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Chemical composition of three dominant myctophid fish, *Diaphus theta*, *Stenobrachius leucopsarus*, and *S. nannochir*, in the subarctic and transition waters of the western North Pacific

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Water, carbon, and nitrogen contents were analysed in both juvenile and adult specimens of Diaphus theta, Stenobrachius leucopsarus, *and* S. nannochir, *which are the dominant myctophid species in the subarctic and transition waters of the North Pacific. The relationship between body length and dry weight, carbon content, and nitrogen content of these three species were expressed as double logarithmic equations. The differences in chemical content among the different size-classes of each species may be associated with reproductive biology.*

Keywords: body length, carbon and nitrogen cycles, myctophid fish, oceanic ecosystems

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Myctophid fish are a major component of the micronektonic fish community in oceanic ecosystems. *Diaphus theta* Eigenmann & Eigenmann, *Stenobrachius leucopsarus* (Eigenmann & Eigenmannn), and *S. nannochir* (Gilbert) are mainly distributed throughout the subarctic and transition waters of the North Pacific Ocean, the Bering Sea, and the Sea of Okhotsk, and they are the dominant myctophid species in these areas (Pearcy, 1964; Pearcy *et al.*, 1977; Willis *et al.*, 1988; Balanov & Il'inskii 1992; Beamish *et al.*, 1999; Watanabe *et al.*, 1999). *Diaphus theta* is a vertically migrant species with distinct day–night habitat separation; *S. leucopsarus* is a semi-migrant species in which part of the population remains in the daytime habitat at night; and *S. nannochir* is a non-migrant species (Pearcy *et al.*, 1977; Frost & McCrone, 1979; Willis & Pearcy, 1982; Watanabe *et al.*, 1999). These species mainly feed on crustacean zooplankton, i.e. copepods such as *Neocalanus* spp. and *Metridia* spp., and euphausiids such as *Euphausia pacifica* and *Thysanoessa* spp., which are key species in the subarctic Pacific ecosystem (Tyler & Pearcy, 1975; Pearcy *et al.*, 1979; Balanov, 1994; Balanov *et al.*, 1995; Moku *et al.*, 2000). Myctophids also play an important role in transporting organic matter from the surface to the deep layer of the ocean. Therefore, ecological studies of myctophids are required to understand energy flow from lower to higher trophic levels, carbon and nitrogen cycles, and the vertical transport of organic materials from the epipelagic to the mesopelagic layers.

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Carbon and nitrogen cycling are commonly used as indicators of energy flow. However, there is insufficient information concerning the chemical composition of myctophids in the subarctic and transition waters of the North Pacific (Butler & Pearcy, 1972; Childress & Nigaard, 1973; Neighbors & Nafpaktitis, 1982; Bailey & Robison, 1986). Most previous studies have attempted to quantitatively clarify the role of these fish in the subarctic Pacific and adjacent seas, but these results were based on one or very few individuals of limited body size (Butler & Pearcy, 1972; Childress & Nigaard, 1973; Bailey & Robison, 1986; Lindsay, 2003). We analysed the relationship between standard length (SL) and wet weight, dry weight, water content, carbon content, and nitrogen content in juvenile and adult specimens of *D. theta*, *S. leucopsarus* and *S. nannochir*. We also discuss the results in relation to the life-history traits of these species.

Samples were collected in the subarctic and transition waters of the western North Pacific. Sampling was performed from onboard a number of vessels: the commercial trawler 'Marusada-Maru' under charter by the Japan Marine Fishery Resources Research Center; the research vessels 'Hakuho-Maru' and 'Tansei-Maru' of the Ocean Research Institute, University of Tokyo; and the fisheries research vessel 'Shunyo-Maru' of the National Research Institute of Far Seas Fisheries. Samples were collected from July 1995 to April 1998 using an otter trawl and a 3-m Isaacs–Kidd midwater trawl (Table 1). Samples were frozen onboard at −20°C or −80°C. After thawing in the laboratory, the samples were measured to the nearest 0.1 mm in SL and weighed to the nearest 0.01 g. In total, 30 individuals were obtained for

Table 1. Sampling data of *Diaphus theta* (Dt), *Stenobrachius leucopsarus* (Sl) and *S. nannochir* (Sn) in the western North Pacific.

Vessel	Date	Sampling locality		Number of specimens examined		
		Latitude	Longitude	Dt	Sl	Sn
'Marusada-Maru'	5 July 1995	41°58.7′N	145°01.8′E	12	–	–
	5 July 1995	41°56.1′N	145°05.8′E	4	–	–
	6 July 1995	41°56.2′N	145°06.6′E	–	8	–
	6 July 1995	41°53.5′N	145°06.1′E	–	9	16
'Hakuho-Maru'	1 November 1997	41°35.3′N	146°41.1′E	6	13	–
	30 September 1998	41°31.4′N	147°01.8′E	2	–	–
	30 September 1998	42°20.9′N	152°00.3′E	3	–	–
'Tansei-Maru'	9 April 1998	38°17.5′N	143°17.0′E	–	–	3
	9 April 1998	38°17.0′N	143°25.4′E	–	–	5
'Shunyo-Maru'	16 April 1998	37°57.4′N	141°58.5′E	3	–	–
			Total	30	30	24

both *Diaphus theta*, ranging from 15.7 to 94.2 mm SL, and *Stenobrachius leucopsarus*, ranging from 25.1 to 92.5 mm SL. Only 24 individuals were obtained for *S. nannochir*, ranging from 31.4 to 107.2 mm SL. These specimens were analysed for growth-associated differences in chemical composition. Each fish was placed on a pre-weighed aluminium sample boat and dried in an oven at 60°C for 2–3 days until it reached a constant weight. The dried fish was then ground to a fine powder in a glass tissue grinder. Samples were kept in a desiccator until analysis. Three samples of each homogenized fish were placed into ultra-clean tin capsules. The carbon and nitrogen contents were analysed using a Fisons NA-1500 elemental analyser (Fisons Instruments, Italy). Values from three samples were used to calculate the mean carbon and nitrogen contents of each fish.

For each species, the relationships between SL (mm) and wet weight (WW in g), dry weight (DW in g), carbon content (C in g), and nitrogen content (N in g) were expressed as follows. These equations are written on a $\log_{10}$ basis because the double logarithmic relationship gave the best fit.

Diaphus theta:

$$\log \mathrm{WW} = 3.10 \log \mathrm{SL} - 4.99 \ (r^2 = 0.981)$$
$$\log \mathrm{DW} = 3.25 \log \mathrm{SL} - 5.76 \ (r^2 = 0.852)$$
$$\log \mathrm{C} = 3.35 \log \mathrm{SL} - 6.16 \ (r^2 = 0.711)$$
$$\log \mathrm{N} = 2.89 \log \mathrm{SL} - 6.34 \ (r^2 = 0.967)$$

Stenobrachius leucopsarus:

$$\log \mathrm{WW} = 3.13 \log \mathrm{SL} - 5.21 \ (r^2 = 0.979)$$
$$\log \mathrm{DW} = 3.11 \log \mathrm{SL} - 5.66 \ (r^2 = 0.971)$$
$$\log \mathrm{C} = 3.17 \log \mathrm{SL} - 5.94 \ (r^2 = 0.963)$$
$$\log \mathrm{N} = 2.99 \log \mathrm{SL} - 6.77 \ (r^2 = 0.954)$$

Stenobrachius nannochir:

$$\log \mathrm{WW} = 3.17 \log \mathrm{SL} - 5.38 \ (r^2 = 0.986)$$
$$\log \mathrm{DW} = 3.36 \log \mathrm{SL} - 6.23 \ (r^2 = 0.982)$$
$$\log \mathrm{C} = 3.50 \log \mathrm{SL} - 6.67 \ (r^2 = 0.980)$$
$$\log \mathrm{N} = 2.89 \log \mathrm{SL} - 6.74 \ (r^2 = 0.940)$$

In *D. theta*, the water and nitrogen contents were lowest for the middle size-class (40–80 mm SL; ANOVA, $P < 0.05$), and the carbon content was highest for middle size-class (ANOVA, $P < 0.05$; Table 2). We observed similar trends in *S. leucopsarus* for water (ANOVA, $P < 0.05$) and carbon contents, although a significant difference in carbon content was only observed between the smallest (<40 mm SL) and middle (ANOVA, $P < 0.05$) size-classes (Table 2). The differences in nitrogen content were significant between the smallest size-class and all other classes (ANOVA, $P < 0.05$). In *S. nannochir*, the water and nitrogen contents (% dry weight) showed a tendency to decrease with growth; in contrast, carbon content tended to increase with growth (Table 2).

Our carbon and nitrogen content results by size-class allow us to more accurately estimate the quantity of carbon and nitrogen bases in the fish biomass, the flow of energy from mesozooplankton to animals at higher trophic levels through myctophid fish, and vertical fluxes from epipelagic to deep-sea systems in the subarctic and transition waters of the North Pacific. Of these three myctophid species, *S. leucopsarus* is a key species in the subarctic Pacific ecosystem (e.g. Beamish *et al.*, 1999). The biomass estimates of *S. leucopsarus* in the western North Pacific, including the western Bering Sea and the Sea of Okhotsk, and in the eastern North Pacific were ~13000 and 300 thousand tons wet weight, respectively (Beamish *et al.*, 1999). Using the mean carbon and nitrogen content percentages quantified in the present study, the estimates of carbon and nitrogen bases contained in the biomass of this species are 2930 and 213 thousand tons, respectively. If the size distributions of all populations are determined, more detailed estimates of biomass carbon and nitrogen could be possible because our dataset includes a greater variety of fish sizes, especially smaller classes, compared to previous studies.

The carbon contents (% wet weight) for *D. theta*, *S. leucopsarus*, and *S. nannochir* ranged from 15 to 24%, which is two to five times higher than values reported for tropical and subtropical myctophid species (Childress & Nygaard, 1973; Childress *et al.*, 1990). This may be attributable to the elevated lipid contents observed in subarctic myctophids compared to tropical and subtropical myctophids (Seo *et al.*, 1996). In addition, our data for the carbon and nitrogen contents in *D. theta* and *S. leucopsarus* are consistent with those reported by Childress & Nygaard (1973), although our analysis included a much wider range of body sizes.

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Table 2. Chemical composition (mean ± standard deviation) of the three myctophid fish.

Species	N	Water (% wet weight)	Carbon		Nitrogen	
			(% wet weight)	(% dry weight)	(% wet weight)	(% dry weight)
Diaphus theta						
<40 mm SL	8	73.9 ± 4.2	14.7 ± 4.8	55.4 ± 9.2	2.5 ± 0.3	9.7 ± 1.6
40–80 mm SL	16	63.3 ± 4.3	24.0 ± 3.5	65.0 ± 3.8	1.7 ± 0.3	4.9 ± 1.5
>80 mm SL	6	73.7 ± 3.2	14.9 ± 3.4	55.8 ± 6.3	2.1 ± 0.3	8.1 ± 1.9
Total	30	68.2 ± 6.7	19.7 ± 6.0	60.6 ± 7.6	2.0 ± 0.4	6.8 ± 2.7
Stenobrachius leucopsarus						
<40 mm SL	6	67.0 ± 1.6	20.7 ± 1.1	62.6 ± 0.9	1.8 ± 0.1	5.4 ± 0.3
40–80 mm SL	16	65.7 ± 1.1	22.8 ± 0.8	66.4 ± 1.5	1.6 ± 0.2	4.6 ± 0.5
>80 mm SL	8	67.5 ± 0.8	21.3 ± 0.8	65.7 ± 1.4	1.6 ± 0.2	4.8 ± 0.5
Total	30	66.4 ± 1.4	22.0 ± 1.2	65.5 ± 2.0	1.6 ± 0.2	4.8 ± 0.5
S. nannochir						
<40 mm SL	3	72.8 ± 3.3	16.5 ± 3.1	60.5 ± 4.0	1.5 ± 0.1	5.7 ± 0.9
40–80 mm SL	8	70.9 ± 1.8	18.8 ± 1.5	64.6 ± 2.0	1.5 ± 0.2	5.1 ± 0.6
>80 mm SL	13	67.7 ± 1.2	22.4 ± 1.2	69.5 ± 1.4	1.2 ± 0.1	3.8 ± 0.4
Total	24	69.4 ± 2.6	20.5 ± 2.7	66.8 ± 3.8	1.3 ± 0.2	4.4 ± 0.9

SL, standard length.

In general, mesopelagic fish have the highest water content and the lowest lipid and caloric contents among deeper-living species, suggesting a relationship between chemical composition and food availability (Bailey & Robison, 1986). While the depth layer used by *D. theta* during the daytime is the shallowest among the three myctophid species examined in this study, and *D. theta* undergoes a diel vertical migration, *S. nannochir* is the deepest-living and non-migratory species (Watanabe *et al.*, 1999). However, except for nitrogen content, there were no clear trends in the water and carbon contents among the three species. This suggests that the biomass of zooplankton prey for *S. nannnochir* in the deep layer is relatively high. In the subarctic Pacific, the biomass of dominant copepods, such as three *Neocalanus* spp., especially *N. cristatus*, which is the main prey of *S. nannochir* (Moku *et al.*, 2000), is very high, maintaining the mesopelagic ecosystem through their seasonal ontogenetic vertical migration from the epipelagic to the mesopelagic layer (e.g. Kobari & Ikeda, 1999, 2001; Tsuda *et al.*, 1999, 2004).

Because males and females were not analysed separately, our data cannot be used to discuss sex-dependent relationships between reproduction and growth. However, it is expected that egg production in females would be influenced by growth and the subsequent changes in tissue chemical composition. Changes in water, carbon, and nitrogen contents may be related to reproduction in these three species. In both *D. theta* and *S. leucopsarus*, females attain maturity at lengths of 55 mm SL and 60–65 mm SL, respectively (Smoker & Pearcy, 1970; Moku, 2000). Accordingly, we observed changes in the chemical contents of these two species in the 40–80 mm SL size-class compared to the <40 mm SL size-class. Individuals in the >80 mm SL size-class exhibited higher water contents and lower carbon contents than did individuals in the 40–80 mm SL size- class, suggesting that female reproduction may have decreased or ceased altogether. In *S. nannochir*, the carbon content and the water and nitrogen contents continued to increase and decrease, respectively, as body size increased. However, *S. nannochir* attains maturity at a larger body size (90 mm SL; Moku, 2000) than do the other two species; thus, these individuals were likely not yet mature. In some myctophid species, including *S. leucopsarus* and *D. theta*, lipid contents increased with increasing fish size (Butler & Pearcy, 1972; Neighbors & Nafpaktitis, 1982). Although these studies did not examine changes in water content with size, lipid content would be related to the water, carbon and nitrogen contents of the three myctophids in this study. In the present study, the samples were collected from spring to autumn. If there were strong relationships between chemical composition and reproduction in these three species, the chemical compositions and lipid accumulation would be strongly related to spawning seasons and it would be necessary to analyse the relationships in detail based on seasonal sampling of the myctophids.

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