

Trophic ecology of three dominant myctophid species in the northern California Current region

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ABSTRACT: The feeding ecology of 3 dominant sympatric myctophid species (*Tarletonbeania crenularis*, *Diaphus theta*, and *Stenobrachius leucopsarus*) in the northern California Current System was investigated based on samples collected in June, August, and September of 2006. All 3 species fed predominantly on *Euphausia pacifica*, the most abundant euphausiid off the central Oregon coast. In contrast, the same 3 lanternfishes showed marked variation in utilization of other principal food categories, and stronger resource partitioning was evident in smaller individuals. The proportion of euphausiids in the diet of *T. crenularis* and *S. leucopsarus* gradually increased with increasing size. *D. theta* at intermediate sizes (31 to 60 mm) preyed heavily upon salps and hyperiid amphipods, whereas the largest specimens consumed mostly euphausiids. *S. leucopsarus* showed little changes in composition of principal food categories between months, while *T. crenularis* and *D. theta* consumed more hyperiid amphipods in June, euphausiids in August, and salps in September. No feeding on salps was recorded in *S. leucopsarus* for the entire study period. All 3 species showed variation in feeding intensity, stomach fullness, state of digestion, and number of prey species and prey items per stomach. A divergence in feeding strategies of these co-occurring lanternfishes appears to reflect their structural morphology and generally conforms to an ecological subdivision of this midwater family into 'active' and 'inactive' species. Active myctophids (*T. crenularis* and *D. theta*) consumed significantly larger amounts of protein-rich prey such as euphausiids, hyperiid amphipods, and salps, while inactive *S. leucopsarus* showed higher preference for slower-moving, lipid-rich *Neocalanus* copepods.

KEY WORDS: Myctophidae · Mesopelagic · *Tarletonbeania crenularis* · *Diaphus theta* · *Stenobrachius leucopsarus* · Feeding ecology · Ecomorphology · California Current

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INTRODUCTION

The northern California Current (NCC) is a highly productive and dynamic pelagic environment in which significant biophysical variability has been recorded on different time scales from seasonal to decadal (Chelton et al. 1982, McGowan et al. 1998). Primary and secondary production in this region fluctuate dramatically due to episodic variability in upwelling intensity throughout the year (Brickley & Thomas 2004, Barth et al. 2005) and are also strongly influenced by periodic El Niño and La Niña events and longer-term regime shifts (Peterson & Schwing 2003). This variability can have pervasive effects on all

trophic levels within this system. The region sustains valuable stocks of commercially exploited nektonic species such as salmon, anchovy, sardine, mackerel, albacore, and hake (Brodeur et al. 2003). In addition to these commercial species, a significant portion of the fish biomass in the NCC region is concentrated in what are called micronektonic fishes, i.e. small mesopelagic taxa such as myctophids, gonostomatids, bathylagids, and juvenile pelagic nekton (Brodeur et al. 2005).

Ubiquitous bioluminescent fishes of the family Myctophidae, commonly known as lanternfishes, are often the dominant component of micronektonic communities in the North Pacific, achieving very high abundances and biomass (Beamish et al. 1999, Brodeur &

Yamamura 2005). Myctophids represent an important trophic link between phytophagous zooplankton such as copepods and euphausiids and higher trophic level organisms such as salmon, tuna, seabirds, and marine mammals (see review in Brodeur & Yamamura 2005). They dominate the fish biomass in oceanic waters of the Northeast Pacific (Pearcy 1977, Gjøsæter & Kawaguchi 1980, Beamish et al. 1999), and their transport onto continental shelves represents an important flux of energy into these systems, as represented in food web models of the California Current (Field et al. 2006).

Three lanternfish species (*Tarletonbeania crenularis*, *Stenobranchius leucopsarus*, and *Diaphus theta*) form the bulk of micronekton fishes found in the NCC. These 3 species were reported to account for two-thirds of all fishes collected in Isaac-Kidd midwater trawl tows in the upper 200 m off Oregon, USA (Pearcy 1964, 1977). Due to their high biomass and widespread distribution and coupled with biological features such as diel vertical migration and strong zooplanktivory, myctophids are widely recognized as significant but poorly understood mediators in the transfer of organic matter from lower to higher trophic levels and to deeper ocean layers (Merrett & Roe 1974, Williams et al. 2001, Brodeur & Yamamura 2005). The sheer biomass of these fishes in the NCC clearly implies that they have a vast potential for competition for food resources with other co-occurring commercial fish species such as juvenile rockfishes *Sebastes* spp. and Pacific hake *Merluccius productus*, but the extent of such ecological interactions remains poorly understood.

In the North Pacific, feeding preferences and general trophodynamics of various lanternfish species were investigated in low- (Clarke 1973), temperate- (Gordon et al. 1985, Moku et al. 2000, Uchikawa et al. 2002, Watanabe et al. 2002), and high-latitude regions (Balanov 1994, Balanov et al. 1995, Nishimura et al. 1999), with more emphasis on the western part of the ocean. Off the coast of Oregon, feeding ecology of the principal myctophid species was studied more than 3 decades ago (Tyler & Pearcy 1975, Pearcy et al. 1979), and the only recent study examining their diet was a geographically limited investigation in Astoria Canyon off Oregon (Bosley et al. 2004). None of these studies examined aspects of trophic ecology that influence interactions among competing groups such as seasonal changes or diet overlap. Studies of such interactions among these species are needed as part of an attempt to understand broader marine ecological frameworks in the NCC. In the present study, we capitalized on extensive lanternfish collections made off Oregon and Washington to describe diet diversity and variability in 3 dominant myctophid species in the NCC region.

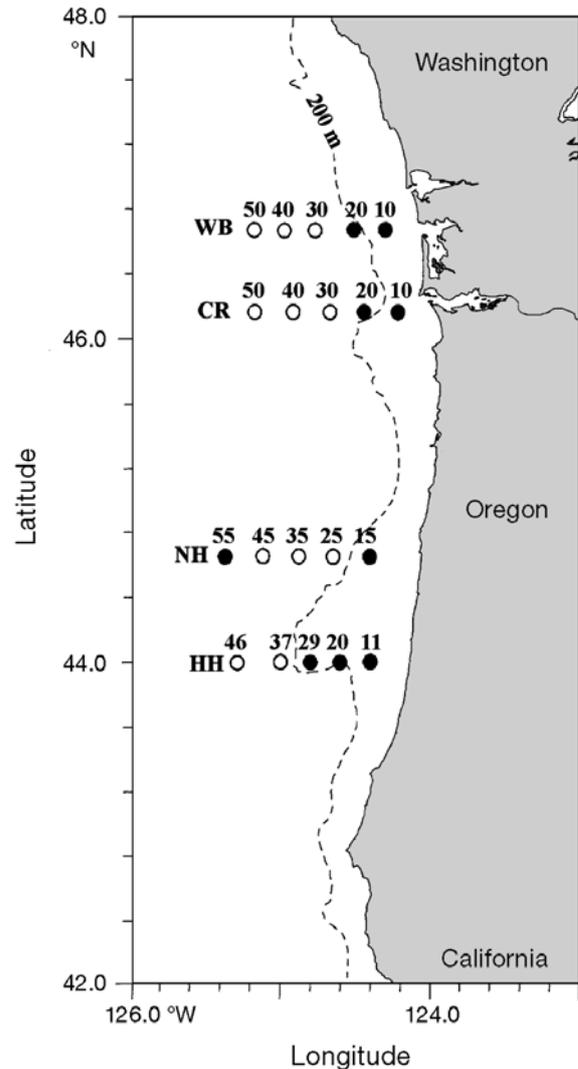


Fig. 1. Transects and stations of the Stock Assessment Improvement Program (SAIP) in 2006. Open circles indicate stations where myctophid specimens used in this study were collected

MATERIALS AND METHODS

Three lanternfish species were collected in June, August, and September during NOAA Stock Assessment Improvement Program (SAIP) cruises in 2006 off the coast of Oregon and Washington, USA. Specimens were collected along 4 transects perpendicular to the coast (Fig. 1) using a Nordic 264 rope trawl fished at night within the 30 to 50 m depth stratum. The trawl had an effective mouth opening of 12 m height and 28 m width (336 m²) based on net mensuration estimates (Emmett et al. 2004), with a 6.1 m long, 3 mm stretched knotless web liner sewn into the cod end. The number of specimens, size range for each species/station, and details of sampling locations are given in Table 1. Trawl samples, initially bulk-frozen at

sea, were thawed in the lab and sorted. The 3 species of myctophids were initially fixed in a 10% formalin/seawater solution and then transferred to 70% ethanol prior to diet analysis. Specimens for dissection were measured (standard length, SL, ± 0.1 mm) and weighed (± 0.0001 g).

The stomachs were then removed, placed into a small Petri dish and examined using a dissecting microscope. Prey organisms in the stomachs were identified to the lowest possible taxonomic level and counted. After blotting to remove excess water, wet weights (± 0.0001 g) were obtained for each prey taxon. Stomach fullness was recorded on a scale from 0 to 5, where 0 = empty, 1 = $\frac{1}{4}$ full, 2 = $\frac{1}{2}$ full, 3 = $\frac{3}{4}$ full; 4 = full, and 5 = distended with thin stomach wall. Even if only 1 small prey item was found, the stomach was classified as category 1. The state of digestion was determined as 0 = well digested, 1 = some items identifiable to major categories, 2 = most items identifiable to major categories, 3 = some items identifiable to species, 4 = most or all items identifiable to species.

Diet relationships of the 3 myctophid species were described using percentages for frequency of occurrence (F), number (Cn), and wet weight (WW) of ingested prey. Based on these indices, an Index of Relative Importance (IRI; Pinkas et al. 1971) was calculated as:

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

for each prey category. Feeding intensity was expressed as stomach content index (SCI):

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

We used 1-way analyses of variance (ANOVAs) to test for differences in feeding intensity and number of prey items/species per stomach, as well as indices of stomach fullness and state of digestion between different size classes and months.

Trophic relationships between different size groups of myctophids were examined using agglomerative hierarchical cluster analysis applied to a matrix of % WW contribution of particular prey category (rows) by size class of 1 of 3 lanternfish species (columns). The data matrix was transformed using arcsine square root transformation prior to analysis. We used a Bray-Curtis dissimilarity coefficient and an upper group middle averaging (UPGMA) algorithm to form the dendrograms. Clustering was conducted using Primer v. 5 (Clarke & Gorley 2001). We also used a multivariate analysis of similarities (ANOSIM) to test for differences in diet based on % WW of particular prey using different months, size groups, and geographical component (north versus south) as factors. The similarity matrix on WW composition of different prey (arcsine square root transformed) was calculated using Bray-Curtis coefficient and then subjected to ANOSIM analysis using Primer (Clarke & Green 1988). To determine which prey taxa were most likely responsible for the patterns detected by ANOSIM, we followed with a similarity percentages (SIMPER) analysis to define the discriminating species for each factor.

Table 1. *Tarletonbeania crenularis*, *Stenobranchius leucopsarus*, and *Diaphus theta*. Sampling location information and number and size range (SL, mm) of myctophid specimens examined. Dates given as mm/dd/yy

Stn	Date	Sampling locality		Bottom depth (m)	No. (size range)		
		Latitude (N)	Longitude (W)		<i>T. crenularis</i>	<i>S. leucopsarus</i>	<i>D. theta</i>
CR-30	6/17/06	46° 9' 36"	124° 40' 37"	732	50 (24–57)	104 (27–74)	12 (35–46)
CR40	6/16/06	46° 9' 43"	124° 55' 19"	853	48 (24–73)	–	–
CR-30	8/10/06	46° 9' 36"	124° 40' 37"	732	–	–	1 (52)
CR-40	8/8/06	46° 9' 43"	124° 55' 19"	853	32 (27–71)	–	–
HH-37	8/8/06	44° 0' 7"	125° 0' 0"	950	–	38 (36–70)	69 (40–67)
NH-25	8/9/06	33° 38' 60"	124° 39' 7"	297	–	–	8 (44–68)
NH-35	8/9/06	44° 39' 7"	124° 52' 48"	435	15 (32–64)	37 (18–47)	–
NH-45	8/8/06	44° 39' 11"	125° 7' 5"	700	–	18 (34–46)	1 (46)
CR-30	8/10/06	46° 9' 36"	124° 40' 37"	732	25 (30–71)	–	–
WB-30	8/11/06	46° 40' 5"	124° 46' 41"	293	27 (31–76)	10 (32–45)	10 (46–70)
WB-40	8/10/06	46° 40' 1"	124° 58' 55"	910	16 (29–70)	–	–
HH-37	9/25/06	44° 0' 7"	125° 0' 0"	950	10 (43–65)	5 (39–73)	18 (19–63)
HH-46	9/25/06	43° 59' 49"	125° 17' 13"	1600	10 (47–70)	–	15 (19–22)
NH-45	9/25/06			700	16 (39–79)	11 (30–48)	1 (54)
NH-35	9/26/06	44° 39' 7"	124° 52' 48"	435	5 (46–68)	3 (43–49)	1 (56)
CR-30	9/27/06	46° 9' 36"	124° 40' 37"	732	10 (44–75)	10 (43–73)	10 (43–57)
CR-40	9/27/06	46° 9' 43"	124° 55' 19"	853	10 (41–80)	9 (41–54)	19 (38–59)
CR-50	9/27/06	46° 9' 43"	124° 10' 41"	1423	44 (28–70)	52 (18–67)	32 (20–58)
WB-40	9/27/06	46° 40' 1"	124° 58' 55"	910	9 (43–64)	6 (40–67)	12 (36–56)
WB-50	9/29/06	46° 40' 12"	124° 10' 59"	1020	–	–	10 (40–57)

RESULTS

In total, stomach contents of 328 *Tarletonbeania crenularis*, 219 *Diaphus theta*, and 303 *Stenobranchius leucopsarus* were analyzed (Table 1). These 3 species overlapped broadly in their length–frequency distributions and had similar length–weight relationships (Fig. 2). In general, feeding incidence was high, with the number of full or partially full stomachs being highest in *D. theta* (96.6%) lowest in *T. crenularis* (86.9%), and intermediate in *S. leucopsarus* (90.4%).

The specimens of *Tarletonbeania crenularis*, ranging from 24 to 80 mm SL, yielded 4592 food items spread over 29 prey categories (Table 2). Food of *T. crenularis*

consisted primarily of euphausiids (70.0% WW), which, along with hyperiid amphipods (13.3%), salps (9.9%), and larvaceans (3.2%), comprised over 95% of the total food items consumed. Euphausiids were also the most frequently found items, followed by hyperiid amphipods, copepods, appendicularians, and salps. Minor prey categories of *T. crenularis* included ostracods, pteropods, and fish remains, which generally occurred at low frequencies (Table 2). Of the taxa identified to species, copepods displayed the highest species richness (11 species), followed by hyperiid amphipods (5 species). Based on overall IRI calculations, the most significant prey for *T. crenularis* were *Euphausia pacifica* (IRI 3532), *Oikopleura* spp. (1173),

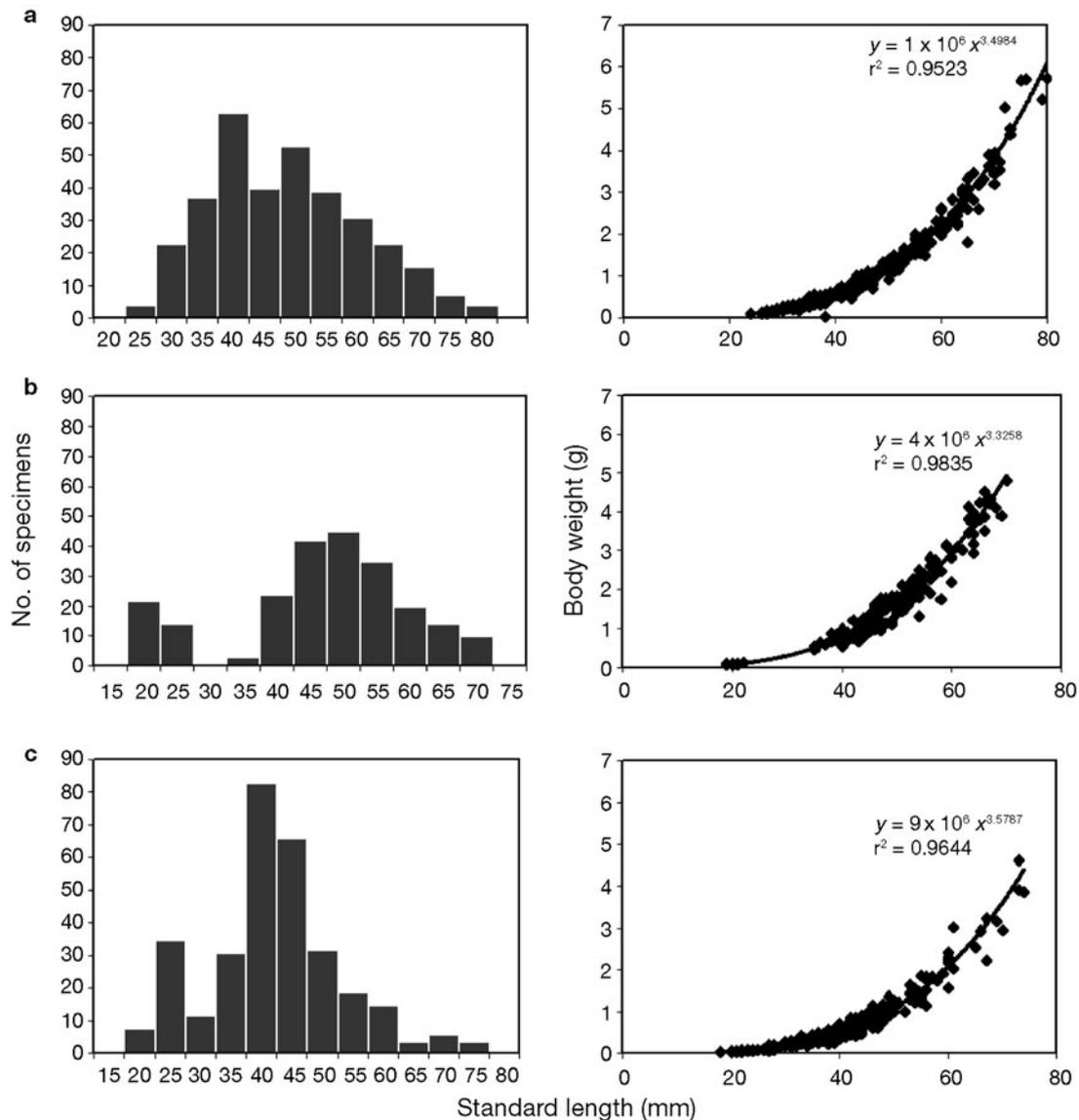


Fig. 2. *Tarletonbeania crenularis*, *Diaphus theta*, and *Stenobranchius leucopsarus*. Length–frequency distributions (left panels) and length–weight relationships (right panels) of (a) *T. crenularis*, (b) *D. theta*, (c) *S. leucopsarus* examined for stomach analysis

Table 2. *Tarletonbeania crenularis*, *Diaphus theta*, and *Stenobranchius leucopsarus*. Diet composition at all stations combined. See 'Materials and methods' for abbreviations

Prey species	<i>T. crenularis</i>						<i>D. theta</i>						<i>S. leucopsarus</i>					
	No.	WW (mg)	F (%)	Cn (%)	WW (%)	IRI	No.	WW (mg)	F (%)	Cn (%)	WW (%)	IRI	No.	WW (mg)	F (%)	Cn (%)	WW (%)	IRI
Radiolaria																		
Unidentified							1	1.7	0.5	0.1	0.1	< 1						
Scyphozoa																		
Unidentified medusa							6	0.9	1.4	0.5	0.0	< 1						
Euphausiacea																		
<i>Euphausia pacifica</i>	280	7046.8	34.1	6.2	68.9	2565	131	1953.8	39.7	11.5	61.9	2914	298	2180.6	50.5	41.9	79.8	6148
Euphausiacea larvae	465	110.9	7.6	10.2	1.1	86	48	18.5	8.7	4.2	0.6	42	30	37.8	3.0	4.2	1.4	17
Euphausiid eggs	3	0.1	0.3	0.1	0.0	< 1												
Unidentified euphausiids						3	3.4	0.9	0.3	0.1	< 1	6	16.1	1.7	0.8	0.6	2	
Total/combined	748	7157.8		16.5	70.0	3532	182	1975.7		15.9	6.6	3331	334	2234.5		47.0	81.8	6881
Amphipoda																		
<i>Cyphocaris challengeri</i>							1	0.8	0.5	0.1	0.0	< 1						
<i>Hyperia medusarum</i>	247	1073.4	12.5	5.4	10.5	199	19	116.5	5.9	1.7	3.7	32	19	68.5	4.3	2.7	2.5	22
<i>Platyscelis</i> sp.							1	15.6	0.5	0.1	0.5	< 1						
<i>Primno macropa</i>	3	21.8	0.6	0.1	0.2	< 1	6	9.3	2.7	0.5	0.3	2	1	3.9	0.3	0.1	0.1	< 1
<i>Streetsia challengeri</i>	1	17.7	0.3	0.0	0.2	< 1												
<i>Themisto pacifica</i>	32	89.4	8.5	0.7	0.9	13	21	85.4	6.4	1.8	2.7	29	41	141.3	9.6	5.8	5.2	105
<i>Vibilia australis</i>	5	33.2	1.5	0.1	0.3	1	1	3	0.5	0.1	0.1	< 1						
Unident. hyperiids	42	128.3	7.6	0.9	1.3	17	15	21.3	6.8	1.3	0.7	14	4	2.9	1.3	0.6	0.1	1
Total/combined	330	1363.8		7.3	13.3	595	64	251.9		5.6	8.0	275	65	216.6		9.1	7.9	261
Copepoda																		
<i>Aetideus pacifica</i>	1	2.5	0.3	0.0	0.0	< 1							10	17.3	2.6	1.4	0.6	5
<i>Calanus marshallae</i>	5	4.1	1.2	0.1	0.0	< 1	9	9.6	3.7	0.8	0.3	4	54	26.7	10.9	7.6	1.0	93
<i>Calanus pacificus</i>	71	38.7	9.1	1.6	0.4	18	19	13	7.8	1.7	0.4	16	6	8.5	2.0	0.8	0.3	2
<i>Candacia bipinnata</i>	31	49.5	7.3	0.7	0.5	9	2	0.1	0.5	0.2	0.0	< 1	1	0.2	0.3	0.1	0.0	< 1
<i>Centropages abdominalis</i>													7	21.1	2.3	1.0	0.8	4
<i>Euchaeta</i> sp.	1	1.5	0.3	0.0	0.0	< 1	8	23.1	3.2	0.7	0.7	5	1	0.6	0.3	0.1	0.0	< 1
<i>Gaidius minutus</i>													2	1.8	0.7	0.3	0.1	< 1
<i>Lucicutia flavicornis</i>																		
<i>Mesocalanus tenuicornis</i>							1	1.2	0.5	0.1	0.0	< 1						
<i>Metridia pacifica</i>	14	5.7	3.0	0.3	0.1	1	57	23.4	13.7	5.0	0.7	78	35	10.7	7.3	4.9	0.4	39
<i>Neocalanus</i> spp.	1	1.5	0.3	0.0	0.0	< 1	3	3.5	1.4	0.3	0.1	1	42	99.9	11.6	5.9	3.7	110
<i>Oithona</i> sp.	1	0.5	0.3	0.0	0.0	< 1												
<i>Oncaena</i> sp.							1	0.9	0.5	0.1	0.0	< 1						
<i>Paracalanus</i> sp.							2	0.6	0.9	0.2	0.0	< 1						
<i>Pseudocalanus</i> sp.	9	2.7	1.5	0.2	0.0	< 1	3	0.2	0.9	0.3	0.0	< 1	7	2.2	1.3	1.0	0.1	1
<i>Rhincalanus nasutus</i>	1	0.3	0.3	0.0	0.0	< 1							1	1.2	0.3	0.1	0.0	< 1
Parasitic copepods	4	1	0.9	0.1	0.0	< 1												
Unident. copepods	64	31.8	11.6	1.4	0.3	20	91	24.8	24.7	8.0	0.8	216	99	52.9	22.4	13.9	1.9	356
total/combined	203	139.8		4.5	1.4	143	196	100.4		17.1	3.2	706	265	243.1		37.3	8.9	2307
Insecta																		
Unidentified	1	0.5	0.3	0.0	0.0	< 1												
Ostracoda																		
Ostracoda	12	14.5	2.4	0.3	0.1	1	33	23.5	12.3	2.9	0.7	45	18	4.6	3.3	2.5	0.2	9
Decapoda																		
Zoea	1	11.9	0.3	0.0	0.1	< 1												
Bivalvia																		
Larvae							3	0.5	1.4	0.3	0.0	< 1						
Gastropoda																		
Larvae	1	0.6	0.3	0.0	0.0	< 1	1	0.4	0.5	0.1	0.0	< 1						
Pteropoda																		
<i>Limacina helicina</i>	5	3.5	1.5	0.1	0.0	< 1	74	58.2	20.1	6.5	1.8	167	9	5.4	2.3	1.3	0.2	3
Unidentified	1	8.9	0.3	0.0	0.1	< 1												
Cephalopoda																		
Paralarva	1	2.4	0.3	0.0	0.0	< 1												
Salps																		
<i>Salpa</i> spp.	645	1003.3	17.1	14.2	9.8	410	306	717.4	34.2	26.8	22.7	1695						
Appendicularia																		
<i>Oikopleura</i> spp.	2588	323.8	19.5	57.0	3.2	1173	274	20.5	14.2	24.0	0.6	348	19	1.1	2.0	2.7	0.0	5
Teleostei																		
Unident. fish remains	6	189.5	1.8	0.1	1.9	4												
Fish scales							3	5.1	1.4	0.3	0.2	1	1	0.2	0.3	0.1	0.0	< 1

hyperiid amphipods (595), *Salpa* spp. (410), and copepods (143), whereas the IRI for other zooplankton categories was mostly <1 (Table 2).

Twenty-five different types of prey from 1143 total identified food items were recorded from specimens of *Diaphus theta* that ranged from 19 to 70 mm SL. Various stages of *Euphausia pacifica* comprised over half of the total prey weight (62.6%), followed by *Salpa* spp. (22.7%) and hyperiid amphipods (8.3%), with the remaining prey categories totaling less than 9% (Table 2). Copepods were the most frequently found items, followed by euphausiids, salps, pteropods, hyperiids, appendicularians, and ostracods. Copepods were also the most diverse prey category (at least 10 species), with *Calanus pacificus*, *C. marshallae*, and *Metridia pacifica* occurring most frequently. At least 5 species of hyperiid amphipods were recorded in the diet of *D. theta*, with *Hyperia medusarum* and *Themisto pacifica* being dominant both by biomass and frequency of occurrence. The most significant prey types for *D. theta* were *E. pacifica* (IRI 2914) and *Salpa* spp. (1695), followed by copepods (706), *Oikopleura* spp. (348), hyperiid amphipods (275), and *Limacina helicina* (167; Table 2).

Twenty-two prey categories were identified in specimens of *Stenobrachius leucopsarus* in the 18 to 74 mm SL size range. The diet of this species consisted mainly of *Euphausia pacifica* (77.8%), and hyperiid amphipods (7.9%), with the remaining categories comprising <15%. The most frequently consumed prey were *E. pacifica*, copepods, and hyperiids, with the 2 latter categories also being the most diverse prey. IRI calculations indicated overall importance of just 2 main prey types, euphausiids (IRI: 6880) and copepods (2307) in the diet of *S. leucopsarus* (Table 2).

Ontogenetic changes in major diet categories

There was a strong tendency of *Tarletonbeania crenularis* toward reliance on just 1 type of prey, namely *Euphausia pacifica*, with increasing size (Fig. 3). The proportion of this prey in diets steadily increased from 20% in specimens 24–30 mm SL to 88% at 71–80 mm SL. The utilization of hyperiid amphipods showed the opposite trend. Hyperiid amphipods comprised up to 39% of WW biomass at 31–40 mm, but this proportion decreased to less than 2% in specimens 61–70 mm. At 20–40 mm SL, the WW biomass values for hyperiid amphipods were greater than for any other large prey category, being exceeded only by *E. pacifica* at larger sizes. A less pronounced decrease was evident in the consumption of salps with growth in *T. crenularis*. In general, the smallest specimens of *T. crenularis* fed heavily on salps, whose

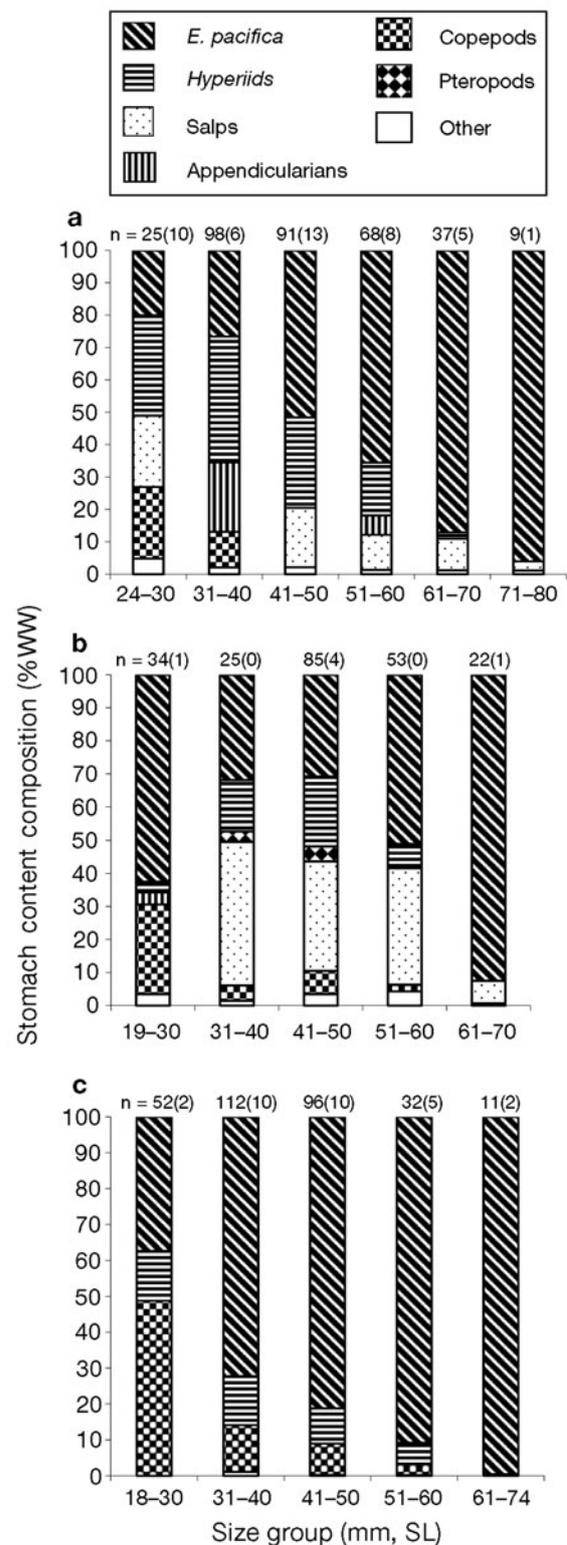


Fig. 3. *Tarletonbeania crenularis*, *Diaphus theta*, and *Stenobrachius leucopsarus*. Wet weight composition (% WW) of prey categories for different size groups in 3 myctophid species: (a) *T. crenularis*, (b) *D. theta*, (c) *S. leucopsarus*. The number of stomachs analyzed and the number of empty stomachs (in parentheses) is shown at the top of each graph

dietary contribution was identical to that of copepods. Unlike salps, which were consumed in detectable quantities even by the largest *T. crenularis*, copepods were only important for fish <40 mm and were found in negligible numbers in stomachs of larger specimens. The larvacean *Oikopleura* sp. was an important prey for 2 *T. crenularis* size categories: 31–40 mm (21.0% WW) and 51–60 mm (6.0%), but contributed less than 2% to the diet of other size categories.

The ontogenetic diet shift in *Stenobrachius leucopsarus* was generally similar to that in *Tarletonbeania crenularis* in that there was a clear increase in the consumption of *Euphausia pacifica* with increasing predator size. However, the dependence on *E. pacifica* with increasing predator size was even more pronounced for this species, where even at a size of 31–40 mm, euphausiids already comprised over 70% of the prey weight. Both hyperiid amphipods and copepods showed a clear decrease in WW percentages with growth of this species. Almost half of the diet (49%) in the smallest specimens of *S. leucopsarus* (18–30 mm SL) was composed of copepods (Fig. 3).

Diaphus theta showed a different pattern of diet change with increasing size. Unlike the other 2 species, its smallest size group (19–30 mm) fed heavily on small euphausiids (62%) and copepods (27%). However, reliance on *Euphausia pacifica* decreased at 31–60 mm, when this species started to consume large quantities of salps, with their dietary contribution ranging from 33 to 43% WW. The amount of hyperiid amphipods consumed by *D. theta* also peaked at these sizes, but the contribution of copepods was minor (2.0 to 7.1%). Among other major prey categories, the pteropod *Limacina helicina* was important in *D. theta* diets at sizes of 31–50 mm (3.1 to 4.5% WW), while *Oikopleura* spp. had a contribution similar to hyperiid amphipods consumed by specimens 19–30 mm SL (Fig. 3).

Between-month variability in major diet categories

Among the 3 myctophid species, *Euphausia pacifica* appeared to be the most important prey type for *Stenobrachius leucopsarus*, and its %WW in the fish stomachs remained practically unchanged for all 3 months, ranging from 77 to 87%, with higher values recorded in August. *Tarletonbeania crenularis* and *Diaphus theta* also consumed a higher percentage of *E. pacifica* during August than in other months. In June and September, however, the role of *E. pacifica* in the diet of *D. theta* was reduced relative to other types of prey (Fig. 4).

Hyperiid amphipods were more important prey for all 3 myctophids in early summer, with dietary contribution

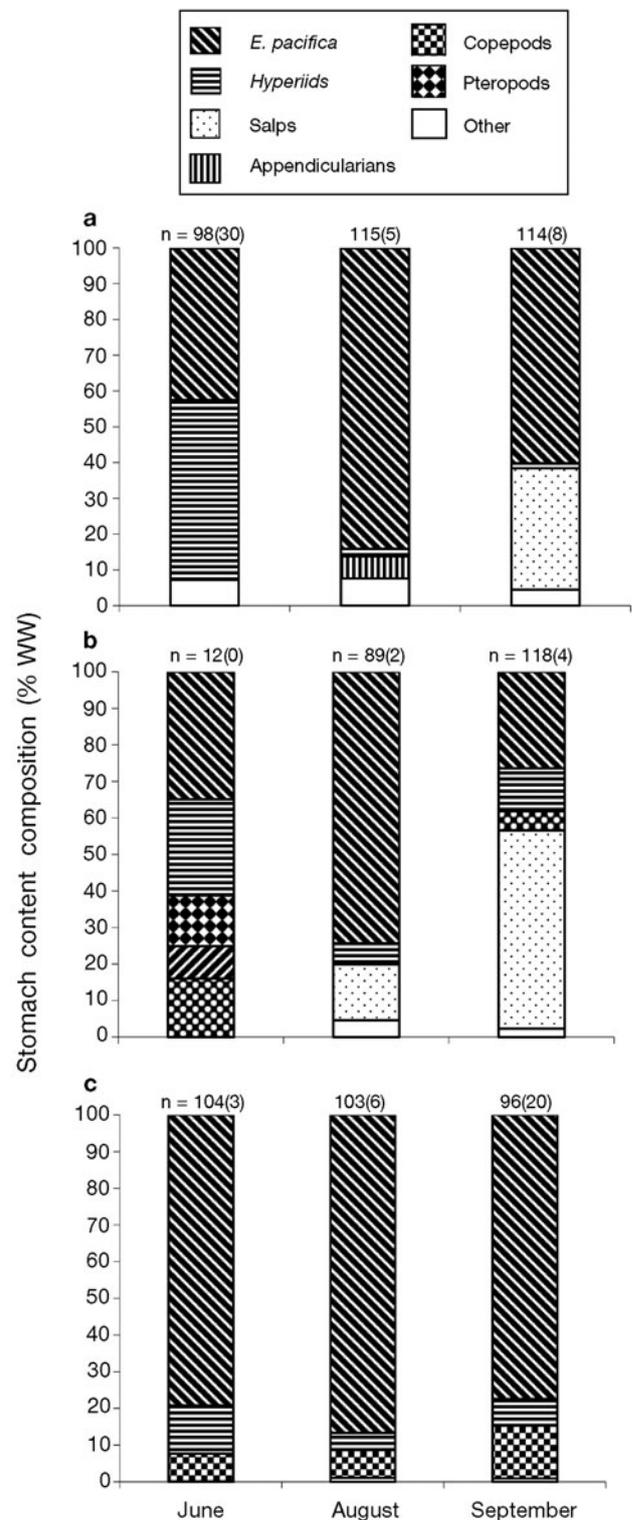


Fig. 4. *Tarletonbeania crenularis*, *Diaphus theta*, and *Stenobrachius leucopsarus*. Between-month variation in different prey categories (% WW) in 3 myctophid species: (a) *T. crenularis*, (b) *D. theta*, (c) *S. leucopsarus*. The number of stomachs analyzed and number of empty stomachs (in parentheses) is shown at the top of each graph

ranging from 13.5% in *Stenobrachius leucopsarus* to 50.3% in *Tarletonbeania crenularis*. In the following months, the proportion of hyperiid amphipods dropped most significantly in *T. crenularis* (to 2.1% in August and 1.5% in September), but these prey were still important for *Diaphus theta* (11.7% in September). Overall variations in hyperiid amphipod consumption were least pronounced in *S. leucopsarus*. This species fed more on hyperiids in June (13.2%) and September (7.3%), but less in August (4.7%). A somewhat similar pattern was evident for *D. theta*, with the highest proportion of hyperiids consumed in June, lowest in August, and intermediate values recorded in September (Fig. 4).

Throughout the study period, calanoid copepods did not play a significant role in the diet of *Tarletonbeania crenularis*. For *Diaphus theta*, however, copepods were somewhat important prey, increasing to 16.0% of total prey biomass in early summer, and then decreasing to less than 2% in August before slightly increasing again in September (5.3%). Variations in copepod biomass were much less pronounced in *Stenobrachius leucopsarus*, with nearly equal proportions consumed in June and August, and a doubling of those proportions in September.

Gelatinous zooplankters (*Salpa* spp.) were recorded as the most significant prey for *Diaphus theta*. Their most intense feeding on salps occurred during September, when salp biomass exceeded 50% of total zooplankton consumed. A lower proportion of salps (15.3%) was eaten by *D. theta* during August, and no

salps were found in specimens collected during June. A similar feeding pattern was found in *Tarletonbeania crenularis*, with 1 *Salpa* sp. specimen recorded in June, 37 in August, and 607 in September, when salps comprised 33.9% of the biomass of all ingested prey (Fig. 4). Unlike the other 2 myctophids, *Stenobrachius leucopsarus* did not feed on salps during the months investigated.

Feeding differences between size classes

With the exception of the largest specimens of *Stenobrachius leucopsarus* (61–74 mm SL), which showed high dissimilarity to all other specimens (possibly due to the small sample size), 3 distinct clusters were formed at a similarity of about 50% (Fig. 5). The bulk of *S. leucopsarus* specimens (18–60 mm SL) formed a cluster with *Tarletonbeania crenularis* (31–40 mm) and *Diaphus theta* (19–30 mm). Close grouping of most sizes of *S. leucopsarus* appeared to be a result of its less diverse diet, which did not include *Salpa* spp. or any significant amounts of *Oikopleura* and *Limacina*. Smaller specimens of *D. theta* (19–30 mm) and *T. crenularis* (31–40 mm SL), joining at a level of about 62% similarity, both fed on appendicularians, which comprised up to 21% WW of biomass for *T. crenularis* at that size range. Similar to *S. leucopsarus*, *D. theta* and *T. crenularis* at this size did not consume any significant amounts of salps.

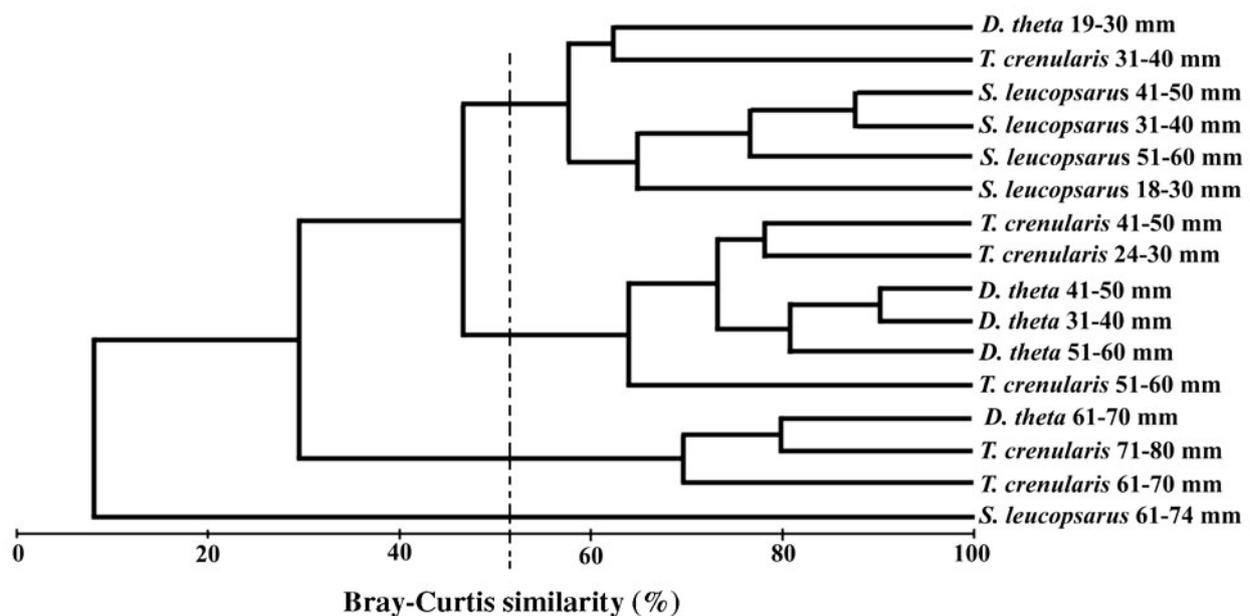


Fig. 5. *Tarletonbeania crenularis*, *Diaphus theta*, and *Stenobrachius leucopsarus*. Feeding differences between different size classes of 3 myctophid species based on WW composition (%) of prey categories. Dashed line indicates cut-off level for groups discussed in text

ranging from 2.0 to 4.4 and decreasing significantly with time. Compared to *Tarletonbeania crenularis* and *Stenobranchius leucopsarus*, total numbers of prey items for *D. theta* were intermediate, with minimal variation among months. Indices for stomach fullness and digestive state showed a significant decrease with increasing size.

Both the total number of prey items and prey species richness decreased from June to September in *Stenobranchius leucopsarus*, with highly significant variations. The number of prey items per stomach in *S. leucopsarus* was lowest among the 3 myctophid species, with mean values ranging from 1.7 to 3.7. Mean numbers of prey species consumed by *S. leucopsarus* were also low compared to the other 2 myctophid species and ranged from 1.3 to 1.9. Stomach fullness and state of digestion values also varied significantly between months, with both of these parameters decreasing steadily with time. On the other hand, changes in %BW were minimal and not significant for *S. leucopsarus* (Table 5).

Among 6 different size classes of *Tarletonbeania crenularis*, no significant variation in feeding intensity or number of prey items ingested was observed. Stomach fullness indices also showed no marked change; however, significant variation was detected in the number of prey species, which was somewhat greater at smaller sizes, and in the state of digestion, which had higher values in larger size classes (Table 6).

Table 5. *Tarletonbeania crenularis*, *Diaphus theta*, and *Stenobranchius leucopsarus*. Monthly variation in feeding parameters (mean \pm SD). SCI: stomach content index, ns: not significant

	June	August	September	p
<i>T. crenularis</i>				
SCI (% BW)	3.7 \pm 3.4	2.5 \pm 2.9	1.9 \pm 2.2	<0.0005
No. of prey items per stomach	12.1 \pm 17.5	25.1 \pm 46.4	10.5 \pm 13.0	<0.005
No. of prey species per stomach	1.8 \pm 0.8	2.0 \pm 1.1	1.7 \pm 0.9	ns
Stomach fullness	2.5 \pm 2.1	3.0 \pm 1.4	2.5 \pm 1.4	<0.05
State of digestion	3.1 \pm 0.8	2.9 \pm 0.9	2.7 \pm 1.2	<0.05
No. of specimens examined	98	115	114	
<i>D. theta</i>				
SCI (% BW)	1.4 \pm 0.7	1.3 \pm 1.5	1.2 \pm 1.18	ns
No. of prey items per stomach	8.7 \pm 4.1	6.3 \pm 10.3	5.8 \pm 4.5	ns
No. of prey species per stomach	4.4 \pm 1.7	2.3 \pm 1.2	2.0 \pm 1.1	<<0.0001
Stomach fullness	3.6 \pm 0.7	2.3 \pm 1.3	2.1 \pm 1.2	<<0.0001
State of digestion	3.2 \pm 0.4	2.9 \pm 1.1	2.5 \pm 1.1	<0.001
No. of specimens examined	12	89	118	
<i>S. leucopsarus</i>				
SCI (% BW)	1.9 \pm 1.8	1.9 \pm 2.2	1.5 \pm 1.9	ns
No. of prey items per stomach	3.7 \pm 2.1	2.4 \pm 1.7	1.7 \pm 0.9	<<0.0001
No. of prey species per stomach	1.9 \pm 1.0	1.6 \pm 0.9	1.3 \pm 0.5	<<0.0001
Stomach fullness	2.6 \pm 1.3	2.2 \pm 1.5	1.6 \pm 1.2	<<0.0001
State of digestion	3.3 \pm 0.7	3.1 \pm 1.1	2.6 \pm 1.1	<<0.0001
No. of specimens examined	104	103	96	

Changes in feeding intensity of *Diaphus theta* were highly significant, with the most intense feeding observed in the smallest specimens (18–30 mm SL) and the lowest values recorded in specimens of 31–60 mm SL. Significant variation was also seen in the number of species ingested per stomach and in the stomach fullness index, with the highest values observed in the smallest size classes. Variations in the state of digestion and number of prey items per stomach were negligible.

All feeding parameters except stomach fullness index were significantly different between size classes in *Stenobranchius leucopsarus*, with the most significant variations in mean number of prey items and number of prey species ingested per stomach. Both of these parameters were greatest at intermediate sizes (31–60 mm SL). Less important were changes in feeding intensity and state of digestion of stomach contents, with SCI values generally decreasing with growth and state of digestion showing an opposite trend (Table 6).

DISCUSSION

Numerous studies worldwide have reported lanternfishes as major consumers of zooplankton in midwater communities (Hopkins & Baird 1977, Hopkins & Gartner 1992, Pakhomov et al. 1996, Brodeur & Yamamura 2005). The 3 myctophids examined in our study fed almost exclusively on zooplankton. The only exception to this pattern occurred in the largest specimens of *Tarletonbeania crenularis*, which occasionally had fish remains in their stomachs. The fish consumed by *T. crenularis* was tentatively identified as *Lipolagus ochotensis*, a common midwater bathylagid found off Oregon.

It is relatively well established that trophic competition in myctophid communities can be significantly reduced through both inter- and intraspecific resource partitioning (Hopkins & Gartner 1992, Gartner et al. 1997), and recent reports have indicated differential feeding patterns in lanternfish larvae as well (Conley & Hopkins 2004, Sassa & Kawaguchi 2005).

In our study, the most common and abundant euphausiid in oceanic waters off Oregon, *Euphausia pacifica*, was by far the most important prey for all 3 species based on IRI val-

Table 6. *Tarletonbeania crenularis*, *Diaphus theta*, and *Stenobrachius leucopsarus*. Variability in feeding parameters between different size groups (SL) of 3 myctophids (mean \pm SD). SCI: stomach content index

<i>T. crenularis</i>	24–30 mm	31–40 mm	41–50 mm	51–60 mm	61–70 mm	71–80 mm	p
SCI (%)	3.1 \pm 2.6	2.0 \pm 2.7	2.9 \pm 2.6	2.6 \pm 3.0	2.5 \pm 2.9	5.3 \pm 4.7	ns
No. of prey items per stomach	12.6 \pm 16.4	21.3 \pm 32.1	10.5 \pm 11.7	21.8 \pm 52.7	12.3 \pm 19.1	10.5 \pm 10.4	ns
No. of prey species per stomach	2.0 \pm 1.0	2.0 \pm 1.0	2.0 \pm 1.0	1.7 \pm 1.0	1.4 \pm 0.8	2.1 \pm 1.2	<0.05
Stomach fullness	2.0 \pm 2.0	2.5 \pm 1.4	2.8 \pm 1.8	2.7 \pm 1.8	2.8 \pm 1.8	3.8 \pm 1.6	ns
State of digestion	2.8 \pm 0.9	2.6 \pm 1.0	3.0 \pm 0.9	3.1 \pm 1.2	3.1 \pm 1.2	3.2 \pm 0.9	<0.05
<i>D. theta</i>	19–30 mm	31–40 mm	41–50 mm	51–60 mm	61–70 mm		p
SCI (%)	2.6 \pm 1.0	1.1 \pm 1.1	1.0 \pm 0.9	1.0 \pm 1.4	1.4 \pm 1.7		<<0.0001
No. of prey items per stomach	8.8 \pm 3.5	4.3 \pm 3.5	5.9 \pm 6.9	7.2 \pm 11.9	3.7 \pm 3.1		ns
No. of prey species per stomach	3.1 \pm 0.9	2.0 \pm 1.2	2.4 \pm 1.5	2.3 \pm 1.2	1.5 \pm 0.9		<<0.0001
Stomach fullness	2.8 \pm 1.2	2.2 \pm 1.2	2.2 \pm 1.2	1.9 \pm 1.1	2.6 \pm 1.6		<0.01
State of digestion	2.8 \pm 0.9	2.7 \pm 0.8	2.6 \pm 1.1	2.5 \pm 1.3	2.8 \pm 1.2		ns
<i>S. leucopsarus</i>	18–30 mm	31–40 mm	41–50 mm	51–60 mm	61–74 mm		p
SCI (%)	2.4 \pm 2.5	1.8 \pm 1.9	1.6 \pm 1.8	1.7 \pm 1.9	0.5 \pm 0.5		<0.05
No. of prey items per stomach	1.6 \pm 1.1	3.3 \pm 2.0	2.7 \pm 2.0	2.3 \pm 1.5	1.7 \pm 1.0		<<0.0001
No. of prey species per stomach	1.2 \pm 0.4	1.8 \pm 0.9	1.7 \pm 1.0	1.5 \pm 0.6	1.1 \pm 0.3		<0.0001
Stomach fullness	1.9 \pm 1.0	2.2 \pm 1.3	2.2 \pm 1.4	2.5 \pm 2.0	2.2 \pm 1.6		ns
State of digestion	2.6 \pm 0.9	3.1 \pm 0.9	3.1 \pm 1.1	3.2 \pm 1.2	3.1 \pm 1.5		<0.05

ues. This accorded with findings of earlier myctophid diet studies at similar latitudes in the Pacific, including those of *Diaphus* (Kosenok et al. 2006), *Notoscopelus* (Uchikawa et al. 2002), *Stenobrachius* (Moku et al. 2000, Balanov et al. 1995), and *Triphoturus* (Imsand 1981). At the same time, dietary differences are more apparent in smaller individuals of our 3 studied species, suggesting stronger competition and resource partitioning prior to the period when all species are able to consume larger, agile, and most abundant prey such as euphausiids.

The higher proportion of euphausiids in all 3 species during August generally agrees with observations of their peak of abundance during late summer (Gómez-Gutiérrez et al. 2005). Alternatively, the mean lengths of August specimens of *Diaphus theta* were significantly greater than those examined in June and September. This may be another reason for the higher proportion of euphausiids consumed during August in this species, considering the patterns in ontogenetic diet shifts observed here and elsewhere (Tyler & Pearcy 1975). However, this would not be the case for *Tarletonbeania crenularis*, in which the mean length of August specimens was not significantly different from those of either June or September.

Copepods were the next most important food category for *Stenobrachius leucopsarus* after euphausiids, similar to what was found for this species in both southern (Collard 1970, Cailliet 1972, Cailliet & Ebeling 1990) and northern regions (Tyler & Pearcy 1975,

Pearcy et al. 1979, Bosley et al. 2004) of the California Current. Interestingly, feeding studies from other regions (e.g. Bering Sea) have repeatedly shown a higher prevalence of copepod biomass in the diet of this species (Gorbatenko & Il'inskii 1991, Balanov 1994). A recent study of *S. leucopsarus* in the Bering Sea suggested that copepods can be important prey items in some seasons (e.g. spring), whereas euphausiids are more important diet items later in the year (Tanimata et al. 2008).

The population of *Stenobrachius leucopsarus* off the coast of Oregon consists of non-migratory and vertically migrating individuals (Pearcy et al. 1979). Our data on the migrating portion of the *S. leucopsarus* population is consistent with earlier findings of ontogenetic diet shift in this species as well as total number of prey items in stomachs (Pearcy et al. 1979). However, Pearcy et al. (1979) recorded a noticeably higher number of copepod prey species, but this was likely due to their larger sample size, as well as their broader vertical coverage of the water column. Overall, copepods were the most species-rich group in all 3 myctophid species examined in our study, with each having 10 to 11 copepod taxa in their diet. In general, the copepod prey species represented a typical species mixture from the offshore copepod assemblage consisting of both Transition Zone species and temperate-subtropical neritic taxa (Morgan et al. 2003).

Based on IRI indices, selectivity for different types of prey was more evenly distributed in *Tarletonbeania*

crenularis and *Diaphus theta*, indicating a more balanced overall food spectrum than in *Stenobranchius leucopsarus*, which had only 2 major prey categories. Beyond the predominance of *Euphausia pacifica*, which had very similar IRI values in both *T. crenularis* and *D. theta*, the 2 species showed some differences in diet, with larvaceans, hyperiids, and salps (in decreasing order of importance) occurring more in *T. crenularis* and salps, copepods, hyperiids, and larvaceans in *D. theta*. Of the less common prey categories, *D. theta* also showed a clear selectivity for shelled zooplankton, such as ostracods and the pteropod *Limacina helicina*.

Night-time vertical distribution of 3 dominant myctophid species off Oregon can be different in terms of their maximum abundance (Pearcy 1964). In general, *Tarletonbeania crenularis* showed the shallowest distribution, with greatest number of individuals recorded above 10 m, *Diaphus theta* was most abundant between 10 and 25 m, and *Stenobranchius leucopsarus* between 25 and 30 m. Although inferred from non-closing fishing gear, these data suggest vertical partitioning of the night-time habitat of these fishes. Such habitat subdivision may affect their night-time feeding, if zooplankton prey species display similar patterns of water column partitioning. However, available information indicates that these lanternfishes are likely to find similar assemblages of prey during their night-time presence in the mixed layer (Mackas & Tsuda 1999).

In view of the differences in feeding between these myctophids, we also note that they belong to 2 different eco-morphological types, according to an informal classification based on *in situ* observations and estimates of swimming ability (Barham 1971). These include the so-called active myctophids, characterized by the presence of a well-developed, gas-filled swimbladder (can be absent in some species) and a relatively low lipid content. Other features of the active lanternfish type include a firm body, often with a slender caudal peduncle, large eyes, and silvery scales. These species are active diel vertical migrants and strongly follow isolumens. Some examples of active myctophids include *Myctophum*, *Protomyctophum*, *Tarletonbeania*, and *Benthoosema* (Barham 1971, Butler & Pearcy 1972, Neighbors & Nafpaktitis 1982). In contrast, inactive myctophids are characterized by a dark body with a deep caudal peduncle, flabby muscles, and relatively small eyes. These species can also migrate to the surface at night, but usually stay deeper and are not attracted by light. Inactive lanternfishes such as *Stenobranchius leucopsarus*, *Triphoturus mexicanus*, and numerous species of *Lampanyctus* are less-active swimmers, have a much higher body lipid content, and often have a fat-invested swimbladder. Species of *Diaphus* do not fall readily into either of the

2 types, occupying a somewhat intermediate position (Bekker 1983). Subsequent studies provided more evidence that active and inactive myctophids differ significantly by lipid and water content and also by the type of lipids they accumulate (wax esters versus triglycerides; Neighbors & Nafpaktitis 1982).

In a typical inactive myctophid, such as *Stenobranchius leucopsarus*, lipids are composed of large quantities of low-density wax esters, which, coupled with a high body-water content, serve as a buoyancy mechanism (Butler & Pearcy 1972, Neighbors & Nafpaktitis 1982). In contrast, triglyceride-rich *Diaphus theta* uses stored lipids as an energy reserve and not for buoyancy control, which indicates its need for more active swimming (Neighbors & Nafpaktitis 1982). *Tarletonbeania crenularis*, as a typical active myctophid, is characterized by firm muscles and skin, non-deciduous scales, and the general appearance of a good swimmer. Morphological differences between the active *T. crenularis* and the inactive *S. leucopsarus* were very apparent upon visual examination of specimens collected from the Nordic trawl: *T. crenularis* showed the best resistance to abrasion in the Nordic trawl cod-end and was often retrieved in excellent condition, whereas the lipid-rich, watery bodies of *S. leucopsarus* suffered the most damage, with most specimens devoid of skin and showing signs of evisceration. Specimens of *D. theta* showed a somewhat intermediate condition during sampling.

Our results suggest that variations in diet among these lanternfishes are a reflection of their structural morphology, differing energy requirements, and general life strategies. In our study, the active myctophid *Tarletonbeania crenularis* consumed significantly higher amounts of fast-moving, protein-rich plankton, such as euphausiids and hyperiid amphipods. *Stenobranchius leucopsarus* consumed the least biomass of these 3 prey taxa, and *Diaphus theta* was intermediate between the other 2. The higher feeding activity of *D. theta* compared to *S. leucopsarus* was also noted in an earlier study (Moku et al. 2000). Considering that species with stronger swimming abilities would presumably have a more extensive foraging range, it is not surprising that *T. crenularis* showed the highest diversity of prey, followed by *D. theta* and *S. leucopsarus*; however, these differences were not pronounced.

In the present study, the more active myctophids *Tarletonbeania crenularis* and *Diaphus theta* consumed significant quantities of salps, a feeding resource apparently containing up to 80% protein (% of total organic content, 6.6% dry weight), but very little lipid (7.6% of total organic content, 0.6% dry weight; Madin et al. 1981). In the Atlantic Ocean, another component of the active group, *Ceratoscopelus warmingtonii*, was found to prey heavily on salps (Kinzer &

Schulz 1985), which comprised 12% by number of the prey items consumed, a value very similar to our data for *T. crenularis*. In sharp contrast, inactive *Stenobrachius leucopsarus* completely avoided eating salps during all months investigated. The most recent study of *S. leucopsarus* in the western part of the North Pacific also did not list salps as part of the diet of this species (Tanimata et al. 2008).

Salp feeding by the active myctophids *Tarletonbeania crenularis* and *Diaphus theta* is rather new information, since gelatinous zooplankton were not previously reported as a significant food component in these species (Tyler & Pearcy 1975). Similarly, the diet of *D. theta* off the Kuril Islands in Russia contained only a minor proportion of salps (Kosenok et al. 2006). On the other hand, salps have often been categorized as unidentified gelatinous material (Mauchline & Gordon 1983), thus obscuring their actual proportions in diets. The significance of salps in feeding has been reported for a number of fish groups, and their importance was stressed for continental slopes and regions around seamounts, islands, and underwater rises, where concentrations can be particularly high (Kashkina 1986). A number of salp species were present off Oregon throughout the year, with maximum abundances for some species (*Salpa fusiformis*, *Iasis zonaria*) recorded during intense summer upwelling conditions, while other species occurred in higher densities during winter (*Thalia democratica*, *Pegea confederata*; Hubbard & Pearcy 1971).

Recent modeling of seasonal food webs on Oregon's inner shelf indicates that large gelatinous zooplankton such as jellyfishes can play a significant role as zooplankton consumers. At the same time, large jellyfishes are rarely consumed by potential predators, leading to a significant diversion of zooplankton production away from higher trophic levels (Ruzicka et al. 2007). Away from the coastal zone, where abundances of smaller gelatinous organisms such as salps or larvaceans are more pronounced, the situation can be drastically different. Considering the extreme growth rates of these organisms (Heron 1972), short generation times, and high fecundities (Alldredge & Madin 1982), as well as their apparent consumption by myctophids in the NCC, models of the pelagic ecosystem will need to consider the energy pathways between these components of the oceanic environment.

The high lipid content, watery muscle tissue, and fat-filled swimbladder suggest less efficient swimming in *Stenobrachius leucopsarus*, and are likely the main causes for its selectivity of less active, slower-moving prey. We observed that *S. leucopsarus* showed a marked preference for large, lipid-rich, deeper-dwelling copepods such as *Neocalanus* (*N. cristatus*

and *N. plumchrus*), which, in terms of WW biomass, comprised over 50% of all copepod specimens identified. Similar selectivity for *Neocalanus* spp. by *S. leucopsarus* was noted in an earlier study off Oregon (Tyler & Pearcy 1975) as well as in the western Pacific (Moku et al. 2000). Adult *Neocalanus* spp. are known to spend late summer, autumn, and early winter at depths of 400 to 2000 m (Miller et al. 1984, Mackas & Tsuda 1999). *Neocalanus* copepods (all adults) found in *S. leucopsarus* stomachs showed a different degree of digestion and were likely consumed at depth prior to or during ascent to surface layers.

Many pelagic copepods contain large quantities of wax esters as energy reserves (Lewis 1967, Falk-Petersen et al. 1987). For diapausing copepods, large sacs of wax esters are suggested as an adaptation for achieving neutral buoyancy in cold, deep waters, so they can minimize energy expenditure while maintaining depth (Lee et al. 2006). Similarly, wax esters are the principal constituents of lipids in *Stenobrachius leucopsarus*. A study on several myctophids suggested that wax esters in pelagic copepods of the genera *Neocalanus* and *Eucalanus* can be directly incorporated into the lipids of lanternfishes (Saito & Murata 1998). This information may help to explain the selectivity for large, lipid-rich copepods and the avoidance of lipid-poor salps by *S. leucopsarus*. Another inactive myctophid, *Lampanyctus alatus*, in the eastern Gulf of Mexico showed a similar high selectivity for large, lipid-rich copepods of the genus *Pleuromamma* (Hopkins & Baird 1985). Further observations on the feeding ecology of particular midwater species and/or ecological groups, put into the context of structural morphology, biochemical composition, and general lifestyles, are needed to better understand the ecomorphological correlates and trophic relationships in the mesopelagic zone.

The current study provides information on lanternfish feeding during summer and early autumn, but no work to date has addressed trophic interactions in this family during winter months. Although there is apparently little change in the offshore copepod communities off Oregon and Washington between summer and winter seasons (Morgan et al. 2003), temporal variation in abundance of other zooplankton groups could be quite pronounced, potentially affecting diet and other trophic characteristics of principal micronektonic fishes. Thus, future emphasis on lanternfish diel feeding chronology, daily rations, standing stocks, and abundance, along with zooplankton prey abundance in the environment, is required to better understand the feeding ecology of these fishes, their actual role as competitors to commercial species, and their overall importance in the oceanic food webs and ecosystem dynamics.

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