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Ontogenetic diel vertical migration of the planktonic copepod *Calanus sinicus* in the Inland Sea of Japan

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Abstract

The ontogenetic diel vertical migration of the planktonic copepod *Calanus sinicus* was investigated in the Inland Sea of Japan in summer 1988, when the water was thermally stratified with a thermocline of ca 5 °C between 35 and 45 m. Stage-specific differences in the diel vertical migration behavior of *C. sinicus* were found. Eggs were spawned primarily within the surface-waters between midnight and dawn by ascending females, and sank gradually to deeper waters until they hatched into nauplii. Non-feeding nauplius stages (NI and II) were distributed throughout the water column, but the first feeding stage (NIII) performed an ontogenetic upward migration. NIV to VI and copepodite (C) stages I to III continuously aggregated in the phytoplankton-rich euphotic layer. However, the depth of the median CI to III populations descended as stage progressed. The onset of prominent diel vertical migration took place in CIV, and the amplitude of vertical migration increased with age, being maximal in adult females (CVI♀). Adult males (CVI♂), however, remained in the layer below 20 m, and did not migrate dielly. The ecological significance of ontogenetic diel vertical migration is discussed.

Introduction

Planktonic copepods of the genus *Calanus* (which consists of 11 species; Bradford 1988), frequently dominate the marine zooplankton community in temperate-, boreal- and arctic-waters. Since they are herbivorous or omnivorous, they occupy the trophic level between phytoplankton or microheterotrophs and large carnivores including fish. Hence, *Calanus* has been one of the most popular subjects for research on copepod biology and ecology (Marshall and Orr 1955).

Calanus sinicus is distributed in the East China Sea, Yellow Sea and coastal waters of Japan (Brodsky 1965, cited by Kidachi 1979a, b) and is regarded as the most southerly distributed species of the genus in the northern hemisphere. This species often constitutes an important component of the zooplankton biomass in continental shelf waters (Lin and Li 1984 in Xiamen Harbor, China; Uye et al. 1986 in the Inland Sea of Japan). However, ecological studies on this species are relatively few, being confined to seasonal occurrence (Hirota 1964, 1979, Kidachi 1979a, b, Lin and Li 1984), reproduction (Lin and Li 1986) and development (Li and Fang 1983, Uye 1988). Diel vertical migration is a well-known phenomenon in planktonic copepods, especially in the genus *Calanus* (Russell 1927, Cushing 1951, Marshall and Orr 1955, Williams 1985, Williams and Conway 1980, 1984), and many explanations (light, gravitation, pressure, endogenous rhythm, avoidance of predation, feeding, etc.) have been suggested as possible factors to induce (Banse 1964). The vertical migratory behavior of *Calanus* has usually been examined only in late copepodites and adults, and little is known about migratory behavior in younger stages. Diel vertical migration of all stages has not been studied for *C. sinicus*, although Kadota (1984) investigated day and night difference in the vertical distribution patterns of CV and adults in Sagami Bay, central Japan.

We have been investigating the population growth and vertical distribution of *Calanus sinicus* in and around the Inland Sea of Japan in order to understand the role of this species in the biological production of this area. This paper describes the diel vertical migration of eggs, nauplii, copepodites and adults sampled in the summer of 1988 when the water was quite thermally stratified.

Materials and methods

A series of samplings were undertaken from the T. and R. V. "Toyoshio Maru" at a station (34°04.22′N, 134°51.25′E, average depth: 57 m, maximum tidal range: 1.45 m) in Kii Channel (Fig. 1), at 3 h intervals between 09.00 on 31 August and 09.00 hrs on 1 September 1988. Water from 12

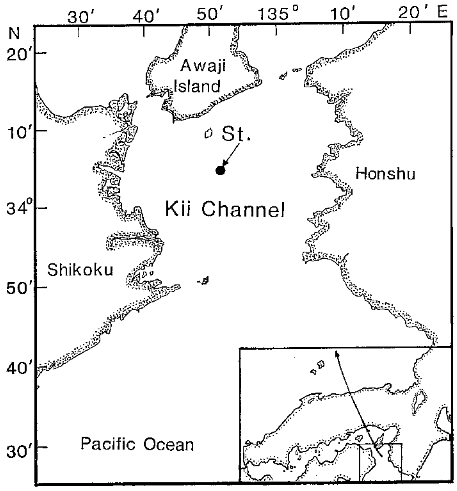

Fig. 1. Kii Channel of the Inland Sea of Japan with location of sampling station (St.)

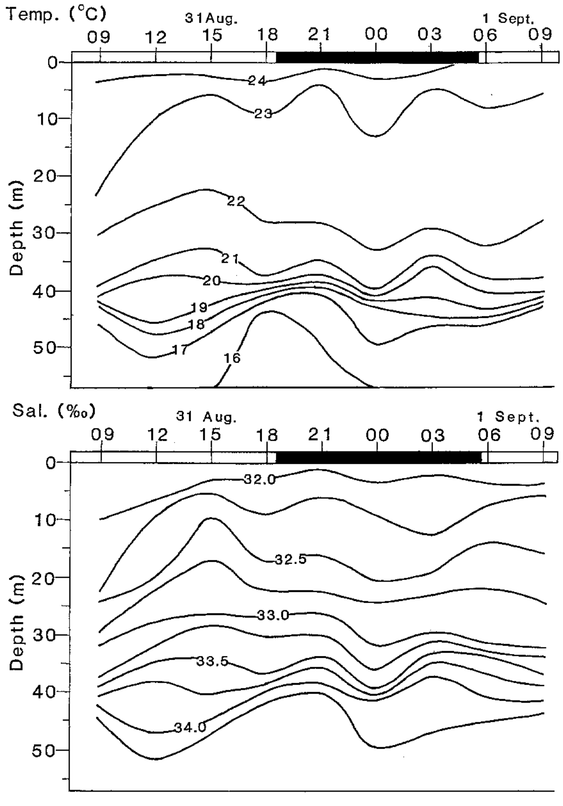

Fig. 2. Diel variation in vertical distribution of temperature and salinity from 09.00 hrs, 31 August, to 09.00 hrs, 1 September, 1988. Open and black bars represent day- and night-time, respectively

depths at 5 m intervals between the surface and 55 m, was pumped on deck using a submersible pump (Ebara, 40BHS-3-6-1.5, hose i.d. = 50 mm, flow rate = 230 l min^{-1}). From each depth, 1.15 m^3 of water was filtered using a conical net with a 96 μm mesh opening. Samples were preserved in 5% formalin-seawater solution and brought back to the land laboratory. Later, all developmental stages, including eggs, of *Calanus sinicus* were counted for each sample. Because of their morphological similarity, nauplius stages (N) I and II were counted together. The count of each developmental stage was converted to individual numbers per unit volume of water. For each developmental stage, the depth of the median population was calculated. The difference in their mean values tested (Students' *t*-test) between daytime (from 06.00 to 15.00 hrs) and night-time (from 18.00 to 03.00 hrs) for the criteria of diel vertical migration.

At 3 h intervals, vertical profiles of temperature and salinity were recorded using a memory STD (Alec Co.). Vertical profiles of chlorophyll *a* concentration were only determined at 12.00 hrs on 31 August and at 00.00 hrs on 1 September. From each depht 100 ml of water was filtered onto glassfiber filters (Whatman GF/C), extracted in 90% acetone, and chlorophyll *a* measured fluorometrically (Turner Designs) following the method of Strickland and Parsons (1972).

Results

Hydrographic conditions

The water column was quite thermally stratified during this investigation: the surface temperature was more than 24 °C and the near bottom temperature was ca 16 °C (Fig. 2). Temperature gradually decreased with depth in the upper 30 m. A thermocline of ca 5 °C was observed between ca 35 and 45 m, although its sharpness and depth varied with time, and probably with tidal cycle (high tide 20.47 hrs on 31 August and 09.28 hrs on 1 September; low tide 14.37 hrs on 31 August and 03.09 hrs on 1 September). Salinity also exhibited considerable change, from less than 32‰ at the surface to more than 34.25‰ near the bottom. The increase in salinity was largest (1.25‰ of increase) from ca 30 to 43 m, coinciding with the thermocline. Chlorophyll *a* concentration was >1 μg l^{-1} in the upper 20 m with a peak concentration of 5.10 μg l^{-1} (Fig. 3).

Sampling efficiency by pump

To evaluate the avoidance capability of *Calanus sinicus* from the stream generated by the pump, copepod density was compared between pump and net (0.45 m diam., 96 μm mesh opening, vertical tow from the bottom to the surface) samples collected at 12.00 and 18.00 hrs on 31 August, and 00.00 and 06.00 hrs on 1 September. The density of copepods sampled by the pump was always lower than that of the net (Fig. 4). Even eggs were undersampled by the pump, suggesting that sampling of the water at 5 m intervals failed to include the depth at which peak egg abundance occurred. The difference in copepod density increased as stages progressed; adult females were least efficiently collected (Fig. 4). We assumed the sampling efficiency of the pump was constant for a given developmental stage during our study.

Diel vertical migration

Calanus sinicus eggs were distributed throughout the water column (Fig. 5), although abundance exhibited remarkable variation throughout the investigation. They were most abundant at dawn (06.00 hrs), decreased progressively to a minimum in the evening (21.00 hrs), and then increased (Table 1). Coinciding with the decrease in abundance, the vertical distribution of eggs varied with time, i.e., the depth of the median egg population moved from 12 m at 06.00 hrs to 37 m at 15.00 hrs, and then rose (Table 2).

NI and II were also distributed throughout the water column, but exhibited more homogeneous distribution than eggs (Fig. 5). Their abundance was relatively constant during the investigation, except at 00.00 and 03.00 hrs when it was higher than the other occasions (Table 1). Their vertical distribution was not significantly different between day and night samples, and the depth of the median population ranged from 23 to 36 m (Table 2).

NIII to VI exhibited essentially similar vertical distribution: the majority of the population was above the thermocline (Fig. 5). Although a part of NIII population remained in the deeper layer, NIV to VI aggregated in the upper 20 m (median depth: 3 to 11 m), where the chlorophyll *a* concentration was higher. Although there was no statistical difference in mean median depth between day and night-time, individuals of NIV to VI, which occurred at the surface, were significantly ($p < 0.03$) more abundant during night-time (in this case from 21.00 to 06.00 hrs) than daytime (from 09.00 to 18.00 hrs). This indicates the occurrence of a small scale diel vertical migration in these stages.

Most of the copepodite stages (C I to III) were restricted to the upper layer throughout the day (Fig. 6), but the daily median depth tended to increase as the stage progressed (Table 2). There was no significant difference in the median depth between day- and night-time (Table 2), indicating that early copepodites did not undergo diel vertical migration.

CIV and V extended their distributional range to nearly the whole water column (Fig. 6), and exhibited clear diel

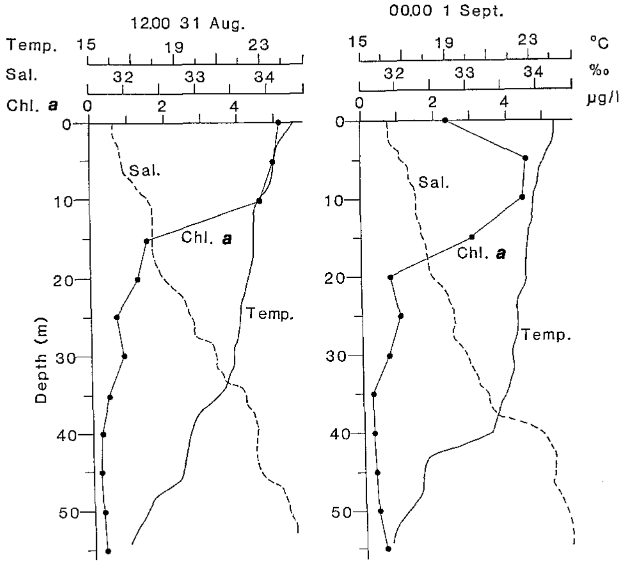

Fig. 3. Vertical profiles of temperature (continuous line), salinity (dashed line) and chlorophyll *a* (continuous line with filled circles) concentration at 12.00 hrs, 31 August, and 00.00 hrs, 1 September, 1988

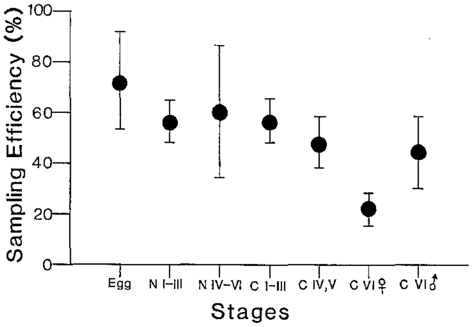

Fig. 4. *Calanus sinicus.* Mean efficiency of developmental stages (N and C refer to nauplius and copepodite, Roman numerals indicate stage) sampled using a submersible pump. Values expressed as percentage of abundance determined by a vertical haul of a 96 µm-mesh plankton net. Vertical bars denote standard deviation of mean

Table 1. *Calanus sinicus.* Variation in average density (m^{-3}, corrected for sampling efficiency) of each developmental stage from 09.00 hrs, 31 August, to 09.00 hrs, 1 September, 1988. Stages are E: egg; N: nauplius; C: copepodite

Stage	Day (hrs)			Night (hrs)				Day (hrs)	
	09.00	12.00	15.00	18.00	21.00	00.00	03.00	06.00	09.00
E	3426	2043	1213	361	204	993	1160	3556	1961
NI, II	347	185	220	280	416	864	798	413	247
NIII	1473	640	356	567	820	1018	198	349	427
NIV	877	403	173	205	92	542	118	137	242
NV	765	177	90	102	63	627	102	75	118
NVI	375	120	98	155	115	495	63	65	48
CI	145	49	71	67	189	162	13	107	165
CII	67	62	60	76	187	102	24	102	105
CIII	34	64	49	93	122	38	73	111	89
CIV	61	67	72	69	76	42	116	59	65
CV	97	80	69	65	82	65	97	78	114
CVI ♀	191	120	493	329	187	213	196	173	307
CVI ♂	33	22	31	22	18	18	31	27	29

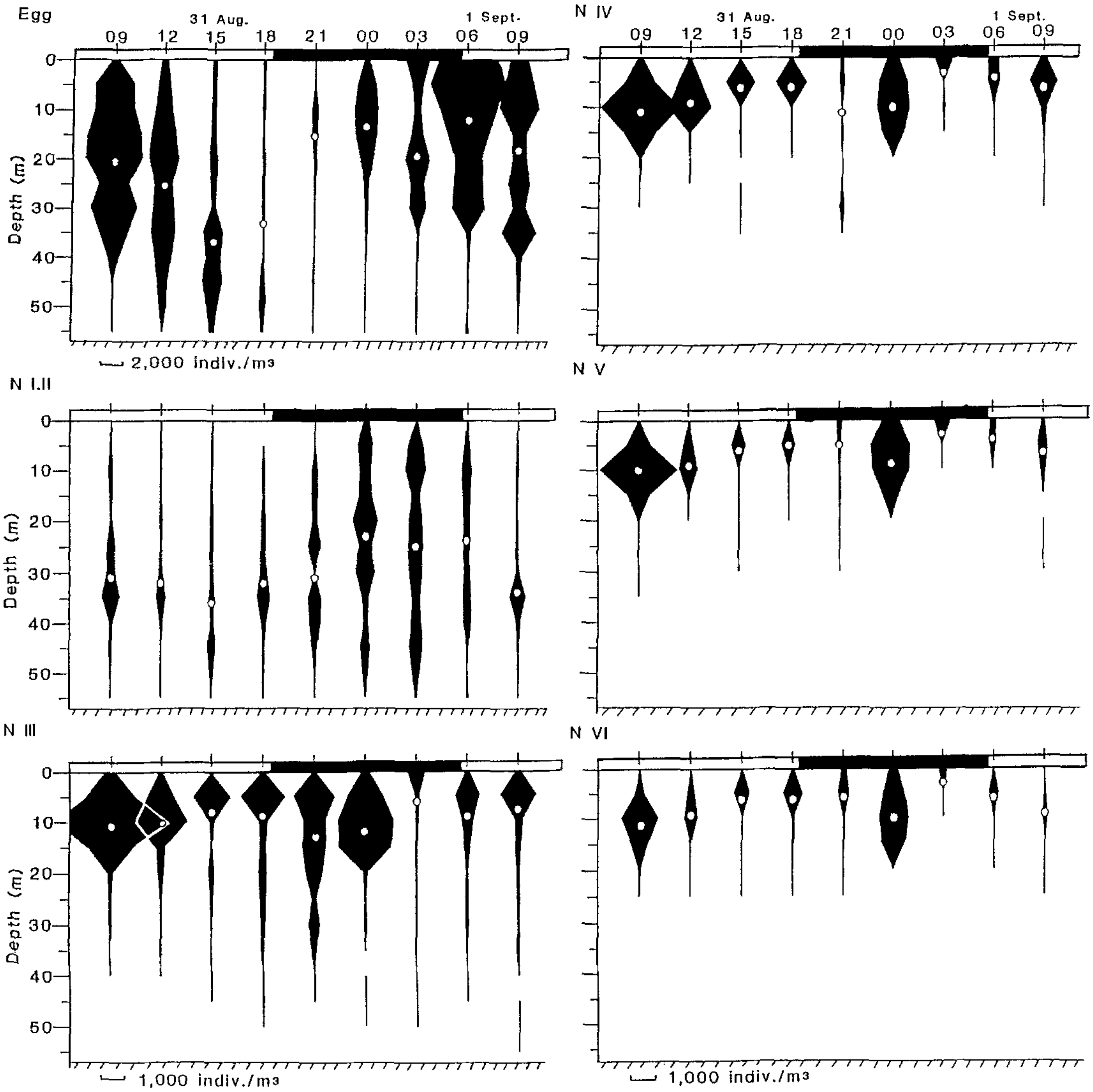

Fig. 5. *Calanus sinicus.* Diel variation in vertical distribution of eggs and nauplii. Open circles indicate depth of median population. Note, numerical scale is different between eggs and nauplii (NI to VI). Open and black bars indicate day- and night-time, respectively

Table 2. *Calanus sinicus.* Variation in depth (m) of median population of each developmental stage. Stages as in Table 1. *p*: Significance; NS: not significant

Stage	Day (hrs)			Night (hrs)				Day (hrs)		Mean		
	09.00	12.00	15.00	18.00	21.00	00.00	03.00	06.00	09.00	Day	Night	*p*
E	20	25	37	33	15	13	19	12	18	22.4	20.0	NS
NI, II	31	32	36	32	31	23	25	24	34	31.4	27.8	NS
NIII	11	10	8	9	13	12	6	9	8	9.5	10.0	NS
NIV	11	9	6	6	11	10	3	4	6	7.5	7.5	NS
NV	10	9	6	5	5	9	3	4	7	7.2	5.5	NS
NVI	11	9	6	6	6	10	3	6	9	8.2	6.3	NS
CI	17	13	8	11	8	13	6	9	12	11.8	9.5	NS
CII	21	15	10	13	10	15	7	12	13	14.2	11.3	NS
CIII	25	20	13	18	14	18	8	20	18	19.2	14.5	NS
CIV	30	29	23	22	19	24	13	36	26	28.8	19.5	<0.03
CV	38	41	35	24	23	25	27	44	42	40.0	24.8	<0.001
CVI ♀	48	47	51	22	17	17	15	48	49	48.6	17.8	<0.001
CVI ♂	43	45	47	46	42	40	43	43	45	44.6	42.8	NS

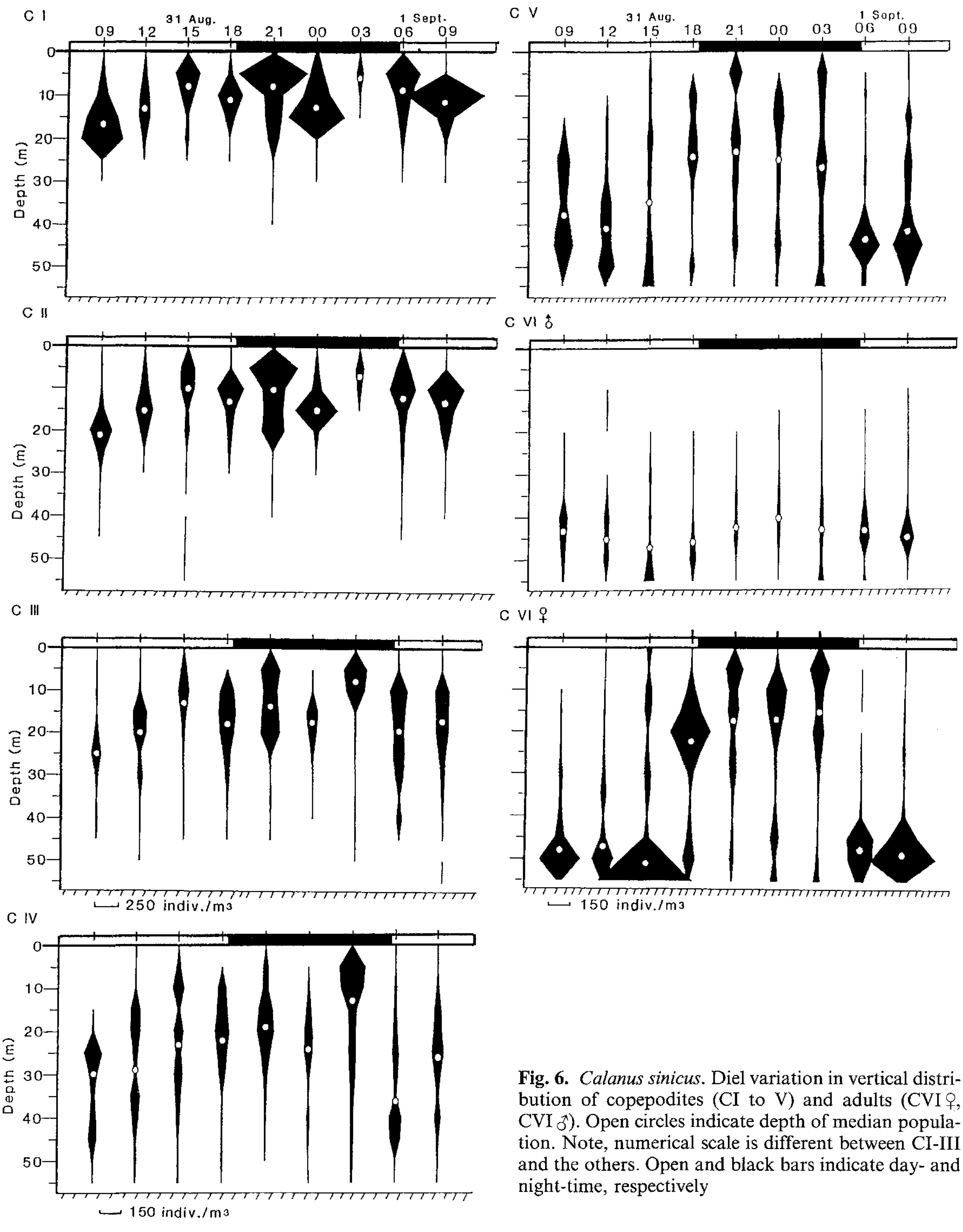

Fig. 6. *Calanus sinicus*. Diel variation in vertical distribution of copepodites (CI to V) and adults (CVI ♀, CVI ♂). Open circles indicate depth of median population. Note, numerical scale is different between CI-III and the others. Open and black bars indicate day- and night-time, respectively

vertical migration (Table 2). CIV migrated within the water column above the thermocline, and CV migrated across the thermocline.

Adult females and males exhibited completely different migration behaviors. Females were distributed throughout the water column, and exhibited strong diel vertical migration (Fig. 6). The majority of the female population migrated upward at dusk, remained in the shallow layer throughout the night, and then descended to below the thermocline before dawn. During the day, females aggregated near the bottom (45 to 50 m) but not immediately above, except for one occasion at 15.00 hrs. The mean night-time median depth of females was 17.8 m, which was shallower than that of CIV and V. In contrast, males were distributed below 20 m (Fig. 6) and the median depth was within, and slightly below, the thermocline (Table 2). No diel vertical migration was observed for males.

Discussion

Previous studies (Cushing 1951, Harding et al. 1951, Marshall and Orr 1955, Mullin 1968, Runge 1985, Williams and

Conway 1987) have demonstrated that *Calanus* spp. lay their eggs in the surface waters at night when they migrate upwards. Eggs and hatched nauplii are thus retained within the surface layer where phytoplankton-food is generally more abundant. A similar spawning behavior was found in this study on *C. sinicus*. The bulk of adult females ascended at dusk, remained within the surface layer and laid their eggs after midnight. Our previous investigation (Uye unpublished data) indicated that *C. sinicus* began spawning after midnight and almost ceased before dawn, with peak spawning occuring around 03.00 hrs. In this investigation, spawned eggs were accumulated in the upper water column and were most abundant at dawn (Fig. 5, Table 1).

Since *Calanus sinicus* eggs are denser than seawater, they sink to progressively deeper layers during development. Since the females did not spawn during the day, the descent of eggs (median depth: 12 m at 06.00 hrs and 37 m at 15.00 hrs, Table 2) would occur solely by sinking. The sinking velocity of *C. sinicus* eggs (average temperature during descent ca 22 °C) is calculated as 67 m d^{-1}, which is similar to that reported by Marshall and Orr (1955) for *C. finmarchicus* (23 to 98 m d^{-1} at 20 °C). The time required for development of *C. sinicus* eggs is 0.7 d at 22 °C (Uye 1988), which means that eggs produced at 00.00 hrs began to hatch at ca 17.00 hrs. A sharp decrease in egg density between 15.00 and 18.00 hrs (1 213 to 361 eggs m^{-3}, respectively) and the gradual increase in NI and II abundance after 18.00 hrs (Table 1) are probably due to this hatching process.

Adult *Calanus sinicus* females cannibalistically prey on their eggs (S. Ohtsuka personal communication). If females and spawned eggs occurred at the same depth, encounter rates would be high. In *C. sinicus,* however, spawning was performed by nocturnally ascending females which left the surface waters before dawn when eggs were most concentrated. Hence, nocturnal spawning behavior, which has been also observed in *Labidocera aestiva* (Marcus 1985), *Acartia tonsa* (Stearns et al. 1989), *Centropages abdominalis* and *Tortanus forcipatus* (Uye unpublished), is of adaptive significance for migratory omnivorous/carnivorous copepods.

Pronounced ontogenetic upward migration occurred in NIII *Calanus sinicus*. We suggest the elevation of the vertical distribution after NIII is primarily related to stage-specific feeding behavior. As in other *Calanus* species (Landry 1983, Peterson 1986), NI and II are non-feeding. They move their appendages infrequently and hence continue to sink. Feeding commences at NIII, and upward migration to the food-rich surface waters is then beneficial. The remaining nauplii and young copepodites are active feeders, and the latter, in particular, are efficient in converting food to growth (their weight specific growth rates are higher than 100% d^{-1} at 20 °C, Uye 1988). By continuous occurrence within the phytoplankton-rich surface layer, these stages can feed and grow at maximum potential rates. For these stages, constant food supply may be important.

Clear diel vertical migration in late copepodites and adult *Calanus sinicus* females is, of course, due to the enhanced swimming ability of these stages. The onset of diel vertical migration may be related to the feeding periodicity of these stages. Their day depths gradually deepen as the stage of development progressed – indicated by their reduced feeding rates during the day. High nocturnal feeding rates have been demonstrated for CV and adult females of *Calanus* spp. (Simard et al. 1985, Harris and Malej 1986, Dagg et al. 1989) although not for CIV. We did not quantify the gut contents of *C. sinicus,* but microscopic observation revealed evidence of feeding periodicity; night-collected CIV, CV and adult females had full, dark gut contents. Their reduced feeding activity during the day may imply their lower growth rates. In fact, the specific growth rates of late copepodites (especially CV) and adult females (i.e., egg production rate) of *C. sinicus* are much lower than those of early copepodites, under even continuous excess food supply (Uye 1988, unpublished data).

There are two alternative hypotheses to explain the selective force behind diel vertical migration of zooplankton. First is the so-called metabolic hypothesis (McLaren 1963, 1974, Enright 1977), i.e., migrating populations achieve some energetic benefit by feeding in warm, phytoplankton-rich surface layer and by converting intaken energy in the cool deep-layer. This hypothesis can be applicable for late copepodites and adult females of *Calanus sinicus,*which experience temperature differences of 2° to 6 °C between day and night. However, this hypothesis can not be verified unless we compare the energetic benefit (e.g. net growth rate) between migratory populations and non-migratory, surface dwelling populations. Further, the metabolic hypothesis is incomplete, as it does not explain why younger developmental stages or adult males do not undergo diel vertical migration. The second hypothesis concerns minimization of population mortality by predation (Zaret and Suffern 1976, Wright et al. 1980, Ohman et al. 1983, Fancett and Kimmerer 1985). The most powerful predators of *C. sinicus,* in our study area, are sardine and anchovy. Since these fish tend to select larger prey (Uotani et al. 1978, Koslow 1981), older stages of *C. sinicus* are more susceptible. Early copepodites may also be threatened by fish predation during the day when most older stages leave the shallow layer. However, the co-occurrence of other copepod species (namely *Paracalanus* sp., *Oithona daviae, O. similis, Corycaeus afficis* and *Microsetella norvegica;* body carbon weight of their adult females = 1 to 3 μg, is larger than and similar to *C. sinicus* CI and II) may alleviate the predation pressure upon young *C. sinicus* copepodites. Hence, predation avoidance is a more reasonable explanation for the selective advantage of ontogenetic diel vertical migration in *C. sinicus.* Considering the above-mentioned feeding behavior of *C. sinicus,* we conclude that growth is a prime aim for young (small, hence less susceptible to fish predation) development stages, and predation avoidance is an important strategy for older stages, in particular adult females. The numerical decline of adult females is a direct effect of the decrease in population recruitment rate.

Huntley and Brooks (1982) and Dagg (1985) have demonstrated that the migratory behavior of copepods is influenced by food availability. When phytoplankton is abundant and individual ingestion rates are high, copepods performed high-amplitude migration. Since the chlorophyll concentration was as high as 4 to 5 $\mu g\ l^{-1}$ in the surface layer during this investigation, the individual ingestion rates might be high. Hence, we expect that the potential migratory behavior of late copepodites and adult females of *Calanus sinicus* was not reduced by food scarcity.

Although Brodsky (1975) assigned *Calanus sinicus* to a category of subtropical species, it is a temperate species. In the central part of the Inland Sea of Japan, this species occurs during the cold season between November and June and disappears when water temperature exceeds 22.8 °C (Hirota 1979). In Xiamen Harbor, China, *C. sinicus* also disappears in June when water temperature warms to above 20 °C (Lin and Li 1984). Further, Uye (1988) found the hatching of *C. sinicus* eggs occurs between 5° and 22.6 °C. However, hatching success is as low as 20% at 22.6 °C. These facts indicate that the thermal range of *C. sinicus* falls between 5° and 23 °C. During this study, the surface temperature (>24 °C) was apparently sublethal to *C. sinicus* and the surface was always avoided by this copepod, except for the nocturnal occurrence of NIV to VI.

In contrast to adult females, the distribution of adult *Calanus sinicus* males was confined to the deeper layer and did not exhibit diel vertical migration. Since males are weak feeders, they do not necessarily undergo feeding migration. In addition, males are probably physiologically less tolerant than females, and hence they avoided high-temperature surface-waters and remained primarily in cool deeper waters throughout the whole day.

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