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Larval feeding habits of *Diaphus garmani* and *Myctophum asperum* (Pisces: Myctophidae) in the transition region of the western North Pacific

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ABSTRACT: We examined the feeding habits of the 2 dominant myctophid larvae, *Diaphus garmani* and *Myctophum asperum*, in the transition region of the western North Pacific. The incidence of feeding by these 2 species was ~10 times higher during the day than at night (66 to 71% vs. 5 to 6%), indicating that both larvae are daytime visual feeders. The prey of the 2 species were quite different: *D. garmani* depended mainly on appendicularian houses and copepod nauplii, while *M. asperum* fed mainly on ostracods and polychaetes. Prey size ingested increased with larval development, while niche breadth was independent of larval size, and did not change during development for either species. The average number of prey consumed by both larvae was 1 to 2 per gut, although an underestimate of prey number for *D. garmani* is possible owing to rapid digestion of fragile appendicularian houses. The number of prey was positively correlated with body length for *D. garmani*, but not for *M. asperum*. Competition for prey among these myctophid larvae and co-existing Japanese anchovy *Engraulis japonicus* larvae is unlikely because of their diet and habitat depth segregation.

KEY WORDS: Myctophid fish · *Diaphus garmani* · *Myctophum asperum* · Larval feeding habits · Appendicularian house · Resource partitioning · Transition region

INTRODUCTION

The transition region of the western North Pacific is located between the Oyashio (subarctic) and Kuroshio (subtropical) fronts (Kawai 1972, Roden 1991). In this region, complicated physical oceanographic structures such as warmwater tongues or streamers and warm or cold-core rings are typically observed, due to strong interactions between the Kuroshio and Oyashio currents (Roden 1991, Sugimoto & Tameishi 1996, Olson 2001). The transition region of the western North Pacific is an important spawning and nursery ground, not only for commercially valuable epipelagic fishes such as anchovy, sardine, and saury, but also for mesopelagic fishes such as those of the families Myctophidae and Bathylagidae (Sassa 2001, Sassa et al. 2002a, 2004b, Moku et al. 2003). The dominance of myctophid fish larvae in oceanic ichthyoplankton assemblages has been reported in various parts of the world's oceans, including the western North Pacific (Ahlstrom 1969, Loeb 1979a,b, Moser & Smith 1993, Olivar & Shelton 1993, Sassa 2001, Sassa et al. 2002b, 2004a). Their larvae are distributed in the productive upper 200 m layer during both day and night (Ahlstrom 1959, Loeb 1979a,b, Sassa et al. 2002b, 2004c), where they feed on small zooplankton (Gorelova & Efremenko 1989, Sabatés & Saiz 2000). Therefore, myctophid larvae have been identified as potential competitors with commercially important fish larvae for prey in oceanic regions (e.g. Ahlstrom 1969, Sassa 2001).

Nevertheless, knowledge of their feeding habits is quite limited and only a few studies have examined myctophid larvae. Gorelova & Efremenko (1989) described the food composition of the 2 dominant myctophid larvae in the Southern Ocean qualitatively and indicated that their primary prey comprised crustacean

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eggs and euphausiid calyptopis. Sabatés & Saiz (2000) examined the feeding habits of 5 species of myctophid larvae in the western Mediterranean and revealed that the larvae consumed mainly copepod nauplii and copepodites. In the transition region of the western North Pacific, the larvae of 3 other myctophids also depend mainly on copepods of all developmental stages, including eggs, nauplii, and copepodites (Sassa 2001). The myctophid larvae select both species-specific and developmental stage-specific sized prey (Sabatés & Saiz 2000).

Diaphus garmani and *Myctophum asperum* are dominant myctophid fishes in the Kuroshio and transition regions of the western North Pacific (Ozawa 1986, Beamish et al. 1999, Sassa et al. 2002a,b, 2003, 2004a,b,c). These species spawn in both regions. The main spawning seasons of *D. garmani* and *M. asperum* in the Kuroshio region are spring to early autumn and late winter to summer, respectively. The start of spawning is delayed for ca. 1 to 2 mo in the transition regions (Sassa et al. 2003, 2004a,b). Since considerable numbers of the larvae which hatch in the Kuroshio region are transported into the transition region by the Kuroshio current, these 2 species are the dominant component of ichthyoplankton assemblages in the transition region off Japan (Sassa et al. 2002a,b, 2003, 2004a,b,c). Larvae of *D. garmani* and *M. asperum* are distributed in the productive epipelagic layer at 20 to 50 m and 40 to 75 m, respectively, during both day and night (Tsukamoto et al. 2001, Sassa et al. 2002b, 2004c). After they metamorphose into juveniles, they start diel vertical migration and nocturnal feeding (Kawaguchi 1977, Watanabe et al. 1999). During winter, their subadult or adult populations are thought to migrate southward from the transition region to the Kuroshio to overwinter (Sassa et al. 2004b).

This study determined and compared the feeding habits of *Diaphus garmani* and *Myctophum asperum* larvae. Feeding incidence, diet composition, prey size, trophic niche breadth, numbers of prey per larvae, and the relationships between morphological variables (body length and mouth size) and feeding habits were examined. During the late 1990s, the population of the Japanese anchovy *Engraulis japonicus* was large in the coastal waters off Japan with the total annual catch reaching 100 000 to 313 000 t (Ministry of Agriculture, Forestry and Fisheries of Japan 2001). Their larval distribution extended from coastal to offshore waters in the transition region and they formed one of the main components of the ichthyoplankton (Kubota et al. 2001, Takahashi et al. 2001). Possible competition for prey among the larvae of the 2 myctophids and Japanese anchovy is also discussed, since their habitats overlap spatiotemporally (Sassa 2001, Sassa et al. 2004b,c).

MATERIALS AND METHODS

Sample collection. Larvae were collected during 4 cruises in the transition region of the western North Pacific in 1997 and 1998 (Fig. 1). Between 23 May and 15 June 1997, a multi-layer closing Motoda MTD net with an 80 cm mouth diameter and a 0.5 mm mesh (Motoda 1971) was towed for 30 min in 10 target depth layers (0, 10, 20, 30, 50, 75, 100, 125, 150, and 200 m) and a 3 m Isaacs-Kidd midwater trawl (IKMT) fitted with a 0.5 or 1.0 mm mesh net was used to sample the upper 100 m depths during the RV 'Hakuho-Maru' cruise (Ocean Research Institute, the University of Tokyo). A rectangular frame trawl with a 2.24 × 2.24 m mouth opening and a 1.59 mm mesh net (Methot 1986, Kubota et al. 2001) was towed obliquely from surface down to ca. 75 m during the RV 'Soyo-Maru' (National Research Institute of Fisheries Science, Japanese Fisheries Agency) cruise on 1 to 6 June 1997. Vertically stratified sampling was also made with a multiple opening-closing net and environmental sensing system (MOCNESS) (0.9 × 1.3 m mouth opening, 0.33 mm mesh net; Wiebe et al. 1985) during the RV 'Wakataka-Maru' cruise on 1 to 13 September 1998, and the

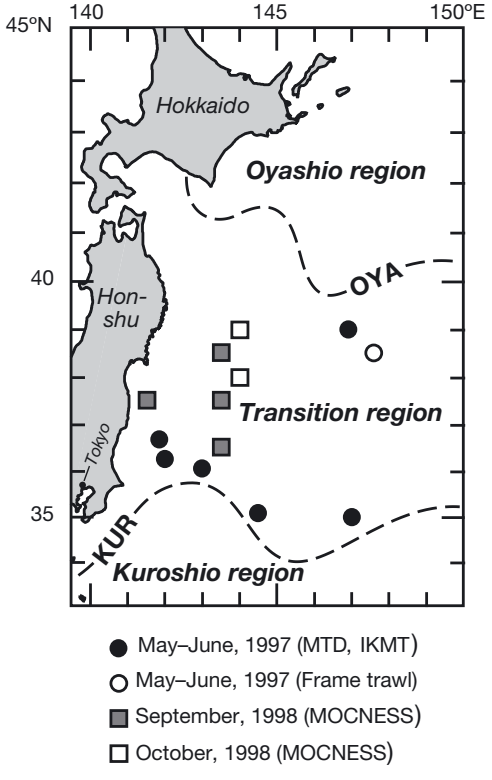

Fig. 1. Sampling localities of fish larvae during the 4 cruises in the transition region of the western North Pacific. The position of the Kuroshio and Oyashio fronts (broken lines) and water masses are shown. KUR and OYA represent the Kuroshio and Oyashio fronts, respectively

RV 'Hakuho-Maru' cruise on 5 to 10 October 1998. Sequential samples were taken from 4 depth strata (0–25, 25–50, 50–150, and 150–250 m) during the RV 'Wakataka-Maru' cruise in September and from 8 depth strata (0–20, 20–40, 40–60, 60–80, 80–100, 100–125, 125–150, and 150–200 m) during the RV 'Hakuho-Maru' cruise in October. Plankton samples were fixed with 10% buffered formalin seawater at sea.

Laboratory analysis. Intact specimens of *Diaphus garmani* and *Myctophum asperum* larvae were sorted for gut content analysis, and 215 and 375 ind. respectively, were examined (Table 1). Before dissection, the body length (BL) and upper jaw length were measured to the nearest 0.1 and 0.01 mm respectively. As BL, notochord length (NL) was measured for preflexion larvae and standard length (SL) for flexion and postflexion larvae. Upper jaw length was measured from the tip of the snout to the posterior end of the maxilla. Hereafter, 'mouth size' refers to upper jaw length, unless otherwise specified (Shirota 1970, Sabatés & Saiz 2000). Larvae size ranged from 3.9 to 10.7 mm (mean ± SD: 7.2 ± 1.7 mm) in *D. garmani* and 3.6 to 15.4 mm BL (8.5 ± 2.5 mm) in *M. asperum* (Fig. 2). These 2 species hatch at ca. 2 mm NL and the yolk is absorbed by the time they reach ca. 3 mm NL (Ozawa 1986, Moser & Ahlstrom 1996, Sassa et al. 2003). This suggests that first feeding occurs at a size of >3 mm NL. The transformation size to juvenile is ca. 11 mm SL for *D. garmani* and 15 mm SL for *M. asperum* (Ozawa 1986, Sassa et al. 2003). Our study covered almost all larval stages after yolk-sac absorption for the 2 species, although we could not examine the 3 to 3.9 mm NL specimens of *D. garmani* and the 3 to 3.6 mm NL specimens of *M. asperum*. Guts were dissected from the body and opened lengthwise with a fine needle. The prey items were identified to the lowest possible taxon and counted. The maximum body width of each prey was measured to the nearest 0.01 mm, using a microscope with an ocular micrometer, along the maximum cross section (hereafter, referred to as 'prey width') that the larvae had had to ingest (Blaxter 1963, Arthur 1976). It was not always possible to measure prey width, since the main dietary components of *D. garmani* and *M. asperum* consist of non-crustaceans without an exoskeleton that are sometimes partially digested and distorted in the gut. We therefore measured only fresh food items.

Table 1. *Diaphus garmani* and *Myctophum asperum*. Numbers of individuals examined for gut contents. –: no larvae caught or examined

	Diaphus garmani	*Myctophum asperum*
May–June, 1997 (MTD, IKMT)	113	148
May–June, 1997 (Frame trawl)	34	227
September, 1998 (MOCNESS)	65	–
October, 1988 (MOCNESS)	3	–
Total	215	375

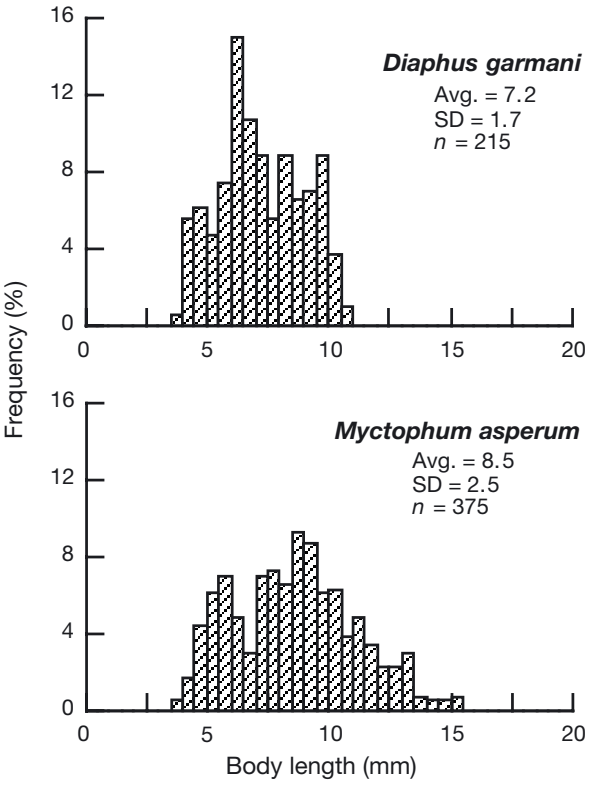

Fig. 2. *Diaphus garmani* and *Myctophum asperum*. Length-frequency distributions of the larvae examined for the gut content analysis

Data analysis. All larvae with identifiable prey in their guts were used for the analysis. Feeding incidence was calculated as the percentage of the total number of larvae with gut contents out of the total number of larvae examined for the day and night samples. The larvae collected between 1 h after sunrise and 1 h before sunset, and between 1 h after sunset and 1 h before sunrise, were considered 'daytime' and 'nighttime' samples, respectively. Feeding incidence was considered a measure of feeding success or the feeding rate in the field.

The diets of the 2 species were described using the percent frequency of occurrence (% F) of a diet item in larvae with food in their guts and the percent of the total number (% N) of diet items examined. The product of % F and% N was taken as an index of the relative importance (IRI) of each diet item.

Intraspecific changes in prey size were examined through larval development. Pearre's trophic niche

width (Pearre 1986) was adopted to analyze the relationship between prey size and predator size. In this analysis, the fish larvae were classified according to body length at 0.1 mm intervals. Only classes with >1 prey item in the gut were further analyzed. The mean and SD of the $\log_{10}$-transformed prey width was calculated for each available size class. This model adopts the SD of the $\log_{10}$-transformed prey sizes as a measure of trophic niche width. The relationship between body length and the corresponding mean and SD of the $\log_{10}$-transformed prey size was examined using linear regression analysis.

Regression analysis was used to determine the relationship between the number of prey in the gut and larval body size. The relationship between body length and upper jaw length was fitted using linear, allometric, and logarithmic formulae using the least squares method.

Table 2. *Diaphus garmani* and *Myctophum asperum*. Diel feeding incidence (%) of larvae in the transition region of the western North Pacific. N: number of larvae examined

Species	Size class (mm BL)	Day		Night	
		%	N	%	N
Diaphus garmani	3.9–7.9	70.8	113	4.2	24
	8.0–10.7	71.2	52	7.7	26
	Total	70.9	165	6.0	50
Myctophum asperum	3.6–7.9	62.3	114	2.2	45
	8.0–11.9	70.5	122	1.6	61
	12.0–15.4	60.0	15	16.7	18
	Total	66.1	251	4.8	124

The Shannon-Wiener diversity index (H') (Shannon & Weaver 1949) was adopted as a measure of prey species diversity.

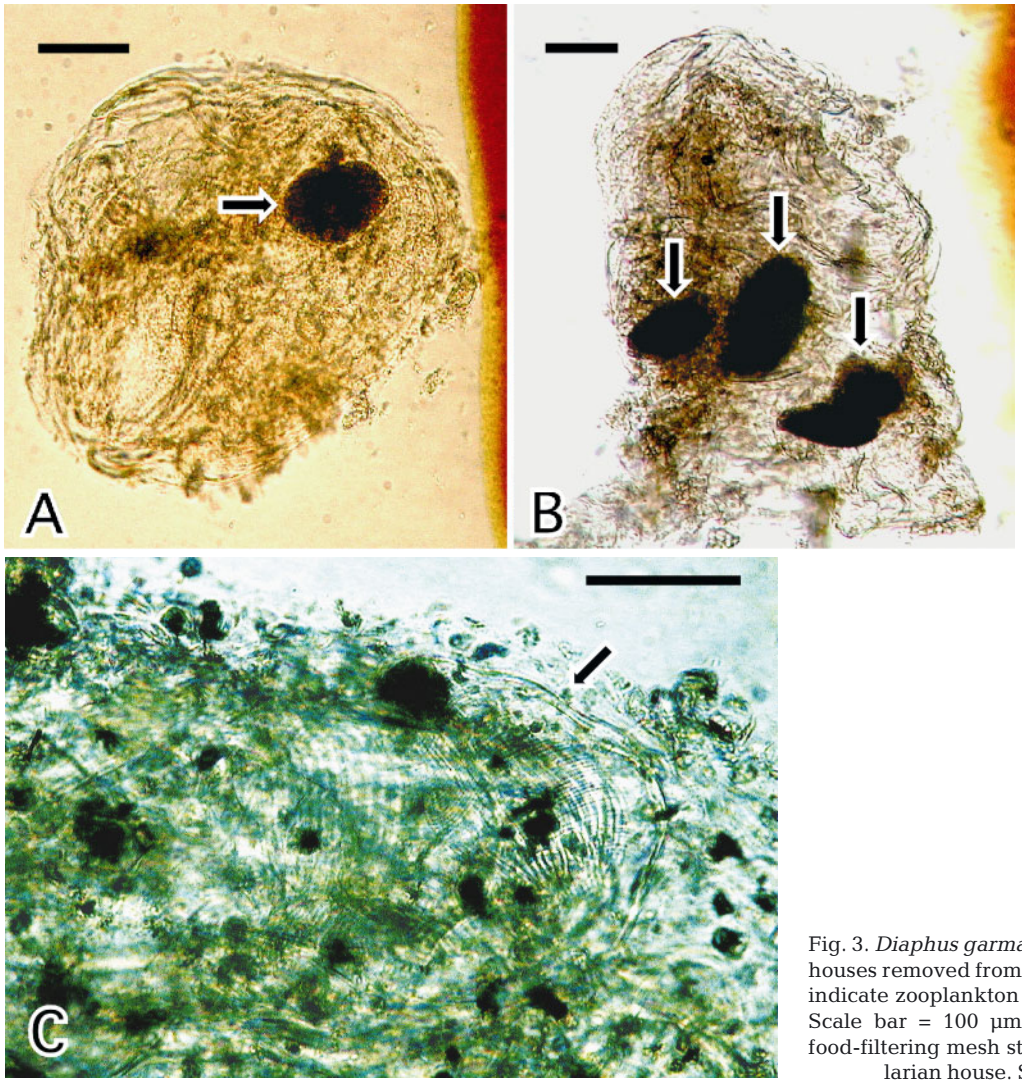

Fig. 3. *Diaphus garmani*. (A,B) Appendicularian houses removed from the guts of larvae. Arrows indicate zooplankton fecal pellets in the house. Scale bar = 100 µm. (C) Minute rectangular food-filtering mesh structure in the appendicularian house. Scale bar = 100 µm

RESULTS

Feeding incidence

The smallest larvae with gut contents were 4.1 mm BL for both *Diaphus garmani* and *Myctophum asperum*. The feeding incidence was ca. 71% in all size classes of *D. garmani* during the daytime, while at night it decreased to <8% (Table 2). More than 60% of all size classes of *M. asperum* larvae had food in their guts during the day (Table 2), while <3% did at night, except for the relatively high value of 16.7% in the 12 to 15.4 mm BL size class (Table 2). These diel changes in feeding incidence indicate that both larvae are daytime, i.e. visual, feeders.

Diet composition and trophic ontogeny

We frequently found transparent objects in the guts of *Diaphus garmani* (Fig. 3A,B). These ranged from 310 to 1150 µm in length and from 200 to 620 µm in width. They were soft capsules with no cellular structures in which net-like filters (pore size: ca. 2 × 4 µm) were usually observed (Fig. 3C). We identified the transparent capsules as appendicularian houses from their morphology (Alldredge 1977, Mochioka & Iwamizu 1996). The structures and size of the net-like filters corresponded to the feeding or incurrent filter of appendicularian houses. The houses sometimes contained 1 to 3 zooplankton fecal pellets (Fig. 3A,B), which had elongated shapes and were 175 ± 53 µm (mean ± SD) (range 75 to 300 µm) in length and 90 ± 30 µm (range 46 to 175 µm) in width.

In *Diaphus garmani* larvae of the 3.9 to 7.9 mm BL size class, appendicularian houses and copepod nauplii dominated and accounted for 32.2% and 31.6% respectively of the total prey identified (Table 3). As the *D. garmani* larvae grew, appendicularian houses became more important as prey, since they formed 70.3% of the total prey identified in the larger size class. Copepod nauplii ranked second, accounting for 8.8%. As a result, the larger size class had an extremely low diversity of prey items with H' = 1.15 (Table 3). In all size classes, appendicularian houses were the dominant prey, while appendicularian bodies accounted for only 2.2%. The index of relative importance (IRI) for appendicularian houses and copepod nauplii was 1353 to 5951 and 158 to 1248, respectively (Table 3). The IRI of other prey taxa was <100, indicating that this species preyed mainly on these 2 prey items during the larval stage.

The larvae of *Myctophum asperum* depended mainly on ostracods, polychaetes, and copepods, which accounted for 81.6 to 86.4% of the total number of prey items identified (Table 4). The IRI values were 760 to 1924 for ostracods and 463 to 1363 for polychaetes (Table 4). Copepod nauplii and copepodites of *Oithona* spp. and *Saphirina* spp. sometimes had a high IRI (116 to 158), while the values of other prey were <100. The diversity of prey items of *M. asperum* was much higher than that of *Diaphus garmani*. *Diaphus garmani* depended mainly on appendicularian houses, while *M. asperum* depended on ostracods, polychaetes, and copepods. Both species consumed copepods, but *D. garmani* fed mainly on eggs and nauplii, while *M. asperum* depended on more developed stages, including nauplii and copepodites of calanoid, cyclopoid, and poecilostomatoid copepods (Table 4).

Table 3. *Diaphus garmani*. Prey composition of the 2 size classes of larvae. Percent of the total number (% N) of diet items and percent frequency of the occurrence (% F) of a diet item among larvae with food in their guts were multiplied, and the product (% N × % F) was taken as an index of relative importance (IRI). –: no occurrence

Size class (mm BL):	3.9–7.9			8.0–10.7		
No. larvae examined	137			78		
No. empty stomachs	56			39		
Total no. prey items	152			91		
Diversity index (H')	1.87			1.15		
Food items	% N	% F	IRI	% N	% F	IRI
Radiolaria	0.66	1.23	0.81	–	–	–
Polychaete	0.66	1.23	0.81	–	–	–
Cladocera: *Evadne* sp.	3.95	7.41	29.24	–	–	–
Ostracoda	–	–	–	1.10	2.56	2.82
Copepoda						
Egg	8.55	11.11	94.99	1.10	2.56	2.82
Nauplius	31.58	39.51	1247.73	8.79	17.95	157.78
Calanoid copepodite						
Calanus spp.	3.95	6.17	24.37	–	–	–
Unidentifiable calanoid	7.24	13.58	98.32	3.30	5.13	16.93
Cyclopoid copepodite						
Oithona spp.	1.32	2.47	3.26	–	–	–
Poecilostomatoid copepodite						
Oncaea spp.	–	–	–	1.10	2.56	2.82
Unidentified copepoda	1.97	3.70	7.29	1.10	2.56	2.82
Euphausiidae						
Egg	1.32	2.47	3.26	–	–	–
Calyptopis	–	–	–	2.20	2.56	5.63
Appendicularians	32.24	41.98	1353.15	72.53	82.05	5950.97
Unidentifiable material	2.63	4.94	13.00	2.20	2.56	5.64
Unidentified crustacean	3.95	4.94	19.49	3.30	7.69	25.36
Unidentified egg	–	–	–	3.30	2.56	8.45

Table 4. *Myctophum asperum*. Prey composition of the 3 size classes of larvae. Percent of the total number (% N) of diet items and percent frequency of the occurrence (% F) of a diet item among larvae with food in their guts were multiplied, and the product (% N × % F) was taken as an index of relative importance (IRI). –: no occurrence

Size class (mm BL):	3.6–7.9			8.0–11.9			12.0–15.4		
No. larvae examined	159			183			33		
No. empty stomachs	87			96			21		
Total no. prey items	120			164			22		
Diversity index (*H'*)	1.89			2.08			1.64		
Food items	% N	% F	IRI	% N	% F	IRI	% N	% F	IRI
Radiolaria	–	–	–	0.61	1.15	0.70	–	–	–
Polychaete	16.67	27.78	462.96	26.22	45.98	1205.49	27.27	50.00	1363.64
Cladocera									
Evadne sp.	1.67	2.78	4.64	5.49	4.60	25.25	–	–	–
Penilia avirostris	0.83	1.39	1.15	–	–	–	–	–	–
Ostracoda	43.30	44.44	1924.44	24.39	31.03	756.94	40.91	33.33	1363.64
Copepoda									
Egg	0.83	1.39	1.15	–	–	–	–	–	–
Nauplius	7.50	12.50	93.75	15.24	10.34	157.58	4.55	8.33	37.90
Calanoid copepodite									
Eucalanus spp.	–	–	–	0.61	1.15	0.70	–	–	–
Euchaeta spp.	–	–	–	0.61	1.15	0.70	4.55	8.33	37.90
Pseudo/Paracalanus spp.	3.33	5.56	18.51	5.49	4.60	25.25	–	–	–
Cyclopoid copepodite									
Oithona spp.	8.33	13.89	115.70	3.05	1.15	3.51	–	–	–
Poecilostomatoid copepodite									
Oncaea spp.	0.83	1.39	1.15	1.22	1.15	1.40	–	–	–
Sapphirina spp.	0.83	1.39	1.15	4.88	9.20	44.90	9.09	16.67	151.53
Unidentified copepoda	–	–	–	0.61	1.15	0.70	–	–	–
Amphipoda	0.83	1.39	1.16	0.61	1.15	0.70	–	–	–
Euphausiidae									
Egg	–	–	–	–	–	–	4.55	8.33	37.90
Calyptopis	0.83	1.39	1.15	–	–	–	4.55	8.33	37.90
Furcilia	1.67	2.78	4.64	1.83	3.45	6.31	–	–	–
Juvenile	–	–	–	0.61	1.15	0.70	–	–	–
Appendicularians	8.33	11.11	92.56	0.61	1.15	0.70	–	–	–
Unidentifiable material	3.33	4.17	13.89	1.83	3.45	6.31	–	–	–
Unidentified crustacean	0.83	1.39	1.16	6.10	11.49	70.09	4.55	8.33	37.88

Prey size and trophic niche breadth

The prey size range of *Diaphus garmani* and *Myctophum asperum* larvae was 70 to 620 µm and 80 to 1950 µm, respectively (Fig. 4). The prey size range widened with development in both species (Fig. 4). The logarithmic average sizes of prey were significantly correlated with larval length (Fig. 4, Table 5; $r^2 = 0.467$, df = 39, $p < 0.001$ for *D. garmani*; $r^2 = 0.435$, df = 46, $p < 0.001$ for *M. asperum*). The rates of change in average prey size with growth (i.e. the slope of mean prey size/larval fish length relationship) for *D. garmani* and *M. asperum* were similar, i.e. 0.060 and 0.058, respectively (Table 5). Niche breadths were independent of larval size, and did not change during larval development (regression analysis for each species, $p > 0.1$, Table 5) with the average niche breadths (SD) of *D. garmani* and *M. asperum* being 0.13 ± 0.07 and 0.19 ± 0.10, respectively.

Up to ca. 11 mm BL, no remarkable difference in mouth size was observed between the 2 species (Fig. 5). The mouth sizes for *Diaphus garmani* of 5 and 10 mm BL were 0.79 and 2.05 mm and those for *Myctophum asperum* of 5, 10, and 15 mm BL were 0.97, 2.10, and 2.76 mm, respectively, based on the formula obtained in Fig. 5. Prey size as a percentage of mouth size for *D. garmani* and *M. asperum* ranged from 7.4 to 53% (mean ± SD, 23.4 ± 8.8%) and 4.8 to 93% (28.6 ± 16.2%), respectively.

Numbers of prey per gut

We examined only daytime samples, since larvae of both species fed mostly during the daytime (Table 2). In *Diaphus garmani*, the number of prey per gut ranged from 0 to 7. The number of prey eaten was positively correlated with body length (Fig. 6; $r^2 = 0.029$, df

Table 5. *Diaphus garmani* and *Myctophum asperum*. Weighted linear-regression analysis of average (log_{10}-transformed) prey width and trophic niche-breadth (SD of log_{10}-transformed prey width) as a function of larval body length. Slope, intercept, corresponding standard errors (SE), and determination coefficients are shown. $^{*}p < 0.05$, $^{**}p < 0.001$

	Intercept	SE	Slope	SE	r^2
Average prey width vs. larval body length					
Diaphus garmani	2.011**	0.074	0.060**	0.010	0.467
Myctophum asperum	2.146**	0.086	0.058**	0.010	0.435
Trophic niche-breadth vs. larval body length					
Diaphus garmani	0.162*	0.048	–0.004	0.007	0.009
Myctophum asperum	0.184*	0.053	0.001	0.006	0.001

= 164, $p < 0.05$), showing an increase in feeding ability with growth. The average numbers of prey were 0.9 and 1.8 ind. per gut in the larvae of 4 to 6 mm and 6 to 10 mm BL, respectively (Fig. 6). The numbers of prey ingested were probably underestimated for *D. garmani* owing to the rapid digestion of fragile appendicularian houses, which were their main prey (Table 3).

In *Myctophum asperum*, the number of prey ranged from 0 to 11 (mean 1.2) per gut and showed no positive relation with growth (Fig. 6; $r^2 = 0.004$, df = 250, $p > 0.1$). This reflected their dependence on the larger prey and a prey size shift with growth (Fig. 4) instead of taking an increased number of small prey. The average number of prey per gut was 1.20 ± 0.43 (mean ± SD) individuals throughout larval development (Fig. 6).

DISCUSSION

Feeding incidence and diurnal feeding

Diaphus garmani and *Myctophum asperum* larvae fed mainly during the daytime in the epipelagic layer, showing that they are visual feeders. This is character-

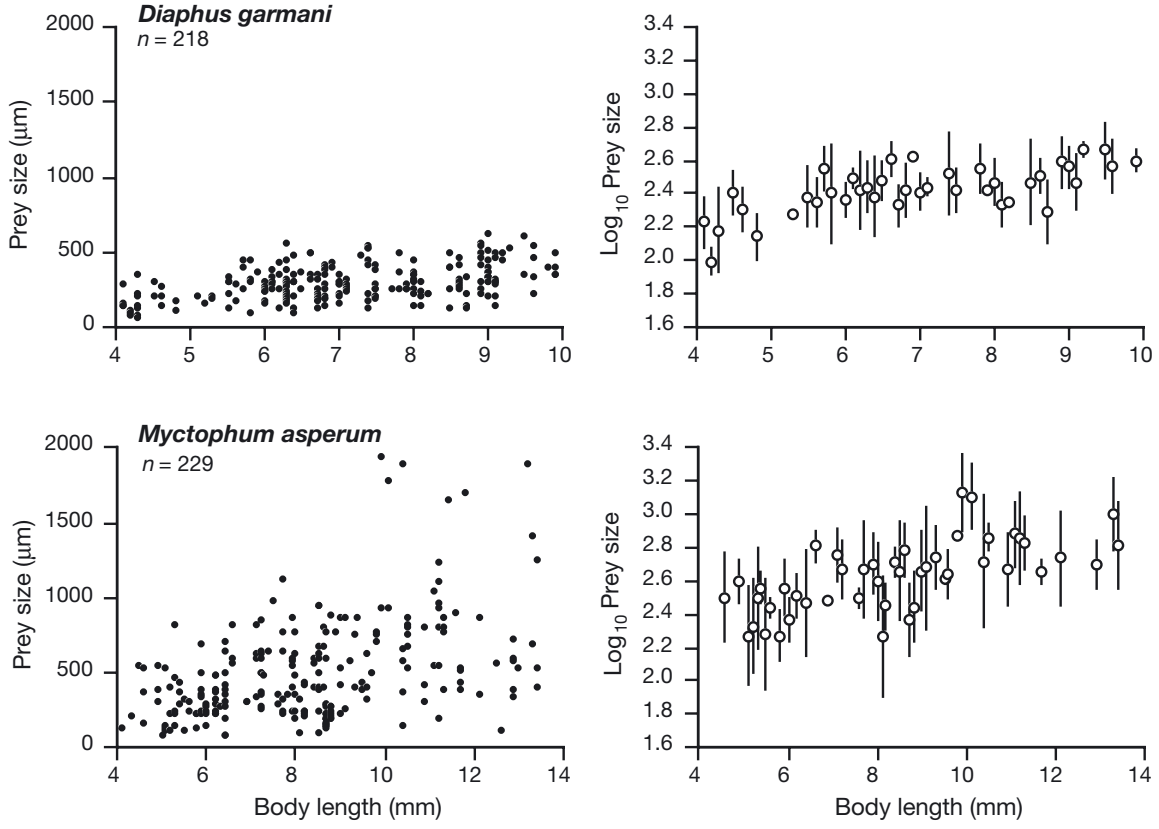

Fig. 4. *Diaphus garmani* and *Myctophum asperum*. Prey size–fish body length relationship for the 2 species. Prey size was measured as the maximum body width. Prey size in the graphs on the left is untransformed raw data, while it is log_{10}-transformed in the graphs on the right

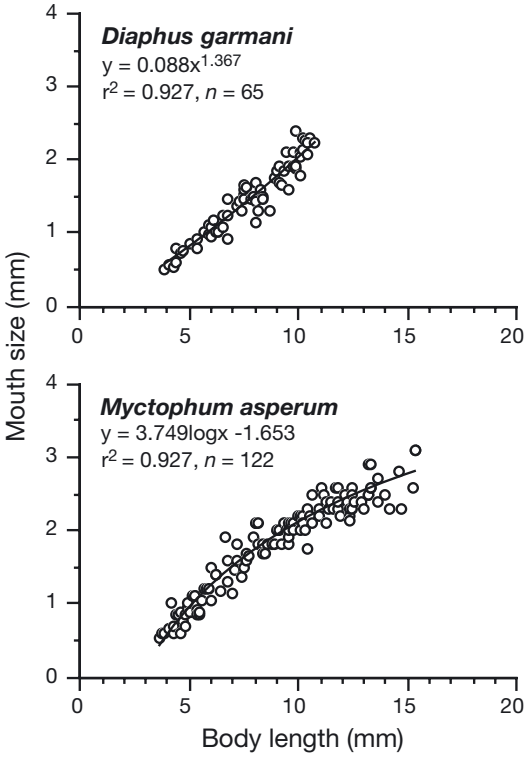

Fig. 5. *Diaphus garmani* and *Myctophum asperum*. Relationship between larval body size and mouth size

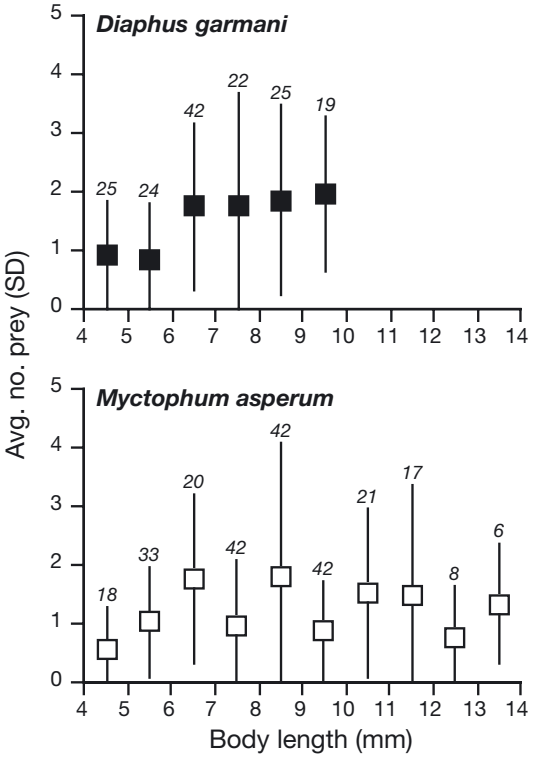

Fig. 6. *Diaphus garmani* and *Myctophum asperum*. Number of prey per gut in relation to body length (mm). Numbers above the bars are the numbers of larvae examined

istic of most larval fish reported to date (e.g. Blaxter 1963, Arthur 1976, Last 1978, Hunter 1981, Uotani 1985, Young & Davis 1990, Sanchez-Velasco et al. 1999, Sabatés & Saiz 2000). *D. garmani* and *M. asperum* start diel vertical migration after metamorphosis from larvae to juveniles, and actively feed in the epipelagic layer at night, exhibiting obvious diel feeding periodicity (Clarke 1973, Watanabe et al. 1999, 2002, Sassa et al. 2002a). Therefore, they change their feeding habits from diurnal to nocturnal feeding after metamorphosis. The relatively high feeding incidence value of 16.7% for the 12 to 15.4 mm *M. asperum* larvae might indicate the beginning of the transition to crepuscular or nocturnal feeding occurring just before the final transformation to the juvenile stage.

Feeding incidence could vary with the digestibility of the prey preferentially consumed by each species. Our results may be underestimates, especially in the larger size classes, since as they grew, the larvae of both species began to feed on soft animals without exoskeletons, i.e. appendicularian houses in *Diaphus garmani* and polychaetes in *Myctophum asperum*. These soft prey would be digested rapidly to an unrecognisable and therefore uncountable state. However, the daytime feeding incidence of *D. garmani* and *M. asperum* increased gradually with development, which would correspond to an increase in their swimming and feeding abilities after fin formation, and the development of the mouth and sense organs such as eyes and lateral lines (Shirota 1970, Hunter 1981, Ozawa 1986, Sassa et al. 2003).

Diet composition

Diaphus garmani larvae fed mainly on appendicularian houses, but appendicularian bodies were rarely detected in their guts. Although little is known about the densities of appendicularian houses in the study area, *D. garmani* larvae might select them, the IRI value for appendicularian houses is very high (Table 3). Several species of pleuronectiform and scombrid larvae feed mainly on appendicularian houses and bodies (Ryland 1964, Last 1978, Uotani et al. 1981, Young & Davis 1990, Fortier & Villeneuve 1996, Sanchez-Velasco et al. 1999). Appendicularian house widths eaten by *D. garmani* larvae ranged from 200 to 620 µm, which are among the smallest appendicularian houses (Alldredge 1977). This suggests that *D. garmani* larvae eat very small juvenile appendicularian houses produced in the first few days of life. The mouth size of *D. garmani* larvae ranged from 790 to 2050 µm (Figs. 4 & 5), which is large enough to swallow

these houses. We examined the gut contents of *D. garmani* collected during May to June and September to October, but no significant seasonal difference was found in the prey composition between early summer and autumn. The houses contain large amounts of organic material, such as phytoplankters, protozoans, and appendicularian fecal pellets. Phytoplankters and protozoans usually remaine on the food-concentrating filters of the houses. In oceanic waters, several species of pelagic crustaceans, such as ostracods, copepods, euphausiids, and decapod larvae, are thought to consume discarded appendicularian houses (Alldredge 1972, 1976, Ohtsuka et al. 1993). Mochioka & Iwamizu (1996) also found that 8 species of anguilloid leptocephali fed selectively on appendicularian houses. These facts strongly imply that discarded appendicularian houses are an important food source for several zooplankton taxa and larval fishes in oceanic waters.

The appendicularian houses sometimes contained 1 to 3 zooplankton fecal pellets averaging 175 µm in length (Fig. 3A,B). The appendicularian fecal pellets are rarely larger than about 1/3 of the trunk length (Ryland 1964). Fecal pellets 175 µm in length would be produced by animals with trunk lengths of at least >500 µm. Appendicularians this size would produce a house too large (ca. 3 mm in width: Alldredge 1977) to be prey for *D. garmani* larvae. It is likely that these are pellets from other planktonic animals, such as copepods or larger appendicularians, which were eaten by the fish larvae separately and combined in the gut. Zooplankton fecal pellets of similar size are also found in the guts of anguilloid leptocephali (Otake et al. 1993, Mochioka & Iwamizu 1996).

Myctophum asperum larvae fed on ostracods from the onset of feeding. The peak abundance of ostracods in the Kuroshio and its adjacent waters is from winter to spring (Hirota 1995), which corresponds with the seasonal peak abundance of *M. asperum* larvae (Sassa 2001, Sassa et al. 2004a,b). Polychaetes were also common prey items for *M. asperum* larvae >8.0 mm SL. Gorelova & Efremenko (1989) also reported that fragments of pelagic polychaete bodies, such as bundles of setae, were frequently found in the gut of *Electrona antarctica* larvae in the Scotia Sea. In our study area, copepods are the numerically dominant component of the zooplankton community, while ostracods and polychaetes are rare (Odate 1994), suggesting possible selective feeding on ostracods and polychaetes by *M. asperum* larvae.

Sabatés & Saiz (2000) examined the feeding habits of 5 coexisting myctophid larvae (*Benthosema glaciale*, *Ceratoscopelus maderensis*, *Hygophum benoiti*, *Lampanyctus crocodilus*, and *Myctophum punctatum*) in the western Mediterranean and found that 88% of the identified prey were copepod nauplii and copepodites. In the transition region of the western North Pacific, myctophid larvae of *Diaphus theta*, *Protomyctophum thompsoni*, and *Tarletonbeania taylori* also depend mainly on copepods, which account for ca. 90% of the total number of prey (Sassa 2001). Although *D. garmani* and *M. asperum* larvae also consumed copepods, the IRI values indicated that *D. garmani* depended much more on appendicularian houses while *M. asperum* depended on ostracods and polychaetes, showing unique species-specific feeding habits. Although *D. garmani* larvae ≤7.9 mm BL depend equally on copepod nauplii and appendicularians, the nauplius size differed markedly between *D. garmani* and the other 3 myctophid larvae studied in the transition region (Sassa 2001). In *D. theta*, *P. thompsoni*, and *T. taylori* larvae, nauplii with widths of 50 to 150 µm accounted for >80% of the total number of prey (Sassa 2001), while in *D. garmani*, those with widths of 150 to 350 µm accounted for 85.1%, i.e. their diet overlap was not significant. These recent studies on the prey composition of myctophid larvae, together with our results, suggest resource partitioning among myctophid fish larvae, which belong to the most speciose fish group in the oceans.

In the worlds' oceans, each species of myctophid has a specific larval distribution depth in the productive epipelagic zone within 200 m of the surface, and none show diel vertical migration (e.g. Ahlstrom 1959, Loeb 1979a,b, Moser & Smith 1993, Sassa et al. 2002b, 2004c). The vertical peak abundance of larvae of *Diaphus garmani* and *Myctophum asperum* was in the 20 to 50 m and 40 to 75 m layers, respectively, in the Kuroshio and transition regions off central Japan (Table 6, Sassa 2001, Tsukamoto et al. 2001, Sassa et al. 2002b, 2004c). The segregation of both diet and habitat between these 2 fish larvae shows that they probably do not compete for prey (Table 6), although final confirmation would involve comparison of diets within the narrow vertical depth of overlap (ca. 40 to 50 m depth) between the 2 species. Juvenile and adult myctophids in the Gulf of Mexico and the western North Pacific reduce competition by partitioning vertical space and zooplankton food resources (Hopkins & Gartner 1992, Watanabe et al. 2002). Larval myctophids would likely adopt similar feeding strategies.

Prey size vs. numbers of prey

Fish larvae forage selectively, eating particles that fall within a preferred size range limited by their mouth size (Shirota 1970, Hunter 1981). The prey of *Diaphus garmani* and *Myctophum asperum* larvae are larger than those of the other 3 myctophid species in the transition region of the western North Pacific,

Table 6. *Diaphus garmani*, *Myctophum asperum*, and *Engraulis japonicus*. Summary of vertical distribution and feeding habits of larvae in the transition region of the western North Pacific. The main prey of myctophid larvae were defined as items accounting for >1000 of IRI. Larval habitat depths are based on Ida (1972), Sassa (2001), Sassa et al. (2002b), and Tsukamoto et al. (2001). The main prey of *E. japonicus* larvae are after Funakoshi (1984), Uotani (1985), Mitani (1988), Uotani et al. (1988), and Hirakawa et al. (1997)

Species	Habitat depth (m)	Main prey
Diaphus garmani		
≤7.9 mm BL	20–50	Appendicularian houses, copepod nauplii[a]
≥8.0 mm BL	20–50	Appendicularian houses
Myctophum asperum		
≤7.9 mm BL	40–75	Ostracods
≥8.0 mm BL	40–75	Ostracods, polychaetes
Engraulis japonicus		
≤7.9 mm BL	0–30	Copepod nauplii[b]
≥8.0 mm BL	0–30	Copepod copepodites

[a]150–300 µm width, [b]50–110 µm width

probably due to the larger mouth size of these 2 species (Table 7). Conversely, the average numbers of prey consumed by the 2 larvae were from 1 to 2 per gut and lower than those of the other species previously studied (Sassa 2001), although the value for *D. garmani* was probably underestimated due to the rapid digestion of fragile appendicularian houses. This suggests that feeding strategy of the 2 species involves taking larger prey instead of taking a large number of small prey. By contrast, the larvae of *D. theta*, *Protomyctophum thompsoni*, and *Tarletonbeania taylori* consumed ca. 3 to 9 times more small prey than *D. garmani* and *M. asperum* in this study (Sassa 2001). Prey size consumed increased with larval growth, and was a fairly constant percentage of mouth size for *D. garmani* and *M. asperum*, i.e. ca. 23 and 29% on average, respectively, which are relatively high values when compared with those of other myctophid larvae in the western Mediterranean (mean 17–22% Sabatés & Saiz 2000) and transition region (mean 10–13% Sassa 2001). The niche breadth of *D. garmani* and *M. asperum* larvae did not increase with growth, which agrees with other studies (e.g. Pearre 1986, Houde 1997, Sabatés & Saiz 2000).

Table 7. Upper jaw length for the larvae of 5 myctophid species at body lengths (BL) of 5 and 10 mm in the transition region of the western North Pacific

Species	Upper jaw length (mm) at 5 mm BL	Upper jaw length (mm) at 10 mm BL
Diaphus garmani	0.79	2.05
Myctophum asperum	0.97	2.10
Diaphus theta[a]	0.33	1.70
Protomyctophum thompsoni[a]	0.48	1.18
Tarletonbeania taylori[a]	0.45	1.38

[a]Data after Sassa (2001)

Possible prey competition between larval myctophids and Japanese anchovy

Larvae of *Diaphus garmani* potentially compete with Japanese anchovy *Engraulis japonicus* for prey in the Kuroshio and transition regions of the western North Pacific, since they are usually occur together, sharing a spatiotemporally similar habitat (Sassa 2001, Tsukamoto et al. 2001). The distribution of *E. japonicus* larvae is centered in the upper 30 m layer during the day (Table 6) (Ida 1972, Sassa 2001, Tsukamoto et al. 2001), and partly overlaps that of *D. garmani* larvae in the 20 to 30 m layer. Larvae of *E. japonicus* ≤7.9 mm BL eat mainly copepod nauplii and shift to copepodite stages of *Oithona* spp. and *Paracalanus* spp. in larvae ≥8 mm BL (Table 6) (Funakoshi 1984, Uotani 1985, Mitani 1988, Uotani et al. 1988). The larvae of *D. garmani* ≤7.9 mm BL also consumed copepod nauplii in this study. However, the nauplius size differed markedly between *D. garmani* and *E. japonicus* and their diet overlap was not significant. In *E. japonicus* larvae, nauplii 50 to 110 µm wide accounted for >80% of the total number of prey, with the peak at 70 µm (Funakoshi 1984, Uotani 1985, Uotani et al. 1988, Hirakawa et al. 1997) (Table 6). This nauplius size is much smaller than those ingested by *D. garmani*, which had a width of 150 to 350 µm and accounted for 85.1% of the total prey number, while the 50 to 110 µm wide nauplii accounted for only 6.4% (Table 6). When they reached 8 mm BL, *D. garmani* started to feed mainly on appendicularian houses, which are not utilized by *E. japonicus*. Based on these results, we conclude that prey competition between *D. garmani* and the Japanese anchovy is not likely.

The impact that larval myctophids have on marine prey resources is important, but knowledge of their feeding ecology in the world's oceans is quite limited. Moreover, little is known about their prey abundance; for example, there is no record of the abundance of appendicularian houses in our study area. In the future, knowledge of (1) the abundance of myctophid larvae, (2) daily rations and gastric evacuation rates of these larvae, (3) daily production of their prey, and (4) prey densities in the field are needed to quantitatively estimate the impact of myctophids on marine prey resources in the transition region of the western North Pacific.

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