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Population structure and life cycle of *Pseudocalanus minutus* and *Pseudocalanus newmani* (Copepoda: Calanoida) in Toyama Bay, southern Japan Sea

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Abstract: Population structure and life cycle of *Pseudocalanus minutus* and *P. newmani* in Toyama Bay, southern Japan Sea, were investigated based on seasonal samples obtained by vertical hauls (0–500 m depth) of twin-type Norpac nets (0.33-mm and 0.10-mm mesh) over one full year from February 1990 through January 1991. Closing PCP nets (0.06-mm mesh) were also towed to evaluate vertical distribution patterns in September 1990, November 1991 and February 1997. *P. minutus* was present throughout the year. The population structure was characterized by numerous early copepodite stages in February–April, largely copepodite V (CV) in May–November, and a rapid increase of adults in November to January. As the exclusive component of the population, CVs were distributed below 300 m in September and November both day and night. These CVs were considered to be in diapause. In February most of the CI to CIV stages were concentrated in the top 100 m. All copepodite stages of *P. newmani* were collected for only 7 months of the year, disappearing from the water column in Toyama Bay from mid-June onward and their very small population recovered in November. Vertical sampling in September failed to collect them down to 1000-m depth. The period of their absence corresponded to the period of seasonal warming of surface waters. Unlike *P. minutus*, *P. newmani* appears to lack the ability to sink to cooler water during the warm summer season in Toyama Bay. Vertical sampling in February revealed that all copepodite stages of *P. newmani* were distributed largely in the top 100 m. From these results, combined with the temperature-generation length relationship established by McLaren et al. (1989a), it is estimated that *P. minutus* and *P. newmani* have two and three generations, respectively, per year. Further, the present results for both *Pseudocalanus* species are compared with those reported from coastal waters in the northwestern Pacific and other regions.

Key words: *Pseudocalanus*, life cycle, vertical distribution, Toyama Bay, Japan Sea

Introduction

The Japan Sea is located in the subarctic being one of the marginal seas in the Pacific Ocean. However its southern upper waters exhibit subtropical characters due to the intrusion of the warm Tsushima Current. Because of this two-layer system, subtropical and boreal

species are often collected together in plankton samples in Toyama Bay, located in the southern Japan Sea (Hirakawa et al. 1992). In recent years, intensive studies of the life cycles of cold-water zooplankton species in Toyama Bay have revealed that primarily epipelagic cold-water species such as *Euphausia pacifica*, *Metridia pacifica*, *Themisto japonica*, *Sagitta elegans* and *Aglantha digitale* maintain their populations in Toyama Bay throughout the year by sinking to cooler depths during high-temperature periods (Iguchi et al. 1993; Hirakawa & Imamura 1993; Ikeda et al. 1992; Terazaki 1993; Ikeda & Imamura 1996).

The genus *Pseudocalanus* includes small particle-feeding (herbivorous) copepods, which often dominate the zooplankton communities in the temperate-boreal neritic waters of the Northern Hemisphere (Corkett & McLaren 1978). Frost (1989) revised the taxonomy of the genus, and *P. minutus* (Krøyer) and *P. newmani* Frost are the only two species of *Pseudocalanus* occurring in the temperate-boreal waters of the northwestern Pacific (Frost 1989). In the Japan Sea, *Pseudocalanus* species (formerly regarded as monotypic, *P. elongatus*) are one of the important components of the epipelagic zooplankton fauna (Zenkevitch 1963), and have been regarded as indicator species of cold water masses (Morioka 1973, 1977; Furuhashi 1975). The southern limit of the distribution of *Pseudocalanus* species in the Japan Sea is considered to be off southwest Honshu (Morioka 1973) or the coast of Korea (Mori 1937). Previously, Sazhin & Vinogradov (1979) observed that *P. elongatus* (= *P. newmani*) is concentrated in the top 25 m in June in the central Japan Sea. Hirakawa et al. (1990) noted that *P. minutus* is distributed below 300 m both day and night in September in Toyama Bay, southern Japan Sea. No other information is presently available for the seasonal vertical distribution and life history patterns of *Pseudocalanus* in the Japan Sea.

The present study aims to reveal the population structure and life cycle of *Pseudocalanus minutus* and *P. newmani* in Toyama Bay, southern Japan Sea, with particular reference to their vertical distribution patterns in response to the seasonally changing thermal regimes in the bay. The present results are compared with those of the same *Pseudocalanus* species living in coastal waters in the northwestern Pacific and other regions.

Materials and Methods

Samples were collected at a station (37°00'N, 137°14'E; bottom depth ca. 1000 m) located in the central part of Toyama Bay (Fig. 1). Paired (twin-type) Norpac nets (45-cm mouth diameter, 0.33- and 0.10-mm mesh; Motoda 1957) were towed vertically from 500-m depth to the surface during mostly daylight hours at 2-week intervals from February 1990 through January 1991 (Hirakawa et al. 1992). The volume of water filtered through the net was estimated from the reading of a Rigosha flowmeter mounted in the mouth of each net.

Day and nighttime vertical distribution patterns of *Pseudocalanus* were examined on three occasions. The stratified vertical tows with a Palumbo–Chun–Petersen (PCP) type closing net (45-cm mouth diameter, 0.06-mm mesh) designed by Kawamura (1989) were made during 8–9 September 1990, 30 November–1 December 1991, and on 23 February 1997. Sampling depth strata were 0–100, 100–300, 300–500, 500–700 and 700–950 m in September 1990 and 0–50, 50–100, 100–150, 150–250, 250–350, 350–500, 500–700 and 700–920 m in November–December 1991 and 0–10, 10–20, 20–30, 30–50, 50–75, 75–100, 100–150, 150–200, 200–300 and 300–500 m in February 1997. These discrete depth samples from different years were used to analyze seasonal changes in vertical distribution patterns of *Pseudocalanus* based on the premise that no interannual variations occurred. All Norpac- and PCP-net samples were immediately preserved in 10% buffered formalin-seawater solution. Temperature

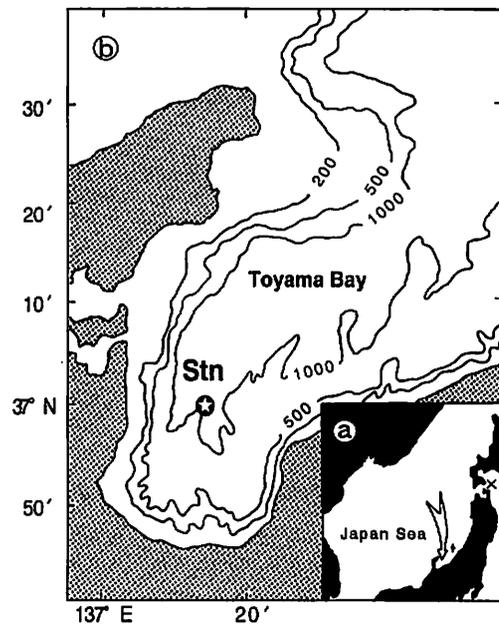


Fig. 1. a. Location of Toyama Bay in the southern Japan Sea. Sampling station of Yamaguchi & Shiga (1997) off Cape Esan is denoted by a cross ($42^{\circ}00'N$, $141^{\circ}30'E$). b. The sampling station (circled star) in Toyama Bay, in which depth contours (1000, 500, and 200 m) are superimposed.

and salinity data were obtained by a CTD system (Neil Brown) at each zooplankton sampling.

At a land laboratory, all copepodite stages of *Pseudocalanus minutus* and *P. newmani* were sorted from a 1/4 aliquot (0.10 mm-mesh Norpac net), entire sample (0.33 mm-mesh Norpac net), or a 7/8 aliquot sample (0.06 mm-mesh PCP net). For identification of copepodite stages Corkett & McLaren (1978) was consulted. The 0.10 mm-mesh Norpac net could retain all copepodite stages (CI to CVI), but the 0.33 mm-mesh Norpac net could retain only the CV and CVI (adult) stages of both species (Yamaguchi, unpublished data). The 0.06 mm-mesh PCP net could catch all naupliar and copepodite stages of both species, but no attempt was made to count naupliar stages because of the difficulty of distinguishing between *P. minutus* and *P. newmani*.

Results

Hydrography

Toyama Bay is a deep canyon, whose 1000 m isobath connects it to the deep basin of the central Japan Sea (Fig. 1). Seasonal changes in temperature and salinity in the top 250 m reflected local meteorological events and intrusions of the warm Tsushima Current (Hirakawa et al. 1992). During this study, temperatures recorded between 0 and 250 m depth ranged from an at depth minimum of $2^{\circ}C$ (February, October and November) to a surface maximum of $26^{\circ}C$ (August), and salinity ranged from a surface minimum of 33.0 PSU (August to November) to a maximum of 34.4 PSU at ca. 100 m (August to September) (Fig. 2). Below 250 m depth, there was almost no seasonal variability; both temperature and salinity were stable at $<4^{\circ}C$ and <34.1 PSU, respectively. Water characterised by temperatures lower than $1^{\circ}C$ and salinity of 34.05–34.10 PSU is termed “Deep-Water” and is widespread over the entire Japan Sea (Nishimura 1969).

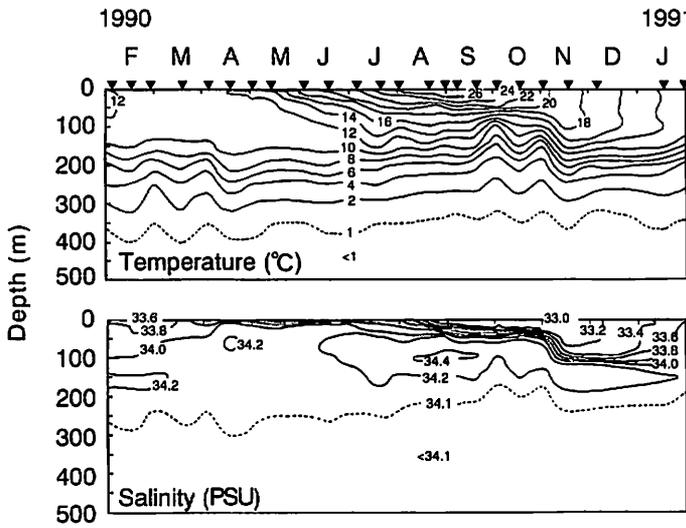


Fig. 2. Temperature and salinity profiles of the top 500 m of the water column at the station in Toyama Bay during the sampling period from February 1990 to January 1991. Sampling dates indicated by triangles on top abscissa.

Abundance and population structure

Sampling precision was examined by comparing the abundance of stage CV and adults of both *Pseudocalanus minutus* and *P. newmani* caught with the paired Norpac nets (0.10- and 0.33-mm mesh). The results of a paired *t*-test indicated that there was no significant difference between the numerical abundances estimated from these two nets (*P. minutus* CV: $t=0.81$, $df=23$, $p>0.4$; adult: $t=0.37$, $df=23$, $p>0.7$, *P. newmani* CV: $t=1.88$, $df=23$, $p>0.7$; adult: $t=1.13$, $df=23$, $p>0.2$). Hence, the CV and adult data from the 0.10 and 0.33 mm-mesh Norpac nets were combined for the following analyses.

Pseudocalanus minutus occurred throughout the year, with a prominent abundance peak in November ($1872 \text{ indiv. m}^{-2}$) and two moderate peaks in late February ($1135 \text{ indiv. m}^{-2}$) and April ($1519 \text{ indiv. m}^{-2}$) (Fig. 3a). The November peak was composed largely of CV with a few adults, whereas the late February and April peaks consisted of younger copepodites. The

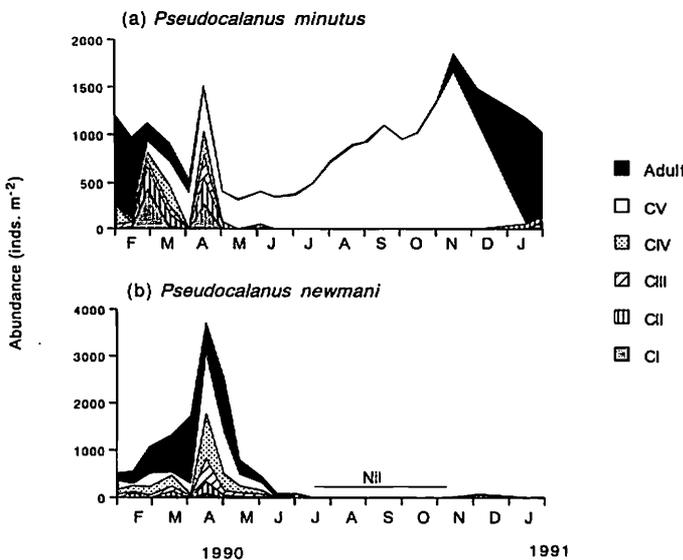


Fig. 3. Seasonal changes in numerical abundance of each copepodite stage of *Pseudocalanus minutus* (a) and *P. newmani* (b) at the station in Toyama Bay.

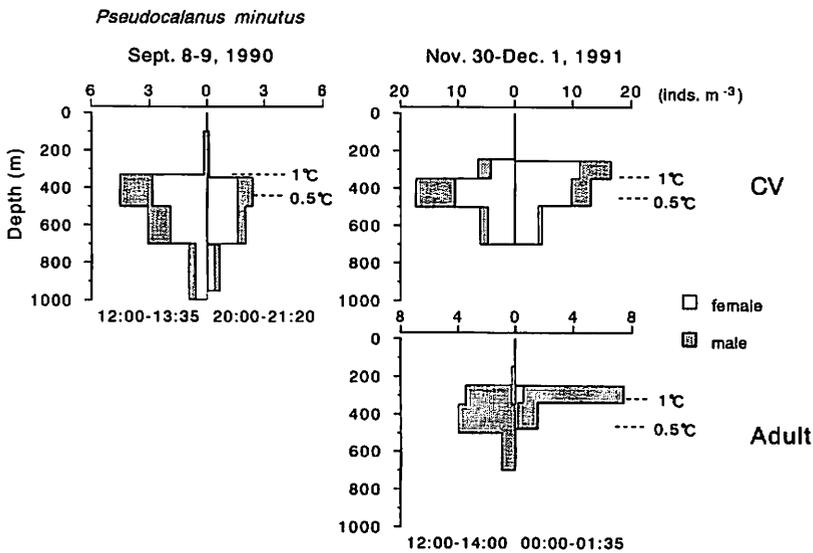


Fig. 4. Vertical distribution of *Pseudocalanus minutus* (CV and adults) on 8–9 September 1990 (left panel) and 30 November–1 December 1991 (right panels) in Toyama Bay. Vertical distribution of temperatures (0.5 and 1.0°C) is superimposed. No adult *P. minutus* found in the September sampling and no *P. newmani* occurred in the September and November/December samplings.

abundance minimum was 335 indiv. m⁻², observed in mid-May when the entire population was comprised of CV indiv. The population in mid-May through November was characterised by the exclusive dominance of CV, and the population abundance increased gradually towards November. From November onward, the abundance of CV decreased while that of adults increased.

Pseudocalanus newmani was found from February 1990 to early June 1990, and its population during that time included all copepodite stages (Fig. 3b). A pronounced numerical peak was seen in April. The abundance of younger copepodite stages peaked in April, but as a whole the proportion of the population comprised of copepodites was lowest in February and March. *P. newmani* was absent entirely from mid-July to late November 1990, but its population recovered slightly from November onward (Fig. 3b). The period in which *P. newmani* did not occur corresponded to a period when water temperatures in the top 100 m exceeded 15°C (cf. Fig. 2).

Vertical distribution

Figure 4 shows the daytime and nighttime vertical distribution patterns of CV (September 1990), and CV and adults of *Pseudocalanus minutus* (November–December 1991). Copepodite stages other than CV and/or adults were not found in either set of samples. These stages of *P. minutus* were more abundant in November–December than in September. Common in both seasons, CV was distributed mostly or entirely between 300 and 700 m and displayed no diel vertical movement. In November–December 1991, adults were dominated by males (female : male = 0.1 : 1) residing at depths between 250 and 500 m. Both adult males and females exhibited no appreciable diel vertical movement. In these September and November–December samples, no *P. newmani* were collected. The few *P. newmani* collected by 0–500 m vertical hauls with Norpac nets in November 1991 (Fig. 3b) were not detected by the

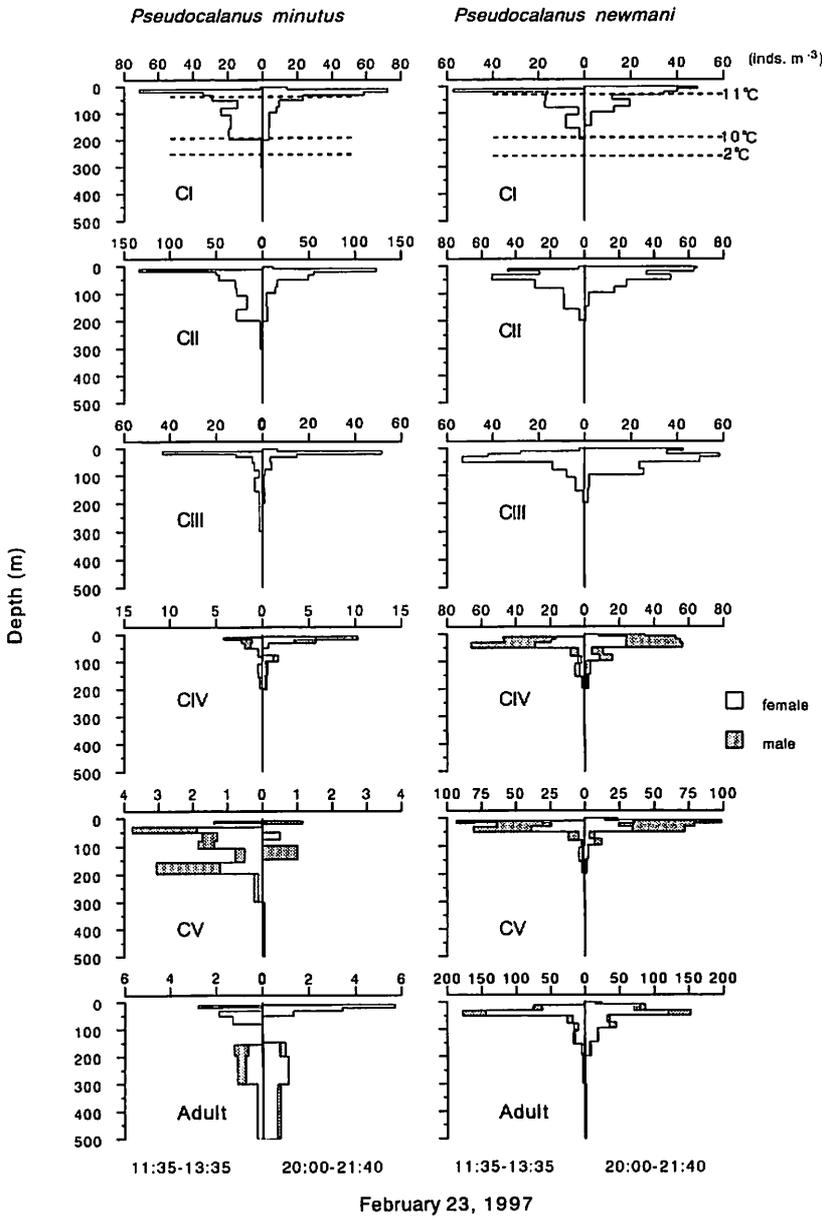


Fig. 5. Vertical distribution of all copepodite stages of *Pseudocalanus minutus* (left panels) and *P. newmani* (right panels) on 23 February 1997 in Toyama Bay. Vertical distribution of temperatures (2, 10 and 11°C) is super-imposed only in top panels. Note that abundance scales are different between panels.

PCP nets. The day and night vertical distributions of *P. minutus* and *P. newmani* in February 1997 are shown in Fig. 5. Early copepodite stages were abundant for *P. minutus*, whereas late copepodite stages were numerous for *P. newmani*. For both species, most of the population was found in the top 100 m where temperatures were $\geq 10^{\circ}\text{C}$. A slight nocturnal ascent to the surface for each copepodite stage was observed for both *P. minutus* and *P. newmani* (Fig. 5). The magnitude of this vertical migration was 2 to 58 m as estimated by calculating weighted mean depth (cf. Bollens & Frost 1989) from day and night vertical distribution patterns of the populations.

Discussion

Life cycle

As herbivorous copepods, *Pseudocalanus minutus* is a primarily arctic, and *P. newmani* is an arctic-temperate species (Frost 1989). The present results show clearly that the active growth and reproductive season of *P. minutus* and *P. newmani* in Toyama Bay is confined to only 3 months of the year (February to April, cf. Fig. 3) when water temperature reaches its annual minimum (the top 100 m, 10–12°C) and phytoplankton abundance reaches its annual maximum (Taniguchi et al. 1997). Within this 3-month period, there occurred two (*P. minutus*) or three abundance peaks (*P. newmani*) of early copepodite stages (CI and CII, Fig. 3). Because of the 2-week sampling interval of this study, it is difficult to judge whether or not these peaks correspond to multiple generations. To resolve this problem, generation length of *P. minutus* and *P. newmani* was estimated from the relationship between generation length and temperature of both species established by McLaren et al. (1989a). For this estimation, the vertical distribution of both species was assumed to be confined to the top 100 m as seen in the results of the vertical distribution survey done in February 1997 (Fig. 5), where the water temperature in the top 100 m during February and April was estimated at 10°C (cf. Fig. 2). Thus, the predicted generation length is 43 d for *P. minutus* and 31 d for *P. newmani*, both of which are consistent with the observed interval between the abundance peaks of early copepodites in the respective species. From this result, two generations of *P. minutus*, and three generations of *P. newmani* were considered to occur at the beginning of the year in Toyama Bay. The dissimilar generation times of *P. minutus* and *P. newmani* may explain the dominance of early copepodite stages for *P. minutus*, and late copepodite stages for *P. newmani* in the PCP net samples collected in February 1997 (Fig. 5).

The present estimate of two generations per year for *P. minutus* in Toyama Bay is greater than the one generation per year estimated in the Bedford Basin (McLaren et al. 1989b), Balsfjorden (Norrbín 1994), and the Greenland Sea (Richter 1994), but consistent with the two generations per year found in Malangen, northern Norway (Falkenhaug et al. 1997). The three generations per year estimated for *P. newmani* in the present study is similar to the results (≥ 3 generations per year) of McLaren et al. (1989b) for the population in Nova Scotia. Regional differences in generation number per year, if any, of both *P. minutus* and *P. newmani* may result from the combined effects of temperature and food phytoplankton conditions in each habitat.

From May onward, the surface temperature increased gradually and reached the annual maximum of $>26^{\circ}\text{C}$ in September. During this high temperature period, *Pseudocalanus minutus* CV resided in the cooler, deeper layers (Fig. 4). The CVs molted to adults by the end of the year, reproduced and repeated the generation in February to April of the next year. A gradual increase in the abundance of CVs from May to November may suggest that the population sank to depths >500 m when surface waters began to warm and gradually returned to shallower depths, as shown in the vertical profiles of the population abundances examined in September and November–December (Fig. 4).

Recently, Ikeda & Hirakawa (1998) determined the oxygen consumption rate and chemical composition of *Pseudocalanus minutus* collected from 400–700 m depths in Toyama Bay during December 1991 and found that they were in diapause, characterized by extremely low oxygen consumption rates and high lipid contents in their bodies. Copepodite Vs of *P. minutus* have been reported in diapause for the populations in the Bedford Basin (McLaren et al. 1989b), Balsfjorden, northern Norway (Norrbín 1994) and the Greenland Sea (Richter 1994).

Richter (1994) noted CVs of *P. minutus* in diapause distributed between 500 and 1000 m in the Greenland Sea, which overlaps the 300–1000 m distributional depth observed for this species in Toyama Bay (cf. Fig. 4).

In contrast to *P. minutus*, *P. newmani* decreased in population size rapidly after forming the annual abundance peak in April. *P. newmani* disappeared from the top 500 m of the water column in Toyama Bay from mid-June onward and their small population recovered in November. The period of their absence corresponded to the seasonal warming of surface waters to temperatures up to 26°C. Since vertical tows extending down to 1000-m depth in September and November–December failed to find *P. newmani*, their population was thought to have collapsed or emigrated to somewhere else during this warm period. The bathymetric distribution of *P. newmani* has been found to be much shallower than *P. minutus* off southwestern Hokkaido (Yamaguchi & Shiga 1997) and this is also the case for the late copepodite stages in Toyama Bay (cf. Fig. 5). According to Yamaguchi & Shiga (1997) a large deposition of lipids in the body as seen in *P. minutus* was not seen in *P. newmani*. The present results suggest strongly that *P. newmani* lacks the ability to sink to cooler water and diapause in order to thrive in the warm summer season in Toyama Bay. However, the mechanism for population recovery in November (Fig. 3) is undetermined.

Regional comparison

Table 1 summarizes the abundance of all copepodite stages and body sizes of adult females of *Pseudocalanus minutus* and *P. newmani* in Toyama Bay (present study) and at a station off Cape Esan (42°00'N, 141°20'E, cf. Fig. 1), northwestern Pacific (Yamaguchi & Shiga 1997). The abundance of all copepodite stages and body sizes of both species in Toyama Bay are different from those off Cape Esan with regard to several aspects. First, the population sizes of both copepods are smaller in Toyama Bay than in those off Cape Esan (the abundance of *P. minutus* in Toyama Bay is 1/20 of that off Cape Esan, and *P. newmani* in Toyama Bay is 1/154 of that off Cape Esan). Second, in terms of relative abundance (annual numerical mean) *P.*

Table 1. Abundance of copepodites (all stages) and prosome length of adult females of *Pseudocalanus* spp. in Toyama Bay and off Cape Esan.

<i>Pseudocalanus</i>	Location	Abundance (indiv. m ⁻²)**			Prosome length (mm)***		Reference
		Max (Month)	Min (Month)	Annual mean	Mean ± 1SD (Range)	Difference (t-test)	
<i>minutus</i>	off Cape Esan	90,552 (May)	349 (Sep.)	18,205	1.17 ± 0.06 (1.02–1.28)	p < 0.01	Yamaguchi & Shiga (1997)
	Toyama Bay	1519* (Apr.)	335 (May)	910	1.03 ± 0.04 (0.91–1.14)		Present study
<i>newmani</i>	off Cape Esan	598,516 (June)	2614 (Sep.)	83,695	0.88 ± 0.04 (0.79–0.95)	p < 0.05	Yamaguchi & Shiga (1997)
	Toyama Bay	3721 (Apr.)	0 (July–Nov.)	537	0.84 ± 0.06 (0.68–0.95)		Present study

* 1872 indiv. m⁻² observed in November was omitted as it was composed exclusively of CV in diapause.

** Abundance data off Cape Esan were from 0–450 m vertical hauls as compared with 0–500 m vertical hauls in this study. *** One hundred adult females were sorted from the samples taken in February at each location.

minutus is more abundant than *P. newmani* in Toyama Bay while the reverse was the case off Cape Esan. Third, the periods of highest annual numerical abundance of early copepodite stages are seen in April (for both *P. minutus* and *P. newmani*) in Toyama Bay, whereas they are in May (for *P. minutus*) and in June (for *P. newmani*) off Cape Esan. Fourth, the body sizes of adult females of both species in Toyama Bay are smaller than those off Cape Esan.

All of these regional, dissimilar features that are seen in the *Pseudocalanus minutus* and *P. newmani* populations in Toyama Bay and off Cape Esan may be explained by differences in thermal conditions, and in the magnitude and production cycle of phytoplankton in these two habitats. The annual range of sea surface temperatures off Cape Esan is 1.5 to 22°C (Fig. 2 in Yamaguchi & Shiga 1997), in contrast to 10 to 26°C in Toyama Bay (Fig. 2). While the temperatures in the top 100 m exceed 10°C only in August to December off Cape Esan, such high temperature conditions are the case throughout the whole year in Toyama Bay (Fig. 2). Chlorophyll-*a* concentrations in Toyama Bay are lower than $1 \mu\text{g l}^{-1}$ during most seasons (Nagata & Nakura 1993), whereas the concentration off Cape Esan is $>1 \mu\text{g l}^{-1}$ from March to November and reaches $7 \mu\text{g l}^{-1}$ in April (Yamaguchi & Shiga 1997). Compared with the populations in Toyama Bay, the greater population sizes of these *Pseudocalanus* species off Cape Esan may be explained by the cooler conditions and a more abundant food supply in the latter habitat. In contrast to off Cape Esan, the higher relative abundance of *P. minutus* over *P. newmani* in Toyama Bay is due to the absence of the latter species during high temperature periods (*P. newmani* occurred throughout the year off Cape Esan). The different timing of the abundance peaks of young copepodites reflect the dissimilar production cycles of food phytoplankton between these two habitats, i.e., the annual peak in phytoplankton abundance occurs in late winter/early spring in Toyama Bay (Taniguchi et al. 1997) but in April off Cape Esan (Yamaguchi & Shiga 1997). Young copepodites of *P. minutus* and *P. newmani* were most abundant one to two months after the peaks in phytoplankton abundance in both habitats. There is a large body of evidence indicating that both higher temperature and lower phytoplankton concentrations are major parameters causing smaller size in adult copepods (McLaren 1974; Corkett & McLaren 1978; Vidal 1980).

While the diel vertical movement of the populations of *Pseudocalanus minutus* and *P. newmani* off Cape Esan was not investigated by Yamaguchi & Shiga (1997), *P. newmani* has been found to be a reverse diel vertical migrator in Dabob Bay, Washington (Ohman et al. 1983). In other regions, both *Pseudocalanus* species have been reported to be non-migrators (e.g. Minoda 1971; Corkett & McLaren 1978) or normal diel vertical migrators (Zagorodnyaya 1975; Afrikova 1976; Kamba 1977; Corkett & McLaren 1978). In the present study, *P. newmani* exhibited a nocturnal ascent to the surface only in February (Fig. 5), though the difference in the day-night vertical distribution pattern of the entire population is almost negligible. *P. minutus* also showed nocturnal ascending behavior of limited magnitude only in February (Fig. 5) and was non-migratory in September and November–December when in diapause (Fig. 4). The reverse diel vertical migration of *P. newmani* in Dabob Bay has been interpreted to result from their avoidance from invertebrate predators such as *Euchaeta* (= *Paraeuchaeta*) *elongata* and *Sagitta elegans* (Ohman et al. 1983; Ohman 1990). These predators also occur in Toyama Bay. Compared with those of Dabob Bay, the abundances of these predatory zooplankters in Toyama Bay are relatively low, by a factor of 1/6 (maximum abundance $1500 \text{ indiv. m}^{-2}$ [0–175 m, Yen 1985] vs $100 \text{ indiv. m}^{-2}$ [0–500 m, Ikeda & Hirakawa 1996] for *P. elongata* [adult female], and $2500 \text{ indiv. m}^{-2}$ [0–175 m, King 1979] vs $550 \text{ indiv. m}^{-2}$ [0–500 m, Terazaki 1993] for *S. elegans*). This suggests that if the presence of predators is the major mechanism causing reverse diel vertical migration in their prey, the predation pressure on *P. new-*

mani is too low to induce this avoidance behavior for this species in Toyama Bay.

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