

# Food habits of threadfin hakeling *Laemonema longipes* along the Pacific coast of northern Japan

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*Food habits of threadfin hakeling Laemonema longipes, the dominant demersal fish in the upper continental slope of the western sub-Arctic North Pacific, were described based upon >1400 specimens collected off north-eastern Honshu Island and south-eastern Hokkaido Island, Japan. Threadfin hakeling depended exclusively on pelagic organisms including copepods Neocalanus cristatus, Euphausia pacifica, shrimps Sergestes similis, firefly squid Watasenia scintillans and myctophids Diaphus theta. Threadfin hakeling showed a clear size-dependent dietary variation, with mesozooplankton and shrimps being important for small- and medium-sized fish ( $\leq 400$  mm standard length (SL)), and myctophids being important for large-sized fish ( $> 400$  mm SL). Since all of these prey undertake diurnal vertical migration, it was concluded that threadfin hakeling take an important role in capturing energy and materials transported from the epipelagic zone to the bathypelagic layer over the upper continental slope. Dietary variation among different areas, seasons and depths were also examined. Of these, areal difference was rather obscure reflecting common prey field in the Tohoku and Doto areas under the prevalence of the North Pacific Intermediate Water, whereas clear seasonal difference was found in the Doto area; the o-group of walleye pollock Theragra chalcogramma was ingested only in the late summer and early autumn in this area.*

**Keywords:** moridae, upper continental slope, bathypelagic zone, micronekton, ontogenetic difference in diet, walleye pollock

Submitted 23 August 2010; accepted 31 January 2011; first published online 13 July 2011

## INTRODUCTION

Threadfin hakeling *Laemonema longipes* Schmidt is a benthopelagic morid fish distributed in the western North Pacific, extending from central Japan through the Okhotsk Sea to the Bering Sea (Cohen *et al.*, 1990). It is one of the dominant species in the upper and middle continental slope area of the Pacific coast of northern Japan, (Yamamura *et al.*, 1998). While being an important prey for marine mammals including fur seal (Wada, 1971), Baird's (Walker *et al.*, 2002; Ohizumi *et al.*, 2003) and sperm whales (Kawakami, 1980), it is one of the few commercially utilized morid species (Meléndez & Markle, 1997). Japanese and Russian trawlers have landed between 33 and 48 thousand tons annually during the last decade (Narimatsu *et al.*, 2008). This species spawns in the subtropical waters adjacent to the Izu Islands, off central Honshu Island. Then the juveniles migrate north along the continental slopes off Tohoku area, north-eastern Honshu Island to the feeding area off southern Hokkaido Island and Kurile Archipelago (Savin, 1993; Nobetsu, 2002), where adults are distributed during summer and autumn. More recently, Hattori *et al.* (2009) pointed out that immature hakeling  $\leq 35$  cm standard length (SL) utilize the southern Tohoku area ( $35^{\circ}50' - 38^{\circ}50'N$ ) as a nursery ground.

Threadfin hakeling may be assumed to be an important component of the upper slope ecosystem in the western

North Pacific. Information on its trophic relationships provides insights into the flow of materials in the relatively unknown upper slope habitat. Very limited information has been available on the feeding habits of this species, and the difficulty that previous authors studying food habits of deep-sea macrourid and morid fish encountered was extremely high incidence of everted stomachs and those with regurgitated contents due to decompressed gas bladders (e.g. Drazen *et al.*, 2001; Jones, 2008). Yokota & Kawasaki (1990) reported that threadfin hakeling from the Tohoku area prey mainly on copepods, euphausiids and lantern fish, whereas Yamamura and his colleagues documented this species as an important predator for *Euphausia pacifica* and micronekton including myctophids and mesopelagic shrimps off Sendai Bay, Tohoku area (Yamamura *et al.*, 1998; Yamamura & Inada, 2001). More recently, Yamauchi *et al.* (2008) found copepods and euphausiids from a total of 13 stomachs of threadfin hakeling captured off the southern coast of Hokkaido Island. The present study provides detailed information on taxonomic composition, spatial, seasonal, ontogenetic and bathymetric variation of diet of threadfin hakeling sampled off north-eastern Honshu Island (Tohoku area) and off south-eastern Hokkaido Island (Doto area).

## MATERIALS AND METHODS

Samples used in the present study were collected in the Tohoku and Doto areas during 1989–2005 (Figure 1). The depths sampled ranged widely both in the Tohoku

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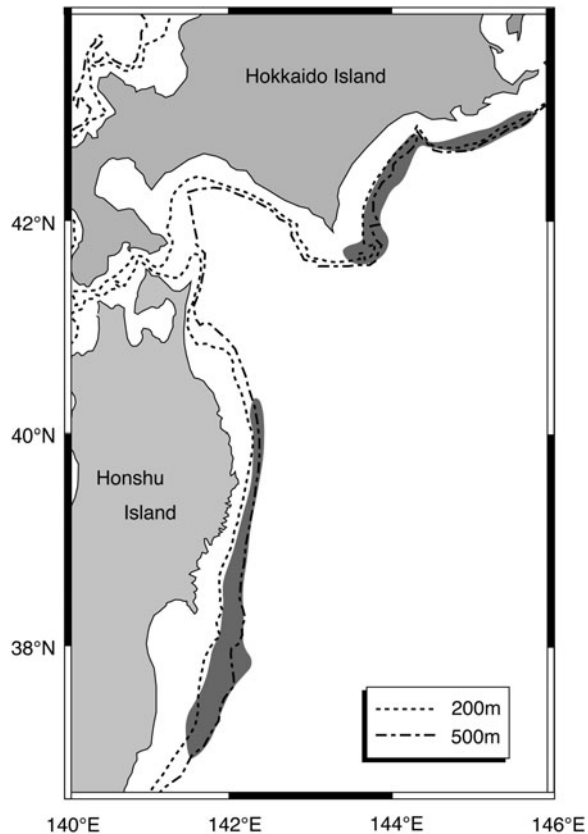


Fig. 1. Map showing the areas of sample collection (shaded areas).

(172–882 m in bottom depth) and Doto (180–874 m) areas. Of the 1413 fish included in this study, 1158 (82.0%) and 149 (10.6%) were taken by bottom trawls and mid-water trawls operated by research vessels, respectively. In addition, 51 (3.6%) and 55 (3.9%) specimens were obtained by bottom trawls and bottom gill nets operated by commercial vessels, respectively. The greatest portion of the fish was collected during daytime, although the exact time of commercial fishing was not known. High incidence (usually >99%) of either everted stomachs, or regurgitated stomachs retained in their mouths, were observed. Therefore, from the catch of each tow of the research vessel, and commercial specimens landed at the fish market, up to 30 fish with neither sign of stomach eversion nor regurgitation were sampled for diet analysis. These were then measured and weighed to the nearest 1 mm and 1 g, respectively, either on-board or in the laboratory. Stomachs were preserved in a 10% formalin–seawater solution. In the laboratory, stomachs were cut open in a Petri dish filled with water, and the contents were removed from the stomach and pylorus. The stomach contents were placed on filter paper, and the excess water was removed by suction. The contents were then sorted and identified to the species level under a stereoscopic microscope to the lowest taxon possible. Sometimes advanced digestive stages of prey prevented us from enumerating prey, especially in copepods. So we did not assess numerical composition of the diets. Each item was dried separately in a drying oven at 52°C for 24 hours and in a desiccator for 36 to 48 hours, and then weighed to the nearest 1 mg.

Data were divided by 10 cm size-class in SL of fish, season (spring and summer: from March to August; autumn and

winter: from September to February) and bottom depth of stations sampled (shallow: ≤450 m; deep: >450 m). The diets were compared using percentage similarity (PS):

$$PS = \sum_i |p_i - q_i|,$$

where  $p_i$  and  $q_i$  are percentage contribution in dry weight (DW) of  $i$ -th prey category, respectively (Schoener, 1970). For the calculation of PS, the following prey categories were included: squids, euphausiids, mysids, euphausiids, shrimps, chaetognaths, mesopelagic fish and walleye pollock. The pair of subsamples with a PS value less than 40% was considered to be substantially different following the criteria given by Ross (1986).

## RESULTS

### Size–frequency distribution of fish

The body lengths of the fish sampled for stomach contents analyses were 37–606 mm SL. The length–frequency distribution of threadfin hakeling clearly differed by area (Figure 2). Whereas a wide size-range of fish were sampled in the Tohoku area, the greatest portion of fish from the Doto area was >400 mm SL fish (89.5%). Most specimens were sampled during spring and early summer (April–July) and were the most numerous in both areas (82.5% and 57.9% in the Tohoku and Doto area, respectively). This geographical and seasonal unevenness in sample numbers reflects the life history of threadfin hakeling stated above.

### Overall diet

Threadfin hakeling depended exclusively upon pelagic and planktonic organisms. In total 46 prey categories were identified from the stomachs of a total of 1413 fish examined (Table 1). Of these, six were benthic or benthopelagic organisms, but represented only <1% in dry weight (%DW) of the diet in any of predator size-classes. Crustacea was most diverse including at least 20 taxa; copepods, euphausiids and decapods were important in this class. Copepods accounted for 0.6 to 45.9%DW of the total diets. *Neocalanus cristatus* (Kröyer) was predominant making up >95% of identifiable copepods in any of the fish size-classes. Euphausiids represented 5.7 to 45.3%DW of the total diets, and *Euphausia pacifica* Hansen was the only significant species (>80%). The sergestid shrimp *Sergestes similis* Hansen was also an important prey item making up >90% of decapod crustacean mass. Fish was second in terms of species number represented by at least 18 species. Eleven of these species occurred only in the stomachs of >400 mm SL fish. Myctophidae was the most important family accounting for >85%DW of fish ingested by any size-class. The most important myctophid was *Diaphus theta* Eigenman and Eigenman, which occurred in all size-classes of fish. Other important species were *Lampanyctus jordani* Gilbert and *L. regalis* Gilbert. Most of the other fish species ingested were also micronekton including gonostomatids, bathylagids and paralepidids. An exception was walleye pollock *Theragra chalcogramma* (Pallas), which occurred in the stomachs of >300 mm SL fish. The pollock found in stomachs of the hakeling were yearlings with standard

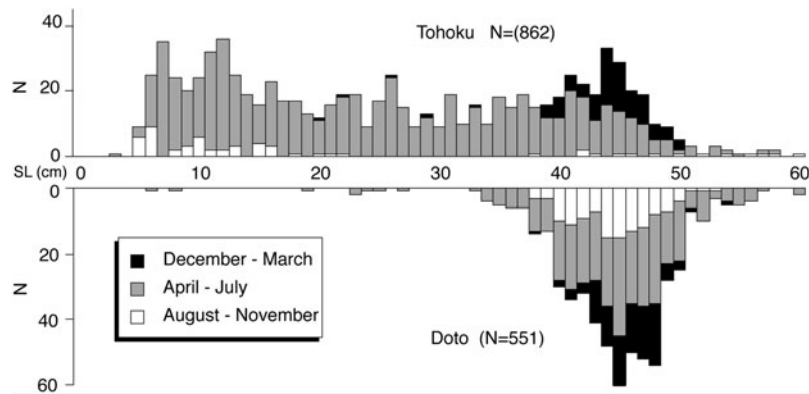


Fig. 2. Body length–frequency distribution of threadfin hakeling, whose stomachs were examined for contents. Specimens from different periods of year are represented by different colours.

lengths of 84 to 118 mm. Japanese anchovy *Engraulis japonicus* (Houttuyn) also occurred, but never as whole specimens, only heads or tails. This suggested that they were not preyed upon but scavenged after they were discarded by Japanese common squids *Todarodes pacificus* Steenstrup, as reported for walleye pollock (Yamamura *et al.*, 2002). Squid was also an important prey taxon, in which firefly squid *Watasenia scintillans* (Berry) predominated (89.0%).

### Ontogenetic variation

The diet of threadfin hakeling changed clearly with fish size. Whereas copepods, euphausiids and shrimps were important for  $\leq 400$  mm SL fish, mesopelagic fish predominated in the diet of  $>400$  mm SL fish (Figure 3). The importance of euphausiids was highest in the diet of  $\leq 100$  mm SL size-class (44.2% DW), and decreased gradually with increasing fish size. Copepods were important for middle-sized fish accounting for 34.4% and 46.0% of DW for 201–300 and 301–400 mm SL size-classes, respectively. Shrimps represented fair amounts of contribution (24.9% DW) in the diets of  $\leq 300$  mm SL fish, and were most important in the diet of 101 to 200 mm SL fish (41.7%). Squids were less important compared with other prey categories mentioned above for small hakeling, but they were third and second in importance in the diets of 301–400 and 401–500 mm SL fish (13.6 and 12.1%, respectively). In the matrix of percentage similarity (Figure 4a), neighbouring pairs of fish size-classes showed medium to high value of similarity ( $\geq 48\%$ ) reflecting the gradualness in the ontogenetic shift of diet, whereas pairs with distant lengths ( $>20$  cm difference in length) showed substantially different diets ( $\leq 35\%$ ).

### Spatial variation

Due to the skewed fish size-distribution in the Doto area (Figure 2), the comparison of fish diet between Tohoku and Doto areas was possible for 301–400 mm and  $>400$  mm SL size-classes. Geographical variation in the diet was less pronounced when compared with ontogenetic variation, with the similarity of diets for same size-class from different areas being  $\geq 72\%$  (Figures 4b & 5). In both areas, copepods were the most important prey for 301–400 mm SL fish (43.5% and 61.1%, respectively). Other prey items of importance in this size-class were, in decreasing order, mesopelagic

fish, squid and euphausiids in the Tohoku area (16.6%, 15.2% and 11.9%, respectively) and euphausiids and mesopelagic fish in the Doto area (19.6% and 10.7%, respectively). In  $>400$  mm SL size-class, mesopelagic fish were equally important in both areas (65.9% and 64.4%, respectively). Other important prey items were squids, which comprised *Watasenia scintillans* (Berry) (17.2%), and euphausiids (11.9%) in the Tohoku area, and euphausiids (12.2%) in the Doto area. Walleye pollock *Theragra chalcogramma* (Pallas) were observed only in the Doto area (4.7%).

### Seasonal variation

Only for  $>400$  mm SL fish were sufficient number of specimens available for the comparison of diet among different seasons and areas (Figure 6). In the Tohoku area, the importance of mesopelagic fish increased from winter (December–March) through spring and early summer (April–July; from 57.1% to 67.1%), while squids became less important (from 28.3% to 11.4%). In the Doto area, seasonal variation was more pronounced, and the opposite seasonal pattern was found in the contribution of mesopelagic fishes; it decreased from winter through spring (from 89.5% to 40.7%). Meso-zooplankton including copepods and euphausiids supplemented the decrease of mesopelagic fish during spring (13.7% and 18.1%, respectively). Dietary similarity among different seasons and areas were generally high reflecting high dependence on micronekton (Figure 4c). One exception was autumn in the Doto area, where walleye pollock was important (33.5%). The pollock ingested were age-0 group with body lengths ranging from 84 to 118 mm SL (mean  $\pm$  SD =  $106 \pm 11$  mm).

### Bathymetric variation

Bathymetric difference of diet was compared in the Tohoku area by bottom depths of sampling stations between the shallow area ( $\leq 450$  m) and deep area ( $>450$  m). The most conspicuous difference between the areas was ontogenetic pattern in contribution of copepods: whereas it got less important for larger fish in the shallow area, the highest contribution was found in the middle size-class (301–400 mm) in the deep area (Figure 7). Instead, shrimps, comprising mainly *Sergestes similis* Hansen, were important for the small size-class in the deep area (37.7%). Euphausiids were more important in the

**Table 1.** Diet of threadfin hakeling *Laemonema longipes* along the Pacific coast of northern Japan, represented as percentage dry weight (DW) composition (W) and percentage frequency of occurrence (F); +, <0.01; unid., unidentified.

Size-classes in standard length	≤100 mm		101–200 mm		201–300 mm		301–400 mm		401–500 mm		≥500 mm	
	W	F	W	F	W	F	W	F	W	F	W	F
Annelida												
Polychaeta (unid.)	–	–	–	–	–	–	–	–	+	0.30	–	–
Chaetognatha	0.67	3.23	0.12	1.79	0.03	0.53	0.03	2.74	0.03	3.63	0.01	1.03
Mollusca												
Cephalopoda (total)	–	–	3.66	–	5.43	–	13.93	–	12.75	–	5.05	–
Decapoda (unid.)	–	–	–	–	0.01	0.53	0.33	1.37	0.31	2.18	0.23	2.06
<i>Watasenia scintillans</i>	–	–	3.66	0.60	5.41	3.82	13.60	7.04	10.35	11.03	1.16	3.09
<i>Enoploteuthis chunii</i>	–	–	–	–	–	–	–	–	0.30	0.15	–	–
Gonatidae (unid.)	–	–	–	–	–	–	–	–	0.02	0.29	–	–
<i>Berryteuthis magister</i> <sup>a</sup>	–	–	–	–	–	–	–	–	0.61	0.29	–	–
<i>Berryeuthis anonychus</i>	–	–	–	–	–	–	–	–	0.06	0.15	–	–
<i>Gonatopsis borealis</i>	–	–	–	–	–	–	–	–	1.11	2.90	3.66	7.22
Crustacea												
Copepoda (total)	10.42	–	16.61	–	34.34	–	45.93	–	5.79	–	0.56	–
Copepoda (unid.)	6.78	8.06	7.24	16.42	8.33	16.56	3.81	38.69	1.99	19.59	0.56	6.19
<i>Neocalanus cristatus</i>	2.72	4.84	9.31	10.75	26.00	26.11	41.95	65.33	3.60	20.17	+	1.03
<i>Eucalanus bungii</i>	0.33	0.81	0.02	0.60	0.01	0.64	0.13	1.51	0.20	3.34	–	–
<i>Metridia</i> sp.	–	–	–	–	–	–	0.01	0.50	+	0.73	–	–
<i>Euchaeta</i> sp.	0.50	0.81	0.02	0.60	–	–	+	0.50	–	–	–	–
<i>Candacia</i> sp.	0.08	0.40	0.02	0.60	0.02	1.91	0.01	2.51	+	1.02	–	–
Mysidacea (unid.)	–	–	0.78	2.39	0.31	3.18	0.02	1.01	0.01	1.02	0.07	2.06
<i>Gnathophausia zoea</i>	–	–	–	–	–	–	0.65	1.01	0.01	1.16	–	–
<i>Eucopia</i> sp. <sup>a</sup>	–	–	–	–	–	–	0.19	0.50	–	–	–	–
<i>Meterithrops microthalma</i>	2.86	2.42	0.85	2.39	0.02	0.64	0.04	1.01	0.01	1.16	–	–
Amphipoda (unid.)	1.42	4.44	0.02	0.60	0.01	0.64	+	0.50	0.02	0.29	–	–
<i>Themisto japonica</i>	1.09	2.42	1.59	5.37	2.90	22.93	0.43	5.94	0.06	7.40	0.01	2.06
<i>Primno abyssalis</i>	–	–	–	–	–	–	0.01	0.46	+	–	0.01	1.03
Euphausiacea (total)	45.29	–	25.97	–	13.1	–	13.0	–	11.65	–	5.68	–
Euphausiacea (unid.)	0.33	1.21	0.53	0.90	0.21	4.46	2.87	8.54	1.89	6.39	1.59	6.19
<i>Euphausia pacifica</i>	44.96	20.97	25.44	23.88	12.88	30.57	9.97	19.10	7.85	32.66	1.28	15.46
<i>Thysanoessa inermis</i>	–	–	–	–	–	–	0.02	0.50	0.56	3.19	1.52	7.22
<i>Th. longipes</i>	–	–	–	–	–	–	0.09	0.50	1.36	5.95	1.29	4.12
Decapod Crustacea (total)	33.55	–	40.82	–	24.93	–	8.72	–	2.76	–	1.46	–
<i>Acanthephyra</i> sp.	–	–	–	–	1.33	0.53	–	–	–	–	0.19	1.03
<i>Bentheogenema borealis</i>	–	–	1.71	1.19	–	–	–	–	0.02	0.15	0.02	1.03
<i>Sergestes similis</i>	33.55	4.84	39.11	18.51	23.60	40.76	8.76	13.57	2.57	10.30	1.25	10.31
Pandalidae sp. <sup>a</sup>	–	–	–	–	–	–	–	–	0.03	0.15	–	–
<i>Neocrangon communis</i> <sup>a</sup>	–	–	–	–	–	–	–	–	0.06	0.44	–	–
<i>Argis lar</i> <sup>a</sup>	–	–	–	–	–	–	–	–	0.08	0.15	–	–
Brachyura	–	–	–	–	–	–	–	–	0.01	0.15	–	–
Vertebrata: Osteichthys												
Pisces (total)	2.93	–	9.57	–	17.95	–	16.49	–	67.11	–	86.38	–

Pisces (unid.)	2.93	0.40	0.50	0.30	0.05	1.27	0.17	1.01	1.87	4.79	1.23	6.19
<i>Synaphobranchus kaupii</i> <sup>a</sup>	–	–	–	–	–	–	–	–	–	–	3.02	1.03
<i>Engraulis japonicus</i>	–	–	–	–	–	–	–	–	0.38	0.15	–	–
<i>Leuroglossus schmidti</i>	–	–	–	–	0.24	0.64	0.50	0.50	0.41	1.16	1.52	2.06
<i>Bathylagus ochotensis</i>	–	–	–	–	–	–	–	–	0.11	0.58	0.41	2.06
<i>Bathylagus milleri</i>	–	–	–	–	–	–	0.48	0.50	0.06	0.04	0.03	1.03
<i>Maurolicus japonicus</i>	–	–	–	–	–	–	–	–	0.03	0.15	–	–
<i>Gonostoma gracile</i>	–	–	–	–	0.11	0.64	0.79	0.50	0.05	0.15	–	–
<i>Cyclothone alba</i>	–	–	0.09	0.30	–	–	–	–	0.10	0.19	0.20	1.03
Myctophidae (total)	–	–	–	–	17.55	–	14.55	–	60.53	–	65.94	–
Myctophidae (unid.)	–	–	3.55	2.09	9.01	7.64	6.73	4.52	7.52	9.29	–	–
<i>Lampanyctus</i> sp.	–	–	–	–	–	–	–	–	0.80	0.29	7.86	8.25
<i>L. jordani</i>	–	–	–	–	–	–	–	–	5.19	1.31	23.83	10.31
<i>L. regalis</i>	–	–	–	–	–	–	–	–	1.45	0.15	20.70	8.25
<i>Diaphus theta</i>	–	–	4.70	0.30	7.51	2.55	7.82	3.02	0.24	0.44	11.44	9.28
<i>Diaphus</i> sp.	–	–	–	–	–	–	–	–	43.34	18.58	–	–
<i>Protomyctophum thompsoni</i>	–	–	–	–	–	–	–	–	0.20	0.29	–	–
<i>Stenobrachius leucopsarus</i>	–	–	–	–	–	–	–	–	1.12	0.73	–	–
<i>S. nannochir</i>	–	–	–	–	–	–	–	–	0.30	0.44	0.08	1.03
<i>Stenobrachius</i> sp.	–	–	–	–	1.04	0.64	–	–	0.38	0.44	0.09	1.03
<i>Symbolophorus californiensis</i>	–	–	–	–	–	–	–	–	–	–	1.94	1.03
Paralepididae sp.	–	–	–	–	–	–	–	–	0.92	0.15	12.41	1.03
<i>Theragra chalcogramma</i>	–	–	–	–	–	–	+	0.50	2.66	1.31	1.62	2.06
Macrouridae sp.	–	–	0.73	0.30	–	–	–	–	–	–	–	–
Unid. digested matter	2.51	2.82	0.60	0.12	0.17	0.64	–	–	0.12	1.74	0.16	2.06
N of stomachs with contents	118		223		157		199		636		79	
Total DW of prey examined	1.2		8.9		28.4		75.5		744.3		197.6	

<sup>a</sup>, benthic organisms.

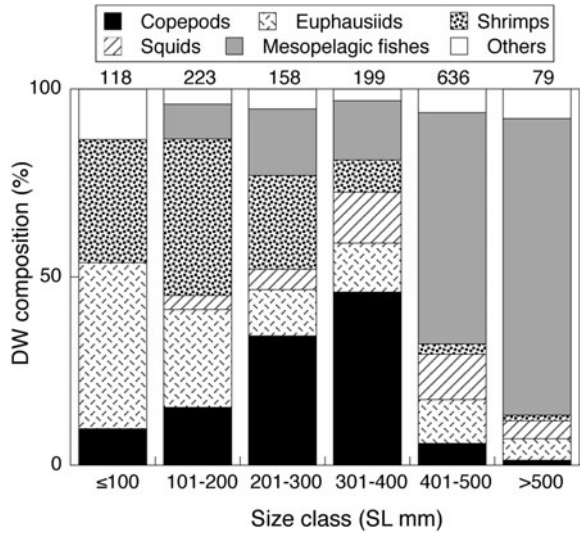


Fig. 3. Ontogenetic variation in the diets of *Laemonema longipes* represented as dry weight composition. Specimens from different areas were combined. Figures above the bar indicate number of specimens containing food.

shallow area (12.6%–24.7%) than in the deep area (0.4%–15.5%). Reflecting the difference, PS value for same size-class from different depth areas was intermediate in ≤30 cm and 30–40 cm size-classes (54% and 58%, respectively; Figure 4d).

DISCUSSION

Previous studies on the food habits of other morid species have emphasized their broad range of diets including both pelagic and benthic prey; Mediterranean codling *Lepidion lepidion* (Risso) (Carrassón *et al.*, 1997), brown hakeling *Physiculus maximowiczii* (Herzenstein) (Fujita *et al.*, 1995) and red cod *Salilota australis* (Günther) (Arkhipkin *et al.*, 2001). In the present study, threadfin hakeling preyed almost exclusively on pelagic and planktonic organisms. This result follows general predictions from its protruded lower jaw. Benthic organisms (e.g. *Synaphobranchus kaupii* Johnson and *Argis lar* (Owen)) occurred in small quantities and comprised species known to occur considerable distance off the sea-bed when feeding (Gordon & Mauchline, 1996, Sedberry & Musick, 1978).

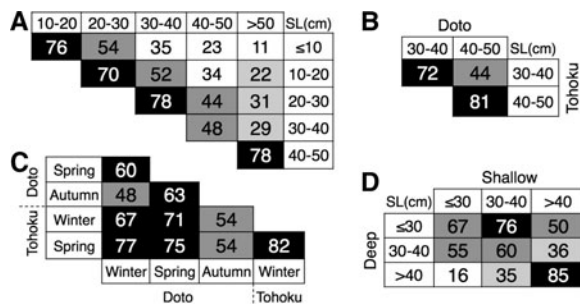


Fig. 4. Matrices of percentage similarity (PS) showing dietary similarity among different fish size-classes (a), geographical areas (b), geographical area and season (c) and depth stratum (d). Thickness of each cell indicate level of similarity: ■: >60%, ▣: 41–60%, ▤: 21–40%, □: ≤20%.

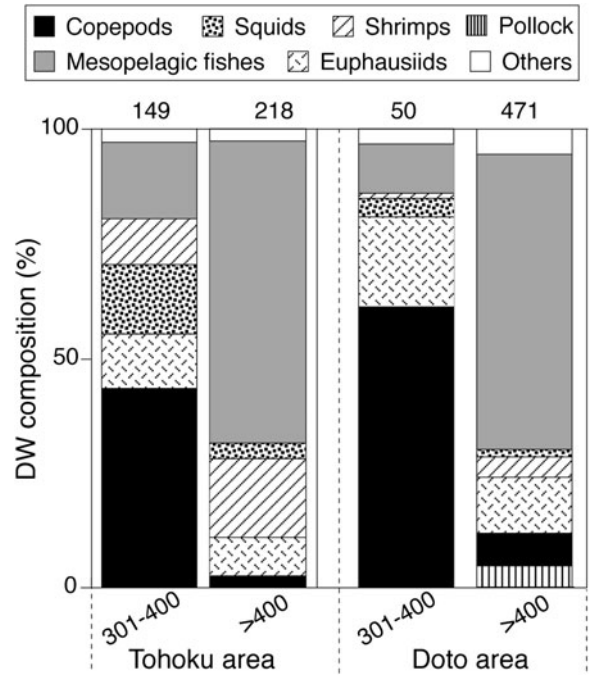


Fig. 5. Geographical variation in the diets of *Laemonema longipes* represented as dry weight composition. Sufficient number of specimens were available for 301–400 mm standard length (SL) and >400 mm SL size-classes.

We analysed the diets of hakeling with neither sign of stomach eversion nor regurgitation. This exclusion may have skewed the depth distribution of specimens toward shallower waters, since fish captured from deeper waters generally represent higher rate of stomach eversion. However, its influence was concluded to be limited because the diets of hakeling from different depth areas showed high similarity (≥60%; Figure 4d). We did not assess the diel variation in feeding

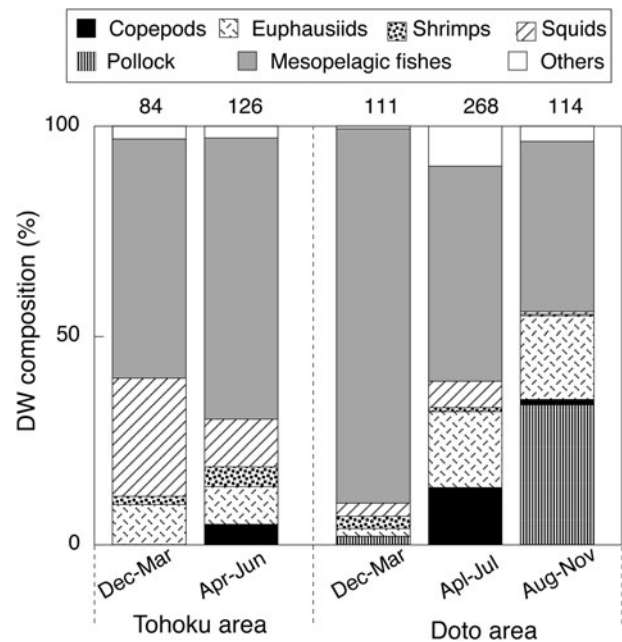


Fig. 6. Seasonal variation in the diets of the >400 mm standard length size-class of *Laemonema longipes* in the different areas, represented as dry weight composition.

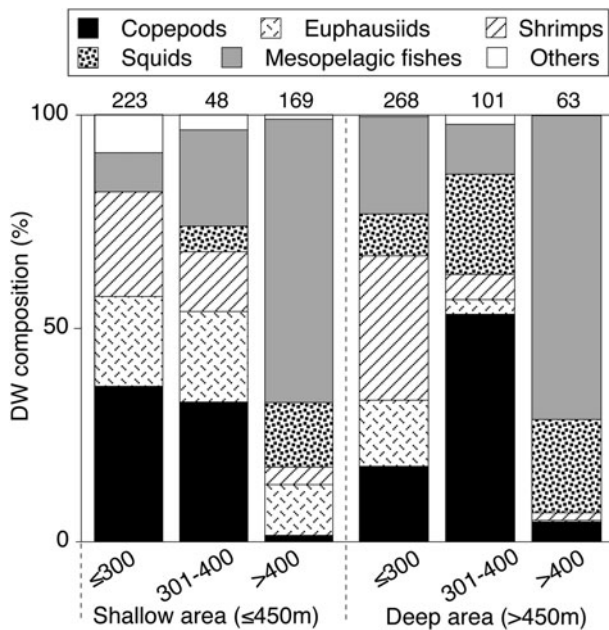


Fig. 7. Bathymetric variation in the diets of the >400 mm standard length size-class of *Laemonema longipes*, represented as dry weight composition. Samples were divided into shallow ( $\leq 400$  m) and deep (>400 m) strata based on bottom depths of sampling stations.

due to the high incidence of stomach eversion and regurgitation. However, different distributions by time of day were observed previously; they are distributed on the sea floor during daytime whereas they stay  $\sim 50$  m above the sea bottom during daytime (Yokota & Kawasaki, 1990; S. Honda, National Research Institute of Fisheries Science, personal communication). This behaviour perhaps reflects their intensive feeding upon pelagic prey during daytime, most of which undergo diurnal vertical migration (e.g. Watanabe *et al.*, 1999; Endo & Yamano, 2006). These vertically migrating animals are important transporters of organic carbon from the epipelagic layer to deeper layer of the ocean (Hidaka *et al.*, 2001; Kobari *et al.*, 2008). Thus, threadfin hakeling plays an important role in capturing the organic carbon transported by the vertically migrating prey organisms in the upper bathypelagic zone.

Fish diets generally shift from small prey to larger prey with ontogeny (Scharf *et al.*, 2000). Threadfin hakeling shifted abruptly from planktivore in  $\leq 400$  mm SL size-classes to piscivore in >400 mm SL fish. However, a reverse size relationship was found in the  $\leq 400$  mm SL size-classes; copepods, the smallest prey item, was more important for larger size-classes whereas the intermediate-sized prey including euphausiids and shrimps were more important in smaller size-classes ( $\leq 200$  mm SL). Based upon the bathymetric comparison of diet (Figure 5), this trend is only evident in deeper waters. Although we have no plausible explanation for this pattern, there would have been some conditions promoting the ingestion of shrimps (copepods) by the fish of small (middle) size-class in the deep area, such as an overlap in vertical distribution.

In the geographical comparison of diets, characteristic prey in the Tohoku area were squids comprised mainly of *Watasenia scintillans* (Berry) and shrimps represented by *Sergestes similis*. Both species are typical transitional species,

which are distributed mainly in the transitional area between cold Oyashio and warm Kuroshio currents (Omori, 1974; Yamamura & Inada, 2001). However, geographical differences in the diet of threadfin hakeling were insignificant with copepods and myctophids dominating in the middle (301–400 mm) and large (>400 mm) size-classes, respectively, in both of the areas (Figure 4). This fact implies that the prey field of threadfin hakeling is basically uniform throughout the Pacific coast of northern Japan under the prevalence of the North Pacific Intermediate Water over the upper-slope zone (Yasuda, 2003).

Seasonal variation of diet was more obvious in the Doto area than in the Tohoku area. The seasonal fluctuation in the abundance of major prey is more fluctuating in the Doto area (Odate, 1994). Mesozooplankton including *Neocalanus cristatus* (Kröyer) and *Euphausia pacifica* Hansen in the Oyashio area show conspicuous seasonality in their abundance. They are abundant during productive spring and summer whereas scarce during less productive autumn and winter (Kobari & Ikeda, 1999; Yamamura, 2004). However, such a variation is less pronounced in the Tohoku area compared to the Oyashio (i.e. Doto) area (Odate, 1994).

Walleye pollock *Theragra chalcogramma* (Pallas) was observed only during late summer and autumn (August–November). The fish preyed upon were age-0 fish, born during the preceding spring and settled in late summer and autumn into the Doto area, their most important nursery (Ito *et al.*, 2004). They are distributed mainly over the continental shelves with bottom depths  $\leq 150$  m, where threadfin hakeling does not occur (Kooka *et al.*, 2009). Therefore, it is probable that some fraction of the age-0 group would have been distributed in deeper waters. Thus, threadfin hakeling was found to be a predator on juvenile walleye pollock, as well as a potential competitor for adult walleye pollock. However, the adverse effects of threadfin hakeling on walleye pollock seems to be very limited, because: (1) juvenile pollock were infrequently ingested and they become less vulnerable as they grow, due to the size-dependent nature of predation (Yamamura, 2004); and (2) the spatial/depth overlap between juvenile walleye pollock and threadfin hakeling is very limited.

In conclusion, threadfin hakeling mainly depend upon pelagic organisms including copepods, euphausiids, shrimps, squids and myctophids, all of which are diurnal vertical migrants. This implies that threadfin hakeling is a counterpart of walleye pollock; whereas the former prosper in the lower continental shelf region, the latter dominates in the upper continental slope region. Due to its dominance in the upper-slope region, threadfin hakeling plays an important role in fixing organic carbon transported into the coastal bathypelagic zone by vertically migrating prey organisms.

## ACKNOWLEDGEMENTS

The authors are grateful to H. Fujiwara, T. Hattori, M. Shimazaki and K. Watanabe for their help in sample collection; captains and crews of FRVs 'Hokko-maru', 'Kaiyo-maru', 'Kaiyo Maru 3', 'Seitoku-maru 2', 'Tanshu-maru' and 'Wakataka-maru' for their assistance at sea; M. Ishiguro for her laboratory assistance. We also wish to thank N. Shiga and T. Komai for their help in

prey identification; and K. Shimazaki, H. Ogi and Y. Sakurai for their encouragements throughout this study.

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