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Title	Comparison of the nutritional transition date distributions of marbled sole larvae and juveniles in Hakodate Bay, Hokkaido
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Citation	Fisheries Science, 75(3), 619-628 https://doi.org/10.1007/s12562-009-0086-0
Issue Date	2009-05
Doc URL	https://hdl.handle.net/2115/38480
Rights	The original publication is available at www.springerlink.com
Type	journal article
File Information	75-3_p619-628.pdf

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Comparison of the nutritional-transition-date distributions of marbled sole larvae and juveniles in Hakodate Bay, Hokkaido

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Abstract To examine survival processes in marbled sole *Pseudopleuronectes yokohamae* larvae, nutritional-transition-date distributions (NTDDs) were compared between larvae and large juveniles (LJs) in Hakodate Bay from 2001 to 2003. NTDDs were used instead of hatch-date distributions because the onset of increment formation coincides with the timing of the transition from endogenous to exogenous nutritional sources for marbled sole. LJs were defined as being large enough to be safe from predation by the sand shrimp *Crangon uritai*. In 2001 and 2002, the ranges of the NTDDs of LJs largely overlapped with those of the larvae. However, in 2003, the early cohort (those whose otolith rings formed before 17 March) disappeared from the NTDDs during and after April, and the NTDDs of LJs were heavily biased toward a later period than those of the larvae. In 2003, Oyashio Coastal Water (<3 °C and ≤33.0 salinity) unexpectedly intruded into the bay in late March and lowered the water temperature from 6.3 °C on 6 March to 4.1 °C on 25 March. One possible cause of mortality in the early cohort of 2003 might be feeding failure caused by the extremely low water temperature.

Keywords diet, larvae and juveniles, marbled sole, mortality, nutritional transition, otolith microstructure analysis, Oyashio Coastal Water, *Pseudopleuronectes yokohamae*.

Introduction

Fluctuations in the recruitment level of marine fishes are mainly determined by variations in survival during the early life stages [1]. The marbled sole *Pseudopleuronectes yokohamae* [2] is a temperate flatfish species that is an important part of bottom-trawl and gill-net fisheries. Hakodate Bay (Fig. 1) is the northernmost habitat of this species, and spawning occurs from late winter (February) to early spring (April) [3], when the water temperatures are the lowest of the year [4]. Therefore, extremely low water temperature might affect larval survival of this species, and consequently date-selective survival processes might occur in this area. In addition, the relationship between the period when larvae are present and seasonal fluctuations in prey densities might be important to their survival (i.e. the match-mismatch hypothesis [5]).

Investigations of the early life history of marbled sole previously were conducted in Hakodate Bay. Transportation of pelagic larvae and immigration of juveniles [6], the feeding ecology of larvae and juveniles [4, 7], and predation by the sand shrimp *Crangon uritai* on demersal larvae and juveniles [8–10] have been studied. The early life history of marbled sole also has been studied in other locations and in the laboratory [11–12]. Otolith daily increments analysis is powerful tool for studying the early life ecology of fishes (e.g. age, growth, and date-selective survival), and otolith microstructure analysis of marbled sole larvae and juveniles provides information about nutrition transition (first feeding) date [13]. However, date-selective survival processes have not been studied for marbled sole.

The purpose of this study was to examine the relationship between the survival of marbled sole larvae and environmental factors in Hakodate Bay. To meet this goal, nutritional-transition-date distributions (NTDDs) were constructed based on otolith microstructure analysis and then were compared between larvae collected in March–April and large juveniles (LJs) collected later in the season. Environmental factors also were contrasted during the phases when larval survival was high and low.

Materials and methods

Study area

In Hakodate Bay, adult marbled sole females spawn their demersal and adhesive eggs on the bottom along a 20 m isobath in the eastern part of the bay mouth near Mt. Hakodate (Fig. 1). In March–April, a strong west-northwesterly wind induces a southward-offshore drift of surface water and a northward-inshore compensatory drift of deeper water in Hakodate Bay. Pelagic larvae are transported mainly into the eastern part of Hakodate Bay by the compensatory drift and are scarce in the western part and out of the bay (e.g. off Moheji, Toubetsu; Fig. 1) [6]. Settled juveniles are abundant off Nanaehama in the inner part of Hakodate Bay (Fig. 1) [14]. Therefore, larvae and juveniles were collected from a five-station transect (bottom depths ranged from 3–20 m) from Nanaehama in the direction of the spawning ground. This transect line was on the course of a ferryboat, and sampling could be conducted while keeping away from

commercial fishing gear.

Hakodate Bay is adjacent to Tsugaru Strait (Fig. 1), and the eastward Tsugaru Warm Current (TWC) flows from the Japan Sea to the Pacific Ocean throughout the year. The TWC is driven by the difference in the sea surface level between the Japan Sea (higher) and the Pacific Ocean (lower). From January to August, cold and less saline Oyashio Coastal Water (OCW) is distributed in the eastern mouth of the Tsugaru Strait [15]. In cold winters, the OCW can intrude into Hakodate Bay when the sea surface level drops because of over-cooling in the Japan Sea.

Sampling and treatment of specimens

In 2001–2003, sampling for larvae and small juveniles of marbled sole was conducted at about 10-day intervals in March–April at five stations (Fig. 1, Table 1). Sampling for LJs was carried out in July at Stns. 3, 5, and 10 on 30 June 2003 and in July 2001–2003. Pelagic larvae were collected in triplicate oblique tows of a plankton net (net-opening diameter: 80 cm; mesh aperture: 0.33 mm; a flow meter was installed at the mouth). Larvae and juveniles distributed near and on the sea bottom were collected by duplicate Hirota's sledge net tows (mouth opening: 60 × 40 cm; mesh aperture: 0.50 mm) [16]. When sampling in June and July, simultaneous tows of two sledge nets were conducted two or three times at each station.

Water temperature and salinity were measured with a CTD (SBE-19, Sea Bird Electronics Inc.,

Bellevue, Washington, USA) from the sea surface to the sea floor. Copepod nauplii are the principal prey for pelagic larvae of marbled sole (4.1–7.0 mm in notochord length) [4]. Water samples were collected with a van Dorn water sampler (6 l volume) at 5 m intervals from the sea surface to the sea floor, and copepod nauplii were concentrated by sieving this water with a hand net (mesh aperture: 0.040 mm). Larvae and juveniles of marbled sole were preserved in a 90% ethanol solution and copepod nauplii were preserved in 5% formalin solution.

The densities of larvae that collected by the plankton net were converted to number per square meters [6, 17–18] based on the rotations of the flow meter, the mouth opening of the net (0.50 m^2), and the length of warp. The catch efficiency of the sledge net was assumed to be 1. Yoshida et al. [19] examined the catch efficiency of Hirota's sledge net for marbled sole juveniles smaller than 44.1 mm in standard length (SL) and reported that the maximum efficiency (38%) occurred at 30.1 mm SL. However, the catch efficiency has not been reported for >44.1 mm SL marbled sole juveniles and for any other flatfish juveniles.

In Hakodate Bay, the pelagic larvae of marbled sole are distributed below the 5 m depth layer of the water column [6]. Thus, the mean density of copepod nauplii for each sampling date (inds./l) was calculated from their densities in water samples collected below the 5 m depth layer (11 samples). Similarly, the mean water temperature (°C) was calculated from the temperatures measured in the same 11 layers. The water mass with <3 °C and ≤33.0 salinity was defined as OCW [15].

If the F_{max}-test showed that the variances were heteroscedastic, data in this study were analyzed using the Kruskal-Wallis test; if the variances were homoscedastic, they were analyzed using a one-way ANOVA. Thereafter, post-hoc pairwise comparisons were conducted with the Steel-Dwass test.

Estimation of nutritional-transition-date distributions (NTDDs)

On each sampling date, 100 individuals (or all specimens for sampling dates with fewer than 100 larvae) of marbled sole larvae or juveniles were randomly chosen. On 9 March 2001, only six larvae were collected (0.14 inds./m^2) and some were broken, so these were not used for otolith analysis. Notochord length (NL) was measured for larvae and SL was measured for juveniles using digital calipers. Individuals for which otolith extraction or preparation failed were omitted from the later analyses.

Lapillar otoliths were extracted and mounted on glass slides with epoxy resin under a dissecting microscope. After lapilli were ground almost to the core with lapping film (9 μm particles), otolith images were magnified under a light microscope with translucent light (× 1000 magnification), and the number of increments was counted using an otolith measurement system (RATOC System Engineering Inc., Tokyo, Japan). See Joh et al. [13] for details about otolith preparation.

For marbled sole, the onset of daily otolith increment formation occurs at the transition from endogenous to exogenous nutritional sources [13], and the timing of the first feeding is delayed several

days after hatching. Therefore, in 2001–2003, the NTDDs were constructed instead of hatch-date distributions. For each sampling date, an individual nutritional-transition date was calculated as subtracting the number of increments from a sampling date. In this study, we did not estimate the means and modes of the NTDDs because the NTDDs were not corrected for differences in cumulative mortality (see Discussion). To confirm the adequacy of the subsampling of larvae and juveniles for the NTDD analysis, larvae and juveniles which were not used for the NTDD analysis (NA larvae and juveniles) were randomly measured their body length up to 50 individuals. Next, the body length distributions of larvae and juveniles were compared between NTDD-analyzed and NA.

The sand shrimp *C. uritai* is a predator of metamorphosing larvae and juveniles [8–10]; other demersal predators of them are rare in Hakodate Bay [20]. Therefore, marbled sole juveniles that were larger than the maximum vulnerable size for sand shrimp predation were assumed to get out of the phase that predation mortality was relatively high. The maximum ratio of body length of predated marbled sole to that of *C. uritai* is 0.32 [8], and the maximum body length of *C. uritai* has been reported to be 48.0 mm in Hakodate Bay [19]. The maximum vulnerable size of marbled sole juveniles was calculated to be 15.4 mm SL by multiplying 48.0 and 0.32. Therefore, large juveniles (LJ: >15.4 mm SL juveniles) collected on 30 June 2003 and in July 2001–2003 were defined as survivors in this study (i.e. they made it through the larval and early juvenile stages). The NTDDs of LJs were compared with those of larvae collected in March–April.

Analysis of digestive tract contents of larvae

To investigate the effect of low water temperature on larval feeding, the digestive tract contents of 31 larvae (or all specimens for sampling dates with fewer than 31 larvae) collected in late March 2001–2003 were identified to the lowest practical taxa and counted. Developmental stages of collected marbled sole larvae were determined by Minami [11]. Stage B larvae, which have already opened their mouth and started feeding but still have the yolk-sac [4, 11], were used for the dietary analysis because 16 stage B larvae that collected on 25 March 2003 were only available for dietary analysis after otolith analysis. Stage B larvae collected in 2001–2002 were used for comparison. Larvae with broken digestive tracts were omitted from the analysis. Data were expressed as the percentage frequency of occurrence (F%, the percentage of larvae that consumed a particular type of prey), percentage in number (N%, the percentage of each prey type consumed to the total number of prey items), feeding intensity (FI, the ratio of the total number of each prey type to the total number of larvae examined), and the feeding rate (the proportion of larvae with prey to the total number of larvae examined).

Results

Nutritional-transition-date distributions (NTDDs)

In 2001–2003, the nutritional-transition date of the larvae generally shifted to later period as sampling seasons passed (Fig. 2). The ranges of the NTDDs of the larvae were 10 March–18 April in 2001, 23 February–14 April in 2002, and 24 February–22 April in 2003. Those of LJs were 19 March–5 April in 2001, 26 February–8 April in 2002, 23 March–20 April in June 2003, and 20 March–11 May in July 2003. In 2001 and 2002, the NTDDs of LJs overlapped with those of larvae collected in March–April. In contrast, in 2003, the NTDDs of LJs were heavily biased towards a later season compared to the NTDDs of the larvae. Moreover, in 2003, the early cohort that changed its nutritional source before 17 March was not represented in the NTDDs of larvae collected during and after April.

Body length distributions

For each sampling date, the body length histograms of NTDD-analyzed larvae were roughly similar to those of NA larvae. In 2001–2003, the ranges of body length were 3.70–10.32 mm NL for NTDD-analyzed larvae and 2.99–10.35 mm NL for NA larvae (Fig. 3). Although the mean NL of NTDD-analyzed larvae (5.78 mm) significantly differed from that of NA larvae (5.96 mm; one-way ANOVA; $P = 0.04$), the difference was small (0.18 mm). In 2003 when the large mismatch of the NTDD occurred between larvae and LJs, the NLs did not significantly differ between NTDD-analyzed larvae and

NA larvae ($P = 0.07$).

Oceanographic environment

Mean water temperatures in March–April differed significantly during 2001–2003 (one-way ANOVA: $P < 0.001$, Fig. 4) and were highest in 2002, medium in 2001, and lowest in 2003 (Steel-Dwass test: all $P < 0.001$). In 2001, the mean water temperature was 6.3 °C in early March and increased to 8.4 °C in late April. In 2003, the mean water temperature on 6 March was 6.3 °C and decreased to 4.1 °C on 25 March, then reached 7.4 °C in late April. On 25 March 2003, OCW (<3ºC and ≤33.0 salinity) intruded into the mid-water layers from offshore (Fig. 5); however, OCW was not observed on 14 March or 1 April. The isohaline (33.0) was located in the 6–9 m depth layers on 25 March and was distributed in the ≤1–3 m depth layer on 14 March and 1 April. OCW was not observed in 2001 and 2002.

During March and April, the density of copepod nauplii differed significantly among the three years (Kruskal-Wallis test, $P < 0.001$; Fig. 6); densities in 2001 and 2003 were equally high but were low in 2002 (Steel-Dwass test: 2001 vs. 2003, $P > 0.05$; 2001 vs. 2002 and 2002 vs. 2003, both $P < 0.001$). In 2001, the mean density in early March was 28.1 inds./l; increased to 83.9 inds./l in late April. In 2002, the mean density in mid-March was relatively low (11.9 inds./l) but increased to 110 inds./l in late April. In 2003, the seasonal change in the mean density of copepod nauplii was small and the mean densities were

relatively high, ranging between 37.3 and 61.5 inds./l.

Diet of stage B larvae in late March

In late March 2001–2003, the feeding rate of stage B larvae ranged from 31% to 45% (Table 2). Diatoms and invertebrate eggs were found in all years. In 2001 and 2002, tintinnids, rotifers, and copepod nauplii also were found, but they were not seen in 2003.

Discussion

In 2001−2003, the nutritional-transition date of the larvae generally shifted to later period as sampling seasons passed (Fig. 2). This phenomenon might be related to our definitions of developmental stages. As the spawning season proceeds, the developmental stages of the cohort-of-the-year advance and the old individuals become juveniles. Naturally, juveniles were not included in larval category, and they were not included in the larval NTDDs. This also means that samples need to be collected several times during a spawning period to determine the duration of time that larvae are present. In this study, sampling was conducted several times at relatively short (about 10 days) intervals in March–April. Thus, we believe that our sampling covered the period during which larvae were present.

Almost all larvae of the early cohort (individuals that switched their nutritional source before 17 March) in 2003 might have die during March. In 2001–2002, the NTDDs of LJs overlapped with those of larvae collected in March–April (Fig. 2). In contrast, in 2003, the range of NTDDs of LJ was heavily biased toward a later period (20 March–11 May), and the early cohort was not detected during and after April. On 6 and 14 March 2003, a large number of larvae were collected (6 March: 350 individuals, 13.6 inds./m^2; 14 March: 1,604 individuals, 9.9 inds./m^2), and all were the part of the early cohort. Thus, a relatively large cohort disappeared in the NTDD in April, June, and July. Late-hatched (young) individuals experienced lower cumulative mortality than early-hatched (old) individuals; therefore, the proportion of early-hatched individuals in the hatch-date distribution was lower and that of late-hatched was higher than the true proportions (mortality effects) [21]. In this study, we did not correct for this mortality because the age-specific mortality of marbled sole larvae has not been clarified. Thus, even in the case where no date-selective mortality occurred, the NTDD of LJs might be biased toward the later season compared to that of the larvae collected earlier. However, the large mismatch of the NTDDs was only observed in 2003, even though the sampling season was the same for all years studied (2001–2003). Moreover, the early cohort did not include in April and in the juvenile sample on 30 June 2003. Thus, we concluded that the large mismatch of the NTDDs in 2003 was the consequence of extremely high mortality of the early cohort and that the early cohort in 2003 was probably removed before April. In 2003, the NL distributions of NTDD-analyzed larvae did not differ from those of NA; therefore,

subsampling bias for the NTDD analysis might be also small.

The mortality of the early cohort in 2003 was probably caused by the extremely low water temperature induced by OCW. OCW intrudes into Hakodate Bay from the Pacific Ocean in cold winters, like that of 2003. Water temperature is an important environmental factor that has both direct and indirect effects on larval growth and survival. Several potential relationships may exist between low water temperature and larval mortality. Previously reported digestive-tract-contents analysis of marbled sole larvae in this area in 1998–2000 suggests that low water temperature might have a greater impact on the feeding intensity of larval marble sole than prey abundance [4]. Copepod nauplii are the principal prey item for most marine fish larvae [22], including marbled sole larvae [4]. In Hakodate Bay, water temperatures during late March–mid-April were higher than 7.5 °C in 1998 and 2000 and lower than 7.5 °C in 1999. The cause of low water temperatures in 1999 was not the intrusion of OCW [4]. Mean copepod naupliar densities in March–April were similar in these years (1998: 18.3–54.2 inds./l; 1999: 15.8–50.7 inds./l; 2000: 15.3–43.1 inds./l). The feeding intensities of marbled sole larvae were high in 1998 (1.33 nauplii/larva) and 2000 (0.93 nauplii/larva) but low in 1999 (0.22 nauplii/larva). From these results, Nakagami [4] concluded that the ability of larvae to capture mobile prey items in 1999 was negatively affected by low water temperature despite the relatively high abundance of nauplii. First-feeding stage larvae mainly feed on mobile prey items such as copepod nauplii and rotifers and on slightly mobile tintinnids and inactive diatoms. As the larvae develop, their preference for copepod

nauplii abruptly increases and diatoms and tintinnids disappear from the digestive tracts of marbled sole larvae >6.1 mm NL [4]. Diatoms are difficult to digest and do not sustain sufficient larval development [22]. Tintinnids have low mobility, are easily digested, and play a role as initial prey items for first-feeding larvae, but they can not support the nutritional requirements of well-developed larvae [23]. In this study, the larvae that disappeared from the NTDDs in 2003 switched their nutritional source before 17 March. When OCW intruded in late March 2003, most of the early cohort might have been well developed and highly dependent on mobile prey items such as copepod nauplii and rotifers as their food source. Therefore, the early cohort might have starved because of their reduced ability to capture mobile prey in water of extremely low temperature.

The failure of stage B larvae to feed on mobile and slightly mobile prey items in late March 2003 supported the premise that feeding is restricted by extremely low water temperature. Marbled sole larvae start feeding at stage B, but feeding rate at this stage is low [4, 11]. In this study, stage B larvae caught on 25 March 2003 fed only on immobile prey items (e.g. diatoms and invertebrate eggs) at 4.1 °C (Table 2). In contrast, in 2001 (7.4 °C) and 2002 (8.5 °C), slightly mobile (tintinnids) and mobile prey organisms (rotifers and copepod nauplii) were observed in their digestive tracts along with immobile prey. The stage B larvae that were collected on 25 March 2003 and analyzed for digestive tract contents were younger than the early cohort. Unfortunately, on 25 March 2003, no stage C and older larvae were available for the diet analysis. Thus, the feeding condition of the early cohort under extremely low water temperature

condition could not be analyzed directly.

Larvae that began feeding around 25 March 2003 when OCW intruded did not disappear from the NTDDs of April and later. Most of the larvae collected on 25 March 2003 were <6 mm NL and might have been at or shortly after the first-feeding stage (Fig. 3), and they endured the severe temperature condition by feeding on immobile prey items such as diatoms and invertebrate eggs (Table 2).

The mean copepod naupliar densities in March 2003 were 2.7–3.2 times greater than those in 2002, when prey densities were the lowest within the 2001–2003 study periods (Fig. 6). Nevertheless; nutritional-transition-date selective mortality occurred in 2003 but not in 2002. Thus, OCW did not cause a decline in naupliar abundance, and the mortality in the early cohort in 2003 cannot be explained by a prey shortage.

In 2003, OCW might have swept marbled sole pelagic larvae from Hakodate Bay toward an area unsuitable for survival via two possible processes: 1) the early cohort in Hakodate Bay were thrust out by OCW or 2) the recession of the OCW removed the pelagic larvae that switched around 25 March away from the bay. On 25 March 2003 when OCW intruded, a greater density of pelagic larvae was observed at offshore stations (11.7 inds./m^2 at Stn. 15 and 8.7 inds./m^2 at Stn. 20) than at inshore stations (2.1–6.3 inds./m^2 at Stns. 3, 5, and 10), and most of the larvae collected might have been at or shortly after the first-feeding stage (<6 mm NL, Fig. 3). If the pelagic larvae were removed from the bay by the recession of OCW, the larvae that changed their nutritional source around 25 March would have

disappeared from the NTDDs after April, but they existed after April (Fig. 2). Marbled sole larvae begin their demersal life before the completion of eye migration [24]. Settled juveniles and well-developed larvae of flatfishes that are distributed near and on the sea bottom are not much affected by the current [25]. Therefore, well-developed individuals of the early cohort likely would not have been advected by the intrusion of OCW. However, our data do not provide direct evidence to reject the hypothesis that the early cohort that still belonged to pelagic stages was advected outside the bay.

The present study described the first investigation of NTDDs for marbled sole larvae. Our results demonstrated that NTDD-selective mortality in marbled sole larvae occurred in conjunction with an unexpected intrusion of OCW in Hakodate Bay. We suggest two possible hypotheses for the occurrence of NTDD-selective mortality in 2003: feeding failure caused by extremely low water temperature and the transfer of pelagic larvae from inside to outside of the bay. Hakodate Bay is the northernmost habitat of marbled sole and the relatively high water temperature here may guarantee larval survival. Therefore, we suggest that thermal transport by the Tsugaru Warm Current is important for the reproduction of marbled sole in their northernmost habitat. Further studies of age-specific mortality of marbled sole larvae are needed, as are studies of the transportation process of pelagic larvae.

Acknowledgements We would like to express our gratitude to Prof. T. Takahashi, Prof. Y. Sakurai and Assoc. Prof. T. Nakatani for their valuable advice during our study. We thank Y. Hiraoka for her support

with dietary analysis. We also thank H. Ishizaki, I. Oda and the members of the Marine Bioresources Ecology Laboratory (Hokkaido University) for their support in field sampling. This work was supported by the Grant-in Aid for Primary Study of Fisheries Encouragement to T. Takatsu from Hakodate City Hall, and by the 21st century COE Program “Marine Bio-Manipulation Frontier for Food Production” of the Ministry of Education, Culture, Sports, Science and Technology of Japan. Our English in this manuscript was polished up by International Science Editing Ltd.

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Figure captions

Fig. 1 The location of sampling stations and isobaths in Hakodate Bay. Solid circles indicate sampling stations used in this study (each numeral shows the depth at each station) and solid squares show the sampling stations of Nakagami et al. [6] for the spatial distribution of larval marbled sole

Fig. 2 Comparison of nutritional-transition-date distributions (NTDDs) of marbled sole larvae and juveniles among sampling dates in 2001–2003. Solid bars showed the NTDDs of LJs (>15.4 mm standard length juveniles collected in June and July). The ranges of arrows show the ranges of the nutritional-transition date of the larvae

Fig. 3 The body length (notochord length and standard length) histograms of NTDD-analyzed and NA larvae and juveniles of marbled sole in 2001–2003. Bars and lines indicate NTDD-analyzed and NA larvae and juveniles, respectively. The number of individuals of the NTDD-analyzed larvae and juveniles were often smaller than those of Fig. 2 because body lengths of some individuals could not be measured due to their broken bodies

Fig. 4 Seasonal changes in the mean water temperature (≥5 m depth layer) in Hakodate Bay from March to April in 2001–2003

Fig. 5 The vertical profiles of water temperature (solid line, °C) and salinity (broken line) on 14 March, 25 March, and 1 April in 2003. The dotted layer indicates the sea floor. The shaded area for 25 March indicates Oyashio Coastal Water (<3.0 °C and <33.0 salinity) mass

Fig. 6 Seasonal changes in mean density of copepod nauplii as a principal prey item for marbled sole larvae in Hakodate Bay (≥5 m depth layer) from March to April in 2001–2003

Table 1 The numbers of sampling casts and the density of larvae collected with a plankton net and that of larvae and juveniles collected with a sledge net

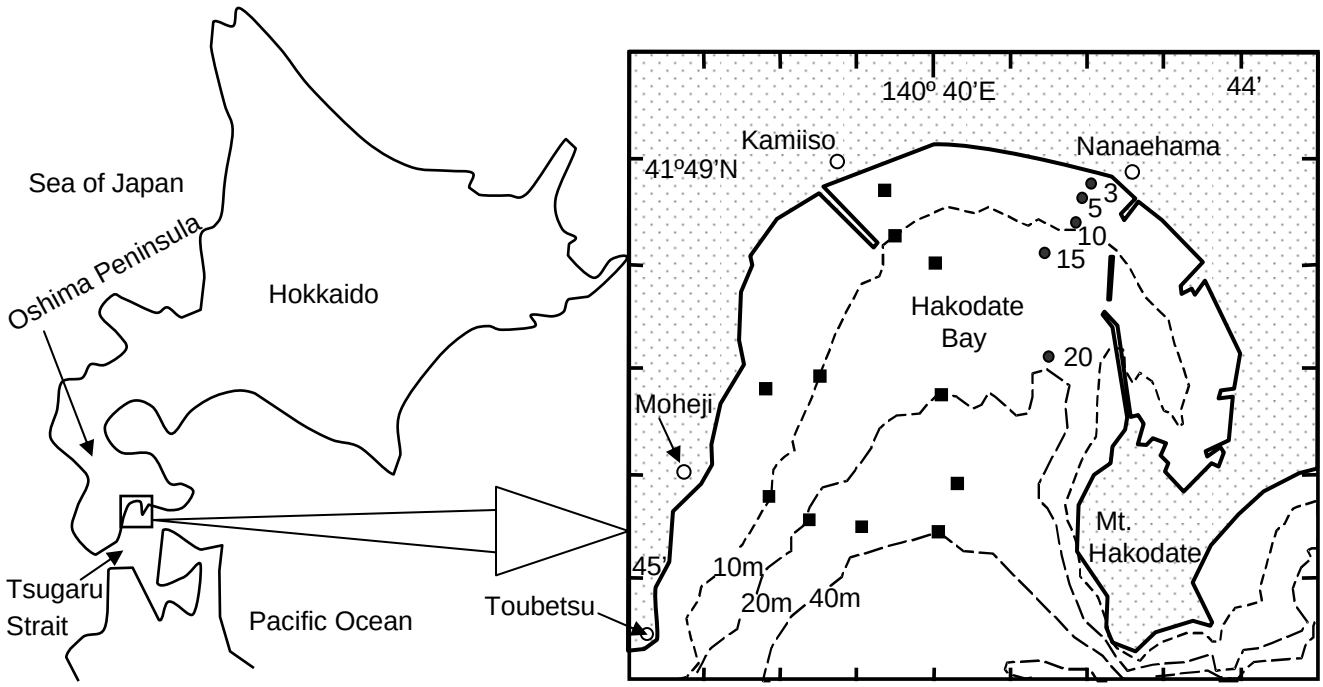
Year	Number of casts			Density of larvae and juveniles		Number of individuals collected	
Date	van Dorn bottle	Plankton net	Sledge net	Plankton net (inds./m^2)	Sledge net (inds./100m^2)	Larvae	Juveniles
2001							
9 March	16	15	10	0.1	0 (0)	6	0
26 March	16	15	10	8.9	0.5 (0)	403	0
6 April	16	15	14	0.7	0 (0)	21	0
25 April	16	15	14	1.1	0.8 (0.0)	54	1
10 July	0	0	18	-	- (0.8)	0	23
2002							
13 March	16	15	5	18.5	3.7 (0)	407	0
25 March	16	15	10	16.9	10.1 (0)	511	0
5 April	16	15	14	61.3	73.7 (0)	2922	0
15 April	16	13	8	2.2	10.3 (2.6)	207	44
24 April	16	15	18	0.1	4.1 (2.2)	127	66
26 July	0	0	12	-	- (2.3)	0	45
2003							
6 March	16	15	10	13.6	0.3 (0)	350	0
14 March	16	15	12	59.8	9.9 (0)	1604	0
25 March	16	15	10	6.4	3.8 (0)	231	0
1 April	16	15	12	5.7	0.1 (0)	179	0
15 April	16	15	12	4.5	1.9 (0)	125	0
25 April	16	15	12	0.2	3.3 (0)	68	0
30 June	0	0	10	-	- (2.0)	0	33
30 July	0	0	13	-	- (1.6)	0	34

Numbers in parentheses represent the density of juveniles.

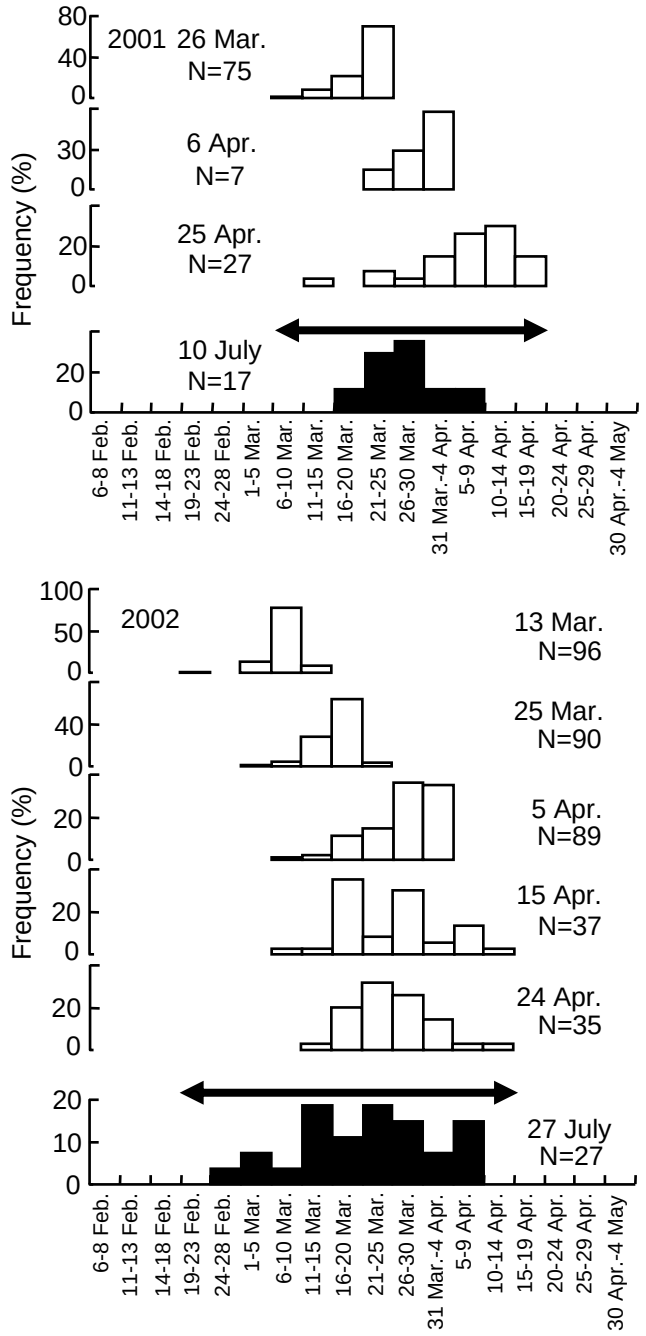
Table 2 Diet of *Pseudopleuronectes yokohamae* stage B larvae by percent frequency (F%), percent by number (N%), and feeding intensity (number of prey/larva, FI) in late March 2001, 2002, and 2003

Sampling date	26 Mar. 2001			25 Mar. 2002			25 Mar. 2003		
Taxon	F%	N%	FI	F%	N%	FI	F%	N%	FI
Diatom	10	16	0.10	17	53	0.31	25	67	0.25
Copepoda nauplius	3	5	0.03	0	0	0	0	0	0
Rotatoria	10	21	0.13	7	12	0.07	0	0	0
Tintinnina	19	37	0.23	7	12	0.07	0	0	0
Invertebrate egg	0	0	0	0	0	0	6	17	0.06
Unidentified	10	21	0.13	14	24	0.14	6	17	0.06
Feeding rate		45			34			31	
Total number of prey		19			17			6	
Number of larvae examined		31			29			16	
Water temperature*		7.4 °C			8.5 °C			4.1 °C	

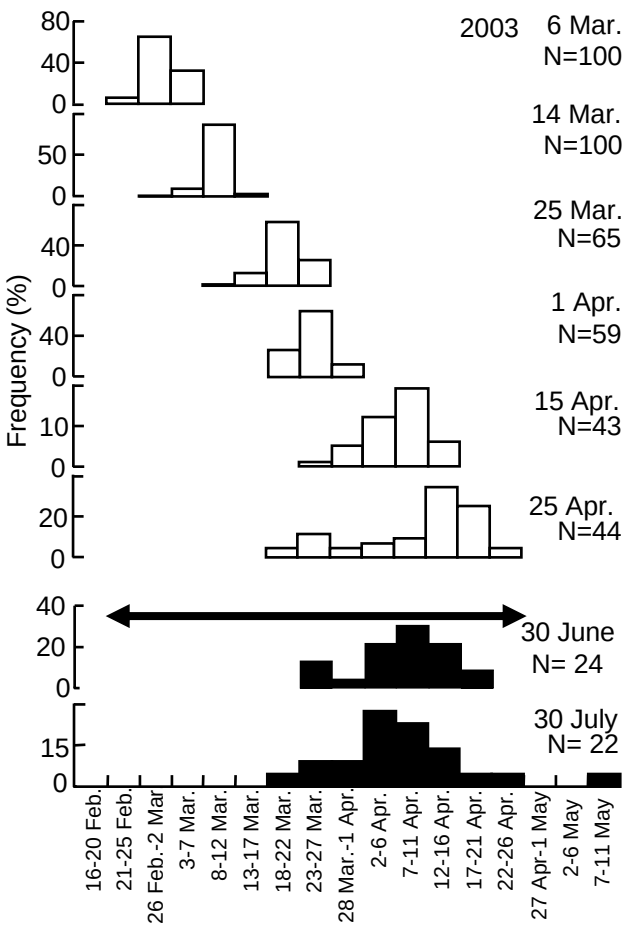
*: mean temperature below the 5 m depth layers.


Sea of Japan
Oshima Peninsula
Hokkaido
Tsugaru
Strait
Pacific Ocean
Toubetsu
140º 40'E
44'
41º49'N
45'
Kamiisso
Nanaehama
Moheji
Hakodate
Bay
Mt.
Hakodate
3
5
10
15
20
10m
20m
40m

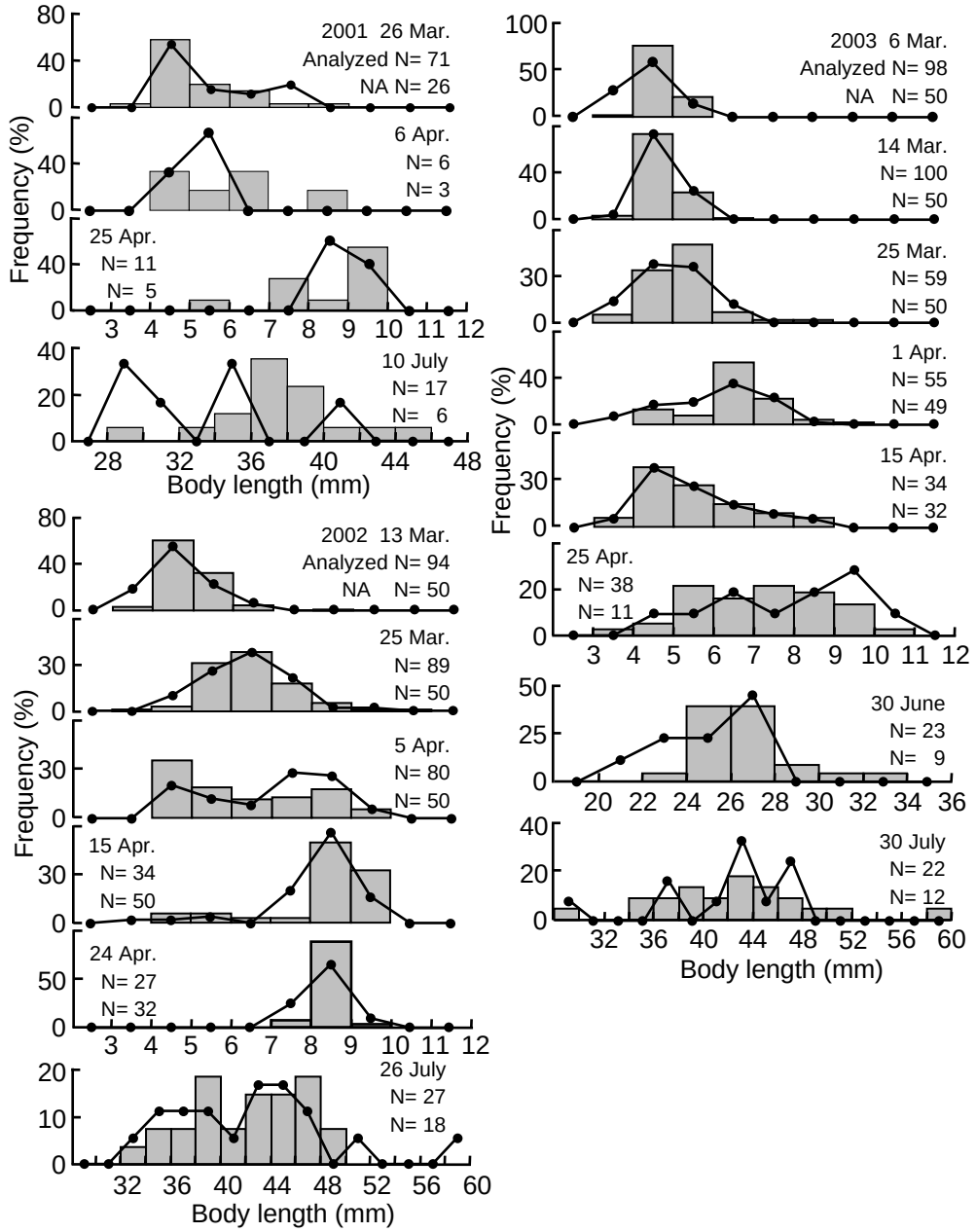
174 mm


2001
26 Mar.
N=75
6 Apr.
N=7
25 Apr.
N=27
10 July
N=17
Frequency (%)
6-8 Feb.
11-13 Feb.
14-18 Feb.
19-23 Feb.
24-28 Feb.
1-5 Mar.
6-10 Mar.
11-15 Mar.
16-20 Mar.
21-25 Mar.
26-30 Mar.
31 Mar.-4 Apr.
5-9 Apr.
10-14 Apr.
15-19 Apr.
20-24 Apr.
25-29 Apr.
30 Apr.-4 May

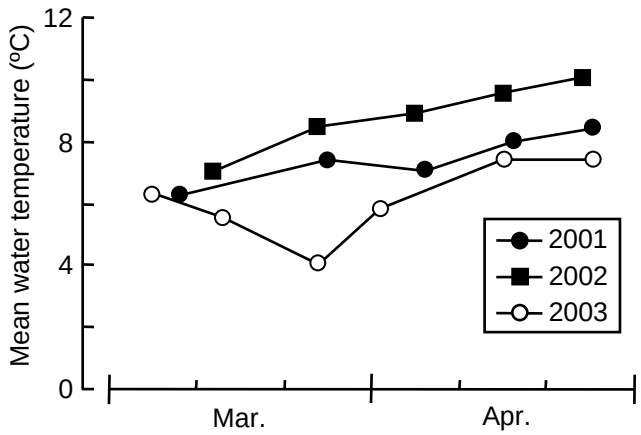
2002
13 Mar.
N=96
25 Mar.
N=90
5 Apr.
N=89
15 Apr.
N=37
24 Apr.
N=35
27 July
N=27
Frequency (%)
6-8 Feb.
11-13 Feb.
14-18 Feb.
19-23 Feb.
24-28 Feb.
1-5 Mar.
6-10 Mar.
11-15 Mar.
16-20 Mar.
21-25 Mar.
26-30 Mar.
31 Mar.-4 Apr.
5-9 Apr.
10-14 Apr.
15-19 Apr.
20-24 Apr.
25-29 Apr.
30 Apr.-4 May


2003
6 Mar.
N=100
14 Mar.
N=100
25 Mar.
N=65
1 Apr.
N=59
15 Apr.
N=43
25 Apr.
N=44
30 June
N= 24
30 July
N= 22
Frequency (%)
16-20 Feb.
21-25 Feb.
26 Feb.-2 Mar
3-7 Mar.
8-12 Mar.
13-17 Mar.
18-22 Mar.
23-27 Mar.
28 Mar.-1 Apr.
2-6 Apr.
7-11 Apr.
12-16 Apr.
17-21 Apr.
22-26 Apr.
27 Apr-1 May
2-6 May
7-11 May

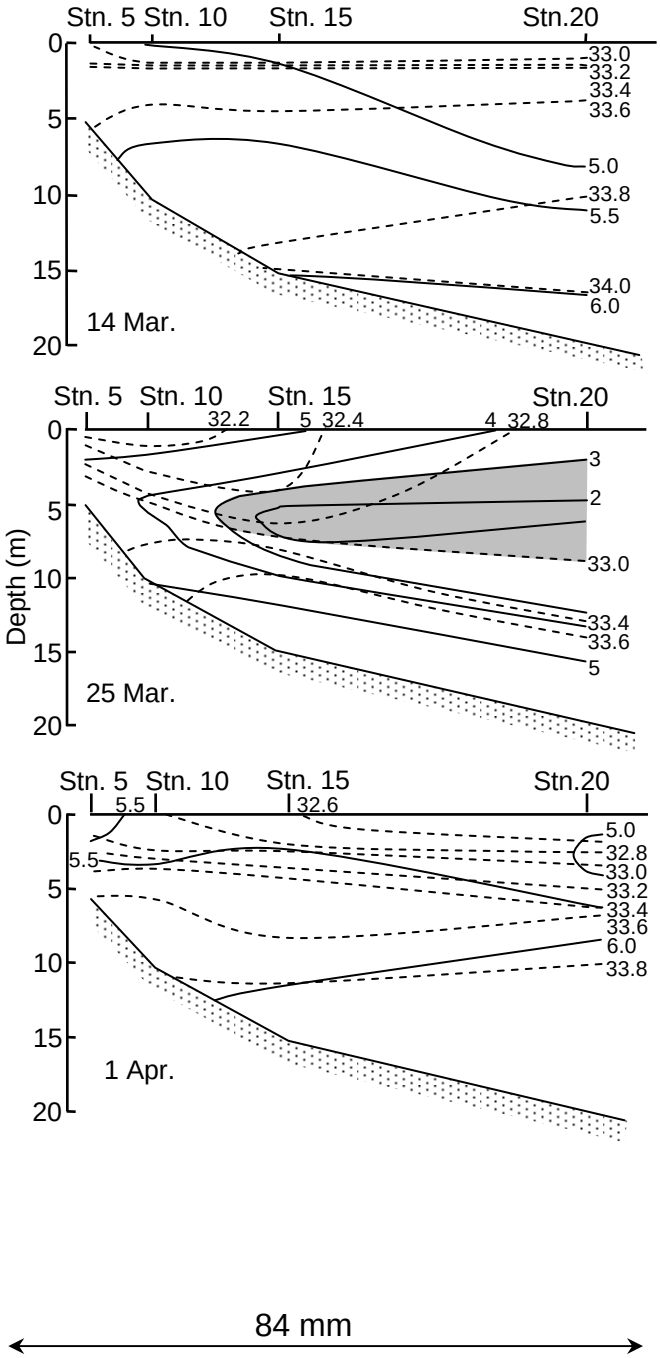
174 mm


2001 26 Mar.
Analyzed N= 71
NA N= 26
6 Apr.
N= 6
N= 3
25 Apr.
N= 11
N= 5
10 July
N= 17
N= 6
Frequency (%)
Body length (mm)
2002 13 Mar.
Analyzed N= 94
NA N= 50
25 Mar.
N= 89
N= 50
5 Apr.
N= 80
N= 50
15 Apr.
N= 34
N= 50
24 Apr.
N= 27
N= 32
26 July
N= 27
N= 18
Frequency (%)
Body length (mm)
2003 6 Mar.
Analyzed N= 98
NA N= 50
14 Mar.
N= 100
N= 50
25 Mar.
N= 59
N= 50
1 Apr.
N= 55
N= 49
15 Apr.
N= 34
N= 32
25 Apr.
N= 38
N= 11
30 June
N= 23
N= 9
30 July
N= 22
N= 12
Frequency (%)
Body length (mm)

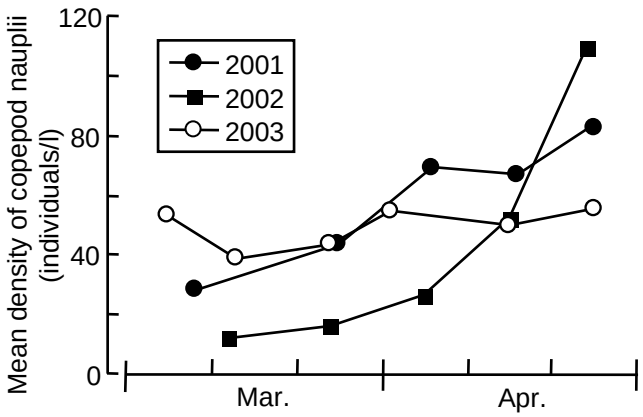
129 mm



84 mm


Stn. 5
Stn. 10
Stn. 15
Stn.20
0
5
10
15
20
33.0
33.2
33.4
33.6
5.0
33.8
5.5
34.0
6.0
14 Mar.
Stn. 5
Stn. 10
Stn. 15
Stn.20
32.2
5
32.4
4
32.8
Depth (m)
3
2
33.0
33.4
33.6
5
25 Mar.
Stn. 5
Stn. 10
Stn. 15
Stn.20
5.5
32.6
5.0
32.8
33.0
33.2
33.4
33.6
6.0
33.8
1 Apr.

84 mm


Mean density of copepod nauplii
(individuals/l)
120
80
40
0
2001
2002
2003
Mar.
Apr.

84 mm

北海道函館湾におけるマコガレイ仔稚魚の内部栄養から外部栄養への転換日分布の比較

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マコガレイ仔魚の生残過程を調べるため、耳石日周輪解析を行い、内部栄養から外部栄養への転換日分布（以下：NTDD）を仔魚と稚魚との間で比較した。2001～2002 年では、仔魚と稚魚の NTDD の範囲はおおむね重複していた。一方、2003 年では 3 月 17 日以前に栄養転換した個体が 4 月以降の NTDD から消失していた。2003 年には 3 月下旬に沿岸親潮が函館湾内へ流入し、湾内の水温が著しく低下した。この著しい低水温により 3 月 17 日以前に栄養転換した仔魚のほとんどが死亡した可能性が示唆された。