Feeding habits of three dominant myctophid fishes, *Diaphus theta, Stenobrachius leucopsarus* and *S. nannochir*, in the subarctic and transitional waters of the western North Pacific

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ABSTRACT: The feeding habits of 3 dominant myctophid fishes, *Diaphus theta* (vertical migrant), *Stenobrachius leucopsarus* (semi-migrant), and *S. nannochir* (non-migrant), were studied in relation to their diel vertical migration patterns using time-series sampling during the summers of 1994 to 1996 in the subarctic and transitional waters of the western North Pacific. *D. theta* and *S. leucopsarus* fed mainly on euphausiids (mainly *Euphausia pacifica*), copepods (mainly *Metridia pacifica* and the *Neocalanus plumchrus/flemingeri* group), and amphipods (mainly the *Themisto japonica/pacifica* group). The prey of *S. nannochir* was mainly copepods, but the species were different from those preyed on by *D. theta* and *S. leucopsarus. D. theta* fed on euphausiids, with 1 feeding peak during the daytime and another at night, but fed on amphipods only at night and on copepods throughout the entire diel cycle. The vertical migratory component of *S. leucopsarus* showed a significant diel feeding periodicity, feeding on euphausiids, copepods, and amphipods from dusk to midnight, while the non-migratory component did not feed actively at nighttime, and had a high frequency of empty stomachs. The non-migratory *S. nannochir* showed no diel feeding periodicity. The average ratio of stomach content weight/body weight was 2.2% during the day and 2.0% at night in *D. theta*, 0.8% during the daytime and 1.1% at night in the migratory *S. leucopsarus*, 0.6% at night in the non-migratory *S. leucopsarus*, and 0.07 to 0.13% (avg. 0.11%) in *S. nannochir*.

KEY WORDS: Myctophid fish · Diet composition · Diel feeding periodicity · Daily ration · Diel vertical migration

INTRODUCTION

In oceanic ecosystems, myctophids are one of the dominant micronektonic fishes, occupying mainly the tertiary trophic level. About 20 myctophid species are distributed in the subarctic and transitional waters of the western North Pacific (Ogawa 1961, Watanabe et al. 1999 and unpubl. data), and most of these species migrate upward every night to feed on zooplankton, especially crustaceans, in the productive epipelagic zone. They might compete for prey with small pelagic fishes like the Japanese sardine, mackerel, and saury, which migrate into the transitional and subarctic regions to feed in the summer, since this area is highly productive and supports one of the richest fisheries in the world. Myctophids are also known to play an important role in transporting organic matter from the surface to the deep sea (Merrett & Roe 1974, Hopkins & Baird 1977). In this area, myctophid fishes are also important prey of larger squid, finned fish, including salmon, cod, and mackerel, and marine mammals such as the fur seal and Dall's porpoise (Mead & Taylor 1953, Japan Fisheries Agency 1965, Naito et al. 1977, Ohizumi et al. 1998, Pearcy et al. 1988). Much less is

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known about myctophid ecology in the western Pacific than in the eastern Pacific (e.g., Pearcy 1964, Tyler & Pearcy 1975, Frost & McCrone 1979, Cailliet & Ebeling 1990). Recently, the myctophid community structure was studied in the western North Pacific, and various modes of diel vertical migration were described in relation to the water-temperature regime (Watanabe et al. 1999). This paper examines the feeding habits of the 3 dominant myctophids, *Diaphus theta* (vertical migrant), *Stenobrachius leucopsarus* (semi-migrant), and *S. nannochir* (non-migrant), and discusses their feeding strategies in relation to their diel vertical migration patterns.

MATERIALS AND METHODS

Samples were collected in the transitional and sub-arctic waters off Japan by the commercial trawler 'Marusada-Maru' under charter to the Japan Marine Fishery Resources Research Center in August 1994, July 1995, and July 1996. Detailed sampling data, including locality, date, time, net depth and net speed, are shown in Table 1. The mouth area of the trawls was 1300 m^2 in 1994 and 490 m^2 in 1995 and 1996, and the respective mesh size of the cod-end each year was 14 × 14, 30 × 30, and 18 × 18 mm.

Commercial trawls of these sizes do not produce significant day-night differences in catches of myctophid species per unit effort (CPUE), suggesting no bias due to visual net avoidance during the daytime, which is inevitable for traditional micronekton nets such as the IKMT and RMT 1+8 (Watanabe et al. 1999). To keep the net at the target depth for discrete depth sampling, net depth and the height of the net mouth were monitored during real time with an acoustic recorder attached to the head rope of the trawl. When casting the trawl, the ship and wire speeds were regulated to minimize the volume of water filtered by the net and the holding effect of the otter boards. During retrieval, the ship moved backwards so that the net was not towed and then the net was hauled in vertically. Using this sampling procedure, contamination from the upper layer is estimated to be <2% of the total catch (Watanabe et al. 1999).

Myctophid species were sorted, frozen aboard ship, and fixed in 10% formalin in the laboratory. Standard length (SL), body wet weight, wet weight of stomach contents, and stomach fullness were measured in fixed specimens. Stomach content index (*SCI*) was calculated as:

$$SCI\,(\%) = (\text{wet wt of stomach contents/body wet wt}) \times 100$$

Stomach fullness was estimated by observing the stomach rugae (Tyler & Pearcy 1975). The stomach rugae were scored on a 4-stage scale: Stage 0, empty stomach; Stage 1, stomach contents recognized, but rugae not distended; Stage 2, rugae partially distended, but recognizable; Stage 3, full stomach, stomach wall distended thin and no rugae recognized.

Table 1. Sampling data in the subarctic and transitional waters of the western North Pacific

| Stn | Sampling locality | | Date | Time | Sampling | Net speed |
	Latitude	Longitude		(horizontal tow)	depth (m)	(knot)
1994						
1-1	40° 58′ N	146° 48′ E	11 Aug	12:35–13:35	320–356	4.3
1-2	40° 56′ N	146° 48′ E	11 Aug	14:20–15:20	430–464	3.6
1-3	40° 55′ N	146° 51′ E	11 Aug	20:15–20:45	25–61	4.4
1-4	40° 52′ N	146° 52′ E	11 Aug	21:10–21:40	60–97	4.4
1-5	40° 52′ N	146° 51′ E	12 Aug	10:10–11:10	520–558	3.8
1-6	40° 55′ N	146° 43′ E	12 Aug	12:05–13:05	650–670	3.4
1995						
2	41° 01′ N	143° 11′ E	16 Jul	20:45–21:45	520–544	3.2
1996						
3-1	40° 00′ N	145° 01′ E	15 Jul	01:00–01:30	60–87	3.0
3-2	39° 58′ N	144° 55′ E	15 Jul	02:45–03:45	220–247	3.4
3-3	39° 58′ N	144° 59′ E	15 Jul	04:20–05:20	320–347	3.4
3-4	40° 01′ N	144° 58′ E	15 Jul	05:50–06:50	420–447	2.8
3-5	40° 02′ N	144° 56′ E	15 Jul	15:10–16:10	630–657	3.0
3-6	40° 01′ N	144° 51′ E	15 Jul	16:50–17:50	530–557	2.9
3-7	40° 01′ N	144° 54′ E	15 Jul	18:30–19:30	450–476	3.5
3-8	39° 58′ N	144° 58′ E	16 Jul	15:57–16:57	320–347	2.7
3-9	40° 01′ N	144° 52′ E	16 Jul	18:23–19:23	125–327	2.5
3-10	40° 01′ N	144° 40′ E	16 Jul	22:30–23:30	530–558	2.9

The state of digestion of each major prey item was staged by the modified method of Pearcy et al. (1979): Stage 1, fresh prey not digested; Stage 2, body shape of prey preserved, but some appendages separated from body; Stage 3, body shape of prey deformed, but identifiable to some higher taxa. Based on these criteria, the ratio of individuals in each digestion stage was calculated for each food item.

Stomach contents were identified to higher taxa. The dominant taxa in the stomachs of specimens collected in August 1994 were identified to species, genera, or family, depending on their state of digestion. The copepod species *Neocalanus plumchrus* and *N. flemingeri* and the amphipod species *Themisto japonica* and *T. pacifica* were treated together as *N. plumchrus/ flemingeri* and *T. japonica/pacifica*, respectively, because of the difficulty in identifying digested material. The wet weight of each food item was measured to the nearest 1 mg. The frequency of occurrence (*F*) of each food item in the total number of stomachs examined (excluding empty stomachs), percentage of each food item to the total number of identifiable food items (*Cn*), and percentage wet weight of each food item to the total wet weight of identifiable food items (*WW*) were calculated for each species as:

$$F_i(\%) = \frac{\text{no. of stomachs including food item } i}{\text{total no. of stomachs with food}} \times 100$$

$$Cn_i(\%) = \frac{\text{total no. of food item } i}{\text{total no. of identified items}} \times 100$$

$$WW_i(\%) = \frac{\text{total wet weight of food item } i}{\text{total wet weight of identified items}} \times 100$$

Using these 3 indices, an index of relative importance (*IRI*, Pinkas et al. 1971) for food item *i* was calculated using the equation:

$$IRI_i = (Cn_i + WW_i) \times F_i$$

This is represented by the size of a rectangle resolved by plotting the 3 values on a 3-way graph.

The number of individuals examined for each analysis is shown in Table 2.

RESULTS

Diet composition

Diaphus theta (a migrant)

Most of the prey items were small crustaceans, mainly euphausiids, copepods, and amphipods (Fig. 1A). Ostracods, chaetognaths, mysids, pteropods, cephalopods, crustacean larvae, and gelatinous zooplankton were minor components. Numerically, copepods were dominant and accounted for 77.1% (*Cn*) of the total identifiable food items, while other items accounted for less than 7% each. In wet weight (*WW*), euphausiids occupied 61.6% of the total prey, followed by copepods (22.1%), amphipods (9.6%), and ostracods (2.1%). The frequencies of occurrence (*F*) of copepods, euphausiids, amphipods, and ostracods were 93.3, 66.4, 48.5, and 48.8%, respectively, while those of the other prey items were relatively low (<17% in total).

The index of relative importance (*IRI*) for copepods was 9255, followed by euphausiids (4549), amphipods (740), and ostracods (359). The *IRI* of other prey taxa was <100, indicating that this species preyed mainly on copepods and euphausiids (Fig. 1A).

The size distribution of the 315 individuals examined was unimodal (Fig. 2). The ratio of euphausiids (largest prey item) to the total weight of identified stomach contents was 39.8 ± 39.8% (avg. ± SD) for 40 to 65 mm standard length (SL) fish and 40.4 ± 38.3% for 66 to 91 mm SL fish at night. The difference was not statistically significant (Mann-Whitney *U*-test, p > 0.05). Therefore, no noticeable shift in prey size occurs with growth over the size range examined.

Prey species composition showed that the dominant identifiable food items were copepods (30.0 to 44.3%), euphausiids (10.9 to 42.0%), and amphipods (7.6 to 25.9%) (Table 3). Among the copepod species, *Metridia pacifica* was dominant numerically, followed by the *Neocalanus plumchrus/flemingeri* group. *Euphausia pacifica* constituted >75% of the euphausiids identified, and the *Themisto japonica/pacifica* group accounted for 84% of the amphipods.

Table 2. *Diaphus theta*, *Stenobrachius leucopsarus* and *S. nannochir*. Number of individuals examined to calculate index of relative importance (*IRI*), stomach content index (*SCI*), and composition of stomach fullness (*SF*) and digestion stage (*DS*). –: no data

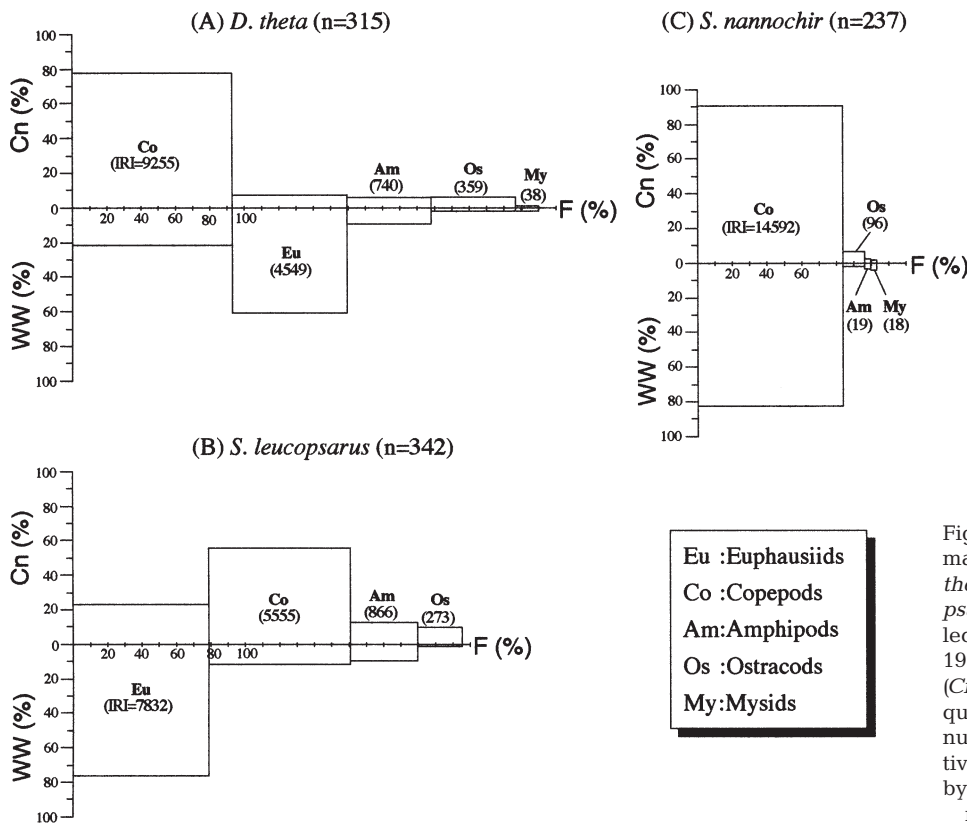| Year | D. theta | | | S. leucopsarus | | | S. nannochir | | |
	IRI	SCI & SF	DS	IRI	SCI & SF	DS	IRI	SCI & SF	DS
1994	135	136	135	162	162	162	55	96	55
1995	–	–	–	–	56	44	–	–	–
1996	180	300	180	180	300	180	168	250	168
Total	315	436	315	342	518	386	223	346	223

Fig. 1. Percent composition of major prey items of (A) *Diaphus theta*, (B) *Stenobrachius leucopsarus*, and (C) *S. nannochir* collected in August 1994 and July 1996 (combined data) by number (*Cn*), wet weight (*WW*), and frequency of occurrence (*F*) in total number of stomachs. Index of relative importance (*IRI*) is represented by size of respective rectangles. n = number of stomachs examined
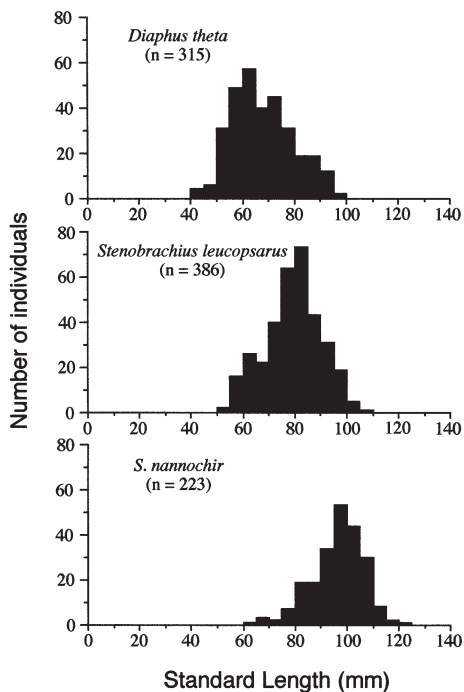

Fig. 2. *Diaphus theta*, *Stenobrachius leucopsarus*, and *S. nannochir*. Size distributions of specimens examined

Stenobrachius leucopsarus (a semi-migrant)

The prey group composition was similar to that of *Diaphus theta* and consisted mainly of crustaceans. Prey items were identified from 8 groups: euphausiids, copepods, amphipods, ostracods, chaetognaths, mysids, cephalopods, and gelatinous zooplankton. Of these, copepods were the most dominant numerically (*Cn* = 55.5%), followed by euphausiids (22.8%), amphipods (12.2%), and ostracods (9.3%) (Fig. 1B), as in *D. theta*. In *WW*, euphausiids accounted for 76.3% of the total stomach contents, far exceeding copepods (11.9%) and amphipods (10.2%). Euphausiids and copepods occurred in ca 80% of the stomachs with contents, while amphipods and ostracods were present in <40% of these stomachs.

The *IRI* values were 7832 for euphausiids, 5555 for copepods, 866 for amphipods, and 273 for ostracods (Fig. 1B), suggesting that this species preyed mainly on euphausiids and secondarily on copepods.

The size distribution of the 386 individuals examined was unimodal, ranging from 50 to 105 mm SL (Fig. 2). The ratio of euphausiids in the identifiable stomach contents by weight was 49.8 ± 45.2% for 55 to 80 mm SL fish and 44.5 ± 45.7% for 81 to 102 mm SL at night.

Table 3. Prey species composition of *Diaphus theta* and *Stenobrachius leucopsarus* collected in different time and depth layers in August 1994, showing numbers of each food item and its percentage (in parentheses) of total number of all food items identified. –: absent

	Diaphus theta				*Stenobrachius leucopsarus*	
Station (Table 1):	1-1	1-2	1-3	1-4	1-3	1-4
Sampling layer (m):	320–356	430–464	25–61	60–97	25–61	60–97
Time (h):	12:35–13:35	14:20–15:20	20:15–20:45	21:10–21:40	20:15–20:45	21:10–21:40
No. of stomachs examined:	36	12	45	43	44	49
Copepoda	128 (34.9)	33 (30.0)	112 (42.1)	211 (44.3)	220 (64.1)	154 (44.0)
Metridia pacifica	48 (13.1)	18 (16.4)	38 (14.3)	108 (22.7)	107 (31.2)	88 (25.1)
M. okhotensis	6 (1.6)	–	5 (1.9)	14 (2.9)	4 (1.2)	1 (0.3)
Neocalanus plumchrus/flemingeri	8 (2.2)	1 (0.9)	40 (15.0)	22 (4.6)	45 (13.1)	31 (8.9)
N. cristatus	3 (0.8)	–	–	1 (0.2)	7 (2.0)	3 (0.9)
Pleuromamma scutullata	4 (1.1)	2 (1.8)	1 (0.4)	7 (1.5)	2 (0.6)	6 (1.7)
P. gracilis	–	–	1 (0.4)	1 (0.2)	–	1 (0.3)
P. abdominalis	1 (0.3)	–	–	1 (0.2)	–	–
Pleuromamma spp.	–	–	–	–	1 (0.3)	1 (0.3)
Eucalanus bungii	4 (1.1)	–	3 (1.1)	8 (1.7)	1 (0.3)	1 (0.3)
Eucalanus spp.	2 (0.6)	1 (0.9)	–	–	–	–
Candacia columbiae	1 (0.3)	2 (1.8)	5 (1.9)	5 (1.1)	16 (4.7)	5 (1.4)
C. norvegica	1 (0.3)	–	–	–	–	2 (0.6)
Scottocalanus helenae	–	–	–	–	–	1 (0.3)
Calanus spp.	1 (0.3)	–	1 (0.4)	–	–	–
Gaidius sp.	–	–	1 (0.4)	–	–	–
Gaetanus kruppi	–	–	1 (0.4)	–	–	–
Aetideidae	3 (0.8)	1 (0.9)	–	2 (0.4)	3 (0.9)	3 (0.9)
Heterorhabdidae	1 (0.3)	–	1 (0.4)	7 (1.5)	–	–
Euchaetidae	3 (0.8)	1 (0.9)	–	3 (0.6)	1 (0.3)	1 (0.3)
Unidentified	42 (11.5)	7 (6.4)	15 (5.6)	32 (6.7)	33 (9.6)	10 (2.9)
Euphausiacea	154 (42.0)	46 (41.8)	70 (26.3)	52 (10.9)	86 (25.1)	80 (22.9)
Euphausia pacifica	120 (32.7)	39 (35.4)	62 (23.3)	39 (8.2)	77 (22.4)	64 (18.3)
Euphausia spp.	3 (0.8)	2 (1.8)	–	–	–	–
Thysanoessa longipes	5 (1.4)	–	–	6 (1.3)	–	5 (1.4)
Thysanoessa spp.	2 (0.5)	–	–	7 (1.5)	–	3 (0.9)
Unidentified	24 (6.7)	5 (4.5)	8 (3.0)	–	9 (2.6)	8 (2.3)
Amphipoda	27 (7.6)	9 (8.2)	69 (25.9)	112 (23.5)	18 (5.2)	59 (16.9)
Themisto japonica/pacifica	24 (6.7)	5 (4.5)	66 (24.8)	104 (21.8)	17 (5.0)	49 (14.0)
Primno abyssalis	1 (0.3)	1 (0.9)	1 (0.4)	2 (0.4)	–	1 (0.3)
Unidentified	2 (0.6)	3 (2.7)	2 (0.8)	6 (1.3)	1 (0.3)	9 (2.6)
Ostracoda	54 (14.7)	22 (20.0)	15 (5.6)	94 (19.7)	18 (5.2)	55 (15.7)
Mysidacea	3 (0.8)	–	–	4 (0.8)	–	1 (0.3)
Chaetognatha	–	–	–	1 (0.2)	1 (0.3)	–
Pteropoda	–	–	–	1 (0.2)	–	1 (0.3)
Cephalopoda	–	–	–	1 (0.2)	–	–

No significant shift in prey size with growth was observed within this size range (Mann-Whitney *U*-test, p > 0.05).

Prey-species analysis also showed that copepods numerically contributed between 34.6 and 64.1% of the total prey items, of which *Metridia pacifica* (25.1 to 31.2%, avg. 28.2%) and the *Neocalanus plumchrus/flemingeri* group (8.9 to 13.1%, avg. 11.0%) were dominant (Table 3). Numerically, euphausiids and amphipods accounted for 22.9 to 25.1% (avg. 24.0%) and 5.2 to 16.9% (avg. 11.1%), respectively, with *Euphausia pacifica* and the *Themisto japonica/pacifica* group dominating the respective taxa (Table 3).

Stenobrachius nannochir (a non-migrant)

Our data indicated that this species almost exclusively preyed on copepods. The *Cn*, *WW*, and *F* values for copepods were 90.4, 82.7, and 84.3%, respectively. The *IRI* value of copepods was 14 592, while that of other prey items was <100 (Fig. 1C).

This species preyed mainly on copepods belonging to the genera *Neocalanus* and *Pleuromamma*, especially *N. cristatus*, which accounted for 28.3 to 42.4% (avg. 35.4%) of the total food items identified, and 33.3 to 45.2% (avg. 39.3%) of the total copepods (Table 4).

Table 4. Prey species of *Stenobrachius nannochir* collected in August 1994, showing numbers of each food item and its percentage (in parentheses) of total number of all food items identified. –: absent

Sampling layer (m):	520–558	650–670
Time (h):	10:10–11:10	12:05–13:05
No. of stomachs examined:	31	24
Copepoda	51 (85.0)	31 (93.9)
Neocalanus cristatus	17 (28.3)	14 (42.4)
N. plumchrus/flemingeri	6 (10.0)	3 (9.1)
Pleuromamma scutullata	9 (15.0)	3 (9.1)
P. gracilis	1 (1.7)	–
Pleuromamma spp.	1 (1.7)	2 (6.1)
Metridia okhotensis	2 (3.3)	1 (3.0)
Eucalanus bungii	2 (3.3)	2 (6.1)
Eucalanus sp.	–	1 (3.0)
Euchaetidae	2 (3.3)	1 (3.0)
Aetideidae	2 (3.3)	–
Unidentified	9 (15.0)	4 (12.1)
Ostracoda	6 (10.0)	2 (6.1)
Amphipoda	1 (1.7)	–
Mysidacea	2 (3.3)	–

Diel feeding periodicity

The numbers of individuals examined to determine the stomach content index (*SCI*), stomach fullness, and digestion condition are given in Table 2.

Diaphus theta

Stomach content weight as a percentage of body weight (*SCI*) fluctuated between 1.2 and 2.7 % (avg. 2.1 %) over 24 h, and the stomachs contained considerable amounts of prey both during the day and at night. However, *SCI* decreased significantly from late afternoon to early night (ANOVA; $F_{(9, 426)}$ = 9.25, p < 0.01) (Fig. 3A).

Diel change in stomach fullness defined by the condition of the stomach rugae indicates that *Diaphus theta* actively feeds throughout the diel cycle, since we observed no clear changes in stomach fullness with time (Fig. 3B). The percentage of full stomachs at Stage 3 peaked (92.0 to 94.0 %) from midnight to dawn, and then gradually decreased throughout the day until early evening, reaching its lowest value (51.2 %) at 21:00 h. The day-night difference was not as remarkable, since 74.0 to 83.3 % of the stomachs were full (Stage 3) during the day. The percentage of Stage 2 stomachs increased as the percentage at Stage 3 decreased, but the percentages of empty and Stage 1 stomachs remained low over 24 h, 0 to 2.9 and 0 to 7.7 %, respectively.

The digestion stages of the major prey groups (euphausiids, copepods, and amphipods) were examined in relation to sampling time (Fig. 4). The occurrence of fresh euphausiids at Stage 1 was bimodal; the first peak was noted at 13:05 h (27.3 %) and the second peak at 20:30 h (18.2 %). These 2 peaks were significant (chi-square test, p < 0.01). The peaks for Stage 1 were followed by peaks for Stages 2 and 3 in succession, reflecting digestion of the euphausiids. Stage 1 copepods occurred throughout the diel period, with a small peak at 14:50 h (26.5 %). The percentage of Stage 1 amphipods was very high (46.7 to 71.1 %) at night, when *Diaphus theta* migrated up to the upper 100 m, but remained below 20.0 % during the daytime.

Stenobrachius leucopsarus

Part of the population of this species often remains in the daytime habitat at night (Pearcy et al. 1977, Cailliet & Ebeling 1990, Watanabe et al. 1999). Therefore, migratory and non-migratory nighttime specimens
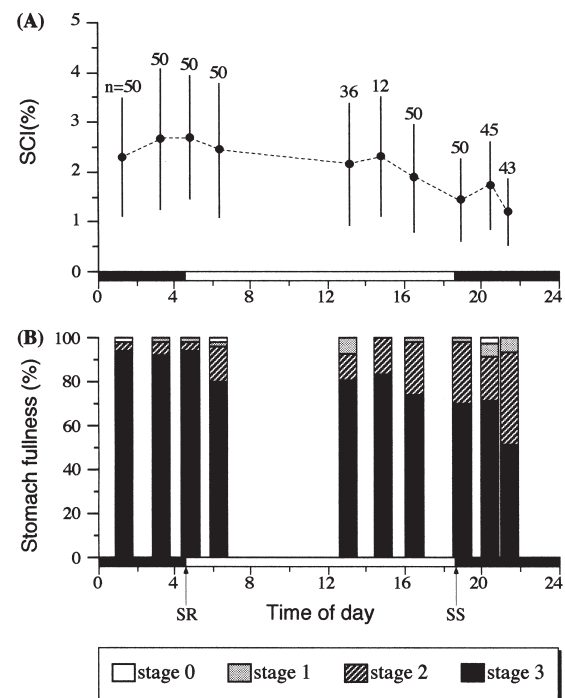

Fig. 3. *Diaphus theta.* Diel changes in stomach fullness. (A) Average stomach content index (*SCI*); vertical bars = SD. (B) Frequency of occurrence of each stage based on condition of stomach rugae (Stage 0 = empty; Stage 1 = contents recognized, but rugae not distended; Stage 2 = rugae partially distended, but recognizable; Stage 3 = full stomach, stomach very distended and no rugae recognized); SR, SS = sunrise and sunset, respectively; n = number of individuals examined

were analyzed separately. The *SCI* tended to be lower during the day, but the day-night difference was not significant (Mann-Whitney *U*-test, p > 0.05) (Fig. 5A). The *SCI* of the non-migratory component collected below 400 m at night was 0.6%, which was significantly lower than that of the migratory component (0.6 to 1.4%, avg. 1.1%) (Mann-Whitney *U*-test, p < 0.01), suggesting that non-migratory individuals do not feed as actively at night.

Diel change in the states of stomach fullness is shown in Fig. 5B. The occurrence of full stomachs at Stage 3 increased from 34.0% at sunset to 82.0% just after midnight and then gradually decreased to 40.0% in the early morning; it then increased to 70.0% at 14:50 h and decreased again to 30.0% 2 h before sun-

Fig. 5. *Stenobrachius leucopsarus*. Diel change in the stomach fullness. (A) Average stomach content index (*SCI*). (B) Frequency of occurrence of each stage based on condition of stomach rugae. ✱ = non-migratory population of *S. leucopsarus*; see Fig. 3 for further details

set. Stomachs at Stages 1 and 2 were found less frequently at night. During the daytime, the percentage of empty stomachs at Stage 0 was 0 to 6.0% (avg. 1.6%); at night, it was 0 to 2.0% (avg. 1.3%) for migratory individuals and 21.4% for non-migratory individuals, which was significantly higher than that of the migrants (chi-square test, p < 0.01).

Diel change in the digestion stage of each prey group in the stomachs also revealed a clear feeding periodicity (Fig. 6). Fresh euphausiids at Stage 1 occurred in 12.5 to 23.0% (avg. 19.2%) of the stomachs examined between dusk and midnight. These percentages were significantly higher than during the daytime (0 to 11.8%, avg. 3.8%) (chi-square test, p < 0.01). Similar tendencies were also observed for copepods and amphipods. The percentage of prey at Stage 1 was significantly lower in non-migrants than in migrants: 12.5 versus 23.3% for euphausiids, 6.5 versus 26.6% for copepods, and 0 versus 72.2% for amphipods (chi-square test, p < 0.01) (Fig. 6).

Stenobrachius nannochir

There was no remarkable diel change in either the *SCI* (ANOVA; $F_{(6, 339)} = 1.12$, p > 0.05) or stomach fullness of this non-migratory species (Fig. 7). The SCI was

Fig. 4. *Diaphus theta*. Diel change in stage of digestion of stomach contents. (Stage 1 = fresh prey, not digested; Stage 2 = shape of prey preserved, but some of appendages or carapaces separated; Stage 3 = prey deformed, but identifiable to higher taxa; 315 stomachs were examined.) SR, SS = sunrise and sunset, respectively
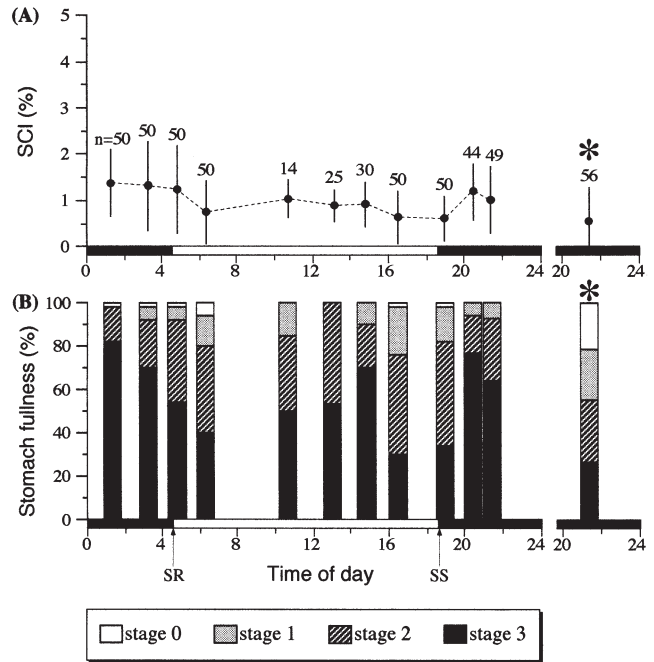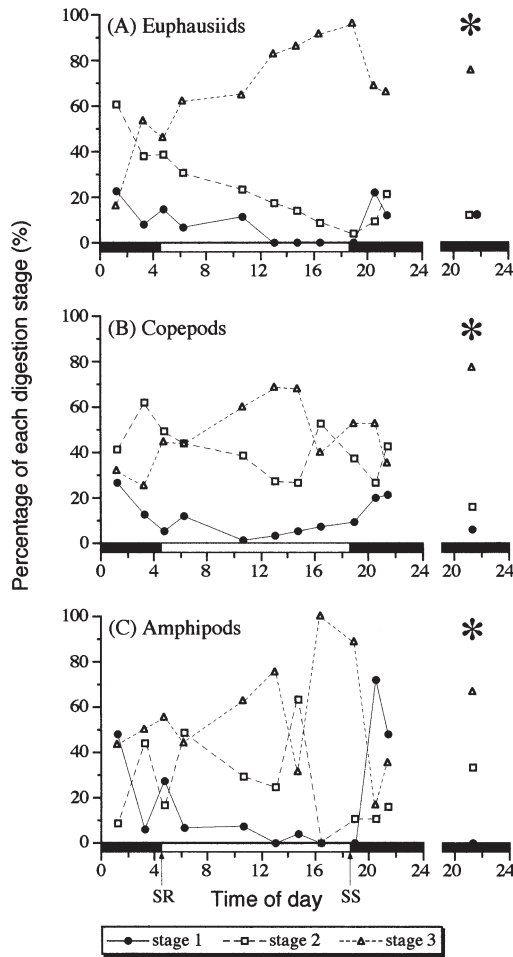
Fig. 6. *Stenobrachius leucopsarus*. Diel change in stage of digestion of stomach contents. 386 stomachs were examined. ∗ = non-migratory population at night; see Fig. 4 for further details

always below 0.13% and usually 10 and 20 times lower than the SCI of migratory *Stenobrachius leucopsarus* and *Diaphus theta*, respectively. Empty stomachs occurred much more frequently than in the other 2 species (11.5 to 44.0%, avg. 26.3% in *S. nannochir* versus 0 to 2.9%, avg. 0.7% in *D. theta* and 0 to 21.4%, avg. 3.1% in *S. leucopsarus*) (Figs. 7B, 3B & 5B, respectively). Percentage of fresh copepods at Stage 1 also did not change significantly throughout the diel cycle (chi-square test, p > 0.05) (Fig. 8).

DISCUSSION

Net feeding

Net feeding has been reported for fish collected with plankton nets because of the high zooplankton prey density in the cod-end (Lancraft & Robison 1980). Hop-

kins & Baird (1975) suggested that the dietary data for mesopelagic fishes collected by a trawl with a 0.333 mm mesh at the cod-end was not heavily biased by net feeding. Our diet analysis should not be biased by net feeding because of the adoption of 14 × 14, 18 × 18, and 30 × 30 mm meshes at the cod-end, which allowed most of the zooplankton prey to pass through.

Diel feeding periodicity

Migratory myctophids are known to actively feed in the epipelagic layer at night, and typically exhibit obvious diel feeding periodicity, especially in subtropical and tropical regions where the zooplankton biomass is rather low and restricted to the epipelagic zone (e.g., Baird et al. 1975, Clarke 1978, Kinzer & Schulz 1985). However, in highly productive regions, such as the subarctic and upwelling or slope water areas, migratory myctophids such as *Diaphus theta*, *Stenobrachius leucopsarus*, *Tarletonbeania crenularis* (Paxton 1967, Tyler & Pearcy 1975, Pearcy et al. 1979, Cailliet & Ebeling 1990), *Benthosema glaciale* (Kinzer 1977), *Diaphus dumerilii*, and *Lepidophanes guentheri* (Samyshev & Schetinkin 1971) have been reported to feed both at night and during the day. Our results also showed active daytime feeding by *D. theta* in the transitional and subarctic western North Pacific, where many prey organisms are available in the daytime mesopelagic layer.
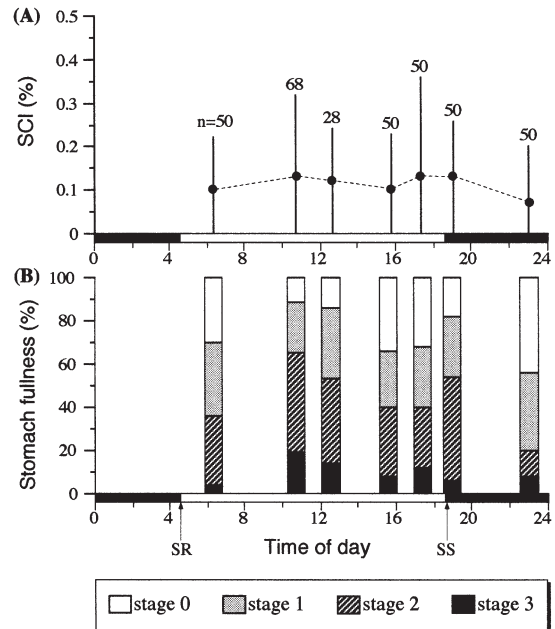

Fig. 7. *Stenobrachius nannochir*. Diel change in stomach fullness. (A) Average stomach content index (*SCI*). (B) Frequency of occurrence of each stage based on condition of stomach rugae. See Fig. 3 for further details

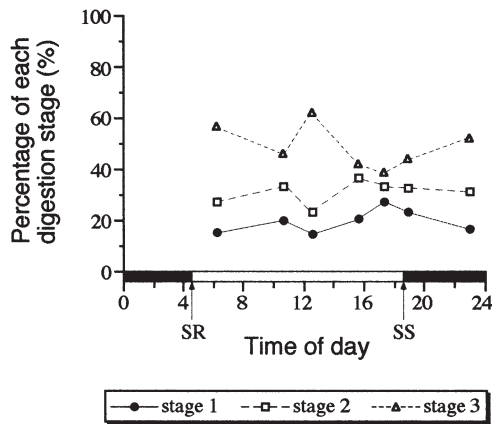Fig. 8. *Stenobrachius nannochir*. Diel change in stage of digestion of copepods in stomachs. 223 stomachs were examined. See Fig. 4 for further details

Diel migration patterns and feeding habits

Diaphus theta is a typical diel vertical migrant and is distributed between depths of 300 and 500 m during the daytime and between depths of 20 and 100 m at night (Watanabe et al. 1999). This species actively fed on euphausiids and copepods both during the day and at night. This can be explained by the overlap of the diel vertical migration depths of *D. theta* and its main prey, *Euphausia pacifica* and copepods belonging to the genera *Metridia* & *Pleuromamma* (Frost & Mc-Crone 1979, Hattori 1989).

Part of the *Stenobrachius leucopsarus* population is migratory and is distributed between 400 and 700 m (mainly 500 to 600 m) during the day and between 20 and 200 m at night, while the remainder of the population often remains in the daytime habitat at night (Pearcy et al. 1977, Watanabe et al. 1999). The migratory component mainly fed on crustaceans at night, and the species composition was similar to that of *Diaphus theta* (Table 3). Pearcy et al. (1979) and Cailliet & Ebeling (1990) suggested that this species feeds both during the daytime and at night, and that the non-migratory component also feeds in the mesopelagic layer at night. However, we only observed active nighttime feeding in the migratory component in the epipelagic layer, while the non-migrants had a significantly higher proportion of empty stomachs at night.

Stenobrachius nannochir is a non-migratory species and is distributed between 500 and 700 m (mainly 600 to 700 m) in our study area (Watanabe et al. 1999). This species showed no diel feeding periodicity, and empty stomachs were observed significantly more frequently than in the other 2 species (chi-square test, p < 0.01). Furuhashi & Shimazaki (1989) also observed no feeding periodicity in this species in the Bering Sea. Clarke

(1978) suggested daytime feeding of the non-migratory sternoptychid fish *Danaphos oculatus* in Hawaiian waters, due to the higher concentration of vertically migrating prey zooplankton in the mesopelagic layer during the daytime. In the subarctic summer, the main prey species of *S. nannochir* was *Neocalanus cristatus* in the diapause stage. These prey are lipid-rich after storing energy in the epipelagic zone, and are abundant at depths >500 m, which corresponds with the habitat of this myctophid species (Miller et al. 1984, Kobari & Ikeda 1999). Furthermore, the total abundance of calanoid copepods is reported to show no diel change in the habitat of *S. nannochir* (Hattori 1989), which would also partly explain the absence of a diel feeding rhythm of this non-migrant.

Daily rations

Estimating the mesozooplankton (especially crustaceans) biomass consumed every night by vertical migratory myctophids is of major interest to fisheries scientists from the view of estimating the carrying capacity of the epipelagic zone. Some researchers have estimated the egestion time of myctophid fishes. In tropical or subtropical regions, the egestion time was estimated to be 6.0 h at 12.0°C for *Lampanyctus mexicanus* (Holton 1969), 4.2 h at 13.0°C for *Diaphus taaningi* (Baird et al. 1975), and 1.9 h at 12.5°C for *Hygophum proximum* (Clarke 1978). In high-latitude waters, the egestion time was reported to be 8.5 h at 3.0°C for *Electrona antarctica* (Rowedder 1979) and 8.0 h at 3.5°C for *E. carlsbergi* (Gerasimova 1991). Since *Diaphus theta* and *Stenobrachius leucopsarus* are distributed in 2 to 4°C waters during the day and in 6 to 8°C waters at night (Watanabe et al. 1999), their egestion times are thought to be 6 to 8 h. The egestion time of *S. nannochir* distributed in the 2 to 4°C layer is thought to be around 8 h. Bajkov (1935) suggested the equation:

daily ration = 24 (h) × average *SCI* (%)/egestion time (h)

Assuming that the egestion time of the 3 species is 8 h, their daily rations are estimated to be 6.3 % of body wet weight for *D. theta*, 3.0 % for the migratory *S. leucopsarus*, and 0.33 % for *S. nannochir*, using the average SCI values of 2.1, 1.0, and 0.11 % over 24 h, respectively. Using estimates of the wet/dry weight ratios for crustaceans (Omori 1969) and myctophids (Butler & Pearcy 1972), the crustacean component of the daily ration is estimated to be 3.3 % of the body dry weight of the fish for *D. theta*, 1.8 % for the migratory *S. leucopsarus*, and 0.14 % for *S. nannochir*. Gartner et al. (1997) reviewed the daily rations of migratory myctophids and reported values from 1.0 to 4.5 % of dry body weight.

The daily ration of non-migratory *S. nannochir* was 1 order of magnitude lower than these values for migrants.

Habitat segregation and resource partitioning

The prey organisms and feeding rhythms of the 3 species examined in this study are depicted in relation to their diel migration patterns in Fig. 9. The diel vertical migration patterns are closely related to feeding strategies and are reflected in life history strategies, affecting life span and modes of growth and reproduction. The main habitat depths of the 3 species are distinct during the day. Only the nighttime habitats of *Diaphus theta* and *Stenobrachius leucopsarus* partly overlap in the upper 100 m layer, but their centers of distribution are different, with a deeper nighttime migration of *S. leucopsarus* (Pearcy 1964, Watanabe et al. 1999). This habitat segregation suggests spatial resource-partitioning among the 3 species. Hopkins & Gartner (1992) suggested resource-partitioning among the myctophid community in the eastern Gulf of Mexico by prey species, prey size, and habitat segregation. Compared with an oligotrophic low-latitude region like the Gulf of Mexico, the competing pressure for resources would be lower in this productive study area. Shifts in prey species and size with ontogeny were not examined, since the specimens examined in this study were subadults and adults >40 mm SL. This remains for future study.

Life style and trade-off in energy demand

Diaphus theta and *Stenobrachius leucopsarus* are reported to need 6 and 8 yr to reach lengths of 117 and 85 mm SL, respectively (Smoker & Pearcy 1970, Childress et al. 1980, Ivanov & Lapko 1994). This difference in age and growth is supported by the higher feeding activity of *D. theta* shown in this study both during the day and at night (Figs. 2 & 3).

The energy requirements of these species might be offset or altered by differences in their metabolic rates, swimbladder morphology, and lipid composition, which are closely related to energy consumption for diel vertical migration or maintaining buoyancy. All 3 species have swimbladders that decrease with body size and have high lipid contents. The swimbladders in some adult *Diaphus theta* are gas-filled and atrophied in others, while large *Stenobrachius leucopsarus* and *S. nannochir* have fat-invested swimbladders (Butler & Pearcy 1972). The diel migration into the high-temperature zone requires energy, not only for regulating swimbladder volume but also for the higher metabolic rate that occurs in the high-temperature epipelagic zone. This is approximately twice as high as that in the mesopelagic zone (Torres et al. 1979). Of the 3 species, *D. theta* needs the most energy, to migrate into and live in the epipelagic layer every night. The active feeding by *D. theta* not only assures energy for its active vertical migration, but also explains its dominance in the myctophid fish community in the subarctic and transi-
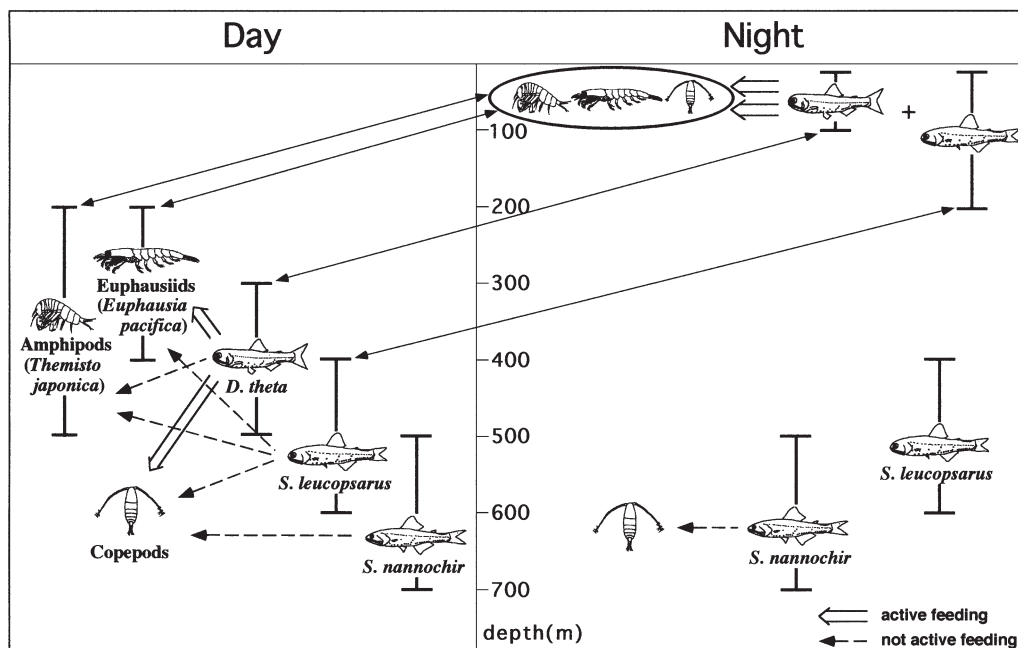

Fig. 9. *Diaphus theta*, *Stenobrachius leucopsarus*, and *S. nannochir.* Feeding habits and diel vertical migration patterns of the 3 myctophid fishes in the subarctic and transitional waters of the western North Pacific

tional waters of the North Pacific (Willis et al. 1988, Watanabe et al. 1999). *S. nannochir* may stay in the low-temperature habitat for 24 h. This assures a lower metabolic rate (Childress 1995), which is more favorable as an adaptation to the low prey-density environment in the lower mesopelagic zone. Its high wax content (12% of body wet weight) and fat-invested swimbladder help to maintain buoyancy without energy expenditure (Butler & Pearcy 1972, Saito & Murata 1996, Seo et al. 1996, Phleger 1998). *S. leucopsarus* has a flexible feeding strategy, intermediate between the other 2 species; part of its population eschews the vertical migration observed in *S. nannochir*. Both *S. leucopsarus* and *S. nannochir* have a high content of wax esters (87.9 to 98.6%) in their total lipids, while the major lipids of *D. theta* are triacylglycerols (68.1 to 87.8%) (Saito & Murata 1996, Seo et al. 1996). Phleger (1998) suggested that wax esters played a role in maintaining neutral buoyancy.

The feeding strategies of these 3 dominant myctophid species suggest a trade-off between the low- and high-energy demands of their differing lifestyles. One species, *Diaphus theta*, has a high-energy lifestyle, migrating into the epipelagic zone where temperatures and prey densities are high. A second species, *Stenobrachius nannochir*, has a low-energy lifestyle, remaining in the lower mesopelagic zone with its low temperatures and prey densities. The third species, *S. leucopsarus*, adopts an intermediate strategy, between the other two.

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