Spatial Distributions of Larval, Newly-Settled, and Benthic Stages of Bivalves in Subtidal Areas Adjacent to Tidal Flats

YASUO TSUTSUMI and HIDEO SEKIGUCHI

Faculty of Bioresources, Mie University

Abstract

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Spatial distributions of planktonic larvae and newly-settled and benthic stages of three species of bivalves (*Ruditapes philippinarum*, *Nuttallia olivacea*, *Musculista senhousia*) were investigated in the subtidal area adjacent to the tidal flats of the Ano and Shitomo Rivers. In all three species the benthic juveniles and adults were very scarce in the subtidal area, while the larvae occurred abundantly there. The newly-settled and benthic bivalves tended to occur at sites near the low water of tidal level water. This suggests that larvae avoid settling on the bottom in the subtidal area but are transported to the lower margin of the tidal flats.

Introduction

As reviewed in HALL (1994) and OLAFSSON et al. (1994), recent work on marine benthic invertebrates has emphasized the role of recruitment processes in the population dynamics and community structure of intertidal and subtidal organisms. Some consider that the distribution and abundance of organisms is mainly determined by pre-settlement processes (e.g., larval availability, and selective or non-selective settlement), while others attribute distribution and abundance to post-settlement processes (e.g., differential mortality at sites after larval settlement). Unfortunately, little work has been done concerning the organisms common in the subtidal zone.

Since 1987 we have worked on the population dynamics and community structure of intertidal organisms, particularly focusing on the larval recruitment processes of the three species of bivalves (*Ruditapes philippinarum*, *Nuttallia olivacea*, *Musculista senhousia*) that are very abundant on the tidal flats of the Ano and
Shitomo Rivers, which flow into the western part of Ise Bay on the Pacific coast of central Japan (Sakai, 1992; Kimura & Sekiguchi, 1993a, b; Tsutsumi, 1994; Sekiguchi et al., 1995). Our preliminary surveys found that these species were very scarce in the subtidal area adjacent to these tidal flats, but common and sometimes very abundant in the subtidal zones of several inlets and neritic areas in central and southern Japan (Tanaka & Kikuchi, 1978; Furuta, 1981). According to Tanaka & Kikuchi (1978), Kimura & Sekiguchi (1993a), and Tsutsumi (1994), the characteristics of populations of M. senhousia on tidal flats differ remarkably depending on locality and also differ from those in the subtidal zone.

In the present paper we examine the occurrence of planktonic larvae and newly-settled and benthic stages of bivalves (juveniles and adults) of the above-mentioned three species in subtidal area adjacent to tidal flats.

Materials and Methods

1. STUDY AREA

The Ano and Shitomo Rivers located in Tsu city flow into the western part of Ise Bay on the Pacific coast of central Japan (Fig. 1). These
Spatial distributions of bivalves in the subtidal zone

rivers are small and short; the Ano River is 27.9 km long and passes through the lowlands of Tsu city and its environs, while the Shitomo River is 14.5 km long and passes through rice fields. Saline water is detected at sites 2.3 km upstream from the river mouth in the Ano River and 5.5 km upstream from the mouth in the Shitomo River (Kimura & Sekiguchi, 1993a).

Although the mouths of the Ano and Shitomo Rivers are adjacent to each other, the tidal flats of these small rivers have different types of sediment. In general, the mean grain size is smaller and the silt-clay content is clearly higher in the Shitomo River than in the Ano River (Kimura & Sekiguchi, 1993b). However, such differences are not found between the subtidal areas adjacent to these two tidal flats (Fig. 2).

2. SAMPLING AND PROCESSING OF BIVALVES

Investigations were done in the subtidal area adjacent to the tidal flats of the Ano and Shitomo Rivers. Twenty-eight sampling stations were established in the subtidal zone, 8 (A-H) of which were located along the low water tidal level (LWTL); the other 20 (1-20) were scattered in the subtidal area within 1.0 km of the shore (Fig. 1). Sampling was done during low water in the daytime in May, September, and December, 1992. The water temperature and salinity were measured at the surface and at 1 m above the bottom at stations 1-20 by employing STD instrument.

Planktonic larvae are defined here as veliger larvae (excluding the early-stage veliger, i.e., the D-shaped veliger). Newly-settled bivalves are defined as specimens with shell lengths of less than 0.3 mm, because juveniles of the bivalves common in tidal flats in Japan grow to a shell length of ca. 200-300 μm very shortly after settlement (Yoshida, 1953; Xu, 1983; Sakai & Sekiguchi, 1992). Small bivalves are defined to be specimens with shell lengths greater than 0.3 mm but less than 1.0 mm, while large bivalves are

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Fig. 2 Spatial distribution of the silt-clay content (%) of sediments in the subtidal zone.
those with shell lengths of 1.0 mm or more.

For sampling the planktonic larvae, plankton nets with mesh-openings of 133 μm were hauled vertically from the bottom to the surface at stations 1-20, this being done once at each station. The samples were immediately fixed with 3% neutralized formalin seawater. The specimens were identified to species according to Sakai & Sekiguchi (1992), but the D-shaped larvae were excluded because of difficulties in identification. Densities of the larvae were recorded as individual numbers per haul.

For sampling the newly-settled and small bivalves, bottom surface sediment was collected at stations 1-20 by using a Smith-McIntyre grab, and then the sediment in the grab was subsampled by using a core sampler (3.4 cm in diameter, 10 cm depth, covering a surface area of 9.08 cm²). Surface sediment was collected at stations A-H by using the same core sampler. One sample was obtained at each station. The sediment was filtered with a sieve having 125 μm mesh-openings, and the specimens were immediately fixed with 5% neutralized formalin seawater dyed with rose bengal. The specimens were identified to species according to Sakai & Sekiguchi (1992). The shell lengths of the specimens were measured to an accuracy of 0.01 mm.

For sampling the large bivalves, sediment was collected at stations 1-20 by using a Smith-McIntyre grab (covering a surface area of 25 × 25 cm), and at stations A-H by using a quadrant frame (covering a surface area of 23.5 × 23.5 cm and 20 cm deep), sampling being performed once at each station. The sediment was then filtered with a sieve having 1.0 mm mesh-openings, and the specimens were immediately fixed with 10% neutralized formalin.

The surface sediment grain sizes were measured at each sampling station. The sediment, which was treated according to Oceanographic Society of Japan (1991), was filtered with a series of sieves: 2.000, 1.000, 0.710, 0.500, 0.355, 0.250, 0.180, 0.125, 0.090, and 0.063 mm mesh-openings. The dry weight of sediment at each station was measured, and we then calculated the silt-clay fraction according to Ozawa & Nojima (1976).

Results

1. ENVIRONMENTAL CONDITIONS IN THE STUDY AREA

The silt-clay content of the sediment varied seasonally and among the sampling stations (Fig. 2). It was 0.05-11.30 % in May, 0.05-8.83 % in September, and 0.02-8.77 % in December. It was in general lower at stations A-H along the low water tidal level than at stations in the subtidal zone.

At stations 1-20 the surface water temperature was 16.8-19.2 °C in May, 28.5-28.9 °C in September, and 12.0-12.9 °C in December. The temperature at the surface was lower by ca. 3 °C than at the bottom in September, while in December, very slight differences in temperature with depth were detected only at the stations located well offshore.

At stations 1-20 the surface salinity was 22.1-27.5% in May, 19.8-23.5% in September, and ca. 30.0% in December. It was higher by ca. 4.5% at the bottom than at the surface in May and September, while it was almost the same throughout the water column in December.

2. DISTRIBUTION OF THE BIVALVES IN THE SUBTIDAL AREA

2.1. Ruditapes philippinarum (Table 1)

In May, September and December, large bivalves were abundant at stations A-H along the LWTL: station H in May, stations D and 3 in September, and station A in December.

Newly-settled and small bivalves were found abundantly at stations along the LWTL and also at neighbouring stations, in May, September, and December.

Planktonic larvae were found at all stations in May, September, and December, though their densities varied remarkably among stations. In May and September the larvae were quite
Spatial distributions of bivalves in the subtidal zone

Table 1  Spatial distributions of densities of the three species of bivalves in the subtidal area adjacent to the tidal flats of the Ano and Shitomo Rivers.

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<th>PL</th>
<th>NS</th>
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L: planktonic larvae; NS: newly-settled bivalves; S: small bivalves; L: large bivalves. Numericals indicate means (upper level) and standard deviations (lower level) of maximal density during the three study intervals (May, September, December) as follows: PL in ind./haul, NS and S in ind./10cm², and L in ind./m². See text for further explanation.
abundant at all stations except those along the LWTL, and they were particularly abundant at
stations 8, 9, 10, 14, and 18 in May. On the other hand, in September they were more abundant at
stations 1-10 near the shore, particularly at station 7.

2-2. Nuttallia olivacea (Table 1)
In May, September, and December, large bivalves were found at stations along the LWTL
and at neighbouring stations. They were particularly abundant at station F in September
and at station A in December.

Newly-settled and small bivalves were found exclusively at stations along the LWTL
and also at neighbouring stations in May, September, and December, though in very low
numbers. In December, only small bivalves were found at station E.

In May and September the planktonic larvae were more abundant at stations along the LWTL
and also at the neighbouring stations, whereas they were more abundant at the offshore sta-
tions 11-20 in December.

2-3. Musculista senhousia (Table 1)
No large bivalves were collected at any station in May, September, nor December.

Newly-settled and small bivalves were not collected at any station in May, but they occurred
abundantly at several offshore stations in September. In December, specimens were found
only at these same offshore stations.

Planktonic larvae were more abundant at the central stations 6-15 than at the offshore sta-
tions 11-20 in May and December, while in September they were more abundant at stations
along the LWTL. Larvae were particularly abundant at station 1 in May and September,
and at station 16 in December.

To summarize, individuals in the benthic phase (the newly-settled, small, and large bi-
valves) of R. philippinarum and N. olivacea were abundant solely at stations along the
LWTL and at neighbouring stations with low silt-clay content in the bottom sediments. M.
senhousia was collected only at several offshore stations in very low numbers. However,
planktonic larvae of all three species were found at all stations, though their densities varied
remarkably by station.

Discussion

Larvae of two species (R. philippinarum, N. olivacea) were found abundantly in the subtidal
areas, while the juveniles and adults were very scarce and were restricted largely to the stations
along the LWTL. But this is not the case with M. senhousia. All three species have always been
collected abundantly on the tidal flats of the Ano and Shitomo Rivers (Sakai, 1992; Kimura &
Sekiguchi, 1993a, b).

What kinds of processes during larval settlement could contribute to the absence of benthic
phase individuals of these three species that are common in the tidal flats? The following three
alternative processes are potentially involved:

(1) The larvae avoid settling on the bottom in the subtidal zone, but continue floating just
above the bottom until they encounter sites where they prefer to settle (the sediment along
the LWTL or on the tidal flats of the rivers). But small numbers of larvae may settle on the bot-
tom at most of the subtidal stations in the present study area.

(2) Except for the sediment along the LWTL
and on the tidal flats, almost all of the larvae
and newly-settled bivalves die very shortly after
settlement anywhere in the whole subtidal zone
in the present study area.

(3) Even though the larvae settle on the bot-
ttom sediment throughout most of the subtidal
zone adjacent to the tidal flats of the rivers, they
are subsequently transported onto the sediment
close to the LWTL and accumulate there. We do
not have evidence yet to falsify any of the above-
mentioned scenarios (1)- (3). However, process
(2) is difficult to accept, because it implies the
mass mortality of larvae or newly-settled
bivalves of these three species very shortly after the larvae settle on the bottom, yet we were not able to find dead shells of newly-settled and small bivalves.

Around river mouths, in general, freshwater or less saline water flushes out toward the sea, while saline water in deep and/or bottom layers intrudes upstream (e.g., Sekiguchi, 1992). According to Wood & Hagriss (1971) and Sekiguchi (1991, 1992), planktonic larvae, particularly later-stage veliger larvae of estuarine bivalves, have been found in the middle to deeper layers around river mouths, and thus the larval population would be retained there without being flushed out to sea. We have not yet obtained data indicating a similar retention mechanism for the larval populations of the above-mentioned three species.

The larvae of the two species R. philippinarum, N. oleracea probably have a chance of reaching the sediment close to the LWTL and on tidal flats of the Ano and Shitomo Rivers if they remain in the deeper layers within the present study area. Furthermore, even though the larvae do settle on the bottom sediment throughout most of the subtidal zone adjacent to the tidal flats of these rivers, they may be transported onto the sediment close to the LWTL and accumulate there; several tens of species of newly-settled and small bivalves have been known to float in water by using drift threads (Sigurjónsson et al., 1976; Lane et al., 1985). Unfortunately, present three species have not yet been confirmed as using drifting threads, though juveniles and adults of R. philippinarum are able to migrate and/or disperse under the sediment (Sai, 1963).

The present study suggests that several processes in larval settlement are essential in explaining the absence of benthic stages of the above-mentioned three species of bivalves in the subtidal zone adjacent to the tidal flats. Luckenbach (1984) showed that the distribution of an estuarine bivalve resulted from differential mortality at sites rather than differential settlement at sites, while Woodin (1985) reached the opposite conclusion regarding the distribution of polychaetes in a mudflat. Also, in an infaunal bivalve more abundant in seagrass beds than in sandflats, two processes (hydrodynamic influence of projecting seagrasses on larval and postlarval settlement, and higher survival after settlement in the seagrass beds) were involved in elevating the bivalve densities in the seagrass beds (Peterson, 1986).

References


Lane, D. J., A. R. Beamont and J. R. Hunter.


和文要旨

堤 康夫・関口秀夫 河口千穂湖に隣接した潮下帯における二枚貝類の浮遊幼生．著生稚貝及び稚・成員の分
Spatial distributions of bivalves in the subtidal zone

布。

安瀬川と志登茂川の河口干瀬に隣接した潮下帯において、3種類の二枚貝類（アサリ、イソシジミ、ホトキスガイ）の浮遊幼生、着底稚貝及び稚・成員の分布を調査した。3種類とも、浮遊幼生は多く出現するのに反し、底生期の稚・成員はごく稀であった。着底稚貝と稚・成員には、干潮の水際近い地点に分布する傾向が見られた。このことは、浮遊幼生が潮下帯に着底するのを避け、河口干瀬の水際近辺に輸送されることを示唆している。

HIDEO SEKIGUCHI
Faculty of Bioresources, Mie University,
1515 Kamihama-cho, Tsu, Mie 514, Japan.