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Vertical Distribution Patterns of Three Mesopelagic *Paraeuchaeta* Species (Copepoda : Calanoida) in the Oyashio Region, Western Subarctic Pacific Ocean

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Abstract

Diel, seasonal, and ontogenetic vertical migration patterns of three *Paraeuchaeta* species (*P. elongata, P. birostrata*, and *P. rubra*) were studied in the Oyashio region during September 1996 through October 1997. Monthly samples were collected with 0.1 mm-mesh closing nets towed through five discrete depths between the surface and $\leq 2,000$ m. Vertical distribution patterns of the whole population were different between the three species, i.e. 310 ± 74 m (annual mean$\pm$1sd) for *P. elongata* ; 800 ± 111 m for *P. birostrata* ; $1,163 \pm 220$ m for *P. rubra*. Among the three species, diel vertical migration (DVM) was observed only for shallow living *P. elongata*. Within the species, stage-specific distribution depths remained unchanged with season. Ontogenetic vertical migration was seen in all the three species, showing a common pattern that was characterized by deeper occurrence of early and late copepodid stages, and shallower occurrence of middle copepodid stages. This ontogenetic vertical migration pattern and species vertical separation within the genus is hypothesized to be related density of the body and reducing predatory mortality in deep layer.

Key words : Mesopelagic, Vertical distribution, Copepoda, *Paraeuchaeta*, Oyashio region

Introduction

During the last two decades, our knowledge about the biology of oceanic calanoid copepods in the subarctic Pacific Ocean has advanced, especially that on large grazing copepods such as *Neocalanus cristatus, N. plumchrus, N. flemingeri*, and *Eucalanus bungii* (Miller et al., 1984 ; Miller and Clemons, 1988 ; Kobari and Ikeda, 1999 ; Tsuda et al., 1999). All of these copepods are epipelagic species although they sink and enter diapause in the mesopelagic zone during part of their life cycles (Miller et al., 1984). Information about the biology of mesopelagic copepods in the subarctic Pacific region is currently limited to four species, *Paraeuchaeta elongata* (Ozaki and Ikeda, 1999 and references therein), *Pleuromamma scutullata* and *Heterorhabdus tanneri* (Yamaguchi and Ikeda, 2000a), and *Gaidius variabilis* (Yamaguchi and Ikeda, 2000b).

Paraeuchaeta species are known to be meso- and bathypelagic inhabitants in the subarctic Pacific (Park, 1994), and *P. elongata, P. birostrata* and *P. rubra* are the most dominant of those species (Brodsky, 1950 ; Park, 1994). Among the three, the depth of distribution increases in the order : *P. elongata-P. birostrata-P. rubra* (Minoda, 1971 ; Sekiguchi, 1975). The shallowest-

living species *P. elongata* has been most extensively studied. It exhibits a nocturnal ascent migration pattern (Minoda, 1971 ; Morioka, 1975 ; Sekiguchi, 1975 ; Ohman, 1990 ; Hirakawa et al., 1990 ; Bollens and Frost, 1991), and feeds on small calanoid copepods (Yen, 1983, 1985) or eggs and larvae of pelagic fish in the epipelagic layer at night (Bailey and Yen, 1983). The life cycle of *P. elongata* is annual (Morioka, 1975 ; Ikeda and Hirakawa, 1996 ; Ozaki and Ikeda, 1999). An unique reverse ontogenetic vertical migration pattern (naupliar and early copepodid stages migrate upward gradually with development) has been documented for the population of *P. elongata* in the southern Japan Sea, a marginal sea of the North Pacific (Morioka, 1975). In contrast to *P. elongata, P. birostrata* and *P. rubra* have been little studied, except for collection of incidental information about their vertical and geographical distribution patterns (Minoda, 1971 ; Sekiguchi, 1975 ; Park, 1994) and their body sizes and brood sizes (Mauchline, 1998). As part of a research program to evaluate the biology of deep-sea zooplankton in the Oyashio region, the present study investigated species-specific vertical distribution patterns, at various time scales, of three *Paraeuchaeta* species. Data were obtained from monthly samples collected with 0.1 mm-mesh closing

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nets from five discrete depth strata between the surface and ≤2,000 m. Results are compared with those on other euchaetid copepods from other regions, and discussed in the light of trophic features in the meso- and bathypelagic realms of the Oyashio region.

Materials and methods

Field samplings

Samples were collected at approximately monthly intervals from September 1996 through October 1997, on board the T.S. *Oshoro-Maru* and T.S. *Hokusei-Maru* of the Faculty of Fisheries of Hokkaido University, R.V. *Tansei-Maru* of the Ocean Research Institute of Tokyo University, R.V. *Hokko-Maru* of the Hokkaido National Fisheries Research Institute, and R.V. *Hokushin-Maru* of the Kushiro Fisheries Experimental Station (Table 1). All samplings were conducted between 41°30′-42°30′N and 145°00′-146°00′E in the Oyashio region off southeastern Hokkaido (hereafter referred to as Site H) (Fig. 1). The Oyashio is a western boundary current of the subarctic circulation in the North Pacific that flows southwestward along the Kuril Islands and Hokkaido until it reaches the east coast of northern Honshu, Japan, where it turns east at about 40° N (cf. Kono, 1997). The Site H of this study is located at the southern end of the Oyashio.

Zooplankton were collected with a closing net designed by Kawamura (1989) (60-cm mouth diameter, 0.1-mm mesh) equipped with a Rigosha flowmeter in the mouth of the net, and a TSK Depth Distance Recorder (Tsurumi Seiki, Yokohama, Japan) or RMD Depth meter (Rigosha, Tokyo, Japan). The net was towed vertically at 1 m s^{-1} through five discrete depth strata : 0-the bottom of thermocline (Th), Th-250, 250-500, 500-1,000, and 1,000- ≤2,000 m (Table 1). Most sampling was conducted at night. To investigate the diel

Table 1. Zooplankton sampling data at Site H (Lat. 41° 30′N-42°30′N, Long. 145°00′E-146°00′E) in the Oyashio region. Discrete sampling strata are : surface-bottom of thermocline (Th), Th-250, 250-500, 500-1,000, and 1,000- ≤2,000 m.

Date	Time (Local time)	Vessel
4 September 1996	1827-2023	*Oshoro-Maru*
19 September 1996	1737-1944	*Hokusei-Maru*
1 October 1996	2325-0205	*Hokusei-Maru*
8 December 1996	0110-0248, 0636-0850	*Hokushin-Maru*
13 January 1997	1000-1200	*Hokko-Maru*
20 February 1997	0230-0510*	*Hokushin-Maru*
17 March 1997	0055-0330	*Hokko-Maru*
11 April 1997	0240-0440, 0820-1030	*Hokusei-Maru*
6 May 1997	2335-0320**	*Hokko-Maru*
4 June 1997	1850-2009***	*Oshoro-Maru*
23 June 1997	2123-2326	*Hokusei-Maru*
2 July 1997	1953-2208	*Hokusei-Maru*
17 August 1997	1945-2139	*Oshoro-Maru*
26 August 1997	1010-1201	*Tansei-Maru*
5 October 1997	2045-2220, 1505-1715	*Hokusei-Maru*

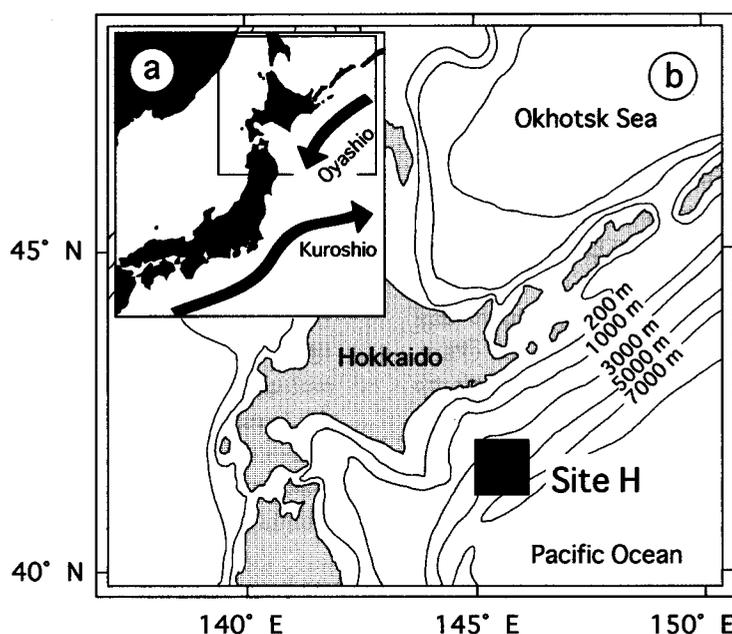Missing strata. *500-1,000, 1,000- ≤2,000 m ; **Th-250, 250-500 m ; ***1,000- ≤2,000 m.

Fig. 1. The Oyashio region in the western subarctic Pacific Ocean (a), and the sampling site ("Site H", shaded) (b). Depth contours (200, 1,000, 3,000, 5,000, and 7,000 m) are superimposed in (b).

vertical migration patterns, a set of day-night samplings was conducted on 8 December 1996, 11 April 1997, and 5 October 1997 (Table 1). After collection, zooplankton samples were preserved immediately in 5% formalin-seawater buffered with borax. Temperature and salinity were determined with a CTD system (Neil Brown, General Oceanics, Miami, USA or Sea Bird Electronics, Washington, USA) at the time of sampling. Chlorophyll *a* concentration data at Site H were supplied by Drs. A. Tsuda, H. Saito, and H. Kasai of the Hokkaido National Fisheries Research Institute.

Identification and enumeration

In the laboratory, *Paraeuchaeta elongata, P. birostrata*, and *P. rubra* were sorted from the whole samples under a dissecting microscope and each copepodid stage counted. The abundance of other congeneric *Paraeuchaeta* species was low (<5%). The identification of copepodid stages was based on the descriptions of Campbell (1934) for *P. elongata*. No description is presently available for *P. birostrata* and *P. rubra* copepodids. To distinguish copepodid 4-5 stages (C4-C5) of the three species, brush-like setae in the ventral margin of the last thoracic segment (*P. elongata* : not present, *P. birostrata* : short and wide, *P. rubra* : long and narrow), and the shape of the end of the last thoracic segment (*P. elongata* : sharply elongated, *P. birostrata* : rounded, *P. rubra* : pointed) were used in this study. Based on the presence of the fifth swimming leg (males) or not (females), identification of males and females was made for the C4 to C6. For species identification of C1-C3, the prosome width was useful, i.e. the prosome width of C1-C3 *Paraeuchaeta* species was bimodal throughout the year, and we designated that specimens with large width (mean±1sd are 0.52±0.02 mm for C1, 0.64±0.03 mm for C2, and 0.78±0.06 mm for C3) as *P. birostrata*, and those with small width (0.35±0.02 mm for C1, 0.41±0.02 mm for C2, and 0.64±0.03 mm for C3) as *P. elongata*. No C1-C3 of *P. rubra* occurred in the samples; presumably this is due to the deeper distribution of this species (>2,000 m) and their species-specific ontogenetic vertical migration pattern (see 'Ontogenetic vertical migration' section in Discussion).

Depth where population resided

To make a quantitative comparison possible, the depth where 50% of the population resided ($D_{50\%}$) was calculated (cf. Pennak, 1943), and the magnitude of vertical migration (diel, seasonal, and ontogenetic) and its statistical significance was estimated and calculated based on the $D_{50\%}$ values. Additional calculations were made to determine the depths at which 25% ($D_{25\%}$) and 75% ($D_{75\%}$) of the population occurred.

Results

Hydrography

Over the study period, surface temperatures ranged from 2°C (March to April 1997) to 18°C (September to October 1996 and 1997) (Fig. 2a). Surface temperatures above 10°C occurred from September to November 1996 and from June to October 1997, when the thermocline was well established at 20-50 m depth. Temperatures below 3°C occurred from February to April 1997, when the top 150 m water column was well mixed vertically. Seasonal temperature ranges decreased with increasing depth. Below 300 m depth, temperatures remained below 3.5°C throughout the year.

Surface salinity ranged seasonally from 32.2 to 34.1‰. Relatively high surface salinities (>33.5‰) occurred from December 1996 to January 1997 (Fig. 2b). Oyashio Water, characterized by salinities between 33.0 and 33.5‰ and temperatures lower than 3°C (Hanawa and Mitsudera, 1987), was observed at 0-150 m from February to April 1997. Less saline water (<33.0‰) recorded near the surface during other months is considered to
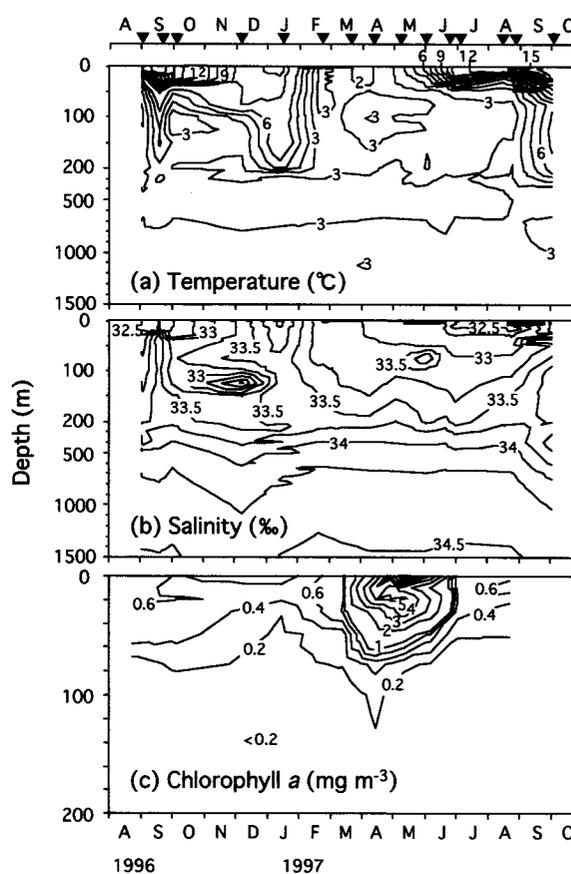

Fig. 2. Seasonal changes in vertical profiles of temperature (°C) (a), salinity (‰) (b), and chlorophyll *a* (mg m⁻³) (c) at Site H. Note the depth scale of (c) is not the same as those of (a) and (b). Solid triangles on top abscissa denote sampling dates.

be derived from the Okhotsk Sea (T. Kono, personal communications). Salinity below 500 m depth changed only slightly throughout the year (range: 34.0-34.5‰).

Phytoplankton biomass, estimated as chlorophyll a concentrations, showed a marked seasonality (Fig. 2c). Chlorophyll a concentrations at the surface were about 0.4 mg m^{-3} from August 1996 to the end of March 1997, then increased rapidly to >9 mg m^{-3} in May 1997, where concentrations above 2 mg m^{-3} extended down to 50 m depth. Surface chlorophyll a concentrations decreased to 2 mg m^{-3} by the end of June and were less than 1 mg m^{-3} toward the end of 1997. Chlorophyll a concentrations below 100 m depth were <0.2 mg m^{-3} throughout the year.

Paraeuchaeta elongata

Most *Paraeuchaeta elongata* populations were distributed between the surface and 1000 m depth throughout the year. Day-night vertical distributions observed on 8 December 1996, 11 April, and 5 October 1997 exhibited a nocturnal ascent pattern of late copepodid stages (C3-C6F) on all occasions (Fig. 3). The magnitude of diel vertical migration was largest in December (range= 10-272 m, mean= 136 m; calculation based on day-night $D_{50\%}$ depth of each copepodid stage) and the least in October (range= 8-144 m, mean= 53 m). Over the entire study period, the nighttime depths of $D_{50\%}$ for the whole population ranged from 223 m (11 April 1997) to 458 m (5 October 1997), but seasonal variations

in the nighttime $D_{50\%}$ were not significant (p=0.54, one-way ANOVA) (annual mean nighttime $D_{50\%}$=310 [±74, 1sd] m, cf. Fig. 6).

Between-stage differences in the nighttime $D_{50\%}$ were significant (p<0.0001, one-way ANOVA, Fig. 3). The differences between females and males were not significant in C4 and C5 (p=0.42, Wilcoxon two-sample test), but significant in C6 (p=0.006), so the data for both sexes were separated only for C6 in Fig. 3. The position of C1 in the water-column was the deepest (annual mean nighttime $D_{50\%}$=810 [±222] m), and the depth of occurrence became gradually shallower from C1 to C3. The C3 occurred at the shallowest depths, with its annual mean nighttime $D_{50\%}$ being 195 (±44) m. During the development from C4 to C6, the distribution depth increased gradually, but the magnitude of this ontogenetic vertical shift (419 m; 614 m of C6M minus 195 m of C3) was smaller than that in C1-C3 (615 m; 810 m of C1 minus 195 m of C3). The C6M was distributed deeper than C6F (annual mean=311 [±136] m).

Paraeuchaeta birostrata

Paraeuchaeta birostrata were found largely between 500 and 1,000 m depth throughout the year. Diel vertical migration patterns of *P. birostrata* were not significant (Fig. 4). Over the entire study period, the nighttime depths of $D_{50\%}$ for the whole population ranged from 646 m (17 August 1997) to 963 m (19
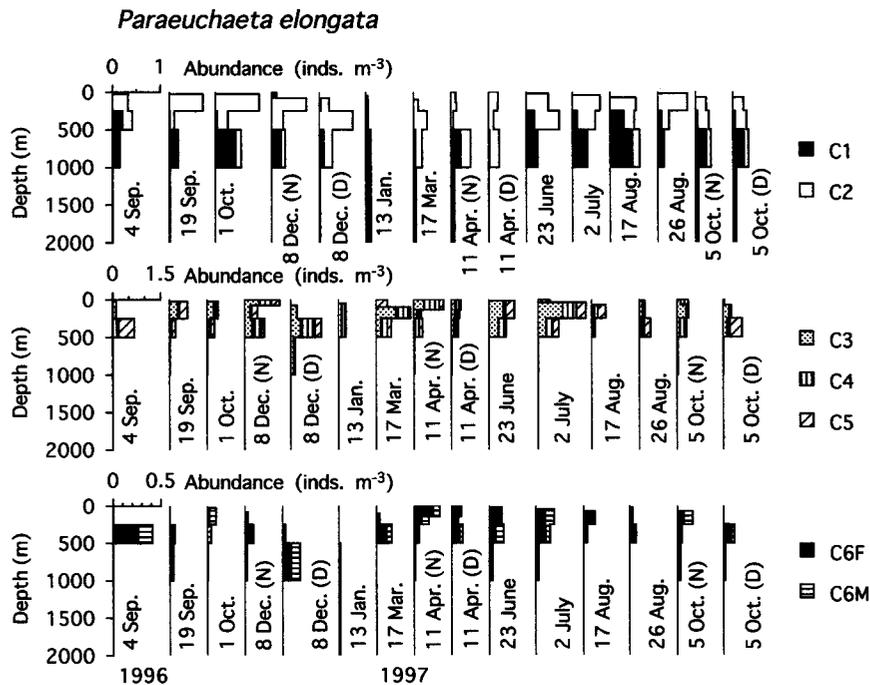

Fig. 3. Vertical distribution of *Paraeuchaeta elongata* in the Oyashio region, western subarctic Pacific. Upper, middle, and lower panels indicate that of C1 and C2, C3-C5, and C6 females and males, respectively. Note that abundance scale of each three panel is not the same. (N): night; (D): day.
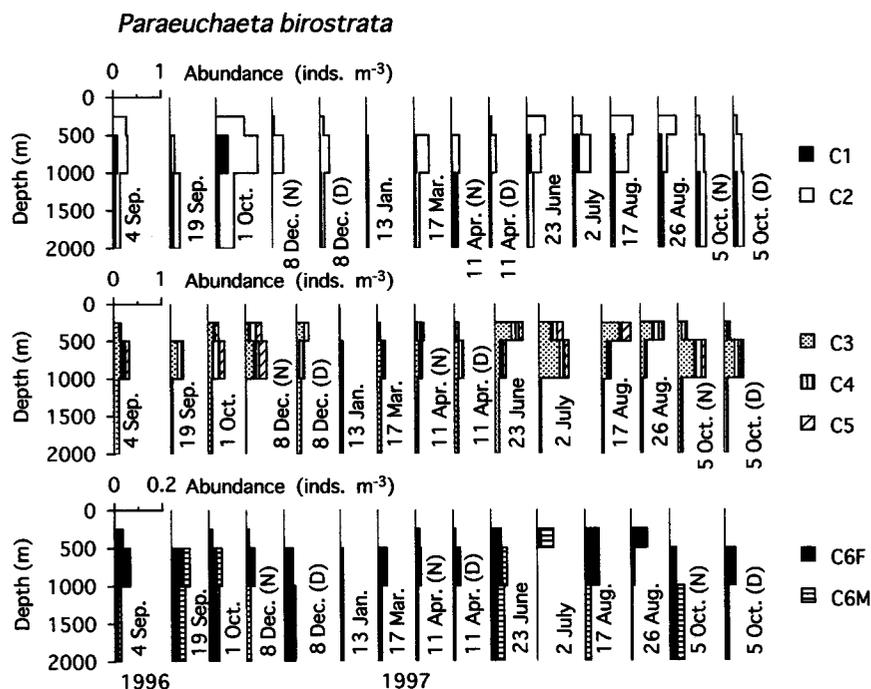
Paraeuchaeta birostrata

Fig. 4. Vertical distribution of *Paraeuchaeta birostrata* in the Oyashio region, western subarctic Pacific. Upper, middle, and lower panels indicate that of C1 and C2, C3-C5, and C6 females and males, respectively. Note that abundance scale of each three panel is not the same. (N) : night ; (D) : day.

September 1996), but seasonal changes in the nighttime $D_{50\%}$ were not significant ($p=0.55$, one-way ANOVA) (annual mean nighttime $D_{50\%}=800$ [±111, 1sd] m, cf. Fig. 6).

Between-stage differences in the nighttime $D_{50\%}$ were significant ($p<0.0001$, one-way ANOVA, Fig. 4). The differences between females and males were not significant in C4 and C5 ($p=0.31$, Wilcoxon two-sample test), but significant in C6 ($p=0.01$), so the data for both sexes were separated only for C6 in Fig. 4. The position of C1 and C6M in the water column was deepest (annual mean nighttime $D_{50\%}=1,051$ [±255] m for C1 and 1,218 [±232] m for C6M), the depth of occurrence became gradually shallower from C1 to C4. The C4 occurred at the shallowest depth, with its annual mean nighttime $D_{50\%}$ being 660 (±116) m. The magnitude of ontogenetic vertical shift was calculated as 558 m (1,218 m of C6M minus 660 m of C4). The C6M was distributed deeper than C6F (annual mean=807 [±232] m).

Paraeuchaeta rubra

Most *Paraeuchaeta rubra* populations resided between 500 and 2000 m depth throughout the year. Diel vertical migration of *P. rubra* was not significant. There were no differences between day and night vertical distribution patterns (as an exception C4 occurred in much shallower depths at night than in daytime on 8 December 1996) (Fig. 5). Over the entire study period,

the nighttime $D_{50\%}$ depths of the whole population ranged from 931 m (2 July 1997) to 1468 m (4 September 1996), but seasonal variations in the nighttime $D_{50\%}$ were not significant ($p=0.67$, one-way ANOVA) (annual mean nighttime $D_{50\%}=1163$ [±220, 1sd] m, Fig. 6).

Between-stage differences in the nighttime $D_{50\%}$ were significant ($p<0.05$, one-way ANOVA, Fig. 5). The C4 stage was found in the shallowest water (annual mean nighttime $D_{50\%}=1,029$ [±299] m), the depth of occurrence becoming gradually greater from C4 to C6. The C6M occurred at the deepest depth, with its annual mean nighttime $D_{50\%}$ being 1,415 (±191) m.

Discussion

Diel and seasonal vertical distributions

Of the three *Paraeuchaeta* species, diel vertical migration (DVM) was observed only for C3-C6 females of the shallow-living *P. elongata* (Table 2). Nocturnal ascent behavior of *P. elongata* has been reported for the populations in the southern Japan Sea (Morioka, 1975 ; Hirakawa et al., 1990), western subarctic Pacific (Minoda, 1971 ; Sekiguchi, 1975), and Dabob Bay in the eastern subarctic Pacific (Bailey and Yen, 1983 ; Yen, 1983, 1985 ; Ohman, 1990 ; Bollens and Frost, 1991). The observed magnitude of the DVM range (53-136 m) of the population in the Oyashio region in this study is consistent with those of previous studies (cf. Bollens and Frost, 1991). Their upward migration is interpreted as
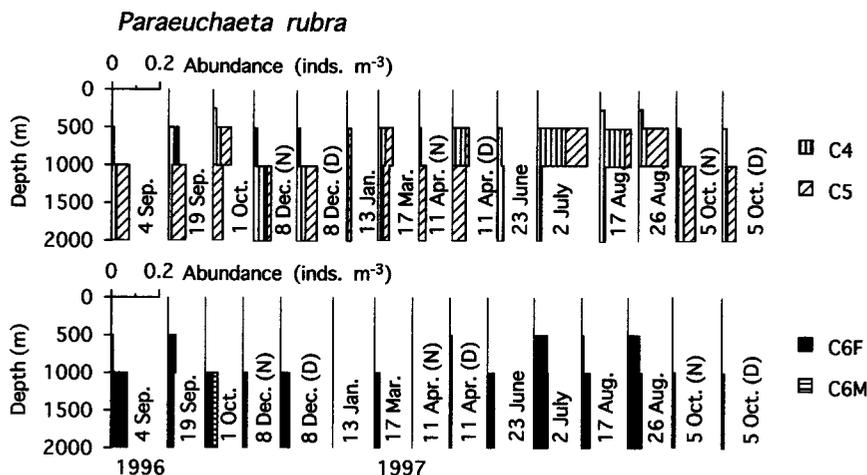
Fig. 5. Vertical distribution of *Paraeuchaeta rubra* in the Oyashio region, western subarctic Pacific. Upper and lower panels indicate that of C4-C5, and C6 females and males, respectively. (N): night; (D): day.
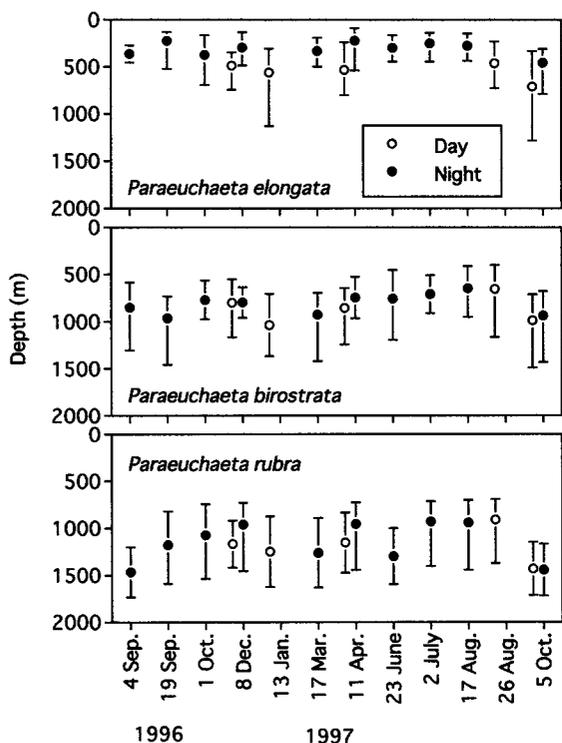

Fig. 6. Seasonal changes in vertical distribution of *Paraeuchaeta elongata* (upper), *P. birostrata* (middle), and *P. rubra* (lower) in the Oyashio region. Bathymetric distribution of the population is defined as depths where 50% of the population was distributed ($D_{50\%}$), and the vertical bars as the range where 25 to 75% of the population ($D_{25\%}$ and $D_{75\%}$) resided.
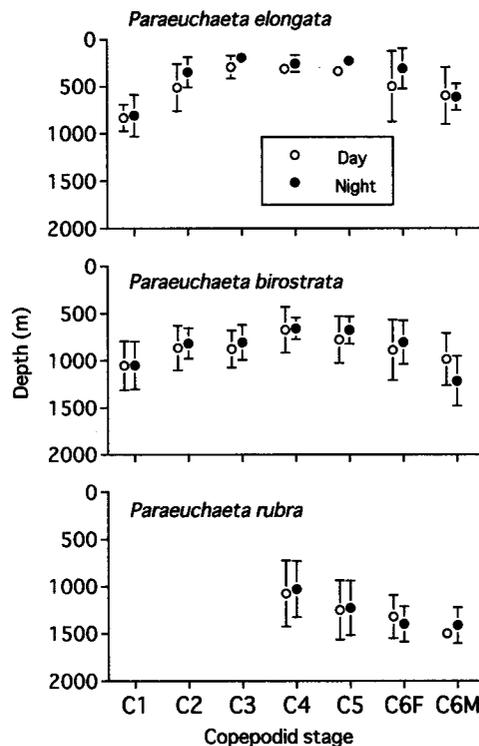
Fig. 7. Annual mean vertical distribution layers of each copepodid stage of *Paraeuchaeta elongata* (upper), *P. birostrata* (middle), and *P. rubra* (lower) in the Oyashio region. Vertical bars indicate one standard deviation. Open and closed symbols indicate daytime and nighttime samplings.

being for feeding at upper layers in the nighttime (Yen, 1983), and their prey items are small calanoid copepods (Yen, 1983, 1985). In contrast to C6F, C6M *P. elongata* remained depths throughout the day (Fig. 7), which may be explained by the fact that C6M *P. elongata* cease feeding (Campbell, 1934; Ikeda and Hirakawa, 1996). In fact, *P. elongata* exhibits little weight

gain from C5M to C6M (Yamaguchi and Ikeda, in this issue). In the present analysis, DVM behavior was not apparent for the deeper-living *P. birostrata* and *P. rubra*. For *P. rubra*, it is noted that their vertical distribution ranges (500-2,000 m, cf. Fig. 5) include only two sampling strata (500-1,000 m and 1,000-2,000 m) thereby the resolution of $D_{50\%}$ is less than that of *P. birostrata*.

Table 2. Summary of vertical distribution of three *Paraeuchaeta* species in the Oyashio region.

Paraeuchaeta	Presence of vertical migration (magnitude : m)			Distribution layer (annual mean nighttime $D_{50\%} \pm 1sd$)
	Diel	Seasonal	Ontogenetic	
elongata	Yes (53–136 m)	No	Yes (615 m)	310 ± 74 m
birostrata	No	No	Yes (558 m)	800 ± 111 m
rubra	No	No	Yes (386 m)*	1163 ± 220 m*

* : Values on vertical distribution of *P. rubra* is underestimated because of no data for C1-C3.

Nevertheless, Kikuchi and Omori (1985) studied vertical distribution of oceanic shrimps down to 6,000 m off the Pacific coast of Japan, and noted that species living above 600 to 1,000 m performed marked diel migrations whereas those at >600 to 1,000 m did not show apparent diel migration.

The three *Paraeuchaeta* species exhibited no appreciable seasonal vertical migration (SVM) (Fig. 6, Table 2), although some studies have shown that the daytime distribution layer of *P. elongata* becomes shallower in spring (Morioka, 1975 ; Ozaki and Ikeda, 1999). As *P. elongata* performs DVM, their daytime distribution depth may be affected by the light intensity, as is known for euphausiids (e.g. Mauchline, 1980). The spring phytoplankton bloom, which occurs in surface layers, may reduce light penetration into the water at that time (cf. Fig. 2c). The consequent reduction in light intensity is considered a possible cause of the shallower diel excursions of *P. elongata* in spring. The limited magnitude of this SVM (100-150 m cf. Ozaki and Ikeda, 1999) also may be masked with the present sampling design. If the penetration of light is the major cue to induce SVM, the absence of SVM for *P. birostrata* and *P. rubra* observed in this study may be explained by little or no light penetration to their resident depths.

For meso- and bathypelagic copepods, an absence of seasonal vertical population shifts has been noted by previous workers (Richter, 1994, 1995 ; Yamaguchi et al., 1999 ; Yamaguchi and Ikeda, 2000a, b). According to Richter (1995), calanoid copepods which perform SVM's in the Greenland Sea are all categorized as particle-suspension feeders on phytoplankton and microzooplankton. It is interesting to note that extensive seasonal migrators (500- ≥ 1,000 m) such as *Neocalanus* spp. (Fulton, 1973 ; Miller et al., 1984 ; Kobari and Ikeda, 1999), *Eucalanus bungii* (Miller et al., 1984), and *Pseudocalanus minutus* (Yamaguchi and Shiga, 1997) in the North Pacific are all categorized as particle-suspension feeders on phytoplankton and microzooplankton. As *Paraeuchaeta* are carnivores, it is not necessary for them to migrate to surface layer to feed on phytoplankton. Their preferred food of small copepods can be found throughout the water column.

Ontogenetic vertical migration

In the Oyashio region, Sekiguchi (1975) noted previously that *Paraeuchaeta elongata* and *P. birostrata* did not undergo ontogenetic vertical migration (OVM), which contrasts with the present results (Fig. 7, Table 2). Sekiguchi (1975) observed only late copepodid stages (after C3 or C4) because of his use of larger mesh nets (0.33 mm) as compared with that (0.10 mm) of this study. The present vertical distribution data of C1 through C6 male these two species show their OVM patterns. In fact, Morioka (1975) evaluated OVM of *P. elongata* in the Japan Sea, and noted that eggs, nauplii, and C1 were distributed in deeper layers and migrated upward during C2-C3. He also noted that C4-C6F commence diel vertical migration (C6M remain at depths as mentioned above). This upward migration during early to middle copepodid stages was also observed for *P. elongata* and *P. birostrata* in the Oyashio region of this study (Fig. 7). This OVM pattern could not be confirmed for *P. rubra* because no C1-C3 stages were taken in the present samples. Presumably, the C1-C3 of *P. rubra* occur at >2,000 m depth. Information about OVM in mesopelagic copepods is currently limited to only a few species belonging to the families Euchaetidae (Morioka, 1975 ; Binet, 1977) and Aetideidae (Richter, 1994 ; Falkenhaug et al., 1997 ; Yamaguchi and Ikeda, 2000b). Although the magnitude of OVM and stage-specific depth distribution differs greatly between species, developmental ascent is a common feature among these copepods. While extensive OVM is known to occur in large epipelagic grazing *Neocalanus* species (Fulton, 1973 ; Miller et al., 1984 ; Kobari and Ikeda, 1999), nature of the OVM in meso- and bathypelagic *Paraeuchaeta* species differs from that of epipelagic *Neocalanus* species in several respects. First, C3-C4 are the shallowest-occurring stages in *Paraeuchaeta* species whereas C1-C5 are shallowest in *Neocalanus* species. Second, the OVM of *Paraeuchaeta*

spp. is not seasonally correlated, but that of *Neocalanus* is closely related to the spring phytoplankton bloom or annual peak of primary production (see Fig. 16 in Miller et al., 1984 ; Fig. 5 in Kobari and Ikeda, 1999). Third, there seems to be no diapause stage in *Paraeuchaeta* species, while diapause is a characteristic of C5 or C6 of *Neocalanus* species in the mesopelagic zone. According to Richter (1995), large epipelagic grazing copepods (such as *Neocalanus*) undergoing deep ontogenetic vertical migrations are likely to experience lower mortality than others wintering at shallower depths. The deeper-layers, through reduction in predation by visual carnivores (both invertebrate and vertebrate) (Vinogradov, 1968), may be regarded as a refuge. This is not only for the diapausing herbivore species in deeper-layers, but also for eggs and juvenile stages of some mesopelagic species, such as the ostracods *Conchoecia pseudodiscophora* (Ikeda and Imamura, 1992) and *Boroecia borealis* (Richter, 1994).

Vertical partitioning within the genus

Euchaetid copepods are known as typical carnivores (cf. Yen, 1982), and can detect hydrodynamic disturbances created by moving prey animals (Yen, 1987, 1988). The relationship between the size of predatory copepods (L_{pred} ; mm) and that of their prey animals (L_{prey} ; mm) has been established experimentally as $L_{prey} = -0.13 + 0.25 L_{pred}$, $r^2 = 0.93$ (Landry and Fagerness, 1988). From this relationship and the size (prosome length) of each copepodid stage of the three *Paraeuchaeta* in this study (Yamaguchi and Ikeda, in this issue), their preferred prey sizes were calculated. The estimated prey size (prosome length of prey copepods) ranged from 0.11-1.11 mm for C1-C6 for *P. elongata*, 0.20-1.29 mm for C1-C6 for *P. birostrata*, and 0.58-1.18 mm for C4-C6 for *P. rubra*. Clearly, the prey sizes of the three *Paraeuchaeta* species overlap considerably, but food competition between the species is unlikely because of their vertical separation (Table 2). Judging from calculated prey size, together with information about its bathymetric distribution and abundance, possible candidate prey animals in the Oyashio region are C5 of *Pseudocalanus* spp. ($L_{prey} = 0.77$ mm, cf. Yamaguchi et al., 1998) for *P. elongata*, C1 of *Gaidius variabilis* ($L_{prey} = 0.76$ mm, cf. Yamaguchi and Ikeda, 2000b) for *P. birostrata*, and C2 of *G. variabilis* ($L_{prey} = 1.07$ mm, cf. Yamaguchi and Ikeda, 2000b) for *P. rubra*.

Considering overlapped prey size mentioned above, similar habitat temperature (ca. 3°C, Fig. 2a) and salinity (34.0-34.5‰, Fig. 2b), and near-synchronized reproduction season of the three *Paraeuchaeta* species (Yamaguchi and Ikeda, 2001), a question may arise ; what factors caused the species-specific differences in the vertical

distribution of them ? We define the specific-gravity index (SGI) of the body as $SGI = DW(PL)^{-3}$, where DW is dry weight (mg) and PL is prosome length (mm), our calculation of SGI based on the data of DW and PL of preserved specimens of C4-C6 (Yamaguchi and Ikeda, in this issue) yielded 0.018 ± 0.004 for *P. elongata*, 0.021 ± 0.002 for *P. birostrata*, and 0.023 ± 0.002 for *P. rubra* (between-species difference ; $p < 0.05$, one-way ANOVA). Among the three *Paraeuchaeta* species compared, it is evident that deeper-living species exhibit greater SGI.

Brood sizes of *Paraeuchaeta elongata, P. birostrata,* and *P. rubra* have been recorded as 26.2, 8.5, and 7.3 eggs, respectively (Yamaguchi and Ikeda, in this issue). From these brood size data, together with likely four successive broods for each species (Mauchline, 1998, 283 p), the lifetime fecundity is estimated as 105 eggs for *P. elongata*, 34 eggs for *P. birostrata*, and 29 eggs for *P. rubra*. From the viewpoint of maintaining stable population, these between-species differences in lifetime fecundity reflect the magnitude of predation mortality in the course of their development, e.g. high fecund species are under higher predation pressure as compared with low fecund. Within the three *Paraeuchaeta* species, the estimated lifetime fecundity decreases with increasing the depth of residence in the order of *P. elongata-P. birostrata-P. rubra*. This observed depth-related decreasing pattern of the lifetime fecundity within the *Paraeuchaeta* spp. is consistent with the hypothesis that pelagic predators decrease exponentially with increasing depth in the ocean (Vinogradov, 1968 ; Mauchline, 1991). Clearly, these depth-related patterns in SGI and lifetime fecundity seen in the three *Paraeuchaeta* species in this study needs to be validated by broad comparison in future, including the other *Paraeuchaeta* species living more deeper layers in the North Pacific.

Acknowledgements

References

Bailey, K.M. and Yen, J. (1983). Predation by a carnivorous marine copepod, *Euchaeta elongata* (Esterly), on eggs and larvae of the Pacific hake, *Merluccius productus. J. Plankton Res.,* **5**, 71-82.

Binet, D. (1977). Cycles biologiques et migrations

ontogenéiques chez quelques copéodes péagiques des eaux Ivoiriennes. *Cahiers ORSTOM, Series Oceanographie,* **15**, 111-138.

Bollens, S.M. and Frost, B.W. (1991). Ovigerity, selective predation and variable diel vertical migration in *Euchaeta elongata* (Copepoda : Calanoida). *Oecologia,* **87**, 155-161.

Brodsky, K.A. (1950). Calanoida of the far-eastern seas and polar basin of the USSR. p. 1-442, Strelkov, A.A. (ed.). *Keys to the fauna of the USSR No. 35,* Moskva, Leningrad (English translation, I.P.S.T., Jerusalem, 1967).

Campbell, M.H. (1934). The life history and postembryonic development of the copepods *Calanus tonsus* Brady and *Euchaeta japonica* Marukawa. *J. Biol. Bd. Can.,* **1**, 1-65.

Falkenhaug, T., Tande, K.S. and Semenova, T. (1997). Diel, seasonal, and ontogenetic variations in the vertical distributions of four marine copepods. *Mar. Ecol. Prog. Ser.,* **149**, 105-119.

Fulton, J. (1973). Some aspects of the life history of *Calanus plumchrus* in the Strait of Georgia. *J. Fish. Res. Bd. Can.,* **30**, 811-815.

Hanawa, K. and Mitsudera, H. (1987). Variation of water system distribution in the Sanriku coastal area. *J. Oceanogr. Soc. Japan,* **42**, 435-446.

Hirakawa, K., Ikeda, T. and Kajihara, N. (1990). Vertical distribution of zooplankton in Toyama Bay, southern Japan Sea, with special reference to Copepoda. *Bull. Plankton Soc. Japan,* **37**, 111-126.

Ikeda, T. and Hirakawa, K. (1996). Early development and estimated life cycle of the mesopelagic copepod *Pareuchaeta elongata* in the southern Japan Sea. *Mar. Biol.,* **126**, 261-270.

Ikeda, T. and Imamura, A. (1992). Population structure and life cycle of the mesopelagic ostracod *Conchoecia pseudodiscophora* in Toyama Bay, southern Japan Sea. *Mar. Biol.,* **113**, 595-601.

Kawamura, A. (1989). Fast sinking mouth ring for Closing Norpac net. *Bull. Jap. Soc. Scient. Fish.,* **55**, 1121.

Kikuchi, T. and Omori, M. (1985). Vertical distribution and migration of oceanic shrimps at two locations off the Pacific coast of Japan. *Deep-Sea Res. A,* **32**, 837-851.

Kobari, T. and Ikeda, T. (1999). Vertical distribution, population structure, and life cycle of *Neocalanus cristatus* (Crustacea : Copepoda) in the Oyashio region, with notes on its regional variations. *Mar. Biol.,* **134**, 683-696.

Kono, T. (1997). Modification of the Oyashio Water in the Hokkaido and Tohoku areas. *Deep-Sea Res. I,* **44**, 669-688.

Landry, M.R. and Fagerness, V.L. (1988). Behavioral and morphological influences on predatory interactions among marine copepods. *Bull. Mar. Sci.,* **43**, 509-529.

Mauchline, J. (1980). The biology of mysids and euphausiids. *Adv. Mar. Biol.,* **18**, 1-677.

Mauchline, J. (1991). Some modern concepts in deep-sea pelagic studies : patterns of growth in the different horizons. p.107-130, Mauchline, J. and Nemoto, T. (eds.). *Marine Biology, its Accomplishment and Future Prospect.* Hokusen-sha, Tokyo.

Mauchline, J. (1998). The biology of calanoid copepods. *Adv. Mar. Biol.,* **33**, 1-710.

Miller, C.B. and Clemons, M.J. (1988). Revised life history analysis for large grazing copepods in the subarctic Pacific Ocean. *Prog. Oceanogr.,* **20**, 293-313.

Miller, C.B., Frost, B.W., Batchelder, H.P., Clemons, M.J. and Conway, R.E. (1984). Life histories of large, grazing copepods in the subarctic ocean gyre : *Neocalanus plumchrus, Neocalanus cristatus,* and *Eucalanus bungii* in the Northeast Pacific. *Prog. Oceanogr.,* **13**, 201-243.

Minoda, T. (1971). Pelagic copepoda in the Bering Sea and the northwestern North Pacific with special reference to their vertical distribution. *Mem. Fac. Fish. Hokkaido Univ.,* **18**, 1-74.

Morioka, Y. (1975). A preliminary report on the distribution and life history of a copepod, *Pareuchaeta elongata,* in the Vicinity of Sado Island, Japan Sea. *Bull. Jap. Sea Reg. Fish. Res. Lab.,* **26**, 41-56.

Ohman, M.D. (1990). The demographic benefits of diel vertical migration by zooplankton. *Ecol. Monogr.,* **60**, 257-281.

Ozaki, K. and Ikeda, T. (1999). Vertical distribution, population structure and life cycle of the mesopelagic copepod *Paraeuchaeta elongata* off Cape Esan, southwestern Hokkaido, Japan. *Plankton Biol. Ecol.,* **46**, 48-53.

Park, T. (1994). Geographic distribution of the bathypelagic genus *Paraeuchaeta* (Copepoda : Calanoida). *Hydrobiologia,* **292/293**, 317-332.

Pennak, R.W. (1943). An effective method of diagramming diurnal movements of zooplankton organisms. *Ecology,* **24**, 405-407.

Richter, C. (1994). Regional and seasonal variability in the vertical distribution of mesozooplankton in the Greenland Sea. *Ber. Polarforsch.,* **154**, 1-87.

Richter, C. (1995). Seasonal changes in the vertical distribution of mesozooplankton in the Greenland Sea Gyre (75°N) : distribution strategies of calanoid copepods. *ICES J. mar. Sci.,* **52**, 533-539.

Sekiguchi, H. (1975). Seasonal and ontogenetic vertical migrations in some common copepods in the northern region of the North Pacific. *Bull. Fac. Fish. Mie Univ.,* **2**, 29-38.

Tsuda, A., Saito, H. and Kasai, H. (1999). Life histories of *Neocalanus flemingeri* and *Neocalanus plumchrus* (Calanoida : Copepoda) in the western subarctic Pacific. *Mar. Biol.,* **135**, 535-544.

Vinogradov, M.E. (1968). *Vertical distribution of the oceanic zooplankton.* Izd. Nauka, Moscow (English translation, I.P.S.T., Jerusalem, 1970).

Yamaguchi, A. and Ikeda, T. (2000a). Vertical distribution, life cycle, and body allometry of two oceanic calanoid copepods (*Pleuromamma scutullata* and *Heterorhabdus tanneri*) in the Oyashio region, western North Pacific Ocean. *J. Plankton Res.,* **22**, 29-46.

Yamaguchi, A. and Ikeda, T. (2000b). Vertical distribution, life cycle and developmental characteristics of mesopelagic calanoid copepod *Gaidius variabilis* (Aetideidae) in the Oyashio region, western North Pacific Ocean. *Mar. Biol.,* **137**, 99-109.

Yamaguchi, A. and Ikeda, T. (2001). Abundance and population structure of three mesopelagic *Paraeuchaeta* species (Copepoda : Calanoida) in the Oyashio region, western subarctic Pacific Ocean with notes on their carcasses and epizoic ciliates. *Plankton Biol. Ecol.,* **48**, 104-

113.

Yamaguchi, A. and Ikeda, T. (in this issue). Reproductive and developmental characteristics of three mesopelagic *Paraeuchaeta* species (Copepoda : Calanoida) in the Oyashio region, western subarctic Pacific Ocean. *Bull. Fac. Fish. Hokkaido Univ.*

Yamaguchi, A., Ikeda, T. and Hirakawa, K. (1999). Diel vertical migration, population structure and life cycle of the copepod *Scolecithricella minor* (Calanoida : Scolecitrichidae) in Toyama Bay, southern Japan Sea. *Plankton Biol. Ecol.*, **46**, 54-61.

Yamaguchi, A., Ikada, T. and Shiga, N. (1998). Population structure and life cycle of *Pseudocalanus minutus* and *Pseudocalanus newmani* (Copepoda : Calanoida) in Toyama Bay, Japan Sea. *Plankton Biol. Ecol.*, **45**, 183-193.

Yamaguchi, A. and Shiga, N. (1997). Vertical distribution and life cycles of *Pseudocalanus minutus* and *P. newmani* (Copepoda ; Calanoida) off Cape Esan, southwestern Hokkaido (in Japanese with English abstract). *Bull. Plankton Soc. Japan*, **44**, 11-20.

Yen, J. (1982). Sources of variability in attack rates of *Euchaeta elongata* Esterly, a carnivorous marine copepod. *J. exp. mar. Biol. Ecol.*, **63**, 105-117.

Yen, J. (1983). Effects of prey concentration, prey size, predator life stage, predator starvation, and season on predation rates of the carnivorous copepod *Euchaeta elongata*. *Mar. Biol.*, **75**, 69-77.

Yen, J. (1985). Selective predation by the carnivorous marine copepod *Euchaeta elongata* : laboratory measurements of predation rates verified by field observations of temporal and spatial feeding patterns. *Limnol. Oceanogr.*, **30**, 577-597.

Yen, J. (1987). Predation by a carnivorous marine copepod, *Euchaeta norvegica* Boeck, on eggs and larvae of the North Atlantic cod *Gadus morhua*. *J. exp. mar. Biol. Ecol.*, **112**, 283-296.

Yen, J. (1988). Directionality and swimming speeds in predator-prey and male-female interactions of *Euchaeta rimana*, a subtropical marine copepod. *Bull. Mar. Res.*, **43**, 395-403.