini & Mazzola 2003). Rau et al. (1989) and Hemminga & Mateo (1996) attributed the significant decrease of $\delta^{13}$C values of phytoplankton and seagrasses with increasing latitude to the effect of temperature on CO$_2$ solubility and, hence, its concentration in seawater. This phenomenon, in which the decrease of water temperature and increasing CO$_2$ solubility results in depleted phytoplankton $\delta^{13}$C values, is applicable to our results. The water temperature after sea ice retreated on 24 March 2005 was 0.3°C, whereas the temperature when the spring bloom of diatoms appeared on 12 April 2004 was 4.6°C. Thus, this difference of water temperature might be one of the factors causing the difference in POM and phytoplankton $\delta^{13}$C values between the sampling dates. Regarding $\delta^{15}$N values, it is known that most of the available nitrate is quickly used and primary production relies largely on recycled ammonia, which is generally depleted in $^{15}$N (Michener & Schell 1994). In our study, the spring bloom of the diatom Chaetoceros sp. on 12 April 2004 would have used much of the available nitrate in the water, and the subsequent generation of recycled ammonia might have resulted in the depleted $\delta^{15}$N of phytoplankton. Another interpretation for reduction of phytoplankton $\delta^{15}$N...
is as follows: if nitrate pool is sufficient in the water column, $\delta^{15}N$ of phytoplankton reduces due to preferential use of $^{14}N$ (Altabet & Francois 1994, Minagawa et al. 2001). This phenomenon might be one of the factors causing the reduction of the phytoplankton $\delta^{15}N$, although the nitrate concentration was not measured in our study. Regarding molar carbon:nitrogen ratios of phytoplankton and POM, the value of 5.7 for phytoplankton was slightly lower than 6.2 for POM. The microzooplankton included in the phytoplankton sample as mentioned above might cause the lower carbon:nitrogen ratio because the carbon:nitrogen ratios of zooplankton species in our study were lower than that of phytoplankton (see Table 3), although the carbon:nitrogen ratio for phytoplankton varies depending on physiological conditions of phytoplankton species (Banse 1974).

Ice algae showed a slightly enriched $\delta^{13}C$ form $-22.3$ to $-21.5\%o$ compared to $-24.1\%o$ of phytoplankton (Table 2). Previous studies obtained similar results (Hobson & Welch 1992, Hobson et al. 1995). The enriched $\delta^{13}C$ value of ice algae might result from a more general phenomenon—that isotopic discrimination in marine plants is related to the thickness of the boundary layers that determine the rate of $CO_2$ or $HCO_3^-$ diffusion (Smith & Walker 1980). Well-defined boundary layers, such as those associated with litoral algae, lead to an accumulation of this discriminated $^{13}C$. The subsequent enrichment in $^{13}C$ of carbon available for photosynthesis would result in enriched $\delta^{13}C$ values of ice algae (Keeley & Sandquist 1992, Simenstad et al. 1993).

Primary diet for consumers

It is clear that phytoplankton is the main contributor to the diets of pelagic consumers such as the copepods *Neocalanus cristatus* and *Pseudocalanus sp.*; however, the main diet of primary benthic consumers, such as amphipods *Atylus sp.* and *Pontogeneia sp.*, is unidentified organic matter. The difference in $\delta^{13}C$ values between suspension-feeding pelagic primary consumers such as copepods (mean value of $-23.6\%o$) and deposit-feeding benthic primary consumers such as amphipods (mean value of $-18.8\%o$) is $4.8\%o$. The range of differences in $\delta^{13}C$ values between phytoplankton and benthic primary consumers and between suspension and deposit feeders seems to be a general trend in coastal (Herman et al. 2000) as well as offshore benthic ecosystems (Hobson et al. 1995, 2002). Herman et al. (2000) demonstrated such differences among benthic primary consumers, and the $\delta^{13}C$ values of suspension feeders (mainly feeding on phytoplankton) were $4-6\%o$ more depleted than those of deposit feeders (mainly feeding on benthic microalgae). However, Mincks et al. (2008) reported that $\delta^{13}C$ value of suspension-feeding bivalve species was within the $\delta^{13}C$ range for deposit feeders. They therefore suggested that the bivalves had been feeding on $\delta^{13}C$-enriched re-suspended sediment. A similar phenomenon was evident in scallops in our study.

The $\delta^{13}C$ values of juvenile and adult scallops *Mizuhopecten yessoensis* were $-19.6\pm0.1\%o$ and $-18.1\pm0.1\%o$, respectively (Table 3). We had assumed that the $\delta^{13}C$ value for scallops would be close to the value for phytoplankton ($-22\%o$) because *M. yessoensis* is a suspension feeder that feeds on organic particles settling from the upper water column to the sediment surface. However, the observed $\delta^{13}C$ value, especially of adult scallops, was highly enriched and close to that of the amphipod *Atylus* sp., a deposit feeder (see Table 3). Le Loc‘h & Hily (2005) reported that the $\delta^{13}C$ value for the scallop *Aequipecten opercularis* (Linnaeus) inhabiting depths of 80–130 m in the Bay of Biscay (Latitude around 40°N) in the northeast Atlantic Ocean was highly enriched ($-16\%o$). From this enriched $\delta^{13}C$ value for *A. opercularis*, which feeds on organic particles suspended in the first 2 cm of the water layer above the sediment surface, they deduced that, in the ecosystem of the sampling site, the quality of the suspended particles changes drastically in the first centimeters of the water column above the sediment and that this change is sufficiently stable over time to induce differences in isotopic signatures in the tissue of consumers. In contrast, they also found that the $\delta^{13}C$ values of benthic suspension feeders, such as ascidians and the polychaete *Hyalinoecia fauveri* Roja, were $-20\%o$ and $-19\%o$, respectively. They suggested that these taxa have $\delta^{13}C$ values more depleted than that of *A. opercularis* because the positions of the inhalant siphons of ascidians and of the apex of the polychaete feeding tube, at 2–5 cm above the bottom, are higher than the interface comprising the layer where the scallops feed. Similarly, the $\delta^{13}C$ value of juvenile scallops ($M. yessoensis$) in our study, hanging in culture cages 20 m above the sediment, would be more depleted than that of the adult scallops on the bottom.

Recently, there have been some reports that benthic detritus, derived from pelagic phytoplankton and assimilated as microbial or meiofaunal biomass, plays an important role in the diet of primary benthic consumers (Langdon & Newell 1990, Posh & Arndt 1996). As a result of the strong carbon fractionation effects of bacterial metabolism, the benthic consumers exhibited greater $\delta^{13}C$ enrichment ($4-5\%o$) than pelagic consumers (Goering et al. 1990, Hobson et al. 1995, Nyssen et al. 2002, Lovvorn et al. 2005, Mincks et al. 2008). Benthic detritus as a main food for primary benthic consumers such as benthic amphipods and scallops might also play an important role in benthic trophic linkages nearshore and offshore along the Okhotsk coast. Large quantities of fresh organic matter (with $\delta^{13}C$ ranging from $-22.8\%o$ to $-24.0\%o$) composed of ice algae, fecal pellets, and detritus derived from seasonal sea ice (Hiwatari et al. 2008) and the spring bloom after the sea-ice retreat, settles on the seafloor along the Okhotsk coast during the sea-ice season and early spring. This fresh organic matter would change the $\delta^{13}C$ enrichment of benthic detritus through the various stages of decomposition as a result of recycling within the microbial loop.
The significant differences between the δ¹³C of the pelagic and demersal fishes clearly reflects the difference in primary diets between the pelagic and benthic food webs (Table 4). The diet of juvenile pink salmon Oncorhynchus gorbuscha and chum salmon O. keta consists chiefly of pelagic copepods (Nagata 2003, Miyamoto 2003). This is reflected in their δ¹³C values, which in this study ranged from −20.4‰ to −22.4‰. The diet of young Japanese sand lance Ammodytes personatus Girard consists of copepods, euphausiids, and amphipods (Miyake 2003). This results in the most enriched δ¹³C value among the pelagic fishes, −20.2‰, and this species would feed on both pelagic and benthic diets. The more enriched δ¹⁵N values among the demersal fishes reflect their benthic diets. Suda et al. (2005) and Fuzawa (2009) investigated the stomach contents of sand flounder Pleuronectes punctatissimus (Steindachner) found along the Mombetsu coast and observed that the diet was composed of benthic invertebrates, such as cumaceans, benthic copepods, mysids, and amphipods. Thus, the δ¹³C value of P. punctatissimus in this study, −17.3‰, reflects their diet.

δ¹⁵N differences resulting from species-specific feeding habits

Differences in δ¹⁵N values among species within crustacean groups are shown in Fig. 2. The δ¹⁵N values identify the consumers’ position in the trophic structure of the food web and suggest the consumers’ feeding pattern as herbivore, omnivore, or carnivore. The δ¹⁵N values of the copepod species varied from 6.5‰ for Pseudocalanus sp. to 11.2‰ for Calanus glacialis. Based on the feeding patterns corresponding to these δ¹⁵N values, Pseudocalanus sp. and Neocalanus cristatus are presumably herbivorous species, Eurytemora herdmani is omnivorous, and Acartia sp. and C. glacialis are omnivorous-carnivorous, respectively. These deduced feeding patterns are consistent with those derived from the shape of the cutting edge on the mandible of the mouth parts in the pelagic copepods (Ito 1970) except for C. glacialis. Recently, however, copepods believed to be herbivorous from earlier studies were observed to feed not only on phytoplankton and detritus but also on microzooplankton (Greene & Landry 1988, Tiselius 1989, Ohtsuka et al. 1996). As a result, Ohtsuka & Nishida (1997) proposed referring to the herbivorous feeders as “particle feeders,” as the copepods exhibit a feeding behavior that adapts to the prevailing diet. In this study, the high δ¹⁵N value of 11.2‰ for C. glacialis, known as a herbivorous species (Mauchline 1998), suggests that they might also feed on microzooplankton during some of their life stages.

The δ¹⁵N of amphipods ranged from 8.1‰ for Atylus sp. to 10.8‰ for Monoculodes sp. (Fig. 2). The δ¹⁵N values of Atylus sp., Paralarcorchestes sp., and Pontogeneia sp. correspond to an omnivorous feeding pattern, and that of Monoculodes sp. suggests an omnivorous-carnivorous feeding pattern. The feeding behavior of amphipods can be approximately determined from the degree of the molar development on the mandible of their mouth parts. The molars of Atylus sp., Paralarcorchestes sp., and Pontogeneia sp. as omnivorous are well developed and well suited to grinding their diets (Lincoln 1979, Barnard & Karaman 1991). On the other hand, the molars of Monoculodes sp. are weakly developed (Moore 1984). Beare & Moore (1994) examined the gut contents of M. gibbosus Chevreux collected from the bottom at 35 m depth off Loch Fyne in Scotland and determined that the species was a specialist predator on harpacticoid copepods. The high δ¹⁵N value for Monoculodes sp. found in this study suggests that this species might also feed on harpacticoid copepods along the Mombetsu coast.

Mysids show marked diurnal vertical migration and therefore link benthic and pelagic food webs (Hanamura 1997, Takahashi & Kawaguchi 1998). Both species found in this study—Archaeomysis ochotensis and Exacanthomysis japonica—would show this same migration and feed on both pelagic and benthic diets. The δ¹⁵N value of 11.6‰ for E. japonica was higher than that of A. ochotensis (9.4‰). The difference in the δ¹⁵N values of these species probably reflects the difference in the diet composition in their respective habitats, A. ochotensis was found at 4–6 m depth and E. japonica at 8–10 m depth in the study area.

Trophic linkages

To construct appropriate trophic linkages, it is necessary to divide the species having clearly different δ¹³C and δ¹⁵N values into trophic groups. In this study, copepods and benthic amphipods were each separated into three groups based on their δ¹³C and δ¹⁵N differences. The copepod groups are copepod I (C-I): Neocalanus cristatus and Pseudocalanus sp.; copepod II (C-II): Eurytemora herdmani; and copepod III (C-III): Acartia sp. and Calanus glacialis. The amphipod groups are amphipod I (A-I): Atylus sp. and Pontogeneia sp.; amphipod II (A-II): Monoculodes sp.; and amphipod III (A-III): Paralarcorchestes sp. The δ¹³C and δ¹⁵N values of the organic matter sources and consumers were plotted, and the pelagic and benthic trophic linkages are clearly distinguishable (Fig. 3). From this plot it became apparent that neither terrestrial plant debris (TPD) nor the seagrass Z. marina (ZO) contributed to the diet of consumers.

In the pelagic trophic linkages, the organic matter source at the first trophic level was phytoplankton and particulate organic matter (PP) with a mean δ¹³C of −23.3‰ and a mean δ¹⁵N of 5.4‰. The second trophic level consisted of the C-I copepod group and the amphipod Themisto japonica (Bovallius) (AT) (mean δ¹³C, −23.6‰; mean δ¹⁵N, 7.9‰). The third level was composed of C-III copepods, euphausiids (ET), and Clione limacine (Phipps) (GC) (mean δ¹³C, −22.3‰; mean δ¹⁵N, 10.8‰). The highest (fourth) level was composed of Sagitta elegans (CS) and fishes such as Oncorhynchus gorbuscha, O. keta (FO), and Clupea pal-
In summary, the present study demonstrates that phytoplankton and benthic detritus constituted the main food sources for primary consumers such as zooplankton and small benthic invertebrate, and that the differences in stable nitrogen isotope ratios were related to species-specific feed-
ing habits of copepods and amphipods crustacean groups, and moreover that there are both pelagic and benthic trophic linkages within the ecosystem in the Okhotsk coast. The results support the idea that the abundance of spring bloom of diatom and ice algae after the retreat of the sea ice sustain fishery resources (i.e. salmon juveniles and scallops) through both the pelagic and benthic trophic linkages in the Okhotsk coast in spring.

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