



Title	Feeding habits of pointhead flounder <i>Cleisthenes pinetorum</i> larvae in and near Funka Bay, Hokkaido, Japan
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Feeding habits of pointhead flounder *Cleisthenes pinetorum* larvae in and near Funka Bay, Hokkaido, Japan

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The feeding habits of pointhead flounder *Cleisthenes pinetorum* larvae were investigated in and near Funka Bay, Hokkaido Island during 10–20 August 2001. As the larvae grew, the principal prey shifted from copepod nauplii (especially, *Oithona similis* and *Pseudocalanus newmani*) as the initial food item to copepodites and an appendicularia *Oikopleura* sp. Nauplii of *Microsetella* sp. were abundant in the sampling area, but few were eaten by the larvae. The number of prey in the larval digestive tracts increased from 08:55 and peaked near sunset, suggesting the larvae are visual day feeders. Nauplii concentrations in the water varied geographically, but the number of nauplii in the larval digestive tracts did not vary. Pointhead flounder larvae in the first feeding stage might not starve in and near Funka Bay in August 2001.

Key words: appendicularia, *Cleisthenes pinetorum*, copepoda, feeding periodicity, flounder, Funka Bay, larva, nauplius

Introduction

The pointhead flounder *Cleisthenes pinetorum* is distributed in coastal areas of Hokkaido Island and the northern part of Honshu Island, Japan. It is caught in and near Funka Bay in Hokkaido by commercial bottom set nets and gill nets. Annual catches were over 5,000 metric tons in the 1960s and 1970s, but decreased sharply in the 1980s, reaching a low of 202 metric tons in 1990. In 2001, the annual catch increased to 1,100 metric tons due to strong year classes during 1990–1992 (Hokkaido Government, 2003). To reveal the cause of stock size fluctuations, a better understanding is needed of how the early life history affects recruitment.

Studies of the early life history of pointhead flounder have clarified the morphologies of eggs and larvae (Kuraue, 1914; Pertseva-Ostroumova, 1961; Okiyama and Takahashi, 1976; Nagasawa, 1990), spatial distribution and feeding habits of pelagic larvae in the northern Japan Sea (Nagasawa, 1990), and seasonal migrations of juvenile and young individuals (Tominaga *et al.*, 2000). In and near Funka Bay, the diel vertical and horizontal distributions of pointhead flounder larvae have also been described (Kurifuji *et al.*, in press), however no studies have examined their diurnal rhythms and geographical differences of feeding habits. An examination of the feeding ecology of pelagic larvae, which

are vulnerable to currents and have high mortality (Houde, 1987), might help clarify the cause of recruitment fluctuation. In this study, we investigated and compared the feeding habits of pointhead flounder larvae in and near Funka Bay among different sampling times and areas.

Materials and Methods

Sampling was conducted aboard the T/S *Hokusei-maru* of Hokkaido University, Faculty of Fisheries at 40 stations on the continental shelf in August 2001 (Fig. 1). The sampling area was divided into four parts: northern part of Funka Bay (NFB), southern part of Funka Bay (SFB), mouth of Funka Bay (MFB), and outside of the bay (OB). Pointhead flounder larvae were collected with a ring net (80 cm diameter and 0.33 mm mesh size) at 35 stations and five Motoda (MTD) nets (56 cm diameter and 0.33 mm mesh size) at five stations on 10–17 August 2001 (Fig. 1, Table 1). The ring net was towed obliquely from 60 m depth to the surface, and the MTD nets were towed horizontally for 10 min at five depths (0, 10, 20, 30 and 40 m). These samplings were conducted during daylight hours (Table 1). In addition, at a station in NFB where larvae were abundant (Fig. 1: C, open square), continual tows were made with the MTD nets by the same method described above at two-hour intervals between 14:40 on 19 August and 15:16 on 20 August 2001 (Table 1). All samples were preserved in a 5% buffered formalin-seawater solution.

In the laboratory, pointhead flounder larvae past the yolk-sac stage were classified into six developmental stages according to Nagasawa (1990): stage A, the digestive tract began to coil but was unlooped; stage B, the digestive tract

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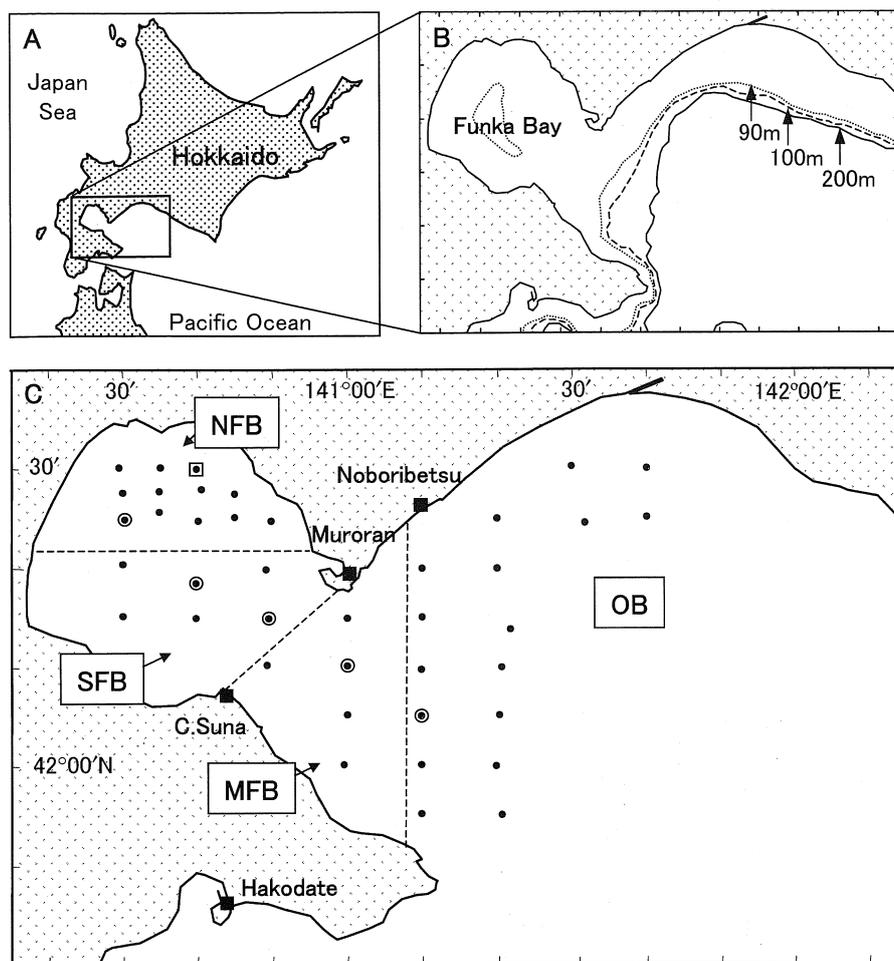


Figure 1. Location of Funka Bay (A), contours of depth (B), and sampling stations of oblique hauls with a ring net from 60-m depth (solid circles) and horizontal hauls with MTD nets (open circles; C). The open square shows the location where MTD nets were sampled 13 times over 24 hours. Funka Bay and its adjacent area were divided into four regions, NFB: northern part of Funka Bay; SFB: southern part of Funka Bay; MFB: mouth of Funka Bay; and OB: outside of the bay.

looped and the notochord tip was straight; stage C, preflexion and the hypural element began to form; stage D, flexion and caudal fin ray appeared; stage E, postflexion and left eye was not visible from the right side; and stage F, upper edge of left eye was visible from the right side.

Digestive tracts were removed from the larvae, and their contents were identified to the lowest possible taxa and counted. These contents were stained with methylene blue for detection of “house rudiments” of *Oikopleura* sp., and they are colorable purple (Takatsu *et al.*, unpublished) and less-digestible than other organs (Flood and Diebel, 1988). “House rudiment” is non-expanded and preliminarily secreted “house”, which is equipped with feeding filters, and if the expanded “house” becomes clogged with prey particles, the animal discards the “house” and expands the “house rudiment” (Alldredge, 1976; Flood and Diebel, 1988). The body length of food items was measured using a

binocular microscope with a micrometer. The second longest three-dimensional length of a prey item generally determines if it can enter a predator’s mouth (Pearre, 1980), so we measured the prey widths (PW; prosome widths of copepod nauplii and copepodites, house rudiment widths of appendicularians, and the length that vertically intersected with the maximum length of other prey items) in the diet. Data on the digestive tracts contents of larvae for different developmental stages and areas were expressed as the percentage frequency of occurrence (F%: the percentage of larvae that fed a particular type of prey) and percentage in number (N%: the percentage that each prey type composed of total number of prey items). For each data set, we tested the homogeneity of variance using the F_{\max} -test, and, if necessary, $\log(x+1)$ transformed the data, then compared between/among samples using one-way ANOVA, the Mann-Whitney test, or the Kruskal-Wallis test. The median PWs

Table 1. Location of sampling stations and sampling times in this study.

Date	Time	Gear*	Location		Date	Time	Gear*	Location	
			Lat. (N)	Long. (E)				Lat. (N)	Long. (E)
2001 Aug.					16	08:30	R	41°55.1'	141° 9.8'
10	16:00	M	42°10.0'	141° 0.0'		09:55	R	41°55.0'	141°20.5'
13	11:35	R	42°30.0'	141°40.0'		11:10	R	42° 0.0'	141°19.8'
	11:51	M	42°30.3'	141°40.4'		12:23	R	42° 5.1'	141°20.2'
	13:30	R	42°25.0'	141°40.0'		13:35	R	42° 9.9'	141°20.6'
	15:00	R	42°24.5'	141°31.7'		14:45	R	42°13.8'	141°21.7'
	16:23	R	42°30.2'	141°29.9'		16:05	R	41°19.9'	141°20.0'
14	06:10	R	42°30.1'	140°29.6'		17:15	R	41°24.9'	141°20.0'
	07:30	R	42°24.8'	140°30.3'	17	07:40	R	42°19.3'	140°38.1'
	08:29	M	42°24.8'	140°30.3'		08:40	M	42°19.3'	140°38.1'
	09:40	R	42°20.3'	140°30.3'		10:05	R	42°27.5'	140°30.0'
	10:52	R	42°15.1'	140°30.3'		11:12	R	42°30.1'	140°35.1'
	12:15	R	42°14.9'	140°39.9'		12:08	R	42°27.6'	140°34.9'
	13:13	R	42°18.3'	140°39.8'		13:00	R	42°25.6'	140°35.0'
	14:20	R	42°24.7'	140°40.1'		14:05	R	42°27.9'	140°40.6'
	15:27	R	42°29.9'	140°40.0'		14:55	R	42°27.4'	140°45.0'
	16:50	R	42°24.7'	140°49.9'		15:40	R	42°25.0'	140°45.0'
15	05:25	R	42°19.8'	140°49.3'	19	15:00	M	42°29.4'	140°40.9'
	06:20	R	42°15.0'	141°50.0'		16:56	M		
	07:07	M	42°15.0'	141°50.0'		18:54	M		
	08:15	R	42°10.1'	141°49.4'		20:57	M		
	10:12	R	42° 0.1'	141°59.6'		22:50	M		
	11:17	R	42° 5.1'	141° 0.0'	20	00:55	M		
	12:20	R	42°10.0'	141° 0.0'		02:59	M		
	13:24	R	42°14.8'	141° 0.0'		04:55	M		
	14:50	R	42°19.9'	141°10.0'		06:55	M		
	15:50	R	42°15.0'	141°10.0'		08:50	M		
	16:51	R	42° 9.7'	141° 9.8'		10:51	M		
16	05:25	R	42° 5.0'	141° 9.8'		12:55	M		
	06:10	M	42° 5.0'	141° 9.8'		14:52	M		
	07:20	R	42° 0.1'	141° 9.8'					

* M: MTD nets towed horizontally; R: Ring net towed obliquely.

of copepod nauplii collected from digestive tracts were compared using Peritz's multiple comparisons (Nagata and Yoshida, 1997). The difference in numerical diet composition among areas and depths, and between day and night were compared using the G-test (Sokal and Rohlf, 1995).

Result

Change in food by developmental stage

Larvae at stages A–B mainly fed on copepod nauplii (N%=79 and F%=50 at stage A, N%=83 and F%=67 at stage B; Fig. 2). Most stage C larvae also fed on copepod nauplii (F%=88), but the nauplii formed a smaller part in the diet (N%=51) than in larvae at stages A–B, and the number of copepodites (N%=18) and the appendicularia *Oikopleura* sp. (N%=20) increased. Five individuals at

stage D fed mainly on copepod nauplii (F%=80, N%=43), copepodites (F%=100, N%=29) and an *Oikopleura* sp. (F%=60, N%=14). Copepodite prey included *Paracalanus* sp. (36%), *Oithona similis* (21%), *Microsetella* sp. (5%), *Pseudocalanus newmani* (3%), and species that could not be identified because of digestion (36%). House rudiments of *Oikopleura* sp. occurred with trunks in the diet frequently, however did not with tails at all. The maximum prey widths fed by larvae increased with increasing larval mouth width (Fig. 3). The median prey widths were 74.7 μ m for copepod nauplii, 130 μ m for copepodites, and 153 μ m for *Oikopleura* sp. Small numbers of bivalve larvae, rotifers (*Trichocerca* sp.), tintinnids, and a species of dinoflagellate were also present (each N% \leq 4). Five individuals in stages E–F fed on polychaete larvae and eu-

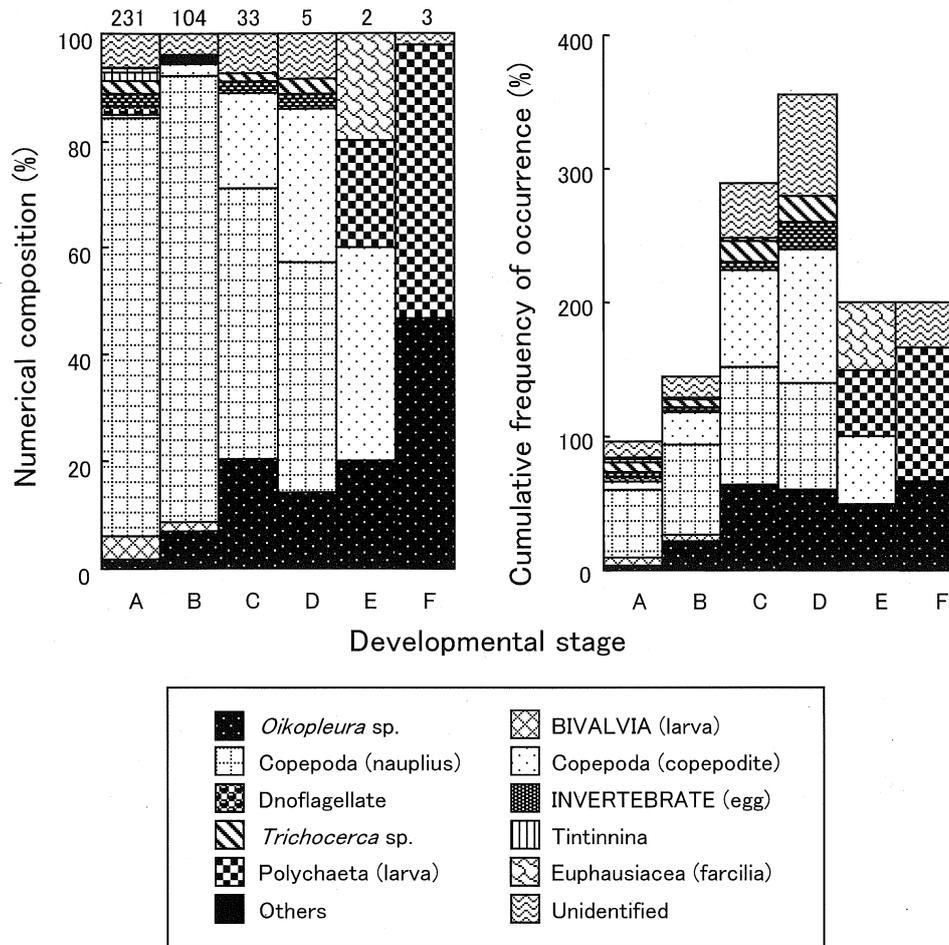


Figure 2. Numerical compositions and percent frequency of occurrence of food items in digestive tracts of *C. pinetorum* larvae by developmental stage in Funka Bay during 10–20 August 2001. Developmental stages of larvae are described in detail in the text. The numeral above each bar shows the number of fish examined.

phausiid farciliae.

As the larvae developed from stage A to stage C, the number that fed on nauplii of *Pseudocalanus newmani* increased (N%: 22–47%), but the number that fed on nauplii of *Oithona similis* and *Paracalanus* sp. both decreased (N%: 45–25%, and 9–3%, respectively; Fig. 4). Nauplii of *Microsetella* sp. were abundant in the water column (27% by the number of all nauplii collected; Kurifuji *et al.*, in press), but few occurred in the diet (N%≤2). The median prosome widths (PWs) significantly differed among the four taxa (Kruskal-Wallis test; $P < 0.001$), and the PW of *P. newmani* was significantly larger than for the three other nauplii (Peritz's multiple comparison test at the 5% level; Table 2).

Diurnal feeding rhythm

In our survey using five MTD nets between 0 and 40 m depth, most larvae were sampled at 20–40 m depth. The numerical composition (N%) of each developmental stage (Table 3) did not significantly differ among depths (G-test;

stage A, $P = 0.95$; stage B, $P = 0.11$; stage C, $P = 0.12$). Therefore we did not distinguish larvae by sampling depth in the analysis of diurnal feeding rhythm. The percentage of larvae with prey of stage A larvae at a station in NFB (Fig. 1) were high in the daytime from 08:55 to 17:01 (83–100%) and decreased at night, with the minimum value (17%) occurring at 05:00 after sunrise (Fig. 5). The percentage of larvae with prey of stage A and stage B larvae were similar. Almost all larvae at stages C–F except for two larvae collected at 01:00 (93%) had prey items in their digestive tracts.

The mean number of all prey items digestive tracts of larvae increased from 15:05 to 17:01, and the peaks occurred before or just after sunset in all stages (Fig. 5). These peak were 7.3 prey/larva at stage A, 18.0 prey/larva at stage B and 16.8 prey/larva for stages C–F. The mean number of prey in the digestive tracts of stage A was low in the morning (07:00; 0.5 prey/larva) and relatively high from 08:55 to 14:57 (3.0–4.4 prey/larva). Larvae at stage B

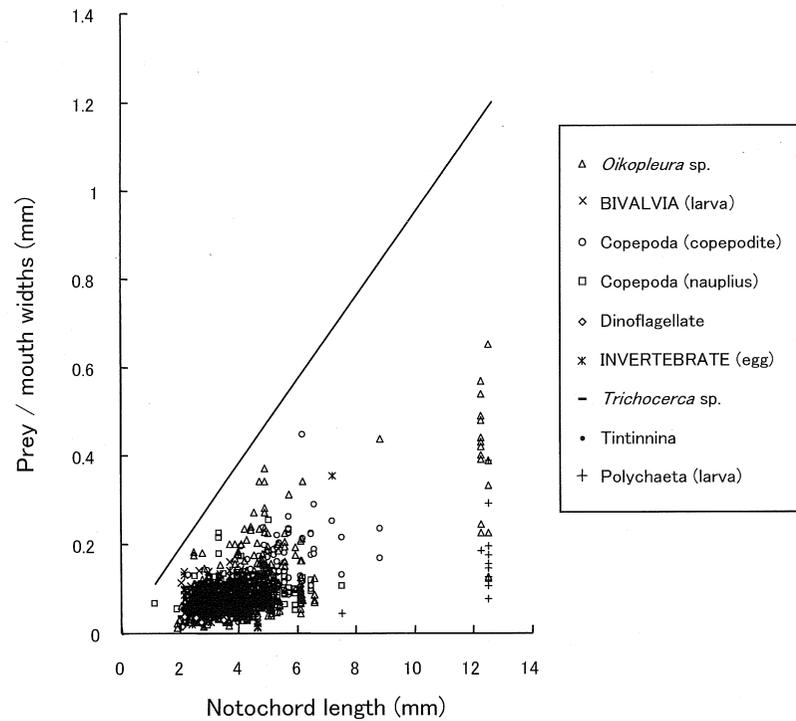


Figure 3. Prey size distribution of food items in digestive tracts of *C. pinetorum* larvae in Funka Bay during 10–20 August 2001. The solid line shows the regression line between notochord length (NL) and mouth width (MW) of larvae ($MW=0.0952NL$, $N=329$, $r^2=0.72$, $P<0.001$).

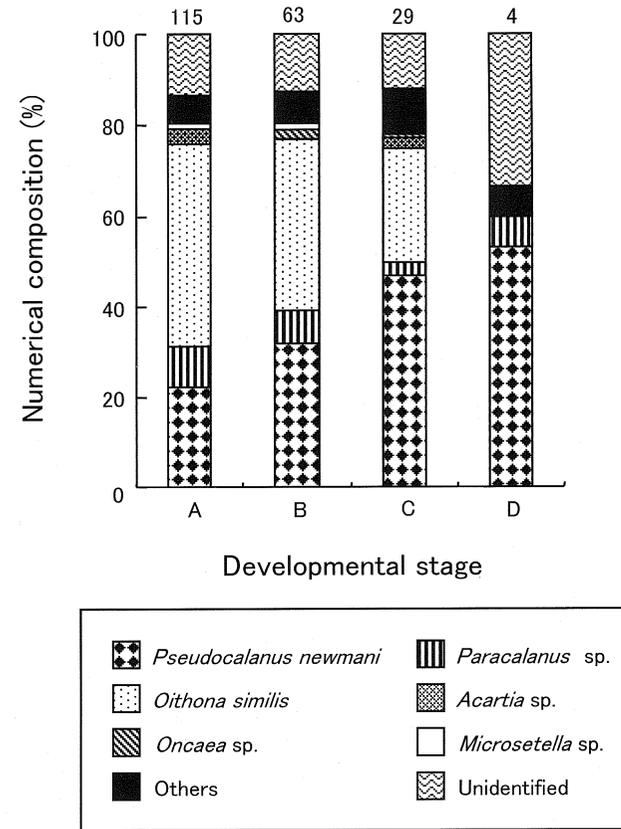


Figure 4. Numerical compositions of copepod nauplii in digestive tracts of *C. pinetorum* larvae by developmental stage. The numeral above each bar shows the number of nauplii identified.

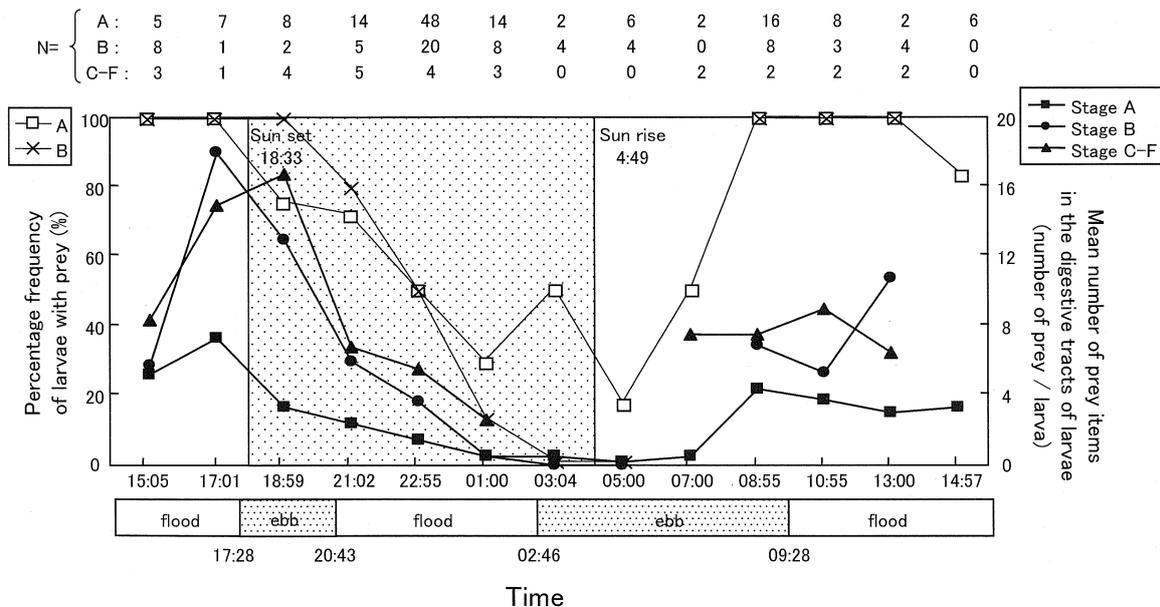
Table 2. Prosome width (PW: μm) of copepod nauplii in the digestive tracts of *C. pinetorum* larvae.

Prey type	10th percentile	Median	90th percentile	N*
<i>Microsetella</i> sp.	47.7	67.5	90.1	18
<i>Oithona similis</i>	49.9	65.7	90.0	364
<i>Paracalanus</i> sp.	38.1	62.5	105	71
<i>Pseudocalanus newmani</i>	63.8	92.5	124	281

* N: sample size.

Table 3. Numerical compositions of food items in digestive tracts of *C. pinetorum* larvae sampled by MTD nets in Funka Bay during 10–20 August 2001.

Developmental stage	A			B			C		
	20	30	40	20	30	40	20	30	40
BIVALVIA (larva)	0	0.9	0	0	0	1.0	0	0	1.0
Copepoda (nauplius)	83.3	93.6	96.5	66.7	83.5	71.8	51.3	51.5	34.8
Copepoda (copepodite)	0	0	0	16.7	1.3	8.7	17.9	20.6	22.0
Dinoflagellate	0	0	0	0	2.5	0	0	0	0
INVERTEBRATE (egg)	3.3	0.9	1.2	16.7	0	0	0	0	0
<i>Trichocerca</i> sp.	0	0	0	0	3.8	1.0	0	1.0	2.8
<i>Oikopleura</i> sp.	0	0	1.2	0	6.3	9.7	23.6	19.6	23.4
Unidentified	13.3	1.8	0	0	1.6	7.8	5.1	7.2	17.0
Number of larvae examined	25	100	26	5	44	24	26	28	12

**Figure 5.** Diurnal changes in mean number of prey items in the digestive tracts of larvae (number of prey/larva) and percentage frequency of *C. pinetorum* larvae had any prey in their digestive tracts by developmental stage. Dotted area shows nighttime and ebb tide. N: number of fish examined.

and in stages C–F had higher values than stage A, but showed similar temporal trends with the stage A larvae. No clear relationship was seen between tides and feeding periodicity, and there was no significant difference between day and night in compositions (N%) in the diet of stage A (G-test; $P=0.09$) and stage B larvae (G-test; $P=0.94$).

Geographical differences of feeding habits

Although the numerical compositions of food items (N%) in the diet of larvae at stage A significantly differed among areas (G-test; $P=0.002$), the larvae fed mainly on copepod

nauplii (43–92%) in all areas during daylight hours (05:25–17:15; Fig. 6). More larvae fed on dinoflagellates and tintinnids in OB than in NFB, SFB and MFB. In contrast, *Oikopleura* sp. and bivalve larvae were not fed in OB. The mean total number of prey items in the digestive tracts of larvae in daytime did not significantly differ among areas (one-way ANOVA; $P=0.66$; Table 4). The taxonomical compositions of copepod nauplii prey and the mean number of the nauplii in the digestive tracts did not significantly differ among areas (G-test; $P=0.45$, one-way ANOVA;

$P=0.08$).

Discussion

Pointhead flounder larvae at the first feeding stage fed mainly on copepod nauplii (Fig. 2), which are the principal prey item for most marine fish larvae (Tanaka, 1980). Stages A–D larvae fed on nauplii of *Oithona similis* and *Pseudocalanus newmani*, and some *Paracalanus* sp., but

fed few *Microsetella* sp. nauplii (1.0% of all nauplii in diet), even though these nauplii composed 27% of all nauplii collected in the study area with nets (Kurifuji *et al.*, 2005). Copepod nauplii have various shapes, for example, *O. similis* is egg-shaped, *P. newmani* and *Paracalanus* sp. are egg-shaped with urosomes, and *Microsetella* sp. is egg-shaped but flattened along the dorso-ventral axis (Koga, 1984). It is likely that the shape of *Microsetella* sp. make it less visible than other nauplii, and this difference in shape may also affect its swimming behavior, and hence, prey selectivity of pointhead flounder larvae.

Our results indicated that the range of prey size that larvae can feed expanded as the larvae grew. The number of larvae that fed on *P. newmani*, the largest of the nauplii taxa fed, increased as the larvae grew (Fig. 4). Also, as the larvae grew, the larval diet shifted to copepodites and an appendicularia *Oikopleura* sp. (Figs. 2, 3) which were larger than the copepod nauplii. The shift from copepod nauplii to copepodites also occurs in pointhead flounder larvae in the northern part of the Japan Sea (Nagasawa, 1990), and such a diet shift is often observed in other larval fishes. However flatfish larvae frequently feed on *Oikopleura* sp. (e.g., Last, 1978; Hasegawa *et al.*, 2003), which is rarely fed by other larval marine fishes (Ikewaki and Sawada, 1991). *Oikopleura* sp. might be a preferable prey item for pointhead flounder larvae because this prey was fed by larvae at similar rates as copepodites (Fig. 2), even though copepodites were approximately five times more abundant than *Oikopleura* sp. in this area in August 2001 (Kurifuji *et al.*, 2005). Flatfish larvae are weak swimmers (Fukuhara, 1988; Bailey *et al.*, 2005), and *Oikopleura* sp. is thought to be easily preyed on by pointhead flounder larvae because of its slow swimming speed (Alldredge, 1976).

Appendicularians feed efficiently within complex mucus filter “houses” on small particles such as nano- and pico-plankton, which are not preyed on by other herbivores including some copepods (Alldredge, 1976; Deibel, 1998). Appendicularians exhibit high metabolic activity, a fast

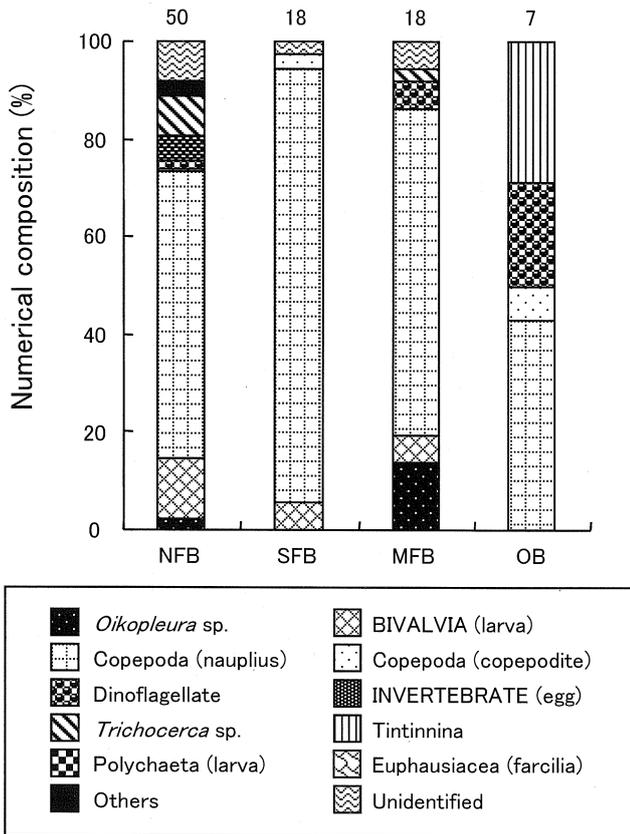


Figure 6. Numerical compositions of food items in digestive tracts of *C. pinetorum* at stage A. Abbreviations of sea areas are defined in Fig. 1. The numeral above each bar shows the number of fish examined.

Table 4. Geographical difference in mean number of prey items in the digestive tract of *C. pinetorum* at stage A, and mean concentration during 10–17 August 2001 of copepod nauplii other than *Microsetella* sp. Data collected in daytime (05:25–17:15) were used. Abbreviations of sampling areas are shown in Fig. 1.

	NFB	SFB	MFB	OB
Number of larvae examined	50	18	18	7
Mean number of all prey items in the larval digestive tracts (\pm SD)	3.0 \pm 3.3	2.2 \pm 3.2	2.0 \pm 1.9	2.0 \pm 2.1
Mean number of copepod nauplii in the larval digestive tracts (\pm SD)	1.8 \pm 2.9	1.9 \pm 3.1	1.3 \pm 1.6	0.86 \pm 0.9
Mean concentration (inds./L)*	35.8	56.5	15.5	20.0

* after Kurifuji *et al.* (2005).

generation time, and rapid short-term population responses to periods of enhanced production (Deibel, 1998). They short-circuit the microbial loop (Azam *et al.*, 1983) by directly transferring energy from very small particles to larval and adult fish (Gadomski and Boehlert, 1984; Gorsky and Fenaux, 1998). On the other hand, copepodites fed on microphytoplankton and microzooplankton (e.g., flagellates and ciliates), but microphytoplankton are less abundant in Funka Bay during the summer (Shinada *et al.*, 2003). Thus copepodites were also considered to depend on the microbial food chain (Shinada *et al.*, 2001). Accordingly, the early life stages of pointhead flounder that feed mainly on *Oikopleura* sp. and copepodites probably depend on the microbial food chain in summer.

Our results suggest pointhead flounder larvae are visual day feeders and feed little at night (Fig. 5). A net study in August 2001 by Kurifuji *et al.* (2005) formed no evidence of diel vertical migration in nauplii or stage A larvae at our sampling station (the open square in Fig. 1). Thus the feeding periodicity was not caused by diel vertical migrations of prey items and larvae. Because many fish larvae are visual feeders (Ryland, 1964), they can not find prey in the dark night environment. The peak of mean number of all prey items in the larval digestive tracts occurred before or just after sunset (Fig. 5). In many fishes, a diel feeding rhythm begins in the larval stages, and these rhythms vary among species (Sakamoto, 1988). Most animals have two feeding peaks: one in the early morning and one in the evening (Katoh, 1973). In some larval and juvenile fishes, two feeding peaks are observed in the field, for example in Japanese horse mackerel *Trachurus japonicus* (Kozasa, 1970) and yellowtail *Soriola quinqueradiata* (Anraku and Azeta, 1967), while a single peak in the afternoon is observed in yellowtail flounder *Limanda ferruginea* (Smith *et al.*, 1978). In pointhead flounder larvae, feeding intensities remained low for ca. 2–4 hours after sunrise, and a single peak occurred near sunset (Fig. 5). It seems probable that pointhead flounder larvae continuously fed in daytime, but they might have had low feeding success.

The number of nauplii in the digestive tracts of stage A larvae did not significantly differ among the four survey areas in daytime (Table 4). However a plankton survey conducted at the same time and place showed concentrations of all copepod nauplii except for *Microsetella* sp. at 20 m depth differed significantly among these areas, mean concentrations of copepod nauplii were higher at SFB (56.5 inds./L) and NFB (35.8 inds./L) than at OB (20.0 inds./L) and MFB (15.5 inds./L; Table 4). Accordingly, the amount of digestive tracts contents did not change when prey concentrations ranged from 15.5 to 56.5 inds./L, which suggests that larvae in the first feeding stage in and near Funka Bay in August 2001 were not starving.

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噴火湾とその周辺海域におけるソウハチ *Cleisthenes pinetorum* 仔魚の摂餌生態

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2001年8月10–20日の期間、北海道噴火湾とその周辺海域においてソウハチ *Cleisthenes pinetorum* 仔魚の摂餌生態を調査した。仔魚は成長とともに、初期餌料であるかいあし類ノープリウス（特に *Oithona similis* と *Pseudocalanus newmani*）からコペポダイトや尾虫類 *Oikopleura* 属の1種へと主要餌生物を移行させていた。 *Microsetella* 属の1種のノープリウスは調査海域に豊富に生息していたが、仔魚にはほとんど摂餌されていなかった。仔魚1個体が摂餌して

いた餌生物の平均個体数は08:55から高くなり、日没前後に最も高い値を示したことから、仔魚は視覚捕食者であることが示された。水域によってノープリウスの密度は変動していたにもかかわらず、仔魚1個体が摂餌していたノープリウスの個体数は異ならなかった。2001年夏季の噴火湾とその周辺海域において、摂餌開始期のソウハチ仔魚の飢餓による死亡の可能性は低いと考えられた。

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