INTRODUCTION

Most marine benthic invertebrates, including bivalves, have complex life histories with benthic and planktonic phases. Scientists have recently focused mainly on the larval recruitment of invertebrates, coined as the supply side of ecology, which includes the dispersal/transport of planktonic larvae, their retention at or return to adult habitats, settlement at the sea bottom and recruitment to benthic populations. Such factors play an important role in the community and population dynamics of invertebrates.

The manila clam *Ruditapes philippinarum* is commercially important to Japan, and is abundant in inter- and subtidal zones from Hokkaido to Kyusyu. Annual catch yields in Japan amounted to 120 000–160 000 metric tons from 1975 to 1987, but yields have decreased drastically since 1987 (Fig. 1). This is also the case for Ariake Sound, particularly in Kumamoto Prefecture, where yields peaked at approximately 65 000 metric tons, which is equivalent to half of the yields in Japan in 1977, and have decreased drastically to one-hundredth of this amount (Fig. 1). Decreasing yields may be possibly a result of overfishing, environmental deterioration and outbreaks of predators.

To restore the catch yields of *R. philippinarum* and maintain satisfactory environments for benthic populations of the clam, larval recruitment and population dynamics, which are determined possibly by pre-settlement or post settlement processes, should be examined. The clam has been studied intensively in Japan. Unfortunately, there is little information on larval recruitment because most studies have focused on benthic phases (e.g. Ikematsu and Matsumoto, Ikematsu, Sekiguchi). Only a few studies have been done on larval recruitment of bivalves due to difficulties in quantitative sampling and the identification of planktonic larvae. Based on Sakai and Sekiguchi’s identification key for planktonic larvae and new settlers of bivalves commonly and abundantly found on Japanese tidal flats, Sekiguchi and his colleagues have studied the larval recruitment of *R. philippinarum*, *Musculista senhousia* and...
Nuttallia olivacea on tidal flats along the western coast of Ise Bay on the Pacific coast of central Japan. The results of their studies are summarized as follows: Seasonal and annual fluctuations of densities of planktonic larvae, new settlers and small to large bivalves in these three species are remarkable, and the larvae released by fall–early winter spawners may contribute mainly to the establishment of benthic populations.

The present study is concerned with the larval recruitment of R. philippinarum in Ariake Sound, to examine the following: (i) seasonal and annual fluctuations of density at each growth stage (planktonic larvae, new settlers and small to large bivalves); (ii) cohorts based on the cohort analysis of shell length distributions; (iii) success/failure of recruitment; (iv) growth stage at which benthic population size is determined; and (v) mechanisms by which benthic populations are maintained.

MATERIALS AND METHODS

Study area

Ariake Sound, with a southward opening, has a surface area of 1700 km² and an average depth of 20 m with a muddy sediment bottom (Fig. 2). Maximal tidal range reaches to 6.5 m in the innermost part of the Sound, and vast tidal flats develop largely in the eastern part with a surface area of 238 km² at the spring tide and a surface area of 110 km² at the neap tide.

Field sampling was carried out biweekly from February 1997 to December 1998 on the tidal flats at the mouths of Midori and Kikuchi Rivers where they flow into the eastern part (Kumamoto Prefecture) of Ariake Sound (Fig. 2). The mouths of the two rivers are 20 km distant from each other. Midori River runs a distance of 78 km with tidal flats originally made by fine sand sediment but of muddy sand recently (hereafter called Kawaguchi). Kikuchi River runs a distance of 71 km and has tidal flats with a muddy sediment (hereafter called Nameishi). Although R. philippinarum was abundant on both flats before 1984, the fishery

Fig. 1 Variations in annual catch yields of the manila clam Ruditapes philippinarum in Japan. Total, total catch yields in Japan.

Fig. 2 Study area in Ariake Sound, southern Japan. Lined areas, sediment exposed to air during high water at the spring tide; hatched areas, sediment of the intertidal zone.
collapsed at Nameishi, and catch yields have decreased drastically at Kawaguchi. To re-establish an active clam fishery at Kawaguchi, the Kumamoto Prefecture Government had fine sands placed on the muddy sand sediment of the flat in 1996.

Sediment characteristics clearly differ between Kawaguchi and Nameishi. The silt-clay fraction is clearly higher at Nameishi than Kawaguchi. The silt-clay fraction at Nameishi is higher in the rainy season (June to early July) and twice as high in the other seasons, whereas at Kawaguchi it is higher in the rainy season and nearly 100 times as high during the other seasons (Table 1). Precipitation was maximal in July and minimal in October in 1997, whereas it was maximal in June and minimal in August in 1998 (Table 2).

For the sampling of bivalves in the benthic phase on the flats, six stations (Sts. A, B, C, D and E within X, and St. Y) were established on Kawaguchi and six sampling stations (Sts. A, B, C, D, E and F) were established on Nameishi (Fig. 3). All stations were exposed to air at ebb tide and were underwater when river discharge increased as a result of too much precipitation with the approach of typhoons. There were also two stations (Sts Z and 2) for sampling planktonic larvae of bivalves at Kawaguchi and Nameishi (Fig. 3). Two samples were collected at each station to reduce the effects of sampling bias as a result of uneven distributions of bivalves on tidal flats. All data were used to estimate density of bivalves in the benthic phase as individuals per 100 cm².

Table 1  Sediment characteristics on the two tidal flats (Kawaguchi and Nameishi, Kumamoto Prefecture)

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<td>Kawaguchi*</td>
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<tr>
<td>St. A</td>
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<td>24.00</td>
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<tr>
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<tr>
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<td>0.97</td>
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<td>Kawaguchi†</td>
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<tr>
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<td>St. F</td>
<td>1.02</td>
<td>1.25</td>
<td>0.86</td>
<td>0.84</td>
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Kawaguchi‡     |              |              |              |              |
| St. A          | 6.74         | 100.00       | 100.00       | 59.1         |
| St. B          | 2.52         | 1.25         | 0.86         | 0.84         |

Table 2  Weather conditions at Misumi, Amakusa, Kumamoto Prefecture

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<th>Feb. 97</th>
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<td>WSW</td>
<td>SSW</td>
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<td>NE</td>
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<td>115.0</td>
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<td>28.3</td>
<td>25.5</td>
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<tr>
<td>Wind direction</td>
<td>SW</td>
<td>WSW</td>
<td>S</td>
<td>NNW</td>
<td>NE</td>
<td>NNE</td>
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<tr>
<td>Wind velocity (m/s)</td>
<td>1.0</td>
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<td>1.1</td>
<td>1.4</td>
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Precipitation, monthly total precipitation; air temperature and wind velocity, average values; wind direction, mostly frequent wind directions.

Sakai and Sekiguchi, counted by species with a dissecting microscope.

New settlers and small to large bivalves were collected from sediment at sampling stations on both flats of Kawaguchi and Nameishi biweekly from February 1997 to December 1998 (Fig. 3). New settlers and small bivalves are aggregated largely within the upper 1.0 cm of the sediment. Two sediment samples were collected at each station during the ebb tide using a core sampler (34 mm diameter, depth 2.0 cm) and filtered with a 125μm mesh sieve. The samples were fixed immediately with 5% buffered formalin and dyed with Rose Bengal to facilitate sorting the bivalves. All specimens were sorted using a suction device, identified according to Xu, and Sakai and Sekiguchi, and counted by species with a dissecting microscope. The shell length of all specimens was measured to the nearest 1.0μm with an ocular micrometer.

Two sediment samples for large bivalves were collected at each station during ebb tide using a core sampler (10 cm × 10 cm × 10 cm, or 25 cm × 25 cm × 10 cm) and filtered with a 1.0 mm mesh sieve. All samples were fixed immediately with 10% buffered formalin. All specimens were sorted, identified and counted. The shell length of all specimens was measured to the nearest 0.1 mm with vernier calipers.

Cohort analysis

Shell length data for the two groups (new settlers and small bivalves, large bivalves) were compiled for all stations on Kawaguchi and Nameishi. Based on these data, cohorts within each group were separated by the method of Akamine, which separates polymodal 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.

RESULTS

Kawaguchi (Midori River flat)

Planktonic larvae

Planktonic larvae were collected at Sts Z and 2 biweekly from April 1997 to December 1998 (Fig. 3) by pumping 200 L of seawater from an intermediate depth (1.5 m) during the flood tide to avoid surface freshwater. The water was then filtered with a 40μm mesh sieve. Samples were fixed immediately with 5% buffered formalin seawater. The temperature and salinity of the pumped water were monitored with a salinometer. All specimens of planktonic larvae (Umbo veliger larvae) of bivalves were identified according to Xu and Sakai and Sekiguchi, and counted by species with a dissecting microscope.

New settlers and small to large bivalves were collected from sediment at sampling stations on both flats of Kawaguchi and Nameishi biweekly from February 1997 to December 1998 (Fig. 3). New settlers and small bivalves are aggregated largely within the upper 1.0 cm of the sediment. Two sediment samples were collected at each station during the ebb tide using a core sampler (34 mm diameter, depth 2.0 cm) and filtered with a 125μm mesh sieve. The samples were fixed immediately with 5% buffered formalin and dyed with Rose Bengal to facilitate sorting the bivalves. All specimens were sorted using a suction device, identified according to Xu and Sakai and Sekiguchi, and counted by species with a dissecting microscope. The shell length of all specimens was measured to the nearest 1.0μm with an ocular micrometer.

Two sediment samples for large bivalves were collected at each station during ebb tide using a core sampler (10 cm × 10 cm × 10 cm, or 25 cm × 25 cm × 10 cm) and filtered with a 1.0 mm mesh sieve. All samples were fixed immediately with 10% buffered formalin. All specimens were sorted, identified and counted. The shell length of all specimens was measured to the nearest 0.1 mm with vernier calipers.
in June (100 ind./200 L), while those in 1998 were somewhat higher in May (300 ind./200 L) than in November (200 ind./200 L). Density peaks of the larvae in mid June 1997 and mid May 1998 may have been laid by spring-early summer spawners, while those in late October 1997 and late November 1998 may have been laid by fall–early winter spawners.

Water temperature and salinity fluctuated remarkably with the season; minimal temperature and maximal salinity occurred in early winter (9.8–11.6°C, 32.42–32.63 PSU) and maximal temperature and minimal salinity occurred from spring to summer (28.7–28.8°C, 24.40–26.45 PSU) (Fig. 4). This may be related to precipitation and freshwater discharge through the two rivers (Kikuchi and Midori Rivers). As indicated in Fig. 4, the density of planktonic larvae in spring to summer peaked during the increase in water temperature and/or decreasing salinity, and peaked during the decrease in water temperature and/or increasing salinity from fall to early winter.

**New settlers**

New settlers were found from May to June 1997 and November 1997 to November 1998 (Fig. 5). Their
Larvae with density peaks in late November 1998 may settle in early January 1999, and density peaks of new settlers may appear in January (Ishii R, unpubl. data, 1998). This suggests that seasonal changes for new settler density may depend on larval density.

Small bivalves were found throughout 1997 except January and September, and found from January to October in 1998 (Fig. 5). Their density fluctuated remarkably with the season, peaking three times in 1997 (late February, early July and early December) and twice in 1998 (early May and mid July). Peaks density fluctuated remarkably with the season, peaking twice in 1997 (early June and December) and in 1998 (May and mid July). The peaks in 1997 were much higher during December (270 ind./100 cm²) than in June (30 ind./100 cm²). Those in July 1998 (30 ind./100 cm²) were somewhat higher than in May 1998 (20 ind./100 cm²). Seasonal changes for new settler density were similar to that of planktonic larvae.


**Small bivalves**

Small bivalves were found throughout 1997 except January and September, and found from January to October in 1998 (Fig. 5). Their density fluctuated remarkably with the season, peaking three times in 1997 (late February, early July and early December) and twice in 1998 (early May and mid July). Peaks
in 1997 were much higher in December (950 ind./100 cm²) than in February (70 ind./100 cm²) and in July (50 ind./100 cm²). Those in May 1998 (120 ind./100 cm²) were higher than in July 1998 (70 ind./100 cm²). Seasonal changes for small bivalves density was almost the same as for planktonic larvae and new settlers.

By comparing seasonal changes of densities for new settlers and small bivalves, density peaks of small bivalves in early July 1997 and May to July 1998 may originate from those of new settlers in spring to early summer 1997 and 1998, while peaks of small bivalves in early December 1997 may originate from those of new settlers in fall to early winter 1997. This suggests that seasonal changes for small bivalve density may be derived from the density of new settlers.

**Large bivalves**

Large bivalves were found from April 1997 to December 1998 (Fig. 5). Their density fluctuated remarkably with the season, peaking once in 1997 (early July), but did not fluctuate remarkably with the season in 1998. Peaks in 1997 were much higher in July (40 ind./100 cm²) than in other months. Seasonal change of large bivalve density was much different from those of planktonic larvae, new settlers and small bivalve density.

By comparing seasonal changes of densities for small and large bivalves, the density peaks of large bivalves in early July 1997 may originate from those of small bivalves, planktonic larvae and new settlers in spring to summer 1997. There were no density peaks of large bivalves in December 1997, which corresponded to those of small bivalves in December 1997 or planktonic larvae in October 1997 and new settlers in December 1997. In 1998, it was difficult to correspond the density peaks of large bivalves with small bivalves or planktonic larvae and new settlers. Seasonal changes for large bivalve density may not always be derived from that of small bivalve density.

**Cohort analysis**

Fourteen cohorts (a’–n’) were identified for new settlers and small bivalves from 1997 to 1998 (Fig. 4). Five cohorts (a’–e’) were found from February to July 1997, three cohorts (f’–h’) from November 1997 to March 1998, and six cohorts (i’–n’) from April to July 1998. None was from August to October of both years.

Eleven cohorts (A’–K’) were identified for large bivalves for both years. Cohort A’ may have come from that in 1996. Cohorts B’–f’ (with the exceptions of cohorts F’, J’, K’) were found in one month, whereas cohort F’, which had the longest appearance period, was found from early July 1997 to mid December 1998. Based on growth curves, cohorts c’ and F’, f’ and H’, and k’ and J’ would appear to come from the same cohort, respectively. Thus, the cohorts c’, f’ and k’ within new settlers and small bivalves succeeded in recruitment.

Density peaks of new settlers and small bivalves appeared in early June 1997, early December 1997 and April and July 1998, corresponding to those of planktonic larvae. The peaks of new settlers may thus be maintained by cohorts c’, f’, k’ and m’. A marked density peak of large bivalves was found only in July to August 1997, corresponding to those of new settlers and small bivalves in early July 1997. In October to December 1997 and 1998, no marked peak was detected, although weak peaks were found for new settlers and small bivalves. Thus, cohorts c’, f’, k’ and m’ within new settlers and small bivalves gave rise to the peaks of new settlers and small bivalves in 1997 and 1998, whereas cohorts g’, j’ and m’ within the new settlers and small bivalves may not have generated peaks of large bivalves in 1998 when density was maintained mainly by cohorts F’, J’ and K’ within large bivalves.

**Nameishi (Kikuchi River flat)**

**Planktonic larvae**

Planktonic larvae were found from May to December of 1997 and 1998, but not in February to April 1997 (Fig. 6). Their density fluctuated remarkably with the season, peaking twice in 1997 (mid June and early November) and in 1998 (early August and mid December). Peaks in 1997 were much higher in November (300 ind./200 L) than in June (20 ind./200 L). Those in 1998 were somewhat higher in December (130 ind./200 L) than in August (100 ind./200 L). Density peaks of larvae in mid June 1997 and early August 1998 may originate from spring–early summer spawning, whereas those in early November 1997 and mid December 1998 may originate from fall–early winter spawning.

Seasonal fluctuations for planktonic larval density was similar in Kawaguchi and Nameishi during both years. But larval density was lower at Nameishi for the two years compared with Kawaguchi.

Seasonal changes in water temperature and salinity were remarkable. Maximal temperature and minimal salinity during summer was 29.8–30.1°C and 20.09–20.39 PSU, and the minimal temperature in winter and maximal salinity in...
spring was 10.3–11.1°C and 32.36–32.41 PSU, respectively (Fig. 7). As indicated in Fig. 6 as well as for Kawaguchi, density peaks of planktonic larvae in spring to summer were found during an increase in water temperature and/or decrease in salinity, whereas at Nameishi they were found during a decrease in water temperature in fall to early winter.

New settlers

New settlers were found from May to June 1997 and November 1997 to August 1998 (Fig. 7). Their density fluctuated remarkably with the season, peaking twice in 1997 (early July and early December) and twice in 1998 (mid May and July to August). The peaks in 1997 were much higher in
December (130 ind./100 cm²) than in July (20 ind./100 cm²). Those in 1998 were somewhat higher during July to August (30 ind./100 cm²) than during May (20 ind./100 cm²). Seasonal changes for new settler density was similar to that for planktonic larval density.

Seasonal fluctuation of new settler density was similar for Kawaguchi and Nameishi in both years. Density of new settlers in 1997 was clearly lower at Nameishi than Kawaguchi, whereas in 1998 it was the same at the two sites.


**Small bivalves**

Small bivalves were found throughout 1997 except during May, September and October and from January to September 1998 (Fig. 7). Their density fluctuated remarkably with the season, peaking

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**Fig. 7** Seasonal and annual fluctuations of densities of new settlers and small to large bivalves of the manila clam *Ruditapes philippinarum* at Nameishi.
Three cohorts (a–c) were identified for new settlers and small bivalves from 1997 to 1998 (Fig. 6). Two cohorts (a, b) were found from June to July 1997 and one cohort (c) from November 1997 to April 1998. None was detected from August to October in 1997, which was when planktonic larvae were not found. Most cohorts continued for 2 weeks and longer. No cohort was detected from September to December in 1998, which was when planktonic larvae were few.

Nine cohorts (A–I) were identified for large bivalves for the two years. Two cohorts (A, B) may come from those in 1996. Cohorts C–D (except cohorts E, F) were found over a period of two months and cohort G was found from mid March 1998 to early December 1998. Cohorts E and F, which appeared suddenly in February 1998, continued for two weeks and disappeared suddenly in March 1998. Based on growth curves, cohorts c and G may belong to the same cohort.

Density peaks of new settlers found in early July 1997, early December 1997 and mid August 1998 corresponded to those of planktonic larvae. Density peaks of small bivalves found in early July 1997 and early December 1997 corresponded to those of new settlers. Hence, peaks of new settlers may have been maintained by cohorts b and c. But density peaks of small bivalves, which were not found in mid August 1998, corresponded to those of new settlers. Density peaks of large bivalves found in early July 1997 corresponded to those of planktonic larvae and new settlers in early June and early July 1997. Those of large bivalves found in late June 1998 corresponded to those of planktonic larvae in early November 1997 and new settlers in December 1997. Thus, cohorts a and b in new settlers and small bivalves maintained the peaks of new settlers and small bivalves. Those cohorts may have succeeded in recruiting but failed to maintain the peaks of large bivalves in July 1997. Density of large bivalves in 1998 may have been maintained by cohorts G and H in large bivalves, probably corresponding to cohort c in new settlers and small bivalves.

**DISCUSSION**

**Larval recruitment**

According to Sagara,23 *R. philippinarum* populations that inhabit waters along the Pacific coast south of Tokyo Bay spawn twice a year in spring to early summer and fall to early winter, whereas those that spawn once a year (in summer) do so in
Larval recruitment of *Ruditapes philippinarum*  

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waters north of the bay. Such geographic differences of spawning events may be a result of water temperature.\(^{23,24}\) The present study confirmed that the spawning season in Ariake Sound is similar to that for waters south of Tokyo Bay (Figs 4,6).

Seasonal changes of new settler density apparently depend on those of larval density (Figs 5,7). Studies on larval recruitment of bivalves are few, except those on tidal flats in Ise Bay along the Pacific coast of central Japan by Sekiguchi and his colleagues.\(^4,5,8,17,18\) Sekiguchi and his colleagues demonstrated that seasonal changes for new settler density depended on those of larval density. On the other hand, seasonal changes for large bivalve density showed much different trends from those of new settler and small bivalve densities (Figs 5,7).

Large bivalves showed density peaks in summer corresponding to those of planktonic larvae, new settlers and small bivalves, which may originate from spawning in spring to early summer (Figs 4,6). This suggests that density peaks of large bivalves during summer may be supported mainly by density peaks of planktonic larvae in early summer. However, large bivalves did not show density peaks in winter corresponding to those of planktonic larvae, new settlers and small bivalves and which may originate from spawning in fall to early winter (Figs 4,6). Thus, a large bivalve density in fall to winter may be determined mainly by environmental factors. Alternatively, according to studies done in Ise Bay by Sekiguchi and his colleagues, cohorts that showed density peaks of planktonic larvae, new settlers and small bivalves of *R. philippinarum* in fall to early winter contributed to forming benthic populations on tidal flats, whereas those in spring to early summer did not.\(^4,5,16-18\)

New settlers and small bivalves of *R. philippinarum* in Ariake Sound showed density peaks in fall to early winter in addition to those in spring to early summer, but the peaks in fall to early winter failed to recruit and thus generate peaks of large bivalves, probably due to environmental factors during the same periods. The same was observed for *M. senhousia*, which is common and abundant on the tidal flats of Ariake Sound (Ishii R, unpubl. data, 1998). Large bivalves of these two species may be killed shortly after recruitment due to environmental factors such as: (i) winter’s lowering of atmosphere and mud/water temperatures; (ii) conditions related to a cold and strong winter monsoon; (iii) emigration to a neighboring subtidal zone; (iv) pathogens; and (v) predation by crabs, fish and shorebirds. Winter’s lowering of temperatures may be excluded in the present case because the lowest atmosphere and water temperatures were 6.5°C (January) and 11°C (January) on average, respectively, as indicated in Table 2 and Figs 4 and 6. Such temperatures are not critical to either species. Bivalves on the tidal flats of Ariake Sound may thus be exposed to other conditions that are driven by a strong cold monsoon in winter (Table 2). This is also true for new settlers and small bivalves.

The ecological role of pathogens and emigration to neighboring subtidal zones may also be excluded in the present case, although dispersal and/or migration does occur for new settlers to large bivalves of *R. philippinarum*.\(^8,25\) The size-dependent killing of species by predators (crabs, gastropods, fish and shorebirds) may be related to the absence of density peaks of large bivalves during winter. Crabs, gastropods and fish may also be excluded because it is difficult to believe that they would have a great influence on recruitment in winter only. Many shorebirds show size-dependent feeding on tidal flats,\(^26\) and migrate to Japanese tidal flats mainly in winter.

**Differences of larval recruitment between the two sites**

Seasonal and interannual density fluctuations of planktonic larvae, new settlers and small bivalves of *R. philippinarum* were similar at the two sites, but this was not the case for large bivalves. Larval recruitment at Kawaguchi and Nameishi differed as summarized in Table 3. For any growth stage from planktonic larvae to large bivalves in 1997, density was much higher at Kawaguchi than Nameishi, whereas in 1998 the reverse was true for large bivalves, although densities of planktonic larvae and small bivalves were higher at Kawaguchi than Nameishi. Larval density may always be much higher at Kawaguchi, hence, large bivalve density is much higher at Kawaguchi as observed in 1997. Certain environmental factors that had a great influence on recruitment at Nameishi, but not at Kawaguchi, may have caused a higher density of large bivalves to occur at Nameishi as observed in 1998.

Two questions arise: (1) why is the density of planktonic larvae of *R. philippinarum* always much higher at Kawaguchi than Nameishi; and (2) what are the environmental factors that favor larval recruitment only at Nameishi? In answer to question 1, there are three alternative hypotheses: (a) the number of released larvae is higher at Kawaguchi as a result of the larger spawning population size, and planktonic larvae are retained much more and larval density is much higher at Kawaguchi; (b) despite the larger spawning population at Nameishi, planktonic larvae are retained
much more and larval density is much higher at Kawaguchi; and (c) spawning population size at Kawaguchi is almost equal to that at Nameishi, but planktonic larvae are retained much more and larval density is much higher at Kawaguchi. Hypothesis a may support the 1997 observation, whereas hypothesis b supports the 1998 observation. Hypothesis c may not be supported by the present study.

Based on the above two hypotheses (a, b), the retention mechanism of planktonic larvae at Kawaguchi, but not at Nameishi, may be related to the fact that the density of planktonic larvae of _R. philippinarum_ is always much higher at Kawaguchi. Although larval retention may be related intimately to environmental characteristics at Kawaguchi, there is not enough information on these environmental features at Kawaguchi.

What are the environmental factors having a great influence on recruitment at Nameishi in 1998? This question may be answered by the predation of shorebirds on the tidal flats at Kawaguchi and Nameishi during winter. The feeding habits of shorebirds on the tidal flats and the differences in shorebird populations at the two sites must be further clarified.

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**Table 3** Differences of larval recruitment of _Ruditapes philippinarum_ between the two tidal flats (Kawaguchi and Nameishi, Kumamoto Prefecture)

<table>
<thead>
<tr>
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<th>Kawaguchi</th>
<th>Nameishi</th>
<th>Kawaguchi</th>
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(○) Higher density; (¥) lower density; (¥¥) nearly equal density.

Planktonic larvae, new settlers and small to large bivalves are defined in the text.


