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Diet of the mesopelagic fish *Notoscopelus japonicus* (Family: Myctophidae) associated with the continental slope off the Pacific coast of Honshu, Japan

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ABSTRACT: The diet of *Notoscopelus japonicus*, one of the dominant mesopelagic fishes in the transitional waters of the western North Pacific, was examined in 106 specimens collected over the continental slope off the Pacific coast of northern Japan during April and October 1996. The prey comprised mainly crustaceans, such as copepods, ostracods, euphausiids and amphipods. *Euphausia pacifica* was the dominant prey, representing 83.1% by number and 72.4% by wet weight of the total diet. Between April and October, there was no shift in prey species consumed, but prey size decreased significantly and prey number per fish stomach increased in October. These results indicate that, in October, *N. japonicus* consumed larger numbers of smaller *E. pacifica*, rather than shifting to other prey taxa. The pronounced importance of *E. pacifica* in the diet was ascribed to its co-occurrence with *N. japonicus* at night in the surface layer and during the daytime in the near-bottom layer.

KEY WORDS: diet, *Euphausia pacifica*, euphausiids, mesopelagic fish, myctophids, *Notoscopelus japonicus*, upper continental slope.

INTRODUCTION

Myctophids are a dominant component of the pelagic ecosystems,¹ where they generally prey on crustacean zooplankton and are consumed by marine birds,² marine mammals³ and fish.⁴ They also form dense aggregations near continental slopes,^{5–8} where they may also play an important role in the near-shore ecosystem.

Notoscopelus japonicus is one of the most dominant myctophids in the transitional western North Pacific.^{9–11} Off the Pacific coast of northern Japan (Tohoku region), especially near the continental slope, *N. japonicus* is heavily consumed by marine mammals, such as the northern fur seal *Callorhinus ursinus*^{12,13} and Dall's porpoise *Phocoenoides dalli*.^{14,15} Furthermore, dominant demersal fishes, such as the Pacific cod *Gadus macrocephalus* and walleye pollock *Theragra chalcogramma*, consume

N. japonicus in this region.¹⁶ Thus, *N. japonicus* plays an important role in transferring organic material from lower trophic levels to higher trophic levels in both the pelagic and the near-bottom layers over the continental slope. In spite of the ecologic importance of *N. japonicus*, no information is available on its feeding habits. The present study reports the diet of *N. japonicus* associated with the continental slope in the Tohoku region.

MATERIALS AND METHODS

Specimens were collected during two demersal fish surveys conducted by the Tohoku National Fisheries Research Institute in April 1996 (R/V Tanshu-Marui) and October 1996 (R/V Wakataka-Marui). During the cruises, a bottom trawl with a mouth opening of 3.3 × 18.2 m was towed at an average ship speed of 3 knots (5.7 km/h). The net had an 8 mm mesh codend lining and was towed for 30 min at fishing depth at each sampling station. The location of stations and detailed sampling data are shown in Fig. 1 and Table 1. A total of 11 tows was made during the day and one was made at

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Fig. 1 Locations of bottom trawl stations. (●) R/V Tanshu-Mar cruise during April 1996; (▲) R/V Wakataka-Mar cruise during October 1996.

dusk (Table 1). Oceanographic observations were made in the area delineated by the latitudes 36°30'N and 38°30'N in April and 36°30'N and 41°30'N in October and the 150 and 1800 m isobaths. Water temperature was measured from the sea surface to just above the sea floor using an expendable bathythermograph (XBT) along five (April; 29 stations) and 10 (October; 61 stations) latitudinal transects.

Fish samples were fixed in a 10% buffered formaldehyde seawater solution at sea and then transferred to 50% isopropyl alcohol in the laboratory. Each fish was measured to the nearest 0.1 mm standard length (SL), weighed to the nearest 0.1 g wet body weight and the stomach was then dissected out. Prey was identified to the lowest taxon possible, counted and weighed to the nearest 0.1 mg. Prey found in the mouth cavity and esophagus of fish was excluded from the analysis because it could have been ingested in the net. Some individuals had digested prey items in their mouth cavities, which indicated an occurrence of regurgitation, but no empty stomachs resulting from regurgitation or everted stomachs were observed, suggesting that regurgitation was negligible for this study. Fish scales (probably from myctophids) and all but one ophiuroid arm found in the stomachs were excluded from the diet analysis, because they were considered to be ingested in the net. The one ophiuroid arm included in the analysis apparently resulted from natural feeding activity because it was surrounded by digested euphausiids. Two copepod species, namely *Neocalanus plumchrus* and *N. flemingeri*, and two amphipod species, namely *Themisto japonica* and *T. pacifica*, were treated as *N. plumchrus/flemingeri* and *T. japonica/pacifica*, respectively, due to the difficulty

Table 1 Sampling data of bottom trawls conducted off the Pacific coast of Honshu, Japan

		Sampling locality		Trawling	Sampling	Specimens	
Data		Vessel	Latitude (N)	Longitude (E)	mid-time (h)	depth (m)	examined
April	12	TM	38°28′	142°02′	07:11	408–415	73
	17	TM	37°31′	141°29′	07:31	410–415	3
	15	TM	36°58′	141°34′	13:44	399–401	1
	19	TM	36°30′	141°16′	09:54	806–813	3
	19	TM	36°45′	141°43′	15:12	1408	1
October	7	WM	39°29′	142°16′	06:37	373–383	17
	8	WM	39°07′	142°10′	06:49	395	1
	8	WM	38°55′	142°22′	15:14	940–946	1
	16	WM	38°05′	142°03′	12:14	406–417	1
	16	WM	38°04′	142°12′	*17:26	796–801	1
	17	WM	38°06′	142°21′	07:07	998–1000	1
	18	WM	37°25′	141°48′	11:05	400–412	3
Total					106		

TM: R/V Tanshu-Mar; WM: R/V Wakataka-Mar.

*Trawling was made after sunset (sunrise: 05.00 h (April), 05.30 h (October); sunset: 18.10 h (April), 17.00 h (October)).

in identification of partly digested materials. A stomach contents index (SCI) was calculated as follows:

$$SCI(\%) = (\text{wet weight total stomach contents} / \text{wet body weight}) \times 100$$

The diet of *N. japonicus* was expressed as the percentage of each prey type of the total number of prey identified (*Cn*), the percentage of each prey type of the total wet weight of prey identified (*WW*) and the percentage of stomachs in which each prey type was found (*F*). Based on these indices, we calculated an index of relative importance (*IRI*):¹⁷

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

for each prey category. The *IRI* for each category was then standardized to %*IRI*:¹⁸

$$\%IRI_i = 100 \times IRI_i / \sum_i^n IRI_i$$

where *n* is the total number of prey categories considered at a given taxonomic level.

To assess the effects of season on diet composition, we compared prey composition (*Cn*% and *WW*%) between April and October using the percent similarity index (*PSI*):¹⁹

$$PSI = 100 - 1/2 \sum_{i=1}^n |p_{x,i} - p_{y,i}|$$

where *p_{x,i}* and *p_{y,i}* are the percentage of the *i*th prey category in the diet for data of April and October, respectively. This coefficient ranges from 0% (no overlap) to 100% (complete overlap). There is no statistical method available to test the significance of *PSI*, so we considered diets to be similar when the *PSI* was 60%, which is the criterion used in published reports.²⁰⁻²² Because this index is sensitive to the taxonomic resolution of prey, we used the lowest taxonomic levels available (generally genus or species).

RESULTS

In the Tohoku region, the position of the Kuroshio front is defined to be where the temperature at 100 m depth is 14°C in April and 16°C in October and the position of the Oyashio front is defined to be where the temperature at 100 m depth is 5°C in April and 7°C in October.^{23,24} The area between these fronts is regarded as transitional waters. In the present study area (Fig. 1), the average temperature at 100 m depth was lower during April (mean $\pm$ SD = 7.7 $\pm$ 1.4°C; 29 XBT stations) than during October (12.5 $\pm$ 2.7°C; 61 XBT stations). Neither

front was observed during April in the study area. During October, the Kuroshio front occurred near 37°N, indicating that all 12 sampling stations were located in transitional waters.

The stomach contents of 106 fish ranging from 108 to 144 mm SL (mean $\pm$ SD = 126.2 $\pm$ 7.8 mm) were examined. Of these, only two individuals had empty stomachs. Median SL did not differ significantly between April (125.8 $\pm$ 8.1 mm) and October (127.5 $\pm$ 6.6 mm) (*U* = 850, *P* = 0.230, Mann-Whitney *U*-test).

The diets in April and October were similar in composition in terms of prey number and weight (*PSI* = 76 and 64% for *Cn* and *WW*, respectively). Therefore, the data from both seasons were combined for later analysis.

The diet of *N. japonicus* included copepods, ostracods, amphipods, euphausiids, decapods and ophiuroids (Table 2), with crustaceans forming the largest portion of the diet (*Cn* = 95.4%; *WW* = 99.8%; *F* = 98.1%). Euphausiids were the most dominant prey taxon (*Cn* = 85.3%; *WW* = 97.2%; *F* = 98.1%), *Euphausia pacifica*, which constituted 97.5 and 95.7% of the total number and wet weight of euphausiids, respectively (Table 2), was consumed by more than 82% of *N. japonicus* examined. Other euphausiid species, such as *Thysanoessa longipes* and *Tessarabrachion oculatum* were also ingested, but in low numbers. Copepods were the second-most important prey taxon by number (7.5%) and frequency of occurrence (23.3%) and comprised more than 10 species, including *Neocalanus cristatus*, *Candacia columbiae* and *Euchaeta rimana*. However, the gravimetric contribution of copepods to the diet was low (< 2.1%). *Sergestes similis*, the only decapod crustacean in the diet, was eaten by 10% of the fish and was the second-most important prey by wet weight (*WW* = 21.4%), but was low in numerical importance (*Cn* = 1.7%). Other prey taxa, such as conchoeciid ostracods, amphipods (*T. japonica/pacifica*) and ophiuroids, accounted for 1.0% of each index. The %*IRI* of euphausiids in the diet was 97.1%, whereas the values for the five other prey taxa were all $\leq$ 1.5% (Table 2).

The *SCI* ranged from 0 to 2.1, with an average of 0.6 in April, and from < 0.1 to 1.6 with an average of 0.7 in October. Prey size ranged from 2.1 to 46.0 mm total length (TL). Prey items larger than 23 mm TL comprised only *S. similis*, whereas those smaller than 9 mm TL comprised copepods and ostracods. Over 70% of prey items ranging from 9 to 23 mm TL were euphausiids. All ingested *E. pacifica* were either juveniles or adults. Of *E. pacifica* ingested in April, 98% were > 13 mm TL, whereas 67% of those ingested in October were > 13 mm TL. *Euphausia pacifica* ingested in April were significantly larger than those ingested in October (*t* =

Table 2 Diet of *Notoscopelus japonicus*

	Cn (%)	WW (%)	F (%)	%IRI
Crustacea (total)	95.4	99.8	98.1	
Copepoda (total)	7.5	2.1	23.3	1.5
<i>Aetideopsis multiserrata</i>	0.1	<0.1	1.0	
<i>Neocalanus cristatus</i>	0.9	0.5	4.9	
<i>Neocalanus plumchrus/flemingeri</i>	0.1	<0.1	1.0	
<i>Candacia columbiae</i>	1.2	0.2	7.8	
<i>Euchaeta rimana</i>	1.3	0.5	3.9	
<i>Euchaeta</i> spp.	0.6	0.4	2.9	
<i>Paraeuchaeta elongata</i>	0.1	0.1	1.0	
Euchaetidae (unidentified)	0.1	<0.1	1.0	
<i>Metridia okhotensis</i>	0.1	<0.1	1.0	
<i>M. pacifica</i>	0.4	<0.1	1.9	
<i>Metridia</i> spp.	0.3	<0.1	1.9	
<i>Pleuromanmma</i> spp.	0.3	<0.1	1.9	
<i>Scottocalanus securifrons</i>	0.1	<0.1	1.0	
Calanoida (unidentified)	1.6	0.3	5.8	
Ostracoda				
<i>Conchoecia</i> sp.	0.1	<0.1	1.0	<0.1
Malacostraca (total)	87.2	97.2	98.1	
Amphipoda				
<i>Themisto japonica/pacifica</i>	0.1	0.1	1.0	<0.1
Euphausiacea (total)	85.3	75.7	92.2	97.1
<i>Euphausia pacifica</i>	8.1	72.4	82.5	
<i>Thysanoessa longipes</i>	0.1	0.5	1.0	
<i>Thysanoessa</i> spp.	0.1	0.4	1.0	
<i>Tessarabrachion oculatum</i>	0.4	0.9	2.9	
Euphausiidae (unidentified)	0.1	0.1	1.0	
Euphausiacea (unidentified)	1.3	1.3	6.8	
Decapoda				
<i>Sergestes similis</i>	1.7	21.4	9.7	1.5
Crustacea (unidentified)	0.6	0.4	3.9	
Ophiuroidea (unidentified)	0.1	0.2	1.0	<0.1
No. identifiable prey item		693		
No. unidentifiable material		1		
No. stomachs containing identifiable prey items		103		
No. stomachs examined		106		
No. empty stomachs		2		

Cn, percentage of identifiable prey of the total number; WW, percentage of identifiable prey of the total wet weight; F, percentage frequency of occurrence of identifiable prey; %IRI, index of percentage relative importance.

5.702, $P < 0.001$, t -test; Fig. 2). In contrast, the number of euphausiids ingested per stomach was significantly higher in October than in April ($U = 291$, $P < 0.001$, Mann-Whitney U -test). There was no significant difference in SCI between April and October ($U = 779$, $P = 0.083$, Mann-Whitney U -test). Furthermore, the SL of fish that preyed on *E. pacifica* did not differ by month (125.0 ± 7.3 and 127.3 ± 6.7 mm in April and October, respectively; $U = 612$, $P = 0.146$, Mann-Whitney U -test).

DISCUSSION

In the depth range (343–1408 m) sampled in the present study, 93% of *N. japonicus* were collected at 373–417 m depth. This range corresponded with the known depth range of vertical distribution of *N. japonicus*, which is 300–500 m in both offshore¹¹ and near-shore (K Uchikawa, unpubl. data, 1998) waters during the daytime. The occurrence of *N. japonicus* near the sea floor on the upper conti-

Fig. 2 Size distribution of *Euphausia pacifica* ingested by *Notoscopelus japonicus*.

mental slope is presumably a result of the interruption of its downward migration by the sea floor.²⁵⁻²⁷ Thus, at bottom depths less than 500 m, this species will be associated with the bottom during the daytime. The few specimens collected in bottom tows at depths > 500 m may have been collected during the net's ascent and descent through the 300–500 m range.

Like other myctophids,^{25,28-31} *N. japonicus* feed mainly on crustaceans. No seasonal dietary shift was observed. This reflects a high dependence on *E. pacifica* in both April and October. *Euphausia pacifica* is one of the most abundant zooplankton in the Tohoku region³²⁻³⁴ and undertakes diel vertical migration (DVM) between 200 and 400 m depths during the daytime and the surface layer at night.³⁴⁻³⁶ Because *N. japonicus* also undertakes DVM,¹¹ it probably occurs at the same depths with *E. pacifica* during both the day and night. In the study area, dense aggregations of *E. pacifica* have been observed not only in the surface layer at night,^{32,37} but also in the near-bottom layer during the daytime.^{38,39} Aggregations of euphausiids in the near-bottom layers are thought to result from the interruption of their downward migration by the shallow sea floor and will increase their exposure to near-bottom predators.^{20,40,41} At depths less than approximately 400 m, *E. pacifica* were presumably trapped near the sea floor during the daytime, which plausibly improved the feeding conditions for *N. japonicus*. Thus, *N. japonicus* would have had access to aggregations of *E. pacifica* both in the surface layer at night and in the near-bottom layer during the daytime. Migrant myctophids feed mainly in the surface layers at night,⁴²⁻⁴⁴ but there are some reports of daytime feeding by migrant myctophids in productive areas, such as subar-

ctic/transitional,³¹ upwelling^{45,46} and upper-slope areas.^{28,29,47-49} Although we have no data on feeding periodicity, it seems likely that active feeding during the daytime by *N. japonicus* enhanced the importance of *E. pacifica* as food.

The average size of prey ingested by *N. japonicus* was 15.5 and 13.8 mm in April and October, respectively. This result indicated that *N. japonicus* ingested larger prey compared with other myctophids; *Diaphus taaningi* (most prey were < 4 mm),⁵⁰ *Lampanyctus alatus* (most prey were < 4 mm)⁵¹ and *Benthosema glaciale* (prey were ≤ 7 mm).⁵² Two factors are probably responsible for the differences. The positive relationship between predator and prey sizes has been widely reported for fish with particulate feeding.⁵³ *Notoscopelus japonicus* examined in the present study had a larger body size compared with the other myctophid fishes cited above and this would have resulted in a larger prey size. Another possibility is size composition of prey available. The predominant prey for *N. japonicus* was *E. pacifica*, which has a far larger body size compared with other common prey for myctophids, such as copepods and ostracods. As discussed below, an enhanced availability of *E. pacifica* in the bottom layer would have resulted in the large prey size of *N. japonicus*. The size of *E. pacifica* ingested by *N. japonicus* was significantly larger in April than in October, whereas the number of euphausiids per fish stomach significantly increased from April to October. Because the median size of *N. japonicus* examined in the present study did not differ seasonally, the decrease in prey size rather reflects the change in the size composition of available prey. In the Tohoku region, *E. pacifica* grows rapidly from 13 to 18 mm TL during March to May and growth is suspended through the winter.⁵⁴ *Euphausia pacifica* matures when it grows to 13 mm TL⁵⁵ and spawns mainly during spring to early summer.^{54,56} In our results, > 98% of *E. pacifica* were > 13 mm TL in April, whereas 67% of *E. pacifica* ingested were > 13 mm TL in October. These results suggest that the difference in size composition resulted from seasonal dynamics of the *E. pacifica* population. Because there was no significant seasonal difference in feeding intensity (SCI), in October *N. japonicus* appears to feed on larger numbers of smaller *E. pacifica* rather than shifting to other prey taxa.

Euphausia pacifica is an important prey for vertically migrating myctophids, such as *Diaphus theta* and *Stenobrachius leucopsarus*, in the north-western North Pacific.³¹ However, unlike *N. japonicus* in the present study, these two myctophids feed heavily on taxa other than euphausiids. Cope-

Pods are generally the major prey of midwater fishes in oceanic regions, whereas euphausiids become more important in areas closer to land.²⁹ Aggregations of euphausiids in the continental slope regions^{38-40,57,58} would enhance the availability and importance of euphausiids as prey. Gartner *et al.*²⁵ suggested that myctophids may approach the bottom not only because of the interruption of downward migration, but also due to the high prey concentrations in the benthopelagic layer over the continental slopes. Therefore, the pronounced importance of *E. pacifica* in the diet of *N. japonicus* is ascribed to the dense aggregation of *E. pacifica* being accessible during both day and night.

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