

Larval Recruitment of the Tropical Mussel *Modiolus philippinarum* (Bivalvia: Mytilidae) in Seagrass Beds

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Abstract: The tropical mussel *Modiolus philippinarum* is common and abundant in seagrass beds in Okinawa Island, southernmost Japan, and is commercially important to local fishermen. In order to elucidate the mechanisms that maintain the difference in density between benthic populations of the mussel within and outside seagrass beds, we monitored temporal variations in densities of the mussel at different developmental stages (planktonic larvae; new settlers; small and large individuals) within and outside seagrass beds in Okinawa Island over one year. Based on these data, the difference in larval density was not significant, but there were significant differences between densities of new settlers (shell length < 250 μm), small individuals (250 μm \leq shell length < 1.0 mm) and large individuals (shell length \geq 1.0 mm), within and outside seagrass beds. Cohort separation was applied to data for shell length distributions of new settlers and small and large individuals, and revealed that larvae mainly settled in July to August. New settlers grew up to about 20 mm in shell length in their first year; their mortality was constant and/or low once individuals had attained shell lengths of about 300 μm . These facts indicate that the much higher density of benthic populations of the mussel within seagrass beds may be determined at and/or shortly following larval settlement, though details of the mechanisms driving the above difference are not yet identified.

Keywords: larval recruitment, *Modiolus*, tropical mussel, seagrass

Introduction

It has been established that density and species diversity of benthic populations and communities are much higher within seagrass beds as compared to neighboring non-seagrass areas (Orth, 1977, 1992). Most previous studies have dealt with the mechanisms by which the difference between benthos densities within and outside seagrass beds may be generated and maintained. A variety of biotic or abiotic factors have been referred to, e.g. the differences in the complexity of habitats (Heck & Crowder, 1990; Heck & Wilson, 1987; Summerson & Peterson, 1984; Bologna & Heck, 2000), prey abundance (Peterson *et al.*, 1984), larval supply (Eckman, 1987; Wilson, 1990) and characteristics or stability of sediments (Orth, 1977, 1992).

In recent studies dealing with dynamics of populations and communities of marine benthic invertebrates (e.g. Underwood & Fairweather, 1989; Olafsson *et al.*, 1994; Underwood & Keough, 2001), the importance of larval recruitment processes as a mechanism by which benthic populations and communities may be generated and maintained has been widely cited, though Olafsson *et al.* (1994) believed that post-recruitment processes may play a more important role than pre-recruitment ones. This is also true for benthic invertebrates within seagrass beds. The canopy structure of seagrass beds reduces the velocity of water movement within the beds (Eckman, 1983, 1987; Fonseca & Fisher, 1986), with the result that detritus and particulate matter in the water may be trapped and retained within the beds, increasing the silt-clay and/or organic matter fraction of the

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bottom sediment (Peterson *et al.*, 1984; Fonseca & Fisher, 1986). Some believe that planktonic larvae of marine benthic invertebrates may also be trapped and retained within seagrass beds like detritus and particulate matter, resulting in a higher larval supply and thus higher larval settlement within the beds (Peterson, 1986; Orth, 1977, 1992; Bologna & Heck, 2000).

Recent studies have partly dealt with larval recruitment of bivalves within seagrass beds (Peterson, 1986; Eckman, 1987; Wilson, 1990; Reusch, 1998; Bologna & Heck, 2000). These studies suggest that larval recruitment processes may determine the difference in densities between benthic populations within and outside seagrass beds. All except Wilson (1990) and Bologna & Heck (2000) dealt mainly with post-recruitment events such as survivorship of new settlers, Wilson (1990) compared larval settlement of benthic invertebrates within and outside seagrass beds based on data for densities of new settlers identified to class level, not to species. Bologna & Heck (2000) investigated the impact of seagrass habitat architecture on bivalve settlement and concluded that structural components of seagrass habitats increased bivalve settlement. Based on the previous studies referred to above, we conclude that for benthic invertebrates the difference in density between benthic populations within and outside seagrass beds has not yet been viewed in terms of larval recruitment processes. This is also true for benthic invertebrates, particularly bivalves, within seagrass beds elsewhere in the Indo-West Pacific.

The tropical mussel *Modiolus philippinarum* is common and abundant within seagrass beds in Okinawa Island, southernmost Japan (Ozawa, 2001). By monitoring temporal variations in densities at different developmental stages (planktonic larvae; new settlers; small and large individuals) of the mussel, the present study examines larval recruitment of the mussel in order to identify the developmental stage at which the difference in density between benthic populations of the mussel within and outside seagrass beds may become established.

Materials and Methods

Study area

Kin Bay is located along the Pacific coast of central Okinawa Island, southernmost Japan (Oceanographic Society of Japan, 1985; Fig. 1). It covers 138 km², with most of the bay less than 30 m deep, and geographically belongs to the Tropical Zone. The bay is separated in the south from Nakagusuku Bay by a causeway connecting Okinawa Island with Henza Island (Fig. 1), though boat transit and bay water exchange occur through three gateways in the causeway. The dense seagrass beds where the present study was undertaken are located in the area west of Henza Island and north of the causeway (Fig. 1). They cover a surface area of about 0.7 km² with a height of about 20 cm throughout the year, and form one of the largest seagrass areas in the coastal region of Okinawa Island. According to Toma (1999) and Ozawa (2001), these beds are composed of 7 seagrass species: *Halophila ovalis*, *Thalassia hemprichii*, *Cymodocea rotundata*, *Cymodocea serrulata*, *Syringodium isoetifolium*, *Halodule uninarvis* and *Halodule pinifolia*.

Sampling was undertaken at 3 stations within and outside the seagrass beds (Fig. 1): Stn. A, where dense seagrasses (mostly *T. hemprichii*) were found throughout the year; Stn. B, close to the margin of the beds, where low density seagrasses (mostly *T. hemprichii*) were found throughout the year, and Stn. C, outside the beds, where no seagrass was found on the sandy sediment bottom. These stations were 100 m apart from each other, and were located parallel to and about 150 m off the causeway. They all lay deeper than 3 m (mean depth at low water of the spring tide).

Environmental conditions

There was no difference in water temperature or salinity between the three stations according to our preliminary surveys. We monitored water temperature and salinity only at Stn. A within seagrass beds from July 1999 to July 2000. Water temperature was measured to the nearest 0.01°C

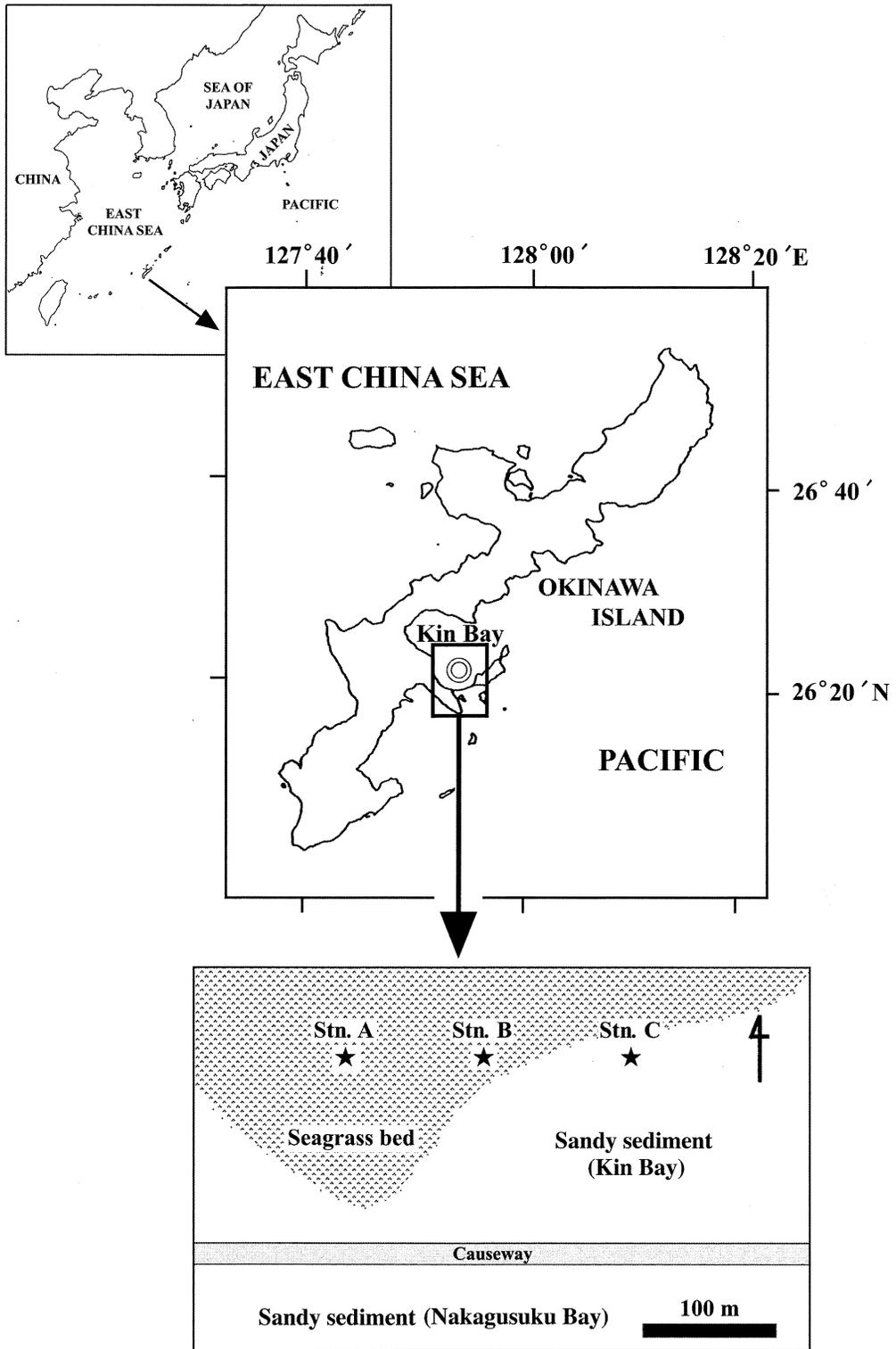


Fig. 1. Study area and sampling location within Kin Bay, Okinawa Island, southernmost Japan. Double circles: sampling site.

at intervals of 2 h using a Continuously Recording Sensor for Water Temperature (StowAway) left on the bottom close to Stn. A. Salinity was then measured to the nearest 0.1 PSU in water samples obtained 30 cm above the bottom at Stn. A, when samplings were made at different developmental stages of *M. philippinarum*, using a Reflection Salinometer (IS/Mill-G) in the laboratory. We calculated water temperature as monthly averages and salinity as the average over the sampling intervals of the mussel.

Seagrass biomass was measured at intervals of one month at Stns. A and B, respectively, from July 1999 to July 2000. Three samples of seagrass together with sediments were collected by divers at each station using a quadrat (20 cm×20 cm) with plastic boards of 20 cm height. After washing the seagrass in water, parts of the sample from above and below bottom surface were dried separately at 80°C for 48 h in an oven and were then weighed to the nearest 0.01 g using an electric balance.

To measure the silt-clay fraction (percentage in dry weight) of the sediment, two samples were collected using a core sampler (76 mm in diameter, depth 10 mm) at each station, at intervals of one week from July to November 1999, at intervals of 2 weeks from December 1999 to March 2000, and at intervals of one week from April to July 2000. After treating the sediment samples following Oceanographic Society of Japan (1986), they were filtered with a sieve (mesh aperture 63 µm), dried at 80°C for 48 h in an oven and weighed to the nearest 0.001 g.

Sampling procedures

Following previous studies (Sakai & Sekiguchi, 1992; Miyawaki & Sekiguchi, 1999, 2000; Ishii *et al.*, 2001a, b), samples were collected of the different developmental stages of the mussel (planktonic larvae; new settlers; small and large individuals). For *M. philippinarum*, we here define 'planktonic larvae' as umbo larvae (later veliger stage) because of a lack of information on the morphological characteristics of D-shaped larvae (earlier veliger stage); 'new settlers' as individuals with a shell length of less than 250 µm following Ozawa & Sekiguchi (2002) who cultured larvae in the laboratory. 'Small individuals' are defined as those with a shell length of between 250 µm and 1.0 mm, and 'large individuals' as those over 1.0 mm.

A variety of definitions of 'recruitment' exist, depending on different taxa and researchers. In general, marine benthic invertebrates with complex developmental stages (*i.e.* planktonic and benthic life stages) show much higher mortality shortly after larval settlement and metamorphosis, but thereafter grow with constant and/or low mortality (Muus, 1973). Following Miyawaki & Sekiguchi (1999, 2000), 'recruitment' is defined here as cohorts of *M. philippinarum* that attain 1.0 mm and more in average shell length.

Planktonic larvae, new settlers and small individuals of bivalves were sorted out from plankton and sediment samples under an optical stereomicroscope, using a suction device (Sakai & Sekiguchi, 1990). Species identification was undertaken for planktonic larvae and new settlers of *M. philippinarum* based on the shell hinge following Sakai & Sekiguchi (1990) and morphological features of shell described by Ozawa & Sekiguchi (2002). Shell lengths of the new settlers and small specimens were measured to the nearest 1 µm using a binocular micrometer on an optical microscope, while large individuals were measured to the nearest 0.1 mm using a vernier caliper.

Planktonic larvae: Divers using a plankton net (22 cm in diameter, mesh aperture 125 µm) collected plankton samples at the three stations (A, B, C) at intervals of three days from July to October 1999, two weeks from November 1999 to March 2000, and one week from April to July 2000, following Ozawa (2001), who determined the main spawning season of *M. philippinarum* in Okinawa Island to be from June to October. The net was vertically towed several times from a point 30 cm above the bottom to the surface at each station, so that the total tow distance of nets was 20 m at each station, equivalent to a filtered water volume of about 760 l. Plankton samples were immediately fixed with 3% neutralized seawater formalin, and deposited in a refrigerator

(4°C) until sorting and examination of the larvae was undertaken under an optical microscope after re-fixation of the samples with 80% ethanol in the laboratory.

New settlers and small individuals: Sampling procedures for new settlers and small individuals are same as outlined for planktonic larvae above, except the following: using a core sampler (76 mm in diameter, depth 10 mm) divers collected two samples of bottom sediments of 10 mm depth at each station. After filtering using a sieve (mesh aperture 125 µm), the remaining sediment was fixed with 3% neutralized formalin seawater and dyed with Rose Bengal to facilitate sorting of the bivalves. These sediment samples were deposited in the refrigerator (4°C) until sorting and examination of the new settlers and small individuals under an optical microscope. In the present study, new settlers and small individuals were not collected from seagrass blades because our preliminary surveys did not indicate the occurrence of specimens there.

Large individuals: Divers used a quadrat (50 cm×50 cm) with plastic boards of 20 cm height to collect two samples of bottom sediment at intervals of one month at each station. At Stns. A and B, however, seagrass was collected in addition to the sediments. After filtering these sediment samples using a sieve (mesh aperture 1.0 mm), the remaining sediment was fixed with 10% neutralized formalin seawater.

Data processing

We examined the difference in densities of planktonic larvae, new settlers and small and large individuals of *M. philippinarum* between the three stations employing a non-parametric two-way Friedman's test and then between each pair of stations (A vs. B, A vs. C, B vs. C) employing a non-parametric Wilcoxon's test using Bonferroni's inequality (Sokal & Rohlf, 1973; Yamamura, 1993) as follows:

$$\text{Bonferroni's inequality } \alpha' = \alpha / {}_kC_2, \text{ i.e. } \alpha' = 0.05 / {}_3C_2 = 0.0167$$

where α' : corrected significant level 0.0167 for any pair of k stations, α : significant level 0.05 for all data sets, ${}_kC_2$: number of pair combinations from k stations and k: number of stations 3.

Data on shell length distributions for 2 groups ('new settlers and small individuals' and 'large individuals') of the mussel were compiled for all the stations. Based on these data, cohorts within each group of the mussel were separated by the method of Akamine (1985), which separates poly-modal length distribution into two or more normal distributions. The growth curve of each cohort was estimated based on the mean shell length of each normal distribution. However, cohort separation for the new settlers and small individuals was carried out based on shell length data for the periods from July to August 1999 and 2000 respectively, because density was too low in the other months to do cohort separation, while that for the large individuals was done based on the data of shell lengths less than 20 mm.

Results

Temporal variations in environmental conditions

Water temperature and salinity: Temporal variations in water temperature and salinity at Stn. A are shown in Fig. 2. It is easy to detect the trend in temporal variations in water temperature but it is difficult to detect any trend in temporal variations in salinity. Despite Okinawa Island geographically belonging to the Tropical Zone, water temperature varied markedly, with a range of 23.4±4.8°C (average±standard deviation), through a year: water temperature was 28.6±0.9°C in July to October when planktonic larvae of *M. philippinarum* were abundantly found but fell to 18.0±0.8°C in December to March of the following year when the larvae were not found (see below). This fall in temperature is driven by the winter monsoon blowing from the mainland of China. Unlike water temperature, however, salinity was almost constant at 34.9±0.4 PSU throughout the year, because

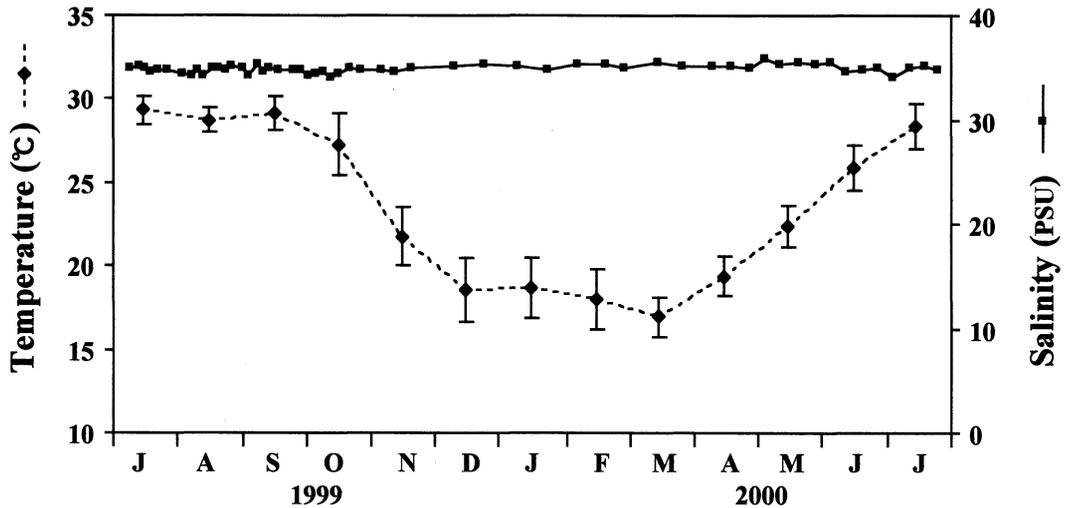


Fig. 2. Temporal variations in mean water temperature and salinity in water just above the bottom at Stn. A within seagrass beds in Kin Bay, Okinawa Island. Vertical lines: standard deviation.

the seagrass beds studied are in a location that is not influenced by freshwater discharge.

Seagrass biomass: Temporal variations in seagrass biomass at Stns. A and B are shown in Fig. 3. It is difficult to detect any trend in temporal variations in seagrass biomass above and below bottom surface. Throughout the year, seagrasses above and below bottom surface were detectable at each station, and their biomass was always higher at Stn. A than at Stn. B. Seagrass biomass above and below the bottom surface was 3.66 ± 1.46 g / 0.04 m² and 11.32 ± 4.43 g / 0.04 m² at Stn. A, respectively, while that was 0.97 ± 0.59 g / 0.04 m² and 3.31 ± 2.43 g / 0.04 m² at Stn. B, respectively. Temporal variations in seagrass biomass above and below bottom surface were not similar to each other at each station.

Silt-clay fraction of sediment: Temporal variations in the silt-clay fraction of sediment are shown in Fig. 4. It is difficult to detect any trend in temporal variations in the silt-clay fraction of sediment. Despite irregular variations being detected through a year, the silt-clay fraction was highest at Stn. A with $6.03 \pm 1.23\%$, intermediate at Stn. B with $2.50 \pm 0.95\%$, and the lowest at Stn. C with $0.86 \pm 0.49\%$ over the year.

Temporal variations in densities for different life stages of the mussel *Modiolus philippinarum*

Planktonic larvae: As indicated in Fig. 5, larvae were abundantly found only during the warmer period from early July to late October 1999 and thereafter from June to July 2000. Their occurrence corresponded to the main spawning season (Ozawa, 2001). Based on the data collected in 1999, 95% of all larvae collected from July to October were found in July and August. There were three peaks of larval density, in middle July, middle August and late September at each station, with the highest density reaching about 75 ind./760 l. As indicated by Ozawa (2001) dealing with the reproduction and spawning of the mussel in the same sites as in the present study, these peaks corresponded to spawning peaks of adults with an interval of about 45 days. The difference in larval density was not significant between stations α ($\chi^2_r=0.21$, $p>0.90$; Table 1), nor between any pair of stations.

New settlers: As indicated in Fig. 5, new settlers were abundantly found in the warmer period, as with larvae, and the highest density was detected in July 1999. Based on the data collected in 1999, there were three peaks of density of new settlers as with larvae. The highest density was

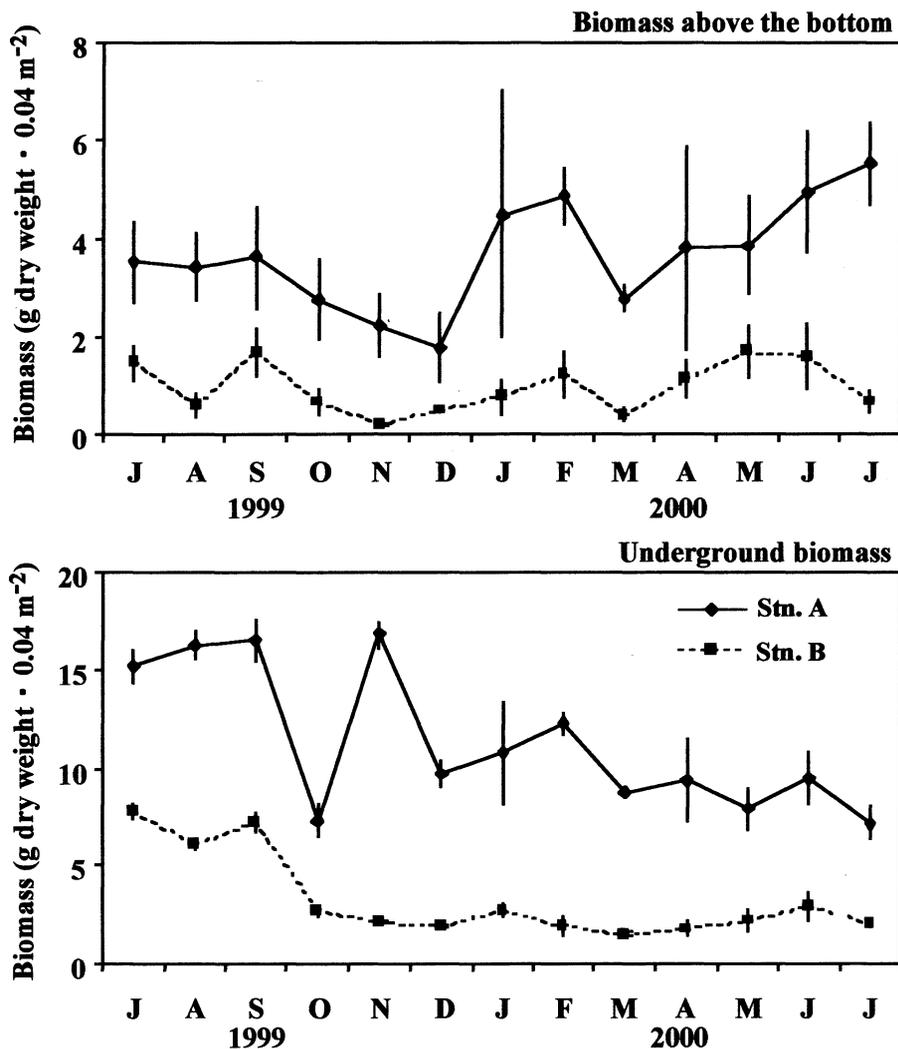


Fig. 3. Temporal variations in seagrass biomass above and below ground in Kin Bay, Okinawa Island. Data for 3 samples at each station were averaged. Vertical lines: standard deviation.

detected at Stn. A with about 19 ind./50 cm². The difference in density of new settlers was significant among stations ($\chi^2=13.16$, $p<0.01$; Table 1). The difference was significant between Stns. A and B and also between Stns. A and C, but not between Stns. B and C. The highest density was at Stn. A.

Small individuals: As indicated in Fig. 5, small individuals were abundantly found from July 1999 to January 2000 and thereafter from June to July 2000. The highest density, about 6 ind./50 cm², was detected at Stn. A in July 1999. It is difficult to detect density peaks of small individuals that correspond to the three peaks of larval and new settler density, respectively. The difference in density of small individuals was significant among stations ($\chi^2=38.56$, $p<0.01$; Table 1), and between any pair of stations, the density being highest at Stn. A, intermediate at Stn. B and lowest at Stn. C.

Large individuals: As indicated in Fig. 5, large individuals were found at Stn. A throughout the

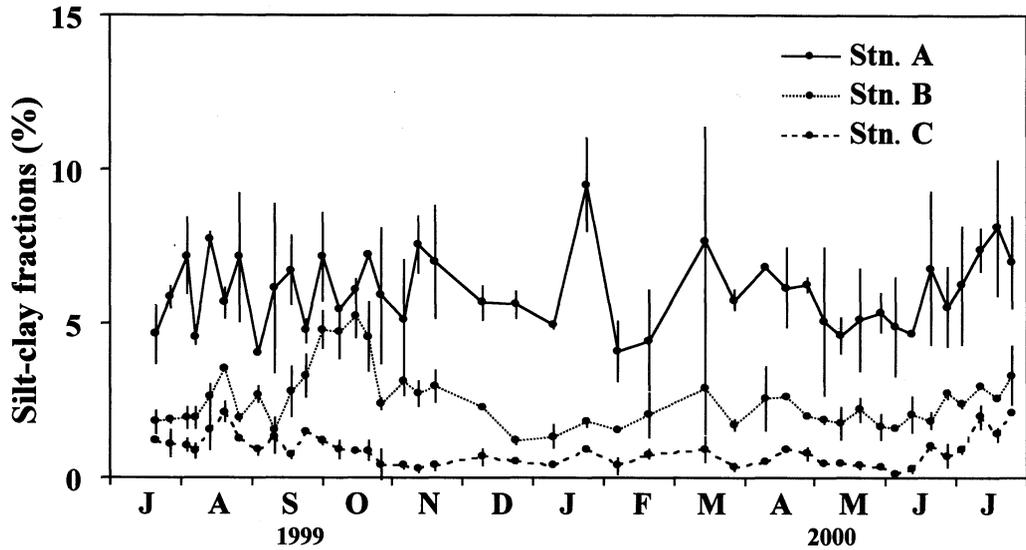


Fig. 4. Temporal variations in the silt-clay fraction of sediment in Kin Bay, Okinawa Island. Data for 3 samples at each station were averaged. Vertical lines: standard deviation.

Table 1. Multiple comparison test for densities of bivalve species between stations.

Stage	<i>Modiolus philippinarum</i>	Other Mytilidae	Other bivalve species
Planktonic larvae	NS	NS	NS
New settlers	A>B C	-	-
Small individuals*	A>B>C	A B>C	A B>C
Large individuals	A>B C	A>B C	A B>C
Cohort F ^{**,***}	A>B C	-	-

NS: Not significant in Friedman's two-way analysis for ranks. See text for further explanations.

*: Densities of new settlers and small individuals were pooled for the other mytilidae and the other bivalve species, respectively.

**: Multiple comparison test was done only for *M. philippinarum*.

***: See text for Fig. 8 for cohort F.

year. In strong contrast to the figures for planktonic larvae, new settlers and small individuals, the density of large individuals was higher between August 1999 and March 2000, with the highest density reaching about 9 ind./0.25 m². Only single individuals were found at Stn. B in December 1999, in March 2000 and in May 2000, while no specimens were found at Stn. C. The difference in density of large individuals was significant among stations ($\chi^2_r=24.57$, $p<0.01$; Table 1). It was significant between Stns. A and B and between Stns. A and C, but not between Stns. B and C. The highest density was found at Stn. A. This is also true for the density of different cohorts as referred to later ($\chi^2_r=22.62$, $p<0.01$).

Cohort separation of the mussel *Modiolus philippinarum*

Temporal variations in shell length distributions of the two groups (the new settlers and small individuals, and the large individuals) are illustrated in Figs. 6 and 7 respectively. New settlers were abundant from July to August while new recruits were found over longer periods, e.g. in April, August to September and December. Based on these data, cohort separation was undertaken

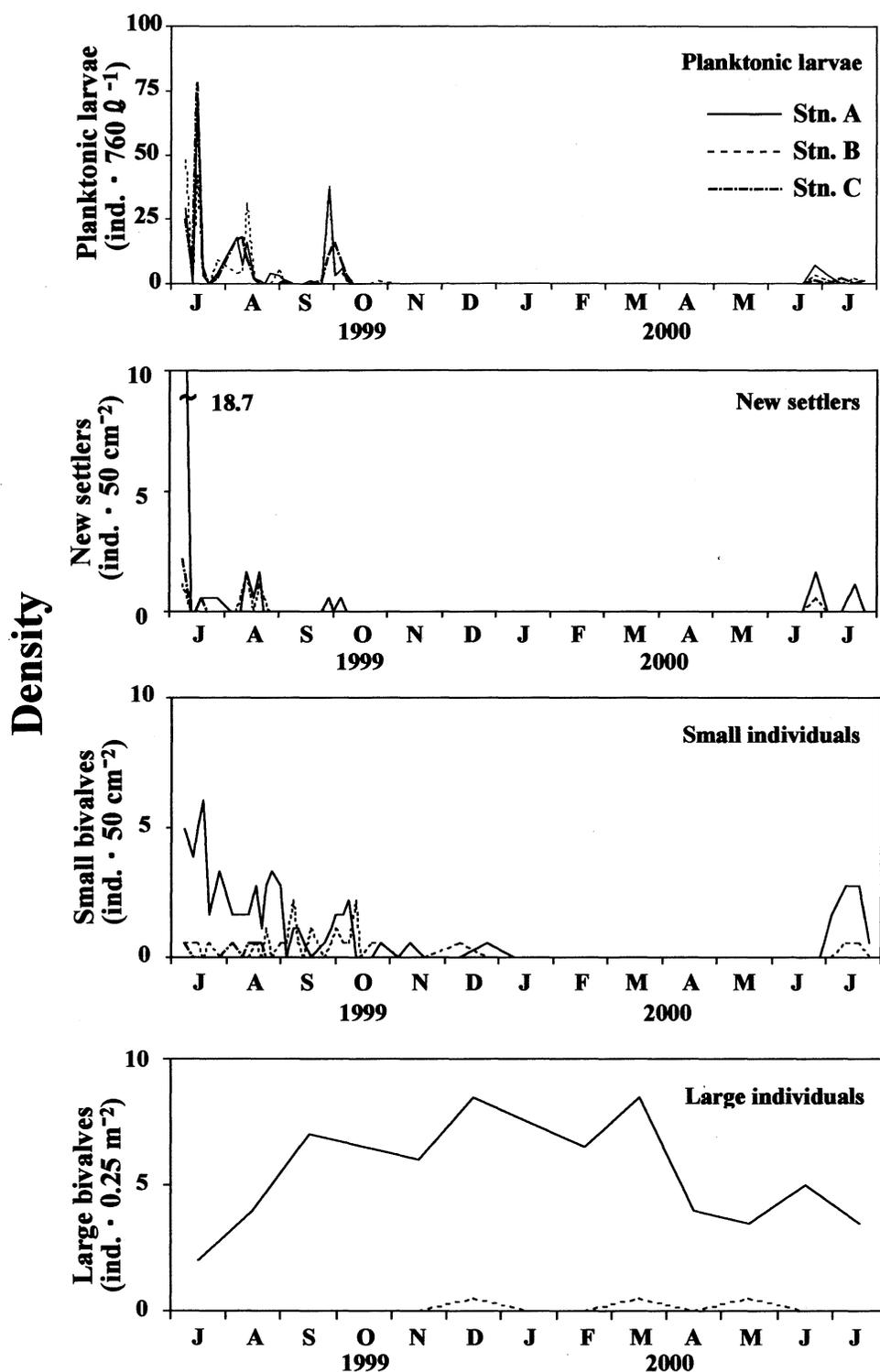


Fig. 5. Temporal variations in densities for planktonic larvae, new settlers, small and large individuals of *M. philippinarum* in Kin Bay, Okinawa Island. Data for 2 samples were averaged except for planktonic larvae. See text for further explanation.

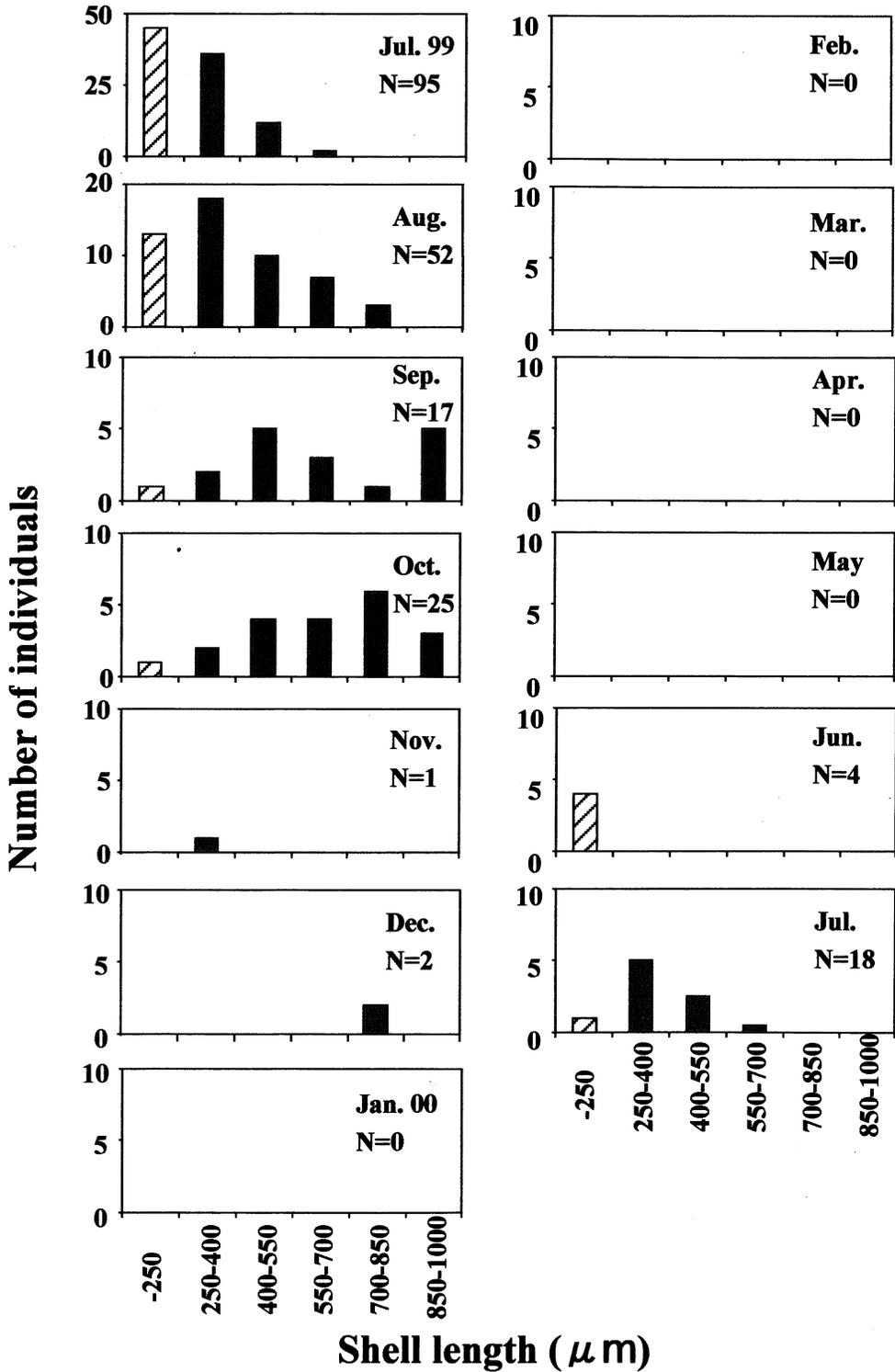


Fig. 6. Temporal variations in shell length distributions of the new settlers and small individuals of *M. philippinarum* in Kin Bay, Okinawa Island. Data for all specimens collected were used. Hatched columns: new settlers; solid columns: small individuals.

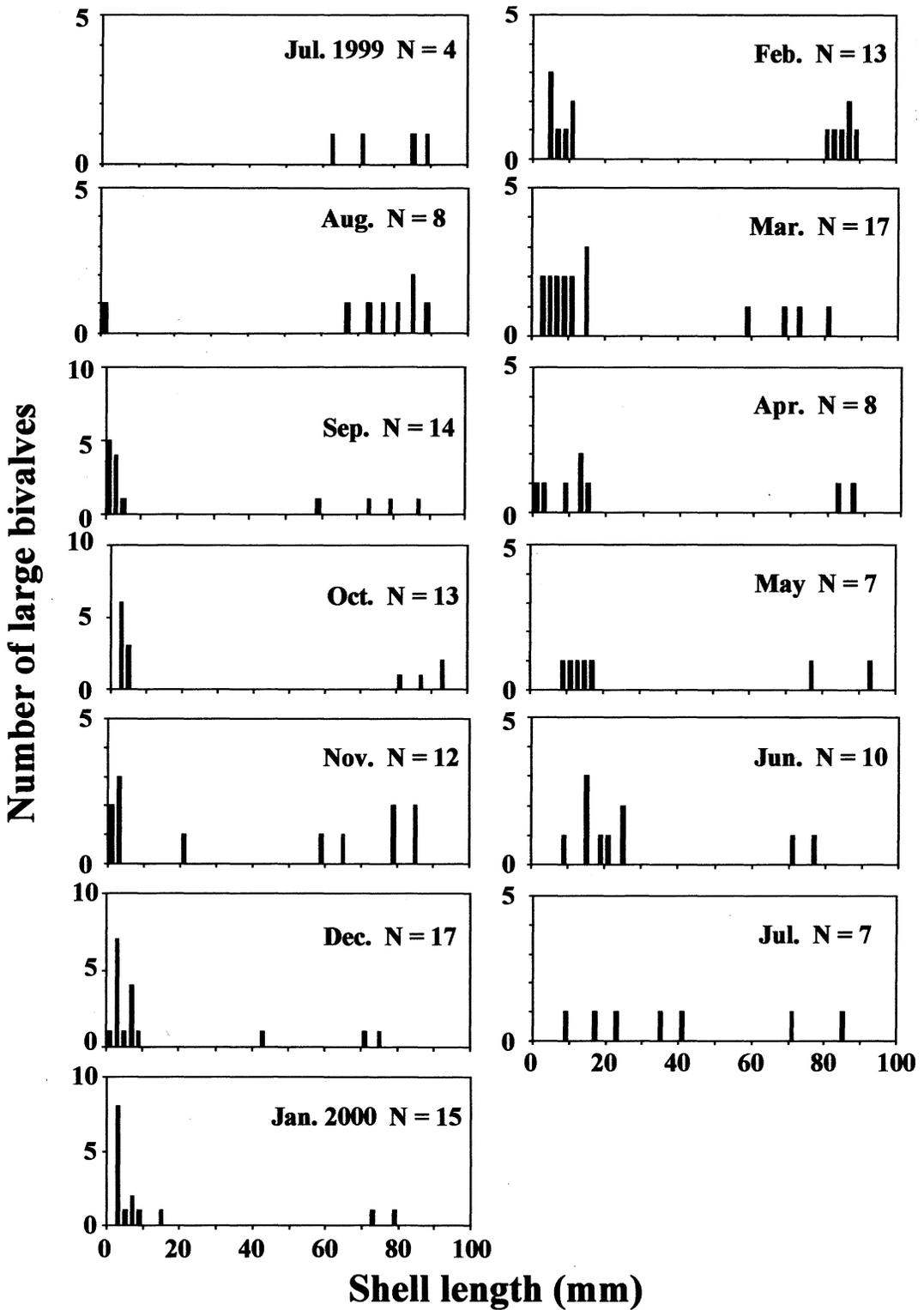


Fig. 7. Temporal variations in shell length distributions of large individuals of *M. philippinarum* in Kin Bay, Okinawa Island. Data for all specimens collected were used.

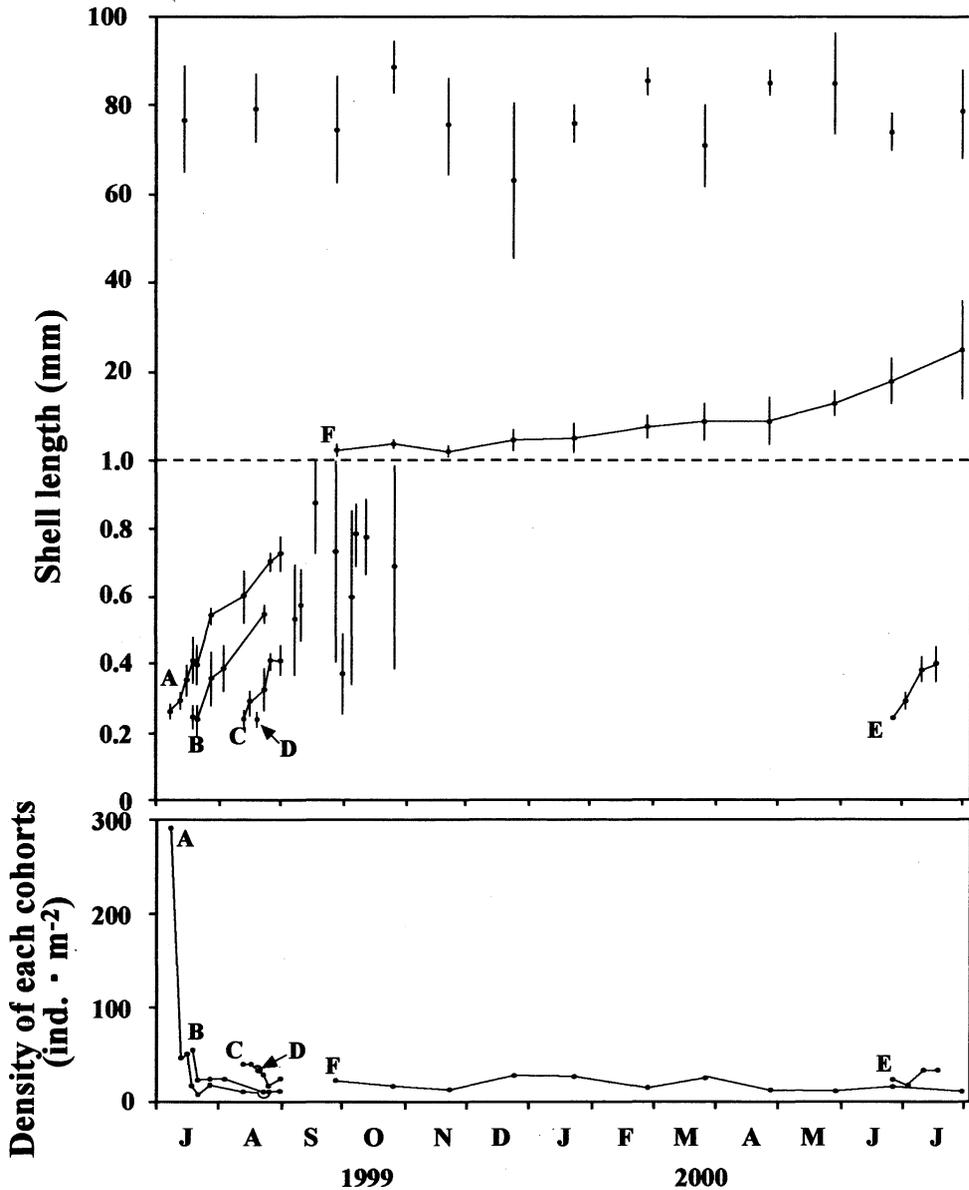


Fig. 8. Cohort separation of *M. philippinarum* in Kin Bay, Okinawa Island. Data for all specimens collected were used. A, B, C, D, E and F: different cohorts. Solid circles and vertical lines in upper 2 figures represent mean and standard deviation, respectively. See text for further explanation.

as shown in Fig. 8. For the new settlers and small individuals, 4 cohorts (A, B, C, D) were clearly identified for the period from July to August 1999 while one cohort (E) was found from June to July 2000. Main recruitment of the mussel, particularly for cohort F, which is absolutely dominant among large individuals, is detected in September to October 1999. As exemplified by cohort A, extremely high mortality occurs shortly after larval settlement. For large individuals, the cohort F (new recruits) was identified, as well as several other older, mixed cohorts. Cohort F reached a shell length of 20 mm in July 2000, about 10 months after larval recruitment in September or October 1999.

Discussion

In terms of the mechanisms by which benthic populations of *M. philippinarum* may be generated and maintained within seagrass beds, the results of the present study are summarized as follows:

- 1) Planktonic larvae were mainly collected in July to August, so new settlers were mainly found for the same period when 4 cohorts (A, B, C, D) were identified as indicated in Fig. 8.
- 2) New recruits of large individuals identified as cohort F were first found in September. The extent to which cohorts of the new settlers and small individuals (A, B, C, D) contributed to establishing the cohort F of large individuals remains unsolved in the present study. Ozawa & Sekiguchi's (2002) work with larval culture of the mussel in laboratory showed that it took about 30–40 days from larval settlement to produce individuals with a shell length of 1.0 mm at a water temperature of 30°C. Similar results were obtained also in the present study, as shown above (Fig. 8).

As indicated in Fig. 8, 4 cohorts (A, B, C, D) of new settlers of the mussel were generated by larvae mainly found in July and August, while larvae found in September and October when water temperature started to rapidly decrease (Fig. 2) failed to clearly establish successful cohorts of small and large individuals. This indicates that larvae of the mussel released in the earlier part of the main spawning period may survive to then establish successful cohorts in recruitment, while those released in the later part may be destined for death due to lower water temperature in October and onward (Fig. 2). This may be supported by the fact that growth of the cohort F was much lower for the period when water temperature rapidly decreased, as shown in Fig. 8.

Extremely high mortality shortly after larval settlement was detected, as exemplified by the cohort A, whereas cohorts of small (shell length about 300 μm and more) to large individuals showed relatively constant, low mortality (Fig. 8). As found by Peterson (1986), Wilson (1990) and Olafsson *et al.* (1994) in the population dynamics of marine benthic invertebrates, this suggests that the strength of mortality shortly after larval settlement may have a greater influence on population dynamics of *M. philippinarum* than larval supply and settlement. Higher mortality shortly after larval settlement driven both by predation and biotic and abiotic disturbance has been reported for several temperate bivalve species (Muus, 1973; Hurlbut, 1991; Imabayashi & Iwatani, 1990; Miyawaki & Sekiguchi, 2000; Newell *et al.*, 2000). Eckman (1987) demonstrated higher mortality among new settlers of two bivalve species inhabiting seagrass beds due to physical and biological disturbance of the sediment.

Although the research has documented the effects of structural habitats on flow and deposition of larvae, there are few detailed investigations that examine how settling organisms use seagrass habitats. It is not established yet whether larvae are deposited on the sediment surface or whether they actively settle on and cling to the fronds and leaves. As shown by Bologna & Heck (2000), larvae of several bivalve species settle on the seagrass blade surface. In the present study, we did not examine whether or not *M. philippinarum* larvae settle on the seagrass blade surface, although our conclusions above are not altered by the possibility that they may use seagrass blades as primary settlement sites (*sensu* Bayne, 1964),

We set out to examine the following two issues:

- 1) How the difference in densities of benthic populations (large individuals) of *M. philippinarum* within and outside seagrass beds may be determined.
- 2) How benthic populations of the mussel may be generated and maintained within the beds.

The results of the present study are summarized as follows: there was no significant difference in larval density of the mussel among the three stations. The difference in densities of the benthic stages (new settlers, small and large individuals) was significant between the three stations, their density being the highest at Stn. A, intermediate at Stn. B and the lowest at Stn. C, though the difference for new settlers was not significant between Stns. B and C. These facts indicate that the dif-

ference in densities between large individuals within and outside seagrass beds may be determined at the new settler stage.

The difference between densities of benthic populations of large individuals of *M. philippinarum* within and outside seagrass beds may be explained by one of the following three scenarios:

1) There is no significant difference between larval density within and outside seagrass beds, but larval settlement is much higher within the beds than outside, with the result that large individuals achieve much higher density within the beds.

2) There is no significant difference between larval density or larval settlement within and outside seagrass beds, but the mortality shortly after larval settlement is much higher outside than within the beds, perhaps coupled with a higher migration rate into the beds from outside. Large individuals would thus eventually achieve a much higher density within the beds.

3) There is significant difference between larval density within and outside the beds, with higher larval density within the beds, and events during the subsequent developmental stages (larval settlement, new settlers, small and large individuals) do not alter this pattern, which is fixed at the larval stage. Accordingly, large individuals attain a much higher density within the beds.

Scenarios 1) and 2) imply that the higher density of larvae released by higher density of large individuals (*i.e.* spawners) within seagrass beds may quickly disperse and fail to generate a difference between larval supply within and outside of the beds.

If the first scenario is accepted, the higher density of large individuals within seagrass beds may be determined by much higher larval settlement within the beds. Then, higher larval settlement of the mussel within seagrass beds may be generated through selective or non-selective and passive larval settlement within the beds. It is difficult to distinguish selective larval settlement from non-selective and passive larval settlement for benthic invertebrates in the field. According to previous studies (Butman, 1986, 1987, 1989; Butman *et al.*, 1988; Snelgrove *et al.*, 1994) that dealt with settlement behavior of planktonic larvae of benthic invertebrates in a flume, the larvae behaved like particulate matter in water and were mainly controlled by water movement, though their behavior played an important role in larval settlement within the boundary layer several mm or cm above the flume bottom. The canopy structure of seagrass beds reduces the velocity of water movement within seagrass beds, and particulate matter in water may thus be trapped and retained within the beds and increase the silt-clay fraction and/or organic matter fraction of bottom sediment (Peterson *et al.*, 1984; Fonseca & Fisher, 1986). This was also found in the present study, as indicated in Fig. 4. The larvae may thus be trapped and retained within the beds like particulate matter in water (Orth, 1977, 1992; Peterson, 1986).

If the second scenario is accepted, the higher density of large individuals of the mussel within seagrass beds may be generated by higher mortality shortly after larval settlement outside the beds and/or by transport and migration of new settlers shortly after larval settlement into the beds from the outside. New settlers and/or early juveniles of some bivalves are able to move or migrate using byssus drifting (Sigurdsson *et al.*, 1976; Lane *et al.*, 1985). Unfortunately, byssus drifting has not been confirmed yet for new settlers and/or early juveniles of *M. philippinarum*. If higher mortality shortly (within 3 days) after larval settlement is detected for the mussel as in other benthic invertebrates studied by Thorson (1950), Sastry (1979) and Hurlbut (1991), the new settler density of the mussel in the present study may not indicate that the strength of larval settlement varies depending on environmental conditions, and thus may not always indicate higher larval settlement within seagrass beds than outside. In order to examine the above two scenarios, we need to measure daily larval settlement and mortality shortly after larval settlement within and outside seagrass beds.

If the third scenario is accepted, the higher density of large individuals of the mussel within seagrass beds may be generated by higher larval density within the beds because events during the following life stages (larval settlement, new settlers, small and large individuals) cannot alter the pattern (higher density within the beds) fixed at the larval stage. The present study showed no

significant difference between larval density within and outside the beds (Table 1, Fig. 5). In the present study, we collected planktonic larvae of the mussel by vertical towing of plankton nets from a depth of 30 cm above the bottom to the sea surface at each station. However, if the larvae of the mussel are concentrated in the water just above the bottom (i.e. within seagrass of a height of about 20 cm above the bottom) and there is significant difference between larval density within and outside the beds, the third scenario has to be accepted, though it is not obvious.

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熱帯海草藻場におけるホソスジヒバリガイの幼生加入過程

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要 約

ホソスジヒバリガイは沖縄本島では主として海草藻場に生息し、隣接する海草のない区域にはほとんど見られない。この海草藻場内外のホソスジヒバリガイの密度差が形成され維持される機構を解明するために、沖縄本島の金武湾の海草藻場内外に定点を設け、各成長段階（浮遊幼生、着底稚貝、小型個体、大型個体）の密度の変動を1年間にわたって調査した。海草藻場内外のホソスジヒバリガイの密度差は、浮遊幼生を除いて、各成長段階において統計的に有意であった。ホソスジヒバリガイの殻長頻度分布に基づくコホート解析の結果によれば、浮遊幼生は主として7月～8月に着底し、着底後1年で約20 mmにまで成長する。着底直後の死亡率は著しく高いが、殻長約300 μ mを越す小型個体の死亡率は低くなり、ほぼ一定となる。これらの事実は、その具体的な詳細は未解明であるが、海草藻場内のホソスジヒバリガイの大型個体の密度は着底直後の死亡率の高低によって決定されており、また海草藻場内外の密度差は着底稚貝の段階において決定されていることを示している。